



## Treefall Age Determination and Gap Dynamics in a Tropical Forest

Miguel Martinez-Ramos, Elena Alvarez-Buylla, Jose Sarukhan, Daniel Pinero

*Journal of Ecology*, Volume 76, Issue 3 (Sep., 1988), 700-716.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198809%2976%3A3%3C700%3ATADAGD%3E2.0.CO%3B2-4>

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

*Journal of Ecology* is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

---

*Journal of Ecology*

©1988 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).

©2002 JSTOR

## TREEFALL AGE DETERMINATION AND GAP DYNAMICS IN A TROPICAL FOREST

MIGUEL MARTÍNEZ-RAMOS\*†, ELENA ALVAREZ-BUYLLA†, JOSÉ SARUKHÁN† AND DANIEL PIÑERO†

*\*Estación de Biología Tropical Los Tuxtlas, Apartado Postal 94, San Andrés Tuxtla, Veracruz, México and Departamento de Ecología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-233, 04510 México D.F., México*

### SUMMARY

(1) Most individuals of *Astrocaryum mexicanum*, a monopodial neotropical understorey palm, endure treefalls that form gaps in the forest, by bending under falling trees and limbs. After one year, a bent palm recovers vertical growth at its terminal meristem and forms a permanent kink in its stem. Previous detailed demographic studies have allowed us to determine with accuracy the passage of time, based on the age-constant rate of stem elongation of the palm.

(2) Using this morphological feature of the palm, together with its high density (300–1230 mature individuals ha<sup>-1</sup>) in a 5-ha tract of rainforest at Los Tuxtlas, Veracruz, México, it was possible for the first time to apply a time scale to the study of gap formation and regeneration dynamics of tropical rainforests. Surviving palms, after being knocked down or bent by treefalls, record gap-forming events for up to 100 years. By using this technique, the age structure of the forest mosaic was obtained at a scale of 25 m<sup>2</sup>.

(3) A high variation in both temporal turnover rates (mean ± S.D. = 47 ± 45 years) and spatial occurrence of treefall disturbances was found; more than 50% of the quadrats suffered disturbance in the last thirty years and 28% suffered more than one disturbance in the last seventy years. These results provide evidence that canopy disturbances capable of promoting the release of suppressed seedlings and saplings of forest trees may occur at the small scale of some tens of square metres.

(4) The long-term treefall patterns analysed (up to seventy years) show that canopy disturbances are a permanent ecological factor in the rainforest environment. Annual rainfall explains more than 50% of the annual variation of the proportion of forest opened to gaps per year.

(5) The yearly disturbance does not indicate the gap availability for species regeneration: for example, a year of high disturbance (e.g. 6.1% of the forest opened to gaps) may have a similar number of sizeable gaps suitable for pioneer regeneration as a year of low disturbance (e.g. 1.5% of the forest opened to gaps).

(6) The results obtained in this study show that the gap-formation process operating at Los Tuxtlas forest promotes a strong temporally and spatially random variation in the physical environment of plants. This heterogeneity may be one of the factors involved in determining the high biological diversity found in most tropical rainforests.

### INTRODUCTION

Treefall disturbances play a crucial role in the structure and dynamic processes of forest communities (Whitmore 1975; Hallé, Oldeman & Tomlinson 1978; Pickett & White 1985). Current research is focused on the mechanisms involved in the so-called 'patch dynamics' (Pickett & White 1985; Sarukhán, Piñero & Martínez-Ramos 1986). Treefalls generate gap dynamics in forest populations; these gap dynamics promote the expression

† Present address: Centro de Ecología, UNAM, Apartado Postal 70-275, México, D.F., 04510, México.

of a floristic–structural mosaic of vegetation which may be subject, by virtue of repeated disturbance events, to recurrent successional phases (Oldeman 1978; Bormann & Likens 1979; Brokaw 1985a; Martínez-Ramos 1985; Martínez-Ramos & Alvarez-Buylla 1986). Although models of gap dynamics have been developed (e.g. Shugart & Darrel 1981), predictive analyses of the patchwork of forest vegetation are pending. If the status of a plant community at any given time is partly the result of disturbance and successional events that have occurred in the past (Harper 1977), historical analyses are needed to predict the future dynamics of forest communities.

In temperate forests, growth rings of fallen and gap-released trees may be used to record treefall events, in order to study the influence of treefalls on the mechanisms responsible for the structure and composition of the forest (Lorimer 1980; Runkle 1981, 1982). The virtual absence of chronologically regular and permanent vegetative structures in tropical trees (e.g. growth rings) (Bormann & Berlyn 1981) has hindered the application of such a method in tropical rain forests. In this paper we show that certain understorey palms can be used to detect the temporal and spatial treefall regimes operating in these communities. An application of this approach is made to investigate some patterns of gap dynamics occurring in a tropical rain forest of south-eastern México.

## METHODS

### *The dating device*

The study was carried out in the tropical rain forest at the Los Tuxtlas Tropical Field Station (Instituto de Biología, Universidad Nacional Autónoma de México) (LTTS), located in the State of Veracruz (18°36'N, 95°07'W), México. The mean annual rainfall at LTTS is about 4500 mm and no month has less than 100 mm of rain. The forest in the 700-ha reserve includes more than 200 tree species and the mean canopy height is about 30 m. Detailed descriptions of the flora, vegetation and environmental conditions occurring at LTTS are given in Piñero, Sarukhán & González (1977), Estrada, Coates-Estrada & Martínez-Ramos (1985), and Ibarra-Manríquez (1985).

Understorey plants of most tropical rain forests receive blows by the falling upper-canopy trees and large branches. This is particularly noticeable in the case of the palm *Astrocaryum mexicanum* Liebm., which represents 20–60% of all trees with diameters at breast height (dbh)  $\geq 3.3$  cm in LTTS (Piñero, Sarukhán & González 1977). It occurs at densities of 300–1230 mature plants (stems from 1–7 m in height)  $\text{ha}^{-1}$  and is distributed almost everywhere in the forest (Piñero, Sarukhán & González 1977). The annual probability of a palm being hit by a falling tree or large branch is 0.0133, because forty-four out of 345 mature individuals were observed to have been knocked or bent down by treefalls in eight 20 m  $\times$  30 m permanent plots used for long-term demographic studies of this species (Sarukhán 1978; Piñero, Martínez-Ramos & Sarukhán 1984), in the period 1975–1985.

If the single apical meristem of *A. mexicanum* is severely damaged or broken off by a blow, the palm dies. In most cases, however, the cylindrical, slender (4–7 cm diameter), woody stem simply bends downwards when hit. The high flexibility and resistance of the trunk, and its firmly anchored root system keep the stem from either breaking or being uprooted. Bent palms have a high chance of surviving. We estimated an annual survivorship rate of 0.9667 by following the fate of 110 bent palms (including recently-bent mature individuals) in our permanent plots between 1981 and 1985.



