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Spatial and Temporal Variation of Seed Rain in a Tropical Lowland Wet Forest¹

Bette A. Loiselle

Department of Biology, Univ. Missouri-St. Louis, 8001 Natural Bridge Rd., St. Louis, Missouri 63121, U.S.A.

Eric Ribbens²

Ecology and Evolutionary Biology, Univ. Connecticut, Storrs, Connecticut 06269, U.S.A.

and

Orlando Vargas

Estación Biológica La Selva, Organizacion para Estudios Tropicales, San Pedro de Montes de Oca, Costa Rica

ABSTRACT

Patterns of seed rain were observed at five forest locations in recent treefall gaps and paired understory sites in a tropical wet forest in northeast Costa Rica. Seed rain was dominated by animal-dispersed species. Overall, significantly more wind-dispersed seeds arrived into treefall gaps than into forest understory. Contrary to expectations, understory sites received a greater seed rain than did gap sites during three of four sample periods over the course of one year. Considerable spatial heterogeneity, however, existed among forest locations, with some forest sites receiving up to three times more seed rain input than others. Results from this seed rain study generally matched those from an earlier study at this site in terms of seed rain volume and dominant plant families. Composition of seed rain was more similar among habitat types (*i.e.*, gap, understory) than among forest locations (*i.e.*, paired sites) suggesting that spatial foraging activity and habitat preference of seed dispersers result in non-random patterns of seed rain. If true, then such patterns have implications for evolution of fruit and seed characters that promote survival and establishment of seeds under certain environmental conditions.

RESUMEN

Se observaron los patrones de "lluvia" de semillas en cinco lugares en el bosque donde existen claros debido a reciente caída de árboles y lugares cercanos a éstos en el sotobosque de un bosque húmedo tropical en el noreste de Costa Rica. Las semillas predominantes en la "lluvia" de semillas corresponden a especies dispersadas por animales. En general, significativamente más semillas dispersadas por viento llegaron a los claros que al sotobosque.

Contrariamente a lo esperado, los sitios en el sotobosque recibieron mayor lluvia de semillas que los los sitios en los claros durante tres de cuatro periodos de muestreo durante el curso de un año. Sin embargo, se encontró amplia heterogeneidad espacial entre los cinco lugares del bosque, recibiendo algunos de éstos una lluvia de semillas tres veces mayor que otros.

Los resultados de volúmen de la lluvia de semillas y familias de plantas dominantes encontrados en este estudio, concuerdan en general con los de un estudio realizado anteriormente en el mismo sitio. La composición de la lluvia de semillas fue más parecida entre tipos de habitat (*i.e.*, claros, sotobosque) que entre las cinco localidades en el bosque sugiriendo que espacialmente, la actividad de forrageo y la preferencia de habitat de los dispersadores, produce patrones no-azarosos de lluvia de semillas. Si ésto es cierto, entonces, tales patrones tienen implicancias para la evolución de aquellos caracteres que- en frutos y semillas- promueven la sobrevivencia y establecimiento de semillas bajo ciertas condiciones ambientales.

Key words: endozoochory; gap; regeneration; seed dispersal; seed rain; tropical forest.

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² Correspondence address: Department of Biology, St. John's University, Collegeville, Minnesota 56321, U.S.A.

FEW SEEDS UNDERGO LONG SEED DORMANCY in tropical lowland wet forests (Ng 1980, Garwood 1983, Saulei & Swaine 1988, Vásquez-Yanes & Orozco-Segovia 1993). Even the classic pioneer species, *Cecropia obtusifolia*, has seeds that have a limited life (<2 yr) in the soil seed bank (Alvarez-Bullya & Martínez-Ramos 1990, Alvarez-Bullya & García-Barrios 1991). The relative absence of dormancy and short lifespan of seeds in lowland wet forests likely is due to the susceptibility of seeds to fungal attack and other mortality risks (Hopkins & Graham 1983, Foster 1986, Osmund *et al.* 1987, Putz & Appanah 1987; see also Brown & Venable 1986). Consequently, with the exception of a few shade-intolerant species where recruitment may be dominated by seeds in the soil seed bank, regeneration of most plant species in these forests is due to recent input of seeds from seed rain and from vegetative sprouting (e.g., Uhl *et al.* 1981, Hopkins & Graham 1983, Putz 1983, Whitmore 1983, Vásquez-Yanes & Orozco-Segovia 1984, Brandani *et al.* 1988, Saulei & Swaine 1988, Alvarez-Bullya & Martínez-Ramos 1990, Alvarez-Bullya & García-Barrios 1991, see also Ribbens *et al.* 1994).

Patterns of seed dispersal and post-dispersal seed and seedling survival are influenced by a multitude of biotic and abiotic factors, as well as by chance events (e.g., Howe 1980, Augspurger 1983, 1984; Clark & Clark 1984, 1989; Hubbell & Foster 1986, 1990; Osmund *et al.* 1987; Sork 1987; Chazdon 1988; Schupp 1988, 1993; Martínez-Ramos & Soto-Castro 1993). Seed shadows of trees are somewhat predictable, especially for trees with large gravity- or wind-dispersed seeds (Augspurger & Franson 1993, Willson 1993). In contrast, animal-dispersed seeds are likely to have more variable spatial distribution of seeds than are plant species dispersed by wind or gravity (Herrera 1985, Howe 1989). For example, for tropical shrubs dispersed by birds, Levey (1988) suggested that because frugivorous birds often concentrate their activities in treefall gaps, gaps may act as recruitment foci and receive a disproportionate number of seeds (see also Hoppes 1988). Secondary dispersal and non-random mortality of seeds and seedlings, however, "shape" this initial seed shadow and thus, affect spatial distribution of later life history stages (*cf.* Janzen 1970, Byrne & Levey 1993, Kaspari 1993, Martínez-Ramos & Soto-Castro 1993).

