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Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species

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Summary

1 We examined how seed size and seedling growth rate influence recruitment success of neotropical pioneer species. We investigated the soil seed bank, and followed seedlings from emergence and establishment to the sapling stage in artificially created gaps in secondary forest on the Barro Colorado Nature Monument, Panamá.

2 To simulate microsite variation within gaps, litter addition/removal and soil disturbance treatments were applied to seedling plots in a factorial design.

3 Seedling emergence was almost three-fold higher in litter-free plots than in control plots.

4 We found a negative relationship between seed mass and seed abundance in the soil, seed mass was positively correlated with seedling emergence success from the seed bank and with seedling survival through to the end of the first dry season.

5 In the 18 months following the first dry season we observed an uncoupling of seed mass from seedling performance. Seedling mortality was now a function of maximum relative growth rate, with higher mortality of fast-growing species attributable to herbivory, notably by shoot-borers.

6 We propose that a seed size-dependent trade-off between dispersal success (selecting for large seed number), and emergence–establishment success (selecting for large seed size) can explain the maintenance of wide variation in seed size among pioneer species. Secondarily, a trade-off between growth rate and susceptibility to herbivores acting at the post-establishment phase may contribute to observed differences in light requirements among pioneer species.

Key-words: gap phase regeneration, herbivory, seedling emergence, seedling establishment, trade-off

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Introduction

Many factors are thought to contribute to species coexistence and the maintenance of life-history diversity in plant communities. These include fine-scale specialization in regeneration requirements and biotic interactions among species (e.g. Harper *et al.* 1961, 1965; Janzen 1970; Connell 1971; Grubb 1977), and the importance of chance events coupled with community-wide recruitment limitation (e.g. Hubbell 1979; Hubbell & Foster 1986; Hurtt & Pacala 1995). Although studies focused at particular life-history stages may indicate that each of these factors play a role, evaluation of their relative importance, and of the interactions among them, requires an integrated study of all juvenile size classes.

Fast-growing pioneer species provide a useful system to examine the life-history correlates of differential recruitment success from the seed to the sapling size class. In tropical forests, pioneers form a small functional group of trees and shrubs characterized by an inability to persist as seedlings in the forest understorey. Previous studies have shown that pioneers recruit predominantly from dormant seeds in the soil (e.g. Guevara Sada & Gómez-Pompa 1972; Lawton & Putz 1988), that species vary in their requirements for seed germination (e.g. Vázquez-Yanes 1974; Vázquez-Yanes & Smith 1982) and seedling establishment (e.g. Riera 1985; Nunez-Farfan & Dirzo 1988), and that species vary in light requirements for sapling growth and survival (Brokaw 1987; Van der Meer *et al.* 1998).

Seed mass is perhaps the most important life-history character influencing recruitment success (e.g. Gross

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1984; Howe *et al.* 1985; Tripathi & Khan 1990; Paz *et al.* 1999; Turnbull *et al.* 1999). In central Panama, seed mass varies over at least four orders of magnitude among coexisting pioneer species (Dalling *et al.* 1997). Small-seeded pioneers are most abundant in the soil seed bank at this site, but they are not more abundant as seedlings in natural gaps (Dalling *et al.* 1998). Consequently, large-seeded species must have much higher per-capita germination, emergence or establishment success than small-seeded pioneers (Dalling *et al.* 1998).

Mortality of larger sized seedlings and saplings may also be important in shaping the distribution pattern of pioneers across gaps (Brokaw 1987). Absolute differences in size among individuals are progressively less likely to be determined by variation in seed mass or timing of seed germination as seedlings grow, with variation in growth rates becoming the major determinant of plant size, and thereby of the outcome of competitive interactions among individuals. At this stage, allocation to defence may largely determine the outcome of interactions with pests and pathogens and may also limit both the population size and distribution of fast-growing species (Kitajima 1994; Kobe 1999).

In this study we examine the mechanisms and life-history correlates of differential recruitment success from the seed to the sapling stage for pioneer species in central Panama. We use artificially created treefall gaps to evaluate simultaneously the relative importance of life-history characters (seed dormancy, seed size, and relative growth rate), and microsite conditions (light, litter and soil disturbance) on pioneer recruitment success. We assess whether species distributions within and across gaps are mostly determined by the composition and abundance of the seed bank, reflecting local dispersal and seed longevity, or by species-specific seed germination, seedling establishment, or post-establishment success in different gap microsites.

Methods

STUDY AREA

The study was carried out in seasonally moist tropical forest in the Barro Colorado Nature Monument (BCNM), Panama (9°10′ N, 79°51′ W). Rainfall at BCNM averages 2600 mm/year, with a pronounced dry season from January through April (Rand & Rand 1982). The flora is described by Croat (1978), and by Foster & Brokaw (1982); in the present paper, species nomenclature follows Croat (1978). Gaps were created on the Buena Vista peninsula, an area of secondary forest *c.* 70 years old, contiguous with Soberania National Park (Denslow & Guzman 2000). Canopy height at this site averages 20 m, with emergent individuals of *Ficus insipida* and *Pseudobombax septenatum*. The canopy is dominated by a diverse assemblage of approximately 30 pioneer tree species, and has a great abundance of palms.

OVERVIEW OF EXPERIMENTAL DESIGN

In July 1997 we located five sites, each of 100 m^2, separated by at least 30 m, within a 5-ha plateau on the western half of the Buena Vista peninsula. All sites were under closed canopy, but lacked trees > 40 cm d.b.h. Within the central 9 m × 9 m of each site we established a square 6 × 6 grid of 36 1 × 1 m plots each separated by 0.5 m wide access strips. We sampled the soil seed bank along the access strips and then felled all trees and shrubs within the sites, and cut lianas back to the gap edge. After gap creation in August 1997, plots were randomly assigned one of six litter removal and soil disturbance treatments simulating a range of natural gap microsites. For the first 8 months (i.e. until April 1998) we recorded all seedling emergence and mortality within the plots. For the following 14 months we recorded the growth, mortality and herbivory rate on up to 10 of the tallest seedlings recruited in each plot.

