Forest Tree Persistence, Elephants, and Stem Scars[1]

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ABSTRACT

Sixteen percent of tree stems 10 cm diameter or greater recorded in seven 1 ha plots in Rabongo Forest, Uganda had stem damage attributable to elephants (*Loxodonta africana*). We propose four strategies that may help tree species persist under these conditions: repellence, resistance, tolerance and avoidance. We sought and found evidence for each strategy. Large, shade-tolerant *Cynometra alexandri* dominated basal area (often >50%) and showed severe scarring. Nearly 80 percent of stems were small pioneer species. Scarring frequency and intensity increased with stem size. Stem-size distributions declined steeply, implying a high mortality to growth rate ratio. Tree species with spiny stems or with known toxic bark defenses were unscarred. Epiphytic figs escaped damage while at small sizes. Mid-successional tree species were scarce and appeared sensitive to elephants. Savanna species were seldom scarred. Taking stem size-effects into account by using a per-stem logistic modeling approach, scarring became more probable with slower growth and with increasing species abundance, and also varied with location. Pioneer and shade-bearer guilds showed a deficit of intermediate-sized stems. Evidence that selective elephant damage is responsible for monodominant *C. alexandri* forests remains equivocal; however, elephants do influence tree diversity, forest structure, and the wider landscape.

Key words: African semi-deciduous rain forest; bark damage; Cynometra alexandri*; herbivory;* Loxodonta africana*; monodominant; species richness; succession; tolerance; Uganda.*

TREE DAMAGE CAUSED BY ELEPHANTS (*LOXODONTA AF-RICANA*) has been reported in closed canopy forests across Africa (Merz 1981, Short 1981, White *et al.* 1993, Höft & Höft 1995). Stems are broken, and bark is stripped and eaten from standing trees (Buechner & Dawkins 1961, Laws *et al.* 1975, Merz 1981, Short 1981, White *et al.* 1993, Höft & Höft 1995). The complete stripping of bark from a stem circumference (ring-barking) generally results in stem death and affects even large stems (Buechner & Dawkins 1961, Laws *et al.* 1975). Bark damage can lead to infection and stem rot (Laws *et al.* 1975). Stem damage is known to reduce mean tree lifetimes (Putz & Milton 1983, Franklin *et al.* 1987, Hennon 1995, Schoonenberg *et al.* 2003). How African forests are ultimately affected remains unclear, although there have been some suggestions.

Natural forest vegetation below 1500 m elevation on deep, well drained soils on the eastern edge of the Albertine Rift Valley, western Uganda, appears to follow a predictable successional sequence from initial forest-tree colonization of grasslands to a monodominant forest of the caesalpinoid legume tree *Cynometra alexandri* (Harris 1934, Eggeling 1947, Hart *et al.* 1989, Sheil 2003). This buttressed, dense-timbered species grows to a large size, is long-lived (Sheil *et al.* 2000), and indicates areas of older forests (Eggeling 1947). Laws *et al.* (1970, 1975) observed that although elephants damaged many tree species, *C. alexandri* trees were largely avoided. This led them to suggest that *C. alexandri*-dominance resulted from elephant pressure. Two lines of evidence provided circumstantial support to this proposition. First is that, in Uganda, *C. alexandri* forests coincide with areas of important historical elephant populations (Eggeling 1947, Langdale-Brown *et al.* 1964, Laws *et al.* 1975, Lock 1977: 404, Howard 1991). The second line of evidence relates to tree composition changes observed in some long-term tree plots in Budongo Forest that have not been visited by elephants since the 1960s. These plots include a pristine 2 ha plot of *C. alexandri* forest in which a marked increase in understory stem density and species numbers remains otherwise unexplained (Sheil & Ducey 2002, Sheil 2003); however, doubts remain. Connell (1978) suggested an alternative interpretation of Laws *et al.*'s observations: he proposed that *C. alexandri* forest develops with or without elephants—by feeding on earlier successional trees, elephants accelerate but do not direct vegetation change. Further explanation of which trees are damaged by elephants, and of how it affects them, can provide some basis for better evaluating these proposals.

Studies addressing impacts of elephants on for-

ests are challenging. For example, manipulative experiments or exclusion plots are usually impractical. Most work on elephant–forest interactions has focused on seedlings and saplings. Yet these small stems are damaged by various animals (Synnott 1975, Kasenene 1984, Tsingalia 1989, Struhsaker 1997) and often recover with little evidence of prior damage (Kruger *et al.* 1997). Our study focused on larger trees and considered stem-scarring patterns and stem-size distributions. Injuries to larger stems are, at least in East Africa, predominantly due to elephants, and leave distinct scars (Laws *et al.* 1975). We propose four general strategies that may help trees persist: repellence, resistance, tolerance, and avoidance.

REPELLENCE.—Trees differ in their appeal to elephants. How elephants select woody foods has been little studied (McCullagh 1969, Short 1981, Theuerkauf *et al.* 2000; *cf.* Jachmann 1989), but spiny, distasteful, or toxic species are likely to be repellent. Laws *et al.* (1975) implied that *C. alexandri* is repellent. *Holoptelea grandis* and *Schrebera arborea* may possess distasteful bark or exudates (Buechner & Dawkins 1961). Repellent species should display little scarring, with stem populations showing continuous regeneration and recruitment into larger classes.

RESISTANCE.—Trees differ in strength and vulnerability to injury. At the whole-tree level, larger strong-timbered species are the most likely to be resistant; however, resistant species may be prone to damage at smaller sizes.

AVOIDANCE.—Trees differ in their capacity to elude damage. Temporal avoidance requires fast progression through vulnerable life stages (Janzen 1971). Such "run for your life" strategies may suit small, fast-growing species. If threats vary in intensity over time, a "wait and see" avoidance tactic may be favored. Species exhibiting this tactic may be over-represented by "safe" life history stages and are not expected to reveal a normal stand-size curve. "Safe stages" might include the seed bank, or tough, large-sized (resistant) adults. Spatial avoidance is possible. For example, species that establish epiphytically may initially avoid elephant damage but become vulnerable to damage at larger sizes.

TOLERANCE.—Trees differ in their ability to recover from damage. While virtually all seedlings and saplings can coppice, low-stature multistemmed species seem especially effective at this (Kruger *et al.*
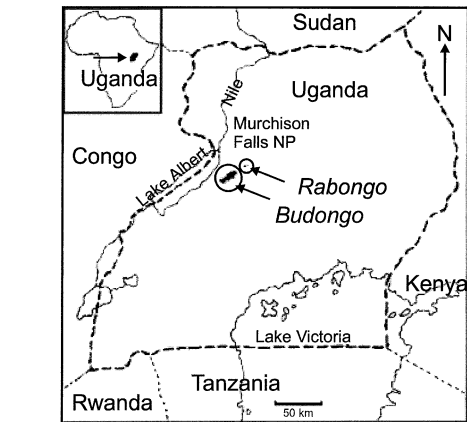

FIGURE 1.   The locations of Rabongo and Budongo forests, Bunyoro, Uganda.

