

# Seed rain during initial colonization of abandoned pastures in the premontane wet forest zone of southern Costa Rica

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**Abstract:** Understanding tropical succession requires insight into propagule availability, which constrains possible woody plant recruitment, yet seed rain composition in multiple post-agricultural sites has seldom been examined. We monitored seed rain for 60 wk in five abandoned pastures in southern Costa Rica, collecting a total of 1 140 688 seeds of 165 morphospecies. Most seeds (80.1%) arrived during the wet season. Species richness was highest in the wet season and greater in forest than in pasture. Seed rain density was greatest at the forest/pasture edge and decreased drastically just a few metres into pastures. In and near the forest, animal-dispersed seeds were more abundant than seeds dispersed by other means, while wind-dispersed taxa increased in relative importance at greater distances from the forest. Total seed input to pastures did not reflect size of adjacent forest fragments, although seed rain density varied more than threefold among sites. Among-site variation in density of regenerating woody seedlings was roughly proportional to among-site variation in seed rain. Morphospecies composition differed significantly among sites. Also, seed rain and woody plant colonists were rather dissimilar in composition, suggesting that while propagule availability is necessary for early woody plant establishment, it is a poor predictor of successional trajectory.

**Key Words:** dispersal limitation, distance, pasture, post-agriculture, seed rain, succession

## INTRODUCTION

Patterns and causes of temporal trends in species composition during tropical secondary succession are poorly known (Finegan 1996). One promising avenue towards resolution of species composition puzzles is to more closely examine the availability of propagules (Pickett *et al.* 1987). For example, in intact tropical forests, dispersal limitation has been identified as the primary cause of the absence of many pioneer species from most gaps, as well as overall constraints on species richness (Hubbell *et al.* 1999). After major disturbance in temperate forests, presence or absence of propagules in a seed bank can drastically alter the trajectory of forest recovery (Peterson & Carson 1996, Schoennagel *et al.* 2003). Similarly, several recent studies of tropical post-agricultural succession have demonstrated that the extreme limitation of propagules constrains woody plant establishment (Aide & Cavelier 1994, Cubiña &

Aide 2001, Duncan & Chapman 1999, Holl 1999, 2002; Holl *et al.* 2000, Nepstad *et al.* 1996). If such limitations are common, then closer examination of propagule availability may explain much of the spatial heterogeneity in patterns of species composition during initial stages of succession. In particular, heterogeneity in propagule availability among sites is acknowledged but little-studied. We know of few studies that address variation in initial succession among replicated post-agricultural sites (Mesquita *et al.* 2001, Peterson & Haines 2000, Uhl *et al.* 1988, Zahawi & Augspurger 1999) and none of these has directly related successional trajectories to propagule abundance patterns.

In abandoned pastures, seed input from off-site is pivotal because other mechanisms of establishment are reduced or eliminated after years of grazing (Holl 1999). The soil seed bank of woody forest plants is usually depleted, and colonization via sprouting is usually not possible due to lack of stumps and logs (Garwood 1989, Vázquez-Yanes & Orozco-Segovia 1996).

Previous studies of tropical seed rain have yielded several generalities. The seed rain in abandoned

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pastures usually contains only a small subset of forest woody species, while wind-dispersed species are often overrepresented (Cubiña & Aide 2001, Holl 1999, Martínez-Garza & González-Montagut 1999). For all species pooled, both species diversity and seed number rapidly decrease at distances of 10–30 m or less from dispersal sources (Aide & Cavellier 1994, Cubiña & Aide 2001, Gorchov *et al.* 1993, Ingle 2003, Martínez-Garza & González-Montagut 1999, 2002) conforming to predictions of dispersal curves for wind-transported seeds (see Greene & Johnson 1996). This fit of total seed rain dispersal curves to the predictions for wind-dispersed species is probably because wind-dispersed species often make up such a large proportion of total seed rain (Ingle 2003). For animal-dispersed species, the dispersal distance and direction from the parent plant depend upon the frugivore's gut passage time and post-feeding movements (Howe 1981, Murray 1988), and therefore dispersal of these species is often very patchy at small scales, with occasional long-distance dispersal occurring even though most seeds are deposited locally. For example, Chavez-Ramirez & Slack (1994) found that seed dispersal by tight-flocking birds was spatially clumped while that of plant species dispersed by birds feeding in loosely associated flocks was much more scattered. Moreover, numerous studies document much greater seed rain of animal-dispersed species beneath isolated pasture trees or shrubs (Carrière *et al.* 2002, Duncan & Chapman 1999, Holl 2002, Nepstad *et al.* 1996). Nevertheless, the remnant tree enhancement of seed rain is not uniform: Slocum & Horvitz (2000) report significant variation in seed rain under remnant trees of different species. Thus, the potential for seed rain to drive among-site variation in succession can be viewed as a larger-scale analogue of the differential colonization beneath versus away from isolated pasture trees.

