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DISPERSAL PATTERNS AND SEED BANK DYNAMICS OF PIONEER TREES IN MOIST TROPICAL FOREST

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Abstract. Seed dispersal patterns and seed persistence in the soil should strongly influence the distribution of pioneer tree recruits in gaps. Nonetheless, seed distribution patterns for pioneers are poorly known, and processes controlling the fate of seeds in the soil have been little explored. We examined patterns of seed rain, seed abundance in the soil, and seed mortality of two common pioneer trees, *Miconia argentea* (Melastomataceae) and *Cecropia insignis* (Moraceae), on Barro Colorado Island, Panama. For each species, we selected four isolated, reproductive trees within a 50-ha forest dynamics plot. Seed rain and soil seed bank samples were collected, respectively, in mesh traps and from soil cores sampled along transects radiating away from the tree crowns.

At below-crown sites, seed rain inputs far exceeded soil seed bank densities measured at the end of the fruiting season. For *Miconia,* the below-crown seed bank in the surface 3 cm of soil accounted for only 23% of seed rain, and for *Cecropia,* only 2%. However for *Miconia,* at distances >5 m from the crown seed bank densities exceeded the annual seed rain input. For both species log seed densities in the seed bank declined linearly with log distance from the crown and also decreased dramatically through the year. The annual loss rate of *Miconia* seeds was >90% below the crown and declined to 65% at 30 m from the crown. The annual loss rate for *Cecropia* was >90% at all distances. Seed losses in the seed bank could be largely attributed to mortality from pathogenic fungi. Fungicide treatment significantly increased seed survival in the soil for both species.

For these two gap-dependent pioneer species, rapid seed-bank turnover rates and logarithmic declines in soil seed density with distance from adults suggested that both the spatial distribution and timing of gap formation may have influenced their chances of successful gap colonization. Recruitment from distant seed sources, or from seeds surviving in the soil after the death of the parent tree, may be relatively rare for these species.

Key words: Cecropia insignis; *gap colonization;* Miconia argentea; *pathogenic fungi; Panama; pioneer; seed dispersal; seed predation; seed rain; soil seed bank.*

INTRODUCTION

Recruitment from transient or persistent soil seed banks has long been considered an important pathway for regeneration of tropical pioneer species (e.g., Symington 1933, Guevara Sada and Gómez-Pompa 1972, Cheke et al. 1979, Hall and Swaine 1980, Lawton and Putz 1988). Studies of tropical forest soil seed banks have found the seeds of pioneers to be abundant (Garwood 1989), burial experiments have shown that the seeds of many pioneer species have the potential for long-term viability in the soil (Uhl and Clark 1983, Perez-Nasser and Vázquez-Yanes 1986, Hopkins and Graham 1987, Murray 1988), and observations of seed germination from soil samples have shown that the soil seed bank is often dominated by species not fruiting locally at the time (Cheke et al. 1979, Hall and Swaine 1980). Nonetheless, temporal and spatial distributions of buried seeds are poorly known, and the underlying processes controlling the fates of seeds are poorly understood (Garwood 1989).

The relative importance of prolonged seed dormancy vs. long-distance seed dispersal for gap colonization remains unresolved because studies of seed dispersal have rarely been integrated with those of the soil seed bank in either temperate or tropical forests (but see Murray 1988, Alvarez-Buylla and Martínez-Ramos 1990, Herrera et al. 1994). Evidence for long-term seed persistence in the soil is not conclusive, because most studies have been carried out under semi-natural conditions using seeds buried in pots or nylon bags where seed predators and soil-borne pathogens may be excluded (Vázquez-Yanes and Smith 1982). Studies of seed persistence under completely natural conditions are rare, and the results are not in agreement. Most seeds of *Calathea ovandensis,* a gap-dependent herb, can persist for several years in the soil under natural conditions (Horvitz and Schemske 1994). In contrast, <8% of seeds of *Cecropia obtusifolia,* the only well-studied pioneer tree, persist for >1 yr (Alvarez-Buylla and Martínez-Ramos 1990).

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TABLE 1. Demographic and life history characteristics of the study species in a neotropical moist forest.

Characteristic	*Cecropia insignis*	*Miconia argentea*
Reproductive dbh† (cm)	20	11
Maximum dbh‡ (cm)	66	39
Density (inds./ha)‖	3.4	1.2
Seed size (mg)†	0.5	0.08
Seed per fruit†	1000–2000	1–80
Dispersal agent§	bat, bird, monkey	bird, monkey, coatimundi
Fruit type¶	achene, aggregated in catkins	berry
Fruiting period#	Feb–June	Mar–July

Note: dbh = diameter at breast height.
† J. Dalling, *unpublished data.*
‡ Largest individual recorded in the 1995 census of the 50-ha plot (R. Condit, S. Hubbell, and R. Foster, *unpublished data*).
‖ Density of reproductive-sized individuals averaged over the 50-ha plot in 1995 (R. Condit, S. Hubbell, and R. Foster, *unpublished data*).
§ Hladik and Hladik (1969), Brokaw (1987).
¶ Croat (1978).
# Foster (1982).

Evidence that seed dispersal characteristics directly influence recruitment patterns of pioneers is also not conclusive, because seed dispersal curves have been measured for only a few pioneer species. Fleming and Heithaus (1981) and Alvarez-Buylla and Martínez-Ramos (1990) found that seed dispersal curves for *Cecropia peltata* and *C. obtusifolia,* respectively, were strongly leptokurtic, with seed densities declining to low levels at distances >30 m from source trees. Similarly, Laman (1996) found strongly leptokurtic seed dispersal curves for two *Ficus* species in Borneo, although up to 45% of the seed crop of the largest fig trees were transported >60 m from the crown. In contrast, Murray (1988) argued that seed shadows for three pioneer shrubs in Costa Rica were not leptokurtic. He inferred seed dispersal distances by radio-tracking their avian dispersal agents and found that only 20–36% of seeds were deposited within 30 m of the parent plant, and that some seeds were deposited >300 m away.

A more detailed understanding of dispersal patterns and seed persistence for tropical pioneer trees should provide important information on the mechanisms that determine the spatial and genetic structure of their populations (Hamrick et al. 1993). If seeds of pioneers are typically dispersed short distances, then their distribution among gaps should be spatially clumped, individual pioneer species should occupy relatively few gaps, and historical local pioneer community composition should be more important than establishment and growth requirements in determining their probability of occupying a gap. On the other hand, if the seeds of pioneers are widely dispersed, then individual species should be found distributed widely across many gaps, and the probability of adult occupancy might instead be determined more by whether appropriate microsites are present that provide species-specific requirements for establishment and growth (Denslow 1980, 1987, Brokaw 1987, Brandani et al. 1988).

In this study, we document the spatial and temporal patterns of seed abundance of two common pioneer tree species in seasonally moist tropical forest in Panama, and examine the processes determining these patterns. In particular we asked: (1) What is the distribution of seed rain, and what proportion of the seed rain becomes incorporated in the soil seed bank?, (2) Do secondary seed dispersal agents and seed predators rearrange seed shadows, and can they account for losses occurring between seed dispersal and seed incorporation into the soil?, (3) Do seed shadows in the soil seed bank ("footprints" sensu Saulei and Swaine 1988) persist seasonally and after the death of the parent tree?, and (4) What is the role of fungi as a seed mortality agent within the soil seed bank?

STUDY AREA AND SPECIES

The study was carried out in seasonally moist tropical forest on Barro Colorado Island (BCI), Panama. Rainfall on BCI averages 2700 mm/yr, with a pronounced dry season from January through April (Rand and Rand 1982). The flora is described by Croat (1978) and by Foster and Brokaw (1982); in the present paper, species nomenclature follows Croat (1978). Investigations of seed distribution patterns were carried out within the Forest Dynamics Project 50-ha plot located on the central plateau of BCI; the plot was established in 1982 and is described in detail by Hubbell and Foster (1983).