FIG. 1. Recovery sequence of *Astrocaryum mexicanum*: (a) stem is bent by a treefall creating a gap (arrowed); (b) bent stem starts turning upwards at the tip of the terminal meristem within one year of being blown down (arrowed); (c) a kink forms at this point (arrowed), and the stem continues growing vertically; (d)  $L_1$  estimates the age at which the palm was blown down and  $L_2$  how long ago the treefall occurred.

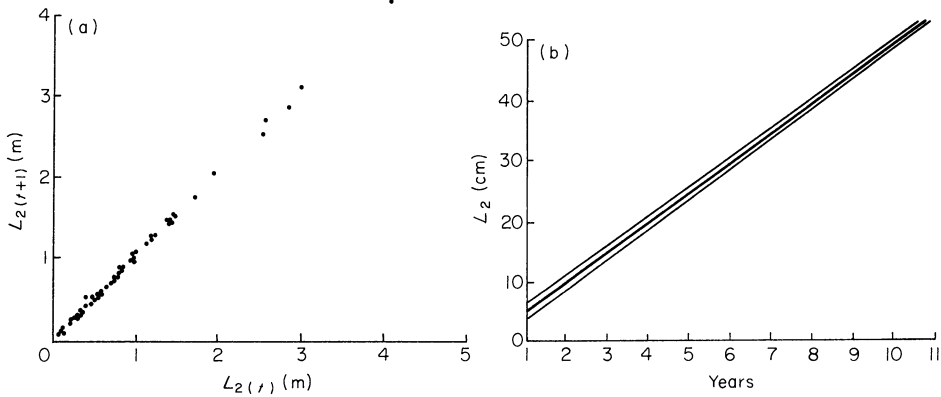


FIG. 2. (a) Relationship between two consecutive measures of  $L_2$  for mature bent palms growing in eight  $20 \text{ m} \times 30 \text{ m}$  permanent plots. Data taken for a four-year period (1981–85) and transformed to a one-year basis; the slope of the linear regression does not differ significantly from an expected value of 1.0 ( $y = 0.048 + 1.01x$ ,  $F'_{97} = 78.33$ ,  $r^2 = 0.9988$ ,  $P < 0.001$ ) and confidence intervals are  $\pm 1.2 \text{ cm}$ ; variates are not autocorrelated (Durbin–Watson test = 1.85;  $P > 0.10$ ). (b) The predicted mean and confidence interval values of  $L_2$ , representing the first ten years after the recovery of a stem palm bent by a treefall.

Surviving bent palms start growing upwards at the tip of the stem within a year after being hit. The bend thus becomes a permanent kink in the stem (Fig. 1). The length of the new trunk formed after the kink ( $L_2$  in Fig. 1) provides a good estimate of the time since the plant was hit; the length of the trunk found before the kink ( $L_1$ ) estimates the age of the palm when it was bent. Palms with  $L_1 \geq 1 \text{ m}$  have an annual mean rate of stem elongation of 4.8 cm (confidence interval = 3.8–5.9 cm;  $P = 0.05$ ), independently of  $L_2$  (Fig. 2a). Given that the confidence intervals predicted for two consecutive annual growth values did not overlap, an age-scale of  $L_2$  on a one-year time basis could be obtained (Fig. 2b). Palms need not be bent fully to the ground level for the dating technique to work.

Through its life span, a mature palm may be subjected to a maximum of four bending events. We have assumed that mortality and growth rates of ‘mono-kinked’ (which represent 89% of total bent palms) and ‘multi-kinked’ palms are the same. In multi-kinked palms, the trunk length interval between two kinks estimates the time elapsed between two consecutive disturbances in the same spot in the forest.

Bent palms with appreciable kinks result from treefalls or large branch falls that may have created a gap in the canopy and therefore can be used to date such events. We have estimated ages above the kink of up to ninety-nine years (4.8 m of  $L_2$ ).

#### *Using the dating tool to study gap dynamics*

In September 1982 we selected a 5-ha study plot established as a transect 100 m wide and 500 m long, extending from the edge into the inner part of the forest. In this plot the following data were collected: (i) location in a staked grid system to the nearest 0.5 m of all bent *A. mexicanum* palms; (ii) the lengths  $L_1$  and  $L_2$  for each bent palm to the nearest cm (for multi-kinked palms, the lengths between kinks were also obtained); (iii) the area occupied by gaps  $\leq$  one year old, according to the gap definition given by Brokaw (1982a); (iv) location of all clearly distinguishable fallen trees (dbh > 10 cm) or large branches, mapped at the scale of the grid system; fallen trees were grouped into three

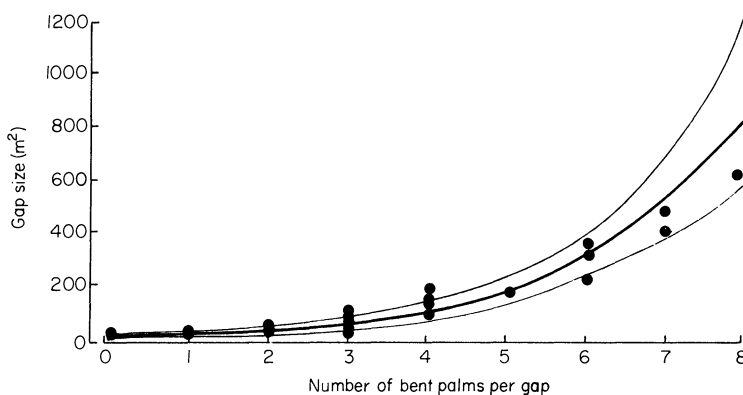


FIG. 3. Relationship between the number of recently bent palms ( $L_2=0$ ) found in one-year old gaps and the gap size;  $y = 11.4e^{0.54x}$ ,  $F'_{31} = 148.9$ ,  $P < 0.01$ ,  $r^2 = 0.822$ .

general types (snapped-off, uprooted and killed-standing); dbh (or diameter above buttresses) and height of snap (where applicable) were also recorded.

