

PREDICTING THE FUNCTIONAL ROLE OF FOREST TREE SPECIES IN RESTORING  
DEGRADED FORESTS: A CASE OF MABIRA FOREST, UGANDA

BY

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MSc. Forestry (2006/HD07/5822U)

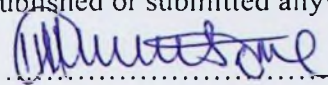


A DISSERTATION SUBMITTED TO SCHOOL OF GRADUATE STUDIES IN PARTIAL  
FULFILMENT FOR THE AWARD OF A MASTER OF SCIENCE IN FORESTRY  
DEGREE OF MAKERERE UNIVERSITY

AUGUST 2009

### Declaration

I Muthalib Baiikitenda Katumba declare that this is my original work and has never been published or submitted anywhere unless stated for any award

  
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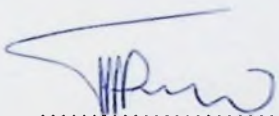
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The cover photo is *Lecaniodiscus fraxinifolius* in fruit

## **Dedication**

To all people who resisted the Central government's plan to give part of Mabira Forest for  
Sugar cane production

## **Acknowledgement**

I would like to thank my Supervisors at the Faculty of Forestry and Nature Conservation Makerere University: Dr. Gerald Eilu and Associate Professor Mnason Tweheyo for guiding me through this research process. I thank Dr. Jan Dick who introduced this idea of functional groups and Ron Smith who taught me how to use multivariate techniques for generating functional groups.

I am also greatly indebted to my field and Laboratory assistants Susan Nansereko, David Mugeni of National Forestry Resources Research Institute, Sebastian Walaita, Kevin Anderu, Joseph Ochwo for helping search the archives for tree seed data. Robert Angutoko and Patrick Katalo for the professional services in climbing even the most difficult tree in Mabira Forest. I also thank David Nkuutu, Martin Mwodi, Leo Twinomuhangi, Judith Ahebwa Kiyangi and all the staff of Mabira Ecotourism Centre for the support during data collection.

I would also like to thank the Director (Mr. J.F.O Esegu) and staff of the National Forestry Resources Research Institute (NaFORRI) for their support and permission to use the institute facilities and equipment. Special thanks to Dr. D.L.N. Hafashimana for his assistance in identifying some of the tree species collected and providing reading material relevant to my research work. Lastly, I thank my family especially my wife Betty for keeping the family together.

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|         |                                                                                                                          |
|---------|--------------------------------------------------------------------------------------------------------------------------|
| DLW     | Dry Leaf Weight                                                                                                          |
| FAO     | Food and agriculture organisation                                                                                        |
| FOREAIM | Bridging Restoration and Multi-functionality in Degraded Forest Landscapes<br>of Eastern Africa and Indian Ocean Islands |
| FTEA    | Flora of Tropical East Africa                                                                                            |
| LA      | Leaf Area                                                                                                                |
| M.a.s.l | Metres above sea level                                                                                                   |
| MFPED   | Ministry of Finance Planning and Economic Development                                                                    |
| MUIENR  | Makerere University Institute of Environment and Nature conservation                                                     |
| N.P.K   | Nitrogen Phosphorous Potassium                                                                                           |
| NBS     | National Biomass Study                                                                                                   |
| NFP     | National Forest Plan                                                                                                     |
| SLA     | Specific Leaf Area                                                                                                       |
| SE      | Standard Error of mean                                                                                                   |

## Summary

This dissertation is structured into three chapters; that is General introduction and two manuscripts. Chapter One describes the background and scope of the study. Chapter Two is titled "Patterns of Specific Leaf area of trees in Mabira Forest Reserve, Uganda". It contains information on the relationship between SLA and tree height, family, leaf type and leaf area. Specific Leaf Area (SLA) was chosen to this study because it's direct relationships to plant physiological processes such as photosynthetic rate. Leaves were collected randomly from selected tree species and leaf area was measured. The leaves were oven dried and SLA is the ratio of Leaf area (LA) and dry leaf weight (DW). SLA varied significantly among trees ( $P < 0.001$ ) and within leaves and leaf types. For instance, there was a significant difference between leaves collected from the Upper, Middle and Lower parts of the crown for 86% of the species in the study. However, the differences did not increase or decrease with crown height. Since SLA has a direct relationship to resource requirements and photosynthetic rates, species with low SLA e.g. *Rinorea ardisiifolia*, *Sterculia dawei* and *Warburgia ugandensis* can be used to restore lowly degraded parts and those with high SLA e.g. *Turraea robusta*, *Vernonia auriculifera* and *Oncoba spinosa* can be used to restore highly degraded parts of the forests

Chapter Three is titled "Deriving functional groups for Mabira Forest tree species and predicting their Potential role in forest Restoration". It presents the functional classification of tree species for Mabira forest reserve. A functional approach based on 18 morphological traits including: Leaf, bark, stem, flower, sex and defence was used to classify 100 tree species into groups of similar ecological function(s). The traits were compiled from literature

about flora of Uganda. Leaf area and Specific Leaf Area were determined from collected and measured leaves as described in Chapter II. Hierarchical cluster analysis with the computer program Genstat was used to generate the groups. Seven functional groups were obtained each represented by 3-39 species. The groups represent species in the various successional stages. I recommend planting the degraded parts with species that are represented in the various functional groups.

## CHAPTER ONE

The first part of the book is devoted to a study of the historical background of the subject. It begins with a brief survey of the history of the subject from the time of the ancient Greeks to the present day. It then goes on to discuss the various theories and methods of research which have been developed in the field. The second part of the book is devoted to a study of the various theories and methods of research which have been developed in the field. It begins with a brief survey of the history of the subject from the time of the ancient Greeks to the present day. It then goes on to discuss the various theories and methods of research which have been developed in the field.

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## GENERAL INTRODUCTION

### Background

About 350 million hectares of tropical forest land have been severely damaged that it won't grow back spontaneously while a further 500 million hectares is either degraded or has re-grown after initial deforestation (FAO, 1997). Such large areas of damaged forest are a major cause of concern to ecologists. Forests provide a variety of socio-economic and ecological goods and services. It's therefore important to conserve them for the benefit of the present and future generations.

Forest degradation has remained a major challenge especially in many tropical countries which hold about 55% of the world's forests (FAO, 1997). Ecologists are now seeking ways of accelerating the restoration of these degraded lands. This has been attempted through planting native or exotic species in the degraded forest lands. However, such efforts have been limited by information on the ecology and function of the various tree species planted in relation to forest ecosystem maintenance and stability, which is vital for making the right decisions on possible interventions. For instance, after evicting encroachers from Mabira forest, efforts were geared towards restoring some of the degraded sites of the forest. *Terminalia spp.* and *Maesopsis eminii* were chosen for restoration.

The choice of native species to use in restoring forests at different levels of degradation is unclear and there is no consensus on the procedures to undertake. Before restoration is done, there is need to know what species existed in this site and what functional role such species were playing in maintaining the ecosystem. Fonseca and Ganade (2001) noted that functions

are many but those involved, for instance, in the maintenance of biogeochemical and hydrological cycles, climate control, decomposition and soil formation, pest control and pollination have to be maintained. It is then this information that can be used to choose the right species for performing the various functional roles as identified for particular degraded forest.

On the other hand, during the course of restoring degraded forests, terminologies such as restoration, rehabilitation or degradation have often been used in different contexts to mean; - bringing the forest back to its original structure, productivity and native species diversity. A degraded site might still contain trees but it has lost at least some of its former ecological integrity. Restoration which aims at re-establishing the presumed structure, productivity and species diversity of the forest originally present at a site is an ideal approach because the ecological processes and functions of the restored forest will closely match those of the original forest. This study will attempt to generate knowledge that could be used to aid the process of restoration.

### **Objectives**

The overall objective of this study is to group tree species with similar functional characteristics and predict their role in restoration of a degraded forest

### **Specific objectives**

1. Derive functional groups using selected tree morphological characteristics
2. Describe the morphological characteristics of generated functional groups
3. Predict the ecological role of the functional groups in restoring a degraded forest.

## Justification

Forests serve many functions at the local, landscape, national and global levels, but only if they are in good health. A healthy forest is one that is able to sustain its complexity while providing for human needs (O'Laughlin *et al.* 1994). Forests provide people with sustainable supplies of clean water, timber, fuel wood and other products and services, and they contribute to the global quest to conserve biodiversity and reduce atmospheric green house emissions. However, drastic changes in the forest cover have taken place globally during the past century and this is threatening their service roles.

In Uganda, the forest cover was reported to be about 10.8 million ha (52%) by 1890. This has however, shrunk to only 5 million ha (24%) of Uganda's land surface area (National Biomass Study, 2003). FAO (2000) estimated the deforestation rate in Uganda to be 55,000 ha per year based on the change in the amount of bush land and woodlands from 1990 to 1995 while the government estimates the rate of land clearance to range from 70,000 to 200,000 ha (MFPED, 1994). These figures imply a deforestation rate of about 2% and this poses a serious challenge because there is no control over use and management of forests on private land.

Reports (NFP 2002), indicate that over 30% of Uganda's Tropical high forests are now degraded and private forests are shrinking more rapidly than government managed forests. As a result, Uganda's biodiversity is declining rapidly (MUIENR, 2000). However, when a species is lost, its functional role within the ecosystem is not known, therefore a functional approach, where species are studied to understand their functions in the ecosystem is a right approach to restoration ecology. However, there are many species in an ecosystem; therefore

a classification system based on their morphological and physiological adaptations would be used to scale down the task of working with many species. The groups generated would then be further scrutinized to determine their functional role within the ecosystem.

Restoring, rehabilitating, managing and protecting forests are very important interventions for continued provision of global ecological services. However, any meaningful restoration process requires the provision of knowledge on key: policy, socioeconomic, legal, institutional, ecological and silvicultural issues that need to be taken into account in the planning and implementation of appropriate strategies and viable options. This study therefore aims at generating information on the silvicultural aspects that can be applied in the restoration of Mabira Forest Reserve and subsequently other tropical forests in Uganda.

METHODS AND STUDY AREA

Location

The study was carried out in Mabira Forest Reserve located between 32° 52' -33° 07'E and 0°24' -0°35' N (Davenport *et al.*, 1996) in central Uganda. The forest covers an area of 306 km<sup>2</sup> and has an altitudinal range of 1070 -1340 m.a.s.l. The forest is approximately 52 km from Kampala city towards the east.

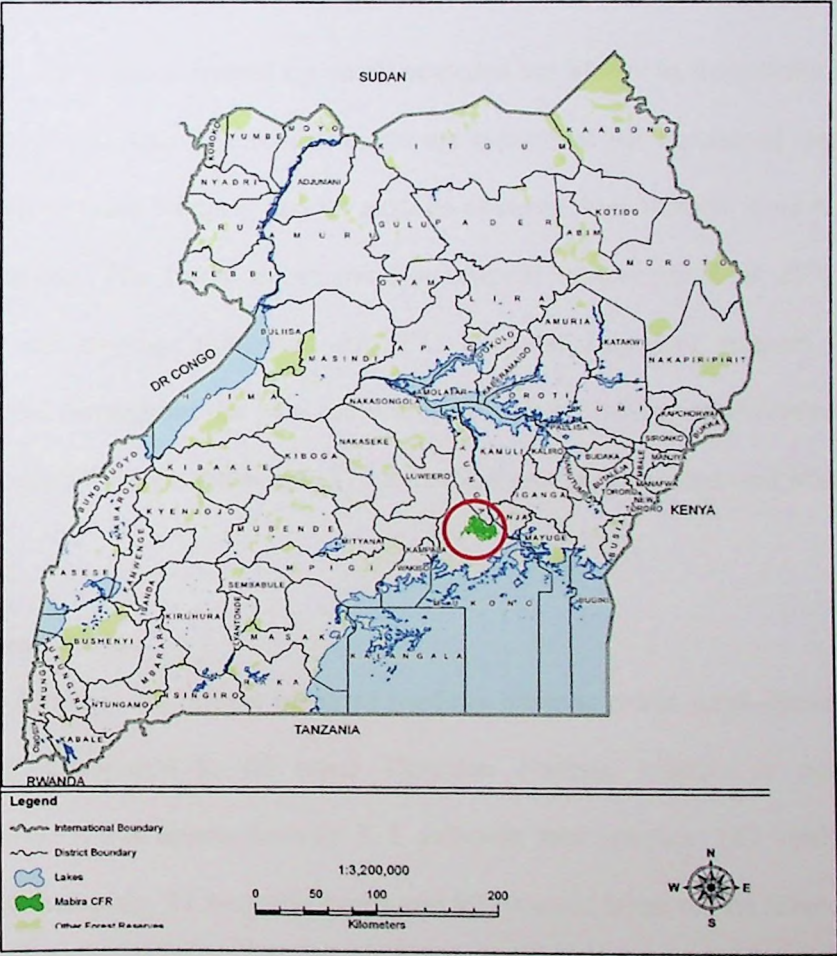


Figure 1: Map of Uganda showing the location of Mabira Forest

### **Soil types**

Most of the underlying rocks are granitic gneiss and granites of the Buganda –Toro system (Pallister, 1959). The rock has undergone chemical weathering over time because of the equatorial climate and humid conditions. The soils are of the ferrallitic types which are in the final stage of tropical weathering. They consist of red soils on slopes and black clays in the valley bottoms often referred to as Buganda catena.

### **Climate**

The climate is characterised by small seasonal variations in temperature, humidity and wind throughout the year. The temperatures are typical of the equatorial region but proximity of the forest to Lake Victoria and an altitude of more than 1000 m have a moderating effect on temperatures. The forest experiences maximum temperatures of 27°C between January – March and average minimum of 22°C between July and August. The rainfall is well distributed throughout the year but with peaks in April-May and October to November. Total annual rainfall ranges between 1375 and 1524 mm (Komutunga and Musiitwa 2001).

### **Flora and Fauna**

Mabira forest is the largest block of medium altitude moist semi-deciduous forest in central Uganda. Compared to 65 other Ugandan Forests, Mabira is described as relatively biodiverse. It has approximately 312 different tree species, 287 bird species, 23 different types of mammals, 21 butterfly types and 97 types of large moths (Davenport *et al.*, 1996). A number of mammals such as the blue and red tail monkeys, pigs, bush bucks and forest duickers (Davenport *et al.*, 1996) still exist in the forest.

Mabira forest is characteristic of vegetation types representing sub-climax or human altered plant communities; consequently, three vegetation sub-types are recognized: young colonizing forest, mature mixed forest and *Celtis* mixed forest. The young colonizing Forest covers approximately 2.7% of the total area and it's mainly in zones of the forest that had been encroached in the past or has undergone unregulated harvesting. The dominant species in these parts are *Broussonetia papyrifera*. Nonetheless, both understory and upper story tree species such as *Diospyros* and *Trelepisium* respectively are occasionally encountered in this forest type but in small quantities.

The Mature mixed forest occupies about 52% of the area (Davenport *et al*, 1996). The lower canopy trees are dominated by *Diospyros abyssinica* and *Funtumia elastica* and the canopy trees include: *Chrysophyllum* and *Albizia* species. Nevertheless, *Celtis* species makes up the highest number of growing stock. Six species of *Celtis*: *C. zenkeri*, *C. wightii*, *C. mildbraedii*, *C. durandii*, *C. africana* and *C. adolfi-friedericii* dominate the *Celtis* Forest type. These species dominate the upper story, therefore giving it the composition and character of a *Celtis* dominated forest type. The *Celtis* species are normally associated with *Albizia glaberrima*, *Albizia ferruginea* and *Chrysophyllum* species.

### **Management history of Mabira Forest Reserve**

Mabira Forest Reserve was gazetted as a central forest reserve under legal notice no. 87 of 1932 with an area of 29,592 ha. This was initially gazetted as a local forest reserve managed by the Buganda Kingdom but later transferred to the central government under statutory instrument 176 of 1968 and therefore its control was vested in the Forestry department. At

its gazettement, there were about 27 human settlement enclaves that were completely or partly surrounded by the forest and these are ecologically part of the forest. These communities and the forest impact on each other in various ways.

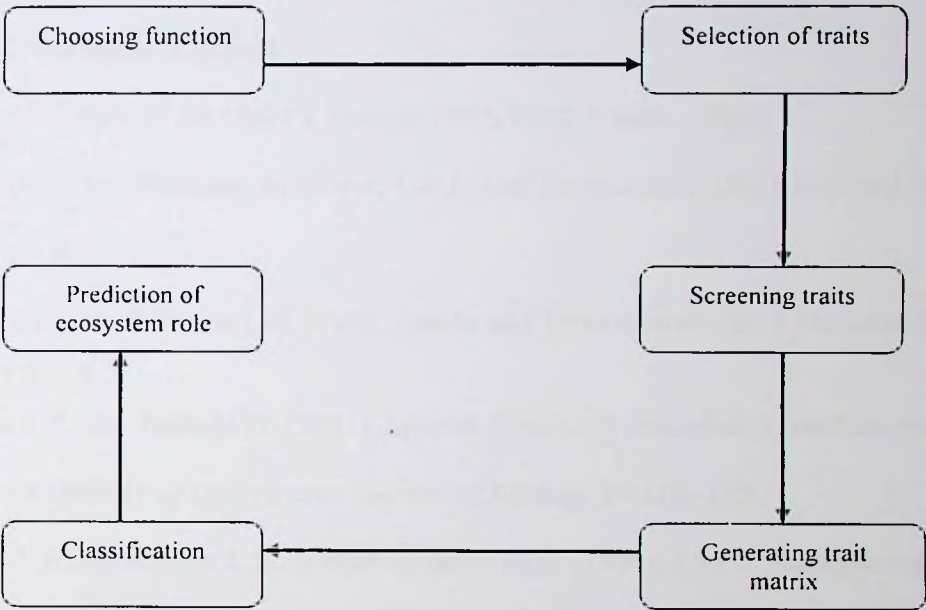
However due political instability in early 1970s, illegal crop farming started resulting in the breakdown of law and order and by 1981, 7860 ha (26.2%) of the forest was already occupied by about 1800 encroachers (Karani *et al.*, 1997). However the government evicted all the encroachers in 1988. The previously encroached sites are dominated by invasive plant species such as *Broussonetia papyrifera* and *Lantana camara*.

