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Long-term tree population dynamics and their implications for the conservation of the Kakamega Forest, Kenya

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Abstract. Long-term studies of tree population dynamics play an important role in identifying the conservation needs of tropical forest ecosystems. We examined changes in tree population structure and composition over an 18-year period (1981–1999) in three plots located at the center of the Isecheno study site in the Kakamega Forest, Kenya, a forest with a history of logging and other anthropogenic disturbance. DBH size class distribution took the shape of an 'inverse J' curve in both 1981 and 1999 and did not differ significantly between the two study periods. Stem density increased significantly during the study with most of the increase occurring in the smallest stem size class (10–14 cm DBH). Nearly all of the most common species in 1981 remained among the most common in 1999, though the density of pioneer species decreased by 21% during the study. Our results suggest that forest in the study plots remained relatively undisturbed and in good condition over the study period. Forest in the plots also appeared still to be recovering from the selective logging of large trees that took place at Isecheno in the 1940s. In addition to our longitudinal study, we compared tree population parameters at three additional Isecheno sites spread over a distance of ~ 1 km that have experienced different histories of disturbance: (i) a lightly human disturbed site (LHD), (ii) a heavily human disturbed site (HHD), and (iii) a cattle disturbed site (CD). While all three sites were selectively logged in the 1940s, the main signs of disturbance today are footpaths at the LHD site, tree stumps at the HHD site, and wide cattle paths at the CD site. Not surprisingly, of the disturbed sites, the LHD site was in the best condition. Trees at the HHD site exhibited extremely poor recruitment into the small size classes, a condition that can probably be attributed to human exploitation of small trees for poles. The CD site appeared to be at an earlier successional stage than the other disturbed sites with its low mean DBH, high overall stem density, and high pioneer species stem density. Browsing and trampling of vegetation by cattle may be the source of the light gaps that have led to the abundance of pioneer species at this site. We conclude that conservation measures applied to central Isecheno, including the establishment of a forest station nearby and ranger patrols, appear to have succeeded, but that the prognosis for the Kakamega Forest in general is bleak if protection efforts are not increased in other parts of the forest, where anthropogenic disturbance remains high. We also note the considerable variation in tree population structure and composition that can occur within a small area depending on the local history of disturbance.

Introduction

Tropical forest ecosystems are important because they act as reservoirs of biodiversity, timber, medicinal plants, and oxygen, and play a critical role in watershed protection (Richards 1996). Over the past century, growing human populations have put increasing pressure on tropical forests, threatening to do irreversible damage to these ecosystems. Long-term studies of tree population dynamics are critical to increasing our understanding of the conservation needs of tropical forest ecosystems (Hubbell and Foster 1992; Condit 1995; Sheil et al. 2000). At least one such study has been conducted in each of the major categories of tropical forests on earth (Condit 1995), yet the number of forests where long-term tree population dynamics have been studied is still relatively small (Connell et al. 1984; Lieberman and Lieberman 1987; Manokaran and Kochummen 1987; Milton et al. 1994; Taylor et al. 1996; Chapman et al. 1997; Lwanga et al. 2000; Hart 2001; Sheil 2001). With the high rate of forest loss and degradation in many tropical regions, studies of long-term dynamics in forests threatened by human activities are particularly valuable.

Humans have affected tropical rainforests in many ways, particularly through logging and agriculture (Whitmore 1984). Several studies have examined the long-term effects of logging on forest structure and composition (Cannon et al. 1994; Plumptre 1996; Chapman and Chapman 1997; Struhsaker 1997). Studies from forests in Uganda in particular have shown that tree regeneration may remain poor even >20 years after logging subsides (Struhsaker 1997), and that forest structure requires >50 years to return to pre-logging conditions (Plumptre 1996). Several studies have also been conducted on the influence of shifting cultivation on forest regeneration. The results of these studies suggest that the rate at which tree regeneration proceeds after agricultural disturbance varies widely between sites, thereby rendering it difficult to predict the rate of recovery for any particular site (Uhl and Jordan 1984; Saldarriaga et al. 1988; Chapman and Chapman 1999; Duncan and Chapman 1999).

As in most tropical countries where human populations are increasing rapidly, forest conservation is a critical issue in Kenya (Rugene 2001; Opala 2002). By the late 1980s/early 1990s only 2% of Kenya remained covered by indigenous forest (Wass 1995), and 80% of this remaining forest cover occurred in agricultural areas with high human densities (Tsingalia 1988). This scenario has produced an ongoing conflict between attempts at forest conservation and the land use needs of Kenya's increasing human population (Tsingalia 1988; Wass 1995). A forest that epitomizes this conflict is the Kakamega Forest, Kenya's only remaining Guineo-Congolian rainforest (Cords and Tsingalia 1982; Kokwaro 1988; Tsingalia 1988). The Kakamega Forest is one of the most important reservoirs of biodiversity in Kenya (Wass 1995), yet it is surrounded by a human population whose density exceeds 175 individuals/km^2 (Tsingalia 1988).

The high human density in the Kakamega area has led to considerable long-term human influence on the forest (Tsingalia 1988; Wass 1995). For example, local people have long used the forest as a thoroughfare for herding cattle to grasslands in the forest interior and as a source of charcoal, fuelwood, gold, honey, medicinal plants, and construction materials (Wass 1995). Furthermore, selective logging operations took place in the forest from the 1930s to 1982, though few official records of this logging have been preserved (Tsingalia 1988). Disturbance levels, however, are not uniform throughout the forest (Kiama and Kiyiapi 2001; personal observation). Several sites, including the site of Isecheno where one of us (M.C.) has been conducting research on nonhuman primates for >20 years, have been afforded some protection via the establishment of forest stations, ranger patrols, and a 1982 presidential decree banning all indigenous tree species exploitation (Tsingalia 1988).

In this paper, we attempt to infer the extent to which these conservation measures have succeeded in protecting the forest at Isecheno over the past two decades by examining both temporal changes and geographical differences in forest structure and composition. First, we use data from vegetation plots established at the center of Isecheno in 1981 and resampled in 1999 to examine changes in the tree population over this period. Second, we compare the results of tree censuses in lightly human disturbed areas at the center of Isecheno with those from currently heavily human disturbed areas and areas intensively used as cattle thoroughfares on the periphery of the site. As the first long-term study of tree population dynamics at Kakamega, our results have important implications for the conservation prospects of this forest. Furthermore, the nature of disturbance at Kakamega (e.g. pole cutting, cattle grazing, past logging) is typical of many managed rainforests and our results may therefore help inform management decisions in other disturbed rainforests as well.

Methods

Study site

Research was conducted at Isecheno study site in the central region of the Kakamega Forest in western Kenya (0°19′ N; 34°52′ E; Elevation 1580 m), ~40 km NW of Lake Victoria. Though the forest encompasses 240 km^2, only ~100 km^2 of this area is actually covered by indigenous forest (Brooks et al. 1999). The remaining portion of the reserve consists of plantations, tea fields, and grasslands (Wass 1995). The indigenous forest at Kakamega has been fragmented into at least two blocks, the largest of which is 86 km^2 and includes Isecheno (Brooks et al. 1999). Isecheno was selectively logged for very large trees in the 1940s (Cords 1987) and suffers from some illegal exploitation (tree felling for poles, liana cutting for removal of dead firewood, honey harvesting) by local people, particularly on its periphery (Cords and Tsingalia 1982; Kokwaro 1988; Tsingalia 1988; personal observation).

