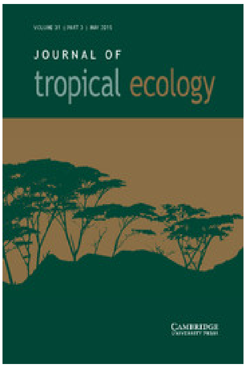

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Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda

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ABSTRACT. The Kibale Forest, western Uganda, is the only site where studies have compared the impact of elephants on rainforest regeneration in logged and unlogged control areas. Elephants used heavily logged areas more than lightly logged and unlogged areas. Forest gaps were used more by elephants than closed-canopy areas and large gaps more than small ones. Gaps were larger in logged than unlogged forest. There were lower densities of young trees (saplings and poles) and a higher incidence of elephant damage to them in heavily logged forest than in lightly logged and unlogged sites. Elephant use of an area and damage to young trees was inversely or unrelated to the density of young trees and directly related to the density of herbaceous tangle. Heavy logging resulted in large areas of herbaceous tangle, which attracted elephants who suppressed forest regeneration by damaging young trees and perpetuating the herbaceous tangle. The tangle directly competed with regeneration of young trees while also attracting elephants and rodents (seed and seedling predators) and facilitating increased windthrow of trees. Selective browsing of young trees by elephants affected rates of regeneration, growth form and species composition. Rather than remove elephants, a more effective and humane approach to long-term management of logging is to reduce logging offtake and incidental damage caused by timber extraction.

KEY WORDS: elephants, forest regeneration, logging, selective browsing.

INTRODUCTION

It has been contended for at least 40 years that elephants (*Loxodonta africana* Blumenbach) living in African rainforests have a propensity to utilize forest clearings and secondary growth more so than closed-canopy, mature forest (Jones 1955, Langdale-Brown *et al.* 1964, Laws 1970, Laws *et al.* 1975). More quantitative studies support this conclusion (Barnes *et al.* 1991, Kasenene 1987; Merz 1981, 1986; Nummelin 1990, Prins & Reitsma 1989, Short 1981, Wing & Buss 1970). It was further suggested that by selectively using these clearings and secondary forests, elephants perpetuated and maintained these plant communities through the impact of browsing and trampling (Eggeling 1947, Jones 1955, Langdale-Brown *et al.* 1964). Nearly 30 years ago it was speculated that this selective use of habitat by elephants prevented forest regeneration in logged areas (Kingston 1967, Laws 1970, Laws *et al.* 1975). None of the earlier studies, however, addressed the issue of how selective logging affects habitat use by elephants and, in turn, how this influences forest regeneration. Specifically, the earlier studies did not compare the impact of elephants in logged and unlogged control areas.

The Kibale Forest of western Uganda has been the site of the majority of ecological work on African elephants living in rainforests (Buss 1990, Kingston 1967, Wing & Buss 1970). It is also the only location where studies have addressed the specific issue of how selective logging affects elephant ecology and, in turn, forest regeneration (Kasenene 1980, 1984, 1987; Lwanga 1994, Nummelin 1990).

This paper has three objectives. The first is to summarize relevant data from the Kibale Forest of Uganda, which indicate that the intensity of selective logging affects the negative impact of elephants on tree regeneration and thereby maintains herbaceous tangles in logged areas of the forest. The second is to make recommendations regarding logging practices that will reduce this impact and which are more compatible with forest regeneration. The third objective is to make suggestions for future research on this issue.

STUDY SITE AND STUDIES

The Kibale Forest is located in western Uganda (0° 13′ to 0° 41′ N, 30° 19′ to 30° 32′ E; elevation 1110–1590 m). It covers 560 km^2 and is comprised of a mosaic of habitat types. Approximately 60% is moist evergreen forest (Kingston 1967, Struhsaker 1975, Wing & Buss 1970).

In this paper we refer to four forest compartments: one was the unlogged control (K30), two were logged (K14 lightly, K15 heavily) and one was heavily logged followed by poisoning of undesirable trees with an arboricide (K13) (Table 1 adapted from Kasenene 1987, Skorupa 1988 and Uganda Forest Department records). These compartments ranged in size from 282 to 622 ha.

Table 1. Study site treatments in Kibale Forest, Uganda. (C = Control, LL = Lightly Logged, HL = Heavily Logged, P = Poisoned.)

			Reduction in % Basal area			Estimated number of trees cut ha^{-1} based on	
Forest comp.	Treatment	Date logged	All species	Commercial species[1]	Volume harvested[2] (m^3 ha^{-1})	Volume conversion	Stump count
K30	C	–	–	–	–	–	–
K14	LL	1969	25	49.5	14	5.1	3.0
K15	HL	1968–69	47	59.7	21	7.4	8.6
K13	HL+P	1968	50.3	82.8	17	6.1	9.8

Modified from Kasenene (1987) and Skorupa (1988).

[1] Based on differences from the control site (K30).

[2] Uganda Forest Department records.

The studies of elephant ecology in Kibale span a period of 30 years. The most extensive and detailed work was conducted by Wing & Buss (1970) between October 1962 and 1965 when elephants were at their highest recorded densities in Kibale. Their study covered the entire forest. No further studies were done on elephants in Kibale until 1978–1979 when Kasenene (1980, 1984) recorded elephant-damaged saplings and poles in eleven 0.81 ha plots located in lightly logged (K14; N = 5) and unlogged (K30; N = 6) compartments. In 1983–1984 Nummelin (1990) counted elephant dung heaps along transects in three forest compartments (K14, 15, 30). During his study of gap dynamics in 1984–1986, Kasenene (1987) collected data on elephant use of gaps and the incidence of elephant-damaged saplings and poles in gaps of four forest compartments of Kibale (K13, 14, 15, 30). In 1992–1993 Lwanga (1994) studied elephant damage to saplings and poles of two emergent tree species in three compartments (K13, 15, 30) and also recorded damage to all species along fresh elephant tracks in K30 and K15.

Selective use of logged forest by elephants

Wing & Buss (1970) demonstrated that the Kibale elephants spent more time and used the woody vegetation more in *Acanthus*–grass–scrub and colonizing forest habitats than expected based on proportional representation of these habitats in Kibale. A detailed analysis of habitat features led them to conclude that utilization by elephants was likely to be greatest in habitats with the following attributes: the understorey herbaceous vegetation is prominent or dominant, the stocking of overstorey trees is light (i.e. open canopy), predominant tree size is small, the area of ground shaded by trees is <75%, soil drainage is poor and slope of land is flat to moderate (20–30°). It seems apparent to us that the critical variable here is the abundance of understorey herbaceous vegetation because it comprises elephant browse. All of the other variables, with the possible exception of slope, obviously enhance proliferation of the herbaceous understorey.

