Soil seed bank, seed removal, and germination in a seasonally dry tropical forest in Veracruz, Mexico

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Abstract: The soil seed bank has a limited role in the seasonal dry tropical forest regeneration process, but seed removal and germination can also be limiting factors during the early forest recovery. In central Veracruz, Mexico, the soil seed bank was determined en five fallows and two forests. Seed bank decreased from fallow to forest (1,303 to 101 seeds m^{-2}); herbs and grasses predominated, thus the similarity between species composition of seed bank and vegetation was low. Seed removal and germination were evaluated for *Acacia cochliacantha*, *Caesalpinia cacalaco*, *Ipomoea wolcottiana*, and *Senna atomaria*, in contrasting habitats represented by pasture, fallow and forest. Seed removal was determined under treatments of total access, rodent exclosure, and insect exclosure. *Caesalpinia* (largest seeds) showed the lowest seed removal (5%), whereas *Senna* (63%) and *Ipomoea* (29%) showed the highest. Rodent exclosure reduced seed removal for *Ipomoea* (medium-sized seeds); and insect exclosure reduced removal for *Senna* and *Acacia* (small seeds). With the exception of *Senna* (18% germination), the scarified seeds displayed the highest germination percentage (53-99%). For all species, germination was higher in forest than in open habitats, only *Senna* seeds presented the lowest germination percentage in the forest habitat. Results suggested that in the dry forest of Veracruz, current seed removal may not limit forest regeneration. We suggest seed scarification of some species for use in restoration activities.
Key words: dry forest, forest recovery, native trees, seed predation, seed scarification, secondary succession.

Resumen: El banco de semillas del suelo tiene un papel limitado en la recuperación de la selva baja caducifolia, pero la remoción y germinación de semillas pueden también ser factores limitantes al inicio de la sucesión. En el centro de Veracruz, México, el banco de semillas del suelo se determinó en cinco acahuales y dos selvas. El banco de semillas disminuyó de acahual a selva (1,303 a 101 semillas m^{-2}). Predominaron hierbas y pastos, por lo que la similitud entre la composición de especies del banco y la vegetación fue baja. La remoción y germinación de semillas se evaluó en *Acacia cochliacantha*, *Caesalpinia cacalaco*, *Ipomoea wolcottiana* y *Senna atomaria* en hábitats contrastantes representados por potrero y selva. La remoción de semillas se determinó bajo tratamientos de acceso total, exclusión de roedores y de insectos. *Caesalpinia* (semilla más grande) presentó la menor remoción (5%), mientras que *Senna* (63%) e *Ipomoea* (29%) presentaron la más elevada. La exclusión de roedores redujo la remoción para Ipomoea (semillas de tamaño mediano), y la exclusión de insectos redujo la remoción de *Senna* y *Acacia* (semillas pequeñas). Con la excepción de *Senna* (18% germinación), las semillas escarificadas presentaron el mayor porcentaje de germinación (53-99%). Para todas las especies, la germinación fue mayor en selva que en hábitats abiertos, únicamente *Senna* presentó un porcentaje de germinación más bajo en selva. La remoción actual de semillas puede no limitar la regeneración. Se recomienda la escarificación de las semillas de algunas especies para actividades de restauración.
Palabras clave: árboles nativos, depredación de semillas, escarificación de semillas, recuperación de selva, selva seca, sucesión secundaria.

Soil seed banks, as well as seed removal and germination, have been studied in relation to the recovery of the seasonally dry tropical forest in abandoned fields (Rico-Gray and García-Franco, 1992; Skoglund, 1992; Miller, 1999; Wijdeven and Kuzee, 2000; Dalling, 2002; Lemenih and Teketay, 2006; Reubens *et al.*, 2007; Maza-Villalobos *et al.*, 2011;

Meave *et al.*, 2012). In dry forests, another important source of forest regeneration is root or stem sprouting (Vieira and Scariot, 2006); however, when propagules are available, forest recovery in open areas may occur through secondary succession (Garwood, 1989; Dalling and Denslow, 1998; Holl, 1999; Holl *et al.*, 2000; Williams-Linera *et al.*, 2011).

The presence of propagules can be the result of seed storage in soil banks, seed rain, and the proximity to the propagule source-forest patches, isolated trees, or secondary vegetation (Holl, 1999; Zahawi and Augspurger, 1999; Wijdeven and Kuzee, 2000; Vieira and Scariot, 2006). Lack of dispersal and competition with seedlings and pastures may limit natural regeneration (Holl *et al*., 2000; Maza-Villalobos *et al*., 2011; Reid and Armesto, 2011). In abandoned areas, seed banks can trigger secondary succession; however, successful seedling establishment is influenced by other selective pressures that affect regeneration patterns, such as animal-plant interactions (e.g., herbivory, seed removal), seed germination, and favorable microenvironments (Skoglund, 1992; Holl *et al*., 2000; Fenner and Thompson, 2005; Aerts *et al*., 2006; Wassie *et al*., 2009).

Seed predation may critically reduce seedling recruitment; therefore, post-dispersal seed removal has been identified as a crucial phase in the regeneration and composition of tropical dry forest communities (Wijdeven and Kuzee, 2000; Jones *et al*., 2003; Briones-Salas *et al*., 2006). A general consensus is that low seed availability in open areas and seed mortality during dispersal are two of the major constraints to natural regeneration (Hammond, 1995; Vieira and Scariot, 2006). Seed size is also an important factor that affects the chances of being eaten or removed. Rodents prefer larger seeds, while small ones are more likely to become buried, which may cause ants and beetles to preferentially select them (Forget and Milleron, 1991; Dalling, 2002; Fenner and Thompson, 2005; Briones-Salas *et al*., 2006; Farwig *et al*., 2008).

Seed germination studies have found more variability between tree species than between habitats (Baskin *et al*., 1998; Holl, 2002). A higher germination rate in sites with vegetation cover than in open areas has been found; there, high humidity and low evapotranspiration may provide more favorable microclimatic conditions (Holl, 1999; Ceccon *et al*., 2006; Wassie *et al*., 2009). Mechanical or chemical scarification or other damage to seed coatings allows water absorption and promotes germination (Camargo-Ricalde and Grether, 1998; Ortega *et al*., 2001; Dalling *et al*., 2011).

In central Veracruz, the seasonally dry tropical forest (SDTF) has been reduced to 7% of its original size, even though one-third of this area is secondary vegetation; previous work has indicated that the fallow period is short, usually no longer than 7-10 years, making old secondary successional sites unavailable (Williams-Linera *et al*., 2011). The working hypothesis were: (1) the size and composition of soil seed banks in successional sites and dry forest habitats do not mirror the aboveground vegetation, (2) the seed removal patterns of selected tree species is higher in open habitats, and (3) the germination potential of selected tree species in contrasting habitats (active pasture, successional sites and forest) will be lower in open habitats.

