Soil Seed Banks and Regeneration of Tropical Rain Forest from Milpa Fields at the Selva Lacandona, Chiapas, Mexico

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ABSTRACT

The traditional milpa agriculture system (slash-burn) of the Lacandon Maya people in eastern Chiapas, Mexico has created and uses a variety of habitat patches including the whole range of seral stages during forest development. This study examines seed bank attributes in habitats associated with slash-burn agriculture and with the more recent expansion of grasslands. We estimated the abundance and floristic composition of seeds in the soil from induced grasslands, milpa fields neighboring early and mature forests, and from secondary forest and mature tropical rain forest (15 samples by site, 2–3 replicated sites per successional stage). A total of 130 species germinated from the soil samples. The seeds of late successional tree species were scarce in all the seed soil samples (<2% of the species). Twenty-five early successional species accounted for ca. 70 percent of all individuals. Soil seed density (but not species richness) increased as milpas and fallows dominated the landscape. Affinity analysis based on presence/absence and abundance data showed a different soil seed bank composition for the grasslands when compared to that of all other successional communities. Our results suggest that current expansion of pastures and agricultural fields modifies seed deposition and storage patterns in the soil that may alter the process of secondary succession. This compromises both the regenerating potential of tropical rain forest in the region, and the sustainability of traditional practices and economic relationships of the Lacandon Maya.

RESUMEN

El sistema de agricultura de roza, tumba y quema de los mayas lacandones genera y hace uso de toda la gama de estados sucesionales del desarrollo forestal. Este estudio analiza el banco de semillas de comunidades asociadas al sistema de agricultura trashumante y a la más reciente ampliación de pastizales inducidos. Se estimó la composición florística y la abundancia de semillas en el suelo de sitios replicados de pastizales, campos de cultivo de milpa, campos en barbecho (acahuales), bosques secundarios y selva alta perennifolia (15 muestras por sitio; 2–3 sitios por etapa sucesional); se incluyeron los bancos de semillas de milpas y acahuales colindantes a áreas con extenso disturbio y en claros dentro del bosque. Un total de 130 especies germinaron de las muestras de suelo al cabo de ocho meses. Las semillas de árboles de etapas avanzadas de la sucesión fueron escasas en todas las comunidades (<2% de las especies). Veinticinco especies pioneras contribuyeron con ca. del 70 porciento del total de individuos. La densidad de semillas en el suelo de milpas y bosques (pero no la riqueza de especies) se incrementó en áreas con mayor abundancia de milpas y acahuales. El análisis de afinidad basado en presencia/ausencia y abundancia mostró que los pastizales tienen un banco de semillas diferente del resto de los hábitats en la región. Los resultados sugieren que la ampliación de pastizales y campos agrícolas favorece cambios en los patrones de aporte y almacenamiento de semillas en el suelo que pueden alterar los procesos de sucesión secundaria. Esto compromete las posibilidades de regeneración del bosque y la sostenibilidad de las prácticas tradicionales y relaciones económicas de los mayas lacandones.

Key words: deforestation; disturbance; forest fragmentation; Maya; pioneer species; shifting cultivation; slash-and-burn agriculture; seedlings; succession; sustainability; weeds.

THE RECENT and widespread deforestation and land use changes in the neotropics are related to the

establishment of pasture for raising livestock (Ewel 1981, Buschbacher *et al.* 1984, Buschbacher 1986, Hecht 1993, Toledo & Ordóñez 1993). The expansion of grassland and agricultural lands increases the distance between the forest "islands" while their ·area decreases, and creates an abrupt edge between the altered habitats and the remaining old-growth forest stands. These factors may reduce population sizes of mature forest tree species, and modify reproductive and dispersal events that determine the

regeneration and invasive potential of the relict populations (Gómez-Pompa *et al.* 1972; Janzen, 1983, 1986, 1987; Saunders *et al.* 1990).

The floristic composition, abundance, and turnover rate of buried seeds in the soil affect the regeneration of tropical forests in different ways (Garwood 1989). The recruitment of new individuals of some tropical trees, mostly early successional species, depends, at least in part, on a seed bank that can remain dormant in the soil until favorable conditions for germination and growth occur (Guevara & Gómez-Pompa 1972, Cheke *et al.* 1979, Garwood 1983, Young *et al.* 1987). Weeds in the seed bank can interfere with tree seedlings and saplings during the earliest stages of forest development (Kellman & Adams 1970, Kellman 1974; Ewel 1986). However, some herbs, shrubs, and pioneer trees in the soil seed bank may facilitate the dispersal and establishment of other more successionally advanced species by providing food and shelter for generalist dispersers (Charles-Dominique 1986; Fleming 1986), and improving or buffering microhabitat conditions, like humidity and temperature (Uhl 1987). After severe disturbance, those plants recruited from the seed bank may provide some protection against soil erosion (Uhl *et al.* 1981).

The traditional land use pattern of the Lacandon Maya people involves the harvest of a diverse array of plant and animal products along a successional sere from milpa fields and grasslands through tropical rain forest (Nations & Nigh 1980, March 1987). The milpa fields include mixed crops of maize, beans, and squash, and are abandoned after 2–3 years of continued cropping due to decreasing harvests and weed invasion. Most of the Lacandon milpa fields (0.5–1.0 ha) are established in the vicinity of dwellings or close to fallow stands (Nations & Nigh 1980). However, some milpa fields are established in newly cleared areas, and some pastures were introduced in the last two decades replacing milpa fields and fallows. The resulting complex habitat mosaic provides an opportunity to evaluate the sustainability of a land use system involving milpa agriculture and extraction of forest products from nearby successional and mature stands.

The objective of this study is to gain understanding on the interactions between a traditional land-use system and the regeneration potential of tropical rain forest species. We examine the abundance and floristic composition of soil seed banks in replicated successional stands ranging from milpa fields and pastures through fallows and tropical rain forest in the Selva Lacandona region, Chiapas, Mexico. In addition, we document the seed bank differences between similarly-aged communities surrounded by early or late successional communities.

STUDY SITES

The study was conducted in the Lacanjá river plains, on the NE border of the Montes Azules Biosphere Reserve, Selva Lacandona, Chiapas, Mexico (16°46'N, 91°08'W, 350–400 m elevation). The climate is warm-humid with an average annual temperature of 25–27°C, and an annual rainfall of 180–220 cm (García 1987). Most of the precipitation (>80%) occurs between June and October. The rendzinic soils are derived from limestone, and support associations of Tropical Rain Forest and Lower Montane Rain Forest (Pennington & Sarukhán 1968, Breedlove 1981, Meave del Castillo 1990). Physiognomic attributes and information by local farmers were used to select the study sites. Most of the best preserved forest stands were close to the Bonampak archaeological site. Secondary forest stands, grasslands, and milpa fields were concentrated in the vicinity of the Lacandon Maya villages of Bethel and Lacanjá-Chansayab.

