RECOVERY OF KAKAMEGA TROPICAL RAINFOREST FROM ANTHROPOGENIC DISTURBANCES

FM Mutiso[1], J Hitimana[2], JL Kiyiapi[3], FK Sang[4] & E Eboh[5]

[1]*South Eastern Kenya University, School of Environment and Natural Resources Management, PO Box 170 Kitui-90200, Kenya; mutifestox@yahoo.com*
[2]*Kabiaga University, School of Natural Resource Management, PO Box 1 Kericho-20201, Kenya*
[3]*Ministry of Education, PO Box 30040-00100, Nairobi*
[4]*University of Eldoret, School of Natural Resource Management, PO Box 1125 Eldoret-30100, Kenya*
[5]*University of Nigeria, Department of Agricultural Economics, Nsukka*

MUTISO FM, HITIMANA J, KIYIAPI JL, SANG FK & EBOH E. 2013. Recovery of Kakamega tropical rainforest from anthropogenic disturbances. Kakamega forest in south-western Kenya has been selectively logged since the 1940s. A study on its recovery from anthropogenic disturbances compared data from studies carried out in 1981, 1999 and 2006 in central Isecheno block of Kakamega forest. In the 2006 study, a low number of species was recorded compared with those of 1981 and 1999. In the undisturbed plots, 13 species were isolated which underwent marked changes in stocking: *Funtumia africana, Antiaris toxicaria, Bersama abyssinica, Blighia unijugata, Cassipourea ruwenzorensis, Celtis mildbraedii, Ficus sur, Markhamia lutea, Polyscias fulva, Sapium ellipticum, Teclea nobilis, Trichilia emetica* and *Trilepisium madagascariense.* In all undisturbed and disturbed (plots and transects) sites, *A. toxicaria* and *F. africana* were among the top 10 most abundant species. Currently, man-made trails are the main disturbance affecting Kakamega forest ecosystem. However, this forest is recovering and maturing towards climax as evidenced by a decline in species diversity, increment in density and diameter at breast height over the 25-year period. There are indications of ecosystem sustainability, resiliency and integrity retention after disturbance.

Keywords: Selective logging, forest recovery, Isecheno, *Solanum mauritianum*, man-made trails, *Funtumia africana,* Kenya

MUTISO FM, HITIMANA J, KIYIAPI JL, SANG FK & EBOH E. 2013. Pemulihan hutan hujan tropika Kakamega daripada gangguan manusia. Hutan Kakamega di barat daya Kenya mengalami tebangan memilih sejak tahun 1940-an. Pemulihan hutan daripada gangguan manusia ditinjau dengan membandingkan data daripada kajian yang dijalankan pada tahun 1981, 1999 dan 2006 terhadap blok Ischeno tengah di hutan Kakamega. Bilangan spesies adalah lebih rendah dalam kajian tahun 2006 berbanding dengan tahun 1981 dan 1999. Sebanyak 13 spesies dijumpai di dalam plot yang tidak diganggu iaitu *Funtumia africana, Antiaris toxicaria, Bersama abyssinica, Blighia unijugata, Cassipourea ruwenzorensis, Celtis mildbraedii, Ficus sur, Markhamia lutea, Polyscias fulva, Sapium ellipticum, Teclea nobilis, Trichilia emetica* dan *Trilepisium madagascariense*. Penstokan spesies tersebut berubah dengan ketara dengan masa. *Antiaris toxicaria* dan *F. africana* merupakan antara 10 spesies terbanyak dalam semua tapak tak diganggu dan yang diganggu (plot dan transek). Pada masa ini, rintis buatan manusia merupakan gangguan utama yang mempengaruhi ekosistem hutan Kakamega. Namun, hutan ini sedang melalui proses pemulihan dan kematangan menuju klimaks. Ini adalah kerana dalam tempoh 25 tahun, kepelbagaian spesies di dalam hutan telah berkurang, bilangan pokok telah bertambah dan diameter pokok pada aras dada juga telah bertambah. Ekosistem menunjukkan tanda-tanda mampan, mudah pulih dan pengekalan ciri selepas gangguan.

INTRODUCTION

Logging damages trees and seedlings, affecting the potential for future crops and consequently the sustainability of the forestry operation (Gaaf 1986, UNO 1994). A high level of damage will change the floristic and faunal composition. Forest health may be defined as a condition whereby a forest has the capacity for recovery from a wide range of disturbances while retaining its ecological integrity. However, when such disturbances are beyond a critical limit, the ecosystem can switch to an alternative state to the detriment of all biota in habitation (Kumar 2001, Mutiso et al. 2011). Unless an ecosystem has in-built resilience to disturbances, the future flora and fauna may be at risk. The greater the change from natural regeneration dynamics,

the more likely that animal food availability and niche distribution will change (UNO 1994). In a long-term study in Budongo forest, Uganda, Plumptre (1996) concluded that even 60–80 years were not enough for a tropical rainforest to completely recover from effects of selective logging. Selective logging leads to gap formation that is the principal site for spontaneous forest rejuvenation whereby a mature tree, often senescent, releases a site for occupation of new individuals (UNO 1994).

