Seed bank versus seed rain in the regeneration of a tropical pioneer tree

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Summary. We used the tropical pioneer tree, *Cecropia obtusifolia* to evaluate the relative importance of different sources of seeds in the regeneration of species that depend on ephemeral sites. We studied seed production in a population established in a 5 ha plot, and dispersal, dormancy and seed predation in two recent treefall gaps (<1 year-old), two building or successional forest patches (10–15 since disturbed), and two mature forest patches (>35 years since disturbed) for a one year period at Los Tuxtlas (Mexico). Flowers and fruits were counted at monthly intervals. Annual fecundity per tree ranged from 1.4×10^4 to 1.4×10^7 seeds. Seeds were continuously available on the trees and on the ground. Average annual seed rain per m^2 (as measured by 0.5×0.5 m seed traps) varied from 184 to 1925 among the six sites. Distance to nearest seed source and patch type explained more than 60% of the seed rain variation among sites. Soil seed density, estimated by counting seeds from ten samples (78.5 $cm^2 \times 10$ cm deep) collected from each site in October and January, ranged among the six sites from 269 to 4485 seeds per m^2 in January and from 204 to 5073 in October. Soil seed viabilities were much lower (17.1% in October and 5.1% in January) than those of rain seeds (48.26%). Annual survivorships of 2.2% were estimated for seeds artificially sown on the soil surface of a gap and a mature patch, and 3.75% in a building patch. In two other experiments seed removal rates ranged from 27% to 98% in 4 days. Removal rates were significantly higher in gap and mature patches than in building patches. Ants (*Paratrechina vividula*) and grasshopper nymphs (*Hygronemobius.* sp.) were the main predators. We draw three main conclusions from our data: (1) Pathogens and predators determine low survivorship of *C. obtusifolia*'s seeds in the soil and a rapid turnover rate (1.07 to 1.02 years) of its seed bank; (2) a continuous and copious seed production and an abundant and extensive seed rain replenish the soil seed pool in patches with different disturbance ages at least up to 86 m from nearest source; (3) more than 90% of the seeds contributing to *C. obtusifolia* seedling recruitment in gaps are less than one year-old. We discuss our results in the context of previous similar studies for tropical forests.

Natural disturbances influence the dynamics of biological communities (Paine and Levin 1981; Sousa 1984), the evolution of species life-history traits (review in Pickett and White 1985), and the coexistence of species (Connell 1978; Denslow 1985; Hubbell and Foster 1987). In tropical forests, chronic treefalls and limbfalls that create canopy gaps are the main modes of small-scale disturbance (Whitmore 1978; Brokaw 1985; Lawton and Putz 1988; Martínez-Ramos et al. 1988). Gap dynamics generates in these forests a mosaic of vegetation patches of different sizes and times since disturbance (Whitmore 1978).

Processes that govern the colonization of different aged patches play a major role in population dynamics (Sousa 1984; Martínez-Ramos et al. 1989; Horvitz and Schemske 1986). For example, mechanisms of temporal (i.e., seed dormancy) and spatial scape (i.e., seed dispersal) should enable successful colonization of species that attain maturity only in ephemeral and unpredictable open spaces such as forest treefall gaps. In fact, theory predicts long term soil seed survival for plant species inhabiting this type of sites (Silvertown 1989). In forest communities, relatively little attention has been paid to the mechanisms determining the propagules' probability of arriving and surviving in different patches (but see Horvitz and Schemske 1986; Martínez-Ramos and Alvarez-Buylla 1986; Augspurger and Franson 1988; Murray 1988; Schupp 1988a; Schupp et al. 1989).

This study discusses the relative importance of several life history attributes by which pioneer species achieve colonization of relatively small and unpredictable sites.

The possibilities include: 1) production of numerous seeds throughout the year, 2) wide dispersal, and 3) long-lived seeds. Additionally, seeds may be differentially dispersed to gaps, or survive better in gaps than elsewhere. Although some of these attributes have been documented for some pioneers (e.g., Vázquez-Yanes 1980; Augspurger and Franson 1988), no study has, to our knowledge, evaluated the importance of these attributes for a particular pioneer species in natural conditions (see reviews in Harper 1977; Sarukhán 1980; Garwood 1989).

Our approach was to evaluate the seed bank versus the seed rain contribution to regeneration by documenting the natural demography of seeds for the common pioneer tree species *Cecropia obtusifolia* (attains maturity only in gaps >100 m^2, Alvarez-Buylla 1986) in a 5 ha plot of the forest mosaic at Los Tuxtlas, México. We measured seed production, and total and viable seedfall and soil seed density in patches with different disturbance ages and at different seasons. From the data on natural sites, we generated hypotheses concerning the mechanisms of seed losses at different stages in their journey from trees to germination sites. We tested some of these hypotheses with experiments. In particular, we focused on the causes of seed losses in the soil.

Materials and methods

Species and the study site

Cecropia obtusifolia Bertol (Moraceae; although placed in the Cecropiaceae by Berg 1978) is an abundant pioneer tree species that colonizes treefall gaps in Los Tuxtlas forest. It grows from the Northern part of the Gulf of México and Pacific coast to the Caribbean Mexican coasts and the coasts of Chiapas, and in Central and South American forests in an altitudinal range of 0–800 m (Pennington and Sarukhán 1968; Ibarra 1985).

C. obtusifolia is a dioecious tree, 20–30 m high (Alvarez-Buylla 1986). Female inflorescence buds give rise to clusters of 4 (12–21 cm long each) spadices. Infructescences are similar in size to pistillate inflorescences; each bears 2700–4700 achenes. These are the dispersal units (hereafter referred to as seeds), they are cylindric, bright brown, 1–2 mm long and 0.8–1.3 mm wide (Alvarez-Buylla 1986). Fruits are eaten and seeds transported by a wide array of birds and mammals (Estrada et al. 1984), and seeds have photoblastic dormancy (Vázquez-Yanes 1979; Vázquez-Yanes and Smith 1982).

