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Soil seed banks in the tropical agricultural fields of Los Tuxtlas, Mexico

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Abstract: To investigate the effects of different land use conditions on the soil seed bank of three crop fields in a tropical rain forest area of the Los Tuxtlas region in southeastern Mexico (Gulf of Mexico coast), we compared the number of species, mean seed density and species composition of seeds. The number of species (33, 45 and 48 species, respectively) was different among fields but mean seed density (total density per field: 10186, 17522 and 33811 seeds m^{-2}) was not different. The crop fields' seed banks were dominated by secondary herbs, and few pioneers species and secondary trees were found. Differences in the number of species and composition are explained on the basis of differences in the surrounding vegetation, the time the crop fields have been used, management practices and the presence of remnant trees in each field.

Resumen: Se comparó el efecto que tienen diferentes condiciones de uso, en el contenido del banco de semillas del suelo en tres campos sembrados con maíz. El estudio se hizo, en la región de Los Tuxtlas, al sureste de México. La comparación se basó en: el número de especies, la densidad de semillas y la composición de especies. El número de especies por campo fue de: 33, 45 y 48 y la densidad de semillas fue de: 10 186, 17 522 y 33 811 semillas m^{-2}, respectivamente. Hubo diferencias en el promedio del número de especies, pero no en la densidad promedio de semillas, entre los tres campos. Las especies secundarias herbáceas y arbustivas fueron las más abundantes en cada uno de los campos. El efecto que tienen las condiciones de uso en el contenido de semillas del banco son, en orden de importancia: 1) la extensión del período de uso del campo, 2) el tipo de vegetación que circunda los campos y 3) la presencia de árboles aislados.

Resumo: Para investigar os efeitos das diferentes condições de uso da terra nos bancos seminais em três parcelas de cultura numa área de floresta tropical de chuvas na região de Los Tuxlas na costa sudeste do Golfo do México, comparou-se a riqueza específica, a densidade média das sementes e a composição das espécies. A riqueza específica (o número de espécies de 33, 45 e 48, respectivamente) era diferente entre as várias parcelas embora a densidade média de sementes (densidade total por campo foi de 10186, 17522 e 33811 sementes por m^{-2}) não fosse diferente. O banco seminal nos solos agrícolas era dominado por ervas secundárias, e por poucas pioneiras e árvores secundárias. As diferenças na riqueza específica e composição são explicadas na base das diferenças na vegetação circundante, tempo de utilização dos campos agrícolas, práticas de gestão e presença de árvores solitárias em cada campo.

Key words: Landscape ecology, secondary succession, slash and burn agriculture, tropical rain forest regeneration,

Introduction

The deforestation of tropical rain forest (TRF) creates fragmented landscapes with a complex mosaic of vegetation. In the Los Tuxtlas region, the rain forest has been reduced to less than 36% of its original area, and is now distributed in fragments of various sizes. Areas used for human activities occupy more than 60% of the area previously covered by TRF, including pastures, crop fields, and urban areas. The original vegetation has been reduced to forest fragments, riparian corridors, living fences and even isolated trees (Guevara *et al.* 2005). The seeds and fruits of the species found in the open sites, secondary vegetation and mature forest are distributed across the landscape mosaic and are potential colonizers of abandoned fields (Guevara *et al.* 1998, 2004). The vegetation of these landscape elements reflects both the availability of propagules after disturbance and their subsequent

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arrival at disturbed sites. These propagules represent the floristic potential of a site and could be an important reserve for the restoration of the original vegetation (Guevara & Gómez-Pompa 1972).

The arrival and permanence of propagules occurs in different ways. Storage in the soil is the best documented. The composition of the soil seed bank determines the initial colonization of a site after a natural or human disturbance, and provides species for the process of vegetation recovery (Cubiña & Aide 2001; Dalling & Denslow 1998; Kellman 1978; Kalamees & Zobel 2002 Wijdeven & Kuzee 2000). In tropical rain forest areas the seed bank has been analyzed mainly in areas with original forest, and has been linked with gap colonization (Dalling & Denslow 1998; Drake 1998; Guevara 1986; Metcalfe & Turner 1998; Whitmore 1983). Only a few studies have focussed on the soil seed bank in other landscape elements such as agricultural fields, open pastures or secondary vegetation (Butler & Chazdon 1998; Dalling & Denslow 1998; Ewel *et al*. 1981; Kellman 1974, 1978; Pèrez & Santiago 2001; Uhl & Clark 1983; Wijdeven & Kuzee 2000).