At mount Elgon, invasion by *Solanum mauritianum* (weed) occurred and out-competed regeneration of all the other once dominant species (Hitimana et al. 2004, 2006). *Solanum* is an early and prolific seeder. It is considered as invasive alien species with unknown economic value, is fast growing and an aggressive gap coloniser associated with forest disturbance. The weed is slowly penetrating into the Kakamega ecosystem (Mutiso 2009) and Mau forests (Mutiso et al. 2011) through gap colonisation. In forest management terms, gap is where the new crop of economic species should arise through successional development (Gaaf 1986, UNO 1994). Similarly, patches in Kakamega forest were reported as centres of new regeneration (Tsingalia & Kassilly 2010). Kakamega forest has undergone various faunal and floristic changes that threaten the health of the ecosystem (Kiama & Kiyiapi 2001). The forest was subjected to selective logging in the 1940s (Fashing et al. 2003, Fashing 2004). Deforestation and degradation activities in the Kakamega forest have changed the climate, vegetation, flora, fauna and even species composition to such an extent that most of the early description of the forest no longer applies (Kokwaro 1988, Farwig et al. 2006). Kakamega forest has been undergoing landuse changes due to logging, agriculture and other anthropogenic disturbances (Miao 2008). Kakamega ecosystem plays critical roles in the livelihood of local people (Momanyi 2007) and in controlling the rainfall in East and Central Africa. Elsewhere, uses, over-exploitation of products and services as well as severe degradation of most of the tropical forests were documented (Guenter et al. 2011).

During their 18-year study in Kakamega, central Isecheno, Fashing et al. (2003) found that the ecosystem was still recovering and that pioneer species declined by 21% between 1981 and 1999 while new species made up the top 10 most abundant species. It is common for species diversity to decline as tropical rainforests pass through the later successional stages after disturbance (Fashing et al. 2003). The study predicted a climax forest in Kakamega composing of a mixed rather than a monodominant rainforest. Kakamega forest is currently characterised by high incidences of man-made trails for ecotourism and those used by Colobus monkey researchers, forest personnel and local communities (Mutiso 2009, Fashing et al. 2003). Ecotourism trails are affecting the ecosystem negatively by opening up the ecosystem to gap coloniser weeds. Similar negative impacts of trails in Kakamega forest such as vegetation trampling, soil erosion, uncoordinated camp sites, pollution and illegal forest activities were documented by Ouma et al. (2011). Common trail impacts include soil erosion, trail wetness or muddiness, creation of parallel secondary treads and informal side trails, vegetation cover loss or composition change, soil compaction and trail widening (Leung & Marion 1999, 2000).

Kiama and Kiyiapi (2001) stated that disturbance in the forest was not uniform throughout the forest and called for urgent surveys to determine the status of the forest remaining outside the relatively well protected sites such as Isecheno and Buyangu. To ascertain the current status of the forest, we carried out a comprehensive analysis of different studies done at the central Isecheno site between 1981 and 2006 (Table 1). To understand the recovery process from past disturbances, we analysed the current disturbances and tree population dynamics.

MATERIALS AND METHODS

Study site

Kakamega rainforest is the only tropical rainforest in Kenya of the Guineo–Congolian type (Kumelachew 2008, Miao 2008). It once stretched across Central Africa to East Africa. Currently, it consists of a large forest block and six forest fragments (Peters et al. 2009). The main forest block is approximately 8245 ha (excluding natural glades) and forest fragments, from 65 to 1370 ha. This study was conducted in central Isecheno of Kakamega forest (Figure 1). The site is at 0° 19' N, 34° 52' E; elevation 1580 m and 40 km north-west of Lake Victoria (Fashing et al. 2003). It was subjected to selective logging in the

Table 1   Tree population parameters in sampled sections of Kakamega forest between 1981 and 2006

Site	Researcher	Area surveyed (ha)	No. of species	H'	Stem ha^{-1}	Mean dbh (cm)
Undisturbed plot 1981	Cords	1.75	58	3.49	378.3	28.7
Undisturbed plot 1999	Forrestel	1.79	56	3.32	414.0	29.7
Undisturbed plot 2006	Mutiso	1.0	47	3.51	563.0	37.2
Low-human-disturbed transect	Fashing	4.15	64	3.33	364.1	32.7
High-human-disturbed transect	Scully	0.85	54	3.54	357.6	42.1
Cattle-disturbed transect	Scully	0.70	52	3.35	582.9	26.5
Low-human-disturbed plot 2006	Mutiso	1.0	45	3.49	470.0	36.5

