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Source: *Vegetatio*, Vol. 71, No. 3 (Aug. 31, 1987), pp. 157-173

Published by: Springer

Stable URL: <http://www.jstor.org/stable/20038178>

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Seed dynamics during forest succession in Costa Rica

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Accepted 16.3.1987

Key words: Forest regeneration, Germination, Seed input, Seed rain: allochthonous, Seed rain: autochthonous, Soil seed bank, Succession, Tropics

Abstract

Soil seed banks and current seed inputs each play a role in tropical succession. We compared the abundance and floristic composition of seeds from these two sources at a Costa Rican site by germinating seeds from the soil, measuring seed inputs for 3 yr, and monitoring the earliest colonists in a forest clearing.

There were an estimated 6800 viable seeds/m² in the soil of 3.3-yr-old vegetation, 9500 seeds/m² in 11-yr-old vegetation, and 7000 seeds/m² in a 75-yr-old forest. An estimated 10100 seeds/m² fell on the soil surface of the young successional vegetation during 3 yr and 3700 seeds/m² fell during that same time in the forest.

Locally produced seeds accounted for about 75% of the seed input to the soil surface early in succession. Seeds dispersed out of young successional vegetation increased the quantity and species richness of the seed input and storage in an adjacent forest. Much of the species richness of the young successional vegetation resulted from seeds dispersed there from other communities by animals.

Deforestation stimulated germination of most seeds in the surface soil of the old forest, including seeds of the dominant canopy tree. The recruitment of seedlings from the soil seed bank numerically overwhelmed that from post-disturbance seed rain and sprouts.

We evaluated patterns of soil seed storage during succession and predicted the ability of vegetation of differing ages to respond to disturbance. Immediately after disturbance the number of seeds in the soil plummeted due to mortality, low inputs, and germination. As the vegetation regrew, the soil seed bank increased to a peak after 4 to 7 yr, then gradually decreased to its pre-disturbance size. High-frequency pulses of disturbance should result in reduced species richness, dominance by species with long-lived seeds, and fast recovery by seedling recruitment from the soil seed bank.

Introduction

The seeds available for regeneration after distur-

bance are influenced by temporal patterns of seed production, by seed dispersal, and by seed longevity (Grubb, 1977; Noble & Slatyer, 1980; Gross & Werner, 1982; Marks, 1983). Knowledge of seed inputs and soil seed banks might be especially important to understanding succession in the humid tropics, where rates of seed turnover are high and

* Journal series number 6459 from the Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida 32611, USA.

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hundreds of species have the potential to become incorporated into the vegetation and/or the soil seed bank (Whitmore, 1983). Devegetated sites, such as those that result from clearing forests for agriculture, have three potential sources of regeneration: seeds present in the soil at the time of disturbance (the soil seed bank), post-disturbance seed inputs, and resprouting trunks and roots.

The soil seed bank is a product of site history (Livingston & Allessio, 1968; Kellman, 1974), previous seed input, and seed losses due to germination and mortality. It may contain allochthonous seeds (i.e., seeds that originate elsewhere and are dispersed onto the site) and/or autochthonous seeds (i.e., seeds produced by plants growing on the site). Results of four studies (Uhl *et al.*, 1981; Putz, 1983; Swaine & Hall, 1983; Guevara, 1986) suggest that soil seed banks are important in the early stages of secondary succession in the tropics, but few data are available to assess temporal changes of those seed banks.

Seed inputs, even in the humid tropics, vary widely over the course of a year (Estrada, 1970; Smythe, 1970; Jackson, 1981; Foster, 1982; Carabias-Lilo & Guevara, 1985; Guevara, 1986), and succession is probably controlled to some extent by seasonal patterns of seed arrival. Immediately after a site is devegetated, all seed rain is allochthonous. As the vegetation recovers, autochthonous seeds also contribute to the seed rain. The relative importance of these two seed sources has never been reported for tropical successional vegetation, in spite of their implications for succession.

Vegetative sprouts are especially important in the tropics on sites that have been manually cleared for shifting agriculture. Because they grow quickly from extensive root systems, sprouts can be numerically important after logging (Saulei, 1984) and are often the largest plants in old field tropical succession (Ewel, 1977; Uhl *et al.*, 1981; Uhl, 1982).

In a humid tropical forest region, we reconstructed the history of changes in the soil seed bank during succession and determined the relative importance of autochthonous and allochthonous seed rains. Finally, we examined the relative importance of the soil seed bank, post-deforestation seed inputs, and vegetative sprouts in regeneration by felling a patch

of forest and measuring seed inputs and regeneration in the clearing.

Study area

The study area is in the Florencia Norte Forest, located at 650 m elevation near Turrialba, Costa Rica (9° 53' N, 83° 40' W) in the Tropical Premontane Wet Forest life zone (Tosi 1969). Mean annual rainfall is 2700 mm and the dry season is normally about 3 to 4 months long. During our 3-yr study monthly rainfall was < 100 mm/month only in March to April 1980, March 1981, and January to April 1982. The soils are of volcanic origin and relatively fertile (Berish, 1983).

The Florencia Norte Forest developed following the abandonment of coffee plantations and/or pasture early in this century. The 30-m-tall canopy is dominated by the tiliaceous tree *Goethalsia meiantha* (Donn.Sm.) Burret, but many other species are present including the trees *Cecropia obtusifolia*, *Cordia alliodora* (Ruiz & Pav.) Oken, *Guarea* sp., *Simarouba amara* Aubl., *Virola koschnyi* Warb., and *Zanthoxylon* sp., plus numerous vines, shrubs, and epiphytes. About 3 ha of this forest were felled in 1971 (Harcombe, 1977) and at the beginning of our 3-yr study (1979) the regrowth on this site was 8 yr old. A 50 by 100 m patch of the forest and about 1 ha of the 8- to 11-yr-old regrowth, in addition to younger vegetation described below, were used for our study (Fig. 1).