## RESULTS

A total of 1280 bent palms ( $L_1 \geq 1$  m) with appreciable kinks were recorded in the 5-ha plot. Palms with one, two, three and four kinks represented 88.8, 10.0, 1.1, and 0.1%, respectively, of the total bent palms. Only 7% of the plot area contained no palms. The number of bent palms per gap increased with the size of the canopy opening (Fig. 3). No bent palms were found in gaps smaller than 5 m<sup>2</sup>. One bent palm represented a median gap area of approximately 25 m<sup>2</sup> (mean  $\pm$  S.D. =  $26.79 \pm 15.22$  m<sup>2</sup>; range = 5–60 m<sup>2</sup>;  $n = 39$ ). Of 112 fallen trunks (dbh > 10 cm) censused on the 5-ha plot, 22% were large limbs of dying trees or growing canopy trees, and 78% were snapped or uprooted trees. Of the eighty-three fallen trees, 26% were uprooted, 69% snapped and 5% died standing. Trees were snapped at various points along the bole, with a tendency for the point of breakage to occur at a height < 2 m above ground (Fig. 4a). No significant difference (Student's  $t$ -test;  $P > 0.10$ ) was found in dbh between uprooted (mean  $\pm$  S.D. =  $62.1 \pm 31.2$ ,  $n = 21$ ) and snapped ( $56.4 \pm 37.5$ ,  $n = 57$ ) trees, and there was a wide overlap of ranges (Fig. 4b).

### Forest mosaic and age structure

In order to illustrate the spatial arrangement of forest patches disturbed at different times, the study plot was divided into 2000 quadrats of 25 m<sup>2</sup> (the median gap area per bent palm). The time since the last disturbance was calculated for each quadrat and each of them was assigned to a five-year-old class (arbitrarily chosen for computing purposes, based on the younger  $L_2$  value of the bent palms found in it). Those mature forest squares without bent palms were assigned an age equal to, or larger than, the tallest undamaged *A. mexicanum* stem found in it ( $\geq 85$  years). The quadrats without bent palms (only 6.8%) but containing pioneer trees were assigned an age equal to the surrounding quadrats with bent palms. Figure 5 is a diagram of the forest mosaic obtained. Although this method provides a good visual idea of spatial heterogeneity of the treefall disturbances in the

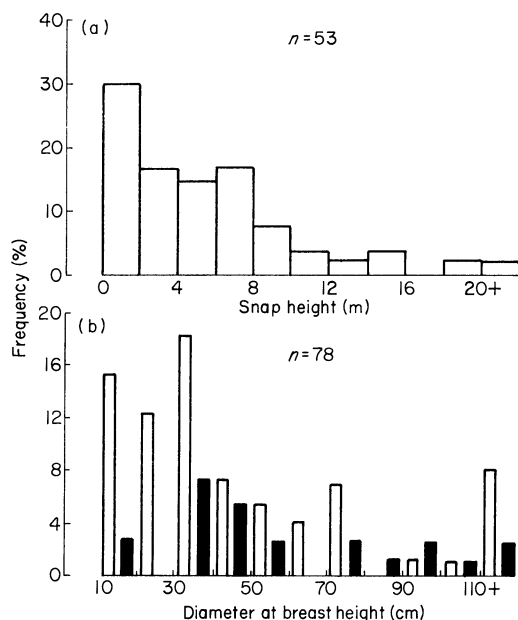


FIG. 4. Patterns of the dynamics of fallen trees at Los Tuxtlas rain forest: (a) snap-height distribution of fallen trees censused on the 5-ha study plot; (b) dbh distributions of snapped ( $\square$ ) vs. uprooted ( $\blacksquare$ ) fallen trees; bars represent percentage values of the total number of fallen trees.

forest, interesting underlying information about gap dynamics is not directly apparent. For example, because the successional age of each quadrat only reflects the most recent disturbance found in it, recurrent treefall events are ignored. A  $\chi^2$ -analysis (using a Poisson model) of the frequency of recurrent treefalls detected per quadrat (mean  $\pm$  S.D. =  $0.46 \pm 0.93$ ) showed that this type of disturbance has not a random spatial distribution ( $\chi^2 = 800.3$ ,  $P < 0.001$ ). The ratio  $S^2/\bar{x}$  (indicating patchiness when its value is significantly higher than one) was 1.83 and shows that quadrats with recurrent treefalls are clumped ( $t = 12.6$ ,  $P < 0.001$ ). This means that some areas of the forest are more frequently disturbed (28% of the quadrats showed between two and seven different  $L_2$  ages) than others (72% of the quadrats showed one  $L_2$  record).

On the other hand, because bent palms died in some quadrats, the frequency of quadrats in the different age-classes is skewed towards old treefall records (46% were older than eighty years) and, therefore, does not reflect an unbiased age structure of forest gaps implicit in the mosaic (Fig. 6a). Taking into account the overlapping of treefalls, we considered all bent palms and their survivorship rates to recalculate the age structure of the patches using the function  $F_x = G(B_x/R^x)$ , where  $F_x$  is the area (in  $m^2$ ) occupied by gaps of 1, 2, 3, ...,  $x$  years old;  $B_x$  is the number of bent palms in the entire 5-ha plot indicating treefalls of age  $x$ ;  $R$  is the estimated mean annual probability of a bent palm of both surviving and not being hit again (= 0.9538) (for multi-kinked palms it was assumed that an old treefall record is lost when a palm already bent is hit again); and  $G$  is the median gap area per bent palm (=  $25 m^2$ ). The  $F_x$  values obtained were grouped into five-year-old classes and expressed as percentages of the total area of the study plot (Fig. 6b). Clearly, the structure obtained is that of young forest because more than half of the plot area was detected to have been disturbed within the last thirty years. This result suggests the