Three replicate sites were chosen for each of the following habitat types, except that only two sites were accessible for types 1 and 4:

1. Mature forest. The canopy tree species (40–50 m high) include *Brosimum alicastrum, Calophyllum brasiliense, Dialium guianense, Guatteria anomala, Poulsenia armata, Terminalia amazonia,* and *Swietenia macrophylla.* Sampling sites were located at least 500 m from milpa fields or early secondary forests.
2. Mid-successional forest. Canopy trees (20–25 m high) include *Ampelocera hottlei, Bursera simaruba, Dendropanax arboreus,* and *Spondias mombin.* The understory tree layer is dominated by *Rinorea hummelii.* Sampling sites were located at least 500 m from severely disturbed habitats.
3. Tree-dominated fallow with four to eight years after abandonment of the milpa field. Canopy trees include *Belotia mexicana, Cecropia obtusifolia, Heliocarpus donnell-smithii, H. appendiculatus,* and *Ochroma lagopus.*
4. Shrub-dominated fallow with two to four years after the last milpa crop and surrounded by mid-successional and mature forests. Dominant shrubs include *Piper aduncum, P. aeroginosibaccum, P. auritum, P. hispidum,* and *Podachaenium eminens.*
5. Shrub-dominated fallow surrounded by fallows

and milpa fields. Dominant species are similar to those of the previous shrub-dominated community.

6. Old-Field with one to two years after milpa abandonment; annual herbs and vines predominate (*Merremia tuberosa, Rivina humilis, Mikania* spp.).

7. Milpa field surrounded by mature forest. The sites were cleared for the first time in December-January, burned in April, and sowed in May before soil core sampling.

8. Milpa field surrounded by fallows and milpa fields. The fallows were cleared in March, burned in April, and sowed in May before soil core sampling.

9. Grassland. Maintained through biennial fires, and almost completely dominated by the African grass *Cynodon nlemfuensis*.

10. Border between new milpa field and mature forest.

11. Border between old milpa field and shrub-dominated fallow.

METHODS

SOIL SAMPLING.—In June 1990, before the end of the dry season, 15 samples of surface soil (30 × 30 cm, and 10 cm deep) were obtained every 5 m along three transects in each replicated site. The uppermost litter strata (approximately 0–5 cm deep) and the subjacent soil (5–10 cm deep) from the mature and mid-successional forests were collected separately. Soil samples between cultivated fields (milpa) and adjacent forested stands were obtained at 0, 5 and 10 m on each side along three transects perpendicular to the border.

Samples were air-dried, sieved (0.25 cm²) to remove litter and rocks, and weighed. Seeds retained by the sieve were returned to the sample. We obtained and weighed soil subsamples of 350 cm³ from each sample. The soil subsamples were taken to the "Jardín Botánico Faustino Miranda", Tuxtla Gutiérrez, Chiapas (530 m elevation) for seed germination (August 1990 through April 1991) under a temperature regime similar to that prevailing in the original habitats. All soil subsamples from the same replicated site were laid individually (< 1 cm depth) on a river sand bed (10 cm depth) in the same bench (150 × 75 × 11 cm). The benches were kept outdoors and were divided with plastic wire into 45 rectangles (15 × 12 cm). The sand bed was watered during five months before these germination tests to remove non-soil seeds. The soil subsamples were watered daily and covered with nylon and wire mesh.

Emerging seedlings were identified (to genus, species or morphospecies), counted, and removed every two weeks during the first month, and then at monthly intervals. Seedling evaluation ceased after no new individuals were observed to emerge in two consecutive months. Species identification was achieved by comparing seedlings with specimens collected in the study sites. Voucher specimens were deposited at the CIES herbarium at San Cristóbal de Las Casas, Chiapas. Seed density of each sample was estimated by dividing number of seedlings germinating per subsample by estimated area of the subsample. The latter was calculated by multiplying area of sample (0.045 m² for forest samples and 0.09 m² for remaining samples) by the proportion of sample analyzed (dry weight of subsample/dry weight of sample). Forest seed density estimates were adjusted (×2) to homogenize data for their analysis.

ANALYSIS.—The regional pattern of diversity of the seedlings emerging from the soil samples was evaluated with affinity analysis (Istock & Scheiner 1987, Scheiner 1992). The Affinity Analysis Program version 4.3 provides Jaccard (absence/presence) and percent similarity (abundance) indices for the data, and computes affinity values using a standardized Wilcoxon signed-rank test. The position of the points in the plot of mean affinity vs. mean similarity shows the extent to which each community represents the overall diversity of the total sample. "Modal sites" are those with high mean similarities, high mean affinities, and having more common species throughout the landscape. "Outlier sites" appear in the left lower corner of this plot. They have few species or only locally common species. Standard errors of estimates are calculated with the jackknife procedure. Mosaic diversity, the slope of the plot between mean affinity vs. mean similarity, depends on the average and dispersion of the pairwise similarities among communities, and the position of each point relative to all other points simultaneously (Scheiner 1992). The mosaic diversity value was compared with distributions generated with bootstrap procedures (50 simulations). Null hypothesis of random reshuffling included constraints on matrix total, abundance or frequency of species in each site, and abundance or frequency of species across all sites (Scheiner 1992).

