DIVERSITY, USE AND RESILIENCE OF WOODY SPECIES IN A MULTIPLE LAND USE EQUATORIAL AFRICAN SAVANNA, CENTRAL UGANDA

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ABSTRACT

Savanna woodlands are vitally important in providing ecological services (e.g. erosion protection, micro-climate) and economic services (e.g. timber, food, fodder non-wood products, and wild-life habitats) that sustain local livelihoods and national economies. Increasing demands and the need for sustainable savanna woodland resource management requires that the ecological, economic, social and cultural values of these resources be explored and brought to the attention of decision makers and the general public. The identification and better understanding of the structure and dynamics of woodland community types, patterns of species distribution and quantitative properties of their diversity is important to the conservation and sustainable management of these woodlands. This study seeks to contribute to a better understanding of Nakasongola woodland community types, species diversity patterns and environment correlates, natural regeneration processes (i.e. sprouting and seedling establishment) and identifying livelihood strategies adopted by households, woody species utilised, and the contribution of charcoal production to household livelihoods. Data on vegetation and environmental variables were collected using 75 rectangular 20 x 50 m (0.1 ha) plots. Data on land use and land cover changes, and relevant associated socio-economic parameters were collected through the analysis of multi-temporal satellite imagery and field observations, as well as interviews of local households and key informants. The basic major livelihood activities for the rural households in this savanna dryland are charcoal production, subsistence crop cultivation and livestock grazing. However, it, sometimes, includes various combinations of activities, i.e. charcoal production and subsistence crop cultivation for both food and cash, and livestock keeping for income generation through selling the livestock products such as milk and, sometimes, the whole animal. At least 24 woody species, including fruit trees (*Mangifera indica* and *Artocarpus heterophyllus*), are frequently harvested, including 16 species that are considered the most utilized for charcoal production. Charcoal production, being the major source of income to the rural households, contributes on average US$ 259 ± 46 (S.E.) per household annually. There were significant differences in charcoal production (Kruskal-Wallis; $H = 31.42$, $p < 0.0001$), producer sale prices per bag of charcoal ($H = 35.62$, $p < 0.0001$), and annual incomes from charcoal production ($H = 32.44$, $p < 0.0001$) per households across the 8 sub-counties. Most of the youth (≤ 20 years old) derive their livelihoods from charcoal production, a small amount of trade, offering labour services, livestock keeping, fishing, bee keeping and earth brick making. Charcoal production, livestock keeping and hunting are carried out particularly by men, whereas, crop cultivation, and collection of fire wood, medicinal plants and fruits are carried out, mainly, by women. However, men are also engaged in cultivation only during the rainy seasons. There have been significant land cover changes in the area during the period 1984 to 2001, resulting in a 64% decrease in dense woodland cover, and an 80% increase in areas under cultivation/settlements. These changes are attributed to significant spatial expansion in agriculture, increased commercialisation of charcoal production, grazing and human population growth.

A total of 44,195 (5,893 plants/ha) woody plants representing 99 species in 67 genera and 31 families were recorded. The most species rich families were Mimosaceae (13), Rubiaceae (9), Moraceae (7), Euphorbiaceae (7), Anacardiaceae (6), Combretaceae (5) and Verbenaceae (5). Density of woody species differed significantly ($F_{2, 72} = 6.3$, $P < 0.003$) among land uses, being higher under charcoal production (7,131 ± 755 plants/ha) and cultivation (6,612 ± 665) areas and significantly lower under grazing lands (4,152 ± 525). Community species composition differed significantly (Global $R_{ANOSIM} = 0.14$, $p = 0.001$) among land use types. All measures of beta-diversity (spatial "turnover" in species composition) showed consistently higher beta-diversity in the grazing land use ($\beta_W = 3.1$; $\beta_T = 3.1$), followed by cultivation ($\beta_W = 2.8$; $\beta_T = 3.0$) and charcoal production ($\beta_W = 2.7$; $\beta_T = 2.8$), suggesting a more heterogeneous spatial distribution of species in the grazing lands. This suggests that variations in the composition and diversity of woody species are to a great extent influenced by land use type and anthropogenic disturbances in this region. Basal area of woody species differed significantly ($F_{2, 72} = 12.0$, $P < 0.0001$) among land uses, being highest under cultivation and charcoal production and significantly lower under grazing. Woody plant density differed ($F_{2,72} = 6.3$, $P = 0.003$) across land-uses, being highest under charcoal production and cultivation and significantly lower under grazing. The species that contributed most to both basal area and density across all the land uses were *Combretum collinum* and *Combretum molle*. However, different species contributed the next most i.e. *Piliostigma thonningii* for grazing; *Albizia zygia* and *Harrisonia abyssinica* for cultivation and *Vepris nobilis* for charcoal production areas. For both basal area and abundance of all woody species, the total variance in species-environmental factor relations (for the combined first four canonical axes) was higher than 50%, suggesting a relatively strong influence of the measured environment variables on species composition and distributions. The CCA points to a significant influence of soil Ca^{2+} and Mg^{2+} in association with grazing on gradients in the composition and structure of woody species in the savanna woodland of Nakasongola.

Resprouting was generally common among the woody species. A total of 2,595 stumps, representing 74 species in 31 families were recorded from all plots. Of these, 98.3% resprouted and were identified to species level. Density of both stumps and total resprout differed significantly ($p < 0.05$) among the land uses, being higher in charcoal production areas than in grazing and cultivation land uses. For the overall pooled data, resprouts per stump differed significantly among land uses ($F_{2, 456} = 7.75$, $p = 0.0005$), being highest in charcoal production (mean ± S.E.; 14 ± 1) and cultivation (13 ± 1) land uses and lowest under grazing areas (10 ± 1). Generally, the mean number of resprouts per stump increased with increasing stump basal diameter (BD), being highest for BD size class > 41 cm. In relation to stump height, the highest mean resprouts/stump was found on stumps with heights ranging from 0.31-0.40 m. Based on pooled species data, regression analyses showed weakly significant negative relationships between BD of leading resprouts and number of resprouts/stump ($r^2 = 0.123$, $p < 0.0001$) and between height of leading resprouts and number of resprouts/stump ($r^2 = 0.068$, $p < 0.0001$). Density of seedlings of woody species differed significantly among land use types (ANOVA; $F_{2, 72} =$

5.9, p = 0.004), being highest for cultivation (3,162 ± 440 individuals ha^{-1}), followed by charcoal production (2,416 ± 295 ha^{-1}) and lowest for grazing (1,629 ± 205 ha^{-1}). Composition of seedlings differed significantly among land use types (Global R_{ANOSIM} = 0.119, p = 0.001). The distributions and densities of some seedlings were explained by gradients in environmental variables, with edaphic factors (i.e. Ca^{2+}, Mg^{2+}, K^{+} and organic matter) and charcoal production being the most important. The first two axes of the Canonical Correspondence Analysis (CCA) explained 41.9% of the variance in species – environmental relations and were a reflection of edaphic and charcoal production land use gradients. All of the 16 highly utilized species were well represented in both the juvenile and adult classes, with gradually declining number of individuals with increasing stem size-class. This indicates that most of these species have high regeneration potential. Juvenile:adult tree ratios >1 and negative DSCD slopes indicate good recruitment and probably successful regeneration for these species. The study revealed land cover changes mainly in the dense and medium dense woodlands, reflected by the increase in open woodland, grasslands and cultivation/settlements. These trends threaten the livelihoods of local communities who are entirely dependent on these natural resources. Sustainable management will require the establishment of suitable integrated community-based institutions and management practices, with support from all key stakeholders (i.e. National Forest Authority (NFA)) and local communities. Maintenance of savanna woodland resources and other ecosystem services essential for human well-being will require an effective legal framework to prevent over-exploitation and give incentives for the protection of the fragile savanna woodland vegetation. An appropriate savanna woodland management policy will be required to guide changes in land use that accommodate the requirements of land users, aided by targeted conservation efforts to all woody plants and particularly for the highly utilized species for charcoal production as well as the multipurpose species. In addition, there is urgent need to build local capacity for improved harvesting and utilization of these tree species. This can be achieved through equipping local users with up to date information as well as observing the existing skills.

***Key words**: Alpha diversity, ANOSIM, beta-diversity, basal diameter (BD), Canonical Correspondence Analysis (CCA), diameter size-class distributions (DSCD), land cover change, land use, livelihood strategies, resprouting, seedling recruitment*

DECLARATION

I declare that this thesis is my own original work. It is being submitted for the degree of Doctor of Philosophy (PhD), within the Faculty of Science, of the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before either in part or in full for any degree or examination in any other University.

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(Signature of candidate)
30th day of September 2010

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DEDICATION

This work is dedicated to my sons

Ian Joel Kairu

and

Ethan Malcolm Kunona.

