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Pioneer species distribution in treefall gaps in Neotropical rain forest; a gap definition and its consequences

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ABSTRACT. An attempt was made to evaluate the consequences of applying a strict definition (Brokaw 1982a) to the delimitation of forest gaps in the field. The northernmost Neotropical rain forest, at Los Tuxtlas, Mexico, was searched for young (1–2 years old) single-event gaps that would meet the criteria of the definition. In 60 ha of rain forest, only 12 such gaps containing pioneer species could be found. Thirty-three pioneer species (shrubs and trees) were used as indicator species for gap conditions. Gap size, measured as projected canopy opening (*sensu* Brokaw 1982a), underestimated from 44 to 515% the size of the area colonized by pioneer species. On average the size of the colonized area was 3.4 times larger than the size of the projected canopy opening. The majority of the pioneer species showed a relative preference for gap borders, an area generally not included in the projected canopy opening. Pioneer plant abundance and density, and species richness and density, did not differ significantly between gap centres and gap borders. Floristical variation was not related to gap size or location in the gap. These findings can be explained if gap environment (to which pioneer plants respond) is seen as the result of many interacting factors, of which size of the canopy opening is only one. It is concluded that the definition for delimiting gaps in the field as proposed by Brokaw (1982a) cannot be regarded a generally applicable definition, and that its value as a comparative standard is doubtful.

KEY WORDS: gap definition, Neotropics, pioneer community, pioneer species distribution, treefall gaps, tropical rain forest.

INTRODUCTION

Vegetation gaps resulting from treefalls are considered to be of great importance for the regeneration of tropical rain forest species (Bazzaz 1984, Brokaw 1985b, Denslow 1980, Hartshorn 1978, 1980, Orians 1983, Pickett 1983, Whitmore 1978, 1982). Consequently it is important to apply a clear and unequivocal definition of 'gap', so that results of research on gap dynamics are comparable between sites. Although many studies on gap-phase regeneration have been carried out in the past (see reviews by Brokaw 1985b and Martínez-Ramos 1985), relatively few provide a clear definition of 'gap' and its spatial delimitation, possibly as a result of the large variation in gap appearance in the field. In most cases the definitions given are general and vague; they refer to gaps as 'canopy opening' or 'hole in the foliage' (e.g. Bazzaz 1984, Oldeman 1978, Richards 1952, Schulz 1960, Whitmore 1984). To date the only strict definition for tropical forests is given by Brokaw (1982a). He defines a gap as:

> A 'hole' in the forest extending through all levels down to an average height of 2 m above ground. The sides of forest openings are irregular in profile, but for a workable definition the side at a particular place on the perimeter is located at the innermost point reached by foliage, at any level at that place on the perimeter.

This definition has been used to delimit the area in which the early stages of the regeneration of plant populations, especially pioneers, are affected as a result of the canopy opening and the associated changes in microclimate (Brokaw 1985a, 1987). It has also been used for estimating the degree of canopy destruction resulting from natural disturbances in the forest (Brokaw 1982b, 1985b).

The question is whether the delimitation of affected space by this definition is proper. Our field observations suggested that the application of Brokaw's (1982a) definition would result in an underestimation of the space in which vegetation structure and plant populations are affected. Two questions emerge: (1) to what extent is the total affected area underestimated by the application of Brokaw's gap definition? (2) is the structure and composition of the pioneer community of the transition zone between the centre of a gap and the surrounding mature forest different from that of the centre istself? In this paper, we assess these two questions. The data were collected during a survey of pioneer plant communities in canopy gaps in the tropical rain forest reserve of Los Tuxtlas, State of Veracruz, Mexico.

STUDY SITE

The Tropical Field Station of Los Tuxtlas is a 700 ha reserve of tropical rain forest in the State of Veracruz, Mexico. It is considered to be the northernmost Neotropical rain forest (18° 35′ N, 95° 07′ W). Canopy height varies from 25 to 35 m. There are no records of recent human disturbance in the reserve, but at present it is surrounded by large clearings, used as pastures and crop fields. These clearings result in a higher rate of treefall disturbance at the forest edges of the forest reserve (Martínez-Ramos 1985, Sarukhán *et al.* 1985).

