EFFECTS OF LOGGING ON ENVIRONMENTAL FACTORS, NATURAL REGENERATION, AND DISTRIBUTION OF SELECTED MAHOGANY SPECIES IN BUDONGO FOREST RESERVE, UGANDA

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DECLARATION

I, JOSEPH B. BAHATI declare that the work presented herein is my own original work, except where otherwise stated and has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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ABSTRACT

This study explored some of the basic environmental factors that affect the natural regeneration of four mahogany species existing in the Budongo Forest Reserve, Uganda. The four species studied are: *Khaya anthotheca, Entandrophragma cylindricum, E. utile* and *E. angolense*. For each species, the biology, ecophysiology, silviculture and management are reviewed. Diverse published reports were critically reviewed and efforts made to highlight their contributions and identify knowledge gaps. Whereas forest understorey light is emphasized as the major hindrance to tropical natural forest regeneration, this study also investigated the effects of past logging in the Budongo forest reserve on soil factors and microenvironments (illumination, photosynthetically active radiation and forest temperature) and on mahogany regeneration.

Three forest categories (“treatments”) including unlogged (one compartment), earlier logged (seven compartments) and later logged (three compartments) were identified from the Budongo forest main block and the two outlying forest patches (Siba and Kaniyo Pabidi). Data were collected from plots established in each compartment. A total of 258 plots were sampled. The plots were 25m x 50m each. Within each plot, mahogany seedlings, saplings and trees were sampled. From the same plots, soil samples were collected and were analyzed for texture, pH and nutrients and compared within and between treatments. Furthermore, illumination, photosynthetically active radiation (PAR) and temperature (below ground, forest floor and forest understorey-air) were evaluated to ascertain whether there were any variations in and between the three treatments.

There was significant difference between the unlogged and the logged treatments ($05 < P \geq 0.01$) in terms of regeneration, edaphic and micro-environmental factors. *K. anthotheca* was observed to be quantitatively the most significant mahogany timber species in Budongo Forest Reserve. Next in abundance were *E. cylindricum* and *E. angolense* respectively. The least important, in terms of regeneration density was *E. utile.* Exploitation generally affected individuals in the larger sizes (≥ 80cm dbh). Differences in light regimes are between logged and unlogged forest tracts. The earlier and later logged treatments were quite similar, but PAR effects were detectable between the extreme forest categories (unlogged vs. later logged). Values of PAR and illumination were lowest in the unlogged forest than in the logged treatments. Contrasts between forest treatments were most marked in the later logged treatment, particularly with illumination and temperature (below ground and on the forest floor). Lower temperatures in the unlogged forest and higher temperatures in the most recently logged compartments were observed. Direct multivariate analysis of data using DCA and CCA techniques showed a significant correlation between local patterns of mahogany regeneration and some of the soil variables, available phosphorus, potassium and total nitrogen being the most important

Given the significance of the role of light/PAR and temperature variations in the treatments sampled, more silvicultural effort, such as enrichment planting and conservation should be placed on compartments that were logged earlier, preferably in the 1960s.

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A:	Area (m^2)
ANOVA:	Analysis of Variance
BFP:	Budongo Forest Project
BFR:	Budongo Forest Reserve
C_3:	Three-carbon photosynthesis
C_4:	Four-carbon photosynthesis
CCA	Canonical Correspondence Analysis
CIPEC:	Centre for the study of Institutions, Population and Environmental Change
CFR:	Central Forest Reserves
Cpt.:	Compartment
DBH:	Diameter at breast height
DCA	Detrended Correspondence Analysis
EL:	Earlier logging
F:	Fluorescence (mol m^{-2} s^{-1})
FAO:	Food and Agricultural Organization of the United Nations
FTEA:	Floral of Tropical East Africa
GIS:	Geographical Information System
Ha:	Hectare (= 10, 000 m^2)
IARC:	International Agricultural Research Institute
LAI:	Leaf Area Index
LL	Later logging
LAR:	Leaf Area Ratio
LFR:	Local Forest Reserves
m:	Meter
Mol:	Amount of substance with Avogadro's number of particles
n:	Number
NBC:	National Biomass Center – Forest Department
NDVI:	Normalized Difference Vegetation Index (dimensionless)
NPK:	Nitrogen Phosphorus and Potassium
PR:	Photosynthetic Rate (μmol m^{-2} s^{-1})
PAR:	Photosynthetically Active Radiation (usually 350-700 nm)
pH:	Negative Logarithm of Hydrogen Ion Activity
Q_e:	Radiant flux (W – J s^{-1})
Q_p:	Photon flux (mol s^{-1})
RGR:	Relative Growth Ratio
RP:	Research Plot

UFD:	Uganda Forest Department
UNEP:	United Nations Environmental Program
UnL	Unlogged
UNESCO:	United Nations Educational, Scientific and Cultural Organization
UNO:	United Nations Organization (New York)
UNSO:	United Nations Sahel Office
WRI:	World Resources Institute
λ :	Wavelength of light

CHAPTER 1

General Introduction

Summary

This chapter provides a general background to the research presented in this thesis. It highlights the factors influencing the regeneration of the four selected mahogany species and provides the scope of the study. The chapter also presents the research problem, the justification of the study and identifies gaps in knowledge of past researches and management strategies by the Forest Department in enhancing the regeneration niche of the four selected mahogany species in the Budongo forest reserve. Finally, the objectives, hypotheses, assumptions and the structure of this thesis are outlined.

1. 1 Background to the study

The gazetted area of Budongo forest is 793km^2. The forest is a moist tropical forest previously managed mainly for timber production, especially the species of mahogany (Harris 1933; Eggeling 1940; Howard 1991; Plumptre and Reynolds 1994). Today, multiple management strategies to meet timber, animal, and tourism interests are pursued (Herd and Longoya 1994). This study focused on the regeneration of four mahogany species. The production of timber by both the mechanized sawmills and pitsawyers has been concentrating on a few mahogany species without consideration of the future stock or possible extinction of these species. This study, therefore, was concerned with four large species belonging to Meliaceae, which occur in Budongo Forest. One species studied was *Khaya anthotheca* (Welw.) C. DC. The other three are species of *Entandrophragma: E. cylindricum* (Sprague) Sprague, *E. utile* (Dawe & Sprague) Sprague and *E. angolense* (Welw.) C. DC.

Indeed, tropical rain forests are biologically diverse and dynamic (Wyatt-Smith 1987), and possess a high order of organization in which physiological, morphological, microclimatic, and ecological features are strongly inter-linked (Brunig 1973, Connel 1978, Huntley 1988). In order to maintain such biological diversity, especially of the economic species, sufficient natural regeneration is required. Natural regeneration involves germination, recruitment, survivorship, and growth of a large number of plants (Kigenyi, 1979; Jonkers, 1987). Rand and Windsor (1976) assert that plant regeneration and distribution follow an ecological pattern. Furthermore, Barnes *et al* (1998), Nobwoshi (1987), and Saluei (1984), suggest that regeneration is not dependent on seeds or plants alone but also on factors of the biophysical environment, such as light, temperature, relative humidity, soil nutrients, soil moisture, and disturbance regimes. In this respect, seeds and seedlings are important in the regeneration process and in order for seeds to germinate and seedlings to grow, adequate active radiation, temperature, soil moisture, and soil nutrients are required (Lamprecht, 1993; Mueller-Dombois, 1975). In Uganda's forests, Eggeling (1952, 1947); Hamilton (1981); FAO (1989); and Synnott (1975) have emphasized the importance of environmental factors in regeneration including the micro-meteorological factors, such as light, temperature and moisture that should be adequate after canopy opening.

In the Budongo Forest, consideration of the requirements for light, photosynthetically active radiation (PAR), temperature, and soil moisture to ensure sufficient regeneration of the mahogany species played a major role in the decisions for harvesting, chemical treatment (arboricide application), and burning for charcoal production of some tree species such as *Cynometra alexandrii* during the 1950s and 1960s (Eggeling, 1947; Dawkins, 1958; Philip, 1965; Paterson 1991; Plumptre 1994 and Bahati, 1995, 1998). From 1911 until the present date, non-systematic tree felling has continuously been carried out in the different compartments of Budongo forest reserve. According to Eggeling (1940, 1947) and Paterson (1991), human effort to plant (enrichment planting) the Budongo forest with mahoganies started in the 1940s to complement the natural regeneration. Unfortunately, the anticipated regeneration patterns for the commercial species, especially the mahogany was not realized (Synnott, 1975/1985; Paterson, 1991; Mwima et al., 2001). Therefore, effective conservation and management of the mahogany species in the Budongo forest required understanding of the roles of the determinant ecological/environmental factors, such as logging, temperature, illumination, etc. More details on the general mahogany regeneration in tropical forests in general and in Budongo Forest in particular are presented in Table 1.1.

1. 2 Scope of the study

In a predominantly mixed forest like Budongo, the factors that affect natural regeneration of tree species are diverse. According to Larcher (1980); Jackson (1969); Marks and Bormann (1872); Hall et al. (1964); Daubenmire (1974) and Plumptre (1975) influencing factors vary from species to species. Also, they vary with the differences in ecological setting, such as tropical forests and savanna grasslands (Kramer and Kozlowski 1960).

For sustainable natural regeneration to take place, the source of seed (i.e. seed trees) must be present. Sufficient moisture, adequate light intensities and quality, PAR, temperature and soil nutrients have to be available (Kramer and Kozlowski 1960). Also, disturbances or damage from animals, insects and fire and sometimes from uncontrolled human interventions have to be controlled or prevented (Struhsaker 1997). Consequently, this study focused on the impact of logging and period since logging on the regeneration of the four mahogany species and assessment of the effect of micro-environmental factors and soil nutrients on the natural regeneration of the mahogany species. The micro-environmental factors studied include illumination, PAR and temperature.

Table 1.1: Facts on tropical regeneration, especially on Budongo Forest Reserve

A. General For Tropical Forests	**Citation**
■ In effective natural regeneration timing of the regeneration niche is crucial.	(Fenner Michael, 1992)
■ Seed bank and seed rain are and will continue to be important in tropical forest restoration. Protection of seed trees must be emphasized in future forestry management.	(Kennedy and Swaine, 1992)
■ Longevity of seed is very low for mahogany species and generally for tropical trees. Mahoganies have no dormancy and have short viability span.	(Bazzar, 1991)
■ Successful regeneration depends on minimizing damage on seedlings, adolescent trees, the soils and drainage patterns.	(Whitmore, 1991)
■ Demographic patterns showed pulse regimes of *Khaya anthotheca* due to many saplings and poles in the undisturbed than in the disturbed and such pulses are self-perpetuating depending on the frequency of the pulses.	(Luken, 1990)
■ 3.3% tree removal reduces canopy by 50%.	(Uhl and Viera, 1989)
■ Loss of seed from predation (rodents), rot, and insect larvae is more severe in gaps than in the closed forest.	(Stuhsaker, 1977)
■ Saplings and pole size were more abundant in habitat surrounding the gaps. Therefore, such environment could provide appropriate environment for the recruitment of *Khaya anthotheca* In gaps they are out competed by fast growing species pioneers, pests, lack of microclimate and other stress factors.	(Stuhsaker, 1977)
B. Particular to Budongo Forest	
■ Mahogany regeneration mostly depends on seed rain rather than on the seed bank.	(Mwima *et al.,* 2001)
■ Because of the lack of timing of logging in the Budongo Forest any seed dispersed are subjected to environmental stress such as high light intensities, desiccation and competition.	(Mwima *et al.,* 2001)
■ The fewer mahogany timber stems present were due to pitsawying	(Mwima *et al.,* 2001; Plumptre, 1995; Bahati, 1995, 1998)
■ Past phenology results (past studies) indicate that maximum seed production for mahoganies seeds takes place when the mother tree attained ≥ 80 cm dbh. This is higher than the Forest Department recommended harvesting of 70 cm dbh.	(Plumptre, 1994)
■ There is high correlation between the larger size trees and the logarithm of seedling density.	(Plumptre, 1994)
■ There has been more volume of mahogany removed from the forest than other species put together, thus making the Meliaceae family members more disadvantaged and less competitive.	(Plumptre 1996)
■ High mortality of seedlings was in the pitsawn-gaps and recently logged areas and regeneration was relatively poor in the gaps and in the controls than the old logged forest tracts.	(Mwima *et al.,* 2001)

Furthermore, measurements of slope, aspect and general vegetation cover (ground and forest canopy), were made and correlated with regeneration, soil and to past harvesting treatment-regimes.

1.3 The research problem

The five aspects of the research problem that formed the basis for this study include:

(i) Budongo forest has been subject to extensive creaming of the mahogany species, but currently, there have been no baseline studies carried out to verify the existing size class structure (saplings, poles, young or mature trees) of the species in question;

(ii) The Ecological requirements for the mahogany species, with regard to the micro-environmental factors have not been adequately researched in Uganda. In the Budongo forest, decisions for harvesting, chemical treatment (arboricide application), and burning for charcoal production of some tree species such as *Cynometra alexandrii* (Dawkins, 1954) were partly based on the need to improve the requirements for light, temperature, and soil moisture that would ensure sufficient regeneration of the mahogany species. However, the specific requirements of the most desired mahogany species have not been studied in their natural ecosystem. Synnott (1975) studied requirements for *E. utile* specifically in nursery environment

(iii) The lack of researched information on the ecology of the mahogany species makes the harvesting practice inconsistent with the natural regeneration dynamics of the forest. Furthermore, artificial planting carried out in the past (in some compartments), was not based on scientific information to adequately take advantage of the openings created during harvesting;

(iv) The extent of degradation of the forest and associated changes of the mahogany regeneration and stocking in Budongo forest following human activities (harvesting and treatment) was not clearly established. However, it was already clear that the overall species mix was greater in the logged than the unlogged compartments (Plumptre et al., 1991; Plumptre, 1994; Plumptre and Reynolds, 1994; Bahati, 1995), and

(v) The mahogany family was often aggregated and treated as a single species. The study examined each of the four species in terms of regeneration dynamics, population structure, and spatial distribution. These were compared with the biophysical, micro-environmental, edaphic factors, and the hydrological pattern in the Budongo forest. Each of the four species was expected to have a different regeneration pattern, population biology, and an ecological environment that determines their spatial distribution.

Thus, this mahogany regeneration study included assessing seedlings (<2.5 cm dbh at root collar) and sapling (>2.5<5 cm dbh or 1.3 m from ground), poles (all sizes) and trees (≥ 10 cm dbh) in relation to edaphic and micro-environmental factors. Poles were assessed, specifically for forest stability and growth of transitional stages and trees to ascertain the availability of seed trees in the Budongo forest. The edaphic factors studied included, soil reaction (pH), organic matter and nutrients (nitrogen, phosphorus, potassium, calcium, sodium and magnesium), while the micro-environmental factors included illumination, PAR and forest temperature. Seed production, dispersal, predation, seed survival and germination were **not** studied. The conceptual framework illustrated in Figure 1.1 explains the scope of the study.

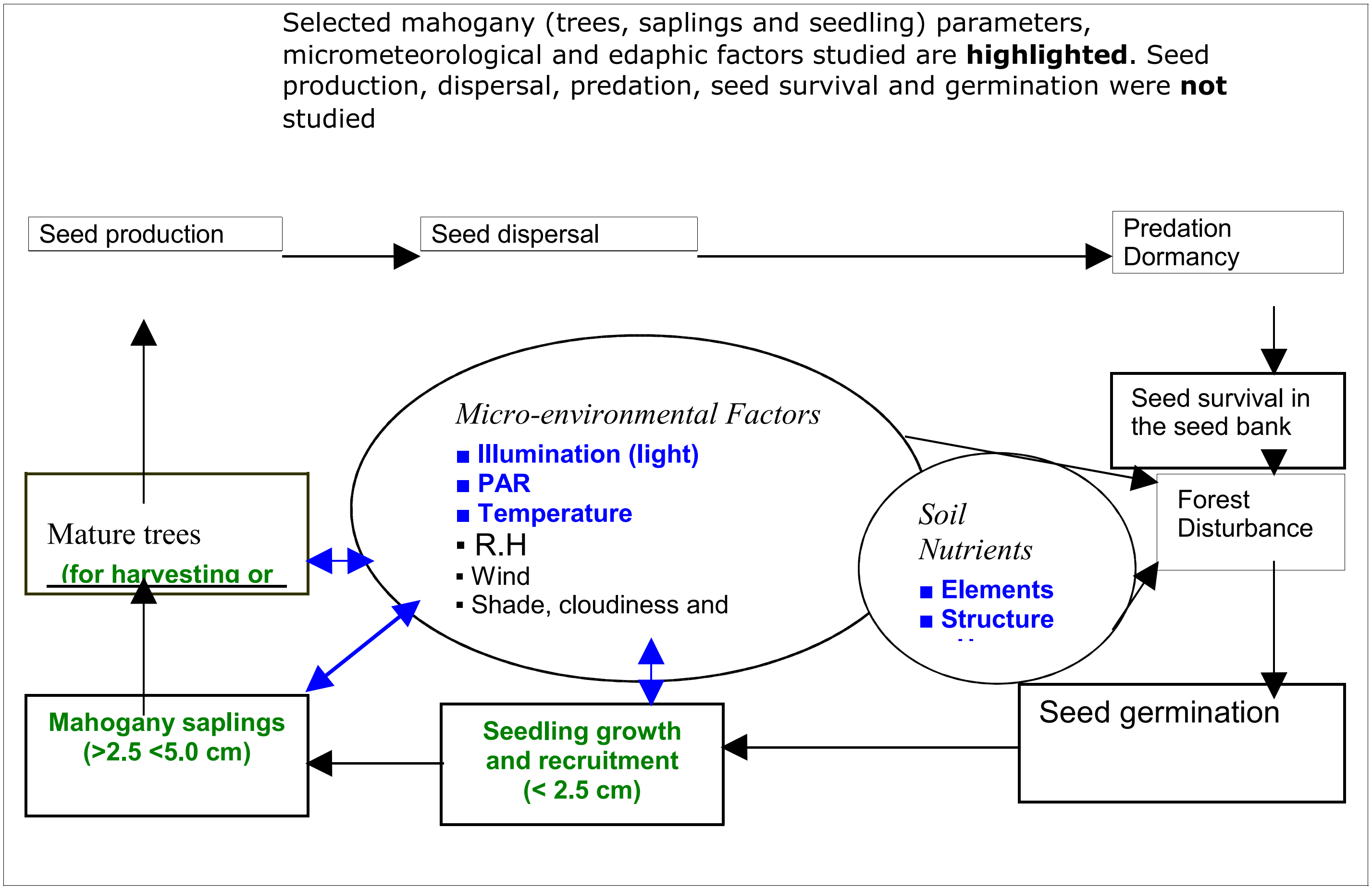

Figure 1.1: Scope of the study- conceptual Framework

Notes: Seedlings were measured at root collar.

1.4 Justification for the study

The mahoganies are an important group of timber species internationally and in Uganda, especially for their high quality timber production. Information on the current status of the four species present in Uganda with regard to their regeneration, population structure, and distribution patterns is lacking and is urgently needed for silvicultural and management decisions. Therefore, the study was undertaken to examine the natural regeneration, population structure, and general distribution of *Khaya anthotheca, Entandrophragma utile, E. angolense* and *E. cylindricum.* Such information is lacking and is needed to map the distribution of the mahogany species and aid in managing sensitive forest habitats. With natural regeneration, population structure, and spatial distribution ascertained, the harvesting of the mahogany species could easily be planned to optimize future production. Also, enrichment planting could easily be undertaken. After all, the importance of forest management in Budongo forest, which was aimed at the improvement of the production of the mahogany timber species, had not been adequately assessed. The present study, therefore, aimed at generating scientific information that could positively contribute to making management decisions geared towards improved future production of the commercial species, especially the valuable mahoganies.

1. 5 Aim and objectives

The main aim of this study was to determine the natural regeneration dynamics and environmental requirements, population structure, and spatial distribution of *K. anthotheca, E. utile, E. angolense* and *E. cylindricum* after the various periods of logging and subsequent ecological changes in Budongo Forest Reserve.

Consequently, the specific objectives were to:

(i) determine the present levels of regeneration, population structure and spatial distribution of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* after various periods of logging in Budongo Forest Reserve,

(ii) explore the effect of edaphic factors (soil texture, pH, organic matter and nutrient levels on the regeneration of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* in Budongo Forest Reserve, in relation to logging history,

(iii) explore the effect of logging on micro-environmental factors, specifically light, PAR and temperature and their influence on the regeneration of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* in Budongo Forest Reserve and

(iv) establish the effect of time since logging on the level of regeneration, structure and distribution of mahogany species.

1. 6 Research hypotheses

In assessing the natural regeneration, population structure, and spatial distribution patterns of the four mahogany species in logged areas of Budongo forest, the following null hypotheses were tested:

1. Natural regeneration of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* is similar in the logged and unlogged forest tracts in Budongo Forest Reserve.

2. Micro-environmental factors have no affect on regeneration, population structure, and spatial distribution of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

3. Forest soil factors (texture, pH and nutrient levels) do not affect the regeneration dynamics, population structure and spatial distribution of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

4. The time-span after harvesting has no effect on the regeneration, structure, and distribution of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

1.7 Research assumption

The study was carried out with the assumption that the condition of the Budongo forest was initially similar. With no human activities, the natural regeneration, species structure and distribution, soil factors and micro-environmental factors, would be similar in the logged as in the unlogged treatment. Also, it was anticipated that the effects of illumination, PAR, temperature, groundcover and canopy cover are the most important micrometeorological factors on the mahogany regeneration, structure and distribution, and that they are interrelated.

1.8 Thesis structure

A total of seven chapters are presented in this thesis as outlined below.

Chapter one is a general introduction. It presents the background for this thesis. It highlights the importance of the micro-environmental factors required for the natural regeneration of mahogany species, which form important forest resources in Uganda. The scope, limitations, and conceptual framework are presented. Also included in this chapter are the aim, research objectives, hypotheses and an assumption.

Chapter two presents a literature review and gives an overview of natural regeneration in closed tropical forests. The chapter starts with a summary of the subsections that build the rationale for addressing the problem of natural regeneration in Budongo forest. A review of natural regeneration in closed tropical forests and the effect of forest understorey illumination (light energy), photosynthetically active radiation (PAR) and temperature on regeneration are discussed. In this chapter, forest management in Uganda and the history of the management of the Budongo Forest Reserve are highlighted. Past ecological and vegetation surveys in Budongo forest, including silvicultural interventions in the regeneration of natural forest species are presented. The ecology of Budongo forest mahoganies: the state of knowledge for the four mahogany species under investigation is highlighted and schematically shown on the Meliaceae Family Dendrogram. Their present theoretical distribution, phenology cycles, dispersal patterns, regeneration behavior and environmental conditions for growth are also discussed.

Chapter three, on materials and methods, starts with the description of the study area and continues by describing the equipment used, study design, and details of the field procedures that were used to collect the quantitative data. The procedure for data analysis is also presented.

Chapter four presents the effect of logging on natural regeneration, structure and distribution in Budongo Forest Reserve. Individual tallies, diameter size classes, height structures, importance values, slope/aspect, crown scores and aspect ratios are presented and compared across the three forest treatments sampled. Species ordinations in the treatments sampled are presented.

Chapter five presents results of the effects of logging on forest soils and subsequently, the effects of forest soils on natural regeneration, structure and distribution of mahogany species in thee Budongo forest.

Chapter six presents results on the effects of logging on microclimate and the effect of microclimatic changes following logging on natural regeneration, structure and distribution of mahogany species in Budongo Forest Reserve, while Chapter seven presents the general discussion, conclusions and recommendations.

CHAPTER 2

LITERATURE REVIEW ON NATURAL REGENERATION IN CLOSED TROPICAL FORESTS

Summary

The purpose of this literature review is to give a general overview of tree regeneration in closed tropical forests and the effects of logging and management on tropical moist forests. Section 2.1 looks at examples of logging and management impacts on closed moist forests in the tropics. A review of natural regeneration and the effects of logging on regeneration, population structure, and distribution are outlined. The effects of climatic, soils, and biotic factors on regeneration are presented in Section 2.2. Also reviewed are forest management in Uganda and the management history of the Budongo Forest in Section 2.3. In Section 2.4, past ecological, vegetation and regeneration studies are presented, while Budongo forest types and natural regeneration are reviewed in Section 2.5. A review of the ecology of the Budongo mahoganies: state of knowledge is presented in Section 2.6. Finally, the lessons learnt are presented in Section 2.7

2.1 Logging and management impacts on closed moist forests in the tropics

Literature from several studies indicates that logging directly affects species composition and the growing stock of the forests ecosystem (Brasnett 1946, Burgess 1971, Brokaw 1982, Finegan 1984, Bazzar and Pickett 1990). Quite often no plans or maps are prepared and several commercial species are felled (Jonkers, 1987; Paterson, 1991). Consequently, the unplanned and un-mapped logging affects the forest's seed rain in the subsequent year. Although the logging impact may encourage a new balance of regeneration, most of the vegetation present before logging is often destroyed, particularly where large gaps are formed (Sandra and Lugo 1990, Mwima *et al.* 2001). Fortunately, when decomposition of debris occurs, which includes the remains of the felled trees; nutrients are released and made available for the development of the residual stand (Jonkers, 1987). Plants growing from seeds use part of these nutrients. Extraction of timber using heavy equipment destroys several plants and soils are compacted (Jonkers, 1987). The end results are reflected in limited regeneration and change in vegetation composition.

It has been reported that the extent of logging impacts are different for different tree size classes. According to Jonkers (1987) and Kasenene (1987), small trees are much more vulnerable to destruction as they suffer severe injury and check back than larger ones (Mwima *et al.* 2001). The damage caused tends to be confined around the tree felled, where the regeneration is affected most. This trend has been reported for Budongo where the mahogany trees were selectively and mechanically removed (Synnott, 1985; Paterson, 1991 Plumptre 1995, Mwima *et al.*, 2001).

Disturbance due to logging or gap creation by natural fall has been shown to have a positive impact on the forest by stimulating species regeneration (Connell 1978, Kasenene 1987, Huntley 1988, Lugo 1988, Reid and Miller 1989). Habitat patchiness resulting from logging influences the composition of tree species and the interactions among them (Reid and Miller 1989). At the same time, population dynamics introduces an independent pattern of variation on diversity and succession (Connell 1978), both of which are influenced by the physical environment (Reid and Miller 1989). Following logging, primary production processes such as photosynthesis, decomposition, nutrient cycling and soil fertility, which follow logging, create forest conditions suitable for species already present (Newbery and Proctor, 1984). A clear understanding of these processes and how they interact is essential for plant growth and development because the overall impact is that the understorey species tend to be different from the canopy species (Reid and Miller 1989).

Areas that are not disturbed show characteristics of climax communities, like the presence of species having superior competitive ability and reduction in diversity, while areas with intermediate frequencies of disturbance often have increased species diversity (Connell, 1978). Disturbance creates conditions conducive for the establishment of fast growing species such as *Maesopsis eminii, Trema orientalis,* and *Polyscias fulva,* which become dominant in the colonizing forest. Jonkers (1987) attributes this to intermediate disturbances with different degrees of frequency and intensity. However, regardless of how static they appear, the mixture of species that make up forest communities and ecosystems change continually. Natural systems that support such communities and ecosystems are maintained by a set of complex interactions and interdependences, which vary over time (Brunig, 1973; Reid and Miller, 1989). This complexity makes it difficult to generalize about the causes of species regeneration, structure and distribution.

Other factors responsible for variations in tropical forest regeneration and spatial distribution are changes in temperature, humidity, rainfall, altitude and soil type (Kelly, 1988; Iremonger and Sidrak, 1988 cited in Snell, 1991). The wide range of microclimates in the tropics offers many environmental niches, which provide highly varied habitats allowing greater species specialization (Connell 1978, 1986 and Kelly 1988). Furthermore, Brunig (1976) argues that variation in vegetation is partly the result of adaptations of plants to the physical and chemical conditions of a site. Connell (1978) supports this position and adds that niche subdivisions are also found along gradients of light, water nutrients and heat and explains forest composition in terms of variation in elevation, slope, aspect, soil type, understorey composition and impacts of previous or current management.

Forest diversity has been shown to increase with increased rainfall or where water is retained (Hall and Swaine, 1976). Research by Hall and Swaine (1976) indicates that some species in wetter areas of tropical forests appear to have greater site variation with limited growth ranges. Increased altitude has been reported to reduce species diversity (UNESCO, UNEP and FAO, 1978). A common explanation here is that many species are not able to survive or sufficiently establish under very cold conditions. Other observations have been made by Brunig (1976), who stated that species diversity is strongly correlated with edaphic variations. As a result, lower diversities tend to be observed in poorer soils (i.e. those with poor structure, texture, aeration, organic matter content, compactness and nutrient composition). Brunig's findings deviates from those by Hall and Swaine (1976) who found diversity to be high on poor soils with low total exchangeable bases. Nonetheless, there still seems to be no clear explanation of the relationship between soil nutrients and species diversity.

Patterns of species distribution in the tropics are little understood (Whitmore, 1990). Only a few tropical forest species have been studied in depth. Before the 1940s, knowledge of species ranges, distribution and basic ecological requirements remained largely unknown (Watt, 1947). Species richness and low frequency per unit area in tropical forests make the above observations questionable (Newbery and Proctor, 1984). A lot, however, has changed in the last 50 years as more ecological research on individual or selected species were completed (Synnott, 1975).

Species occurrence in natural forests has been described in different ways. For example, Huntley (1986) reported that in some forests species occur in clumps. He gives three possible reasons for such occurrence namely, accumulation of seeds by animals or birds depositing them in one place, seed dispersal occurring over a very limited distance or presence of suitable microclimates for successful regeneration at that site. Similar reasons are also given by Hubbell and Foster (1986) about seed dispersal mechanisms in natural forest ecosystems.

In summary, it can be said that species diversity, structure and distribution pattern are dictated by physical, chemical, biological and environmental factors. A combination of these factors on population dynamics means that no particular species can dominate the forest. Species abundance, therefore, depends on fecundity, seed dispersal, establishment within a variety of environments, microclimatic characteristics, and natural competition (Connell, 1978; Whitson and Massey, 1981).

2.2 The effects of climate, soil and biotic factors on regeneration

2.2 1 Effects of climatic factors

Climatic factors relevant to the present study were identified as water, light, PAR and temperature. These climatic factors are important for forest regeneration, species structure and composition.

2.2.1.1Effect of water on regeneration

Disruption of the hydrological cycles through logging may lead to reduction of the amount and or change in the distribution of rainfall, which affects forest temperature and amount of evapotranspiration in the forest (Dickinson 1982).

This is a concern for natural regeneration as seed dispersal should coincide with sufficient moisture in the regeneration niche (Mwima et al. 2001). Budongo forest reserve experiences two rainy and two dry seasons (Eggeling, 1947; Landale-Brown *et al*., 1964; Plumptre, 1994 1995 and Bahati, 1995). It is in the dry seasons that mahogany seeds are dispersed (Plumptre 1995). Mahogany seeds have high viability and no dormancy periods (Mwima *et al.* 2001), so lack of water can be the most important single factor limiting plant regeneration, growth and productivity throughout the world (Turner 1980). Most often the effects of water stress on physiological processes of the plant are studied along with the effects of temperature on plants, for the two are strongly related in a forest ecosystem. Photosynthesis (food manufacturing), nutrient absorption and transpiration in plants takes place with the interaction of both water and temperature. Therefore, they influence the morphology and physiology mechanisms of plants (Turner, 1980)

2.2.1.2 Light

There are five reasons why solar radiation is important in forest regeneration. These are thermal effects, absorbed energy, photomorphogenesis, photocybernetic effects and photodestructive effects. Thermal effects involve radiation, which is the mode of energy exchanged between plants and the aerial environment (Whitmore 1966). Radiation provides the main energy input to plants, with much of this energy being converted to heat and driving other radiation exchange and processes such as transpiration (Bjorkman 1972, Tang Yanhong *et al.* 1996). Absorbed energy is solar radiation absorbed through photosynthesis, which is used in the synthesis of energy rich chemical bonds and reduced carbon compounds (Bjorkman 1972, Bjorkman and Ludov 1972). Photomorphogenesis involves light, which plays an important role in the regulation of growth thus affecting the structure, crown shape and development of the plant (Hesketh 1963, Hubbell and Foster 1983). Photocybernetic effects induce the germination of seed (e.g. breaking of dormancy) or flowering in plants (e.g. plant photoperiodism). Finally, photodestructive effects are mutagenesis, have short wavelength with high energetic radiation including the ultraviolet as well as X and γ-radiation damage the living cells, particularly affecting the structure of the genetic material and causing mutation (Treshow 1970, Taylorson and Borthwick 1969).

The fittest and most viable seed is the one which happens by chance to fall in a favorable gap (Webb 1847, Web et al. 1972, Uhl and Viera 1989). For a seed to be successful, dispersal should coincides with the on-set of rains (Webb et al. 1972). The process of regeneration starts after seed dispersal, when the dispersed seed may or may not be followed by a period of dormancy. Mahogany species are in the non-dormancy category and are dispersed during the dry season. Consequently, the process of germination starts once adequate environmental requirements are available. Dispersal, dormancy and time of germination constitute what Fenner (1992) termed the regeneration niche. Also, seed germination and plant survival in the seed bank depends on the response to various environmental factors, such as illumination (light) inside the forest. Many of these factors have important interactions when operating simultaneously. For example, response to light are often influenced by temperature, response to nitrogen interacts with light, and so on.

Furthermore, vegetation (species) composition also depends on plant competition. Individual plants compete for light, temperature, moisture and nutrients. For example, plant survival in the forest may depend on different abilities to tolerate overshadowing. It is readily appreciated that forest canopy dominants exert an influence on the ground cover. Therefore, differences in regeneration requirements may provide an important means of maintaining species diversity.

2.2.1.3 Photosynthetically active radiation

Photosynthesis is a photochemical process expressed in terms of Quanta per second per unit area and is functional in the wavelength 350-700 nm within which the absorbed light energy is transformed into chemical energy in photoautotrophic plants. Therefore, for photosynthesis to take place, light must be in the wavelength (λ) of 350-700 nm. This applies whether photosynthesis is taking place in dim or bright light, night (C3) or day (C4) photosynthesis. Consequently, it is the wavelength that is critical where plant photosynthesis is concerned. Any forest condition that presents extreme change in wavelength below or beyond this 350-700 range causes an imbalance in plant performance, which results in weak and poor stands.

Photosynthesis is a function of illumination intensity. However when a series of light intensities are used, like in a forest environment, due to varied canopy opening regimes, then the rate of photosynthesis presented as a function of light intensity changes. This change requires correcting the measurements to express real photosynthesis. This correcting factor is known as the photon flux density (PFD), which is expressed as:

Lux X $10^{14} = \mu m s^{-1} m^{-2}$

$^{\text{Where}}$ μm = micromoles

S =second

m = meters

Thus, at low illumination the rate of photosynthesis is proportional to the illumination rate, but with high illumination, the rate of photosynthesis is dependent on the source of illumination (light). In order for photosynthesis to take place, the plants must have sufficient photosynthesis pigments absorbing the whole wavelength spectrum (Daubenmire 1974; Szeicz 1975; Campbell 1996; Tang Yanhong et al. 1996).

Taylorson and Borthwick (1969) noted that light absorbed by chlorophyll is poorly used for photosynthesis whereas light absorbed by accessory pigments is transferred to chlorophyll and readily utilized in photosynthesis. Furthermore, Treshow (1970) reported that the genetic make-up of plants varies and is greatly influenced by the microenvironment. It is the microenvironments that this study addressed in order to evaluate photosynthesis response of the mahogany species in the unlogged and logged compartments of Budongo forest reserve.

2.2.1.4 Effect of forest temperature on forest regeneration and forest structure

In tropical forest ecosystems, the optimum rate of photosynthesis occurs at 20 to 35^{0}C (Bjorkman *et al.* 1980). However, the rate of dark respiration tends to increase with rising temperature up to the point at which injury to the protoplasm begins to occur. As a result high night temperatures are particularly injurious to plants.

Temperature is important during germination. The imbibed water into the seed induces the germination process at an optimal temperature, but shortage leads to seed and seedling death (Enderson 1974; Mooney, Bjorkman and Collatz 1977). In addition, temperature is critical in the breakdown of protein and ammonia released in plants during establishment (Bjorkman and Badger 1977). Thus, the activities of plant enzymes change with changes of temperature in the environment.

Insufficient light in the understorey in Budongo forest, due to the dense canopy and the absence of a young stock of mahogany in the understorey, led to important management decisions such as intensive logging, arboricide treatment and charcoal burning. All were aimed at creating an environment that would promote the regeneration of the mahogany species. The driving factor for the above management intervention (Howard 1991, Paterson 1991, Plumptre and Reynolds 1995, Plumptre 1995, Bahati 1995) was to improve light in the understorey (forest illumination) although temperature could also have been a significant factor. Therefore, in addition to assessment of the importance of light in the forest understorey, this study also examined the existing temperature at three levels: (a) below ground (regeneration niche), (b) at the forest floor level and (c) understorey air-temperature at 2 meters above the ground to find out if there was any correlation between mahogany regeneration and forest understorey temperature.

2.2.2 Forest soils

The most notable characteristics of tropical forest ecosystem soils are that they are highly weathered, highly leached and oligotrophic (i.e. nutrient poor) (Myers 1992). Tropical forest are predominantly composed of brown earth, rich in allumimium and poor on most of the major nutrients such as nitrogen, phosphorus and potassium. However, these nutrients are usually locked up in tree and other forest vegetation biomass (Huntley, 1986; Howard, 1991 and Randolph, 1998). Tropical forest soils support a vast number of plant and animal species of varying physical rotations (Howard, 1991). Plants such as the herbal colonizers last one to two seasons and later die, while trees may last up to 120 years. These varying rotation periods and the subsequent forest decomposition influence nutrient cycling, capabilities in moisture retention in the soil, fertility, regeneration, forest structure, composition and productivity (Myers 1992). Although tropical forests are oligotrophic and comprise of only seven percent of the earth's land surface, they contain between two and four millions of the five to ten million plant and animal species. In Uganda, the Budongo forest reserve consists of over 400 plant species and over 150 animal (vertebrate) species (Howard 1991). Therefore, one complex by-product of the high species diversity of tropical forests is the complex web of interactions that connects the resident plant and animal species and soils. Myers (1992) finds it hard to visualize the scale of biological richness in a tropical high forest, and far more difficult to imagine the complexity of interactions between animals and plants and between them and their physical environment including soils.

One of the noteworthy manifestations of the complexity of tropical forests is the process of soil nutrient cycling (Myers 1992; Park 1992) Despite being generally characterized by old, highly weathered and highly infertile soils (see table 2.1 below), tropical forests are highly productive habitats. The explanation of this paradox lies in the highly adapted forms of nutrient cycling that have evolved over long periods of stability in tropical forest ecosystems. Unlike temperate forest ecosystems, where most of the nutrients released from decaying plant and animal materials are stored within the soil and then made available for growing plants, most of the nutrients in tropical forest ecosystems are held in the living tissues of the vegetation itself (Jordan 1985).

Table 2.1: General distribution of main soil types in humid tropics (% of total land area)

General soil group	**Africa**	**Asia**	**Latin America**	**Total humid Tropics**
Acid, infertile solis (Oxisols and Utisols)	56	38	82	63
Moderately fertile, well-drained soils (Alfisols, Vertisols, Mollisols, Andepts, Tropepts, Fluvents)	12	33	7	15
Poor drained soils (Aquepts)	12	6	6	8
Very infertile sandy soils (Psamments, Spodosols)	16	6	2	7
Shallow soils (Lithic, Entisols)	3	10	3	5
Organic soils (Histosols)	1	6	-	-

Source: National Research Council (1982:50)

In addition, on the tropical forest floor, there exists a nutrient-conserving mechanism. For example, tree roots, which extend 100 meters along the surface of the ground form a dense network. Some aerial roots even emerge from the soil and climb-up tree trunks in order to be able to capture nutrients before they enter the soil. The root mat is extraordinarily efficient at absorbing nutrients washed into the soil, whether from rainfall or rotting vegetation (Stark and Jordan 1978).

