Forest Restoration in Abandoned Agricultural Land: a Case Study from East Africa

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Abstract: *Millions of hectares of tropical forests have been converted to agricultural land and abandoned, so it is important that we understand the process of forest recovery and comprehend how pathways are modified by different types of disturbance in different geographic regions. In a 4-year case study, we quantified the pattern of forest recovery following clearing and 3 years of cultivation of a moist-evergreen forest in Uganda. Long-term observation (746 hours) of frugivore visitation to the regenerating area demonstrated that birds were frequent visitors (5.8 birds/hour), whereas large mammalian frugivores rarely used the area. Frugivore visitation rates facilitated seedling recruitment that averaged 0.51 seedlings/m^2 from 22 tree species by the end of the study. Recruitment included species with large seeds, despite the fact that seed-eating rodents were almost twice as abundant in the regenerating area than in mature forest. By the end of the study, however, only 20 trees were ≥0.5 m tall, and no trees were ≥2 m tall. This slow recruitment reflected high seedling mortality and dominance of the area by elephant grass (*Pennisetum purpureum*) and the herb* Acanthus pubescens*. After 4 years, trees ≥0.5 m tall attained a biomass of only 8.92 kg/ha, whereas the biomass of* P. purpureum *and* A. pubescens *had reached 35,500 kg/ha and 18,100 kg/ha respectively. We provide an initial assessment of two programs designed to enhance restoration of abandoned agricultural lands: planting of cuttings to act as dispersal foci and sowing of seeds. Our results showed that density of seedlings growing in the management plot where we sowed seeds (0.35 seedlings/m^2) and in the plot where we established cuttings (0.30 seedling/m^2) was lower than in the control plot (0.51 seedlings/m^2). This East African site was only lightly disturbed, yet tree recovery was occurring slower than in heavily degraded sites described from South America. The rate of recovery seemed to be strongly determined by interactions between tree seedlings and* P. purpureum *and* A. pubescens.

Restauración de Bosques en Tierras Agriculturales Abandonadas: Caso de Estudio en Africa Occidental

Resumen: *Millones de hectáreas de bosque tropical han sido convertidas a tierras agriculturales y abandonadas; por ello, es importante que entendamos el proceso de recuperación del bosque y comprendamos como sus posibles vías son modificadas por diferentes tipos de perturbación en diferentes regiones geográficas. En un caso de estudio de cuatro años de duración, cuatificamos los patrones de recuperación del bosque posterior a un clareo y tres años de cultivo en un bosque tropical húmedo siempreverde de Uganda. Observaciones de largo plazo (746 horas) de visitas de frugívoros a las áreas de regeneración demonstraron que las aves fueron visitadores frecuentes (5.8 aves/hora), mientras que mamíferos frugívoros grandes utilizaron el área en raras ocasiones. Las tasas de visita de frugívoros facilitó el reclutamiento de plátulas y promedió 0.51 plántulas/m^2 para 22 especies de árboles al final del estudio. El reclutamiento incluyó especies con semillas grandes a pesar del hecho de que la abundancia de roedores que se alimentan de semillas fue doble en la zona en regeneración que en el bosque maduro. Sin embrago, al final del estudio solo 20 árboles tuviéron ≥0.5 m de altura y no hubiéron árboles de ≥2 m de altura. Este reclutamiento lento refleja una alta mortalidad de plántulas y la dominancia en el área del pasto elefante (*Pennisetum purpureum*) y la hierba* Acanthus pubescens*. Después de 4 años, los árboles de >0.5 m de altura obtuvieron una biomasa de tan solo 8.42 kg/ha, mientras que la biomasa de* P. purpureum *y* A. pubescens *alcanzó 35,500 y 18,100 kg/ha respectivamente. Proveemos una evaluación inicial de dos programas diseñados para incrementar la restauración de tierras agriculturales abandonadas: siembra de esquejes que actúen como dispersores y siembra de semillas.*

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Nuestros resultados muestran que las densidades de plántulas creciendo en los lotes manejados donde se sembraron semillas (0.35 plántulas/m^2) y en los lotes donde se establecieron esquejes (0.30 plántulas/m^2) fueron más bajas que en los lotes control (0.51 plántulas/m^2). Este sitio Africano fué perturbado solo ligeramente, sin embargo, la recuperación de los árboles ocurre mas despacio que en sitios altamente degradados descritos para Sudamérica. la tasa de recuperación parece estar altamente degradados descritos para Sudamérica. La tasa de recuperación parece estar altamente determinada por interacciones entre las semillas de los árboles y P. purpureum *y* A. pubescens.

Introduction

Tropical forests and the animals they support are increasingly threatened by accelerating rates of forest conversion and degradation (Lanly 1982; Brown & Lugo 1990). Converted land is generally agriculturally unproductive, biologically impoverished, and more flammable than the forests it replaces (Uhl & Buschbacher 1985; Uhl 1987). Comparative data are generally not available to allow generalizations about the process of succession that follows different types of disturbance or the effectiveness of different forms of human intervention designed to facilitate recovery.

