Within-Gap Spatial Heterogeneity and Seedling Performance in a Mexican Tropical Forest
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The internal heterogeneity of gaps was investigated by comparing (1) the floristic composition and structural organization of colonizing seedlings and (2) the performance of two selected species, *Cecropia obtusifolia* and *Heliocarpus appendiculatus*, in permanent quadrats established in the root and crown zones of fallen trees in the tropical rain forest of Los Tuxtlas, Mexico.
Considerable differences were found between the two zones regarding number of species and diversity; likewise, the floristic similarity of quadrats of the two zones was always lower than that of the quadrats of the same zone (root or crown). The exclusive species of each zone, or even the shared species were present with different density or size (or both), leading to different hierachical organizations.
Two of the dominant species of both zones, *C. obtusifolia* and *H. appendiculatus*, were compared by a more detailed study of plant demography, including their standing levels of herbivory. It was found that *C. obtusifolia* survived better in the crown than in the root zone while *H. appendiculatus* showed the opposite response. Though many seedlings died due to unknown reasons, herbivory (by insects) accounted for a large proportion of the mortality of the plants: mortality rates were higher for seedlings that had previously been heavily damaged, than for seedlings that were intact or slightly damaged. Physical damage, especially from falling objects was also an important source of mortality. These causes of mortality varied somewhat between the two zones.
We conclude that, in addition to the spatial heterogeneity created by the occurrence of gaps in the forest, within gap heterogeneity also affects the performance of species and the dynamics of the forest.

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Introduction

Small-scale spatial heterogeneity is receiving increasing attention as an important environmental feature affecting the ecology and evolution of plants and animals (see Strobeck 1974, Wilson 1980, Turkington and Aarssen 1984). Spatial heterogeneity of the physical environment may promote heterogeneity of the biotic environment which, in turn, differently affects the performance and fate of individuals in different parts of the local environment. For example, Dirzo (1984) has suggested that spatial heterogeneity in regimes of herbivory upon individuals of *Trifolium repens* within a population would select for well defended plants in areas where herbivore pressure is high, and for competitive plants (though poorly defended) in areas of low pressure. Likewise, Coley (1983a) suggests that spatial heterogeneity could account for the great variation in herbivory rates found among conspecific individuals in tropical rain forests.

In tropical rain forests, the continuous production of natural disturbances generated by tree- or limb-falls is a process that causes a great degree of spatial heterogeneity (Whitmore 1975, 1978, 1982, Brokaw 1982a, b, 1985, Martínez-Ramos 1985). Such heterogeneity has been considered as a fundamental factor promoting and

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maintaining much of the tree species-richness that characterizes these communities (Connell 1978, Denslow 1980). Indeed, Orians (1982) suggested that the heterogeneity created by tree fall gaps could enhance the rich flora of tropical forest systems; moreover, he has stressed that the gap itself has an internal spatial heterogeneity (the root, the bole and the crown zones of the fallen tree) with different environmental regimes which could lead to the "specialization" of pioneer (colonizing) species into different "guilds" that survive and grow better in a particular zone of the gap. An extension of this argument would imply that different pioneer species should have different success in different zones of the colonizable gaps (see Orians 1982).

While several authors have documented the marked differences in the floristic organization of the tropical rain forest as a whole, as influenced by the occurrence of tree fall gaps (Aubréville 1938, Richards 1952, van Steenis 1958, Schulz 1960, Whitmore 1975, Hallé et al. 1978), very few data have been provided regarding the floristic differences that may occur within a given rain forest gap. With a few exceptional cases (e.g., Brandani et al. 1987), not only is the existence of marked floristic contrasts between different zones of the gap poorly documented, there are also essentially no data demonstrating that different colonizing species establish preferentially in different gap zones and/or whether they perform differently and have therefore different success within the spatial heterogeneity of the gap.

In the present paper we report data of a study directed to assess 1) whether there are different floristic assemblages in different zones of a gap by looking at the community of seedlings that colonize the gap; 2) the performance, in different zones of a gap, of the seedlings of two selected species in the tropical rain forest of Los Tuxtlas, in southeast Mexico. For the floristic analyses we carried out surveys of the seedlings present in two contrasting zones of the gap (the root and crown zones of the fallen tree), at different times soon after the gap was created. For the analysis of seedling performance we monitored survival and growth of two species in the two gap zones (root and crown). Additionally, we measured herbivory as an environmental factor affecting the performance of the species because it has been argued that this is an important factor in the ecology of gap-colonizing species in tropical rain forests (Hartshorn 1978, 1980, Coley 1980, 1983a, b).

Materials and methods

The study site

The study was carried out at Los Tuxtlas Tropical Research Station, located in the State of Veracruz, in southeast Mexico. The vegetation of the area is wet tropical rain forest. The forest is rich in species with trees of up to 35 m (Piñero et al. 1977). The mean yearly temperature is 27°C; total yearly rainfall averages 4700 mm. The area has a short "dry season" (around March–May) in which rainfall is reduced but not absent, and a long wet season that extends to the winter months (December–February). This winter season is of great ecological importance for the zone; during this time of the year strong northerly winds (locally called "nortes") are common and are associated with marked decreases in temperature (6°C on average; minimum records as low as 10°C); this season accounts for up to 18% of the total yearly rainfall. Other details of the vegetation and the physical environment are described in Lot-Helgueras (1976) and Piñero et al. (1977).

An important feature of the site is the considerable occurrence of natural disturbances due to tree- or limb-falls. The forest is extremely dynamic, with an estimated average turnover rate of 67 yr on average for different zones of the forest (Martínez-Ramos and Alvarez-Buylla 1986). The major occurrence of these disturbances is in the wet season but with a marked peak in the months of November-February, corresponding to the season of "nortes".

The study gaps

For this study two large gaps (ca. 600 m^2 each) were used. One of these (site I) was created in July 1982 by the fall of a large *Ficus* sp. (Moraceae) tree. The other gap (site II) was opened on October, 1981, by the fall of a large *Spondias radlkoferii* (Anacardiaceae). The two gaps were east-west oriented, in direction of the slope. Both gaps had three distinct zones: root, bole and crown; however, only the root (in site I) and crown (in site II) zones were studied. The reason for using two different gaps was that colonization on the different zones starts at different times. In the crown zone of a given gap, colonization is delayed probably due to the instability of the substrate – branches, twigs, leaves are continuously breaking and decaying.

