

SEED DISPERSAL AND POTENTIAL FOREST SUCCESSION IN ABANDONED AGRICULTURE IN TROPICAL AFRICA

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Abstract. Natural forest succession on human-disturbed lands is often slow because the resources necessary for succession are depleted. In such landscapes, forest succession may be dependent on arrival of seeds from off-site, many of which are dispersed by fruit-eating animals. We studied bat and bird seed dispersal in a deforested agricultural area adjacent to Kibale National Park, Uganda. Seed rain was monitored for 6 mo in short (<0.5 m) and tall (2–5 m) grassland, and below short (1–3.5 m), medium (3.5–10.0 m), and tall (≥ 10.0 m) isolated trees within grassland. Seed rain (numbers of seeds and seed species) under trees of all heights was greater than in short or tall grasslands. Bats dispersed seeds mostly below tall trees, while birds dispersed seeds mostly below both tall and mid-sized trees. More seeds and seed species were dispersed under tall trees than below short trees. Within 150 m of the forest there was no relationship between the seed rain under trees and the distance to the forest edge. Nearly half of the >11 200 seeds collected were from hemiepiphytic *Ficus* that are unable to grow from the ground. One-third of collected seeds were from shrubs, and most of the remainder were from trees. Nearly all tree and shrub seeds collected (>99%) were species typically found in disturbed grassland, not in forest. These results suggest that in this African region, forest succession may proceed very slowly on degraded lands.

Key words: deforestation; degraded lands; disturbance; forest regeneration; fruit bats; Kibale National Park, Uganda; old field succession; restoration; seed dispersal.

INTRODUCTION

Degraded tropical landscapes are expanding in area as forests are converted to unsustainable pasture or cultivation and then abandoned (Nepstad et al. 1991, Brown and Lugo 1994). Human disturbance to these areas often depletes resources needed for natural regeneration (e.g., seed banks) and forest succession may depend on arrival of wind- or animal-dispersed seeds (Da Silva et al. 1996, Nepstad et al. 1996). In many tropical regions, frugivorous bats and birds are the predominant dispersers of pioneer woody plants, playing an important role in their early establishment (Uhl et al. 1981, Vieira et al. 1994, Da Silva et al. 1996).

Animal-dispersed seed rain can be low on deforested agricultural or pastoral lands because these lands initially offer little to foraging frugivores. However, remnant forest trees or early colonizing trees offer food and/or perch sites to frugivores, and thus may receive more zoochorous seed rain than treeless areas (Uhl 1987, Vieira et al. 1994). Seedling establishment may be more likely below these trees than in nearby treeless areas since competition with grasses is less (Vieira et al. 1994), seed and seedling predation can be lower (Nepstad et al. 1991, but see Kolb 1993), soil nutrients can be more abundant (Vieira et al. 1994), and humidity and temperature can be more favorable for seedlings

(Uhl et al. 1982). Lower temperatures and fuel-load below isolated trees may protect seeds and seedlings from fire (Kuusipalo et al. 1995). Eventually, seedlings recruited below these isolated trees may become tree patches that continue to facilitate forest succession (Guevara et al. 1986, Kolb 1993).

Trees in a deforested landscape may vary in their attractiveness to frugivores (McDonnell 1986). Bat and bird seed dispersers may prefer tall trees or perches if they offer greater foraging opportunities, visibility, and/or vantage. However, in past studies no consistent relationship between tree height and seed rain has emerged (McDonnell 1986, Guevara et al. 1992). Frugivore use of a tree may also be determined by the tree's position in the landscape, in particular, distance from forest edge (Willson and Crome 1989, Guevara et al. 1992). Through variation in their attractiveness to frugivores, tree characteristics may influence seed dispersal and plant recruitment patterns in deforested areas.

We investigated animal-mediated seed dispersal in a deforested agricultural area immediately adjacent to tropical forest in Kibale National Park, Uganda. Large areas of the southern third of the park's forest, the Southern Corridor, were converted to cropland by settlers in the 1970s and 1980s. After relocation of settlers out of the park in 1992, these lands were abandoned. Now dominated by tall grasses, forest succession on these abandoned lands seems very slow. Interested in forest regrowth on these lands, we addressed three main

questions: *where* are seeds dispersed in this deforested landscape, *what* types of seeds are dispersed, and *who* is dispersing the seeds?

The spatial distribution of seed rain was examined in four ways. First, because bats and birds may be more likely to visit trees than grassland, we hypothesized that seed rain would be greater below isolated trees than in adjacent grassland. Second, because tall trees offer more foraging area and, possibly, greater safety from predators than short trees, we hypothesized that seed rain would be greater below tall trees than either mid-sized or short trees. Third, although the forest is potentially a large source of seeds and frugivores, forest-dwelling seed dispersers may avoid cleared areas to reduce their risk of predation (Janzen et al. 1976, Wegner and Merriam 1979, Janzen 1990) or to concentrate their foraging where food is more abundant. Thus, we hypothesized that seed rain below trees would be negatively correlated with distance from forest edge. Fourth, we hypothesized that fruit production by trees would increase non-conspicuous seed rain below those trees. Since *Musa* spp. (banana) can persist in abandoned cropland, seed rain below several fruiting *Musa* plants was also sampled. Collected seed rain was described in terms of plant growth forms and disturbance regimes. We also described the forms of animal-dispersed seeds to infer differences between bird and bat seed dispersal.

