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Seed Dynamics of Early and Late Successional Tree Species in Tropical Abandoned Pastures: Seed Burial as a Way of Evading Predation

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Abstract

We explored different treatments to enhance the probability of sowed seeds of two early successional (ES, *Cecropia obtusifolia* and *Ochroma pyramidale*) and two late successional (LS, *Brosimum costaricanum* and *Dialium guianense*) species to escape predation and germinate in abandoned cattle-raising pasture fields in Southeastern Mexico. ES species were sown in groups of 50 seeds under three treatments: invertebrate exclusion, burial, and exposition to seedeaters. LS species were sown in groups of 10 seeds under three treatments: vertebrate exclusion, burial, and exposition to seedeaters. We registered seed predation and germination 2, 4, 8, 16, 32, and 64 days after the initial sowing. Overall, ES showed higher predation rates (mean ± SE = 0.45 ± 0.07 seed seed^{-1} day^{-1}; *n* = 3) than LS species (0.09 ± 0.02 seed seed^{-1} day^{-1}). *Cecropia obtusifolia* was completely predated in all treatments after 8 days. Burial and exclusion treatments reduced final predation in circa 6% for *O. pyramidale*, relative to that of exposed seeds (85% after 8 days); most germination occurred in buried seeds (3.7%). In *B. costaricanum,* burial enabled germination by 10%; exposed and excluded seeds were removed 100%. *Dialium guianense* showed 12% germination in buried seeds and circa 20% of the seeds were not removed after 64 days. Direct sowing would be a recommended rainforest restoration practice for species with relatively large seeds if deposited in groups and buried. Studies which address variation across numerous sites are necessary in order to generate more consistent seed predation patterns and rainforest restoration principles in tropical pastures.

Key words: **abandoned pasture fields, direct sowing, early and late successional species, germination, Mexico, rainforest restoration, seed predation.**

Introduction

Tropical rainforest regeneration can be delayed or impeded by ecological barriers related to propagule scarcity (i.e., seed dispersal limitation, depleted seed and seedlings banks, and the lack of resprouts), habitat degradation, or a combination of both (Holl 1999). In general, seed predation is a strong barrier against natural regeneration in abandoned tropical humid pastures (Nepstad et al. 1996; Notman & Gorchov 2001; but see Aide & Cavelier 1994), as well as tropical dry (e.g., Hammond 1995) and temperate (e.g., Ostfeld et al. 1997) old-field systems. Protecting seeds against predation, permitting them to reach the seedling stage, is an important goal of tropical restoration programs (Camargo et al. 2002; Woods & Elliott 2004).

The probability of seed predation depends on seed characteristics, such as animal preferences, energetic and chemical content, seed mass, pulp presence, and color (Holl & Lulow 1997; Camargo et al. 2002; Peña-Claros & De Boo 2002). Abundance and identity of potential seedeaters, such as rodents, beetles, and ants (Nepstad et al. 1996; Vasconcelos 1999; Notman & Gorchov 2001; Dunn 2004), also influence predation probabilities. Both suits of variables combine and generate particular seed–animal interactions that may strongly change in space and time (Janzen 1971; Holl & Lulow 1997; Guariguata & Pinard 1998).

Few studies have explored the potential implications of predator exclusion as a way of increasing seedling establishment. To our best knowledge, only a few studies have tested exclusion treatments to reduce seed predation in tropical cattle pastures. In these systems, Holl and Lulow (1997) observed significantly lower predation rates in excluded seeds (average 0.006 seeds day^{-1}) than in exposed seeds (0.1529 seeds day^{-1}) for a variety of tropical tree and shrub species. Notman and Gorchov (2001) registered 90% predation by rodents in exposed seeds and less than 10% predation in exclusion treatments, caused mainly by insects. Woods and Elliott (2004) observed no effect of exclusion against rodents, due to heavy predation by ants, but did observe germination enhancement due to seed burial. Thus, in two of three studies, exclusion seems to increase seed survival substantially.

