Soil Seed Banks and Regeneration of Neotropical Dry Deciduous and Gallery Forests in Nicaragua

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Photograph 1.
Firewood extraction from the Chacocente Wildlife Refuge, Nicaragua, which is a typical anthropogenic disturbance of tropical dry forests
Photo by Guillermo Castro-Marin.

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RÉSUMÉ

RÔLE DES BANQUES DE SEMENCES DU SOL DANS LA RÉGÉNÉRATION DES FORÊTS SÈCHES DE FEUILLUS ET DES FORÊTS-GALERIES EN ZONE NÉOTROPICALE DU NICARAGUA

Le déclin des forêts sèches tropicales et la nécessité de les restaurer sont aujourd'hui des réalités largement reconnues. Pour la restauration de forêts dégradées, la première étape consiste toujours à quantifier les niveaux réels et potentiels de régénération naturelle, en analysant le rôle des banques de semences du sol dans la dissémination de propagules. Pour cette étude, nous avons évalué la composition, la densité et la distribution spatiale de la banque de semences du sol et des populations de jeunes plants dans les forêts sèches de feuillus et les forêts-galeries du refuge de Chacocente au Nicaragua. Au total, 17 espèces ont été repérées dans la banque de semences du sol dans la forêt de feuillus, avec une densité de semences viables de 466 semences/m^2. Dans la forêt-galerie, 24 espèces ont été repérées dans la banque de semences du sol, avec une densité viable de 1 257 semences/m^2. Une analyse spatiale de la banque de semences a révélé des répartitions par paquets ou uniformes dans les deux types de forêts, suivant les essences. La densité globale des jeunes plants dans les forêts à feuillus et les forêts-galeries s'établissent respectivement à 6 250 et 6 600 individus/ha. En termes de distribution spatiale, les peuplements de jeunes plants sont répartis par paquets ou uniformément, suivant les essences. La similitude entre banque de semences du sol, couche de jeunes plants et végétation aérienne est faible sur les deux sites. Cela permet de conclure que le nombre d'espèces dans les banques de semences du sol et la quantité de semences stockées dans le sol sont relativement faibles. La régénération est abondante pour certaines essences mais faible pour d'autres. Il convient donc d'assister le processus de régénération naturelle par ensemencement direct, établissement de jeunes plants et aménagement des sites afin d'améliorer les conditions de prise et de croissance des jeunes plants.

Mots-clés : forêt tropicale sèche, banque de semences du sol, distribution spatiale, index de Morisita, restauration.

ABSTRACT

SOIL SEED BANKS AND REGENERATION OF NEOTROPICAL DRY DECIDUOUS AND GALLERY FORESTS IN NICARAGUA

Today, the depletion of tropical dry forests and the need for their restoration are well recognized. In restoring degraded forests, the first step is to quantify the actual and potential levels of natural regeneration, examining the role of soil seed banks as propagule donors. In this study, we assessed the composition, density and spatial distribution of the soil seed bank and seedling populations in dry deciduous and gallery forests of the Chacocente Wildlife Refuge in Nicaragua. A total of 17 species were found in the soil seed bank of the deciduous forest, with a viable seed density of 466 seeds/m^2. In the gallery forest, a total of 24 species were found in the soil seed bank with a viable seed density of 1257 seeds/m^2. The spatial analysis of the soil seed bank revealed clumped and uniform distributions in both forests, depending on the species. The total seedling density in the deciduous and gallery forests was 6250 and 6600 individuals/ha, respectively. The spatial distribution of seedling populations varied from clumped to uniform depending on the species. The similarity between the soil seed bank, seedling layer and above-ground vegetation was low in both forest sites. It may be concluded that the number of seed bank species and the quantity of soil-stored seeds are relatively low. Regeneration was abundant in some species, but poor in many others. The natural regeneration process should therefore be assisted through direct seeding, planting seedlings and manipulation of the site to improve environmental conditions for seedling establishment and growth.

Keywords: tropical dry forest, seedling bank, spatial pattern, Morisita's index, restoration.

RESUMEN

PAPEL DE LOS BANCOS DE SEMILLAS DEL SUELO EN LA REGENERACIÓN DE BOSQUES SECOS DE FRONDOSAS Y DE GALERÍA EN LA ZONA NEOTROPICAL NICARAGÜENSE

El declive de los bosques secos tropicales y la necesidad de restaurarlos son realidades ampliamente aceptadas hoy en día. Para la restauración de bosques degradados, la primera etapa sigue consistiendo en cuantificar los niveles reales y potenciales de regeneración natural, analizando el papel de los bancos de semillas del suelo en la diseminación de propágulos. Para este estudio, se evaluó la composición, densidad y distribución espacial del banco de semillas del suelo y de las poblaciones de plantitas silvestres en los bosques secos de frondosas y los bosques de galería del refugio de Chacocente en Nicaragua. Se identificó un total de 17 especies en el banco de semillas del suelo en el bosque de frondosas, con una densidad de semillas viables de 466 semillas/m^2. En el bosque de galería, se identificaron 24 especies en el banco de semillas del suelo, con una densidad viable de 1257 semillas/m^2. El análisis espacial del banco de semillas reveló distribuciones agrupadas o uniformes en ambos tipos de bosque, dependiendo de las especies. La densidad global de plantas jóvenes en los bosques de frondosas y en los de galería es, respectivamente, de 6250 y 6600 individuos/ha. En cuanto a la distribución espacial, los rodales de plantas jóvenes se reparten por grupos o uniformemente, dependiendo de las especies. El índice de similitud entre el banco de semillas del suelo, la capa de plantas jóvenes y la vegetación aérea es bajo en ambos sitios. Esto permite concluir que el número de especies en los bancos de semillas del suelo y la cantidad de semillas almacenadas en el suelo es relativamente escaso. La regeneración es abundante en algunas especies, pero baja en otras. Por ello, es conveniente ayudar al proceso de regeneración natural mediante siembra directa, establecimiento de plantas jóvenes y adecuación de los sitios para mejorar las condiciones de arraigo y crecimiento de las plantas jóvenes.

Palabras clave: bosque tropical seco, banco de semillas del suelo, distribución espacial, índice de Morisita, restauración.

Introduction

Tropical dry forests are among the most severely degraded and threatened forest ecosystems in Central America (Janzen, 2002). Historically, these forest formations have been extensively converted into other land uses, such as crop fields and/or range lands (Gillespie, 1999). Forest remnants probably represent less than 2% of the original dry forest along the Pacific coast of Mesoamerica, an area extending from Panama to western Mexico (Sabogal & Valerio, 1998). Nicaragua is the largest country in Central America (land area ca. 130 000 km^2), and its tropical dry forest areas cover ca. 2 500 km^2, representing 2.1% of the total forest cover (Roldan, 2001). Tropical dry forests have been under heavy pressure from, among others, extensive ranching during the 1960s and 1970s (Janzen, 2002). In addition, since the beginning of the last century, there has been extensive harvesting of commercially valuable species for export, such as *Swietenia humilis, Guaiacum sanctum, Cedrela odorata, Dalbergia retusa* and *Bombacopsis quinatum*.

