EARLY GROWTH AND INSECT HERBIVORY OF *NEOBOUTONIA MACROCALYX* SEEDLINGS IN DIFFERENT SIZED GAPS IN KIBALE NATIONAL PARK

BY

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DECLARATION

I hereby declare that the work presented in this thesis is the result of my own investigation except where otherwise stated. It has never been submitted in part or whole for any degree in this university or any other institution of higher learning.

Signed …………………. ………………………..
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This thesis has been submitted to Makerere University with our approval as university supervisors

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Dr. Fred Babweteera Date

DEDICATION

This thesis is dedicated to the God Almighty, the provider of wisdom, my mother, sisters and brothers.

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DEFINITION OF TERMS

Gap: A real projection of canopy opening reaching within 2m of ground at least 40 m^2 (Brokaw, 1982). This study considered both the natural tree fall gaps and those created as a result of logging.

Logging: The work of felling trees, cutting them into logs and transporting the logs to saw mills or market.

Canopy: The uppermost layer in a forest formed by crowns of trees. It can also be called crown canopy.

Herbivory: The consumption of plants without necessarily killing them.

Growth: An increase in the size of an organism or part of an organism, usually as a result of an increase in the number of cells. Growth of an organism may stop at maturity, as in the case of humans and other mammals, or it may continue throughout life, as in many plants.

Survival: A state of remaining alive or a natural process resulting in the evolution of organisms best adapted to the environment

ABSTRACT

Gap size is considered as a key factor to tree colonization and succession. Small gaps often show a species compositon that is distinctly different from larger gaps. This species niche differentiation is influenced by plant life and herbivory. Early growth, survival and insect herbivory of *Neoboutonia macrocalyx* seedlings in different sized gaps in Kibale National Park were investigated. The aim of this study was to assess the regeneration potential of *Neoboutonia macrocalyx* seedlings in gaps of different sizes in Kibale National Park. To achieve this aim, data were collected from *Neoboutonia macrocalyx* seedlings planted in 22 gaps in Kibale National park. For each gap, the gap size and canopy openness were determined. Gaps were grouped into small (≤ 500 m^2), medium ($>500 \leq 1000$ m^2) and large (>1000 m^2). Four plots of 50x50cm were established in each gap. In each plot, ten *N. macrocalyx* seeds were sown. After one month, the following growth parameters were observed monthly in each gap for a period of six months: seedling height (cm), leaf area (cm^2), total number of leaves and number of new apical leaves developed per month. Herbivory was determined by calculating the percentage of leaf area missing and seedling survival was determined by counting the number of seedlings that were still alive at the end of the experiment (six months).It was found that seedling growth increased with increase in gap size and herbivory was higher in small gaps than in large gaps. Seedling survival was higher in large gaps than small gaps. These results indicate that regeneration of *N. macrocalyx* is best in gaps that are over $1000m^2$. It is recommended that *N. macrocalyx* should be used in large gaps as a colonizing tree species to restore the lost forest trees and enrichment planting should be encouraged where natural regeneration has failed.

CHAPTER ONE

1.0 Introduction

1.1 Background

Tree fall disturbances play a crucial role in the structure and dynamic processes of forest communities (Whitmore, 1975, Halle *et al,*.1979). Tree falls generate gap dynamics in forest populations, which promote the expression of a floristic- structural mosaic of vegetation that may be subject, by virtue of repeated disturbance events, to recurrent successional phases (Olderman, 1978; Bormann and likens, 1979; Brokaw, 1985; Martinez-Ramos and Alvarez- Buylla, 1986).

Canopy gaps are integral of every primary forest ecosystem, no matter whether it is a temperate or tropical forest. They can be caused by various factors including landslides, strong winds, logging and injury or death of individual trees. Landslides and uprooting may open up the soil to the mineral horizon. Other causes may not affect soil structure so drastically. Many fast growing shade intolerant pioneer species are adapted to canopy disturbance and they need light gaps to establish and reach maturity. Late successional canopy tree species often tolerant shade juveniles, but most of them also require disturbance of forest canopy to reach reproductive maturity (Hartshorn, 1980; Whitmore, 1989).

Gap size is considered a key factor in determining colonization by trees (Arriaga, 2000; Brokaw, 1985; Denslow, 1980; Whitmore, 1989, 1996). Small gaps often show a species compositon that is distinctly different from larger gaps (Arriaga, 2000). Some of the parameters which are associated with gap are light availability and quality (Barton *et al.*, 1989, Denslow *et al.*, 1998), herbivory (Pearson *et al.*, 2003) and nutrient availability (Denslow *et al.*, 1998). Canopy gaps could be regarded neither as homogeneous environment nor as sharply delimited (Brandani etal,. 1988, Dalling and Hubell 2002; Ntinez- Farfan and Dirzo 1988; Whitmore, 1996).

Plant species composition and diversity changes from the gap edge to the center (Hartshorn, 1981). Garwood (1989) proposed that, in small gaps the growth of seedlings and suppressed saplings is promoted, where as large gaps are dominated by pioneer species which arrive mainly by seed rain or to a limited amount, are in the soil seed bank (Vasquez- Yanes and Orozco – Segovia, 1993). As a result, species composition is related to gap size. Within small gaps, no own succession series starts in contrast to big gaps which allow for secondary succession to establish. Two aspects determine the further development of a canopy gap; first, the colonizing species, which are adapted to the special conditions within gaps and secondly, the subset of species that were present and survived gap creation.

The process of canopy perforation, and hence the formation of canopy gaps, drives the regeneration cycle of the tropical rainforest. Canopy gaps constitute small to mid-scaled disturbances created by the fall of the structural elements of the forest. In places where gaps are formed, new forest patches start to regenerate and grow until they eventually reach a stage of maturity, from which gaps are formed again.

Disturbance is ubiquitous in forest ecosystems (Attiwell 1994; Rogers 1996). Defined as any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett 1985), disturbance determines forest species composition, structure, and process. Furthermore, disturbances exert their influence over a wide range of temporal and spatial scales. It promotes changes in resource fluxes, changes that lead to some form of reorganization of the disturbed patch or gap at structural and functional levels that may be similar or dissimilar to predisturbance levels. Resource levels and inputs are changed and species respond accordingly.

Studies of regeneration in tropical forests have highlighted the importance of canopy gaps, typically resulting from tree falls, in determining forest structure (Denslow, 1980, 1987; Brown & Whitmore, 1992; Whitmore & Brown, 1996). The concept of gap partitioning rests on the assumption that ability to take advantage of gaps of different sizes involves a set of characters on which natural selection can operate (Whitmore & Brown, 1996). Therefore, it seems reasonable that if the frequency of gap formation, size of gaps and the duration of periods of release differ among regions, then the benefits of different strategies of gap partitioning will also differ. Thus, tree communities in different regions may differ in the proportion of species adapted to exploit gaps of different sizes. A number of authors have used similar logic to explain the structure of particular communities and have suggested that the disturbance regimes over evolutionary time will influence the composition of particular communities for example the monsoon forests (Whitmore, 1974, 1990) and Amazonian caatinga (Comes & Grubb, 1996).

Gap formation in the forest leads to rapid tree recruitment and redevelopment of the canopy (Brokaw, 1985a; Denslow, 1987). Gaps induce significant changes in the gap microclimate compared with the forest understory and as a result, the germination, establishment, growth and reproduction of many gap plants are increased (Denslow, 1987). Gaps maintain high pioneer tree density and diversity (Brokaw, 1985, Lawton & Putz,

1988) as well as high liana species diversity (Schnitzer & Carson, 2001). However, gaps do not appear to maintain species diversity of non pioneer, shade- tolerant trees (Uhl *et al*., 1988; Hubbell *et al*., 1999; Schnitzer & Carson, 2001). Patterns of plant growth and other ecological processes are thought to vary as a function of gap size, because gap size directly affects light levels and microclimates (Denslow & Hartshorn, 1994) and nutrient availability (Whitmore, 1996). Changes in miroclimates as a result of gap formation have got influence on the distribution of insect herbivores and seedling survival in gaps of different sizes. Annual rates of leaf damage are higher in tropical forests than in temperate broad-leaved forests. Herbivory averages 7.1% per year in the temperate zone, and 11.1% for shade-tolerant species in the humid tropics. Rates of damage to gap specialists are even higher (48.0%), but they comprise less than 15% of the individual trees in tropical forests (Hubbell and Foster, 1986).

1.2 Statement of the Problem

Kibale National Park (KNP) has been severely affected by agricultural encroachment and commercial logging, and these are the main causes of forest fragmentation in Uganda (Obua, 1996). Ecotourism is a major economic activity in the park. Although under strict protection, KNP is still the main source of firewood, building poles, bush meat and medicines for the majority of the local people living in its immediate neighbourhood (Obua, 1988). The forest was subjected to different levels of selective logging, which is expected to cause different ecological changes and therefore the survival of many tropical forest species may depend on their ability to adapt to disturbed forest environment. However, recent studies demonstrate that tree regeneration following large scale disturbance can be slow or possibly arrested, decreasing the conservation value of disturbed forests (Chapman and Chapman, 1997). In KNP, many abandoned logging gaps showed little forest recovery 30 years after selective logging and previously logged areas are dominated by herbaceous growth, primarily *Acanthus pubescens* (Chapman and Chapman, 1997). This is consistent with the generally held view that the tree communities in Africa include relatively few aggressive colonizing tree species that can invade large gaps (Dean & Milton, 1995; Richards, 1996; Chapman & Chapman, 1997). Previous studies have been carried out on tree seedling growth and survival in forest gaps and forest understory in KNP (Chapman & Chapman, 2004). However, there is lack of knowledge on how gaps of different sizes influence seedling growth, herbivory and seedling survival in Kibale National Park. This study was part of the research that focused on diversity and species richness of herbivores, intensity of herbivory and regeneration of *Neoboutonia* species in Uganda. Therefore, for practical reasons, the project did amodel study with one tree species (*Neoboutonia macrocalyx*) and its abundant and highly diverse fauna of leaf feeding insects and was the most available pioneer tree species in the research area.

1.3 Overall objective of the study

To assess the regeneration potential of *Neoboutonia macrocalyx* seedlings in gaps of different sizes in Kibale National Park

1.4 Specific objectives

1. To investigate if gap size influences growth of *Neoboutonia macrocalyx* seedlings.
2. To determine the variations in insect herbivory on the leaves of *Neoboutonia*

macrocalyx seedlings in different sized gaps.

3 .To examine the variations in *Neoboutonia microcalyx* seedling survival in gaps of different sizes.

1.5 Hypothesis

1. Growth of *Neoboutonia macrocalyx* seedlings is not influenced by gap size
2. There are no variations in insect herbivory on the leaves of *Neoboutonia macrocalyx* seedlings in different sized gaps
3. There are no variations in *Neoboutonia macrocalyx* seedling survival in gaps of different sizes.