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LIST OF SYMBOLS AND ACRONYMS

ANOSIM:	ANalysis Of SIMilarity
ANOVA:	Analysis of Variance
Av.P:	Available Phosphorous
BA:	Basal Area
Ca:	Calcium
CCA:	Canonical Correspondence Analysis
DBH:	Diameter at Breast Height
DEM:	Digital Elevation Model
DEP:	District Environmental Profile
DRH:	Diameter at Reference Height
DSCD:	Diameter Size-Class Distributions
FAO:	Food and Agriculture Organization
GPS:	Global Positioning System
H':	Shannon-Weiner Index of Diversity
ISODATA:	Interactive Self-Organizing Data Analysis Technique
K:	Potassium
MEA:	Millennium Ecosystems Assessment
MEMD:	Ministry of Energy and Mineral Development
Mg:	Magnesium
N:	Nitrogen
Na:	Sodium
NEMA:	National Environmental Management Authority
NFA:	National Forest Authority
OM:	Organic matter
pH:	Alkalinity/ Acidity
PRA:	Participatory Rural Appraisal
RMSE:	Root Mean Square Errors
SIMPER:	SIMilarity PERcentages
SRTM:	Shuttle Radar Topography Mission
SSI:	Semi Structured Interview
UBOS:	Uganda Bureau of Statistics
UTM:	Universal Transverse Mercator
WGS:	World Geodetic System

GLOSSARY OF FREQUENTLY USED TERMS

(see references cited below in “References” under Chapter 1: Introduction)

Alpha-diversity: The diversity in woody species at individual sites (e.g. plots, quadrants) within a habitat or community (Magurran, 2004; Legendre *et al.,* 2005).

Beta-diversity: The rate of change of species diversity along a gradient from one site or habitat to another (Whittaker 1972; Magurran, 2004).

Disturbance: Any event in time that disrupts ecosystems, changes the community or population structure, resource availability or physical environment (White & Pickett, 1985; Osborne, 2000).

Woodland: All wooded areas with 5-20 per cent tree canopy cover, where the canopy is composed of a single stemmed, woody plants greater than 5 m in height. It includes dense, medium dense and open woodlands.

Cultivated land: Area under crop, orchard and/or fallow or land cleared for raising crops.

Human livelihood: Various means of supporting life and meeting individual and community needs. It can be expressed in cash, kind or both, in addition to associated social institutions. Thus, formal and informal employment streams, land-based resources such as crops, livestock and secondary resources, as well as social and economic capital.

Land cover: The ecological state and physical appearance of the land surface (e.g. closed forests, woodlands, or grasslands) (Turner & Meyer, 1994; Brandon, 2001)

Land use: The manner in which human beings employ the land and its resources (e.g. for agriculture, grazing, logging, etc. (Brandon, 2001).

Livelihood strategy: The range and combination of activities and choices that people make and undertake - ways of combining and using assets - in order to achieve their livelihood goals (DFID, 1999).

Regeneration: The establishment of new tree cohorts (Bernier & Ponge, 1994) or population recruitment arising from seeds and seedling establishment or vegetative growth (stem coppicing or root suckering).

Resprouting: The terms coppicing/resprouting/sprouting have been used interchangeably in literature. For the purpose of this study, resprouting is used to denote shoots growing from the stem or stem base of a woody plant following damage e.g. from harvesting or tree/branch fall.

Root sucker: Shoots growing from root crown following damage.

Species diversity: The variety of life (Osborne, 2000; Magurran, 2004).

Species richness: The number of woody species per unit area (Magurran, 2004).

Woody plants: Collective term for trees, shrubs and lianas (Lawes *et al.,* 2004).

CHAPTER 1

General introduction

1.0. INTRODUCTION

1.1. Background

Savannas cover 60% of Sub-Saharan Africa (Scholes & Walker, 1993), and globally they are home to over 30% of the world's population (Solbrig *et al.*, 1991). They have an unusual vegetation formation because of a co-dominance of herbaceous (particularly grasses) and woody plants, forming either savanna grasslands or woodlands. The woody plants within the savanna woodlands of Sub-Saharan Africa and many other parts of the world form an important structural diversity for plant and animal biota, which is so important for human livelihoods.

Savanna woodlands, for example the miombo woodlands, are reported to be vitally important in providing ecological (e.g. erosion protection, micro-climate amelioration, habitat for a wide range of organisms, carbon sequestration, etc.) and economic services (e.g. timber, food, fodder, non-wood products, and wild-life habitats) that sustain local livelihoods and national economies (Scholes & Archer 1997; Chidumayo, 1997; http://www.fao.org/DOCREP/005/w4442E/w4442e04.htm, accessed 15/9/2005). Throughout Sub-Saharan Africa they contribute considerably to household livelihoods by providing fuel, fodder, medicine, products of cultural importance and food security, and potentially supplementing incomes (Shackleton, 1997; Luoga *et al.,* 2000; Dovie *et al.,* 2002, Shackleton *et al.,* 2002; Kristensen & Lykke, 2003). For example, fuelwood from woodlands provides many people, especially the poor rural households, with a primary source of energy (Eberhard, 1990). In Africa, it is estimated that the number of people using fuelwood and other biomass fuels will rise by more than 40% to about 700 million between 2000 and 2030 (Arnold & Persson, 2003). It is projected that by the year 2030, charcoal consumption in Africa would be at least five times the consumption of the 1970s (Table 1), greatly threatening the survival of savanna woodlands. Hence, there is an urgent need for sustainable use and management of savanna woodlands aided by scientific data. With the ever increasing human population and rural households continued reliance on fuelwood as the primary energy source, utilization of savanna woodlands is high and they are increasingly threatened (Geldenhuys, 1997; Luoga *et al.,* 2004). Indeed, a number of livelihood strategies that involve harvesting of woody plants for charcoal production, firewood and other subsistence uses are common and can influence the dynamics of savanna vegetation.

Table 1. FAO projections of wood fuel consumption to year 2030 in Africa.

Year	**1970**	**1980**	**1990**	**2000**	**2010**	**2020**	**2030**
Fuel wood (million cubic meters)	261.1	305.1	364.6	440.0	485.7	526.0	544.8
Charcoal (million tons)	8.1	11.0	16.0	23.0	30.2	38.4	46.1
Charcoal: Fuel wood ratio	1:32	1:28	1:23	1:19	1:16	1:14	1:12

1.2. Species diversity, anthropogenic disturbances and edaphic factors in savanna ecosystems

Species diversity is an important parameter of a plant community and one of the major criteria for nature conservation. Savanna woodlands are endowed with high plant and animal species diversity and high levels of endemism (Homewood & Brockington, 1999). For example the core of the southern African savanna woodland biome contains about 5,780 plant species, of which 43% are endemic (Cowling, 1984). However, there is widespread concern that savanna woodland ecosystems, with unique and valuable biodiversity resources, are being lost (Rennolls & Laumonier, 2000) as a result of both natural and anthropogenic disturbances and mismanagement (O'Connor, 2005). Savanna woodlands are continuously being exposed to severe large-scale changes through the cutting of woody plants for charcoal and fuelwood, creation of pastures, accidental or intentional fires (Gerhardt & Hytteborn, 1992; Rennolls & Laumonier, 2000; Luoga *et al*., 2002; MEA, 2005a & b). With increasing human population, these ecosystems are being overexploited (Kristensen & Lykke, 2003) leading to increased loss of woodland cover and declining tree species diversity. Yet, tree species diversity is an important aspect of savanna woodland ecosystem diversity (William-Linera, 2002), and sustainability of most dry savanna ecosystems depends on trees and other woody plants. On the other hand, this threatens the provision of sustainable ecosystem services and goods which are essential for sustainable rural livelihoods. Hence, the conservation of savannas ecosystems is becoming increasingly important for the development of sustainable land use systems and human well-being.

Species diversity is connected to ecosystem dynamics and environmental quality, and a change in species diversity is often used as an indicator of anthropogenic or natural disturbances in an ecosystem (Liu & Brakenhielm, 1996). In addition, measures of species diversity play a central role in ecology and conservation biology (Noss & Cooperrider, 1994; Magurran, 2004). Disturbance has three principal components (i.e. scale, intensity and frequency) within which Connell (1978) contends that variation in magnitude correlates with variation in diversity. The type, intensity and duration of disturbance shape the characteristics of populations, communities and ecosystems (Averill *et al.,* 1994). Disturbance has many important effects on communities and ecosystems, including enhancing or limiting biological diversity, causing input or losses of dead organic matter and nutrients that affect productivity and habitat structure, and creating landscape patterns that influence many ecological factors, from movements and densities of organisms to functional attributes of ecosystems (Dale *et al.,* 2000). Therefore, characterization of biodiversity through inventories can be useful in the planning of operations that aim to conserve biodiversity (Belbin, 1995; Faith & Walker, 1996; Vanclay, 1998). However, conservation strategies for sustaining biodiversity must consider that species richness and ecological processes are controlled by parameters operating at a wide array of scales (Baudry *et al.*, 2000).

