

Seed limitation in a Panamanian forest

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Summary

1 The role of seed limitation in tropical forests remains uncertain owing to the scarcity of experimental evidence. We performed seed addition experiments to assess seed limitation for 32 shade-tolerant tropical forest species and monitored the natural seed rain of 25 of these species for 17 years.

2 One, two or five seeds were sown into 0.0079-m² plots for large- ($n = 5$ species), medium- ($n = 5$) and small-seeded species ($n = 22$), respectively. The experiment was replicated at 69 sites, placed in groups of three at 23 locations. Seedling establishment was evaluated after 1 and 2 years in paired seed addition and control plots. Natural seedling emergence and understorey plant density were also measured.

3 Median natural seed rain was 0.31 seeds m⁻² year⁻¹ per focal species.

4 Seed addition enhanced seedling establishment in 31 and 26 of the 32 species after 1 and 2 years, respectively. Mean number of focal species' seedlings after 2 years was 0.002 seedlings in control plots and 0.12, 0.37 and 0.60 seedlings in seed addition plots for large-, medium- and small-seeded species, respectively.

5 A 25 seeds added treatment increased seedling establishment by ≥ 2.0 -fold over the five seeds added treatment after 2 years.

6 Community-wide recruitment and understorey plant density were strongly seed-limited. The natural density of understorey plants averaged 12 plants m⁻² and was significantly less than for seedlings of the single focal species in plots with ≥ 2 seeds added 2 years earlier.

7 The number of established seedlings per seed added was independent of seed size.

8 Treatment (adding zero or five seeds), species identity and location all affected seedling establishment for the 11 small-seeded species represented at all sites, with treatment and its interactions accounting for 86% of the explained variation.

9 Our results suggest that seed limitation plays a dominant role in seedling recruitment and understorey plant community assembly in tropical forests. Although strong seed limitation may set the stage for species-neutral community assembly, the species differences in seedling establishment rate and its spatial variation demonstrate an important role for species-specific processes.

Key-words: community ecology, dispersal assembly, Panama, seed addition experiment, seed limitation, seed size, seedling ecology, seedling recruitment, tropical ecology, tropical forest

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Introduction

Seed limitation refers to the failure of seeds of a given plant species to arrive at suitable sites in sufficient numbers

to establish as seedlings (Nathan & Muller-Landau 2000; Levin *et al.* 2003). Seed addition experiments have demonstrated that the failure of seeds to arrive limits recruitment in temperate herb communities (Tilman 1997; Ehrlén & Eriksson 2000; Rand 2000; Turnbull *et al.* 2000; Foster & Tilman 2003; Foster *et al.* 2004). Seed limitation may limit the scope for pairwise

competitive interactions between species because direct competition between sessile plants is restricted to near neighbours whose zones of resource depletion overlap. In extreme cases, seed limitation may also limit competition among all individuals by keeping total plant density at low levels (Wright 2002). Thus, seed limitation may contribute to the maintenance of species richness by slowing competitive dynamics (Hurt & Pacala 1995; Hubbell *et al.* 1999; Hubbell 2001; Schupp *et al.* 2002).

In contrast to temperate herbaceous communities, the role of local-scale seed limitation is unclear in tropical forests. Makana & Thomas (2004) performed seed addition experiments for two light-demanding African tree species and found that both were strongly seed-limited. Indirect evidence for seed limitation comes from seed trap studies, which suggest strong seed limitation in many tropical forest plant species (Hubbell *et al.* 1999; Dalling *et al.* 2002; Murray & Garcia-C. 2002; Terborgh *et al.* 2002). Additional evidence for seed limitation is provided by autocorrelation in the spatial distribution of tropical plants that occurs independently of environmental variation (Dalling *et al.* 1998; Valencia *et al.* 2004) and by correlations between seedling distributions and seed rain density predicted from seed trap studies (Dalling *et al.* 2002). These indirect measures cannot provide conclusive evidence for seed limitation, however, because it is unclear which sites are suitable for germination and seedling establishment (Levine & Murrell 2003). Furthermore, community-level seed production can be very high in tropical forests. For example, seed rain density averages 965 seeds $\text{m}^{-2} \text{year}^{-1}$ for seeds with minimum dimension larger than 1.0 mm on Barro Colorado Island, Panama (Harms *et al.* 2000) and ≥ 500 seeds $\text{m}^{-2} \text{year}^{-1}$ for seeds with minimum dimension larger than 1.5 mm at Cocha Cashu, Peru (Terborgh *et al.* 2002). Hence, it is far from clear whether seed input limits total seedling recruitment in tropical forests (Terborgh *et al.* 2002; Wright 2002). In fact, Webb & Peart (2001) argued that community-wide seed dispersal in an Indonesian forest approached the level at which seed dispersal limitation is unimportant in curtailing competitive exclusion.

Here, we test directly for local-scale seed limitation for 32 shade-tolerant species in old-growth tropical moist forest in Panama using seed sowing experiments (Turnbull *et al.* 2000). We asked the following questions:

1. Is seedling recruitment of individual species seed-limited?
2. Is seedling recruitment of the plant community as a whole seed-limited?
3. What is the relative importance of species identity, location, seed limitation and their interactions as controls of seedling recruitment? An important role for location or a location-by-species interaction would provide evidence that not all sites are equally suitable for germination and seedling establishment of all shade-tolerant species.

Materials and methods

STUDY SITE AND SPECIES

Barro Colorado Island (BCI; 9°09' N, 79°51' W) supports tropical semi-deciduous forest (Croat 1978; Foster & Brokaw 1996; Leigh 1999). Annual precipitation averages *c.* 2600 mm, and the climate is seasonally dry. Elevation ranges between 27 and 160 m a.s.l. About half the forest is old-growth, at least parts of which have escaped agriculture for 2000 years or more (Leigh 1999). Detailed descriptions of the climate, geology and biota of BCI can be found in Croat (1978), Gentry (1990), Leigh *et al.* (1996) and Leigh (1999). The 32 study species include 18 families and a wide range of growth forms and all 32 are relatively shade-tolerant (Table 1). Nomenclature follows Croat (1978) as updated by Condit *et al.* (1995) with two additional changes: *Cephaelis ipecacuanha* and *Virola surinamensis* have been renamed as *Psychotria ipecacuanha* (Brot.) Stokes and *V. nobilis* A. C. Sm., respectively.

