

Forest Regeneration in Logged and Unlogged Forests of Kibale National Park, Uganda¹

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ABSTRACT

Processes of forest regeneration in two unlogged areas and in three areas that were logged nearly 25 years ago were quantified in Kibale National Park, Uganda. For forests to recover from logging, one would predict recruitment and growth processes to be accelerated in logged areas relative to unlogged areas, facilitating increased recruitment of trees into the adult size classes. We examined this prediction first by determining the growth of 4733 trees over a 51 to 56 month period and found that growth rates in the most heavily logged area were consistently slower than in the two unlogged areas. In contrast, the lightly logged forest had similar growth rates to unlogged areas in the small size classes, but trees in the 30 to 50 cm DBH size cohort exhibited elevated growth rates relative to the unlogged areas. Mortality was highest in the heavily logged areas, with many deaths occurring when healthy trees were knocked over by neighboring treefalls. We found no difference in the density or species richness of seedlings in the logged and unlogged forests. The number of seedlings that emerged from the disturbed soil (seed bank+seed rain) and initially seed-free soil (seed rain) was greater in the logged forest than in the unlogged forest. However, sapling density was lower in the heavily logged areas, suggesting that there is a high level of seedling mortality in logged areas. We suggest that the level of canopy opening created during logging, the lack of aggressive colonizing tree species, elephant activity that is concentrated in logged areas, and an aggressive herb community, all combine to delay vegetation recovery in Kibale Forest.

Key words: logging; phenology; recruitment; seed dispersal; seed rain; tropical forest management; Uganda.

TROPICAL FORESTS ARE BEING LOGGED OR converted to agricultural land at an ever increasing rate. One estimate suggests that most of the world's tropical forests will be affected by commercial logging or other severe human disturbances within the next 20 years (Johns & Skorupa 1987). As a result, there will be an increased tendency to relog previously harvested areas, to restore degraded areas to productive lands, and to manage harvest sites more effectively. In all of these situations it will be necessary to predict the direction and time scale over which regeneration will occur and understand the processes that will influence the time scale.

For effective long-term management of harvest areas, estimates of forest recovery rate are vital to establishing appropriate cutting cycles. Early estimates of cutting cycles were simply based on typical growth rates of tropical trees and average levels of felling damage (Dawkins 1959) and ignored processes that could alter rates of regeneration. Inventory data and estimates of the growth and mortality rates of cohorts of trees have been used to provide the basis for harvesting schedules (e.g., Vanclay 1989). However, such models use the mean growth rate which may be inappropriate and

use unreliable mortality estimates which ignore episodic and spatially clumped mortality events (Putz 1993). Putz (1993) suggests that such stand models should be restricted to areas with conditions similar to the sites on which the model's parameters were based. If present models have only restricted application, it may be more effective to develop models based on a better understanding of how different logging practices and ecological parameters affect the processes of regeneration (e.g., seedling establishment, tree recruitment, growth, fruiting phenology, tree mortality). Important parameters include: soil fertility (Ewel 1980), the extent and rate of herb or shrub layer growth (Fitzgerald & Selden 1975, Brokaw 1983, Kasenene 1987), the probability of fire inhibiting regeneration in the flammable degraded landscape (Uhl & Buschbacher 1985, Uhl *et al.* 1988, Woods 1989, Uhl & Kauffman 1990), the nature and extent of animal damage to logged forests (Osmaston 1959, Wing & Buss 1970, Fox 1976), the nature of skid damage, soil compaction, and erosion following logging and bulldozer activity (Uhl *et al.* 1982, Cannon *et al.* 1994), and the level of extraction (Wilkie *et al.* 1992).

In this study, we quantify processes of forest regeneration in two unlogged areas and in three areas that were logged nearly 25 years ago at dif-

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ferent intensities. For forests to recover from logging, one would predict recruitment and growth processes to be accelerated in logged areas relative to unlogged areas, facilitating increased recruitment of trees into the adult size classes. We examined this prediction first by determining the growth of 4733 individually marked trees over a 51 to 56 month period and by quantifying the mortality rate and source of mortality for trees in logged and unlogged areas. We quantified the potential for recruitment into the seedling class by measuring seed rain, estimating the number and diversity of seeds in the soil, and by monitoring tree fruiting patterns to determine the frequency with which fresh seeds were locally available. Finally, we measured seedling density and stand structure in logged and unlogged forests.

METHODS

STUDY SITE AND SPECIES.—Kibale National Park (766 km²), located in western Uganda (0°13'–0°41' N and 30°19'–30°32' E) near the base of the Ruwenzori Mountains, is a moist evergreen forest, transitional between lowland rain forest and montane forest (Wing & Buss 1970, Skorupa 1988). About 60 percent of the park is tall forest with a 25–30 m canopy. The remainder of the park is composed of a mosaic of swamp, grassland, pine plantations, and colonizing forest (Wing & Buss 1970). The Kibale forest received the protected status of a National Park in 1993. Prior to this date, the area had been Forest Reserve (gazetted in 1932) with the stated goal of providing a sustained production of hardwood timber (Osmaston 1959). A planned polycyclic felling cycle of 70 years was initiated, and it was recommended that the logging open the canopy by approximately 50 percent through the harvest of trees over 1.52 m in girth (Kingston 1967). Twenty-seven hardwood species were recommended for harvesting.

The selection of study sites is a particularly important issue for this study, since few pre-logging data concerning the forest composition of different areas are available. In this study we attempt to compare various properties of logged areas to control areas that have not been logged. However, we have no means of insuring that the control and treatment areas did not differ prior to logging. Thus, observed differences may not be due to the site's logging history alone. To attempt to address this problem, we have selected two unlogged control sites, which we contrast with three logged sites. By having two control areas we can examine

whether the variance between unlogged sites is of a reduced or similar magnitude to the variance between unlogged and logged sites. Therefore, our study was conducted in five areas in the National Park. Four areas were adjacent to the Makerere University Biological Field Station at Kanyawara, and the fifth site was at another field station 10 km to the south at Ngogo. Kanyawara is situated at an elevation of 1500 m and Ngogo is at 1350 m. Within each site there are elevational changes from hill tops to valley bottoms of 150–200 m (measured with a Paulin Micro Surveying Altimeter). Kanyawara exhibits slightly cooler temperatures (annual mean daily minimum 1977 to 1994 = 16.4 ± 0.4 °C; maximum = 23.3 ± 0.6 °C; 1977 to 1984 = 16.2 ± 0.4 °C; maximum = 23.3 ± 0.6 °C) than Ngogo (annual mean daily minimum; 1977 to 1984 = 16.7 ± 0.4 °C; maximum = 24.2 ± 0.6 °C). Mean annual rainfall has averaged 167 cm (1977–1994; 157 cm 1977–1984) at Kanyawara. Ngogo receives slightly less precipitation with a mean annual rainfall of 149 cm (1977–1984).

The forest area at Kanyawara is considered a *Parinari* forest, which is distinguished on photo aspect maps by large spreading crowns of *Parinari excelsa*. Ground surveys indicate that this forest type can be divided into major subtypes, however ground sampling also suggests that all of these subtypes are very similar in terms of cumulative basal area, canopy cover, and stem density (Kingston 1967). Such features generally vary by only approximately 5 percent across even the most dissimilar of the *Parinari* forest subtypes (Kingston 1967, Skorupa 1988). The presence of *P. excelsa* and the subdominants found near Kanyawara (*Aningeria altissima*, *Olea welwitschii*, *Newtonia buchananii*, and *Chrysophyllum gorungosanum*) have been thought to indicate climax forest between 1370 and 1525 m (Osmaston 1959). Ngogo, at 1350 m, has some features of lower elevation forests. *P. excelsa* is still present, but the forest is very mixed with *Chrysophyllum* spp. and *Celtis* spp. being common.

