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Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil¹

Karen D. Holl²

Center for Conservation Biology, Stanford University, Stanford, California 94305 U.S.A.

ABSTRACT

Vegetation, seed rain, seed germination, microclimate, and soil physical and chemical parameters were measured in a recently abandoned pasture and adjacent primary rain forest in southern Costa Rica. The goal of this study was to assess the importance of these factors in limiting forest regeneration in abandoned pastures. Seed rain of animal dispersed species decreased dramatically in the pasture >5 m from the forest/pasture edge; fewer wind dispersed seeds fell in the pasture than in the forest, but the difference was much less than for animal dispersed seeds. Percent seed germination of most species studied was similar in the forest and in pasture with grasses; seed germination was lower during the dry season in areas of pasture cleared of grasses. Air temperature, vapor pressure deficit (VPD), and photon flux density (PFD) were much higher in the pasture than in the forest at 1 m above the ground. VPD and PFD at ground level and soil temperature were similar in the pasture and the forest, indicating that pasture grasses strongly modify microclimatic conditions near the soil surface. The lowest gravimetric water content recorded in the pasture during the dry season was 0.5 and leaf relative water contents of the two species measured in the forest and pasture were identical, suggesting that plants in the pasture were not water stressed. Levels of most soil nutrients were lower in the pasture as compared to the forest; however, aboveground and root biomass for seedlings grown in pasture and forest soils did not differ significantly. Although a number of factors impede forest recovery in abandoned pastures, these results suggest that the most important limitation is lack of seed dispersal.

RESUMEN

Se evaluó la vegetación, la dispersión de semillas, la germinación de semillas, el microclima, y las condiciones físicas y químicas del suelo en un pastizal recientemente abandonado y un bosque húmedo primario en el sur de Costa Rica. El motivo del estudio fue evaluar la importancia de estos factores como limitantes en la regeneración del bosque en pastizal abandonado. La cantidad de semillas dispersadas por animales disminuyó drásticamente en el pastizal a más de 5 m del borde entre el mismo y el bosque; la cantidad de semillas dispersadas por el viento fue más bajo en el pastizal que en el bosque, pero la diferencia fue menor que para las semillas dispersadas por animales. El porcentaje de germinación de la mayoría de las semillas de las plantas estudiadas fue similar en el bosque y en el pastizal con gramas. Sin embargo, la germinación fue más baja en áreas sin gramas durante la época seca. La temperatura del aire, el déficit de presión de vapor (VPD), y la densidad del flujo de fotones (PFD) fueron más altos en el pastizal que en el bosque medidos a 1 m por encima del nivel del suelo. El VPD y la PFD al nivel del suelo y la temperatura del suelo fueron similares en el pastizal y en el bosque, lo que indica que las gramas modifican sustancialmente las condiciones microclimáticas cerca del suelo. El contenido gravimétrico de agua del suelo más bajo registrado durante la época seca fue 0.5 y los contenidos relativos de agua de dos especies de plantas en el bosque y el pastizal fueron idénticos, lo que sugiere que las plantas en el pastizal no sufrieron stress por falta de agua. Los niveles de nutrientes en el suelo fueron más bajos en el pastizal que en el bosque; sin embargo, la biomasa de hojas, tallos, y raíces de plántulas que crecieron en suelo de pastizal y de bosque no fueron estadísticamente diferentes. Aunque varios factores limitan la recuperación del bosque en áreas de pastizal, estos resultados sugieren que el factor más importante es la falta de dispersión de semillas.

Key words: andisol; Costa Rica; pasture grasses; phosphorus; restoration; succession; seed dispersal; soil compaction; soil nutrients.

WHEREAS RATES OF TROPICAL DEFORESTATION are difficult to calculate, they are unquestionably high. Recent estimates of tropical moist forest land area

in Latin America range from 416–687 million ha (reviewed in Grainger 1993). The vast majority of the forest clearing in Latin America is for agricultural purposes, in particular to create pastureland for cattle grazing (Amelung & Diehl 1992, Fearnside 1993). Extensive deforestation has caused excessive erosion and associated water quality degradation in Costa Rica (Hartshorn 1982, Ramírez & Maldonado 1988), as well as in most other tropical

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² Current address: Environmental Studies Department, University of California, Santa Cruz, California 95064 U.S.A.

countries. Tropical deforestation has profound effects on carbon cycling (Houghton 1995), the hydrological cycle (Lean & Warrilow 1989, Shukla *et al.* 1990), and the conservation of biodiversity (Wilson 1988).

In Latin America, agricultural lands are often abandoned due to declining productivity and changing economic incentives (Uhl *et al.* 1988, Aide *et al.* 1995). This process of clearing and abandonment has led to large areas of highly degraded lands that are often slow to recover, particularly in areas of intense disturbance with agricultural machinery (Buschbacher *et al.* 1988, Uhl *et al.* 1988). A few studies in recent years have investigated factors limiting recovery of tropical forest in pastureland (*e.g.*, Uhl 1987, Buschbacher *et al.* 1988, Nepstad *et al.* 1991, Aide & Cavelier 1994, Fernandes & Sanford 1995, Nepstad *et al.* 1996). Results of these studies suggest that a number of factors may impede tropical forest recovery in areas of pastureland, including a lack of soil nutrients, soil compaction, competition with aggressive, non-native pasture grasses, seasonal drought, low rates of seed colonization, and seed and seedling predation. However, the relative importance of these factors in limiting recovery has varied greatly among studies and, in some cases, results have been contradictory.

The goal of this research was to investigate the importance of factors limiting the early stages of forest regeneration in an abandoned pasture in southern Costa Rica. Three specific questions were addressed: (1) how widely are seeds dispersed from the nearby forest into the abandoned pasture?; (2) are seeds of woody species able to germinate in the pasture?; and (3) to what extent do (a) microclimatic conditions and (b) soil physical and chemical parameters limit seedling establishment and growth? I compare these results to related studies in order to identify site-specific differences that influence the relative importance of these factors in limiting forest recovery. Identifying the rate-limiting step(s) of succession in highly degraded lands is necessary to develop techniques for facilitating the recovery process and restoring biodiversity and ecosystem services (MacMahon 1987).

METHODS

SITE DESCRIPTION.—This study was conducted in primary, seasonal montane wet forest (Holdridge *et al.* 1971) and abandoned pasture adjacent to the Las Alturas Biological Station in southern Costa Rica (8°57'N, 82°50'W, 1500 m elev.). Average an-

nual rainfall is *ca* 3000 mm, more than 95 percent of which normally falls between April and December (Instituto Costarricense de Electricidad, pers. comm.). Average annual maximum and minimum temperatures are 24.6 and 13.2°C, respectively (Instituto Costarricense de Electricidad, pers. comm.).