EXPERIMENTAL DESIGN

The rain of seeds and flowers was censused weekly from 1 January 1987 to 21 May 2003, using 200 seed traps set along 2.7 km of trails within a 50-ha forest dynamics plot (Wright & Calderón 1995; Wright *et al.* 2005). Each seed trap consisted of a square, 0.5-m² PVC frame supporting a shallow, open-topped, 1-mm mesh bag, and suspended 0.8 m above the ground on four PVC posts. Traps were located at 13.5-m intervals on alternating sides of the trail and randomly between 4 m and 10 m from the trail so that distances between nearest traps averaged 18.9 ± 3.6 m (± 1 SD). All flowers, seeds, fruits, capsules and other reproductive parts of plants that fell into the traps were identified to species level and counted (only presence was recorded for flowers). Fruits and seeds were further categorized as aborted, immature, mature (endosperm filled), or damaged by insects or vertebrates. The number of undamaged, mature fruit was multiplied by the species-specific average seed : fruit ratio and added to the number of undamaged seeds to estimate the total number of viable seeds falling into each trap for each species.

Seeds were sown into 0.0079-m² plots between March and October 2000 as each species matured fruit. Just one species was sown into each plot. Seedling establishment was evaluated near the end of the next two wet seasons in October–November 2001 and again in November–December 2002. Number of leaves and stem height (measured from the ground to the tip of stem) were recorded for the tallest seedling of the focal species in each plot during the 2001 and 2002 censuses. We refer to the period between sowing and the 2001 census as the first year and the period between the 2001 and 2002 censuses as the second year.

The experiment was replicated at 69 closed-canopy sites in old-growth forest. The 69 sites occurred in groups

Table 1 Descriptions of the 32 study species, including family (names lack the -aceae suffix), growth form (GF: H = herb, L = liana, S = shrub, U = treelet, M = medium-sized tree, T = large tree), seed dry mass and natural seed rain quantified for 17 years and 200 0.5-m² traps as population-level seed production (the mean \pm SD number of seeds captured standardized to a square metre basis) and seed arrival (the number of traps that captured one or more seeds). NA = data not available

Species	Family	GF	Seed mass (g dry weight)	Seed production (m ⁻² year ⁻¹)	Seed arrival (no. of traps)
<i>Beilschmiedia pendula</i>	Laur-	T	3.8761	0.78 \pm 0.74	179
<i>Brosimum alicastrum</i>	Mor-	T	0.6472	5.20 \pm 3.99	172
<i>Calophyllum longifolium</i>	Clusi-	T	1.9501	0.07 \pm 0.07	87
<i>Chrysochlamys eclipes</i>	Clusi-	S	0.0962	0.00 \pm 0.00	4
<i>Cupania sylvatica</i>	Sapind-	U	0.1187	0.02 \pm 0.03	51
<i>Eugenia nesiotica</i>	Myrt-	M	0.3465	0.01 \pm 0.02	36
<i>Faramea occidentalis</i>	Rubi-	U	0.1962	8.89 \pm 12.32	200
<i>Geophila repens</i>	Rubi-	H	NA	*	*
<i>Gustavia superba</i>	Lecythid-	M	4.8342	0.62 \pm 0.60	144
<i>Herrania purpurea</i>	Sterculi-	U	0.1847	0.01 \pm 0.04	2
<i>Hybanthus prunifolius</i>	Viol-	S	0.0182	11.63 \pm 8.07	200
<i>Lacistema aggregatum</i>	Lacistem-	U	0.0107	0.01 \pm 0.03	12
<i>Mouriri myrtilloides</i>	Melastomat-	S	0.0447	0.42 \pm 0.27	184
<i>Ocotea whitei</i>	Laur-	T	NA	0.08 \pm 0.13	59
<i>Oenocarpus mapora</i>	Arec-	M	1.3327	0.91 \pm 0.70	199
<i>Paullinia turbacensis</i>	Sapind-	L	0.0925	0.10 \pm 0.11	115
<i>Pharus latifolius</i>	Po-	H	NA	*	*
<i>Pouteria reticulata</i>	Sapot-	T	0.4310	0.31 \pm 0.41	166
<i>Prioria copaifera</i>	Fab-	T	22.6387	0.17 \pm 0.11	152
<i>Psychotria deflexa</i>	Rub-	S	0.0026	0.01 \pm 0.02	3
<i>Psychotria emetica</i>	Rub-	S	0.0030	*	*
<i>Psychotria horizontalis</i>	Rub-	S	0.0040	1.54 \pm 1.06	185
<i>Psychotria ipecacuanha</i>	Rub-	S	0.0060	*	*
<i>Psychotria limonensis</i>	Rub-	S	0.0066	0.01 \pm 0.03	6
<i>Psychotria marginata</i>	Rub-	S	0.0075	0.01 \pm 0.01	19
<i>Sorocea affinis</i>	Mor-	S	0.0777	0.40 \pm 0.41	153
<i>Streptochaeta sodiroana</i>	Po-	H	NA	*	*
<i>Streptochaeta spicata</i>	Po-	H	NA	*	*
<i>Streptogyne americana</i>	Po-	H	NA	*	*
<i>Tabernaemontana arborea</i>	Apocyn-	T	0.0694	0.86 \pm 0.78	189
<i>Trichilia tuberculata</i>	Meli-	T	0.1196	22.75 \pm 22.66	200
<i>Virola nobilis</i>	Myristic-	T	1.6382	0.45 \pm 0.16	153

*Seeds were never captured for the seven study species that are always shorter than the 80-cm-high traps as adults.