The importance of treefall gaps to plant regeneration in tropical forests has been noted by many investigators (e.g., Hartshorn 1983; Denslow 1980, 1987; Brokaw 1985; Clark & Clark 1992). Although early studies established a dichotomy be-

tween shade-intolerant and shade-tolerant species, such a dichotomy is too simplified, since plant species fall along a continuum of light (and associated microenvironmental factors) gradients with respect to regeneration probabilities and growth responses (Denslow 1980, Clark & Clark 1992). Moreover, the importance of biotic factors (e.g., predation, susceptibility to pathogens) also varies among forest microenvironments, and thus affects recruitment probabilities for plants in complex ways (e.g., Augspurger 1984, Schupp & Frost 1989, Kaspari 1993, Notman 1994).

In this study, we investigated the effect of forest location (five sites) and habitat (gap, understory) on seed rain in a Costa Rican tropical wet forest over a nine-month period. This study thus complements a previous study at the same site that investigated seed rain into recent treefall gaps (Denslow & Gomez 1990). Specifically we ask whether location or habitat effects were more important in influencing the number and composition of emerging seedlings from seed rain traps. Additionally, we investigated whether certain dispersal mechanisms (*i.e.*, endozoochory, wind, *etc.*) affected seed arrival at different forest locations or habitats. Because regeneration patterns reported here are influenced by post-dispersal events (*i.e.*, time since arrival in trap and germination), this study is not able to critically examine all of the ecological processes involved in patterns of seed rain and seedling recruitment. Nonetheless, we feel that the patterns presented here are useful for evaluating recruitment probabilities for seeds arriving into gap and forest understory, as well as evaluating spatial heterogeneity in seed rain.

Such evaluation is important because the spatial dispersion of seeds forms the template for later regeneration and recruitment patterns. Predictable, or at least non-random, patterns of seed dispersion have very different implications for forest regeneration and ultimately, conservation of these species rich forests than do random patterns of seed dispersion. Thus, understanding the patterns and processes of spatial recruitment of seeds is essential, and indeed, necessary to understand later recruitment patterns and organization of forest plant communities (*cf.* Osmund *et al.* 1987).

METHODS

This study was conducted in undisturbed forest at Estación Biológica La Selva, a field station operated by the Organization for Tropical Studies (OTS) in northeast Costa Rica. La Selva receives approximately 3900–4000 mm rain annually (Hartshorn