The primary forest is part of the Las Tablas Protected Area (19,602 ha), which is contiguous with La Amistad Biosphere Reserve. The forest directly abuts the pasture, forming an abrupt, linear forest/pasture edge. The 5 ha pasture where the study was conducted is part of a mosaic of agricultural land uses covering *ca* 2500 ha. This pasture was cleared 25 years ago using heavy machinery. The land was used 15 years for the cultivation of coffee and then 10 subsequent years for cattle grazing. Cattle were removed from the pasture in February 1995, at the initiation of the study. At that time, the pasture vegetation consisted predominantly of nonnative grasses such as *Axonopus scoparius*, *Digitaria decumbens*, and *Melinis minutiflora*. Isolated trees, primarily *Inga edulis* Mart. and *Inga punctata* Willd., were scattered throughout the pasture.

Vegetation, microclimate, and soil nutrients were measured in six 12 × 12 m plots in the forest and pasture. In both the forest and pasture, three plots each were located at 25 and 250 m from the forest/pasture edge. At each distance from the edge, plots were separated by *ca* 100 m. Plots in the pasture were located at least 4 m from the edge of the canopy of isolated trees. Plots were located at two distances from the forest/pasture edge to measure whether recovery differed with distance from the edge. However, in few cases did initial measurements vary with distance from the edge. Therefore, results reported here are combined unless otherwise noted.

VEGETATION.—The vegetation in the forest and pasture was surveyed in the six 12 × 12 m plots using a stratified random sampling procedure. Percent cover of herbaceous vegetation and woody vegetation <1 m tall was measured in four 1-m² plots. Shrubs and small trees (1–5 m in height) were marked and their cover recorded in two 4 × 4 m plots. All trees >5 m tall in the 12 × 12 m forest plot were marked and their diameter at breast height (DBH) recorded. Because pasture plots were deliberately located away from the few isolated trees, the DBH of all trees within the 5-ha pasture study area were recorded to quantify the basal area of trees.

All plants were identified to the lowest possible

taxonomic group. Seedlings of tree species could not always be distinguished and were assigned to morphological groups. Plots were marked and surveyed between January and April 1995, but were revisited periodically during the following year to collect flowering specimens. Voucher specimens were deposited at the University of Costa Rica Herbarium. Taxonomic authorities are listed in the text only for species that are not included in Appendix 1.

Importance values were calculated for the species in each vegetational stratum (Mueller-Dombois & Ellenberg 1974). The importance value was calculated as the sum of the relative cover and relative frequency for herbs and shrubs. For trees, the importance value was calculated as the relative number of individuals and relative basal area. Since a measure of frequency and abundance was included for each layer, the sum of importance values in each layer totaled 200; values reported here are the largest importance value from the three layers. Vines and lianas were included with the strata in which they were most abundantly represented.

SEED RAIN.—Seed rain was measured between 1 May 1995 and 30 April 1996 along three transects that passed through the marked plots. Along each transect, seed traps were placed at the forest/pasture edge and at distances of 5, 15, 25, 50, 75, 125, and 250 m from the edge into both the pasture and forest. Seed traps consisted of fine-mesh hardware cloth suspended in an inverted pyramid below 0.5×0.5 m wood frames raised above the ground by 0.5 m legs. Traps were emptied twice monthly. All visible, apparently healthy seeds (except grasses) were separated from leaves and other debris, identified to morphospecies, and counted. Seeds of pasture grasses were not counted, as the focus of this study was on seed rain of successional and forest species. Seeds were identified to the lowest possible taxonomic group by collecting flowering and fruiting specimens of plants and comparing them to collections at the California Academy of Sciences, Costa Rican National Herbarium, and the La Selva Biological Station. Species composition of trees and shrubs over each trap was recorded in order to estimate the percentage of seeds that were dispersed beyond the plant canopy in comparison to those that dropped directly below fruiting plants.

To estimate seed predation in traps, twice during the study period (August 1995 and February 1996), five seeds of nine species were marked, placed in each of six traps in both the pasture and forest, and recounted at the next sampling date. As *ca* 95 percent of marked seeds remained after two

weeks, seed loss due to predation was considered negligible.

SEED GERMINATION.—To determine whether seeds of woody species would germinate if dispersed into the pasture, germination success was monitored in three habitats: pasture with grasses, pasture cleared of grasses, and forest. Six species were chosen that were all small-seeded, woody species that were collected in pasture seed traps, indicating that they are dispersed into the pasture. Germination of three species that are dispersed during the dry season, *Heliocarpus appendiculatus* Turcz., *Psychotria goldmanii*, and *Solanum acerifolium* Dunal, was monitored beginning in February 1996. Germination of three species dispersed during the rainy season, *Hasseltia floribunda*, *Miconia donaeana* Naudin, and *Saurauia montana* Seem., was monitored beginning in May 1996. Germination was monitored weekly for a three month period. Seeds that had germinated were removed at each census period.

Twenty-five seeds of each species were placed on the soil surface (to mimic natural dispersal) in $8 \times 8 \times 7$ cm pots filled with pasture soil that had been heated at 200°C for 4 hr to kill existing seeds. An additional control pot was placed at each location; no germination of the study species was observed in these pots. Five pots of each species were placed in each of the habitats separated by *ca* 10 m. Each pot was covered with a 1.3-cm metal mesh and coated with a sticky, insect trapping cream (Tanglefoot[®]) to prevent seed predation by insects and small rodents, which was shown to be high in a previous study (Holl & Lulow 1997). In cleared plots, grass was cut at the soil surface using a mechanical trimmer. Resprouts were removed by hand during the study.

MICROCLIMATE AND WATER STATUS.—Air temperature, relative humidity, and photon flux density (PFD) were recorded at 5 cm and 1 m height in order to compare microclimatic conditions in the forest and pasture for germinating seeds/young seedlings and saplings, respectively. Soil temperature was recorded at a depth of 5 cm. Microclimatic measurements were made at four points in each of the six plots in the forest and pasture and at 24 points in the pasture where grasses had been cleared. Measurements were made between 1100 and 1300 h on four clear days over a period of two weeks in mid-February 1996 (dry season). Plots were randomly measured so that an equal number of measurements were taken in each habitat type on a single day. Instantaneous microclimate mea-

surements were not made during the rainy season because continually changing cloud cover rendered temporal variation sufficiently high to prevent between site comparisons, and microclimatic differences between habitats are much lower during the rainy season (Holl, pers. obs.).