In the agricultural fields of Los Tuxtlas there is wide variation in several factors, including the use, size, and type of crop planted, among others. Seed banks in agricultural soils are comprised of different sets of species. The main set includes weeds (*sensu* Kellman 1980) and pioneer trees and shrubs. The other, smaller group includes late secondary trees and rain forest species (Guevara *et al*. 2004). Disturbance of the original forest (logging, burning etc.) usually eliminates the seed bank of rain forest species. Agricultural use and pasture management (weeding, ploughing, grazing, etc.) decrease the seed density of the pioneer tree species linked to forest gap colonization, and favour the growth of secondary weeds (Dalling & Denslow 1998; Kellman 1980).

We compare the number of species, mean seed density and species composition of the soil seed bank in three agricultural fields of different ages, with the surrounding vegetation and management practices in the Los Tuxtlas region.

Materials and methods

Study site

The three fields studied are situated in the region of Los Tuxtlas, southeastern Veracruz at 18^0 05′, 18^0 45′ N and 94^0 35′, 95^0 30′ W on the Gulf coast of Mexico. The volcanic mountain range of Los Tuxtlas dates from the Oligocene to the Recent, and the soil is made up mainly of sand and ashes. The climate is hot and humid with a mean annual precipitation of 4500 mm and a mean annual temperature of 27^0C (Soto 2004). The region is covered by a mosaic of vegetation dominated by cattle pastures and different kinds of crop fields that surround the remaining tropical rain forest fragments (Castillo-Campos & Laborde 2004).

Field A was cleared by slash and burn, used for cattle grazing for a few months and is located on a gentle slope of 3–4^0 with small mounds. It is surrounded by other cultivated fields and rain forest. There were two remnant trees left in the field: *Ficus* sp. and *Pouteria campechiana* (H.B. & K.) Baehni. Field B was cleared the same way, used for cattle grazing and then used continuously for maize crops for over 20 years. The field is surrounded by the local village, old secondary growth and a newly cleared area. It has four remnant trees: two individuals of *Ficus* sp., a *Ceiba pentandra* Gaertn. and a *Nectandra ambigens* (S.F. Blake) C.K. Allen, which has a strangler fig (*Ficus colubrinae* Stand.) growing on it.

Field C was cleared the same way, and has been used for maize for the last 10–12 years. It is surrounded by young secondary growth and rain forest. There are three remnant trees: two individuals of *Ficus insipida* Willd. and a *Pouteria sapota* (Jacq.) H.E. Moore & Stearn.

Sampling was done randomly at 73 sites using a 1 m^2 frame. Soil cores were taken at each site from two opposite corners of the frame. Part of each site was located under the canopy of a remnant tree. The core was 8 cm in diameter and 8 cm deep, with a surface area of 50.2 cm^2 and a volume of 401.6 cm^3.

Each soil core was soaked in water for 24 h to soften the aggregates, and then sieved with a series of three sieves under running tap water. The high aggregation of soil particles required slow rubbing by hand to successfully complete the sieving process. Residues were air-dried and packed in envelopes for the future extraction of seeds. This technique prevented seed damage and simplified seed extraction by producing subsamples with particles and seeds of the same size. No germination occurred at this stage. The seeds were then removed with the aid of a dissecting microscope. The smallest sized sieve only allowed for the loss of very small seeds, such as orchid seeds.

The seeds were counted for each sample and identified using a reference seed collection for the secondary species reported for the region. Results for cores from each site were averaged. Seed density values were transformed according to the following scale: 1:1; 2:2; 3:3–4; 4:5–8; 5:9–16; 6:17–32; 7:33–64; 8:65–128; 9:129–more.