Tsingalia (1988) describes the Kakamega Forest as consisting of four layers: top canopy, middle canopy, lower canopy, and herb layer. In most areas, including Isecheno, the canopy is somewhat open and emergents rarely exceed 45 m. Based on lists compiled by Tsingalia (1988) and Mutangah et al. (1992), pioneer species at Kakamega include *Acanthus* sp., *Albizia grandibracteata*, *A. gummifera*, *Bridelia micrantha*, *Celtis africana*, *Croton macrostachyus*, *C. megalocarpus*, *Dombeya burgessiae*, *Erythrina abyssinica*, *Harungana madagascariensis*, *Maesa lanceolata*, *Markhamia lutea*, *Polyscias fulva*, *Solanum giganteum*, and *Trema orientalis*.

Rainfall at Kakamega averages approximately 2000 mm per year, with reported figures ranging from 1956 mm (Kokwaro 1988; Gathua 2000 – measured in a nearby town over 40–60 years, from 1923 to 1998) to 2215 mm (Cords 1987 – measured at the study site, from 1976 to 1981). Average minimum monthly temperatures range from 11 to 21 °C while average maximum monthly temperatures range from 18 to 29 °C (Cords 1987).

Data collection

Long-term tree population dynamics in a single undisturbed area

Changes in tree population dynamics were studied over an 18-year period through the monitoring of three vegetation plots located at the center of Isecheno. These plots of 0.77 ha (Plot 1), 0.49 ha (Plot 2), and 0.49 ha (Plot 3) were established in 1981 by Cords (1984). Plots were chosen so as not to be intersected by trails through the forest and to be representative of the least disturbed areas of forest at Isecheno. Plots were broken down into 10 m × 10 m subplots and the perimeters of these subplots were demarcated with flagging. The species identity and girth at breast height (GBH) of all trees $\geqslant 30$ cm GBH (~ 10 cm DBH) were recorded. GBH measurements were then converted to DBH values so as to be comparable to most other studies of tropical rainforest tree populations (Condit 1995).

Cords' three plots were relocated and recensused by Forrestel in 1999. Relocation of these plots was made possible by the detailed descriptions of the plots' locations provided by Cords' maps and field notes from 1981. The area surveyed in Plots 2 and 3 remained unchanged while the area surveyed in Plot 1 increased slightly to 0.81 ha in 1999. Data on species identity, GBH, and DBH in 1999 were gathered via the same methods as in 1981.

Comparisons between areas with different disturbance regimes

A study of tree population structure in peripheral regions of Isecheno with different disturbance regimes was conducted by Scully in 2000. Scully's results from disturbed areas would ideally be compared with Forrestel's 1999 results from relatively undisturbed areas. However, Scully enumerated trees along existing trails (i.e. transects) rather than in plots, thereby rendering comparisons between her results and Forrestel's results problematic. We attempted to avoid this problem by comparing Scully's results to those produced from data collected by Fashing in 1998 along existing trails in the same general area where Forrestel's plots were located. Fashing's transects were more disturbed than Forrestel's plots by virtue of their following existing trails, yet they could still be classified as relatively lightly disturbed (lightly human disturbed or LHD) since they are exploited primarily by humans as footpaths. Trails were generally 1–2 m wide and used by monkey researchers, tourists, forestry department personnel, and occasionally local people traveling through the forest.

In the studies by both Fashing and Scully, tree species identity and GBH were recorded for all trees $\geqslant 30$ cm GBH whose trunks were located within 5 m on either side of the transect. GBH measurements were then converted to DBH values. Transects consisted of a series of adjacent 25 × 10 m segments that followed existing trails through the forest. At Fashing's LHD site, a total of nine transects were censused through a relatively homogeneous area for a total of 4.15 ha surveyed.

In Scully's study, two peripheral areas at Isecheno were evaluated. First, Scully censused 0.85 ha of transects at a site (heavily human disturbed or HHD) which was located near a tea field and human settlement on the western edge of Isecheno. Local people are regularly spotted in this area and signs of ongoing forest disturbance (e.g. pole cutting and firewood collection) have been present throughout the past two decades. Second, Scully censused 0.70 ha of transects at another site located deeper within the forest on the eastern periphery of Isecheno. Though it is located further from human settlement and is therefore less accessible than the HHD site, this second site (cattle disturbed or CD) has been used regularly over at least the last two decades as a cattle path by local people en route to a distant glade. The HHD and CD sites are within ~ 0.5 km of the central Isecheno site censused by Cords, Forrestel and Fashing, and were also subjected to the selective logging of the 1940s.

Data analysis

We updated the names of several species identified by Cords in 1981 to follow the taxonomic conventions of Beentje (1994) used by the other authors of this paper. Basal area (BA) was not calculated for any of the sites discussed in this paper due to the inclusion of both buttressed and non-buttressed trees in GBH measurements. Heavily buttressed trees do not make up a large proportion of the trees at Isecheno, but their inclusion in GBH measurements could nevertheless lead to large overestimates of BA (Sheil 1995).

Species–area curves were generated by plotting cumulative number of species against area sampled using randomly selected 10 m × 10 m subplots in the plot-based studies and 50 m × 10 m subplots in the transect-based studies. Because the area included in transect samples differed widely between sites, the rarefaction method was used to estimate species richness at these sites. Rarefaction was conducted using the free software program 'Rarefact' available online at http://www2.biology.ualberta.ca/jbrzusto/rarefact.php. Species diversity (H') was calculated using the Shannon–Wiener diversity index and species evenness (J) was calculated via the evenness index (Kent and Coker 1992). Because data were most often not normally distributed, all statistical tests in this paper are nonparametric and two-tailed. Significance level was set at $P \leqslant 0.05$ for all tests.

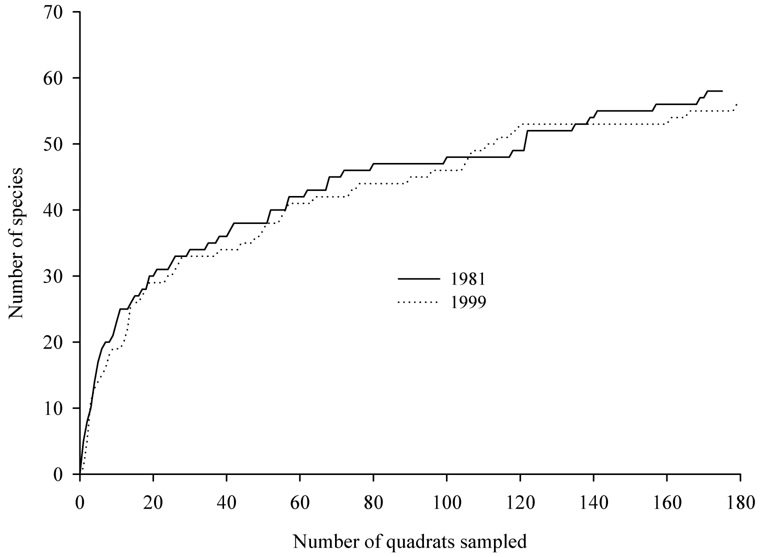


Figure 1. Cumulative species–area relationships for the undisturbed plots in 1981 and 1999. Each quadrat represents an area of 0.01 ha.

