

Disturbance Effects on the Seed Bank of Mexican Cloud Forest Fragments¹

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ABSTRACT

The density and floristic composition of the soil seed bank was assessed in six cloud forest fragments with different levels of human disturbance in central Veracruz, Mexico. A total of 8416 seeds germinated in 60 soil samples, at 5-cm depth, corresponding to 107 species, 85 genera, and 48 families. Significant differences were found among study sites in seed densities with values ranging from 873 to 3632/m². Tree species contributed 20 percent of the total soil seed bank in four sites and herbs accounted for the majority of the species in each site. Among tree species, *Trema micrantha* displayed the highest seed density, accounting for 84 percent of the germinated seeds. In general, the tree species composition of the soil seed bank did not closely reflect the composition of the tree community. Results suggest that disturbance produced by human activities (trail use, selective cutting of trees, livestock) may influence the size and composition of the soil seed bank in forest fragments. Sites where human activity has been reduced showed the highest proportion of dormant seeds.

RESUMEN

La densidad y composición florística del banco de semillas del suelo se determinó en seis fragmentos de bosque de niebla con distinto nivel de alteración humana, en Veracruz, México. Un total de 8416 semillas germinaron en 60 muestras de suelo, correspondientes a 107 especies, 85 géneros y 48 familias. Se encontraron diferencias significativas entre los sitios de estudio, con valores desde 873 a 3632 semillas/m². La mayoría de las especies fueron hierbas y en cuatro de los sitios las especies arbóreas contribuyeron un 20 por ciento al total de semillas del banco del suelo. Entre las especies arbóreas, *Trema micrantha* (L.) Blume (Ulmaceae) presentó la mayor densidad de semillas (84% de las semillas germinadas). En general, la composición de especies arbóreas en el banco del suelo no reflejó la composición de la comunidad de árboles en cada sitio. Los resultados sugieren que la alteración causada por actividad humana (uso de senderos, tala selectiva y pastoreo) puede influir en el tamaño y composición del banco de semillas del suelo en fragmentos de bosque. Los sitios donde la actividad humana es reducida tienen la mayor proporción de semillas latentes.

Key words: anthropogenic disturbance; cloud forest; diversity; fragmentation; México; regeneration; soil seed bank; tropical montane forest; Veracruz.

THE SEED BANK IS AN AGGREGATION OF UNGERMINATED VIABLE SEEDS buried in the soil, on the soil surface or litter layer, potentially capable of replacing adult plants (Baker 1989, Garwood 1989, Simpson *et al.* 1989). In tree species, the recruitment of new individuals to a population depends, in part, on the seed bank that remains in the soil until favorable conditions for germination and growth occur (Lawton & Putz 1988, Garwood 1989, Quintana-Ascencio *et al.* 1996, Osumi & Sakurai 1997, Dalling *et al.* 1998). The seed bank has therefore been considered an important factor in the regeneration of communities after either natural or anthropogenic disturbance (Saulei & Swaine 1988, Pickett & McDonnell 1989, Thompson 1992, Quintana-Ascencio *et al.* 1996).

Soil seed bank studies provide information about size and floristic composition of the seed bank (Hopkins & Graham 1983, Williams-Linera 1993) and its dynamics (Saulei & Swaine 1988; Dalling *et al.* 1997, 1998). Also, these studies reveal regeneration potential from buried seeds both in conserved forest (Alvarez-Buylla & Martínez-Ramos 1990, Dalling *et al.* 1998) and forest subjected to

human disturbance (Rico-Gray & García-Franco 1992, Quintana-Ascencio *et al.* 1996, Osumi & Sakurai 1997, Fujisaka *et al.* 1998, Butler & Chazdon 1998, Dupuy & Chazdon 1998, Miller 1999, Lyaruu *et al.* 2000). Seed bank dynamics are influenced by the composition of standing vegetation (Pickett & McDonnell 1989, Dalling & Denslow 1998), because input to the seed bank is determined by the seed rain (Simpson *et al.* 1989). Seed bank losses may result from physiological properties of seeds, which influence germination, dormancy, and viability (Garwood 1989, Dalling *et al.* 1997) or by seed death as a result of animal predation, pathogen attack, deep burial, or natural senescence (Fenner 1985, Baker 1989). These inputs and outputs directly control seed density, species composition, and the genetic composition of the seed bank (Simpson *et al.* 1989). Variation in seed bank density and floristic composition is also related to geographical location (Williams-Linera 1993), season (Garwood 1989), distance to reproductive conspecifics (Dalling *et al.* 1997), forest age, and distance from the nearest disturbance (Fenner 1985, Thompson 1992).