Average annual rainfall in the area is 4639 mm and the mean annual temperature is 24.6°C (data of the meteorological station of Coyame, located at a distance of 35 km from the study site). A relatively dry period occurs, usually from March until May. The topography of the area is characterized by steep slopes (23–38% on average, Martínez-Ramos, unpublished data). Soils are classified as vitric andosols (FAO/UNESCO 1975), and are relatively rich in N, P and K (Bongers *et al.*, in press). Descriptions of the flora, vegetation, and ecology of the forest of Los Tuxtlas can be found in Gomez-Pompa *et al.* (1976), Gomez-Pompa & del Amo (1985), Ibarra-Manriquez (1985), Bongers *et al.* (in press) and Popma *et al.* (in press).

METHODS

To study the effect of gap characteristics on pioneer community composition, we censused young gaps (1–2 years old, age determined according to the method described by Martínez-Ramos 1985) in about 60 ha of primary forest. We used the definition proposed by Brokaw (1982a) to delimit the gaps in the field. Only single-event gaps were included in the census, and we concentrated our study on the community of pioneer species. These pioneer species regenerate and thrive under elevated light conditions and not below the intact forest canopy (Martínez-Ramos 1985, Vazquez-Yanes 1980, Vazquez-Yanes & Orozco-Segovia 1984). In an area of about 60 ha we detected approximately 400 gaps. Among these, only 12 were single-event gaps of 1–2 years old. The remainder were either too old to be included in the analysis, or consisted of a combination of several gaps of unequal age, or did not extend through all vegetation layers (which made them unsuitable according to Brokaw's (1982a) definition).

In each gap included in the analysis we located the perimeter and centre of the canopy opening above it. From this point eight lines were laid out at regular angular intervals and in fixed directions. Two areas were delimited along these lines: the 'projected canopy opening' (*sensu* Brokaw 1982a), and the 'total affected area' indicated by the presence of young pioneer plants with a height over 0.5 m. Subsequently the 'total affected area' was subdivided into two parts, a 'gap centre area' and a 'gap border area' (Figure 1). The 'gap centre area' lies at the gap's centre and is of the same shape as the 'total affected area', but its linear dimensions in all eight directions are proportionally shortened (by a factor 0.7) in such a way that its area was approximately half of the 'total affected area'. The remainder was called the 'gap border area'. Gap centre and gap border are defined here in a pragmatic way, to make sure that they are approximately equal in size, thus avoiding species-area effects. All pioneer plants at least 0.5 m tall were counted by species for the centre and border areas separately. These counts were used, transformed on a $\log_2$ basis, for an analysis of community composition using indicator species analysis, a polythetic divisive classification method (Hill *et al.* 1975, program TWINSPAN, Hill 1979). Gap centre and gap border areas were treated as separate units in the analysis, and only species that occurred in more than three units were included to avoid distortions due to rare species.