The study was conducted at Los Tuxtlas field station of the Instituto de Biología, Universidad Nacional Autónoma de México (18°35'N, 95°07'W) in Veracruz, México. The station's 700 ha of virgin forest has been classified as Evergreen Tall Tropical Forest (Miranda and Hernández-Xolocotzi 1963) with a 30 m canopy height. Mean annual rainfall is 4600 mm and mean annual temperature 25° C.

Permanent study plot

All reproductive females ($N = 42$; DBH > 10 cm) of *C. obtusifolia* found in a 5 ha (100 × 500 m, E-W oriented) plot of primary forest were mapped and tagged in December 1983. Individuals were spatially segregated; the smallest ones growing in recent gaps (<5 cm DBH; <1 year-old) and the rest in patches of different ages after disturbance; oldest patches, with 25 m tall *C. obtusifolia*, were aged around 35 years-old according to the treefall dating method of Martínez-Ramos et al. (1988).

Seed production

All floral buds, and clusters of mature and immature inflorescences and infructescences for each female tree were counted visually by climbing nearby trees of the same height as the tree being monitored. Censuses were made at monthly intervals during one year (February 1984–March 1985). To estimate maturation and abscission rates of infructescences, a sample of accesible floral buds of one female tree were marked in May, June, July, August and September of 1985 (5, 10, 13, 19 and 11 buds respectively for each month), and a sample of floral buds of three other females were marked in June, 1985 (13, 21 and 19 buds in each tree). All these trees were found outside the 5 ha plot. The marked buds were recensused every 20 days until all buds and fruits fell to the ground, or matured and were taken by frugivores. To calculate individual fecundities we estimated number of seeds per infructescence in females of different sizes (see Alvarez-Buylla 1986 for collection and counting details). We collected 207 infructescences from 11 trees: 38 from two trees 10.1–20.0 cm of 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.

Seed rain

To compare seed rain (total input of new seeds) among sites with different disturbance ages and at different distances from fruiting *C. obtusifolia*, we monitored total and viable seed rain in six sites in the 5 ha plot. We used Whitmore's (1978) characterization of the forest mosaic to distinguish three types of patches: newly opened gaps (<1 year since formed); building patches (2–35 years since disturbed and dominated by shade-intolerant or pioneer species); and mature patches (>35 years since disturbed, dominated by shade-tolerant species).

Since it was not possible to find the three types of patches in all the range of distances to nearest seed source in the 5 ha plot, and to guarantee equal representation of all patch types, two gaps, two building and two mature patches were selected randomly and ten traps were placed randomly within each patch. In addition, we measured the distance of each trap to the nearest fruiting *C. obtusifolia*. Gaps had areas between 200 and 300 m^2, 0–2 m average canopy and were formed by natural treefalls in November–December 1983. One had fruiting *C. obtusifolia* 0.5 to 8 m away and the other one 19 to 30 m away. The building patches had been opened by single natural treefalls between 1973 and 1975. Both had canopy heights between 20–25 m, but one was dominated by a mature population of 20–25 m tall *C. obtusifolia* and traps were 0 to 10 m from nearest seed source. The other building patch had only one juvenile *C. obtusifolia* and traps in it were 50 to 86 m from nearest seed source. The mature patches (>50 years since disturbed) had a 28 m high canopy, and traps were 9.7 to 28 m from nearest seed source.

Each trap was set on 15 cm wooden legs and consisted of a 0.5 × 0.5 × 0.10 m tray of 5 cm wire mesh covered with a nylon sheet that retained *C. obtusifolia* seeds but allowed water drainage. Every month, from March 1984 through February 1985, each sheet was removed and a new sheet set in place. We did not see signs of mammal predation (e.g., holes in trap sheets) or birds perching on traps, but we could not account for predation by invertebrates between collections. Sheets were transported to the laboratory where all *C. obtusifolia* seeds from each trap were separated and counted under a dissecting microscope. Seed viability was tested by germination under optimal conditions (25° C and 8 h light per day, Vázquez-Yanes and Smith 1982) in petri dishes with agar and 250 ppm (per l of agar) of gibberelic acid to break induced dormancy (Vázquez-Yanes, pers. com.). We verified that the percentage of germination under these conditions corresponded to the actual seeds' viabilities by applying the tetrazolium test (Moore 1973) to a sample of 200 fresh seeds and to some of the seeds collected in the first samples.

Soil seeds

We estimated soil seed content by counting total seeds in samples and performing viability tests of seeds recovered. Two soil collections were made: one in January 1984, before the peak of seed production of *C. obtusifolia;* and another one after the peak of seed production in October 1984. At each collection date 10 cylindrical soil cores (10 cm diameter and 10 cm deep) were taken from random points in each of the same six sites as for the seed rain and distances to nearest seed sources were also measured.

For each sampling point all litter was collected from within a 25 cm² frame centered over each core. Nine of the 10 cores per site were stratified in two samples (0–5 and 5–10 cm deep) and the other one in three (0–5, 5–10, and 10–15). Each litter and soil sample was separated using N° 10 and N° 30 sieves; the soil was water-sieved and the final sample was allowed to dry in the shade at room temperature. All *C. obtusifolia* seeds were separated and counted under a dissecting microscope and viability tests were conducted as above.

Seed survivorship experiment

To obtain a direct estimate of seed life-span in natural soil conditions, five plots (50 × 50 cm) were randomly established in each of three sites: the one year-old gap far from *C. obtusifolia;* the 14 year-old building patch dominated by *C. obtusifolia;* and one of the mature patches. Mature infructescences were collected from 10 females. Infructescences were cut open longitudinally and seeds were scraped off, spread on paper and let to dry in the dark at room temperature. Seeds were cleaned manually until completely devoid of pulp. Dry seeds were mixed and homogenized. From these seeds, 100 were sown on top of 8 cm diamter × 10 cm deep cores of commercial potting soil (with no *C. obtusifolia* seeds; germination trials showed that soil type did not affect germination) inside a wire mesh cylinder (mesh size = 3 cm). This enabled free passage of arthropods in the soil and facilitated relocalization and collection of stocks. The soil used was of a slightly different color from forest soil and this helped to confirm that no soil was displaced by water currents during the experiment.