Disturbance by human activities affects seed bank size and composition. When the anthropogenic disturbance is more intense or more frequent than the natural disturbance regime, the forest shows a larger seed bank. These large banks are mostly composed of secondary species with changes in diversity and life form

¹ Received 26 August 2003; revision accepted 29 November 2004.

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proportions (Fenner 1985, Saulei & Swaine 1988, Garwood 1989, Pickett & McDonnell 1989, Quintana-Ascencio *et al.* 1996, Dupuy & Chazdon 1998, Leckie *et al.* 1999, Arevalo & Fernández-Palacios 2000). The rate at which the seed bank returns to predisturbance size and composition is influenced by the degree of isolation, size, and severity of disturbance, and the regeneration strategy of the colonizing species (Garwood 1989). Seed density and species number in soil seed banks in relation to human disturbance have been investigated in a number of studies (Rico-Gray & García-Franco 1992, Quintana-Ascencio *et al.* 1996, Osumi & Sakurai 1997, Fujisaka *et al.* 1998, Dupuy & Chazdon 1998, Miller 1999, Lyaruu *et al.* 2000); however, the of human disturbance effect on seed banks of Neotropical cloud forests has not been studied.

The hypothesis investigated in the current study was that forest fragments with high levels of disturbance have the largest and most diverse seed banks mainly composed of pioneer species and herbs, while in contrast, the seed bank of the least disturbed forest is small, less diverse, and dominated by tree species. We ranked the study sites by measures of human disturbance, and examine the relationships between the degree of disturbance and seed bank size and composition.

METHODS

STUDY AREA.—This investigation was undertaken in six native forest fragments located in central Veracruz, Mexico. The type of vegetation corresponds to tropical montane cloud forest (TMCF) or *bosque mesófilo de montaña*, *sensu* Rzedowski (1978). The field sites were the Ecological Park (EP), Las Cañadas (LC), Xolostla (XO), Banderilla (BA), Rancho Viejo (RV), and Acatlan (AC; Table 1). A detailed description of how these forest fragments were characterized in terms of vegetation structure, soil characteristics, and disturbance regime can be found in Williams-Linera (2002). Because the vegetation structure of cloud forests vary in many features (*e.g.*, Kapelle *et al.* 1996, Challenger 1998), parameters such as tree density and basal area are not good indicators of disturbance (Williams-Linera 2002). Since fragments near towns and/or crossed by trails are accessible to people who cut trees, branches, or gather fuel wood (Hamilton *et al.* 1995, Williams-Linera 2002), the distance to towns, number of trails, and livestock presence in the forest are good indicators of disturbance. Human activities inside the forest can be inferred by frequency of main (at least 50-cm width) or secondary trails (less than 50-cm width). Trail frequency was classified into three categories: low (<5 trails crossing the fragment), intermediate (5–10 main trails crossed by secondary trails), and high (>10 main trails crossed by several secondary trails). Livestock was assessed by the presence of feces of cattle or goats. Two of the fragments, EP and LC, are currently ecological reserves protected by the Instituto de Ecología, A.C. and its owner, respectively. Disturbance categories were estimated as a combination of distance to towns, trail frequency, cut tree number, livestock presence, and protection status. The ranks based on the disturbance categories are: XO, RV, and BA are fragments with high disturbance, EP and LC

TABLE 1. Characteristics of the forest fragments in central Veracruz, Mexico. Altitude, geographical coordinates, area (ha), town at <1 km, and soil compaction (kg/cm²). Trees > 5 cm dbh: density (ind/ha), basal area (m²/ha), and total number of cut trees (ind/0.1 ha). Presence of livestock, trail frequency, status: protected (P) or not protected (NP) and disturbance category (1 = high, 2 = intermediate, and 3 = low; adapted from Williams-Linera 2002). Density (ind/m²) of shade-intolerant seedlings in the forest floor (Alvarez-Aquino 2002) and seeds in the soil seed bank (this study).