of three at 23 locations, sited every 100 m along the trails in old-growth forest in the south-western part of BCI. At each location three replicate sites were chosen, essentially at random, except that all sites were at least 3 m from the nearest trail, sites were separated from one another by 2–5 m, and canopy gaps *sensu* Brokaw (1982) and large palms were avoided. Although much topographic and edaphic variation was sampled, including the two major soil types on BCI (Leigh 1999), using the trail system introduced some bias away from steep slopes and swamps (Svenning *et al.* 2004). At each site, paired seed addition and control plots separated by 15 cm were established for each species. Each seed addition and control plot was delimited by a 10-cm-diameter circle of 5-cm-high aluminium mesh to prevent seeds from being washed away by rain. We found no indications that the mesh reduced seed predation. Unknown vertebrates removed a large fraction of the seeds weighing ≥ 0.3 g added to our experimental plots within a few days (J.-C.S., personal observation). Furthermore, in a pilot study ants were observed climbing the mesh to retrieve aril-coated

seeds of *Paullinia turbacensis* placed inside plots. Finally, total annual seedling emergence rates in the control plots (see Results) were similar to those observed in other studies on BCI (*c.* 10–40 seedlings m⁻² in Daws *et al.* in press). Several species were seeded into fewer than 69 sites (Table 2; range = 12–69 sites, average = 54.6). One, two and five seeds were added per plot for large- (2.0–22.6 g dry weight), medium- (0.3–1.6 g) and small- (0.03–0.2 g) seeded species, respectively. The few species with no available seed mass data (Table 1) were placed in a seed mass class based our field experience. For all study species seed dimensions are given directly or can be inferred from the species descriptions in Croat (1978). An additional plot with 25 seeds added was established for seven of the small-seeded species at 29–60 sites (average = 40). Seeds were collected distant from the experiment and were dropped into the experimental plots within 1–3 days. Plots were placed to avoid all naturally occurring plants and were maintained by removing naturally emerging seedlings of non-focal species and loosening litter suspended on the aluminium mesh during the first year.

Table 2 The outcome of the seed addition experiments 1 and 2 years after sowing (plain and bold type face, respectively). *n* refers to the number of paired seed addition (SA) and control (C) plots. Seeds refer to the number of seeds added to each SA plot. Seedling presence refers to the number of SA plots with focal species present as a seedling. Stem height and number of leaves are given as means (± 1 SD) for the largest focal species' seedling in each SA plot. Number of seedlings is the mean (± 1 SD) number of seedlings present for the SA and C plots. *P* is the significance level for a one-tailed sign test comparing number of seedlings for paired SA and C plots, except for the 25-seed addition treatments where the sign test compares paired 25-seed and five-seed SA plots