We used Nested-ANOVA and Kruskal-Wallis tests (Zar 1984, Sokal & Rohlf 1981) to compare the number of seeds and number of species among
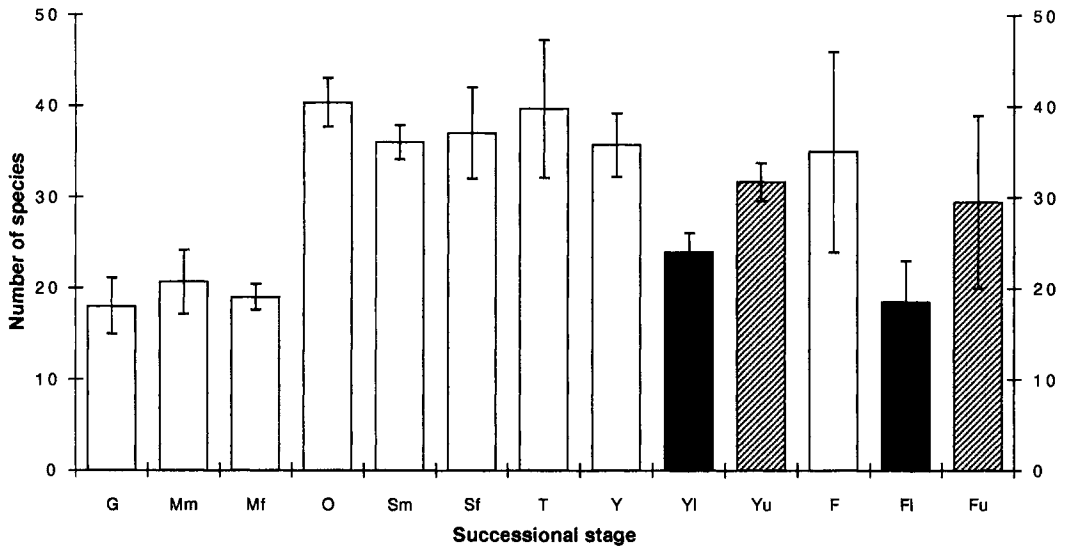
FIGURE 1.   Mean species number (± 1 SE, $N = 2$–3 sites) in the soil seed bank of different stages of the successional gradient of tropical rain forests at the Selva Lacandona, Chiapas, Mexico. Grassland: G; Milpa field surrounded by fallows and other milpa fields: Mm; Milpa field surrounded by mature forest: Mf; Old-Field: O; Shrub-dominated fallow surrounded by fallows and milpa fields: Sm; Shrub-dominated fallow surrounded by mid-successional and mature forests: Sf; Tree-dominated fallow: T; Mid-successional forest: Y; Mature forest: F, u and l indicate upper and lower soil strata, respectively.

habitat conditions. The gradients of species richness and seed number in the borders were analyzed with Spearman correlation tests (Siegel 1956).

RESULTS

FLORISTIC COMPOSITION AND SPECIES RICHNESS.—A total of 130 vascular plant species from at least 32 families germinated from all samples throughout the eight-month period. Eleven morphospecies could not be assigned to any family (see Appendix). Asteraceae (22%), Poaceae (10%), Fabaceae (6%), Euphorbiaceae (6%), Rubiaceae (5%), and Solanaceae (5%) accounted for about half of all species. Herbs (55%), vines (5%), and early successional shrubs (15%), and trees (9%), accounted for most of species in all habitat conditions. The relative abundance of seeds of early successional trees and shrubs, such as *Belotia mexicana, Cecropia* spp., *Cordia alliodora, Heliocarpus* spp., *Piper* spp., and *Trema micrantha,* tended to increase with habitat age, while the seeds of weedy herbs decreased (see Appendix).

The number of species in the soil seed bank differed among habitat conditions (Kruskal-Wallis test; $H = 19.3$, $N = 25$ replicated sites, $P < 0.02$, forest soil strata pooled; $H = 22.2$, $N = 30$, $P < 0.02$, forest soil strata separated; Fig. 1). Fallow

habitats showed the highest species richness (range was 32 to 52 species), which decreased in the lower soil strata of more advanced communities (14–27), and in the soil of milpa fields and grasslands (13–26). There were more species in the upper soil layer of the mid-successional and mature forests than in the lower one.

The number of species along the transect between milpa and fallow showed no trend (Fig. 2a). The 20 m wide border between milpa fields and mature forest had fewer species than that between milpa and fallow ($H = 5.2$, $N = 30$, five replicated distances $\times$ three replicated sites $\times$ two border types, $P < 0.05$). Species number decreased from the mature forest side (12 to 10 species) towards the milpa (6 to 4 species; Spearman correlation, $t = 4.8$, d.f. $= 13$, $P < 0.001$; Fig. 2b).

SEED DENSITY.—Total density of seeds in the soil differed among habitat conditions (730,829.68 MS among community types, 161,334.73 MS among sites within community types, 21,238.46 MS within sites, 10, 19 and 420 degrees of freedom respectively, $N = 450$ samples, F community type $= 4.53$, $P < 0.002$, F sites $= 7.60$, $P < 0.001$, forest soil layers separated; Fig. 3). The highest seed abundance was found in the shrub-dominated fallow surrounded by fallows and milpa fields (4600
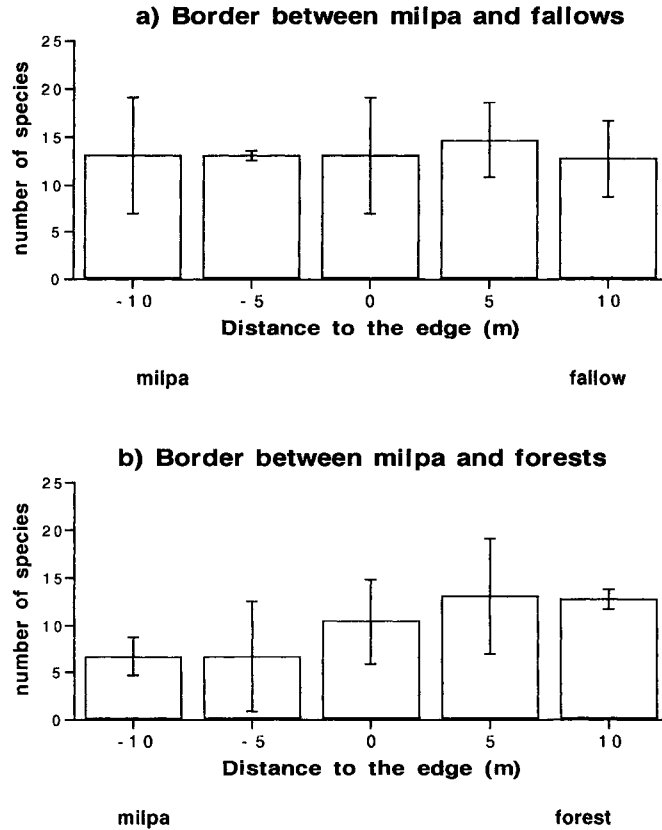
FIGURE 2. Mean species number (± 1 SE, $N = 3$ sites) in the soil of the border between (a) milpa fields and fallows, and (b) milpa fields and mature forests. Negative values are distances from the edge towards the milpa side; positive values indicate distances to the forest or fallow sides.

seeds m^{-2}), and the lowest in the grassland (969 seeds m^{-2}), the mature forest (715 seeds m^{-2}, forest soil strata pooled), and the milpa field surrounded by forest (437 seeds m^{-2}). One-third of the species in the soil samples of the mid-successional and mature forests were restricted to these communities and had very low densities, including shrubs and trees such as *Ficus* sp., *Psychotria* spp., *Spondias mombin*, and *Zanthoxylum kellermanii*.