Results

Long-term forest dynamics in central Isecheno

Species–area curves for both 1981 and 1999 are approaching asymptotes, suggesting that both censuses detected most of the species in the study area (Figure 1). Number of species recorded dropped slightly from 58 (including six unidentified) in 1981 to 56 (including three unidentified) in 1999 (Table 1). Species diversity fell from 3.49 to 3.32 (5%) and species evenness fell from 0.86 to 0.82 (5%) over the same period.

Stem density increased from 378.3 stems/ha in 1981 to 414.0 stems/ha in 1999. When plots from 1981 and 1999 are divided into a series of 10 m × 10 m subplots, stem density per subplot is significantly higher in 1999 than in 1981 (Wilcoxon signed ranks test: $Z = -2.40$, $P = 0.017$). Mean DBH also increased slightly from 28.7 ± 0.9 cm in 1981 to 29.7 ± 1.1 cm in 1999. However, when the 1981 and 1999 plots are divided into a series of 10 m × 10 m subplots, mean DBH per subplot does not differ significantly between studies (Wilcoxon signed ranks test: $Z = -0.03$, $P = 0.997$).

The size class distributions of stems in both 1981 and 1999 exhibit a roughly negative exponential, or 'inverse J', curve (Figure 2). When trees are divided into eight DBH categories (10–19, 20–29, 30–39, 40–49, 50–59, 60–69, 70–79, ≥80 cm), there is no significant difference in size class distributions between study periods (Kolmogorov–Smirnov test: $\chi^2 = 2.45$, $P = 0.290$). However, the relative

Table 1. Comparison of tree population parameters at Isecheno study sites.

Site	Researcher	Area surveyed (ha)	# species	*H′*	Stems/ha	Mean DBH
Undisturbed plot 1981	Cords	1.75	58 (50)[a]	3.49	378.3	28.7
Undisturbed plot 1999	Forrestel	1.79	56 (45)	3.32	414.0	29.7
Low human disturbance transect	Fashing	4.15	64 (49)	3.33	364.1	32.7
High human disturbance transect	Scully	0.85	54 (51)	3.54	357.6	42.1
Cattle disturbed transect	Scully	0.70	52 (52)	3.35	582.9	26.5

[Note: Because of methodological differences, comparisons between plots and transects should be regarded with caution.] [a]Number in parentheses is the number of species from randomly selected quadrats covering a total of 0.70 ha.

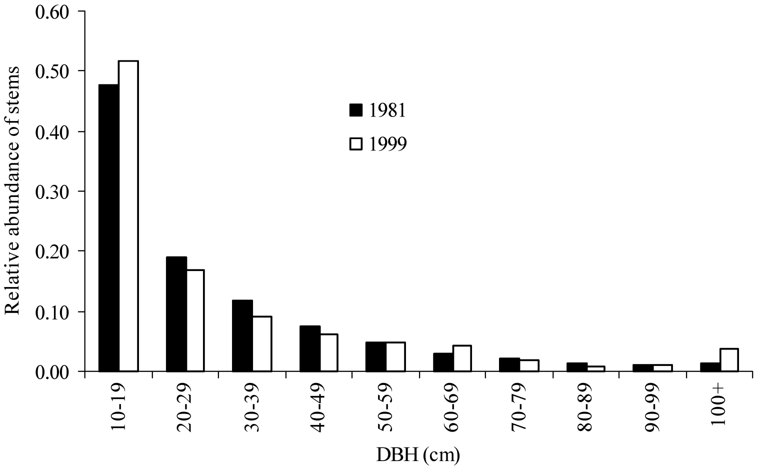


Figure 2. Stem size class distribution (⩾ 10 cm DBH) in the undisturbed plots in 1981 and 1999.

abundances of very small (10–14 cm) and very large (⩾ 100 cm) trees increased considerably from 1981 to 1999. Very small stems accounted for only 29.9% of all stems in 1981 but accounted for 35.9% of all stems in 1999. Very large stems accounted for only 1.4% of all stems in 1981 but accounted for 3.6% of all stems in 1999.

Eight species recorded in 1981 were no longer present in 1999, while nine species identified in 1999 were not recorded in 1981 (Table 2). Twenty-two (42%) of the 52 species identified in 1981 decreased in abundance, 15 (29%) increased, and 15 (29%) remained at nearly the same abundance (changed by ⩽ 1.0 stem/ha) over the next 18 years. Only three species not recorded in 1981 were found to have reached densities of ⩾ 1.0 stem/ha by 1999.

Table 2. Density of $\geqslant$30 cm GBH trees (stems/ha) in Cords' 1981 undisturbed plots, Forrestel's 1999 recensus of those plots, Fashing's lightly human disturbed (LHD) transects, Scully's heavily human disturbed (HHD) transects, and Scully's cattle disturbed (CD) transects.

Species (Family)	Undisturbed plots 1981	Undisturbed plots 1999	LHD transects	HHD transects	CD transects
Acrocarpus fraxinifolius (Leguminosae)	2.3	0.0	0.2	4.7	0.0
Alangium chinense (Alangiaceae)	0.0	3.9	1.0	0.0	8.6
Albizia gummifera (Mimosaceae)	11.4	7.8	8.4	2.4	8.6
Aningeria altissima (Sapotaceae)	9.1	8.9	7.0	2.4	7.1
Antiaris toxicaria (Moraceae)	36.6	48.0	38.1	50.6	25.7
Bequaertiodendron oblanceolatum (Sapotaceae)	8.6	11.7	8.4	2.4	8.6
Bersama abyssinica (Melianthaceae)	5.1	3.9	1.2	1.2	1.4
Bischoffia javanica (Euphorbiaceae)	0.6	0.6	2.9	3.5	8.6
Blighia unijugata (Sapindaceae)	16.0	14.0	10.4	4.7	8.6
Bridelia micrantha (Euphorbiaceae)	6.3	0.6	2.2	4.7	24.3
Canthium keniense (Rubiaceae)	0.0	0.0	1.7	0.0	1.4
Casaeria battiscombei (Flacourtiaceae)	1.7	4.5	1.7	4.7	5.7
Cassipourea ruwensorensis (Rhizophoraceae)	2.9	8.4	6.0	2.4	11.4
Celtis africana (Ulmaceae)	13.7	10.6	18.6	15.3	11.4
Celtis gomphophylla (Ulmaceae)	20.6	27.4	21.2	22.4	12.9
Celtis mildbraedii (Ulmaceae)	0.0	0.6	0.0	0.0	0.0
Chaetacme aristata (Ulmaceae)	8.6	5.6	6.3	17.6	2.9
Chrysophyllum albidum (Sapotaceae)	2.9	1.1	1.0	0.0	2.9
Cordia africana (Boraginaceae)	10.3	5.0	8.2	7.1	4.3
Cordia millenii (Boraginaceae)	0.0	0.0	0.0	0.0	1.4
Craibia brownii (Papilionaceae)	0.0	0.0	0.2	0.0	0.0
Croton macrostachyus (Euphorbiaceae)	3.4	0.6	0.0	1.2	0.0
Croton megalocarpus (Euphorbiaceae)	16.0	14.5	14.9	16.5	35.7
Croton sylvaticus (Euphorbiaceae)	12.0	9.5	6.7	5.9	8.6
Cupressus sp. (Cupressaceae)	0.0	0.0	1.0	0.0	0.0
Diospyros abyssinica (Ebenaceae)	3.4	2.8	2.4	7.1	1.4
Dovyalis macrocalyx (Flacourtiaceae)	0.0	0.0	0.7	0.0	0.0
Drypetes gerrardii (Euphorbiaceae)	1.1	0.0	0.0	0.0	0.0
Ehretia cymosa (Boraginaceae)	5.1	3.4	2.2	4.7	2.9
Erythrina abyssinica (Papilionaceae)	0.0	0.0	0.0	1.2	0.0
Fagaropsis angolensis (Rutaceae)	0.0	0.0	1.0	0.0	4.3
Ficus exasperata (Moraceae)	21.1	25.1	30.4	8.2	17.1
Ficus lutea (Moraceae)	0.6	1.1	0.2	2.4	1.4
Ficus natalensis (Moraceae)	0.0	0.6	0.2	0.0	1.4
Ficus ovata (Moraceae)	0.0	0.0	0.2	0.0	0.0
Ficus sur (Moraceae)	7.4	8.9	8.9	4.7	1.4
Ficus sycomorus (Moraceae)	1.1	0.0	0.0	0.0	0.0