### **Scope of the study**

The focus of this study is on the use of tree morphological and physiological characteristics to group species with similar ecological functions together and use the resultant groups in predicting their role in restoring a degraded forest. Morphological traits were obtained from literature and field observations. However, physiological characteristics are difficult and expensive to measure. As such, Specific Leaf Area (SLA), a variable that has direct relationships with a number of physiological characteristics such as photosynthetic rate (Meziane and Shipley 2001) was the most appropriate variable to measure.

Tree characteristics (traits) for 100 species were selected based on their function in establishment, growth and survival in a forest ecosystem from relevant literature. The traits were subjected to multivariate analyses using Genstat computer package. The functional groups were generated and tested for robustness. Basing on their most significant characteristics in forming the groups, they were described and their potential role(s) in

restoration of the forest was predicted. The research strategy for constructing the functional groups is summarised in Figure 2.



Adapted from; Boutin, C and Keddy, P.A. 1993

Figure 2: Research strategy for constructing functional groups of plants

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## CHAPTER TWO

## Patterns of Specific leaf Area of trees in Mabira Forest Reserve, Uganda

### Abstract

Plant size, the environment and other intrinsic growth factors influence plant establishment and survival. Tropical plants therefore tend to adapt both morphologically and physiologically in response to light. Because light is mainly captured by leaves and processed into energy, we studied the Specific Leaf Area (SLA) of 117 tree species in Mabira Forest, central Uganda. The objective was to (i) determine the specific leaf area of Mabira forest tree species (ii) determination of the variation of SLA with tree height and (iii) to determine the relationship between SLA and leaf type. A total of 30 leaves were collected randomly from each tree crown. The leaves were scanned and their areas measured. They were then oven dried at 70°C until constant weight and weighed (precision 0.01g). The leaf types comprised both simple and compound. Compound leaved trees had a lower mean SLA (145.6cm<sup>2</sup>/g) than simple leaved species (mean 172.7). Passifloraceae and Flacourtiaceae had the highest mean SLA (492.5 and 467.2 (cm<sup>2</sup>/g) respectively). Violaceae and Guttiferae had the lowest mean SLA (81.3 and 89.9 cm<sup>2</sup>/g respectively). There were significant differences between leaves collected from the Upper, Middle and Lower parts of the crown ( $P < 0.05$ ) for 86% of the species but the differences did not consistently increase or decrease with crown height. For instance, there was no significant difference in the SLA of leaves picked at the lower and middle parts of the crown for 37% of the species in the study. Since SLA has a direct relationship to resource requirements and photosynthetic rates, species with low SLA e.g. *Rinorea ardisiifolia*, *Sterculia dawei* and *Warburgia ugandensis* can be used to restore lowly degraded parts and those with high SLA e.g. *Turraea robusta*, *Vernonia auriculifera* and *Oncoba spinosa* can be used to restore highly degraded parts of the forests.

**Key words:** Leaf Area, leaf dry weight, Tree crown and Leaf type

## INTRODUCTION

The physical structure of plants such as leaves, roots and stems contribute in different ways to growth and survival of plants. The leaves for instance, are primarily responsible for the capture and conversion of radiant energy. Other organisms especially the fauna depend on plants because their leaves are able to convert the radiant energy into a usable form. To understand the growth and survival strategies of plants, the role various plant parts play in species survival in the ecosystem needs to be understood.

Plants adjust their leaf characteristics to capture light because this is one of the most limiting resources for plant growth and survival in a tropical forest ecosystem, (Poorter, 2001). Leaf area, thickness and consequently Specific Leaf Area (SLA); play an important role in plant function (Vile *et al.*, 2005). This is because the amount of light absorbed by a leaf and the diffusion of carbon dioxide through its tissues, at least partially depend on its leaf thickness (Syvertsen *et al.*, 1995).

As knowledge of plant function can be inferred from Specific Leaf Area this is an important variable in plant growth models. SLA relates dry matter production and leaf area expansion, to light interception and consequently photosynthesis (Gary *et al.*, 1993). The rate of leaf photosynthesis per unit area strongly depends on leaf nitrogen content and photosynthetic components (Terashima *et al.*, 2006). SLA was found to be a much more accurate predictor of photosynthetic capacity than using a simple area based approach (Reich *et al.*, 1998). Species with higher SLA tend to have higher net photosynthetic capacity per unit leaf (Reich *et al.*, 1998) than those with lower SLA. Specific Leaf Area was chosen for assessment in

this study because it is relatively easy to measure compared to other physiological processes and is related to a number of physiological processes such as photosynthetic rate (Meziane and Shipley, 2001; Reich *et al.*, 1998). SLA plays a major role in leaf functioning and is related to species strategies of resource acquisition and use. It can also be used to predict the nitrogen content and gas exchange of leaves (Meziane and Shipley, 2001).

Relatively large leaves may have fitness benefits derived from a greater boundary layer thickness for heat exchange, thus maximizing photosynthetic gains under cooler, moister and more shaded environments (Gates, 1980). However, these benefits must be considered against the potential costs of having large leaves and the greater susceptibility to wind damage and the need for more support tissue in the leaf. Larger leaves generally have less nitrogen per unit dry mass and hence relatively low photosynthetic capacity (Niinemets *et al.*, 2006).

On the other hand, relatively small leaves, because of higher heat exchange capacity, are often considered to be advantageous in hot, dry, high light and low nutrient environments (Westoby, 2002). Smaller leaves allow more efficient vertical distribution in a multilayered crown and they are associated with reduced leaf expansion time (Moles and Westoby, 2000). This is advantageous during desiccation and will accordingly favour the survival of such plants in drier environments. Smaller leaves may also reduce losses due to herbivory.

A key question among ecologists is why some plants possess larger leaves even under high light conditions. Kleiman *et al.*, (2007) noted that in most woody deciduous plants,

prevalence of small leaf size is not simply a result of a prevalence of small plant size but possibly because most environments, during most of the evolutionary history of land plants, may have been relatively hot and dry, and/or with relatively low nutrients. This favoured the evolution of species with the relatively small leaves that are apparently adapted to these environmental conditions.

Some tree species may have small leaves and high specific leaf area not because relatively small leaves are usually more adapted than larger leaves, but because relatively higher leafing intensity common in small leaved species is usually more adaptive than lower leafing intensity common with broad leaved species (Kleiman *et al.*, 2007). Tree species, as a result, adapt accordingly to prevailing environmental conditions and this aligns their physiological capacity to suite the growth environment. The proportion of large or small leaves in a semi – deciduous forest such as Mabira is not known, moreover, the prevalence of species with leaves of the different sizes in degraded sites is not known.

Studies of physiological processes are expensive and time consuming but quick solutions to some of the prevailing challenges such as forest degradation and biodiversity loss are needed. As such, identifying surrogate variables that can directly relate to the physiological process of plants is a useful tool that can aid faster decision making on type of species to protect or plant that may play a significant role in restoring degraded forests. Because plants adapt physiologically to prevailing environmental conditions, SLA can aid in the prediction of the type of species that will enhance the restoration of a degraded forest because of its direct

relationship to leaf nitrogen (Meziane and Shipley, 2001) and Phosphorous and Potassium (Santiago and Wright, 2007) factors that influence photosynthetic rates.

In this study, we measured the specific leaf area of tree species of Mabira Forest to address the following specific questions: What is the Specific Leaf Area (SLA) of selected tree species in Mabira Forest? How does SLA vary among the different families? Does SLA and Leaf Area (LA) vary with tree height? Does leaf type influence SLA? The information on specific leaf area will be one of the traits to be used when deriving tree species functional groups in chapter III of this study. The physiological behavior of the species can help in predicting their growth characteristics in forest ecosystems.

## METHODS AND STUDY AREA

### Location

The study was carried out in Mabira Forest Reserve located between 32° 52' and 33° 07'E and 0°24' -0°35' N (Davenport *et al.*, 1996) in central Uganda. The forest covers an area of 306 km<sup>2</sup> and has an altitudinal range of 1070 -1340 m.a.s.l. The forest is approximately 52 km from Kampala city towards the east.

### Soil types

Most of the underlying rocks are granitic gneiss and granites of the Buganda –Toro system (Pallister, 1959). The rock has undergone chemical weathering over time because of the equatorial climate and humid conditions. The soils are of the ferrallitic types which are in the final stage of tropical weathering. They consist of red soils on slopes and black clays in the valley bottoms often referred to as Buganda catena.

### Climate

The climate is characterised by small seasonal variations in temperature, humidity and wind throughout the year. The temperatures are typical of the equatorial region but proximity of the forest to Lake Victoria and an altitude of more than 1000 m have a moderating effect on temperatures. The forest experiences maximum temperatures of 27°C between January – March and average minimum of 22°C between July and August. The rainfall is well distributed throughout the year but with peaks in April-May and October to November. Total annual rainfall ranges between 1375 and 1524 mm (Komutunga and Musiitwa 2001).

## Flora and Fauna

Mabira forest is the largest block of medium altitude moist semi-deciduous forest in central Uganda. Compared to 65 other Ugandan Forests, Mabira is described as relatively biodiverse. It has approximately 312 different tree species, 287 bird species, 23 different types of mammals, 21 butterfly species and 97 types of large moths (Davenport *et al.*, 1996). A number of mammals such as the blue and red tail monkeys, pigs, bush bucks and forest duickers (Davenport *et al.*, 1996) still exist in the forest.

Mabira forest is characteristic of vegetation types representing sub-climax or human altered plant communities; consequently, three vegetation sub-types are recognized: young colonizing forest, mature mixed forest and *Celtis* mixed forest. The young colonizing Forest covers approximately 2.7% of the total area and it's mainly in zones of the forest that had been encroached in the past or has undergone unregulated harvesting. The dominant species in these parts are *Broussonetia papyrifera*. Nonetheless, both understory and upper story tree species such as *Diospyros* and *Trelepisium* respectively are occasionally encountered in this forest type but in small quantities.

The Mature mixed forest occupies about 52% of the area (Davenport *et al.*, 1996). The lower canopy trees are dominated by *Diospyros abyssinica* and *Funtumia elastica* and the canopy trees include: *Chrysophyllum* species and *Albizia* species. Nevertheless, *Celtis* species makes up the highest number of growing stock.

Six species of *Celtis*: *C. zenkeri*, *C. wightii*, *C. mildbraedii*, *C. durandii*, *C. africana* and *C. adolfi-friedericii* dominate the *Celtis* Forest type. These species dominate the upper story, therefore giving it the composition and character of a *Celtis* Dominated forest type. The *Celtis* species are normally associated with *Albizia glaberrima*, *Albizia ferruginea* and *Chrysophyllum* species.

### **Management history of Mabira Forest Reserve**

Mabira Forest Reserve was gazetted as a central forest reserve under legal notice no. 87 of 1932 with an area of 29,592 ha. This was initially gazetted as a local forest reserve managed by the Buganda Kingdom but later transferred to the central government under statutory instrument 176 of 1968 and therefore its control was vested in the Forestry department. At its gazettelement, there were about 27 human settlement enclaves that were completely or partly surrounded by the forest and these are ecologically part of the forest. These communities and the forest impact on each other.

However due political instability in early 1970s, illegal crop farming started resulting in the breakdown of law and order and by 1981, 7860 ha (26.2%) of the forest was already occupied by about 1800 encroachers (Karani *et al.*, 1997). However the government evicted all the encroachers in 1988. The previously encroached sites are dominated by invasive plant species such as *Broussonetia papyrifera* and *Lantana camara*.

### **Sampling design**

One hundred seventeen tree species for the study were pre-selected from the Mabira biodiversity report (Davenport *et al.*, 1996). The species represent the most common tree

species of Mabira forest. Leaves were collected from tree species randomly identified within the forest but with a diameter of at least 10 cm. A total of 10 mature leaves were collected randomly from top, middle and lower parts of the crown. Mature leaves were observed to be relatively less shiny and the entire leaf has fully acquired the natural green colour (personal observation). The 30 leaves were collected from each tree to minimise the effect of perforations on some leaves to the total mean leaf area and weight.

To determine whether there were differences in leaf sizes collected from the upper, middle and lower parts of the crown, 30 leaves were collected from each of the three crown levels of the first 28 tree species encountered during data collection. The upper part was the highest point of the tree crown that climber would comfortably reach while the lower part comprised of the lowest branches of the tree crown. Leaves were collected from two replicates for *Diospyros abyssinica*, *Funtumia elastica*, *Milicia excelsa* and *Tabernaemontana holstii*. Leaves were collected from one or two crown levels for some tree species such as *Vernonia amygdalina* that did not have an easily distinguishable canopy structure or were too weak to support the tree climber to collect the top leaves.

All leaves were collected by professional tree climbers who used ropes and spiked boots to access the tree canopy. The leaves were kept in polythene bags and transported to a station within the forest where they were stored in a refrigerator at 10°C and later retrieved for leaf area determination. The maximum duration between collection and leaf area measurement was 48 hours. Data on maximum tree height were compiled from publications about Flora of

Uganda such as Hamilton, (1991) and the Flora of Tropical East Africa (Royal Botanical Gardens Kew -Series))

### **Measurement of Leaf Area**

The petiole of each fresh leaf was cut off using a pair of scissors and the leaf blade was spread flat on the bed of a Scanner (BENQ 5000 series) and scanned at a resolution of 300 dots per inch (dpi). Leaf area was determined by exporting the scanned image of the leaf to the computer software "Compu Eye, Leaf and Symptom Area" (Bakr, 2005). The software provides an easy method for measuring total leaf area. The software runs using Microsoft Visual Basic 6. It divides the image into small squares and assesses the average colour of every square, where the area of these square units could be adjusted between 0.1 and 1.0 mm<sup>2</sup> (Bakr, 2005). The squares are counted by the software to give the total leaf area. The software was calibrated prior to determination of total leaf area by scanning a conventional ruler at 300dpi and exporting ruler readings into the software. To evaluate the accuracy of the software, an object with known area was scanned at 300 dpi resolution and using the calibrated software, the scanned image was analyzed by the software to confirm the area.

### **Determination of dry leaf weight**

The already scanned leaves were placed in paper bags and oven dried (Gallen Kamp Oven) at 70 °C to constant weight. The leaves were weighed on a Mettler PJ 3600 (precious 0.01g) measuring scale to obtain dry weight. The Specific Leaf Area was calculated as the area of leaf per unit dry weight.

## Data analysis

Data analyses were done using the computer software Genstat Discovery Version 3 and Microsoft Excel. Analysis of Variance was performed to investigate the differences between SLA at the three crown levels; low mid and top. The Least Significant Difference (LSD) between the mean SLA at various levels of the crown was calculated. SLA differences or similarities between crown levels were denoted by a letter superscript. Mean SLA, and the respective F- probabilities were generated for each of the species. A Generalised linear model was performed to investigate the relationship between SLA and tree height, family and leaf type. Leaf types were converted into a four-point scale reflecting the level of disassociation of the leaf or leaflets from the midrib i.e. 1= simple, 2= bifoliate and trifoliate, 3 = paripinnate and imparipinnate, 4= bipinnate and digitate. This was done in order to have sufficient data in each category. A correlation matrix was generated to show the relationships between variables such as Leaf Area, Dry Leaf Weight, Tree height and Leaf type. Summaries of Specific Leaf Area, Leaf Area and their respective Standard Errors were generated using Genstat and Excel. All these tests were performed at 95% confidence interval.

RESULTS

Specific Leaf Area (SLA) of Mabira Forest tree species

There was variation in SLA among trees growing in Mabira forest. The variation was observed among species even with similar characteristics such as Leaf Type, Maximum Height at maturity, Canopy Level and family (Appendix 1). Specific Leaf Area differs significantly ( $P<0.001$ ) between species. The lowest SLA's were observed in: *Myrianthus holstii* and *Piptadeniastrum africana* while the highest SLA's were calculated for *Turraea robusta* and *Oncoba spinosa* (Appendix 1) tree species. The mean SLA for all the species was  $163\text{ cm}^2\text{g}^{-1}$  (S.E. =46). Relatively short trees (0-10m) had higher SLAs (Mean=  $218\text{ cm}^2\text{g}^{-1}$ , S.E. =40) than taller trees (>51 m) with mean SLA  $111\text{ cm}^2\text{g}^{-1}$  (S.E. 13.1), (Figure 2).

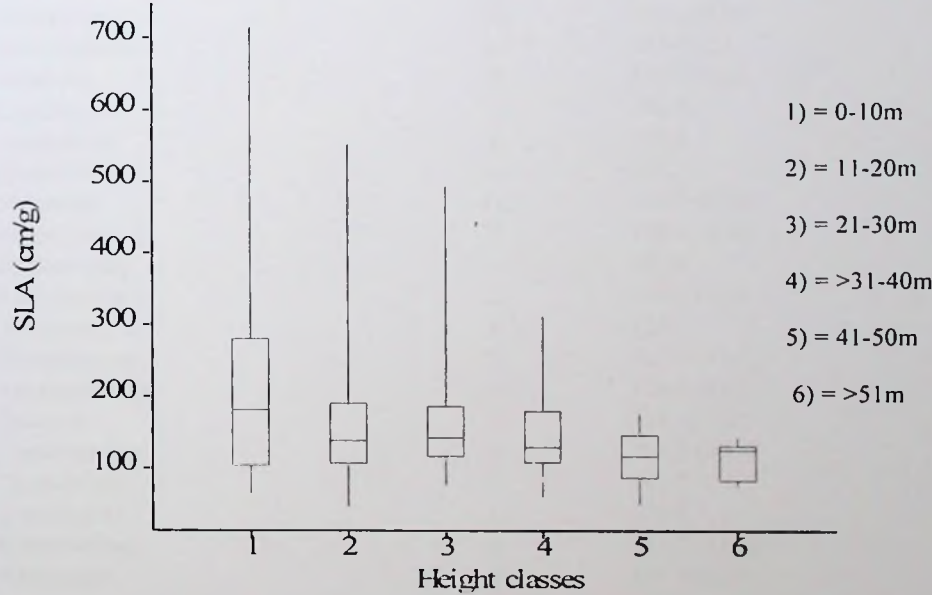


Figure 1: Mean Specific Leaf Area of tree species in six height categories of Mabira Forest

Among families, Passifloraceae and Flacourtiaceae had the highest mean SLA while

Guttiferae and Violaceae had the lowest (Table 1). However, 16 families were represented by one species only. The family in which a tree belongs significantly influences the SLA of that tree species ( $P= 0.03$ ) (Appendix 2).

