

The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon

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Abstract

Seed dispersal and forest regeneration were studied on a 30 × 150 m strip cleared by 'strip-cutting,' a system of forest management designed for sustained yield (Hartshorn 1989), in high terrace rain forest in the Department of Loreto, Peru. After one year the strip was dominated by seedlings of a few bat- and bird- dispersed pioneer tree species (*Cecropia* spp., Melastomataceae, and *Alchornea triplinervia*); stump sprouts from cut trees and saplings that survived the clearing were less numerous. The density of saplings (> 2 m in height) surviving the clearing was 903 per hectare; 94% of these survived the subsequent 18 months. About 30% of 417 stumps (> 7.5 cm diameter at breast height) resprouted within 3 months, with an additional 10% sprouting in the subsequent 10 months. Sprouting frequency was greater for small stumps than large and varied greatly among plant families. Seed deposition over this year was much lower in the interior of the strip, both in species richness and numbers of seeds, than within the forest; strip edges were intermediate in richness and number. The decline in seed input from forest to edge to strip, both in species and in numbers of seeds, was most pronounced for bird-dispersed taxa (primarily Melastomataceae); bat- and wind- dispersed taxa were more evenly distributed. The similarity in bat species composition between the strip and nearby primary forest was higher than the similarity in bird species composition between these habitats, reflecting a failure of many forest bird species to venture into the strip. The predominance of *Cecropia* spp. and other pioneers of minimal commercial value in the regeneration question the sustainability of strip-cutting. Subsequent succession and future tree species composition on the cleared strip will depend not only on the survivorship and growth of sprouts, survivors, and seedlings, but also on responses of different seed-dispersing animal taxa to changes in the species composition and structure of the vegetation in the strip.

Introduction

Natural forest management for sustained yield is considered an alternative to deforestation in tropical rain forests (Mergen & Vincent 1987; Buschbacher 1990). One system of forest manage-

ment for sustained timber yield that holds great promise is the strip-cut system (Hartshorn 1989; Anonymous 1990; Buschbacher 1990). In this system long, narrow (30–40 m) strips are clearcut and all timber is extracted. This width was selected to simulate the diameter typical of natural

treefall gaps, which are the principal sites of natural regeneration of many valuable light tropical hardwoods (Hartshorn 1980, 1989). Animal, rather than mechanical, traction is used in order to minimize compaction of the soil. No seedlings are planted in the strips; rather natural regeneration from seeds and stump sprouts is permitted. Silvicultural treatments may be applied to improve the representation of desirable tree species. In a forest managed according to this scheme, a small percentage of the surface area will be cut each year, for the first 30–40 years. After this time, timber would be extracted from the regenerated forest in the oldest strips. The first implementation of this strip-cut system has been in the Palcazu Valley in Peru, as part of a joint United States Agency for International Development (AID) and Peru Instituto Nacional de Desarrollo (INADE) development project (Hartshorn 1989; Anonymous 1990).

Before the strip system is implemented on a large scale, it is necessary to evaluate its potential for long-term sustainability. A key factor in the determination of sustainability is the species composition of the forest that regenerates after logging. That species composition may be shaped by four modes of regeneration: advance regeneration (surviving seedlings and saplings), sprouting, germination of dormant seeds in the seed bank, and dispersal of seeds from the forest. We are investigating the contribution of each mode, with particular focus on seed dispersal, to forest regeneration after strip cutting in a lowland rainforest site in the Peruvian Amazon. The seed dispersal research is further focused on the role of birds and bats, as these are among the principal dispersal agents of Neotropical rain forest trees (Howe & Smallwood 1982). By investigating the spatial and temporal patterns of seed dispersal we hope not only to help evaluate the sustainability of strip-cutting, but also to suggest changes to parameters such as strip width and season-of-cutting that may increase the abundance of desired tree species. In this paper we report on major trends observed during the first year of our study.

Methods

Study site and climate

This research was done at the Centro de Investigaciones Jenaro Herrera (CIJH) (4° 55' S, 73° 40' W), a field station operated by the Instituto de Investigacion de la Amazonia Peruana (IIAP) and located on the Ucayali River approximately 140 km south of Iquitos. Long-term records show a mean annual precipitation of 2800 mm, with a relatively dry period from June to September (Spichiger et al. 1989).