H' = Shannon–Wiener index; dbh = diameter at breast height
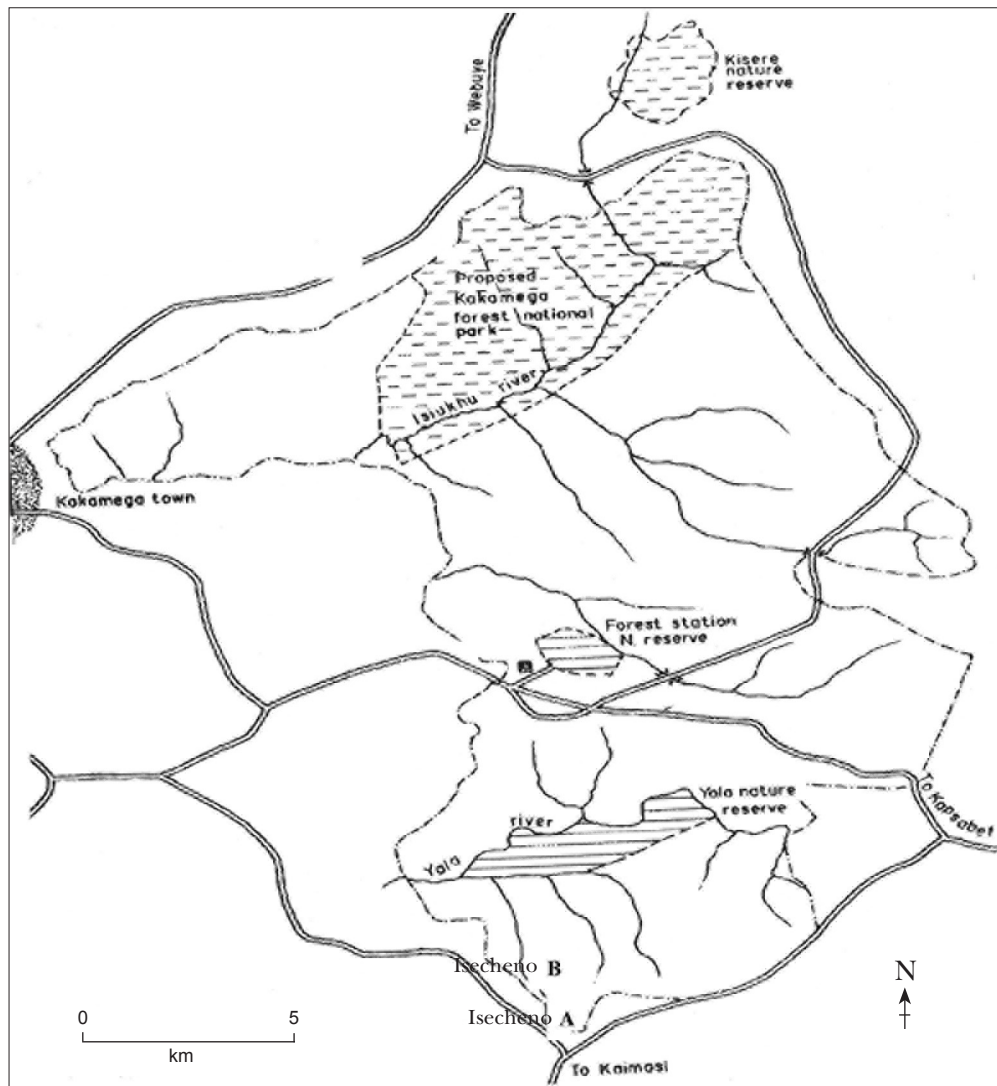
Figure 1   Map of Kakamega forest showing Isecheno A and B

1940s (Fashing et al. 2003). Other anthropogenic activities such as fuelwood extraction, charcoal making, extraction of building and craft materials as well as medicinal products are common (Momanyi 2007, Lung & Schaab 2008). Pioneer species at Kakamega include *Acanthus* sp., *Albizia grandibracteata, Albizia gummifera, Bridelia micrantha, Celtis africana, Croton macrostachyus, Croton megalocarpus, Dombeya burgessiae, Erythrina abyssinica, Harungana madascariensis, Maesa*

lanceolata, Markhamia lutea, Polyscias fulva, Solanum giganteum and *Trema orientalis.* The forest covers approximately 28,200 ha. The area is slightly slopy; soils are well-drained, deep, dark brown, friable sandy loams with pockets of poorly-drained soils. Rainfall averages approximately 2000 mm year^{-1} (Fashing et al. 2003), ranging from 1956 mm (Kokwaro 1988; measured in a nearby town over 40–60 years from 1923 till 1998) to 2215 mm (Cords 1984; measured at the study site from 1976 till 1981). The mean annual temperature ranges from 28 to 32 °C, with maximum at 11 °C and minimum, 13 °C.

Data collection

To evaluate the long-term tree population dynamics of central Isecheno site, we used maps and field notes from research works done by Cords in 1981 (Cords 1984) as well as Fashing, Forrestel and Scully (Fashing et al. 2003) to relocate the plots. Plots were subdivided into 5 m × 5 m subplots and the identity and diameter at breast height (dbh) of all trees ≥ 5cm were recorded. A 1-ha plot was also established in the relatively disturbed area in central Isecheno. Data from disturbed site were compared with similar ones collected in the same region in previous studies. Efforts were made to evaluate and document the current disturbances in both undisturbed and disturbed plots. All studies between 1981 and 2006 used tree density and dbh as well as disturbance regimes to study tree population dynamics.

Data analysis

The current anthropogenic disturbances were subjected to analysis of variance (ANOVA) to detect and isolate significant statistical differences in their occurrences. Spearman correlation analysis was conducted to isolate any correlations. Density and mean dbh of species in the sampled area were calculated. Species diversity was calculated using the Shannon–Wiener index (H'):

$$H' = [N \times \ln N - \Sigma(n_i \times \ln n_i)]/N$$

where n_i = number of individual of species i and $N = \Sigma n_i$.

