Post-dispersal removal of seeds of pioneer species from five Panamanian forests

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(*Accepted 5 April 2004*)

Abstract: Variation among forests in environmental and biotic conditions may strongly influence seed fate with important consequences for the abundance and distribution of plant species. Here we examine the post-dispersal seed removal rates of six pioneer species (*Cecropia peltata, Miconia argentea, Luehea seemannii, Trema micrantha, Apeiba aspera* and *Jacaranda copaia*) from the soil surface at five sites in Panama varying in elevation (0–1100 m) and seasonality (0–4 mo dry season). We compared removal rates of washed seeds placed in vertebrate exclosures, invertebrate exclosures, and unprotected controls in January and June. Overall, removal rates of unprotected seeds were similar among sites. Almost all seed removal could be attributed to litter ants in two subfamilies (Myrmicinae and Ponerinae). Little or no removal was recorded from invertebrate exclosures while vertebrate exclosures had no effect on removal either in lowland and montane forests. Seed removal rates were high for four animal-dispersed species (mean 45% removed over 2 d), whereas two wind-dispersed species were largely untouched (mean 2% removed). These results indicate that seed dispersal characteristics, rather than site characteristics, may be the strongest determinant of the post-dispersal seed fate of pioneers.

Key Words: environmental gradient, litter ants, seed dispersal, seed removal

INTRODUCTION

Recruitment of pioneer species during gap-phase regeneration is often dependent upon successful establishment from the soil seed bank (Cheke *et al.* 1979, Dalling & Hubbell 2002, Guevara Sada & Gómez-Pompa 1972, Lawton & Putz 1988, Whitmore 1983). For establishment to take place, however, seeds must survive the activities of secondary dispersers and predators, avoid fungal infection, and remain sufficiently close to the soil surface for successful seedling emergence to occur. Seed burial experiments, radiocarbon dating, and comparisons between seed rain and soil seed densities indicate that species vary markedly in the capacity to survive these hazards, with seed persistence time for pioneers varying from a few weeks or less up to several decades (Alvarez-Buylla & Martínez-Ramos 1990, Dalling *et al.* 1997,

Murray & Garcia 2002, J. W. Dalling & Brown, unpubl. data).

Seed fate may be primarily determined by seed size and morphology. Small-seeded species (< 1 mg seed mass) are frequently removed by litter ants at the soil surface (Levey & Byrne 1993), are susceptible to fungal pathogens (Dalling *et al.* 1998), and are only capable of successfully emerging from the surface few millimetres of soil (Pearson *et al.* 2002). Seed relocation by litter-dwelling ants in the forest understorey may increase chances of seedling recruitment for pioneer species (Levey & Byrne 1993) since microsites suitable for germination and establishment are often patchy and scarce. However, most seed removal by ants probably results in seed predation (Levey & Byrne 1993). In contrast, seeds > 10 mg may exceed the maximum size that can be removed by litter ants (Kaspari 1996), or may have seed coats too thick for ants to penetrate (O'Dowd & Hay 1980). However, larger-seeded species may be more attractive to vertebrate seed predators.

Community-wide patterns of seed fate may also be influenced by site characteristics. The activity of seed

Table 1. Location and characteristics of the five study sites.

Site	Location	Elevation (m)	Rainfall (mm y^{-1})	Forest type
Parque Metropolitano	8°58′N, 79°34′W	50	1740	seasonal semi-deciduous
Barro Colorado Island	9°10′N, 79°51′W	70	2700	seasonal semi-deciduous
Fort Sherman	9°17′N, 79°58′W	70	3500	aseasonal wet forest
Cerro Campana	8°40′N, 79°52′W	800	2700	pre-montane wet forest
Fortuna	8°43′N, 82°14′W	1100	3300	montane wet forest

predators is likely to vary substantially along environmental gradients in tropical forests. Leaf litter ants rapidly remove small seeds and fruit from the soil surface at lowland sites, but their activity is positively correlated with soil moisture availability (Kaspari & Weiser 2000, Levings & Windsor 1984). Litter ants also decline in abundance at high elevation (McCoy 1990, Olson 1994, Samson *et al.* 1997), so that in contrast to lowland sites, they may be relatively unimportant as sources of seed loss in montane forest (Murray & Garcia 2002). Rather less is known about the relative importance of vertebrates as predators of small seeds, although some evidence suggests that they may play a more important role in montane than in lowland forests (Murray & Garcia 2002; K. G. Murray, personal communication).

