Seed Availability as a Limiting Factor in Forest Recovery Processes in Costa Rica

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Abstract

Abandoned pastures and secondary forests are increasingly prominent features of tropical landscapes. Forest regrowth on abandoned pastures is generally slow and virtually limited to regeneration from seeds from external sources, since agricultural activities alter site conditions. We hypothesize that seed availability is a major limiting factor in forest recovery on abandoned pastures. This hypothesis was tested by studying the seed bank, seed rain, and seed predation in a small pasture (1 ha) situated in a forest-pasture mosaic in northwestern Costa Rica. The tree seed density in the pasture seed bank was much lower (21/m²) than the density in the seed bank of a neighboring secondary forest (402/m²). Within a period of five weeks, 23 tree seeds entered the pasture by seed rain. This number is low compared to densities found in closed forests but higher than densities reported in other studies where virtually no seeds were found beyond 20 m from the forest edge. Possibly the small size of the pasture with seed sources nearby and the small-scale landscape mosaic enhance seed dispersal. Predation limits the seed density in pastures, with 42% of the woody species consumed by predators. The low seed density in the seed bank, and hampered recruitment combined with significant losses, pose severe restrictions to forest recovery on abandoned pastures. Moderate land use, and small sized clearings with seed sources nearby may increase the pace of recovery. Nevertheless, forest establishment may still take a considerable time. Thus, enlarging the available pool of species may be a worthwhile management strategy.

Key words: abandoned pasture, Costa Rica, forest recovery, forest restoration, seed availability, seed dispersal, seed predation, seed rain, soil seed bank, tropics.

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Introduction

Tropical forests are being cut at an alarming rate, and the loss of biodiversity due to these deforestation activities has become a worldwide concern (McNeely et al. 1990; Sawyer 1990). The cleared areas are often used for cattle grazing and are abandoned after several years (Buschbacher 1986), resulting in a fragmented landscape of grasslands and secondary and mature forests (Saldarriaga et al. 1988; Brown & Lugo 1990).

In the past, abandoned areas have largely been neglected. More recently however, it has been recognized that secondary forests on these formerly abandoned areas may provide a variety of functions: production of woody and non woody forest products; protection of watershed areas; use as a buffer for mature forests; and preservation of species diversity (Brown & Lugo 1990; Finegan 1992; Aide et al. 1995). Understanding the processes of forest recovery is, therefore, of paramount importance (Soulé & Kohm 1989).

In general, most field studies on forest recovery were done on large and/or severely disturbed sites, concentrating on a chronosequence of secondary forests (Purata 1986; Saldarriaga et al. 1988; Kappelle et al. 1996), or following recruitment after abandonment or in plantations (Uhl et al. 1981; Swaine & Hall 1983; Haggar et al. 1997; Parrotta et al. 1997). A conceptual framework for the recovery of forest after disturbance was developed by Bazzaz (1984). Although initially for natural treefall gaps, the framework can be extrapolated to abandoned fields (Garwood 1989; Uhl et al. 1990). The closure of opened areas depends on the availability of invaders, from the extension of branches in small gaps, to the germination of seeds in large open areas (Bazzaz 1984). Forest recovery on abandoned pastures is often very slow (Uhl et al. 1988; Aide et al. 1995). In general, intensive agricultural activities eliminate the possibilities for advance regeneration and resprouting (Whitmore 1983; Uhl et al. 1988, 1990). Thus, forest recovery on abandoned pastures may be largely limited by the availability of seeds. Nevertheless, the processes that determine the assemblage of species, available for the initial establishment on abandoned sites, are still poorly understood and quantified (Swaine & Hall 1983; Purata 1986; Garwood 1989; Janzen & Vázquez-Yanes 1991; but see Aide & Cavelier 1994; Nepstad et al. 1996).

Seed availability can be characterized by three components: the presence, the gains, and the losses. The presence is confined to the viable seed bank, which may be altered by the duration, intensity, and frequency of agricultural activities (Uhl et al. 1981; Garwood 1989). Gains by seed rain may be affected by the size and nature of the open site, and by the availability of seed sources. Seed vectors do not readily cross or enter open areas due to a lack of food sources, perching sites, and visibility to predators (Charles-Dominique 1986; Aide & Cavelier 1994; Nepstad et al. 1996; Wunderle 1997). Loss of viable seed may be caused by a variety of factors such as germination, unfavorable environments, pathogens, or predation (Louda 1989; Parker et al. 1989; Hammond 1995; Hau 1997).

We hypothesize that seed availability is a major limiting factor in forest recovery on former agricultural areas. In this paper we focus on the seed availability in a small abandoned pasture, located in a small scale forest-pasture mosaic in northwestern Costa Rica. We will address the following components: (1) the presence of seeds in the seed bank; (2) the colonization of seeds by seed rain; and (3) the loss of seeds due to seed predation.

