

23 Soil Seed Bank Changes Along a Forest Interior–Edge–Pasture Gradient in a Costa Rican Montane Oak Forest

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23.1 Introduction

Past tropical deforestation has given rise to landscape mosaics of old-growth fragments, successional forest patches, crop fields and pasturelands (Laurance et al. 1997; Chap. 16). Differently shaped and sized patches are separated from each other by a variety of edges. At those edges, microclimatic variables such as light intensity and duration, relative humidity, air temperature, and soil factors differ significantly over short distances (Lovejoy et al. 1983; Williams-Linera 1990; José et al. 1996; Laurance et al. 1997; Chap. 19). As a result, plant community structure and composition change along gradients from the tropical forest interior, across the edge, into non-forest vegetation (Lopez de Casenave et al. 1995; José et al. 1996; Oosterhoorn and Kappelle 2000; Chaps. 13 and 19). The importance of soil seed banks as sources for tree recruits at such edges has long been recognized (e.g., Young et al. 1987; Garwood 1989; Parker et al. 1989; Teketay and Granström 1995; Quintana-Ascencio et al. 1996; Dalling and Denslow 1998; Cubiña and Aide 2001; Chap. 19).

However, since most studies have been conducted in tropical lowlands, it still remains unclear to what extent these trends fully apply to patchy landscapes in tropical montane forest regions. This is of special interest, recognizing that harsh environmental conditions on tropical mountains reduce forest recovery rates significantly (Ewel 1980). For instance, Kappelle et al. (1995, 1996, and Chap. 17) estimate that Costa Rican montane oak forests recovering from slash-and-burn and subsequent grazing will need at least about a century to return to their old-growth state, in terms of non-epiphytic structure and species composition – assuming forest seed sources are nearby. For this reason, we studied the size and composition of soil seed banks along a montane oak forest interior–edge–pasture gradient in Costa Rica. The insights

gained will be particularly useful to conservation efforts directed at the ecological restoration of fragile montane oak forests in the Neotropics (Holl and Kappelle 1999).

23.2 Study Area

The study was carried out in the montane cloud forest zone (2,300–2,800 m a.s.l.) of the Los Santos Forest Reserve (Dota County) and Tapantí-Río Macho National Park (El Guarco County) in the western part of Costa Rica's Cordillera de Talamanca. Average annual rainfall is 2,100–3,000 mm, and average annual temperature varies in the range 12–14.5 °C, depending on altitude. The dry season lasts from early January to late April (Herrera 1986). Soils are derived from volcanic ash, are acid (pH 3.5–5.5), and moderately fertile. Natural vegetation is 30–50 m tall, evergreen broad-leaved oak forest (Kappelle 1996; Chap. 10). Since the early 1950s, conversion of the region's oak forests into grasslands and croplands has led to a complex landscape mosaic (Helmer 2000). After abandonment of low-production pasturelands in the late 1970s and early 1980s, stands of successional forests have developed along edges of old-growth forests and productive pastures (Kappelle and Juárez 1995; Chap. 30).

23.3 Methods

23.3.1 Site Selection and Transect Establishment

From a set of black-and-white aerial photographs (1992; scale 1:60,000), we selected four 10-ha old-growth montane oak forest fragments bordering patches of grass-dominated, 30±5 year old pastures: Alto Roble de Copey de Dota (AR), La Damita del Guarco (LD), Providencia de Dota (PR), and San Gerardo de Dota (SG). Patches were located at 09°34'–09°42'N, 83°50'–83°55'W, and 2,380–2,710 m altitude. At each site, a 150-m-long transect was laid out, running from the forest interior (–50 m) through the abrupt edge (0 m) into the exterior (i.e., pasture; +100 m), perpendicular to the forest edge. As recommended by Fraver (1994) and José et al. (1996), the edge was delimited by the bases of bordering mature forest tree stems. Changes in standing vegetation structure and terrestrial vascular plant species composition along transects are published elsewhere (Oosterhoorn and Kappelle 2000).

23.3.2 Soil Seed Bank Sampling and Seed Germination

Topsoil samples were collected along four transects at a depth of 0–5 cm over an area of 35×35 cm at distance intervals of 5, 15, 30 and 50 m from the forest–pasture edge into the old-growth forest, and at 5, 15, 30, 50, 75 and 100 m from the edge into the pasture. An additional sample was taken at the edge itself, i.e., at a distance of 0 m, reaching 11 samples per transect and 44 samples in total. Samples were processed within 2–3 days of collection, and placed in an on-site (2,630 m altitude) greenhouse with a transparent plastic roof allowing for 60–80 % total sunlight. Following Thompson et al. (1996), each sample was thoroughly mixed, evenly divided, and spread in a 2.5-cm layer over two round 30-cm-diameter seed trays containing a layer of sterilized soil covered with a 1-cm layer of seed-free gray sand. Eight trays were filled only with sterilized soil and were used as controls to detect any seed contamination. Trays were hand-watered daily. Seedling mortality was negligible (<1 %).