Twenty-five early successional species accounted for *ca.* 70 percent of the total number of individuals in any habitat condition, including the trees *Cecropia* spp. (mostly *C. obtusifolia* and some *C. peltata*), *Heliocarpus appendiculatus, H. donnell-smithii, Trema micrantha*, the shrubs *Piper auritum, P. hispidum, Podachaenium eminens*, and the herbs *Acalypha diversifolia, Baccharis trinervis, Borreria ocymoides, Eupatorium* spp. (3 undetermined species), *Euphorbia hypericifolia, Iresine* spp., *Solanum* sp., *S. americanum, Mikania aromatica, M. cordifolia*,

M. micrantha, Neurolaena lobata, Witheringia nelsonii, and Species 59 (Asteraceae). All these species showed different abundance among the several habitat conditions (Kruskal-Wallis test, $P < 0.001$ in all cases). Among these generally abundant species, only *Iresine* spp., *S. americanum*, and Species 59 were well represented in grasslands (see Appendix). *Cecropia* spp., *Solanum* sp., *S. americanum, Mikania micrantha, Piper auritum, P. hispidum*, and Species 59 were found in all successional stands. Among tree species, *Cecropia* spp., *Heliocarpus* spp., and *Trema micrantha*, had their highest seed density in mid-successional forests and fallows.

Seed density was homogeneous along transects between milpa fields and fallows ($t = 0.81$, d.f. $= 13$, $P > 0.05$, Fig. 4a). Seed abundance at the edge of the old-growth forest with the newly open milpa field was higher (2500–4000 seeds m^{-2}) than in similarly aged forested stands located away from milpa fields and fallows (700–1300 seeds m^{-2},
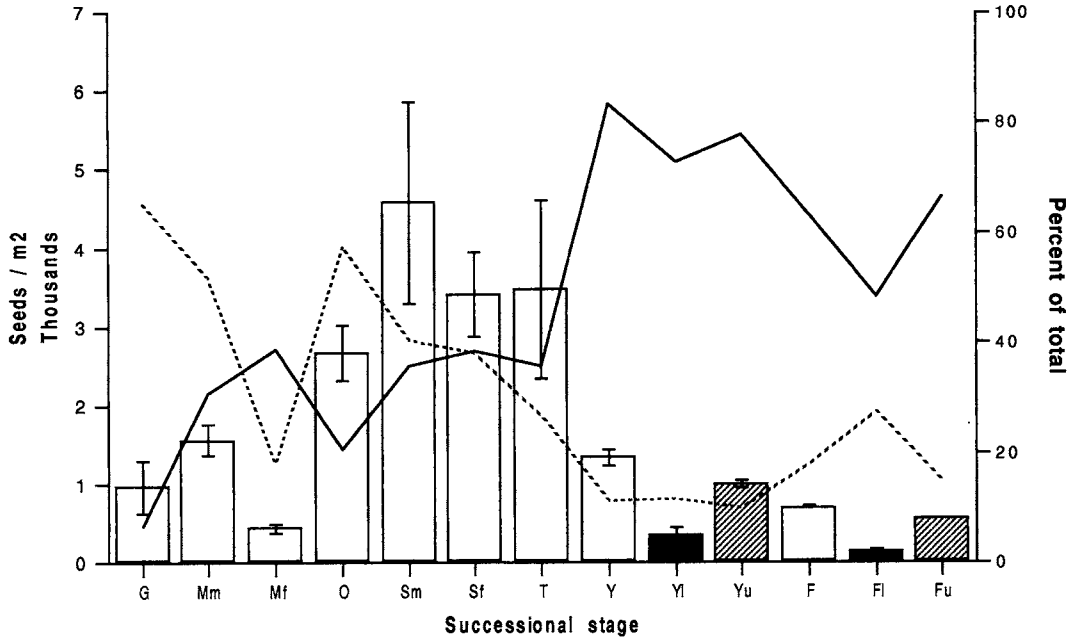
FIGURE 3.   Mean seed number (± 1 SE, $N = 2$–3 sites) in the soil of different successional stages of tropical rain forests at the Selva Lacandona, Chiapas, Mexico. Community identification as in Figure 1. Percent of seeds of woody species: continuous line. Percent of seeds of herb species: broken line.

Figs. 3 and 4b). Seed density decreased from *ca.* 4000 seeds m^{-2} on the old-growth forest side to less than 1,000 seeds m^{-2} in the new milpa field ($t = 3.44$, d.f. = 13, $P < 0.01$, Fig. 4b).

REGIONAL DIVERSITY.—Observed mean similarities (0.27 $\pm$ 0.04 for Jaccard and 0.25 $\pm$ 0.05 for percent similarity) were significantly different from "random communities" ($P < 0.001$; using Z statistic) when matrix totals (0.12 $\pm$ 0.002 and 0.06 $\pm$ 0.003) or site totals (0.11 $\pm$ 0.001 and 0.07 $\pm$ 0.002) were held constant. However, they were not different when species totals were constrained (0.27 $\pm$ 0.001 and 0.22 $\pm$ 0.005). Observed mosaic diversities (4.6 $\pm$ 0.08 and 3.2 $\pm$ 0.07, respectively) were significantly different from those of any of the "random communities". Mosaic diversity was intermediate when species totals were constrained (6.96 $\pm$ 0.46 and 4.68 $\pm$ 0.20), and highest when site totals (8.11 $\pm$ 0.24 and 9.16 $\pm$ 0.52) or matrix totals (9.3 $\pm$ 0.35 and 9.45 $\pm$ 0.7) were held constant.

Seed assemblages from fallows and upper soil strata of old-growth forests, which had the highest abundance and species richness of pioneer herbs, shrubs and trees, could be identified as modal sites (Figs. 5 and 6). Soil seed banks of pastures had the

least similar seed flora, and were consistently identified as outliers (more than 1 s.d. from the mean affinity). The relative position of seed assemblages from the upper and lower soil layers of the old-growth forests suggests a floristic contrast between superficial and buried seed banks (Figs. 5 and 6).

