



Unfavorable successional pathways and the conservation value of logged tropical forest

COLIN A. CHAPMAN^{1,2,*} and LAUREN J. CHAPMAN^{1,2}

¹*Department of Zoology, University of Florida, Gainesville, FL 32611, USA;*

²*Wildlife Conservation Society, 185th Street and Southern Boulevard, Bronx, NY 10460, USA; *Author for correspondence (e-mail: cchapman@zoo.ufl.edu; fax: +1-352-392-3704)*

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Abstract. Conservation agencies are increasingly advocating that the survival of many tropical forest species may depend on disturbed forests and are directing scarce conservation resources to managing logged forests. This requires critical evaluation. In this 10-year study, we quantify tree community dynamics in three selectively logged areas harvested at different intensities and compare their recovery to two unlogged areas in Kibale National Park, Uganda. Over the 10 years, 527 of the original 4840 tagged trees (≥ 10 cm DBH) died; while the mortality rate was highest in the heavily logged area, it was only significantly greater than one of the unlogged sites. The density of new trees varied significantly among areas being highest in the lightly logged area, but the density of new recruits in the heavily logged area did not differ from the unlogged areas. Overall, the more heavily logged areas had higher growth rates than the unlogged or lightly logged areas. However, there was no difference among areas in the magnitude of the change in basal area; and in both 1990 (20+ years post-harvest) and 2000 the basal area in the heavily logged area was significantly less than the unlogged areas. In general, findings from the heavily logged area suggest that the expectation that in logged areas a number of processes of forest regeneration will be accelerated relative to unlogged forest was not met. Thus, 30+ years after logging evidence suggests that forest recovery will be slower than expected. We also present evidence to suggest that the climate in the region is changing, which may account for changes in the population dynamics of certain species in the unlogged forests.

Introduction

Although tropical forests cover only 6% of Earth's arable surface, they harbor roughly half of all known species (National Research Council 1992). It is clear that the future of these highly diverse ecosystems is threatened by ever-escalating rates of forest conversion and degradation (Brown and Lugo 1990; Chapman and Peres 2001). The FAO (1999) estimated that tropical countries are losing 127,300 km² of forest annually. Less than 5% of the world's tropical forests are legally protected from human exploitation, and many of these legally protected areas are subjected to illegal exploitation (Redford 1992; Fa et al. 1995; Oates 1996). Furthermore, many tropical species are locally endemic or are rare and patchily distributed (Struhsaker 1975; Richards 1996). Such restricted distributions predispose such species to increased risk of extinction when habitats are modified (Terborgh 1992), because national parks,

even if effectively protected, will fail to conserve species whose ranges do not fall within a protected area. As a result, many conservation and development agencies suggest that conservation of many tropical forest species will depend on the capacity of disturbed forests to support their populations (Struhsaker 1997; Putz et al. 2000; Fimbel et al. 2001). The most prevalent form of disturbed forest habitat with conservation potential is selectively logged forest (Frumhoff 1995; Struhsaker 1997). It is estimated that between 5 and 6 million ha of tropical forest is logged each year (FAO 1990).

At a time of tightening budgets, the decision to place scarce conservation resources into managing logged forests requires critical evaluation. Fundamental assumptions of this strategy are that the successional pathway that follows logging is one that will lead to an ecosystem similar to the pre-disturbance one, that this will happen in a reasonably short period, and that the resulting ecosystem will support a similar richness as the original one. The rationale for accepting these assumptions is largely based on the general forestry principle that logging creates gaps in the forest canopy; these gaps increase light intensity reaching the forest floor or subcanopy, which in turn accelerates growth of existing trees (Fox 1976; Putz et al. 2000). It is also assumed that logged forest will recover significantly before the forest is scheduled to be re-harvested, before the land is acquired by agriculturalists and converted to farm land, and/or before the successional pathway is altered by the effects of fire that can be encouraged by logging (Oates 1995; Holdsworth and Uhl 1997; Peres 1999).

Over the past 3 decades, a system of permanent plots has been established in the tropics (Hubbell 1979; Condit 1995; Taylor et al. 1996; Sheil 1997). One aim of establishing these plots is to provide a baseline to monitor change in tree communities that may relate to climate change (Condit et al. 1996). These plots also provide an extremely valuable resource for forest managers, as these data can be used to evaluate the potential profit of different timber species based on their growth rate (Condit et al. 1993a, 1996; Taylor et al. 1996). If the conservation and development communities are going to advocate placing scarce conservation resources into managing logged forests, then it is important to provide information from long-term plots concerning how the tree community in logged forests changes over time and how these forests respond to climate change.

The objective of this 10-year study was to evaluate the recovery of the tree community in three selectively logged areas in Kibale National Park, Uganda that were harvested at different intensities and compare their recovery to two unlogged areas. Monitoring was started 20+ years after the logging was completed. We evaluate mortality, growth, recruitment rates, and changes in basal area of the entire tree community, and of select species. We consider the successional pathways these forests exhibit and their potential future tree community structure and composition. We also evaluate long-term climate data to assess whether specific changes in tree community composition could be driven by climate change.