Both areas appear to lack aggressive colonizing tree species. *Musanga cecropioides* is not found in the area, and while trees such as *Polyscias fulva* and *Trema orientalis* are in the region, these species do not seem to invade gaps quickly. In a study of tree-fall gaps in Kibale National Park, we have been unable to find any species whose seedlings are typically found in treefall gaps (Chapman *et al.* pers. obs.). This is in marked contrast to a number of studies in the Neotropics which have defined pioneers as species whose saplings are typically found

only in gaps (Hartshorn 1980, Brokaw 1985). Furthermore, a study at Kibale documented that of the species tested a third grew faster in the understory than in either small or large gaps (Chapman & Chapman 1996). In contrast, studies from Central America (Augsburger 1984, Brokaw 1985, Pompa & Bongers 1988) document that the growth of all species was enhanced in gaps.

Ngogo has not been commercially exploited for timber. At Kanyawara there are unlogged areas and areas that have been harvested to various intensities. An area of approximately 300 ha at Kanyawara (compartment K-30) has not been commercially harvested, however, prior to 1970, a few large stems (0.03–0.04 trees/ha) were removed by pit-sawyers in this area. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa 1988), and this area is considered as a second unlogged site. An area of approximately 390 ha of forest (compartment K-14) was lightly and selectively harvested between May and December 1969 (averaging 14 m³/ha or approximately 5.1 stems/ha). Twenty-three tree species were removed, with only 9 species contributing 94 percent of the total timber harvest (Kasenene 1987, Skorupa 1988). Harvest was not evenly distributed in this area (Struhsaker 1997). As a result of the heterogeneity, we divided this compartment into two areas: a moderately logged area and a lightly logged area, where stump and gap enumeration suggests only a few selected trees were removed (Kasenene 1987). The final area is a 360 ha section of forest (compartment K-15) that was heavily and selectively cut between September 1968 and April 1969. Total harvest averaged 21 m³/ha or approximately 7.4 stems/ha (Skorupa 1988). A total of 18 tree species were harvested, with 9 species contributing more than 95 percent of the harvest volume (Kasenene 1987, Skorupa 1988).

SAMPLING METHODS.—Permanent vegetation transects (200 m × 10 m) were established at each study site with the location of transects selected at random from within the existing trail system. This system of trails (approximately 200 km) was established in a grid system along compass bearings and was designed to provide access to the forest. The trails do however avoid some areas, such as the very swampy valley bottoms. We established 26 transects at Kanyawara in January 1990 (unlogged $N = 12$ transects, lightly logged $N = 5$, moderately logged $N = 4$, heavily logged $N = 5$), providing a total sampling area of 5.2 ha. Twenty-four transects

were established at Ngogo in May 1990, producing a total sampling area of 4.8 ha. Each tree ≥ 10 cm Diameter at Breast Height (DBH) within 5 m of each side of the trail was individually marked with a numbered aluminum tag and measured (DBH). Kanyawara and Ngogo transects provided a total of 2111 and 2622 individually labelled trees, respectively.

Slope, the amount of light reaching near to the ground, and the density of ground vegetation (trees, herbs, shrubs, and grasses) were recorded for all transects at 20-m intervals. Light was ranked by looking directly up into a 100 mm diameter tube covered with a grid consisting of 9 cells and counting the number of grid cells in which light could be seen. A measure of ground vegetation was determined 2 m off the trail every 20 m by counting all stems less than 2 m in height within a 1-meter radius circle. There was no difference between areas in any of these variables (ground vegetation— $F = 1.44$, $P = 0.258$; light— $F = 0.28$, $P = 0.839$; slope— $F = 2.11$, $P = 0.128$).

Phenological information on the tagged trees has been recorded monthly since January 1990 at Kanyawara and since May 1990 at Ngogo. Each month, we documented the stage of leaf development (leaf bud, young leaves, mature leaves; visually assessed through binoculars) and noted the presence or absence of flowers and ripe fruits for all trees. The abundance of fruit on a tree was ranked on a 0 (no fruit) to 4 (a heavy fruit set) scale. The tree's ability to produce fruit was indexed as DBH. To verify the validity of using DBH in this manner, we measured the DBH of a subset of fruiting trees (*Uvariopsis congensis*— $N = 7$, *Tabernaemontana holstii*— $N = 12$, *Myrianthus arboreus*— $N = 10$, *Rothmania urcelliformis*— $N = 12$). Subsequently, we collected and weighed all the fruits on these trees. For each species, DBH was positively correlated with fruit biomass (Chapman *et al.* 1992). As a means of contrasting the relative fruit production of the different areas, fruit abundance was indexed in two ways: (1) as the total number of fruiting trees/ha multiplied by their fruit abundance rank and (2) as the sum of the DBH of each individual fruiting tree/ha multiplied by the fruit abundance score for that tree.

During these monthly phenology samples, the death of any tagged tree was recorded, and it was noted if 1) the tree died standing, 2) if the tree died standing, then subsequently lost most of its branches and fell, or 3) if a healthy tree was knocked over by another falling tree. In August 1994, the DBH of the trees was remeasured (at the

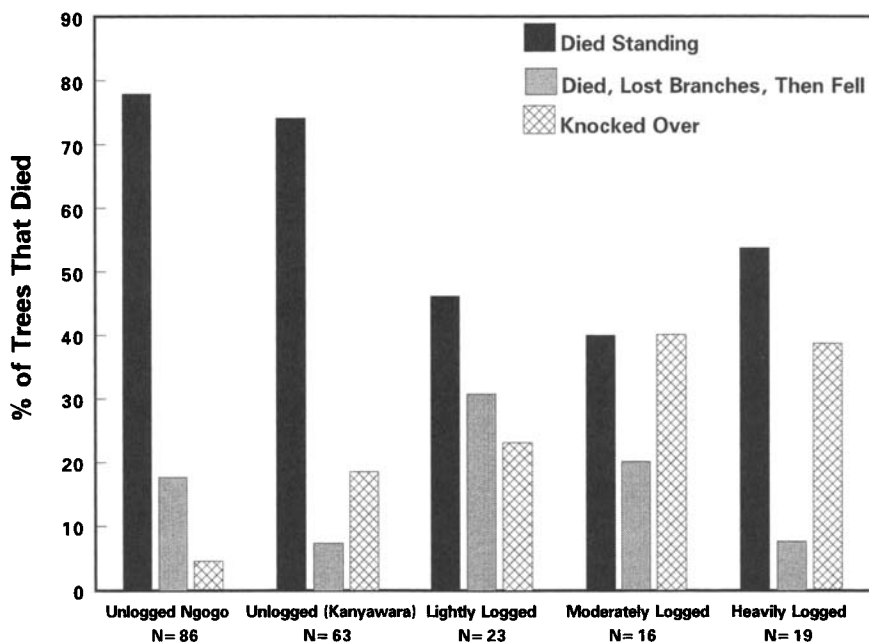


FIGURE 1. The proportion of tagged trees that died in different fashions in areas of Kibale National Park that were unlogged (Ngogo, Kanyawara) or had been logged at different intensities.

location of the tag) providing growth data over 56 months at Kanyawara and 51 months at Ngogo.

At Kanyawara, all trees less than 10 cm DBH, but greater than 1 m tall were measured (DBH and height) between May through July 1992 using the same transects, but with a strip width of 2 m. A total of 10,358 poles were enumerated, of which we were able to identify 92 percent to species.