The seed density and the number of species of the seed bank data were not normally distributed. A Kruskal-Wallis one way analysis of variance on ranks was used to analyze these data and we used Dunn's method as the multiple comparison procedure. We compared the species composition among fields using the Sorensen index. To obtain a similarity pattern for the different fields, Ward's method with average linkage clustering was applied to a similarity matrix based on the density scale described above using the relative Sorensen Ratio as a distance measure (PC Ord 4, McClune & Mefford 1999). In addition, we obtained an ordered table for each of the fields. Finally, Detrended Correspondence Analysis (program PC Ord 4, McCune & Mefford 1999) was applied to explain the variation in floristic composition among fields.

Nomenclature follows MEXU (the Mexican National Herbarium), UNAM (the Universidad Nacional Autónoma de Mexico) and the Flora of Veracruz Floristic List (Sosa & Gómez-Pompa 1994).

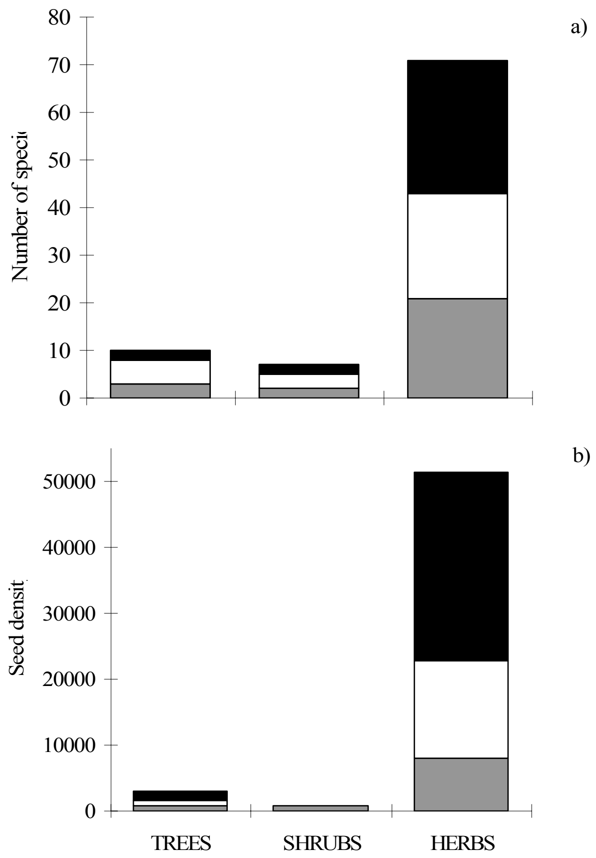

Fig. 1. Species richness (a) and seed density m^2 (b) groupd by growth forms, in three crop field; ■ Field A, □ Field B and ░ Field C, in soils samples of Los Tuxtlas, Mexico.

Results

The number of seed species and seed density

Seeds were classified into 43 taxa and unknowns. Unidentified seeds represented only a small proportion (10%) of all seeds. The mean number of species in the soil was different among sites (H= 29.71, P <0.001). A multiple comparison shows that the mean number of species in Field C was more than twice that of Field A. Although the total number of seeds per square meter between crop fields seems to be different, the mean seed density per field was not different (H= 5.016, P= 0.081), varying from 161.7 in Field A to 536.7 seeds m^{-2} in Field C (Table 1).

The seed bank consisted almost entirely of the seeds of secondary herbs (33 species and 51399 seeds m^{-2}). Across sites, herbs accounted for 52.4% of the taxa that could be assigned a growth form (Fig. 1a), but accounted for 92.9% of the total seed density (Fig. 1b). In Field C the seed bank contained significantly more seeds of herbs than Fields A or B. Herbs contributed 94.7% to the Field C seed bank and trees only 5.2%. In Field A, herbs accounted for 83.9% of the total seed bank, and trees only 8.7%. Shrub density was low at the three sites, but Field A had significantly more shrub species (Chi-square= 15 289; P < 0.001).

Time of use and management practice

The number of species (Chi-square=6.12, P=0.047) and seed density (Chi-square=13.63, P=0.001) were significantly related to the number of years that the field has been used and to the management of the field.