Species that underwent marked density changes between 1981 and 2006 were isolated. The top 10 most abundant species in the various studies were recorded.

RESULTS

Although the undisturbed plot was located in the interior of the forest, incidences of disturbances were evident. The most prevalent disturbance in the low-human-disturbed site was footpath (Figure 2). A Spearman correlation analysis showed positive correlation between tree cutting and dead branch/stump ($r_s = 0.57$, n = 10, p = 0.015) in the undisturbed plot. A similar relationship was observed between tree
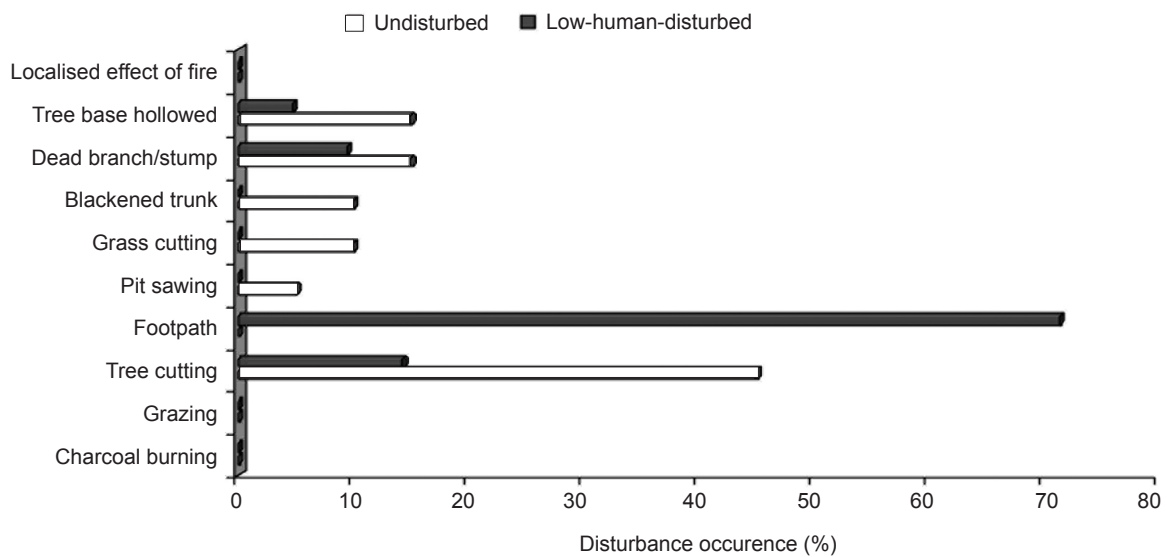
Figure 2   Anthropogenic disturbance occurrence (%) in sampled sections of Kakamega forest in 2006

cutting and footpath (r_s = 0.49, n = 10, p = 0.008) in the low-human-disturbed site. Significant differences (p = 0.008) in the prevalence of anthropogenic disturbances existed.

Lower number of species was recorded in 2006 compared with 1981 and 1999 (Table 1). However, higher density and mean dbh were observed in 2006 except for high-human-disturbed and cattle-disturbed transects respectively (Table 1).

All plots and transects were located in central Isecheno block of Kakamega forest (Figure 1). Cords and Forrestel used the same plots (see Table 1).

The 2006 study captured newcomers: *A. grandibracteata, Bosguiea phaberos, Clausena anisata, Hagenia abyssinica, Morus lactea* and *Macaranga kilimandscharca* (Table 2). Apart from *B. phaberos* and *M. lactea*, the other