DISCUSSION

A considerable body of work has accumulated about tropical forest succession following natural gap formation in preserved forests (see for example Gómez-Pompa *et al.* 1991). However, the regeneration, interference, and facilitation potential of the weedy flora, which may predominate in the soil seed banks of disturbed habitats, has received less attention, and this mostly in relation to slash and burn agriculture (Kellman 1974, Ewel 1981, Uhl *et al.* 1981, Uhl 1987, Young *et al.* 1987, see review by Garwood 1989 and other references cited therein). Gaining insight about the effects of landscape-level disturbance during the restoration processes in highly fragmented habitats becomes a high priority, as most neotropical forests are being replaced by pasture lands, plantations, and early secondary forest vegetation (Janzen 1986, 1987).

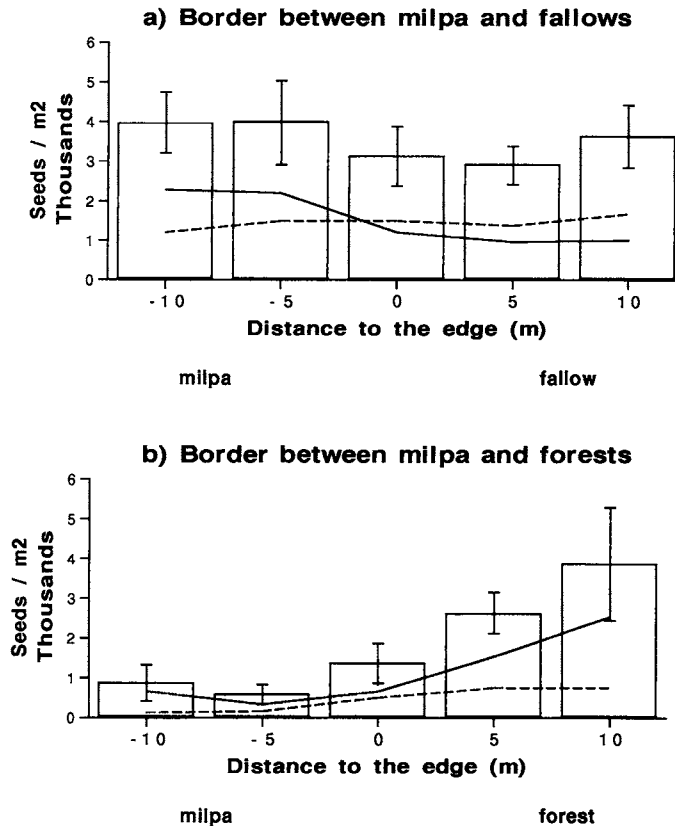Short-term milpa agriculture is one of the most

a) Border between milpa and fallows

milpa   fallow

b) Border between milpa and forests

milpa   forest

FIGURE 4.   Mean seed number (± 1 SE, $N = 3$ sites) in the soil of the border between (a) milpa fields and fallows, and (b) milpa fields and mature forests. Negative values are distances from the edge towards the milpa side; positive values indicate distances to the forest or fallow sides. Mean seed number of woody species: continuous line. Mean seed number of herbs: broken line.

frequent land-use systems to be established by poor farmers immediately after clearing of old-growth tropical rain forests (Nye & Greenland 1960). However, sustained-yield milpa agriculture, as practiced by traditional lowland Maya peasants, is associated with the maintenance of a wide array of diverse successional communities at various stages of recovery (Cowgill 1962, Nations & Nigh 1980, Mauricio Leguízamo et al. 1984, Levy-Tacher et al. 1991). Milpa abandonment is forced by soil nutrient depletion, and a progressive infestation by a weedy flora which may remain dormant in soil seed banks for long periods (Nye & Greenland 1960, Kellman & Adams 1970). In this study, the species richness and density of seeds in the soil increased from early successional open communities to a peak in fallows 4–12 years old, and decreased again in late seral communities.

Los Tuxtlas tropical rain forest reserve in south-ern Veracruz (Mexico) includes 600 ha of undisturbed forest mostly surrounded by pasture and permanent agriculture lands. In soils from this isolated forest, Guevara & Gómez-Pompa (1972) obtained a similar unimodal pattern with 2672 seeds m^{-2} in a two-month old secondary growth stand, 4051 seeds m^{-2} in a milpa-derived 5-yr fallow, and only 689–862 seeds m^{-2} in two old-growth forest stands. Young et al. (1987) found the same general pattern of seed abundance in the soil in a successional sere at Turrialba, Costa Rica. They proposed as its causes the initial effect of fire, the subsequent accumulation of dormant seeds of pioneer species in fallow stands, the loss of their viability in mid-successional and mature forests, and their replacement by non-dormant seeds from late successional shrub and tree species (Young et al. 1987).

The relationship between seed abundance and vegetation age is affected by the successional attri-
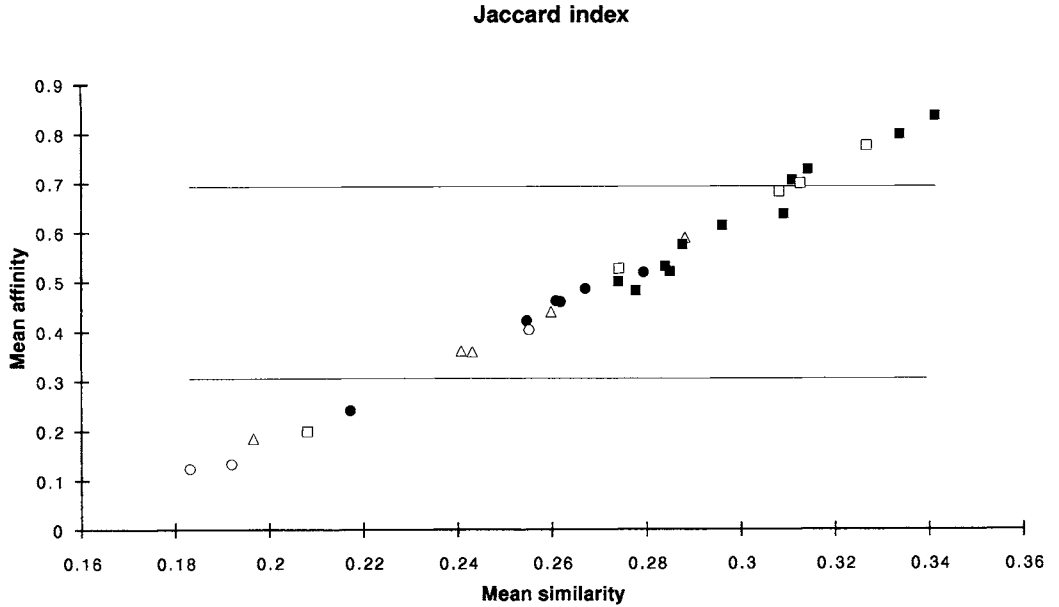
Jaccard index

