Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees

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Summary

1 We examined the abundance and distribution patterns of pioneer seeds in the soil seed bank, and of pioneer seedlings in 53 recently formed gaps, in a 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama. The aim was to assess the importance of dispersal limitation (failure of seeds to arrive at all sites suitable for their germination) and establishment limitation (failure of seeds having reached a site to germinate successfully and establish as seedlings) in determining patterns of gap occupancy.

2 The abundance of seeds in the soil seed bank was strongly negatively correlated with seed size, but was not correlated with the abundance of reproductive-sized adult trees in the plot. In contrast, the abundance of pioneer seedlings > 10 cm height in natural gaps was strongly correlated with adult abundance, but was not correlated with seed size.

3 Seedlings were non-randomly distributed among gaps, but seedling abundance was not directly related to gap size, and there was no evidence of partitioning of the light environment of gaps by small seedlings. Large differences in growth and mortality rates among species were observed after 1 year, and this may result in the gap size partitioning previously found in saplings of the same species.

4 Seedlings of most species, particularly those with large seeds, were relatively more abundant than expected in gaps close to their conspecific adults. Proximity to reproductives, and by inference dispersal limitation, therefore exerts some effect on seedling distribution. None the less, large differences between seed and seedling abundances for some species, and low seedling occupancy rates in some gaps close to adult conspecifics, suggest that seedling emergence probabilities and species-specific establishment requirements may also be important determinants of local abundance.

Keywords: dispersal limitation, establishment limitation, gap, gap light environment, seedling establishment

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Introduction

Attempts to understand the coexistence of tree species in tropical forests have focused on biotic interactions and the specialized regeneration requirements of the species concerned (Grubb 1977; Denslow 1980, 1987), and on how history and probabilistic processes can predict the dynamic properties of plant communities (Hubbell & Foster 1986a). While chance and biology are both undoubtedly important, probabilistic and deterministic processes have rarely been compared. This is partly due to the complexity of scaling up from detailed autecological studies that emphasize the interactions among a few species in species-rich communities. One approach to this problem is to examine in detail mechanisms underlying the coexistence of a single functional group of species. An advantage of this approach over selecting species at random from the entire community is that it addresses subtle differences among apparently ecologically similar species.

Pioneer species (which are characterized by an inability to persist as seedlings in the forest under-

storey) form a small functional group of tropical trees that are attractive for study since their recruitment sites can be defined and measured (e.g. Brokaw 1982a; Popma *et al.* 1988; but see Lieberman *et al.* 1989) and because processes of growth and mortality are played out rapidly. Extensive work carried out by Brokaw (1982b, 1985a,b, 1986, 1987) has highlighted differences in regeneration requirements among a subset of the *c.* 40 pioneer species on Barro Colorado Island (BCI), Panamá. Much of Brokaw's work concerned the effects of gap size on pioneer abundance and species composition, and he found convincing evidence for different gap size requirements for three pioneer species that were based on both mortality patterns and growth performance of saplings (Brokaw 1987). He further argued that a performance hierarchy evident across gaps of different sizes should also be manifested across the gradient from the gap centre to the gap edge. More recently, Brown (1996) found some evidence for gap partitioning within a large gap for three dipterocarp species. However, in contrast to Brokaw's findings, the relative growth performance among the species remained unchanged from the gap centre to the forest edge, and was instead due solely to differential seedling mortality.

Other studies have stressed the importance of within-gap heterogeneity for the maintenance of tree species diversity. On BCI, pioneers in general appear to be most abundant on mineral soil and may be more abundant in large gaps than in small gaps in part because large gaps are more likely to be caused by treefalls that resulted in soil disturbance (Putz 1983). In French Guyana, some, but not all, pioneers are more abundant on tip-up mounds of fallen trees (Riera 1985), and in lowland forest at La Selva, Costa Rica, Brandani *et al.* (1988) found that many tree species were associated with different zones (root, bole and crown) within gaps, and suggested that these association patterns resulted from non-random mortality of seedlings, rather than the differential germination patterns observed by other workers (Raich & Gong 1990).

None the less, gap size differences and within-gap heterogeneity appear to be insufficient to explain the coexistence of large numbers of apparently similar gap-dependent species (Denslow 1995). Species distribution patterns within and among gaps are known to be clumped (Brokaw 1986, 1987; Brandani *et al.* 1988) but the importance of limited seed dispersal and seed availability in the seed bank has not been examined. These factors may reduce competitive interactions to only a subset of species present in each gap. Recent evidence indicates that the soil seed bank of pioneer species is much more dynamic than was previously thought (Alvarez-Buylla & Martínez-Ramos 1990; Chandrashekara & Ramakrishnan 1993; Dalling *et al.* 1997, 1998), with turnover rates for some species of little more than 1 year. Similarly, while pioneers have traditionally been considered to

be capable of substantial long-distance seed dispersal of 750 m or more (Holthuijzen & Boerboom 1982; Denslow & Gomez-Diaz 1990) these reports are based on inferred rather than measured seed sources. Seed shadows have rarely been measured directly for pioneer species, but in all cases examined seed densities decline to low levels 30–60 m beyond the crowns of adult individuals (Alvarez-Buylla & Martínez-Ramos 1990; Laman 1996; Dalling *et al.* 1997).

Recent theoretical work has shown that strong dispersal limitation can promote species richness by greatly slowing competitive exclusion (Tilman 1994; Hurtt & Pacala 1995). Under dispersal limitation, gap sites are frequently not won by the best competitor in the community but by the best competitor among the restricted set of species that arrives at the gap site. Although steady-state dispersal limitation has been postulated to be a widespread phenomenon among chalk grassland perennials, and large-seeded shade-tolerant tropical tree species (Grubb 1986; Silman 1996), the possibility that it is also strong in small-seeded, highly dispersive pioneer species has not been considered previously. Nevertheless, high dispersability may actually be a sign that dispersal limitation has been a strong selective force during the evolution of pioneer life histories.

In this study we used the annual canopy height survey carried out in the 50-ha forest dynamics plot on BCI to locate a large sample of newly formed canopy gaps within a mapped forest stand. Focusing on a group of 24 known pioneer taxa, we looked for evidence of gap size partitioning, and for dispersal limitation (strictly speaking, seedling emergence limited by the proximity of conspecific adults). Specifically we asked:

1 What is the size distribution of gaps, and how is the abundance of seedlings related to it?
2 How does the abundance distribution of pioneer seedlings compare with that of seeds in the soil seed bank and adult trees?
3 Do species show differential growth responses to light availability?
4 Are seedling dispersion patterns skewed towards adult plants, and does the proximity to adults explain any variation in seedling abundance among gaps?

Methods

STUDY AREA

The study was carried out in seasonally moist tropical forest on Barro Colorado Island (BCI), Panamá (9°10′N, 79°51′W). Rainfall on BCI averages 2600 mm year^{-1}, with a pronounced dry season from January until April (Rand & Rand 1982). The flora and vegetation of BCI have been described by Croat (1978) and by Foster & Brokaw (1982). Geology and hydrology have been described by Dietrich *et al.*

(1982). Investigations 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).

SELECTION AND CENSUSING OF GAP SITES

To locate recent treefall gaps within the 50-ha plot, we used data from the canopy height census that has been conducted annually (except for 1994) within the plot using the procedure described in detail by Hubbell & Foster (1986b) and Welden *et al.* (1991). Canopy height was assessed using a range pole at the intersection point of each 5 m × 5 m subplot, and the maximum canopy height was divided into the following size classes: 0–2 m, 2–5 m, 5–10 m, 10–20 m, 20–30 m and > 30 m. In March 1996 we identified all the potential new treefall gap sites ($n = 70$) as sample points that were < 5 m height in 1995 but had been > 20 m in 1993, and that were at least 40 m from the edge of the 50-ha plot. Contiguous low canopy sample points were considered as single gaps, and the area of the gap was estimated from the number of low canopy points within it. Hence an isolated low canopy point was considered to represent a gap < 25 m², and each additional low canopy point increased the gap size by 25 m².