In this study we examine removal rates of seeds of six pioneer species at five sites in Panama differing in rainfall, seasonality and elevation. We test whether species varying in seed mass and primary dispersal mode show differing removal patterns among sites, and use two exclosure treatments to evaluate whether removal is attributable to invertebrate or vertebrate predators and dispersers. We predict that invertebrate seed removal should increase with decreasing seasonality in the lowlands, and decrease with increasing elevation. We predict that vertebrate seed predation will only be important for the largest-seeded species (> 10 mg dry mass).

METHODS

Study sites and species

The study was carried out from October 2000 to June 2001 at five sites varying in elevation, rainfall and

seasonality, in the Republic of Panama (Table 1). Work was conducted within old-growth or old secondary forest (> 80 y) at all these sites except Parque Metropolitano. Since accessible stands of old-growth lowland forest no longer occur along the Pacific coast of central Panama, work at Parque Metropolitano was conducted in secondary forest approximately 60 y old, with a canopy dominated by long-lived pioneer and second-growth species (e.g. *Luehea seemannii*, *Anacardium excelsum*).

For seed removal experiments, we chose six pioneer species varying in seed size and dispersal characteristics common among the lowland sites (Table 2). All six species are common in the soil seed bank on Barro Colorado Nature Monument (BCNM). Four species are bird or mammal dispersed. Of these, *Cecropia peltata* (Cecropiaceae) and *Miconia argentea* (Melastomataceae) produce multi-seeded fleshy fruits and *Trema micrantha* (Celtidaceae) produces fleshy single-seeded fruits. *Apeiba aspera* (= *A. membranacea*, Tiliaceae, in Croat 1978) produces hard, spine-covered, multi-seed fruits that are either opened by monkeys in the canopy or by rodents on the ground. Individual *Apeiba* seeds are coated in an oily mesocarp that adheres strongly to the seeds. Our remaining two species are wind dispersed. *Luehea seemannii* (Tiliaceae) has a single elongated wing (samara) 1 cm long. *Jacaranda copaia* (Bignoniaceae) has a membranaceous circular wing surrounding the seed 2 cm in diameter. Detailed descriptions of these species (henceforth identified by genus name only) including their range distributions are found in Croat (1978).

Seed removal experiments

Seeds of all species were collected at BCNM. Seeds of *Trema*, *Cecropia* and *Miconia* were washed to remove all fruit pulp.

Table 2. Characteristics of species chosen for seed removal experiments. Sites: M = Parque Metropolitano, B = Barro Colorado Island, S = Fort Sherman, C = Cerro Campana, F = Fortuna.

Species	Seed mass (mg)	Primary dispersal agent	Seed morphology[1]	Sites present
Miconia argentea (Sw.) DC.	0.08	monkey, bird	pyramidal	M, B, S, C
Cecropia peltata L.	0.5	monkey, bird, bat	obovoid	M, B, S, C
Luehea seemannii Tr. & Planch.	1.0	wind	samara	M, B
Jacaranda copaia (Aubl.) D. Don.	4.7	wind	winged disc	M, B, S
Trema micrantha (L.) Blume*	1.4	bird	ovoid	M, B, S, C, F
Apeiba aspera Spruce	14.2	monkey	irregular ovoid	B, S

[1] Morphology of diaspore after primary dispersal.

* 'small-seeded morphotype' *sensu* Silvera *et al.* (2002).

Seeds of *Apeiba* were collected from fruits opened and discarded on the ground. Although *Apeiba* seeds were thoroughly washed small fragments of fruit pulp remained adhered to the seeds. Seeds of *Luehea* and *Jacaranda* were collected from unopened capsules. Seeds of all species were stored in an air-conditioned room before use. In October–November 2000 we set up 60 seed removal stations (10 stations for each of the six study species) at each of the five sites. Stations were randomly assigned to a seed species and were at least 5 m apart along a randomly located transect. Some stations were relocated to avoid treefall gaps. Each station consisted of a pair of 9-cm-diameter, upside-down Petri dishes, 10 cm apart, sheltered by a transparent 0.8-m² plastic tent to protect our seeds from being washed off by rain or contaminated by other falling seeds. One dish was assigned to an 'ant-free' treatment made by smearing 1 cm around the edge of the dish with Tanglefoot ® (Tanglefoot Co., Grand Rapids, Michigan, USA), a sticky paste that prevented crawling insects from moving onto the plate. The other dish remained untreated. Each dish received 10 seeds of one of the six species.