FIGURE 5.   Affinity Analysis graph for presence/absence data on seeds in the soil of successional stages of tropical rain forests at the La Selva Lacandona, Chiapas, Mexico. Community identification as in Figure 1: Fu and Yu, open squares; F1 and Y1, open triangles; T, Sf, Sm, and O, filled squares; Mf and Mm, filled circles; G open circles. Communities with affinity value above the upper line have more than 1 SD above the mean and are defined as modal; communities with affinity value below the lower line have more than 1 SD below the mean and are defined as outliers.
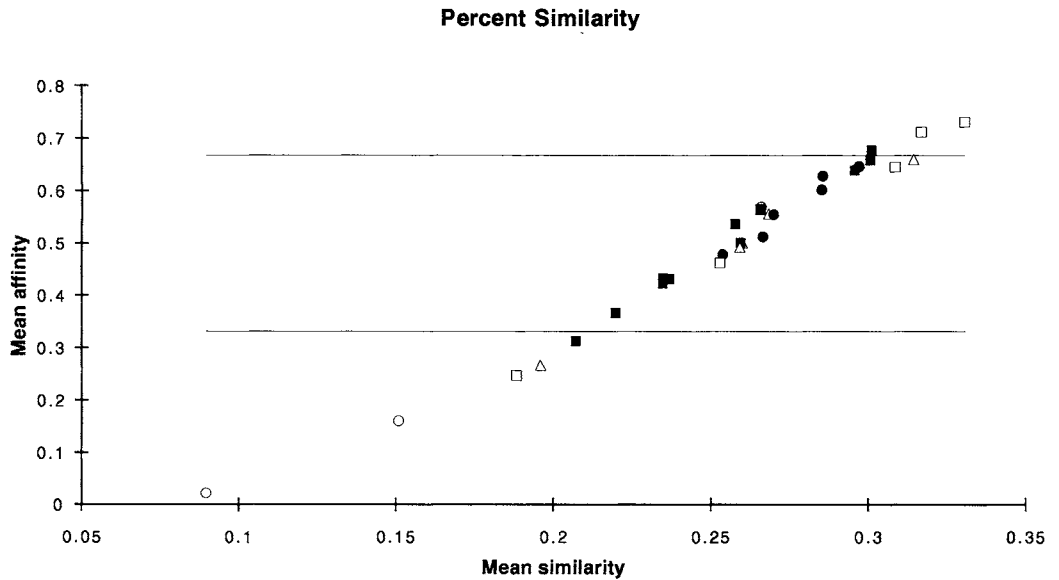
Percent Similarity

FIGURE 6.   Affinity Analysis graph for abundance data on seeds in the soil of successional stages of tropical rain forests at the La Selva Lacandona, Chiapas, Mexico. Community identification as in Figure 5.

butes of the surrounding landscape patches and the complexity of the regional mosaic. Purata (1986) found that old-field and fallow succession at Los Tuxtlas, Veracruz, is influenced by the floristic composition and disturbance regime of neighboring vegetation. In our study sites, the density of seeds in the soil of all kinds of seral stages increases as disturbed habitats dominate the landscape; however, no trend was found for species richness. Milpa fields established in recently cleared old-growth forest show a lower number of seeds (437 seeds m^{-2}, 17–21 species) than those milpas surrounded by fallows and agricultural areas (1562 seeds m^{-2}, 16–26 species). Also, the seed abundance of young fallows bordering forest stands (3421 seeds m^{-2}) was lower than those close to milpa fields, grasslands, and other fallows (4603 seeds m^{-2}), indicating that farmers can avoid weed infestation by clearing mature forest. The abundance of buried seeds in mature forest stands located far away from agricultural lands was lower (1339 seeds m^{-2}) than in similar stands bordering with milpa fields (2500–4000 seeds m^{-2}). In the heavily disturbed Belize River Valley, Kellman (1974) found higher seed densities in soils from permanently cultivated fields (7623 seeds m^{-2}), grasslands (5226 seeds m^{-2}), and early (4-yr; 4524 seeds m^{-2}) to late fallows (20-yr, 10171 seeds m^{-2}). These data suggest that seeds of weeds may increase in the soil as deforested areas become more widespread and permanent.

The establishment of pastures for raising livestock is the main cause of deforestation in tropical America (Ewel 1981, Buschbacher et al. 1984, Buschbacher 1986, Hecht 1993). Affinity analysis considering the presence/absence and abundance of species in our data showed the contrasting composition of seed banks in the soil of grasslands from those of all the other successional communities. This result suggests that the persistence and expansion of grasslands would provoke a severe impoverishment of soil seed floras in neotropical regions.

The seeds of late successional trees were scarce in the soil seed banks from all habitat types in the landscape (<2% of the species in any of our study sites). Previous studies have shown short longevities for the seeds of primary tree species common in the Selva Lacandona region (Moreno-Casasola 1976, Vázquez-Yánes & Orozco-Segovia 1984). In a related study we observed the seasonal arrival of seeds and the occurrence of seedlings of many primary species in the same old-growth forest stands (Carrillo-Arreola, 1992, Quintana-Ascencio & Carrillo-Arreola, pers. obs.), suggesting that their regeneration depends on germination of recently released

seeds and the periodical renewal of a reserve of immature individuals (Brokaw 1985).

Pioneer tree species contributed most of the seeds in fallows and mature forests, but their abundance decreased markedly in open communities. Seeds of pioneer and late secondary tree species buried in soil often have longer viability and dormancy than primary species (Vázquez-Yánes & Smith 1982, Garwood 1989, Vázquez-Yánes & Segovia 1984, Pérez-Nasser 1985, Orozco-Segovia 1986). However, Alvarez-Buylla & Martínez-Ramos (1990) showed that the regeneration of Cecropia obtusifolia, a common neotropical early successional tree species, may rely mostly on recently arrived seeds. Although C. obtusifolia seeds have the ability to remain dormant for several years (Vázquez-Yánes 1976, Vázquez-Yánes & Smith 1982), they usually suffer high death rates under field conditions which lowers their contribution to the bank of viable seeds in the soil (Martínez-Ramos & Alvarez-Buylla 1986, Alvarez-Buylla & García Barrios 1991). The abundance of many pioneer tree seeds in the soil of forested tropical lowland communities may be sustained by the massive seed production typical of these species (Alvarez-Buylla & García Barrios 1991).

