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THE INFLUENCE OF MECHANIZED SELECTIVE LOGGING, FELLING INTENSITY AND GAP-SIZE ON THE REGENERATION OF A TROPICAL MOIST FOREST IN THE KIBALE FOREST RESERVE, UGANDA

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John Massan Kasenene

has been accepted towards fulfillment
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Peter G. Murphy
Major professor

Date December 21, 1987

THE INFLUENCE OF MECHANIZED SELECTIVE LOGGING, FELLING INTENSITY AND GAP-SIZE ON THE REGENERATION OF A TROPICAL MOIST FOREST IN THE KIBALE FOREST RESERVE, UGANDA

By

John Massan Kasenene

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ABSTRACT

THE INFLUENCE OF MECHANIZED SELECTIVE LOGGING, FELLING INTENSITY AND GAP-SIZE ON THE REGENERATION OF A TROPICAL MOIST FOREST IN THE KIBALE FOREST RESERVE, UGANDA

By

John Massan Kasenene

This study was conducted in the Kibale Forest Reserve in Western Uganda. The reserve is Equatorial in position (0° 13' to 0° 41'N and 30° 19' to 30° 32'E) with a medium altitude tropical moist forest. The effects of a mechanized polycyclic felling system on the forest was characterized through study of species composition, structure and the regeneration of tree species with the uncut mature forest as the control. Four contiguous forest tracts, including the control, the lightly cut, the heavily cut, and heavily cut and arboricide-treated forest, were surveyed.

The results clearly indicate that mechanized selective timber harvesting in species-rich tropical moist forest was hard to control and incompatible with minimizing damage and disturbances or creation of forest gaps characteristic of natural forest disturbances. The mean gap size for lightly cut forest was $467m^2$ (range 75 to $1800m^2$) whereas natural tree fall gaps in control forest averaged $256m^2$ (range 100 to $663m^2$). The mean gap size in heavily cut forest was very large, $1307m^2$ (range 73 to $7100m^2$) for heavily cut, and $938m^2$ (range 227 to $3313m^2$) for heavily cut and treated forest.

Mechanized selective logging had detrimental effects on the forests of the reserve which led to drastic decreases in sapling, pole, and tree species richness, distribution, density, diversity, and basal areas for all tree species, including desirable timber or primary forest species. There was also increased tree mortality through windthrows in heavily cut areas where annual rates of 1.7, 1.3, and 3.3 trees/ha for uncut, lightly cut and heavily cut forests, respectively, were observed.

Successful tree seedling, sapling and pole growth was observed at felling intensities below $14m^3$/ha and gap sizes below $650m^2$, whereas regeneration where 17 to $21m^3$/ha of commercial timber had been mechanically removed, and where gaps above $650m^2$ were created, was impoverished. Based on the sapling and pole species richness of unlogged mature forest (control), the forest regeneration 20 years post-felling was less by 28.1% in lightly cut, less by 48.9% in heavily cut and less by 70.8% in heavily cut and treated forest areas. This reflects the effects of the logging system, logging intensity and disturbances in the forests 20 years ago. The chemical treatments contributed to further lowering of the diversity of tree regeneration in heavily cut and treated areas.

It appears, therefore, that the heavily selectively cut tracts of the reserve might have to recover for longer periods than the usual 70 years of harvest cycle for anything resembling an exploitable forest to reappear. Timber extraction through controlled systems that could remove between 2 and 4 canopy trees/ha would cause relatively minor damage to the forest. Pitsawing and forms of polycyclic systems that are more labor intensive than machine based could, if properly controlled, create gaps and disturbances similar to natural tree falls and be very compatible with long term sustained yield timber exploitation of tropical moist forest reserves.

This dissertation is dedicated to
the memory of my brother ISRAEL.

ACKNOWLEDGEMENTS

The author's work alone is by no means the only factor responsible for the accomplishment of a doctoral dissertation. This therefore gives me opportunity to acknowledge the many individuals, organisations and societies who provided support and assistance during the course of my study.

I thank the office of the President, The National Research Council, Uganda and the Uganda Forest Department for giving me permission to conduct research in Uganda and the Kibale Forest Reserve in particular.

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Dr. George Petrides and Dr. Donald Dickmann. To all of them I am most grateful.

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NOMENCLATURE OF PLANTS CITED IN THE TEXT

TREE SPECIES

Albizzia gummifera (Gmel.) C. A. Sm.
Aningeria altissima (A. Chev) Aubrev. & Pellegr.
Antiaris toxicaria (Rumph. ex. Pers.) Lesch.
Aphania senegalensis (Juss. ex Bernh.) Radlk.
Blighia unijugata Bak.
Bosquiea phoberos Baill.
Carapa grandifolia Sprague
Celtis africana Burn. f.
Celtis durandii Engl.
Chaetacmea aristata Planch.
Chrysophyllum gorungosanum G. Don.
Clausena anisata (Willd.) Oliv.
Cordia millenii Bak.
Cynometra alexandri C. H. Wright
Diospyros abyssinica (Hiern) F. White
Entandrophragma utile (Dawe & Sprague) Sprague
Fagara macrophylla (Oliv.) Engl.
Fagaropsis angolensis (Engl.) Dale
Funtumia latifolia (Stapf) Stapf ex Schltr.
Lovoa swynnertonii Bak. f.
Maesa lanceolata Forrsk.
Markhamia platycalyx (Bak.) Sprague
Mimusops bagshawei S. Moore
Neoboutonia macrocalyx Pax
Newtonia buchananii (Baker) Gilb. & Boutique
Olea welwitschii (Knob.) Gilg. & Schellenb.
Parinari excelsa Sabine
Piptadeniastrum africanum (Hook. f.) Brenan
Pterygota mildbraedii Schott. & Endl.
Pygeum africana Hook. f.
Strombosia scheffleri Engl.
Symphonia globulifera L. f.
Teclea nobilis Del.
Trema guineensis Ficalho
Trichilia splendida A. Chev.
Uvariopsis congensis Nov.
Wurbagia ugandensis Sprague

NON-TREE SPECIES

Aspilia africana (Pers.) C. D. Adams
Bidens pilosa L.
Brillantaisia nitens Lindau
Cymbopogon afronardus Schult.
Fleurya urophylla Mildbr.
Imperata cylindrica Beav.
Mimulopsis solmsii Schweinf.
Monechma subsessile Hochst.
Palisota schweinfurthii C. B. Cl.
Pennisetum purpureum Schum.
Pollia condensata C. B. Cl.

Nomenclature after Daydon (1895), Eggeling and Dale (1951) and Hamilton (1981).

GENERAL INTRODUCTION

Historical Background to the Study

The study was conducted in Uganda, a land-locked equatorial country bordered by the Sudan to the North, Kenya to the East, Tanzania and Rwanda to the South and Zaire to the West (Figure 1). Uganda is blessed with a diversity of freshwater lakes, rivers, swamps and great mountain ranges. Consequently, a diversity of habitats occur in the country. Most habitats are transitional between the lowland tropical rain forests of Zaire to the West and the dry savanna of Kenya to the East.

Uganda has several forest reserves, mostly concentrated in the western part of the country (Figure 1). They are government controlled and protected reserves (Kingston, 1967), established to serve several functions, such as protection reserves (e.g. the Ruwenzori and Mount Elgon) or reserves for limited and controlled exploitation. The first legal status of the Kibale Forest Reserve was through gazetting as a crown forest in 1932 and being made a Central Forest Reserve in 1948. It was not until 1963 that consolidated gazetting was effected with the reserve officially covering an area of 560 sq km (Kingston 1967). Two areas within the reserve, one 59.8 km^2 and other only

Figure 1. Approximate locations of major Forest Reserves and geographical features of Uganda. The Forest Reserves include: 1-Zoka, 2-Budongo, 3-Bugoma, 4-Itwara, 5-Kibale (where the research was conducted), 6-Ruwenzori, 7-Kasyoha-Kitomi, 8-Kalinzu, 9-Maramagambo, 10-Impenetrable, 11-Mgahinga, 12-Malabigambo, 13-Mabira and 14-Mount Elgon.

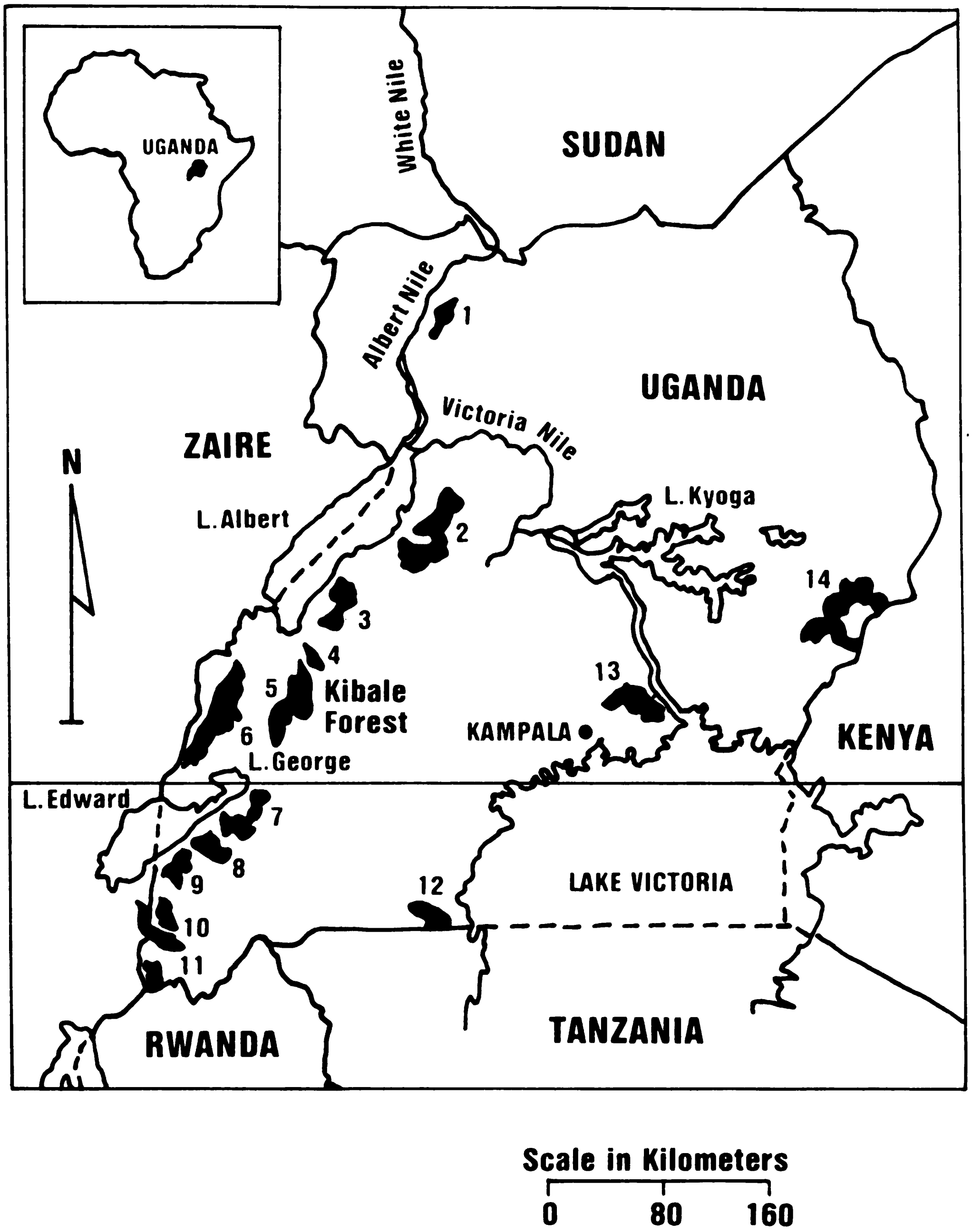
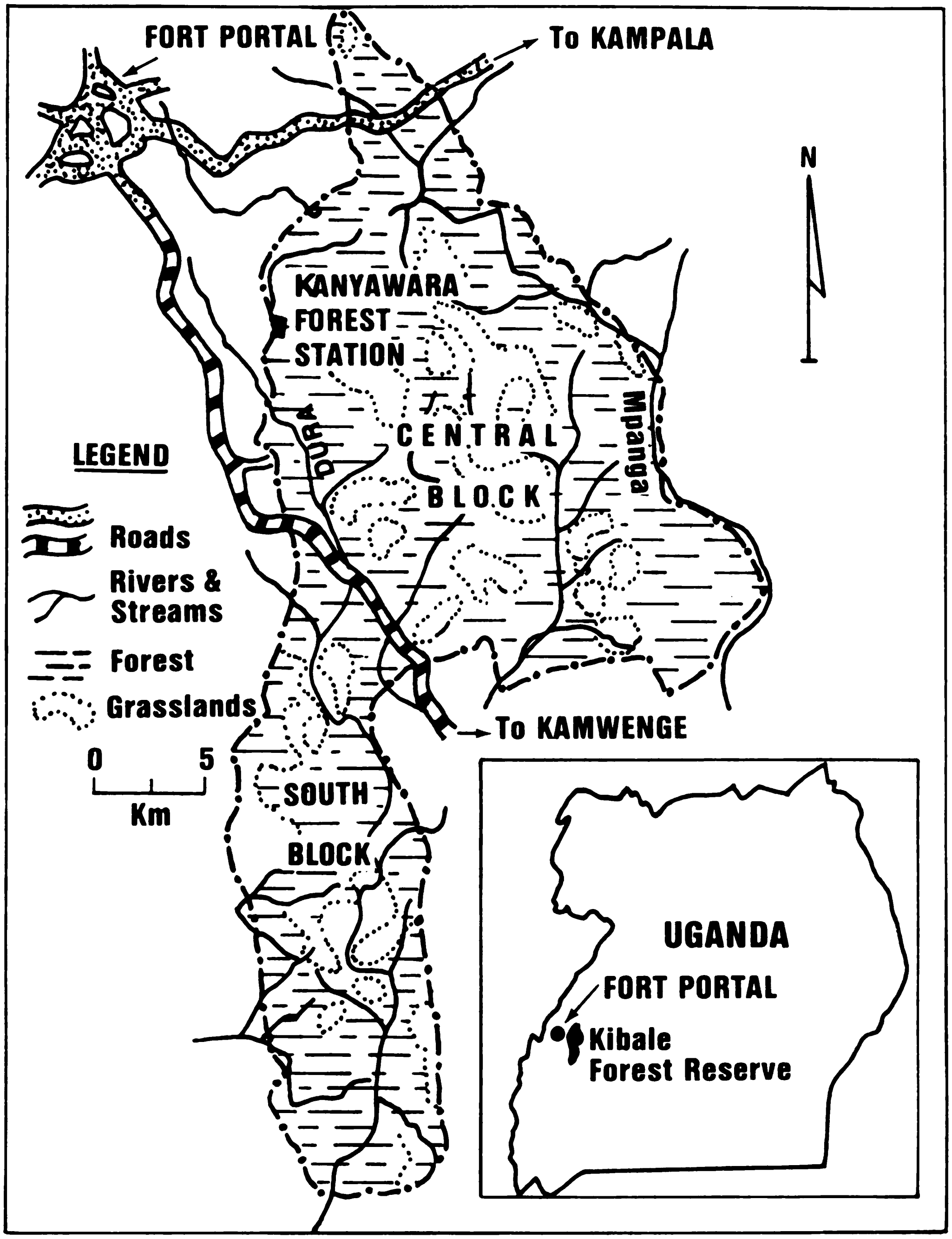

UGANDA
White Nile
SUDAN
Albert Nile
1
UGANDA
Victoria Nile
ZAIRE
N
L. Albert
2
L. Kyoga
14
3
4
5
Kibale Forest
13
6
KAMPALA
KENYA
L. George
0°
L. Edward
7
8
9
12
LAKE VICTORIA
10
11
RWANDA
TANZANIA
Scale in Kilometers
0
80
160

Figure 2. The Kibale Forest Reserve: Showing approximate location of areas protected as Nature Reserves (NR) and the research plot (RP-703) where part of this study was conducted.


FORT PORTAL
To KAMPALA
N
KANYAWARA
FOREST
STATION
DURA
CENTRAL
BLOCK
Mpanga
LEGEND
Roads
Rivers & Streams
Forest
Grasslands
0 5
Km
To KAMWENGE
SOUTH
BLOCK
UGANDA
FORT PORTAL
Kibale
Forest Reserve

2.0 km^2 were declared Nature Reserves (Figure 2) where any form of human interference with nature is strictly prohibited. Another area, 1210 ha, also within the reserve, was designated as Research Plot 703 to promote research.

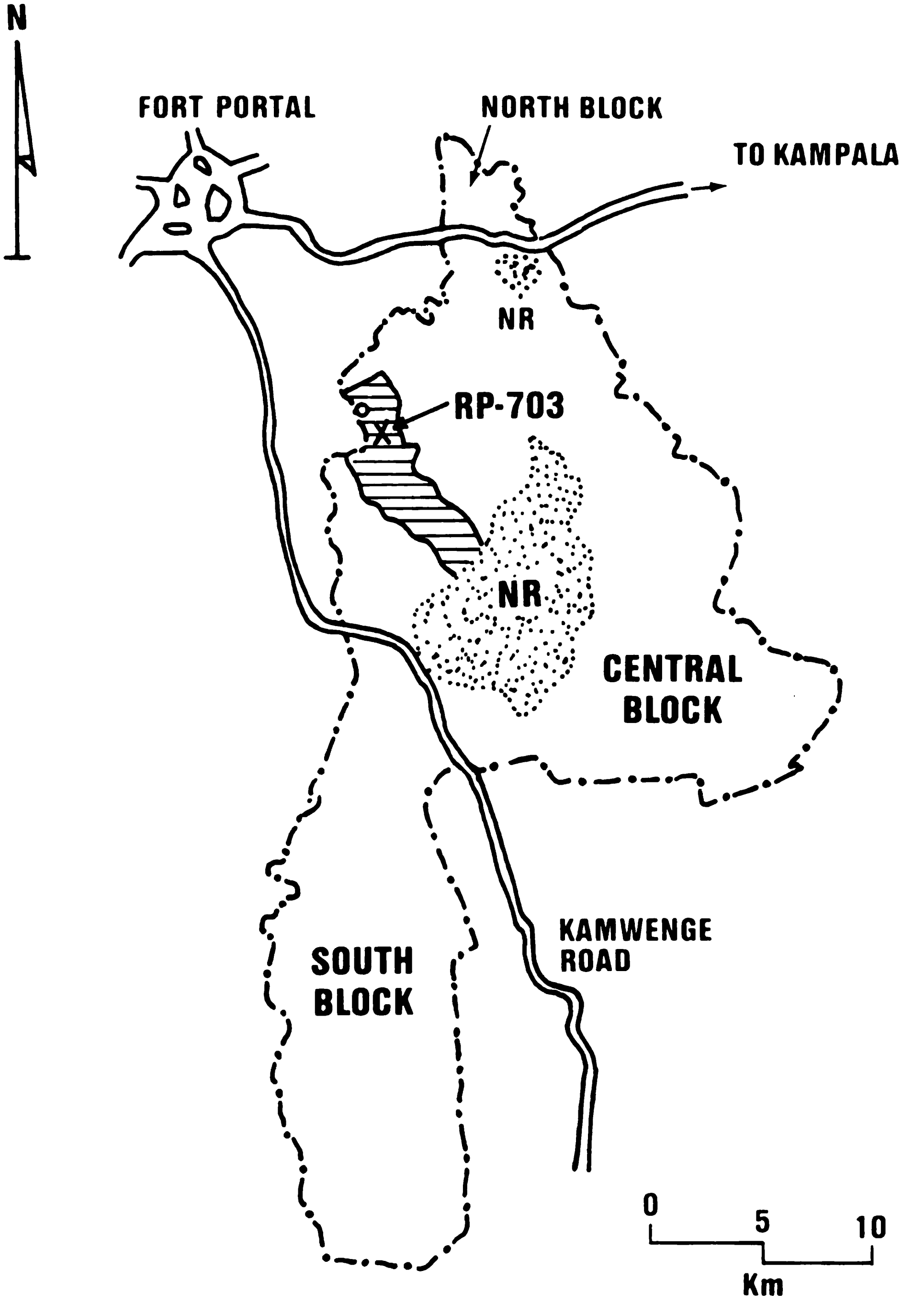
In Uganda, like elsewhere in the tropics, the major cause of forest destruction centers on the conversion of forests to agricultural land, uncontrolled cutting of trees for fuelwood, timber and building poles, and poaching of game (Goodland 1980; Committee on Res. Priorities in Trop. Biol. 1980). With the ever increasing human population as the ultimate cause of forest destruction, the situation in Uganda is expected to be complicated or worsened by changing demographic and social circumstances, economic uncertainty, lack of modern forest laws, and ineffective enforcement of these laws.

The area of Uganda's land now under closed natural forest is well below the 4.6% estimated in 1958 (Langdale-Brown 1960, cited by Hamilton 1984). Currently, the Uganda Forest Department administers 7720 km^2 of natural forest and this represents only 3.3% of Uganda's total area (FAO-UNEP 1981). The Forest Department accepted a system adopted by the sawmillers during the first half of this decade which was a modified form of monocyclic system (Whitmore 1975), apparently destructive to species-rich tropical forests. Trees were harvested regardless of size or rarity and no enrichment planting was undertaken. Extensive damage was done to the remaining trees, poles, seedlings and saplings by the practice of dragging logs over long distances to extraction roads. Sawmill operations of this kind are now underway in Budongo, Mabira and Itwara Forest Reserves. The Forest Department authorities are reluctant to abandon such forest felling practices as there is a lack of strong evidence to challenge the appropriateness of the system. To resolve the predicament, the Kibale Forest Project proposed a study of the current status of regeneration under a range of forest disturbance regimes incuding mechanized logging.

Location of the Study Site and Climate

The Kibale Forest Reserve is a government controlled reserve in Kaborole District, Western Uganda. It is situated approximately 24 km. east of the foothills of the Mountains of the Moon (Ruwenzori) and 10 km from the town of Fort Portal (Figure 3). It is equatorial in position (0° 13' to 0° 41' N and 30° 19' to 30 ° 32' E) and lies on an undulating plateau slightly tilted to the south (Kingston 1967, Wing and Buss 1970). The altitude varies between 1590 m in the northern extreme of the forest to 1110 m in the south. The Fort Portal-Kampala road cuts the reserve in the northern part while the Fort Portal-Kamwenge road cuts it in the South. The three forest blocks formed by the road cuts include the North Block (13.55 km^2) the Central Block (361.51 km^2) and the South Block (184.49 km^2). The reserve forms a long strip running north and south for 56 km on its longest axis (Kingston 1967) and covers an area of 560 sq. km. Numerous hills, valleys, swamps and streams cause

Figure 3. Map of Kibale Forest Reserve showing the position of the three Forest Blocks, major river systems and the extent of forest and grasslands. This study was conducted in the Central Block of the reserve near Kanyawara Forest Station.


N
FORT PORTAL
NORTH BLOCK
TO KAMPALA
NR
RP-703
NR
CENTRAL BLOCK
SOUTH BLOCK
KAMWENGE ROAD
0
5
10
Km

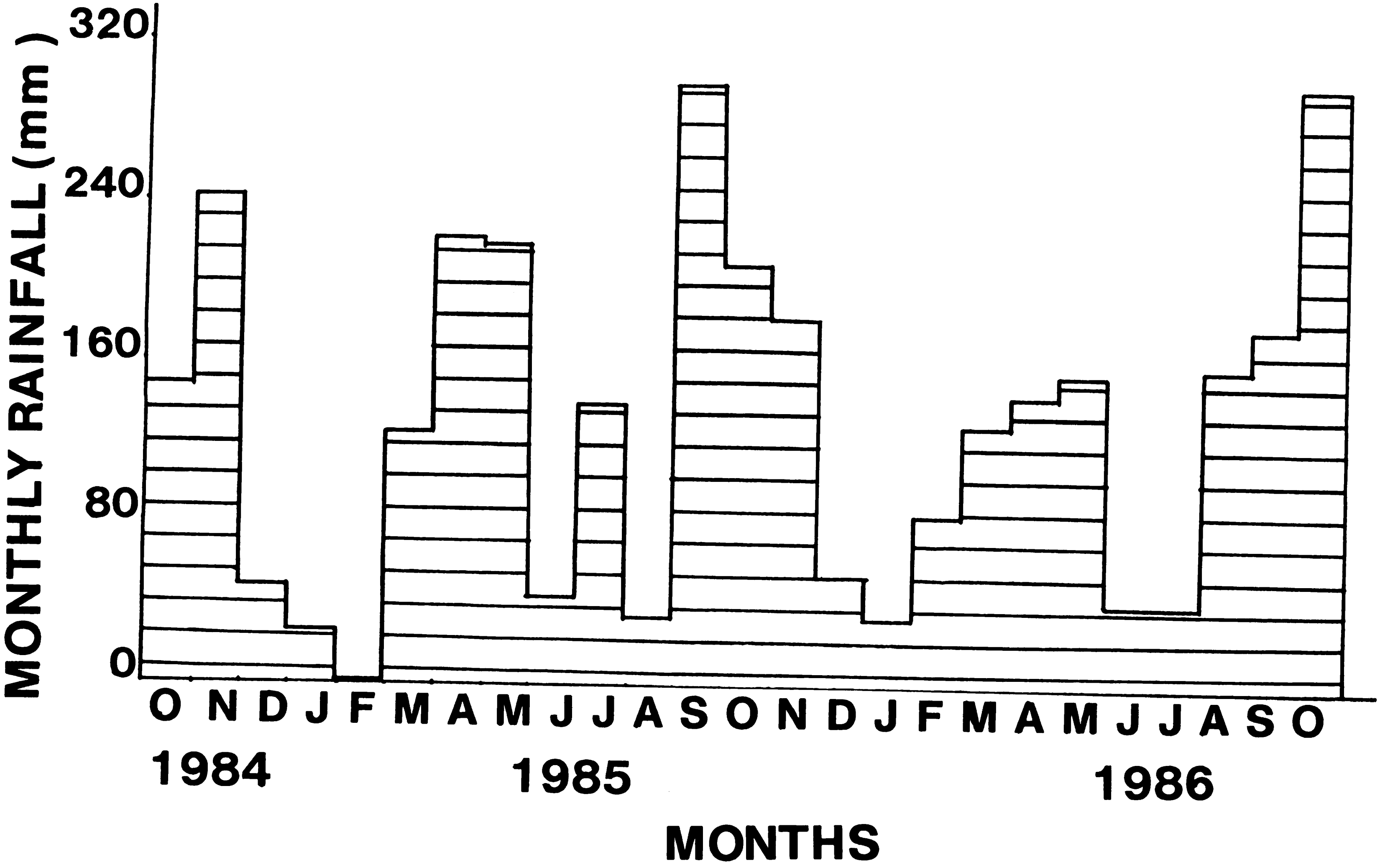
altitudinal differences in the relief. The streams feed into the two major rivers, Mpanga and Dura, which flow southwards into Lake George. The South Block is 6 km north of the Queen Elizabeth (formerly Ruwenzori) National Park.

The rainfall is low to moderate (mean annual preciptation 1700 mm) and distributed in two nearly equal maxima and minima (Kingston 1967, Struhsaker 1975). The typical two wet seasons are March to May and September to November and the two dry seasons are in December to February and June to August (see Figure 4). However, the onset of both wet and dry seasons varies from year to year as does their intensity. Locally, there is more rain in the north than in the south of the reserve. Wind is generally mild, being strongest immediately prior to and during the convectional rainstorms. Because of the elevation, the temperature of the reserve is constantly low compared to those of most equatorial regions (Wing and Buss 1970) and is stable over the years with an annual average of 20.5 ^{o}C (Struhsaker's Weather Records 1977-1979). The reserve forest is distinguished from lowland tropical rainforest on account of greater altitude, lower temperature and lower rainfall but is physiognomically similar (Langdale-Brown et al. 1964).

Geology and Soils

The geology and soils of the Kibale Forest have been extensively described by Osmaston, 1959; Harrop, 1962, Lang-Brown and Harrop, 1962; and Langdale-Brown *et al*. 1964. Two

Figure 4. Monthly rainfall at Kanyawara during the study period. Data were obtained from Dr. Thomas Struhsaker's weather records.


MONTHLY RAINFALL (mm)
320
240
160
80
0
O N D J F M A M J J A S O N D J F M A M J J A S O
1984
1985
1986
MONTHS

types of rocks formed in the Precambrian period and underlain by undifferentiated acid gneisses constitute the major substrate of the reserve. The Toro System overlying these rocks forms prominent ridges mainly of quartzite and sometimes schists and phyllites which are intruded by amphibiolites, gneisses and granites (Lang-Brown and Harrop 1962 and Harrop 1962). Some hills in the reserve have layers of hard laterite exposed on them.

About 90% of the reserve contains red ferrallitic soils. The northern 2/3 consists mainly of ferrallitic sandy clay loams while part of the remaining south has sandy loams (Harrop 1962, Van Orsdol, 1983). These soils are deeply weathered, shallow and stony and show little differentiation into distinct horizons. Such lateritic soils, therefore, have very few weatherable minerals and are consequently infertile. Any sustained agricultural production on these ferrallitic soils will definitely require heavy investment in fertilization. The remaining 10% of the reserve has eutrophic soils overlying a base of volcanic ash. These are characterized by high contents of weatherable minerals and so are excellent for agriculture. Such soils are limited to the western edge of the reserve in Mpokya and Isunga areas where the problems of agricultural encroachment on the reserve and forest destruction are the highest.

Vegetation and Animals

The Kibale Forest is a medium altitude transitional, moist forest falling between dry tropical and wet tropical rainforest (Struhsaker 1975, Van Orsdol 1983, 1986). The major habitat types of the forest reserve include swamp forest and grasslands which intersperse with the forest to form a mosaic of vegetation (Figure 3). Of the 560 km^2 of the reserve, only 350 km^2 are composed of forest and the remainder is swamp and grasslands (Lockwood Consultants 1974). The grassland communities are essentially similar to those found in savanna-woodland, i.e. tall grassland communities in high rainfall areas with *Pennisetum purpureum*, *Imperata cylindrica* and *Cymbopogon afronardus* species dominating. The grasslands occupy the hilly summits and are historically a result of past human settlement and hunter's fires which maintain their integrity by rendering natural colonization by tree species impossible.

In general, the northern, central and southern blocks of the reserve vary in dominant tree species and consociations. Osmaston (1959), Langdale-Brown et al. (1964) and Wing and Buss (1970) found *Parinari excelsa* the dominant species in the mature types north of the reserve (circa 1500 m altitude) but with *Strombosia scheffleri*, *Aningeria altissima*, *Newtonia buchananii*, *Olea welwitschii* and *Carapa grandifolia* as typical associates. These form the richest timber types in the forest. In the Central Block (1200-1500 m altitude) the forest is of a mixed type

dominated by species of *Chrysophyllum gorungosanum*, *Celtis africana*, *Markhamia platycalyx* and *Diospyros abyssinica* with *P. excelsa* occuring in low numbers. The South Block (1200 m altitude) is dominated by species of *Olea welwitschii* , *Pterygota mildbraedii* and *Piptadeniastrum africanum* and a mixture of *Lovoa swynnertonii*, *Diospyros abyssinica* and *Markamia platycalyx* forests. However, the lower altitudes and river valleys in the South Block are occupied by pure stands of Ironwood, *Cynometra alexandri*, with *Celtis durandii*, *Celtis africana*, *Diospyros abyssinica* and *Wurbagia ugandensis* sparsely present.

In the Central Forest Block, the high forest is a mixture of deciduous and evergreen tree species with evergreens predominant. Trees rise to over 55 m in the mature forest (Struhsaker 1975, Wing and Buss 1970) and exhibit a closed canopy of stratified tree crowns. Here, the undergrowth is sparse and characterized by shade tolerant herbs and shrubs. Plants such as *Palisota schweinfurthii*, *Pollia condensata* and a variety of broad leaved forest grasses and ferns abound. Selective felling up to 1969 resulted in about 35% of the northern and a big part of the central forest block being harvested (Struhsaker 1975). This caused giant gaps in the forest canopy which allow direct sunlight to reach the forest ground. Consequently, the dense growth of herbaceous and non-woody vegetation dominated by *Acanthus* species characterizes the secondary forests.

The Kibale Forest Reserve supports one of the richest arrays of fauna of any forest in East Africa (Van Orsdol, 1983, 1986). Prominent among these are the eleven species of non-human primates. These include the rare and endangered red colobus monkey (*Colobus badius*), black and white monkey (*Colobus guereza*), the chimpanzee (*Pan troglodytes*), red tail monkey (*Cercopithecus ascanius*), blue monkey (*Cercopithecus mitis*), lhoesti monkey (*Cercopithecus lhoesti*), mangabey (*Cercocebus albigena*) and olive baboon (*Papio anubis*). The red colobus in the reserve represent the only remaining viable population of this species in Uganda (Struhsaker 1975).

The common terrestrial mammals in the reserve include two species of red and blue duikers (*Cephalophus harveyi* and *C. monticola*, respectively), bush buck (*Tragelaphus scriptus*), bush pig (*Potamochoerus porcus*), warthog (*Phacochoerus aethiopicus*) and the buffalo (*Syncerus caffer*). Kibale is also a very important sanctuary for the African elephant (*Loxodonta africana*) population. After felling operations in the Kibale forest in 1968, elephant control by shooting was practiced. This, combined with excessive poaching a few years after the culling, has severely reduced the elephant populations to very low levels (Eltringham and Malpas 1980). The waterbuck (*Kobus defassa*), sitatunga (*Tragelaphus spekei*) and the giant forest hog (*Hylochoerus meinertzhageni*) also utilize the reserve.

The carnivore population, as reported by Struhsaker (1980) (and personal observation) include the lion (*Panthera leo* - an occasional visitor to the reserve), leopard (*P. pardus* - very rare), golden Cat (*Felis aurata*), serval (*F. serval*), African civet (*Viverra civetta*), palm civet (*Nandinia binotata*) ratel (*Mellivora capensis*) and the Congo clawless otter (*Aonyx congica*).

Of the small mammals, the rodents are diverse and ubiquitous. Their role as consumers and possible predators in the food chain is beginning to be recognized through the studies of Isabirye-Basuta (1979) and Kasenene (1980). The data base is still small, however, compared to the studies on grassland rodents in the Ruwenzori (now Queen Elizabeth) National Park (Delany, 1964b, Cheesman 1975). Except for some non-human primates and some small rodents, no accurate censuses or estimates have been made on the other mammal residents of the reserve.

The avifauna of Kibale forest is also rich. Joseph Skorupa of the University of California, Davis (unpublished) has listed over 325 species occurring in 46 families. Some of these include the crowned hawk eagle (*Stephonoaetus coronatus*), martial eagle (*Polemaetus bellicosus*), giant blue turaco (*Corythaeola cristata*), gray parrot (*Psittacus erithacus*) and the black and white casqued Hornbill (*Bycanistes subcylindricus*). The Kibale ground thrush (*Zoothera kibalensis*) was first described in 1979 and has not been reported from anywhere outside of Kibale forest.

More details and description of the forest flora and fauna and general history of the reserve can be obtained from Kingston, 1967; Wing and Buss, 1970; Struhsaker, 1975; Isabirye-Basuta, 1979; and Kasenene 1980.

The Study Context, Objectives and Hypotheses

In Uganda, the greatest threats to the integrity of tropical forest ecosystems include increased consumer and commercial demands locally and across the borders, the omnipresent and increasing human population and the consequent demand for agricultural land. Specifically, the problems of agricultural encroachment and human settlement in the reserves, poaching, rampant firewood collection and charcoal burning for both home and local markets and, worst of all, uncontrolled selective logging (mechanised and pitsawing) are prevalent. The effects of these disturbance factors on the forest reserve are only in initial stages of assessment and still poorly understood. The official government policy towards the tropical forests is still rapid exploitation for timber and the methods employed are uncontrolled and destructive. Lack of adequate information on how much destruction logging systems impose on the forest prompted this study. Currently, the recommended method for forest exploitation is polycyclic, where a given forest tract is selectively felled once every 70 years (Kingston 1967). Considering the fact that this system employs heavy machinery, it definitely cannot minimize damage in species-rich tropical forests. I therefore question the appropriateness of these polycyclic systems, which, because of too intensive felling, turn into a monocyclic system in the actual exploitation of species-rich tropical forests. It is inevitable that we have to exploit our forest resources but the methods recommended for exploitation should minimize disturbance to important biological processes (Tie 1973, Ashton 1978).

The Kibale forest's heterogeneity in terms of vegetation communities, topography, soils and most importantly, level of disturbances (human induced and natural) made it suitable for my study. Therefore, I aimed at assessing the human impact on the forest resource base and the forest's response to both anthropogenic and natural forms of disturbance. Forest disturbances generate forest gaps of various configurations and sizes. Natural tree falls (and thus forest gaps) are considered to form an important integral component of the forest dynamics (Hartshorn 1978, Schenske and Brokaw 1981). Therefore, I hypothesized that the rate and level of forest disturbance (thus the rate and extent of forest gap formation) are inversely related to tree species diversity and density, rate of forest recovery and general regeneration success of desirable canopy or timber species.

The major objectives of the study were:

1) Characterization of the mature and secondary forest communities of the reserve with respect to plant

species composition, diversity, structure and regeneration.

2) Quantification and analysis of the frequency, extent and major causes of forest disturbances or forest gaps in the mature and secondary forest communities.

3) Determination of the influence of natural and human induced forest gaps on forest vegetational parameters such as density, diversity, frequency of occurrence, predation levels, recruitment and mode of regeneration (with adjacent undisturbed forest serving as the control).

4) Comparison of the results of the study with related studies conducted in other tropical forests in order to understand the dynamics of tropical moist forest, more generally, under the influence of disturbances.

It is hoped that the elucidation of tree death rates, recruitment into gaps and regenerational dynamics of the tropical moist forest under a range of disturbance regimes should add to our understanding of their dynamics. This should form a basis for the development of meaningful plans for maintenance of tropical moist forest productivity and for accelerating the recovery of exploited areas.

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PART I

THE COMPOSITION, STRUCTURE AND REGENERATION OF SELECTIVELY CUT AND UNCUT FOREST TRACTS OF THE RESERVE

INTRODUCTION

Tropical Forest Disturbances and the Need for Research

The rate at which tropical forest ecosystems are being indiscriminately converted and/or transformed poses a threat to their integrity and future existence (Richards, 1964; Sanderson and Loth, 1965; Brenan, 1973; Fosberg, 1973; TIE Report, 1973; Longman and Jenik 1974, Chapman 1975, IUCN, 1975; Brazier *et al*. 1976, USAID, 1978; Goodland, 1980; Lugo and Brown, 1981; and Uhl *et al*. 1985). Estimates of rates of tropical deforestation and other forms of forest disturbance that lead to degradation are variable and range from 50,000 to 300,000 Km^2 per year (Bolin 1977, IUCN 1980, and Woodwell 1978). By some estimates, total elimination of mature tropical forests from the surface of the earth is expected to occur shortly after the year 2000 (Richards 1973, Global 2000 Report 1980). Large forest tracts in Central America, West Africa, and South East Asia are already approaching depletion (Myers 1980, Plumwood and Routley 1982). In Africa, forest destruction is estimated at approximately 2 million ha/year and the rate of forest destruction in Uganda must be correspondingly high (FAO-UNEP 1981).

It is well established that once the structural and functional elements of a tropical rainforest are seriously disrupted, they become very difficult to re-establish (Gomez-Pompa et al. 1974; IUCN, 1975; Whitmore, 1975; Poore, 1976; USAID, 1978; UNESCO, 1978; Ewel, 1980; Plumwood and Routley 1982 and Uhl et al. 1982). Thus, tropical forests qualify for designation as "fragile ecosystems" which are highly susceptible to human forms of disturbance (TIE Report 1973, Myers, 1980).

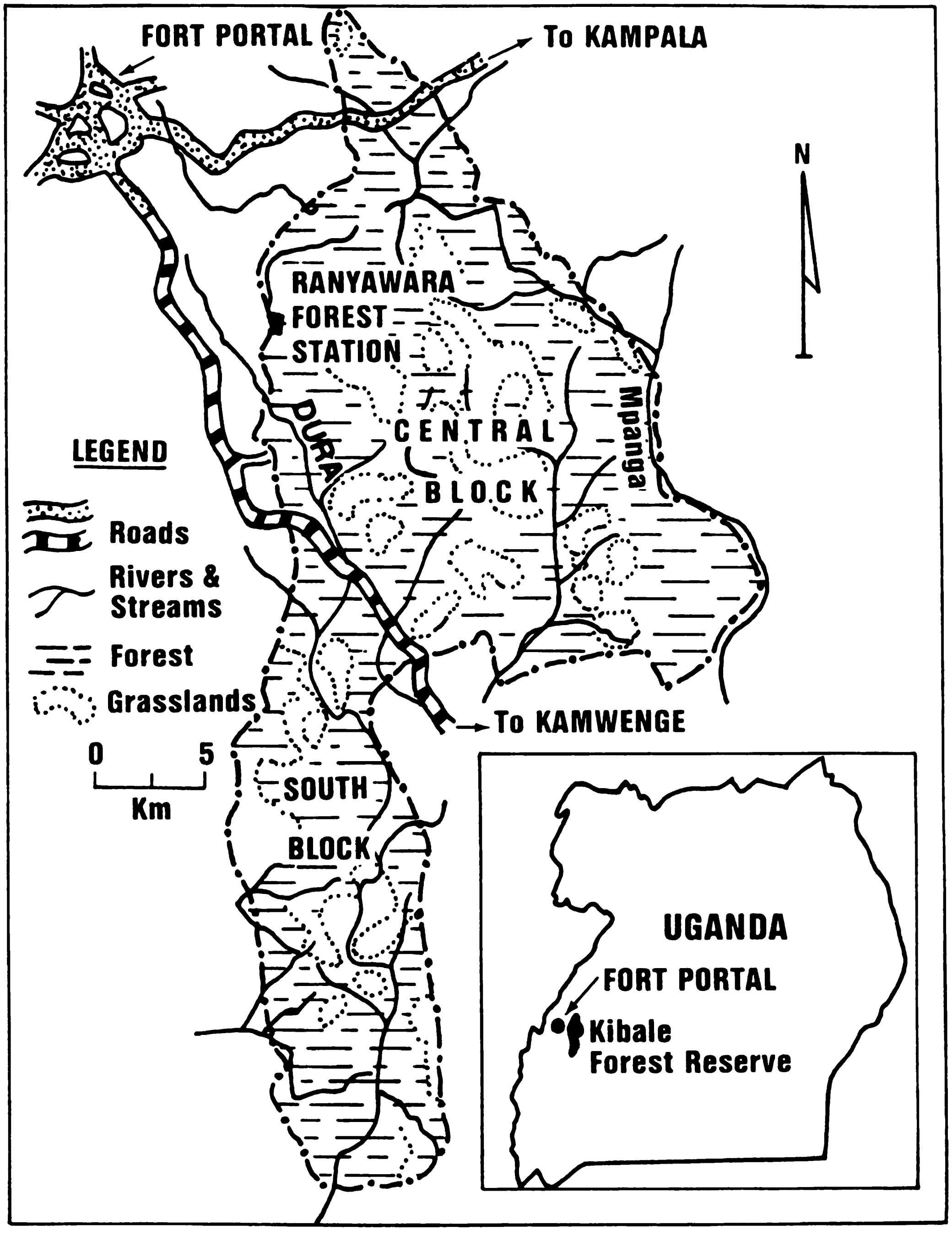
Tropical deforestation is of special concern because of its potential impacts on genetic diversity (Myers 1979) and biogeochemicl cycles (Longman & Jenik, 1974, Poore 1976, IUCN, 1975; Wadsworth 1978 and Jordan and Herrera 1981). The impact of tropical forest felling and burning is potentially of importance to world climate patterns because of its relationship to the global carbon cycle (Bolin 1977, Wong, 1978; 1979; Woodwell et al., 1978). Again, tropical deforestation has been shown to have important local impacts on nutrient cycles, soil organisms and stored propagules, all of which have long term effects on site recovery (Jordan and Herrera, 1981; Ewel et al., 1981; Uhl et al. 1982 b, Putz 1983, 1984, Lugo and Murphy 1986).

Most studies in the tropics have concentrated on forests of humid climates even though they account for a relatively small portion of the forested landscape (Brown and Lugo 1982, Murphy and Lugo 1986 a,b). Of the total global extent of tropical forest, Brown and Lugo (1982) estimated 25% was tropical and subtropical wet and rainforest, 33% was tropical and subtropical moist forest and 42% was tropical and subtropical dry forest (sensu Holdridge 1967). The tropical moist and dry forests are very little studied in spite of their extensive global distribution and role in supporting human populations (Murphy and Lugo 1986 a,b). Considerable ecological attention is now being given to formerly neglected successional ecosystems (Ewel, 1977, Goodland 1980, Uhl *et al*. 1982 b, 1985) for all categories of tropical forests. The major reason is that successional ecosystems have positive net yield and therefore potential for production of food and fiber for human needs (Ewel 1977). Secondly, successional ecosystems occupy tremendous areas, principally because of shifting agriculture, logging operations, and abandonment of futile ventures, e.g. improved cattle pastures in lowland forests (Ewel 1971, 1980; Ewel *et al*. 1977, Uhl *et al*. 1985, Goodland 1980). Therefore, research on how tropical forests recover from a range of disturbance regimes should help government planners and developers avoid costly mistakes in land use.

General Management History of the Study Compartments and Plots

The Kibale Forest Reserve (henceforth called the reserve) was selected for this study (Figure 1). It represents one of the best examples of medium altitude tropical moist forest ecosystems in East Africa (Struhsaker, 1975). It is a transitional moist forest between dry

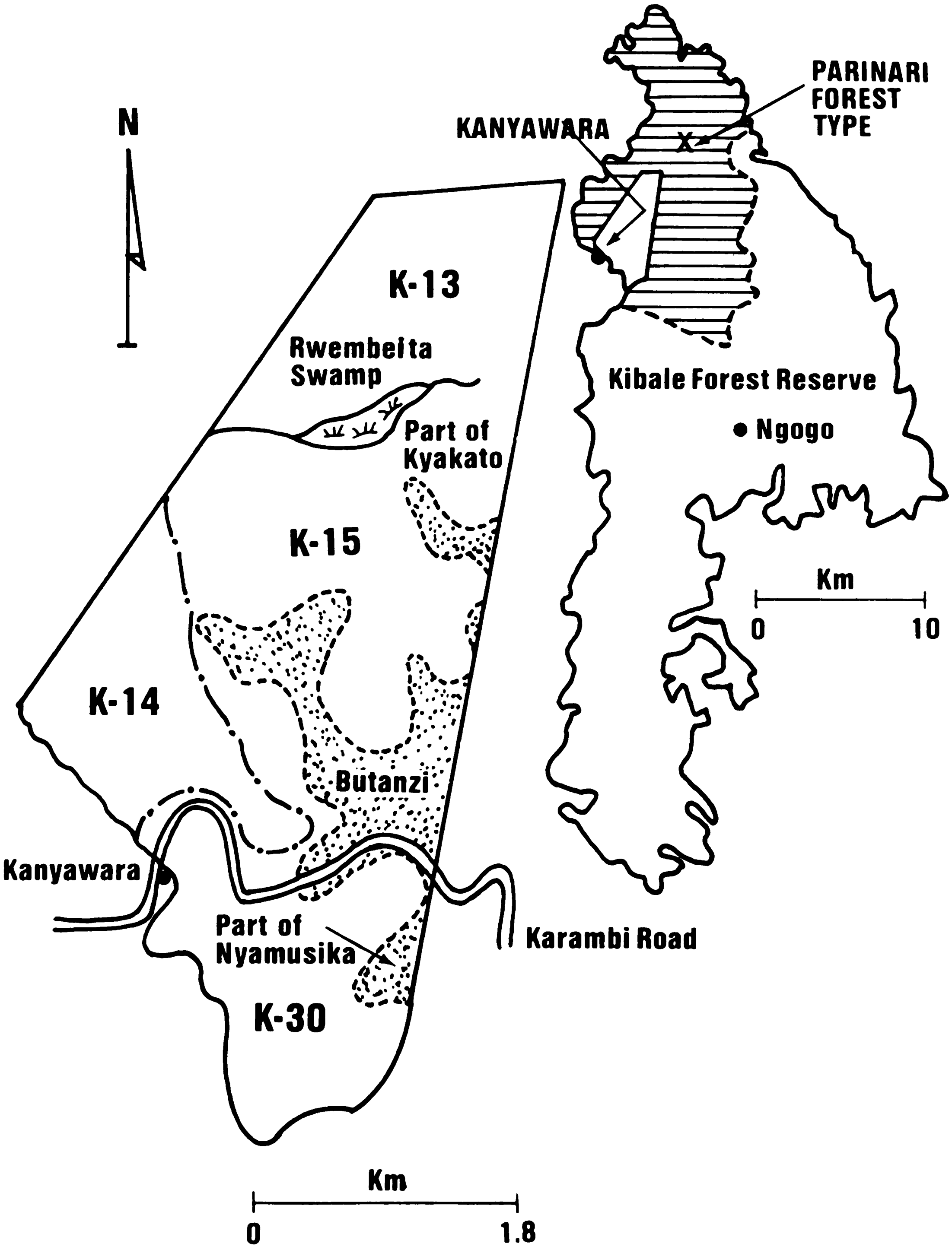
Figure 1. Map of Uganda showing the position of Kibale Forest Reserve. The Reserve is administratively divided into the North Block, Central Block and South Block. The whole reserve is a mosaic of 7 forest types.