At each low canopy site we recorded how the gap had been formed (branch fall; standing dead tree; tree snapped; tree uprooted; multiple treefall). At sites consisting of a single low canopy sample point, we established a grid of 36 1-m² plots centred on the sample point. We sampled more than the 25 m² projection of the canopy opening on the forest floor, since the effects of treefall gaps on seedling establishment can extend beyond the edge of the canopy opening (Popma *et al.* 1988). For large gaps the grid size was incremented by 30 m² for each additional contiguous low canopy sample point.

Within each 1-m² subplot we searched for all seedlings from a list of 24 pioneer taxa that had been drawn up prior to the study (see Species selection below). All seedlings of these taxa > 10 cm in height were tagged and their height measured. Additionally we recorded, but did not tag, all seedlings of these taxa < 10 cm in height. Seedlings were treated as individuals, except for *Cecropia* in three adjacent 1-m² plots in one gap that contained 30, 40 and 50 seedlings aggregated together in bird or bat faecal clumps. These clumps were counted as single individuals for analyses. All seedlings were recorded as either rooting in the soil or in elevated microsites (e.g. on fallen trunks and roots). From previous studies (Dalling *et al.* 1995, 1997, 1998; Dalling & Denslow 1998) we are confident that we can identify these taxa even at the cotyledonary stage. In March 1997 we remeasured the height of all tagged seedlings and recorded whether seedlings had been damaged and resprouted.

Estimates of seed abundances in the soil seed bank for 17 pioneer tree species were based on 192 soil samples of 0.251 collected at 0–3 cm depth every 3 months over a 1-year period along transects laid out around eight reproductive-sized pioneer trees scattered throughout the 50-ha plot. Correlations between seed bank density, seed size and seedling abundance in the plot were performed using values for the highest seed bank density for each species over the year. Details of the sampling methodology for the seed bank study, and of the seed bank dynamics of individual species, are provided in Dalling *et al.* (1997, 1998). Data on seed size are from Dalling *et al.* (1997) with additional collections made on BCI during 1996.

SPECIES SELECTION

Twenty-four species (henceforth called 'focal species'; Table 1) were chosen for inclusion in the study, based upon patterns of seedling distribution we have observed on BCI, regeneration requirements of species reported in the literature (Putz 1983; Brokaw 1985a, 1987; Garwood 1986), and on our capacity to identify very small seedlings. We included three multispecies taxa, *Cecropia*, *Spondias* and *Zanthoxylum*, because they are common in gaps on BCI even though we are unable to identify them to species as small seedlings. Analyses were carried out at the generic level on the seedlings and adults of these taxa. Since a continuum of light requirements exists for tree species growing on BCI, we could not delineate a definitive pioneer guild; however, for all studied species for which data are available ($n = 14$) a high proportion of recruits reaching > 1 cm d.b.h. are found in gaps (Welden *et al.* 1991) and have high scores in the demographic index of Condit *et al.* (1996), indicating high growth, high mortality and a strong tendency to recruit into gaps. We also included one shade-tolerant species, *Alseis blackiana*. *Alseis* was included for comparison since it is common in gaps, common in the soil seed bank (Dalling *et al.* 1997) and apparently rare or absent in the forest understorey as a small seedling despite the persistence of larger seedlings and saplings in the shade (J. Dalling, personal observation).

LIGHT MEASUREMENTS

We assessed the light environment of gaps and of individual seedlings in October–November 1996 using hemispherical (fisheye) photography. To characterize gaps we took one photograph at each of the 5 m × 5 m grid intersections within gaps, at 1 m above the ground. To characterize the light environment of seedlings, we randomly selected up to 40 seedlings of each species, ranging between 10 cm and 40 cm in height in the initial census in February–March 1996. Actual sample sizes for individual species varied (range $n = 12$–35) since many seedlings initially recorded in March were dead or had resprouted by Nov-

Table 1 Demographic and life-history characteristics of the focal species. Reprod. d.b.h. = diameter at breast height at first reproduction. Density measurement is for reproductive-sized individuals. A = animal dispersed; W = wind dispersed. Abundance in the surface 3 cm of the seed bank + = < 10 seeds m^{-2}; + + < 50 seeds m^{-2}; + + + > 50 seeds m^{-2} (data from Dalling *et al.* 1997)

Taxa	Reprod. d.b.h. (cm)	Seed mass* (mg)	Dispersal agent	Recorded in seed bank?
Alchornea costaricensis Pax & Hoffm.	20	38.50	A	+
Alseis blackiana Hemsl.	20	0.12	W	+ + +
Annona spraguei Saff.	8	40.40	A	−
Apeiba membranacea Spruce ex Benth.	30	14.20	A	+
Casearia arborea (L. C. Rich) Urban	20	1.65	A	+
Cecropia spp. L.	8–30	0.5–0.6	A	+ + +
Ceiba pentandra (L.) Gaertn.	60	65.00	W	−
Cordia alliadora (R. & P.) Cham.	20	12.50	W	−
Croton billbergianus Müll. Arg.	5	24.0	A	+
Ficus insipida Willd.	40	1.60	A	+ +
Guazuma ulmifolia Lam.	20	4.60	A	+
Jacaranda copaia (Aubl.)	30	4.70	W	+ +
Luehea seemannii Tr. & Planch.	30	1.90	W	+ +
Miconia argentea (Sw.) DC	11	0.08	A	+ + +
Ochroma pyramidale (Cav.) Urban	20	6.60	W	+
Palicourea guianensis Aubl.	1	14.30	A	+
Pseudobombax septenatum (Jacq.) Dug.	40	88.30	W	−
Sapium caudatum Pitt.	20	64.00	A	−
Solanum hayesii Fern.	4	2.40	A	+
Spondias spp. L.	30	746–1426	A	+
Terminalia amazonica (J. F. Gmel.) Exell	30	3.80	W	−
Trema micrantha (L.) Blume	20	3.90	A	+ +
Turpinia occidentalis Croat	20	40	A	−
Zanthoxylum spp.	20–30	11–36	A	+ +

*Air-dry diaspore masses are given (without wings). For *Spondias* the diaspore is a fibrous endocarp. Seed mass for *Turpinia* is estimated from seed dimensions in Croat (1978).

ember, and we only report data for the 10 most common species. The height at which photographs were taken depended on plant size, but was always < 5 cm from the shoot apex.

Photographs were taken with Kodak Tri-X pan ASA-400 black and white film (Eastman Kodak, Rochester, NY) using a Nikkor 8-mm hemispherical lens and a Nikon FM2 camera (Nikon, Melville, NY). Photographs were analysed using the video image analysis program CANOPY (Rich 1989; Rich *et al.* 1993). Images were input through a Sanyo CCD VDC3824 video camera fitted with a Nikkor 55 mm Micro lens, and the digitized video image (512 × 480 pixels) displayed on a Panasonic WV-5410 monitor. One of us (KS) was responsible for setting the threshold image intensity value classifying the openings and vegetation for all photographs. Although this determination involves subjectivity, practised operators can achieve a high degree of repeatability (Rich *et al.* 1993 and references therein).

The indirect site factor (ISF), defined as the proportion of diffuse skylight, and the direct site factor (DSF), defined as the proportion of direct sunlight under a canopy relative to that in the open, were used to calculate an estimated global site factor (GSF). GSF is defined as the total proportion of global radiation under a plant canopy relative to that above it, and is the weighted sum of ISF and DSF (Rich 1989; Canham *et al.* 1990). [GSF] = $p_i t_i$[ISF] + $p_d t_d$[DSF], where p_i is the proportion of diffuse skylight, p_d is the proportion of direct sunlight received above the canopy, and t_i and t_d are the proportions of diffuse skylight and direct sunlight that are transmitted through the canopy. For our estimated GSF, we assume that incident radiation was split evenly between diffuse and direct radiation (i.e. p_d and p_i both = 0.5; Canham 1988).