Table 2. Continued.

Species (Family)	Undisturbed plots 1981	Undisturbed plots 1999	LHD transects	HHD transects	CD transects
Ficus thonningii (Moraceae)	0.6	0.0	1.9	2.4	1.4
Funtumia africana (Apocynaceae)	31.4	50.3	28.9	12.9	44.3
Harungana madagascariensis (Guttiferae)	3.4	0.0	1.9	7.1	94.3
Heinsenia diervillioides (Rubiaceae)	1.7	5.6	0.0	1.2	5.7
Khaya anthotheca (Meliaceae)	0.0	0.0	0.0	11.8	0.0
Kigelia africana (Bignoniaceae)	0.0	0.0	0.0	1.2	0.0
Kigelia moosa (Bignoniaceae)	0.6	0.6	1.4	3.5	0.0
Lepidotrichilia volkensii (Meliaceae)	0.6	0.0	0.0	0.0	0.0
Maesa lanceolata (Myrsinaceae)	0.0	0.0	0.5	0.0	0.0
Maesopsis eminii (Rhamnaceae)	2.9	0.6	1.0	2.4	12.9
Manilkara butugi (Sapotaceae)	1.1	0.6	2.2	1.2	2.9
Margaritaria discoidea (Euphorbiaceae)	5.7	0.0	2.4	0.0	1.4
Markhamia lutea (Bignoniaceae)	18.3	21.8	10.8	12.9	5.7
Milicia excelsa (Moraceae)	0.6	1.7	4.8	1.2	0.0
Monodora myristica (Annonaceae)	0.0	0.0	0.5	0.0	0.0
Morus mesozygia (Moraceae)	0.6	6.1	3.6	5.9	5.7
Olea capensis (Oleaceae)	5.7	5.0	6.5	5.9	1.4
Oncoba spinosa (Flacourtiaceae)	0.0	0.0	0.0	0.0	1.4
Phyllanthus inflatus (Euphorbiaceae)	0.0	3.9	0.0	0.0	0.0
Phyllanthus sp. (Euphorbiaceae)	0.0	0.6	0.0	0.0	0.0
Polyscias fulva (Araliaceae)	9.1	11.7	6.0	20.0	34.3
Premna angolensis (Verbenaceae)	4.0	2.2	1.7	2.4	0.0
Prunus africana (Rosaceae)	0.6	0.6	3.1	14.1	8.6
Psidium guajava (Myrtaceae)	0.0	0.0	0.0	0.0	12.9
Rawsonia lucida (Flacourtiaceae)	0.0	0.6	0.0	0.0	4.3
Rinorea brachypetala (Violaceae)	0.0	4.5	1.0	0.0	5.7
Rothmannia urcelliformis (Rubiaceae)	0.6	0.0	0.0	0.0	0.0
Sapium ellipticum (Euphorbiaceae)	1.1	1.1	3.9	5.9	11.4
Solanum mauritianum (Solanaceae)	0.0	0.0	1.4	7.1	0.0
Spathodea campanulata (Bignoniaceae)	0.6	1.1	0.7	0.0	0.0
Strombosia scheffleri (Olacaceae)	7.4	17.3	8.7	8.2	44.3
Strychnos mitis (Loganiaceae)	0.0	0.6	0.0	0.0	0.0
Strychnos usambarensis (Loganiaceae)	0.0	0.0	1.0	3.5	1.4
Syzygium guineense (Myrtaceae)	0.0	0.0	0.0	0.0	5.7
Teclea nobilis (Rutaceae)	15.4	14.0	11.8	3.5	2.9
Teclea sp. (Rutaceae)	0.0	0.0	1.2	0.0	0.0
Toona ciliata (Meliaceae)	0.0	0.6	4.1	2.4	0.0
Trema orientalis (Ulmaceae)	5.1	0.6	0.5	0.0	0.0
Trichilia emetica (Meliaceae)	5.1	4.5	2.9	2.4	4.3

Table 2. Continued.

Species (Family)	Undisturbed plots 1981	Undisturbed plots 1999	LHD transects	HHD transects	CD transects
Trilepisium madagascariense (Moraceae)	16.0	16.8	21.2	5.9	15.7
Vangueria apiculata (Rubiaceae)	0.6	0.6	0.0	2.4	0.0
Vangueria volkensii (Rubiaceae)	0.0	0.0	4.3	0.0	0.0
Vitex keniensis (Verbenaceae)	0.0	0.0	1.0	1.2	1.4
Zanthoxylum gillettii (Rutaceae)	6.9	9.5	7.7	9.4	22.9
Zanthoxylum mildbraedii (Rutaceae)	0.0	0.0	1.0	1.2	0.0
Unidentified[a]	4.6	2.2	1.0	1.2	0.0
Total	378.2	414.4	364.1	358.4	582.9