	EP	LC	XO	BA	RV	AC
Altitude (m)	1250	1340	1450	1470	1500	1840
Latitude N	19°30'	19°11'	19°32'	19°35'	19°30'	19°40'
Longitude W	96°56'	96°59'	96°58'	96°56'	97°0'	96°51'
Area (ha)	29	40	6.6	6.2	19.8	4.1
Town	Yes	No	Yes	Yes	No	No
Compaction	11.1	15.2	11.5	11.3	12.5	10.7
Tree density	1120	1370	1170	1320	1700	360
Basal area	61.31	35.32	45.53	40.67	89.35	37.71
Cut/0.1 ha	4	0	13	7	6	2
Livestock	None	None	None	Some	Some	Some
Trail	Medium	Low	High	Medium	High	Low
Status	P	P	NP	NP	NP	NP
Disturbance	2	2	1	1	1	3
Seedlings/m ²	3.22	1.34	4.73	2.72	1.03	0.72
Seed/m ²	303	1759	224	130	156	48

are sites with intermediate disturbance, and AC is a fragment with low disturbance (Table 1).

SAMPLING DESIGN.—In each forest fragment, a single 100 × 100 m plot was established at least 30 m from any forest edge. Soil samples were collected at the end of January 1999. Fresh litter was removed from the soil surface, and twelve soil samples (30 × 30 cm, 5-cm depth) were collected randomly within each plot. Samples were transported in black plastic bags and stored in the laboratory prior to the germination assessment.

SEED GERMINATION.—Within 1 week of collection, soil samples were placed in a screened greenhouse under a clear plastic roof in the Botanical Garden of the Instituto de Ecología, A.C. Irradiance (PAR) inside the greenhouse ranged from 15 to 20 percent of full sunlight and the mean value of red:far-red ratio of irradiance was 1.1 (measured with a Red/Far-Red Sensor, SKR 110, Skye Instruments Ltd., Llandrindod Wells, UK). Mean temperature was 0.4°C lower than outside the greenhouse. The Botanical Garden is located in a region of tropical montane cloud forest at an altitude of 1300 m. The temperature regime was similar to that of the sampled sites.

Two samples from each site were autoclaved (115°C for 1 h) and used as controls to detect contamination by wind-dispersed seeds from vegetation surrounding the greenhouse. The soil of the remaining ten samples from the six sites was spread over 60 plastic

trays (40 × 40 cm) in a thin layer (to a depth of 2–2.5 cm). The trays were positioned randomly in the greenhouse and randomly rearranged at regular intervals. In order to maintain soil moisture the trays were hand-watered every 1–2 d.

The density and composition of the seed bank were determined by observing seedling emergence once a week during a 10-mo period. Emerging seedlings were counted, and identified to genus or species. On the basis of literature reports and field observations, tree species were classified as shade tolerant or pioneers. In the control samples, germinated seeds of the herb *Taraxacum officinale* were recorded; therefore, this species was eliminated from the counts. After identification, seedlings were removed. Germination evaluation ceased after no further germination was observed during three consecutive months.

Seedlings that were difficult to identify were transplanted into pots and grown until identification was possible. Species were identified by comparing seedlings with herbarium specimens or with plants collected in the sites. Voucher specimens were deposited at the Herbarium XAL of the Instituto de Ecología, A.C. Nomenclature follows Flora of Veracruz (Sosa & Gómez-Pompa 1994). Pioneer tree species (*Trema micrantha*, *Hedyosmum mexicanum*, *Heliocarpus americanus*, *Heliocarpus mexicanus*, *Rapanea myricoides*, *Acacia pennatula*, and *Buddleia cordata*) were classified as such on the basis of literature, field observation, and personal communication with people involved in the study of this kind of vegetation. The complete list of species and the number of seedlings germinated in the soil samples from each site can be obtained on request to the correspondence author.