Twenty years later after a major decline (approximately 40–80%) in elephant densities due to poaching and, in a much smaller sample, Nummelin (1990) reached a similar conclusion to that of Wing & Buss (1970). He found 6.3 times more elephant dung in heavily logged forest (K15) than in the near-by unlogged forest (K30). Lightly logged forest (K14) had similar amounts of dung to the unlogged forest. This greater visitation rate by elephants can likewise be related to denser ground vegetation in the heavily logged than unlogged forest (Basuta & Kasenene 1987; Kasenene 1980, 1984, 1987; Lwanga 1994).

Kasenene (1987) found that the frequency of elephant visits and the number of forest gaps used by them was significantly greater in both heavily and lightly logged forest than in the unlogged control. Gaps were largest in the heavily logged forest, intermediate in lightly logged, and smallest in unlogged forest. The extent of ground-vegetation cover was strongly correlated with gap size, being greatest in heavily logged, and least in the control forest (Kasenene 1987).

Selective browsing by elephants and size class of trees

Wing & Buss (1970) sampled all size classes of woody plants (N = 118,618) along line transects throughout Kibale and found that 20.8% of all the stems examined had been damaged by elephants. Approximately 75% of all woody stems used by elephants were <2.5 cm dbh and 97.5% were <10.2 cm dbh (representing approximately 13.7% of all stems <10.2 cm dbh, Table 16 in Wing & Buss 1970). Lwanga's (1994) data are consistent with these results. He found that 25% of all saplings and poles (>1–<14 cm dbh) along fresh elephant paths were damaged. Lwanga's slightly higher figure may be due to his much smaller sample and the fact that he sampled along elephant browsing paths rather than uniformly spaced line transects.

Elephants browsed woody stems 1.3 to <2.5 cm dbh significantly more than expected and woody stems >2.5 to 122 cm dbh significantly less than expected. There was no significant selectivity for or avoidance of larger size classes (Wing & Buss 1970).

The data and analysis by Wing & Buss (1970) clearly demonstrate that in rainforests the greatest impact of elephants on woody vegetation and forest dynamics is on the smaller and usually younger plants. We would add to this the observation that elephant damage to larger trees (>30 cm dbh) is usually in the form of bark damage which exposes the wood to attack by beetles and fungi. Trees with this type of damage often, if not usually, live and reproduce many years (>30) after the initial damage is inflicted (also see Short 1981). For example, in Kibale no correlation was found between mortality rates and incidence and extent of elephant-caused bark damage among adult trees of five upper canopy species (Struhsaker *et al.* 1989). Furthermore, the recruitment of saplings into the pole size class was extremely poor for many canopy tree species as indicated by the very low population densities of poles (7–14 cm dbh) (Struhsaker *et al.* 1989). Based on this information, we focus our attention on the impact of elephants on the smaller size classes of trees.

Most of the elephant damage to trees has been classified as breakage (97.3% of total utilization, Wing & Buss 1970), eating terminal twigs and leaf stripping (86%, Short 1981) or snapping (86.2%, Lwanga 1994). This type of damage is usually not fatal, but it probably affects the subsequent growth rate and form of the tree, which could be of considerable significance to the timber industry. As Laws *et al.* (1975) emphasize, removal of the lead stem by elephants probably suppresses growth in young trees and, we would add, this may partly explain the poor recruitment into the pole size class. The end result is suppressed forest regeneration with all of its implications for species composition and community ecology.

Density of tree saplings and poles in logged vs *unlogged forest*

Kasenene (1987) found that the density of tree saplings (>5 cm dbh) and poles (<13 cm dbh) (all species combined) were both inversely related to the intensity of logging ($P < 0.0001$ for both size classes in four compartments:

Table 2. Differences (Mann–Whitney U-test) in number of *Mimusops bagshawei* and *Strombosia scheffleri* stems (dbh ≥2.5 cm and < 10 cm) per 250 m^2 plot among mature (K30), logged (K15) and logged-and-poisoned (K13) forest compartments of the Kibale Forest, Uganda (from Lwanga 1994).

Species	Forest type	Number of stems/ plot ±SD	Number of plots	z	P
Mimusops	Logged	0.042 ±0.202	213		
bagshawei	Mature	0.278 ±0.623	194	−5.13	<0.0001
	Logged + poisoned	0.010 ±0.098	105		
	Mature	0.278 ±0.623	194	−4.71	<0.0001
	Logged + poisoned	0.010 ±0.098	105		
	Logged	0.042 ±0.202	213	−1.57	0.11
Strombosia	Logged	0.338 ±0.905	213		
scheffleri	Mature	0.433 ±0.904	194	−1.83	0.07
	Logged + poisoned	0.533 ±0.019	105		
	Mature	0.433 ±0.904	194	−0.88	0.38
	Logged + poisoned	0.533 ±0.019	105		
	Logged	0.338 ±0.905	213	−2.47	0.01

K13, 14, 15, 30, see Table 1). The heavily logged and poisoned compartment had the lowest sapling and pole densities, being only 25–33% that of the unlogged forest. Even the lightly logged forest had significantly lower densities of saplings and poles than the unlogged control (Kasenene 1987).

Using line-transect sampling, Lwanga (1994), in a detailed study of two upper canopy tree species, found differences in the densities of saplings and poles (>2.5 to <10 cm dbh) between the heavily logged and unlogged compartments (Table 2). Densities of young *Mimusops bagshawei* S. Moore were significantly greater in unlogged than either heavily logged (K15) or heavily logged and poisoned (K13) compartments P <0.0001, but there was no difference in densities between the two logged sites (Table 2). In contrast, the density of young *Strombosia scheffleri* Engl. was significantly less in the heavily logged (K15) compartment than in the unlogged (K30) and heavily logged/poisoned (K13) sites, which did not differ from one another (Table 2).

In a much smaller sample which consisted of enumerating saplings and poles (>1.0 to <14 cm dbh) of all species along fresh elephant paths, Lwanga (1994 and unpublished data) found 441 stems in a 0.19 ha sample of unlogged (K30) forest compared to only 161 stems in a sample of 0.19 ha in the heavily logged forest (K15).

These studies support the conclusion that the greater use of logged areas by elephants is not related to higher densities of saplings and poles. Furthermore, elephant browsing likely contributes to the lower densities of young trees in logged forest.