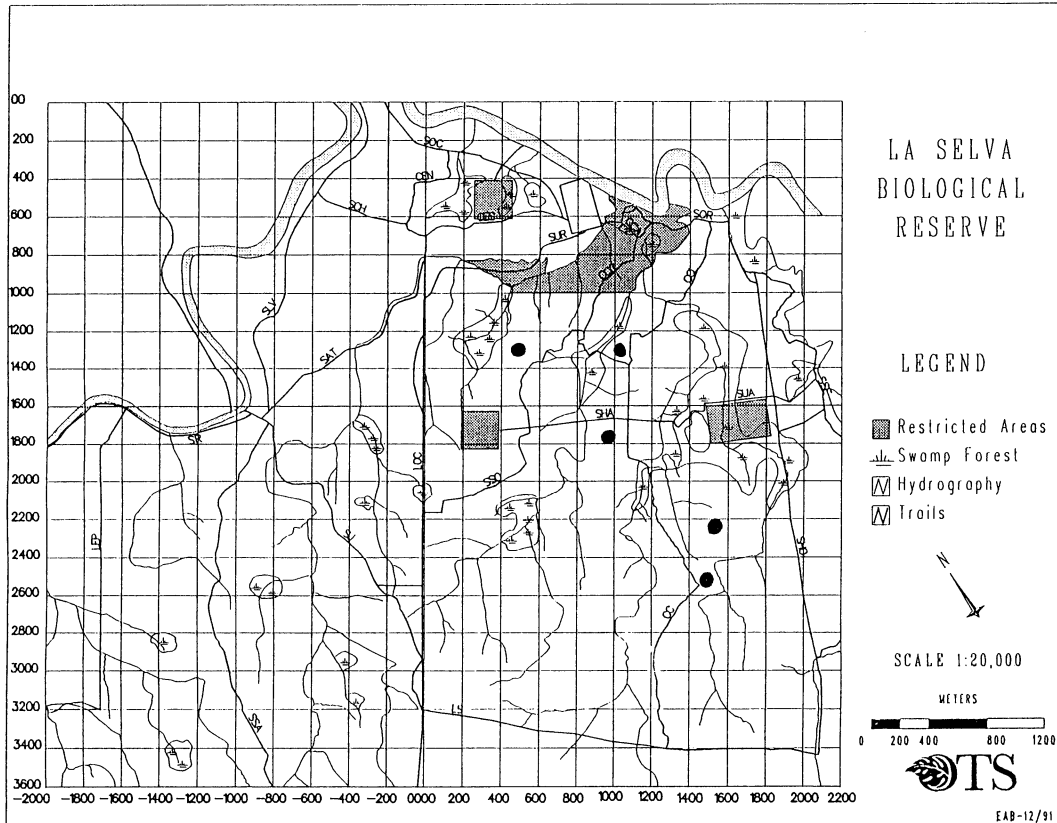


FIGURE 1. Location of paired sites (shown by black circles) within the undisturbed forest of "old" La Selva. Sites were located in forest adjacent to the following trail markers and were from 25–200 m off the trails. Approximate trail locations were Camino Central 375 m, 1100 m and 1350 m (hereafter, CC 375, CC 1100, CC 1350); Camino Circular Cercano 1150 m (CCC 1150); and Sendero Suroeste 240 m (SSO 240). At each site, 8 traps (0.2 m² each) were placed in a treefall gap and in adjacent forest understorey for a total of 16 traps per site.

1983). The main dry season lasts from January or February to March or April with a shorter, less pronounced dry season in September or October. Forest at this site is classified as tropical wet forest following Holdridge (1967) life zones (Hartshorn & Peralta 1988). A complete description of this site is available in McDade *et al.* (1994; and refs. therein).

In early March 1990, we searched for recent treefall gaps (<3 months old) in mature forests on the eastern half of La Selva. Our criteria were that the treefalls resulted from the tip up of a canopy tree and that treefall gaps were at least 300–400 m distance from each other in order to cover a wide area within the La Selva forest. Five treefall gap sites were selected on residual soils (Fig. 1).

Ground litter and vegetation were cleared in ca. 16 m² area near the upper bole and crown area in

order to facilitate placement of seed traps. In each of the cleared areas, 8 traps (0.4 m × 0.5 m), constructed of a wood frame and fine nylon mesh base, were placed in a slight depression at ground level. Traps were evenly spaced within the area cleared in the gap. For each treefall gap, a paired understorey site under closed canopy was selected 30–40 m away in a random compass direction. Eight traps were placed over an approximately equivalent area as in treefall gap sites.

We filled each trap with sterilized soil between 11–12 March 1990 (old alluvium soil collected from near the laboratory clearings was sterilized by setting in a microwave on high setting for 15 minutes, or by heating in a drying oven at 110°C for 3–4 hours). We returned and collected soil from seed traps on 4 occasions during the next year (6 April, 1 June, 3 August, 23 December). While in

the field, seedlings found in each trap were carefully collected for transfer to shadehouses. Soil from each trap was then collected and kept in separate bags. Emptied seed rain traps were filled with fresh sterilized soil. We elected to use this seed trap method rather than above ground traps due to high rates of decomposition at the site. The latter method is a direct estimate of seed rain, whereas our method is affected by mortality and secondary removal after seed arrival. Due to time constraints we could not empty traps on a regular basis (*i.e.*, weekly) to ensure that seeds did not decompose between visits, and thus used sterilized soil traps instead. Soil collected from the seed traps was transferred on the same or next day to shallow trays located in 20 percent full-light shadehouses in the laboratory clearing. This light level was selected because it approximates light levels found in treefall gaps at La Selva and because it matched that used in a previous seed rain study at this site (Denslow & Gomez 1990).

Shadehouse trays were filled (approx. 2 cm deep) with sterilized sand, and soil from seed traps was spread on top in separate trays divided by wooden cross pieces. Plastic sheets were placed over the shadehouse benches (about 1.5 m above bench throughout) to prevent further contamination by incoming seeds and protect emerging seedlings from heavy rainfall. Germinating trays were kept moist by frequent watering with a fine mist. Controls to test the efficiency of soil sterilization were established in shadehouses alongside seed rain traps. Plant species that appeared in controls were considered to represent inadequate sterilization of soil or seeds arriving after trays were established in the shadehouse. Controls only very rarely had emerging seedlings and will not be discussed further.

We checked for germinating seedlings on a weekly basis, scoring the number and identity (when known) of each seedling until the next collection date (2–4 months later or March 1991 for the final collection). Thus seedlings were allowed to emerge over at least a two-month period. Under similar germination conditions, Denslow and Gomez (1990) reported that more than 96 percent of seeds collected from traps germinated within a two-month period. If seedlings were not identifiable, they were transferred to a separate tray, given a unique morpho-species identity and allowed to grow until identification was possible. In many cases, plant identification only was possible to the genus level, and thus, species number as used here is conservative. Voucher specimens of each seedling were collected and stored in the La Selva herbarium. Several seed-

lings died before identification was possible; these seedlings were used in analyses dealing with numbers of seedlings and morphospecies, but were not used in analyses comparing species composition among sites (see below).

It is important to note that because of the time between collection of soil from seed traps, seeds may have germinated and died in the field or have undergone mortality due to predator or pathogen attack, and thus are not recorded here. This presents a bias in this study, particularly if probability of germination and survival differed among forest location or habitat types. Nonetheless, this mortality likely reflected conditions in the field for incoming seeds and thus reflects recruitment probabilities for seeds.