Two strips, each 30 by 150 m, were cut in primary lowland rain forest on high terrace. A few large trees of selected species had been removed from this forest approximately 15–20 years earlier, but its canopy was intact. Soils were sandy clay loam with pH 3.6–4.0 (unpubl. data). All analyses reported here refer to the first of these strips, cleared at the end of the rainy season (April – May 1989). This strip was on level topography, with its long axis running north–south. The families best represented in the canopy were Lecythidaceae, Leguminosae, and Sapotaceae; Burseraceae were particularly numerous in the midstory.

A reference collection of seeds was developed from plant specimens with ripe fruit collected from the forest and from disturbed areas. Plant identifications were made by Fernando Cornejo and Rodolfo Vasquez. Voucher specimens will be deposited at the Herbarium Herrense at CIJH at the completion of this project.

Clearing

Lianas and understory palms were cut in December 1988; trees greater than 5 cm dbh were cut 24 April–9 May 1989, beginning with the smallest diameter classes and progressing to larger classes. Wherever possible we avoided cutting trees smaller than 5 cm dbh. Directional felling was used to ensure that all crowns landed within the 30 m strip. Six large trees located near the edge of the strip but leaning out were not felled. Botanical specimens were collected from each felled

tree. Stumps were tagged with the number used for the botanical specimen.

Eight of the large trees were sawn into boards within the strip using a 'tableadora' consisting of a chainsaw mounted on a carriage. Some of the other wood was processed as roundwood, 'sinchinas,' and charcoal (Cornejo & Gorchoy, in prep.). All forest products were removed by human labor; neither machines nor draft animals entered the strip. Unused logs were removed from the strip in order to simulate site conditions that would predominate after the more complete utilization planned for this management system (Anonymous 1990). These logs were deposited in the adjacent forest.

Regeneration

Small trees (< 5 cm dbh but > 2 m in height) that survived the clearing were tagged and measured in June 1989, shortly after the strip was cleared, and again in November 1990. The northernmost 15 m and southernmost 15 m were excluded from this inventory because these areas were subject to a different environment (e.g. more shade) than the rest of the strip.

Twenty transects, each 0.5 m wide and extending across the strip (30 m) were inventoried in July 1989 and July 1990. In the first inventory all stems that had survived the clearing, no matter how small, were marked with a spot of red paint, so that this advance regeneration could later be distinguished from new seedlings. In the second inventory, we counted all stems taller than 50 cm; only stems classified as trees are analyzed here. Tree stems were classified as stump sprouts (even small diameter stems were examined for evidence of cutting and resprouting), advance regeneration (present in 1989 inventory but not sprouts), or seedlings. Only the tallest stem was counted on stumps with multiple sprouts.

In August 1989 and again in June 1990 we censused stumps of trees > 7.5 cm dbh for the number of sprouts and height of the highest sprout.

Seed traps

Ninety six seed traps were placed within the strip on 15 June 1989, shortly after clearing was completed. Each trap consisted of a nylon cloth supported by a plastic frame measuring 50 cm × 50 cm standing 40 cm above the ground. Traps were placed in six columns of 16 traps each; columns were located 2.5, 7.5, and 12.5 m from the west edge of the strip, and 2.5, 7.5, and 12.5 m from the east edge (Fig. 1). Two additional columns of 16 traps each were placed in the forest 25 m east and 25 m west of the strip (Fig. 1). Within each column, adjacent traps were 7.5 m apart.

At semi-monthly intervals for 12 months the cloths were collected and replaced by clean cloths. The contents of each cloth were carefully checked for seeds and fruits, which were identified with the aid of the reference collection. When intact fruits were recovered the number of seeds contained within was counted or was estimated using the average from a sample of fruits of that species. In order to expedite the detection and counting of seeds less than 1 mm in diameter, we passed the contents of the forest and edge traps through a fiberglass screen with 1 mm square openings and separately inspected the fractions that did and

Outline of strip showing location of seed traps

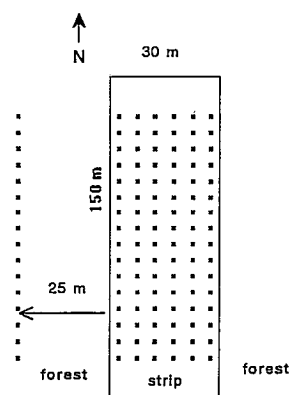


Fig. 1. Location of seed traps in and near the 30 × 150 m logged strip. Eight columns of 16 traps each were positioned in June 1989: two columns in the forest (25 m west and 25 m east of the strip) and six columns within the strip (2.5 m, 7.5 m, and 12.5 m from the west edge and the same distances from the east edge).

did not pass. Beginning with the fifth semi-monthly collection we mixed the material that passed the screen and then inspected a randomly chosen half. Preliminary trials revealed that nearly all species present in the entire sample were detected in the subsample, because when very small seeds were found they were usually in large numbers. Seed counts from the inspected half were then doubled to approximate their abundance in the entire trap.