FORT PORTAL
To KAMPALA
N
RANYAWARA
FOREST
STATION
DURA
CENTRAL
BLOCK
Mpanga
LEGEND
Roads
Rivers & Streams
Forest
Grasslands
0 5
Km
To KAMWENGE
SOUTH
BLOCK
UGANDA
FORT PORTAL
Kibale Forest Reserve

tropical forest and wet tropical rain forest (Langdale-Brown et al. 1964, Osmaston 1959a). According to the Holdridge (1967) Life Zone Classification, the reserve would fall between the dry and moist tropical forest zones. But Whittaker's (1975) classification, based on mean annual precipitation and temperature would put the Kibale forest formation into the tropical seasonal forest category. The forest in the reserve was described by Osmaston (1959a) on a 1:200,000 scale vegetation map as tropical high forest which is equivalent to tropical rain forest as described by Richards (1952). The entire study was conducted in the distributional limits of the Parinari forest type (Kingston 1967, Figure 2) near Kanyawara Forest Station. The presence of mature P. excelsa with its subdominant associates of canopy tree species such as A. altissima, C. gorungosanum, N. buchananii and O. welwitschii is used as an indicator of the climax forest between 1370 m and 1525 m altitude (Kingston 1967).

The reserve was established to provide sustained production of hardwood timber and production of softwoods from plantations established in the grasslands (Kingston 1967). The forest is supposed to be exploited on a planned felling cycle of 70 years. A system of silviculture, near to clear felling (uncontrolled polycyclic system) is extensively practiced and pitsawing also allowed. The recommended logging was supposed to open up the canopy by approximately 50% and trees over 1.52 m (5 feet) in girth

Figure 2. Map of Kibale Forest Reserve showing the approximate position of the study area and relative location of timber compartments included in the study. The Butanzi, Kyakato and Nyamusika hills have been planted with exotic species of Pines and Cypress. The shading indicates the distributional limits of the *Parinari* forest type.


N
KANYAWARA
PARINARI
FOREST
TYPE
K-13
Rwembeita
Swamp
Part of
Kyakato
K-15
K-14
Butanzi
Kanyawara
Part of
Nyamusika
K-30
Karambi Road
Kibale Forest Reserve
Ngogo
Km
0
10
Km
0
1.8

(at breast height or above buttresses) were to be harvested (Kingston, 1967, Forest Dept. Records, Fort Portal). A total of 27 desirable or merchantable hardwood species was recommended for harvesting. However, the recommendations were inadequate because the unrecommended tree species and small size classes were allowed to be cut at the sawmiller's discretion. In some of the cut compartments, felling was followed with chemical treatment of undesirable residual trees (weeds) with arboricides, a process called "refining" (Kingston 1967).

My study plots were all located in the central part of the reserve (Central Block) where the altitude varies between 1350 m and 1550 m (Figure 1 & 2, see general introduction for details of climate, vegetation, geology, soils and animals). Mechanized selective felling up to 1969 resulted in about 35% of the northern and central forest blocks being harvested (Struhsaker 1975). In the central block, the cut and uncut forest tracts are adjacent, separated only by a motorable track (Figure 2). In comparison with the uncut, the cut forest has an open upper tree canopy, with much sunlight reaching the ground. The understory is thick and dense forming an impenetrable tangle of climbers, creepers and herbs (Kasenene 1980, 1984). Repeated elephant incursions in the cut areas are contributing to what appears to be vegetation suppressed at an early recovery stage (Kasenene 1980). In addition, the elephants destroy woody plants in the seedling/sapling stage either by trampling, browsing, uprooting, barking or topping. The few large trees, mostly with defects such as hollow or crooked boles, or of undesirable species, were left scattered in the cut areas at the time of cutting in 1969. These could serve as important seed sources for regeneration but in the semi-open environment of felled areas, they become susceptible to wind and storm damage (Skorupa and Kasenene 1984).

The Study Plots

These were located in cut (K-13, K-14 and K-15) and uncut (K-30) forest compartments of the reserve (Figure 2). Each study plot had a previously established grid system of trails used for access in primate and other research conducted by the Kibale Forest Project. Compartment 30 (K-30) includes about 300 ha of relatively undisturbed mature forest. Prior to 1970, an extremely low density of 3 to 4 large stems/km^2 were removed by pitsawyers (Struhsaker 1975, Skorupa & Kasenene 1984) and this seems to have had very little impact on the integrity of the forest. The Compartment has been protected from further pitsawing activities since 1970 but has been a site of extensive research on primates and other aspects of forest biology and ecology. Compartment K-30, therefore, is ideally suited to serve as control. Compartment 14 (K-14) includes nearly 390 ha of secondary forest that was selectively cut between May and December 1969. Selective harvesting was light, removing, on the average, 14 m^3/ha (saleable volume only) and leaving behind a lightly disturbed forest. Logs of 23 tree species were removed with only 9 species contributing 94% of the total timber harvested (Skorupa, unpublished; Uganda Forest Dept. Records).

Compartment 15 (K-15) includes about 360 ha of forest that was heavily selectively cut between September 1968 and April 1969. Total harvest removed, on average, 21 m^3/ha from K-15. The 100 ha area included in the study plots was extremely heavily disturbed. A total of 18 tree species was harvested with only 9 of them contributing more than 95% of the harvested volume. Both K-14 and K-15 residual forest areas were untreated with arboricides after the harvest. Compartment 13 (K-13), the northern-most part of the study area (Figure 2), was heavily selectively harvested between the months of April and August 1968. Total harvest averaged 17 m^3/ha (i.e. actual saleable volume on record). Trees of 28 desirable or merchantable species were felled with only 9 species contributing 91% of the harvest volume. The study plot was located in the part of K-13 that was heavily cut and treated with arboricides. However, it should be noted that more timber trees were destroyed through damage during road construction, hauling of logs and crushed trees than indicated by saleable volumes recorded by the Uganda Forest Department at Fort Portal.

The results of timber stock enumerations prior to forest exploitation show significant local variations in densities of individual species, but total forest density, basal area, forest canopy cover and species diversity were relatively constant for all subtypes of Parinari forest (Kingston 1967).

The major objective of this study was to characterize the mature and secondary forest communities of the central part of the reserve with respect to the effect of selective timber harvesting on composition, structure and regeneration of the forest.

METHODS

The forest sites selected for intensive vegetation and regeneration studies included the selectively felled compartments (K-13, K-14, & K-15) and the adjacent mature and undisturbed forest (K-30). All these compartments are located within the *Parinari* forest type (Kingston 1967), (Figure 2). Compartment-30 (K-30) which shows very little evidence of recent human disturbances was used as control in the study of the effects of selective logging on the composition, structure and regeneration of the forest in the reserve. Composition, structure and regenerational characteristics were compared between the uncut mature forest site (K-30) and the three selectively felled secondary forest sites (K-13, K-14, K-15). Regeneration was assessed through the analysis of seedling and sapling abundance and distributions, by size class. In addition to the major objective of the study, an attempt was made to obtain an index of the level of forest exploitation independently of the Forest Department's volume records.

Level of Forest Exploitation

It is often difficult to convert the forest department's output records, in cubic meters of wood, into density of trees harvested per forest area. Therefore, enumeration of cut tree stumps was undertaken to estimate the level of forest exploitation in terms of density. To enumerate the partially or sometimes completely covered tree stumps in cut forests, a modified form of game census method (Struhsaker, pers. comm.) was devised and adopted. For game censuses, the method relies on the target animal advertising its presence by noise or flight. Then its location is marked and distance to the line of travel (or trail) recorded. The width of the strip sampled is taken as twice the observed average distance at which the animals were flushed (Leopold, 1948). Similarly, for purposes of this study, all cut tree stumps that could be seen within various distances astride the trail were counted and their perpendicular distances from the trail measured. Censusing of stumps involved slow walk ($\simeq$ 2 km/hr), visual scanning of either side of the trail for stumps and recording. There was no straying off the trail except when a stump was spotted and measurements of distance to the trail were to be taken. The number of stumps seen or observed were plotted against their perpendicular distances from the trail. The perpendicular distance at which the slope of frequency of occurrence of stumps declined drastically was taken as half the effective width of the strip sampled. Double this distance, therefore, gave the estimated width of the strip along the trail that was sampled for cut tree stumps. The area of forest sampled was then calculated by multiplying the estimated width of the strip by the length of the censused trails. Consequently, the level of forest exploitation in terms of density was calculated.

Forest Vegetation Composition and Structure

In each forest tract, previously established trails were followed for tree, pole and sapling enumerations and sampling of other vegetational features. The direction of travel along the trails was variable. At every junction, the direction of movement was randomly determined. Sample plots were established at every 120 m interval along the trails. Each sample plot measured 5 m x 20 m. All trees (≥ 13 cm dbh), poles (>5 cm and <13 cm dbh) and saplings (> 2 cm and < 5 cm dbh) within 2.5 m on either side of the trail and in the sample plot were measured. For every tree, pole or sapling, its species, diameter at breast height (dbh) (in this study, breast height was fixed at 1.3 m from the ground or base of the tree) and condition (e.g., dead or alive, crown broken, wounded, number of wounds or scars) were recorded. On-site identification of trees depended on keys and descriptions of the common tree species of Uganda by Eggeling and Dale (1951), and Hamilton (1981). Trees were identified based on leaf shape, trunk shape, presence of latex or other sap and various characteristics of outer and inner bark including color, odor, thickness, and texture. Unidentified trees were given their local name, described and voucher specimens collected, dried and pressed for subsequent identification and deposition at the Makerere University Herbarium. Sometimes it was impossible to collect specimens of giant trees. These were mapped, and marked with aluminum tags bearing identification code names. Mr. Katende, Curator of Makerere University Herbarium, was hired and helped in onsite identification of marked trees and plants in the study plots. The sampling intensity per forest compartment studied was based on the species area curves for saplings, poles and trees.

Estimates of forest canopy cover were made by eye and checked by measurements of the amount of light penetrating into the forest using a Weston light meter. An area of approximately 10 m x 10 m (ground measurements) of the forest canopy, centered in the sample plot was scanned from the ground at random points and % canopy cover estimated. Estimates involved mental comparison of the amount of holes in the canopy through which one could see the sky and the area shaded by the canopy. At every canopy cover scanning point, light readings were taken and very soon after, a forest gap light reading was taken as well. The light meter was calibrated in foot candles.

A subplot of 2 m x 5 m was located in the middle of each 5 m x 20 m plot for forest understory and ground vegetation sampling. The subplot was subdivided into 4 smaller plots of 1 m x 2.5 m. All living plants rooted within each of the 4 smaller plots were identified, counted and recorded. Estimates of percent ground vegetation cover (gvc) by plants under 1.3 m height were made. This was done by standing on the edge of the smaller plots, looking down upon the ground vegetation and estimating the amount of ground vegetation cover against open ground. Again, voucher specimens of unidentified plants and tree seedlings were collected, labelled and pressed for future identification and deposition at the Makerere University Herbarium. A compass and clinometer were used to determine both the aspect and general slope of the plots studied.

The collected data were then used to calculate or estimate density (#/ha) dominance (m^2/ha), and importance values (IV) and ranks of desirable and some important non-desirable tree species that dominate the canopy. Importance value (IV) was calculated as based on the sum of relative frequency, relative density and relative dominance. The widely used Shannon-Wiener and Simpson diversity indices (Krebs 1972, Brower and Zar 1984) were calculated for trees, poles, and sapling classes.

RESULTS

Level of Forest Exploitation

In compartment 13, (K-13) the length of the trail censused for cut tree stumps was 4.3 km. The estimated mean strip width from trail to stumps (by frequency distribution of stumps with respect to perpendicular distance from the trail) was approximately 5.1 m. The sampled strip therefore was estimated to be twice this mean strip width i.e. 2 x 5. 1 m. The area sampled in K-13 was then estimated to be 4300 x 10.2 m^2 or 4.39 ha. With a total of 43 cut tree stumps counted within the estimated sample strip width, the estimate of density of trees removed from K-13 was 43 ÷ 4.39 or 9.8 trees/ha. Similarly, in K-14, 28 tree stumps were counted in 6.94 km. of 13.5 m wide sample strip. Thus an area of 9.37 ha was estimated resulting in a level of harvest of 3.0 trees/ha. In K-15, the length of the census trail was 6.53 km and the estimated width of the strip 10.1/m. Thus the forest area sampled for cut tree stumps was 6.9 ha. With 56 tree stumps counted within the sample strip, an index of harvest of 8.50 trees/ha was estimated. In K-30, the length of the census strip and width were 7.18 km and 29.8 m, respectively. With only 3 cut tree stumps observed, the estimated index of harvest was very low, approximately 0.14 trees/ha. The majority of tree stumps observed were in advanced stages of rotting and decomposition. Thus, few stumps could be identified to species level with certainty.

Table 1, shows estimates of the amount of forest harvest in the four compartments. Estimates of density (#/ha) by conversion from volume data (Skorupa unpublished) or by direct enumeration of cut tree stumps (this study) are also included. Our estimates for density of forest trees harvested varied in values but were not different in depicting the level of forest exploitation for the forest compartment studied ($U=10$, $N_1 = N_2 = 4$, $P > 0.10$, one tailed test), (Sokal and Rohlf 1981). In both cases, the trend was similar. The heavily cut forest areas showed higher indices of forest exploitation than lighly cut or uncut forest tracts (Table 1).

Forest Vegetation Composition and Structure

Tree species diversity

Two common measures of species diversity are the Simpsons index (Ds) and the Shannon-Wiener-Index (H') (Krebs 1972, Smith 1974 and Brower and Zar, 1984).

In this study, the Simpsons Index was defined

$$\text{as } Ds = 1 - \frac{ni\ (ni-1)}{N(N-1)}$$

In general form, the Shannon-Wiener formula is written as: $H' = -pi \log_2 pi$. However, in the calculation of

Table 1. Volume of Commercial timber outtake (m^3/ha) and the estimated density (#/ha) for selectively cut compartments. All estimates exclude rejected amounts of cut wood.

Parameters estimated	FOREST COMPARTMENTS				Source of Information
	K13	K14	K15	K30	
Total Volume m^3/ha	17	14	21	2-3t[a]/km	Skorupa & Kasenene 1984
Density (#/ha) by conversion from Volume	6.1	5.1	7.4	(0.02-0.03)[a]	Skorupa (Unpubl.)
Density (#/ha) by stump census	9.8	3.0	8.6	0.14	This study

[a] Pitsawyers removed on the order of 2-3 trees/km in the past (Skorupa and Kasenene 1984).

Table 2. Diversity index values for saplings (>2cm <5 cm dbh), poles and small trees (>5 cm <13 cm dbh) and large trees (> 13 cm dbh) in selectively cut (K-13, K-14, K-15) and uncut (K-30) forest tracts of the reserve; n is the number of plots, each 5 m x 20 m.

	FOREST COMPARTMENTS			
Measures of Diversity	K-30 (n=49)	K-14 (n=46)	K-15 (n=45)	K-13 (n=43)
Species Richness	b			
Saplings	57(18)	55(19)	48(17)	37(16)
Poles & trees	53(13)	51(14)	45(12)	39(13)
Trees	38(15)	54(14)	39(12)	49(17)
# of individuals/species				
Saplings	17.1(15.2)	11.0(10.6)	7.5(6.9)	4.9(5.6)
Poles and Trees	10.1(8.3)	7.0(7.4)	4.5(3.6)	3.6(3.9)
Trees	7.5(8.0)	5.8(9.2)	6.2(4.5)	4.0(4.4)
Simpson's Diversity (Ds)				
Saplings	0.95(0.89)	0.95(0.95)	0.95(0.89)	0.95(0.87)
Poles & trees	0.91(0.83)	0.95(0.83)	0.96(0.88)	0.94(0.88)
Trees	0.94(0.88)	0.94(0.82)	0.92(0.79)	0.96(0.90)
Shannon-Wiener Diversity (H)				
Saplings	5.1(3.6)	4.8(4.2)	4.7(3.6)	4.7(3.4)
Poles and Trees	4.6(2.9)	4.8(3.0)	4.9(3.1)	4.7(3.3)
Tree	4.5(3.4)	4.9(3.0)	4.4(2.2)	5.1(3.6)
H max.				
Saplings	5.8(4.2)	5.8(4.2)	5.6(4.1)	5.2(4.0)
Poles and trees	5.7(3.7)	5.7(3.8)	5.6(3.6)	5.3(3.7)
Trees	5.3(3.9)	5.8(3.8)	5.3(3.6)	5.6(4.1)
Equitability, (E)				
Saplings	0.88(0.86)	0.83(1.0)	0.84(0.88)	0.90(0.85)
Poles and trees	0.81(0.78)	0.84(0.79)	0.88(0.86)	0.88(0.89)
Trees	0.85(0.87)	0.81(0.79)	0.83(0.61)	0.91(0.88)

Figures in brackets represent desirable tree species.

indices (Table 2) the modified form (Smith 1974) used was defined as:

$$H = 3.322\ [\log_{10} N - (ni \log_{10} ni)/N]$$

The maximum species diversity index (H max.) was also calculated using the relationshp:

$$H\ max. = \log_2 S \text{ or } 3.322 \log_{10} S.$$

Estimation of tree species evenness or Equitability (E) involved the relationshp:

$$E = \frac{H}{H\ max.}$$

In these indices,

Ds = Simpson's species diversity index

H = the Shannon-Wiener index of species diversity

S = the number of species observed

3.322 = a conversion factor, $\log_{10}$ to $\log_2$

N = total number of individuals of all the species

ni = number of individuals of a species

Table 2, exhibits six common measures of species diversity. The simplest measure of diversity was the number of species or species richness encountered in the four forest compartments studied. Clearly, the uncut forest shows the highest tree species richness in the sapling and pole size classes. The lightly cut forest (K-14) was ranked second to uncut and the heavily selectively cut forests shared the third and fourth position. However, the cut forest tracts tended to have more species in the tree size classes than uncut forest.

Uncut forest (K-30) also had the highest number of individuals per species, for all size classes, than any of the selectively cut forest tracts. The lightly selectively cut forest ranked second in this respect and the heavily selectively cut forest (K-15 and K-13) ranked in the third and fourth positions, respectively. With respect to Shannon-Wiener diversity index, the uncut forest had the highest diversity of tree saplings. The lightly cut forest, ranked second and heavily cut areas shared the third position. This was also true for the maximum possible diversity estimates for the four forest tracts studied. High indices of equitability for saplings, poles and trees were also exhibited by both the cut and uncut forest tracts (Table 2). The desirable or canopy tree species followed the trend of species diversity indicated above. The unlogged forest showed the highest tree species richness, highest numbers of individuals per species and high equitability. As expected of lightly cut forest, K-14 was placed second in all diversity measures and the heavily cut (K-15) in the third and heavily cut and treated forest in the fourth position.

Another measure of species diversity considered in this study was the species-area curves for the four forest compartments (Fig. 3 and 4). Species-area curves were plotted to assure that the majority of tree species within the study compartments had been observed, but also provided important comparative information on the species richness of

Figure 3. Cumulative increase in the number of species of saplings (>2<5 cm dbh) poles and small trees (>5<13 cm dbh) and large trees (≥13 cm dbh) with corresponding increase in forest area sampled in lightly cut (K-14) and uncut (K-30) forest tracts of the reserve.

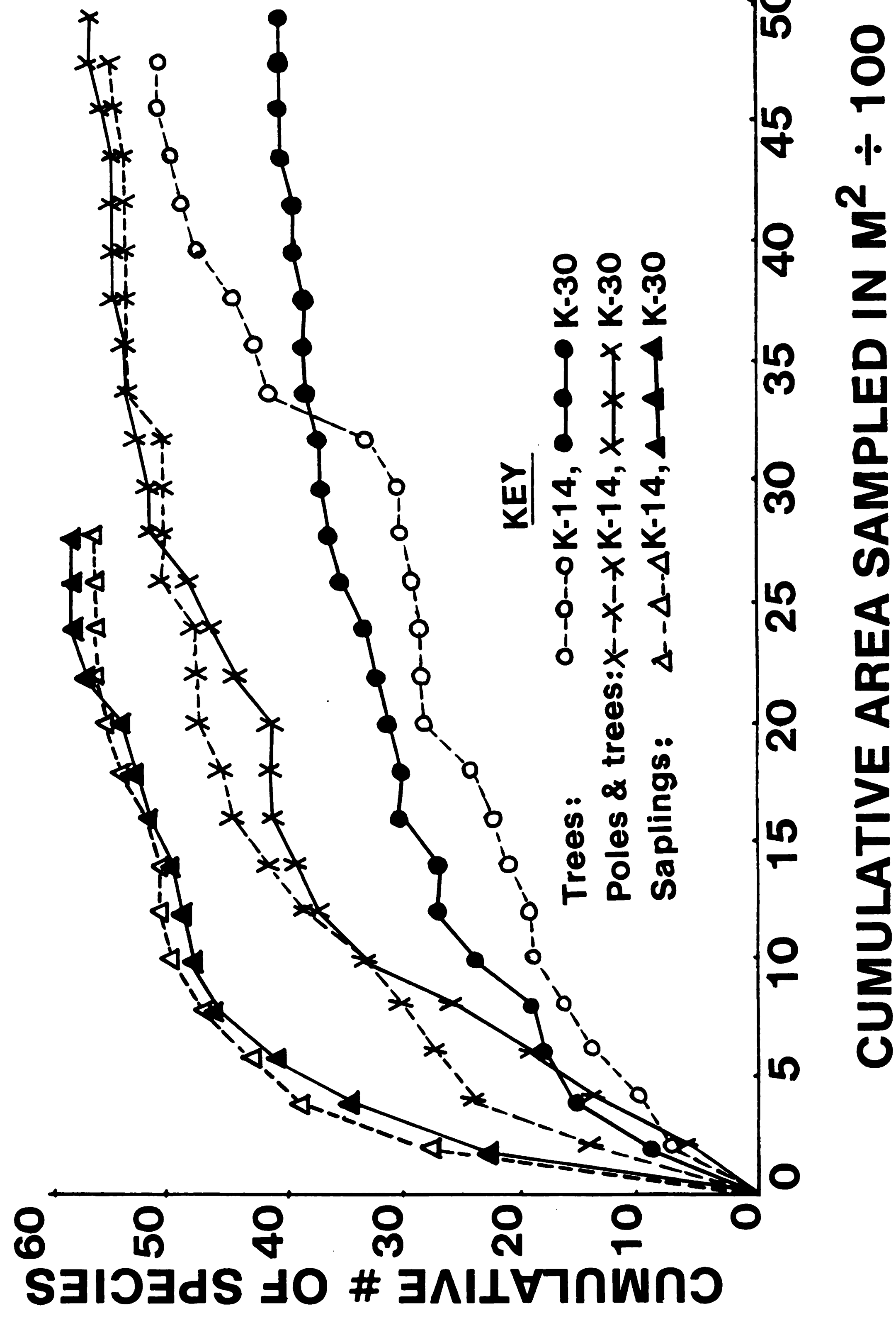
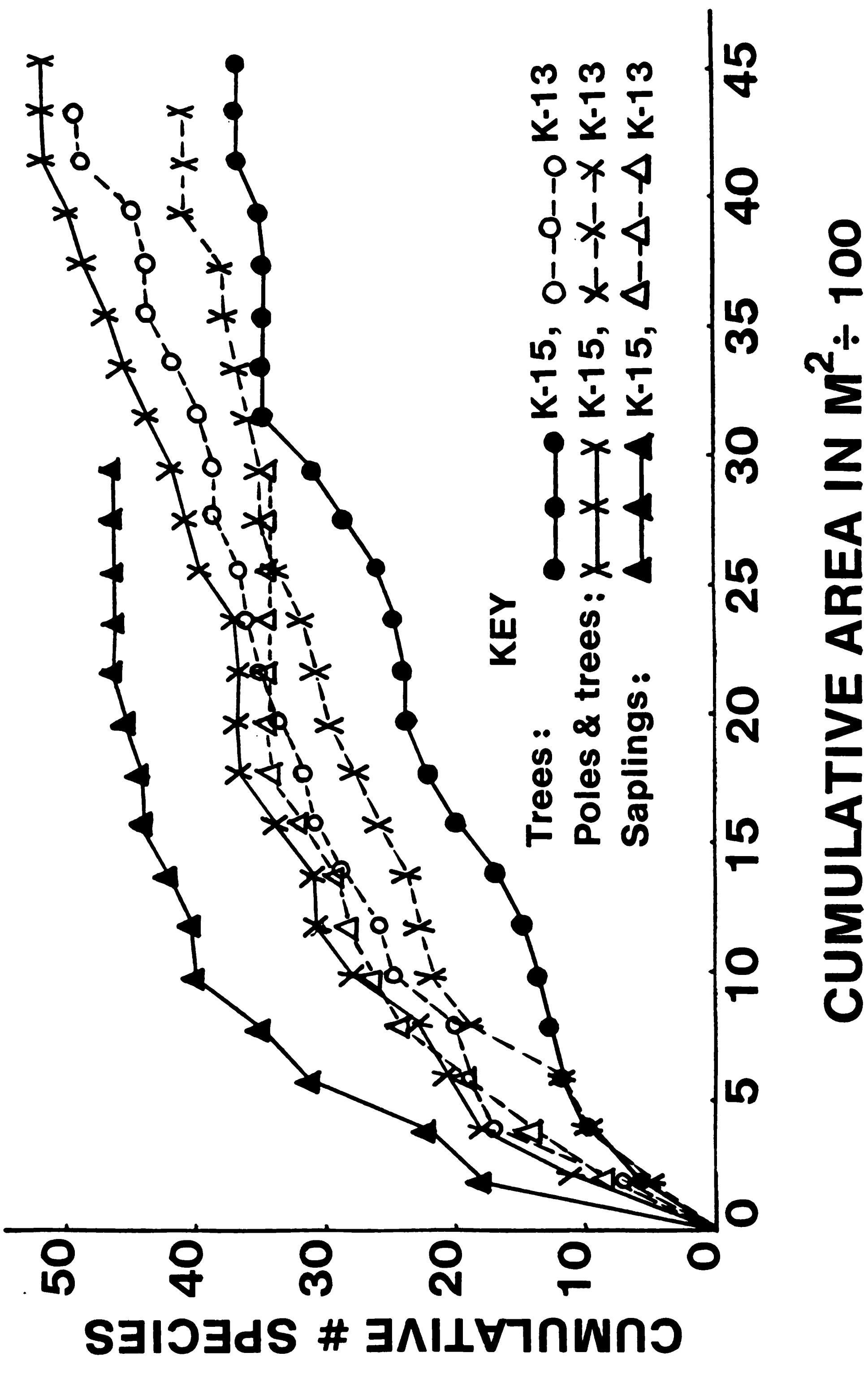

CUMULATIVE # OF SPECIES
0
10
20
30
40
50
60
0
5
10
15
20
25
30
35
40
45
50
CUMULATIVE AREA SAMPLED IN M² ÷ 100
KEY
Trees: o--o--o K-14, ●—● K-30
Poles & trees: ×--×--× K-14, ×—× K-30
Saplings: △--△--△ K-14, ▲—▲ K-30

Figure 4. Cumulative increase in the number of species of saplings (>2 cm <5 cm dbh) poles and small trees (>5 cm <13 cm dbh) and large trees ($\geq$13 cm dbh) with corresponding increase in forest area sampled in heavily selectively cut and treated forest (K-13) and the heavily cut but untreated forest (K-15) of the reserve.


CUMULATIVE # SPECIES
0
10
20
30
40
50
CUMULATIVE AREA IN M^2 ÷ 100
0
5
10
15
20
25
30
35
40
45
KEY
Trees : K-15, K-13
Poles & trees : K-15, K-13
Saplings : K-15, K-13

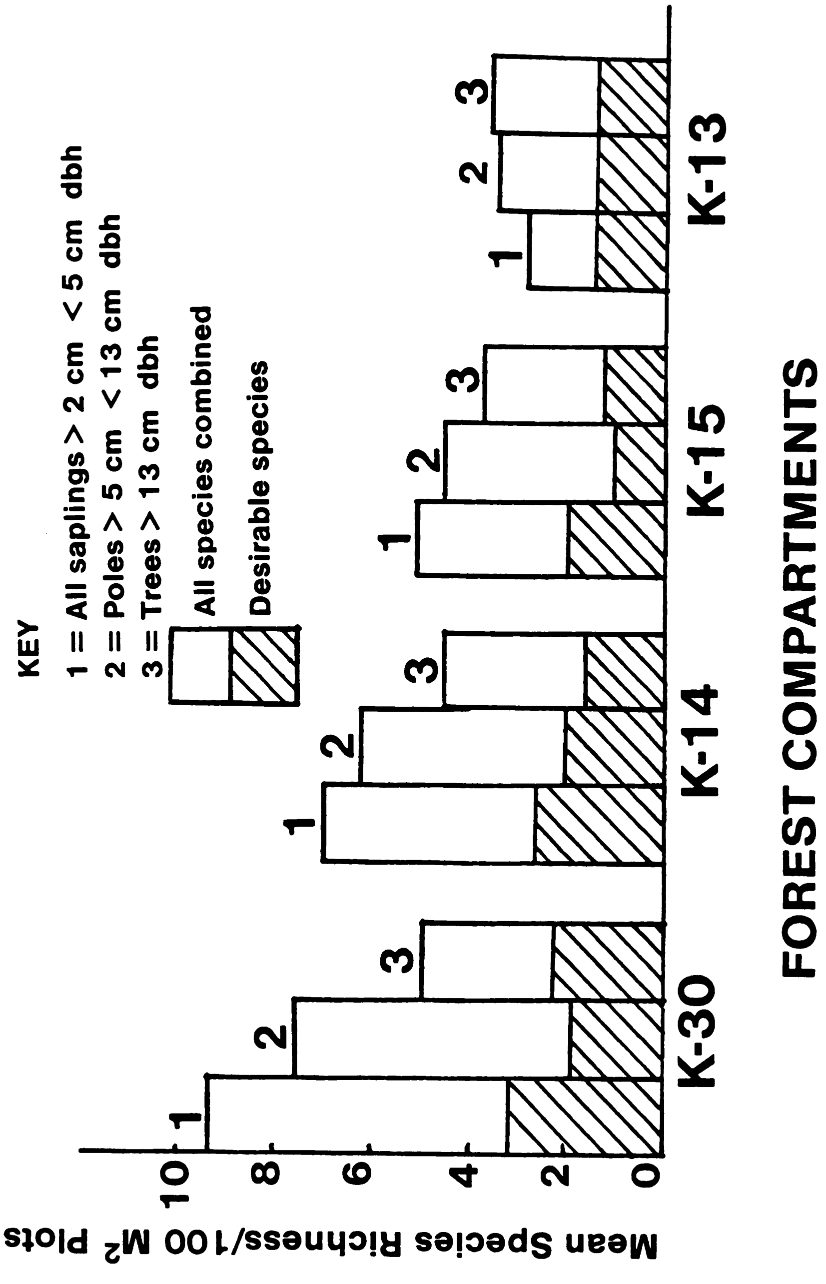
trees, poles and saplings in relation to increasing size of forest areas sampled.

Figures 3 and 4 show species area curves for three size classes for each forest compartment studied. Curves were plotted for trees ($\geq$ 13 cm dbh), poles (>5 cm <13 cm dbh), and tree saplings (>2 cm <5 cm dbh) It was thought that segregation of size classes would give a better estimate of the level of sampling of the study plots. In the lightly cut and uncut forest tracts (K-14 and K-30 respectively) the curves for trees and poles approached asymptotes in just about 0.45 to 0.50 ha of complete sampling, and within 0.25 to 0.30 ha for the sapling size classes (Fig. 3). However, for the heavily selectively felled forest areas (K-13 and K-15), only the sapling size classes plateaued after 0.25 to 0.30 ha of sampling. The curves for the tree and poles size classes continued to rise even after 0.50 ha of sampling (Fig. 4).

Except for the tree size classes, the species-area curves for poles and sapling size classes for uncut and lightly cut forest tracts were similar (Fig. 3). This indicated similarity in the number of tree species per area of forest sampled. The species-area curves for heavily cut forest tracts (Fig. 4) were different for all tree size classes compared. Using K-30 species-area curves as a standard, the curves for K-13 and K-15 fall under those of K-30 for the respective size classes (Figs. 3 and 4). The curves also show that there were more tree species in the sapling size classes per area sampled in uncut and lightly cut than in heavily cut forest tracts. These results suggest negative effects of logging on tree species diversity.

Measures of species richness for the four forest compartments were further analyzed and compared using oneway ANOVA and Duncan's Multiple Range Test (Appendix Table 1). With the exception of K-13 vs. K-15, and K14 vs. K30 plot pairs, all other pairs compared had significantly different species richness of trees ($\geq$ 13 cm dbh) per sample plot ($F = 7.83$, $P \leq 0.0001$). As expected, the plots in uncut forest had the highest mean number of tree species per sample plot, the lightly cut forest had the second highest and the heavily cut forests the lowest (third and fourth position, Fig. 5). For pole tree species richness, only the K-13 vs. K-15 plot pair showed similarities; all other pair combinations differed ($F = 22.638$, $P < 0.0001$). Again, plots in uncut forest had higher pole species richness than those in cut forests. But within the cut forest category, the plots in lightly cut forest had higher pole species richness than plots in heavily cut forest areas. Thus the order of importance for tree pole species richness was K-30> K-14> K-15> K-13. Important results pertaining to forest regeneration were exhibited by tree sapling classes (Appendix table 1, Fig. 5). There were highly significant differences for sapling species richness among all plot pair combinations of the four forest compartments ($F = 35.500$ $P<<$

Figure 5. Mean species richness for sample plots in uncut (K-30), lightly cut (K-14), heavily cut (K-15), and heavily cut and treated (K-13) forest tracts of the reserve.


Mean Species Richness/100 M^2 Plots
0
2
4
6
8
10
1
2
3
K-30
K-14
K-15
K-13
KEY
1 = All saplings > 2 cm < 5 cm dbh
2 = Poles > 5 cm < 13 cm dbh
3 = Trees > 13 cm dbh
All species combined
Desirable species
FOREST COMPARTMENTS

0.0001). The uncut forest had the highest mean number of sapling species per sample plot, the lightly cut forest was ranked second and the heavily cut forests followed in the third and fourth positions. The lightly cut forest (K-14) had 72.9%, heavily cut forest (K-15) had 51.1% and the heavily cut and treated forest (K-13) only 29.2% of the sapling species richness exhibited in uncut forest (K-30). It was also noted with concern that within the heavily selectively cut and treated forest (K-13), the sapling species richness was very low compared to the species richness of poles and trees (Fig. 5). This trend was not exhibited by any of the other forest compartments studied. The forest management practice of treatment of residual forest after felling with arboricides may account for the observed depression in the sapling species richness in compartment-13.

For the desirable trees, there were more species per plot in uncut than any of the cut forest areas ($F = 7.062$, $P<0.0001$). The desirable pole species showed significant difference only in three pairs of plots ($F = 6.876$, $P<0.0002$). The desirable pole species richness was similar for the plot pairs of uncut and lightly cut forest and for the two heavily cut forest tracts. However, the similarity in the pole species richness for the plots in K-13 and K-30 was difficult to explain. The desirable sapling species richness were significantly different for three obvious plot pairs, K-13 and K-14, K-13 and K-30, and K-15 and K-30 ($F =$

11.07, P<0.0001). But sample plots of uncut and lightly cut forest and those of heavily cut forests (K-13 & K-15) had similar sapling species richness. The observed differences in tree, pole and, more importantly, sapling species richness suggest that selective timber harvesting could have been the main cause or influence.

Tree density and basal area

Estimation of the density of trees and juvenile size classes for the selectively cut and uncut forest tracts of the reserve was thought to give an insight into the degree of forest exploitation, disturbance, and an indication of the success of forest regeneration 20 years later. Table 3, and Appendix table 1 show mean density estimates for tree, poles, and sapling classes for the study compartments. The densities within the three size classes were compared among the compartments using ANOVA and Duncan's Multiple Range Test (Appendix Table 1). As expected, there was significant difference in the density of trees between uncut, lightly cut and heavily selectively cut forest (F = 9.750, P<0.0001). As depicted in Table 3, uncut forest (K-30) exhibited the highest tree density with lightly cut forest in the second position and K-15 and K-13 in the third and fourth positions, respectively. All logged study plots, except for K-14, differed significantly from the control plot (K-30) in forest vegetation composition (Appendix table 1). Among the logged study plots, only the K15-K13 pair showed similarity in tree density. A similar trend was

Table 3. Results of forest vegetation sampling in uncut mature forest (K-30), lightly cut (K-14), heavily cut (K-15) and heavily cut and treated forest (K-13) in the reserve. Measurements included saplings (>2 cm <5 cm dbh), poles and small trees (>5 cm <13 cm dbh) and large trees (≥13 cm dbh). N is the number of plots each 5 m x 20 m.

	FOREST COMPARTMENTS			
Parameters	K-30 (n=49)	K-14 (n=46)	K-15 (n=45)	K-13 (n=43)
<u>Density (#/ha) ÷ 100</u>				
Saplings	29.3 (13.1)[a]	23.7 (19.7)	13.4 (11.0)	7.1 (4.9)
Poles	13.6 (5.6)	9.2 (5.0)	6.0 (4.1)	4.1 (2.6)
Trees	6.5 (2.1)	6.0 (2.2)	4.7 (2.5)	4.4 (2.2)
Desirable Saplings	9.8 (7.5)	7.7 (6.1)	4.6 (3.9)	3.4 (3.0)
Desirable Poles	2.6 (2.1)	2.7 (2.4)	1.2 (1.2)	1.7 (1.4)
Desirable Trees	2.9 (1.8)	2.3 (1.9)	1.4 (1.4)	1.6 (1.4)
<u>Basal Area (m^2/ha)</u>				
Saplings	2.0 (0.9)	1.5 (1.1)	0.8 (0.7)	0.4 (0.4)
Poles	7.1 (3.4)	4.6 (2.3)	2.8 (2.0)	2.0 (1.4)
Trees	99.9 (73.6)	54.6 (54.1)	65.9 (54.5)	38.3 (37.1)
All Combined	109.1 (73)	60.7 (54.7)	69.4 (55.0)	40.7 (37.2)

a = Standard deviation of the mean

exhibited for the poles, where even the lightly cut and uncut forest plots differed in their pole density (F = 39.143, P<0.0001). There was a highly significant difference in the density of saplings among all plot pair combinations for the four forest compartments (F = 34.596, P<<0.0001). The order of seedling density was K30> K14> K15> K13. The heavily cut forests (K-13 and K-15) showed similar tree densities for the desirable species but all other pair combinations were significantly different (F = 8.591, P<0.0001). The existence of a difference in density of desirable trees between K-14 and K-30 study plots could have resulted from the effects of harvesting which was selective with respect to size and prime tree species. The plots in uncut and lightly cut forest had higher pole density than those in cut forests (F = 6.832, P<0.0001) and within the cut forests, K-14 had higher densities. Again, the most striking density results were those of sapling classes where the heavily selectively cut forest plots showed similar but very low densities and the lightly cut and uncut forest plots very high densities (F = 12.993, P<0.0001).

There was considerable variation in basal area estimates for the four forest compartments and for the trees, poles and sapling classes (F = 9.791, 42,033 and 42.425 respectively, all P<0.0001). The contribution by saplings and poles to basal area estimates was very small (table 3). By virtue of high densities of big trees, K-30 plots had highest basal area estimates for all size classes considered. However, tree basal area for heavily selectively cut forest (K-15) was slightly higher than for lightly cut forest but the two were not significantly different ($P>0.05$).

In K-30, the desirable timber trees and poles combined and saplings contributed only 27.4% and 33.4% respectively, of the total density. The results for K-14 are comparable to those for K-30. The desirable timber trees and poles contributed 32.9% of the total density while saplings contributed only 32.5% of the total sapling density. In the heavily selectively cut forest tracts, K-15 and K-13, the desirable trees and poles accounted for 24.3% and 38.8%, respectively, of the total tree and pole densities. The desirable saplings also showed relatively high percentage contributions of 34.3% (K-15) and 47.9% (K-13) of the total tree sapling density. The high estimate values in K-13 might have been influenced by small numbers which often tend to inflate percentages. Although it was almost 19 years since the forest was felled, forest composition with respect to tree density and basal area showed great variations between the compartments (Table 4). Great differences in percent reduction of densities of trees, poles, and saplings was observed for the differently managed forest compartments (Table 4). With the exception of only one positive increase for the density of poles of desirable species in lightly logged forest, the general trend of density of trees, poles

Table 4. Percent reduction in density and basal area of trees, poles and saplings in selectively cut forest compartments of the reserve. K-30 was uncut and was used as control. N is the number of plots each 5 m x 20 m.

	COMPARTMENTS			
	K-30	K-14	K-15	K-13
Parameters	(n=49)	(n=46)	(n=45)	(n=43)
Density (#/ha) 100	No/ha	% REDUCTION		
Saplings	29.3	19.1	54.3	75.8
Poles	13.6	32.4	55.9	69.9
Trees	6.5	7.3	27.7	32.4
Desirable Saplings	9.8	21.4	53.1	65.3
Desirable Poles	2.6	128.6*	53.9	34.6
Desirable Trees	2.9	20.7	51.8	44.8
Basal Area (m^2/ha)				
Saplings	2.0	25.0	60.0	80.0
Poles	7.1	35.2	60.6	71.8
Trees	99.9	45.3	34.0	61.7
All Combined	109.0	44.4	36.4	62.7

* There was a positive post-harvest increase in the density of tree poles.

and saplings following logging was negative. The negative trend in density was more pronounced in heavily cut than lightly cut forest. This was also true for the basal area of trees, poles and saplings (Table 4). It is suggested that the magnitude of the differences in the density or basal area for the different size classes and compartments were a reflection of the intensity of exploitation and forest disturbance.

In general terms, therefore, the plots in uncut forest (K-30) had the highest species richness and diversity and the highest density and basal area for all size classes considered. The lightly cut forest (K-14) ranked second while the heavily selectively cut forest (K-15) and heavily selectively cut and treated forest (K-13) ranked third and fourth respectively. However, the non-desirable timber species accounted for the majority of species richness and diversity (Fig. 5), and a greater percentage of density and basal area (Table 3), for all size classes in all forest tracts studied than did the desirable or canopy tree species. Therefore, it appears that the great differences between the study plots in vegetation composition reflect, to a greater extent, the intensities of logging disturbance and in a minor way the inherent natural variations. The differences in tree, pole and sapling species richness for all trees in general and desirable tree species could be explained based on the effects of selective logging with respect to size and species.

Importance Values of tree species

Like most tropical forests, the forest areas studied had high species diversity values reflecting the absence of any tendency for individual tree species to dominate the community. However, the best measure for the importance of a species in a community should incorporate measures of basal area, extent of spatial distribution and population size (Curtis and McIntosh, 1951). Consequently the importance values (IV.) recorded in table 5, were obtained by summing values of relative dominance, relative frequency and relative density of tree species. The importance values of desirable timber species (also dominant canopy tree species) and a few important non-desirable species were computed for the four tracts studied (Table 5).

In uncut and selectively cut forest tracts some non-desirable canopy and understory tree species ranked within the top ten in importance (Table 5). A non-desirable but canopy tree species, Diospyros abyssinica, was ranked first in uncut mature forest and was in second, third and seventh rank positions in selectively cut forests of K-15, K-14 and K-13, respectively. Similarly, Celtis durandii, and two other understory species, Teclea nobilis and Uvariopsis congensis ranked in the top ten species in importance for compartments K-30, K-14 and K-15 but were very low in importance in compartment-13. Each forest compartment studied had a different tree species at the top of the list of importance values. In K-14, Markhamia platycalyx was

Table 5. Importance Values (IV) and ranks for desirable (also forest canopy) and some non-desirable timber species for uncut (K-30) and selectively cut (K-14, K-15, K-13) forest tracts of the reserve.

Tree Species	Importance Values (IV)				Importance Ranks			
	K-30	K-14	K-15	K-13	K-30	K-14	K-15	K-13
A. *altissima*	14.1	7.4	1.1	7.6	11	16	20	12.0
A. *toxicaria*	10.8	7.9	2.0	6.6	13	15	19	17
B. *unijugata*	6.7	9.8	17.2	21.2	17	12	7	6
C. *africana*	10.6	14.0	21.1	2.3	14	9	4	20
C. *durandii* *	21.9	23.6	35.5	27.4	6	5	3	3
C. *gorungosanum*	7.3	1.5	3.1	3.7	16	22	18	18
C. *millenii*	4.6	8.6	9.9	2.6	19	14	12	4
D. *abyssinica* *	25.2	25.2	41.8	20.9	1	3	2	7
F. *macrophylla*	1.1	2.2	10.9	10.9	22	21	10	9
F. *angolensis*	1.4	3.5	4.3	7.3	21	19	16	14
F. *Latifolia*	24.5	20.1	10.4	8.6	3	7	11	11
L. *swynnertonii*	24.8	11.0	0.6	2.6	2	11	22	19
M. *platycalyx*	17.4	36.6	18.1	19.5	9	1	6	8
M. *bagshawei*	23.4	4.2	7.9	1.9	5	18	5	21
N. *buchananii*	4.7	13.0	9.1	22.9	18	10	13	5
O. *welwitschii*	17.7	17.3	51.3	38.1	8	8	1	2
P. *excelsa*	12.9	9.1	13.0	1.1	12	13	8	22
P. *africana*	0.0	2.7	0.6	7.1	23	20	21	15
S. *scheffleri*	15.7	24.5	8.0	41.0	10	4	14	1
S. *globulifera*	9.1	1.6	0.0	7.0	15	23	23	16
T. *nobilis* *	23.7	28.6	18.3	7.5	4	2	5	13
T. *splendida*	4.3	5.3	3.6	8.9	20	17	17	10
U. *congensis* *	17.8	22.1	12.1	0.0	7	6	9	23

*Non-desirable species were not felled in harvesting.
[a] One (1) indicates highest and 23 lowest rank.

most important, Olea welwitschii and Strombosia scheffleri ranked in top places of importance for K-15 and K-13, respectively. No one tree species had similar importance value indices in each of the four forest compartments studied. Consequently, there was no significant correlation between importance values and ranks of tree species when comparing K-30 and K-15, K-30 and K-13, K-14 and K-13, and K-15 and K-13. However, there was significant positive correlation between importance values and ranks of tree species when comparing K-30 and K-14 ($r = 0.670$, $P<0.01$) and K-14 and K-15 ($r = 0.628$, $P<0.01$).