Table 1: Mean Specific Leaf Area (SLA) per family and Standard error of the mean in parentheses

| Family         | Number of species | Mean SLA (cm <sup>2</sup> /g) (SE) |
|----------------|-------------------|------------------------------------|
| Passifloraceae | 1                 | 492.5                              |
| Flacourtiaceae | 2                 | 467.2 (246.8)                      |
| Myrsinaceae    | 1                 | 342.8                              |
| Simaroubaceae  | 1                 | 327.1                              |
| Asteraceae     | 2                 | 303.4(44.3)                        |
| Verbenaceae    | 1                 | 284.5                              |
| Rutaceae       | 4                 | 214.9(36.3)                        |
| Loganiaceae    | 1                 | 211.6                              |
| Rosaceae       | 1                 | 204.4                              |
| Rubiaceae      | 4                 | 178.6(36.3)                        |
| Ulmaceae       | 7                 | 169.8 (16.8)                       |
| Apocynaceae    | 5                 | 167. 8(22.3)                       |
| Meliaceae      | 10                | 166.2 (43.6)                       |
| Euphorbiaceae  | 10                | 165.0(33)                          |
| Fabaceae       | 17                | 150.1(20.2)                        |
| Lauraceae      | 1                 | 146.4                              |
| Annonaceae     | 1                 | 144.6                              |
| Bombacaceae    | 1                 | 143.1                              |
| Moraceae       | 11                | 141.7 (22.2)                       |
| Sapotaceae     | 7                 | 134,8(11.6)                        |
| Balanitaceae   | 1                 | 132.4                              |
| Sapindaceae    | 2                 | 129.9 (7.9)                        |
| Araliaceae     | 1                 | 127.7                              |
| Boraginaceae   | 3                 | 127.5 (13.7)                       |
| Anacardiaceae  | 3                 | 124.8 (9.9)                        |
| Oleaceae       | 2                 | 122.3(18.8)                        |
| Combretaceae   | 2                 | 121.2 (19.8)                       |
| Rhamnaceae     | 1                 | 116.7                              |
| Burseraceae    | 1                 | 116.1                              |
| Bignoniaceae   | 4                 | 111.2 (11.3)                       |
| Agavaceae      | 2                 | 105.5 (6.9)                        |
| Ebenaceae      | 1                 | 97.4                               |
| Guttiferae     | 1                 | 89.9                               |
| Sterculiaceae  | 3                 | 89.7                               |
| Violaceae      | 1                 | 81.3                               |
| Canellaceae    | 1                 | 68.5                               |

### Specific Leaf Area and Leaf type

The leaf types recorded are categorised as: compound (35.9%) and simple (64.1%). Within the compound leaves, five types were found; bifoliolate (2.3%), digitate (6.8%), trifoliolate (6.8%), paripinnate (20.5%), bipinnate (27.3%), imparipinnate (36.4%) (Figure 2).

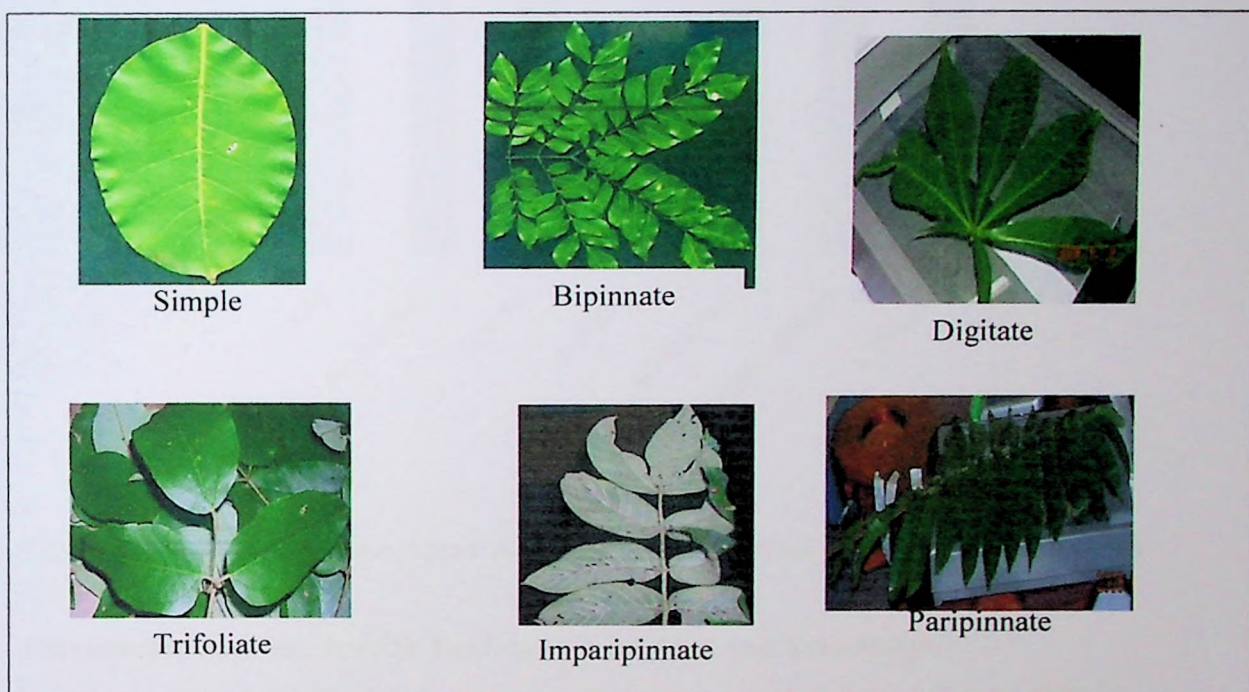


Figure 2: Leaf types encountered during leaf collection

Tree species with trifoliolate leaves had the highest mean SLA and palmate leaves had the lowest SLA (Figure 3). Bifoliolate was represented by one species *Balanites wilsoniana* (Appendix 1). Generally, compound leaved trees had a lower SLA (mean =  $145.7\text{cm}^2\text{g}^{-1}$ , S.E. = 10.5) than simple leaved tree species (Mean SLA =  $173\text{cm}^2\text{g}^{-1}$ , S.E. = 13.1). However, the difference between the means was not significant at 5% (LSD = 37.6). Leaf type however significantly influences ( $P = 0.04$ ) SLA (Appendix 2).

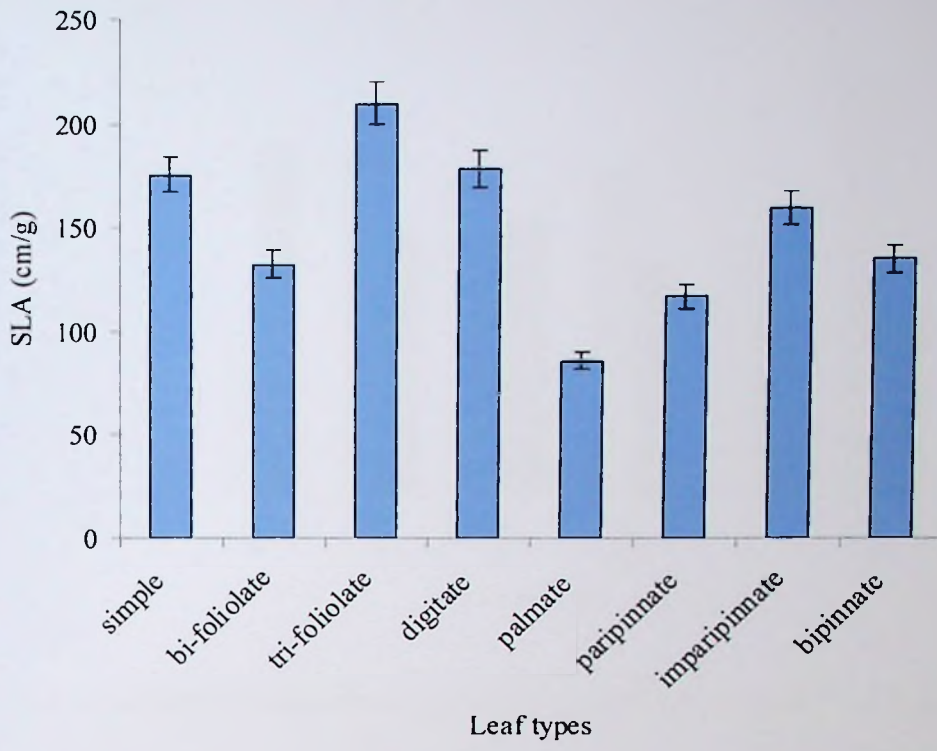


Figure 3: Mean Specific Leaf Area among leaf types measured in Mabira Forest Reserve

**Relationship between Specific Leaf Area, Leaf Area and Tree Height**

There is a weak negative correlation between SLA and tree height ( $r^2 = -0.263$ ). As tree height increases, the SLA of most tree species decreases (Figure 4). Increase in tree height was however accompanied by increased leaf area of trees (Figure 4). Even so, there was a very weak positive overall correlation ( $r^2 = 0.070$ ) between leaf area and maximum tree height. However, the heights considered are those compiled from literature on various flora of Uganda but not measured directly from sampled tree species. A generalised linear model revealed that SLA is significantly negatively associated with tree height ( $P = 0.03$ ) (Appendix 2).

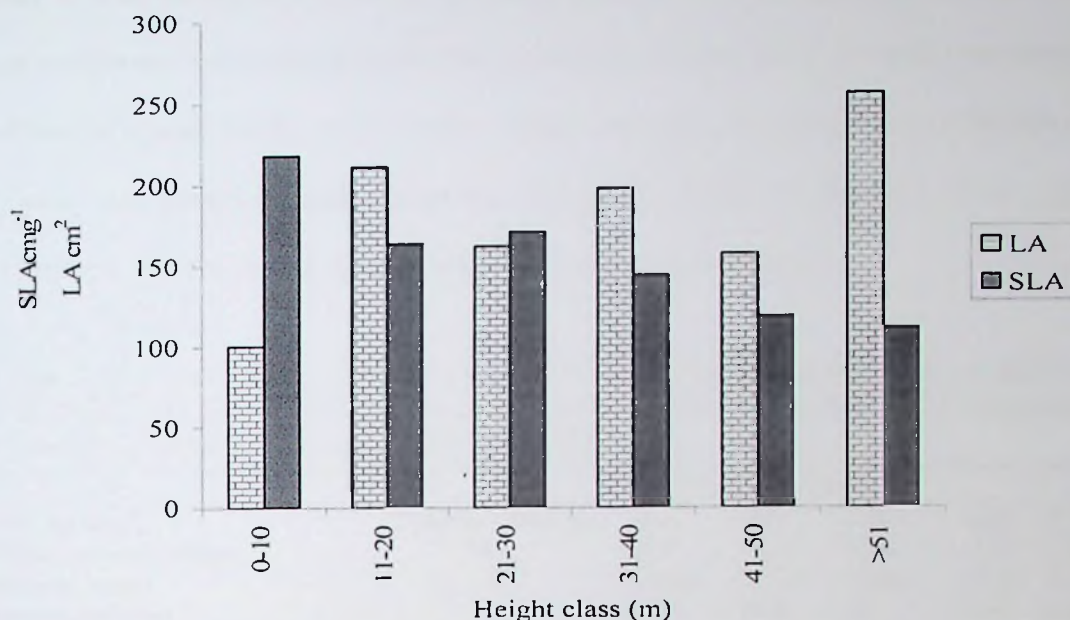


Figure 4: Variation of Specific Leaf Area (SLA) and Leaf Area (LA) with tree height

#### Specific Leaf Area at different levels of the crown

There was a significant difference ( $P = 0.01$ ) between leaves collected at the top, middle and lower crown levels for most species found in Mabira Forest Reserve. The SLAs of leaves collected at the top, middle and lower parts of the crowns of 83% of the species showed a significant difference ( $P < 0.05$ ) (Table 3). There was no significant difference in SLA for leaves collected from the lower and middle crown level of 37% of the tree species sampled. For 40% of the species, SLA of leaves collected from the lower crown level was not significantly different from top level while in 43% of the species; SLA of leaves collected from the middle crown level was not significantly different from the top level leaves.

Only 17% of the species showed a significant difference in SLA for leaves collected from the top, middle and lower crown levels. The differences did not however show a consistent trend within the crown levels. For instance, *Prunus africana*, *Alstonia boonei*, *Milicia excelsa*, *Croton macrostachyus* and *Diospyros abyssinica* (Table 2) did not show significant differences in SLA among leaves collected at various crown levels.

Table 2: Number of leaves sampled, Mean SLA, Least Significant Difference (LSDs) and F-probabilities for selected tree species at various crown levels. Similarity letter superscript between levels denotes no significant difference in SLA.

| Tree species                           | Number of leaves | Mean SLA (cm/g)     |                    |                     | LSD   | F- prob. |
|----------------------------------------|------------------|---------------------|--------------------|---------------------|-------|----------|
|                                        |                  | Low                 | Mid                | Top                 |       |          |
| <i>Albizia grandibracteata</i>         | 95               | 91.5 <sup>a</sup>   | 72.2 <sup>b</sup>  | 85.7 <sup>a</sup>   | 10.72 | 0.003    |
| <i>Alstonia boonei</i>                 | 92               | 120.0 <sup>ab</sup> | 113.5 <sup>b</sup> | 130.6 <sup>a</sup>  | 15.73 | 0.107    |
| <i>Antiaris toxicaria</i>              | 91               | 67.4 <sup>a</sup>   | 62.9 <sup>a</sup>  | 51 <sup>b</sup>     | 9.83  | 0.002    |
| <i>Bequaertiodendron oblanceolatum</i> | 95               | 134.9 <sup>a</sup>  | 122.9 <sup>b</sup> | 103.4 <sup>c</sup>  | 7.42  | 0.001    |
| <i>Blighia unijugata</i>               | 94               | 131.7 <sup>a</sup>  | 111.6 <sup>b</sup> | 121.9 <sup>ab</sup> | 11.34 | 0.003    |
| <i>Celtis gomphophylla</i>             | 94               | 189.2 <sup>b</sup>  | 189.6 <sup>b</sup> | 210.2 <sup>a</sup>  | 17.89 | 0.034    |
| <i>Celtis zenkeri</i>                  | 95               | 204.1 <sup>a</sup>  | 180.1 <sup>b</sup> | 181.4 <sup>b</sup>  | 11.04 | 0.001    |
| <i>Chrysophyllum albidum</i>           | 83               | 85 <sup>a</sup>     | 78.9 <sup>b</sup>  | 85.5 <sup>a</sup>   | 5.97  | 0.045    |
| <i>Chrysophyllum muerense</i>          | 90               | 173 <sup>a</sup>    | 177.6 <sup>a</sup> | 157.8 <sup>b</sup>  | 9.37  | 0.001    |
| <i>Cordia millenii</i>                 | 94               | 102.4 <sup>a</sup>  | 78 <sup>b</sup>    | 63.5 <sup>c</sup>   | 9.00  | 0.001    |
| <i>Croton macrostachyus</i>            | 90               | 62.7 <sup>a</sup>   | 63.8 <sup>a</sup>  | 68.1 <sup>a</sup>   | 7.37  | 0.318    |
| <i>Diospyros abyssinica</i>            | 184              | 106.1 <sup>a</sup>  | 111.1 <sup>a</sup> | 110 <sup>a</sup>    | 10.74 | 0.442    |
| <i>Ficus exasperata</i>                | 92               | 88.3 <sup>a</sup>   | 45.1 <sup>b</sup>  | 44.3 <sup>b</sup>   | 9.62  | <.001    |
| <i>Ficus ovata</i>                     | 82               | 115 <sup>b</sup>    | 144 <sup>a</sup>   | 95.7 <sup>c</sup>   | 18.20 | <.001    |
| <i>Ficus vallis-choudae</i>            | 96               | 204.8 <sup>a</sup>  | 127.1 <sup>b</sup> | 107.1 <sup>c</sup>  | 10.02 | <.001    |
| <i>Funtumia elastica</i>               | 191              | 151.1 <sup>a</sup>  | 132.8 <sup>b</sup> | 122 <sup>b</sup>    | 14.26 | <.001    |
| <i>Maesopsis eminii</i>                | 90               | 114.9 <sup>b</sup>  | 129.2 <sup>a</sup> | 105.9 <sup>b</sup>  | 10.85 | <.001    |
| <i>Markhamia lutea</i>                 | 95               | 127.9 <sup>b</sup>  | 172.9 <sup>a</sup> | 106.3 <sup>b</sup>  | 22.08 | <.001    |
| <i>Milicia excelsa</i>                 | 180              | 81.1 <sup>a</sup>   | 72.9 <sup>b</sup>  | 75.2 <sup>ab</sup>  | 10.43 | 0.098    |
| <i>Mimusops bagswawei</i>              | 93               | 149.5 <sup>a</sup>  | 141.6 <sup>a</sup> | 131.4 <sup>b</sup>  | 9.59  | 0.001    |
| <i>Monodora myristica</i>              | 94               | 154 <sup>a</sup>    | 180.1 <sup>a</sup> | 100.4 <sup>b</sup>  | 12.17 | 0.002    |
| <i>Morus mesozygia</i>                 | 93               | 204.5 <sup>a</sup>  | 149.3 <sup>c</sup> | 170.4 <sup>b</sup>  | 18.65 | <.001    |
| <i>Prunus africana</i>                 | 75               | 208.8 <sup>a</sup>  | 199.3 <sup>a</sup> | 204 <sup>a</sup>    | 45.01 | 0.652    |
| <i>Sapium ellipticum</i>               | 96               | 95.2 <sup>b</sup>   | 80 <sup>c</sup>    | 110.5 <sup>b</sup>  | 7.21  | <.001    |
| <i>Sterculia dawei</i>                 | 91               | 39.8 <sup>a</sup>   | 22 <sup>b</sup>    | 25.9 <sup>b</sup>   | 9.82  | <.001    |
| <i>Pachystela brevipes</i>             | 96               | 119.4 <sup>b</sup>  | 153.6 <sup>a</sup> | 154.3 <sup>a</sup>  | 10.96 | <.001    |
| <i>Tabernaemontana holstii</i>         | 175              | 141.1 <sup>a</sup>  | 136.4 <sup>a</sup> | 110.7 <sup>b</sup>  | 14.50 | <.001    |
| <i>Vepris nobilis</i>                  | 96               | 123.7 <sup>ab</sup> | 115.1 <sup>b</sup> | 129.5 <sup>a</sup>  | 8.97  | 0.01     |

Leaves were collected from crown levels: Low = lower, Mid = middle and Top = top parts of the crown

### Relationship between Leaf area and dry leaf weight

Up to 77% of the species exhibited a positive linear relationship ( $r^2 \geq 0.5$ ) between leaf area and leaf dry weight (Appendix 1) some species e.g. *Beilschmedia ugandensis* exhibited a strong positive relationship ( $r^2 = 0.87$ ) (Figure 5a) while *Warburgia ugandensis* showed weak positive ( $r^2 = 0.144$ ) (Figure 5b). Species such as *Vernonia amygdalina* and *Albizia gummifera* however exhibited a weak negative correlation ( $r^2 = -0.110$  and  $-2.466$  respectively (Appendix 1). *Tetrapleura tetrepetra* exhibited no correlation ( $r = 0.004$ ) (Figure 5c). The correlation for 17% of the species was  $\leq 0.4$  and only 6% of the species had negative correlation coefficient (Appendix 1).