In early 1979, portions of the vegetation in Harcombe's plot and surrounding forest were felled and burned. Afterwards, four experimental vegetation types (described in Ewel *et al.*, 1982 and Blanton & Ewel, 1985), separated from one another by narrow footpaths, were established in a randomized block design with six blocks. Each 35 by 35 m block was surrounded by untouched 8-yr-old vegetation and forest remnants. Two of those treatments are of concern in this study. One was a temporal sequence of monocultures: two crops of maize (*Zea mays* L.), followed by cassava (*Manihot esculenta* Crantz), then a timber tree, *Cordia alliodora*. The monocultures were kept well weeded and did not produce seeds during the study period. The other

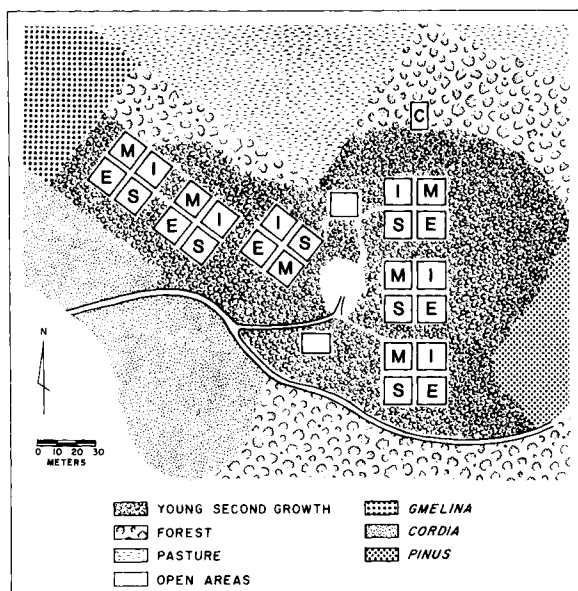


Fig. 1. Map of the study site. The four vegetation types used in this study were the old, second-growth forest in the northeast corner, a portion of which we cleared (labelled C); the second-growth vegetation that surrounded the square plots and was about 8 yr old at the beginning of this 3-yr study; six plots (labelled S) that contained successional vegetation that was 9 months old at the start of the study; and six plots (labelled M) that contained crop monocultures. Plots labelled E contained enriched successional vegetation and plots labelled I contained an imitation of successional vegetation.

treatment consisted of pioneer vegetation that appeared spontaneously and without intervention by the investigators. During our 3-yr study this vegetation increased in age from 9 to 46 months, stand leaf area index changed from 2.1 to 3.3, aboveground biomass increased from 950 to 2000 g/m², dominants grew from 5.3 to 12.5 m tall, and the number of species (all six blocks combined) increased from 81 to 233 (J. Ewel, unpubl.).

There were two other vegetation types in each of the six blocks. One of these, an imitation of successional vegetation, contained only species introduced to the site by us, so it was possible to discount seeds produced there and caught in traps. The other community, called enriched successional vegetation, was identical to the successional vegetation except that we regularly added vast numbers of seeds to each plot as part of a related research

project. Seeds added by us were not native to the site, and none of them appeared in the seed traps.

Methods

Voucher specimens were identified and deposited at the National Museum of Costa Rica. Species difficult to distinguish as seedlings (e.g., *Cecropia insignis* from *C. obtusifolia*, or *Piper* spp. from one another or from *Pothomorphe umbellata*) were placed in the smallest taxon to which we could confidently assign them. Because of their importance to succession and colonization, we also determined the life forms and modes of dispersal of the species whose seeds we encountered.

Seeds in the soil

On 21 to 23 June 1982 we sampled seeds in the soil beneath the forest, the then 11-yr-old vegetation, and the then 3.3-yr-old successional vegetation. A bulk density sampler (diameter = 8.5 cm) was used to collect samples from 0 to 4 cm (including surface litter), 4 to 10 cm, and 10 to 20 cm depths at each sample point. In the forest one core was taken at each of three locations about 10 m apart, at least 20 m from the forest edge. In the 11-yr-old vegetation one core was taken at each of 12 locations in the area surrounding the six blocks containing the young, experimental plant communities. The sampling locations were about 2.5 m outside the blocks, one near the topographic low of each block and the other near the topographic high to reduce effects due to water-mediated movements of seeds. The soil in the 3.3-yr-old vegetation was sampled at 12 points, two cores in each of the six blocks.

Samples were transported to a seed-proof shade-house where they were randomly assigned to flats containing sterilized sand. The soil from each sample was spread to a thickness of about 1 cm on top of the sand. All samples were watered daily and were checked for the presence of seedlings weekly through the first 6 weeks and less frequently for the next 19 weeks. Most seeds germinated within 6 weeks. The soil was stirred at week 14, but little ad-

ditional germination resulted. Seedlings that could not be identified immediately were marked and allowed to grow larger.

Six control flats of sterilized sand and soil placed in the shadehouse and monitored for about 6 months yielded no seedlings, indicating that there was no contamination of samples by seeds entering the shadehouse. There were some substrate contaminants, as the methyl bromide used to sterilize the sand proved ineffective in killing all of the seeds. It was easy to distinguish these contaminants, however, because they were unique species and appeared only on the edges of the flats away from our samples.

Because the time required for seedling emergence is a crucial factor governing the early stages of succession, we recorded the germination times of the seeds from the soil samples. Germination times were recorded with a precision of 2 or 3 days in the first 6 weeks and of about 1 week thereafter. Out of 1858 germinated seeds, 43 (2.3%) were not included in this analysis because of uncertainty as to exactly when they had germinated.

To obtain an estimate of soil seed storage at a time of year other than June, we took ten more soil cores from the 11-yr-old vegetation on 7 October 1982. A sharpened 20-cm diameter plastic cylinder was pounded 4 cm into the ground at 6 m intervals to obtain the samples. These samples were treated like the others and monitored until 14 December 1982.

Seed inputs

Seed rain was estimated by monitoring germination of seeds caught in traps. The traps were 0.175 m² rectangular metal flats containing soil from the site that had been sterilized in an autoclave. Steam-sterilization of this soil affects early growth of seedlings, but not seed germination (Williams-Linera & Ewel, 1984). One flat was placed in each of the six replications of the successional vegetation and of the monoculture, and three were placed near the centre of the forest, about 10 m apart. All traps were placed in depressions, such that the soil in the flat was approximately level with the surrounding

soil surface. After 4 weeks the flats were removed from the field and placed in a screened shadehouse. Each 4-week sampling period was followed by 4 weeks of no sampling. Seed inputs for these unsampled time intervals were estimated by averaging values from the sampling periods prior to and following the unsampled intervals. The first sampling period began when the successional vegetation was 9 months old (17 December 1979). Sampling was terminated > 3 yr later (24 January 1983) after 21 sampling periods.

In the shadehouse the flats were watered daily and inspected for seedlings every 3 to 4 weeks. Plants that could be identified were recorded and removed, while the others were left until further growth allowed identification. Monitoring continued for 1.5 months (sampling periods 1 to 7) or 4.5 months (periods 8 to 21). Three control flats were placed in the shadehouse with the others to correct for contamination by seed entry into the shadehouse.

This seed trapping method was compared with two others – 27 by 27 cm screen traps and 15 by 25 cm sticky traps – for the 4 week period from 6 September to 4 October 1982. The numbers of seeds caught in screen traps, sticky traps, and sterilized-soil traps were not significantly different (Waller-Duncan *k*-ratio *t* test on log-transformed data); all data presented in Results are from the sterilized-soil traps.