The major forest canopy tree species which are also desirable timber species, such as Parinari excelsa, Mimusops bagshawei, Lovoa swynnertonii, Newtonia buchananii, Aningeria altissima, and Chrysophyllum gorungosanum were very poorly distributed and had very low densities for all size classes, especially in selectively cut forest tracts. Consequently, they had very low importance value indices and ranked very low in importance. The relative frequency, relative density and relative dominance, and consequently importance values of desirable species or canopy tree species, were very low in cut forest areas compared to uncut but non-desirable tree species showed higher values for all four forest tracts. However, some non-desirable understory species such as Uvariopsis congensis and Teclea nobilis had high importance values and ranks in uncut and lightly cut forest tracts, low values and ranks in K-15 and were almost absent in K-13 plots.

Other measures of forest structure and composition

An analysis of variance and Duncan's multiple range test revealed that all logged study plots (Table 6) differed significantly from the control plot (K-30) in forest canopy cover (F = 52.30 , P<0.0001). All pairwise comparisons between uncut, lightly cut and heavily cut study plots showed that forest canopy cover was dissimilar (Table 6) However, study plots in K-30 (control plot) had the highest canopy cover averages, with lightly cut forest (K-14) ranked second and heavily selectively cut forest K-15 and K-13 in third and fourth positions, respectively. Relative to canopy cover for the control plot (K-30), cover was 19.8% less in K-14, and 47.9% and 61.7% less in K-15 and K-13 respectively. There was also a strongly inverse relationship between forest canopy cover and the amount of light reaching inside the forest for all study plots.

High amounts of sunlight reach inside the forest in heavily cut forest areas (Table 6). An analysis of variance and Duncan's multiple range test revealed that all logged study plots, except K-14, differ significantly from the control plot (K-30) in the amount of sunlight penetrating into the forest (F = 42.895 P<0.0001). Percent canopy cover and % gap light inside the forest were significantly negatively correlated at P<0.05 for K-14 and K-30 only (r = -0.359 and r = -0.306 respectively, Pearson's correlation).

Table 6. Summary of the results of forest canopy cover, percent gap light inside the forest, and forest ground vegetation cover in cut and uncut forest tracts of the reserve.

	FOREST COMPARTMENT			
PARAMETERS	K-30	K-14	K-15	K-13
% Forest canopy cover	58.5 (10.4)[a]	46.9 (14.9)	30.5 (16.9)	22.4 (14.6)
% Gap light inside forest	7.9 (9.4)	9.3 (8.5)	27.9 (19.9)	39.2 (20.1)
% Ground vegetation cover (GVC)	24.1 (16.3)	40.8 (23.2)	60.8 (23.4)	71.4 (22.8)
% Slope of Plots	28.0 (7.7)	14.7 (10.1)	15.8 (8.7)	16.3 (10.4)

a = Standard deviation of the mean

All logged study plots differed significantly from the control plot in the amount of ground vegetation cover (gvc) (F = 52.142, P<0.0001). All pairwise comparisons among uncut, lightly cut and heavily cut study plots were significantly different. The control plot (K-30) had the lowest of all gvc estimates, K-14 the second lowest and the heavily cut forest areas the highest gvc estimates (Table 6). Pearson's correlation between % gvc and amount of sunlight reaching into the forest were highly significantly positive for all study plots (all P<0.0001) except K-14. However, the relationship between % gvc and the amount of forest canopy cover were strongly negative for all study plots (all P<0.0001).

The % slope of study plots in cut forest tracts differed significantly from those in uncut forest (F = 21.80, P<0.0001. ANOVA and Duncan's test). The average % slope for K-30 plots was, 28.0% and 14.74%, 15.8% and 16.28% for K-14, K-15 and K-13 plots respectively. However, there was no significant difference in the slope of study plots among the cut forest tracts, indicating similarity in terrain. The influence of topograhpic relief on observed differences in forest composition parameters may be small, at least for the selectively cut forest tracts.

Intraplot vegetation parameter comparisons

Within uncut mature forest (K-30) there was no significant correlation between large tree and the juvenile tree species richness or density (Table 7a). Further, there

Table 7a. Pearson's correlations between forest vegetation parameters of uncut forest (K-30) in the reserve.

Parameter	Tree Classes		A	B	C	D	E	F	G	H	I	J	K	L	M
	Trees	A													
Species richness	Seedlings	B													
	Saplings	C													
	Desirable Trees	D	XX												
	Desirable Saplings	E			XX										
	Trees	F	XX	X		XX									
Density #/ha	Saplings	G			XX		XX								
	Desirable trees	H	XX			XX		XX							
	Desirable Saplings	I			XX		XX		XX						
	% Forest Canopy Cover	J													
Other measures	% Gaplight in Forest	K		$\overline{X}$								$\overline{X}$			
	% Ground Veg. Cover	L		$\overline{XX}$								$\overline{XX}$	X		
	% Slope of Plots	M													

X = Significant at $P<0.05$

XX = Highly significant at $P<<0.01$

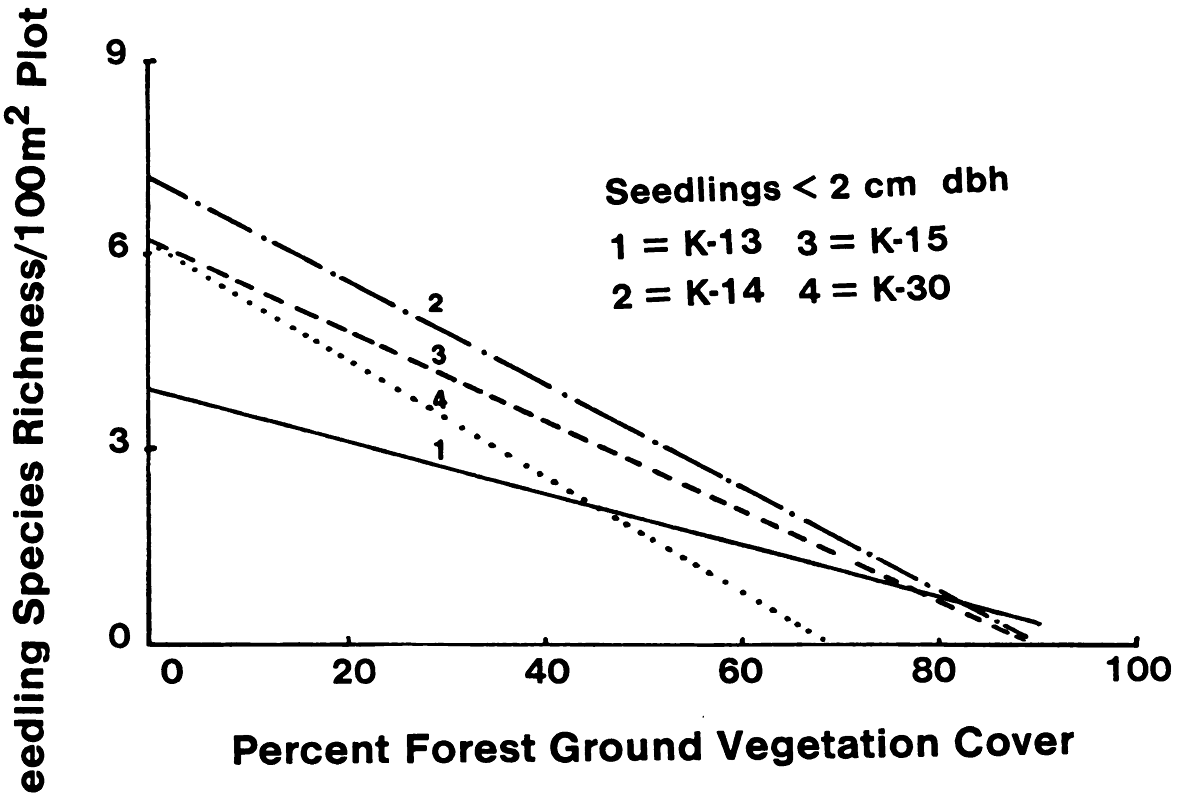
$\overline{X}$ = Significantly inverse

was no correlation between tree species richness or density and other measures of forest composition and structure (see Table 7a). The relationship between seedling species richness and the amount of light reaching inside the forest was significantly negative ($r = - 0.288$, $P<0.045$). Similarly, a highly significant negative correlation between % ground vegetation cover (gvc) and tree seedling (but not sapling) species richness was observed ($r = -0.517$ $P<0.001$, Fig. 6). However, the amount of sunlight reaching inside the forest was negatively related to forest canopy cover but positive in relation to the amount of gvc inside the forest. Therefore, this suggests that excessive destruction of the forest canopy could be detrimental to seedling and sapling regeneration.

For the lightly cut forest tract (K-14), the high tree species richness and density was positively related to forest canopy cover, as was tree seedling and sapling species richness and density (Table 7b). Here, the amount of light reaching inside the forest was negatively correlated with both forest canopy cover, species diversity and density of desirable tree species. Again, the strongly negative relationship between % gvc and the seedling and sapling species richness and density was realized (Table 7b, Fig. 6, 7).

For the heavily selectively cut forest tract (K-15), the big tree species richness and density were positively correlated with the seedling and sapling species richness,

Figure 6. Correlations between seedling (<2 cm dbh) and sapling (>2 cm <5 cm dbh) species richness and the level of forest ground vegetation cover of the study plots in the reserve.


Seedling Species Richness/100m² Plot
9
6
3
0
0
20
40
60
80
100
Percent Forest Ground Vegetation Cover
Seedlings < 2 cm dbh
1 = K-13 3 = K-15
2 = K-14 4 = K-30
2
3
4
1

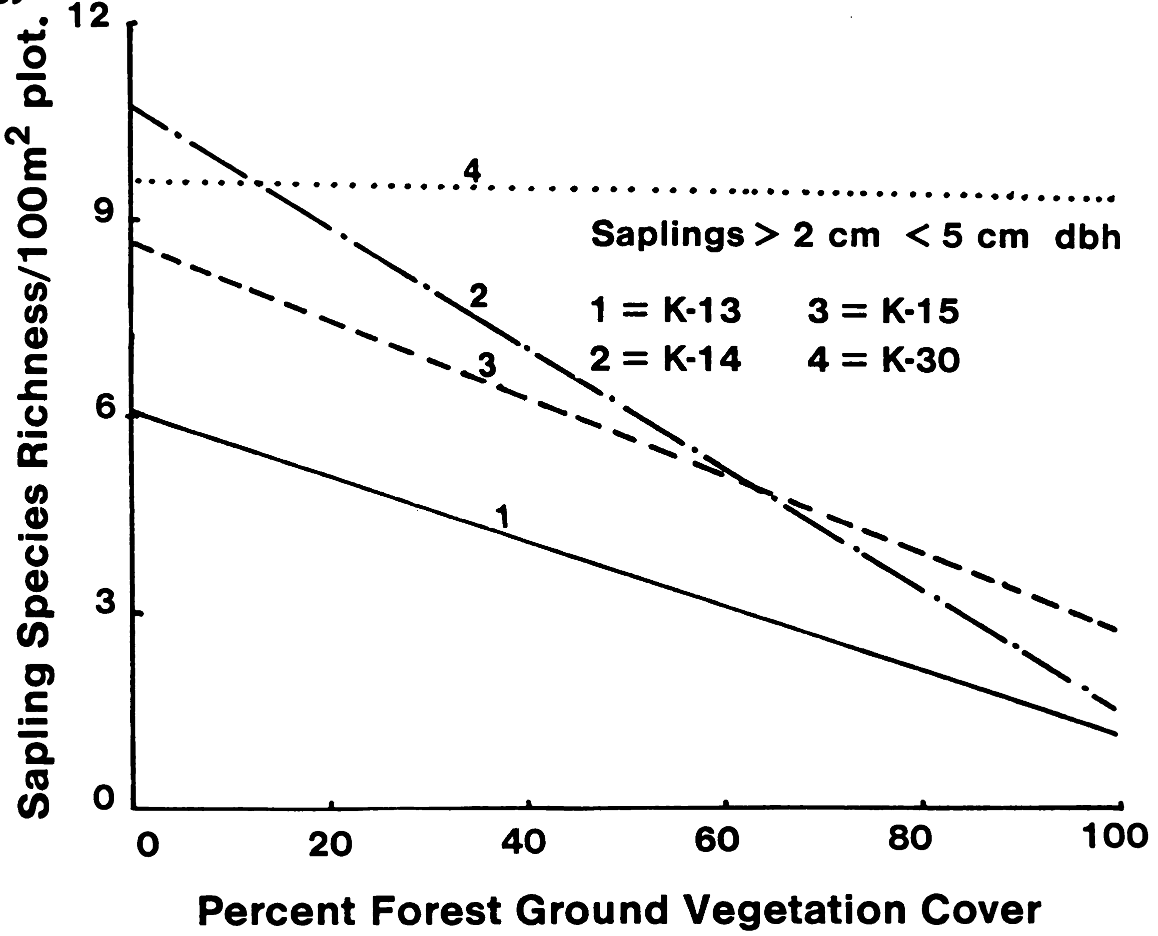

Sapling Species Richness/100m² plot.
12
9
6
3
0
0
20
40
60
80
100
Percent Forest Ground Vegetation Cover
Saplings > 2 cm < 5 cm dbh
1 = K-13 3 = K-15
2 = K-14 4 = K-30
4
2
3
1

Table 7b. Pearson's correlations between forest vegetation parameters of lightly cut forest (K-14) in the reserve.

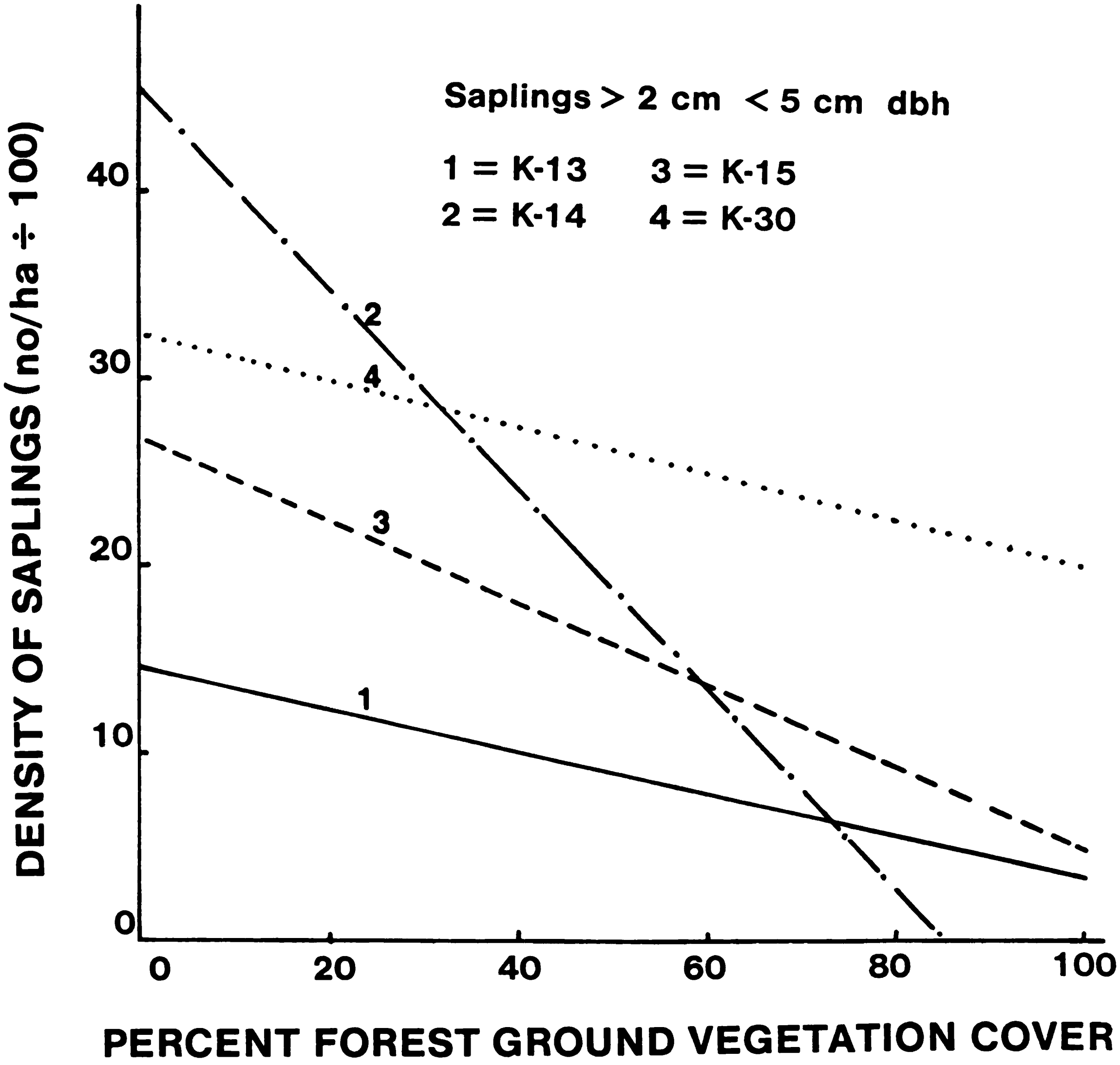
Parameter	Tree Classes		A	B	C	D	E	F	G	H	I	J	K	L	M
	Trees	A													
Species richness	Seedlings	B													
	Saplings	C		XX											
	Desirable Trees	D	XX												
	Desirable Saplings	E		XX	XX										
	Trees	F	XX	XX	XX	XX									
Density #/ha	Saplings	G		XX	XX		XX								
	Desirable trees	H	XX		XX	XX		XX	XX						
	Desirable Saplings	I		XX	XX		XX		XX						
	% Forest Canopy Cover	J	X	XX	X			XX	XX						
Other measures	% Gaplight in Forest	K				$\overline{XX}$				$\overline{XX}$		$\overline{XX}$			
	% Ground Veg. Cover	L		$\overline{XX}$	$\overline{XX}$		$\overline{XX}$	$\overline{XX}$	$\overline{XX}$		$\overline{XX}$	$\overline{XX}$			
	% Slope of Plots	M													

X = Significant at P<0.05

XX = Highly significant at P<<0.01

$\overline{X}$ = Significantly inverse

Figure 7. Correlation between sapling density (#.ha 100) and percent forest ground vegetation cover of the study plots in the reserve.


Saplings > 2 cm < 5 cm dbh
1 = K-13
3 = K-15
2 = K-14
4 = K-30
DENSITY OF SAPLINGS (no/ha ÷ 100)
0
10
20
30
40
0
20
40
60
80
100
PERCENT FOREST GROUND VEGETATION COVER
1
2
3
4

density of saplings, and forest canopy cover but negatively related to the amount of light reaching inside the forest and ground vegetation cover. However, the forest canopy cover was positively correlated with the seedling and sapling species richness and density but negatively related to ground vegetation cover. The amount of ground vegetation cover in the forest understory was postively correlated with the intensity of light penetrating into the forest. However, both the ground vegetation cover and the amount of light penetrating into the forest were strongly negatively correlated to seedling and sapling species richness and density (Table 7c Figs. 6 & 7).

The heavily selectively cut and treated forest tract (K-13) showed vegetation correlation patterns similar to K-15. The species richness of big trees was positively correlated, though weakly, with sapling species richness and forest canopy cover, but negatively with the amount of gap light reaching inside the forest (Table 7d). Again, the juvenile tree classes were positively correlated with the level of forest canopy cover. The amount of forest ground vegetation cover was again strongly negatively correlated with juvenile tree species richness and density and the level of forest cover but positively with the amount of sunlight penetrating into the forest.

Table 7c. Pearson's correlations between forest vegetation parameters of heavily selectively cut forest (K-15) in the reserve.

Parameter	Tree Classes		A	B	C	D	E	F	G	H	I	J	K	L	M
	Trees	A													
Species richness	Seedlings	B	XX												
	Saplings	C	X	XX											
	Desirable Trees	D	XX	X											
	Desirable Saplings	E	XX	X	XX										
Density #/ha	Trees	F		XX	XX	X	XX								
	Saplings	G		XX	XX		XX	XX							
	Desirable trees	H	XX	X		XX		X							
	Desirable Saplings	I	XX	X	XX		XX	XX	XX						
Other measures	% Forest Canopy Cover	J	X	XX	X			XX	X						
	% Gaplight in Forest	K	$\overline{X}$	$\overline{X}$				$\overline{XX}$							
	% Ground Veg. Cover	L	$\overline{XX}$	$\overline{XX}$	$\overline{XX}$		$\overline{X}$	$\overline{XX}$	$\overline{XX}$		$\overline{X}$	$\overline{XX}$	$\overline{XX}$		
	% Slope of Plots	M			X		XX				XX				

X = Significant at P<0.05
XX = Highly significant at P<<0.01
$\overline{X}$ = Significantly inverse

Table 7d. Pearson's correlations between forest vegetation parameters of heavily selectively cut and treated forest (K-13) in the reserve.

Parameter	Tree Classes		A	B	C	D	E	F	G	H	I	J	K	L	M
Species richness	Trees	A													
	Seedlings	B													
	Saplings	C	X	X											
	Desirable Trees	D	XX												
	Desirable Saplings	E			XX										
Density #/ha	Trees	F	XX			XX									
	Saplings	G		X	XX		XX								
	Desirable trees	H	XX			XX		XX							
	Desirable Saplings	I		X	XX		XX		XX						
Other measures	% Forest Canopy Cover	J	XX		XX		XX	X	XX		XX				
	% Gaplight in Forest	K	$\overline{X}$									$\overline{XX}$			
	% Ground Veg. Cover	L		$\overline{XX}$	$\overline{XX}$				$\overline{XX}$		$\overline{X}$	$\overline{XX}$	X		
	% Slope of Plots	M													

X = Significant correlation, $P<0.05$

XX = Highly significant at $P<<0.01$

$\overline{X}$ = Significantly inverse

Regeneration in Mature and Secondary Forest Communities

Tree Size-Class distribution

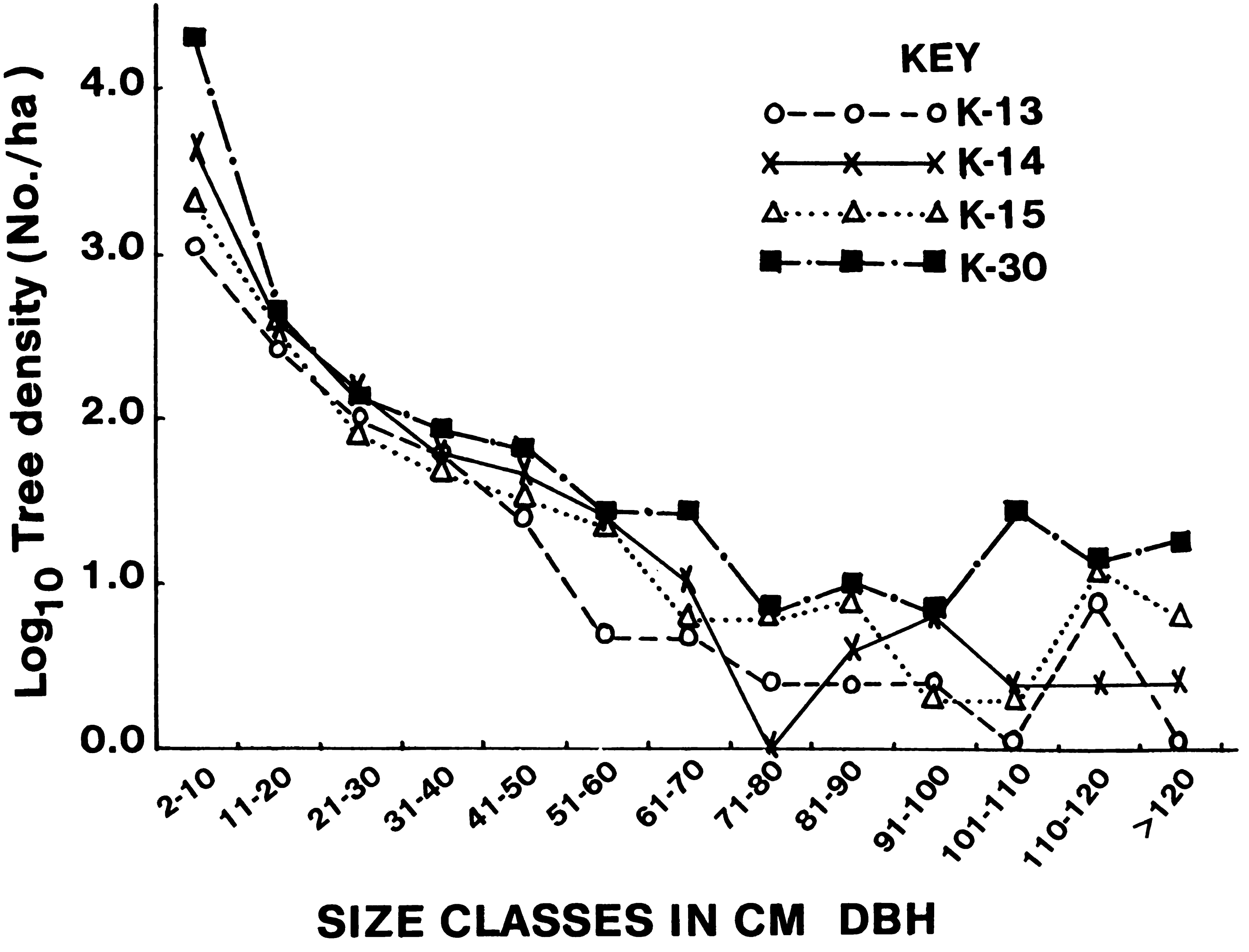
The size class distribution of both desirable and non-desirable timber species combined are shown in Table 8, and Fig. 8. For all forest tracts studied, there was heavy stocking in the smaller tree size classes (> 2 cm < 10 cm dbh) and intermediate stocking in the middle classes (> 11 cm ≤ 40 cm dbh) but very low stocking densities for the larger size classes. In all cases, and for all size classes but one, the plots in uncut mature forest displayed the highest stocking densities. In one intermediate size class (≥ 21 cm < 30 cm dbh) the plots in lightly cut forest (K-14) exhibited one of the highest stocking densities, 19.8% more than the density of the same class in uncut forest. It was suggested that light felling and slight opening of the canopy encouraged more regeneration and growth of pre-existing and new fast growing species which resulted in the big increase in stocking. Again, most understory species like _U. congensis_ and _T. nobilis_, which exhibit no large trees, showed extremely high stocking densities in the smaller and intermediate size classes. They also seem to be regenerating continuously in all compartments except the heavily cut and treated forest (K-13). One should also note that the effect of selective cutting and intensity of cutting and/or treatment were detrimental to both the seedling/sapling classes and larger tree size classes (Table 8, Fig. 8). The contribution of the desirable or canopy

Table 8. Percent size class distribution of tree species in the study compartments of the reserve and potential contribution to the possible maximum standing stock since harvest with K-30 as a control (=100%).

	Size classes in cm dbh				
Study Plot	>2<10	>11<20	>21<30	>31<50	>50
K-30	96.2 100	2.0 100	0.63 100	0.64 100	0.6 100
K-14	83.8 16.6	9.4 89.4	4.0 119.8*	1.6 47.5	1.3 44.3
K-15	80.2 10.1	10.6 64.3	3.0 56.9	3.5 66.0	2.7 58.1
K-13	70.4 5.6	16.1 61.8	6.8 82.5	5.2 62.3	1.5 19.9

* There was positive post harvest increase in density.

Figure 8. Stand curves for uncut forest (K-30) lightly cut forest (K-14), heavily selectively cut forest (K-15) and the heavily selectively cut and treated forest tract (K-13) of the reserve.


KEY
K-13
K-14
K-15
K-30
Log$_{10}$ Tree density (No./ha)
4.0
3.0
2.0
1.0
0.0
2-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
101-110
110-120
>120
SIZE CLASSES IN CM DBH

tree species to the density and distribution of trees in the various size classes was small (see tree density and basal area). Clearly, selective felling disrupted the distribution and compositon of the desirable trees in cut areas. This was reflected in importance values and ranks of species (Table 5) and the great fluctuations in tree stand curves for size classes above 60 cm dbh (Fig. 8). Tree species such as A. altissima, B. unijugata, C. africana, C. gorungosanum, C. millenii, M. bagshawei, N. buchananii, O. welwitschii, P. excelsa and T. splendida which were particularly sought during felling had the lowest representatives in all size classes studied and for all cut forest tracts. Even some of the largest and often most valuable timber species such as P. excelsa and O. welwitschii showed significant deficiencies both in the smaller and intermediate size classes in all study plots. The greater proportion of individuals of these species was in size classes greater than 50 cm dbh. They also show poor regeneration under semi-open forest canopies. It was thought that such species, deficient in seedling, sapling and pole size classes, might require forest gaps for successful regeneration.

Tree seedling and sapling dynamics

Throughout this chapter, it has been emphasized that the non-desirable timber species contributed significantly to tree species richness, distribution, density and dominance and thus were ranked high in importance (Table 5).

The contribution by desirable timber species to sapling and pole species richness and density was relatively small in all study plots (Table 9). In this section, I focus on the nature and level of regeneration of the 19 desirable or canopy tree species and the four important non-desirable species (Appendix table 2). The 19 desirable species were mostly the canopy trees which exceed 50 cm dbh at maturity.

In heavily selectively cut and treated forest (K-13), tree species with large numbers of saplings, poles and small trees included N. buchananii, B. unijugata, S. scheffleri and D. abyssinica in that order of importance. Together, they constituted 56.3% of sapling regeneration, 36.1% of pole regeneration and 50.6% of sapling and pole regeneration of the desirable and the four important non-desirable species (Appendix table 2). For the lightly cut forest (K-14), the order of abundance of tree sapling species regeneration was L. swynnertonii > N. buchananii > B. unijugata > S. scheffleri > A. toxicaria. These species formed 63.9% of the regeneration of desirable sapling species but 33.9% of the regeneration of both desirable and non-desirable sapling species in the understory. In the heavily selectively cut forest (K-15), the desirable tree species with large numbers of saplings and poles included B. unijugata (in the lead) followed distantly by N. buchananii, C. africana, F. macrophylla and S. scheffleri in that order. These accounted for 39.8% of desirable sapling regeneration in the understory. Under semi-closed canopy conditions of

Table 9. Sapling and pole distribution in cm dbh size-classes for the four study areas.

Study Area	# Plots Sampled	Parameter Examined	Saplings (>2 cm <5 cm dbh)		Poles (>5 cm <10 cm dbh)	
			Desirable	Undesirable	Desirable	Undesirable
K-30	49	Density *	1203.4	19321.8	167.4	871.9
		#/species	63.3	345.0	12.0	12.0
K-14	46	Density *	800.0	2665.3	230.4	682.5
		#/species	42.1	48.5	16.5	13.7
K-15	45	Density *	519.9	1648.7	91.1	386.4
		#/species	30.6	34.3	9.1	9.7
K-13	43	Density *	377.4	840.3	109.3	288.4
		#/species	23.6	22.7	7.8	7.6

* Density = #/Ha, #/species = mean number of individuals/species

K-30, L. swynnertonii had the highest amount of regeneration, M. bagshawei followed in second place, F. latifolia in third and N. buchananii in fourth. These four formed 48.5% of the regeneration of desirable sapling species, 30.9% of the regeneration of desirable sapling and pole classes combined, and 32.8% of all desirable and non-desirable sapling and pole classes.

Of the nineteen common desirable species in the study plots, seven had large numbers of saplings and poles under closed canopy and six under opened up canopies whereas the rest seemed to have no special preferences (Appendix table 2). Under closed canopy, saplings of L. swynnertonii, M. bagshawei, T. splendida, A. toxicaria, C. gorungosanum and F. latifolia were abundant. All non-desirable species, mostly the understory types such as U. congensis and T. nobilis, were also very well represented in the sapling regeneration under closed canopy. However, the most successfully regenerating desirable species under open canopies included B. unijugata, F. macrophylla, O. welwitschii and N. buchananii. Although L. swynnertonii, N. buchananii, A. altissima, M. bagshawei and C. africana species had large numbers of saplings and poles in mature forest, a greater percentage of the mature trees was either already dead or dying. In K-30 plots, mature N. buchananii trees had suffered 100% mortality and L. swynnertonii over 80%. The mortality of trees of the other three species was much lower: 14% of C. africana, 17% of A. altissima, and only 3.3% of M. bagshawei. Most were poorly represented in the pole and intermediate size classes but the sapling classes were abundantly represented.

Table 10 shows the results of intercompartment correlation analysis of the density of the saplings and poles of the nineteen desirable and some non-desirable species in the study plots (Appendix table 2). The desirable sapling species regeneration in uncut and lightly cut study plots was similar. The lightly cut (K-14) and heavily cut (K-15) plots also showed similar amounts of desirable sapling regeneration. The third pair which showed similarity in sapling regeneration was the two heavily selectively cut forest tracts (K-15 vs. K-13). All other paired comparisons were significantly different. Similarly, paired comparisons between uncut forest, lightly cut forest and heavily cut forest (K-15) showed that their desirable pole species regeneration was similar. However, all other paired comparisons with the heavily cut and treated forest were significantly different.

Table 10. Correlative comparisons of the density of desirable and some important non-desirable tree saplings and poles of the study plots.

	Saplings (>2 cm <5 cm dbh)				Poles (>5 cm <13 cm dbh)			
Study Plots	K-30	K-14	K-15	K-13	K-30	K-14	K-15	K-13
K-30			all df = 21				all df = 21	
K-14	r=0.778 P<0.01				r=0.880 P<0.01			
K-15	r=0.273 NS	r=0.577 P<0.01			r=0.452 P<0.05	r=0.668 P<0.01		
K-13	r=0.045 NS	r=0.182 NS	r=0.571 P<0.01		r=0.367 NS	r=0.333 NS	r=.276 NS	

DISCUSSION

The Uganda Forest Department employs a polycyclic system in the exploitation of the natural forest in the reserves. Natural regeneration in the cut forests was expected without application of special silvicultural measures if cutting was followed by intensive elephant control (Kingston, 1967). A 70-year rotation cycle of forest exploitation was anticipated. Only commercially desirable species $\geq$ 1.52 m girth at breast height (gbh) were recommended for felling (Kingston, 1967), but the sawmillers also cut trees below 1.52 gbh. Consequently, heavy timber exploitation ranging from 14.0 m^3/ha in lightly cut to over 21 m^3/ha in heavily cut forest tracts ensued. In light of the current state of forest recovery 20 years after cutting, e.g. basal area, 55.7%, 63.6% and 37.3% and forest canopy cover, 80.2%, 52.1% and 38.3% of uncut forest in lightly cut, heavily cut and heavily cut and treated forests, respectively, the 70- year rotation may not be feasible in heavily cut areas.

When carried out with care and on a rational basis, selective timber havesting could be one of the most ecologically sound options for forest management causing minor disturbances akin to natural tree falls (Goodland, 1980; Fearnside, 1983; Uhl et al., 1985). However, several factors interact to make mechanised selective timber harvesting much more detrimental than it would appear (Uhl et al., 1985; Skorupa and Kasenene, 1984; this study). In the first instance, the cutters are not the land owners and have no vested interest in doing the work carefully. The cutters are likely to fell all potentially harvestable trees, with no regard to minimum girth recommendations, thus resulting in undersize trees being cut. Usually, the bulldozers that follow cause damage to many seedlings, saplings and poles during the hauling of logs to extraction roads. The whole method of timber harvesting is lacking in adequate control.

To overcome the difficulty of conversion of outtake records in cubic meters to density of trees removed per forest plot, as a measure of intensity of harvest, a tree stump census method was devised. Although it was almost 19 years since forest exploitation, the decomposing tree stumps, or at least the heartwood portions, were still standing. This indicates that the hardwood forest stumps, under secondary forest conditions, require more than 20 years to rot away. The two methods of estimating level of forest exploitation in terms of density, i.e. conversion from data in cubic meters (Skorupa, unpublished), and direct tree stump census (this study), provided similar estimates of the level of forest exploitation. Direct tree stump censuses can, therefore, be very useful where there are no records of volume of exploitation. It is very likely that the understory vegetation cover, which was variable for the study compartments, had a strong influence on the number of tree stumps seen and distance at which the tree stumps were observed. This might have affected the estimates of the effective width of sample strips and density of observed tree stumps. After all, the method assumed that all cut tree stumps were still present and easily discernible in spite of partial decomposition.

The estimates of level of forest exploitation in the reserve were in accord with African tropical forest management schemes where it is common practice to harvest between 5 and 25 cubic meters of commercially desirable wood/ha (Fontane et al., 1978). This level of exploitation is often dictated by the need for adequate short term cash returns typical of capital intensive forestry (Whitmore 1975; IUCN, 1975; USAID, 1978; Skorupa and Kasenene, 1984). Usually, capital intensive mechanised timber harvesting in the tropics destroys on the order of 50% (33 to 66%) of the original stand (Fox, 1968; Ewel and Conde, 1976; Johns, 1983; Skorupa and Kasenene, 1984; Uhl et al., 1985). In spite of all this extensive forest destruction during felling, only 10% or less of the stand is actually harvested (Fox, 1968; Johns 1983). So, it is difficult to assess the full impact of forest logging based only on volume and level of harvest of a few commercially desirable species. The official Forest Department's extraction data or records do not show the volume or density of trees, poles, saplings or seedlings damaged or killed by tree crushes or by the mechanical handling of logs from the forest to extraction roads. Available evidence all indicates that even the removal of 20 cubic meters of commercial timber or less/ha results in considerable damage to the forest (Ewel and Conde, 1976; Skorupa and Kasenene, 1984; Uhl et al., 1985). In lightly cut areas, removal of $\leq 14 \text{ m}^3$ of commercially valuable timber/ha seems to have caused tolerable forest destruction and disturbances, for high levels of recovery of the forest structure and composition and high amounts of forest tree regeneration have occurred. However, the forest compartments K-13 and K-15, which had approximately 17 and 21 m^3 of actual volume of commercial timber mechanically removed/ha, respectively, seem to have been over-exploited, causing extensive forest destruction and disturbance. This level of exploitation may have been detrimental for the medium altitude tropical moist forest, as such forests are characterised by lower numbers of species and lower volume of potentially harvestable timber than typical lowland tropical forests (Richards, 1964, 1973; Whitmore, 1975).

Judging from the amount of deviation of selected ecosystem variables, e.g. vegetation composition, structure and level of regeneration etc., from a reference mature forest, 20 years post cut, the heavily selectively cut forests were substantially disturbed and degraded. Species diversity has been one of the basic concepts of ecology used to characterise communities and ecosystems (Gomez-Pompa et al., 1972; Richards, 1973; DeJong, 1975; Whitmore, 1975). Consequently, two commonly applied indices, the Simpson's (Ds) and Shannon-Wiener (H') diversity indices were used to characterise the cut and uncut forest tracts of the reserve. Both indices are known to be sensitive to changes in the numbers of species and the distribution of individuals amongst the species (i.e. evenness or equitability, E) (Krebs, 1972; DeJong, 1975; Barbour et al., 1980 and Brower and Zar, 1984). Species richness, as the simplest and least ambiguous index of species diversity (Green, 1979) was also compared between cut and uncut forest compartments.

Deducing from the maximum species diversity index (H max), all forest compartments, cut and uncut, exhibited high tree, pole and sapling species diversity indices for all tree species combined (H = 4.4 to 5.1), but low diversity indices for desirable species (H = 2.2 to 4.2). The unlogged forest leads in the diversity of tree sapling with lightly cut forest in second place and heavily felled areas in last position. This seemed to agree with the intensity of disturbance the forests had experienced. However, the high equitablity indices for all study compartments clearly indicates multispecies dominance of the forests studied.

The fact that the species-area curves approached or were leveling off after only 40 or less 100 m^2 sample plots, for all size classes in mature and lightly cut forests indicated that a representative number of species had been observed within the study plots. This could be attributed to the high density of trees for all size classes in the mature and lightly cut forests. However, the values of tree species richness observed in this study (37 to 57 species/0.5ha), were lower than those reported for tropical wet forests (Richards, 1952; Whitmore, 1975; Uhl et al., 1980; Hartshorn, 1980), but higher than those reported for tropical dry forests (Murphy and Lugo, 1986a, b). The equitability component of diversity was relatively high, except for the heavily selectively cut forests.

Significant differences in species diversity, richness and equitability still prevail among uncut, lightly cut and heavily selectively felled forest tracts. In the heavily cut forests, 61.1 to 67.6% and 60 to 80% of the large tree and pole classes, respectively, included pioneer and fast growing secondary forest species which were uncommon in mature and lightly cut forests. The sapling classes too (50 to 60%) were dominated by non-desirable weedy species. Pure stands of Trema guineensis, a fast growing pioneer species, were found mainly in the heavily felled forest tracts. Timber stock enumerations prior to forest exploitation showed that tree diversity was relatively constant for all subtypes of Parinari forest (Kingston, 1967). Therefore, it is very unlikely that physical variation and natural phenomena, alone, could explain the great differences in species richness, diversity and equitability for the cut and uncut forest tracts within a single Parinari forest type.

Differential logging intensity, ensuing disturbances and treatment, are thought to account for the large part of the differences exhibited. The Forest Department's post felling silvicultural practice of poisoning non-commercial residual trees (weeds), could also account for the 21.9%, 12.9% and 2.0% further depression of floral diversity of saplings, poles and trees, respectively, in the heavily cut and treated forest tracts of the reserve.

The species diversity and richness were not the only characteristics affected by logging in the reserve. Directly and/or indirectly, heavy selective logging resulted in decreases in the sapling, pole and tree density, distribution and basal area. Light selective cutting decreased the density of saplings, poles and trees by 19.1, 32.4 and 7.3%, respectively, while heavy selective cutting by 54.3, 55.9 and 27.7% respectively. Light selective cutting increased the density of desirable poles to 128.6% (i.e. 28.6% more than in uncut mature forest) whereas heavy cutting has reduced it by 34.6 to 53.9%. However, the greatest reduction in the density of saplings, poles and trees was observed in the heavily cut and treated forests where percentage decreases of 75.8, 69.9 and 32.4% respectively have been recorded. The same general trend applies for the basal areas of saplings, poles and trees. The reductions in densities, distribution and basal areas seemed to correspond to the intensity of exploitation and treatment.

The drastic decreases in density, distribution and basal area have also led to low importance values of the desirable timber or canopy species. This is due to the fact that felling was selective with respect to size and prime species. Selection for size and prime species during cutting may also explain the low correlations between importance values and ranks of tree species in uncut and heavily cut forests or lightly cut and heavily cut forests. However, the significant positive correlations between importance values and ranks of tree species in uncut and lightly cut forests were clear indications of high forest recovery rates in lightly selectively cut than heavily cut forests.

Accompanying drastic decreases in density and basal areas of trees were serious reductions in forest canopy cover, more especially in heavily cut areas. In selective felling, the maximum recommended level of reduction of closed canopy cover lies between 40 and 50% (Kingston, 1967, Uhl _et_ _al._, 1985). But in the actual cutting of the forest in the reserve, this was not adhered to. Twenty years after, the forest canopy cover in lightly cut, heavily cut and heavily cut and treated forests was still 19.8%, 47.9% and 61.7%, respectively, less than that in uncut mature forest. Consequently, the high intensities of sunlight reaching into the forest encourage the growth and development of a dense tangle of impenetrable herbs, climbers and non-woody shrubs. The dense understory was strongly negatively correlated with seedling and sapling regeneration of both desirable and non-desirable species. Generally, the slightly open forest canopy as in uncut and lightly cut forests, encouraged more regeneration and provided protection to natural regeneration of hardwood species including the desirable timber species, at the expense of a thick understory of herbs and non-woody shrubs. Therefore, many of the vegetational differences between uncut, lightly cut and heavily cut forest tracts were a result of habitat modification by selective felling operations and not initial differences in the habitat conditions.

In the Budongo forest, Uganda, Philip (1965) observed adequate natural regeneration of valuable timber species after felling and poisoning of weedy species. But most studies concerned with forest regeneration and recovery after felling operations or other forms of disturbances (e.g. Eggeling, 1947a; Richards, 1964; Whitmore 1975; Synnott, 1975; Uhl et al., 1985, 1982b and this study) contradict Philip's observations. However, it does appear that differences in level and type of disturbance are very important in forest regeneration and recovery. Most studies suggest that selective logging encourages the regeneration of colonizing or secondary forest species with only a small representation of primary forest species in intermediate stages of succession (Richards, 1964; Uhl et al., 1985). Forest communities which have undergone clear cutting or have had any severe disruption show decreases in numbers of K-selected species and increases in opportunistic or r-selected species.

In their natural habitats, characterised by low light conditions, seedlings and saplings of primary forest species apparently possess adaptive mechanisms which permit them to undergo long periods of suppression and still recover after a disturbance (Richards, 1972; Whitmore, 1975; Gomez-Pompa _et al._, 1976). However, these shade-tolerant species differ with respect to optimal light intensities for growth (Marquis _et al._, 1986; Lugo, 1970). As the results of this study also suggest, the logged or desirable primary forest species may have found post-logging light conditions (i.e. 3.5 to 5.0 times more in heavily cut than uncut forest) unsuitable for their own regeneration. Tree species such as _U. congensis_ and _T. nobilis_ are characteristic understory species of the reserve and probably are shade- requiring in habit. Their impoverished distribution, lower densities, lower dominance and absence in heavily cut and significantly disturbed forests in the reserve may suggest failure to survive in altered microhabitat and forest climate. In a red fir forest in Sierra Nevada, California, Ustin _et al._ (1984) also found that high light intensities on open sites were inhibitory to red fir seedling regeneration. They suggested that seedlings were absent from high light plots because of temperature and water stresses induced by higher irradiances early in the growing season.

Observations in this study and those of Langdale-Brown _et_ _al._ (1964) and Kingston (1967), suggest severe lack of regeneration of _P._ _excelsa_ and _O._ _welwitschii_ in the high forest of the reserve. These were the dominant tree species in some parts of the reserve and often the largest trees. The scarcity of saplings, poles and small trees in the understory shows that their populations may be unstable and declining as a component of the system. In African forests, poor regeneration of dominant species, as was the case in this study, may indicate changing composition of the community (Langdale-Brown _et_ _al._, 1964; Richards, 1964). The changes may be part of the normal process of development of a successional forest towards a stable climax state.

In the Budongo forest, Uganda, Eggeling (1947), Brasnett (1946) and Synnott (1975) suggested that lack of adequate seed supply after cutting was responsible for the low species diversity and limited regeneration of trees in the secondary forest. Over-exploitation of mature trees and treatment of over-mature and defective desirables with arboricides reduces the potential seed sources for forest regeneration. Other major factors germane to heavy forest logging that have been shown to suppress forest regeneration include: drastic changes in biotic components (e.g. rodents and insects, Janzen, 1971; Synnott, 1975; Isabirye-Basuta, 1979; Kasenene, 1980, 1984), changes in microlimatic conditions of the forest (Richards, 1964; Whitmore, 1978; Gomez-Pompa, 1976) and physical-chemical changes in the soils (Armson et al., 1973; Putz, 1983). However, other observers suggest that recovery of a felled forest may depend on either the persistence of adequate primary forest tree species on the spot as adult refuges (Synnott, 1975; Kasenene, 1980, 1984; this study), regeneration from dormant soil seed banks (Whitmore, 1975; Putz, 1983a; Uhl and Jordan, 1984; Young, 1985), survival of pre-existing seedlings, saplings and sprouts (Uhl et al., 1982b, 1985 and Murphy and Lugo, 1986a) or the possibility of colonisation from outside (Richards, 1964, Gomez-Pompa et al., 1972, Liew and Wong, 1973; Poore, 1976 and Hartshorn, 1978). However, seed viability for some trees may be very short and successful regeneration may occur only under closed or slightly altered forest conditions. In the heavily selectively cut forest tracts of the reserve, a combination of factors, including excessive felling of the mature trees, the killing of undesirable and defective desirable trees with arboricides and windthrows (Skorupa and Kasenene, 1984) drastically reduced the number of reproductively mature trees. Seed supply may have been locally inadequate, contributing to low potential for natural regeneration. Therefore, in selective felling, much effort should be geared toward minimizing the impact of deforestation. The crucial matter in the felling system should be to control the damage done.

