Role of dispersal in the recruitment limitation of neotropical pioneer species

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Summary

1 We examined the importance of seed dispersal in predicting the pioneer seedling
composition in recent gaps in a forest plot on Barro Colorado Island (BCI), Panama.
We characterize seed dispersal for 13 taxa from seed rain data collected over 13 years
in 200 mesh traps, and for an additional species from germination from soil samples
collected in one year. We describe seedling distribution patterns from a complete census
of all seedlings of these 14 taxa present in 36 treefall gaps.

2 A maximum likelihood model, incorporating both distance to adult trees and tree
size, fitted observed seed rain to traps quite well for all taxa.

3 The ability to predict seedling recruit number per gap varied greatly among taxa.
For 8 of 14 taxa, regression models incorporating predicted seed rain were significantly
better predictors of seedling recruitment than models in which recruitment probability
was assumed constant in all sites.

4 To see if variation in local dispersal patterns determined the community composition
of gaps, we examined the relative abundances of these 14 pioneer taxa in the 36 gaps. We
found that taxon abundances were significantly positively correlated with abundances
predicted from seed dispersal models and seed–seedling regressions for 27 out of 36
gaps.

5 Overall, we find evidence that limited seed dispersal is an important factor contribut-
ing, together with factors affecting post-dispersal recruitment success, to seedling
distribution patterns in gaps.

Key-words: dispersal limitation, gap, seed limitation, seedling distribution pattern, seed-
ling establishment

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Introduction

Limits to seed dispersal may be a major factor contrib-
uting to the maintenance of diversity in species-rich
plant communities (e.g. Levin 1974; Platt & Weis 1977;
Tilman 1994; Hurtt & Pacala 1995). This is because the
failure of seeds of superior competitors to arrive at
suitable microsites provides the opportunity for less
competitive species to take their place, thus slowing
competitive exclusion. Empirical support for dispersal
limitation comes from numerous seed addition
experiments that show that seed availability may limit

the population growth of many species, particularly in
early successional habitats (reviewed by Turnbull *et al.*
2000).

The importance of seed limitation, however, needs to
be assessed in the context of post-dispersal establish-
ment success (Nathan & Muller-Landau 2000). Traits
that favour seed dispersal (small seed size, reproductive
synchrony) may be unfavourable to subsequent seed-
ling establishment, either because microsites favoura-
ble for the emergence or establishment of small-seeded
species are rare (a trade-off between seed and microsite
limitation), or because seedlings are eliminated by
larger seeded competitors (competition-colonization
trade-off; Turnbull *et al.* 1999). None the less, analyses
of both dispersal and establishment requirements
remain rare due to the limited area that can monitored

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in experimental manipulations of seed dispersal, and due to insufficiently detailed evaluation of post-dispersal recruitment success (Clark, Beckage *et al.* 1999; Turnbull *et al.* 2000).

An alternative to experimental manipulations of seed dispersal is to describe spatial variation in natural seed rain patterns. Although many studies have mapped seed distributions around isolated adults (e.g. Cremer 1966; Hoppes 1988; Kitajima & Augspurger 1989; Dalling *et al.* 1998b), difficulties arise in scaling dispersal characters of individual trees to the population level. The focal tree-based approach requires large sample sizes if it is adequately to characterize both size-fecundity relationships and interannual variation in individual and population-level seed production. These samples are difficult to acquire, and may provide anomalous results if isolated trees differ from the overall population in the activity of their pollinators, seed predators or dispersal agents (Ribbens *et al.* 1994).

More recently, a method for determining dispersal functions of plants has become available that is not dependent on identifying the maternal tree of each seed produced. This inverse-modelling approach uses maximum-likelihood analysis to locate parameter values for dispersal functions that result in the best fit to observed seed rain data (Ribbens *et al.* 1994; Clark, Silman *et al.* 1999). Application of this method potentially allows spatial variation in seed rain to be characterized over landscape scales with sufficient detail to develop predictive models. Calibration of the dispersal model requires only sample seed density data and information on the sizes and locations of reproductive adults. Nonetheless, important caveats in the use and interpretation of this method need to be acknowledged. The data are generally sufficient only to fit models with a small number of free parameters, restricting the shape of possible seed shadows, just as sparse data in ordinary analyses may make it impossible to fit anything but a linear model. The resulting seed dispersal fit is only the best among those simple models that were tried, and thus may not well describe the complex and individually variable seed shadows that result from fruit consumption and movement patterns of a suite of vertebrate seed dispersers.

In this study we use maximum-likelihood techniques to fit models of seed production and seed dispersal and then apply these models to estimate seed rain to a set of treefall gaps occupied by seedlings of an assemblage of neotropical pioneer species. This is a diverse group of tree species dependent upon canopy disturbances for successful seedling recruitment. Earlier studies have examined potential mechanisms that might permit the coexistence of these species, including among-species variation in seed germination (Pearson *et al.* 2002) and seedling establishment requirements (Dalling & Hubbell 2002), and in seedling growth performance (Brokaw 1985, 1987; Dalling & Hubbell 2002). In addition, a study of the spatial dispersion pattern of

seedlings revealed the potential importance of limits to dispersal in structuring this tree community (Dalling *et al.* 1998a). Here we take a more detailed look at seed limitation of pioneers defined as the failure of seeds to arrive at all sites suitable for recruitment. We combine our existing data on the distribution pattern of pioneer seedlings within gaps with a model of seed dispersal to examine whether estimated seed rain can predict among-gap variation in seedling abundance within species, and relative abundances of species within gaps.

Methods

STUDY SITE AND SPECIES

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 to April (Windsor 1990). The flora and vegetation of BCI have been described by Croat (1978) and by Foster & Brokaw (1982). Investigations were carried out within the Forest Dynamics Project 50-ha plot, on the central plateau of BCI. The plot was established in 1982 and all trees > 1 cm diameter at breast height (d.b.h.) have been mapped and measured in 1985, 1990, 1995 and 2000. The plot is described in detail by Hubbell & Foster (1983). Nomenclature follows Croat (1978).

We sought data for species that are considered pioneers (i.e. with a high proportion of individuals > 1 cm d.b.h. being found in gaps, Welden *et al.* 1991). This, together with high scores in the demographic index of Condit *et al.* (1996), indicates high growth and mortality rates and a strong tendency to recruit into gaps. The 14 taxa for which sufficient seed was collected to allow analysis varied over four orders of magnitude in seed mass, in stature from shrubs to emergent trees, and in the size at which reproduction is initiated from 1 to 20 cm d.b.h. (Table 1). One species is ballistically dispersed, five are wind dispersed and the remainder primarily by birds, bats and primates. The capacity for seed dormancy is less well studied for these species, but ranges from 0 months in *Cordia alliadora* to at least 2 years in *Apeiba aspera* (Dalling *et al.* 1997).