Here we present findings from a larger study of factors limiting forest regeneration in five abandoned pastures adjacent to forest fragments in the premontane wet forest zone of southern Costa Rica. We have described early successional patterns, potential facilitation of woody plant colonization by rotting logs, and seed predation in our study sites in separate publications (Jones *et al.* 2003, Peterson & Haines 2000). Larger rain-forest fragments have higher diversity of plants and animals than smaller ones (MacArthur & Wilson 1967) and thus should be greater source pools for recolonization of adjacent patches. Therefore, we would expect pastures adjacent to larger forest fragments to have more dense and diverse seed rains. Also, compared to animal-dispersed species we expect wind-dispersed taxa to have consistently longer-tailed distributions with distance from the forest edge since animal dispersers tend to stay near the edge while winds continue out into the open (da Silva *et al.*

1996, Ingle 2003, Slocum & Horvitz 2000). This study quantified seed rain and tested the following hypotheses: (1) Seed rain density and diversity will decrease dramatically within a few tens of metres of forest edge. (2) Among-site variation in seed rain density and diversity will be proportional to forest fragment size. (3) Wind-dispersed species will disperse farther and more uniformly than animal-dispersed species, thereby comprising an increasing proportion of the seed rain at greater distances from the forest. (4) Because of greater production and disperser activity in the wet season, seed rain density and diversity will be greater in the wet season than in the dry season.

## METHODS

### Study area

We conducted our research in a landscape mosaic of forest fragments and pastures near the Las Cruces Biological Station, canton Coto Brus, Puntarenas Province, southern Costa Rica (8°47'N, 82°57'W). Pre-settlement vegetation was tropical premontane moist forest (Hartshorn 1983), but extensive clearing for cattle pasture in the 1950s and 1960s has left a predominantly agricultural landscape with scattered forest remnants (Juarez 1994). Elevation of the area ranges from 800 to 1500 m asl. The climate is only slightly seasonal with average annual precipitation of 3820 mm and average annual temperature of 20.7 °C; the wettest month is October, with an average of 660 mm of precipitation, while the driest month is February (70 mm) (L. D. Gomez, pers. comm.).

In June 1996, we leased (from local landowners) five active pasture sites within 3 km of one another and fenced them to exclude cattle. These sites (sites 1–5) were chosen to have a straight forest edge that bordered on active pasture, but with fences to prevent cattle encroachment into the forest. The pasture sites range in size from 0.26 to 0.63 ha with a mean size of 0.37 ha. The forest fragment adjacent to site 1 is 240 ha in size. Those adjacent to sites 2 and 3 are 10 and 3 ha respectively while sites 4 and 5 are both adjacent to a 25-ha fragment. When we started our study the pasture vegetation was a mixture of grasses, predominantly *Cynodon nlemfuensis* and *Urochloa* spp., and was grazed to a height of roughly 10–50 cm. There were no tree seedlings apparent above the grasses and only a few scattered canopy-size (i.e. > 10 m tall) trees remained in the pastures from the pre-settlement forest (Peterson & Haines 2000). All sites except site 4 had been converted to pasture prior to 1981, and aerial photographs from 1992 showed all sites to be active pastures. For additional information about the sites see Jin *et al.* (2001), Jones *et al.* (2003) and Peterson & Haines (2000).

## Seed rain

Within each field site, two parallel transects ('ridge' and 'slope') were established perpendicular to the forest/pasture boundary. The transects within each site were widely separated and encompassed the topographic variability within the pastures. Seed traps were established in pairs (5 m between the traps of a pair), at 5 and 20 m into the forest, at the boundary (0 m), and at 2.5, 5, 15, 30 and 50 m into the pastures. A total of 160 traps was established, with 32 traps (8 pairs per transect) in each of five sites.

The circular seed traps covered an area of 0.145 m<sup>2</sup> each. The traps (70 cm tall) were constructed from modified woven plastic grain bags suspended as an inverted cone from a circular wire frame. To minimize artificial seed input to traps from bird defecations, an additional wire perch, shaped into a somewhat larger circle, was attached approximately 10 cm above and slightly outside of the upper lip of each trap. Birds that were attracted to perch on the seed traps and would otherwise defecate into the trap should land on the outer wire and defecate outside the traps.

