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Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama

J. W. DALLING^{a1}, M. D. SWAINE^b and NANCY C. GARWOOD^c

^a *Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948*

^b *Department of Plant and Soil Science, University of Aberdeen, Aberdeen AB9 2UD, U.K.*

^c *Botany Department, Natural History Museum, London SW7 5BD, U.K.*

ABSTRACT. Seasonal changes in the densities of dormant seeds in the soil around eight pioneer trees in the 50-ha Forest Dynamics Plot, on Barro Colorado Island, Panamá were studied, and how seed dispersal and seed dormancy influenced patterns of seed abundance and distribution were examined. Twenty-four, 3-cm-deep soil samples were collected on 30 m transects radiating out from each of the trees in each of four time-intervals through the year, and four 21-cm-deep samples were collected beneath the focal tree crowns. In the surface 0–3 cm of soil, germinable seed densities of all species combined declined from a peak of 1090 seeds m⁻² in the mid-wet season in August, to 330 seeds m⁻² by the end of the wet season in November. In contrast, at soil depths >3 cm, there was little variation in soil seed bank density through the year. Some variation in soil seed bank density for individual species could be accounted for by distance to reproductive conspecifics. Among species, abundance in the soil was negatively correlated with seed size. Seed persistence varied greatly among species at this site; after 1 y of burial in mesh bags, seed germinability of four species was near zero, while four other species showed no consistent decline in seed germinability after >2 y of burial. For at least one species, *Trema micrantha*, prolonged seed dormancy was also possible under natural conditions. Twenty-five percent of *Trema* seeds extracted from the soil at a site occupied by an isolated *Trema* tree that died between 1982 and 1985 were still germinable in 1994.

KEY WORDS: Barro Colorado Island, pioneer, seed burial, seed dispersal, seed dormancy, soil seed bank.

INTRODUCTION

Widespread seed dispersal and the capacity for seed dormancy are thought to be two key reproductive traits that allow pioneers to colonize ephemeral gap sites in tropical forests (Guevara & Gomez-Pompa 1972, van Steenis 1958, Whitmore 1983). Empirical studies have clearly demonstrated the importance of germination from dormant seeds for regeneration in gaps (Lawton & Putz 1988, Prévost 1981, Putz & Appanah 1987, Uhl *et al.* 1981, Young *et al.* 1987), and seed dispersal measurements indicate that seeds of pioneers can be transported up to several hundred metres (Denslow & Gomez-Diaz 1990, Murray

¹ Correspondence author: Jim Dalling, Email: dallingj@bci.si.edu, Fax: (Panamá) 507-2723065.

1988). Theoretical studies indicate that the advantage of these two traits is interdependent (Venable & Brown 1988, Venable & Lawlor 1980), so that the advantage to pioneer species of seed dormancy is only apparent when coupled to seed dispersal (Murray 1988).

Nonetheless, the duration of seed dormancy varies greatly among pioneer species. Estimates of seed survival based on burial of seeds in mesh bags or boxes have shown that while seeds of some species retain close to 100% germinability after 2 y, other species show marked reductions in germinability in under 1 y (Hopkins & Graham 1987, Perez-Nasser & Vázquez-Yanes 1986). Direct measurements of seed inputs and seed losses from the soil indicate that some pioneers have very rapid seed bank turnover rates. More than 90% of seeds of *Cecropia obtusifolia*, and *Cecropia insignis* disappear from the seed bank within a year (Alvarez-Buylla & Martinez-Ramos 1990; Dalling *et al.* 1997). For *Miconia argentea*, seed persistence varies with distance from the parent tree; annual losses from the seed bank declined from >90% below the crowns of fruiting trees to 70% at 30 m from the nearest tree (Dalling *et al.* 1997). Since direct measurements have only been made for a very limited number of pioneers it is unclear whether these high turnover rates reflect methodological differences, differences among sites, or variation among species in their seed persistence in the soil.

Pioneer species should also exhibit differences in their mean and median seed dispersal distances, reflecting differences in seed size, seed crop sizes, and seed dispersal agents. Since the length of seed shadows is proportional to the total number of seeds released (Dirzo & Dominguez 1986, van der Plank 1960), the allocation of reproductive resources into large or small seeds should influence seed distribution patterns within the forest stand. Likewise, seed dispersal agents also influence seed distribution patterns. Wind-dispersed pioneer and non-pioneer species tend to have flatter seed dispersal curves with modes more distant from the source tree than vertebrate-dispersed species (Dirzo & Dominguez 1986, Willson 1993, Willson & Crome 1989), and among vertebrate-dispersed species seed shadows can also be affected by behavioural attributes of the dispersers (Gorchov *et al.* 1993, Murray 1988).

Differences in dispersal and seed dormancy characteristics among pioneers should be reflected in spatial and temporal variation in the composition of the soil seed bank. In this study we describe how the soil seed bank community varies seasonally around eight focal trees within a large census plot. Since soil seed banks tend to be dominated by one or a few species (Garwood 1989), we supplement field data with experimentally buried seeds retained within nylon mesh bags, and look for evidence of 'seasonally transient' versus 'persistent' seed banks (*sensu* Garwood 1989). Finally, we attempt to determine what factors control seed abundances in the soil.

STUDY SITE

The study was carried out on Barro Colorado Island (BCI), Panamá. Rainfall on BCI averages 2700 mm y⁻¹, with a pronounced dry season from January until April (Rand & Rand 1982). The flora and vegetation of BCI is described by Croat (1978), and by Foster & Brokaw (1982). Geology and hydrology are described by Dietrich *et al.* (1982). Investigations of seed distribution patterns were carried out within the Forest Dynamics Project 50 ha plot, on the central plateau of BCI. The plot is described in detail by Hubbell & Foster (1983). Nomenclature follows Croat (1978).

METHODS

Sampling the soil seed bank

Measurements of the abundance and composition of the soil seed bank were made seasonally within the 50-ha Forest Dynamics Plot on BCI. The sampling regime described here was designed for an accompanying study (Dalling *et al.* 1997) that examined the seed rain and soil seed bank dynamics of the two commonest pioneer tree species on BCI. For that study, four reproductive-sized individuals of each of *Miconia argentea* (Sw.) DC, and *Cecropia insignis* Liebm. were selected from the 1990 census data of the 50-ha plot that were at least 50 m from the nearest reproductive sized conspecific tree. These individuals were chosen primarily to generate seed dispersal curves for individual trees with a minimal contribution of seeds from neighbouring conspecifics. Herein we examine the seed abundances of species *other than Miconia and Cecropia* around these trees. We acknowledge that these eight sample sites are scattered through the plot and not randomly located in the forest, and are centred around sites which presumably share a similar disturbance history. An implicit assumption is that the abundance of seeds of the two focal species does not affect the dynamics of the seed bank of other species at these sites.

For each of the *Miconia* and *Cecropia* trees, the projection of the centre point of the crown was used as the point of origin for four transects laid out along a bearing chosen at random within each of the cardinal quadrants. On each transect, one sample was taken from beneath the crown, at one-third and two-thirds the distance between the crown centre and crown edge, and at 5, 10, 20 and 30 m from the crown edge. The initial set of soil samples was collected at the beginning of the wet season in May 1993. Repeated soil samples were collected within 30 cm from the initial samples during August and November 1993, and February 1994.