SEED DISTRIBUTION DATA

For all taxa except *Miconia argentea*, seed rain data were collected using 200 square traps regularly spaced along 2.7 km of trails within the 50-ha plot (Fig. 1; average distance between nearest neighbour seed traps is 18.9 ± 3.6 m, SD). Each trap consists of a 0.5-m² PVC frame supporting a 1-mm mesh bag suspended 0.8 m above the ground on four PVC posts. To avoid problems near the plot edge, beyond which we had no information on adult trees, we excluded all samples taken from the 12 traps within 20 m of the plot edge, leaving 188 traps. An average of 5.2 (2.8%) of these

Table 1 Species (D = dioecious), principle dispersers (A = avian; P = primate; R = rodent; W = wind; B = ballistic), diaspore mass without wings (mg), estimated minimum reproductive size (cm d.b.h), number of reproductive-sized individuals in the plot in 1995, Pearson regression coefficient of log (actual seed rain + 1) against log (fitted seed rain + 1), median dispersal distance, fecundity (seeds cm^{-2} basal area), dispersal parameters p and u, and clumping parameter, k, of the fit of seed rain to traps, and χ^2 value of likelihood ratio tests vs. the null model (all species $P < 0.001$)

Taxa	Dispersal	Diaspore mass	Repr. d.b.h.	n	r^2	Dispersal (m)	Fecundity seeds cm^{-2}	p	u	k	χ^2
Alchornea costaricensis (D)	A	38.50	13	135	0.44	1.3	33.5	0.61	0.8	0.16	118.9
Alseis blackiana	W	0.12	13	784	0.58	3.2	907.2	0.94	9.2	0.30	190.2
Apeiba aspera	P, R	14.20	20	141	0.23	3.2	7.8	0.80	7.6	0.06	34.4
Casearia arborea	A, P	1.65	13	88	0.38	1.9	128.3	0.92	3.2	0.03	32.3
Cecropia insignis (D)	A, P	0.50	20	182	0.26	0.8	225.6	0.32	0.1	0.08	30.7
Cordia alliodora	W	12.50	13	54	0.49	7.0	18.1	0.63	24.5	0.20	77.3
Croton billbergianus	B	24.0	3	367	0.87	2.2	2.6	0.73	2.9	0.78	46.1
Jacaranda copaia	W	4.70	20	193	0.73	21.2	67.3	0.81	328.8	2.00	253.5
Luehea seemannii	W	1.90	20	64	0.64	8.2	273.7	0.62	32.7	0.98	288.3
Miconia argentea	A, P	0.08	7	121	0.64	51.5	6109.7	0.16	39.9	1.76	42.3
Palicourea guianensis	A	14.30	1	1055	0.30	5.6	50.5	0.57	15.1	0.20	61.5
Spondias spp.	P, R	740–1430	20	18	0.21	26.2	0.8	0.17	10.9	0.29	48.1
Terminalia amazonia	W	3.80	20	22	0.51	83.1	61.3	0.67	3807.2	1.96	149.8
Zanthoxylum spp. (D)	A, P	11–36	20	108	0.11	0.8	22.7	0.45	0.2	0.50	16.2

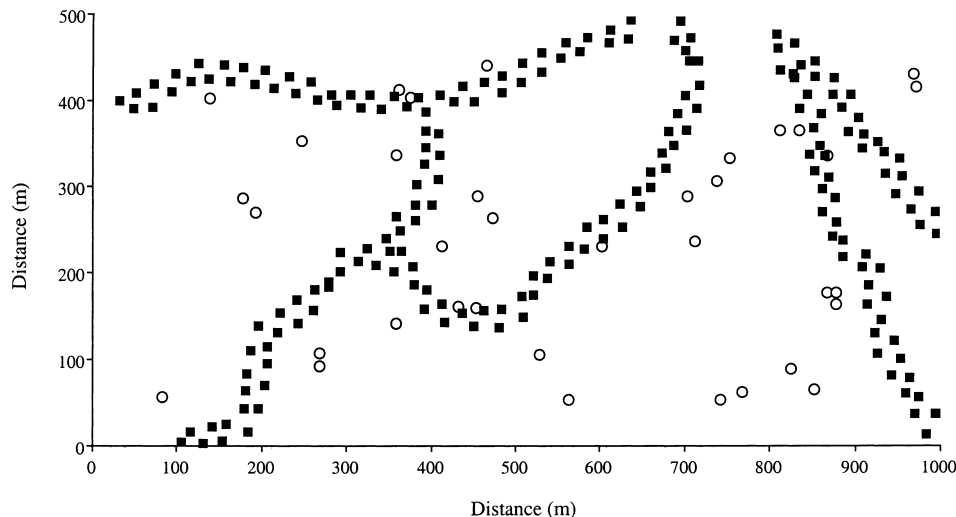*Apeiba aspera* = *Apeiba membranacea* (Croat 1978).

Fig. 1 Location of gaps (○) and seed rain traps (■), within the 50-ha forest dynamics plot.

were located in sites with a canopy height of less than 5 m in any given year (cf a value of 3.5% for the total 50, R. Condit, unpublished data). All seeds, fruits and seed-bearing fruit fragments > 1 mm in diameter falling into the traps have been removed, identified to species, and recorded every week since January 1987 (Wright & Calderón 1995; Wright *et al.* 1999). In this study we use seed rain data from January 1987 until December 1999. For each species, the counts of mature fruits falling during this interval were multiplied by the average number of seeds per fruit (S. J. Wright, unpublished data) and added to the counts of simple seeds to obtain the estimated total number of seeds per trap.

For *Miconia argentea*, one of the most abundant pioneer species on the plot and the dominant species in the soil seed bank (Dalling *et al.* 1997), seed trap data were not available because its seeds are smaller than the mesh size of the traps. Data on the distribution of *Miconia* seeds were taken instead from a study of soil seed bank dynamics (Dalling *et al.* 1997, 1998b). Soil samples were collected from two locations below the centre of the crown, and at 5, 10, 20 and 30 m from the crown edge along each of four transects radiating from the crown of four *Miconia* and four *Cecropia* trees present in the plot ($n = 192$ samples). Samples were collected in May 1993 using a 10.3-cm diameter, 3-cm deep soil corer. Soil samples were placed in a growing-house and the viable seed density estimated from counts of seedlings that emerged over the following 6 weeks (Dalling *et al.* 1995). Interpretation of dispersal patterns for *Miconia* requires caution as variation in seed bank densities includes both variation in dispersal and post-dispersal seed losses from the soil.

SEEDLING DISTRIBUTION DATA

We used annual data on canopy height in the 50-ha plot to locate 36 treefall gaps formed between 1993 and 1995 (Fig. 1). We established a grid of 1-m² plots across the central portion of each gap and searched for all seedlings (individuals < 1 cm d.b.h) of 24 pioneer species (Dalling *et al.* 1998a), but data are presented only for the 14 most abundant in the seed rain. Seedling locations were mapped to the nearest square metre. However, large parts of many of these gaps were not suitable for pioneer seedling recruitment, as they were either deeply shaded by vegetation that survived the treefall, or were covered by course debris that impeded seed germination or seedling establishment. We therefore limit our analyses to the 670 potential 'recruitment sites', defined as 1-m² plots occupied by at least one pioneer seedling. The number of these recruitment sites within each gap varies from 2 to 60 (mean = 19, SD = 16). As we found no significant difference in the light environment of recruitment sites occupied by different pioneer species (Dalling *et al.* 1998a), we assume all sites to be equally colonizable by the different pioneer species. Seedlings of *Zanthoxylum ekmanii* (formerly *belizense*), *Z. juniperum* (formerly *procerum*) and *Z. setulosum*, and of *Spondias mombin* and *S. radlkoferi* have similar life-histories and were not distinguished to species in the field. Seed and seedling analyses for these two groups were therefore conducted at the genus level, and henceforth we refer to analyses of 'taxa' rather than 'species'. Additional information on the selection and censusing of gap sites is provided in Dalling *et al.* (1998a).