Observations of seed removal were conducted simultaneously on 30 of the 60 stations. At 10h00 seeds were placed on alternate stations at least 10 m apart along the transect. Seed removal was recorded every hour until 16h00. Stations were re-censused the following morning starting at 10h00 and hourly until 16h00. A final census of the number of remaining seeds was made at 09h00 on the third day. At 10h00 on the third day fresh seeds were placed out on the remaining 30 stations and monitored as above. Specimens of ants carrying seeds were collected at the stations. Ants were removed from Petri dishes only when large numbers of ants had recruited to a station. Otherwise, ants were collected from around the Petri dish just after seed removal. Ant removal may therefore have reduced removal rates in a few instances (see also Kaspari 1993). Vouchers of ants collected during the experiments are deposited in a collection on BCI.

A second set of experiments was carried out at the same study sites with a subset of species in May–June 2001. At the same locations in each site as used in the first set of experiments we set up stations with different treatments. On this occasion, one of each pair of Petri dishes was enclosed within an 11-cm-diameter, 30-cm-high cylinder constructed from 0.6-mm steel mesh designed to exclude vertebrate seed removal. Because of limited seed supply,

stations were set up for three of the species: *Apeiba*, *Luehea* and *Cecropia*. In contrast to the first experiment, we used *Luehea* seeds from which the wing had been removed. Seeds were placed out in stations at 10h00 and observations made at 11h00 and every 2 h until 15h00. We repeated the observations the following day starting at 10h00 and hourly until 15h00. A final census of the number of remaining seeds was made at 09h00 on the third day. Ants were collected as above.

Data analysis

Differences in seed removal among species, treatments and sites were compared using analysis of deviance. Since the dependent variable, remaining seed number, is discrete, and the data are overdispersed (with the variance:mean ratio > 1), we assumed a negative binomial error distribution. All models were fitted by maximum likelihood methods using Crawley's negative binomial errors macro implemented in the statistical program GLIM 3.7 (Crawley 1993).

RESULTS

Effect of exclosure treatments on seed removal

Most seed removal we observed could be attributed to small invertebrates. Over the total observation period, no seeds of *Cecropia* or *Miconia* were removed from the insect exclosure treatment. Likewise, minimal numbers of *Trema* (6/500), *Luehea* (3/500) and *Jacaranda* (1/500) seeds disappeared, the latter two species perhaps moved by the wind. Only the larger-seeded *Apeiba* had substantial numbers of seeds removed from the insect exclosure treatment, predominantly from the higher-elevation sites of Cerro Campana (20/100 seeds), and Fortuna (32/100 seeds). Only five *Apeiba* seeds were removed from the insect exclosure treatment at the remaining three sites. Given the low removal rate from the insect exclosure treatment, the mesh cage treatment designed to exclude vertebrates was not expected to influence removal rates except for *Apeiba*. In fact, we found no cage effect on removal for any of the three species tested (*Cecropia*, *Luehea* and *Apeiba*, F = 0.7; df = 1, 270; P > 0.05; Table 3). Finally, removal of the samara wing from *Luehea* seeds did not substantially increase rate of seed removal (Table 3).

Table 3. Mean per cent seed removal ± SE from vertebrate caged and uncaged stations in May–June 2001. Wings were cut off seeds of *Luehea*.

Species	Metropolitano Caged	Metropolitano Uncaged	BCI Caged	BCI Uncaged	Sherman Caged	Sherman Uncaged	Campana Caged	Campana Uncaged	Fortuna Caged	Fortuna Uncaged	All sites Caged	All sites Uncaged
Apeiba	29 ± 4	27 ± 4	36 ± 4	35 ± 3	60 ± 12	68 ± 4	98 ± 6	100 ± 0	80 ± 3	72 ± 3	61 ± 4	61 ± 4
Cecropia	58 ± 4	74 ± 4	18 ± 3	17 ± 3	18 ± 3	29 ± 3	27 ± 4	34 ± 5	44 ± 5	49 ± 4	33 ± 4	41 ± 4
Luehea	11 ± 3	17 ± 2	8 ± 2	5 ± 8	3 ± 4	8 ± 0.8	4 ± 1	25 ± 3	4 ± 1	3 ± 0.7	6 ± 2	12 ± 2

Table 4. Number of seed stations from which at least one seed was removed ('stations visited', n = 10) and mean per cent number of seeds removed ± SE at each study site for seeds exposed to insects in October–November 2000.