We identified any fruiting plants above each seed trap. This enabled us to distinguish between fruits and seeds that fell from the parent plant from those that were truly dispersed, and analyze the latter data separately.

Species were determined to be dispersed by birds, bats, or both based on the presence of their seeds in fecal samples obtained from captured animals (below). Species were considered wind-dispersed if their diaspores contained wings or plumes or if seeds dispersed passively from capsules that remained on the plant.

Bird and bat capture

In order to determine the dispersal mode of the seeds reaching the strip, and to document seasonal and successional changes in the use of the strip by potential dispersal agents, we netted birds and bats in the strip monthly from June 1989 through May 1990. To determine the broader habitat use of animals that visited or colonized the strip, we netted both taxa in primary forest (monthly) and a strip of approximately 15 year-

old secondary forest 1 km from the strip (for five of the 12 months). Bats were also netted in agroforestry plantations and open areas near the CIJH buildings (six months). Nylon mist-nets were set for bats on one to three nights and for birds on one to four days per site per month. In the strip nets were set primarily along the perimeter. In the forest sites nets were primarily set along (for birds) or across (for bats) trails.

Captured animals were kept in cloth bags for at least one hour, identified, and released. Each bag was inspected for fecal material; if present this was carefully inspected for insect parts and intact seeds. Seeds found in feces were identified with the aid of the reference collection.

Bat and bird species composition in the different habitats was compared using the Index of Similarity $I = 2C / A + B$ where C equals the number of species shared between the two habitats and A and B are the numbers of species in each of the two habitats (Krebs 1985). This index ranges from 0 (no overlap) to 1.0 (complete overlap).

Results

Regeneration

Fourteen months after clearing, 743 arborescent stems taller than 0.5 m were found on the 20 0.5 m wide transects across the strip, equivalent to 2.48/m² or 24,800/ha. Most of these (72%) were classified as seedlings, 19% as stump sprouts, and 9% as advance regeneration; seedlings predominated in all size classes (Table 1).

Table 1. Mean \pm standard error number of advanced regeneration (survivors), new seedlings, and stump sprouts of tree taxa, grouped by stem height category, in 20 15 m² (30 m \times 0.5 m) transects in the strip, July 1990. Only the tallest sprout was counted on each stump.

Regeneration Class	Height category (m)				Total
	0.5-1.0	1.0-1.5	1.5-2.0	> 2.0	
Adv. regeneration	1.2 \pm 0.3	0.6 \pm 0.2	0.4 \pm 0.1	1.3 \pm 0.3	3.4 \pm 0.5
Seedlings	9.6 \pm 0.8	6.0 \pm 0.7	4.5 \pm 0.6	6.8 \pm 0.9	26.8 \pm 1.6
Stump sprouts	3.0 \pm 0.3	2.0 \pm 0.3	0.9 \pm 0.2	1.0 \pm 0.2	6.9 \pm 0.5
Total	13.8 \pm 0.9	8.6 \pm 0.8	5.8 \pm 0.7	9.0 \pm 1.1	37.2 \pm 1.8

The majority of the 537 tree seedlings belonged to a few taxa of pioneers: four *Cecropia* species (45%), several species of Melastomataceae (11%), and *Alchornea triplinervia* (Euphorbiaceae) (8%). In contrast, the advance regeneration and stump sprouts included a diversity of mature forest trees. The family best represented in the advance regeneration was Burseraceae. Among sprouting stumps, the most numerous families were Lecythidaceae (especially *Eschweilera bracteosa*), Leguminosae (especially *Inga* spp.), Melastomataceae, Burseraceae (especially *Prostium* spp.), and Meliaceae (especially *Guarea* spp.).

Within the central 120 meters of the strip, 325 small trees (> 2 m in height) survived the felling of the larger trees, representing a density of 903 trees per hectare. Of these, 307 (94%) were alive when recensused in Nov. 1990 (18 months after clearing), 7 (2%) were dead, and 11 (3%) were not found and presumed dead.