Species composition

The Sorensen index showed that species composition between fields was very similar, with Field A most different from the others (A *vs.* B= 0.77; A *vs.* C= 0.8 and B *vs.* C= 0.9). Nevertheless, a few species were highly abundant in all three fields. The most abundant species was *Amaranthus hybridus* L. with a mean seed density of 9198 seeds m^{-2} (15% of total seeds), followed by *Melampodium divaricatum* DC. A secondary composite (7932 seeds m^{-2}; 13%), *Hyptis verticillata* Jacq. (7867 seeds m^{-2}; 13%), *Panicum*

Table 1. Mean seed density of identified species for soil samples in three crop fields in Los Tuxtlas.

Species	Family	Field A	Field B	Field C	Mean
Acalypha diversifolia Jacq.	Euphorbiaceae		32	10	14.0
Achyranthes sp. L.	Amaranthaceae		4		1.3
Amaranthus hybridus L.	Amaranthaceae	26	28	9,144	3066.0
Ardisia crispa A. DC.	Myrsinaceae	26			8.7
Asclepias sp. L.	Asclepiadaceae			30	10.0
Axonopus compressus (Sw.) Beauv.	Poaceae	2,110	982	1,024	1372.0
Bidens pilosa L.	Asteraceae	6		53	19.7
Cecropia obtusifolia Bertol.	Cecropiaceae		32		10.7
Commelina diffusa Zoll. ex C.B.Clarke.	Commelinaceae	412	2,736	1,584	1577.3
Crotalaria sp. Dill. ex L.	Leguminosae	12	4	34	16.7
Cyperus sp. L.	Cyperaceae	26	1,590	149	588.3
Eleusine indica (L.) Gaertn.	Poaceae	496		370	288.7
Erechtites hieracifolia Raf. ex DC.	Asteraceae			4	1.3
Euphorbia hyssopifolia L.	Euphorbiaceae	12		4	5.3
Euphorbia sp. L.	Euphorbiaceae		16	64	26.7
Ficus insipida Willd.	Moraceae	750	536		428.7
Ficus obtusifolia Kunth	Moraceae		108	1,554	554.0
Hyptis atrorubens Poit	Lamiaceae	12	112	324	149.3
Hyptis verticillata Jacq.	Lamiaceae		158	7,709	2622.3
Iresine celosia L.	Amaranthaceae	1,350	90	20	486.7
Lasiacis sp. Hitchc.	Poaceae		16		5.3
Melampodium divaricatum DC.	Asteraceae	474	7,058	400	2644.0
Mimosa pudica L.	Mimosaceae		28		9.3
Monarda sp. L.	Lamiaceae		36	2,570	868.7
Myriocarpa longipes Liebm.	Urticaceae		4		1.3
Panicum germinatum Forsskal	Poaceae	1,324	136	3,944	1801.3
Panicum trichoides Sw.	Poaceae			104	34.7
Paspalum conjugatum P.J. Bergius	Poaceae	254	1,200	150	534.7
Paspalum sp. L.	Poaceae			10	3.3
Phytolacca rivinoides Kunth & Bouche	Phytolaccaceae	310	16	4	110.0
Sapium lateriflorum Hemsl.	Euphorbiaceae		4		1.3
Scleria melaleuca Rchb. ex Schltdl. & Cham.	Cyperaceae	20	8	14	14.0
Sida rhombifolia L.	Malvaceae			24	8.0
Siparuna andina A. DC.	Monimiaceae	6			2.0
Solanum nigrum L.	Solanaceae	434	36	130	200.0
Solanum rudepanum Dunal	Solanaceae	482	20	70	190.7
Syngonium podophyllum Schott	Araceae	6			2.0
Talinum sp. Adans.	Portulacaceae	136	262	344	247.3
Tetrorchidium rotundatum Standley	Euphorbiaceae	68	20	10	32.7
Trema micrantha Blume	Ulmaceae	12			4.0
Tripogandra serrulata (Vahl) Handlos	Commelinaceae	82	204	370	218.7
Urera caracasana Griseb.	Urticaceae	696	74	24	264.7
Verbesina sp. L.	Asteraceae			2	0.7
Number of species		33	45	48	
Seed density of identified species		9,542	15,550	30,247	
Seed density of 20 unidentified species		644	1,972	3,564	
Seed density (seeds m^{-2})		10,186	17,522	33,811	

germinatum Forsskal (5404 seeds m^{-2}; 9%) and *Commelina diffusa* Zoll. ex C.B.Clarke (4732 seeds m^{-2}; 8%) which together account for 58% (Table 1).