| | Metropolitano | | BCI | | Sherman | | Campana | | Fortuna | | All sites |
	Stations visited	Removal %	Stations visited	Removal %	Stations visited	Removal %	Stations visited	Removal %	Stations visited	Removal %	Removal %
Miconia	6	40 ± 4	7	43 ± 4	5	33 ± 2	5	28 ± 1	6	42 ± 2	37 ± 3
Cecropia	8	70 ± 15	7	56 ± 15	7	29 ± 12	4	17 ± 10	7	33 ± 1	41 ± 10
Luehea	1	10 ± 10	2	2 ± 1	1	2 ± 2	0	0	0	0	3 ± 2
Jacaranda	0	0	2	3 ± 2	0	0	0	0	0	0	0.6 ± 0.6
Trema	8	55 ± 1	10	80 ± 10	9	23 ± 9	7	49 ± 15	9	35 ± 8	49 ± 10
Apeiba	8	29 ± 1	10	96 ± 3	8	64 ± 13	8	31 ± 10	9	54 ± 10	55 ± 12
All species*	30	49 ± 9	34	69 ± 11	29	37 ± 9	24	31 ± 7	31	41 ± 5	45 ± 6.6

*Excluding *Luehea* and *Jacaranda*.

Variation in removal rates among sites and species

Here we only consider the fate of seeds exposed to insects in October–November 2000 (Table 4). Removal rates were strikingly different for seeds with primary dispersal by wind versus animals. Samaras of the wind-dispersed *Luehea* were untouched at two of the sites, and only few seeds were removed from each of the remaining three sites. Similarly only three winged seeds of *Jacaranda* were removed from BCI and untouched elsewhere (Table 4). In contrast, a substantial fraction of the four animal-dispersed seeds were removed over the same time period, ranging from 17% for *Cecropia* at Campana to 96% for *Apeiba* at BCI (Table 4).

For the four animal-dispersed species, we found a significant effect of site on seed removal (F = 2.46; df = 4, 180; P < 0.05), but no significant effect of species (F = 0.97; df = 3, 180; P > 0.01) or site × species interaction (F = 0.89; df = 12, 180; P > 0.01). Differences among sites in seed removal could be attributed to the higher removal at BCI (mean 69%) than at the other sites (mean 39%; Table 4). Explanations for this site effect are unclear, and suggest higher litter invertebrate densities may be present at BCI than elsewhere. The site effect was no longer significant when BCI was omitted from a recoded analysis of deviance model.

Ant species distribution at the seed baits

We observed 20 ant species belonging to two subfamilies (Myrmicinae and Ponerinae) during the seed removal experiments ran in October–November 2000. The genus with the most species was *Pheidole*, with four species encountered in the three lowland sites and eight species in the higher-elevation sites. Although half of the ant species were observed at more than one site, no ant species were found in both lowland and higher-elevation sites (Table 5). Most species observed in the lowlands were recorded at more than one site, whereas most species

Table 5. Ant species observed harvesting seeds from the removal experiment in October–November 2000. Abbreviations as for Table 2.

Ant species	Seeds harvested	Site
Myrmicinae		
Cyphomyrmex sp. 1	*Luehea, Cecropia*	M
Cyphomyrmex sp. 2	*Luehea*	M
Pheidole biconstricta (Mayr) (1)*	*Cecropia*	M, B, S
Pheidole biconstricta (Mayr) (2)*	*Trema*	M, B, S
Pheidole multispina	*Miconia, Apeiba*	M, B, S
Solenopsis (*Diplorhoptrum*) sp.	*Miconia, Apeiba*	M, B, S
Pheidole sp. 1	*Apeiba*	M, B
Pheidole sp. 2	*Cecropia, Apeiba*	C
Pheidole sp. 3	*Cecropia, Apeiba*	C, F
Pheidole sp. 4	*Cecropia, Miconia*	C, F
Pheidole sp. 5	*Cecropia, Trema*	C
Pheidole sp. 6	*Cecropia*	C
Pheidole sp. 7	*Cecropia, Apeiba, Trema*	F
Pheidole sp. 8	*Cecropia, Miconia, Apeiba*	F
Pheidole sp. 9	*Cecropia, Apeiba*	F
Monomorium sp.	*Cecropia*	C
Trachymyrmex cornetzi (Wheeler)	*Cecropia*	M, B
Sericomyrmex urichi (Mayr)	*Cecropia*	M, B, S
Wasmannia auropunctata (Roger)	*Miconia, Apeiba*	M, B, S
Ponerinae		
Gnamptogenys sp.	*Apeiba*	C

* Different in some morphological traits perhaps two infra-specific taxa.

from the higher-elevation sites were found either at Cerro Campana or Fortuna.