Although the primary dry forest has almost disappeared along the Pacific coast, there are remaining fragments or patches of dry forests (Janzen, 2002). These remaining fragments are considered to be the most endangered ecosystems in the lowland tropics, and immediate restoration measures are urgently needed (Janzen, 2002). Restoration or, more strictly speaking, ecological restoration, is defined by the Society for Ecological Restoration as “the process of assisting the recovery and management of ecological integrity. Ecological integrity includes a critical range of variability in biodiversity, ecological processes and structures, regional and historical context, and sustainable cultural practice”. Four possible methods for restoring natural vegetation exist: (i) natural regeneration, (ii) direct seeding, (iii) planting seedlings, and (iv) incorporating restoration goals in plantation programs (Lamb *et al.*, 1997; Vallejo *et al.*, 2006). Natural regeneration is the cheapest approach for rehabilitating degraded forest ecosystems, provided that the previous disturbance has left some residuals (e.g. soil seed banks, mother trees or root shoots) that can serve as “succession primers”. The first step in any forest restoration endeavour is therefore a site assessment to quantify actual and potential levels of natural regeneration, to examine the presence of “succession primers” and to determine whether intervention is needed to accelerate the natural regeneration process (Wijdeven & Kuzee, 2000).

In the restoration of plant communities in degraded forests, the idea of exploiting soil seed banks may sound attractive. The soil seed bank refers to all viable seeds and fruits present on or in the soil and associated litter/humus. Soil seed banks can be either transient, with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than 1 year (Simpson *et al.*, 1989). They exhibit spatial and temporal variations, reflecting their initial dispersal onto the soil and subsequent movement (Simpson *et al.*, 1989). The pool of long-lived seeds in the soil accumulates over many decades and forms a source of propagules that ensures continual occupation of a site after disturbances, while serving as a gene pool by buffering genetic changes in the population. An understanding of soil seed bank dynamics in degraded forests, which include gains through seed rain, losses due to seed predation, seed death and transfer into the active seed bank to germinate and form a seedling bank, is paramount before deciding whether intervention is needed to assist the natural regeneration process. Natural regeneration is also heterogeneous across the landscape, depending on seed dispersal, viability, dormancy, predation, herbivory, rainfall and topographic, edaphic and light conditions (Khurana & Singh 2001; Enoki & Abe 2004). Determining the spatial patterns of natural regeneration is therefore also essential in designing an appropriate restoration technique.

Photograph 2.
A typical Neotropical dry forest formation in the Chacocente Wildlife Refuge, Nicaragua
Photo by Guillermo Castro-Marin.

This study was carried out at Chacocente Wildlife Refuge in Nicaragua, which was established in 1983 to protect the remaining fragments of tropical dry forest along the Central American Pacific coast as well as the nesting beaches of endangered species of marine turtles, the olive ridley (*Lepidochelys olivacea*) and leatherback (*Dermochelys coriacea*) (Anonymous, 2002). Despite natural and anthropogenic disturbances (photograph 1) due to commercial timber extraction (of species such as *Swietenia humilis, Cedrela odorata, Bombacopsis quinata, Dalbergia retusa, Guaicum sanctum*), illegal felling for local consumption, conversion to agricultural lands and fire (Roldan, 2001), the Chacocente Wildlife Refuge is still one of the relatively intact dry forest formations with distinct dry deciduous (photograph 2) and gallery (photograph 3) forests. It thus offers invaluable opportunities for research on the restoration of degraded tropical dry forests in Central America. The general aim of this study was to gain knowledge about the soil seed bank and the extent of natural regeneration in dry deciduous and gallery forests that can be used for the restoration of such disturbed forest ecosystems. The specific objectives were:
1) to determine the composition, density, and spatial distribution of the soil seed bank,
2) to determine the floristic composition, density and spatial distribution of naturally regenerating seedlings of woody species, and
3) to analyze the relationships between the soil seed banks and the standing vegetation in dry deciduous and gallery forests.

Materials and Methods

Study area

The study was carried out in Chacocente Wildlife Refuge (11°30' - 11°35' N and 86°08' - 86°14' W), on the south-west Pacific coast of Nicaragua (figure 1). The Refuge consists of closed dry deciduous forest (1 099 ha), gallery forest (471 ha), open low forest (1 842 ha), fallows (554 ha), cropland (311 ha), grassland (294 ha), and beach areas (71 ha) (ANONYMOUS, 2002). The gallery forest, defined as narrow patches along the fringes of semi-permanent watercourses, occurs along the main water course, the Río Escalante. Chacocente has a 7-month dry season with less than 50 mm precipitation per month. During the rainy season (June-October), rainfall is irregular with many days without rainfall (ANONYMOUS 2002). Mean annual precipitation during the last 14 years (1990-2003) was 1 422 mm, with a maximum in 1995 (1 962 mm) and a minimum in 1991 (991 mm). Mean monthly maximum and minimum temperatures were 28.3ºC and 26.2ºC respectively. Soils in the dry deciduous forest type are classified as Vertic and Ferric Luvisols (SABOGAL & VALERIO 1998) while those in the gallery forest are Eutric Fluvisols.