Methods

Study site

Kibale National Park (766 km²) is located in western Uganda (0°13'–0°41' N and 30°19'–30°32' E) near the foothills of the Ruwenzori Mountains (Struhsaker 1975, 1997; Chapman et al. 1997; Chapman and Lambert 2000). The park consists of mature, mid-altitude, moist semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; primarily *Cupressus lusitanica*, *Pinus patula*, *P. caribaea*, and *Eucalyptus* spp.; Chapman and Lambert 2000). Mean annual rainfall in the region is 1749 mm (1990–2001, or 1547 mm from 1903–2001, see evidence of climate change below); the mean daily minimum temperature is 14.9 °C; and the mean daily maximum temperature is 20.2 °C (1990–2001; Chapman and Chapman, unpublished data). Rainfall is bimodal, with two rainy seasons generally occurring from March to May and September to November.

Kibale forest received national park status in 1993. Prior to 1993, it was a forest reserve, gazetted in 1932 with the goal of providing a sustained production of hardwood timber (Osmaston 1959). A polycyclic felling cycle of 70 years was initiated, and it was recommended that logging open the canopy by approximately 50% through the harvest of trees over 1.52 m in girth (Kingston 1967). This history of logging led to varying degrees of disturbance among sites. We selected five sites to study using 0.2 ha permanent vegetation plots. Three of these sites were logged at different intensities in the late 1960s and two were unlogged. Four areas are adjacent to one another at the Kanyawara study site (1500 m, two of which are combined for statistical comparisons), and the fifth site is at Ngogo (1350 m), approximately 10 km to the south.

Foresters have classified Kanyawara as a *Parinari* forest, distinguished on photo aspect maps by the large spreading crowns of *Parinari excelsa*; a valuable timber tree (Kingston 1967; Skorupa 1988). The presence of *P. excelsa* and the subdominants found near Kanyawara (*Aningeria altissima*, *Olea welwitschii*, *Newtonia buchananii*, and *Chrysophyllum gorungosanum*) are thought to indicate a climax forest between 1370 and 1525 m (Osmaston 1959). Ngogo has some features of lower elevation forest. These two forests, although located only 10 km apart, differ in tree species composition (Chapman et al. 1997). At Ngogo, *P. excelsa* is still present, but the forest is very mixed with *Chrysophyllum* spp. and *Celtis* spp. being common. Of all species found at either site ($n = 104$) only 52% were found at both sites. If rare species (< 1 individual ha⁻¹) are excluded, the two sites share 72% of the species (Chapman et al. 1997). There were also shifts in the relative abundances of the fauna between these two sites (Struhsaker 1997).

The K-15 forestry compartment at Kanyawara is a 347 ha section of forest that experienced high-intensity selective felling from September 1968 through

April 1969. Harvest averaged $21 \text{ m}^3 \text{ ha}^{-1}$ or approximately $7.4 \text{ stems ha}^{-1}$ (Skorupa 1988; Struhsaker 1997); however, incidental damage was much higher. It is estimated that approximately 50% of all trees in this compartment were destroyed by logging and incidental damage (Skorupa 1988; Chapman and Chapman 1997). A total of 18 tree species were harvested, with nine species contributing more than 95% of the harvest volume (Kasenene 1987; Skorupa 1988).

Forestry compartment K-14, a 405 ha forest block, experienced low intensity selective felling from May through December 1969 (averaging $14 \text{ m}^3 \text{ ha}^{-1}$ or $5.1 \text{ stems ha}^{-1}$). Twenty-three tree species were harvested, with nine species accounting for 94% of before harvest volume. Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa 1988; Struhsaker 1997). Harvest was not evenly distributed in this forestry compartment (Struhsaker 1997; Chapman and Chapman 1997). As a result, we divided this compartment into two study sites: a moderately logged area (Mikana, adjacent to the K-15 compartment) and a lightly logged area (called K-14), where stump and gap enumeration suggests only a few trees were removed (Kasenene 1987).

K-30 is a 282-ha area that has not been commercially harvested. However, prior to 1970, a few large stems (0.03–0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa 1988; Struhsaker 1997). Hence, compartment K-30 serves as one of the control areas. As a control, we are assuming that differences between the unlogged K-30 compartment and the neighboring logged compartments (K-14, K-15) are due primarily to the effects of logging. However, we have no means of ensuring that the control and treatment areas did not differ prior to logging. The final site, Ngogo, differs in tree composition from K-30 (Chapman et al. 1997), and has not been logged. By having two controls we can start to examine whether variance between unlogged sites is similar or less than variance between unlogged and logged sites.