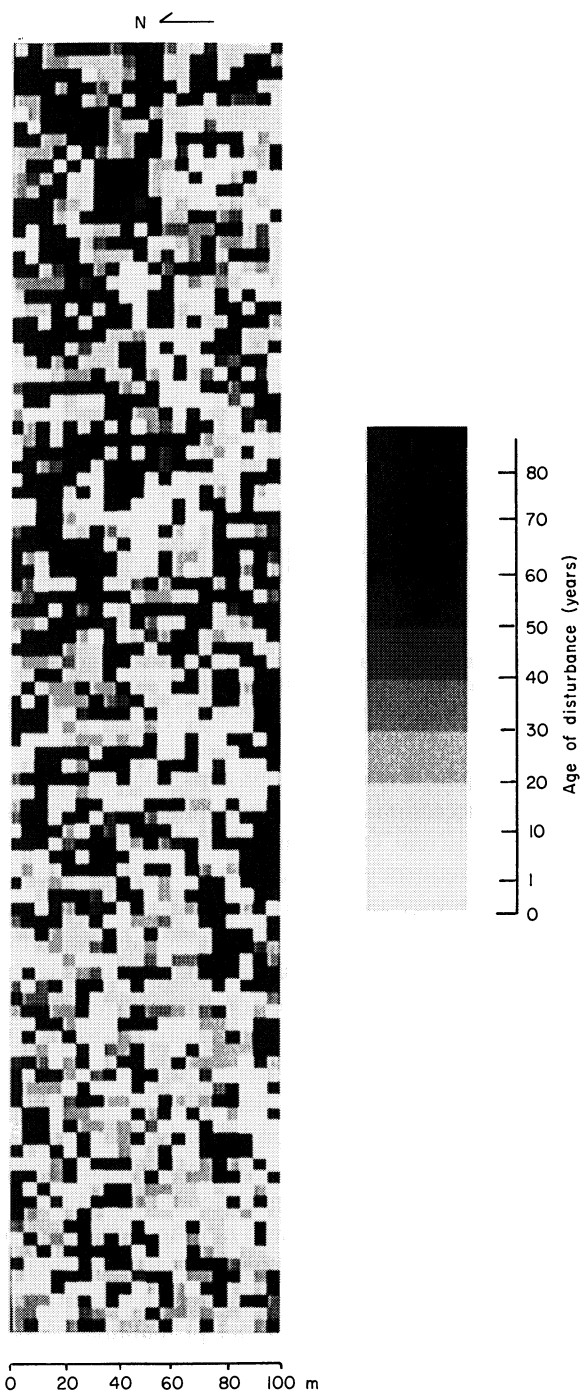


FIG. 5. Representation of the spatial distribution of forest patches disturbed at different times in 5 ha of tropical rain forest at Los Tuxtlas. The squares represent 5 m x 5 m quadrats and the shades of grey indicate the age of the last treefall detected in each quadrat. The scale on the right-hand side of the figure is composed of ten categories of ten-year periods, starting from white, which indicates gaps less than one year of age, and ending with black, for patches over eighty years old.



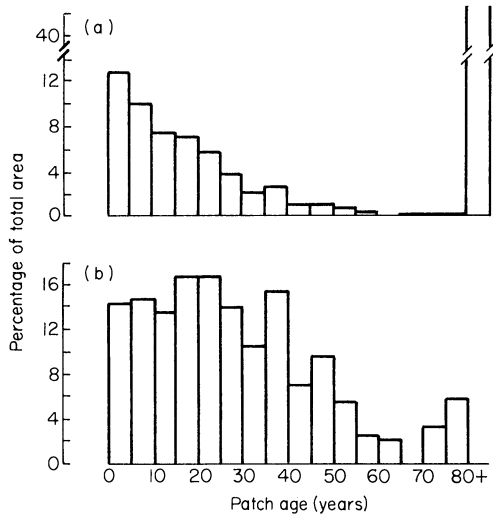


FIG. 6. Age structure of 5 ha of tropical rain forest at Los Tuxtlas: (a) the percentage values for each age category (in years) obtained from the forest mosaic; (b) the corrected age structure estimated using the function  $F_x = G(B_x/R^x)$ ; see text for explanation.

existence of a short rotation period (the mean time in which 100% of a forest area is covered by gaps (Pickett & White 1985)) of the forest in the study plot. The total sum of percentage values of the age structure obtained for treefalls of up to eighty years old (150%) gives an estimate of the rotation period of about fifty-three years.

#### *Long-term patterns*

In order to investigate some temporal variations of the gap-formation regime operating in the study plot, a second analysis was made. This was based on a plotless method involving the use of all bent palms, and the use of different  $L_2$  values of multi-kinked palms as independent time estimators. Bent palms were classified in  $L_2$  annual categories (Fig. 2b). It is clear that a certain reduction of bent palms occurs with time, because not all palms hit by falling tree or branch survive to the oldest recorded age (Fig. 7a). Age-specific survivorship rates ( $S_x$ ) were estimated in two ways: (i) from the age structure of  $L_2$  of the bent palms censused in the study plot, and (ii) using  $S_x = a^x$ , where  $a = 0.967$ , the estimated annual survivorship rate of bent palms in the permanent plots. Both estimations coincide fairly well for the first thirty years of  $L_2$  (Fig. 7b), but no so later on; apparently, some palms recording older treefalls in the 5-ha plot die at a higher rate than that estimated for a four-year period in our permanent plots.

Estimations of the proportion of forest canopy area opened to gaps per year in the period of seventy years (1912–82) were obtained by means of the function  $PGA_x = [(B_x/S_x)G]/P$ , where  $B_x$  is the number of surviving bent palms in year  $x$ ,  $S_x$  is the probability of survival to that year (obtained from the age structure of  $L_2$  (cf. Fig. 6b)),  $G$  is the median gap area per bent palm (= 25 m<sup>2</sup>) and  $P$  the total plot area (= 50 000 m<sup>2</sup>). Clearly, both the frequency and the intensity of disturbance vary with time (Fig. 8a). Peaks and valleys in the histogram reflect years of high and low rates of gap formation, and are not affected by the calculation of survivorship rates; for example, two years reflecting high forest disturbance (1949 and 1971) are more than twenty years apart and have a similar number

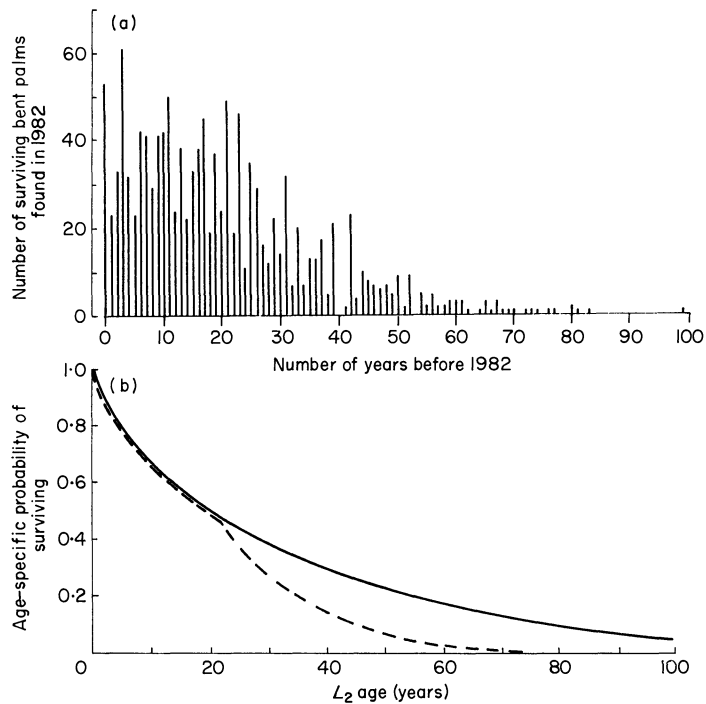


FIG. 7. Long-term temporal components of the treefall-gap regime found with the aid of *Astrocaryum mexicanum* as a dating device. (a) Number of surviving mature palms bent yearly before 1982. (b) Age-specific survivorship rate ( $S_x$ ) of bent palms; these probabilities were obtained using: (i) the age structure (on the basis of ten-year-long age-classes) of  $L_2$  values of the bent palm population censused in the study plot and employing a vertical life-table technique (-----), and (ii) using the exponential  $S_x = 0.967^x$  (——).

of bent palms (Fig. 7a); therefore, we deduce that 1949 must have been a year with a greater rate of disturbance than 1971 (Fig. 8a). On the other hand, fluctuations in numbers of bent palms could result from variations in the size of the cohorts of palms susceptible to bending each year. This is not the case, because population size and structure of mature *Astrocaryum mexicanum* palms are at equilibrium (Piñero, Martínez-Ramos & Sarukhán 1984). The annual gap rates estimated are positively correlated with the annual rainfall (Fig. 9). An autocorrelation analysis (Roughgarden 1975) showed that the estimated annual gap opening rates fluctuated without a predictable temporal pattern.

