Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree — an evaluation of the climax–pioneer paradigm for tropical rain forests

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Summary

1. Demography and allometry of the dioecious tree *Cecropia obtusifolia* were studied in a 5-ha permanent plot at Los Tuxtlas rain forest, Mexico. Treefall gaps were aged and a significant positive correlation was found between gap age and tree size. Active regeneration of the species was suggested by the high proportion (>35%) of young individuals. The population was highly clumped among young juvenile trees and became less aggregated as density within-gaps decreased among older trees. New and successful recruitment was restricted to recently formed (<3 years since opened) and large (>100-m^2) gaps. Oldest individuals (35 m high) were growing in 37-year-old gaps.

2. Tree height and stem diameter increased allometrically with a slope <1·5 in trees >0·3 m tall. The margin between the actual tree diameter (d) and the theoretical minimum buckling diameter ($d_{min.}$) declined exponentially from *c.* 20 in juvenile trees to almost 1 in the oldest trees (>30 years old). Whilst the number of leaves remains fairly constant before branching, it increases linearly as the number of branches increase. Changes in area per leaf during the life cycle yield an overall allometric pattern between tree height and total leaf area.

3. Seed and seedling mortality was >99%. Reduced light, falling debris, movement of rotting logs and soil dryness were important mortality factors in pre-reproductive stages. Oldest adults died standing, apparently due to senescence. Maximum life expectancy is reached when trees attain a non-suppressed canopy position (*c.* 20 m high). Individuals showed high growth rates (a stem-diameter increment of up to 2 cm year^{-1}). Growth-rate variation in juvenile stages seem to be related to high environmental heterogeneity. In adult stages the number of conspecifics growing in the same gap seems to affect diameter growth rate negatively. First reproduction occured at about 3 years of age (when 10 cm in diameter) and increased with age. Annual fecundity rates of individuals ranged from $1·4 \times 10^4$ to $1·4 \times 10^7$ seeds and increased allometrically with stem diameter and number of branches.

4. The most important environmental filter in the life-cycle of *C. obtusifolia* operates from the seedling to the juvenile stage. This finding does not support the suggestion that pioneer limitation to gap regeneration is determined during germination. The allometric and demographic traits of *C. obtusifolia* correspond to those expected for a shade-intolerant species that colonizes ephemeral sites, and they contrast with those of purported shade-tolerant tree species reported in the literature. However, rather than finding two clearly distinguishable types of life-histories, a continuum of demographic life-cycles was found. Therefore, the dichotomous pioneer–climax framework should be viewed as a means of identifying the extremes of a continuum of tree life histories.

Key-words: life histories, pioneer species, treefall gaps and patch dynamics, unpredictable environments

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Introduction

Swaine & Whitmore (1988) have distinguished two broad life-history types in tropical trees: light-demanding pioneers that germinate, establish and grow to maturity only in treefall gaps; and climax species that germinate and establish in the shade and often attain maturity when juveniles are released from suppression. Published demographic studies of tropical trees do not enable an evaluation of such a climax−pioneer dichotomy, because complete life tables have not been obtained for any of the so-called pioneer tree species. For arboreal tropical rain-forest species, detailed survivorship and reproductive schedules are only known for the understorey palms *Podococus barteri* (Bullock 1980), *Astrocaryum mexicanum* (Piñero, Martínez-Ramos & Sarukhán 1984) and *Chamaedorea tepejilote* (Oyama 1990); and for the canopy-forming, long-lived trees *Penthacletra macroloba* (Hartshorn 1972), *Omphalea oleifera* (Palomeque 1988) and *Brosimum alicastrum* (Peeters 1983, 1991).

This paper reports the first demographic study for a tropical pioneer tree species, part of a long-term programme started in 1983 documenting the population dynamics of *Cecropia obtusifolia*, the most abundant pioneer tree in rain-forest gaps at Los Tuxtlas, Mexico. Because it has been possible to reconstruct the treefall history at the sites where the individuals were growing (Martínez-Ramos *et al.* 1988), this paper also provides a quantitative evaluation of the gap-dependence hypothesis for *C. obtusifolia*. The paper focuses on the demography of established individuals. Seed demography has been treated in detail elsewhere (Alvarez-Buylla & Martínez-Ramos 1990; Alvarez-Buylla & García-Barrios 1991). To evaluate the climax−pioneer paradigm, the demographic patterns obtained for *C. obtusifolia* was contrasted with those reported in the literature for purported non-pioneer tropical tree species in Mexican rain forests.

In this study, the following questions were specifically addressed:

1. What allometric growth patterns does a purported pioneer species have during its life cycle and how are these related to its demographic patterns?
2. What type of spatial distribution and population size structure does it have?
3. How are gap age and plant age (or size) related for a pioneer species?
4. What are the growth, survivorship and fecundity schedules of a pioneer tree species and how do these compare with those of non-pioneer trees?
5. What environmental factors, especially those related to gaps, correlate with the variation in demographic traits between individuals?
6. What are the life-cycle stages at which the most important numerical changes occur?

Materials and methods

SPECIES AND STUDY SITE

Cecropia obtusifolia Bertol. (Moraceae), is the most abundant pioneer tree species in treefall gaps at Los Tuxtlas rain forest, Veracruz, Mexico (Fig. 1). Its geographic distribution extends along the Pacific and Atlantic Mexican coasts, and in Central and South American forests over an altitudinal range of 0−800 m (Pennington & Sarukhán 1968; Ibarra 1985). This and other *Cecropia* species are among the most abundant pioneers of other neotropical forests (Hartshorn 1978).

C. obtusifolia is a dioecious, myrmecophilous, 20−35-m-tall tree, with a monopodial trunk and tiers of first-order branches, morphologically identical to the trunk, and with lateral flower buds (Fig. 1). Such traits correspond to Rauh's architectural model (Hallé, Oldeman & Tomlinson 1978). Female inflorescence buds give rise to clusters of three to five spadices, 12−21 cm long. Each spadix bears 2700−4700 achenes. These dispersing units (hereafter termed seeds) are cylindrical, bright brown, 1−2 mm long and 0·8−1·3 mm wide (Alvarez-Buylla 1986). Fruits are eaten and seeds transported by mammals and birds (Estrada, Coates-Estrada & Vazquez-Yanes 1984). Seeds have photoblastic dormancy (Vázquez-Yanes & Smith 1982) and the seed-bank of the species has a turnover rate of *c.* 1 year at Los Tuxtlas (Alvarez-Buylla & Martínez-Ramos 1990; Alvarez-Buylla & García-Barrios 1991).

The study was conducted at Los Tuxtlas Tropical Field Station (owned by the Institute of Biology, Universidad Nacional Autónoma de México), in south-eastern Veracruz, Mexico (18°35′N, 95°07′W). The 25−40-m-high canopy forest in the 700-ha reserve has been classified as Evergreen Tall Tropical Forest (*sensu* Miranda & Hernández 1963) and corresponds to the Wet Tropical Forest of Holdrige's classification (Holdrige 1967). Mean rainfall and temperature are 4600 mm year^{-1} and 25 °C, respectively. Vegetation, soils and climates of the site have been described elsewhere (Lot-Helgueras 1976; Chizón 1984; Bongers *et al.* 1988).