The traps in the weed-free monoculture only received seed inputs from other vegetation types. Therefore, the seeds they caught provided an estimate of allochthonous seed rain in the adjacent successional vegetation. Autochthonous seed inputs within each of the six plots containing young successional vegetation were calculated as the total number of seeds trapped there, minus the seed rain in the monoculture plot within the same block. Negative values were set equal to zero.

The biases that might have entered into the estimates of autochthonous seed rain depend, in part, on the seed-donor vegetation surrounding each plot. In five of the six blocks, the successional vegetation and the monoculture each bordered similar kinds of vegetation as the other (Fig. 1), so we take the estimates of seed rain on these plots to be unbi-

ased. In the sixth block (third from the left in Fig. 1) the monoculture bordered two communities that probably donated large quantities of seeds (succession and enriched succession) whereas the successional vegetation bordered two communities from which seeds were not dispersed (monoculture and imitation). This would have resulted in an overestimation of allochthonous, and an underestimation of autochthonous, seed inputs in the successional vegetation.

Forest clearing

To determine the relative importances of the soil seed bank, post-deforestation seed dispersal, and vegetative sprouts in post-deforestation regeneration, an 8 by 14 m plot in the 75-yr-old forest was cleared. Before felling, the plot contained 72 vascular plant species. Of these, 22% were trees, 18% shrubs, 15% forbs, 13% epiphytes, 13% herbaceous vines, 13% lianas, 3% palms, and 3% grasses. The vegetation was felled on 16 and 17 September 1982. Logs were removed from the site and 4 days later slash and most litter were raked off to reduce their germination-inhibiting effects (Sydes & Grime, 1981). Because one edge of the plot was coincident with the southern edge of the forest, it received direct sunlight during much of the day.

On 21 September eight 0.5 m² plots were established along the long axis of the clearing. We recorded seedling and sprout emergence and mortality on four of these plots for 10 weeks by marking individual plants at 2 week intervals.

The other four plots, at alternate locations in the row, were designated as harvest plots. Beginning at week 4, and every 2 weeks thereafter until week 10, the vegetation on one randomly chosen plot was harvested. The plants were counted and sorted by species and origin (seed, sprout, or, in the case of a few epiphytes that fell into the plots, intact plant). All samples were dried at 70 °C, then weighed. The heights of the three tallest plants in each unharvested plot were measured to the nearest 0.5 cm at the same 2-week intervals.

To estimate the importance of post-disturbance seed inputs in the early stages of succession, twelve

2 m² exclosures were constructed in the clearing. Each exclosure was a 125 by 160 cm frame, 40 cm above the ground, its top covered with 1 mm² mesh and its sides covered with muslim. Six pairs of exclosures were placed, 75 cm apart, in two parallel rows, and one randomly chosen member of each pair was used to exclude seed input. Seeds found on the top of the other exclosure each day were identified and counted, then placed on the soil under the exclosure in approximately the same location at which they would have arrived had the screen not been present.

After 9 weeks a 0.5 m² vegetation sample was taken from beneath each exclosure. All plants were cut at ground level, classified to species and origin, counted, dried at 70 °C, and weighed.

To check the effectiveness of the exclosures in preventing seed input, two 0.175 m² flats of autoclaved soil were placed in the clearing and covered with the same type of screen that topped the exclosures. Five seeds of four species germinated in these two flats, showing that the screen did not prevent all seed input. However, this leakage was probably equal in both treatments.

Seed inputs were estimated independently using two 0.175 m² flats of autoclaved soil placed in the clearing. At the conclusion of the experiment these flats were moved to a screened shadehouse. There they were watered daily for 5 months and monitored periodically for seedlings.

Results

Soil seed storage

Density

An estimated 6800 to 9500 seeds/m² were present in the top 20 cm of soil in the three communities sampled (Fig. 2). These estimates are based on germinated-seed counts from cores (mean number of seeds per core \pm S.E.) of 38 ± 6 in the 3.3-yr-old vegetation, 54 ± 13 in the 11-yr-old community, and 40 ± 4 in the forest. Coefficients of variation for 0 to 20 cm samples were 51%, 83%, and 16%, respectively.

After square-root transformations to equalize

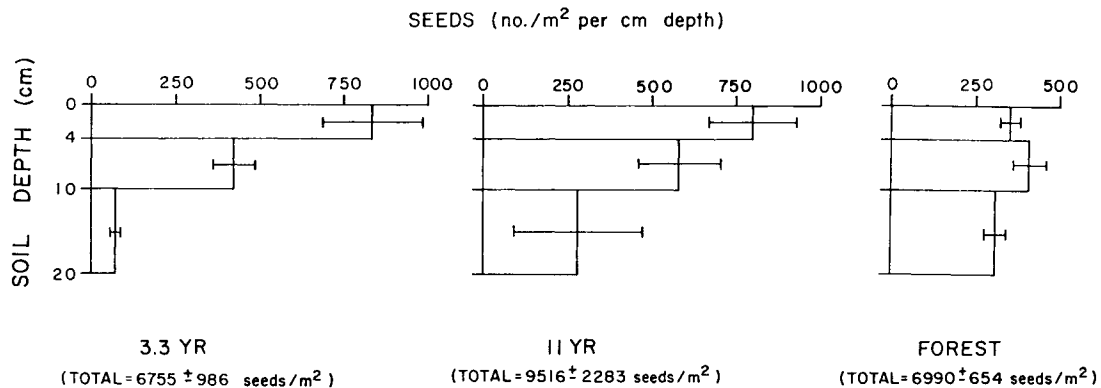


Fig. 2. Soil seed storages in the three communities. Seed density is expressed as mean number of seeds/m² per centimeter depth \pm S.E.

the variances, comparisons among communities were made using the Waller-Duncan k -ratio t -test. The 3.3-yr-old and 11-yr-old stands and the forest had total seed storages (0 to 20 cm) that were not significantly different ($\alpha = 0.05$), but there were significant differences in the surface soils (0 to 4 cm); the surface soil of the forest contained less than half as many seeds as that of the two younger stands. Densities at 4 to 10 cm were not significantly different among the three communities. Below 10 cm there were significantly fewer seeds under the 3.3-yr-old vegetation than under the forest; the number of seeds at that depth under the 11-yr-old vegetation was intermediate.

In October there were the equivalent of 1889 ± 643 seeds/m² in the top 4 cm of soil of the 11-yr-old community, which was not significantly different ($p = 0.17$) from the 3201 ± 518 present in June.

Species composition

Fifty-nine species (or groups of species), the most abundant of which are enumerated in Table 1, were found in the 27 cores. There were 47 species in the 11-yr-old vegetation, 40 in the 3.3-yr-old community, and 21 in the forest, where species richness was probably underestimated because it was sampled with only three cores.