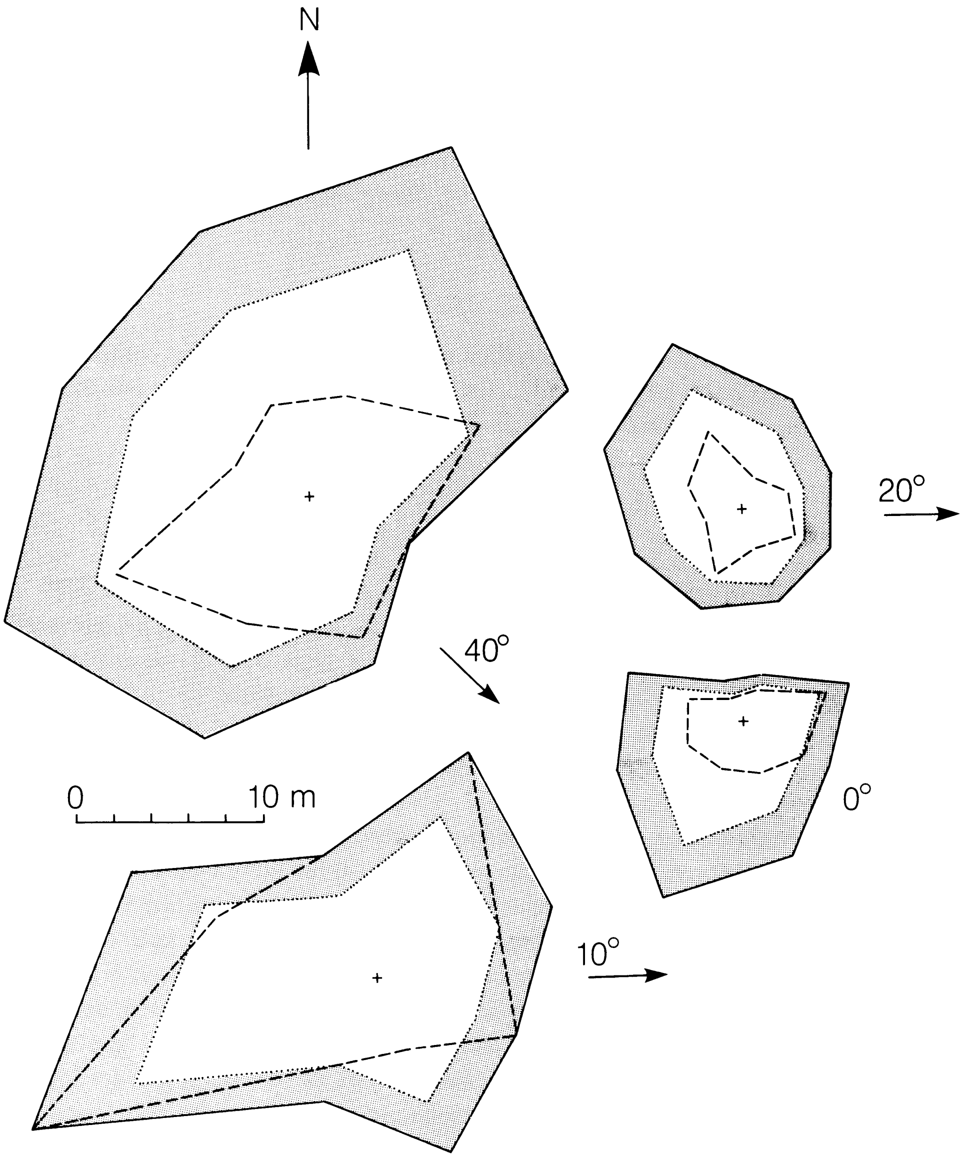

Figure 1. Maps of four canopy gaps from the Los Tuxtlas rain forest. Shown is the total affected area colonized by pioneers (———), the projected canopy opening (- - - -), and the gap centre area (. . . . .). The gap border area is shaded. Arrows indicate the upward direction of the land surface slopes, and values indicate their steepness (degrees).

RESULTS

Gap characteristics

Table 1 gives a summary of the characteristics of the gaps sampled and the pioneer communities recorded there. Four of these gaps were caused by falling branches, three by uprooted trees, and five by trees snapped above ground level.

Table 1. Characteristics of gaps and pioneer communities for twelve gaps of the Los Tuxtlas rain forest.