Four 1 m^2 permanent observation quadrats (POQs) were established in each of the two zones. The POQs were marked by four aluminium pegs (1 m tall) sunk into the corners of the quadrat. A removable grid of 25 subquadrats (20 × 20 cm) temporarily attached to the pegs was used to locate the seedlings that established within the 1 m^2 area. Soon after the establishment of the four POQs, one of them in the crown zone (site II) was destroyed due to the fall of a large branch, leaving only three POQs in this zone.

Floristic composition and structure of the seedling communities

On all the POQs of both zones, a record was made of all the seedlings (> 5 cm height) present on three recording dates in relation to the time in which the gap of site I was formed: two months after (September, 1982), seven months after (February, 1983) and one year after (July,

Tab. 1. Summary of the floristic parameters (no. of species, diversity index (H'), and evenness (E)) in the POQs from two tree-fall gaps at Los Tuxtlas during three recording dates. Mean values and their standard deviations are given for each zone (root, crown) on each recording date.

Time	Zone	POQ	No. of spp.	Density	H'	E
Sep 1982	Root	1	20	57	1.228	0.943
		2	13	78	0.683	0.613
		3	20	86	0.843	0.647
		4	24	82	1.228	0.889
	$\bar{X}$		19.25	75.75	0.995	0.773
	S		4.57	12.91	0.239	0.167
	Crown	1	10	45	0.616	0.616
		2	7	32	0.576	0.682
		3	9	39	0.724	0.759
	$\bar{X}$		8.66	36.66	0.639	0.686
	S		1.52	6.50	0.062	0.072
Feb 1983	Root	1	18	52	1.090	1.086
		2	13	61	0.746	0.671
		3	24	61	1.242	0.900
		4	27	63	1.259	0.879
	$\bar{X}$		20.50	59.25	1.08	0.830
	S		6.24	4.92	0.205	0.106
	Crown	1	12	26	0.832	0.771
		2	6	17	0.557	0.716
		3	9	20	0.854	0.895
	$\bar{X}$		9.0	21.0	0.748	0.794
	S		3.0	4.58	0.135	0.091
Jul 1983	Root	1	18	36	1.156	0.921
		2	10	36	0.454	0.454
		3	28	72	1.371	0.947
		4	24	51	1.268	0.919
	$\bar{X}$		20.0	48.75	1.062	0.810
	S		7.83	17.03	0.414	0.237
	Crown	1	13	31	0.962	0.864
		2	7	17	0.656	0.775
		3	7	18	0.767	0.908
	$\bar{X}$		9.0	22.0	0.795	0.849
	S		3.43	3.43	0.155	0.067

1983). The seedlings were identified to species or genus whenever possible (approx. 70% of the total). Those that could not be identified were given arbitrary code names.

In order to obtain a numerical idea of the structural organization of the seedling communities an importance value (IV) was calculated for each species on each POQ. The IV was defined (after Curtis 1959, Kershaw and Looney 1985, see also Sarukhán 1968) as:

$$IV = Fi + Di + DXi$$

where Fi, the relative frequency of the ith species, is the number of 20 × 20 cm subquadrats in which the species was present divided by the total number of subquadrats (i.e. 25); Di, the relative density of the ith species, is the number of individuals of the species per 1 m^2 quadrat divided by the total number of individuals in the 1 m^2 quadrat, and DXi, the relative dominance of the ith species, was the combined product of the plant's height x number of leaves x the estimated mean leaf area (defined as the sum of the products of leaf length and width), divided by the total dominance of all species.

Demography of two selected species

Two species, *Cecropia obtusifolia* Bertol. (Moraceae) and *Heliocarpus appendiculatus* Turcz. (Tiliaceae), were selected for a more detailed demographic analysis. These species were chosen because they are the most conspicuous arboreal elements in secondary vegetation, both naturally- and artificially-induced in southeastern Mexico (Ramos-Prado et al. 1982, Núñez-Farfán 1985). The seedlings of both species present in all POQs were individually numbered and marked with a plastic tag (Dymo); the precise location of each plant was marked on a map.

At monthly intervals we recorded plant survival, growth (measured by height, number of leaves, and mean leaf area) and an estimate of herbivory. Herbi-

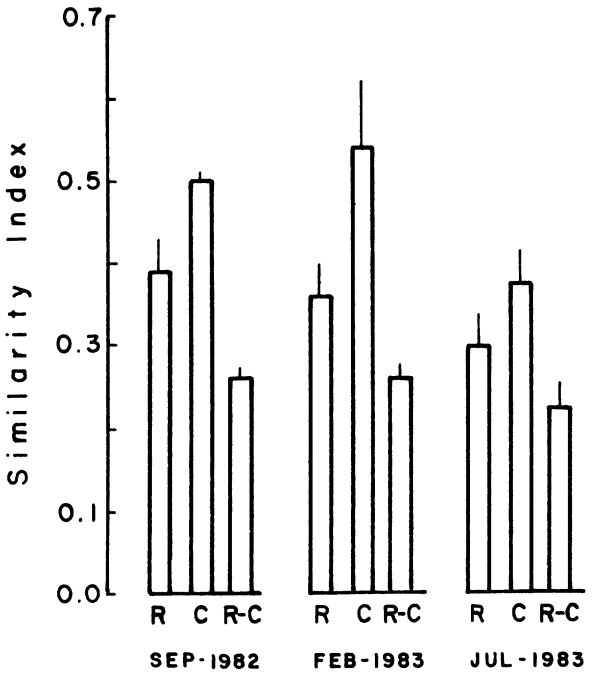

Fig. 1. Floristic Similarity (mean value of Sørensen's Index +1 SD) between POQs located in the root zone (R), crown zone (C), and between POQs from the two zones (R–C) during three recording dates.

vory was estimated on the basis of categories (per leaf) of area eaten: 0, intact; 1, < 10%; 2, 10–25%; 3, 25–50%; 4, 50–75%; 5, 75–100%. The score of each individual leaf was used to define an index of herbivory (IH) per plant (and also per species) as:

$$IH = \sum_{i=1}^{5} (Li)\,(i) / n$$

where i is the category of damage (from 0 to 5), Li is the number of leaves in the ith category of damage and n is the total number of leaves on the plant. Similar indices have been used by other workers (e.g., Stanton 1975, Fox and Morrow 1983, Dirzo 1984). Additionally, the occurrence of different types of damage by insects on the leaves, was also recorded.