Species	<i>n</i>	Seeds	Seedling presence (no. SA plots)	Stem height (cm)	No. of leaves	No. of seedlings per SA plot	No. of seedlings per C plot	<i>P</i>		
<i>Beilschmiedia pendula</i>	69	1	14	23.8 \pm 9.5	3.6 \pm 3.1	0.20 \pm 0.41	0.01 \pm 0.12	0.00049		
			9	34.5 \pm 12	6.6 \pm 3.9	0.13 \pm 0.34	0.00 \pm 0.00	0.0020		
<i>Brosimum alicastrum</i>	69	2	7	15.0 \pm 7.1	2.9 \pm 2.2	0.13 \pm 0.42	0.00 \pm 0.00	0.0078		
			6	17.5 \pm 6.9	2.7 \pm 1.2	0.10 \pm 0.35	0.00 \pm 0.00	0.016		
<i>Calophyllum longifolium</i>	69	1	10	28.4 \pm 10.2	5.3 \pm 3.1	0.14 \pm 0.35	0.00 \pm 0.00	0.00098		
			6	45.1 \pm 23.0	10.3 \pm 6.7	0.09 \pm 0.28	0.00 \pm 0.00	0.016		
<i>Chrysochlamys eclipes</i>	20	5	1	4.3	4	0.05 \pm 0.22	0.00 \pm 0.00	0.50		
			1	6.2	6	0.05 \pm 0.22	0.00 \pm 0.00	0.50		
<i>Cupania sylvatica</i>	29	5	21	8.3 \pm 1.9	3.5 \pm 2.4	0.90 \pm 1.14	0.00 \pm 0.00	0.00003		
			16	8.9 \pm 3.0	4.8 \pm 1.9	0.62 \pm 0.94	0.00 \pm 0.00	0.00024		
			29	25	21	8.7 \pm 1.9	3.0 \pm 1.9	2.76 \pm 2.68	0.00 \pm 0.00	0.00002
<i>Eugenia nesiotica</i>	23	2	14	19.4 \pm 4.0	15.6 \pm 6.6	1.00 \pm 0.90	0.00 \pm 0.00	0.00005		
			13	24.8 \pm 4.0	20.8 \pm 11.4	0.91 \pm 0.90	0.00 \pm 0.00	0.00012		
			69	5	42	8.9 \pm 3.0	2.0 \pm 1.1	1.48 \pm 1.58	0.04 \pm 0.21	9 \times 10 ⁻¹³
<i>Faramaea occidentalis</i>	69	5	23	10.8 \pm 3.6	5.3 \pm 2.3	0.90 \pm 1.54	0.03 \pm 0.17	5 \times 10⁻⁷		
			69	5	37	3.6 \pm 4.9	4.4 \pm 2.8	0.84 \pm 0.95	0.00 \pm 0.00	7 \times 10 ⁻¹²
<i>Geophila repens</i>	69	5	20	14.5 \pm 30.5	16.4 \pm 43.4	0.39 \pm 0.67	0.00 \pm 0.00	9 \times 10⁻⁷		
			69	1	11	19.6 \pm 4.5	5.5 \pm 2.8	0.16 \pm 0.37	0.00 \pm 0.00	0.00049
<i>Gustavia superba</i>	69	1	7	29.1 \pm 5.3	9.7 \pm 5.2	0.10 \pm 0.30	0.00 \pm 0.00	0.0078		
			55	5	34	13.3 \pm 3.1	4.1 \pm 1.9	1.56 \pm 1.62	0.00 \pm 0.00	6 \times 10 ⁻¹¹
<i>Herrania purpurea</i>	55	5	28	15.5 \pm 4.3	4.1 \pm 1.5	1.05 \pm 1.28	0.00 \pm 0.00	4 \times 10⁻⁹		
			60	5	33	6.1 \pm 2.1	4.4 \pm 1.9	0.92 \pm 1.06	0.00 \pm 0.00	1 \times 10 ⁻¹⁰
<i>Hybanthus prunifolius</i>	60	5	20	9.2 \pm 4.2	5.6 \pm 2.6	0.52 \pm 0.85	0.00 \pm 0.00	1 \times 10⁻⁶		
			60	25	35	7.5 \pm 2.8	5.6 \pm 2.6	2.78 \pm 3.45	0.00 \pm 0.00	0.0069
			26	11.3 \pm 4.6	5.1 \pm 2.9	1.42 \pm 2.25	0.00 \pm 0.00	0.012		
<i>Lacistema aggregatum</i>	39	5	31	8.7 \pm 5.7	6.6 \pm 3.8	2.21 \pm 1.66	0.00 \pm 0.00	5 \times 10 ⁻¹⁰		
			27	15.2 \pm 13.0	9.9 \pm 7.6	1.74 \pm 1.57	0.00 \pm 0.00	7 \times 10⁻⁹		
			30	25	25	8.7 \pm 3.4	6.4 \pm 2.1	5.83 \pm 4.96	0.00 \pm 0.00	0.00077
<i>Mouriri myrtilloides</i>	69	5	21	13.3 \pm 10.3	8.2 \pm 3.9	3.13 \pm 2.83	0.00 \pm 0.00	0.0085		
			69	5	19	10.9 \pm 2.5	10.7 \pm 6.7	0.67 \pm 1.29	0.00 \pm 0.00	2 \times 10 ⁻⁶
			16	15.0 \pm 3.5	28.5 \pm 18.4	0.48 \pm 0.99	0.00 \pm 0.00	0.00002		
<i>Ocotea whitei</i>	69	1	21	42.7 \pm 17.2	8.6 \pm 11.6	0.30 \pm 0.46	0.00 \pm 0.00	5 \times 10 ⁻⁷		
			14	55.8 \pm 28.7	30.9 \pm 62.6	0.20 \pm 0.41	0.00 \pm 0.00	0.00006		
<i>Oenocarpus mapora</i>	69	2	18	5.9 \pm 0.91	1.9 \pm 0.2	0.43 \pm 0.78	0.00 \pm 0.00	4 \times 10 ⁻⁶		
			18	6.8 \pm 1.5	3.1 \pm 1.1	0.42 \pm 0.76	0.00 \pm 0.00	4 \times 10⁻⁶		
<i>Paullinia turbacensis</i>	12	5	9	11.2 \pm 3.6	5.3 \pm 2.5	1.50 \pm 1.31	0.00 \pm 0.00	0.0020		
			9	13.4 \pm 4.9	7.0 \pm 2.2	1.50 \pm 1.31	0.00 \pm 0.00	0.0020		
<i>Pharus latifolius</i>	69	5	33	5.4 \pm 2.8	5.1 \pm 2.1	0.99 \pm 1.28	0.01 \pm 0.12	2 \times 10 ⁻⁹		
			19	9.1 \pm 6.4	6.6 \pm 3.5	0.41 \pm 0.75	0.00 \pm 0.00	2 \times 10⁻⁶		
<i>Pouteria reticulata</i>	69	2	33	14.3 \pm 2.8	6.1 \pm 3.0	0.65 \pm 0.76	0.00 \pm 0.00	1 \times 10 ⁻¹⁰		
			25	16.3 \pm 4.0	8.3 \pm 5.4	0.42 \pm 0.60	0.00 \pm 0.00	3 \times 10⁻⁸		
<i>Prioria copaifera</i>	68	1	8	53.2 \pm 24.9	2.8 \pm 2.0	0.12 \pm 0.32	0.00 \pm 0.00	0.0039		
			4	63.6 \pm 33.4	7.3 \pm 3.4	0.06 \pm 0.24	0.00 \pm 0.00	0.063		
<i>Psychotria deflexa</i>	69	5	19	3.5 \pm 1.1	4.5 \pm 1.6	0.48 \pm 0.88	0.00 \pm 0.00	2 \times 10 ⁻⁶		
			4	7.7 \pm 2.2	7.5 \pm 3.5	0.09 \pm 0.37	0.00 \pm 0.00	0.063		
<i>Psychotria emetica</i>	69	5	23	2.4 \pm 0.8	2.7 \pm 1.4	0.42 \pm 0.72	0.00 \pm 0.00	1 \times 10 ⁻⁷		
			0	—	—	0.00 \pm 0.00	0.00 \pm 0.00	—		
<i>Psychotria horizontalis</i>	69	5	35	2.9 \pm 7.9	3.3 \pm 1.3	0.94 \pm 1.17	0.01 \pm 0.12	3 \times 10 ⁻¹¹		
			7	5.1 \pm 1.3	6.9 \pm 1.9	0.17 \pm 0.59	0.01 \pm 0.12	0.035		
<i>Psychotria ipeacacuanha</i>	69	5	16	2.7 \pm 0.9	2.9 \pm 1.8	0.30 \pm 0.60	0.00 \pm 0.00	0.00002		
			3	7.3 \pm 0.8	9.0 \pm 2.0	0.04 \pm 0.21	0.00 \pm 0.00	0.13		
<i>Psychotria limonensis</i>	69	5	20	5.6 \pm 2.9	6.1 \pm 3.2	0.52 \pm 0.95	0.01 \pm 0.12	1 \times 10 ⁻⁶		
			13	11.8 \pm 7.2	7.8 \pm 2.8	0.33 \pm 0.82	0.01 \pm 0.12	0.00012		
			54	25	23	5.9 \pm 2.8	5.8 \pm 2.6	1.65 \pm 3.19	0.02 \pm 0.14	0.061
<i>Psychotria marginata</i>	41	5	18	10.1 \pm 4.9	6.9 \pm 2.9	0.72 \pm 1.28	0.02 \pm 0.14	0.032		
			41	5	11	4.6 \pm 1.7	6.7 \pm 4.1	0.51 \pm 0.98	0.00 \pm 0.00	0.00049
			7	7.5 \pm 3.5	7.6 \pm 2.8	0.24 \pm 0.58	0.00 \pm 0.00	0.0078		
	35	25	16	4.0 \pm 1.6	4.9 \pm 3.1	1.54 \pm 3.11	0.00 \pm 0.00	0.032		
			6	6.1 \pm 1.9	7.7 \pm 3.9	0.63 \pm 1.93	0.00 \pm 0.00	0.62		