Methods

Study area. The study area is located in the SDTF region of central Veracruz, Mexico (19° 17' N, 96° 26' W; 19° 10' N, 96° 32' W; altitude: 97-230 m). In forests fragments, some dominant tree species are *Bursera fagaraoides*, *B. simaruba*, *Calyptranthes schiedeana*, *Heliocarpus donnellsmithii*, *Ipomoea wolcottiana*, *Luehea candida*, and *Tabebuia chrysantha*, whereas in the early successional sites, dominant species are *Acacia cochliacantha*, *A. cornigera*, and *Guazuma ulmifolia*. Mean annual precipitation is 957 mm (range: 502-1,467 mm), with a dry season from October to May. Mean minimum and maximum temperatures are 20 and 31 °C, respectively. The dominant soil units are Cambisol and Vertisol with exposed rock. In this area, we selected eight study sites corresponding to different habitats: one active pasture (P1), five fallows with different years of abandonment (S1-S5), and two forest fragments (F1-F2; Table 1). A detailed description of each site can be found in Williams-Linera and Lorea (2009) and Williams-Linera *et al*. (2011).

Soil seed bank. The soil was collected from five fallow sites and two forest fragments in late May 2008, just before the onset of the rainy season that triggers seed germination (Table 1). At each study site, ten soil samples (30 cm × 30 cm and 5 cm depth) were collected on plots previously established for vegetation studies (Williams-Linera and Lorea, 2009; Williams-Linera *et al*., 2011). The soil samples were transported to a greenhouse located on the campus of the University of Veracruz in Xalapa. They were placed in 70 trays (53 × 26 cm) in layers of approximately 5 cm depth. Four control trays with autoclaved sterilized soil were located randomly in the greenhouse. Trays were watered every day during the seven-month period. Emerging seedlings were identified, counted and removed from the trays to reduce shade. Unidentified seedlings were transplanted to pots and grown until identification became possible; seedlings were identified and deposited in the University of Veracruz XALUV herbarium. Although dormant seeds may not show using this technique, germination may provide a more reliable method than directly extracting and counting the seeds from the soil (Gross, 1990).

Plant species. Four native tree species were selected to test germination and seed removal. They were abundant and represented different seed dispersal modes: *Acacia cochliacantha* (animal-dispersed), *Ipomoea wolcottiana* (wind-dispersed), and *Caesalpinia cacalaco* and *Senna atomaria* (self-dispersed). *Acacia cochliacantha* and *S. atomaria* can be considered as early successional or pioneer trees and the other species as late succesional or forest species (Williams-Linera *et al*., 2011). Hereafter, they will be referred to by genus only. Seeds were collected between May and August 2007, when fruit production peaks (GWL, unpubl. data).

Table 1. Characteristics of the study sites in the seasonally dry tropical forest region of central Veracruz, Mexico. P1 is active pasture, S1-S5 are early successional sites, F1-F2 are forest sites. Studies are soil seed bank (SSB), seed removal (SR), and seed germination (SG). Age (time since abandonment) and land use history were determined based on information from local inhabitants and corroborated using historical land-use maps associated with legal documents constituting *ejidos* (1920-1960); modified after Williams-Linera *et al.* (2011).

| Site	Latitude N	Longitude W	Altitude m	Area ha	Study	Age yr	Land use
P1	19° 17′0″	96° 28′ 57″	40	1.5	SG, SR	-	active pasture with isolated trees
S1	19° 21′ 47″	96° 34′ 8″	220	1.0	SSB	1	cop fallow. Deforested for ca. 100 year. Used for mango, papaya, beans and corn. Burned annually
S2	19° 17′ 1″	96° 28′ 29″	130	0.7	SSB, SG	1	pasture fallow. Deforested in 1998 to grow *Panicum maximum*. Continuously used for cattle
S3	19° 21′ 59″	96° 32′ 44″	250	0.5	SSB	3.3	pasture fallow. Deforested for ca 50 years. Used as farmyard to milk 6–8 cows during 15 years. With isolate trees
S4	19° 11′ 4″	96° 32′ 10″	230	0.4	SSB	4.3	pasture fallow. Deforested for ca. 33 year. Used to raise cattle for 20 year. Few trees
S5	19° 17′ 34″	96° 27′ 7″	175	0.4	SSB	6.3	pasture fallow. Deforested for ca. 100 year. Used to grow *Brachiaria* as forage for donkeys
F1	19° 16′12″	96° 29′ 39″	97	21.1	SSB, SG	-	forest
F2	19° 10′ 4″	96° 33′ 0″	221	1.5	SSB	-	forest

Five to ten mature trees of each species were selected, and at least 50 fruits were collected per tree and stored in paper bags. Seeds were separated from fruit; only seeds that had a good appearance (fully grown and without evidence of rot or insect damage) were chosen and subsequently selected using the flotation in water method.

Since the probability of successful seedling establishment in the face of environmental hazards increases with seed mass, the seed volume was calculated from linear dimensions, assuming an ellipsoidal shape and using the equation proposed by Dias and Ganhão (2012). Ten seeds of each species were randomly chosen and measured to the nearest mm. Seed mass varied by 5-6 orders of magnitude among species. *Caesalpinia* seeds had the largest volume (V = 243.8 mm^3, se = 17.3), followed by *Ipomoea* (V = 109.8 mm^3, se = 5.4); seeds of *Senna* (V = 21.1 mm^3, se = 1.2) and *Acacia* (V = 17.3 mm^3, se = 2.5) were smaller and statistically similar to each other (Kruskal-Wallis test, χ^2 = 34.2, $P <$ 0.0001).

Seed removal. Seed removal was studied during the rainy season using three treatments: total access to animals, and the exclusion of rodents or exclusion of insects. To exclude insects, we used 20 × 20 × 10 cm boxes made of wire mesh with 0.5 cm^2 openings, and open tops and walls coated with Vaseline to keep insects from entering. To exclude rodents, we used 20 × 20 × 10 cm boxes made of wire mesh with 1 cm^2 openings and closed tops. At site P1, twelve trees were chosen in open areas. Boxes were placed at ground level un-der the crown of each tree at least 0.50 m from the trunk. For each species, 25 seeds were placed in one Petri dish per box; three treatments with four replications were located around each tree. A total of 144 boxes (per species, 12 open, 12 inaccessible to insects, and 12 inaccessible to rodents) were checked daily during the first week and every other day for the following three weeks.