The single most common species in the soil of Field A was the grass *Axonopus compressus* (Sw.) Beauv., which was present in all soil samples but only accounted for only 7% of total seeds, followed by *Iresine celosia* L. and *P. germinatum*. It is worth noting that in these sites three species accounted for 47% of the seeds. At Field B, *M. divaricatum* accounted for 40% of the seeds and together with *C. difusa*, *Cyperus* sp. and *Paspalum conjugatum* P.J. Bergius accounted for 71% of the seeds at this site.

In Field C, the site with the highest number of species, eight species each had densities of more than 1000 seeds m^{-2}, and together accounted for 87% of the seeds. *A. hybridus* was the most abundant species with 27% of the seeds at this site and 15% of all the seeds collected (Table 1).

The cluster dendrogram (Fig. 2) shows two large groups. Group I contains only Field A sites with species dispersed by birds, such as *F. insipida*, *Phytolacca rivinoides* Kunth & Bouche, *Solanum nigrum* L., *Trema micrantha* (L.) Blume, *Siparuna andina* A. DC. and *Urera caracasana* Griseb. The common species *H. verticillata* and *Monarda* sp. L. are absent from these sites. There are two clear subgroups: one comprised of sites that are poor in species (less than 5 species), and one of sites that are rich in species (more than 10 species).