Elephant damage to saplings and poles in logged vs *unlogged forest*

Kasenene's (1980, 1984) data from line transects demonstrate a significantly higher incidence of elephant damage to saplings and poles (0.5 m tall to

Table 3. Differences in elephant damage to saplings and poles (0.5 m tall to ≤12.7 cm dbh) of 23 selected species in unlogged (K30) and lightly logged (K14) forest in Kibale Forest, Uganda (data from Kasenene 1980, 1984).

	Densities (numbers ha^{-1})			
	Unlogged (K30)		Lightly logged (K14)	
Species	Intact	Damaged	Intact	Damaged
Parinari excelsa	22.1	0	25.7	0.9
Celtis durandii	28.8	2.2	28.8	3.2
Celtis africana	30.4	5.0	32.3	8.4
Conopharyngia holstii	35.4	0	30.4	0.8
Cassipourea ruwensorensis	46.0	0	34.8	5.0*
Markhamia platycalyx	40.3	10.1	36.4	12.3
Strombosia scheffleri	65.5	0	101.2	13.8*
Aningeria altissima	65.5	0	41.9	6.8*
Trichilia splendida	82.1	3.7	36.2	10.7*
Leptonychia mildbraedii	93.8	0	59.3	3.1
Pancovia turbinata	103.5	1.8	27.6	2.5
Chaetacme aristata	117.7	0	126.4	2.8
Funtumia latifolia	121.3	5.3	91.4	5.1
Chrysophyllum gorungosanum	139.0	0	27.3	4.6*
Antiaris toxicaria	158.4	10.7	77.2	20.2*
Monodora myristica	175.7	14.7	57.0	6.8
Mimusops bagshawei	214.2	0	89.3	11.6*
Lovoa swynnertonii	232.0	6.9	94.0	7.1
Newtonia buchananii	301.1	14.9	174.3	33.7*
Diospyros abyssinica	289.1	32.1	228.0	14.6
Bosqueia phoberos	311.7	21.0	48.1	15.6*
Symphonia globulifera	529.2	0	81.7	7.7*
Teclea nobilis	639.3	3.2	608.4	20.8*

* = Significant G-test, $P \leq 0.05$ (critical $\chi^2 = 3.841$), df = 1. When $N < 200$, Yate's correction for continuity applied; when $N > 200$, Williams's correction applied.

<12.7 cm dbh) of 23 tree species in lightly logged than unlogged forest (9.2% *vs* 3.3%; $\chi^2 = 97.2$, df = 1, $P < 0.001$). His transects covered a total of 1.35 ha from six plots in unlogged (K30) and 1.13 ha from five plots in logged (K14) forest. We analysed this same data set by species and found that significantly more saplings and poles were damaged among 11 of the 23 species in the lightly logged than in the unlogged forest (Table 3, all plant names from Eggeling & Dale 1952 and Hamilton 1981). No species had more damaged individuals in the unlogged than in the lightly logged forest.

Comparing the densities of undamaged (normal) and broken (coppicing and stem sprouts) stems of saplings and poles in the gaps of the four study compartments in Kibale, Kasenene (1987) found highly significant differences. Undamaged saplings and poles were most abundant in gaps of unlogged forest and decreased in density with increasing intensity of logging (Figure 1). Conversely, the percentage of damaged stems varied directly with the intensity of logging, being greatest in the heavily logged and poisoned compartment (93%) and lowest in the unlogged forest (58%). Although some of this damage may have

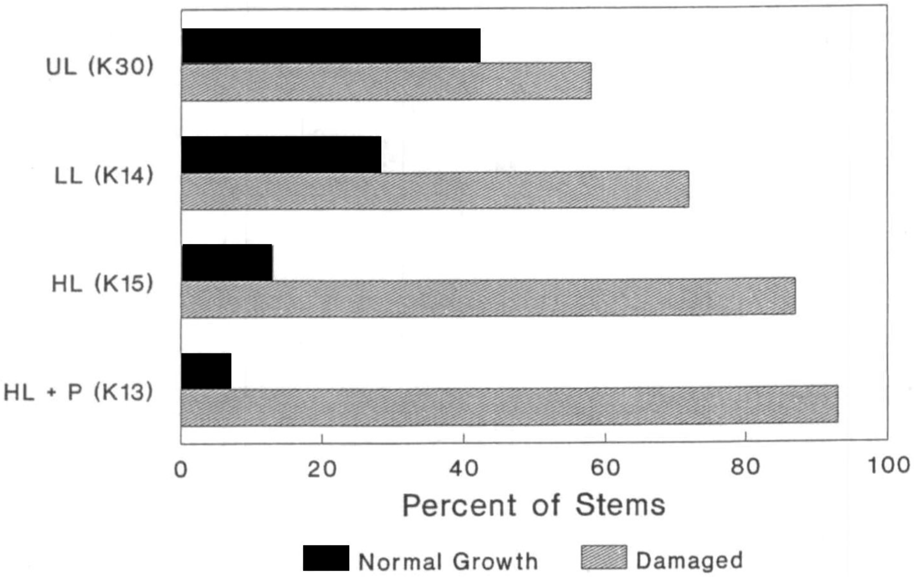

Figure 1. The percentage of saplings and poles (>1.5–10 cm dbh) of canopy tree species in forest gaps that were damaged (coppicing or sprouting from a broken stem) apparently by elephants increased with the intensity of logging in Kibale. UL = unlogged mature forest, LL = lightly logged, HL = heavily logged and LP + P = heavily logged followed by poisoning (adapted from Kasenene 1987).

been due to factors other than elephants (e.g. windfalls), the pronounced dissimilarity in damage between species suggested that the majority of the differences in damage between forest compartments was due to contrasts in elephant use. Direct damage from the logging operation itself is discounted because the studies were done 16–18 years after logging.

Differences between plots in gaps and closed canopy indicate that elephants selectively browsed in forest gaps rather than in closed-canopy forest. The percentage of damaged saplings and poles was at least 6–10 times greater in gaps than in the closed-canopy forest (Kasenene 1987).

In line-transect samples, Lwanga (1994) found significantly greater elephant damage to the saplings and poles of *Mimusops* and *Strombosia* in heavily logged and heavily logged plus poisoned compartments than in the unlogged control (Table 4). In contrast, when Lwanga (1994 and unpublished data) sampled saplings and poles (>1.0 to <14 cm dbh) of all species along fresh elephant paths, he found a higher percentage (28.1% in K30) were damaged in the unlogged than the heavily logged (17.4% in K15) forest. Our analysis of these data showed that these differences were significant whether all species were compared ($\chi^2 = 6.63$, df = 1, $P = 0.01$) or only those 11 species with selection ratios of >1.19 and common to the samples from both compartments ($\chi^2 = 5.56$, df = 1, $P < 0.025$). However, when only *Mimusops* and *Strombosia* were compared, the two sampling methods indicated similar trends. A greater percentage was damaged in the logged than unlogged sample; 100% *vs* 81% for

Table 4. Differences in numbers of *Mimusops bagshawei* and *Strombosia scheffleri* stems that were damaged (snapped, bent or pushed over) among mature (K30), logged (K15) and logged-and-poisoned (K13) forest compartments of Kibale Forest, Uganda (same data set as Table 2). Figures in parentheses are the expected values (from Lwanga 1994).