Natural plant communities are usually not at equilibrium and thus species diversity as a community parameter is subject to change through time due to both intrinsic forces, for example mortality and regeneration, and extrinsic forces such as fire, gap creation and pollution deposition (Liu & Brakenhielm, 1996). An underlying assumption of many woodland ecological studies is that plant communities are largely influenced by the dominant species in an association (Sagers & Lyon, 1997). Understanding the distributions of the largest and most abundant woody species will lead to an understanding of plant communities as a whole (Eyre, 1980). Furthermore, the presence of a species at a given site is determined by habitat quality (Duelli, 1997), while diversity within a patch may also depend on the structure of the surrounding landscape. Therefore, the composition of a landscape is one of the key factors explaining species richness at the regional scale (Dunning *et al.*, 1992; Dale *et al.*, 2000; Wagner *et al.*, 2000). Within a landscape, edaphic factors (i.e. soil moisture and nutrients) are widely accepted as the primary determinants of woodland structure and function (Walker & Noy-Meir, 1982; Tothill & Mott, 1985; Frost *et al.*, 1985). The interplay of soil moisture and nutrients are modified by fire, herbivory (by wild and domestic animals) and humans, commonly termed secondary determinants (Frost *et al.*, 1986; Skarpe, 1992; Scholes & Walker, 1993; Scholes & Archer, 1997). Studies have also shown that variability in species richness between land uses can be explained by a variety of factors that include internal factors like habitat quality (Dauber & Wolters, 2000), external factors such as spatial-temporal dynamics (Purtauf *et al.*, 2001; Waldhardt & Otte, 2003), boundary characteristics (Fagan *et al.*, 1999) or neighbourhood effects (Tilman & Downing, 1994).

1.3. Land cover and land use changes

Land use is defined as the manner in which human beings employ the land and its resources (e.g. for agriculture, grazing, logging, etc.), while land cover is the ecological state and physical appearance of the land surface (e.g. closed forests, woodlands, or grasslands; Turner & Meyer, 1994; FAO, 1997; Brandon, 2001). Land cover is a fundamental variable that impacts on and links many parts of the human and physical environments. It is regarded as the single most important variable of global change affecting ecological systems (Vitousek, 1994).

Land cover and land use change have occurred throughout the history and continue to occur in most parts of the world, as populations have changed and human civilizations have risen and fallen (e.g. Perlin, 1989; Turner *et al.*, 1990). The primary cause of land cover and land use change worldwide is the human population and the way people use and manage land (Kates *et al*., 1990; Liu *et al.*, 1993; Turner *et al.*, 1990; Riebsame *et al.*, 1994; Diamond & Noonan, 1996; Dale *et al*., 2000; Gobin *et al*., 2001). The most potent forces for change acting on vegetation are the effects of changing land use arising from direct effects of an expanding human population and associated infrastructure (e.g. habitat destruction for agriculture, human settlement, overgrazing, etc.) and indirect effects (e.g. socio-cultural factors, political systems, pollution, etc.; Grime, 1997; Dale *et al.*, 2000; MEA, 2005b). Humans are reducing the capacity of ecosystems to cope with change through a combination of top-down (e.g. overexploitation of top predators) and bottom-up impacts (e.g. excess nutrient influx) as well as through alterations of disturbance regime and with climatic change (Paine *et al.*, 1998; Nyström *et al.*, 2000; Worm *et al.*, 2002). As such, land use directly and indirectly influences environmental conditions, which play a major role in the dynamics and changes in landscapes.

Forests and grasslands, in particular, have undergone large changes (Houghton, 1995), and it is estimated that between 1700 and 1980, the area of forests and woodlands decreased globally by 19%, and grassland and pasture by 8%, while croplands increased by 466% (Richards, 1990). Land use changes that alter natural disturbances are likely to cause changes in species abundance and distribution, community composition and ecosystem function (Yarie *et al*., 1998). Studies have also shown that variability in species richness between land uses can be explained by a variety of factors that include internal factors like habitat quality (Dauber & Wolters, 2000), external factors such as spatial-temporal dynamics (Purtauf *et al.*, 2001; Waldhardt & Otte, 2003), boundary characteristics (Fagan *et al.*, 1999) or neighbourhood effects (Tilman & Downing, 1994).

Shifting cultivation (whereby fields are cleared, burnt and cultivated for short periods and then fallowed), grazing and burning play a key role in the modification and transformation of savanna landscapes including the miombo woodlands (Frost *et al.*, 1985). The different kinds of shifting cultivation practiced in the miombo woodland of Zambia have led to deforestation (Araki, 1992; Ministry of Environment and Natural Resources, 1994), with attendant loss of top-soil organic matter and available phosphorus (Chidumayo & Kwibisa, 2003), leading to loss of soil productivity. Ethiopia's long term human occupation of the woodlands accompanied by shifting cultivation and extensive cattle grazing activities, in combination with localized human population pressure, has resulted in heavy deforestation, loss of biodiversity and impoverishment of ecosystems (Yirdaw & Luukkanen, 2003). Moreover manipulation of vegetation through land use practices that cause loss of habitat quality may result in loss of income, environmental services, national food security and tourism revenues, habitat degradation and biodiversity loss (Blaisdell *et al.,* 1970; MEA, 2005a), consequently compromising human well-being.

The prevailing land use practices in many of Africa's savanna woodlands do not represent optimum resource management of particularly woody plants. Yet the sustainability of most dryland ecosystems depends heavily on trees and other woody plants. Hence, in a country like Uganda, for the sustainable management of important savanna resources, it is important to evaluate the magnitude, pattern, and type of land use and land cover changes and projecting the consequences of such change to their conservation (FAO, 2004; MEA, 2005b). However, the recognition that ecological processes occur within a temporal setting and that they change over time is fundamental to analyzing their effects on land use. Size, shape, and spatial relationships of habitat patches on the landscape affect the structure and function of ecosystems. On the other hand, the responses of the land to changes in use and management by people depend on the expression of the fundamental principles of nature, i.e. time, species, place, disturbance and landscape (Dale *et al*., 2000).

1.4. Wood harvesting to meet livelihood needs

High population growth on limited land combined with difficult economic circumstances, often made worse by adverse climatic conditions such as drought, constrain rural incomes, consequently, encouraging people to increase reliance on the woodlands for additional agriculture and pastureland (Chipika & Kowero, 2000). Furthermore, such conditions provide an incentive to rural communities to increase harvesting of woodland products for sale to supplement incomes, hence causing deforestation and/or degradation of the woodlands. In southern African countries, the high dependency of urban and rural households on firewood and charcoal for cooking is one of the major causes of deforestation. This raises fears about land degradation because of loss of soil productivity (Chidumayo, 1989; Moyo *et al.,* 1993). Heavy reliance on wood fuels can result in a range of negative environmental impacts, with both local and global consequences, including forests/woodlands loss and degradation, health problems for charcoal producers and households where biofuels are combusted (Ezzati & Kammen, 2001), and increased greenhouse gas emissions (Blailis *et al.*, 2005). It is estimated that extraction of wood from tropical forest/woodlands for timber, charcoal production and fuelwood constitute 68% of the proximate causes of deforestation in Africa, 89% in Asia and 51% in Latin America (Geist & Lambin, 2001). It has been shown that impacts of wood harvesting of savanna woodlands are usually higher close to the village and decrease with distance from settlements (Grundy *et al.*, 1993; Vermeulen, 1996; Shackleton, 1993; Luoga *et al.*, 2002).

1.5. Fire

In most African savanna ecosystems, fires result from charcoal burning, preparation of land for crop cultivation (slash and burn practices), and intentional burning of old dry grass and killing ticks by livestock keepers (MEA, 2005b). Such anthropogenic fires are a major disturbance factor, and may be a controlling factor determining patterns of species richness mainly in savanna ecosystems (Hoffman, 1998). Indeed, fire is a pivotal ecological factor that influences the functional response of woody plants in habitats prone to such disturbance (Clarke *et al.,* 2005) and may produce as much as a third of total global emissions from biomass burning (Andrea, 1991). However, the impacts of fires on ecosystem functions and dynamics are influenced by fire intensity and frequency. But the frequency with which fires occur in an ecosystem and their intensity is influenced by the vegetation within which they occur (Averill *et al.*, 1994). Frequent burning, similar to the case for most equatorial African savannas, can be a major constraint for reproduction of woody species and reducing top-soil organic matter and nitrogen (Hoffmann, 1998). Excessive intensity and frequency of fire can lead to irreversible changes in ecological processes such as loss of soil organic matter, erosion, loss of biodiversity, and habitat changes for many plant and animal species (MEA, 2005b). For example, in the miombo woodlands, it has been predicted that increased fire will expand savanna grassland areas at the expense of wooded areas (Desanker *et al.*, 1997).

Although savanna plants are reported to be adapted to burning (through persistence or resprouting), most of them cannot survive the rigours of repeated burning especially for seed-based recruitment (Clarke *et al.,* 2005). Nevertheless species composition of plant communities may be maintained after fire (Traband & Lepart, 1981). Therefore, clearly understanding the effects of burning on the savanna plant dynamics is necessary for predicting the long term effects of current fire regimes on woody species (Pivello & Norton, 1996). There is also a growing realization that fire regimes can have profound effects on community dynamics (Bond & Midgley, 2001), and this has led to intensive efforts to model the response of plants to fire (Vesk & Westoby, 2004).