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With the aim of favoring new productive systems that maintain biodiversity and ecosystem services, the Mexican Government has recently launched programs that economically support alternative sustainable land uses. Local people are now interested in ways of establishing productive secondary forests, preferably at low costs and through simple technology methods (Comisión Nacional Forestal 2006; X. Garcia-Orth, personal observations). The purpose of this study is to provide useful knowledge for restoration practitioners working in degraded tropical ecosystems where seed predation may be a strong regeneration barrier. We studied the dynamics of sown seeds of four rainforest tree species with contrasting life histories (two pioneer and two mature forest species) in recently tropical abandoned pastures. We included exclusion and burial treatments for all species to enhance the probability of seed survival and germination, and test alternative restoration practices. Because small seeds of pioneer species are adapted to forest gap colonization, have low maternal resources and low secondary metabolite content (Vázquez-Yanes & Orozco-Segovia 1993), we hypothesized that these seeds would suffer high removal by invertebrates, but faster germination rates in the exclusion and burial treatments. On the other hand, we hypothesized that the large-seeded mature forest species would suffer high removal rates when exposed (mainly due to vertebrate presence), but very low removal rates when excluded or buried, showing lower removal rates overall. The high energetic seed content of large-seeded species would mean high antiherbivore defenses (Janzen 1969), and therefore lower predation rates (Camargo et al. 2002; Moles et al. 2003).

Methods

Study Site

The study was carried out at the Marqués de Comillas region, Chiapas, Southeast Mexico (lat 16°01′N, long 90°55′W). The region covers an area of 200,970 ha, delimited by the Lacantún River in the West and North, by the Guatemalan border in the South, and by the Salinas River in the East and North (Arreola 1996). Once completely covered with rainforest, now the landscape at this region is constituted by a matrix of forest remnants, secondary forests, and agricultural lands. The original rainforest cover area has been reduced to less than half in the past three decades (De Jong et al. 2000).

The climate of the region is humid and warm, with a mean annual temperature of 24.8°C, and a mean temperature of 18°C during the coldest month (February). Mean annual rainfall is circa 3,000 mm, with the highest precipitation occurring between June and September. A short dry season, with less than 60 mm per month, occurs between February and April (García 1987; Siebe et al. 1995). Different kinds of soils have been identified in the area according to the parent material where they have developed (i.e., recent alluvium from the Lacantún River, sandstone, luthite, and limestone; FAO 1988). Tropical rainforest is the predominant vegetation type and it varies in structure and composition across geomorphologic landscape units differing in soil and topography (García-Gil & Lugo 1992; Ibarra-Manríquez & Martínez-Ramos 2002). Land tenure is mainly communal, and economical activities include agriculture (such as maize, beans, and peppers) and extensive livestock herding, mainly cattle (Lazcano-Barrero et al. 1992; Arreola 1996).

Studied Pasture Fields

Three active cattle pasture fields, circa 6 ha in extension each, were selected for this study. Hereafter, these will be addressed as site-1, site-2, and site-3. All sites were located in low-hill, poor sandy soil areas (Siebe et al. 1995) and separated by at least 4 km. Sites had similar land-use history: original vegetation consisted of rainforest, which was cut and burned for the first time between 1985 and 1990. Maize was grown for 2–3 years, after which forage grasses were established. The sites were burned every 1 or 2 years although used as cattle pasture (Table 1). In July 2004, an area of 1.4 ha in each pasture was fenced to exclude cattle and left undisturbed. The experiment was initiated in July 2005.

Table 1. Characteristics of the three pasture sites where the experiment took place at Marqués de Comillas, Southeast Mexico.

Site	*Average Ground Cover (All Species) (%)*	*Dominant Herb and/or Grass Species*	*Family*	*Proportional Ground Cover per Species per* m^2 *(%)*	*Average Number of Herb Species per* m^2	*Distance to Closest Forest Remnant (m)*	*Closest Remnant Age*
Site-1	100	*Panicum* spp.	Poaceae	70–90	4.1	100	Mature (>80 yr)
		Desmodium spp.	Mimosaceae	70–80			
		Axonopus spp.	Poaceae	60–80			
Site-2	78	*Scleria* spp.	Cyperaceae	40–90	9	100	20 yr
		Panicum spp.	Poaceae	35–40			
		Sida rhombifolia	Malvaceae	10–30			
Site-3	82	*Andropogon* spp.	Poaceae	80–100	3.7	200	Mature (>80 yr)
		Axonopus spp.	Poaceae	70–100			
		Echinochloa spp.	Poaceae	40–60			

Seed Collection and Treatments

In each study pasture, we established five plots of 5 × 5 m which were cleared of grass with *machete* to set seed containers on the ground, and make seed finding and counting possible (see details below). The plots were separated by 5 m along a 50-m transect which was established 70 m from any isolated tree located inside the fenced area.