PERMANENT STUDY PLOT

A population was studied in a 500-m × 100-m permanent plot for which the forest dynamics and spatial distribution of gaps had been obtained in detail (Martínez-Ramos *et al.* 1988). Brokaw's (1982) definition of gaps was adopted, and the minimum gap size considered was 25 m^2. A 5-m × 5-m grid system was established in the plot. In each of the 2000 quadrats of the grid, the area occupied by recent gaps (<1 year old) and the age of the last treefall were recorded as indicated by Martínez-Ramos *et al.* (1988). *C. obtusifolia* individuals taller
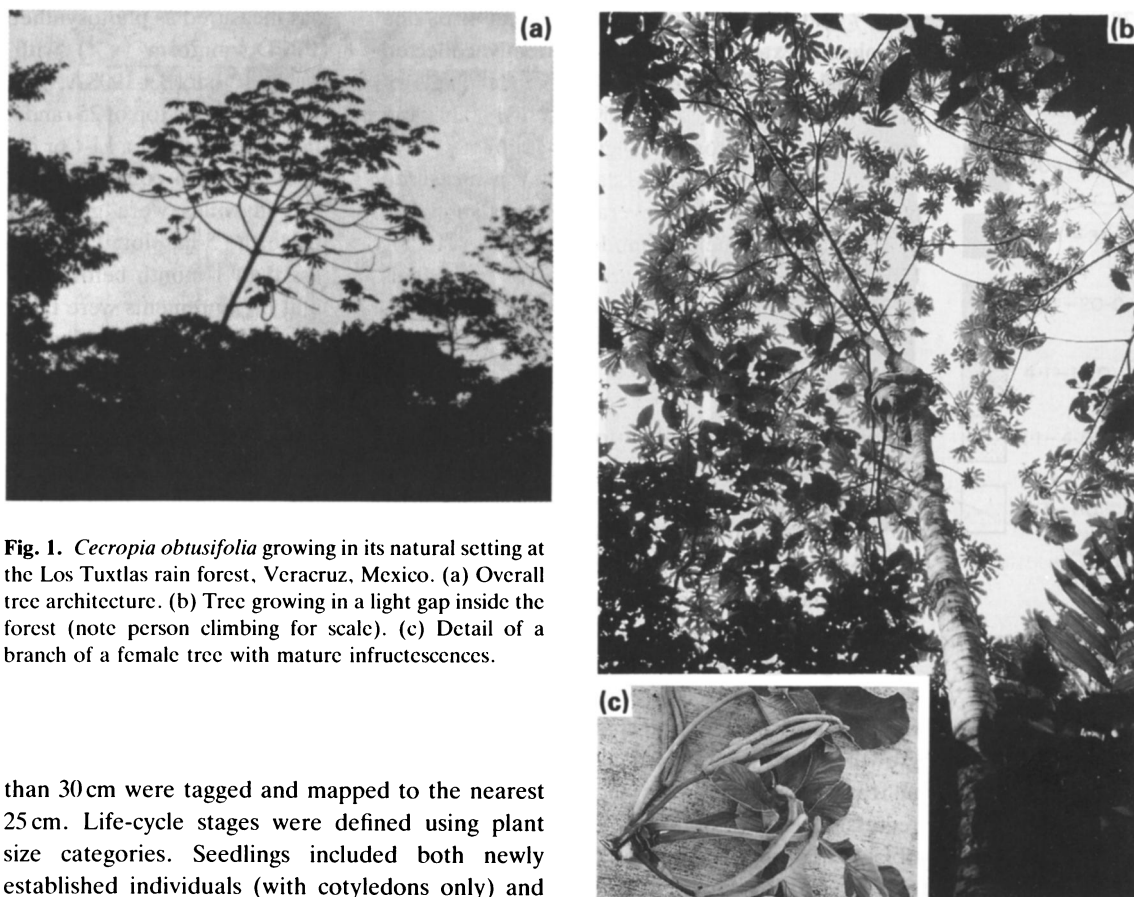
Fig. 1. *Cecropia obtusifolia* growing in its natural setting at the Los Tuxtlas rain forest, Veracruz, Mexico. (a) Overall tree architecture. (b) Tree growing in a light gap inside the forest (note person climbing for scale). (c) Detail of a branch of a female tree with mature infructescences.

than 30 cm were tagged and mapped to the nearest 25 cm. Life-cycle stages were defined using plant size categories. Seedlings included both newly established individuals (with cotyledons only) and plants with entire leaves and with stems up to 3 mm in diameter (*c.* 30 cm tall). Juveniles included plants 0·3−4 cm in stem diameter, generally taller than 30 cm, with lobed leaves, which were colonized by ants and were unbranched. In order to get a better evaluation of the demographic changes related to plant size, and to conserve as large a sample size as possible, this juvenile stage was divided in two substages: juvenile I (0.3−1 cm in stem diameter) and juvenile II (1·1−4 cm). Pre-reproductives included trees of 4·1−10 cm in stem diameter, mostly unbranched and without reproductive structures. Mature individuals were >10 cm in stem diameter, branched, and with at least one reproductive structure during the year of study. The criterion followed in the juvenile stage was also used to categorize mature trees in substages that had the following stem diameters: I, 10·1−20 cm; II, 20·1−30 cm; III, 30·1−40 cm and IV, 40·1−50 cm.

Seedling survivorship and growth were documented in six 0·25-m × 0·25-m plots in a recently formed gap (<6 months old). In September 1983 several patches with high (400−640 seedlings m^{-2}), medium (176−320 seedlings m^{-2}) and low (90−112 seedlings m^{-2}) density were located in the gap. In these patches, two 25-cm × 25-cm permanent quadrats per density were randomly established. In each quadrat an aluminum grid, delimited by four right-angled aluminum pegs into which the grid fitted exactly, was used to map and relocate seedlings. All seedlings were mapped (to the nearest

0·5 cm) and their total height, leaf and cotyledon number measured. Seedlings were tagged with a small numbered stalk and a nylon thread around each, and recensused monthly until March 1984.

In December 1983 all juvenile, pre-reproductive and reproductive individuals in the 5-ha plot were measured. Total height was recorded with tapes, rods or clinometer depending on height. Paint marks were placed above the first adventitious root (*c.* 0·1−0·15 of total height) in pre-reproductive and mature trees and 1·3 m high in juvenile individuals, or 10 cm below the apical meristem if they were shorter. Just above the mark, stem diameter was measured with a conventional plastic vernier in juveniles or with a wooden caliper in individuals of later stages. Additionally, one paint mark, at the same height as the former, was placed at both sides of the stem to facilitate the remeasurement of stem diameter at exactly the same position in subsequent censuses. For each individual, total number of leaves and of first-order branches (if present) were counted. In adults this was done by climbing nearby trees of the same height as the tree being monitored. Because of the simple architecture and the large leaf size of *C. obtusifolia* trees, these countings were quite accurate. Additional observations were made, such as presence or absence of ants and cause of death. Juveniles were re-censused after 4, 7 and 12 months; pre-reproductive and mature individuals

after 7 and 12 months. To estimate leaf size, one completely extended leaf was randomly collected from each of 37 mature and 20 juvenile plants of varying height (1·6−12 m). These individuals were randomly chosen from trees growing along a forest trail outside the study site. Leaf area was measured by cutting each leaf into several segments and using a Li-Cor area meter (model Li-3000, Li-Cor, Lincoln, NB, USA). Leaf are data for individuals <1·6 m tall came from Núñez-Farfán (1985).

ALLOMETRIC PATTERNS

Despite the fact that plant-form variables covary (King 1990), standard regressions were used to describe allometric patterns. This was done in order to enable comparisons with previously published allometric relationships. To correct the effect of autocorrelation in the regression model, the method proposed by White, Haun & Gow (1988) was used. Tree height was used as the independent variable in the regression models, because height influences the light environment and space available for plant growth (D.A. King, personal communication). In all cases, variables were log-transformed before regressions were obtained. Allometric relations obtained by measuring many trees at a single time may be used to infer growth patterns if it is assumed that individual trees follow the same such pattern throughout their life (D.A. King, personal communication). Hence, inferences about growth patterns from the allometric relations obtained are only valid for *Cecropia obtusifolia* trees that established inside the rain forest studied.

SEED PRODUCTION

Floral buds and clusters of mature and immature inflorescences and infructescences for each female and male tree were visually counted by climbing nearby trees of the same height as the tree being monitored. Monthly censuses were made from December 1983 to March 1984. Estimates of rates of maturation (Alvarez-Buylla & Martínez-Ramos 1990) guaranteed that reproductive structures were not counted twice in consecutive censuses. To calculate individual fecundities from the above data, the numbers of seeds per spadix in females of different sizes were estimated (see Alvarez-Buylla (1986) for details). We collected 207 spadices from eleven trees, 38 from two trees 10·1−20·0 cm in diameter at breast height (dbh), 97 from five trees 20·1−30·0 dbh, 48 from two trees 30·1−40·0 dbh and 32 from two trees 40·1−50·0 dbh.

MEASUREMENT OF INCIDENT LIGHT

In November 1984, on a clear, sunny day, photosynthetically active radiation (PAR; 400−700 nm)

was measured as photosynthetic photon flux density (PPFD; $mmol\,m^{-2}\,s^{-1}$) with a Li-Cor quantum sensor (model Li-190SA, Li-Cor) that was placed horizontally on top of 25 randomly selected juveniles until the needle of a Li-Cor quantometer (model Li-185A, Li-Cor) connected to the sensor stabilized. The juveniles were growing in two nearby gaps inside the 5-ha plot; 12 were alive and 13 had died less than 1 month before light was measured. Ten light measurements were taken from 07.30 to 15.30 hours for each plant. Individual plants were assigned a random number and light was measured from individual 1 to individual 25, then from 25 to 1 and so on, until 10 measurements were completed for each individual. Maximum time elapsed between first and last individual in each reading was 12 min. It was not possible to have a reference light measurement, but it is valid to use the PAR readings to compare the relative light microclimate of dead and living individuals.