1.6 Justification of the study

Such information is useful in planning of forest management practices and conservation decisions. This has provided information on regeneration ecology of natural forest ecosystems. The information generated in this study is important in understanding the processes of colonization and establishment of early successional stands, and could be used to improve on the regeneration of tropical forest gaps. Information on seedling growth and herbivory can also be used in restoration of degraded forests, since it suggests the potential pioneer tree species that can regenerate and colonize well in tropical forest gaps.

CHAPTER TWO

2.0 Literature Review

2.1 The importance of gap size in forest regeneration

Gap size is the most important characteristic of gaps, because it often correlates with biologically functional parameters (Denslow, 1980, Turner, 1990, Turner & Newton, 1990, Denslow & Hartshorn, 1994). Gap size is important in forest regeneration as it influences environmental factors such as light, air and soil temperature and relative air and soil humidity. Hence, the greater the gap size the more variable its microclimate tends to be when compared to the condition under closed forest canopy. Light intensity, soil temperature and air temperature increase while humidity decreases as gap size increases (Torquebiau, 1988; Brown, 1993; Endler, 1993). However, the climatic difference in a gap is not due to its size *per se*, but also on the architecture and arrangement of surrounding tree crown (Endler, 1993). The distribution of solar radiation is mainly determined by the forest architecture and tree canopies (Steege, 1994). The environment in a gap is strongly dependent on the size of the gap and the larger the gap, the greater the amount of radiation incident on the forest floor, resulting into higher temperatures and light levels, lower humidity and soil moisture. It has been suggested that such microclimatic differences influence the species composition in gap (Enright *et al*., 1993). In fact, the theories of niche differentiation are all hinged around gap size (Swaine and Whitmore, 1988, Turner, 1990, Osunkjoya *et al*., 1993, Poorter, 1998).

2.2 Seedling establishment and regeneration in forest gaps

When a rain forest is exploited for timber, a secondary forest, different from the original primary forest develops (Whitmore 1975, Poore 1976, Woodwell 1978). Poore (1976) suggests that recovery of exploited forest will depend on either coppicing of old stumps, regeneration from dormant seeds and established seedlings or recolonization from outside. Several physical features of tropical high forest that are altered by logging have been suggested to variably influence the regeneration of shade tolerant and light demanding forest species (Richards 1964, Whitmore 1978, Hartshorn 1978). Amongst others, are changes in macro and microclimatic conditions and changes in forest soil chemistry.The lush understory growth that follows disturbance also ensures strong competition for light, space and soil nutrients in addition to supporting high densities of seed and seedling predators (Janzen 1970, 1971; Synnott 1975; Jeffrey 1977; Isabirye- Basuta 1979)

Seedling growth is strongly limited by canopy openness. Most species increase their growth rates as canopy openness is increased. Generally, light availability on the forest floor is between 1-2% of the light above the canopy (Zagt & Werger, 1998). Hence, any moderate opening of the canopy leads to enhanced growth. When the canopy is opened too widely, it is likely that the slow growing, typical mature or climax forest species will be overtopped by the inherently fast growing pioneer species or strangled by lianas, which profit most from the increased light availability. In large gaps, in approximately one month, the pioneer species out compete the more slow growing shade tolerant species, irrespective of the initial size difference. Such pioneers intercept most of the light and continue to respond with vigorous growth, while the smaller shade tolerant species are left behind in the shade. However, when the canopy begins to close, it is also true that the light demanders die off and the shade tolerants slowly dominate the former gaps.

2.3 Effects of canopy openness on insect herbivores

At the community level, tree felling increases insect abundance and species richness but reduces community evenness and such responses have typically been attributed to intermediate levels of disturbance (Connel 1979; Petraits *et al*., 1989).

Moderate levels of disturbance in tropical rain forests often increase insect species richness, particularly of butterflies by increasing habitat heterogeneity (Spitzer *et al*., 1997). Large natural gaps (450- 900 m^2, average 34% canopy openness) support higher insect abundance and diversity including species in genus *Chrysomelidae*, *Membracidae* and *Cicadellidae* than do small gaps (Charles, 1998). As certain species tolerate the new conditions induced by disturbance better than others, evenness in the communities may decrease and overall insect abundance particularly of sap-sucking insects may increase. However, increase of abundance largely occurs among those species with wide ecological tolerances and large geographical ranges (Hamer *et al.,* 1997; Spitzer *et al.,* 1997) while more ecologically restricted species may decline. Further, dominant competitors with poor dispersal abilities might become extinct (Tilman *et al.,* 1994). The canopy openness often triggers leaf production of rain forest plants in forest gaps (Bongers and Popma, 1990) and herbivores usually depend on the presence of young foliage in rain forests (Wolda, 1983).

2.4. Seedling growth and herbivory

In most cases, it is the juveniles and not germinating dormant seeds that replace canopy adults (Schupp *et al.*, 1989). Although shade-tolerant species can survive for years in the low light understory in the tropical forests, the growth of both trees (Brokaw, 1985; Hladik and Blanc, 1987) and understory herbs (Smith, 1987) respond positively to increased light availability. The availability of light is a fundamental determinant of tree seedling growth and survival in forests (Chazdon, 1988). Numerous studies have investigated the traits of plants specialized to grow at high irradiance in canopy gaps and at low irradiance in the forest understorey (Bazzaz, 1979; Bazzaz and Pickett, 1980; Canham *et al*. 1996; Grubb *et al.*1996; Walters and Reich, 1996). For example, Walters and Reich (1996) showed that generally the same morphological adaptations existed for rapid growth of five deciduous tree species in high and low light conditions including a high specific leaf area (SLA), a high net assimilation rate (NAR), and a high relative allocation to leaf mass and leaf area.

Specialization to light environments might also be manifested as a negative relationship between growth rates at high irradiance and mortality in shade for comparisons across species. This has been observed when tree species differing widely in shade tolerance have been compared in both temperate (Kobe *et al*, 1995) and tropical (Hubbell and Foster, 1992) tree floras. The relationship is consistent with cross overs in photosynthetic rates in response to variation in irradiance if the high mortality of potentially fast growing species in shade is driven by their inability to maintain a positive carbon balance at low irradiance (Givnish, 1988). However, an alternative hypothesis proposes that the rank order of species growth rates is maintained across irradiance conditions (Kitajima, 1994, 1996; Poorter, 1999). According to this hypothesis, the high mortality of potentially fast growing species at low irradiance is associated with low investment in morphological and biochemical characteristics that confer defence against herbivores and pathogens, such as thicker, more lignified leaves and production of secondary chemicals (Kitajima, 1994; Cornelissen *et al*, 1998; Poorter, 1999). For example, Coley *et al*.,(1985) argued that slower growing species with longer lived leaves have an increased investment in anti- herbivore defences, while faster growing species rely on their ability to rapidly replace tissue removed by herbivores to maintain a high photosynthetic area, and consequently a high growth rate. At low irradiance, fast growing species are unable to replace tissue lost to herbivores because high respiration rates result in net photosynthetic rates that are not sufficient to maintain a positive carbon balance (Loach, 1967; Boardman, 1977; Coley *et al*., 1985; Kitajima, 1994).

Herbivores can be a major cause of leaf loss in forests, reducing plant growth (Crawley, 1983). In a year, herbivores remove 7.5% and 10.9% of the leaf area on average in temperate and tropical forests, respectively. In the shaded understory, carbon gain is low and loss of leaf area is predicted to have a greater negative effect on plant growth than in high light environments (Coley *et al.,* 1985). Some factors that influence herbivore damage rates are leaf age, leaf quality, plant size and variations in weather patterns that may affect herbivore population size. Many studies have demonstrated that young leaves are preferred by herbivores and receive higher levels of damage than mature leaves (Milton, 1979; Rockwood & Glander, 1979; Rausher, 1981; Coley, 1983). Higher damage rates on young leaves have been ascribed to lower levels of leaf toughness, higher levels of water and nitrogen and in some cases, lower levels of secondary defenses (Coley and Aide, 1991). Along with effects of leaf age, light can affect leaf characteristics that influence herbivore feeding behavior. Light levels affect leaf structure, toughness and nutritional quality (Scriber and Slansky 1981), and levels of defensive compounds in leaves (Bryant *et al.*, 1983; Mole *et al.*, 1988). How these differences translate into actual herbivore damage varies between studies; some studies have demonstrated higher herbivory rates on plants in high light environments (Bigger, 1981; Lincoln and Mooney, 1984; Harison, 1987), while others have shown higher damage rates in low light environments (Rice *et al.*, 1979; Maiorana, 1981)

2.5 Ecology of *Neoboutonia macrocalyx*

Neoboutonia macrocalyx Pax (Euphorbiaceae) is a pioneer tree which grows in light gaps of medium altitude tropical rain forests (Chapman *et al.*, 1999). The growth of *N. macrocalyx* is not limited to primary forests; it is present in partially logged and secondary forests (Kasenene & Roininen, 1999). *Neoboutonia macrocalyx* inhabits sites which are secondary forest, river valleys or low–lying areas where water fluctuations are low (Chapman *et al.*, 1999). This species produces leaves continuously throughout the year (Roininen & Kasenene, unpubl. data).

Such pioneer species provide a particularly suitable study system because they respond rapidly in terms of growth and mortality to resource availability (Wright & Cornejo, 1990, Wright, 1991).

Neoboutonia macrocalyx trees are 10-20 meters tall with a canopy width of 7 to 12 meters. Leaf abscission occurs from the base of shoot, and thus the abscised leaves are the oldest on a shoot (Hamilton, 1991). Based on the earlier research conducted in KNP, it seems that the insect feeding pattern on *N. macrocalyx* tree is caused by relatively random visits of a highly mobile free-feeding guild (Roininen & Kasenene unpublished data).

2.6 Importance of *Neoboutonia macrocalyx*

Neoboutonia macrocalyx is very important for the production of paper pulp (Eggling, 1951). The communities around Kibale National Park use the tree for poles and rafters for construction and firewood (Kakudidi, 1999). The species is also important culturally as it is used against witch craft. It is used medicinally for the treatment of stomach ache and in abortion. The communities around Kibale National Park have incorporated *Neoboutonia* species into their agroforesty systems and management of woodlots for construction and firewood resources. However, the use is not extensive, although it could be a good tree for agroforestry because it pumps nutrients from deep soil layers and due to its deep rooted system, it does not compete with agricultural crops (Kasenene, unpublished data). The tree may also be an important medicine for the local chimpanzee population, which occasionally eat the roots and bark (Jeremiah. S. Lwanga pers.com).The wood is soft and is used for making boxes, crates, beehives and stools.