1997). Tolerance may be especially exhibited by "sapwood trees," which do not form heartwood, maintain healing ability deep within the stem, and even allow some tolerance of ring barking (Watson 1934, Fisher 1981, Ng 1986). Such species may persist despite damage and heavy scarring. Expected size distributions are unclear, but an ability to persist as coppice stems and as larger resistant stems implies a potential for bimodal size-class distributions.

Generalizing from plant defense theory suggests that rapid growth (avoidance) and damage recovery (tolerance) are high energy strategies likely to suit fast-growing and well illuminated species like pioneers and savanna species. Preemptive investment strategies like strength (resistance) and chemical defense (repellence) seem suited to slower-growing, shade-tolerant species (Wells 1976, Coley *et al.* 1985, Loehle 1988, van der Meijden *et al.* 1988). Based on these ideas, we predicted that pioneer and savanna species (being palatable and less resistant) would suffer higher levels of damage and depletion than shade tolerant species like *C. alexandri*.

METHODS

STUDY SITE.—Rabongo is a small, 4 km² forest within the Murchison Falls National Park and has been described by Buechner and Dawkins (1961) and Laws *et al.* (1975). The larger Budongo Forest lies 20 km to the southwest (Fig. 1; Eggeling 1947). The sites share a similar elevation (*ca* 1000 m), climate, gentle topography, ancient nonvolcanic soils, and flora (Eggeling 1947, Buechner &

TABLE 1. *Stem damage class scoring used in Rabongo (applied to lowest 4 m of stem).*

Class	Definition (implied loss of bark)
0	No clear damage
1	Localized damage, remains ≥3/4 unringed at worst height[1]
2	Semi-ringed, <3/4 to ≥1/4 unringed at worst height
3	<1/4 unringed at worst height
4[2]	Total ringing somewhere <1 m wide or with remaining bark ≥25% of ringed area
5	Total bark stripping ≥1 m wide all the way around (bark less than <25%)

[1] "Worst height" means at the level where a tape wrapped around the stem—to minimize the measured circumference as in normal stem measurement conventions—would encounter the highest proportion of damaged surface as a proportion of the measurement. Usually, such measurement was not needed and the classes were readily applied.
[2] Damage in this class need not be lethal. There are three reasons: (1) scarring does not always involve deep damage and living tissue remains present; (2) scars of different ages can overlap; and (3) there are species that can survive ring-barking.

Dawkins 1961, Laws *et al.* 1975). Human impacts appear negligible at Rabongo. Fires in the surrounding grassland sometimes impact the forest edges (Buechner & Dawkins 1961).

Several studies of elephants have been conducted in the region (Buechner *et al.* 1963; Laws *et al.* 1970, 1975; Eltringham & Malpas 1980); these are of "savanna" elephants (*Loxodonta africana africana*), which have no specific dependence upon forests. While Budongo once may have had *ca* 700 resident animals (Laws *et al.* 1975), only animals ranging over the surrounding wooded grasslands visit Rabongo. Estimates of elephant populations in Murchison Falls National Park imply a considerable decline during the 1960s and 1970s (Eltringham & Malpas 1980); however, the remaining elephants continue to visit Rabongo relatively often and animal numbers have increased through the 1990s (D. Sheil, pers. obs.; Uganda national parks, pers. comm.).

RABONGO TREE DATA.—We established seven square 1 ha plots in Rabongo. The area was stratified into forest types according to distinct canopy textures identified from aerial images. A grid was laid over this classified image and random number Cartesian coordinate pairs were generated to objectively select sites in each forest type (resolution *ca* 5 m). These locations were found on the ground by reference to features visible on the images, and a further pair of random numbers were used to offset the first plot corner (north and east ± 10 m) to avoid local systematic biases. One plot (6) was located at the edge of the forest.

In each plot, all stems 10 cm DBH (diam at 1.3 m or above any buttresses or deformities) or greater were identified to species, mapped, and measured. Each plot was divided into 25 20 x 20

m grid squares. In each of these squares, 20 percent of the area was assessed for saplings (DBH < 10 cm and height > 1.5 m) in a central circular sub-plot with 2.52 m radius. The lower 4 m of each stem was assessed for scars. A "scar" was defined as an unambiguous sign of tusk damage to the stem, even if the stem had subsequently healed. We were unable to judge if such scarring was associated with feeding and/or other aspects of elephant behavior. Nor could we devise a reliable means of aging scars. Stem damage was assessed at the stem circumference (below 4 m), where a tape encounters the highest proportion of damaged surface. Scores (0 to 5) were determined by the extent of ring-barking or "ringing" (Table 1).

GUILDS AND SPECIES CHARACTERS.—Guild designations follow Hawthorne (1995, 1996; Sheil *et al.* 2000). Pioneers are consistently well exposed ("early successional"); shade bearers are consistently found in shade ("late successional"). Non-pioneer light demanders (NPLDs) are relatively shaded as seedlings but become relatively exposed at larger sizes ("mid-successional"). As light patterns are related to moisture and general exposure in closed forest conditions, we concurred with Hawthorne (1995) in distinguishing species usually found in open woodland ("savanna species") and in wet areas ("swamp species"). We also placed species with epiphytic establishment in a distinct guild. Species names, authorities, and guilds are listed in the Appendix for species recorded (≥10 cm DBH) in the plots.

Growth data for many species found in Rabongo were recorded at five long-term plots in nearby Budongo (Sheil 1997a, b). These plots provided individual stem measures over six decades. Per-species growth means are the average value of all in-

terval records from all (undisturbed) periods for all stems. Four plots had some interventions, and periods of growth immediately following these events were excluded. These data summaries provided our best available predictions of per-species stem growth in Rabongo.

Various additional species characteristics were considered for comparative evaluations. Large spines are common on the stems of *Chaetachme aristata*, *Dicrostachys cinerea*, and *Oncoba spinosa*. Bark toxicity has been little studied (Watt & Breyer-Brandwijk 1962, Gartlan *et al.* 1980, Waterman 1983, Hamilton 1991). But it is known that *Antiaris toxicaria* has a toxic latex, and bark of both *Strychnos mitis* and *Erythrophleum suaveolens* contains powerful toxic alkaloids (Hamilton 1991). Spines, burrs, epicormic buds, and various bark characteristics (Malan & van Wyk 1993) are all likely to influence the ease of large-scale bark stripping and could be investigated further as forms of repellence or resistance; however, apart from spines—which we consider "repellence" (above)—the influence of these characteristics has not been assessed.