The two species chosen for this study (Table 1) are the most common pioneer tree species on BCI, and also the most abundant tree species within the soil seed bank (Putz 1983, Dalling et al. 1995, 1997). *Cecropia insignis* Liebm. (Moraceae) is a dioecious tree ranging from Nicaragua to Colombia and occurs in seasonally moist lowland, wet lowland, and pre-montane wet rain forests (Holdridge et al. 1971, Croat 1978). *Miconia argentea* (Sw.) DC. (Melastomataceae) ranges from southern Mexico to Panama and occurs in dry forests, pre-montane wet forests, and tropical wet forests

(Holdridge et al. 1971, Croat 1978). During the dry season and early wet season, both species produce fruit containing numerous very small zoochorously dispersed seeds. In *Miconia,* seeds are borne in fleshy berries, whereas *Cecropia* produces single-seeded achenes that are aggregated into catkins (hereafter referred to as "fruits").

METHODS

Selection of focal trees

In order to examine the shape of seed shadows produced by single pioneer trees, we used data from the 1982, 1985, and 1990 censuses of the 50-ha plot to select four reproductive-sized *Miconia argentea* trees, and four female reproductive *Cecropia insignis* trees. Each tree was ≥40 m away from any site occupied by a reproductive-sized conspecific during the existence of the plot. To examine the persistence of seeds in the soil, we also selected sites within the plot that had contained reproductive-sized trees prior to the 1990 plot census. For *Miconia,* three replicate sites were found which had contained living trees in 1985 that were dead in 1990, and three sites that contained living trees in 1982 that were dead in 1985. All sites were at least 30 m from the nearest living reproductive-sized *Miconia.* Treefall gap sites were excluded. For *Cecropia,* no detailed attempt was made to survey sites occupied by dead trees, because data on the sex of these trees from the 1982 and 1985 plot censuses were incomplete.

Measurements of seed rain

In 1993, four 0.25-m^2 traps lined with 0.2-mm nylon mesh were placed at random below the crowns of the four focal *Miconia* trees, and three of the focal *Cecropia* trees. Each week during the period of fruit production and dispersal (1 March to 30 June), all fruits and seeds were collected from the traps. The number of seeds within fruits was estimated based on fruit size. For *Miconia,* the seed content of fruits was weakly related to fruit diameter (regression, $r^2 = 0.23$, $F = 6.70$, df = 1, 23, $P = 0.016$), but there was no relationship between the proportion of seeds that were viable and fruit size (regression, $r^2 = 0.004$, $F = 0.008$, df = 1, 23, NS). Therefore to estimate seed number within fruits, individual fruits were measured with calipers and separated into three size categories with different mean seed numbers (<2 mm, mean = 21 viable seeds per fruit; 2–3 mm, mean = 31 viable seeds per fruit; >3 mm, mean = 49 viable seeds per fruit). Fruits >3 mm were typically blue or black and are hereafter considered "mature". After removal of the intact fruits, the remaining material collected from *Miconia* traps was dried in an oven at 60°C for 48 h, thoroughly homogenized, and a subsample taken from which individual seeds were counted under a dissecting microscope. A similar procedure was used for *Cecropia*: the number of seeds embedded in whole or partial "fruits" (catkins) was estimated based on weighed subsamples of fruits, and the number of individually dispersed seeds (achenes) was estimated from subsamples examined under a microscope. For both species, seed samples were placed in petri dishes in a growth chamber (Percival, Model I-35; 12 h dark at 25°C, 12 h light at 30°C, 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$, red/far red ratio = 1.65), and percentage germination was recorded.

In 1994, we collected additional seed rain samples from around the same four *Miconia* trees throughout the fruiting season from March until May. Similar mesh-lined traps were used, but the four traps were positioned along one randomly located transect at sites below the crown, and at 5 m, 10 m, and 20 m from the crown edge of each tree. Limited resources prohibited our establishing a similar sampling regime for *Cecropia.* Because of low densities of *Miconia* seeds in more distant traps, it was not practical to count individual seeds by hand. Instead, all the samples were initially sorted to remove large litter fragments and then rinsed through a filter paper using a 0.5% sodium hypochlorite solution to surface-sterilize seeds and litter fragments. The filter papers were subsequently placed in petri dishes in a growth chamber (conditions as in previous paragraph), and emergent seedlings counted weekly over the following 8-wk period. In June 1994, 2 wk after the end of the fruiting season, three 0–3 cm depth, 250-cm^3 soil samples were collected at a distance of 50 cm from three of the four sides of each of the mesh traps. Emergence of *Miconia* seedlings from the soil samples was measured according to the methods below (see *Methods: Spatial and temporal variation in soil seed bank density*).

Predation and secondary dispersal of Miconia

Ants are potentially important dispersers and consumers of small seeds on the forest floor. To examine how patterns of seed rain are altered by secondary dispersal and predation on the soil surface, we measured fruit and seed removal rates at four equidistant points below the crown of each of the *Miconia* focal trees, and at four sites 30 m away from the crown. At each sample point, a small amount of leaf litter was removed, and three microscope slides were placed on the soil surface. Microscope slides were sheltered from rain under a 0.25-m^2 plastic roof raised 30 cm above the ground. Experiments were carried out once, and on separate days, for each focal tree, during the middle of the *Miconia* fruiting period in May 1994. At 1000 each day, the three slides were covered with 500 pulp-free *Miconia* seeds, 10 mature *Miconia* fruits, and 10 immature *Miconia* fruits, respectively. Censuses of fruit removal were made after 30 min, 90 min, and hourly over the following 4 h. During this period, direct observations of fruit and seed removal by ants were made. Where possible, nest sites of foraging ants were marked. After 24 h, a final count was made of the fruit

remaining at each sample point, and the remaining seeds were collected for counting in the laboratory.

Spatial and temporal variation in soil seed bank density

Spatial distribution patterns of seeds in the soil and their changes over time were examined by repeated sampling of the soil seed bank from 24 cm deep soil cores taken beneath the crown of the focal trees, and from 3 cm deep cores collected on transects radiating away from the crowns. At below-crown sites cores were made using a 6 cm deep, 10.3 cm diameter open-ended soil corer flanked by an aluminum collar that prevented soil from falling into the core hole. The core was subdivided into 3 cm deep subsamples that were measured volumetrically in the field. Successive samples were removed from the core hole to give six soil samples from 0–3, 3–6, 6–9, 9–12, 15–18, and 21–24 cm soil depth. Samples from 12–15 and 18–21 cm were discarded to save greenhouse space. Three cores were collected at random locations under each of the four *Miconia* and *Cecropia* trees; samples were collected in March 1993 (*Miconia* only), and again in June, September, and December 1993 (both species). Three additional cores (0–24 cm, sampled as above) were also collected from random locations within the 25-m^2 subplots occupied by dead trees, and single cores collected at three control sites unoccupied by *Miconia* and *Cecropia* at least since the establishment of the plot in 1982.

The projection of the center point of the crown of each living focal tree was used as the point of origin for four transects laid out along a bearing chosen at random within each of the four cardinal quadrants. On each transect, two soil samples were taken from below the crown, at one-third and two-thirds the distance between the crown center and crown edge, and four additional samples were taken at 5 m, 10 m, 20 m, and 30 m away, respectively, from the crown edge. Additional soil samples were taken from sites at least 50 m from the nearest reproductive sized *Miconia* or *Cecropia* recorded in the 1990 plot census, and at least 50 m from the plot edge (to exclude potential effects of trees just beyond the plot boundary). Each sample was taken using a 10.3-cm diameter, 3 cm deep soil corer to yield 250 cm^3 of soil. The initial set of samples was collected in May 1993; repeat samples were collected at the same sites during August 1993, November 1993, and February 1994.