The yearly estimated proportions of forest area opened to gaps are not normally distributed (Fig. 8b). The inverse values of these proportions give a mean forest turnover rate of  $47 \pm 45$  (mean  $\pm$  S.D.;  $n = 70$ ) years (median = 34 years; coefficient of skewness = 3.36,  $P < 0.05$ ). A similar turnover rate is obtained for the last thirty years (1952–82) using both  $S_x = 0.967^x$  ( $44 \pm 17$  years) and the age structure of  $L_2$  values ( $42 \pm 16$  years) as the age-specific survivorship rates of bent palms (cf. Fig. 7b). It should be noted, however, that the variance of the turnover rate estimation is larger for the sample of seventy years. This means that (i) episodes of high and low disturbance have occurred for long periods of time, or (ii) mortality of bent palms increases sample errors with time, or both. The second possibility is remote because many late records (up to forty years before 1982) show the same or higher number of bent palms than more recent years (Fig. 7a).

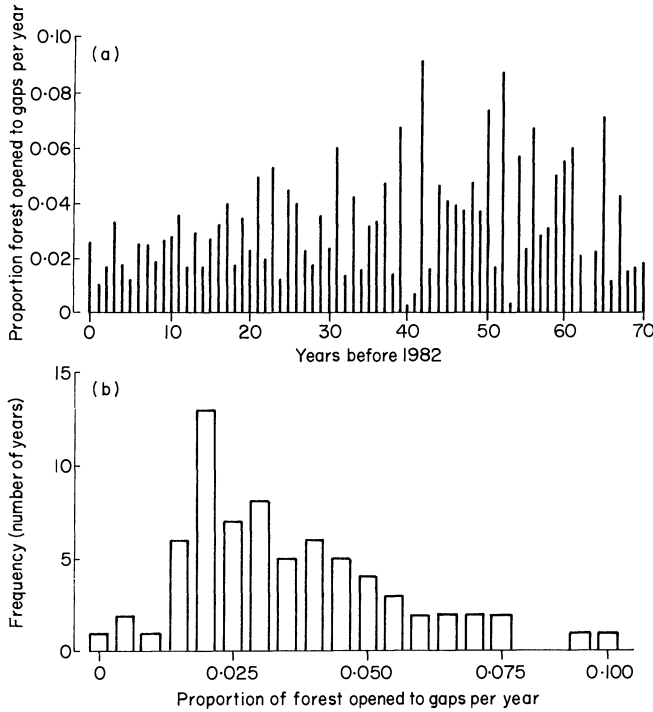


FIG. 8. (a) The predicted yearly fraction (from 1912–82) of forest canopy area opened to gaps (gap proportion) in the 5-ha plot studied; the values were obtained by means of the function  $PGA_x = [(B_x/S_x)G]/P$  (see text). (b) Frequency distribution of gap proportion values for seventy years in the period 1912–82.

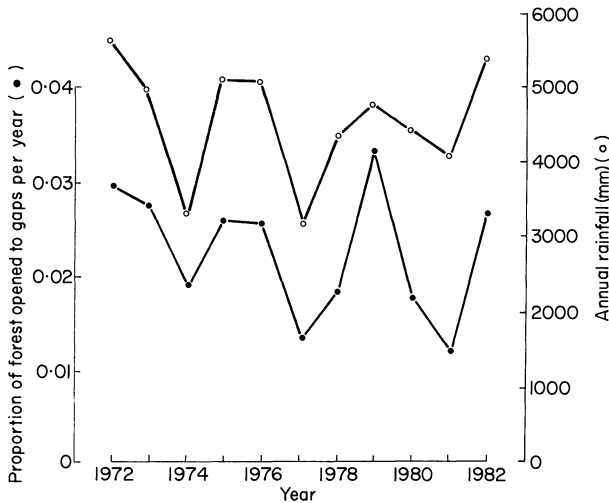


FIG. 9. Long-term patterns of rates of gap formation and rainfall in the Los Tuxtlas forest. The annual rainfall values come from the available meteorological records at LTTS (Estrada, Coates-Estrada & Martínez-Ramos 1985). Points are positively correlated ( $r^2 = 0.51$ ;  $P < 0.01$ ).

*Yearly variability in the formation of gaps of different sizes*

Spatial and temporal variation in gap formation may affect the relative abundances of species in different regeneration guilds. In neotropical rainforests, large gaps ( $> 200 \text{ m}^2$ ) favour the regeneration of pioneer species while small gaps favour the regeneration of persistent canopy species (Denslow 1980; Hartshorn 1980; Bazzaz 1984; Brokaw 1985a,b; Martínez-Ramos 1985). We analysed the frequency distribution of gap sizes in years with different degrees of disturbance to show the change in the availability of gaps of different sizes through time (see Appendix for calculations). The distributions obtained (Fig. 10) show that the gaps available to the different regeneration guilds change drastically through time, even between years with similar degrees of treefall disturbance. This means, for example, that years with low or high disturbance rates are not necessarily bad (Fig. 10d) or good years (Fig. 10a), respectively, for the regeneration of pioneer trees.