Table 2   Density of ≥ 5cm diameter at breast height (dbh) trees in all plots

Species	Undisturbed			Disturbed			
	Plot 1981	Plot 1999	Plot 2006	LHD transect	HHD transect	CD transect	LHD plot 2006
Acrocarpus flaxinifolius	2.3	0.0	0.0	0.2	4.7	0.0	0.0
Alanguium chinanse	0.0	3.9	0.0	1.0	0.0	8.6	0.0
Albizia gummifera	11.4	7.8	2.0	8.4	2.4	8.6	1.0
Aningeria altissima	9.1	8.9	18.0	7.0	2.4	7.1	20.0
Antiaris toxicaria	36.6	48.0	50.0	38.1	50.6	25.7	40.0
Acanthus pubescens	0.0	0.0	2.0	0.0	0.0	0.0	4.0
Albizia grandibracteata	0.0	0.0	0.0	0.0	0.0	0.0	2.0
Bequaertiodendron oblancealatum	8.6	11.7	0.0	8.4	2.4	8.6	0.0
Bersama abyssinica	5.1	3.9	6.0	1.2	1.2	1.2	4.0
Bischofia javonica	0.6	0.6	2.0	2.9	3.5	8.6	0.0
Blighia unijugata	16.0	14.0	23.0	10.4	4.7	8.6	20.0
Bridelia micrantha	6.3	0.6	0.0	2.2	4.7	24.3	0.0
Bosquiea phaberos	0.0	0.0	13.0	0.0	0.0	0.0	17.0
Canthium keniense	0.0	0.0	0.0	1.7	0.0	1.4	0.0
Casaeria battiscombei	1.7	4.5	0.0	1.7	4.7	5.7	0.0
Cassipourea ruwensorensis	2.9	8.4	21.0	6.0	2.4	11.4	17.0
Celtis africana	13.7	10.6	0.0	18.6	15.3	11.4	0.0
Celtis gomphophylla	20.6	27.4	0.0	21.2	22.4	12.9	0.0
Celtis mildbraedii	0.0	0.6	10.0	0.0	0.0	0.0	12.0
Chaetacme aristata	8.6	5.6	2.0	6.3	17.6	2.9	4.0
Chrysophyllum albidum	2.9	1.1	0.0	1.0	0.0	2.9	0.0
Cordia africana	10.3	5.0	2.0	8.2	7.1	4.3	2.0
Cordia millenii	0.0	0.0	0.0	0.0	0.0	1.4	0.0
Craibia brownii	0.0	0.0	37.0	0.2	0.0	0.0	22.0
Croton macrostachyus	3.4	0.6	0.0	0.0	1.2	0.0	0.0
Croton megalocarpus	16.0	14.5	3.0	14.9	16.5	35.7	5.0
Croton slyvaticus	12.0	9.5	6.0	6.7	5.9	8.6	2.0
Cuppressus sp.	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Celtis durantii	0.0	0.0	28.0	2.4	7.1	1.4	18.0
Clausena anisata	0.0	0.0	1.0	0.0	0.0	0.0	3.0
Clausena mildbraidii	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diospyros abyssinica	3.4	2.8	0.0	2.4	7.1	1.4	0.0
Dovyalis macrocalyx	0.0	0.0	23.0	0.7	0.0	0.0	27.0
Drypetes gerrardii	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Ehretia cymosa	5.1	3.4	0.0	2.2	4.7	2.9	0.0
Fagaropsis angolensis	0.0	0.0	0.0	0.0	1.2	0.0	0.0
Ficus exasperata	21.1	25.1	0.0	30.4	8.2	17.1	4.0
Ficus lutea	0.6	1.1	2.0	0.2	2.4	1.4	2.0

(continued)

Table 2 (continued)

Species	Undisturbed			Disturbed			
	Plot 1981	Plot 1999	Plot 2006	LHD transect	HHD transect	CD transect	LHD plot 2006
Ficus ovata	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Ficus sur	7.4	8.9	13.0	8.9	4.7	1.4	7.0
Ficus sycomorus	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Ficus thonningii	0.6	0.0	0.0	1.9	2.4	1.4	0.0
Funtumia africana	31.4	50.3	117.0	28.9	12.9	44.3	103.0
Harungana madagascariensis	3.4	0.0	2.0	1.9	7.1	94.3	0.0
Heinsenia diervillioides	1.7	5.6	0.0	0.0	1.2	5.7	0.0
Hagenia abyssinica	0.0	0.0	4.0	0.0	0.0	0.0	2.0
Khaya anthotheca	0.0	0.0	0.0	0.0	11.8	0.0	0.0
Kigelia africana	0.0	0.0	0.0	0.0	1.2	0.0	0.0
Kigelia moosa	0.6	0.6	0.0	1.4	3.5	0.0	0.0
Lepidotrichilia volkensii	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Maesa lanceolata	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Maesopsis eminii	2.9	0.6	0.0	2.2	1.2	12.9	0.0
Manilkara butugi	1.1	0.6	0.0	2.2	1.2	2.9	0.0
Margaritaria discoidea	5.7	0.0	0.0	2.4	0.0	1.4	0.0
Markhamia lutea	18.3	21.8	26.0	10.8	12.9	5.7	12.0
Milicia excelsa	0.6	1.7	0.0	4.8	1.2	0.0	0.0
Monontora myristica	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Morus mesozygia	0.6	6.1	0.0	3.6	5.9	5.7	0.0
Morus lactea	0.0	0.0	13.0	0.0	0.0	1.4	0.0
Macaranga kilimandschrica	0.0	0.0	1.0	0.0	0.0	0.0	1.0
Olea capensis	5.7	5.0	1.0	6.5	5.9	1.4	3.0
Oncoba spinosa	0.0	0.0	0.0	0.0	0.0	1.4	0.0
Phyllanthus inflatus	0.0	3.9	0.0	0.0	0.0	0.0	0.0
Phyllanthus sp.	0.0	0.6	0.0	0.0	0.0	0.0	0.0
Polyscias fulva	9.1	11.7	16.0	6.0	20.0	34.3	12.0
Premna angolensis	4.0	2.2	0.0	1.7	2.4	0.0	0.0
Prunus africana	0.6	0.6	2.0	3.1	14.1	8.6	4.0
Psidium guajava	0.0	0.0	0.0	0.0	0.0	12.9	0.0
Rawsonia lucia	0.0	0.6	5.0	0.0	0.0	4.3	11.0
Rinorea brachypetala	0.0	4.5	0.0	1.0	0.0	5.7	0.0
Rothmannia urcelliformis	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Sapium ellipticum	1.1	1.1	14.0	3.9	5.9	1.4	6.0
Solanum mauritianum	0.0	0.0	5.0	1.4	7.1	0.0	2.0
Spathodea campanulata	0.6	1.1	0.0	0.7	0.0	0.0	2.0
Strombosia scheffleri	7.4	17.3	3.0	8.7	8.2	44.3	5.0
Strychnos mitis	0.0	0.6	0.0	0.0	0.0	0.0	0.0
Strychnos usambarensis	0.0	0.0	0.0	1.0	3.5	1.4	0.0
Syzygium guineense	0.0	0.0	0.0	0.0	0.0	5.7	0.0
Teclea nobilis	15.4	14.0	29.0	11.8	3.5	2.9	11.0
Teclea sp.	0.0	0.0	0.0	1.2	0.0	0.0	0.0
Toona ciliata	0.0	0.6	0.0	4.1	2.4	0.0	0.0
Trema orientalis	5.1	0.6	3.0	0.5	0.0	0.0	5.0
Trichilia emetica	5.1	4.5	21.0	2.9	2.4	4.3	29.0
Trilepisium madagascariensis	16.0	16.8	22.0	21.2	5.9	15.7	14.0
Vangueria apiculata	0.6	0.6	0.0	0.0	2.4	0.0	0.0
Vangueria volkensii	0.0	0.0	6.0	4.3	0.0	0.0	0.0
Vitex keniensis	0.0	0.0	0.0	1.0	1.2	0.0	0.0
Zanthoxylum gillettii	6.9	9.5	4.0	7.7	9.4	22.9	2.0
Zanthoxylum mildbraedii	0.0	0.0	0.0	1.0	1.2	0.0	0.0
Unidentified	4.6	2.2	0.0	1.0	1.2	0.0	0.0
Total	378.2	414.4	563.0	364.1	358.4	582.9	470.0