Six cylinders were inserted into the soil at random positions in each 0.5 × 0.5 m plot and the seeds were covered with a 1 cm layer of the soil that kept seeds from being blown by the wind (a total of 3000 seeds sown in each site, six sets of 100 in each of the 5 plots per site). Finally, each plot was covered by a 1 m² transparent plastic sheet suspended 1 m above the ground to intercept the rain of new seeds. Newly germinating seedlings in the field were monitored and removed every 15 days during the first two months and monthly thereafter. To make sure that seedlings that germinated and died between monitorings were not considered as removed, we searched carefully for dead seedlings. Furthermore, opened seed coats from already germinated seeds coincided with the number of germinated seeds registered in the field.

Every two months, one core from each of the five plots at each site (15 cores collected every two months) was randomly selected and processed as described for the soil collections. No changes, that could indicate movement due to water currents, were detected on the level of soil inside the baskets. The cores were stored in two black bags to minimize activation of germination before processing. Samples were processed and dried in the dark at room temperature five to seven days after collection.

Seeds recovered were classified as germinated (when the radicle was extended), whole, or damaged. To distinguish between dormant and dead seeds the undamaged whole seeds were tested for viability through germination under optimal conditions as described above. The initial viability (90%) was also obtained for the stock of seeds used in the experiment. As a control, a stock of seeds for those used in the experiment were kept in the laboratory and every two months they were tested for viability in the same growth chambers used for the seeds recovered from the soil. Two

petri dishes with 50 seeds each were used for this purpose and the control viabilities varied between 85% and 94%.

Seed predation experiments

To identify seed predators of *C. obtusifolia*, a pile of dry seeds devoid of pulp (seeds processed as above) was placed on the ground inside the forest and observed for 2 periods of 1.5 h during the day in August 1987. Insects attracted by the seeds were collected. Another pile of around 3000 seeds was placed 1 m from a nest of the most commonly collected ants (*Parathrechina vividula*). We observed the ants collecting for 1 h.

Two experiments were designed to test seed removal rates. Seeds used in these experiments were collected and processed as in the survivorship experiment. In May 1985, pairs of petri dishes (8 cm diameter) were placed at 2 m intervals along each of two randomly selected perpendicular transects (20 m long) in an 18 year-old building patch. Fifty seeds of *C. obtusifolia* were placed in each petri dish; one dish was covered with 2.5 mm plastic mesh and the other one was left uncovered. Seed losses and seed predators were recorded in the following four days, with site visits between 10 a.m.–12 a.m. daily.

In August 1987 a second experiment was performed using lower seed densities. In two randomly selected mature patches, two gaps and two building patches, 10 points were randomly selected at both sides of a randomly selected transect. The gaps and mature patches were more than 10 m from nearest seed source and the building patches were < 10 m. Three petri dishes, each with 10 seeds of *C. obtusifolia*, were placed at each point. One petri dish was covered with its lid with 4 holes (2 × 1 cm) at equidistant points around its base to enable free entrance of arthropods. The other two dishes were left uncovered. One was lined with tanglefoot to trap insects attracted by the seeds. A 30 cm² sheet of 3 mm plastic mesh with three wooden poles was placed 50 cm over each group of three dishes to avoid direct rain splashing. Dishes were collected after 4 days and number of damaged and lost seeds were counted. Insects trapped and those observed eating the seeds were collected and sent for identification.

Data analyses

To evaluate the effect of distance to seed source and patch type on the seed rain and the soil seed content we used log-linear models (Everitt 1977). Seed frequencies (either seeds per trap or seeds per sample) were taken as the dependent variable. The independent variables considered by the models were: (a) distance to the nearest fruiting tree; (b) patch type, a categorical variable with three levels (gap, building and mature), and (c) site, a categorical variable with six levels. We compared the proportion of the variation in seeds per trap or per sample (for the rain and seed bank respectively) explained by three alternative models. The first one assumed that each of the six sites is unique (five degrees of freedom), and the second simpler and more parsimonious model included the effect of distance to nearest fruiting tree and patch type (3 degrees of freedom). A third model, also with five degrees of freedom, included the interaction between distance and patch type.

The fitting of the log-linear model was done through Generalized Linear Models (GLM) described originally be Nelder and Wedderbum (1972, see also McCullagh and Nelder 1983). The deviance of a GLM measures the discrepancy between the data and the fitted values. In the case of log-linear models fitted to frequency data, the deviances are asymptotically distributed as χ^2. The change in deviance when a new term is fitted is also distributed as χ^2 and can be used to test the validity of the new term (Ezcurra et al. 1987).

Analyses of variance (ANOVA) were used to compare seeds per infructescence among trees of different DBH's and to compare number of predated seeds among different patch types. Differences
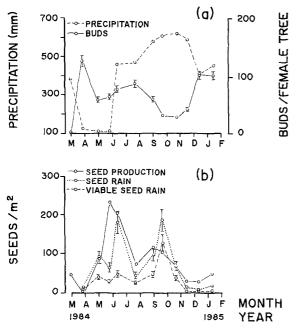
Fig. 1. a Reproductive phenology of *Cecropia obtusifolia* and rainfall regime at Los Tuxtlas (data taken at the station for the year 1984–85 by the staff of UNAM). The average number of floral buds and one standard error are reported for each month ($n = 42$ female trees per month), b seasonal variation in mean seed rain/m² and seed production/m² in *Cecropia obtusifolia* at Los Tuxtlas. Mean seed rain and one standard error are reported for each month ($n = 60$ seed rain traps per month). Average seed production per month was obtained by dividing total seeds produced in 5 ha plot per month by total area (5 ha)

among averages were tested with multiple comparison tests. Differences between germination percentages were tested with t_s statistic. Correlation analysis was used to compare average seed density among sites in the rain and in the soil (Sokal and Rohlf 1981). Frequency distributions were compared with the Kolmogorov-Smirnov test (Siegel 1980).

Results

Seed production and seed rain

Annual fecundity per tree ranged from 1.4×10^4 to 1.4×10^7 seeds and average seeds per infructescence was estimated to be 2727 ($n = 2$; s.d. $= 595$) and 4612 ($n = 9$; s.d. $= 602$) for trees smaller and greater than 20 cm DBH, respectively. ANOVA and an a posteriori test showed that trees 10.1–20.0 cm DBH produced fewer ($P < 0.05$) seeds per infructescence than larger trees.