Results

Structure and floristic composition

A total of 86 different species were recorded on all the POQs. Seventy-two different species were found in the root zone whereas the crown zone only had 33. A full list of the species is given in the Appendix. Thus, the two zones were colonized by a rich but numerically different floristic potential (Tab. 1). Throughout the study period there were marked differences between the zones in the mean number of species, number of individuals and diversity (as defined by the Shannon-Wiener index), with greater values always being found in the root zone. Statistically significant differences ($P < 0.05$) exist between the mean number of species and individuals in September, 1982. In February, 1983, the same tendencies remained and the diversity index was also significantly greater ($t = 40.08$, $P < 0.01$; see Poole 1974 for the test of comparison) in the root zone. All three parameters were again significantly greater ($P < 0.05$) in the root zone than in the crown zone on the third recording date.

Some of the species that appeared throughout the study period were shared by both zones of the gap; however, many of them were exclusive to one or the other zone. This tendency was quantitatively assessed by means of Sørensen's Similarity Index (see Greig-Smith 1983). Fig. 1 shows the mean similarity value between the POQs of each zone (root, crown) and between the POQs of both zones for three recording dates. The floristic similarity was always greater within than between zones. The lowest similarity values were, on all three dates, those of the between-zone comparison. The greatest similarity was found among the crown zones. The order of floristic similarity was, for the three recording dates, crown zone > root zone ≫ between-zones. This result suggests that these two zones of a given gap are colonized by a different floristic assemblage that might determine a different floristic potential for gap regeneration.

Fig. 2 shows a hierarchical arrangement of the most important species (up to ten) for each of the POQs of both sites at the three dates. The most noticeable feature of this analysis is the considerable skewness in the ordering of species, i.e., one (or a few) of the species present on each POQ is markedly "dominant". This is more evident in the crown (Fig. 2B) than in the root zone (Fig. 2A). Other differences between the zones are also apparent. The single most important species in the root zone (Fig. 2A) varied between POQs for a given date and between dates for a given POQ (e.g. POQs 1, 3 and 4), though in some cases (e.g. (POQ 2; Fig. 2A) the single most important species remained throughout. The most important species in this zone included *Cecropia obtusifolia* (POQs 1 and 2 in Sep, 1982; POQ 2 in Feb and Jul, 1983), *Cissus gossypiifolia* (POQs 3 and 4 in Sep, 1982), *Heliocarpus appendiculatus* (POQ 3 and 4 in Feb and Jul, 1983), and *Robinsonella mirandae* (POQ 1, Feb, 1983). In great contrast, in the crown zone (Fig. 2B), *Cecropia obtusifolia* was, by far, the most important species in all POQs on all recording dates. Other important species (although considerably less so than *C. obtusifolia*) were *Acalypha skutchii* and *Hiraea fagifolia*. *H. appendiculatus*, a very important species in the root zone, was among the ten most important species in four instances (POQ 1 in Sep 1982 and Jul, 1983; POQ 3 in Sep, 1982 and Feb, 1983). Despite these marked differences between the two zones, *C. obtusifolia* and *H. appendiculatus* are clearly

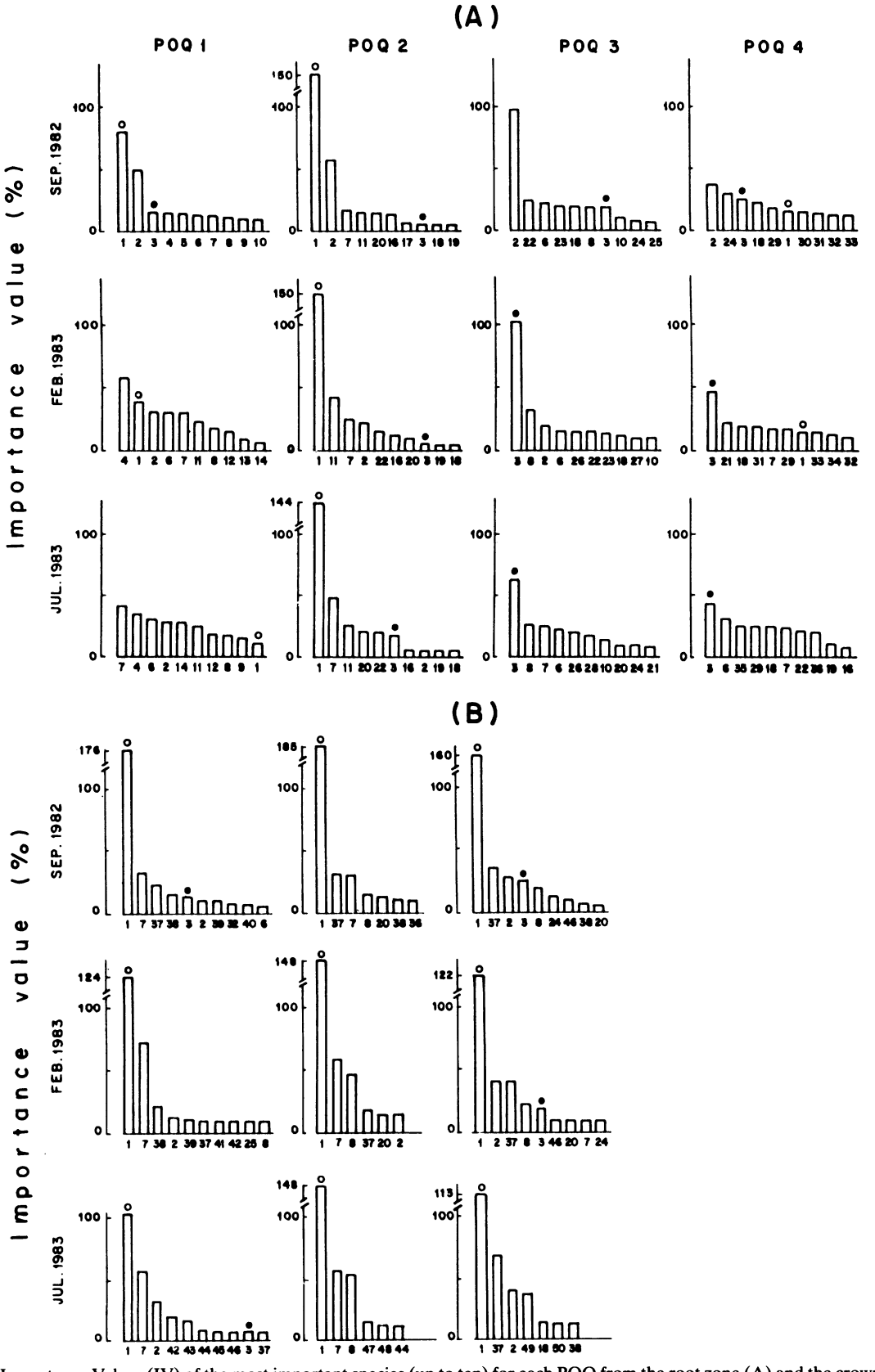

Fig. 2. Importance Values (IV) of the most important species (up to ten) for each POQ from the root zone (A) and the crown zone (B) during three dates after the onset of regeneration at Los Tuxtlas. Each number on the X-axis corresponds to one species, whose name is given in the Appendix. Note the positions of *Cecropia obtusifolia* (○) and *Heliocarpus appendiculatus* (●).