We also considered sapwood species. While many Ugandan forest trees appear to lack distinct heartwood (Eggeling & Dale 1952), species classification currently remains too speculative for community analyses. We are certain of only one species, *A. toxicaria* (R. Plumptre, pers. comm.), which also has toxic latex.

ANALYSES.—We investigated if species showed a common ranking in relative degree of scarring across plots. Given differing numbers of species per plot and issues of nonindependence, multiple rank correlations proved analytically unwieldy to present and interpret. We developed a single "all-plots" permutation-based test based on the null hypothesis of random rankings in each plot. Denoting the rank of species i at plot j as $r(i,j)$, then the relative rank is defined as $\rho(i,j) = r(i,j)/N_j$, where N_j is the number of species in plot j. Our measure of consistency for species i, $d(i)$, is the interquartile range of $\rho(i,j)$ across plot j, $j = 1, 2 \ldots 7$. The null distribution of our test statistic D, defined as the sum of $d(i)$ across all species, can be estimated with a randomized permutation test (Manly 1991). At each plot, we assigned the rank of each species by randomly selecting a number without replacement from the numbers $1, 2 \ldots N_j$. After performing these randomizations for all plots, we computed the relative rank of each species at each plot and proceeded to compute the consistency statistic. By repeating these randomizations, we estimated the distribution of D under the null hypothesis. The P-value was estimated from the proportion of simulated D-values less than the observed value.

We used generalized linear models (GLM; McCullagh & Nelder 1989, Barnett 2004) with a logit link function (logistic regression) to estimate the probability of a stem being scarred. This framework provides statistical power and tractability unavailable with conventional selection indices. We modeled the odds ratio of a stem being scarred as a function of independent variables using the following equation: $[P(Y = 1)]/[1 - P(Y = 1)] = e^{x'\beta}$, where $x'\beta = \beta_0 + \beta_1$ variable $- 1 + \beta_2$ variable $- 2 \ldots$. $P(Y = 1)$ is the probability of being scarred. Note that given this formulation, e^{β} is the odds ratio of being scarred when a predictor variable increases by one unit. We fitted candidate models and identified those with the lowest Akaike information criterion (AIC; Akaike 1974).

As with any regression type model, the assumption is that error occurs in the response, but not in the explanatory variables. Two explanatory variables, species abundance and the mean growth rate, were estimated at the species rather than at the stem level. Uncertainties associated with these estimates were not included in the basic models. One solution would be models in which the individual values are assumed to contain individual measurement errors (Carroll *et al.* 1995); however, some exploratory simulations of intraspecific variation in mean growth showed that the likely effect of such variation on our results was negligible.

Evaluating stem-size distribution requires consideration of multiple processes, and we found no defensible and analytically tractable *a priori* models. Exploratory approaches appeared more helpful. We examined stem-size distributions of each guild against a Weibull distribution. This distribution is characterized by two parameters called the scale and shape parameters, α and β, and gives the number of stems, N_k, in a defined diameter class DBH_{k-1} to DBH_k as $N_k = N(exp[-\alpha DBH_k^\beta] - exp[-\alpha DBH_{k-1}^\beta])$, where N is the total number of stems. This function is very successful at fitting real stem-size distribution data (Bailey & Dell 1973, Vanclay 1994, Alder 1995) and is popular with modelers dealing with uneven-age stands (Hyink & Moser 1979, Kamziah *et al.* 2000, Návar & Corral 2000). The scale parameter is approximately equal to the median DBH while the shape parameter controls the skewness of the distribution. Most forms of the distribution show either a simple decline or a unimodal form. Depending on the shape

parameters, the distribution is skewed to the left, symmetrical, or skewed to the right; multiple peaks are not possible. Our assumption was that a stem population that is near equilibrium would have a sampled DBH distribution that can be closely approximated by a Weibull distribution. If the actual distribution departs substantially, the nature of these differences may be ecologically revealing. We used the chi-square goodness of fit test (Daniel 1990). For each test, the DBH classes were chosen such that less than 20 percent of the classes had expected values below 5.

RESULTS

FOREST VEGETATION AT RABONGO.—Forest-wide collections yielded 174 tree species, most occurring at very low densities. The Rabongo tree flora appeared to be a subset of Budongo's, but mid-successional species (*i.e.,* NPLDs) were much less abundant. The seven 1 ha plots contained a total of 2452 stems (all ≥10 cm DBH) yielding 71 species (Appendix). Nineteen of these species (27%) were represented by a single stem, and a further 12 (17%) had five or less. Plot stem densities (≥10 cm DBH) varied from 252 to 522 stems/ ha, and species richness ranged from 24 to 44 species/ ha. The majority of stems in all plots (77% of the total) were pioneer species. *Diospyros abyssinica* was the most common species in all but plot 1, while *C. alexandri* dominated basal area in all but the forest edge vegetation recorded in plot 6 (Table 2; >50% in four plots).

Holoptelea grandis and *D. abyssinica* had relatively continuous stem-size distributions but few other species were represented at intermediate stem sizes (20–60 cm DBH; Appendix). Thirty-one species (44%) occurred only in the smallest size class (10–20 cm DBH), and three only in the largest (≥60 cm). Two species, *Trichilia dregeana* and *S. mitis*, had no stems in the 20–60 cm DBH range, despite possessing both smaller and larger stems. *Cynometra alexandri* was rare at small sizes (<50 cm DBH) and did not appear to be regenerating. Small diameter (<10 cm DBH) strangler figs were abundant (*Ficus thonningii, F. pseudomangifera,* and *F. sansibarica*).

SCARRING.—Within the seven plots, 401 stems (16% of stems ≥ 10 cm DBH) had scars attributable to elephants. Damage varied from 29 to 108 scarred stems/ha (Table 2). Damage on buttressed and fluted stems was generally confined to the narrow outer edge of the flange, distant from the body of the stem. Using a permutation approach to assess rank consistency for the 46 species occurring in two or more plots (see Methods), we found that these species had a significantly similar ranking in relative degree of scarring across the seven plots (D = 7.73, $P < 0.001$; 1000 null model permutations).

Grouping species records by stem abundance highlights the fact that species with moderate abundance (10 spp. with 10 to 19 stems total) showed the least amount of damage, whereas both scarce and common species (24 and 4 spp., respectively) showed a higher incidence of damage (Fig. 2). Within the 10–20 cm DBH class, only *D. abyssinica, H. grandis, Rinorea beniensis, Rothmannia urcelliformis* (all $P < 0.05$), and *Monodora myristica* ($P < 0.001$) had significantly above average scarring, while *Caloncoba crepiana* ($P < 0.001$), *Premna angolensis* ($P < 0.01$), *Margariteria discoidea* ($P < 0.05$), and the epiphytically established *F. thonningii* ($P < 0.05$) were below average.