Seeds of four abundant forest tree species were used: two small-seeded, early successional species (ES, *Cecropia obtusifolia* and *Ochroma pyramidale*), and two large-seeded, late successional species (LS, *Brosimum costaricanum* and *Dialium guianense*) (Table 2). We will refer to species by genus name hereafter. Our species selection included species that would usually reach pastures by animal (*Cecropia*) and wind dispersal (*Ochroma*), and species with limited dispersal into pastures (*Brosimum* and *Dialium*). Except *Cecropia*, the rest of the species are useful for local resource management, that is, wood production and/or nutritional value for cattle and people (Table 2; Vázquez-Yanes et al. 1999).

Except *Ochroma* (collected in March 2005), all seeds were collected 2 days before the start of the experiment. *Cecropia* seeds were collected from two mature trees located less than 4 km from experimental sites. Seeds were rinsed with water to remove fruit tissue and dried with absorbent paper. *Ochroma* seeds were collected from naturally fallen fruits belonging to more than 10 roadside mature individuals, and the cotton-like tissue containing seeds was removed by hand. Seeds were stored in paper bags in the shade at the study area, until the start of the experiment. *Brosimum* and *Dialium* fruits were collected from 3 to 10 different individuals located in forest remnants close to the studied pastures. Fruits were picked up from the ground, rinsed with water to remove fruit tissue, and dried with absorbent paper.

For setting seeds of ES species, we used inverted cone-shaped containers (7 cm diameter, 10 cm depth) made with metal mesh (5-mm aperture), filled with commercial garden soil. We used commercial garden soil in order to facilitate finding the small seeds. Local soil was coarse and not homogenous, making it easy to lose ES species seeds. Fifty seeds were used per experimental container. Three treatments were applied to the seeds: burial, exclusion from invertebrates, and complete exposition. Seeds in the burial treatment were sown and covered with garden soil up to 0.3 cm. Seed germination of photoblastic (*Cecropia*) or thermoblastic (*Ochroma*) seeds could be affected by the soil cover. However, it has been shown that the exposure of seeds of *C. obtusifolia* to direct sun light for short periods (>10 min) are enough to activate seed germination mechanisms (Vázquez-Yanes & Smith 1982). Other studies have registered quantifiable germination rates in *C. obtusifolia* seeds covered with soil (Alvarez-Buylla & Martínez-Ramos 1990). For *Ochroma*, soil temperature changes operating in the open field at 0.3 cm depth are enough to promote germination (Vázquez-Yanes et al. 1999).

Invertebrate exclusion was achieved by placing the seeds at the soil surface and a fine nylon cloth mesh (less than 0.1 mm aperture) was fixed over the containers. The cloth covered half of the container's height and was held tightly by rubber bands. Although seeds were accessible from belowground (if invertebrates dug across the section of the container without cloth), the seeds were unreachable from the surface level. Exposed seeds were placed on the surface of the garden soil without any protection. The surface of the ground barely surpassed the containers' height, making them not visible at ground level. During each census, one container from each plot was removed from the ground and placed inside a plastic bag for transportation to the laboratory, where seeds were separated from the commercial garden soil with the help of a thin painting brush under a stereoscopic microscope and registered as germinated (seeds with an emerged radicle), damaged (with evidence of invertebrate partial consumption or fungal tissue), or present. Censuses were made 2, 4, 8, 16, 32, and 64 days after the start of the experiment. Five containers were removed at each census per species per site.

For LS species, we used 10 seeds per deposition spot. The treatments applied to the seeds were burial, protection from vertebrates, and complete exposition. For the burial treatment, we made wire mesh (5-mm aperture) box-shaped containers (5 × 5 × 10 cm), half-filled with local soil. The seeds were placed in the containers and

Table 2. General attributes of the four tree species studied at Marqués de Comillas, Southeast Mexico.