Tab. 2. The dynamics of seedling populations of *Cecropia obtusifolia* and *Heliocarpus appendiculatus* in the two zones (root, crown) of the gaps studied. The numbers are m^{-2}.

	C. obtusifolia		*H. appendiculatus*	
	Root	Crown	Root	Crown
A) No. of individuals Sep, 1982	16.5	22.66	3.0	1.66
B) No. of individuals Oct, 1984	0.25	2.33	1.25	0.0
C) Net gain	−16.25	−18.67	−1.75	−1.66
D) New individuals appearing between Sep 1982–Oct 1984	5.0	3.33	2.75	1.0
E) Individuals lost from the populations between Sep 1982–Oct 1984	37.5	23.66	4.0	2.66
F) Individuals present at Sep 1982 but lost by Apr 1984	32.25	20.33	1.75	1.66
G) Percentage survival from Sep 1982–Oct 1984 (B/A × 100)	1.5	10.29	41.66	0.0

important floristic elements in the colonization of gaps – the former markedly so in the crown zone and the latter in the root zone.

The demography of C. obtusifolia and H. appendiculatus seedlings

Plant survival and population dynamics

We followed the fate of individually marked seedlings of *C. obtusifolia* and *H. appendiculatus*, to gather basic demographic information on the dynamics of colonization. Tab. 2 shows the dynamics of the seedling populations of both species on both sites, on a per meter square basis. *C. obtusifolia* started with a much greater density than *H. appendiculatus* in both the root and crown zones. The densities of *C. obtusifolia* were, respectively, 5.5 and 13.6 times greater than those of *H. appendiculatus* at the beginning of the study. However, towards the end of the study period, 25 months later (October, 1984), the density of *H. appendiculatus* was marginally greater than that of *C. obtusifolia* (1.25 vs 0.25 seedlings m^{-2}) in the root zone. The survival of *C. obtusifolia* was extremely poor in the root zone. Most of the survivors were in the crown zone, whereas the opposite was true for *H. appendiculatus*.

The number of individuals lost from the populations between September 1982 and October 1984 was extremely high for *C. obtusifolia* (156) and small for *H. appendiculatus* (24). The percentages of survival of individuals from September 1982 to October 1984 (both sites pooled), were very low indeed: 5.9% for *C. obtusifolia* and 29.4% for *H. appendiculatus*. Although there were some recruitments for both species (Tab. 2), these were not enough to compensate for the intense mortality and hence the populations markedly declined.

The time-course of survival for both species in both zones is shown in Fig. 3. *C. obtusifolia* (Fig. 3A) survived about equally well in both zones for the first 11 months after establishment but after this period the risk of death was considerably higher in the root zone, whereas survival decreased only slightly in the crown zone. By the end of the study (October, 1984), survival was ca. 11% in the crown zone and less than 2% in the zone of the roots. In contrast, *H. appendiculatus* (Fig. 3B) suffered intense mortality in the crown zone and by March 1983 (six months after establishment) the pop-

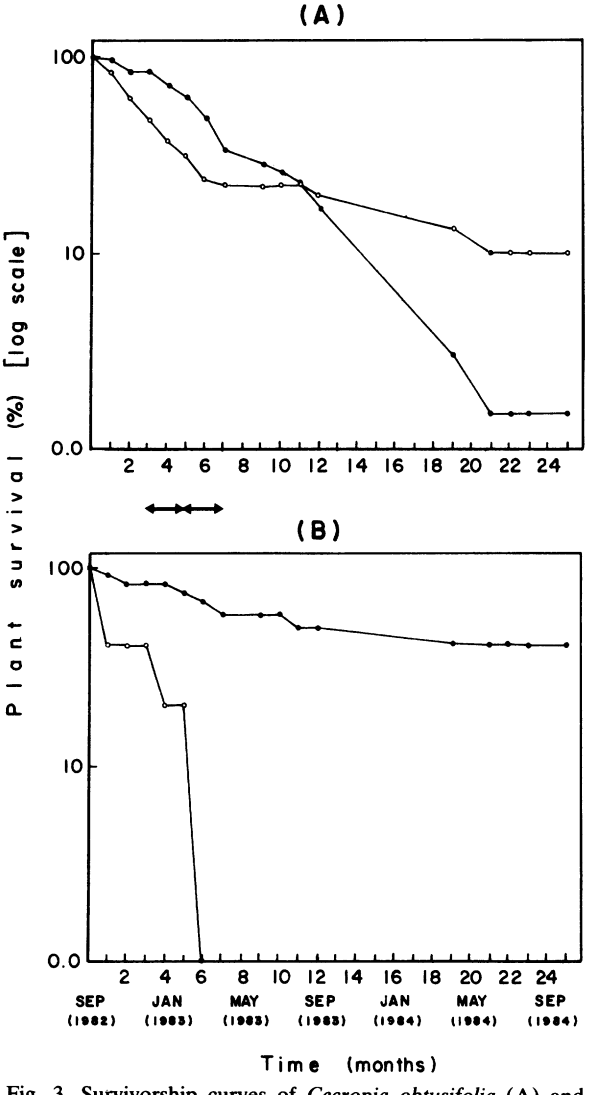

Fig. 3. Survivorship curves of *Cecropia obtusifolia* (A) and *Heliocarpus appendiculatus* (B) seedling populations growing in the root zone (●) and in the crown zone (○) of the gap. (Arrows indicate the period when contingency analysis between herbivory and survivorship were made; see Tab. 3).