DATA ANALYSIS.—The variables measured were germinated seed density and species composition. Data on seed density were log transformed and analyzed using a one-way analysis of variance (ANOVA) to test the effect of site on seed density. The effect of site on density of pioneer tree species, number of all species in the seed bank, and number of individuals per species were analyzed using

a Kruskal–Wallis test, as the data were not normally distributed. Statistical analyses were performed using Minitab (Release 13 12.1, 1998).

The Jaccard coefficient for presence-absence data (Magurran 1996) estimated the similarities between seed bank species composition among sites, and the similarities between seed bank and canopy vegetation by genera within each site. The coefficient (J) was calculated according to the formula:

$$J = j/a + b - j \quad (1)$$

where, j is number of taxa common to two samples, a is the total number of taxa in location a , and b is the total number of taxa in location b . The values of the coefficient may range between 0, if the sites had no species or genera in common, and 1, for complete similarity. Species diversity in the seed bank of each study site was measured using H , the Shannon Diversity Index (Magurran 1996).

To elucidate whether the variations in seed bank (size and composition) were related to site characteristics, Spearman's rank correlation coefficients were calculated between the soil seed banks total and pioneer tree seed densities, species number, and Shannon diversity index with vegetation structure (basal area and density of trees ≥ 5 cm dbh) and altitude, forest fragment area, and soil compaction.

RESULTS

A total of 8416 seeds germinated in the 60 soil samples, corresponding to 107 species, 85 genera, and 48 families. Germinated seed densities varied from 873 to 3632 seeds/m², with density at LC higher than at other sites (one-way ANOVA, $F = 6.58$, $df = 5$, $P < 0.01$, Table 2). Species number in the soil seed banks differed among sites, and the lowest number of species was found in AC (Kruskal–Wallis test; $X^2 = 18.86$, $N = 60$, $P < 0.01$, Table 2). Densities of pioneer tree species in the seed banks differed among

TABLE 2. The variables recorded in six forest fragments in central Veracruz, México are germinated seed (mean \pm 1 SE), seed density (seeds/m²), pioneer tree seed density (seed/m²), number of species, Jaccard coefficient between tree genera in the soil seed bank and the forest overstory, and common species in each seed bank.

Sites	Germinated seeds	Density	Pioneer	Spp no.	Jaccard coefficient	Common species
EP	1244 \pm 116	1382	303	59	0.428	<i>Trema micrantha</i> , <i>Moussonia deppeana</i> , <i>Cestrum lanatum</i> , <i>Gnaphalium americanum</i> , <i>Ageratina</i> sp., <i>Mikania scandens</i> , <i>Desmodium</i> sp.
LC	3269 \pm 543	3632	1759	65	0.357	<i>Trema micrantha</i> , <i>Conostegia</i> sp., <i>Cestrum lanatum</i> , <i>Sellaginella galeotti</i> , <i>Piper amalago</i> , <i>Vitis bourgaeana</i> .
XO	925 \pm 138	1027	225	54	0.416	<i>Trema micrantha</i> , <i>Solanum</i> sp., <i>Hoffmania excelsa</i> , <i>Cestrum lanatum</i> , <i>Viola</i> sp., <i>Sellaginella martensii</i> , <i>Lasiacis</i> sp., <i>Vitis bourgaeana</i> , <i>Mikania scandens</i> .
BA	1218 \pm 300	1353	130	51	0.416	<i>Turpinia insignis</i> , <i>Trema micrantha</i> , <i>Moussonia deppeana</i> , <i>Lasiacis</i> sp., <i>Gnaphalium americanum</i> <i>Desmodium</i> sp.
RV	974 \pm 133	1082	156	48	0.583	<i>Trema micrantha</i> , <i>Moussonia deppeana</i> , <i>Conostegia</i> sp., <i>Rubus schiedeanae</i> , <i>Lasiacis</i> sp., <i>Passiflora membranacea</i>
AC	786 \pm 121	873	48	38	0.125	<i>Trema micrantha</i> , <i>Hamelia</i> sp., <i>Phytolacca icosandra</i> , <i>Panicum</i> sp., <i>Sonchus oleraceus</i> .