Soil samples were taken with a 10.3-cm diameter, 3-cm deep, soil corer to yield a 250-cm³ soil sample at each site. Samples were transported in black polythene 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. Seeds

were 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 over which to record seedling emergence were determined experimentally in advance (Dalling *et al.* 1995). Seedling trays were located at random within two shadehouses in the laboratory clearing on BCI, under conditions ranging from 15 to 25% full sun, and maximum daily temperature fluctuations of 27–35 °C measured at the soil surface. Seedlings were identified and removed weekly; unidentifiable seedlings were marked with colour-coded toothpicks and allowed to grow up until at least morphotypes could be assigned to them. Four additional trays containing autoclave-sterilized forest soil (116 °C for 1 h) were included with each set of soil samples, as controls for contamination. Seedlings of two species, *Chrysothemis fredrichsthaliana*, and *Pilea microphylla* germinated in these control trays, and were excluded from seedling counts.

An additional series of soil samples was collected to investigate the depth distribution of seeds within the soil. Soil samples were taken with 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. Soil samples were measured volumetrically in the field, and successive samples 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. Samples from 12–15 and 18–21 cm were discarded to save greenhouse space. Three cores were collected at random points beneath the crowns of each of the four *Miconia* and *Cecropia* trees sampled above, and three additional cores were collected at random sites within the plot at least 30 m from the nearest *Miconia* or *Cecropia* tree. Initial samples were collected in June 1993, and repeat samples taken in September and December 1993. Soil samples were treated exactly as those collected along transects.

Additional sampling for Trema trees

Analysis of the spatial distribution of *Trema micrantha* seeds from the 0–3 cm soil cores collected around the *Miconia* and *Cecropia* trees indicated that high densities of *Trema* seeds were present in sites >30 m from the nearest reproductive-sized conspecific recorded in any census of the 50-ha plot. In order to examine the capacity of *Trema* seeds to persist beyond the death of the parent tree we therefore collected additional 0–24 cm soil cores in July 1994, beneath the crowns of living *Trema* trees, and at sites occupied by *Trema* in previous plot censuses but that had since died. Sampling of *Trema*, however, was constrained by its rarity in the plot, and was limited to three cores collected at each of three living reproductive sized trees, sites occupied by three trees that died between 1985 and 1990, and one tree that died between 1982 and 1985. One additional core was collected at each of three ‘control’ sites at least 50 m from the nearest site occupied by a *Trema* during the existence of the plot. Since *Trema* seeds are relatively large (3.0 mg), they were sieved directly out of the

soil, and germinated in petri-dishes in a growth chamber (12 h dark at 25 °C; 12 h light at 30 °C, 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$, red-far red light ratio = 1.65).

Survival of artificially buried seeds

Since seeds of many species are present in the seed bank at too low a density to detect seasonal changes in their abundance under field conditions, we examined the change in germinability of fresh seeds enclosed within mesh bags buried 3 cm deep in the soil. Fresh, mature seed of thirteen species were collected when available, cleaned and sorted in a darkroom beneath far-red light (red–far red ratio = 0.3) into lots of 20, 25 or 30 seeds, mixed with *c.* 5 cm³ of sterile forest soil (autoclave sterilized at 115 °C for 1 h), and enclosed within 0.5 mm mesh size nylon bags. For each species, the bags were buried at one site in a grid beneath an intact forest canopy, with bags separated from each other by 20 cm. Seed burial sites were at least 30 m away from the nearest reproductive conspecific. For each species, additional seed samples were dried in the oven at 70 °C for 48 h to measure diaspore mass.

To determine the initial germinability of the seed lot prior to burial, three randomly chosen nylon bags were cut open and spread out on a double layer of moist filter paper within petri dishes. Petri dishes were placed in a growth chamber (conditions as above) and checked for germination until 2 wk after no more new seedlings emerged. Subsequently, three bags of each species were disinterred at 3-mo intervals, and germinated in petri dishes, as above. Nylon bags that were found to be damaged when disinterred were discarded and replacement bags were collected. No attempt was made to distinguish rotten/disappeared versus germinated seeds.

Species for which some temperature scarification was known to increase germination (*Apeiba membranacea*, *Luehea seemannii*, and *Trichospermum mexicanum*, 2 min at 70 °C; *Guazuma ulmifolia*, 10 min at 70 °C; *Ochroma pyramidale*, 30 s at 100 °C; Acuña & Garwood 1987, Garwood 1986) were given the treatment after removal from the field; and for each of these species an additional bag was collected at each interval and left unscarified. Species without a scarification requirement were *Cecropia insignis*, *Cecropia obtusifolia*, *Cordia alliodora*, *Jacaranda copaia*, *Miconia affinis*, *Miconia argentea*, *Solanum hayesii*, *Trema micrantha* ‘brown’ and *Trema micrantha* ‘black’. *Trema micrantha* ‘brown’ and ‘black’ refer to two morphotypes with different seed sizes and coloration. Only the ‘black’ morphotype is found within the 50-ha plot. The ‘brown’ morphotype is restricted to the laboratory clearing and lake margin of BCI (J.W. Dalling & K. I. Silvera, unpubl. data).

Data analysis

Seed counts for each sample were (log (n + 1) transformed and analysed by repeated measures analysis of variance (ANOVA) using SYSTAT (Wilkinson *et al.* 1992). For the purposes of the ANOVA, each of the eight focal *Miconia* and *Cecropia* trees (and three control sites for depth samples) were treated as

random blocks. Distance from the focal tree was not treated as a factor in the ANOVA, since multiple regressions of soil seed bank density versus distance, and tree (block) were not significant for any of the four census intervals ($r^2 = 0.01-0.03$; $df = 2, 189$; $P > 0.05$). The analysis of seasonal changes in seed density with soil depth was also performed using repeated measures ANOVA. To account for lack of independence among successively removed soil samples from within the same core hole, soil depth treatments were nested with cores, and soil cores nested within sites. For both repeated-measures ANOVAs 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.

The α log series diversity index was used for comparisons of seed bank diversity by census interval and by soil depth, as it is relatively insensitive to sample size, and to the abundance of the commonest species (Magurran 1988). Alpha diversity could not be calculated for soil depths > 12 cm because of low seed density and species poorness. To test whether the relative abundance of species changed through the year we compared the species ranking of species present in all four census periods using the Friedman ranking test.

To investigate the spatial distribution pattern of seeds, the 50-ha plot data set was used to calculate the distance from each sample location to the nearest reproductive-sized tree recorded in the 1990 census of the 50-ha plot (reproductive size classes estimated by R. Foster, unpubl. data), for each species recorded in the soil seed bank. Sample sites which were closer to the plot edge than to the nearest reproductive tree of that species were excluded. For each species, data for the census period when that species was most abundant were used in a regression of soil seed bank density versus distance. To avoid problems of inconstant variance and negative seed counts that might be predicted using a normal errors linear regression model, we analysed the data using generalized linear modelling techniques (McCullagh & Nelder 1989) implemented in the GLIM statistical package (Crawley 1993). We assumed Poisson distributed errors and employed a linear model with a log-link function. Hypothesis testing was carried out using the χ^2 -test on differences in deviance. The appropriateness of the assumption of Poisson errors was checked by comparing the residual deviance with the residual degrees of freedom after fitting the explanatory variable. Large relative values of the residual deviance indicate overdispersion which may result in overestimation of significance levels. In order to account for this, the deviance was rescaled by an appropriate Heterogeneity Factor (HF), the ratio of the residual deviance to the degrees of freedom (McCullagh & Nelder 1989). For multi-species taxa (e.g. *Zanthoxylum* spp.), the distance to the nearest individual of any species in the taxa was used.

Changes in percentage seed germination with time for seeds buried in nylon bags were analysed by linear or log-linear regression. No attempt was made at

polynomial curve fitting to seed germination data, since periodic declines in seed germination resulting from seed dormancy could not be distinguished from random seed mortality.