CALCULATION OF SEED LIMITATION AND ITS COMPONENTS

To explore the degrees and kinds of limits to colonization success of pioneers, we calculated measures of seed limitation, source limitation and dispersal limitation (Clark *et al.* 1998; Nathan & Muller-Landau 2000; Muller-Landau *et al.* 2002) at the 0.5-m² scale of each trap for periods of 1, 2 and 4 years using data on seed arrival into the 200 seed traps in the plot. *Seed limitation* is defined as the proportion of traps not receiving seeds of the focal species over the time period. *Source limitation* reflects constraints on seed arrival into traps due to limited numbers of seeds available overall; it is defined as the proportion of traps not receiving seeds if seeds are uniformly and randomly distributed among traps. *Dispersal limitation*, in contrast, reflects how seed arrival is further reduced by limited seed dispersal above and beyond constraints due to limited seed number; it is defined as 1 (proportion of traps receiving seeds)/(proportion of traps that would receive seeds if seeds were randomly distributed). Thus, altogether (1-seed limitation) is equal to the product of (1-source limitation) and (1-dispersal limitation) (Muller-Landau *et al.* 2002).

FITTING SEED PRODUCTION AND DISPERSAL

We used data on the location and number of seeds in seed traps or of viable seeds in soil samples together with locations and sizes of adult trees to fit the probability of seed arrival as a function of distance from an adult tree (the dispersal kernel), and to fit fecundity as a function of tree size for each taxon. Starting from a set of parameters specifying these functions, we calculated expected seed rain to each seed rain trap (or soil sample) as the sum of contributions from the seed shadows of conspecific adult trees on the plot. Contributions from each tree were determined by distance to trap and tree size according to parameter values. We searched for the parameter values that produced the best fit to the observed seed rain using maximum likelihood methods (Ribbens *et al.* 1994; Clark, Silman *et al.* 1999). We assumed that trees smaller than two-thirds of the species-specific adult size (as estimated by Robin Foster, personal communication) produced no seeds (S. J. Wright, unpublished data). Above these cut-offs (Table 1), we assumed that average seed production per tree was proportional to basal area, following Ribbens *et al.* (1994), Clark *et al.* (1998), and Clark, Silman *et al.* (1999a), with a single fitted parameter, β, for seed production per cm² basal area.

We fitted seed dispersal kernels using the flexible 2-parameter 2Dt model introduced by Clark, Silman *et al.* (1999):

$$f(x) = \frac{p}{\pi u \left(1 + \dfrac{x^2}{u}\right)^{p+1}} \qquad \text{eqn 1}$$

where $f(x)$ is the probability density of seeds at a distance x from a parent tree, and p and u are fitted parameters; that is, $f(x)\,dA$ is the expected proportion of the total seedfall to be found in an area dA at distance x from the parent tree. Clark, Silman *et al.* (1999) obtain this function by combining a two-dimensional Gaussian distribution – which is expected under random movement with a fixed stopping time – and a gamma distribution of the Gaussian parameter, representing variation among different dispersal agents. This model provided a better fit than exponential or Gaussian models (Clark, Silman *et al.* 1999; Nathan & Muller-Landau 2000). The distribution of observed values for seed rain into traps around expected values was assumed to follow a negative binomial distribution (Clark, Silman *et al.* 1999). The clumping parameter, k, of the negative binomial was thus the fourth and final fitted parameter. Low values of k correspond to high variances in observed values around the expected values. The likelihood of the observed seed trap data (S, the set of all seedfalls Sj into individual traps j) given a particular set of parameter values (g, a and k) was thus calculated as

$$L(S|\beta,p,u,k) = \sum_{traps\ j} \frac{\Gamma(k + \hat{S}_j)}{\Gamma(k)S_j!}\left(\frac{k}{k + \hat{S}_j}\right)^k \left(\frac{\hat{S}_j}{k + \hat{S}_j}\right)^{S_j}$$

$$\text{eqn 2}$$

where $\hat{S}_j$ is the expected seed rain into trap j under the model, with fecundity parameter β and dispersal parameters p and u (equation 1). We then found the parameter values that maximized the likelihood function.

For each taxon, we used a likelihood ratio test to compare the best-fit seed rain model with a null model that assumed uniform expected seed rain across the plot (Rich 1988; Ribbens *et al.* 1994; Clark *et al.* 1998; Clark, Silman *et al.* 1999). For illustration of the goodness of fit, we also present Pearson's r^2 values for the correlation between model fits and observed seed densities. For calculations of these correlations, densities were first transformed as log (seed number + 1), to reduce deviations from normality (Zar 1974). For most species, the absolute counts of seeds in traps are mostly low, and thus we do not expect high r^2 values even when the model is a very good reflection of the dispersal process. For example, where 0.1 seeds are expected per square metre, even a perfect fit to the model will result in zero seeds observed nine times out of 10 and one seed observed one time out of 10, and both these possibilities will result in substantial residuals and lowered Pearson r^2 values.

Finally, our seed rain models assume that seed arrival depends only on distance from source trees, and is unaffected by local habitat, including the presence of gaps (Augspurger & Franson 1988; Wenny & Levey 1998). To test for disproportionate arrival of seeds to gaps, we used non-parametric Mann–Whitney *U*-tests to compare the residuals of seed rain model fits for traps in sites with low canopy height (gaps) with those with high canopy height. We chose non-parametric tests because the distribution of residuals deviates strongly from normal. Canopy height was measured annually on a 5×5 m grid across the entire 50-ha plot from 1987 through to 1996 (Hubbell & Foster 1986; Welden *et al.* 1991). For each trap location we used the height of the nearest canopy sampling point. Sites were classified as low-canopy if a canopy height of 5 m or less was measured in two or more of the 12 years. If there is disproportionately high dispersal of seeds to gaps, then we would expect that the residuals in low-canopy sites would tend to be larger (and more often positive) than those in high-canopy sites. *Miconia* was excluded from this analysis as all soil samples were collected from understorey locations.

ANALYSES OF AMONG-GAP VARIATION IN SEEDLING NUMBERS WITHIN TAXA

For each taxon, we investigated whether information on expected seed rain to each gap explained among-gap variation in seedling numbers. Expected seed rain was calculated for each 1-m² plot that was potentially colonizable by pioneer seedlings, which we defined as any plot containing at least one seedling of a pioneer species. Although seed rain estimates and seedling abundances were available at the scale of 1-m² plots within gaps, we analysed results at the level of the whole gap to avoid pseudoreplication. As plots within a gap

had very similar expected seed rain and distances to nearest adult for any given taxon, we simply used the average of these quantities for each gap as our independent variables.

We first fit a model in which the probability of a seedling emerging was assumed constant across all 1-m² plots, independent of seed rain. Thus the expected number of seedlings of a taxon in a gap, R, was assumed linearly proportional to the total area of recruitment sites, n present in the gap (measured as the total number of 1×1 m plots with pioneer seedlings):

$$R = a_c n \quad \text{(constant model)} \qquad \text{eqn 3}$$

where a_c is a fitted taxon-specific parameter giving the expected number of seedlings per plot. We call this the constant model, and use it as a basis of comparison for the seed-rain-dependent models.