Overall stem abundance decreased rapidly with stem size while scarring increased in frequency and intensity (Fig. 3). The most severe scarring occured on large *C. alexandri* stems (Table 3). All guilds showed increased scarring with size; ultimately, scarring became more common than non-scarring in shade-tolerant as opposed to pioneer species (Fig. 4). The pattern for NPLDs suggested that damage was rare at smaller sizes—but there were few stems over 10 cm DBH.

Considering each species separately, larger trees were more often damaged than smaller stems. For 17 of the 27 species with sufficient data ($N \geq 4$ in the larger stem size classes), the 10–20 cm DBH class had less scarring than stems >20 cm, with seven ties recorded ($P = 0.0013$, binomial test). The rank of total per-species basal area against proportion of stems scarred was also significantly related ($\tau = 0.304$, $P = 0.006$, $N = 30$). Examined on a per-species basis for those 32 species with available information (see Methods), there was a nonsignificant but negative trend in the rank correlation between species growth rate and scarring incidence ($\tau = -0.230$, $P = 0.085$ $N = 32$; Fig. 5). Although a per-stem summary suggested that scarred stems possesseed a higher estimated mean growth rate than non-scarred stems (0.456 vs. 0.441 cm/yr), this difference was also not significant ($P = 0.063$; Kruskal–Wallis).

Species with spiny stems were not scarred: *C. aristata* (no scars in 10 stems), *D. cinerea* (0 in 18), and *O. spinosa* (0 in 13). Three species known for toxic alkaloids were also unharmed: *A. toxicaria* (no

TABLE 2. *Summary descriptions of the seven 1 ha plots established in Rabongo. All figures relate to stems 10 cm DBH or greater unless otherwise stated.*

Plot	1	2	3
Includes forest edge	No	No	No
Total N ($\geq$10 cm DBH)	522	266	335
Total N ($\geq$40 cm DBH)	21	22	25
BA m²/ha total	19.94	26.07	27.39
Total species	24	26	44
Most abundant species (N)	*Holoptelea grandis*	*Diospyros abyssinica*	*D. abyssinica*
	287	157	130
Most dominant species (m²/ha)	*Cynometra alexandri*	*C. alexandri*	*C. alexandri*
	6.91	16.56	13.78
Pioneers (N)	484	233	242
Non-Pioneer Light Demanders (N)	3	10	18
Shade bearers (N)	26	19	59
Swamp species (N)		1	3
Savanna/woodland species (N)	7	2	4
Strangler species (N)	2	1	8
Unclassified species (N)			1
C. alexandri (N)	7	10	12
Count of damaged stems total	108	57	55
and by class (1, 2, 3, 4)	77, 22, 6, 3	41, 9, 7, 0	35, 9, 8, 3

scars in 5 stems), *S. mitis* (0 in 5), and *E. suaveolens* (0 in 13).

We used a logistic model to examine per-stem probability of scarring as a function of stem diameter and species abundance with plot identity included as a cofactor. All these explanatory terms proved significant (Table 4; model 1). Increased stem size and stem membership of more abundant species both increased the likelihood of a stem being scarred; for each centimeter increase in diameter, an average stem was 3–4 percent more likely to be scarred, and with an increase in species abundance of 10 stems/ha, scarring rose by *ca* 3 to 4 percent. There were also significant differences among plots. These analyses confirmed that the probability of scarring was a function of stem size, species identity, and location.

Analysis of scarring, stem size, and available growth data (note that here the model included only those 32 species for which per-species mean growth rate estimates were available) revealed a significant negative relationship with per-species growth, in addition to the relationships described in model 1 for stem diameter and plot (Table 4; model 2). We also assessed a model that included both species abundance and growth data (Table 4; model 3). Again, all terms were significant. Based on AIC, we could conclude that model 3 was the best model (rerunning model 1 based only on the 32 species used in models 1 and 2 gave: model 1, AIC = 853.11; model 2, AIC = 851.25; model 3,

AIC = 835.58). More importantly, the form and magnitude of the relationships were consistent across these models, suggesting that relatively distinct components of variation were being addressed. Model 3 implies that for each additional centimeter in diameter, an average stem was 4 percent more likely to be scarred, and controlling for stem size, an increase in a species abundance of 10 stems/ha increased the mean incidence of scarring by *ca* 21 percent. Because faster-growing species are often larger, we now see that the influence of growth was confounded in the per-species univariate approaches but is revealed as two distinct components in the per-stem GLM approach. Once stem size was considered, species that grew faster were less likely to be scarred (a decrease of *ca* 20%/mm/yr).

STEM-SIZE DISTRIBUTIONS.—Only a single scarred stem was recorded from the savanna guild. The diameter distribution for this guild did not depart significantly from a Weibull distribution (P = 0.121). In contrast, significant deviation was found for pioneers ($P < 0.001$), NLPDs ($P < 0.001$), and shade bearers ($P < 0.001$). For both the pioneer and shade-bearer guilds, comparison with the Weibull distribution suggested a deficit of stems in the middle of the distribution. We interpreted this as likely due to mortality, *i.e.* unrecorded dead trees. Thus, there was an apparent dearth of pioneers up to at least 30 cm DBH, while for shade

TABLE 2. *Extended.*

4	5	6	7
No	No	Yes	No
252	508	289	280
24	26	6	30
22.72	21.38	8.98	26.25
26	41	32	27
D. abyssinica	*D. abyssinica*	*D. abyssinica*	*D. abyssinica*
124	*132*	*54*	*109*
C. alexandri	*C. alexandri*	*Margaritaria discoidea*	*C. alexandri*
14.70	5.44	1.92	15.15
180	380	213	217
23	19	32	4
32	84	35	46
14	19	6	10
3	3		3
	3	3	
14	6	1	14
37	59	29	56
28, 6, 3, 0	53, 5, 1, 0	27, 1, 1, 0	49, 4, 3, 0

bearers the deficit continued up to 80 cm DBH. The small number of NPLD observations precluded further interpretation.