The most abundant species also occurred with greatest frequency in the cores. There were highly positive (Spearman rank correlation coefficients ranged from 0.62 to 0.93) and significant (p always

< 0.02) correlations between the estimated mean numbers of seeds of individual species and the number of cores where those species were found. An exception was an unidentified solanaceous forb that had 147 seeds in one core but was not found elsewhere. Species found in $> 90\%$ of the cores were *Pothomorphe umbellata* in the 3.3-yr-old vegetation and *Cecropia* spp., *Phytolacca rivinoides*, *P. umbellata*, and *Solanum umbellatum* in the 11-yr-old vegetation and the forest.

Many species were present in the surface soil (0 to 4 cm), but absent or rare deeper (4 to 20 cm) in the soil: 28 of 40 species in the 3.3-yr-old vegetation, 21 of 47 species in the 11-yr-old vegetation, and 7 of 21 species in the forest. The seeds of others increased in number at deeper soil depths or were only found there: 12 in the 3.3-yr-old vegetation, 25 in the 11-yr-old community, and 14 in the forest. In the forest, the five species that were most common in the seed banks of all three communities (see paragraph above) had more seeds per centimeter depth from 4 to 20 cm than in the surface soil.

The total number of species encountered in the 11-yr-old stand dropped from 31 in June to 26 in October, even though twice as much surface area (1571 cm²) was sampled in October. Seven of the species found in June were not found in October, while twelve species found in October had not been encountered in June.

Forbs, shrubs, and grasses/sedges were the three life forms that together accounted for $> 70\%$ of the species and $> 65\%$ of the individuals in the soil

Table 2. Representation of plant life forms among the species found in soil samples and in seed traps. Total number of seeds in 0 to 20 cm soil samples was 450 in the 3.3-yr-old vegetation, 648 in the 11-yr-old vegetation, and 119 in the forest. Total number of seeds found in seed traps was 5418 in the young successional vegetation and 1005 in the forest.

Life form	Seeds in the soil						Seed inputs			
	3.3-yr-old vegetation		11-yr-old vegetation		Forest		Young successional vegetation		Forest	
	Percent of seeds	Number of species	Percent of seeds	Number of species	Percent of seeds	Number of species	Percent of seeds	Number of species	Percent of seeds	Number of species
epiphyte	< 1	1	0	0	1	1	< 1	2	2	3
forb	25	13	47	14	29	6	20	32	29	18
grass/sedge	11	7	5	8	2	1	9	8	2	6
herbaceous vine	12	4	10	4	5	2	6	8	3	4
liana	0	0	3	2	2	2	< 1	2	2	4
shrub	41	13	24	14	34	8	46	17	22	8
tree	6	2	5	3	15	1	11	5	9	4
unknown	5	0	6	2	12	0	7	1	31	1
Total	100	40	100	47	100	21	100	75	100	48

seed bank in each community (Table 2).

Fleshy, multiple-seeded fruits accounted for 79% of the seeds and 48% of the species whose seeds were found in the forest soil, but the soil seed banks of the other stands were not dominated by a single diaspore dispersal type (Table 3).

Germination

Modal germination time of all species combined was 3 weeks (Fig. 3) and 89% of the seeds had germinated by 6 weeks. The species whose seeds were relatively abundant fell into two groups. One group included species that germinated very quickly (mo-

Table 3. Representation of diaspore dispersal types among the species found in soil samples and in seed traps. Total number of seeds in 0 to 20 cm soil samples was 450 in the 3.3-yr-old vegetation, 648 in the 11-yr-old vegetation, and 119 in the forest. Total number of seeds found in seed traps was 5418 in the young successional vegetation and 1005 in the forest.

Diaspore dispersal type	Seeds in the soil						Seed inputs			
	3.3-yr-old vegetation		11-yr-old vegetation		Forest		Young successional vegetation		Forest	
	Percent of seeds	Number of species	Percent of seeds	Number of species	Percent of seeds	Number of species	Percent of seeds	Number of species	Percent of seeds	Number of species
Biotic: fleshy, 1 – 2 seeds	6	3	3	5	< 1	1	8	11	2	4
fleshy, > 2 seeds	53	13	40	13	79	10	43	20	32	13
hooked appendages	3	1	4	1	< 1	1	13	3	< 1	1
subtotal	62	17	47	19	< 81	12	64	34	< 35	18
Abiotic: winged, plumed	14	6	9	6	6	3	4	9	2	6
explosively ejected	< 1	1	< 1	2	0	0	< 1	2	< 1	2
subtotal	< 15	7	< 10	8	6	3	< 5	11	< 3	8
No obvious adaptation	18	13	17	14	4	3	22	25	7	17
Unknown	6	3	26	6	9	3	9	5	56	5
Total	100	40	100	47	100	21	100	75	100	48

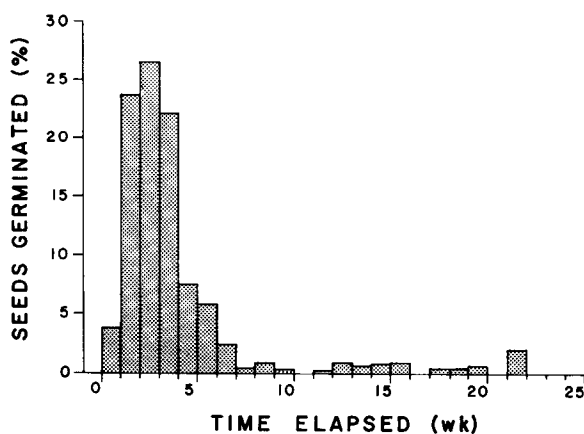


Fig. 3. Germination time distribution for seeds ($n = 1815$) from all soil samples. In addition to the 27 soil cores taken as part of this study, the graph includes data from 12 additional cores taken in two adjacent plant communities with similar seed-bank floras.

dal time of 2 weeks): *Clibadium surinamense*, *Digitaria ciliaris*, *Hyptis pittieri*, *Neurolaena lobata*, *Phytolacca rivinoides*, *Solanum nigrescens*, and *Vernonia patens*. Species in the other group took about twice as long to germinate (modal time of 4 weeks): *Cecropia* spp., *Heterocondylos vitalbis*, *Manettia reclinata*, *Piper* spp., *Pothomorphe umbellata*, and the unidentified solanaceous species. Seeds of longer-lived species tended to germinate more slowly than those of shorter-lived species: the modal germination time of grasses and sedges was 2 weeks; that of forbs was 2 weeks; shrubs, 3 weeks; vines and lianas combined, 4 weeks; and trees, 4 weeks.