For adult individuals an index of overtopping tree crowns was obtained by counting the number of crowns that overtopped 50% or more of the crown of each mature individual of *C. obtusifolia*. The numbers of contiguous conspecific crowns were also counted.

AGE ESTIMATE

Patch age was determined using the stems of the abundant understorey palm *Astrocaryum mexicanum* (Martínez-Ramos *et al.* 1988). Palms are bent during treefalls and most recover vertical growth leaving a clear kink on the palm stem that marks the time elapsed from the last treefall event that could have produced a canopy gap. This dating tool has an estimation error of c. 1 year (Martínez-Ramos *et al.* 1988) and was used to age *Cecropia obtusifolia.* by assigning trees the age of the last treefall detected in the patch where they were growing. For the Los Tuxtlas forest, patch ages have been estimated up to 100 years after disturbance (Martínez-Ramos *et al.* 1988).

Results

POPULATION STRUCTURE

Spatial distribution

Of a total of 60 recent gaps (<1 year since last disturbance) found in the 5-ha plot in 1983, 52 (86·6%) were smaller than 50 m², two were 50−100 m² in area, and six were larger than 100 m². The population of *C. obtusifolia* shows a patchy spatial pattern; youngest and smallest established individuals grow generally in recently opened (<1 year since opened) gaps, whilst older plants grow in in-
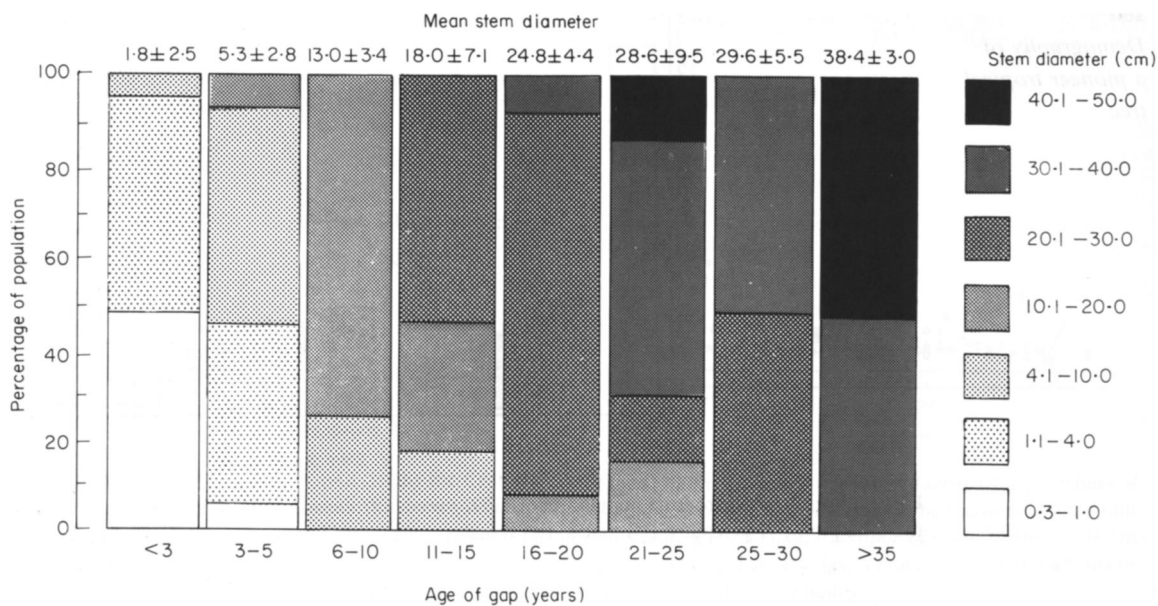
Mean stem diameter

1·8±2·5 5·3±2·8 13·0±3·4 18·0±7·1 24·8±4·4 28·6±9·5 29·6±5·5 38·4±3·0

Stem diameter (cm)

- 40·1 − 50·0
- 30·1 − 40·0
- 20·1 − 30·0
- 10·1 − 20·0
- 4·1 − 10·0
- 1·1 − 4·0
- 0·3 − 1·0

Fig. 2. Population structure of *Cecropia obtusifolia* at Los Tuxtlas, Veracruz, Mexico in gaps of increasing age (years) since disturbance. Number of individuals per size category as in Table 3.

creasingly older gaps up to 35 year since disturbance (Fig. 2). This yields an overall aggregated pattern of spatial distribution in the forest. A decrease in the within-patch plant density as gaps age coincides with a less aggregated pattern among established individuals of increasing size (and presumably increasing age) (Table 1). Female and male individuals considered separately are randomly distributed.

Sex ratio and spatial association of sexes

A 1·5:1 female:male sex ratio was found in the 5-ha forest population of *C. obtusifolia*. This ratio was not significantly different from 1:1 ($\chi^2 = 2·81$; $P > 0·05$). Trees of both sexes seem to be randomly distributed in space in relation to each other ($\chi^2 = 1·03$; $P > 0·05$).

Size distribution

C. obtusifolia presented a left-skewed trunk-diameter frequency distribution in the 5-ha plot, which suggests active regeneration in the population (Fig. 3). The population structure in gaps of increasing age (Fig. 2) and the size−age relationship (Fig. 4) shows that recruitment of *C. obtusifolia* coincides with gap formation; few individuals recruit to the 1-cm-stem-diameter category after 2 years of gap formation, and none after 4. In gaps older than 25 years only trees $\geqslant 30$ cm in stem diameter were found. Males and females had similar size structures (Fig. 3; Kolmogorov−Smirnov $D = 9$, $P > 0.05$). The oldest trees ($n = 2$) were found in gaps of up to 37 years since last disturbance and were >35 cm in stem diameter and 35 m tall.

Table 1. Density and spatial distribution of *Cecropia obtusifolia* in the 5-ha plot at Los Tuxtlas, Veracruz, Mexico

Life-cycle stage	Stem diameter (cm)	Density (individuals ha⁻¹)	Clark & Evans' (1954) dispersion index†
Total population	>0·3	28·4	0·5073***
Non-reproductive	<10	14·4	0·2008***
Juvenile I	0·3−1	4·8	−
Juvenile II	1·1−4·0	5·8	−
Pre-reproductive	4·1−10·0	3·8	−
Reproductive	>10	14·0	0·7720*
Female		8·4	0·9340
Male		5·6	0·9627

† <1 indicates an aggregated pattern, 1 indicates a random distribution and >1 indicates an overdispersed pattern. A Z-test was used to test the significance of the departure of the Clark and Evan's values from 1 (Poole 1974); * $P < 0·05$, ** $P < 0·001$, *** $P < 0·0001$.
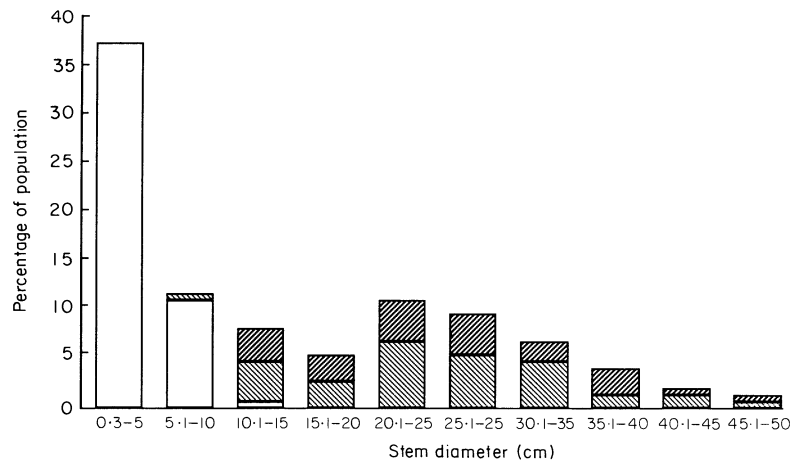
Fig. 3. Overall structure for a population of *Cecropia obtusifolia* at Los Tuxtlas, Veracruz, Mexico (*n* = 142) established in the 5-ha plot: (□) juveniles; (▨) males; (▧) females.
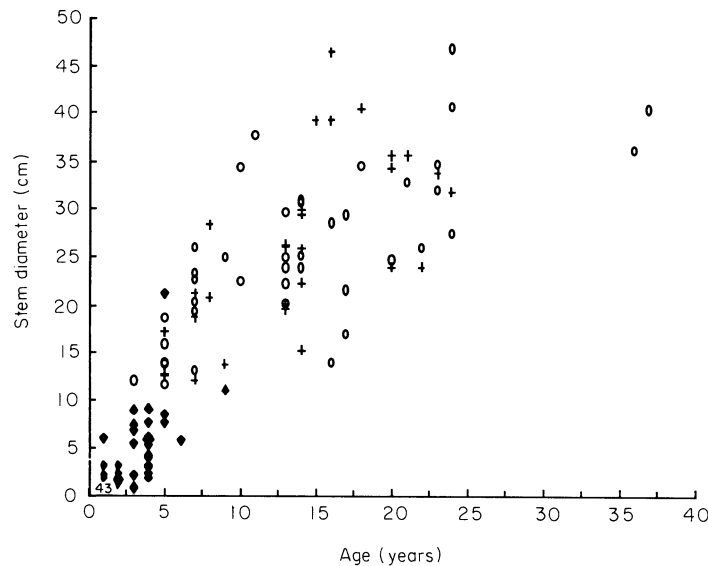