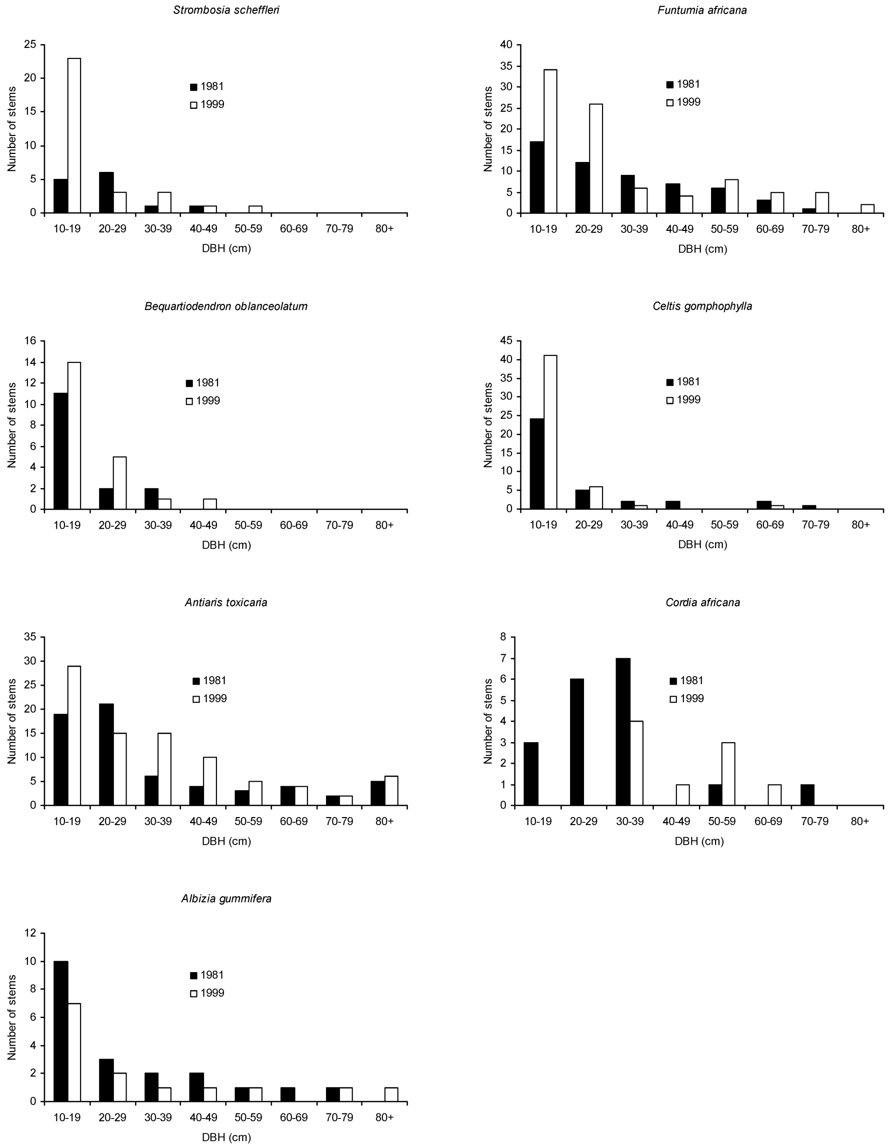
[a] Includes 6 species for undisturbed plots 1981, 3 species for undisturbed plots 1999, 1+ species for LHD transects, 1 species for HHD transects, and 0 species for CD transects.

Statistically significant changes in stem density for individual species could not be detected because no species was represented by $\geqslant 100$ stems (Condit 1995). However, there were several relatively common species ($\geqslant 10$ stems/ha during either survey) that underwent marked changes in density ($\geqslant 30\%$) between 1981 and 1999 (Figure 3). Among these species, stem density increased in *Strombosia scheffleri* by 134%, *Funtumia africana* (syn. *F. latifolia*) by 60%, *Bequartiodendron oblanceolatum* by 36%, *Celtis gomphophylla* (syn. *C. durandii*) by 33%, and *Antiaris toxicaria* by 31%. Stem density decreased markedly in only two common species: *Cordia africana* by 51% and *Albizia gummifera* by 32%.

Of the top 10 species in terms of stem density in 1981, nine remained in the top 10 in 1999. The only change involved *Celtis africana*, a pioneer species, dropping out of the top 10 and being replaced by *Strombosia scheffleri*, a climax species. Stem densities of all pioneer tree species combined fell from 86.7 stems/ha in 1981 to 68.2 stems/ha in 1999, a decline of 21%. Most pioneer species present at Isecheno exhibited very poor recruitment into the smaller stem size classes between 1981 and 1999 (Figure 4).

Comparison of sites with different disturbance regimes

The species–area curve for the LHD site is approaching an asymptote, but the smaller areas surveyed in the HHD and CD sites resulted in species–area curves for these sites that have yet to level off (Figure 5). A total of 64 species (1 unidentified) were recorded in the LHD forest, 53 species (1 unidentified) in the HHD forest, and 52 species (0 unidentified) in the CD forest (Table 1). However, when rarefaction is used to account for differences in area sampled, species richness is estimated at 50.1 (±2.5) in the LHD area, 53.0 (±0.0) in the HHD area, and 48.4 (±1.6) in the CD area. Controlling for area sampled by analyzing a randomly selected sample of 14 0.05 ha subplots in each study area, species diversity (H') was 3.33 in the LHD forest, 3.54 in the HHD forest, and 3.35 in the CD forest, while



Strombosia scheffleri

Funtumia africana

Bequartiodendron oblanceolatum

Celtis gomphophylla

Antiaris toxicaria

Cordia africana

Albizia gummifera

Figure 3. Stem size class distributions (⩾10 cm DBH) of species that underwent marked changes in density (⩾30%) between 1981 and 1999.

species evenness (*J*) was 0.86 in the LHD forest, 0.90 in the HHD forest, and 0.85 in the CD forest.

Stem density was much higher in the CD area (582.9 stems/ha) than in the HHD (357.6 stems/ha) or LHD (364.1 stems/ha) areas (Table 1). In fact, when 14 0.05 ha subplots are randomly chosen from each area, stem density per subplot differs sig-