Finally, the effects of adult density and seed size on seed abundance in the soil were examined for the 11 commonest tree species (Appendix 1) using linear regression. For each species, the total mean seed density was chosen from the census period when that species was most abundant. Data on adult (reproductive-sized) density are from the 1990 census of the 50-ha plot. Estimates of the minimum reproductive sizes of individual species are from R. Foster (unpubl. data).

RESULTS

Density and diversity of the soil seed bank

The density of germinable seeds in the surface 0–3 cm soil cores varied significantly with site ($F = 2.1$; $df = 7,187$; $P < 0.05$) and with season ($F = 97.3$, $df = 3,552$; $P < 0.001$; Figure 1a), reaching a peak of 1090 (± 60) seeds m^{-2} , in the mid-wet season in August 1993, and declining to 330 (± 30) seeds m^{-2} in the late wet season in November 1993 (means ± 1 S.E.). In May 1993, on average eight seedlings emerged from each soil sample (range 0–43 seedlings). There was no interaction between sites and the census period ($F = 1.5$; $df = 21,552$; $P > 0.05$), indicating that seasonal changes in soil seed bank density occur independently of local site effects. Individual species mostly showed the same trends in seasonal variation in soil seed bank density as for the data combined across species. All the commonest species had the lowest seed densities in November 1993, but the amplitude of seasonal variation differed among species (Appendix 1). Seasonal variation in the seed abundances of *Miconia* and *Cecropia* are recounted in detail elsewhere (Dalling *et al.* 1997), and are not included in any of the analyses reported here.

Fluctuations in the density of the soil seed bank were matched by changes in species richness (Figure 1b), and in the a diversity index (Figure 1c). Differential seed mortality among species through the year was insufficient to affect the relative abundance ranking of the commonest species (Figure 2a; Friedman's test = 52.8, $df = 15$, $P < 0.001$; Kendall's coefficient of concordance = 0.88). Throughout the year, *Alseis*, *Ficus* spp., *Zanthoxylum* spp. and *Trema* accounted for >80% of tree seeds (Appendix 1).

Germinable soil seed densities from 0–21 cm soil cores collected beneath the crowns of focal trees reveal that fluctuations in seed densities are almost entirely restricted to the surface 0–3 cm of soil (Figure 3a,b). While log soil seed bank densities declined linearly with log soil depth (Table 1), for seasonal fluctuations in seed density there was a suggested interaction between burial depth and census interval ($F = 1.5$; $df = 30,240$; $P < 0.06$). A post-hoc contrast of the depth \times time interaction showed that seasonal changes in seed density at 0–3 cm depth are significantly different from the mean of all other soil

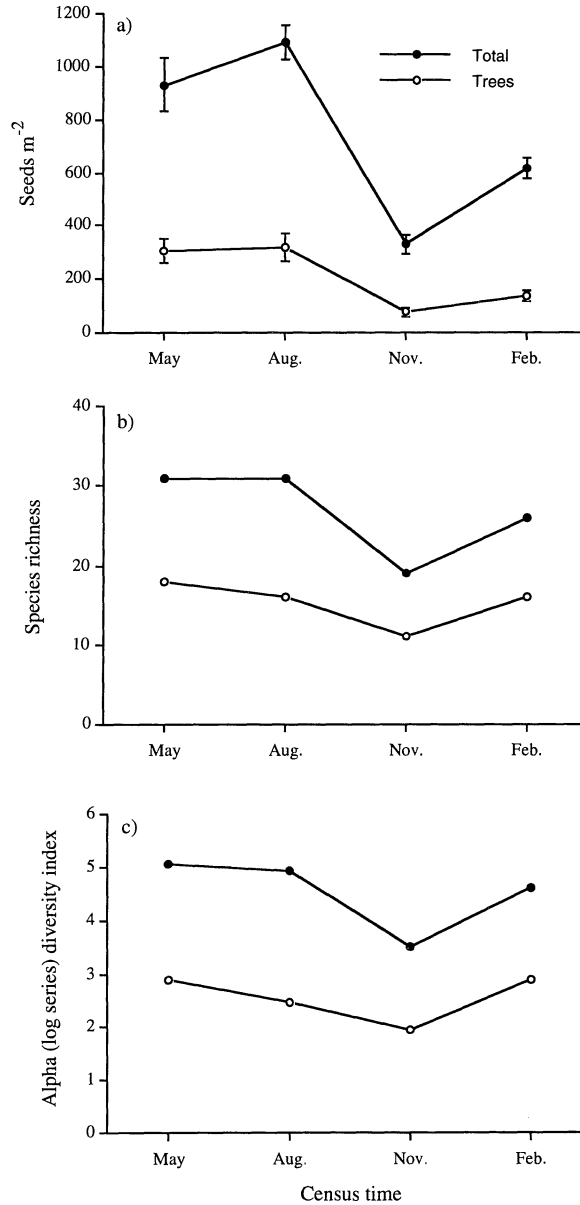


Figure 1. Changes in (a) mean total seed bank density, and mean tree seed bank density (\pm SE), means are of 24 samples collected at each of eight focal trees; (b) total species richness and tree species richness, and (c) α log-series diversity index for all taxa, and for trees only, germinated from 0–3 cm depth soil samples collected at four census periods 1993–1994 on Barro Colorado Island.

depths ($F = 16.5$; $df = 1,96$; $P < 0.001$). Clearly seeds that are immediately buried to >3 cm are much more likely to persist in the soil.

The species richness of the seed bank declined with soil depth (Figure 3c), but remained relatively unchanged across the three census intervals. In the

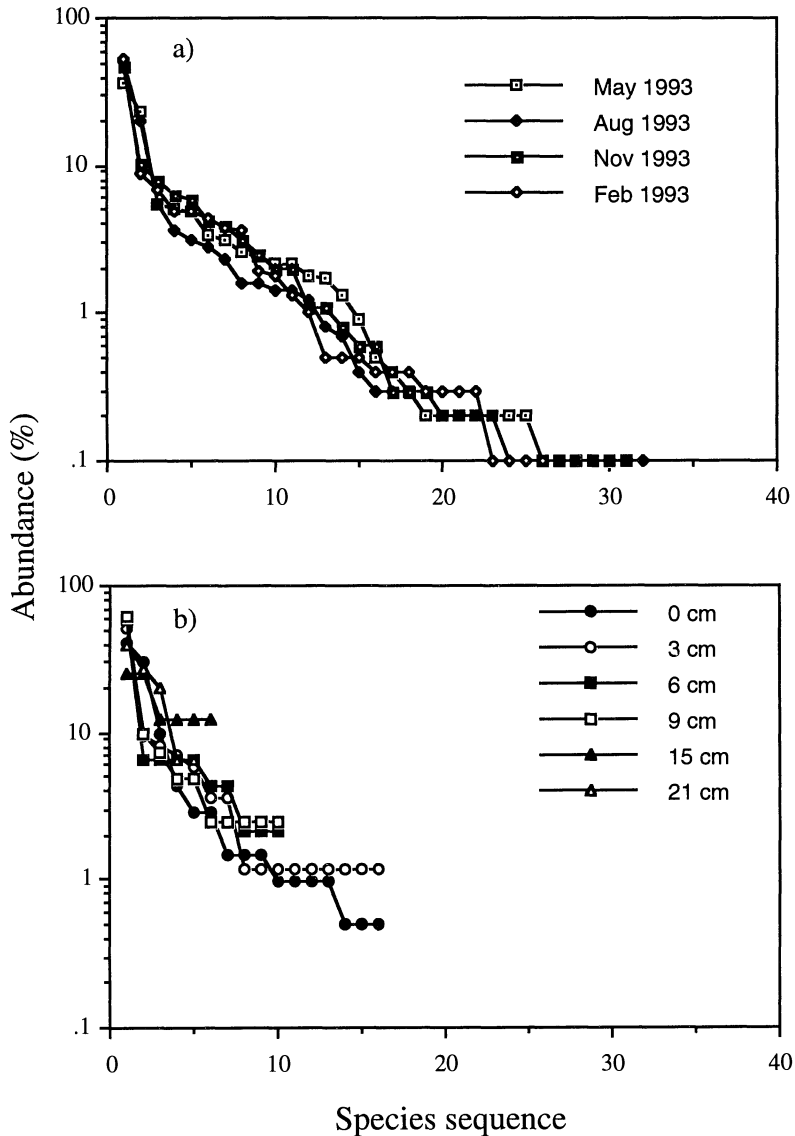


Figure 2. Rank abundance plot of species present in (a) the 0–3 cm depth soil samples collected on transects at four census periods, and (b) in consecutive 3-cm deep soil samples (12–15 and 18–21 cm excluded) during June 1993.

