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Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama

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Abstract. We used a forest chronosequence at the Barro Colorado Nature Monument (BCNM) to examine changes in the abundance and species composition of seeds in the soil during forest succession. At each of eight sites varying from 20 yr to 100 yr since abandonment, and at two old-growth (> 500 yr) forest stands, we established two 160-m transects and sampled the surface 0 - 3 cm of soil in cores collected at each 5 m interval. Seed densities were estimated from the number of seedlings germinated from the soil over a six-week period. Contrary to expectation, neither the density of the soil seed bank, nor species richness or diversity were directly related to age since abandonment, but the density of the soil seed bank was correlated with the abundance of seed-bank-forming species in the standing vegetation. In marked contrast to published studies, herbaceous taxa were rare even in the youngest stands, and the common tree species, which accounted for most seeds in the soil, were present in all stands. The pioneer tree *Miconia argentea* (*Melastomataceae*) was the single most common species in the seed bank, accounting for 62 % of seeds and present in 92 % of soil samples. Rapid recovery of the vegetation of young regrowth stands on BCNM, when compared to sites elsewhere may be partly due to allochthonous seed rain from nearby mature forest stands and the lack of seed inputs of weeds and grasses from agricultural and pasture lands which may inhibit forest succession.

Keywords: Barro Colorado Nature Monument; Forest regeneration; Forest succession; Germinable-seed bank; Pioneer.

Abbreviations: BCNM = Barro Colorado Nature Monument; BCI = Barro Colorado Island.

Nomenclature: Croat (1978).

Introduction

Studies of tropical forest succession have highlighted the importance of the soil seed bank as a source of recruits following disturbance (Prévost 1981; Uhl et al. 1981; Putz & Appanah 1987; Young et al. 1987; Lawton & Putz 1988; Garwood 1989). Since the turnover rates of tropical soil seed banks are high, and apparently few species produce long-persistent seeds (Alvarez-Buylla & Martínez-Ramos 1990; Alvarez-Buylla & García-

Barrios 1991; Chandrashekara & Ramakrishnan 1993; Dalling et al. 1997, 1998), the disturbance history, current seed rain, and recent floristic composition of individual sites are likely to strongly influence the soil seed bank community (Guevara & Gómez-Pompa 1972; Epp 1987; Young et al. 1987; Quintana-Ascencio et al. 1996).

The objective of this study was to examine the extent to which the soil seed bank reflects the early floristic composition of regrowth stands, and continues to be influenced by forest development through succession. Saulei & Swaine (1988) have argued that changes in soil seed bank density and composition following logging in Papua New Guinea could be largely explained by the input of seeds from a succession of *in situ* colonizing plants reaching maturity. Similarly, Young et al. (1987) working in young regrowth stands in Costa Rica found that locally produced seeds accounted for about 75 % of the seed input to the soil surface early in succession, although allochthonous seed inputs accounted for most of the species richness.

Indeed, the composition of the soil seed bank and the standing vegetation may diverge only late in succession. Garwood (1989) noted that whereas the composition of the seed bank floras of late secondary forest (Hopkins & Graham 1984), young regrowth (De Foresta et al. 1984; Young et al. 1987) and pastures (Kellman 1974; Marks 1983) reflected that of the standing vegetation, the seed banks of widely separated mature forest stands were more similar to each other than to the standing vegetation from which they were sampled (De Foresta et al. 1984; Hopkins & Graham 1984).

Temporal changes in soil seed bank composition and its similarity to the standing vegetation can best be inferred by sampling across chronosequences of sites sharing similar climatic and edaphic conditions and, where possible, similar initial disturbance regimes. As yet, only a few studies have compared the floristic composition of the soil seed bank in young regrowth stands, and in stands up to 100 yr old (Young et al. 1987; Rico-Gray & García-Franco 1992), and to our knowledge, only one study has compared young stands with adjacent mature forest (Dupuy & Chazdon 1998).

Here we examine the abundance and composition of the soil seed bank along a chronosequence of 10 stands ranging from 20 yr old to > 500 yr in sites bordered mostly by mature and old secondary forest on the Barro Colorado Nature Monument (BCNM) in Panama. We predicted that the abundance and composition of seeds in the soil would be strongly affected by stand age. Specifically we expected to find three characteristics. 1. The youngest sites would have high and homogeneous seed densities, dominated by herbaceous species, and high light-demanding pioneers (e.g. *Ochroma pyramidale*, *Trema micrantha*; Vazquez-Yanes 1974; Brokaw 1987). 2. In stands of intermediate age, large gaps should be rare (Knight 1975; Yavitt et al. 1995), pioneers requiring much light should decline in abundance, and the initial colonizing vegetation should be replaced by more shade tolerant species unrepresented in the soil seed bank. 3. In old-growth stands seed abundance and diversity should increase in comparison to stands of intermediate age as the standing vegetation matures and a larger range of gap sizes are formed by the death of emergent trees. Increased heterogeneity in forest structure should also increase local variability in the seed bank, reflecting the past and present distribution of treefall gaps and pioneer trees in the forest.

Material and Methods

Study area

The study was carried out at the Barro Colorado Nature Monument (BCNM), in Central Panama (9° 10' N, 79° 51' W). The monument comprises a 1500 ha island – Barro Colorado Island (BCI) – and surrounding mainland peninsulas that were formed in 1914 when the Chagres river was dammed to create Gatun lake. BCI has been under constant protection since it was declared a nature reserve in 1923. About half of the island is young forest, mostly a hundred or more years old, and still recovering from old agricultural clearings. The rest of the island is covered with older forest little disturbed in the last 400 yr, except for some selective logging in the last century, and wind damage since the creation of Lake Gatun (Foster & Brokaw 1982; Piperno 1992). Mainland peninsulas adjacent to Barro Colorado Island were added to the Barro Colorado Nature Monument in 1977. These sites have been disturbed more recently, in some cases up to 20 yr ago (see section below 'stand selection').