Fig. 4. Gap-age–plant-size relationship ($r^2 = 0.772$; $n = 142$; $P < 0.05$) for *Cecropia obtusifolia* individuals >0.3 m tall (*n* = 142) at Los Tuxtlas, Veracruz, Mexico. Gap age was estimated using *Astrocaryum mexicanum* stems (Martínez-Ramos *et al*. 1988). Numbers of points overlaping are indicated: (◆) juveniles; (○) females; (+) males.

ALLOMETRIC PATTERNS

Small seedlings with two epigeous cotyledons (*c.* 0.15 cm²) emerge from the small seeds (2–4 mm long) of *C. obtusifolia*. The number of leaves per plant (range 0–8) increases allometrically with height (Table 2) in seedlings up to 7 cm tall. In taller seedlings (8–15 cm), leaf number (range 2–6) varies greatly between individuals of the same size, and height and leaf number are not correlated (Table 2). Leaf area is fairly constant in early life, and starts increasing slowly as plants grow from the seedling to the juvenile stage. In juveniles, leaf morphology changes from entire to lobed (at leaf number 8–10). This change coincides with the colonization of stems by ants of the genus *Azteca*, and production of glycogen-rich bodies at the base

of leaves (see also Núñez-Farfán & Dirzo 1989). The area of each leaf increases rapidly thereafter until the main stem branches and reproduction begins, at which point it decreases again (Fig. 5). Area per leaf in mature trees of different sizes was not measured, but we have observed a decrease

Table 2. Allometry of height (*H*) and number of leaves (*N*) on *Cecropia obtusifolia* seedlings at Los Tuxtlas rain forest, Mexico. Slope corresponds to linear models of log *N* as a function of log *H*

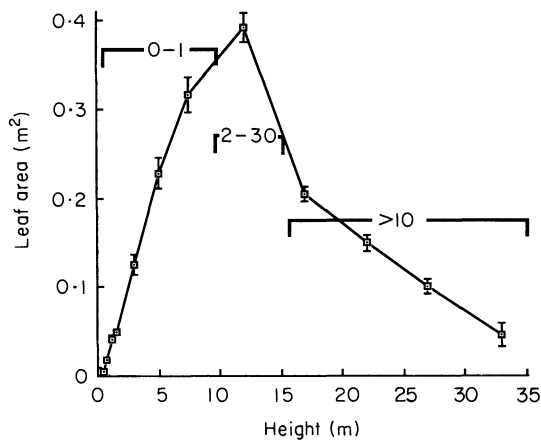| Height	95% confidence limits of slope	*n*	r^2	*P*
1–7 cm	0.336–0.492	202	0.471	<0.05
8–15 cm	−1.290 to −0.272	19	0.281	>0.05

Fig. 5. Leaf size as a function of tree height for *Cecropia obtusifolia* individuals at Los Tuxtlas, Veracruz, Mexico. Brackets indicate height categories with a given number of branches shown on each bracket. Mean area per leaf and 95% confidence intervals are graphed at the upper limit of height categories. Sample sizes for first to last categories: 30, 6, 3, 1, 4, 7, 3, 6, 10, 10, 13, 4. Fist four data points from Núñez-Farfán (1985).

in leaf size of oldest (>30-year-old) and tallest (>30-m-tall) trees.

Stem diameter is allometrically related to height in *C. obtusifolia* juvenile, pre-reproductive and
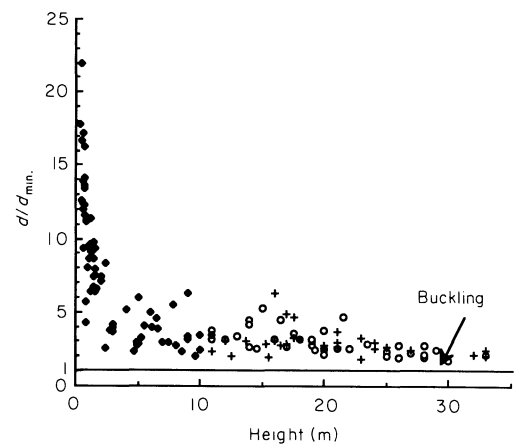
Fig. 7. Stem diameter (d) safety factor (d/d_{min}, where d is actual stem diameter and $d_{min.}$ is the theoretical minimum buckling diameter) of *Cecropia obtusifolia* trees >0·3 m tall growing at Los Tuxtlas, Veracruz, Mexico: (◆) juveniles, (○) females, (+) males.

mature plants (Fig. 6a). The few trees departing from the power model had been broken by falling debris. The allometric constant is significantly different from 1 (Fig. 6a) and the safety factor in *C. obtusifolia* decreases as trees grow in height, although after 5 m tall, the actual safety factor decreases very slowly (Fig. 7). This factor is esti-
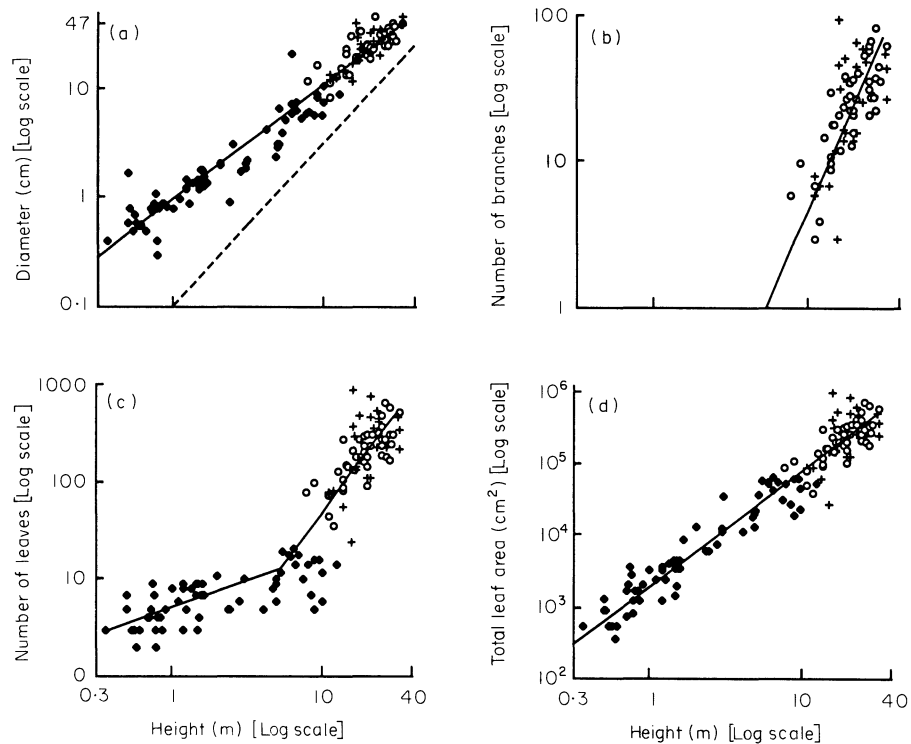
Fig. 6. Vegetative development of *Cecropia obtusifolia* individuals >0·3 m tall ($n = 142$) at Los Tuxtlas, Veracruz, Mexico. (a) Allometry of stem diameter (D) and height (H): $\log D = 1·069 \log H - 0·018$; $r_{adj.}^2 = 0·953$; $P < 0·0001$ (dashed line corresponds to McMahon's (1973) buckling-limit relationship: $\log D = 1·5 \log H - 0·1$). (b) Number of first-order branches (B) as a function of height: $\log B = 2·396 \log H - 1·739$; $r_{adj.}^2 = 0·558$; $P < 0·0001$. (c) Number of leaves (L) as a function of height for unbranched individuals: $\log L = 0·558 \log H - 0·701$; $r_{adj.}^2 = 0·515$; $P < 0·0001$, and for branched individuals: $\log L = 2·108 \log H - 0·439$; $r_{adj.}^2 = 0·488$; $P < 0·0001$. (d) Allometry of total leaf area (A) and tree height: $\log A = 1·617 \log H + 3·275$; $r_{adj.}^2 = 0·937$; $P < 0·0001$. In all cases the best-fit model is given, corrected for autocorrelation and heteroscedasticity when necessary (White, Haun & Gow 1988): (◆) juveniles, (○) females, (+) males.

mated as the ratio of the observed diameter (d) and the minimum diameter at a given height to prevent buckling ($d_{min}.$), according to the theory of McMahon (1973).