We fit linear and nonlinear models for the dependence of seedling number on seed rain. In the linear model, the expected seedling number per plot in each gap is proportional to the average seed rain per plot in that gap, $\bar{S}$. Thus the total seedling number in a gap is proportional to the total expected seed rain, that is, to the number of plots times the seed rain per plot:

$$R = a_l n \bar{S} \quad \text{(linear seed model)} \qquad \text{eqn 4}$$

with the single fitted parameter, now designated a_l, interpretable as the average seed-to-seedling transition probability (the average number of seedlings per seed). This model implicitly assumes density-independent seedling establishment. We also fit a power law model,

$$R = a_n n \bar{S}^{b_n} \quad \text{(nonlinear seed model)} \qquad \text{eqn 5}$$

which allows for density-dependent seedling establishment. For $b_n < 1$, seed-to-seedling transition probability is negatively density-dependent, while for $b_n > 1$, it is positively density-dependent.

Finally, for comparison, we also fit a model in which expected seedling number per plot was a power law function of the average distance to the nearest conspecific adult from plots within the gap, $\bar{D}$:

$$R = a_d n \bar{D}^{b_d} \quad \text{(nonlinear distance model)} \qquad \text{eqn 6}$$

Distance to nearest adult is a commonly measured proxy for seed rain used in place of seed input data in analyses of dispersion patterns (Dalling *et al.* 1998a), despite the known problems with this assumption (Nathan & Muller-Landau 2000).

As the dependent variable, actual seedling number, is discrete, and the data were over-dispersed (with the variance : mean ratio > 1), we assumed a negative binomial error distribution. All models were fit by maximum likelihood methods using the nonlinear fitting function in SYSTAT version 7 (SPSS Inc., Chicago, USA), with a user-defined loss function specifying

Table 2 Components of dispersal limitation (see text) averaged over 1, 2 and 4 years of seed collection in 200 traps

	Mean number of seeds m^{-2} in traps (years)			Mean number of traps hit (years)			Mean seed limitation			Mean source limitation			Mean dispersal limitation		
	1	2	4	1	2	4	1	2	4	1	2	4	1	2	4
	1	2	4	1	2	21.3	0.96	0.93	0.89	0.01	< 0.01	< 0.01	0.96	0.93	0.89
Alchornea	15.6	31.1	62.3	7.9	13.2	156.0	0.68	0.47	0.22	< 0.01	< 0.01	< 0.01	0.68	0.47	0.22
Alseis	118.0	236.0	472.1	63.4	106.8	17.0	0.96	0.94	0.92	0.19	0.04	< 0.01	0.95	0.94	0.91
Apeiba	4.8	9.7	19.3	7.8	11.3	8.0	0.97	0.97	0.96	0.03	< 0.01	< 0.01	0.97	0.97	0.96
Casearia	36.8	73.5	147.0	5.2	6.7	34.3	0.93	0.89	0.83	0.23	0.17	< 0.01	0.77	0.73	0.83
Cecropia	29.8	59.5	119.0	13.5	21.7	40.0	0.90	0.86	0.80	0.41	0.16	0.03	0.82	0.83	0.79
Cordia	1.9	3.9	7.8	19.3	28.0	4.7	0.99	0.99	0.98	0.94	0.89	0.79	0.41	0.61	0.73
Croton	0.1	0.3	0.5	1.7	3.0	199.0	0.39	0.03	0.01	0.22	< 0.01	< 0.01	0.25	0.03	0.01
Jacaranda	76.9	153.9	307.7	121.6	194.5	196.3	0.24	0.06	0.02	< 0.01	< 0.01	< 0.01	0.24	0.06	0.02
Luehea	111.2	222.3	444.7	151.8	188.3	30.3	0.95	0.91	0.85	0.74	0.55	0.39	0.52	0.67	0.70
Palicourea	0.9	1.8	3.5	10.1	18.8	36.0	0.94	0.90	0.82	0.82	0.66	0.44	0.61	0.70	0.68
Spondias	0.4	0.8	1.7	11.4	20.3	194.7	0.29	0.10	0.03	0.10	0.01	< 0.01	0.21	0.09	0.03
Terminalia	7.1	14.2	28.5	142.2	179.5	50.7	0.92	0.86	0.75	0.50	0.25	< 0.01	0.70	0.81	0.75
Zanthoxylum	3.7	7.4	14.7	15.8	28.5										

negative binomial errors. Models were compared using the Akaike Information Criterion (AIC), defined as the negative log-likelihood plus two times the number of parameters. This criterion effectively weighs improvements in fit (likelihood) against increased model complexity (Hilborn & Mangel 1997; Burnham & Anderson 1998). The best model has the lowest AIC value.

ANALYSES OF RELATIVE ABUNDANCES OF PIONEER TAXA WITHIN GAPS

Finally, we examined the extent to which variation in seed rain can explain local variation in the relative abundance of pioneer taxa. We calculated expected seedling abundances of each taxon in each gap using predicted seed rain combined with first the linear and then the nonlinear fitted models for seedling number as a function of seed rain.

For each gap, we examined the Pearson correlations of the actual seedling abundances with both sets of predicted seedling abundances. Abundances were first log-transformed as $\log_{10}$ (abundance + 1). For comparison, we also calculated expected seedling numbers in each gap under the assumption that the probability of seedlings of each taxon establishing is the same across all gaps, and thus depends only on the relative abundance of that taxon overall (and not on local seed rain). That is, we calculated expected seedling numbers of each species in each gap as the relative abundance of that taxon overall times the number of seedlings in the gap, and then calculated Pearson correlations on log-transformed abundances as before.

Results

SEED LIMITATION

Seed limitation is strong for all but a few of the smallest seeded and best dispersed taxa, *Jacaranda*, *Luehea* and *Terminalia* (Table 2). For eight of 13 pioneer taxa, an average of > 90% of traps failed to receive any seed in 1 year. Seed limitation remained high for most taxa even when seed rain was summed over 4 years. However, high seed limitation values for the smallest-seeded taxa *Alseis* and *Cecropia* in part reflect undercounts of seeds in traps as some seeds of these taxa pass through the mesh traps or may go undetected. For *Miconia*, we could not calculate seed limitation directly from soil sample data because sample locations were biased towards *Miconia* trees.