Seed inputs

During the first year germination was monitored in the shadehouse for 1.5 months after each trapping period. If seeds in the traps germinated at the same rate as those from the soil cores (Fig. 3), seed rain during the first year may have been underestimated by about 10%. However, it is likely that seeds in the soil seed bank germinated more slowly, on average, than freshly trapped seeds, so the error is probably < 10%.

Quantities

During the 3 yr that we trapped seeds in the young successional vegetation, we caught 5418 individuals (the equivalent of 10075/m² when estimates for unsampled periods are included) comprised of 75 species. Annual seed input was remarkably constant: 3560 seeds/m² during the first year of trapping (when the vegetation was 0.7 to 1.7 yr old), 3300 seeds/m² during the second year, and 3215 seeds/m² during the third. Approximately nine seeds fell on each square meter every day.

In the adjacent forest (where there were only three traps) we caught 1005 individuals (3740/m²). More than half of those seeds (562, or 2090/m²) fell in the first year, only 311 (or 1155/m²) were trapped in the second year, and still fewer (132, or 490/m²) were caught in the third.

Coefficients of variation of the numbers of seeds trapped during any sampling period were high (32 to 673 in the successional vegetation and 37 to 174 in the forest), indicating considerable patchiness in seed rain. Only two species were ever found in all six traps in the young successional vegetation at one time: *Phytolacca rivinoides* and *Mikania micrantha*.

Species composition

More species were trapped in the young successional vegetation than in the forest (75, compared to 48), but we used only half as much trap surface-area in the forest. The ever-increasing species-time curves (Fig. 4) suggest that more species would have been captured with further sampling in both communities. Ten species had seed-input rates > 100 m⁻² yr⁻¹ (Table 1).

Shrubs and forbs accounted for 65% of the species trapped over the 3-yr study period in the young successional vegetation and 54% of those trapped in the forest (Table 2). Together these two life forms contributed 64% of all seeds and 61% of all species trapped in both communities.

Diaspores without obvious dispersal mechanisms (principally legumes, grasses, and sedges) and fleshy-fruited, multiple-seeded fruits together accounted for 60% of both the individuals and the species trapped over the 3-yr study period in the young successional vegetation and the forest com-

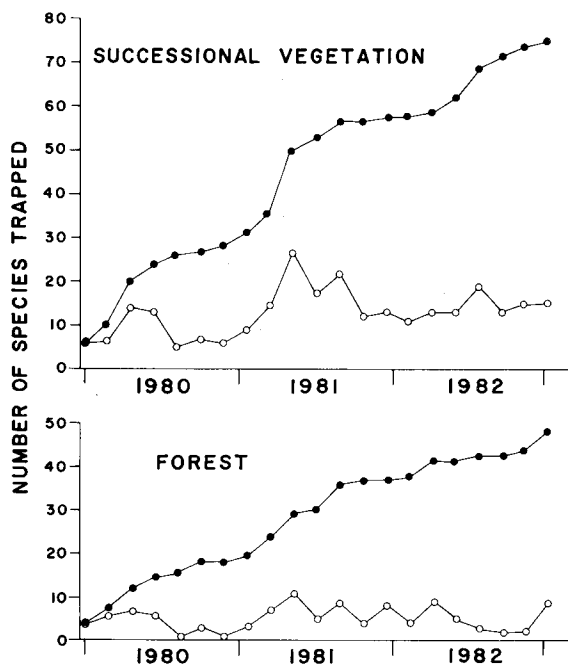


Fig. 4. Number of species (open circles) and cumulative number of species (closed circles) caught in seed traps in the young successional stand and the forest.

bined. Neither seeds from fleshy fruits containing few seeds nor those from wind-dispersed diaspores (winged or plumed) accounted for $> 8\%$ of the seeds caught in either community (Table 3). Species with biotically mediated dispersal (fleshy fruits or those with hooked appendages) made up 58% of all seeds captured.

Seasonal patterns

The numbers of seeds trapped in the young successional vegetation varied throughout the year, but peak seed rain tended to accompany or follow dry periods (Fig. 5). In the forest, the peaks of seed input in both 1980 and 1981 came early in the rainy season; there was no well-defined peak in 1982, when seed inputs were much lower.

In the young successional vegetation the number of species in traps tended to oscillate, but the oscillations were not synchronous with seasonal changes (Fig. 4). There were no discernible seasonal patterns of oscillations in the number of species trapped in the forest.

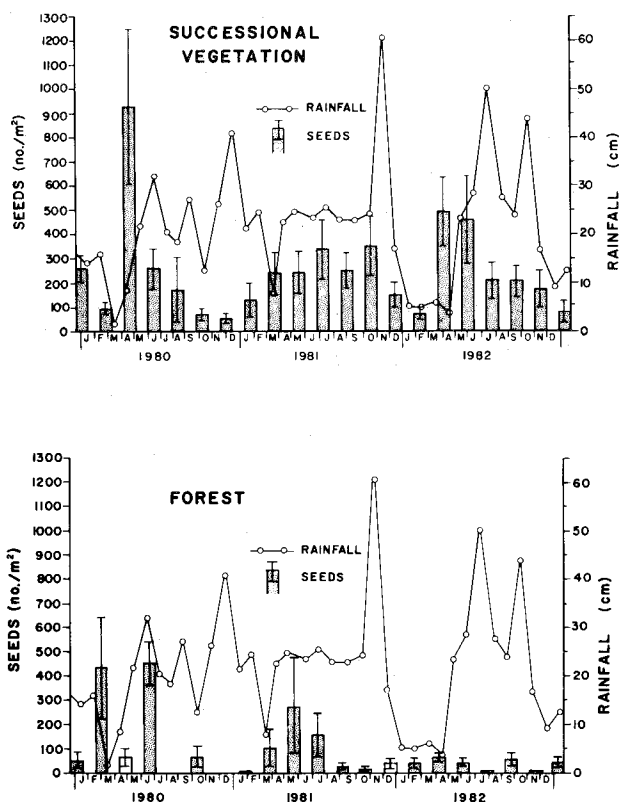


Fig. 5. Seed input in the young successional stand and the forest during the 3-yr study. Input is expressed as mean number of seeds/m²/4 weeks \pm S.E.

Seasonal patterns of seed input were evident among the species caught in the traps in the successional vegetation (but not those trapped in the forest). Seven common species (or groups of species) were caught in all months: *Bocconia frutescens*, *Cecropia* spp., *Clibadium surinamense*, *Panicum trichoides*, *Paspalum decumbens*, *Solanum nigrescens*, and *S. umbellatum*. A second group of species dispersed seeds only during the rainy season: *Borreria laevis*, *Palicourea guianensis*, *Panicum maximum*, *Piper* spp., *Pothomorphe umbellata*, and *Vernonia brachiata*. Two common species, *Vernonia patens* and *Acalypha macrostachya* Jacq., dispersed seeds only from March to June, the transition between the dry season and the rainy season. *Phytolacca rivinoides* and *Solanum schlechtendalianum*, were trapped every month except September to November, the end of the rainy season.