SUMMARY AND CONCLUSION

The composition, structure and regeneration of uncut mature forest and selectively cut secondary forest tracts of the Kibale Forest Reserve were investigated to determine the effects of mechanized selective timber harvesting. The mature and secondary forest communities both exhibited high species diversity and equitability which indicated lack of forest dominance by any one tree species. The species-areas curves for saplings, poles and trees reached asymptotes in less than 0.5 ha of cumulative area sampled. This suggests high stand densities for the three size classes examined. The species richness observed for the mature high altitude tropical moist forest averaged 49 to 57/0.5 ha and was lower than those reported for lowland tropical moist or rainforests but high compared to tropical dry forests. However, the average values of basal areas of trees, poles and saplings combined were high (40.7 to 109.1 m^2/ha) compared to those reported for tropical wet or rainforest (20-75 m^2/ha) and tropical dry forests (17 to 40 m^2/ha). A combination of high stand densities for the three size classes studied and inclusion of the saplings and poles in the sample, may have caused the inflation of the values for basal areas.

In high altitude tropical moist forest, mechanised selective timber exploitation in excess of 14 m^3/ha of commercially desirable timber was observed to be destructive to the forest structure, composition and regeneration. The forest compartments which had 17 and 21 m^3/ha of actual volume of commercial timber mechanically removed appear to have been overexploited, causing extensive damage and disturbance to the forest. In contrast, the lightly cut forest had 14 m^3 of commercial timber per hectare removed, and high amounts of forest regeneration and recovery have occurred. Directly and/or indirectly, heavy selective logging resulted in drastic decreases in equitability, basal area, density and species richness of saplings, poles and small tress and large trees. The reductions in equitability, density and basal area also led to low importance values of desirable timber or canopy species since forest felling was selective with respect to size of trees and prime species.

Corresponding to drastic decreases in density and basal areas of trees were serious reductions in forest canopy cover of the heavily cut areas. Consequently, high intensities of sunlight, deleterious to primary forest seedling and sapling species regeneration, induced a dense tangle of herbs, climbers and non-woody shrubs. The dense understory was itself strongly negatively correlated with seedling and sapling regeneration of both desirable and non valuable tree species. Thus, great structural and compositonal differences between uncut, lightly cut and heavily selectively cut forest tracts of the reserve still existed at the time of sampling, 20 years post cut. Physical variation and natural phenomena alone could not explain the great differences in species richness, diversity and equitablity for uncut, lightly cut and heavily selectively cut, and cut and treated forest tracts of the reserve. Differential logging intensity, ensuing problems of forest disturbance and arboricide treatment were evidently the major cause.

The uncut mature forest exhibited the highest levels of species richness, density and basal areas for trees, poles and saplings of both the desirable timber or canopy species and non-valuable tree species. In this respect, the lightly selectively cut forest followed closely in second place, the heavily cut in third and the heavily cut and treated forest in fourth position. The gradations in tree species diversity, density, basal area and level of forest regeneration in terms of sapling and pole species richness, density and equitability of both desirable and non-valuable timber species, 20 years after selective felling closely corresponded to the intensity of felling and felling with treatment. Treatment of the residual forest weeds with arboricides was suspected to be the major cause of further depression in the floristic diversity of both desirable and non-desirable species in the heavily cut and treated forest tracts of the reserve.

Conclusion

Because of the intensity of such operations, the damage inflicted by mechanical logging operations is often much more severe than that of pitsawyers (Kasenene 1984, Skorupa and Kasenene 1984, Struhsaker pers. comm.). Modified forms of a polycyclic felling system (Whitmore 1975) that are slightly more advanced than pitsawing conceivably could be managed in ways compatible with maintaining the dynamic structure and functions of the forest. Timber extraction through controlled polycyclic systems that could remove between 2 and 4 canopy trees/ha would be akin to natural tree fall disturbance causing small gaps in the forest canopy (Whitmore 1975, Herbert and Beveridge 1977, Uhl *et al*. 1985) and the damage done to the forest would be relatively minor. Therefore an important goal of rational forest exploitation should be to manipulate the forest canopy to create gaps of a size that favor the growth and development of the chosen species.

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Appendix Table 1, **Summary of analysis of variance and Duncan's Multiple Range test on some forest vegetation enumeration parameters.**

Parameters		Species richness				Density #/ha				Basal area m^2/ha			
		1	2	3	4	1	2	3	4	1	2	3	4
	1	-				-				-			
Trees	2	*	-			*	-				-		
	3		*	-			*	-		*		-	
	4	*		*	-	*		*	-	*	*	*	-
	1	-				-				-			
Poles	2	*	-			*	-			*	-		
	3		*	-			*	-			*	-	
	4	*	*	*	-	*	*	*	-	*	*	*	-
	1	-				-				-			
Saplings	2	*	-			*	-			*	-		
	3	*	*	-		*	*	-			*	-	
	4	*	*	*	-	*	*	*	-	*	*	*	-
Desirable Trees	1	-				-				-			
	2		-			*	-				-		
	3			-			*	-		*		-	
	4	*	*	*	-	*	*	*	-	*	*	*	-
Desirable Poles	1	-				-							
	2	*	-			*	-						
	3		*	-			*	-					
	4			*	-			*	-				
Desirable Saplings	1	-				-							
	2	*	-			*	-						
	3			-			*	-					
	4	*		*	-	*		*	-				

1 = K-13
2 = K-14
3 = K-15
4 = K-30
* = Pairs of groups significantly different at the 0.05 level or lower.

Appendix Table 2. Estimates of density of desirable species saplings (Sa) and Poles (Po) for the study plots.

Tree Species	COMPARTMENTS							
	K-30		K-14		K-15		K-13	
	Sa	Po	Sa	Po	Sa	Po	Sa	Po
A. altissima	40.8	2.1	21.7	2.2	2.2	2.2	9.3	11.6
A. toxicaria	134.7	8.2	73.9	13.1	13.3	0.0	27.9	7.0
B. unijugata	85.7	2.1	113.1	6.5	128.9	11.1	83.7	23.3
C. africana	44.9	2.1	60.9	26.1	48.9	22.2	0.0	2.3
C. durandii *	40.8	26.5	17.4	26.1	26.7	26.7	18.6	30.2
C. gorungosanum	40.8	2.1	14.4	6.5	22.2	0.0	18.6	0.0
C. millenii	12.2	8.2	4.4	2.2	8.9	11.1	0.0	9.3
D. abyssinica *	106.1	40.8	60.9	21.7	84.4	24.4	46.5	9.3
F. macrophylla	8.2	2.1	13.1	6.5	44.4	11.1	18.6	4.7
F. angolensis	8.2	2.1	13.1	13.1	8.9	6.7	9.3	2.3
F. latifolia	85.7	44.9	21.7	73.9	31.1	13.3	9.3	14.0
L. swynnertonii	277.6	20.4	143.5	8.7	0.0	2.2	9.3	0.0
M. platycalyx	28.6	46.9	26.1	39.1	13.3	17.8	4.7	16.3
M. bagshawei	118.4	12.2	43.5	6.5	22.2	0.0	4.7	0.0
N. buchananii	65.3	0.0	104.4	10.9	62.2	2.2	107.0	9.3
O. welwitschii	8.2	2.1	43.5	0.0	31.1	2.2	9.3	2.3
P. excelsa	16.3	0.0	17.4	4.4	22.2	2.2	0.0	0.0
P. africana	0.0	0.0	8.7	6.5	4.4	0.0	4.7	4.7
S. scheffleri	44.9	30.6	78.3	32.6	31.1	4.4	46.5	30.2
S. globulifera	53.1	2.1	17.4	0.0	0.0	0.0	14.0	0.0
T. nobilis *	187.8	71.4	252.2	93.5	88.9	36.7	23.3	11.6
T. splendida	53.1	2.1	69.0	0.0	22.2	2.2	37.2	11.6
U. congensis *	204.1	28.6	295.7	23.9	75.6	31.1	0.0	0.0

* = Non-desirable timber species

PART II

MODE OF TREE DEATH AND GAP CREATION IN SELECTIVELY CUT AND UNCUT FOREST TRACTS OF THE RESERVE

INTRODUCTION

Tropical forests have often been described as mosaics of patches of different sizes and ages of regrowth originating in gaps created by falling trees (Richards, 1952; Whitmore, 1975, 1978; Brokaw, 1982a, b; Pickett, 1983; Putz et al., 1983). Forests are often subject to many scales of disturbance ranging from the fall of an individual tree or branch to the flattening of large areas by earthquakes, hurricanes or wind and storm throws (Leigh, 1982; Foster and Brokaw, 1982). Tropical forest patchiness has also been largely attributed to several other factors including microtopography, landslides, various forms of tree death, animal activity, wind and storm throws, forest disturbances from selective logging and clearing for agriculture, settlements and roads amongst others (Eggeling, 1947; Longman and Jenik, 1974; Hartshorn, 1978; Denslow, 1980; Brokaw, 1982a; Putz and Milton, 1982; Foster and Brokaw, 1982; Putz et al., 1983; Pickett, 1983; Sousa, 1984; Skorupa and Kasenene, 1984; Brokaw, 1985a, b; and Lieberman et al., 1985).

Several workers have suggested that the natural rate of tree falls constitutes a very important integral component of the climax forest dynamics (Richards, 1952; Gomez-Pompa *et al.*, 1972, 1974; Hartshorn, 1978, 1980; Schenske and Brokaw, 1981; and Pickett, 1983). For example, many canopy tree species have been observed to depend on gaps for establishment and growth to maturity (Richards, 1952; Whitmore, 1975; Hartshorn, 1978, 1980; Brokaw, 1982b; Pickett, 1983). Seeds of some forest tree species do germinate under closed forest canopy but their seedlings must subsequently be in a gap to ensure further growth and establishment (Denslow, 1980; Brokaw, 1982b). Other groups of tree species survive as suppressed saplings in closed forest until a gap is formed above them. Then they respond by either reducing growth and eventualy dying (Burgess, 1970; Meijer, 1970; Liew and Wong, 1973) or accelerating growth and surviving (Richards, 1952; Whitmore, 1975; and Gomez-Pompa *et al.*, 1972).

Pioneer tree seedlings emerge in gaps of all sizes (Brokaw, 1982a) but their optimum growth and survival are restricted to large forest gaps (Richards, 1952; Whitmore, 1975; Hartshorn, 1978; Denslow, 1980; Brokaw, 1982a; and Pickett, 1983). Therefore, tree falls and consequent forest gap formations are a very important source of environmental heterogeneity (Whitmore, 1975, 1978; Hartshorn, 1978) which has ramifications for ecological diversification and evolution of rainforests (Connell, 1978; Denslow, 1980; and Sousa, 1984). Denslow (1980) and Pickett (1983) have written comprehensive literature synopses of tropical tree species ecological limitations, adaptations and response to

gaps of specific size ranges and modes of formation.

In many forest communities, the most common natural disturbance is the death of canopy trees. These deaths occur in a variety of ways which may include tree uproots, snaps, or death while standing (Brokaw, 1982a; Putz, 1983; Putz and Milton, 1982; Putz _et_ _al._, 1983). Each of these types of disturbance has a different effect on the species composition in regenerating patches of the forest (Brokaw, 1982a; Putz and Milton, 1982; Putz _et_ _al._, 1983). Richards and Williamson (1975) regard gaps, both natural and artificially generated, as dynamic patches for forest regeneration and recovery. However, selective felling has been observed to foster more frequent and severe windfalls (Herbert and Beveridge, 1977).

The existence of large gaps or exposed areas, even in mature forest, has been suggested to be the cause of fast turnover rates for some tropical rainforests (Brokaw, 1982a; Foster and Brokaw, 1982). Denslow (1980) suggested that human induced changes in the size frequency distribution of gaps, by either increasing or decreasing the rate of gap formation, will result in the gradual loss of species. The preceding observations and predictions suggest high tree fall rates for forests where there has been extensive forest disturbance through felling. This could be detrimental to forest regeneration and recovery since the few, usually defective desirable tree species left behind after felling are exposed and may not withstand wind pressure. Their falls would also contribute to the damage of young regeneration and to the further expansion of gaps (Longman and Jenik, 1974; Brokaw, 1982). Accordingly, if conservative use of a tropical forest ecosystem is to be achieved, the utilization scheme should be formulated with respect to likely impacts upon some important dynamic processes of the forest. Consequently, the study of tree mortality rates, with particular emphasis on the dynamics of tree falls in mature and secondary forest communities, was undertaken in the Kibale Forest Reserve. Thus, the main objective for conducting the study was to establish whether selective timber harvesting (light and heavy) had any significant influence on the rates of tree falls, thus gap formation. Secondly, the study was intended to check on whether there were any correlations between rainy seasons and tree falls and possible causes of falls. Finally, an objective was to compare mortality rates observed in this study to mortality rates reported for Neotropic and Malaysian forests to determine whether there were any similarities which might imply applications of similar or different forest management plans.

METHODS

Intensive systematic censusing of freshly fallen trees and large branches began in November, 1984, and ran through June, 1986. Tree and big branch fall censuses were conducted in the lightly selectively cut (K-14), heavily selectively felled (K-15), and uncut mature forest (K-30) compartments of the reserve. All three study compartments are located within Parinari forest type (Kingston, 1967). The mature, undisturbed forest (K-30), located adjacent to the lightly cut forest (K-14), was used as a control. Treefall census routes were permanently marked out in the three forest compartments indicated above. The census routes followed previously established grid lines or trails (Fig. 1 and 2) which are maintained for primate studies. A strip enumeration of all fallen trees encountered on either side of census route was conducted every second and third day of the month following the previous counts. Only new falls, subsequent to the previous, were counted. All tree and big branch falls which caused an observable hole or light gap in the forest canopy and all other trees brought down by the major fall were included in the counts.

Actual censusing of treefalls involved slow walk (≃ 2Km./hr.), visual scanning of either side of the trail

Figure 1. Sectors of study compartments 14(K-14) and 30(K-30) showing tree fall census routes along which tree falls were enumerated for 21 consecutive months. Only a few numbered or lettered grid lines or trails have been included in order to enhance clarity of the census route (thick line).

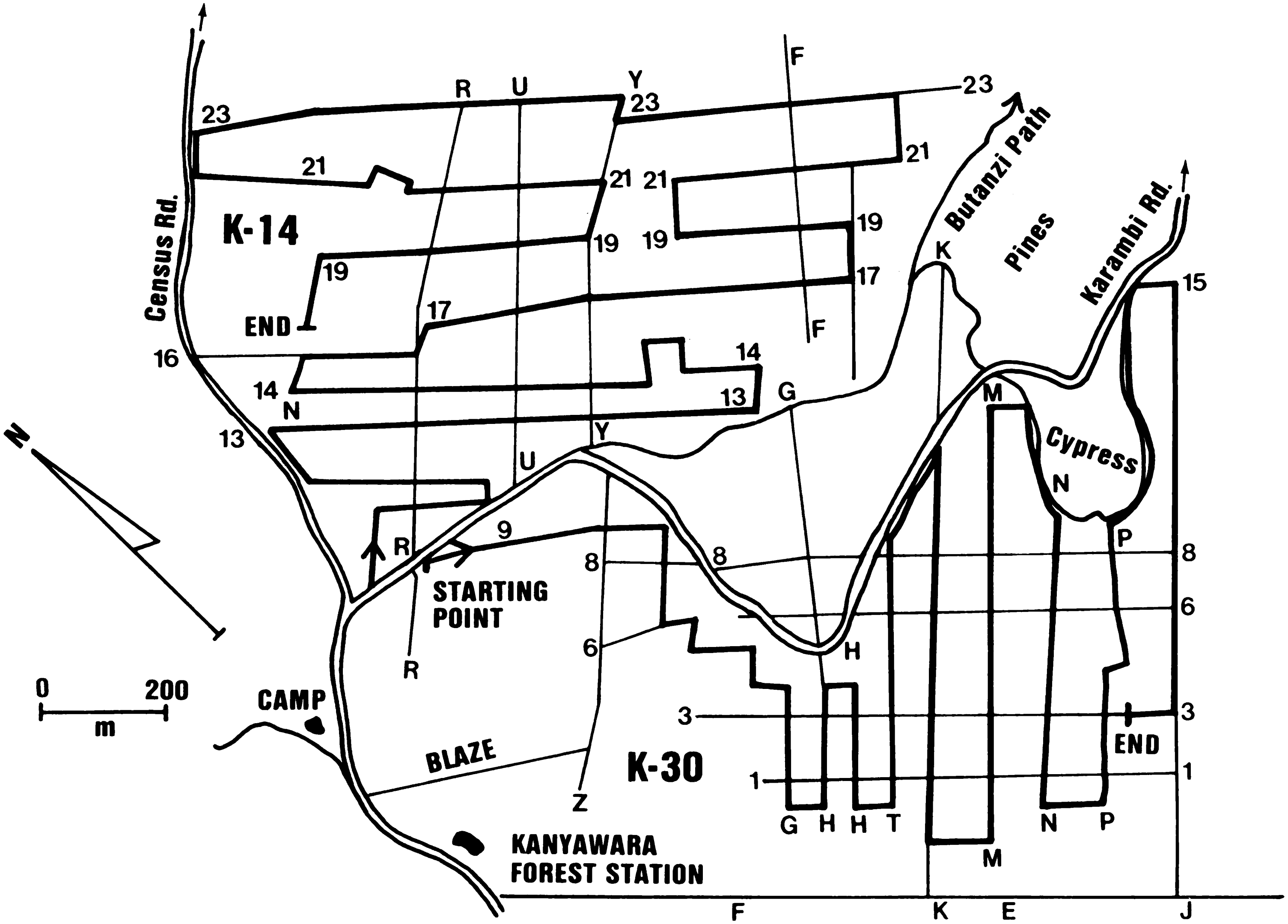
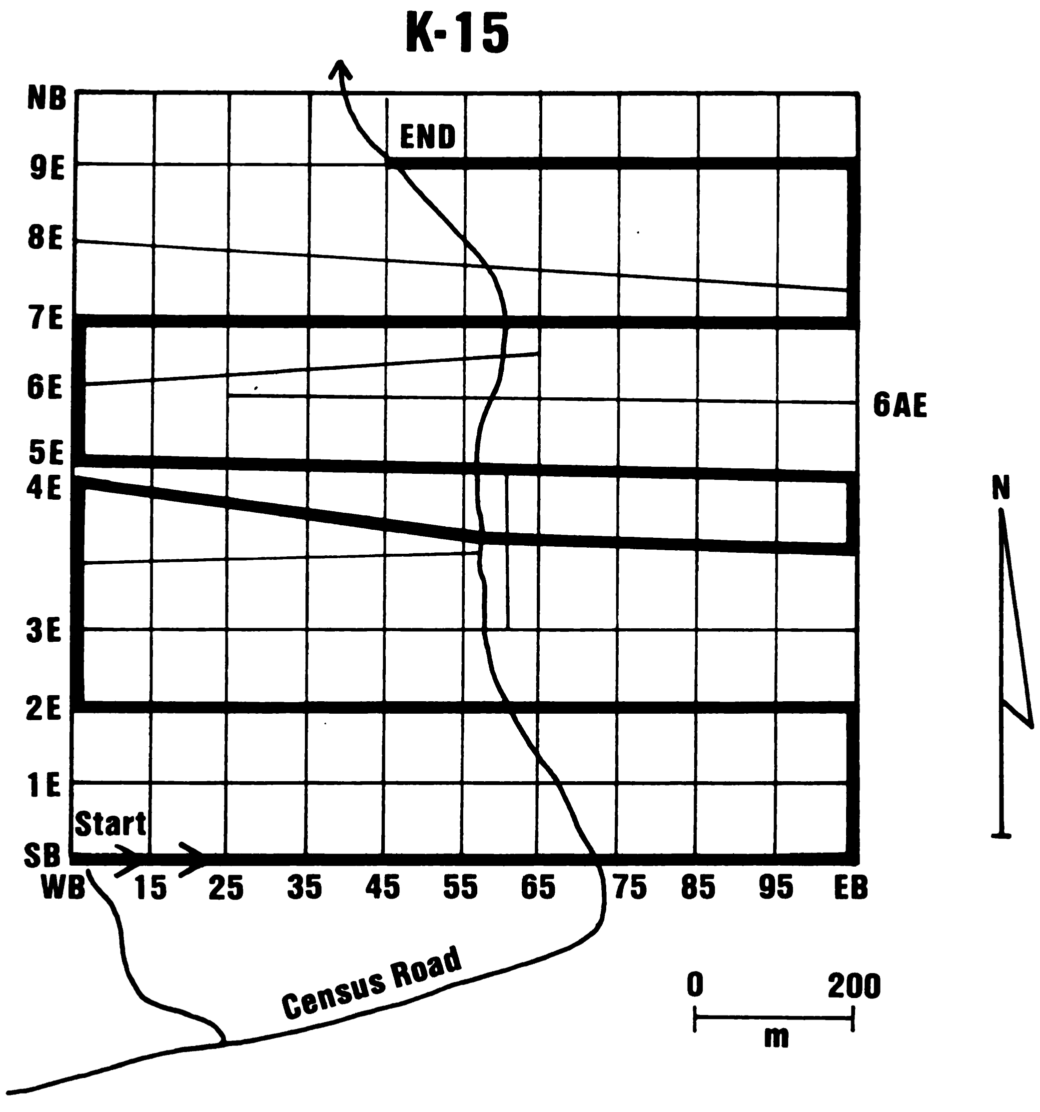

Census Rd.
Butanzi Path
Pines
Karambi Rd.
K-14
K-30
Cypress
STARTING POINT
END
END
BLAZE
CAMP
KANYAWARA FOREST STATION
N
0
200
m
R
U
Y
F
23
21
19
17
16
14
13
9
8
6
3
1
15
K
E
J
G
H
T
M
N
P
Z

Figure 2. Sectors of study compartment 15(K-15) showing the treefall census route (thick line) along which tree fall enumerations were conducted for 21 consecutive months.


K-15
NB
9E
8E
7E
6E
5E
4E
3E
2E
1E
SB
WB
15
25
35
45
55
65
75
85
95
EB
END
Start
6AE
N
Census Road
0
200
m

for treefalls, and recording. There was no straying off the census trail until a tree or branch fall was spotted. Measurements of the perpendicular distance from the trail to the tree or branchfall were made using a tape measure. The diameter of the fallen trunk(s) at 1.3m from the root plate (for uproots), and the diameter of the snapped tree(s) at 1.3m from the ground, were measured. The tree was identified to species following Eggeling and Dale (1951) and Hamilton (1981). The fallen tree condition with regard to whether the tree was live, dead, had heart rot or hollowed center in case of snaps, was noted.

The modes of tree death were categorised as tree snaps, uproots and dead standing. Large limbfalls which caused gaps were classified as branchfalls. Tree snaps included treefalls which had breaks anywhere above the ground level but below the branches. Tree uproots involved soil disturbance and presence of root plate. Trees which broke in the canopy above the lower branches were recorded as branchfalls. Where a combination of both tree snaps and uproot occured, the fall was designated as uproot. Both live and dead trees involved in the falls were counted but recorded separately. The location of the fallen tree was mapped and the fall marked with tapes and aluminum tags bearing dates of first observation and major tree species involved in the fall. A similar method, following the same census trails as for tree falls, was employed in the censusing of dead standing trees, at three-month intervals.

The measurements of the perpendicular distance from the trail to tree falls, branch falls or dead standing trees and the number of falls or dead standing trees observed were used to plot graphs of frequency distribution such as those in Figure 3. The distance at which the slope of occurrence of falls or dead standing trees began to decline permanently to 2% or less of the total counts was taken as half the effective width of the strip sampled. The area of forest strip sampled was then calculated by multiplying the estimated width of the strip by the length of the census trail. The density of falls and dead standing trees in terms of #/ha was then calculated.

The measurements of diameter of trees involved in falls and dead standing were used in estimating the size-class range of standing stock that was susceptible. The susceptible species population densities and density of susceptible trees per study plot were obtained from the tree enumeration data of Part One of this study. The percent rates of falls (snap, uproot and branchfalls) and dead standing trees per study area were then calculated thus:

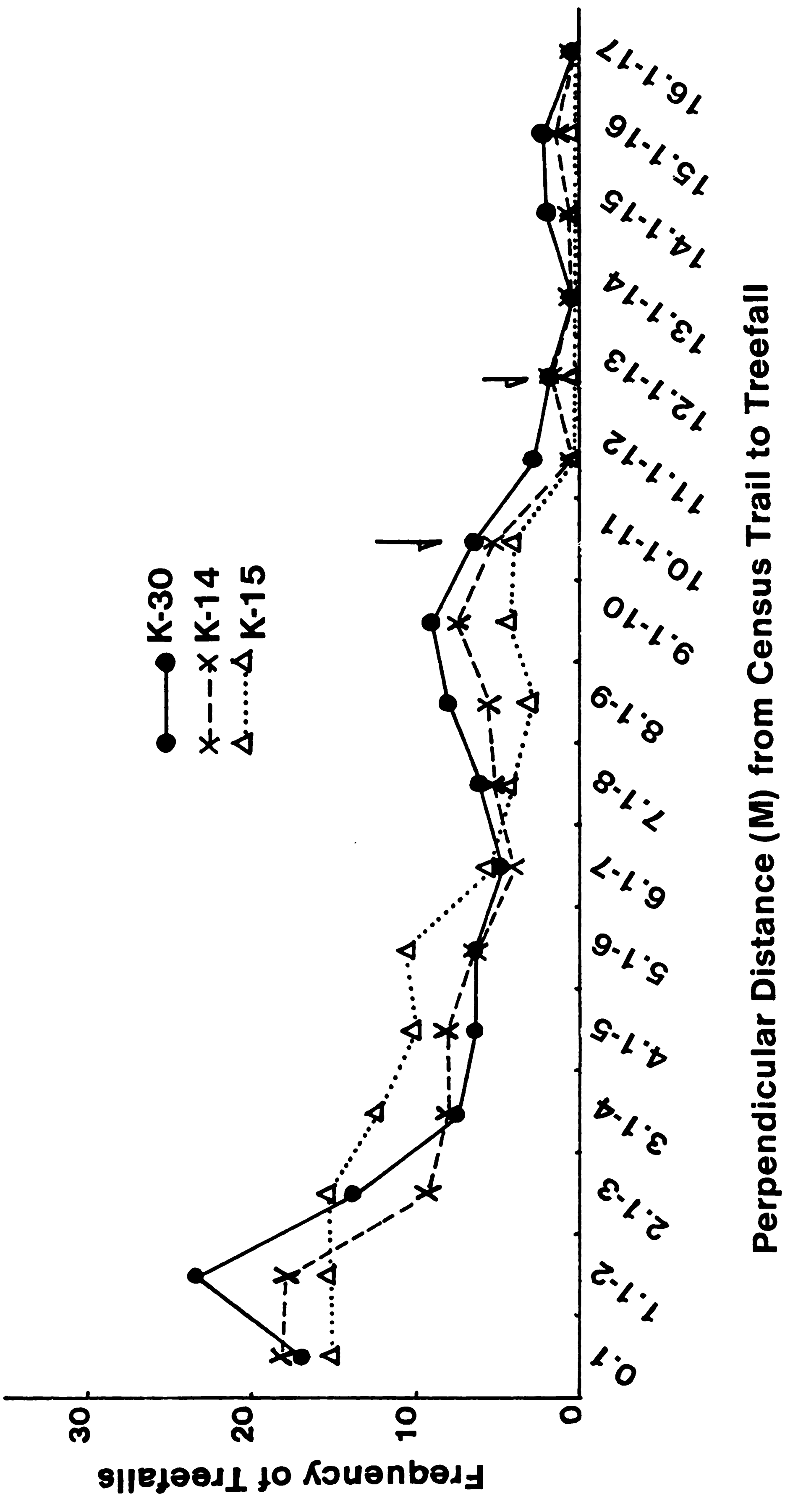
$$\text{Monthly rate} = \frac{DX \times 100}{DS}$$

$$\text{Annual rate} = \frac{12\bar{D}X \times 100}{20 \times DS}$$

Where

DX = Monthly density of tree fall or dead standing trees.

Figure 3. Frequency distribution of tree falls with respect to their perpendicular distance of location in the census strip from the census trail. The 2% or lower cut off points for K-14 and K-15 treefalls were estimated at 10m and at 12m for K-30.


K-30
K-14
K-15
Frequency of Treefalls
0
10
20
30
0.1
1.1-2
2.1-3
3.1-4
4.1-5
5.1-6
6.1-7
7.1-8
8.1-9
9.1-10
10.1-11
11.1-12
12.1-13
13.1-14
14.1-15
15.1-16
16.1-17
Perpendicular Distance (M) from Census Trail to Treefall

$\overline{DX}$ = Mean monthly density of tree falls or dead standing trees.

DS = Density of susceptible trees per study area.

12 and 20 = Months in a year and months of sampling, respectively.

The time it would take all susceptible trees in each compartment to have fallen (average life expectancy) was estimated by dividing the density (No./ha) of susceptible trees by total live tree falls/ha/year. However, it was assumed that constant rates of tree falls per compartment per year would be maintained.

The data for the first month of tree death sampling (October, 1984) was only used as base line for subsequent samples. It was never included in the statistical computations due to uncertainties regarding the time over which observed tree falls had occurred.

RESULTS

Comparison of Treefalls in Cut and Uncut Mature Forest

The lengths of the census routes were 7.18km, 6.94Km, and 6.64Km for uncut (K-30), lightly cut (K-14), and heavily selectively cut (K-15) forests, respectively. Estimates of census strip widths were 20m for both lightly and heavily cut forests (K-14 and K-15 respectively) and 24m for the uncut mature forest. Consequently, forest areas of 13.88ha, 13.28ha and 17.23ha for K-14, K-15 and K-30, respectively, were sampled for tree falls.

Intra-Compartment Comparisons

The monthly densities (#/ha) of tree and branch falls were compared (Appendix Tables 1, 2 and 3) within each of the three compartments. The Mann-Whitney U-test for large samples (n=20 months) was used to compare the mode of tree and branch falls within the study compartments. The U-value was computed from the relationships:

$$U = n_1 n_2 + \frac{n_1(n_1+1)}{2} - R_1 \text{ or}$$

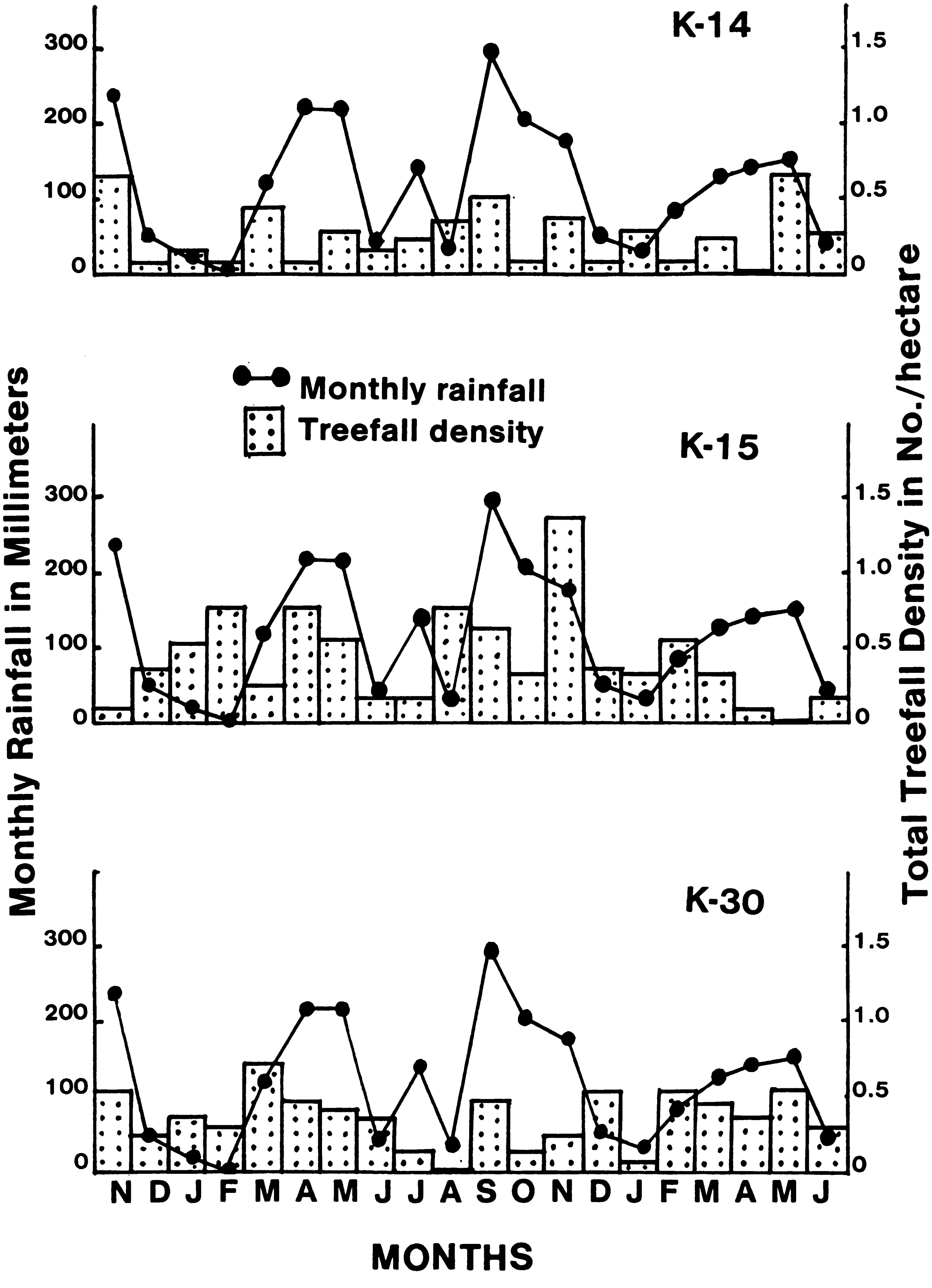
$$U = n_1 n_2 + \frac{n_2(n_2+1)}{2} - R_2$$

where R_1 and R_2 were the sums of the ranks assigned to groups whose sizes were n_1 and n_2 respectively (see Siegel, 1956; pp. 119-120).

Within the lightly cut forest tract (K-14), there was no significant difference between the densities of live and dead branch falls, tree snaps, tree uproots or a combination of tree snaps and uproots involved in the falls (all $P>0.05$, Mann-Whitney U-test-one tailed test) among months. However, there were more monthly tree snaps than uproots ($U=106$, $n_1=n_2=20$, $P<0.01$ one tailed test). Both tree snaps and uproots were independent of whether the tree was live or dead ($X^2=0.333$, $P>0.455$). With the exception of total tree falls (combined snaps and uproots, $r=0.420$, $P<0.05$) all other forms of falls i.e. branchfalls, tree snaps and tree uproots were not significantly correlated with monthly rainfall (Fig. 4).

The heavily selectively cut forest (K-15) displayed a different pattern of tree falls (Appendix Table 2). The densities of live and dead branchfalls and live and dead tree uproots were similar. There were more live tree snaps than dead tree snaps ($U=119$. $n_1=n_2=20$ $P<0.025$ one tailed test) and the total tree falls (snaps + uproots) had more live than dead trees involved in the falls ($U=120$, $n_1=n_2=20$ $P<0.025$). As for K-14, there were also more tree snaps than uproots ($U=134$ $n_1=n_2=20$, $P<0.05$). However, in the heavily selectively cut forest, live trees exhibited a higher tendency to snap than uproot ($X^2=3.34$, $X^2_{0.05}$ $[1]=3.84$)

Figure 4. Monthly density of total tree falls (snaps + uproots) for the lightly cut (K-14), heavily selectively cut (K-15) and uncut mature forest (K-30) compared with monthly rainfall (●——●).


K-14
K-15
K-30
300
200
100
0
1.5
1.0
0.5
0
Monthly rainfall
Treefall density
Monthly Rainfall in Millimeters
Total Treefall Density in No./hectare
N D J F M A M J J A S O N D J F M A M J
MONTHS

compared to lightly cut forest (K-14) though the tendency was not strongly significant. For the heavily cut forest, the correlations between rainfall and tree falls was extremely low and not significant (Fig. 4).

In the control plot (K-30) the density of dead branch falls was higher than live branch falls ($U=93.5$, $n_1=n_2=20$, $P<0.01$) and the density of dead tree uproots was also higher than that of live tree uproots ($U=120$, $n_1=n_2=20$, $P<0.25$). However, there were no differences between the density of live and dead tree snaps or total tree falls (all $P>0.05$, Mann-Whitney U-test, Appendix Table 3). In contrast with K-14 and K-15 tree falls, the density of tree snaps and uproots was similar. As with lightly cut forest, the tree snaps and uproots were independent of tree condition, dead or live ($X^2=2.82$, $P>0.05$). However, there were significant positive correlations between big branch falls and rainfall ($r=0.428$, $P<0.05$) and also for tree uproots and rainfall ($r=0.427$, $P<0.05$). All other treefall correlations with rainfall were not significant.

Of the total trees dead or dying in the lightly selectively cut forest (i.e. treefalls + dead standing stock = 142), 34.5% died because the trunks snapped, 14.1% of them were uprooted and 52.1% died standing. Of the tree falls and dead standing stock, 79.6% was by already dead trees at the time of sampling and 21.1% by live treefalls. Of the 134 trees involved in tree falls and dead standing trees in the heavily selectively cut forest (K-15), 53.0% died from tree snaps, 26.1% from uproots and 18.7% died standing. Live tree falls constituted 54.5% of tree falls and dead standing stock and dead trees the remaining 45.5%. For uncut mature forest, the proportion of dead standing trees was comparable to lightly cut forest. Of the 237 tree falls and dead standing trees recorded, 22.8% were tree snaps, 27.8% tree uproots and 48.5% were dead standing trees. Again, the proportion of live tree falls (21.1%) and dead trees (78.9%) involved in tree falls and dead standing stock were comparable to lightly cut forest. Heavy selective felling seems to have encouraged high rates of tree snaps, most of which were live, but lowered tree deaths through uproots and dead standing. This could be the real case since most large trees, some of which were overmature and thus prone to die standing or uproot, were removed by the felling process.

Intercompartment Comparisons

Diameter measurements of trees that were involved in falls and dead standing trees were used to fix the size class range and density of standing stock that was prone to tree fall death (Table 1). All trees above 15cm dbh were susceptible to falls or death while standing. However, trees below the 15cm dbh cut off point were also involved in tree falls, but trees greater than 15cm dbh were most frequently subject to tree falls and dead standing trees in the majority of study plots.

Table 1. Parameters of tree death rates for the lightly cut forest (K-14), heavily selectively cut (K-15) and uncut mature forest (K-30) of the reserve.

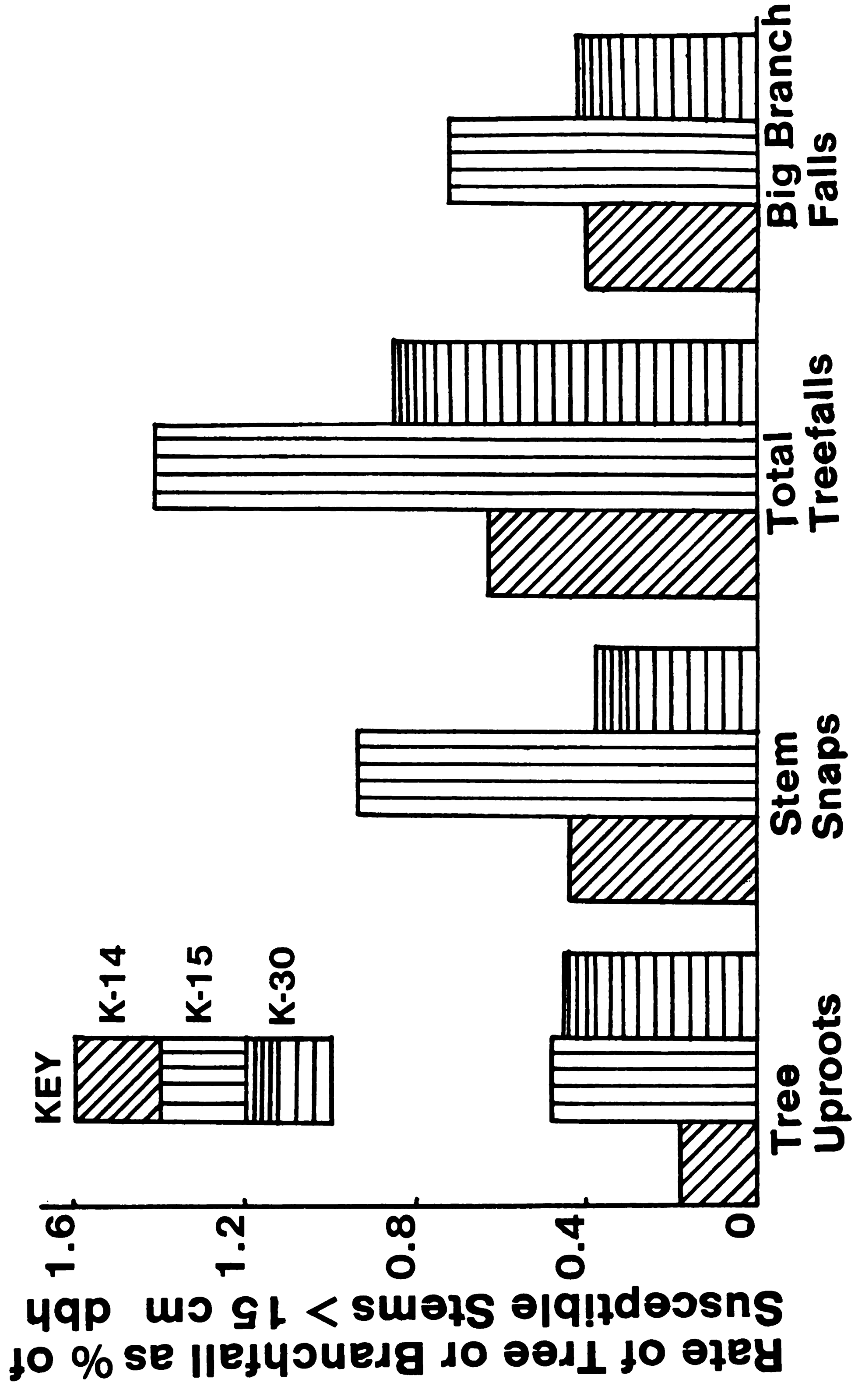
Parameters	Study Plots		
	K-14	K-15	K-30
Forest area (ha) sampled/month	13.88	13.28	17.23
Density (#/ha) of susceptible trees	470.3	351.1	501.7
Total trees fallen (L+D)	68	109	122
Tree snaps/ha/yr (L+D)	2.08	3.25	1.91
Percent snaps /ha/yr (L+D)	0.44	0.93	0.38
Tree uproots/ha/yr (L+D)	0.86	1.67	2.33
Percent uproots/ha/yr (L+D)	0.18	0.48	0.46
Total falls/ha/yr (L+D)	2.94	4.92	4.24
Percent of falls/ha/yr (L+D)	0.63	1.41	0.85
Total live tree falls	30	73	50
Total live tree falls/ha/yr	1.30	3.30	1.74
Percent of deaths/ha/yr	0.27	0.94	0.35
Average life expectancy* (yrs)	361.8	106.4	288.4
Branchfalls/ha/yr	1.90	2.53	0.42
Percent branch falls	0.40	0.72	0.42
<u>Dead standing trees (DST)</u>			
Forest area sampled	24.98	30.54	28.72
Mean DST/month	73.81	25.01	115.02
DST/ha/month	2.95	0.82	4.0
Percent DST/ha/month	0.63	0.23	0.80

* Computed by dividing the susceptible tree density by total live treefalls/ha/year. L=Live, D=Dead.

Tree and branchfall density data (Appendix Tables 1, 2, and 3) were transformed into rates (as percent) of tree fall/ha/susceptible tree and then compared between compartments. The non-parametric comparison by STP (Simultaneous Test Procedure of Dwass and Gabriel, an unplanned test for equal sample sizes), a substitute for single classification ANOVA (Sokal and Rohlf, 1981; p. 438) was used in comparisons. The calculated critical value of $Us_{0.05}[3,20]$ was 286.63 and only values of Us equal or greater than the critical value were considered significant.

In paired comparisons, the heavily selectively cut forest (K-15) had higher monthly rates of tree snaps than the lightly cut (Us=285) and uncut forest (Us=293). There were no significant differences between the rates of tree snaps in lightly cut and uncut forest tracts (also see Fig. 5, Table 1). For tree uproots, again, the heavily selectively cut forest had higher rates than the lightly cut forest (Us=283, weakly significant). The rates of tree uproots in uncut mature forest were also higher than in lightly cut forest (Us=305). However, the heavily selectively cut and uncut forest had similar rates of tree uproots (Us=201 Ns, Fig. 5, Table 1). The rates of total tree falls (i.e. uproots and snaps combined) for the heavily selectively cut forest were also significantly higher than for lightly cut (Us=295.5) or uncut forest (Us=276, weakly significant). But the rates of total tree falls in lightly cut and uncut forest tracts were not significantly different

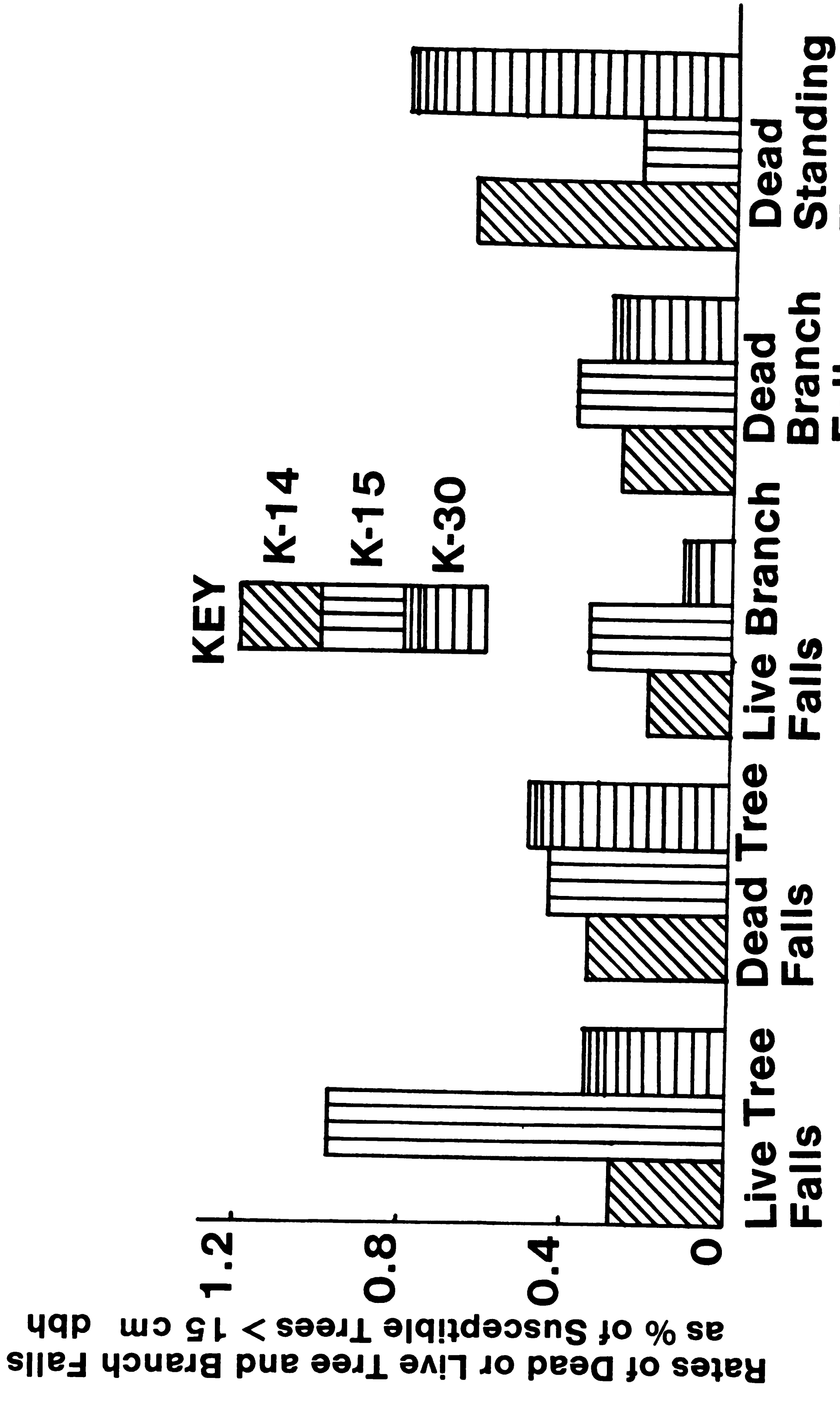
Figure 5. Rate of tree and branch falls in terms of the density of tree uproots, stem snaps and big branch falls (i.e.No/ha/year) expressed as the percentage of the density (#/ha) of susceptible trees in lightly cut (K-14), heavily selectively cut (K-15) and uncut (K-30) forest tracts of the reserve.