Methods

Study Site

Research was conducted from January to July 1995 at the Ecolodge San Luis and Biological Station, situated at the head of the San Luis valley at an elevation of 1,100 m, in Guanacaste Province, northwestern Costa Rica (10°17′N, 84°48′W). There is a pronounced dry season, from January until the end of May. Soils are classified as Andepts, derived from volcanic ash, rich in organic matter, of medium texture and moderate fertility (Vásquez-Morrera 1991). The study site is a small pasture of 125 m × 75 m surrounded by secondary forests (>40 years) and patches of mature forest, with the exception of the northeastern side. The forest consists of a variety of tree species such as *Cecropia obtusifolia*, *Trema micrantha*, *Sapium oligoneurum*, *Ulmus mexicana*, *Heliocarpus americanus*, *Ficus* sp., *Dendropanax arborea*, and *Inga* sp. The pasture was cleared in 1975 and moderately grazed for the following 18 years. Two years prior to our field study in 1995, the pasture was officially abandoned, although sporadic grazing for short periods still occurred for another 1.5 years. The vegetation in the pasture is dominated by *Cynodon dactylon* (Poaceae), an introduced African grass species.

Seed Bank

The soil seed bank of the pasture and nearby secondary forest was assessed for species composition by collecting 10 soil samples (0.4 × 0.4 m, 5 cm depth) from random locations in both pasture and forest. Before the samples were emptied into flats (0.4 × 0.4 m, 7 cm depth), stones, leaves, and roots were removed with the aid of a coarse sieve. The 20 flats were then placed in a shadehouse and left to germinate for a period of three months, when germination had stopped. The flats were relocated to a different place in the shadehouse each week. When necessary they were watered and weeded. Every other week, new seedlings were identified and counted. Voucher species were replanted in canisters, and several seedlings of each species were pressed and stored. The shadehouse was covered with shade cloth, to prevent seeds from entering the flats.

Seed Rain

Soil for the seed rain experiment was collected from the pasture, at a depth greater than 1.5 m where the presence of seeds was assumed to be negligible. The soils in the study area are classified as Andepts and were, therefore, presumed to be adequate for the experiment. Seed rain was determined by randomly placing flats with soil (0.4 m × 0.4 m, 5 cm depth) in the pasture. All flats were covered with wire mesh (0.5 inch) to inhibit seed predation. Two groups of five flats were placed in the pasture for a period of 17 days, so that a total of 10 samples was collected in five weeks. Every other week, seedlings were identified and the total number of individuals recorded until germination stopped. When necessary, the samples were watered and weeded. The same soil was used for four control flats (0.4 m × 0.4 m, 5 cm depth) that were placed in the shadehouse, to determine if seeds were able to pass through the shade cloth. A few small seeds were observed in the control flats, and results were corrected for all flats accordingly.

Seed Predation

Seed predation in the pasture was assessed for two assemblages of seeds; the actual assemblage (pasture seed bank composition) and a richer one (forest seed bank composition). Five pairs of flats with pasture soil (0.4 m × 0.4 m, 5 cm depth) and five pairs of flats with forest soil (0.4 m × 0.4 m, 5 cm depth) were placed at random locations in the pasture. Of each pair, one flat was covered with wire mesh (1.25 cm) to inhibit seed predation by vertebrates. For both pasture and forest samples, the soil was first mixed to obtain a homogeneous sample set. Ingrowth and coverage by grasses were regularly prevented. After three months, when germination had ceased, species and abundances were recorded.

Analysis

Differences between the forest and pasture seed bank and between seed rain periods were analyzed with the two-tailed Student's *t*-test, assuming unequal variances. The diversity of the forest and pasture seed bank was determined with the Shannon-Wiener diversity index, $H' = -\Sigma p_i \mathrm{LN} p_i$. Differences in seed predation between open and protected flats were calculated with the Student's *t*-test, paired for means.

Results

Seed Bank

In total, 4,134 individuals per m^2, representing 59 species, germinated in the pasture seed bank. A significantly smaller number, 1,576 individuals per m^2, germinated in the forest seed bank (Student's *t*-test: $p < 0.01$). Nevertheless, 69 species were identified in the forest seed bank. The average number of species per sample did not vary greatly between pasture and forest samples (26.6 and 30.3, respectively). In both seed banks, 25 individuals per m^2 could not be identified.

The pasture seed bank contained significantly more individuals and species of grasses and herbs than the forest seed bank (Fig. 1; Student's *t*-test: $p < 0.01$). Grasses contributed 45% to the pasture seed bank, and herbs 33%. In the forest seed bank, herbs accounted for 16% of the total number of individuals, and grasses only 0.4%. Vine abundance was low in both pasture and forest seed bank, but forest soil contained significantly more vine species (Student's *t*-test: $p < 0.05$). Shrubs formed a substantial part of the pasture seed bank (21%), and dominated the forest seed bank (57%). Forest soil also contained significantly more shrub species than pasture soil (Student's *t*-test: $p < 0.001$). The number of tree seedlings and species was significantly higher in the forest seed bank than in the pasture seed bank (Student's *t*-test: $p < 0.001$). Trees contributed 26% to the forest soil and only 1% to the pasture soil. Overall, the number of woody species (trees and shrubs combined) was significantly higher in the forest seed bank (Student's *t*-test: $p < 0.001$), but the number of woody seedlings was not significantly different. In total, 83% of the seedlings in forest soil were woody, and 22% of the individuals in pasture soil were woody.