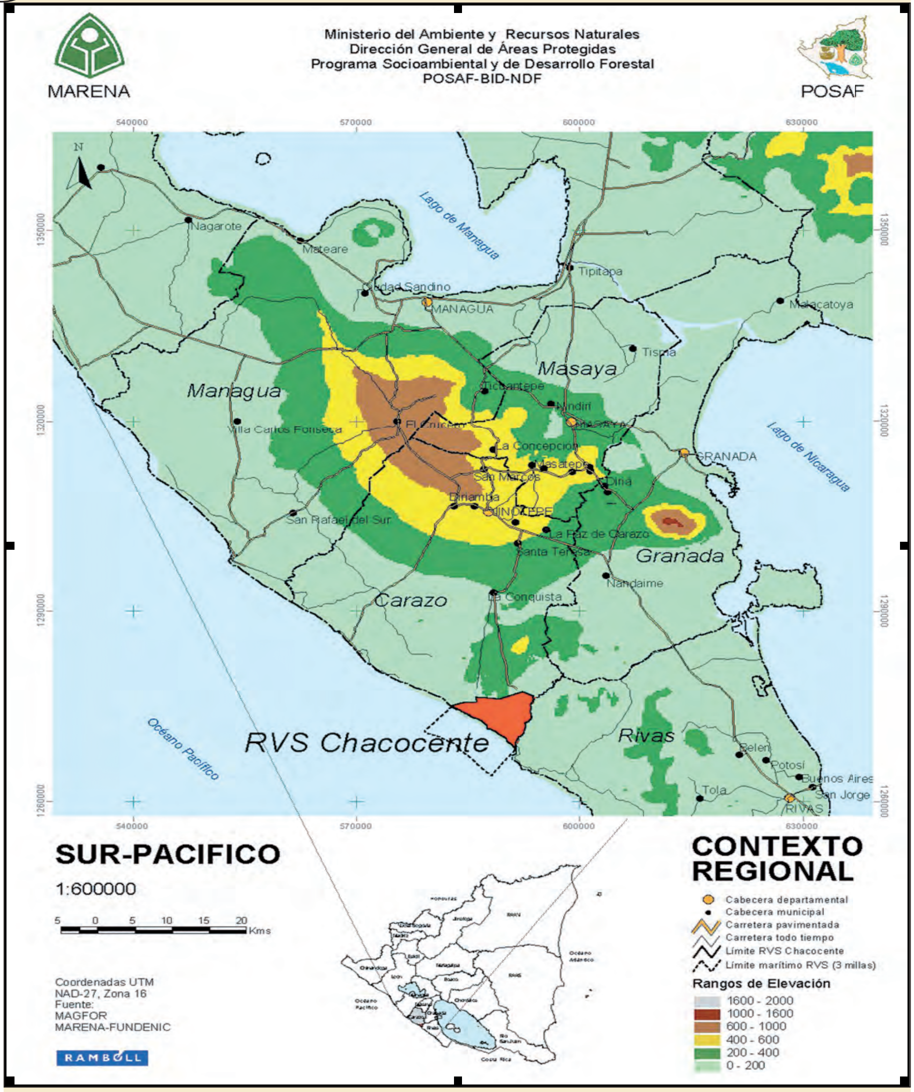

Figure 1.
Location of the Chacocente Wildlife Refuge, Nicaragua, where the present study was conducted.

Soil seed bank assessment

In each of the dry deciduous and gallery forests, two permanent sample plots were established in 1994 by Universidad Nacional Agraria, Managua, Nicaragua, to monitor changes in biodiversity. The area of each permanent plot was 1.0 ha, as in the case of most biodiversity monitoring plots in the Neotropics, and each was further divided into 25 subplots of 20 × 20 m to carry out detailed inventories. In each subplot (20 × 20 m) within each forest type, two quadrats measuring 15 × 15 cm were laid in opposite corners in order to get a better representation of the soil sample (figure 2). From each quadrat, four soil layers of 3 cm thickness each to a depth of 12 cm (0-3, 3-6, 6-9 and 9-12 cm) were collected using a sharp knife and spoon. Soil samples taken from each quadrat within a subplot were mixed to form a soil composite, in order to reduce variability within the sub plots. The soil samples per subplot were then put in separate plastic bags with the relevant information. To recover seeds from the soil, the soil samples were sieved with different mesh sizes ranging from 0.5 mm to 5 mm, on the assumption that seed sizes of most woody species fall within this range. The viability of seeds recovered by sieving was determined by germination and cutting tests after they were identified. Germination tests were carried out with Jacobsen's apparatus at 20 ± 2°C with illumination of *ca.* 20 mE m^{-2} s^{-1} (Fluorescent lamp F 40 W / 33 RS cool white light) for six weeks. After six weeks of incubation, the viability of seeds that had not germinated was assessed by cutting. Seeds with a firm white embryo were considered viable while seeds that were covered with fungi, collapsed when pinched and had grey, yellow, or brownish embryos were considered dead (TEKETAY & GRANSTRÖM, 1995; BASKIN & BASKIN, 1998).

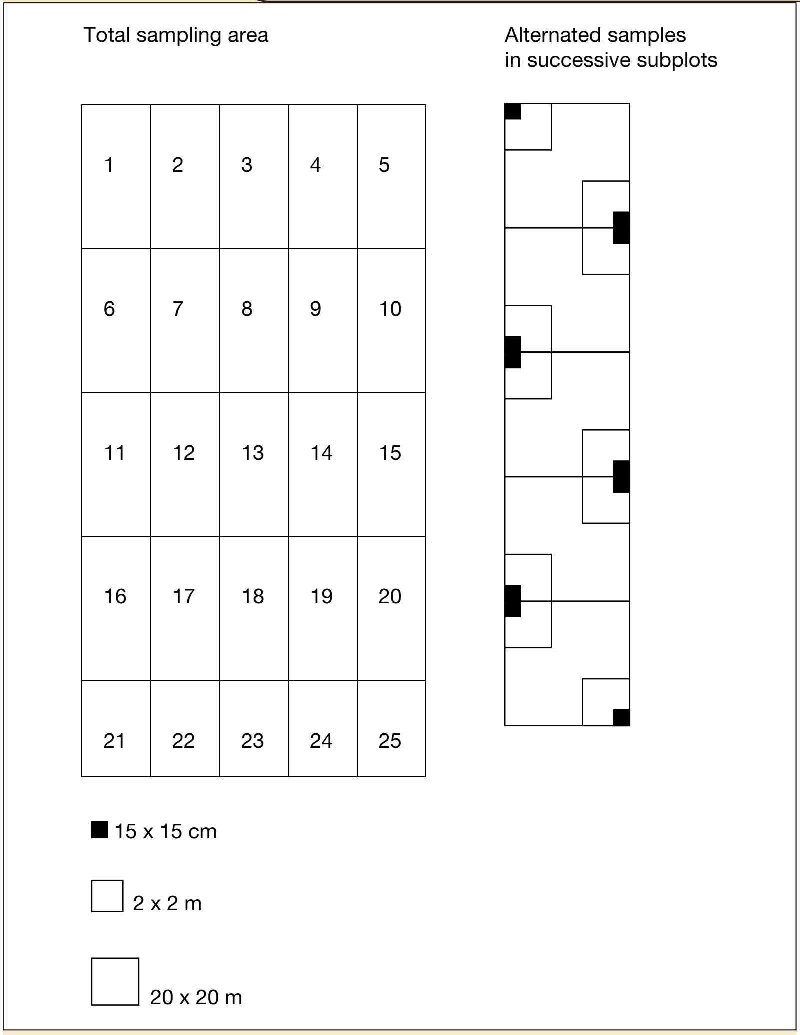

Figure 2.
Lay-out of sampling design employed for assessing the soil seed bank, seedling populations and aboveground vegetation in the dry deciduous and gallery forests of the Chacocente Wildlife Refuge, Nicaragua.

Inventory of the standing vegetation

Species composition and the number of individuals making up the standing vegetation (seedlings, saplings and mature trees) were assessed in each of the permanent plots. In this study, seedlings were considered as individuals ≤ 150 cm in height (Teketay, 1997), saplings as individuals between 1.5 and 4 m in height, and mature trees as individuals ≥ 5 cm in diameter at breast height (dbh). To assess seedling populations, two quadrats of 2 × 2 m were laid in opposite corners of each 20 x 20 m subplot (figure 2), while the populations of both saplings and mature trees were assessed in each of the 25 subplots (20 × 20 m).