Seed germination. Seed germination experiments were conducted in laboratory and field conditions using two treatments consisting of mechanical scarification and one control. Scarification consisted of a small cut in the seed coat made with a knife, care being taken not to damage the embryo. Control and scarified seeds were immersed in distilled water for a period of 24 hours. Subsequently, sets of 50 seeds were placed in four Petri dishes for each treatment; cotton was used as substrate and kept wet with distilled water to a saturation point during the whole experiment. In the lab, germination was evaluated in a germination chamber (Lab-Line Instruments INC.) with temperature varying from 25 to 30 °C, and 12-hour photoperiod. Germination in the field was conducted in forest, fallow, and pasture habitats during the rainy season. In each, we established four 1 × 1 m plots, one for each species. Eight Petri dishes (four with control seeds and four with scarified seeds) were placed on each plot. The 96 Petri dishes were buried at 3 cm with removal of litterfall; they were protected with wire mesh boxes 20 × 20 × 10 cm placed at ground level. We counted germinated seeds daily for one week and then every other day.
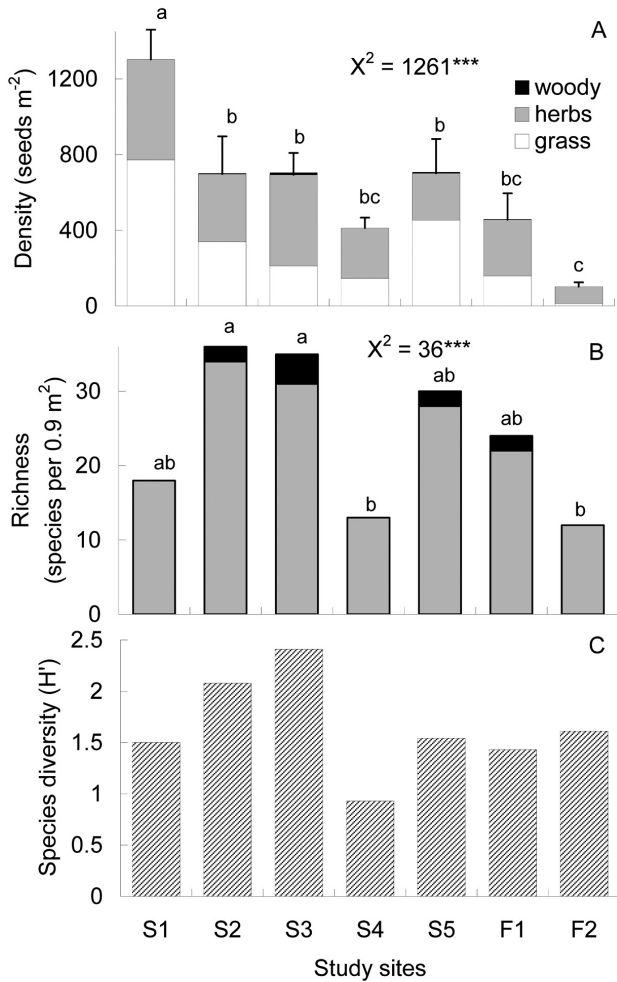
Figure 1. Soil seed banks in the seasonally dry tropical forest region of central Veracruz, Mexico. A) Seed density (mean and one s.e.) and life forms, B) number of species and, C) Shannon diversity Index. *** is $P < 0.001$, and different letters indicate significant differences.

Statistical analyses. Differences in soil seed bank density and richness were analyzed using generalized linear models, since data were counts a Poisson distribution and logarithmic link function were used to test differences in total density, richness, and life forms. Shannon diversity indices were estimated as $H' = -\Sigma p_i \ln p_i$. The Chao-Jaccard Index was calculated to analyze similarity between seed bank species abundance using EstimateS version 7.5 software (Colwell, 2005). This index has a value of 1 for identical species composition and 0 when assemblages are completely dissimilar. Absence-presence of species between seed banks and woody vegetation were compared, but since they were predominantly different, the index was not calculated.