1.6. Resilience in Social-Ecological Systems (SES)

A resilient social system is one with the capacity to survive different types of change, be it from a political, social or natural disturbances such as woodland/forest fires, poor harvest, etc (Gunderson, 2000). Humans plan and fantasize as to how the feature will turn out. They can choose to make changes to certain structure and functions in the society. Preferences and values of people are not necessarily invariable, nor do they exist in a social and cultural vacuum. Rather, they are formed and reformed as part of social process (Folke, 2003). Ecological processes and the feedbacks that they can create between human actions and human well-being are thought to be important for human societies (Cumming *et al.,* 2005a). Whereas, managing for resilience implies maintaining options in a world of rapid change in which surprise is likely and the future unpredictable, hence, resilience is forward looking (Folke *et al.*, 2002). It may be possible to assess SES thresholds retrospectively, through historical analysis of case studies, especially in applications of resilience to pressing environmental problems (Carpenter *et al.*, 2005), as well as using potential surrogates of resilience, i.e. variables through which the persistence of SES emerging through change can be assessed (Berkers & Seixas, 2005). According to Carpenter *et al*. (2005) “a resilience surrogate is a proxy used to assess resilience in a social ecological system”. Surrogates are different from indicators because they are forward-looking rather than measures of the current or past state. In order to build resilience, there are four categories of factors, i.e.: (i) learning to live with change, (ii) nurturing diversity for reorganization and renewal, (iii) combining different kinds of knowledge and (iv) creating opportunity for self organization (Berkers & Seixas, 2005). Woodlands in Nakasongola District, central Uganda, tend to be human-dominated and are used intensively for charcoal production and extraction of firewood and building poles. The woodlands are geographically bounded and readily identifiable as integrated systems of human and nature. Therefore, they are regarded as a social–ecological system (SES).

1.7. Theoretical considerations

One concern with the utilization of savanna woodlands for fuelwood, charcoal and other products through human harvesting of woody plants is whether these savanna ecosystems are resilient to such anthropogenic disturbances. A number of theories/hypotheses including the Ecological Resilience Hypothesis and Intermediate Disturbance Hypothesis have been put forward to explain the influence of disturbance regimes on ecosystem resilience and species diversity. As regards species diversity, the are two general classes of hypotheses; the neutral and the niche-based (i.e. differentiation hypothesis) that have been put forward to explain the origin and maintenance of variation in species composition (Pitman *et al.,* 2001; Hubbell, 2001) among communities within a geographic region.

In savanna ecosystems there may be various livelihood strategies, which are a response to socio-economic conditions at any point in time. In explaining the livelihood strategies adopted in the rural communities a number of theories that include the Induced Innovation and Boserupian theories (Boserup, 1965; Binswanger & Ruttan 1978; Ruthenberg, 1980) have been put forward.

1.7.1. Ecological resilience

Resilience is the ability to return to a steady state following a perturbation (Pimm, 1984; O'Neill *et al*., 1986; Tilman & Downing, 1994; Tilman, 1996). While ecological resilience is defined as the amount of disturbance that an ecosystem could withstand without changing self-organized processes and structures (defined as alternative stable states) (Gunderson, 2000). The definition for ecological resilience emphasizes conditions far from any stable steady-state, where instabilities can flip a system into another regime of behaviour, which is to another stability domain (Walker *et al.,* 1996; Holling, 1996; Gunderson, 2000; Gunderson *et al*., 2002). It describes the capacity of an ecosystem to cope with disturbances, such as storms, fire and pollution, without shifting into a qualitatively different state. Thus, a resilient ecosystem is one which has the capacity to withstand shocks and surprises, and if damaged to rebuild itself. The process of rebuilding after disturbance promotes renewal and innovation. Without resilience, ecosystems may become vulnerable to the effects of disturbance that previously could be absorbed (Folk *et al.,* 2002). Linked social-ecological systems are often difficult to manage and understand due to their non-linear and multi-scale dynamics, the potential for rapid change in system drivers, their sensitivity to external perturbations, and the reflexivity of human action (Bennet *et al.,* 2005). There is one most important uncertainty about ecosystems at the present time, the question of how much change they can cope with before the provision of ecosystem services is compromised (Carpenter, 2002). If ecosystems are relatively resilient, they will be able to absorb anthropogenic impacts without the loss of essential structure or functions (Cumming *et al.,* 2005b). From a practical stand point, resilience theory provides a conceptual foundation for sustainable development (Folke *et al.,* 2002).

Ecosystems are resilient when ecological interactions reinforce one another and dampen disruptions (Peterson *et al.*, 1998). Such a situation may arise due to compensation when a species with an ecological function similar to another species increases in abundance as the other declines (Holling, 1996), or as one species reduces the impact of a disruption on another species (Peterson *et al.*, 1998). However, human actions may cause loss of resilience through removing response diversity, whole functional groups of species or whole trophic levels impacting on ecosystems via emissions of waste and pollutants and climatic change, and altering the magnitude, frequency, and duration of disturbance regimes to which the biota are adapted (Folke *et al.*, 2004). Disturbance dynamics affect and are affected by species and their ecological functions (D'Antonio & Vitousek, 1992). Consequently, the processes regulating contagious disturbances (e.g. fire, diseases, and insect outbreaks) are as much determinants of ecological resilience as are more local interactions among species (Peterson *et al.*, 1998). Loss of resilience through the combined and often synergistic effects of disturbance pressures can make ecosystems more vulnerable to changes that previously could be absorbed (Folke *et al.*, 2004).

Despite the impacts of human disturbance, some studies have shown that savanna vegetation appears to be resilient to it, with individual plant species, communities and vegetation formations re-establishing themselves despite major fluctuations (Belsky, 1987; Dublin, 1995) through regeneration. However, studies of regeneration ecology of tropical trees indicate that the mechanisms of regeneration vary from species to species (Brokaw, 1985; Swaine & Whitmore, 1988; Garwood, 1989; Whitmore, 1989, 1991; Fenner, 1995). Regeneration in woodlands can be achieved through seedlings recruitment and coppicing or resprouting. Many woody plants can resprout, and many ecosystems are dominated by resprouters (Bond & Midgley, 2001). The ability to coppice, which refers to the production of "vegetative shoots at the base of the stump" (van Wyk & van Wyk, 1997), is an efficient means by which woody plants regain biomass lost during disturbances such as frequent fires (Bellingham & Sparrow, 2000). Resprouting after harvesting is a key component of regeneration in miombo (Luoga *et al.*, 2004), and the ability of damaged trees to regrow from the remaining stump has been regarded as a key attribute to the resilience and productivity of savannas (Shackleton, 2000). Several studies have revealed that coppicing/resprouting is generally the primary regeneration mechanism in dry woodland sites, where stumps and roots remain in place (Murphy & Lugo, 1986; Murphy *et al.,* 1995). Trees of the savanna woodlands of south central and eastern Africa resprout from roots and stumps once the above ground parts have been removed or killed by harvesting or fire damage (Frost *et al.,* 1986; Grundy, 1995; Luoga *et al.,* 2004). In savanna communities, resprouting plays a major role in the process of post-fire succession, and has been considered as a simple regrowth of long-lived plants present in pre-fire stands (Luoga *et al.*, 2004).

On the other hand, biodiversity has been found to play a crucial role in natural ecosystems (e.g. savanna woodlands) resilience by spreading risks through having many species performing the same essential function (such as photosynthesis or decomposition) and if species in such “functional groups” respond in different ways to disturbance. Then, species can replace or compensate for each other in times of disturbance providing insurance, and making it possible for ecosystems to reorganise after disturbance (Folke *et al.,* 2002). It has also been experimentally demonstrated that in small systems, over ecologically brief periods, increased species richness increases the efficiency and stability of some ecosystem functions (Tilman, 1996; Tilman *et al.*, 1996). According to Folke *et al.* (2004), biological sources of renewal and reorganization for ecosystem resilience consists of functional groups of biological legacies and mobile link species and their support areas in larger landscapes or seascapes. For example large trees serve as biological legacies after fire and storms in forest ecosystems (e.g. Elmqvist *et al.,* 2001), and seed banks and vegetative propagules play the same role in the tundra ecosystems (Vavrek *et al.,* 1999). Furthermore, a number of observations suggest that biodiversity at larger spatial scales (i.e. landscapes and regions) ensures that appropriate key species for ecosystem functioning are recruited to local systems after disturbance or when environmental conditions change (Peterson *et al.,* 199; Nystrom & Folke, 2001; Bengtsson *et al.,* 2003). Thus, ecosystems seem to be particularly resilient if there are many species performing the same function, and species within such functional groups respond in different ways to disturbances (Folke *et al.,* 2002; Walker *et al.,* 2002; Allison & Hobbs, 2004).