Table 2 Continued

Species	<i>n</i>	Seeds	Seedling presence (no. SA plots)	Stem height (cm)	No. of leaves	No. of seedlings per SA plot	No. of seedlings per C plot	<i>P</i>
<i>Sorocea affinis</i>	69	5	42	7.6 ± 2.2	2.5 ± 1.3	1.39 ± 1.43	0.00 ± 0.00	2 × 10 ⁻¹³
			28	9.6 ± 2.8	4.0 ± 1.8	0.80 ± 1.11	0.00 ± 0.00	4 × 10⁻⁹
<i>Streptochaeta sodiroana</i>	54	5	29	4.6 ± 2.0	4.8 ± 2.2	1.28 ± 1.46	0.00 ± 0.00	2 × 10 ⁻⁹
			19	7.2 ± 3.0	5.7 ± 2.9	0.63 ± 0.98	0.00 ± 0.00	2 × 10⁻⁶
	30	25	21	6.1 ± 2.1	3.9 ± 1.6	5.40 ± 5.36	0.00 ± 0.00	0.0022
			17	7.4 ± 2.2	5.9 ± 2.7	2.00 ± 2.55	0.00 ± 0.00	0.011
<i>Streptochaeta spicata</i>	30	5	18	7.8 ± 3.6	7.7 ± 2.9	1.33 ± 1.45	0.00 ± 0.00	4 × 10 ⁻⁶
	60	5	36	4.1 ± 1.7	3.7 ± 1.6	1.27 ± 1.33	0.02 ± 0.13	1 × 10 ⁻¹¹
			23	7.8 ± 6.9	5.9 ± 3.1	0.77 ± 1.18	0.02 ± 0.13	2 × 10⁻⁷
	42	25	29	4.1 ± 1.5	3.3 ± 1.4	4.14 ± 5.28	0.02 ± 0.15	0.00009
			18	8.0 ± 5.2	6.0 ± 4.5	2.17 ± 3.81	0.02 ± 0.15	0.0059
<i>Tabernaemontana arborea</i>	48	5	18	14.4 ± 5.4	5.8 ± 3.3	0.75 ± 1.16	0.00 ± 0.00	4 × 10 ⁻⁶
	69	5	37	9.2 ± 1.5	4.4 ± 1.7	1.39 ± 1.65	0.00 ± 0.00	7 × 10 ⁻¹²
			32	10.3 ± 2.1	7.2 ± 2.5	0.96 ± 1.29	0.00 ± 0.00	2 × 10⁻¹⁰
<i>Virola nobilis</i>	69	2	14	15.2 ± 5.8	2.1 ± 2.0	0.23 ± 0.49	0.00 ± 0.00	0.00006
			1	30.0	0.0	0.01 ± 0.12	0.00 ± 0.00	0.50

Naturally emerging seedlings were identified, counted and removed approximately monthly during the first year, except during the dry season (January–April 2001) when seedling emergence was negligible. The object of this weeding was to be able to evaluate the limitation of recruitment by seed arrival without confounding competitive interactions. Weeding turned out to have little or no impact on focal species' recruitment (see Results).

To estimate natural densities of plants in the understorey (defined as plants with d.b.h. < 5 cm), we censused all plants in 10-cm-diameter plots located randomly c. 1.5 m away from each *Hybanthus prunifolius* and *Faramaea occidentalis* experiment ($n = 138$ 'natural density' plots) during the 2001 census. A small flag was thrown backwards over one shoulder to locate the centre of each plot randomly with the caveat that plots were not allowed to contain large trees.

DATA ANALYSES

We used sign tests to assess species-level seed limitation by comparing the number of seedlings established in paired control and seed addition plots for each focal species (Zar 1996). Sign tests were used because observed values were highly skewed and covered a limited range. We also used sign tests to assess community-wide seed limitation by comparing the total number of seedlings (focal species' seedlings established after 1 year plus all other non-focal species' seedlings emerging during the first year) in paired control and seed addition plots for each of the four seed addition levels (i.e. one, two, five or 25 seeds added). The sign tests were one-tailed given the expectation that seed addition could raise, but not lower, seedling recruitment. Probabilities were computed using binomial coefficients for the species-level

tests and a normal approximation for the community-wide tests because of the larger sample size (Zar 1996). We also evaluated community-wide seed limitation by comparing the natural densities of all herbaceous and woody plants in the 138 'natural density' plots with the densities of focal species' seedlings for the four seed addition levels using Wilcoxon two-sample tests.

We evaluated the effect of weeding by comparing the number of focal species' seedlings establishing in seed addition plots with and without naturally emerging seedlings using a one-way ANOVA; by definition only seed addition plots with naturally emerging seedlings were weeded. We assessed the effect of seed mass on the mean number of seedlings produced per seed using a second ANOVA to compare species from the three seed size categories described previously (see Experimental design above). The 32 species were replicates for the analysis of seed mass.

We determined the relative effects of seed addition (zero or five seeds added), species identity ($n =$ the 11 species sown at all 69 sites), location ($n = 23$) and their interactions on the number of focal species' seedlings established per plot after 1 year using a three-way ANOVA. Species and treatment were treated as fixed effects and location as a random effect. We computed *F*-ratios following Quinn & Keough (2002) and variance components using the estimated mean square approach (Quinn & Keough 2002). We note that variance components for fixed and random factors have different interpretations, namely as the estimated variance between the group means for the specific populations sampled and between all possible group means, respectively (Quinn & Keough 2002). To enhance comparability between the variance components one could also treat location as a fixed factor. However, this changes the

individual variance components by $< 0.3\%$ (data not shown). The limited numbers of seedlings in the one- and two-seed addition plots prohibited analyses of variation in seedling numbers per plot for the medium- and large-seeded species. For ANOVA, the response variables were square-root transformed to improve normality and residual plots were investigated as a check thereof. Analyses were performed in Microsoft® Office Excel 2003 (Microsoft Corporation, Washington, USA) and JMP 5.0 (SAS Institute Inc. 2000).