0–3 cm sub-samples, where the germinable soil seed density declined by 68% over the June value, the number of taxa remained more or less constant, suggesting that some density-dependent thinning of the seed bank may occur. This contradicts the earlier result showing that diversity tracks seed density in the 0–3 cm soil cores taken over a wider area (Figure 1a–c). However, far fewer depth samples ($n = 24$) were collected than transect samples ($n = 192$) at each time interval, and differences in these results may result from sampling error.

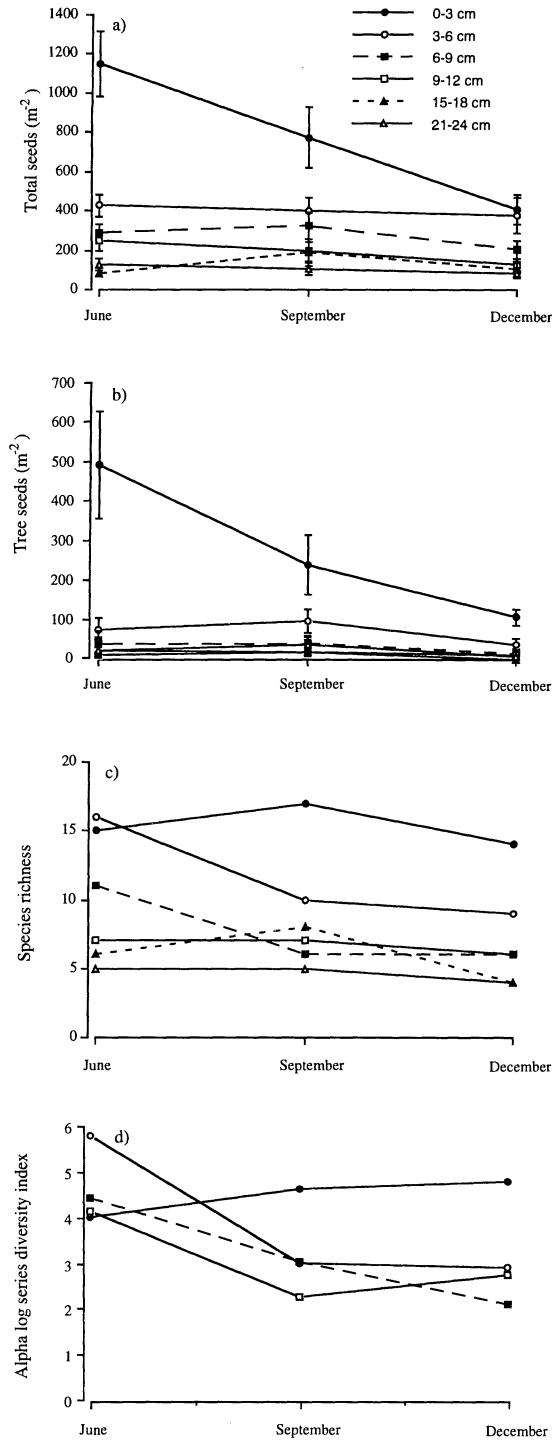


Figure 3. Changes in (a) mean total soil seed bank density (\pm SE), (b) mean tree soil seed bank density (\pm SE) as in (a), (c) total species richness, and (d) α log-series diversity index, including all taxa, germinated from consecutive 3-cm deep soil samples (12–15 and 18–21 cm excluded) at three census periods during 1993. Means are of three samples collected at each of eight focal trees.

Table 1. Regression equations relating total germinable seed number (y) to soil depth (x) during the three census periods.

Census period	Equation	r^2	df	F	P
June 1993	$\ln(y + 1) = -0.08x + 2.24$	0.54	1,64	75.10	<0.001
September 1993	$\ln(y + 1) = -0.06x + 2.04$	0.38	1,64	38.70	<0.001
December 1993	$\ln(y + 1) = -0.06x + 2.04$	0.32	1,64	28.69	<0.001

Alpha diversity for the surface 0–12 cm of soil in June 1993 (Figure 3d) did not decline with increasing soil depth despite decreasing seed density and species richness. This may be partly due to the relative abundances of species in the soil becoming more even with increasing depth, as reflected in the rank abundance plots (Fig. 2b). Nonetheless, the abundance ranking of species in June 1993 did not change significantly with soil depth (Friedman's test = 48.9, $df = 14$, $P < 0.001$; Kendall's coefficient of concordance = 0.59).

For *Trema*, sampling around the focal *Miconia* and *Cecropia* trees showed that relatively high seed densities (>1000 seeds m^{-2}) were found in some soil samples >50 m from the nearest reproductive-sized conspecific tree (see below). Subsequent sampling around sites in the plot occupied by living and dead *Trema* trees, revealed that the highest density of *Trema* seeds was found at a site where a *Trema* tree had died between 1982 and 1985, and where 25% of the intact *Trema* seeds sieved out of the soil were still germinable (Figure 4). No *Trema* seeds at all were found in three 'control' sites >50 m from the nearest *Trema* tree recorded in any plot census.

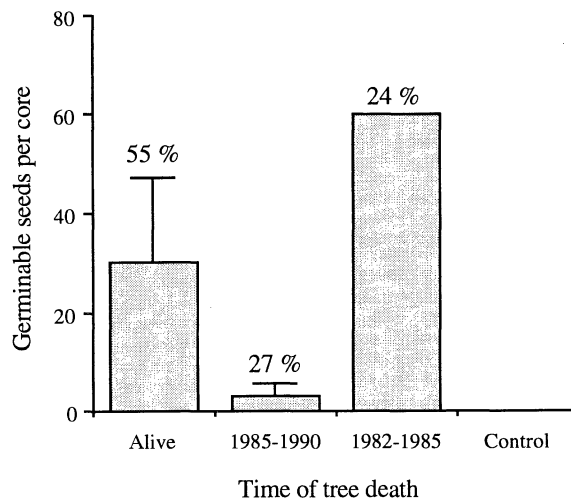


Figure 4. Mean number of germinable seeds extracted per core (0–24 cm), and percentage germinability of extracted seeds collected beneath the crown of living *Trema* trees ($n = 3$), trees that died between 1985 and 1990 ($n = 3$), between 1982 and 1985 ($n = 1$), and at sites unoccupied by *Trema* trees since 1982 ($n = 3$ sites).