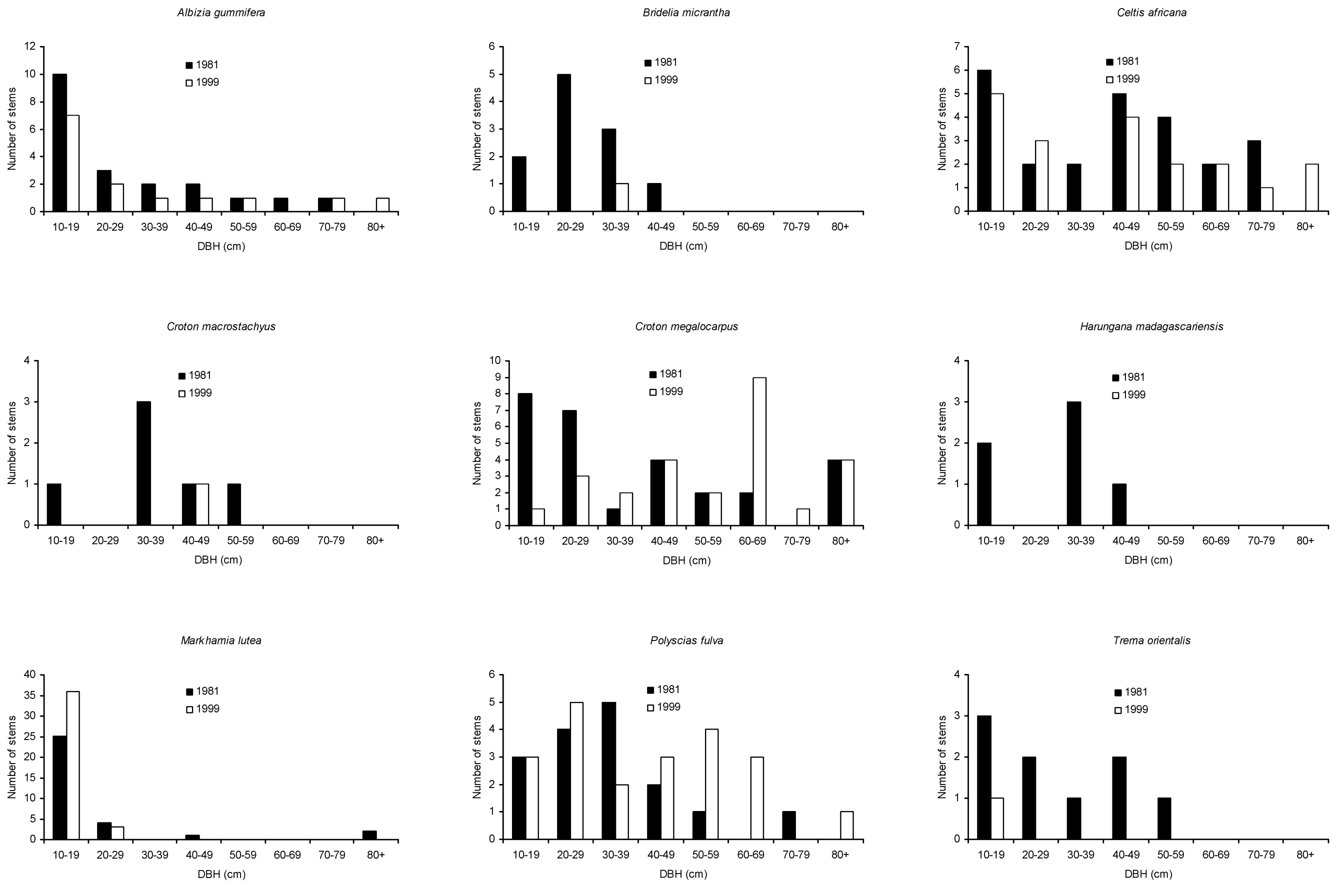


Figure 4. Stem size class distributions ($\geqslant 10$ cm DBH) of pioneer species in the 1981 and 1999 plots.

nificantly between the three areas (Kruskal–Wallis test: KW = 96.2, df = 2, $P < 0.001$). However, a *post hoc* comparison between treatments (Siegel and Castellan 1988) reveals that only the differences between the LHD and CD areas and between the HHD and CD areas are significant. Stem density of pioneer species was much higher in the CD area (214.3 stems/ha) than in the HHD (81.3 stems/ha) and LHD areas (63.8 stems/ha). Mean DBH also differed considerably between areas and was much larger in the HHD area (42.1 ± 1.8 cm) than in the CD (26.5 ± 1.0 cm) and LHD (32.7 ± 0.7 cm) areas (Table 1).

The size class distributions of stems differ markedly among sites (Figure 6). When trees are divided into eight DBH categories (10–19, 20–29, 30–39, 40–49, 50–59, 60–69, 70–79, $\geqslant 80$ cm), there are significant differences in size class distributions between the three sites (Kolmogorov–Smirnov test: $\chi^2 = 86.6$, $P < 0.0001$). Much of this variation results from the vast differences in relative abundance of small stems (10–19 cm DBH) across sites. In fact, the percentage of small stems is so low in the HHD area that it is the one area in this study that does not conform to an inverse J distribution.

Discussion

Long-term tree population dynamics in central Isecheno

The results of our long-term study suggest that the forest in the central plots at Isecheno has remained in good condition since monitoring began in 1981. We base our positive assessment of the forest's condition on several key results. First, DBH class distribution took the shape of an 'inverse J' curve (Mori et al. 1989) in both 1981 and 1999, an indication that the forest has consistently maintained a size class distribution typical of a natural rainforest over the past 18 years (Richards 1996). Second, DBH class distribution did not differ significantly between the two study periods, suggesting that the tree community has been structurally stable over the course of our study (Swaine et al. 1987; De Oliveira and Mori 1999). Third, rates of tree species immigration and emigration during our 18-year study at Isecheno were similar to those described over a 14-year period for Kade Forest, Ghana, where Swaine et al. (1987) concluded that species composition in the forest was relatively stable. Lastly, the fact that 9 of the 10 densest species in 1981 remained in the top 10 in 1999 indicates that the identities of the species that predominate at Isecheno have changed little over the past two decades.

There is also evidence that the forest in our central study plots at Isecheno is still maturing towards climax forest. For example, the major pioneer species present in 1981 declined by 21% over the next 18 years and most exhibited poor recruitment into the smaller stem size classes. Furthermore, the one new species that entered the top 10 in 1999 was a climax species (*Strombosia scheffleri*), while the species that dropped out was a pioneer species (*Celtis africana*). The decline in species diversity at Isecheno also suggests that the forest was still maturing during

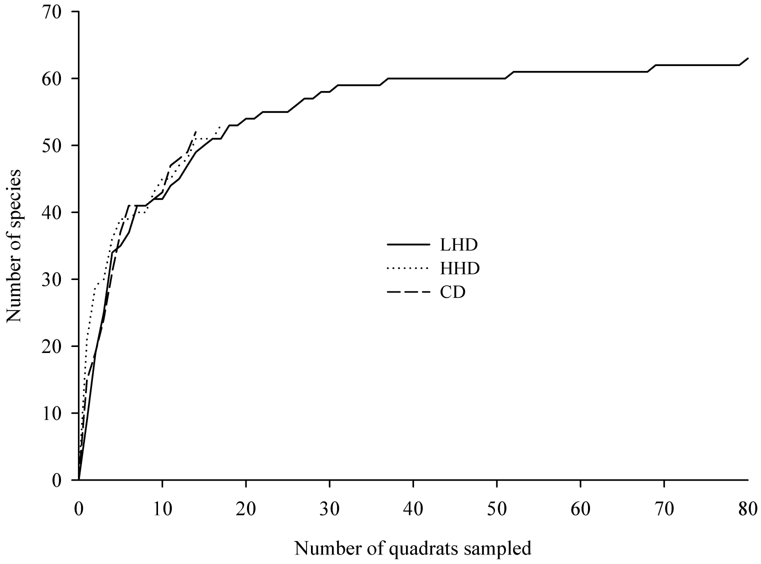


Figure 5. The cumulative species–area relationships for the lightly human disturbed (LHD), heavily human disturbed (HHD), and cattle disturbed (CD) transects. Each quadrat represents an area of 0.05 ha.

our study, since it is common for species diversity to fall as a tropical rainforest passes through the later successional stages after disturbance (Connell 1978; Crow 1980). These results suggest that the forest in central Isecheno is still recovering from the selective logging of large trees that occurred at the site in the 1940s. This scenario is supported by the fact that two of the three species most heavily exploited by loggers at Kakamega in the past (*Antiaris toxicaria*, *Funtumia africana*, *Croton megalocarpus*; Tsingalia 1988) underwent unusually large increases in stem density between 1981 and 1999.