METHODS

Study site

The study site was located near the Makerere University Biological Field Station at Kanyawara (hereafter Kanyawara) in Kibale National Park, Uganda (0°34' N, 30°21' E). This 766 km² park is a mosaic of mid-elevation moist evergreen forest, swamp forest, papyrus swamp, selectively logged forest, exotic tree plantations, and tall grassland (Kingston 1967). Kanyawara experiences two periods of seasonal rainfall, March to May, and September to November, with rain averaging 167 cm/yr, (range = 157–186 cm, period = 1977–1994).

The study site was an approximately 150 × 250 m area of deforested cropland, with one long edge adjacent to protected mature forest (Fig. 1, Plate 1). Cropland extended many kilometers beyond the other borders of the study site. Between half of the study site and the forest was 5–7 year-old abandoned cultivation (~4500 m²), with tall trees (>10 m) dominating an understory of herbs and short grasses. Between the other half of the study site and the forest was low (5–10 m) secondary forest (~3100 m²) of unknown history. Because neither of these latter areas were typical of degraded lands in the Southern Corridor, they were not sampled.

The area was partially active cropland under the supervision of field station managers. Within it was fal-

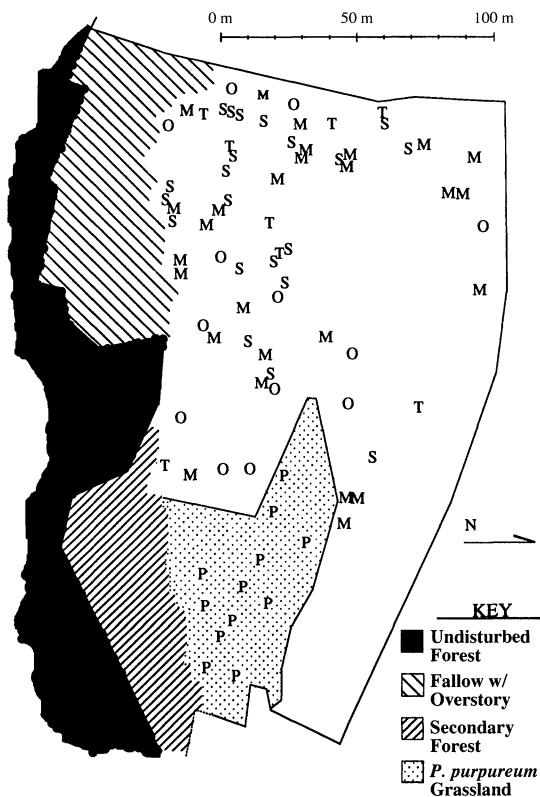


FIG. 1. The study area located on degraded agricultural land immediately adjacent to the Kibale National Park, Uganda. To the south of the study area was forest, while active cropland extended in all other directions. Recently abandoned fallow, active cultivation, and a small *Musa* and *Eucalyptus* plantation were within the borders of the study area. Letters indicate the location of seed traps in short (O) or tall (P) grassland areas, and the positions and heights of short (S), medium (M), or tall (T) trees below which seed rain was sampled.

low of short grasses, forbs, and vines (~9500 m²), low-growing crops (e.g., ground nuts, sweet potato; ~7600 m²), fallow of *Pennisetum purpureum* grass (~4000 m²), a *Musa* plantation (~2500 m²), and a plantation of *Eucalyptus globulus* (3–10 m high, ~1600 m²; Fig. 1). Human activity on the land was low, mostly restricted to the *Musa* plantation. *Musa* fruits were harvested before ripening and their presence probably did not affect the abundance of most frugivores. Throughout these areas were scattered trees of a variety of heights. These were either remnants from the original forest, pioneers, or planted exotics (e.g., *E. globulus*). This mixture of habitats was typical of degraded agricultural areas in the Southern Corridor soon after abandonment, and is probably similar to many abandoned croplands throughout the humid tropics.

Seed trap placement

We sampled seed rain in three habitats: below isolated trees; at sites with low herbaceous cover (mostly



PLATE 1. A view of the study area adjacent to Kibale National Park, Uganda. Note the edge of the *Musa* plantation to the left, a tall tree (a snag with an epiphytic fig; ht > 10m) in the center, and a short tree (ht < 3.5 m) to the right. In the foreground is the short grassland habitat, and the natural forest is in the background. Photograph by R. Scot Duncan.

grasses, ≤ 0.5 m in height), representing most cropland immediately after abandonment (hereafter short grassland); and in *P. purpureum*-dominated areas (hereafter tall grassland) representing the predominant habitat of abandoned lands in the region after 2–3 yr of fallow (Fig. 1).

We classified trees into three height categories: short, height = 1.0–3.5 m; medium, $3.5 < \text{height} < 10.0$ m; and tall, ≥ 10.0 m. In this classification, short trees would be enveloped by *P. purpureum* grasses within approximately a year after land abandonment, while medium height and tall trees would be emergent. Tall trees were at much lower densities than trees in the other height categories. Tree heights were re-measured at the study's end (6 mo later), and initial and final heights were averaged to yield the values used in analyses.

We collected seed rain on durable plastic sheets loosely stretched and stapled to wooden frames (mean seed trap area = 0.554 m^2 , SD = 0.025, range = 0.49–0.62 m^2). Each frame was elevated on 20–25 cm tall legs to reduce seed removal by animals. Seed removal from these seed traps in degraded cropland is low (e.g.,

<1% of 150 seeds were removed from 5 traps during 6 d, for each of 2 species, *Celtis durandii* and *Albizia grandibracteata*).