In the heavily logged and the unlogged areas of Kanyawara, 600 m transects were sampled to determine the distance (visually estimated) between adjacent trees. While many trees in both areas were in close proximity, there were a number of instances where there was a considerable distance between adjacent trees because of previous logging activities or because of natural treefalls. These data on canopy opening are augmented with published data from the same areas where the 40 gaps (logged area—areas of extraction, unlogged forest—tree falls) were measured per forest (Kasenene 1987). The edge of these gaps was determined by the presence of light demanding species (e.g., *Trema orientalis*, *Mimulopsis solmsii*) and by taking light meter readings.

To determine the density of seedlings (from germinating seeds to plants 1 m tall) in heavily logged and unlogged areas we counted, in May 1992, the seedlings in twenty 1 m² randomly lo-

cated quadrats. All trees within a 10 m radius or that had canopies overhanging the sampling site were identified and measured (DBH) to determine if it was probable that the seedling resulted from a dispersal event or from fruitfall.

To estimate the abundance and species composition of buried seeds, 30 locations in the heavily logged forest and 30 locations in unlogged forest at Kanyawara were randomly selected, and 0.5 m² by 5 cm deep soil samples were collected. In the unlogged forest, sites within 20 m of a tree fall were rejected. Thirty collections (15 logged, 15 unlogged) were made during June 1990, and 30 collections were made in July 1991. The soil was sifted, and all seeds greater than 1 mm in diameter (approximately the size of fig seeds) were extracted. The species identity of seeds was determined by comparing unknown seeds to a seed catalog of 174 species made by collecting fruits directly from known plant species. Seeds that could not be identified were assigned a "type" number and placed in the catalog. When sufficient seeds of an unidentified type were available (seeds were also being collected at that time from animal dung), they were planted and grown for identification (Chapman 1989). We estimated the proportion of the seeds in the soil sample that could have simply fallen

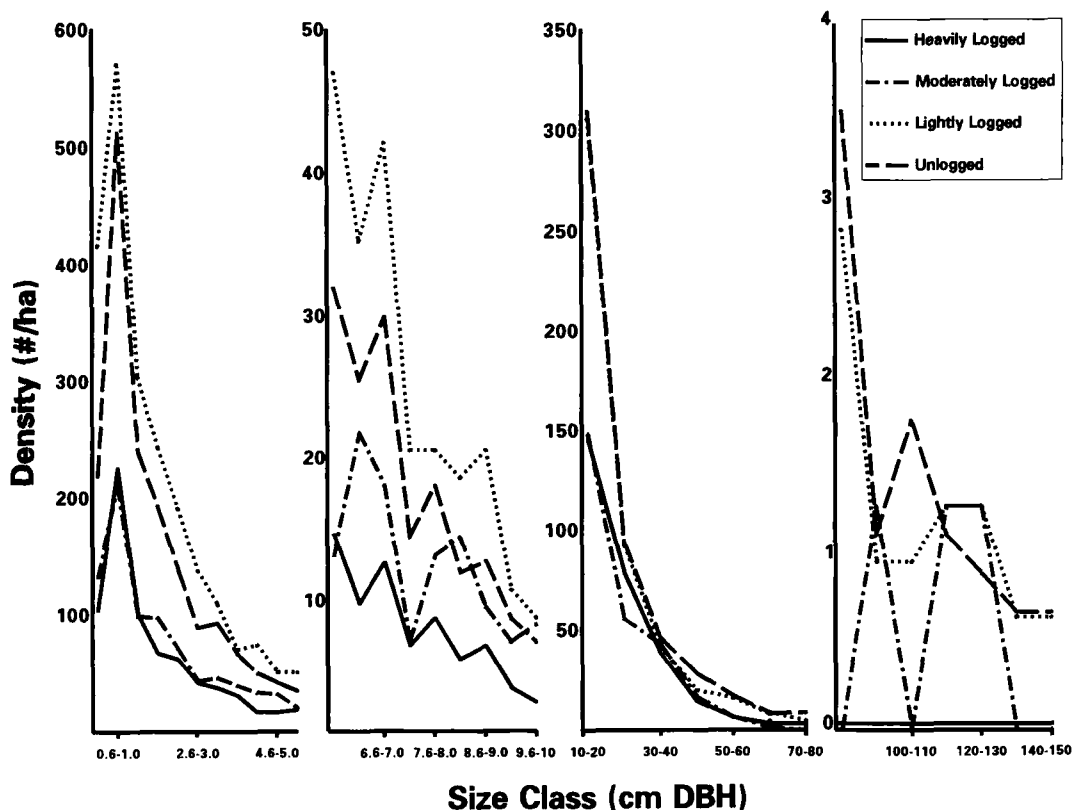


FIGURE 2. The density of different sizes of trees from 0.1 cm DBH to > 150 cm DBH in four areas that have been undisturbed or have been logged at different intensities. Note that the scales on the Y axes change for each panel (see the text for descriptions of the methods used to calculate density for each of the different size classes).

from overhanging trees and what proportion were potentially dispersed, by identifying and measuring (DBH) of trees within a 10 m radius of the site or trees that were further, but which had canopies overhanging the site. We quantified differences between the heavily logged and the unlogged forests at Kanyawara in the number of seedlings establishing in newly disturbed soil (seed bank + recent seed rain) and those that arrived subsequent to disturbance (seed rain). Two soil-filled trays were placed at randomly selected grid locations in each forest. One tray contained surface soil dug from that location and placed in the tray. This sample represented both the seeds present in the soil at the time the station was established (seed bank) and those seeds that arrived subsequently (seed rain). The soil in the other tray was taken back to camp and boiled, killing all seeds, and thus represented only the seed rain. To verify that boiling killed all of the seeds, we placed boiled soil in the

greenhouse; no seedlings emerged in 24 months. Seedling emergence in both trays was recorded two months later. Because we are examining relative differences between areas, the effect of boiling on soil chemistry should not create a systematic bias. Therefore, no attempt was made to examine any physical changes in the soil resulting from boiling.

To document the fate of seeds in the different areas, seeds ($N = 42$) from 6 species were placed along a transect which was divided into twelve 0.5 m² areas. In each of the 12 areas, 10 *Uvariopsis congensis*, 10 *Chrysophyllum* sp., 10 *Tabernaemontana holstii*, 4 *Mimusops bagshawei*, 4 *Pseudospondias microcarpa*, and 4 *Monodora myristica* were spread throughout the 0.5 m² area. Every second month, two 0.5 m² areas were randomly selected from the transect and excavated to determine which seeds still remained in the soil or if any had germinated. Tree nomenclature follows Hamilton (1991).

TABLE 1. The density and basal area (3 size classes and total basal area (cm²/ha)) of trees in areas of Kibale National Park, Uganda that have been logged to different intensities or have not been logged. * Indicated that Kingston (1967) classified these species as timber quality trees.