Species and size class	Forest type	Number of damaged stems	Number of intact stems	χ^2 (df = 1)	P
Mimusops bagshawei	Mature	16 (20.6)	38 (33.4)		
(dbh ≥2.5–10 cm)	Logged	8 (3.4)	1 (5.6)	4.573	<0.05
Minusops bagshawei	Mature	0	13		
(dbh ≥10 cm)	Logged	1	0		
Strombosia scheffleri	Mature	11 (27.6)	75 (58.4)		
(dbh ≥2.5–10 cm)	Logged	40 (23.4)	33 (49.6)	31.15	<0.001
	Mature	11 (29.3)	75 (56.7)		
	Logged + poisoned	36 (17.7)	16 (34.3)	44.39	<0.001
	Logged	40 (44.4)	33 (28.6)		
Strombosia scheffleri	Logged + poisoned	36 (31.6)	16 (20.4)	2.11	>0.1
(dbh ≥10 cm)	Mature	0 (3.1)	71 (67.9)		
	Logged	4 (0.9)	16 (19.1)	8.316	<0.01
	Mature	0 (2.3)	71 (68.7)		
	Logged + poisoned	3 (6.7)	18 (20.3)	5.15	<0.05
	Logged	4 (3.4)	16 (16.6)		
	Logged + poisoned	3 (3.6)	18 (17.4)	0.005	>0.1

Mimusops and 100% *vs* 66.7% for *Strombosia*. Note that these percentages are much higher than those in Table 4.

Although some of these differences may be due to sample size, the comparison indicates the importance of sampling method, particularly the spatial array, in examining the impact of elephant browsing; random or systematic *vs* elephant selected. For example, of the 11 species common to the elephant-path samples from both compartments, those having selection ratios of >1.19 were 2.6 times more abundant in the unlogged (118 stems) than the logged (46) sample. This suggests that the elephants were selectively using parts of the unlogged forest, seeking out those areas with higher densities of preferred tree species.

Selective browsing by elephants

The extensive and detailed study by Wing & Buss (1970) clearly established that the Kibale elephants are very selective browsers. Of the 250 woody species enumerated in their study, 108 were browsed significantly more than expected, 91 as expected and 51 species were browsed less than expected. Similarly, Laws *et al.* (1975) demonstrated selective browsing by elephants in the Budongo Forest of Uganda.

Selection ratios were computed for 23 tree species from the line-transect data of Kasenene (1980, 1984; Table 5). The selection ratio for a species is the quotient of the proportional contribution of that species to the total number of browsed plants divided by its proportional contribution to the total number of plants enumerated. A ratio greater than one indicates the species was selectively

Table 5. Elephant damage to tree saplings and poles in Kibale Forest, Uganda (line-transect data from Kasenene 1980, 1984).

	Unlogged			Lightly logged		
Species	% of total K30	% of all damaged K30	Selection ratios % of damaged/ % of total K30	% of total K14	% of all damaged K14	Selection ratios % of damaged/ % of total K14
Parinari excelsa	0.6	0.0	0.000	1.1	0.4	0.382
Celtis durandii	0.8	1.7	2.146	1.3	1.5	1.090
Celtis africana	0.9	3.8	4.292*	1.7	3.8	2.246*
Conopharyngia holstii	0.9	0.0	0.000	1.3	0.4	0.273
Cassipourea ruwensorensis	1.2	0.0	0.000	1.7	2.3	1.363
Markhamia platycalyx	1.3	7.7	6.044*	2.1	5.6	2.748*
Strombosia scheffleri	1.6	0.0	0.000	4.8	6.3	1.308
Aningeria altissima	1.6	0.0	0.000	2.1	3.1	1.527
Trichilia splendida	2.2	2.8	1.300	2.0	4.9	2.486*
Leptonychia mildbraedii	2.4	0.0	0.000	2.6	1.4	0.534
Pancovia turbinata	2.7	1.4	0.514	1.3	1.2	0.916
Chaetacme aristata	3.0	0.0	0.000*	5.4	1.3	0.240*
Funtumia latifolia	3.2	4.0	1.269	4.1	2.3	0.578
Chrysophyllum gorungosanum	3.5	0.0	0.000*	1.3	2.1	1.559
Antiaris toxicaria	4.3	8.1	1.904*	4.1	9.3	2.257*
Monodora myristica	4.8	11.1	2.327*	2.7	3.1	1.156
Mimusops bagshawei	5.4	0.0	0.000*	4.2	5.3	1.254
Lovoa swynnertonii	6.0	5.3	0.876	4.3	3.2	0.763
Newtonia buchananii	8.0	11.3	1.420	8.8	15.5	1.766*
Diospyros abyssinica	8.1	24.4	3.022*	10.2	6.7	0.654
Bosqueia phoberos	8.4	15.9	1.904*	2.7	7.2	2.672*
Symphonia globulifera	13.3	0.0	0.000*	3.8	3.5	0.938
Teclea nobilis	16.2	2.4	0.151*	26.5	9.5	0.360*
Totals (N. ha^{-1})	3973	132		2376	218	

* = Significant χ^2, $P < 0.05$, df = 1. Expected values of damaged and undamaged trees (based on total proportions for all 23 species combined) were compared to observed values.

browsed, whereas a ratio less than one indicates it was avoided (Crawley 1983).

In the unlogged (K30) forest, six of the 23 species were selectively browsed, whereas five species were avoided (i.e. selection ratios significantly different from unity, Table 5). The lightly logged (K14) forest also had six species that were selectively browsed, but only two species that were avoided. Nine species had similar significant selection ratios or trends in both logged and unlogged forest; selected for: *Celtis africana*, *Markhamia*, *Trichilia*, *Antiaris*, *Monodora*, *Newtonia* and *Bosqueia*; avoided: *Chaetacme* and *Teclea*. In contrast, at least four species had different trends in selection ratios between the two compartments: *Chrysophyllum*, *Mimusops*, *Diospyros* and *Symphonia* (Table 5). Thus, although more young trees were damaged by elephants in lightly logged forest (Table 3), elephant selectively in feeding was similar, if not slightly greater, in the unlogged forest (Table 5).