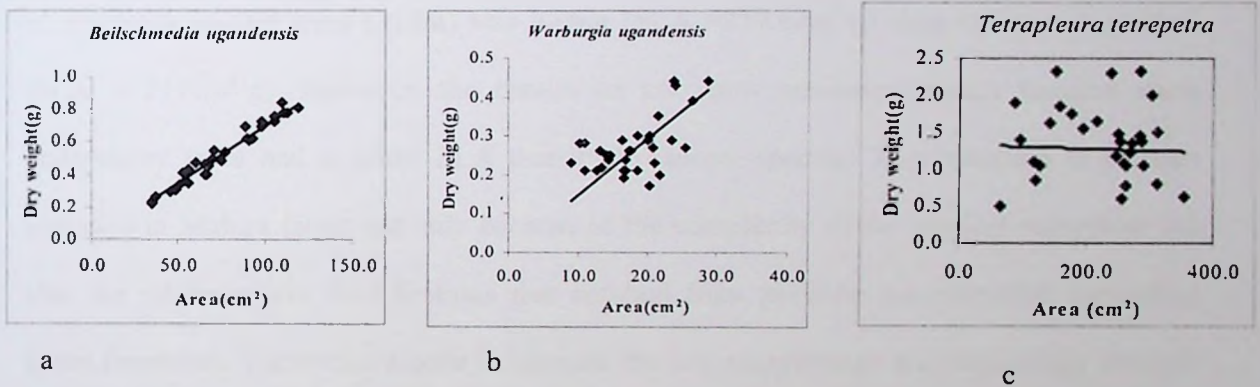


Figure 5: Scatter plots of leaf area and dry leaf weight of selected tree species

## DISCUSSION

### Specific Leaf Area of Mabira Forest tree species

Specific Leaf Area greatly varied between tree species in this study. It varied with tree height, leaf type, crown level and family. These findings are similar with Reich *et al.*, (1999) who obtained varying SLAs for tree species in six different ecosystem sites in both North and South America forests. Significant differences of SLA were also observed between trees and understorey species in a study carried out in a lowland tropical forest in Central Panama (Santiago and Wright (2006). The SLA was between  $38.7\text{cm}^2/\text{g}$  and  $266.8\text{cm}^2/\text{g}$  for trees and  $166.2\text{cm}^2/\text{g}$  and  $298.3\text{cm}^2/\text{g}$  for understorey species. Our findings also reveal that mean SLA of relatively shorter trees ( $\leq 10\text{m}$ ) was higher ( $\text{SLA} = 217.6\text{cm}^2/\text{g}$ ) than taller trees ( $> 50\text{m}$ ) ( $\text{SLA} = 111\text{cm}^2/\text{g}$ ). However, the results do not show consistent trends because some understorey trees had a lower SLA than high canopy species. This variation is perhaps expected in Mabira forest not only because of the complexity of the tropical ecosystem but also the micro-habitat modifications that resulted from previous un-controlled harvesting forest resources. These could have influenced the leaf morphology and physiology through nutrient loss, erosion and others thereby contributing to the observed results of SLA.

Generally taller trees had a lower SLA than shorter trees confirming findings of Rozendaal *et al.* (2006) and Goncalves *et al.* (2005) who found higher SLAs in shade (shorter trees) than in sun leaves (taller trees). However, the trend exhibited by the Mabira tree species were not consistent with those of Rozendaal *et al.*, (2006) because there were wide ranging variations in SLA irrespective of the level of canopy in which species grow.

For instance, *Rhus vulgaris* that grows to about 6m tall had a lower SLA than *Prunus africana* that grows up to 40 metres. This is probably because Mabira forest has undergone a series of irregular harvests and encroachment for agricultural production that opened up parts of the forest for a long time. These activities greatly contributed to nutrient loss that some areas of the forest were being colonised by common savannah species. A number of savannah species e.g. *Acacia hockii* and *A.polyacantha* were observed growing in some parts of the forest. According to Hoffmann *et al.*, (2005), SLA of forest species was 52% greater than that of savannah species. Therefore, *Rhus vulgaris*, a typical savannah species could not have a higher SLA than *Prunus Africana*, a known forest species. The high SLA in forest conditions in their study was attributed to the higher concentrations of N, P and K of the forest as opposed to savannah woodlands. This perhaps explains the higher SLA in *Rhus vulgaris* which is a common woodland species in Uganda.

Leaves that are exposed to light in the canopy are smaller and thicker (Rozendaal *et al.*, 2006, Vile *et al.*, 2005), to prevent overheating and because of this, their photosynthetic capacity is increased through nitrogen capture. Goncalves *et al.*, (2005) in their study of *Swietenia macrophylla* grown under shade and the sun found a higher SLA (SLA =  $178\text{cm}^2/\text{g}$ ) under shade than in the sun (SLA =  $57.4\text{cm}^2/\text{g}$ ). The low SLA for *Swietenia macrophylla* grown under the sun was also associated with higher macronutrient concentrations of Nitrogen, Phosphorous and Potassium. These nutrients significantly influence photosynthetic capacity (Meziane and Shipley, 2001). This implies that such species have higher photosynthetic rates in sun conditions. Tree species that exhibited low SLA, such as *Entandrophragma utile* and *Antiaris toxicaria* are typical upper-storey trees in

Mabira and since low SLA is also associated with thicker leaves (Reich *et al.*, 1998) to resist desiccation due to excessive temperatures, the low SLA obtained for these species is consistent with the above studies and implies that high canopy trees adapt thicker leaves to enhance photosynthetic rates in sunny conditions.

### **Specific Leaf Area at different crown levels**

Leaves that grow in the shaded under-storey, where light is a limiting resource, increase efficiency of light capture through a high SLA (Evans and Poorter, 2001) resulting from high biomass allocation to leaves. As an adaptation, such leaves are thin and feathery because wind and desiccation stresses are lower in the under-storey (Poorter, 1999). However, results from this study contradict by showing that some top leaves (that are more exposed to sunlight) have relatively higher SLA than middle and lower crown leaves. This lack of consistency for most species perhaps is good indicator of the effect of the degradation the forest has undergone. The degradation probably created changes in the structure of the canopy that exposed the lower crown leaves to high sunlight intensities and this probably influenced the adaptation to dissipate off heat and resultantly led to the observed low SLA in some lower crown leaves.

### **Relationship between leaf area and dry leaf weight**

A linear relationship between leaf area and dry weight was obtained for most tree species. However, several differences were observed during leaf collection and measurement. Meziane and Shipley (2001) noted that SLA plays a major role in leaf functioning and is related to the species strategy for resource acquisition and use. Because leaves were picked

from different sites in the forest, at different times of the day, some species could have had high nutrient levels at the time of leaf collection which perhaps influenced the dry weight. Therefore, the dry leaf weight of some species could have been higher or lower than expected resulting in the lack of correlation in some species. On addition, some leaves were perforated by birds and caterpillars and this might have led to a difference between the observed and actual dry leaf weight.

## CONCLUSIONS

Specific Leaf area greatly varies among tree species of Mabira forest. This could be probably due to several biotic and abiotic factors that were not part of this study.

SLA is negatively correlated to tree height. As the height of most trees increases, the SLA reduces. However, this was not consistent for all tree species of Mabira Forest.

Leaf type and family of species significantly influence the SLA of tree species. However, level of tree crown at which leaves were collected did not show a significant influence on leaf area and SLA.

SLA is an important and quick to measure variable that can be used to deduce the response of various physiological and morphological characteristics of plants to any ecosystem changes. For instance we illustrated that SLA is negatively correlated to tree height and leaf area. However, differences in light intensity especially where leaves were collected could be a major influence that will need further research.

## **RECOMMENDATIONS**

Factors that influence the SLA of tree species need to be investigated in detail to understand its relationship to other tree traits. Also the role of such traits in maintenance the ecosystem can be clearly understood.

The relationship between SLA and other morphological and physiological adaptations need to be studied to fully understand the functional role of species in ecosystem processes. this is because some of the results obtained in this study could not be conclusively explained.

The functioning of some physiological processes in trees can be predicted rather than determined by use of proxy variables such as SLA. For instance, we can predict that thicker leaves (i.e. lower SLA) that have probably more chloroplasts have higher photosynthetic rates than species with high SLA. However, this may not be true in all situations because of other biotic and abiotic factors in a tropical forest such as shade, soil and competition for resources e.g. nutrients. Nonetheless, this study is an insight into the physiology of tropical tree species.

## **ACKNOWLEDGEMENT**

We thank the European Union for funding this research under the FOREAIM Project through the Faculty of Forestry and Nature Conservation, Makerere University and all partners in this project. We thank Ron Smith at the Centre for Ecology and Hydrology, U.K. for his part in training me in data analysis techniques and the tree climbers, Robert Angutoko and Patrick Katalo for their services.

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## APPENDICES

### Appendix 1: Specific leaf area, family, leaf type and correlation coefficient for dry weight and leaf area for 117 tree species studied in Mabira Forest

| Species name                                       | Family         | Leaf type     | Number of Leaves sampled | Tree Maximum growth height | Mean Leaf Area | Leaf Area and dry weight Correlation coefficient ( $r^2$ ) | SLA   |
|----------------------------------------------------|----------------|---------------|--------------------------|----------------------------|----------------|------------------------------------------------------------|-------|
| <i>Acacia hockii</i> (De Wild)                     | Fabaceae       | bipinnate     | 14                       | 6                          | 5.99           | 0.564                                                      | 66.8  |
| <i>Acacia polyacantha</i> (Hochst.ex A. Rich)      | Fabaceae       | bipinnate     | 19                       | 8                          | 99.69          | -0.695                                                     | 141.5 |
| <i>Albizia coriaria</i> (Welw.ex.Oliv)             | Fabaceae       | bipinnate     | 31                       | 36                         | 183.61         | 0.733                                                      | 64.6  |
| <i>Albizia ferruginea</i> (Guill. & Perr.)         | Fabaceae       | bipinnate     | 28                       | 45                         | 219.77         | 0.662                                                      | 167.6 |
| <i>Albizia glaberrima</i> (Schumach. & Thonn.)     | Fabaceae       | bipinnate     | 31                       | 30                         | 119.50         | 0.829                                                      | 114.4 |
| <i>Albizia grandibracteata</i> (Taub.)             | Fabaceae       | bipinnate     | 94                       | 20                         | 80.06          | 0.508                                                      | 83    |
| <i>Albizia gummifera</i> (J.F.Gmel)                | Fabaceae       | bipinnate     | 33                       | 20                         | 126.39         | -2.466                                                     | 128   |
| <i>Albizia zygia</i> (DC.)Macbr                    | Fabaceae       | bipinnate     | 18                       | 30                         | 86.29          | 0.819                                                      | 89.7  |
| <i>Alstonia boonei</i> (De Wild)                   | Apocynaceae    | simple        | 125                      | 65                         | 47.12          | 0.382                                                      | 126.6 |
| <i>Aningeria altissima</i> (A. Chev.)              | Sapotaceae     | simple        | 31                       | 50                         | 40.81          | 0.803                                                      | 118.3 |
| <i>Antiaris toxicaria</i> (Rumph. ex.pers.) Lesch. | Moraceae       | simple        | 91                       | 40                         | 20.47          | 0.415                                                      | 60.7  |
| <i>Baikiaea insignis</i> (Benth.)                  | Fabaceae       | imparipinnate | 16                       | 35                         | 326.39         | 0.443                                                      | 124   |
| <i>Balanites wilsoniana</i> (Dawe & Sprague)       | Balanitaceae   | bi-foliolate  | 60                       | 30                         | 38.49          | 0.392                                                      | 132.4 |
| <i>Beilschmiedia ugandensis</i> (Rendle)           | Lauraceae      | simple        | 30                       | 45                         | 75.17          | 0.960                                                      | 146.4 |
| <i>Bequaertiodendron oblanceolatum</i> (S.Moore)   | Sapotaceae     | simple        | 95                       | 15                         | 51.78          | 0.596                                                      | 120.2 |
| <i>Bersama abyssinica</i> (Fresen.)                | Meliaceae      | imparipinnate | 19                       | 15                         | 583.08         | 0.873                                                      | 141.6 |
| <i>Blighia unijugata</i> (Bak.)                    | Sapindaceae    | paripinnate   | 94                       | 25                         | 27.00          | 0.834                                                      | 122   |
| <i>Bombax buonapozense</i> (P.Beauv.)              | Bombacaceae    | digitate      | 31                       | 75                         | 107.55         | 0.904                                                      | 143.1 |
| <i>Bridelia micrantha</i> (Hochst.) Baill.)        | Euphorbiaceae  | simple        | 32                       | 13                         | 48.35          | 0.787                                                      | 101.5 |
| <i>Canarium schweinfurthii</i> (Engl.)             | Burseraceae    | imparipinnate | 10                       | 40                         | 682.16         | 0.885                                                      | 116.1 |
| <i>Celtis africana</i> ((Burm.f.)                  | Ulmaceae       | simple        | 48                       | 35                         | 14.85          | 0.596                                                      | 214.2 |
| <i>Celtis gomphophylla</i> (Engl.)                 | Ulmaceae       | simple        | 94                       | 15                         | 36.66          | 0.608                                                      | 196.2 |
| <i>Celtis mildbraedii</i> (Engl.)                  | Ulmaceae       | simple        | 28                       | 50                         | 19.59          | 0.509                                                      | 103.8 |
| <i>Celtis wightii</i> (Planch.)                    | Ulmaceae       | simple        | 62                       | 20                         | 63.81          | 0.487                                                      | 111.8 |
| <i>Celtis zenkeri</i> (Engl.)                      | Ulmaceae       | simple        | 95                       | 40                         | 71.16          | 0.886                                                      | 188.9 |
| <i>Chrysophyllum albidum</i> (G.Don)               | Sapotaceae     | simple        | 95                       | 60                         | 168.30         | 0.856                                                      | 86    |
| <i>Chrysophyllum muerense</i> (Engl.)              | Sapotaceae     | simple        | 90                       | 40                         | 50.11          | 0.908                                                      | 169.7 |
| <i>Clausena anisata</i> (Willd.)                   | Rutaceae       | imparipinnate | 15                       | 10                         | 128.62         | 0.997                                                      | 258.8 |
| <i>Cola gigantea</i> (A. Chev)                     | Sterculiaceae  | simple        | 47                       | 35                         | 994.38         | 0.653                                                      | 121.8 |
| <i>Combretum molle</i> (G.Don)                     | Combretaceae   | simple        | 32                       | 17                         | 102.14         | 0.869                                                      | 101.4 |
| <i>Cordia africana</i> (Lam.)                      | Boraginaceae   | simple        | 31                       | 15                         | 188.31         | 0.917                                                      | 138.4 |
| <i>Cordia millenii</i> (Baker)                     | Boraginaceae   | simple        | 31                       | 35                         | 246.86         | 0.521                                                      | 100.3 |
| <i>Craibia brownii</i> (Dunn.)                     | Fabaceae       | imparipinnate | 25                       | 20                         | 179.52         | 0.629                                                      | 163.2 |
| <i>Croton macrostachyus</i> (Delile)               | Euphorbiaceae  | simple        | 90                       | 5                          | 119.70         | 0.799                                                      | 64.9  |
| <i>Croton megalocarpus</i> (Hutch)                 | Euphorbiaceae  | simple        | 24                       | 40                         | 64.15          | 0.938                                                      | 311.4 |
| <i>Croton sylvaticus</i> (Krauss)                  | Euphorbiaceae  | simple        | 29                       | 30                         | 40.21          | 0.577                                                      | 139.1 |
| <i>Diospyros abyssinica</i> (Hiern) F.White)       | Ebenaceae      | simple        | 96                       | 40                         | 28.41          | 0.469                                                      | 97.4  |
| <i>Dovyalis macrocalyx</i> (Oliv.) Warb.)          | Flacourtiaceae | simple        | 29                       | 8                          | 12.56          | 0.695                                                      | 220.4 |
| <i>Dracaena fragrans</i> (L.) Ker-Gawl             | Agavaceae      | palmate       | 32                       | 5                          | 179.73         | 0.821                                                      | 112.4 |