During the first 5 years *C. obtusifolia* individuals are monopodial with a few (three to 20) large leaves near the apical meristem. Branching and first reproduction coincide at a height of 7–12 m. Before branching, total leaf area per tree increases by augmentation in leaf size rather than by increments in leaf number (Fig. 6c,d). Juvenile individuals have only three to 10 fairly large leaves, and pre-reproductive trees, which are still unbranched, bear three to 20 very large leaves. Before branching leaf size attains its maximum (Fig. 5) and once branching starts, area per leaf decreases, but an increase in number of leaves as new branches are formed yields a constant allometric rate (1·617) of total leaf area increase as trees grow in height (Fig. 6d). In mature individuals, the rate of crown expansion (branch and leaf number) as a function of the tree's stem diameter and height growth rates is allometric and significantly higher than in non-reproductive individuals (Fig. 6b,c). Stem diameter explains a greater proportion of the variation in crown size ($r^2_{branches} = 0.761$ and $r^2_{leaves} = 0.683$; $n = 70$, $P < 0.0001$) than height, and such variation for a given height is higher in mature than in non-reproductive trees (Fig. 6b,c). Male and female trees showed similar allometric patterns (Fig. 6).

Demographic analyses of *C. obtusifolia* were based on stem diameter because this trait is more commonly used in other studies, and it is highly correlated to the other vegetative traits ($r^2 = 0.94$, 0·87 and 0·84 for height, number of branches and number of leaves, respectively). We also consider branch number after maturation, because it is tightly related to total leaf area (Fig. 8; $r^2 = 0.979$) and number of available lateral floral buds ($r^2 = 0.67$).

DEMOGRAPHIC PATTERNS AND CAUSES OF VARIATION

Survivorship

C. obtusifolia had type-III (Pearl & Miner 1935; Deevey 1947) survivorship curve (Table 3, and see Fig. 12 later), i.e. the highest mortality rates were registered during the seed and seedling stages and the lowest at the mature ones. Nonetheless, there was a slight increase in mortality at the last mature stage (Table 3).

High pre- and post-dispersal mortality rates operate on seeds. Some seeds lost viability inside frugivorous vertebrates which may act as seed dispersers (Vázquez-Yanes & Orozco-Segovia 1986); in the soil, most seeds died due to attacks of ants and pathogens (Alvarez-Buylla & Martínez-Ramos 1990). Of all seeds produced in the 5-ha in
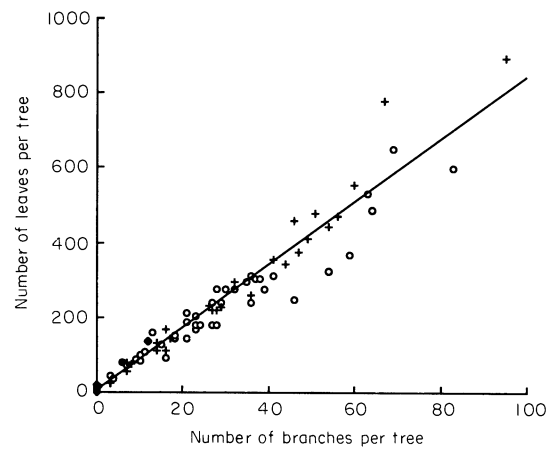

Fig. 8. Number of leaves (L) as a function of number of branches (B) in *Cecropia obtusifolia* trees >0·3 m tall ($n = 142$) at Los Tuxtlas, Veracruz, Mexico. Best-fit model graphed: $L = 8.35B + 3.58$; $r_{adj.}^2 = 0.959$; $P < 0.0001$; the model was corrected for autocorrelation and heteroscedasticity according to White, Haun & Gow (1988): ($\diamond$) juveniles, ($\circ$) females, ($+$) males. All juveniles (unbranched and <10 leaves) close to origin.

one year, only 40% reached the soil, and only half of these were viable. After a year, an average of 2·87% seeds remained viable in the soil. The rest were lost due to predation and pathogen attack, and 0·53%, 2·2% and 4·4% germinated in mature, successional and gap sites, respectively (Alvarez-Buylla & Martínez-Ramos 1990). The seed to seedling transition is therefore equal to 0·278%.

The greatest numerical loss in the population occurred during the seedling stage (Table 3). All originally labelled seedlings died after 167 days. This loss of seedlings seems not to be related to natural enemies because pathogen attack and damage due to herbivores were rare at this stage. Seedling survivorship was positively related to plant size (as measured by total height and number of leaves), but the number of cotyledons and the month of emergence did not affect seedling survivorship significantly (Table 4). Size variation, however, is not always relevant for survivorship. For example, a group of seedlings, established on top of a falling trunk in one gap, died when the trunk decomposed and buried the seedlings. Among other factors determining seedling survivorship, light availability seems to be important. Seedling survivorship increased with gap size (Spearman rank correlation $r_s = 0.772$; $n = 11$ gaps, $P < 0.05$). However, some seedlings completely exposed to sunlight died, apparently due to soil dryness.

Most juvenile trees died due to shading, to falling debris, or to movement of their rooting substrate when established on top of rotting trunks (Table 3). At the time light measurements were taken, dead juvenile (I and II) individuals were located in sites that received significantly less PAR from 7.30 to

Table 3. Life-stage-specific annual mortality rates and causes of death of *Cecropia obtusifolia* individuals in the 5-ha plot at Los Tuxtlas, Veracruz, Mexico from December 1983 to December 1984

Life-cycle stage and stem diameter (cm)	n	Patch age (years)	Mortality rate	Cause of death* 1	2	3	4	5
Seeds on trees	63 926 000†	—	0·7978	Predation, loss of viability				
Seed rain viability	12 762 034‡	—	0·9574	Predation, pathogen attack, loss				
Established individuals								
<0·3 (seedling)	177 800§	<0·5	>0·99¶a	0	0	0	0	100
0·3−1 (juvenile I)	24	<1	0·875b	15	0	79	0	6
1·1−4·0 (juvenile II)	29	1−4	0·586c	5	37	53	0	5
4·1−10 (pre-reproductive)	19	1−9	0·235d	20	0	80	0	0
10·1−20 (mature I)	18	3−17	0·053de	20	0	0	0	80
20·1−30 (mature II)	31	7−24	0·032e	0	0	0	100	0
30·1−40 (mature III)	16	10−36	0·063de	0	0	0	100	0
40·1−50 (mature IV)	5	16−37	0·200	0	0	0	100	0

* Mortality causes listed for seeds (from Alvarez-Buylla & Martínez-Ramos 1990). The percentages of established individuals dying due to each of the five causes of death identified are given: 1, physical damage due to falling branches; 2, rotting of trunk that served as rooting substrate; 3, shading; 4, senility; 5, unknown.

† Total seed production from annual fecundities of trees in the 5-ha plot.

‡ Total seed rain (viable) in the 5-ha plot estimated from seed trapping (from Alvarez-Buylla & Martínez-Ramos 1990).

§Total number of seedlings estimated by adding the products of the expected number of viable seeds in the soil of each patch type in the 5-ha plot, and the germination probability in each patch type (from Alvarez-Buylla & García-Barrios 1990).

¶After 167 days all seedlings marked died; hence annual mortality was estimated to be >0·99. Letters indicate which mortality rates are significantly different ($P < 0.05$) according to a generalized linear model (two last categories pooled for this analysis).