Closely associated with the root mats are fungi-root combinations known as *mycorrhizae*. These *mycorrhizae*, together with their associated symbiotic bacteria, are essential to the health of many tropical trees, including the mahoganies. They are the main conduits through which tree roots recover phosphorous, zinc, copper, molybdenum and other minerals from the leaf litter on the forest floor. *Mycorrhizae* grow on or near the surface layers of the feeder roots of plants, where they work in close symbiotic relationship with their plant hosts. By colonizing the roots, the fungi enhance the functioning of root systems. They enable plants to absorb more minerals from the soil and also help to resist root pathogens, withstand drought and tolerate other adverse conditions. In return for this support, the fungi obtain energy from their plant hosts in form of fixed carbon (Stark and Jordan 1978).

2.2.3 Effect of biotic factors (animals, canopy and ground covers) on regeneration

Tall undergrowth in the forest, especially indisturbed compartments, are detrimental to regeneration. They attract animal browsers, predators or pathogens and lead to seedling mortality (Janzen 1970, Augspurger 1983, Augspurger and Kelly 1984). Synnott (1975) showed that mortality of *E. utile* seedlings due to these agents was high in the Budongo forest reserve. Furthermore, Eggeling (1947) reported that at the start of the rains, seedlings on the forest floor are abundant, but these gradually disappear with the onset of drought in the understorey microclimate. It has been suggested that animals (e.g. rodents or squirrels) are partly responsible for the disappearance (Johns 1992, Plumptre and Reynolds 1994, Mwima et al. 2001).

In severe seedling damage situations, squirrels and rodents can be eliminated from the site by constructing a wire mesh. Individual shelter-guards can further enhance their protection from gnawing mammals. In addition, guards promote fast growth compared to species that are not guarded (Watt, 1947).

It is not known whether this type of damage by animals is severe enough in Budongo forest to warrant individual seedling guard protection.

A forest community includes more than trees (Wyatt-Smith 1995, Barnes et al. 1998, Whittmann et al. 2002). Other indicators of a normal forest are the plants that comprise groundcover and to what extent the canopy is open to direct sunlight (Whitmann et al 2002). The amount of groundcover influences regeneration in both positive and negative ways. Firstly, the groundcover provides suitable microenvironments and nurses the young plant during the early stages of development (Snedaker 1970, Bazzar and Pickett 1990, Sandra and Lugo 1990). The young plant is not conspicuous to predators (large herbivores) at the early stages during regeneration (Roche 1978, Schupp and Frost 1989). Secondly, groundcover competes with seedlings for light, nutrients and soil moisture, which limits and controls plant growth (Howard 1991, Bowers and Dooley 1993). Sometimes, groundcover can be a host to pests that may later be hazardous to the young regeneration (Ross 1981, Brewer and Rejmanek 1999). Furthermore, in logged forests or gaps, ground vegetation cover is diverse and forms important food for terrestrial animals, which disperse seeds into the disturbed sites (Kasenene, 1984).

In tropical forest ecosystems, canopy cover affects crown shape, which is important in plant ecology as this influences the type of regeneration that grows on the forest floor (Sandra and Lugo 1990). Crown shape is a response to light or as a result of plant genetic make-up influenced by the micro-environment (Ross, 1981; Brokaw, 1985; Bazzar and Pickett, 1990; Bowers and Dooley, 1993; Caldwell and Pearcy, 1994). Crown shape is assessed by crown score, which is a measure of how the crown is exposed to direct light radiation (Cadwell and Pearcy 1994). Plant crown exposure is influenced by the crown of surrounding trees, saplings, climbers, and lianas (Mwima *et al*., 2001). Since regeneration may be shade tolerant, light demanding or a mix of the two, it is essential that crown dynamics is understood in order to manage the diversity of regeneration that exist in forest ecosystems.

2.3 Management history of the Budongo Forest Reserve

The reservation of Budongo Forest started in the 1932 after the first aerial survey covering 500 km² of the forest (Eggeling, 1947) followed by ground enumeration (FAO, 1989). The management of the forest, however, started much earlier. For example, in 1922 planting of *Khaya anthotheca*, *Entandrophragma* species and *Maesopsis eminii* was attempted in parts of Biiso block (FAO, 1989) in order to increase the stand density. This was after realizing that the upper and middle layers of the forest canopy lacked seedlings. Earlier attempts through enrichment planting were nearly unsuccessful because of the closed forest canopy that allowed little light to reach the undergrowth and as a result natural regeneration was poor. Regeneration failure was also partly due to grazing and browsing by wild game. Destruction by elephants, buffaloes, antelopes, wild pig, bushbucks, and rodents also posed a serious problem to enrichment planting (Philip, 1965; Synnott, 1975; FAO. 1989). Controlled shooting was initiated in order to reduce the animal population and to save the seedlings, but this method too was unsuccessful.

Budongo forest was also managed for production of wild rubber, which was tapped from *Funtumia elastica* (Preuss) Stapf. The history of rubber tapping in Budongo dates as far back as 1942 when about 40 tonnes of rubber was produced per annum. The activity was gradually replaced by the taungya system introduced in Nyakafunjo in the 1940s as a way of establishing plantations in Budongo (Paterson, 1991). The method was cheap to the Forest Department and simple enough for the local people to adopt and practice.

From the 1940s, research initiatives focused on the silviculture of indigenous timber species with trials of both natural and artificial methods of regeneration (FAO, 1989). Later, investigations of fast growing species particularly *K. anthotheca* (mahogany) was made. Selection of trees and the establishment of research plots were carried out. Periodic assessments of species in the research plots were conducted to guide management decisions. In the 1950s and 1960s, arboricide (2, 4,5-T and 2,4-D in 1:2 proportions and mixed with diesel) was applied to trees that were then undesirable (weed species), to open up the canopy and encourage the spread of the mixed forest species, especially mahogany (Plumptre, 1996; Philip, 1965). Appendix 1 shows the logged and treated compartments, when they were logged and the quantity of timber removed.

During the late 1960s and 1970s, the high demand for charcoal forced the Forest Department to reduce and finally eliminate other refining practices, such as arboricide treatments in Budongo (Ndemere, 1997) (Appendix 2). Previously, much of the charcoal burning had been done on public land outside the forest reserve. However, these resources became depleted and the Forest Department attracted private charcoal dealers into the forest reserve to utilize the wood that remained after felling. The introduction of large-scale charcoal production helped in some ways to get rid of arboricidal treatments.

2.4 Past ecological, vegetation survey and regeneration studies in Budongo Forest Reserve

2.4.1 Ecological studies

Eggeling (1947) landmark paper on the ecology of the Budongo forest identified the reserve as one of the few rain forests that was still increasing in size since the 1930’s. This paper describes the stages of natural succession with an emphasis on woody species succession and provides a detailed description of the structure and composition of a representative tropical moist evergreen (Tall Grassland agro-ecological zone) forest in Uganda. Eggeling (1947) identified three succession stages (Figure 2.1). These stages included: (1) the colonising forest occupied by light demanding species; (2) a mixed forest transition to (3) a climax forest dominated by shade-tolerant species.

Figure 2.1: Map of Budongo Forest Reserve showing the forest successional stages in 1950s

Source: Budongo Forest Management plan 1997-2007

These forests are often considered when a 'natural' regeneration and silvicultural management is needed.

In addition, Langdale-Brown's (1960) Memoirs detailed findings of the ecological survey of the vegetation of Uganda including Budongo Forest Reserve. The survey was designed as an aid to agricultural development in Uganda. Consequently, the main themes of the survey were with particular application to forestry and agriculture. Two themes were relevant to this study:

i Census of the existing botanical resources.

ii Understanding vegetation as an indicator for soil characteristics, such as texture, drainage and correlation of plants with specific soil conditions as an aid to pedological interpretations of aerial photographs. Today, understanding Uganda's vegetation is essential and applicable to characterizing vegetation/soil relations using Geographical Information System (GIS) applications.

The description of the Budongo Forest vegetation (moist semi-deciduous forest) is detailed in Langdale-Brown (1960) and Langdale-Brown *et al.* (1964). Langdale-Brown's (1960) mapping of plant communities in Uganda was based on determining and distinguishing between, stable, unchanging plant communities in equilibrium with their local environment and unstable, transient plant communities, which normally gave way to others after a shorter or longer period of time.

Furthermore, Synnott (1975) systematically investigated the factors affecting the survival and growth of seeds and seedlings of *Entandrophragma utile* (Dawe and Sprague) Sprague in Budongo forest and Nyabyeya nursery in Uganda. He investigated seed viability from the time of seed-fall to the start and end of the rainy season. Synnott investigated the nutrient content of the *E. utile* seed and sowed the seed in the forest to monitor germination, survival and growth of the seedlings in addition to monitoring the causes of seedling death. The studies of Synnott (1975) were followed by Plumptre (1994), who emphasized that the change from polycyclic to monocyclic logging (selective logging to clear felling) in the 1950s greatly affected the functional dynamics of the Budongo forest. Monocyclic logging aimed at creating sufficient canopy openings, which would favour the germination and early establishment of the desirable mahogany species. The change to monocyclic logging was introduced with mechanized logging to ensure an economic recovery from the investments made. This approach drastically changed the microclimate, affected the soil structure regimes, removed major seed producers and damaged the remaining stock of the pole and young mahogany stems. In addition, Plumptre (1995) noted that there was limited stock of seed trees due to government policy to reduce the diameter at breast height (dbh size class) of harvestable trees from 80 cm to 50 cm dbh. Mahogany species are seed prolific at larger dbh, estimated at ≥ 80 cm.

Earlier studies (Bahati 1995, 1998) reviewed the transitional changes the Budongo forest reserve went through since reservation in 1932. After reservation, Uganda Forest Department had the mandate to assess the stock and manage the forest reserve. Twenty years later, the Forest Department realised that the most desired species were not represented in the understorey because of insufficient light. Timber harvesting was intensified To open the forest canopy. In addition, killing of the undesirable trees using arboricide and charcoal burning of the residual stand was encouraged to further open the canopy. However, it was not known how much light was optimal, and what consequences accompanied the intensity of harvesting, chemical treatment and charcoal burning. Enrichment planting, which was then a policy to increase the stock of the mahogany species, was summarily abandoned in 1960s because seedling survival, growth and recruitment were low.

Almost about the same time, Obua *et al.* (1998) investigated the perception of the communities on the long-term benefits/losses and changes that had taken place in Budongo forest reserve. The investigations indicated that community attitudes and perceptions about the forest management were not the same then (1990s) as previously (during 1950s and 1960s). Residents of the surrounding communities harvested at will and took no responsibility for the reduced forest cover. They were not consulted and involved in making management strategies for the forest, but were seen as destroyers of the forest. The communities depended on the forest for energy, building poles, medicine, handicraft materials and sometimes for food. The consequence of the above community-forest interactions, especially in canopy opening and forest regeneration are also not known.

Mwima *et al*. (2001) noted that forest-felling intensity in Budongo forest was high and the forest was being altered continuously. The mahogany seed trees were found only in some compartments and absent in others. As a result, mahogany regeneration, which mostly depends on seed rain rather than on seed-bank, was getting affected. Also, because of the timing of logging and the rainy season, any dispersed seed were subjected to environmental stress such as short light intensities, desiccation and plant competition thus leading to inadequate recruitment.

2.4.2 Vegetation survey studies

In his Botanical Mission of the Uganda Protectorate, Dawe (1906) noted that Budongo Forest was the most valuable timber forest within the limit of the Uganda Protectorate. The forest was well watered by several streams of fair size and precipitation was very high. Temperature at the time was on average a maximum of 24 ^{0}C and a minimum of 16 ^{0}C.

Dawe (1906) had a mission to find out the stock of the *Funtumia elastica* in the Uganda Protectorate and found that throughout all parts of Budongo, *F. elastica* was fairly abundant, except in such localities where *Cynometra alexandri* (Muhimbi) were predominant. Even then *Funtumia* grew in association with the muhimbi. Dawe (1906) found out that of the other rubber trees, *Clitandra cymulosa* was only sparsely distributed. *Landolphia landolphioides* was found in the moist parts especially in small quantities in the outlying forest areas and rarely in the more central area. Also, *L. florida* was occasionally found and both *L. owariensis and L. comorensis,* were present on the outskirts of the forest

Dawe (1906) asserts that the most important timber species of the Budongo belong to the mahogany order – Meliaceae. He noted that what appears to him to be the most valuable one was a new species of *Entandrophragma* (*Pseudocedrela)*, which he and Sprague described and named as *Entandrophragma utile*. It is an immense tree, with very valuable timber. The tree (*E. utile*) is easily distinguished in the forest by its clavate capsules, which are usually found lying at the base of the tree and are about 15-25cm (6-10 inches) long. There are five valves and dehiscent from a 5-angled pithy axis. The seeds have a long wing at one end. It is especially abundant in the Biiso part of the forest.

Khaya anthotheca was another valuable timber tree that Dawe (1906) found throughout the forest. It is also recognized by its capsules, which are usually found at the base of the tree. They are globose and dehisce, usually by four valves from a four-winged pithy axis. Its brown seed are oval in outline and slightly winged at the margins.

On the Budongo forest outskirts (i.e. in rather open parts of the forest), *Maesopsis emin*ii trees are found. They are tall straight trees, which are used along Lake Victoria shores for making canoes. This species is known in Bunyoro, where Budongo is located as Muhongera. Other trees recorded as important by Dawe (1906) are *Erythrophloeum suaveolens*, which provide teak-like wood. It is one of the most common tree species of Budongo forest and attains enormous dimensions. *E. suaveolens* has a clear bole and reaches up to 15m (50 feet) in height. Many are 1.5-1.8m (5-6 feet) in diameter at 1.5m (5 feet) from the ground. *Cordia milenii,* is also *a* rather important and common tree affording a useful and tough timber. It is normally recognized by its white cup-shaped flowers and egg-shaped fruit, the pericarp of which, when it decays, forms a gelatinous mass on the ground. It is known in Bunyoro as Mutumba and used for making native drums. *Balsamocitrus dawei* is also an important tree species of Budongo forest and is locally used for fragrance. This is predominant in the Biiso area. Several other important species were recorded by Dawe (1906). *Dracontomelum,* which is a *Canarium*-like species and is known locally as Mulio is usually eaten by wild pigs and sometimes by locals. *Celtis phillipensis*, is a large tree also found in the Biiso forest area. *Chrysophyllum africanum*, a distinct tall tree with rufous foliage and a bronze colour contrasts strongly from the other trees. *Milicia excelsa* (Muvule), *Cynometra alexandri* (Muhimbi), *Balanites wilsoniana* (Lukanyu) and *Alstonia boonei* (Musoga) are also Budongo forest species. According to Dawe (1906), the soils around Budongo are fertile with great possibilities for agriculture.

There are two seasons in Budongo Forest Reserve. The wet and dry seasons. Furthermore, each of these seasons is subdivided into the little season and the great season. For example, the little dry season occurs from June to July, while the great dry season occurs from December until late February. These two seasons affect the flowering, fruit-formation and seed-dispersal of trees in the Budongo Forest Reserve (Dawe, 1906).

After Dawe (1906), Troup (1922) gave a report of his visit to the Uganda Protectorate in 1921. The objective of the visit was to visit Uganda forests, assess their conditions, evaluate the condition of the country's general forestry sector and make recommendations for future administration and management of forests in Uganda. Budongo Forest Reserve is one of the forests that was visited.

In 1921 Budongo Forest was evaluated as being in good condition. The most common tree was *Cynometra alexandri* (Muhimbi), which is very plentiful in the forest. *Entandrophragma* (Miovu) occurred in moderate quantities and reached a large size. Other trees reported in this report include *Khaya anthotheca, Lovoa, trichiliioides*, *Milicia excelsa, Alstonia boonei, Chrysophyllum albidum, C. africanum, Piptadeniastrum africanum, Psydrax parviflora, Pouteria altissima, Celtis* species*, Parkia filicoides, Sapium ellipticum, Maesopsis eminii, Pycnathus angolensis, Canarium schweinfurthii, Cordia milenii, Casia sieberiana, Erythrophloeum suaveolens, Trichilia dregeana, T. preuriana, T. rubescens, Funtumia elastica* (once used for tapping rubber) and various species of *Ficus.*

According to Troup (1922), timber at the time of the survey was cut on a small scale by hand. Provision had been made for the construction of a sawmill. The construction of the sawmill was initially meant to provide high quality furniture timber for export and to provide railway sleepers.

By 1922, the percentage of timber in Uganda was very small (with approximately 7% of country was closed canopy forest cover) when compared with most timber producing countries, such as France (with 18% of country under forest cover) and Germany (26% of country under forest cover). Even then, such countries were unable to supply all their timber requirements. In Uganda therefore, timber resources were in short supply. Troup noted that Uganda would be able to meet its own timber requirements provided existing forests were strictly maintained and systematically managed. Importing timber would be expensive due to the country's geographic location. Therefore, it was important that the country be self-supporting for timber. Troup (1922) envisaged future general development and a raising standard of living and consequently a high demand for timber.

Troup (1922) raised the important question of who should engage in timber convertion. The dilemma was between giving the mandate to a Government agency of lessees and licensees or small permit holders. The Troup report recommended a Government agency for the following reasons:

- The area to be dealt with is not so vast as to preclude the work being carried out by Government,

- Most timber was supplied to Government Departments. It was easy for the Government Forest Department to deal with other Government Departments,
- Government was in a better position than any private agency to bring to notice and develop markets for the various timbers then were unknown or imperfectly known,

- The regeneration and felling strategy (canopy cover opening) would require careful execution under a regular programme. The Forest

Department would have a free hand in carrying this out if it arranged to do the timber conversion itself,

- Government was likely to make more timber profit out of the forests by directly converting round wood into timber, and

In the Troup report, felling, extraction and regeneration were considered simultaneously and the Forest Department was better positioned to carry out these operations carefully to avoid damage to the forest.

Then, Eggeling (1940) indicated that in all the East African territories under the British Administration, the Budongo Forest in Uganda stood out as the one with the largest marketable quantities of mahogany timber. Budongo Forest is an outlier of the Ituri forest of the Democratic Republic of Congo and also resembled in many respects the mahogany forests of West Africa.

Eggeling (1940) noted three main blocks of the forest (Budongo proper and the two small blocks of Siba and Kaniyo Pabidi) combining to a total area of approximately 265.5 km^2 (165 square miles). According to Eggeling (1940), Budongo Forest was shunned before the arrival of Europeans. It was undisturbed until the beginning of the 20th century, when commercial development started with the tapping of wild rubber (*Funtumia*) in 1905. Tapping attracted those seeking employment and operation continued until 1910 when the price for wild rubber declined. During this period, Budongo was considered solely as a source for rubber and no attention was paid to its timber.

In 1910, Dawe sketch-mapped the whole forest identifying a large majority of the timber species and made a 0.26% enumeration of all trees exceeding 0.6m (2 feet) diameter at breast height (dbh). It is remarkable that the findings at that time agreed with the map prepared from aerial and enumeration surveys of the forest in 1932, 22 years later (Harris, 1933).

In 1919, Forest Department exploitation of timber started. However, during the previous nine years small quantities had been cut by other Government Departments in the outskirts of the forest. Sawing was by hand. Only mahogany was cut and there was no prescribed cut. The project was abandoned in 1922.

The first sawmill began operation in 1925, being constructed on a European estate outside the forest and operating with trees cut on permit. This sawmill operated intermittently until 1930, when the owner went into liquidation.

In August 1930, Messrs. Buchannan's (Budongo) Sawmills was granted a license to exploit timber from a small portion of the main forest block. In 1934, this enterprise was granted a ten-year exclusive (harvesting all tree species) license in the Budongo series of the mahogany circle as prescribed in the Working Plan. As replanting was not a responsibility of the licensee, all regeneration work was completed by the Forest Department

Eggeling (1940) noted that the high-forest blocks of Budongo were islands in a sea of grass. They were surrounded on all sides by annually fire-swept savanna in which *Terminalia brownii* and *Combretum* dominated the woody species. The transition from forest to savanna was abrupt and the edge of the forest sharply defined. Forest expansion was most rapid in the fertile

Acanthus pubescens dominated areas where the scanty shade and less luxuriant grass-growth were ideal for the regeneration of *Maesopsis eminii*, the primary tree colonizer. In less fertile areas where *Acanthus* was absent, especially on highly laterite ridges, expansion was less rapid. Here *Sapium ellipticum, Spathodea campanulata, Croton macrostachyus, Albizia coriaria, A. ferruginea, A. glaberrima, Margaritaria discoidea, Trema orientalis, Prunus africana* and *Caloncoba crepiniana* all played an important part. Gradually transitional woodland (forest without a closed canopy) forms. In effect, on fertile areas, *Acanthus* invades grassland, *Maesopsis* invades the *Acanthus* communities and *Khaya* and other associated species mentioned above invade *Maesopsis* (Eggeling, 1940). Based on timber characterization, Eggeling (1940) identified four main forest types in the following proportions:

Woodland (no mahogany, *Cynometra* or *Maesopsis*) (2%)

Forest swamps (no mahogany, *Cynometra* or *Maesopsis*) (2%)

Maesopsis forest (dominant) (4%)

Mahogany and ironwood forest mix 92%

Woodland contained no species of economic value. The Budongo forest swamps predominantly had rattan canes (*Calamus deerratus*) and herbs. Forest swamps, too, are unimportant for timber species. Swamps were treeless or dotted with *Phoenix reclinata, Pseudospondias microcarpa, Mitrogyna stipulosa, Spondianthus preussii, Parkia filicoidea, Cathormion altissimum* and *Erythrina mildbraedii*. Eggeling noted that except where the ground was permanently waterlogged, *Khaya, Cynometra* and *Alstonia* were found. The *Maesopsis* forest had *Maesopsis* predominating, while the mahogany and ironwood forest exhibited a five layer forest: topmost, main, third, second and ground layer.

The topmost layer of the mahogany and ironwood forest was not continuous and consisted of the emergents, mainly *Cynometra* and mature mahogany trees. Other species found in this layer were *Milicia excelsa, Bombax buonopozense, Trilepisium madagascariensis, Klainedoxa gabonensis* and *Mildbraediodendron excelsum*. The main layer contained *Alstonia boonei, Ricinodendron heudelotii, Erythrophloeum suaveolens, Holoptelea grandis, Pterygota macrocarpa, Cola caricaefolia, C. gigantean, Cordia millenii, Celti*s spp, *Balanites wilsoniana, Chrysophyllum* sp. and *Albizzia* sp. The younger stocks of *Cynometra* and mahogany were also found in this layer. The third layer consisted of the same species as above, but at lower frequencies and abundance. The second layer, mainly saplings and poles, was the best defined and consisted of *Lasiodiscus mildbraedii, Celtis brownii, Rinorea angustifolia, R. brachypetala* and *Glenniea africana*. The ground layer consisted of shrubs and herbs.

The silvicultural aims of Budongo forest were to provide facilities for profitable exploitation whilst ensuring the preservation of the existing type of forest; secondly, to provide for flexible, but conservative regulation of the yield; and thirdly, to provide for the Forest Department to increase the stock of valuable indigenous species in all suitable forest localities. Therefore, efforts were directed at raising mahogany species (especially *Khaya anthotheca* and *Entandrophragma angolense)*. In the Main Block, artificial regeneration occurred in the logged compartments and was carried out a year after exploitation. In the Siba block, natural regeneration was the target. No record is available of any particular regeneration strategy for the Kaniyo Pabidi block. From 1929 until 1934 approximately 417 acres of exploited forest were enriched. After 1934, an average of 352 acres per year were artificially regenerated. The total area of artificially regenerated forest in Budongo by 1939 was 2177 acres (Eggeling, 1940).

In the Siba block, where natural regeneration was the strategy, the mahogany in the non-*Cynometra* portion of the forest were so well represented in the young class that no silvicultural work was necessary beyond the freeing of natural seedlings and saplings. Unfortunately in the *Cynometra*-abundant portion of the forest mahogany no longer regenerated. Experiments to induce natural regeneration proved disappointing with many of the saplings bent and twisted.

Paterson (1991) detailed the initial contact of the Budongo Forest Reserve with the Colonial Forestry Administration explaining the subsequent reduced fire frequency and the control of roaming large wild mammals (e.g. elephants) in the early 1900. Forest colonization was high, but species dispersed by animals were greatly checked. Paterson noted the ecological research at that time and emphasized the sustainable management in the 1940s, 1950s and 1960s in which yield (round wood removal) and silvicultural prescriptions were done for the benefit of the forest, wildlife, surrounding communities and government. Due to political instability and lack of effective monitoring/supervision of harvesting activities in the late 1970s and early 1980s there was concern for the continued existence of the most harvested species from the forest (i.e. the mahogany species).

2.4.3 Regeneration (artificial and natural) studies in Budongo forest: past silvicultural effort

Eggeling's (1940) account of the Budongo Forest Reserve between 1929 and 1939 clearly indicates that both artificial and natural methods of mahogany regeneration were still at the experimental stage, but he regarded both methods as promising. Transplants and stump plants of mahogany grew satisfactorily in Budongo Forest Reserve, but both types of plants had the disadvantage that a relatively long period of weeding was necessary before the young tree was clear of the undergrowth.

2.4.3.1 Types of planting

Several methods of regeneration establishment were tried. Initially, it was either planting along narrow lines or group planting. Later, line-group planting was adopted.

1. Line planting

Narrow lines 0.91 m (3 feet) wide were planted with two years old transplants 30 cm-45 cm (1-1.5 feet) high. Seven years after planting these lines no longer required annual cleaning and ten years after planting the best saplings were 6m (20 feet) high. A sufficient number of trees survived giving a higher mahogany stock than in the original forest, but many were suppressed by the heavy shade inevitable in narrow lines (Eggeling, 1940).

2. Group planting

Similar transplants were also planted in groups of 3-5 in felling gaps. Where necessary to ensure regular distribution, additional gaps were opened to give three groups to the acre. Here, too, enough trees survived to replace the number removed in felling. However, owing to greater exposure, there was higher plant mortality in-group planting than in line planting, and more beating-up was required. In groups, the higher exposure to light caused greater initial growth, but this was offset later by the fact that the group environment did not have the same “growing-up” power as found in the line environment (Eggeling, 1940).

There was nothing to choose between the two methods with regard to shoot borer damage, to which *K. anthotheca* was very susceptible, although *E. angolense* seemed immune.

Stumps at first appeared to give better results than transplants, but it was found that although stumps often shoot strongly soon after planting, they frequently did so before they were properly rooted. Not long afterwards the new shoots died back and, although death of the stump seldom resulted, there was a considerable lag between the initial dieback and the re-growth after the roots had formed. Transplants moved during a resting-stage, stood the shock of lifting much better than did plants, which were growing actively, as the leading shoots of the latter usually died back. Stumps prepared from plants in a resting condition escaped dieback. For successful transplanting, the resting stage and perfect weather had to coincide. Stumps, on the other hand, could be planted in any but the driest weather. Because of this last advantage, stumps were planted almost exclusively at Budongo in the years 1934-38. Establishment was satisfactory but costs remained higher than desirable, owing to the amount of weeding required.

By 1938, the various disadvantages of group- and line-planting had been realized. Narrow lines were too dark, while wide lines were too costly. Both types, if planted throughout became attractive to animals. Felling gaps were particularly exposed. For efficient control of groups, mapping was essential but very expensive. Lines did not suffer from this disadvantage of exposure. Therefore, from the consideration of the merits and demerits of the two methods, “line-group” planting was adopted.

In the line-group method, narrow lines running east to west were cut through the regeneration area at intervals of 45.7 m (150 feet). Along these lines, line-groups measuring 6 m x 3 m (20 feet by 10 feet) were opened every 31m (100 feet), and in each group three mahogany trees were planted 1.5m (5 feet) apart in a row. The plants were mulched, partly to keep the soil moist and partly to keep weeds down. Enriched-felling gaps encountered along the lines were treated as line-groups.

Line-groups were not fully exposed to direct light until a month or two after planting, initial shade being beneficial to establishment. The line-group method gave easier control and a more even distribution of plants than group planting. In addition, it made fuller use of felling gaps, gave more favourable conditions of light and shade, and was less wasteful of plants than line-planting.

The new line-group method with its various advantages was further boosted by the information on the planting of mahogany (*K. anthotheca*) and *Milicia excelsa* (then *Chlorophora excelsa*) in the Ivory Coast, West Africa. In Ivory Coast, plants 1.5 – 2 meters high were planted. Consequently, mahogany seedlings in the nurseries were left to grow to the required height stripped of their leaves and planted. Results were so successful that two years later (in 1939), stumps and small transplants of mahogany ceased to be planted at Budongo.

The nurseries for *K. anthotheca, E. angolense,* and *E. utile* were located within the forest and cleared of all growth except the light-crowned trees of the topmost storey. The beds were left unshaded, but those of *E. utile* required heavy shade for the first year. The exact nursery requirements of *E.*

cylindricum, one of the four mahogany species in the present study were not assessed.

If mahogany seeds were sown after the early rains had started, no watering was required. Plants took 2-4 year (mostly 3 years), to be lifted. They were taken from the beds, stripped of their leaves, root pruned to leave a good-sized main root and planted. Striplings were lifted when making no growth, otherwise, the fresh succulent leader died back and growth was checked.

By using striplings in line-groups, Eggeling (1940) concluded that regeneration costs were reduced greatly. Ninety percent of planting became successfully established. Beating-up costs were reduced and, because large size plants were used, no weeding was required. The average growth rate of striplings per year was 0.6m (2 feet) of growth and the total period of tending was reduced from seven years to four.

On natural regeneration studies, three natural regeneration experiments were carried out in Siba Block (1931-1935)

EXPERIMENT 1: Natural regeneration immediately after exploitation

In the year following exploitation during 1931, twenty-three felling gaps in 17 acres of forest from which all exploitable mahogany had been removed were hoed clear of undergrowth prior to the ripening of seed on the remaining mother/seed trees. There was at least one mother tree on every acre.

EXPERIMENT 2: Natural regeneration four years before exploitation

3.6 hectares (8 acres) of an area likely to form part of the fifth annual felling coupe were treated in the year during which the first coupe was exploited. All mahogany and all second-storey species were left unfelled, with the exception of young regeneration of the reserved species. All undergrowth less than 7.5cm (3 inches) in diameter at 0.3m (1 foot) from the ground was cleared around mahogany seedlings. In addition, undesirable upper-storey species were frill-poisoned if ring barking had proved an unsuccessful means of killing them. Very little regeneration resulted.

EXPERIMENT 3: Natural regeneration four years after exploitation, with preliminary clearing nine years before exploitation

7.7 hectares (17 acres) of an area likely to form part of the ninth annual felling coupe were treated in the year during which the first coupe was exploited. All mahoganies and reserved species were retained and all undesirable middle-storey and upper-storey species were felled. For four years, the area was left unattended. In the fifth year, the lower level of the understorey and the coppice growth from the trees felled in the first clearing would be removed in anticipation of mahogany seeding.

Whether or not Experiment 3 proved successful, it implied such an expensive method of obtaining natural regeneration that for practical purposes it had to be ignored. Experiment 2, which cost a little less than Experiment 1, but gave poorer results, suffered from the disadvantage that it was difficult to forecast several years in advance just where a felling coupe would be located. Experiment 1 was the most promising of the three. However, the average cost for the natural regeneration option in Experiment 1 was more than the line-group planting in the artificial regeneration described above.

It is worth noting that Experiment 1 (but not Experiment 2 or 3) was carried out in the forest area where mahogany regenerates satisfactorily without assistance. It is doubtful if the experiment would have had even its limited success, if it had been carried out in the main Siba block where Mahogany is scarcer and *Cynometra* more abundant (Eggeling, 1940).

With the above background, this study was therefore undertaken to investigate the present distribution of the mahogany species and how the forest microenvironments have been modified to promote or prevent their natural regeneration. Microclimatic (light, rainfall, temperature) and edaphic conditions in Uganda's natural forests are important determinants of the regeneration development, distribution, composition and structure of the forest species. The forest history influenced by (a) humans, through commercial harvesting and ecological management, and (b) natural processes, through natural catastrophes (e.g. wind throw and animal damage), influence the way light, rainfall and temperature interact with forest vegetation (Eggeling, 1940).

Budongo Forest Reserve with an extensive history of timber-harvesting and ecological management in Uganda is suitable for this study since all appropriate compartments logged at different dates exist. Therefore, this study was aimed at an in-depth investigation of the effects of the light, photosynthesis, temperature and forest soils on the natural regeneration of the most harvested mahogany species.

2.5 Effect of forest types on natural regeneration in Budongo Forest Reserve

2.5.1 Forest types

Landale-Brown *et al.* (1964) noted that Budongo forest reserve contained over a quarter of the growing stock of timber in Uganda, much of it mahogany. It was also the best-known forest because it had been the focus of much work by the Forest Department (Eggeling 1947; Dawkins 1956; Langdale-Brown *et al.* 1964; Philip 1965, 1967; Naluswa 1970; Karani 1994; Plumptre and Reynolds 1994; Bahati 1995; Kamugisha and Nsita 1997). Consequently, three successional stages were identified and two ecotones between them.

The first successional stage is colonizing forest, which has two forms: on the deeper and better soils *Maesopsis eminii* (Engl.) is predominant, while on shallow poor soils *Olea welwitschii (*Knobl.*), Sapium ellipticum (*Baill.*)* and *Margaritaria discoideus (*Webster.*)* are successfully established. According to Eggeling (1947), these colonizing forest species may last for only one generation since most of them will not regenerate under shade and are replaced by mixed forest species. The second successional stage is a mixed forest, which has a great diversity of large tree species, including mahoganies such as *K. anthotheca* and *Entandrophragma* species (Eggeling 1947; Langdale-Brown et al. 1964). This stage may last for more than a generation, as mixed forest species are able to regenerate in gaps. But Dawe (1954) noted that in a mature-developed mixed forest mahoganies suffer a shortage of the smaller sizes, which has important ecological implications.

The third successional stage is a climax forest, which has *Cynometra alexandri* as the dominant species. The climax is mostly on shallow stony soils, valley bottoms with impeded drainage. However, Osmaston (1959) indicated that although *Cynometra* is predominant in the climax-poor soils, it is not necessarily going to replace all the mixed forest species. What may happen is for *Celtis* spp. and perhaps *Chrysophyllum* spp. to be the major constituents, while mahoganies will be scarce. The present study was conducted to verify and evaluate the above assertions.

2.5.2 Natural regeneration in Budongo Forest Reserve

The major influence on the ecology of Budongo forest has predominantly been human activities. Plumptre and Reynolds (1994) have reported that as a result of more than 60 years of logging, most of the reserve (about 623 km^2) has been exploited. Harvesting and treatments carried out to encourage regeneration of the valuable timber species have been well documented by Paterson (1991) and Plumptre and Reynolds (1994).

Initially, harvesting intensity in Budongo was low about 20 m^3 ha^1 and consisted of a two tier system in which the largest trees in the compartments were harvested at approximately 40 year intervals (allowed dbh was 120 cm and later reduced to 70 cm dbh). FAO (1989) reported that due to the low harvesting intensity, natural regeneration met a lot of competition from residual trees left by the saw millers. From 1959 up to the late 1960s a monocyclic system in which Budongo was to be virtually clear-felled on an 80-year rotation was introduced. This system enabled the opening of the crown canopy much more than would have been if a 40-year rotation were maintained (Karani 1994).

2.6 Ecology of the Budongo mahoganies: state of knowledge

The plant family *Meliaceae* is among the more useful to man because of its high quality timbers and for the ease with which some species can be grown in plantations (Eggeling and Harris, 1939; Pennington and Styles, 1975). The family is confined to the tropics and often grows in a variety of habitats from rain forests to mangrove swamps and semi-deserts (White 1962 1975). For example, in tropical Mexico and Central America, *Meliaceae* are abundant in the upper storey of the high evergreen forest (e.g. *Swietenia*). In Africa, the dominant high forest emergents, *Khaya, Entandrophragma* and *Lovoa* are important as timber species. In Malaysia, they form an important component of the understorey of the lowland forests (e.g. *Chisocheton* and *Aglaia*). Some members of the family are shrubs (*Turraea*), while (*Neregamia* and *Munronia)* are small suffrutices with a woody rootstock. Furthermore, all species of Meliaceae are woody; the majority being trees ranging from forest giants down to small trees.

The classification of the *Meliaceae* into family, subfamily, genera, subgenera and species has been in effect since 1789 (Pennington and Styles 1975). Meliaceae consists of 4 subfamilies: 1) *Melioideae,* 2) *Quivisianthoideae*, 3) *Capuronianthoidea* and 4) *Swietenioideae*.

Of importance to this study is the subfamily Swietenioideae, which consists of three tribes and 13 genera. One of the tribes is the Swietenieae consisting of nine genera that includes *Khaya* and *Entandrophragma*. There are six species of *Khaya*, four of these are on mainland Africa, and the other two are endemic to Madagascar and the Comoros. The genus *Entandrophragma* consists of 11 species (Figure 2.2).

Many meliaceae have unisexual flowers, but always with well-developed flowers of the opposite sex. In contrast to most rudimentary structures, the shapes and positions of these, relative to other parts of the flower, are remarkably constant within species and genera and even tribes but vary greatly between them (Eggeling and Harris 1939; Pennington and Styles 1975; Mabberley 1997).

This study is concerned with four large species belonging to the Meliaceae, which occur in Budongo Forest. One is *Khaya anthotheca* (Welw.) C. DC. The other three are species of *Entandrophragma: E. cylindricum* (Sprague) Sprague, *E. utile* (Dawe & Sprague) Sprague and *E. angolense* (Welw.) C. DC.

2.6.1 The Meliaceae in Budongo Forest Reserve, Uganda

Budongo forest consists of four main forest types three of which are in phases of ecological succession namely *Cynometra* climax (32 %), mixed forest (60 %) and colonizing forest (6 %). The fourth, the swamp forest, is found along streams and covers about 2 % of the area (Eggeling 1947; Webb 1947).

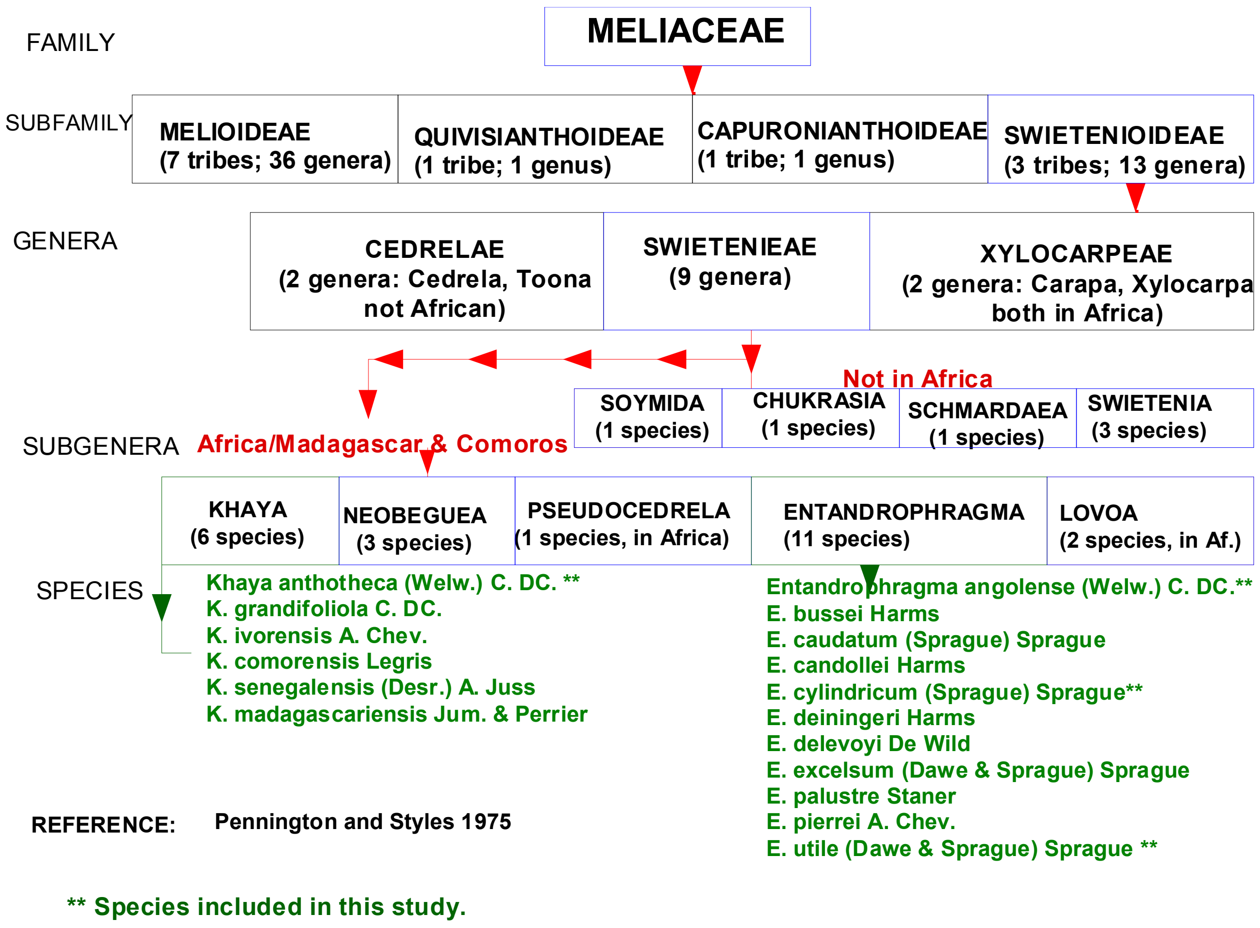

Figure 2.2: An overview of the *Meliaceae* family and species selected for the study

The mahogany species in the proposed study have variable ecological requirements (Eggeling and Harris, 1939). Therefore, for effective silvicultural management, it is important that these ecological variations are understood. The phenology; flowering patterns and ecological requirements of the four selected species are described below.