Species	Unlogged (Ngogo)				Unlogged (Kanyawara)				Lightly logged		
	Density	Basal area			Density	Basal area			Density	Basal area	
		10-30	30-50	>50		10-30	30-50	>50			10-30
* <i>Albizia gummifera</i>	—	—	—	—	1.25	550	1588	0	2138	10.00	3481
* <i>Aningeria altissima</i>	—	—	—	—	1.47	119	0	93,603	93,722	2.00	515
<i>Aniaria toxicaria</i>	—	—	—	—	0.42	143	0	0	143	2.00	190
<i>Aphania senegalensis</i>	3.13	918	2992	0	1.67	814	0	0	814	1.00	795
<i>Balanites wilsoniana</i>	1.67	323	0	4071	1.67	505	0	10,725	11,230	—	—
<i>Bersame abyssinica</i>	—	—	—	—	—	—	—	—	—	—	—
<i>Blighia unijugata</i>	0.42	0	350	1357	0.83	246	0	0	246	—	—
<i>Bosqueia phoberos</i>	5.63	2122	6290	5873	49.58	15,703	1390	0	17,093	29.00	11,162
<i>Casipourea ruwensorenensis</i>	5.00	1584	0	1584	6.67	1939	0	6677	8616	4.00	51
<i>Celtis africana</i>	1.25	193	4539	18,117	4.17	1092	0	16,270	17,362	13.00	2763
<i>Celtis durandii</i>	57.71	26,526	26,356	63,198	47.08	18,680	28,018	81,551	128,249	46.00	19,597
<i>Chaetacme aristata</i>	4.79	2143	2858	822	17.08	6574	3269	0	9843	10.00	4552
<i>Chrysophyllum</i> sp.	64.17	23,264	25,352	51,459	2.50	324	1273	17,821	19,418	1.00	238
<i>Clausena anisata</i>	0.42	161	0	161	—	—	—	—	—	1.00	327
<i>Coffea canephora</i>	0.42	161	0	161	0.42	212	0	0	212	1.00	608
* <i>Cordia abyssinica</i>	0.42	47	572	6599	0.42	267	0	0	267	6.00	4605
* <i>Cordia millenii</i>	—	—	—	—	0.42	187	0	0	187	—	—
* <i>Croton</i> sp.	0.21	51	0	51	0.42	196	0	0	196	—	—
<i>Dasylopsis</i> sp.	8.50	2183	0	2183	2.50	3134	0	0	3134	1.00	190
<i>Diospyros abyssinica</i>	68.96	25,082	34,101	22,108	40.00	15,239	15,088	22,703	53,030	60.00	24,521
<i>Dombeya mukou</i>	3.33	1293	2359	0	9.58	4679	5497	1987	12,163	6.00	2652
<i>Erythrina abyssinica</i>	—	—	—	—	—	—	—	—	—	1.00	1214
<i>Euaenia eminens</i>	0.63	427	0	427	1.25	575	0	0	575	3.00	1715
* <i>Fagara angolensis</i>	0.21	80	0	80	0.83	517	0	0	517	—	—
* <i>Fagaropsis angolensis</i>	2.50	420	378	1870	2.08	474	743	10,891	12,109	1.00	164
<i>Ficus exasperata</i>	0.42	—	—	—	3.75	1126	0	28,871	29,996	5.00	2056
<i>Ficus mucosa</i>	0.63	—	—	—	—	—	—	—	—	—	—
<i>Ficus natalensis</i>	0.36	—	—	—	0.42	—	—	—	—	—	—
<i>Ficus ovata</i>	0.21	—	—	—	—	—	—	—	—	1.00	—
<i>Ficus sansibarica</i>	2.50	—	—	—	1.46	—	—	—	—	5.00	—
<i>Ficus saussureana</i>	0.42	—	—	—	0.42	—	—	—	—	—	—
<i>Ficus trichopoda</i>	0.42	—	—	—	—	—	—	—	—	—	—
<i>Funtumia latifolia</i>	36.25	11,475	24,021	15,678	33.33	12,844	11,217	24,094	48,155	—	—
<i>Kigelia moosa</i>	0.83	246	0	246	3.75	1605	0	0	1605	1.00	173
<i>Leptonychia mildbraedii</i>	2.29	698	0	698	35.42	11,028	662	0	11,690	9.00	3875

TABLE 1. Continued.

Species	Unlogged (Ngogo)				Unlogged (Kanyawara)				Lightly logged			
	Basal area				Basal area				Basal area			
	Density	10-30	30-50	>50	Total	Density	10-30	30-50	>50	Total	Density	10-30
<i>Linociera johnsonii</i>	7.29	3399	1233	0	4632	5.42	2224	2296	1944	6465	1.00	604
* <i>Lovoa swynnertonii</i>	2.50	110	1811	26,967	28,888	0.83	0	0	11,208	11,208	—	—
<i>Macaranga</i> sp.	0.42	115	0	0	115	—	—	—	—	—	—	—
<i>Maesa lanofolata</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Markbarmia placycalyx</i>	24.79	11,147	8868	3219	23,234	50.42	20,337	22,683	13,458	56,477	46.00	15,588
<i>Milletia dura</i>	7.71	2837	0	0	2837	3.75	515	2079	0	2594	8.00	3035
<i>Mimusops bagshawei</i>	3.13	0	800	31,787	32,586	3.33	0	2255	31,580	33,835	—	—
<i>Mitragyna rubrostipulata</i>	0.42	47	0	2398	2445	—	—	—	—	—	—	—
<i>Monodora myrsinitica</i>	0.42	0	0	2226	2226	0.42	0	0	1873	1873	—	—
<i>Myrianthus arboreus</i>	—	—	—	—	—	2.08	724	843	0	1567	4.00	1740
<i>Neoboutania macrocalyx</i>	7.92	4177	2728	0	6905	1.25	105	1485	0	1591	6.00	3959
* <i>Newtonia buchananii</i>	2.08	0	0	56,438	56,438	—	—	—	—	—	1.00	460
* <i>Olea welwitschii</i>	3.33	1575	0	27,024	28,599	3.33	546	802	15,224	16,572	3.00	1750
<i>Oncoba rouledegi</i>	0.42	279	0	0	279	—	—	—	—	—	1.00	257
<i>Pancovia turbinata</i>	2.29	277	1292	4629	6198	10.42	3564	2266	0	5830	1.00	308
<i>Parinari excelsa</i>	0.21	0	0	1250	1250	2.06	0	2287	58,240	60,527	—	—
<i>Pleiocarpa pycnantha</i>	1.04	227	0	0	227	0.29	121	0	0	121	—	—
<i>Polycalis fulva</i>	0.21	73	0	0	73	0.83	447	0	0	447	1.00	1145
<i>Premna angolensis</i>	4.38	1684	2655	4485	8824	5.00	344	4112	6616	11,072	—	—
<i>Pseudospondias microcarpa</i>	1.25	173	792	30,905	31,870	2.08	483	0	44,441	44,924	—	—
<i>Pterygota milbraedii</i>	10.83	822	3137	229,047	233,006	—	—	—	—	—	—	—
<i>Pygum africanum</i>	0.21	154	0	154	154	—	—	—	—	—	—	—
<i>Rauvolfia vomitaria</i>	2.08	703	1053	0	1756	1.25	166	0	0	166	3.00	817
<i>Rochmannia urcelliformis</i>	5.00	1275	0	0	1275	—	—	—	—	—	—	—
<i>Sapium</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—
<i>Spathodea campanulata</i>	2.71	683	1479	4449	6612	0.83	0	960	5796	6756	—	—
* <i>Strombosia scheffleri</i>	3.13	283	3887	9467	13,636	12.08	918	8880	38,212	48,010	1.00	1104
<i>Strychnos mitis</i>	0.21	44	0	0	44	7.50	2006	6071	4253	12,331	2.00	925
<i>Symphonia globulifera</i>	—	—	—	—	—	0.42	0	1122	4337	5459	—	—
<i>Tabernaemontana holstii</i>	34.58	12,109	1705	0	13,814	4.58	1575	0	0	1575	6.00	1821
<i>Tarenna pavettoides</i>	4.38	1367	0	0	1367	4.58	505	0	0	505	—	—
<i>Teclea nobilis</i>	3.75	2722	1101	0	3823	17.50	7613	0	0	7613	29.00	10,019
<i>Trema guineensis</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Trichilia splendida</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Uvariopsis congensis</i>	100.83	42,678	1583	0	44,261	60.42	24,486	653	0	25,139	29.00	12,051
<i>Vangueria apiculata</i>	—	—	—	—	—	—	—	—	—	—	1.00	227
<i>Warburgia stuhlmannii</i>	0.83	201	0	0	201	—	—	—	—	—	—	—

TABLE 1. Extended.