Microclimate measures were recorded using a LI-1000 data logger. Air temperature and soil temperature were recorded using LI-1015 and LI-1016 temperature sensors; relative humidity was recorded using a Humitter 50U; and PFD was recorded using an LI-190SA quantum sensor. Air temperature and relative humidity sensors were protected from direct shortwave radiation by a white wooden shield. Relative humidity was converted to vapor pressure deficit using ambient air temperature at the same height (Jones 1983).

Soil moisture was measured four times: 21 November 1995 (end of the rainy season), 29 January 1996 (mid-dry season), 28 February 1996 (end of the dry season), and 16 February 1997 (mid-dry season). Three soil cores were removed from 0–15 cm in each of the six plots in the forest and pasture and the six plots in the pasture cleared of grasses. Cores within a plot were separated by at least 1 m. Cores were weighed, dried at 105°C for 24 hr, and reweighed. Composite soil samples from the three plots located at 25 m from the edge in the pasture and forest were collected for determination of soil moisture curves. Soil moisture curves relating gravimetric water content to water potential over a range of soil moistures were determined using an SC-10 thermocouple psychrometer and an NT-3 nanovoltmeter. Rainfall data since 1984 (the earliest available) were obtained from the Instituto Costarricense de Electricidad for a weather station located *ca* 1 km from the study site.

The relative water content (Koide *et al.* 1989) of seedlings of two trees that were naturally present in both the forest and pasture, *Inga edulis* and *Ocotea whitei*, was measured on 27–28 February 1996. Single leaves were removed from five individuals of each species in the forest and the pasture and were immediately placed in a sealed plastic bag containing a moistened paper towel. Leaves were removed individually from bags, surface dried, and weighed to the nearest milligram within 0.5 hr of their removal from the plant. The leaf petioles were then submerged in water, recut, and left for 24 hr, after which they were reweighed for saturated mass, dried at 105°C for 24 hr, and their dry masses determined.

SOIL.—In June 1995, 2.5 cm diameter soil cores

were removed from 0–5 and 5–25 cm depths at ten locations in each 12 × 12 m plot and composited. These layers were chosen as previous studies in volcanic soils in the tropics suggest that most available nutrients are concentrated in the top 5 cm (Rosemeyer 1990, Ewel *et al.* 1991, Schlather 1995). In the forest, the depth of the litter layer was measured at each point and the litter was removed before sampling. There was no measurable litter present in the pasture at the time of sampling.

Resin-extractable phosphorus (Cooperband & Logan 1994) was determined on field moist soils within 48 hr of sample collection. This method removes the most biologically available phosphorus (Hedley *et al.* 1982). All further analyses were done within two weeks at the Soils Laboratory of the College of Agriculture at the University of Costa Rica following standard methods currently used by soil testing laboratories in the country (Díaz-Romeu & Hunter 1978).

Samples were dried at 40°C for 48 hr and passed through a 2-mm sieve. Soil pH in H₂O was determined electrometrically using a soil:water volume ratio of 1:2.5. Total nitrogen was determined using the standard Kjeldahl technique (Bremner & Mulvaney 1982). The carbon content of the samples was analyzed using the Walkley-Black wet digestion method (Allison 1975) using a correction factor of 1.33 for incomplete recovery of organic carbon (Bornemisza *et al.* 1979) and a ratio of organic matter to organic C of 1.67. P and K were extracted using the modified Olsen method (Díaz-Romeu & Hunter 1978). The Olsen method for P extraction removes labile P on the soil particle surfaces, as well as some microbial P (Hedley *et al.* 1982). Ca and Mg were extracted with an unbuffered 1 mol/liter KCl solution (Díaz-Romeu & Hunter 1978). Cations were measured using an atomic absorption spectrometer. Exchangeable acidity was measured by extraction with 1 mol/liter KCl followed by titration with 0.1 mol/liter NaOH. Effective cation exchange capacity (CEC_e) was determined as the sum of the extracted Ca and Mg, the K extracted with the modified Olsen solution, and the exchangeable acidity. Acid saturation is the percentage of CEC_e accounted for by exchangeable acidity. Subsamples of each of the three replicates at each distance from the forest/pasture edge were composited, and phosphorus retention rates were calculated (Blakemore *et al.* 1987).

Because it is difficult to assess the nutrients available to plants, bioassay studies were used to compare growth rates in pasture and forest soils.

Growth rates of three tree species of different successional stages, *Cecropia polyphlebia* Donn. Sm., *Calophyllum brasiliense*, and *Beilschmiedia ovalis*, were compared. *C. polyphlebia* is a common pioneer species; *B. ovalis* is a mature forest species; and *C. brasiliense* is found regularly in the mature forest, but is considered well adapted to the poor soil and stressful microclimatic conditions often observed in degraded pastures (Nichols & González 1991).

Soil was collected from 0–30 cm depth at ten locations in the forest and pasture. Soil from each habitat was mixed and placed in 11.5 cm diameter \times 30 cm deep nursery bags. Twenty seedlings of each species, ca 5 cm in height, were transplanted into bags with each soil type. Seedlings were exposed to full sunlight and irrigated with river water as needed during the dry season. Once a month, a thin layer of leaf litter was placed on the seedlings grown in forest soil to simulate leaf fall. After six months, aboveground and root biomass of seedlings were separated, washed, dried at 60°C to constant mass, and weighed.

Bulk density was measured in three layers (0–5, 6.5–15, and 16.5–25 cm) at three points just outside each plot. Bulk density was measured using an 8.5 cm diameter by 5 cm high thin-walled steel cylinder. The cylinder was hammered in vertically for the top layer. For the two lower layers, the core was extracted horizontally to avoid compaction between layers. Because of limited oven space, a 15–20 g subsample was dried at 105°C for 24 hr. For 12 samples, the entire sample minus the subsample was dried. The correlation between the values calculated using the full sample and subsample was $r = 0.99$.

Instantaneous infiltration rates were measured on a single day in late November 1995, at the end of the rainy season. Infiltration rates were measured at three points <1 m outside of the three plots 25 m from the forest/pasture edge in both the pasture and forest. Metal cylinders (15.5 cm diameter) were inserted 5 cm into the soil. The time necessary for the water level to drop from 2 to 1 cm was measured for ten consecutive periods. This number was chosen as 10 cm is the maximum amount of rain that falls in a single day at the site.