Sampling methods

At each site, we established permanent vegetation plots (200 m \times 10 m) with the location of plots selected at random from within the existing trail system. We established 26 plots at Kanyawara in January 1990 (unlogged (K-30) = 12 plots (mean number of trees/plot = $97 \pm 6.3 \text{ SE}$), lightly logged (K-14) = 5 (mean $88 \pm 4.6 \text{ SE}$), moderately logged (Mikana) = 4 (mean $57 \pm 2.8 \text{ SE}$), heavily logged (K-15) = 5 (mean = 59 ± 9.5)), providing a total sampling area of 5.2 ha. Twenty-four plots were established at Ngogo in May 1990 producing a total sampling area of 4.8 ha (mean number of trees/plot = $144 \pm 6.2 \text{ SE}$). Each tree with a diameter at breast height (DBH) ≥ 10 cm within 5 m of each side of the trail was individually marked with a numbered aluminum tag and

measured (DBH). This provided an initial sample of 2111 trees at Kanyawara (1067 unlogged, 296 K-15, 524 K-14, 227 Mikana) and 2622 trees at Ngogo.

Plots were resurveyed approximately 10 years after their establishment (May 2000). All tagged trees were located and new trees with a DBH ≥ 10 cm were identified and tagged. If a tree had died, the cause of death was determined where possible. Determining the cause of death was facilitated by the fact that all plots were used in a phenology study from 1990 to 1996 (Chapman et al. 1999) and mortality was monitored. We noted if (1) the tree died standing, (2) the tree died standing then subsequently lost most of its branches before falling, (3) the tree appeared to be healthy until it fell, and (4) an apparently healthy tree was knocked over by another falling tree. Growth of trees was assessed over the 10 years by contrasting the initial and final DBH measurement. Both measurements were made where the tree tag was affixed to the tree.

We contrast the rate of population change of all species and display these results graphically. These results should be considered preliminary, as Condit et al. (1993a,b) recommend that the minimum sample size for statistical confidence in tree population changes is 100 stems per species. Given that we were only sampling stems ≥ 10 cm DBH and a number of the common species have clumped distribution patterns, we only have a few species that have more than 100 stems in all areas.

Rainfall data were available between 1903 and 1971 from Government of Uganda meteorological records for the town of Fort Portal (approximately 20 km west of Kanyawara), between 1972 and 1989 from T.T. Struhsaker (Kanyawara), and from 1989 to present from our data (Kanyawara).

For statistical comparisons each transect was considered an independent unit and comparisons were made among areas that had been subjected to different levels of harvest. Percent data were arcsine square root transformed. For statistical comparisons of mortality rates, density of recruits, and change in basal area, transects K-14 (Mikana, $n = 4$) and K-15 ($n = 5$) were combined. For growth rates, each tree was considered independent and thus Mikana and K-15 were not combined.

Results

Over the 10 years, 527 of the original 4840 trees died in the five sites. While the mortality rate was highest in the heavily logged area, it was only significantly greater than the unlogged Ngogo site ($F = 3.75$, $P = 0.017$; *post hoc* test $P = 0.003$), which was also less than the Kanyawara unlogged site ($P = 0.045$; Figure 1). There was no overall difference in causes of death among areas ($\chi^2 = 3.28$, $P > 0.10$). The six most common species at the Kanyawara sites had different mortality rates among areas (Figure 2). For example, the mortality rate of *U. congensis* was highest in the heavily logged area, while for *F. latifolia* mortality was lowest in this forestry compartment.