LHD = low-human-disturbed transect, HHD = high-human-disturbed transect, CD = cattle-disturbed transect

species had very low densities. Species such as *Acrocarpus flaxinifolius, Alanguium chinanse* and *Bequaertiodendron oblancealatum* were captured in previous studies but absent or occurred in low densities in the 2006 study. *Antiaris toxicaria, Blighia unijugata, Funtumia africana, M. lactea, P. fulva, Strombosia scheffleri, Teclea nobilis* and *Trilepisium madagascarensis* each contributed ≥ 10 stems ha^{-1} in most of the sites. These eight species contributed largely to the overall density. However, *Cassipourea ruwenzorensis, Celtis durantii, Dovyalis macrocalyx, Sapium ellipticum* and *Trichilia emetica* contributed largely to the overall density in 2006 but none or very little in the previous studies. On the contrary, *C. africana, Celtis gomphophylla, C. megalocarpus, Ficus exasperata* and *Zanthoxylum gillettii* contributed largely to the overall density in previous studies but none or very little in 2006.

In the undisturbed plots of 1981, 1999 and 2006, 13 species underwent marked density changes (Table 3). The 13 contributed 43.5% of overall density in 1981, 49.2% in 1999 and 65.4% in 2006. Recruitment of *Celtis mildbraedii* and *S. ellipticum* into mature stages seemed to have occurred greatly between 1981 and 2006. While *A. toxicaria* had the highest density in 1981, *F. africana* seemed to have taken the lead in 1999 and 2006. Significant differences (p = 0.012) and strong positive correlations in density changes in 1981, 1999 and 2006 (r_s = 0.079, n = 12, p = 0.001) were recorded.

Funtumia africana and *A. toxicaria* were among the top 10 most abundant species occupying position one and two respectively in the undisturbed plots of 1981, 1999 and 2006 (Table 4). In 1999, *C. gomphophylla* and *Croton slyvaticus* dropped from the top 10 and newcomers *B. oblancealatum* and *S. scheffleri* came in to take position nine and five respectively. Between 1999 and 2006, five more species had dropped out and were replaced by newcomers. In the disturbed transects and plot, species not only frequently changed their positions among the top 10 but also dropped out and were replaced by newcomers.

DISCUSSION

In the low-human-disturbed site, high presence of footpaths was due to the frequency of human activities in the forest. For over a decade, a research on the Colobus monkeys had been going on and trails had been regularly cleared to facilitate this. A trail is not only an indicator of forest disturbances but also leads to a chain of other disturbances (Mutiso 2009) such as tree cutting, fuelwood extraction and charcoal making. Vegetation trampling and soil erosion along the trails in Kakamega forest were reported as significant disturbances (Ouma et al. 2011). Forest disturbances in Kakamega forest were reported to be due to human activities such as fuelwood extraction, charcoal making,

Table 3　　Species that underwent marked changes in density between 1981 and 2006

Species	1981	1999	2006
Funtumia africana	31.4	50.3	117.0
Antiaris toxicaria	36.6	48.0	50.0
Bersama abyssinica	5.1	3.9	6.0
Blighia unijugata	16.0	14.0	23.0
Cassipourea ruwensorensis	2.9	8.4	21.0
Celtis mildbraedii	0.0	0.6	10.0
Ficus sur	7.4	8.9	13.0
Markhamia lutea	18.3	21.8	26.0
Polyscias fulva	9.1	11.7	16.0
Sapium ellipticum	1.1	1.1	14.0
Teclea nobilis	15.4	14.0	29.0
Trichilia emetica	5.1	4.5	21.0
Trilepisium madagascarensis	16.0	16.8	22.0
Total	164.4	204.0	368.0