Species	Lightly logged			Moderately logged			Heavily logged			Total		
	Basal area			Basal area			Basal area					
	30-50	>50	Total	Density	10-30	30-50	>50	Total	Density		10-30	30-50
* <i>Albizia gummifera</i>	0	0	3481	3.75	1787	2530	0	4317	—	—	—	—
* <i>Avingeria altissima</i>	0	0	515	2.50	0	0	29,228	29,228	2.00	801	0	0
<i>Antiaris toxicaria</i>	0	0	190	—	—	—	—	—	—	—	—	—
<i>Aphania senegalensis</i>	0	0	795	2.50	1547	0	0	1547	1.00	629	0	0
<i>Balanites wilsoniana</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bersame abyssinica</i>	—	—	—	—	—	—	—	—	2.00	1008	0	0
<i>Blighia unijugata</i>	—	—	—	—	—	—	—	—	2.00	231	0	0
<i>Bosqueia phoberos</i>	0	0	11,162	25.00	11,259	0	5290	16,548	10.00	2427	0	0
<i>Cassipourea ruwensorensis</i>	0	15,710	15,761	3.75	736	0	0	736	7.00	2945	0	12,636
<i>Celtis africana</i>	0	136,546	139,309	17.50	5408	6493	0	11,901	33.00	11,441	28,550	6435
<i>Celtis durandii</i>	26,172	37,423	83,193	16.25	3524	19,637	7307	30,468	1.00	1404	0	0
<i>Chaetacme aristata</i>	0	0	4552	3.75	1753	2010	0	3763	—	—	—	—
<i>Chrysophyllum</i> sp.	0	0	238	1.25	347	0	0	347	—	—	—	—
<i>Clauseria anisata</i>	0	0	327	—	—	—	—	—	—	—	—	—
<i>Coffea canephora</i>	0	0	608	—	—	—	—	—	6.00	1147	5472	0
* <i>Cordia abyssinica</i>	0	0	4605	—	—	—	—	—	4.00	11,538	0	0
* <i>Cordia millenii</i>	—	—	—	—	—	—	—	—	1.00	648	0	0
* <i>Croton</i> sp.	—	—	—	1.25	430	0	0	430	52.00	25,143	27,353	23,321
<i>Dasylops</i> sp.	0	0	190	—	—	—	—	—	—	—	—	—
<i>Diospyros abyssinica</i>	44,115	12,299	80,935	40.00	16,811	27,034	6976	50,820	—	—	—	—
<i>Dombeya mukou</i>	4432	4297	11,381	6.25	3578	2011	0	5589	—	—	—	—
<i>Erythrina abyssinica</i>	0	0	1214	2.50	899	0	0	899	11.00	4185	2221	0
<i>Euadenia eminenis</i>	0	0	1715	1.25	0	2630	0	2630	1.00	312	0	0
* <i>Fagara angolensis</i>	0	0	164	8.75	2306	0	0	2306	2.00	665	0	0
<i>Ficus exasperata</i>	0	21,505	23,561	2.50	908	0	4988	5896	—	—	—	—
<i>Ficus mucoso</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ficus natalensis</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ficus ovata</i>	—	—	—	1.25	—	—	—	—	—	—	—	—
<i>Ficus sansibarica</i>	—	—	—	—	—	—	—	—	2.00	—	—	—
<i>Ficus saussureana</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ficus trichopoda</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Funtumia latifolia</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Kigelia moosa</i>	0	0	173	17.50	10,037	0	0	10,037	27.00	12,281	1608	0
<i>Leptonychia mildbraedii</i>	0	0	3875	1.25	588	0	0	568	5.00	1308	4547	0
	0	0	3875	1.25	341	0	0	341	—	—	—	—

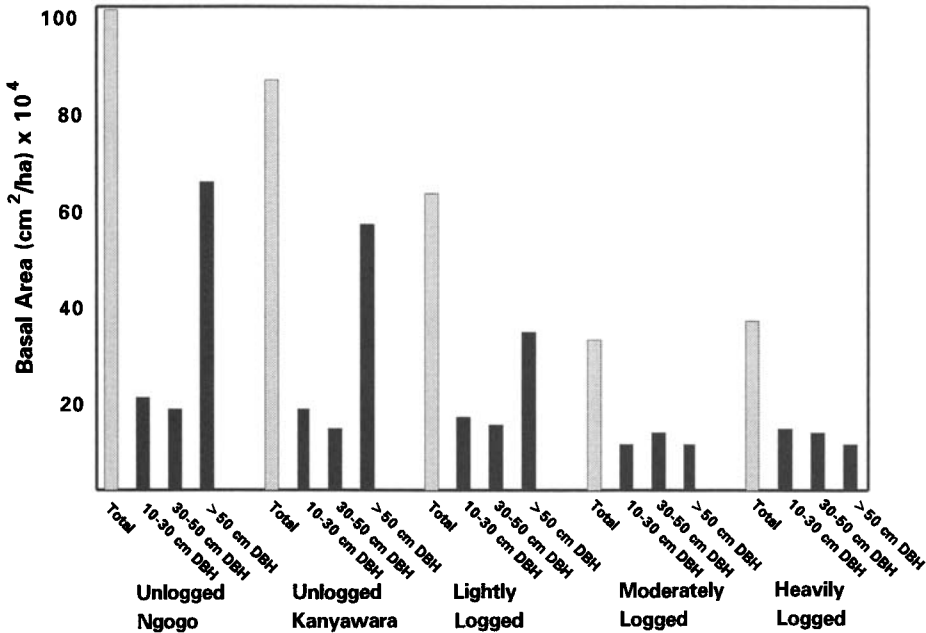


FIGURE 3. The basal area (cm²/ha) of trees (>10 cm DBH) from transects in forests in Kibale National Park, Uganda which have experienced different logging regimes or have not been logged.

RESULTS

TREE MORTALITY.—The unlogged area at Ngogo had fewer trees die over the time frame of the study than any of the other sites (1.10% of trees >10 cm DBH per year, $N = 86$, mean DBH = 24.0 cm). At Kanyawara the unlogged area had 1.24 percent of monitored trees die each year ($N = 63$, mean DBH = 27.3 cm), and the lightly logged forest had a similar death rate (1.27%, $N = 23$, mean DBH = 24.0 cm). In contrast, the moderately logged area (1.62 percent of trees >10 cm DBH per year, $N = 16$, mean DBH = 22.1 cm) and the heavily logged areas (1.48%, $N = 19$, mean DBH = 29.1 cm) exhibited higher mortality.

Compared with the logged areas, the two unlogged areas had more trees die standing ($X^2 = 13.88$, $P < 0.01$), and fewer apparently healthy trees die as a result of being knocked down by adjacent tree falls ($X^2 = 17.18$, $P < 0.005$; Fig. 1). In all areas a similar proportion of trees died standing, then over the years, lost their branches, and finally fell ($X^2 = 4.52$, $P > 0.1$; Fig. 1). When these trees did fall, they typically did little damage to neighboring trees, since little of their canopy branches remained, and few, if any, vines remained attached to the dead tree.