Our results from Isecheno are consistent with Plumptre's (1996) conclusion from a long-term study in the Budongo Forest, Uganda, that even 60–80 years might not be enough time for forest structure to completely recover from selective logging. Unlike at Budongo, however, we have no record of what mature forest at Kakamega looks like and whether the climax stage is mixed rainforest or monodominant rainforest. The fact that Isecheno is not currently close to being dominated by one or several self-replacing shade tolerant tree species (Eggeling 1947; Connell and Lowman 1989; Hart et al. 1989) even 60 years after selective logging, however, suggests that the climax stage at Kakamega is characterized by mixed rather than monodominant forest.

It is encouraging that, despite the intense population pressure in the Kakamega region, forest in the central study plots at Isecheno showed no overt signs of disturbance and appeared to improve in condition between 1981 and 1999. An alternative viewpoint, which can only be ruled out completely through continued long-term monitoring, is that the forest in the study plots has been disturbed in recent

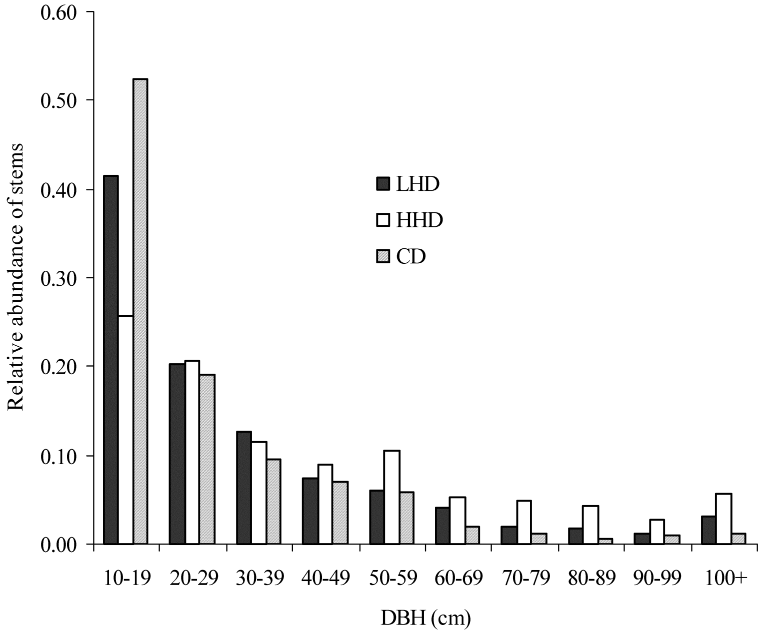


Figure 6. Size class distribution of stems ⩾10 cm DBH in the LHD, HHD, and CD transects.

decades, but that the impacts of this human exploitation were not perceptible in our study due to the variables we took into account and the scales of time and space we considered. For example, our study did not examine parameters such as growth and mortality for individual species that are often monitored in other long-term studies (Manokaran and Kochummen 1987; Milton et al. 1994). Furthermore, it is possible that definitive changes in forest structure occurred in trees <10 cm DBH, a size class we did not monitor (Hubbell and Foster 1992). Lastly, the time scale considered in our study may have been too short for the deleterious effects of human population pressure to be apparent. Some conservationists argue that the effects of low intensity environmental degradation can remain imperceptible for considerable periods of time before the true extent of the damage they have wrought is expressed (Barnes 1990).

Comparison between areas with different levels and types of disturbance

Tree population parameters differed considerably among the three disturbed study sites. The low mean DBH, high overall stem density, and high pioneer species stem density suggest that the CD site is at an earlier stage of succession than the other disturbed sites. This situation is not surprising considering the negative impact cattle are known to have on regeneration in South American forests (Veblen et al. 1992; Relva and Veblen 1998). By recurrently browsing and trampling undergrowth along the CD transect at Isecheno (personal observation), cattle may be responsible for creating persistent light gaps which facilitate the success of pioneer species and prevent the emergence of shade-tolerant later successional species. Despite its earlier successional stage, this area holds some conservation promise in that it is relatively distant from human settlement, making it somewhat more impractical as a source of wood products. Thus, if cattle herding could be eliminated, the forest might continue regenerating relatively unimpeded at this site.

The prospects for the other intensively disturbed site, HHD, are less promising. The most striking feature of the tree population at this site is that it fails to conform to the inverse J distribution typical of natural rainforests (Richards 1996). The high proportion of large DBH stems suggests recruitment into the smaller size classes is very poor at this site. This poor recruitment is almost certainly due to the site's location on the edge of the forest adjacent to a tea field and human settlement. Local people appear to be heavily exploiting this site as a source of small stems to be used as building materials. For example, the density of the tree species most preferred for pole-cutting in the Kakamega Forest, *Funtumia africana* (Tsingalia 1988), is 2.2–3.4× higher at the other two disturbed sites than it is at the HHD site. Furthermore, only 1 of the 11 *F. africana* stems recorded at the HHD site belonged to the smallest size class, indicating poor recruitment for this species. Considering the ongoing human disturbance and extremely poor overall recruitment that results from it, the forest at this site is likely to remain unnatural for years to come. Only if the human exploitation is curtailed will this site begin the process of increasing recruitment into the small size classes again.

Not surprisingly, the LHD site appears to be in the best condition of the disturbed sites. Though comparisons between transects and plots must be made cautiously, tree population parameters for the LHD site are generally more similar to those for Forrestel's nearby relatively undisturbed plots than they are to those for the other disturbed sites. The major differences in tree population parameters between the LHD transects and Forrestel's plots are that the overall stem density is 12% lower and the density of stems in the smallest size class is 29% lower in the LHD transects. These results indicate poorer recruitment in the LHD transects than in the plots, which suggests there may be some illegal pole-cutting even in this area by local people. Nevertheless, the inverse J distribution and the population parameters that generally resemble those for the nearby plots suggest that the LHD transects are in the best condition of the three disturbed sites.

Conclusions and recommendations

Our long-term research suggests that conservation activities carried out in central Isecheno over the past few decades have been effective. Because of its proximity to the forest station and perhaps also its location in the heart of an area where scientists have conducted biological research over the past three decades (Zimmerman 1972; Cords 1987; Copeland et al. 1996; Fashing 2001), central Isecheno has not suffered from the disturbance that has clearly affected the HHD and CD sites on its periphery. While it is encouraging that central Isecheno appears to have fared well in recent years, it is alarming to contemplate the level of disturbance that might be occurring further afield if areas like the HHD and CD sites less than 1 km away are in such poor condition.

Indeed, the heterogeneity in forest condition over small spatial scales revealed by our study underscores the challenges of making representative surveys in forests like this one, where human influence is not uniformly distributed in space. In the Kakamega Forest, surveys are urgently needed to determine the status of the forest remaining outside of the relatively well-protected sites like Isecheno and Buyangu (Mutangah et al. 1992; Kiama and Kiyiapi 2001). Further long-term research on tree population dynamics in both undisturbed and disturbed regions of the forest will be critical to improving our understanding of the levels and types of disturbance the forest can withstand before adverse effects begin to emerge. With the high human population in the region, it will be difficult to terminate illegal activities in the forest, but protection efforts will need to increase if much forest is to remain outside of the few areas which are currently effectively protected.

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References

Barnes R.F.W. 1990. Deforestation trends in tropical Africa. African Journal of Ecology 28: 161–173.