The forest at BCNM is semi-deciduous, although only a small fraction of the tree species lose their leaves for more than a few days. Rainfall at the laboratory clearing on BCI averages 2700 mm/yr, with a pronounced dry season from January through April (Windsor 1990).

The flora is described by Croat (1978), and by Foster & Brokaw (1982). Geology and hydrology are described by Dietrich et al. (1982), and Stewart et al. (1980).

Stand selection

Sites were selected to replicate stand ages across a long chronosequence. Histories of forest clearance, land use, and subsequent regrowth of fallow vegetation were confirmed by examination of aerial photographs (1926, 1955, 1966, 1973, 1979, 1983), contemporaneous descriptions of Barro Colorado Island (Chapman 1929; Kenoyer 1929; Standley 1933; additional sources reviewed in Foster & Brokaw 1982), and interviews with scientists, farmers and forest guards. 10 stands at least 4 ha in area were selected to include two stands each with the following approximate times in fallow: 20, 40, 70, 120 and two old growth sites > 500 yr (Fig. 1). Although the precise time of abandonment could not be determined, we are confident of the rank order of these approximate ages.

All stands except one, PED (see Fig. 1 for stand abbreviations), are located within the BCNM under management of the Smithsonian Tropical Research Institute. With the exception of PED, forests were not subject to further management or manipulation subsequent to their abandonment. PED (ca. 20 yr old) may be used for occasional fire wood collection. Stands are located on basalt and sandstones. Soil bulk density and pH, an indicator of soil nutrient status, did not vary significantly among stands (J. Denslow unpubl. data).

Sampling of the soil seed bank

At each of the 10 forest sites, except SAI, we established two parallel 160 m transects at least 20 m apart. At SAI space only permitted one transect. All trees > 5 cm DBH were identified in 16 contiguous 10 m × 10 m quadrats along each transect. Saplings and shrubs (>1 m tall and < 5 cm DBH) were counted and identified in 32 contiguous 5 m × 5 m quadrats along the same quadrat and nested within the tree quadrats.

Due to a shortage of growing-house spaces on BCI, we collected soil samples on two occasions at each site. For all sites, except ZET, samples were collected in 1995. In mid-August we collected the first 13 soil samples taken at each 10-m interval along each transect, starting at 0 m and finishing at 130 m. Six weeks later, we collected another 13 samples from each transect, starting at 5 m along the transect and finishing at 135 m. Samples from the ZET site were collected in the same way, and at exactly the same time of year in 1996. Collections were made in August-September as this is the period of peak abundance and species richness of seeds in the soil seed bank on BCI (Dalling et al. 1997).
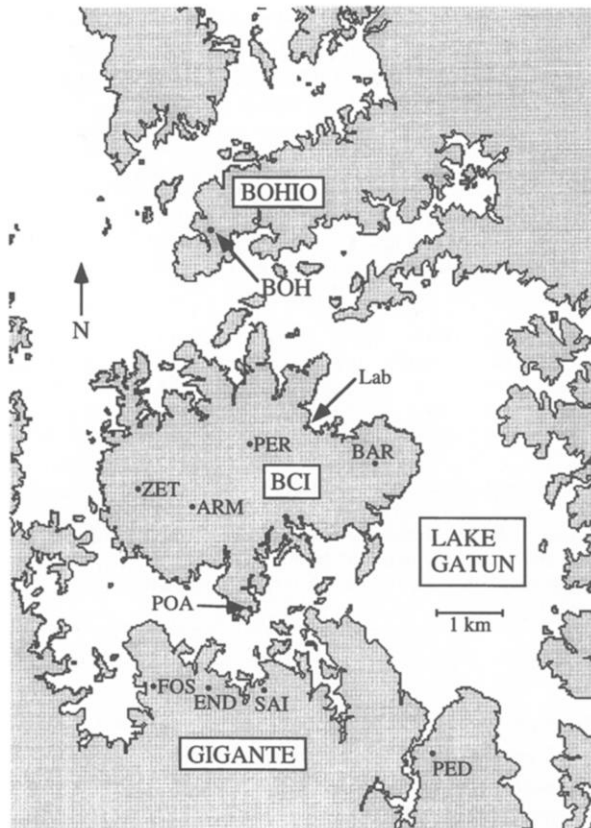
Fig. 1. Map showing the locations of the 10 forest stands. BCI = Barro Colorado Island. Sites are named for adjacent trails or peninsulas: ARM = Armour; BAR = Barbour; BOH = Bohio; END = Enders; FOS = Foster; PED = Pedro Gomez; PER = Pearson; POA = Poachers; SAI = Saíno; ZET = Zetek.

Although the amplitude of seasonal variation in seed abundance varies among species, most species show the same trends in seasonal variation as for the seed bank community as a whole (Dalling et al. 1997).