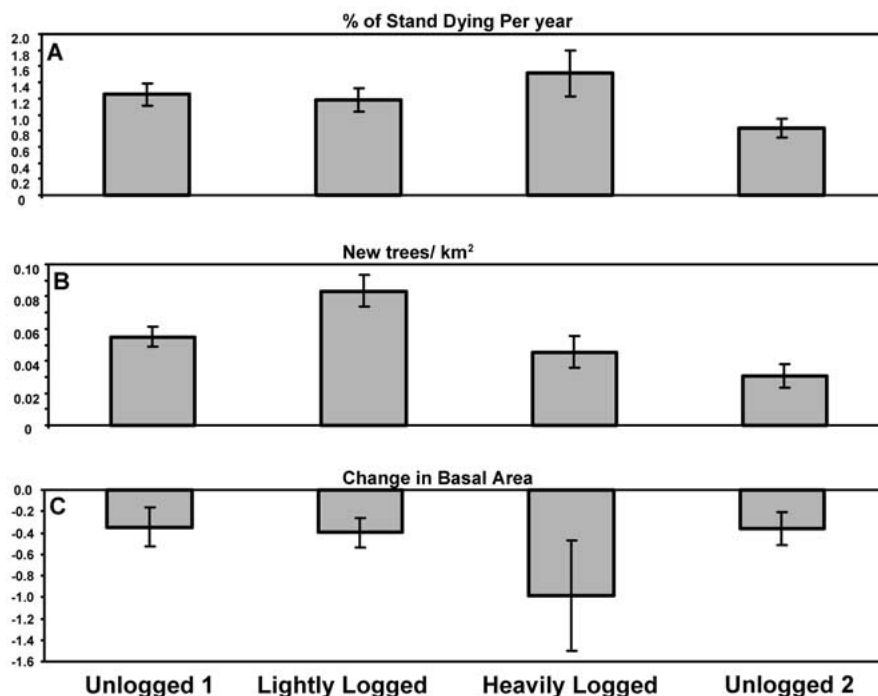


Figure 1. (A) The percentage of the stand that died (\pm SE) in logged and unlogged areas of Kibale National Park, Uganda over 10 years ($F = 3.75$, $P = 0.017$; significant *post hoc* tests, heavily logged (K-15 and Mikana) site differed from unlogged 2 (Ngogo), $P = 0.003$, and unlogged 1 (K-30) differed from unlogged 2, $P = 0.045$), (B) The density (number/km²) of new stems (≥ 10 cm DBH; \pm SE) recruiting into these areas ($F = 7.164$, $P < 0.001$; lightly logged differed from unlogged 1 $P = 0.039$, unlogged 2 $P < 0.001$, and heavily logged $P = 0.008$; unlogged 1 differed from unlogged 2 $P = 0.014$). (C) The percent change in basal area (\pm SE) in these logged and unlogged areas ($F = 1.222$, $P = 0.313$).

The density of trees that recruited into the ≥ 10 cm DBH size class was greater in the lightly logged area than in any other area ($F = 7.164$, $P < 0.001$; unlogged Kanyawara $P = 0.039$, unlogged Ngogo $P < 0.001$, heavily logged $P = 0.008$; Figure 1). Recruitment into the heavily logged area was less than the unlogged area immediately adjacent to it, but this difference was not statistically significant. Considering all of the species that had more than 10 individuals recruited into this size class over the 10 years illustrates variation in species recruitment among sites (Figure 3).

When we considered all stems, we found consistent differences among sites in growth rates (Table 1). In general, the more heavily logged areas had higher growth rates than the unlogged or lightly logged areas, but there were some inconsistencies in this pattern on a species-by-species basis and there were considerable differences in growth rates of the six most abundant species at Kanyawara in the different areas (Table 1). Growth rates of *C. durandii* and

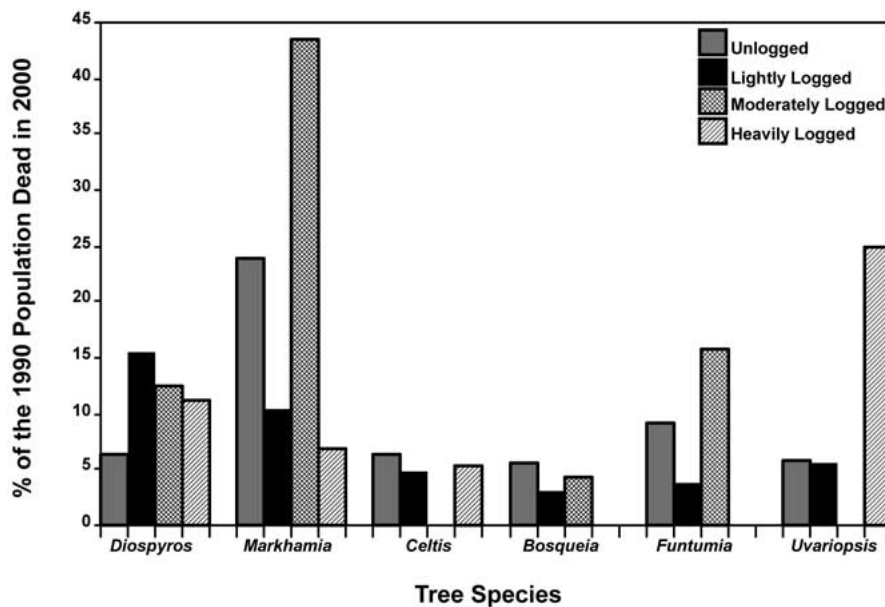


Figure 2. The percentage of trees (≥ 10 cm DBH) dying over a decade in four areas of Kibale National Park, Uganda. The six most abundant tree species at Kanyawara are depicted and include *Bosqueia phoberos* (shade tolerant), *Celtis durandii* (large gap species), *Diospyros abyssinica* (shade tolerant), *Funtumia latifolia* (shade tolerant), *Markhamia platycalyx* (large gap species), and *Uvariopsis congensis* (shade tolerant).

F. latifolia were higher in the moderately and heavily logged areas than in the lightly logged and unlogged areas. Both of these species colonize disturbed areas as soon as a canopy of early pioneers is establishing (i.e., typically 5–7 years after a major disturbance). *D. abyssinica* is similarly very common in areas about a decade after disturbance; however, its growth rate did not differ among forestry compartments.

Considering all species together, the basal area in the different sites decreased over the 10 years (paired t -test $t = 5.209$, $P < 0.001$; paired by transect). This likely represents the death of a few large individuals and the fact that recruitment into the ≤ 10 cm DBH size class in the gaps they leave behind was not assessed. There was no difference among sites in the magnitude of the change in basal area ($F = 1.222$, $P = 0.313$; Figure 1). However, basal area differed among areas (1990 $F = 10.481$, $P < 0.001$; 2000 $F = 11.636$, $P < 0.001$). The heavily logged area had a smaller basal area than either of the unlogged forests (K-30 2000 $P = 0.003$, Ngogo $P < 0.001$), but the lightly logged area did not differ in basal area from the unlogged area immediately adjacent to it ($P = 0.754$). The basal area of the two unlogged forests differed ($P = 0.030$), with the basal area at Kanyawara being 20% less than Ngogo.