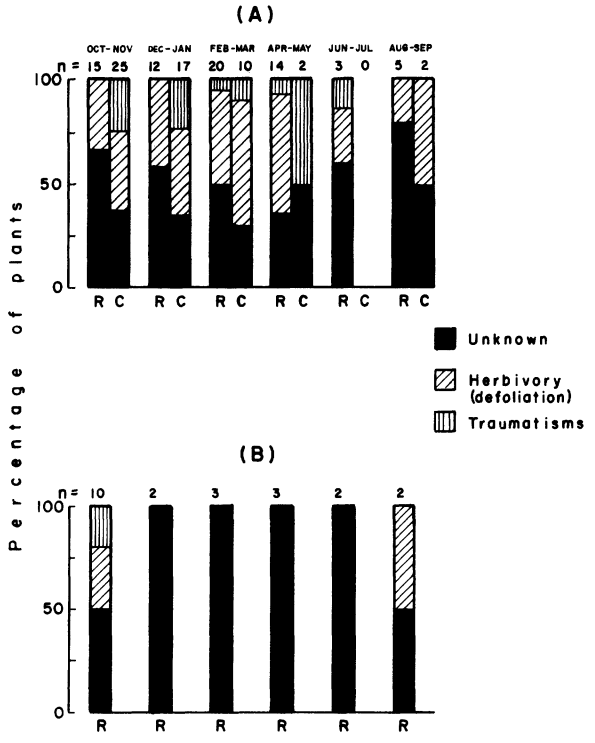

Fig. 4. Causes of death for *Cecropia obtusifolia* (A) and *Heliocarpus appendiculatus* (B) seedlings in the root (R) and in the crown (C) zones along one year after establishment. The numbers (n) indicate the plants that were dead, at those recording times.

ulation had disappeared. On the other hand, death rates were much lower in the root zone, with about 40% of the individuals still alive at the end of the study. Thus, clearly there was a strong differential survival: *C. obtusifolia* survived better in the crown zone whereas *H. appendiculatus* did so in the root zone.

Herbivory and other possible causes of plant death

Using the data on deaths occurring during two consecutive months, we assessed the possible causes of plant death (Fig. 4). A considerable proportion of the plants of both species died of unknown causes. On a bimonthly basis, the percentage of plants that died due to unknown reasons ranged, for *C. obtusifolia*, from 30% (Feb–Mar, 1983 in the crown zone) to 80% (Aug–Sep, 1983 in the root zone). For *H. appendiculatus* (pooled data from both sites) the values ranged from 50 to 100%, although the much reduced number of plants (and deaths) in this species precludes a reliable assessment. For those plants whose causes of death could be identified with some certainty, the two main agents were traumatisms (injuries) and herbivory. Traumatisms were caused mainly by the fall of branches, twigs, loose stems of lianas, or other objects from the surrounding upper vegetation. In this category are included traumatisms associated with the breakage of unsuitable substrate (e.g. decaying branches), in particular in the crown zone. Herbivory-associated death includes defoliation and damage by pathogens that, in this forest, is largely associated with damage by defoliating insects (see Dirzo 1987).

The foliage of *C. obtusifolia* presented a variety of types of damage (mining, skeletonization, cut edges, etc.) that varied from three to eight different types. For *H. appendiculatus* the corresponding range was also three to eight. However, despite this variety of types of damage, in general there was one (or few) predominant type(s) of damage so that the diversity of types of damage present on each month (Shannon-Wiener index) was rather low (range 0.36–2.72 for *C. obtusifolia*, 0.13–0.71 for *H. appendiculatus* (see Núñez-Farfán 1985, Núñez-Farfán and Dirzo 1985)). In all cases the evidence of damage was scars caused by insects (mainly Lepidoptera, Coleoptera, and Orthoptera) rather than by vertebrates (browsing, pull-out).

The levels of damage as defined by the index of herbivory (see Materials and methods) are shown in Fig. 5. For *C. obtusifolia* there was a higher level of damage in the crown zone soon after the establishment of the seedlings, but later on the differences between zones were not so marked. Nevertheless, the overall difference is significant (Mann-Whitney's $U = 31$; $P < 0.05$), with plants in the crown zone having, in general, higher levels of damage. Additionally, there is evidence of seasonality in the levels of herbivory with a noticeable decline in the late dry season and early wet season (April–June). The index of herbivory ranged from 0.40 (equivalent to 4% leaf area damaged) at the beginning of the study for the plants in the root zone, to a maximum of 2.22 (equivalent to up to ca. 30%) some months

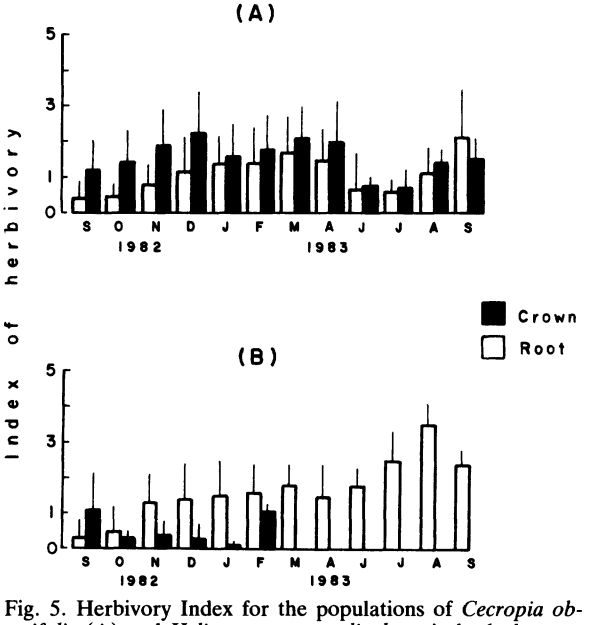

Fig. 5. Herbivory Index for the populations of *Cecropia obtusifolia* (A) and *Heliocarpus appendiculatus* in both the root and the crown zones of the gap. The values represent the mean +1 SD. (For a description of the Index see text).

Tab. 3. A contingency analysis of the survival of *Cecropia obtusifolia* between two recording dates (Dec 1982–Feb 1983 and Feb 1983–Apr 1983; pooled values) in relation to the intensity of damage (leaf area eaten) by herbivores. (Expected numbers for each cell in parenthesis).

Individuals	Leaf area damage (%)			
At time t+1	0–10	> 10 < 50	> 50	Σ
Surviving	34 (29.81)	61 (57.14)	5 (13.04)	100
Dead	14 (18.19)	31 (34.86)	16 (7.95)	61
Σ	48	92	21	161

$\chi^2 = 15.33$, $P < 0.005$

after, in the zone of the crown. For *H. appendiculatus* in the root zone there was a steady increase in herbivory from 0.32 at the beginning of the study to 3.5 one year after. No seasonal changes in damage rates are evident in *H. appendiculatus*. In the crown zone there was an oscillating pattern of herbivory up to February 1983, after which all individuals in this zone died (cf. Fig. 3). The yearly averages of damage levels were 1.34 (equivalent to a maximum of 15.1% leaf area eaten) for *C. obtusifolia* and 1.33 (equivalent to a maximum of 15% leaf area eaten) for *H. appendiculatus*.