Much of our knowledge concerning regeneration of damaged habitats is based on investigations of temperate systems (Hutnik & Davis 1973; Johnson & Bradshaw 1979; Cairns 1980, 1988*a*, 1988*b*; McDonald & Stiles 1983), but using this information to predict regeneration in tropical areas may be misleading (Lugo 1992). For example, most temperate areas lack major groups of seed dispersers that are important in the tropics (e.g., frugivorous primates and bats). Not only is there a paucity of studies of regeneration in the tropics, but the available studies are biased toward the Neotropics. Unfortunately, applying what is known from Neotropical studies to other tropical areas of the world may be inadequate. For example, it may be inappropriate to apply results from the Amazon to mid-elevation African forests. Unlike a number of South American forests, mid-elevation African forests have few small-seeded colonizer genera (Chapman et al. 1999), no leaf cutter ants (*Atta*), and few trees that rely on wind dispersal. Wind-dispersed trees constitute 15% of forest tree species in Brazil (Uhl 1988) but only 2% in Uganda (C.A.C. and L.J.C., unpublished data).

Several factors can delay or stop regeneration in degraded areas, and the importance of these factors will probably vary geographically. Agricultural activities can lead to topsoil erosion or nutrient exhaustion (Uhl et al. 1982; Aide & Cavelier 1994); stump sprouting may be limited and seed banks depleted from repeated burning or weeding (Uhl et al. 1985; Nepstad et al. 1996); source plants that contribute new seeds may be distant or scarce (Guevara et al. 1986); and frugivore dispersers may not be attracted to degraded areas (Duncan & Chapman 1999). Even if seeds or sprouts are available in a degraded area, regeneration may not proceed because the microenvironment may be unsuitable (Brown & Lugo 1994); aggressive herbaceous growth may dominate (Walker 1994); the tree community of a region may lack species that can take advantage of the conditions found in large gaps (Chapman et al. 1999); seed and seedling predation may be extremely high (Nepstad et al. 1996); or human-initiated fires may prohibit succession from proceeding (Uhl & Kauffman 1990). In general, data on the importance of these factors are scarce, so examining geographical variation of their importance is not possible. Data on how different tree communities respond to large gap formation, however, indicate that geographical variation can be dramatic. For example, Augspurger (1984) and Brokaw (1985) examined recruitment of several tree species in different conditions in Panama and found that all the species exhibited higher growth and survival in the sun than in the shade. Similarly, Pompa and Bongers (1988) documented that in Mexico the growth of all species examined was enhanced in large and small gaps, and in large gaps the growth was more rapid than in small gaps. Ganzhorn (1995) reported that in Madagascar almost all overstory tree species regenerate best in gaps larger than gaps created by the collapse of a single tree. In contrast, research in Uganda demonstrated that for some species, growth in small gaps was not faster than growth in the understory, and that for most species there is higher mortality for seedlings grown in large gaps than for those in the understory (Chapman et al. 1999).

In a 4-year case study, we quantified the pattern of recovery of forest following clearing and cultivation in Kibale National Park, Uganda. First, we considered the pattern of seedling establishment and mortality in light of what plant forms dominate the regenerating lands. Second, we considered the role of seed dispersers and seed predators in forest recovery by quantifying visitation rates of birds and other frugivores, seed rain, and changes in rodent abundance. Third, we estimated the biomass of establishing trees, herbs, and grasses. To facilitate regional comparisons, these descriptions were made by methods similar to those used in many other Neotropical studies. Finally, we made an initial assessment of two management programs designed to enhance restoration of abandoned agricultural lands: (1)

planting cuttings to act as dispersal foci and (2) sowing seeds.

Methods

Study Site

Kibale National Park (766 km^2) is located in western Uganda, just east of the Ruwenzori Mountains (lat 0°13′–0°41′N, long 30°19′–30°32′E). Kibale is composed of mature moist-evergreen forest, swamp, grassland, plantation, abandoned agricultural land, and colonizing forest (Struhsaker 1975; Chapman & Chapman 1997). Our study was conducted near Makerere University Biological Field Station. This area is located at an elevation of 1500 m and receives an annual rainfall of 1700 mm (1984–1996) that is bimodal in distribution. May through August and December through February tend to be drier than other months. On average, the first rains of the year (March–April) are less severe than the second rains (September–November). Despite these bimodal trends, year-to-year variation in the magnitude, onset, and duration of wet and dry seasons is high. Mean daily minimum temperature is 15.5° C, and mean daily maximum temperature is 23.7° C (1990–1996).

We quantified the pattern of forest recovery following clearing and 3 years of cultivation of a moist-evergreen forest. Foresters have classified the forest that was originally on this site as a *Parinari* forest, distinguished on photo aspect maps by large, spreading crowns of *Parinari excelsa* (Kingston 1967; Skorupa 1988). The presence of *P. excelsa* and the subdominants (*Aningeria altissima, Olea welwitschii, Newtonia buchananii*, and *Chrysophyllum gorungosanum*) are thought to indicate a climax forest between 1370 and 1525 m (Osmaston 1959). Detailed enumeration of the tree community of this area is provided by Chapman et al. (1997).

We selected this area in which to quantify regeneration because it was one of a few areas of abandoned agricultural land within the northern section of the national park; so it was possible to exclude fire for the duration of the project. In addition, detailed information was available on its history of land use. It was a mixed-crop plot (the last crops were corn [*Zea mays*] and yams [*Dioscorea*]) that had been used for 3 consecutive years and then abandoned. As is typical for this area of Uganda, most trees were removed by the farmer, the area was burned, remaining logs were removed, the soil was hoed by hand, and stumps were removed. Each year before planting, the area was burned and hoed to remove colonizing grasses. Two plantings were made each year. This area was directly adjacent to a 300-ha portion of relatively undisturbed natural forest known as forestry compartment K-30 (Skorupa 1988). Prior to 1970, a few large stems (0.03–0.04 stems/ha) were removed from this area by pitsawyers, but this extremely low level of extraction had little effect on the structure of the forest (Skorupa 1988; Struhsaker 1997).