We randomly chose 22 short, 25 medium, and 8 tall trees for seed rain sampling. A minimum of 0.5% of the crown area of selected trees was sampled, using ≤ 5 seed traps per tree. Thus, taller trees often had >1 seed trap below them, with seed rain averaged among the traps. Also, we roughly standardized the total area sampled within each tree height category, resulting in fewer large trees sampled than medium or short trees. Distances from sampled trees to the nearest forest edge were also measured.

We randomly placed seed traps below tree crowns, with no sampling below overlapping crowns of adjacent trees. Sampled trees had crown diameters ≥ 1.0 m and were ≥ 1.0 m taller than surrounding herbaceous vegetation (within 1.0 m of crown). Trees within 5 m of the road bounding one edge of the study site were excluded since frugivores might avoid them. Trees in the tall grassland and plantations of *E. globulus* and *Musa* were not sampled, although 1–2 *E. globulus* trees per tree height category were sampled outside the plantations.

We also placed seed traps at 13 random locations in short grassland where traps were >1.0 m from the crowns of nearby trees and shrubs. Twelve tall grassland locations were also randomly chosen for sampling. These sites had $\geq 75\%$ *P. purpureum* cover and were >1.0 m from crowns of adjacent trees or shrubs. Trails ≤ 1.0 m wide were cut through the *P. purpureum* area to access seed traps.

For the five sampled trees that produced ripe endozoochorous fruits during the study, non-conspecific seed rain was compared between fruiting and non-fruiting periods. A *G* test goodness-of-fit (single classification, extrinsic) was used to compare expected and observed seed numbers below each tree during fruiting and non-fruiting periods (defined by the presence or absence of ripe fruit), using William's correction factor to adjust for low sample sizes ($N = 2$ treatments; Sokal and Rolf 1981). Restricting comparisons within each tree controlled other variables that could possibly affect seed rain (e.g., numbers of fruits produced).

We conducted a preliminary survey to see if fruiting *Musa* spp. attract frugivores and increase seed rain. Six *Musa* scattered across the study site were haphazardly selected and their fruits allowed to ripen in situ. A seed trap below each plant's single fruit cluster was monitored during fruiting and non-fruiting periods; no more than two of these *Musa* had ripe fruits at the same time.

Seed trap monitoring

We checked seed traps daily during six sampling intervals between August 1994 to January 1995, spanning a wet and dry season (mean sampling interval = 14.2 d; SD = 8.1 d; range = 7–29 d; each interval separated by >14 d). Total sampling effort among seed

traps varied due to occasional trap damage (mean = 87 d, SD = 2.8 d; range = 72–89 d).

Since heavy rains could wash seeds off traps, we attempted to check seed traps before any rainfall. If rain fell before checking (≥ 5.0 mm of rainfall in < 2 h), that day's data were excluded (rain was monitored 1 km from the site). These are probably conservative criteria since greater volumes seemed necessary to wash seeds off traps.

We searched traps for animal-dispersed seeds and fruits. Seed species largely reliant on wind or gravity dispersal were excluded; such species comprise a minor component of trees at Kibale. Seeds within an individual defecation, fruit, or bat wadge (a compressed pellet of fiber and seed spit-out by fruit bats; sensu Goodall 1986) were kept distinct from other samples. Seeds and fruits of the same species as the sampled tree were excluded from analysis if that tree was fruiting; seeds and fruits from overhanging, fruiting epiphytes were also excluded. Collected seeds were identified and counted; the few crushed seeds collected were excluded. For fruits with many small seeds (e.g., *Ficus* spp.) seed numbers were sometimes based on mean seed counts of collected fruits. We identified seeds using a reference collection and Hamilton (1990).

Seed rain description

We described seed rain in terms of density (no. seeds·m⁻²·d⁻¹), species richness per day (no. seed species·m⁻²·d⁻¹), and species richness per study (no. seed species·m⁻²·80 d⁻¹). Standardization for sampling area and time was necessary since seed trap sizes and the number of days sampled varied. We quantified species richness over two time scales because there is a limited pool of plant species in the region, and given enough sampling time, all seed traps or habitats could receive all species available. Species richness per day for a trap was the average daily number of seed species among all sampling days. Species richness per study was the total number of seed species collected for 80 randomly chosen days, since this was the lowest total of sampling days among all seed traps.

We classified seeds into seven plant growth forms: trees, shrubs, climbers, herbs, crops, *Ficus*, and unknown. Trees were woody species > 3.0 m tall when mature, shrubs were woody species 0.5–3.0 m tall, climbers (vines) were non-self-supporting species, and herbs were nonwoody, nonclimbing species growing < 1.0 m tall. Crops were any agricultural species. The fruits of most crops were harvested before they attracted frugivores. Most unknown seeds were probably climbers, herbs, and shrubs, as these were poorly represented in the reference collection. The *Ficus* seeds could only be identified to genus. *Ficus* was its own plant growth form category because one of nine *Ficus* species at Kanyawara is a shrub, one is freestanding, and seven species are hemi-epiphytes; thus, *Ficus* seeds could not be categorized with confidence as trees. *Ficus*

do not appear to be important in forest succession at Kanyawara, as they are not typically found regenerating in abandoned cropland. Each species was categorized as typically found in mature forest or disturbances based on Hamilton (1990) and our own observations.

We recovered five deposition forms of animal-dispersed seeds: bird dung, unknown dung, dropped fruit, bat wadge, and source-unknown. Bird dung was identified by having white uric acid present. Since bird dung may not contain visible uric acid, it can closely resemble bat dung. We classified these ambiguous samples as unknown dung, although this likely underestimated bird seed dispersal. Dropped fruit included both whole and partial fruits. Source-unknown seeds were those with no indication of how they arrived; many were probably bird regurgitations.