To assess the possible demographic impact of herbivory, a correlative analysis was made by separating the individuals of both species into three categories of damage (0–10, 10–50, > 50% of leaf area eaten) at a given point of time, and then calculating their probability of survival some time after. There were sufficient numbers to apply this analysis only for the period Feb–Apr, 1983 (see Fig. 3), and only for *C. obtusifolia*. The results are shown in Tab. 3. The contingency analysis shows that heavily defoliated individuals (> 50% leaf area removed) had a significantly greater probability of death between recording dates, than those individuals that were undamaged or very slightly damaged (< 10% of leaf area eaten) ($\chi^2 = 15.3$, $P < 0.005$). Individuals of intermediate levels of damage, contributed very little to the significance of the analysis. Moreover, since mortality is heavier in the crown zone at the period of this analysis (Fig. 3) it is likely that the intense herbivory (Fig. 5) is, at least partly, responsible for this mortality, while the heavier mortality that occurred towards the end of the study at the root zone (cf. Fig. 3), is related to other causes.

Discussion

This study clearly demonstrates the existence of considerable differences in floristic/structural arrays and seedling performance associated with the internal spatial heterogeneity of gaps. Nevertheless, when interpreting the results of this study, it should be remembered that the comparisons between the gap zones were made using two different gaps. This study design was necessary because of the following difficulties: (1) at Los Tuxtlas the different zones of a gap (e.g., root, bole, crown) appear to be colonized at different times (J. Núñez-Farfán, R. Dirzo pers. obs.). In general, the instability of the substrate in the crown zone delays colonization and establishment for several months. Thus, the study of different zones of the same gap, although more realistic, confound the effects of the spatial heterogeneity with those of temporal heterogeneity. (2) When a gap is produced, not always are its different zones suitable for study. For example, in the gap created by the fall of the *Ficus* tree (our site I), the crown fell on a locally steeper terrain that made the establishment of permanent quadrats very difficult and also not comparable to those of the root zone. Likewise, the root zone of the other fallen tree (our site II), was located close to the foraging area of a leaf-cutting ant colony that might have prevented the comparable study of seedling performance and herbivory. Our study emphasizes spatial heterogeneity by the use of two comparable gaps – both similar in size, orientation, soil, general topography and not too far apart (ca. 200 m) from each other. However, the study of experimentally created and controlled gaps (e.g., Smith 1987, N. Brokaw, pers. comm.), may be a more suitable option.

Bearing these considerations in mind, however, a number of preliminary conclusions emerge from the study that warrant further work.

The analysis of the seedling community showed a marked contrast in the floristic assemblage of the root and crown zones. These results are in aggreement with those of Orians (1982) and Brandani et al. (1987). The fact that we detected a very low floristic similarity between zones quite early in the colonization process (Fig. 1) indicates that there might have been differential germination and establishment of seedlings. This suggests a number of studies directed to determine whether the floristic contrast is due to different seed banks and, if so, what determines the differences. The possibility that differential seed banks may be due to differential dispersal within a gap has not been studied so far. On the other hand, it is known that different species have seeds with different germination requirements, but the contrasts have been documented for seeds of pioneer vs not-pioneer species (Whitmore 1983, Vázquez-Yanes and Orozco-Segovia 1984). Much less is known about differences in germination biology within the guild of early colonizing species.

The floristic differences were accompanied by structural contrasts in the colonizing guild; different, or even the same species in the two zones showed different orders of "dominance" (based on their value of importance). These structural contrasts may be due both to differential establishment and also to differences in plant performance between the zones. The latter was

clearly illustrated by the demographic behaviour of *C. obtusifolia* and *H. appendiculatus* in the root and crown zones. It appears that the ecological characteristics of each zone constitute environmental regimes of contrasting hostility to each of the two species studied. What are the ecological features that determine these differences in plant performance? A number of obvious physical factors (soil conditions, light, substrate, etc.) may be quite different between the zones, and although detailed studies have been made on their spatial variation (e.g., Chazdon and Fetcher 1984), no characterizations seem to have been made at this scale of spatial heterogeneity. Variation of nutrients in the soil (nitrogen and phosphorus) after the gap formation has been studied by Vitousek and Denslow (1986). Their results indicate that there are differences in nutrient availability between zones within a gap. Thus, such results support our findings (see also Orians 1982, and Bazzaz 1984, for hypothetical explanations). Likewise, biotic factors such as mycorrhizae, pathogens or herbivores, may differ and affect plants distinctly in the different zones of a gap. Again, these seem not to have been assessed at this level of heterogeneity.

We found differences in herbivory between the root and crown zones in the case of *C. obtusifolia*, the plants from the crown zone having a greater level of damage. Additionally, we found evidence that herbivory may increase the plant death rates and therefore, some of the differences in survival of *C. obtusifolia* between the zones may be determined by differences in herbivory pressure. Thus, as Hartshorn (1978) pointed out, the fate of individual plants within a gap may be determined by herbivores. Again, although spatial differences in herbivory have been found for tropical forest trees (Coley 1983a, 1987), variation at this level of heterogeneity has not been documented previously.

Apart from the deaths due to unknown reasons and herbivory, trumatisms accounted for a large proportion of plant deaths in *C. obtusifolia*. This cause of mortality was more evident in the crown zone where the substrate is more unstable and where the twigs or branches of other neighbouring trees damaged by the falling crown regularly fall down. Nevertheless, most of the surviving individuals of *C. obtusifolia* were found in the crown zone; in *H. appendiculatus*, in contrast, though establishment was poor in the crown zone, none of those plants survived there (cf. Tab. 3). It appears that *C. obtusifolia*'s prop roots, stem flexibility and reiteration capacity of the stem of this species allow it to survive in the unstable and accident-prone zone of the fallen crown. These characteristics do not seem to be present in *H. appendiculatus*.

The striking floristic and structural differences in the seedling community as well as the marked differences in their survival described here, point to the possibility that besides the much discussed and well-documented heterogeneity of tropical forests caused by forest gaps (Ricklefs 1977, Strong 1977, Connell 1978, Denslow 1980, Brokaw 1982b, Orians 1982, Brandani et al. 1987) there is another source of spatial heterogeneity (Orians 1982) within gaps, that may play an important role in determining the success of particular species and may also, ultimately, affect the dynamics of the forest. Finally, the results of this study have some bearings on niche theory, because they suggests that two ecologically similar species divide up what might have been considered to be a uniform gap.

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References

Aubréville, A. 1938. La forét coloniale: les brousses secondaires en Afrique Ecuatoriale, Cote D'Ivore, Cameroun. – Revue Bois Tropiques 2: 24–35.