DATA ANALYSIS.—We used two-way analysis of variance (Model III ANOVA) to examine the importance of forest location (5 locations, random effect) and habitat (gap or understory, fixed effect) in determining number of plant species or individuals occurring in seed traps; each collection date was treated in separate ANOVA models as length of time between collections varied. We tested for normality of dependent variables using Wilks-Shapiro test (Sokal & Rohlf 1981). When necessary, we natural log-transformed dependent variables to meet assumptions of normality for ANOVA.

To examine whether the distribution of seeds dispersed by different modes (*i.e.*, wind, gravity, *etc.*) differed among forest location or between habitats, we used chi-square contingency analyses. First, we characterized seedlings into dispersal modes according to literature accounts (Croft 1978, Hammel 1986, Loiselle & Blake 1990) and personal observations: endozoochory, wind, epizoochory, mechanical (*i.e.*, ballistic, gravity), and unknown. To compare seed dispersal modes among forest locations, all trap data within a paired site were combined. To examine differences in the importance of seed dispersal mode to seed rain as a function of habitat, we combined all traps within either gap or understory habitats by sampling dates; this allowed us to examine whether seasonal differences in dispersal mode occurred as well.

The above analyses consider primarily abundance measures and ignore composition of seed species arriving at seed trap locations. Consequently, we used cluster analyses to examine similarities in seed species composition as a function of forest location and habitat. If arrival of seeds is highly heterogeneous and based on local sources, then we might predict that forest location (*i.e.*, paired sites)

TABLE 1. Number of individuals of species germinated from seed traps placed in gap and forest understory habitats during four collection periods at Estación Biológica La Selva, Costa Rica. Seeds are divided into known dispersal modes; those not able to be classified into a dispersal mode are not shown here. Results of Chi-square contingency analyses testing for significant differences in the distribution among dispersal modes between gap and understory are shown.

	Number of individuals			Number of species		
	Gap	Understory	χ^2	Gap	Understory	χ^2
April						
Endozoochory	95	149	= 0.62	14	17	= 0.96
Wind	5	12	$P > 0.80$	2	4	$P > 0.80$
Epizoochory	22	36		4	4	
Mechanical	9	15		2	1	
Total	131	212		22	26	
June						
Endozoochory	57	192	= 41.9	15	18	= 0.60
Wind	14	6	$P < 0.001$	4	3	$P > 0.90$
Epizoochory	14	30		2	2	
Mechanical	18	7		3	2	
Total	103	235		24	25	
August						
Endozoochory	38	336	= 9.4	14	20	= 3.65
Wind	2	6	$P < 0.05$	1	5	$P > 0.30$
Epizoochory	2	11		1	7	
Mechanical	9	25		2	2	
Total	51	378		18	34	
December						
Endozoochory	553	291	= 6.09	27	34	= 2.17
Wind	65	21	$P > 0.10$	7	5	$P > 0.50$
Epizoochory	85	56		4	3	
Mechanical	1	0		1	0	
Total	704	368		39	42	

forms the basis of clusters, rather than habitat type. If, on the other hand, differential seed rain occurred in gap and understory habitats due to foraging activities of animals or wind currents, then we might expect that gap sites would be more similar to each other than to understory sites and vice versa. We used cluster analyses that are hierarchical, agglomerative, and polythetic (Sneath & Sokal 1973); cluster analyses were run using PCORD (McCune 1991).

The data matrix used in cluster analyses were total number of seedlings emerged (all dates combined) for each plant species by location and habitat (*i.e.*, gap site 1, understory site 1, gap site 2, . . . , gap site 5, understory site 5). The data matrix was simplified by removing all species for which family was unknown or for which species only were represented by one record. This resulted in a data matrix of 83 species by 10 sites. Data were relativized by row and column totals in order to weight species and sites equally. This step was taken as we were primarily interested in understanding similarities

among sites due to species composition, rather than abundance of seed rain. We report results from cluster analysis using group average (UPGMA) as this produced dendrograms with the least percent chaining when compared with other methods of clustering used (*i.e.*, nearest neighbor or single linkage).

RESULTS

A total of 2355 seedlings from at least 47 plant families and 112 plant species were recorded from seed traps over the course of this study; 132 seedlings were not identified to any plant family. The range in the average density of seedlings recorded per seed trap varied from 13.90 seedlings/m² to 82.95 seedlings/m²; the maximum number of seedlings recorded from any one trap during any sampling collection was 154 seedlings (770 seedlings/m²).

Number of seedlings recorded varied between habitat types as well as among locations within the

TABLE 2. Number of individuals or species germinated from seed traps placed at five locations in forest at Estación Biológica La Selva, Costa Rica. Seeds are divided into one of four known dispersal modes. Results of Chi-square contingency analyses testing for significant differences in the distribution among dispersal modes and forest locations are shown. See Figure 1 for locations of sites within La Selva.