All samples were transported in black polyethylene bags, stored in an air-conditioned laboratory at 25°C, and processed within 48 h of collection. Soil samples were spread evenly to a depth of 0.5 cm in seedling trays containing a 1 cm deep layer of moist, seed-free sand, and the seeds allowed to germinate over a 6-wk period. Since both the rate and the amount of seedling emergence are highly sensitive to soil depth, the optimum depth to spread soil, and the time period over which to record seedling emergence were determined experimentally in advance (Dalling et al. 1995). As a control against contamination, four additional trays containing autoclave-sterilized soil (116°C for 1 h) were included with each set of soil samples. Seedling trays were placed at random on benches covered by clear plastic within two screened growing houses in the laboratory clearing on BCI, under conditions ranging from 15% to 25% full sun. Trays were hand-watered daily, and seedling emergence from soil flats was recorded at weekly intervals.

Causes of seed mortality in the soil: the role of fruit maturity and fungi

Initial observations of below-crown seed rain of *Miconia* indicated that it consists of vertebrate-dispersed individual seeds, fallen mature fruit, and large numbers of fallen immature fruit. Seeds of immature fruits have a markedly less pigmented testa than those of mature fruits, suggesting that the testa of seeds from immature fruits may be less durable. Since seeds derived from immature fruit are largely confined to the area beneath the crown of their mother, differences in seed mortality in below-crown sites and sites away from the crown might result from differential mortality among these seed types.

Consequently, in May 1994 we investigated the effect of fruit maturity on the survival of *Miconia* seeds buried in nylon bags in the soil. We defined mature fruits as those that were >3 mm diameter, soft, and dark blue-purple, and immature fruits as <2 mm diameter, hard, and green. Seeds were washed out of mature and immature fruits in a darkroom under low intensity, far-red enriched light, counted into lots of 50 seeds, and incorporated into 0.2 mm nylon mesh bags containing 3 cm^3 of autoclave-sterilized soil. In May 1994, six bags of each fruit type were buried level with the soil surface in a grid at each of three understory sites at least 30 m from the nearest reproductive *Miconia* tree. Initial seed viability was determined by transferring the contents of three additional nylon bags of each fruit type into petri dishes, and germinating seeds in a growth chamber (conditions as in *Methods: Measurements of seed rain,* above). Half of the buried bags were recovered after 3 mo, and the remaining bags after 6 mo. Seeds were germinated as for other seed bank samples.

In June 1994 we investigated the role of soil fungi as seed mortality agents for both *Miconia* and *Cecropia* by applying fungicide to seeds enclosed within nylon mesh bags and buried in the soil. Mature fruits were collected from the crowns of three *Miconia* and also from three *Cecropia* trees, seeds were washed and mixed in a darkroom, and sorted into lots of 50 seeds (*Miconia*) and 30 seeds (*Cecropia*). Fungicide-treated seed lots were thoroughly coated with powdered Captan fungicide (N-trichloromethylthio-4-cyclahexene-1,2-dicarboximide), whereas control seeds were un-

treated. The seed lots were incorporated into nylon bags as above, and the bags buried level with the soil surface at three site types in the 50-ha plot: (1) Four bags of untreated seeds, and four bags of Captan-treated seeds were buried at random locations beneath the crown of each of the four focal conspecific trees. (2) Four bags of untreated seeds were buried beneath the crown of each of the four focal heterospecific trees. (3) Four bags of untreated seeds, and four bags of Captan-treated seeds, were buried 30 m from the edge of the crown of each of the four conspecific trees (one bag of each treatment in each of the four cardinal quadrants).

At monthly intervals during the wet season between July and November, the Captan-treated bags were retreated with fungicide by immersing them in 10 g/L Captan solution. The bags were allowed to dry for a few minutes, and then reburied. Untreated bags were removed and replaced, but were not soaked since the soil was already at or near field capacity. In December 1994 (1 mo after the final Captan retreatment), bags were removed from the plot, and the seeds germinated in petri dishes in a growth chamber (conditions as in *Methods: Measurements of seed rain,* above).

Data analysis

Seed densities were normalized by log transformation prior to analyses. Vertical and horizontal distribution patterns of seeds in the soil at each census were examined using multiple linear regressions. For seeds dispersed by animals and wind (as opposed to ballistic dispersal), the shape of the seed shadow generally conforms to a semi-log function (Willson 1993); however in some cases curve fits may be better with other functions, such as a negative power function (Okubo and Levin 1989), or a double log function (Willson 1993, Laman 1996). We fitted both semi-log and double-log transformed data to linear regression models. In almost all cases, double-log transformations represented by the equation $\ln y = b(\ln x) + a$ (where y is seed density, and x is soil depth or distance from the focal tree) yielded the best fit, and only these regression equations are reported. Below-crown soil samples were coded as 0 m distance.

Analyses of variance were performed using the MGLH procedures in SYSTAT (Wilkinson et al. 1992). Effects of census interval, focal tree, and distance or soil depth on seed density were analyzed by mixed-model, repeated-measures ANOVA. Focal tree was treated as a random effect, and distance or soil depth as fixed effects. The Greenhouse-Geisser adjustment of F tests of between-subjects factors with multiple degrees of freedom in the numerator was used to avoid possible violations of the equal covariance (circularity) assumption. This tends to be a conservative adjustment to biases in the covariance matrix that inflate F statistics (Maxwell and Delaney 1990).

Effects of time since tree death, focal tree, and soil depth on seed density were analyzed as a nested mixed-model ANOVA. Tree was treated as a random effect and was nested within the fixed effect of time since tree death. Changes in the distribution of seeds with soil depth for different times since tree death were examined by analysis of covariance of the homogeneity of slopes of regressions of log-transformed seed density on soil depth (Zar 1984). Effects of fruit ripeness and duration of burial on seedling emergence from *Miconia* seeds enclosed in mesh bags were analyzed by repeated-measures ANOVA, with fruit ripeness and burial site coded as between-subjects fixed factors, and repeated measures occurring in the dimension of time. Effects of fungicide treatment, tree, and site type (below conspecific, below heterospecific, or 30 m away from crown) on seed survival in nylon bags were analyzed using mixed-model ANOVA. Treatment and site type were treated as fixed factors, and tree as a random factor.

Annual seed loss rates (l) were calculated using the equation $l = 1 - (N_1/N_0)^{1/t}$, where N_0 and N_1 are seed counts at the beginning and the end of the measurement period t (Sheil et al. 1995). To compare loss rates at different distances from the focal tree, the measurement period of May 1993–February 1994 was used for *Miconia* (i.e., $t = 0.75$ yr) and August 1993 to February 1994 for *Cecropia* ($t = 0.5$ yr). For soil depth cores, the period June 1993 to December 1993 ($t = 0.5$ yr) was used for both species. The inter-census period used to estimate annual loss rates was dependent on the length of time between fruiting events; *Miconia* trees fruited until just before the census in May 1993, whereas *Cecropia* trees continued to fruit until June 1993. Since seed densities increased at some sites distant from focal trees, or at deep soil layers, data were pooled from the four transects at each tree, and from the three depth cores sampled below each tree crown. Percentage loss values were arcsine transformed, and analyzed by regression and one-way ANOVA. As calculated here, annual loss (l) is the reciprocal of the "seed bank turnover rate" of Alvarez-Buylla and Martínez-Ramos (1990).

Comparisons of removal rates among fruit types and individual seeds of *Miconia,* and between sites, were made using the Mantel-Haenszel chi-square test (Tables procedure, SYSTAT, Wilkinson et al. 1992). This statistic tests for the association between two binary variables (fruit type and seed removal) while controlling for a stratification variable (focal tree).

Results

Seed rain inputs and secondary dispersal

For both *Miconia* and *Cecropia,* subsamples of seed rain collected in 1993 and germinated in growth chambers had >90% viability. Mean below-crown seed rain inputs for *Miconia* were 40 100 seeds·m^{-2}·yr^{-1}, based on the census carried out in 1993 (Table 2). The majority of seeds captured were within fallen immature

TABLE 2. Seed density in the below-crown seed rain and in the soil seed bank immediately following the fruiting season (means ± 1 SE), and percentage reduction in seed density from the total seed rain to the seed bank, in a study of seed dynamics in a moist tropical forest.