The contents of each trap were removed at 1–3-wk intervals over a 60.5-wk period from 20 September 1996 to 17 November 1997. At the laboratory, seeds were removed from leaf litter onto a 0.5-mm screen with brushes and running water. Seeds were counted, sorted into numbered morphotypes, and identified to the lowest possible taxon (family, genus or species). A reference seed collection was created from the trap samples and from our voucher herbarium specimens. We modified our laboratory protocol in March 1997 to ensure we were not missing any of the extremely small seeds (Melastomataceae, etc.). Therefore, the number of small seeds recorded prior to this change may be artificially low. All seeds trapped were included in the analysis except for Gramineae (Poaceae) which were excluded. This study was part of a larger effort examining factors limiting forest regeneration in abandoned pastures, therefore our focus is on species other than the existing dominant graminoid vegetation in the pastures.

## Statistical analysis

We tested seed rain density and species richness for significant effects of site, transect, distance, and season, using Kruskal–Wallis one-way ANOVA and Wilcoxon signed-rank tests. When testing seed rain density and richness (raw number of morphospecies) for site and transect effects, we pooled pairs of seed rain traps. Because transects are nested within site, we tested for transect effects separately for each site. Tests of richness used richness of morphospecies. To characterize distance-

from-forest effects on seed rain, we used both linear regression of log-log transformed data, as well as non-linear regression. Distance-from-forest regression used only data from traps at the boundary (0 m), and 2.5, 5, 15, 30 and 50 m from forest. To test familial composition for effect of distance, site and season, we used two-way G-tests of independence (Sokal & Rohlf 1994). A two-way G-test of independence was used to test for differences in morphospecies composition among pasture sites. Statistical testing was done with Sigma-Stat 3.0 (SPSS Inc., Chicago).

We calculated species accumulation curves by site, for traps, transects and sampling periods pooled, using seed rain in the forest (including boundary traps), versus seed rain in the pasture ( $\geq 2.5$  m from boundary). Accumulation was calculated on the basis of seeds, rather than traps. We used EcoSim 7 software (Acquired Intelligence, Inc. & Kesey-Bear, Jericho, VT), with 500 randomizations. In all species accumulation calculations, the melastomataceous *Miconia tonduzii* was excluded because of excessive numbers of seeds, which overwhelmed the software.

## RESULTS

We collected a total of 1 140 688 seeds (excluding Gramineae) between 20 September 1996 and 17 November 1997. They represented a total of 165 morphospecies belonging to 65 identifiable taxa including 26 families, and 31 genera (Table 1). Only 717 (0.06%) of the seeds were unidentifiable to family. The vast majority (96.9%) of seeds were from species in the Melastomataceae (predominantly *Miconia*, *Conostegia*, *Topobea* and *Blakea*, all of which are animal-dispersed; Gentry 1993), with the next most common families being animal-dispersed Cecropiaceae (1.3%), Marcgraviaceae (0.7%), Moraceae (0.2%) and wind-dispersed Asteraceae (0.2%). Identification beyond family level was problematic for most Asteraceae seeds (except *Neomirandea*) because the seed morphology of the taxa in our area is poorly known. At least 97.4% of the seeds were from trees.

Seed rain density did not differ significantly between transects within sites (Wilcoxon Signed-Rank tests,  $P > 0.1$  in all cases). Also, for four of the five sites, there was no difference between transects in species richness (Wilcoxon Signed-rank tests,  $P > 0.1$  in four cases;  $P < 0.01$  for site 4, Figure 1); therefore, transects were pooled in all subsequent analyses.

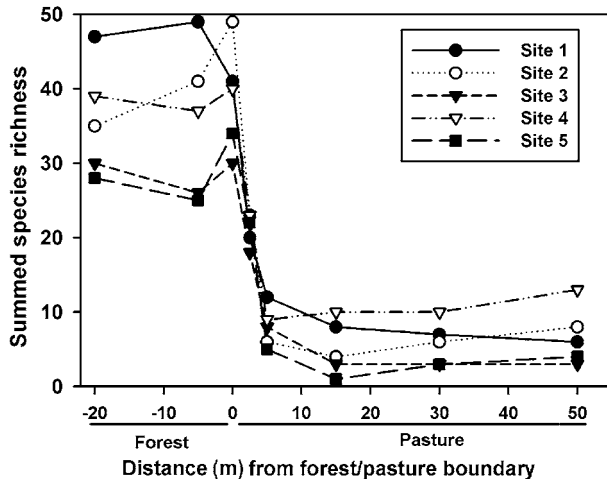
Roughly 80.1% of all seeds were collected during the wet season (May–November) although the difference in number of seeds collected by season was not significant (Mann–Whitney,  $T = 6900$ ,  $P = 0.308$ ). There were a total of 78 different morphospecies collected during the dry season and 144 during the wet season. Dry-season

**Table 1.** The ten most abundant morphospecies in the pasture seed traps at the five study sites. 100 traps in abandoned pastures were monitored between 20 September 1996 and 17 November 1997. Classification based on information in Gentry (1993), Haber *et al.* (1996), Maas & Westra (1993), Zamora *et al.* (2000, 2004).