Buds of female inflorescences were produced seasonally (Fig. 1a), with maximum activity during driest months. Buds opened into flowers mostly during the winter rainy season (December to February), with a secondary flowering peak during the summer rainy season (June to September). The highest fruiting peak occurred during May–June, at the onset of the rainy season, but mature fruits were available all year long (Fig. 1b).

C. obtusifolia's seed production and seed rain showed similar seasonal patterns (Fig. 1b). However, higher seedfall than seed production in the 5 ha plot suggests
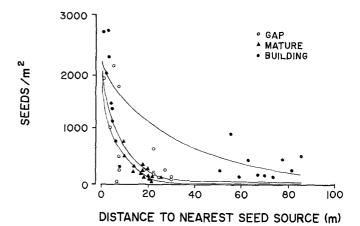

DISTANCE TO NEAREST SEED SOURCE (m)

Fig. 2. Best fit log-linear model for *Cecropia obtusifolia* seed rain versus distance to nearest seed source in gap, building and mature patches at Los Tuxtlas forest. The fitting of the model was done through GLM using seeds per trap as the dependent variable and patch type and distance to nearest seed source as independent variables; estimated parameters were converted to seeds/m² by multiplying by four and only statistically significant parameter estimates were considered to construct the curves (see data analyses for more details on GLM). The general equation for the model is $Y = e^{(7.020 - 0.037 \text{Dist} + 0.742 P_2 - 0.932 P_3)}$. The superior line corresponds to the building, the middle one to the gap and the bottom one to the mature patch

an influx of seeds from outside the plot during September to October. Seed losses from the trees to the ground are apparent during the rest of the year. Seed rain could be underestimated due to invertebrate predation in traps (see methods), but predispersal seed predation could have also occurred (e.g., Estrada et al. 1984; Charles-Dominique 1986). Pathogen attack or senescence seem important sources of seed loss right after seeds leave the trees, especially during May to July when the proportion of viable seeds in the rain decreased (Fig. 1b).

Newly dispersed viable seeds were widely and patchily dispersed in space. Seed inputs were detected up to 86 m from the nearest source. The probability of finding at least one of *C. obtusifolia's* newly dispersed seeds in 0.25 m² of forest floor is above 0.8 per month from May through December and is never less than 0.4 for the rest of the year. The spatial distribution of newly dispersed seeds of *C. obtusifolia* was highly heterogeneous, however, and most traps received a low number of seeds (see Martínez-Ramos and Alvarez-Buylla 1986; Fig. 2). The aggregation index obtained by the ratio of the variance to the mean of the annual number of seeds per trap was very high ($s^2/x = 440$; $n = 60$). *C. obtusifolia's* dispersal in fecal loads may explain this high aggregation index.

Seeds falling in sites far from fruiting *C. obtusifolia* had greater viabilities than those falling close to seed sources. To avoid confounding patch and distance effects we compared seed viabilities between the gap close and that one far from seed sources ($427/1091 = 39.1\%$ and $160/209 = 76.6\%$ respectively; $t_s = 12.47$; $P < 0.0001$), and we did the same thing for the far and near building patches ($558/1917 = 29.1\%$ and $190/339 = 56.2\%$; $t_s =$

Table 1. Analysis of deviance for the effect of distance to nearest seed source and patch type (i.e., mature, gap or successional) on number of seeds of *C. obtusifolia* per seed rain trap. A poisson error distribution and a logarithmic link function were assumed. The degrees of freedom (D.F.) correspond to the model considered in each case and the difference of deviance of each model with respect to total deviance (constant) is equal to the χ^2 approximation that had associated P values <0.001 in all cases (see methods section and text for more details on GLM). (A) Total seeds, (B) viable seeds

A

Model	Deviance	D.F.	χ^2 Approx.	r^2
Constant	51119	—	—	—
Site	18871	5	32248	0.6308
Patch + distance	18648	3	32471	0.6353
Patch + distance + patch × distance	13315	5	37804	0.7395

(B)

Model	Deviance	D.F.	χ^2 Approx.	r^2
Constant	13211	—	—	—
Site	7960	5	5251	0.3975
Patch + distance	8080	3	5131	0.3884
Patch + distance + patch × distance	6478	5	6733	0.5097

10.23; $P<0.0001$). Both mature patches were relatively far (10 to 28 m) from seed sources and their seeds' viabilities were relatively high (73.5% and 62.1%).

Total and viable seed rain was a positive log-linear function of distance to nearest fruiting *C. obtusifolia* and was also significantly affected by patch type (Table 1 and Fig. 2). A simpler generalized linear model, that incorporates the effect of distance to nearest seed source and patch type, explained a similar proportion of the variation in number of seeds among traps than the less parsimonious model that assumed each site to be different from each other. In all cases shown in Table 1 the χ^2 approximation was statistically significant ($P<0.001$). Models that only considered either patch type or distance explained a smaller and not significant proportion of the variation in the number of seeds per trap. A third model, that incorporated the interaction between distance and patch type, explained a greater proportion of the variation than the site model using the same degrees of freedom (Table 1).

The best fit log-linear models for seeds per m^2 versus distance to nearest seed source, considering those parameters that were statistically different from zero according to a t test, represent approximations of the dispersal curve of *C. obtusifolia* in each patch type (Fig. 2). These curves suggest that in mature patches seedfall decreases with distance faster than in building and gap patches and that at equal distances from nearest seed source seedfall is predicted to be higher in building than in gap or mature patches.
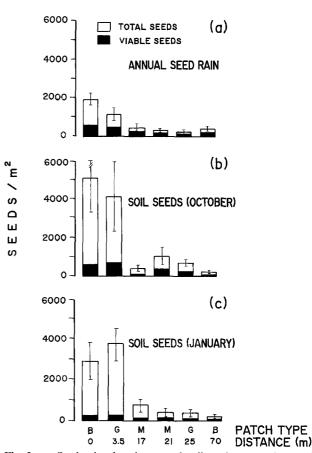