Results

NATURAL SEED RAIN

The natural seed rain ranged from $0.00 \text{ m}^{-2} \text{ year}^{-1}$ to $22.8 \text{ m}^{-2} \text{ year}^{-1}$ (median = 0.31) for the 25 focal species that, as adults, are taller than the 80-cm-high traps (Table 1). This contrasts strongly with experimental seed densities of 1–25 seeds per 0.0079 m^2 . The mean number of traps where seeds of a species arrived was closely related to mean seedfall density (Fig. 1). After 17 years, the cumulative percentage of the 200 possible traps reached by seeds varied from 0% to 100% among the 25 focal species (median = 152; Table 1).

SPECIES-LEVEL SEED LIMITATION

Seed addition enhanced seedling establishment significantly in 31 of 32 species after 1 year and in 26 of 32

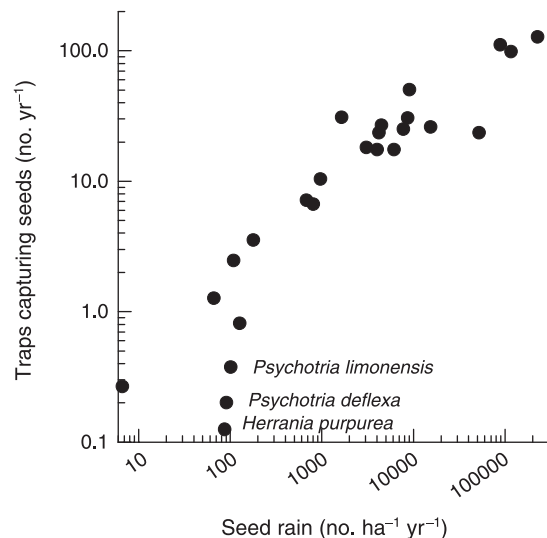


Fig. 1 Seed arrival increases with population-level seed production. Seed arrival on the vertical axis is the mean number of 0.5-m^2 traps (out of 200 in total) that captured a seed of the species. Seed production on the horizontal axis is the mean number of seeds captured standardized to a hectare basis. Means are for 17 years. Symbols represent the 25 study species that are taller than the 80-cm tall traps. The seven remaining study species are always shorter than the traps and were never captured as seeds. Two outliers, *Psychotria limonensis* and *P. deflexa*, bear many fruit below 80 cm. The final outlier, *Herrania purpurea*, is a small cauliflorous treelet that often displays its fruit below 80 cm.

species after 2 years (Table 2). The one species that showed no evidence of seed limitation, *Chrysochlamys eclipes*, produces many sterile seeds (S.J.W., personal observation), and these would not have been distinguished before sowing. The mean number of focal species' seedlings ($\pm 1 \text{ SD}$) per 0.0079 m^2 seed addition plots was 0.19 ± 0.07 ($n = 5$ species), 0.49 ± 0.35 ($n = 5$ species) and 0.99 ± 0.51 ($n = 22$ species) seedlings for large-, medium- and small-seeded (five-seed treatment) species after 1 year and 0.12 ± 0.05 , 0.37 ± 0.35 and 0.60 ± 0.47 seedlings after 2 years, respectively. In contrast, mean seedling number of single focal species was only 0.003 ± 0.009 and 0.002 ± 0.007 seedlings in the control plots ($n = 32$ species) after 1 and 2 years, respectively. The 25-seed addition treatment increased seedling establishment over the five-seed addition by 2.7-fold to 3.7-fold (mean increase 3.6-fold $\pm 0.38 \text{ SD}$) after 1 year and by 2.0-fold to 3.4-fold (mean increase 2.5-fold $\pm 0.51 \text{ SD}$) after 2 years (Fig. 2), with the one-tailed sign test significant at $P < 0.05$ for six of seven species for both censuses (Table 2).

Most seedlings that established in the seed addition plots survived and grew during the second year (Table 2). Many achieved impressive stem lengths, the largest being 135 cm in *Ocotea whitei*, 100 cm in *Prioria copaifera*, 88 cm in *Calophyllum longifolium* and 64 cm in *Beilschmiedia pendula* (all large-seeded canopy species), 57 cm in the treelet *Lacistema aggregatum* and 140 cm in the trailing herb *Geophila repens* (both small-seeded).

Weeding had little impact on focal species' recruitment. No wildings emerged during the first year in 70% of the one-seed, 74% of the two-seed, 77% of the five-seed and 67% of the 25-seed addition plots where focal species' seedlings established ($n = 64, 86, 558$ and 170 plots, respectively). Furthermore, the number of focal species' seedlings in these plots did not differ significantly from the number of focal species' seedlings in plots where non-focal species' seedlings did emerge and were subsequently removed by weeding (ANOVA, $r^2 = 0.005$, $P = 0.08$ and $r^2 = 0.003$, $P = 0.46$ for the five- and 25-seed addition plots, respectively). The number of naturally emerging seedlings was too limited to allow similar analyses for the one- and two-seed addition plots.

COMMUNITY-WIDE SEED LIMITATION

The total number of seedlings (focal species' seedlings established after 1 year plus all other non-focal species' seedlings emerging during the first year) was greater in the seed addition plots than in the control plots for all treatments [proportion of non-zero differences with greater number of seedlings in the seed addition plot: 59% (one-tailed sign test $P < 0.05$), 77% ($P < 0.0005$), 82% ($P < 0.0005$), 87% ($P < 0.0005$) for the one-, two-, five- and 25-seed addition treatments, $n = 165, 149, 761$ and 218 non-zero differences, respectively; Table 3].