TABLE 3. Seed density (seeds/m²) by life form in the soil seed bank of the six forests fragments in central Veracruz, Mexico.

Sites	Seed density (seeds/m ²)					
	EP	LC	XO	BA	RV	AC
Trees	352	1824	224	253	222	50
Shrubs	417	689	293	444	164	183
Herbs	517	908	378	357	293	448
Grasses	64	129	107	280	351	192
Vines	32	82	25	19	52	0
Total	1382	3632	1027	1353	1082	873

sites (Kruskal–Wallis test; $X^2 = 32.73$, $N = 60$, $P < 0.01$, Table 2). LC had the highest percentage of pioneer tree seeds (48%), followed by EP (22%), XO (22%), RV (14%), BA (10%), and AC (5%). Among tree species, *T. micrantha* accounted for 84 percent of the germinated seeds, and displayed the highest seed density in all but one site, BA, where *Turpinia insignis* was more abundant. The most abundant shrub was *Moussonia deppeana* with densities higher than 120 seeds/m² in EP and BA. The most abundant herbs were *Gnaphalium americanum*, *Lasiacis* sp., *Viola* sp., and *Panicum* sp. Vines were present in five of the study sites and the most common genera were *Coccocypselum*, *Desmodium*, *Mikania*, *Passiflora*, *Smilax*, and *Vitis*.

Tree species contributed 20 percent of the total soil seed bank in four of the sites. In LC and AC, the contribution was 50 and 6 percent, respectively. Herbs accounted for the majority of species in each site. In five of the sites herbs accounted for 48–73 percent of all germinated species, while in LC herbs represented 29 percent of the seed bank (Table 3). In LC, we recorded the highest number of species (65), 43 percent of which were herbs and 15 percent were trees. AC showed the lowest number of species (38) with 51 percent herbs and 10 percent trees. With the exception of RV, where 20 percent of the species were trees, tree species represented approximately 11–16 percent of the total number of species in each site. Compositae (16%), Solanaceae (8%), Rubiaceae (7%), Campanulaceae (4%), Graminae (4%), Passifloraceae (4%), and Verbenaceae (4%) accounted for 47 percent of the species.

Seed species diversity in the soil banks differed among sites (Kruskal–Wallis test; $X^2 = 18.49$, $N = 60$, $P < 0.01$). XO had the highest Shannon diversity Index ($H = 3.07$), whereas LC ($H = 2.33$) had the lowest. Diversity values in EP ($H = 2.92$), BA ($H = 2.90$), AC ($H = 2.75$), and RV ($H = 2.69$) were intermediate and similar to each other.

Seven woody plant species were common to the seed banks of all sites (*Clethra mexicana*, *T. micrantha*, *R. myricoides*, *Rubus schiedeanus*, *Baccharis* sp., *Cestrum lanatum*, and *Hoffmania excelsa*). Nine species (*Quercus* sp., *Boerhavia* sp., *Citharexylum ligustrinum*, *Durante repens*, *Hamelia* sp., *Ocotea psychotrioides*, *Perrottetia ovata*, *Solanum nigrescens*, and *Urea* sp.) were found in the seed banks of one or two sites only. The Jaccard coefficients between pairs of sites

TABLE 4. Floristic similarity between pairs of study sites. Values are Jaccard coefficients and number of shared species are between parentheses.

Site	LC	XO	BA	RV	AC
EP	0.53 (43)	0.53 (39)	0.57 (40)	0.49 (35)	0.31 (23)
LC	—	0.45 (37)	0.43 (35)	0.45 (35)	0.30 (24)
XO	—	—	0.52 (36)	0.52 (35)	0.28 (20)
BA	—	—	—	0.50 (33)	0.37 (24)
RV	—	—	—	—	0.28 (19)

indicated that the seed bank composition of AC is less similar to the other sites composition. The seed banks of BA and EP shared 70 percent of the species, mainly shrubs and herbs (Table 4).