SIZE CLASSES AND GROWTH RATES.—If one examines

tree size class frequency distributions (stand curves) for each of the areas with different logging histories at Kanyawara, a number of trends are apparent (Fig. 2). In the smallest size classes (0.1–5 cm and 5–10 cm DBH), the lightly logged area had a greater density of trees than the unlogged area. Between 10 and 80 cm DBH, the two forests showed similar densities. In the largest size classes, however, the lightly logged area had fewer trees than the unlogged area. The difference in the larger size class may represent the trees that were removed during the logging operation. In contrast, the density of all size classes of trees was consistently lower in the moderately logged and heavily logged areas relative to the unlogged area. There were no large trees (> 80 cm DBH) found on the transects in the heavily logged area.

Similar trends are revealed by examining the basal area (cm²/ha) of the different forests (Table 1, Fig. 3). Overall, the two unlogged sites had larger basal area values than the unlogged sites. The average basal area of the unlogged forests was 32 percent greater than the lightly logged forest, 65 percent greater than the moderately logged forest, and 62 percent greater than the heavily logged forest (Fig. 3). The lightly logged forest had values similar or greater than the unlogged forest in the smaller size classes.

Trees in the most heavily logged area had the slowest growth rate of any of the areas (trees > 10

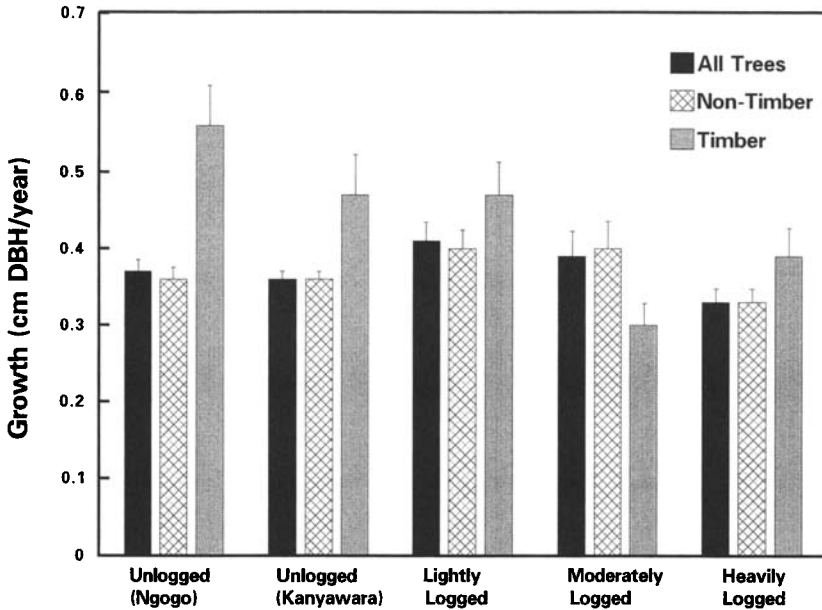


FIGURE 4. The annual growth rate in cm DBH for all trees, non-timber trees, and timber trees in areas of Kibale National Park that were unlogged (Ngogo, Kanyawara) or had been logged at different intensities.

cm DBH). Trees in moderately and lightly logged areas had a slightly faster growth rate than either of the unlogged areas (Fig. 4). If one only considers those species of trees listed as timber trees (Kings-ton 1967, Table 1), timber trees had a faster than average growth rate in all of the areas, with the exception of the moderately logged area. The difference in growth rates between timber and non-timber trees was most pronounced in the two unlogged areas (Fig. 4).

Growth rates of different size classes varied between areas. The most heavily logged area had consistently slower mean growth rates than the other areas (Fig. 5). In contrast, trees in the lightly logged area had similar growth rates as other areas in the smaller size classes, but showed elevated growth rates for trees 30 to 50 cm DBH. Trees in the moderately logged area exhibited an intermediate pattern, but had slower growth rates than in the unlogged areas in all but the smallest size classes.

GAPS.—The average distance between the branches of adjacent trees along the transect established to assess the size of gaps in the unlogged area was estimated to be 1.2 m. 42 percent of the trees were in direct contact, 74 percent of the canopy gaps between adjacent trees were 1 m wide or less, while gaps of 1–2 m represented 16 percent of the distance between trees. Large gaps in excess of 5 m

represented only 2 percent of the unlogged forest. Along the transect in the heavily logged area, the average distance between neighboring trees was 2.1 m, and only 25 percent of the logged forest had trees with connected canopies. 59 percent of adjacent trees were separated by distances of 1 m or less. Large canopy gaps (> 5 m) represented 12 percent of the sample in the logged transect.

These data correspond with the trend documented by Kasenene (1987), in which the areas of 40 randomly selected treefall or logging gaps were measured. The average gap size decreased from heavily logged (mean = 1307 m², range = 73–7100 m²), to lightly logged (mean = 467 m², range = 75–1800 m²), to the unlogged forest (mean = 256 m², range = 100–663 m²).

SEEDLING DENSITY AND RICHNESS.—There was no difference between seedling density in the heavily logged and unlogged forests of Kanyawara ($t = 0.847$, $P = 0.403$, $N = 60$, unlogged = 20.9 seedlings/m², heavily logged = 16.3 seedlings/m²), nor in the number of species of seedlings found in the quadrats ($t = 0.827$, $P = 0.169$, $N = 60$, unlogged = 5.1 seedling species/m², heavily logged = 4.8 seedling species/m²). Similarly, the number of seedlings that could have come from trees directly above the sampling site did not vary between logged and unlogged areas ($t = 0.454$, $P = 0.653$,

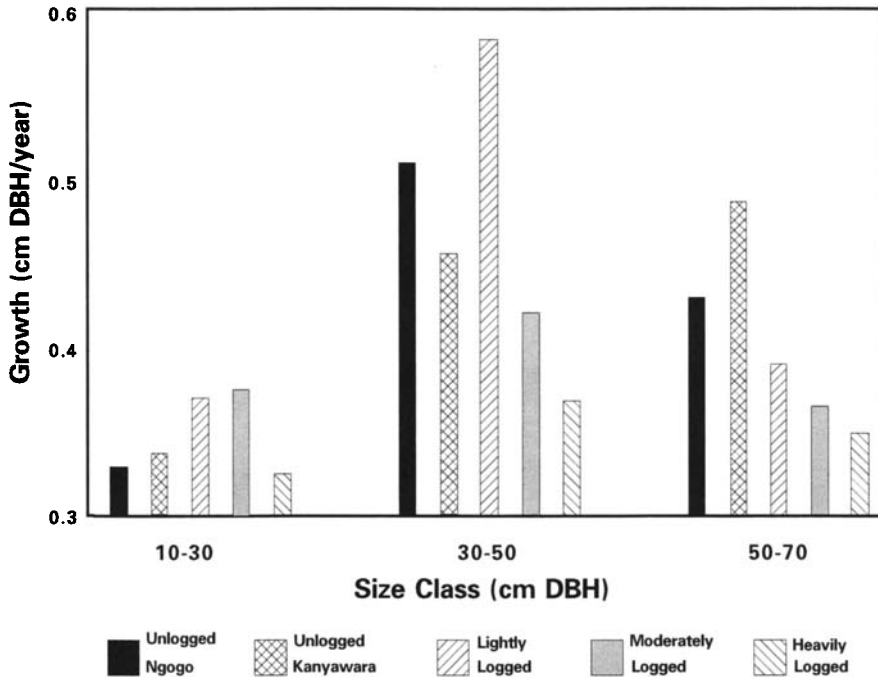


FIGURE 5. The mean annual growth rate in cm DBH for three size classes of trees in areas that were unlogged (Ngogo, Kanyawara) or had been logged at different intensities.