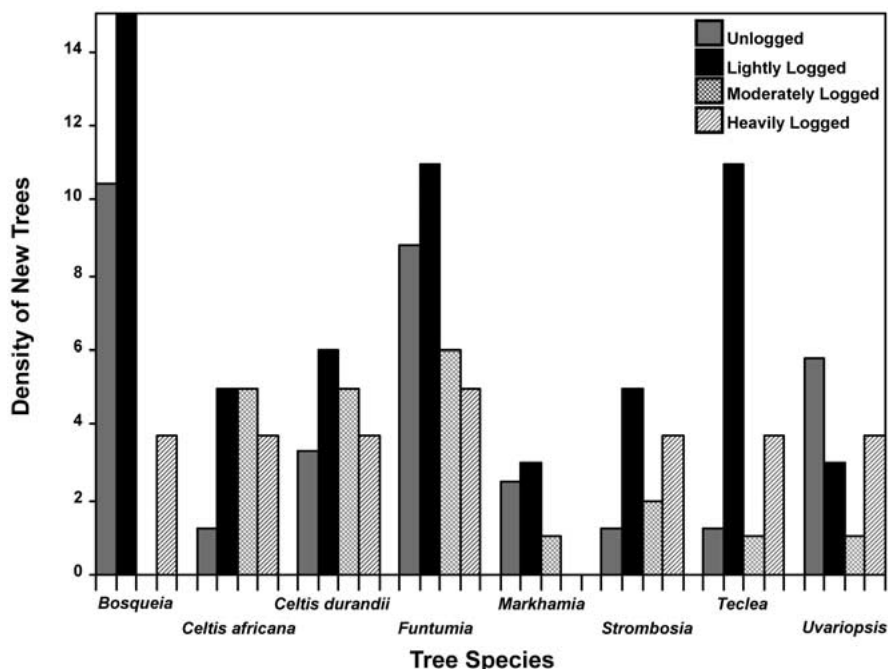


Figure 3. The density (individuals/ha) of trees recruiting into the ≥ 10 cm DBH size class between 1990 and 2000 in Kibale National Park, Uganda. Only those species that had more than 10 new individuals are presented (*B. phoberos*, *Celtis africana*, *C. durandii*, *F. latifolia*, *M. platycalyx*, *Strombosia scheffleri*, *Teclea nobilis*, and *U. congensis*).

When considering changes in basal area on a species-by-species basis, a number of interesting among-site differences are evident (Figure 4). For example, the basal areas of *F. latifolia* and *B. phoberos* increased in all areas, while those of *M. platycalyx* and *D. abyssinica* declined in all areas. The total basal area of *C. durandii* declined slightly in the unlogged area of Kanyawara, in the lightly logged area it increased slightly, while in the moderately and heavily logged areas it increased dramatically (Figure 4).

Of the 58 species found in the unlogged forestry compartment at Kanyawara, 20 species declined in abundance, 19 increased in abundance, and numbers were unchanged for 19 populations (Figure 5). The distribution of increases and declines was very similar in the unlogged, lightly logged, and heavily logged areas of Kanyawara; however, the moderately logged area had more species that showed moderate declines in abundance (Figure 4). At Ngogo, the distribution was similar to those at Kanyawara, excluding the moderately logged area, but there were more species that showed an increase in abundance. Of the 89 species found in the Ngogo plots, only 13 declined in

Table 1. The growth (cm DBH) of all trees (>10 cm DBH) and the six most abundant tree species over a 10-year period in areas of Kibale National Park, Uganda, that have experienced different histories of logging. ANOVA was used to test for differences in growth rates among compartments for all species and for the six most abundant species. The *a posteriori* Scheffe test was used to detect differences between pairs of sites.

| Forestry compartment | All species ¹ | <i>D. abyssinica</i> ² | <i>C. durandii</i> ³ | <i>F. latifolia</i> ⁴ | <i>B. phoberos</i> ⁵ | <i>U. congensis</i> ⁶ | <i>M. platycalyx</i> ⁷ |
|--------------------------------|--------------------------|-----------------------------------|---------------------------------|----------------------------------|---------------------------------|----------------------------------|-----------------------------------|
| (1) Unlogged (K30) | 2.16 | 2.56 | 2.55 | 4.78 | 1.55 | 1.32 | 1.25 |
| (2) Lightly logged (K14) | 2.45 | 2.83 | 2.51 | 5.45 | 1.43 | 1.35 | 2.80 |
| (3) Moderately logged (Mikana) | 3.74 | 3.58 | 7.91 | 7.96 | | 2.10 | 1.48 |
| (4) Heavily logged (K15) | 4.19 | 2.84 | 4.33 | 7.86 | 1.62 | 1.18 | 1.77 |
| (5) Unlogged (Ngogo) | 2.54 | 2.21 | 2.24 | 4.04 | 3.85 | 1.67 | 1.74 |

¹F = 10.70, *P* < 0.01 (1 dif 3,4, 2 dif 4 3 dif 4,5).