The similarity between soil seed bank and overstory tree species composition was greatest at RV (Table 2). In general, tree species composition of the soil seed bank did not reflect the composition of the tree community. Taking into account all the species recorded in all the fragments, 40 percent of the tree species found in the soil seed bank were not present in the overstory.

Soil seed density, species number, and diversity index were not significantly correlated with vegetation structure. However, seed density of pioneer tree species was positively correlated with fragment area ($r = 0.88$, $P = 0.01$). Soil seed densities of all species and pioneer tree species were correlated with soil compaction ($r = 0.82$, $P = 0.04$, and $r = 0.94$, $P = 0.005$, respectively). Species number in the seed bank was negatively correlated with fragment area ($r = -0.94$, $P = 0.005$), and positively with soil compaction ($r = 0.82$, $P = 0.04$). Altitude was not significantly correlated with any seed bank variable.

DISCUSSION

Soil seed bank size and composition are influenced by disturbance regimes (Thompson 1992), human activities inside the forest, and land use patterns in adjacent areas (Dupuy & Chazdon 1998). In our fragments the main causes of disturbance were people walking through the forest, gathering of fuelwood, selective cutting of trees, and grazing livestock. Germinated seed densities recorded in this study are comparable to densities found in temperate and tropical lowlands, and montane forests (Oosting & Humphreys 1940, Hall & Swaine 1980, Hopkins & Graham 1983, Saulei & Swaine 1988, Williams-Linera 1993, Dalling *et al.* 1997, Dalling & Denslow 1998, Miller 1999). However, our values are lower than those reported from disturbed or secondary forests where weedy species seeds are predominant (*e.g.*, 4600 seeds/m² in Quintana-Ascencio *et al.* 1996, 4535 seeds/m² in Butler & Chazdon 1998, 6854 seeds/m² in Dupuy & Chazdon 1998). The comparison suggests that, although our sites displayed a disturbance gradient, the level of disturbance was moderate.

Primary forest or forests subjected to little disturbance have relatively small seed banks because the shade-tolerant species seed

input (usually canopy trees) is low and produces a transient seed bank (Garwood 1989, Thompson 1992). In contrast, when disturbance is frequent seed banks are large (Fenner, 1985, Quintana-Ascencio *et al.* 1996, Leckie *et al.* 1999) as a result of the persistent seed bank of shade-intolerant species (Garwood, 1989). AC had the lowest seed bank density presumably because it is the least disturbed fragment, and is dominated by *Fagus*, a shade tolerant species. Contrary to expectation, the site with the highest seed density (LC) is not the most disturbed fragment. This may be related to the presence of disturbed areas surrounding the forest, to past forest disturbance, or to the lack of gaps and the consequent accumulation of dormant seeds of shade-intolerant species (Osuni & Sakurai 1997). Although fragment area and pioneer tree seed density are correlated, the large fragments (LC and EP) are less disturbed than smaller sites.

Forests surrounded by disturbed areas (agriculture and pastures) have high seed bank species diversity because of the additions of pioneer or secondary forest species (Fenner 1985, Quintana-Ascencio *et al.* 1996, Arevalo & Fernández-Palacios 2000). XO, one of the most disturbed sites, showed the highest diversity and was surrounded by disturbed areas. The largest area (LC) had the lowest seed bank diversity, due to the very high density of *Trema* seeds, which require light to stimulate germination.

In mature tropical forests with closed canopies, trees dominate the seed bank, whereas in disturbed or secondary forests with open canopies the seed bank may be dominated by herbs (Garwood 1989, Leckie *et al.* 1999). In this study, disturbance was infrequent in sites with the highest (LC) and lowest (AC) densities of tree seeds in the seed bank, due to the accumulation of *Trema* seeds in LC and the transient seed bank of *Fagus* in AC. Our sites adjacent to pastures (RV and BA) had the highest grass seed density as has been reported in a tropical forest in Costa Rica, where grasses were more abundant in forest surrounded by pastures (Dalling & Denslow 1998, Dupuy & Chazdon 1998).