GAP CREATION AND SEED BANK SAMPLING

The artificially created gaps were similar in size to most tree fall and branch fall gaps where the majority of pioneer recruits are found on BCNM (Dalling *et al.* 1998). However they differ from natural gaps in an important respect in that we removed all ‘advance regeneration’ (seedlings and saplings present at the time of gap formation) and all woody debris which fell into the gap as it was cut. Small seedlings and saplings were removed from the seedling plots by cutting the stems at ground level to avoid soil disturbance, and re-sprouts were cut back every month until December 1998, and every 3 months until June 1999.

We collected 21 soil samples from the access paths between plots in each gap, with each sample taken at a random location between different, adjacent plots. Soil samples were excavated using a 6-cm deep, 10.3 cm diameter open-ended soil corer flanked with an aluminium collar that prevented soil from falling into the core hole. The core was subdivided into 0–1 cm, 1–3 cm and 3–6 cm deep subsamples that were measured volumetrically in the field. Samples were collected in mid-July 1997, less than 1 week prior to gap creation, and just after the end of the 3–4 month fruiting season for most pioneers in the BCNM (Foster 1982; Dalling *et al.* 1997). Therefore, with the exception of two pioneer taxa with prolonged fruiting seasons (*Ficus* spp. and *Cecropia* spp.), seedlings of pioneers that emerged in our plots during the first 9 months of the study must have originated from the seed bank rather than from new seed rain.

All soil samples were transported in black polyethylene bags, stored in an air-conditioned laboratory at 25 °C, and processed within 48 h of collection. Soil samples were spread evenly to a depth of 0.5 cm in seedling trays containing a 1-cm deep layer of moist, seed-free sand, and the seeds allowed to germinate over a 10-week period (Dalling *et al.* 1995). As a control against contamination, four additional trays containing autoclave-sterilized soil (116 °C for 1 h) were included with each set of soil samples. Seedling trays were placed at random on benches covered by clear plastic within two screened growing houses in the laboratory clearing on BCI, under conditions ranging from 15% to 25% full sun. Trays were hand-watered daily, and seedling emergence from soil flats was recorded at weekly intervals. Seedlings that could not be identified after 10 weeks were individually potted and grown up until identification could be made.

TREATMENTS AND SITE MEASUREMENTS

The 36 seedling plots in each gap were randomly assigned to six different treatments generated by the combination of three litter treatments (unmanipulated, litter addition and litter removal), and two soil-disturbance treatments (disturbed and undisturbed). These treatments were designed to simulate the principal microsite conditions found in natural gaps (Orians 1982; Brandani *et al.* 1988): litter removal and soil disturbance partially mimics the root plate area of natural treefall gaps, and litter addition mimics the portion of the gap occupied by the fallen tree crown. At the start of the experiment litter was transferred from litter removal plots to the top of existing litter in the litter addition plots to form a layer approximately 5 cm deep. Fresh litter fall was removed from the litter-removal plots every week for the first 9 months of the experiment. Disturbance was simulated by turning over the surface 3 cm of soil with a fork. We also determined the probability of seedlings being covered by freshly fallen leaves during early establishment by burying toothpicks at four random locations within each of the 12 litter-free plots in each gap. Only the 2 mm diameter blunt end of the toothpick, simulating the initial cotyledon area of a small-seeded pioneer, protruded from the soil. The presence or absence of litter covering toothpicks was recorded weekly from September 1997 until May 1998.

Finally, as a measure of site conditions among and within the gaps, we took one hemispherical photograph in October 1997 1 m above the centre of each litter-free plot in each gap. Photographs were taken with Kodak Tri-X pan ASA-400 black and white film (Eastman Kodak, Rochester, New York) using a Nikkor 8 mm hemispherical lens and a Nikon FM2 camera (Nikon, Melville, New York). Percent canopy openness for each image was calculated using the video image analysis program CANOPY (Rich 1989; Rich *et al.* 1993).

MEASUREMENTS OF SEEDLING EMERGENCE AND GROWTH

All new seedling recruits appearing in the seedling plots were censused every 2 weeks for the first 8 weeks (i.e. until October 1997), and subsequently monthly until the end of the dry season in mid-April 1998. To follow seedling survival we marked all individuals with coloured toothpicks and mapped seedling locations within plots to the nearest 10 cm. Most seedlings were identifiable at the cotyledon stage (to genus in the case of *Cecropia*, *Piper*, *Ficus* and *Zanthoxylum*). We consider this 8-month period (July 1997–April 1998) to constitute the period of 'seedling establishment'.

In January 1998, we tagged and measured the height of the 10 tallest seedlings in each plot (including non-pioneer recruits, but excluding lianas that had adopted a climbing habit). Heights were remeasured monthly until June 1998, every 2 months until December 1998, and every 3 months until June 1999. We consider April 1998–June 1999 to be the 'post-establishment' period. The few individuals that outgrew the initially tallest 10 seedlings in each plot were not added to the census; however, seedlings that died during the census period were replaced by the next tallest previously unmarked/untagged individual in the plot.

By mid-September 1998 herbivore damage appeared to be common and we conducted a one-time census of damage to all seedlings of the 13 taxa recorded in the plots. For each seedling we recorded height, proportion of total leaf area consumed by herbivores in categories of 0, < 50, and > 50% leaf area removed, and whether the leading shoot of the seedling had died-back or been consumed.

STATISTICAL ANALYSES

A comparison of the species relative abundance in the soil seed bank and among seedlings that emerged in the litter-free plots pooled from each gap was made using ordination. We calculated the Jaccard similarity index for the seed and seedling composition of each gap using only the 15 most abundant taxa present in the seed bank of all gaps combined. The matrix was analysed using Non-metric Multidimensional Scaling (NMS) ordination (PC-ORD; McCune & Mefford 1997), a technique that yields readily interpretable configurations of sites on a minimal number of dimensions.