Table 4　　Top 10 large trees (based on density) in all plots

Species	Undisturbed			Disturbed			
	1981	1999	2006	LHD transect	HHD transect	CD transect	LHD plot 2006
Antiaris toxicaria	36.6	48.0	50.0	38.1	50.6	25.7	40.0
Funtumia africana	31.4	50.3	117.0	28.9	12.9	44.3	103.0
Ficus exasperata	21.1	27.4	–	30.4	8.2	17.1	–
Celtis gomphophylla	20.6	–	–	21.2	22.4	12.9	–
Markhamia lutea	18.3	21.8	26.0	10.8	12.9	–	–
Croton megalocarpus	16.0	14.5	–	14.9	16.5	–	–
Blighia unijugata	16.0	14.0	23.0	10.4	–	–	20.0
Celtis africana	13.7	10.9	–	18.6	15.3	11.4	–
Strombosia scheffleri	–	17.3	–	8.7	8.2	44.3	
Croton slyvaticus	12.0	–	–	–	–	–	–
Bequaertiodendron oblancealatum	–	11.7	–	–	–	–	–
Aningeria altissima	–	–	–	–	–	–	20.0
Craibia brownii	–	–	37.0	–	–	–	22.0
Teclea nobilis	–	–	29.0	–	–	–	–
Dovyalis macrocalyx	–	–	23.0	–	–	–	27.0
Trilepisium madascariense	16.0	16.8	22.0	21.2	–	15.7	–
Cassipourea ruwenzorensis	–	–	21.0	–	–	–	17.0
Trichilia emetica	–	–	21.0	–	–	–	29.0
Clausena anisata	–	–	–	–	17.6	–	–
Khaya anthotheca	–	–	–	–	11.8	–	–
Diospyros abyssinica	–	–	–	–	–	–	–
Harungana madagascarensis	–	–	–	–	–	94.3	–
Bridelia micrantha	–	–	–	–	–	24.3	–
Maesopsis eminii	–	–	–	–	–	12.9	–
Bosquiea phaberos	–	–	–	–	–	–	17.0
Celtis durantii	–	–	–	–	–	–	18.0

– = Species that were not among the top 10 most dense species or absent at the time of the study; LHD = low-human-disturbed, HHD = high-human-disturbed, CD = cattle-disturbed

construction and craft industries (Bleher et al. 2006, Momanyi 2007). Differences in disturbance incidence are due to the fact that their prevalence is not uniform (Kiama & Kiyiapi 2001). For instance in the current study, ecotourism trails led to a number of other forest exploitation activities in the disturbed site, while only a few disturbances were evident in the undisturbed site. The sites also experienced selective logging in the 1940s (Lawes et al. 2000, Fashing et al. 2003, Bleher et al. 2006). However, the current forest structure indicates a forest in the process of stabilising, which may take many years. According to Plumptre (1996), even 60–80 years might not be enough for a forest structure to completely recover from selective logging. Despite the intense population pressure in the Kakamega region, forest in the central study sites showed no obvious sign of disturbance and appeared to improve between 1981 and 1999 (Fashing et al. 2003). In the absence of man-made trails for ecotourism development, the greater part of Kakamega forest would not be highly disturbed. For instance, Ouma et al (2011) reported that the high level of trail impacts in the northern part of the Kakamega forest was attributed not

only to tourist visitation but could also be due to illegal use of forest resources (e.g. firewood, grass, medicinal plants) by the adjacent forest community. Tree cutting should be controlled to allow the forest to mature (Barnes 1990, Kumar 2001, Fashing et al. 2003, Mutiso 2009). Effects of ecotourism trails on the long-term tree population dynamics and recovery of Kakamega forest should be conducted since there are no major differences in tree species composition in both disturbed and undisturbed sites.

Differences in species number may be largely attributed to the size of the sampled area. While the current study did a total enumeration of the 2 ha sampled, other researchers sampled more or less than 1 ha except for Fashing et al. (2003). Different sampling designs (plots or transects) were used and could make comparison less authoritative. However, in the current study, the use of larger plots (2 ha) and complete enumeration of all the study parameters as opposed to previous studies gave better understanding of tree population dynamics. The results were comparable since all plots and transects were located in central Isecheno block of Kakamega forest. The reduced number of species coupled with rapid increase in the density and overall mean dbh were, however, a reflection of a maturing forest towards climax, 66 years after the 1940s selective logging. While some studies showed that species diversity peaked at mid-climax, others showed it peaked at climax (Mc-queen 1991). It is common for species diversity to decline as a tropical rainforest passes through the later seral stages (Fashing et al. 2003). Though there is no record of what mature forest at Kakamega will look like and whether the climax stage will be a mixed or monodominant rainforest, the fact that Isecheno is not currently close to being dominated by one or several self-replacing shade-tolerant tree species even 60 years after selective logging suggests that the climax stage at Kakamega will be characterised by a mixed forest community (Fashing et al. 2003). Similar study in Mau tropical forests (Mutiso et al. 2011) documented a recovery process characterised by individualistic successional pathway. A high species diversity implies that there is sharing of resources between many codominant species. The high H' is a clear indication that many species have remained unchanged over the period (Mc-queen 1991). Similar high species diversity was recorded by

Akwee et al. (2010) in Kakamega forest. It is, however, difficult to authoritatively state when species diversity is expected to peak in Kakamega. Generally, species diversity is believed to be low in extreme conditions and high in optimum conditions. In relation to succession, diversity is either highest in a climax forest or peaks in mid-succession towards climax forest (Mc-queen 1991).