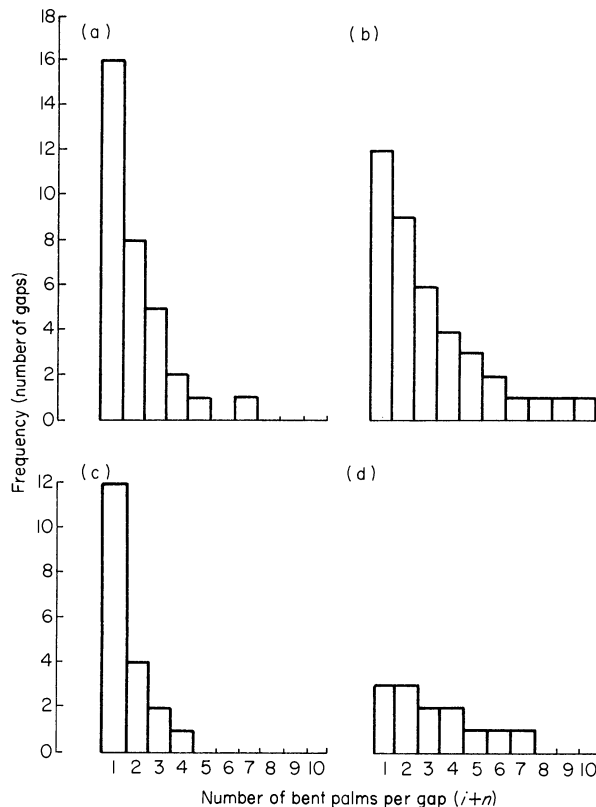


FIG. 10. The gap-size frequency distribution predicted for years with high and low treefall disturbance rates. High: (a) 1979, annual proportion of forest canopy opened to gaps (APFG)=0.0335; (b) 1961, APFG=0.0608. Low: (c) 1977, APFG=0.0150; (d) 1958, APFG=0.0179. The gap sizes ( $\text{m}^2$ ), estimated according to Fig. 3 for each  $i+n$  category, are: 1 = 15–24; 2 = 27–41; 3 = 47–70; 4 = 78–122; 5 = 131–213; 6 = 217–379; 7 = 357–676; 8 = 583–1212; 9 = 951–2179; 10 = 1548–3926.

## DISCUSSION

Tropical rain forests are mosaics of disturbed patches for which an age structure exists. As with the life-tables of populations of long-lived organisms, the dynamics of these mosaics and the processes generating the age structure can be vertically analysed, if some time-scale relevant to the 'forest life-cycle' is obtained. In this work we suggest a method for obtaining such a pivotal time-scale in a tropical forest. The biological properties of *Astrocaryum mexicanum* and the information available on this palm make it a suitable tool for dating treefall disturbances. The continuous monopodial growth of the palm shows little variation among individuals bent during temporal environmental changes, so the length of the trunk gives an extremely good estimate of time (the total statistical error being less than one year). Such a situation contrasts with growth in diameter of the trunk of many tropical trees, which often varies greatly between individuals and between years (Bormann & Berlyn 1981), and commonly leads to large inaccuracies in the age determination of tropical trees using trunk diameters (e.g. Lieberman & Lieberman 1985; Peralta *et al.* 1987). On the other hand, the high density of mature palms facilitates the detection of gaps as small as 5 m<sup>2</sup>; all gaps larger than 50 m<sup>2</sup> had bent palms (Fig. 3). The gaps without bent palms (those < 25 m<sup>2</sup>) produced by falling branches represented only 22% of the area opened to gaps in 1982 in the study plot. These ephemeral gaps, quickly closed by the lateral growth of the crown of surrounding trees, may only be important in stimulating temporary seedling and sapling growth of shade-tolerant species (Whitmore 1975; Denslow 1980; Hartshorn 1980; Brokaw 1985b).

The possibility of ageing bent individuals and the fact that the population of mature palms is in equilibrium, allowed an age-specific survivorship rate curve to be obtained for bent palms. This kind of data is fundamental for making inferences about the long-term treefall gap regimes using perishable time indicators. J. H. Fox (personal communication) has developed a model to calculate the percentage of error in estimating a community turnover rate using such indicators (in our case the palms): the model considers the annual mean mortality rate of the indicators and the mean fraction of area disturbed per year. According to his model, our turnover estimations have an accuracy greater than 80%.

Two major points emerge from the analyses outlined: (i) a strong spatial heterogeneity exists for disturbance ages at a scale as small as 25 m<sup>2</sup>, and (ii) the turnover process of the forest studied has a high degree of temporal variation. We do not know to what extent the spatial heterogeneity found in disturbance ages corresponds to an environmental heterogeneity. Certainly, newly formed gaps (< 5 years) are environmentally different from older forest patches (Denslow 1980; Chazdon & Fetcher 1984). Young gaps are the sites in which recruitment by rapid growth of established seedlings or saplings of most rainforest tree species takes place (Whitmore 1975; Denslow 1980; Hartshorn 1980; Pickett 1983; Brokaw 1985a,b; Martínez-Ramos 1985). Moreover, considerable inter-gap variation in environment may exist as a result of the different modes in which a treefall occurs. Uprooted trees disturb both the soil and canopy microenvironment, snapped-off trees alter mainly the above-ground conditions, and dead-standing trees open only small gaps in the canopy (Whitmore 1975). These treefall types may affect differentially the gap-regeneration mechanisms of tropical rain forest populations (Putz *et al.* 1983; Bazzaz 1984).

The long-term treefall patterns obtained (Fig. 5) show that canopy disturbances are a permanent ecological factor in the forest environment. It would appear that treefall

disturbances may be a selective agent with a potential to shape ecological and evolutionary attributes of plant populations in tropical rainforests.

Annual rainfall was found to be a significant force in determining the rate of gap formation. In Central American rain forests a strong relationship between treefall occurrence and monthly rainfall has been detected (Brokaw 1982b). Assuming that higher treefall rates increase recruitment probabilities for gap-dependent species, it has been suggested that rainfall fluctuations may have a controlling role on the recruitment processes of rainforest communities (Martínez-Ramos & Alvarez-Buylla 1986).

In mature temperate forests, the estimated mean proportion of gap area opened per year varies within a narrow range (0.005–0.02) (Runkle 1985). It has been suggested that the spatial and temporal regimes of treefall disturbance, and not the mean disturbance rate, are the ecologically relevant features for the processes involved in community organization (Runkle 1982, 1985). For example, the degree of temporal and spatial variance in treefall rates could play an important role in generating diversity (Connell 1978).

The mean turnover rates obtained for tropical rain forests lie in the range of values for temperate ones (Brokaw 1985a; Martínez-Ramos 1985). Therefore, the mean degree of disturbance rate cannot be taken as a key element in understanding why plant diversity in tropical rain forests is higher than in temperate ones. On the other hand, it has been proposed that forests with very low or very high frequency of disturbance may both be conducive to low diversity, because small groups of either fugitive, fast-growing species or highly competitive slow-growing species are, respectively, selected in each situation (Connell 1978; Hubbell 1979). Yet two forests with equal levels and frequencies of treefall disturbance might differ in diversity, because the range and frequencies of the gap sizes produced could differ both spatially and temporally. A high temporal and spatial variance in gap availability implies that regeneration of different species will be favoured in different years, and therefore diversity could increase. In contrast, a low variance would imply that the regeneration of a similar group of species will be favoured year after year, and therefore diversity could remain constant.

The above situation may take place if propagule production of species is maintained constant through time. Pioneer species tend to produce seeds regularly both between and within years, but many long-lived persistent species produce fruits in short periods of time and in several cases the fruiting occurs irregularly among years (Janzen 1978; Carabias & Guevara-Sada 1985); these persistent species, however, maintain long-lived seedling banks that stand waiting for gaps to open and stimulate their growth (Martínez-Ramos 1985; Martínez-Ramos & Alvarez Buylla 1986). High diversity may be favoured in communities where strong interspecific differences in the seeding schedules and seedling bank dynamics operate coupled with a high variability in rates of gap formation (Chesson & Warner 1981; Orians 1982).