Further evidence for community-wide seed limitation comes from comparisons of natural densities of all herbaceous and woody plants (0.094 ± 0.399 plants per

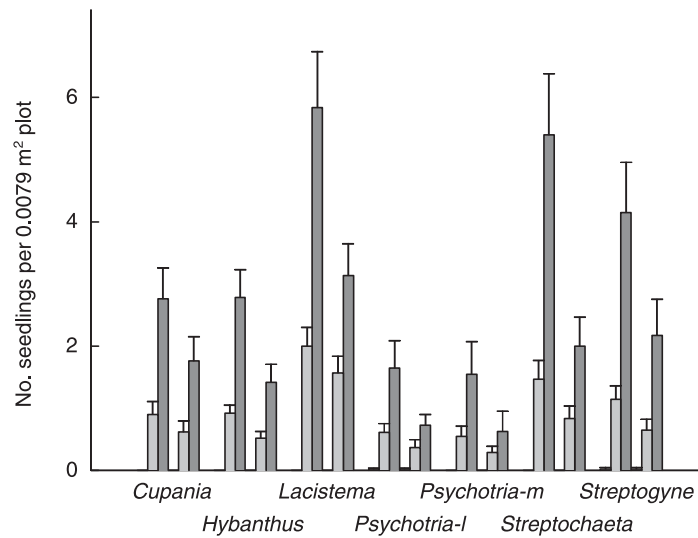


Fig. 2 Mean focal species' seedling densities in control (white bars), five-seed addition (light grey) and 25-seed addition (dark grey) plots for *Cupania sylvatica* ($n = 29$ plots per treatment), *Hybanthus prunifolius* ($n = 60$), *Lacistema aggregatum* ($n = 30$), *Psychotria limonensis* ($n = 54$), *P. marginata* ($n = 35$), *Streptochaeta sodiroana* ($n = 30$) and *Streptogyne americana* ($n = 42$). For each species, seedling densities after 1 or 2 years are given by three bars to the left or right, respectively. Note that the white bars are absent or very small owing to the zero or low densities in the control plots. Only sites with all three treatments represented were included. Error bars give the standard error of the mean.

Table 3 Evidence for community-wide seed limitation. Entries are the mean number of seedlings (1 SD) that recruited and survived until the first census (2001) for the focal species in the seed addition (SA) plots, that emerged during that same year for all non-focal species in the SA plots and that emerged during that same year for all species in the control plots. Means and SDs were calculated over all species in each seed size category

Plot type	Seedling type	Seed size (no. of seeds added)			
		Small (5)	Small (25)	Medium (2)	Large (1)
SA	Focal species	0.96 (1.30)	3.22 (4.27)	0.41 (0.70)	0.19 (0.39)
SA	Other species	0.36 (0.80)	0.52 (0.90)	0.35 (0.90)	0.38 (1.22)
Control	All species	0.36 (0.77)	0.48 (0.96)	0.30 (0.73)	0.38 (0.62)
No. of seeds added		5	25	2	1
No. of SA plots of each type		1207	280	299	344

0.0079-m² plot, mean \pm SD calculated for 138 plots) with the densities of focal species' seedlings present in seed addition plots. Even after 2 years, focal species' seedling densities were significantly greater than natural densities of all understory plants for the two-seed (mean 0.291 ± 0.607 seedlings per 0.0079-m² plot, Wilcoxon's two-sample test, $P = 0.0001$, $n = 299$ plots), five-seed (mean 0.544 ± 1.030 , $P < 0.0001$, $n = 1207$ plots) and 25-seed (mean 1.579 ± 2.551 ; $P < 0.0001$, $n = 280$ plots) addition, but not for the one-seed (mean 0.116 ± 0.321 , $P = 0.11$, $n = 344$ plots) addition treatment. Natural densities are lower than natural emergence rates owing to the death of many seedlings during their first year post-germination.

RELATIVE IMPORTANCE OF SEED LIMITATION, SPECIES IDENTITY AND LOCATION

The mean number of seedlings produced per seed added did not differ among the three seed size categories [Table 4; $F_{2,29} = 0.22$, $P = 0.81$ for 2001 and $F_{2,29} = 0.36$,

Table 4 The number of focal species' seedlings per seed added (mean \pm 1 SD) 1 and 2 years after sowing for small- (five-seed treatment), medium- and large-seeded species. Means and standard deviations are calculated over species

	2001	2002
Small seeds (22 spp.)	0.20 ± 0.10	0.12 ± 0.09
Medium seeds (five spp.)	0.24 ± 0.17	0.19 ± 0.18
Large seeds (five spp.)	0.19 ± 0.07	0.12 ± 0.05

$P = 0.70$ for 2002 for one-way ANOVAS comparing the mean number of seedlings per seed among the five large-, five medium- and 22 small-seeded species (five-seed treatment)].

Treatment (adding zero or five seeds), species identity, location and their interactions collectively explained a large proportion of the variation in the number of focal species' seedlings established after 1 year for the 11 small-seeded species sown at all 69 sites ($r^2 = 62.0\%$). All main effects and interactions contributed significantly

Table 5 Three-way factorial mixed-effects analysis of variance of the number of focal species' seedlings (square-root transformed) per 10-cm-diameter plot ($n = 1518$) in relation to treatment (fixed effect: zero or five seeds added), species identity (fixed effect: the 11 small-seeded species represented at all 69 sites, $n = 11$) and location (random effect; $n = 23$) 1 year after seed addition. Variance components were computed using the estimated mean square approach (Quinn & Keough 2002)

	d.f.	Sum of squares	<i>F</i> ratio	Estimated variance component (%)
Species	10	20.34	6.88****	2.7
Location	22	17.56	4.06****	2.0
Treatment	1	124.87	156.60****	35.0
Species \times Location	220	65.06	1.50****	3.5
Species \times Treatment	10	18.42	6.61****	4.9
Location \times Treatment	22	17.54	4.05****	3.9
Species \times Location \times Treatment	220	61.28	1.42***	5.8
Error	1012	199.08		42.2

*** $P < 0.001$; **** $P < 0.0001$.

to the explained variance (Table 5). Treatment alone explained 60.6% of the explained variance; all interactions involving treatment explained another 25.3%; and the species, location and species–location interaction collectively explained just 14.2% of the explained variance (Table 5).