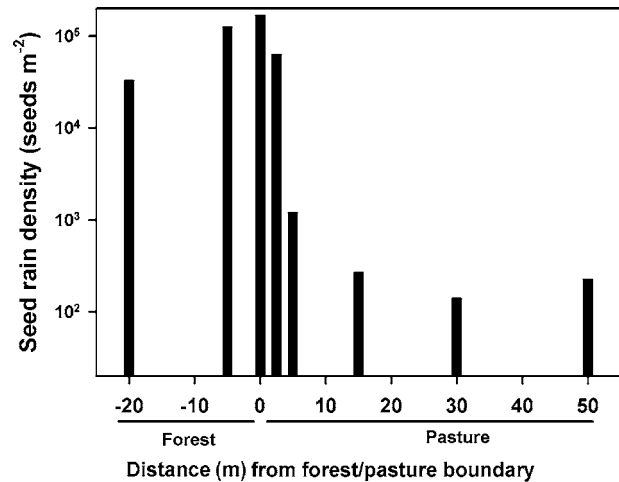
	Family	Species	No. of seeds	Dispersal agent
Site 1	Melastomataceae	<i>Miconia tonduzii</i>	40284	Bird
	Marcgraviaceae	<i>Marcgravia</i> sp. A	310	Bird
	Asteraceae	<i>Neomirandea</i> sp.	255	Wind
	Euphorbiaceae	<i>Croton draco</i>	216	Explosive
	Euphorbiaceae	<i>Sapium sebiferum</i>	146	Bird
	Asteraceae	Unknown 1	67	Wind
	Unknown	Unknown 2	38	?
	Melastomataceae	Unknown 3	34	Bird
	Asteraceae	Unknown 4	15	Wind
	Tiliaceae	<i>Heliocarpus appendiculatus</i>	14	Wind
Site 2	Melastomataceae	<i>Miconia tonduzii</i>	43826	Bird
	Marcgraviaceae	<i>Marcgravia</i> sp. A	2199	Bird
	Melastomataceae	Unknown 3	1432	Bird
	Marcgraviaceae	<i>Marcgravia</i> sp. B	544	Bird
	Tiliaceae	<i>Heliocarpus appendiculatus</i>	61	Wind
	Cecropiaceae	<i>Cecropia obtusifolia</i>	60	Bird, bat
	Unknown	Unknown 5	38	?
	Asteraceae	Unknown 6	13	Wind
	Unknown	Unknown 7	9	?
	Asteraceae	Unknown 4	8	?
Site 3	Melastomataceae	<i>Miconia tonduzii</i>	64286	Bird
	Melastomataceae	Unknown 3	394	Bird
	Asteraceae	Unknown 8	158	Wind
	Asteraceae	<i>Neomirandea</i> sp.	23	Wind
	Asteraceae	Unknown 6	22	Wind
	Solanaceae	<i>Lycianthes synanthera</i>	13	Bird
	Solanaceae	<i>Solanum</i> sp.	12	Bird
	Cecropiaceae	<i>Cecropia obtusifolia</i>	11	Bird, bat
	Euphorbiaceae	<i>Hyeronima oblonga</i>	5	Bird, mammal
	Marcgraviaceae	<i>Marcgravia</i> sp. B	5	Bird
Site 4	Melastomataceae	<i>Miconia tonduzii</i>	9313	Bird
	Melastomataceae	Unknown 3	797	Bird
	Marcgraviaceae	<i>Marcgravia</i> sp. B	397	Bird
	Asteraceae	Unknown 4	235	Wind
	Moraceae	<i>Ficus</i> sp.	226	Bird
	Solanaceae	<i>Solanum ferrugineum</i>	224	Bird, mammal
	Asteraceae	<i>Neomirandea</i> sp.	188	Wind
	Asteraceae	Unknown 9	132	Wind
	Cecropiaceae	<i>Cecropia obtusifolia</i>	107	Bird, bat
	Asteraceae	Unknown 8	41	Wind
Site 5	Melastomataceae	<i>Miconia tonduzii</i>	21181	Bird
	Melastomataceae	Unknown 3	765	Bird
	Marcgraviaceae	<i>Marcgravia</i> sp. A	359	Bird
	Unknown	Unknown 10	120	?
	Euphorbiaceae	<i>Hyeronima oblonga</i>	89	Bird, mammal
	Melastomataceae	Unknown 11	78	Bird
	Cecropiaceae	<i>Cecropia obtusifolia</i>	33	Bird, bat
	Asteraceae	<i>Neomirandea</i> sp.	23	Wind
	Solanaceae	<i>Solanum ferrugineum</i>	21	Bird, mammal
	Moraceae	<i>Ficus</i> sp.	17	Bird