DISCUSSION

GENERAL.—The distribution of scars across stems was not random. Our results confirmed that scars are more likely among larger stems, on more common species, on slower-growing species, and that incidence varies with location. *Cynometra alexandri* dominated in most areas of the forest, but the hypothesis that elephants directly favor it was not supported. Looking at all stems together, the rapid decrease of stem abundance with size implies a high mortality to growth ratio. The parallel size-related increase in severity and frequency of scarring suggests that these patterns are linked and that elephants are influencing stand structure. The general rarity of stems in some size classes and the high
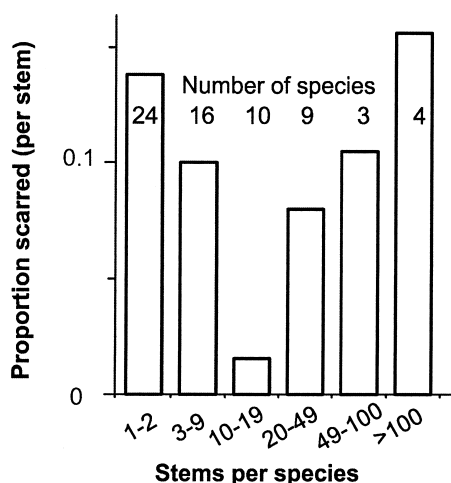

FIGURE 2.   Species grouped by abundance in the 10–20 cm DBH range versus proportion scarred. The number of species in each class is given.
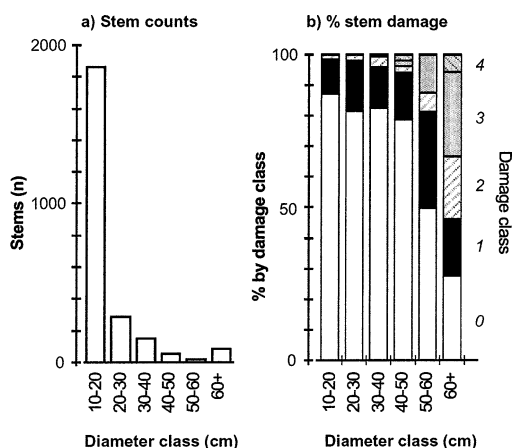

FIGURE 3.   Stem size distribution (a) and percentage scarring by stem size and scar class (b) as defined in Table 1.

TABLE 3. *Intensity and proportion of scarring (stems DBH ≥ 10 cm) for pooled records from the seven 1 ha plots.*

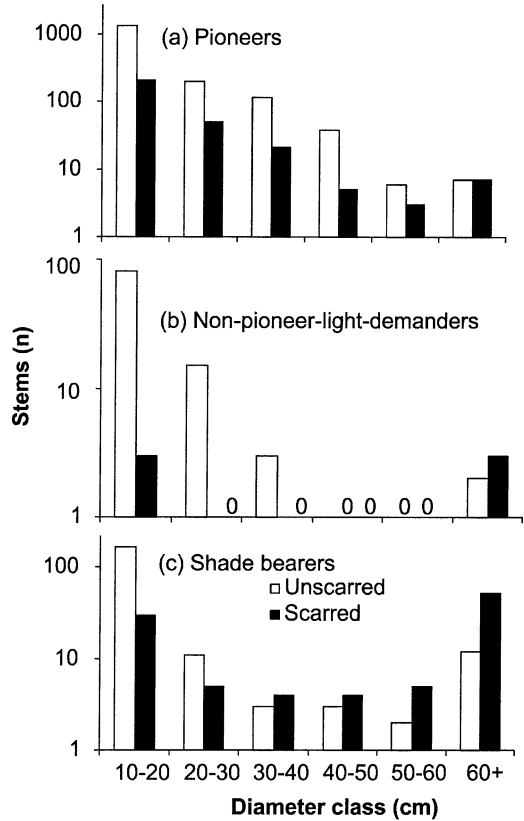| Damage class	0	1	2	3	4	5
Total stems	2051	310	56	29	6	0
Total species	58	27	11	13	2	0
Prevalent species and % of the class	*Diospyros abyssinica* 33	*D. abyssinica* 40	*Cynometra alexandri* 30	*C. alexandri* 58	*C. alexandri* 83	

FIGURE 4.   Abundance of scarred and unscarred stems by stem size for the three most common species guilds. Empty classes are labeled "0."

abundance of pioneers appear, at least in part, related to the presence of elephants.

DO ELEPHANTS AFFECT TREE SPECIES PERSISTENCE?—Our approach was to predict and seek patterns. While the underlying mechanisms remain unproven, each of the four proposed strategies gained support.

REPELLENCE.—Neither spiny stemmed nor toxic bark species were scarred. Buechner and Dawkins (1961) proposed that *H. grandis* and *S. arborea* were repellent, having directly observed that the pungent scent of cut *H. grandis* bark repelled elephants (Buenchner & Dawkins 1961; C. Dawkins, pers. comm.). The continuous stem-size distributions of *H. grandis* and *S. arborea* indeed suggest repellence, as does that for *D. abyssinica* (Appendix). The above average scarring within the 10–20 cm interval for *H. grandis* and *D. abyssinica* re-
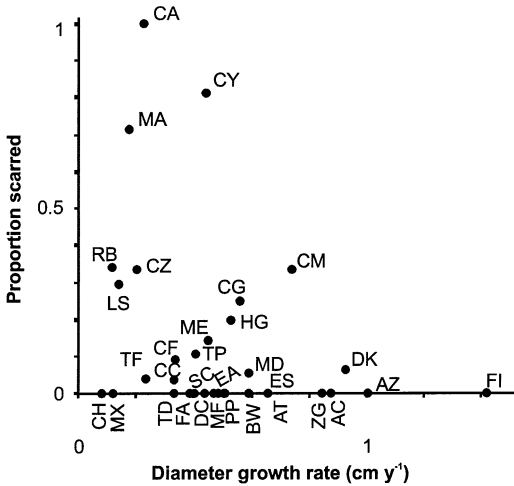
FIGURE 5.   Species plotted according to proportion of stems showing scars (all stems ≥ 10 cm DBH) and estimated mean growth. Growth data use the mean species growth recorded from five long-term Budongo plots (but not including periods five years after silvicultural treatments). Species labels: AC, *Albizia coriaria*; AT, *Antiaris toxicaria*; AZ, *Albizia zygia*; BW, *Blighia welwitschii*; CA, *Crossonephalis africanus*; CC, *Caloncoba crepiana*; CF, *Coffea canephora*; CG, *Cola gigantean*; CH, *Chaetachme aristata*; CM, *Cordia millenii*; CY, *C. alexandri*; CZ, *Celtis zenkeri*; DC, *Dicrostachys cinerea*; DK, *Dombeya kirkii*; EA, *Erythrina abyssinica*; ES, *Erythrophleum suaveolens*; FA, *Fagaropsis angolensis*; FI, *Ficus sur*; HG, *Holoptelea grandis*; LS, *Lepisanthes senegalensis*; MA, *Monodora angolensis*; MD, *Margaritaria discoidea*; ME, *Milicia excelsa*; MF, *Majidea fosteri*; MX, *Mildbraediodendron excelsum*; PP, *Psydrax parviflora*; RB, *Rinorea beniensis*; SC, *Spathodea campanulata*; TD, *Trichilia dregeana*; TF, *Tapura fischeri*; TP, *Trichilia prieuriana*; ZG, *Zanha golungensis*.

mains striking. Some forms of repellence may prevent almost any bark damage, while others merely reduce its severity. Bark damage may result not only from bark-eating but also occurs when small trees are pushed to allow feeding from the crowns.