Species	Source†	Seed density (no./m²)		
		Seed rain	Seed bank	% reduction
Miconia	mature fruit	5800 ± 3400		
	immature fruit	29 200 ± 13 300		
	individual seeds	5100 ± 2500		
	total seeds	40 100 ± 19 700	9100 ± 2900	77
Cecropia	catkins	41 200 ± 17 700		
	individual seeds	24 800 ± 2900		
	total seeds	66 000 ± 20 200	1600 ± 500	98

† Condition in which seeds were dispersed.

fruits (accounting for 73% of the total seed rain), whereas much smaller percentages were contained in ripe fruit (14%) and individually dispersed seeds (13%). Comparison of the total below-crown seed rain with the number of germinable seeds in the surface soil (0–3 cm) immediately after the fruiting season in May 1993 indicated that only 23% of the seed rain survived through the fruiting season to become incorporated into the surface soil layer of the seed bank (Table 2). Mean below-crown seed rain densities for *Cecropia* were 66 000 seeds·m^{-2}·yr^{-1} (Table 2). Like *Miconia,* the majority of the below-crown seed rain inputs were also from seeds dispersed within catkins (62%). Only a very small fraction (2%) of the below-crown seed rain of *Cecropia* was incorporated into the surface soil seed bank (Table 2).

In 1994, comparison of the total seed rain and the initial seed bank densities following the fruiting season for *Miconia* showed that seed loss rates were strongly dependent on distance from the focal tree crown (Fig. 1). While the input of seed rain exceeded that incorporated into the seed bank by 950% in below-crown sites in 1994, seed rain only accounted for 12% of seeds incorporated into the seed bank at 20 m from the crown.

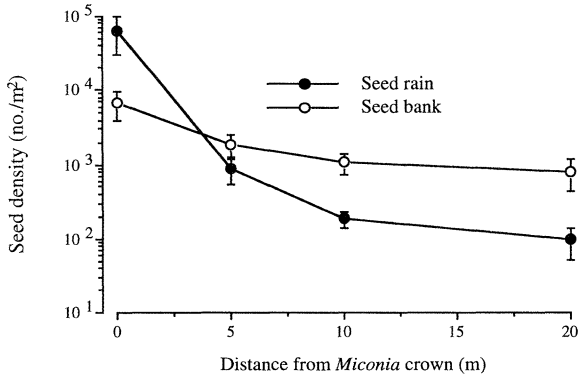

FIG. 1. Seed rain and soil seed density (mean ± 1 SE) measured at four *Miconia* trees in 1994 (n = 1 transect per tree). Seed rain data were gathered during March through May 1994; seed bank values are from June 1994, for 0–3 cm soil depth.

Since the slope of the regression of log seed rain density vs. distance from focal tree was steeper than that of the log seed bank density vs. log distance (Student's t = 25.6, df = 28, $P < 0.001$), proportionally fewer seeds were incorporated into the seed bank close to the focal tree than farther away.

There were clear differences in the fates of mature fruits, immature fruits, and pulp-free individual seeds. Very few immature fruits were removed over the 24-h collection period, although significantly more fruits were removed at 30 m from the crown (16%), than below the crown (2%) (χ^2 = 20.5, df = 1, $P < 0.001$) of focal trees. In contrast, 87% of mature fruits were removed from below the crown after 24 h and 91% at 30 m (χ^2 = 1.8, df = 1, NS). The removal rate of individual seeds was intermediate between mature fruits and immature fruits, and was the same below the crown (56%), and at 30 m from the crown (55%) (χ^2 = 3.5, df = 1, NS)

One ant species (*Ectatomma ruidum*) accounted for all the observed removal of *Miconia* fruit during the 5.5-h period of observation. Since *Ectatomma* ants carried fruits above the surface of the litter, they could be relatively easily followed from the sample points to their nest entrances. The foraging distance for *Ectatomma* averaged only 1.67 ± 0.24 m ([mean ± 1 SE], range = 0.67–5.17 m, n = 24 observations). Foraging distances >3 m were only observed on three occasions and only occurred when fruits were transferred between ants. Very little removal of individual *Miconia* seeds occurred during the observation period, but >50% of seeds were removed over 24 h.

Spatial and temporal variation in soil seed bank density

For both species log soil seed densities declined linearly and significantly with log soil depth beneath the focal tree crown (Table 3). For *Miconia,* seed densities declined from 6000 ± 3000 seeds/m² (mean ± 1 SD) in the surface 0–3 cm to 1400 ± 1200 seeds/m² at 21 cm soil depth in June 1993, and from 500 ± 130 seeds/m² at the surface to 300 ± 170 seeds/m² at 21 cm by December 1993 (Fig. 2a). Following the fruiting season

TABLE 3. Repeated-measures ANOVA for effect of tree, soil depth, and census period on soil seed density, in a study of seed dynamics in a Panamanian moist forest.

Source of variation	*Miconia*			*Cecropia*		
	df	MS	*F*	df	MS	*F*
Between subjects						
Tree	3	0.52	27.8***	3	0.23	11.5***
Depth	5	0.83	39.5***	5	0.91	22.8***
Tree × Depth	15	0.02	1.1	15	0.04	2.4*
Error	48	0.02		48	0.02	
Within subject						
Census time	3	5.10	79.1***	2	0.10	1.6
Census time × Tree	9	0.16	2.4*	6	0.18	2.7*
Census time × Depth	15	0.26	4.1***	10	0.18	2.7**
Census time × Tree × Depth	45	0.05	0.7	30	0.06	0.9
Error	141	0.06		96	0.07	

Notes: Repeated measures occurred on census time (3-mo intervals). Analyses were performed on log([value] + 1)-transformed data. *Miconia* data have one missing value. Means are presented in Fig. 2.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

in June 1993, soil depth accounted for 60% of variation in seed density, declining to only 6% by December 1993. The virtual disappearance of the effect of soil depth on seed density is partly accounted for by the very high seed loss rates beneath the crown, such that few seeds were recorded in soil samples by December. For *Cecropia,* seed densities varied from 2000 ± 400) seeds/m^2 in the surface 0–3 cm of soil to 200 ± 100 seeds/m^2 at 21–cm depth in June 1993, and from 600 ± 400 seeds/m^2 at the surface to 75 ± 60 seeds/m^2 at 21 cm in December 1993 (Fig. 2b). Regressions of seed density on soil depth showed a pattern similar to that of *Miconia.* Following the fruiting season in June 1993, soil depth accounted for 54% of variation in seed density, declining to 22% by December 1993. In both species, there was a significant interaction between census time and soil depth (Table 3), so that relative rates of decline in seed densities through time were lower at greater soil depths.

For both *Miconia* and *Cecropia,* log seed densities also declined linearly and significantly with log distance from the focal tree crown (Table 4). For *Miconia,* seed densities decreased from 9100 ± 5800 seeds/m^2 below the crown and 550 ± 300 seeds/m^2 at 30 m from the crown in May 1993, to 950 ± 470 seeds/m^2 below the crown and 250 ± 300 seeds/m^2 at 30 m in February 1994 (mean ± 1 SD) (Fig. 3a). Immediately after the end of the fruiting season, in May 1993, distance from crown accounted for up to 57% of variation in seed density, but only for 36% of density variation by February 1994. The repeated-measures ANOVA showed that while seed densities declined significantly at all distances with census time (Table 4), the decrease was proportionally greater at sites below the focal tree crown than at sites farther away (census time × distance interaction, Table 4).