2.6.1.1 *Khaya anthotheca* (Welw.) C.DC.

K. anthotheca is medium to large sized, usually evergreen and up to 45-60 m tall. When mature, *K. anthotheca* has a large crown up to 10-20 m in diameter. It has spreading branches with a radius up to 20 m. The bole may reach over 3m in diameter. In Budongo forest, buttresses are present on mature stems. The bark is moderately thick in the open, but thin and smooth in a closed forest understorey. It exhibits small-scattered tubercles and circular flaking in old trees.

In Uganda, among the meliaceae timber species, *K. anthotheca* is predominant and naturally growing in Budongo and Bugoma forests. It’s seed is dispersed from March to June and in October (Synnott, 1985). *K. anthotheca* is generally propagated by seed, but can also be propagated by layering, root and shoot cuttings, and grafting in a poly-propagator (Pennington and Styles 1975). Efforts are being made to propagate the species by tissue culture. On the African continent, *K. anthotheca* is distributed in Sierra Leone, Tanzania, Angola, Zambia, Malawi, Mozambique and Guinea (Styles and White 1991).

Although it’s best to harvest the ripe fruits from the tree, fruit collection within 1-2 days of natural dropping also gives satisfactory results. *K. anthotheca* seeds have short viability period and show no dormancy regimes before germination (Synnott 1975, Mwima et al. 2001).

In Budongo Forest Reserve, *K. anthotheca* is reported to flower from January to April, then again in September. Fruits take 10-14 month to mature (Eggeling and Harris, 1939). Thus fruits are ready for seed dispersal almost one year after flowering from January to April and again July to August (Synnott 1985).

K. anthotheca regenerates well in colonizing and secondary forest, but with little recruitment in the undisturbed forests due to heavy shade (Hawthorne, 1995). *K. anthotheca* is common in old gaps within a forest environment. It occurs on deep, fertile and moderately moist soils. According to Eggeling and Harris (1940), *K. anthotheca* is the first high-forest tree to follow *Maesopsis eminii* in the colonization of proximal grassland. The species regenerates and grows best in deep fertile soils with more soil moisture than the other mahogany species. Its optimal regeneration niche is along riverbanks and degraded forest patches (Katende *et al.*, 1995; Eggeling and Harris, 1939).

K. anthotheca seed is vulnerable to attack by borer and sought after by small rodents. *K. anthotheca* saplings and young trees are susceptible to shoot borer (*Hypsipyla*) attack. Eggeling and Harris (1939) and Taylor (1960) suggest that *K. anthotheca* require light, and grows faster in old gaps. In Nigeria, Anon (1952 1957), Kemp (1961), Webb (1964) and Jackson (1973) reported that, although the mature trees occurred throughout the forests, regeneration was greatest in the outer boundary areas, where the canopy was not completely covered.

K. anthotheca prefers to germinate and initially grow under semi-open light-environments, but cannot withstand competition (Mwima *et al*. 2001); Katende *et al.* 1995). *K. anthotheca* responds well to organic and chemical fertilisers.

Young *K. anthotheca* stumps coppice well and evidence of the species coppicing in Budongo Forest are known (Naluswa, 1970). It is not known if such coppices can survive to maturity.

Hawthorne (1993) noted site differences where *K. anthotheca* was naturally regenerating. For example, in a closed forest ecosystem, seedlings can become established, but rarely survive more than two years, whereas seedlings under more open canopy (e.g. in gaps, along boundaries or where the forest had been treated), often survived 10 years, and probably to maturity. Therefore, the conclusion made by the above studies was that Khaya is a "pioneer" in the transition from savanna to forest. Also, Hawthorne (1993) asserts that regeneration in immediately logged forest is very sparse. He indicates that regeneration does not benefit from extensive disturbance.

K. anthotheca is found naturally from 120-1470m altitudes, but can grow at elevations up to 1525m (Styles and White 1991).

The highest temperature recorded in Budongo Forest Reserve, where the species grows and the study was conducted is 36.7 ^{0}C (Katende *et al.,* 1995). Minimum temperatures of 9.5 ^{0}C have been recorded. Although *K. anthotheca* trees can tolerate extreme temperatures, seedlings are more sensitive.

Good *K. anthotheca* growth has been observed in areas with an annual rainfall of about 900 mm. On well-drained soils, up to 2500 mm rainfall is tolerated, but then fruiting is generally poor. *K. anthotheca* is a lowland rain forest/riparian species (Pennington and Styles, 1975). Mean monthly precipitation in Budongo forest varies between 762 mm (January) to 4750 mm (November) (FAO, 1984).

Soil texture suitable for *K. anthotheca* may range from sandy-loam to heavy clay. The soil pH may vary from 6 to 9, but best growth occurs on soils with a pH of 6.2-7.0 (Katende *et al.,* 1995). *K. anthotheca* prefers medium textured fertile soils, but still performs better than most other mahogany species on less fertile soils.

2.6.1.2 *Entandrophragma cylindricum* (Sprague) Sprague

In Uganda, *E. cylindricum* is of relatively small size, but when mature, it is taller than mature *K. antotheca.* The tree attains 61-64 m height when mature (Eggeling 1952).

E. cylindricum is usually an evergreen tree, with a large crown up to an average of 10-25m in diameter. Diameter at breast height may reach over 3m on mature trees. Buttresses are small when they exist. The bark is moderately thick in the open, but thin in a closed forest understorey. It exhibits small-scattered tubercles and long-cylindrical and irregular flaking towards the base in old trees.

In Uganda, *E. cylindricum* appears in limited quantities in Mengo (Kyagwe) and Namamve (Eggeling 1952). On the African continent, *E. cylindricum* is well distributed in Sierra Leone, Angola and cultivated in Kenya (Nairobi Arboretum). In Uganda, and in Budongo Forest in particular, *E. cylindricum* is not widely spread (Synnott 1985; Katende *et al.,* 1995).

Synnott (1985) noted that *E. cylindricum* in Budongo Forest starts flowering in January and May. Fruits are fully formed by September. The fruit is a smooth, ellipsoidal-cucumber shaped (4-8 cm long). When ripe it is red-brown and contains the seeds. Although it's best to harvest the ripe fruits from the tree, fruit collection within 1-2 days of natural dropping also gives satisfactory results and is more practical.

Propagation is mainly from seed. Where seeds are normally sown in the nursery, they are tended to for 12-18 months before being transplanted in the forest environment (Synnott 1975). Seedbeds should be watered sparingly and soil should be kept loose to prevent caking. In Budongo Forest, predation from insects and rodents is prevalent (Eggeling, 1952). Propagation from shoot cuttings is not as successful as with *K. anthotheca.*

Under favourable moisture conditions, natural regeneration of *E. cylindricum* is usually profuse within a distance of 150m from the mother tree since seed is distributed by gravity and wind. Unfortunately, *E. cylindricum* prefers to germinate and initially grow under semi-open light-environments, but cannot withstand competition, especially from grasses. *E. cylindricum* responds well to organic and chemical fertilisers (Katende et al. 1995).

E. cylindricum is found naturally from 1100-1500 m altitudes, but can grow at elevations up to 1600 m (Styles and White 1991).

2.6.1.3 *Entandrophragma utile* (Dawe and Sprague) Sprague

This is a large tree species that can attain 50 m in height with massive branches. It is an evergreen with a round and large-spreading crown up to 10-25 m in diameter. Diameter at breast height may reach 2-5 m when mature. Buttresses are occasionally present. The bark is moderately thick in the open, but thin in a closed forest understorey. The bark is grey-brown cracked and fissured into squarish scale like pieces.

E. utile is shade-tolerant until fully established and appears to exist purely in the transition from mixed to the climax forest where it overshadow and out-competes other species (Eggeling, 1952; Synnott, 1985). It dominates the main canopy and understorey layers in the forest and is prominent in the old colonizing and old mixed forest although less evident in arboricide-treated areas.

In Uganda *E. utile* has been widely recorded (Mwima *et al*., 2001; Plumptre, 1994; Bahati, 1995; Howard, 1991; Eggeling, 1952; Eggeling and Harris, 1939). Specimens of *E. utile* were recorded in Acholi in 1933, Bunyoro in 1962 and Mengo (Kyagwe) in 1932. However, of the four mahogany species in the present study, it is the rarest in Budongo forest (Katende *et al.*, 1995). Disturbance of the environment inhibits its regeneration and growth.

In Budongo forest reserve, *E. utile* trees start flowering in February (Eggeling and Harris, 1939). Formation of mature fruits takes more than a year. Seed dispersal starts in February, through October and December. To date, matures trees are found along the "Royal Mile" and in the unlogged part of the forest.

Regeneration of *E. utile* is by seed. Trials on propagating the species by tissue culture are being made. Although it's best to harvest the ripe fruits from the tree, fruit collection within 1-2 days of natural dropping also gives satisfactory results. Unfortunately, *E. utile* seeds have a short viability period, have no dormancy and are favoured by larvae of insects found in the forest undestorey (Pennington and Styles, 1975).

Therefore, timing of seed dispersal in relation to the rainy season is essential for regeneration to take place (Mwima et al., 2001). Under favourable moisture conditions, natural regeneration of *E. utile* is usually within a distance of 50 m from the mother tree since seed is distributed by gravity and wind. Dispersal occurs during the dry season. This species prefers to germinate and initially grow under closed canopy with minimum light-temperature environments. It responds well to organic and chemical fertilisers (Hawthorne, 1995). In Budongo Forest Reserve, *E. utile* seedling growth is slow because the roots develop slowly (Sawyer, 1960). For example, seedlings attain 1m or less in 4 years (Synnott, 1975). In Budongo Forest Reserve, seedlings suffer higher mortality than other *Entandrophragma* species due to predation by antelope and rodents. Also, they suffer from Hypsiphyla shoot borers (Synnott, 1975). The seedlings are more sensitive than other *Entandrophragma* species and rapidly affected by drought and changes in exposure to sun (Synnott, 1975; Taylor, 1960). The seedlings are physiologically well suited to the deep shade of the forest floor. Light availability is noted to be a limiting factor on seedling growth. In unshaded environments, seedlings are stunted and may die (Synnott, 1975).

2.6.1.4 *Entandrophragma angolense* (Welw.) C.D.C. (Meliaceae)

E. angolense is an evergreen tree up to 35-55 m tall with a round, large crown up to 10-20 m diameter. Of the major mahogany timber species, *E. angolense* has the straightest bole when mature (Katende *et al.*, 1995; Eggeling and Harris, 1939). It has spreading branches and in Budongo Forest, diameter at breast height may reach over 3.5 m. Buttresses are more developed in *E. angolense* than any of the other *Entandrophragma* species. The bark is moderately thin in a closed forest understorey. It exhibits small-scattered tubercles and short cylindrical flaking in old trees. Young stems are smooth.

In Uganda, the distribution of *E. angolense* is recorded in Itwara (Kabarole), Kalinzu (Bushenyi), Budongo (Masindi & Hoima) and Mt. Elgon (Mbale) forests (Eggeling, 1952). In Budongo forest, *E. angolense* is not widely spread, since it requires fertile, well-drained and well-aerated soils (Eggeling 1952; Synnott 1975; Katende et al. 1995).

On the African continent, *E. angolense* is documented to be more abundant in Tanzania, Democratic Republic of Congo, and Malawi than in Uganda (Eggeling and Harris 1939). In Kenya, it is cultivated in the Nairobi Arboretum. It is the least preferred of mahogany species for timber in this study because it easily warps and twists if converted into products while green (Hawthorne, 1995; Katende et al 1995).

In Budongo forest, *E. angolense* is generally propagated by seed, which are dispersed in January, June and July (Eggeling, 1952). Plumptre (1995) noted that trees with a larger diameter (≥ 80 cm) have shown profuse seed production. *E. angolense* grows at forest edges and in thickets and prefers to germinate and initially grow under semi-open light-environments. Under favourable moisture conditions, natural regeneration of *E. angolense* is usually profuse within a distance of 200m from the mother tree, as seed is distributed by gravity and wind. Seedlings require shade for the first few years (Eggeling and Harris, 1939). The species has been over-harvested and is not as common as it used to be in the 1960s (Synnott 1985). Initial clearing and later some shade are required before establishment (Katende *et al.*, 1995).

2.7 Lessons learnt

In this review, the lessons learnt include: (a) logging is the most significant controllable activity affecting natural regeneration in the tropics including Uganda's natural forest, (b) the importance of water, light, photosynthesis, temperature and canopy manipulation in promoting mahogany regeneration is particularly identified and emphasized in most literature and (c) tree regeneration, especially for mahoganies, depends on prevailing climatic, edaphic, biotic and altitudinal conditions inside the forest. Plumptre (1994) and Paterson (1991) have indicated that harvesting of mahogany species over the last 60 years from the Budongo forest has greatly compromised and reduced the stock of seed trees in the forest. Consequently, there are two scenarios that support and contest the role of timber harvesting as a catalyst for mahogany regeneration in Budongo Forest. On one hand, Brasnett (1946), Dawkins (1956), Eggeling (1940), and Eggeling (1947) support canopy opening with the assumption that the operation would support mahogany regeneration. However, Bahati (1995 and 1998), Howard (1991) Paterson (1991) Philip (1965 1967) and Naluswa (1970) have suggested that the opening of the forest canopy through timber harvesting has resulted in physical conditions that may not have favoured mahogany regeneration. Studies in other forests have noted that in an open environment, predation on seedlings by herbivores is common (Kasenene, 1984, 1991; Johns 1988; Hartshorn, 1990). Also, insect pests take advantage of the suitable environment in which young regrowth is vulnerable to attack (Burgess, 1971;

Uhl and Viera, 1989; Verissimo *et al.*, 1992). Young seedlings are trampled on and some seedlings and saplings are destroyed (Marn and Jonkers, 1981). Therefore, this study was designed to investigate the factors that affect the regeneration, structure and distribution of selected mahogany species and how these may have been influenced by earlier (previous) or later (recent) timber harvesting.

CHAPTER 3

MATERIALS AND METHODS

Summary

This Chapter starts with a brief background of the country and description of the study area, the *Budongo Forest Reserve.* It describes the location, climate, edaphic profiles, biodiversity, ecology and human activities in and around the Budongo Forest Reserve and states the justification for selecting the study *treatments and* compartments*.* A list of equipment used in the study, slope correction factors and the survey team are presented in section 3.3. The study design and distribution of sample plots are presented in section 3.4. Section 3.5 presents data collection methods and procedures. Subsection 3.5.1 gives a general lay out of samples. Subsection 3.5.2 contains details of regeneration data collection methods and procedures. Section 3.5.2.1 presents the definition for regeneration and the methods used for its assessment. Soil sampling methods are presented in Section 3.6. Section 3.7 details data collection methods of forest illumination, PAR, temperature, and ground and canopy covers. Assessment of stumps is in section 3.8, while measurements of slope angles and determination of aspect are in section 3.9. Finally, data summarization and statistical analyses are described in subsection 3.10.

3.1 Country background

Uganda is a relatively small landlocked country lying astride the equator in east-central Africa. It occupies about 236,000 km^2 *of the central African plateau, north of Lake Victoria. It is bordered by the Democratic Republic of*

Congo to the west, Kenya to the east, the Sudan to the north, and Rwanda and Tanzania to the south (FAO, 1984). The climate in Uganda is influenced by its latitudinal position, altitude and topography (Howard, 1991). It has a bimodal rainfall pattern (April-May and October-November), both with an average of 1,000-1,500mm of rain per annum. The Northeast constitute the driest region, while the wettest regions include the Rwenzori area (mountains of the moon) and the islands of Lake Victoria as well as the highlands of the Southwest. The mean temperatures are also influenced by altitude and follow the patterns of the rainfall (Howard, 1991; Langdale-Brown and Wilson, 1964).

Uganda lies on a very ancient sandy clay loamy soil, which is reasonably fertile, but highly weathered (Howard, 1991; Paterson, 1991; Langdale-Brown and Wilson, 1964). However, the Budongo forest reserve lies on more fertile soils (ferrisols, lithosols and histosols), which are associated with the more recent landforms and extremely high biodiversity along the western rift (Howard, 1991).

The population of Uganda has risen sharply in the last few decades. By 2002 the country had an estimated population of 24.5 million (preliminary population and household census, 2002) from 3.2 millions in 1920s. With an annual growth rate of 3.67% (between 1980 to 1990), the population is predicted to reach 53.14 million by the year 2025 (World Resources Institute, 1997). World Resources Institute (1997) ranks Uganda as Africa's fourth most densely populated country, after Rwanda, Burundi and Nigeria. Uganda is predominantly an agricultural country with the majority (83%) of the labour force engaged in subsistence farming (Howard, 1991; Hamilton, 1984). Therefore, agriculture and forestry will continue to play important roles in the economy (Hamilton, 1984).

The present study was conducted in Budongo Forest Reserve (Figure 3.1), which is located in the Districts of Masindi (consisting of the Main and Kaniyo Pabidi Blocks) and Hoima (consisting of Siba Block) in Western Uganda.

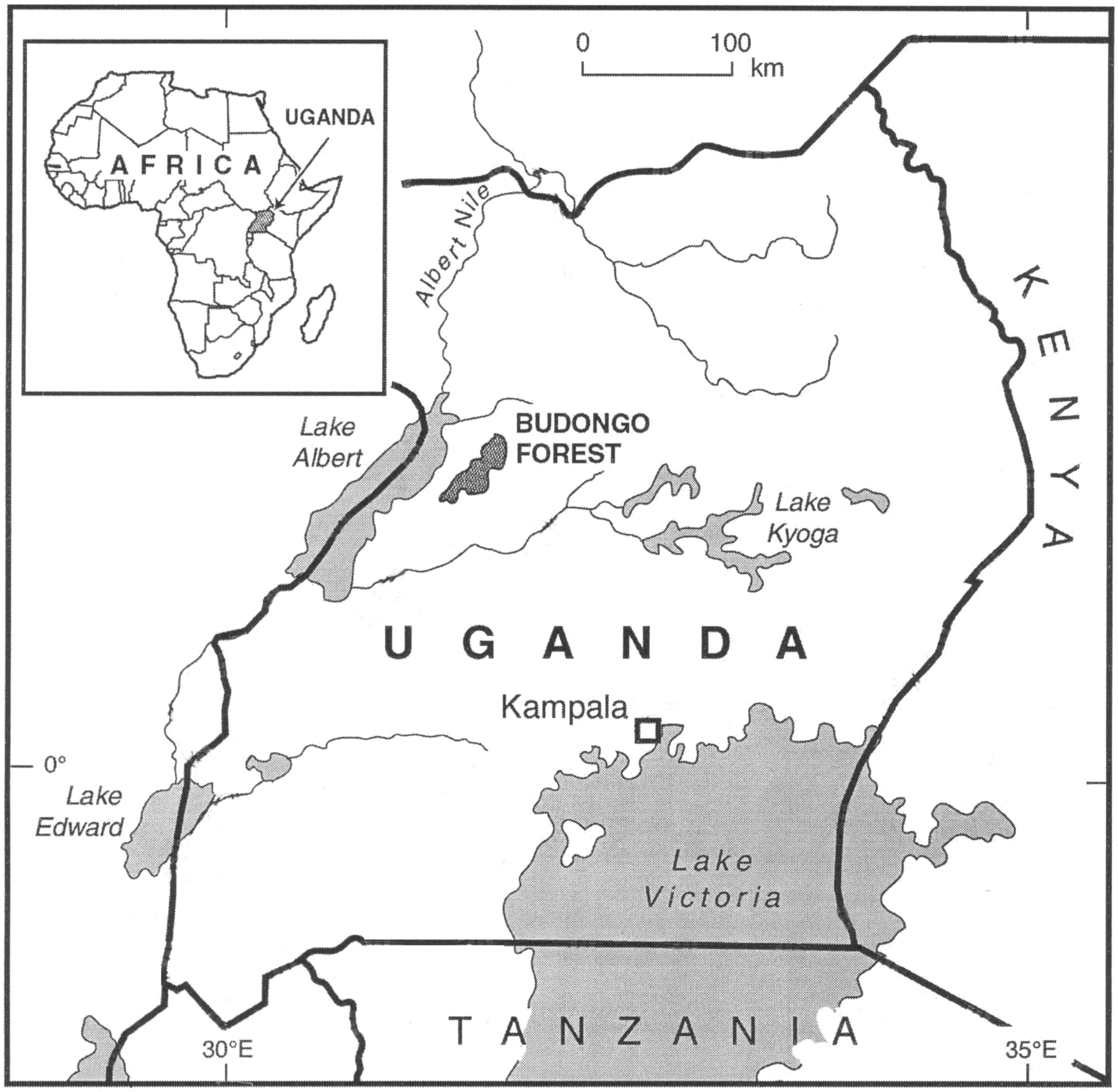

Figure 3.1: Location of Budongo Forest Reserve

3.2 Budongo Forest Reserve: description

Budongo Forest, 1°37'-2°3'N; 31°22-31°46'E is located at the top of an escarpment east of Lake Albert near the eastern edge of the western rift valley, in Masindi and Hoima Districts. The forest reserve is contiguous with

Murchison Falls National Park and Karuma Game Reserve in the North, and Bugungu Game reserve in the West. It is about 14 km from Masindi town on Butiaba road and approximately 15 km from Masindi town on Murchison Falls National Park road (Ndemere 1997).

The terrain is gently undulating with a general downhill slope to the NNW. Two main rivers (Sonso and Waisoke) and several small streams drain the forest. The underlying rocks are ancient gneisses, schists and granulites of the basement complex, overlain by the Bunyoro series sediments in a small area of the Siba block (Howard, 1991). The soils are ferralitic, mainly sandy to sandy clay loam of low to moderate fertility. The area has a bimodal rainfall with a peak in the March-May period and another in the September-November period. The mean average annual rainfall is 1150-1500 mm. The mean minimum daily temperature ranges from 17°C in April to 20°C in October. The corresponding mean maximum daily temperature ranges from an average of 28°C in July to 29°C in January. Temperature averages 22.8 °C, which sometimes drops to about 16 °C (FAO, 1984).

The soils in Budongo Forest Reserve are mostly of volcanic origin and the vegetation includes savannah grassland species such as Aspilia *sp*., Brachiaria brizantha, Cymbopogon afronardus, *Hyparrhenia filipendula, H. dissoluta, H. rufa, Panicum maximum, Sporobolus pyramidalis, tall elephant grass (*Pennisetum purpureum) *and a mosaic of forests (woodland, tropical, artificial timber plantations and agroforestry forests) (Langdale-Brown, 1960). Human activities around the forest are gradually changing this type of vegetation (Rwabwoogo, 1997). Agriculture is the major economic activity around Budongo forest with commercial sugarcane and tobacco growing at the forest's edge. Other central and local Government forest reserves around Budongo forest, which influence the utilization of the Budongo Forest Reserve, are shown in Table 3.1. All consist of a mix of mahogany and other species.*

Around the Siba Block, human activities are mainly agricultural with an emphasis on food such as Musa *sp. (Banana*), *Manihot esculenta (Cassava), Eleusine coracana (Millet) and cash crops such as Camellia sinensis (tea) and* Nicotiana tabacum *(Tobacco). Other commercial crops are Phaseolus vulgaris (Beans),* Zea mays *(Maize) and Arachis hypogaea (Groundnuts). The high population pressure around the forest has forced people to cultivate marginal areas around the Siba Block (NEMA, 1997). Timber harvesting takes place in the forests listed in Table 3.1.*

3.2.1 Budongo forest biodiversity status

The forest comprises mostly medium elevation moist semi-deciduous forest. In addition, it consists of some grassland areas capable of supporting forest cover. According to Howard (1991), in Budongo forest there are approximately 240 tree species (56% of Uganda's total). Several tree species are listed as endangered, four of which, including K. anthotheca, E. cylindricum, E. utile and E. angolense, are also listed in the same classification. The forest also has approximately 150 species of forest birds (49% of the country's total); 5 species of diurnal forest primates (42% of the country's total) and 42 species of forest swallowtails and charaxid butterflies (60% of the country's total) (Howard, 1991; Ndemere, 1997). The list of plant species mentioned in this thesis is shown in Appendix 3.

Table 3.1: *Central and Local Government Reserves around Budongo Forest Reserve*

A: Central Forest Reserves

Hoima Central Forest Reserves (CFR)				Masindi Central Forest Reserves (CFR)		
Code	Forest Name	Area (ha.)		Code	Forest Name	Area (ha.)
HO/01	Budongo (part)	637		MS/01	Budongo (part)	81, 893
HO/02	Bugoma	41, 144		MS/02	Fumbya	425
HO/03	Bujawe	4, 869		MS/03	Kaduku	583
HO/05	Ibamba	313		MS/04	Kasokwa	73
HO/06	Kahurukobwire	1, 088		MS/05	Kasongoire (part)	1216
HO/07	Kandanda-Ngobya	2, 556		MS/06	Kibeka	9, 570
HO/09	Kyahaiguru	422		MS/07	Kigulya Hill	391
HO/10	Kyamugongo	117		MS/09	Kitonya Hill	293
HO/11	Mpanga	544		MS/10	Maseege	951
HO/12	Mukihani	3, 619		MS/11	Masindi	39
HO/13	Wambabya	3, 429		MS/13	Musoma	278
HO/14	Kasongoire (part)	1, 873		MS/14	Nsekuro Hill	132
				MS/15	Nyabyeya	347
				MS/16	Nyakunyu	466
				MS/17	Nyamakere	3, 898
				MS/18	Rwensama	127
				MS/19	Sirisiri	492
Total	12 Forests			Total	17 Forests	
B: Local Forest Reserves						
Hoima Local Forest Reserves (LFR)				Masindi Local Forest Reserves (LFR)		
Code	Forest Name	Area (ha.)		Code	Forest Name	Area (ha.)
HO/04	Hoima	5		MS/08	Kirebe	49
HO/08	Kijubya	34		MS/12	Masindi Port	18
Total	2 Forests			Total	2 Forests	

Notes: *Central Forest Reserves (CFRs) are managed by the Central Government and their routine management is by the Forest Department. Local Government manages Local Forest Reserves (LFRs) and their routine management is by the District Administration. All the forests listed in the table above contain mahogany.*

3.2.2 The study treatments (compartments)

Budongo forest reserve consists of three parts, two of which can be considered as patches - Siba and Kaniyo Blocks (Figure 3.2). Most of the biological research on Budongo has, in the past, concentrated on the Main Block consisting of Biiso, Nyakanfunjo, and Waibira blocks (Eggeling 1940; Eggeling 1947; Langdale-Brown et al. 1964; Paterson 1991; and Plumptre and Reynolds, 1994; Ndemere 1997; Bahati 1998; Obua et al.*, 2000; Mwima* et al.*, 2001). This study located sample plots both in the main forest and in the two forest patches.*

3.2.3 Justification for treatment and compartment selection

Budongo Forest Reserve is divided into 68 compartments. One compartment (N15) is a strict nature reserve and represents the unlogged forest. Howard (1991) proposed a zonal division of the forest in which additional compartments (earlier and later logged) are also identified.

For purpose of comparing between logged and unlogged forest, compartment N15 was identified as the unlogged. As earlier indicated, Budongo forest consists of a main block and two discrete patches (Siba and Kaniyo Pabidi). At least one compartment was located in each of the two forest patches to identify where the pattern of mahogany regeneration was most abundant.

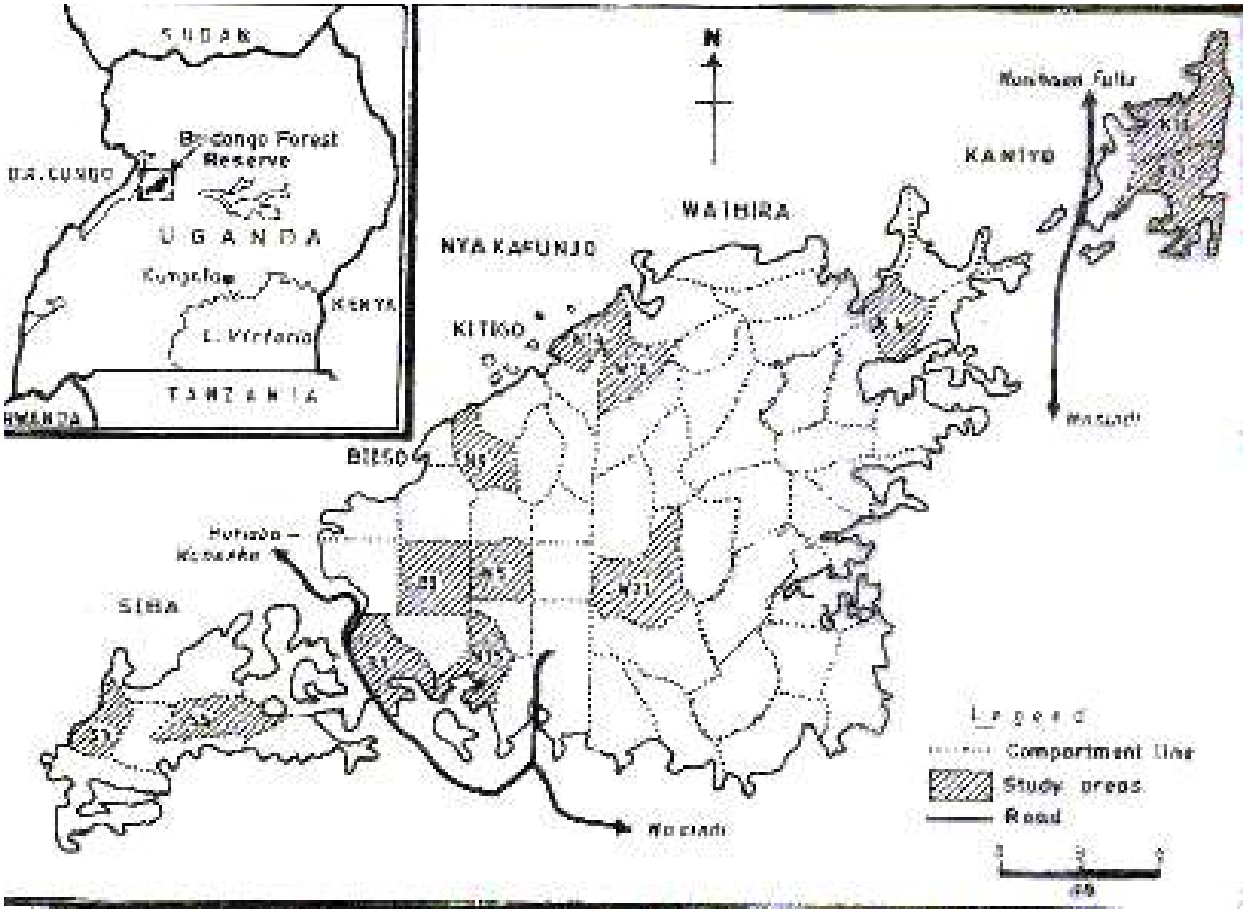

Figure 3.2*: Location of Study Area (Compartments)*

Note: *1. Compartments S3 and S5 are in Siba Block (Patch)*

Compartments N15, N14, N9, N5, B3, B1, W16, W21, W25, W40 are in the Main Block and compartment K4 and K12 are in the Kaniyo Pabidi Block (Patch).

2. Compartment N15 is the unlogged treatment (UnL). Compartments N14, N9, N5, S5, S3, B3, W16 make the earlier logged treatment (EL), while compartments B1, W21, and K4 make the later logged treatment (LL)

For comparison between treatments, this study evaluated and compared mahogany regeneration, soils and micro-environmental factors in samples of the forest logged between the 1930s and the 1990s. The earlier logging (at least 34 years ago) comprised the areas logged in the 1930s-1960s. Compartments N14, N9, N5, S5, S3, B3 and W16 were in the earlier logging category. The later logging (logged within the last 34 years), comprised the areas logged in the 1970s-1990s. Compartments B1, W21 and K4 were in the *later logging category. The unlogged compartment (N15) represented the unlogged treatment (see Appendix 1).*

3.3 Equipment used, slope correction and survey team

3.3.1 List of equipment

The list of equipment and coding forms used during the study for recording tree, sapling and seedling individuals, and recording the microenvironment parameters are detailed in Table 3.2.

Table 3.2: *Equipment used during the study*

List of equipment			
A	Linear distance ■ 50m fiber glass tape ■ 100m wire-rope tape marked at 0.5m interval	F	Illumination ■ Light meter (Lux)
B	DBH ■ DBH tape ■ DBH Caliper ■ Linear tape for extremely large stems.	G	*Photosynthetically Active Radiation (PAR)* ■ Quantum sensor LQ 250
C	Height ■ Suunto clinometer ■ Haga altimeter	H	Slope angles and aspect ■ Suunto clinometer ■ Hand-held compass
D	*pH* ■ pH-moisture meter	I	Soil sample collection and transect cutting ■Hoes ■ Machetes (Panga) ■ Spade and shovel

E	*Temperature (below, F. floor and understorey air-temp)* ■ Thermocouple	J	Record keeping ■ Coding sheets ■ Sample charts

3.3.2 Correction for slope

The following correction factors were used to correct instrument readings to obtain true horizontal sampling plots. Table 3.3 below shows the slopes encountered, correction factor and total study area sampled.

Table 3.3: *Slope angles and slope correction factors across the study area*

Slope (Degrees)	Correction factor	Area of study area in hectare
0^0->5^0	0.08	3201.6
≥ 5^0 <10^0	0.23	2950.2
≥ 10^0 <12.5^0	0.31	250.5
≥ 12.5^0 <15^0	0.49	211.7
≥ 15^0 <17.5^0	0.71	395
≥ 17.5^0 <20^0	0.97	311
≥ 20^0	1.28	153
Total		**7473**

Note: *The study areas in Budongo Forest in the different slope-angle categories determined from National Biomass Center GIS coverages and topography data*

Source for slope correction factors: *User's Manual-Suunto clinometer (Forest slope/angle-measuring hypsometer)*

3.3.3 The Field Team

The field team was made up of the PhD. student, three Field Assistants and two Game Guards.

3. 4 Study design, selection, distribution of samples and sampling intensity

3.4.1 Study design

The procedure for data collection included selecting and identifying the boundaries of the compartment to be sampled. Then, two perpendicular transects were laid from the center of each sampled compartment and extended to the edges of the compartment. Transects were laid in the north-south and east-west directions

3.4.2 Selection of samples

The rationales for selecting the study compartments (treatments) were based on their location, size and dates of last logging. The main block located in the center of the reserve covers the largest area, while then Siba patch located in the southern and Kaniyo Pabidi patch located in the northern part of the forest reserve are smaller. In Budongo forest reserve, there is only one strict nature reserve, which in this study is known as the unlogged compartment. This compartment is more or less uniform in species structure and composition. In this study, this area forms the unlogged treatment. The earlier logged treatment constitutes the largest area of the forest. Due to varying logging intensities in these areas in the past, it is more diverse. Therefore, the greatest number of compartments investigated (7) came from this treatment. The diversity in the later logged treatment is not as high as in the earlier *logged area. Consequently, fewer (three) compartments in this area were investigated.*

Furthermore, the selection of compartments was aimed at capturing representative populations of the selected mahogany species from the main block and the two forest patches (Table 3.4).

Table 3.4: *Treatment categories and number of compartments sampled during the field survey*

Treatment category	**Compartments**	**Location and number of compartments**		
		Main Block	Siba	Kaniyo Pabidi
Not logged (control)	N15	1 (n=24)		
Earlier logging (1930s-1980s)	N9, B3, N14, N5, W16, W21	6 (n=140)		
	S3,		1 (n=22)	
Later logging (1970s-1980s)	K4			1 (n=24)
	B1, S5	2 (n=48)	1 (n=24)	
Total		**8 (n=188)**	**2 (n=46)**	**1 (n=24)**

Note: *The number in brackets is of sample plots*

3.4.3 Sampling intensity

Two compartments had 20 and 22 plots, but the rest of the compartments had 24 plots (Table 3.4). The percentage of the area sampled in the different compartments to total study area were unlogged (13%), earlier logging (8%) and later logging (8%). The intensity of sampling (percentage of samples to *treatments) was unlogged (0.3%), earlier logging (0.4%) and later logging (0.3%) (Table 3.5).*

Within each compartment, plots were randomly selected and data (mahogany regeneration and trees, ground and canopy cover, soil samples, illumination, PAR and temperature) were measured or estimated. The plots were 25m x 50m each.

***Table 3.5:** Samples and intensity of sampling across the study area*

Treatment	**Compartment**	**Percentage (%) of total study area**	**Percentage (%) of treatment**
Unlogged	N15 (n=24)	13	0.3
Earlier logging (1950s-1960s)	N14 (n=24)	5	0.7
	N9 (n=24)	6	0.6
	N5 (n=20)	7	0.4
	S3 (n=22)	11	0.3
	B3 (n=24)	7	0.5
	W21 (n=24)	11	0.3
	W16 n=24)	9	0.4
Later logging (1970s-1980s)	B1 (n=24)	14	0.3
	S5 (n=24)	7	0.6
	K4 (n=24)	10	0.4
Total	**11**	**100**	**4.8**

***Note:** The number in brackets is of sample plots*

3.4.4 Study matrix

The study design-matrices in Tables 3.6 and 3.7 below show the levels at which the survey was conducted. To compare data between treatments, the unlogged (Compartment N15) was compared to data-averages from the earlier logged (compartments N14, N9, N5, S3, B3, W21 and W16) and later logged (compartments B1, S5 and K4). Also, data averages from earlier logged treatments were compared to the later logged treatment. Eleven compartments consisting of 258 plots were sampled.