2.7 Lepidopteran fauna in Kibale

Little is known a bout the lepidopteran fauna in Kibale, and elsewhere in Uganda (Plumptre *et al.*, 2007). However, 94 species of the family Nymphalidae have been recorded from KNP including species in subfamilies Acraeinae, Charaxinae, Nymphalinae and Satyrinae (Molleman *et al.*,2006*)*. In addition, species of Lycaenidae and Hesperidae have also been found. Further, 42 species of Saturniidae, 65 species of Sphingidae (Howard *et al*, 1996), 23 species of papilionidae and 12 species of Pieridae have been identified (Chapman,un published). On *Neoboutonia* most of the species found in Kibale have been moths. Geometridae are the largest group followed by Gelechiidae, Lymatriidae and Noctuidae. Also species of Nolidae, Oecophoridae, Pyralidae, Lasiocampidae, Saturniidae. Limacodidae, Carposinidae, Arctiidae, Psychidae, Notodontidae and Nymphalidae have been identified.

CHAPTER THREE – STUDY AREA DESCRIPTION AND METHODS

3.1 Introduction

This chapter presents a brief description of Kibale National Park, its management history and methods used to carry out the study. The study area is described in section 3.2 and the methods are presented in section 3.3.

3.2 Description of Kibale National Park

3.2.1 Location and size

The study was conducted in the Kanyawara area of the Kibale National Park for the period of six months. The Park lies in Kabarole District (formerly Toro District) of western Uganda. It covers an area of 560 km^2 (Kingston, 1967; Struhsaker, 1975) It runs along a north- south axis about 56 km and is located near the edge of the western great Rift Valley, lying only 24 km east of the Rwenzori Mountains. The reserve is equatorial (0^o 13 to 0^o 41`N and $30^o$ 19` to 30^o 32`E). Altitude within the reserve ranges from 1,590 m in the north to 1,110 m in the south (Struhsaker, 1975). The park has a series of undulating hills and valleys with variations in relief rarely exceeding 150-180m vertically (Wing and Buss, 1970). Water is abundant throughout the forest with streams and swamps in nearly all the numerous valleys. All the water courses eventually empty in either the Dura River or the Mpanga River, both of which drain into Lake George (Wing and Buss, 1970; Struhsaker, 1975).

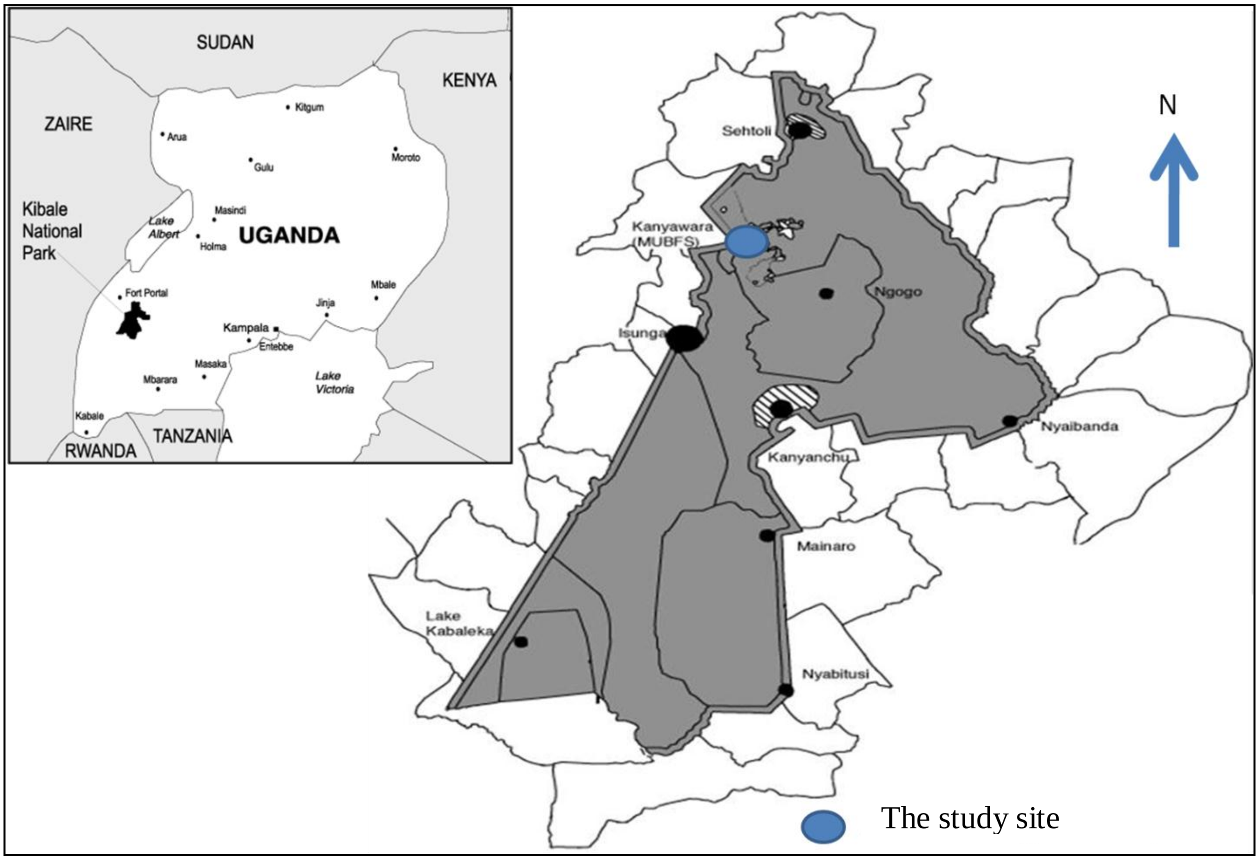

Figure 1: Map of Kibale National Park

3.2.2 Climate

Fossil leaves described by Kingston (1967) indicate that climatic conditions and forest composition have remained essentially unchanged for the past 1000 -10000 years. Similar much of East Africa, rainfall is bimodal in distribution, occurring in two distinct rainy seasons: March-May and August-November, possibly due to low land deforestation (Fleming, 1986). Mean annual rainfall increased from 1,622 mm during 1977-1991; (Struhsaker, 1997) to 1,700 mm during 1990-1996 (Chapman & Chapman un publ.data).The effects of increased rainfall in KNP have not been studied, but it may be significant, because compared to more low- lying forests, the relatively high altitude of Kyanyawara around KNP, results in a relatively low evapo-transpiration rate; meaning more moisture is available for plant growth (Langdale-Brown *et al.*, 1964). Kyanyawara shows little seasonal variations in temperature. Mean daily maximum temperatures range from 21-25 ^{o}C with a mean daily temperatures of 23.7 ^{o}C and mean daily low temperatures range_ between 14-17 ^{o}C with a mean daily minimum temperature of 15.5^{o}C (1990-1996; Chapman & Chapman, un publ.data). The dry seasons are in the month of December to February and June to August, but the latter is hotter than the former (Kingston, 1967).

3.2.3 Vegetation in Kibale

The vegetation of the National Park ranges from grasslands and thickets to forest, forming a complex and irregular mosaic of vegetation (Wing and Buss, 1970). Only 60% of the National Park is dominated by trees, the remaining 40% is composed of grasslands, woodlands, thickets, colonizing forest, papyrus swamps and plantations of exotic trees (Wing and Buss, 1970). Classification of the high forest in KNP ranges from moist evergreen forest (but closely related to moist montane forest) to low land tropical (having affinities to both montane rain forest and mixed tropical deciduous forest) (Langdale *et al.*, 1964; Kingston, 1967; Skorupa, 1988). Though most trees rarely reach heights above 40m, Oates (1974) describes the canopy height of the forest in the northern sector of the KNP, as a stratified, discontinuous upper canopy at a height of 25-50m. While swamp vegetation occurs in many valley areas, comprising mainly *Veronina* and *Acanthus* spp and sometimes solely *Cyperus papyrus*. Hill top ridges in KNP are often grassy with *Pennisetum purpureum, Imperata cylindrica,* and *Cymbopogon afronardus* species dominating.

Langdale and Harrop (1962) suggest that Kibale grass hill tops are artifacts of past forest clearance and cultivation by humans. Others however speculate that grassy hilltops result from poor soil conditions caused by the erosion of volcanic deposits into valley bottoms, after which fire perpetuates and maintains grassy conditions (Mahaney *et al.,* 1997). The northern sector of the forest has been classified as Parinari forest, because the upper canopy is dominated by the large conspicuous emergent *Parinari excelsa* trees. Co-dominants in this area include *Carapa grandifolia*, *Aningeria altissima, Newtonia buchananii, Olea welwitschii*, *Celtis africana, Strombosia scheffleri* and *Mimusops bagshawei.* As one moves to the south of KNP, these species become less common and *Pterygota mildbreadii*, and *Chrysophyllum albidum* become obvious elements of the forest (Kingston 1967; Struhsaker 1975). Close to the southern end of the reserve, the forest is dominated by *Cynometra alexandrii.* An estimated 229 tree species are found in the Kibale National Park, some of which are important timber species such as *Cordia millenii*, *Entandrophragma angolense* (naturally rare) and *Lovoa swynnertonii* listed as endangered species. Non timber tree species of economic importance include wild robusta coffee (*Coffea canephora*)

3.2.4 Soils, Geology and Drainage

Nutrient rich sandy loams and sandy clay loams cover 90% of the park. Such soils are concentrated in the northern part of the park and in the valleys of the Mpanga and Dura rivers and their tributary streams (Oates 1974). The Kyanyawara area of the forest reserve exhibits predominantly red, well drained soils of the ferrallitic group, classified as a dark gray to red sandy loams or sandy clays underlain by strongly folded and metamorphosed sedimentary rocks of Precambrian age (Lockwood Consultants Ltd, 1973, as cited in Mc key *et al*, 1978)

3.2.5 Logging history of Kibale National Park

Kibale Forest received National Park status in 1993. Prior to 1993, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing a sustained production of hardwood timber (Osmaston, 1959). The felling cycle of 70 years was initiated, and it was recommended that logging should open the canopy by approximately 50% through the harvest of trees over 1.52 m in diameter at breast height (Kingston, 1967). This logging led to varying degrees of disturbance among sites.

The area around Makerere University Biological Field Station (MUBFS) is called Kanyawara; named after the nearby village. Foresters have classified Kanyawara as a Parinari forest, distinguished on photo aspect maps by the large spreading crowns of *Parinari excelsa*; a valuable timber tree (Kingston, 1967; Skorupa, 1988). The presence of *P. excelsa* and the subdominants found near Kanyawara (*Aningeria altissima, Olea welwitschii, Newtonia buchananii*, and *Chrysophyllum gorungosanum)* are thought to indicate a climax forest between 1370 m and 1525 m elevation above sea level (Osmaston, 1959).

The forest has 3 forestry compartments just the area around kanyawara that have been disturbed in different fashions. The K-15 forestry compartment at Kanyawara is a 347 ha section of forest that experienced high intensity selective felling from September 1968 through April 1969. Total harvest averaged 21 m^3/ha or approximately 7.4 stems/ha

(Skorupa, 1988; Struhsaker, 1997); however, incidental damage was much higher. It is estimated that approximately 50% of all trees in this compartment were destroyed by logging and incidental damage (Skorupa, 1988; Chapman and Chapman, 1997). A total of 18 tree species were harvested, with nine species contributing more than 95% of the harvest volume (Kasenene, 1987; Skorupa, 1988).