Species	*Family*	*Successional Status*	*Dispersal Vector*	*Seed Dry Mass (g)*	*Species-Related Benefits*
Cecropia obtusifolia Bertol.	Cecropiaceae	ES	Bird and mammal	0.0009	Ecological
Ochroma pyramidale (Cav. ex Lam.) Urb.	Malvaceae	ES	Wind	0.0068	Ecological, productive
Brosimum costaricanum Liebm.	Moraceae	LS	Bird and mammal	0.92	Ecological, productive
Dialium guianense (Aubl.) Sandwith.	Fabaceae	LS	Bird and gravity	0.25	Ecological, productive, alimentary, medicinal

Mean dry seed mass is as reported from Ibarra-Manriquez et al. (2001).

covered with local soil. Containers were placed in handmade holes (5 × 5 × 10 cm) in the ground. To exclude seeds from vertebrate seedeaters, we made small cages (15 × 15 × 5 cm) with wire mesh (5-mm aperture). Seeds were placed directly over the pasture floor and the cages were placed over them, firmly fixed to the ground with metal hooks. Invertebrates could remove the seeds through the wire mesh. Exposed seeds were placed directly on the pasture floor and kept in one spot with a circular metal ring (1 cm high), though seeds remained completely accessible to seedeaters. Censuses were made 2, 4, 8, 16, 32, and 64 days after the start of the experiment. Subsequently, we combed through the soil to find buried seeds of LS species. The remaining seeds were counted and placed back in the container as originally. During each census, seeds were registered as germinated, damaged, or present. Each plot had six containers for each treatment, for a total of 30 containers inspected at each census, per species, per site.

Data Analyses

Observations for each species within plots and sites were not independent from one another, so we added up the total of seeds per species per treatment per site. For ES species, the bundle of 50 seeds in each of the five plots was added up, resulting in an accumulated proportion of remaining or germinated seeds out of a total of 250 seeds per site per census date. For LS species, the six observations in each of the five plots (60 seeds per plot) were added up and resulted in a proportion of remaining seeds out of a total of 300 seeds per site for each census. Because seed predation was more than 90% after 8 days for ES species and after 16 days for one of the two LS species (see Results), we assessed the influence of treatments on initial seed predation rates restricting the analysis to the early census periods. We obtained initial predation rates as $[(\log N_f) - (\log N_i)]/t$, where N_f is the remaining number of seeds, N_i is the initial number of seeds, and t is the number of days from the sowing date to the final census (8 days for ES species, and 16 days for LS species). For each species and treatment, we report a men (± SE) predation rate from three site values. We used survival analyses (Cox's proportional hazard model) to determine the effects of treatments on mean time of seed survival. Because sites could not be considered as replicates (due to variation regarding land-use history, surrounding forest matrix, and structural composition of pasture vegetation), we carried out survival analysis for each species at each site separately. Conclusions were derived from the results' regularity across sites. For *Cecropia,* a survival model with constant hazard, no censoring, and exponential error structure with reciprocal link function was defined (following criteria given by Crawley 1993). For the rest of the species (where a few seeds remained alive at the end of the study), a survival model with constant hazard, censored data, and Poisson error structure with log link function was defined (Crawley 1993). To evaluate effects of site and treatments on the final proportion of germination (64 days after sowing date), we used an Analysis of Deviance which considered a binomial error and a logistic link function, following criteria given by Crawley (1993). In these analyses the deviance explained by each factor can be considered to be an approximated χ^2 value (Crawley 1993).

Results

Seed Predation

ES Species. Lumping all treatments and sites, ES species were consumed faster (mean ± SE = 0.48 ± 0.07 seed seed^{-1} day^{-1}) than LS species (0.09 ± 0.02 seed seed^{-1} day^{-1}). In all species, rates of seed predation were very high during the first 16 days of observation and diminished after 32 days (Figs. 1 & 2). For ES species, 40% of all seeds were removed within the first 48 hours, and within the first 4 days we observed more than 50% predation.