23.3.3 Seedling Emergence Monitoring

Seedling emergence was monitored weekly over a 6-month period (April–September 1996). Although the soil was not checked for seeds that remained without germination in the period following the monitoring phase, seedling emergence after 6 months was extremely low. Germinated seedlings were counted, and carefully removed immediately after identification or after a morphologic species code was confidently assigned. Morphospecies were subsequently identified in the herbarium. Seedlings were removed to reduce shading and competition. Collected specimens were identified by specialists and deposited at herbaria (CR, INB, USJ). Seedling species were classified with respect to their life form in trees, shrubs, herbs (including grasses, sedges and forbs) and climbers. Species were categorized according to their dispersal mode (anemochorous, zoochorous, autochorous, hydrochorous, or unknown), on the basis of data presented by Wijtzes (1990), expert knowledge, and own observations. Ferns were excluded from all data analyses.

23.3.4 Quantitative Data Analysis

Counts data showed a Poisson distribution and were log transformed [$\log(n+1)$] to normalize variance. Data were analyzed with a one-way or two-way ANOVA to test for differences between distance from edge and site location. Site–habitat interactions were not analyzed, as only one transect was run per site. Levels of seed bank diversity of both forest and pasture soils were estimated using Shannon–Wiener's diversity index:

$$H' = -\sum (p_i) \cdot (\log_2 p_i)$$

in which p_i is the proportion of emerged seedlings found in the i th species in a sample (Magurran 1988). Similarity between pairs of soil seed samples was assessed using Sørensen's quantitative similarity index for presence-absence data (Magurran 1988). Applying the same similarity index, soil seed bank composition was compared to seed plant species composition of standing vegetation for each sample distance along the 150-m-long axis. For this purpose, we used presence-absence data for standing vegetation in 10×10 m quadrates, as provided by Oosterhoorn and Kappelle (2000).

23.4 Seedling Abundance and Diversity

During 6 months of monitoring, in all 4,940 seedlings were counted of which 97 % was identified to species level. A total of 1,203 emerged from forest soil, and 3,737 from pasture soil samples. Seedlings per sample ranged from eight (forest) to 462 (pasture). Average density was 491 seedlings/m² for forest samples and 1,271 for pasture samples. The number of seeds found in pasture samples was significantly higher than that in forest samples ($P < 0.01$).

Seedlings belonged to 80 species (68 genera, 37 families), Asteraceae (16 species) and Solanaceae (eight species) being most important. *Physalis* and *Solanum* had three species each. Half of all 4,940 seedlings belonged to only two genera: *Hydrocotyle* (1,446 seedlings, 29.3 %) and *Gnaphalium* (1,030 seedlings, 20.9 %). Species were classified into nine pioneer trees (*Bocconia*, *Brunellia*, *Malva*, *Monnina*, *Oreopanax*, *Sida*, *Vaccinium*, *Viburnum* and *Wigandia*), 17 shrubs, 48 herbs and six climbers. Trees represented 0.3 % of all seedlings, whereas shrubs totaled 20.0 %, herbs 76.8 %, and climbers less than 0.01 %. Pastures were significantly richer in herb seedlings than were forests ($P < 0.001$). Shannon-Wiener's diversity index H' ranged from 0.41 in pasture to 3.5 in forest. A lower seedling per species ratio was observed toward the end of the 6-month monitoring period.

23.5 Seed Dispersal Strategies

A total of 3,849 seedlings belonged to 36 species with an anemochorous (wind) dispersal strategy (655 seedlings in forest samples, and 3,194 in pasture), whereas 585 seedlings in 22 species were zoochorous (bird and/or mammal dispersed; forest: 467; pasture: 118), and another 506 seedlings in 22 species had an unknown or different dispersal mode, e.g., autochorous or

hydrochorous (forest: 81; pasture: 425). Animal-dispersed seeds were significantly more abundant ($P<0.001$) in forest samples than in pasture, whereas wind-dispersed seeds were significantly more important ($P<0.001$) in pasture than in forest.