KEY
K-14
K-15
K-30
Rate of Tree or Branchfall as % of Susceptible Stems > 15 cm dbh
1.6
1.2
0.8
0.4
0
Tree Uproots
Stem Snaps
Total Treefalls
Big Branch Falls

(Us = 244.5, NS, see also Fig. 5, Table 1). However the rates for total branch falls (i.e. live+dead) for all paired plot comparisons showed no significant differences among compartments (all Us<272, NS, see also Fig. 5 and Table 1).

Comparisons of live and dead trees or big branches involved in falls were also performed (Fig. 6 Table 1). Of the total tree falls, live tree falls formed 67% in heavily cut, 44% in lightly cut and 41% in uncut mature forest. The heavily selectively cut forest also exhibited higher monthly rates of live tree falls than the lightly cut forest (Us=295) or uncut mature forest (Us=274 weakly significant). The montly rates of live tree falls for uncut and lightly cut forest tracts were not significantly different (Us=219 NS). Consequently, estimate of the time it would take all susceptible trees in K-14, K-15 and K-30 to have fallen (average life expectancy) followed a pattern opposite to that of the rates of live trees falls. The average life expectancy for trees in the lightly selectively cut forest was the highest (361.8 years), followed by uncut mature forest (288.4 years) and heavily selectively cut forest (106.4 years) (X^2=134.01, P<0.005). These results should be taken as crude estimates due to the short sampling period and lumping of several age classes of trees including saplings, poles, small trees and large trees. However, with the average life expectancy of trees in uncut mature forest (288.4 years) as a standard, the average expectancy of further life of trees in heavily cut forest seems to have

Figure 6. Rates of live and dead tree and branch falls (No/ha/yr) and monthly estimates of the density of dead standing trees (No/ha/month) expressed as percentage of the density of susceptible trees in lightly cut (K-14), heavily selectively cut (K-15) and uncut (K-30) forest tracts of the reserve.


Rates of Dead or Live Tree and Branch Falls
as % of Susceptible Trees > 15 cm dbh
1.2
0.8
0.4
0
Live Tree Falls
Dead Tree Falls
Live Branch Falls
Dead Branch Fall
Dead Standing Trees
KEY
K-14
K-15
K-30

been substantially reduced, while that for trees in lightly cut forest increased. Natural variation alone could not explain these great differences in average life expectancy of trees from differently managed forest compartments. Differential selective logging was suspected to have contributed significantly to these differences and could account for the greatest part of the differences.

For dead tree fall rates, there were no significant differences among the study compartments (all Us.$\leq$263.5 NS) (Figure 6). Although live and dead branch fall rates were not significantly different for all paired comparisons, the tendency for higher rates of live branch falls in the heavily cut forest was apparent (Fig. 6). Clearly, the lightly cut and uncut forest tracts had similar higher densities of dead standing trees ($Us=47$ $n_1=n_2=11$, $P>0.05$) than the heavily selectively cut forest ($Us=26$, $n_1=n_2=11$, $P<0.025$, one tailed test, also see Fig. 6). There was no correlation between rates of tree falls for all study compartment pair combinations (all $r\leq0.112$, $n=20$, $P>0.05$). This suggests that differences in forest management (in this case, different levels of felling intensity) alters the forest's dynamics of tree falls.

Table 2 shows the density of desirable and some important non-desirable timber or canopy species involved in tree mortality. Excessive removal of large desirable tree species from K-15 apparently did not lead to reductions in treefalls but the escalation of it. All the seventeen major

Table 2. Density (#/ha) of desirable and some important non-desirable* timber or canopy tree species involved in tree falls, and dead standing trees in cut and uncut forest tracts of the reserve.

Tree Species	Tree Falls			Dead standing		
	K14	K15	K30	K14	K15	K30
A. altissima	0.0	0.15	1.33	0.04	0.0	0.56
A. toxicaria	0.0	0.08	0.0	0.0	0.0	0.0
B. unijugata	0.0	0.15	0.06	0.0	0.03	0.0
C. africana	0.57	0.38	0.64	0.08	0.03	0.10
C. durandii*	0.36	0.12	0.23	0.04	0.0	0.0
C. gorungosanum	0.07	0.08	0.46	0.0	0.03	0.07
C. millenii	0.07	0.08	0.06	0.08	0.07	0.0
D. abyssinica*	0.50	1.66	0.41	0.08	0.03	0.0
F. macrophylla	0.07	0.08	0.0	0.0	0.0	0.07
F. angolensis	0.0	0.23	0.11	0.0	0.0	0.07
F. latifolia	0.50	0.08	0.52	0.04	0.0	0.03
L. swynnertonii	0.0	0.08	0.35	0.0	0.0	0.59
M. platycalyx	0.58	0.08	0.29	0.36	0.10	0.14
M. bagshawei	0.07	0.08	0.75	0.04	0.0	0.07
N. buchananii	0.22	0.08	0.06	0.08	0.07	0.03
N. macrocalyx*	0.36	1.66	0.12	0.04	0.16	0.03
O. welwitschii	0.29	0.90	0.34	0.08	0.23	0.0
P. excelsa	0.14	0.23	0.23	0.0	0.0	0.0
P. africana	0.0	0.08	0.06	0.0	0.0	0.0
S. scheffleri	0.29	0.15	0.29	0.08	0.0	0.30
T. guineensis*	0.50	0.68	0.0	1.64	0.0	0.0
$\bar{X}$	0.22	0.34	0.30	0.13	0.04	0.10
$S\bar{x}$	0.21	0.49	0.32	0.35	0.06	0.17

canopy or desirable tree species were among tree falls in heavily cut forest; fifteen tree species were involved in uncut and only eleven species in lightly cut forest. The density of individuals of desirable species involved in treefalls was significantly higher for heavily cut, relative to uncut forest ($T=54$, $n=20$, $P<0.025$, one tailed Wilcoxon's signed rank test) or lightly cut forest ($T=32.5$, $n=21$, $P<0.005$). However, the density of individuals of desirable species involved in treefalls for uncut and lightly cut forest was not significantly different. This may imply that for the heavily selectively cut forest (K-15), the few large desirable trees which were left behind because of defects, e.g. crooked boles, heart rot or hollowed center, could not withstand post felling conditions.

In lightly cut forest, 90% of the dead standing trees in the small size classes ($\geq 6<20$cm dbh) were of the pioneer species, *T. guineensis*. *M. platycalyx* formed the highest percentage of the dead standing desirable tree species (12.16%) while species of *Cordia*, *Newtonia*, *O. welwitschii*, and *S. scheffleri* were in the second place, each contributing about 2.7% of dead standing stock. Species of *A. altissima*, *M. bagshawei* and *F. latifolia* together contributed 4.05% of the dead standing stock.

In the heavily cut forest, the total number of dead standing trees was low for obvious reasons; the most susceptible mature and overmature trees were removed during felling and by consequent tree falls. However, one of the

most prized timber species, *Olea welwitschii* (or Elgon olive), had the highest percentage (28%) of dead standing stock while *M. platycalyx* was second with 12% and *N. buchananii* and *C. millenii* together formed 16%. Trees of *N. macrocalyx*, a pioneer species, formed 18.28% of the dead standing stock while the major portion of the remaining 26% was formed by non-desirable tree species. Here, the percentage estimates for dead standing species are inflated because of the small number of trees involved in dead standing stock.

In the mature forest (K-30), the dead standing species were dominated by *Lovoa* (14.9%), *Aningeria* (14.0%) and *Strombosia* (7.9%). These species also had the largest number of large individuals in the samples. In combination, *N. buchananii*, *M. bagshawei*, *F. lalifolia*, *C. africana*, *M. platycalyx*, *F. macrophylla* and *C. gorungosanum* constituted 13.16% of the dead standing stock.

Diameter Class Distribution of Tree Falls

Within plot comparison of size classes of tree snaps and uproots showed no significant differences for all the study compartments (all $U_{0.05}[2,11] \geq 42.5$, Mann-Whitney U-test, Siegel, 1956). Intercompartment comparisons of size class distribution of trees involved in tree fall deaths also showed no differences in all possible plot pair combinations (all $Us \leq 74$, $U_{0.05}[3,11] = 96.19$, STP, Sokal and Rohlf, 1981, p. 438). However, the pattern of distribution of tree falls was variable between compartments (Fig. 7, Appendix Table 4).

Figure 7 shows the frequency of the various categories of tree snaps, uproots and total tree falls (snaps + uproots) in each diameter class. Tree fall peaks differed for the cut and uncut forest tracts but the peaks for cut forests were generally similar (Fig. 7). However, Figure 8 presents the same information of total tree falls in a more instructive form; the density of tree falls (No/ha) as a percentage of the density of living stems in the corresponding diameter classes. The heavily selectively cut forest had one minor tree fall peak in the lower size classes, between 20 and 40 cm dbh and a major peak in the intermediate size classes, between 60 and 70 cm dbh. The lightly cut forest also had two tree fall peaks, a minor one between 40 and 50 cm dbh and a major peak between 70 and 80 cm dbh. However, some high tree fall levels were recorded for size classes above 100 cm dbh. For uncut forest, tree fall peaks included a minor one between 30 and 40 cm dbh and a major peak between 70 and 80 cm dbh. The major tree fall peaks for uncut and lightly cut forests were similar in dbh range but not in magnitude. The major tree fall peaks for both cut and uncut forest tracts occurred between 60 and 80 cm dbh with the heavily selectively cut forest having the highest, lightly cut forest second highest and the uncut mature forest in third position. The high tree falls in the lower size classes (20 to 40 cm dbh) could be largely a

Figure 7. Size class (10 cm dbh interval) distribution of tree falls (No/ha) attributed to stem snaps and tree uproots in lightly selectively cut (K-14), heavily selectively cut (K-15) and uncut (K-30) forest tracts of the reserve.

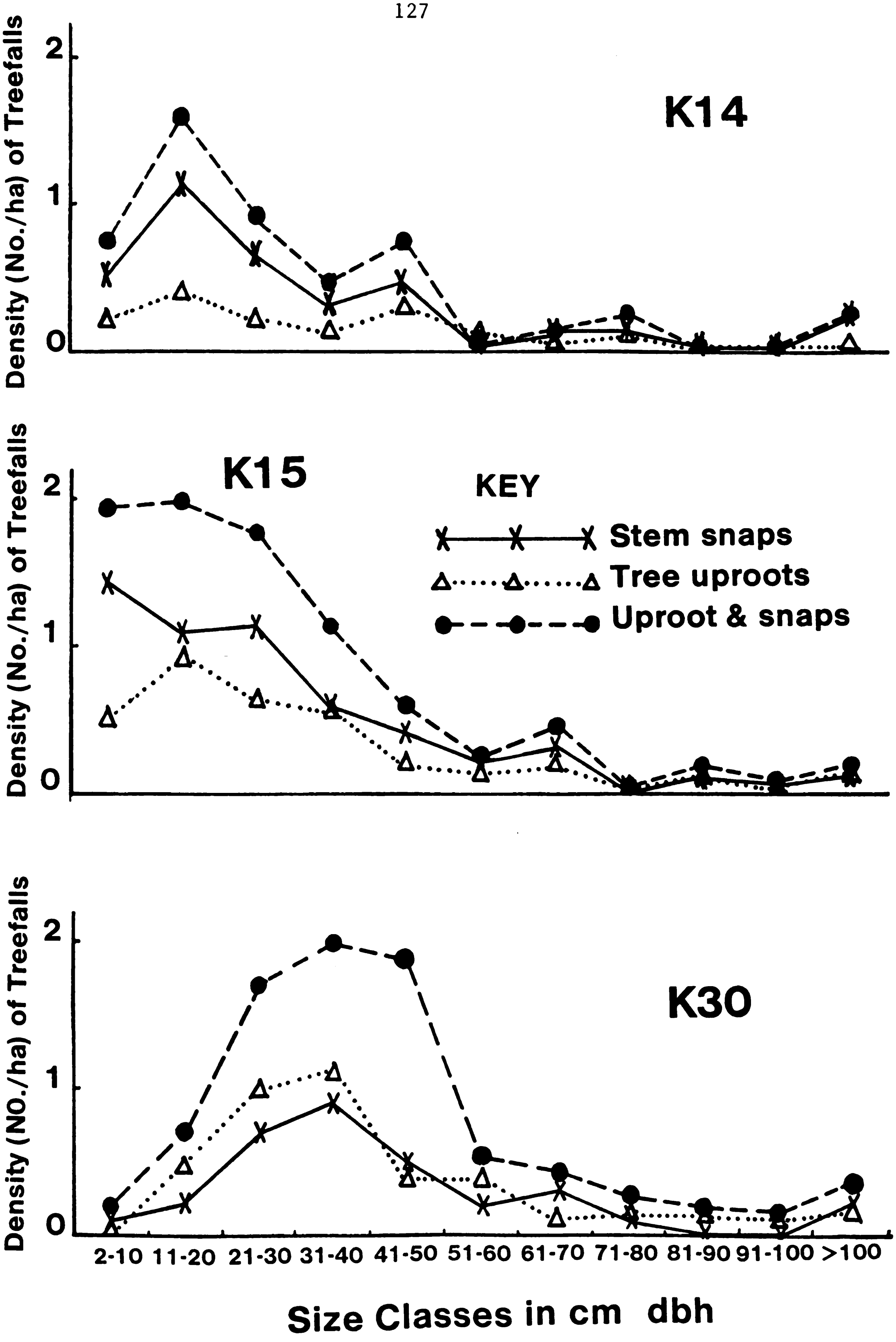
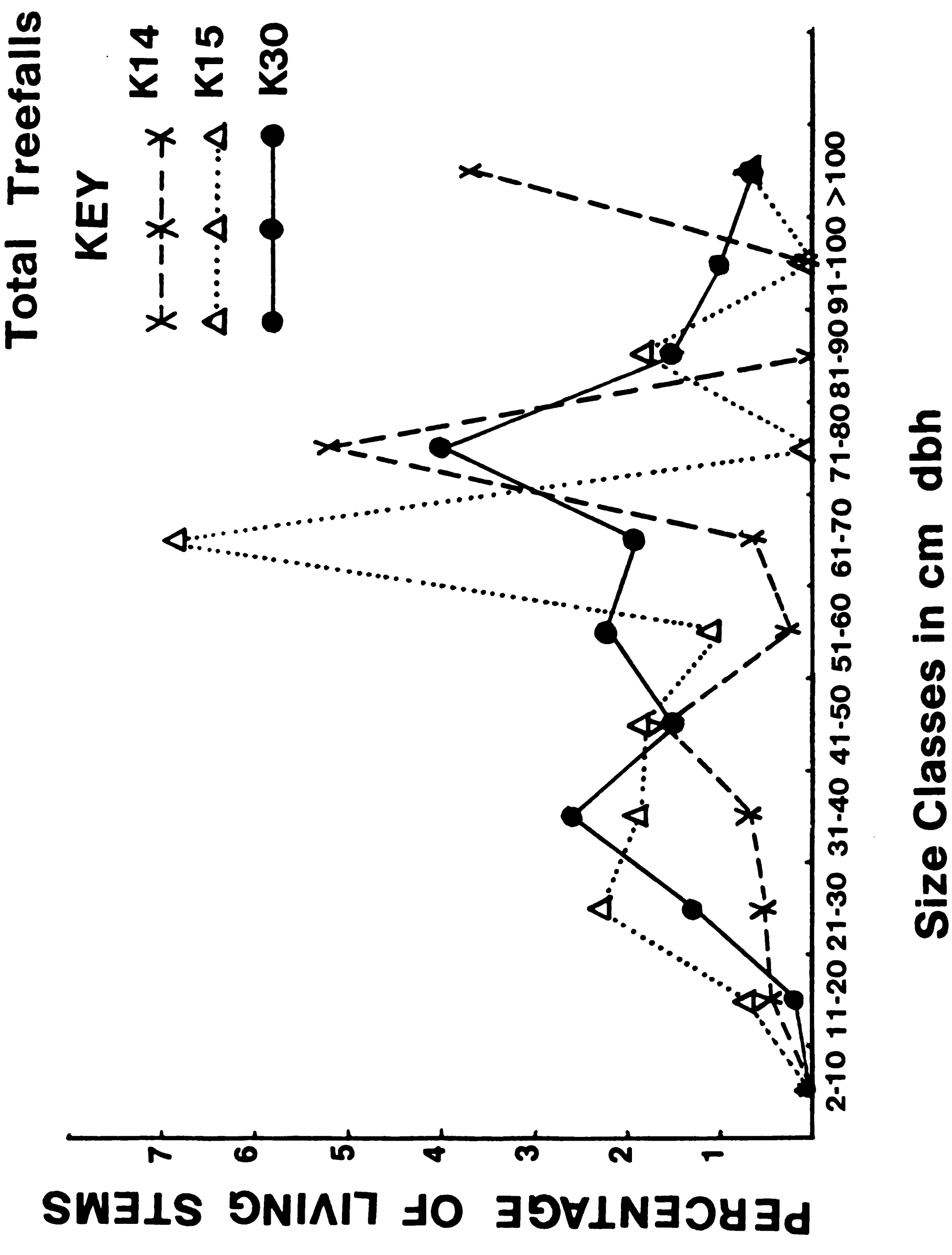

Density (No./ha) of Treefalls
2
1
0
K14
Density (No./ha) of Treefalls
2
1
0
K15
KEY
Stem snaps
Tree uproots
Uproot & snaps
Density (NO./ha) of Treefalls
2
1
0
K30
2-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
>100
Size Classes in cm dbh

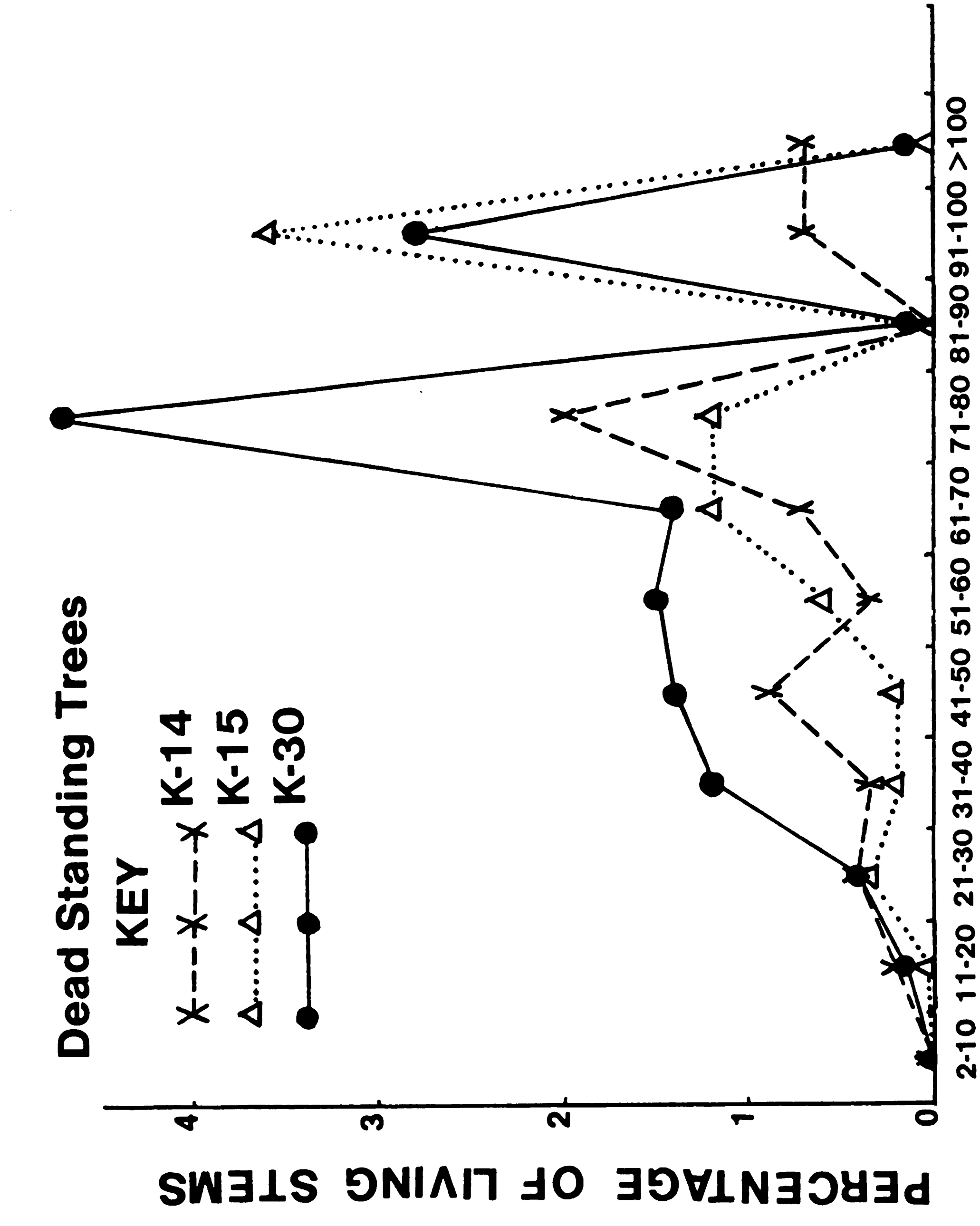
Figure 8. Frequency distribution of diameter at breast height (10 cm dbh interval) of total tree falls (snaps + uproots) expressed as percentages of the density (No/ha) of living stems in the same diameter class in lightly cut (K-14), heavily selectively cut (K-15) and uncut (K-30) forest tracts of the reserve.


Total Treefalls
KEY
K14
K15
K30
PERCENTAGE OF LIVING STEMS
7
6
5
4
3
2
1
2-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
>100
Size Classes in cm dbh

function of large tree falls which may also break many smaller trees. Whenever there was a major tree fall, several saplings, poles and small trees were brought down as well. With the exception of lightly cut forest, very few trees $\geq$90 cm dbh were involved in tree falls. Selective tree harvesting could explain such observation for heavily cut forest (K-15), but the uncut mature forest also exhibited lower mortality in the large size classes. This may suggest that intact forests have the ability to guard against large tree falls.

For dead standing trees, the differences between size class distribution in lightly cut and heavily cut forest, or in lightly cut and uncut forest, were not significant. But the size class distribution of dead standing trees in heavily selectively cut and uncut mature forest were weakly significantly different ($Us=95$ while $Us_{0.05}[3,11]= 96.19$, STP). As with tree falls, the uncut forest showed a peak in dead standing trees between 70 and 80 cm dbh, but in this case the larger size classes were also well represented in tree deaths with a peak between 90 and 100 cm dbh. Higher percentages of tree deaths were also recorded for intermediate size classes between 30 and 60 cm dbh (Fig. 9, Appendix table 4). The heavily selectively cut forest showed higher levels of tree deaths between 60 and 80 cm dbh with a peak in the large size classes between 90 and 100 cm dbh. As in uncut mature forest, the lightly selectively cut forest had high levels of tree deaths in the intermediate

Figure 9. Frequency distribution of the diameter at breast height (10 cm dbh interval) of dead standing trees expressed as the percentage of the density (No/ha) of living trees in the same diameter class in lightly cut (K-14), heavily selectively cut (K-15) and uncut (K-30) forest tracts of the reserve.


Dead Standing Trees
KEY
K-14
K-15
K-30
PERCENTAGE OF LIVING STEMS
0
1
2
3
4
2-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
>100
Size Classes in cm dbh

size classes between 30 and 60 cm dbh with a peak between 70 and 80 cm dbh. The first major peaks of dead standing trees for both cut and uncut forest tracts occurred between 60 and 80 cm dbh with uncut forest having the highest peak, lightly cut forest in second place and heavily selectively cut forest in the third position. However, the second major peaks of tree deaths occurring between 90 and 100 cm dbh were dominated by the heavily selectively cut forest, uncut forest in the second and lightly cut forest in the third position. In general, all tree mortality curves were skewed to the left.

DISCUSSION

Comparison of Tree Falls in Cut and Uncut Mature Forests

The study of tree fall dynamics employed a strip census method in order to include representative samples of the topography and vegetation of the Central Kibale Forest Reserve. Brokaw (1982a) used a similar method for the same reasons, to cover as much of the representative forest vegetation and topography as possible. Unlike other workers who predetermined the size class ranges of trees and tree falls to be examined (Brokaw, 1982a Putz and Milton, 1982) I considered all tree size classes that were involved in the falls. As in Putz *et al.* (1983), fallen trees in small size classes ($\leq$10cm dbh) as well as large canopy type trees or "gap formers" were all considered in sampling. The small size classes were included because of their importance in forest regeneration and potential recovery after various forms of natural and human disturbances.

There is extreme variability in the predominant mode of tree deaths for different forests in the same or different regions (Brokaw, 1982a; Putz and Milton, 1982; Putz *et al.*, 1983). The results of this study also suggest that even within the same forest type, especially where there have been differential management practices, variations in rates and modes of tree mortality were extremely high (Appendix tables 1 to 3). However, most studies, including the present one show three prevalent types of tree death, including tree snaps, tree uproots and death while standing (Runkle, 1982; Putz and Milton, 1982; Putz _et_ _al._, 1983; Harcombe and Marks, 1983). In this study, the predominant modes of tree death included tree snaps for the heavily selectively cut forest, and tree snaps, tree uproots and death while standing for the lightly cut and uncut mature forests.

More dead trees than live were involved in tree falls in uncut and lightly cut but not in heavily selectively cut forest. In the heavily selectively cut forest, mostly live trees (67%) were involved in tree falls. In the lightly selectively cut forest, 34.5% and 14.1% of tree falls occurred through tree snaps and uproots, respectively. The heavily selectively cut forest had 53% and 26.1% of the tree falls occurring through tree snaps and uproots, respectively, while the uncut mature forest had 22.8% and 27.8% of tree falls as snaps and uproots, respectively.

Similarly, Runkle (1982) found that of gap making trees, 67% and 19% were tree snaps and uproots, respectively. The damage to tropical hardwood plantations in Western Samoa, mainly through tree snaps and uproots accounted for only 15% (Wood, 1979). In a _Fagus-Magnolia_ forest in Texas, a five year sample showed 21% and 0% of the trees that fell were snaps and uproots, respectively

(Harcombe and Marks, 1983). On Barro Colorado Island, Panama, of the fallen trees in a specified area and period, 70% were snapped and 25% uprooted (Putz et al., 1983) while in an old forest on the same island, 52% had snapped trunks and 17% were uprooted (Putz and Milton, 1982). At La Selva in Costa Rica, of the dead tree individuals over a 13 year period, 26% died standing, 31% had fallen and 7% were found buried under tree falls (Lieberman et al., 1985). In other forests, however, the major mode of tree deaths was tree uproots instead of snaps. In a tropical forest in Nigeria, uprooting accounted for 30% of tree deaths (Jones, 1956) while tree snaps were 27.2% (extrapolated from frequency curves). For *Tilia-Carpinus* and *Pinus-Quercus* forests in Poland, tree uproots (48%) predominated over tree snaps (7%) (Falinski, 1978). The results of this study were in concert with the observations of Lieberman et al. (1985) that mortality rates were independent of tree sizes ≥ 10 cm dbh. However, small to middle-story trees (≥ 20 cm < 80 cm dbh) were more susceptible to tree fall death than large trees ≥ 90 cm dbh. With the exception of heavily selectively cut forests, this study could also add that tree falls were independent of tree condition, dead or alive but slightly biased towards dead trees.

Of the tree deaths involving tree snaps, tree uproots and dead standing trees in lightly cut and uncut forest tracts, 79.6% and 78.9%, respectively, were already dead trees at the time of sampling. But for the heavily selectively cut forest, dead tree falls and trees which died standing formed 45.5% of total tree deaths. With the exception of heavily selectively cut forest (54.5%), the percentages of live tree falls for the lightly cut (20.4%) and uncut mature forest (21.1%) were relatively low. It was obvious that heavy selective logging removed most of the large desirable trees from the heavily cut and lightly cut tracts and that there was no felling in the mature forest. Therefore, high levels of dead tree falls and dead standing trees would only be expected for uncut mature forest.

Several studies in other tropical and temperate forests also show variable and high amounts of trees which died while standing (Sousa, 1984). For example, in mesic forest in eastern U.S.A., Runkle (1982) found that 10% of the gap-making trees died standing. In a Fagus-Magnolia forest in Texas, U.S.A., 77% of the trees that died did so before they fell over (Harcombe and Marks, 1983). In a Tilia-Carpinus and Pinus-Quercus forest in Poland, of the trees that died, 45% were dead standing (Falinski, 1978). Also, in lowland Dipterocarp forest in Malaysia, trees mostly died standing and very few died through snaps or uproots (Putz and Appanah, Ms). In an old forest on Barro Colorado Island, 14% of tree mortality was by trees which died while standing (Putz and Milton, 1982) and all others through snaps and uproots. In Costa Rica, 26% of the trees that died over a 13 year period did so while standing (Lieberman et al., 1985). So the predominant modes of tree deaths, including tree snaps, tree uproots and death while standing can be variable locally and regionally, but ubiquity implies their importance in the dynamics of forests.

The preliminary results of ongoing long term research (now in 13th year of observation) on tree mortality, encompassing a larger area (42 ha) of uncut study compartment (K-30) in the reserve show higher levels of die-offs of some primary forest species (Struhsaker, Geither and Kasenene--unpublished). Large, mature individuals of five canopy tree species including *N. buchananii*, *L. swynnertonii*, *A. altissima*, *C. africana* and *M. bagshawei* are particularly involved in the die-offs. These are some of the upper canopy species that attain heights at maturity of from 30 m to 60 m (Eggeling, 1951) and are common to abundant in some parts of the reserve. The mature populations of *N. buchananii* and *L. swynnertonii* have already had 100% and 80% mortality, respectively. The mortality levels in *A. altissima* (17%), *C. africana* (14%) and *M. bagshawei* (3.3%) are lower than in the previous two species. The majority of dead *Newtonia* and *Lovoa* trees had already fallen by the time of the study and thus made little contribution to the estimates of tree falls and trees which die while standing. However, the questions regarding the cause of the massive die-offs of these important timber or primary forest species remain unresolved and call for another study.

In the reserve, the proportions of tree falls and dead standing trees for all three compartments showed increases and high levels from 20 to 40 cm dbh class; at which point there was a break and no further increase until the 60 cm dbh class. This indicates high death rate among trees less than 40 cm dbh. This may be because of the fast growing and short lived species of small size in cut forests or the death of many small trees caused by large tree falls. The short lived pioneer species such as T. guineensis and N. macrocalyx in cut forest tracts seem to have matured and were in senescence only 20 years after selective felling. However, their death (most died while standing) was more pronounced in lightly cut, thus less disturbed, forest, than heavily felled areas where there was extensive forest disturbance and large gaps.

In uncut and lightly cut forest, the high death rates among trees of 60 cm dbh upwards, the mature middle-story and emergent individuals could be attributed, mainly, to old age and senescence. But in heavily cut areas, the high death rates through live tree snaps may be taken as indicating high incidences of wind damage. However, the death rates among trees $\geq$ 60 cm dbh were irregular, perhaps because of the small number of trees involved. The rapid rises of death rates with increasing size of trees, in both cut and uncut forests, suggest unstable, all-aged populations.

The predominant modes of tree deaths clearly vary from forest to forest, suggesting that many factors, in simple or complex interactions, were in control. Variations in modes of tree deaths are regarded as important for rain forests because they create heterogeneous sites vital for forest regeneration, ecological diversity and evolution (Armson and Fesseden, 1973; Connell, 1978; Denslow, 1980 and Sousa, 1984). In the Kibale Forest, it appears that selective felling altered the mode and rate of tree deaths in favor of tree snaps, where more live than dead trees were involved. For example, the annual rate of live tree falls/ha was 1.30 for the lightly cut, 3.30 for the heavily selectively cut and 1.74 for uncut mature forest.

Selective forest felling previously has been observed to foster more frequent and severe wind throws (Herbert and Beveridge, 1977). The existence of large gaps or exposed areas even in mature forest has been suggested to result in high turnover rates for some tropical rainforests (Brokaw, 1982a; Foster and Brokaw, 1982). Denslow (1980) suggested that human-induced changes in the size frequency distribution of gaps by either increasing or decreasing the rate of gap formation will result in gradual loss of species. Human-induced changes in forest structure through felling, for example, might account for the high rates of live tree falls in the heavily selectively cut areas of the Kibale forest. The few large trees which were left behind after felling (usually the defective desirable species) were exposed to the vagaries of nature and suffered heavy mortality. This could be detrimental to forest regeneration and recovery because excessive mortality of the few mature desirable trees could reduce the potential seed sources in addition to crushing young trees or creating more extensive gaps (Longman and Jenik, 1974; Foster and Brokaw, 1982; Kasenene, 1984).

In spite of the short period of sampling tree falls in the Kibale Forest Reserve, mortality rate estimates (no/ha/yr) for disturbed forest sites were comparable to those of Malaysian forests but not forests on Barro Colorado Island (Table 3). At La Selva, Hartshorn (1978) estimated rates of tree fall at 1/ha/year. Brokaw (1982a) also arrived at an estimate of one gap/ha/year which could be taken as one canopy tree/ha/year for a forest on Barro Colorado Island. These rates are comparable to Kibale forest estimates of 1.30 and 1.74 trees/ha/year for lightly cut and uncut mature forests, respectively. Previously, mortality rates of 1.30 and 1.40 trees/ha/year had been established for the same forest tracts (Skorupa and Kasenene, 1984) and are consistent with the current rates. However, the heavily selectively cut forest exhibited higher mortality rates (6.2 trees/ha/year) in the previous study (Skorupa and Kasenene, 1984) and the current rate is also high (3.30 trees/ha/year) compared to lightly cut and uncut forests. This indicates almost constant mortality rates for the less disturbed (uncut and lightly cut) forests but

Table 3. Tree Mortality records from Barro Colorado Island, Malaysia and Uganda, East Africa.

Site	Size class range gbh	Area sampled ha.	No. of trees	No. of deaths/ha. (/year)	Average lifetime yrs.	Observation period yrs.	Authority
Barro Colorado Island							Putz and Milton
Young Forest	60	5	833	78(15.6)	57	5	1982
Old Forest	60	2	328	17(3.4)	96	5	1982
Sungei Menyala							
Malaysia							Wyatt-Smith 1966
Disturbed site	61	0.4	107	31(2.6)	41	12	in Putz and Milton
Primary forest	61	1.6	334	69(5.8)	58	12	1982
Bukit Lagong							
Malaysia							Wyatt-Smith 1966
Disturbed site	61	0.4	95	12(1.2)	79	10	in Putz and Milton
Primary forest	61	1.6	449	55(5.5)	82	10	1982
Kibale Forest,							
Uganda							
Heavily cut forest	47	13.3	351	5.5(3.3)	106	1.66	This study
Lightly cut forest	47	13.9	470	2.16(1.3)	361	1.66	This study
Uncut mature forest	47	17.3	502	2.90(1.7)	288	1.66	This study

variable rates over time in the more disturbed (heavily cut) forest. The different mortality estimates for the heavily cut forest in 1984 (6.2 trees/ha) and 1987 (this study, 3.30 trees/ha) could suggest that there have been drastic reductions in the amount of susceptible trees over a short period of time. Similarly the pattern of tree deaths on Barro Colorado Island shows higher mortality rates for young or disturbed forests than for undisturbed mature forest while the converse was true for Malaysian forests (Putz and Milton, 1982; Table 3). There were great variations in forest areas sampled, lower size class limits for trees studied, and the length of observation period for the different studies of tree mortality (e.g. Hartshorn, 1978; Brokaw, 1982a; Putz and Milton, 1982; Putz et al., 1983; Harcombe and Marks, 1983; Skorupa and Kasenene, 1984; Lieberman et al., 1985; this study). These variations might have influenced the results differently for the different forests thus possibly leading to questionable comparisons and incorrect conclusions.

In the forest tracts studied, there were few trees above 61cm gbh and very few of them were involved in tree falls. Therefore, it was irrelevant to calculate the life expectancy of trees using only the large size classes as has been the practice in other studies (Putz and Milton, 1982). I propose that the best estimates of life expectancies of trees should be the ones that reflect the life expectancy of the whole forest as well. So the inclusion of all tree size

classes that were physically involved in treefall deaths was emphasized. After all, when a large tree falls, it brings down with it many small to intermediate size class trees because of their usually high density. The life expectancies for trees in the heavily selectively cut, lightly cut and uncut forest tracts were variable and high (Table 3). The comparatively low expectancy of further life (106 yrs.) for trees in the heavily selectively cut forest could be accounted for by the low densities of trees in the small to intermediate size classes and the high rates of live tree falls. However, the high expectancy of further life in lightly cut forest (361 years) could also be attributed to the preponderance of small to intermediate size trees and lower mortality in the large tree classes. Although the small to intermediate size class trees were abundant, the high mortality in the large size classes gave the uncut mature forest a relatively higher turn over rate (288 years) than the lightly cut forest. Again, variations in forest areas sampled, tree size class limits and the length of observation period might have influenced the results from the different forests studied including Kibale, thus limiting comparisons and conclusions. However, the general trend was longer expectancy of further life for trees in lightly disturbed and primary forests and a shorter one for trees in heavily disturbed forests. Natural variation alone may not explain the great difference in tree mortality and life expectancy of trees in lightly and

heavily disturbed forest sites of the reserve. Human disturbances through differential felling intensities were suggested to have been the major initiator of observed variations. The influence of heavy selective felling on the dynamics of tree fall deaths was still strong 20 years later.

A number of workers have observed clear cut seasonal peaks in tree falls for other tropical and temperate forests (Hartshorn, 1978; Sarukhan, 1978; Falinski, 1978 in Brokaw 1982a; Brokaw, 1982a). These observers attributed seasonality in tree mortality to seasonally wet soil and consequent loosening of roots or seasonal high winds associated with heavy rain. We would expect high correlations between tree falls and rainfall. However, total tree falls (snaps + uproots), tree uproots and branch-falls were positively correlated with rainfall only in the lightly cut and uncut mature forest. There were no significant correlations between rainfall and tree falls for the heavily cut forest where tree falls seemed to occur at high levels for all months in the year and asynchronous with rainfall. In both cut and uncut forest compartments, tree snaps had no significant correlations with rainfall. This strongly suggests that factors other than rainfall and associated wind were also influencing tree falls, especially in the heavily selectively cut forest. If seasonally wet soil and consequent loosening of roots are important for tree uproots (Hartshorn, 1978; Whitmore, 1978; Brokaw, 1982;

Pickett, 1983; Putz et al., 1983) then gusty winds are also important for tree snaps. The high incidences of live tree snaps in the heavily cut forest, higher rates of tree snaps than uproots in both cut and uncut forest tracts and the low correlations between tree falls and rainfall suggest gusty winds to be an important control of tree falls in the reserve. In the Kibale forest, it was common for windy weather to precede periods of rainfall, and within the wet season not all windy weather was necessarily followed by heavy rain (personal observation). This could partly explain the low correlations between rainfall and all modes of tree falls. Brokaw (1982a) suggested that rain trapped by leaves and associated vines, epiphytes and bark of trees creates substantial "rain load" which could also account for more tree snaps than uproots. A combination of factors, including rainfall, wind and possibly rain load, may have contributed to the variations in tree falls for the differently managed forest tracts of the reserve. Thus as predicted, more tree falls (including snaps, snaps and uproots together) occurred in the heavily selectively cut forest where scattered large trees were not buffered from wind pressure. In lightly cut and uncut mature forest, the presence of many large trees may have provided protection to large and small trees against gusty winds, explaining the fewer tree falls relative to heavily cut forest.

Several ultimate factors, including shallow rootedness, insect and fungus damaged stems and roots, steepness of terrain and landslides (Brokaw, 1982a; Putz and Milton, 1982; Putz *et al.*, 1983; Sousa, 1984) and animal damage (Eggeling, 1947) have also been observed to strongly influence treefalls. Shallow rootedness was common among big tree uproots. Incidences of heart rot or hollowed boles were not widespread among tree snaps. However, elephant damage to trees through uproots (sapling classes) and tree snaps (pole classes) was widespread, especially in the heavily selectively cut forest. It has been reported that trees on the edges of large gaps are subject to more wind induced mechanical stresses than trees in the forest interior. Mechanical damage suffered during earlier treefalls and sun scald of exposed tree trunks all lead to greater likelihood of treefalls in heavily cut forests (Lawton and Putz, manuscript).

Another dimension to factors influencing tree snaps, uproots or mortality rates is wood density, wood strength and tree size (Putz *et al.*, 1983). Larger trees are more prone to uproot than snap, and trees of high wood strength and density would also be expected to uproot more frequently than snap (Putz *et al.*, 1983). The pattern and level of tree snaps and uproots in the selectively cut forests seemed to agree with the prediction. There were more tree snaps than uproots, possibly because of the abundance of low density, low wood strength species characteristics of secondary forests. However, the mature forest with high densities of large trees and primary forest species of high

density and strength had similar levels of tree uproots and snaps. This did not contradict the predictions of Putz et al. (1983) completely if the three study areas were considered together. There were more tree deaths through uproots in the mature forest than selectively cut secondary forests. One other variable introduced in my tree fall samples was the small tree size classes. It could be that only the large tree classes (≥60cm gbh) used in earlier studies were more responsive to the effects of heavy rain and wind and result in high correlations between treefalls and rain fall. Evidently, human disturbance was very important in the alteration of the seasonal rhythms of treefall dynamics of the studied forests of the reserve. The degree of alteration or variation in treefall dynamics depended on the level of forest disturbance.

SUMMARY AND CONCLUSIONS

Twenty months of intensive systematic censusing of freshly fallen trees and big branch falls in lightly cut (K-14), heavily selectively cut (K-15) and uncut mature forest (K-30) were undertaken for the purpose of esbablishing whether heavy selective timber harvesting had any influence on the dynamics of tree falls and trees which died while standing. The forest areas sampled were estimated at 13.88ha for K-14, 13.28ha for K-15 and 17.23ha for K-30. Censuses were conducted every second or third day of the month following the previous counts and only new tree falls subsequent to previous falls were enumerated.

Within lightly cut forest (K-14), the densities of dead and live tree snaps and dead and live tree uproots and thus dead and live tree falls were similar. However, the density of tree snaps was higher than that of the uproots. In the heavily selectively cut forest, tree falls were dominated by live tree snaps. For the mature forest, the density of dead tree uproots was higher than for live but the density of dead and live tree snaps were similar. In contrast with K-14 and K-15, the density of tree uproots and snaps was similar.

Of the total tree mortality observed in K-14 (142 trees), 34.5% were tree snaps, 14.1% were uproots and 52.1% died standing. Live tree falls formed 21.1% of the deaths while 79.6% was by trees already dead at the time of sampling (i.e. dead tree falls + dead standing trees). Total tree mortality for K-15 included 134 trees where 53% were tree snaps, 26.1% were uproots and 18.7% died standing. However, live tree falls constituted 54.5% of tree fall deaths while already dead trees formed 45.5%. The partitioning of 237 tree deaths for K-30 was 22.8% tree snaps, 27.8% uproots and 48.5% dead standing trees. The proportion of live tree falls (21.1%) and dead trees (78.9%) was comparable only to K-14.

The die-offs of several canopy tree species in the mature forest of the reserve seemed a cause for alarm and calls for immediate research and action. For example, the species populations of Newtonia and Lovoa have already had 100% and over 80% mortality, respectively, and the causes of the death have not been established. The high percentages of dead tree falls or dead standing trees in K-14 or K15 could be accounted for largely by the die-offs of the short lived pioneer species of Trema and Neoboutonia. They seem to be dying off only 20 years after selective felling. However, their deaths were more pronounced in lightly, as compared to heavily, disturbed forest. The populations of pioneer species in the mature forest was insignificant,

which implies low levels of disturbances or a preponderance of small gaps.

Among the study plots, the rates of tree snaps and uproots were higher in K-15 than K-14 or K-30, but K-14 and K-30 had similar rates. Again, the rates of total tree falls (uproots + snaps) for K-15 were much higher than for K-14 or K-30, whereas K-14 and K-30 had similar rates. Again, K-15 exhibited higher rates of live tree falls than K-14 or K-30 but live tree fall rates were similar for K-14 and K-30. It appears that selective felling altered the mode and rate of tree deaths in favor of tree snaps where more live than dead trees were involved. Consequently, the average life expectancy for trees in K-14 was highest (361.8 years) followed by K-30 forest trees (288.4 yrs) and K-15 trees (106.4 years).

The mortality rate estimates for the mature or primary forests were very variable. The annual rates of live tree falls/ha were 1.30 for K-14, 3.30 for K-15 and 1.74 for K-30. The pattern of tree size class distribution of tree fall deaths were also variable between compartments. In general, the tree mortality curves for both cut and uncut mature forests were skewed to the left. It was suggested that the damage caused by a few large trees to many small ones during tree falls contributed to high mortality rates in the small tree classes.

The mortality of desirable timber species in K-15 was significantly higher than that in K-14 or K-30. Selective removal of many large desirable trees from K-15 did not lead to reductions in later tree falls but seemed to escalate it. This implies that the few large desirable trees which were left behind after felling, mainly because of defects, were exposed to various natural forces and suffered heavy mortality. This could be detrimental to the forest regeneration and recovery since excessive mortality of such trees would drastically reduce the seed source and populations necessary for ample forest regeneration and recovery. In addition, excessive falls of remnant trees would crush the young regeneration and create more extensive gaps.

Natural variation alone could not explain the great variations and differences in the mode of tree deaths, tree mortality rates and life expectancy of trees from the forests which were differentially managed 20 years earlier. Human disturbances through differing felling intensities were suggested to have been the major initiator of observed variations upon which the proximate and ultimate natural forces acted to produce current differences and variations in tree mortality 20 years later.

CONCLUSION

Can rates of natural tree falls help guide us in the management of natural forests? Except for disturbed forest sites, the natural rate of tree falls for primary and mature tropical forests so far reported range from one tree/ha/year to 5.8 trees/ha/year. For the reserve, the number of dead standing trees/ha was 4.0 while the rate of tree falls for the lightly selectively cut forest was 1.30 trees/ha/year. The lightly selectively cut forest looked less disturbed and maintained low mortality levels over the years. With respect to variations among the differently managed forests in the reserve, an average harvest intensity of 3 to 4 canopy trees/ha is suggested and could be compatible with minimizing damage to the forest structure and composition in Ugandan forests in general and the Kibale forest in particular. This would simulate the natural rates of tree falls which constitute an important integral component of the mature forests' dynamics.