Gap number	1	2	3	4	5	6	7	8	9	10	11	12	Total
						Gap characteristics							
Size of PCO* (m^2)	12	19	20	23	31	51	73	79	84	127	137	223	
Size of centre (m^2)	18	56	57	50	58	61	147	55	71	128	261	169	1131
Size of border (m^2)	19	61	58	52	60	76	158	59	78	146	291	164	1222
Size of TAA† (m^2)	37	117	115	102	118	137	305	114	149	274	552	333	
Elevation (m)	185	200	205	245	340	160	315	390	215	210	320	249	
Slope (%)	25	20	20	0	35	20	45	35	15	25	40	10	
Aspect	SE	E	E	–	N	NE	N	E	NE	SE	SE	E	
Mean height of surrounding vegetation	16.8	19.3	20.0	22.3	22.2	24.1	16.3	22.7	17.3	27.0	19.4	16.7	
						Community structure							
No. of species in centre	5	6	9	4	6	7	13	9	5	20	15	4	
No. of species in border	3	6	6	6	5	10	16	18	10	15	15	5	
No. of species in TAA†	5	8	10	6	8	13	17	18	11	22	18	6	
No. of indiv. in centre	16	20	34	41	36	7	120	22	31	65	122	6	520
No. of indiv. in border	14	48	28	24	64	21	163	50	57	42	231	18	760
No. of indiv. in TAA†	30	68	72	65	100	28	283	72	88	107	353	24	

* PCO is projected canopy opening; † TAA is total affected gap area.

Slope varied between 0 and 45 degrees, slope aspect ranged from north through east to south. The mean height of the surrounding vegetation (measured at eight points on the circumference of the projected canopy opening) varied between 16.3 and 22.7 m (but individual point values ranged from 9 to 35 m). It is obvious that the gaps were rather different in many features. The most important result is that the area colonized by pioneer species was always larger than the area of the canopy opening by vertical projection (Figure 1). Also, the latter was not necessarily concentric with the colonized area (Figure 1).

The size of the projected canopy opening and the size of the total affected area were significantly correlated ($R = 0.74$, $P < 0.01$), but variance seemed to become larger at larger gap sizes (Figure 2). Total affected area was from 44 to 515% larger than the projected canopy opening; on average it was 3.4 ± 1.6 (SD) times as large.

Pioneer species distribution

In order to assess whether individual species showed preferences for either border or centre areas, the relative abundance of a species in the two areas was calculated (Table 2). These figures indicate tendencies, as sample size was too small to determine the significance of this predominance. Because we are dealing with pioneer species only, it was expected that most of them would show a clear preference for the centre area. However, only four species showed this pattern. One species was equally abundant in gap centres and borders, while eleven species showed a relative predominance in gap borders. The remaining seventeen species were (arbitrarily) considered to be too infrequent ($\leqslant 3$ gaps) to make any conclusions about their possible preferences.

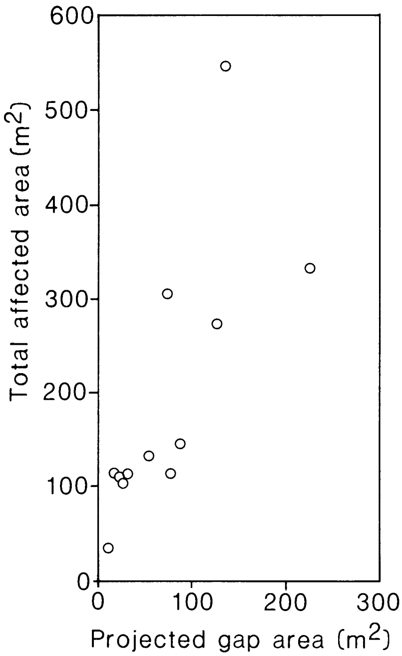

Figure 2. Relation between size of total affected area and size of projected canopy opening. Pearson Correlation $R = 0.74$, $P < 0.01$.

Pioneer communities

Compared in terms of pioneer plant abundance (number of pioneer plants per gap, given in Table 1) and density (number of plants m^{-2}), and species richness (number of pioneer species per gap, Table 1) and density (number of species m^{-2}), no significant differences between gap centre and gap border areas could be found.

Nevertheless the data suggested considerable differences for some variables. For example, the total number of pioneer plants found in all gap borders was 135% (corrected for the small difference in area between a gap's centre and its border) of the total for all gap centres. The mean difference per gap however, was only 20 ± 34.6 (SD) plants, which was not significantly different from 0 ($t = 2.00$, NS).