1.7.2. Intermediate Disturbance Hypothesis

The Intermediate Disturbance Hypothesis is an ecological hypothesis, which proposes that diversity will be highest at sites that have had an intermediate frequency of disturbance that prevents competitive exclusion and will be lower at sites that have experienced very high or very low disturbance frequencies (Grime, 1973; Connell, 1978). High diversity (species richness) is expected in regions with intermediate levels of disturbances. Therefore, disturbance is an important mechanism for producing spatial heterogeneity within patches (Chaneton & Facelli, 1991; Collins, 1992). Disturbance not only change the immediate material fluxes, but also affect the composition of species within the system. For example, areas suitable for growth are opened which were previously occupied by other species now weakened by disturbance or killed, the remaining surviving organisms may spread or new species enter (Schulze *et al.,* 2002). Whereas, number of species decreases in the absence of external disturbance (Hobbie *et al.,* 1994). The idea that ecosystems are in equilibrium with their environment has been proven incorrect. Short-term variability of climate and the occurrence of small or large spatial “catastrophes” cause continuous change in the biogeochemical conditions and turnover of the participating species (Schulze *et al.,* 2002). In relation to charcoal harvest in savanna woodlands of Uganda, we expect that parts of woodlands exposed to intermediate harvesting will have high species regeneration rates and be able to withstand the disturbance pressures, as compared to those that are over-harvested.

Species responses to disturbances are governed primarily by their life history and physiological traits and by the characteristics of the disturbance (Gomez *et al.*, 1999). Species traits are especially important in determining the potential of species to establish and to persist following disturbance (Chambers, 1995). In the southern African savannas, the survival of the cut stem and growth rate of the resultant coppice shoots is believed to be influenced by several plant related factors, including height and size of the shrub height of cutting and root/shoot ratio after felling (Shackleton, 1997; Kaschula *et al.*, 2005a). However, regeneration and persistence of tree species is sometimes dependent on a particular disturbance event (e.g. Sterwart & Rose, 1990; Cho & Boerner, 1991; Welden *et al.*, 1991). For example, some species might require a large scale disturbance, while others may mainly regenerate in a single tree fall gap. Disturbance frequency is an important determinant of the relative frequency of resprouting at the community level (White & Picket, 1985; Midgley, 1996; Kruger *et al.*, 1997). In addition, disturbance history is a major factor controlling local variation in community structure and that passive recovery by woody vegetation is constrained by both climatic and biological factors (Gomez *et al.*, 1999). Hence an evaluation of the relative importance of soil compaction and anthropogenic disturbances in influencing resilience and persistence of woody plants is essential for developing conservation priorities (William-Linera, 2002). Furthermore, understanding the factors affecting coppice growth of a species, such as environmental conditions and harvesting techniques is, therefore, vital in order to develop models for sustainable fuel use (Kaschula *et al.*, 2005b), and management of woodland resources (Shackleton, 1993, 2000). Although coppice growth is an important species-specific trait that strongly influences fuelwood production and regeneration, patterns of coppice growth are poorly understood in African savannas (Bellingham & Sparrow, 2000).

1.7.3. The Niche differentiation hypothesis and neutral theory of biodiversity

The neutral theory of biodiversity considers that species distribution results from stochastic demographic processes and the processes like limited dispersal ability create locally autocorrelated spatial patterns which maintain biodiversity (Hubbell, 2001). In contrast, the niche differentiation hypothesis focuses on the importance of niche differentiation for diversity maintenance; and both exogenous factors such as environmental variation (often soil type and topography), and endogenous factors such as light and/or successional status (Chesson, 2000; Chase & Leibold, 2003) have been proposed as major niche dimensions controlling species distribution in tropical ecosystems.

1.7.4. Induced Innovation Theory

According to the "Induced Innovation Theory" historical changes in socio-economic conditions (particularly increased population density and market development) lead to changes in relative input and output prices, and therefore the types of strategies and specific options considered by natural resource dependent communities (Boserup, 1965; Binswanger & Ruttan, 1978; Ruthenberg, 1980). While the livelihood approach states that the type of activity undertaken and the amount on income earned by a household is a function of the assets at its disposal (Barrett *et al.,* 2005, Brown *et al.,* 2006). Hence, the mechanisms adopted to meet every day needs may vary from household to household depending on their resource endowments.

1.8. Description of the study area

The present study focused on an African equatorial multiple use savanna of Nakasongola District located to the south of Lake Kyoga in central Uganda, and lying at $0^0 40'$- $1^0 41'$ N and $31^0 57'$ - $32^0 48'$ E. The District covers about 3,424 km^2 most of which is woodland and grassland savanna vegetation and only about 322 km^2 (10%) are open water and wetlands. The area has a human population of about 128,126 (41 people/km^2; 50.2% males and 49.8 females; 2000 National Housing Census), scattered within the eight sub-counties (i.e. administrative sub-divisions) namely; Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata that constitute the District (Figure 1; Uganda Bureau of Statistics, 2002). About 95.3% of the total population lives in rural areas and entirely depend on the land resources (Uganda Bureau of Statistics, 2002).

This savanna receives mean annual rainfall ranging from 500 – 1000 mm, which is concentrated into two wet seasons (March to May and August to November); but rainfall amounts and reliability is higher in the south, declining gradually to the north. The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C, respectively. The topography of the area undulates between 1,036 m and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al.,* 1967).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964). This is a natural savanna woodland or woodland of mixed deciduous trees 3 to 12 m high and grasses 0.3 to 1.3 m high at maturity. However, the cover of the grass layer varies with season, which is often patchy and is subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirki*i subsp. *mildbraedii, A. senegal,* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983). The vegetation formations and dynamics of the area seem to be influenced by anthropogenic factors, rainfall and soils. Given the nature of the rainfall patterns and vegetation formations, the major land uses practices in this savanna seem to be livestock grazing, subsistence crop cultivation, charcoal production and fuelwood extraction. However, there is a succession of change in land use over time with areas used for charcoal production being later used for cultivation, while cultivated areas may subsequently be used for grazing. With most of the household livelihood strategies heavily dependent and based on woodland resources, a number of land use practices within a particular area are constantly changing (USAID report, 2002). Hence, a particular area can experience a multiple of land uses within a particular period of time.

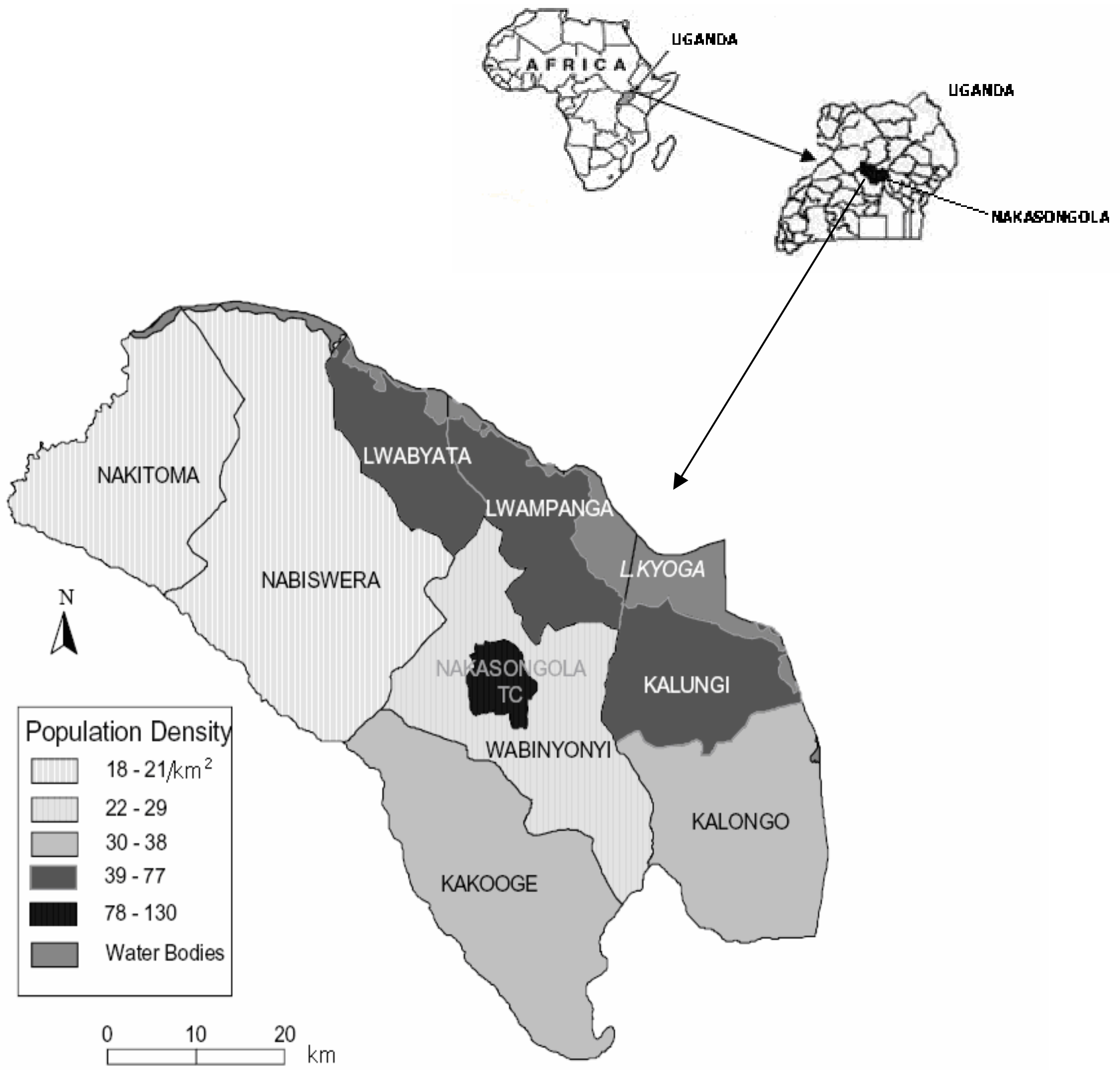

Figure 1. Map of Nakasongola District showing the eight constituent sub-counties and their human population density. In-set is a map of Africa showing Uganda and a map of Uganda showing Nakasongola District shaded. (TC: Town centre; L. Kyoga: Lake Kyoga).