At least 26 rodent species have been trapped or seen in Kibale (Struhsaker 1997), and many of these species are seed predators (Basuta 1979). The rodents that are seed predators could potentially shape the trajectory of the regeneration. Because the abundance of different rodent species varies between habitats within Kibale and among years (Basuta & Kasenene 1987), the manner with which they influence forest regeneration could change over time.

Seedling Establishment and Mortality

A 30 × 50 m area was selected and subdivided into 15, 10 × 10 m subplots with corners marked with tall wooden stakes. To facilitate comparison with previous studies, the size and shape of this area were made the same as in prior studies in South America (Jordan & Uhl 1978; Uhl 1987; Saldarriaga et al. 1988). The location, size, and identity of any remaining trees were determined. Tree seedling establishment and mortality were monitored in the plot approximately every 3 months for 44 months (September 1993–April 1997). Each 10 × 10 m subplot was searched for seedlings, and every tree seedling encountered was identified and marked with an aluminum tree tag tied with a loose string to the base of the seedling. Every month an effort was made to find as many seedlings as possible. As the grass/herbaceous vegetation became progressively more dense, it became increasingly difficult to locate new seedlings, so seedlings were discovered only when they reached a larger size. Because of this bias, the seedling establishment and mortality rates that we report should be considered minimum rates.

Dominant Cover and Aboveground Living Biomass

We quantified changes in plot vegetation every 4 months. Four quadrats (65 × 65 cm) were placed systematically in each subplot, with each quadrat 2 m from the center of the subplot in each of four compass bearings (north, east, south, and west). We described the dominant plant form in the quadrat, estimated the percentage of bare ground, and ranked light availability at ground level on a scale of 1 to 4 (4 being full sunlight).

To estimate aboveground living biomass of trees for each year of the study, regression equations were built between tree height and dry weight for a set of trees harvested from forest patches outside of the park (n = 28, trees ≥0.5–2 m in height, no tree had exceeded 2 m by the end of the study, Uhl 1987). The species selected were those commonly found in the subplots (*Albizia grandibracteata, Bridelia micrantha, Diospyros abyssinica, Erythrina abyssinica, Maesa lanceolata, Mille-*

tia dura, Pygeum africanum, Sapium ellipticum), and the sample of harvested trees approximated the relative abundance of the species in the study area. Height was measured after the tree was harvested by cutting it at ground level. Subsequently, leaves were separated from stems and trunk, and the material was air dried by hanging it under a tin roof that provided rain protection but permitted airflow. Leaves were placed in mesh bags, whereas stems and trunk were simply tied together. Samples were allowed to dry until they reached a constant dry weight.

Regression equations between tree height and dry weight were established from this sample (log dry weight = 0.00452 (height in cm) + 1.476; $r^2 = 0.791$, $p < 0.0001$, $n = 28$). Subsequently, the dry weight of every tree ≥0.5 m tall was calculated for the trees in the regenerating area. We selected these procedures to facilitate comparison with studies conducted in South America (Jordan & Uhl 1978; Uhl 1987; Saldarriaga et al. 1988).

In the last 2 years of the study, grasses (primarily elephant grass [*Pennisetum purpureum*]) and herbs (primarily *Acanthus pubescens*) constituted a significant component of the biomass. Thus, in the final sampling period (April 1997) the height of all *A. pubescens* stems was measured ($n = 161$), and a regression equation was built between *A. pubescens* height and dry weight for a set of plants harvested from forest patches outside of the national park (dry weight = 0.7165 (height in cm) − 885.243; $r^2 = 0.584$, $p < 0.004$, $n = 12$). Using these equations, we estimated the dry weight of *A. pubescens* in the plot. *P. purpureum* grows in dense clusters that can dominate large sections of land. We then estimated the proportion of each 10 × 10 m subplot dominated by *P. purpureum*. Subsequently, we harvested 12, 1-m^2, randomly selected *P. purpureum* areas by cutting all stems at ground level. Samples were dried to determine biomass.

Seed Rain

Seed traps were used to assess the quantity of seeds falling onto the plot (Chapman et al. 1994). Traps were durable plastic sheets loosely stretched and stapled to 0.5-m^2 wooden frames. Each frame was elevated on legs 20–25 cm tall to reduce seed removal by seed predators. Rain was permitted to drain by cutting a 4 × 4 cm hole in the center of the trap and covering the hole with 1 × 1 mm plastic mesh. This mesh size was used because McClanahan and Wolfe (1987) demonstrated that 1.4 mm mesh is smaller than the expected size for bird-dispersed seeds. Seed removal from these seed traps in abandoned crop land is low (i.e., <1% of 150 seeds were removed from five traps during 6 days for each of two species, *Celtis durandii* and *Albizia grandibracteata*; these species are common in regenerating areas and vary in seed size). Fifteen seed traps were placed randomly throughout the regenerating area. Traps were monitored once a week for the first 10 months of the study. The contents were transferred into individually labeled plastic containers and transported to the lab, where they were sorted. When possible, we identified the animal that had deposited the seed onto the trap (e.g., if it was found to have white uric acid it was identified as bird dung; Duncan & Chapman 1999). After 1 year, grasses and herbs were beginning to grow over many of the traps. Because falling seeds could be deflected by overhanging vegetation, traps were removed.