summed species richness (mean =  $6.70 \pm 0.634$  (range: 0–21) morphospecies per trap pair) was significantly lower than wet-season summed species richness (mean =  $10.4 \pm 1.01$  (range: 0–33) morphospecies per trap pair; Mann–Whitney,  $T = 5780$ ,  $P = 0.024$ ). The

distribution of seeds among families differed between seasons (two-way G-test of independence, season vs. family category,  $P < 0.001$ ; Table 2). Also, within each site, seeds were relatively more abundant in traps further from the forest/pasture boundary during the wet season



**Figure 1.** Summed non-graminoid seed rain richness in five abandoned Costa Rican pastures and adjacent forest fragments. Species richness (raw number of morphospecies) at each distance from the pasture/forest boundary at each of the five study sites with all collection dates, traps and transects combined.



**Figure 2.** Seed rain density ( $\text{seeds m}^{-2}$ ) in five abandoned Costa Rican pastures and adjacent forest fragments. Density versus distance from pasture/forest boundary with all collection dates, sites, transects and traps combined.

**Table 2.** Familial composition of seed rain by season. Numbers represent total number of seeds collected during the season.

Family	Wet season	Dry season
Melastomataceae	903 311	201 494
Cecropiaceae	3225	11,372
Euphorbiaceae	1261	213
Solanaceae	1160	420
Asteraceae	874	1968
Moraceae	715	2035
Tiliaceae	34	2053
Others	3442	7111
Total	914 022	226 666

(two-way G-test of independence, season vs. distance category,  $P < 0.001$  in all cases, Sokal & Rohlf 1994).

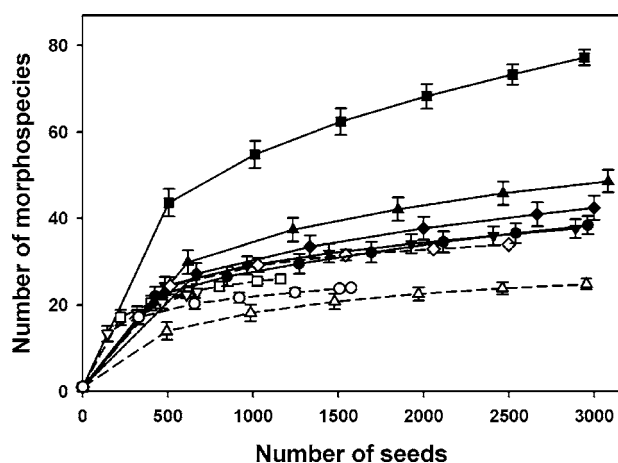
Sites varied over three-fold in total seed rain, from 119 579 seeds in site 5, to 402 066 seeds in site 2, however, these totals were not significantly different between sites (Kruskal–Wallis,  $H = 3.08$ ,  $P = 0.545$ ). Notably, total seed rain in pasture seed traps ( $> 5$  m from forest) showed a very different among-site pattern, with site 2 receiving by far the most seeds, and sites 3 and 5 the least. Summed species richness per trap-pair within a site was not significantly different between sites (Kruskal–Wallis,  $H = 5.86$ ,  $P = 0.210$ ). However, composition at the level of morphospecies differed significantly among pasture sites (Table 1). A two-way G-test of independence, using five sites and the 20 most abundant morphospecies (excluding the super-abundant *Miconia tonduzii*) was highly significant ( $P < 0.001$ ).