Table 4. *Cecropia obtusifolia* seedling survival after 69 and 167 days of emergence for different categories of height, number of leaves, number of cotyledons and month of emergence in 1983

Categories	n	Probability of survival for† 69 days	167 days
Seedling height (cm)			
<1·0	27	0·07	0·00
1·1−2·0	49	0·25	0·02
2·1−3·0	14	0·36 $G = 8·7134*$	0·00 $G = 4·0104*$
3·1−4·0	7	0·29	0·14
4·1−5·0	4	0·25	0·25
No. of leaves			
0	13	0·00	0·00
1	1	0·00	0·00
2	40	0·25	0·00
3	27	0·22 $G = 7·8952*$	0·04 $G = 7·6096**$
4	14	0·29	0·07
>4	6	0·33	0·17
No. of cotyledons			
0	2	0·00	0·00
1	5	0·40 $G = 0·1914$	0·00
2	94	0·21	0·03
Month of emergence			
September	101	0·22	0·03
October	20	0·35 $G = 3·1324$	0·10 $G = 0·1804$
November	12	0·42	0·08
December	3	—	0·00

† A *G*-test was used to test for differences among survivorships: * $P < 0.05$; ** $P < 0.01$. Continuous lines link statistically equal ($P > 0.05$) survivorships according to a multiple STP test (Sokal & Rohlf 1981).

15.30 hours (mean ± SE: $192 \cdot 6 \pm 7 \cdot 9$ mmol m^{-2} s^{-1}; $n = 13$) than sites where surviving individuals were found ($265 \cdot 8 \pm 25 \cdot 4$ mmol m^{-2} s^{-1}; $n = 12$) (Mann–Whitney U-test = 46; $P < 0 \cdot 05$).

Oldest and largest mature trees die standing; their trunk breaks off at the tip, they lose branches, their leaves become smaller, and apparently they are attacked by wood pathogens.

Growth

Newly established ($0 \cdot 5 - 15$-cm-tall) seedlings had an average height growth rate of $1 \cdot 5$ cm month^{-1}. Variability observed around this average value was related to the seedlings' emergence time. Early seedlings grew faster ($1 \cdot 5$ cm month^{-1}; $n = 101$) than later ones ($0 \cdot 65$ cm month^{-1}; $n = 32$) ($F_{2,127} = 8 \cdot 32$, $P < 0 \cdot 001$).

Mean growth rate, as measured by annual stem-diameter increments, increases with size at juvenile and pre-reproductive stages up to a maximum value of 2 cm year^{-1} (Fig. 9). Just at the beginning of the mature stage, this trend is reversed: growth rate of mature trees decreased with size (Fig. 9). Juvenile II plants showed the highest growth-rate variability (Fig. 9). This inter-plant variation seems to be the consequence of an increased within- and between-gap environmental heterogeneity as gaps age. For example, juvenile II plants in sites with high PAR had greater growth rates than those in sites with lower PAR ($r^2 = 0 \cdot 49$, $n = 14$, $P < 0 \cdot 01$), and juveniles growing in large gaps (>200 m^2) had significantly higher growth rates ($3 \cdot 14 - 3 \cdot 54$ cm year^{-1}, $n = 3$ gaps) than those in smaller gaps ($0 \cdot 14 - 1 \cdot 86$ cm year^{-1}, $n = 8$ gaps) (Mann–Whitney U-test = 0, $P = 0 \cdot 006$).

Gap size and the number of conspecific *C. ob-*
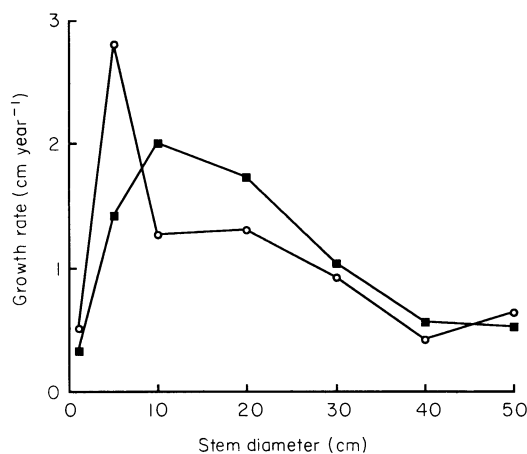
Fig. 9. Annual average mean (■) diameter growth rates and its standard deviation (○) as a function of plant size of *Cecropia obtusifolia* at Los Tuxtlas, Veracruz, Mexico. Values are plotted at the upper limit of each size category. The number of individuals per category is given in Table 3.

tusifolia plants in a gap seem to affect growth variation in an interactive manner. In gaps less than 16 years old, the number of conspecifics and the individuals growth rate were positively correlated ($r_s = 0 \cdot 715$, $n = 18$ patches, $P < 0 \cdot 01$), suggesting that gap size is not only important for recruitment but also an indicator of the level of resource availability (e.g. light) for growth during pre-reproductive stages. This trend was reversed in older gaps ($r_s = -0 \cdot 542$, $n = 9$ patches, $P < 0 \cdot 01$), probably because the establishment of several conspecific mature trees in large gaps results in some sort of intraspecific interference as trees grow and reproduce. The fact that *C. obtusifolia* trees do not have contiguous or overtopping conspecific crowns, suggests that such putative interference occurs underground rather than among crowns for light interception. Only seven, one and three of the 70 mature individuals had one, two and three contiguous conspecific crowns, respectively. Moreover, 90% of mature trees did not have a crown of any species covering 50% or more of its own crown.

Fecundity

In both male and female trees, the smallest mature individuals found in the 5-ha plot had a stem diameter of 10 cm and a height of $7 - 12$ m. These sizes coincided tightly with tree branching (Fig. 6b). Using gap age as an estimator of tree age, an age at first reproduction of about 3 years (Fig. 4) was estimated.

Annual size- or age-specific fecundity rates (seeds per year per female) depend on the (i) number of spadices produced per year per branch, (ii) number of branches per tree, and (iii) number of seeds per spadix. The annual production of spadices was linearly and positively related to number of branches (Fig. 10). Spadices produced by trees at the mature-I stage contained significantly fewer seeds (mean ± SE = 2227 ± 410) than those of trees in later mature stages (4612 ± 201). These two trends yielded allometric relationship between fecundity and size for mature trees (Fig. 11a). Although fecundity also showed a positive relationship with age, stem diameter or crown size (number of branches per tree) explained about twice the amount of variation observed in individual fecundity than tree age (Fig. 11b). Despite these relationships, there was a noteworthy degree of fecundity variation between individuals of about same size (up to $1 \cdot 5$ orders of magnitude, Fig. 11). This variation could be related to intraspecific interactions between trees because fecundity rates were found to be inversely related to number of mature trees per gap, although the correlation coefficient between number of conspecifics per patch and fecundity was only marginally significant ($r = -0 \cdot 44$, $n = 20$ patches, $0 \cdot 10 > P > 0 \cdot 05$).
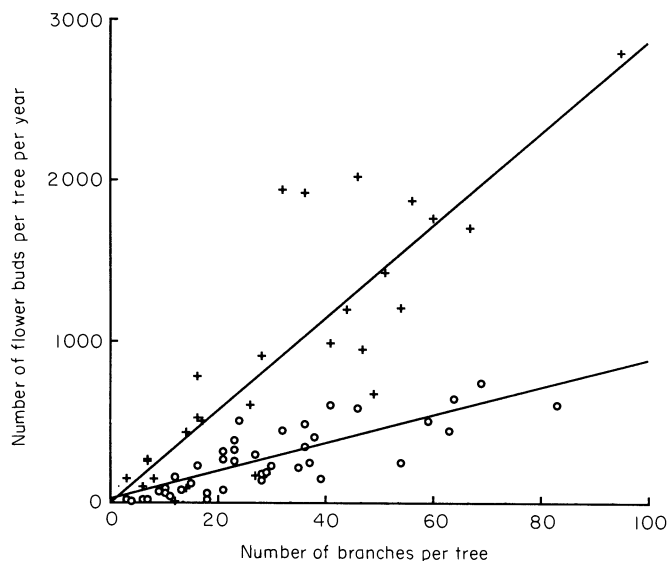
Fig. 10. Annual number of flower buds produced (F) in male ($+$; $n = 28$) and female ($\circ$; $n = 42$) *Cecropia obtusifolia* as a function of number of branches (B) per tree at Los Tuxtlas, Veracruz, Mexico. Males: $F = 27 \cdot 7$ (B); $r_{adj.}^2 = 0 \cdot 7440$; $P < 0 \cdot 0001$. Females: $F = 7 \cdot 9594$ (B); $r_{adj.}^2 = 0 \cdot 6642$; $P < 0 \cdot 0001$. In both cases the best-fit linear models are given, autocorrelation and heteroscedasticity corrected when necessary (White, Haun & Gow 1988).
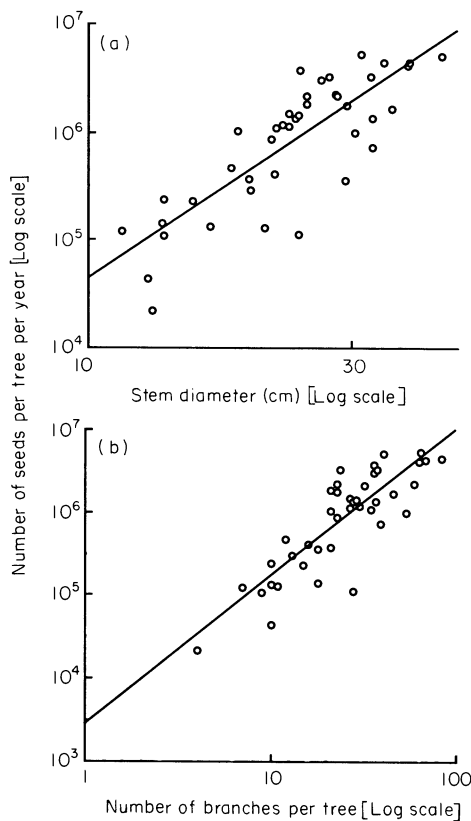
Fig. 11. Fecundity rate as a function of size and age of *Cecropia obtusifolia* tree ($n = 42$) at Los Tuxtlas, Veracruz, Mexico. (a) Allometry of number of seeds produced per year (m_x) and stem diameter (D): log $m_x = 1 \cdot 327 + 3 \cdot 303$ log D; $r_{adj.}^2 = 0 \cdot 677$; $P < 0 \cdot 0001$. (b) Allometry of number of seeds produced per year and number of branches (B): log $m_x = 3 \cdot 5729 + 4 \cdot 6897$ log B; $r_{adj.}^2 = 0 \cdot 726$; $P < 0 \cdot 0001$. In both cases best-fit model is given; no significant autocorrelation or heteroscedasticity found in either.