For the seed removal experiment, all seeds were observed during a month; survivorship curves were analyzed as censored data with the product-limit (Kaplan-Meier) survival analysis. This is a nonparametric test for comparing the
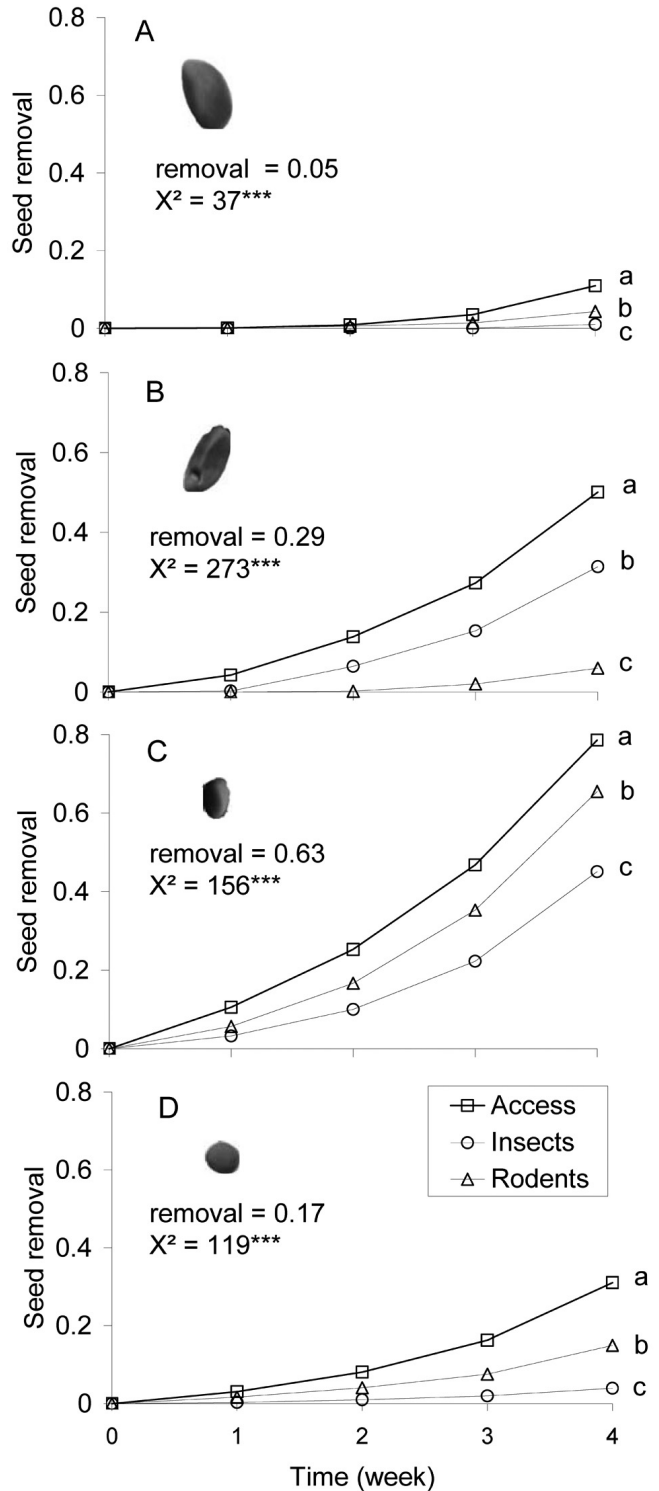
Figure 2. Seed removal proportions for treatments of total access, insect exclusion and, rodent exclusion in open areas (P1) in the seasonally dry forest region of central Veracruz, Mexico. Species are arranged in decreasing order of seed volume: A) *Caesalpinia cacalaco*, B) *Ipomoea wolcottiana*, C) *Senna atomaria*, and D) *Acacia cochliacantha*. *** is $P < 0.001$, and different letters indicate significant differences.
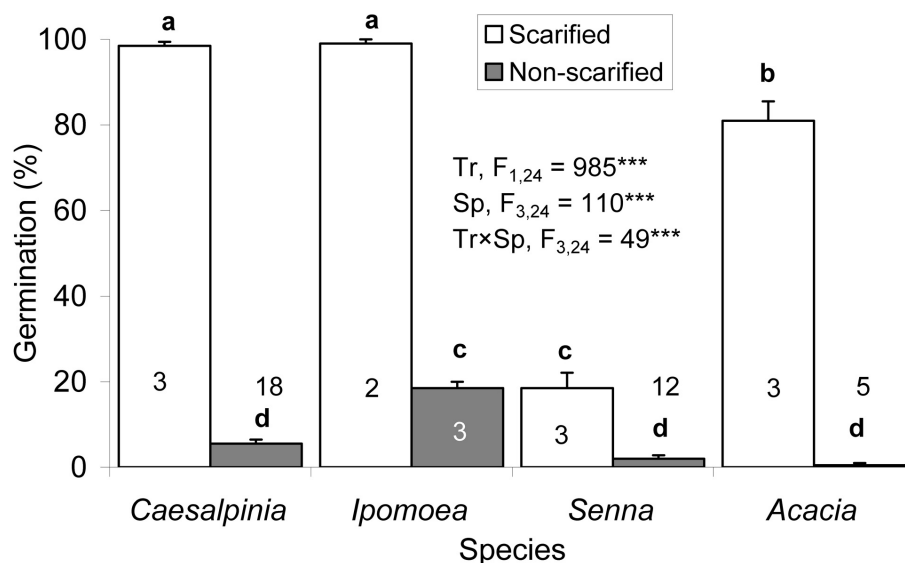
Figure 3. Seed germination percent in lab conditions for scarified and control seeds of each selected species. Numbers are L50 or number of days taken for the germination of 50% of the seeds. Tr: treatment, Sp: species, Tr × Sp: treatment-species interaction. Values are mean and one s.e.; *** is $P < 0.001$ and different letters indicate significant differences.

distribution of life-spans of groups; Wilcoxon statistics was used to test homogeneity between groups. Statistical analyses were performed using JMP version 6.0 software.

Germination data percentages were arcsine transformed, and two-way ANOVAs were used to test for differences between treatments (scarification and control) and habitats (forest, fallow, and pasture) per species. When significant differences were detected, means were compared using a Tukey-HSD test.

Results

Seed bank. In total, 3,946 seedlings were recorded in the soil seed bank of the study sites, corresponding to 25 families represented by 51 genera, 83 species, and three morphospecies, although graminoid species (grasses and sedges) were not identified (Appendix 1). The most abundant families were Cyperaceae-Poaceae (47.7%), Acanthaceae (15.2%), Euphorbiaceae (9.9%), Malvaceae (6.9%), Asteraceae (6.6%), and Fabaceae (1.8%). Life forms were unequally represented, with very few trees and abundant herbs (including sedges and grasses; Figure 1). Seed density ranged from 101 to 1,303 seeds m^{-2}. Overall, germinated seeds significantly decreased from the most disturbed site (S1) to the forest (F1 and F2) (Figure 1A). Richness varied from 13 to 36 species (Figure 1B), and the Shannon diversity index was between 0.93 and 2.41 (Figure 1C). When soil seed bank composition was compared using the Chao-Jaccard Index, we found that fallows S2, S3, and S4 were highly similar. Furthermore, the soil seed bank of the two forest sites was similar between themselves and S4 too (Table 2). However, seed bank in fallow S1 differed from all others.

The species composition found in soil seed banks and woody vegetation was dissimilar (Chao Jaccard Index = 0). Only *Acacia cochliacantha*, *Bursera cinerea*, and *Caesalpinia cacalaco* were found in both the seed bank and standing vegetation of the same site. However, seeds from species not present as adult plants such as *Ipomoea wolcottiana*, *Piscidia piscipula*, and *Senna atomaria* were found in seed banks (Appendix 1).

Seed removal. Seed removal was significantly different among species ($\chi^2 = 1493$, df = 3, $P < 0.0001$) and treatments ($\chi^2 = 409$, df = 2, $P < 0.0001$). Overall, *Senna* and *Ipomoea* had the highest percentage of seed removal; as could be expected, for all species the highest percentage of seed removal was recorded when seeds were offered with complete access to animals (Figure 2). The species with the largest seeds (*Caesalpinia*) showed the lowest seed removal

Table 2. Similarity between pairs of soil banks estimated according to the Chao Jaccard Index for seed species abundance in the seasonally dry forest region of central Veracruz, Mexico. S1-S5 are early successional sites, F1-F2 are forest sites. Values in bold type indicate more similarity between sites.