Frugivore Visitors and Rodent Abundance

To quantify diurnal frugivore activity in the study plot, observations were made from a tower 3 m tall approximately 20 m from the western edge of the regenerating area (da Silva et al. 1996). Observations were initiated shortly after the area was cleared and were made once every 2 weeks until May 1996 (34 months). All birds flying over the area were counted, and any bird perching within the area was recorded. We grouped birds into two categories, small passerines and large seed dispersers (e.g., hornbills [*Bycanistes subcylindricus*]). For primates and ungulates, the length of time each species spent in the area was noted. Observations started shortly after dawn and were made for an average of 9 hours each day, for a total observation time of 746 hours.

To evaluate patterns of rodent abundance, we used standard Sherman live traps (7.6 × 8.9 × 22.9 cm) baited with a mixture of ripe bananas (approximately 60% by weight), maize flour (30%), and powdered peanuts (10%). This bait is effective in attracting a wide range of small mammals (Cheesman & Delany 1979) and has been successfully used in a number of studies conducted in Kibale (Basuta 1979; Basuta & Kasenene 1987; Struhsaker 1997). One trap was set in the middle of each 10 × 10 m subplot (total $n = 15$) in the late afternoon and checked early the following morning. Captured rodents were identified and released. Rodent capturing was conducted 38 times between September 1993 and June 1996, 570 total trap nights.

Management Strategies to Promote Regeneration

We assessed the relative merits of two potential management programs: (1) planting cuttings to act as foci for seed dispersal and (2) sowing seeds. We used two 20 × 40 m plots that were in the same area as the control plot (the plot previously described) and that had a similar history. Within the first experimental plot, two *Erythrina abyssinica* cuttings and three *Ficus* spp. (*F. brachylepis, F. natalensis, F. dawei*, 1.5 m tall) cuttings were planted in each 10 × 10 m subplot. In the second experimental plot, we examined the effect of sowing seeds. We selected species that typically are described as pioneers

(Hamilton 1991; Katende et al. 1995) or that are commonly found growing in disturbed areas around Kibale (Chapman et al. 1999). We used *Albizia grandibracteata* (100 seeds in each subplot, for a total of 800 seeds), *Cordia abyssinica* (100 seeds in each subplot, for a total of 800 seeds), *Trema orientalis* (400 seeds in each subplot, for a total of 3200 seeds), and *Maesa lanceolata* (400 seeds in each subplot, for a total of 3200 seeds). The number of seeds used was based on seed size (more seeds for small-seeded species) and availability. For the two treatments we quantified seedling growth and mortality, dominant cover, frugivore visitors, and rodent abundance following the procedures outlined previously.

Results

Seedling Establishment and Mortality

The rate of tree seedling establishment was slow during the first 2 years following abandonment but increased rapidly in years 3 and 4 (Fig. 1a). Seedling mortality also increased in the last 2 years of the study and showed a pattern of higher mortality in the dry season (Fig. 1b). By the end of the 44 months of the study, only three individual trees had reached ≥1 m in height (*Acrocapus fraxinifolius*, *Persea americana* [Avocado], and *Maesa lanceolata*), and only 20 trees were ≥0.5 m tall. *A. fraxinifolius* was introduced to East Africa from Southeast Asia and is planted as a source of fuelwood (Katende et al. 1995). Avocado is an exotic that was introduced for its edible fruits, probably when the area was cleared. *M. lanceolata* is a fast-growing native tree.

The number of tree species in the plot increased linearly; 22 species were present after 44 months (Fig. 1c). Despite this steady increase in species richness, a few species dominated the recruiting tree community: *Milletia dura, Diospyros abyssinica, Maesa lanceolata*, and *Bridelia micrantha* constituted 76.2% of all seedlings (Fig. 2). The majority (91%) of the species that established on the plot had fleshy fruits or dry dehiscent pods; only 9% (2 out of 22) were wind-dispersed. Some of the establishing seedlings in both the control and experimental plots were large-seeded species (e.g., *Mimusops bagshawei* [1.7 cm long, SD ± 1.7], *Monodora myristica* [1.8 cm long, SD ± 1.8], *Uvariopsis congensis* [1.3 cm long, SD ± 1.2]) that are dispersed by large frugivores.

Dominant Cover

The vegetative cover in the plot was assessed 11 times between November 1993 and April 1997 (41 months) at approximately 4-month intervals. The first year of growth was dominated by short grasses (primarily *Cynodon dactylon*) and short herbs (primarily *Bidens pilosa*). *Pennisetum purpureum* soon became established and gradually dominated the area (Fig. 1d). Associated with the increased dominance of *P. purpureum* was a decline in both diversity (Simpson's index) and species richness of the plants dominating the 60 sampling plots and a decline in the amount of bare ground available for colonization (Fig. 3). Near the end of the study, *Acanthus pubescens* became more abundant and was replacing *P. purpureum* (Fig. 1d). Observations made on lands near the regenerating area that have been abandoned for longer periods suggest that in some areas *A. pubescens* is capable of eventually replacing *P. purpureum* to form a dense monospecific stand. Trees rarely dominated any sampling quadrats (only 3% of the quadrats during one sample period), and at the end of the sampling none of the quadrats was dominated by trees.