Fig. 3a–c. Seed rain abundance and soil seed content in gap (G), building (B) and mature (M) forest patches at Los Tuxtlas. (a) Annual seed rain; (b) soil seeds (October collection); (c) soil seeds (January collection). The mean density of total seeds per square metre and one standard error are reported ($n=10$ for each patch type). The distance from the midpoint of the patch to the edge of the crown of the nearest fruiting tree of *Cecropia obtusifolia* is reported underneath patch types

The distribution of *C. obtusifolia*'s seed rain among the phases of the forest mosaic is given by the product of the average seed rain/m^2 in each type (Fig. 3a) and the area covered by each patch type. We provide here an estimate of the mosaic level seedfall based on the average estimates we obtained for patches in two distance categories (far: >5 m; and near: <5 m from seed source) for each patch type. This estimate should be accurate because seedfall drops drastically with distance (Fig. 2). From a map with all the fruiting trees of *C. obtusifolia* and the areas covered by each patch type for the 5 ha plot (Alvarez-Buylla 1986; Martínez-Ramos et al. 1988), we estimated the area in gap and building phases with and without fruiting *C. obtusifolia* nearby, and the area covered by mature patches. Only around 40% of the 6.4×10^7 seeds of *C. obtusifolia* estimated to have been produced in one year by the 5 ha plot population were recovered in the seed rain of that year. Of these seeds, gaps (1.13% of the 5 ha plot) received around 3%, building patches (33.59% of area) 43%, and mature patches (64.35% of area) 54%.

Table 2. Analysis of deviance for the effect of distance to nearest seed source and patch type (i.e., mature, gap or successional) on number of seeds of *C. obtusifolia* per soil sample. A poisson error distribution and a logarithmic link function were assumed. The degrees of freedom (D.F.) correspond to the model considered in each case and the difference of deviance of each model with respect to total deviance (constant) is equal to the χ^2 approximation that had associated P values <0.001 in all cases (see methods section and text for more details on GLM). The first value corresponds to the January collection and the second one to the October collection. (A) Total seeds, (B) viable seeds

(A)

Model	Deviance	D.F.	χ^2 Approx.	r^2
Constant	136857–251353	—	—	—
Site	60539–154406	5	76318–96947	0.5576–0.3857
Patch + distance	67827–149578	3	69030–101775	0.5044–0.4049
Patch + distance + patch × distance	66904–136808	5	69953–114545	0.5111–0.5443

(B)

Model	Deviance	D.F.	χ^2 Approx.	r^2
Constant	3981–95608	—	—	—
Site	2746–71715	5	1235–23893	0.3102–0.2499
Patch + distance	3563–74820	3	418–20788	0.1050–0.2174
Patch + distance + patch × distance	2845–62023	5	1136–33585	0.2854–0.3513

Soil seeds

The similarity between the spatial pattern of seed density in the rain and in the soil suggests that the soil seed stock is explained, to a great extent, by the seed rain created by the present adult population in the 5 ha plot (Fig. 3). Average total seed rain and soil seed content in October (after peaks of the species fruit production) per site were significantly correlated ($r = 0.914$, $n = 6$, $P < 0.05$), and correlation of seed rain and seed content in January ($r = 0.791$, $n = 6$, $P < 0.1$) was marginally significant.
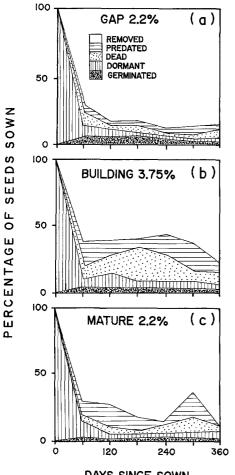
Total and viable soil seeds per sample in October and January were a positive log-linear function of distance to nearest seed source and were also significantly affected by patch type (Table 2). Although the models explained a smaller proportion of the variation in soil than in rain seed content, the model that incorporated the distance and patch type effects also explained a similar or greater proportion of the variation than the model that assumed each site to be unique. In all cases the χ^2 approximation had an associated P value less than 0.001. Models that considered either patch type or distance explained a smaller proportion of variation in soil seeds than any of these two models, while a model considering the interaction term explained a greater proportion of the variation (Table 2). For October total and viable seeds and January total seeds parameters were statistically different from zero ($P < 0.001$) according to a t test; for January viable seeds the y ordinate and the slopes of gap and mature patches were equal.

Comparisons of viable rain and soil seed densities suggest that seeds accumulate in the soil for slightly over one year (Fig. 3). Total *C. obtusifolia's* seeds recovered from soil collections made before and after the species highest peaks of seed production were very high (Fig. 3a and b). However, viabilities of soil seeds were much lower than those of rain seeds maybe due to pathogens or senescence.

The distribution of total and viable seeds in the soil profile also suggests that pathogens and predators are important depleting factors of the seed bank. Old seeds, in deeper soil strata, had lower viabilities than fresh ones, found near the soil surface. Predation is suggested because very few seeds become buried below 5 cm. Seventy-seven percent of total soil seeds were found in the topmost 5 cm of soil. Only 2% of the seeds were collected 10–15 cm below the surface, and these were all nonviable. In comparison, seeds recovered from 0–5 and 5–10 cm depths had average viabilities of 13.8% and 6.0%, respectively.

Seed survivorship

Viability estimates for seeds taken from trees, from seed rain traps and from soil samples suggest that *Cocropia obtusifolia's* seeds lose viability at high rates after leaving the trees. Freshly collected seeds from mature infructescences had viability percentages greater than 85% ($n = 2000$), viabilities dropped to 48.4% ($n = 945$) in the newly dispersed seeds, and to 17.1% ($n = 1,618$) and 5.1% ($n =$

Fig. 4a–c. Dynamics of the population of seeds of *Cecropia obtusifolia* introduced in the soil of (a) a gap, (b) a building and (c) a mature patch at Los Tuxtlas. The final survivorship probability is reported for each patch type. Seeds with arrested germination plus seedlings germinated in the field are included under the category of germinated seeds in this Figure

1,147) in those collected from the soil in October and January, respectively.