Beentje H.J. 1994. Kenya Trees, Shrubs and Lianas. National Museums of Kenya, Nairobi, Kenya.

Brooks T.M., Pimm S.L. and Oyugi J.O. 1999. Time lag between deforestation and extinction in tropical forest fragments. Conservation Biology 13: 1140–1150.

Cannon C.H., Peart D.R., Leighton M. and Kartawinata K. 1994. The structure of lowland rain-forest after selective logging in West Kalimantan, Indonesia. Forest Ecology and Management 67: 49–68.

Chapman C.A. and Chapman L.J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. Biotropica 29: 396–412.

Chapman C.A. and Chapman L.J. 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. Conservation Biology 13: 1301–1311.

Chapman C.A., Chapman L.J., Wrangham R., Isabirye-Basuta G. and Ben-David K. 1997. Spatial and temporal variation in the structure of a tropical forest. African Journal of Ecology 35: 287–302.

Condit R. 1995. Research in large, long-term tropical forest plots. Trends in Ecology and Evolution 10: 18–22.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Connell J.H. and Lowman M.D. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. American Naturalist 134: 88–119.

Connell J.H., Tracey J.G. and Webb L.J. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain-forest tree diversity. Ecological Monographs 54: 141–164.

Copeland R.S., Okeka W. and Corbet P.S. 1996. Treeholes as larval habitat of the dragonfly *Hadrothemis camarensis*. Aquatic Insects 18: 129–147.

Cords M.A. 1984. Mixed Species Groups of *Cercopithecus* Monkeys in the Kakamega Forest, Kenya. Ph.D. Thesis, University of California, Berkeley, California.

Cords M. 1987. Mixed species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. University of California Publications in Zoology 117: 1–109.

Cords M. and Tsingalia H.M. 1982. A Report on Harmful Exploitation of Indigenous Forest in Kakamega (to the Ministry of Tourism and Wildlife). Wildlife Conservation and Management Division, Government of Kenya, Nairobi, Kenya.

Crow T.R. 1980. A rain forest chronicle: a 30 year record of change in structure and composition at El Verde, Puerto Rico. Biotropica 12: 42–55.

De Oliveira A.A. and Mori S.A. 1999. A central Amazonian terra firme forest. I. High tree species richness on poor soils. Biodiversity and Conservation 8: 1219–1244.

Duncan R.S. and Chapman C.A. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecological Applications 9: 998–1008.

Eggeling W.J. 1947. Observations on the ecology of Budongo rain forest, Uganda. Journal of Ecology 34: 20–87.

Fashing P.J. 2001. Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. Behavioral Ecology and Sociobiology 50: 219–230.

Gathua J.M. 2000. Intraspecific Variation in Foraging Patterns of Redtail Monkeys (*Cercopithecus ascanius*) in the Kakamega Forest, Kenya. Ph.D. Thesis, Columbia University, New York.

Hart T.B. 2001. Forest dynamics in the Ituri Basin (DR Congo): dominance, diversity, and conservation. In: Weber W., White L.J.T., Vedder A. and Naughton-Treves L. (eds), African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective. Yale University Press, New Haven, Connecticut, pp. 154–164.

Hart T.B., Hart J.A. and Murphy P.G. 1989. Monodominant and species-rich forests of the humid tropics: causes of their co-occurrence. American Naturalist 133: 613–633.

Hubbell S.P. and Foster R.B. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. Oikos 63: 48–61.

Kent M. and Coker P. 1992. Vegetation Description and Analysis: A Practical Approach. CRC Press, Boca Raton, Florida.

Kiama D. and Kiyiapi J. 2001. Shade tolerance and regeneration of some tree species of a tropical rain forest in western Kenya. Plant Ecology 156: 183–191.

Kokwaro J.O. 1988. Conservation status of the Kakamega Forest in Kenya: the easternmost relic of the equatorial rain forests of Africa. Monographs in Systematic Botany Missouri Botanical Garden 25: 471–489.

Lieberman D. and Lieberman M. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969–1982). Journal of Tropical Ecology 3: 347–358.

Lwanga J.S., Butynski T.M. and Struhsaker T.T. 2000. Tree population dynamics in Kibale National Park, Uganda 1975–1998. African Journal of Ecology 38: 238–247.

Manokaran N. and Kochummen K.M. 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. Journal of Tropical Ecology 3: 315–330.

Milton K., Laca E.A. and Demment M.W. 1994. Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. Journal of Ecology 82: 79–87.

Mori S.A., Rabelo B.V., Tsou C.H. and Daly D. 1989. Composition and structure of an Eastern Amazonian forest at Camaipi, Amapa, Brazil. Boletim do Museu Paraense Emilio Goeldi, Serie Botanica 5: 3–18.

Mutangah J.G., Mwangangi O. and Mwaura P.K. 1992. Kakamega Forest: A Vegetation Survey Report. Kenya Indigenous Forest Conservation Project, Nairobi, Kenya.

Opala K. 2002. Kenya: unlucky pawns in forests plunder. Daily Nation (January 22) 2002: 4–5.

Plumptre A.J. 1996. Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. Forest Ecology and Management 89: 101–113.

Relva M.A. and Veblen T.T. 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. Forest Ecology and Management 108: 27–40.

Richards P.W. 1996. The Tropical Rain Forest: An Ecological Study. Cambridge University Press, Cambridge, UK.

Rugene N. 2001. State challenged on conservation. Daily Nation (April 19) 2001: 4–5.

Saldarriaga J.G., West D.C., Tharp M.L. and Uhl C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76: 938–958.

Sheil D. 1995. A critique of permanent forest plot methods and analysis with examples from Budongo Forest, Uganda. Forest Ecology and Management 77: 11–34.

Sheil D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. Plant Ecology 155: 183–199.

Sheil D., Jennings S. and Savill P. 2000. Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest. Journal of Tropical Ecology 16: 765–800.

Siegel S. and Castellan N.J. Jr. 1988. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Struhsaker T.T. 1997. Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation. University of Florida Press, Gainesville, Florida.

Swaine M.D., Hall J.B. and Alexander I.J. 1987. Tree population dynamics at Kade, Ghana (1968–1982). Journal of Tropical Ecology 3: 331–345.

Taylor D.M., Hamilton A.C., Whyatt J.D., Mucunguzi P. and Bukenya-Ziraba R. 1996. Stand dynamics in Mpanga Research Forest Reserve, Uganda, 1968–1993. Journal of Tropical Ecology 12: 583–597.

Tsingalia M.H. 1988. Animals and the Regeneration of an African Rainforest Tree. Ph.D. Thesis, University of California, Berkeley, California.

Uhl C. and Jordan C. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65: 1460–1476.

Veblen T.T., Mermoz M., Martin C. and Kitzberger T. 1992. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conservation Biology 6: 71–83.

Wass P. 1995. Kenya's Indigenous Forests: Status, Management, and Conservation. IUCN, Gland, Switzerland.

Whitmore T.C. 1984. Tropical Rain Forests of the Far East. Clarendon Press, Oxford, UK.

Zimmerman D.A. 1972. The avifauna of the Kakamega Forest, western Kenya, including a bird population study. Bulletin of the American Museum of Natural History 149: 257–339.