Parametric analyses of the seed rain data were not possible due to strongly zero-skewed distributions. Nonparametric Kruskal-Wallis tests were used to contrast seed rain categories. When significant differences were detected, post hoc Mann-Whitney *U* tests were used to determine which pairs of tree height categories differed (Day and Quinn 1989). Although not typically presented with nonparametric data, means and standard deviations are presented in addition to medians to facilitate comparisons to other studies.

RESULTS

Spatial patterns of seed rain

Seed rain in short and tall grassland was much lower than that under isolated trees (Fig. 2). Only one seed trap in short grassland received any seeds of fleshy-fruited species (nine small *Trema orientalis* fruits on a branch apparently blown to the trap during a storm). Only three tall grassland traps received seeds of fleshy-fruited species (three tree, 31 climber, and three shrub seeds). Seed density and species richness (per day and per study) for all tree height categories were greater than in short and tall grassland (Mann-Whitney *U*, $P < 0.005$ for all comparisons). Short and tall grasslands did not differ for any of the seed rain variables (Mann-Whitney *U*, $P = 0.268$ for all comparisons; Fig. 2).

Seed density (seeds·m⁻²·d⁻¹) differed among tree height categories (Kruskal-Wallis, $H = 8.51$, $P < 0.014$). Seed density at short trees was lower than at tall trees, but seed density at short and medium height trees was similar, as was seed density between medium height and tall trees (Fig. 2). There was a trend for lower median seed density as tree height declined, but mean seed density was greatest below medium height trees.

Short trees received fewer species per day (seed species·m⁻²·d⁻¹) than medium height and tall trees (Kruskal-Wallis, $H = 11.54$, $P < 0.003$, Fig. 2); species richness was similar between medium height and tall trees (Fig. 2). Species richness per study (seed spe-

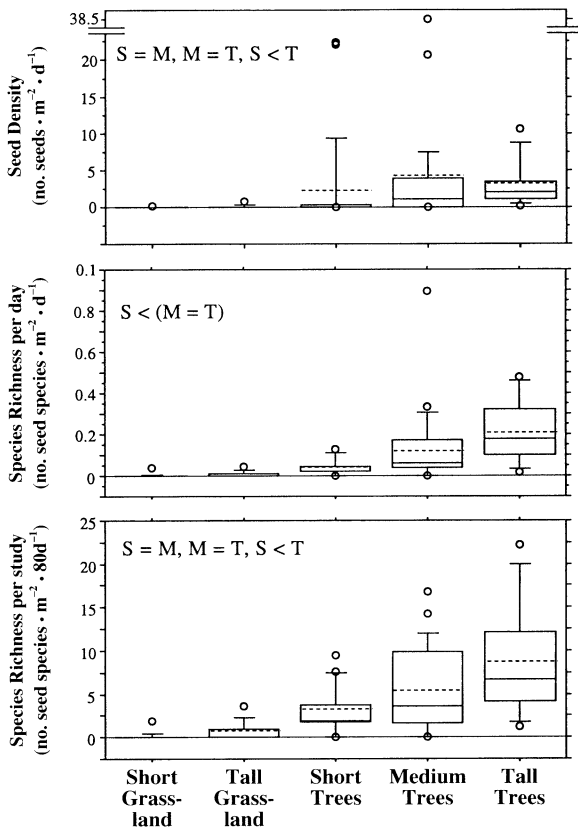


FIG. 2. Seed rain collected in five habitats in a degraded agricultural area. Seed rain is displayed in box plot distributions in terms of seed density (no. seeds·m⁻²·d⁻¹), species richness per day (no. seed species·m⁻²·d⁻¹), and species richness per study (no. seed species·m⁻²·80 d⁻¹). Each box contains the 25th–75th percentiles, and T bars show the bounds of the 10th and 90th percentiles. Solid lines within boxes show medians (50th percentile), and dashed lines show means; circles depict outliers. Within each graph, Mann-Whitney comparisons of the seed rain variable among the tree height categories are presented (short [S], medium [M], and tall [T] trees). The equals sign (=) indicates no difference between two categories, and the < symbol indicates one category significantly less than the other ($P < 0.05$) or less than either of two categories within parentheses. Note the broken axis on the seed density plot.

cies·m⁻²·80 d⁻¹) differed among tree height categories (Kruskal-Wallis, $H = 7.00$, $P < 0.030$), with similar species richness between short and medium height trees, and between medium height and tall trees; tall trees had greater species richness per study than short trees (Fig. 2). For both species richness measures, there was a trend for lower species richness with decreasing tree height.

We found no significant correlations between the three seed rain variables and nearest distance to forest edge, whether tree height categories were analyzed separately or combined ($P > 0.05$ for all comparisons). Distances from trees to forest edge were similar among the three tree height categories (short trees, mean = 62 m, SD = 24; medium height trees, mean = 66 m, SD

= 34; tall trees, mean = 65 m, SD = 33; Kruskal-Wallis, $H = 0.340$, $P = 0.844$). Correlations of seed rain and distance were not feasible for short and tall grassland sites since seed rain there was so low.

Of the 55 trees sampled, 27 were species producing fleshy fruits. Five of these fruited during the study, and non-conspicuous seed rain densities below them differed between fruiting and non-fruiting periods ($G > 13.7$, $P < 0.005$, all trees). Four trees had greater than expected seed density during their fruiting periods (fruiting mean = 28.1 seeds·m⁻²·d⁻¹, SD = 33.3; non-fruiting mean = 6.2 seeds·m⁻²·d⁻¹, SD = 10.9), but one tree had greater seed density when not fruiting (0.32 and 0.76 seeds·m⁻²·d⁻¹, fruiting and non-fruiting, respectively).