Our survivorship experiment provided a direct estimate of soil seed survivorship and an alternative evaluation of the causes of seed death operating in natural conditions (Fig. 4). The number of viable seeds recovered during the experiment decreased drastically within two months of sowing date. After one year, only 2.2%, 3.7% and 2.2% of the seeds sown in the gap, building and mature patches respectivley remained dormant. High removal rates in sown seeds suggest that predation is the main cause of seed losses in the soil; some seeds were recovered with signs of predation. The damage ranged from small central perforations to complete fragmentation of the seeds. Whole but non-viable seeds represented a relatively small proportion of the seeds sown.

Seed outputs from the soil due to germination were mainly registered during the first two months of the experiment (Fig. 4). The greatest percentage of germination in the field (seedlings with extended cotyledons) was registered in the gap (4.4%), although some seeds germinated in the building (2.2%) and mature (0.53%) patches.

Seed predation

Ants and grasshopper nymphs appear to be the main predators of *C. obtusifolia*. Two ant species (*Paratrechina vividula*) [Nylander], family Myrmicinae, tribe Lasiini, and *Atta cephalotes* [Linne], family Myrmicinae, tribe Attini) were observed carrying seeds of *C. obtusifolia* to their nests; *Solenopsis geminata* (Fabricius) (family Myrmicinae, tribe Solenopsidini) ants were sometimes attracted by the seeds. *Paratrechina vividula* removed approximately 3000 seeds in 1.5 h from a pile placed 1 m from their nest. Only empty or broken seeds were left by the ants; the rest were taken into the nest (>15 cm deep) and none of the seeds were dropped on the way during this trial. Nymphs of a Grillidae (Nemobini, *Hygronemobius* sp.) were seen eating seeds leaving small perforations in the centre of seeds.

In the first predation experiment we registered very high rates of predation and seed removal. In the uncovered dishes 55% of the seeds were removed or eaten in situ after the first day and only 4% of the seeds were recovered undamaged after 4 days. In the mesh-covered dishes 72% of the seeds were recovered with no signs of predation after 4 days. Most seed remains and some ants were still inside the dishes; the mesh size proved to be too small for the ants' free passage.

In the second experiment, where the number of seeds per dish was lower, the rate of seed removal was also lower than in the first experiment. The distribution of seeds per dish after 4 days was bimodal, suggesting that once animals discovered a dish of seeds all of them may have been taken. Mean number of seeds in the dishes after four days was around 7 (95% confidence limits: 5.8–7.6) for the covered dishes with 2×1 cm holes, and around 6 (95% confidence limits: 4.7–6.7) for the uncovered ones. The frequency distribution of seeds/dish in open and covered dishes were equal ($D = 0.15$; $2 < P < 0.3$), suggesting that invertebrates were probably the primary seed predators.

Patch type had a statistically significant effect on average number of seeds removed per site according to an ANOVA with two replicates per patch type ($F = 22.026$, and $F = 7.568$; $P < 0.01$ and $P < 0.06$ for uncovered and covered dishes respectively). Seed removal in gap and mature patches from uncovered dishes was higher (by an a posteriori STP test at $P < 0.05$) than in building patches.

Discussion

Four adaptive traits have been proposed to explain how pioneer or shade-intolerant species colonize newly opened gaps in tropical forests: long-term dormancy; germination cued to environmental gap conditions; co-

pious and continuous seed production; and wide and long-distance dispersal (Gómez-Pompa et al. 1972; Vázquez-Yanes 1980).

Soil seed survivorship

Previous studies have directly documented long-term survivorship (up to 5 yr.) of seeds of tropical pioneers. In these studies, however, seeds were protected from predators (see review in Whitmore 1983 and particular studies in Holthuijzen and Boerboom 1982; Pérez-Nasser 1985; Vázquez-Yanes and Orozco-Segovia 1985; Hopkins and Graham 1987; Murray 1988). Our data show that seeds of *C. obtusifolia* have short life spans in the soil natural conditions. Our survivorship experiment yielded an average annual survivorship of only 2% (0.02) (Fig. 4) that corresponds to an average seeds' life-span of 9 days, assuming that the number of days a seed lives in the soil has a geometric probability distribution. This survivorship implies a mean seed bank turnover rate (the average number of years for the renewal of all seeds in the soil $= 1/1{-}0.02$) equal to 1.02 yr. We obtained a very similar turnover rate when we compared the average number of viable seeds in the annual rain and in the October soil collections (soil seeds/rain seeds $= 1.07$ yr.; from data in Fig. 3), and the turnover rate would be even faster if we considered the January collection. These turnover rates imply that all viable seeds of *C. obtusifolia* are renewed in the soil of Los Tuxtlas approximately every 1.02 to 1.07 years. Data collected by other researchers for *C. obtusifolia* also suggest low viabilities of soil seeds and seed bank turnover rates of around one year in natural conditions at Los Tuxtlas (Vázquez-Yanes and Orozco-Segovia 1986; Salmerón 1984; Guevara 1986).

What causes seed loss in the soil?

The main causes of soil seed loss are senescence, predators, pathogens, and germination (Harper 1977). No previous study has evaluated the relative role of all these factors in the seed bank dynamics of tropical species (see reviews of past work in Sarukhán 1980; Whitmore 1983; Garwood 1989).

Predation and pathogen attack. Around sixty percent of *C. obtusifolia*'s seeds, kept dry in the laboratory, remain viable at least five years after collection (personal observation). Hence the rapid loss of viability of whole seeds of *C. obtusifolia* in natural conditions is due to the attack of pathogens or the action of some environmental factors not present in laboratory conditions (e.g., humidity).

Our study showed that predation and pathogen attack are the main causes of *C. obtusifolia*'s seed loss at Los Tuxtlas. Our survivorship experiment suggested that predation is the main cause of seed loss. In this experiment whole dead seeds, perhaps lost due to pathogens, represented a small proportion of seed loss. High

and non-uniform removal rates suggested that recruiting ants responding to high densities of food sources were the main predators during the experiments (Fig. 4). *Paratrechina vividula* ants might be among the main predators of *C. obtusifolia*. Although we did not observe ants eating seeds we saw them taken to their nests (>15 cm deep, R. Carroll, pers. comm.) where most seeds probably are eaten or die. Seeds with signs of predation represented 8.59%, 13.57% and 4.3% of sown seeds for the mature, building, and gap patches respectively; these were probably eaten by grasshopper nymphs (*Hygronemobius* sp.).