Apart from our data, there is no information available at present on the long-term temporal regime of treefall disturbances occurring in tropical rain forests. Based on the spatial and temporal variance of gap formation observed at LTTS, we can state two general hypotheses: (i) species diversity is higher in tropical rainforests in part because both the temporal and spatial variance of disturbance in these communities is higher than it is in temperate forests, and (ii) within the tropics, forests with different disturbance variances must differ in species diversity. Year-long favourable growth conditions, niche differentiation, specific plant–animal relationships, biogeographic refuges, and several other phenomena have been postulated as the reason for such highly diverse communities

in the tropics (Leigh 1982; Prance 1982); none of these hypotheses is exclusive, and a combination of factors may be the source of high biological diversity in the wet tropics.

The dating method used for the LTTS forest permits an exploration of the history of a given gap-formation regime and an understanding of its relationship with the structure and dynamics of a tropical rainforest. How generally applicable may this age dating method be? To what extent can understorey palms of other tropical rain forests be used as dating tools? This depends on the population density and the demographic information available on the species. In Mexican and Central American rainforests, individuals of several palm species (of genera such as *Chamaedorea*, *Bactris* and *Geonoma*, and of other species of *Astrocaryum*) have treefall kinks in their stems (M. Martínez-Ramos, personal observation). However, other palm species might not have the same population attributes (high abundance, longevity, low variance in growth rate and high survivorship rates) found in *A. mexicanum* in LTTS and other areas of south eastern Mexico (Vite 1985). In such situations the use of ecologically similar groups of understorey palm species, whose population and demographic attributes are well known, could be used as multispecies treefall dating tools. Besides the understanding of community structure and dynamics of the tropical rainforests, information such as we have obtained in this study may be important in the design and protection of tropical forest reserves, and may offer a basis for the future manipulation of forest diversity and composition through controlled disturbances.

#### ACKNOWLEDGMENTS

We thank J. Corona, Centro Científico IBM de México, for the computer analysis of Fig. 5; A. López and J. Núñez-Farfán for field assistance. D. Janzen, R. Dirzo, S. H. Bullock, J. H. Fox, M. Franco, G. Harshorn, M. Crawley and P. Balvanera kindly commended on an earlier draft of the manuscript, and J. H. Fox made many helpful suggestions. This study was carried out partially with the aid of a grant from the Consejo Nacional de Ciencia y Tecnología (CONACyT, México) and supported by the Los Tuxtlas Tropical Field Station, Instituto de Biología, Universidad Nacional Autónoma de México.

#### REFERENCES

- Bazzaz, F. A. (1984). Dynamics of wet tropical forests and their species strategies. *Physiological Ecology of Plants of the Wet Tropics* (Ed by E. Medina, H. Mooney & C. Vázquez-Yanes), pp. 233–243. Dr. W. Junk, The Hague.
- Bormann, F. H. & Likens, G. E. (1979). *Pattern and Process in a Forest Ecosystem*. Springer-Verlag, New York.
- Bormann, F. H. & Berlyn, M. (1981). *Age and Growth Rate of Tropical Trees*. Yale University Press, New Haven.
- Brokaw, N. V. L. (1982a). The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, **14**, 158–160.
- Brokaw, N. V. L. (1982b). Treefalls: frequency, timing and consequences. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (Ed by E. G. Leigh, Jr, A. S. Rand & D. M. Windsor), pp. 101–108. Smithsonian Institution Press, Washington, D.C.
- Brokaw, N. V. L. (1985a). Treefalls, regrowth and community structure in tropical forests. *The Ecology of Natural Disturbance and Patch Dynamics*. (Ed by S. T. A. Pickett & P. S. White), pp. 53–69. Academic Press, New York.
- Brokaw, N. V. L. (1985b). Gap phase regeneration in a tropical forest. *Ecology*, **66**, 682–687.
- Carabias, J. & Guevara-Sada, S. (1985). Fenología de una selva tropical húmeda y en una comunidad derivada; Los Tuxtlas, Ver. *Investigaciones sobre la Regeneración de Selvas en Veracruz, México. Vol. II* (Ed by A. Gómez-Pompa & S. del Amo), pp. 27–66. INIREB-Alhambra, México.