Seedlings in the pasture soil consisted of 33 families and 54 genera. The three most abundant families were *Cyperaceae* (43%), *Malvaceae* (11%), and *Caryophyllaceae* (10%). *Asteraceae* and *Solanaceae* were the most species rich families with 13 and 6 species, respectively.

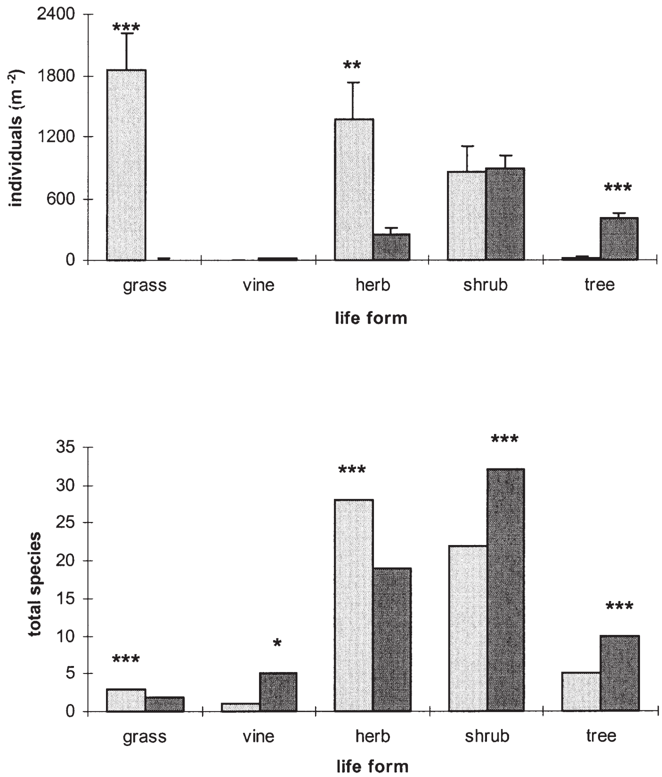

Figure 1. Life form distribution of germinated seedlings in the pasture (light bars) and forest seed bank (dark bars), for mean number of individuals (± 1 SE) (top figure) and total number of species (bottom figure). Significant differences in mean number of individuals and mean number of species between pasture and forest seed bank are indicated with: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$ (Student's *t*-test for independent samples).

The seedlings in forest soil consisted of 33 families and 56 genera. The three most abundant families were *Solanaceae* (42%), *Asteraceae* (18%), and *Piperaceae* (11%). *Solanaceae* and *Asteraceae* were the most species rich families, with 9 and 10 species, respectively.

Relatively few species dominated the seed banks. The three most common species contributed 57% to the seedlings in pasture soil, and 38% to the seedlings in forest soil (Appendix 1). The overall Shannon-Wiener diversity index (H′) was lower for the pasture seed bank (2.3) than for the forest seed bank (3.0). Also, the diversity per sample was significantly lower for the pasture seed bank (1.9), compared to the forest seed bank (2.6) (Shannon-Wiener index (H′); Student's *t*-test: $p < 0.001$).

All tree species can be classified as pioneer species (E. Bello 1995, personal communication; Swaine & Whitmore 1988). The five most common trees were *Acnistus arborescens*, *Trema micrantha*, *Cecropia obtusifolia*, *Croton* sp., and *Lansiantheae fructicosa* (Appendix 1).

Seed Rain

Seed rain was collected for a period of five weeks. In total, 70 seedlings emerged per m^2. Of these seedlings only *Cecropia obtusifolia* (which accounted for 22.6 seedlings per m^2) could be identified. The number of *Cecropia obtusifolia* seedlings was significantly less in the second half of the study period, compared to the first half ($6.3/m^2$ and $16.3/m^2$, respectively; Student's *t*-test: $p < 0.05$), although overall seedling density differed only slightly.

Seed Predation

Predation did not affect the total number of seedlings and mean number of species in the protected and non-protected pasture soil samples. In the forest soil samples, predation significantly reduced the total number of seedlings (44%) and the mean number of species (23%; 6 species) (Student's *t*-test: $p < 0.05$).