Seeds of *Cecropia* were removed faster than any other species: 80% predation by day 4 and 100% predation after 8 days of observation (Fig. 1). Overall, the predation rate for *Cecropia* was the highest of all studied species (0.598 ± 0.018 seed seed^{-1} day^{-1}). Seed predation rate was not significantly different among treatments in any site for this species. *Ochroma* showed the second fastest predation rate (0.310 ± 0.117 seed seed^{-1} day^{-1}; Fig. 3) with more

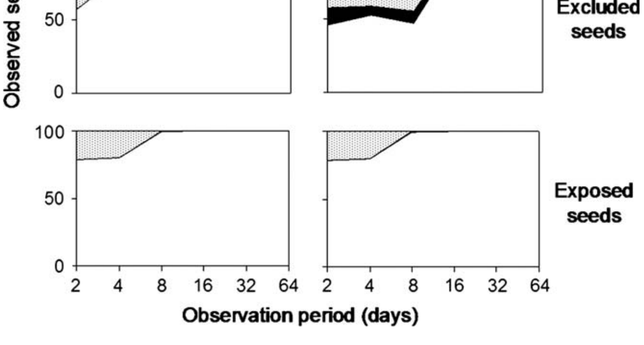

Figure 1. Dynamics (along a 64-day period) of seeds from two ES species (*Cecropia* and *Ochroma*) sown under different treatments in abandoned pasture fields at Marqués de Comillas, Southeast Mexico. Areas correspond as follows: percentage of remaining seeds (dotted), percentage of germinated seeds (gray), percentage of damaged seeds (black), and percentage of removed seeds (blank). Values correspond to averaged sites (see text for details).

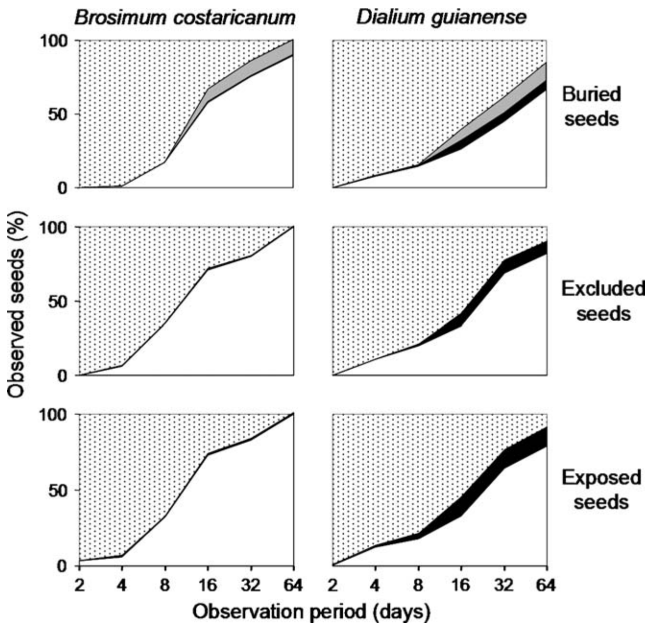

Figure 2. Dynamics (along a 64-day period) of seeds from two LS species (*Brosimum* and *Dialium*) sown under different treatments in abandoned pasture fields at Marqués de Comillas, Southeast Mexico. Areas correspond as follows: percentage of remaining seeds (shaded), percentage of germinated seeds (gray), percentage of damaged seeds (black), and percentage of removed seeds (blank). Values correspond to averaged sites (see text for details).

than 60% of seeds removed after 32 days, and 92–100% predation at the end of the experiment. Buried seeds were almost completely removed by day 32, excluded seeds were completely removed by day 16, and exposed seeds were completely removed by day 8 (Fig. 1). Significant differences between treatments in removal rates were recorded within each site ($\chi^2 > 11.7$, df $= 2$, $p < 0.001$).

LS Species. Lumping all treatments and sites, LS species showed 20% predation after 8 days, and 70% predation after 64 days of observation, except for *Dialium* when buried (66.6% predation, 64 days). *Brosimum* showed a strong increase in predation from circa 20 to 90% in most treatments, between 8 and 16 days of observation (Fig. 2). Differences in predation rates were observed between sites and treatments within some sites (Fig. 3). Overall predation rate for *Brosimum* was 0.146 ± 0.031 seed seed^{-1} day^{-1}. Site-1 and site-3 exhibited significant differences in seed predation rates between treatments ($\chi^2 > 19.4$, df $=$ 2, $p < 0.001$). *Dialium* seeds showed the lowest predation rates of all studied species (0.028 ± 0.002 seed seed^{-1} day^{-1}). For this species, the main increase in predation occurred between 16 and 32 days of observation (Fig. 2). Predation of *Dialium* varied significantly between sites (Fig. 3), and more than 20% of the seeds remained at the end of the observation period. Exposed and excluded seeds exhibited higher predation percentages (circa 60%) after 32 days of observation, whereas buried species showed similar predation percentages until the end of the experiment (Fig. 2). Significant differences in predation rates were observed between treatments in site-1 and site-2 ($\chi^2 > 16.4$, df $= 2$, $p < 0.001$). *Dialium* was the only species to show seeds that were not removed or germinated by the end of the experiment.