- Chazdon, R. & Fetcher, N. (1984). Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology*, **72**, 553–564.
- Chesson, P. L. & Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **117**, 923–943.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, **203**, 1299–1309.
- Denslow, J. (1980). Gap partitioning among tropical forest trees. *Biotropica*, **12** (Supplement), 47–55.
- Estrada, A., Coates-Estrada, R. & Martínez-Ramos, M. (1985). La Estación de Biología Tropical Los Tuxtlas: un recurso para el estudio y conservación de la selvas del trópico húmedo. *Investigaciones sobre la Regeneración de Selvas en Veracruz, México. Vol. II* (Ed. by A. Gómez-Pompa & S. del Amo), pp. 379–393. INIREB-Alhambra, México.
- Hallé, F., Oldeman, R. A. A. & Tomlinson, P. B. (1978). *Tropical Trees and Forests: an Architectural Analysis*. Springer-Verlag, Berlin.
- Harper, J. L. (1977). *Population Biology of Plants*. Academic Press, London.
- Hartshorn, G. (1978). Tree falls and tropical forest dynamics. *Tropical Trees as Living Systems* (Ed by P. B. Tomlinson & M. H. Zimmermann), pp. 617–638. Cambridge University Press, Cambridge.
- Hartshorn, G. (1980). Neotropical forest dynamics. *Biotropica*, **12** (Supplement), 26–30.
- Hubbell, S. P. (1979). Tree dispersion, abundance and diversity in a tropical rain forest. *Science*, **199**, 1302–1310.
- Ibarra-Manríquez, G. (1985). *Estudios preliminares sobre la flora leñosa de la Estación de Biología Tropical Los Tuxtlas, Veracruz, México*. Bs. Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Janzen, D. H. (1978). Seeding patterns of tropical trees. *Tropical Trees as Living Systems* (Ed by P. B. Tomlinson & M. H. Zimmermann), pp. 83–128. Cambridge University Press, Cambridge.
- Leigh, E. G., Jr (1982). Why are there so many kinds of tropical trees? *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (Ed by E. G. Leigh, Jr, A. S. Rand & D. M. Windsor), pp. 63–66. Smithsonian Institution Press, Washington, D.C.
- Lieberman, M. & Lieberman, D. (1985). Simulation of growth curves from periodic increment data. *Ecology*, **66**, 632–635.
- Lorimer, C. G. (1980). Age structure and disturbance history of southern Appalachian forest. *Ecology*, **61**, 1169–1184.
- Martínez-Ramos, M. (1985). Claros, ciclos vitales de los árboles tropicales y la regeneración natural de las selvas altas perennifolias. *Investigaciones Sobre la Regeneración de Selvas Altas en Veracruz, México. Vol. II* (Ed by A. Gómez-Pompa & S. Del Amo), pp. 191–239. INIREB-Alhambra, México.
- Martínez-Ramos, M. & Alvarez-Buylla, E. (1986). Gap dynamics, seed dispersal and tree recruitment: the case of *Cecropia obtusifolia* at Los Tuxtlas, México. *Frugivores and Seed Dispersal* (Ed by A. Estrada & T. H. Fleming), pp. 323–346. Dr. W. Junk, Dordrecht.
- Oldeman, R. A. A. (1978). Architecture and energy exchange of dicotyledonous trees in the forest. *Tropical Trees as Living Systems* (Ed by P. B. Tomlinson & M. H. Zimmermann), pp. 535–560. Cambridge University Press, Cambridge.
- Orians, G. H. (1982). The influence of tree falls on tropical forest species richness. *Tropical Ecology*, **23**, 255–279.
- Peralta, T., Hartshorn, G., Lieberman, D. & Lieberman, M. (1987). Reseña de estudios a largo plazo sobre composición florística y dinámica del bosque tropical en La Selva, Costa Rica. *Ecología y Ecofisiología de Plantas en los Bosques Mesoamericanos* (Ed by D. A. Clark, R. Dirzo & N. Fetcher). *Revista de Ecología Tropical* (Supl. 1), **35**, 23–40.
- Pickett, S. T. A. (1983). Differential adaptation of tropical species to canopy gaps and its role to community dynamics. *Tropical Ecology*, **24**, 68–84.
- Pickett, S. T. A. & White, P. S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Piñero, D., Sarukhán, J. & González, E. (1977). Estudios demográficos en plantas: *Astrocaryum mexicanum* Liebm. I. Estructura de las poblaciones. *Boletín de la Sociedad Botánica de México*, **37**, 69–118.
- Piñero, D., Martínez-Ramos, M. & Sarukhán, J. (1984). A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *Journal of Ecology*, **72**, 977–991.
- Prance, G. T. (1982). *Biological Diversification in the Tropics*. Columbia University Press, New York.
- Putz, F. E., Coley, D., Lu, K., Montalvo, A. & Ariello, A. (1983). Uprooting and snapping of trees: structural determinants and ecological consequence. *Canadian Journal of Forest Research*, **13**, 1011–1020.
- Roughgarden, J. (1975). A simple model for population dynamics in stochastic environments. *American Naturalist*, **108**, 649–664.
- Runkle, J. R. (1981). Gap regeneration in some old-growth forest of the eastern United States. *Ecology*, **62**, 1041–1051.
- Runkle, J. R. (1982). Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63**, 1533–1546.
- Runkle, J. R. (1985). Disturbance regimes in temperate forests. *The Ecology of Natural Disturbance and Patch Dynamics* (Ed by S.T.A. Pickett & P.S. White), pp. 17–33. Academic Press, New York.
- Sarukhán, J. (1978). Studies on the demography of tropical trees. *Tropical Trees as Living Systems* (Ed by P. B. Tomlinson & M. H. Zimmermann), pp. 163–184. Cambridge University Press, Cambridge.



- Sarukhán, J., Piñero, D. & Martínez-Ramos, M. (1985). Plant demography: a community level interpretation. *Studies on Plant Demography: a Festschrift for John L. Harper* (Ed by J. White), pp. 17–31. Academic Press, London.
- Shugart, H. H., Jr & Darrel, C. W. (1981). Long-term dynamics of forest ecosystems. *American Scientist*, **68**, 647–652.
- Whitmore, T. H. (1975). *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford.
- Vite, F. (1985). *La estrategia de asignación de energía de Astrocaryum mexicanum Liebm. (Palmae)*. Bs. Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.

(Received 27 January 1987; revision received 22 June 1987)

## APPENDIX

*Calculation of gap-size distributions using bent palms*

The gap-size frequency distributions were obtained as follows: (i) the locations of bent palms were plotted in a coordinate system; (ii) neighbouring bent palms of the same  $L_2$  age found in a radius of 12 m were grouped (12 m is the mean length of a large fallen limb or tree forming a canopy gap at the LTTS (M. Martínez-Ramos, unpublished data); (iii) the frequency of groups with 1, 2, 3, ...,  $i$  neighbour bent palms was obtained; (iv) using the age-specific survivorship rate ( $S_x$ ) (Fig. 7b), the binomial distribution  $P_{i+n} = S_x + [1 - (S_x)]^{i+n} [(i+n)! S_x^i (1 - S_x)^n] / i! n!$  was employed to calculate the probabilities for each group to come from an original one composed of  $i+0, i+1, i+2, \dots, i+n$  bent palms, assuming that the probability of losing a treefall record is independent of the loss of another one (this is, in our case, an approximation of 90%, because the multi-kinked palms were included in the analysis, in which case the probability is not independent); (v) the frequency of groups with  $i$  bent palms were multiplied by their respective standardized  $P_{i+n}$  probabilities, and the products which resulted for each  $i+n$  value were added; (vi) the predicted frequency of groups with no survivors ( $i=0$ ) were added to the frequencies obtained for each group composed by  $i+n$  individuals. Further details are given in Table 1.

TABLE 1. Predicted frequency of gaps formed in 1979 containing  $i+n$  bent palms (bottom row, in entire values). The left column indicates the frequency of groups (in parentheses) with  $i$  survivor bent palms found in 1982 in the 5-ha study plot at Los Tuxtlas. The elements of the matrix were generated by a binomial model and indicate the frequency of groups coming from an original one composed of  $i+n$  bent palms (in parentheses are the probabilities given by the model for each  $i+n$  value). The frequencies were calculated by multiplying  $i$  by their respective standardized probabilities. Excepting the first row, which indicates the predicted frequency of  $i+n$  groups with no bent palm survivors, the sum of the probabilities in each row is 1.06. Only values of frequencies larger than 0.1 are shown.

$i$	Number of bent palms per gap ( $i+n$ )							
	1	2	3	4	5	6	7	8
0	1 (0.0959)							
1 (18)	14.7 (0.9041)	2.8 (0.1734)	0.4 (0.249)	0.1 (0.0032)				
2 (7)		5.2 (0.8174)	1.4 (0.2352)	0.3 (0.0451)	0.1 (0.0072)			
3 (5)			3.3 (0.7390)	1.3 (0.2835)	0.3 (0.0680)	0.1 (0.0130)		
4 (1)				0.6 (0.6681)	0.3 (0.3204)	0.1 (0.0922)		
5 (0)								
6 (0)								
7 (1)							0.5 (0.4938)	0.4 (0.3788)
Total number of gaps	16	8	5	2	1	0	1	0