In the pasture soil samples, only the number of grasses was significantly affected by predation (Fig. 2; Student's *t*-test: $p < 0.05$). The total number of grasses was reduced by 52%. In the forest soil samples, the number of herbs and shrubs were significantly affected by predation (Student's *t*-test: $p < 0.05$). Herbs were reduced by 80% and shrubs by 52%. Also, the number of shrub species was significantly smaller (25%; 4 species; Student's *t*-test: $p < 0.05$) in the non-protected forest soil samples. The number of tree seedlings was reduced by 30% due to predation, but differences were not significant. Thus, the total seedling density of woody species declined significantly (42%; Student's *t*-test: $p < 0.05$), as well as the number of woody species (21%; 5 species; Student's *t*-test: $p < 0.001$). Herbs suffered more predation than trees (Student's *t*-test: $p < 0.05$). Although shrubs and trees were affected by predation, no significant differences could be detected per species and between species.

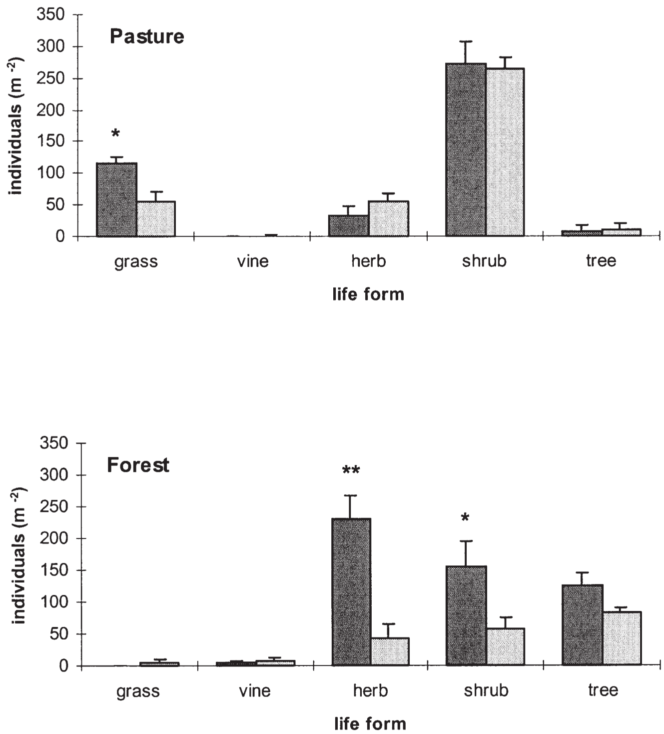

Figure 2. Differences in the mean number (± 1 SE) of germinated seedlings per life form in amount of predation. Protected (dark bars) and non-protected (light bars) soil samples are shown for pasture soil (top figure) and forest soil (bottom figure). Significant differences between protected and non-protected soil samples are indicated with: * = $p < 0.05$; ** = $p < 0.01$ (Student's *t*-test, paired samples for means).

Discussion

Seed Bank

Seed banks of pasture and forest differ dramatically in both seed density and composition. The seed density in pasture soil is more than twice the density in forest soil. However, the pasture seed bank is dominated by grasses and herbs with few trees, while the forest seed bank consists mainly of shrubs and trees. Our results are consistent with other studies. Trees are rare in the seed banks of post-agricultural areas (Table 1). We found only 21 germinated tree seedlings per m^2, representing 1% of the total seed density. This coincides with a reported range of 0–130 tree seeds per m^2 (0.6% average; Garwood 1989). Deforestation, soil disturbance, and weeding enhance germination, causing a depletion of the original forest seed bank (Uhl et al. 1981, 1988; Garwood 1989; Aide et al. 1995). Furthermore, burning and a dense grass layer may inhibit or prevent germination, inducing a decrease in viability of the remaining seeds in time (Uhl et al. 1981; Nepstad et al. 1991). Thus, agricultural activities lead to a distinct seed bank composition, dominated by ruderal species with low tree propagule availability (Garwood 1989).

The composition of the sampled forest seed bank has characteristics of both mature and secondary forest seed banks (Table 1). However, the density of shrub seeds is high compared to seed banks in both forest types, which may be due to the high density and close proximity of shrubs in the area. The study site is situated in a small-scale fragmented landscape of abandoned agricultural fields and secondary and mature forests, which might enhance shrub abundance. It could also be attributed to the floristic composition in the region, as shrubs are also very common in mature forests (Kuzee et al. 1994).

Table 1. Comparison between the agricultural field (pasture) and forest seed bank of this study and various other seed bank studies. Indicated are: total seed density, species richness per sampled area, and seed density per life form, for agricultural fields, and secondary and mature forests.

		Seed Density	*Species Richness (area in cm²)*	*Grasses/Herbs*	*Shrubs*	*Trees*
Agricultural fields						
This study	mean/m²	4,183	59 (16,000)	3,224	861	21
	% of total			78%	21%	1%
Other studies[a]	mean/m²	4,927	16 (4,000)–54 (2,280)	4,080	426	34
	% of total			87%	7%	0.6%
	range/m²	[370–7,623]		[717–6,287]	[0–1,800]	[0–130]
Secondary forests						
This study	mean/m²	1,576	68 (16,000)	254	886	402
	% of total			16%	57%	26%
Other studies[a]	mean/m²	3,350	21 (660)–67 (1,140)	1,254	228	375
	% of total			40%	9%	19%
	range/m²	[334–4,051]		[104–8,382]	[0–616]	[0–613]
Mature forests						
Other studies[a]	mean/m²	354	4 (640)–64 (30,000)	74	36	208
	% of total			18%	12%	61%
	range/m²	[163–862]		[0–440]	[0–82]	[60–653]

[a]Derived from review by Garwood (1989).