STATISTICAL ANALYSES.—I tested the relationship between seed rain and distance from the forest/pasture edge using linear regression. The independent variables were distance into the forest and pasture from the edge, and the dependent variables were

the logarithm of the number of animal and wind dispersed seeds.

Two-sample *t*-tests were used to compare measurements in the pasture and forest (e.g., soil nutrients and aboveground and root biomass in bioassay studies). One-way ANOVA was used to compare percent seed germination and gravimetric water content in the three habitat types (forest, pasture with grass, pasture cleared of grass); values were arcsine transformed as they are proportions. Air temperature, soil temperature, and VPD were compared using three-way ANOVA, including the three main-effects of habitat type, distance to the forest/pasture edge, and height above the soil surface, and interaction terms. Tukey's LSD multiple comparison procedure was used to separate habitat groups when habitat was found to be a significant factor in an ANOVA. Air temperature and soil temperature data were log transformed to meet assumptions of normality and homoscedasticity. Because PFD levels varied by two orders of magnitude in the forest and pasture and, therefore, strongly deviated from normality even after transformation, PFD data were not analyzed statistically. Throughout, results in which $P < 0.05$ are reported as significant.

RESULTS

VEGETATION.—Forest and pasture plant species with importance values >1 are listed in Appendix 1. Common species in the forest included: *Litachne pauciflora* and *Pavonia schiedeana* in the herb layer; *Ardisia* sp., *Meliosma idiopoda*, and *Piper* spp. in the shrub layer; and *Ocotea floribunda*, *Prunus annularis*, *Sorocea trophoides*, and *Symphonia globulifera* in the tree layer. The pasture was dominated by the exotic pasture grasses listed previously; other common herbaceous species in the pasture included *Elephantopus mollis*, *Hydrocotyle nubigena*, and *Spermacoce assurgens*.

Whereas there was a greater number of herbaceous species in the pasture than in the forest, overall species richness was ca four times higher in the forest. No species were found in sample plots in both the forest and pasture. However, in the pasture, there were a few isolated individuals of trees commonly observed in the forest, such as *Gordonia fruticosa* and *Ulmus mexicana* Liebm.

Herbaceous cover was much higher in the pasture ($87.4 \pm 14.5\%$) than in the forest ($30.8 \pm 12.7\%$). Shrub cover and total basal area in the forest sample plots were 66.3 ± 27.0 percent and

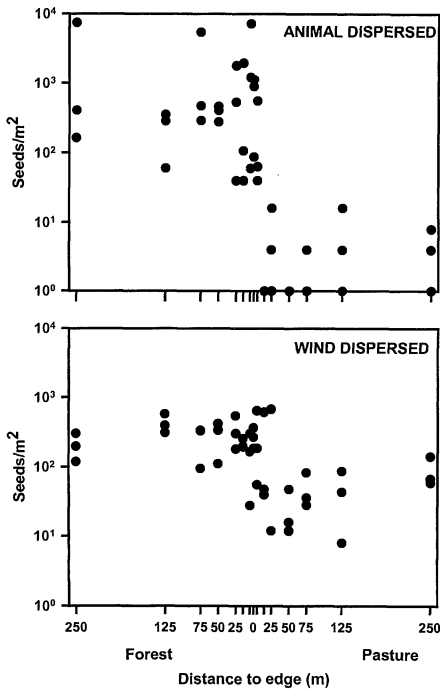


FIGURE 1. Number of animal dispersed (upper) and wind dispersed (lower) seeds falling as a function of distance into the pasture and forest. Seeds were collected between 1 May 1995 and 30 April 1996.

44.7 ± 21.3 m²/ha, respectively. Basal area of trees in the pasture was 1.9 m²/ha.

SEED RAIN.—Of the 10,499 seeds collected, all but 149 were identified to family and all but 1688 were identified to genus or species. The majority of seeds not identified below the family level were in the Asteraceae. An average of 1670 seeds/m² (range 57–7328) fell in forest traps and 190 seeds/m² (range 0–684; not including grasses) fell in pasture traps over the 1-yr study period; there was high variation within each habitat type. The peak of animal dispersed seeds was in the first half of the rainy season (May and June), whereas most wind dispersed seeds fell during the dry season (January and February).

The number of animal dispersed seeds decreased sharply on the pasture side of the forest/pasture edge (Fig. 1); few such seeds (3 seeds/m²) were recorded beyond 5 m of the forest/pasture edge. The number of wind dispersed seeds recorded in the pasture was about half the amount falling in the forest (141 vs. 275 seeds/m²; Fig. 1). Neither

the number of animal dispersed nor wind dispersed seeds was significantly related to distance from the edge in either the forest or pasture ($P > 0.05$ in all cases).

A total of 17 morphospecies of seeds were recorded in seed traps in the pasture, but only six of those species were recorded beyond 5 m from the forest edge. Four wind dispersed seed types comprised the vast majority of seeds recorded in the pasture: *Clematis dioica*, *Heliocarpus appendiculatus*, *Ulmus mexicana*, and Asteraceae. The only animal dispersed genus recorded in pasture traps beyond 5 m of the forest edge was *Solanum*. All five of these plants are present in the pasture. *H. appendiculatus* and *U. mexicana* exist as remnant trees. *C. dioica* and a number of species of *Solanum* are present in the occasional shrub patches below remnant trees. Herbs, vines, and shrubs in the Asteraceae are present in both the forest and pasture.

In contrast, 63 morphospecies were recorded in the forest, of which 82 percent were animal dispersed. *Ficus* was by far the most common genus in the forest, accounting for ca 55 percent of all trapped seeds. Other common species in the forest included: *Alchornea glandulosa* Poeppig, *Ardisia* sp., *Cecropia polyphlebia*, a few species of Solanaceae, and the same wind dispersed species common in the pasture. None of the seeds recorded in the pasture fell from plants in the immediate vicinity of the traps, whereas 57–68 percent of seeds falling in the forest were from plants whose canopy was over the seed traps.

SEED GERMINATION.—Percent seed germination ranged from 0–53 percent. During the dry season, seed germination was significantly lower for all species in pasture plots cleared of grasses than in pasture plots with grasses (Table 1); however, during the rainy season, percent seed germination was similar for all species in these two habitats. Seed germination was not significantly different for four of the species when comparing pasture with grasses and forest (Table 1). Two of the species, *Hasseltia floribunda* and *Solanum acerifolium*, showed higher percent germination in the pasture with grass compared to the forest, and one species, *Saurauia montana*, germinated more often in the pasture cleared of grass than in the forest.