Data analysis

The soil seed flora was identified to species level with the assistance of Faculty members of Universidad Nacional Agraria (Nicaragua) and relevant literature (Salas, 1993). The standing vegetation (seedlings, saplings and mature trees) was also identified to species level. Density and vertical distribution of seeds in the soil as well as the density of seedlings were determined using simple mathematical calculations. Sorensen's similarity index (Krebs, 1999) was used to compare the similarity between the species composition of the soil seed bank and the above-ground vegetation (seedlings, saplings and mature trees) as well as between seedlings and the upper canopy using the following formula:

$$S_s = \frac{2a}{2a+b+c}$$

S_s(Sorensen's similarity coefficient), a (number of seed bank/seedling/sapling and adult tree species present in deciduous forest and gallery forest), b (number of seed bank/seedling/sapling and adult tree species present in the gallery forest but not in the deciduous forest), c (number of seed bank/seedling/sapling and adult tree species in the deciduous forest but not in the gallery forest). Sorensen's coefficient ranges from zero (no species in common) to 1.0 (identical set of species).

The spatial distribution of seeds and seedlings across the study site was analyzed using the standardized Morisita index, which is independent of population density and size (Krebs, 1999). First, Morisita's index (I_d) was calculated using the following formula:

$$I_d = Q\sum_{i=1}^{Q} X_i(X_i-1)/N(N-1)$$

Where X_i (the number of seeds/seedlings of a species in i subplots), Q (the number of subplots) and $N = \sum X_i$. Then two critical values for Morisita's index were calculated using the following formulae:
Uniform index =

$$M_u = \frac{\chi^2_{.975} - n + \sum x_i}{(\sum x_i) - 1}$$

Clumped index =

$$M_c = \frac{\chi^2_{.025} - n + \sum x_i}{(\sum x_i)}$$

Where $\chi^2_{.975}$ and $\chi^2_{.025}$ (values of chi-squared with (n-1) degrees of freedom that has 97.5% and 2.5% of the area to the right, respectively); X_i (Number of seeds/seedlings in subplot) i and n (Number of subplots). The standardized Morisita index (I_p) was then calculated with one of the following three formulae:

Photograph 3.
The evergreen gallery forest along the Río Escalante in Chacocente Wildlife Refuge, Nicaragua
Photo by Guillermo Castro-Marin.

1) $I_p = 0.5 + 0.5\left(\frac{I_d - M_c}{n - M_c}\right)$;

When $I_d \geq M_c > 1.0$,

2) $I_p = 0.5\left(\frac{I_d - 1}{M_u - 1}\right)$;

When $M_c > I_d \geq 1.0$, or

3) $I_p = -0.5\left(\frac{I_d - 1}{M_u - 1}\right)$;

When $1.0 > I_d > M_u$

The standardized Morisita index of dispersion ranges from -1 to +1 with 95% confidence limits at ± 0.5. A random pattern gives a value of zero, a clumped pattern is above zero and a uniform pattern below zero (Krebs, 1999). In the analysis of spatial patterns, species with at least two seeds or seedlings were considered.

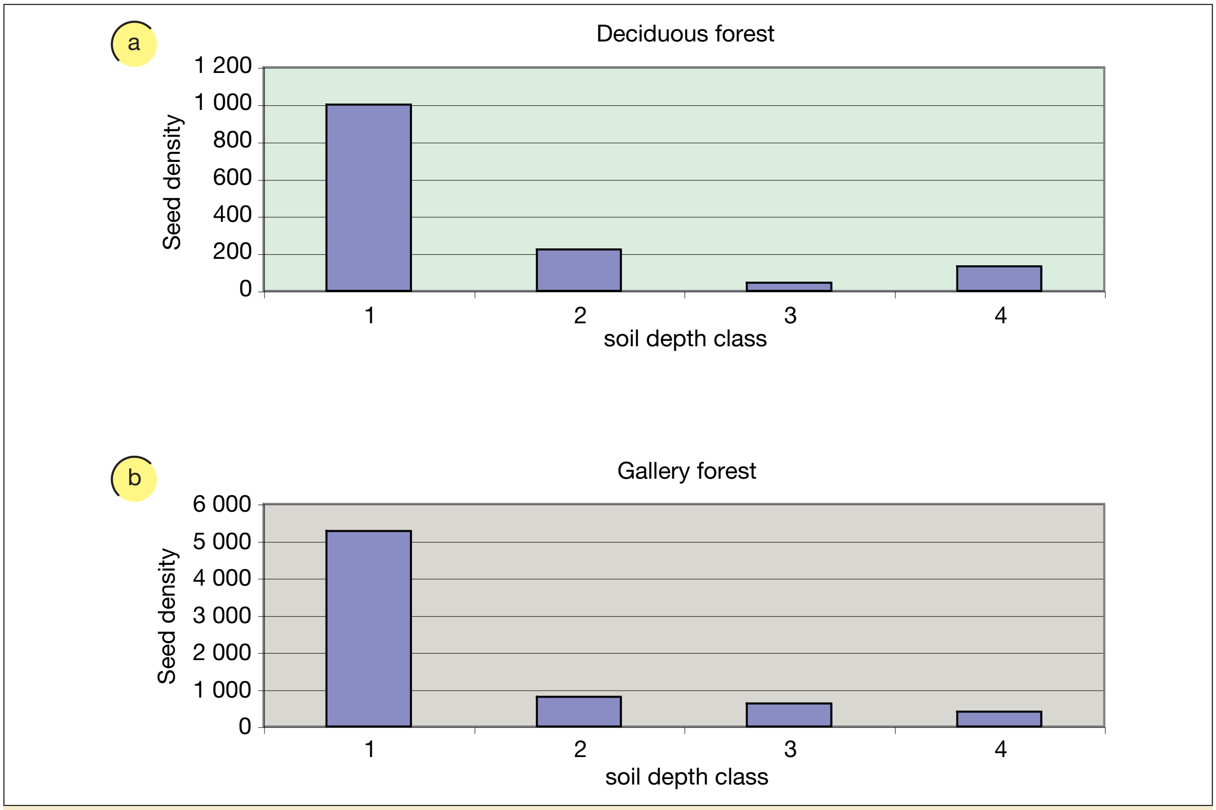

Figure 3.
Vertical distribution of seeds recovered from soil samples collected from deciduous (a) and gallery (b) forests. Chacocente Wildlife Refuge, Nicaragua.

Table 1.
Density (seeds/m^2), frequency and viability of seeds recovered from soil samples.