Seed Rain

Despite the low tree seed density in the pasture seed bank, we found a total input of 22.6 tree seeds per m² in five weeks, all *Cecropia obtusifolia.* This is relatively high compared to most seed colonization studies in open areas (Appendix 2).

Several studies indicate that the number of dispersed tree seeds is inversely related to the distance to seed sources and/or perching sites, whether it is the forest edge (McClanahan 1986; Purata 1986; Nepstad et al. 1991; Parrotta 1993; Aide & Cavelier 1994), or remnant trees in agricultural fields (Guevara et al. 1986; Janzen 1988; Guevara & Laborde 1993; Nepstad et al. 1996). The majority of dispersed seeds are found under remnant trees, and within 20 meters from the forest edge. Away from the edge, colonization is almost absent (Appendix 2). The high density of seeds found by Saulei and Swaine (1988) may be attributed to clear felling and a high seed production of a dominant herb (Saulei & Swaine 1988). Seed rain densities under remnant trees coincide with densities found in closed forests, demonstrating the importance of remnant trees as regeneration nuclei (Janzen 1988). Our seed rain densities correspond to those found in edges, and strip-cuts and gaps in closed forests (Appendix 2). The relatively high colonization rate may be due to the small size of the pasture, with distances to forest edges between 10 and 60 meters, and the presence of remnant trees. Possibly, a small-scale forest-pasture mosaic increases the abundance of seed vectors important for open areas, and induces seed vector movements through these areas. However, we sampled for a short period and, because seed rain varies within the year (Young et al. 1987; Saulei & Swaine 1988), the amounts found may be biased. Nevertheless, *Cecropia obtusifolia* can be found in the seed rain year round (Young et al. 1987), and most species in our region produce seeds from September to January (W. A. Haber & E. Bello unpublished study).

Birds and bats are the most important seed vectors for tropical tree species, particularly for the colonization of open sites (Howe & Smallwood 1982; Charles-Dominique 1986; Gorchov et al. 1993; Wunderle 1997). Birds need perches to defecate, while bats can defecate in flight (Fleming & Heithaus 1981; Charles-Dominique 1986; Nepstad et al. 1990), thus dispersing seeds more readily into open areas. All identified seeds in our study are *C. obtusifolia* seeds, normally dispersed by bats. Cattle and deer may be regarded as another seed vector for open areas. The dung pats may contain a variety of successional species, create gaps in the vegetation, and provide favorable germination conditions (Uhl & Clark 1983; Janzen 1984; Nepstad et al. 1991; Malo & Suárez 1995).

Seed Predation

The initial number of tree seeds in pastures is apparently too small to be detected and/or affected by seed predators. However, our results suggest that with higher seed densities, composed of naturally occurring assemblages, predation limits the available pool of species. In total, 42% of the woody individuals were subject to predation in the forest seed samples, and the number of woody species declined 21%. Aide and Cavelier (1994) found an average predation rate of 50% for eight tree species in a pasture, and Hammond (1995) detected an average predation rate of 65% in abandoned fields. In abandoned shifting cultivation plots, predation ranged from 35 to 100% among species, with an average of 80% (Uhl 1987). Nepstad et al. (1996) found predation rates higher than 80% for most species.

Remarkably, our experiment indicates that, although the number of woody seeds declines significantly, trees become the most dominant life form in terms of seed density (Fig. 2). However, we have no indications to suggest that this shift in composition also positively affects forest recovery.

Most studies indicate that predation rates vary among species (Uhl 1987; De Steven 1991; Aide & Cavelier 1994; Hammond 1995; Hau 1997). Several studies indicate that predation is positively related to seed density and seed size (De Steven 1991; Reader 1993; Hulme 1994; Hammond 1995). In contrast, Nepstad et al. (1990, 1996) reported that small seeds were more severely subject to predation than large seeds, probably due to the presence of seed predators such as ants and small rodents (Nepstad et al. 1996). Holl and Lulow (1997) and Hau (1997) detected no relation between seed size and predation rates. We found no significant differences between predation rates of species, but this may be due to low initial densities per species. Aide and Cavelier (1994), Kollmann and Pirl (1995), and Hau (1997) stated that predation rates are higher in forest than in open grasslands, although Hammond (1995), Nepstad et al. (1991, 1996), and Holl and Lulow (1997) detected no difference or a negative correlation. Vegetation cover, even in grasslands, possibly provides protection for seed predators and may thus have a considerable effect on seed predation (Gill & Marks 1991; Reader 1993; Hulme 1994).