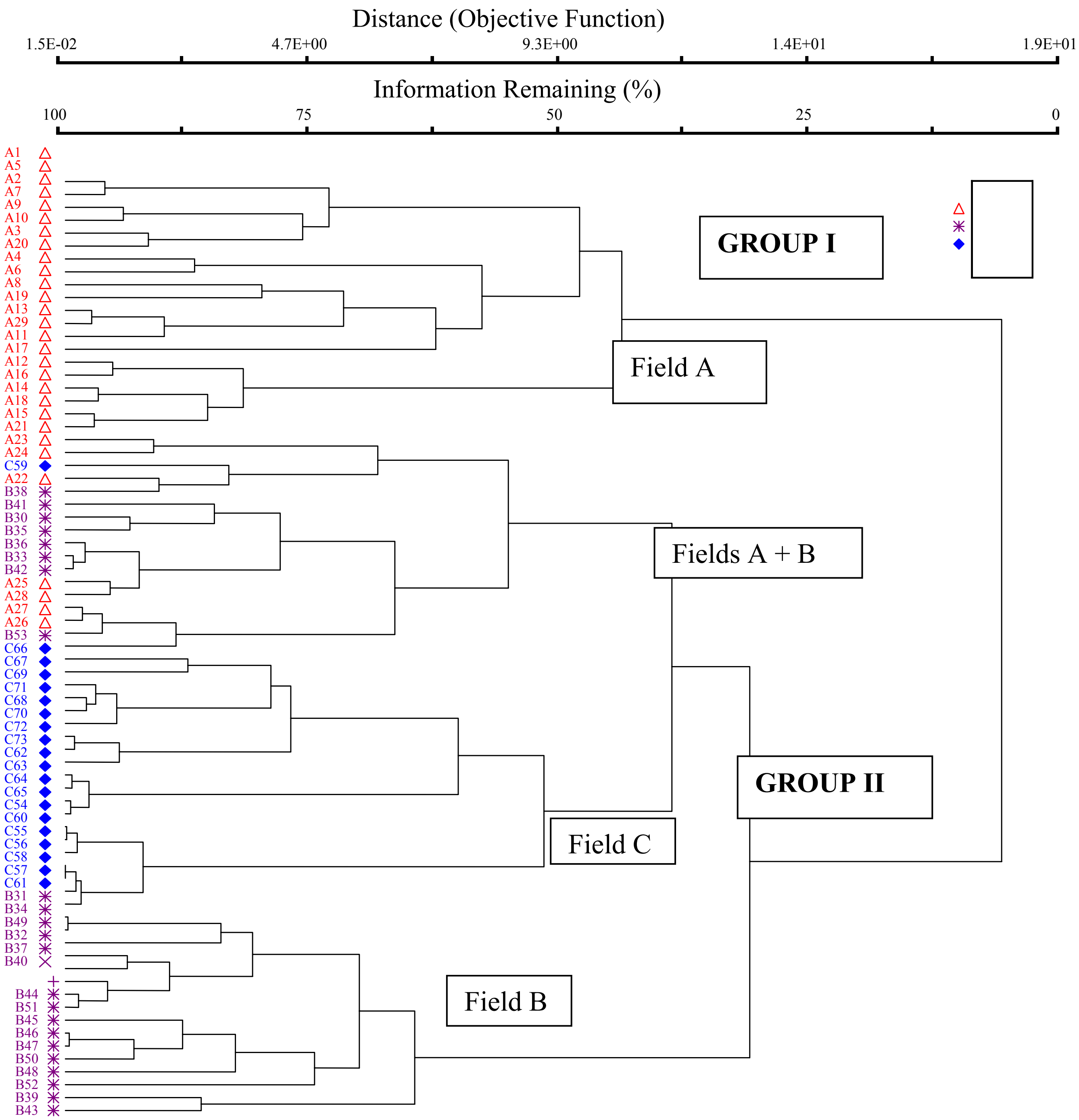

Fig. 2. Cluster dendrogram classification of all sites based on Sorensen Index similarity, obtained with PC Ord 4 (McClune & Mefford 1999).

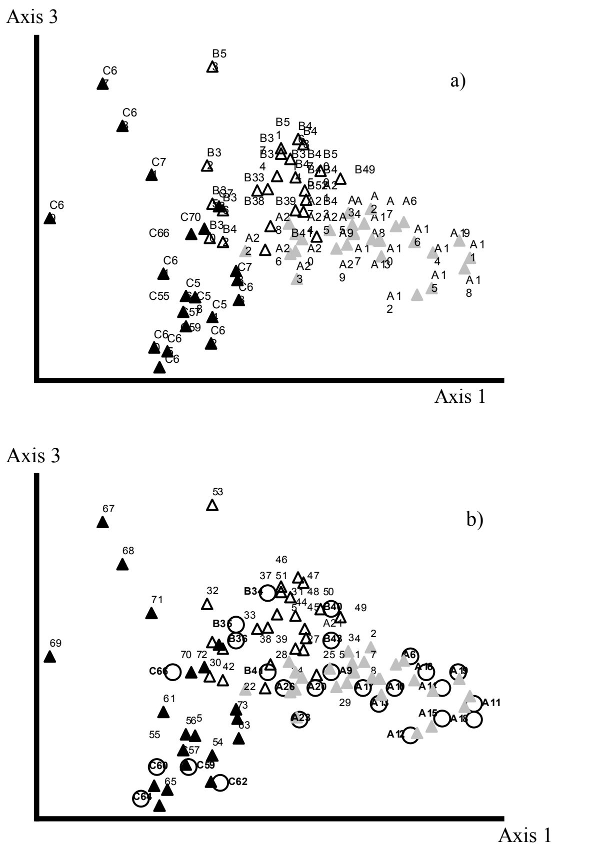

Fig. 3. (a) Ordination analysis by Princeipal component Analysis in three crop fields; A=▲ B=△, C= ▲ (b) Oridnation analysis, encircled numbers are canopy sites. (McClune & Mefford 1999).

In Group II, grassland species predominate, i.e. *A. compressus, P. conjugatum* and *P. germinatum*. Group II also has three subgroups. The first group is formed mainly of sites from Fields A and B and only one Field C site. *M. divaricatum* and *C. difusa* dominated and there were only a few grass seeds, although in some sites there were high numbers of *A. compressus*. The second subgroup had only sites from Field C with high densities of herbaceous seeds (*A. hybridus, C. diffusa, H. verticillata*), a few grass seeds (*A. compressus, P. geminatum*), and some seeds of a tree species, *Ficus obtusifolia* Kunth. In some of the samples there was a very high number of *F. obtusifolia* seeds, because during sampling this tree was fruiting. In the third subgroup, with only sites from Field B, herbaceous seeds (*M. divarictum, C. diffusa, Cyperus* sp.) and grass seeds (*P. conjugatum*) were the prevailing types.