$N = 60$, unlogged = 8.2, heavily logged = 6.0). Interestingly, there was a tendency for seedlings from “desirable” timber trees (as classified by Kingston 1967, Table 1) to be more common in the heavily logged area (mean = 2.75), than in the unlogged area (mean = 1.1, $t = 1.82$, $P = 0.076$).

seeds were found in soil samples from the unlogged and logged areas. Six species of seeds were only found in the unlogged forest, 4 species were only found in the heavily logged area, and 3 species were found in both areas (Table 2). On average, the number of species found at a sampling site was higher in the unlogged (mean = 2.2, $N = 30$ sampling sites), than in the heavily logged area (mean

SEED BANK AND SEED RAIN.—Fifteen species of tree

TABLE 2. The species of tree seeds found in soil samples from logged and unlogged areas in the Kibale National Park, Uganda. A “*” indicates that Kingston (1967) classified these species as timber quality trees.

Species	# of seeds		# of sites with that species		Density of adults	
	Unlogged	Logged	Unlogged	Logged	Unlogged	Logged
<i>Uvariopsis congensis</i>	207	0	9	0	60.4	4.0
<i>Celtis durandii</i>	370	555	15	5	47.1	33.0
<i>Diospyros abyssinica</i>	1	28	1	8	40.0	52.0
* <i>Parinari excelsa</i>	8	1	3	1	2.1	—
<i>Mimusops bagshawii</i>	0	172	2	0	3.3	—
<i>Randia</i> sp.	1	0	1	0	—	—
<i>Drypetes</i> sp.	0	2	0	2	—	—
* <i>Olea welwitschii</i>	0	179	0	5	3.3	2.0
<i>Pseudospondias microcarpa</i>	6	0	2	0	2.1	—
* <i>Aningeria altissima</i>	0	2	0	2	1.5	2.0
<i>Dasylepis eggelingi</i>	0	1	0	1	2.5	1.0
<i>Teclea nobilis</i>	1	0	1	0	17.5	1.0
<i>Strychnos mitis</i>	5	0	1	0	7.5	—

= 1.4, $N = 30$, Mann-Whitney $P = 0.021$). In contrast, there was a tendency for the number of seeds found in the seedbank in the heavily logged area (mean = 36.9) to be higher than in the unlogged forest (mean = 22.6, Mann-Whitney $P = 0.066$). However, for both areas, these averages were highly skewed by a few sites with a large number of seeds from one species. None of the species of trees found in the samples are classified by Hamilton (1991) as being pioneer species, or as being frequently found in disturbed areas.

96.3 percent of the seeds came from locations with the same species above or within 10 m of the site. The proportions were similar in the logged (96.8 %) and unlogged forests (95.5%; $X^2 = 1.70$, $P > 0.1$). However, only 58.7 percent of the species found in the sampling sites had parent trees above the site or within 10 m. Forest types were again similar in this respect (logged 57.1%, unlogged 60.0%, $X^2 = 0.05$, $P > 0.1$).

As previous research in Kibale would suggest (Lwanga 1994, Chapman and Chapman 1996), seeds placed along the transects in both logged and unlogged areas experienced high levels of predation. Within 2 months, 76 percent of the seeds placed in the unlogged forest and 70 percent of the seeds in the logged forest had disappeared. Disappearance rate varied considerably among species after the first 2 months. Eight months after establishing the plots, 93 percent and 88 percent of the seeds placed in the unlogged and logged forests had disappeared, respectively. No seeds were found in either area when samples were collected after 10 and 12 months. When sifting through the soil from these stations, seed fragments were often found, suggesting that rodents were responsible for some seed mortality and potentially for the disappearance of many other missing seeds.

In both forest types, the disturbed soil representing both the seed bank and seed rain had more seedlings (unlogged forest mean = 0.93, logged forest mean = 11.7) than the boiled soil representing only seed rain (unlogged forest mean = 0, logged forest mean = 1.2; Mann-Whitney $U = 2.63$, $P = 0.009$), suggesting that seeds lying dormant in the soil contribute to tree replacement. For both treatments, plots in the logged forest had a greater number of seedlings emerging than the unlogged forest (seed bank + seed rain—Mann-Whitney $U = 3.06$, $P = 0.002$, seed rain—Mann-Whitney $U = 4.29$, $P < 0.001$).

PHENOLOGY.—Both indices of fruit production indicated that more fruit was produced in unlogged

than in logged areas (Table 3). Among logged areas, fruit production was higher in K-15 than K-14 at Mikana (Table 3). However, in terms of maintaining frugivore abundance, particularly species with small home ranges, the number of months with very low fruit production may be particularly important. In the unlogged areas, low fruit abundance scores (fruiting trees/ha*score) occurred in very few months (scores < 50: Ngogo = 5 out of 51 months, Kanyawara = 7 out of 56 months). Low fruit scores occurred much more frequently in logged areas (scores < 50: light logged = 17 out of 51 months, moderate logged = 34 months, heavily logged 14 months).

DISCUSSION

One would envision that 25 years should be sufficient to detect processes facilitating compensatory recruitment in logged areas. Although many processes of forest dynamics differed between the unlogged areas of Kibale and the logged forests, we found several lines of evidence to suggest that compensatory processes are not operating in the heavily logged area. Mortality was highest in the heavily logged areas with many deaths resulting from healthy trees being knocked over by neighboring tree falls (Kasenene 1987). Tree growth rates in the most heavily logged areas were consistently slower for all size classes. The stand curves suggest that the density of all size classes of trees was consistently lower in the heavily logged areas than in the unlogged areas. Consequently, many of the gaps created by harvesting in these heavily logged areas still exist and have not been filled in by new tree growth. In contrast, the most lightly logged area had similar growth rates to the unlogged areas in the small size classes, but trees in the 30 to 50 cm DBH size cohort exhibited elevated growth rates relative to the unlogged area. The stand curves indicate that in the smallest size classes the most lightly logged area had a slightly greater density of trees than the unlogged areas, but otherwise the stand curves are similar up to the largest size classes.

These observations raise the question of what creates differences between lightly and heavily logged areas and why there is little evidence of compensatory recovery in the heavily logged area. We suggest these patterns relate in part to response by the plant community in Kibale to the gap conditions created by logging. In the lightly logged area, gaps were small, and conditions altered by the opening of the canopy would not be changed across as large an area as in the heavily logged area

TABLE 3. Annual fruit production for each of the five areas examined that are either unlogged or were logged at differing intensities in the late 1960's in Kibale National Park, Uganda. The method of indexing fruit production is explained in detail in the methods, and briefly as a footnote.

Forests Year	Fruit production ¹		# of months ¹ /year < 50	Fruit production ²	
	Mean	SD		Mean	SD
Unlogged (Kanyawara)					
1990	90.9	63.0	3	2878	1243
1991	104.0	47.8	2	2917	991
1992	108.5	39.9	0	4337	1302
1993	131.7	68.6	0	3867	1489
1994	117.1	51.7	2	3946	2121
Average between years	110.4	54.4	1.4	3589	1429
Unlogged (Ngogo)					
1990	42.6	39.9	3	1519	1308
1991	125.4	87.2	0	3840	2348
1992	153.3	47.9	0	5013	1247
1993	84.1	33.2	2	2371	754
1994	91.3	28.5	0	2463	2037
Average between years	99.3	47.3	1	3041	1539
Lightly logged					
1990	62.6	31.6	5	1816	1026
1991	65.3	50.0	6	2084	1733
1992	110.0	20.7	0	3951	713
1993	87.5	41.1	3	2431	1068
1994	123.0	48.9	3	3355	2079
Average between years	89.7	37.9	3.4	2728	1324
Moderately logged					
1990	28.3	14.4	11	566	331
1991	32.6	15.5	10	646	353
1992	80.2	19.1	1	1661	491
1993	32.4	18.2	9	703	387
1994	61.7	24.0	3	1068	605
Average between years	47.0	18.2	6.8	928	433
Heavily logged					
1990	65.4	35.1	4	1980	1137
1991	69.1	28.5	5	2246	1048
1992	136.0	26.1	0	4208	1135
1993	81.5	24.9	2	2490	813
1994	114.7	52.4	3	2885	1662
Average between years	93.5	33.4	2.8	2762	1159

¹ The total number of fruiting trees/ha multiplied by their fruit abundance rank.