Table 3.6: *Matrix for comparison between treatments*

Compartments	Earlier logging (1950s-1960s aggregated)							Later logging (1970s-1980s aggregated)		
	N14	N9	N5	S3	B3	W21	W16	B1 n=24	S5 n=24	K4 n=24
N15 (n=24)	*							*		
N14 (n=24)										
N9 (n=24)										
N5 (n=20)										
S3 (n=22)										
B3 (n=24)										
W21 (n=24)	*									
W16 (n=24)										

Note: *n=24 are samples in a compartment.* * *indicates inter-treatment comparisons.*

Table 3.7: *Matrix for comparison within treatments*

Treatment	Compartment	Earlier logging							Later logging		
		N14	N9	N5	S3	B3	W21	W16	B1	S5	K14
Unlogged	N15 (n=24)	*	*	*	*	*	*	*	*	*	*
Earlier logging (1950s-1960s)	N14 (n=24)		*	*	*	*	*	*	*	*	*
	N9 (n=24)			*	*	*	*	*	*	*	*
	N5 (n=20)				*	*	*	*	*	*	*
	S3 (n=22)					*	*	*	*	*	*
	B3 (n=24)						*	*	*	*	*
	W21 (n=24)							*	*	*	*
	W16 (n=24) \\								*	*	*
Later logging (1970s-1980s)	B1 (n=24)									*	*
	S5 (n=24)										∀
	K4 (n=24)										

Note: *n=24 are samples in a compartment. ∀ indicates inter-compartment comparisons.*

3.5 General layout of samples and regeneration data collection methods

3.5.1 General layout of sample plots

In each compartment sampled, two transects, perpendicular to each other were laid from the center, where a cross-trench was marked. The cross transects (north-south and east-west) were extended to the compartment edges. A hand compass was used to determine the North-south and East-west directions. Sample plots, each 50 m X 25 m were laid randomly along and off the transects. The north south transect was sampled first followed by the east west transect (Figure 3.3). A minimum of 20 sample plots and a maximum of 24 sample plots per compartment were assessed (see Table 3.4 above). At each sample plot, data on mahogany trees and regeneration (saplings and seedlings), illumination, PAR and temperature were assessed and recorded. Soil samples (top and subsoil) from each compartment were collected from which soil chemical analyses were performed.

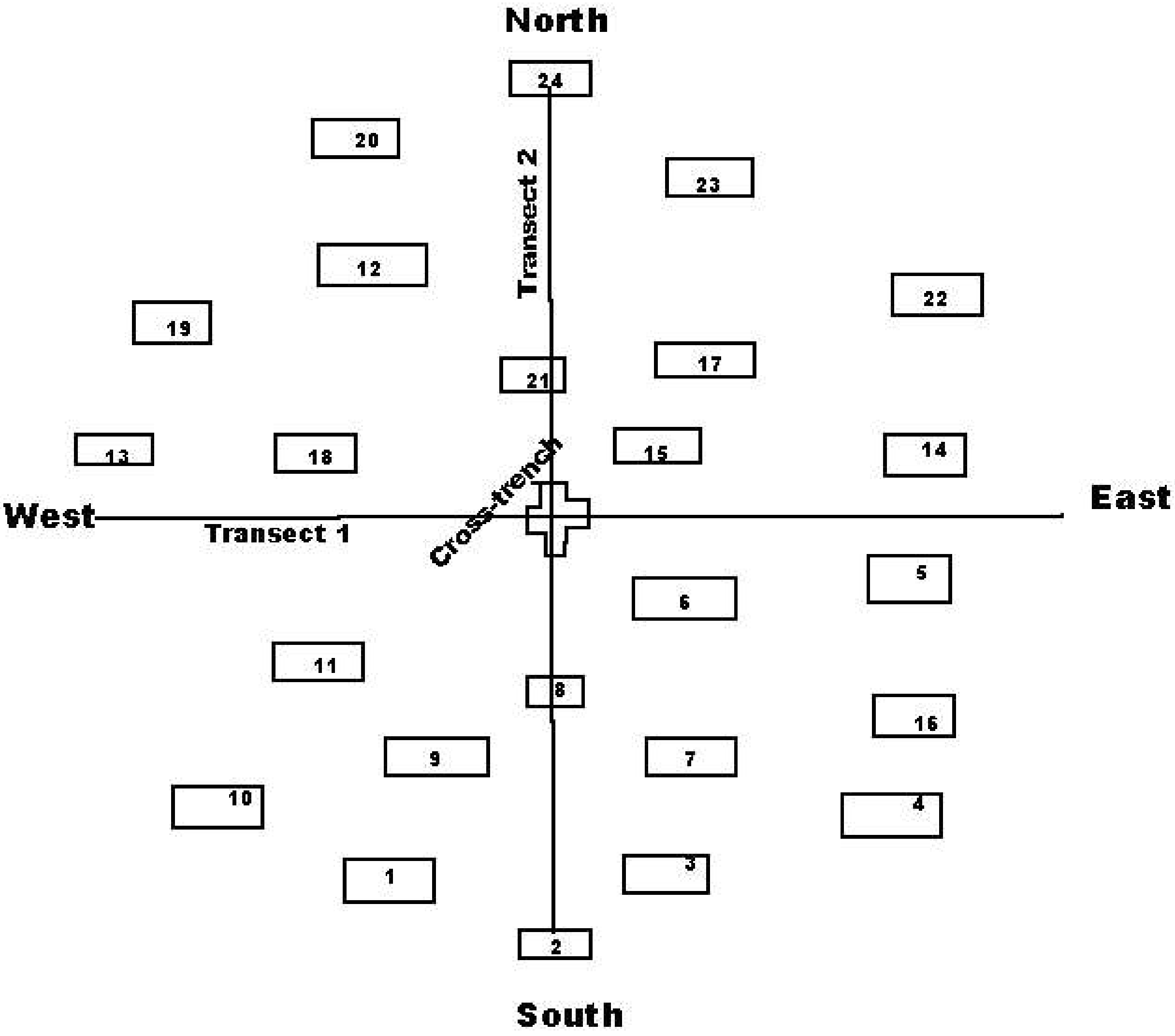

Figure 3.3: *Sketch map of the distribution of sample plots in a compartment. This design was specifically for compartment 21*

3.5.2 Regeneration data-collection methods and procedures

3.5.2.1 Definitions

In this study, mahogany tree stems ≥30 cm DBH were sampled. Sapling individuals were defined as individuals ≥2.5 and <5.0 cm at root collar, while seedling individuals were from a germinating seed that could be identified (with well formed leaves) to <2.5 cm at root collar. The other mahogany *growth forms assessed were poles (>5 and <10 cm dbh) and small trees (>10 and <30 cm dbh).*

In addition, crown depth was the distance in meters from the first main branch on the stem (timber height) to the top most point of the crown. Crown diameter was the mean of 2-3 horizontal distances taken perpendicular to each other of a tree or sapling's crown edges. In this study, the mean of two readings was recorded as the crown diameter.

3.5.2.2 General assessment of the mahogany individuals

*Two perpendicular transects (north-south and east-west directions), were centrally located in each of the compartments sampled (Figure 3.3 above). A hand-held compass was used to determine the directions. Along and off each transect, the sampling points for each compartment were determined using random numbers (100 – 500) beginning from each of the transect edges. Any random number picked from the random numbers was the distance in meters from the edge (starting point) of the transect or from one sample to the center of a subsequent sample. At the established center of each sampling point, a rectangular plot of 50 X 25 m was located and marked with colour flags (Snell, 1991; Raunkiaer 1934). Within each plot, a total count of all the trees, small trees, poles, saplings and seedlings of the four species (*K. anthotheca, E. utile, E. angolense, *and* E. cylindricum) *were determined. For trees, poles and saplings, measurements included DBH, height, crown depth and crown width. As earlier mentioned all plants with ≤ 2.5 cm diameter measured at root collar were considered as seedlings.*

A 50 X 25 m plot is appropriate for sampling and comparing natural forest ecosystems after different intensities of selective harvesting. The method *permits estimation of the density of individuals per unit area (Cottam et al. 1953; Cottam and Curtis, 1956). Crown depth and crown width were recorded for trees, poles, and saplings only. Crown depths were estimated by subtracting individual timber height (point of first branching) from total height, while estimation for crown diameter was by use of a linear tape taken on the forest floor at two cross-sectional points corresponding to the crown and the average recorded.*

Addition ecological observations of possible relevance, such as number of tree falls, presence of climbers, ground and canopy covers, presence of epiphytes, animal damage, insect infestation and number of defected stems in each sample plot were also recorded. Ground and canopy cover were estimated using Ostrom's (1992; 1998) method. The method employs a 100% scale, where a completely covered sample is represented by 100%, while a completely exposed sample is represented by 0%. Visual assessment was used to indicate the intermediate scales. The results of these observations from the different compartments were to allow detection of any quantitative and qualitative changes and compare these to mahogany regeneration, population structure and distribution after years of timber harvesting.

3.5.2.3 Seedling, sapling, pole, and tree measurements

All mahogany individuals in the seedling, sapling, pole and tree size classes located within the sample plot (50 m X 25 m) were identified to species level and measured. Seedlings were only counted.

For saplings, poles and small trees, a diameter tape or a diameter caliper was used, while for buttressed and extremely large tree stems, a linear tape was used and diameter calculated. Diameter was measured for the tree, pole and sapling classes at breast height (1.3 m on upper side of the stem) from the ground. For seedlings, only diameters at the root collar were measured. A hypsometer (Suunto clinometer) was used to estimate height. Diameters for buttressed or very large trees were measured using a linear tape measure, above the buttress where applicable.

Individual tree, pole, sapling and seedling crowns depths were estimated by employing the Pythagoras theorem of base distance measurement. The instrument (Haga altimeter), which was already calibrated to read off the height, was used if you were a certain fixed distance from the base of the tree. All counts and measurements were recorded on a coding sheet.

3.6 Soil Sampling layout and sample collection

3.6.1 Soil sampling layout

The soil-sampling layout across the study area followed a similar pattern with the sampling of the mahogany individuals (see Figure 3.3). The same plots were used and at least 20 soil cores (compartment N5 consisting of top and subsoil) were sampled in each compartment (Table 3.8). Hoes, machetes (pangas), spades and shovels were used. For each profile pit, topsoil and subsoil were carefully separated, labeled and packed for transportation to the soil analysis laboratory at Makerere University Soil Science Laboratory.

Table 3.8: *Total number of soil samples across the study area*

Treatment	**Compartment**	**Number of samples**		
		Top soil	Subsoil	Total
Unlogged	N15	24	24	48
Earlier logging (1950s-1960s)	N14	24	24	48
	N9	24	24	48
	N5	20	20	40
	S5	24	24	48
	S3	22	22	44
	B3	24	24	48
	B1	24	24	48
Later logging (1970s-1980s)	W2	24	24	48
	W16	24	24	48
	K12	24	24	48

Note: 258 samples of topsoil and 258 samples of subsoil were collected and analyzed.

3.6.2 Soil sample collection

Soil corers (Sanchez 1976) were used to obtain topsoil samples. Subsoil was collected after digging a soil profile to ascertain the distinction between the two layers. Topsoil samples were collected at < 15 cm depth. Below that depth, subsoil samples were collected (Steiner 1990). The collected samples were stored in plastic bags. Labels indicating study site, date, and soil type (top or subsoil) were tagged on the plastic bags. The analysis for total nitrogen, available phosphorous, extractable potassium, pH, cation exchange capacity (CEC), organic carbon, Na, Ca, Mg and soil structure were carried out on each sample collected.

3.6.3 Soil sample analysis

3.6.3.1 Texture

In this study, two methods were employed to determine the particle size distribution in the soil samples collected. These were the quantitative analysis followed by use of the Stoke's law approach. These two methods are based on the fact that (a) particles settle out of soil-water suspension in order of decreasing size, and (b) the specific gravity of a soil suspension is directly related to the total quantity of soil material still in suspension.

- ***Quantitative analysis***

Separation of the gravel and sand was by shaking on a standard soil sieve (0.2 mm x 0.2 mm) and then determining the percentage of material retained on each sieve by weighing. Only 100 g of soil representing both top and subsoil were weighed for analysis.

- ***Stoke's law***

The analysis of the silt and clay particles was determined by the material that remained in a water suspension as a function of the time that the suspension was allowed to stand. For maximum accuracy the suspension was completed at specific time (1 hour) intervals in a pipette. In addition, a soil hydrometer (ASTM 152H) was used to measure the change in specific gravity of the soil suspension over 3 hours at 20 ^{0}C (Jackson, 1958). The hydrometer uses the Bouyoucos scale, expressed as the percent by mass (g) of soil in suspension. Two samples, each weighing 100 g representing the top and subsoil of soil were analyzed.

3.6.3.2 Soil reaction - pH

Soil samples from both the top soil and subsoil of each plot were separately diluted with distilled water. Thereafter, 0.01 M $CaCl_2$ *solution was added to a mixture of soil/distilled water in a pH gauge to measure and record the pH values. The values obtained represented the pH of the soil solution under actual field conditions in the compartments sampled.*

3.6.3.3 Organic matter

The amount of organic matter available in the soil samples (100 g of top and subsoil) was determined by using the wet combustion method, which was based on the oxidation with chromic acid and the use of an indicator solution (Walkley-Black method) (Black, 1965). The Walkley-Black method is dependent upon the oxidation of the active organic content of the soil sample by chromic acid in the presence of excess concentrated sulphuric acid. The remaining chromic acid is then back titred with a ferrous sulfate (indicator) solution.

3.6.3.4 Total Nitrogen (N)

Determination of total nitrogen available in the soil samples was carried out using the Kjeldahl technique. In the Kjeldahl procedure, nitrogen is converted to $(NH_4)\ SO_4$ *by a catalyzed digestion* (K_2SO_4)*. The* K_2SO_4 *elevates the boiling point of the concentrated* H_2SO_4*, which allows the reaction to go to completion at 360* ^0C*. On completion of digestion, the compound is made strongly alkaline by addition of concentrated NaOH, and ammonia is then distilled by steam distillation into a solution of boric acid* (H_3BO_4)*. The ammonia neutralizes the boric acid. Back titration of neutralized boric acid with standardized* H_2SO_4*, gives a quantitative determination of the amount of nitrogen in the soil sample. The procedure given above follows Black (1965) and Allen (1989).*

3.6.3.5 Available Phosphorous (P)

The available phosphorus was determined by extraction of phosphorus from 100 g of soil sample (top and subsoil respectively) followed by a colorimetric test for the concentration of phosphorus. The combination of HCl and NH_4F *dissolved aluminum and iron phosphates by its complex ion formation with these metal ions in an acid solution (Jackson, 1958).*

In determining the amount of available phosphorus in the soil samples, the following chemical reagents were used: (1) HCl and NH_4F *– extraction solution (2) ammonium molybdate, (3) dilute stannous chloride solution, (4) primary phosphate standard, 50 ppm, (5) secondary phosphate standards (0.0, 0.4, 0.8, 1.2).*

3.6.3 6 Exchangeable Potassium (K)

The amount of potassium available in the soil sampled was determined with the use of two chemical reagents mixed with 100 g of separate soil samples (top and subsoil). The two reagents are: (1) NH_4Oac *(ammonium acetate, adjusted to pH 7.0) and (2) standard potassium solution. The actual values of potassium were read off from an absorption spectrophotometer and the procedures followed are described in Allen (1989) and Black (1965).*

3.6.3.7Calcium, Sodium and magnesium

The above three nutrients (calcium, sodium and magnesium) were extracted with ammonium acetate (Okalebo et al., 1993) and determined by flame photometer (sodium) and atomic absorptiometer (calcium and magnesium).

3.7 Forest illumination, PAR and temperature measurements

3.7.1 Illumination (forest understorey light) measurements

A light meter (Model LQ 250) was used to take understorey forest illumination (Lux). All illumination measurements were recorded between 12:00 p.m. and 3:00 p.m. This time-range was adopted after a pilot field trial to determine the minimal variation of instrument readings during daylight. In all the compartments, the time 12:00 p.m. to 3:00 p.m. showed the least illumination value variation. Illumination measurements were made at two levels: (a) at the center of each sample plot, (b) at the individual growing position of all the encountered mahogany regeneration individuals (seedling and saplings) and (c) at the center of gaps encountered within the plot.

3.7.2 Photosynthetically Active Radiation (PAR) measurements

Direct measurements of photosynthesis in quanta units (μms^{-1}m^{-1}) were recorded at the center of each sample plot and at the individual mahogany regeneration (seedlings and saplings). A quantum (Photon Lux Density, LQ 250) sensor was used. With the quantum base-instrument in one hand, the other hand moved the quantum sensor up to the seedling and sapling center. A digital value in μms^{-1}m^{-2} was recorded after a stable record on the instrument screen was registered. At every pole, small and large mahogany stems, readings of PAR were also taken and recorded.

3.7.3 Temperature measurements

Using a tele-thermocouple (Bentel, 2000), temperatures below ground, at the forest floor and forest understorey-air were measured and recorded. Like illumination, all temperatures were recorded between 12:00 p.m. and 3:00 p.m. Temperature measurements were made as follows:

- *at the center of each sample plot, three readings were taken (below ground, on the forest floor and understorey forest-air). These three readings at the center of the plot were to serve as control readings for that particular plot and*

- *at the individual growing position of all the encountered mahogany seedlings and saplings.*

Temperatures were read to the nearest degree. The purpose for the control temperature readings were to investigate the variations caused by the overlapping canopy on the different regeneration size classes (seedlings and saplings).

3.8 Assessment of ground and canopy cover

Ground and canopy cover were estimated using the methods detailed in Ostrom (1998).

3.9 Assessment of forest slope angles and aspect

3.9.1 Forest slope angles

At each sample plot slopes of (1) top ridges, (2) mid-ridges, (3) valley bottoms, and (4) swampy areas were recorded. The information obtained was important in verifying the effects of topography on the density and distribution of mahogany individuals in the forest ecosystem. Slope angles were measured from the center of the sample plot using a Suunto clinometer.

3.9.2 Aspect.

In this study aspect was defined as the direction where water would naturally flow in a given plot in the forest. Aspect is important in forest ecosystem hydrology and was measured with a handheld compass. Like slope angles, slope aspects were measured from the center of the sample plot.

3.10 Data summarization, ordination and statistical Analyses

3.10.1 Data summarization

Data are presented in tables and as sums, means, sample variance, standard errors and standard deviations before statistical analysis, ordination and comparisons were carried out.

3.10.2 Ordinations

Canonical and Detrended Correspondence analyses (CCA and DCA) as well as Principal Component Analysis (PCA) were used to order the mahogany trees and regeneration species first within the three treatments (unlogged, earlier logged and later logged). The species were also ordered along the different biophysical and environmental gradients of slope/aspect, soils, illumination, PAR, ground/canopy covers and temperatures.

3.10.3 Statistical analyses

3.10.3.1 Analysis of variance (ANOVA)

The treatments (unlogged, earlier logged and later logged) and parameters (e.g. individual tallies, densities, temperature, illumination, PAR, crown score, aspect ratio, canopy and ground covers) were analyzed using nested ANOVA on MINITAB (version 10.2) SPSS, (version 11) and SAS (version 8) statistical programs. Minitab is the most convenient for normalization of soil samples. SPSS is convenient for ANOVAs, correlation and regression analyses, while SAS is most convenient for the discriminant analysis. P-values are quoted in the text.

Comparisons of variances from the different treatments and to determine significant differences were performed using tukey's test). Tukey's test) was used because the analysis aimed at comparing within-variances of three treatments (unlogged, earlier logged and later logged) and finding where significant differences lied. Where necessary, t-tests were also used.

3.10.3.2 Regression, correlation, multicollinearity effects, autocorrelation, homoscedasticity and heteroscedasticity distributions

3.10.3.2.1 Regression

Relating two or more parameters measured on the same mahogany individual, multiple regressions and correlations were used (Ricker, 1984). The slope of the log sample plots were analyzed as follows:

The data were subject to multiple regression where the slope of geometric mean regression, v, was calculated as $v = \alpha/r$

The 95% and 99% confidence limit of v was calculated as

$$V \pm t \times \surd (V^2 ((1-r^2)/ (n-2))$$

Where t = the student test for n – 2 degree of freedom, and n is the total number of values used in the regression. Slopes with two values of V (V1 x V2) were compared by a t-test, using the following equation:-

$$T = \frac{V2 - V1}{V2^2 ((1- r^2)/(n_2-2)) + (V1^2 ((1- r^2)/ (n_2-2))}$$

The calculation was compared with tables of t values with n1 + n2 – 4 degree of freedom.

In this study, multiple regressions were used while employing sets of data from each category of compartment studied (the unlogged, earlier logging in 1950s-1960s and later logging in the 1970s-1980s). The dependent and independent variables were as follows:

- ⊗ *Soil nutrient levels, reaction, organic matter and soil texture as independent variables and mahogany individuals (trees, saplings and seedlings) as dependent variables.*

- ⊗ *Illumination, Photosynthetically active radiation (PAR) and temperatures as the independent variable and regeneration (seedlings and saplings) densities and dominance as dependent variables*

- ⊗ *Illumination, Photosynthetically active radiation (PAR) and temperatures as the independent variable and mediating biophysical factors (slope angle, slope aspect), species crown diameter, species crown depth, and ground/canopy cover as dependent variables.*

3.10.3.3 Multicollinearity effects and autocorrelation - Measures of variable association

In this study, it was anticipated that the effects of illumination, PAR, temperature, groundcover and canopy cover are the most important microenvironmental factors affecting mahogany regeneration, structure and distribution, and also that they were interrelated. First, MINITAB was used to indicate the variables that are significantly associated using Pearson correlation coefficients. Second, SAS was used to perform a disrciminant analysis to indicate which of the variables were significant and the order of importance. The SAS statement, PROC STEPDISK METHOD STEPWISE computes several statistics that describe the relationships between two of the variables of the contingency table, giving Pearson coefficients. According to Agresti (1996), using Pearson coefficient is appropriate for ordinal variables such as for illumination, PAR, temperature, ground and canopy covers. The Pearson correlation describes the strength of the linear association between the variables and has the range .

3.10.3.4Homoscedasticity and heteroscedasticity distributions

Homoscedasticity and heteroscedasticity distribution types on individuals across the study area were ascertained for the different mahogany species in response to the different soil and microenvironmental parameters. Homoscedasticity distribution refers to a homogeneous scatter of points around the regression line indicating that variability of the observed variable from the mean is the same. Heteroscedasticity refers to a nonhomogenous scatter. Also, measurements of the crown shape for the four mahogany species were obtained by estimating the ratio of crown depth and crown *diameter (Aspect Ratio) and scatter plots to show variation in compartments versus mahogany species aspect ratio for each compartment were mapped on a graph.*

Graphs and stand tables (importance value tables) from seedling, sapling and tree field-measurements were computerized to facilitate concise characterization of each of the four species (expressed per ha) in terms of abundance, structure and distribution.

CHAPTER 4

RESEARCH RESULTS PART 1:

EFFECT OF LOGGING ON REGENERATION, STRUCTURE AND DISTRIBUTION OF SELECTED MAHOGANY SPECIES IN BUDONGO FOREST RESERVE, UGANDA

Summary

This chapter presents results from the study conducted in the Budongo forest reserve, Uganda, between June and November 2000 and December 2000 to February 2001. The aim of the study was to determine the effect of logging on population status of Khaya anthotheca, Entandrophragma cylindricum, E. utile *and* E. angolense *in the forest. This chapter presents data on these species and compares the situation in a) unlogged, b) forest earlier logged more than 32 years ago (1930s and 1960s) and c) forest later logged within 34 years (1970s and 1980s). The numbers of individuals with variable height and in different diameter size-class distributions are presented. Importance values for saplings and trees are presented and similarities and contrasts indicated. Thereafter, crown diameter/crown depth and crown score are examined as indications of the responses of mahogany population to logging and exposure to light.*

4.1 Introduction

Ecological plant succession is an orderly and directional process of community development that involves predictable changes in species structure with time (Zedler and Zedler 1969). Barnes et al. (1998) further describes succession as the compositional change of plant species, which takes place in an environment where human activities have been withdrawn over an extended period of time. Therefore, different stages in succession are characterized by differences in relative species frequency, abundance and dominance (Bell and Bellairs 1992; Bell *et al*. 1993; Randolph 1998). Unless interrupted, succession, structural changes and plant distribution patterns never stop until a climax of a more or less homogenous ecosystem is reached. This study examines their successional process by investigating the distribution of four mahogany species after selective logging in the Budongo Forest Reserve. The time of logging has been categorized as earlier logged (logged at least 32 years ago, in the 1930s and 1960s) and later logged (within 32 years, in the 1970s and 1980s). Comparisons of the data collected are made with those from an unlogged compartment.

4.2 Distribution of mahogany seedlings, saplings, poles, small and large trees

Khaya anthotheca was the best represented of the four species in the samples studied, perhaps because it showed more tolerance of an open canopy condition. Nevertheless, it equally showed tolerance for shade in the unlogged and the earlier logged compartments. Except for compartment N9 (sapling class in the earlier logged) and K4 (small tree in the later logged), the species is represented in all the compartments surveyed (Table 4.1). Compartment W16 (earlier logged) had the highest seedling density (33 seedlings per hectare), while compartment W21 (earlier logged showed the most sapling density (6 saplings per hectare). Compartments W21 and W16 (earlier logging) each showed densities of 7 poles per hectare (Table 4.1).

Likewise, compartments W21 and W16 (earlier logging) had the highest small tree densities (13 and 14 trees per hectare respectively). The compartment with the highest number of *K. anthotheca* large tree density was W16 (earlier logging) with 8 large trees per hectare (Table 4.1). Following *K. anthotheca* in representation was *E. cylindricum* with average densities of 2 seedlings per hectare, 1 sapling, 1 small tree and 1 large trees per hectare in the unlogged treatment (Table 4.1).

Table 4.1: Distribution of mahogany seedlings, saplings, poles, small and large tree densities (No./ha.) across the study area

	K. anthotheca					*E. cylindricum*					***E. utile***					***E. angolense***				
Treatment	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT
N15 *(unlogged)*	14	3	6	7	4	1	0	0	0	1	2	0	1	1	1	2	1	0	1	2
Averages	**14**	**3**	**6**	**7**	**4**	**1**	**0**	**0**	**0**	**1**	**2**	**0**	**1**	**1**	**1**	**2**	**1**	**0**	**1**	**2**
N14	8	1	2	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1
N9	3	0	1	6	1	3	1	1	1	0	0	0	0	1	1	1	2	1	1	0
N5 *Earlier logged*	2	1	5	8	1	4	2	1	1	0	1	0	1	0	0	3	2	3	1	1
S3	4	1	1	5	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
B3	7	1	1	7	2	3	0	1	3	2	2	0	0	0	1	1	1	1	0	0
W21	3	6	7	13	4	2	2	1	2	0	0	0	0	1	0	2	2	0	1	0
W16	33	3	7	14	8	1	1	1	0	1	0	3	1	2	0	1	2	1	1	0
Averages	**9**	**2**	**4**	**8**	**3**	**2**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**1**	**1**	**1**
B1	12	4	4	7	2	8	3	3	4	0	0	1		0	1	8	3	1	0	0
S5 Later	4	3	3	8	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
K4	22	1	1	0	2	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0
Averages	**13**	**3**	**3**	**5**	**2**	**3**	**1**	**2**	**2**	**0**	**1**	**1**	**1**	**0**	**1**	**4**	**1**	**1**	**0**	**0**
GRAND TOTAL	112	24	38	76	25	23	9	9	11	4	7	6	3	5	6	21	14	7	5	4
					275					**56**					**27**					**51**

Se = Seedlings 0 - >2.5 cm root collar
Sa = Saplings > 2.5 ≤ 5.0 cm root collar
Po = Poles > 5.0 ≤ 10.0 cm dbh
ST = Small trees > 10.0 <30 cm dbh
LT = Large trees ≥ 30 cm dbh

The third most represented species during the field survey was *E. angolense*. The compartments with the highest densities of regeneration were compartments B1 (later logging with 8 seedlings, 3 saplings, 3 poles and 4 small trees per hectare; and compartment N5 (earlier logging) with 4 seedlings, 2 saplings, 1 pole and 1 small tree per hectare (Table 4.1). *E. utile* had the least mahogany densities recorded in this study. The unlogged treatment showed the highest average density representation with 2 seedlings, 1 pole, 1 small and 1 large tree per hectare.

4.2.1 Comparison of mahogany size-class densities within and between treatments

When all mahogany size-classes were compared for the four studied species, there were significant differences across treatments (0.05 <p > 0.01) (Table 4.2). The differences are probably due to differences in species size-class responses to different forest environments prevailing in the three treatments.

Table 4.2: One-way analysis of variance for mahogany size-classes across treatments

Size-class	***Source of Variation***	***SS***	***MS***	***F***	***P-value***
Se	Between treatments	227.67	75.89	31.4023	***** 8.94E-05
	Within size-class	19.33	2.42		
Sa	Between treatments	8.00	2.67	8	***** 0.005395
	Within size-class	2.67	0.33		
Po	Between treatments	22.00	7.33	6.769231	****** 0.018804
	Within size-class	8.67	1.08		
ST	Between treatments	78.25	26.08	26.08333	***** 0.000175
	Within size-class	8.00	1.00		
LT	Between treatments	10.25	3.42	5.857143	****** 0.023401
	Within size-class	4.67	0.58		

Note: ** = 0.05 < p > 0.01 * = p < 0.01

Se = Seedlings	0 - >2.5 cm root collar
Sa = Saplings	> 2.5 ≤ 5.0 cm root collar
Po = Poles	> 5.0 ≤ 10.0 cm dbh
ST = Small trees	> 10.0 <30 cm dbh
LT = Large trees	≥ 30 cm dbh

K. athotheca seedlings showed the most variability across treatments with a sample variance of 7, while saplings showed the least variability. *K. anthotheca* seedlings, saplings and small trees showed negative skew, an indication that regeneration was not normally distributed across treatments due to other factors other than the availability of the larger tree size classes, which showed no skew (Table 4.3). *E. cylindricum* and *E. utile* showed no variations, while seedlings and large trees of *E. angolense* showed variability across treatments (Table 4.3). Apart from *E. angolense*, saplings of the other species were negatively skewed (Table 4.3).

Table 4.3: Species size-class distribution, sample variance and skewness within treatments

	K. anthotheca					***E. cylindricum***					***E. utile***					***E. angolense***				
Treatment	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT
Unlogged (UnL)	**14**	**3**	**6**	**7**	**4**	**1**	**0**	**0**	**0**	**1**	**2**	**0**	**1**	**1**	**1**	**2**	**1**	**0**	**1**	**2**
Earlier (EL)	**9**	**2**	**3**	**8**	**3**	**2**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**1**	**1**	**1**
Later (LL)	**13**	**3**	**3**	**5**	**2**	**3**	**1**	**2**	**2**	**0**	**1**	**1**	**1**	**0**	**1**	**4**	**1**	**1**	**0**	**0**
$\sum X$ *(Sum)*	36	8	12	20	9	6	2	3	3	2	4	2	3	2	3	8	4	2	2	3
Mean	12.0	2.7	4.0	6.7	3.0	2.00	0.67	1.00	1.00	0.67	1.3	0.7	1.0	0.7	1.0	2.7	1.3	0.7	0.7	1.0
Standard Error	1.5	0.3	1.0	0.9	0.6	0.58	0.33	0.58	0.58	0.33	0.3	0.3	0.0	0.3	0.0	0.7	0.3	0.3	0.3	0.6
SD	2.6	0.6	1.7	1.5	1.0	1.00	0.58	1.00	1.00	0.58	0.6	0.6	0.0	0.6	0.0	1.2	0.6	0.6	0.6	1.0
Sample Variance	7.0	0.3	3.0	2.3	1.0	1.00	0.33	1.00	1.00	0.33	0.3	0.3	0.0	0.3	0.0	1.3	0.3	0.3	0.3	1.0
Skewness	-1.5	-1.7	1.7	-0.9	0.0	0.00	-1.73	0.00	0.00	-1.73	1.7	-1.7	0.0	-1.7	0.0	1.7	1.7	-1.7	-1.7	0.0

Notes: Se = Seedlings 0 - >2.5 cm root collar

Sa = Saplings > 2.5 ≤ 5.0 cm root collar
Po = Poles > 5.0 ≤ 10.0 cm dbh
ST = Small trees > 10.0 <30 cm dbh
LT = Large trees ≥ 30 cm dbh
SD = Standard deviation
UnL = Unlogged
EL = Earlier logging
LL = Later logging

On comparing the unlogged, earlier and later logged treatments, density results show highest variability in the later logged forest tracts (standard error, 2.0) than in the unlogged and earlier logged forest tracts. For example, total density for *K. anthotheca* indicated sample variance in the later logged as 20.2, unlogged as 18.7, while in the earlier logged as 10.5 (Table 4.4). Tukey test results show significant differences between earlier and later logged treatments (q = 0.00507) and between the unlogged and later logged forest tracts (q = 0.041). Sample variance for E. cylindricum was 1.3 in the later logged and in the unlogged and earlier logged, it was 0.3 and 0.2 respectively. Tukey test result for *E. cylindricum* densities between the unlogged and earlier logged was q = -2.52, between unlogged and later logged was q = -2.121 and between earlier and later logged was q = -0.73. All the treatments were generally similar. The earlier logged forest tracts showed the least variability in species density.

The forest treatments with the highest density of *Khaya anthotheca* did not necessarily contain the highest densities of the other mahogany species studied. In general, *E. cylindricum, E. Utile* and *E. angolense* showed very low densities across the study area. Therefore, it is not easy, at this time, to conclude on the best forest treatment where the species regenerated most based on logging alone.

Across the three treatments, the regeneration patterns for sapling densities were generally lower compared to the seedling and the larger size-classes (poles, small and large trees) (Table 4.4).

Table 4.4: Species size-class distribution, sample variance and skewness across treatments

Size-class	*K anthotheca*			*E. cylindricum*			*E. utile*			*E. angolense*		
	UnL	EL	LL	UnL	EL	LL	UnL	EL	LL	UnL	EL	LL
Se	**14**	**9**	**13**	**1**	**2**	**3**	**2**	**1**	**1**	**2**	**2**	**4**
Sa	**3**	**2**	**3**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**2**	**1**
Po	**6**	**3**	**3**	**0**	**1**	**2**	**1**	**1**	**1**	**0**	**1**	**1**
ST	**7**	**8**	**5**	**0**	**1**	**2**	**1**	**1**	**0**	**1**	**1**	**0**
LT	**4**	**3**	**2**	**1**	**1**	**0**	**1**	**1**	**1**	**2**	**1**	**0**
∑x (Sum)	34	25	26	2	6	8	5	5	4	6	7	6
Mean	6.8	5.0	5.2	0.4	1.2	1.6	1.0	1.0	0.8	1.2	1.4	1.2
Standard Error	1.9	1.4	2.0	0.2	0.2	0.5	0.3	0.0	0.2	0.4	0.2	0.7
SD	4.3	3.2	4.5	0.5	0.4	1.1	0.7	0.0	0.4	0.8	0.5	1.6
Sample Variance	18.7	10.5	20.2	0.3	0.2	1.3	0.5	0.0	0.2	0.7	0.3	2.7
Skewness	1.5	0.6	1.9	0.6	2.2	-0.4	0.0	0.0	-2.2	-0.5	0.6	1.7

Notes:

Se = Seedlings 0 - >2.5 cm root collar
Sa = Saplings > 2.5 ≤ 5.0 cm root collar
Po = Poles > 5.0 ≤ 10.0 cm dbh
ST = Small trees > 10.0 <30 cm dbh
LT = Large trees ≥ 30 cm dbh
UnL = Unlogged
EL = Earlier logging
LL = Later logging
SD = Standard deviation

Only the variations between treatments were significantly different at 0.05 < p > 0.01 significant level (Table 4.5).

Table 4.5: Mahogany species variations within and between treatments

Species	*No. of treatments*	*Sum*	*Average*	*Variance*		
K. anthotheca	3	105.6	35.2	77.2		
E. cylindricum	3	16	5.3	12.3		
E. utile	3	6.5	2.2	3.4		
E. angolense	3	20	6.7	9.3		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between treatments	2123.42	3	707.81	27.70	**0.000141**	4.07
Within species	204.41	8	25.55			
Total	2327.83	11				

Note: The three treatments are unlogged, earlier and later logged forest tracts

4.3 Diameter size-class distribution

From the results, it is evident that *K. anthotheca* is a more numerous and more important species in Budongo forest than the *Entandrophragma* species. For example, *K. anthotheca* seedlings showed a stand density of 14 seedlings per hectare in the unlogged treatment, while the earlier logged treatment showed a stand density of 9 stems per hectare and the later logged treatment showed a stand density of 13 seedlings per hectare. There is a correlation between the density of regeneration of mahogany species and the density of the larger sizes (Table 4.6). When *K. anthotheca* is compared to the *Entandrophragma* species, *Khaya* regeneration across the treatments may be described as adequate, while the regeneration of the *Entandrophragma* species can be described as poor or scanty (Table 4.6).

Table 4.6: Mahogany diameter size-class distribution in Budongo Forest Reserve treatments

Species	**Treatment**	**Diameter size-classes (Density = No./ha.)**					**Total density**	
		Se	Sa	Po	ST	LT		
K. athotheca	UnL	**14**	**3**	**6**	**7**	**4**	34	**85**
	EL	**9**	**2**	**3**	**8**	**3**	25	
	LL	**13**	**3**	**3**	**5**	**2**	26	
E. cylindricum	UnL	**1**	**0**	**0**	**0**	**1**	2	**16**
	EL	**2**	**1**	**1**	**1**	**1**	6	
	LL	**3**	**1**	**2**	**2**	**0**	8	
E. utile	UnL	**2**	**0**	**1**	**1**	**1**	5	**14**
	EL	**1**	**1**	**1**	**1**	**1**	5	
	LL	**1**	**1**	**1**	**0**	**1**	4	
E. angolense	UnL	**2**	**1**	**0**	**1**	**2**	6	**19**
	EL	**2**	**2**	**1**	**1**	**1**	7	
	LL	**4**	**1**	**1**	**0**	**0**	6	
	∑x (Sum)	54	16	20	27	17		
	Mean	4.5	1.3	1.7	2.3	1.4		
	SD	4.74	0.98	1.67	2.80	1.16		

Notes:

Se = Seedlings 0 - >2.5 cm root collar
Sa = Saplings > 2.5 ≤ 5.0 cm root collar
Po = Poles > 5.0 ≤ 10.0 cm dbh
ST = Small trees > 10.0 <30 cm dbh
LT = Large trees ≥ 30 cm dbh
UnL = Unlogged
EL = Earlier logging
LL = Later logging
SD = Standard deviation

For all the four species studied, most of the individuals found were in the seedling, sapling, pole and small tree size-classes showing vigorous growth at the early stages of mahogany regeneration. However, from seedling to sapling densities, there is a decline in density in all the species studied (Table 4.6) indication of high sapling mortality. A total sum of 16 saplings (mean 1.3 ± 0.98) was observed compared to 54 seedlings (mean 4.5 ± 4.7) and 20 poles (mean 1.7 ± 1.67). From ecological observations on the large tree size-class in the field in the logged compartments (earlier and later logged), the remaining large stems were stunted, defective and probably left behind as uneconomical during logging. With intensive mechanical logging in 1950s-1960s and the onset of hand sawing (1970s-1980s), reduction of the minimum diameter policy (i.e. cutting all trees having ≥70cm) meant more larger trees were exploited. It is possible that during mechanical logging and the use of large poles in bed-construction associated with hand sawing, there was increased mortality of the residual and intermediate diameter size-classes (Table 4.6).

Results from the study area again show *K. anthotheca* as the most important, especially in the unlogged forest tracts (Table 4.5). Total densities for the *Entandrophragma* species show high densities in the earlier logged forest tracts. For example, *E. utile* shows total densities of 5 stems per hectare in the earlier and unlogged forest tracts, while total density in the later logged forest tracts were 4 stems per hectare (Table 4.6).

Also, total density for *E. angolense* was high in the earlier logged forest than the unlogged and later logged forest tracts, an indication that these two species were favourably growing in semi-closed forest environments. Total density for *E. cylindricum* was high in the later logged forest tracts an indication that this species was favourably growing in a more open and recently logged forest environment (Table 4.6).

4.4 Estimated seedling, sapling, pole and tree density, basal area and volume

Based on the estimated stem density, basal area and volume per hectare, *K. anthotheca* is again the most important (Table 4.7). In the unlogged treatment, *K. anthotheca,* shows the highest stock of the seedlings (14 seedlings per hectare) compared to the earlier logged (9 seedlings per hectare) and later logged compartments (13 seedlings per hectare) (Table 4.7).