For most taxa, the number of seeds available was a less important contributor to seed limitation than was limited dispersal of available seeds; dispersal limitation was greater than source limitation in 10 of 13 pioneer taxa. Source limitation, the proportion of traps that would fail to receive seeds under conditions of random dispersal, showed large interspecific variation, ranging from < 0.01 for *Alseis* and *Luehea* to 0.94 for *Croton* (Table 2). This reflects the great variation in population-level seed availability, arising from differences in adult abundance and in seed production per adult. Taxa with small adult stature and large seed size (*Croton* and *Palicourea*) were very strongly source limited, as were rarer pioneer taxa (individual *Spondias* and *Zanthoxylum* species, not shown). However, many taxa had low source limitation, especially when seed rain was summed over multiple years: 10 of 13 taxa had source limitation < 0.01 over 4 years. By contrast, only the fecund, wind-dispersed taxa *Jacaranda*, *Luehea* and *Terminalia* had dispersal limitation ≤ 0.02 over 4 years (also ≤ 0.25 per year). Their low dispersal limitation is especially impressive considering their relatively low adult abundances; only 22 reproductive-sized *Terminalia* trees were present in the plot. The highest dispersal limitation was present in animal-dispersed taxa that had abundant seeds but distributed them poorly: *Alchornea*, *Apeiba* and *Casearia*.
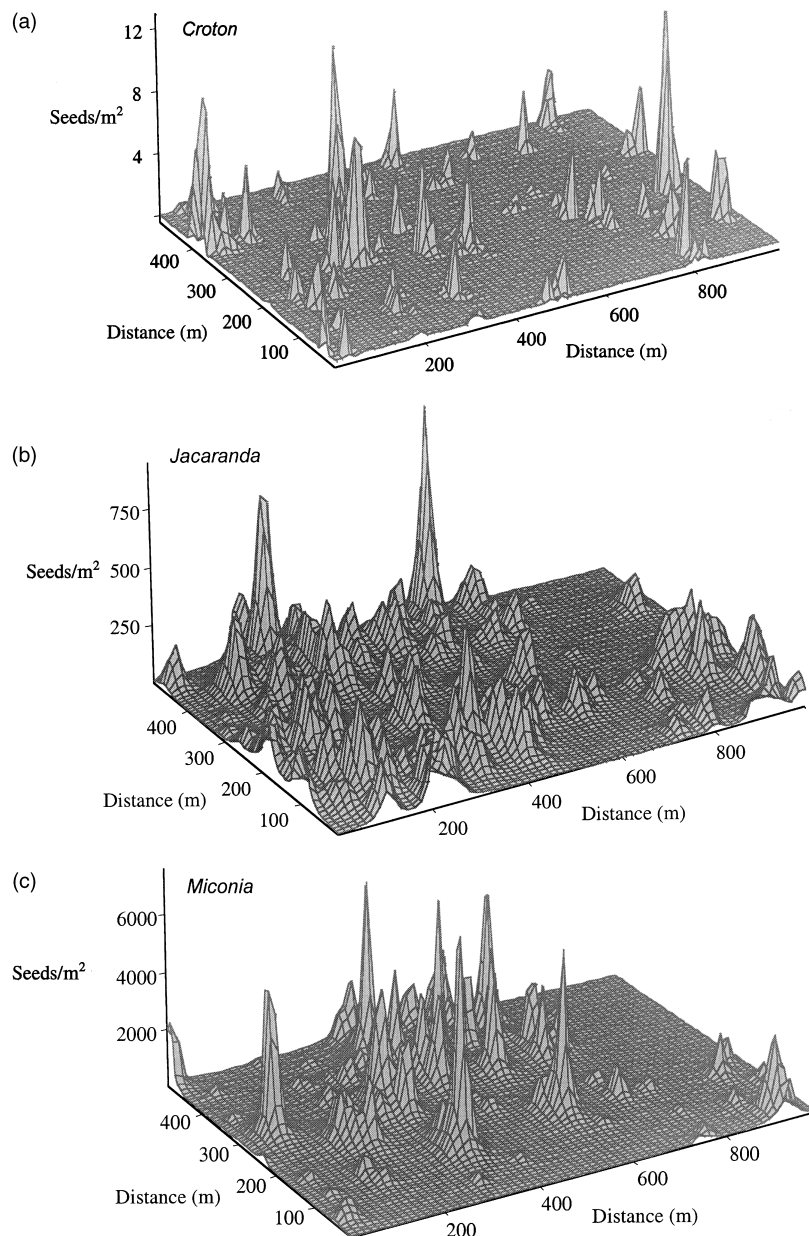
Fig. 2 Expected seed rain m^{-2} fit to each 100-m^2 subplot with the 50-ha forest dynamics plot (excluding a 10-m band around the plot perimeter), for three pioneer taxa with contrasting dispersal syndromes: (a) *Croton bilbergianus*, a subcanopy tree with explosively dispersed seeds; (b) *Jacaranda copaia*, a wind-dispersed canopy tree; and (c) *Miconia argentea*, a monkey- and bird-dispersed canopy tree.

SEED PRODUCTION AND DISPERSAL

Fourteen taxa were sufficiently abundant in seed rain traps, or in the soil seed bank (> 10 sites reached by seeds) to make it possible to fit functions for seed production and seed dispersal. Fits of seed rain to traps were significantly better than random for all taxa (Table 1; $\chi^2 > 16$; $P < 0.001$). Good fits of fitted against actual seed rain ($r^2 > 0.45$) were obtained for the five wind-dispersed, and one ballistically dispersed taxa, as well as for the very small-seeded, animal-dispersed *Miconia* censused from the soil seed bank. The other animal-dispersed taxa had poorer seed rain fits (*Zanthoxylum*, *Spondias*, *Palicourea*, *Cecropia*, *Casearia* and *Apeiba*) (Table 1). Median seed dispersal distances

were very sensitive to model parameters, and varied from < 1 m to > 80 m (Table 1). Spatial patterns of predicted seed rain across the whole plot are illustrated for three taxa (*Croton*, *Jacaranda* and *Miconia*) varying in seed and source limitation (Fig. 2).

For most taxa, residuals of fitted seed rain were not significantly different for the 34 traps that were located in areas of low canopy height (gaps) for 2 or more years of the study compared with the 154 traps that consistently had high canopy heights (understorey). Non-parametric Mann–Whitney *U*-test statistics showed significantly different residuals in gap areas only for *Palicourea*, where the residuals were indeed higher in gaps ($n = 154,34$; $Z = 3.57$, $P < 0.001$). In this species, expected seed rain per square metre was four

Table 3 Fitted parameters (*a*, *b* and *k*) and the log likelihood (*L*) of four models predicting seedling numbers in gaps for each species. R_s is the total number of seedlings of the species in all gaps; Gaps is the number of gaps in which seedlings of the species appear. Boldface indicates the best model for each species (the model with the lowest AIC)

Taxa	R_s	Gaps $R > 0$	Constant a_c	k_c	$-\ln L_c$	Linear seed a_l	k_l	$-\ln L_l$	Nonlinear seed a_n	b_n	k_n	$-\ln L_n$	Nonlinear distance a_d	b_d	kDa	$-\ln L_d$
Alchornea	45	20	**0.08**	**1.87**	**53.8**	0.48	0.38	64.4	0.09	0.11	1.96	53.4	0.13	−0.15	1.87	53.7
Alseis	309	30	**0.43**	**1.11**	**102.2**	0.01	0.47	116.3	0.43	0	1.11	102.2	0.43	0	1.11	102.2
Apeiba	81	16	0.10	0.61	58.7	0.22	0.37	61.1	**0.12**	**0.32**	**0.77**	**56.6**	1.29	−0.79	0.72	57.2
Casearia	34	7	0.03	0.20	29.3	0.03	0.20	28.1	**0.02**	**0.40**	**0.79**	**24.9**	3.75	−1.55	0.50	25.9
Cecropia	299	25	**0.42**	**0.65**	**100.7**	0.06	0.38	108.2	0.35	0.08	0.66	100.6	0.71	−0.16	0.66	100.5
Cordia	33	7	0.03	0.17	29.3	**0.05**	**2.8×10^5**	**21.7**	0.06	0.90	2.4×10^5	21.4	343.79	−2.59	5.96	23.7
Croton	115	8	0.16	0.09	43.2	**21.19**	**0.09**	**42.9**	1.57	0.51	0.10	42.5	524.52	−2.68	0.11	41.7
Jacaranda	106	22	0.15	0.92	70.1	0.00	0.94	68.9	**0.02**	**0.52**	**1.40**	**66.0**	1.93	−0.79	1.13	67.9
Luehea	102	19	**0.14**	**0.68**	**65.0**	0.01	0.42	69.2	0.14	0	0.68	65.0	0.06	0.21	0.69	65.0
Miconia	188	23	**0.23**	**0.72**	**81.9**	0.00	0.51	85.5	0.89	−0.24	0.74	81.7	0.60	−0.26	0.74	81.6
Palicourea	136	24	0.19	1.16	75.8	0.43	0.87	79.2	**0.24**	**0.40**	**2.67**	**69.9**	0.62	−0.51	2.01	72.2
Spondias	21	10	0.03	0.43	34.5	**0.21**	**0.42**	**34.1**	0.10	0.59	0.47	33.9	0.30	−0.57	0.42	34.1
Terminalia	19	2	0.01	0.03	13.0	**0.00**	**0.06**	**12.0**	0.00	1.05	0.06	12.0	1.45	−1.35	0.15	11.4
Zanthoxylum	49	14	**0.06**	**0.66**	**46.8**	0.13	0.35	50.2	0.07	0.15	0.69	46.6	0.17	−0.30	0.69	46.6

times higher in gap than understorey traps due to the relative proximity of source plants, while observed seed rain was 19 times higher in traps in gaps.