Three fruiting *Musa* received very little or no seed rain during both fruiting and non-fruiting periods. Fruits of one *Musa* plant were eaten by baboons (*Papio anubis*), another was eaten by bats and baboons, and the third was eaten only by bats. However, no baboon dung was found in the area, and bat wadges collected from traps contained few seeds ($N = 2$ seeds at one *Musa*). The three other *Musa* averaged >100 seeds/d and between 1–3 species/d during the fruiting period. During non-fruiting periods, only one of these received any seed rain (mean seeds/d = 0.7, SD = 4.9). Most seeds at these *Musa* were in bird and unknown dung, with very few in bat wadges.

Composition of seed rain

The majority of seeds we collected below trees were of three plant growth forms: *Ficus* seeds (49.0%, $N = 5516$), shrub seeds (34.3%, $N = 3858$), and tree seeds (14.1%, $N = 1593$, Appendix). Climbers, herbs, and crops were not numerically important, contributing <3.0% of all seeds collected. Most seeds collected below short and tall trees were *Ficus* (88.3% and 75.3%, respectively; Fig. 3), but most seeds at medium height trees were shrub species (65.1%), with far fewer *Ficus* seeds (10.9%; Fig. 3).

We restricted comparisons of tree height categories within plant growth forms to *Ficus*, tree, and shrub seeds since few seeds were collected from other plant growth form categories (Appendix). Seed densities for these plant growth forms differed among the tree height categories (Kruskal-Wallis, *Ficus*, $H = 10.02$, $P = 0.007$; tree, $H = 10.47$, $P = 0.005$; shrub, $H = 8.09$, $P = 0.004$). *Ficus* seed rain below short and medium height trees was similar (Mann-Whitney U , $P = 0.925$), but both categories had less *Ficus* seed rain than tall trees (Mann-Whitney U , $P = 0.004$ and $P = 0.006$, respectively). Tree seed rain between medium height and tall trees was similar (Mann-Whitney U , $P = 0.910$), but seed rain below either tree category surpassed that at short trees (Mann-Whitney U , $P = 0.004$ and $P = 0.001$, respectively). Similarly, shrub seed rain was similar between medium height and tall trees (Mann-Whitney U , $P = 0.396$), but both tree categories

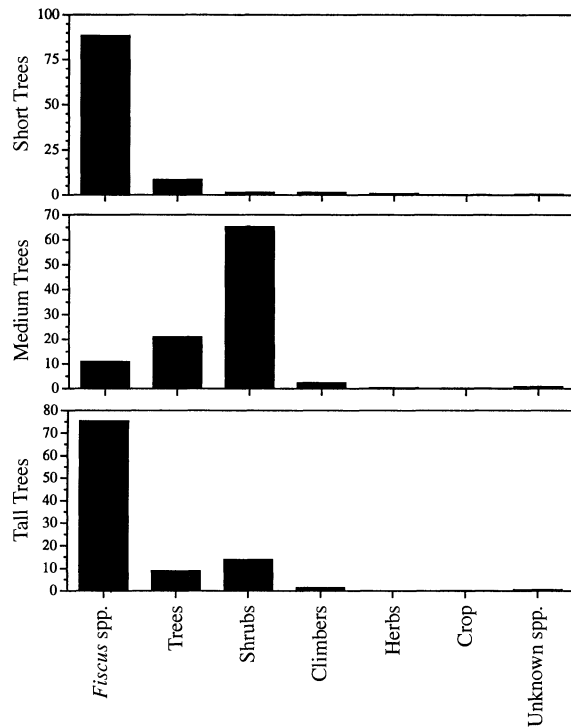


FIG. 3. Three tree height categories and the percentage of their seed rain belonging to seven plant form categories.

had more shrub seeds than short trees (Mann-Whitney U , $P = 0.001$ and $P = 0.019$, respectively).

Most tree and shrub seeds collected were species that typically grow in disturbed grasslands or agricultural fallow, not in forest tree fall gaps. Among the 11 tree species collected, eight usually grow in disturbances. Of these eight species, *Measa lanceolata*, a short tree producing many small fruits packed with tiny seeds, contributed the vast majority of seeds (1423 seeds, 89.4% of all tree seeds). *T. orientalis* was the second most important of the tree species (141 seeds, 8.9% of all tree seeds). This tree is a midsized pioneer species that produces single-seeded small fruits. The three mature forest tree species contributed very few seeds (0.93% of all tree seeds) and included *C. durandii* (13 seeds), *Diospyros abyssinica* (1 seed), and *Allophylus abyssinicus* (1 seed). Similarly, only one of seven shrub species collected below trees typically grows in undisturbed forest (*Ensete ventricosum*, 1 seed, 0.03% of all shrub seeds). Most shrub seeds were *Piper umbellatum* (3408 seeds, 88.3% of all shrub seeds) and *Lantana camara* (245 seeds, 6.4% of all shrub seeds).

The seed dispersers

Seed rain below trees was split into five deposition form categories, and within each deposition form, tree height categories were compared using the three seed rain variables (Tables 1 and 2). Seed rain in the source-unknown category was very low and not included in

these analyses (142 seeds, <1.3% of all seeds). When bird dung seed rain was compared among tree height categories, short trees received significantly fewer seeds and seed species than medium height and tall trees, whose seed rain was similar (Table 2). For unknown dung, the only difference among tree height categories was that short trees received fewer seeds than tall trees. For bat wadage seeds, short and medium height trees received similar numbers of seeds and species, with both categories receiving less than tall trees. Finally, for dropped fruit, differences among tree height categories were only detected for species richness per study, where tall trees received more species than medium height trees (Table 2).