Of 417 stumps of trees > 7.5 cm dbh, 129 (31%) had one or more living sprouts three months after cutting (August 1989). Ten months later, an additional 56 stumps had sprouted, whereas only 14 that had sprouts in the earlier census lacked them in the latter, raising the total to 171 (41%). Likelihood of sprouting was related to tree diameter: smaller trees (7.5–15 cm dbh) were more than twice as likely to sprout as larger trees (> 30 cm dbh) (Fig. 2). Among the best represented plant families, frequency of sprouting was highest among trees in the Vochysiaceae, Lecythidaceae, Leguminosae, and Lauraceae (Table 2).

Seed rain

Seeds of 115 species have been identified to date from the 128 seed traps over the first year after clearing. The families represented by the most species are Melastomataceae (19 spp.) and Moraceae (13 spp.).

Based on diet records, 20 of these species were dispersed by bats. The most frequently trapped bat-dispersed species were *Cecropia ficifolia*, *C.*

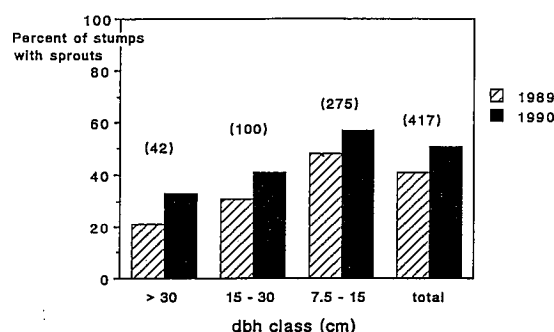


Fig. 2. Percentage of stumps in the logged strip with one or more sprouts three months (August 1989) and 13 months (June 1990) after clearing, for three diameter classes and for all stumps > 7.5 cm dbh. Dbh refers to diameter of the tree when it was cut, not of the stump or the sprout. Number of stumps in each diameter class is given in parentheses.

Table 2. Number of stumps (> 7.5 cm dbh) in the strip, number and percentage of these stumps with sprouts in June 1990, and net gain in this number since August 1989 (3 months after clearing), for the 12 plant families with the most stumps.

Family	Number of stumps		Net gain '89 to '90
	Total	Sprouting	
Lecythidaceae	59	43 (73%)	11
Burseraceae	38	10 (26%)	6
Leguminosae	37	19 (51%)	1
Sapotaceae	32	13 (41%)	1
Euphorbiaceae	31	7 (23%)	4
Myristicaceae	28	5 (18%)	2
Moraceae	21	4 (19%)	0
Lauraceae	20	10 (50%)	2
Melastomataceae	20	0 (0%)	0
Rubiaceae	11	3 (27%)	-3
Vochysiaceae	11	9 (82%)	0
Annonaceae	10	2 (20%)	0
Other	99	46 (46%)	18
Total	417	171 (41%)	42

membranacea, *C. distachya* (Moraceae), *Piper aduncum* (Piperaceae), and *Vismia* spp. (Hypericaceae).

Of 23 species recovered in the traps that were dispersed by birds, about half are in the Melastomataceae, including three of those most frequently trapped: *Miconia minutiflora*, *M. poeppigii*, and *Ossaea cucullata*. Other common bird-

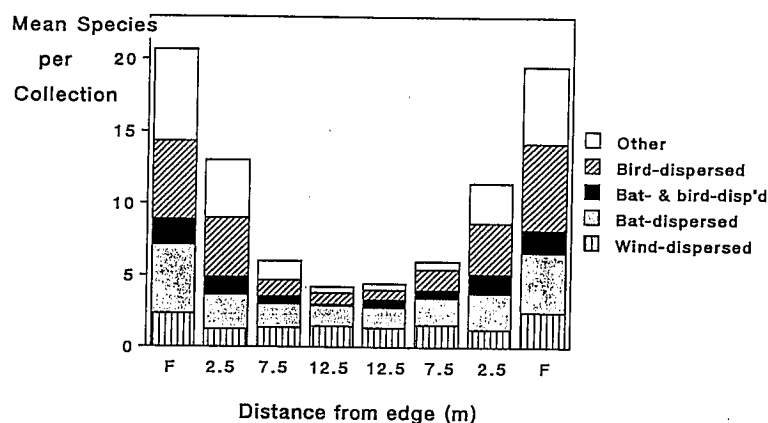


Fig. 3. Mean number of plant species represented by seeds in seed traps per semi-monthly collection, over the first year after clearing (June 1989–June 1990). Each bar represents a column of 16 traps (total area 4 m²) located in the forest (F) 25 m from the strip or within the strip, 2.5 m, 7.5 m, or 12.5 m from the forest. Left to right on the graph corresponds to west to east (Fig. 1). Plant species are categorized by dispersal mode.

dispersed taxa were *Souroubea guianensis* (Marcgraviaceae), *Coussapoa parvifolia* (Moraceae), and *Alchornea triplinervia* (Euphorbiaceae). Three frequently trapped genera included bird- and bat-dispersed taxa with seeds that could not be distinguished: *Marcgravia* (Marcgraviaceae), *Philodendron* (Araceae), and *Ficus* (Moraceae).