Seed bank density in relation to the distribution of reproductive trees

In order to examine whether some variation in seed density was attributable to the proximity of reproductive conspecifics we plotted the number of emergent seedlings of individual species against distance to the nearest reproductive-sized conspecific (Figure 5). For six taxa, *Acalypha* spp., *Alseis*, *Ficus* spp., *Piper* spp., *Trema* and *Zanthoxylum* spp. there were significant, but weak regressions between the seed count per sample at the census interval when the soil seed bank density for that species was highest, and distance from the nearest reproductive conspecific (or congeneric) tree in the 50-ha plot (Table 2). For *Piper* and *Trema*, although regressions were significant, they explained only a trivial percentage ($\leq 6\%$) of variance in seed density between sample sites. For the remaining species, distance explained between 15 and 33% of variance (Table 2).

Survival of artificially buried seeds

In common with samples collected from the soil seed bank, seeds of many, but not all species buried in nylon bags also showed rapid declines in germinability over a year (Table 3; Figure 6). Seeds of the shade intolerant species *Cordia alliodora* had no capacity to remain dormant, and germinated inside the mesh bags immediately after burial in the soil (J. W. Dalling, *pers. obs.*). Germinability of seeds of three other species, *Jacaranda*, *Luehea*, and *Cecropia insignis* neared, or reached zero before 2 y of burial. For the remaining species, burial mostly resulted in some decline in percentage germination, however, in many cases there was considerable variation in percentage germination between census dates, and between replicates disinterred at each census date. In the case of the 'brown' morphotype of *Trema* seedling emergence actually increased during burial to reach 80% after 28 mo. Species requiring a scarification treatment to break dormancy (*Apeiba*, *Guazuma*, *Luehea*, *Ochroma* and *Trichospermum*), appeared to retain the need for scarification even after prolonged burial in the soil (Figure 6). Only *Apeiba* fully lost the need for scarification during the course of the experiment, and even then, only after 22 mo of burial.

Seed size and abundance in the seed bank

Abundance in the soil seed bank of the 11 commonest tree species was independent of adult density in the 50-ha plot ($r^2 = 0.06$; $F = 0.44$; $df = 1,9$; $P > 0.05$), but there was a significant positive regression of seed abundance on seed size ($r^2 = 0.65$; $F = 16.6$; $df = 1,9$; $P < 0.05$).

DISCUSSION

Brokaw (1986) predicted that the capacity of pioneers to germinate from dormant buried seeds in response to environmental cues should uncouple the timing of dispersal from the timing of seedling emergence. This appears to be true on BCI where six out of the ten commonest pioneer species present in the seed

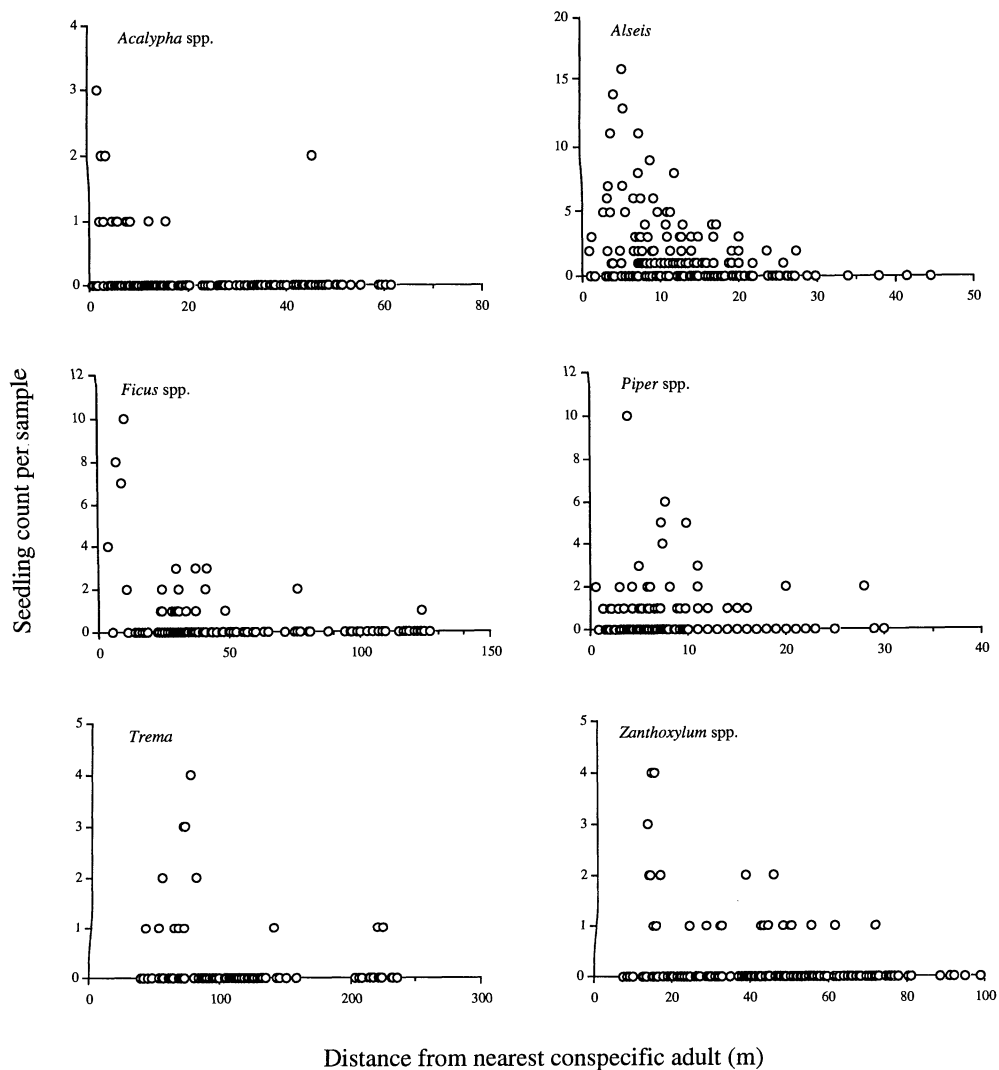


Figure 5. Scatterplots of seedling counts per sample (0–3 cm) versus the calculated distance from the sample site to the nearest reproductive-sized conspecific (or congeneric). Seed counts are taken from the census period when that species was most abundant (Appendix). Note that the scale changes between species. Regression equations, coefficients and probability values are given in Table 2.

Table 2. Poisson-errors-model linear regression of the number of emergent seedlings per soil sample versus distance to the nearest reproductive-sized conspecific. HF is the heterogeneity factor (see Methods). See also accompanying Figure 5.

Species	Equation	χ^2	r^2	n	HF	P
<i>Acalypha</i> spp.	$y = e^{(-0.09x - 1.05)}$	15.3	0.15	191	1.0	<0.001
<i>Alseis blackiana</i>	$y = e^{(-0.10x + 1.58)}$	44.3	0.19	191	2.6	<0.001
<i>Ficus</i> spp.	$y = e^{(-0.07x + 1.36)}$	70.4	0.33	146	1.2	<0.001
<i>Piper</i> spp.	$y = e^{(-0.05x - 0.35)}$	4.8	0.03	190	1.5	<0.05
<i>Trema micrantha</i>	$y = e^{(-0.01x - 0.49)}$	6.5	0.06	115	1.0	<0.05
<i>Zanthoxylum</i> spp.	$y = e^{(-0.05x - 0.30)}$	32.7	0.18	191	1.0	<0.001