DATA ANALYSIS

Seedling dispersion patterns of individual species were examined using a nearest neighbour analysis of pioneer seedlings to conspecific (or congeneric) adult trees of reproductive size. Data from both the 1990 and the 1995 censuses of the 50-ha plot were used to find nearest adults, since the exclusive use of the 1995 census may have excluded individuals that died shortly before or after gap formation in 1993–94, whereas exclusive use of the 1990 census may have excluded rapidly growing individuals of species that are reproductive at small diameters (e.g. *Palicourea* and *Croton*). Reproductive sizes were estimated from fruit censuses carried out in the 50-ha plot (J. Dalling, unpublished data; S.J. Wright, J. Pavon & A. Jara-

millo, unpublished data). For most species, adult census year (1990 vs. 1995) and small changes in the estimated size-at-reproduction had only a very small effect on the median distance between adult and seedling.

We used the Kolmogorov–Smirnov two-sample test to test the null hypothesis that the distribution of seedlings of a target species is identical to that of all focal species with respect to the distribution of adults of the target species. In principle the analysis is similar to that described by Hamill & Wright (1986). For each target species we generated a cumulative frequency curve of distances of seedlings to the nearest reproductive-sized conspecific adult (or congeneric adult for *Cecropia* spp. and *Zanthoxylum* spp.) and compared it to a cumulative frequency curve generated from the distribution of seedlings of all 24 focal species vs. adults of the same target species. The statistic for the two-sample Kolmogorov–Smirnov test is defined by the module of the maximum difference between the cumulative distributions (D_{max}) and the sample sizes of the curves to be compared (n_1, n_2). The level of significance was calculated from the observed value for D_{max} using the expression:

$$P = 2e - [(2 (n_1 n_2) (D_{max})^2)/(n_1 + n_2)]$$

where P is the smallest level of significance at which the null hypothesis is rejected (Pacheco & Henderson 1996). Although our application of this test violates the assumption of mutual independence between the two populations being compared (seedlings of the target species are included in the sample of all focal species), this remains a conservative test of dispersion differences since departures in the cumulative frequency distributions can only result from over or under-representation by species other than the target species. We included the target species in the all-focal species curve since many plots contained only one seedling (often that of the target species). Seedlings that were closer to the edge of the 50-ha plot than to the nearest target adult were excluded from the analysis, hence the sample size for the all-species accumulation curve varies slightly between species.

To analyse effects of distance from the nearest adult conspecific on within-gap seedling abundance we used generalized linear modelling techniques (McCullagh & Nelder 1989) implemented in the GLIM statistical package (Crawley 1993). To avoid problems of inconstant variance and negative seedling counts that might be predicted with a normal errors linear regression model, and to account for large differences in seedling number between gaps (range 2–184), we carried out a weighted regression on the proportion of all focal seedlings in each gap belonging to the individual target species. The proportional response variable was modelled using binomial errors and a logit link function, with the total number of focal seedlings in each gap as the binomial denominator. Hypothesis testing was carried out using the χ^2 test on differences in

deviance. The appropriateness of the assumption of binomial errors was checked by comparing the residual deviance with the residual degrees of freedom after fitting the explanatory variable.

Results

GAP CHARACTERISTICS

We identified 53 gap sites from 70 low-canopy sites recorded in the 1995 canopy height survey. Most of these sites (83%) consisted of a single, isolated low canopy point and were therefore considered as gaps of $< 25 \, \text{m}^2$ (Hubbell & Foster 1983). Few gaps consisted of two or more contiguous low canopy sites (two sites $n = 4$; three sites $n = 3$; four sites $n = 1$; five sites $n = 1$). While all the gaps $> 25 \, \text{m}^2$ contained seedlings of at least one of the focal species, 17 (39%) gaps of the $< 25 \, \text{m}^2$ lacked seedlings of the focal species. Gap size was not related to seedling density for either seedlings $< 10 \, \text{cm}$ height, $> 10 \, \text{cm}$ height or all seedlings combined (d.f.$_{1,33}$; $F = 1.5$–3.1; $r^2 = 0.04$–0.09).
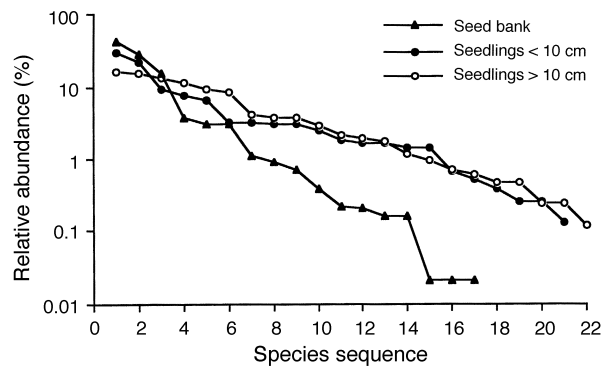
We could determine the origin of gap formation for all gaps occupied by focal species and for half the gaps unoccupied by any focal seedling. Most gaps (48%) resulted from branch or crown fall. Fewer gaps resulted from trees snapped at the base (15%), uprooted trees (15%) or standing dead trees (19%). Only 11% of gaps were clearly the result of multiple treefalls. Microsite conditions within gaps reflected these different modes of formation, with different amounts of woody debris (mean cover = 13%, range 1–33%) and liana loads (S. Schnitzer, unpublished data) reflecting different amounts of crown material deposited into the gap. Although we did not investigate in detail association patterns between species and within gap microsites, some species established more or less frequently than expected in elevated sites on fallen debris (Table 2). After 1 year such seedlings were equally likely to survive as those established in the soil (Yates-corrected $\chi^2 = 2.29$, d.f. = 1, NS).

SPECIES DIVERSITY AND SEEDLING ABUNDANCE PATTERNS

We found seedlings $< 10 \, \text{cm}$ height for all of our 24 focal species except *Ceiba*, *Pseudobombax* and *Sapium*, and seedlings $> 10 \, \text{cm}$ height for all species except *Trema* and *Ochroma*. Species varied greatly in abundance (Fig. 1 and Table 2), ranging from three species represented by single individuals up to *Cecropia* representing 29% of all seedlings $< 10 \, \text{cm}$ height. Relative abundance plots for seedlings $< 10 \, \text{cm}$ and $> 10 \, \text{cm}$ in height were very similar, and there was greater evenness of relative abundance of seedlings than of seeds in the soil seed bank (Fig. 1; this was also true comparing only the 17 taxa present both in the seed bank and seedling census).

Table 2 Number of occupied gaps, number of seedlings < 10 cm height and > 10 cm height, and a comparison of seedling numbers recruiting in terrestrial vs. elevated microsites in 36 gap sites. *P*-values refer to under (–) or over-representation (+) of elevated seedlings compared with the expected seedling number based on all species combined. Species with no observed elevated seedlings were given a value of 1 for calculation of *G* statistics

Species	Total seedlings Gaps occupied	< 10 cm	> 10 cm	Terrestrial	Elevated	G	P
Alchornea	20	13	32	45	0	2.4	NS
Alseis	29	171	139	300	10	0.6	NS
Annona	13	3	15	18	0	2.1	NS
Apeiba	16	50	31	81	0	3.9	*Under
Casearia	7	24	10	34	0	2.1	NS
Cecropia	25	345	70	387	28	7.1	**Over
Ceiba	1	0	2	2	0	–	–
Cordia	7	14	18	32	0	2.1	NS
Croton	8	19	97	115	1	4.2	*Under
Ficus	4	11	4	14	1	0.2	NS
Guazuma	6	2	8	10	0	2.7	NS
Jacaranda	22	72	34	90	16	20.7	***Over
Luehea	19	23	79	101	1	3.4	NS
Miconia	23	57	131	179	9	0.3	NS
Ochroma	1	1	0	1	0	–	–
Palicourea	25	25	112	137	0	7.7	**Under
Pseudobombax	1	0	1	1	0	–	–
Solanum	4	11	4	15	0	2.3	NS
Sapium	1	0	1	1	0	–	–
Spondias	10	5	16	21	0	2.1	NS
Terminalia	2	13	6	19	0	2.1	NS
Trema	1	2	0	2	0	–	–
Turpinia	2	4	5	9	0	3.6	NS
Zanthoxylum	14	23	24	45	2	0.0	NS
Total		888	839	1659	68		

Fig. 1 Rank abundance plots for pioneer tree species present in the soil seed bank (data from Dalling *et al.*, 1997), present as seedlings < 10 cm height in gaps, and present as seedlings > 10 cm height in gaps on Barro Colorado Island, Panama. Seven species occurred as seedlings but were not present in the seed bank.