Seed Availability and Forest Recovery

Forest clearing and subsequent agricultural activities often limit the set of recovery pathways to a mature and diverse forest (Whitmore 1983; Uhl et al. 1988; 1990; Aide et al. 1995). This paper clearly indicates that seed availability is a major limiting factor in forest recovery in three important ways: (1) tree seed density in pasture seed banks is low, (2) the immigration of new recruits is hampered, and (3) seed predation seriously limits the available pool of species.

Not only is seed availability limited, but several studies indicate or suggest that the potential available assemblage of species may also be restricted. First, the tree seed composition in seed banks is virtually limited to pioneer species (Garwood 1989), such as *Cecropia obtusifolia* and *Heliocarpus americanus* in this study. Most of the pioneer species have the capacity of long viability and/or dormancy, in contrast to most mature forest tree species (Whitmore 1983; Vázquez-Yanes & Orozco Segovia 1984). Second, the main seed vectors for open areas, birds and bats, disperse generally only small, light weight seeds of pioneer species, opposed to the larger, heavier seeds of mature forest species (Charles-Dominique 1986; Nepstad et al. 1990, 1996). Finally, larger seeds with a higher energy content (often mature forest species) are more attractive to seed predators than small seeds, which may be difficult to find in grasslands (De Steven 1991; Hammond 1995). These factors may thus result in a limited and skewed assemblage of species available for forest recovery processes (Charles-Dominique 1986; Nepstad et al. 1990, 1996; Aide & Cavelier 1994).

Various aspects of these general trends may be questionable, however. Mature forest and pioneer species have a wide and overlapping range of seed sizes, both including species capable of persisting in the soil seed bank (irrespective of seed size) for a substantial period of time (Grubb 1996, 1998; Metcalfe & Turner 1998). Species with small seeds can be dispersed by birds and bats (Charles-Dominique 1986) but also risk predation by small rodents and ants (Nepstad et al. 1996).

Forest recovery is seriously hindered due to the limited availability of seeds. Small-sized clearings, moderate land use intensity, and a fine scaled landscape mosaic, result in higher seed inputs, and possibly increase the rate of forest recovery. However, forest establishment, on small and large and/or severely degraded sites, may still take a considerable period of time. Human interference in the recovery process may be regarded as a valuable option, considering the possible functions and values of secondary forests. In a related study, we added soil from the forest (seed bank) to various treatments of the pasture vegetation. The experiments indicated that the addition of seeds from the forest soil, irrespective of treatment, greatly increased the density of germinated tree seedlings (Kuzee & Wijdeven unpublished study). Thus, an artificial increase in seed availability may be one of the crucial components.

Acknowledgments

We are grateful to Profs. Drs. Diana and Milton Lieberman for their hospitality and scientific and logistical support. We would like to thank Dr. Frans Bongers for his valuable advice and criticism, and Ad van Hees, Dr. John Parrotta, and an anonymous reviewer for their helpful comments on earlier drafts of the manuscript. We thank Margaret Still, Bud Watson, and the personnel of the Ecolodge San Luis and Biological Station for their assistance, and Eric Bello for the identification of the seedlings. This study was supported by a Mellon Foundation grant to Profs. Drs. Diana and Milton Lieberman.

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Appendix 1. Species list and seed densities for plants from the pasture and forest seed bank. Nomenclature follows Haber (1991).