Bazzaz, F. A. 1984. Dynamics of wet tropical forests and their species. – In: Medina, E., Mooney, H. A. and Vázquez-Yanes, C. (eds), Physiological ecology of plants of the wet tropics. Junk, The Hague, The Netherlands, pp. 233–243.

Brandani, A., Hartshorn, G. S. and Orians, G. H. 1987. Internal heterogeneity of gaps and tropical tree species richness. – J. Trop. Ecol. In press.

Brokaw, N. V. L. 1982a. The definition of treefall gap and its effect on measures of forest dynamics. – Biotropica 14: 158–160.

– 1982b. Treefalls: frequency, timing, and consequences. – In: Leigh, E. G., Rand, A. S. and Windsor, D. M. (eds), The ecology of a tropical forest. Seasonal rhytms and long-term changes. Smithsonian Inst. Press, Washington, DC, pp. 101–108.

– 1985. Treefall, regrowth, and community structure in tropical forests. – In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbances and patch dynamics. Academic Press, New York, pp. 53–69.

Chazdon, R. L. and Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. – J. Ecol. 72: 553–564.

Coley, P. D. 1980. Effects of leaf age and plant life history patterns on herbivory. – Nature, Lond. 284: 545–546.

– 1983a. Intraspecific variation in herbivory on two tropical tree species. – Ecology 64: 426–433.

– 1983b. Herbivory and defensive characteristics of tree species in a lowland tropical forest. – Ecol. Monogr. 53: 209–233.

– 1987. Patrones en las defensas de las plantas: ò Porqué los herbivoros prefieren ciertas plantas? – In: Clark, D. A., Dirzo, R. and Fetcher, N. (eds), Ecología y ecofisiología de plantas en los bosques mesoamericanos. Rev. Biol. Trop. 34 (supl. 1): 151–164.

Connell, J. H. 1978. Diversity in tropical rainforest and coral reefs. – Science 199: 1302–1310.

Curtis, J. T. 1959. The vegetation of Wisconsin. An ordination of plant communities. – Univ. of Wisconsin Press, Madison, WI.

Denslow, J. S. 1980. Gap partitioning among tropical forest trees. – Biotropica 12 (suppl.): 47–55.

Dirzo, R. 1984. Herbivory: a phytocentric overview. – In: Dirzo, R. and Sarukhán, J. (eds), Perspectives on plant population ecology. Sinauer, Sunderland, MA, pp. 141–165.

– 1987. Estudios sobre interacciones planta-herbívoro en Los

Tuxtlas, Veracruz. – In: Clark, D. A., Dirzo, R. and Fetcher, N. (eds), Ecología y ecofisiología de plantas en los bosques mesoamericanos. Rev. Biol. Trop. 34 (supl.): 119–131.
Fox, L. and Morrow, P. A. 1983. Estimates of damage by herbivorous insects on *Eucalyptus* trees. – Aust. J. Ecol. 8: 139–147.
Greig-Smith, P. 1983. Quantitative plant ecology. 3rd ed. – Univ. of California Press, Berkeley and Los Angeles, CA.
Hallé, F., Oldeman, R. A. A. and Tomlinson, P. B. 1978. Tropical trees and forests: an architectural analysis. – Springer, Berlin.
Hartshorn, G. S. 1978. Treefalls and the tropical forest dynamics. – In: Tomlinson, P. B. and Zimmerman, M. H. (eds), Tropical trees as living systems. Cambridge Univ. Press, New York, pp. 617–638.
– 1980. Neotropical forest dynamics. – Biotropica 12 (suppl.): 23–30.
Kershaw, K. A. and Looney, J. H. H. 1985. Quantitative dynamic plant ecology. 3rd ed. – Edward Arnold, London.
Lot-Helgueras, A. 1976. La estación de biología tropical Los Tuxtlas: pasado, presente y futuro. – In: Gómez-Pompa, A., Vázquez-Yanes, C., Del Amo, S. and Butanda, A. (eds), Investigaciones sobre la regeneración de selvas altas en Veracruz, México. Ed. CECSA, México, pp. 31–69.
Martínez-Ramos, M. 1985. Claros, historia de vida de los árboles y la dinámica de la regeneración natural de las selvas altas perennifolias. – In: Gómez-Pompa, A. and Del Amo, S. (eds), Investigaciones sobre la regeneración de las selvas altas en Veracruz, México. vol. II. Ed. Alhambra, México, pp. 191–239.
– and Alvarez-Buylla, E. 1986. Seed dispersal, gap dynamics and tree recruitment: the case of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. – In: Estrada, A. and Fleming, T. (eds), Frugivores and seed dispersal. Junk, The Hague, The Netherlands. pp. 333–346.
Núñez-Farfán, J. 1985. Aspectos ecológicos de especies pioneras en una selva húmeda de México. – B. Sc. Thesis, Facultad de Ciencias, UNAM, México.
– and Dirzo, R. 1985. Herbivoría y sucesión en una selva alta perennifolia. – In: Gómez-Pompa, A. and Del Amo, S. (eds), Investigaciones sobre la regeneración de selvas altas en Veracruz, México. vol. II, Ed. Alhambra, México, pp. 313–332.
Orians, G. H. 1982. The influence of tree-falls in tropical forests on tree species richness. – Trop. Ecol. 23: 255–279.
Piñero, D., Sarukhán, J. and González, E. 1977. Estudios demográficos en plantas. *Astrocaryum mexicanum* Liebm. estructura de las poblaciones. – Bol. Soc. Bot. Mex. 37: 69–118.
Poole, R. W. 1974. An introduction to quantitative ecology. – McGraw-Hill, NY.
Ramos-Prado, J. M., Delgado Rueda, M., Del Amo, S. and Fernández, E. 1982. Análisis estructural de una área de vegetación secundaria en Uxpanapa, Veracruz. – Biotica 7: 7–29.
Richards, P. W. 1952. The tropical rain forest. – Cambridge Univ. Press, Cambridge.
Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. – Am. Nat. 111: 376–381.
Sarukhán, J. 1968. Análisis sinecológico de las selvas de *Terminalia amazonia* en la planicie costera del Golfo de México. – M. Sc. Thesis, Colegio de Posgraduados de Chapingo, México.
Schulz, J. P. 1960. Suriname. – Verh. K. Ned. Akad. Wet., Afd. Natuurkunde, Tweed. Reeks, Deel LIII: 1. Amsterdam.
Smith, A. 1987. Respuesta de hierbas del sotobosque tropical a claros ocasionados por la caída de árboles. – In: Clark, D. A., Dirzo, R. and Fetcher, N. (eds), Ecología y ecofisiología de plantas en los bosques mesoamericanos. Rev. Biol. Trop. 34 (supl.): 113–119.
Stanton, N. 1975. Herbivore pressure on two types of tropical forests. – Biotropica 7: 8–11.
Steenis, C. G. G. J. van 1958. Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. – Proc. Symp. Humid Trop. Veg., Kandy. UNESCO, Paris, pp. 159–165.
Strobeck, C. K. 1974. Sufficient conditions for polymorphism with n niches and m mating groups. – Am. Nat. 108: 152–156.
Strong, D. R., Jr. 1977. Epiphyte loads, treefalls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. – J. Biogeogr. 4: 215–218.
Turkington, R. and Aarssen, L. W. 1984. Local-scale differentiation as result of competitive interactions. – In: Dirzo, R. and Sarukhán, J. (eds), Perspectives on plant population ecology. Sinauer, Sunderland, MA, pp. 107–127.
Vázquez-Yanes, C. and Orozco-Segovia, A. 1984. Ecophysiology of seed germination in the tropical humid forests of the world: a review. – In: Medina, E., Mooney, H. A. and Vázquez-Yanes, C. (eds), Physiological ecology of plants of the wet tropics. Junk, The Hague, The Netherlands, pp. 37–50.
Vitousek, P. M. and Denslow, J. S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. – J. Ecol. 74: 1167–1178.
Whitmore, T. C. 1975. Tropical rain forest of the far East. – Clarendon Press, Oxford.
– 1978. Gaps in the forest canopy. – In: Tomlinson, P. B. and Zimmerman, M. H. (eds), Tropical trees as living systems. Cambridge Univ. Press, New York, pp. 639–655.
– 1982. On pattern and process in forests. – In: Newman, E. I. (ed.), The plant community as a working mechanism. Blackwell, Oxford, pp. 45–59.
– 1983. Secondary succession from seed in the tropical rain forest. – Forest. Abstr. 44: 767–779.
Wilson, D. S. 1980. The natural selection of populations and communities. – The Benjamin/Cummings Publ. Co., California.