Seed distribution patterns and losses through the year for *Cecropia* were somewhat different from *Miconia* (Fig. 3b). Seed densities initially increased between May 1993 and August 1993, as trees continued to fruit, then declined from 1600 ± 1000 seeds/m^2 below the crown and 300 ± 100 seeds/m^2 at 30 m away from the crown in August 1993, to 400 ± 100 seeds/m^2 below the crown and 200 ± 180 seeds/m^2 at 30 m in February 1994 (mean ± 1 SD). Distance from crown accounted for only 34% of variance in seed density in August and only 10% by February 1994. In contrast to *Miconia,* there did not appear to be a distance-dependent component to seed loss in *Cecropia.* While seed densities declined significantly with census time, the census time × distance interaction was not significant (Table 4).

For *Miconia,* mean annual seed losses (Fig. 4a) remained consistently high (>90%) up to 18 cm soil depth, but were significantly lower at 21–24 cm (one-way ANOVA on tree means, $F = 6.3$, df = 5, 18, $P < 0.01$; a posteriori Tukey hsd multiple comparison $P < 0.05$). For *Cecropia,* mean annual seed losses varied greatly among focal trees, and although there was a trend of decreasing seed loss with depth, it was not significant (Fig. 4a; one-way ANOVA on tree means: $F = 1.4$, df = 5, 18, NS).

The presence of a distance effect on seed loss in *Miconia* is also apparent from the calculated annual loss rate (l). For both species the below-crown loss rate was >90% for both *Miconia* and *Cecropia* (Fig. 4b). However, whereas the loss rate for *Miconia* declined with distance from the crown (regression, $r^2 = 0.97$, $F = 82.0$, df = 1, 3, $P < 0.01$), the loss rate for *Cecropia* was not related to distance (regression, $r^2 = 0.69$, $F = 6.7$, df = 1, 3, NS).

Persistence of Miconia *seeds following tree death*

Total *Miconia* seed densities beneath the crown declined exponentially with time since tree death ($\ln y = -0.23x + 4.65$, $r^2 = 0.79$, df = 1, 8, $P < 0.001$, Fig. 5). This decline was evident throughout the soil depth

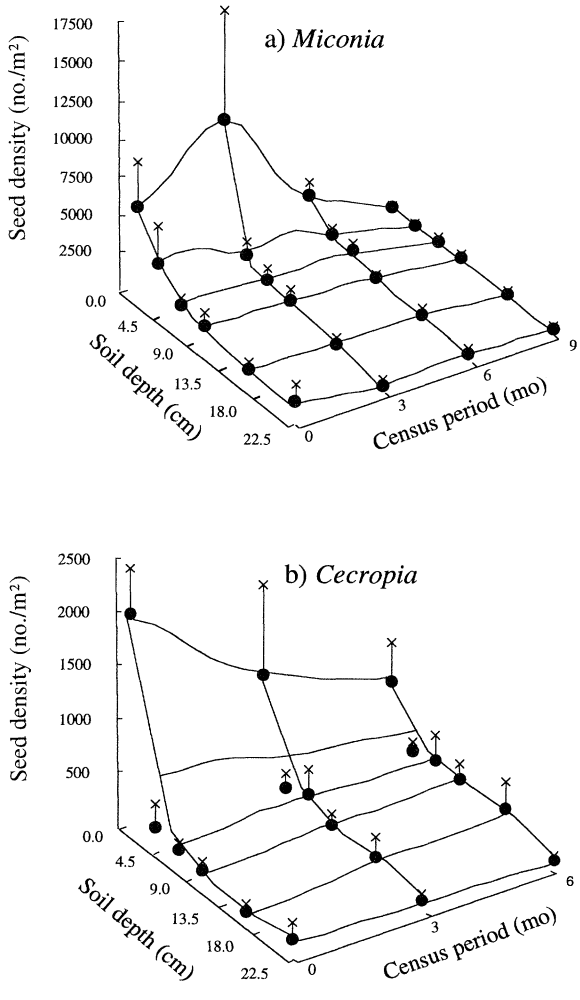

FIG. 2. Seed density (●; mean and 1 SD) of (a) *Miconia*, and (b) *Cecropia* as a function of soil depth (below-crown sites) and census interval (n = 4 trees per species). Census times are March (t = 0), June, September, and December 1993. The surface is fitted using distance-weighted least squares in SYSTAT (McLain 1974, Wilkinson et al. 1992).

profile. In the surface 0–3 cm of soil, seed densities declined from 5700 ± 2900 seeds/m² (mean ± 1 SD) below living trees, to 900 ± 440 seeds/m² at sites occupied by *Miconia* trees that died between 1985 and 1990 (average 5.5 yr since tree death), and to 550 ± 40 seeds/m² in sites occupied by *Miconia* trees that died between 1982 and 1985 (average 9.5 yr since tree death). Declines were similar at 21–24 cm soil depth, ranging from 640 ± 550 seeds/m² below living trees, to 170 ± 80 seeds/m² at sites 9.5 yr since tree death. At control sites unoccupied by *Miconia* trees since at least 1982, seed densities varied from 270 ± 290 seeds/m² at 0–3 cm soil depth, to 40 ± 60 seeds/m² at 21–24 cm.

Both the time since tree death and the identity of the focal tree individual significantly affected seed density (Table 5). Seed densities from around living *Miconia* trees were significantly higher than those around trees that had died between 1985 and 1990 ("Dead 1990"), and were somewhat higher (but not significantly so) at "Dead 1990" sites than at sites where trees died between 1982 and 1985 ("Dead 1985"). Seed densities at "Dead 1985" sites were not significantly greater than at control sites unoccupied by *Miconia* since 1982 (Table 5). In contrast to changing seasonal patterns in seed density with depth observed for living *Miconia* trees (Fig. 2), the slopes of seed density vs. depth were not significantly different among sites occupied by living and dead *Miconia* trees in March 1993 (ANCOVA, F = 1.30, df = 3, 9, NS).

Effects of fruit maturity and soil fungi on seed mortality

There was no effect of fruit maturity, site, or duration of burial on seedling emergence for *Miconia* seeds buried for 3 or 6 mo in nylon mesh bags (repeated-measures ANOVA, all tests nonsignificant). After 6 mo of burial, 75% of seeds from immature fruits, and 68% of seeds from mature fruits, produced emergent seedlings.

In the fungicide experiment there was a significant effect of burial location (below conspecific, below heterospecific, or 30 m away from either species) on the germinability of untreated seeds of both *Miconia* and *Cecropia* (two-way ANOVA, F = 5.2, df = 2, 86, $P < 0.01$), with the two species responding similarly to burial location. Post hoc tests of differences among locations revealed that germination was higher at sites 30 m away from conspecific crowns than below conspecific crowns (Tukey hsd, $P < 0.01$), whereas differences between below-conspecific and below-heterospecific crowns were not significant (Tukey hsd, $P > 0.05$) (Fig. 6).

The application of fungicide had significant effects on seed germinability (Fig. 6 and Table 6). The fungicide treatment reduced mortality below the crown by 47% for *Miconia* and by 39% for *Cecropia*. At sites 30 m from the nearest conspecific crown, fungicide still reduced seed mortality, but overall effects were smaller (27% reduction for *Miconia* and 33% for *Cecropia*). For *Miconia* there was a significant effect of location (below crown vs. away from crown) as well as fungicide treatment, whereas for *Cecropia* there was a strong effect of treatment, but not of location (Table 6).

DISCUSSION

Spatial and temporal dynamics of pioneer seeds

Analysis of the seed bank dynamics of *Miconia argentea* and *Cecropia insignis* indicated that there were two important stages at which seed losses could occur for pioneer species. Firstly, a very large proportion of seeds dispersed below the crown either were removed or died immediately after dispersal. Secondly, there is

TABLE 4. Repeated-measures ANOVA for effect of tree, distance from crown, and census time on soil seed density, in a study of seed dynamics in a neotropical moist forest.