|                                                 |                |               |     |    |         |        |       |
|-------------------------------------------------|----------------|---------------|-----|----|---------|--------|-------|
| <i>Dracaena steudneri</i> (Engl.)               | Agavaceae      | palmate       | 32  | 18 | 993.20  | 0.700  | 98.7  |
| <i>Drypetes ugandensis</i> (Rendle) Hutch       | Euphorbiaceae  | simple        | 62  | 20 | 74.55   | 0.682  | 149.5 |
| <i>Ehretia cymosa</i> (Thonn.)                  | Boraginaceae   | simple        | 32  | 20 | 72.14   | 0.873  | 143.7 |
| <i>Entada abyssinica</i> (Steud. ex A. Rich)    | Fabaceae       | bipinnate     | 17  | 10 | 143.40  | 0.296  | 181.8 |
| <i>Entandrophragma angolense</i> (Welw.)        | Meliaceae      | paripinnate   | 16  | 50 | 686.85  | 0.925  | 115.4 |
| <i>Entandrophragma cylindricum</i> (Sprague)    | Meliaceae      | paripinnate   | 31  | 55 | 376.88  | 0.238  | 124.9 |
| <i>Entandrophragma utile</i> (Dawe & Sprague)   | Meliaceae      | paripinnate   | 10  | 50 | 641.99  | 0.517  | 87.1  |
| <i>Erythrina abyssinica</i> (Lam.)              | Fabaceae       | tri-foliolate | 32  | 12 | 178.20  | 0.835  | 173.7 |
| <i>Erythrina excelsa</i> (Bak.)                 | Fabaceae       | tri-foliolate | 32  | 30 | 160.28  | 0.836  | 343.1 |
| <i>Fagaropsis angolensis</i> (Engl.)            | Rutaceae       | imparipinnate | 16  | 20 | 211.96  | 0.906  | 126.9 |
| <i>Ficus exasperata</i> (Vahl.)                 | Moraceae       | simple        | 63  | 25 | 62.42   | 0.806  | 165.1 |
| <i>Ficus mucuso</i> (Welw. ex Warb.)            | Moraceae       | simple        | 27  | 30 | 85.80   | 0.841  | 165   |
| <i>Ficus natalensis</i> (Hochst)                | Moraceae       | simple        | 35  | 30 | 22.22   | 0.886  | 130.9 |
| <i>Ficus ovata</i> (Vahl)                       | Moraceae       | simple        | 26  | 15 | 191.62  | 0.762  | 195.6 |
| <i>Ficus sur</i> (Engl.)                        | Moraceae       | simple        | 60  | 20 | 73.93   | 0.723  | 303.5 |
| <i>Ficus vallis-choudae</i> (Del.)              | Meliaceae      | simple        | 96  | 20 | 98.04   | 0.710  | 146.3 |
| <i>Flueggea virosa</i> ((Willd.) Voigt)         | Euphorbiaceae  | simple        | 31  | 7  | 11.86   | 0.570  | 388.8 |
| <i>Funtumia africana</i> (Benth.)               | Apocynaceae    | simple        | 30  | 30 | 81.51   | 0.939  | 219.7 |
| <i>Funtumia elastica</i> (Preuss)               | Apocynaceae    | simple        | 96  | 40 | 80.45   | 0.007  | 138.3 |
| <i>Guarea cedrata</i> (A. Chev.)                | Meliaceae      | paripinnate   | 29  | 45 | 105.52  | 0.558  | 139.2 |
| <i>Hallea stipulosa</i> (DC.) Kuntze            | Rubiaceae      | simple        | 28  | 30 | 227.18  | 0.752  | 117.4 |
| <i>Harrisonia abyssinica</i> (Oliv.)            | Simaroubaceae  | imparipinnate | 31  | 12 | 46.09   | 0.910  | 327.1 |
| <i>Harungana madagascariensis</i> (Poir)        | Guttiferae     | simple        | 35  | 25 | 43.86   | 0.012  | 89.9  |
| <i>Holoptelea grandis</i> (Hutch)               | Ulmaceae       | simple        | 64  | 50 | 57.20   | 0.816  | 171.5 |
| <i>Khaya anthotheca</i> (Welw.)                 | Meliaceae      | paripinnate   | 10  | 60 | 577.70  | 0.645  | 74.2  |
| <i>Kigelia africana</i> (Lam.) Benth.)          | Bignoniaceae   | imparipinnate | 68  | 18 | 358.12  | 0.235  | 121.3 |
| <i>Lannea welwitschii</i> (Hiern) Engl.)        | Anacardiaceae  | imparipinnate | 22  | 30 | 465.07  | 0.500  | 144.4 |
| <i>Lecaniodiscus fraxinifolius</i> (Bak.)       | Sapindaceae    | paripinnate   | 26  | 18 | 69.03   | 0.940  | 137.8 |
| <i>Leptonychia mildbraedii</i> (Engl.)          | Sterculiaceae  | simple        | 95  | 10 | 21.27   | -0.370 | 70.9  |
| <i>Lovoa trichilioides</i> (Harms.)             | Meliaceae      | paripinnate   | 32  | 40 | 292.92  | 0.325  | 115.6 |
| <i>Maesa lanceolata</i> (Forsk)                 | Myrsinaceae    | simple        | 31  | 5  | 132.47  | 0.783  | 342.8 |
| <i>Maesopsis eminii</i> (Engl.)                 | Rhamnaceae     | simple        | 90  | 30 | 16.81   | 0.588  | 116.7 |
| <i>Manilkara dawei</i> (Stapf) Chiov.           | Sapotaceae     | simple        | 30  | 25 | 21.57   | 0.642  | 174.2 |
| <i>Margaritaria discoidea</i> (Baill.) Webster) | Euphorbiaceae  | simple        | 32  | 25 | 128.32  | 0.717  | 112.3 |
| <i>Markhamia lutea</i> (Barker) Sprague)        | Bignoniaceae   | imparipinnate | 95  | 15 | 69.39   | 0.824  | 135.3 |
| <i>Mildbraediodendron excelsum</i> (Harms.)     | Fabaceae       | paripinnate   | 30  | 50 | 131.69  | 0.919  | 132.6 |
| <i>Milicia excelsa</i> (Welw.)                  | Moraceae       | simple        | 180 | 45 | 78.86   | 0.351  | 76.4  |
| <i>Mimusops bagswawei</i> (S. Moore)            | Sapotaceae     | simple        | 93  | 40 | 42.56   | 0.642  | 140.9 |
| <i>Monodora myristica</i> (Gaertn.) Dunal)      | Annonaceae     | simple        | 94  | 30 | 108.01  | 0.393  | 144.6 |
| <i>Morinda lucida</i> (Benth.)                  | Rubiaceae      | simple        | 32  | 18 | 67.91   | 0.864  | 269.2 |
| <i>Morus mesozygia</i> (Sim.)                   | Moraceae       | simple        | 93  | 45 | 32.38   | 0.627  | 175   |
| <i>Myrianthus holstii</i> (Engl.)               | Moraceae       | palmate       | 32  | 20 | 1575.71 | 0.761  | 46.5  |
| <i>Neoboutonia macrocalyx</i> (Pax)             | Euphorbiaceae  | simple        | 25  | 25 | 308.68  | 0.553  | 180.8 |
| <i>Olea welwitschii</i> (Knobl.)                | Oleaceae       | simple        | 31  | 25 | 77.97   | 0.233  | 141.1 |
| <i>Oncoba spinosa</i> (Forssk.)                 | Flacourtiaceae | simple        | 10  | 10 | 75.40   | 0.478  | 714   |
| <i>Pachystela brevipes</i> (Baker) Engl.        | Sapotaceae     | simple        | 96  | 35 | 20.51   | 0.054  | 134.5 |
| <i>Parkia filicoidea</i> (Welw. ex Oliv)        | Fabaceae       | bipinnate     | 11  | 30 | 112.78  | -0.285 | 338   |
| <i>Paropsia guineensis</i> (Oliv.)              | Passifloraceae | simple        | 62  | 25 | 48.60   | 0.759  | 492.5 |
| <i>Piptadeniastrum africanum</i> (Hook.f.)      | Fabaceae       | bipinnate     | 29  | 50 | 54.44   | 0.888  | 51    |
| <i>Polyscias fulva</i> (Hiern) Harms)           | Araliaceae     | imparipinnate | 10  | 30 | 997.10  | 0.141  | 127.7 |

|                                                    |               |               |     |    |        |        |       |
|----------------------------------------------------|---------------|---------------|-----|----|--------|--------|-------|
| <i>Prunus africana</i> (Hook.f.) Kalkman           | Rosaceae      | simple        | 75  | 40 | 38.27  | 0.569  | 204.4 |
| <i>Pseudospondias microcarpa</i> (A. Rich.) Engl.) | Anacardiaceae | imparipinnate | 18  | 30 | 331.68 | 0.876  | 117.2 |
| <i>Rauvolfia vomitoria</i> (Afzel.)                | Apocynaceae   | simple        | 25  | 20 | 284.82 | 0.927  | 224.6 |
| <i>Rhus vulgaris</i> (Meikle)                      | Anacardiaceae | tri-foliolate | 32  | 6  | 41.03  | 0.946  | 112.9 |
| <i>Ricinodendron heudelotii</i> (Baill.) Heckel)   | Euphorbiaceae | digitate      | 32  | 45 | 39.62  | 0.844  | 106.2 |
| <i>Rinorea ardisiaeflora</i> (Welw.ex Oliv.)       | Violaceae     | simple        | 10  | 10 | 73.07  | 0.820  | 81.3  |
| <i>Rothmannia urcelliformis</i> (Hiern)            | Rubiaceae     | simple        | 32  | 10 | 28.84  | 0.810  | 205.1 |
| <i>Sapium ellipticum</i> (Krauss) Pax)             | Euphorbiaceae | simple        | 96  | 20 | 39.95  | 0.516  | 95.2  |
| <i>Schrebera arborea</i> (A. Chev.)                | Oleaceae      | simple        | 32  | 15 | 56.78  | 0.708  | 103.6 |
| <i>Spathodea campanulata</i> (P.Beauv.)            | Bignoniaceae  | imparipinnate | 20  | 15 | 531.75 | 0.769  | 82.6  |
| <i>Sterculia dawsoni</i> (Sprague)                 | Sterculiaceae | simple        | 30  | 30 | 180.58 | 0.774  | 76.5  |
| <i>Stereospermum kunthianum</i> (Cham.)            | Bignoniaceae  | imparipinnate | 25  | 13 | 220.01 | 0.930  | 105.4 |
| <i>Strychnos mitis</i> (S. Moore)                  | Loganiaceae   | simple        | 32  | 24 | 17.89  | 0.913  | 211.6 |
| <i>Tabernaemontana holstii</i> (K.Schum.)          | Apocynaceae   | simple        | 175 | 10 | 217.42 | 0.616  | 129.9 |
| <i>Terminalia glaucescens</i> (Benth.)             | Combretaceae  | simple        | 32  | 13 | 166.57 | 0.853  | 141.1 |
| <i>Tetrapleura tetraptera</i> (Schumach. & Thonn.) | Fabaceae      | bipinnate     | 30  | 30 | 220.90 | -0.939 | 188.6 |
| <i>Treculia africana</i> (Decne)                   | Moraceae      | simple        | 31  | 25 | 181.19 | 0.839  | 89.9  |
| <i>Trelepisium madagascariensis</i> (Baill)        | Rutaceae      | simple        | 62  | 30 | 20.73  | -0.214 | 186   |
| <i>Trema orientalis</i> (L.) Bl.                   | Ulmaceae      | simple        | 30  | 12 | 43.85  | 0.702  | 202.2 |
| <i>Trichilia dregeana</i> (Sond.)                  | Meliaceae     | imparipinnate | 30  | 30 | 92.60  | 0.799  | 167.2 |
| <i>Turraea robusta</i> (Guerke)                    | Meliaceae     | simple        | 27  | 12 | 51.06  | 0.854  | 550.9 |
| <i>Vangueria apiculata</i> (K.Schum.)              | Moraceae      | simple        | 50  | 15 | 90.91  | 0.668  | 149.8 |
| <i>Vepris nobilis</i> (Baill.)                     | Rubiaceae     | simple        | 96  | 12 | 56.90  | 0.678  | 122.8 |
| <i>Vernonia amygdalina</i> (Delile)                | Asteraceae    | simple        | 20  | 4  | 350.71 | 0.597  | 347.7 |
| <i>Vernonia auriculifera</i> (Hiern)               | Asteraceae    | simple        | 21  | 10 | 63.54  | -0.110 | 259.1 |
| <i>Vitex amboniensis</i> (Guerke)                  | Verbenaceae   | digitate      | 15  | 15 | 297.65 | 0.358  | 284.5 |
| <i>Warburgia ugandensis</i> (Sprague)              | Canellaceae   | simple        | 32  | 42 | 18.07  | 0.144  | 68.5  |
| <i>Zanthoxylum gillettii</i> (Engl.)               | Rutaceae      | imparipinnate | 13  | 30 | 530.32 | 0.654  | 288   |

## Appendix 2: Generalized Linear Model output for effect of selected variables on SLA

| Change                     | d.f. | s.s.   | m.s.   | v.r. | F pr. |
|----------------------------|------|--------|--------|------|-------|
| +Tree height               | 1    | 0.3154 | 0.3154 | 9.6  | 0.003 |
| + Number of leaves sampled | 1    | 0.1134 | 0.1134 | 3.4  | 0.067 |
| + Leaf type                | 1    | 0.1459 | 0.1459 | 4.4  | 0.039 |
| +Family                    | 35   | 1.9982 | 0.0571 | 1.7  | 0.023 |
| Residual                   | 78   | 2.57   | 0.033  |      |       |

### CHAPTER THREE

## **Deriving functional groups for Mabira Forest tree species and predicting their potential role in forest restoration**

### **Abstract**

This study was done to: derive functional groups among tree species of Mabira Forest; describe the characteristics of derived functional groups; and predict the role of each functional group in restoring a degraded forest. We used a functional approach based on 18 morphological characteristics e.g. Leaf, bark, stem, flower, sex and defence to classify 100 tree species into groups of similar characteristics. The characters were compiled from literature about flora of Uganda. Leaf area and Specific Leaf Area were determined by collecting leaves and measuring leaf area using "Compu eye leaf area" computer software. Hierarchical cluster analysis with Genstat was used to generate the groups. Seven functional groups were obtained each represented by 3-39 species. The groups include: Compound leaved forest non dependent species, Relatively short simple leaved pioneers, Simple leaved secondary successional species, Simple leaved forest interior species, Undefined group, Compound leaved secondary succesional species and Compound leaved shade tolerant species. The groups represent species in the various successional stages. We recommend replanting recently degraded sites with: Short-simple leaved pioneers (Group Two), Simple leaved secondary successional (Group 3) for medium degraded sites and compound leaved shade tolerant species (Group Seven) in areas that experienced disturbance more than 20 years ago.

**Keywords:** *Restoration, Forest ecosystem and classification*

## INTRODUCTION

Large areas of the world's tropical forests have been degraded, with the resultant loss of species diversity (Lamb, 1998). Forest degradation is one of the major challenges facing conservationists and the rate at which it is occurring appears to be increasing (FAO, 1997). For instance, Uganda's deforestation rate stands at about 2% (FAO) due to the increased interest in the utilization of forest resources to improve livelihoods through productive agriculture, resource exploitation, industrialization and urbanisation. A key question is how do we aid restoration of biodiversity over such large areas of tropical forest that are struggling with natural recovery?

In many cases, natural recovery is unlikely to succeed because the degraded site is often subject to recurrent disturbances such as fire, grazing or continued illegal harvesting of resources. In other cases, natural succession may allow recovery to occur but this is only possible if sufficient residual forest remains nearby to act as a source of germplasm for the recovering forest (Lamb, 1998). The critical ecological dilemma is that when a species is lost, we do not know what function is lost with it; therefore, we need to understand the role of all ecosystem components in maintaining its complexity and use such knowledge in undertaking any conservation efforts. Ecologists are working towards aided restoration. However, ecosystems are characterised by large numbers of plant and animal species. As a result, the task of understanding the role(s) of individual species in ecosystem maintenance is quite cumbersome using conventional research approaches. This can be over-come by generating classes of species that are more likely to perform a given function in the ecosystem basing on their observed characteristics.

Classifying forest ecosystem components into groups of species that perform similar ecological function(s) (i.e. functional classification) is a simplified approach that would aid decision making on choice of species for spatial or sequential introduction in the recovering ecosystem. Functional classification has been used in various ways e.g.; predicting ecological effects of global change (Wooward and Diament, 1991), understanding ecosystem processes (Arndt, 2006; Chapin *et al.*, 1996) and describing vegetation types (Semenova and Van der maarel., 2000). This approach which aims at understanding the behaviour of plants in relation to their growth environmental conditions (Semenova and Van der maarel. 2000) is needed in tropical ecosystems to simplify descriptions and predictions of forest dynamics (Gitay *et al.*, 1999).

There are several approaches used by ecologists in classifying plants but the method used depends on the interest of the scientist. However, Box (1996) suggested that using a structural-functional approach to classifying plants permits the use of visible structural attributes of species as surrogates for functional patterns. However, function is very difficult to define because plants change with environmental conditions, along gradients and evolutionarily, therefore, functional traits have to be carefully chosen to reflect important or valued elements (Craig *et al.*, 2005). The selection of function in this study was based on the purpose of this study i.e. restoration. Therefore, morphological and physiological characteristics that influence growth and survival in a forest ecosystem were selected for this study.

Gitay and Noble (1997) described three approaches for developing functional classifications: subjective, deductive and data driven. A data driven approach was chosen for this study because multivariate techniques are used to generate clusters of species based on a set of morphological characters. Such data are available and the resultant outputs can be easily interpreted. Boutin and Keddy (1993) recommended; identifying the function, selection of functional traits, screening the traits, forming a similarity matrix and classification as the strategy for constructing functional groups. The generated functional groups are then used to make simple predictive ecological models depending on the interest of the researcher. The functional groups can then be further investigated to determine their role restoration and general ecosystem functioning.

### **Functional classification and ecosystems stability**

Ecosystems are maintained when local climate, soil resource supply, disturbance regimes and functional groups alternate within stable boundaries (Chapin *et al.* 1996). Sustainable ecosystems are therefore those that maintain diversity of major functional groups and productivity. Continued species extinction invariably leads to irreversible degradation of ecosystem functions (Fonseca and Ganade, 2001). The functions are many but those involved, for instance, in the maintenance of biogeochemical and hydrological cycles, climate control, decomposition and soil formation, pest control and pollination have to be maintained (Fonseca and Ganade, 2001).

Functions are maintained by different species of the ecosystem but some species could locally go extinct without a substantial loss in ecosystems (Walker, 1992). The loss could be

probably because some species in a particular functional group play similar roles. Evaluating the degree of functional redundancy can be done by generating functional groups for forest ecosystem components. However, this requires an agreed definition of a functional group (Fonseca and Ganade. 2001). This study is focussing on classification of species in relation to their potential role in the recovery of a degraded forest ecosystem.

### **Tree species adaptation to ecosystem processes**

Different tree species adapt in various ways to survival in their successional hierarchy. Several authors (e.g. Connell and Slatyer, 1977) have described the sequence of succession. These authors agree that certain species usually appear first because they have evolved “colonizing” characteristics such as the ability to produce large numbers of propagules, have good dispersal powers, survive in dormant state for a long time, and grow quickly to maturity. On the other hand, later successional species exhibit buttressing as an adaptation for support among taller trees (Archibold, 1995), compound leaves (Givinish, 1988), and leaf replacement (deciduousness) are more likely an adaptation for heat dissipation (Gates *et al.*, 2005). Re-sprouting (Noble and Slatyer, 1980) and vegetative reproduction (McIntyre *et al.* 1995) found these adaptations to be important in post disturbance regeneration. Therefore, these structural attributes that are adaptations for growth at the various stages of forest development can be the basis for determine the best suite of species for restoration of a degraded forest system.