The ordination results (Fig. 3a) also show a field subdivision, which corresponds to the classification results. Along the x axis a species richness gradient can be interpreted, with higher numbers towards the left of the ordination space (where Field C sites predominate), and poorer sites towards the extreme right (Field A sites). This gradient also shows many bird-dispersed species (*F. insipida, U. caracasana, Eleusine indica* (L.) Gaertn. and *Solanum rudepanum* Dunal) towards Field A sites, with *A. compressus*, *I. celosia* L. and *P. germinatum* as the most abundant herb species. Field C had high numbers of grasses and secondary species. Many sites had *Ficus* spp., but other bird-dispersed species were poorly represented.

The ordination shows a clear separation among the three fields (Fig. 3a). Cumulative variance for the first two axes accounted for 26.9%. Field A was more spread along the X axis. Sites where the seeds of bird-dispersed species predominate were found towards the extreme right of the ordination space, while sites with seeds from grass species were found closer to the other two fields. If we consider whether a tree canopy was present for each site (Fig. 3b), we observe that most of the "canopy" sites are found in the lower part of the graph. Apparently, they make up a particular set of species that determines part of the floristic variation (e.g. *F. obtusifolia* and *Tripogandra serrulata* (Vahl) Handlos). This tendency was clear in Fields A and C, but not so much in Field B. However, we did not find any relationship between the number of species and the presence of a tree canopy.

Discussion

The total number of species (63) and the number of species of each field (33, 45 and 48) are close to the mean values reported for other tropical fields. These range from 34 (tropical wet forest in Costa Rica, Butler & Chazdon 1994) to 69 species (in a secondary forest in Costa Rica, Wijdeven & Kuzze 2000). Lower numbers were obtained by Uhl & Clark (1983) in extremely poor conditions in Venezuela.

Our data are similar to those obtained from a mature forest. Guevara (1986) reported 46 species in the seed bank of rain forest sites at Los Tuxtlas, but low numbers were also recorded beneath the canopy of isolated trees in pastures, with 78 species (Guevara & Sánchez-Ríos unpubl. data).

Total seed density at Los Tuxtlas was higher than in the secondary growth stands (8331 and 14535 seeds m^{-2}) and old growth stands (2258–2 659 seeds m^{-2}) reported for Costa Rica (Dupuy & Chazdon 1998).

The mean seed density in crop fields was greater than that of undisturbed rain forest soils, where a mean seed density of 279 ± 29 seeds m^{-2} (Guevara 1986) and 1 01.4 ± 78 seeds m^{-2} (Guevara & Sánchez-Ríos unpubl. data) were registered.

The crop field seed bank was dominated by secondary herbs and there were few trees, while the forest seed bank consisted mainly of shrubs and pioneer trees such as *U. caracasana*, *Cecropia obtusifolia* Bertol., *T. micrantha* and *Heliocarpus appendiculatus* Turcz. (Guevara 1986; Guevara & Sánchez-Ríos unpubl. data). These results are similar to those of other studies where herbs dominated the soil seed bank (Dupuy & Chazdon 1998).

If we relate the position of the sites in the three fields to some of the site characteristics, we observe that Field C, the largest, is richest in species (48) and also has the highest seed density. This field is completely surrounded by young secondary growth and rainforest vegetation. Its seed bank contains many grassland and secondary species, but also a few secondary growth species. Field A on the other hand has the lowest number of species and the lowest seed density. It was surrounded by arboreal vegetation on only one quarter of its circumference.