Comparisons of seed rain and soil collections (see Fig. 3) suggest that pathogen attack is also an important cause of seed loss. While the difference in total seeds between January and October is relatively small, viable seeds in January were fewer than in October (Fig. 3), suggesting that pathogens and not predators are the main causes of seed loss. Several factors may explain the discrepancy between these and the seed bank experiment results. Some slightly eaten seeds might have been considered as whole biassing the difference between the January and October total soil seed contents (Fig. 3). The experiment could have overestimated, on the other hand, removal rates because seeds were sown in high densities and close to the surface. *C. obtusifolia* dispersal in fecal loads may produce, however, natural local densities similar to those used in our experiment (Fleming and Heithaus 1981; Brokaw 1986). Finally, the relative role of predators and pathogens on *C. obtusifolia*'s seed bank seems to vary spatially and temporally (see Vázquez-Yanes and Orozco-Segovia 1985; Bosh and Vázquez-Yanes 1985; Pérez-Nasser 1985). In any case, direct evaluations of the relative effect of these two seed loss causes should be pursued in the future.

Our results suggested that spatial variation in predation rates depend in part on the sites' disturbance age. The survivorship and predation experiments suggested that seed survivorship in building patches was higher than in mature patches. In building patches with fruiting *C. obtusifolia* an abundant seed rain (ca. 2,000 seeds/m^2/year) might satiate predators. But differences in abundance and diversity of predators in gaps and in closed forest could also account for differential survivorship. Grasshopper predation was higher in building than in gaps or mature patches (Fig. 4). Differences in abundance and predation rates among patch types have been documented only for rodents (Emmons 1982), but *C. obtusifolia*'s seeds are not eaten by rodents at Los Tuxtlas (Sánchez-Cordero, unpubl. data). Our results corroborate this because predation rates were equal in open and mammal-protected dishes, but not in ant-protected dishes.

Germination. Arrested and successful germination also caused numerical loss in the seed bank of *C. obtusifolia*. We registered arrested germination in some of the seeds recovered from the survivorship experiment, but these accounted only for 0.1%, 0.6% and 1.5% (total germination in Fig. 4 minus germination in the field) of seed loss in the gap, building and mature patches respectively.

Processing of samples could have initiated the germination of these seeds (but see methods). In such a case, our survivorship estimates would be slightly underestimated.

This study confirms that seeds of *C. obtusifolia* germinate preferentially in gaps (Vázquez-Yanes and Orozco-Segovia 1984). Seedling emergence was higher in gaps (4.4%) than in building and mature patches, but they were not as high as expected from germination trials in petri dishes (Vázquez-Yanes and Orozco-Segovia 1985), perhaps because of the high rates of seed predation and pathogen attack suffered by *C. obtusifolia*. The small germination percentages in building and mature patches contrast with the expectation that *C. obtusifolia*'s seeds only germinate in large gaps (Vázquez-Yanes and Smith 1982; Vázquez-Yanes and Orozco-Segovia 1985). However, some seeds may be able to germinate in more limited light conditions than others because of genetic or phenotypic variability expressed in natural conditions (Vázquez-Yanes and Orozco-Segovia 1986; Cano, Martínez-Ramos and Alvarez-Buylla, unpublished work). Secretion of gibberelic acid by the soil microflora might also stimulate germination in light-limited environments (Bosch and Vázquez-Yanes 1985) when seeds are in direct contact with soil microflora.

How is the seed pool replenished?

The copious and continuous seed production, and the dispersal of *C. obtusifolia*'s seeds up to 86 m from seed sources (Figs. 1 and 2) by a wide array of frugivores (Estrada et al. 1984), seem to be important in replenishing this species' seed pools in sites that may open to gaps within the short life-span of its seeds.

The copious production and continuous (but with seasonal peaks) availability of seeds in *C. obtusifolia* (see Fig. 1) is typical of other pioneer tropical species dispersed by animals (Howe and Smallwood 1982; Whitmore 1983). We lack direct evidence on fruit removal, but other studies have documented that *C. obtusifolia*'s seeds are dispersed by many birds and mammals at Los Tuxtlas (Estrada et al. 1984). The difference between number of buds (1.1×10^4) and clusters of mature infructescences (3.6×10^3; one cluster of four infructescences develops from each bud) suggests high removal between our monitorings. That the difference was due in part to frugivory between censuses and not only to premature bud abscission is supported by data gathered from trees with marked buds outside the 5 ha plot. Neither buds or mature infructescences were counted twice in consecutive months, because they disappeared 25–28 days after they were visible. Considering that 30% of the buds and none of the immature infructescences abscissed before maturation, an approximate relative difference of 48% ({[buds-fruits] − proportion of abscissed bud × [buds-fruits]}/buds) between buds and clusters of infructescences could be explained partly by frugivory between censuses. We can not, however, rule out pre dispersal seed predation.

We found that seeds far from seed sources had higher viabilities than those collected close to fruiting *C. obtusifolia*. Increased ability to germinate due to treatment in the guts of dispersers is one possible explanation for this finding (see Vázquez-Yanes and Orozco-Segovia 1986). This is unlikely, however, because seeds collected directly from trees had high viabilities (i.e., >90%). It is likely, however, that more unripe fruits fall under tree canopies in comparison to seeds taken by frugivores.

We have provided approximations of *Cecropia obtusifolia*'s dispersal curves in each patch type. Although the exact quantitative predictions of our models must be taken with caution due to unbalanced sampling (see methods and Fig. 2), our data show that distance to nearest seed source, patch type, and the interaction of these two, explain an important proportion of the variation of *C. obtusifolia*'s seedfall (Table 1). Gaps seem to receive greater seedfalls only if found close to a seed source. Preferential seed rain to gaps has been documented only for wind-dispersed seeds at Barro Colorado Island (BCI) (Augspurger and Franson 1988). Our model also suggests that building patches receive greater seedfalls at equal distances from source than gaps or mature patches. Higher seedfall in building patches may be explained by the association of this patch type to the presence of mature pioneers (see also Levey 1988). Also because *C. obtusifolia* is an animal dispersed species, we expect sites with perches for dispersers (building and mature) to receive higher seedfalls than sites without perches (gaps). In fact, we observed that traps located near the centre of the gaps received fewer seeds than those close to the gap edges (data not shown). The fact that neither of the two mature patches had seed sources as close as one of the gaps or building patches may explain why, at equal distances from seed sources, the model predicted similar seedfalls in mature patches and gaps.