More tentatively, repellence may also be operating for *Trichilia* spp. and *Tetrapleura tetraptera* (Appendix), along with the entire guild of savanna species (Table 5). Thus, contrary to prediction, evidence of repellence was not associated with shade tolerant species. Indeed, the GLM analyses showed that faster-growing species were less likely to be scarred, once size was accounted for, which did not correspond to our simple expectations concerning repellence (but see avoidance below). The advantages or costs of such repellence may not be as we suspected. Are forest edge and savanna species somehow different? Evolution in restricted (*e.g.,*

riverine) patches, on forest edges, or for scattered populations within seasonal regions that maintain large densities of herbivores, could conceivably be a powerful spur to anti-herbivore defenses—suggesting a key contrast with the majority of forest interior species.

RESISTANCE.—Large trees, including *C. alexandri*, appear to persist through strength and resistance. The clearest evidence of this is the inference drawn from the abundance of very large as opposed to intermediate-sized stems. Size gives a plausible advantage in both stem breakage and ring-barking. Considering the physical stability of stems, the nature of stem form, rooting, and also the distribution and implications of rotten and hollowed stems, merit further study (McMahon & Kronauer 1976, Mattheck *et al.* 1994). Heavy buttressing is unusually prevalent on many species in west Ugandan forests (Hamilton 1991). Buttresses provide stability (Smith 1972, Black & Harper 1979), are an impediment to ring-barking, and greatly increase bark area in the likely damage zone. In addition, damage on buttressed and fluted stems is often confined to the narrow outer edge, distant from the body of the stem (D. Sheil, pers. obs.), where rot is presumably less likely to spread to the heartwood. A possible relation between elephants and prevalence of buttressing warrants consideration.

AVOIDANCE.—That faster growth is related to less scarring at a given stem-diameter size supports the principle of temporal avoidance. The abundance of pioneers at Rabongo may reflect their per-lifetime advantage in reaching reproductive life stages.

The epiphytic juveniles of *F. pseudomangifera*, and *F.* c.f. *sansibarica* were strikingly common at Rabongo but larger mature stems remained rare, consistent with the truncated size distribution we had predicted. In contrast, larger *F. thonningii* stems were common and remained unscarred, suggesting repellence.

TOLERANCE.—The only certain sapwood species, *A. toxicaria*, was rare, poisonous, did not reach large sizes, and was totally unscarred. The GLM models showed that even after controlling for size effects and species-growth, abundance was positively associated with higher scarring, which suggests differential survival. How tropical trees react to wounding (Shain 1979, Loehle 1988, Schoonenberg *et al.* 2003) and the ecology of stem rot re-

TABLE 4.   *Results from a general linear model of the probability of a stem being scarred as a function of stem diameter and species abundance with plot as a factor.*

	Estimate	Error	Probability
Model 1. $x'\beta = \beta_0 + \beta_1 DBH + \beta_2$ (species abundance) $+ \gamma_j$, j = 1, 2, ... 7; AIC = 1991.50, N = 2451[1]			
Intercept	−2.19	0.159	$<2 \times 10^{-16}$
DBH	0.034	0.003	$<2 \times 10^{-16}$
Species abundance ($\times$ 100)	0.048	0.018	0.008
Plot 2[2]	−0.238	0.197	0.23
Plot 3	−0.461	0.194	0.018
Plot 4	−0.718	0.225	0.00148
Plot 5	−0.706	0.181	0.00018
Plot 6	−0.713	0.232	0.0020
Plot 7	−0.366	0.198	0.064
Model 2. $x'\beta = \beta_0 + \beta_1 DBH + \beta_2$ (per-species growth) $+ \gamma_j$; AIC = 851.25, N = 1007			
Intercept	1.11	0.354	0.0018
DBH	0.033	0.00346	$<2 \times 10^{-16}$
Per-species growth	−1.59	0.638	0.013
Model 3. $x'\beta = \beta_0 + \beta_1 DBH + \beta_2$ (species abundance) $+ \beta_3$(per-species growth) $+ \gamma_j$; AIC = 835.58, N = 1007			
Intercept	−1.16	0.381	0.0024
DBH	0.040	0.0041	$<2 \times 10^{-16}$
Species abundance ($\times$ 100)	0.272	0.072	0.00017
Per-species growth	−4.22	1.065	7.4×10^{-5}

[1] AIC of model 1 is not comparable to those of models 2 and 3 since the number of observations involved are different. Using only the 1007 observations for which growth data are available, model 1's AIC is 853.11.
[2] Plot 1 = 0 = reference. There are significant differences among plots in all models, but these were similar and are shown only for model 1.

quire attention (Scheffer & Cowling 1966, Shigo 1985).

COMMUNITY CHANGE.—Historically, Budongo has not experienced the intensity of elephant impacts seen at Rabongo, and the Budongo elephant populations were eliminated in the 1970s. Differences between Budongo and Rabongo may reflect the influence of elephants. Mid-successional species (NPLDs), especially Sapotaceae and Meliaceae, were scarce at Rabongo but abundant in Budongo (Eggeling 1947, Sheil *et al.* 2000). It was the elephants' clear preference for valued NPLD species (*e.g., Khaya anthotheca* and *Entandrophragma* spp.) that led to elephant culling at Budongo (Leggat 1965, Laws *et al.* 1975, Dawkins & Philip 1998). This difference supports the proposition that mid-successional species are relatively intolerant of elephants. A comparison with changes in species abundance across the long-term plots at Budongo showed a relative increase in the abundance of species absent from Rabongo, while species that were more common at Rabongo were, in general, becoming rarer in Budongo (D. Sheil 2003, pers obs.).

What brings animals to one area rather than to another remains uncertain: local species-level density-dependent processes (Connell 1978, Barnes 1983) appear overly simplistic. Wider patterns of food availability in time and space are likely important. The significant plot effect revealed in the GLM analyses may have reflected site-specific factors that attract elephants (Western 1975, Klaus *et al.* 1998, Vanleeuwe & Gautier-Hion 1998, Ba-

TABLE 5.   *Diameter distributions by main tree guilds assessed by χ^2 against a Weibull pattern.*

		Parameter estimates				
Guild	N	Scale, α	Shape, β	χ^2	df	P-value
Pioneer	1949	0.118	1.018	214.67	6	<0.001
NPLDs	109	0.120	0.828	20.23	3	<0.001
Shade bearers	300	0.054	0.615	108.63	10	0.001
Savanna/woodland	62	0.136	1.513	2.42	1	0.121

baasa 2000). Indeed, several deep pools of water in the vicinity of Rabongo and a ranger post made it a safe haven from poachers. Alternatively, the differences may have been related to differences in vegetation.