Compartment K-14, a 405 ha forest block, experienced low intensity selective felling from May through December 1969 (averaging 14 m3/ha or 5.1 stems/ha). Twenty-three tree species were harvested, with nine species accounting for 94% of harvest volume. Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa, 1988; Struhsaker, 1997). Harvest was not evenly distributed in this forestry compartment (Struhsaker, 1997; Chapman and Chapman, 1997). As a result, this compartment was divided into two areas: a moderately logged area (Mikana) and a lightly logged area, where stump and gap enumeration suggests only a few selected trees were removed (Kasenene, 1987)

Compartment 30 covers 300 ha of mature forest and has been classified as parinari forest (Osmatson, 1959) determined by the presence of *parinari excels Sab. (Chrysobalanaceae) and subdominants (Aningeria altissima)*. Based on the stump counts, two to three trees per km^2 were felled from the area pior 1970 but this had little impact on the compartment as whole (Skorupa, 1988). Within K30, there are valleys and hilltops that cause elevation changes of 150 to 200 metres (Chapman and Chapman, 1997).

3.3 Methods

3.3.1 Selection of study areas

The non random selection of gaps was done because experimentally there was a need to Choose gaps of different sizes available. A transect walk was done to purposively select the gaps. Twenty four gaps whose sizes vary from 112 m^2 to1493 m^2 and 40 years old were selected in compartments 14 and 30 . Some of the gaps were created as a result of natural tree fall while others were a result of human activities such as selective logging done about 40 years ago.

3.3.2 Field data collection

3.3.2.1 Measurement of gap size

In measuring the size of gaps, the gap edges were considered as woody vegetation at the height of 2 m tall (Browkaw, 1982). Distances from the estimated centre of the gap to the edges were measured in eight compass directions (0, 45, 90, 180,135, 225, 270, and 315 degrees) and a sketch map of the gap was drawn. The compass points on the edge of the gap were joined on the map and eight triangles were formed. The areas of the triangles were computed to obtain gap sizes (Jans *et al.,* 1993).

3.3.2.2 Selection of sample plot design

Four plots of 50 x 50 cm were randomly established in every gap (i.e. 4 replicates per gap). In each plot, ten *N. macrocalyx* seeds collected from old *N. macrocalyx* trees with in the same Kibale National Park were sown. The experiment was establishment in the month of October 2006 during the rain season to ensure germination of seeds. In order to maintain uniform spacing between sown seeds in every plot in a gap, two parallel lines separated by 10 cm were established in each plot. Five *N.* macrocalyx seeds were sown singly along each line at a spacing 5cm.

3.3.2.3 Measurement of canopy openness

The amount of light passing in forest canopy and reaching the ground in every selected gap was measured using a spherical densitometer (Lemmon, 1956). In taking canopy openness measurements, the observer stood at one point in the middle of the plot and held the densiometer at the elbow height from the ground with its screen facing upwards. For each plot, measurements were taken in four compass directions (North, East, South and West) in percentages and then averaged. Light data collection was taken for 14 days throughout the experiment.

3.3.2.4 Measurement of seedling growth

The following growth variables were determined monthly on every seedling per plot, starting at one month after sowing and was done throughout the experiment for six months

- Seedling height (cm)
- Leaf area (cm^2)
- Number of leaves
- Number of new apical meristem leaves developed per month

A meter rule was used to measure the height of seedlings. This was done by placing the meter rule vertically from the ground to the apical meristem of the seedling. The midrib of each leaf was measured to determine its leaf area. Leaf number per seedling was determined by counting the total number of leaves on each seedling. During every assessment, all leaves were marked with plastic tags in order to facilitate identification of newly emerged leaves in subsequent assessments.

3.3.2.5 Seedling survival

Seedling survival was determined by recording the number of seedlings that survived for the whole period of the experiment (six months). At the end of six months, seedlings show the capacity to continue growing, show their potential survival and the extent of herbivory. Counting the number of seedlings that survived was done in all plots within a gap and recording the percentage of seedlings surviving in every gap.

3.3.2.6 Measurement of insect herbivory

Measurement of insect herbivory started two weeks after germination when leaves had established well and there was the need to measure herbivory at that early stage when the leaves are very young and more prone to insect herbivores. The level of seedling herbivory was determined weekly by measuring leaf area missing and the midrib length (from apex to the petiole where the leaf begins). For every leaf, the area missing was determined by placing the leaves on a graph paper with the scale of 1x1cm photocopied on plastic transparences. The leaf area missing was determined by counting the number of squares covered by defoliated patches on the leaf. In most cases, the leaf margins were intact, although the lamina may be heavily damaged by larval feeding. In some cases, where the leaf margins were partly damaged beyond recognition, the other half of the same leaf was used to estimate the edge.

An earlier study of 159 *N .macrocalyx* leaves from KNP (Roininen, un published data) found a highly significant relationship between leaf area (y) and midrib length (x)

(R^2 = 0.99, $P<0.001$) and established a model for establishing leaf area of *N. macrocalyx* as: $Y = 5.03x + 0.83x^2$. This regression model was used in the present study to determine total leaf area.

3.3.3 Data Analysis

The data were entered checked and organised in Excel computer program and organized for analysis in SPSS statistical package. The following statistical procedures were used;

Simple linear regression in SPSS statistical programme was used to determine a relationship between canopy openness and gap size. Similary, linear regression was used to determine the relationship between growth of *N .macrocalyx* seedlings and gap size (objective 1). The measured dependent variables for growth included; mean seedling height per gap, leaf numbers per seedling in every gap , total leaf area on seedlings per gap and number of new apical leaf growth on every seedling per gap and the independent variable was gap size.

ANOVA was used to test for variations in insect herbivory on the leaves of *N. macrocalyx* seedlings between different sized gaps (objective 2) that were categorized as small, medium and large gaps. Gaps with sizes of ≤ 500m^2 were categorized as small N=12, between 500 but ≤ 1000m^2 as medium gaps N=5 and

>1000_m^2 as large gaps N=5. Herbivory between gaps was determined by comparing the mean percentage leaf area missing between different categories of gaps. The data were arcsine square root transformed to ensure homogeneity of variances.

The variations in survival of *N. macrocalyx* seedlings between gaps of different sizes (objective 3), was also determined by ANOVA. This was done by comparing the differences in percentage seedling survival between three gap categories.

CHAPTER FOUR

4. RESULTS

4.1 Relationship between gap size and canopy openness

The linear regression showed a significant positive relationship between gap size and canopy openness ($R^2=0.51$ $P<0.05$) *(Figure2)*

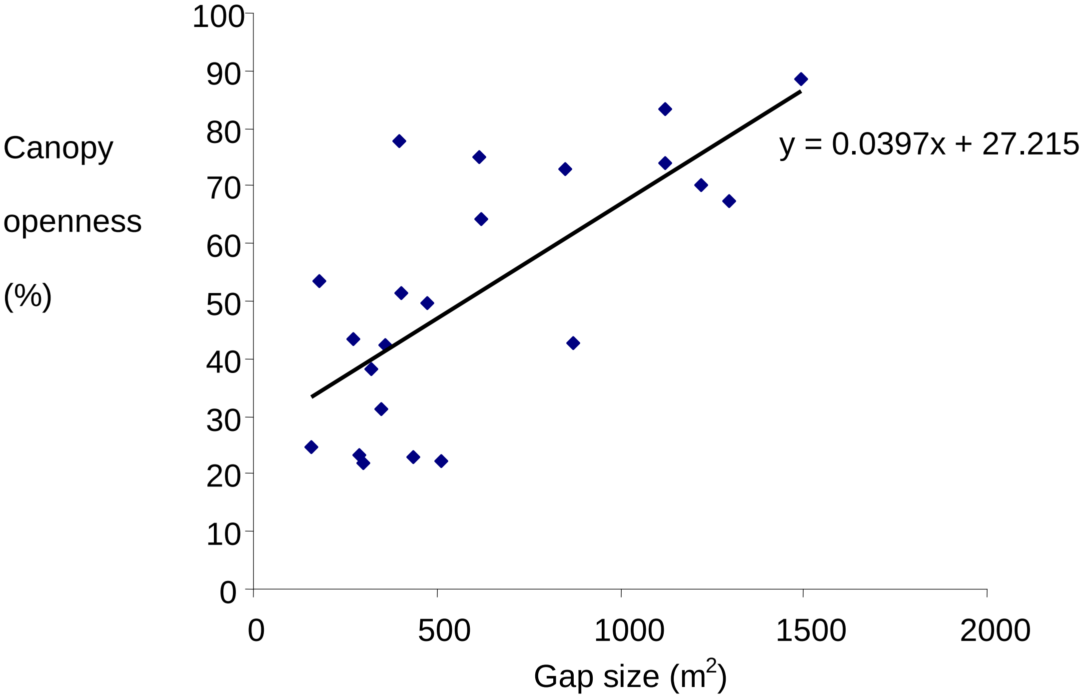

Figure2. Relationship between gap size and canopy openness in Kibale National Park, Uganda.

4.2 Relationship between gap size and growth of *Neoboutonia macrocalyx* seedlings

There was a significant positive relationship between mean seedling height measured after six months and gap size (R^2 $=0.55$, $P<0.05$) *(Figure3)*.