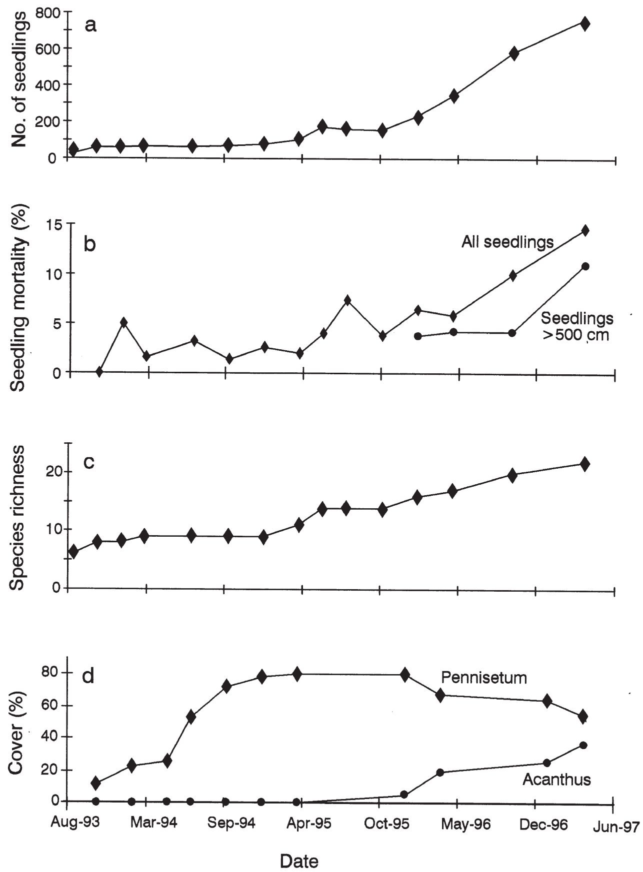

Figure 1. Components of the regeneration process that took place in a 30 × 50 m area of abandoned agricultural land that was converted from moist-tropical forest in Kibale National Park, Uganda: (a) number of seedlings found in the regenerating area, (b) percentage of seedlings dying between sampling periods, (c) species richness of seedlings over time, and (d) percentage of quadrats dominated by Pennisetum purpureum *(elephant grass) and* Acanthus pubescens*.*

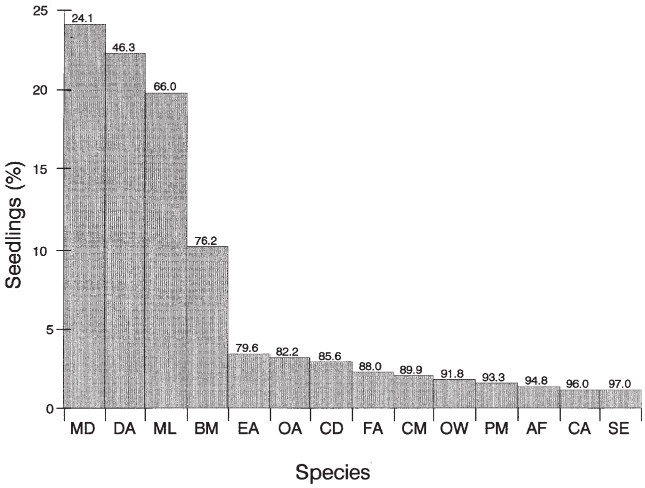

Figure 2. Composition of the seedling community found in an abandoned agricultural land converted from moist-tropical forest in Kibale National Park, Uganda, 4 years after abandonment. The cumulative composition of the community is presented above each bar describing a specific species: MD, Milletia dura*; DA,* Diospyros abyssinica*; ML,* Maesa lanceolata*; BM,* Bridelia micrantha*; EA,* Erythrina abyssinica*; PA,* Pygeum africanum*; CD,* Celtis durandii*; FA,* Fagaropsis angolensis*; CM,* Croton macrostachyus*, OW,* Olea welwitschii*, PM,* Persea americana*, AF,* Acrocapus fraxinifolius*; CA,* Celtis africana*, SE,* Sapium ellipticum *(nomenclature follows Hamilton 1991).*

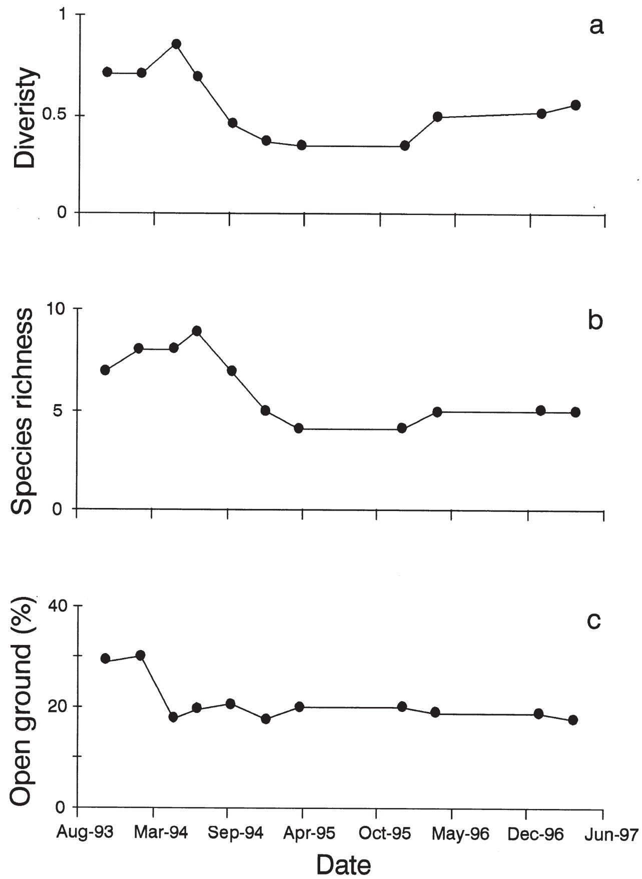

Figure 3. Changes in (a) diversity (Simpson's index) and (b) species richness of all plants dominating 60 sampling plots (65 × 65 cm) and (c) amount of open ground available for colonization found in abandoned agricultural land that was converted from moist-tropical forest in Kibale National Park, Uganda.