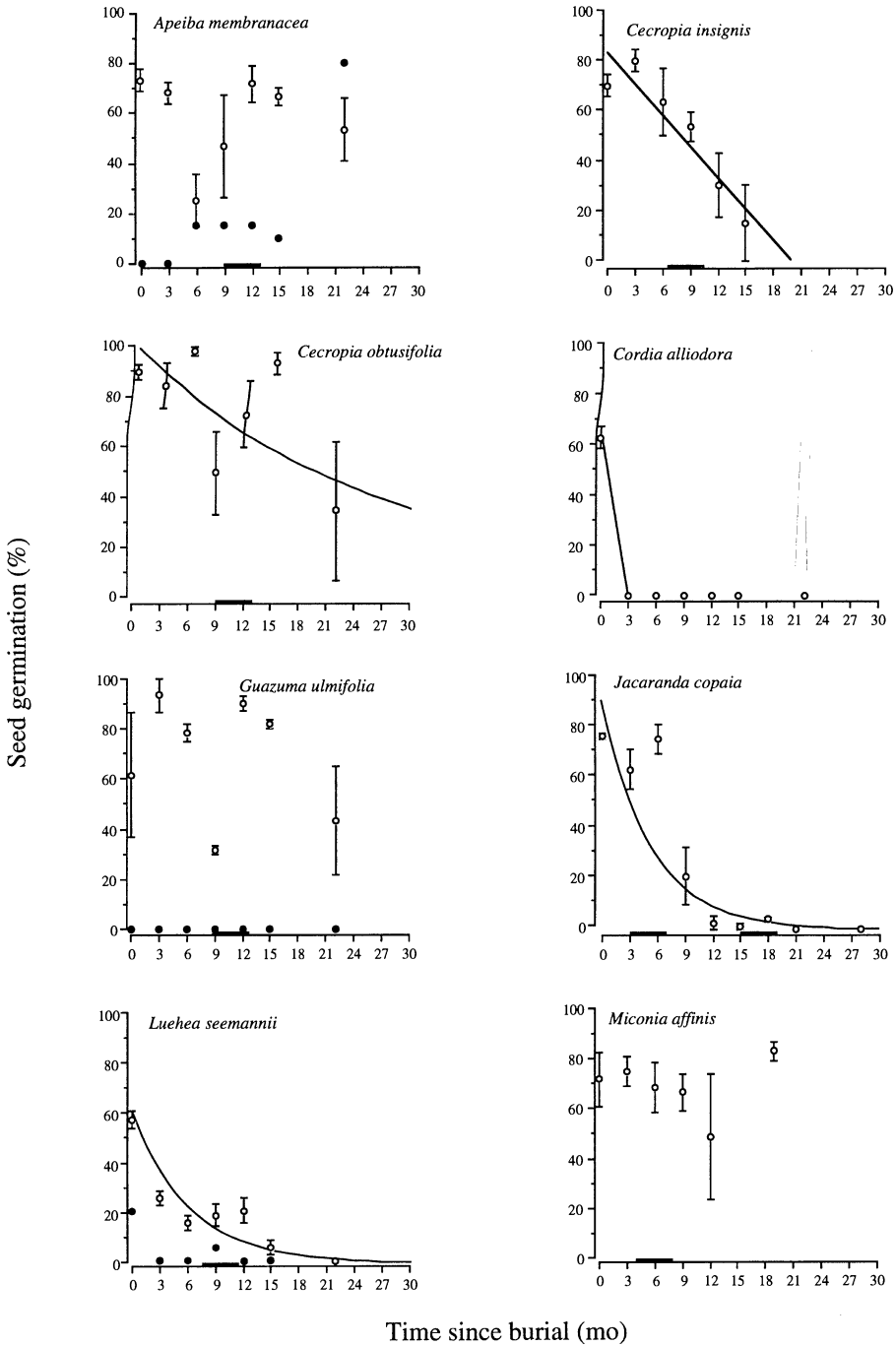


Figure 6. Percentage germination of seeds enclosed within nylon mesh bags and buried for varying periods in the soil (n = 3 bags per time interval, ± SE). Closed circles are germination values for seeds that were not scarified after removal of the bag from the soil (n = 1 bag). The black horizontal bar above the X-axis represents timing of the dry season. Regression equations, coefficients and probability values are given in Table 3.

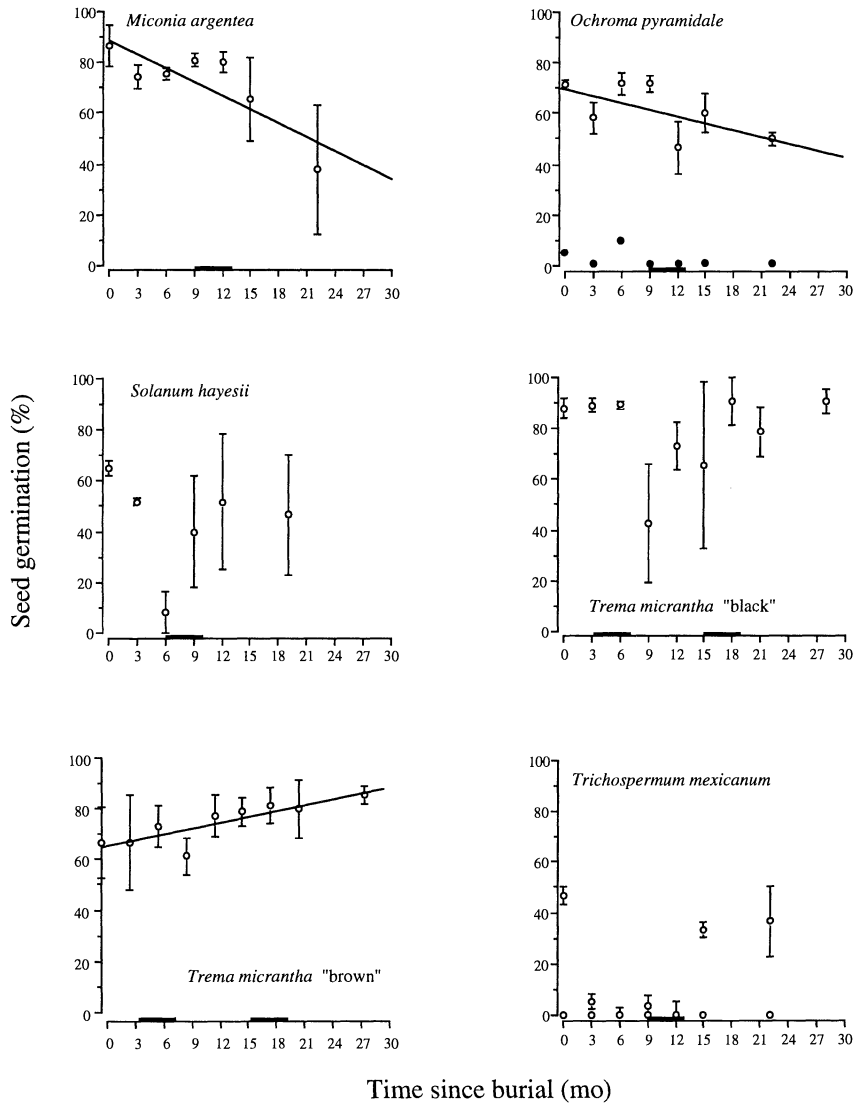


Figure 6. Continued from previous page.

bank fruit in the late dry season during March and April and only two species, *Trema* and *Jacaranda* consistently fruit during the peak period of gap formation 4–5 mo later in August or September (Appendix 1; Brokaw 1982, Foster 1982). Germinable soil seed bank densities at or near the soil surface remained at their highest level through May and August, but declined dramatically in November, probably as a result of pathogenic mortality of seeds (Dalling *et al.* 1997). Some decline in seedling emergence however may also be attributable to changing weather patterns. November days are generally rainy or overcast,

Table 3. Regression equations relating percentage germination of seeds enclosed within nylon mesh bags to time since burial. See Figure 6.