Forest Location:	Number of individuals					Number of species				
	CC 1100	CC 1350	CCC 1150	CC 375	SSO 240	CC 1100	CC 1350	CCC 1150	CC 375	SSO 240
Dispersal mode										
Endozoochory	216	164	713	386	232	41	40	56	61	44
Wind/water	32	10	12	25	52	10	5	7	9	7
Epizoochory	30	65	29	42	90	9	9	11	8	1
Mechanical	29	11	10	18	16	6	3	2	6	5
Total	307	250	764	471	390	66	57	76	84	57
$\chi^2 =$			289.4					7.38		
P-value			<0.001					>0.80		

La Selva forest. Except for the December collection period, understory habitats had more emerging seedlings than did gap habitats (Table 1). Moreover, when all dates were combined, the number of emerging seedlings was found to vary three-fold among forest locations (Table 2). Thus, considerable spatial heterogeneity exists in recruitment patterns.

PATTERNS ASSOCIATED WITH DISPERSAL MODE.—Emerging seedlings from the traps were dominated (>70%) by individuals with endozoochorous dispersal in all samples and habitat types (Table 1). This was not a surprising result given the prevalence of this dispersal mode among tree and shrub species at La Selva (Frankie *et al.* 1974, Opler *et al.* 1980, Howe & Smallwood 1982). Distribution of seedlings by dispersal mode, however, differed significantly between gap and understory sites (all forest locations combined) during June and August collection periods ($X^2 > 9.4$, $P < 0.05$, $df = 3$); no significant pattern in dissemination of seeds by dispersal mode was found during April and December collections (Table 1). More seedlings of endozoochorous seeds emerged from understory sites than expected in both June and August. Indeed, when all collection periods were combined and dispersal mode patterns reexamined, the significant difference in the distribution of emerging seedlings from seed traps held ($X^2 = 25.2$, $P < 0.001$, $df = 3$), but this difference was due almost entirely to the greater propensity of wind-dispersed seedlings to occur in gap sites than in understory sites (these cell chi-squares accounted for 87% of the total chi-square). We found no differences in the distribution of plant species occurring in gap or understory sites as a

function of dispersal mode during any collection period (Table 1).

Significant heterogeneity existed in the distribution of seedlings among dispersal modes when the five forest locations were compared (all sampling periods and habitat types combined) ($X^2 = 289.4$, $P < 0.0001$, $df = 12$). In particular, forest near the end of the Camino Circular Cercano ("Near Loop Trail"), which had the greatest seed-rain input overall, also had more endozoochorous and fewer wind-dispersed seeds in seed traps when compared to other forest locations (Table 2). No significant difference in the distribution of seed dispersal modes, however, was found in the number of plant species recorded from seed traps among these locations (Table 2).

EFFECT OF FOREST LOCATION AND HABITAT TYPE ON SEED RAIN.—Results of ANOVA models reveal the importance of both habitat type and forest location in influencing seed rain patterns (Table 3, Figs. 1 & 2). The relative importance of these two factors, however, differed among sampling periods. For example, more seeds and seed species were disseminated into understory habitats regardless of forest location from the August collection (Fig 3). In contrast, differential numbers of seed and seed species were disseminated among forest locations during June and December sampling periods, but the pattern of recruitment into gap and understory habitats differed among locations, as indicated by significant or nearly significant interaction terms, making interpretation of the location effect difficult (Table 3, Figs. 1 & 2). Thus, considerable variation existed in recruitment patterns across the study period with