Most of the frequent species showed a relative predominance in either the gap centres or the gap borders (Table 2). This does not necessarily imply that the species lists of the pioneer communities in the gap centre and border areas differ. The results from the species and samples classification are shown in Table 3. The first species group resulting from the first division (group '0' in Table 3) consists of species considered to be 'large gap' pioneers which require high light levels for their regeneration: *Cecropia obtusifolia* (Barton 1984, Martínez-Ramos & Alvarez-Buylla 1986), *Trema micrantha* (Brokaw 1987), *Heliocarpus appendiculatus* (Barton 1984), *Piper hispidum* (Gomez-Pompa & Vazquez-Yanes 1985), *Piper auritum* (Gomez-Pompa & Vazquez-Yanes 1985),

Table 2. Proportion of gaps with a higher (f-centre), equal (f-equal) or lower (f-border) abundance of each pioneer species in gap centre relative to gap border. Species are ordered in terms of their relative preference for centre or border of gap.

	Frequency (number of gaps)	f-centre	f-equal	f-border
Species predominating in gap centres				
Cecropia obtusifolia (Moraceae)	6	1	0	0
Urera elata (Urticaceae)	6	0.83	0.17	0
Heliocarpus appendiculatus (Tiliaceae)	7	0.71	0	0.29
Piper lapathifolium (Piperaceae)	7	0.57	0.14	0.29
Species equally important in gap centres and gap borders				
Urera caracasana (Urticaceae)	7	0.43	0.13	0.43
Species predominating in gap borders				
Omphalea oleifera (Euphorbiaceae)	8	0.13	0	0.87
Robinsonella mirandae (Malvaceae)	4	0.25	0	0.75
Myriocarpa longipes (Urticaceae)	10	0.20	0.10	0.70
Acalypha skutchii (Euphorbiaceae)	9	0.22	0.11	0.66
Schaueria calycobractea (Acanthaceae)	12	0.17	0.25	0.58
Piper hispidum (Piperaceae)	7	0.29	0.14	0.57
Piper amalago (Piperaceae)	8	0.22	0.22	0.56
Hampea nutriformis (Malvaceae)	4	0.25	0.25	0.50
Stemmadenia donnell-smithii (Anacardiaceae)	4	0.25	0.25	0.50
Trema micrantha (Ulmaceae)	4	0.25	0.25	0.50
Siparuna andina (Monimeaceae)	4	0.25	0.25	0.50
Low frequency species				
Carica papaya (Caricaceae)	3	1	0	0
Spondias radlkoferi (Anacardiaceae)	2	1	0	0
Heliconia bihai (Musaceae)	1	1	0	0
Acalypha diversifolia (Euphorbiaceae)	1	1	0	0
Cestrum sp. (Solanaceae)	1	1	0	0
Xanthosoma sp. (Araceae)	3	0.67	0	0.33
Solanum sp. (Solanaceae)	3	0.67	0	0.33
Potomorphe umbellatum (Piperaceae)	3	0.33	0.33	0.33
Piper auritum (Piperaceae)	3	0.33	0.33	0.33
Alchornea latifolia (Malvaceae)	1	0	1	0
Piper umbellatum (Piperaceae)	2	0.50	0	0.50
Trichospermum mexicanum (Tiliaceae)	2	0.50	0	0.50
Tetrochidum rotundatum (Euphorbiaceae)	3	0.33	0	0.66
Neurolaena macrocephala (Asteraceae)	3	0	0.33	0.66
Erythrina folkersii (Legumniosae)	2	0	0	1
Cnidosculus multilobus (Euphorbiaceae)	1	0	0	1
Ochroma pyramidale (Bombacaceae)	1	0	0	1

Urera caracasana and *Urera elata*. The species in the second group (group '1' in Table 3) are classified as 'small gap' pioneers, which are known to regenerate under lower, as well as higher light levels. They include *Acalypha skutchii, Myriocarpa longipes* (Bongers & Popma, unpublished data), *Piper amalago* (Gomez-Pompa & Vazquez-Yanes 1985), *Schaueria calycobractea* and even a late secondary canopy species, *Omphalea oleifera* (Bongers & Popma, unpublished data).