Species	Equation	r ²	df	F	P
<i>Cecropia insignis</i>	$y = -0.66x + 16.1$	0.61	1,16	25.4	<0.001
<i>Cecropia obtusifolia</i>	$\ln(y) = -0.05x + 3.1$	0.28	1,21	5.6	0.013
<i>Jacaranda copaia</i>	$\ln(y) = -0.13x + 2.9$	0.70	1,25	58.6	<0.001
<i>Luehea seemannii</i>	$\ln(y) = -0.13x + 2.3$	0.79	1,19	72.6	<0.001
<i>Jacaranda copaia</i>	$\ln(y) = -0.13x + 2.3$	0.79	1,25	58.6	<0.001
<i>Miconia argentea</i>	$y = -0.55x + 27.0$	0.23	1,21	5.5	0.029
<i>Ochroma pyramidale</i>	$y = -0.19x + 14.2$	0.26	1,19	6.6	0.038
<i>Trema micrantha</i> 'brown'	$y = 0.19x + 16.3$	0.15	1,25	4.4	0.046

and daily temperature fluctuations are lower than for the rest of the year (Windsor 1990).

The declines in soil seed bank density and species richness with increasing soil depth observed here have been generally reported for other tropical forest soils (Cheke *et al.* 1979, Enright 1985, Holthuijzen & Boerboom 1982, Hopkins & Graham 1983, Putz 1983, Young 1985). More striking are the differences in the seasonal changes in seed bank density in the different soil layers. While in the 0–3 cm soil layer, the total soil seed bank density declined by 68% between June and December 1993, the decline over the same period in the 3–6 cm layer was only 12%. Clearly rates of seed loss are highly dependent on soil depth; measurements of annual 'turnover' of the seed bank (e.g. Alvarez-Buylla & Martínez-Ramos 1990, Chandrashekara & Ramakrishnan 1993) need to take this into account.

Deeply buried, and therefore more persistent seeds may be important for establishment in gaps where there has been no recent seed rain. For most species however, regeneration from deeply buried seeds will be dependent upon soil disturbance, since very small-seeded pioneers only have sufficient seed reserves to emerge through the surface few millimetres of soil (J.W. Dalling, unpubl. data; Guzmán-Grajoles & Walker 1991, Molofsky & Augpurger 1992). As a consequence, Garwood (1989) concluded that deeply buried seeds are unlikely to account for much regeneration following gap formation except on the bare soil around uprooted trees. Indeed, pioneer seedling and saplings often are aggregated on the tip-up mounds of uprooted trees (Brandani *et al.* 1988, Putz 1983, Riera 1985), but these sites only represent a small proportion of the total gap area.

Since most of the common pioneer trees on BCI fruit concurrently, and the seeds of almost all species have some capacity to persist in the soil, species relative abundances did not change much through the year. However, while many species were present in low densities in the soil, only a small number of species were common in the seed bank (Appendix 1). Seed size alone accounts for a large proportion of variation in soil seed bank density among species, while proximity to reproductive trees accounts for some variation in soil seed bank density among sites for a few species. Saulei & Swaine (1988) argued that

soil seed bank densities and composition in Papua New Guinea could be largely explained by the input of seeds from a succession of *in situ* colonizing plants reaching maturity, and that inputs from more distant sites were minor. In support of this view, evidence here and elsewhere show that for many pioneer species seed densities decline logarithmically with distance from the crown (Alvarez-Buylla & Martínez-Ramos 1990, Dalling *et al.* 1997, Fleming & Heithaus 1981).

Persistence time of seeds in the soil varies greatly among species, providing evidence for both seasonally transient and persistent soil seed banks. In addition to *Cordia alliodora*, which had no capacity to remain dormant in the soil, seeds of two other wind dispersed species, *Luehea seemannii* and *Jacaranda copaia*, showed an almost complete loss of germinability within 1 y of burial in mesh bags. If these mesh bags had been buried closer to the soil surface, perhaps loss of germinability would have been even more rapid. Since seedlings of these species are unable to persist in the understorey they may be restricted to colonizing a sub-set of available tree-fall gaps in the forest. *Cordia*, for example, fruits in April–May, and its seeds germinate at the onset of the first rains surviving for only a couple of months in the shaded understorey. Since successful regeneration in gaps for pioneers is apparently related to early colonization of the gap site (Garwood 1986, Kennedy & Swaine 1992), *Cordia* may be limited to colonizing gaps that form during the dry season, and first month of the following wet season. Likewise, *Jacaranda* fruits synchronously biennially (S. J. Wright, unpubl. data) during the mid-wet season from July to September. While this represents the peak time of gap-formation on BCI, *Jacaranda* may be excluded from colonizing at least half of available gap sites.

Short-term seed viability though, does not appear to be a constraint for all wind-dispersed species (c.f. Swaine & Hall 1983). *Ochroma* retained 70% of its initial germinability after 22 mo of burial, and *Trichospermum*, while displaying low germination through the first year, retained 84% germinability after 22 mo of burial. The dry season did not obviously correlate with periods of high and low germinability of seeds (e.g. *Apeiba*, *Solanum*, and *Trichospermum*; Figure 6), and variation among replicates and time intervals is more likely to be due to occasional high mortality of seeds following microbial colonization of bags (Vazquez-Yanes & Smith 1982).

In the bird-dispersed tree, *Trema micrantha* independent confirmation of prolonged seed germinability was obtained from the recovery of germinable seeds from isolated sites at which *Trema* trees had died between 1985 and 1990, and 1982 and 1985. This suggests that the high density seed patches found for *Trema* >50 m from the nearest individual recorded through the history of the plot represent seed shadows from trees that existed prior to the establishment of the plot in 1982. Similar observations were made by Alexandre (1978) for *Trema guineensis* in the Ivory Coast; he also found local patches of up to 3000 seeds m⁻² which he attributed to the one time presence of a *Trema* tree now long disappeared.

Not all viable seeds in the soil can be included in the germinable seed bank. Some species may have seeds that remain innately dormant (i.e. unable to respond to environmental cues to germinate) for prolonged periods in the soil. These species may be under-represented in soil seed bank density measurements based on seedling counts. Unscarified seeds of *Trichospermum*, *Ochroma* and *Guazuma* failed to germinate in a growth chamber even after 15 and 22 mo of burial. For *Apeiba*, the germinability of unscarified seeds only reached that of scarified seeds after 22 mo of burial. This is contrary to the expectation that prolonged burial leads to a gradual abrasion or decay of the seed coat, and the consequent, relatively rapid release from innate dormancy (Fenner 1985). Although the growth chamber conditions we used to trigger germination may not adequately simulate environmental changes associated with gap formation (particularly fluctuations in temperature and soil moisture availability), our data suggest that wind-dispersed seeds with hard seed coats, and unscarified animal dispersed seeds, may remain in the soil for several years before they can respond to gap formation. Such seed behaviour conflicts with notions of optimal germination strategies for species with dormant seeds (Cohen 1966).

The need for extreme scarification treatments shown in some of these species (e.g. *Ochroma*, *Apeiba*, *Trichospermum*) may represent the cost of developing a long-lived seed bank. Freshly dispersed seeds may need to be physically well protected in order to avoid seed predators and pathogens that are active predominantly on the soil surface. Even *Trema*, which is unresponsive to artificial scarification with hot water, acid or physical abrasion, has greatly delayed germination of freshly dispersed seeds (>3 mo delay) versus seeds buried for one year (<4 wk-delay), under the same environmental conditions (J. W. Dalling & K. I. Silvera, unpubl. data).