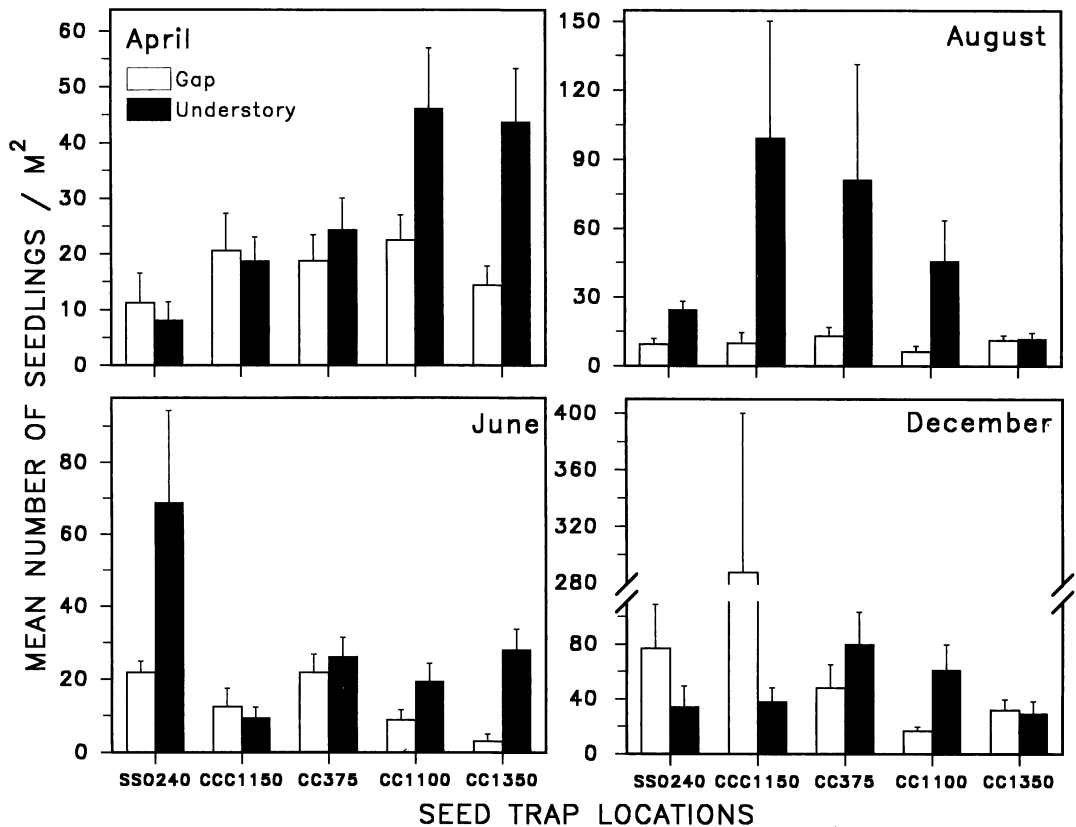


FIGURE 2. Mean number of seedlings per m² emerged from seed traps as a function of habitat type and forest location (see Fig. 1) for 4 collection dates during 1990. Seed rain traps were originally placed in the field on 11–12 March.

no single factor emerging as a determinant of seed rain patterns.

COMPOSITION OF SEED RAIN AMONG FOREST LOCATIONS AND HABITAT TYPES.—Seeds from six plant families (Cecropiaceae, Graminae, Melastomataceae, Piperaceae, Rubiaceae, Tiliaceae) accounted for 65 percent of all emerging seedlings from traps during the course of this study (Table 4). Approximately 10 percent (11 species) of the seed species recorded in this study occurred in 9 or 10 of the seed trap sites (*i.e.*, 5 locations \times 2 habitats). Important tree and liana species among this ubiquitous group included *Aristolochia constricta*, *Cecropia insignis*, *Pinzona coriacea*, *Hyeronima laxiflora*, *Miconia multispicata*, and *Trema interrigma*. The first species is wind-dispersed, whereas the remaining species are endozoochorous and dispersed primarily by birds. When compared to a null model of equal occurrence between gap and understorey sites, we found that

22 of 36 plant species (*i.e.*, those with >10 seedlings emerged from seed traps) showed significant nonrandom patterns ($X^2 > 4.09$, $P < 0.05$, $df = 1$); 7 were significantly more abundant in gaps and 15 in understorey sites (Table 5).

In general, based on seed species composition, sites in the same habitat type (*i.e.*, gap or understorey sites) were more similar in species composition than were sites located in the same patch of forest (*i.e.*, paired understorey and gap sites) (Fig. 4). Exceptions to this were that the seed composition found in understorey traps located near CC 1350 m was more similar to its paired site than to other understorey sites; and gap site near CC 375 m clustered with understorey sites prior to joining other gap sites. Moreover, gap and understorey sites did not cluster together based on their general proximity. The two closest sites were located in forest 100–200 m east of CC 1100–CC 1350 m, yet they were relatively well separated in the cluster dendrogram.

TABLE 4. Number of emerging seedlings from seed traps placed in gap and understory habitats (all seed traps and forest locations combined). Only plant families with more than 10 individuals shown here; families with less than 10 individuals are noted.

Plant family	Gap	Under- story	Total
Annonaceae	4	10	14
Araceae	18	26	44
Aristolochiaceae	46	16	62
Begoniaceae	25	6	31
Cecropiaceae	49	216	265
Commelinaceae	11	5	16
Compositae	18	60	78
Dilleniaceae	16	23	39
Eleocarpaceae	9	18	27
Euphorbiaceae	25	49	74
Flacourtiaceae	4	14	18
Gramineae	105	74	179
Haemodoraceae	10	3	13
Labiatae	25	9	34
Melastomataceae	96	130	226
Myristicaceae	0	15	15
Phyllolaccaceae	4	10	14
Piperaceae	31	105	136
Rubiaceae	414	197	611
Solanaceae	20	19	39
Tiliaceae	12	98	110
Ulmaceae	22	39	61
Verbenaceae	6	9	15

Other plant families with 10 or fewer emerging seedlings: Acanthaceae, Apocynaceae, Bignoniaceae, Boraginaceae, Bromeliaceae, Cactaceae, Caryophyllaceae, Clethraceae, Clusiaceae, Convolvulaceae, Cyclanthaceae, Heliconiaceae, Loganiaceae, Malpighiaceae, Malvaceae, Marantaceae, Mimosaceae, Myrsinaceae, Onagraceae, Palmae, Rhamnaceae, Smilacaceae, Vitaceae.

DISCUSSION

Tropical wet forest at La Selva is rich in plant species (ca. 2000 species) and is characterized by its dynamic nature (e.g., Lieberman & Lieberman 1987, Lieberman *et al.* 1990, Hartshorn 1990, McDade *et al.* 1994). Indeed, anyone who has spent more than a few days at this site, particularly if one is attempting to walk straight transect lines off trail, is well aware of the seemingly large portions of the forest in some stage of gap regeneration. Gap sites have been identified as important sites for plant recruitment, as well as for foraging sites for several frugivorous birds (Hartshorn 1983, Denslow *et al.* 1986, Levey 1988, Alvarez-Bullya & García-Barrios 1991, Clark & Clark 1992). The prevalence of animal-dispersed plant species, many of which are primarily dispersed by birds, together with in-

creased bird activity in forest gaps, have led Levey (1988) to suggest that gaps may act as recruitment foci for plants. Differential input of seeds into gaps, however, may be counterbalanced by mortality if seed and seedling survival are disproportionately low in gaps. Schupp & Frost (1989) demonstrated increased seed predation on *Welfia georgii*, a common subcanopy palm, in forest gaps relative to understory at La Selva. Such a pattern may reflect increased rodent abundance in forest gaps (Emmons 1982). Notman (1994), however, found that for *Macoubea guianensis* (Euphorbiaceae) significantly lower levels of seed predation occurred in and near large forest clearings (30 × 100 m) than in forest understory.