Effects of plot treatments and seed mass on seedling mortality to the end of the first dry season, and at the post-establishment phase were analysed using generalized linear modelling in GLIM (v. 3.77; Royal Statistical Society, London, UK). To avoid problems of inconstant variance and negative mortality rates that might be predicted when normal errors models are applied to proportion data, we assumed binomial error distributions, used the total sample size from which each observed proportion was drawn as the binomial denominator, and employed a linear model using a logit link function (Crawley 1993). 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 variables. Large relative values of the residual deviance indicate overdispersion which may result in overestimation of significance levels. To account for this, the deviance was rescaled by an appropriate 'heterogeneity factor', the ratio of the residual deviance to the degrees of freedom (McCullagh & Nelder 1989). Hypothesis testing on overdispersed data was carried out using an *F*-test rather than a Chi-squared test (Crawley 1993).

Comparisons of emergence and establishment success among pioneer species were restricted to the litter-free plots, and to the 15 most abundant pioneer species present in the soil seed bank, because of limited sample sizes. Post-establishment seedling mortality analyses included both the pioneer species that recruited from the seed bank and seedlings of species that recruited from seed rain following gap creation. Binomial errors were employed in regressions using proportional seedling emergence or mortality as the dependent variable; regressions of seed and seedling abundances on seed mass were log-transformed prior to analysis with normal error structures.

Results

SOIL SEED BANK COMMUNITY

A total of 38 taxa were identified from seedlings germinated from the soil seed bank samples. The majority of taxa were trees or shrubs (23), followed by herbs (10), and lianas (5). Seed mass data for the most abundant taxa are given in Table 1. Seed densities were significantly higher at Gap 3 than for other sites (ANOVA $F_{4,100} = 8.41$; Bonferroni post-hoc test, $P < 0.05$), because of high densities of *Miconia argentea* seeds at this site (Table 1). This was the most abundant species in every site, but otherwise seed bank composition varied markedly across the gaps, with the sedge *Rhynchospora cephalotes* particularly abundant in Gap 1, the tree *Trema micrantha* in Gaps 3 and 5, and the trees *Cecropia obtusifolia* and *Cecropia peltata* in Gap 4. The early pioneer seedling communities of these gaps strongly reflected their seed bank compositions (Fig. 1).

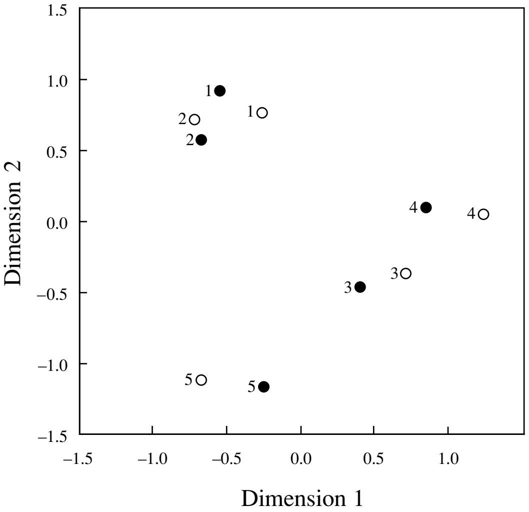

Fig. 1 Non-metric Multidimensional Scaling Ordination of relative abundance data for the 15 most abundant seed bank taxa in the 5 gaps. Closed circles: seed bank data; open circles: seedlings that emerged in the first 8 months of the study.

LIGHT ENVIRONMENTS AND LITTER FALL REGIMES

Canopy openness varied significantly among gaps (ANOVA $F_{4,55} = 4.25$; $P < 0.001$), however, post-hoc comparisons were significant only between the brightest site, Gap 5 (mean 13.2%, SD = 0.03) and the darkest site, Gap 4

Table 1 Total mean seed density (±1 SE), total number of identifiable taxa, and mean seed density for the 15 most abundant taxa in the top 0–6 cm of soil ordered by abundance. The study was carried out in a seasonally moist tropical forest in Panama. Air dry seed mass (mg), and life-form (T = shrub/tree, H = herb, C = climber) are given for each species in parentheses. Soil samples ($n = 21$ per site) were taken 1 week prior to gap formation

Gap site	1	2	3	4	5
Mean seed density (m^{-2})	1390 (± 150)	1070 (± 110)	3180 (± 450)	1720 (± 230)	1850 (± 140)
Total number of taxa	21	22	23	23	23
Miconia argentea (0.08) (T)	440	390	2160	840	800
Melastomataceae[1] (0.007) (T)	80	90	190	150	340
Cecropia spp[2]. (0.68) (T)	90	110	130	210	110
Piper spp. (0.04) (T)	170	60	130	100	70
Rhynchospora cephalotes (0.97) (H)	330	110	10	50	0
Ficus insipida (0.175) (T)	30	70	110	120	70
Trema micrantha (3.9) (T)	50	30	110	20	140
Miconia affinis (0.24) (T)	100	90	10	10	40
Apeiba tibourbou (12.0) (T)	10	0	10	60	70
Trichospermum mexicanum (2.7) (T)	10	10	50	10	50
Alseis blackiana (0.12) (T)	10	10	10	20	20
Scleria secans (10.4) (C)	10	20	0	20	10
Passiflora vitifolia (3.3) (C)	0	0	0	30	0
Apeiba membranacea (14.2) (T)	0	0	0	0	20
Zanthoxylum spp. (11–36) (T)	0	0	10	10	0

[1] Unidentified taxa distinct from *Miconia argentea* and *Miconia affinis*.

[2] Potentially both *Cecropia obtusifolia* and *Cecropia peltata* were present but congeners could not be distinguished at the cotyledon stage. All larger individuals included in growth censuses were *Cecropia peltata*.

(mean 8.5%, SD = 0.03). Canopy openness did not affect either total seedling emergence in litter-free plots or seedling survival to April 1998 ($F_{1,58}$ = 2.9 and 3.1, respectively).

Mean (±1 SE) initial standing leaf litter dry weight at the start of the experiment was estimated at 209 ± 18 g m^{-2} (n = 5). In addition to a large standing crop of litter, high litter fall rates in both gaps and understorey sites probably affected seedling recruitment in initially litter-free sites. For species with small initial seedling sizes (e.g. *Alseis blackiana*, *Cecropia* spp., *Miconia argentea*) one month's growth or more may be necessary before seedlings are sufficiently large to survive when covered by falling leaf litter. The proportion of toothpicks that were covered at least once per month by leaf litter in gaps varied between 0.3 in the mid-late wet season and nearly 0.6 in the late dry season.