Probably, the highest density of the larger-size trees (mother trees) influenced the presence of the high levels of *K. anthotheca* regeneration. *E. cylindricum* saplings were, however, mostly found in the earlier logged (basal area = 0.002 m^2 per hectare) and later logged treatments (basal area = 0.003 m^2 per hectare). Despite the presence of the large sizes, *E. cylindricum* saplings, poles and small trees were not recorded in the unlogged treatment (Table 4.6). *E. utile* saplings, poles, small and large trees were predominantly recorded in the unlogged and earlier logged treatments, which may be due to the closed or semi-closed tree canopy-environments prevailing in these two treatments.

Table 4.7: Density (No./ha.), basal area (m^2/ha.) and volume (m^3/ha.) of seedlings, saplings, poles, small and large tree across the study area

Treatment	**Parameter**	**Khaya anthotheca**					**Ent. cyl**					**Ent. utile**					**Ent. ang**				
		Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT	Se	Sa	Po	ST	LT
Unlogged Control (n=24)	Density	**14**	**3**	**6**	**7**	**4**	**1**	**0**	**0**	**0**	**1**	**2**	**0**	**1**	**1**	**1**	**2**	**1**	**0**	**1**	**2**
	Basal area	**-**	0.01	0.08	0.32	13.6	-	0	0	0	5.7	-	0	0.01	0.05	4.9	-	0.005	0	0.08	10.4
	Volume	-	0.07	0.57	1.63	203.5	-	0	0	0	92.8	-	0	0.09	0.16	86.0	-	0.03	0	0.39	176.0
Earlier logging 1930s-1960s (n=162)	Density	**9**	**2**	**4**	**8**	**3**	**2**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**1**	**1**	**1**
	Basal area	-	0.07	0.04	0.65	4.14	-	0.002	0.01	0.05	0.24	-	0.004	0.008	0.05	0.36	-	0.01	0.02	1.32	0.32
	Volume	-	0.05	0.33	1.88	19.83	-	0.02	0.06	0.11	0.99	-	0.004	0.03	0.33	4.43	-	0.01	0.07	0.62	7.60
Later logging 1970s-1980s (n=72)	Density	**13**	**3**	**3**	**5**	**2**	**3**	**1**	**2**	**2**	**0**	**1**	**1**	**0**	**0**	**1**	**4**	**1**	**1**	**0**	**0**
	Basal area	-	0.61	0.03	0.31	2.84	-	0.003	0.02	0.02	0	-	0.002	0	0	0.14	-	0.009	0.008	0	0
	Volume	-	0.15	0.04	1.75	4.62	-	0.03	0.14	1.35	0	-	0.011	0	0	2.84	-	0.03	0.04	0	0

Note: n= are samples in the treatment

Se = Seedlings 0 - >2.5 cm root collar
Sa = Saplings > 2.5 ≤ 5.0 cm root collar
Po = Poles > 5.0 ≤ 10.0 cm dbh
ST = Small trees > 10.0 <30 cm dbh
LT = Large trees ≥ 30 cm dbh

Finally, the larger sizes of *E. angolense* were not recorded in the later logged treatment even when the corresponding smaller sizes (seedling, saplings and poles) were recorded (Table 4.7).

Furthermore, Detrended Correspondence Analysis (DCA) results of the distribution of seedlings and saplings showed variations in species response to the three treatments (unlogged, earlier and later logged) (Figure 4.1). *K. anthotheca* and *E. utile*, which are not closely associated suggests that the two species grow in similar microenvironments. They are predominantly distributed along axis 2 in the earlier logged treatment. *E. angolense* and *E. cylindricum*, which are not closely associated suggests that these two species grow in different microenvironments. For example, the results show that *E. angolense* predominantly appeared in the earlier logged treatment, while *E. cylindricum* predominantly appeared in the transition between the earlier and later logged treatment. Also, DCA results suggest that there exist close association between regeneration and the larger sizes. For example the large and small trees of *K. athotheca* and *E. angolense* are associated to their respective seedling and sapling (regeneration) size-classes (Figures 4.1).

The unlogged treatment showed no predominant mahogany regeneration, although *E. utile* predominantly appeared in the transition between the earlier and the unlogged treatments (Figure 4.1).

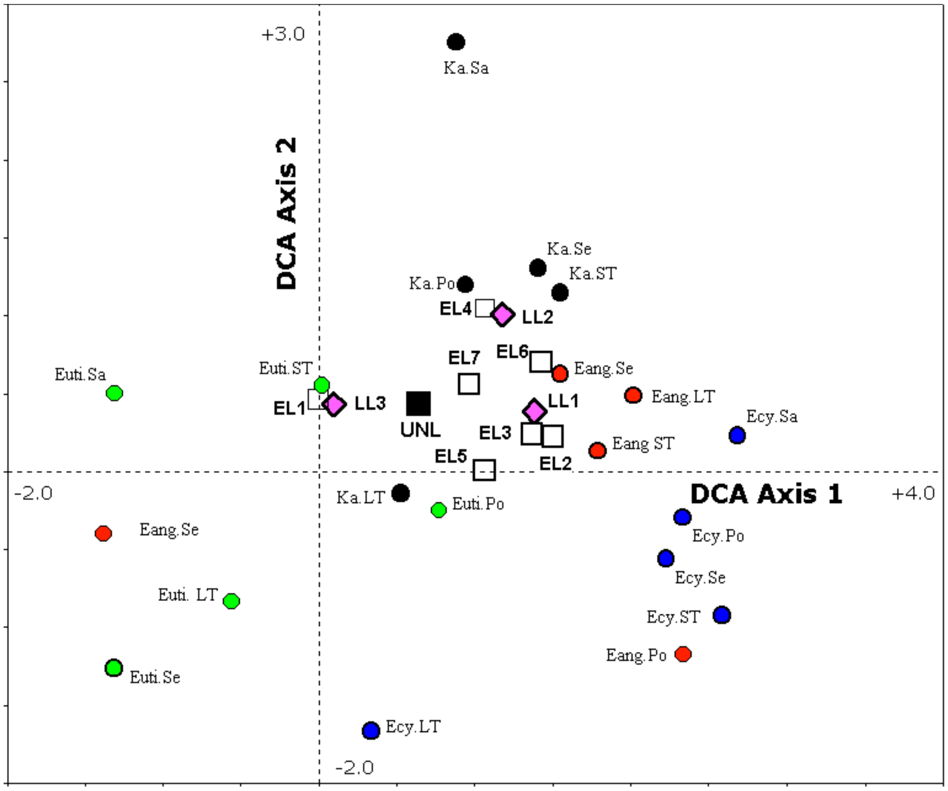

Figure 4.1: Detrended Correspondence Analysis of the selected mahogany species in the three treatments: unlogged, earlier and later logging. Eigenvalues and percentage variances are given in Table 4.8

Note: ■ UnL = Unlogged; □ EL = Earlier logging and 🟪 LL = Later logging

● Ka.Se, Ka.Sa, Ka.Po, Ka.ST and Ka.LT represent *K. anthotheca* seedlings, saplings, poles, small and large trees.

🔵 Ecy.Se, Ecy.Sa, Ecy.Po, Ecy.ST and Ecy.LT represent *E. cylindricum* seedlings, saplings, poles, small and large trees.

🟢 Euti.Se, Euti.Sa, Euti.Po, Euti.ST and Euti.LT represent *E. utile* seedlings, saplings, poles, small and large trees.

🔴 Eang.Se, Eang.Sa, Eang.Po, Eang.ST and Eang.LT represent *E. angolense* seedlings, saplings, poles, small and large trees.

Table 4.8: Detrended correspondence analysis showing correlation of species ordination axes with eigenvalues and percentage variances

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues	0.171	0.063	0 .020	0 .013	0.524
Lengths of gradient	1.506	1.043	.810	1.075	
Cumulative percentage variance of selected mahogany species (size-class) data	32.7	44.8	48.6	51.1	

The detrended correspondence analysis suggests that variations between treatments explain 44.8 percentage of the differences in species distribution (Table 4.8). In comparing the distribution of the different mahogany size-classes along the three treatments, the results show that the species predominantly prefer transition forest tracts. For example, all mahogany seedlings and saplings studied are predominantly distributed in the transitions between the unlogged and later logged treatments and between the later and earlier logged treatments (Figure 4.1). Also, results show clusters of pole and small trees in the earlier and unlogged treatments. The large trees predominantly appeared in the transitions between the earlier and the unlogged treatment and between the unlogged and later logged (Figure 4.1). It was, however observed during the survey that most of the large trees in the later logged treatment were the defective ones left behind after logging.

The predominant distribution of mahogany seedlings in close association with the large trees in the earlier and later logged treatments (Figure 4.1) emphasizes the importance of mother/seed trees in natural forest management. This finding confirms Plumptre (1994), who noted that mahogany species produce seeds when the mother tree attains ≥80 cm dbh and that there is high correlation between large size trees and the logarithm of seedling density in Budongo Forest Reserve. Exploitation as shown in the later logged treatment is generally associated with fewer individuals in the large sizes (Figure 4.1).

4.5 Mahogany regeneration and stability

High densities of *K. anthotheca* were recorded in the unlogged and later logged forest tracts than in earlier logged compartments (Figure 4.3). Two explanations are possible. First, the abundant presence of mother trees in the unlogged forest compartment and secondly, *K. anthotheca* regeneration being a function of open forest environments. *K. anthotheca* saplings drastically reduced from seedling densities of 9-14 stems per hectare to 2-4 sapling stems per hectare, which probably suggests a problem of high mortality in the transition from seedlings to sapling size classes (Figure 4.2a). At pole and small tree size-classes, the forest environment in the earlier logged compartments show higher densities (Figure 4.2a).

E. cylindricum and *E. utile* show consistent stability in the earlier logged forest compartments with irregular patterns in the unlogged and later logged forest compartments. Thus, regeneration of seedlings and saplings for the above two species (*E. cylindricum* and *E. utile*) were in the range of 1 – 2 stems per hectare, especially in the earlier logged compartments (Figure 4.2b-c). Probably, these two species are shade or semi-open tolerant species.

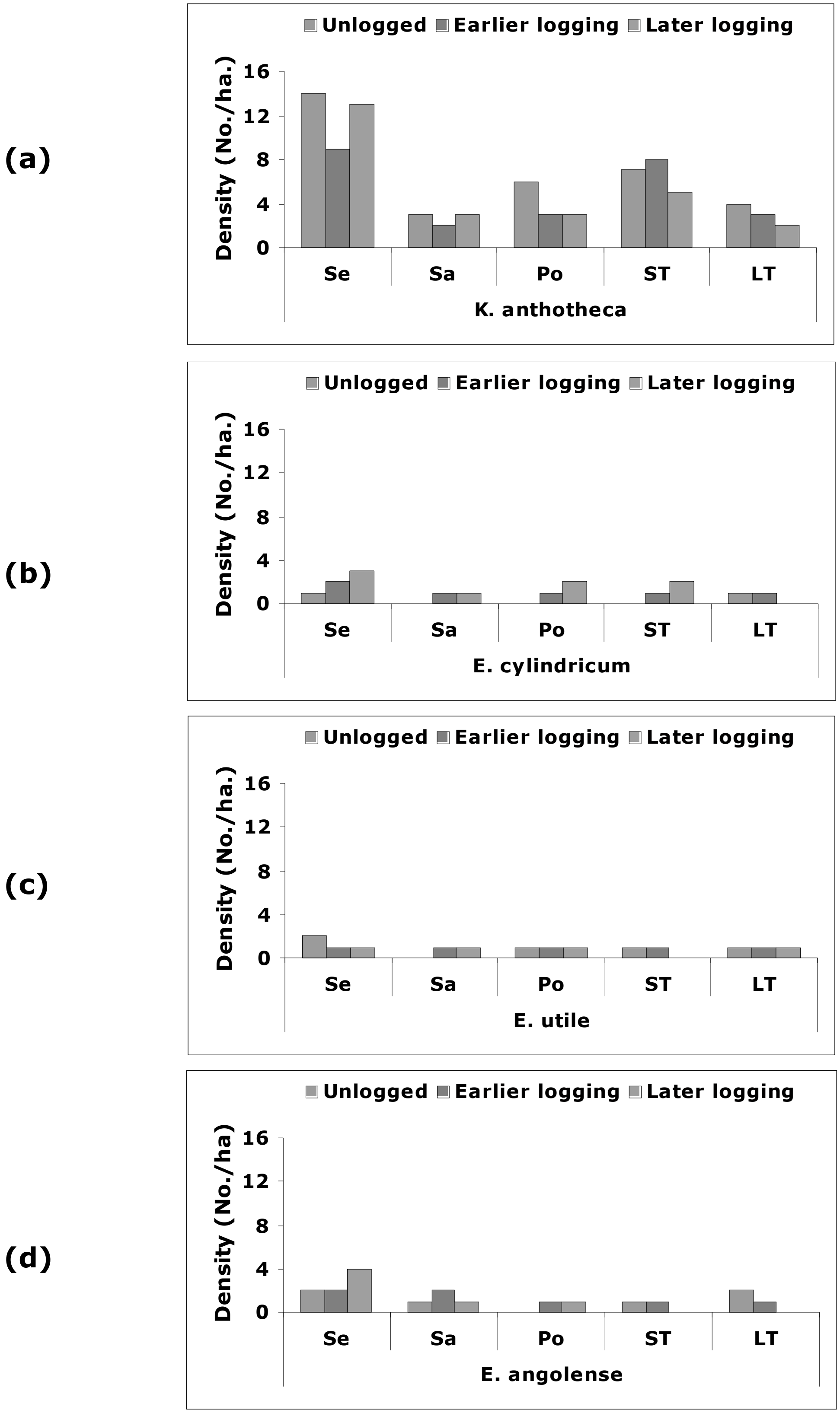

Figure 4.2a-d: Mahogany stability in size-classes across treatments

Note:

Se =	Seedlings	0 - > 2.5 cm root collar	Sa =	Saplings	> 2.5 ≤ 5.0 cm dbh
Po =	Poles	> 5.0 ≤ 10.0 cm dbh	ST =	Small trees	> 10.0 < 30.0 cm dbh
LT =	Large tree	> 30 cm dbh			

In contrast to the above scenario, *E. angolense* seedlings appeared more favoured in the later logged compartments (Figure 4.2d). Again, this suggests that *E. angolense* regeneration is most favoured in open forest environments. The larger size-classes (pole and small trees) are most favoured in the earlier logged treatment (Figure 4.2d).

4.6 Importance Value (IV) results

The importance value represents a sum of three forest measurements divided by three. These measurements are: (1) relative frequency, (2) relative density and (3) relative dominance. Tables 4.9 shows the three measures separately tabulated. The three measures are separated so that it is possible to discern if the IV is influenced by relative frequency and relative density or to tell if the influence is from all the three measures. Also, the table shows how the selected mahogany species are related to each other along the three measures.

Relative frequency measures show how often the species was represented in sample plots by at least one representative individual in relation to other species, while relative density measures the density of the species in the sampled area in relation to the density of the other species under investigation. Relative dominance is a measure of an allometric aggregation of basal area, height and crown-cover and represents the species dominance in relation to the dominance of the other species under investigation. Relative measures range from 0.1 to 1.

Thus, Table 4.9 show the three relative measures for the trees and saplings, their importance values and rank across the three treatments.

Table 4.9: Mahogany Mean Relative Density, Relative frequency and Relative Dominance compared

Treatment	*Mahogany trees*																			
	Rel. freq.				**Rel. density**				**Rel. domin.**				**IV**				**Rank**			
	Ka	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**
Unlogged Control (n=24)	0.66	0.04	0.08	0.22	0.79	0.11	0.08	0.02	0.82	0.11	0.06	0.01	0.76	0.09	0.07	0.08	**1**	**2**	**4**	**3**
Earlier logging 1950s-1960s (n=162)	0.59	0.12	0.13	0.16	0.59	0.12	0.13	0.15	0.71	0.10	0.08	0.10	0.63	0.11	0.11	0.14	**1**	**3**	**3**	**2**
Later logging 1970s-1980s (n=72)	0.57	0.07	0.14	0.21	0.54	0.07	0.14	0.20	0.68	0.04	0.12	0.16	0.6	0.06	0.13	0.19	**1**	**4**	**3**	**2**
Mean	**0.61**	**0.08**	**0.12**	**0.20**	**0.64**	**0.10**	**0.12**	**0.12**	**0.74**	**0.08**	**0.09**	**0.09**	**0.41**	**0.06**	**0.08**	**0.11**	1	3	4	2
	Mahogany saplings																			
	Rel. freq.				**Rel. density**				**Rel. domin.**				**IV**				**Rank**			
	Ka	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**	**Ka**	**Eu**	**Ec**	**Ea**
Unlogged Control (n=24)	0.70	0.00	0.20	0.10	0.80	0.00	0.10	0.10	0.80	0.00	0.10	0.10	0.77	0.00	0.13	0.01	**1**	**4**	**2**	**3**
Earlier logging 1950s-1960s (n=162)	0.49	0.20	0.14	0.23	0.53	0.16	0.11	0.21	0.53	0.16	0.11	0.21	0.52	0.10	0.12	0.22	**1**	**4**	**3**	**2**
Later logging 1970s-1980s (n=72)	0.76	0.20	0.03	0.13	0.73	0.17	0.03	0.10	0.73	0.17	0.03	0.10	0.74	0.18	0.03	0.11	**1**	**2**	**4**	**3**
Mean	**0.65**	**0.13**	**0.12**	**0.15**	**0.69**	**0.11**	**0.08**	**0.14**	**0.69**	**0.11**	**0.08**	**0.14**	**0.42**	**0.09**	**0.05**	**0.11**	1	4	3	2

Note: n= are samples in the treatment
Ka = *Khaya anthotheca*
Eu = *Ent. utile*
Ec = *Ent. cylindricum*
Ea = *Ent. angolense*

The results suggest that *K. anthotheca* is the most frequent, dense and dominant in both trees and saplings. For example, *K. anthotheca* shows mean relative frequency of 0.61, relative density of 0.64 and relative dominance of 0.74 for trees and relative frequency of 0.65, relative density of 0.69 and relative dominance of 0.69 for saplings. Furthermore, *K. anthotheca* trees show higher importance value than all the *Entandrophragma* species studied. The results consistently show higher relative values (frequency, density and dominance) for trees in the unlogged treatment than in the earlier and later logged treatments (Table 4.9). However, *K. anthotheca* saplings are more frequent in the unlogged and later logged than in earlier logged treatments, more dense in the unlogged than in the later or earlier logged treatments, and more dominant in the unlogged than in the earlier and later logged treatments (Table 4.9). *K. anthotheca* is higher in density across most size-classes analyzed.

Thus, the IV results across the sampled compartments again show that *K. anthotheca* is the most important of the selected species studied, while *E. utile* and *E. cylindricum* are the least important.

4.7 Crown symmetry and physiognomy: Crown score

Crown score is a measure of how far the crown is exposed to direct light radiation. It is an indication of the openness of the growing condition for plant individuals, influenced by the crowns of surrounding trees, saplings, climbers and lianas (Caldwell and Pearcy 1994). An entirely exposed crown (growing in the gap or open) is represented by crown score 1, while an entirely covered crown is represented by a score of 4. Intermediate crown exposures are represented by intermediate scores of 2 and 3 respectively (Table 4.10).

Table 4.10: Crown score description

Crown score	**Description**	**Further comments**
1	Exposed	Complete open with 100% exposure
2	Mostly exposed	At least 75% exposed crown
3	Mostly covered	At least 75% covered crown
4	Covered	Completely covered with 100% crown closure

4.7.1 Mean crown-scores for trees

Generally, results of tree mean crown-scores for mahoganies show no clear pattern. However, *Khaya anthotheca* appears to be growing mostly in exposed environments. In the later logged treatment, *K. anthotheca* is growing in a completely exposed environment (Figure 4.3).

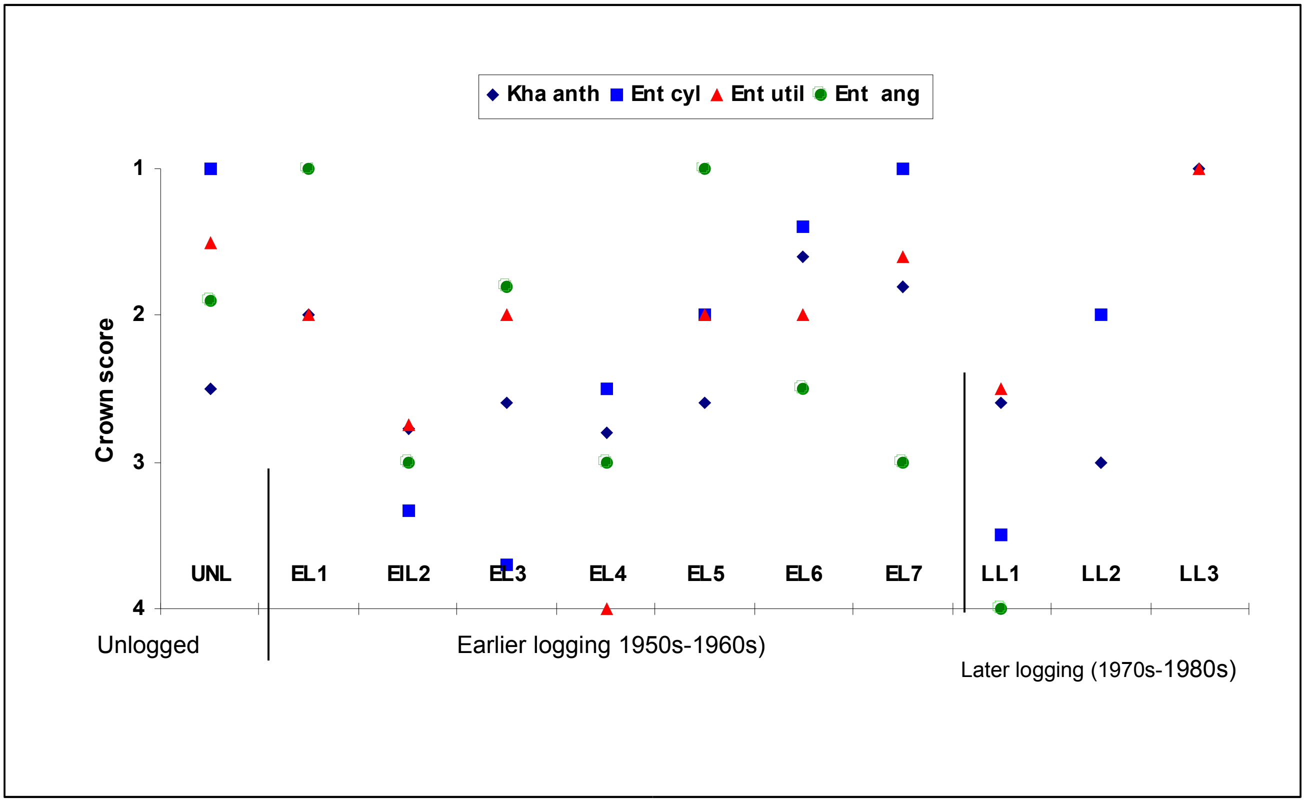

Figure 4.3: Tree mean crown-score

In unlogged, earlier and later logged compartments *E. cylindricum* appears in mostly exposed environments in some compartments, though in other compartments, it is growing in the mostly covered environments (Figure 4.3). However, *E. utile* is predominantly growing in the mostly exposed environments, except in compartment S5 (earlier logged) where it appears in the completely covered environments.

In some earlier logged compartments, *E. angolense* is growing in completely open areas, while in the unlogged, it is growing under a moderately or completely covered crown. Generally, therefore, mahogany species respond differently to forest understorey environments, but appear to flourish and grow favourably in the mostly exposed/covered environments with 75% cover (see Figure 4.3 above). Therefore, mahogany trees appear to grow in environments influenced by either the availability of the parent trees, site factors or other tree species in their proximity, which affects the immediate canopy environments.

4.7.2 Mean crown-scores for saplings

Saplings of *K. anthotheca* appear in the mostly covered environments. The exception was in one of the sampled sites in earlier logged, where the species was growing in a mostly exposed environment. From the results, *E. cylindricum* saplings were growing in the moderately closed to completely closed environments (Figure 4.4). Like *K. anthotheca* and *E. cylindricum*, *E. utile* was predominant in moderately closed environments, although exceptions were observed in two of the sampled sites in the earlier logged forests where the species was growing in mostly exposed open environments (Figure 4.4).

The results also indicate that *E. angolense* saplings are found in the mostly closed to completely closed environments. The exception is in only one of the sampled sites in the earlier logged forest tracts, where it is represented in a completely closed environment (Figure 4.4 above). The pattern for trees with regard to crown-score is not clearly defined and seems to be species dependent, while generally, the young trees prefer closed and semi-closed environments.

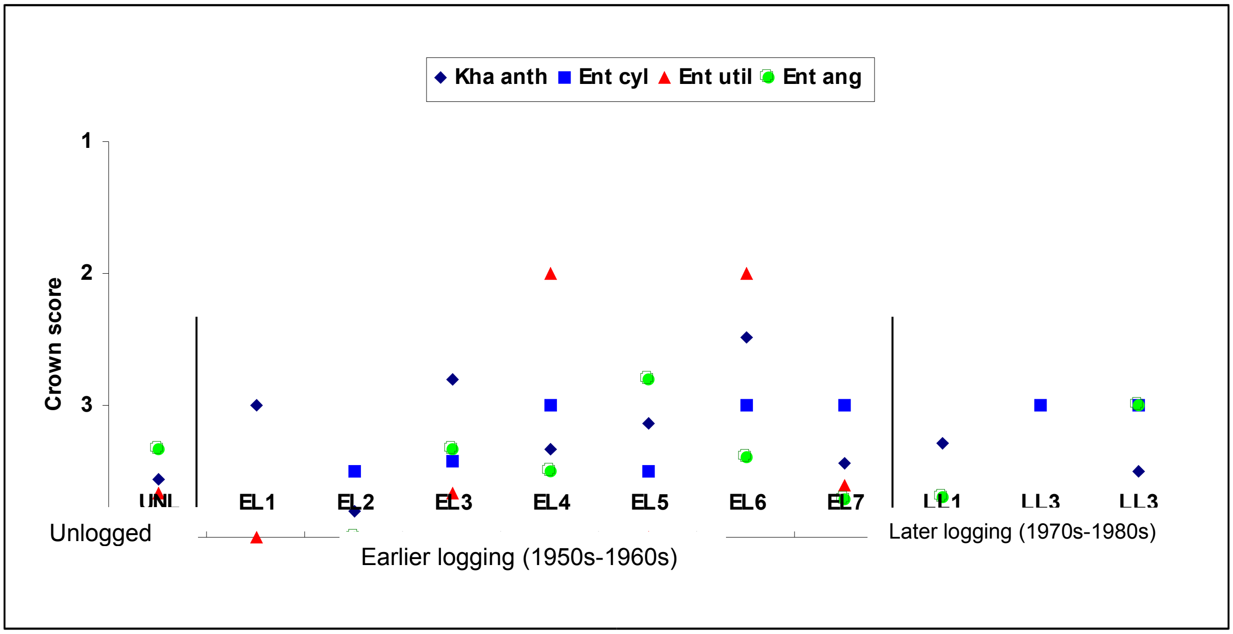

Figure 4.4: Sapling mean crow-score

4.8 Crown symmetry and physiognomy: crown aspect ratio

Crown aspect ratio is a photo-morphogenetic response of plants to light (Russell *et al.* 1988). In a forest environment, the crown depth is related to the crown diameter to derive a measure of the crown shape (aspect ratio). Aspect ratio is crown depth divided by crown diameter (Glen 1988).

In some species, aspect ratio may be a result of the genetic composition of the plant, but in most cases, it is a response of plant to genetics within species and the light environment (Hesketh and Moss, 1963; Björkman, 1972; Bazzar *et al.*, 1990; Barnes *et al.*, 1998). Under full light, a crown diameter is wider than its depth, while in a limited light environment; mahogany plants develop a cathedral-like crown. In this study, Table 4.11 shows the categories under which aspect ratio was investigated.

Table 4.11: Categorizing aspect ratio for mahogany in Budongo Forest Reserve

Category	**Description**	**Likely individual shapes**	**Likely forest types**
>1	▪ Restricted light environment ▪ Mostly covered ▪ Covered	▪ Bell-shaped ▪ Cathedral-like	▪ Closed forest
1	▪ Mostly exposed crown in open with other plant individuals in close proximity	▪ Oval/flat-shaped with crown diameter almost equivalent to crown depth	▪ Earlier logged ▪ Lightly exploited forest
<1	▪ Complete exposed (both on top and sides)	▪ Oval/flat-shaped with crown diameter greater than crown depth	▪ Recently logged ▪ Heavily exploited

4.8.1 Tree mean aspect ratio

Results from physiognomic measurements of crown depth and diameter in Budongo forest shows an uneven distribution for the trees. This is probably due to the variations of light environment in the forest.

K. anthotheca was in the aspect-ratio category 1 (crown depth=crown width), which represents a mostly exposed crown in the open with other plant individuals in close proximity (Figure 4.5). Individuals in this category were flat-shaped, with crown diameter almost equivalent to crown depth. From the aspect-ratio point of view *K. anthotheca* grow in earlier logged and lightly exploited forest type.

In the unlogged, earlier logged and later logged treatments, *E. cylindricum* was represented in open gaps with flat-shaped crowns. In this category, the crown diameter is greater than crown depth (Table 4.11 and Figure 4.5). *E. utile* trees were predominantly represented in the mostly exposed (≥0.5 <1) category. In this category, individuals are flat-shaped with crown diameter almost equivalent to crown depth. The individuals are mostly found in earlier logged and lightly exploited forest types (Table 4.11 and Figure 4.5).

E. angolense appears in all the three categories (Figure 4.5) an indication that this species is a generalist and growing in both the unlogged and the logged treatments (earlier or later logged). In the unlogged forest (UnL), *E.*

angolense appeared in the complete open gaps or heavily exploited forest-types.

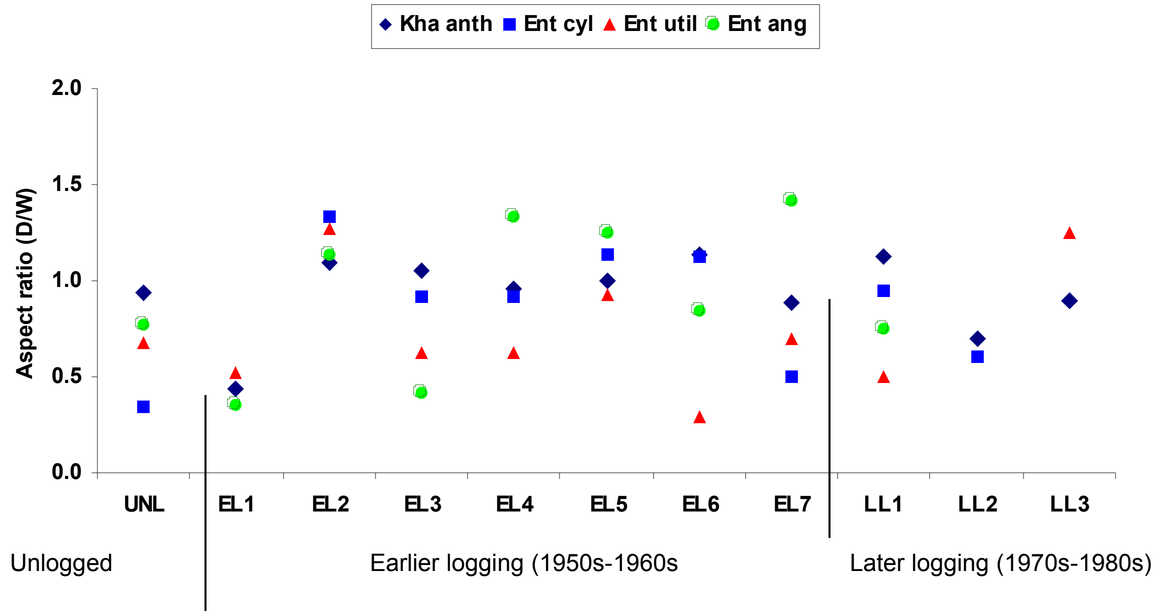

Figure 4.5: Tree mean aspect ratio

In some earlier logged (EL6) and later logged areas (LL1), it was represented in mostly exposed or lightly exploited forest-types, while in earlier logged forests (EL2, EL4 and EL6), the species was represented in covered or mostly covered environments and had bell-shaped crowns (Table 4.11 and Figure 4.5).

4.8.2 Mahogany sapling mean aspect ratio

Saplings mean crown measurement results show relatively dome-shaped distributions. This dome-shaped characteristic is especially evident in earlier logged compartments. It is likely that the earlier logged compartments provide microenvironments in which the saplings are flourishing, even for *E. utile,* which shows extreme variations (Figure 4.6). Individual species mean aspect-ratio results are described below.

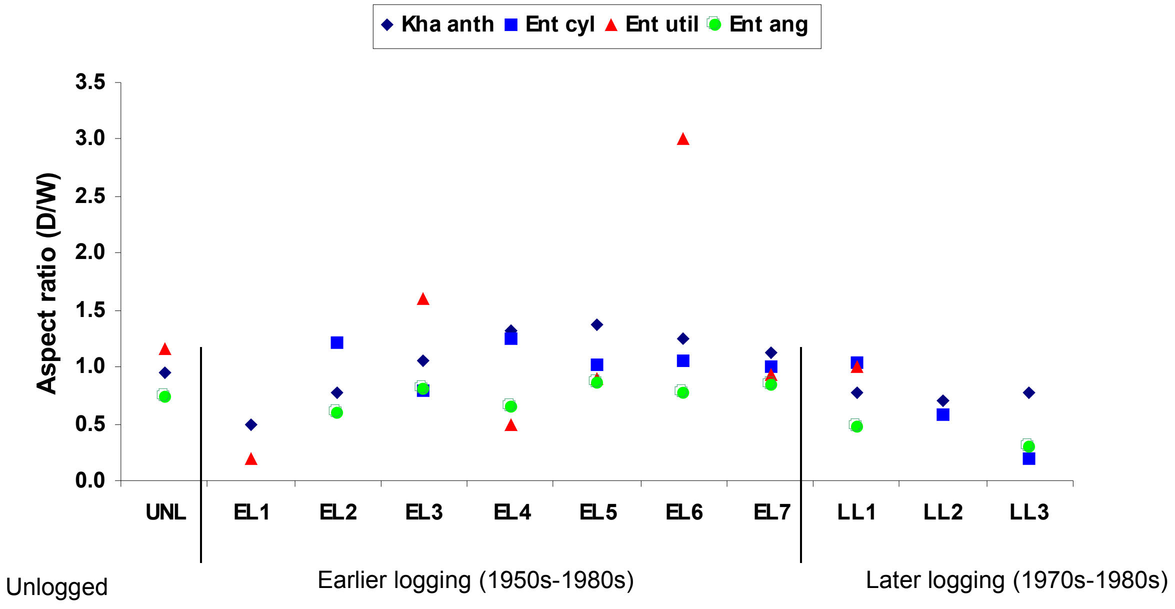

Figure 4.6: Sapling mean aspect ratio

In earlier logged forest tracts (EL1 and EL2) and later logged forests (LL1, LL2 and LL3), *K. anthotheca* was represented in the <1 aspect-ratio category (Figure 4.6) In the unlogged forest (UNL) and two sites in earlier logged forests (EL3 and EL6), the species was represented in the 1 aspect-ratio category. In three other sites in the earlier logged forest (EL4, EL5 and EL7), *K. anthotheca* was represented in the mostly covered category (Figure 4.6).

E. cylindricum was absent in the unlogged forest (UnL). In later logged forest tracts, the species was represented in the <1 category, with flat-shaped crowns. In this category, individuals are completely exposed both on the top and at the sides. In Budongo forest, such characteristics are evident in later logged compartments or heavily logged forests (see Figure 4.6 above).

Of the four mahogany species investigated, mean aspect-ratio patterns for *E. utile* saplings show random patterns across the study area (Figure 4.6) In most sites of the earlier logged forests, *E. utile* was growing in a completely closed environment, while in one site (EL1), the species was represented in completely exposed environments. Crown shapes were both cathedral-like and flat-shaped respectively (see Figure 4.6). *E. angolense* saplings were mostly represented in the <1 category, the complete exposed environments (Figure 4.6). The species was absent in EL1 (earlier logged), LL2 and LL2 (later logged forest tracts.

4.9 Chapter discussion

This chapter has evaluated and presented mahogany distribution (seedlings, saplings, poles, small and large trees) across the study areas. Estimated densities, basal areas and volume per hectare, importance values and regeneration stability have been analyzed and presented. Summary tables and trend figures are presented. In addition, mean crown score and aspect ratio were calculated for individual trees and saplings and compared across the three treatments in the study: a) unlogged, b) earlier logged (1930s-60s) and c) later logged (1970s-80s).

For all the four mahogany species studied, most of the diameter size-classes distribution densities were in the seedling, sapling, pole and small trees, showing a vigorous young post-exploitation crop in areas logged in the past (earlier and later logged). *K. anthotheca* is the most important species showing the most relative frequency, relative density and relative dominance. Generally, regeneration was higher where numbers of mature mother trees existed.

In comparing the distribution and structure of the four mahogany species along the three forest treatments, the ordination results show that the four species predominantly were unevenly distributed across the three treatments. The distribution patterns of seedlings and saplings (regeneration) as the pole show strong association to their respective larger size-classes. From the results logging explain only 44.8% distribution. The remaining percentage may be explained by either environmental factors, past arboricide treatment or animal and insect damages. Furthermore, the Tukey and Students T-test results show positive and significant differences mostly between the unlogged and later logged compartments and to some extent between the unlogged and earlier logged compartments ($0.05 < p > 0.01$). These differences have important silvicultural implication to forest regeneration and regeneration establishment post logging.

The observations that the species are distributed in all the compartments (unlogged and logged) with high variations may attest to influences beyond simply physical and some biological. The effect of soil structure, reaction (pH), organic matter, nutrient levels and forest microenvironments may also be contributing to the natural regeneration, general structure and distribution of mahogany species in the forest. More in-depth investigation and results with regard to these factors are presented in the next chapters.

CHAPTER 5

RESEARCH RESULTS PART 2: THE EFFECT OF LOGGING ON SOIL NUTRIENT AVAILABILITY AND CONSEQUENCES ON MAHOGANY REGENERATION IN BUDONGO FOREST RESERVE, UGANDA

Summary

This chapter has five sections. Section 5.1 is an introduction. Section 5.2 presents data analysis. The results of soil texture, soil reaction, organic matter and nutrient levels related to the logging history are presented in Section 5.3. Results are presented in summary, T-test and Pearson product moment correlation coefficient tables. Relationships between regeneration and soil variables are presented in Section 5.4, while Section 5.5 presents the discussion of the chapter results.

5.1 Introduction

Soil nutrient availability is among the most important factors affecting ecological processes within forest ecosystems. It influences plant germination, growth rate and plant survival, soil physical properties, microbial activity and nutrient uptake efficiency (Ralston, 1964; Buckman and Brady, 1968; Treshow, 1970; Pritchett, 1979; & Horton *et al.*, 1984).

Factors influencing soil nutrient cycles have been studied extensively. Baver *et al.* (1972) and Pritchett (1979) summarized the factors involved as a) parent material, b) heat loss from the soil through the insulating effect of plant cover, c) litter layer, and (d) tree canopy. The parent material influences the rate and ease with which weathering and formation of bonds with other soil elements will proceed, while the vegetation cover on the soil forms a blanket that influences heat exchange. The latter interface affects the process of nutrient cycling near the soil surface. The accumulation of a litter layer together with the presence of the organic matter reflects the health and fertility of the ecosystem and to silviculturalists influence the quality of a forest site (Barnes *et al.*, 1998).