Source of variation	*Miconia*			*Cecropia*	
	df	MS	*F*	MS	*F*
Between subjects					
Tree	3	0.17	5.7**	0.15	3.8*
Distance	4	2.12	30.3***	0.73	36.5***
Tree × Distance	12	0.07	2.0*	0.02	0.5
Error	76	0.03		0.04	
Within subject					
Census time	3	7.99	136.0***	0.99	14.1***
Census time × Distance	12	0.33	5.6***	0.11	1.5
Census time × Tree	9	0.14	2.5*	0.07	0.9
Census time × Distance × Tree	36	0.04	0.7	0.06	0.9
Error	228	0.05		0.07	

Notes: Repeated measures occurred on census time (3-mo intervals). Analyses were performed on log([value] + 1)-transformed data. Means are presented in Fig. 3.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

a rapid decline in seed density within the soil seed bank through the year.

The immediate postdispersal seed banks represented only 23% (*Miconia*) and 2% (*Cecropia*) of the below-crown seed rain. For *Miconia,* most postdispersal seed losses may have resulted from the activities of ants foraging in the litter layer. Almost all mature *Miconia* fruits experimentally placed at below-crown sites were removed by *Ectatomma* ants within 24 h. Although these ants rarely traveled >2 m before entering the nest, *Ectatomma* may have contributed substantially to the vertical dispersal of seeds as nest sites were at >30 cm depth and waste material did not return to the soil surface (J. Dalling, *personal observation*). In contrast to mature fruit, individual seeds were removed only by small ants that typically nest in the leaf litter (e.g., *Pheidole* spp., *Solenopsis* spp.). These ants eventually removed >50% of experimentally placed seeds. Given the high nest density of litter ants on BCI (Levings and Franks 1982), these ants were also unlikely to carry seeds long distances, but they may have been important in moving seeds to favorable microsites if some seeds escaped predation (cf. Levey and Byrne 1993). Fallen immature fruits were unattractive to ants and only 2% were removed from beneath the crown over a 24-h period. However, seeds from immature fruits (29 200 seeds/m^2) probably made an important contribution to the seed bank, since there were insufficient individual seeds (5100 seeds/m^2) to account for the below-crown seed bank density at the soil surface immediately after the fruiting season (9100 seeds/m^2), and most fallen mature fruits would have been deeply buried.

Seeds in the soil showed rapid declines in density over time. In both species, secondary losses of seeds from within the surface 3 cm of the soil seed bank were >90%/yr beneath the crown. These values are similar to loss rates for the only other well-studied tropical pioneer, *Cecropia obtusifolia* (93–98%/yr; Alvarez-Buylla and Martínez-Ramos 1990). Annual loss rates for *Cecropia insignis* on BCI were not dependent on distance. Similarly, annual seed loss rates for *Cecropia obtusifolia* in Mexico were not dependent on distance to the nearest fruiting adult, and they did not differ between forest patch types of differing age and structure (Alvarez-Buylla and Martínez-Ramos 1990). In contrast, annual loss rates for *Miconia* were dependent on distance, and thus also dependent on density because of the correlation between seed density and distance from the parent tree. Distance- or density-dependent seed predation or seedling mortality has been frequently reported for nonpioneer trees with larger seeds (e.g., Wilson and Janzen 1972, Augspurger 1983, Gilbert et al. 1994) and may have a role in the maintenance of diversity in tropical forests (Janzen 1970, Connell 1971). This is the first report of density-dependent seed losses within the seed bank of a tropical pioneer.

The overall pattern of seed rain input and losses from the soil seed bank for *Miconia* (Fig. 7) showed that many seeds were deeply buried beneath the crown and that seeds also accumulated in the soil at sites >10 m from the crown despite very low measured seed rain inputs. This seed fate diagram is incomplete because we did not sample the deeply buried seed pool beyond the crown; seed bank dynamics in this pool may be distinct from below-crown sites because intact mature and immature fruits were not dispersed to these sites, and because the relative contribution of seeds from other dispersal agents may be different. At below-crown sites, it seems unlikely that deeply buried seed stocks could have arisen from a slow process of seed percolation through the soil, given the high rates of seed mortality at the soil surface. Instead we suggest that seeds became deeply buried because of soil cracking in the final months of the dry season (Smela 1987; J. Dalling and R. Murillo, *unpublished data*), or were moved through the soil by a variety of biotic agents such as earthworms (Grant 1983), dung beetles (Estrada and Coates-Estrada 1991), and ants (Roberts and

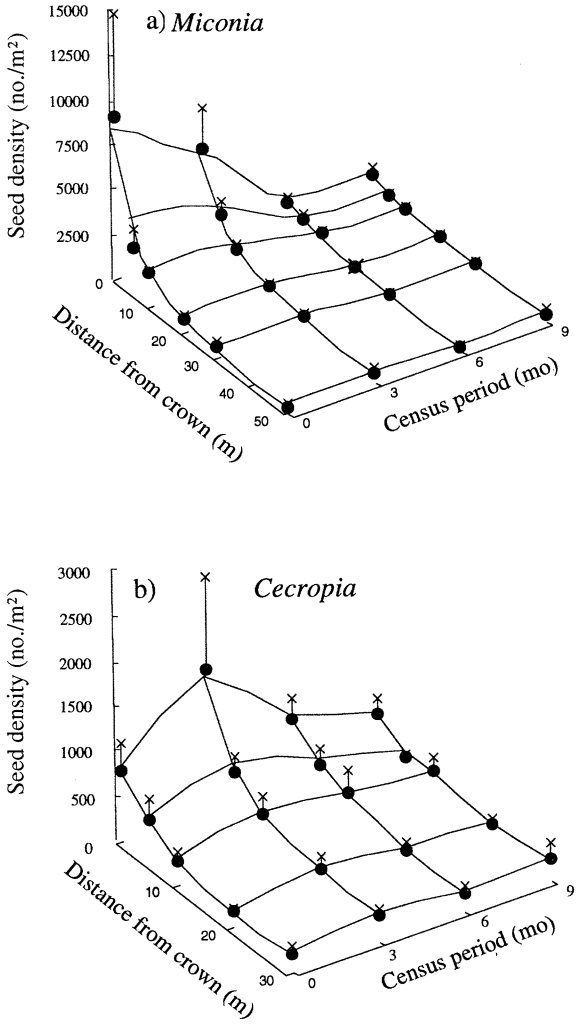

FIG. 3. Seed density of (a) *Miconia,* and (b) *Cecropia* (●; mean and 1 SD, $n = 4$ trees per species) as a function of distance from crown, and census interval. Census times are May ($t = 0$), August, and November 1993 and February 1994. The surface is fitted using distance-weighted least squares in SYSTAT (McLain 1974, Wilkinson et al. 1992).

Heithaus 1986, Levey and Byrne 1993). Consequently, we caution against using the vertical distribution of seeds as an estimate of seed longevity in tropical forests (cf. Leck 1989, Kjellsson 1992, Teketay and Granstrom 1995).

We found evidence that deeply buried seeds survived longer in the soil than seeds near the soil surface, as reported for some temperate agricultural species (Rampton and Ching 1970, Taylorson 1970). However, the causes of seed loss in tropical forests and temperate agricultural systems may differ. Whereas seed losses near the soil surface in agricultural systems have been largely attributed to germination, we did not observe any recently germinated seedlings of *Miconia* or *Cecropia* at any of our transect sites. Thus, germination does not appear to be a major factor accounting for seed loss from the surface soil under the canopy on BCI (but see Li et al. 1996). Instead we suggest that differential seed losses may result from lower pathogen activity in deep soil layers. The role of these deeply buried seeds for the regeneration of these species remains unclear. Buried seeds would be brought to the soil surface on tip-up mounds formed by uprooted fallen trees, and pioneer seedlings are more abundant on tip-ups than in other areas of tree-fall gaps (Putz 1983). Nonetheless, it is still uncertain whether their higher abundance here results from germination of previously buried seeds or from enhanced germination of recently dispersed seeds on the newly exposed bare soil. Also, tip-ups are absent from many treefall gaps, and, where present, only represent a small fraction of the gap area. Hence the contribution of deeply buried seeds to pio-