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 taken from 0 - 3 cm depth since seed abundance and diversity is highest in this layer, and represents the greatest soil depth from which many seed bank species can successfully emerge (J. Dalling unpubl. data). Although deeper soil layers may contain a different composition of long-dormant seeds, a disproportionately greater sampling effort would have been needed to record them since log seed density declines linearly with soil depth on BCI (Dalling et al. 1997). Samples were transported in black polythene bags, stored in an air-conditioned laboratory at 25 °C, and processed within 48 h of collection. Each sample was spread evenly to a depth of 0.5 cm in seedling trays containing a 1-cm deep layer of moist, seed-free sand. Four additional trays containing autoclave-sterilized soil (116 °C for 1 h)

were included with each set of soil samples as controls for contamination. Although seedling emergence was recorded over only a six-week period we are confident that we were able to census the great majority of germinable seeds. An earlier experiment conducted at this site has shown that the rate of seedling emergence is very sensitive to the depth at which soil is spread in the greenhouse; for soil spread to a depth of 0.5 cm, > 90 % of the seedlings recorded after 18 weeks emerged during the first six weeks in the growing house (Dalling et al. 1995).

Seedling trays were arranged in a randomized design on benches and covered with a clear plastic roof within two screened growing houses in the laboratory clearing on BCI. Light levels (PAR) ranged from 15 % to 25 % full sun. Trays were hand-watered daily and seedling emergence from soil flats was recorded at weekly intervals. Seedlings that could not be identified after six weeks were individually potted and grown up until determination was possible (usually to species). Seedlings of two abundant and species-rich genera, *Cecropia* and *Piper*, were too numerous to handle this way; only a subsample of individuals were further identified to species during the second sampling period.

Comparisons of the seed bank with the composition of the tree overstory are based on the census of all trees ≥ 5 cm DBH recorded from the transect. Tree species were considered to be 'seed-bank forming' if more than one seed was recorded germinating from any of the soil samples collected. Taxa were assigned to growth form categories (trees and shrubs, herbs, and lianas) according to species descriptions in Croat (1978).

Data analysis

Seedling emergence counts from each soil sample were log (count + 1) transformed and analysed in a nested, repeated measures analysis of variance (ANOVA), using the general linear model function in SYSTAT (Wilkinson et al. 1992). To examine differences in seedling densities between 'young' and 'old' forest sites, we contrasted the four sites < 70 yr old with the remaining six older sites. We consider 70 yr as a breakpoint between young and old sites because fast-growing pioneers reach their maximum recorded DBH on BCI in 40 - 60 yr (Condit et al. 1993). After 70 yr of regrowth we assume that some of the initial regrowth will be dying back, and that some later recruits will be reaching reproductive maturity. Results of the analysis including and excluding the ZET site (sampled a year later in 1996) are very similar, and ZET is included in the results reported here. Fisher's α log series diversity index was used for calculations of seed bank diversity because it is relatively insensitive to sample size, and to the abundance of the commonest species (Magurran 1988).

Comparison of the species composition of the seed bank with the tree community at each site was made using Sörensen's similarity index for presence-absence data: $C_s = 2\,j/(a+b)$, in which j is the number of species common to seed bank and tree community, a is number of species in the seed bank, and b is number of species in the tree community. Stands were ordinated using Nonmetric Multidimensional Scaling (PROC MDS, Anon. 1997). NMS is an iterative technique based on ranked distances of n entities on k axes which seeks to minimize the stress of the k-dimensional configuration (e.g. Prentice 1977). The distance matrix was based on Sörensen's similarity index: $1 - C_s$; seeds of 23 species were involved. Taxa containing several indistinguishable species, as well as taxa occurring in only one stand were deleted from the data set for the purposes of the ordination. Only seeds of tree species were included (App. 1).

The relationship between soil seed bank density and the abundance of seed bank forming tree species in the stand was examined using Pearson correlation. The arcsine-transformed proportion of the number of trees in the stand that form soil seed banks was regressed against log-transformed stand age. Similarly, seed abundances for individual species were regressed against log stand age using arcsine transformed values of the proportion of total seeds belonging to each species at each site. In all cases normal errors model linear regression was performed using the GLIM statistical package (GLIM 3.77, Anon. 1985; Crawley 1993). Weighting of sites by either the total number of trees or total number of seeds did not affect the outcome of these analyses.

Results

Abundance of buried seeds

Emergent seedlings were classified into 72 taxa and unknowns. Unidentified seedlings contributed only a small proportion (< 10 %) of all emergent seedlings (App. 1). Seedling densities differed significantly among sites, varying from 800 seeds/m² at PEA (for site abbreviations, see Fig. 1), up to 3100 seeds/m² at FOS (Fig. 2a; Tables 1, 2). Seed densities also declined significantly between the first and second census (mean for all sites = 1860 seeds/m² vs. 1440 seeds/m²), independent of site, although censuses were only six weeks apart (Table 2). The regression of seed density with forest age was not significant (Fig. 2a), though the four youngest forest sites (FOS, END, PED, SAI) had significantly higher seed densities than the remaining older forest sites ($F = 13.1$, df = 1,228, $p < 0.001$). The coefficient of variation of seed density, species richness, and Fisher's α (log series)

Table 1. Age, stem density, basal area, and affinities between the tree community (> 5 cm DBH) and the soil seed bank (SSB) community using Sörensens qualitative similarity index (C_s). See legend to Fig. 1 for full site names.