SEEDLING EMERGENCE AND PRE-ESTABLISHMENT SURVIVAL

Seedling emergence commenced 2 weeks after gap formation in early August 1997. Emergence rates remained high through the wet season but declined almost to zero by the beginning of the dry season in early to mid December (160 days post-gap formation; Fig. 2). Total seedling emergence over the first 280 days up to the end of the first dry season was significantly different among sites, with highest emergence in Gap 3, reflecting variation in soil seed bank density among sites (mixed model ANOVA on log-transformed seedling counts; $F_{4,149}$ = 11.6; $P < 0.001$). Litter treatment had a strongly significant effect on emergence ($F_{2,149}$ = 194.4; $P < 0.001$); litter removal increased seedling emergence almost threefold over control plots, whereas litter addition reduced seedling emergence almost by half (Fig. 2a). There was a tendency towards higher seedling emergence in plots with soil disturbance at each level of the litter treatment (Fig. 2a), but this effect was not statistically significant ($F_{1,149}$ = 1.8). The proportion of seeds in the soil seed bank that emerged as seedlings was very low. For the treatment with the highest seedling emergence (litter removed and disturbance), 7.1 ± 1.4% (mean ± SE) of the estimated standing crop of seeds in the top 0–6 cm of soil emerged over the period August 1997–April 1998. For the treatment with lowest seedling emergence (litter addition, no disturbance) only 1.3 ± 0.6% emerged.

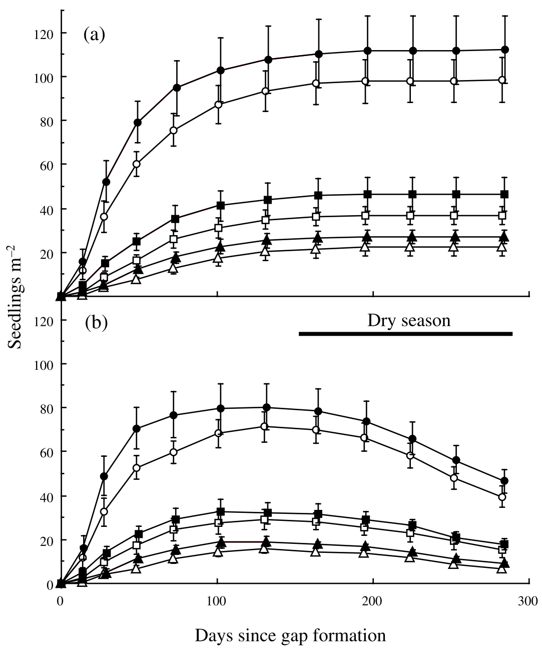

Fig. 2 (a) Cumulative emergence of seedlings (±1 SE), and (b) seedlings surviving until the end of the first dry season following gap creation (the 'pre-establishment' phase) in litter removed treatments (○), controls (□) and litter addition treatments (△). Filled symbols indicate soil disturbance treatment. Symbols are staggered to reveal error bars.

In total 61% of seedlings that emerged following gap formation had died by the end of the first dry season (Fig. 2b). Analysis of deviance performed on proportional mortality in April 1998 showed that there were no significant effects of soil disturbance on seedling mortality, and no interaction effects between litter cover, disturbance or gap. Site had a highly significant effect on mortality, varying from 50% in Gap 2 to 73% in Gap 3 ($F_{4,149}$ = 35.0; $P < 0.01$). There was also a significant effect of litter ($F_{2,149}$ = 5.9; $P < 0.01$) attributable to higher mortality in the litter addition plots (66%). There was no significant difference between mortality in litter removal (58%) and control treatments (60%; ANODEV performed on recoded full model $F_{10,49}$ = 0.91).

Comparisons among species in the litter-free plots indicate that seed mass can be a strong determinant of seed bank abundance, emergence success and establishment success among species in this system. Smaller seeded species were more abundant than larger seeded species in the 0–6 cm deep soil seed bank (r^2 = 0.48; $F_{1,13}$ = 12.1; $P < 0.01$, Fig. 3a), and seed bank abundance in turn had a positive effect on total seedling emergence (r^2 = 0.50; $F_{1,13}$ = 13.0; $P < 0.01$). However, a higher *percentage* of seeds of larger seeded pioneers successfully emerged from the soil seed bank during the first 9 months (r^2 = 0.63; $F_{1,13}$ = 22.5; $P < 0.01$; Fig. 3b). One explanation for this pattern might be that pioneers with different seed sizes differ in the maximum soil depth from which they are potentially capable of emerging. To test this idea, we recalculated the proportion of seedlings successfully emerging from different fractions of the soil seed bank. We used seedling emergence data from the 0–1 cm deep soil layer for the smallest pioneers (< 1 mg seed mass), the 0–3 cm deep soil layer for intermediate sized species (1–10 mg seed mass), and 0–6 cm deep soil layer for the largest pioneers (> 10 mg). These categories were based on the observed maximum burial depths from which different pioneer species could emerge in a growth chamber experiment (Pearson *et al.* 2002). For the recalculated regression, there was no longer a significant effect of seed mass on proportional emergence (r^2 = 0.21; $F_{1,13}$ = 3.4).