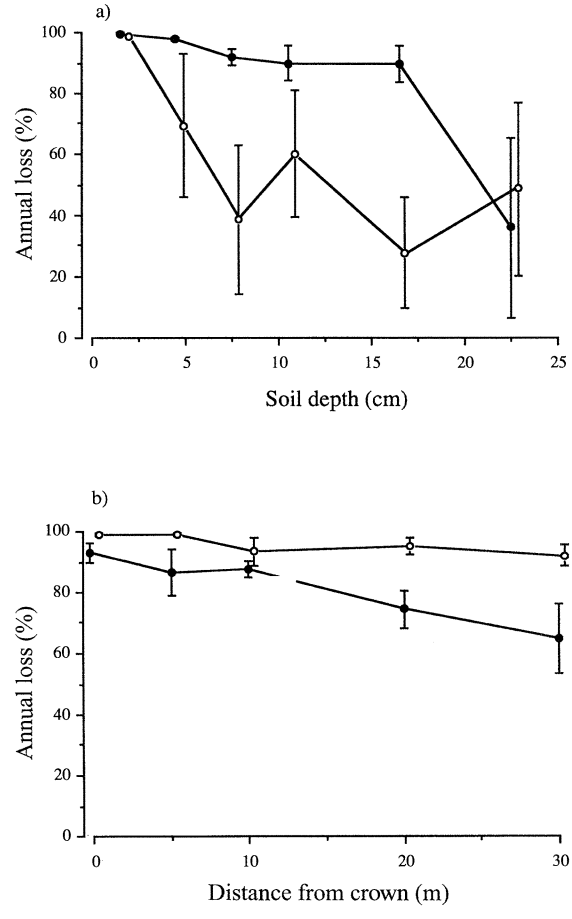

FIG. 4. Relationship between mean annual rate of seed loss (l) for *Cecropia* (○) and *Miconia* (●) and (a) soil depth beneath the crown and (b) distance from the crown of the focal tree. Values for the depth comparison are derived from changes in seed density between June 1993 and December 1993 for both species. Values for the distance comparison are derived from changes in seed density between May 1993 and February 1994 for *Miconia,* and August 1993 and February 1994 for *Cecropia.* All values are means (±1 SE) pooled by tree.

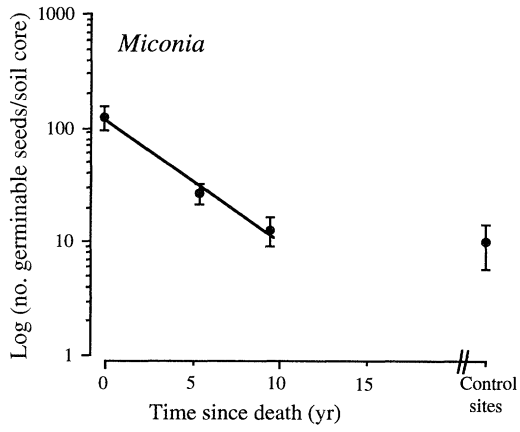

FIG. 5. Regression of log(seed number per core 0–24 cm depth) for *Miconia*, vs. time since the death of the last *Miconia* tree to occupy the site. Soil samples were collected in March 1993 from sites with living trees (n = 4 trees), trees that died between the 1985 and 1990 plot census (n = 3 trees), and trees that died between the 1982 and 1985 plot census (n = 2 trees). Control sites were unoccupied by *Miconia* trees since at least 1982.

neer regeneration in gaps may be small on a per-unit-area basis. In the absence of soil disturbance, seedling recruitment is typically limited to the uppermost layers of the soil representing only a small fraction of the total soil seed bank (Thompson 1992). In a growth chamber, seedlings of *Miconia* and *Cecropia* only successfully emerged from burial depths of <1 cm and ≤3 cm, respectively (J. Dalling, *unpublished data*).

At the soil surface, the seed bank density >5 m beyond the crown greatly exceeded measured seed rain inputs for *Miconia* (Fig. 7). However, given the annual loss rate in the seed bank, and the measured seed rain input at 20 m from the nearest *Miconia* crown, it would have been impossible to build up the measured seed bank stock at this site within the reproductive lifetime of the tree. This suggests inconstant seed rain input, inconstant seed bank loss rates, or an underestimation of seed rain inputs to the soil using our method. We consider the last possibility more likely because of the problem of extracting and separating a small number of very small seeds from the large amount of leaf litter also collected by the seed traps.

The high loss rate of seeds in the soil reported here are representative of most, but not all, pioneer species on BCI (Dalling et al. 1997). For *Trema micrantha* we found >20% viability of seeds sieved out of the soil at sites where *Trema* trees had died 4–9 yr previously (Dalling et al. 1997). Moreover, patches extending over areas of several m^2, with high densities of seeds of this species were found 20–30 m from the nearest conspecific adult recorded in any census of the 50-ha plot, suggesting that seeds of *Trema* may have survived in the soil from prior to the plot's establishment in 1982 (Dalling et al. 1997). Long-term seed persistence may have been selected for in this species, as *Trema* requires larger gaps than either *Miconia* or *Cecropia* for seedling and sapling growth (Brokaw 1987) and these gaps are rare on BCI.

TABLE 5. ANOVA for effects of time since tree death and focal tree on *Miconia* soil seed density.

Source of variation	df	MS	F
Time since tree death	3	1.48	15.00***
Tree	9	0.10	3.2*
Error	14	0.03	
Contrasts:			
Alive 1993 vs. dead 1990	1, 9	1.50	15.3**
Dead 1990 vs. dead 1985	1, 9	0.36	3.7*
Dead 1985 vs. control	1, 9	0.02	0.2

Notes: Trees are nested within time since tree death. Analyses were performed on log([value] + 1)-transformed data. Means are presented in Fig. 5.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Role of fungi as agents of seed mortality in the soil seed bank

Evidence is accumulating that fungal pathogens may regulate the distribution and abundance of plant populations in tropical forests (Augspurger 1983, 1984, Gilbert et al. 1994), but experimental studies on the

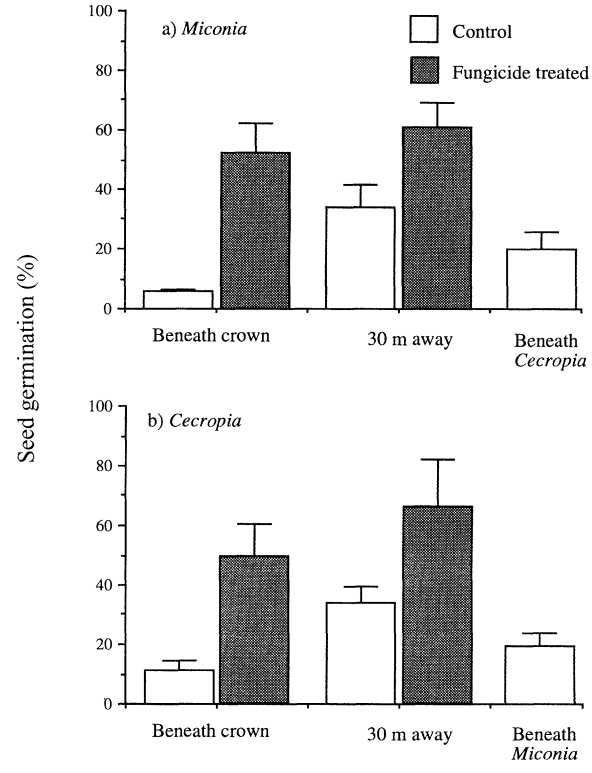

FIG. 6. Percentage seed germination (mean and 1 SE) of control (untreated) and fungicide-treated seeds from nylon bags buried below conspecific crown sites, at sites 30 m away from any *Miconia* or *Cecropia* crown, and below the crown of the heterospecific species.

TABLE 6. ANOVA for the effect of tree, fungicide treatment, and location, on survival of seeds buried in nylon bags in a neotropical moist forest.