We may speculate that the dispersers foraging and regurgitating or defecating behaviors in different patch types might underly the significance of the distance-patch interaction term in the third model we tested. For example, in gaps, frugivores probably have to fly for longer distances until they find a new perch or foraging site, and seeds are retained longer and hence their availability decreases more slowly with distance from source. Other studies have documented different abundances of dispersers and fruit sources in mature and gap patches (Schemske and Brokaw 1981; Brokaw 1986; Levey 1988). No study has related seed sources, seed rain and frugivore abundance and behavior in the same tropical forest (but see Hoppes 1987 and 1988 for a temperature example).

Seed bank versus seed rain in the regeneration of Cecropia obtusifolia

No study has, to our knowledge, combined forest and seed dynamics data that enable indirect estimates of seed survivorship (see Alvarez-Buylla and García-Barrios 1990), or the importance of the seed bank versus the seed rain in the regeneration of tropical trees. Previous

studies that have determined origin of seeds directly have compared seedling emergence in gaps from sterilized (seed rain contribution) and fresh soil (seed rain plus seed bank) (Putz and Appanah 1987; Lawton and Putz 1988), or seedling emergence in sites with and without seed rain exclusion (Young et al. 1987). Their results suggest that most seedlings recruit from the soil (see review in Garwood 1989).

Garwood (1989) suggests that some of the above studies might exaggerate the contribution of the seeds in the seed bank (soil) versus those in the seed rain (dispersed into the gap after formed) due to technical problems (e.g., diminished seedling survival in sterilized soil). But most importantly, their data for individual species show that the proportion of soil to rain seed contribution ranged from less than 50 to more than 90% among species, suggesting much variation in soil seed survivorship among tropical trees.

To quantitatively determine the contribution of dispersal in time and space, the forest as well as the seeds' dynamics have to be considered. A model that incorporates these two dynamics estimates that more than 90% of *Cecropia obtusifolia*'s seedlings that recruit into gaps at Los Tuxtlas come from either seeds that were recently dispersed to the site (i.e., the year prior to gap formation) or seeds dispersed into the gap shortly after the gap forms (Alvarez-Buylla and Garcia-Barrios 1990). That *C. obtusifolia* regenerates mainly from seeds less than one year-old due to high predation and pathogen attack rates in the soil is further supported by the empirical results of this paper (Tables 1 and 2; Figs. 3 and 4), and by the fact that soil of fields far away from recent seed sources lack *C. obtusifolia* and other pioneers (Janzen 1983; Guevara 1986).

Assuming that gaps are available for colonization during one year, we estimate that around 50% of *C. obtusifolia*'s seedlings should come from dormant soil seeds, and 50% should originate from new seedfall to already opened gaps. This estimate is derived from the fact that the soil seed content is mainly explained by that year's seed rain because the turnover rate of the species seed bank is of around one year. The relative contribution of soil and rain seeds is probably affected, however, by factors operating in natural conditions that were not considered in this average estimate. For example, if gaps are available for colonization for less than a year after the treefall occurs (e.g., Murray 1988), the relatvie contribution of soil seeds would be greater than we estimated (e.g., Putz and Appanah 1987; Young et al. 1987; Lawton and Putz 1988). In fact, *C. obtusifolia*'s seedlings established early after gap formation have greater survivorships and growth rates than those established later (Alvarez-Buylla 1986). However, if buried seeds have lower chances of germinating than new seeds, or seedlings emerging from them have lower chances of maturing, the above calculations would be overestimating the relative contribution of soil seeds. In one gap, only seedlings from new seed rain of *C. obtusifolia* that were established on top of the trunk survived after one year; and many adults have remainders of rotting logs underneath (Alvarez-Buylla 1986).

Conclusions

Our study constitutes one of the first attempts to evaluate the relative importance of seed sources in the colonization of forest gaps (see also Horvitz and Schemske 1986; Murray 1988). In this study we have shown that seeds of *Cecropia obtusifolia* have short life-spans in the soil due to high seed predation and pathogen attack rates, and that its large seed crops and dispersal by various birds and mammals replenish the soil seed pool of all patch types at least up to 86 m from nearest source. Hence, the previously accepted statement that early pioneers persist for long periods as dormant seeds in the soil can not be generalized. Because pathogens and predators are probably important in mediating the effect of seed dispersal on plant fitness and population dynamics of other pioneers, future studies should directly evaluate their relative role in the species' soil seed dynamics.

The comprehensive approach to determining seed dynamics that we have presented here, including seed rain, soil seed densities, seed viabilities and seed removal in different components of the forest mosaic has been rarely achieved before. With our data we have attempted to quantify these parameters within different forest patch types, thereby enabling aerial estimations of seed dynamics within the entire forest unit. This approach should prove vital in the future in developing more of a landscape-level understanding of the role of seed production and dispersal in spatio-temporal aspects of plant distribution. Studies to obtain more accurate estimates of such parameters will be time-consuming and labor-intensive, because they should consider great forest extensions and many replicate sites (Garwood 1989). Factors other than patch type and distance to nearest seed source should also be considered (e.g., Schupp 1988 b).

If dispersal determines most of the abundance and composition of seed pools in gaps due to short-lived soil seeds of dominant pioneers such as *C. obtusifolia*, the process of tree-by-tree replacement in forests may be influenced by the spatial relationships of these species' mature trees and gaps. For example, if gaps open close to mature pioneer trees more frequently than expected by chance (e.g., Lawton and Putz 1988), pioneers should not require a long-term soil seed accumulation, or a long-distance dispersal to reach recently opened large gaps.

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