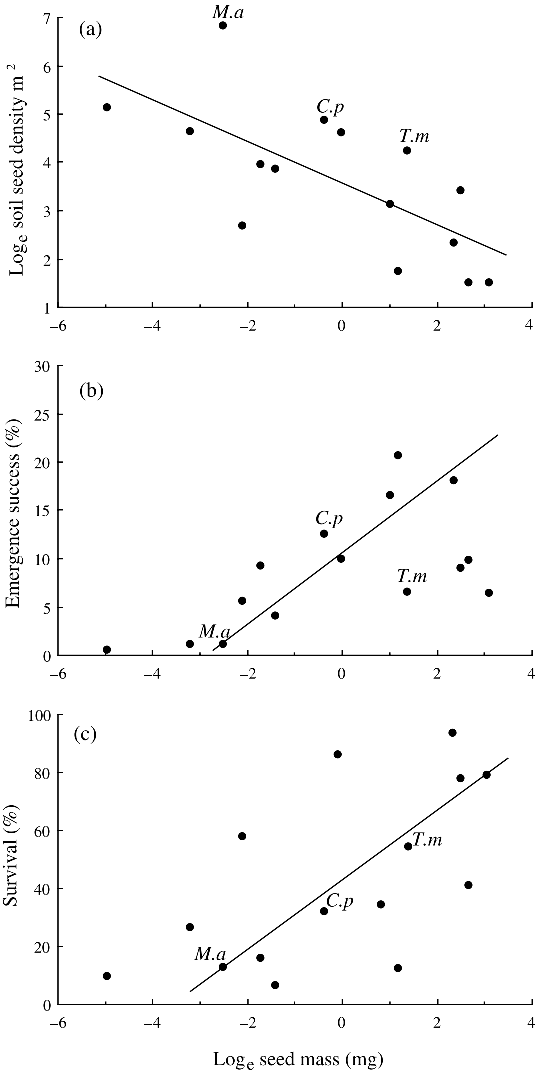

Fig. 3 Regressions of (a) log(seed density m^{-2}) in the surface 0–6 cm of soil, (b) percentage of seeds present in the surface 0–6 cm of soil emerging as seedlings up to April 1998 against log(seed mass), and (c) percentage of seedlings that emerged that survived to April 1998, against log(seed mass). Data for the 15 most abundant species in the soil seed bank and litter-free plots only. Three common pioneer species are identified: *Cecropia peltata* (*C. p*); *Miconia argentea* (*M. a*) and *Trema micrantha* (*T. m*).

Neither seed mass nor seed bank density alone (0–6 cm depth) significantly affected seedling abundance at the end of the first dry season ($r^2 = 0.03$ and 0.13, respectively). However, a multiple regression including both seed mass and seed bank density is quite a strong predictor of the abundance of surviving seedlings ($r^2 = 0.53$; $F_{2,13} = 7.4$; $P < 0.01$). This multiple regression reflects the significant positive effect of seed mass on percentage survival of seedlings that emerged ($r^2 = 0.43$; $F_{1,13} = 10.0$; $P < 0.01$; Fig. 3c).

RECRUITMENT OF NON-PIONEERS

In the establishment phase up to the end of the first dry season, seedling communities were dominated by 15 pioneer species. These species accounted for 95% of seeds that emerged in the soil seed bank study, and 66% of the 10 410 seedlings in the seedling plots that emerged and survived long enough to be identified to at least a morphotype. By April 1998, the relative importance of these species had declined, accounting for 56% of the 4069 surviving seedlings. Five additional non-seed bank species absent from the germinable soil seed bank (three shrubs and trees: *Psychotria deflexa*, *Psychotria racemosa* and *Byrsonima spicata*; and two lianas: *Tetracera portobellensis* and *Mascagnia nervosa*) accounted for a large proportion of the remaining recruits (13%) and surviving seedlings (22%). Individuals of these species were proportionally much more abundant than pioneers in the litter addition plots (accounting for 41% of surviving seedlings in April 1998, compared with 31% of survivors belonging to the 15 pioneer species) and they were less abundant in the litter-free plots (where they accounted for only 15% of surviving seedlings, compared with 65% belonging to the 15 pioneer species).

POST-ESTABLISHMENT SEEDLING MORTALITY AND GROWTH

In the post-establishment phase, seedling censuses were restricted to the 10 tallest free-standing individuals in each plot. However, fewer than 10 free-standing seedlings were present in the initial census in some of the plots, and significantly fewer of the litter-addition and control plots combined (39 of 120 plots) contained a full complement of seedlings compared with the litter-removal plots (57 of 60 plots; Fisher Exact test $P < 0.01$). Moreover, despite high seedling mortality, differences in the number of seedlings per plot persisted until the end of the study.

The total marked seedling population declined from 1665 to 1086 individuals during the census period. The 15 pioneer taxa accounted for 42% of individuals at the beginning of the census and declined to 32% at the last census. Most notably, the population size of the most common species, *Cecropia peltata*, declined dramatically during this period from 312 to 40 individuals, whereas the population size of *Miconia argentea* increased from 17 to 66 individuals, reflecting net recruitment of individuals into the census to replace lost individuals (Fig. 4a). The most abundant non-seed bank species in the census were *Tetracera portobellensis* ($n = 206$ individuals in January 1998), 38 of which became climbers during the study and were dropped from the census, and *Byrsonima spicata* ($n = 142$), which was represented among the 10 tallest individuals in four of the five gaps in June 1999.

In addition to high mortality, *Cecropia peltata* also showed negative mean seedling height growth for a prolonged period during the census (Fig. 4b), reflecting widespread and repeated damage to seedling apices from insect herbivores. The fast-growing pioneer tree, *Trema micrantha*, also suffered from insect herbivore damage during this period but mostly recovered by