1.9. Rationale of the study

In Sub-Saharan Africa, savannas make up most of the tropical and subtropical woodland cover, from which rural households derive a wide range of products (including food, medicine, and fuelwood), for both subsistence and income generation (e.g. Luoga *et al.,* 2000; Braedt & Standa-Gunda, 2000; Dovie *et al.,* 2003; Letsela *et al.,* 2003; Kituyi, 2004; Dovie *et al.,* 2004; Botha *et al.*, 2005). In southern and eastern African regions, miombo woodlands are economically important for the supply of timber, poles, firewood, charcoal, medicines, food, fibre and carvings (Chidumayo, 1988; SADC, 1993; Luoga *et al.,* 2000; Shackleton, 2002). In Uganda, forests and savanna woodlands supply well over 90% of its energy requirements, and it is reported that in 2001, the Uganda Forest Department was earning about US$336,134 a year from timber sales (Moyoni, 2001). At the same time, these woodlands are used as grazing land by pastoralists, and cleared for shifting subsistence crop cultivation and establishment of cattle ranches. Thus, they can make a significant contribution to local and national production and economic growth. However, some of the household livelihood activities might be leading to biodiversity loss and reductions in the abundance or elimination of valuable species that support both livestock and human livelihoods.

Although Uganda's savanna woodlands, like those of other Sub-Saharan African countries, are of environmental and socio-economic importance, and faced with serious management challenges, few studies have been carried out on them, as compared to the local tropical rainforests. Like their other counterparts on the continent, they are relatively poorly known, both in terms of their species diversity and resilience to both anthropogenic and natural disturbances (Grainger, 1999). Given the attention accorded to their management, there seems to be little appreciation in government and planning of their importance for rural livelihoods and their contribution to the informal economy. Yet, studies elsewhere (e.g. Luoga *et al.,* 2000; Shackleton, 2002; Kituyi, 2004) have revealed that woody species in dryland woodlands are used for charcoal production, fuelwood and building poles. However, information on the ecological diversity and regeneration potential of a number of important plants, particularly the highly utilised woody species used for charcoal production, is insufficient

The currently changing climate, increasing demands for the conservation and improvement of dry woodlands, and control of desertification, necessitates a sound understanding of the nature, dynamics and production potential of savanna woodland systems. Moreover, in order to utilise and manage sustainably the available natural resources to their full potential, without causing long-term damage, it is important to precisely describe and classify land use and land cover changes in order to define sustainable land use systems that are best suited for each place (FAO, 1998). Furthermore, planning sustainable management of existing land uses in the area requires studies of the structure, composition, and ecological functioning and resilience of the savanna woodlands. Understanding of the influence of land use practices and environmental factors on patterns of plant species diversity, woodland plant composition and dynamics is of great importance in the process of land use and management, as it aids effective conservation, planning and management (Solbrig *et al.,* 1992; Walker & Stefan, 1996). Information on plant population dynamics under the current disturbance regimes is needed to foresee the trends of community changes in the future. Furthermore, since the woodlands of Uganda, like those of other African countries, are subjected to various anthropogenic disturbances, their future sustainable management and conservation requires a consideration of their resilience to such disturbances. A better understanding of biological diversity and ecosystem resilience is important in the active adaptive management and governance of resilience, required to sustain or create desired ecosystems states (Folke *et al.,* 2004). Understanding the contexts for how people respond to and shape periods of change and how society reorganises following change seems to be a largely neglected and poorly understood issue (Gunderson & Holling, 2002). So far, there is little experience with estimating resilience of SES, and little understanding through empirical study of resilience in SES (Carpenter *et al*., 2005) particularly in the savanna woodlands of Uganda. Yet, the building of resilience in integrated human and nature systems or social –ecological systems (SES) is key for sustainability (Berker & Seixas, 2005). It is important that society is flexible and knowledgeable about how nature exists and functions because nature is dynamic (Adger, 2000). While attaching monetary values to natural resources (both timber and non-timber woodland products), can aid decision making to assess planning and development alternatives to allocate scarce human and financial resources, reconcile conflicting demands, plan land uses, and determine compensation levels for loss of resources (Shackleton *et al.,* 2002; Luoga *et al*., 2002).

1.9.1. Aims and Objectives of the study

This thesis aims to contribute to our understanding of woody plant diversity, distribution, use and resilience as well as land-cover change in a multiple land use equatorial African savanna in relation to human utilisation of woodland resources and edaphic factors. The main aim is further broken into a series of specific objectives that form the basis of six study chapters (i.e. Chapters 2 to 7) that are included in this thesis. The six studies (i.e. Chapters 2 - 7) included in this thesis had the following specific objectives:

i. To identify household livelihood strategies and assess the economic contribution of charcoal production to rural livelihoods.
ii. To analyse land cover and associated land use changes during 1984, 1995 and 2000 (Landsat images), with a view to assessing the influence of human utilization on the woodland resources.
iii. To determine and compare woody species diversity (richness and evenness, and alpha and beta diversity) in the identified major land use types (charcoal production, cultivated and grazing land).
iv. To describe the interrelations between the woody species composition with the corresponding site environmental (e.g. topographical gradients, and soil chemical and physical factors), and anthropogenic (human induced) factors.
v. To assess the level of human harvesting of woody plants and their responses to harvesting and other forms of anthropogenic disturbances through resprouting.
vi. To investigate seedling recruitment in relation to environmental factors and the population structure of woody species, with a view to determining resilience to harvesting and other anthropogenic disturbances.

In addressing these objectives, the following hypothesis/theories; (i) the induced innovation theory (Chapter 2), (ii) the niche differentiation hypothesis (Chapter 4, 5, and 7), and (iii) ecological resilience (Chapter 6 and 7) are considered.

1.9.2. General approach to the study

The study took a trans-disciplinary approach, using methods across disciplines (i.e. ecology, remote-sensing, social and economic) to address the research objectives. By integrating social and economic information with environmental information about the savanna ecosystems, the approach can explicitly link human utilisation to biological capacity of the ecosystems to sustain the utilization.

Based on these major land cover and the three land use practices namely grazing, cultivation and charcoal production (hereafter referred to as grazing, cultivation, charcoal production respectively), representative villages (areas) in each of the eight sub-counties were located (with the help of local leaders, and the Natural Resource and Environmental Officials) and targeted for woody vegetation sampling. Thus, in each sub-county, at least three transects were laid, each representing one of the three major land use types. The locations of the transects were selected randomly but taking into consideration the homogeneous nature of the area for a particular land use type, and an area sufficient enough to accommodate at least three 20 x 50 m (0.1 ha) plots with a separation distance of 200 metres from each other. The 20 x 50 m plot size is the standard area for work on vascular plant species richness in savanna woodlands. It has been widely used in studies of the vegetation of tropical woodlands and forests (e.g. Luoga *et al*., 2000; Dupré 2001; Duque *et al*., 2002; Witkowski & Garner, 2008). Transects were laid radiating away from the source of disturbance as it was hypothesised that in villages where subsistence activities are paramount there are gradients in resource availability, which decrease with increasing distance from the source of disturbance. A total of 25 transects representing 75, 0.1 ha plots were laid, with each sub-county contributing 3 transects except for Nabiswera which had 4 transects. The additional three plots were an attempt to include a highly overgrazed area in Nabisweera sub-county. Hence, in each land use type, 24 plots were sampled, except for "grazing" which had 27 plots.

To detect changes in land cover, at least two time-period data sets are required (Jenson, 1986). In this case three date (1984, 1995 and 2000/1) ortho-rectified, multi-temporal Landsat data sets UTM/WGS84 images were used to map the changes of the vegetation in order to understand the variability in land cover changes. The history of land use and causes of land cover changes within the eight sub-counties in the study area were obtained at least over the past 10 years through field observations, as well as interviews (i.e. semi-structured interviews) with local people and key informants living around and within the woodlands.

Semi-structured interviews were also used to collect data on livelihood strategies, savanna woodland resource use, and trends in woodland cover. The semi-structured nature enables 'key topics to be gathered from all respondents, while allowing the respondents the flexibility to define those topics within their contextual understanding' (O'Higgins, 2007). The interview was carried out on an individual basis, to minimise peer influence and improve the quality of data (Phillips & Gentry, 1993), and all the responses were recorded. The data collection methods for each of the study objectives are described in detail under each respective study chapter (i.e. Chapters 2-7).