SEED RAIN AS A PREDICTOR OF AMONG-GAP VARIATION IN SEEDLING NUMBERS WITHIN TAXA

Incorporating seed rain improved predictions of seedling abundance in gaps for 12 of 14 taxa, as reflected by higher likelihoods for the nonlinear seed model than for the constant model (Fig. 3, Table 3). However, increases in likelihood using the density-dependent model were not always large enough to offset the increased number of parameters in this model. After adjusting likelihood for parameter number using the Akaike information criterion we found that the constant model best described six taxa, the linear seed model four taxa and the nonlinear seed model four taxa (best models in bold in Table 3). There were no taxa for which the nonlinear distance model was preferred overall. For most taxa, nonlinear fits using distance to the nearest reproductive sized conspecific alone were inferior to nonlinear fits using predicted seed rain based on all adults and the fitted seed shadow model; the exceptions in which fits were slightly but not significantly superior (difference in likelihoods was less than one) were *Cecropia*, *Croton*, *Miconia* and *Terminalia*.

In a few cases, fitted parameter values are outside the expected range. In the linear seed model, we expect the fitted parameter a_l to be the mean number of seedlings per seed and thus to be between zero and one; however, for *Croton* it is 21. We suspect that this reflects long-term seed dormancy, which has previously been observed in a congener (Teketay & Granstrom 1997). The seed-to-seedling results for this species are dominated by two gaps in which large numbers of seedlings were observed (39 and 54, respectively), while less than two seeds were expected to arrive (Fig. 3). In both these gaps, adult *Croton* trees were present in the 1980 census, but dead by the time of the 1990 census. Thus these trees were not included as potential seed sources in our calculations of expected seed rain, which would cause predicted seed rain to underestimate available seeds because it fails to consider a long-lived seed bank.

For the nonlinear seed model, we expect the fitted exponent b_n to be between zero and one, reflecting negative density-dependent seedling establishment (Harms *et al.* 2000). However, the value for *Miconia* is negative (−0.24), suggesting that seedling number goes up as seed density decreases. The value for *Terminalia* is greater than one (1.05), although not significantly so; values greater than one correspond to positively density-dependent establishment. For two species, *Alseis* and *Luehea*, the best fits are obtained for exponents of zero, which reduce the nonlinear seed model to the constant model. For *Alseis*, the exponent in the nonlinear distance model, b_d, was also zero; for *Luehea*, it was positive, suggesting that seedling number increases as distance from adult increases. In the case of both *Luehea* and *Miconia*, the fits for the nonlinear models suggest that either seed rain and distance to nearest adults are poorly predicted or known, or else they are unimportant as determinants of seedling density variation among these gaps.

SEED RAIN AS A PREDICTOR OF RELATIVE ABUNDANCE OF TAXA WITHIN GAPS

The relative abundance of pioneer taxa varied among gaps, from those dominated by one or two otherwise uncommon taxa (e.g. gap #10 dominated by *Croton*, gap #16 dominated by *Palicourea*), to those with even representation of several common taxa. These differences are reflected in the variation in Pearson correlation coefficients for each gap between actual seedling
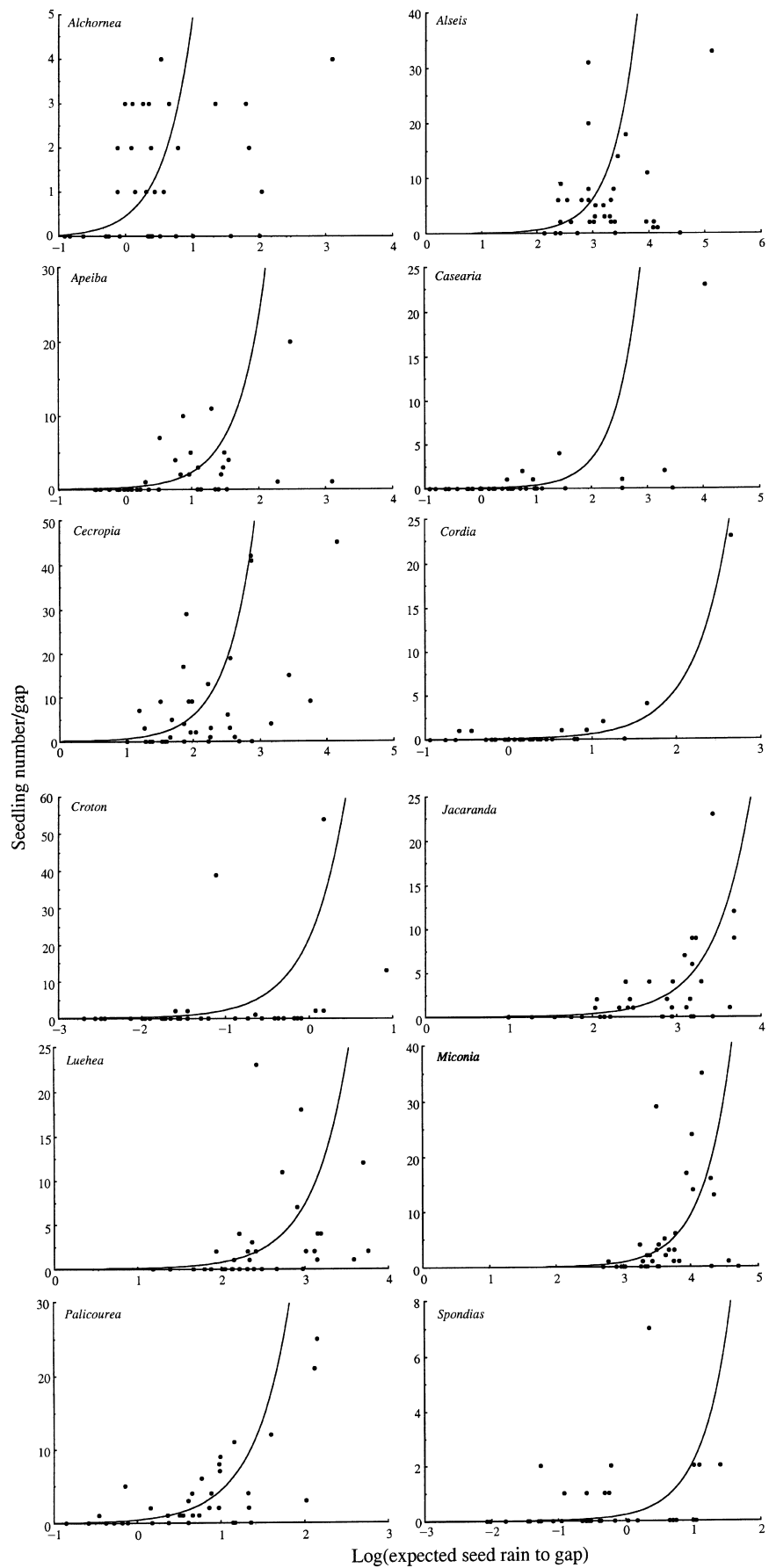
Fig. 3 Regression of seedling number per gap against $\log_{10}$ (expected seed rain to gap). Curve fit is for the linear seed model (Table 3), where total seedling recruitment per gap is proportional to the total expected seed rain times the average seed-to-seedling transition probability (the average number of seedlings per seed).
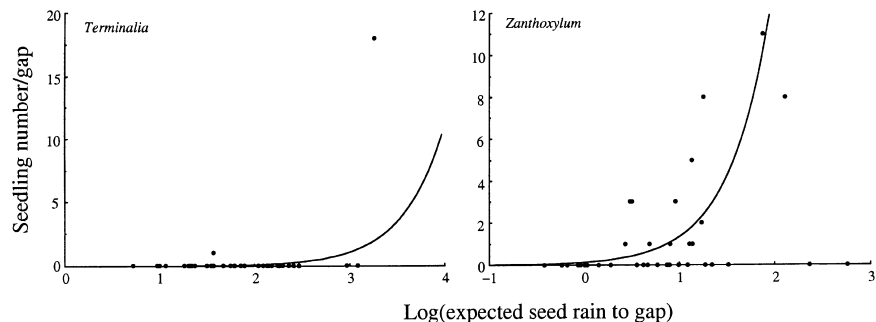
Fig. 3 *continued*