Family	Genus and Species	Density (m^2) Pasture	Forest	Life Form[a]
ACANTHACEAE	*Justicia* sp.1	1.9	23.1	H
	sp.2		1.9	S
	Pseudoranthemum cuspidatum (Nees) Radlk.	0.6		H
AMARANTHACEAE	*Achyranthes aspera* L.	0.6		H
ARACEAE	*Anthurium* sp.		1.3	H
ASCLEPIADACEAE	*Asclepias curassavica* L.	231.9		S
ASTERACEAE	*Ageratina bustamenta* (DC.) R. King & H. Robinson	4.4	2.5	S
	Ageratum microcarpum (Benth. ex Oersted) Hemsley	1.9		H
	Baccharis trinervis (Lam.) Pers.		5.0	S
	sp.	2.5	7.5	S
	Cirsium mexicanum DC.	3.1	0.6	H
	Conyza apurensis Kunth	10.0	8.8	H
	Critonia morifolia (Miller) R. King & H. Robinson	16.3	38.8	S
	Jaegeria hirta (Lagasca) Less.	3.1		H
	Lasianthaea fruticosa (L.) K. Becker	1.9	45.6	T
	Liabum bourgeaui Hieron.	2.5		S
	Melanthera nivea (L.) Small	1.9		S
	Podachaemium eminens (Lagasca) Schultz-Bip.	18.8	161.9	H
	Verbesina crocata (Cav.) Less. ex DC.	1.3	5.6	S
	Vernonia patens Kunth	6.9	3.8	S
BORAGINACEAE	*Cordia* sp.		3.1	T
	Tournefortia glabra L.		13.8	S
BRASSICACEAE	*Brassica juncea* (L.) Czerniak.	24.4	1.9	H
	Cardamine fulcrata Greene	21.9	3.1	H
CAMPANULACEAE	*Lobelia xalapensis* Kunth	2.5	1.9	H
CAPPARIDACEAE	*Podandrogyne decipiens* (Triana & Planchon) Woodson	0.6	15.6	S
CARYOPHYLLACEAE	*Cerastium glomeratum* Thuill.	63.8		H
	Stellaria ovata Willd. ex Schldl.	337.5	4.4	H
CECROPIACEAE	*Cecropia obtusifolia* Bertol., cf.	0.6	51.3	T
CHENOPODIACEAE	*Chenopodium* sp.	10.6		H
COMMELINACEAE	*Tinantia standleyi* Steyerm.	5.6	0.6	H
	Tripogandra serrulata (Vahl) Handlos	23.1		H
	sp.	82.5		H
CYPERACEAE	*Cyperus hermaphroditus* (Jacq.) Standley	1778.1	5.6	G
EUPHORBIACEAE	*Croton draco* Cham. & Schldl.		0.6	T
	sp.		48.1	T
	Ricinus sp.		14.4	S
	Sapium oligoneurum Schumann & Pittier		5.6	T
LAMIACEAE	*Hyptis mutabilis* (L. Rich.) Briq.	8.1	1.9	S
	Marsypianthes chamaedrys (Vahl) Kuntze		1.9	S
LYTHRACEAE	*Cuphea infundibulum* Koehne	13.1	0.6	S
MALVACEAE	*Sida haenkeana* Presl	461.9	8.1	S
MARANTACEAE	*Achyronthes* sp.	2.5	10.0	H
MIMOSOIDEAE	*Mimosa* sp.	21.9	0.6	H
OXALIDACEAE	*Oxalis debilis* Kunth	170.6	1.3	H
PAPAVERACEAE	*Bocconia frutescens* L.	2.5	0.6	S
PAPILIONOIDEAE	*Crotalaria* sp.	3.1		H
PASSIFLORACEAE	*Passiflora adenopoda* DC.	2.5	1.9	V
	biflora Lam.		1.9	V
PHYTOLACCACEAE	*Petiveria alliacea* L.	0.6	23.8	S
	Phytolacca icosandra L.		7.5	S
	Rivina humilis L.		2.5	S
PIPERACEAE	*Piper auritum* Kunth	1.3	136.9	S
	sp.		35.6	S
POACEAE	*Digitaria abyssinica* (Hochst.) Stapf	25.6		G
	Paspalum candidum (Humb. & Bonpl.) Kunth	55.0	0.6	G
RANUNCULACEAE	*Clematis dioica* L.		1.9	V
ROSACEAE	*Rubus rosifolius* Smith	52.5	13.8	S

Continued

Appendix 1. Continued.

Family	Genus and Species	Density (m^2) Pasture	Forest	Life Form[a]
RUBIACEAE	*Mitracarpus hirtus*	95.0	2.5	H
	Psychotria sp.1		4.4	S
	sp.2		8.1	S
SCROPHULARIACEAE	*Stemodia* sp.	5.0	0.6	H
SOLANACEAE	*Acnistus arborescens* (L.) Schldl.	13.8	154.4	T
	Cestrum racemosum Ruiz López & Pavón		0.6	S
	Solanum acerifolium Dunal		2.5	S
	americanum Miller	0.6	16.3	H
	aphyodendron S. Knapp		6.3	S
	hispidum Pers.	19.4	204.4	S
	sp.	4.4		S
	umbellatum Miller	0.6	49.4	S
	Witheringia sp.1		3.8	S
	sp.2	1.9	228.1	S
TILIACEAE	*Heliocarpus americanus* L.	1.3	3.1	T
ULMACEAE	*Trema micrantha* (L.) Blume	3.8	86.9	T
	Ulmus mexicana (Liebm.) Planchon		4.4	T
UMBELIFERA	*Hydrocofile* sp	235.0	1.3	H
URTICACEAE	*Phenax hirtus* Sw.) Wedd.	25.0	10.6	S
	mexicanus Wedd.		1.9	H
	rugosus (Poiret) Wedd.	1.3		H
	Pilea sp.	154.4	6.3	H
	Urera baccifera (L.) Gaudich.	1.3	25.0	S
VERBENACEAE	*Verbena litoralis* Kunth	63.8		H
VITACEAE	*Cissus verticillata* (L.) Nicholson & Jarvis		2.5	V
	Vitis tiliifolia Humb. & Bonpl.		1.3	V

[a]Life form: G = grass; V = vine; H = herb; S = shrub; T = tree.

Appendix 2. Seed rain studies in various environments, ordered on distance to forest edge.