The Selva Lacandona represents some of the northernmost, more extensive, and best preserved remnants of tropical rain forest in Mexico and Central America. Most of the pristine habitats on the Mexican side are included in the Montes Azules Biosphere Reserve. As with many neotropical reserves, most of these forests are surrounded by extensive disturbed habitats (Hartshorn 1983, Janzen 1987). The results of this study suggest that the current expansion of pastures and agricultural fields in the Selva Lacandona modify soil seed bank characteristics. The resulting changes in the pattern of seed deposition and storage in the soil may alter the process of secondary succession. Competition with increasing numbers of weeds may decrease rates of establishment of tree seedlings in recently abandoned fields and fallows (Uhl 1987), while the declining abundance of early successional tree species, presumably providing necessary microhabitat conditions for the establishment of late successional tree species, may hinder recovery of mature forest.

The traditional Maya milpa system takes advantage of successional processes that replenish soil nutrients and eliminate competitive plants (Collier 1975, Hernández-Xolocotzi 1993). However, these conditions only occur if rather long fallow periods are involved (>20–25 years). This study shows that short forest return times may result in increasing

weed abundance, and as a consequence, decreasing harvesting rates (Bye 1993). The widespread replacement of forest and agricultural fields by pastures is provoking vegetation changes, including the invasion of exotics and the decline of most woody species. This alteration seems to compromise not only the regenerating potential of tropical rain forest in the region, but also the sustainability of traditional practices and economic relationships of Lacandon Maya farmers.

ACKNOWLEDGEMENTS

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APPENDIX. Mean absolute density (seeds m⁻² of species present in the soil seed (and spore) bank of successional stages of tropical rain forest at the Selva Lacandona, Chiapas, Mexico. Mature forest: Fu, Fl, u and l indicate upper and lower soil strata, respectively (adjusted × 2); Mid-successional forest: Yu, Yl; Tree-dominated fallow: T; Shrub-dominated fallow surrounded by mid-successional and mature forests: Sf; Shrub-dominated fallow surrounded by fallows and milpa fields: Sm; Old-field: O; Milpa field surrounded by mature forest: Mf; Milpa field surrounded by fallows and milpa fields: Mm; Grassland: G; Border between milpa field and mature forest: Bmf; Border between milpa field and shrub-dominated fallow: Bms. Life forms: U = unknown, H = herb, V = vine, S = shrub, T = tree, F = fern; cross symbol for the non-empty cells with less than 130 seeds m⁻² (range 42–250), correspond on average to one germinated seed from the subsample.

Species	Life form	Fu	Fl	Yu	Yl	SF	T	Sm	O	Mf	Mm	G	Bms	Bmf
Actinidiaceae														
Saurauia scabrida Hemsl.	S			+	+									
Amaranthaceae														
Amarantbus hybridus L.	H							+						
Iresine spp.¹	H	+		+		408	361	278	262		287	156	248	+
Anacardiaceae														
Spondias mombin L.	T	+		+										
Araceae														
Species 99	V						+						+	+
Asclepiadaceae														
Marsdenia macrophylla (Humb. & Bonpl.) Fourn.	V	+	+											
Asteraceae														
Aster sp. 112	H							+	+					
Baccharis trinervis (Lam.) Pers.	S	+				+	+	544	+			+	+	
Conyza canadensis (L.) Cronq.	H	+				283	+	+	+	+		+	+	
Eupatorium macrophyllum L.	H								+	+				
Eupatorium sp. 11	U	+		+		+	+	+	+	+	+		+	
Eupatorium sp. 49	H								+	+				
Eupatorium sp. 82	U	+		137		+	+		+	+	+	+	+	188
Liabum discolor (Hook. & Arnot.) Benth. & Hook.	S		+		+									
Melampodium divaricatum (Rich.) DC.	H	+	+						+					
Melanthera nivea (L.) Small	H	+							+					
Mikania aromatica Oerst.	H	+				+	167		+	+	+			
Mikania cordifolia (L.f.) Willd.	H		+		+	+	+	+	151	+	+	+	+	139
Mikania micrantha H.B.K.	H	+		+		+	+	+	163	+		+	+	+
Neurolaena lobata (L.) R. Br.	H					+	+		377	+		+		+
Podachaenium eminens (Less.) Sch.-Bip.	T	+				+	+	701	+		146		761	
Pseudoelephantopus spicatus (Juss.) Rohr.	H	+				+		+	+					
Salmea scandens (L.) DC.	H			+			+	+	+					
Schistocarpha eupatorioides (Frenzl) Kuntze	H	+				+	+	+	+	+		+	+	+

APPENDIX. *Continued.*

Species	Life form	Fu	Fl	Yu	Yl	SF	T	Sm	O	Mf	Mm	G	Bms	Bmf
Sonchus oleraceus L.	H	+	+				+	+	+	+	+			+
Vernonia cinerea (L.) Less.	U					+	+	+	+	+	+	+	+	+
Species 20	H						152	+	186					+
Species 26	H	+	+	+				+	+	+	+		+	
Species 59	H	+		+		+	+	+	+	+	+		130	+
Species 75	H		+	+	+	+						+		
Species 126	U											+		
Species 132	U		+	+										
Specie 133			+											
Begonia glabra Aublet	H					+								
Bombacaceae														
Ochroma lagopus Sw.	T								+					
Boraginaceae														
Cordia alliodora (Ruiz & Pavón) Oken	T			+			+	+					+	
Rocbefortia sp. 102	S						+		+					
Caryophyllaceae														
Arenaria sp. 107	H	+												
Commelinaceae														
Commelina erecta L.	H		+											
Cucurbitaceae														
Melothria pendula L.	V				+				+					
Cyperaceae														
Cyperus sp. 45	H											+		
Rhynchospora radicans Schl. & Cham.	H						+	+	+			369		
Euphorbiaceae														
Acalypha diversifolia Jacq.	S	+	+	+	+	+	255	+	+	+	135		+	+
Chamaesyce hypericifolia (L.) Millsp.	H					+		911	358		210	+	+	
Chamaesyce byssopifolia (L.) Small	H							+						
Euphorbia graminea Jacq.	H									+				
Euphorbia heterophylla L.	H								+					
Plukenetia sp. 101	V						+							
Plukenetia sp. 111	V						+							