Results of this seed rain study were similar to that conducted in treefall gaps by Denslow and Gomez (1990). In both studies, Rubiaceae dominated the seed rain input in gaps. Moreover, 11 of 15 families with the greatest number of seedlings emerging from traps were shared between the two studies (see Table 4 for this study). Additional important families from Denslow and Gomez (1990; Table 1) were Annonaceae, Caesalpinaceae, Combretaceae, and Haemodoraceae. Contrary to previous expectations, we found that forest gaps did not act as recruitment foci, and in general contained fewer emerging seedlings from seed traps than did forest understory sites. This finding, however, is complicated by two factors—forest location and placement of seed traps. Seed traps located in gap habitats were placed near the center of the gap (*cf.* Denslow and Gomez 1990), rather than near gap edges. Gap centers, at least for the first 3–4 months of the study, had fewer perch sites available for birds and had a more open canopy overhead; these two factors may limit seed rain input by animals that have ingested seeds. Moreover, in some locations at some periods during the year, gap sites had significantly more seeds than did forest understory. Thus, considerable spatial and temporal heterogeneity occurred in abundance of seeds arriving into forest environments. Other seed rain or dispersal studies also have reported significant spatial variation in seed rain input (e.g., Howe & Primack 1975, Fleming & Heithaus 1981, Hopkins & Graham 1983, Denslow & Gomez 1990, Martínez-Ramos & Soto-Castro 1993).

Despite this heterogeneity in seed rain input, gap sites were more similar to each other in seed species composition than they were to understory sites, indicating nonrandom patterns of seed rain (Fig. 4). Moreover, a large proportion of the species (61%) tested for nonrandom occurrence between habitats showed significant associations with either

TABLE 5. Species showing significant associations with either gap or understory habitats. Results of Chi-square tests are shown as the number of gap or understory locations (of a total possible 5) where species was recorded.

Species	χ^2	P <	Gap	Understory
Gap species				
<i>Aristolochia constricta</i>	14.52	0.001	5	5
<i>Begonia</i> sp.	22.00	0.001	1	1
Graminae sp.	16.01	0.001	5	5
<i>Hyptis obtusifolia</i>	7.53	0.01	3	4
Melastome unid.	7.14	0.01	2	1
Rubiaceae unid.	391.00	0.001	2	4
<i>Geophila</i> sp.	15.38	0.001	4	3
Understory species				
<i>Philodendron</i> sp.	5.82	0.05	4	5
<i>Cecropia insignis</i>	105.20	0.001	5	5
<i>Erechtites hieracifolia</i>	24.65	0.001	4	5
<i>Chamaesyce</i> sp.	4.09	0.05	5	5
<i>Hyeronima laxiflora</i>	4.76	0.05	2	2
<i>Laetia procera</i>	4.57	0.05	2	5
<i>Paspalum</i> sp.	5.45	0.05	4	5
<i>Miconia multispicata</i>	11.31	0.001	5	5
<i>Otoba novogranatensis</i>	15.00	0.001	0	3
<i>Peperomia serpens</i>	44.60	0.001	2	3
<i>Piper</i> sp.	27.00	0.001	0	1
Rubiaceae unid.	146.20	0.001	3	4
<i>Hamelia patens</i>	14.20	0.001	1	3
<i>Apeiba membranaceae</i>	72.10	0.001	3	4
<i>Trema integerrima</i>	4.74	0.05	4	5

gap or understory sites (Table 5). For a few of these species it is possible that significant associations with gap or forest understory habitat is really a reflection of the proximity of nearby reproductive adults, as seedlings only were recorded at one or two locations. Denslow and Gomez (1990), however, did not find any relationship between nearby adults (*i.e.*, within 50 m) and composition of seed rain in treefall gaps at La Selva. In a Mexican wet forest, approximately 50 percent of the seed rain was attributable to seeds arriving from outside the local area (*i.e.*, 25 m \times 25 m plot) (Martínez-Ramos and Soto-Castro 1993).

The dynamic nature of tropical forests, however, means that treefall gaps are frequently forming, expanding, and being filled in during the building phase. For recruitment of individual plant species, the importance of these events will depend on the patch (*i.e.*, new gap, building phase, mature forest, *etc.*) transition probabilities, probability of seed arrival, seed survival, and seed life span in each patch (Alvarez-Bullya & García-Barrios 1991). We do not have data on seed life spans in the soil, nor data on whether differential seed survival occurs among our forest locations or habitats over the period between seed arrival and germination in the shadehouses. Except for the December time period, the

maximum time between arrival of a seed and movement to shadehouses was two months. Nonetheless, our seed rain patterns may be influenced by post-dispersal processes affecting seeds in the soil.