Changes in the rank order of abundance of species, and its relationship to seed size, were analysed using Spearman's rank correlations (Table 3). Whereas rank abundance of seeds in the soil was negatively correlated with seed size but not correlated with adult abundance, rank abundance of seedlings < 10 cm height was negatively correlated with seed size, and positively correlated with both seed bank rank abundance and adult rank abundance. Although correlated with seedlings < 10 cm height, the only other rank correlation for seedlings > 10 cm was with adult abundance ($r_s = 0.90$), indicating that the relative abundances of pioneer species are mostly set during emergence and early establishment. Some of these changes in relative abundance appear to result from poor establishment success of small-seeded species. Excluding the shade-tolerant species *Alseis*, there was also a significant positive correlation between the magnitude of change in relative abundance from the seed bank to the seedling layer (> 10 cm height) and seed size ($r_s = 0.52$, $n = 16$, $P < 0.05$).

Seedlings of individual species were not evenly dis-

Table 3 Spearman's rank correlation tests among rank abundance of seeds in the soil seed bank (Dalling *et al.* 1997), seedling abundances and adult abundances. Sample sizes are smaller for comparisons with the soil seed bank since only 17 of the seedling taxa germinated from the soil (*n*: number of species, r_s: correlation coefficient, *P*: level of significance, NS if $P > 0.05$)

	n	r_s	*P*
Seed size *vs*:			
Seed bank density	17	−0.74	< 0.01
Seedlings < 10 cm	24	−0.58	< 0.01
Seedlings > 10 cm	24	−0.32	NS
Adults	24	−0.19	NS
Seed bank density *vs*:			
Seedlings < 10 cm	17	0.54	< 0.05
Seedlings > 10 cm	17	0.26	NS
Adults	17	0.08	NS
Seedlings < 10 cm *vs*:			
Seedlings > 10 cm	24	0.86	< 0.01
Adults	24	0.83	< 0.01
Seedlings > 10 cm *vs*:			
Adults	24	0.90	< 0.01

tributed among the gaps. This clumped distribution pattern was indicated by comparison of the species' accumulation rates in sequentially sampled gaps, which were lower than expected when compared with curves from a null-model (similar results were found considering only seedlings < 10 cm or > 10 cm height). The null curve was generated by allocating seedlings randomly to gaps, but with the overall seedling abundance distribution across gaps maintained (Fig. 2; $n = 50$ randomizations). For all seedlings combined, an average of 10 gaps would need to be sampled to encounter 75% of the focal species, whereas only six gaps would have been needed if the seedling population was randomly distributed.
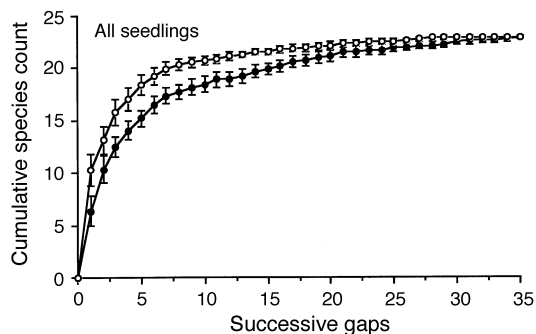
Fig. 2 Observed (closed circles) and null-model (open circles) species accumulation curves for pioneer tree species present in successively sampled gaps on BCI. Data are for all seedlings (< 10 cm and > 10 cm). Null-model species accumulation curves were generated by randomly assigning seedlings to gaps while maintaining the observed abundance distribution. Error bars are 95% confidence intervals ($n = 50$ randomizations).

GAP LIGHT ENVIRONMENTS

Gap size effects

Single hemispherical photographs taken at the canopy height survey points did not reveal any relationships between seedling abundance and the light regime. Most surprisingly, there was no significant difference in the measured light conditions of gap sites lacking any individuals of our target species ($n = 17$; mean GSF = 0.162, SE ± 0.02) and light conditions of occupied gap sites ($n = 34$; mean GSF = 0.172, SE ± 0.01; $d.f._{1,49}$, $F = 0.23$, NS). For occupied gaps, there was no relationship between seedling density and light conditions for seedlings < 10 cm height, > 10 cm height, or all seedlings combined ($r^2 = 0.00$–0.01).

Species responses to light conditions

In contrast to gap-level light measurements, light measurements made at the individual seedling level revealed significant effects on growth for most species even though sample sizes were often small (Fig. 3 and Table 4). Two species for which light effects on growth were undetectable were *Alseis* and *Cordia*. Many *Alseis* seedlings were in relatively dark microsites and grew very little over the year. In contrast to all other focal species, *Cordia* seedlings appeared not to respond to higher light microsites by growth. This may have been the result of very heavy herbivory of all *Cordia* seedlings in the census by a specialist cassidine chrysomelid beetle *Ischnocodia annulus* (J. Dalling, personal observation; D. Windsor, personal communication). Excluding *Alseis* and *Cordia*, we found no evidence that the remaining species responded differentially to light (ANOVA test of homogeneity of slopes, $d.f._{1,7}$, $F = 1.79$, NS).