Seed rain density was highest at the forest/pasture edge and decreased somewhat into the forest at all sites, but decreased drastically and significantly with distance from the pasture/forest boundary (Figure 2). Considering

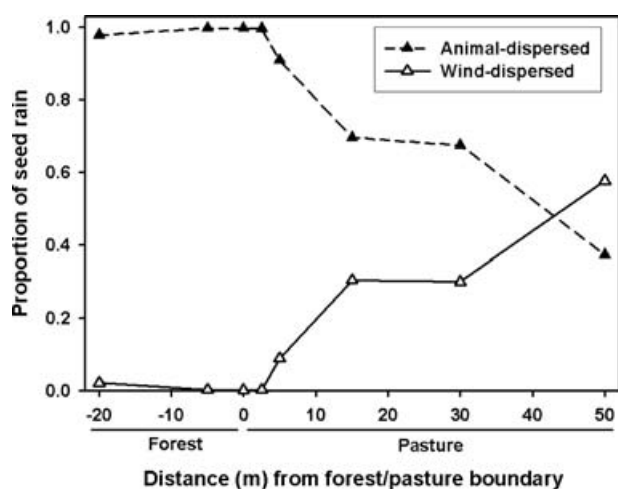
only traps from the boundary or pasture, in all sites the linear regression of log density versus log distance from forest was highly significant ( $P \leq 0.005$  in all cases,  $R^2 \geq 0.51$  in all cases). Although the decline in seed input with distance differed somewhat among sites, for all sites pooled, the seed rain at 35 and 50 m from forest was a mere 0.08–0.14% of that at the forest/pasture boundary. The relationship of seed rain (all species pooled) to distance from forest followed the negative exponential suggested by Greene & Johnson (1996); very closely in sites 1, 2 and 4 ( $R^2 > 0.99$  in all three sites), and less closely in sites 3 and 5 ( $R^2 = 0.563$  and  $0.657$ , respectively).

Not surprisingly, given the density patterns above, within each site species richness was lower at every distance into the pasture than at either the pasture/forest boundary or in the forest itself (Figure 1). With all sites combined, seeds from 99 morphospecies representing 24 of the 26 identifiable families were collected at the boundary (absent were Cyclanthaceae and Heliconiaceae with totals of 3 and 1 seeds respectively). A total of 120 morphospecies was present in the forest samples and 67 in the pasture, although only 12 of the 26 families contributed to the seed rain 5 m or more into the pasture. Only Asteraceae and Tiliaceae (both wind-dispersed) and Marcgraviaceae and Solanaceae (both animal-dispersed) were present at every distance into both habitats (forest, pasture).

Species accumulation curves show that the per-seed species richness in all sites was substantially greater in forest than in pasture (Figure 3). Indeed, the species accumulation curves for the forest traps reflect forest fragment size, since site 1 forest traps are in the largest forest fragment, followed by those from site 2, and then the other sites.



**Figure 3.** Per-seed species accumulation in the seed rain by site, for forest seed traps and pasture seed traps at five sites in southern Costa Rica. Transects, distances within forest or pasture, and sampling dates pooled. Species accumulation calculated based on 500 randomizations. Error bars are 1 SD. Forest means and standard deviations indicated with solid symbols and lines. Pasture data shown using the same symbol shape as adjoining forest, but with open symbols and dashed lines. Squares indicate site 1, triangles site 2, inverted triangles site 3, diamonds site 4 and circles site 5. *Miconia tonduzii* (Melastomataceae) excluded from all accumulation calculations, because it increased seed abundance to a level that could not be analysed by available software.



**Figure 4.** Proportional composition of total seed rain by dispersal mode in five abandoned Costa Rican pastures and adjacent forest fragments. Frequency of animal and wind-dispersed seeds versus distance from pasture/forest boundary with all collection dates, sites, transects and traps combined. 'Animal' includes morphospecies dispersed predominantly by birds, bats or other mammals.

With all sites combined, animal-dispersed seeds composed the majority of the seed rain at all distances from the forest/pasture boundary except 50 m into the pasture (Figure 4). At that distance wind-dispersed seeds were the

most common. Seeds dispersed by explosive, ballistic or unknown mechanisms made up less than 1% of the total seed rain at all distances except for 30 and 50 m into the pasture where they constituted 2.7 and 5.1% of the total, respectively.

Although animal-dispersed taxa were numerically dominant over seeds from other dispersal types, the relative abundances of seeds from different dispersal modes was site- and distance-dependent. In site 2, animal-dispersed seeds were more abundant than seeds dispersed in other ways, at all distances. However, at the other four sites, wind-dispersed seeds became most abundant at distances far from the forest. Within each of the five sites, G-tests showed highly significant ( $P < 0.001$  in all cases) shifts in relative abundances of animal vs. wind-dispersed seeds, across the various distances.

Many of the morphospecies collected from our seed traps had very localized distributions or very low abundance. Of the 165 morphospecies recognized, 68 were found only in a single pair of seed traps. The much lower diversity of species collected from pasture seed traps is reflected in the fact that 96 taxa were collected only in forest traps. Forty-seven morphospecies were represented by only 1 seed, and another 17 by only two seeds.