In conclusion, few generalizations can be made about the seed ecology of pioneers. On BCI, pioneers exhibit a variety of seed sizes, seed dormancy patterns, timing of reproduction, and seed dispersal agents. Future studies aimed at understanding co-existence among pioneers need to examine how both seed dispersal, and seedling establishment requirements might select for combinations of these traits, and the trade-offs that exist between them.

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Appendix 1. Fruiting season, seed size and mean seed densities for species of trees, shrubs, herbs and lianas from 192 soil cores (0–3 cm depth), taken around four *Miconia* and four *Cecropia* focal trees at four census periods. Totals are given with 1 S.E in parentheses. Maximum frequency refers to the percentage of soil samples in which the species was present, during the census interval in which its seed density was highest.

Species	Fruiting season ^a	Dispersal agent ^b	Seed size (mg) ^c	Density (m ⁻²)				Max. frequency (%)
				May 1993	Aug. 1993	Nov. 1993	Jan. 1994	
Trees								
<i>Alseis blackiana</i>	Mar–May	W	0.12	170.7	190.1	22.5	43.8	54.2
<i>Ficus</i> spp. ^d	All year	A	0.15–2.0	40.0	30.0	14.4	18.1	14.6
<i>Zanthoxylum</i> spp. ^e	Sept; Jan–Mar	A	11–36	23.8	26.9	8.8	24.4	14.1
<i>Trema micrantha</i>	All year	A	3.90	22.5	22.5	17.5	23.8	13.5
<i>Luehea seemanii</i>	Mar–June	W	1.90	15.0	8.1	2.5	5.0	12.0
<i>Jacaranda copaia</i>	July–Sept	W	4.70	3.8	13.1	1.9	0.6	9.4
<i>Apeiba membranacea</i>	Feb–Apr	A	14.20	9.4	6.9	2.5	6.3	6.3
<i>Cecropia obtusifolia</i>	Feb–Aug	A	0.59	6.9	3.8	0.6	0.0	3.7
<i>Alchronea costaricensis</i>	June	A	38.50	3.1	0.6	0.0	2.5	2.6
<i>Croton billbergianus</i>	Aug–Sept	E		1.9	1.3	0.0	1.3	0.5
<i>Solanum hayesii</i>	Apr–July	A	2.40	1.3	2.5	4.4	2.5	3.7
<i>Trattinickia aspera</i>	Jan–June	A	285.00	1.3	1.9	0.6	0.6	1.0
<i>Palicourea guianensis</i>	Oct–Nov	A	14.30	1.3	1.9	0.0	1.3	1.6
<i>Casearia arborea</i>	Aug–Oct	A	1.52–1.78	1.3	2.5	0.0	1.9	2.1
<i>Brosimum alicastrum</i>	All year	A	459–852	0.6	0.0	0.0	0.0	0.5
<i>Trupimia occidentalis</i>	Aug–Oct	A		0.6	0.0	0.0	0.0	0.5
<i>Fareamea occidentalis</i>	Nov–Jan	A		0.6	0.0	0.0	0.0	0.5
<i>Guazuma ulmifolia</i>	Feb–Apr	A	3.58–4.73	0.6	0.0	0.0	0.0	0.5
<i>Miconia affinis</i>	Jun–Oct	A	0.24	0.0	2.5	1.3	1.9	2.1
<i>Ochroma pyramidale</i>	Apr–July	W	6.60	0.0	0.6	0.0	0.0	0.5
<i>Spondias mombin</i> ^f	Aug–Oct	A	769–1426	0.0	0.0	0.0	0.6	0.5
<i>Guettardia foliacea</i> ^f	Oct–Dec	A		0.0	3.1	0.0	1.3	1.0
Herbs, shrubs, lianas								
Other Melastomataceae ^g	—	—	0.007–0.35	270.1	492.7	105.0	265.1	80.7
<i>Piper</i> spp. ^h	—	A	0.04–3.2	36.3	53.1	6.9	21.9	22.9
<i>Hamelia</i> spp.	—	A	0.046–0.097	35.6	34.4	4.4	34.4	15.1
Monocotyledons ⁱ	—	—	—	18.8	13.1	9.4	18.8	11.5
Unknown No. 1	—	—	—	17.5	0.0	0.0	0.0	11.5
Compositae ^j	—	W		15.6	15.0	5.6	8.8	8.9
<i>Acalypha</i> spp. ^k	—	E	0.43–2.5	13.1	15.6	13.1	9.4	8.7
Unknown No. 2	—	—		12.5	11.9	0.6	2.5	8.3
<i>Hybanthus prunifolius</i>	Feb–Apr	E	12.5–13.1	1.3	1.3	0.0	0.0	1.0
Rubiaceae	—	—		1.3	0.6	0.0	0.0	1.0
<i>Davila nitida</i>	May–June	A	8.5	1.3	0.0	0.0	0.0	1.0
<i>Mouriri myrtilloides</i>	sporadic	A	85.9	0.6	0.0	0.0	0.0	0.5
<i>Mascagnia hippocrateoides</i>	June–July	W		0.6	0.0	0.0	0.0	0.5
<i>Passiflora</i> spp.	—	A	2.8–3.7	0.0	0.6	0.0	0.0	0.5
<i>Clusia odorata</i>	sporadic	A	4.83–5.04	0.0	0.6	0.0	0.0	0.5
Unknown No. 3	—	—		0.0	1.9	0.0	0.6	1.6
<i>Thinouia myriantha</i>	Apr–May	W	65.3	0.0	0.6	0.0	0.0	0.5
<i>Chamaesyce</i> sp.	—	E	0.24	0.0	0.0	1.3	0.0	0.5

Appendix 1. (cont.)

Species	Fruiting season ^a	Dispersal agent ^b	Seed size (mg) ^c	Density (m ⁻²)				Max. frequency (%)
				May 1993	Aug. 1993	Nov. 1993	Jan. 1994	
<i>Psychotria</i> sp.	—	A	3.36–25.2	0.0	0.0	0.0	1.3	1.0
<i>Vitis tiliifolia</i>	Feb–June	A	9.95	0.0	1.9	0.0	1.9	1.0
Hippocratiaceae	—	W		0.0	0.6	0.0	0.0	0.5
Unidentified				203.8	125.7	105.0	115.0	
<i>Miconia argentea</i> ^d	Mar–May	A	0.08	496.4	433.9	122.5	157.6	81.2
<i>Cecropia insignis</i> ^d	Mar–June	A	0.68	197.6	258.9	142.6	162.6	75.0
Total tree seeds ^m				304.5 (47.0)	318.3 (50.7)	76.9 (16.0)	135.7 (20.1)	
Total seed density ^m				932.9 (99.0)	1087.9 (65.3)	328.3 (33.1)	615.2 (38.2)	

^a From Croat (1977), Foster (1982) and J. Dalling, *personal observation*.

^b From Foster (1982). A = Animal, W = Wind, E = Explosive.

^c Dry mass including dispersal structures. Data from this study and N. Garwood (unpubl. data).

^d Mostly *F. costaricana*.

^e Mostly *Z. belizense*.

^f Multi-seeded endocarps.

^g Various small-seeded species, excluding *Miconia argentea* and *M. affinis*.

^h Mostly *P. cordulatum*.

ⁱ *Commelina*, *Costus* and *Heliconia*.

^j Mostly *Chromolaena odorata*.

^k Both *A. diversifolia* and *A. macrostachya*.

^l 'Background' seed densities calculated from samples collected from around heterospecific focal trees only.

^m Excluding *Miconia* and *Cecropia*.