Table 3. TWINSPAN classification of the pioneer plant stands in centres and borders of twelve gaps in the Los Tuxtlas rain forest. Species with a frequency less than four units were excluded from the analysis. These are given at the bottom of the table. Values are transformed according to the following scale: 1 = 1, 2 = 2, 3 = 3-5, 4 = 6-11, 5 = 12-23, 6 = 24-47, 7 = > 48 individuals. Circles indicate small gaps (total affected area less than 200 m^2), squares are large gaps (total affected area greater than 200 m^2), open symbols denote gap borders, closed symbols gap centres.

	Gap number																								Species classification	
Species	10 ■	10 □	11 ■	11 □	6 ●	7 ■	7 □	5 ●	8 ●	8 ○	1 ●	2 ●	2 ○	3 ●	3 ○	6 ○	9 ●	9 ○	1 ○	4 ●	4 ○	12 ■	12 □	5 ○	level 1	level 2
Cecropia obtusifolia	4	3	4	3	1	2	1	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	a
Piper auritum	.	.	2	2	.	4	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	a
Robinsonella mirandae	1	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	0	a
Stemmadenia deonnell-smithii	2	2	1	2	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	0	a
Trema micrantha	1	1	1	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	0	a
Carica papaya	4	3	4	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	a
Siparuna andina	3	2	3	3	.	3	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	0	a
Potomorphe umbellatum	1	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	a
Heliocarpus appendiculatus	3	2	4	4	1	2	1	.	4	2	.	.	.	1	.	.	.	3	.	.	.	.	.	.	0	b
Piper hispidum	1	1	3	3	.	.	5	5	.	1	3	.	.	2	3	.	.	.	.	.	1	1	2	.	0	b
Urera caracasana	4	4	3	1	2	2	3	.	3	4	.	1	1	.	.	.	.	2	.	.	.	.	.	.	0	b
Urera elata	2	.	1	1	.	5	3	2	3	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	0	b
Neurolaena macrocephala	.	.	.	.	1	.	2	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	0	b
Xanthosoma sp.	.	.	.	.	.	2	.	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	0	b
Acalypha skutchii	.	2	.	.	.	.	.	.	1	4	4	3	6	5	4	3	4	5	4	2	2	1	2	.	1	a
Hampea nutriformis	2	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	2	.	.	.	.	.	.	1	a
Omphalea oleifera	.	.	.	.	.	1	6	4	1	2	1	.	.	.	1	1	.	.	2	1	1	2	3	6	1	a
Piper amalago	4	4	.	.	.	3	5	1	1	3	1	1	2	.	.	.	1	1	.	3	1	.	3	2	1	a
Schaueria calycobractea	1	1	6	7	.	7	7	5	.	3	1	4	4	3	4	4	5	5	1	6	5	.	4	6	1	a
Myriocarpa longipes	1	1	5	6	.	.	4	.	1	2	1	.	4	2	.	1	3	3	.	.	.	.	.	1	1	b
Piper lapatifolium	2	3	3	.	.	1	1	2	.	.	.	.	.	4	4	1	1	.	.	.	.	.	.	.	1	b
Sample classification level 1:	a	a	a	a	a	a	a	a	a	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b		
level 2:	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1		
Low frequency species excluded from analysis																										
Spondias radlkoferi	3	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Piper umbellatum	2	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Alchornea latifolia	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cnidosculus multilobus	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cestrum sp.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Tetrorchidum rotundatum	.	.	.	1	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.		
Trichospermum mexicanum	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.		
Erythrina folkersii	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.		
Helioconia bihai	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.		
Solanum sp.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.		
Acalypha diversifolia	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.		
Ochroma pyramidale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.		