## DISCUSSION

The size (1.14 million non-Gramineae seeds collected), duration (14 mo) and complexity (five sites) of our study make it unique among tropical seed rain studies, and enable us to not only confirm several extant generalizations, but also to reveal previously undocumented patterns. Consistent with other work, we found a pronounced dependence of seed rain density and composition on time of year: most seeds (80.1%) fell during the wet season (May–November) and over 99% of these were animal-dispersed. Similarly, Holl (1999) found the peak dispersal of animal-dependent seeds in the first half of the rainy season. In a study of frugivorous bird movements, da Silva *et al.* (1996) found bird activity in the Amazonian pastures was highest in the wet season. Dry-season seed rain had a much higher percentage of Cecropiaceae (5.6% vs. 0.4% in the wet season), Asteraceae (1.0% vs. 0.1% in wet season) and Tiliaceae (1.0% vs. <0.004% in wet season); because many of the common species in these families are typical early successional colonists, sites open during the dry season may consequently differ in vegetation species composition compared to sites open in the wet season. However, due to the very high abundance of seeds during the wet season, sparsely vegetated or open ground that is available to woody plant propagules in that season may be more quickly colonized than areas open in the dry season, potentially accelerating the initial rate of succession.

Seed rain density was very heterogeneous among sites, varying more than 3-fold overall, and more than 7-fold for pasture seed traps. Yet this variation among sites does not parallel among-site differences in tree and shrub colonization: in 1998, density of woody colonists (> 1 m tall) in the pastures at sites 1–5 was 2.6, 2.4, 0.3, 17.2 and 4.2 stems per 100 m<sup>2</sup>, respectively (Peterson & Haines 2000). The much greater colonist density and seed rain in site 4 suggests a positive relationship, but this is not apparent when comparing the other sites (e.g. no similarity in rank order of remaining sites). Thus it appears that seed rain density can explain only part of the large differences among sites in initial tree and shrub density. We have shown elsewhere (Peterson & Haines 2000) that after seed arrival, the next important filter on seedling establishment is competition with the pasture grasses. It appears that woody forest seedlings rarely establish in intact graminoid vegetation, but much more readily colonize some kinds of favourable microsites that circumvent the inhibition by grasses such as rotting logs or small-scale open areas (Peterson & Haines 2000, unpubl. data). Therefore the availability of such microsites is a pivotal filter between seed abundances resulting from seed rain patterns, and abundances of woody seedlings and saplings.

The total number of seeds collected within a given pasture was not proportional to the size of the adjacent forest fragment. Similarly, while site 1, which is adjacent to the largest fragment, did have the highest species richness, the lowest species richness was not found near the smallest fragment but rather next to one of intermediate size.

There were also dramatic differences among sites in taxonomic composition of the seed rain (Table 1), but such differences are not paralleled by differences in tree and shrub composition among the sites (Peterson & Haines 2000). In the seed rain reported here, as well as in avian faecal samples collected in the same sites (Werner 2004), Asteraceae seeds were numerically dominant in site 4 pasture traps, yet in the successional vegetation, melastomes were predominant in that site (Peterson & Haines 2000). In site 3, initial vegetation was dominated by Melastomataceae (*Miconia tonduzii*), Caprifoliaceae (*Viburnum costaricanum*) and Solanaceae (*Solanum ferrugineum*), while seed rain composition was predominantly taxa in the Asteraceae. Similarly, *Croton draco* was the most abundant tree in site 1 (Peterson & Haines 2000), but *Croton* seeds account for only 0.52% of the pasture seed rain at that site. At the coarse scale, the among-site differences in colonizing vegetation composition appear unrelated to overall composition of the seed rain, although fine-scale variation in composition (unpubl. data) clearly shows such an influence due to abundant regeneration of a particular species near fecund adults of that species (e.g. *Croton draco* near the forest

boundary in site 1; pers. obs.). As alluded to above, our related work suggests that certain species are suited to regeneration in particular microsites, or their dispersal mechanism may preferentially deposit their seeds in particular microsites (e.g. defecation of *Miconia* seeds by birds on rotting logs). Thus, while among-site variation in composition of colonizing woody plants is influenced somewhat by seed rain, the availability of microsites is also an important influence.