Site	Age (yr)	Stems (ha⁻¹)	Basal area (m²ha⁻¹)	SSB spp[1]	SSB trees[2] (%)	Shared[3]	C_s
SPED	~ 20	1038	26.5	14	169 (16.3)	8	0.144
SAI	~ 20	2108	18.3	15	569 (33.2)	4	0.138
END	~ 40	1154	23.3	16	184 (16.0)	9	0.175
FOS	~ 40	985	21.2	16	200 (20.3)	6	0.152
BOH	~ 70	832	28.1	13	113 (13.5)	7	0.177
POA	~ 70	1038	47.7	10	147 (14.2)	9	0.186
BAR	~ 100	1481	28.3	9	94 (6.3)	6	0.148
PER	~ 100	1060	36.6	12	84 (8.0)	7	0.156
ARM	> 500	1347	23.2	10	103 (6.5)	7	0.136
ZET	> 500	1341	29.0	15	153 (11.4)	10	0.213

[1] Number of seed bank forming species (species represented by more than one seed in the combined seed banks of all sites);
[2] Total number of trees/ha in the stand which are seed bank forming species (expressed as a percentage of all trees);
[3] Number of tree species in common between the seed bank and standing vegetation.

diversity were all independent of forest age (Fig. 2b-d).

The seed bank consisted almost entirely of seeds of trees and shrubs. Across sites, lianas and herbs accounted for 36 % of the taxa that could be assigned a growth form, but they accounted for only 2.2 % (S.E.=0.3) and 3.9 % (S.E = 2.3) of the total seed abundance respectively (App. 1). Only Pearson site had an unusually high proportion of herbaceous seeds (25 %), but this was entirely due to a large number of *Begonia filipes* germinants from a single sample. Contrary to expectation, and even excluding *B. filipes*, the four youngest forest sites had fewer herbaceous seeds than the six older sites ($\chi^2 = 10.9$, df $= 1, p < 0.001$), though the younger sites did have more liana seeds ($\chi^2 = 34.2$, df $= 1, p < 0.001$).

Affinities with the standing vegetation and among sites

The abundance of seed-bank-forming tree species in the stand was not related to stand age (df $= 1,8, F = 2.3$, n.s), but was a good predictor of the soil seed bank density beneath that stand ($r = 0.75, n = 10, p < 0.05$). However, few of the tree species in the stand were represented in the soil seed bank, and the similarity between the tree composition and seed bank composition was not related to stand age (Table 3). Although seed bank forming species constituted a higher proportion of trees in the four younger forest sites than in the six older sites, the seed bank composition was not more similar among young sites ($C_s = 0.15$) than among older sites ($C_s = 0.16$; t-test: $t = 0.68$, df $= 7, p = 0.51$). Ordination results (Fig. 3) also show that the stand
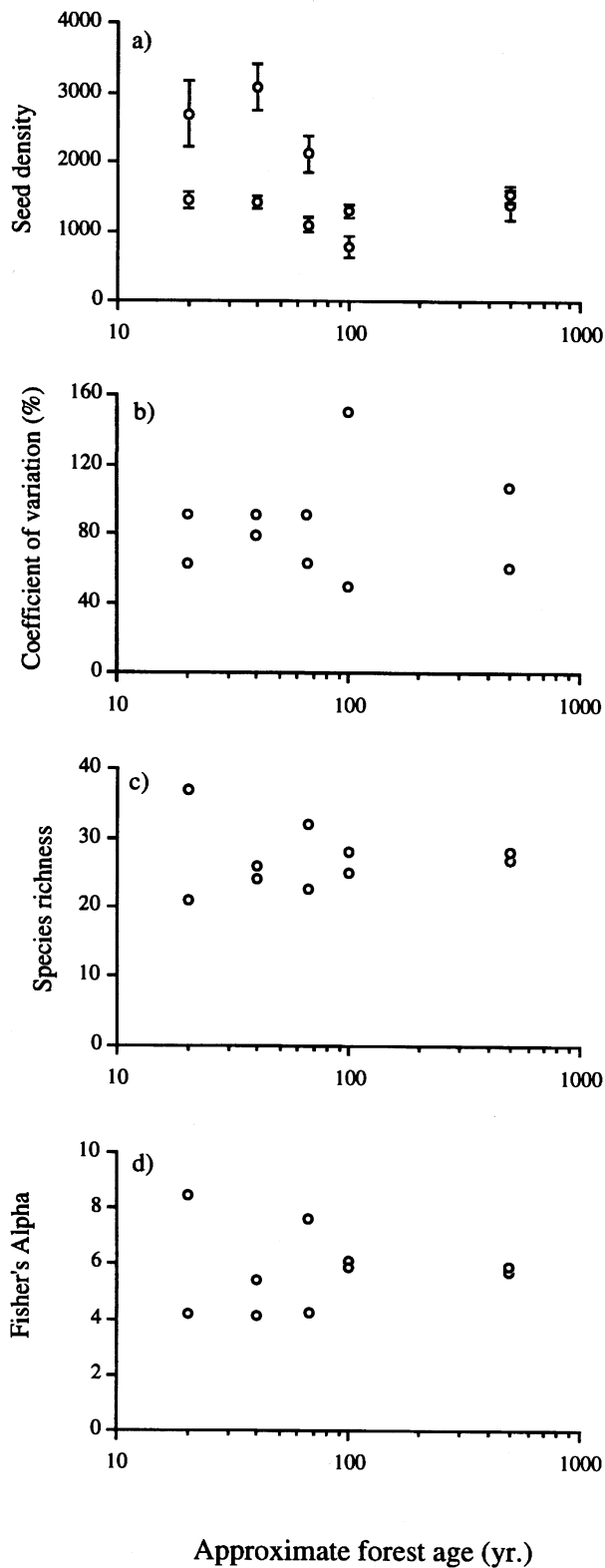
Fig. 2. a. Total soil seed density (seeds/m²); b. Coefficient of variation of total seed density (%); c. Species richness; d. Fisher's α log series diversity versus stand age.

Approximate forest age (yr.)

Table 2. Nested repeated measures ANOVA of log (count + 1)-transformed total seedling counts. Transects are nested within sites. Repeated measures on the census period (September and November).