MICROCLIMATE AND WATER STATUS.—Microclimate measurements are shown in Table 2. Air temperature was $>5^{\circ}\text{C}$ higher in the pasture than in the forest during the dry season and did not differ significantly with grass cover and height above the soil

TABLE 1. Mean percent seed germination of six woody species in forest and pasture with and without grasses. Values are means \pm 1 SD. $N = 5$ pots with 25 seeds for each habitat. Means with the same letter are not significantly different ($P < 0.05$) across habitat type based on Tukey's LSD. Dry mass of seeds is based on a sample of 20–30 seeds.

Species	Seed dry mass (mg)	Pasture with grass	Pasture without grass	Forest
Dry season				
<i>Heliocarpus appendiculatus</i>	4.7	37 \pm 15 (a)	2 \pm 2 (b)	28 \pm 11 (a)
<i>Psychotria goldmanii</i>	4.3	35 \pm 22 (a)	0 \pm 0 (b)	36 \pm 17 (a)
<i>Solanum acerifolium</i>	1.8	44 \pm 11 (a)	11 \pm 9 (b)	3 \pm 5 (b)
Rainy season				
<i>Haseltia floribunda</i>	6.3	53 \pm 5 (a)	37 \pm 14 (ab)	30 \pm 11 (b)
<i>Miconia donaeana</i>	<0.1	12 \pm 15 (a)	8 \pm 10 (a)	0 \pm 0 (a)
<i>Saurauia montana</i>	0.3	7 \pm 9 (ab)	25 \pm 16 (a)	1 \pm 1 (b)

surface. Soil temperature was similar in the forest and in the pasture with thick grass cover, but was much higher and varied greatly in areas of the pasture cleared of grasses. Vapor pressure deficit (VPD) was much higher in the pasture than in the forest at 1 m above the soil surface. At 5 cm from the soil surface, VPD was higher in the pasture below grasses than in the forest, but was lower than in pasture cleared of grasses. Similarly, PFD was *ca* 100 times higher in the pasture at 1 m, but was comparable to the forest at ground level. Not surprisingly, microclimate variables in the pasture did not differ significantly with distance from the forest/pasture edge. VPD in the forest was higher at 25 m than at 250 m from the edge (0.91 ± 0.14 kPa vs. 0.71 ± 0.07 kPa, $N = 12$); the same was true for air temperature ($23.5 \pm 1.3^\circ\text{C}$ vs. $22.2 \pm 0.3^\circ\text{C}$, $N = 12$).

Soil moisture was higher in the forest than in the pasture at all measurement periods (Fig. 2). Soil moisture was significantly higher below pasture grasses than in areas cleared of grasses in February 1997. The lowest gravimetric water content recorded was 0.5 in one of the cleared areas, which corresponded to a water potential of -0.02 MPa. Soil moisture curves conducted in the laboratory indicated that water potential dropped below -1.5 MPa, which commonly is considered permanent wilting point (Taiz & Zeiger 1991) at gravimetric water contents of *ca* 0.25 and 0.31 for forest and pasture soils, respectively.

Average values for leaf relative water content measured at the end of February 1996 were identical in the forest and pasture for both of the species measured (*Inga edulis*: Forest 0.97 ± 0.03 , Pasture 0.97 ± 0.05 ; *Ocotea whitei*: Forest 0.98 ± 0.04 , Pasture 0.98 ± 0.02 ; $N = 5$).

SOIL.—The soil at this study site was originally classified at a scale of 1:200,000 as an andic humitropept (Pérez *et al.* 1979). However, analyses from this study show that it has many of the characters of Andisols discussed by Mohr *et al.* (1972) and Sanchez (1976), including $\text{pH} > 5.5$, high organic matter, low available P due to high fixation rates, and low bulk density (Table 3; Fig. 4). Acidity and pH did not vary significantly between habitats in either the 0–5 or 5–25 cm layer. Values for extractable Ca, Mg, and K, CEC_e, percent organic matter, and percent total N were significantly higher in the forest than in the pasture in both layers. The amount of extractable cations in the forest, particularly in the upper layer, was extremely high. P levels were low in both habitats. Resin-extractable phosphorus (REP) was significantly higher in the forest, while bicarbonate-extractable phosphorus (BEP) did not differ between the two habitats. Average litter depth in the forest was 1.6 ± 0.3 cm, whereas there was no measurable litter in the pasture.

Neither the aboveground nor the root biomass differed significantly in soil types for any of the three species of tree seedlings grown in bags with pasture and forest soil (Fig. 3).

Bulk density was low in both the forest and pasture (Fig. 4). Pasture soils were significantly more compacted in all layers; the largest difference was in the 0–5 cm layer. Differences in soil compaction resulted in infiltration rates in the pasture and forest that varied by two orders of magnitude; the average time for infiltration of 10 cm of water into the pasture soil was 193 min (range 43–299 min) compared to 1.5 min (range 0.7–3.7 min) in the forest.

TABLE 2. Air temperature (T_{air}), soil temperature (T_{soil}), vapor pressure deficit (VPD), and photon flux density (PFD) in primary forest and open pasture with and without grasses. All measurements were made on clear days in February 1996 between 1100–1300 h. Values are means \pm 1 SD. $N = 24$ for each location.^a

Location	T_{air} (°C)		T_{soil} (°C)		VPD (kPa)		PFD ($\mu\text{mol}/\text{m}^2/\text{s}$)	
	5 cm	1 m	-5 cm	1 m	5 cm	1 m	5 cm	1 m
Forest	22.8 \pm 1.1 ^a	22.9 \pm 1.1 ^a	17.6 \pm 0.4 ^a	0.86 \pm 0.16 ^a	0.75 \pm 0.16 ^a	0.86 \pm 0.16 ^a	27 \pm 56	10 \pm 8
Pasture with grass cover	28.3 \pm 1.0 ^b	28.1 \pm 1.0 ^b	18.3 \pm 1.4 ^a	1.72 \pm 0.21 ^b	1.13 \pm 0.20 ^b	1.72 \pm 0.21 ^b	35 \pm 46	2139 \pm 116
Pasture without grass cover	28.7 \pm 0.7 ^b	28.2 \pm 0.8 ^b	26.0 \pm 2.0 ^b	1.79 \pm 0.20 ^b	1.58 \pm 0.28 ^c	1.79 \pm 0.20 ^b	2132 \pm 95	2115 \pm 99

^a Means with the same letter are not significantly different ($P < 0.05$) across habitat type based on Tukey's LSD.