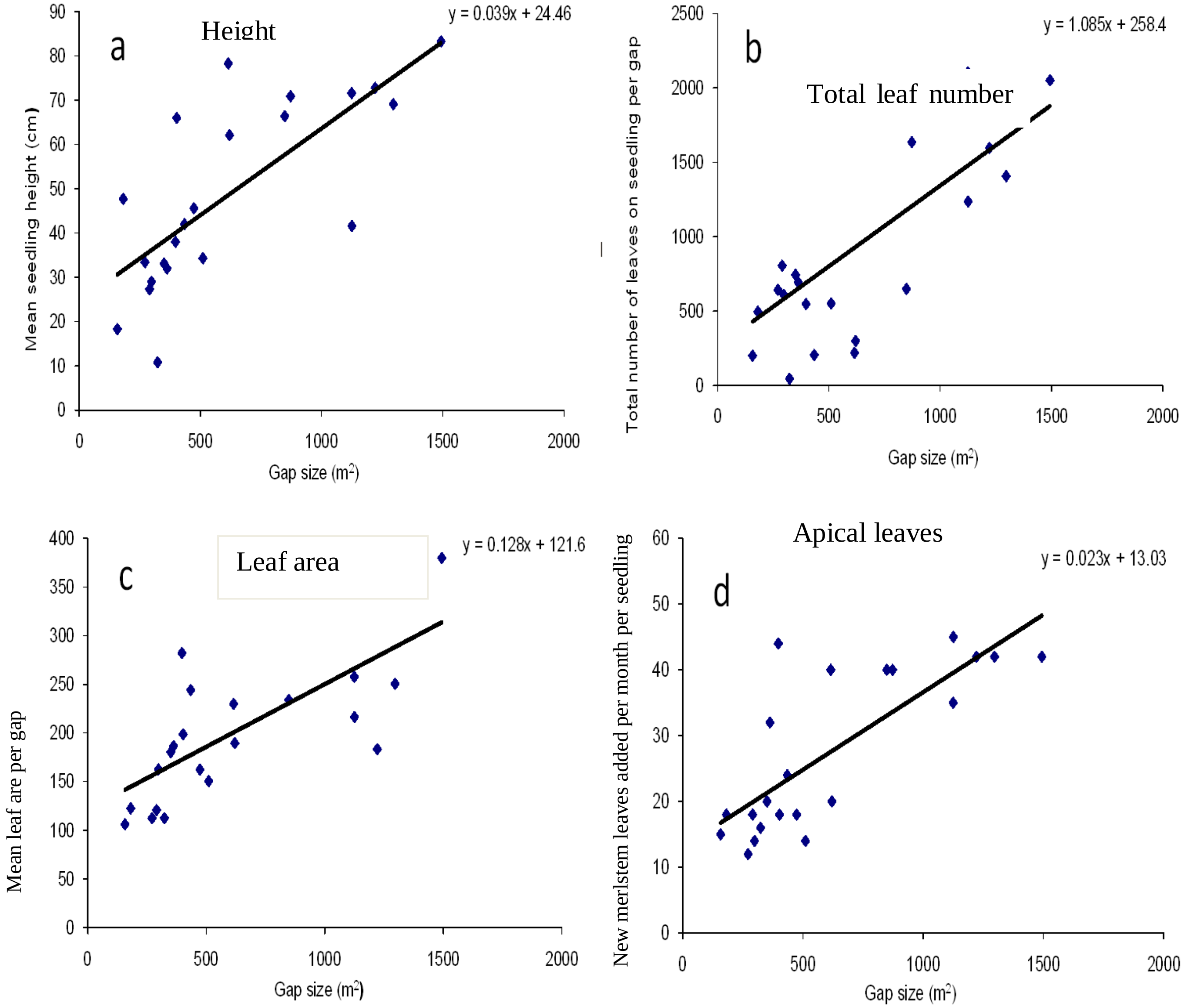

Figure3. Relationships between gap size and *N. macrocalyx* seedling height, total leaf numbers, leaf area and number of new apical leaves per month in Kibale National Park.

Similarly, a linear regression analysis showed that there was a positive and significant relationship between gap size and total number of leaves on seedlings in gap (Figure3b) ($R^2=0.42$, $P<0.05$).

The linear regression analysis showed a positive and significant linear relationship between mean total leaf area per gap and gap size *(*$R^2 = 0.48$, $P < 0.05$*) (*Figure 3c*)*

There was a positively and highly significant relationship between total number of new apical leaves added per unit time on every seedling and gap size (Figure 3d) ($R^2 = 0.59$, $P<0.05$). This means that the number of new apical meristem leaves per month on every seedlings increased with increasing gap size.

4.3 Insect herbivory on *Neoboutonia macrocalyx* seedlings in different gap sizes.

There was a significant difference in herbivory on *Neoboutonia macrocalyx* seedlings between different gap categories *(*$F_{2, 19} = 20.5$, $P<0.05$*)*. Mean percentage leaf area missing was significantly higher *(*$P<0.05$*)* in smaller gaps compared to medium and large gaps *(*Figure 4*)*. However, the mean percentage leaf areas missing in medium and large gaps were not significantly different *(*$P>0.05$, Figure 4*)*.

Gaps with sizes of ≤ 500 m^2 were categorized as small N=12, between 500 but ≤ 1000 m^2 as medium gaps N=5 and >1000 m^2 as large gaps N=5).

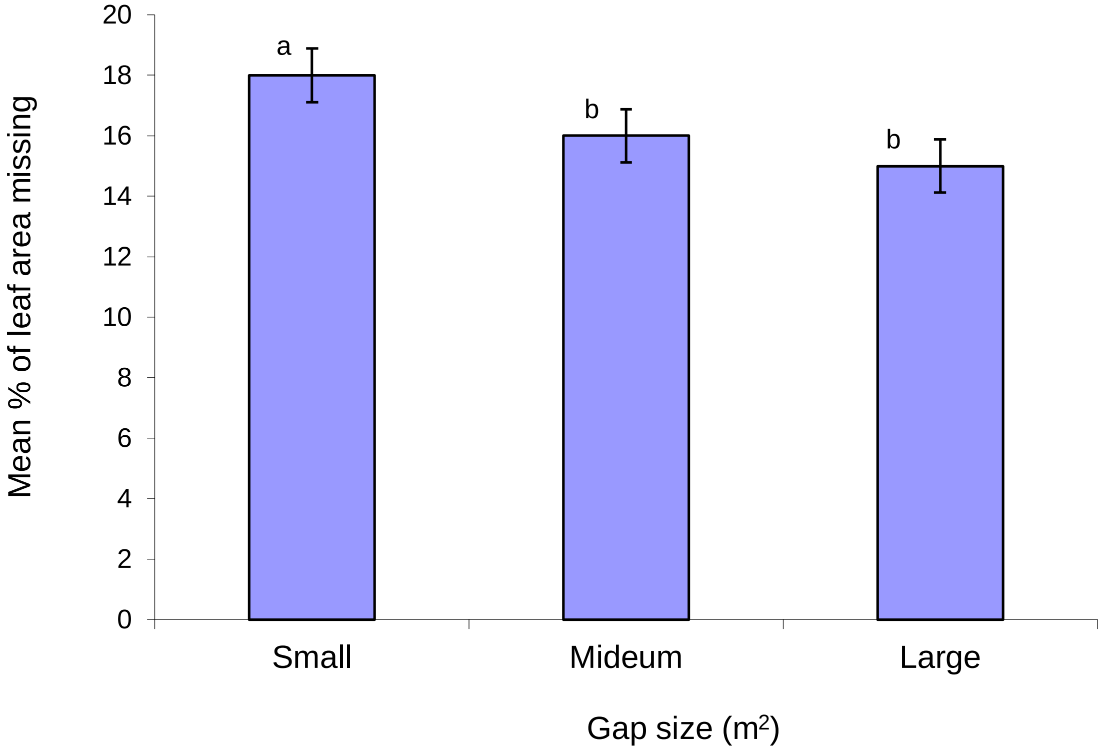

Figure 4. Mean percentage of leaf area missing per leaf of *Neoboutonia macrocalyx* seedlings in different gap sizes. Bars with different letters show significance difference while those with same letter indicate non significant difference.

4.4 Variations in seedling survival between gaps of different size

There were significant differences in mean percentage seedling survival between small, medium and large gaps ($F_{2, 19} = 3.87, P<0.05$). The highest seedling survival (72%) was observed in large gaps and this was significantly higher than the seedling survival observed in medium (56%) and small (51%) gaps (Figure 5). There was no significant difference in seedling survival in small and medium gaps. However, there was significant difference observed in percentage survival of seedlings growing in medium and large gaps. Similarly there was significant difference between large and small gaps (*P<0.05*, Figure5*)*.

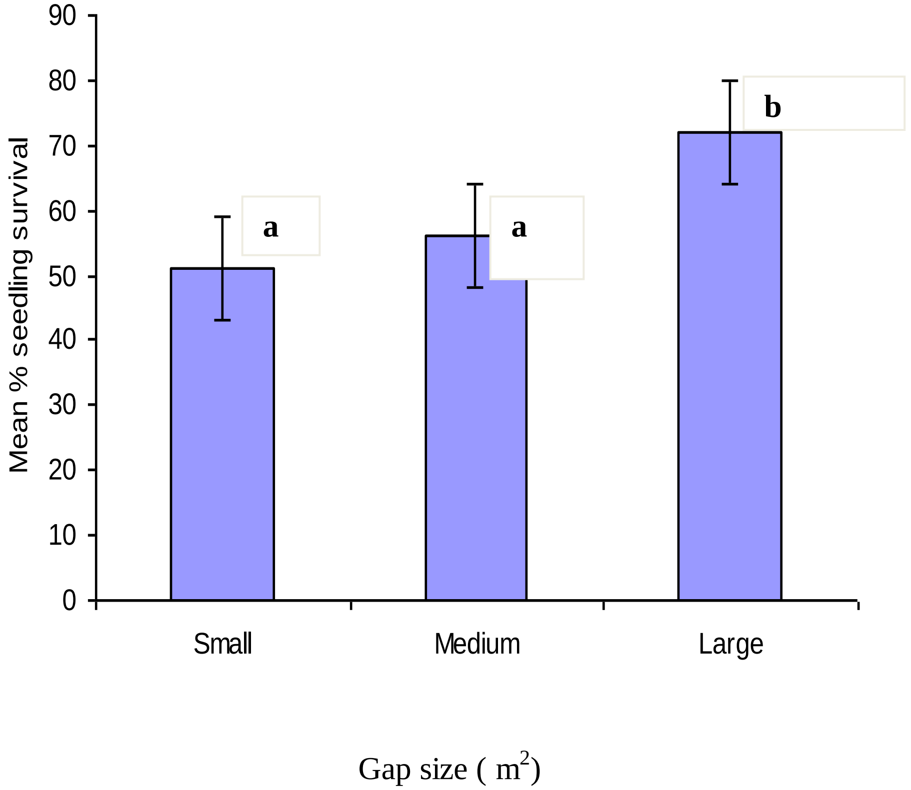

Figure 5. Mean percentage survival of *Neoboutonia macrocalyx* seedlings in different gapsizes in Kibale National Park. Bars with different letters show significance difference while those with same letters indicate non significance *($P<0.05$*)

Plate.1. Measuring growth of *Neoboutonia macrocalyx* seedlings in forest gaps of Kibale National Park.

Plate.2. *Neoboutonia macrocalyx* seedlings growing in a forest gap invaded by herbaceous vegetation in Kibale National Park.

CHAPTER FIVE

5. DISCUSION

5.1 Relationship between gap size and canopy openness

There was a strong relationship between gap size and canopy openness (Figure 2).This means that large gaps received more light. Light regimes in gaps depend more on gap size than the orientation and shape of the gap, local topography and height of the surrounding canopy trees (Dens low's 1987). A large area gap may receive less light than a medium area gap if the surrounding canopy is taller. Therefore, the total light availability is a better estimate of the effective gap area (Whitmore, 1996).

5.2 Seedling growth in gaps of varying sizes

The results showed that there was a higher height gain by the seedlings in large or more open gaps than small size gaps(Figure 3a). This is probably due to increased light reaching the forest floor and this increases soil temperatures that speed up soil microbial activities and soil decomposition releasing nutrients available for plant growth. There is also increase in light levels that enhances photosynthetic processes and hence result in vigorous growth of *N. macrocalyx* seedlings. The larger forest gaps have significantly more light, soil moisture and higher temperatures (Denslow *et al.*, 1998).