Aboveground Living Biomass and Seed Rain

Tree biomass was extremely low throughout the study. It increased steadily over the first 3 years (year 1 = 6.39 kg/ha, year 2 = 10.08 kg/ha, year 3 = 10.74 kg/ha) but declined in year 4 (8.92 kg/ha). The decline reflected an increased mortality rate in trees 0.5–1 m tall and the slow recruitment into this size class. This increased mortality corresponded to the time when *P. purpureum* dominated and *A. pubescens* abundance was increasing. By year 4, the biomass of *P. purpureum* and *A. pubescens* averaged 35,500 kg/ha and 18,100 kg/ha, respectively.

We monitored 15, 0.5-m^2 seed-rain traps over the first 254 days of the study. During this period only three *Maesa lanceolata* fruits were found on the traps (see also Duncan & Chapman 1999). No fecal material was associated with the seeds, so it is likely that either an animal carrying the fruits dropped them or the seeds were blown onto the trap.

Frugivore Visitors and Rodent Abundance

We assessed frugivore visitation rates to the study area based on 746 hours of observation over 34 months. During this period 3831 birds flew over (n = 1920) or perched (n = 1911) in the plot. Large frugivorous mammals entered the plot on three occasions: chimpanzees (*Pan troglodytes*, in a group of 3), black-and-white colobus (*Colobus guereza*, not typically seed dispersers, in a group of approximately 11), and bushbuck (*Tragelaphus scriptus*; known to disperse seeds, a solitary individual). Although large frugivores rarely entered the regenerating area, their activity may have been significant. For example, most chimpanzee defecations contain seeds (98.5%), and a single defecation will on average contain 22 large seeds from 2.8 species (Wrangham et al. 1994). Further, many of the seeds dispersed by animals like chimpanzees are often large and of different species from those dispersed by small birds. Hornbills are very large frugivorous birds, known to disperse seeds of many fruiting tree species, including species with large seeds (Kalina 1988). Hornbills flew over the regenerating area on 116 occasions but never landed in the plot.

Frugivore visitation rose quickly after abandonment due to a number of bird species eating seeds of the short grasses that quickly became established (Fig. 4). As the short-grass species were replaced by *P. purpureum*, frugivore visitation declined. Thereafter, visitation increased gradually as the *P. purpureum* was replaced by *A. pubescens.* The fact that seedling recruitment was slow in the first 2 years of this study and peaked only after frugivore visitation increased suggests that seeds present in the soil seedbank were not a major source of seedling recruitment.

Three species of rodents made up the majority of the animals captured and released (*Praomys jacksoni, Hylomyscus stella, Lophuromys flavopunctatus*), and there was no major change in the proportions of these species over time. Through analyses of stomach contents of rodents in Kibale National Park, Basuta (1979) found that fruit and seeds constituted between 50% and 65% of the diet of both *P. jacksoni* and *H. stella. L. flavopunctatus* was more insectivorous, but fruit and seeds still made up over 35% of its diet. Considering all three species as potential seed predators, we found few seed predators in the area immediately after the land was abandoned, but within 3 months the number of seed predators increased dramatically. Within 9 months, trap success had declined (Fig. 5).

Contrasting the capture success from the regenerating area to unlogged areas of Kibale indicates that the relative intensity of seed predation is higher in regenerating land than in forest. Two studies have been conducted in Kibale using methods similar to those employed here (same traps and bait but different years; Kasenene 1980, 1984; Muganga 1989). The trap success of these studies averaged 12.4%, whereas trap success in our plot averaged 22.9%.

Management Strategies to Promote Regeneration

At the conclusion of the study, the density of seedlings in the management plot in which we sowed seeds (0.35 seedlings/m^2) and in the plot in which we planted cuttings (0.30 seedlings/m^2) was lower than in the control plot (0.51 seedlings/m^2). In the plot where seeds were sown, there was little evidence of increased recruitment of the species used in the trial. We spread 800 *Cordia abyssinica* seeds throughout the plot, but no seedlings of this species were found until 4 years later, when one was found. We placed 3200 *Trema orientalis* seeds in the plot, and no seedlings of this species were found. Similarly, 3200 *Maesa lanceolata* seeds were spread throughout the plot, and only two seedlings of this species were found in the first 4 years (far fewer than the control plot, where 36 seedlings were found by year 4). The only species for which recruitment increased as a result of seeding was *Albizia grandibracteata* (100 seeds were sown in each subplot, for a total of 800 seeds). Within 3 months of sowing *A. grandibracteata* seeds, 16 seedlings had established, and seedling density at the end of the study was higher in the experimental plot (0.035 seedlings/m^2) than the control plot (0.008 seedlings/m^2).