Source of variation	df	MS	F	P
Between Subject				
Site	9	1.20	13.21	< 0.001
Transect	9	0.10	1.09	0.37
Error	228	0.09		
Within Subject				
Census date	1	1.00	14.50	0.002
Census date × site	9	0.09	1.29	0.245
Census date × transect	9	0.03	0.42	0.926
Error	228	0.07		

configuration was not significantly correlated with estimated stand age, though clusters based on stand location (Barro Colorado Island, Gigante Peninsula, Bohio Peninsula; cf. Fig. 1) do suggest some grouping (cf. Table 1).

Individual species abundance and distribution patterns

The single most common species in the soil seed bank of BCNM is the melastome tree *Miconia argentea* (*Melastomataceae*) present in 91 % of all soil samples, and accounting for > 60 % of all seeds in the seed bank (App. 1). Only at ARM was its abundance surpassed by another taxon (unknown species of *Melastomataceae*). No other taxon accounted for more than 10 % of seeds, though *Piper* spp. were present in nearly half of all samples (App. 1).

Individual species differed markedly in their seed abundances across sites (Fig. 4). Relative abundances of three taxa (*Alseis blackiana*, *Piper* spp., and *Rubiaceae* spp) were significantly related to forest age. Relative abundances of *A. blackiana* and *Rubiaceae* increased with forest age ($r^2 = 0.57$; $F = 10.6$; df = 1,8; $P < 0.05$) and ($r^2 = 0.49$; $F = 7.7$; df = 1,8; $P < 0.05$) respectively, whereas the relative abundance of *Piper* spp. decreased with forest age ($r^2 = 0.73$; $F = 21.5$; df = 1,8; $P < 0.001$). Coefficients of determination for absolute abundance (seedling counts at each site) rather than relative abundance (proportion of seedlings emergent from each site) were similar, but slightly lower for all species. For some taxa, e.g. *Chromolaena odorata*, *Luehea seemannii* and *Trema micrantha*, seed densities differed in sites of similar age. However, given the rarity of pioneer trees within these stands, these differences in seed abundance could result from the presence or absence of only one or two trees near each site. For example, no adult *T. micrantha* trees were recorded in any of the vegetation samples on
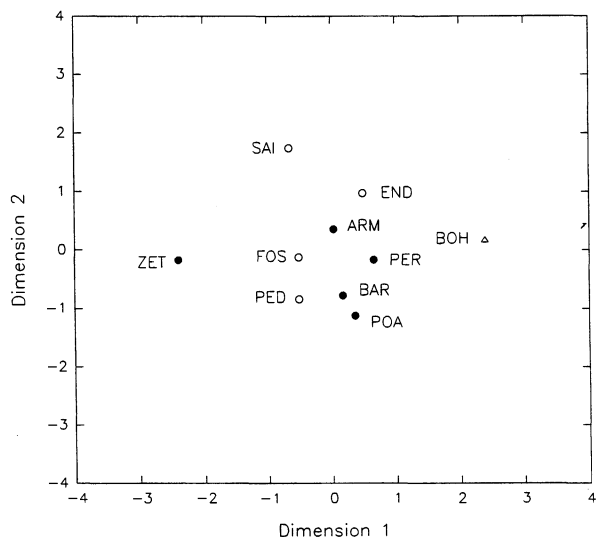
Fig. 3. Nonmetric Multidimensional Scaling ordination of 10 stands based on the composition of the seed bank. Filled circles: Barro Colorado Island; open circles: Gigante Peninsula; triangle: Bohio Peninsula (see Fig. 1 for site locations).

any of the sites even though *T. micrantha* was present in the seed bank at every site (App. 1).

As expected, trees that become reproductive only at large diameters (e.g. *Alseis blackiana* > 20 cm DBH, *Ficus insipida* > 40 cm DBH, *Luehea seemannii* > 30 cm DBH; R. Foster unpubl. data) were largely absent from the seed bank of the youngest sites. These sites were dominated by shrubs and trees with fast growth rates, e.g. *Trema* and *Cecropia*, or which are reproductive at small diameters, e.g. *Chromolaena odorata* < 1 cm DBH, *Miconia argentea* > 10 cm DBH, *Piper* spp. < 1 cm DBH; R. Foster, J. Dalling, unpubl. data).

Discussion

Our results, which show relatively small changes in seed abundance across a chronosequence are in marked contrast with previous studies that have found the soil seed bank density to be much higher in younger than older stands (Guevara & Gómez-Pompa 1972; De Foresta & Prévost 1986; Young et al. 1987; Rico-Gray & García-Franco 1992; Quintana-Ascencio et al. 1996; Dupuy & Chazdon 1998). A possible explanation for this difference is that peaks in seed abundance in the soil occur very early in succession and may have already disappeared in our youngest sites. Certainly in almost all previous studies the youngest stands were younger (range 8 - 19 yr) than the sites examined here.

Nonetheless, we did find that variance in soil seed

density was quite high within stands, and among stands of similar age (particularly the younger ones). We found no evidence of increasing variance in seed density with increasing stand age, as would be predicted if the distribution of seed bank forming trees becomes more patchy. In fact, in a comparable study in lowland wet forest in Costa Rica, Dupuy & Chazdon (1998) found that soil seed densities were high and spatially variable in young forest, and low and relatively homogeneous in old forest. The sampling regime in this study may not have been adequate to detect patchiness within stands, however the variation in seed density among stands may largely result from differences in the local abundance of seed bank forming tree species in the stand. Indeed, the abundance of seeds and seed bank trees were strongly positively correlated. Any additional role of biotic factors (e.g. seed predator and pathogen communities) or abiotic factors (e.g. soil structure) on seedling emergence remain unclear.