	Species	Family/Subfamily	LF**	Density	Frequency%	Viability
A	Dry deciduous forest					
	Allophylus psilospermus	Sapindaceae	T	333	24	20
	*Bixa orellanea**	Bixaceae	S	22	4	100
	Caesalpinia coriaria	Caesalpinioideae	T	22	4	100
	Canavalia sp.*	Caesalpinioideae	H	133	8	100
	Casearia tremula	Flacourtiaceae	T	22	4	0
	Cenchrus echinatus	Poaceae	G	22	4	0
	Centrosema sp.	Papilionoideae	L	67	8	0
	Chomelia speciosa	Rubiaceae	T	133	16	50
	Eleusine indica	Poaceae	G	67	4	0
	Hybanthus attenuatus	Violaceae	L	22	4	0
	Lysiloma divaricatum	Mimosoideae	T	244	20	0
	Myrospermum frutescens	Papilionoideae	T	44	8	0
	Paspalum sp.	Poaceae	G	67	12	0
	Stemmadenia obovata	Apocynaceae	T	89	12	75
	Tabernaemontana sp.	Apocynaceae	T	22	4	0
	*Tithonia rotundifolia**	Asteraceae	H	22	4	100
	*Trichilia hirta**	Meliaceae	T	67	8	100
B	Gallery forest					
	Achotocarpus nigricans	Achotocarpaceae	T	22	4	0
	Alvaradoa amorphoides	Simaroubaceae	T	2 511	48	19
	Apeiba tibourbou	Tiliaceae	T	111	16	0
	Bursera simarouba	Burseraceae	T	67	8	100
	Cenchrus echinatus	Poaceae	G	22	4	100
	*Chomelia speciosa**	Rubiaceae	T	556	36	28
	Coursetia elliptica	Papilionoideae	T	111	8	0
	Cucumis anguria	Cucurbitaceae	H	22	4	0
	Erythroxylum havanense	Erythroxylaceae	T	67	8	0
	Esenbeckia litoralis	Rutaceae	T	22	4	0
	Guazuma ulmifolia	Sterculiaceae	T	689	20	13
	Karwinskia calderonii	Rhamnaceae	T	178	24	13
	Luehea speciosa	Tiliaceae	T	1 289	28	26
	Phyllanthus amarus	Euphobiaceae	H	267	16	0
	Pithecellobium saman	Mimosoideae	T	22	4	0
	Priva lappulacea	Verbenaceae	H	156	4	0
	Sida acuta	Malvaceae	H	133	4	0
	Sida rhombifolia	Malvaceae	H	67	4	0
	*Simarouba glauca**	Simaroubaceae	T	511	16	17
	Spondias mombin	Anacardiaceae	T	22	4	0
	Tabernaemontana sp.	Apocynaceae	T	22	4	0
	Terminalia oblonga	Combretaceae	T	133	8	0
	Trichilia hirta	Meliaceae	T	67	8	0
	Waltheria americana	Sterculiaceae	H	22	4	0

* Seeds with physical dormancy
** LF = Life forms (T = trees, G = grass, H = herbaceous plants)

Results

Composition and density of the soil seed bank

The total number of species recovered from the soil samples collected in the deciduous forest was 17, representing trees, shrubs, herbs, grasses and climbers (table IA). Fabaceae made up the dominant family with five species, followed by Poaceae with three species. The total number of seeds obtained from all soil samples collected down to a depth of 12 cm was 63, corresponding to a total density of 1 400 seeds/m², and a viable seed density of 466 seeds/m². Trees made up a major component of the soil seed bank, and the most abundant species in the soil seed flora were *Allophylus psilospermus* and *Chomelia speciosa* with 24% and 16% of frequency of occurrence in the sample plots, respectively. In the gallery forest, the total numbers of species and seeds recovered from all soil samples were 24 and 319, respectively. Trees had the highest number of species (17) and seeds (288), accounting for 90% of the total seed density (7 088 seeds/m²) and 98% of the total viable seed density (1 257 seeds/m²), while the remaining 10% was distributed between herbs and grasses (table IB). The tree species with significant representation in the soil seed bank were *Alvaradoa amorphoides*, *Chomelia speciosa, Luehea speciosa, Guazuma ulmifolia*, and *Simarouba glauca,* with a frequency of 48, 36, 28, 20 and 16% respectively.

The seeds of most species recovered from the deciduous forest did not germinate and the cutting test also revealed that they were dead (table IA). Some species, such as *Chomelia speciosa* and *Stemmadenia obovata*, had a high proportion of viable seeds, as determined by the cutting test. In contrast, some seeds of *Allophylus psilospermus* had undifferentiated embryos when closely examined after dissection. Species with hard seed coats, such as *Canavalia* sp., responded positively to germination after mechanical scarification. It should be noted that most of the species with 100% seed viability had one or two seeds in total. A similar trend was observed for seeds recovered from soil samples taken from the gallery forest, where only eight species showed some germination (table IB). After dissection, most of the seeds appeared to be empty or had dead embryos, for example *Simarouba glauca*.

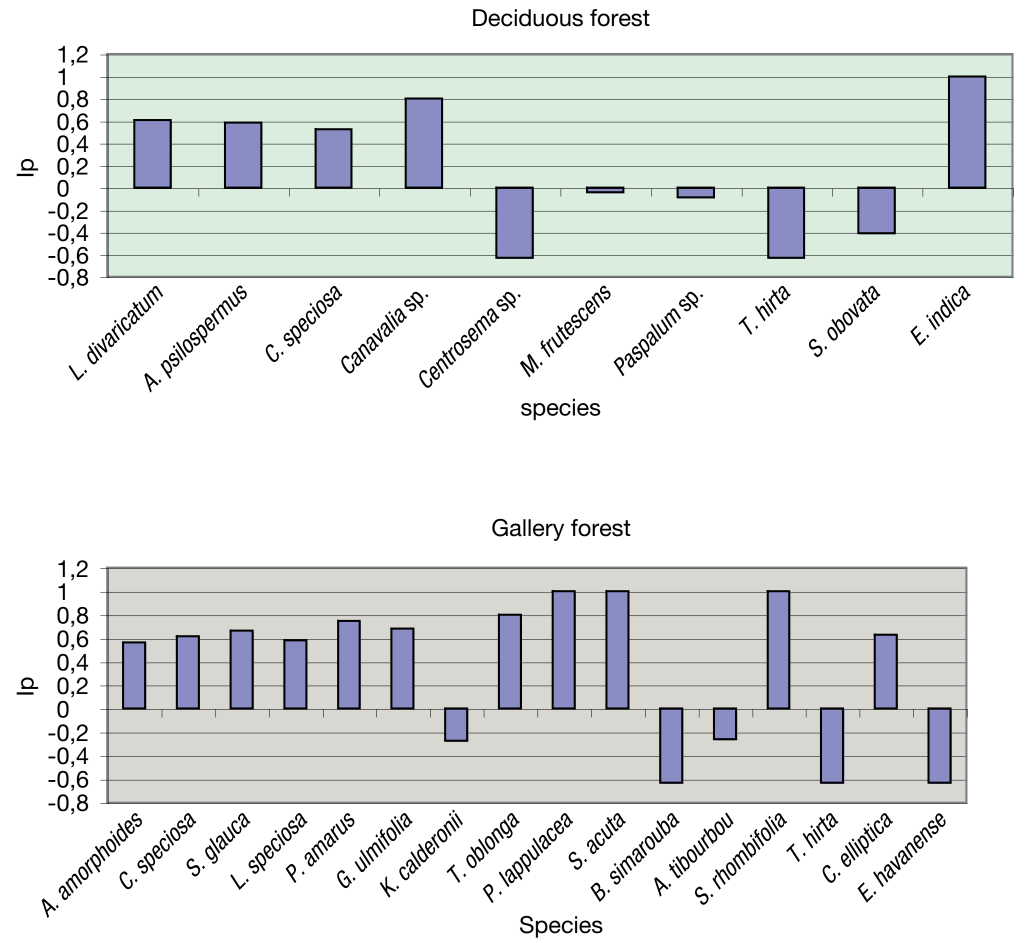

Figure 4.
Spatial distribution of soil seed banks in the dry deciduous and gallery forests. Chacocente Wildlife Refuge, Nicaragua (Ip = Standardized Morisita's index).