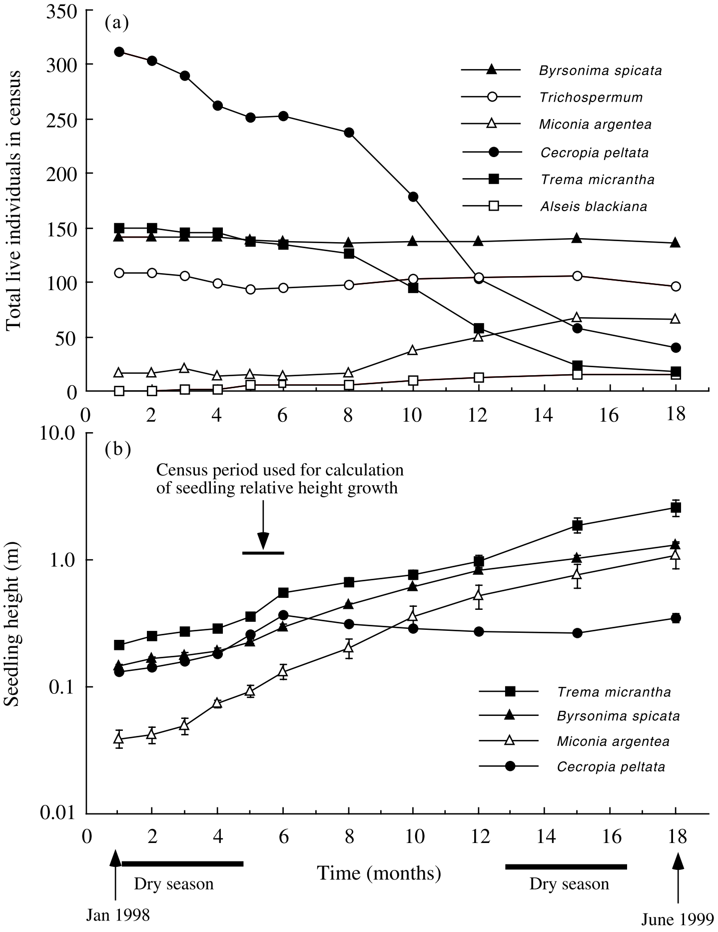

Fig. 4 (a) Total number of individuals of selected species present in 180 1 m^2 plots in five gaps. Only the 10 tallest free-standing seedlings in each plot were included in the census from January 1988 to June 1999. Seedlings that died during the census were replaced by the next tallest free-standing individual present in the plot. (b) Growth curves for selected tree species over the same period.

March 1999. In contrast, *Miconia argentea* was unaffected by shoot damage and mean seedling height exceeded that of *Cecropia peltata* by October 1998 (Fig. 4b). For subsequent, interspecific comparisons of relative height growth we use the May–June 1998 census period after the onset of the wet season and prior to the outbreak of stem-boring and meristem-feeding insects, to calculate species' maximal growth rates.

In the post-establishment phase, seedling relative growth rate, rather than seed mass, was the most important determinant of continuing recruitment success. Considering together the pioneer (n = 7) and non-seed bank tree species (n = 7) with > 20 seedlings in the initial census, we found a significant positive relationship between the maximal relative growth rate recorded in May–June 1998 and proportional seedling mortality from January 1998 to June 1999 ($r^2 = 0.66$; d.f. 1,12; $F = 23.3$; $P < 0.01$; Fig. 5a). In contrast, seed mass was not a significant factor in a multiple regression of proportional seedling mortality on maximal relative height growth rate and seed mass (removal from maximal model; $F = 1.8$; d.f. 1,10; NS).

Loss of the apical growing shoot rather than severe defoliation appears to be a significant source of damage to these seedlings. Only one species, *Alseis blackiana*, had a large proportion (> 40%) of severely defoliated individuals in September 1998, while more than half the individuals of 5 out of 13 species suffered apical damage (Table 2). Species with the highest maximal growth rates also had the highest proportion of individuals suffering apical damage ($r^2 = 0.61$; d.f. 1,11; $F = 17.3$; $P < 0.01$; Fig. 5b). We observed that in some cases apical damage was severe and frequent enough to kill the seedlings. In the case of *Cecropia peltata*, in which leaf tissue is arrayed around the young shoots close to the seedling apex, breakage of the stem by insect herbivores also resulted in the complete loss of leaf area. Direct and indirect impacts of shoot damage are reflected in the positive relationship between proportion of individuals of a species with shoot damage and proportional mortality ($r^2 = 0.56$; d.f. 1,9; $F = 11.8$; $P < 0.05$; Fig. 5c).

Discussion

IMPACT OF INITIAL FLORISTIC COMPOSITION ON GAP REGROWTH

Although our five gaps were all located within a small area (5 ha), we found striking differences in the seed

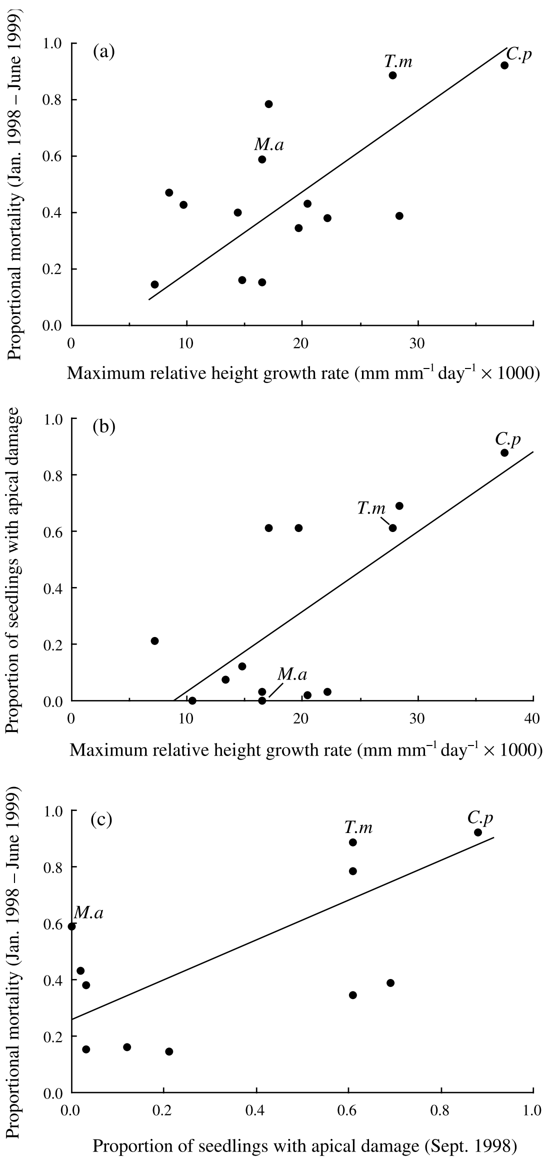

Fig. 5 (a) Regression of the proportion of seedlings marked in January 1998 dying between January 1998 and June 1999, and species-specific maximum relative height growth rate measured between May and June 1998 ($n = 14$ species). (b) Regression of proportion of seedlings censused in September 1998 exhibiting damage to the apical shoot against the species-specific maximum relative height growth rate measured between May and June 1998 ($n = 13$ species). (c) Regression of proportion of seedlings marked in January 1998 dying between January 1998 and June 1999 against proportion of seedlings censused in September 1998 exhibiting damage to the apical shoot ($n = 11$ species). Three common pioneer species are identified: *Cecropia peltata* (*C. p*); *Miconia argentea* (*M. a*) and *Trema micrantha* (*T. m*).