According to Binkley (1995), plant life is constructed from a surprisingly small quantity of elements, such as are required for plant growth and development. In this respect, these elements are either macro-nutrients, which are required in relatively large amounts or micronutrients, which are required in relatively small amounts. Although micronutrients are required in small amounts, they are all, none-the-less important in the biochemical functioning of forest stands (Sanchez, 1976).

5.1.1 Soil texture

Chapter 3, detailed the materials used and procedures applied to collect soil samples from the unlogged, earlier and later logged compartments within Budongo Forest. Soil samples were collected from the top and sub-soil respectively and kept in separate polythene bags for texture and nutrient analysis. A depth of 0 to 15 cm was chosen as topsoil because surface soil has greater temperature fluctuations than the subsoil (Pritchett 1979, Gent et al. 1983).

5.1.2 Soil reaction (pH) and organic matter content

The amounts of organic matter combined with levels of clay are important in enhancing early plant growth after germination in forest ecosystems. According to Money (1978), clay-organic matter cohesion helps retention of soil fertility as the rate of leaching is reduced. The pH levels in the soils further complicate the clay-humus cohesions. Therefore, the amount of organic matter and pH were evaluated in both top and sub soils, which were later compared within and between the three treatments sampled.

5.1.3 Soil nutrients

The methods described in Chapter 3 were used to collect soil samples. The collected samples were prepared for laboratory analysis first by air-drying for about 24 hours and passing through a 2 mm sieve and second by testing for pH, levels of organic matter, nitrogen, available phosphorus, potassium, sodium, calcium, magnesium, sand, clay and silt.

5.2 Data analysis

The soil laboratory results were transformed for normality using MINITAB statistical software. After normalization, the data were subjected to one-way analysis of variance. Duncan's New Multiple range Test was run on the SAS computer programme to separate least significant differences (LSD) in soil nutrients within and between compartments (i.e. unlogged, earlier and later logged compartments). Student's t-test analyses were done on data collected from pH, organic matter, nutrient levels and soil texture. Also done were comparisons of mahogany regeneration with soil texture, pH and organic matter soil nutrient levels.

5.3 Results of soil texture: Sand, clay and silt

5.3.1 % Sand

The later logged forest tracts showed the most within treatment variations compared to the unlogged and earlier logged treatments. The later logged treatment had the greatest accumulation of sand with an average of 58.4% sand in the topsoil and 48.4% in the subsoil. The unlogged treatment had the lowest percentage of sand with an average of 52% sand in the topsoil and 45% in the subsoil and (Table 5.1).

The most between-treatment variations were detected between the earlier and later logged treatments (p=0.243) compared to the unlogged and earlier logged treatment (p=0.952) and between unlogged and later logged treatment (p=0.42) (0. 05 ≤P > 0. 01). There was no significant difference in sand proportions across the three treatments. Tables 5.2a-c and 5.3a-c show variations in soil texture, pH, organic matter and soil nutrients in the top and subsoil.

Table 5.1: Means of soil texture in top and sub soils across treatments

		Top soil (%)			Subsoil (%)		
Compartment	**Treatment**	**Sand**	**Clay**	**Silt**	**Sand**	**Clay**	**Silt**
N15 (n=24)	Unlogged (n=24)	52	29	19	36	45	20
Averages		**52**	**29**	**19**	**36**	**45**	**20**
N14 (n=24)	Earlier logged (1930s-1960s) (n=162)	54	24	22	33	49	18
N9 (n=24)		54	27	19	31	50	18
N5 (n=20)		54	26	20	38	41	21
S3 (n=22)		60	19	21	41	36	23
B3 (n=24)		44	40	17	45	38	17
W21 (n=24)		58	21	22	49	34	17
W16 (n=24)		50	32	18	52	33	14
Averages		**53.4**	**27.0**	**19.6**	**41.3**	**40.4**	**18.3**
B1 (n=24)	Later logged (1970s-1980s) (n=72)	60	19	21	**47**	**33**	**21**
S5 (n=24)		60	18	22	**52**	**26**	**22**
K4 (n=24)		55	22	23	**47**	**38**	**16**
Averages		**58.4**	**19.7**	**21.9**	**48.4**	**32.1**	**19.5**

Note: n= are sample plots in compartments/treatments

5.3.2 % Clay

The earlier logged forests had the most within-treatment variations in clay content than the later and unlogged treatments. The unlogged treatment showed the highest amounts of clay, with an average percent of 29 in the topsoil and 45 in the subsoil. The lowest amount of clay proportions was in later logged treatment with an average percentage of 19.7 in the topsoil and 32.1 in the subsoil (Table 5.1). The earlier logged was intermediate.

Table 5.2a-c: Analysis of variance: variations in soil texture, pH, organic matter, and soil nutrients between treatments in **topsoil**

(a) Unlogged vs. earlier logging

Treatment	Soil element	p-values	F-value	P > 0. 01 ≤ 0. 05
Unlogged vs. earlier logging	PH	0.042	7.48	S
	Organic matter	0.050	30.13	S
	Nitrogen (N)	0.235	16.25	NS
	Avail. Phosphorus (P)	0.117	6.23	NS
	Potassium (K)	0.092	21.82	NS
	Sodium (Na)	0.130	12.85	NS
	Calcium (ca)	0.241	13.33	NS
	Magnesium (Mg)	0.015	5.55	S
	Sand	0.952	8.38	NS
	Clay	0.224	9.49	NS
	Silt	0.731	2.36	NS

(b) Unlogged vs. later logging

Treatment	Soil element	p-value	F-value	P > 0. 01 ≤ 0. 05
Unlogged vs. later logging	PH	0.0024	1.301	S
	Organic matter	0.045	26.484	S
	Nitrogen (N)	0.132	14.284	NS
	Avail. Phosphorus (P)	0.050	5.476	S
	Potassium (K)	0.0112	19.180	S
	Sodium (Na)	0.0358	11.295	S
	Calcium (ca)	0.281	11.717	NS
	Magnesium (Mg)	0.143	4.878	NS
	Sand	0.419	7.366	NS
	Clay	0.220	8.342	NS
	Silt	0.297	2.074	NS

(c) Earlier vs. later logging

Treatment	Soil element	p-value	F-value	P > 0. 01 ≤ 0. 05
Earlier vs. later logging	PH	0.144	1.227	NS
	Organic matter	0.044	24.676	S
	Nitrogen (N)	0.099	13.471	NS
	Avail. Phosphorus (P)	0.216	5.165	NS
	Potassium (K)	0.139	18.089	NS
	Sodium (Na)	0.283	10.653	NS
	Calcium (ca)	0.290	11.051	NS
	Magnesium (Mg)	0.014	4.601	S
	Sand	0.243	7.031	NS
	Clay	0.0365	7.867	S
	Silt	0.0025	14.956	S

Note: S represents significant, while NS represents non-significant

Table 5.3a-c: Analysis of variance: variations in soil texture, pH, organic matter, and soil nutrients between treatments in the **subsoil**

(a) Unlogged vs. earlier logging

Treatment	Soil element	p-value	F-value	P > 0. 01 ≤ 0. 05
Unlogged vs. earlier logging	PH	0.026	8.320	S
	Organic matter	0.301	1.477	NS
	Nitrogen (N)	0.153	0.114	NS
	Avail. Phosphorus (P)	0.131	1.550	NS
	Potassium (K)	0.231	0.100	NS
	Sodium (Na)	0.111	0.059	NS
	Calcium (ca)	0.207	1.870	NS
	Magnesium (Mg)	0.014	5.520	S
	Sand	0.030	7.069	S
	Clay	0.204	7.695	NS
	Silt	0.121	3.612	NS

(b) Unlogged vs. later logging

Treatment	Soil element	p-value	F-value	P > 0. 01 ≤ 0. 05
Unlogged vs. later logging	PH	0.0264	14.127	S
	Organic matter	0.027	12.261	S
	Nitrogen (N)	0.141	10.097	NS
	Avail. Phosphorus (P)	0.014	21.324	S
	Potassium (K)	0.021	8.085	S
	Sodium (Na)	0.001	17.050	S
	Calcium (ca)	0.219	1.597	NS
	Magnesium (Mg)	0.013	20.444	S
	Sand	0.027	12.037	S
	Clay	0.318	2.572	NS
	Silt	0.011	13.085	S

(c) Earlier vs. later logging

Treatment	Soil element	p-value	F-value	P > 0. 01 ≤ 0. 05
Earlier vs. later logging	PH	0.024	11.094	S
	Organic matter	0.328	1.224	NS
	Nitrogen (N)	0.114	0.095	NS
	Avail. Phosphorus (P)	0.314	1.285	NS
	Potassium (K)	0.121	0.083	NS
	Sodium (Na)	0.110	0.049	NS
	Calcium (ca)	0.419	1.550	NS
	Magnesium (Mg)	0.013	10.431	S
	Sand	0.028	5.860	S
	Clay	0.019	6.379	S
	Silt	0.011	12.994	S

Note: S represents significant, while NS represents non-significant

Thus, clay proportions decreased with canopy opening. In comparing between treatments, significant differences were detected between earlier and later logged treatments (P=0.0365) (Table 2). All other potential pairs, such as comparisons between unlogged and earlier logging, between unlogged and later logging and between unlogged and all logged treatments) were generally similar and not significantly different (05 ≤ P > 0. 01) (Tables 5.2a-c and 5.3a-c).

5.3.3 % Silt

The highest within-treatment variations were detected in the later logged treatment compared to the unlogged and earlier logged treatment. The earlier logging had the highest amount of silt with an average of 21.9% in top soil and 19.5 in subsoil compared to the unlogged treatment with an average of 19% in top soil and 20% in sub soil and the earlier logging with an average of 19.6% in top soil and 18.3% in sub soil. The unlogged treatment showed the least within-treatment variations (Table 5.1). In comparing the three treatments, silt proportions were significantly different between earlier and later logged treatment (p=0.025) (05 ≤ P > 0. 01). Other potential pairs, such as comparisons between unlogged and earlier logging, between unlogged and later logging and between unlogged and all logged treatments were not significantly different (Tables 5.2c and 5.3c).

5.3.4 Soil reaction (pH) and organic matter levels

5.3.4.1 Soil reaction (pH)

From the pH average results, the topsoil showed relatively similar reaction levels across the study area. The earlier logged treatment showed the most within-treatment variations compared to the unlogged and later logged treatments. The unlogged was the most neutral with an average of 6.67 in top soil and an average of 6.17 in subsoil. The later logging showed the most acidic soils with an average of 6.35 in topsoil and 5.92 in sub soil (Table 5.4). The sub soils were, in most cases more acidic than the topsoil across treatments (Table 5.4). In comparing the unlogged, earlier and later logged treatments, soil reaction (pH) decreased with canopy opening (i.e. the later logged treatment showed the most acidic soils compared to the unlogged and earlier logged treatments. Significant differences were detected between the unlogged and earlier logging (p=0.042) and between unlogged and later logging (p=0.0024) (0. 05 ≤ P > 0. 01). Comparison between earlier and later logging was not significantly different for topsoil (Tables 5.2c and 5.3c).

5.3.4.2 Organic matter

The unlogged treatment showed the most within-treatment variations compared to the earlier and later logged treatments.

Table 5.4: Average pH and organic matter content within and between treatments

Compartment	Treatment	*Top soil*		*Subsoil*	
		PH	**OM (%)**	**pH**	**OM (%)**
N15 (n=24)	Unlogged (n=24)	6.68	7.07	6.17	1.75
Averages		**6.68**	**7.07**	**6.17**	**1.75**
N14 (n=24)	Earlier logged (1950s-1960s) (n=162)	7.05	7.96	5.91	2.85
N9 (n=24)		6.76	8.57	9.44	2.25
N5 (n=20)		6.69	8.37	5.96	1.70
S3 (n=22)		6.83	9.51	6.19	2.02
B3 (n=24)		6.18	6.56	5.68	1.67
W21 (n=24)		6.46	7.34	5.73	1.56
W16 (n=24)		6.19	6.97	5.71	1.49
Averages		**6.59**	**7.90**	**6.37**	**1.93**
B1 (n=24)	Later logged (1970s-1980s) (n=72)	6.18	5.57	5.87	1.67
S5 (n=24)		6.61	7.77	6.21	2.67
K4 (n=24)		6.26	7.11	5.69	1.67
Averages		**6.35**	**6.82**	**5.92**	**2.00**

Note: (n=24) are sample plots in compartments

The earlier logged treatment showed the highest accumulation of organic matter with an average of 7.90 % in the topsoil and 1.93 % in the subsoil. The later logged treatment showed the least organic matter levels with an average of 6.82 % in the topsoil and 2.0 % in the subsoil (Table 5.4). Organic matter levels were consistently higher in the topsoil than in the sub soils in all the samples (Table 5.4). In comparing the three treatments, the earlier logged compartments showed more organic matter content compared to the unlogged and the later logged compartments. A significant difference was detected between the unlogged and earlier logged treatment (p=0.050). Also a significant difference was detected between the unlogged and later logged treatment (p=0.045), but comparison between the earlier and later logged forests were not significantly different (p=0.074) (0. 05 ≤ P > 0. 01) (Tables 5.2c and 5.3c).

According to Barnes *et al*. (1998), most forest soils range from extremely acid (pH 4.0) to slightly acid (pH 6.9) and the pH levels of particular forest site depends substantially on the amount of organic matter additions (e.g. dead and decomposing leaves, twigs and other stem parts). From the results, the amount of organic matter in Budongo forest, especially in the earlier logged forest tracts probably influenced the pH levels in the topsoil (Table 5.4).

5.3.4 Results of nutrient levels

5.3.4.1 Nitrogen (N) (%)

The earlier logged forests showed the most within-treatment variations compared to the unlogged and later logged treatments. The later logged treatment showed the least within-treatment variations. Nitrogen content was highest in the unlogged forest with an average of 0.54% in the topsoil and 0.19% in the subsoil (Table 5.5). In comparing the unlogged, the earlier and the later logged treatments, nitrogen levels were decreasing with decreasing canopy cover (Table 5.5). The decrease in nitrogen levels from the unlogged treatment, through the earlier to the later logged treatments is shown in both the topsoils and in the sub soils (Table 5.5).

Table 5.5: Average nutrient levels (N, avail. P, K, Na, Ca, Mg) between treatments

Compartment	Treatment	Topsoil						Subsoil					
		N	Avail. P	K	Na	Ca	Mg	N	Avail. P	K	Na	Ca	Mg
		(%)	ppm	m-mol/100g soil				(%)	ppm	m-mol/100g soil			
N15 (n=24)	Unlogged	0.54	2.99	0.66	0.075	12.39	3.48	0.19	1.01	0.39	0.04	9.53	2.99
Averages		**0.54**	**2.99**	**0.66**	**0.075**	**12.39**	**3.48**	**0.19**	**1.01**	**0.39**	**0.04**	**9.53**	**2.99**
N14 (n=24)	Earlier logged (1930s-1960s)	0.51	2.75	0.66	0.076	13.56	3.85	0.15	1.43	0.33	0.04	8.58	2.78
N9 (n=24)		0.59	2.7	0.68	0.08	12.36	3.61	0.18	0.93	0.36	0.04	7.37	2.53
N5 (n=20)		0.54	3.48	0.66	0.07	12.76	3.47	0.13	1.00	0.28	0.03	9.54	3.10
S3 (n=22)		0.55	5.25	0.69	0.08	14.74	3.52	0.1	2.22	0.30	0.03	11.13	3.02
B3 (n=24)		0.43	3.11	0.50	0.06	9.83	2.78	0.18	3.64	0.27	0.04	6.53	2.42
W21 (n=24)		0.41	4.09	0.56	0.06	13.03	3.45	0.11	3.89	0.17	0.03	8.44	2.63
W16 (n=24)		0.39	4.65	0.42	0.08	8.92	2.74	0.16	5.89	0.20	0.03	7.07	2.54
Averages		**0.49**	**3.72**	**0.60**	**0.03**	**1.86**	**0.49**	**0.14**	**2.71**	**0.27**	**0.03**	**8.38**	**2.72**
B1 (n=24)	Later logged (1970s-1980s)	0.27	6.6	0.40	0.05	12.92	2.78	0.16	4.11	0.26	0.03	10.31	2.56
S6 (n=24)		0.51	5.34	0.62	0.07	14.85	3.79	0.11	3.27	0.32	0.03	12.48	3.09
K4 (n=24)		0.37	4.27	0.49	0.06	12.23	3.27	0.14	3.67	0.21	0.03	7.31	2.36
Averages		**0.38**	**5.40**	**0.50**	**0.04**	**9.03**	**2.35**	**0.14**	**3.68**	**0.26**	**0.03**	**10.03**	**2.67**

Note: n= sample plots in compartments

Although not significantly different, the comparison between the unlogged with later logged treatments showed the most distinct between-treatment variations (p=0.0841). All the three treatments were generally similar in total nitrogen (Tables 5.2 and 5.3).

5.3.4.2 Available phosphorus (ppm)

Within treatment variations of available phosphorus was highest in the later logged treatment. The least within-treatment variations were detected in the unlogged forest. Also, the highest content of phosphorus was in the later logged treatment with 5.4 ppm in the topsoil and 3.68 ppm in the subsoil (Table 5.5). In comparing the unlogged, the earlier and the later logged treatments, available phosphorus increased with canopy opening (Table 5.5).

Increasing accumulation of available phosphorus from the unlogged, through the earlier to the later logged compartments are evident in both the top and sub soils (Table 5.5). A significant difference was detected between the unlogged forests and the later logged forests (p=0.05). Other potential pairs (unlogged vs. earlier and earlier vs. later) were not significantly different (0. 05≤ P > 0. 01) (Tables 5.2 and 5.3).

5.3.4.3 Potassium (K) (m-mol/100g soil)

Highest within-treatment variations were detected in the later logged treatment. The least was in the unlogged treatment. Accumulation of potassium was highest in the unlogged forest with an average of 0.66 m-mol/100g soil in top soil and 0.39 m-mol/100g soil in subsoil. The later logged treatment showed the least potassium accumulation (Table 5.5). To compare the unlogged, earlier and later logged treatments, potassium decreased from the unlogged, through the earlier logged to the later logged treatment (Table 5.5). A significant difference was detected between the unlogged treatment and the later logged treatment (p=0.0112). Also, the unlogged was significantly different from the logged (aggregated) (p=0.046). Other potential pairs, such as comparisons between unlogged and earlier logged treatment and between earlier logging and later logging were not significantly different (0. 05≤ P > 0. 01) (Tables 5.2 and 5.3).

5.3.4.4 Sodium (Na) (m-mol/100g soil)

The earlier logged treatment showed the highest within-treatment variations (sample variance of 0.003) compared to the unlogged treatment (sample variance of 0.0007) and the later logged treatment (sample variance of 0.0008). The treatment with the most sodium content was the unlogged with an average of 0.075 m-mol/100g soil in the top soil and 0.04 m-mol/100g soil in the subsoil. The later logged showed the least sodium content (Table 5.5). In comparing the three treatments, sodium decreased from the unlogged, through the earlier to the later logged treatments (Table 5.5). The unlogged treatment was significantly different from the later logged treatment (p=0.0358). Also significantly different was the comparison between earlier and later logged treatment (p=0.0503). Other potential pairs, such as unlogged vs. later logged and unlogged vs. earlier logged were not significantly different (0. 05 ≤ P > 0. 01) (Tables 5.2 and 5.3).

5.3.4.5 Calcium (Ca) (m-mol/100g soil)

The highest within-treatment variations were detected in earlier logged. The least variations were in the unlogged treatment. The unlogged treatment showed the highest amounts of calcium (average of 12.39 m-mol/100g in the topsoil and 9.53 m-mol/100g in the subsoil). Results indicate that the earlier logged treatment presented the least amount of calcium (see Table 5.5 above). No significant differences were detected between treatments. They were generally similar in calcium content (Tables 5.2c and 5.3c).

5.3.4.6 Magnesium (Mg) (m-mol/100g soil)

Highest within-treatment variations were detected in the later logged forests (sample variance of 1.1 m-mol/100g soil). The least was detected in earlier logging (sample variance of 0.941 m-mol/100g soil). Accumulation of magnesium was highest in the unlogged forest with an average of 3.48 m-mol/100g soil in topsoil and 2.99 m-mol/100g soil in subsoil (see Table 5.5 above). In comparing the three treatments, a significant difference was only detected between the unlogged and all logged treatments (p=0.0488) (0. 05 ≤ P > 0. 01). Other potential pairs (unlogged vs. earlier logged; unlogged vs. later logged and earlier vs. later logged) were not significantly different. Generally, magnesium was decreasing from the unlogged, through the earlier to the later logged treatments both in the top and sub soils (see Table 5.5 above).

5.4 Relationships of mahogany regeneration with soil texture, pH, organic matter and nutrients

All mahogany regeneration showed negative correlations with soil texture, pH, organic matter and most soil nutrients. Only available phosphorus consistently showed positive correlation with regeneration (Table 5.6).

For example, *K. anthotheca* seedlings were negatively correlated to pH, nitrogen, potassium, calcium and magnesium (Table 5.6). The unlogged treatment with most concentration of nitrogen negatively affected the density of seedlings and saplings (r=-0.51). Seedlings of *E. cylindricum* were negatively correlated to mostly organic matter and sodium, while the pole size-class were negatively correlated to mostly pH, organic matter, nitrogen, AVP, sodium, potassium and magnesium (Table 5.6). *E. utile* seedlings were mainly negatively correlated to soil texture and AVP (r=-0.60), while the saplings were negatively correlated to nitrogen, potassium, calcium and magnesium. Seedlings of *E. angolense* were mostly negatively correlated to organic matter, nitrogen, AVP and sodium. *E. angolense* saplings were mostly negatively correlated to magnesium (r=0.52) (Table 5.6).

Table 5.6: Pearson product moment correlation coefficients (r) between the different tested soil variables with mahogany regeneration

Soil Variable	**K. anthotheca**			***E. cylindricum***			***E. utile***			***E. angolense***		
Top soil	Se	Sa	Po	Se	Sa	Po	Se	Sa	Po	Se	Sa	Po
Sand	-0.31	0.34	0.02	0.10	0.31	0.19	-0.69	-0.19	-0.10	0.35	0.06	-0.28
Clay	0.26	-0.29	0.03	-0.01	-0.23	-0.10	0.63	0.16	0.16	-0.28	0.07	0.32
Silt	-0.18	0.21	-0.12	-0.21	0.04	-0.14	-0.36	-0.12	-0.36	0.06	-0.37	-0.43
PH	-0.54	-0.36	-0.21	-0.40	-0.32	-0.53	-0.01	-0.41	-0.27	-0.40	-0.35	-0.13
Org. matter	-0.46	-0.49	-0.32	-0.52	-0.35	-0.58	-0.23	-0.36	-0.39	-0.56	-0.28	0.01
Nitrogen	-0.51	-0.51	-0.23	-0.45	-0.47	-0.59	0.14	-0.51	-0.24	-0.59	-0.32	0.05
AVP	0.18	0.45	0.11	0.36	0.39	0.56	-0.60	0.25	0.20	0.60	0.27	-0.11
Potassium	-0.65	-0.40	-0.24	-0.41	-0.39	-0.58	0.11	-0.65	-0.31	-0.47	-0.35	-0.06
Sodium	0.05	-0.44	-0.03	-0.60	-0.48	-0.59	-0.10	0.11	-0.03	-0.64	-0.23	-0.05
Calcium	-0.64	0.04	-0.25	-0.11	-0.05	-0.13	-0.31	-0.57	-0.34	0.07	-0.29	-0.32
Magnesium	-0.57	-0.20	-0.20	-0.48	-0.35	-0.54	-0.08	-0.51	-0.44	-0.45	-0.52	-0.29
Subsoil	Se	Sa	Po	Se	Sa	Po	Se	Sa	Po	Se	Sa	Po
Sand	0.40	0.59	0.33	0.05	0.16	0.35	-0.33	0.38	0.05	0.18	0.05	-0.16
Clay	-0.16	-0.56	-0.26	-0.12	-0.18	-0.39	0.42	-0.17	-0.05	-0.26	-0.06	0.12
Silt	-0.64	-0.05	-0.19	0.21	0.05	0.11	-0.12	-0.61	0.05	0.33	-0.02	0.05
PH	-0.32	-0.42	-0.34	0.09	0.00	0.03	-0.27	-0.28	-0.22	-0.14	0.19	0.10
Org. matter	-0.41	-0.34	-0.46	-0.33	-0.43	-0.27	-0.13	-0.22	-0.49	-0.38	-0.57	-0.32
Nitrogen	-0.57	-0.24	-0.02	0.26	-0.05	0.12	0.54	0.18	0.35	0.10	0.19	0.16
AVP	0.32	0.50	0.30	0.09	0.20	0.39	-0.33	0.66	0.09	0.17	0.19	-0.15
Potassium	0.62	-0.46	-0.32	-0.07	-0.39	-0.25	0.31	-0.45	0.02	-0.13	-0.25	-0.06
Sodium	-0.38	-0.42	-0.31	-0.11	-0.42	-0.29	0.60	-0.25	-0.18	-0.33	-0.21	-0.12
Calcium	-0.18	0.23	0.05	0.06	0.05	0.12	-0.33	-0.36	0.08	0.28	-0.11	-0.15
Magnesium	-0.41	0.01	0.19	-0.18	-0.12	-0.24	-0.02	-0.41	0.20	-0.06	-0.18	0.10

Note: Whereas the response of mahogany regeneration to available phosphorus (AVP) was generally positive, the response to soil texture, pH, organic matter and other soil nutrients was generally negative.

5.5 Chapter Discussion

The results show significant negative correlations between soil texture (top and sub soil) and *E. utile* regeneration across the treatments sampled. The other studied mahogany species showed weak negative correlations. The sand proportions in both earlier and later logged forest tracts were texturally identical.

In the subsoil, clay proportions are more pronounced compared to sand and silt, especially in the unlogged forest. Also, clay proportions are pronounced in the unlogged and earlier logged treatments with distinct variations between the compartments. For example, clay proportions in compartment N5 (earlier logging) are closely similar to clay proportions in the unlogged forest, but significantly different from clay proportions in compartments N9 and N14 (earlier logged), which are texturally similar (Table 5.1). Compartments W21 and W6 (later logged) showed identical soil textural proportions, which probably explain the present distribution and structure of the mahoganies across the study area presented in the previous chapter.

Soil pH is defined as the negative logarithm of the hydrogen ion concentration. Soil pH or soil reaction is an indication of the acidity or alkalinity of soil and is measured in pH units. As the amount of hydrogen ions in the soil increases as the soil pH decreases thus becoming more acidic. The pH scale goes from 0 to 14 with pH 7 as the neutral point. From pH 7 to 0 the soil is increasingly more acidic and from pH 7 to 14 the soil is increasingly more alkaline or basic. In Budongo forest, the soils were generally in the range of pH 5 to 7 (Table 5.4).

According to Barnes *et al.* (1998), the effect of soil pH on the solubility of minerals or nutrients is great. Before plants can use a nutrient, it must be dissolved in the soil solution. Most minerals and nutrients are more soluble or available in basic soils than in neutral or acid soils. For example, phosphorus is never readily soluble in the soil but is most available in soil with a pH of 6.5. Extremely and strongly acid soils (pH 4.0-5.0) can have high concentrations of soluble aluminum, iron and manganese, which may be toxic to the growth of some plants. A pH range of approximately 6 to 7 promotes the most ready availability of plant nutrients. The present results suggest that the earlier logged treatment presented the most conducive soil reaction levels to enhanced mahogany regeneration.

Whitemore (1990) and Greig-Smith (1983) noted that some tropical forest plants tolerate strong acid soils and grow well, while some plants do well only in slightly acid to moderately alkaline soils. However, a slightly alkaline (pH 7.4-7.8) or higher pH soil can cause a problem with the availability of iron causing chlorosis of the leaves which will put the species under stress leading to species decline and eventual mortality. The soil pH can also influence plant growth by its effect on activity of beneficial microorganisms (e.g. bacteria) that decompose soil organic matter. This microbial activity is hindered in strong acid soils, therefore preventing organic matter from breaking down, resulting in an accumulation of organic matter and the tie up of nutrients, particularly nitrogen, that are held in the organic matter.

Forest soils tend to become acidic as a result of carbon dioxide from decomposing organic matter and root respiration dissolving in soil water to form a weak organic acid and from formation of strong organic and inorganic acids, such as nitric and sulfuric acid, from decaying organic matter. The impulse effect from decomposing organic matter in the later logged treatment probably explains the persistent higher levels of acidity than in the earlier and unlogged treatments.

In investigating the contribution of logging on changes in the organic matter levels in Budongo forest, the earlier logging showed the highest deposits compared to the unlogged and later logged treatments (Table 5.4). Organic matter is the vast array of carbon compounds in soil. Originally created by plants, microbes, and other organisms, these compounds play a variety of roles in nutrient, water, and biological cycles. Thus, soil texture, especially soils with 20-25 % clay and silt proportions are important for organic matter formation in tropical soils (Money, 1978). Both organic and clay particles hold on to nutrients electrochemically - like a magnet holds on to iron filings. Fine-textured soils can hold much more organic matter than sandy soils for two reasons. First, clay particles form electrochemical bonds that hold organic compounds. Second, decomposition occurs faster in well-aerated sandy soils (Money, 1978). The unlogged and earlier logged treatments had the most deposits of clay and silt.

The amount of nutrients that the organic compounds and clay could carry and make available to plants is called the soil's cation exchange capacity (CEC). According to Barnes *et al.* (1998), Whitmore (1990) and Greg-smith (1968) soils with up to 6% organic matter support plants in dry spells, roots grow more easily, soil compaction and erosion are reduced, and soil organism are supported for the many soil processes. This is a general phenomenon evidenced more in the earlier logged and unlogged treatment than in the later logged treatment.

Organic matter also affects nutrient cycles by chelating (chemically holding on to) nutrients, and preventing them from becoming insoluble and therefore unavailable to plants. For example, humic substances help make iron available to plants, even in medium-to-high pH soils. In forestry, organic matter is important as food for microorganisms, insects, worms, and other organisms, and as a habitat for some larger organisms (Whitmore, 1990). The organic soil organisms degrade potential pollutants and help bind soil particles into larger aggregates. Well-aggregated, crumbly soil allows good root penetration, improves water infiltration and reduces erosion (Money, 1978). Also, high temperatures speed up the decomposition of organic matter. The later and earlier logged treatments probably had generally higher temperature conditions compared to the unlogged because of the amount of canopy cover differences.

Nutrients for healthy plant growth are divided into three categories: primary, secondary and micronutrients. Nitrogen (N), phosphorus (P) and potassium (K) are primary nutrients, which are needed in fairly large quantities compared to the other plant nutrients. Calcium (Ca) and magnesium (Mg) are secondary nutrients, which are required by the plant in lesser quantities but are still essential for good plant growth. Zinc (Zn) and manganese (Mn) are micronutrients, which are required by the plant in very small amounts. Most secondary and micronutrient deficiencies are easily corrected by keeping the soil at the neutral pH value (Barnes et al., 1998).

The major impact that extremes in pH have on plant growth is related to the availability of plant nutrients or the soil concentration of plant-toxic minerals. In highly acid soils, aluminum and manganese can become more available and more toxic to the plant. Also at low pH values, calcium, phosphorus and magnesium are less available to the plant. At pH values of 6.5 and above, phosphorus and most of the micronutrients become less available (Barnes et al., 1998). Therefore, nitrogen credits have been developed for some plant residues. Recommended nutrient credits account for the fact that not all of the nutrients in organic material will be available to plants during regeneration. The organic compounds must be broken down by microorganisms and transformed into inorganic forms that plants can use. Generally, little fresh tree residue will decompose after logging. Only herbaceous plants decompose quickly and these are important during after-logging germination, since their nutrients are made available to plants. Smaller amounts of nutrients from tree residues are available in subsequent years (Whitemore, 1990). Each specific organic to inorganic conversion by microorganisms has a characteristic amount of carbon in proportion to nitrogen (ratio). A low carbon-to-nitrogen ratio means the material is high in nitrogen. Plant materials with a high C:N ratio (low nitrogen) decompose slowly and may trigger nitrogen deficiency in plants as they decompose (Money, 1978).

Plants depend on microbes to break down organic matter and make the nutrients available to them. Most microbes get energy from carbon compounds such as sugars, carbohydrates, fats, and other substances. After logging, plant residues (trunks, branches and leaves) deposited into the soil trigger a feeding frenzy and a burst in microbial growth. To grow, microbes need carbon for energy and nitrogen to build proteins (Barns *et al.*, 1998). For every twenty to thirty carbon atoms they consume, they use about one nitrogen atom. If that nitrogen is not available from the newly added organic material, microbes will take it from the soil, and deprive growing plants of nitrogen. Plant materials with C:N ratios less than 30:1 will not trigger temporary nitrogen deficiency. The nitrogen is not lost from the soil since it is still present in the cells of microbes but plants cannot use it. During this initial decay process, microbes are giving off large amounts of CO_2 to the atmosphere and the carbon-to-nitrogen ratio of the remaining organic material declines (Money, 1978 and Barnes *et al.,* 1998). Microbial activity slows because the remaining compounds are more recalcitrant (difficult to decompose). At this point, nitrogen from the dying microbes becomes available to plants. According to Ssali (2000), Barnes *et al*. (1998), Greig-Smith (1983) and Whitemore (1990), soil organic matter has a C:N ration of 10:1, composted soil 10-30:1, corn stover 60:1, while sawdust has a C:N ration of 100-400:1. If the ratio is less than 20:1, the residue has more than 2% nitrogen, and nitrogen will be quickly available to growing plants. If the ratio is more than 40:1, the residue has less than 1% nitrogen, and N will be tied up (unavailable to plants) for a few months or years, or much longer in the case of low-nitrogen woody materials. Probably the C:N ratio applies to the logging situation in Budongo and has had an influence on mahogany regeneration as shown by the response of the mahogany regeneration in the three treatments.

Finally, the results from this chapter suggest that logging in the Budongo Forest Reserve, contributed mainly to changes in organic matter and nutrient levels across treatments. These changes have a bearing on the regeneration, structure and distribution of the mahogany species in the forest. The low and negative correlation coefficients (r shown in Tables 5.6 above), suggest a negative cause/effect relationship between soil and mahogany regeneration in Budongo Forest Reserve. The above information is important for silvicultural management and prescriptions. A relationship of mahogany regeneration with forest soils would be complete after the effect of the microenvironment, such as illumination, PAR, temperature, ground and canopy cover that goes along with forest soil nutrient cycling is known. Data from illumination, PAR, ground and canopy cover are presented in the next chapter.

CHAPTER 6

RESEARCH RESULTS PART 3:
EFFECT OF ILLUMINATION, PAR, TEMPERATURE, GROUND AND CANOPY COVER ON THE REGENERATION OF SELECTED MAHOGANY SPECIES IN BUDONGO FOREST RESERVE

Summary

This chapter has three sections. Section 6.1 presents an introduction. It highlights the aim, objectives and presents the justification for studying forest environments in relation to mahogany regeneration. Brief descriptions on data collection methods for forest light regimes, PAR and temperature are presented. Section 6.2 presents the results. Comparisons and contrasts within and between treatments across the study area are given. Detrended correspondence analysis (DCA) and Canonical correspondence analysis (CCA) results show gradient relationships between mahogany seedlings and saplings, and environmental variables in the three treatments across the study area. Also, regression relationships between illumination, PAR, temperature, ground and canopy cover are presented. The Section also relates logging with physical landscape, ground and canopy covers. Gradient analysis of environmental factors with regeneration and a Pearson Correlation Matrix and the order of the observed significant microenvironments at the time of sampling are presented. Section 6.3 presents discussions for the chapter.

6.1 Introduction

Understorey forest illumination, photosynthetically active radiation (PAR) and temperature are among the most important micro-climatic factors affecting ecological processes within forest ecosystems. They influence plant regeneration, growth and survival, soil physical properties, microbial activity, relative humidity, and nutrient uptake efficiency (Ralston, 1964; Buckman and Brady, 1968; Treshow, 1970; Pritchett, 1979; & Horton *et al.,* 1984).

Factors influencing illumination, PAR and soil temperature variations have been studied extensively. Baver *et al*., (1972) and Pritchett (1979) summarized the factors involved as the albedo effect, depth of penetration of solar radiation through the canopy, latent heat in evapotranspiration, heat loss from the soil through the insulating effect of plant cover, aspect of direction of slope, litter layer, tree canopy and forest ground cover. Ghuman and Lat (1981) and Barnes *et al.* (1998) concluded that the transference of heat energy produced at the soil surface by incident solar radiation was the main cause of temperature changes in the atmosphere near the ground and in the soil.

Investigations on the effects of logging on forest illumination, PAR and temperature in tropical forests have been completed. Studies reported by Synnott (1975), Björkman (1972), Björkman and Ludlow (1972), and Steemann and Willemoes (1971) provide insight into the role of illumination, PAR and temperature on the germination and growth of forest plants, especially relating to soil-surface conditions in the timber-harvested forests. How does illumination, PAR or temperature gradients compare, for example, under unlogged, mature secondary forest (earlier) and a recently (later) logged forest? To answer the above question, measurements of forest illumination, PAR and temperature regimes below the ground, on the forest floor and forest understorey air in the different sites logged at different times are required. Forest temperature is measured using numerical solutions of a basic heat flow equation. For example, Hanks *et al.* (1971) and Ghuman and Lal (1981) utilized initial land boundary conditions and thermal characteristics of soils to predict forest temperature regimes and variability. Smith et al. (1964) showed that forest temperature could be inferred from open-air temperature. Watson (1980) reported significant correlations (r=0.92 to 0.95) between mean annual and seasonal soil temperatures monitored below surface level, with corresponding mean air temperature. Synnott (1975) examined and recommended a range of appropriate temperatures required for the regeneration of *E. utile* in a nursery setting. This study therefore, examined the effect of light, PAR and temperature regimes under various conditions within a natural forest setting on the development of the regeneration of mahogany species in Budongo forest.

6.1.1 Aim and objectives.

The aims and objectives of studying the effect of illumination, PAR and temperature on natural regeneration of mahogany species in Budongo forest reserve were to:

a) investigate and compare the temperature measured below ground, at the forest floor and in the understorey in the unlogged, earlier logged (at least 32 year ago) and later logged compartments (within 32 year). Later, these comparisons were correlated to the seedling and sapling densities found in the three forest treatments

b) investigate and compare illumination and PAR in the three treatments and later correlated to the seedling and sapling densities and

c) assess the relationships and effect of time after logging between mahogany regeneration (seedlings and saplings) with environmental variables, in the three treatments.

The information on the above relationships would be useful for estimating suitable forest illumination, PAR and temperature in relation to choice of silvicultural treatment, such as creating forest gaps for enrichment planting. In addition, this information may help in understanding the effect of canopy opening on forest understorey illumination, PAR and temperature several years after logging. Observations of significant differences in illumination, PAR and temperature in logged and unlogged forest areas would suggest the need for appropriate silvicultural prescriptions to reduce or prevent forest degradation in general and encourage regeneration and forest recovery that normally follows logging.

6.1.2 Justification for environment data and data collection methods

Two sets of data from the study area were collected in August – November and December – February. In and around Budongo Forest Reserve, the period August to November is wet, while December to February is dry. The significance for selecting the two periods (August – November and December-February) was to compare and contrast the variations of forest understorey light, PAR and temperature regimes within and between the treatments in relation to the regeneration density and distribution of the selected mahogany species. The two climatic extremes (wet and dry periods) were expected to have very strong influence on mahogany regeneration, growth and development.

6.2 Results

Data were summarized to show comparisons across the treatments. Thereafter, the data were subjected to t-test analyses at $0.05 < p > 0.010$ and $p < 0.01$ levels of significance. The analysis was run on a MINITAB computer programme to separate significant differences in illumination, PAR and temperatures readings within and between treatments. A t-test analysis was appropriate when comparing variables from two comparable treatments. The means and standard deviations were determined on average data collected (illumination, PAR, temperature, ground and canopy cover). An ordination (Canonical correspondence analysis) was performed on the selected mahogany regeneration for correlation with the underlying environmental factors.