Based on fruit and seed morphology we determined that 20 other species were wind dispersed. The two most frequent wind-dispersed species were *Adelobotrys marginata* (Melastomataceae) and *Ladenbergia magnifolia* (Rubiaceae).

The dispersal mode of the remaining 49 species has yet to be determined; they are grouped as 'other' in these analyses. Most (25) of these species are probably bird-dispersed, based on morphology and taxonomic affiliation. Other species have morphologies suggesting dispersed by arboreal or terrestrial mammals, or by both mammals and birds; for some species the dispersal mode is unknown.

The average number of species per semi-monthly collection was highest for the columns of traps in the forest, intermediate for the traps near the edge, and lowest in traps in the interior of the strip (Fig. 3). This pattern was most pronounced for bird-dispersed species. Wind-dispersed species were encountered at similar frequencies in all positions, while the spatial pattern

for bat-dispersed species was intermediate (Fig. 3).

Twenty of the species with seeds in the traps had a fruiting individual located above one or more of these traps. Seeds recovered from traps below these fruiting conspecific adults were scored as 'fallen' rather than 'dispersed' in the following analysis.

The density of dispersed seeds was much greater in the forest than in the interior of the strip, 7.5 m or 12.5 m from the edge; traps 2.5 m from the edge showed intermediate density (Fig. 4). Fallen seeds showed a less regular pattern (Fig. 4), due primarily to numerous fruits fall-

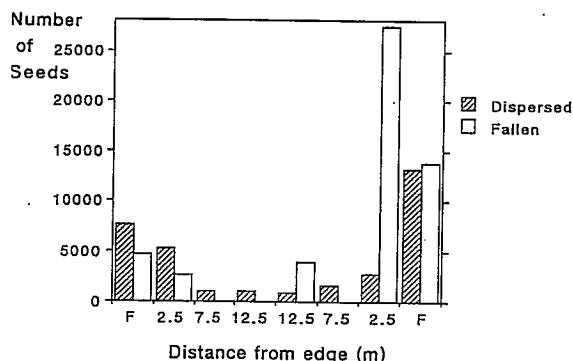


Fig. 4. Total number of dispersed and fallen seeds recovered from seed traps over the first year after clearing. Columns of seed traps are labelled as in Fig. 2. See text for definitions.

Table 3. Density of seeds of six taxa deposited in and near the strip over the first year after clearing. At each position seeds were collected from 32 traps, each 0.25 m². Forest traps were 25 m from the edge of the strip. Densities are per m².

Dispersal mode & species	Total seeds	Position			Forest
		Strip, distance from edge			
		12.5 m	7.5 m	2.5 m	
Bird					
<i>Ossaea cucullata</i>	1528	0.62	5.88	12.12	172.38
<i>Miconia poeppigii</i>	540	0.62	0.62	21.00	45.25
Bat					
<i>Cecropia ficifolia</i>	843	23.88	25.38	31.50	24.62
<i>Piper aduncum</i>	724	14.62	5.62	29.25	41.00
Wind					
<i>Adelobotrys marginata</i>	2666	70.88	102.25	32.62	127.50

ing from an epiphytic *Philodendron* directly onto one of traps near the east edge and to fruits falling from an fruiting individual of *Phytolacca rivinoides* to a trap 12.5 m from the east edge.

The decline in seed input from forest to edge to strip interior was much greater for bird-dispersed seeds than for seeds dispersed by bats or wind. This pattern is illustrated by the density of the seed rain at each distance for five plant species well-represented in the traps and free of the confounding presence of a fruiting individual above one of the traps. For one bird-dispersed melastome, *Miconia poeppigii*, the seed rain near the edge of the strip was half that in the forest, while for another, *Ossaea cucullata*, it was more than an order of magnitude lower (Table 3). For both melastomes, the seed rain near the center of the strip was about two orders of magnitude lower than that in the forest. In contrast, one bat-dispersed species, *Piper aduncum*, showed less than an order of magnitude decline in seed density from forest to edge to center, and another, *Cecropia ficifolia*, showed little difference in seed rain among locations (Table 3.) The most common wind-dispersed species, *Adelobotrys marginata*, dispersed seeds to similar densities in the forest and strip interior, but to lower density at the edge (Table 3).