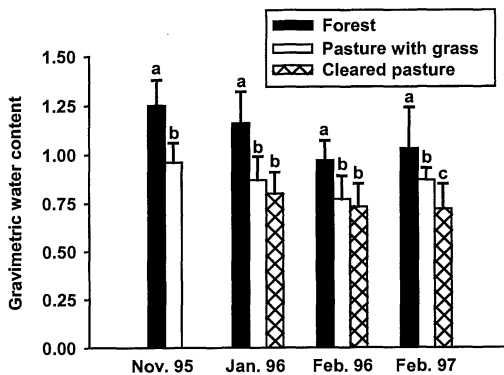


FIGURE 2. Gravimetric soil water content in primary forest and pasture with and without grass on 21 November 1995, 29 January 1996, 28 February 1996, and 16 February 1997. $N = 18$ for each location. Error bars represent 1 SD. Means with the same letter are not significantly different ($P < 0.05$) across habitat type. Tukey's LSD was used for three way comparison and a t -test was used for two way comparison.

DISCUSSION

SEED RAIN.—Forest plant species are rarely found in recently abandoned pastures and the seeds of most tropical forest plants rapidly lose viability (Garwood 1989, Vázquez-Yanes & Orozco-Segovia 1993); therefore, succession in abandoned pastures is dependent upon recently dispersed forest seeds. This and previous studies clearly demonstrate that lack of seed dispersal is a major factor limiting forest regeneration in abandoned pastureland; few seeds of animal dispersed, woody species fall beyond 5 m of the forest edge in areas of pasture without trees or shrubs (Willson & Crome 1989, Kolb 1993, Aide & Cavellier 1994, Vieira *et al.* 1994). The vast majority of tropical forest seeds have adaptations for animal dispersal (Howe 1984); yet many tropical forest birds and mammals rarely venture into open areas (Sisk 1991, Cardoso da Silva *et al.* 1996).

Whereas 140 wind dispersed seeds/ m^2/yr were recorded in the pasture, all but one were of only four seed types. Previous empirical (Willson & Crome 1989) and theoretical (Greene & Johnson 1996) studies suggest that numbers of wind dispersed seeds decline in relation to distance from the forest/pasture edge. In this study, such a trend was not observed. However, the four types of wind dispersed seeds commonly found in pasture traps were from plants already present in the pasture, which would explain the lack of such a pattern.

This study, as well as many previous studies

TABLE 3. Soil nutrients in the forest and pasture at two depths. CEC_e = Effective cation exchange capacity; REP = Resin-extractable phosphorus; BEP = Bicarbonate-extractable phosphorus; OM = Organic matter. Values are means \pm 1 SD. $N = 6$ for each habitat type for all variables except P retention, for which $N = 2$.^a

Soil character	0–5 cm			5–25 cm		
	Forest	Pasture	Sig	Forest	Pasture	Sig
pH (in H ₂ O)	5.7 \pm 0.2	5.6 \pm 0.2	NS	5.7 \pm 0.1	5.8 \pm 0.1	NS
Ca (cmol/kg)	25.9 \pm 5.1	6.5 \pm 1.3	***	8.1 \pm 3.9	2.1 \pm 0.6	*
Mg (cmol/kg)	11.0 \pm 2.9	2.4 \pm 1.0	***	3.3 \pm 1.2	0.6 \pm 0.3	**
K (cmol/kg)	0.79 \pm 0.26	0.30 \pm 0.06	**	0.30 \pm 0.08	0.15 \pm 0.07	**
Acidity (cmol/kg)	0.56 \pm 0.09	0.92 \pm 0.53	NS	0.49 \pm 0.15	0.54 \pm 0.31	NS
CEC_e (cmol/kg)	38.2 \pm 6.8	10.1 \pm 1.8	***	12.1 \pm 4.8	3.3 \pm 0.8	*
OM (%)	28.0 \pm 4.2	17.0 \pm 2.9	***	16.0 \pm 1.6	12.7 \pm 3.2	*
N (%)	1.10 \pm 0.10	0.80 \pm 0.12	**	0.74 \pm 0.07	0.60 \pm 0.12	*
REP (mg/kg)	4.0 \pm 0.5	0.2 \pm 0.2	***	1.3 \pm 0.2	0.7 \pm 0.2	***
BEP (mg/kg)	10.7 \pm 3.2	9.0 \pm 3.7	NS	6.3 \pm 1.7	4.9 \pm 1.6	NS
P retention (%)	88.1 \pm 1.5	96.7 \pm 0.4	*	97.0 \pm 0.7	98.1 \pm 0.2	NS

^a Values in different habitats in each layer were compared using a *t*-test. NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

(e.g., Foster 1982, Augspurger & Franson 1988, Kolb 1993), showed that seed rain varies greatly over small distances both in pastures and forests. High variability in seed dispersal is one cause of the patchy recovery commonly observed in most early-successional ecosystems.

SEED GERMINATION.—While seed dispersal appears to be a major factor limiting recovery, a subsequent question is whether forest seeds dispersed into the pasture are indeed able to germinate. In this study, germination success for seeds of woody species placed in the pasture under grass was generally higher than for seeds placed in the forest, suggesting that lack of seed germination is not a major

factor limiting recovery. It is interesting that none of these species germinated more in areas cleared of pasture grasses, given the low PFD below pasture grasses. High light conditions have been shown to favor germination of early-successional woody species in some studies (Whitmore 1983, Everham *et al.* 1996); however, other studies have shown that many woody species can germinate at relatively low light levels (Augspurger 1984, Vázquez-Yanes & Orozco-Segovia 1993, Metcalfe 1996). Results of this study, as well as research by Aide and Cavellier (1994) and González Montagut (1996) in pastures of Puerto Rico and Mexico, respectively, show that some species have higher germination rates in areas of grass than in areas cleared of vegetation. These

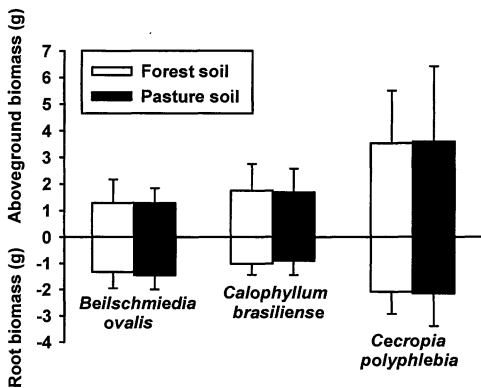


FIGURE 3. Comparison of aboveground and root biomass for three tree species grown in pasture and forest soil. $N = 17$ –20 for each species in each soil. Error bars represent 1 SD.