Discussion

This seed addition experiment demonstrated that seedling recruitment was strongly seed-limited for 31 of 32 shade-tolerant species in an old-growth tropical moist forest and that subsequent seedling survival was sufficiently high that significant effects of added seeds persisted for 2 years for 26 species. The experiment also produced strong evidence that the plant community as a whole was severely seed-limited in terms of both seedling recruitment and total understorey plant density. The total of number of focal species' seedlings surviving 1 year plus all non-focal species' seedlings emerging during the first year was significantly increased by all seed addition treatments. Furthermore, the average focal species' seedling density when 2–25 seeds were added per 0.0079-m² plot (≥ 37 seedlings m⁻² after 2 years) greatly exceeded average natural understorey plant densities on BCI (12 plants m⁻², this study) and in other lowland neotropical forests [Cocha Cashu, Peru: 20 plants m⁻² (Terborgh *et al.* 2002); La Selva, Costa Rica: 9–15 seedlings m⁻² (Marquis *et al.* 1986)]. Seed arrival clearly affects the species composition as well as the overall density of seedlings in the tropical forest understorey. Because seed arrival provides the spatial template for processes occurring in later ontogenetic stages, strong seed limitation of seedling recruitment is likely to have profound consequences for the adult plant community as well, although experimental demonstration of this will be difficult for long-lived species.

We included several herbaceous species, and after 2 years at least one (*Geophila repens*) achieved reproductive size (1.4 m stem length; cf. Croat 1978) in a seed addition plot. Furthermore, seedlings of several other species also grew to rather large size over the 2 years of

the study and the surviving seedlings of all species generally experienced positive growth in both years (Table 2). Hence, there is no indication that seedlings emerging after seed addition in otherwise unoccupied understorey sites should have a particularly low chance of reaching later ontogenetic stages. The strong seed limitation documented here suggests that tropical forest understorey plant communities are strongly influenced by seed arrival patterns, in particular given the likely absence of strong competitive dynamics in this stratum of the forest. Acting together with seed limitation, competitive suppression by the overstorey and herbivory cause understorey plant density to be low and hence there is little scope for direct competitive interactions among understorey plants (Wright 2002).

Nathan & Muller-Landau (2000) emphasized the importance of adding seeds at variable densities to provide information on seedling recruitment at saturating seed arrival densities. The addition of 25 vs. five seeds per 0.0079-m² plot elicited a strong increase in seedling recruitment for shade-tolerant species with seed mass < 0.2 g. Consequently, the saturating seed rain density must be > 5 seeds per 0.0079 m² for these species. There is an indication that 25 seeds per 0.0079 m² might be approaching saturation because the increase in recruitment (on average 3.6-fold) was less than the increase in the number of seeds added (5-fold). Regardless, following Nathan & Muller-Landau (2000) the high seedling densities achieved by the addition of 25 seeds per 0.0079 m² provide the best estimate of the absolute degree of seed limitation. The observed rain of seeds with minimum dimension > 1 mm averages 7.6 seeds per 0.0079 m² year⁻¹, including a large proportion of seeds from light-demanding species in old-growth forest on BCI (Harms *et al.* 2000). Hence, even the five-seed addition rate is likely to exceed the annual seed rain for all shade-tolerant species combined, and certainly far exceeds the combined natural seed rain (0.44 seeds per 0.0079 m² year⁻¹) of the 32 shade-tolerant study species (Table 1).

Seed limitation may be caused by insufficient seed numbers (source limitation) or non-uniform seed

distribution patterns (dispersal limitation) (Clark *et al.* 1998; Muller-Landau *et al.* 2002; Schupp *et al.* 2002). Muller-Landau *et al.* (2002) found both strong source and dispersal limitation in *Beilschmiedia pendula* and negligible source and moderate dispersal limitation in *Trichilia tuberculata* at our study site. Our experiment does not allow separation of these two components of limitation for individual species; however, the strong relationship between the proportion of sites where seeds arrive and population-level seed production suggests that source limitation may generally be most important at the species level (Fig. 1). Dispersal limitation can be discounted at the community level.

The estimated strength of seed limitation varies with temporal scale because the chance that a seed arrives can only increase with the passage of time (Muller-Landau *et al.* 2002). Summing seed rain over long periods may be misleading, however, because it ignores temporal variability in site favourability and hence the importance of being present when 'windows of opportunity' open (Schupp *et al.* 2002).

We found that the seedling establishment rate per seed added did not differ between small-, medium- and large-seeded species, in contrast to several previous reports from BCI (e.g. Harms *et al.* 2000; Dalling & Hubbell 2002) and general meta-analyses (Moles & Westoby 2002, 2004). A relationship between seedling establishment and seed size may have emerged if the very smallest seeds, e.g. of *Miconia* or *Ficus* spp., had been included. However, in a study of 18 BCI tree species Augspurger (1984) likewise found no correlation between seed size and seedling survival rate under shade. Our impression from the field was that strong vertebrate predation on large seeds both before and after germination equalized overall establishment. A large proportion of the medium and large seeds added to our experimental plots were altogether removed, often within a few days of placement (J.-C.S., personal observation).

Seed addition, species identity, location and their interactions all had significant effects on seedling establishment for the 11 small-seeded, shade-tolerant species that were represented at all experimental sites in this study (Table 5). Differential establishment among locations and species with similar sized seeds could reflect many ecological differences, including attributes of microsites (e.g. light and moisture availability, proximity to pests) and attributes of species (e.g. shade and drought tolerance, pest defence). Niche differences with respect to edaphic conditions and light availability are well documented for the BCI flora (Kitajima 1994; Harms *et al.* 2001; Engelbrecht & Kursar 2003; Svenning *et al.* 2004). Specialized pests and pathogens could also cause seed and seedling survivorship to vary spatially, being low close to an adult conspecific or where conspecific density is high (Hyatt *et al.* 2003; Janzen 1970) as has indeed been shown for many of our study species on BCI (Condit *et al.* 1992, 1994; Schupp 1992; Harms *et al.* 2000; Wright *et al.* 2005). Nonetheless, the seed addition treatment and interactions involving the seed

addition treatment collectively accounted for 86% of the explained variance in seedling recruitment in our experiment (Table 5).

We conclude that seed limitation strongly influences the local species composition of the understorey seedling community and limits the overall density of understorey plants on BCI and that site and species identity also have strong effects on establishment after seeds arrive. Strong seed limitation may set the stage for neutral dispersal-assembly of the shade-tolerant plant community on BCI (Hubbell 2001). However, the species differences in average seedling establishment per seed and its variation among sites demonstrate that niche differences among species and/or negative density dependence also affect community structure (Harms *et al.* 2000; Svenning *et al.* 2004; Wright *et al.* 2005).

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