Browse selection ratios were also computed for saplings and poles enumerated along fresh elephant trails in unlogged and heavily logged forest (Lwanga 1994 and unpublished data, Table 6). The differences in selection ratios between forest compartments along fresh elephant paths were even less apparent than in the line-transect data of Kasenene. In Lwanga's sample, six species were selectively damaged by elephants and six species avoided in the unlogged forest (i.e. selection ratios significantly different from one, Table 6). Only four species in the heavily logged forest (K15) had significant selection ratios. The relatively low number of species with significant selection ratios in K15 was probably due to the much smaller sample size there than in unlogged K30. Although 0.19 ha were sampled in both forest compartments, there were 2.7 times more saplings and poles in unlogged K30 (N = 441) than the heavily logged K15 (N = 161). The four species selectively browsed in K15 were also selectively browsed in the unlogged forest (Table 6). Trends in selection ratios were similar for most other species sampled in both compartments. These data support the earlier conclusion that, although cumulative elephant damage to young trees was greater in heavily logged than unlogged forest, selective browsing was similar between these compartments.

Consistency in the selection ratios derived from these two sampling methods varied between species. For example, *Antiaris* was selectively browsed in both studies, whereas *Teclea* and *Chaetacme* were avoided. In contrast, selection ratios for at least five species were inconsistent between the two studies. *Mimusops* and *Strombosia* were selectively browsed on elephant paths, but either avoided or browsed as expected on the line transects. *Newtonia* was selectively browsed on paths and in logged areas regardless of sample method, but not selected for in the K30 line-transect data. *Celtis africana* was browsed as expected on elephant paths, but selected for on the transects. Perhaps the greatest discrepancy between methods was that found for *Diospyros*, which was strongly avoided in the path sample, but strongly selected for in the transect data for K30.

Table 6. Selection ratios of elephant damage to saplings and poles (≥1.0–<14 cm dbh) along recently used elephant paths in unlogged (K30) and heavily logged (K15) parts of Kibale Forest, Uganda (data from Lwanga, unpublished). Numbers of stems enumerated (N) are in parenthesis.

Only species occurring in the samples of both K30 and K15 are considered here. In the entire sample, there were ≥50 species in K30 and 40 species in K15.

Species	Selection ratios and (N)	
	Unlogged (K30)	Heavily logged (K15)
Chrysophyllum gorungosanum	0.89 (4)	5.75 (1)(*)
Mimusops bagshawei	2.88 (21)*	5.75 (2)(*)
Newtonia buchananii	3.56 (17)*	5.75 (3)*
Strombosia scheffleri	2.37 (12)*	5.75 (2)(*)
Ficus exasperata	3.56 (2)*	4.31 (4)*
Antiaris toxicaria	3.11 (24)*	3.83 (3)*
Blighia unijugata	3.11 (8)*	2.88 (12)*
Celtis africana	0.51 (7)	1.92 (6)
Ficus urceolaris (*asperifoolia*)	1.78 (12)	1.44 (8)
Teclea nobilis	0.26 (41)*	0 (9)
Markhamia platycalyx	1.19 (6)	0 (3)
Trichilia splendida	1.42 (5)	0 (2)
Chaetacme aristata	0.51 (7)	0 (6)
Vangueria apiculata	0.89 (4)	0 (3)
Conopharyngia holstii	0.97 (11)	0 (5)
Dasylepis eggelingii	0.2 (18)*	0 (2)

The following species were encountered along elephant paths in the samples of both K30 and K15, but were not damaged. Numbers indicate stems enumerated, first for K30 then K15: *Diospyros* (11)* (7), *Cassipourea* (11)* (5), *Oncoba spinosa* (10)* (4), *Celtis d.* (5) (8), *Clausena anisata* (3) (3), *Randia urcelliformes* (4) (3), *Millettia dura* (1) (4), *Psychotria* sp. (5) (13), *Fagaropsis angolensis* (5) (6), *Coffea eugenioides* (1) (3), *Uvariopsis congensis* (7) (7), *Kigelia moosa* (5) (5), *Monodora* (4) (1), *Linociera johnsonii* (5) (2), *Pleiocarpa pyenantha* (7) (2), *Randia malleifera* (21)* (4), *Myrianthus arboreus* (4) (3), *Premna angolensis* (1) (1).

* = Significant χ^2, $P < 0.05$, df = 1. Expected value of damaged and undamaged trees (based on total proportions for all species combined) were compared to observed values.

(*) = Sample too small (see Everitt 1977).

Several factors may account for these differences in results between the two methods. First, the sample was much smaller along the elephant paths (N = 602 stems, Lwanga 1994) than the line transects (N = 7174; Kasenene 1980, 1984). Secondly, the spatial array of the samples were very different; Kasenene's more closely approached a uniform or random sample and Lwanga's was determined by the elephants and followed their foraging paths. Thirdly, there were temporal differences; Lwanga was recording on average much more recent signs of browsing than Kasenene. Fourthly, the logging damage was much greater in Lwanga's sample area (K15) than Kasenene's (K14). Finally, there was a 14-year interval between their studies.

Selection ratios were also computed from the data of Wing & Buss (1970, their Appendix IV, Table 1) for comparison with those computed for Kasenene's and Lwanga's data. Here there are even greater differences in sample size and spatial distribution. Wing & Buss (1970) had an enormous sample over

Table 7. Under canopy tree species with high selection ratios reported from three separate studies in the Kibale Forest, Uganda.

	1962–1964	1978–1979		1993	
Species	Forest-wide[1]	Unlogged (K30)	Lightly logged (K14)[2]	Unlogged (K30)	Heavily logged (K15)[3]
Antiaris toxicaria	2.85	1.90	2.26	3.11	3.83
Blighia unijugata	2.80	n/a	n/a	3.11	2.88
Bosqueia phoberos	2.95	1.90	2.67	2.72	n/s
Celtis africana	3.42	4.29	2.25	0.51	1.92
Ficus exasperata	0.96	n/a	n/a	3.56	4.31
Funtumia latifolia	1.65	1.27	0.58	0.26	n/s
Lovoa swynnertonii	2.85	0.88	0.76	3.56	n/s
Mimusops bagshawei	3.21	0	1.25	2.88	5.75
Monodora myristica	1.69	2.33	1.16	0	0
Newtonia buchananii	2.12	1.42	1.77	3.56	5.75
Parinari excelsa	1.17	0	0.38	n/s	5.75
Strombosia scheffleri	2.66	0	1.31	2.37	5.75
Trichilia splendida	2.20	1.30	2.49	1.42	0

[1] Wing & Buss (1970). All woody plants >1.8 m tall or >1.27 cm diam. at ground level. Largest sample of three studies.