Successional changes

Even though the numbers of seeds trapped in the successional vegetation were remarkably constant from year to year, there were important successional changes in the life forms represented by seeds trapped during the 3-yr-period. Seeds of common, fast-maturing forbs (e.g., *Cardamine axillaris*, *Phytolacca rivinoides*, and *Solanum nigrescens*) were most abundant during the first year of sampling, while seeds of other vines, shrubs, and trees became more abundant with vegetation age.

While various modes of dispersal were represented in commonly trapped species throughout the 3 yr of sampling, biotically dispersed seeds (fleshy-fruited or having hooks) accounted for 93% of the seeds trapped during our first year of measurement, but only 51 and 69% during the second and third years, respectively. The abundance of seeds adapted for biotic dispersal during the first year reflects their high rate of production in the very young successional vegetation; more of these biotically dispersable seeds probably fell into the traps from overhanging vegetation than were delivered there by animals.

Annual changes in seed rain in the forest were related to changes in the composition of the contiguous successional vegetation. For example, the pioneer forbs *Cardamine axillaris*, *Emilia fosbergii* Nicols. and *Phytolacca rivinoides* were absent or sparse in the forest patch, yet together they made up 45% of the forest's seed in the first year. In the second year two species of *Solanum*, sparse in the forest but abundant in the successional vegetation, dominated the forest's seed inputs. Seed inputs to the forest in year 3 were substantially lower than they had been during the first two years, even though the forest's species composition had not changed dramatically. After first-year dominance of the forest seed rain by forbs (47%), shrubs and trees accounted for 71% of the seeds in year 2 and 46% in year 3.

Allochthonous and autochthonous seed rain

The most commonly trapped seeds were species already present in the community. Even though the layout of our plots within blocks may have biased our results toward the low side (see Methods), we

estimate that autochthonous seeds comprised at least 74% of the total seed input over the 3-yr-period (Table 1). The proportion of seed rain that was autochthonous ranged widely among sampling periods, from 37% in 14-month-old vegetation to 99% in 31-month-old vegetation. However, total autochthonous seed rain varied little from year to year and exhibited no seasonal or successional patterns.

Over the 3-yr study, fewer species arrived in monoculture seed traps (51) than in those located in the successional vegetation (75), although the number of species and cumulative number of species caught followed similar temporal patterns in the two communities. Thirty-six (48%) of the species found in traps in the successional vegetation were not encountered in monoculture traps and 13 (25%) of the species trapped in the monoculture were never encountered in the natural regeneration. This may have been due to small sample sizes or it may indicate that some species were preferentially dispersed into one or the other of the two communities.

Species in seed rain compared to species in the soil seed bank

Through June, 1982, when soil samples were taken, 77 species were encountered in soil samples or seed traps in the young successional stand. Thirty-seven species were found only in traps, 15 were only in soil samples, and 25 were found in both. The shared species comprised 90% of all seeds counted.

Some species (e.g., *Cardamine axillaris*, *Paliourea guianensis*, *Panicum trichoides*, *Solanum schlechtendalianum*) had few seeds in the soil despite high seed inputs in the months prior to our soil sampling (Table 1). Others had seed inputs that were substantially smaller than soil seed storage (e.g., *Manettia reclinata*, *Neurolaena lobata*, and *Solanum jamaicense*). These might have gradually accumulated in the soil or they might have been deposited there in large numbers in the past and retained their viability. The most dramatic examples of large soil seed storages and low input were *Piper* spp. and *Pothomorphe umbellata*, which had two or three orders of magnitude more seeds in the soil than had arrived on the site during the previous 2.5 yr. No life form or diaspore dispersal type was

exclusively associated with either low storage and high input or high storage and low input.

Post-deforestation recovery

Succession in the forest clearing was rapid. A total of 2406 individuals emerged in 12 weeks on the four 0.5 m² plots. The rate of emergence dropped rapidly after 2 weeks and from weeks 8 to 12 only about 7 plants/m² emerged weekly. Mortality reached a high of 40 deaths m⁻² wk⁻¹ after 4 weeks, but declined to about half that rate thereafter. Much mortality was caused by herbivores; many missing stems had been cut near ground level, and we saw no evidence of fungal attack. The net result of emergence and mortality was a stand of plants that reached mean densities of 1000 individuals/m² within 4 weeks and maintained that density through week 12.

Forbs and herbaceous vines accounted for most biomass (> 25% each) until week 10. Most shrubs started growth slightly later than the forbs and vines, then increased in both numbers and biomass between weeks 8 and 10. At week 10, when the heights of the tallest plants on sample plots averaged 24 cm, shrubs accounted for 29% of the individuals and 27% of the total biomass of 26 g·m⁻². During the 10 weeks immediately after forest clearing tree biomass never represented more than 6% of the total.

A survey of the clearing 12 weeks after revegetation revealed 52 species, 21 of which had been present on the plot before it was revegetated. Of those 52 species, 29% were forbs, 19% herbaceous vines, 15% trees, 13% shrubs, 10% grasses or sedges, 4% lianas, 4% epiphytes, and 6% unknown. Regeneration was dominated by plants that grew from seeds: of the 52 species, 83% originated solely from seeds, 8% were entirely of sprout origin, 4% were found as both seedlings and sprouts, and three species of epiphytes apparently fell from surrounding trees. More than 98% of the plants counted on the harvest plots were seedlings, although sprouts were larger and collectively represented about 4% of the aboveground biomass.

Most of the 21 species that were present both be-

fore and after creation of the clearing regenerated from seeds rather than sprouts. They included several trees: *Cecropia* spp., *Cordia alliodora*, *Goethalsia meiantha*, *Sorocea pubivena* Hemsl., and *Trema micrantha* (L.) Blume. However, four of the 21 species regenerated only vegetatively; vines were especially prone to resprout.

Post-clearing seed rain was not an important source of seedlings. During the 9-week sampling period seed input was only 15 ± 6 seeds/m² as measured by the number of seeds that landed on the screens or 11 ± 11 seeds/m² as measured by the number of seeds trapped and germinated in sterilized soil. Except for one *Aristolochia* sp. *samara*, all of the 175 seeds that fell on the screens appeared to have arrived in droppings of birds and/or bats. Inputs of new seeds were temporally and spatially patchy. On 45 of 63 sampling days no seeds arrived, and seeds were found on more than one of the six screens on only 5 days.