Seed rain densities were greatest at the forest/pasture edge and decreased with distance into either the forest or pasture. Similar to Holl *et al.* (2000), we found much higher seed densities in the forest fragments than in the adjacent abandoned pastures (Figure 2), but seed rain declined dramatically at distances more than 2.5 m into the pasture (Figure 2). Numerous other researchers have found that density and diversity of seed rain decrease with distance (Aide & Cavelier 1994, Cubiña & Aide 2001, Gorchoy *et al.* 1993, Ingle 2003, Martínez-Garza & González-Montagut 1999, 2002; Nepstad *et al.* 1991; but see Holl 1999 for the absence of distance effect). This trend fits with the findings of da Silva *et al.* (1996) that most frugivorous bird movements over abandoned pastures are limited to a band < 80 m from the forest edge. Similarly, Slocum & Horvitz (2000) noted that mammalian dispersers restricted their movements to areas very near forest edges. Working in the same five sites used in our study, Werner (2004) collected fewer seeds from avian faecal samples in the pastures than the forest fragments even though he captured more seed-carrying birds in the pastures. Thus, the obvious cause of a rapid decline in animal-dispersed seed inputs with distance is the limited movement of frugivorous birds into pastures, coupled with those birds carrying small seed loads.

Although we have observed birds visiting trees in our sites, few of them were frugivorous. Most were either hummingbirds (Trochilidae) visiting Ericaceae flowers, slate-throated redstarts (*Myioborus miniatus*) foraging for insects, or common bush-tanagers (*Chlorospingus ophthalmicus*). While common bush-tanagers, with their varied diet of insects, spiders, fruit and nectar, are known to eat fruits of Melastomataceae and Ericaceae, we never observed this behaviour in our pasture sites (Stiles & Skutch 1989, unpubl. data).

Despite the general dramatic decline with distance, there is conflicting evidence over whether animal-dispersed or wind-dispersed seeds move farther. Cubiña & Aide (2001) found that only three species and 0.3% of the collected seeds managed to move > 4 m from the forest edge in their study in Puerto Rico, and two of those three species were wind-dispersed. Our observations in four sites revealed that wind-dispersed seeds were relatively more common at increasing distances from forest. Nevertheless, despite this general trend, site 2 did

not follow our expectations – even at 50 m from forest, a large majority of the arriving seeds were animal dispersed. We can identify no characteristic of site 2 that would explain this difference.

Many of the animal-dispersed seeds captured far into the pastures were from *Solanum* and related taxa in the Solanaceae (*Cestrum*, *Lycianthes*; Table 1, Figure 4); this is consistent with the finding of Holl (1999) that the only animal-dispersed woody genus that had seed input into her traps > 5 m from forest, was *Solanum*. In Amazonian work, Nepstad *et al.* (1996) report that *Solanum crinitum* is an important early colonist of large pastures, and that it subsequently facilitates establishment of other woody species. In contrast to Ingle's work in the Philippines (Ingle 2003), several studies in the neotropics (this study, Loiselle *et al.* 1996, Young *et al.* 1987) have found higher densities of seeds from animal-dispersed species than from wind-dispersed species. We suggest that while broad generalizations are possible about differences in dispersal distance for wind vs. animal dispersal, the idiosyncracies of any given site may deflect that site from the generally expected pattern.

We note that even controlling for the vastly greater raw number of seeds in the forest seed traps, per-seed species richness in the forest seed rain was much greater in all sites than in the corresponding pasture seed traps (Figure 3). As expected, the largest forest fragments had the most diverse seed rain on a per-seed basis (site 1 in the largest forest fragment), while per-seed diversity was much less in smaller fragments (sites 3 and 5).

The regeneration potential of abandoned pastures can be measured by the seed rain they receive (Martínez-Garza & González-Montagut 1999). However, while constraints on seed dispersal and seedling inhibition by grasses are primary limitations on recovery, seed predation, nutrient or light limitation, or seedling herbivory also can lead to very protracted recovery times in some cases (Aide & Cavelier 1994, Holl *et al.* 2000, Wijdeven & Kuzee 2000). Nevertheless, the five sites we studied had more abundant seed rain (this study; consisting of at least 97% tree seeds) compared with other Costa Rican pastures (Wijdeven & Kuzee 2000), experienced moderate levels of seed removal for most species (Jones *et al.* 2003) and had rapid re-establishment of woody plants (Peterson & Haines 2000). While early successional woody vegetation composition differs from that expected on the basis of seed rain, in this fine-scale mosaic landscape it nevertheless appears that propagule availability of a variety of small-seeded woody species is not a severe constraint on woody plant establishment. However, our seed rain findings, vegetation dynamics, and other observations suggest that large-seeded mature-forest species are absent from current seed rain, and may take decades or longer to establish.

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