Elephants usually prefer to eat pioneer species (Höft & Höft 1995; *cf.* Theuerkauf *et al.* 2000). Feedback loops may occur; open areas offer more feeding opportunities for elephants, and the damage they cause, in turn, maintains or increases openness (Eggeling 1947, Buechner & Dawkins 1961, Campbell 1991, Höft & Höft 1995). Such feedback may influence forest types. In the Shimba Hills, Kenya, Höft and Höft (1995) concluded that elephant activity "arrested" forest succession because the damage promoted regeneration of the most browsed species, the "early successional" and fast-growing *Leptonychia usambarensis* (Sterculiaceae). In contrast, less intense elephant pressure at Budongo appears to have allowed, or favored, the development of late successional *C. alexandri* forests (Laws *et al.* 1975). Rabongo is intermediate, with an abundance of pioneers and dominance by shade-tolerant species. As long as sufficient elephant influences are maintained, our expectation is that *H. grandis* and *D. abysinnica* will persist or even increase at Rabongo (Buechner & Dawkins 1961). At sufficiently high densities, elephants may selectively purge the forests of mid-successional species, thus leaving either late or early successional species or, as in Rabongo, both. By selecting for specializations that require high energy availability or defensive investments (Janzen 1971, van der Meijden *et al.* 1988, Fineblum & Rausher 1995, Tuljapurkar & Wiener 2000), browsers may thus accentuate the evolutionary division between pioneer and shade-tolerant species (*cf.* Swaine & Whitmore 1988, Turner 2001).

DOES THE CREATION OF *C. ALEXANDRI* FOREST DEPEND ON ELEPHANTS?—Large *C. alexandri* trees were severely damaged by elephants and saplings were scarce. Unless juveniles grow and recruit at remarkable rates, such size distribution implies a population decline. There is no suggestion of repellence in these patterns. We suggest a "wait and see" avoidance tactic with large-sized, long-lived adults as the resistant life history stage; adult trees dominate the canopy and maintain a seed rain, waiting for and monopolizing rare regeneration opportunities. Occasional possibilities for recruitment may be key—suggesting an intermittent nonequilibrium process similar to that proposed to explain the persistence of woodland with heavily grazed

grasslands (Prins & van der Jeugd 1993). Such a process is distinct from the direct elephant-driven selection proposed by Laws *et al.* (1975) at Budongo; however, Rabongo does appear to have been under much higher elephant densities than was Budongo during Laws *et al.*'s (1975) observations.

THE BIGGER PICTURE.—Our analyses imply distinct patterns involving scarring and stem-size distributions. Spiny and toxic tree species were unscarred. Epiphytic figs also appeared to escape damage, at least while at small sizes. Stem-size distributions of most species declined steeply and 20 percent of stems possessed clear scarring attributable to elephants. In general, larger stems were more frequently scarred. Once this effect was accounted for, damage was significantly more common on both slower-growing and on more abundant species. Savanna species were seldom scarred and possessed near-continuous size distributions. Pioneer and shade-bearer guilds showed a stem deficit at intermediate sizes. Contrary to prior suggestions, *C. alexandri* was heavily scarred and was not successfully regenerating. Although our results do not indicate that elephants lead directly to domination of the forest by *C. alexandri*, they do imply selective processes that can operate more strongly against some species than against others. Species like *C. alexandri* may dominate not because of continuous pressures, but rather perhaps through durability and longevity—and the occasional regeneration opportunities that arise.

The emerging picture implies tree species with differing strategies, sensitivities, and responses. Trends in composition will be influenced by elephants, and are thus determined in turn by various processes that affect these animals. Relative population growth of each tree species will likely change as animal abundances vary, bolstering or indeed eroding stand diversity. Depending on densities, elephants may accelerate (Connell 1978), modify (Buechner & Dawkins 1961, Laws *et al.* 1975), or even halt (Höft & Höft 1995) succession.

Whether shade-tolerant *C. alexandri* or pioneer species like *H. grandis* and *D. abysinnica* are ultimately favored at high elephant densities, elephants can clearly exert considerable influence on tree community dynamics. Animal–vegetation feedback will influence ultimate outcomes, but will not work in isolation as successional status also depends on other disturbance processes and animals are themselves influenced by changes in the larger landscape. Such interactions complicate models that relate successional status with associated species-richness

patterns (*cf.* Eggeling 1947, Connell 1978, Sheil & Burslem 2003).

Abundances of large forest herbivores have changed globally but we remain ill equipped to anticipate the implications. Although our study is helpful, the deductions are imprecise and in many cases provisional; much remains unclear. For example, edge effects may be important; in Rabongo, no tree is more than a few hundred meters from an edge. Fire also merits closer appraisal (Buechner & Dawkins 1961). In contrast to Uganda, some African forests have reported sizeable elephant populations with little evident tree damage (Ghana: Dudley *et al.* 1992; Congo, Ituri: T. Hart, pers. comm.). In any case, stem damage is not the only ecological influence on forests. For example, some tree species may be dependent on elephants for seed dispersal and seedling establishment (Hawthorne & Parren 2000, Theuerkauf *et al.* 2000, Cochrane 2003). Our study can neither confirm nor refute the ultimate decline of any tree species based on available information.

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APPENDIX

Total stem counts by species for the seven 1 ha plots in Rabongo and the proportion of each with evidence of stem damage. Species nomenclature follows Flora of Tropical East Africa (Various authors 1952 et seq.) or more up-to-date determinations provided by staff at the Royal Botanic Gardens, Kew. Guild designations follow Hawthorne (1995, 1996; Sheil et al. 2000) and are given here by codes: 1: pioneers; 2: non-pioneer light demanders (NPLDs); 3: shade bearers; 4: swamp species; 5: savannah/woodland species; 6: strangler fig species; 0: unclassified.