With the exception of the relatively shade-tolerant species *Alseis*, there was no evidence that seedlings of the focal species partitioned the light environment (Fig. 4). In a pair-wise comparison of light conditions experienced by seedlings of different species, the only significant difference found was between *Alseis* and *Cecropia* seedlings (Bonferroni adjusted posthoc comparison, $P < 0.05$). None the less, some partitioning of the light environment may appear as seedlings continue to grow and die. After 1 year there were dramatic differences in both growth and mortality rates between species. Annual mortality ('*m*' of Sheil *et al.* 1995) varied between 9% (*Casearia* and *Alseis*) and 85% (*Jacaranda*), and relative height growth varied from 7.5×10^{-4} cm cm^{-1} day^{-1} for *Alseis* to 3.6×10^{-3} cm cm^{-1} day^{-1} for *Cecropia*. Furthermore, for species that had > 10 individuals in the initial census there was a trend of increasing mortality with growth rate (Pearson correlation, $r = 0.47$, $n = 14$, $P = 0.09$; Fig. 5).
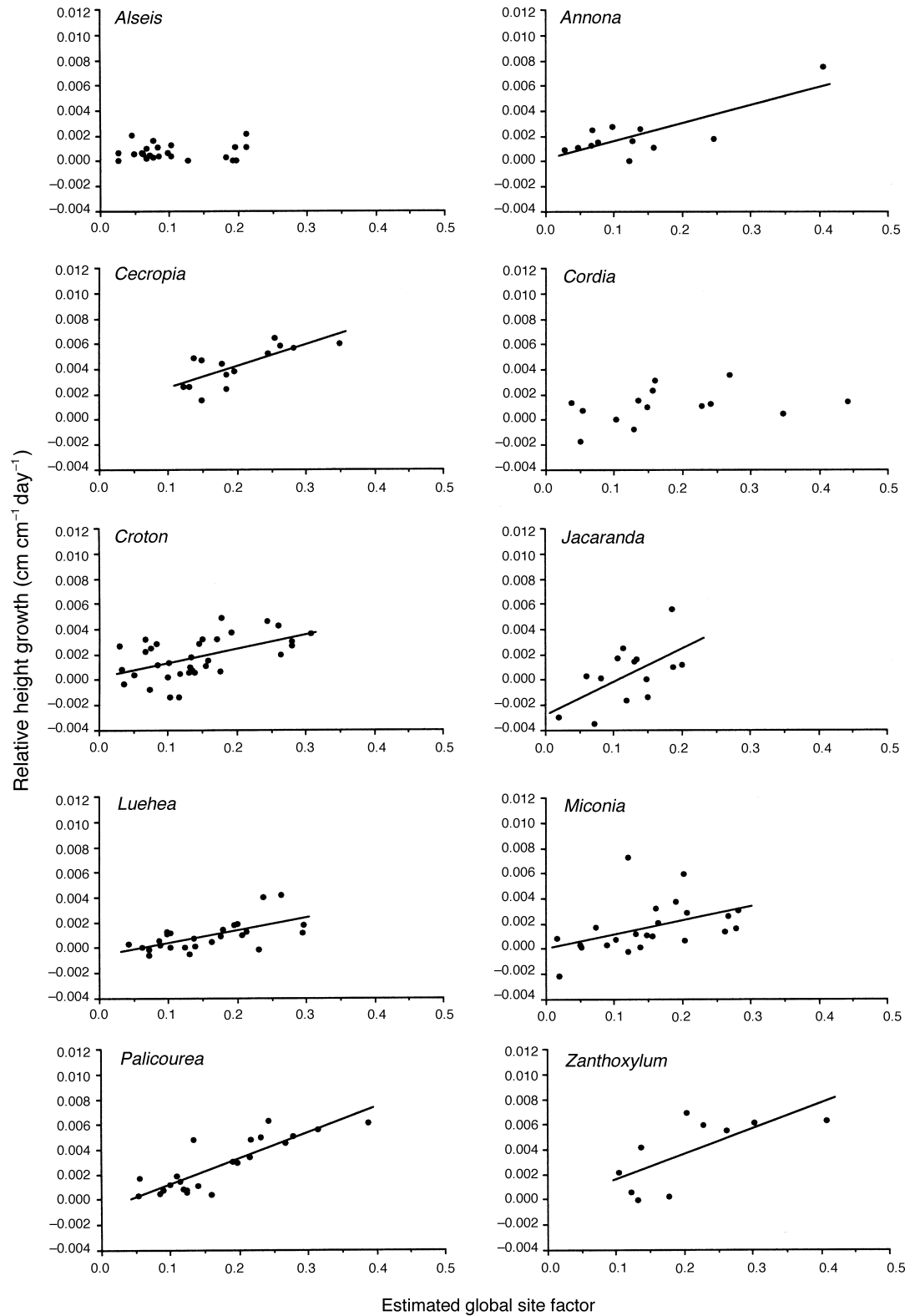
Fig. 3 Relationships between light measured as the estimated global site factor using hemispherical photo analysis and the relative height growth for pioneer tree species on BCI measured after 7 months for 10 species growing in 35 gaps. Regression equations are given in Table 4.

Table 4 Regression equations and probabilities for significant relationships (Fig. 3) between seedling relative height growth ($cm\ cm^{-1}\ day^{-1}$) and the above-plant estimated global site factor (GSF) light measurement taken with a hemispherical lens in November 1996

Species	Regression equation	r^2	n	P
Annona	$y = 0.014x - 0.0002$	0.61	12	0.0026
Cecropia	$y = 0.016x - 0.0009$	0.55	14	0.0024
Croton	$y = 0.011x - 0.0002$	0.27	35	0.0015
Jacaranda	$y = 0.026x - 0.0028$	0.35	14	0.0260
Luehea	$y = 0.010x - 0.0006$	0.39	26	0.0007
Miconia	$y = 0.011x - 0.0006$	0.19	23	0.0392
Palicourea	$y = 0.020x - 0.0008$	0.72	23	0.0001
Zanthoxylum	$y = 0.020x - 0.0004$	0.49	10	0.0250
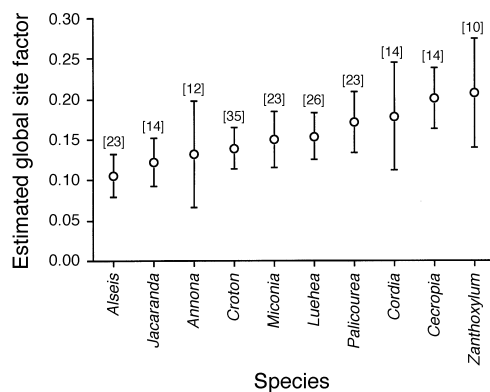
Fig. 4 Estimated global site factor ($\pm$ 95% confidence intervals) for seedlings of 10 species of pioneer trees on BCI ranked by their mean values. Sample sizes are given in brackets above each species.
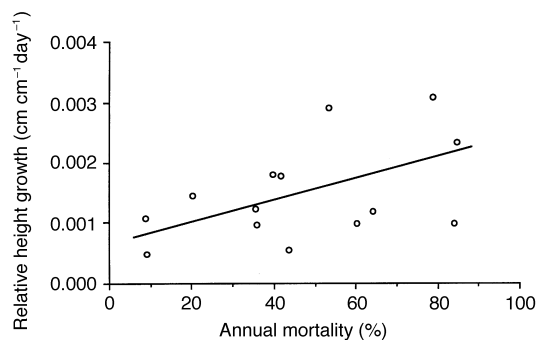
Fig. 5 Correlation between annual mortality rate and height-growth rate for the 14 species of pioneer trees on BCI with > 10 individuals in the initial census.

EVIDENCE FOR DISPERSAL AND EMERGENCE LIMITATION

Seedling dispersion relative to adults

Distributions of the seedlings of most species were significantly skewed towards their conspecific adults when compared to the distribution of seedlings of all focal species to the same adult trees (Fig. 6 shows the 10 most common species). The most marked effects were found for the understorey shrub *Palicourea*, the mid-story tree *Croton*, and the canopy trees *Jacaranda* and *Zanthoxylum* spp. None the less, even seedlings of the very small-seeded and very abundant canopy tree *Alseis*, and of the very small-seeded pioneer tree *Miconia*, were significantly skewed towards adults. Seedlings of *Alchornea*, the least abundant of the species tested, did not differ from expected in their distribution pattern, and *Luehea* seedlings were significantly skewed away from adults (Fig. 6). Excluding *Alchornea*, D_{max} (the maximum difference between cumulative distributions) was positively correlated with seed size (Spearman's rank correlation, $r_s = 0.77$, $n = 9$, $P < 0.05$).

*Between gap seedling abundance patterns*

Comparisons of species abundance on a per-gap basis, and expressed as the proportion of all focal seedlings present in the gap (Fig. 7), reveal some differences compared with the seedling dispersion patterns described above. While *Alseis* and *Cecropia* showed no apparent effect of distance on the proportion of seedlings in the gap, most species had wedge-shaped distributions with both high and low occupancy rates in gaps close to adults, but only low rates in distant gaps. For three species, *Apeiba*, *Croton* and *Jacaranda*, there were significant negative relationships between the proportion of seedlings in the gap and distance from the nearest conspecific adult (binomial regression; Fig. 7).