Germination

No germinated seeds of *Cecropia* were recorded throughout the experiment (Fig. 1). *Ochroma* showed germinated seeds 4 days after sowing and continued until 32 days of observation, when 7.4% germination was recorded (Fig. 1). Higher germination percentages were observed in the burial treatment, though some germination also occurred in the exposed seeds in some sites (Fig. 4A).

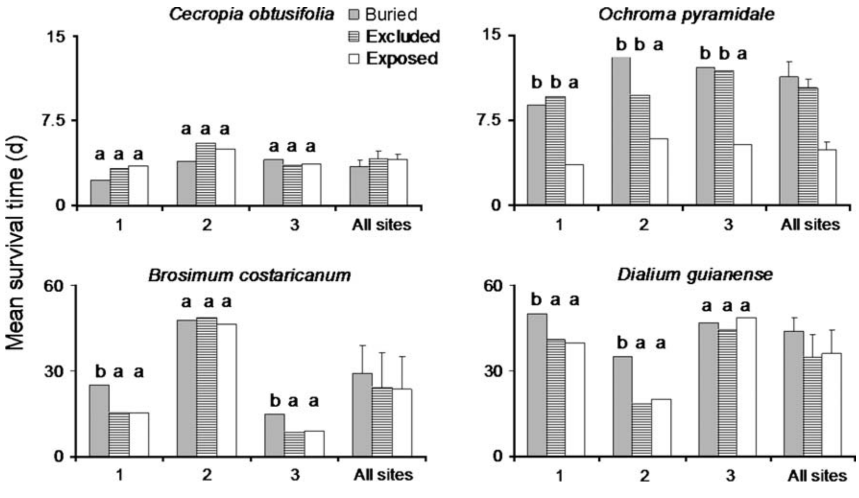

Figure 3. Mean seed survival time (d) estimated (Cox's proportional hazard survival analysis) for two ES and two LS species at Marqués de Comillas, Southeast Mexico. Numbers in the *x*-axis represent sites. Different letters indicate significant statistical differences among treatments within each species. Bars represent plus one SE.

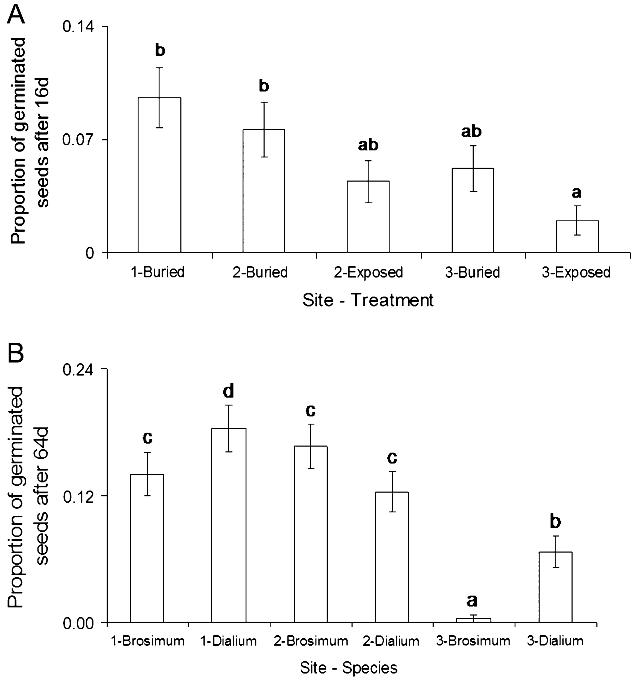

Figure 4. Final proportion of total observed germinated seeds after 64 days for (A) *Ochroma* and (B) *Brosimum* and *Dialium* in abandoned pasture fields at Marqués de Comillas, Southeast Mexico. Bars represent ± SEs. Different letters indicate significant statistical differences.