In conclusion, plant recruitment at La Selva appeared to be affected by a combination of both location and habitat. Considerable variation in recruitment probabilities existed across forest sites at La Selva, most likely due to spatial heterogeneity in fruit availability and activity of frugivorous vertebrates. These data highlight the importance of the dispersal event to recruitment probabilities for plants. For many plant species, seeds appear to be disseminated in a nonrandom fashion with some species having greater probabilities of occurring in treefall gaps than others. Such nonrandom patterns may promote the selection for seed and/or seedling characteristics that are adapted to these microsites. Certainly, seed and seedlings are expected to experience different survival probabilities between gap and understory habitats. Survival in these two different microhabitats is affected by intrinsic (*e.g.*, plant characteristics), as well as extrinsic (*e.g.*, predation, herbivory, mortality due to disturbance, *etc.*) factors (*e.g.*, Kitajima 1992, Kitajima & Augspurger 1989, Clark & Clark 1989, Dirzo & Dominguez 1986, Dirzo & Miranda 1990). Moreover, the conditions

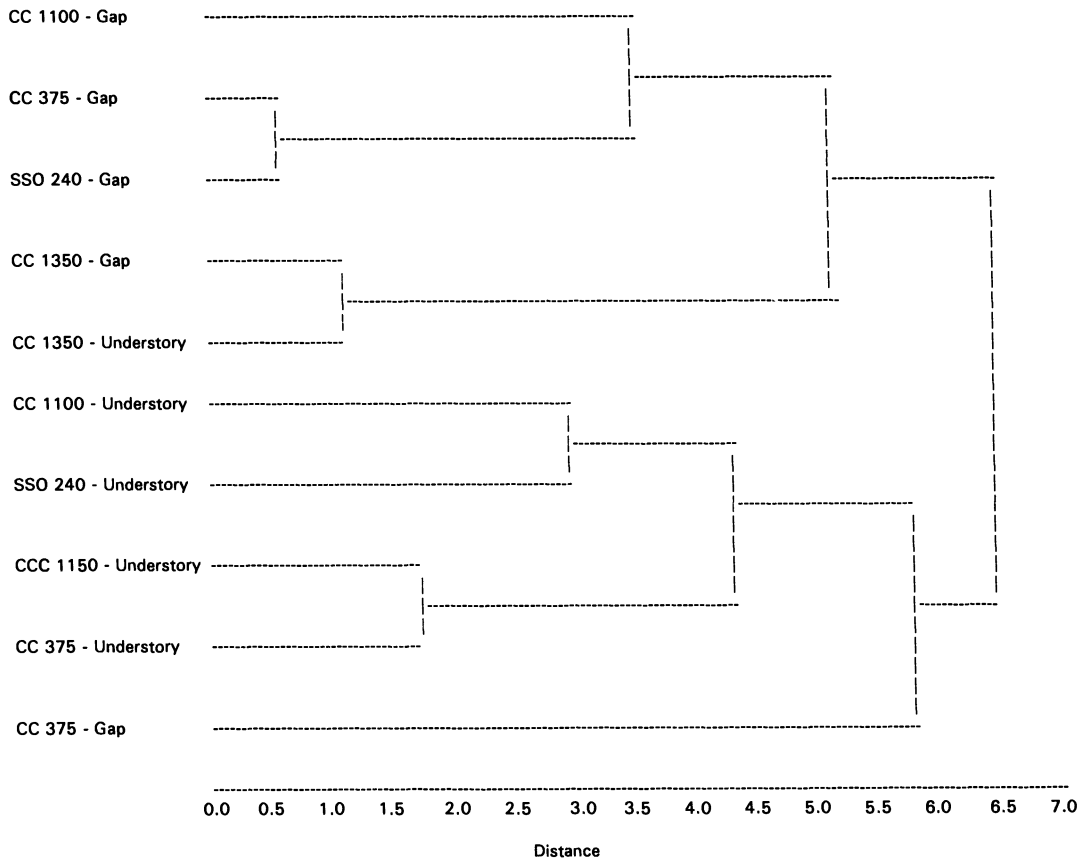


FIGURE 4. Results of dendrogram using group average clustering methods to group 10 sites (5 forest locations \times 2 habitat types; habitat types paired within locations) based on seed species composition from seed traps. Plant species with only one record, as well as plant species not identified to any plant family, were deleted from this cluster analysis. See Figure 1 for location of sites within La Selva forest.

within any location where seeds arrive vary temporally and likely affect seed survival probabilities (Alvarez-Bullya & García-Barrios 1991). Consequently, as Schupp (1993) has argued, understanding plant recruitment and regeneration in tropical forest depends on identifying the relative importance of the dispersal event and post-seed dispersal factors to seed and seedling survival (see also Alvarez-Bullya & García-Barrios 1991). Such processes likely are "shaped" by horizontal (spatial variation in fruit availability) and temporal heterogeneity (variation in plant phenological patterns) and the interaction between the two as these affect fine-scale patterns in disperser foraging activities and seed dissemination. Future research in this area in tropical rain forests would best be directed toward understanding the processes involved in nonrandom dissemination

of seeds by animal dispersers, and the consequences of such patterns of dispersal for the evolutionary dynamics of tropical plants.

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