Bat and bird species composition

A total of 292 bats belonging to 33 species were netted in the strip; over all four sites 1214 bats (49 species) were netted. The species composition of bats netted in the strip was more similar to that of the nearby primary forest (24 species shared, $I = 0.79$) than it was to the secondary forest or open areas (Table 4). For all pairs of sites, the similarity in bat species netted was high (≥ 0.59).

The five most frequently netted bats, both in the strip and overall, were frugivores: *Carollia per-*

Table 4. Number of bat species netted in each habitat and index of similarity between habitats, June 1989–May 1990.

Site	# Captures	# Species	Similarity with:		
			Secondary forest	Strip	Open areas
Primary forest	422	28	0.67	0.79	0.64
Secondary forest	213	26		0.71	0.59
Strip	292	33			0.66
Open areas	287	28			
Total	1214	49			

Table 5. Number of bird species netted in each habitat and index of similarity between habitats, June 1989–May 1990.

Site	# Captures	# Species	Similarity with:	
			Secondary Forest	Strip
Primary forest	206	55	0.58	0.54
Secondary forest	132	38		0.53
Strip	150	45		
Total	488	79		

spicillata, *C. brevicauda*, *Artibeus lituratus*, *A. jamaicensis*, and *Phyllostomus hastatus*. The seeds most frequently obtained from fecal samples of the two *Carollia* species were *Vismia* spp. and *Piper* spp. The other three bat species, which are larger, most frequently had seeds of *Cecropia* spp. in their feces, including the four *Cecropia* species which regenerated in the strip.

We netted 150 birds (45 species) in the strip; 488 birds (79 species) over all three sites. Only 27 of the 45 species were also captured in the nearby primary forest ($I = 0.54$). A comparable level of similarity ($I = 0.53$) was found between the strip and the secondary forest (Table 5).

Frugivores (Columbidae, Pipridae, Thraupidae, and Turdidae) accounted for a similar proportion of captures (27%–29%) at all three sites. The fruit-eating birds most frequently captured in the strip were the White-crowned Manakin *Pipra coronata*, the Blue-crowned Manakin *Pipra pipra*, and the Fulvous-crested Tanager *Tachyphonus surinamus*; these species were also frequently netted in primary and secondary forest. A wide diversity of seeds was recovered from the feces of each of these bird species; the plant family best represented was the Melastomataceae.

Discussion

Regeneration mode

Some of the regenerating trees classified as seedlings may have actually been present before the

clearing but their paint mark was lost. Studies that do not mark advance regeneration (e.g. Hartshorn 1989) probably group such plants as 'seedlings.' Other 'seedlings,' both in our study and others, may be sprouts from very small diameter stems that were broken near ground level during clearing, and which subsequently grew so as to obscure the break. The caveat that not all 'seedlings' actually germinated after the clearing applies not only to the following discussion but to other studies using similar methods.

The density of tree seedlings ≥ 50 cm in height we observed 14 months after clearing (17,900/ha) was about 65% higher than the density reported for two strip cuts in the Palcazu Valley censused after 2 and 2.5 years (Hartshorn 1989). Further sampling at our site will reveal whether stems thin to a comparable density in the second year. At both sites, the high stem density indicates a great potential for silvicultural treatments to favor desired tree species, although it does not obviate concern about their low abundance.

One of the tree species represented by the most seedlings in the strip 14 months after clearing, *Cecropia membranacea*, had seeds present in the seed bank (unpubl. data). However, this species also was dispersed by bats into the strip during the first months after clearing, so the relative importance of the seed bank vs. newly dispersed seeds to this species' regeneration is not known. In a tropical forest in Mexico the seed bank of *C. obtusifolia* is rapidly depleted by predators but continually replenished by the seed rain (Alvarez-Buylla and Martinez-Ramos 1990). The other tree species with seedlings in the strip were not represented in the seed bank, hence their presence is attributable to the seed rain.