The presence of newcomer species is a clear indication that the forest is still in the process of maturing. The fact that the newcomers are still in low densities and are not some of the known self-replacing plants, it is highly possible that they may not be among the most dominant species at climax. Since *B. phaberos* and *M. lutea* are featured among the 17 most species rich category, it is highly possible that the two are among the climax species. Though succession seems to be in progress, characterised by the disappearance of some pioneer species and replacement by newcomers, this study cannot authoritatively state which factor among tree species competitive ability, environment or climatic condition is playing a key role. The succession in Kakamega forest resembles the intermediate model which is a mixture of species positions in succession. According to Bray's criterion, intermediate model is a sequence of species arrivals, with the latest one establishing before the demise of the earliest (Mc-queen 1991). There is a need for an important facilitation and inhibition in Bray's succession model (Mc-queen 1991) where inhibition is shown, apparently by early arrivals of tree species, with their disappearance soon after and a later renewed continued establishment of the same species.

Fertile soils and good climatic conditions in Kakamega translate into high biological diversity, function and productivity (Mutiso 2009). High species diversity in Kakamega forest was reported to be attributed to habitat structure, physical environments, climatic conditions, competition and nutrients that favoured plant growth (Akwee et al. 2010). Such stable sustainability will confer codominant species a competitive advantage over other self-replacing species in the succession cycle (Fashing et al. 2003). According to Mc-queen's resource–ratio model, a temporal gradient of availability of limiting resources such as nitrogen and light levels were relevant to forest succession. The stable rainfall regimes in Kakamega, minimal disturbances and high

species diversity accounted for its sustainability (Fashing et al. 2003). Hitimana et al. (2006) and Mutiso (2009) cautioned the dangers of *S. mauritianum* weed if it found its way into the ecosystem. Similar concerns were expressed by Mutiso et al. (2011) in a study in Mau forests.

Increase in density of individual species and overall density can be attributed to stable regeneration regimes and recruitment. However, it is yet to be established whether *S. ellipticum* and *C. mildbraedii* which increased drastically in 2006 could be some of those species that appeared spasmodically through the succession but with their first prominence at 66 years. While most of these 13 species (Table 3) may persist in varying quantities throughout the succession, it appears that *F. africana* and *A. toxicaria* will be major components of the climax forest. The differences in the 13 species are largely due to environmental and climatic factors, which may have acted additively to the advantage of the species. As the stand matures, changes in soil conditions, organic matter, nitrogen and light levels occur and have impact on subsequent changes in species density and diversity.

While at this stage when the main species of the mature forest are present, chances are that at the final seral stage, there will be a reduction in species richness and density because some of the pioneers including other shade-intolerant species will probably disappear or will be surviving under less optimum conditions to warrant meaningful contribution. As the stand matures, self-thinning will be taking place, resulting in lower density. In relation to both young and older stands, there is reduction in species richness and stocking as a stand passes through various seral stages (Mc-queen 1991). Fragmentation of Kakamega forest had been reported to be modifying the species richness or community composition in the past (Schleuning et al. 2011).

Although over the 25-year period, some species seemed to have either dropped out from the top 10 placings and replaced or changed positions, it is still early to authoritatively state the exact climax community in Kakamega forest. However, it is highly possible that *F. africana* and *A. toxicaria* will be among the climax species because they have remained unchanged over time. Despite the past and present anthropogenic disturbances, Kakamega forest is a mosaic of near primary and secondary forests of different seral stages (Kumelachew 2008). Disturbance plays a

major role in the succession process in Kakamega. Disturbances were reported to fragment the forest block (Miao 2008), open patches for regeneration (Tsingalia & Kassilly 2010) and reduce forest cover (Lung & Schaab 2010). In transects disturbed in 1981 and 1999, tree species frequently changed their positions and were dropped or replaced. Following disturbance, gap colonisers such as *S. mauritianum* aggressively invaded such patches (Hitimana et al. 2004, Mutiso 2009).

CONCLUSIONS

Man-made trails were the main disturbance affecting the ecosystem. The ecosystem was still maturing towards climax as evidenced by a decline in species diversity. It was on its way to recovery from selective logging of the 1940s. The increment in density and mean dbh over 25 years was a measure of ecosystem sustainability and an indicator of ecosystem resilience and integrity retention. The climax forest would likely be a mixed rather than a monodominant rainforest as evidenced by the high species diversity. Many species codominated and *F. africana* as well as *A. toxicaria* would be among the climax species. We strongly recommend regulation of man-made trails in the Kakamega ecosystem. Increase in the density of the alien weed *S. mauritianum* is of concern. Trails offer suitable sites for aggressive invasion by the weed and subsequent out-competing of the natural regeneration of other species. There is a need to study the effects of man-made trails on the long-term tree population dynamics of Kakamega forest.

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