DISCUSSION

Spatial patterns of seed rain

Seed rain below isolated trees far surpassed that in treeless areas at Kibale. This pattern has been found in other systems and supports the idea that tree and shrub recruitment in deforested landscapes will largely begin below isolated trees (Guevara et al. 1986, Kolb 1993, Vieira et al. 1994).

Tall trees generally received more seed rain than short trees, perhaps because they offer more foraging opportunities or increased protection from predators. This suggests tall trees may recruit more seedlings, especially since their shade may create a better environment for seedling germination and survival than the smaller crowns of short trees (Nepstad et al. 1991, Guevara et al. 1992). However, within all tree height categories, we found great variability in seed rain among trees. Thus, factors other than tree height must influence seed rain at isolated trees.

Differences among tree height categories for plant form and deposition form could have resulted if different frugivore species used trees of different heights, or if the same frugivore species differentially used trees of dissimilar heights. For example, the long-ranging Black-and-white Casqued Hornbills (*Ceratogymna subcylindricus*) were only seen using tall trees, while short-ranging species such as Speckled Mousebirds (*Colius striatus*) and Yellow-vented Bulbuls (*Pycnonotus barabatus*) were mostly seen in short or medium height trees. In addition, mousebird flocks often foraged in low growing vegetation, including short trees, but perched for long periods (10–30 min) in canopies of medium height trees. Others have examined the relationship between perch height and seed rain in degraded landscapes, but no consistent pattern has emerged (McDonnell 1986, McClanahan and Wolfe 1987, Guevara et al. 1992). While perch height can influence seed rain, the strength of this effect may vary. For example, McDonnell (1986) suggested perch height relative to neighboring perches, not absolute height, has the most influence in attracting birds. Similarly, trees above a certain height may be regarded

TABLE 1. Medians and means (± 1 SD) of seed rain variables from deposition forms of seeds collected below trees of three height categories.

Deposition form	Statistic	All trees	Tall trees	Medium trees	Short trees
Seed density					
Bird dung	median	0	0.3	0.1	0
	mean (± 1 SD)	0.83 (± 2.39)	0.38 (± 0.29)	1.52 (± 3.36)	0.20 (± 0.82)
Unknown dung	median	0	0.3	0	0
	mean (± 1 SD)	1.03 (± 3.63)	0.40 (± 0.40)	2.11 (± 5.22)	0.03 (± 0.09)
Bat wadge	median	0	0.3	0	0
	mean (± 1 SD)	0.19 (± 0.79)	1.22 (± 1.84)	0.02 (± 0.12)	0.01 (± 0.04)
Dropped fruit	median	0	0	0	0
	mean (± 1 SD)	1.02 (± 4.29)	0.55 (± 1.55)	0.28 (± 1.41)	2.03 (± 6.52)
Source-unknown	median	0	0	0	0
	mean (± 1 SD)	0.04 (± 0.10)	0.04 (± 0.03)	0.06 (± 0.15)	0.01 (± 0.03)
Species richness per day					
Bird dung	median	0	0	0	0
	mean (± 1 SD)	0.03 (± 0.06)	0.05 (± 0.05)	0.05 (± 0.08)	0.01 (± 0.02)
Unknown dung	median	0	0	0	0
	mean (± 1 SD)	0.04 (± 0.08)	0.06 (± 0.10)	0.06 (± 0.10)	0.01 (± 0.03)
Bat wadge	median	0	0	0	0
	mean (± 1 SD)	0.01 (± 0.04)	0.06 (± 0.09)	<0.01 ($\pm <0.01$)	<0.01 (± 0.01)
Dropped fruit	median	0	0	0	0
	mean (± 1 SD)	<0.01 (± 0.01)	0.01 (± 0.01)	<0.01 ($\pm <0.01$)	<0.01 (± 0.01)
Source-unknown	median	0	0	0	0
	mean (± 1 SD)	0.02 (± 0.04)	0.03 (± 0.02)	0.02 (± 0.05)	0.01 (± 0.03)
Species richness per study					
Bird dung	median	0	3.0	1.7	0
	mean (± 1 SD)	1.91 (± 3.02)	3.65 (± 3.46)	2.65 (± 3.50)	0.42 (± 1.14)
Unknown dung	median	0	1.8	0	0
	mean (± 1 SD)	2.25 (± 3.41)	3.41 (± 4.79)	2.84 (± 3.67)	1.15 (± 2.17)
Bat wadge	median	0	1.0	0	0
	mean (± 1 SD)	0.29 (± 0.82)	1.52 (± 1.51)	0.07 (± 0.34)	0.08 (± 0.39)
Dropped fruit	median	0	0.2	0	0
	mean (± 1 SD)	0.22 (± 0.59)	0.54 (± 0.85)	0.07 (± 0.36)	0.26 (± 0.66)
Source-unknown	median	0	2.0	0	0
	mean (± 1 SD)	1.44 (± 2.35)	2.45 (± 2.23)	1.49 (± 2.48)	1.02 (± 2.22)

equally by perching birds and bats (T. C. Moermond, *personal communication*).