Whereas pioneer species of little commercial value predominated among seedlings, the advance regeneration and sprouting stumps included a diversity of commercially valuable species characteristic of later successional stages. Sprout density at 14 months (4600 sprouting stumps/ha) was about twice that in the Palcazu strips at 2 and 2.5 years (Hartshorn 1989). There is no indication that half of these sprouting stumps will die over the next year, as only 3% died between August

1989 and June 1990, far fewer than the number of inactive stumps that sprouted during this period. Nearly all stumps had multiple sprouts; if more than one survive this may lead to a bushy growth form and low timber yield. We have initiated experiments on thinning stems of common species to a single sprout to determine the effect on survivorship and growth.

The high density of saplings that survived the clearing operation and the first year of succession indicates that advance regeneration may play an important role in forest regeneration. For those commercially valuable tree species with poorly dispersed seeds and low sprouting frequency, these saplings may represent the only way to regenerate in the logged strip. Cutting these saplings during the systematic clearing of the understory before the felling operation (Anonymous 1990) eliminates this advance regeneration. Continued research on the survivorship and growth of advance regeneration, stump sprouts, and seedlings will elucidate the contribution of each mode to the regeneration of the forest.

Dispersal agents and spatial pattern

The tendency for bird-dispersed seeds to disperse within the forest or to the strip edge, while bat- and wind-dispersed seeds tend to disperse relatively evenly to forest, edge, and strip interior, is apparent both in the number of species of each dispersal mode represented in traps (Fig. 3) and in the number of seeds of frequently encountered species (Table 3). The paucity of wind-dispersed *Adelobotrys* seeds in traps near the forest edge, compared to those in the forest and strip interior, suggests that air patterns in clearings may disfavor seed deposition near the edge.

The tendency for bats, rather than birds, to disperse seeds to clearings has been reported for other Neotropical sites. In French Guiana, Charles Dominique (1986, see also De Foresta et al. 1984) found that in the forest and under large trees in clearings more seeds were dispersed during the day (by birds) than at night (by bats), whereas in clearings (5–10 m from the forest) and

the interior of a gap, deposition of seeds occurred only at night. They attributed this pattern to the tendency for birds to defecate while perched and for bats to defecate in flight. Similarly, Thomas et al. (1988) found that for a savanna tree of *Muntingia calabura* (bird- and bat-dispersed) in Costa Rica, the proportion of seed-bearing feces found beneath the tree, as opposed to 5 and 15 m away, was greater during the day than at night. Those authors suggested that birds remained in the tree while processing fruits whereas bats carried fruits to feeding roosts and occasionally defecated in flight. Differences in the likelihood of transport from forest to open areas between bat- and wind-dispersed taxa on one hand and bird- and mammal-dispersed taxa on the other was proposed as the explanation for the predominance of bat- and wind-dispersed species in the early stages of primary succession on river meanders in southeastern Peru (Foster et al. 1986).

The high deposition of bird-dispersed seeds in traps 2.5 m from the edge may be attributable to defecation by birds while perched; many of the edge traps were located beneath branches of forest trees. Perch availability may be a major determinant of where seeds are deposited by birds within the strip, as it is in old fields in eastern North America (McDonnell & Stiles 1983). To test whether traps with more cover have greater input of bird-dispersed seeds we recorded the branch density at various heights and the light level above each trap; these data remain to be analyzed.

Although the movement patterns of birds and bats may change with the vegetation structure later in succession, the first year's results lead us to predict that increasing the width of the logged strip would result in an increase in the ratio of bat- and wind-dispersed species to bird-dispersed species in the regeneration. Narrower strips should favor bird-dispersed species, as well as decrease the predominance of pioneers; however, the large crown diameters of emergent trees means that they could not be felled completely within narrower strips.

Dispersers and succession

The greater similarity in bat vs. bird species composition among sites reflects the tendency for many bats to travel long distances and traverse diverse habitats during foraging (Heithaus & Fleming 1978). Capture of a bat in a particular habitat does not necessarily indicate it was foraging there, particularly when the capture is on a forest trail. For bats, the fact that the strip's community was more similar to that of nearby primary forest than to more distant sites with early successional vegetation, hints that many forest bats venture into the clearing. On the other hand, the abundance of seeds of pioneer *Cecropia* spp. in the seed traps indicates that at least some individuals of the large frugivorous bats that disperse these seeds visited the strip after foraging in early successional areas.

The bird community using the strip in the first year after clearing was as similar to that of nearby primary forest as to that of secondary forest, but we predict that as the strip's plant community develops into secondary forest, the bird community will converge toward that typical of secondary forest. We also predict that the number and diversity of frugivorous birds utilizing the strip will increase as the forest regenerates, and this will lead to an increase in the deposition of bird-dispersed seeds. Over the first year, however, capture rates have not increased.