1.9.3. Structure of the thesis

The thesis consists of eight chapters arranged in a thematic progression beginning with an introduction chapter (Chapter 1) followed by six study results chapters (Chapters 2-7), and a synthesis chapter (Chapter 8). In Chapter 1, the general background for developing this research and a description of the study area are presented. The six study results chapters (i.e. Chapters 2-7) are autonomous and written in a format of scientific papers each with a complete abstract, introduction, methods, results, discussion and conclusion sections. Hence, there are repetitions of some items or their parts (e.g. study area description and sampling design) among these chapters. Of these, Chapter 2 reports on the household livelihoods and incomes generated from charcoal production. This is followed by Chapter 3 which reports on the land use and land cover changes due to the influence of human utilization on the woodland vegetation and the implications for sustainable management of these woodlands. In Chapters 4 and 5, the structure, composition (i.e. species richness, diversity) and distribution of the woody species are described in relations to major land uses and environmental gradients. In Chapters 6 and 7, the different aspects of natural regeneration (i.e. resprouting and seedling recruitment) of woody species and the 16 woody species highly utilized for charcoal production are described in relation to major land uses and environmental gradients within the multiple use savanna. Finally, Chapter 8 presents a general discussion and synthesis, which serves as the bridge between the different main chapters (i.e. Chapters 2 - 7). It also includes directions for future work and thoughts on the implications of this research for the better understanding of savanna woodlands, and the influences of humans on woodland resources, and, hence, the sustainable management of savanna woodlands.

References

Adger, W.N. 2000. Social and ecological resilience: are they related? *Progress in Human Geography* 24: 347-364.

Allison, H.E. & Hobbs, R.J. 2004. Resilience, adaptive capacity and the "Lock in Trap" of the western Australian agricultural region. *Ecology and Society* 9(1): 3. [online]URL:http://www.ecologyandsociety.org/vol9/iss1/art3/

Andrea, M.O. 1991. Biomass burning: its history, use and distribution and its impact on environmental quality and global change. pp. 3-21. In: Levine, J.S. (Ed.) Global Biomass Burning: Atmospheric, Climatic and Biospheric Implications. MIT Press, Cambridge, Massachusetts.

Araki, S. 1992. The role of miombo woodland ecosystem in chitemene shifting cultivation in northern Zambia. *Journal of Plant Information MAB* 11: 8-15.

Arnold, M. & Person, R. 2003. Reassessing the fuelwood situation in developing countries. *International Forestry Review* 5: 379-383.

Averill, R.D., Larson, L., Saveland, J., Wargo, P. & Williams, J. 1994. Disturbance Process and Ecosystem Management. Vegetation Management and Protection Report.

Barrett, C.B., Bezuneh, M., Clay, D.C. & Reardon, T. 2005. Heterogeneous constraints, incentives and income diversification strategies in rural Africa. Q*uarterly Journal of International Agriculture* 44(1): 37-60.

Baudry, J., Burel, F., Thenail, C. & LeCaeur, D. 2000. A holistic landscape ecological study of the interactions between farming activities and ecological patterns in Brittany, France. *Landscape Urban Plan* 50: 119-128.

Belbin, L. 1995. A multivariate approach to the selection of biological reserves. *Biodiversity and Conservation* 9: 951-963.

Bellingham, P.J. & Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409-416.

Belsky, A.J. 1987. Re-vegetation of Natural and human caused disturbances in the Serengeti National Park, Tanzania. *Vegetatio* 70: 51-59.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U. & Folke, C. 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32: 389-396.

Bennett, E.M., Cumming, G.S. & Peterson, G.D. 2005. A Systems Model Approach to Determining Resilience Surrogates for Case Studies. *Ecosystems* 8: 945-957.

Berkers, F. & Seixas, C. 2005. Building Resilience in Lagoon Social-Ecological Systems: A Local-Level Perspective. *Ecosystems* 8: 967-974.

Bernard, R.H. 1996. "Qualitative data, quantitative analysis". *The cultural Anthropology Methods Journal* 8 (1): 9-11.

Bernier, N. & Ponge, J.F. 1994. Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. Soil Biology & Biochemistry 26: 183-220.

Binswager, H.P. & Ruttan, V. 1978. Induced Innovation. Technology, Institutions and Development: John Hopkins University Press.

Blailis, R., Ezzati, M. & Kammen, D. 2005. Mortality and greenhouse gas impacts of biomass and petroleum energy futures in Africa. *Science* 308: 98-103.

Blaisdell, J.P., Duvall, V.L., Harris, R.W., Lloyd, R.D. & Reid, E.H. 1970. Range research to meet new challenges and goals. *Journal of Range Management* 23: 227-234.

Bond, J.W. & Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16: 45-51.

Bond, W.J. & Van Wilgren, B.W. 1996. Fire and Plants. *Population and Community Biology Series* 14. Chapman and Hall.

Boserup, E. 1965. The conditions of agricultural growth: The economics of agrarian change under population pressure. London, George Allen and Unwin Ltd.

Botha, J., Witkowski, E.T.F. & Cock, J. 2005. A review of nurseries as conservation or social forest outreach tools. *International Journal of Biodiversity Science and Management* 1: 33-49.

Braedt, O. & Standa-Gunda, W. 2000. Woodcraft markets in Zimbabwe. *International Tree Crops Journal* 10: 367-84.

Brandon, R.B. 2001. Mapping Rural Land Use & Land Cover Change in Carroll County, Arkansas Utilizing Multi-Temporal Landsat Thematic Mapper Satellite Imagery. Thesis University of Arkansas. http://www.cast.uark.edu/local/brandon_thesis /index.html

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

Brown, D.R., Stephens, E.C., Ouma, J.O., Murithi, F.M. & Barrett, C.B. 2006. Livelihood stratergies in the rural Kenyanhighlands. *African Journal of Agricultural and Resource Economics* 1(1): 21-36.

Carpenter, S.R. 2002. Ecological futures: building an ecology of the long now. *Ecology* 83(8): 2069-2083.

Carpenter, S.R., Westley, W. & Turner, M.G. 2005. Surrogates for Resilience of Social-Ecological Systems. *Ecosystems* 8: 941-944.

Chambers, J.C 1995. Disturbance, life history strategies, and seed fates in alpine herb field communities. *American Journal of Botany* 82: 421-433.

Chaneton, E.J & Facelli, J.M. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* 93: 141-155

Chase J.M. & Leibold M.A. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31: 343-366.

Chidumayo, E.N. & Kwibisa, L. 2003. Effect of deforestation on grass biomass and soil nutrient status in miombo woodland Zambia. *Agriculture, Ecosystem and Environment* 96: 97-105.

Chidumayo, E.N. 1988. Estimating fuelwood production and yield in regrowth dry miombo woodland in Zambia. *Forest Ecology Monograph* 24: 59-66.

Chidumayo, E.N. 1989. Land use, deforestation and reforestation in the Zambian copper belt. *Land Degradation and Rehabilitation* 1: 209-216.

Chidumayo, E.N. 1997. Miombo Ecology and Management: An Introduction. Intermediate Technology Publications, London. pp. 166

Chipika, J.T. & Kowero, G. 2000. Deforestation of woodlands in communal area Zimbabwe: is it due to agricultural policies? *Agriculture, Ecosystems and Environment* 7: 175-185.

Cho, D.S & Boerner, R.E.J. 1991. Canopy disturbance patterns and regeneration of Quercus species in two Ohio old-growth forests. *Vegetatio* 93: 9-18.

Clarke, P.J., Knox, K.J.E., Willis, K.E. & Campbell, M. 2005. Landscape patterns of woody plant response to crown fire: Disturbance and productivity influence sprouting ability. *Journal of Ecology* 93: 544-555.

Collins, S.L.1992. Fire frequency and community heterogeneity in tall grass prairie vegetation. *Journal of Ecology* 73: 2001-2006.

Connell, J.H. 1978. Diversity in Tropical Rainforests and Coral Reefs. *Science* 199: 1302-1310.

Cowling, R.M. 1984. A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. *Bothalia* 15: 175-227.

Cumming, G.S., Alcamo, J., Sala, O., Swart, R., Bennett, E.M. & Zurek, M. 2005a. Are Existing Global Scenarios Consistent with Ecological Feedback? *Ecosystems* 8: 143-152.

Cumming, G.S., Barnes, G., Perez, S., Schmink, M., Sieving, K.E., Southworth, J., Binford, M., Holt, R.D., Stickler, C. & Van Holt, T. 2005b. An Exploratory Framework for the Empirical Measurement of Resilience. *Ecosystems* 8: 975-987.

D'Antonio, C.M. & Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* 23: 63-87.

Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.H., Huntly, N., Naiman, R.J., Riebsame, W.E., Turner, M.G. & Valone, T.J. 2000. Ecological Principles and Guidelines for Managing the use of Land. *Ecological Applications* 10(3): 639-670.

Dauber, J. & Wolters, V. 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biology and Biochemistry* 32: 93-99.