Appendix. Floristic list of the species present only in the root zone (R), only in the crown zone (C), or in both (B) zones of the trefall-gaps at Los Tuxtlas. Code numbers correspond to the species cited in Fig. 2.

Species	Code no.	Zone	Family
Aphelandra aurantiaca	10	R	Acanthaceae
Odontonema callistachyum	8	R	Acanthaceae
Iresine diffusa	34	R	Amaranthaceae
Cymbopetalum baillonii	50	C	Annonaceae
Fornsteronia viridescens	46	B	Apocynaceae
Stemmadenia donnell-smithii		R	Apocynaceae
Anthurium pentaphyllum	18	B	Araceae
Dieffenbachia seguine	9	R	Araceae
Not identified Ar. 1	8	B	Araceae
Not identified Ar. 2		R	Araceae
Not identified Ar. 3	24	R	Araceae
Not identified Ar. 4	27	B	Araceae
Philodendron saggitifolium		R	Araceae
Syngonium podophyllum	26	R	Araceae
Not identified Beg. 1		R	Begoniacea
Anemopaegma chrysanthum	29	R	Bignoniaceae
Ochroma pyramidale		R	Bombacaceae
Cordia megalantha		C	Boraginaceae
Carica papaya	14	R	Caricaceae
Eupatorium galeottii		R	Compositae
Neurolaena lobata	19	R	Compositae
Ipomoea batatas	30	R	Convolvulaceae

Ipomoea phillomega	31	R	Convolvulaceae
Acalypha skutchii	7	B	Euphorbiaceae
Croton schiedeanus	48	C	Euphorbiaceae
Sapium nitidum	32	R	Euphorbiaceae
Tetrorchidium rotundatum		B	Euphorbiaceae
Pleuranthodendron lindenii		R	Flacourtiaceae
Not identified Poa. 1	13	R	Poaceae
Salacia megistophylla		R	Hippocrateaceae
Dussia mexicana	42	C	Fabaceae
Spigelia palmeri	20	B	Loganiaceae
Hiraea fagifolia	37	C	Malphigiaceae
Not identified Mal. 1	43	C	Malphigiaceae
Robinsonella mirandae	4	R	Malvaceae
Trichilia breviflora		R	Meliaceae
Trichilia martiana	38	B	Meliaceae
Trichilia moschata		C	Meliaceae
Cecropia obtusifolia	1	B	Moraceae
Poulsenia armata		R	Moraceae
Pseudolmedia oxyphyllaria	22	R	Moraceae
Trophis mexicana	25	B	Moraceae
Heliconia bihai	12	R	Musaceae
Astrocaryum mexicanum		R	Arecaceae
Chamaedorea tepejilote		R	Arecaceae
Passiflora helleri		R	Passifloraceae
Piper auritum	11	R	Piperaceae
Piper hispidum	16	R	Piperaceae
Piper sp.	36	B	Piperaceae
Phytolacca rivinoides	33	R	Phytolaccaceae
Polypodium sp.		R	Polypodiaceae
Not identified Rub. 1	39	C	Rubiaceae
Not identified Rub. 2		B	Rubiaceae
Psychotria faxlucens	23	R	Rubiaceae
Psychotria simiarum		R	Rubiaceae
Zanthoxylum kellermanii	47	C	Rutaceae
Cupania glabra	17	R	Sapindaceae
Paullinia costaricensis	44	C	Sapindaceae
Serjania goniocarpa		R	Sapindaceae
Pouteria durlandii		R	Sapotaceae
Selaginella sp.	15	R	Selaginellaceae
Lycianthes heteroclita		R	Solanaceae
Not identified Sol. 1	21	R	Solanaceae
Not identified Sol. 2		R	Solanaceae
Not identified Sol. 3		C	Solanaceae
Solanum schlechtendalianum		R	Solanaceae
Heliocarpus appendiculatus	3	B	Tiliaceae
Trema micrantha	35	R	Tiliaceae
Trichospermum mexicanum	5	R	Tiliaceae
Urera caracasana	6	R	Urticaceae
Urera elata		R	Urticaceae
Orthion oblanceolatum	49	B	Violaceae
Cissus gossypiifolia	2	B	Vitaceae
Not identified A		C	
Not identified B		R	
Not identified C	45	C	
Not identified D	40	B	
Not identified E		B	
Not identified F		C	
Not identified G	41	B	
Not identified H		R	
Not identified I		R	
Not identified J		R	
Not identified K		R	
Not identified L		R	
Not identified M		R	