Similarities between species composition in the soil seed bank and the overstory vegetation have also been related to forest disturbance (Pickett & McDonnell 1989). In undisturbed or old forests, the seed banks are composed almost exclusively of species absent or rare in the forest vegetation and are different in composition from the canopy (Hall & Swaine 1980, Hopkins & Graham 1983, Saulei & Swaine 1988, Thompson 1992, Dupuy & Chazdon 1998, Leckie *et al.* 1999), because primary species dominate the forest and pioneer species dominate the seed bank. In contrast, habitats with frequent disturbance are dominated by pioneer species and may share several species (Fenner 1985, Thompson 1992, Lyaruu *et al.* 2000). AC and LC, sites of low and intermediate disturbance differed most in species composition between the seed bank and the overstory vegetation.

Shade-tolerant species such as *Fagus grandifolia* var. *mexicana*, *Ilex tolucana*, *Symplocos coccinea*, and *Persea americana*, were found in the overstory vegetation but not in the soil bank. Some pioneer tree species (such as *Heliocarpus* in EP and RV) may be absent from the seed bank even when they are present as trees or seedlings, perhaps due to lack of coincidence between a fruiting event and time when the seed bank was sampled (Dupuy & Chazdon 1998), heavy predation (Lyaruu *et al.* 2000), or high mortality immediately after

dispersal. Other species were found only in the soil seed bank as has been reported in lowland and montane tropical forests (Hall & Swaine 1980, Saulei & Swaine 1988, Dalling & Denslow 1998) owing to their seed dormancy (Dalling *et al.* 1997). Some pioneer tree species have very rapid turnover, such as *Cecropia* sp. where 90% of seeds disappear from the seed bank within a year (Alvarez-Buylla & Martínez-Ramos 1990), while others such as *T. micrantha* demonstrate prolonged seed persistence (Dalling *et al.* 1997). Dominance of *Trema* has previously been reported in soil banks from tropical forests (Williams-Linera 1990, Quintana-Ascencio *et al.* 1996, Dalling *et al.* 1997, Dalling & Denslow 1998, Fujisaka *et al.* 1998).

Some shade-intolerant species, such as *T. micrantha*, require soil surface disturbance and lower canopy cover to increase light transmittance and stimulate germination (Whitmore 1996, Oosterhoon & Kappelle 2000). Higher emergence of pioneer species was found after soil surface disturbance by humans (Williams-Linera 1990, Osuni & Sakurai 1997). A comparison between seed and seedling densities (pioneer species only) in the study sites indicated that LC was the site with the highest ratio of seeds in the soil bank to seedlings in the forest floor. In contrast, XO and BA (sites in which people collect soil), displayed the lowest ratio of seeds in the soil bank to seedlings. In LC and EP, high *Trema* seed densities in the soil seed bank were enhanced by rare losses by germination (no seedlings were found in the fragments). In LC, the fragment with the highest seed density, large tree gaps required for *Trema* seed to germinate (Dalling *et al.* 1998) were not present. Additionally, in LC the highest value of soil compaction was recorded, which may increase seed density because compaction reduces germination and seedling establishment (Whitmore 1990), while less compacted soils facilitate seed germination increasing seed bank losses.

Our initial hypothesis that fragments with high levels of disturbance have the largest and most diverse seed banks was partially rejected. We conclude that fragments with intermediate levels of disturbance, as well as more disturbed sites, showed large seed banks dominated by shade-intolerant tree species. Minor, but frequent, soil disturbances due to human activities inside the forest may cause variation in seed densities and seed bank composition by enhancing germination. Consequently, fragments where human activity has been reduced showed the highest proportion of dormant seeds.

ACKNOWLEDGMENTS

The research was supported by a CONACYT grant to the senior author (scholarship no. 117686), and by the European Commission as part of the SUCRE Project (ERBIC18CT970146) and the BIOCORES project (ICA4-CT-2001-10095). We thank Maria de Jesus Peralta, Javier Tolome, and Leticia Cruz for assistance with fieldwork, and Colin Legg and Richard Ennos for advice.

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