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Appendix

Table 1. Monthly distribution and density (No./ha) of tree and branch falls in lightly selectively cut forest (K-14).

Mode of Gap Formation	State of tree or branch	1984			1985											1986						$\bar{X}$	Sx
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun		
Big branch falls	Live	.22	.14	0	0	.07	0	0	.29	.14	.14	.14	.07	.07	.07	0	0	0	.07	0	.07	.07	.07	.08
	Dead	.22	0	.07	.07	.14	.21	.28	.36	.14	.07	0	0	.14	.07	.07	0	.07	0	0	.07	.07	.09	.10
	Total	.44	.14	.07	.07	.21	.21	.28	.65	.28	.21	.14	.07	.21	.14	.07	0	.07	.07	0	.14	.14	.16	.14
Tree snap	Live	.50	0	0	0	0	.21	.07	0	0	.14	.28	.14	0	.22	0	.07	.07	.14	0	.14	0	.07	.09
	Dead	.14	.43	.07	.14	.07	.21	0	.07	.07	0	.07	.07	.07	.14	.07	.07	0	.07	0	.22	.14	.10	.10
	Total	.64	.43	.07	.14	.07	.42	.07	.07	.07	.14	.35	.21	.07	.36	.07	.14	.07	.21	0	.36	.14	.17	.14
Tree uproot	Live	.14	.07	0	0	0	0	0	.14	0	0	0	.14	0	0	0	.15	0	0	0	.15	.07	.04	.06
	Dead	0	.15	0	0	0	0	0	.07	.07	.07	0	.15	0	0	0	0	0	0	0	.14	.07	.04	.06
	Total	.14	.22	0	0	0	0	0	.21	.07	.07	0	.29	0	0	0	.15	0	0	0	.29	.14	.08	.10
Snap + uproot	Live	.64	.07	0	0	0	.21	.07	.14	0	.14	.28	.28	0	.22	0	.22	.07	.14	0	.29	.07	.11	.11
	Dead	.14	.58	.07	.14	.07	.21	0	.14	.14	.07	.07	.22	.07	.14	.07	.07	0	.07	0	.36	.21	.13	.14
	Total	.78	.65	.07	.14	.07	.42	.07	.28	.14	.21	.35	.50	.07	.36	.07	.29	.07	.21	0	.65	.28	.24	.19

Appendix

Table 2. Monthly distribution and density (No./ha) of tree and branch falls in heavily selectively cut forest (K-15).

Mode of Gap Formation	State of tree or branch	1984			1985												1986							
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	$\bar{X}$	Sx
Big branch falls	Live	0	0	.15	.08	.15	.08	.08	.08	.23	.08	.23	.15	.08	.30	.15	0	.08	0	.08	0	0	.10	.08
	Dead	.15	.08	0	.15	.38	.08	.23	.08	.30	.08	.30	.08	.08	0	0	0	0	.23	.08	0	0	.11	.12
	Total	.15	.08	.15	.23	.53	.16	.31	.16	.53	.16	.53	.23	.16	.30	.15	0	.08	.23	.16	.08	0	.21	.16
Tree snap	Live	0	0	.23	.15	.38	.08	.45	.30	.08	.08	.45	.30	.15	.98	.08	0	.23	.08	.08	0	0	.21	.23
	Dead	.08	0	.15	0	.08	.08	.15	.08	.08	.08	0	.08	0	.08	.08	0	.08	.23	0	0	.08	.07	.06
	Total	.08	0	.38	.15	.46	.16	.60	.38	.16	.16	.45	.38	.15	1.06	.16	0	.31	.31	.08	0	.08	.28	.25
Tree uproot	Live	0	0	0	.08	.23	0	.08	.16	0	0	.23	.08	.08	.30	.08	.15	.08	0	0	0	0	.08	.09
	Dead	0	.08	0	.30	.08	.08	.08	0	0	0	.08	.15	.08	0	0	.08	.15	0	0	0	.08	.06	.07
	Total	0	.08	0	.38	.31	.08	.16	.16	0	0	.31	.23	.16	.30	.08	.23	.23	0	0	0	.08	.14	.13
Snap + uproot	Live	0	0	.23	.23	.61	.08	.53	.46	.08	.08	.68	.38	.23	1.28	.16	.15	.31	.08	.08	0	0	.28	.31
	Dead	.08	.08	.15	.30	.16	.16	.23	.08	.08	.08	.08	.23	.08	.08	.08	.08	.23	.23	0	0	.16	.13	.08
	Total	.08	.08	.38	.53	.77	.24	.76	.54	.16	.16	.76	.61	.31	1.36	.24	.23	.54	.31	.08	0	.16	.41	.33

Appendix
Table 3. Monthly distribution and density (No./ha) of tree and branch falls in uncut mature forest (K-30).

Mode of Gap Formation	State of tree or branch	1984			1985												1986							
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	$\bar{X}$	Sx
Big branch falls	Live	0	.17	0	.06	.12	.17	0	0	.12	.06	.06	0	0	0	.06	0	0	0	.12	.06	0	.05	.06
	Dead	.29	.12	.18	0	.06	.06	.23	.18	.12	0	.17	.23	.18	.29	.06	0	.12	.06	.12	.12	.18	.12	.08
	Total	.29	.29	.18	.06	.18	.23	.23	.18	.24	.06	.06	.23	.18	.29	.12	0	.12	.06	.24	.18	.18	.17	.08
Tree snap	Live	.46	.06	.06	.12	.06	.12	0	.12	.12	0	0	.12	0	.12	.29	.06	.17	.06	.06	0	.06	.08	.07
	Dead	.17	.12	.12	.06	.06	.06	.12	.12	.06	.06	0	.06	0	0	0	0	.17	.17	.12	.23	.06	.08	.07
	Total																						.16	.09
Tree uproot	Live	.29	.17	0	.06	.17	.24	.06	.12	.12	0	0	.12	.06	0	.12	0	0	0	0	.17	0	.07	.07
	Dead	.46	.17	.06	.12	.06	.30	.29	.06	.06	.06	0	.18	.06	.12	.12	0	.17	.23	.17	.12	.17	.13	.09
	Total	.75	.34	.06	.18	.23	.54	.35	.18	.18	.06	0	.30	.12	.12	.24	0	.17	.23	.17	.29	.17	.20	.13
Snap + uproot	Live	.75	.23	.06	.18	.18	.36	.06	.24	.24	0	0	.24	.06	.12	.41	.06	.17	.06	.06	.17	.06	.15	.11
	Dead	.63	.29	.18	.18	.12	.36	.41	.18	.12	.12	0	.24	.06	.12	.12	0	.34	.40	.29	.35	.23	.21	.13
	Total	1.38	.52	.24	.36	.30	.72	.47	.42	.36	.12	0	.48	.12	.24	.53	.06	.51	.46	.35	.52	.29	.35	.18

Appendix

Table 4. Size class distribution of trees in terms of density (No./ha) of stem snaps, tree uproots and dead standing trees in selectively cut (K-14, K-15) and unout mature forest (K-30).

Size classes in cm dbh.		2-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	>100
	Dead standing	0.72	0.72	0.64	0.20	0.40	0.08	0.08	0.08	0.00	0.04	0.04
K-14	Tree snap	0.50	1.15	0.64	0.29	0.43	0.00	0.07	0.14	0.00	0.00	0.22
	Tree uproot	0.22	0.43	0.22	0.14	0.29	0.07	0.00	0.07	0.00	0.00	0.00
	Uproot + snap	0.72	1.58	0.86	0.43	0.72	0.07	0.07	0.21	0.00	0.00	0.22
	Dead standing	0.07	0.10	0.26	0.10	0.07	0.13	0.08	0.08	0.00	0.08	0.00
K-15	Tree snap	1.43	1.05	1.13	0.60	0.38	0.15	0.30	0.00	0.08	0.00	0.08
	Tree uproot	0.45	0.90	0.60	0.45	0.23	0.08	0.15	0.00	0.08	0.00	0.08
	Uproot + snap	1.88	1.95	1.73	1.05	0.61	0.23	0.45	0.00	0.16	0.00	0.16
	Dead standing	0.03	0.49	0.49	0.94	0.80	0.35	0.31	0.28	0.07	0.17	0.07
K-30	Tree snap	0.12	0.23	0.70	0.87	0.52	0.17	0.29	0.12	0.00	0.00	0.17
	Tree uproot	0.06	0.46	0.99	1.10	0.35	0.35	0.12	0.12	0.12	0.06	0.17
	Uproot + snap	0.18	0.69	1.69	1.97	0.87	0.52	0.41	0.24	0.12	0.06	0.34

PART III

POST LOGGING PLANT DYNAMICS IN FOREST GAPS

INTRODUCTION

Forest Gaps and Forest Regeneration

Gap creation and filling has been recognized as a major influence on community structure and species interaction. Many moist or rain forest species require or are stimulated by the gaps (Richards, 1952; Gomez-Pompa et al., 1972; Whitmore, 1975; Denslow, 1980; Brokaw, 1982a; Pickett, 1983; Putz, 1983; Uhl et al., 1985). The ecological effects of gaps can be related to their structure, mode of formation and size (Richards, 1952; Whitmore, 1975; Denslow, 1980 and Pickett, 1983). Major causes of gaps and larger disturbances in tropical forests include physical and biological factors such as landslides, gusty winds, storms and lightning, animal activity, death of trees, selective logging (mechanized and pitsawing), agricultural encroachment and human settlement, firewood collecting and charcoal burning (Longman and Jenik, 1974; Whitmore, 1975; IUCN, 1975; UNESCO, 1978; Hartshorn, 1978, 1980; USAID, 1978; Brokaw, 1982a; Putz and Milton, 1982; Putz, 1983a, Uhl et al., 1984, 1985; Dittus, 1985; Lieberman et al., 1985 and Pimentel et al., 1986).

In Ugandan tropical moist forests, the major disturbance factors include agricultural encroachment, uncontrolled timber exploitation for timber and firewood, energy, construction and trade and rampant poaching of game. These problems are bound to increase in light of the ever increasing human population growth rate, currently estimated to be between 3.2% and 3.5% per annum (Hamilton, 1984). The omnipresent social and economic problems, poor land use practices and lack of sound management of natural resources such as forests (Hamilton, 1984; Van Orsdol, 1983) are bound to aggravate the situation.

In Uganda as elsewhere in the tropical forest regions, there appears to be no clear solution to the increases in tropical forest disturbances that accompany the demands for more tropical forest land and forest products, both of which are directed by the human population problems (Richards, 1964; Brenan, 1973; Fosberg, 1973; Chapman, 1975; Orington, 1975; Brazier _et_ _al._, 1976 and USAID, 1978). Amidst these challenges, there is great lack of knowledge regarding the minimum disturbance levels that can be allowed during forest exploitation without destroying the integrity of the structure and function of the tropical forest for sustained use (TIE Report, 1973; Downes, 1974 and IUCN, 1975).

Richards and Williamson (1975) and Webb _et_ _al._ (1972) regard forest disturbances and gaps, both naturally and human generated, as dynamic patches of forest regeneration and recovery. However, the disruption of tropical rainforest composition, structure and function through a range of disturbance regimes has often been observed to lead

to impoverished secondary forests (Gomez-Pompa et al., 1972; Hartshorn, 1980; Uhl et al., 1984 and Odum, 1985). Consequently, tropical rainforests were appropriately described as "fragile ecosystems" sensitive to disturbance (TIE Report, 1973). Once disturbed, the only hope of their regeneration and some recovery depends on either coppicing, regeneration from soil seed banks and established seedlings, or recolonization from outside the disturbance site (Richards, 1952; Whitmore, 1975; Gomez-Pompa et al., 1974; Ewel et al., 1981; Uhl et al., 1982b; Putz, 1983; Uhl et al., 1985, Young, 1985; Marquis et al., 1986). However, Richards (1964) and Whitmore (1975) observed that seedlings and saplings of more extreme shade tolerant species do not usually survive in extensive gaps and that seedling establishment and survival was an inverse function of gap size.

In Uganda, commercial timber harvests involve a mechanized polycyclic system (Whitmore, 1975) where the forest canopy is supposed to be opened up by 50% (Kingston, 1967; Uganda Forest Dept. Records). In the Kibale Forest, the northern 1/3 of the central block where this research was conducted was mechanically selectively felled between 1968 and 1969 creating giant gaps in the forest canopy. However, the southern 2/3 is still intact mature forest with small to medium gaps created by natural tree falls. There is a paucity of information on the impact of mechanized polycyclic felling systems on the structure, composition, function and the regeneration of the resultant secondary forest. However, in other forests, a number of workers have observed significant reductions in species diversity of seedlings and saplings following selective forest felling and equate the reductions to ecological instability (Odum, 1963, 1969; Westhoof, 1971; Herbert et al., 1977; Poore, 1976).

My hypothesis was that the level of forest disturbance and gap size were inversely related to tree sapling and pole abundance, diversity, and the general regeneration success of desirable timber or canopy tree species. Therefore the study of the level of forest regeneration in natural tree fall gaps and comparison with the regeneration in human induced gaps should help us understand the effects of mechanized selective logging on species rich tropical moist forest and the requirements for regeneration of commercially desirable or canopy tree species. Our understanding of the dynamics of tropical moist forest regeneration under a range of disturbance regimes, including natural tree fall disturbances, should also help us in the establishment of minimum disturbance levels the forest could sustain and yet maintain its natural function. Development of appropriate management plans for sustained productivity of existing forest and success in improving the regeneration of already heavily exploited and disturbed areas may depend heavily on the knowledge of the dynamics of forest regeneration after various intensities and modes of disturbances.

This study was designed to determine the ecological effects of forest gaps, natural and human induced, on the floristic composition, abundance and regeneration of saplings and poles of desirable timber or primary forest species and important non-desirable tree species in a tropical moist forest. Secondly, the relative contribution of coppicing and sprouts, soil seed banks, and seed rain from outside the disturbance sites was to be evaluated.

METHODS

Field work began in August 1984 with a survey of the four forest compartments (K-13, K-14, K-15 and K-30), each of which had had a different history of management (see part I). All four compartments were located in the central part of the Kibale Forest Reserve near Kanyawara Forest Station. In the lightly cut (K-14) and uncut (K-30) mature forests, the existing system of trails running south-east and north-west were walked searching for gaps within 10 to 20m of the trail. For the heavily felled forest (K-15), the 100m interval system of trails running east and west were walked and all discernible gaps within 10 to 20m of the trail marked and mapped. The heavily selectively cut and treated forest (K-13) had no trail grids. A grid system of 100m x 200m was established in late August, 1985 covering an area of 30 ha and a linear distance of 5.8 Km.

The entire linear distance of the grid was walked and all recognizable gaps marked and mapped. For the selectively cut forests (K-13, K-14 and K-15), the gaps with cut tree stumps and/or waste tree trunks were marked. In uncut mature forest (K-30), gaps with tree or big branch falls were considered for marking, mapping and later selection. This study concentrated on late gap phase-early building phase (see Whitmore, 1975; Hartshorn, 1980 and Brokaw, 1985) stage of forest gap succession. This stage was characterized by young trees, mostly shade tolerant (since the majority of sapling species in the gaps also appeared in the adjacent forest understory), and a few shade intolerant tree species.

Gap ages for K-13, K-14 and K-15 were deduced from the time the forest trees were cut. However, for K-30, the natural forest gaps which had characteristic gap vegetation species of size-ranges similar to those in selectively cut forest gaps were selected for sampling. A total of 52, 51 and 56 gaps were identified and marked with identification numbers in K-13, K-14 and K-15, respectively, whereas 86 gaps were marked in uncut mature forest (K-30). A table of random numbers was used to select 40 gaps per forest compartment which were measured, mapped and permanently marked with metal tags bearing identification numbers and date of first sampling (Figures 1 & 2). These were designated for intensive two-year and longer term study. All new gaps encountered after the selection of the 40 study gaps in each forest compartment were also marked with identification numbers and dates of first observation and mapped for future studies.

The size (in area, m^2) of a selected gap was determined by a combination of two methods: a) visual estimation of the edges of the gap based on such cues as presence and extent of light demanding vegetation, e.g. <u>Brillantaisia</u>

Figure 1. Approximate location of the 40 randomly selected forest gaps per forest compartment used for gap vegetation studies in lightly selectively cut (K-14) and uncut (K-30) forest tracts of the reserve.

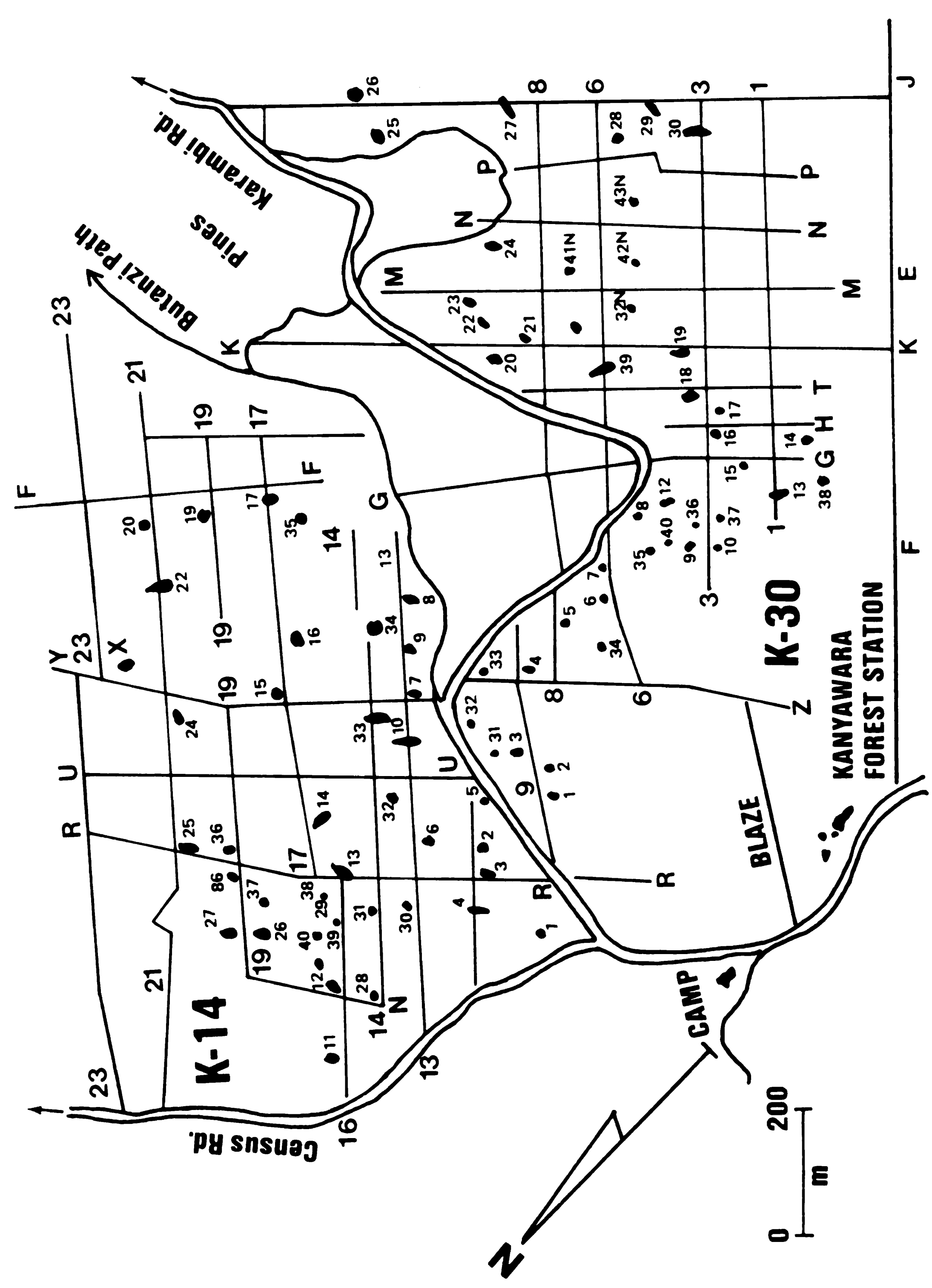
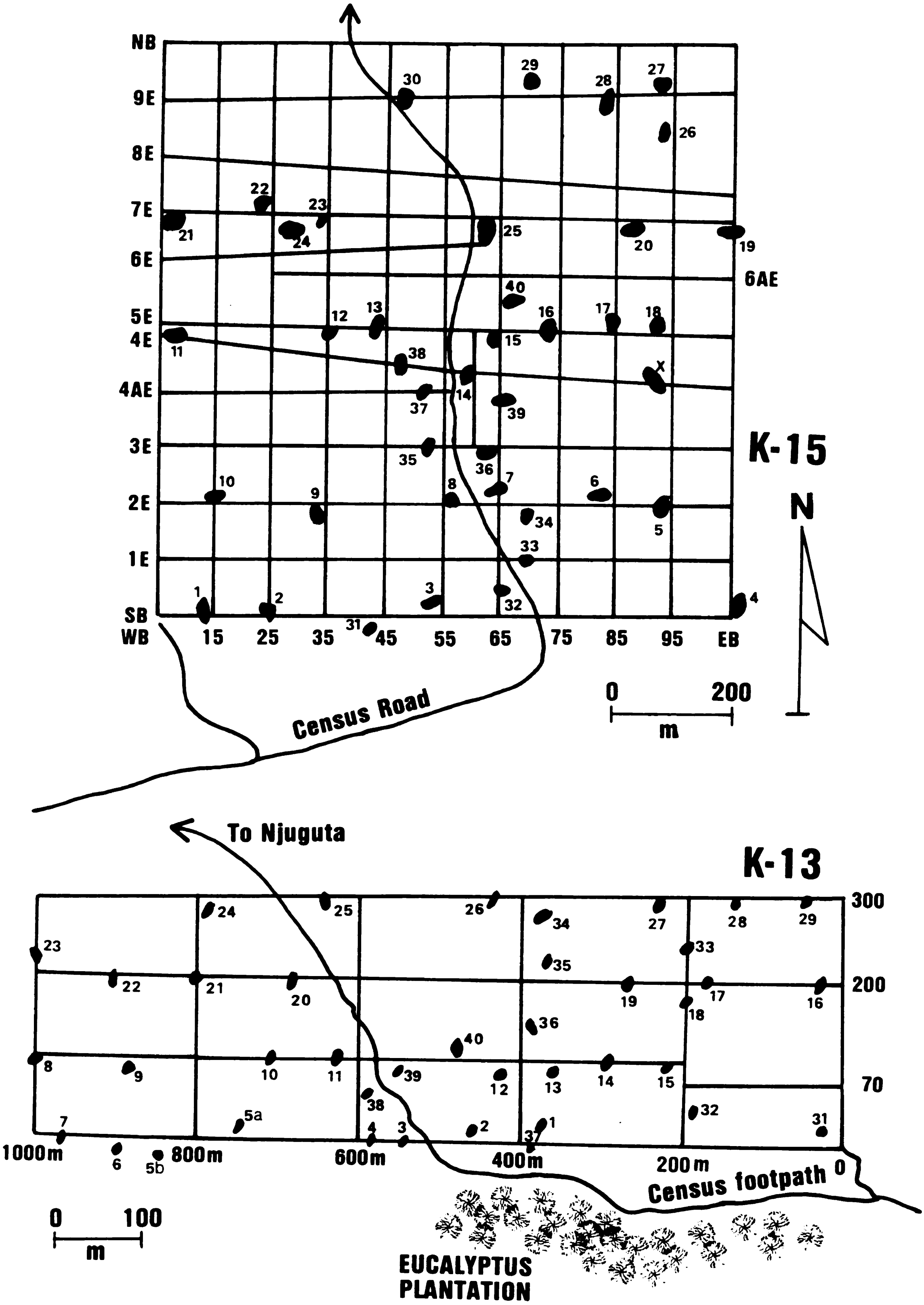

Census Rd.
Karambi Rd.
Butanzi Path
Pines
K-14
K-30
CAMP
BLAZE
KANYAWARA
FOREST STATION
N
0
200
m

Figure 2. Approximate location of 40 randomly selected forest gaps per compartment used for gap vegetation studies in the heavily selectively cut forest (K-15) and heavily selectively cut and treated forest (K-13) in the reserve.


NB
9E
8E
7E
6E
6AE
5E
4E
4AE
3E
2E
1E
SB
WB
15
25
35
45
55
65
75
85
95
EB
K-15
N
0 200
m
Census Road
To Njuguta
K-13
300
200
70
1000m
800m
600m
400m
200m
0
Census footpath
0 100
m
EUCALYPTUS
PLANTATION

nitens, Mimulopsis solmsii and Trema guineensis, which often filled the gaps to the forest/gap interface; b) light meter readings at random points in the forest surrounding the gap. The mean of 10 light readings was taken as representative of the surrounding forest. The interface between gap edge and forest where the gap light declined dramatically to almost surrounding forest levels was marked as the gap edge. Light readings were taken between 11:30 am and 2 pm on days when the sky was relatively clear. Trails were then cut in the gap or the tape measure was pulled through the gap vegetation from a fixed position to the gap edges and measurements taken. Access trail cutting depended on the shape of the gap. If the gap was circular, at least eight radii were cut from the fixed position in the center to the forest edge. If it was long and wide, a base line trail was cut following the longest axis of the gap and other trails crossed it at right angles ending at the forest edge. The size of the gap (area in m^2) was determined from scale drawing of gap configuration on graph paper.

Gap Tree Sapling and Pole Enumeration

After estimation of the gap size, an attempt was made to sample 40% of the gap area for saplings and poles using the trails cut in the gaps. A five meter wide strip along selected trails (2.5 m either side of trail) was sampled. All tree saplings and pole class trees (range $\geq$1.5cm to 10cm dbh) encountered in the sample strip were measured (dbh, cm) and identified to species following Eggeling 1951 and

Hamilton 1981. Voucher specimens of unfamiliar tree saplings and poles were collected, labeled and pressed for future identification at, and deposition with, the Makerere University Herbarium. The effect of logging on forest sapling and pole regeneration was studied by comparing species richness and abundance in cut forest gaps with the same parameters in uncut mature forest gaps. The effect of logging intensity on tree sapling and pole regeneration was also studied by comparing species richness and density of saplings and poles in forest gaps of similar sizes. The effect of post felling treatment with arboricides was studied by comparing species richness and density of saplings and poles in gaps of similar sizes in the two heavily felled forest tracts (K-13 and K-15), one of which (K-13), was treated with arboricides. The effect of gap conditions on forest sapling and pole regeneration was studied by comparing sapling and pole species richness and density in gaps and adjacent surrounding forest. For each of the 20 randomly selected gaps (out of the 40 gaps/ compartment) four 10m x 10m quadrats were established directly opposite the two major axes that crossed the gap perpendicularly in the middle. The quadrats were located 7m to 10m into the forest. Data collection was as described earlier for gap sapling and pole enumerations.

Gap Ground Vegetation Cover (gvc.)

Within each gap, two $4m^2$ quadrats were established and marked with metal tags for long term sampling. Each quadrat was subdivided into four 1m^2 subplots. All living plants rooted within each of the four 1m^2 subplots were identified and their number and frequencies recorded. Visual estimate of the percentage GVC by plants under 1.3m height was made. Voucher specimens of unfamiliar plants were collected, labeled and pressed for subsequent identification at the Makerere University Herbarium. The mean of at least three gvc recordings, 2 dry season (January and June) and one wet season (October) was obtained.

Herbivory and Seed Predation in Forest Gaps

Thirty marked gaps in forest compartments K-14, K-15 and K-30 were visited at the end of each month to examine animal disturbance and intensity of browsing on tree seedlings, saplings and poles. All ninety gaps were sampled on the same day. Sampling involved recording of the presence of incursions and the nature of vegetation disturbance, e.g. trampling, browsing, snapping, uprooting or barking, by tree species.

Seed predation trials on four seed species which could be obtained in large numbers were conducted. Twenty to 30 marked gaps in each forest compartment were used for seed placement. Two seed placement sites, one in the gap center and other at the gap edge, were located in each gap. The number of seeds per placement or pile varied depending on seed size and abundance of available seeds. Only one tree seed species was used per predation trial. The experiment was run until 80% or more of the seeds had been eaten or had become infested with fungus. Recordings for all three forest tracts were done on the same day. Recording involved the number of days elapsed since placement, number of seeds eaten and number remaining per pile. Then the rates of seed disappearance or predation were calculated using the relationship:

$$r = \frac{E}{Pts}$$

Where r = rate of seed predation (seeds/pile/day)
E = total seeds eaten
P = total number of seed placements
t = time (days) since day of placement and
s = number of seeds per pile.

Sources of Plant Recruitment into Forest Gaps

Soils were collected from forest gaps (gap soil) and from under closed or semi-closed forest adjacent to the gap (forest soil) in uncut and selectively cut forest compartments. Samples of the top 10cm of surface soil with bits of litter were collected from $1m^2$ plots. The soil was transferred to screened nursery beds fixed on a raised stand (1.3m above ground) to avoid contamination and seed or seedling predation. Two soil samples from K-14 (one from forest and other from gap) were each thinly spread on a flat iron sheet and thoroughly heated over a fire to sterilise them. These were also placed in the screened nursery bed. The littered surface soil and sterilized soils were spread thinly on top of soil removed from below 10cm depth of each sample. Two replicate trials per gap and adjacent forest soil were run. Each germination trial included 14 soil samples, seven from the forest gaps and a corresponding seven from the forest surrounding the gaps. Fiberglass netting of 1mm x 1mm mesh was used to screen the nursery. The nursery was then lightly thatched with young elephant grass to reduce exposure of the soil to excessive insolation. The plots were watered every evening except on rainy days.

Two $4m^2$ plots (plant regeneration plots = PRP) were also established in 20 of the selected forest gaps in each forest compartment to examine the contribution of buried seeds and seed rain to forest regeneration. The four treatments of the $1m^2$ quadrants in the $4m^2$ PRP were:

a) $1m^2$ subplot with vegetation removed
b) $1m^2$ subplot with vegetation removed and screened
c) $1m^2$ subplot with vegetation and surface soil removed
d) $1m^2$ subplot with vegetation left intact.

Monthly checks of the nursery and PRP and counts and classification of seedlings germinated from buried seeds or seeds dispersed into the gaps were made. Unfamiliar plants were tagged with identity numbers and left to mature for easier identification. For each forest or forest gap plot sampled, two soil seed germination trials were conducted. One was begun in December of 1984 and run through June of 1985. The second one was set up in late June, 1985, and also ran for seven months. Each trial ran for nearly seven months, under the assumption that the majority of seeds should have germinated by then. However, 20 months of observation on the PRP in forest gaps were accomplished.

Mode of Tree Sapling and Pole Regeneration in Gaps

A total of 25 forest gaps was sampled in each forest compartment. Five meter wide strips following the two major or longest axes that crossed the gap perpendicularly in the middle were sampled for tree saplings and poles which were either growing normally (N), coppicing (C) or stem sprouting (SS). The saplings and poles which had no signs of breaks or bark injury were classified as normal (N). Where the main stem was doubly bent, dry or with signs of deterioration while bent, and a dominant side branch taking off from the stem, the sapling or pole was designated stem sprout (SS.). In coppices, the main stem was snapped or broken with sprouts taking off from the stock. The number of breaks and coppices per desirable species sapling or pole stem was also counted. No attempt was made to determine the contribution of root sprouts to gap regeneration because destructive sampling was prohibited in the reserve.

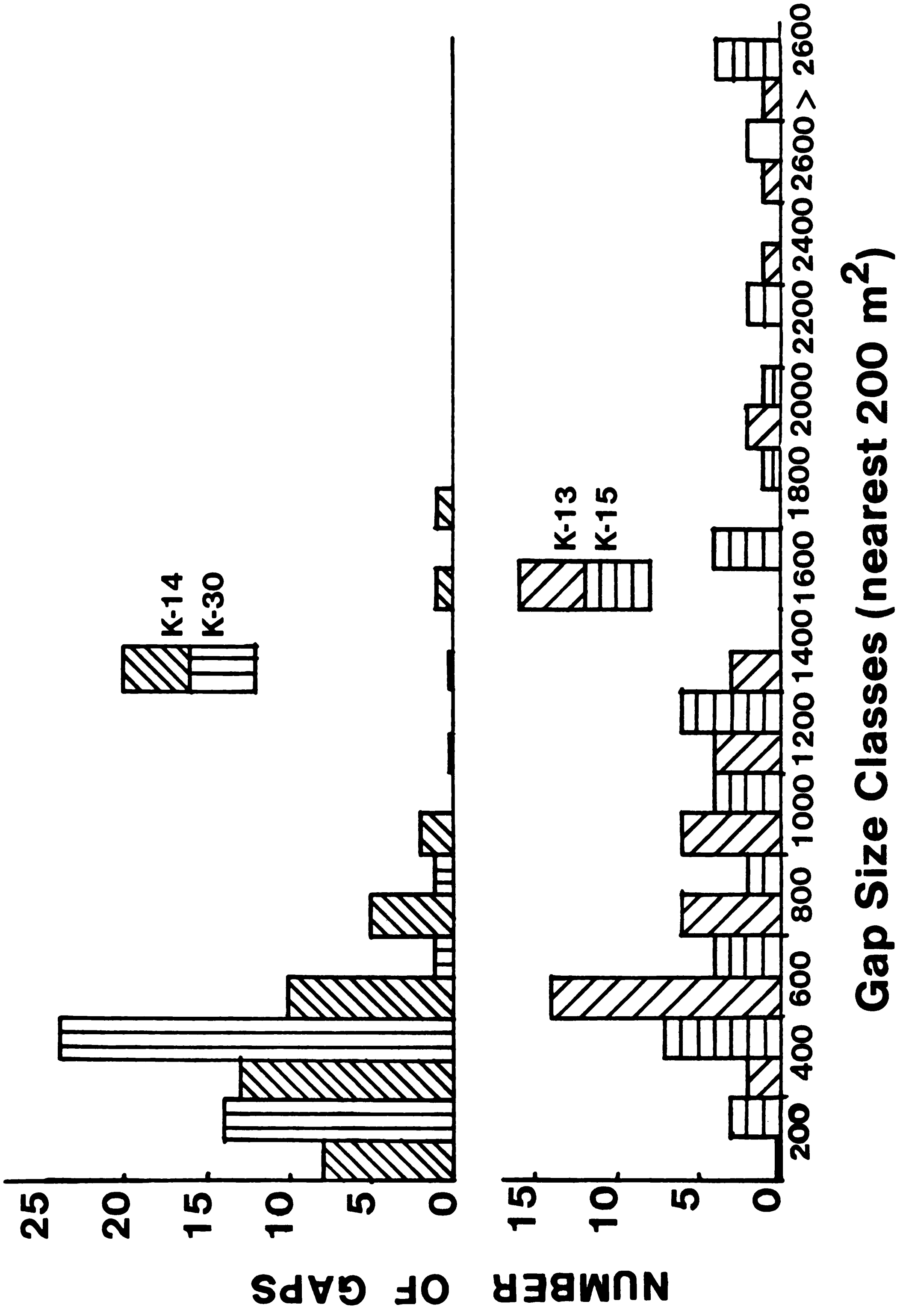
RESULTS

Natural and Artificial Forest Gaps

The non-parametric multiple comparison by STP (Simultaneous Test Procedure of Dwass, Sokal and Rohlf, 1981, p. 437) was used to analyze gap sizes of uncut and selectively cut forest tracts (see Appendix table 1, 2, 3 and 4). The calculated critical value for $U_{0.05}[4, \infty]$ was 1066.7. Except for the forest gaps of pair comparison K-13 Vs K-15 (U=880), the forest gap sizes for all other plot pair comparisons were significantly different (all $U \geq 1135$). As expected, the heavily selectively felled forest (K-13 and K-15) exhibited the highest gap size means ($938m^2$ and $1307m^2$, respectively) and ranges ($227m^2$ to $3313m^2$ and $73m^2$ to $7100m^2$, respectively). The lightly cut forest tract (K-14) showed a lower mean ($467m^2$) and range ($75m^2$ to $1800m^2$) while the naturally formed gaps in uncut mature forest (K-30) had the lowest mean ($256m^2$) and range ($100m^2$ to $663m^2$).

Figure 3 clearly shows that only a small percentage of gaps, 55% and 40%, in the heavily cut forests of K-13 and K-15 respectively, were within the $200m^2$ to $800m^2$ gap size class range. However, the greater percentage of forest gaps, 90% and 100%, in lightly cut (K-14) and uncut (K-30) forest tracts, respectively, were within the same gap size

Figure 3. Size class distribution of 40 randomly selected gaps in uncut mature forest (K-30), lightly selectively cut forest (K-14), heavily selectively cut forest (K-15), and heavily selectively cut and treated forest (K-13) tracts of the reserve.

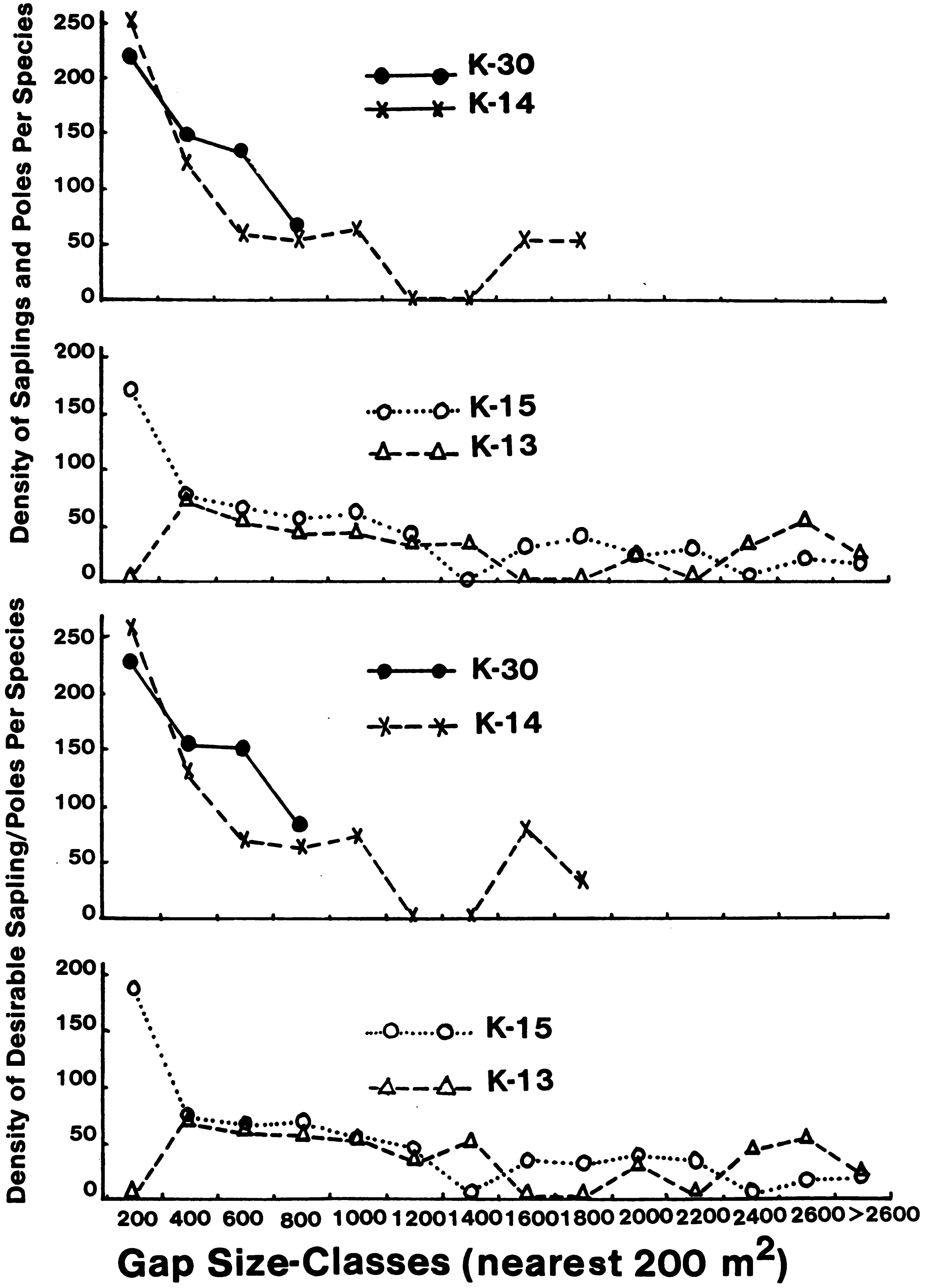

NUMBER OF GAPS
25
20
15
10
5
0
15
10
5
0
K-14
K-30
K-13
K-15
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
2600
2600 >
Gap Size Classes (nearest 200 m²)

class range. The gaps in K-13, K-14, and K-15 were a result of multiple tree removals during selective felling and consequent wind and storm throws. The gaps in uncut forest, K-30 were mainly due to tree falls caused by wind and/or heavy storms. Consequently, the majority of forest gaps in the heavily felled forests were larger than those in the lightly cut and uncut forest tracts. Therefore, selective forest felling resulted in the formation of gaps larger than those characteristic of natural forest disturbances such as windfalls.

Forest Gap Sizes and Sapling and Pole Regeneration

In the heavily selectively cut and treated forest (K-13) the correlation between gap size and sapling and pole species richness or density was not significant. It was likely that the low correlation was influenced by the low species richness and density due to treatment effects, rather than factors controlled by gap size. In K-15, both the species richness and density of saplings and poles of all species combined and desirable tree species were significantly negatively correlated with gap size (all $r \leq -0.459$, $n = 40$, $P<0.01$). Even the density of desirable tree saplings and poles per species was negatively correlated with gap size ($r=-0.488$, $P<0.01$, Fig 4). For K-14, the species richness and density of saplings and poles of all species combined and desirable tree species were also significantly negatively correlated with gap size (all $r \leq 0.514$, $P<0.005$). Again, the density of desirable saplings

Figure 4. The density (No/ha) of saplings and poles of all tree species combined and desirable tree species ($\geq$1.5 cm to 10 cm dbh) per species in the forest gaps of lightly selectively cut (K-14), uncut mature forest (K-30) and the heavily selectively cut (K-15) and heavily selectively cut and treated (K-13) forest tracts of the reserve.


Density of Saplings and Poles Per Species
250
200
150
100
50
0
K-30
K-14
200
150
100
50
0
K-15
K-13
Density of Desirable Sapling/Poles Per Species
250
200
150
100
50
0
K-30
K-14
200
150
100
50
0
K-15
K-13
200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400 2600 >2600
Gap Size-Classes (nearest 200 m2)

and poles per species was strongly negatively correlated with gap size ($r=-0.536$, $P<0.005$, Fig 4). In spite of the small gap sizes and low range, the tree saplings and poles in the gaps of K-30 were also responsive to variations in gap size. The species richness of tree saplings and poles of all tree species combined and desirable tree species were highly negatively correlated with gap size ($r=-0.601$ and $r=-0.619$, respectively, all $P<0.005$). The density of saplings and poles of all species combined, desirable tree species, and the density of desirable tree saplings and poles per species, were also significantly negatively correlated with gap size (all $r\leq-0.435$ and $P\leq0.01$).

Tree sapling and pole species richness, and density of saplings and poles per species, tended to fluctuate most, tending downwards in larger (>650m^2) than smaller gaps less than 650m^2 in size (Appendix tables 1-4, Fig. 4). The majority of natural gaps (97.5%) in uncut mature forest (K-30) fell below the 650m^2 gap size range. The gap sizes with the highest tree sapling and pole species richness and density, and number of individual saplings and poles per species, for K-13, K-14, K-15, and K-30, also fall within the 200m^2 and 650m^2 size range.

There was a highly significant difference between mean tree sapling and pole species richness in the gaps of cut and uncut forest tracts ($F=40.43$, $P<0.005$). The Duncan's multiple range test also showed that the mean species richness of saplings and poles of all species combined were lower and similar for K-13 and K-15 gaps whereas they were higher and similar for K-14 and K-30 forest gaps. For desirable tree sapling and pole species, the gaps in uncut and lightly cut forest had higher levels of species richness than gaps in heavily cut or heavily cut and treated forests (F=37.82, P<0.005). Again, the means of desirable tree sapling and pole species in the gaps of K-13 and K-14 were low and similar while those in K-14 and K-30 gaps were high and similar. The gaps in the heavily felled and treated forest (K-13) had the least while those in uncut forest tract had the highest means of desirable tree sapling and pole species richness.

Similarly, the mean densities of saplings and poles of all tree species and desirable species in the gaps of uncut, lightly cut and heavily cut forests were significantly different (F=43.33 and F=47.70, respectively, all P<0.001). The Duncan's test also showed that the mean densities of tree saplings and poles in the gaps of heavily cut forests were similar and lower than the mean densities in the gaps of lightly cut and uncut mature forest. Therefore, ranking of the densities of saplings and poles in the forest gaps was K-30>K-14>K-15>K-13. Except for the K-13 vs K-15 plot comparison, all other gap plot pair comparisons of the density of sapling and poles per species were significantly different (all $U \geq 1130$, critical $U_{0.05}(4,40)=1066.7$. STP.). The gaps in uncut mature forest had the highest densities per species followed closely by the gaps in lightly cut forest and those in heavily selectively cut forest (Appendix tables 1-4, Fig. 4).

The percent ground vegetation coverage of the study gaps in the four forest compartments was also compared using STP (see Sokal and Rohlf, 1981). As before, the calculated critical value of $U_{0.05}(4,\infty)$ was 1066.7. All gap plot pair comparisons of percent ground vegetation cover (gvc) showed highly significant differences (all $U \geq 1133.5$). The hierarchy in gap gvc ranking was K-13>K-15>K-14>K-30. In general, gaps in selectively cut forest tracts supported higher densities of herbaceous and non woody plant species forming denser gvc than gaps in uncut forest. Light-demanding species were frequently more dominant in cut forest gaps than uncut forest. In some cases, a few gap species such as Fleurya urophylla, Brillantaisia nitens, Aspilia africana, Monechma and Mimulopsis sp. dominated the dense gvc almost to the exclusion of other species in gaps of cut forests. The gvc was poorly correlated with forest gap sizes in K-13, K-15, and K-30 but not in K-14 ($r=0.382$, $P<0.05$). In K-13 and K-15 most forest gaps were large with relatively high and uniform gvc. In K-30 gaps, the gvc was mostly low and variable among gaps. However, the correlations between forest gap gvc and the species richness and density of saplings and poles of all tree species, desirable tree species, and the density of desirable tree saplings and poles per species, in K-13 and K-15, were all significantly negative (all $r \leq -0.339$ and $r \leq -0.383$

respectively, and $P<0.05$). This was also true for K-14 forest gap gvc but the correlations in this case were more strongly negative (all $r \leq -0.560$, $P<0.01$). For the naturally formed gaps in uncut forest, the gap gvc had no significant relationship with the sapling and pole species richness and density. However, the tendency towards an inverse relationship between gvc and tree sapling and pole species richness and density was present.

The effect of logging intensity and chemical treatment on forest regeneration was analyzed by comparing the species richness and density of desirable tree saplings and poles in forest gaps of similar sizes. Sixteen gaps of similar sizes (all $U_{(16,16)} \geq 117.5$ while $U_{0.05(16,16)} = 83$ Mann-Whitney U-test, Siegel, 1956) were selected from the 40 study gaps for each of the three forest tracts (K-14, K-15 and K-30). These were used to study the effects of logging intensity on forest gap tree sapling and pole regeneration for lightly cut, heavily selectively cut and uncut forest tracts.