[2] Kasenene (1980, 1984). Twenty-three selected species, 0.5 m tall to ≤12.7 cm dbh.

[3] Lwanga (1994). All woody plants ≥1.0–<14 cm dbh. Smallest sample of three studies and along fresh elephant paths.

n/a = data not available.
n/s = none in sample.

the entire forest collected during a time when elephant numbers were very much greater. In spite of major differences in sampling, a comparison was made of these three studies to see if any patterns might emerge over the 30-year period. Selection ratios were compared for 13 upper canopy tree species with high ratios that occurred in at least two of the studies (Table 7). Three species (*Antiaris*, *Bosqueia* and *Newtonia*) had high selection ratios in all three studies and all five samples. Three others (*Celtis africana*, *Strombosia* and *Trichilia*) had high ratios in four of the five samples. Two more (*Blighia* and *Ficus exasperata*) were high in all but one of the samples where they occurred or were reported. The remaining five to six species had striking inconsistencies between the samples. It would appear that elephant selectivity is sufficiently strong for saplings and poles of some tree species as to be obvious regardless of the sampling methods. It may be significant that three of the eight species with typically high selection ratios are Moraceae.

Density-dependent browsing by elephants

Studies of the relationship between elephant damage and density of the trees being fed upon demonstrate interspecific variation in woodlands of east Africa. At least four patterns appeared to occur, depending on the species concerned (Barnes 1983). The proportion of trees killed: (1) increased with tree density; (2) decreased with tree density; (3) was independent of tree density; or (4) a fixed number of trees was killed per elephant regardless of tree or elephant density (Barnes 1980, 1983; Western & Van Praet 1973).

We analysed data in Wing & Buss (1970, their Tables 2 & 17 and Figure 15) and found no correlation between the abundance of woody stems (area times density) in nine different habitat types and use of the habitat type by elephants as measured either by dung counts or incidence of damage to woody stems (Spearman's rank correlation, $r_s = -0.17$ in both tests). This indicates that damage is not associated with overall density of woody stems (regardless of species) and, together with the negative r_s, supports the idea that elephants often selectively browse areas with abundant herbaceous tangle and relatively low densities of woody stems.

We examined Kibale data of Kasenene (1980, 1984) for density-dependent damage to saplings and poles (0.5 m tall to <12.7 cm dbh) of all species combined. A regression of stem density against percentage of stems damaged (arcsin transformation) for 23 species revealed no significant relationship ($P > 0.05$) in either the unlogged (K30) ($F_s = 0.2$, regression coefficient = -0.0016) or lightly logged (K14) ($F_s = 2.15$, regression coefficient = -0.0159) forest. The negative regression coefficient suggests an inverse relationship between elephant damage and sapling/pole density, particularly in the logged area, but it was not significant, probably because of large differences between species.

Density-dependent elephant damage for individual species cannot be examined in the conventional manner for the studies by Kasenene and Lwanga because their samples were combined and expressed as only two plots (logged *vs* unlogged). However, an indication of density-dependent relationships can be gained by plotting the differences in total tree densities against differences in densities of damaged trees (saplings and poles) between the logged and unlogged study plots (Figures 2 and 3). Species in the upper left quadrat of these figures had more damage and lower densities in the logged than unlogged forest, whereas those in the lower left quadrat had less damage and lower densities in the logged than unlogged forest, etc.

Both studies indicate major differences between species. Equally striking are the apparent differences between the studies. Kasenene's data indicate inverse density-dependent damage for most species, while Lwanga's data suggest that for most species damage is positively related to density. Three species clearly show opposite patterns between the two studies. Damage to *Newtonia*, *Mimusops* and *Antiaris* is positively related to density in Lwanga's study (Figure 3), but inversely related in Kasenene's (Figure 2). For *Teclea*, damage appears to be independent of density in Lwanga's results, but inversely related to density in Kasenene's, while *Strombosia* damage was positively density dependent in both studies. Some of the difficulties in comparing these two studies have been discussed earlier, but these differences do emphasize the potential importance of methodology in understanding density-dependent elephant damage.

Lwanga's (1994) detailed study of two upper canopy species provides additional insight into the issue of density-dependent elephant damage. In the case

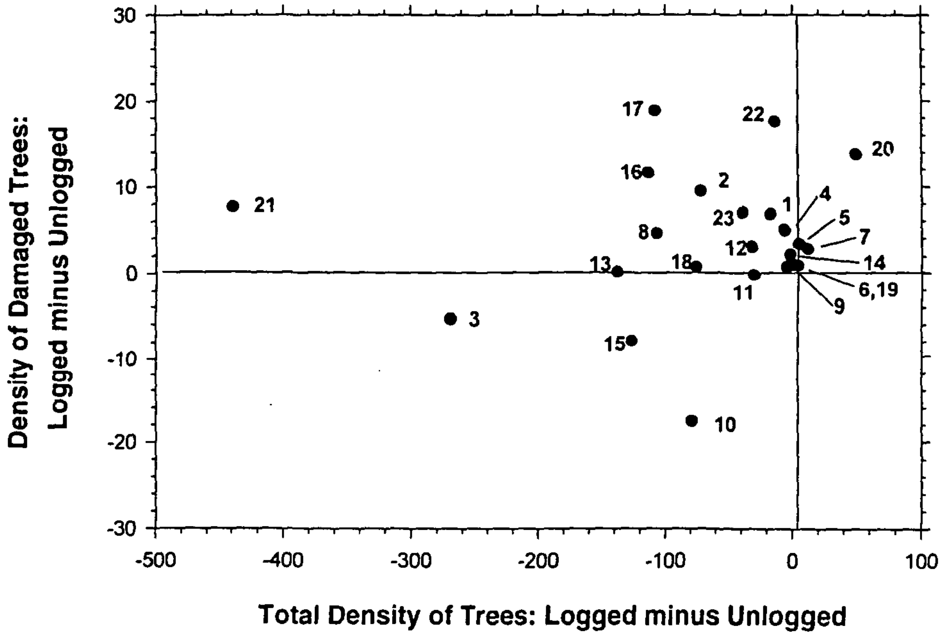

Figure 2. Indices of density-dependent elephant damage to saplings and poles (0.5 m tall to <12.7 cm dbh) along pre-established and uniformly spaced transects indicate inverse density dependence when samples (individuals ha^{-1}) from unlogged (K30) and lightly logged (K14) forest were compared (see text) (adapted from Kasenene 1980, 1984). 1: *Aningeria*, 2: *Antiaris*, 3: *Bosqueia*, 4: *Cassipourea*, 5: *Celtis a.*, 6: *Celtis d.*, 7: *Chaetacme*, 8: *Chrysophyllum gorungosanum*, 9: *Conopharyngia*, 10: *Diospyros*, 11: *Funtumia*, 12: *Leptonychia*, 13: *Lovoa*, 14: *Markhamia*, 15: *Monodora*, 16: *Mimusops*, 17: *Newtonia*, 18: *Pancovia*, 19: *Parinari*, 20: *Strombosia*, 21: *Symphonia*, 22: *Teclea*, 23: *Trichilia*. (Table 3 gives the full names.)