	S2	S3	S4	S5	F1	F2
S1	0.04	0.12	0.00	0.08	0.02	0.01
S2		**0.59**	**0.59**	0.16	0.07	0.10
S3			**0.54**	0.22	0.27	0.15
S4				0.14	**0.38**	**0.44**
F1					0.12	0.13
						0.38
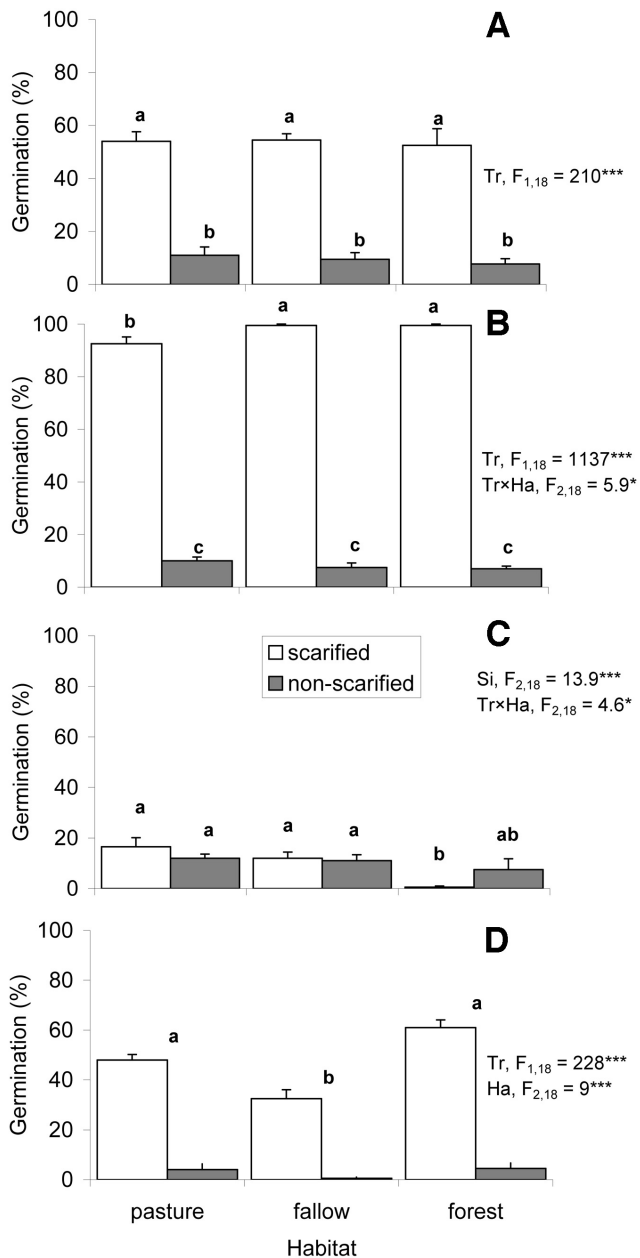
Figure 4. Seed germination percent in field conditions for scarified and control seeds of each selected species in forest, fallow and pasture habitat in the seasonally dry forest region of central Veracruz, Mexico. A) *Caesalpinia cacalaco*, B) *Ipomoea wolcottiana*, C) *Senna atomaria*, and D) *Acacia cochliacantha*. Tr: treatment, Ha: habitat, Tr × Ha: treatment-habitat interaction. Only the significant effects are displayed. Values are mean and one s.e.; * is $P < 0.05$, *** is $P < 0.001$, and different letters indicate significant differences.

rate (Figure 2A). The treatment of rodent exclosure reduced seed removal for *Ipomoea*, which has medium-sized seeds (Figure 2B); the insect exclosure treatment reduced seed removal for species with small seed size, such as *Senna* (Figure 2C) and *Acacia* (Figure 2D).

Seed germination. Under laboratory conditions, seed germination was significantly higher for seeds with mechanical scarification treatment than for untreated seeds, and was significantly different among species (Figure 3). For scarified seeds, the highest percentages were recorded for *Ipomoea* (99.0%) and *Caesalpinia* (98.5%) seeds, followed by *Acacia* (81.0%) and Senna (18.5%). In field conditions, scarified seeds also had a significantly higher germination percent for all species (47.2-97.2%) except *Senna* (9.7%; Figure 4). Species showed differences in germination percentage. *Caesalpinia* did not display significant differences between habitats (Figure 4A), while *Ipomoea* seed germination was higher in fallow and forest than in pasture (Figure 4B). Germination percentage for *Acacia* seeds (Figure 4D) was higher in forest and pasture than in the fallow habitat, whereas germination in the forest was the lowest for *Senna* seeds (Figure 4C).

Discussion

Soil seed bank density in early successional and forest habitats was within the range found for tropical dry forests, with a trend toward more germinated seeds at more disturbed sites (70-855 seed m^{-2}, Rico-Gray and García-Franco,1992; 700-1,000 seeds m^{-2}, Miller, 1999; 466-1,257 seed m^{-2}, Uasuf *et al.*, 2009; 806-3,150 seed m^{-2}, Maza-Villalobos *et al.*, 2011). In our study, land-use history does not have a clear effect on seed bank characteristics, however, a site used for agriculture for a long time (S1, Table 1) had the highest seed density and lower richness than the abandoned sites planted with exotic grasses and the forest sites. In Ethiopia, changes in soil seed density did not show any trend with cultivation time (Lemenih and Teketay, 2006), but in Oaxaca, Mexico, Meave *et al.* (2012) found that seed bank density tended to increase with the time of use of the agricultural fields. Whereas, along a chronosequence of abandoned pastures and forest sites in Chamela, Mexico, Maza-Villalobos *et al.* (2011) reported a reduction in the seed density.

Previous studies have shown that the species composition of soil seed banks in SDTF and successional sites are dominated by grasses and herbs, with scarce native forest species (Garwood, 1989; Rico-Gray and García-Franco, 1992; Miller, 1999; Tekle and Bekele, 2000; Lemenih and Teketay, 2006; Reubens *et al.*, 2007; Salazar *et al.*, 2011; Meave *et al.*, 2012). Here, a few woody species were found in the soil bank, mostly at the successional site (S3) with high species richness both in the seed bank and vegetation; however, the soil seed bank on the forest habitats contained just two seeds from woody species. Similarity between the composition of seed banks and woody vegetation was near zero. Soil was collected before the rainy season to sample the transient plus persistent bank (Fenner and Thompson, 2005); thus, scarceness of woody species may indicate that SDTF species did not form a persistent seed bank and germinate after dispersal during the rainy season (Salazar *et al.*,

2011). At early successional sites, the limited representation of woody species in seed banks may be due to their distance from propagule sources (Garwood, 1989; Wijdeven and Kuzee, 2000; Lemenih and Teketay, 2006; Salazar *et al.*, 2011), absence of seed dispersers such as birds (Jiménez and Armesto, 1992; Rico-Gray and García-Franco, 1992), high predation rates (Hammond, 1995; Jones *et al.*, 2003; Briones-Salas *et al.*, 2006), or the use of fire for land clearing (Miller, 1999).