Nor did post-clearing seed rain have much influence on the biomass, species richness, or density of the early successional vegetation. Aboveground biomass at week 9 (41.5 ± 8.7 g·m⁻²) and the number of species present (mean = 28/0.5 m², range = 20 to 36) did not differ significantly between plots that received new seed input and those that did not. Plant density was significantly higher ($p = 0.04$) in the plots that did not receive post-disturbance seed inputs than in those that did, but the differences were modest (1021 ± 252 compared to 912 ± 216 plants/m²).

Discussion

Grubb (1977) emphasized that many aspects of reproduction must be considered in attempts to explain community patterns and species richness. Factors such as seed production, the distance and timing of seed dispersal, and post-dispersal seed longevity were probably important determinants of the species richness of potential colonists on our site. Autochthonous seed rain reflected on-site seed production, allochthonous seed inputs provided a combined measure of off-site seed production and

dispersal, and the soil seed bank revealed information about longevity.

The 119 species we encountered either in soil cores or in seed traps probably represented many combinations of seed production, dispersal, and longevity. Presumably they ranged from species that produced copious quantities of widely dispersed, long-lived seeds to those that produced few, poorly dispersed seeds that either germinated or succumbed shortly after dispersal. Species that produced small numbers of seeds and/or poorly dispersed seeds with short lives would seem to be nonadaptive, yet most of the ± 350 species that colonized our site during the three years that we monitored seed rain apparently fell into this unlikely category; they did not appear with significant frequency in either soil samples or seed traps. Many species seem to have high post-germination survival, but do not produce prodigious quantities of seeds that are either well dispersed or long-lived.

Most congeners had quite different ratios of seed storage to input, which reflect differences in seed longevity, the timing of dispersal, and seed production. The four *Solanum* species, all of which have fruits that are fleshy, multiple-seeded, and 5 to 20 mm in diameter, illustrate how such differences might endow closely related species with different regeneration niches. Seeds of *S. nigrescens*, a forb, were trapped primarily in 0.7- to 1.7-yr-old vegetation, which contained reproductive adults of that species. One year later, there were approximately 100 seeds/m² of *S. nigrescens* in the surface soil, suggesting that its seeds are at least moderately long-lived. The other three *Solanum* species were shrubs that matured 1 to 3 yr later; their seeds were trapped in greatest abundance when the vegetation was > 1.7 yr old. *Solanum jamaicense* had low seed inputs in the successional vegetation, but a large seed population in the soil; this species is probably a long-lived constituent of the soil seed bank. *Solanum schlechtendalianum*, in contrast, had few seeds in the soil, but a large seed input (439 seeds m⁻² yr⁻¹) in the third year, when the vegetation was 2.7 to 3.7 yr old. *Solanum umbellatum* had both high rates of seed production and long-lived seeds.

The early colonists on our site included several

species that produced massive quantities of seed. However, like other pioneer species, they did not succeed themselves: their seeds either died, became incorporated into the soil seed bank (from which they would presumably stand some chance of recolonizing later), or were dispersed to other sites. In no case did copious seed production result in immediate, abundant regeneration at the site where the seeds were produced.

Although most seeds we trapped originated in the stands being studied, much of the vegetation's species richness resulted from allochthonous seeds. Most species whose mode of dispersal could be inferred had seeds adapted for animal dispersal (see also Swaine & Hall, 1983; Foster, 1982; and Guevara, 1986). The diversity of regenerating tropical forests is clearly dependent on animals.

The numbers of seeds in the top 4 cm of soil did not change from June to October in the 11-year-old vegetation. The observed differences in species composition may have been real and caused by seasonal changes or by June-to-October succession; alternatively, they might have been artifacts of inadequate sampling. It would be surprising, however, if seasonal changes did not occur in tropical soil seed banks. Garwood (1983), for example, described four groups of species having different seasonal timings of both seed dispersal and germination. The relative abundances of seeds in the soil of each of these groups would presumably fluctuate accordingly.

It is beneficial for a species to be a member of the on-site soil seed bank only if the vegetation is likely to be destroyed within the lifetime of its seeds. The germination of long-lived seeds is usually stimulated by the environmental changes associated with disturbance, such as increases in light (Vázquez-Yanes, 1976) or temperature fluctuations (Thompson *et al.*, 1977; Guevara, 1986). On sites such as ours, with a history of recurrent disturbance, the soil seed bank is large and plays a dominant role in early succession, just as it does in other fluctuating environments (Van der Valk & Davis, 1978; Roberts, 1981). Whereas mature tropical forests may have 25 to 1000 seeds/m² in their surface soils (Keay, 1960; Bell, 1970; Guevara & Gómez-Pompa, 1972; Liew, 1973; Ashton, 1978;

Cheke *et al.*, 1979; Hall & Swaine, 1980; Uhl *et al.*, 1981, 1982; Putz, 1983; Hopkins & Graham, 1983; Uhl & Clark, 1983; Guevara, 1986), the soil beneath secondary tropical forests contains many more, often 1000 to 8000/m² (Guevara & Gómez-Pompa, 1972; Ewel *et al.*, 1981).

The soil of the 75-yr-old forest we studied, which was contiguous to young vegetation, contained three times as many seeds as an equal-aged forest about 150 m away (Young, 1985). Although seed rain (in seeds m⁻² day⁻¹) is relatively low in intact tropical forests (0.04, Hopkins, 1970; 0.4, Jackson, 1981; 0.2, Foster, 1982; 0.1, Uhl & Clark, 1983), forests near successional vegetation receive an order of magnitude more seeds (1.5 to 8.3, Cheke *et al.*, 1979; 3.4, this study), as do treefall gaps in mature forest (2.4 to 7.8, Brokaw, 1980) and early successional vegetation (9.2, this study).

Janzen (1983) inferred several potential impacts of human-modified habitats on the composition of surrounding ecosystems. Two such impacts were evident at our site: 1) the communities studied shared a common seed-bank flora of successional species and 2) there was massive export of seeds from successional vegetation to nearby forests. As the abundance of secondary forests and forest edges increases in the tropics, post-deforestation regeneration will no doubt become increasingly dominated by successional species with long-lived seeds.

Succession and soil seed storage

The number of seeds per unit volume of surface soil tended to decrease with increasing vegetation age, while seed density in subsurface soil tended to increase with age. The abundance of seeds in the surface soil of young vegetation was probably a direct result of the high rate of inputs from the overtopping successional plants, many of which were prolific seed producers. For example, from December 1979 to January 1983 approximately three times the number of seeds fell in the 3.3-yr-old vegetation as in the forest. It is likely that some of the seeds on the surface succumbed to pathogens and seed predators, some germinated, and some

eventually trickled downward through soil cracks, tunnels of invertebrates, and root channels to become the subsurface seed bank that characterized older vegetation. These deeply buried seed populations might be relatively stable; Rampton & Ching (1970) showed that seeds buried to 18 cm survived longer than seeds of the same species buried closer to the surface.