Seeds of LS species only germinated in the burial treatment (Fig. 2). Germination was recorded initially at the 8-day census, and continued to occur throughout the experiment (Fig. 2). *Brosimum* showed 10.3% germination after 64 days; the rest of the seeds had been completely removed. Buried seeds of *Dialium* showed 12.4% germination after 64 days (Fig. 4B). Significant differences in final germination percentages were observed between sites (Fig. 4B).

Discussion

Removed seeds may be secondarily dispersed and not always predated (Vander Wall et al. 2005). However, we are certain that most removed seeds in our study were predated because most of the experimental containers exhibited fragments of damaged seeds (except for *Cecropia* seeds, which were either present or removed, but not damaged). Both the small- and large-seeded species we studied suffered higher predation levels in open pasture fields. However, the small-seeded pioneer species were removed faster than primary species, as originally hypothesized. Other studies have recorded similar results in recently abandoned agricultural fields (Nepstad et al. 1996; Holl 2002; Peña-Claros & De Boo 2002; Fornara & Dalling 2005; but see Aide & Cavelier 1994) or nonaltered habitats (Moles et al. 2003). In our study sites, a parallel experiment showed low seedling recruitment throughout 2 years of monitoring (X. Garcia-Orth, personal observations), possibly due to high seed predation. This study has also documented limited seed dispersal and a limited seed bank that could also explain the low recruitment rates. Similar results have been reported for tropical old fields elsewhere (e.g., Wijdeven & Kuzee 2000). The present study suggests that under conditions of high seed predation, exclusion may reduce predation rates in some sites and for some species, but burial will be necessary to attain germination (see also Woods & Elliott 2004). However, direct sowing in pastures is not always a guarantee of seedling emergence and establishment, presumably due to competition between seedlings and grass vegetation, especially in small-seeded species (Camargo et al. 2002).

Studies which address direct seed sowing show that seed removal tends to be lower as seed size increases (e.g., Nepstad et al. 1996; Holl 2002; Jones et al. 2003; but see Peña-Claros & De Boo 2002), at least within a particular habitat type (Moles et al. 2003). Furthermore, the probability of seedling emergence also increases with seed size in old fields (Holl 1999, 2002; Zimmerman et al. 2000; Camargo et al. 2002; Hooper et al. 2002; but see Holl & Lulow 1997) and natural forest habitats (e.g., Paz et al. 1999). Our results concur with these studies as small-seeded species were removed at faster rates and at higher levels than large-seeded species. Ease of transportation may influence the seed species chosen by different animals (Nepstad et al. 1996). In our pasture sites, small seeds were preferred by small invertebrates (e.g., ants of the genus *Solenopsis* and *Pheidole*), whereas larger seeds were preferred by leaf-cutter ants (*Atta* spp.) and rodents. Ants have observed to be stronger removal vectors than rodents in tropical agricultural lands (Woods & Elliott 2004).

Similar to our experiment, high seed predation rates have been observed in the genus *Cecropia* (>80%) only after few hours or days of deposition in open fields (Nepstad et al. 1996; Fornara & Dalling 2005). In fact, it has been shown that copious seed rain is needed to replenish the seed bank of *Cecropia obtusifolia*, exhausted by heavy seed predation rates (>95% in few days, Alvarez-Buylla & Martínez-Ramos 1990) in mature forest. Thus, seeds of *Cecropia* are generally labile to consumption by insect granivores. Matrix population models indicate that when seed rain is poor or null, regeneration is impeded (Alvarez-Buylla & Garcia-Barrios 1991). At our study pasture fields, we recorded seed rain density of less than one seed per square meter (X. Garcia-Orth, unpublished data), which is three orders of magnitude lower than the one recorded in forest habitats (Alvarez-Buylla & Martínez-Ramos 1990). In order to insure regeneration under conditions of low seed rain, it may be necessary to manually sow seeds and protect them against granivores. Alternatively, to avoid the high risk of mortality at the seed stages, juveniles of *Cecropia* could be raised in greenhouses and transplanted to open fields (Kobe 1999).