Species richness was also unrelated to stand age. Although seed abundance has been a good predictor of species richness in other studies (Young et al. 1987; Dalling et al. 1997; Dupuy & Chazdon 1998) they were not correlated across these stands. In fact, other seed bank studies have found little or no change in species richness across chronosequences (Rico-Gray & García-Franco 1992; Quintana-Ascencio et al. 1996) despite changes in species composition. The species composition of the seed bank at BCNM remained remarkably similar across stands. Trees and shrubs accounted for, on average, 94 % of all seeds at all sites and many common tree and shrubs, e.g. *Cecropia* spp. *Trema micrantha* and *Chromolaena odorata*, remained common at all sites. One single tree species *Miconia argentea* was most abundant at every stand except Armour, and was present in 92 % of all soil samples collected. However some species were more abundant in younger or older stands; trees with faster growth rates and/or smaller reproductive diameters were better represented in the younger stands, while trees reproductive only at large diameters were largely absent from the younger stands.

In striking contrast with all previous studies, in which herbaceous species have dominated the seed bank of young regrowth stands (Saulei & Swaine 1988; Rico-Gray & García-Franco 1992; Quintana-Ascencio et al. 1996; Dupuy & Chazdon 1998) herbaceous taxa were almost completely absent on BCNM and made up only 1.1 % of seeds sampled in the four youngest stands. Although herbs and lianas were present at all sites, and accounted for 36 % of the taxa, weeds and grasses were completely absent. These results are in common with earlier studies of the seed bank from old-growth forest on BCI which also found very few
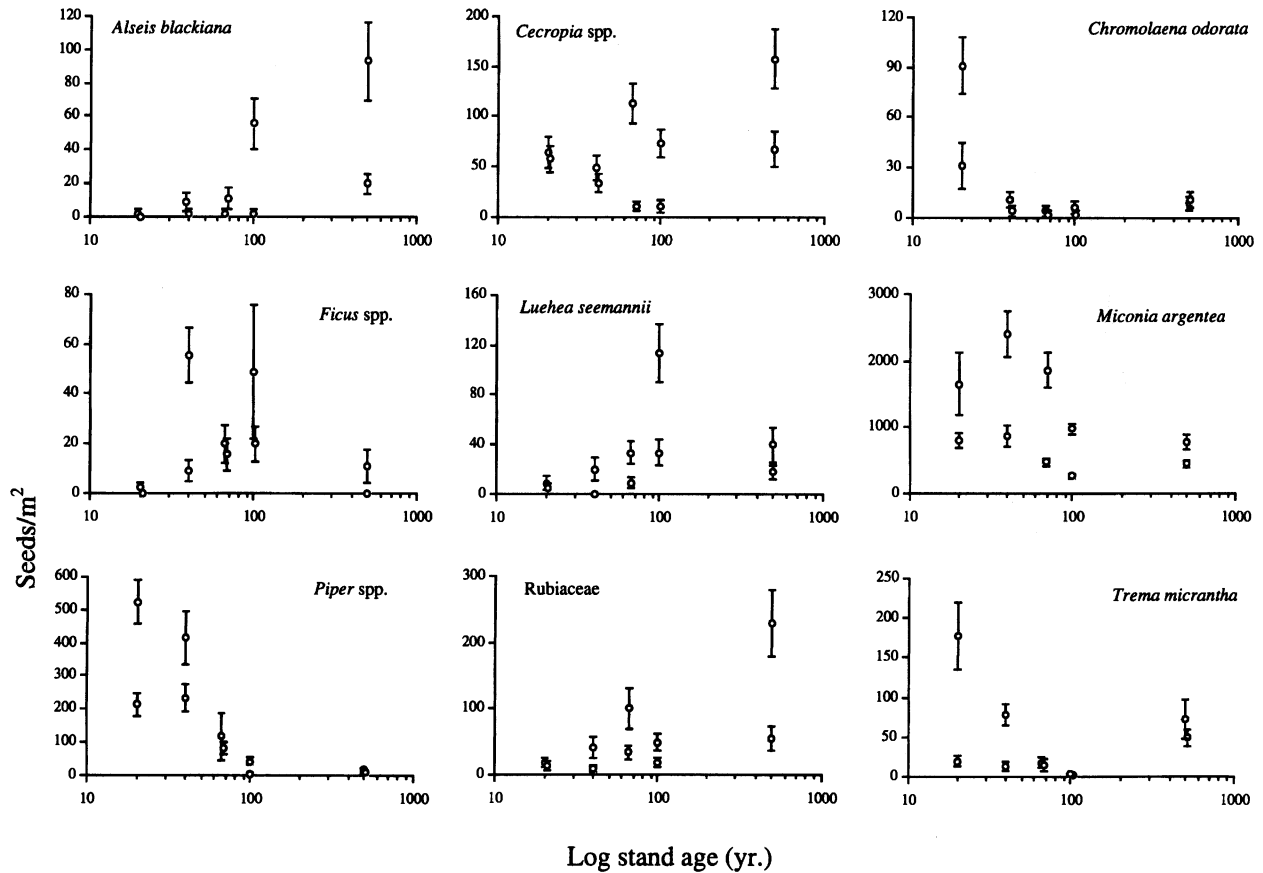
Fig. 4. Individual species abundances (seeds/m²; Mean ± 1 S.E.) versus stand age. Regressions reported in the text were performed on relative abundances.

herbaceous species, and no grasses (Dalling et al. 1995, 1997).