In the first year of the study, birds were frequently seen perching on the cuttings that had been planted in the second experimental plot, suggesting that these cuttings could act as foci for seed dispersal. However, there

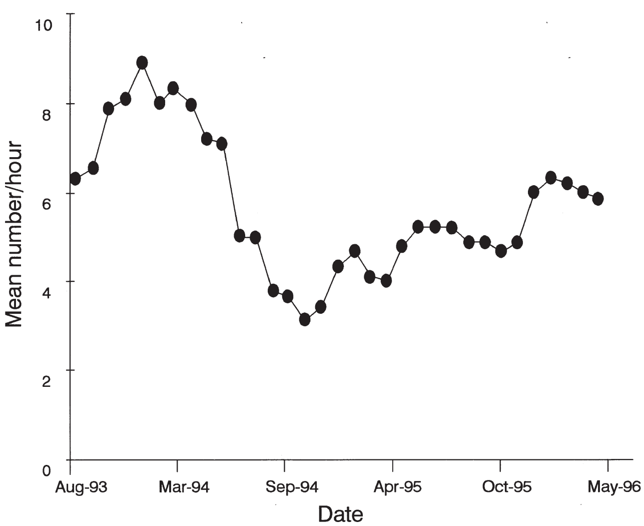

Figure 4. Mean number of frugivores (primarily birds) entering an area of abandoned agricultural land converted from moist-tropical forest in Kibale National Park, Uganda, over the duration of the study (3-month running mean).

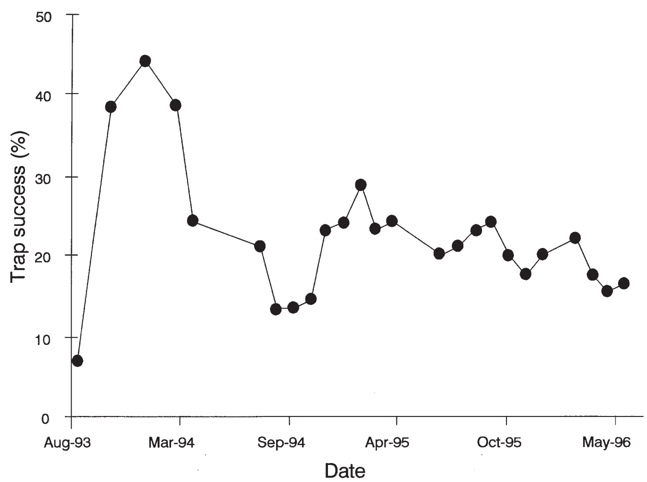

*Figure 5. Percentage of baited rodent traps that were successful at catching seed predatory rodents (*Praomys jacksoni, Hylomyscus stella, Lophuromys flavopunctatus*) during different sampling periods (3-month running mean).*

also were perches, such as tall grass stems, available in the other areas, and over the entire study there was little inter-plot difference in avian visitation (control, 38.3 birds/hour/ha; seeds sown, 41.9 birds/hour/ha; cuttings, 40.0 birds/hour/ha). By the third year, grasses had started to overtop the cuttings, and by the fourth year the cuttings, although often healthy and growing, were submerged under *P. purpureum.* Trap success in capturing rodents was similar among the three plots (control, 22.9%; seeds sown, 25.9%; cuttings, 21.3%) and showed similar changes over time.

Discussion

General Findings

Although our investigation is a case study of one site, surveys throughout Kibale National Park and surrounding areas suggest that the recovery of forest quantified on the plot was typical for the region (Struhsaker 1997; C.A.C. & L.J.C., personal observation).

In comparison to other forms of land use typical in tropical regions (e.g., clearing for pastures, Uhl et al. 1982; Buschbacher et al. 1992; Nepstad et al. 1996), disturbance to this East African site was relatively light. The area was used for only 3 years, it was adjacent to undisturbed forest, the topsoil was not eroded or compacted, and no exotic grasses or weeds appeared to inhibit regeneration. The hoeing, however, did remove trees that would resprout. Despite this light level of modification, the pathway of forest succession was not favorable for forest recovery (as scaled by comparisons to other sites: Uhl & Jordan 1984; Uhl 1987; Nepstad et al. 1996). Frugivore visitation rates appeared to be sufficient to facilitate seedling recruitment that averaged 0.51 seedlings/m^2 from 22 tree species by the end of the 4-year study. This recruitment was dominated by small-seeded species but did include some large-seeded species that probably required dispersal by large frugivores. This level of recruitment was surprising given that seed-eating rodents were almost twice as abundant in the regenerating area as in mature forest. Despite this initial establishment success, however, by the end of the study only 20 trees were ≥0.5 m tall, only 3 trees had reached ≥1 m in height, and no trees were ≥2 m tall. This slow recruitment corresponded to high levels of mortality in the larger seedling size classes near the end of the study and with the dominance of the area by *P. purpureum* and *A. pubescens*, both native to the region. Corresponding to this pattern of recruitment, tree biomass was extremely low throughout the study, whereas the biomass of both *P. purpureum* and *A. pubescens* reached high levels by the end of the study.

These observations are in marked contrast to descriptions of succession following slash-and-burn agriculture in the Amazon. In his study in the upper Rio Negro region of the Amazon, for example, Uhl (1987) described regeneration in a plot the same size as the one established in Kibale. In the first year after abandonment, he found 17 trees ≥2 m tall; during the second and third years the pioneer tree genus *Vismia* had grown to form a partially closed canopy at 8 m; and by the fourth year 667 individuals were ≥2 m tall. The aboveground biomass in Uhl's study was dominated by trees, and by the fourth year it was 2861 g/m^2. The pattern of tree recovery described at Kibale is similar to that described from some heavily modified sites in South America (Uhl et al. 1982; Nepstad et al. 1996). Buschbacher et al. (1992) quantified tree density (≥2 m tall) in abandoned pastures after light, moderate, or heavy use (heavy use involved use of bulldozers to clear all vegetation and woody debris). Although there was a great deal of variation in the density of trees on heavily used lands, after 8 years the density of trees ≥2 m tall was as low as 0.6 individuals/ha.