Site	Site Size	Distance to Forest Edge (m)	Total Seed Rain (m^{-2})	Period (wks)	Seed Rain (m^{-2}/5 wks)	Remarks	Source
Forest		−5 to −40	394.7	52.0	38.0	tree seeds	Saulei & Swaine 1988
Forest		−25	4,812.5	52.0	462.7	disp. + fallen	Gorchov et al. 1993[a]
Forest		−5 to −10	496.8	105.0	23.7		Walker & Neris 1993
Forest			336.6	156.0	10.8	tree seeds	Young et al. 1987
Forest			3740.0	156.0	119.9	all seeds	Young et al. 1987
Forest			1,162.8	65.1	89.3		Devoe 1989
Forest		−10	80.0	4.4	90.9		Aide & Cavelier 1994[a]
Landslide edge		−2 to 0	346.1	105.0	16.5		Walker & Neris 1993
Landslide edge		−2 to 0	51.4	105.0	2.4		Walker & Neris 1993
Pasture edge		0	80.0	4.4	90.9		Aide & Cavelier 1994[a]
Landslide edge	1,555 m^2	2	225.0	13.1	85.9		Myster & Fernandez 1995
Landslide edge	25,000 m^2	2	416.0	13.1	158.8		Myster & Fernandez 1995
Forest strip cut	30 × 150 m	2.5	937.5	52.0	90.1	dispersed	Gorchov et al. 1993[a]
Forest strip cut	30 × 150 m	2.5	4,625.0	52.0	444.7	disp. + fallen	Gorchov et al. 1993[a]
Pasture		5	6.0	4.4	6.8		Aide & Cavelier 1994[a]
Forest strip cut	30 × 150 m	7.5	312.5	52.0	30.0	dispersed	Gorchov et al. 1993[a]
Open site	25 ha	5–10	2.8	0.1	140.0		Charles-Dominique 1986
Pasture		10	1.0	4.4	1.1		Aide & Cavelier 1994[a]
Forest strip cut	30 × 150 m	12.5	250.0	52.0	24.0	dispersed	Gorchov et al. 1993[a]
Forest strip cut	30 × 150 m	12.5	1,100.0	52.0	105.8	disp. + fallen	Gorchov et al. 1993[a]
Small gap			28.3	7.7	18.4		Charles-Dominique 1986
Gap	4–>135 m^2		4.5	52.0	0.4	tree seeds	Lawton & Putz 1988
Gap	4–>135 m^2		28.1	52.0	2.7	all seeds	Lawton & Putz 1988
Gap			364.8	65.1	28.0		Devoe 1989
Gap			4.6	39.2	0.6		Putz & Appanah 1987
Gap	250–350 m^2		49.0	4.4	55.7		Denslow & Gomez Diaz 1990
Landslide	1,555 m^2	15	83.3	13.1	31.8		Myster & Fernandez 1995
Landslide	2,450 m^2		97.1	105.0	4.6		Walker & Neris 1993
Landslide	4,470 m^2		8.3	105.0	0.4		Walker & Neris 1993
Slash-burn site	2,500 m^2		0.0	17.4	0.0	*Cecropia*	Uhl et al. 1981
Slash-burn site	2,500 m^2		0.1	17.4	0.0	all seeds	Uhl et al. 1981
Slash-burn site	2,500 m^2		0.0	2.0	0.0		Uhl et al. 1981
Pasture		20	0.0	4.4	0.0		Aide & Cavelier 1994[a]
Pasture	10,000 m^2	15–60	22.5	5.0	22.5	tree seeds	This study
Pasture	10,000 m^2	15–60	70.0	5.0	70.0	all seeds	This study
Open site	25 ha	50	0.0	6.4	0.0		Charles-Dominique 1986
Clearing		15–95	7.9	26.0	1.5	tree seeds[b]	Saulei & Swaine 1988
Clearing		15–95	829.3	26.0	159.5	all seeds[b]	Saulei & Swaine 1988
Forest clearing	112 m^2		1.4	9.0	0.8	tree seeds	Young et al. 1987
Forest clearing	112 m^2		13.0	9.0	7.2	all seeds	Young et al. 1987
Pasture			1.8	26.1	0.3	tree seeds	Nepstad et al. 1990
Pasture	10 ha	100–350	2.4	52.0	0.2		Nepstad et al. 1996
Mined site		60–240	2.0	87.1	0.1		McClanahan & Wolfe 1993
Snags		60–240	340.9	87.1	19.6		McClanahan & Wolfe 1993
Remnant tree			52.0	1.6	162.5		Charles-Dominique 1986
Remnant tree			440.2	26.1	84.3	tree seeds	Guevara & Laborde 1993
Remnant tree			710.0	26.1	136.0	all seeds	Guevara & Laborde 1993
Remnant tree			711.8	26.1	136.4	tree seeds	Nepstad et al. 1990
Remnant tree		100–350	990.0	52.0	95.2		Nepstad et al. 1996

[a]Values are derived from graphs.
[b]First six months after clearing.