For *Ochroma*, direct sowing may demand high energy input due to high predation rates and the low seed germination rates (Camargo et al. 2002), at least in pastures (Levy-Tacher & Duncan-Golicher 2004). In our study area, previous attempts to establish *Cecropia* and *Ochroma* in abandoned pastures through direct sowing have failed. Regardless of high seed sowing density (groups of 50–100 seeds sown every 3 × 3 m in 20 × 100–m plots, 36 plots distributed in six different pasture fields in total), no seedling recruitment was recorded possibly due to observed heavy seed predation by ants (Martínez-Ramos, unpublished data). The present study exhibited that exclusion decreased predation significantly, but seeds germinated mainly in the burial treatment. If seeds of *Ochroma* are introduced in open pastures, exclusion and burial will be needed. However, as with *Cecropia*, we recommend to transplant juveniles into pastures (Miyawaki 2004; but see Camargo et al. 2002).

Both LS species were heavily predated by vertebrate and invertebrate vectors, contrary to our hypothesis. Since our experimental design only tested seed predation by rodents, we could not quantify seed predation by invertebrates, particularly leaf-cutter ants that were observed to consume *Dialium*. Nevertheless, as excluded and exposed treatments showed no significant difference, we can infer seed predation by invertebrates is, if not higher, at least as strong as seed predation by vertebrates. Though overall seed predation rates were different among sites for *Brosimum*, we believe this species is generally attractive to rodents and has little probability of surviving in pastures if not excluded and buried. It is relevant to mention that *Brosimum* was also removed under exclusion cages, indicating predation by invertebrates. *Dialium* seeds contain secondary metabolites (i.e., protease inhibitors) potentially poisonous for some seedeaters (Calderón et al. 2001), possibly one of the reasons that allowed seeds of this species to remain after 64 days of observation. Similar to *Ochroma*, germination only occurred in large-seeded species when buried.

Our study shows that seed predation of large-seeded species is highly site specific and patchy, even within the apparently homogeneous pasture field landscapes. Other studies have also registered differences within pastures for some large-seeded species (Holl & Lulow 1997; Jones et al. 2003) and may indicate heterogeneous distribution of small vertebrate (e.g., Sánchez-Cordero & Martínez-Gallardo 1998) and invertebrate seedeaters (Mull & MacMahon 1997) among microsites. Therefore, it is important to emphasize that the efficacy of direct sowing of large seeds will depend on site characteristics. In contrast, small seeds were highly predated in all sites, indicating that insect seedeaters are abundant across all sites. Because insect seedeaters are highly active at several depths through soil layers, superficial protection would be insufficient for avoiding invertebrate access to the seeds. However, it is important to mention that our study is limited regarding the number of pastures in which we explored seed predation. As the number of sites considered increases, patterns in seed predation may be more clearly understood (e.g., Moles et al. 2003).

In addition to directly sowing seeds, restoration attempts in tropical pastures must also consider monitoring and nurturing seedling development. In direct sowing attempts, high survival and germination are more likely if seeds are sown during the rainy season. On one hand, a more varied array of resources would be available for seedeaters, perhaps allowing satiation and reducing predator pressure over sown seeds. On the other hand, the pasture floor is moist, increasing germination probability (Blain & Kellman 1991). Furthermore, during the rainy season the emerging seedlings have better conditions to grow. During the dry season, we predict higher seed predation rates and lower germination levels. Finally, as pointed out before, considering the high predation and low germination levels suffered by sowed seeds of ES species (Camargo et al. 2002), we recommend the transplanting of juveniles over the sowing of seeds (Miyawaki 2004; Martínez-Garza et al. 2005). Nevertheless, the costs of raising and transplanting juveniles need to be considered (Martínez-Ramos & Garcia-Orth 2007).

Implications for Practice

- Seed removal by animals represents an important barrier to rainforest regeneration in abandoned pasture fields.
- Small-seeded, ES species are heavily predated (>90%) by invertebrates. Therefore, the transplant of seedlings/saplings may be a more effective way to establish pioneer species in abandoned pastures than direct seed sowing.
- Large-seeded, LS species may be sown directly in the open field if sown in groups, buried, and protected against invertebrate and vertebrate seedeaters.

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