Spatial distribution of the soil seed bank

The vertical distribution of seeds recovered from soil samples collected from the deciduous forest showed high density in the litter layer (0-3 cm) and a gradual decrease in density with increasing depth up to 9 cm and a slight increase afterwards (figure 3a). Of the total number of seeds recovered, 71% were found in the litter layer and 16%, 3% and 9% in the three successive soil layers, respectively. Although the seeds of most species were entirely confined to the litter layer, those of a few species were represented at different depths, albeit in small numbers. The vertical distribution of seeds recovered from soil samples in the gallery forest showed a similar decreasing trend with increasing depth (figure 3b). From the total number of seeds recovered, 74% were found in the litter layer and 11%, 9% and 6% in the three successive soil layers. Most of the seeds of some species were entirely confined to the litter layer while some species were distributed through all depths, although in small numbers. The horizontal distribution of the soil seed bank in the deciduous forest showed both clumped and uniform patterns, depending on the species (figure 4). The five species with a clumped distribution were *Lysiloma divaricatum, Allophylus psilospermus, Chomelia speciosa, Canavalia* sp. and *Eleusine indica*, which also had a fairly high frequency of occurrence in the plots compared to the remaining five species with uniform distribution. In the gallery forest, the majority of the species displayed a clumped distribution. However, a few species, such as *Karwinskia calderonii, Bursera simarouba* and *Trichilia hirta*, showed a uniform distribution (figure 4).

Table 2.
Density of naturally regenerating seedlings (individuals/ha) and their frequency of occurrence in sample plots.

	Species	Family/Subfamily	Density	Frequency
A	Dry deciduous forest			
	Acacia costaricencis	Mimosoideae	200	8
	Allophylus psilospermus	Sapindaceae	50	4
	Allophylus racemosus	Sapindaceae	50	4
	Bursera simarouba	Burseraceae	50	4
	Caesalpinia exostema	Caesalpinioideae	150	12
	Capparis pachaca	Capparidaceae	500	32
	Casearia corymbosa	Flacourtiaceae	200	12
	Casearia tremula	Flacourtiaceae	150	8
	Coccoloba caracasana	Polygonaceae	50	4
	Cordia gerascanthus	Boraginaceae	800	20
	Diospyrus nicaraguensis	Ebenaceae	50	4
	Esenbeckia litoralis	Rutaceae	150	12
	Guarea glabra	Meliaceae	50	4
	Gyrocarpus americanus	Hernandiaceae	50	4
	Haematoxylon brasilleto	Caesalpinioideae	50	4
	Jacquinia aurantiaca	Theophrastaceae	1 400	36
	Lonchocarpus minimiflorus	Papilionoideae	900	20
	Myrospermum frutescens	Papilionoideae	50	4
	Pithecellobium dulce	Mimosoideae	50	4
	Pithecellobium platylobum	Mimosoideae	50	4
	Simarouba glauca	Simaroubaceae	50	4
	Spondias mombin	Anacardiaceae	50	4
	Stemmadenia obovata	Apocynaceae	700	12
	Thounidium decandrum	Sapindaceae	350	20
	Zizyphus guatemalensis	Rhamnaceae	100	8
B	Gallery forest			
	Acacia costaricencis	Mimosoideae	50	4
	Calycophyllum candidissimum	Rubiaceae	100	8
	Capparis pachaca	Capparidaceae	500	32
	Casearia corymbosa	Flacourtiaceae	50	4
	Coccoloba caracasana	Polygonaceae	50	4
	Guaiacum sanctum	Zigophyllaceae	300	24
	Gyrocarpus americanus	Hernandiaceae	1 900	36
	Karwinskia calderonii	Rhamnaceae	50	4
	Pithecellobium saman	Mimosoideae	650	16
	Randia aculeata	Rubiaceae	650	36
	Senna atomaria	Caesalpinioideae	50	4
	Simarouba glauca	Simaroubaceae	750	28
	Spondias mombin	Anacardiaceae	150	8
	Stemmadenia obovata	Apocynaceae	50	4
	Thounidium decandrum	Sapindaceae	900	20
	Trichilia moschata	Meliaceae	350	20
	Zizyphus guatemalensis	Rhamnaceae	50	4

Species composition and density of seedling populations

The total number of species recorded from the dry deciduous forest was 25 (table IIA). Most of the species belonged to the Fabaceae (Papilionoideae, Mimosoideae and Caesalpinioideae). The total seedling density was 6250 individuals/ha and the mean was 250 ± 69 individuals/ha. The species with 10 or more individuals were *Stemmadenia obovata, Lonchocarpus minimiflorus, Cordia gerascanthus, Capparis pachaca* and *Jacquinia aurantiaca*. In addition, these species had the highest frequency of occurrence in the plots surveyed. In the gallery forest, a total of 17 species and 132 individuals were recorded (table IIB). The families most represented were Fabaceae, Rubiaceae and Rhamnaceae with three, two and two species, respectively. The total density was 6600 individuals/ha with a mean of 388 ± 118 individuals/ha. The species most represented were *Simarouba glauca, Pithecellobium saman, Randia aculeata, Thounidium decandrum, Capparis pachaca* and *Gyrocarpus americanus*. Similarly, these species were more frequent in the plots surveyed.

Spatial distribution of seedling populations

The spatial distribution of naturally regenerated seedlings in the deciduous forest showed both clumped and uniform distributions, depending on the species (figure 5). Of the 12 species that had more than one seedling, six exhibited a clumped distribution (photograph 4) and the remaining six displayed a uniform pattern of distribution. Similarly, the seedling population of four species from the gallery forest exhibited a clumped distribution while six species displayed a uniform pattern (figure 5).

Photograph 4.
Patchiness in the regeneration of seedlings of some species resulting in clumped distribution in dry deciduous forest of the Chacocente Wildlife Refuge, Nicaragua
Photo by Guillermo Castro-Marin.

Similarity between the soil seed banks, seedlings and the above-ground vegetation

Within each forest community, similarity between the soil seed flora and the seedling layer was low (table III). In the deciduous forest, four species, namely *Allophylus psilospermus, Casearia tremula, Myrospermum frutescens and Stemmadenia obovata,* were found in both the soil seed bank and the seedling layer. The soil seed bank and the seedling layer in the gallery forest also had four species in common: *Karwinskia calderonii, Pithecellobium saman, Simarouba glauca and Spondias mombin*. The same trend was observed when comparing the species composition of the soil seed bank and saplings/trees. Species in common between the soil seed bank and saplings/trees were *Allophylus psilospermus*, *Casearia tremula*, *Caesalpina coriaria*, *Chomelia speciosa*, *Lysiloma divaricatum*, *Myrospermum frutescens* and *Stemmadenia obovata* in the deciduous forest, and *Achotocarpus nigricans, Bursera simarouba, Guazuma ulmifolia, Karwinskia calderonii, Pithecellobium saman, Simarouba glauca, Spondias mombin, Terminalia oblonga* and *Trichilia hirta* in the gallery forest. The similarity in species composition between the seedling and sapling/tree layers was relatively higher in the deciduous than the gallery forest (table III). It was found that the understory and the overstory had 22 species in common in the deciduous forest and 15 species in the gallery forest.