data of the 14 taxa and expectations of equal-sized seedling samples drawn at random from the seedling population of all gaps ($0.08 < r_{constant} < 0.81$; Table 4). In total, we found significant positive correlations between actual gap data and these random seedling assemblages for 16 out of 36 gaps. Random assortment of seedlings to gaps was the highest correlate of actual seedling relative abundance for six gaps (Table 4).

Expected seedling numbers calculated from predicted local seed rain and the fitted seedling models were better correlates of actual seedling abundances, especially for the nonlinear model. The linear model produced somewhat lower mean correlations than the random assortment model, but more significant correlations (19) and was the highest correlate in more cases (10). The nonlinear seed model, which had the highest mean and median correlations, produced significant correlations in 27 gaps (75% of the total), and was the best correlate in 20 gaps. Note that for *Alseis* and *Luehea*, the nonlinear seed model is identical to the constant model; thus, use of the nonlinear models for all species effectively mixes truly nonlinear models for 12 taxa with constant models for two taxa. In general, gaps with seedling abundances that were poorly correlated with random seedling samples were also poorly correlated with seedling abundances predicted from seed rain (e.g. gaps 6 and 31; Table 4).

Discussion

PREDICTING SEED DISPERSAL AND ESTABLISHMENT PATTERNS FOR PIONEERS

This study shows that seed trap and seed bank data can be used successfully to fit models of seed rain over a continuous landscape for pioneer taxa with a wide variety of dispersal syndromes (Table 1). As might be expected, wind and ballistically dispersed taxa tended to show lower variance between fitted and actual seed rain than did monkey, bird and rodent dispersed seeds. In the case of vertebrate dispersal, our model may not adequately describe the complex foraging patterns of animals, or it may fail to include a significant contribution of long-distance dispersal of seeds from outside the plot. However, good fits of the seed rain data did

not necessarily lead to good predictions of seedling abundance. Taxa varied in the overall fit of the seed-to-seedling regression models, and taxa differed in whether regression models based on predicted seed rain yielded better fits than our null model, in which seedling number is a function of the colonizable area of the gap (Table 3).

The observed variation in seed rain model fits is a reflection of variation both in dispersal characteristics, and in our ability to characterize seed rain. None the less, some influence of life-history does emerge. The best overall regression fits were found for three of the least abundant pioneer taxa with relatively high fecundity (*Casearia*, *Cordia* and *Terminalia*). Good fits are expected for these taxa if a few gaps are located close to fruiting trees while most gaps are located at the limits of the dispersal range. Indeed seedlings of each of these taxa dominated only one out of 36 gaps (Fig. 3). Moderate fits were obtained for many of the larger-seeded taxa with relatively low fecundity (*Alchornea*, *Apeiba*, *Croton*, *Spondias* and *Zanthoxylum*), while the poorest fits were found for the smallest-seeded taxa (*Alseis*, *Cecropia* and *Miconia*).

Life-history variation among species also explained whether seedling abundance models assuming constant seedling densities or those assuming seed-rain-dependent densities were preferred. The constant model was preferred for small-seeded taxa with very high reproductive output (*Alseis*, *Cecropia*, *Luehea* and *Miconia*), and in dioecious taxa for which our ability to predict seed rain patterns was poor (*Alchornea*, *Cecropia* again, and *Zanthoxylum*). The remaining taxa for which seed rain significantly improved predictions of seedling distributions tend to be less common on the plot (*Casearia*, *Cordia*, *Spondias*, *Terminalia*), or have larger seeds and shorter dispersal distances (*Apeiba*, *Croton*, *Palicourea*). Despite these differences in model fits among taxa we found that seed rain was a good predictor of the community composition of pioneers within gaps. In our null model, in which seedling abundances were predicted from their overall abundance across all gaps, we found significant correlations with actual seedling abundances for only 16 out of 36 gaps. Predictions of seedling abundance based on local seed rain gave a substantial improvement, with significant correlations for 27 of 36 gaps (Table 4).

Table 4 Correlations between actual and predicted seedling community composition in each gap for the 14 abundant pioneer taxa for which seed and seedling models could be fit. Area is the total area of the gap available for colonization, species is the number of these 14 species that are present, and seedlings is the total number of their seedlings. Mean Pearson's correlation coefficients of the log (actual seedling abundances + 1) with log (expected seedling abundances + 1) are given (i) where expected seedling abundances were calculated using a null model in which the probability of seedlings of a species establishing depends only on its overall abundance ($r_{constant}$), (ii) using predicted seed rain and the fitted linear seed models (r_{linear}) and (iii) using predicted seed rain and the fitted nonlinear seed models ($r_{non-linear}$). Coefficients > 0.53 are significant ($P < 0.05$); the highest coefficient for each gap is in bold

Gap	Area (m^2)	Species	Seedlings	$r_{constant}$	r_{linear}	$r_{non-linear}$
1	60	11	156	0.36	0.75	**0.79**
2	58	11	128	0.77	0.52	**0.80**
3	43	11	113	0.37	**0.56**	0.49
4	51	10	101	0.62	0.64	**0.67**
5	34	10	68	0.77	0.70	**0.88**
6	22	10	32	0.15	0.07	**0.22**
7	18	10	108	**0.71**	0.60	0.69
8	18	10	54	0.42	−0.04	**0.47**
9	31	9	53	0.52	**0.62**	0.58
10	26	9	96	0.42	**0.65**	0.63
11	54	8	183	0.75	0.76	**0.79**
12	14	8	19	0.53	**0.70**	0.64
13	15	7	24	0.51	0.65	**0.70**
14	13	7	25	**0.57**	0.24	0.56
15	11	7	22	**0.38**	0.11	0.36
16	23	6	48	0.44	0.54	**0.64**
17	21	6	62	**0.64**	0.51	0.55
18	15	6	38	0.56	0.35	**0.57**
19	15	6	24	0.54	0.17	**0.71**
20	15	6	25	0.49	0.52	**0.56**
21	12	6	14	0.70	0.36	**0.74**
22	10	6	15	0.59	0.57	**0.70**
23	9	6	13	0.34	0.28	**0.40**
24	12	5	19	**0.81**	0.67	0.73
25	6	5	7	0.48	**0.63**	0.62
26	4	5	12	0.35	−0.05	**0.37**
27	10	4	11	0.50	**0.60**	0.56
28	9	4	13	0.57	**0.66**	0.65
29	8	4	13	**0.64**	0.32	0.61
30	6	3	7	0.56	0.55	**0.65**
31	4	3	5	0.08	−0.11	**0.11**
32	6	2	8	0.52	0.48	**0.59**
33	6	2	9	0.31	0.13	**0.32**
34	2	2	2	0.21	**0.37**	0.28
35	6	1	8	0.53	**0.72**	0.58
36	3	1	2	0.55	0.68	0.59
Median				0.52	0.54	0.60
Mean				0.51	0.46	0.58
Number significant				16	19	27
Best correlate				6	10	20