of *Mimusops*, the data indicated inverse density dependence because there was greater elephant damage to saplings and poles in the heavily logged forest (K15), which had lower densities of *Mimusops* than the unlogged (K30, Tables 2 and 4). In contrast, data for *Strombosia* indicated density independence. There were higher densities of *Strombosia* saplings and poles in both the unlogged (mature, K30) and heavily logged and poisoned (K13) than in the heavily logged (K15) compartment. However, in spite of significant differences in density, elephant damage was equally high in both logged compartments (K13 and K15) and higher than in the unlogged (K30) forest (Tables 2 and 4). In other words, elephant damage to young *Strombosia* trees was significantly greater in the heavily logged areas than the unlogged, mature forest regardless of density.

All of the data presented in this section support the hypothesis that elephants are using the logged parts of the forest more heavily than the unlogged forest for reasons other than densities of young trees. The higher damage by elephants to young trees in logged forest cannot be related to higher densities of these young trees compared to unlogged, mature forest. We suggest that the greater use of logged forest by elephants overrides the effect of any density-dependent relationships between browse damage and density of young trees.

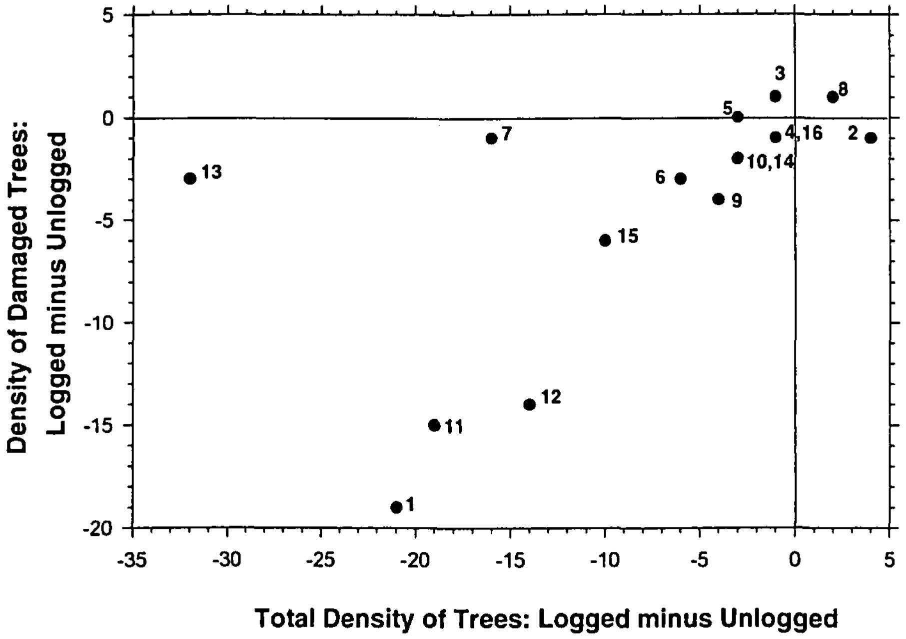

Figure 3. Indices of density-dependent elephant damage to saplings and poles (>1 to <14 cm dbh) along fresh elephant browsing paths indicate positive density dependence for most species when samples (individuals ha^{-1}) from unlogged (K30) and heaviy logged (K15) forest are compared (see text) (from Lwanga 1994 and unpublished data). 1: *Antiaris*, 2: *Blighia*, 3: *Celtis a.*, 4: *Chaetacme*, 5: *Chrysophyllum g.*, 6: *Conopharyngia*, 7: *Dasylepis*, 8: *Ficus exasperata*, 9: *Ficus asperifolia*, 10: *Markhamia*, 11: *Mimusops*, 12: *Newtonia*, 13: *Teclea*, 14: *Trichilia*, 15: *Strombosia*, 16: *Vangueria*. (Table 3 gives the full names.)

DISCUSSION AND CONCLUSIONS

It has been concluded that the excessive damage caused by mechanized logging in Kibale sets off a chain of ecological events that ultimately result in hindrance, if not complete suppression, of natural forest regeneration (Struhsaker 1987). In parts of Kibale there has been little, if any, forest regeneration 25 years after logging. Elephants have been considered to be of major importance in this process. The data we present here add support to this conclusion and help to refine our understanding of the process.

Intensive logging creates large gaps and opens the forest canopy (e.g. Kasenene 1987) (Figure 4). This changes the microclimate on the forest floor and enhances the growth of a herbaceous and semi-woody tangle (Kasenene 1987). Elephants are, in turn, attracted to this tangle as a food source. This conclusion is supported by the data showing a positive correlation between elephant use of an area and the density of vegetative ground cover and a negative correlation between use and density of young trees. The fact that elephant damage to young trees is higher in heavily logged than unlogged forest demonstrates that elephant browsing pressure depends not only on species selectivity and perhaps density, but on the landscape and plant-community composition (i.e. digestibility) as a whole.

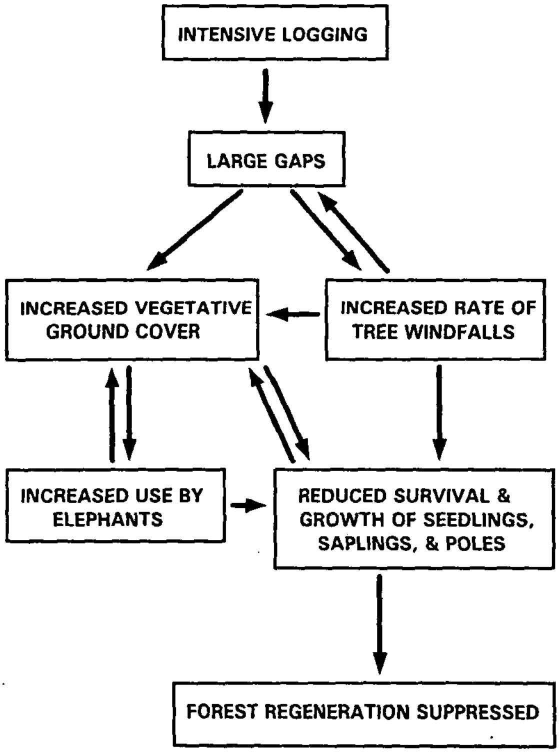

Figure 4. Impact of intensive, selective logging on vegetation, elephants and forest regeneration.