Clearly, the species composition of the soil seed bank is not greatly different in young and old growth forests on BCNM, and it appears that seed banks have either recovered more rapidly, or have been less affected by disturbance than has been reported elsewhere. Although we could not sample comparable sites < 20 yr old at BCNM, and we lack detailed information on the land-use practices carried out prior to abandonment, we can suggest some explanations for the differences in the seed banks of young secondary forests on BCNM at other sites.

The dominance of herbaceous species described in other studies and, in particular, by forbs and grasses with prolific seed production, suggests that the pre- and immediate post-abandonment vegetation have exerted a stronger influence on regrowth at sites other than BCNM. Numerous studies have now documented the influence of allochthonous seed rain from adjacent pastures and cultivations on the seed bank of fragments of mature or older secondary forest (Purata 1986; Young et al. 1987; Quintana-Ascencio et al.

1996), and that subsequent regeneration following disturbance to these stands can be strongly inhibited by the weeds and grasses already present in the soil seed bank (Purata 1986; Uhl et al. 1981; Quintana-Ascencio et al. 1996).

In contrast, at BCNM the unusual situation prevails in which young successional stands remained isolated from large cultivated areas either by Lake Gatun or by remaining blocks of primary forest. Under these conditions allochthonous seed rain into abandoned cultivations would more likely have been composed of primary and secondary forest species, including species that do not form a soil seed bank. The relatively intact bird and mammalian frugivore community at BCNM may also have assisted movement of primary forest species into young regrowth, and surrounding patches of mature forest may have acted as seed sources from which seeds were spread into adjacent regrowth.

As deforestation has continued in and around the Panama Canal watershed, and with it the spread of the exotic grasses we doubt whether newly abandoned cultivations surrounding BCNM would have developed in the same way as those reported here. Indeed

many disturbed areas within the watershed now appear to be stalled in a seasonally burned yet persistent grassland entirely dominated by the introduced rhizomatous grass *Saccharum spontaneum* L.

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App. 1. Abundance (mean and relative)* and frequency (%) (n = 494) of emergent seedlings in the 10 forest stands: ARM = Armour; BAR = Barbour; BOH = Bohio; END = Enders; FOS = Foster; PED = Pedro Gomez; PER = Pearson; POA = Poachers; SAI = Saíno; ZET = Zetek.

Species	ARM	BAR	BOH	END	FOS	PED	PER	POA	SAI	ZET	Mean ab.	Rel. ab.	Percent Frequency
Trees and shrubs													
Miconia argentea	448.7	975.1	473.1	875.1	2405.5	799.6	266.5	1861.3	1657.0	784.0	1054.6	61.86	91.70
Piper spp.[1]	17.8	6.7	117.7	235.4	415.4	213.2	42.2	82.2	524.2	15.5	167.0	9.80	46.36
Melastomataceae[2]	493.1	31.1	122.2	8.9	0.0	46.6	17.8	0.0	4.4	42.2	76.6	4.49	14.78
Cecropia spp.[3]	157.7	11.1	113.3	33.3	48.9	64.4	73.3	11.1	57.8	66.6	63.7	3.74	33.40
Rubiaceae spp.[4]	55.5	17.8	100.0	8.9	42.2	17.8	48.9	33.3	13.3	228.8	56.6	3.32	22.67
Trema micrantha	48.9	2.2	20.0	13.3	77.7	20.0	44.4	15.5	177.7	73.3	49.3	2.89	21.46
Luehea seemannii	17.8	113.3	33.3	20.0	0.0	8.9	33.3	8.9	4.4	40.0	28.0	1.64	16.40
Chromolaena odorata	8.9	6.7	4.4	11.1	4.4	91.1	2.2	2.2	62.2	11.1	20.4	1.20	11.34
Alseis blackiana	20.0	55.5	2.2	8.9	2.2	2.2	2.2	11.1	0.0	93.3	19.8	1.16	11.34
Ficus spp.[5]	11.1	48.9	20.0	55.5	8.9	2.2	20.0	15.5	0.0	0.0	18.2	1.07	11.74
Acalypha diversifolia	20.0	4.4	15.5	26.7	2.2	0.0	8.9	0.0	40.0	0.0	11.8	0.69	5.87
Jacaranda copaia	4.4	0.0	0.0	2.2	4.4	2.2	0.0	4.4	0.0	86.6	10.4	0.61	5.26
Apeiba membranacea	8.9	6.7	0.0	0.0	22.2	20.0	4.4	15.5	0.0	0.0	7.8	0.46	5.06
Zanthoxylum spp.[6]	2.2	6.7	0.0	4.4	2.2	2.2	24.4	0.0	0.0	2.2	4.4	0.26	3.44
Solanum hayesii	0.0	2.2	0.0	0.0	8.9	6.7	0.0	2.2	4.4	13.3	3.8	0.22	3.04
Trichospermum mexicanum	0.0	0.0	0.0	0.0	8.9	11.1	0.0	0.0	8.9	0.0	2.9	0.17	1.62
Hyeronima laxiflora	0.0	2.2	2.2	0.0	0.0	2.2	0.0	15.5	0.0	0.0	2.2	0.13	1.42
Guazuma ulmifolia	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	8.9	2.0	0.12	1.01
Ochroma pyramidale	4.4	0.0	0.0	2.2	0.0	6.7	0.0	0.0	4.4	0.0	1.8	0.10	1.21
Spondias spp.[7]	8.9	0.0	2.2	0.0	0.0	0.0	2.2	0.0	0.0	0.0	1.3	0.08	0.61
Casearia arborea	0.0	2.2	0.0	0.0	0.0	4.4	2.2	2.2	0.0	0.0	1.1	0.07	1.01
Alchornea costaricensis	0.0	0.0	2.2	2.2	0.0	0.0	2.2	2.2	0.0	2.2	1.1	0.07	1.01
Miconia affinis	2.2	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	6.6	1.1	0.06	0.81
Croton billbergianus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.9	0.0	0.9	0.05	0.40
Tetrathylacium johansenii	2.2	0.0	2.2	0.0	0.0	0.0	0.0	0.0	4.4	0.0	0.9	0.05	0.61
Byrsonima spicata	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	4.4	0.9	0.05	0.61
Psychotria marginata	0.0	2.2	2.2	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.7	0.04	1.42
Solanum sp. #2	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	4.4	0.7	0.04	0.61
Margaritaria nobilis	0.0	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.4	0.03	0.20
Terminalia amazonica	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.03	0.40
Trattinnickia aspera	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.4	0.03	0.40