6.2.1 Illumination, PAR and temperature variations during the wet (August to November) and dry (December to February) periods

6.2.1.1 Wet period: August to November

Comparisons of mean illumination, PAR and temperature levels for the August to November period are shown in Table 6.1.

In the August to November wet period, comparisons for illumination within treatments was highest in the earlier logged forest tracts (sample variance of 33 lux). The unlogged and later logged forest tracts showed sample variances of 6.6 and 22 lux, respectively. In comparing the unlogged forest and earlier logged forest tracts, there were significant differences in compartments S3, N9, W21 N5, and B3. Compartments W16 and N14 were not significantly different ($0.05 < P > 0.01$) (Table 61). At significant level testing $P < 0.01$, compartments S3 and N9 show significant differences. The most significant differences in illumination were observed between the earlier and later logged forest tracts ($p=0.05$) and between the unlogged and later logged forest tracts ($p=0.034$). This suggests that the difference between the earlier and later logged forests is probably due to levels of logging intensity and amount of recovery of the forest structure in the earlier logged compartments. The unlogged forest showed almost similar illumination conditions to the earlier logged treatment.

Table 6.1: Significant differences for Illumination. PAR and temperature levels within and between treatments for August to November

Treatment	Illumination (Lux)											
	Earlier Logged (compartments)								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged		**	**	*		**	*	**	*	*		
	Photosynthetically Active Radiation (PAR) ($\mu ms^{-1}m^2$)											
	Earlier Logged (compartments)								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged			**	*			*	*	*	**		
	Forest understorey- air temperatures (^0C)											
	Earlier Logged (compartments)								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged						*			*			
	Forest floor temperatures (^0C)											
	Earlier Logged Compartments								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged						*						
	Below ground temperature (^0C)											
	Earlier Logged Compartments								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged	*	*	**	*	**	*		**	**			

*** = 0.05 < P >0.01 ** = P <0.01 blanks indicate no significance**

N.B: Illumination and below ground temperatures show significant differences between the unlogged and earlier logged compartments

The compartments in the table above show areas with significant differences. Eleven compartments were sampled.

Comparisons between the earlier and the later logged treatments were not significantly different

Variations in PAR within treatments were higher in the later logged forest tracts (sample variance of 100 $\mu ms^{-1}m^2$) than in the earlier logged (sample variance of 72 $\mu ms^{-1}m^2$) and least in the unlogged forest (sample variance of 39.7 $\mu ms^{-1}m^2$). Comparisons between the unlogged compartment and earlier logged compartments show significant differences in compartments N9, W21 and N5. Compartments W16, S3, N14 and B3 are not significantly different from unlogged (0.05 < P >0.01). At significant level testing P <0.01, compartments N9 show significant difference from the unlogged (Table 6.1).

In comparing treatments, the most significant different in PAR were observed between the unlogged and earlier logged forest tracts (p=0.05). Comparisons between the earlier and later logged forest tracts (p=0.77) and between the unlogged and later logged forest tracts (p=0.15) show no significant differences. Thus, the result suggests that PAR conditions in the earlier logged forests were significantly different from the unlogged forest tract.

Understorey air temperature variations within treatments were similar, all showing an average temperature of 22 ^{0}C. However, sample variance in the later logged forest tracts showed the highest value (mean sample variance of 2.4 ^{0}C) compared to the unlogged forest tracts (mean sample variance of 1.9 ^{0}C) or the earlier logged forest tracts (mean sample variance of 1.35 ^{0}C). The most observed significant differences in understorey air temperature were between the unlogged and later logged forest tracts (p=0.046). Comparisons between the unlogged and earlier logged forest tracts (p=0.10) and between earlier and later logged forest tracts (p=0.21) were not significantly different. At compartment level, comparisons between the unlogged compartment and earlier logged compartments show a significant difference in compartment B3 only (0.05 < P >0.01) (Table 6.1).

Like the understorey air temperatures, forest floor temperature variations within treatments were the same in the earlier and later logged forest tracts showing an average of 22 ^{0}C. The unlogged treatment had an average of 21.8 ^{0}C. Sample variance in the earlier logged forest tracts showed the highest value (sample variance of 3.29 ^{0}C) compared to the later logged treatment (mean sample variance of 1.9 ^{0}C) and the unlogged forest tracts (sample variance of 1.62 ^{0}C). The highest variations in forest floor temperature were between the unlogged and later logged forest tracts (p=0.37). Comparisons between the unlogged and earlier logged forest tracts (p=0.51), between earlier and later logged forest tracts (p=0.89) and between the unlogged and all the logged forests (p=o.46) were not significantly different.

Variations in below ground temperatures within treatments were highest in the earlier logged forest tracts (sample variance of 0.41 ^{0}C) than in the later logged (sample variance of 0.29 ^{0}C) and in the unlogged forest (sample variance of 0.18 ^{0}C). Consequently, differences between belowground temperatures were significantly different between unlogged and earlier logged forests tracts (p=0.05) and between earlier and later logged forest tracts (p=0.00008). Comparisons between unlogged and later logged (p=0.29) and between unlogged and earlier logged forest tracts (p=0.27) were not significantly different.

6.2.1.2 Dry period: December to February

Variations within treatments and comparisons of mean illumination, PAR and temperature levels between treatments for the dry (December to February) period are shown in Table 6.2.

In December, which is a dry period, variations for illumination within treatments was highest in the earlier logged forest tracts (sample variance of 32.42 lux).

Table 6.2: Significant differences for illumination, PAR and temperature levels within and between treatments for December to February

Treatment	**Illumination (Lux)**											
	Earlier Logged (Compartments)								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
UnLogged		**	**	*		*	*	**		**	**	**
	Photosynthetically Active Radiation (PAR) ($\mu ms^{-1}m^{2}$)											
	Earlier Logged (compartments)								Later Logged (compartments)			
Unlogged	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged			**			*	*	*			**	
	Forest understorey air- temperatures (^{0}C)											
	Earlier Logged Compartments								Later Logged Compartments			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged	**	**	**	**	**	**	**	**				
Unlogged									**	**	**	**
Earlier Logged												**
	Forest floor temperatures (^{0}C)											
	Earlier Logged (compartments)								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged	**	**	**	**	**	**	**	**				
Unlogged									* **	* **	* **	* **
Earlier Logged												* **
	Below ground temperatures (^{0}C)											
	Earlier Logged (compartments)								Later Logged (compartments)			
	W16	S3	N9	W21	N14	B3	N5	Aggregated	B1	S5	K4	Aggregated
Unlogged	*	*	*	*	*	*	*	*				
Earlier logged									*	**		*

*** = 0.05 < P >0.01 ** P= <0.01 blanks indicate no significant difference**

N.B: Illumination, Temperatures in the understorey, on the forest floor and below ground were significantly different

The compartments in the table above show forest tracts with significant differences when compared to unlogged or earlier logged. Eleven compartments were sampled.

PAR and understorey air temperatures were not significantly different between the earlier and later logged treatments.

The unlogged forest tracts showed the least within sample variances of 3.26 lux, while the later logged forest tracts showed sample variance of 25.49 lux.

Comparisons between the unlogged compartment and earlier logged forest tracts showed significant differences ($p=0.019$), specifically in compartments S3, N9, W21 and N5. Compartments W16, N14 and B3 were not significantly different from the unlogged compartment ($0.05 < P > 0.01$) (Table 6.2). At a significance level of $P < 0.01$, only compartments S5 and N9 showed significant differences (Table 6.2). Also significantly different were observed in the comparisons between the unlogged and later logged forest tracts ($p=0.0018$) and comparisons between the unlogged and all logged compartments aggregated ($P=0.0092$). Variations in PAR within treatments were highest in later logged forest tracts (sample variance of 115.1 $\mu ms^{-1}m^{2}$) than in the earlier logged (sample variance of 78.4 $\mu ms^{-1}m^{2}$) or the unlogged forest (sample variance of 44.26 $\mu ms^{-1}m^{2}$). Comparisons between the unlogged compartment and earlier logged forest tracts showed the highest differences ($p=0.068$) with significant difference in compartments N9, B3 and N5 ($0.05 < P > 0.01$), and compartment S3 and N9 ($P= < 0.01$).

For both the understorey (air temperatures) and the forest floor, comparisons between the unlogged and earlier logged compartments show significant differences for compartments W16, S3, N9, W21, N14, B3 and N5 ($P= < 0.01$). Likewise, in comparing the unlogged compartment with all the earlier logged compartments, there was significant difference at both $P= < 0.01$ (Table 6.2). The below ground temperatures show significant differences for compartments W16, S3, N9, W21, N14, B3 and N5 at $P= 0.05 < P > 0.01$ (Table 6.2).

6.2.2 Relationships between illumination, PAR and Temperature with the selected mahogany regeneration

Using the regression technique, relationships for forest illumination, PAR and temperatures (in the understorey, on the forest floor and below ground) with mahogany regeneration (seedling and saplings) were obtained. The regressions were performed at 95 percent significance levels.

In the unlogged treatment, the negative illumination coefficient of determination value (r^2= -0.120) was influential in the regeneration of *K. anthotheca* seedlings*.* The saplings show coefficient of determination of r^2= 0.18. *E. utile* seedlings showed a coefficient of determination of r^2= 0.740, while the saplings showed a coefficient of determination of r^2= 0.688. The species *E. utile* appears to be influenced by levels of illumination and suitable to closed forest environments (unlogged). From the results, *E. cylindricum* seedlings showed r^2= 0.124, while the saplings showed a coefficient of determination of r^2= 0.127. Seedlings of *E. angolense* showed a coefficient of determination of r^2= 0.038, while the saplings showed a coefficient of determination of r^2= 0.022. Therefore, the results suggest that illumination explains 74 % of the occurrence of *E. utile* seedlings and 69% of the occurrence of *E. utile* saplings*. E. angolense* and *K. anthotheca* regeneration showed the least effects from illumination at the time of sampling (Table 6.3).

Relationships between PAR and regeneration show no significant differences for *K. anthotheca* and *E. cylindricum*. The positive and low r^2 values suggest that in the unlogged treatment, the two species survive relatively better than the regeneration for *E. utile* and *E. angolense* (Table 6.3)

Table 6.3: Multiple regression showing coefficient of determination between the environmental parameters-Illumination, PAR and temperature,

and mahogany seedlings (a) and saplings (b) in the unlogged treatment

Species	Environmental parameters (r^2)					
				Temperatures		
		Illumin	PAR	Understorey air	F.floor	Below ground.
E. cylindricum	A	0.124	0.041	0.044	0.019	0.127
	B	0.127	0.089	0.056	0.074	0.003
E. utile	A	0.740	0.098	0.209	0.022	0.122
	B	0.688	0.069	0.308	0.121	0.023
E. angolense	A	0.038	0.097	0.394	0.099	0.027
	B	0.022	0.061	0.423	0.141	0.108
K. anthotheca	A	-0.120	0.037	0.263	0.034	-0.042
	B	0.180	0.076	0.439	-0.058	-0.181

Note: A represents seedlings, while B represents saplings

Relationships for the understorey air-temperature with mahogany regeneration were generally low for *E. utile* (seedling, r^2=0.209 and saplings r^2=0.308), *E. angolense* (seedling, r^2=0.394 and saplings r^2=0.423), and *K. anthotheca* (seedling, r^2=0.263 and saplings r^2=0.439). However, *E. cylindricum* (seedling, r^2=0.044 and saplings r^2=0.056), did not show significant correlations. The low coefficients of determination suggest a weak relationship of the understorey air-temperature with mahogany regeneration, especially for *E. cylindricum* (Table 6.3).

Surface and belowground temperatures in the unlogged treatment show low and weak relationship with regeneration (Table 6.3). Probably, this is due to the dense canopy cover, which limits evaporation from the forest floor. The forest floor conserves moisture for longer periods. However, *K. anthotheca* regeneration consistently shows low and negative relationships with the below ground temperatures (seedling, r^2= -0.042 and saplings r^2= -0.181) (Table 6.3).

The relatively high correlation between PAR and regeneration (r^2=0.98) in the earlier logging plots indicate that there is sufficient confidence in the computations of PAR as a function for the mahogany seedlings in the earlier logged compartments of study area (Table 6.4). For example, the low correlation between illumination (r^2=0.1) and forest floor temperature (r^2=0.02) for the *K. anthotheca* seedlings in the earlier logged compartments indicated little confidence in this relationship of illumination (radiation) and soil temperature below ground (Table 6.4).

The three levels of temperatures (understorey-air, forest floor and below ground) influenced mahogany regeneration differently. For example, understorey air temperature influenced *E. angolense* seedlings by 94 % and saplings by 23 %. Alternatively, understorey-air temperature had the least influence (r2= 0.09 and 0.08) on the seedlings and saplings for *E. utile* (Table 6.4).

Below ground temperatures results show high coefficients of determination for *E. cylindricum*, *E. angolense* and *K. anthotheca*. *E. utile* shows the least relationship to forest floor temperatures. *E. utile* and *K. anthotheca* regeneration show the least relationship to forest floor temperatures (Table 6.4).

Table 6.4: Multiple regression showing coefficient of determination between the environmental parameters-Illumination, PAR and temperature, and

mahogany seedlings (a) and saplings (b) in the earlier logged treatments

Species		Environmental parameters (r^2)				
				Temperatures		
		Illumin	PAR	Understorey air	F.floor	Below ground.
E. cylundricum	A	0.420	0.98	0.440	0.270	0.900
	B	0.001	0.89	0.560	0.003	0.740
E. utile	A	0.270	0.41	0.090	0.220	0.220
	B	0.290	0.38	0.080	0.230	0.210
E. angolense	A	0.210	0.97	0.940	0.270	0.990
	B	0.110	0.60	0.230	0.080	0.410
K. anthotheca	A	0.100	0.93	0.630	0.020	0.810
	B	0.030	0.76	0.390	0.040	0.580

Note: A represents seedlings, while B represents saplings

The data from Budongo forest reserve suggest that the response of seedlings and saplings to temperature is more strong in the later logged forest tracts than in the unlogged and earlier logged (Table 6.5). This is because Logging opens forest canopy, which affects temperature dynamics in a forest ecosystem (Paterson 1991, Mwima *et al.* 2001), The below ground and understorey air-temperature results across treatments show an unstable equilibrium that explains the pattern of mahogany regeneration in Budongo forest as influenced by illumination as well. The later logged compartments show a more open crown forest than the earlier logged and unlogged compartments, which allows more solar radiation to be absorbed by the soil surface influencing mahogany regeneration in Budongo Forest Reserve.

Table 6.5: Multiple regression showing coefficient of determination between the environmental parameters-Illumination, PAR and temperature, and mahogany seedlings (a) and saplings (b) in the later logged treatments

Species	**Environmental parameters (r^2)**					
				Temperatures		
		Illumin	PAR	Understorey air	F.floor	Below ground.
E. cylundricum	A	0.420	0.980	0.532	0.305	0.991
	B	0.001	0.890	0.678	0.003	0.821
E. utile	A	0.270	0.410	0.109	0.249	0.244
	B	0.290	0.380	0.097	0.260	0.233
E. angolense	A	0.210	0.970	1.137	0.305	0.949
	B	0.110	0.600	0.278	0.090	0.455
K. anthotheca	A	0.100	0.930	0.762	0.023	0.899
	B	0.030	0.760	0.472	0.045	0.644

NB: A represents seedlings, while B represents saplings

6.2.3 Slope, aspect, ground and canopy cover

6.2.3.1 Slope

From the results, there is no significant difference within and between treatments ($0.05 \leq p > 0.01$). This is probably because Budongo forest consists predominantly of undulating topography with the highest mean slope of 3.4^0 in earlier logged forests with a standard deviation ±2.30. The lowest mean slope of 2.63 was encountered in the unlogged forest tracts, while the highest slope variance was in the earlier logged forest tracts (Table 6. 6).

Table 6.6 Comparisons of slope, ground and canopy cover within treatments

Treatment	Slope			Groundcover			Canopy cover		
	Mean	SD	Sample Variance	Mean	SD	Sample Variance	Mean	SD	Sample Variance
UNL (n=24)	2.63	1.84	3.38	13.46	4.62	21.39	32.08	11.12	123.73
EL (n=162)	3.42	2.28	5.20	18.03	10.54	111.07	32.66	19.22	369.26
LL (n=72)	3.15	1.66	2.75	23.00	11.83	139.89	49.74	19.31	372.79
All logged (n=234)	3.34	2.11	4.45	19.56	11.16	124.65	37.91	20.76	431.12

The goodness of fit test (G-test) significantly re-enforces the assumption that Budongo forest is an undulating terrain tilted towards the west (Table 6.7).

Table 6.7: Budongo Forest Reserve: Goodness of fit (G) test of aspect of slope

Slope Aspect (n=258)	**Probability of G**	Remarks
South and West Vs North and East	0.001	Significant
South and East Vs North and West	0.001	Significant
Includes William's correction	0.0753	

Note: n=258 are total number of samples in the study area

6.2.3.2 Slope aspect

Across the study area, slope was predominantly facing west and southwest (Figure 6.1). The results show the later logged predominantly facing the Northeast direction, while the unlogged forest was predominantly facing the south. The aspects of slope within the later logged treatment were generally similar, while the earlier logged treatment plots were the most diverse (Figure 6.1).

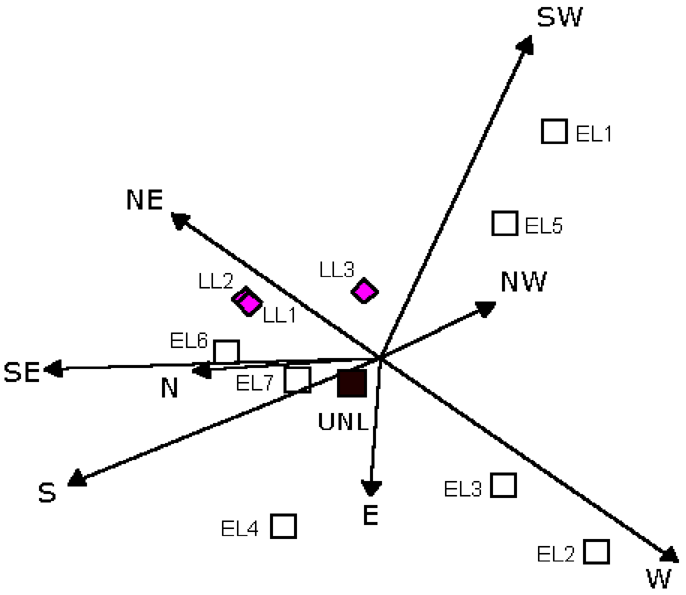

Figure 6.1: Slope-aspect across the study area showing predominance in the south, west and southwest directions.

Note: UNL represents unlogged forest. EL and LL represents earlier and later logged forest tracts respectively. A total of 258 samples were investigated.

6.2.3.3 Forest groundcover

The highest within treatment variation was in the later logged forests compared to the earlier logged and the unlogged forest (Table 6.6). In comparing the unlogged forest and the earlier logged, there were significant differences detected in groundcover at $0.05 \leq p > 0.01$ test level ($p=0.038$). However, two out of seven sampled sites in the earlier logged forest were not significantly different at $P < 0.01$ test level (Table 6.8).

Comparisons between the unlogged and later logged forest tracts were significantly different at $0.05 \leq p > 0.01$ test level ($p=0.0002$). No significant difference was detected at $P < 0.01$ test level. In comparing the earlier and later logged treatments, only one out of three sites in the later logged forest was significantly different at P ≥0. 01 <0. 05 test (Table 6.8).

Table 6.8: T-test result of slope, ground and canopy covers at different dates of timber harvesting in Budongo Forest Reserve, Uganda

Treatment	Significance level	Parameter		
		Slope	Groundcover	Canopy cover
Unlogged Vs Earlier logged	*	NS	NS	N9, S3, W16
	**	NS	W21, W16	N9, S3. B3, W16
Unlogged Vs Later logged	*	NS	B1, S5, K4	
	**	NS	NS	NS
Early Vs Later logged	*	NS	S5	NS
	**	NS	NS	NS
Unlogged vs. logged	*	NS	B1, S5, K4	B1
	**	NS	W21, W16	N9, S3. B3, W16

* = 0.05 ≤ p > 0.01 ** = P <0. 01 NS = Not significant

Note: N9, S5, B1, S5, S3 and W21 are compartments that show significant difference out of the 11 compartments sampled. 258 samples were studied.

6.2.3.4 Forest canopy cover

The highest variations in canopy cover were within the later logged forests compared to the earlier logged and the unlogged forest (Table 6.6). Significant canopy differences were detected between the unlogged forest and later logged forest tracts (p=0.00052) and between earlier and later logged forest tracts (p=0.00089). In comparing the unlogged with the later logged treatment, one out of three compartments sampled was significant at the P ≥0. 01 <0. 05 significant level (see Table 6.8 above).

When comparing the unlogged and all the logged compartments, there was significant difference p <0.01 test level (see Table 6.8 above). The unlogged was not significantly different from the earlier logged forests in term of ground vegetation cover.

6.2.4 Gradient analysis of environmental factors with selected mahogany regeneration

Figure 6.2 shows the distribution patterns of forest environments (soils, illumination, PAR, temperature, ground and canopy cover) across the study area. In the unlogged forest, the effects were mainly from understorey-air and forest floor temperatures. In earlier logged forest tracts, the effects were generally from illumination, PAR and soil reaction (pH), while in the later logged compartments, the effects were mainly from illumination, groundcover and below ground temperatures.

The earlier and later logged forest tracts showed similar environmental characteristics. To a forest ecologist, such sites would require similar silvicultural prescriptions. For example, site LL1 (later logged), EL6 (earlier logged), LL2 (later logged) and EL4 (earlier logging) were similar (Figure 6.2). Also, the results show that the earlier logged forest tracts were close to the unlogged (UNL) forest than the later logged. The closeness indicates similar environmental characteristics between treatments.

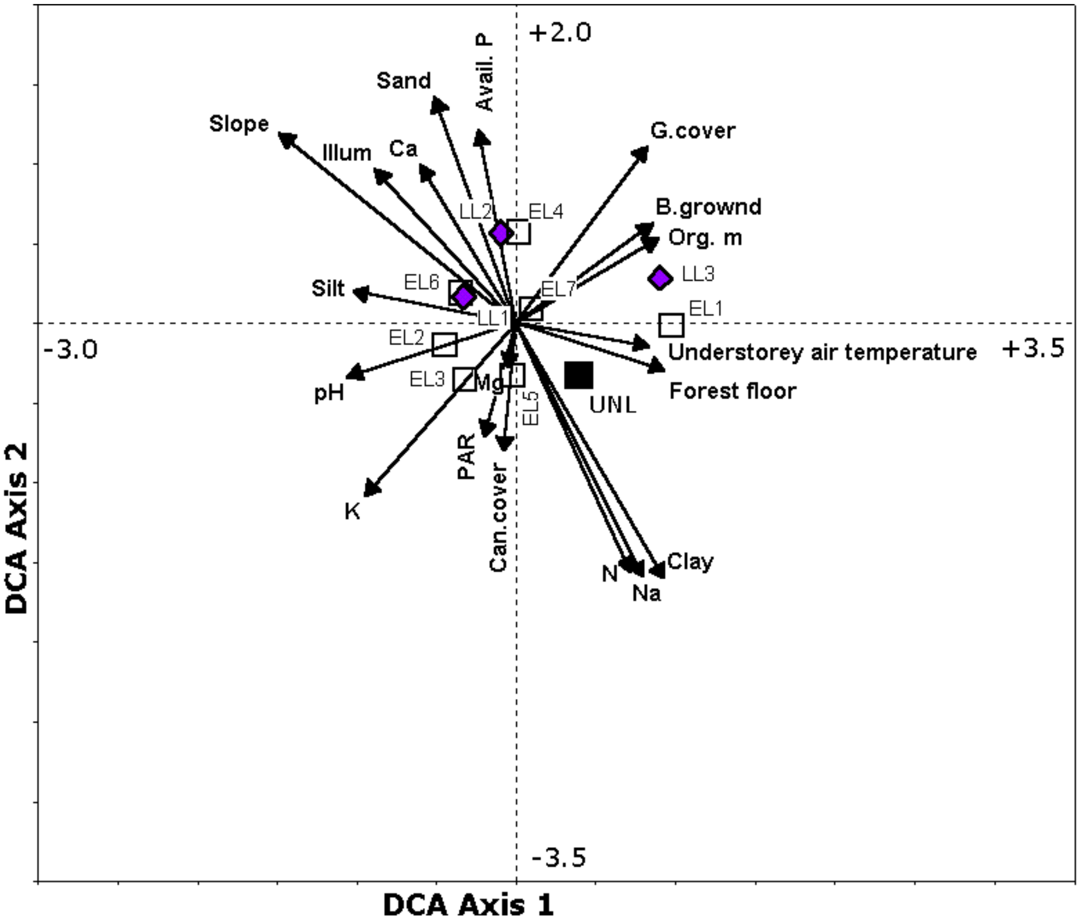

Figure 6.2: Detrended Correspondence Analysis showing forest environments across the three treatments (unlogged, earlier and later logged). 258 samples in 11 compartments were studied. Table 6.9 shows the eigenvalues and cumulative percentage variances in the two axes.

Note:

■ represents unlogged treatment (UnL)

□ represents seven sites in earlier logged treatment (EL)

🟪 represents three sites in later logged treatment (LL)

Table 6.9: Eigenvalues, length of gradient and cumulative percentage variance along the two axes

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues	0.171	0.063	0 .020	0 .013	0.524
Lengths of gradient	1.506	1.043	.810	1.075	
Cumulative percentage variance of selected mahogany species (size-class) data	36.7	54.4	52.3.6	53.2.1	

The cumulative percentage variance along the two axes (Table 6.9 above) suggests that the logging and edaphic factors explain 54.4 percent of the observed mahogany regeneration in the treatments sampled with the soil explaining 8.6 percent variance (i.e. logging explained 44.8 percent variance).

Furthermore, the canonical correspondence analysis of the selected mahogany species with the environmental factors showed that the distribution patterns of mahogany regeneration occurred most in the treatment with adequate illumination and below ground temperature (Figure 6.2). Of the four species, the most affected were *E. cylindricum* and *Ent. angolense*. *K. anthotheca* responded most to temperature on the forest floor and in the understorey. Finally, *E. utile* responded most in forest tracts where PAR was most prevalent (Figure 6.3).

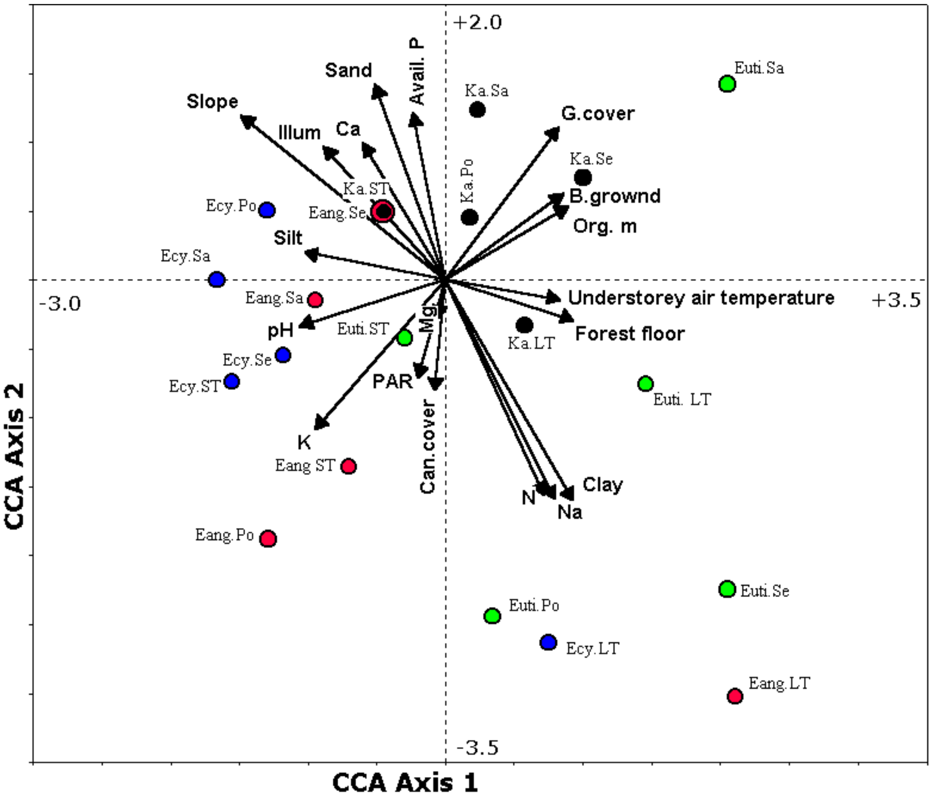

Figure 6.3: Canonical Correspondence Analysis showing the response of selected mahogany species to environmental factors (soils illumination, PAR, temperature, ground and canopy cover). 258 samples in three treatments were studied. Table 6.10 shows the eigenvalues and cumulative percentage variances in the two axes.

Note

● Ka.Se, Ka.Sa, Ka.Po, Ka.ST and Ka.LT represent *K. anthotheca* seedlings, saplings, poles, small and large trees.

🔵 Ecy.Se, Ecy.Sa, Ecy.Po, Ecy.ST and Ecy.LT represent *E. cylindricum* seedlings, saplings, poles, small and large trees.

🟢 Euti.Se, Euti.Sa, Euti.Po, Euti.ST and Euti.LT represent *E. utile* seedlings, saplings, poles, small and large trees.

🔴 Eang.Se, Eang.Sa, Eang.Po, Eang.ST and Eang.LT represent *E. angolense* seedlings, saplings, poles, small and large trees.

Table 6.10: Eigenvalues, length of gradient and cumulative percentage variance along the two axes

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues	0.171	0.063	0 .020	0 .013	0.524
Lengths of gradient	1.506	1.043	.810	1.075	
Cumulative percentage variance of selected mahogany species (size-class) data	39.9	69.5	72.1	72.9	

The cumulative percentage variance along the two axes (Table 6.10 above) suggests that the logging and environmental factors explain 69.5 percent of the observed mahogany regeneration in the treatments.

The relative distribution of the mahogany seedlings and saplings with the environmental variables in the three treatments showed that *E. angolense* saplings, *E. utile* saplings *K. athotheca* saplings and *E. cylindricum seedlings* were mostly influenced by illumination. The analyses of data also show strong correlation of *E. utile seedlings* to understorey-air and surface temperatures, while *E. utile* small trees were strongly correlated to mostly PAR (Figure 6.3).

6.2.5 Multicollinearity and correlation matrix of the illumination, PAR and temperature across the study area

Variables, such as illumination, PAR and temperature are interrelated (Barnes *et al.,* 1998; Björkman (1972),). Their effects on forest regeneration, present a complexity to address in isolation if the effect of each microenvironmental variable in the study is to be determined. Forest environments are further complicated by the groundcover and the influence of the canopy openings, which are also thought to influence light and temperature dynamics inside the forest.

Data of illumination, PAR, temperature, groundcover and canopy cover were subject to a partial correlation to determine the variables that were significantly correlated. Pearson's Correlation using MINITAB v.10.2 was applied. Thereafter, a discriminant analysis, using SAS V.8 was performed to show the observed significant microenvironments across the study area at the time of sampling. Table 6.11 shows Pearson Correlation results of the microenvironments across the study area, while Table 6.12 shows the order of the observed significant microenvironments.

Below ground and surface temperatures were significantly correlated. Also significantly correlated were the surface and forest understorey air-temperatures. Illumination against PAR and groundcover against canopy cover were also significant, but these had weak correlation coefficients of $r \leq 0.5$ (Table 6.11).

Table 6.11: Multicollinearity: Pearson product-moment correlation matrix of the microenvironment variables across the study area (n=258)

	Illumination (Lux)	PAR (µms^{-1}m^2)	Temperature (^{0}C)			
			Below ground	F. floor	Understorey air	Groundcover
PAR (µms^{-1}m^2)	0.248 *	_				
Below ground (^{0}C)	NS	NS	_			
Forest floor (^{0}C)	NS	NS	0.743**	_		
Understorey air (^{0}C)	NS	-0.151*	0.688 *	0.812**	_	
Groundcover ($^{\%}$)	0.210*	NS	0.336*	NS	NS	_
Canopy cover ($^{\%}$)	0.135*	NS	NS	NS	NS	0.343 *

Note: n=258 is total number of samples
The values in the Table are of *Pearson product-moment correlation coefficient*
* P ≥ 0 01 < 0. 05
** P< 0.01
NS = not significant

Discriminant analysis results indicate that for the microenvironments studied in Budongo forest, illumination, temperatures below ground and at the forest floor temperatures, canopy and groundcovers had the most impact on mahogany regeneration compared to PAR and understorey-air temperatures (Table 6.12). Therefore, forest management that emphasizes production and natural regeneration need to consider logging intensity and other available information (e.g. ground and canopy covers, soil property, rainfall patterns, etc.) to help define harvesting intensities. At the time of forest sampling, understorey air temperatures were not significantly influencing mahogany regeneration (seedlings and saplings respectively) (Table 6.12).

Table 6.12: Discriminant analysis: sample coefficient of determination on microenvironment variables against mahogany regeneration (seedling and sapling densities)

	Seedlings		**Saplings**	
Variable	**r^2**	**P-value**	**r^2**	**P-value**
Illumination (Lux)	0.9355	**	0.6829	**
Below ground (^0C)	0.7214	**	0.5266	**
Forest floor (^0C)	0.5767	**	0.4209	*
Canopy cover (%)	0.5153	**	0.3761	*
Groundcover (%)	0.3374	*	0.2463	*
PAR $(\mu ms^{-1}m^{2})$	0.1508	*	0.1100	NS
Understorey air-temp. (^0C)	0.1014	NS	0.0740	NS

Note: * P ≥ 0 01 < 0. 05 ** P< 0.01 NS=Not significant

6.3 Chapter discussion

Difference in forest illumination (light) is really between logged and unlogged forest, but PAR effects are detectable only between the extreme forest categories (unlogged v*s.* most recently logged). PAR and illumination should be lowest in the unlogged forest. Based on the mahogany population densities for both saplings and seedlings in the three treatments, it is clearly shown that the earlier logged compartments are more suitable for regeneration management than the unlogged and later logged compartments. In Budongo Forest, the microenvironment (illumination) influenced by the time after logging (earlier and later logging) significantly affected sapling and seedling response across the study area.

Illumination and the below ground temperature variations are consistently significant to mahogany regeneration in both the wet and dry periods. Only PAR does not show significant variations between these periods. These detected differences may be related to several interacting factors such as the degree of soil-surface cover, vegetation in the proximity, and wind flow at the time of sampling. In the later logged forest tracts, the canopy was most open, which influenced both the solar radiation and illumination. The results show a strong relationship between illumination and temperature across treatments. The importance of solar radiation to forestry lies in the dependence of germination, growth and plant development on photosynthesis and the dependence of photosynthesis on illumination.

In related studies by Van Wijk and Vries (1963), the principal cause of variation of understorey forest temperatures was the changing intensity of short-wave radiation. Absorption and transmission of both the long and short wave radiation, especially in the soil layer, takes place in a fraction of a millimeter thickness. The temperatures in the topsoil layer fluctuate in the course of time and season (wet or dry), corresponding to alternative intervals of heat storage and release of heat into the surrounding environment (Fenner 1992).

Furthermore, Cunningham (1963) suggested that although the soil temperature is not a periodic function of time owing to the variability of weather, it has many features in common with a periodic function. If the soil is covered with dense vegetation, the upper soil-layer forms a surface where a considerable fraction of the incoming radiation is absorbed. The remaining part of temperature is absorbed in the lower region of the vegetation and at the soil surface. The transfer of heat from the surface into the top layer of the soil occurs in the same manner as with a bare surface. Under equal climatic conditions, the daily maximum temperature of the covered surface will be lower than the bare surface, owing to the shading effect of the vegetation. The same illumination and temperature characteristics are observed in the present study, where more open vegetation in later logged compartments experienced considerable fractions of the incident radiation reaching the soil surface. Studies conducted in other forest ecosystems confirm this observation (Geig, 1966; Moehring, 1968; Henderson, 1981; Montgomery and Askew, 1983; and Butera, 1986).

Also, Pritchett (1979) reported that specific heat and conductivity are two inherent properties of soils that influence their temperature. In this study, the soils in the August to November survey probably had a higher moisture content. Barnes *et al.* (1998) noted that moist soils have relatively high thermal conductivity but because of their high specific heat, they do not get as hot as dry soils. This supports the finding of this study showing that temperatures under the August to November survey had generally lower mean temperatures (below ground and forest floor) compared to the December to February survey. This is likely due to high conductivity, which results from the fact that water that fills pore spaces is a better conductor of heat than air that fills pores of dry soils. Similarly, Synnott (1975) noted that hydraulic conductivity of soil increases with temperature increase at all moisture contents.

Therefore, for any silvicultural intervention to be done, stable temperatures below ground and on the forest floor and sufficient illumination are required since their fluctuations may markedly influence mahogany regeneration. From the results, illumination is the most important across the three treatments since light intensities during germination, growth and even in the understorey (sapling and pole stage) are primarily responsible for the selected mahogany response. There is a seasonal difference in the temperature conditions in the forest with generally more uniform conditions for one type of forest in August to November (wet conditions), but more contrast in effect in December to February (drier condition). This suggests that the quality of forest cover affects the understorey conditions. There was lower temperatures in the unlogged forest and higher temperatures in the most recently logged forest compartments.

Given the significance of the role of illumination, photosynthesis and temperature variations in the compartments sampled, especially temperatures below ground and on the forest floor, it is reasonable to suggest that more silvicultural prescriptions should simulate the earlier logged compartment conditions. This represents the most ideal ecological condition for mahogany regeneration compared to the unlogged and later logged forest tracts and even then, operational decisions should be placed on the first compartments that were logged such as N9 and N5.

CHAPTER 7

General Discussion, Conclusions and Recommendations

Summary

This Chapter has six sections. Section 7.1 introduces the chapter and makes references to the aim, objectives, and hypotheses of the study, which are in Chapter 1. Also, the chapter makes reference to the literature review and the results chapters. The four hypotheses for the study are then reviewed and discussed in the next four Sections (7.2 – 7.5). Conclusions for the study are presented in Section 7.6, while recommendations are presented in Section 7.6.1.

7.1 Introduction

Central to this study was to investigate the effect of logging and the periods since logging, and whether with reasonable confidence it could be confirmed that the various environmental variables in Budongo Forest were related to mahogany regeneration (seedlings and saplings) across the study area. Younger (1985) warned that it is possible to draw a sample indicating a relationship when, in fact there is no relationship in the population. This caution was heeded throughout the study.

Random samples were surveyed in the three treatment areas: unlogged (control), earlier logged (1930s to 1960s) and later logged (1970s to 1980s). Objectives and hypotheses were formulated in chapter 1 (pages 8-9) to test whether the identified microenvironmental and physical factors would show any significant relationship with the regeneration of the selected four mahogany species in the Budongo Forest, Uganda. The null hypotheses were:

1. Natural regeneration of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* is the same in the logged and unlogged forest tracts in Budongo Forest.

2. Forest soil (texture, pH, organic matter and nutrient levels) does not affect the regeneration dynamics, population structure and spatial distribution of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

3. Microenvironmental factors (light, PAR, temperature, ground and canopy cover) have no effect on regeneration, population structure, and spatial distribution of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

4. The time-span after logging (harvesting) has no effect on the regeneration, population structure and spatial distribution of *K. anthotheca, E. utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

7.2 Hypothesis 1

$H_{O:}$ Natural regeneration of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* is the same in the logged and unlogged forest tracts in Budongo Forest Reserve.

Out of the four mahogany species investigated, *K. anthotheca* was the best represented in terms of density, frequency, dominance and importance value and. This trend may be due to the tolerance of this species to extreme forest environments (open and closed canopy). However, the earlier logged compartments showed higher densities of trees than the unlogged treatment, which also had higher densities than the later logged treatment.