We found little evidence from our dispersal model that seed rain to gap sites was higher than seed rain to understorey sites. Augspurger & Franson (1988) have suggested that seeds of wind-dispersed species might have disproportionately higher dispersal probabilities into gaps because of local wind turbulence patterns, while at least one bird species in montane forest preferentially disperses seeds to gaps (Wenny & Levey 1998). The one taxon for which we found significantly higher residuals of model fits in low-canopy sites was *Palicourea*, a bird-dispersed shrub. However, our analyses are only a weak test of this hypothesis. The seed trapping study was not designed to contrast captures in gaps vs. understorey sites and consequently only a small

proportion of the 200 traps are in gaps in any given year. Nevertheless, our results do suggest that disproportionate arrival of wind-dispersed seeds to gaps is at most a weak influence on pioneer species seed rain compared with the sizes and locations of source trees.

RELATIVE IMPORTANCE OF SEED VS. ESTABLISHMENT LIMITATION

Community-wide seed limitation appears to play a key role in the maintenance of diversity as a non-equilibrial process slowing rates of competitive exclusion. However, analyses of seedling recruitment in relation to seed abundance indicate that almost all tropical tree

species, including pioneers, are likely to be strongly establishment-limited as well as seed-limited (Hubbell *et al.* 1999; Harms *et al.* 2000; Dalling & Hubbell 2002; Muller-Landau *et al.* 2002). The relative strength of seed vs. establishment limitation might be expected to be largely dictated by seed size. The high fecundity of small-seeded species should mean that they are less likely to be seed limited; however, small-seeded species have much lower seed to seedling transition probabilities than do large-seeded species (Harms *et al.* 2000). The consequence of seed size mediated variation in seed and establishment limitation is an equilibrial competition-colonization trade-off (Hastings 1980; Tilman 1994), that also acts to increase local species coexistence (Chave *et al.* 2002; Muller-Landau *et al.* 2002).

For pioneers, the probability of post-dispersal seedling recruitment is determined by seedling emergence and seedling establishment probabilities, both of which are correlated with seed size (Dalling & Hubbell 2002). Low transition probabilities in small-seeded pioneers are also associated with a more restricted range of microsite conditions favourable to establishment. For example, seed germination of small-seeded pioneers is light sensitive and inhibited by leaf litter on the soil surface (Vázquez-Yanes *et al.* 1990), whereas larger-seeded pioneers are light insensitive and capable of germinating under litter (Pearson *et al.* 2002). Similarly, small-seeded pioneers are more drought sensitive during the first few months of seedling establishment (Engelbrecht *et al.* 2001). Strong microsite limitation may, in part, explain the small or insignificant effect of seed rain on seedling recruitment for the smallest-seeded taxa *Cecropia* and *Miconia* (Fig. 3). For *Alseis*, the failure of seed rain to improve predictions of seedling number may reflect both microsite limitation and some survival in the shade of seedlings that recruited in earlier gap events (Dalling *et al.* 2001).

ROLE OF SEED DORMANCY AND POST-DISPERSAL SEED PREDATION

Captures to seed traps may fail to adequately characterize seed dispersal patterns of pioneers if seeds are capable of prolonged seed dormancy. Trials of seed survival in the soil have not been completed for all the taxa included here, but do vary from a few weeks or months (*Cordia*, *Jacaranda*) to at least several years (*Apeiba*; Dalling *et al.* 1997). For species with very short seed dormancy, the timing of gap formation in relation to the timing of seed dispersal may be more important than the proximity of reproductive conspecifics in determining recruitment success. In contrast, higher than expected seedling recruitment may reflect long-term survival of seeds, as we suspect for *Croton*, where reproductive-sized trees that died prior to 1990 were located close to gaps with large numbers of seedling recruits. Similarly prolonged seed dormancy has also been suggested for *Trema micrantha*, an uncommon pioneer on the plot, based on high density seed patches

distant from any recorded conspecific adult (Dalling *et al.* 1997).

Interspecific variation in the pattern and intensity of post-dispersal seed predation and secondary dispersal may also significantly affect primary seed shadows. Detailed studies of seed bank dynamics of *Miconia* and *Cecropia* show higher rates of incorporation of *Miconia* than *Cecropia* seeds into the seed bank, but stronger density-dependent seed mortality within the seed bank for *Miconia* (Dalling *et al.* 1998b). Ant removal of seeds from the soil surface is also a strong determinant of seed fate (Levey & Byrne 1993). Animal-dispersed seeds of *Miconia*, *Cecropia* and *Apeiba* are more attractive to ants than wind-dispersed seeds *Luehea* and *Jacaranda* (Fornara and Dalling, unpublished data).

FUTURE DIRECTIONS

A more complete understanding of how dispersal and establishment processes contribute to recruitment limitation will require more detailed assessments of gap and microhabitat conditions than attempted here. In this study, gaps were located in 1996 based on the comparison of canopy height measurements made in 1993 and 1995. Gaps we censused may therefore have been between 1 and 3 years old. As most pioneer seedling recruitment occurs within the first few months after gap formation (Garwood 1986; Dalling & Hubbell 2002), differential mortality of seedlings prior to the gap census may have influenced our results. Large differences in mortality rates have been shown among the pioneer species studied here in the first 2 years after seedling emergence, reflecting variation in seed mass and growth rate (Dalling & Hubbell 2002). We suggest that an even stronger effect of seed rain on the seedling composition of gaps would be found with larger sample sizes and more consistency of the timing of seedling censuses. Many of the gaps recorded here were small and contained few seedlings of the focal species (Table 4).

More accurate predictions of recruitment patterns will also require more detailed descriptions of within-gap microsites (Lepage *et al.* 2000). Pioneer species differ in their ability to colonize nurse logs (Dalling *et al.* 1998a) and may differ in their ability to recruit in gaps containing leaf litter (Guzmán-Grajales & Walker 1991; Molofsky & Augspurger 1992). These descriptors of microsite quality are likely to be much better predictors of seedling abundance and composition than is gap size (Brandani *et al.* 1988; Dalling *et al.* 1998a). Finally, there is a clear need for better estimates of seed longevity. Understanding the time-scale under which seeds persist in the soil will indicate the extent to which limited dispersal in space can be compensated for by seed dormancy. These future studies will yield a much more complete understanding of how life history characters influence recruitment limitation and will provide information on how to influence recruitment patterns through forest management (Guariguata 2000).

Acknowledgements

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