²F = 1.30, *P* = 0.27.

³F = 17.02, *P* < 0.01 (3 dif all, 4 dif 1,2).

⁴F = 5.22, *P* < 0.01 (1 dif 3,4).

⁵F = 0.034, *P* = 0.97.

⁶F = 0.03, *P* = 0.81.

⁷F = 1.08, *P* = 0.359.

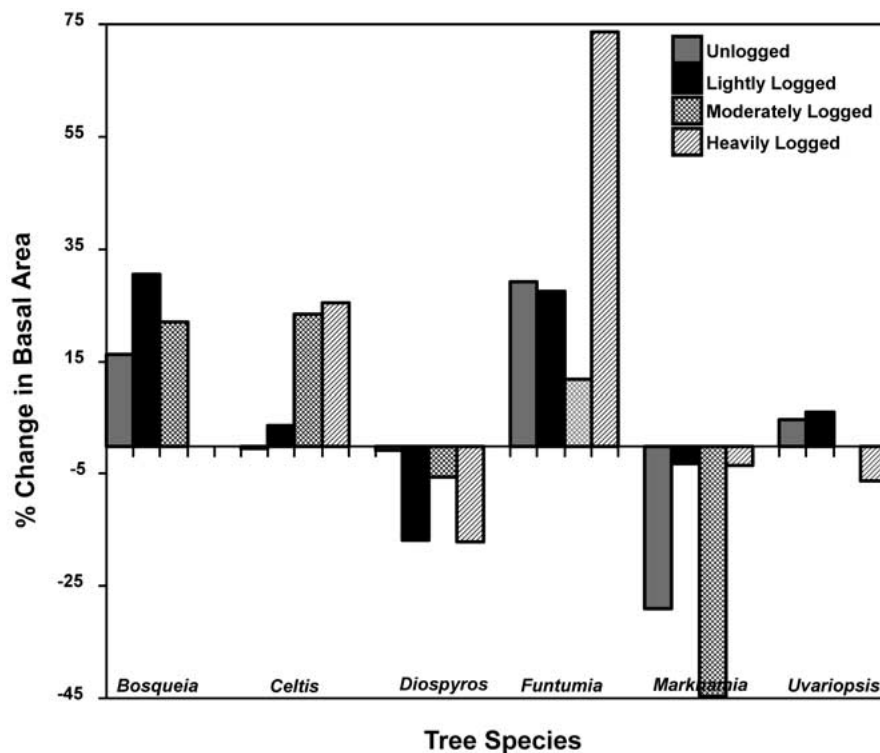


Figure 4. The percent change in basal area of the six most common tree species in areas that have different histories of logging in Kibale National Park, Uganda (*B. phoberos*, *C. durandii*, *D. abyssinica*, *F. latifolia*, *M. platycalyx*, and *U. congensis*).

abundance, 54 remained unchanged, and 19 increased in abundance. In the heavily logged area, *Trema guinensis* showed dramatic declines. In 1990, there were 19 individuals in the plots. In 2000, there was only one remaining individual. *T. guinensis* is a pioneer species that quickly establishes after disturbance, thus the decline likely represents the senescence of individuals that recruited shortly after logging.

There were large changes in abundance for some species in the undisturbed forest that are not so easily understood. For example, 103 *M. platycalyx* trees were found in the 1990 enumeration in the unlogged forest of Kanyawara, while by the second census 20 stems had died. There was little change in the species richness over the 10 years, with the exception of the heavily logged forest where species richness declined by 5.1% and the moderately logged forest where species richness increased by 5% (unlogged Kanyawara 0%, lightly logged 2%, Ngogo 2.2%).

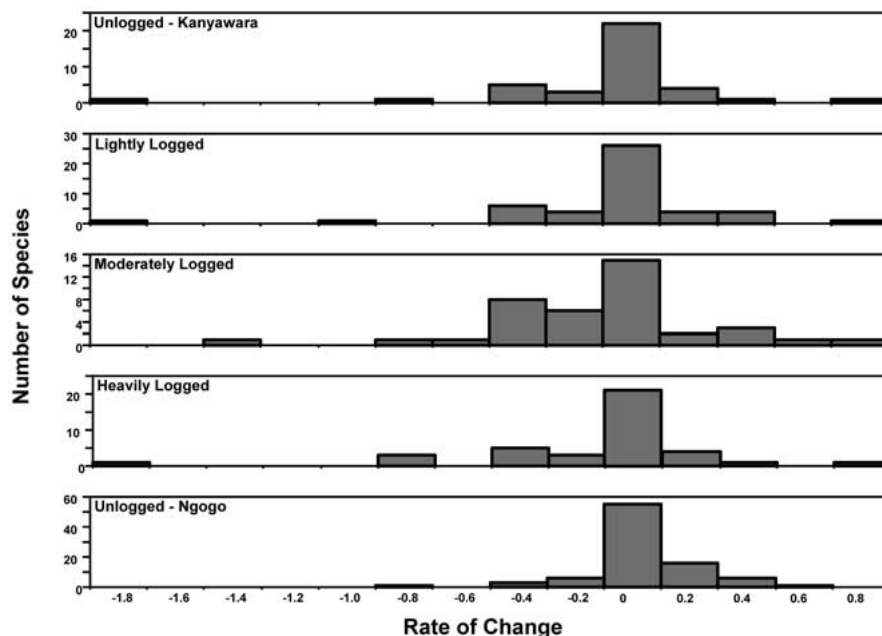


Figure 5. Distribution of population growth rates for tree species (≥ 10 cm DBH) over a 10-year period for areas of Kibale National Park, Uganda, that have experienced different histories of logging.