As others have found, seed rain below trees was not correlated with distance from forest, suggesting recruitment below trees may not be strongly dependent on the forest as a seed source at the distances we used (Willson and Crome 1989, Guevara et al. 1992). Negative relationships between seed rain and distance from forest in treeless areas seem limited to near the forest edge (Charles-Dominique 1986, Aide and Cavelier

1994), suggesting distance may be important early in forest successions (Myster and Pickett 1992).

The fruiting tree and *Musa* surveys suggest that fruit availability at plants in degraded areas can sometimes increase seed rain. The primates visiting *Musa* may have dispersed seeds of forest species rarely dispersed by bats and birds into croplands. Others have also reported low seed rain to isolated trees during fruiting periods (Willson and Crome 1989, Guevara and Laborde 1993). Willson and Crome (1989) suggested

TABLE 2. Comparisons of seed rain variables from the tree height categories (short [S], medium[M], and tall [T] trees) within each of the deposition form categories. The numbers are *P* values of Kruskal-Wallis comparisons of tree height categories.

Deposition form	Seed rain variables		
	Seed density	Species richness per day	Species richness per study
Bird dung	<0.001 S < (M = T)	<0.001 S < (M = T)	<0.001 S < (M = T)
Unknown dung	0.009 (S = M; M = T; S < T)	0.056	0.080
Bat wadge	<0.001 (S = M) < T	<0.001 (S = M) < T	<0.001 (S = M) < T
Dropped fruit	0.073	0.058	0.010 (S = M; M < T; S = T)

Notes: Mann-Whitney pairwise comparisons of tree height categories are presented when significant differences were detected ($P \leq 0.05$).

these patterns could result from frugivores taking fruits to feeding perches or defending fruiting plants, or seed predators consuming most fruits.

Composition of seed rain

Seed arrival is just the first step in a many-phased process leading to tree establishment. Many post-dispersal factors alter recruitment after seed arrival. For example, seed predation may vary among seeds deposited in different forms (Chapman 1989, Willson and Whelan 1990, Moegenburg 1994). However, because seed rain can be the primary source of propagules in many heavily degraded systems, it may still guide future patterns of plant colonization. Below, we offer several predictions of future forest succession on the recently abandoned lands for Kibale and similarly degraded habitats based on the seed rain analyses.

Nearly half (49%) of all seeds collected below trees on the study site were *Ficus* species. Most of these were probably from two large hemi-epiphytic *Ficus* trees on the site that fruited, and, thus, these seeds were unable to establish. Most other seeds collected were from shrubs (34%), and relatively few were from trees (14%). In addition, very few tree and shrub seeds were of forest species (<1%); a surprisingly low proportion considering the vast seed source of the nearby forest. This finding and the lack of a distance effect on seed rain suggest that few birds and bats are crossing from forest into cropland, or that they transport few forest seeds into cropland when they do. Thus, forest succession on Kibale's degraded lands may be delayed by low recruitment of tree seeds.

The low number of tree seeds dispersed onto Kibale's degraded lands suggests succession may differ from degraded Neotropical systems where tree seeds have been reported to be over half the seed numbers dispersed and one-fourth of dispersed species (Guevara and Laborde 1993, Da Silva et al. 1996). Most tree seeds dispersed into degraded Neotropical systems were of small-seeded pioneer species that quickly colonize disturbances (e.g., *Cecropia* spp.; Guevara and

Laborde 1993, Da Silva et al. 1996). Unlike many tropical regions, Kibale seems to lack such assertive pioneer trees (Chapman et al., *in press*), partially explaining the low proportion of tree seeds relative to other studies. This, and the lack of non-pioneer forest species dispersed (<1%), suggests that forest succession on degraded lands at Kibale may be exceptionally slow.

More shrub than tree seeds were dispersed into abandoned cropland at Kibale, suggesting shrubs may dominate initial succession. The potential importance of colonizing shrubs should not be overlooked, especially where forest succession is slowed or prevented by grasses or climbers. Where trees are incapable of colonizing, shrubs that establish may serve as "nurse plants," providing microclimates more conducive to tree seedling establishment than surrounding areas of grassland (Nepstad et al. 1991, Vieira et al. 1994). Furthermore, many shrub species produce fleshy fruits that attract frugivores, thus increasing future seed rain in degraded areas (Vieira et al. 1994, Da Silva et al. 1996).

The seed dispersers

Using bird dung and bat wadges to indicate bird and bat seed dispersal, it seems birds preferred medium height and tall trees over short trees, whereas bats dispersed seeds mainly below tall trees. While seed species richness from birds surpassed that from bats when measured over the entire study, on several occasions outside of sampling intervals, bats dropped fruits and seeds of two large-seeded forest trees not present on the study site (*Chrysophyllum gorungosanum* and *Symphonia globulifera*), suggesting that bats can contribute a unique component to seed rain in degraded areas.

It is unclear what proportions of dropped fruit and unknown dung seeds were contributed by birds vs. bats. Bird contributions to seed rain were probably underestimated since many frugivorous birds produce dung lacking uric acid. We collected few bat wadges at short and medium height trees, suggesting they are not used as bat feeding perches. If so, dropped fruit and unknown dung seed rain at these trees was probably from

birds or flying bats. Furthermore, megachiropteran fruit bats seem to ingest and defecate few seeds of small-seeded fruits (Izhaki et al. 1995), which are the seeds dominating seed rain at these trees. Fruit bats often carry fruit from trees to nearby feeding perches, whereas birds tend to feed within fruiting trees (McDonnell and Stiles 1983, Thomas et al. 1988, Charles-Dominique 1991). Thus, dropped fruit below tall trees may be mostly from bats, but the origin of dropped fruit at short and medium height trees is unclear.