Next in importance and quantity, were densities of *Entandrophragma cylindricum*, which like *K. anthotheca* was high in the earlier logged compartments (logged in 1950s-1960s). The lowest densities were recorded in the recently logged compartments (logged 1970s –1980s). On the other hand, densities of *E. angolense* were highest in the unlogged forest and least in the recently logged forest tracts. This trend may be due to the fact that the species is more shade tolerant, which seems to support the assertion made by Eggeling and Harris (1939) and Pennington and Styles (1975) that *E. angolense* flourishes and grows more rapidly in semi-closed forest environment than in open environments.

E. utile trees were the least often encountered. Probably, the tree was over harvested both in the earlier (1930s – 1960s) and later (1970s – 1980s) logging periods and has not yet recovered its stocking across the study area. Another likelihood is that it is a poor regenerator both in closed and open forest conditions where other factors, such as temperature or light are controlled for.

The distribution of *Khaya anthotheca* saplings followed similar distribution trends as the *K. anthotheca* trees with the highest densities recorded in the earlier logged compartments. The seedlings were most abundant in the logged treatments; especially logged tracts in the 1960s and 1970s, an indication that open forest canopy environments in association with the high densities of the remaining mahogany species in the forest lead to successful regeneration.

For the four mahogany species studied, most observations were of individuals in the 10-19.9 cm and 20-29.9 cm diameter size-classes, showing a vigorous young post exploitation crop in areas logged in the past. The unlogged (control) treatment had the highest densities of the larger (≥ 80cm dbh) trees since such large sizes were harvested from the earlier and later logged treatments. According to Plumptre (1994, 1996); Howard (1991) and Paterson (1991) the reduction of the minimum diameter permitted for cutting firstly from 120 cm to 80 cm dbh and secondly, from 80 cm down to 60 cm has greatly compromised the stock and quality of the mahogany seed trees currently in the production areas of the forest. Furthermore, when there was political instability (1970s to early 1980s), there was a lack of effective monitoring/supervision of harvesting activities. Harvesting and yield regulations, especially the recommended minimum diameter allowed to be cut were not followed (Paterson, 1991). In the present study, exploitation is generally associated with fewer individuals in the larger sizes. *Khaya anthotheca* showed more consistent diameter representation, while *Entandrophragma utile* showed an extremely irregular and unstable trend in diameter size-class distribution across the treatments.

Based on the present results, diameter size-class distribution across the study area presents a high correlation indicating that the current status of mahogany regeneration and distribution in Budongo Forest Reserve is affected by the previous logging history of the forest. For example, the results from the Canonical Correspondence Analysis suggest that most seedlings and saplings were prevalent in compartments associated with the unlogged and earlier logged forest tracts. It just follows that this is where large size/seed trees are growing and were recorded. In the unlogged forest tract, seedlings were observed in areas showing natural disturbances.

Trees of *K. anthotheca* and *E. cylindricum* showed greater average heights in the latter logged treatment than in the earlier logged treatment, suggesting that the local environment was conducive to support rapid height growth. It is not clear what lowest dbh of logged trees was the growth rate of these trees. Not surprisingly however, *E. angolense* and *E. utile* trees in the unlogged treatment showed higher average height measurements than in the logged compartments. Probably, this suggests that the two species are shade tolerant and attain normal heights in shaded forest environments. A long-term experiment is required to confirm this.

K. anthotheca showed higher importance value (IV) results than the *Entandrophragma* species studied. *Khaya* dominated all the parameters including relative frequency, relative density and relative dominance. Also, the results suggest that *K. anthotheca* relative IV parameters were higher in later logged compartments than in earlier logged. As previously mentioned, *K. anthotheca* is a light demanding species and more likely to proliferate successfully in semi-open forest environment. Similar IV trends were shown by *E. cylindricum*, whose IV was lowest in the unlogged treatment.

In the unlogged compartment, *E. angolense* trees showed the highest stem basal area and volume. *K. anthotheca* contributed most in basal area terms in both the earlier and later logged compartments. *Entandrophragma utile* had the lowest basal area, but still had higher projected basal area values in the unlogged control compartment than in the later logged treatment.

Khaya anthotheca saplings and *E. utile* seedlings were the highest represented in the unlogged compartment. However, in the logged (both earlier and later logged) compartments, *E. utile* representation was significantly reduced. In two out of three later logged compartments, no saplings of *E. utile* were found. Also, *E. utile* was the least important, with its seedlings missing from the earlier logged treatment.

K. anthotheca seedlings were the most represented in both the unlogged and logged compartments, which confirms findings by Mwima *et at.* (2001); Pennington and Styles (1975) and Eggeling and Harris (1939) that *Khaya anthotheca* seedlings are shade tolerant, becoming light demanders at later (mature pole and tree) stages of development.

Generally, results of tree mean crown scores showed no clear pattern. However, *Khaya anthotheca* appeared to be growing mostly in exposed environments and a similar trend was shown by *E. cylindricum.* Both *E. utile* and *E. angolense* were growing mostly in more closed environments.

However, mean crown-scores for *K. anthotheca* saplings showed that the species was predominant in mostly covered and semi-covered environments.

Furthermore, results from physiognomy measurements (aspect ratio) showed uneven distribution for trees. This is probably due to variations of the light environments inside the forest. For example, aspect ratios for *K. anthotheca* were mostly in the exposed category. Individuals in this category show flat-shaped or oval crowns in which crown diameter is almost equivalent to crown depth. Such aspect ratios were evident for individuals growing in the earlier logged treatment.

From growth patterns of both crown scores and aspect ratio on the four mahogany species investigated, there are indications that the unlogged and the years after logging (earlier and later logging) have influenced mahogany tree and sapling symmetry and physiognomy (shapes) in Budongo Forest. The results indicate that both crown-scores and aspect ratios show trends that relate to mahogany sapling and tree distribution and successional stages of the forest after logging.

7.3 Hypothesis 2

$H_{O:}$ Forest soil (texture, pH, organic matter and nutrient levels) does not affect the regeneration dynamics, population structure and spatial distribution of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* in Budongo Forest Reserve.

Proportions of sand were generally similar across the study area. Clay proportions were higher in the earlier logged compartments and lowest in the recently logged. Silt proportions were highest in the earlier logging and lowest in the recently logged compartments. Generally, silt distribution trends were relatively stable in the three treatments compared with the clay and sand trends across the study area.

From the texture results, of the 11 compartments studied (for top and sub soils) three showed predominantly loamy soils, three samples were clay loam, one sample was silt clay, two samples were sandy clay and two were sandy loam. The soil structure classifications above were based on Money (1978).

Soil reaction (pH) levels were higher in the earlier logged compartments and lower in the recently logged treatment. Likewise, higher organic matter levels were recorded in the earlier logged than in the recently logged treatment. In nutrient level terms, nitrogen was highest in the unlogged and lowest in the recently logged compartments. Phosphorus, potassium, sodium and magnesium were higher in the unlogged/earlier logging treatments than in the recently logged treatment. Calcium was highest in the recently logged compartments.

Soil structure, soil reaction, organic matter and soil nutrients are important for forest regeneration both during germination and during early growth. Soil structure is important for suitable soil aeration and free moisture movement within the soil and between the soil and plant roots interface.

Soil reaction (pH levels) may limit the distribution of species on an ecosystem landscape (Barnes et al., 1998; Bazzar and Pickett, 1990; Baver et al., 1972). The mean pH values in the Budongo Forest were relatively uniform, although comparatively higher values (alkaline) were recorded in the earlier/unlogged treatments compared with the recently logged treatment, which had more acidic soils. Also, the decomposition and formation of organic matter from dead plants and animals requires suitable moisture, temperature and air regimes to take place. From the results, suitable temperatures for residue decomposition are evident in the earlier logged compartments.

The amounts of organic matter combined with levels of clay in forest ecosystems are important in enhancing early plant growth after germination.

According to Money (1978), clay-organic matter cohesion helps retention of soil fertility as the rate of leaching is reduced.

Nitrogen, phosphorus and potassium are required for formation of chlorophyll and function as catalysts for root/nutrient uptake in plants (Larcher, 1980; Mayer and Poljakoff-Mayber, 1963). These nutrients were highest in the earlier and unlogged compartments. Consequently, it indicates that plant seeds, if dispersed in the area could benefit more where nutrient levels are high than in areas where levels are low, such as in the recently logged treatment.

Even when the treatments may have been different before logging, results from the present study indicate that the unlogged and the years after logging is reflected in the variations of soil reaction (pH) organic matter and soil nutrient levels across the study area. Logging in Budongo Forest Reserve has contributed to changes in nutrient levels across the forest logged at different dates. Significant differences were detected in potassium (K; p=0.011), sodium (Na; p=0.03) and magnesium (mg; p=0.049) levels, especially between the unlogged and later logged forest tracts. Based on the individual mahogany species density per hectare and their corresponding diameter size-class distributions, height structures, crown symmetry and physiognomy, soils in Budongo forest are concluded to relate to mahogany regeneration, structure, abundance and successional stages (seedlings, saplings and trees) of the forest after logging.

7.4 Hypothesis 3

$H_{O:}$ Microenvironmental factors (light, PAR and temperature) have no effect on regeneration, population structure, and spatial distribution of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* in Budongo.

Higher temperature values were more prevalent in the recently logged compartments than in the earlier or unlogged. This was due to more direct exposure to radiation than in the earlier logged compartments or the unlogged compartment. In addition, the variations are probably due to increasing moisture loss by evaporation as a result of the removal of vegetative cover as well as the insulating humus during logging. Variations between the earlier logged compartments and the unlogged compartment were low and insignificant.

The forest light levels (illumination and PAR) are likewise consistently lower in the unlogged treatments than the logged treatments. The canopy cover percentages were significantly lower in the recently logged treatment, which suggests more incident solar radiation and light compared to the unlogged treatment, where the canopy cover percentage closure was higher. Conditions, such as light, PAR and temperature in earlier logging (e.g. N14, N9, B1), seem to encourage mahogany seedling regeneration, but growth into sapling is encouraged by conditions as in the late logged forest tracts.

Based on the distribution of individuals tallied and their diameter class, height structure, crown symmetry and physiognomy, there are indications that the conditions in unlogged forest and the post logging forests had differently influences on temperature, illumination and PAR in the study area

Pennington and Harris (1975); Synnott (1975) and Eggeling (1940, 1947, 1952) noted that mahogany species are shade tolerant, especially during the early stages of development. *Khaya anthotheca* is particularly shade tolerant. The present study suggests similar trends as the four mahogany species were quantitatively more numerous in the earlier logged compartments than in the recently logged compartments.

Consequently, temperature and forest light show strong relationships to mahogany regeneration, distribution and successional stages of the forest (seedlings, saplings and trees) in Budongo Forest Reserve.

Findings from the present study indicate that there is no significant effect from a difference in slope angles and slope aspect between the unlogged and the logged and between the earlier and later logged compartments. This is probably because Budongo Forest is predominantly on a flat terrain consisting of a gently undulating topography. However, in-depth investigations on the effect of valleys and riverine environments on mahogany regeneration, distribution and successional stages of the forest is essential, but was not part of the present study.

Between the unlogged forest and the forests earlier logged, a significant difference in forest groundcover was detected (p=0.038). Also significantly different were comparisons between the unlogged and later logged forest tracts (p=0.0002), an indication that the unlogged and the years after logging (both earlier and later) have influenced the forest ground cover across the study area. Results showed strong inverse correlation between groundcover and regeneration of *E. cylindricum* (r=-0.52) and a positive correlation for *E. angolense* (r=0.49).

The estimated canopy cover percentages across the study area indicated a significant difference between the unlogged and the logged compartments, but earlier and later logged compartments were not significantly different. Correlation between canopy and ground cover was weak (r=0.02), an indication that groundcover vegetation was predominantly shade tolerant species and not directly influenced by canopy cover. Consequently, from findings of both groundcover and canopy cover percentages respectively; it is reasonable to conclude that the regeneration, distribution and successional stages of the four selected mahogany species relate to logging and years after logging. In a forest environment, illumination and temperature are important, especially for shade and semi-shade tolerant species. Silvicultural efforts need to emphasize ground and canopy cover as these two regulate the amount of light and solar radiation reaching the forest floor and the understorey environment.

7.5 Hypothesis 4

$H_{O:}$ The time-span after logging (harvesting) has no effect on the regeneration, population structure and spatial distribution of *Khaya anthotheca, Entandrophragma utile, E. angolense,* and *E. cylindricum* in Budongo Forest.

From the results, there are indications that the years after logging have influenced the distribution and actual numbers of mahogany tree individuals in Budongo Forest Reserve. For example, the earlier logged compartments showed relatively higher mahogany seedling densities (22 tree, 13 saplings and 32 seedling per hectare). The later logged forest tracts showed average densities of 16 trees, 6 saplings and 21 seedlings per hectare, while the unlogged forest tract showed the least seedling densities (19 seedlings per hectare) even when the tree density was highest (24 trees per hectare).

From the aggregated IV results across the study area, the earlier logged treatment had the highest IV for both trees and saplings. In effect, time since logging is important and has influenced mahogany regeneration development, growth and distribution of the various tree size-classes in the Budongo Forest Reserve.

Key findings from the soil samples, stem densities, diameter classes, height structures, crown symmetry and crown physiognomy in the three treatments studied suggest and give evidence that years after logging result in significant differences in mahogany regeneration, distribution and successional stages (seedlings, saplings, poles, small and large trees) in Budongo Forest Reserve.

Brown and Lugo (1982) noted that under a forest environment, canopy opening affect soil mineralization and waste decomposition. They occur under suitable moisture, light and temperature conditions. From the study, a limitation of calcium, available phosphorus, and potassium were recorded in later logged forest tracts, while organic matter was most prevalent in the unlogged and earlier logged forest tracts. The combination of fertility and presence of seed trees enabled the many seedlings and saplings to grow, especially in the earlier logged forest tracts.

The unlogged forest showed a closed canopy environment with the least levels of illumination and lowest mahogany regeneration. Likewise, the later logged compartments were more open, showing higher levels of illumination, with the highest amount of groundcover and moderate densities of sapling and seedling compared to the earlier logged treatment which had the highest densities of saplings and seedlings.

Direct multivariate gradient analyses of data suggest a significant correlation between mahogany regeneration (seedlings and saplings) and some of the soil variables: potassium, sodium, magnesium and total nitrogen. Also, the mahogany regeneration and distribution patterns follow the different forest types, which represent the three forest treatments sampled during the study. The earlier logged treatment showed the most abundant mahogany regeneration (Appendix 4). The results confirm Walaga (1994) and Plumptre (1996) who noted the existence between the local patterns of tree species distribution and soil patterns in the Budongo forest and increasing plant biodiversity from the east to west of the forest.

The microenvironmental factors that were limiting to mahogany regeneration (seedlings and saplings) at the time of the study were illumination, PAR and below ground temperature, which are influenced by forest growth after logging. The forest growth, in turn, is influenced by the soil environment, a medium for plant growth. The results suggest that the earlier logged forest, which mostly is in the western part of the forest, had the most abundant mahogany regeneration. Therefore, time after logging affected the regeneration and structure of mahogany species in Budongo Forest Reserve.

7.6 Conclusions and recommendations

7.6.1 Conclusions

The following conclusions and recommendations have been arrived at through this study.

- *K. anthotheca* was found to be the most dominant and quantitatively most important of the mahogany timber species in the study area. While *K. anthotheca* may develop more light tolerant leaves than the *Entandrophragma* species (Pennington and Styles 1975), they easily adapt morphologically to wider variations of growth situations, which in turn may explain why it is found in a wider range of forest environments (unlogged and logged) in Budongo Forest than the other three species.

- The population of the *Entandrophrama species*, is very low, especially the *E. cylindricum* and *E. utile*. The recently logged compartments persistently showed the least individual densities compared to the earlier logged compartments, which showed the highest individual densities and consequently higher levels of mahogany regeneration.

- Results from the study suggest that slope did not exert any influence on the regeneration, structure and distribution of mahogany species because Budongo forest terrain is generally flat.

- Logging in Budongo Forest Reserve, Uganda has contributed to changes in some nutrient levels across the forest. Higher soil nutrients (especially K, Na, and Mg) are in the earlier logged compartments compared with the unlogged and the recently logged compartments. Soil reaction (pH) and organic matter as well as texture and fertility (soil nutrients) in Budongo Forest Reserve show trends that relate to mahogany regeneration, distribution and successional stages (seedling, saplings and trees) of the forest after logging.

- Illumination, temperatures below ground and temperatures at the forest floor were the most significant microenvironmental factors across the study area, particularly in the earlier logged compartments. The earlier logged compartments have the highest stock of mahogany seedlings, saplings and trees.

- There is a seasonal difference in the temperature conditions in the forest with generally more uniform conditions among the forests in June, but more contrasting conditions in December. This study suggests that the quality of forest cover affects the understorey conditions, which affects mahogany regeneration.

- Also, the difference in light regimes is really between logged and unlogged forest, but PAR effects are detectable only between the extreme forest categories (unlogged *vs.* most recently logged).

7.6.2 Recommendations

Key recommendations from the present study are in two categories. Category one is recommendations for silvicultural management, while category two is recommendations for future research.

7.6.2.1 Recommendations for silvicultural management

- If the management of Budongo for timber is to rely on natural regeneration of the *K. anthotheca* and *Entandrophragma* species for its future crop then some trees of larger diameter size-class must be identified and left as mother trees in each compartment. Effort must be made to protect them from being felled. Individuals tallied were predominantly in the 10-19.9 cm and 20–29.9 cm diameter size-classes. The optimal size-class recommended for logging by Forest Department is a tree ≥ 80 cm dbh.

- Other than natural regeneration, the compartments showing crowded seedlings may be systematically treated through silvicultural operation, such as thinning and transplanting, provided the temperature and canopy cover pattern of the compartments are monitored. There needs to be a method of redistributing seedlings/wildlings from a high concentration area to a low concentration area through artificial planting (enrichment). Larger striplings (three years old with leaves stripped off) may be better suited for this purpose (Eggeling, 1940). In the 1940s and 1950s, younger 9 months old seedlings were used and subsequently suffered due to competition for light, moisture and nutrients (Philip, 1965).

- Given the significance of the role of light and temperature variations in the compartments sampled, it is reasonable to suggest that more silvicultural emphasis should simulate conditions in the earlier logged treatment). Even then, the operational decisions should be based on thorough knowledge of the conditional attributes exhibited in compartments that were logged earlier such as compartments N9 and N5.

7.6.2.2 Recommendations for future research

This study, conducted in three treatments (unlogged, earlier and later logging), provides a great example of how canopy cover manipulation by silvicultural management may be beneficial to some tree species regeneration and stocking over time.

From the results, earlier logged compartments provide more suitable regeneration niches than the unlogged and later logged. If forest management in Budongo forest is concerned about the stability and population of desired forest species, emphasis must be placed on establishing techniques to monitor:

- How logging can predispose the forest to other disturbances. Logging, for examples exposes the forest to insects/birds as well as increased solar radiation that greatly affects the regeneration and growth especially of shade tolerant species.

- How silvicultural interventions lead to deviation from the natural forest recovery process. The importance of silvicultural operations is to maintain the forest interior microenvironments suitable for species regeneration, health and productive growth.

- Strategies used by species to survive logging as well as other natural disturbances. This ecological information is important to the continued commercial forest operations especially targeting the mahoganies and other commercial species in the forest.

- Seasonal effects on the recovery process, including phenological conditions prior to and immediately after logging.

- Techniques to assess how quickly the forest habitat and ecosystem recover after logging.

- Now that forest soil patterns, temperature variations, forest light regimes, individual stocking and distribution patterns of the four mahogany timber species in Budongo forest is established, individual focused research (auto-ecology) may be conducted. This would strengthen capabilities to manipulate regeneration and growing conditions at the seedling, sapling and pole stages.

- The present study did not address species competition, yet competition both interspecific and intraspecific may be a problem in Budongo Forest Reserve. In this situation, mahogany species can be out-competed, die, flourish or get stunted. Pena-claros and de-Boo (2002) noted that species have a regeneration ecology that is closely tied to the physical and biotic factors of the site, where it establishes. Seedlings must not only survive in the site, but also compete with seedlings of their own as well as other species already established (Swaine and Whitmore 1988; Ralson 1984; Snedaker 1970). This situation may be present and affecting the ecology and regeneration of mahogany species in the Budongo Forest Reserve. Future research could include a component on species competition and the impact of animals, insects, herbivores and predators of seeds and seedlings.

- While the results and conclusions made above are sufficient to make this study stand alone, the study remains somewhat incomplete until the perspective from the new Forest Sector policy issues and the concerns for forest users, especially timber users in Uganda are known. A more comprehensive study would include carefully structured qualitative analysis to link the forest data, social and policy concerns. This would then link the constitutional (policy), collective (joint forest management) and operational (routine management), which are jointly important in the future management of natural forests in Uganda.

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Appendix 1:

This appendix shows compartments logged and arboricide-treated in Budongo Forest Reserve. The appendix indicates dates of logging and treatment, and volume of timber removed. Any missing values or any numbers that are questionable are followed by a "?" The appendix only shows timber removed by sawmills and does not include timber removed by pitsawyers, as the records are incomplete for this. The number of plots from Forest Department inventory for each compartment is also given.

***Source**:* Plumptre (1996)

Compartment	Area (ha)	Date Logged	Total (m^3ha^{-1})	Mahogany (m^3 ha^{-1})	Date treated	Arboricide ($1ha^{-1}$)	Inventory plots
Biiso block							
B1 ♦	582	1935	19.9	12.3	1957-58	?	10
		1981-92	21.5	12.9	None	-	-
B2	600	1936-38	40.2	33.9	1958-59	20.4	11
B3 ♦♦	867	1939-40	34.9	23.7	1959-60	?	15
B4	748	1941-42	34.8	19.8	1955-57	20.4	17
		1985-92	**Some pitsawing**				
B5	871	1943-44	34.2	25.2	1960-61	42.6	6
B6	394	1943	14	10.4	1961-63	42.6	7
B7	288	1944	20.2	14.7	?	?	10
Nyakafunjo block							
N1	412	1945	58.7	47.1	1962-63	?	5
N2	630	1945-47	46.2	33.1	1955-56	11.1	14
N3	620	1947-52	80	39.1	1959-61	22	12
N4	341	1952-54	94	48	1960-62	?	5
N5 ♦♦	568	1954	51.5	41.2	1963-64	38.1	10
N6	600	1956-57	59.8	49.4	1956-58	41.6	10
N7	474	1958-59	31.9	26.1	1957-58	44.8	1
N8	498	1957-58	25.7	20.8	1957	47	11
N9 ♦♦	498	1958-59	15.2	10.7	1958	42.3	6
N10	618	1959-60	30.2	23.5	1958-60	50.4	6
N11	564	1960	26.5	21.7	1958-60	42.6	10
N12	389	1960	3	2.5	1958-60	32.9	2
N13	610	1960	13	8.5	1960	40.3	10
N14 ♦♦	535	1961-62	?	?	None		10
N15	777	*Unlogged*	(Strict Nature Reserve)		None		8
Waibira block							
W16 ♦♦	543	961-62	21.7	14.3	1961-62	?	3
W17	609	Unlogged			None		-
W18	681	1960-61	28.8	19.3	1960-62	43.6	11
W19	886	1962-63	25.6	16.3	1961-63	41.4	16
W20	569	1963/64	30.8	20.3	1962-63	41.4	1
W21 ♦♦	1116	1963-64	36.1	23.9	1963-64	29.1	13
W22	1036	1965-67	35.9	23	1966	?	10
W23	736	1966-68	26.4	18.5	1966	?	6
W24	710	1967-69	14.2	9.3	1966-67	?	13

W25	1181	1968-69	9.6	5.4	1970-71	?	10
W26	781	1970-71	30.6	19.1	1971-72	36	0
W27	791	1970-71	?	?	1970-71	46.5	0
W28	1010	1972-73	51.4	29.1	1972-73	29.5	2
W29	744	1972-74	64	40.5	None		6
W30	580	1974-75	8.1	7.5	None		3
W31	689	Unlogged			None		7
W32	968	Unlogged			None		0
W33	731	Unlogged			None		11
W34	751	Unlogged			None		6
W35	680	Pitsawn	?	?	None		5
W36	591	Pitsawn	?	?	None		10
W37	566	1978-82	22.2	10.7	None		11
W38	422	1983	(Partially pitsawn)		None		12
W39	667	1974-76	43.5	25.5	None		2
W40	996	Pitsawn	?	?	None		3
W41	691	Pitsawn	?	?	None		1
W42	804	Pitsawn	?	?	None		14
W43	829	Pitsawn	?	?	None		6
Kaniyo Pabidi block							
K1	177	1970-72	11.7	9.4	?		10
K2	533	1970-72	3.1?	2.3?	?		10
K3	330	1977			None		2
K4 ♦	630	1987-92	20.7	12.6	None		2
K5	311	1985-87	25.6	17.2	None		4
K7	526	1987-89	11.1	9	None		2
K8	169	1986-89	31.5	15.1	None		0
K11	420	Unlogged			None		6
K12	1097	Unlogged	(Current evidence of pitsawing)		None		17
K13	625	Unlogged	(Current evidence of pitsawing)		None		4
Siba block							
S1	810	1963-69	40.9	23.5	1972-73	34.4	10
S2	602	1969-70			1971-72	40	2
S3 ♦♦	528	1966-70			?		0
S4	799	1972-77	28.9				16
S5 ♦	829	1971					13
S6	588	1971			1972-75		9
S7	686	1990			none		9
S8	446	1979/90	48.3	26.3	none		6

Note: ♦♦ indicates compartments sampled in the earlier logged category, while

♦ indicates compartments sampled in the later logged category.

N15, the strict nature reserve was the control treatment and for this study considered as the unlogged.

Previous history of Siba Block: S1-S8 were logged in 1928-35. Total timber removed was 70, 600 m^3; 13.4 m^3 ha^{-1}. Volume of mahogany cut was 49.085 m^3; 9.3 m^3 ha^{-1}. Compartments in Siba were numbered differently in 1930s and the logging followed vegetation types rather than compartments

Appendix 2

TROPICAL FOREST MANAGEMENT/SILVICULTURAL PRESCRIPTIONS (Philip *et al.* 1964)

1. Pre-Logging Refining:

(1) Objective: To create conditions in the forest, at the same time of felling, in which the regeneration of desirable tree species can get established and to minimize felling damage.

(2) Method: climber cutting and poisoning all weed (non-merchantable species) and defective or over-mature stems of desirable trees using a mixture of 3 percent Finopal in heavy diesel is done from 6 to 9 months prior to felling. The arboricide is sprayed onto the stem bole in a band 30 cm wide, except on tree species that are known to be resistant, which need frilling are: *Dombey*a spp., *Melanodiscuss* spp., *Alstonia boonei*, *Bosqueia phoberos*, *Celtis* spp., *Croton macrostachus*, *Ricinodentron heudelotii*, *Sapium ellipticum*, *Trichilia* spp., *Ficus* spp. and *Cynometra alexandri*. *C. alexandri* is frilled, but the sprayed band is retained at 30 cm wide to ensure a good percentage kill. Each forest compartment is subdivided by cut lines into a grid of square plots of 4 ha each, with each plot treated in two sweeps on a 100 m front.

Post-Logging Refining with Arboricide (Budongo Forest Reserve, Uganda):

(1) Objective: To remove weed tree species, defective stems and over-mature trees that are impeding the growth of established regeneration.

(2) Method: The operation is very similar to pre-logging refining, except that it is done in areas, which have been recently harvested, and that treatment units may be enlarged to 6 ha. The minimum size of tree stems treated is 8cm DBH. In some forest compartments, nursery raised seedlings of desirable tree species such as mahogany are planted in gaps and sometimes in lines. The planted seedlings are tended by weeding and climber cutting until they are established.

Appendix 3

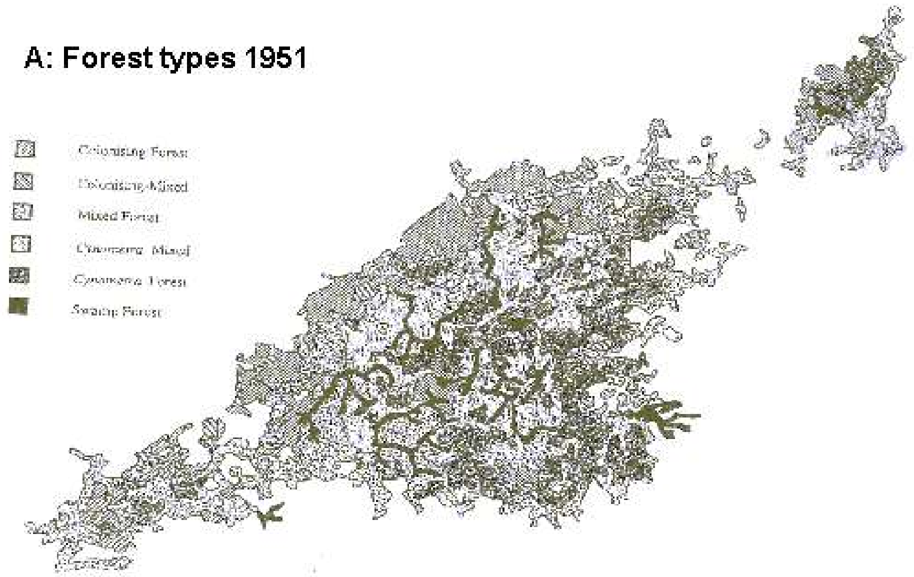
List of species mentioned in this thesis

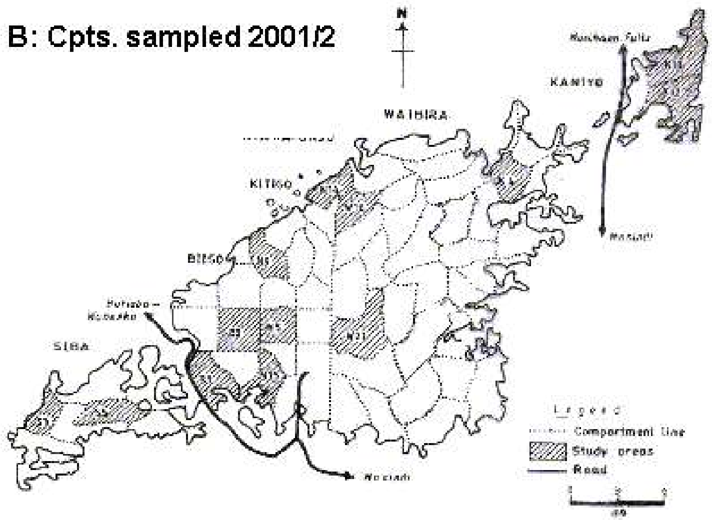
Species	**Family**
Acanthus pubescens (Oliv.) Engl.	Acanthaceae
Aglaia agglomerata Merrill & Perry	Meliaceae
Albizia coriaria Oliv.	Mimosaceae
Albizia ferruginea (Guill. & Perr.) Benth.	Mimosaceae
Albizia glaberrima (Schum. And Thonn.) Benth.	Mimosaceae
Albizia sp.	Mimosaceae
Alstonia boonei De Wild.	Apocynaceae
Andropogon schirensis A. Rich.	Poaceae
Anthericum speciosum Rendle	Anthericaceae
Arachis hypogaea	Leguminoceae
Asparagus sp.	Asparagaceae
Aspilia abyssinica Oliv. & Hiern	Compositae
Balanites wilsoniana *Dawe & Sprague*	Balanitaceae
Balsamocitrus dawei Stapf	Rutaceae
Bombax buonopozense P.Beauv.	Bombacaceae
Brachiaria brizantha (A. Rich.) Stapf	Poaceae
Brachiaria decumbens Stapf	Poaceae
Calamus deerratus Mann. & Wendl.	Arecaceae
Caloncoba crepiniana (De wild. & Th.Dur.) Gilg	Flacourtiaceae
Camellia sinensis (L.) Kuntze	Theaceae
Canarium schweinfurthii Engl.	Burseraceae
Cassia sieberiana DC.	Caesalpiniaceae
Cathormion altissimum (Hook.f.) Hutch. and Dandy	Rhizophoraceae
Celtis mildbraedii Engl.	Ulmaceae
Celtis phillipensis Planch	Ulmaceae
Celtis sp.	Ulmaceae
Celtis zenkeri Engl.	Ulmaceae
Chisocteton fragrans Hiern	Meliaceae
Chrysophyllum africanum A. DC.	Sapotaceae
Chrysophyllum albidum G. Don	Sapotaceae
Chrysophyllum sp.	Sapotaceae
Clitandra cymulosa Benth.	Apocynaceae
Coffea canephora Froehn.	Rubiaceae
*Cola caricaefolia (*G. Don) K. Schum.	Sterculiaceae
Cola gigantea A. Chev.	Sterculiaceae
Combretum sp.	Combretaceae
Cordia millenii Bak.	Boraginaceae
Croton macrostachyus Delile	Euphorbiaceae
Cymbopogon nardus (L.) Rendle	Poaceae
Cynometra alexandri C.H. Wright	Caesalpiniaceae
Dombeya kirkii *Mast.*	Sterculiaceae
Dracontomelon dao *(Blanco) Merr. & Rolfe*	Anacardiaceae

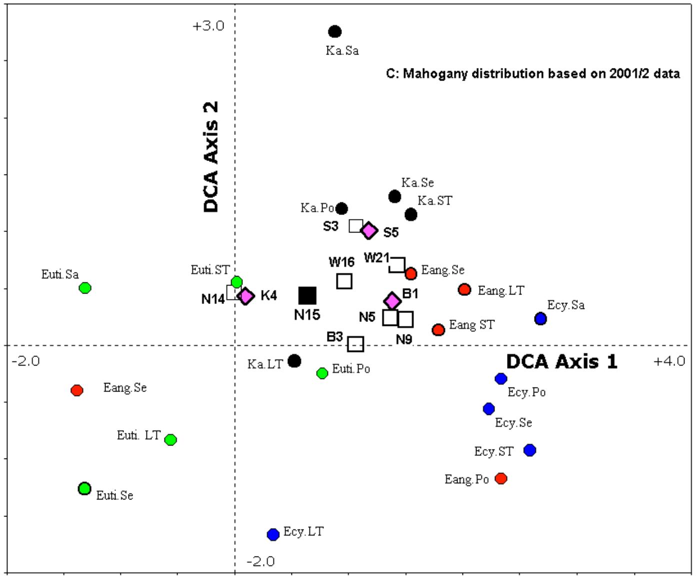
Eleusine coracana (L.) Gaertn.	Poaceae
Entandrophragma angolense (Welw.) C.DC.	Meliaceae
Entandrophragma bussei Harms	Meliaceae
Entandrophragma candollei Harms	Meliaceae
Entandrophragma caudatum *(Sprague) Sprague*	Meliaceae
Entandrophragma cylindricum (Sprague) Sprague	Meliaceae
Entandrophragma delevoyi De wild	Meliaceae
Entandrophragma excelsum (Dawe & Sprague) Sprague	Meliaceae
Entandrophragma palustre Staner	Meliaceae
Entandrophragma pierrei A. Chev.	Meliaceae
Entandrophragma utile (Dawe & Sprague) Sprague	Meliaceae
Erythrina mildbraedii Harms	Papilionaceae
Erythrophleum suaveolens (Guill. & Perr.) Brenan	Caesalpiniaceae
Ficus sp.	Moraceae
Ficus sur Forssk.	Moraceae
Funtumia elastica (Preuss) Stapf	Apocynaceae
Glenniea africana (Radlk.) Leenh.	Sapindaceae
Holoptelea grandis (Hutch.) Mildbr.	Ulmaceae
Hyparrhenia filipendula (Hochst) Stapf	Poaceae
Hyparrhenia rufa (Nees) Stapf	Poaceae
Hyparthelia dissoluta (Steud.) Clayton	Poaceae
Khaya anthotheca (Welw.) C. DC.	Meliaceae
Khaya comorensis Legris	Meliaceae
Khaya grandifolia Thompson.	Meliaceae
Khaya ivorensis A. Chev.	Meliaceae
Khaya madagascariensis Jum. & H. Perrier	Meliaceae
Khaya senegalensis (Desr.) A. Juss.	Meliaceae
Klainedoxa gabonensis Engl.	Irvingiaceae
Landolphia comorensis (Bojer) Pichon	Apocynaceae
Landolphia landolphioides (Hall. F.) A. Chev.	Apocynaceae
Landolphia owariensis P. Beauv.	Apocynaceae
Lasiodiscus mildbraedii Engl.	Rhamnaceae
Leptonychia mildbraedii Engl.	Sterculiaceae
Lovoa trichilioides Harms	Meliaceae
Lychnodiscus cerospermus Radlk.	Sapindaceae
Maesopsis eminii Engl.	Rhamnaceae
Manihot esculenta Crantz	Euphorbiaceae
Margaritaria discoidea (Baill.) G. L. Webster	Euphorbiaceae
Mildbraediodendron excelsum Harms	Papilionaceae
Milicia excelsa C. C. Berg	Moraceae
Mitragyna stipulosa Kuntze	Rubiaceae
Munronia delevayi Franch	Meliaceae
Musa sp.	Musaceae
Naregamia africana (Welw.) Exell	Meliaceae
Nicotiana tabacum *L.*	Solanaceae
Olea welwitschii Gilg & Schell.	Oleaceae
Panicum maximum Jacq.	Poaceae
Parkia filicoidea Oliv.	Mimosaceae
Pennisetum purpureum Schumach.	Poaceae
Phaseolus vulgaris L.	Papilionaceae)
Phoenix reclinata Jacq.	Arecaceae

Piptadeniastrum africanum (Hook. f.) Brenan	Mimosaceae
Polyscias fulva (Hiern) Harms	Araliaceae
Pouteria altissima (A. Chev.) Baehni	Sapotaceae
Prunus africana (Hook. f.) Kalkman	Rosaceae
Pseudospondias microcarpa (A. Rich.) Engl.	Anacardiaceae
Psydrax parviflora (Afzel.) Bridson	Rubiaceae
Pterygota macrocarpa K. Schum.	***Sterculiaceae***
Pycnanthus angolensis (Welw.) Warb.	Myristicaceae
Ricinodendron heudelotii (Baill.) Heckel	Euphorbiaceae
Rinorea angustifolia Thou.) Baill.	Violaceae
Rinorea brachypetala (Turez.) O. Ktze.	Violaceae
Saccharum officinarum L.	Poaceae
Sapium ellipticum (Krauss) Pax	Euphorbiaceae
Sesamum indicum L.	Pedaliaceae
Spathodea campanulata P. Beauv.	Bignoniaceae
Spondianthus preussii Engl.	Euphorbiaceae
Sporobolus pyramidalis P. Beauv.	Poaceae
Terminalia brownii Fresen.	Combretaceae
Trema orientalis (L.) Blume.	***Ulmaceae***
Trichilia dregeana Sond.	Meliaceae
Trichilia prieuriana A. Juss.	Meliaceae
Trichilia rubescens Oliv.	Meliaceae
Trilepisium madagascariense DC.	Moraceae
Turraea sp.	Meliaceae
Zea mays L.	Poaceae

Appendix 4: Vegetation types in 1951 and status of mahogany regeneration and structure in 2001/2


A: Forest types 1951


B: Cpts. sampled 2001/2


C: Mahogany distribution based on 2001/2 data

Note:

- Regeneration for all the mahogany species studied is higher where numbers of mature mother trees existed.

- Mahogany regeneration is more pronounced in compartments located in the mixed forest types than in the *Cynometra* and swamp forest types.

- The regeneration and distribution patterns of *K. anthotheca* and *E. angolense* is random and generally more of generalists, while *E. cylindricum* and *E. utile* are generally more of specialists for specific ecological niches in the earlier and later logged forest tracts.

- The present results confer with Walaga (1994) that there exist significant correlation between local patterns of tree species distribution and some of the soil variables, especially potassium, sodium and percentages of clay and silt. Soil variables in the earlier logged compartments were strongly correlated to mahogany distribution patterns in Budongo Forest Reserve.

- Therefore, the present results suggest that the western part of the forest (Biiso and Nyakanfunjo), which is more of a mixed forest type supports more mahogany regeneration than the more *Cynometra* central and eastern part of the forest.