However, adaptation of tree species to a particular environment rarely depends on a single attribute; rather an integrated functioning of a whole suite of characters. It is therefore

important to employ methods which aim to harness variation in a wide range of traits to form groups of functionally similar plants. Adaptation to germinate and grow under varying environmental conditions depends on both physiological and morphological characters and this was the basis for choice of characters. The question here nevertheless is how do we use this knowledge on adaptation to facilitate quicker restoration of a forest that is at different levels of recovery?

The purpose of this study was to generate groups of functionally similar woody species from Mabira Forest and use the groups to predict their suitability in restoration of the forest. The objectives of the study were to: 1). derive functional groups using selected morphological characteristics; 2). describe the morphological characteristics of generated functional groups; and 3). predict the role of the functional groups in restoring the various parts of a degraded forest. The findings will assist in selection of species that are adapted in space and time for restoration of Mabira Forest and ultimately other tropical forests.

## **METHODS AND STUDY AREA**

### **Location**

The study was carried out in Mabira Forest Reserve located between 32° 52' -33° 07'E and 0°24' -0°35' N (Davenport *et al.*, 1996) in central Uganda. The forest covers an area of 306 km<sup>2</sup> and has an altitudinal range of 1070 -1340 m.a.s.l. The forest is about 52 km from Kampala city towards the east.

### **Soil types**

Most of the underlying rocks are granitic gneiss and granites of the Buganda –Toro system (Pallister, 1959). The rock has undergone chemical weathering over time because of the equatorial climate and humid conditions. The soils are of the ferrallitic types which are in the final stage of tropical weathering. They consist of red soils on slopes and black clays in the valley bottoms often referred to as 'Buganda catena.

### **Climate**

The climate is characterised by small seasonal variations in temperature, humidity and wind throughout the year. The temperatures are typical of the equatorial region but proximity of the forest to Lake Victoria and an altitude of more than 1000 m have a moderating effect on temperatures. The forest experiences maximum temperatures of 27°C between January – March and average minimum of 22°C between July and August. The rainfall is well distributed throughout the year but with peaks in April-May and October to November. Total annual rainfall ranges between 1375 and 1524 mm (Komutunga and Musiitwa 2001).

## Flora and Fauna

Mabira forest is the largest block of medium altitude moist semi-deciduous forest in central Uganda. Compared to 65 other Ugandan Forests, Mabira is described as relatively biodiverse. It has approximately 312 different tree species, 287 bird species, 23 different types of mammals, 21 butterfly and 97 large moth species (Davenport *et al.*, 1996). A number of mammals such as the blue and red tail monkeys, pigs, bush bucks and forest duickers (Davenport *et al.*, 1996) still exist in the forest.

Mabira forest is characteristic of vegetation types representing sub-climax or human altered plant communities; consequently, three vegetation sub-types are recognized: young colonizing forest, mature mixed forest and *Celtis* mixed forest. The young colonizing Forest covers approximately 2.7% of the total area and it's mainly in zones of the forest that had been encroached in the past or has undergone unregulated harvesting. The dominant species in these parts are *Broussonetia papyrifera*. Nonetheless, both understory and upper story tree species such as *Diospyros* and *Trelepisium* respectively are occasionally encountered in this forest type but in small quantities.

The Mature mixed forest occupies about 52% of the area (Davenport *et al.*, 1996). The lower canopy trees are dominated by *Diospyros abyssinica* and *Funtumia elastica* and the canopy trees include: *Chrysophyllum* species and *Albizia* species. Nevertheless, *Celtis* species makes up the highest number of growing stock.

Six species of *Celtis*: *C. zenkeri*, *C. wightii*, *C. mildbraedii*, *C. durandii*, *C. africana* and *C. adolfi-friedericii* dominate the *Celtis* Forest type. These species dominate the upper story, therefore giving it the composition and character of a *Celtis* Dominated forest type. The *Celtis* species are normally associated with *Albizia glaberrima*, *Albizia ferruginea* and *Chrysophyllum* species.

### **Management history of Mabira Forest Reserve**

Mabira Forest Reserve was gazetted as a central forest reserve under legal notice no. 87 of 1932 with an area of 29,592 ha. This was initially gazetted as a local forest reserve managed by the Buganda Kingdom but later transferred to the central government under statutory instrument 176 of 1968 and therefore its control was vested in the Forestry department. At its gazettelement, there were about 27 human settlement enclaves that were completely or partly surrounded by the forest and these are ecologically part of the forest. These communities and the forest impact on each other in various ways.

However due political instability in early 1970s, illegal crop farming started resulting in the breakdown of law and order and by 1981, 7860 ha (26.2%) of the forest was already occupied by about 1800 encroachers (Karani *et al.*, 1997). However the government evicted all the encroachers in 1988. The previously encroached sites are dominated by invasive plant species such as *Broussonetia papyrifera* and *Lantana camara*.

### **Sampling design**

Mabira Forest was clustered into utilization zones by the Forest Department –the body that was then charged with managing all government forest reserves and these zones determine

the management approach of the forest (Figure 1). The major utilization zones include: 1) Production zone, where harvesting of timber and wood was permitted. Concessions were given to timber dealers to harvest but because of poor supervision of the activities, concessioners would surpass the permitted harvesting levels seriously degrading the forest; (2) buffer zone: this was a zone permitted for recreational purposes and minimum impact harvesting. (3) Strict nature reserve was preserved for research and monitoring the health of the forest. However the forest under-went immense management problems that resulted in haphazard harvesting in almost all parts of the forest. The zoning for this study is therefore directly linked to these old management zones. The zoning was majorly based on the nature of current vegetation and history of management and these classes form the basis for restoration. Seven classes were obtained for the Mabira forest reserve and are described below:

#### **(i) Recently abandoned sites**

Trees in these parts of the forest were heavily harvested for timber and fuel wood. Subsequently annual crops such as Maize and Sweet potatoes were grown by the encroachers. The sites were abandoned in the last 1-3 years. The vegetation was mainly comprised of herbs and grasses and they were characterised by tree stumps of felled trees. A few species such as *Albizia glaberrima*, *Vernonia auriculifera* and others were beginning to sprout in these sites.

#### **(ii) Disturbed 3-10 years ago**

Logging took place 3-10 year ago but the site was abandoned because high quality timber and charcoal trees were finished. Many of the sites in this category were characterised by

young trees less than 10cm diameter but there was plenty of invasive species such *Broussonetia papyrifera* and a few less desirable mature trees mainly *Ficus spp.* There were some cocoa trees in some of these sites indicating some abandoned agricultural activities.

### **(iii) Young secondary forest**

This forest is assumed to have been abandoned 10-20 years ago because there was regeneration of typical forest species such as *Celtis spp.*, *Maesopsis eminii*, *Blighia unijugata* and others. However, most of the species were of low diameter class (0-20cm) but with occasional mature trees of low class timber including *Ficus mucosa*. Invasive species such *Broussonetia papyrifera* and *Lantana camara* could occasionally be encountered in this site.

### **(iv) Old secondary forest**

This was last disturbed 21-30 years ago. *Celtis spp.*, *Trichilia dregeana* and *Antiaris toxicaria* could be seen in this site. Tree diameter was varying but there were saplings of species such as *Lovoa trichilioides*, *Holoptelea grandis* and *Maesopsis eminii* that was at least over 40 cm in diameter. Occasionally, undergrowth would be encountered in some parts of the sites but overall, the forest was showing signs of recovering from previous degradation.

### **(v) Very old secondary forest**

This could have been disturbed 30-55 years ago but there were also occasional gaps of recent felling of trees in the last 5-10 years. This was probably a sign of illegal activities in the site. Most of these sites were the buffer zones in the old zoning by the Forest department. Tree

species such as *Albizia zygia*, *Milicia excelsa* that were over 40 cm in diameter were occasionally found. Forest undergrowth was rare but there were many tree saplings and seedlings.

**(vi) Almost intact secondary forest**

These sites were presumed to have been disturbed over 55 years ago and by nature of management, they were supposed to be “strict nature reserve”. However, due to breakdown of rule of law, some of the sites were degraded through illegal harvesting of forest resources. The site has been undergoing un-interrupted recovery over time. The dominant trees were *Celtis* species but there was observable representation of other important tree species in this forest site.

**(vii) Presumably undisturbed forest**

This site was mostly found in what was described as “strict nature reserve”. These strict nature reserves were highly protected by the forest managers because they were left purposely for research and monitoring the health of the forest. The forest floor was mainly composed of vegetation commonly found in mature forests such as *Marantochloa* species and dead wood and leaf litter.



Figure 1: Map of Mabira Forest Reserve showing the management zones and data collection sites

### Morphological characteristics for functional analysis

Data on the morphological characteristics of the selected tree species were compiled from publications on trees and shrubs of Uganda. Literature used include: Hamilton (1991), Katende *et al.* (1995), and Flora of Tropical East Africa (FTEA) (series). Leaf traits were measured and assessed as described in Chapter 2. A total of 18 morphological characteristics selected for cluster analysis are described in Table 1.

Table 1: Morphological characteristics compiled for the 100 tree species in the study

|                          | Description                                                        | Previous use by author                                  |
|--------------------------|--------------------------------------------------------------------|---------------------------------------------------------|
| <b>Site conditions</b>   |                                                                    |                                                         |
| Elevation                | Minimum and Maximum altitude (masl)                                |                                                         |
| Eco-type                 | Common growing habitat                                             |                                                         |
| FTEA Zone (U1-U4)        | Geographical ranges (floral regions) for Uganda                    |                                                         |
| <b>Traits</b>            |                                                                    |                                                         |
| <b>Leaf</b>              |                                                                    |                                                         |
| Leaf retention           | Deciduous or evergreen species                                     | Archibold (1995)                                        |
| Leaf area                | cm <sup>2</sup>                                                    | Box (1996)                                              |
| Leaf texture             | (Upper and lower )Smooth, rough                                    |                                                         |
| Specific leaf area (SLA) | cm <sup>2</sup> /g                                                 |                                                         |
| Leaf type                | Simple or compound,                                                |                                                         |
| Leaf shape               | Elliptic, oblong etc.                                              |                                                         |
| Compound leaf type       | Bipinnate, trifoliolate, bifoliolate, paripinnate or imparipinnate |                                                         |
| <b>Bark</b>              |                                                                    |                                                         |
| Bark thickness           | Thick or thin                                                      | Hegde <i>et al.</i> (1998)                              |
| Bark colour              | Observed bark colour                                               |                                                         |
| Bark texture             | Smooth to rough                                                    |                                                         |
| <b>Reproductive</b>      |                                                                    |                                                         |
| Flower sex               | Unisexual or bisexual                                              | Archibold (1995)                                        |
| Inflorescences           | Yes or No                                                          |                                                         |
| Multi-stems              | Present or not                                                     |                                                         |
| Resprouting ability      | Yes or No                                                          | McIntyre <i>et al.</i> (1999), Noble and Slatyer (1980) |
| <b>Others</b>            |                                                                    |                                                         |
| Successional status      | Pioneer, secondary or climax                                       | Hafashimana (2001)                                      |
| Height                   | Maximum (m)                                                        | McIntyre <i>et al.</i> (1999)                           |
| Buttresses               | Present or absent                                                  | Smith (1979)                                            |
| Growth rate              | Slow to fast                                                       |                                                         |

A number of traits that probably are more associated with growth and survival of a species in an ecosystem e.g. number of seeds or fruits, fruit type, dispersal and pollinator agents are missing in this study because data on these traits were not readily available and could not be determined because of the short duration and limited financial resources that were available for this study.

### **Selection of tree species for functional analysis**

The selection of species for this study was based on availability of data for the most common species naturally growing in Mabira Forest. Data sought was mainly the tree morphological characteristics and Specific Leaf Area. A total of 100 species was selected from 33 plant families each represented by 1-18 species. Species selection was based on the availability of at least 75% of the data required on the 18 traits selected for functional analysis. The major growth forms include: 15 shrubs, 28 medium sized tree species and 57 tall tree species.

### **Data analysis**

Multivariate techniques were used to analyse the data in Genstat Discovery 3. Agglomerative hierarchical cluster analysis was used to form the groups. Cluster analysis encompasses a number of techniques and methods for grouping objects of similar kind into respective categories. Cluster analysis is an exploratory data analysis tool which aims at sorting different objects into groups such that the degree of association between two objects is maximal if they belong to the same group and minimal if they do not (Payne *et al.*, 2003).. Euclidean distance (the square root of the sum of the squared differences between values for the items) was used to form the similarity matrix. The Average Link method was used to generate a dendrogram. The Average link method defines the similarity between clusters as the average of the similarities of that characteristic within members of the cluster. A dendrogram was used to graphically show the various groups generated using this method and indicate the similarity index at which the groups were formed.

To test the validity of the groups generated, the Group Average link method was used to compare the species aggregated into the various functional groups. The method uses an

average of all the samples in any two merging clusters and the original clusters are replaced by their mean, weighted by cluster size (Payne *et al.*, 2008). The groups obtained by the two Link methods were then compared for any similarities. The robustness of the linkages and groups formed, were determined using Mann-Whitney U test to identify traits that were most important at each sub-division of the dendrogram. This test was suitable because the data were ordinal. Descriptive statistics such as percentages and means were carried out using SPSS 12.0. Description of functional groups was based on traits that were found to important in forming the groups. The group names are derived from the most significant discriminating traits in the formation of a particular functional group. All statistical tests were done at 95% Confidence Interval.

## RESULTS

### Functional groups of Mabira forest tree species

Seven functional groups were defined (Figure 2) after testing for robustness and similarity between groups. The groups were formed at 78% similarity index. Group three had the highest (39) and Group Five had the lowest (3) number of species (Appendix 1). The most important discriminating characteristics at the first division in the dendrogram were: Fruit shape, Leaf type, compound leaf shape and Leaf retention while Tree height, Leaf area and resprouting ability were the most significant traits at the sixth division of the dendrogram (Table 2).

Table 2. P- Values for the most significant traits at each division of the dendrogram generated using the Mann-Whitney U test

| Traits              | Division in the Dendrogram |        |        |       |        |        |
|---------------------|----------------------------|--------|--------|-------|--------|--------|
|                     | 1                          | 2      | 3      | 4     | 5      | 6      |
| Eco-type            |                            | 0.027  |        |       |        |        |
| Multi-stems         |                            | 0.000* |        |       | 0.005  |        |
| Height(m)           |                            | 0.004  |        |       |        | 0.001  |
| Buttresses          |                            |        |        |       |        |        |
| Bark colour         |                            | 0.037  |        |       |        |        |
| Bark texture        |                            |        |        | 0.021 | 0.026  |        |
| Leaf type           | 0.005                      |        |        |       |        |        |
| Compound leaf type  | 0.003                      |        |        |       | 0.000* |        |
| Leaf texture        |                            | 0.028  |        |       | 0.025  |        |
| Leaf area           |                            |        |        |       |        | 0.010  |
| Flower sex          |                            |        |        | 0.038 |        |        |
| Inflorescences      |                            |        |        |       |        |        |
| Resprouting ability |                            | 0.014  |        |       |        | 0.000* |
| Growth rate         |                            |        |        |       |        |        |
| Succession level    |                            |        |        |       |        |        |
| Leaf shape          |                            |        | 0.001* |       |        | 0.030  |
| Specific Leaf Area  |                            |        |        |       |        |        |
| Leaf retention      | 0.040                      |        |        |       | 0.038  |        |

\*highly significant between divisions

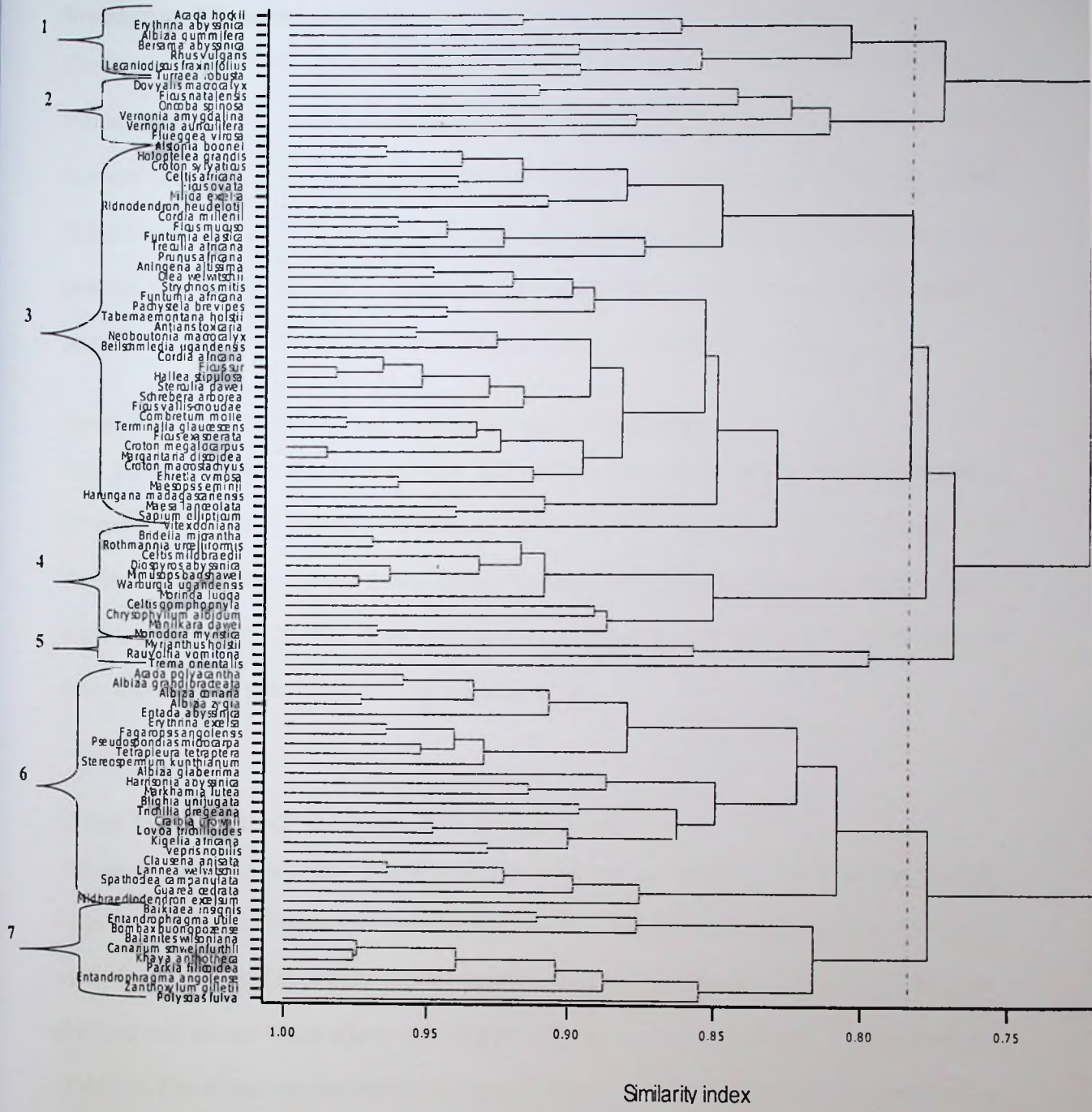


Figure 2: Functional Groups of tree species generated using Average Link method formed at 78% similarity index indicated by the dotted line

### **Description of functional groups**

The description of the groups below is based on the traits that were most dominant in formation of each of the functional groups. Species found in a particular group are presumed to contribute in a similar way to ecosystem processes because they have developed similar characteristics to play that function. This description also will also help to determine the potential role of the species in a particular functional group in restoration of the degraded parts of Mabira Forest. Below is a description of the seven functional groups:

#### **Group One: Compound leaved forest non dependent species**

This group consists of seven species that include: *Acacia hockii*, *Albizia gummifera*, *Erythrina abyssinica*, *Bersama abyssinica*, *Lecaniodiscus fraxinifolius*, *Rhus vulgaris*, and *Turraea robusta*. The species in this group are deciduous, multi-stemmed and do not have buttresses (Appendix 1). Six of the species are compound leaved (Appendix 2) and attain a mean maximum height of about 13 metres (Table 3).