Discussion

Previous studies have considered *C. obtusifolia* as a typical pioneer tree species (Hartshorn 1978; Vázquez-Yanes 1980). The results presented here provide quantitative evidence for some of the demographic traits previously attributed to this type of species: (i) a strongly aggregated spatial distribution, (ii) a size coincidence among individuals found in gaps of similar age (Figs 2 and 3), (iii) relatively high growth rates; (iv) early maturation; and (v) high fecundity rates. In addition, this study has pinpointed critical life-history traits of *C. obtusifolia* and the ecological factors that may be important for the species' population dynamics at Los Tuxtlas rain forest.

The recruitment of *C. obtusifolia* is determined both by spatial and temporal components of gap dynamics. The species' seed fall in a gap depends on the distance to seed sources, the survivorship of seeds in the soil of different patch types, and the forest dynamics (Alvarez-Buylla & Martínez-Ramos 1990; Alvarez-Buylla & García-Barrios 1991). Once seeds reach a gap, the size of the canopy opening affects the rates of successful germination and establishment. Most of the gaps formed at Los Tuxtlas, which are $<100 \, m^2$ in area (Martínez-Ramos *et al.* 1988), are not suitable for the establishment of mature *C. obtusifolia* trees probably due to insufficient light availability in small gaps. Field and laboratory observations suggest that such a constraint affects seedling establishment rather than seed germination (Alvarez-Buylla & Martínez-Ramos 1990; M. Cano, M. Martínez-Ramos & E.R. Alvarez-Buylla, unpublished data). Accordingly,

the seedling—juvenile I transition probability was about 20 times lower than the seed—seedling one (cf. the quotients juvenile/seedling and seedling/seeds on trees from data in Table 3). The survivorship and growth of seedlings and juvenile trees were affected by gap size and light availability. However, other factors such as physical damage, soil dryness and herbivore attack (Núñez-Farfán & Dirzo 1989) also caused mortality at this stage. Light availability probably also determines the temporal limitation of successful colonization of *C. obtusifolia*, which occurs only during the first 2 years after the formation of large gaps.

The fast germination response and high growth rates of *C. obtusifolia* may be interpreted as traits adapted to the colonization of large gaps. Fast germination has been documented by other studies in the laboratory (Vázquez-Yanes & Smith 1982) and in field gaps (M. Cano, M. Martínez-Ramos & E.R. Alvarez-Buylla, unpublished data). Most seeds germinate during the first week after sowing. Such fast germination and rapid growth rates may avoid light interception and interference caused by re-growth of the plant community within gaps (Brokaw 1987). Such regrowth has been shown to reduce the high levels of light availability typical of recently opened gaps to levels typical of the mature understorey (Fetcher, Oberbauer & Strain 1985). On the other hand, fast growth rates may enable the acquisition of a sufficiently thick stem for ant colonization at a younger age. This may be favourable if the ant association prevents or ameliorates the negative demographic effects of herbivory on *C. obtusifolia* plants (Schupp 1987).

The growth pattern of *C. obtusifolia* maybe also interpreted in terms of its colonizing habit. For colonizing species limited mainly by light, King (1981) has proposed a growth model that suggests that very low buckling margins or safety factors will maximize the height growth rates of forest-grown trees. For *C. obtusifolia* a growth pattern of stem diameter in relation to height with relatively low safety factors was found, especially in pre-reproductive and mature trees (Fig. 7). Selection for height growth, rather than strength and longevity, is expected in shade-intolerant species, and an allometric design with low safety margins facilitates rapid height growth by lowering the biomass needed to achieve a certain height (King 1981). The safety factors obtained of *C. obtusifolia* are only approximate because hardwood parameters (from McMahon 1973) were assumed (Fig. 6a,b). In *C. obtusifolia* a lower safety factor is expected, due to its low wood density and hollow trunk (Barajas 1985). However, the safety factor is expected to be larger because of a light-weight crown with hollow branches.

The allometric pattern found in *C. obtusifolia* indicates that it grows in height until death, but if it continued to grow with the same allometric pattern it would eventually reach the buckling limit. Maybe such mechanical strain and an incapacity to alter the allometric relationship between diameter and height growth (for some unknown reason) promotes senility processes, and constitutes one of the factors that explains the maximum longevity attained by this species inside Los Tuxtlas forest. In fact, we have observed that when adult trees begin to die, the trunk tip usually breaks and trees continue to lose the rest of the leaves and branches until death. It would be interesting to determine the maximum life spans and heights attained by trees with different loads of epiphytes and vines that are likely to affect the trees' safety factors. However, epiphytes and vines are rare on *C. obtusifolia* trees at Los Tuxtlas (personal observations). The energetic compromise between growth and reproduction, which is suggested by the decrease in growth rates after the onset of reproduction, as well as the apparently high reproductive effort (suggested by the large numbers of flowers and fruits produced in males and females) of older trees, may be another factor determining the relatively short life-span of *C. obtusifolia* in forests.

Fecundity seems to be limited also by gap size. The space available for crown growth determines the number of branches that may be produced. Because branch number has a positive allometric relationship with floral bud number, gap size limits the potential fecundity of trees of a given age. However, a negative interference effect on growth and fecundity seems to be occurring in those gaps where intraspecific density of mature trees is high.

COMPARISON WITH OTHER TROPICAL TREE SPECIES

Complete life-table data for tropical tree species are scarce (see reviews in Sarukhán 1978, 1980; Córdova 1985), but the comparison of the available demographic information may be useful to evaluate the pioneer—climax categorization (Swaine & Whitmore 1988) of tropical-tree species' life histories. The discussion here will be mainly restricted to Mexican species.