In our study, some tree species were found in both the seed bank and vegetation, while others species were identified in the soil but not in standing vegetation. Those seeds may have arrived due to seed rain, since nearby forest patches, isolated trees that provide shade for livestock, and living fences could act as propagule sources (Holl, 1999; Ceccon *et al.*, 2006). Seed banks have been considered a limited tool in regenerating dry forest vegetation because an almost total absence of seeds from woody species (Lemenih and Teketay, 2006; Reubens *et al.*, 2007; Uasuf *et al.*, 2009; Reid and Armesto, 2011; Salazar *et al.*, 2011). However, in Nicaragua, Uasuf *et al.* (2009) found a 20% similarity between seed bank and standing vegetation; in Tanzania, Lyaruu *et al.* (2000) reported several species in common, and in Chamela, Mexico, Maza-Villalobos *et al.* (2011) found that during succession the soil seed banks change and, herb and grass species may be replaced in abundance and diversity by woody species.

Seed removal may produce considerable seed losses (Wijdeven and Kuzee, 2000; Briones-Salas *et al.*, 2006). In this study, the highest seed removal rate occurred in the total access treatment, as has been observed in other SDTF studies (e.g., Hammond, 1995; Briones-Salas *et al.*, 2006). Species removal agents may be small mammals such as rodents or invertebrates such as ants. Here, insects seem to be the most important seed removers. In Chiapas, Hammond (1995) found that seed removal by vertebrates is greater in early successional sites after shifting agriculture than in mature forest or at sites abandoned for more than 30 years. In Costa Rica, Jones *et al.* (2003) reported more removal in abandoned pasture adjacent to forest fragments than far from the edge; and that interspecific differences in seed removal rates were consistent with the hypothesis that in pasture, larger seeds are removed less than smaller seeds. In our study, the largest seeds are relatively small compared to the seeds of species that occur in secondary forest (Khurana and Singh, 2001; Fenner and Thompson, 2005). Nevertheless, *Caesalpinia*, the species with the largest seeds, was removed, or at least, despite the fact that it has been found as one of the most removed seed by rodents in Chamela (Briones-Salas *et al.*, 2006) and, that rodents are abundant in our study area and are represented by at least eight species (Gómez-Alanis, 2010). *Ipomoea* (medium-size seed) and *Senna* (small-size seed) had the highest percentage of seed removal. In the case of *Ipomoea* seeds, a lower removal with rodent exclosure suggests that rodents were the main predator.

In addition, direct field observations indicated that ants also remove these seeds, as substantial amounts of seeds were found around ant nests. *Ipomoea* presented a vast seed production that can be directly related to the observed high seed removal (CAA, *pers. obs*). Several authors have found this denso-dependent mechanism of higher removal rates when seed density is high (Hammond, 1995; Fenner and Thompson, 2005; Briones-Salas *et al.*, 2006).

In this study, seed removal was relatively low in comparison with values reported for other SDTF sites (98%, Hammond, 1995; 42%, Wijdeven and Kuzee, 2000); thus, current removal rates may not be a limiting factor for regional forest regeneration. Still, before seed germination and seedling establishment take place other barriers such as seed scarification and microhabitat became apparent. Mechanical seed scarification resulted in substantially higher germination percentage, both in lab and field conditions, except for *Senna* seeds. Our results suggest that the other species (*Acacia*, *Caesalpinia*, and *Ipomoea*) need to be mechanically scarified to absorb water to enhance germination; otherwise, germination percentage is low and spread out over time. *Senna* as a pioneer tree, displayed lower germination in the shaded forest habitat, but also in the light-controlled germination chamber, thus *Senna* seeds may have a non-physical dormancy and variation in seed dormancy among populations (Lacerda *et al.*, 2004).

Caesalpinia displayed similar germination percentage in different habitats, whereas *Ipomoea* and *Acacia* had higher germination in forest habitat. In SDTF, germination and early seedling establishment mainly depend on water availability; therefore, lower germination in pasture and fallow are probably due to water stress (Lieberman and Li, 1992; Fenner and Thompson, 2005; Ceccon *et al.*, 2006; Wassie *et al.*, 2009). Scarification is required because the hard and impermeable seed coat prevents the passage of water to the embryo (Cervantes *et al.*, 1996; Camargo-Ricalde and Grether, 1998; Fenner and Thompson, 2005; Wassie *et al.*, 2009; Maza-Villalobos *et al.*, 2011). Seed dormancy prevails in SDTF species, but increased germination after mechanical scarification has been reported for several legume tree seeds (*Acacia cochliacantha*, Cervantes *et al.*, 1996; *Mimosa tenuiflora*, Camargo-Ricalde and Grether, 1998; *Caesalpinia paraguariensis*, Ortega *et al.*, 2001). Under natural conditions, scarification may depend on the effect of avian gut-passage (Reid and Armesto, 2011), but other authors have suggested that in a dry environment, temperature fluctuations on the soil surface can soften the seed coat and allow germination (Moreno-Casasola *et al.*, 1994; Ortega *et al.*, 2001; Fenner and Thompson, 2005).

Conclusions

This study suggests that the soil seed bank of disturbed SDTF habitats is very unlikely to contribute to forest re-

covery since there is no resemblance between the species composition of seed bank and vegetation. The effect of seed removal may not be a limiting factor for recovery in open areas: most seeds of the selected species suffered low removal rates. Furthermore, several seed species showed physical dormancy that broke after scarification. For restoration activities, seeds need to be mechanically scarified in order to achieve a high germination rate. In the study area, the presence of woody vegetation and the proximity to forest fragments may provide early support for forest recovery.

Acknowledgments

Literature cited

Aerts R., Maes W., November E., Negussie A., Henry M. and Muys B. 2006. Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Orea europaea* ssp. *cuspidata* seeds. *Forest Ecology and Management* **230**:23-31.

Baskin J.M., Nan X. and Baskin C.C. 1998. A comparative study of seed dormancy and germination in an annual and a perennial species of *Senna* (Fabaceae). *Seed Science Research* **8**:501-512.

Briones-Salas M., Sánchez-Cordero V. and Sánchez-Rojas G. 2006. Multi-species fruit and seed removal in a tropical deciduous forest in Mexico. *Canadian Journal of Botany* **84**:433-442.

Camargo-Ricalde S.L. and Grether R. 1998. Germinación, dispersión y establecimiento de plántulas de *Mimosa tenuiflora* (Leguminosae) en México. *Revista de Biología Tropical* **46**:543-554.

Ceccon E., Huante P. and Rincón E. 2006. Abiotic factors influencing tropical dry forests regeneration. *Brazilian Archives of Biology and Technology* **49**:305-312.

Cervantes V., Carabias J. and Vázquez-Yañez C. 1996. Seed germination of woody legumes from deciduous tropical forest of southern Mexico. *Forest Ecology and Management* **82**:171-184.