Additionally, litter from fallen trees contributes to an initial influx of nitrogen and phosphorus (Vitousek and Denslow, 1986). These changes lead to higher productivity in gaps, which increases seedling establishments, survival and growth (Denslow, 1987).

Under field conditions, severe competition for light with neighbouring plants also usually occurs, particularly in high-light environments such as canopy gaps. In such high-light environments, earlier vertical growth is advantageous for seedling establishment (Ross and Harper, 1972; Seiwa, 2000) because the light conditions experienced by the seedlings are dramatically improved with increasing seedling height (Givnish, 1982). When a big gap is opened, more pioneer species regenerate quickly (Whitmore, 1975). Such pioneer species can compete among themselves and eventually trigger the growth in height of *Neoboutonia macrocalyx* seedlings so as to compete favourably in more open gaps. This is because, increase in canopy opening promotes dominance of lianas and this could affect the competitive ability of tree species (Schnitzer *et al,* 2000; Schnitzer and Bongers 2000).
The average seedling height at the end of study in both gaps (small, medium and large gaps was 55.6cm

Similarly, the results showed that seedlings growing in large gaps or more open gaps had more of leaves than those growing in less open gaps (Figure 3b). Apart from the increase in light, significant increases in the availability of nutrients and water in forest gaps have been reported to increase number of seedlings (Veenendaal *et al.,* 1996; Denslow *et al.,* 1998; Ostertag, 1998)

Soil moisture contents can be higher in gaps due to the combined effects of: (a) an increased input of rain through a higher through fall (Jetten 1994) and water drip from gap bordering tree crowns (Geiger, 1965), (b) a slower depletion of soil water reserves through reduced root density (Ostertag, 1998; Sanford, 1990), and (c) a reduced leaf area index (Jetten, 1994).

These conditions in more open gaps lead to availability of nutrients such as nitrogen to the seedlings and establish their shoot structures easily and have the capacity to replace the lost ones through herbivory or any other physical injuries made on leaves. This is in line with the findings of Coley *et al.*,(1985) who argued that slower growing species with longer lived leaves have an increased investment in anti- herbivore defences, while faster growing species rely on their ability to replace rapidly tissue removed by herbivores to maintain a high photosynthetic area, and consequently a high growth rate. *Neoboutonia macrocalyx* showed this characteristic of quick growth and replaced quickly the damaged leaves by insect herbivores in large gaps. At low irradiance, fast growing species are unable to replace tissue lost to herbivores because high respiration rates result in net photosynthetic rates that are not sufficient to maintain a positive carbon balance (Loach, 1967; Boardman, 1977; Coley *et al.*, 1985; Kitajima, 1994).

However, this contradicts with studies by Brouwer (1996) and Meinzer *et al.,* (1995), who found that, soil moisture contents can also be lower in gaps due to higher radiation loads, which lead to desiccation of the top soil through evaporation and higher transpiration rates of gap plants or gap bordering trees which have their roots extended into the gap.

Seedlings growing in more open gaps had leaves with large total leaf area (figure 3c). This means that a high leaf number indicates that plants were well established, and implies as well a large photo synthetically active leaf area.

The total number of new apical leaf meristem increased with increase in gap size (Figure 3d). This is probably be due to higher light intensity in large gaps that enhances photosynthesis. This could probably be due to the characteristics behaviour of some quick growing tree species in open areas that lose their leaves and have the capacity to quickly replace them (Coley *et al.*, 1985). This may lead to continuous development of new apical leaves that replace the lost ones. Canopy openness in large gaps often triggers leaf production of rain forest plants in gaps (Bongers and Popma, 1990). This is what was observed in *N. macrocalyx* seedlings that were growing in large gaps

5.3 Seedling herbivory and gap size

Seedling herbivory was highest in small gaps and lowest in large gaps (Figure 4). This indicates that seedlings in small gaps were more susceptible to herbivore attack than those in large gaps. Differences in plant chemistry, local microclimate or predation rates on leaf herbivores have been suggested as possible causes for the decrease in herbivory in disturbed forest areas. Earlier studies showed that lepidopteran larvae respond negatively to disturbance (Arnold and Asquith, 2002). This therefore led to the prediction that there is a lower density of lepidopteran larvae in large gaps compared to small gaps hence the reduced herbivory in large gaps. Factors that influence insect abundance include density dependent and density independent factors. Density dependent factors are common regulators of insect abundance, accounting for 80% (Woiwod and Hanski, 1992, Brook and Bradshaw, 2006). One of the most important factors influencing herbivore abundance is their food resources, *i.e.* leaves, flowers and fruits. The existence of these food resources lead to changes in the abundance of resource specialists (Basset 1999, 1991, Van Schaik *et al.,* 1993, Novotny and Basset, 1998). The quantity of young leaves correlates with the number of leaf chewing insect species (Basset, 1996). This is due to two factors: First, increased amount of leaves means more resources in terms of food and oviposition sites.

Secondly, palatable young leaves with high water content offer a high quality food source for both specialist and generalist species. Predation is another density dependent factor. Ants have been identified as one of the key predators in tropical forests (Novotny *et al*., 1999, Floren *et al.,* 2002, Loiselle and Farji- Brener, 2002). Also other animals such as birds, lizards and bats exert predation pressure to herbivorous insects (Gradwohl and Greenberg, 1982; Dial and Roughdarden, 1995; Van Bael and Brawn, 2005; Kalka *et al*., 2008). This is possible because in large gaps there is quick growth of seedlings and attain greater heights hence exposing herbivorous insects on the leaves to be picked by their natural enemies

Density independent factors are usually weather factors of which temperature is one of the most important (Price, 1997). Most insects are poikilothermic and small temperature changes can influence growth and reproductive activity of insects (Wolda, 1988). Water (rainfall, humidity, moisture content) availability is another important regulatory factor in tropical forests (Didham and Springate, 2003). Because of their small bodies and high metabolic rates, insects are very sensitive to desiccation (Wigglesworth, 1972). Desiccation is especially a problem in the upper canopy where daily fluctuations in temperature and moisture deficit are the most extreme (Parker, 1995).

The canopy typically has a hotter, drier and windier microclimate as well, which may severely affect many insect herbivores (Lowman, 1985). Low temperatures that are available in small gaps as a result of less open forest canopy provide a favourable environment for some of the lepidopteran larvae (insect herbivores). These are soft bodied and therefore more susceptible to desiccation due to heat resulting from the high temperatures in large gaps. The low temperatures in less open gaps probably increase the abundance of insect herbivores, hence leading to more seedling damage as recorded in this study.

Insect herbivores usually depend on the availability of young palatable leaves than mature leaves in rain forests (Novotny *et al,* 2003). However, fast growing seedlings in large gaps possibly exhibit vigour and therefore less vulnerable to herbivory and also there is a possibility that herbivores could be opportunists attacking stressed plants. Fast growth of seedlings in large gaps characterized by greater heights, expose insect herbivores to their natural enemies.. For example, canopy birds, lizards and bats may feed on caterpillars that eat the leaves of trees and hence exerting predation pressure to herbivorous insects (Gradwohl and Greenberg, 1982; Dial and Roughdarden, 1995; Van Bael and Brawn, 2005; Kalka *et al*, 2008). A study by Van Bael and Brawn (2005) revealed that predation by birds decreased arthropod densities in drier forest sites but not in the wetter sites with lower leaf production. Further, Richards and Coley (2007) showed significantly higher predation rates on insect herbivores in gaps than understorey that had lower food availability for herbivores. This is therefore in line with the results of this study that showed that herbivory decreased in big sized gaps possibly due to reduced herbivore communities as the result of the above mentioned factors.

However, the mean percentages in seedling herbivory in the medium and large gaps were not significantly different implying that the conditions which determine the levels of seedling damage by herbivores in medium and large gaps were similar.

5.4 Variations in seedling survival in gaps of different sizes

Seedling survival was highest in large gaps, followed by medium gaps and lowest in small gaps (Figure 5). This means that seedling survival increased with increasing gap size. This was probably caused by more light reaching the forest floor in large gaps which favours the survival of plants especially light demanders (pioneer species) such as *Neoboutonia macrocalyx*. Leaves of tropical pioneer tree typically photosynthesize and respire at higher rates than later successional canopy or understory species (Bazzaz and Pickett, 1980). Pioneer trees, for example, are typically characterized by light induced seed germination, high tissue nitrogen and phosphorous concentration, low wood density, early reproductive maturation and high fecundity, as well as high rates of plasticities of photosynthesis and respiration (Swaine and Whitmore,1988; Raaimakers *et al.,* 1995; Reich *et al.,* 1995; Ackerly, 1996). Combination of some or all of these traits may enable a species to successfully colonize open microsites, but at the same time may limit their ability to persist in low light environment.

Survival increased in big gaps possibly due to availability of soil nutrients such as nitrogen which favours continuous growth of seedlings and ability to replace damaged leaves (King, 1994). In big and more open canopy gaps, there is rapid growth of herbaceous vegetation which in most cases competes and over top the regenerating trees. However, *Neoboutonia macrocalyx* was able to survive in big gaps due to its height advantage and could not easily be over topped by herbaceous weeds in high light environment found in big gaps (Plate.2). In less open canopy gaps or small gaps, there was less light available for maximum photosynthesis in seedlings. This is especially caused by the shadow created by the big branches of the neighbouring trees at the edge of the gap. The seedlings become short and stunted with few pale light green leaves (Personal observation).Forest disturbance that leads to formation of forest gaps affect the herbivore communities negatively (Arnold and Asquith, 2002). Therefore, higher seedling survival in large gaps is possibly due to decreased rates of herbivory in large gaps and this ensures that seedling growth is not retarded while enhancing high seedling survival.

5.5 Implications for conservation

The majority of logged tropical forests are left to naturally regenerate following logging as this is the most economically viable option (Johns, 2004). From the previous studies, natural regeneration was good for Kibale but with some hinderances such as trampling and feeding by elephants (Lawes and Chapman, 2005) and denser herbaceous vegetation that grow after logging (Nummelin, 1992). However, *N. macrocalyx* at the age of five months was able to compete with the herbaceous vegetation but in some gaps some seedlings were trampled over by elephants. The results of this study, large gaps (of > 1000 m^2) showed good, growth and survival of colonizing species such as *Neoboutonia macrocalyx*. Gaps of size less than 1000 m^2 , regeneration was not good and colonizing trees failed to establish and fully colonize the gaps in case of this study.

CHAPTER SIX

6. CONCLUSION AND RECOMMENDATIONS

- Growth of *Neoboutonia macrocalyx* seedlings increased with increase in gap size.
- Herbivory on the leaves of *Neoboutonia macrocalyx* seedlings was lower in large gaps than in small sized gaps.
- Survival of *Neoboutonia macrocalyx* seedlings was highest in large gaps, followed by medium gaps and was lowest in small gaps.