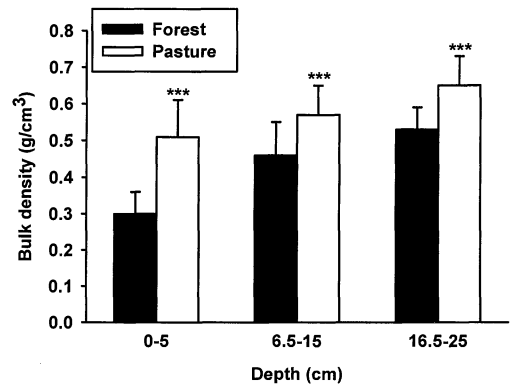


FIGURE 4. Bulk density of pasture and forest soil in three layers. $N = 18$ for each habitat type. Error bars represent 1 SD. Values in different habitats in each layer were compared using a *t*-test. *** = $P < 0.001$.

results suggest that grasses may facilitate germination by reducing high soil temperatures and seed desiccation, particularly during dry periods.

MICROCLIMATE AND WATER STATUS.—A third goal of this study was to determine the extent to which microclimatic conditions influence forest recovery. As discussed previously, stressful microclimatic conditions appeared to affect seed germination in the pasture during the dry season. However, despite large differences in air temperature, VPD, and PFD in the pasture and forest at 1 m above the soil surface, seedlings in the pasture did not appear to be limited by available water.

Previous research in tropical forests has suggested that high temperatures and lower moisture availability in pastures compared to forests may result in water stress for plants (Nepstad *et al.* 1991, 1996) and may limit seedling establishment and survival (Uhl 1987). Nepstad *et al.* (1991) reported that soil water potential in the top 15 cm of soil of an abandoned pasture in the Brazilian Amazon was below -1.5 MPa for a number of weeks during the dry season. In related research, xylem pressure potential was two to five times lower for seedlings planted in a pasture compared to those planted in treefall gaps (Nepstad *et al.* 1996).

There are a number of possible explanations for the differences between my results and those of other studies. First, available moisture may not be limiting at this site because of the relatively short dry season (*ca* 3 mo) compared to other sites with longer dry seasons (up to 6 mo). Second, the results may reflect the fact that rainfall was above average during the study period. Interannual variability in rainfall is high at this study site and it is possible that plants experience drought stress during drier years. However, soil gravimetric water content was measured in February 1997 after a period of 30 days with only 4.8 mm of rain and was still twice what is considered wilting point (Taiz & Zeiger 1991), suggesting that a very lengthy period with no rain would be necessary before plants experienced drought stress.

A third reason for the lack of observed water stress in the pasture for the two species studied may be the dense grasses, which may facilitate forest recovery in highly degraded pastures by reducing evaporation from the soil (Aide & Cavelier 1994). Above and belowground competition with pasture grasses has been suggested as a major factor that limits growth of certain plant species in tropical pastures (Nepstad *et al.* 1991, Guariguata *et al.* 1995, González Montagu 1996, Sun & Dickinson

1996). However, data from this and a previous study (Aide & Cavelier 1994) suggest that pasture grasses have a complex effect on forest recovery. The results reported here do not test whether grasses inhibit growth; however, previous research has shown strong effects of direct above and belowground competition on woody plant growth at this site (Holl 1998).

Finally, relative water content was measured only for two species, and these species may have adaptations to compensate for reduced water levels, possibly explaining the lack of observed water stress. Clearly, measurements must be taken over a number of years and on a range of species before conclusive statements can be made about the degree of water stress at this site.

SOIL.—The final question addressed in this research was whether soil chemical and physical parameters limit recovery. Most previous research in the tropics has indicated that plants are commonly limited by phosphorus (Golley *et al.* 1975, Vitousek 1984, Ewel 1986), although there are exceptions (Vitousek *et al.* 1987, Tanner *et al.* 1992). Low levels of available P are common in volcanic soils because binding of this element with clay results in high P retention rates (Uehara & Gillman 1981). In the current study, REP was below what is considered limiting for plant growth (Landon 1984) in the forest and even lower in the pasture. BEP was similar in both habitat types and was in the middle range compared to previous studies on volcanic soils (Rosemeyer 1990, Cooperband & Logan 1994, Fernandes & Sanford 1995, Kappelle *et al.* 1995, Schlather 1995).

In the current study, percent organic matter and most nutrient levels were extremely high in the forest, which is typical for volcanic soils (Mohr *et al.* 1972, Tanner 1977, Rosemeyer 1990, Kappelle *et al.* 1995). Whereas most nutrient levels were lower in the pasture than in the forests, organic matter, N, Ca, and Mg levels were still within the medium to high range for tropical soils (Sanchez 1976, Landon 1984). Only extractable K levels were moderate to low in the pasture (Landon 1984, Ewel *et al.* 1991). Similarly, most other studies comparing nutrient levels in pasture and forest have reported lower levels of cations in the pastures than in primary and secondary forests (Krebs 1974, Montagnini & Sancho 1990, Aide & Cavelier 1994, Reiners *et al.* 1994). Although organic matter and N levels were high, a large portion of the nutrients in volcanic soils may not be available to plants due to slow mineralization (Sanchez 1976).

Despite the extremely low P levels in the pasture, growth rates of seedlings grown in pasture and forest soils did not differ. This result suggests that either nutrient levels were not limiting or that nutrients were equally limiting in both soil types. Previous bioassay studies have suggested that seedlings grown in pasture soils are more nutrient limited than those grown in forest soils (Aide & Cavelier 1994, G. E. Eckert, pers. obs.). Tropical forest soils are extremely variable with respect to their mineralogy and management history (Sanchez 1976, Landon 1984), which largely accounts for site-specific differences in the extent to which nutrient availability limits forest recovery.

The bulk density values recorded in this study were extremely low in the forest, but were comparable to those reported previously for volcanic soils (Trouse & Humbert 1961, Mohr *et al.* 1972, Vance & Nadkarni 1992). As in most prior studies (*e.g.*, Lal & Cummings 1979, Reiners *et al.* 1994), soil compaction was much higher in the pasture. Although the effects of compaction were not directly measured in the current study, even small differences in soil compaction can affect root growth, gas exchange, and infiltration rates (Trouse & Humbert 1961). For example, Trouse and Humbert (1961) reported reduced root growth at bulk densities as low as 0.56 Mg/m³. Differences in soil compaction may also affect seed germination (Sun & Dickinson 1996).