App. 1, cont.

Species	ARM	BAR	BOH	END	FOS	PED	PER	POA	SAI	ZET	Mean ab.	Rel. ab.	Percent Frequency
Lianas													
Mikania leiostachya	28.9	0.0	6.7	60.0	4.4	33.3	4.4	6.7	44.4	8.9	19.8	1.16	9.51
Vitis tiliifolia	0.0	0.0	0.0	6.7	8.9	13.3	4.4	0.0	22.2	0.0	5.6	0.33	3.64
Aristolochia sp.	2.2	2.2	4.4	31.1	0.0	2.2	0.0	0.0	0.0	2.2	4.4	0.26	1.62
Apocynaceae	0.0	0.0	0.0	0.0	4.4	4.4	0.0	0.0	8.9	0.0	1.8	0.10	1.42
Gouania lupuloides	0.0	0.0	0.0	0.0	2.2	6.7	0.0	0.0	0.0	4.4	1.3	0.08	1.42
Passiflora sp.	0.0	2.2	0.0	0.0	0.0	2.2	0.0	2.2	0.0	0.0	0.7	0.04	0.61
Davilla sp.	2.2	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.4	0.03	0.40
Prionostemma aspera	0.0	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.4	0.03	0.20
Stigmaphyllon sp.	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.03	0.40
Tournefortia sp.	0.0	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.4	0.03	0.40
Cissus sp.	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.4	0.03	0.40
Herbs													
Begonia filipes	0.0	0.0	0.0	0.0	0.0	2.2	135.5	0.0	0.0	0.0	13.8	0.81	0.61
Gibasis geniculata	13.3	13.3	17.8	0.0	0.0	0.0	33.3	4.4	0.0	0.0	8.2	0.48	5.47
Drymonia serrulata	8.9	8.9	11.1	8.9	0.0	15.5	8.9	0.0	4.4	0.0	6.7	0.39	4.86
Compositae	2.2	0.0	0.0	2.2	2.2	4.4	0.0	0.0	17.8	2.2	3.1	0.18	2.02
Chrysothemis sp.	2.2	0.0	2.2	2.2	0.0	17.8	2.2	0.0	0.0	0.0	2.7	0.16	1.21
Monocotyledoneae	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	24.4	2.7	0.16	1.82
Costus sp.	0.0	4.4	2.2	0.0	2.2	4.4	0.0	2.2	0.0	0.0	1.6	0.09	1.21
Heliconia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.3	0.0	1.3	0.08	0.40
Vernonia sp.	0.0	0.0	0.0	0.0	2.2	2.2	0.0	0.0	0.0	0.0	0.4	0.03	0.40
Anthurium sp.	0.0	2.2	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.03	0.40
Unidentified													
Morph#1	0.0	2.2	0.0	0.0	2.2	0.0	0.0	0.0	13.3	0.0	1.8	0.10	0.81
Morph#3	0.0	2.2	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.04	0.40
Unknown	4.4	2.2	8.9	4.4	6.7	11.1	8.9	20.0	4.4	22.2	9.3	0.55	5.87
Total	1401.5	1341.6	1115.0	1434.9	3096.3	1472.6	797.4	2127.9	2700.9	1560.9	1704.9	100.00	

*Occurring once with lowest abundance (2.2), **Trees and shrubs**: ARM: *Psychotria acuminata*; BOH: *Castilla elastica, Clusia* sp., *Cordia bicolor, Ocotea* sp., *Psychotria* sp., *P. horizontalis, P. limonensis*; END: *Allophyllus psilospermus, Gustavia superba, Turpinia occidentalis*; POA: *Lindackeria laurina, Oenocarpus panamanus*; ZET: *Calophyllum longifolium, Palicourea guianensis*; **Lianas**: POS: *Mesechites trifida*; PED: *Maripa panamensis*; **Herbs**: BAR: *Tripogandra* sp.; POS: *Hebeclinium macrophyllum*; PER: *Nautilocalyx panamensis*; **Unidentified**: ARM: Morph#2; ZET: Morph#4, Morph#5.

[1]*Piper marginatum, P. aequale, P. colubrinum, P. reticulatum*, and *Potomorphe (=Piper) umbellatum*; [2] Various minute seeded species, excluding *Miconia argentea* and *M. affinis*; [3] *Cecropia insignis* and *C. obtusifolia*; [4] Various minute seeded species, mostly *Hamelia*; [5] *Ficus insipida* (mostly), *F. yoponensis, F. perforata, F. colubrini*, and *F. citrifolia*; [6] *Zanthoxylum belizense, Z. panamense, Z. procerum* and *Z. setulosum*; [7] *Spondias mombin* and *S. radlikoferai*.