The shape of the survivorship curve of *C. obtusifolia* is similar to that of other tropical tree species studied to date (Fig. 12a). Among these, however, the life span of *C. obtusifolia* is the shortest and its losses from the seed to the juvenile stages are the greatest (Fig. 12a). As expected, the pattern of future life expectancy of *C. obtusifolia* contrasts with that of tropical non-pioneer trees (Fig. 12b). The species attains maximum life expectancy at *c.* 10 years old when it reaches a non-suppressed canopy position (*c.* 20 cm in stem diameter and 20—25 m tall). Fecundity continues to increase monotonically after this size (Figs 11
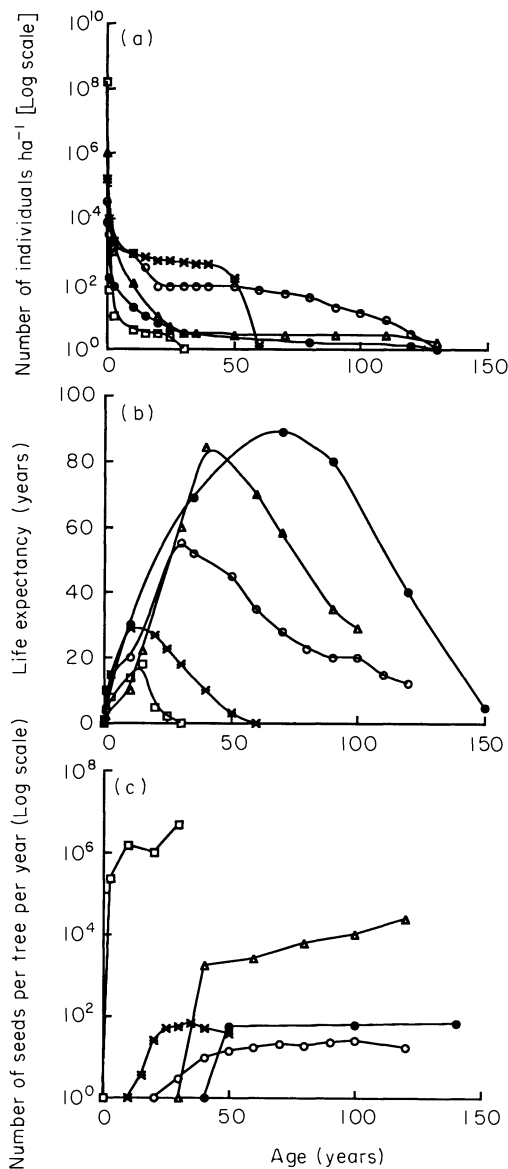
Fig. 12. Demographic patterns for pioneer and non-pioneer tropical tree species. Age-specific (a) survivorship curves, (b) life-expectancy patterns, and (c) annual fecundity patterns. Data from this study (*Cecropia obtusifolia* (□)), and modified from Piñero, Martínez-Ramos & Sarukhán (1984; *Astrocaryum mexicanum* (○)), from Peters (1983; *Brosimum alicastrum* (△)), from Oyama (1987, 1990; *Chamaedorea tepejilote* (*)), and from Palomeque (1988; *Omphalea oleifera* (●)).

and 12c). *Omphalea oleifera* (Euphorbiaceae), a late secondary canopy tree whose seedlings are released from suppression by gaps, also attains maximum life expectancy, at Los Tuxtlas, when it reaches the canopy several years after having reproduced for the first time (Palomeque 1988). In contrast, the other species reach maximum life expectancy before attaining canopy height when they reach the age of first reproduction (Fig. 12b).

Growth rates of *C. obtusifolia* are among the fastest reported for tropical trees (e.g. Córdova 1985; Lieberman & Lieberman 1987; Peralta *et al.*

1987), and such average high and continuous growth rates have been associated with a pioneer life-history pattern (Vázquez-Yanes 1980). In contrast, annual height growth rates of understorey palms (e.g. *Astrocaryum mexicanum*, *Podococcus barteri*, *Chamaedorea tepejilote*) range from 0 to 12 cm (Bullock 1980; Piñero, Martínez-Ramos & Sarukhán 1984; Oyama 1990), around 10 times slower than those of *C. obtusifolia*. Girth growth rates are also relatively high in *C. obtusifolia*, but lower than other pioneer trees (e.g. *Trema micrantha*; Brokaw 1987).

The fecundity pattern of *C. obtusifolia* also contrasts with that of other tropical trees. It reaches the reproductive stage 10 times faster than the understorey palm *A. mexicanum* (Fig. 12c; see also Piñero, Martínez-Ramos & Sarukhán (1984) in the same forest). At Los Tuxtlas, we know of only one other shade-intolerant tree, *Carica papaya* L. (Caricaceae), that matures faster (1 year old) than *C. obtusifolia* (personal observation). Early maturation is related to an increased life-time seed production. Also, individual annual fecundity of female *C. obtusifolia* is much greater than that of *A. mexicanum* and *Omphalea oleiphera*, in the same forest, and than that of *Brosimum alicastrum* (Moraceae) in northern Veracruz (Peters 1991). Fecundity increase with plant age and size in *C. obtusifolia*, as in the other tropical tree species studied. However, whilst in *C. obtusifolia* fecundity increases continuously until death, in other species fecundity reaches a plateau or it decreases after a maximum (Fig. 12c).

Comparisons of demographic patterns among species should bear in mind their different architectures and allometries. In *C. obtusifolia* first reproduction is closely associated with first branching at a stem diameter of 10 cm (3–5 years old) and hence age and size at first reproduction are determined by factors triggering branching. The mechanisms governing these patterns deserve further study. The restricted individual variation in branching size suggests that branching is either triggered by an internal size-dependent mechanism, or by environmental factors (e.g. PAR) that have narrow variability among establishment sites of newly branching (7–12-m-tall) individuals inside the forest.

Maximum potential fecundity and the pattern of fecundity during the life span of a tree also seems to be determined by its architecture. In *C. obtusifolia* fecundity is constrained by the number of branches, and hence by the number of axillary buds that may potentially be differentiated into flowers (which arise laterally). The allometric pattern of fecundity as a function of plant size is therefore constrained by the pattern of crown expansion as trees grow in stem diameter and height. However, an increased number of seeds per infructescence in older mature trees (>20 cm in stem diameter) also contributes to

the increased fecundity in larger plants. The continuous expansion of the tree crown yields a continuous increase in fecundity as trees age and grow. This is the case for *Brosimum alicastrum* (Fig. 12c), which also produces lateral floral buds (Peters 1983). In contrast, fecundity of most palms is constrained by the availability of axillary buds, and by leaf production that only occurs at the apical meristem. In these species the continuous increase in fecundity in early life may be explained by a progressively increasing number of floral buds that may mature as light availability increases whilst palms grow. Once palms reach maximum height and the maximum number of floral buds that may mature is attained, the fecundity curve reaches a plateau. Such a pattern is found in the two palm species that have been studied in Mexico (Fig. 12c). This same fecundity pattern is observed in both the upper-canopy tree *Omphalea oleifera* and the palm *A. mexicanum*, which have contrasting architectures (Fig. 12c).

Allometric patterns maybe also important in explaining differences in species'' longevities. A small safety factor, as found in *C. obtusifolia* and other shade-intolerant tree species (King 1981), may contribute to the relatively short life spans of these species. In contrast, long-lived species have greater safety factors (D.A. King, personal communication). Longevity patterns in tropical tree species are perhaps also explained by an energetic trade off between survivorship and reproduction. In fact, Fig. 12 suggests that age at first reproduction and maximum life span are positively correlated in the Mexican tree species studied to date.

Conclusion

In this study it was shown that *Cecropia obtusifolia* is a shade-intolerant species with a short life span, early maturation, and high growth, mortality and fecundity rates. These traits correspond to those expected by the theory of evolution of life histories for species that grow in unpredictable environments (Stearns 1977). Non-pioneer tropical tree species tend to have opposite life-history traits. However, it is important to note that rather than two clearly distinguishable types of life history, a continuum of demographic patterns has been found. This is true when looking at only five different tree species (Fig. 12). In the context of these results, the usefulness of a dichotomous classification to assign species to one of two life-history types is limited. Therefore, the pioneer–climax framework (Swaine & Whitmore 1988) should be viewed as a means of identifying the extremes of a continuum of tree life histories (Whitmore 1989), rather than as a means of categorization. The existence of a continuum of life histories does not support the idea of a strong evolutionary convergence among many tree species

within a few guilds (Hubbell & Foster 1986). Rather, such a continuum suggests that species may experience many different evolutionary routes.

Whitmore (1989) has distinguished pioneer from non-pioneer tree species based on their incapacity to germinate in the understorey. This and previous studies (Alvarez-Buylla & Martínez-Ramos 1990; Alvarez-Buylla & García-Barrios 1991) show, however, that this is not a generalizable assumption. The strict limitation to establishment in gaps in *C. obtusifolia* operates mainly at the seedling and juvenile stages, rather than at the germination stage. A first environmental sieve, determined by the photosensible system of seeds of *C. obtusifolia* (Vázquez-Yanes & Smith 1982) and the availability of gaps, operates during germination. Numerous seeds germinate, however, in sites where conditions are not adequate to attain maturity, such as small gaps, building and mature patches (M. Cano, M. Martínez-Ramos and E.R. Alvarez-Buylla, unpublished data). It is in the seedling–juvenile transition that the second and numerically most important environmental filters operate. We therefore propose that Swaine and Whitmore's dichotomous classification be used for initial characterization. However, a fuller understanding of the diversity of life histories in tropical forest communities demands detailed demographic studies. Such studies, although time-consuming and laborious, may contribute important data for the assessment of mechanisms involved in community, population and evolutionary processes in tropical rain forests.

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