Concluding remarks

We should note that our results apply only to strips set in a matrix of primary forest. In a forest managed by the strip clear-cut system, up to half the area will eventually be cleared; strips cleared late in the first rotation and in subsequent rotations will be bordered on at least one side by young forest. Species that thrive in the strips and reproduce within the cutting cycle (30–40 years), such as *Cecropia* spp., *Vismia* spp., and *Alchornea triplinervia*, should increase in abundance in such a managed forest. However, such pioneer trees are generally of little or no timber value. Tree

species that do not regenerate in the strips or have long generation times are susceptible to extinction. Communities of seed-dispersing animals will shift in favor of species able to use the new habitats and fruit resources.

Although the movement patterns of dispersal agents and their deposition of seeds of species deemed valuable may be shaped by modifying parameters such as strip width or cutting date, the basic premise of natural regeneration relies on the presence of seed dispersal agents. Some disperser taxa may become locally extinct in a managed forest due to hunting or destruction of roost sites (bats), but their dispersal services may be replaced by other frugivorous taxa (Hallwachs 1986). Of potentially greater impact is the extinction of many disperser species due to the loss of a 'keystone' or 'pivotal' plant species utilized during seasons of resource scarcity (Howe 1984, Terborgh 1986). If such plant species are not capable of regenerating and reproducing in logged strips, it is crucial that they be included in parcels protected from logging or that they be spared from felling.

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References

- Alvarez-Buylla, E. R. & Martinez-Ramos, M. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84: 314–325.
- Anonymous. 1990. Manejo de bosques naturales de la selva alta del Peru. Un estudio de caso del Valle del Palcazu.

- Documento tecnico. INADE-APODESA, AID, Ronco Consulting Corp., & Centro Cientifico Tropical, Lima.
- Buschbacher, R. J. 1990. Natural forest management in the humid tropics: ecological, social, and economic considerations. *Ambio* 19: 253-258.
- Charles Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. In: Estrada, A. & Fleming, T. H. (eds), *Frugivores and seed dispersal*. Dr W. Junk, Dordrecht.
- De Foresta, H., Charles Dominique, P., Erard, Ch., & Prevost, M. F. 1984. Zoochorie et premiers stades de la regeneration naturelle apres coupe en foret guyanaise. *Rev. Ecol. (Terre Vie)* 39: 369-400.
- Foster, R. B., Arce B., J., & Wachter, T. S. 1986. Dispersal and the sequential plant communities in Amazonian Peru floodplain. In: Estrada, A. & Fleming, T. H. (eds), *Frugivores and seed dispersal*. Dr W. Junk, Dordrecht.
- Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*), the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). In: Estrada, A. and Fleming, T. H. (eds), *Frugivores and seed dispersal*. Dr W. Junk, Dordrecht.
- Hartshorn, G. S. 1980. Neotropical forest dynamics. *Biotropica* 12 (Suppl.): 23-30.
- Hartshorn, G. S. 1989. Application of gap theory to tropical forest management: natural regeneration on strip clear-cuts in the Peruvian Amazon. *Ecology* 70: 567-569.
- Heithaus, E. R. & T. H. Fleming. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomidae). *Ecol. Monogr.* 48: 127-143.
- Howe, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biol. Cons.* 30: 261-281.
- Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.
- Krebs, C. J. 1985. *Ecology: the experimental analysis of distribution and abundance*. 3rd ed. Harper and Row, New York.
- McDonnell, M. J. & Stiles, E. W. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56: 109-116.
- Mergen, F. & J. R. Vincent (eds.) 1987. *Natural Management of Tropical Moist Forests*. Yale Univ., New Haven, CT.
- Spichiger, L., Meroz, J., Loizeau, P.-A., & Stutz de Ortega, L. 1989. *Contribucion a la Flora de la Amazonia Peruana. Los Arboles del Arboretum Jenaro Herrera. Vol. 1. Conservatoire et Jardin Botaniques de Geneve, Switz.*
- Terborgh, J. 1986. Community aspects of frugivory in tropical forests. In: Estrada, A. & Fleming, T. H. (eds) *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.
- Thomas, D. W., Cloutier, D., Provencher, M., & Houle, C. 1988. The shape of bird- and bat-generated seed shadows around a tropical fruiting tree. *Biotropica* 20: 347-348.