#### **Group Two: Relatively short, simple leaved pioneers**

This group comprises of six simple leaved tree species that include: *Dovyalis macrocalyx*, *Ficus natalensis*, *Flueggea virosa*, *Oncoba spinosa*, *Vernonia amygdalina* and *Vernonia auriculifera* species (Appendix 1). The species have the highest Mean Specific Leaf Area (MSLA) and lowest Mean Maximum Height (MMH) i.e. 343 cm<sup>2</sup>/g and 12 m respectively (Table 5). The group has the highest number of species described as pioneer (Figure 4). The growth rates are described as fast medium and very fast for three, one and two species respectively.

### **Group Three: Simple leaved secondary successional species**

There are 39 species in this group (Appendix 1). All the species (100%) are single stemmed and have simple leaves. Most of the species (56%) do not possess buttresses 15% have medium sized buttresses and the rest have relatively big buttresses. In the functional category, 62% fall in the intermediate while 23% are pioneer (Figure 4). This group has 41% of species described as fast growing while 38.5% are medium growth rates (Figure 3). When cut, 69% of the species in this group will be able to coppice (Appendix 2).

### **Group Four: Simple leaved forest interior species**

This group is made up of 11 species. The species are single stemmed and possess simple elliptic leaves. Most of the species (82%) do not possess buttresses but the bark for 64% of the species can be described as rough (Appendix 2). The group has 82% intermediate successional species (Figure 4) and 28% are climax species. The mean maximum height is about 31m with an average SLA of  $140 \text{ cm}^2/\text{g}$  (Table 3).

### **Group Five: Undefined group**

This group contains three species i.e.: *Myrianthus holstii*, *Rauvolfia vomitoria*, and *Trema orientalis*. They are simple leaved, evergreen, have a smooth bark but with no buttresses. The three species are able to coppice when cut. The mean SLA is  $120 \text{ cm}^2/\text{g}$  and Maximum height is about 17m tall (table 3). *Trema orientalis*, often described as pioneer in literature was not placed in group two that was dominantly of pioneer species.

### **Group Six: Compound leaved secondary successional species**

This group has 24 species which are single stemmed and compound leaved (Appendix 1 and 2). Most of the tree species (54%) in this group can be described as having medium or low growth rates (Figure 3). The flower sex is bisexual for 79% (Appendix 2) of the species and

63% are intermediate successional species (Figure 4). The species attain mean maximum height of 24 m and SLA of  $149\text{cm}^2/\text{g}$  (Table 3).

#### **Group Seven: Compound leaved shade tolerant species**

The majority of species in this group attain a mean maximum height of 30m and mean SLA of  $155\text{ cm}^2/\text{g}$ , (Table 3). The species in this group have compound pinnate leaves, straight boles and rarely develop multi-stems. Most of the species (70%) are deciduous and 60% have buttresses (Appendix 2). Common shade tolerant species such as *Entandrophragma utile*, *Khaya anthotheca* and others are in this group.

#### **Growth rates among Functional Groups**

Groups 2, 3 and 5 had the highest number of species that are relatively very fast growing (Figure 3) while group 6 and 1 had highest number of relatively slow growing species. Groups 2 and 5 had the most species described as pioneers while groups 4 and 7 had the highest number of intermediates and climax species (Figure 4).

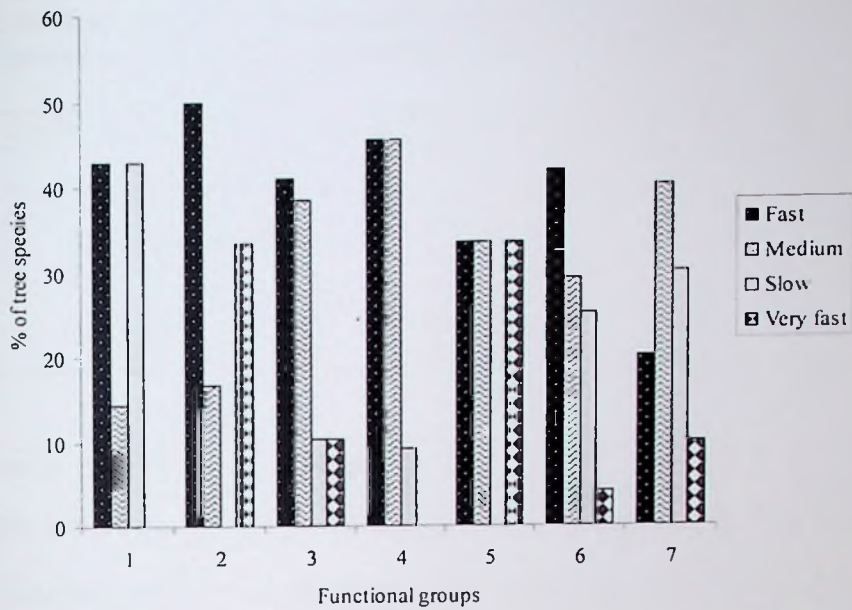


Figure 3: Percentage of tree species in the various growth rate descriptions for derived Functional Groups of Mabira Forest

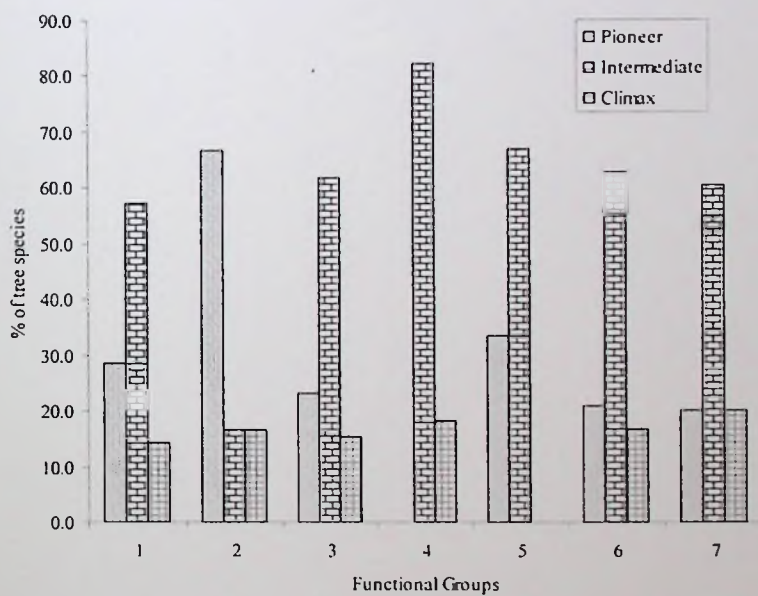


Figure 4: Percentage of species in the various successional hierarchies for the derived Functional Groups of Mabira Forest

Table 3: Number of tree species for derived Functional groups with their respective Mean Specific Leaf Area, Maximum Height and Standard Error (in parentheses) for 100 tree species clustered using Average Link method for Mabira Forest Reserve

| Group | Number of species | Mean Specific Leaf Area (cm/g) (S.E) | Mean Maximum Height (m) (S.E) |
|-------|-------------------|--------------------------------------|-------------------------------|
| 1     | 7                 | 182 (62.9)                           | 13 (2.1)                      |
| 2     | 6                 | 343(83.0)                            | 12(3.8)                       |
| 3     | 39                | 166(12.6)                            | 28(2.1)                       |
| 4     | 11                | 140(19.0)                            | 31(5.0)                       |
| 5     | 3                 | 120(45.1)                            | 17(2.7)                       |
| 6     | 24                | 149(13.2)                            | 24(2.4)                       |
| 7     | 10                | 155(27.4)                            | 43(4.9)                       |

### Robustness of the Functional Groups

To test the robustness of the Functional groups generated using Average Link method, another clustering method - Group Average link method was applied to the same data. The results were used to compare the type and genuineness of the species generated in each of the group in Average Link method that would be used in restoration of Mabira Forest Reserve.

### Functional groups generated using Group Average link method

Using the Group Average link method, seven groups were generated. The groups were however formed at 80% similarity index (Figure 5) unlike with the Average Link method where they were formed at 78%.

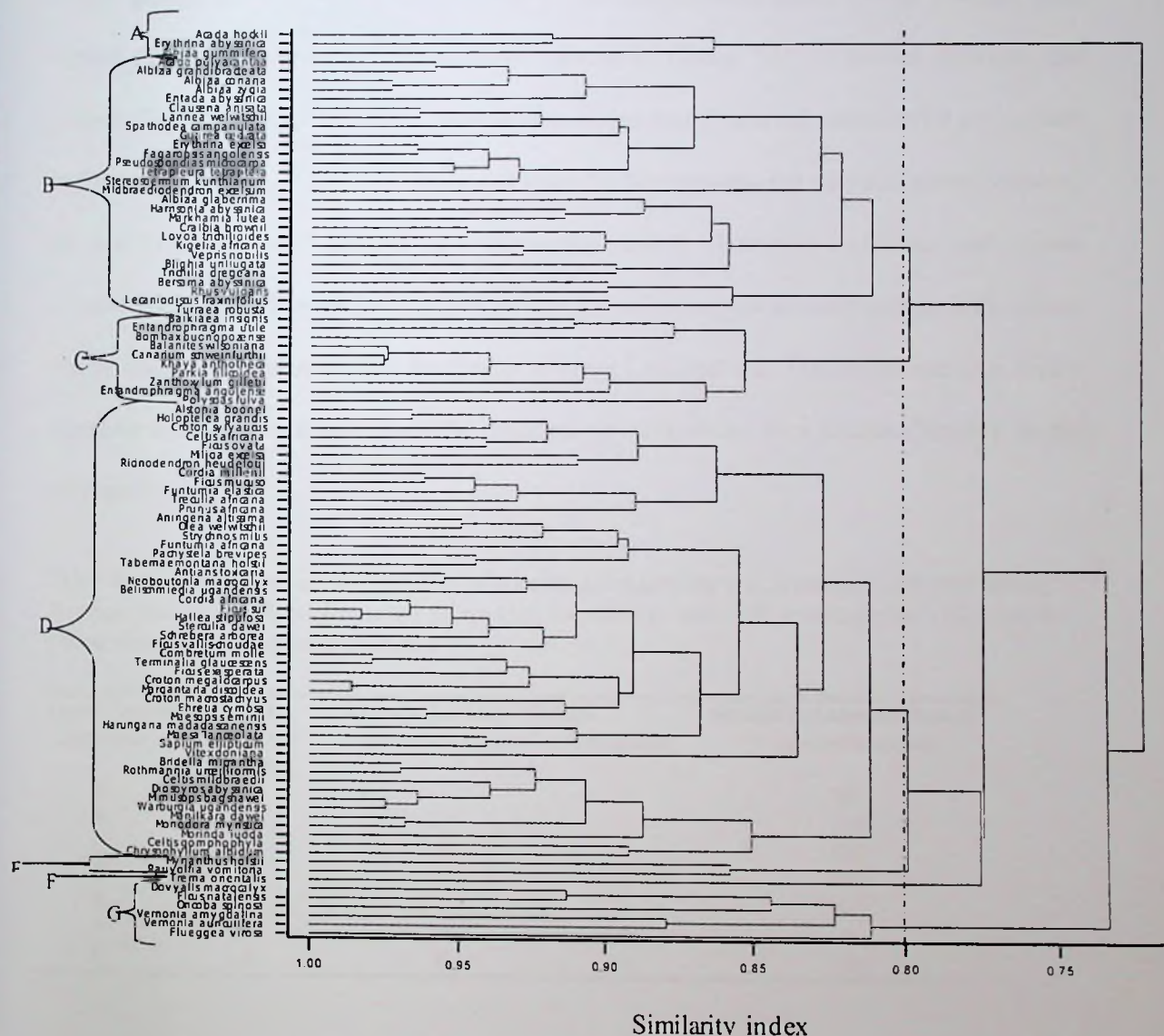


Figure 5. Functional groups of tree species generated using Group Average link method along a similarity index. Groups were formed at 80 % similarity (dotted line).

### Comparison of the generated of groups by the two linking methods

Groups 2 and 7 (Figure 2) (Average Linkage method) and group C and G (Figure 5) (Group Average Link Method) had equal number and type of species resolved in the various groups. However, for groups 1, 5, and 6 of Average Linkage, many of the species were present in similar groups in A, E and B respectively of the classification using Group average Link method (Table 3). For instance, the three species of Group "A" of Group Average link method (Figure 5) (*Acacia hockii*, *Albizia gummifera* and *Erythrina abyssinica*) are present in Group 1 of Average Linking method (Figure 2). Nonetheless the classifications based on the two Link methods, showed that *Myrianthus holstii*, *Rauvolfia vomitoria* and *Trema orientalis* -Group 5 (Figure 2) could not be categorised in respect to other groups with almost similar characteristics even with the Group Average Link method. The difference was *Trema orientalis* that was separated from the other species and placed in a unique Group F as the only species.

Table 4: A comparison of the number of species generated by the Average Link and Group Average link methods and number of species common in both link methods for 100 Mabira Forest Reserve tree species grouped

| Group Average Method |                   | Average Linkage Method |            | Similarity between groups |
|----------------------|-------------------|------------------------|------------|---------------------------|
| Group code           | Number of species | Number of species      | Group code | % of similar species      |
| A                    | 3                 | 7                      | 1          | 43                        |
| B                    | 28                | 24                     | 6          | 100                       |
| C                    | 10                | 10                     | 7          | 100                       |
| D                    | 50                | 39                     | 3          | 100                       |
| E                    | 2                 | 3                      | 5          | 67                        |
| F                    | 1                 | 11                     | 4          | 0                         |
| G                    | 6                 | 6                      | 2          | 100                       |

## DISCUSSION

Functional groups have been generated using morphological characteristics and the groups appear to make ecological sense because species which, for example have characteristics for pioneer (Group 2), secondary succession (Group 3) and late successional characteristics (Group 7) have been placed in different Functional Groups. This kind of classification is useful for selection of species for restoring the various parts of the degraded forest. This grouping conforms to what Kohler *et al.*, (2000) found when they classified species according to their successional status in Sabah's rain forests in Malaysia. They generated three Functional groups of species that included early, mid and late successional. Their results showed that Sabah's rain forests had 68% late successional, 26% mid and 7% early successional species. However, we obtained 18%, 71% and 11% respectively for late, mid and early successional species in this study. This indicates that the two forests are less comparable in terms of species structure probably because of differences in forest age and health of two forests. Mabira Forest has fewer late successional species probably because of its recent history where there was uncontrolled exploitation and encroachment that left some parts of the forests without mature trees.

On the other hand, the two studies differed in approach because Kohler *et al.* (2000) used wood density, timber groups and height to generate the functional groups unlike this study that was based on qualitative descriptions of several morphological characteristics that influence growth and survival in the forest for the classification. Although these results can be used for the intended purpose, several traits that have been found to be better predictors of growth rates such as seed type, seed number, and wood density are missing in this study.

This may have significantly contributed to the lack of consistency in the results as compared to other studies. Many of these traits were difficult to find in Literature while others required field collections that were not possible because of the short duration for this study.

Using the morphological classifications, Mabira Forest showed an overlap of species between the early, mid and later successional stages. This conforms to what Gitay *et al.* (1999) found when they generated 10 functional groups for a subtropical rainforest in Australia using a subjective, morphological and data driven classification methods. They found one group of species largely associated with earlier stages of succession while two groups were largely associated with later successional stages and mid-successional species occurred in both groups.

This trend is expected in the normal structure forest ecosystems because there are no clear cut boundaries among the three successional categories. For instance, *Polyscias fulva* a known open gap species was placed in Group 7. *P. fulva* is compound leaved and therefore possesses a large leaf area as opposed to most pioneers that are simple leaved. The most important traits for the formation of Group 7 were Leaf Area, Tree Height and Copping ability and its leaf size explains why it was placed in Group 7 rather than Group Two of the early successional species.

### **Functional groups and forest restoration**

Predicting the role each functional group will play to restore the degraded forest ecosystem is probably not straight forward because many factors influence species' adaptation and

survival. Edaphic and microclimatic factors have some influence but were not part of this assessment. We can however predict which species can be used to restore the different parts of the forest with some confidence using their morphological characteristics as described by various authors. Whitemore (1989) for instance described pioneers as species that produce numerous small well dispersed seeds and fast growing to fill the gaps and Easdale *et al.*, (2007) noted that species which generally have low SLA, evergreen leaf phenology, high leaf dry matter content or small leaf area are generally more tolerant to infertile soils. Therefore, using this knowledge, we can predict the role of each functional group in restoration of Mabira forest.