Comparisons between forest communities showed low similarity in soil seed flora (table III). The species of soil seed flora that were common to both forest communities were *Cenchrus echinatus, Chomelia speciosa, Tabernaemontana* sp. and *Trichilia hirta*. Similarity in the species composition of the seedling layer between the two forest communities was relatively higher than for soil seed flora. The common species were: *Acacia costaricensis, Capparis pachaca, Casearia corymbosa, Coccoloba caracasana, Gyrocarpus americanus, Simarouba glauca, Spondias mombin, Stemmadenia obovata, Thounidium decandrum* and *Zizyphus guatemalensis.*

Discussion

Soil seed banks

Results from this study revealed that most plant species in the dry deciduous and gallery forests accumulate small quantities of viable seeds in the soil. The lack of reserves of long-lived seeds in the soil of tropical dry forests can be attributed to a number of factors. First, the seeds of several woody species are large with a high moisture content, which is indicative of adaptation to immediate germination and seedling establishment under the forest canopy (Teketay, 1997; Wassie & Teketay, 2006). By immediate germination and establishment, many trees and shrubs form large seedling populations in the forest. This is evidenced by the low similarity found in this study (19% for both dry deciduous and gallery forests) between the seed bank and the seedling bank. Secondly, those seeds that do not germinate are consumed by predators or succumb to attack by micro-organisms (Thompson, 2000). We observed exit holes made by emerging larvae or adult insects in seeds of *Myrospermum frutescens* and *Chomelia speciosa* collected from the deciduous forest and in seeds of *Chomelia speciosa*, *Simarouba glauca*, *Spondias mombin* and *Coursetia elliptica* collected from the gallery forest. Several species of *anobiid* beetles feeding regularly on the fruits and seeds of some plant species, such as *Guazuma ulmifolia* and *Pithecellobium saman*, have been observed (Janzen, 1988) Thirdly, consumption of flowers and developing ovules at an early stage of reproductive growth influences the build-up of the soil seed bank (Thompson, 2000). The number of viable seeds may be reduced by pre-dispersal predation, such as attacks by larvae on still soft full-sized seeds of *Cedrela odorata* (Janzen, 1988). Our findings concur with previous studies in several primary or secondary forest formations in the tropics (Teketay & Granström, 1995; Wijdeven & Kuzee, 2000).

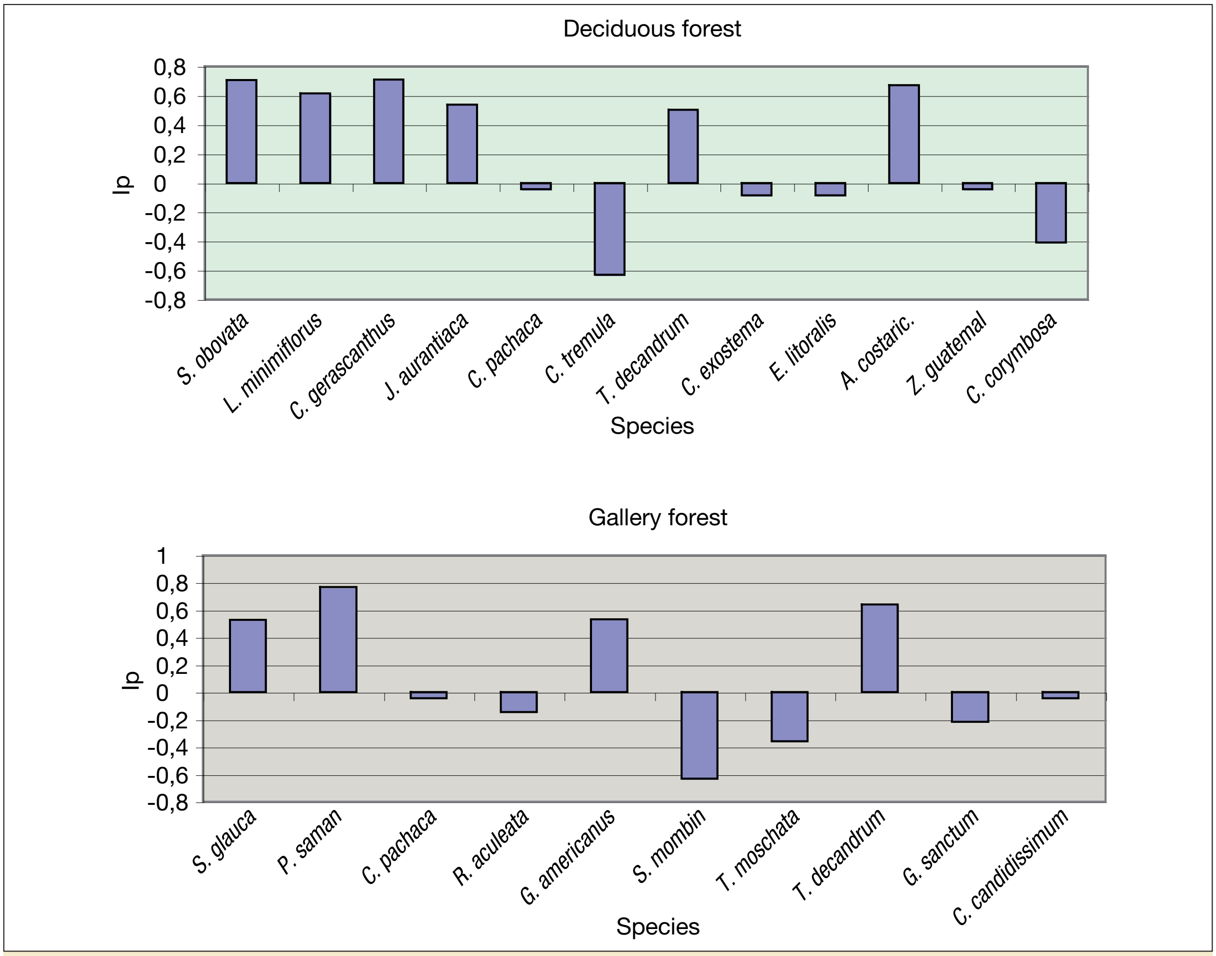

Figure 5.
Spatial distribution of seedling populations in the dry deciduous and gallery forests. Chacocente Wildlife Refuge, Nicaragua (Ip = Standardized Morisita's index).