² The sum of the DBH of each individual fruiting tree multiplied by the fruit abundance score for that tree expressed on a per hectare basis.

which had much larger gaps. Although it is generally thought that canopy species survive and grow better in gaps than in the understory (Brokaw 1985, Putz 1993), this is not always the case. Evidence from Kibale suggests that there are few species of trees capable of taking advantage of high light levels and colonizing gaps. A study which monitored the fate of dispersed seeds and seedlings at Kibale documented that a third of the species tested grew faster in the understory than in either small or large gaps (Chapman & Chapman 1996).

Furthermore, Kibale appears to lack aggressive colonizing tree species. *Musanga cecropioides* is not found in the area, and while trees such as *Polyscias fulva* and *Trema orientalis* are in the region, these species do not seem capable of quickly invading gaps. In a study of treefall gaps in Kibale National Park, we have been unable to find any species whose seedlings are typically found in treefall gaps, and a survey of treefall gaps in unlogged forest did not locate any seedlings of *Polyscias fulva* and *Trema orientalis* (Chapman *et al.* pers. obs.).

The lack of aggressive colonizing tree species at Kibale and the potential that many trees may require shade to grow and survive may contribute to the fact that many of the large canopy openings in the heavily logged area are presently dominated by aggressive herbs and shrubs (primarily *Acanthus pubescens*). Kasenene (1987) documented that logged areas in Kibale had more ground vegetation cover 10 to 15 years post-harvest than unlogged areas. He also found a negative correlation between seedling and sapling richness and the density of ground vegetation. Once a dense herb or shrub layer is established, it may inhibit seedling and sapling survival. We found no difference in the density or species richness of seedlings in the logged and unlogged forests. Further, the number of seedlings that emerged from the disturbed soil (seedbank + seedrain) and initially seed-free soil (seed rain) was greater in the logged forest than in the unlogged forest. However, sapling density was much lower in the heavily logged areas. Therefore, it appears that there is much lower recruitment into the sapling class in logged than unlogged area. A number of studies have similarly shown that when mature tropical forest is cut, colonizing woody and herbaceous species quickly invade (e.g., Fitzgerald & Selden 1975, Brokaw 1985, Vanclay 1993).

There is evidence that elephants may also inhibit tree regeneration of heavily logged areas of Kibale. Elephants use heavily logged areas more than lightly logged and unlogged areas, use gaps more than closed-canopy areas, and appear to be attracted to areas with dense stands of herbaceous growth which are common in logged areas (Struhsaker *et al.* 1996). This results in higher elephant damage to young trees in heavily logged than unlogged forests (Struhsaker *et al.* 1996). Evidence from stand curves in Budongo (Laws *et al.* 1975) and Kibale (Osmaston 1959) and examination of previous damage to felled trees (Laws *et al.* 1975) suggest that regeneration of the stand is not continuous and implicates concentrated elephant activity as the cause of slowed regeneration in comparison with forests where elephants are absent (Laws 1970). The fact that the stand curves we present do not show an increased density of individuals at this pole size, suggests that this damage may eventually lead to increased mortality rates of the pole size class.

Effective forest management depends on understanding the processes influencing regeneration under

different conditions. In Kibale, the level of exploitation and the size of the gaps formed in the lightly logged area were apparently appropriate to encourage tree regeneration in a "reasonable" period of time. In contrast, the sizes of gaps created by the logging intensity conducted in the heavily logged area appear to have resulted in very slow or arrested succession. This may relate to the paucity of pioneer tree species that can take advantage of large gaps, an aggressive herbaceous community that does well in large gaps, and elephant activity which is concentrated in large gaps that the logging created.

The problems faced by forest managers are likely to be site dependent, creating a situation where identifying research priorities is difficult (Putz 1993). From case studies such as this one, however, key processes can be identified and their generality can subsequently be tested at other locations. Three parameters appear to be particularly important in influencing post-logging tree regeneration in Kibale: 1) The intensity of harvest. Harvesting intensity largely determines the degree to which the canopy is opened. In Kibale, trees in areas in which the canopy was opened to a greater extent had slower growth rates and higher mortality rates relative to unlogged or less intensively logged areas. This finding suggests that the increased light in logged areas does not necessarily correspond to increased growth and survival of trees. 2) The tendency for an aggressive herb/shrub layer to become established and persist. This may be related to the nature of the specific plants and animals that are interacting. Kibale has only a few species of quickly invading secondary growth trees, an overall low diversity of tree species, and shrub species that seem very aggressive and persistent. 3) The role of elephants as agents of disturbance. Elephant activity may be important in Kibale because elephants preferentially forage in logged areas to gain access to the abundant shrub layer.

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Call for Nominations for 1998 Honorary Fellow of the Association for Tropical Biology

In 1963, the Association for Tropical Biology established the election of Honorary Fellows as “persons of long distinguished service to tropical biology.” This is the highest award given by the Association. Recently elected Fellows include Dr. Donald Stone, Dr. Betty Meggers, and Dr. José Sarukhán.

Any member of ATB wishing to nominate a candidate for the 1998 award should submit a 1–2 page letter justifying the nomination, along with the nominee’s curriculum vitae, to the Chair of the Nominating Committee, ATB Past-President Deborah Clark (e-mail: daclark@sloth.ots.ac.cr; mail: INTERLINK-341, P.O. Box 02-5635, Miami, Florida 33152) by 15 February 1998. All nominations will be distributed to the Nominating Committee, which will forward the final selection to the ATB Council for approval. The 1998 Honorary Fellow will be announced at the Annual Meeting of ATB in Baltimore.

HONORARY FELLOWS OF THE ASSOCIATION FOR TROPICAL BIOLOGY:

Aguayo, Carlos G.	Hubbell, Theodore H.	Robyns, Walter
Ali, Salim	Humbert, Henri	Romer, Alfred S.
Bailey, Irving W.	Hutchinson, John	Sarukhán, José
Baker, Herbert G.	Keck, David D.	Schmitt, Waldo L.
Bequeart, Joseph	Krauss, Beatrice H.	Simpson, George Gaylord
Borgmeier, Thomas	Lam, Herman J.	Sioli, Herald
Bourliere, F.	Lanjouw, J.	Smith, A. C.
Brade, Alexandre Curt	Lankester, Charles H.	Smith, Lyman B.
Brass, Leonard J.	Manter, H. W.	Snyder, Thomas E.
Birkill, Henry Isaac	Mathias, Mildred E.	St. John, Harold
Cárdenas, Martin	McClure, Floyd A.	Stone, Donald E.
Cheesman, L. Evelyn	Meggers, Betty	Taylor, W. Randolph
Corner, E. J. H.	Metcalfe, Charles Russell	Travassos, Lauro
Costa-Lima, Angelo Moreira	Mayr, Ernst	Uvarov, Boris P.
Dobzhansky, Theodosius	Phelps, William H.	Van der Vecht, Jan
Enders, Robert	Popenoe, Wilson	Van Steenis, C. G. G. J.
Gleason, Henry Alan	Richards, Owain W.	Verdoorn, Frans
Holttum, R. E.	Richards, Paul	Wetmore, Alexander
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