Group Two species in this study has more species with pioneer characteristics than species in other groups. *Vernonia amygdalina* and *Flueggea virosa* and others in this group are described as fast growing. Therefore, such species would be used to restore completely-degraded sites of Mabira Forest Reserve. The sites can include areas that were disturbed less than 3 years ago. These species would provide habitats for seed-dispersers such as birds that would bring in germplasm of other species especially of the secondary succession category and also suppress weeds because of their fast growth.

Group Three of the “Simple leaved secondary successional” species would be most appropriate for restoring sites that have been under natural regeneration for over three years. Many pioneer species would have colonised and occupied as much area as possible to provide a favourable environment for the species in this group to germinate and survive. Tree species such as *Harungana madagascariensis*, *Holoptelea grandis*, *Maesopsis eminii*,

*Margaritaria discoidea* and others in this group has various characteristics e.g. medium growth and medium SLA that fit well in various stages of forest recovery.

Late successional species grow slowly in early stages and will require some degree of shading to survive as juveniles but later dominate the upper canopy, hence exposing their leaves to intense heat. Archibold (1995) described buttressing in trees as an adaptation for support among taller trees and Gates *et al.*, (2005) associated compound leaves to adaptation for heat dissipation. Group Seven of “Compound leaved shade tolerant” species such as *Entandrophragma angolense*, *Entandrophragm utile* and *Parkia filicoidea* are relatively tall, compound leaved, deciduous, buttressed and have single stems. Therefore, they can be used for restoration of forest sites that have undergone natural regeneration for over 30 years because of the adequate shade that is availed by the medium successional species that are already established in these sites.

Whereas restoration invariably seeks a direct and full return to the indigenous, historic ecosystem, plant re-introduction is an expensive, risky option that commits personnel to long-term monitoring and management. Therefore it is important to assess the methods to be employed and the risks they present because different tree species can vary dramatically in growth and survival in the forest ecosystem.

## CONCLUSION

Seven functional groups have been derived for the 100 tree species using multivariate techniques based on 18 traits. Overlap of species among functional groups probably arises because of use of qualitative data, complexity of the forest ecosystem as well as disturbance that provided considerable variation. That limits decision making to a more subjective rather than one backed by quantitative data.

Literature on morphological descriptions of trees species can be useful tool for quickly compiling information about species. However, the data available are incomplete in most publications and therefore needs to be augmented by field observations and measurements. For instance, a number of useful morphological and physiological characteristics such as, photosynthetic rate, wood density, number of seeds and dispersal mechanisms were difficult to find from publications on flora Uganda. These perhaps give a better understanding of adaptation of species to perform certain functions in an ecosystem.

Functional roles need to be maintained by ensuring even distribution of species in the functional groups. This study has illustrated an irregular distribution of species across the groups and this raises the question of functional loss. Functional loss can result if ecosystems are species poor, functionally rich and having species un-evenly distributed across functional groups (Fonseca and Ganada, 2000). Therefore, additional functional roles of the generated functional groups need to be investigated and Groups that are observed to be functionally rich but with low species number need to be reinforced with new species to guard against functional loss in a forest ecosystem.

## RECOMMENDATIONS

Plant recommended specie(s) of a particular functional group for the various sites of the degraded forest to enhance their growth success. However, if the most appropriate species is missing, then a surrogate species within the same functional group can be selected for replanting the site.

Before any forest restoration process is done, a thorough study to understand the state of forest ecosystem and the role of various ecosystem components in its maintenance has to be conducted. This will enrich the decisions made especially on the type and approach of restoring such sites.

Additional studies are required to determine the best traits for measuring functional roles of plants. This would ease choice of traits in functional ecology.

Forest restoration can be a very cost-effective measure to regain the ecological and protective functions of forest ecosystems but to this, political support to make forest restoration an attractive undertaking; acceptance by and collaboration with those stakeholders directly concerned with the forest; a commitment that the forest will be kept as a permanent forest estate and protected from further disturbances; and provision of resources both financial and human for the undertaking are needed.

## **Acknowledgement**

We thank the European Union for funding this research under the FOREAIM project and all other partners. Special thanks to Ron Smith at the Centre for Ecology and Hydrology (CEH) who taught me how to use multivariate techniques in Genstat software.

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## Appendices

### Appendix 1: Tree species considered for functional analysis, functional groups generated and their families for 100 tree species of Mabira Forest Reserve

| Species                                            | Family         | Method of Group formation |                  |
|----------------------------------------------------|----------------|---------------------------|------------------|
|                                                    |                | Average Linkage           | by Group Average |
| <i>Bersama abyssinica</i> (Fresen.)                | Miliaceae      | 1                         | B                |
| <i>Lecaniodiscus fraxinifolius</i> (Bak.)          | Sapindaceae    | 1                         | B                |
| <i>Rhus vulgaris</i> (Meikle)                      | Anacardiaceae  | 1                         | B                |
| <i>Turraea robusta</i> (Guerke)                    | Miliaceae      | 1                         | B                |
| <i>Acacia hockii</i> (De Wild.)                    | Leguminoceae   | 1                         | A                |
| <i>Albizia gummifera</i> (J.F.Gmel)                | Leguminoceae   | 1                         | A                |
| <i>Erythrina abyssinica</i> (Lam.)                 | Leguminoceae   | 1                         | A                |
| <i>Doryalis macrocalyx</i> (Oliv.) Warb.)          | Flacourtiaceae | 2                         | G                |
| <i>Ficus natalensis</i> (Hochst)                   | Moraceae       | 2                         | G                |
| <i>Flueggea virosa</i> ((Willd.) Voigt)            | Euphorbiaceae  | 2                         | G                |
| <i>Oncoba spinosa</i> (Forssk.)                    | Flacourtiaceae | 2                         | G                |
| <i>Vernonia amygdalina</i> (Delile)                | Compositae     | 2                         | G                |
| <i>Vernonia auriculifera</i> (Hiern)               | Compositae     | 2                         | G                |
| <i>Alstonia boonei</i> (De Wild)                   | Apocynaceae    | 3                         | 4                |
| <i>Aningeria altissima</i> (A. Chev.)              | Sapotaceae     | 3                         | D                |
| <i>Antiaris toxicaria</i> (Rumph. ex.pers.) Lesch. | Moraceae       | 3                         | D                |
| <i>Beilschmiedia ugandensis</i> (Rendle)           | Lauraceae      | 3                         | D                |
| <i>Celtis africana</i> ((Burm.f.)                  | Ulmaceae       | 3                         | D                |
| <i>Combretum molle</i> (G.Don)                     | Combretaceae   | 3                         | D                |
| <i>Cordia africana</i> (Lam.)                      | Boraginaceae   | 3                         | D                |
| <i>Cordia millenii</i> (Baker)                     | Boraginaceae   | 3                         | D                |
| <i>Croton macrostachyus</i> (Delile)               | Euphorbiaceae  | 3                         | D                |
| <i>Croton megalocarpus</i> (Hutch.)                | Euphorbiaceae  | 3                         | D                |
| <i>Croton sylvaticus</i> (Krauss)                  | Euphorbiaceae  | 3                         | D                |
| <i>Ehretia cymosa</i> (Thonn.)                     | Boraginaceae   | 3                         | D                |
| <i>Ficus exasperata</i> (Vahl.)                    | Moraceae       | 3                         | D                |
| <i>Ficus mucuso</i> (Welw.ex Warb.)                | Moraceae       | 3                         | D                |
| <i>Ficus ovata</i> (Vahl.)                         | Moraceae       | 3                         | D                |
| <i>Ficus sur</i> (Engl.)                           | Moraceae       | 3                         | D                |
| <i>Ficus vallis-choudae</i> (Del.)                 | Moraceae       | 3                         | D                |
| <i>Funtumia africana</i> (Benth.)                  | Apocynaceae    | 3                         | D                |
| <i>Funtumia elastica</i> (Preuss)                  | Apocynaceae    | 3                         | D                |
| <i>Hallea stipulosa</i> (Kuntze)                   | Rubiaceae      | 3                         | D                |
| <i>Harungana madagascariensis</i> (Poir)           | Guttiferae     | 3                         | D                |
| <i>Holoptelea grandis</i> (Hutch)                  | Ulmaceae       | 3                         | D                |
| <i>Maesa lanceolata</i> (Forsk)                    | Myrinaceae     | 3                         | D                |
| <i>Maesopsis eminii</i> (Engl.)                    | Rhamnaceae     | 3                         | D                |
| <i>Margaritaria discoidea</i> (Baill.) Webster)    | Euphorbiaceae  | 3                         | D                |
| <i>Milicia excelsa</i> (Welw.)                     | Moraceae       | 3                         | D                |
| <i>Neoboutonia macrocalyx</i> (Pax)                | Euphorbiaceae  | 3                         | D                |

|                                                    |               |   |   |
|----------------------------------------------------|---------------|---|---|
| <i>Olea welwitschii</i> (Knobl.)                   | Oleaceae      | 3 | D |
| <i>Pachystela brevipes</i> (Baker) Engl.           | Sapotaceae    | 3 | D |
| <i>Prunus africana</i> (Hook.f.) Kalkman           | Rosaceae      | 3 | D |
| <i>Ricinodendron heudelotii</i> (Baill.) Heckel    | Euphorbiaceae | 3 | D |
| <i>Sapium ellipticum</i> (Krauss) Pax              | Euphorbiaceae | 3 | D |
| <i>Schrebera arborea</i> (A. Chev.)                | Oleaceae      | 3 | D |
| <i>Sterculia dawei</i> (Sprague)                   | Sterculiaceae | 3 | D |
| <i>Strychnos mitis</i> (S. Moore)                  | Loganiaceae   | 3 | D |
| <i>Tabernaemontana holstii</i> (K. Schum.)         | Apocynaceae   | 3 | D |
| <i>Terminalia glaucescens</i> (Benth.)             | Combretaceae  | 3 | D |
| <i>Treculia africana</i> (Decne)                   | Moraceae      | 3 | D |
| <i>Vitex doniana</i> (Sweet)                       | Verbenaceae   | 3 | D |
| <i>Bridelia micrantha</i> (Hochst.) Baill.)        | Euphorbiaceae | 4 | D |
| <i>Celtis gomphophylla</i> (Engl.)                 | Ulmaceae      | 4 | D |
| <i>Celtis mildbraedii</i> (Engl.)                  | Ulmaceae      | 4 | D |
| <i>Chrysophyllum albidum</i> (G. Don)              | Sapotaceae    | 4 | D |
| <i>Diospyros abyssinica</i> (Hiern) F. White)      | Ebenaceae     | 4 | D |
| <i>Manilkara dawei</i> (Stapf) Chiov.              | Sapotaceae    | 4 | D |
| <i>Mimusops bagswawei</i> (S. Moore)               | Sapotaceae    | 4 | D |
| <i>Monodora myristica</i> (Gaertn.) Dunal)         | Annonaceae    | 4 | D |
| <i>Morinda lucida</i> (Benth.)                     | Rubiaceae     | 4 | D |
| <i>Rothmannia urcelliformis</i> (Hiern)            | Rubiaceae     | 4 | D |
| <i>Warburgia ugandensis</i> (Sprague)              | Canellaceae   | 4 | D |
| <i>Myrianthus holstii</i> (Engl.)                  | Moraceae      | 5 | E |
| <i>Rauvolfia vomitoria</i> (Afzel.)                | Apocynaceae   | 5 | E |
| <i>Trema orientalis</i> (L.) Bl.                   | Ulmaceae      | 5 | F |
| <i>Acacia polyacantha</i> (L.f.) Wild              | Leguminosae   | 6 | B |
| <i>Albizia coriaria</i> (Welw.ex.Oliv              | Leguminosae   | 6 | B |
| <i>Albizia glaberrima</i> (Schumach. & Thonn.)     | Leguminosae   | 6 | B |
| <i>Albizia grandibracteata</i> (Taub.)             | Leguminosae   | 6 | B |
| <i>Albizia zygia</i> (DC.) Macbr                   | Leguminosae   | 6 | B |
| <i>Blighia unijugata</i> (Bak.)                    | Sapindaceae   | 6 | B |
| <i>Clausena anisata</i> (Willd.)                   | Rutaceae      | 6 | B |
| <i>Craibia brownii</i> (Dunn.)                     | Leguminosae   | 6 | B |
| <i>Entada abyssinica</i> (Steud.ex. A Rich)        | Leguminosae   | 6 | B |
| <i>Erythrina excelsa</i> (Bak.)                    | Leguminosae   | 6 | B |
| <i>Fagaropsis angolensis</i> (Engl.)               | Rutaceae      | 6 | B |
| <i>Guarea cedrata</i> (A. Chev.)                   | Miliaceae     | 6 | B |
| <i>Harrisonia abyssinica</i> (Oliv.)               | Simaroubaceae | 6 | B |
| <i>Kigelia africana</i> (Lam.) Benth.)             | Bignoniaceae  | 6 | B |
| <i>Lannea welwitschii</i> (Hiern) Engl.)           | Anacardiaceae | 6 | B |
| <i>Lovoa trichilioides</i> (Harms.)                | Miliaceae     | 6 | B |
| <i>Markhamia lutea</i> (Barker) Sprague)           | Bignoniaceae  | 6 | B |
| <i>Mildbraediodendron excelsum</i> (Harms.)        | Leguminosae   | 6 | B |
| <i>Pseudospondias microcarpa</i> (A. Rich.) Engl.) | Anacardiaceae | 6 | B |
| <i>Spathodea campanulata</i> (P. Beauv.)           | Bignoniaceae  | 6 | B |
| <i>Stereospermum kunthianum</i> (Cham.)            | Bignoniaceae  | 6 | B |
| <i>Tetrapleura tetraptera</i> (Schumach. & Thonn.) | Leguminosae   | 6 | B |
| <i>Trichilia dregeana</i> (Sond.)                  | Miliaceae     | 6 | B |
| <i>Vepris nobilis</i> (Delile.)                    | Rutaceae      | 6 | B |

|                                               |              |   |   |
|-----------------------------------------------|--------------|---|---|
| <i>Baikiaea insignis</i> (Benth.)             | Leguminosae  | 7 | C |
| <i>Balanites wilsoniana</i> (Dawe & Sprague)  | Balanitaceae | 7 | C |
| <i>Bombax buonopozense</i> (P. Beauv.)        | Bombacaceae  | 7 | C |
| <i>Canarium schweinfurthii</i> (Engl.)        | Burseraceae  | 7 | C |
| <i>Entandrophragma angolense</i> (Welw.)      | Miliaceae    | 7 | C |
| <i>Entandrophragma utile</i> (Dawe & Sprague) | Miliaceae    | 7 | C |
| <i>Khaya anthotheca</i> (Welw.)               | Miliaceae    | 7 | C |
| <i>Parkia filicoidea</i> (Welw. ex Oliv)      | Leguminosae  | 7 | C |
| <i>Polyscias fulva</i> (Hiern) Harms)         | Araliaceae   | 7 | C |
| <i>Zanthoxylum gillettii</i> (De Wild.)       | Rutaceae     | 7 | C |

**Appendix 2: Percentage of tree species in the various groups with the different characteristics**

| Trait (characteristic)    | Functional Groups |     |     |     |     |     |     |
|---------------------------|-------------------|-----|-----|-----|-----|-----|-----|
|                           | 1                 | 2   | 3   | 4   | 5   | 6   | 7   |
| <b>Eco-type</b>           | % of species      |     |     |     |     |     |     |
| Forest edge               | 14                |     | 3   |     | 33  | 13  |     |
| Forest generalist         | 29                |     | 36  | 27  | 67  | 17  | 20  |
| Forest interior           |                   |     | 26  | 55  |     | 29  | 70  |
| Forest non dependent      | 43                | 100 | 26  | 18  |     | 33  | 10  |
| River-lake-shore          |                   |     | 3   |     |     |     |     |
| Woodland                  | 14                |     | 8   |     |     | 8   |     |
| Multistems present        |                   |     | 100 | 100 | 67  | 100 | 100 |
| Multistems absent         | 100               | 100 |     |     | 33  |     |     |
| Buttresses absent         | 100               | 100 | 56  | 82  | 100 | 75  | 40  |
| Small buttresses          |                   |     | 15  |     |     | 4   |     |
| Buttresses present        |                   |     | 28  | 18  |     | 21  | 60  |
| Compound leaved           | 86                |     |     |     |     | 100 | 100 |
| Simple leaved             | 14                | 100 | 100 | 100 | 100 |     |     |
| Coppicing-Yes             | 29                | 83  | 31  | 18  |     | 8   | 100 |
| Coppicing No              | 71                | 17  | 69  | 82  | 100 | 92  |     |
| Fast growth               | 43                | 50  | 41  | 45  | 33  | 42  | 20  |
| Medium growth             | 14                | 17  | 38  | 45  | 33  | 29  | 40  |
| Slow growth               | 43                |     | 10  | 9   |     | 25  | 30  |
| Very fast growth          |                   | 33  | 10  |     | 33  | 4   | 10  |
| Climax species            | 14                | 17  | 15  | 18  | 0   | 17  | 20  |
| Intermediate species      | 57                | 17  | 62  | 82  | 67  | 63  | 70  |
| Pioneer species           | 29                | 67  | 23  |     | 33  | 21  | 10  |
| <b>Maximum height</b>     |                   |     |     |     |     |     |     |
| 0-10                      | 29                | 83  | 8   | 9   |     | 13  |     |
| 11_20                     | 71                |     | 26  | 27  | 100 | 42  |     |
| 21_30                     |                   | 17  | 33  | 18  |     | 29  | 40  |
| 31_40                     |                   |     | 21  | 18  |     | 8   | 20  |
| 41_50                     |                   |     | 10  | 18  |     | 8   | 20  |
| ≥ 51                      |                   |     | 3   | 9   |     |     | 20  |
| <b>Specific Leaf Area</b> |                   |     |     |     |     |     |     |
| >100                      | 14                |     | 18  | 27  | 33  | 17  | 20  |
| 101_200                   | 71                | 17  | 54  | 55  | 33  | 71  | 60  |
| 201_300                   |                   | 33  | 18  | 18  | 33  | 8   | 10  |
| 301_400                   |                   | 33  | 10  |     |     | 4   | 10  |
| > 400                     | 14                | 17  |     |     |     |     |     |