The sapling and pole species richness for all tree species combined in the gaps of the heavily cut forest and the lightly cut forest (K-15 vs K-14), and lightly cut and uncut forest (K-14 vs K-30), were not significantly different ($U=91$ and $U=104$, respectively and $P>0.05$). However, the gaps in heavily selectively cut forest (K-15) had lower sapling species richness than the gaps in uncut forest ($U=85$, $P=0.05$). These results indicate that both light and heavy selective logging tended to reduce tree sapling and pole species richness of the gaps created by felling. But the level of reduction depended heavily on the intensity of felling. Thus, light selective felling similar to that in K-14 was similar to the natural tree falls and less destructive to sapling and pole regeneration of all tree species in the gaps created.

The influence of logging was more clearly demonstrated by the changes in species richness and density of saplings and poles of desirable or canopy tree species. The forest gaps in lightly cut and uncut forest tracts had similar species richness of desirable tree saplings and poles (U=90.5, P>0.05). However, the forest gaps in heavily selectively felled forest had lower species richness of desirable tree saplings and poles than gaps in lightly cut or uncut forest (U=34 and U=22.5, respectively, all P<0.001). These results suggest that logging affected the species richness of saplings and poles of desirable timber or forest canopy species more than the species richness of saplings and poles of all tree species in general. Consequently, the gaps of heavily selectively cut forest (K-15) had lower density of desirable tree saplings and poles per species than the gaps in lightly cut (U=54, P<0.01) or uncut mature forest (U=20, P<0.001). In contrast, the gaps in lightly cut and uncut forest tracts had similar densities of desirable tree saplings and poles per species (U=94, P>0.05).

To test the effect of post felling chemical treatments, the sapling and pole regeneration in eighteen pairs of gaps of similar sizes ($U=155$, $P>0.05$) from the 40 marked gaps in heavily cut and heavily cut and treated forests were compared. The species richness of tree sapling and pole regeneration in the gaps of heavily cut forest (K-15) was higher than that in the gaps of heavily cut and treated forest ($U=60$, $P<0.01$). The sapling and pole species regeneration in the gaps of lightly cut forest was 90.1% of the species richness in K-30 gaps, that in the heavily selectively cut forest 78.4%, and that in the heavily cut and treated forest gaps only 40.8%. Post felling treatment with arboricides could account for most of the 37.6% depression of tree sapling and pole species in treated forest gaps, relative to heavily cut but untreated plots. Correspondingly, the density of sapling and pole regeneration, and density of saplings and poles per species, was higher in the gaps of heavily cut forest than in heavily cut and treated forest (all $U\leq51$, $P<0.01$). However, the species richness and density of desirable tree saplings and poles per species were not significantly different, although 21.2% and 25.7% lower, respectively, in K-13 than K-15 forest gaps.

Finally, the effect of gap conditions on tree regeneration was examined by comparing the species richness and density of saplings and poles in the gaps and plots located in the forest tracts surrounding the gaps (Table 1).

Table 1. Average sapling and pole ($\geq$1.5cm<10cm dbh) species richness/m^2 and density (#/ha) for the 20 randomly selected gaps (G) and adjacent forest plots (F) for each of the selectively cut (K-14 and K-15) and uncut (K-30) forest tracts of the reserve.

Study plots		All sapling & pole spp. richness/m2	Desirable sapling & pole spp. richness/m2	Density of sapling & pole/species	Density of Desirable sapling & poles/species
K-14	F	0.19 (0.03)*	0.06 (0.01)	225.4 (67.4)	221.9 (68.2)
	G	0.13 (0.07)	0.04 (0.02)	113.6 (78.2)	138.5 (103.3)
K-15	F	0.14 (0.03)	0.041 (0.015)	189.04 (42.46)	191.9 (83.4)
	G	0.06 (0.04)	0.019 (0.015)	69.14 (55.30)	67.5 (63.9)
K-30	F	0.21 (0.05)	0.07 (0.02)	288.4 (76.6)	256.4 (76.7)
	G	0.16 (0.05)	0.05 (0.02)	173.5 (68.6)	194.0 (127)

* Standard deviation of the mean.

For each forest compartment, the tree saplings and poles in 20 pairs of gaps and corresponding forest plots were compared. The Wilcoxon matched pairs signed rank test (T) was used.

In lightly cut forest (K-14) the forest plots adjacent to the gaps harbored higher species richness of all tree species, and desirable tree species, than did the corresponding forest gaps (T=16.5, P<0.005 and T=22, P<0.01 respectively). The species richness of all tree species combined, and desirable tree species in forest gaps was 31.6% and 33.3% lower, respectively, than that in adjacent forest plots. Similarly the forest plots in K-14 had higher densities of sapling and pole species for all tree species and desirable tree species than the forest gaps (T=7 and T=9, respectively, all P<0.005). The density of all tree species combined and desirable tree species in forest gaps was 49.6% and 37.6% lower, respectively, than that in adjacent forest plots.

Evidently, the gaps in heavily selectively cut forest (K-15) experienced serious reductions in tree species richness and density. The species richness of saplings and poles of all three species and desirable tree species in forest gaps and forest plots were highly significantly different (T=4 and T=23 respectively all P<0.05). The species richness of saplings and poles of all tree species and desirable tree species in the forest gaps was 57.2% and 53.7% lower, respectively, than that in adjacent forest plot. Consequently, the density of tree saplings and poles per species for all species and desirable tree species was higher in the forest plots than corresponding gaps ($T=1$ and $T=0$, respectively, all $P<0.005$). Furthermore, the density of saplings and poles per species, for all tree species and desirable tree species, in forest gaps was 63.4% and 64.8% lower, respectively, than that in adjacent forest plots.

For the uncut mature forest, the forest gaps also exhibited lower sapling and pole species richness for all tree species and desirable tree species than the corresponding forest plots ($T=1.5$, $P<0.005$ and $T=24$, $P<0.02$, respectively). However, the percent reduction of tree saplings and poles in the forest gaps was relatively lower than in selectively cut forests which had a predominance of large gaps. The species richness of saplings and poles of all tree species and desirable tree species in the forest gaps was 23.8% and 28.6% lower, respectively, than that in surrounding forest plots. The density of saplings and poles per species for all tree species and desirable tree species was also lower in the forest gaps than corresponding forest plots ($T=10$ and $T=48.5$ respectively, all $P<0.05$). The density of saplings and poles per species for all tree species and the desirable tree species, in forest gaps was 40% and 24.2% lower, respectively, than that in adjacent forest plots.

Forest disturbances through both light and heavy felling and even natural tree falls had a tendency to reduce

gap sapling and pole species richness and density of saplings and poles. However, the level and significance of reduction was related to the intensity of felling and the nature of disturbance as well. It seems that felling alone could not explain the paucity of saplings and poles in the gaps of selectively cut forest tracts. Other consequences of forest felling may have significantly contributed to impoverished regeneration of saplings and poles in forest gaps.

Except for the non-desirable pioneer species or forest gap specialists such as *Trema guineensis* and species of *Neoboutonia*, most tree species regenerating in the gaps were also present in adjacent forest tracts. Even the 18 common desirable timber or canopy tree species in the central forest reserve were common both in the forest gaps and plots in adjacent forest surrounding the gaps (Table 2). The density of the common, desirable timber or canopy tree species was similar for forest gaps and forest plots in K-14 but significantly different in K-15 where forest plots had higher densities than forest gaps ($T=32.5$, $P<0.01$). However, there was strong evidence of higher tree sapling and pole densities of the common desirable timber or canopy tree species in the naturally formed forest gaps than in forest plots ($T=9$, $P<0.005$) in uncut mature forest. These results imply that most of the sapling and pole regeneration in the forest gaps was from pre-existing seedlings and saplings which survived the impact of gap creation. Many

Table 2. The density (No./ha) of saplings and poles (range >1.5cm≤10cm dbh) of the common desirable timber or canopy tree species in the central forest reserve regenerating in forest gaps (G) and forest plots (F) adjacent to the gaps in selectively cut (K-13, K-14, K-15) and uncut (K-30) forest tracts.

	K-13	K-14		K-15		K-30	
Tree Species	G	F	G	F	G	F	G
A. <u>altissima</u>	46.8	25	22	10	10.4	13.3	37.8
A. <u>toxicaria</u>	25.6	35	64.1	1.7	8.2	98.3	134.4
B. <u>unijugata</u>	105.0	151.7	110	90	46.5	91.7	151.2
C. <u>africana</u>	0.54	40	29.7	21.7	12.0	20	33.6
C. <u>gorungosanum</u>	14.1	18.3	16.3	5.0	3.8	26.7	44.8
C. <u>millenii</u>	0.0	3.3	7.7	0.0	1.1	0.0	8.4
F. <u>macrophylla</u>	0.54	3.3	9.6	3.3	2.2	5.0	11.2
F. <u>angolensis</u>	7.1	16.7	5.7	5.0	3.8	5.0	8.4
F. <u>latifolia</u>	2.7	58.3	33.5	31.7	9.8	71.7	106.4
L. <u>swynnertonii</u>	0.0	86.7	89.0	3.3	15.3	136.7	168
M. <u>platycalyx</u>	6.0	58.3	50.7	76.7	12.6	61.7	46.2
M. <u>bagshawei</u>	0.0	48.3	37.3	16.7	3.8	48.3	78.4
N. <u>buchananii</u>	56	63.3	141.6	68.3	33.3	121.7	217
O. <u>welwrtschii</u>	12	5.0	11.5	36.7	9.3	6.7	4.6
P. <u>excelsa</u>	5.4	5.0	2.9	10.0	3.3	5.0	2.8
S. <u>scheffleri</u>	29.4	68.3	100.5	11.7	14.8	21.7	58.8
S. <u>globulifera</u>	4.9	5.0	11.5	1.7	2.2	175	229.6
T. <u>splendida</u>	10.9	68.3	43.1	10	4.9	45	75.6
$\bar{X}$	18.17	42.2	43.7	22.4	11.0	53.0	78.7
Sx	27.16	38.4	41.3	27.9	11.7	52.51	73.2

more tree seedlings and saplings of the common desirable timber or canopy species were able to survive and continue growth into the sapling and pole classes in the commonly small to medium natural gaps than the characteristically larger gaps created by logging.

In all forest compartments the saplings and poles of *Blighia unijugata*, *Newtonia buchananii*, *Lovoa swynnertonii*, *Funtunia latifolia* and *Antiaris toxicaria* seem to be regenerating more successfully than other species in both forest gaps and forest understory. However, they exhibited some tendency towards higher densities in forest gaps than forest understory. *Symphonia globulifera* was poorly regenerating in all cut forest tracts, gaps, or forest plots while abundant regeneration in gaps and understory of uncut mature forest was observed. Some dominant canopy tree species such as *Olea welwitschii*, *Parinari excelsa*, *Fagara macrophylla*, and *Fagaropsis angolensis* showed no regeneration site preferences and had very low sapling and pole regeneration in both forest gaps and forest understory.

Herbivory and Seed Predation in Forest Gaps

Preliminary data on forest gap utilization by elephants suggest that their impact on the regeneration of some important timber or canopy tree species in large gaps created by felling can be significant (Table 3). The frequency of elephant incursions into the logged forest areas and the number of forest gaps used as browsing sites were higher in selectively cut than uncut mature forests

Table 3. The frequency of elephant incursions and percentage of marked forest gaps used by the elephants as browsing sites in lightly cut (K-14), heavily selectively cut (K-15) and uncut forest (K-30) in the reserve.

Year and months of observation		No. of elephant incursions			Mean % marked gaps visited			Types of tree sapling & pole damage observed		
		K-14	K-15	K-30	K-14	K-15	K-30	K-14	K-15	K-30
1984	3	3	3	1	18.7	45.9	4.4	5*	5	1(d)
1985	12	7	8	2	9.1	35.0	3.3	5	5	0
1986	6	0	0	0	0	0	0	0	0	0

* Types of damage include: barking, defoliation, pushover, snapping and uprooting.

(all $T \leq 2$, $P < 0.005$, Wilcoxon's test). Consequently, elephant damage to gap vegetation, including herbs, shrubs and tree species was high for the selectively cut forest tracts. The seedlings, saplings and poles of a few canopy tree species, such as *A. toxicaria*, *L. swynnertonii*, *N. buchananii*, *A. gummifera* and *B. phoberos* seemed more prone to elephant damage than other species. The seedlings, saplings and poles of these species were killed through all five modes of feeding damage, i.e. barking, total defoliation, pushing over, snapping and uprooting. The saplings of *Lovoa*, *Antiaris* and *Bosquiea* were particularly subject to uprooting. However, more observations and data are still needed before firm conclusions can be made.

Seed predation trials were intended to show whether there were different levels of seed predation at increased intensities of forest exploitation. Within the study compartments, the rates of seed predation, with respect to gap center or edge, were not different. With the exception of *Aphania* seeds, the rates of seed predation were slightly higher in the gaps of selectively cut forest than in uncut forest gaps (Table 4). The half life of seed piles (i.e. the time it took 50% of the seeds to disappear) were generally shorter, and very short in the case of *Mimusops* seeds, in the gaps of selectively cut forest relative to uncut forest gaps. There were weakly significant differences between the rates of seed predation of *Trichilia* in the gaps of cut and uncut forest tracts but no

Table 4. Rates of seed predation in forest gaps of lightly cut (K-14), uncut (K-30) and heavily selectively cut (K-15) forest tracts of the reserve.

Tree seed species	Study Plot	Seedpile size (# seeds)	Half-life of seed piles	Mean rate (r) of seed predation (seeds/pile/day)
Aphania senegalensis	K-14	8	0.7	0.62
	K-15	8	2.0	0.33
	K-30	8	1.1	0.46
Mimusops bagshawei	K-14	4	7.0	0.10
	K-15	4	2.4	0.20
	K-30	4	13	0.04
Trichilia splendida	K-14	3	1.5	0.45
	K-15	3	1.5	0.45
	K-30	3	1.8	0.29
Uvariopsis congensis	K-14	5	2.3	0.24
	K-15	5	2.0	0.26
	K-30	5	2.3	0.17

differences in the predation rates of Aphania and Uvariopsis seeds. However, the gaps in cut forest tracts exhibited higher rates of Mimusops seed predation than gaps in uncut forest [U=2, P<0.001 (K-14 vs K-30), and U=0, P<0.001 (K-15 vs K-30), Mann-Whitney U-test]. There was no difference between Mimusops seed predation rates in the gaps of lightly cut and heavily cut forest (P>0.159). Deducing from the way seeds were eaten, the chips of seed or seed coat, and sometimes fecal pellets left on seed pile sites, rodents appeared to be the main seed predators. Again, the database was small; more tree seed species need to be tested before firm conclusions may be drawn.

Sources of Plant Recruitment Into Forest Gaps

Table 5 shows the summary of the species richness and density of plants germinated in 1m^2 plots of forest soil and forest gap soil from compartments K-14, K-15 and K-30. Single classification ANOVA and Duncan's multiple range test (Sokal and Rohlf, 1981) were used to compare the species richness of plant seedlings germinated in 1m^2 plots of the top 10cm of forest and gap soils. For the forest soils, there were no significant differences in species richness of tree seedlings sprouted from the soils of lightly cut (K-14) uncut (K-30) or heavily cut forest (K-15). Except for the forest soils from K-14 and K-30 (F=9.05, P<0.005), the forest soils from K-14 and K-15, K-15 and K-30, had similar numbers of shrub species. The soils from uncut forest had the least, whereas those from the lightly cut, intermediate

Table 5. Mean plant species richness and density (No./m^2) germinated in 1m^2 plots of the top 10cm of forest soil (F) and gapsoil (G) from K-14, K-15 and K-30 and grown in screened nursery.

Plant life form	$\bar{X}$ No. Plant Species K-14(n=28)	 K-15(n=28)	 K-30(n=28)	$\bar{X}$ Density of Plants K-14(n=28)	 K-15(n=28)	 K-30(n=28)
	F G	F G	F G	F G	F G	F G
Tree seedlings	2.3, 1.3	3.0, 1.3	3.4, 1.6	43.2, 1.6	33.7, 2.3	57.3, 15.1
Shrub species	1.0, 2.0	2.4, 3.0	3.9, 1.4	7.9, 26.9	12.6, 48.4	17.7, 20.9
Herbaceous species	18.0, 6.4	23.0, 8.9	11.3, 5.0	256.4,478.7	243.3,709.0	125.9,270.0
Vines and climbers	1.1,10.8	3.9, 1.4	2.7, 1.0	3.6, 4.6	9.6, 7.3	4.9, 4.6
$\bar{X}$ No. Species & Density	22.4,10.8	32.3,14.6	21.3, 9.0	310.2,512.2	299.2,767.0	205.8,310.6

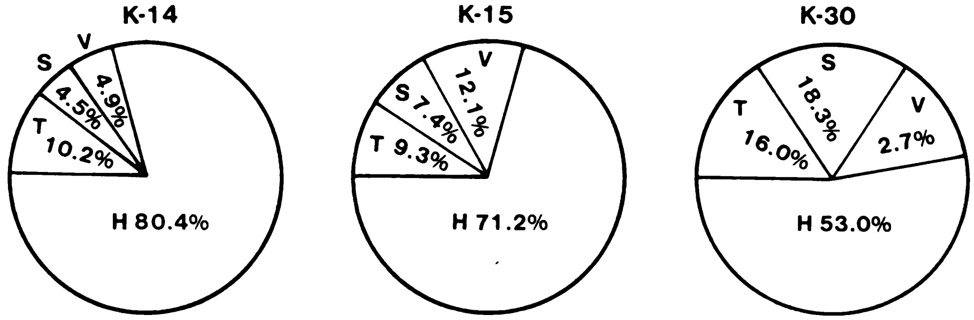
F = Forest soil
G = Forest gap soil

and heavily selectively cut forest had the highest species richness of herbaceous seedlings (F=20.60, P<0.005). The vine and climber species richness was higher for the soils from uncut and heavily cut forest than for lightly cut (F=4.57, P<0.025). When all plant seedlings were considered together, the soils from uncut and lightly cut forest had lower plant species richness than soils from heavily cut forest (F=9.96, P<0.005). However, all forest soil seed bank germination trials were dominated by non-woody seedling species with soils from the heavily cut forest in the lead (Fig. 5).

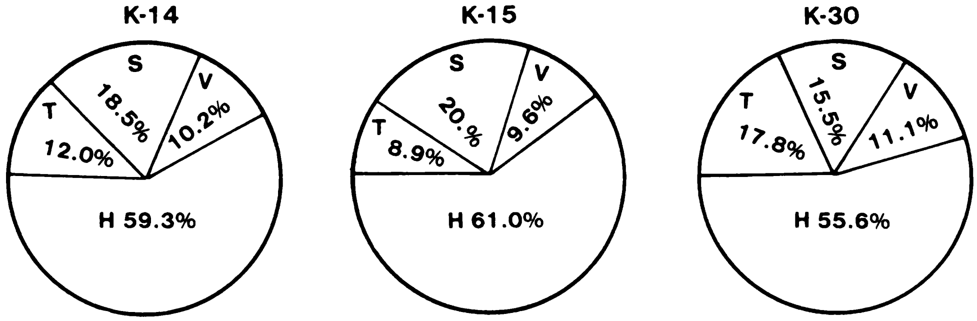
The sterilized soils from K-14 forest had the lowest plant species richness of all soils examined. Only two plants of elephant grass (Pennisetum sp.) and ten of black jack (Bidens sp.) sprouted from the sterilized soil. These two species never reappeared in the plots of other soils from the forest or forest gaps enclosed in the screened nursery. This was possibly a case of contamination. Of the germinated seedlings from the forest soils of K-14, K-15 and K-30, tree seedling species richness was only 10.3%, 9.3% and 16.0% of the species richness, respectively, while herbaceous plants constituted 80.4%, 71,2% and 53.1%, respectively (Fig. 5).

Similarly, the forest gap soils from uncut, lightly cut and heavily selectively cut forests exhibited no significant differences in the species richness of germinated tree, vine and climber seedlings. For the shrub and herbaceous plants,

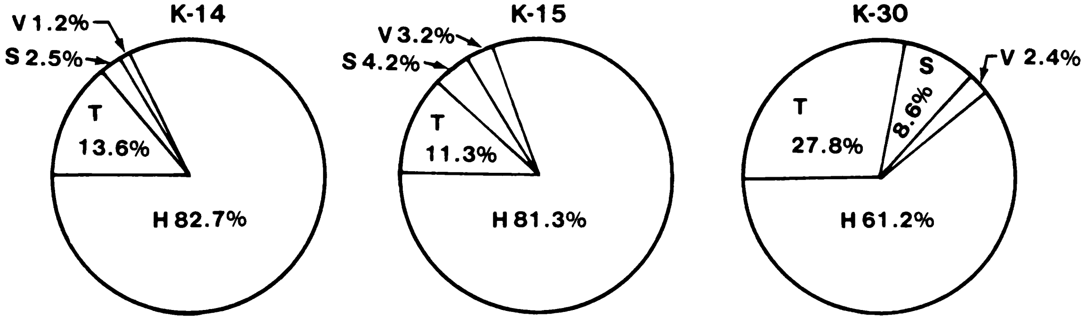
Figure 5. Percent contribution of the four plant life forms to plant species richness and density of plants (No/m^2) germinated in $1m^2$ plots of the top 10 cm of forest soil and gap soil collected from forest gaps and forest plots adjacent to the gaps, respectively, in lightly cut (K-14), heavily selectively cut (K-15) and uncut mature forest (K-30) and grown in screened nursery. T=tree seedlings, S=Shrub species seedlings, H=herbaceous species seedlings and V=vines and climber seedlings.



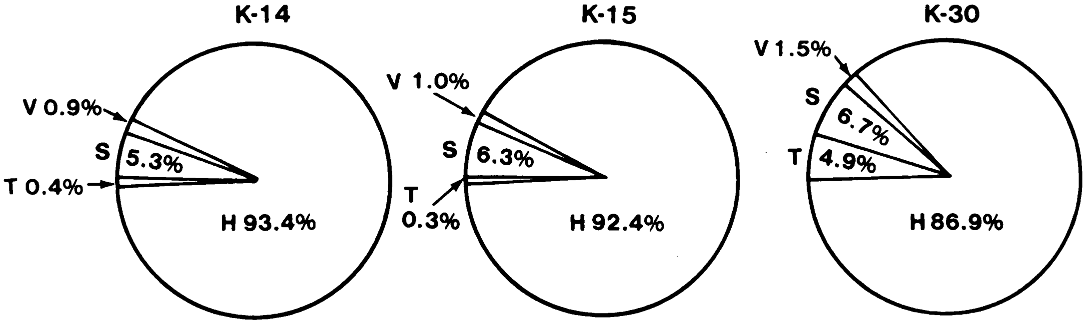
a. Mean seedling species richness (Forest Soil)



b. Mean seedling species richness (Forest-gap Soil)



c. Mean seedling density $(\#/m^2)$ (Forest Soil)



d. Mean seedling density $(\#/m^2)$ (Forest-gap Soil)

the soils from uncut forest gaps had the lowest species richness while those from heavily cut forest had the highest, with soils from lightly cut forest intermediate ($F=6.84$, $F=7.19$, respectively, all $P \leq 0.01$). When all plant seedlings were considered together, the soils from uncut and lightly cut forest gaps had lower plant species richness than those from heavily cut ($F=5.1$, $P<0.025$). The majority of germinated plant seedlings in the forest gap soils were also of herbaceous species (Fig. 5). Of the germinated seedling species from the gap soils of K-14, K-15 and K-30, only 11.9%, 8.9% and 17.7% were tree species, respectively. In contrast, the herbaceous species constituted 58.9%, 61.0% and 55.6% of the germinated seedling species in K-14, K-15 and K-30 forest gap soils, respectively. The vines, climbers and shrub species formed the remainder (Fig. 5).

The Mann-Whitney U-test (Sokal and Rohlf, 1981) was also used in paired comparisons of species richness of plants germinated in forest soils and forest gap soils. The forest soils from under the forest tracts, irrespective of whether the forest was heavily cut, lightly cut or uncut, exhibited higher tree species richness (all $U \geq 48$, $P<0.001$), higher herbaceous species richness (all $U=49$, $P<0.001$) and higher vine and climber seedling species richness (all $U \geq 39$, $P<0.05$) than forest gap soils. For shrubs, gap soils in the heavily cut forest tended to have higher species richness than forest soils from lightly cut and uncut forest. Comparisons of all germinated plant species combined also

showed that forest soils had higher plant species richness than forest gap soils (all $U \geq 49$, $P < 0.001$).

Comparison of the density of seedling sprouts from the forest soils and gap soils using ANOVA and Duncan's test showed a different pattern from that of plant species richness. The densities of tree seedlings, shrub seedlings and non-woody plants germinated from the forest soils of K-14, K-15 and K-30 were not different. The overall mean densities of plants germinated from the forest soils of the three forest compartments were also not different. Only the densities of vine and climber seedlings from the soils of K-15 were higher than those from K-14 or K-30 forest soils ($F=4.24$, $P<0.05$). With the exception of tree seedling densities, where K-30 gap soils had the highest ($F=4.33$, $P<0.05$), the densities of seedlings of shrubs, herbaceous plants, vines and climbers germinated from the gap soils of the three forest compartments were not different. Again, the overall mean density of plants germinated from the gap soils from the three forest compartments was similar.

However, paired comparisons using the U-test showed that the densities of tree seedlings germinated from forest soils were generally higher than from forest gap soils (all $U \geq 38$, $P \leq 0.05$). The density of shrubs, vines and climbers was not different between forest and forest gap soils. However, the forest gap soils from heavily felled forest tracts had higher densities of herbaceous seedlings than forest soils from uncut, lightly cut or heavily cut forest

tracts (all $U \geq 40$, $P \leq 0.05$) whereas all other plot pair comparisons had similar densities. Because of the extremely high non-woody species densities, the forest gap soils from the heavily cut forest also had higher densities of seedlings of all four life forms considered together than forest soils from under uncut, lightly cut or heavily cut forest tracts (all $U \geq 44$, $P \leq 0.01$). All other possible plot pair comparisons had similar densities.

Within the study compartments, the mean species richness and density of seedlings of vines, shrubs and trees germinated from the forest soils of K-30 were low and significantly different from the species richness and density of herbaceous seedlings ($F=23.8$, and 24,07, respectively, all $P \leq 0.005$, ANOVA and Duncan's' test, Fig. 5). For lightly cut forest (K-14) the trend was similar to K-30 forest soil. The species richness and density of vines, shrubs and tree seedlings were similar and lower than the richness and predominance of herbaceous seedlings ($F=272.9$ and 7.9 respectively all $P \leq 0.005$, ANOVA). The mean species richness and density of vines, shrubs and trees germinated from forest soils of K-15 were also very low compared to species richness and density of herbaceous seedlings ($F=77.82$ and 29.85, respectively, all $P<0.005$, Fig. 5).

Within-compartment comparisons of seedling sprouts from gap soils of K-14, K-15, and K-30 showed that the species richness and densities of tree, shrub, vine and climber seedlings were similar but quite low and different from the extremely high species richness and density of herbaceous seedlings (all $F \geq 21.3$, $P < 0.005$, ANOVA and Duncan's test, Fig. 5). This implies that seed banks in both forest and gap soils were abundantly rich in seeds of herbaceous species but extremely impoverished in seeds of tree species. In addition, the forest gap soils were more impoverished in both herbaceous plant species richness and tree species richness and abundance than forest soils.

The majority of tree seedling species germinated from the forest soil and forest gap soils belonged to the so called 'non-desirable' timber species (Table 6). Most were the fast growth, gap or secondary forest colonizers with a few characteristic of middle and understory species. Of the commercially desirable timber species, only _Celtis_ _africana_ appeared in the forest and forest gap soils and _Cordia millenii_ in forest soils from uncut forest, but all in extremely low densities. _Trema_ _guineensis_ was the only pioneer gap species well represented in the soil seed pools of forest and forest gaps. However, the forest soils had higher seedling densities of _Trema_ than forest gap soils (Table 6). In general, the forest soils from uncut mature forest had higher tree seedling species richness and abundance than forest soils from selectively cut forest tracts or gap soils (Table 6). However, the rarity of seedlings of commercially desirable timber or canopy species

Table 6. Mean density (No./m^2) and frequency of occurence (100%=1) of tree seedlings germinated from $1m^2$ plots of the top 10cm of forest soil and forest gap soil tended in screened nursery. No. of $1m^2$ plots for K-14, K-15 and K-30 were equal, n=14.

Tree species	Forest Soil			Forest Gap Soil		
	K-14	K-15	K-30	K-14	K-15	K-30
Celtis durandii	22.8, 1.0	6.2, 1.0	12.2, 0.8	1.3, 0.3	0.2, 0.5	3.0, 0.8
Celtis africana	2.4, 0.2	0.0, 0.0	2.4, 0.6	0.4, 0.2	0.5, 0.2	0.2, 0.1
Trema guineensis	16.8, 0.4	25,0, 1.0	35.2, 1.0	0.0, 0.0	1.0, 0.1	11.5, 0.8
Teclea nobilis	0.2, 0.2	0.0, 0.0	4.0, 0.8	0.4, 0.1	0.0, 0.0	0.0, 0.0
Neoboutonia sp.	0.0, 0.0	1.0, 0.3	0.0, 0.0	0.0, 0.0	0.6, 0.3	0.0, 0.0
Chaetacmea aristata	0.0, 0.0	0.0, 0.0	1.0, 0.1	0.0, 0.0	0.0, 0.0	0.4, 0.2
Clausena anisata	0.0, 0.0	0.8, 0.1	0.0, 0.0	0.0, 0.0	0.0, 0.0	0.0, 0.0
Diospyros abyssinica	0.0, 0.0	0.0, 0.0	0.0, 0.0	0.2, 0.1	0.0, 0.0	0.0, 0.0
Cyphomandra betacea	0.0, 0.0	0.6, 0.2	1.0, 0.1	0.0, 0.0	0.0, 0.0	0.0, 0.0
Cordia millenii	0.0, 0.0	0.0, 0.0	0.6, 0.1	0.0, 0.0	0.0, 0.0	0.0, 0.0
Maesa lanceolata	0.0, 0.0	0.0, 0.0	0.9, 0.4	0.0, 0.0	0.0, 0.0	0.0, 0.0
Unidentified	0.0, 0.0	0.2, 0.1	0.4, 0.1	0.0, 0.0	0.0, 0.0	0.0, 0.0
Total Tree Species	4	6	9	4	4	4
Mean Density	42.2	33.8	57.7	2.3	2.3	15.1

in the forest and forest gap soil seed banks was of concern with regard to forest regeneration.

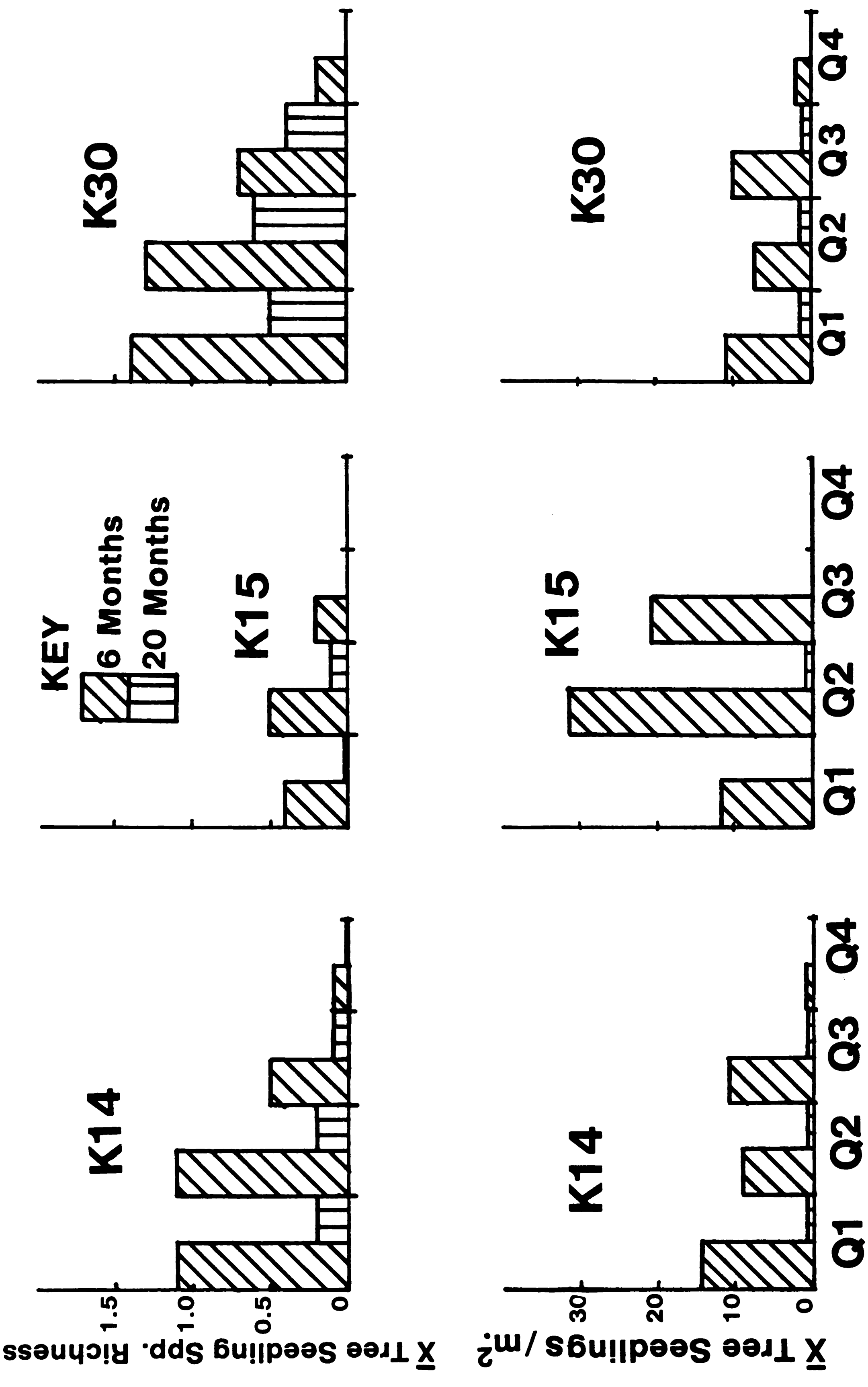
Gap Soil Seed Banks and Incoming Seed Dispersal

This experiment was designed to demonstrate the potential contribution of buried seeds and seeds newly dispersed into the gaps, and the influence of existing vegetation, on forest gap regeneration. Appendix Table 5 shows averages for plant life forms germinated in the 20 PRP in forest gaps of the selectively cut (K-14 and K-15) and uncut forest tracts. The general trend was similar to that of forest gap soil seed germination trials where tree seedlings showed the lowest species richness and density while the herbaceous seedlings showed the highest. However, the plant species richness and density observed in PRP were much lower than those realized from forest soil seed pools or forest gap soils seed pools germinated under screened nursery conditions (all $P<0.01$). This may suggest seed or seedling predation or failure of some seeds to germinate under forest gap conditions which were different from the nursery conditions. In K-14, K-15 and K-30 gaps, the mean seedling species richness of trees, shrubs, vines and climbers that germinated from the PRP was lower than that of herbaceous sprouts ($F=8.36$, 13.53 and 12.47, respectively, all $P\leq0.01$ and Duncan's test). This was another clear indication of the abundance of viable seeds of herbaceous compared to tree species in the forest gap soils. The results also imply that successful tree regeneration in forest gaps could only come from seed dispersal into the gaps or further growth and development of seedlings already established at the time of disturbance.

There were significant differences between treatment means as well. For all the study plots (K-14, K-15 and K-30), the PRP with vegetation removed, vegetation removed and screened, or vegetation and surface soils removed, had similar and higher plant species richness than PRP with all vegetation left intact ($F=4.10$, 4,42 and 7.06 respectively, all $P\leq0.05$ and Duncan's test). The density of herbaceous sprouts in the PRP of K-14, K-15 and K-30 was also very high compared to that of tree, shrub, vine or climber sprouts (all $F\geq20.93$, $P<0.005$). There were significant differences between treatment means with Q_1 and Q_2 having the highest densities, Q_3 intermediate and Q_4 the lowest. Surprisingly, the quadrants with vegetation and surface soils removed also had higher plant species richness and density of newly germinated seedlings than quadrants with vegetation left intact (all $P<0.025$, Mann-Whitney U-test, Fig. 6). This strongly suggests that gap vegetation had a strong suppressive influence on the germination and establishment of newly dispersed and buried seeds in forest gaps.

In total, seven tree species germinated in K-14 PRP. These included *T. guineensis*, *C. durandii*, *C. africana*, *M. Lanceolata*, *D. abyssinica*, *T. nobilis* and *M. bagshawei*. The PRP in K-30 gaps had five of the species in K-14 (except *M. lanceolata* and *C. africana*) plus *C. gorungosanum* and *D.*

Figure 6. Comparison of tree seedling species richness and density of tree seedlings (No/m^2) newly germinated in $1m^2$ manipulated gap plots in forest gaps of K-14, K-15 and K-30 after 6 months and 20 months.


X̄ Tree Seedling Spp. Richness
1.5
1.0
0.5
0
X̄ Tree Seedlings /m²
30
20
10
0
K14
K15
K30
KEY
6 Months
20 Months
Q1
Q2
Q3
Q4

mukole. The PRP in K-15 had only four tree seedling species of C. durandii, C. africana, T. guineensis and M. dura. However, only two tree seedling species, C. durandii and D. abyssinica, were more frequent, but in low numbers, in most PRP of the three forest tracts. All PRP quadrants had lost the greater percentage of newly germinated plants, more especially tree seedlings by the twentieth month of experimentation (Fig. 6). For both the six month and 20 month period of observations, there were no newly germinated and established tree seedlings in the quadrants with all vegetation left intact in K-15 gaps. However, by the twentieth month, all PRP quadrants in the forest gaps of K-15 had lost all new tree seedlings established in them during the experimentation (Fig 6). This demonstrated an extremely high mortality of tree seedlings in forest gaps of heavily selectively felled forest relative to gaps in lightly cut or uncut forest tracts.

Mode of Tree Sapling and Pole Regeneration in Gaps

The modes of sapling and pole regeneration (normal growth, coppicing and stem sprouts) were compared within and between gaps in forest tracts which had had different management histories by using ANOVA and Duncan's multiple range test. Within the heavily cut and heavily cut and treated forests (K-15 and K-13) the differences between the mean density of saplings and poles with normal growth, coppices and stem spouts were highly significant ($F=22.55$ and $F=79.08$, respectively, all $P<0.001$). In both plots the

means of coppices were higher than the means of normal growth or stem sprouts (2.0(N),4.2(SS) 9.5(C)) K-15 and 1.9(N),2.9(SS) 19.9(C)K-13, see Table 7, Fig 7). However, the means of normal growth and stem sprouts were similar. For the lightly cut forest (K-14), the differences among the mean density of normal growth, coppices and stem sprouts were significant (F=10.06, P<0.005) and larger mean densities of coppices among the sapling and pole regeneration, relative to normal growths or stem sprouts, were observed (11.5(SS)15(N) 26(C)). In uncut forest gaps as well, the differences among the means of normal, coppices and stems sprouts were significant (F=9.31 P<0.005) and the means of normal and coppices were similar while stem sprouts were low but the three were not separated by Duncan's test (3.96(SS) 8.2(C)8.24(N)).

Between-plot comparisons showed highly significant differences between the means of normal sapling and pole regeneration in the gaps of K-13, K-14, K-15 and K-30 (F=32.36 P<0.001). The ranking of the mean density of normal growth sapling and poles was K-30 > K-14 > K-15 > K-13 (Fig. 7).

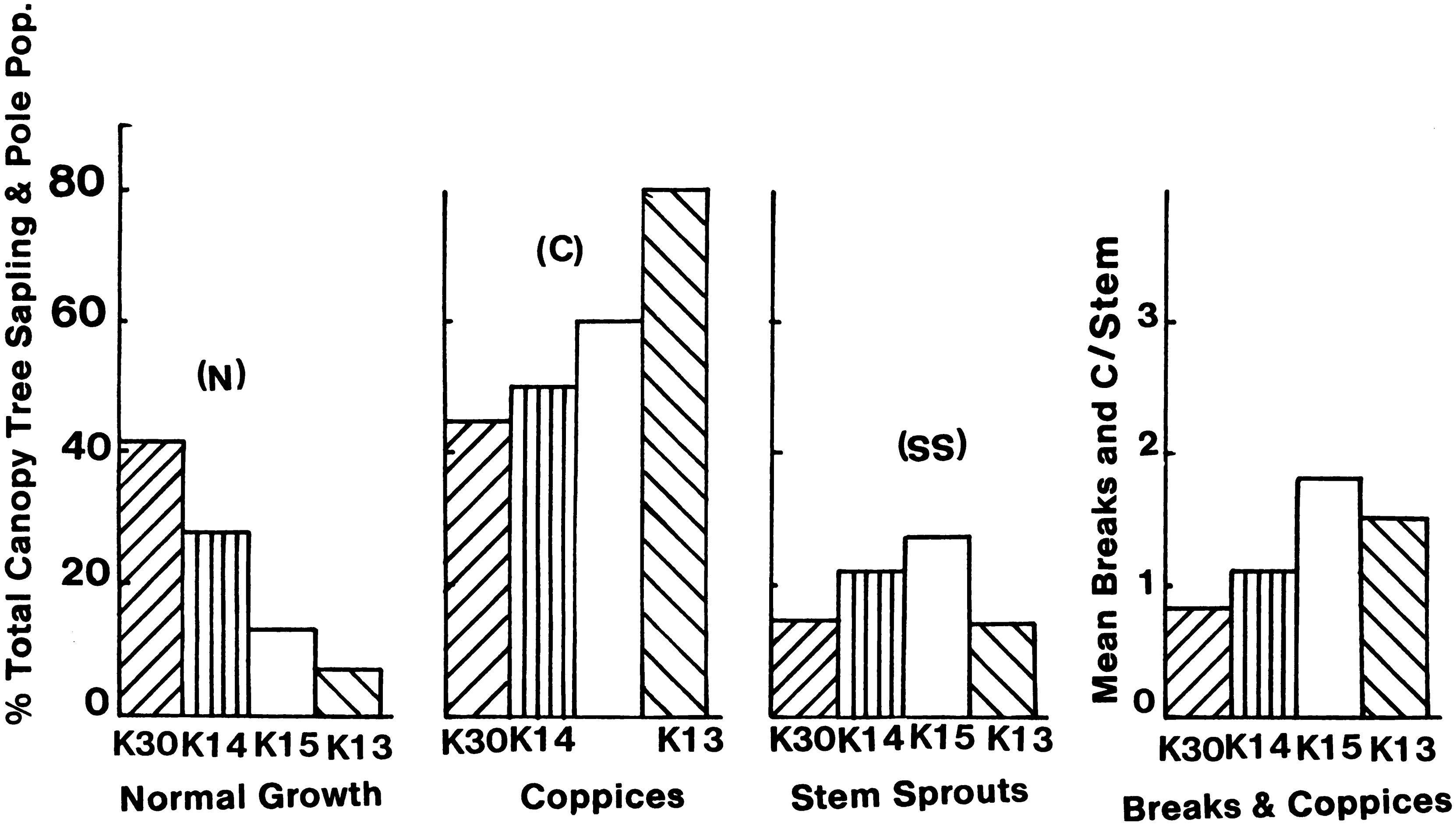
Although the means of coppices in the gaps of K-14 and K-30 looked high (the effect of high sapling and pole densities), the proportions of gap tree sapling and pole regeneration as coppices were lower than in gaps of K-13 and K-15 (Table 7, Fig. 7). However, the gaps in cut forest tracts exhibited higher percentages of tree sapling and pole

Table 7. Mean canopy tree sapling and poles ($>1.5\text{cm}\leq10\text{cm}$ dbh) density (no./ha) per species and percent species population (in brackets) regenerating with normal stems (N), as coppices (C) or as stem sprouts (SS) in the forest gaps of uncut (K-30), lightly cut (K-14) and heavily selectively cut (K-15) and heavily selectively cut and treated forest (K-13) in the reserve.

Study plot	Mean density per species no/ha/sp	Normal growth no/ha/sp	Coppices no/ha/sp	Mean breaks stem no/stem	Stem sprouts no/ha/sp
K-13	24.7	1.9 (7.7)	19.9 (80.6)	1.5	2.9 (13.5)
K-14	53.2	15.0 (28.2)	26.7 (50.2)	1.1	11.5 (21.6)
K-15	15.7	2.0 (12.7)	9.5 (60.5)	1.8	4.2 (26.8)
K-30	71.5	29.9 (41.8)	32.2 (45)	0.8	10.4 (14.5)

no/ha/sp = density per species

Figure 7. Mean percent canopy tree species population of saplings and poles regenerating with normal stems (N), as coppices (C) or as stem sprouts (SS) in the forest gaps of uncut (K-30), lightly cut (K-14), heavily selectively cut (K-15), and heavily selectively cut and treated forest (K-13) in the reserve.


% Total Canopy Tree Sapling & Pole Pop.
0
20
40
60
80
(N)
K30
K14
K15
K13
Normal Growth
(C)
K30
K14
K13
Coppices
(SS)
K30
K14
K15
K13
Stem Sprouts
Mean Breaks and C/Stem
0
1
2
3
K30
K14
K15
K13
Breaks & Coppices

coppices than the gaps in uncut mature forest. Similarly, with the exception of K-13, the gaps in cut forest tracts also had higher percentages of stem sprouts than gaps in uncut mature forest. The low mean of stem sprouts in K-13 gaps was due to lower sapling and pole densities and higher percentages of tree regeneration as coppices.

In summary, the mode of canopy tree sapling and pole regeneration in forest gaps was variable. The gaps in lightly cut and uncut forest tracts had high percentages of normal sapling and pole growth while the regeneration in gaps of heavily cut forests was predominantly coppices. Even the mean number of breaks or snaps per stem followed by successful coppicing was higher for the saplings and poles in selectively cut plots than for uncut mature forest gaps (Fig. 7). However, forest gap regeneration by stem sprouts was small compared to coppices or normal growth saplings and poles but relatively significant in gaps of selectively cut forests.

The seedlings and saplings of most canopy tree species had great potential for coppicing after breaking or snapping. Appendix Table 6 was included to demonstrate the phenomenon of coppicing which was widespread and important in the regeneration of saplings and poles of canopy tree species. However, some canopy tree species seedlings and saplings seemed more prone to breakage or snaps than others but were successful in coppicing. In the gaps of heavily cut forests (K-13 and K-15) canopy tree species of Newtonia, *Lovoa*, *Aningeria*, *Blighia*, *Antiaris*, and *Funtumia*, were high on the list as coppices, with 70% to 90% of their saplings and poles showing signs of breaks or snaps and coppicing. Almost the same species as in K-13 and K-15 were affected in the gaps of lightly cut and uncut forests. However, only a few of their saplings and poles (mean = 51%), relative to K-13 and K-15, had signs of breaks and coppicing. These results seem to indicate frequent gap seedling and sapling disturbances and provide indirect evidence of higher animal usage of larger forest gaps in selectively cut forest relative to the small to medium gaps in uncut forest tracts. Selective browsing by animals may explain why only a few, perhaps preferred, saplings and poles of primary forest species were prone to breaking and coppicing.

DISCUSSION

Natural and Artificial Forest Gaps

The forest gaps studied were heterogeneous in terms of size, configuration and mode of creation, not just "vertical holes" in the forest canopy extending to within 2 meters of the forest floor (as defined by Brokaw, 1982a, 1982b, 1985). In this study, forest gaps were distinguished both by the extent of distribution of light demanding gap vegetation, and gradients of gap light from gap center to surrounding forest some distance inside the forest. Variations in the definitions of forest gaps make comparisons of gap sizes, shapes and frequency somewhat difficult (Brokaw, 1982b). However, some idea of variations in gaps formed in different tropical regions can be achieved.