23.6 Changes Along the Forest Interior–Edge–Pasture Gradient

Seed density increased from the forest interior (490.8 germinated seeds per m^2) across the edge into the pasture (1,270.5 seeds per m^2) for all species, and also for wind-dispersed species alone (Fig. 23.1A–C). A *Hydrocotyle*-dominated seedling peak occurred in the pasture at 30 m from the edge. Forest soil samples ($n=20$; 55 species) and pasture soil samples ($n=24$; 55 species) did not show any significant difference in species richness (# of species per sample). Species richness did not change significantly along the forest interior–edge–pasture gradient (Fig. 23.1D–F). The average number of zoochorous seed plant species per sample, however, was significantly higher in the forest than in the pasture ($P<0.001$), and the average number of anemochorous species per sample was higher in pasture than in forest ($P<0.05$). Compared to forest samples, the seedling/species ratio for all species combined was significantly higher in pasture soil samples ($P<0.01$; Fig. 23.1G).

Similarity between pairs of forest soil seed bank samples was higher (0.48–0.66) than that between pairs of pasture samples (0.32–0.56; Table 23.1), indicating a greater variety in species compositions of pasture soil seed banks. Although soil seed banks (this study) did not reflect standing vegetation (Oosterhoorn and Kappelle 2000) very highly, soil seed bank composition was significantly more similar to the standing floristic composition in pastures than in forests (Table 23.2): mean Sørensen's similarity index $C_s \pm 1 \text{ SE} = 0.0175 \pm 0.05$ in forest, and 0.065 ± 0.014 in pastures; unpaired t test: $t = -2.68$, $\text{df} = 8$, $P = 0.028$. The mean number ($\pm 1 \text{ SE}$) of species shared by standing vegetation in 100- m^2 quadrats and associated soil seed bank was 2.30 ± 0.25 .

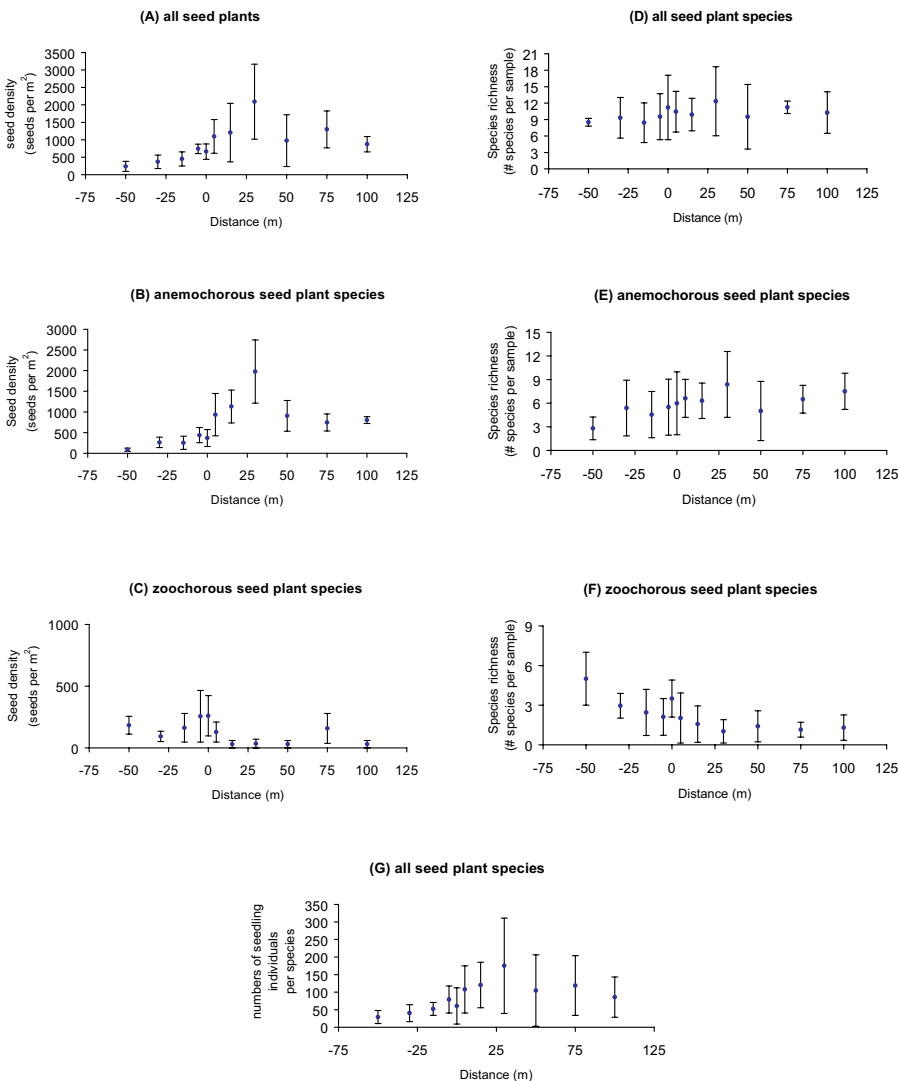


Fig. 23.1A–G. Seed density, species richness, and seedling number measured per distance unit along the forest interior–edge–pasture gradient for seed plant species that emerged from the soil seed bank samples. **A** Seed density ($n=4$; # of germinated seeds per m²; mean and SD) for all species. **B** Seed density for anemochorous species only. **C** Seed density for zoochorous species only. **D** Species richness ($n=4$; # of species per sample; mean and SD) for all species. **E** Species richness for anemochorous species only. **F** Species richness for zoochorous species only. **G** Seedling numbers per species for all species ($n=4$; mean and 1 SE)