Discussion

ABUNDANCE PATTERNS OF PIONEER SPECIES

Species' relative abundances changed markedly from the soil seed bank community to the seedling community, but relative abundances of seedlings were very similar to relative abundances of adults. Seed
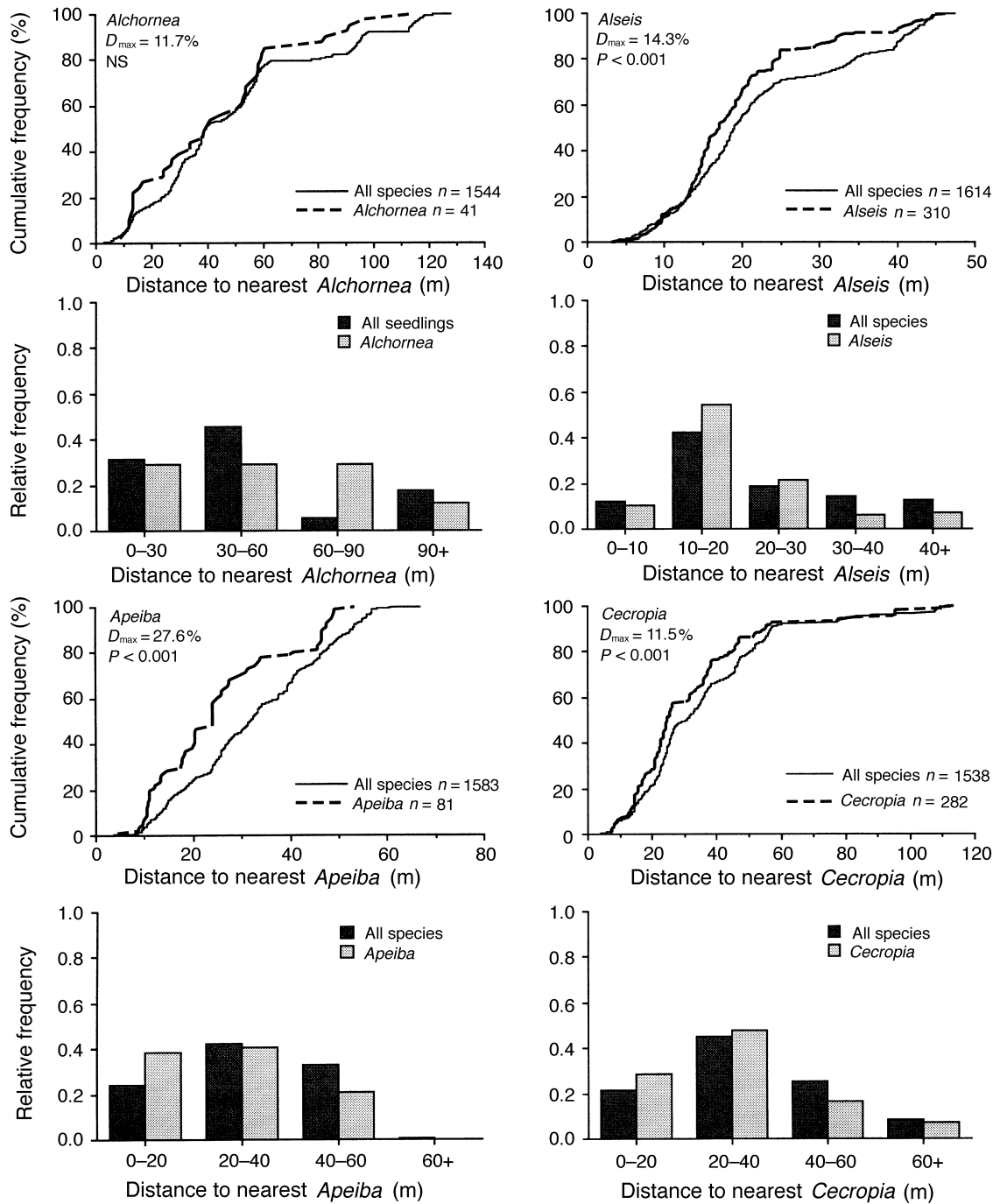
Fig. 6 Distribution of seedlings relative to adults for the 10 most common species. Upper panels: cumulative distribution of relative frequencies of distance from the nearest reproductive-sized adult of a target species (i) for seedlings of the target species (thick broken line), and (ii) for all focal species (thin solid line). Note: the all-species distribution represents the expected distribution pattern of the target species assuming no dispersal limitation, and no distance or density-dependent effects on its recruitment. Lower panels: relative frequencies of the target species and all species taken at four classes of distance from adults of the target species. Note differences in scale between species.

germination, seedling emergence and early establishment probabilities therefore appear to be very important determinants of abundance for pioneers. Whereas the rank abundance of seeds in the soil seed bank was strongly negatively correlated with seed size, the strength of the relationship with seed size declined after seedling emergence, and for seedlings > 10 cm high seed size was uncorrelated with abundance. The

declining importance of seed size results, in part, because some relatively large-seeded species, such as *Palicourea* and *Croton*, that were very rare in the seed bank became common as seedlings, whereas the relative abundance of small-seeded species dropped from the seed bank to the seedling layer (e.g. from 43% to 16% for *Miconia*, and from 28% to 8% for *Cecropia*).
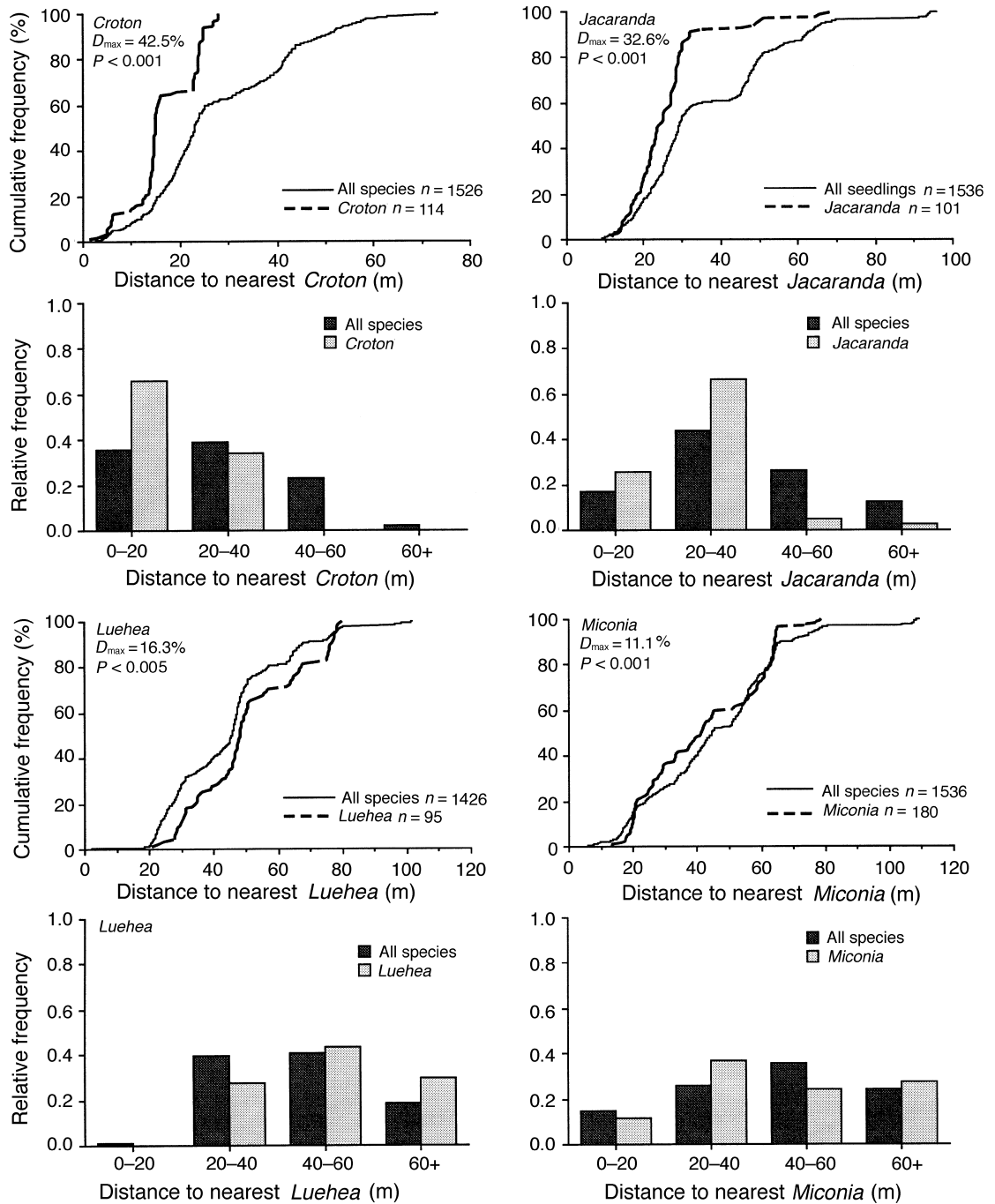
Fig. 6 *continued*

Differences between seed bank and seedling relative abundances may reflect variation in the relative importance of direct dispersal into gaps vs. emergence from the soil as recruitment pathways for different species. However, direct seeding into existing gaps is probably important for very few pioneers on BCI: fruit production is limited to a few months per year for all the species in this study (Foster 1982), and almost all show some seed dormancy (Table 1).