Source of variation	*Miconia*			*Cecropia*		
	df	MS	*F*	df	MS	*F*
Tree	3	1.5	1.3	3	0.03	0.03
Fungicide	1	29.1	17.2*	1	13.6	29.6***
Location	1	6.4	18.2*	1	3.5	1.1
Tree × Fungicide	3	1.7	1.5	3	0.5	0.5
Tree × Location	3	0.4	0.3	3	3.2	3.3*
Fungicide × Location	1	3.2	9.3	1	0.1	0.2
Tree × Fungicide × Location	3	0.3	0.3	3	0.6	0.6
Error	43	1.1		36	1.0	

Notes: Analyses were performed on log([value] + 1) count data of seed germination. Means are presented in Fig. 6.
* $P \leq 0.05$, *** $P < 0.001$.

effects of fungal pathogens in natural plant communities are still rare (Harper 1990, Alexander 1992). Fungi have been suggested as mortality agents in both tropical and temperate soil seed banks (Martínez-Ramos and Alvarez-Buylla 1986, Burdon 1987, Garwood 1989, Alvarez-Buylla and Martínez-Ramos 1990), but only two previous studies have directly investigated the proportion of seed mortality attributable to fungal pathogens. Lonsdale (1993) found that a Benlate fungicide treatment reduced mortality of dormant buried

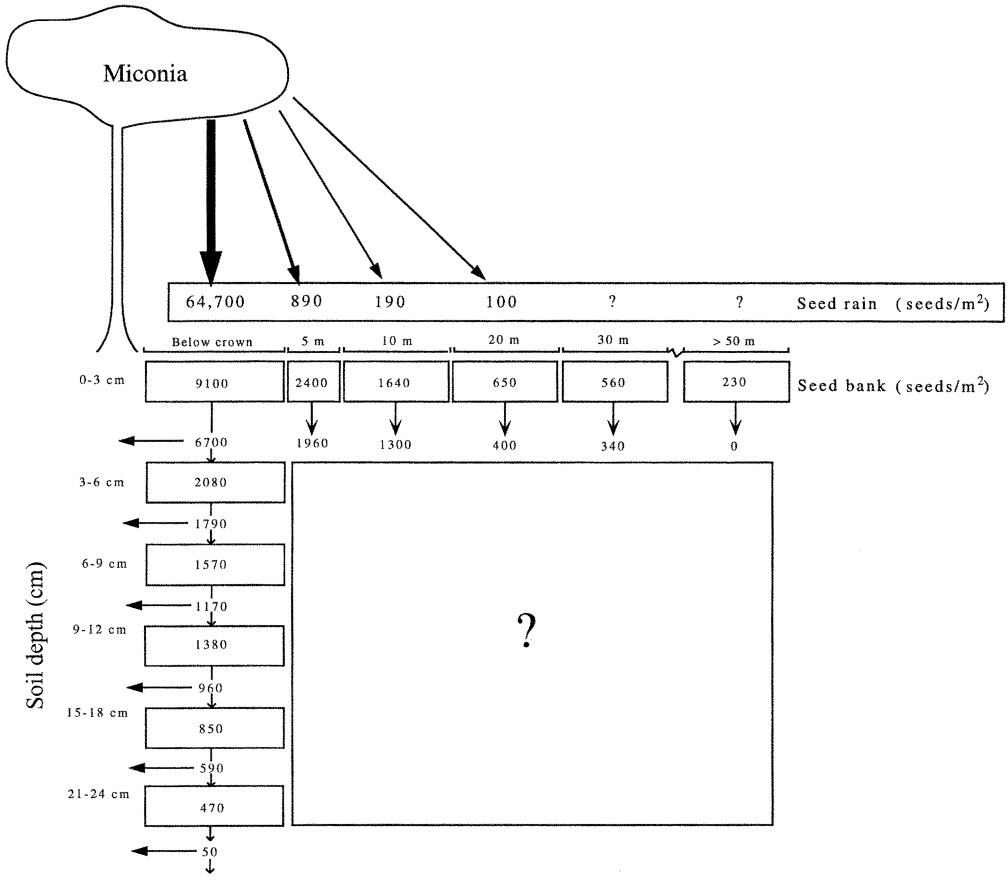

FIG. 7. Annual seed fate diagram for *Miconia*. Arrows from the canopy represent annual seed rain input to the soil. Values in boxes in the seed bank represent the observed seed density following the fruiting season in May 1993 (for 0–3 cm depth) or June 1993 (for 3–24 cm depth). Values with arrows outside boxes represent measured seed losses during the year (May 1993–February 1994, or June–December 1993). Seed losses may be the result of mortality or transition to lower soil layers.

seeds of an invasive nonnative shrub, *Mimosa pigra,* in northern Australia by 10–16%. Given the relatively small effect of the fungicide, Lonsdale concluded that few seeds are killed by fungal pathogens. However, this value for *Mimosa* may be unnaturally low if host-specific fungi are absent from its introduced environment. In contrast, Crist and Friese (1993) argued that fungi play an important role in soil seed dynamics in a semiarid shrub-steppe. They attributed the majority of losses of seeds enclosed within mesh bags to fungal pathogens and decomposition, and further suggested that nonlethal seed-infecting fungi might also affect seed bank dynamics by reducing the attractiveness of seeds to granivorous ants.

In this study, treatment of seeds with a fungicide reduced mortality by up to 47% in *Miconia* and 39% in *Cecropia.* Given the magnitude of this effect, it seems likely that most observed seed losses from within the soil seed bank can be attributed to mortality from fungal pathogens. Moreover, the finding that differences in mortality of *Miconia* seeds were largely attributable to location effects (comparisons of below-crown sites vs. sites 30 m away), while fungicide effects on mortality of *Cecropia* seeds were largely independent of location, is consistent with the finding of distance-dependent effects on seed losses from the seed bank for *Miconia,* but not for *Cecropia.* The extent to which seed-infecting fungi are specific to their hosts needs to be further addressed; it has potentially important influences on pioneer community dynamics.

Implications of seed bank dynamics on the structuring of pioneer tree communities

Now that we have a more thorough understanding of the nature of pioneer seed shadows, we can start to examine how seed dispersal interacts with gap formation and seed survival to generate patterns of seedling recruitment. The finding that soil seed densities of *Miconia* and *Cecropia* declined rapidly with time since seed dispersal and also with distance from the crown is significant, because it implies that both the time of gap formation relative to seed dispersal, and the spatial distribution of gaps, may have a role in determining the probability of a gap becoming occupied by any particular pioneer. Thus this study also offers support to Saulei and Swaine's (1988) assertion that distant dispersal of pioneer seeds into forest is a relatively insignificant contribution to the soil seed bank of primary forest, and that soil seed banks are composed mainly of overlapping seed "footprints" reflecting the current, and in some cases the former, distribution of adult trees.

In the case of pioneers with very small seeds, such as *Miconia* and *Cecropia,* these "footprints" might be quite large. Throughout the year, and at sites 30 m from the nearest adult, both species maintained seed densities of >200 seeds/m^2. Given such prodigious seed output and an adult density of >1 tree/ha, one might not expect any distance-dependent effects on their probabilities of gap occupancy. However, preliminary data indicate that the distribution of seedlings of *Miconia* and *Cecropia* in new treefall gaps on BCI is significantly aggregated towards their conspecific adults when compared with their expected distribution, based on the location of seedlings of 19 other pioneer species present in the same treefall gaps (J. Dalling, S. Hubbell, and K. Silvera, *unpublished manuscript*). These findings suggest that further attention should be given to whether seedling recruitment of tropical trees is limited by dispersal. Even for pioneer trees, which are often assumed to be highly dispersive (Guevara Sada 1974, Whitmore 1975), dispersal limitation may significantly slow competitive exclusion (Hurtt and Pacala 1995) and provide an additional axis to traditional habitat partitioning (e.g., Denslow 1980, Putz 1983, Riera 1985, Brokaw 1987, Denslow 1987, Brandani et al. 1988) as a mechanism for species coexistence.

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