Discussion

Our data indicate that both the logged and the unlogged forests of Kibale are changing. For the logged areas, some of the change is likely due to succession following logging, and the nature of the change appears to be influenced by the intensity of timber extraction. For example, the decline in the abundance of *T. guinensis*, an early successional species, likely represents the senescence of individuals that recruited at the time of logging. However, the changes in some species in the undisturbed forest are not so easily understood, and suggest that other factors may have contributed to the observed changes. For example, rainfall data collected since 1903 indicates that the region is becoming moister (Figure 6); in fact, there is a significant rank correlation between year and annual rainfall ($r_{sp} = 0.401$, $P < 0.001$; see also Struhsaker 1997). If a drought year is considered one with less than 1300 mm of rain, then there is also a significant decline in the number of drought years in a decade over the last century ($r_{sp} = 0.850$, $P = 0.002$). The importance of climate change or other non-logging effects is suggested by the fact that the unlogged forests have changed with regard to a number of the parameters we considered. Interestingly, if it is climate change that is driving changes in the unlogged forest

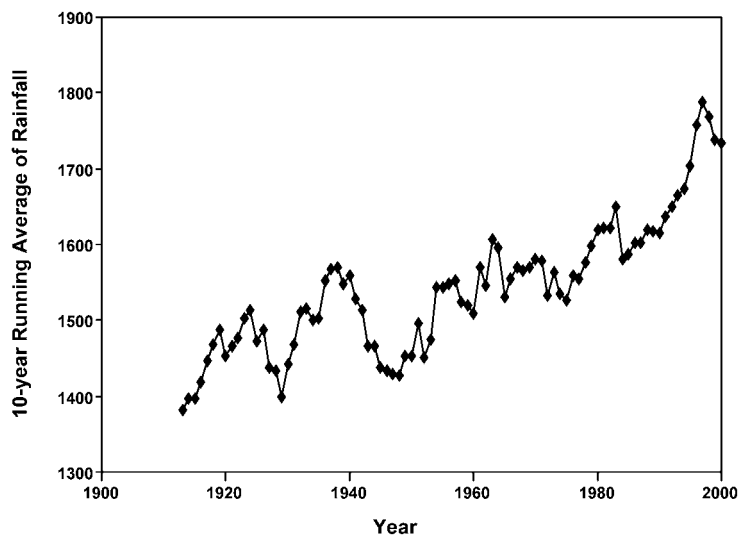


Figure 6. The 10-year running average of the annual rainfall in the area of Kibale National Park, Uganda.

communities, it is not necessarily influencing the two unlogged areas in the same manner, since the unlogged forests of Ngogo and Kanyawara changed in different ways over the 10 years. Sheil (1997) found no evidence for effects of changes in rainfall on stem growth in the Budongo forest that lies less than 200 km northeast of Kibale. The data in Sheil's study consisted of stem measurements spanning 6 decades (see also Eggeling 1947; Sheil 1995; Plumptre 1996). A number of species in Kibale exhibited decreases in the proportion of trees that fruited each year between 1970 and 2000 (Chapman et al., unpublished data). For example, *A. altissima* and *P. excelsa* fruited consistently in the 1970s and early 1980s, but have rarely fruited in the 1990s. Somewhat ironically, the Kanyawara region of Kibale is considered a *Parinari* forest by early foresters (Osmaston 1959; Kingston 1967). Whether this represents a permanent change for these species or part of a long-term cycle is not known; however, if these species continue to fruit poorly, their dominance will likely decline over time. Clearly, there is a need for increased efforts to monitor long-term change in tropical forest communities in relation to climate change.

Lwanga et al. (2000) described tree populations dynamics at Ngogo over a 23-year period (1975–1998) using a different set of plots than the ones used here and enumerating only those trees greater than 10 m tall. There are a number of similarities between the findings of our studies. Lwanga et al. (2000) documented a 3% decline in species richness and we found a 2.2% decline. Both studies documented an overall decline in stem number, but the magnitude of the decline differed (Lwanga et al. 2000 – 8%, this study – 4.7%). Lwanga et al.

documented a 1.6% decrease in basal area, while we documented a 0.4% decrease. These differences may arise from a number of sources. Lwanga et al.'s study is over a longer duration than this one, so patterns may be changing. Alternatively, the differences may simply reflect sampling methods.