Table 23.1. Sørensen’s similarity index (C_s) values for pairs of forest soil seed bank samples, and for pairs of pasture soil seed bank samples at four sampled transect sites in Costa Rica’s montane oak forest–pasture zone (see main text for full names and locations of transect sites AR, LD, PR and SG)

	Forest soil samples				Pasture soil samples			
	AR	LD	PR	SG	AR	LD	PR	SG
AR	–	0.50	0.66	0.48	–	0.32	0.41	0.56
LD		–	0.56	0.59		–	0.42	0.38
PR			–	0.63			–	0.53
SG				–				–

Table 23.2. Sørensen’s similarity index (C_s) values for pairs of sampled soil seed bank (this study) and standing vegetation (census data from Oosterhoorn and Kappelle 2000) per distance unit along the forest interior–edge–pasture gradient for four sampled transect sites in Costa Rica’s montane oak forest–pasture zone. The edge sample at a distance of 0 m was excluded from this analysis

Dist. (m)	Forest				Edge 0	Pasture					
	50	30	15	5		5	15	30	50	75	100
AR	0.15	0.04	0.05	0.12	–	0.35	0.11	0.50	0.11	0.20	0.77
LD	0.04	0.04	0.03	0.03	–	0.07	0.22	0.13	0.00	0.13	0.33
PR	0.06	0.05	0.07	0.12	–	0.17	0.18	0.08	0.17	0.37	0.33
SG	0.00	0.00	0.00	0.11	–	0.13	0.11	0.25	0.18	0.24	0.24
Mean	0.06	0.03	0.04	0.10	–	0.18	0.16	0.24	0.12	0.24	0.42
1 SE	0.03	0.01	0.01	0.02	–	0.06	0.03	0.09	0.04	0.05	0.12

23.7 Conclusions

Mean soil seed densities for this study’s forest and pasture are within ranges known from tropical lowland soil seed banks (150–900 seeds per m² for forest, and 370–7,623 for pastures; Garwood 1989), and similar to values for Colombian cloud forest (Giraldo and Uribe 1994). Soil seed bank species richness did not change significantly along the distance gradient, though it does along a Mexican lowland maize cropland–edge–forest gradient (Quintana-Ascencio et al. 1996). Richness was lower than in other studies (Williams-Linera 1993), possibly due to the relatively short monitoring period of the present study (see also Chap. 19). Species that need a longer period to successfully germinate may not have been recorded (Brown 1992). Furthermore, as it was not possible to spread the soil samples in very thin layers over the trays, an underestimation of the actual seed bank size and composition may have occurred

(Brown 1992; Dalling et al. 1997). Proportions of shrub and herb seedlings in forest soil samples were relatively high in comparison to known ranges (Garwood 1989).

In tropical lowland forests, seed dispersal by animals is much more important than wind dispersal (Howe and Smallwood 1982; Walker and Neris 1993; Chaps. 13, 18, 19 and 26). The contrasting importance of wind dispersal in this tropical montane study is probably due to the high number of herbs of temperate origin, such as *Arenaria*, *Conyza*, *Gnaphalium*, *Hieracium*, *Holcus*, *Plantago*, *Rumex*, *Senecio*, *Sonchus* and *Valeriana* (Kappelle et al. 1992). The dominance of wind-dispersed seeds we recorded in forest soils is known to occur in many tropical forests (Young et al. 1987; Aide and Cavalier 1994; Quintana-Ascencio et al. 1996; Dalling and Denslow 1998). The large proportion of wind-dispersed herb seeds in both forests and pastures is consistent with population dynamics theory stating that *r*-strategists tend to produce larger quantities of small, light seeds that are better protected against predation and can form long-lived soil seed banks (Garwood 1989; de Steven 1991). In the present study, soil seed banks did not closely reflect standing vegetation, particularly in forest samples. This implies that standing vegetation is not a good proxy for soil seed banks in these forests.

Dedication We dedicate this chapter to the late Menno Oosterhoorn, friend and colleague, who whole-heartedly supported our fieldwork and data analysis in the late 1990s.

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