DISCUSSION

In this study we examined removal rates of seeds of four animal- and two wind-dispersed pioneer species placed on the soil surface at five sites varying in seasonality and elevation. Seeds were obtained from tree crowns or from freshly fallen intact fruits and were cleaned of fruit pulp and air-dried before initiating the experiment. Although fruit or faecal material may alter the attractiveness of seeds to secondary dispersers (Byrne & Levey 1993, Kaspari 1993, Loiselle 1990, Pizo & Oliveira 1999) this initial treatment allowed us to assess the role of seed size and morphology as factors influencing seed

removal. Despite this pre-treatment, a dramatic difference remained between the fate of animal- and wind-dispersed seeds. Overall, in October–November 2000, between 17 and 96% of three animal-dispersed seeds were removed from unprotected treatments over 47 h, versus 1–3% for the two wind-dispersed species.

Differences in removal rates between animal- and wind-dispersed seeds could have several explanations. Small particles of fruit pulp or other residues present on the seed coat might have acted as a residual attractant to some ant species, particularly in the case of *Apeiba* seeds, where oily mesocarp tissue remained firmly attached to the seeds. A second possibility is that the large wings on *Luehea* and *Jacaranda* seeds may have hindered seed removal. This also seems unlikely as attempts to remove the seeds were not observed in the field, and because removal of the wings of *Luehea* seeds in May–June 2001 did not substantially increase removal rates relative to other species (Table 3). One final possibility is that invertebrate seed predators may discriminate against wind-dispersed seeds based on their lower seed moisture content (Augspurger 1988).

Most seed removal could be attributed to ants at all sites. Seeds placed on the centre of Petri dishes and surrounded by a barrier of Tanglefoot ® to exclude non-volant invertebrates had very low removal rates (overall < 1% for all species except *Apeiba*). Seeds protected from removal from larger vertebrate seed predators by 0.6-mm steel mesh exclosures had similar removal rates as unprotected controls. An exception to this pattern was substantial losses of *Apeiba* seeds from Tanglefoot ® exclosures in the two higher-elevation sites, which suggest predation by vertebrates might play a role for the largest seeds used in our experiment.

However, removal rates for *Apeiba* were not significantly different between caged and un-caged treatments (Table 3; see Results). Instead, *Apeiba* seed loss at the higher-elevation sites might be accounted for by the activity of large cockroaches (Blattaria), which were occasionally observed removing *Apeiba* seeds from stations at Fortuna and Cerro Campana but were not observed at the lowland sites. Failure to find evidence for vertebrate seed predation may indicate that the seeds we selected were too small to be attractive to rodents, or alternatively, that the structures used in the experiment may have repelled them.

Patterns of ant abundance and diversity along elevational gradients are as yet poorly defined. In general, insect diversity has been found to peak at mid-elevations (Janzen 1973, Janzen *et al.* 1976, but see Wolda 1987). Similarly ant diversity and density peak at 400–800 m elevation in the Philippines (Samson *et al.* 1997), and at 800–1000 m in Panama, declining to low levels by 1500 m (Olson 1994). Here, we found no evidence of a significant difference in removal rates of seeds that we could attribute to variation in overall ant activity between the lowland and higher-elevation sites. Seed removal rates were similar among sites with the exception of high rates at BCI (Table 4), and could be attributed to many ant species (Table 5). Clearly litter-ant communities in the lowland and higher elevation sites differed in species composition, but our records of seed removal were not sufficiently detailed to evaluate the specificity of ants to particular species. Nonetheless, the finding that three ant species (*Pheidole biconstricta*, *Trachymyrmex cornetzi* and *Sericomyrmex urichi*) which were common at least in two of the three lowland sites (Table 5), were observed removing seeds of only a single species (*Cecropia peltata*) is suggestive of some dietary niche partitioning among the litter ants, as has been observed based on seed size (Kaspari 1996).

Overall, our results suggest that seed morphology and dispersal characteristics play a more important role than site characteristics in the post-dispersal seed fate of neotropical pioneers. Further studies need to determine whether the clear differences in removal rates between animal- and wind-dispersed species observed here can be broadly generalized, and should include sites at higher elevations than included here to determine how leaf-litter ants influence recruitment patterns of small-seeded species.

ACKNOWLEDGEMENTS

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