Colwell R.K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5.

Dalling J.W. 2002. Ecología de semillas. In: Guariguata M.R. and Kattán G. Eds. *Ecología y Conservación de Bosques Neotropicales*, pp. 345-375, Libro Universitario Regional, Cártago.

Dalling J.W. and Denslow J.S. 1998. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. *Journal of Vegetation Science* **9**:669-678.

Dalling J.W., Davis A.S., Schutte B.J. and Arnold A.E. 2011. Seed survival in soil: interacting effects of predation, dormancy and the soil microbial community. *Journal of Ecology* **99**:89-95.

Dias L.S. and Ganhão E. 2012. Extending the range for accurate estimation of seed volume from incomplete linear dimension data. *Seed Science and Technology* **40**:129-133.

Farwig N., Bleher B., von der Gönna S. and Böhning-Gaese K. 2008. Does forest fragmentation and selective logging affect seed predators and seed predation rates of *Prunus africana* (Rosaceae)? *Biotropica* **40**:218-224.

Fenner M. and Thompson K. 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge.

Forget P.M. and Milleron T. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* **87**:596-599.

Garwood N.C. 1989. Tropical soil seed Banks: a review. In: Allessio L.M., Thomas P.V. and Simpson R.L. Eds. *Ecology of Soil Seed Banks*, pp. 149-209, Academic Press, San Diego.

Gómez-Alanis, C. 2010. Análisis multicriterio para la determinación de áreas prioritarias para la conservación de elementos bióticos y culturales en el bosque seco del centro de Veracruz, México. Master Thesis. Instituto de Ecología, A.C., Xalapa. 135 pp.

Gross K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology* **78**:1079-1093.

Hammond D.S. 1995. Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. *Journal of Tropical Ecology* **11**:295-313.

Holl K.D. 1999. Factors limiting rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* **31**:229-242.

Holl K.D. 2002. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology* **90**:179-187.

Holl K.D., Loik M.E, Lin E.H.V. and Samuels I.A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* **8**:339-349.

Jiménez H.E. and Armesto J. 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. *Journal of Vegetation Science* **3**:579-586.

Jones F.A., Peterson C.J. and Haines B.L. 2003. Seed predation in Neotropical pre-montane pastures: site, distance, and species effects. *Biotropica* **35**:219-225.

Khurana E. and Singh J.S. 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. *Environmental Conservation* **28**:39-52.

Lacerda D.R., Filho J.P.L., Goulart M.F., Ribeiro R.A. and Lovato M.B. 2004. Seed-dormancy variation in natural populations of two tropical leguminous tree species: *Senna multijuga* (Caesalpinoideae) and *Plathymenia reticulata* (Mimosoideae). *Seed Science Research* **14**:127-135.

Lemenih M. and Teketay D. 2006. Changes in soil seed bank composition and density following deforestation and subsequent cultivation of a tropical dry Afromontane forest in Ethiopia. *Tropical Ecology* **47**:1-12.

Lieberman D. and Li M. 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. *Journal of Vegetation Science* **3**:375-382.

Lyaruu H.V., Eliapenda S. and Backéus I. 2000. Floristic, structural and seed bank diversity of a dry Afromontane forest at Mafai, central Tanzania. *Biodiversity and Conservation* **9**:241-263.

Maza-Villalobos S., Lemus-Herrera C. and Martínez-Ramos M. 2011. Successional trends in soil seed banks of abandoned pastures of a Neotropical dry region. *Journal of Tropical Ecology* **27**:35-49.

Meave J.A., Flores-Rodríguez C., Pérez-García E.A. and Romero-Romero M.A. 2012. Edaphic and seasonal heterogeneity of seed banks in agricultural fields of a tropical dry forest region in Southern Mexico. *Botanical Sciences* **90**:313-329.

Miller P.M. 1999. Effects of deforestation on seed banks in a tropical deciduous forest of western Mexico. *Journal of Tropical Ecology* **15**:179-188.

Moreno-Casasola P., Grime J.P. and Martínez M.L. 1994. A comparative study of the effects of fluctuations in temperature and moisture supply on hard coat dormancy in seeds of coastal tropical legumes in Mexico. *Journal of Tropical Ecology* **10**:67-86.

Ortega B.P., De Viana M.L., Larenas G. and Saravia M. 2001. Germinación de semillas de *Caesalpinia paraguariensis* (Fabaceae): agentes escarificadores y efecto del ganado. *Revista de Biología Tropical* **49**:301-304.

Reid S. and Armesto J.J. 2011. Avian gut-passage effects on seed germination of shrubland species in Mediterranean central Chile. *Plant Ecology* **212**:1-10.

Reubens B., Heyn M., Gebrehiwot K., Hermy M. and Muys. 2007. Persistent soil seed banks for natural rehabilitation of dry tropical forests in northern Ethiopia. *Tropicultura* **25**:204-214.

Rico-Gray V. and García-Franco J.G. 1992. Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *Journal of Vegetation Science* **3**:617-624.

Salazar A., Goldstein G., Franco A.C. and Miralles-Wilhelm F. 2011. Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas. *Seed Science Research* **21**:103-116.

Skoglund J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science* **3**:357-360.

Tekle K. and Bekele T. 2000. The role of soil seed banks in the rehabilitation of degraded hillslopes in southern Wello, Ethiopia. *Biotropica* **32**:23-32.

Uasuf A., Tigabu M. and Odén P.C. 2009. Soil seed banks and regeneration of Neotropical dry deciduous and gallery forests in Nicaragua. *Bois et Forêts des Tropiques* **299**:49-62.

Vieira D.L.M. and Scariot A. 2006. Principles of natural regeneration of topical dry forests for restoration. *Restoration Ecology* **14**:11-20.

Wassie A., Sterck F.J., Teketay D. and Bongers F. 2009. Tree regeneration in Church forests of Ethiopia: effects of microsites and management. *Biotropica* **41**:110-119.

Wijdeven S.M.J. and Kuzee M.E. 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology* **8**:414-424.

Williams-Linera G. and Lorea F. 2009. Tree species diversity driven by environmental and anthropogenic factors in tropical dry forest fragments of central Veracruz, Mexico. *Biodiversity and Conservation* **18**:3269-3293.

Williams-Linera G., Alvarez-Aquino C., Hernández-Ascención E. and Toledo M. 2011. Early successional sites and the recovery of vegetation structure and tree species of the tropical dry forest in Veracruz, Mexico. *New Forests* **42**:131-148.

Zahawi R.A. and Augspurger C.K. 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica* **31**:540-552.