Most studies have dealt with natural tree fall gaps (Whitmore, 1978; Hartshorn, 1978; Brokaw, 1982a, 1982b, 1985) and important regional differences do occur. In Malaysian forests single tree falls of large canopy individuals may cause gaps of 400 m^2 (Whitmore, 1975, 1978) while mean gap size at La Selva, Costa Rica was only 89 ± 88 m^2 (Hartshorn, 1978). Brokaw (1985) studied gap phase regeneration in tree fall gaps ranging from 20 to 705 m^2 in a tropical moist forest on Barro Colorado Island, Panama.

Larger forest gaps have also been known to result from entanglements by lianas or rare catastrophic events (Whitmore, 1978; Pickett, 1983; Hart, 1986). The most extensive gaps in tropical rain forests occur in the cyclone belts between 10^{o} and 20^{o} North and South of the Equator (Whitmore, 1978) where cyclones can destroy many square kilometers in a single storm.

The mean size of gaps in Malaysian forests is $400m^2$ with a maximum of $600m^2$ formed by trees falling simultaneously (Poore, 1968). Longman and Jenik (1974) reported that liana entangled tree falls could even result in gap areas of 0.5ha. In Cameroon forests, Bullock (1980) reports the mean natural gap size as 400 m^2 where the main tree fall damaged 5.2 to 6.2 adjacent trees of 15 to 25 m tall. In this study the mean gap size for lightly cut forest was $467m^2$ (range 75 to $1800m^2$) and the naturally formed gaps in mature forest averaged $256m^2$ (range 100 to $663m^2$). These were similar to those reported from other tropical forest studies. However, all these were small compared to the mean sizes of gaps created by heavy selective logging. The mean gap size in heavily cut forest was $1307m^2$ (range 73 to $7100m^2$) while that for heavily cut and treated forest was $938m^2$ (range 227 to $3313m^2$). In the reserve, natural tree falls and gap creation were random events well separated in time and space. In contrast, selective logging was systematic, highly selective with respect to tree species and size, and occurred within a short span of time over large areas of forest. Thus, giant forest gaps, unparalleled in the natural tree fall gap size ranges, were created.

In the central forest reserve, the mid slopes of a hilly terrain were richer in desirable timber species (Isabirye-Basuta, 1979; Kasenene, 1980) and were felled the heaviest, leading to a patchwork of regrowth and relatively large remnant forest tracts as was the case in lightly cut forest. In the heavily cut forests, a combination of high desirable tree species richness and predominance of *Olea welwitschii* (a highly prized timber species) in large size classes led to excessive exploitation, almost clear felling.

We have to recall the fact that in the reserve, selective logging was uncontrolled (Skorupa and Kasenene, 1984). The sawmillers cut trees below the recommended girth classes thus leading to extensive destruction of the canopy and forest stand. Clearly, uncontrolled selective logging results in the formation of larger gaps than are ecologically beneficial for forest dynamics (Denslow, 1980). Surprisingly enough, the resultant secondary forest was expected to have naturally recovered and be ready for another cycle of harvesting in only 70 years. However, 20 years later, the forest canopy in heavily selectively felled forests was still wide open, allowing plenty of light into the gaps while adequate regeneration of desirable tree species appears to be in jeopardy.

Sapling and Pole Regeneration Relative to Forest Gap Sizes

Mechanized selective logging resulted in the formation of large forest gaps quite different in size, configuration and mode of formation from the small to medium natural tree fall gaps. The differences between tree sapling and pole regeneration in logged forest gaps and natural gaps could provide useful information regarding the requirements for regeneration of commercially desirable or primary forest tree species (Pickett, 1983; Whitmore, 1975, 1978; Hart, 1986). Thus, forest gap regeneration of saplings and poles in late gap phase-early building phase of the forest growth cycle (Whitmore, 1975; Hartshorn, 1980; Brokaw, 1985) was studied. Whitmore (1978) emphasized that because of the overlap, the three gap phases are only abstractions and not separate entities. However, the gap phase consists mainly of juvenile trees, seedlings and saplings while the building phase is mainly a pole forest which grows into the mature phase of the cycle.

After forest gaps are formed there are four possible modes of revegetation. In the first instance, the seedlings and saplings present in the shaded forest understory, if relatively undamaged by the disturbance, contribute substantially to forest regeneration (Ewel, 1977; Pickett, 1983; Uhl, 1983; Augspurger, 1984; this study). Secondly, the sprouts from cut or crushed stems of seedlings and saplings produce new growth for gap regeneration (Uhl, 1983; this study). Thirdly, plants recolonise the forest gaps by the germination of seeds in the soil, where the majority of seeds may be of pioneer or weed species. Fourthly, the seeds from surrounding forest or distant trees may be dispersed into the gaps for tree regeneration (Richards, 1952; Whitmore, 1975, 1978; Putz, 1983; Augspurger, 1984).

Most studies of tropical forest gaps and forest regeneration, and the results of this study, show that different tree species succeed in gaps of different sizes (Knight, 1974; Hartshorn, 1978, 1980; Whitmore, 1975, 1978; Denslow, 1980; Pickett, 1983). There is also a growing consensus that successful regeneration of many forest trees may actually depend on the combined influences of gap size, gap configuration and mode of gap formation (Whitmore, 1975, 1978; Hartshorn, 1978; Denslow, 1980; Pickett, 1983; this study). The strongly inverse relationship between gap-size or intensity of forest exploitation and the species richness and density of saplings and poles, for all tree species in general and desirable tree species in particular, seems to support this view.

As this study indicates, small to medium forest gaps caused by natural tree falls have been observed to favor the growth and success of seedlings and saplings of advance regeneration or suppressed juveniles of primary forest species in the understory (Richards, 1964; Knight, 1974; Hartshorn, 1978; Whitmore, 1975, 1978; Gomez-Pompa et al. 1972). However, in very large gaps, advance regeneration may often respond with reduced growth and eventual death

(Richards, 1964; Burgess, 1970; Meijer, 1970; Liew and Wong, 1973; Whitmore, 1975, 1978; Sousa, 1984; this study), while pioneer plants invade and grow vigorously (Eggeling, 1947; Meijer, 1970; Whitmore, 1975, 1978, 1980; Synnott, 1975; Ewel, 1980; Putz, 1983; Brokaw, 1985). Brokaw (1982b, 1985), while studying gap phase regeneration on Barro Colorado Island, Panama, observed dramatic shifts in density and heavy mortality of primary forest seedling and sapling species in forest gaps >150m^2. Whitmore (1975, 1978), observed successful growth of surviving individuals of primary forest tree species in artificially generated gaps of 0.1ha while they were suppressed by lush growth of secondary forest pioneers in 0.2 to 0.3ha gaps.

Other studies too have indicated significant reductions in species diversity of seedlings and saplings following selective forest felling operations and point to post felling stress and/or ecological instability as the major cause (Westhoof, 1971; Poore, 1976; Herbert and Beveridge, 1977; Odum, 1985). It is not fully understood as to which gap conditions stimulate the seedlings and saplings of canopy tree species to commence and continue growth upwards (Whitmore, 1975, 1978; Pickett, 1983). These conditions are believed to vary from species to species (Lugo, 1970; Sousa, 1984; Marquis _et_ _al._, 1986) or even for single species at different stages of development.

For the majority of forest gaps, including those in this study, the principal environmental change that could

easily influence seedlings and sapling regeneration was alteration of the radiation balance (Whitmore, 1975, 1978; Pickett, 1983; Lee, 1978, 1987). This has also been shown to initiate changes in a number of related factors embracing the physical, chemical and biological environments important for gap seedling and sapling regeneration (Armson _et al._, 1973; Whitmore, 1978; Bullock, 1980 and Putz, 1983). Amounts of daylight reaching into the closed tropical forest have been estimated at 2% of ambient light (Pickett, 1983) and large forest gaps receive between 50 and 100% of ambient daylight. In addition, the duration of insolation, which is variable for the small and large gaps, may also influence forest gap tree regeneration. Usually, small forest gaps caused by natural tree falls are directly insolated for approximately 2hrs per day compared to 6 or 8hrs for large clearings (Pickett, 1983; Lee, 1978, 1987).

Generally, the seedlings and saplings of primary forest species prefer natural habitats of low light conditions and have adaptive traits for prolonged suppression and recovery after a gap is created above them (Richards 1952, 1964; Gomez-Pompa _et al._, 1972; Whitmore, 1975, 1978; Pickett, 1983). Gap creation increases the availability of resources, including light which stimulates increased performance of either advance regeneration or pioneer and weed species depending on the size of the gap (Whitmore, 1978; Pickett, 1983). Therefore, the fact that shade tolerant species require optimal light intensities for growth and survival and that the optimas differ among species (Lugo, 1970; Augspurger, 1984; Sousa, 1984; Marquis _et al._, 1986) may partly explain the reduced seedling, sapling and pole regeneration in large gaps relative to small or medium gaps. The majority of seedlings and saplings of the logged desirable or primary forest species do not usually find large forest gaps characteristic of mechanised selective logging suitable for their own regeneration (Whitmore, 1975, 1978; Sousa, 1984; Uhl and Buschbacher, 1985; this study). The extremely low seedling, sapling and pole regeneration, in terms of species richness, density and number of individuals per species, for all tree species in large gaps but abundant regeneration of the same species in forest plots adjacent to the gaps, strongly supports the preceding observations.

Differential logging intensities and associated forest disturbances and arboricide treatments might also account for the low regeneration potential, especially in the gaps of heavily selectively cut forest. During mechanized selective felling, sawmillers in Uganda usually cut most potentially harvestable trees, felling many more than are actually harvested (Skorupa and Kasenene, 1984). Excessive felling of large trees alone directly affects the would-be advance regeneration through crushes and burial of seedlings and saplings in debris. Subsequently, bulldozers usually follow, smothering and killing many seedlings and saplings during the hauling of logs to extraction roads (Kasenene, 1980; Struhsaker, pers. comm.). Several factors interact and make mechanized selective logging more destructive than it was designed to be. It is clear that the heavily felled forest tracts suffered the greatest disturbance and damage, still reflected in extremely low levels of forest gap regeneration 20 years later.

Furthermore, the poor correlations between gap size and tree seedling, sapling and pole regeneration in gaps of heavily felled and treated forest could suggest the compounded effect of gap size, intensity of disturbance and arboricide treatment. The magnitude of the differences in forest tree regeneration in gaps of similar sizes in two heavily cut forests, where one of them had post felling chemical treatment to kill "weed trees", were too big to be explained by natural variation only. The post felling chemical treatments with arboricide could account for most of the 37.6% depression of tree sapling and pole species in treated forest gaps, relative to heavily cut but untreated forest gaps. In concert with the predictions, the small to medium gaps in unlogged mature forest had the highest regeneration of tree seedlings, saplings and poles, while the gaps in lightly cut forest were ranked second. The level of tree seedling, sapling and pole regeneration in the large forest gaps of heavily selectively cut forest were ranked third and those in heavily felled and treated forest a distant fourth. These findings were not unique to this study. During an ecosystem recovery study in Amazonia, Uhl

et al., (1985) also observed that increased intensity of forest disturbance changed the early vegetation succession from primary forest tree species (cut treatment) to successional woody species (cut and burned treatment) and to forbs and grasses (cut and bulldozed treatment).

The low potential regeneration of desirable or canopy tree species in large gaps has occasionally been blamed on lack of adequate seed populations dispersed to the gaps (Brasnett, 1946; Eggeling, 1947; Synnott, 1975 and this study). Selective logging usually removes most seed bearing trees, and leftovers of overmature and defective individuals of desirable species which would otherwise provide seeds are commonly frilled, poisoned and killed to help forest regeneration (Forest Dept. Records, F/P). This so called "refining" process might have contributed to serious reductions in the local seed supply, thus resulting in low potential for desirable tree species regeneration, especially in gaps of heavily selectively felled forest sites.

Although the recommended level of reduction of forest canopy during selective felling lies between 40 and 50% (Kingston, 1967; Uhl et al., 1985), more extensive reductions often occur because of the problems already cited. Consequently, high light intensities reach into the forest and gaps and encourage the growth and development of a dense tangle of herbs, climbers and non-woody shrubs. The strongly inverse relationship between the dense gap ground story growth and the tree seedling and sapling regeneration suggests strong competition and suppression of tree regeneration by weeds. Earlier studies by Brasnett, (1946), and Synnott (1975) in Budongo forest, Uganda, also showed that the thick ground-vegetation cover that normally follows forest felling was extremely inhibitory to successful tree regeneration. They suggested strong competition for light between the juvenile trees and the thick vegetation cover, root competition for space and nutrients, and actual physical damage of climbers and lianas (also Putz, 1984), to be contributing to reduced regeneration of trees in major forest gaps. The whole method of mechanized selective timber harvesting, if uncontrolled and carelessly carried out as has always been the case in Ugandan forest, can be extremely damaging to the species-rich tropical forest. It has the potential to impoverish and degrade the species composition and spatial arrangements of future secondary forest communities.

The Ideal Gap Size

In the reserve 100% of the forest gaps formed by natural tree falls and 83% of those formed by light forest cutting were between 75 m^2 and 700 m^2 in area. The mean gap size in lightly cut forest (467 m^2), and the gap size range of naturally formed gaps in mature forest (100-663 m^2), were similar to commonly formed natural gaps in tropical forests of other regions (Whitmore, 1975, 1978; Poore, 1968; Hartshorn, 1978; Brokaw, 1985). In contrast, a

lower percentage of forest gaps formed by heavy selective felling (40% in K-15 and 47% in K-13) fell within the same gap size range as natural tree fall gaps; the larger percentage (60% in K-15 and 53% in K-13) were over 700 m^2.

The gap sizes with the highest tree sapling and pole regeneration in terms of species richness, density and number of individuals per species for uncut, lightly cut and heavily cut forest tracts were all below 650 m^2 in size. Tree seedling, sapling and pole regeneration for all species and desirable or primary forest species was low and followed a downward trend in forest gaps exceeding 650 m^2. Therefore, for the reserve, forest gaps between 500 m^2 and 600 m^2 seem to form the upper limits of forest gap sizes where after a disturbance, successful regeneration of trees including the desirable timber or primary forest species could be expected naturally. Therefore, if a maximum of four distantly located canopy trees are to be selectively harvested per hectare of forest, then the total gap area created by felling should never exceed 2400 m^2/ha. This also implies that four adjacent mature trees should never be felled at the same time in the same felling cycle, in order to avoid the detrimental effects of large gaps on forest regeneration.

In earlier studies, timber extraction through strictly controlled polycyclic systems that create 3 to 6 canopy gaps per hectare have been found almost akin to natural tree fall disturbance and result in the formation of small gaps in the

forest canopy (Whitmore, 1975; Herbert and Beveridge, 1977; Uhl et al., 1985) and the damage done to the forest is relatively minor. In the lightly cut forest, removal of 3 to 5 canopy trees per hectare seems to have had little effect on natural forest regeneration. The lightly cut and uncut mature forest tracts of the reserve have approximately 3 to 4 dead-standing canopy trees/ha. The removal of four canopy trees/ha may also resemble natural tree death, and result in the formation of small gaps in the forest canopy and minor damage to the forest. Previously established seedlings and saplings of primary forest species have often been observed to grow to maturity in small to medium sized natural forest gaps where weedy species are naturally excluded (Richards, 1964; Knight, 1974; Hartshorn, 1978; Whitmore, 1978; Pickett, 1983 and Brokaw, 1985).

Herbivory and Seed Predation in Forest Gaps

Compared to temperate forests, tropical evergreen or semi-deciduous forests do not provide strong, regular seasonal pulses of resources (Muller, 1978) and forest gaps might provide important although partially unpredictable pulses (Pickett, 1983). Therefore, forest gaps might attract animals which interact either positively or negatively with gap plant regeneration (Wing and Buss, 1970; Janzen, 1970, 1971; Evans, 1974; Kasenene, 1980; Pickett, 1983; and this study). The luxuriant ground vegetation that normally follows heavy selective logging provides palatable fodder, cover, and ideal nesting sites for animals and insects (Wing and Buss, 1970; Isabirye-Basuta, 1979; Kasenene, 1980, 1984; Merz, 1983; Short, 1983). Evans (1974) has shown that insect populations usually increase in forests which have been degraded and left to regenerate naturally. Insects are known to damage substantial amounts of seeds both in pre and post dispersal condition (Janzen, 1971). Although insect damage to forest tree seeds and seedlings is not easily discernible, Janzen (1970, 1971), Synnott (1975), Bradford et al. (1977) and Flowerdew and Gardner (1978) have demonstrated that insects can destroy significant amounts of seeds in a single seed crop. Insects are ubiquitous, highly diverse in food habits and several magnitudes greater in population density than any of the common mammalian seed predators (Orians et al., 1974; Struhsaker, and Matti-Nummelin, pers. comm.).

Like insects, forest rodents are also ubiquitous and can sustain high population densities in modified forest environments (Delany, 1971; Fleming, 1975; Jeffrey, 1977; Isabirye-Basuta, 1979; Kasenene, 1980, 1984). Modification of primary forest by felling has often been associated with drastic increases in small rodent diversity, population densities and biomass (Delany, 1971; Jeffrey, 1977; Isabirye-Basuta, 1979; Kasenene, 1980). Associated rodent increases vary with the type and degree of modification of the primary forest (Delany, 1971; Jeffrey, 1977) and extensive changes in forest ecology following felling are presumed to be responsible for the changes in rodent population dynamics. As in Delany (1971) and Synnott (1975), earlier studies by the author (Kasenene, 1980, 1984) and Isabirye-Basuta (1979) on rodent ecology and biology in the Kibale forest also show that heavily selectively felled and regenerating forests support higher rodent species diversity and density than lightly cut and uncut forest tracts. Earlier studies in the reserve (Isabirye-Basuta, 1979; Kasenene, 1980, 1984) and those of Delany (1975), Fleming (1975), and Synnott (1975) clearly demonstrated that most rodent species were ecologically important forest seed as well as young seedling predators. Seedlings were selectively browsed and young seedlings with cotyledons still attached were more susceptible to rodent predation and more easily killed than other seedlings (Kasenene, 1980, 1984).

The results of this study and several previous studies (Janzen, 1970, 1971; Delany, 1971; Synnott, 1975, 1977; Field, 1975; Bradford et al., 1977; Isabirye-Basuta, 1979; Kasenene, 1984) emphasize the economic and ecological importance of rodent seed predation with regard to forest regeneration. Synnott (1975) observed very high mortality rates among the seeds and seedlings of Entandrophragma utile due to predation by rodents. Bradford et al. (1977); also found that rodents could very easily damage 75% of Scheelea palm seeds in a single seed crop. Flowerdew et al. (1978) attributed the major portion (75%) of the loss of Ash seeds prior to germination to small rodents. The preliminary

results of the forest gap seed pile predation trials strongly suggest that rodent seed predation can be more significant in the large gaps of the heavily selectively felled forests than in the small to medium gaps in uncut or lightly cut forests. Where heavy timber exploitation has occurred, the seed supplies and seed populations of desirable tree species could be locally inadequate (Synnott, 1975). Therefore the characteristic increases in rodent populations and density (due to invasion and multiplication of colonizing species) following felling might drastically decrease the seed and seedling populations, thus limiting adequate natural regeneration. However, several factors including seed pile size, seed chemical defense, presence of other preferred foods and season of seed placement might have also influenced the results and rates of seed predation in forest gaps (Janzen, 1978; Wilson and Janzen, 1972, Ng 1978, Kasenene, 1980).

Very few studies have focused on the influence of big game on the composition, structure and regeneration of tropical forests. In the Ituri forest of Zaire (Hart, 1986), the large forest gaps were frequently visited by Okapi (*Okapia johnsoni*) and none of the marked pioneer seedlings were present after two years of observation. In a large scale survey of the Kibale forest, Uganda, Osmaston (1959a) and Wing and Buss (1970) found no significant effect of big game such as elephants (*Loxodonta africana* Blumenbach) on the forest structure and composition.

However, the studies of Short (1983) and Merz (1986) in West African forests show that big game, including elephants, prefer secondary forests and/or forest gaps (Hart, 1986) to undisturbed mature forests. All these observations agree with the preliminary findings of this study and my earlier observations (Kasenene, 1980, 1984). It is probable that the luxuriant ground vegetation that develops following forest exploitation provides attractive and palatable fodder for the elephants for they frequent and browse in large forest gaps more often than in small tree fall gaps in mature forest (Kasenene, 1980, 1984, this study).

Eggeling (1947) found that elephants could be a limiting factor in the natural development of vegetation wherever they occur in big numbers. While browsing, they destroy woody plants in the seedling, sapling and even pole stage by a combination of methods including trampling, defoliation, topping, uprooting and barking (Eggeling, 1947; Kasenene, 1984; this study). Therefore, elephants can be important ecological pests of regeneration areas. Their frequent incursions into secondary forests and gaps encourage the perpetuation of the herbaceous tangle "Elephant climax" (Wing and Buss, 1970) where juvenile trees are smothered by climbers and sometimes killed, thus impeding forest regeneration. Therefore, the economic and ecological importance of browsers such as elephants on the forests should be assessed with respect to specific interactions with forest regeneration and consideration of

all discernible forms of animal damage to trees. In the case of elephants, we should also note that intensity of utilization of forest varies with the degree of modification or disturbance of the primary forest.

The large forest gaps in heavily selectively felled forests were preferred and more frequently used by elephants than small to medium size gaps in lightly cut or uncut forest tracts. This implies that the impact of elephants on forest gap regeneration could be controlled if the methods of forest exploitation were controlled to create small to medium gaps. After all, in addition to fertilizing the forests with dung-manure, elephants form an indispensable forest component as large seed dispersers. However, my data on herbivory and seed predation in forest gaps are still limited and fragmentary and pose many problems, but I feel they demonstrate the potential impacts animals can have on large forest gap regeneration and emphasize the need for long term research.

Sources of Plant Recruitment into Forest Gaps

In the study of soil seed banks, germination is usually selected for evaluation of soil seed crop instead of direct counts and identification of seeds in the soil which are extremely tenuous and difficult (Guevara & Gomez-Pompa, 1972). The raised and screened germination stand or house used in this study was meant to protect the soil samples from seed contamination and seed and seedling predation. Earlier studies and the results of this study all indicate

the presence of significant dormant seed pools beneath tropical mature forests (Gomez-Pompa et al., 1972; Guevara and Gomez-Pompa, 1972; Harcombe, 1977; Ewel et al., 1981; Pickett, 1983; and Young, 1985, among others). The number of seeds stored in the soil often referred to as seedcrop, seedpool, seedbanks or floristic potential (Guevara and Gomez-Pompa, 1972; Pickett, 1983), are an important factor in the initiation of secondary succession after forest clearance (Guevara and Gomez-Pompa, 1972; Augspurger, 1984; Young, 1985). However, the results of most studies, including this one, clearly show that by far the most important floristic components of the soil seed banks are large-gap (pioneer, weed or secondary) species (Guevara and Gomez-Pompa, 1972; Ewel et al., 1981; Pickett, 1983).

It is difficult to compare the populations of viable seeds in tropical forest soils from the same or different regions, for there are no standard experimental procedures (Ewel, 1981; Young, 1985). Most often, the germination experiments by different researchers have involved different numbers and sizes of samples, different durations of germination trials, and most importantly, different soil sample depths (Table 8). However, the results clearly suggest that soil seed banks of different tropical forests were highly variable in plant species richness (Table 8). Again, the soil seed banks of forests which had had some forms of human disturbance had even higher species richness than those under mature forest. But where there had been

Table 8 Comparison of soil seed germination results for some tropical rain forests.

Location	Forest type	Depth (cm)	No. of spp.	Seeds/ m^2	Reference
Mexico	High evergreen	0-12 0-12	26 13	344-862 175-689	Guevara & Gomez-Pompa 1972
Panama	Tropical	0-10	48	742	Putz 1983
Nigeria	Tropical moist	0-6.3 0-6.3	17 32	128 211	Keay 1960.
Ghana	Moist-semi deciduous	0-4	30	633	Hall & Swaine 1980
Ghana	Dry-semi decidious	0-4	43	696	1980
Costa Rica	Humid Secondary Forest	Surface	67	8000	Ewel *et al.* 1981
	+ mulching	Surface	51	6000	1981
	+ burning	Surface	37	3000	1981
Uganda	High altitude tropical moist	0-10	22	204	This study
	Lightly felled	0-10	23	310	This study
	Heavily felled	0-10	33	299	This study
	Forest Gaps.				
	Mature forest	0-10	9	311	This study
	Lightly felled	0-10	11	512	This study
	Heavily felled	0-10	15	767	This study

maximum forest disturbance, both natural and artificial, e.g. in forest gaps, the soil seed banks were extremely impoverished in species richness compared to those under mature or secondary forest. However, the low species richness in the gaps is compensated for by high population densities.

As with species richness, the mean number of seeds germinated from soils sampled from beneath the forests were also variable for the different tropical areas. Soil samples from tropical second growth forest and agricultural areas had generally higher numbers of viable seeds than soils from mature forest sites. However, all the values of number of viable seeds/m^2 indicated in the table were considerably lower than the value reported from 3-year-old vegetation on abandoned farm land in the Everglades of south Florida, 30,125 seeds/m^2 (Ewel and Conde, 1979). Their average values for the mature communities were also high, ranging from 500 to 6000 seeds/m^2. These observations therefore suggest that the dormant seeds in the soil seed banks under forest conditions germinate in response to improved resources in the gaps. However, most of the germinated plant species are survived by only a few which successfully establish themselves in the gaps. And the gap soil seed banks continue to be under heavier seed rain, mainly from the few gap species that almost exclusively establish themselves in the new sites or gaps.

In the Kibale the preceding observations were strongly supported by the preponderance of herbaceous plants, vines and climbers, and non-woody shrubs that germinated from the surface soils of manipulated plots located within the forest gaps. The contribution by incoming dispersal to large gap tree seedling and sapling recruitment was very small and extremely lacking in seeds of primary forest species. It seemed that only a few secondary forest trees on the periphery of the gaps were able to disperse their seeds into the gap plots although only a few seeds actually germinated and contributed to the seedling pools in the manipulated plots. However, for the whole 20-month period of observation, no new tree seedlings were observed to germinate and establish in the gap plots with all vegetation left intact. Again, the tree seedlings that were able to germinate in the forest gap plots with vegetation removed, vegetation and top soil removed, and previously screened plots with screens removed six months later, did not survive 20 months of observation. Clearly these observations suggest high seed and seedling mortality, which could have been caused by predation or over exposure to high insolation in large forest gaps. Furthermore, the dense gap vegetation of herbs, shrubs, vines and climbers competitively excludes or suppresses the germination and establishment of all tree species including pioneer, secondary and primary forest species.

The most striking observation about all soil seed banks for different tropical rainforests, including those from the reserve, was the lack of primary forest or canopy tree species (Guevara and Gomez-Pompa, 1972; Ewel et al., 1981; Pickett, 1983; Augspurger, 1984). It is believed that lack of seed dormancy among most primary forest species causes them to germinate within a few weeks of shedding (Whitmore, 1975, 1978; Ng, 1978), and this accounts for their scarcity in forest soil seed banks. However, under certain circumstances, this quick germination is advantageous in ensuring survival power of such species through avoidance of seed predation and fungal attack (Gomez-Pompa et al., 1972). Again, a combination of other factors, including temporal variation in fruiting behavior (e.g. Whitmore, 1975), low seed population, and large seed size (relatively inefficient for dispersal) could have made some primary forest species unavailable for large forest gaps, especially where forest exploitation selected for particular prime species.

The failure of primary forest tree species to invade and regenerate in large forest disturbances in the Ituri forest of Zaire (Hart, 1986) also suggested several controlling factors. Hart (1986) found that even after 40 years of abandonment, the seedlings of shade tolerant dominants from mature forest had not invaded the secondary growth and abandoned garden sites, although the remnant mother trees were no more than several meters away. It is inevitable that primary forest species build up seedling and

sapling populations within the shaded understory until gaps are formed, allowing further growth (Pickett, 1983; Augspurger, 1984; this study). Therefore, the importance of seed dormancy and seed banks in forest regeneration after a large disturbance is primarily restricted to pioneers or large-gap species while the regeneration of small gap or primary forest species is mainly by suppressed seedling and sapling pools in the shaded forest understory.

In the reserve, the majority of seedlings and saplings of canopy tree species that were regenerating in the forest gaps were also found in the understory of adjacent forest tracts. This further supports earlier observations that non-pioneering primary forest species were limited to suppressed seedlings as the primary mode of regeneration after major disturbances. However, these seedlings and saplings suffered great stem damage, probably during gap formation, and were subject to even more damaging episodes after gap formation.

The majority of canopy tree seedlings, saplings and poles in large forest gaps were classed as coppices because they had had several well spaced stem breaks or snaps and successful coppicing. The higher frequency of well spaced stem breaks and coppicing for seedlings and saplings in forest gaps than in adjacent forest understory suggested frequent episodes of forest gap seedling and sapling disturbance. The seedlings and saplings in large forest gaps were more susceptible to damage, most of which could be attributed to frequent tree and branch falls into the gaps or animal browsing.

However, the most important observation was that the majority of seedlings and saplings of desirable timber or primary forest species, in the tropical moist forest studied, demonstrated great ability to recover by stem coppices or sprouts after a disturbance and injury. Therefore, the low populations of seedlings and saplings of primary forest tree species in large forest gaps suggest their inability to survive in extremely open gap conditions, poor competition with the aggressive weeds that take over the gaps, or destruction through severe damage, such as complete defoliation and barking or uprooting. Thus the results of soil seed bank studies and the observed mode of tree seedling and sapling regeneration all indicate that a primary forest cannot be restored if all trees from adjacent areas are destroyed. If it is absolutely necessary to harvest a forest, protection of suppressed seedlings and saplings of primary forest species should be given priority for the successful regeneration of the desirable tree species in the secondary forest.

SUMMARY

In Uganda, the three major threats to the integrity of tropical forest resources include agricultural encroachment, uncontrolled timber exploitation, and rampant poaching of game. However, this study concentrated on the influence of mechanized selective felling on the development of forest gaps and the consequent ecological effects of gaps, on the regeneration of tree species.

A total of 40 randomly selected gaps were examined in each of the four forest compartments comprising the uncut mature forest (K-30), lightly cut forest (K-14), heavily felled forest (K-15), and heavily felled and treated forest (K-13). In selectively felled forest, gaps with cut tree stumps and/or waste tree trunks were studied, while in mature forest, gaps which had tree or big branch falls and characteristic gap vegetation of size ranges (height and dbh.) similar to that in selectively cut forest gaps were considered. Since it had been almost 20 years since felling, the majority of forest gaps selected were in the late gap phase-early building phase stage of gap succession, characterized mainly by tree seedlings, saplings and poles.

The mean gap size for lightly cut forest was 467 m^2 (range 75 to 1800 m^2) and the natural tree fall gaps in

mature forest averaged 256 m^2 (range 100 to 663 m^2). The mean gap size in heavily cut forest was 1307 m^2 (range 73 to 7100 m^2) while that for heavily felled and treated forest was 938 m^2 (range 227 to 3313 m^2). An attempt was made to sample 40% of each gap area. All tree saplings and poles encountered within a 5m wide belt transect following the cut access trails were enumerated, measured (dbh), and identified to species level and mode of origin (coppices, stem sprouts or normally growing). The influence of herbivory on forest gap tree regeneration was assessed from monthly recordings of animal incursions and the nature of associated damage (e.g. trampling, browsing of tree seedlings, saplings and poles). Seed predation trials were also run for some primary forest tree species to test the fate of seeds that come into the forest gaps through dispersal. Finally, other potential sources of recruitment into forest gaps, including soil seed banks, were examined by soil seed germination experiments in protected nursery beds.

Multiple tree removals during selective felling and consequent wind and storm throws in felled forests resulted in the formation of gaps larger than the small to medium gaps characteristics of natural tree falls. All forest gaps created by natural tree falls and 83% of those produced by light forest cutting ranged between 75 and 700 m^2 in size. These were similar in size to most commonly formed natural gaps observed in other forests in different tropical regions. However, only a small percentage of forest gaps formed by heavy selective felling (40% and 47% in K-15 and K-13, respectively) were within the natural tree fall gap size range while 53 to 60% included large gaps greater than 800 m^2.

Success of tree seedling and sapling regeneration was inversely related to gap size. Tree seedling, sapling and pole regeneration was high in gap sizes below 650 m^2 but extremely low, impoverished or suppressed in forest gaps greater than 650 m^2. Consequently, the large forest gaps that resulted from heavy selective felling and associated disturbances had the poorest levels of regeneration of tree species.

However, gap size alone did not seem to account for the extremely low regeneration of tree species in the extensive gaps from heavy selective logging. Heavy logging definitely changed the structure and composition of the mature forest through the removal of most primary forest and large seed bearing trees. Logging intensity was related to degree of physical damage and disturbance to suppressed seedling and saplings in the forest understory. The post harvest chemical treatments and resultant deaths of treated non-commercial and overmature, or defective primary forest trees also seem to have contributed significantly to reduced gap regeneration of all tree species and primary forest species in particular. It has not been ascertained whether the arboricide mixture used in spraying (3% Finopal D/T, i.e.

0.5 liter of Finopal D/T per 18 liters of diesel) was species specific or easily biologically degradable. Other factors germane to heavy selective felling, such as dense gap ground vegetation cover, rodent seed predation, and destructive browsing by big game, may have played a larger role in the reduction of tree regeneration in large forest gaps than in small to medium natural tree fall gaps.

The soil seed banks from underneath the forest canopy and in forest gaps in cut and uncut forests were dominated by large-gap plants, including pioneer, herbaceous, shrub, and vine species. Of the seedlings germinated from forest soils of K-14, K-15 and K-30, only 10.3%, 9.3% and 16% were of tree species while herbaceous plants formed 80.4%, 71.2% and 53.1%, respectively. The density of the sprouted seedlings followed the same trend. For the gap soil seed banks in K-14, K-15, and K-30, tree species formed 11.9%, 8.9% and 17.7% of the germinated seedling species, respectively. The density of the sprouted tree seedlings in K-14, K-15 and K-30 soils formed only 0.3%, 0.3% and 4.9%, respectively, and the herbaceous plants constituted the largest remaining percentages. Except for _C. africana_ and _C. millenii_, which germinated from the forest soil seed banks and _M. bagshawei_ and _A. toxicaria_ in the manipulated gap plots in K-30 only, the majority of tree seedling species which sprouted from the forest and gap soil seed banks belonged to a few non-desirable secondary forest species. The seeds of the only clearly defined gap

specialist and pioneer tree species in the reserve, *Trema guineensis*, were well represented in both forest and gap soil seed banks. The only predictable mode of successful regeneration of desirable timber or primary forest species after felling disturbance was the release of suppressed seedlings and sapling pools in the forest understory.

CONCLUSIONS

When carried out with great care, creating on the average 2 to 4 canopy gaps/ha, selective tree harvesting could be a minor disturbance, akin to natural tree falls which are an important component of the tropical forest dynamics. The disturbances associated with selective felling are supposed to be moderate enough to open a gap but not so much that the suppressed understory tree seedlings and saplings are killed. However, respect for the recommendations for logging and careful logging practices are the exception in tropical rain forests. Thus, mechanised felling in species rich, and uneven growth, tropical moist forest is incompatible with minimizing damage. Large forest gaps of a size that hinder the regeneration of most desired or primary forest species are created. Available evidence suggests that mechanized selective timber harvesting has detrimental effects on tropical forest ecosystems by causing major disturbances and destruction that lead to serious reductions in diversity of tree species, including the desirable timber or canopy tree species, and even the herbaceous and non-woody shrubs. The following list includes a few consequences of uncontrolled selective logging:

- drastic changes in the structure and composition of the mature forest;
- extensive destruction and reduction of the forest canopy;
- intensive and extensive forest disturbances;
- increased tree mortality through windthrows and widening of gaps;
- formations of unnaturally large forest gaps;
- increased daylight penetration, intensity and duration in the forest gaps;
- development of dense and persistent gap vegetation composed of herbs, shrubs, vines and climbers;
- intense competition between gap vegetation and tree seedlings and saplings;
- increased seed and seedling predation, mostly by rodents;
- increased frequency of gap utilization by browsers thus causing sapling destruction;
- reduced tree and pole species diversity;
- reduced tree seedling and sapling species diversity;
- impoverished forest regeneration in general; and
- very low regeneration of desirable timber or primary forest species.

These responses seem to be gradually jeopardizing the structure, condition, stability and appearance of the residual secondary forest community. Twenty years after the felling operations, there appears to be no positive sign of

recolonization of the large forest gaps by primary forest species. The gaps are open, densely covered with herbs, vines and climbers and non-woody and woody shrubs and are thus still subject to frequent disturbances by browsers. In the most heavily exploited areas of the reserve it appears very unlikely that another harvest of valuable timber species could take place, as previously anticipated (Kingston, 1967), 70 years from the last forest harvest. This makes uncertain the very first management objective of establishing the forest reserve, i.e. to realize maximum economic, sustained production of natural hardwood timber. The time required for degraded forests to recover varies depending on the intensity of disturbance, and most studies (e.g. Uhl et al. 1982, 1985) suggest very long periods stretching from hundreds to thousands of years. Therefore, the prognosis is that in the Kibale tropical moist forest reserve, extremely long periods of time, longer than the proposed 70 years of the harvest cycle, will be required for anything resembling a forest worthy of exploitation to reappear, after large, high intensity disturbances.

Therefore, whenever it is necessary to harvest the forest reserve or any other forest, more effort should be put into minimizing the impact of exploitation to reduce the need for intensive silviculture to ensure future timber harvests. The methods employed in the exploitation of species-rich tropical moist forest should emphasize low disturbance levels where small to medium forest gaps are created. This will partially ensure protection of the suppressed seedling and sapling pools of the primary forest species and enhance the successful natural regeneration of the desirable timber species in the secondary forest. Since mechanized timber exploitation is incompatible with minimizing destruction and disturbances in species-rich tropical forests, it should be discouraged. Pitsawing and other forms of polycyclic felling systems that are more labor intensive than machine-based systems, and which would create small to medium gaps akin to natural tree falls, could if properly controlled be very compatible with long term sustained yield timber exploitation. Meanwhile, a modified form of the polycyclic felling system, slightly more advanced than pitsawing, should be studied and developed. The basis for forest exploitation should be to create forest gaps of a size that favor the growth and development of desirable timber or primary forest species without creating the need for intensive post felling silvicultural treatments. Such treatments would be costly, and their implementation uncertain, due to the usual lack of capital and adequately trained and interested man power.

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Appendix

Table 1. Size-class distribution of 40 randomly selected gaps and the distribution of saplings (sa) and poles (P) ($\geq$1.5cm <10cm dbh) in the gaps of heavily selectively cut and treated forest (K-13).

Gap-Size-Classes m^2	50- 200	200- 400	400- 600	600- 800	800- 1000	1000- 1200	1200- 1400	- -	- -	1800 2000	- -	2200 2400	2400 2600	>2600
No. of Gaps	0	2	14	6	6	4	3	0	0	2	0	-	-	-
$\bar{X}$ tree sp. richness	0	7	8.8	7.7	7.7	11	16	0	0	15	0	12	13	4
$\bar{X}$ desirable spp richness	0	4.5	4.0	3.3	3.5	6.8	6	0	0	6	0	6	9	3
$\bar{X}$ Sa/P density #/ha	0	497.1	469.3	323	365.8	406.7	580.5	0	0	321.5	0	433.7	687.7	87.7
$\bar{X}$ desirable sa/p density (#/ha)	0	313.2	234.2	182.6	204.7	254.3	306.1	0	0	178.6	0	268.5	491.2	70.2
Sa/P. density/ species	0	71.0	53.3	41.9	47.5	37.0	36.3	0	0	21.4	0	36.1	52.9	21.9
Desirable Sa/p density/species	0	69.6	58.6	55.3	58.5	37.4	51.0	0	0	29.8	0	44.8	54.6	23.4
% ground veg. cover	0	83	82	89	86	78	78	0	0	90	0	90	60	90

Appendix

Table 2. Size-class distribution of 40 randomly selected gaps and the distribution of saplings (Sa) and poles (P) ($\geq$1.5cm <10cm dbh) in the gaps of lighthly selectively cut forest (K-14).

Gap-Size-Classes m^2	50- 200	200- 400	400- 600	600- 800	800- 1000	1000- 1200	1200- 1400	1400- 1600	1600 1800
No. of Gaps	8	13	10	5	2	0	0	1	1
$\bar{X}$ tree sp. richness	25.3	23.8	19.5	24.6	11.5	0	0	17	22
$\bar{X}$ desirable tree spp. richness	8.2	7.8	7.1	8.4	7.0	0	0	8	9
$\bar{X}$ Sa/P density #/ha	6397	2976	1196.8	1323.6	787.1	0	0	949.4	1487.9
$\bar{X}$ desirable tree Sa/P. density (#/ha)	2172.8	1039.7	503.6	558.4	517.6	0	0	651	392.2
Sa/P density/ species	252.8	125	61.4	53.8	68.4	0	0	55.8	55.1
Desirable Sa/p density/species	265	133.3	70.9	66.5	73.9	0	0	81.4	35.7
% ground veg. cover	40	59.2	65	70	65	0	0	70	60

Appendix

Table 3. Forest gap size-class distribution of 40 randomly selected gaps and the distribution of tree saplings (Sa.) and poles (P) ($\geq$1.5cm <10cm dbh) in the gaps of heavily selectively felled forest (K-15).

Gap-Size-Classes m^2	50-200	200-400	400-600	600-800	800-1000	1000-1200	1400-1600	1600-1800	1800 2000	2000 2200	2400 2600	>2600
No. of Gaps	3	7	4	2	4	6	4	1	1	2	2	4
$\bar{X}$ tree sp. richness	17.0	16.4	19.5	25	18.5	21.2	21.8	10	15	11	13.5	14.8
$\bar{X}$ desirable spp richness	4.3	4.3	4.5	6	7.3	6	4.5	7	2	3.5	4.5	4.5
$\bar{X}$ Sa/P density #/ha	2912.8	1228.2	1328.7	1389.3	1139.4	890.7	714.4	394.5	334	302.9	242.1	232.1
$\bar{X}$ desirable sa/p density (#/ha)	804.2	318.5	306	428.3	399	275.7	156.5	219.2	73.1	114.8	71.5	81.6
Sa/P. density/ species	171.3	74.9	68.1	55.6	61.6	42	32.8	39.5	22.3	27.5	17.9	15.7
Desirable Sa/p density/species	187	74.1	68	71.4	54.7	46	34.8	31.3	36.5	32.8	15.9	18.1
% ground veg. cover.	56.7	75.7	75	85	71.3	77.5	77.5	80	70	65	87.5	80

Appendix

Table 4. Size class distribution of 40 randomly selected gaps and the distribution of saplings and poles ($\geq$1.5cm <10cm dbh) in naturally formed tree fall gaps of uncut mature forest (K-30).

Gap size classes, m^2	50-200	200-400	400-600	600-800	800-1000	1000-1200
Number of gaps	14	24	1	1	0	0
$\bar{X}$ tree species richness	8	25.0	30.0	32.0	-	-
$\bar{X}$ desirable tree spp. richness	8.0	8.7	9.0	11.0	-	-
$\bar{X}$ sapling/Pole density (#/ha)	5158.0	3686.4	4066.4	2061.2	-	-
$\bar{X}$ desirable tree Sa/p density	1847.5	1339.3	1369.3	877.6	-	-
Sa/Po. density/species	218.6	147.5	135.5	64.4		
Desirable Sa/p density/ species	230.9	153.9	152.1	79.8	-	-
% ground vegetation cover	46.8	50.8	25.0	50.0	-	-

Appendix

Table 5. Mean species richness and density (No./m^2) of plants newly germinated in manipulated gap plots of K-14, K-15 and K-30. n=20 gaps for K-14, K-15 and K-30.

Quadrants	Q1			Q2			Q3			Q4		
Compartments	K-14	K-15	K-30	K-14	K-15	K-30	K-14	K-15	K-30	K-14	K-15	K-30
<u>Species richness</u>												
Tree seedlings	1.1	0.4	1.4	1.1	0.5	1.3	0.5	0.2	0.7	0.1	0.0	0.2
Shrubs species	1.1	1.1	1.2	1.0	0.7	0.7	0.8	0.8	0.5	0.1	0.1	0.0
Herbaceous plants	3.1	3.2	4.2	4.1	2.4	4.0	3.5	3.3	2.4	0.2	0.6	0.7
Vines and Climbers	0.5	0.9	0.9	0.7	1.0	1.5	1.0	0.7	0.4	0.1	0.1	0.2
$\overline{X}$ species/m^2	5.8	5.5	7.7	6.9	4.6	7.5	5.8	5.0	4.0	0.5	0.8	1.1
<u>Density No./m^2</u>												
Tree seedlings	14.3	11.7	10.5	8.7	31.1	6.7	10.4	20.5	9.6	0.3	0.0	1.5
Shrub species	25.1	3.5	13.5	5.2	4.9	2.7	19.0	21.8	5.5	0.1	0.2	0.0
Herbaceous plants	165.1	236	102.2	223	276	99	39.1	104.2	16.1	0.9	11	1.9
Vines and Climbers	18	6.5	3.2	0.7	9	4.8	1.1	2.9	10.4	0.2	0.1	0.3
$\overline{X}$ density	206.3	257.7	122.4	237.6	321	113.2	69.6	149.4	31.6	1.5	11.3	3.7

Q_1 = 1m^2 Quadrants with vegetation removed.
Q_2 = as in Q_1 plus screening.
Q_3 = as in Q_1 plus surface soils removed.
Q_4 = 1m^2 Quadrants with all vegetation left intact.

Appendix

Table 6. The density (No./ha) and percent species population (on the right) of canopy tree species saplings and poles (range ≥1.5cm <10cm dbh) regenerating with normal stems (N), as coppices (C) or as stem sprouts (SS) in 25 forest gaps of uncut mature forest (K-30).

Tree Species	Total density (no/ha)	Normal growth (no/ha)	Coppices (no/ha)	Mean breaks stem (no/stem)	Stem sprouts (no/ha)
A. altissima	27.2	13.6, 50	13.6, 50	1.0	0,0
A. toxicaria	138.7	38.1, 31.9	95.2, 64.4	1.9	5.4, 3.7
B. unijugata	87.0	46.2, 53.1	29.9, 34.4	0.9	10.9, 12.5
C. africana	51.7	24.5, 47.4	13.6, 26.3	0.7	13.6, 26.3
C. gorungosanum	78.9	29.9, 37.9	21.8, 27.6	0.8	27.2, 34.5
C. millenii	5.4	2.7, 50	0,0	0.0	2.7, 50
F. macrophylla	10.9	0,0	10.9,100	1.5	0,0
F. angolensis	21.8	10.9, 50	10.9, 50	0.5	0,0
F. exasperata	29.9	0,0	29.9,100	0.9	0,0
F. latifolia	157.8	40.8, 24.5	78.9, 47.3	1.1	38.1, 28.3
L. swynnertonii	190.0	87.1, 45.7	84.3, 44.3	1.2	19.0, 10
M. platycalyx	13.5	5.4, 40	5.4, 40	0.3	2.7, 20
M. bagshawei	54.4	21.8, 40	13.6, 25	1.0	19, 35
N. buchananii	204	87.1, 42.7	84.3, 41.3	0.6	32.6, 16
O. welwitschii	0.0	0,0	0,0	0.0	0,0
P. excelsa	5.4	0,0	5.4,100	1.0	0,0
S. scheffleri	27.1	19.0, 70	5.4, 20	1.0	2.7, 10
S. globulifera	168.6	100.6, 45.2	59.8, 26.8	0.6	8.2, 28
T. splendida	87.0	21.7, 25	49, 56.3	1.0	16.3, 18.7
$\overline{X}$	71.54	29.9, 41.8	32.2, 45	0.84	10.4, 15.4
Sx	68.0	31.4, 20.9	32.4, 29.7	0.46	12.0, 15.0