Table 2 Percentage of individuals with apical damage, and with ≥ 50% loss of leaf tissue for the 13 taxa from a seasonally moist tropical forest in Panama censused in September 1998

Species	n	Apical damage (%)	Leaf damage (%)
Alseis blackiana	26	8	42
Apeiba tibourbou	167	61	11
Byrsonima spicata	154	12	0
Cecropia peltata	264	88	28
Ficus insipida	31	61	0
Jacaranda copaia	30	3	0
Lindackeria laurina	29	21	0
Luehea seemannii	61	3	2
Miconia argentea	106	0	0
Psychotria racemosa	286	3	0
Trema micrantha	114	60	2
Trichospermum mexicanum	148	69	1
Zanthoxylum spp.	16	0	6

bank composition among sites. These differences resulted primarily from the great abundance of one or a few species at each site (e.g. *Miconia argentea* at gap 3; *Cecropia* spp. at gap 4; *Trema micrantha* at gap 5) representing localized seed dispersal from one or more reproductive pioneer trees in the canopy surrounding each site (J. Dalling, personal observation). Gaps in old-growth forest sites are, on average, less likely to be dominated by the seeds of a single species because pioneer species occur at lower frequency in the forest canopy in these sites (Dalling & Denslow 1998), and consequently few gaps are likely to be within a few metres of a reproductive-sized pioneer. None the less, even in old-growth forest the disturbance history and recent floristic composition of individual sites should strongly influence the composition of the soil seed bank (Guevara & Gómez-Pompa 1972; Epp 1987; Young *et al.* 1987; Saulei & Swaine 1988; Quintana-Ascencio *et al.* 1996).

Only a small fraction (< 10%) of the standing crop of the seed bank in the top 6 cm of soil germinated, or emerged in the field and survived for long enough to be included in our seedling censuses (see also Williams-Linera 1990). However, the composition of the initial seedling flora strongly reflected the composition of the seed bank (Fig. 1). The 15 most abundant species present in the seed bank (> 95% of seeds) accounted for two-thirds of identifiable seedlings that emerged over the first 8 months of the study. Over time, as new seeds arrived, the relative importance of these pioneer species diminished, accounting for slightly over half of the seedlings that survived until the end of the first dry season, and one-third of the tallest free-standing individuals 2 years after gap formation. This was due to high mortality among some of the most abundant pioneers in the seed bank (e.g. *Cecropia peltata* and *Trema micrantha*), and the high survivorship of a few non-pioneer species that recruited later (e.g. *Byrsonima spicata*, and *Psychotria racemosa*).

GAP MICROSITE EFFECTS ON RECRUITMENT SUCCESS

Heterogeneity in gap microsites has long been thought to be important for the maintenance of pioneer tree species diversity (Orians 1982; Putz 1983; Barton 1984; Riera 1985; Brandani *et al.* 1988; Popma *et al.* 1988; Van der Meer *et al.* 1998). In this study we were able to determine how variation in litter cover affects both community-wide and species-specific recruitment probabilities, and to assess the relative importance of this factor at early life-history stages.

Litter had a dramatic impact on seedling recruitment. We found three times as many seedling recruits in litter removal plots than in plots without litter manipulation, and a smaller, but significant negative effect of litter addition on seedling survival during the first year. Although seed germination and seedling emergence of small-seeded species are known to be most strongly inhibited by surface litter (Vázquez-Yanes *et al.* 1990; Guzmán-Grajales & Walker 1991; Molofsky & Augspurger 1992; Metcalfe & Grubb 1997) we found little evidence that the standing litter crop played a selective role favouring large-seeded pioneers in this system. None the less, litter fall into initially litter-free microsites may have a significant impact on the establishment success of small-seeded species. During the mid-late wet season when most gaps are formed (Brokaw 1982), and when seed bank densities are highest (Dalling *et al.* 1997), we found that 30% of buried toothpicks in gaps were covered by at least one fallen leaf each month. Small seedlings that emerge from small seeds are more likely to be completely covered by fallen litter, and lack resources to grow around or through litter fragments (Metcalfe & Grubb 1995). Soil disturbance did not affect seedling emergence. Therefore the high density of pioneer seedlings observed on tip-up mounds (Putz 1983) may have more to do with the absence of litter than with soil disturbance.

In contrast, light availability had little effect on recruitment success. In part this might be explained by the uniformity of light environments; canopy openness varied by < 15% between measurement points, but even 'large-gap' pioneers (*sensu* Brokaw 1987), such as *Trema* and *Cecropia*, were observed to germinate at gap edges (see also Li *et al.* 1996). Some individuals of *Trema* were observed to set seed in these gaps by August 1999 only 2 years after seedling emergence. Perhaps in natural gaps, within-gap heterogeneity in light availability, including shading from advance regeneration, would be sufficient to generate differential germination patterns among suites of pioneers, as has been suggested (Raich & Gong 1990).

SEED SIZE AND ESTABLISHMENT SUCCESS

Seed mass was a strong predictor of both seed abundance and seedling recruitment success. Whereas small-seeded pioneers were more abundant in the seed bank (see also Dalling *et al.* 1997), we found a positive effect of seed mass on both emergence probability from the seed bank and on seedling survivorship to the end of the first dry season in litter-free plots. An implicit goal of many seed bank studies is the prediction of post-disturbance seedling recruitment patterns, yet differences in seed mass among species influencing emergence or establishment have not been given consideration (e.g. Swaine & Hall 1983; Hopkins & Graham 1987; Saulei & Swaine 1988; Quintana-Ascencio *et al.* 1996; Dupuy & Chazdon 1998). This study indicates that predictions of the early regrowth of pioneers should be based on seed bank data, seed size data, and information on litter coverage.