Changes in abundance may result instead from a trade-off between dispersal and establishment or from differences in the habitat requirements of pioneer species. Here we find some evidence suggesting such a trade-off because the change in relative abundance from the seed bank to the seedling layer was positively correlated with seed size. Both emergence and establishment probabilities may be important components of this trade-off. In a growth chamber experiment, species varied considerably in the burial depth from which they emerged successfully. Whereas larger-seeded species such as *Apeiba* and *Solanum* successfully emerged from 5-cm burial, the small-seeded pioneers *Miconia* and *Cecropia* were only capable of emerging from the surface few millimetres of soil (J.
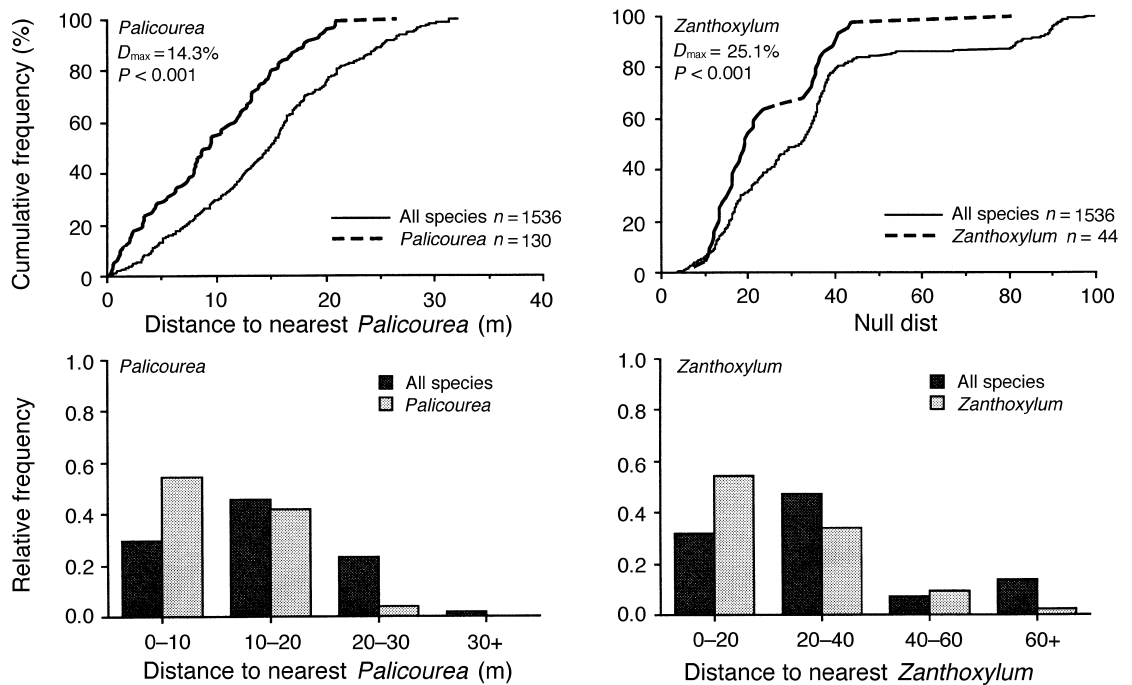
Fig. 6 *continued*

Dalling, unpublished data). Similarly, the presence of surface litter has a strong inhibitory effect on seed germination and emergence, with the smallest seeded species being most susceptible (Vázquez-Yanes *et al.* 1990, Guzmán-Grajales & Walker 1991; Molofsky & Augspurger 1992; Dalling 1995; Metcalfe & Grubb 1995). Once emerged, small seedlings from small seeds may also be more susceptible to damage and herbivory, uprooting by birds and mammals, and desiccation during the dry season (e.g. Clark & Clark 1989; Grubb 1996; Harms & Dalling 1997).

EVIDENCE FOR HABITAT SPECIALIZATION

Although seedling abundance varied enormously within gaps, we failed to find an effect of gap size on seedling density, either when gap size was expressed as the number of contiguous low canopy sites, or using the estimated GSF index of light taken at each gap sample centre point. This is in contrast to the strong correlation found by Brokaw (1982b) in the same patch of forest for saplings > 1 m height. This difference may be because most gaps in our study were small (25 m² on our scale; < 100 m² by Brokaw's (1982a) definition), whereas Brokaw's study included numerous gaps > 300 m². Seedling density may be unresponsive to small changes in canopy openness in very small gaps (see Fig. 1 in Brokaw 1982b), or perhaps the difference results from greatly reduced light availability in the seedling layer as opposed to the sapling layer of gaps.

In examining how habitat requirements for seedling establishment and early growth differed among species, we focused on potential partitioning of the light environment and on one extreme comparison of the potential conditions for seedling emergence (use of the terrestrial vs. elevated sites). Hemispherical photographs have been used successfully in previous studies to characterize the light environment of individual plants (Pearcy 1983; Newell *et al.* 1993; Rich *et al.* 1993; Olesen 1994) and in this study we found a positive relationship between seedling relative height growth and light availability (as estimated GSF) for eight out of 10 species.

None the less, we failed to find species-specific responses to light. With the exception of the relatively shade-tolerant species *Alseis*, neither the mean light environments of seedlings nor the growth responses to light were significantly different between species. While this may be because sample sizes were small, differences in growth rates among gap-dependent species with different carbon allocation patterns may be counteracted by differences in herbivore loads among well and less well defended plants (Coley & Barone 1996).