Therefore, from this study, the following are recommended.

- ➢ *Neoboutonia macrocalyx* species should be planted in large gaps since it has proved to be good colonizing tree specie in large forest gaps to restore the status of large and persistent gaps.
- ➢ There is need for future research to establish tree species that can survive well in gaps with limited light insolation and also species that have the capacity to recover quickly from damages and other injuries caused by mammals , pathogens and other damaging agents.
- ➢ There is need for future studies on the effects of herbaceous vegetation on tree regeneration in forest gaps since these colonize gaps where natural regeneration occurs.

REFERENCES

Ackerly, D.D (1996). Canopy structure and dynamics: integration of growth processes in tropical pioneer trees, pages 619-658 in S.S. Mulky, R.L Chazdon and A.P Smith. Editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York, U.S.A.

Arnold, A.E and Asquith, N.M (2002).Herbivory in a fragmented tropical forest: Patterns from islands at Lago Gatun, Panama. *Biodiv Cons* 11: 1663-466.

Arriaga, L (1979). Gap phase regeneration in tropical montane cloud forest of north- eastern Mexico. *Journal of tropical Ecology,* 16:535-562.

Attiwell, P.M (1994). The disturbance of forest ecosystem: the ecological basis for conservation management. *Forest ecology and management*. 63: 247-300

Basset. Y. (1991). Leaf production of an overstorey rain forest tree and its effects on the temporal distribution of associated insect herbivores. *Oecologia* 88:211-219.

Bazzaz, F.A. (1979). The physiological ecology of plant succession. *Annual Review of E cology and systematic*,10, 351-271.

Bazzaz, F.A and Pickett, S.T.A (1980). The physiological of ecology of tropical succession: a comparative review. *Annual review of Ecology and systems*. 11: 287-310.

Bigger, M (1981). Observation on the insect fauna of shaded and un shaded Amelorrado cocoa. Bulletin of Entomological Research 71:107-119.

Bongers, F and Popma, J (1990). Leaf dynamics of seedlings of rain forest species in relation to canopy gaps. *Oecologia, vol*. 82; page 122-127

Bormann, F.H and Likens, G.E (1979).*Pattern and Process in a forest Ecosystem* Springer-Verlag, New York inc. 253 pp

.**Brokaw, N.V.L (1982).** Tree falls: frequence, timing and consequences. Pages 101-108 in E.G. Leigh, A.S. Rand and D.M.Windsor, editors. *The ecology of tropical forest*: Seasonal rhythms and long term changes. Smithsonian institution Press, Washington, D.C, U.S.A.

Brokaw, N.V.L (1985[a]). Gap-phase regeneration in a tropical forest. *Ecology.* 66: 682-687.

Brokaw, N.V.L (1985). Tree falls, regrowth and community structure in tropical forests. In: The Ecology of Natural Disturbance and Patch Dynamics (Eds S. T. A. Pickett & P. S. White).

Brown, N (1993). The implications of climate and gap microclimate for seedling growth

Bryant, J.P, F.S.Chipin, 111 and D.R.Klein (1983). Carbon /nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357-368.

Canham, C.D, Berkowitz, A.R, Kelly, V.R, Lovett, G.M, Ollinger, S.V, Schurr, J. (1966). Biomass allocation and multiple resource limitation in tree seedlings. *Can J For Res* 26: 1521-1530

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

Chapman, C.A. and Chapman, L.J. 1997. Forest regeneration in logged and un logged forests of Kibale National Park, Uganda. *Biotropica* 29:353-257.

Chapman, C.A., and Chapman, Chapman, L.J., Kaufman, L. and Zanne, A.E. 1999. Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. *African Journal of Ecology*.37: 81-91.

Chazdon, R.L (1988). Sunflecks and their importance to forest understorey plants. *Adv Ecol Res* 18: 1-63

Coley, P. D (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209–233

Coley, P.D and T.M. Aide (1991). A comparison of herbivory and plant defenses in temperate and tropical broad leafed forests. In P.W. Prices, T.M.Lewinsohn, W.W.Benson and G.W.Fernandes, editors. *Herbivory: tropical and temperate perspectives*. John Wiley and Sons, New York, USA, pp. 25- 49.

Coley, P.D., J. P .Bryant, and F.S.Chapin, 111 (1985). Resource availability and plant anti-herbivore defence.*Science* 230:895-899.

Connell, J.H (1979).Tropical rain forests and coral reefs as open non equilibrium systems. In *population dynamics,* ed. RM Anderson, B.D Turner, L.R Taylor, pp 141-61. Oxford / London: Black well Sci.

Crawley, M. J (1983). Herbivory: the dynamics of animal-plant interactions. Blackwell Scientific Publications, Oxford, UK

.**Dalling, J.W and Hubbell, S.P. (2002).** Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecolog*y 90:557-568

Denslow, J.S. (1980). Gap partitioning among tropical rain forest trees. *Biotropica*, 12 (Suppl.), 47- 55

Denslow, J. S. and Hartshorn, G. S (1994). Tree fall gap environments and forest dynamic processes pp 120-127 in McDade, L.A; Bawa, K.S; Hespenheide, H.A and Hartshorn, G.S. (eds) La Selva: *Ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, U.S.A.

Denslow, J.S. (1987). Tropical rain forest gaps and tree species diversity. Ann. Rev. Ecol.

Denslow, J.S., Ellison, A.M and Sanford, R.E (1998). Tree fall gap size effects on above and below ground processes in tropical wet forest. *Journal of ecology.* 86: 597-609.

Dial R. and Roughgarden, J (1995). Experimental removal of insectivores from rain forest canopy: Direct and indirect effects. Ecology. 76:1821-1834.

Didham, R.K. and Sprigate, N.D (2003). Determinants of temporal variation in community structure. In Basset. Y, Novotny.V, Miller.S.E, Kitching, R.L (eds)

Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge, pp 28-39.

Endler, J.A (1993). The color of light in forests and its implications. *Ecological monographs* 63:1–27.

Engling, W. J (1951). The indigenous trees of the Uganda protectorate. Government

Enright, N. J. , R. M. Bartlett , and C. R. De Freitas (1993). Patterns of species composition, recruitment, and growth within canopy gaps in two New Zealand kauri (*Agathis australis*) forests. N.Z. J. Bot 31:361–373.

Fleming T.H (1986). Secular changes in Costarican rainfall: Correlation with elevation. *Journal of tropical ecology*, 2:87-91.

Givnish, T.J (1982) . On the adaptive significance of leaf height in forest herbs. *American Naturalist* **120:**353–381.

Givinish, T.J (1988). Adaptation to sun and shade, a whole plant perspective. *Australian Journal of Plant Physiology 15:63-92.*

Grodwohl, J. and Greenberg, R (1982). The effect of asingle species of a vian predator on the arthropods of aerial leaf litter. *Ecology* 63:581-583

Grubb, P.J, Lee, W.G, Kollmann, J, Bastow Wilson. J.(1996). Interaction of irradiance and soil nutrient supply on growth of ten European tall- shrub species and *Fagus sylvatica*. J Ecol 84: 827-840

Halle, F, Olderman, R. A.A and Tomlinson, P. B (1979). Tropical Trees and Forests on Architectural Analysis Springer- Verlag, Berlin

Hamilton, A.C (1991). *A field guild to Uganda forest trees*. Makerere University Printery, Kampala.

Hamer, K.C, Hill, J.K, Lace, L.A, Langan, A.M (1997). Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *J Biogeogr* 24:67-75

Howard, P; Davenport, T and Matthews, R (1996). Kibale National Park Biodiversity Report. Forest department, Kampala.

Isabirye-Basuta, G.M (1979). The ecology and biology of small rodents in the Kibale forest, Uganda. Msc. Thesis, Makerere University.

Hubbell, S.P and R.B.Foster (1986). Canopy gaps and the dynamics of aneotropical forest. Pages 77-96 *in* M.J.Crawley, editor. Plant ecology. Blackwell Scientific, Oxford, England.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler B.,Wright S.J and Loode LAO S (1999). Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554-557.

Jans, L., Poorter, L., Van Rompaey, R.SA.R. & Bongers, F (1993). Gaps and forest zones in tropical moist forest in Ivory coast. *Biotropica* 25, 258-269.

Janzen, D.H (1970). Herbivores and the number of tree species in tropical forests. *Am.Naturalist*, 14: 501-528

Janzen, D.H (1971). Escape of juvenile *Dioclea megacarp* (Leguminosae) Vines from predators in a deciduous tropical forest. *AM.* Nat. 105:97-112 Johnns, A.G (2004). Timber production and biodiversity conservation in tropical rain forests. Cambridge University Press, Cambridge.

Kakudidi, E. K (1999). Ethnobotanical study in and around Kibale National Park, western Uganda. PhD thesis, Makerere University, Kampala.

Kalka, M.B, Smith, A.R, and Kalko, E.K.V (2008). Bats limit arthropods and herbivory in a tropical forest. Science 320-71.

King, D.A (1994). Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* 81:948-957.

Kingston B (1967). Working plan for Kibale and Itwara central forest Reserves. Forest Department, Entebbe, Uganda.

Kasenene, J.M (1987). The influence of the mechanized selective logging, felling intensity and gap-size on the regeneration of a moist forest in the Kibale Forest Reserve, Uganda. PhD Dissertation, Michigan state University, East Lansing.

Kasenene, J.M, Roininen, H (1999). Seasonality of insect herbivory on the leaves of *Neoboutonia macrocalyx* in the Kibale National Park, Uganda. Afr J Ecol 37:61-68

Kitajima, K (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling torerance of 13 tropical trees. *Oecologia* 98:419-428.

Kitajima, K (1996). Ecophysiology of tropical tree seedlings.pp 559- 597 in Mulkey, S.S., Chazdon, R.L and Smith, A.P (eds). *Tropical plant ecophysiology*. Chapman and Hall, London.

Kobe, R.K, Pacala, S.W, Silander, J.A, Canham, C.D (1995). Juvenile tree survivorship as a component of shade torerance. *Ecol Appl* 5: 517-532

Lang Brown J.R and Harrop J.F (1962). The ecology and soils of the Kibale grasslands, Uganda. East African Agricultural and Forestry journal, April: 264-272.

Langdale- Brown I, Osmaston H.A and Wilson J.G (1964). The Vegetation of Uganda and its bearing on land-use. The Government printer, Entebbe, Uganda.

L**awes, M. J and Chapman,C.A (2005)**. Does the herb *Acanthus pebescens* and / or elephants suppress tree regeneration in disturbed Afrotropical forest? *Forest Ecology Manag* 221:278-284.

Lemmon, R.E **(1956).** Aspherical Densiometer for estimating forest overstory density *light and light quality from hemispherical photographs.* Tropenbos Document 3,

Lincoln, D.E., and H.A.Mooney (1984). Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. *Oecologia* (Berlin) 64: 173-176.