It is clear that regeneration of tropical forest vegetation in abandoned pasture is limited at all early-successional stages: colonization, establishment, growth, and survival. Lack of seed availability appears to be the overriding factor limiting forest recovery in tropical pastures. Not only is dispersal of forest seeds into open areas minimal, the few seeds that do arrive are commonly subjected to high rates of predation (Janzen 1971, Uhl 1987, Nepstad *et al.* 1990, Aide & Cavelier 1994, Holl & Lulow 1997). Questions of drought stress and nutrient limitation become moot if seeds of forest

species are not dispersed into the pasture. Therefore, efforts to facilitate recovery must focus on strategies to elevate seed dispersal, such as planting native tree seedlings to increase canopy architecture, installing bird perching structures, or artificially establishing shrubs that rapidly mature and fruit, thereby attracting seed dispersers.

If barriers to seed dispersal are overcome, a number of interrelated factors may influence seed germination, as well as seedling growth and survival. However, their relative importance varies greatly with climate, soil type, existing vegetation, and management history. The degree to which drought stress affects recovery is highly variable over spatial and temporal scales, depending on the length and severity of the dry season. Nutrient limitation is strongly influenced by soil type, climate, and past land use, further complicating the interaction among these variables. Given the variability in the relative importance of these factors, it is essential to identify rate-limiting factors at individual sites in order to be able to design site-specific management plans to accelerate forest recovery.

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Appendix 1. *Vegetation species list. 1 = importance value 1–5; 2 = importance value 5–25; 3 = importance value >25.*

Pasture herbs		<i>Hoffmannia dotae</i> Standl.	1
<i>Acmella oppositifolia</i> (Lamarck) R. K. Jansen	1	<i>Hoffmannia</i> sp.	1
<i>Ageratum conyzoides</i> L.	1	<i>Inga</i> sp. 1	1
<i>Axonopus scoparius</i> (Flügge) Kuhlman	3	<i>Inga</i> sp. 2	1
Bignoniaceae	2	<i>Meliosma idiopoda</i> Blake	2
<i>Castilleja</i> sp.	1	<i>Meliosma glabrata</i> (Liebm.) Urb.	1
<i>Clematis dioica</i> L.	1	<i>Mollinedia costaricensis</i> Donn. Sm.	1
<i>Digitaria decumbens</i> Stent	3	<i>Mortoniendendrum pentagonum</i> (Donn. Sm.) Miranda	1
<i>Dryopteris patula</i> (Sw.) Underw.	1	Myrtaceae	1
<i>Elephantopus mollis</i> H. B. K.	2	<i>Oreopanax</i> sp.	1
<i>Heterocondylus vitalbae</i> (DC.) R. M. King & H. Rob.	2	<i>Philodendron</i> sp. 1	1
<i>Hydrocotyle nubigena</i> Rodríguez	1	<i>Philodendron</i> sp. 2	1
<i>Iresine diffusa</i> H. & B.	1	<i>Picramnia teapensis</i> Tul.	2
<i>Melinis minutiflora</i> Beauv.	3	<i>Piper aduncum</i> L.	1
<i>Oxalis stricta</i> L.	1	<i>Piper</i> sp. 1	1
<i>Paspalum</i> sp.	2	<i>Piper</i> sp. 2	2
<i>Piper arboreum</i> Aubl.	1	<i>Pleuropetalum sprucei</i> (Hook.f.) Standl.	1
<i>Pteridium aquilinum</i> (L.) Kuhn	1	<i>Pseudolmedia oxyphyllaria</i> Donn. Sm.	1
<i>Rubus rosaefolius</i> Sm.	1	<i>Psychotria</i> spp.	1
<i>Sida rhombifolia</i> L.	1	<i>Psychotria goldmanii</i> Standl.	1
<i>Solanum umbellatum</i> Mill.	1	Rubiaceae	1
<i>Spermaceoce assurgens</i> Ruiz & Pav.	2	<i>Sapium</i> sp.	1
<i>Sporobolus</i> sp.	1	<i>Sloanea</i> sp.	1
<i>Stellaria ovata</i> Willd. ex Schltld.	1	<i>Smilax</i> sp.	1
Forest herbs		Forest trees	
Araceae sp. 1	2	<i>Alchorneopsis floribunda</i> (Benth.) Müll. Arg.	2
Araceae sp. 2	1	Arecaceae	1
<i>Calathea</i> sp.	2	<i>Beilschmiedia ovalis</i> (S. F. Blake) C. K. Allen	2
<i>Costus</i> sp.	1	<i>Cupania</i> sp.	1
<i>Diplazium</i> sp.	1	<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	1
<i>Litbache pauciflora</i> (Sw.) Beauv. ex Poir	2	<i>Eugenia</i> sp.	2
<i>Paullinia</i> sp.	2	<i>Ficus</i> spp.	1
<i>Pavonia schiedeana</i> Steud.	3	<i>Gordonia fructifera</i> (Schrader) H. Keng	1
<i>Pharus parvifolius</i> Nash	1	<i>Hasseltia floribunda</i> H. B. K.	2
<i>Tradescantia zanonii</i> (L.) Sw.	1	<i>Hyeronima oblonga</i> (Tul.) Müll. Arg.	2
Forest shrubs		Lauraceae	2
<i>Ardisia</i> sp.	2	Melastomataceae	1
Arecaceae	1	<i>Meliosma subcordata</i> Standl.	1
Araliaceae	1	<i>Ocotea floribunda</i> (Sw.) Mez	3
<i>Calophyllum brasiliense</i> Camb.	1	<i>Ocotea glaucosericea</i> Rohwer	1
<i>Campyloneurum</i> sp.	1	<i>Ocotea whitei</i> Woodson	1
<i>Celastrus liebmannii</i> Standl.	2	<i>Ocotea</i> spp.	1
<i>Cestrum megalophyllum</i> Dunal	1	<i>Phoebe cinnamomifolia</i> (H. B. K.) Nees	2
<i>Chamaedorea allenii</i> L. H. Bailey	2	<i>Prunus annularis</i> Koehne	2
<i>Chamaedorea pinatifrons</i> (Jacq.) Oerst.	1	<i>Pseudolmedia spurea</i> (Sw.) Griseb.	2
<i>Crossopetalum enervium</i> Hammel	1	<i>Sideroxylon portoricense</i> Urb.	2
<i>Desmopsis</i> sp.	1	<i>Sorocea trophoides</i> W. C. Burger	2
<i>Euterpe</i> sp.	2	<i>Symphonia globulifera</i> L. f.	2
<i>Heisteria acuminata</i> (Humb. & Bonpl.) Engl.	1	<i>Symplocos</i> sp.	1