APPENDIX.   *Continued.*

Species	Life form	Fu	Fl	Yu	Yl	SF	T	Sm	O	Mf	Mm	G	Bms	Bmf
Tetrorchidium rotundatum Standl.	T	+		+	+				+					
Fabaceae														
Acacia glomerosa Benth.	H	+	+	+	+		+							
Desmodium sp. 106	H							+				+		
Vigna umbellata (Thunb.) Ohwi & Walpers	V		+					+						
Vigna sp. 1	V				+					+			+	+
Species 10	H		+						+					
Species 34	H								+	+				
Species 8	H							+					+	
Species 68	H					+		+						
Labiatae														
Hyptis capitata Jacq.	H								+			+	+	
Species 48	H								+		+			
Moraceae														
Cecropia spp.[2]	T	139	+	390	140	776	364	157	+	+	+	+	+	279
Ficus sp. 81	T	+	+	+	+	260	272	238	+	+	+	+	+	
Species 95	U	+	+	+	+	+	+	+		+	+	+	+	
Musaceae														
Heliconia sp.	H						+							
Piperaceae														
Piper auritum H.B.K.	S	+	+	261	+	+	+		+	+	+	+	243	
Piper hispidum Sw.	S	+	+	189	+	+	+		+	+	+	+	157	144
Piper sp. 94	S	+		+				+					+	
Pothomorphe peltata (L.) Miq.	S		+	+	+	+	+	+		+			+	
Poaceae														
Andropogon sp.	H													
Brachiaria fasciculata (Sw.) Parodi	H						+		+	+				
Digitaria bicornis (Retz.) Koeler	H		+							+				
Digitaria horizontalis Willd.	H			+		+	+	+				+		
Digitaria sp. 47	H					+	+		+		+	+		
Eleusine indica (L.) Gaertn.	H								+			+		
Leptochloa virgata (L.) Beauv.	H				+	+	+	+	+			+		
Oplismenus hirtellus (L.) Beauv.	H		+					+						+
Paspalum sp. 46	H		+				+		163			+		+

APPENDIX. *Continued.*

Species	Life form	Fu	Fl	Yu	Yl	SF	T	Sm	O	Mf	Mm	G	Bms	Bmf
Paspalum sp. 69														
Species 52	H				+				+					
Species 85	H								+		+			
Species 88	H								50			+		
Polypodiaceae														
Species 115	F	+	+	+		+	+			+			+	
Species 116	F	+	+	+	+	159	298	+					+	
Species 118	F	+				+								
Species 119	F		+	+		+	+							
Species 120	F				+		+							
Species 121	F				+		+							
Porrulacaceae														
Species 73	H			+		+	+	+	+					
Rhamnaceae														
Gouania lupuloides (L.) Urban	S	+				+	+	+	+				+	
Rubiaceae														
Borreria ocymoides (Burm.) DC.	H					+	+	+	+	+	+		+	
Crusea sp. 103	H			+		+			+		+			
Hamelia patens Jacq.	S				+	+	+					+		
Psychotria chiapensis Standl.	S			+							+			
Psychotria limonensis Krause	S					+		+						
Psychotria sp. 77	S			+						+				
Species 62	S					+	+	+		+	+			
Rutaceae														
Zanthoxylum kellermanii P. Wilson	S	+												
Schizaceae														
Lygodium venustum Sw.	F					+			+	+			+	+
Scrophulariaceae														
Bacopa sp.	H													
Stemodia verticillata (Miller) Sprague	H								+		+	+	+	
Solanaceae														
Capsicum annum L.	H						+							
Physalis philadelphica Lam.	H						+				+			

APPENDIX.   *Continued.*

Species	Life form	Fu	Fl	Yu	Yl	SF	T	Sm	O	Mf	Mm	G	Bms	Bmf
Solanum americanum Miller	H	+	+	+	+	+	+	532	+	+	149	+	441	+
Solanum sp. 7	U	+	+	+	+	+	+	+	+	+	+	+	+	+
Solanum sp. 13	U	+	+	+	+	+	+	+		+	+	+	+	+
Witheringia nelsonii (Fern.) A. T. Hunziker	S	+	+	+	+	+	+	+	+	+		+	+	+
Species 29	H	+	+	+	+	+			+	+				
Tiliaceae														
Belotia mexicana (DC.) Schum.	T	+	+	+	+	+	266		+	+	+		+	472
Heliocarpus spp.[3]	T	+	+	+	+	+	+	+	+					+
Triumfetta semitriloba Jacq.	S						+	+						
Ulmaceae														
Ampelocera hottlei Standl.	T			+							+	+		
Trema micrantha (L.) Blume	T	209	+	305	+	+	+	155	+		+	+	+	+
Urticaceae														
Pilea microphylla (L.) Liebm.	H	+		+	+	261	+			+	+	+	157	
Urera eggersii Hieron.	S	+	+	+	+					+			+	+
Verbenaceae														
Lippia sp. 25	H							+						
Priva lappulacea (L.) Pers.	H					+		+	+	+	+	+		+
Vitaceae														
Cissus gossypiifolia Standl.	V			+	+									
Vitis tiliifolia (Humb. & Bonpl.) ex Roem. & Schult.	V			+	+		+							
Unidentified														
Species 4	H	+						+	+					
Species 6	U		+										+	
Species 41	H			+										
Species 42	H			+			+			+			+	+
Species 64	H			+			+	+		+	+	+		+
Species 65	U			+	+		+	+	+			+	212	+
Species 70	H		+	+	+	+	+		+	+	+	+	+	+
Species 97	H					+	+		+	+	+	+	+	+
Species 104	S	+		+				+	+	+	+	+		+
Species 108	H													+
Species 109														+
Total	Mean	557	155	988	352	3421	3484	4592	2635	437	1562	969	1863	3520

APPENDIX. *Continued.*

Species	Life form	Fu	Fl	Yu	Yl	SF	T	Sm	O	Mf	Mm	G	Bms	Bmf
	SE[4]	6	2	47	93	534	1128	1096	348	56	206	340		
	SE[5]	82	17	150	40	395	337	419	279	58	165	174		
Site differences[6]		de	e	c	e	ab	ab	a	bc	e	cde	de		
Species richness		44	31	53	38	54	64	56	63	34	36	34	45	36

[1] Includes *Iresine celosia* L. and *I. diffusa* Humb. & Bonpl.
[2] Includes *Cecropia obtusifolia* Berrol. and *C. peltata* L.
[3] Includes *Heliocarpus appendiculatus* Turcz. and *H. donnell-smithii* Rose.
[4] Standard error within sites ($N = 2–3$).
[5] Standard error within samples ($N = 30–45$).
[6] Sites with distinct letter are significantly different at $P < 0.05$.