As might be expected given the variation in the intensity of disturbance and the characteristics of the lands studied, the time estimated for disturbed lands to reach an aboveground biomass value characteristic of mature forest is highly variable. Early descriptions of recovery time for abandoned tropical fallows suggested that only 30–40 years would be required to reach a biomass equivalent to that of a mature forest (Snedaker 1970; Lugo et al. 1974; Scott 1977); these studies have been criticized, however. Most important, after initially increasing linearly with time, the rate of biomass accumulation plateaus for a period because biomass accumulation of living trees is offset by the death of short-lived pioneers (Saldarriaga et al. 1988). Saldarriaga et al. (1988) suggest that it might require 200 years following slash-and-burn agriculture for the area to attain the biomass of mature forest. Similarly, Buschbacher et al. (1992) suggest that 200 years might be required for recovery on moderately used pastures, whereas Uhl et al. (1982) estimate that roughly 100 years would be required for areas of caatinga forest in the Amazon and more than 1000 years for sites cleared by bulldozers. Because the biomass of trees declined between years 3 and 4 or our study, we cannot calculate the time to recovery for the Kibale site; available evidence, however, suggests that it may be long.

Why is the recovery of forest at Kibale slow given the modest level of disturbance? Uhl and Jordan (1984) reviewed studies reporting aboveground dry biomass; average biomass 4 years after abandonment was 3559 g/m^2. In Kibale the aboveground dry biomass of trees, *P. purpureum*, and *A. pubescens*, was 5374 g/m^2. This value suggests that the site has the capability to support high levels of regeneration, but herbs and grasses dominate, not trees. Considering the number and diversity of seedlings found in the plot in the later years, seeds appear to be arriving, and the density of seedlings suggests that they can germinate and establish. But seedlings seem unable to grow through dense stands of *P. purpureum* and *A. pubescens.* Thus, the pathway of succession appears to have been deflected from one leading to forest to one dominated by either *P. purpureum* or *A. pubescens.*

A number of documented cases have shown that disturbed areas become dominated by aggressive pioneering herbs, vines, grasses, and/or shrubs, and decades after the disturbance pioneer trees may still be largely absent from such sites (Brokaw 1983; Kasenene 1987; Walker 1994; Walker et al. 1996). The literature on logging of tropical forests also provides a rich source of anecdotal descriptions that suggest that tree regeneration following logging can be retarded by establishment of an aggressive herb or vine layer (Fox 1976; Yap et al. 1995; Pinnard et al. 1996).

Our findings echo the conclusions of others who have examined succession on disturbed lands in suggesting that many factors influence the pathway of succession (Ewel 1980; Uhl 1987). Our findings, however, highlight the importance of considering interactions between plants in determining the rate and trajectory of plant succession. The site in Kibale was lightly disturbed, yet tree recovery occurred at a rate slower than that described for even heavily degraded sites in South America. The rate of recovery seems to be strongly determined by interactions between tree seedlings and *P. purpureum* and *A. pubescens*, which dominate the area.

Evaluating Management Strategies to Promote Regeneration

Both of the programs we examined, planting of cuttings to act as dispersal foci and sowing of seeds, were designed to increase seed input, a factor repeatedly identified as limiting forest recovery (Uhl 1987, 1988; Nepstad 1989; Nepstad et al. 1990, 1996; da Silva et al. 1996). Unfortunately, the time when sown seeds were likely germinating corresponded to the period of highest rodent density, so the success of this treatment might have been different if seeds were sown when rodent densities had declined. This illustrates the complexity of interactions in the recovery process and suggests that manipulations made at different times could have very different effects.

The second program was based on the idea that cuttings would act as dispersal foci. Because deforested agricultural or pastoral lands offer little to foraging frugivores, animal-dispersed seed rain to such areas is typically low (Duncan & Chapman 1999). A number of studies have, however, documented that remnant forest trees offering food and/or perches to frugivores produce elevated levels of seed rain (Uhl 1987; Willson & Crome 1989; Nepstad et al. 1991, 1996; Guevara & Laborde 1993; Vieira et al. 1994). Furthermore, the microhabitat below such trees may be more suitable for germination and establishment than nearby treeless areas (Kellman 1980; Uhl et al. 1982; Guevara et al. 1986, 1992). All of these studies suggest that planting cuttings should be a profitable management strategy. Unfortunately, during the first 2 years when the cuttings were used as perches, rodent density was high. When rodent density declined, *P. purpureum* had grown to a height at which it formed a canopy above the cuttings.

The failure of these potential management strategies illustrates the need for more descriptions of regeneration in a wider variety of settings in many geographic regions. These results and the documentation that regeneration in the area was slow also call for more detailed and extensive investigations into other management strategies that might facilitate regeneration. When attempts are made to manage lands that require human intervention to assure forest ecosystem rehabilitation, it has been suggested that tree plantations should be considered as a means of restoring the productivity of the land (Lugo 1992; Parrotta et al. 1997). The premise underlying this suggestion is that plantation trees can act as shelter trees permitting indigenous trees to grow; then the plantation trees are harvested, paying for the restoration effort. Studies in Kibale (Chapman & Chapman 1996; Zanne 1998) have shown that the species richness of indigenous trees was high in plantations, suggesting that this might be a profitable mechanism to encourage regeneration on abandoned agricultural lands in East Africa.

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