The conservation value of logged forest is dependent on the speed and nature of the post-logging forest recovery process and the ability of the animal populations to respond to the recovery. For logged forest to have high conservation value, the forest would need to recover significantly before the forest is scheduled to be reharvested in a polycyclic logging scheme, before the land is acquired by agriculturalists and converted to farm land, and/or before the successional pathway is altered by fire that can be encouraged by logging. As a result, one would hope to see that the environmental conditions that exist after logging favor some process of forest regeneration, either decreased tree mortality, increased recruitment, or greater tree growth. The mortality rate was highest in the heavily logged area, and it was significantly greater than in one of the unlogged sites. Recruitment into the heavily logged area was less than in the unlogged area immediately adjacent to it, but this difference was not statistically significant. The heavily logged areas had higher growth rates than the unlogged or lightly logged areas; however, this did not compensate for the higher mortality rates. There was no difference among sites in the magnitude of the change in basal area, but the heavily logged area had a smaller mean basal area than either of the unlogged forests 30+ years after the logging. These findings suggest that in heavily logged areas recovery will be very slow. This throws doubt on the universal acceptance of the FAO categorization of secondary forest greater than 60–80 years as primary forest (Brown and Lugo 1990). In contrast, the density of trees that recruited into the ≥ 10 cm DBH size class was greater in the lightly logged area than in any other area and by the end of the study the basal area of the lightly logged area did not differ from the neighboring unlogged area.

There is evidence that animal populations in heavily logged sites in Kibale are not recovering, possibly in response to the slow rate of forest recovery. For example, a recent study in the same sites as studied here (Chapman et al. 2000) demonstrated that group densities for redtail and blue monkeys (*Cercopithecus ascanius*, *C. mitis*) were significantly lower in logged compared to undisturbed forests and that their populations declined between censuses conducted approximately 11 and 28 years after logging. Although red colobus (*Procolobus badius*) densities were significantly lower in logged compared to undisturbed forests, their populations were in a state of recovery. In contrast, black-and-white colobus (*Colobus guereza*) densities were significantly higher in logged compared to undisturbed forests, suggesting that their populations do well in some disturbed habitats. Approximately 23 years after logging, duiker (*Cephalophus monticola* and red duiker – species identity is not known) populations were still significantly higher in unlogged than in logged sites (Struhsaker 1997). With respect to the impact of logging on the bird community of Kibale, in the heavily logged

site a number of forest interior specialists were absent, cavity-nesting species were rare, and the bird community was dominated by a single generalist species (Dranzo 1995).

These findings call for an evaluation of how typical it is for regeneration following logging to be slow. Unfortunately, these data are difficult to obtain, as they require measurements of growth and survival on individually marked trees over a number of years from both logged treatment and unlogged control areas. Cannon et al. (1994) found that there was only limited evidence of canopy development after 8 years in a selectively logged forest in West Kalimantan. In Budongo Forest Reserve, Uganda, Plumptre (1996) found that 50 years of regeneration was not long enough for the forest structure to recover to the levels of unlogged forest for all variables measured, including basal area and crown height. In contrast, data on stand dynamics from a logged Costa Rican forest between 1988 and 1996 suggests that it will only take 20 years before a selectively logged area where 4 tree ha⁻¹ were harvested (mean volume of 10.1 m³ ha⁻¹) will reach the basal area of undisturbed mature lowland forest (Finegan and Camacho 1999). Similarly, approximately 30 years post harvest involving intensive harvest, girdling, and climber cutting, Manokaran (1996) found similar basal areas in harvested and control sites. Efforts to model forest growth and yield after logging suggest a relatively rapid recovery (Vanclay 1989; Spathelf and Durlo 2001).

In Kibale, it seems clear that recovery in the heavily logged site is not rapid. Two factors seem to be important in leading to this unfavorable successional pathway; a dense competitive herbaceous layer and elephants (*Loxodonta africana*). Following logging in Kibale, conditions appear to be favorable for the formation of a dense herbaceous layer that is often dominated by *Acanthus pubescens* (Kasenene 1987; Paul et al. in press). Subsequently, elephants are attracted to these areas to feed and their feeding habits deter tree regeneration and appear to promote maintenance of the herbaceous layer (Wing and Buss 1970; Laws 1994; Struhsaker et al. 1996). Struhsaker et al. (1996) found that elephants in Kibale used heavily logged areas more than lightly logged or unlogged areas, and elephant use of an area and damage to young trees are directly related to the density of herbaceous tangle.

Given that mid-elevation tropical forests have primarily been replaced by agriculture in East Africa (Struhsaker 1987), intervention may be appropriate to speed the recovery process. It is noteworthy that the successional pathway that the lightly logged forest followed post-logging is more quickly leading to forest recovery. There is likely a threshold of harvest intensity above which widespread establishment of a dense herbaceous layer is promoted. Identifying this threshold would be very useful for the long-term management of forests similar to Kibale National Park (Sist et al. 1998).

Our results should not be interpreted to imply that efforts of conservation agencies to manage logged tropical forests are misguided. Rather, we suggest that a balance is needed between efforts directed towards managing logged forests and efforts to preserve undisturbed tracks of land. We believe our study

does highlight the need to understand the successional pathways that forests in different parts of the globe follow after disturbance.

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