The clear differences in the species composition of the fields studied reflect differences in the soil and in agricultural conditions, and are in accordance with the findings of Kellman (1980), which revealed heterogeneities within fields. Such local differentiation can be explained by the following factors: a. the vegetation surrounding the field acts as an important source of propagules. As found by Uhl *et al.* (1981) for the Amazon basin, both the time needed by plants to colonize successional sites and the species composition of these sites are influenced by the dispersal strategies of the surrounding flora. Field A is the most recently cleared area and is still in contact with the forest and riparian vegetation. This is reflected in its low seed density and the considerable proportion of bird-dispersed species. On the other hand, Field C was relatively rich in species because it was surrounded by a lot of forest and had been used for a longer time. Weed seeds were the main cause of this higher number of species. b. Standing trees function as perching sites, thus promoting selective seed input, especially of bird-dispersed species (Dunn 2000; Guevara & Laborde 1993; Guevara *et al.* 1986, 1998; Harvey 2000 a,b; Holl *et al.* 2000; Otero-Arnaiz *et al.* 1999; Toh *et al.* 1999) since many of these remnant trees have berries or fleshy fruits and rely on animals, mainly bats and birds, for their dispersal (Guevara & Laborde 1993; Galindo-González *et al.* 2000; Laborde 1996;). Several studies have found that in comparison with the surrounding open pasture, the vegetation growing beneath the canopy of remnant trees has a much higher density and the number of species of zoochorous woody plants (Guevara & Laborde 1993; Guevara *et al.* 1998; Holl 1999; Otero-Arnaiz *et al.* 1999; Slocum 2001), and may function as forest regeneration nuclei (Guevara *et al.* 1998, 2004). This may explain why the soil seed bank beneath the canopy of isolated trees has a much higher density and richness of zoochorous woody species than crop fields studied by Guevara *et al.* (2004).

The difference in the number of seed species under canopy sites and in open sites in our fields is another feature of the pasture conditions described in Guevara *et al.* (1986, 1998) with regard to the established plants. In our crop field seed bank, the greater number of species under the canopies was not a result of bird-dispersed species, as might be expected, but rather of secondary herbs. This can be explained by the fact that the seeds of bird-dispersed species do not accumulate, and if as in pastures, they are not able to germinate directly under protected conditions, they do not persist. If we compare our results with those from undisturbed forest and stands of secondary vegetation, we find that the seeds of pioneer tree species and shrubs are also rare (Dupuy & Chazdon 1998). We would expect the small seeds of pioneer species to be abundant in the crop field's soil because of their abundant seed rain and dormancy capabilities, but our data showed the opposite. For example *C. obtusifolia,* one of the most common and abundant pioneer species in the soil of the forest (Álvarez-Buylla 1986; Orozco-Segovia 1986; Salmeron 1984; Vázquez-Yanes &) and beneath the canopy of isolated trees in pastures (Guevara *et al.* 2004), is absent from the crop fields we sampled. This could be explained by the preferential predation of small seeds by ants and rodents (González-Montagut 1996; Quiroz & Valenzuela 1995).

The lower abundance of seeds belonging to pioneer species in the fields, as compared to secondary sites and undisturbed rain forest, could be a result of the limited new seed input from pioneer species. Many of these species are bird-dispersed and the absence of perching sites in open fields implies low seed deposition. The scarcity of pioneer species combined with the high number of weed seeds limits the rate of secondary succession. This has actually been found for abandoned sites in the same area where *M.*

divaricatum covers 20% of secondary sites and 60% of rain forest, and where trees are absent (Purata 1986).

The high dispersability of weedy species in these fields can be compared with soil seed bank data for forest edges and secondary stands in this area (Guevara & Gómez-Pompa 1972; Salmeron 1984). Young stands of secondary vegetation have a soil seed bank with 33 species, 84.8% of which are weeds, and which include 99% of the total number of seeds. The forest soil had 30 species, of which 63.3% were weeds, and which included 65.5% of the total number of seeds. In this regard we agree with Kellman (1980) who said that the shift from indigenous to pantropical weeds is related to the change from shifting cultivation to permanent agriculture.

The soil seed bank is highly variable, throughout both the year and the sites of the region. This results from the peculiar conditions for the arrival and permanence of the seeds that are a product of the ecological history of each site, and of the changes in the immediate surroundings. In this study, the influence of the surrounding vegetation seems clear. Although the effect of remnant trees found in previous studies was not clearly detected, our results do verify that these trees attract many seeds that germinate immediately. Information about the seeds in the soil is essential for understanding the process of natural forest regeneration in a fragmented landscape such as Los Tuxtlas. However, the comparability of our results with those of other studies is limited owing to the great differences in the sites and the time of the year the sampling took place.

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