As yet, the mechanism behind the lower establishment success of smaller seeded pioneers remains unclear (Fig. 3c). For the same physiological tolerance to shade, Grubb & Metcalfe (1996), and Grubb (1998) have argued that plants may make many 'risky' small seeds or fewer larger 'safe' seeds. Smaller seeds give rise to seedlings more liable to suffer high mortality from drought, physical disturbance by animals or falling debris, and to suffer overtopping if they are adjacent to seedlings from larger seeds under favourable conditions. In this study we rarely observed seedling uprooting by birds and mammals, and seedling densities were seldom high enough for overtopping to occur. Instead, we suspect that most early post-emergence mortality can be attributed to desiccation during short dry spells in the wet season. The top few millimetres of soil dried very rapidly in gap sites exposed to direct solar radiation. Significantly elevated mortality rates have been shown for recently germinated pioneer seedlings in large gaps during dry periods lasting only 4 days (Engelbrecht *et al.* 2001).

GROWTH RATE AND POST-ESTABLISHMENT SEEDLING SURVIVAL

We observed an uncoupling of seedling survivorship from seed mass after the first dry season. At this post-establishment stage, seedlings of the smallest seeded species had presumably grown sufficiently to escape the mortality hazards associated with small absolute size. Instead, we found a positive relationship between a species maximum relative height growth rate and its mortality rate over the 18 month post-establishment period. We found no effect of seed mass on the seedling relative growth rate in this study or in a related pot experiment using 12 pioneer species (J. Dalling, unpublished data).

A positive relationship between high-light growth rate and low-light seedling mortality has been found previously in both temperate and tropical forests (Kobe *et al.* 1995; Pacala *et al.* 1996; Kobe 1999), and for pioneer and shade tolerant species on BCI in a pot experiment (Kitajima 1994). A trend towards higher mortality in the fastest-growing pioneer species was also found for seedlings censused in natural treefall gaps (Dalling *et al.* 1998). Kitajima (1994) interpreted this relationship as a trade-off acting through species-specific allocation patterns either to leaf area, promoting growth, or to other morphological or physiological traits that confer resistance to pathogens and herbivores, thereby promoting survivorship. Consistent with this view we found that fast growing pioneers do indeed suffer higher rates of herbivore damage than slower growing ones (Fig. 5b; see also Coley 1983a, Coley 1983b).

Interestingly, we found that most lethal herbivore damage could be attributed to stem-boring insects rather than foliovores. Stem borers that attack tropical trees have not received much attention, except for *Hypsipyla* (Lepidoptera: Pyralidae), which attacks and often kills saplings of economically important Meliaceae (e.g. Grijpma & Gara 1970; Newton *et al.* 1998). This may be because their damage is more difficult to assess than foliovores (Coley & Barone 1996). Alternatively, their impact may be limited to a small group of fast-growing species that provide sufficient quantities of soft, rapidly expanding apical tissue for larval development, and are unprotected by ants or trichomes (e.g. Fiala *et al.* 1989; Letourneau 1997; Letourneau & Barbosa 1999).

Seedling mortality at the post-establishment phase dramatically altered the relative abundance of pioneers in our gaps. Large population decreases for some species may in part reflect the attraction of host specialist herbivores to unnaturally high seedling densities in our gaps. None the less, at least one species, *Cecropia peltata*, was almost eliminated from all our gaps by stem-boring insects, including from those gaps where its initial population size was small. The lethality of herbivore damage may also be dependent on seedling size. *Cecropia peltata* individuals were all still in a monopodial growth phase at the time of stem-borer attack, and had not yet been colonized by *Azteca* ants. Although some resprouting did occur after attack, very little refoliation took place and seedlings slowly died over the following months. In contrast, *Trema micrantha* was attacked by insect herbivores, and possibly vertebrate browsers later in the second year when plants had already branched repeatedly. These attacks were insufficient to kill all the growing shoots and most plants survived.

IMPLICATIONS FOR THE MAINTENANCE OF PIONEER SPECIES DIVERSITY

Detailed studies of species-specific recruitment probabilities provide an important step in determining the life-history stages at which variation in performance among species can promote the maintenance of diversity in this functional group. Here we show that recruitment success of pioneers is strongly affected by interspecific variation in dispersal, seedling establishment success and seedling growth characteristics. In this study in secondary forest, species abundance in the seed bank varied dramatically over quite small spatial scales (< 100 m). Dispersal limitation, coupled with post-dispersal seed predation, may be a significant factor maintaining the local species richness of pioneers by slowing competitive exclusion (Tilman 1994; Hurtt & Pacala 1995). Until recently, factors that determine seed bank composition, such as seed size, local abundance of reproductive pioneers, fruiting phenology, dispersal mechanism, and post-dispersal seed fate, have received little attention compared to those affecting post-disturbance seedling establishment.

Although small seed size, and consequently high fecundity, should confer a dispersal advantage to pioneers, seed size among pioneers on BCNM varied over four orders of magnitude. We showed that variation in seed mass may be maintained by a trade-off between selection for dispersal favouring small seeds vs. selection for establishment success favouring large seed mass. This trade-off is not necessarily a competition–colonization trade-off (e.g. Skellam 1951; Armstrong 1976; Tilman 1994; Turnbull *et al.* 1999), as seed densities may be too low for direct seedling competition to occur while seedlings are still dependent upon initial seed resources. Instead, small-seeded pioneers arrive at microsites never occupied by larger seeded species, but have lower probabilities of recruitment at all microsites.

A second, apparently independent trade-off, between growth rate and mortality rate may also influence the species composition of gaps after seedling establishment. In general we observed declines in the population sizes of the fastest growing pioneers (e.g. *Trema micrantha* and *Cecropia peltata*) and an increase in the relative importance of slower growing pioneers (e.g. *Miconia argentea*). Comparisons of growth and mortality over a wider range of gap sizes will show whether these fast growing species escape herbivory, or better tolerate herbivory in high light conditions, providing the mechanism for apparent gap size partitioning among pioneers observed by Brokaw (1987).

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