Appendix 1. Floristic composition of soil seed banks in a seasonally dry tropical forest region of central Veracruz, Mexico. S1-S5 are early successional sites; F1-F2 are forest sites. Values are total number of germinated seeds per species per 0.9 m² at each site.

Family	Species	S1	S2	S3	S4	S5	F1	F2
Tree								
Burseraceae	*Bursera cinerea* Engl.	0	0	0	0	0	1	0
Convolvulaceae	*Ipomoea wolcottiana* Rose	0	3	0	0	3	1	0
Fabaceae	*Caesalpinea cacalaco* Bonpl.	0	0	3	0	0	0	0
	Senna atomaria (L.) Irwin & Barneby	0	0	1	0	0	0	0
Shrub								
Euphorbiaceae	*Croton reflexifolius* Kunth.	0	1	0	0	0	0	0
Fabaceae	*Acacia cochliacantha* Humb.& Bonpl.	0	0	4	0	2	0	0
	Gliricidia sepium (Jacq.)Kunth ex Walp.	0	0	1	0	0	0	0
	Piscidia piscipula (L.) Sarg.	0	0	2	0	0	0	0
Herbaceous								
Acanthaceae	*Blechum brownei* Juss.	0	0	0	0	0	1	0
	Elytraria imbricata (Vahl.) Pers.	0	27	49	220	49	200	52
	Ruellia inundata Kunth.	0	0	1	0	0	0	0
Amaranthaceae	*Achirantes* sp.	0	0	0	0	3	0	0
	Achirantes aspera L.	0	0	0	0	1	0	0
	Amaranthus tricolor L.	0	0	0	0	0	0	1
Asteraceae	*Ageratum houstonianum* Mill.	0	0	0	0	0	1	0
	Baltimora recta L.	0	2	0	0	18	0	1
	Bidens pilosa L.	0	0	0	2	0	0	0
	Delila biflora (L.) Kuntze	0	0	0	2	0	1	0
	Lagascea sp.	0	2	0	0	0	0	0
	Lagascea molis Cav.	47	0	35	0	12	11	1
	Porophyllum macrocephalum DC.	0	0	0	0	0	9	0
	Sabazia sarmentosa Less.	0	0	0	0	0	0	1
	Thitonia tubiformis (Jacq.)	83	0	27	0	5	0	0
	Zaluzania triloba (Ort.) Pers.	0	0	0	0	1	0	0
Boraginaceae	*Heliotropium angiospermum* Murray	0	0	0	0	0	0	4
	Heliotropium indicum L.	0	0	0	0	0	2	0
	Heliotropium procumbens Mill.	0	2	0	0	0	0	0
Brassicaceae	*Brassica* sp.	0	0	12	0	0	1	0
Campanulaceae	*Lobelia* sp.	0	25	4	0	0	0	0
Capparidaceae	*Cleome* sp.	0	1	0	0	0	1	0
	Cleome aculeata L.	3	0	0	0	0	0	0
	Cleome viscosa L.	0	7	34	0	23	1	0
Commelinaceae	*Comelina* sp.	0	0	0	0	0	0	6
	Commelina diffusa Burm.F.	0	0	2	0	0	0	0
Convolvulaceae	*Evolvulus alisinoides* (L.) L.	0	0	0	0	1	0	0
Euphorbiaceae	*Acalypha adenostachya* Mull.Arg.	0	2	0	0	1	0	0
	Acalypha alopecuroide Jacq.	22	2	86	2	51	0	0
	Acalypha unibracteata Müll.Arg.	0	5	1	0	1	0	0
	Chamaecyse sp.	11	0	0	0	0	0	0
	Chamaecyse hipericifolia (L.) Millsp.	13	0	2	0	0	0	0

Appendix 1. Continuation

Family	Species	S1	S2	S3	S4	S5	F1	F2
	Euphorbia sp. 1	0	0	1	0	0	0	0
	Euphorbia sp. 2	15	6	0	0	13	0	0
	Euphorbia sp. 3	8	82	0	0	0	0	0
	Euphorbia sp. 4	0	0	2	0	0	0	0
	Euphorbia sp. 5	5	14	11	0	2	0	1
	Euphorbia heterophylla L.	0	0	0	0	0	3	0
	Euphorbia hirta L.	0	22	0	1	1	0	4
Fabaceae	*Chamaecrista* sp.	0	1	0	0	3	0	0
	Chamaecrista nictitans (L.) Moench.	0	18	0	0	1	0	0
	Crotalaria sp.	0	1	0	0	0	0	0
	Desmodium sp. 1	0	0	2	1	0	0	1
	Desmodium sp. 2	0	7	0	0	0	4	0
	Desmodium sp. 3	0	0	0	0	1	0	0
	Desmodium sp. 4	11	8	0	0	1	0	0
Malvaceae	*Abutilon* sp.	0	1	0	0	0	0	0
	Allowissadula sessei (Lag.) D.M.Bates	1	25	60	0	22	0	0
	Sida sp.	120	4	0	0	0	0	0
	Sida acuta Burm.F.	0	16	0	4	0	0	0
	Sida spinosa L.	0	3	0	0	0	2	0
	Wissadula periplocifolia C.Presl.	0	0	5	0	2	0	6
Nyctaginaceae	*Boerhavia erecta* L.	13	0	4	0	0	0	0
	Okenia sp.	0	1	61	0	0	17	0
Onagraceae	*Ludwigia* sp.	0	0	0	1	0	0	0
Oxaliaceae	*Oxalis* sp.	0	0	0	0	0	0	3
	Oxalis clematodes R.Knuth	0	2	2	4	0	0	0
Portulacaceae	*Portulaca* sp.	0	17	1	0	1	0	0
Rubiaceae	*Borreria* sp.	126	0	0	0	0	0	0
Scrophulariaceae	*Calceolaria* sp.	0	0	0	0	3	0	0
	Capraria frutescen (Mill.) Britton	0	3	2	0	0	0	0
Solanaceae	*Solanum* sp.	0	6	2	0	1	2	0
	Solanum nigrum L.	0	2	8	0	4	0	0
Sterculiacea	*Melochia lupulina* Sw.	0	7	0	0	0	0	0
Tiliaceae	*Corchorus siliquosus* L.	0	0	0	0	2	0	0
Verbenaceae	*Priva aspera* Kunth.	0	0	16	1	0	7	0
Violaceae	*Hybanthus attenuatus* (Humb. & Bonpl.)	0	0	0	0	1	0	0
Sedge and grass								
Cyperaceae and Poaceae		695	306	190	131	407	142	10
Unknown	Undetermined	0	0	3	1	0	4	0
Total		1,173	631	634	370	636	411	91