After 1 year, however, differences in growth rates and mortality rates among species were clear, and there was a tendency for growth and mortality to be positively correlated. In a greenhouse study on BCI, Kitajima (1994) found comparable results for 13 mostly shade-intolerant species. She found that the species with the highest relative growth rates (RGR) in sun also had the highest RGR in shade, and that mortality rates in shade were positively correlated with RGR in both sun and shade. She interpreted these results as consistent with a growth-mortality trade-off acting through species-specific allocation patterns either to leaf area or to other morphological
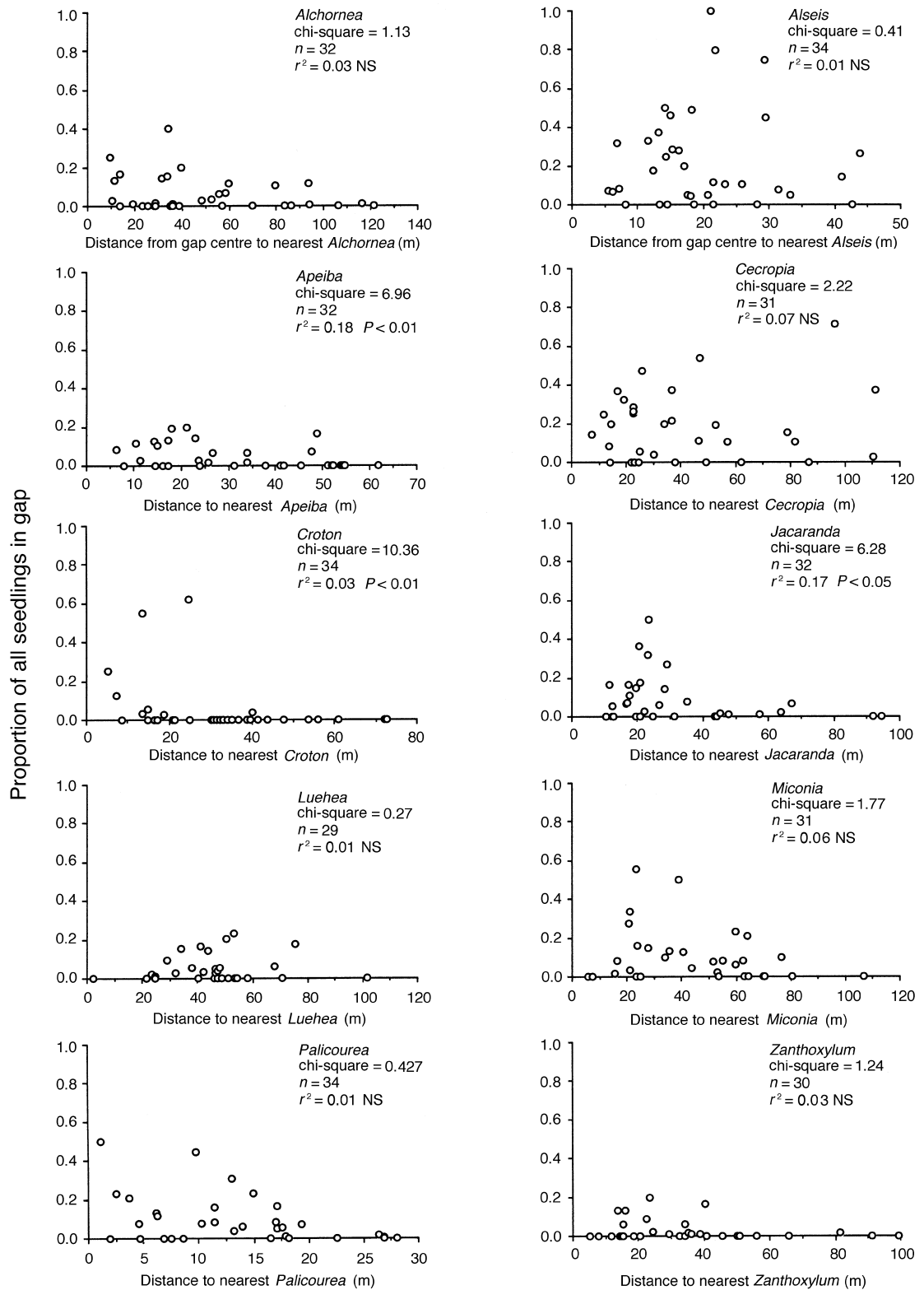
Fig. 7 Relationship between distance of a gap to the nearest reproductive-sized individual of a target species, and the proportion of all focal seedlings within that gap belonging to the target species. Data were analysed by weighted binomial regression and significance tested against the χ^2 distribution (1 d.f.).

traits that confer resistance to pathogens and herbivores. The large differences in growth and mortality among pioneers we report here suggest that a similar trade-off may be at work, and that this might explain

the different distribution patterns of saplings of three pioneer species found by Brokaw (1987). Assuming that RGR rankings among species remain the same throughout early growth, then pioneers with the high-

est RGR would be increasingly limited to sites with the highest light availability if, in lower light sites, rates of carbon assimilation were too low to replace tissue lost to herbivores and pathogens. In contrast, species with lower RGR would have lower rates of tissue loss because of greater allocation to defensive traits and would have lower mortality rates in more shaded sites.

The effect of within-gap heterogeneity in recruitment sites on pioneer distributions on BCI has already been highlighted (Putz 1983), and the differential establishment success in elevated vs. terrestrial sites found here provides further evidence. The role of factors other than light in determining establishment success in gaps (e.g. root competition and nutrient availability, litter, damage from falling debris) requires more attention for their importance to be assessed.

IMPORTANCE OF DISPERSAL LIMITATION

Seed distribution patterns in relation to adults suggest that some dispersal limitation operates for most common pioneer species on BCI (Fig. 6). As expected from a seed size vs. seed number trade-off, the effects of dispersal limitation for small-seeded pioneers were slight, but the degree to which seedling distributions were skewed towards conspecific adults was positively correlated with seed size. On a presence–absence per-gap basis, however, the effect of dispersal on gap occupancy is less clear, and few species were so dispersal limited as to be completely absent from distant gaps. Instead, most species showed triangular distributions of seedling relative abundances with respect to distance to reproductive-sized conspecifics (Fig. 7). This may suggest that dispersal limitation provides an upper boundary to the potential number of seedlings able to colonize a site, and that other factors influence seedling abundances within individual sites, or it may reflect the importance of making more detailed assessments of the fruit production and dispersal parameters of individual species. In our analysis, the only parameter for dispersal limitation was the distance to a reproductive-sized individual. In reality, seed shadows of wind-dispersed species are unlikely to be symmetrical, seed crops presumably increase with tree diameter and not all trees fruit annually.

Hamill & Wright (1986) examined how juvenile distribution patterns can differ from cumulative frequency distributions representing a null model of randomly distributed juveniles. Simulations based on limited seed dispersal and a consequent clumping of juveniles close to conspecific adults yielded similar results to those found here for the majority of pioneers (Fig. 6), but so did an alternative scenario in which adults and juveniles both show a preference for particular underlying patch types within the forest. Such a result might be expected if individual species differ in their ability to colonize different edaphic or topographic sites within the 50-ha plot. However, little

evidence exists for such habitat preferences among pioneers. Harms (1997) used a Monte-Carlo simulation to generate comparative null distributions of stems > 1 cm d.b.h. across five different habitat types (high plateau, low plateau, slope, stream and swamp) within the 50-ha plot. Of the 24 focal species we examined in this study, only five showed habitat associations; *Alseis* stem density was negatively associated with the small swamp site in the plot, and *Cordia*, *Miconia*, *Palicourea* and *Terminalia* were negatively associated with slope sites.

Seedling dispersion patterns relative to seed dispersion patterns may also be strongly affected by post-dispersal seed predation, and it is important to point out that what we have examined is, strictly speaking, emergence limitation rather than dispersal limitation. If seed predation is positively density-dependent, as occurs for *Miconia* (Dalling *et al.* 1998), then seedling densities close to adults may be lower than expected. However, if dispersal limitation is strong enough, with most seeds aggregated around adults, then quite strong density-dependence may not greatly affect the shape of the dispersal curve, and density dependence itself may go undetected (Hubbell 1979). In the case of *Luehea*, the seedling dispersion pattern suggests that density-dependent effects can overcome those of dispersal limitation. *Luehea* seedling abundances were *lower* than expected up to 40 m from the nearest adult (Fig. 6). This is consistent with observations of *Luehea* seed rain and seed abundance in the soil seed bank: while seed rain densities decline logarithmically with distance from adults, germinable seed densities from the soil seed bank are low and independent of distance from adults (J. Dalling, unpublished data).

Uniform or patchy density-independent seed predation and low seedling emergence probabilities may also affect seedling dispersion patterns. Strong density-independent seed mortality has been found for both pioneer and non-pioneer species (Gryj & Domínguez 1996; Dalling *et al.* 1998), and may accentuate apparent dispersal limitation by reducing the probability of seedling emergence at the tail of the seed dispersal curve. The extent to which differential seedling emergence probabilities among species might also modulate the effects of dispersal limitation is unknown. In the two studies we are aware of, less than 10% of the estimated seed pool emerged as seedlings under gap conditions (Williams-Linera 1990; Kennedy & Swaine 1992), but species-specific emergence rates have not been measured.

MAINTENANCE OF DIVERSITY OF GAP-DEPENDENT SPECIES

Seed dispersal, seed germination and early establishment, as well as seedling growth and mortality, all seem to play a role in determining the patterns of pioneer abundance and distribution. Seed dispersal and dormancy parameters ultimately determine which

gap sites are reached by individual species, and appear to have most influence on the larger seeded species with small seed crops. In contrast, small-seeded species may be most constrained by their seed germination and seedling emergence probabilities, as suggested by their decline in relative abundances from the soil seed bank to the seedling layer. Finally, differences in growth and mortality rates among species with different carbon allocation patterns may explain observed patterns of gap partitioning observed in sapling size classes (Brokaw 1987), but not observed for seedlings.

Acknowledgements

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