Few studies have compared fruit bat and bird seed dispersal in different habitats within disturbed areas. Da Silva et al. (1996) reported greater seed rain from birds than bats in degraded pasture in Brazil, but bats were the main dispersers of the first trees established in pastures. Bird seed dispersal was low until these pioneer trees established. Others have found that bat seed dispersal in degraded areas can surpass bird seed rain, and usually consists of pioneer tree species (Thomas 1982, Fleming 1988, Thomas et al. 1988, Gorchov et al. 1993). Charles-Dominique (1986) found that birds dispersed more seeds than bats at remnant trees in clearcuts, but bat seed rain exceeded bird seed rain below shrubs. These studies suggest bats may be more likely to disperse seeds into degraded areas lacking trees, while bird seed dispersal becomes increasingly important as trees establish (Da Silva et al. 1996). However, fruit bat densities in Africa seem to be lower than densities of their microchiropteran counterparts in the Neotropics (Findley and Wilson 1983). Having few pioneer tree species and few fruit bats to disperse them, Kibale seems to lack what are key components of forest succession in many other tropical regions.

Strategies promoting forest succession

The results of this study suggest that unassisted forest succession on degraded croplands in East Africa will proceed slowly. Plant recruitment in degraded areas may include few trees and will probably be limited to areas below isolated midsized and tall trees (>3.5 m). Areas surrounding these trees will be dominated by dense grassland, which may prevent the establishment of the few seeds that reach there. Furthermore, during dry periods these grasslands often burn, eliminating many colonizing trees and perpetuating grass dominance. This is evident at Kibale where grasslands still exist 100 yr after abandonment (Kingston 1967).

Facing these formidable barriers to forest succession, managers may want to facilitate forest regeneration on degraded lands in Kibale and similar systems. Management strategies are more likely to be successful and less costly in time and labor when they rely on natural processes. If the major limitation to succession is the lack of arriving seeds, a temporary crop of fruit-producing plants could be planted to attract frugivores and increase seed rain. This cover crop could create a microclimate favorable to seedling establishment. *Musa* spp. could be used since we found high levels of seed

rain below half the fruiting *Musa* we studied. The other *Musa* were visited by primates that may have dispersed seeds of forest species rarely dispersed by bats and birds. Trials would be needed to determine how long *Musa* would persist after planting, whether tree seedlings could establish below them, and how well the seedlings would grow. Another way to facilitate forest succession on degraded lands is to establish tree plantations of species that can tolerate the harsh conditions of these landscapes and allow recruitment of tree seedlings below them (Lovejoy 1985, Brown and Lugo 1994, Kuusipalo et al. 1995). Although plantations may facilitate forest succession in degraded lands, this strategy should be studied carefully before implementation.

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APPENDIX

Plant form category, species, typical habitat, and total number of seed species collected in five different habitats in a degraded agricultural area near the Kibale National Park, Uganda.

Plant form category	Seed species†	Typical habitat‡	Tall trees	Medium trees	Short trees	Short grassland	Tall grassland
Climber	<i>Diplocyclos palmatus</i>	D	2				
Climber	<i>Mamordica foetida</i>	D	2	3			
Climber	<i>Rubus</i> spp.	D	24	94	27		
Climber	sp. R	D			1		
Climber	sp. W	MF		2			
Climber	sp. X	D		4			
Climber	<i>Ureca hypsiloides</i>	U	20	7	1		31
Crop	<i>Musa</i> spp.	D		1			
Crop	<i>Piper nigrum</i>	D			3		
Crop	<i>Morus</i> spp.	D	3	6			
<i>Ficus</i>	<i>Ficus</i> spp.	U	2845	552	2119		
Herb	<i>Solanum nigrum</i>	D		9	15		
Shrub	<i>Ensete ventricosum</i>	MF	1				
Shrub	<i>Hoslundia opposita</i>	D	16	28			
Shrub	<i>Lantana camara</i>	D	121	114	7		3
Shrub	<i>Lantana trifolia</i>	D	71	68	21		
Shrub	<i>Piper umbellatum</i>	D	311	3094			
Shrub	sp. H	D	2				
Shrub	sp. C	U	1				
Tree	<i>Allophyllus abyssinicus</i>	MF	1				
Tree	<i>Cordia abyssinica</i>	D			1		
Tree	<i>Bridelia micrantha</i>	D	2				2
Tree	<i>Celtis africana</i>	D		8	1		
Tree	<i>Celtis durandii</i>	MF	9	2	1		1
Tree	<i>Diospyros abyssinica</i>	MF	1				
Tree	<i>Measa lanceolata</i>	D	186	1037	188		
Tree	<i>Polyscias fulva</i>	D	8	1	1		
Tree	<i>Prunus africana</i>	D	1				
Tree	<i>Sapium ellipticum</i>	D		1			
Tree	<i>Trema orientalis</i>	D	127	2	3	9	
Unknown	sp. A	U		27			
Unknown	sp. E	U		2			
Unknown	sp. K	U	6		3		
Unknown	sp. M	U		3			
Unknown	sp. O	U	1				
Unknown	sp. CC	U			1		
Unknown	sp. JJ	U	1				
Unknown	sp. KK	U			1		
Unknown	sp. OO	U	1				
Unknown	sp. RR	U	1				
Unknown	sp. TT	U		2			
Unknown	sp. UU	U			3		
Unknown	untyped spp.	U	8	5			

† Unidentified seeds were typed and given letter designations.

‡ The typical habitat of species was categorized as mature forest (MF), disturbances (D), or unknown (U).