Species [Family]	Guild	N per DBH class (cm)						Prop. Scarred
		≥10<20	≥20<30	≥30<40	≥40<50	≥50<60	≥60	
Albizia coriaria Oliv. [Fabaceae subfam. Mimosoideae]	5	1						0.000
Albizia glaberrima (Schumach. & Thonn.) Benth. [Fabaceae subfam. Mimosoideae]	1	2	6	6	5			0.000
Albizia zygia (DC.) J. F. Macbr. [Fabaceae subfam. Mimosoideae]	2	5	2					0.000
Antiaris toxicaria Leschenault var. *usambarensis* (Engl.) C. C. Berg [Moraceae]	2	9	3	1				0.077
Blighia unijugata Bak. [Sapindaceae]	3	7						0.000
Blighia welwitschii (Hiren) Radlk. [Sapindaceae]	2		1					0.028
Caloncoba crepiana (De Wild. & T. Durand) Gilg. [Flacourtiaceae]	1	107						0.250
Celtis zenkeri Engl. [Ulmaceae]	2	6			2			0.000
Chaetachme aristata Planch. [Ulmaceae]	1	10						0.091
Coffea canephora Froehner [Rubiaceae]	3	11						0.250
Cola gigantea A. Chev. [Sterculiaceae]	3	4	1					0.250
Cordia millenii Bak. [Boraginaceae]	1	4	1	1	1		1	0.000
Craibia brownii Dunn [Fabaceae subfam. Papilionideae]	3	4						0.250
Crossonephalis africanus (Radlk.) Leenh. [Sapindaceae]	3					1	1	1.000
Cynometra alexandri C. H. Wright [Fabaceae subfam. Caesalpinioideae]	3	1			1	3	60	0.828
Dicrostachys cinerea (L.) Wight & Arn. [Fabaceae subfam. Mimosoidea]	1	7	6	4		1		0.000
Diospyros abyssinica (Hiern). F. White [Ebenaceae]	1	524	163	103	24	3	3	0.171
Dombeya kirkii Mast. [Sterculiaceae]	5	11	3	2				0.063
Duranta repens L. [Verbenaceae]	3	1						0.000
Erythrina abyssinica DC. subsp. *abyssinica* [Fabaceae subfam. Papilionoideae]	1		1					0.000
Erythrophleum suaveolens (Guill. & Perr.) Brenan [Fabaceae subfam. Caesalpinioideae]	1	1						0.000
Erythroxylum fischeri Engl. [Erythroxylaceae]	1	12	1					0.000
Fagaropsis angolensis (Engl.) Dale [Rutaceae]	0	1						0.000
Ficus exasperata Vahl [Moraceae]	1	1						0.500
Ficus polita Vahl subsp. *polita* [Moraceae]	5	1			1			0.000
Ficus pseudomangifera Hutch. [Moraceae]	6	2	3					0.000
Ficus c. f. *sansibarica* Warb. (not fertile) [Moraceae]	6	13		1			1	0.067
Ficus saussureana DC. [Moraceae]	4	3						0.000
Ficus sur Forssk. [Moraceae]	1	1						0.000
Ficus thonningii Bl. [Moraceae]	5	23	3					0.000
Ficus varifolia Warb. [Moraceae]	1	1						0.000

APPENDIX   *Continued.*

Species [Family]	Guild	N per DBH class (cm)						Prop. Scarred
		≥10 <20	≥20 <30	≥30 <40	≥40 <50	≥50 <60	≥60	
Holoptelea grandis (Hutsch.) Mildbr. [Ulmaceae]	1	457	43	16	11	3	4	0.187
Hoslundia opposita Vahl [Labiatae]	1	1						0.000
Keetia zanzibarica (Klozsch) Bridson [Rubiaceae]	1	88	1					0.090
Khaya grandifoliola C. D. C. [Meliaceae]	2	11	8	3				0.000
Kigelia africana (Lam.) Benth. [Bignoniaceae]	2	21	2					0.043
Lepisanthes senagalensis (Poir.) Leenh. [Sapindaceae]	3	15	3	5	2	2		0.296
Majidea fosteri (Sprague) Radlk. [Sapindaceae]	2						1	0.000
Margaritaria discoidea (Baill). Webster [Euphorbiaceae]	1	22	9	2	1		3	0.027
Markhamia lutea (Benth.) K. Schum. [Bignoniaceae]	1	21	1					0.174
Mildbraediodendron excelsum Harms [Fabaceae subfam. Caesalpinioideae]	2					1	1	0.000
Milicia excelsa (Welw.) C. C. Berg [Moraceae]	1	5	1				1	0.143
Monodora angolensis Welw. [Annonaceae]	3	7						0.714
Monodora myristica (Gaertn.) Dunal [Annonaceae]	3	1						1.000
Multidentia crassa (Hiern) Bridson & Verdc. [Rubiaceae]	0	1						0.000
Ochna afzelii R. Br. ex. Oliv. [Ochnaceae]	5	1						0.000
Oncoba spinosa Forsk [Flacourtiaceae]	5	13						0.000
Oxyanthus speciosus DC. subsp. *globosus* Bridson [Rubiaceae]	3	33						0.061
Parkia filicoidea Oliv. [Fabaceae subfam. Mimosoideae]	2	1						0.000
Premna angolensis Geurke [Verbenaceae]	1	62	6					0.015
Pseudospondias microcarpa (A. Rich.) Engl. [Anacardiaceae]	4	1						1.000
Psydrax parviflora (Afzel.) Bridson [Rubiaceae]	1	17	1					0.000
Pterygota mildbraedii Engl. [Sterculiaceae]	2						3	0.667
Rauvolfia vomitoria Afzel. [Apocynaceae]	1	110	5					0.183
Rinorea beniensis Engl. [Violaceae]	3	50	6					0.232
Rinorea oblongifolia (C. H. Wright). Chipp [Violaceae]	3	2						0.500
Robmannia urcelliformis (Hiern) Bullock ex Robyns [Rubiaceae]	3	23	3					0.346
Schrebera arborea A. Chev. [Oleaceae]	1	22	1	4	1	2		0.200
Securinega virosa (Roxb. ex. Willd.) Baill. [Euphorbiaceae]	1	1						0.000
Spathodea campanulata P. Beauv. [Bignoniaceae]	1	1						0.000
Strychnos mitis S. Moore [Loganiaceae]	3	5						0.000
Tabernaemontana holstii K. Schum. [Apocynaceae]	3	2					1	0.000
Tapura fischeri Engl. [Dichapetalaceae]	3	20	1	1	3	1		0.038
Tetrapleura tetraptera (Schum. & Thonn.) Taub. [Fabaceae subfam. Mimosoideae]	1	7	2				1	0.000
Trichilia dregeana Sond. [Meliaceae]	0	3						0.000

APPENDIX *Continued.*

Species [Family]	Guild	N per DBH class (cm)						Prop. Scarred
		≥10 <20	≥20 <30	≥30 <40	≥40 <50	≥50 <60	≥60	
Trichilia prieuriana A Juss. [Meliaceae]	3	16			1		2	0.105
Turraea floribunda Hochst. [Meliaceae]	1	6						0.000
Vernonia amygdalina Del. [Compositae]	1	9						0.222
Vitex doniana Sweet [Verbenaceae]	5	2	1					0.000
Xylopia parviflora (A. Rich). Benth. [Annonaceae]	2	28	2				1	0.065
Zanha golungensis Hiern. [Sapindaceae]	5	1						0