The samples are grouped according to the predominance of one or the other species group in them. The samples group 'a' (characterized by species group '0') is formed by centre and border areas of large gaps (total affected area >200 m^2), centre areas of small gaps (total affected area <200 m^2) and one border area of a small gap. Samples group 'b' (characterized by species group '1') is formed by centre and border areas of small gaps, and the centre and border area of one large gap. A second order division of the samples as well as of the species groups is indicated at the sides of the table. It is clear that no division between gap centre and gap border areas occurred.

These results suggest that floristic variation is partly related to gap size, but not to location within a gap.

DISCUSSION

The vertical projection of the canopy opening was not an adequate estimate of the area affected by that opening. The area of the projected canopy opening consistently underestimated the area affected by a particular canopy gap as indicated by the presence and frequency of colonizing pioneer species. The relation between projected canopy opening and total affected area as shown in Figure 2, suggests that the underestimation was not systematic. The transition zone between a gap and the surrounding mature forest was generally not included in the projected canopy opening. Nevertheless, this transition zone can be an important site for colonization by pioneer species.

More species showed a preference for gap borders than for gap centres, even with our crude distinction between centre and border areas. No general differences in structure and floristic composition could be detected between colonizing pioneer assemblages in gap centre areas and gap border areas. In almost any individual gap however, important differences could be pointed out between centre and border areas.

Two main groups emerged from the species classification (Table 3). The first species group comprised three species showing a relative predominance in gap centre areas, as well as five species predominating in gap border areas (cp. Table 2). These species may be generally characterized as 'large gap' species. The second species group contained almost exclusively (6 out of 7) species showing a relative predominance in gap border areas, and may be characterized as 'small gap' species. However, neither species group is restricted to large or small gaps, nor to gap centre or gap border areas. This can be understood if the 'gap environment' is seen as a result of the interaction between size of the canopy opening, surface inclination, slope aspect, height of the surrounding vegetation, daily and seasonal variation in the position of the sun, and gap origin. This interaction can cause the border of the gap to appear environmentally like a centre, with a corresponding structure and composition in the pioneer community. Likewise, similar interactions can cause a small gap to appear like a large one and vice versa. The conclusion seems justified that gap borders and gap centres can be equally important as far as early colonization is considered, and that they should therefore be included in any study concerning the effect of treefall gaps on population and vegetation dynamics of forests. Hence, the definition of treefall gaps as proposed by Brokaw (1982a) is too restrictive to be ecologically appropriate.

Two other drawbacks of Brokaw's (1982a) definition can be mentioned. The first one is the requirement of a canopy opening to extend through all vegetation layers in order to be considered a gap. Canopy gaps that do not meet this requirement, or gaps that occur only in the understorey are very frequent in the forest. In these partial gaps growth and/or survival of juvenile individuals of upper-canopy tree species and recruitment and reproduction of understorey trees, shrubs, and herbs is affected (Brokaw 1985a, Clark and Clark *in press*, Sarukhán *et al.* 1984). Second, it is doubtful if direct comparisons between different sites based on the size of the projected canopy opening alone will be very realistic. For example a gap in a high forest will have a smaller influence at ground level than an equally-sized gap in a lower forest. For the same reason, comparisons between geographically different sites should always take into account the position of the sun in estimating the location of the truly affected area below a canopy opening.

The implications of loosening the restrictions imposed by the definition proposed by Brokaw (1982a) could be far reaching. Gap size would increase considerably, and forest turnover rates calculated from gap size frequency would be much faster than previously estimated.

In a later paper, Brokaw (1987), stressed some of the limitations of his definition, but he continues to use it. We suggest that the gap definition proposed by Brokaw should be modified into an ecologically more meaningful one. This is not a simple task, as it would necessarily involve long term and detailed measurements of the changes in the microenvironment caused by treefall gaps, and plant response thereon. An *a posteriori* bio-assay, as applied in this study, can be used to ascertain (locally) the appropriateness of the use of an *a priori* gap definition. However, for comparison among forests a definition based on a bio-assay cannot be used because the bio-assay itself is a variable. An *a priori* definition based on physical gap characteristics is necessary. As such Brokaw's definition is a starting point.

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