Loech, K (1967). Shade tolerance in tree seedlings. Leaf photosynthesis and respiration in plants raised under artificial shade. *New Phytol* 66: 607-621

Loisselle, B.A and Farji-Brener, A.G (2002). What's up? An experimental comparison of predation levels between canopy and understory in tropical wet forest. *Biotropica* 34:327-330

Lowman,M.D (1985). Temporal and spatial variability in insect grazing of the canopies of five Australian rain forest tree species. *Aust.J.Ecol.*10:7-24

Maiorana, V.C (1981). Herbivory in the sun and shade. *Biological journal of the Linean society*. 15:151-156.

Martinez- Ramos, M and Alvarez- Buylla, E (1986). Gap dynamics, seed dispersal and tree recruitment *the case of Cecropia obtusifolia* at Los Tuxtlas,Mexico *frugivore and seed dispersal* (Ed by A Estrada and T.H. Fleming), pp 323-346 Dr .w.Junk, Dordrecht

Milton, K (1979). Factors influencing leaf choice by howler monkeys: *a test of some hypotheses of food selection by generalist herbivores*. American Naturalist 114:362-378.

Molleman, F; Kop,A; Brakefield, P.M; DeVries, P.J; Zwaan, B.J (2006). Vertical and temporal patterns of biodiversity of fruit feeding butterflies in a tropical forest in Uganda. *Biodiversity Conservation*. 15:107-121

Novotny, V. Basset.Y. Auga J, Boen, W. Dal.C. Drozd.P, Kasbal .M, Isua. B, Kutil.R, Manumbor.M, Molem.K (1999). Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. *Austral Journal of Ecology* 24:477-483

Novotny, V, Basset Y, Kitching R.L (2003). Herbivore assemblages and their food resources. In Basset Y, Novotny V, Miller S.E, Kitching R.L (eds) *Arthropods of tropical forests*: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge, pp 40-53

Nummelin, M (1992).Invertebrate herbivory in the forest floor vegetationof virgin and managed forest sites in the Kibale Forest, Western Uganda. *African Journal of Ecology*. 30:213-222.

Oates J.F (1974). The ecology and behaviour of the black and white colobus monkey (colobus guereza Ruppell) in East Africa. PhD. Dissertation, University of London.

Obua, J. (1996). Conservation and ecotourism in Kibale National Park. PhD. thesis, University of Wales, Bangor.

Obua, J. (1998). Park resource use and user attitudes towards conservation in Kibale National Park, western Uganda. *Uganda Journal of Agricultural Sciences. 3*: 47-52.

Olderman, R.A.A (19780). Archetecture and energy exchange of dicotyledonous trees in the forest. *Tropical trees as a living systems* (ed by P.B Tomlinson and M.H Zimmerman)pp 535-560 Cambridge University Press, Cambridge.

Osmatson, H.A (1959). Working plan for the Kibale and Itwara central forest reserves Toro district, Western Province, Uganda. First revision. Forest Department, Kampala, Uganda.

Osonkjoya, O. O., Ash, J; Hopkins, M.S; Graham, A.W and Hopkins, M.S (1993). Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *Journal of tropical Ecology*. 9: 1-18.

Ostertag, R. (1998). Belowground effects of canopy gaps in a tropical wet forest. *Ecology* 79:1294-13

Ostlie, K. R., and L. P. Pedigo (1984). Water loss from soybeans after simulated and actual insect defoliation. *Environmental Entomology.* 13: 1675–1680.

Parker, G.G (1995). Structure and microclimate of forest canopies. In lowman, M.D,

Pearson, T.R.H., Burslem, D.F.R.P., Mullins, C.E. & Dalling, J.W. (2003). Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view. *Functional Ecology,* 17, 394- 402.

Pickett, S.T.A and White, P.S (1985).*The Ecology of Natural Disturbance and Patch Dynamics Academic Press, New York*

Plumptre, A.J ; **Davenport,T.R.B**; **Behangana, M; Kityo, R; Eilu**, **R; Ssegawa, P; Ewango,C; Meirte, D; Kahindo C; Herremans,M; Peterhans JK; Pilgrim JD; Wilson, M; Languy, M ; Moyer, D (2007).** The biodiversity of the Albertine Rift. *Biology Conservation.* 134:178-194.

Poore, D (1976). The values of tropical moist forestecosystems and the environmental consequences of their removal. *Unsylva*, 28: 112-113.

Pooter, L (1998). Seedling growth of Bolivian rain forest tree species in relation to light and water availability. PhD thesis, Utrecht University, The Netherlands.

Poorter, L (1999). Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology*. 13: 396-410

Price. P (1997). Insect ecology (3rd ed).John Wiley & Sons , Inc. New York.
Prints, Entebbe.

Putz, F.E (1984). The natural history of lianas on Barro-Colorado island Panama. *Ecology*. 65: 1713-1724.

Raaimakers, D.R.G., A. Boot; P.Dijkstra; S. Pot and T. Pons (1995). Photosynthetic rates in relation to leaf phosphorous content in pioneer versus climax tropical rain forest trees. *Oecologia* . 102: 120- 125

Rausher, M.D (1981). Host plant selection by *Battus philenor* butterflies: the roles of predation, nutrition and plant chemistry. *Ecological monographs.* 5:1-20.

Reich, P.B; D.S. Ellsworth, and C. Uhl (1995). Leaf carbon and nutrient assimilation and conservation in species of differing successional status in oligotrophic Amazonian forest. *Functional Ecology*. 9: 65-76

Richards, P.W (1964). *The tropical rain forest: an ecological study*. Cambridge University Press.

Richards, L.A & P.D, Coley (2007). Seasonal and habitat differences affect gaps and understorey of tropical forest. Oikos 116:31-40.

Rice, K, Brokaw, N & Thompson, J (2004). Liana abundance in Puerto Rican forest. *Forest ecology and management*. 190:33-41

Rockwood, L.L and K.E. Glander (1979). Howling monkeys and leaf cutting ants: comparative foraging in a tropical deciduous forest. *Biotropica* 11: 1-20.

Rogers, P (1996). Disturbace ecology and Forest management: a review of the literature. USDA Forest service

Rose, S.A (1997). Long term seedling demography after gap creation in the tropical rain forest in Guyana. Tropenbos Guyana reports 79-1.

Ross, M.A and Harper JL (1972). Occupation of biological space during seedling establishment. *Journal of Ecology.* 60:70–88.

Schnitzer, S.A. and Bongers, F (2002). The ecology of lianas and their role in forests. Trends in Ecology and Evolution 17: 223-230.

Schnitzer, S.A. and Carson, W.P. (2001). Tree fall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82, 913–919.

Schnitzer, S.A., Dalling, J.W. & Carson, W.P (2000). The impact of lianas on tree on tree regeneration in tropical forest canopy: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*. 88: 655-666.

Schupp, E.W, H.F.Howe, C.K. Augspurger and D.J.Levey (1989). The arrival and survival in tropical tree fall gaps. Ecology 70: 562-564

Scriber, J.M and F. Slansky (1981). *The nutritional ecology of immature insects. Annual Review of Entomology* 26: 183-211. Seedlings (Ed. M. D. Swaine).UNESCO and Parthenon Publishing, New York.

Seiwa, K (2000). Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. *Oecologia* 123:208–215.

Skorupa J.P (1988). The effects of selective Timber harvesting on Rain forest primates in Kibale forest, Uganda. PhD. dissertation, university of California, Davis.

Steege, H. Ter (1994). *Hemiphot: an MS-DOS program to analyze vegetation indices, light and light quality from hemispherical photographs.* Tropenbos Document 3, Tropenbos, Wageningen, Netherland.

Struhsaker, T.T(1975). *The red colobus monkey. University of Chicago* Press, Chicago, USA.

Struhsaker, T.T (1997). Ecology of an African rain forest: Logging in Kibale and the conflict between conservation and Exploitation. University of Florida Press Gainesville.

Struhsaker, T.T. 1998. Ecology of an African rain forest: logging in Kibale and conflict between conservation and exploitation. University Press of Florida, Gainesville.

survival in tropical tree fall gaps. Ecology. 70:562-564.

Swaine, M.D. & Whitmore, T.C. (1988). On the definition of ecological species groups in tropical rain forest. *Vegetatio,* 75, 81-86

Synnot, T.J (1975). Factors affecting the regeneration and growth of seedling of *Entandrophrogma utile* (Dawe and Sprague). Sprague in Budongo forest and Nyabyeya Nursery- Uganda. PhD. Thesis, Makerere University.
Syst. 18, 431–451.

Tilman, D, May, R.M, Lehman, C.L & Nowak, M.A (1994). Habitat destruction and the extinction debt. *Nature,* 371:65-66.

Torquebiau, E.F (1988). Photosynthetically active radiation environment, patch dynamics and architechture in a tropical rain forest in Sumatra. *Aust. J. Plant Physiol. 15: 327- 342*

Uhl, C., Clark, K., Dezzao, N. & Maquino, P (1988). Vegetation dynamics in Amazonian tree fall gaps. Ecology 69, 751–763.

Van Schaik, C.P, Terborgh, J.W, Wright, J.S (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Ann Rev Ecol Syst* 24:353-377

Veenendaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K. & Mullins, C.E (1996). Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology* 8

Whitmore, T.C (1975). *Tropical rain forests of the far_ east.* Oxford University Press.

Whitmore, T.C (1978). Gaps in the forest canopy. *In: Tropical trees as living systems*. (Eds.P.B.Tomlinson and H.H.Zimmerman) Cambridge University Press.

Whitmore, T.C. (1996). A review of some aspects of tropical rainforest seedling ecology with suggestions for further enquiry. In: The Ecology of Tropical Forest Tree seedlings (Ed. M. D. Swaine). UNESCO and Parthenon Publishing, New York.

Wigglesworth, V.B (1972). The principles of insect physiology. Chapman and Hall. London

Woiwood, I.P and Hanski, I (1992). Patterns of Density Dependence in Moths and Aphids. J Anim Ecolo 61:619-629

Wolda, H (1988). Insect seasonality: Why? Annu Rev Ecol Syst 19: 1-18.

Wright, S.J, Cornejo, F.H (1990). Seasonal drought and leaf fall in a tropical forest. Ecology 71: 1165-1175

Wright, S.J (1991). Seasonal drought and the phenology of understorey shrubs in a tropical moist forest. Ecology 72: 1643-1657

Wright, S.J. & Loo Delao, S. (1999). Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283, 554–557.

York, U.S.A

Zagt, R. J (1997). Tree demography in the tropical rain forest of Guyana. Tropenbos-Guyana series 3.Tropenbos-Guyana Programme, Georgetown, Guyana. PhD thesis, Utrecht University, The Netherlands.

Zagt, R.J. and Wenger, M.J.A (1998). Community structure and demography of primary species in tropical rain forest. Pp 193-220 in Newbery, D.M.; Brown, N.; Prins, H.H.T. (eds.) *Dynamics of tropical communities*. Blackwell Scientific Publishere, Cambridge, UK.