A diagram (Fig. 6) showing the probable successional changes in surface-soil seed storage (0 to 4 cm) on the study site was constructed from our data and earlier estimates of seed densities.

In 1979, Ewel *et al.* (1981) found 67 species and about 8000 seeds/m² in successional vegetation that was approximately 8 yr old at the time of their study (i.e., the 11-yr-old vegetation we studied 3 yr later). Felling that vegetation reduced storage over the next 3 mo to about 6000 seeds/m² and 51 species, although the density decline was not statistically significant. The slash on the site was burned in March of that year, and the fire significantly reduced seed storage to < 3000 seeds/m² and 37 species.

The hypothesized decline in the weeks following the fire is based on our observation that approximately 85% of the seeds in the surface soil germinated after we cleared the patch of forest in 1982 (i.e., about 1200 plants/m² emerged in 12 weeks, most were seedlings, and there had been 1400/m² seeds in the top 4 cm of soil). At this point, soil seed storage would have been at its low, consisting

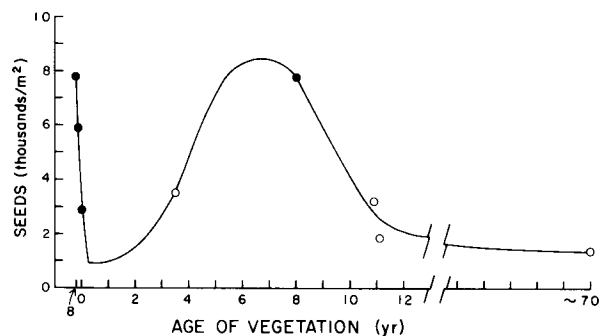


Fig. 6. Trends in surface soil (0 to 4 cm) seed storage during succession. The data points are from Ewel *et al.* (1981) (closed circles) and this study (open circles). The 8 accompanied by an arrow near the origin refers to the age of the vegetation in 1979, when the site was cleared.

perhaps of as few as 450 seeds/m² in the surface soil.

Thereafter, the number of seeds in the soil began to increase. The seed bank increased slowly at first, due to the absence of on-site seed production. For example, we caught only 36 ± 19 seeds/m² (11 species) in a pilot trapping experiment during the 2 weeks immediately after the 1979 burn and 11 to 15 seeds/m² during the first 63 days after the 1982 forest clearing. Uhl *et al.* (1981) captured no seeds during 2 weeks on a newly burned site. Guevara & Gómez-Pompa (1972) found that 2-month-old regrowth had only 45% as many soil seeds as 5-yr-old vegetation. However, by the time our stand was 3.3 yr old, soil seed populations were as dense and species-rich as they had been just after the burn. Many of those seeds were produced by plants on the site.

Two lines of evidence lead us to infer that soil-seed densities would peak about 4 to 7 yr after deforestation: 1) large quantities of seeds would have accumulated because inputs were high from late 1979 through 1982 and germination was probably low beneath the dense vegetation, and 2) Ewel *et al.* (1981) observed large numbers of seeds in the soil of 8-yr-old vegetation. After this peak the soil seed bank would then decline as some seeds lost their viability and the vegetation became dominated by species that were less prolific. Estimates of surface-soil seed storage in both the 11-yr-old community and the forest follow this pattern.

The shape of the soil-seed-storage curve (Fig. 6) might typify many kinds of successional vegetation, even though the numbers of seeds in the soil are likely to vary substantially among sites. The magnitude of the temporal fluctuations would be damped on sites that are so isolated that they never acquire large populations of those species that form soil seed banks. As deforestation advances, however, such sites are fast becoming the exception rather than the norm of the humid tropics.

This model helps to explain why sites supporting vegetation of different ages respond so differently after deforestation. For example, post-deforestation successional vegetation in the primary forest studied by Uhl *et al.* (1981) was sparse and depauperate in comparison with the exuberant regrowth we ob-

served or that Harcombe (1977) described from his earlier study at our site. Such dramatic differences may be determined less by abiotic site characteristics such as soil fertility than by soil seed storage at the time of deforestation.

Response to disturbance

Recruitment from the soil seed bank numerically overwhelmed that from the post-disturbance seed rain in our experimental clearing. The 85% recruitment from the surface-soil seed bank that we observed is much higher than other values in the literature (reviewed by Harper, 1977 and Roberts, 1981), most of which range from 1 to 10%.

Most of the seeds in the soil at our site began germination within a few weeks, as has been reported by others who worked in the tropics (Kellman, 1978; Hall & Swaine, 1980; Hopkins & Graham, 1983). Within weeks the ground was covered by dense vegetation that contained all of the life forms present in the 75-yr-old forest. This diversity of life forms arose from seeds stored in the soil. Putz (1983), Hall & Swaine (1980), Hopkins & Graham (1983), and Guevara (1986) also found that tropical soil seed banks included a broad array of life forms. This contrasts sharply with the temperate zone, where herbs account for most long-lived seeds (Roberts 1981).

That early flush of successional vegetation included 29% of the species (including the dominant tree) found in the forest. Most of these clearly originated from the soil seed bank or from sprouts, but there were a few species whose seeds arrived afterwards in the form of infrequent and spatially patchy seed inputs.

Primary forests of the humid tropics are fragile (*sensu* Gómez-Pompa *et al.*, 1972), in part because many of their species have poorly dispersed, short-lived seeds. Once such forests are destroyed, their original floristic composition returns very slowly, even if deforestation is not accompanied by soil degradation (Whitmore, 1982). The regeneration of secondary forests, such as the one we studied, is a different matter. Many common successional species have well-dispersed and/or long-lived seeds, so

forest destruction is quickly followed by regeneration. Where secondary tropical forests must be harvested to serve human needs, this resiliency invites the development of management practices that take advantage of the useful successional species that regenerate profusely.

Acknowledgements

This research was funded by National Science Foundation grants DEB 78-10721, DEB 80-11136, and BSR-8506373. We thank the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) for land and facilities; Martin Artavia, Luis Coto, Donald Hazlett, and Manuel Rivera for assistance in the field; John Cornell for statistical advice; Gary Hicks, Charles Johnson, and Michael Kelly for computer programming; George Fuller and Dawn Greene for illustrations; and Peter Feinsinger, Donald Hazlett, Martin Kellman, Dennis Knight, Diane Lorenz, Ronald Myers, Laurie Parendes, Francis Putz, Melissa Savage, Michael Swaine, and Thomas Veblen for reviews.

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