It is interesting to note that the seeds of four species from the deciduous forest and two species from the gallery forest exhibit physical dormancy, and germinate fairly well after mechanical scarification. These species possibly form a persistent soil seed bank. Dormancy favours the accumulation of seeds in soils (Teketay & Granström, 1995; Wassie & Teketay, 2006) and is selected for in most tropical dry forest species in response to long dry seasons and unreliable rainy periods (Baskin & Baskin, 1998). In viable non-dormant seeds that accumulate in fairly large numbers in the soil, dormancy may be induced if the seeds are dispersed under dense canopy or buried in the soil (Teketay & Granström, 1995).

The spatial distribution, both vertical and horizontal, of seeds of different species and forest communities varied greatly. The spatial distribution of seeds in the soil is primarily a function of the dispersal process. The number of seeds that falls on a particular area depends on a multitude of factors, such as height, distance and concentration of the seed source, seed dispersal, nature and activity of dispersal agents and spatial heterogeneity of the parent plants in the field (Shaukat & Siddiqui, 2004). These variations may reflect differences among species in terms of seed longevity in the soil, modes of seed dispersal and subsequent movement, seed predation, and probably differences in the slope of the landscape and local edaphic conditions where the seeds land. Similar results have been reported from studies made in other dry forest formations (Teketay & Granström, 1995; Senbeta & Teketay, 2002).

Similarity in the species composition of the soil seed bank and the standing vegetation was low for both dry deciduous (20%) and gallery (25%) forests. Several studies have shown a similar pattern of dissimilarity between the seed bank and standing vegetation (Teketay & Granström, 1995; Senbeta & Teketay, 2002), suggesting that regeneration of woody species from seeds in these tropical dry forests would be hampered by the removal of mature individuals in the standing vegetation. This, in turn, implies that restoration of tropical dry forests would be difficult and slow to accomplish if they are severely degraded.

Table 3.
Comparison of species similarity, based on Sorensen's index, between soil seed flora, seedlings and above-ground vegetation (saplings and mature trees) within and between forest communities.

Within forest community	Deciduous	Gallery
Soil seed bank vs. seedling layer	0.19	0.19
Soil seed bank vs. sapling/tree layer	0.20	0.25
Seedling vs. sapling/tree layers	0.58	0.46
Between forest communities	Gallery forest	
Deciduous forest	Soil seed bank	Seedling layer
Soil seed bank	0.19	
Seedling layer		0.47

Seedling populations

The seedling populations in the deciduous and gallery forests were represented by 25 and 17 species, respectively. Fabaceae had the largest number of species in the deciduous forest and Fabaceae, Rubiaceae and Rhamnaceae in the gallery forest. Fabaceae make up the dominant tree and shrub family in most dry Neotropical forests (Sabogal & Valerio, 1998; Gillespie *et al.*, 2000), and Rubiaceae in gallery forests (González *et al.*, 2006). In the deciduous forest, five species, namely *Capparis pachaca*, *Cordia gerascanthus*, *Jacquinia aurantiaca*, *Lonchocarpus minimiflorus* and *Stemmadenia obovata* had ≥ 500 seedlings/ha. Similarly, *Gyrocarpus americanus*, *Thounidium decandrum*, *Simarouba glauca*, *Randia aculeata Pithecellobium saman* and *Capparis pachaca* had seedling densities ≥ 500 individuals/ha. Except for *S. obovata*, *Pithecellobium saman* and *Simarouba glauca*, other species were not encountered in the soil seed bank. This indicates that seedling banks could be a strategy for the persistence of these species in the community. A similar finding was reported from a dry Afromontane forest where some species completely lack long-lived reserves of seeds in the soil (Teketay, 1997). Many climax species are shade tolerant, germinating and becoming established in the shaded understory, thus build seedling banks. For example, *L. minimiflorus* regenerated abundantly on gentle and steep slopes under partial shading (photograph 5) in the dry forests of Nicaragua (Castro-Marin, 2005). The most suitable environmental conditions for the germination of *Calycophyllum candidissimum* were those with no direct sunlight (Morales, 2004). Some species respond positively to gaps, as their seeds require light to germinate (pioneer species). *Tabebuia ochracea*, *Gyrocarpus americanus* and *Lysiloma divaricatum* regenerate well under canopy gaps (Morales, 2004). Similarly, abundant regeneration of

G. americanus was observed in gaps that are completely exposed to direct sunlight on our study (GONZALEZ, 2005).

The spatial distribution of seedlings varies from species to species in both deciduous and gallery forests. Clumped or aggregated spatial patterns are very common among species in tropical forests (HUBBELL, 1979; CONDIT *et al.*, 2000). Poor dispersal of propagules and limitations to recruitment (soil nutrients, light, moisture, etc) may result in such patterns (BUNYAVEJCHEWIN *et al.*, 2003). Consequently, resource-based niche differentiation results in habitat specialization, so that different species are best suited to different habitats, where they are competitively dominant and relatively more abundant. The distribution pattern of trees is affected by numerous biotic and abiotic factors and their interaction, but topography is a major physical factor which affects the composition, growth, and distribution of tropical forests (ENOKI & ABE, 2004). The refuge (study site) has an irregular landscape with altitudes increasing inland from sea level to ca. 300 m above sea level (ANONYMOUS, 2002). In the deciduous forest, this irregularity of the relief can be clearly observed. In contrast, gallery forests occur on flat land. Different slope gradients may have positive or negative effects on seedling establishment. *Haematoxylon brasiletto* occurred mainly on flat land (TÖRNQVIST, 2004), and was almost absent at higher altitudes, while *C. candidissimum* mainly appeared in fairly undisturbed lowland forests, close to the coast. Although this species was represented in the deciduous forest, close to the coast, higher densities of saplings and mature trees of *C. candidissimum* were found in the gallery forest, where a flat relief is predominant. On the other hand, optimal conditions for the establishment of *L. divaricatum, T. ochracea* and *G. americanus* were on steep slopes (MORALES, 2004).

For both forest communities, the similarity in species composition between the seedling population and the overstory vegetation was low. This lack of correspondence, among others, may be caused by biotic factors such as herbivory, or by abiotic factors such as tree fall. When comparing the understory vegetation of the gallery and deciduous forests, only a few species that were present in the gallery forest were represented in the deciduous forest, which could be attributed to specific niche requirements of the constituent species.

Photograph 5.
Regeneration under partial shading in dry deciduous forest of the Chacocente Wildlife Refuge, Nicaragua
Photo by Guillermo Castro-Marin.

Conclusion:

implications for restoration

Results from this study suggest a paucity of soil seed banks in both forest communities, so that soil seed banks may not be an effective propagule donor for natural species regeneration. In addition, analysis of the spatial pattern of soil seed banks revealed patchiness, which in turn has significant consequences for the distribution of naturally regenerating individuals across the landscape. Although some species regenerated abundantly in both forest communities, the majority were less well represented. Restoration measures should therefore be introduced to assist the natural regeneration process, such as direct seeding, planting seedlings of less abundant species and manipulation of the sites to improve site-related factors for seedling establishment and survival. As this study did not attempt to explain factors that cause low seed density in the soil, further study is recommended to describe rates of predation, dispersal mechanisms, seed rain and germination ecology.

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