Having been attracted to the logged forest by the higher concentrations of herbaceous tangle resulting from the logging operation, the elephants both directly and indirectly cause increased damage and mortality to young trees. This, in turn, decreases the density of young trees and perpetuates the preponderance of the herbaceous tangle.

An important point to emphasize is that the herbaceous tangle associated with heavy logging also appears to suppress tree regeneration by direct competition with seedlings and saplings, and not only by attracting elephants (Kasenene 1987). Rodents are predators of seeds and seedlings and typically their numbers are directly correlated with dense ground vegetation cover (Basuta & Kasenene 1987, Lwanga 1994). Usually, rodent population densities were higher in logged than unlogged forest in Kibale (Basuta 1979, Basuta & Kasenene 1987; Kasenene 1980, 1984; Muganga 1989), but exceptions have been documented (Lwanga 1994). The very open canopy of the heavily logged forest not only enhances the development of herbaceous tangle, but results in an increased incidence of windthrown or windsnapped trees (Kasenene & Murphy 1991, Skorupa & Kasenene 1984). This, in turn, perpetuates canopy openness and tangle formation. The open conditions created by heavy logging also change the microclimate, which may adversely affect survival of seedlings and saplings of some species through higher and more variable temperatures and desiccation.

Thus, although the development of a dense and extensive herbaceous tangle is initiated by heavy logging, its perpetuation is enhanced by elephant browsing and windfalls. The competitive and suppressive action of the tangle and elephant browsing act to prevent forest regeneration. Furthermore, although seed and seedling predation by rodents and insects plays an important role in regeneration, levels of predation on these stages are generally very high throughout the forest. The most striking and measurable difference between heavily logged and unlogged forest are the lower densities of young trees and the higher incidence of elephant damage to them in heavily logged forest (e.g. Lwanga 1994).

The combination of intense and selective browsing of young trees by elephants in the heavily logged forest not only appears to reduce tree density and affects the physical form of the trees which survive, but also shapes the tree-species composition of the post-logging habitat.

Much of the ecological research on African elephants living in rainforests has concentrated on their role as frugivores and seed dispersers (e.g. Alexandre 1978, Merz 1981, Short 1981, White 1994, White *et al.* 1993). Certainly, elephants play a very important role in this regard, particularly for some species, such as *Balanites wilsoniana*, for which they may be the only seed dispersers (e.g. Chapman *et al.* 1992, Struhsaker 1987). However, the work summarized here, as well as in Laws *et al.* (1975), suggest to us that the greatest impact of elephants on rainforest dynamics and structure is in terms of their browsing on tree saplings and poles. The studies in Kibale clearly indicate that this aspect of elephant ecology will become increasingly important as human activities, such as logging, shifting agriculture and forest removal increase in pace with Africa's human population growth (3–4%y^{-1}).

Recommendations for logging practices

The studies summarized here have implications for the management of logging. In the past, killing elephants was the recommended method for dealing with their impact on post-logging forest regeneration (e.g. Laws *et al.* 1975). Laws *et al.* (1975) went so far as to conclude that: 'The presence of elephant is thus incompatible with economic timber production.' Ironically, these same authors point out that despite the extensive killing of elephants (about 600 per year in one administrative district alone during 1961–1968) and an overall estimated reduction of the elephant population by 64% in the same area between 1946 and 1971, there was still a problem of forest regeneration in logged areas. Furthermore, it was estimated that from 1971 to 1980 elephants were reduced by 90% in Uganda (Douglas-Hamilton 1983) and by 80% in Kibale alone (Nummelin 1990), yet heavily logged forests still had poor regeneration.

The studies on post-logging regeneration support the conclusion that when logging was heavy (>25% basal area removal), forest regeneration was greatly hindered and may be suspended. In more lightly logged forests (<25% basal area removal), forest regeneration was better and elephant damage was much less. Even in the absence of elephants, heavy logging impedes forest regeneration.

Contrary to previous management recommendations, we suggest that, rather than focus on removing elephants, attention be given to logging methods which mimimize their impact on the forest ecosystem and mimic natural forest dynamics. This ecological approach to management of natural forests essentially eliminates or at least greatly reduces and simplifies post-harvest management, thereby reducing costs, while at the same time achieving natural forest regeneration and conserving wildlife of old-growth forest. The perspective of this type of management is conservative and long term.

Specific recommendations include the following: (1) reduce logging offtake and incidental damage such that the resulting canopy opening is well below 20% (5–10% would be safer); (2) avoid creating forest gaps >300 m^2, i.e. prohibit cutting of adjacent trees and encourage directional felling, thereby avoiding multiple-tree gaps; (3) gaps created by felling should be spaced as far apart as possible (>50 m); (4) increase minimum felling size class to >100 cm dbh; (5) mimic natural forest dynamics (i.e. a natural treefall rate of 1–2%y^{-1}), which means a conservative harvest rate of about one mature tree (>100 cm dbh) per ha per 100y; (6) use low-impact harvest techniques to reduce incidental damage such as from logging roads and skid tracks, e.g. pitsawing (Struhsaker 1987).

Recommendations for future research

Our understanding of the relation between logging practices, elephant browsing and forest regeneration would be improved, as would our ability to develop more appropriate management practices by the following: (1) more studies of the problem in a greater number of sites – the problem here is finding control plots because most forests in east and west Africa have already been logged to some degree; (2) long-term monitoring of specific plots to evaluate long-term effects of elephant damage on growth and survival of young trees and to better understand the effect of time on detectability of elephant damage; (3) more replicates with finer-grain analysis to better understand ecological variables affecting elephant use of an area and damage to young trees, including intensity of logging and incidental damage, density of young trees and proximity to other resources such as large gaps, water holes, swamps, large areas of herbaceous tangle, old-growth forest, etc.; (4) establish elephant exclosure plots to better understand the relative role of elephants in forest regeneration compared to other factors, such as competition from herbaceous tangle and seed and seedling predation by rodents and insects; and (5) conduct similar research in the rainforests of south-east Asia where logging intensity is usually much greater than in Africa and where the majority of research on elephant ecology has been done in the dry forests of Sri Lanka (e.g. Ishwaran 1983, Mueller-Dombois 1972) and India (e.g. Sukumar 1989).

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