Department for International Development (DFID). 1999. Sustainable livelihoods Guidance sheets. from http://www.eldis.org/vfile/upload/1/document/0901/sectio2.pdf. Accessed on 9.04.2009.

Desanker, P.V., Frost, P.G.H., Justice, C.O. & Scholes, R.J. 1997. The Miombo Network: Frame work for a terrestrial transects study of land use and land cover change in the Miombo ecosystems of Central Africa. IGBP Report No. 41. International Geosphere-Biosphere Programme, Stockholm, also available at http://www.miombo.gecp.virginia.edu

Diamond, H.L. & Noonan, P.F. 1996. Land use in America: report of sustainable use and land project. Island Press, Washington DC.

Dovie, B.K., Shackleton, C.M. & Witkowski, E.T.F. 2002. Direct-use values of woodland resources consumed and traded in a South African village. *International Journal of Sustainable Development and World Ecology* 9: 269-283.

Dovie, D.B.K, Witkowski, E.T.F. & Shackleton, C.M. 2004. The fuelwood crisis in Southern Africa-relating fuelwood use to livelihoods in a rural village. *GeoJournal* 60: 123-133.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2003. Direct-use value of smallholder crop production in semi-arid rural South African village. *Agricultural Systems* 76: 337-357.

Dublin, H. 1995. Vegetation dynamics in the Serengeti Mara ecosystem: the role of elephants, fire and other factors. pp. 71-90. In: Sinclair, A & Arcese, P. (Eds.) Serengeti II: dynamics, management, and conservation of an ecosystem. Chicago University Press, Chicago.

Duelli, P. 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agricultural Ecosystem and Environment* 62: 81-91

Dunning, J.B., Danielson, B.J. & Pulliam, H.R., 1992. Ecological process that affect populations in complex landscapes. *Oikos* 65: 169-175.

Dupré, C. 2001. Regional and local variation in plant species richness. Acta Universitatis Upsaliensis. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 641. Uppsala. ISBN 91-554-5064-4. pp. 32.

Duque, A., Sanchez, M., Cavelier, J. & Duivenvoorden, J.F. 2002. Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology* 18: 499-525.

Eberhard, A.A. 1990. Energy consumption patterns and supply problems in underdeveloped areas of South Africa. *Development Southern Africa* 7: 335-346.

Elmqvist, T., Wall, M., Berggren, A.L., Blix, L., Fritioff, S. & Rinman, U. 2001. Tropical forest reorganization after cyclone and fire disturbance in Samoa: remnant trees as biological legacies. *Conservation Ecology* 5:10. <http://www.consecol.org/vol5/iss2/art10>.

Eyre, F.H. 1980. Forest covers types of the United States and Canada. Society of American Foresters, Washington, D.C.

Ezzati, M., Singer, B. & Kammen, D. 2001. Towards an integrated framework for development and economic policy: the dynamics of environmental Kuznets curves. *World Development* 29: 1421-1434.

Fagan, W.F., Cantrell, R.S. & Cosner, C. 1999. How habitat edges change species interactions. *Journal of American Nature* 153: 165-183.

Faith, D.P. & Walker P.A. 1996. Environmental diversity: on the best possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation* 5: 399-415.

FAO, (undated). Management of natural resources in dry tropical zones. FAO Corporate Document Repository: <http://www.fao.org/DOCREP/005/w4442E/w4442e 04.htm>. Accessed on 15/9/2005.

FAO, 1997. Africover Land Cover Classification. FAO, Rome, Italy.

FAO, 1998. World Reference Base for Soil Resources. FAO, ISRIC and ISSS, Rome, Italy.

FAO, 2004. Land Cover Classification System. Land Cover Topic Centre. Rome, Italy.

Fenner, M. 1995. Ecology of seed banks. pp. 507-528. In: Kigel, J., Gallili, G. (Eds.), Seed development and germination. Marcel Dekker, New York.

Folke, C. 2003. Social-Ecological Resilience and Behavioural Responses. International Centre for Research on Natural Resources and the Environment, Stockholm University, Sweden.

Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C.S., Walker, B., Bengtsson, J., Berkes, F., Colding, J., Danell, K., Falkenmark, M., Moberg, M., Gordon, L., Kaspersson, R., Kautsky, N., Kinzig, A., Levin, S.A., Mäler, K.G., Ohlsson, P., Ostrom, E., Reid, W., Rockström, J., Savenije, S. & Svedin, U. 2002. Resilience and sustainable development: Building Adaptive capacity in a world of transformation. ICSU Series on Science for

Sustainable Development No. 3, 2002. International Council for Science, Paris and Report for the Swedish Environmental Advisory Council No. 1. Ministry of the Environment, Stockholm.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology and Systematics* 35: 557-581

Frost, P., Menaut, J.C., Walker, E., Medina, E., Solbrig, O.T. & Swift, M. 1985. Response on Savanna to Stress and Disturbance: A proposal for a collaborative Programme of Research. Biology International Special Issue 10. IUBS, Paris.

Frost, P.G., Medina, E., Menaut, J.C., Solbrig, O., Swift, M. & Walker, B.H. (Eds.) 1986. *Response of Savanna to Stress and Disturbance*. Biology International Special Issue 10. IUBS, Paris.

Garwood, N.C. 1989. Tropical soil seed banks. pp. 149-209. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.) Ecology of soil seed banks. Academic Press, New York.

Geist, H.J., Lambin, E.F. 2001. What Drives Deforestation? A Meta-analysis and Underlying Causes of Deforestation based on Sub-national Case study Evidence. Louvaine-la- Neuve (Belgium): LUCC International Project Office, LUCC Report Series no. 4.

Geldenhuys, C.J. 1997. Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa. *Forest Ecology and Management* 99: 101-115.

Gerhardt, K. & Hytteborn, H. 1992. Natural dynamics and regeneration methods in tropical dry forests-an introduction. *Journal of Vegetation Science* 4: 95-102.

Gobin, A., Campling, P. & Feyen, J. 2001. Spatial analysis of rural land ownership. *Landscape and Urban Planning* 55:185-194.

Gomez Sal, A., Rey Benayas, J.M., Lopez-Pintor, A. & Rebollo, S. 1999. Role of disturbance in maintaining a savanna-like pattern in Mediterranean *Retama* sphaerocarpa shrub land. *Journal of Vegetation Science* 10: 365-370.

Grainger, A. 1999. Constraints on modelling the deforestation and degradation of open woodlands. *Global Ecology and Biogeography* 8: 179-190.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.

Grime, J.P. 1997. Biodiversity and ecosystem function: The Debate deepens. *Science* 277:1260-1261.

Grundy, I.M. 1995. Regeneration and management of *Brachystegia spiciformis* Benth and *Julbernadia globiflora* (Benth). Troupin in miombo woodlands, Zimbabwe. D. Phil. Thesis. Unpublished. University of Oxford. Oxford.

Grundy, I.M., Campbell, B.M., Balebereho, S., Cunliffe, R., Tafangenyasha, C., Fergusson, R. & Parry, D. 1993. Availability and Use of Trees in Mutanda Resettlement Area, Zimbabwe. *Forest Ecology and Management* 56: 243-266.

Gunderson, L., Holling, C.S. & Peterson, G.D. 2002. Resilience. The earth system: *Biological and Ecological Dimensions of Global Environmental Change* 2: 530-531.

Gunderson, L.H. & Holling, C.S. (Eds.) 2002. Panarchy: Understanding Transformations in Systems of Humans and Nature. Island Press, Washington, DC. pp. 507

Gunderson, L.H. 2000. Ecological Resilience in Theory and Application. *Annual Review of Ecology and Systematics* 31: 425-439

Hobbie, S.E., Jensen, D.B. & Chapin, E.S. III. 1994. Resource supply and disturbance as control over present and future plant diversity. pp.385-408. In: Schulze, E.D. & Mooney, H.A. (Eds.) Biodiversity and ecosystem function. Springer-Verlag, New York, USA.

Hoffmann, W.A. 1998. Post-burn reproduction of woody plants in Neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* 35: 422-433.

Holling, C.S. 1996. Engineering resilience versus ecological resilience. pp. 31-44. In: Schulze, P (Ed.) Engineering within ecological constraints. National Academy Press, Washington DC, USA.

Homewood, K. & Brockington, D. 1999. Biodiversity, conservation and development in Mkomazi Game Reserve, Tanzania. *Global Ecology and Biogeography* 8: 301-313.

Houghton, R.A. 1995. Land use change and the carbon cycle. *Global Change Biology* 1: 275-287.

Hubbell, S.P. 2001. *The unified theory of biodiversity and biogeography*. University Press, Princeton. 390 pp.

Jenson, J.R. 1986. *Introductory Digital Image Processing.* Prentice Hall: New Jersey.

Kaschula, S.A., Twine, W.C. & Scholes, M.C. 2005a. The effect of catena position and stump characteristics on the coppice response of three savanna fuelwood species. *Environmental Conservation* 32: 76-84.

Kaschula, S.A., Twine, W.E. & Scholes, M.C. 2005b. Coppice harvesting of fuelwood species on a South African common: utilizing scientific and indigenous knowledge in community based natural resource management. *Human Ecology* 33: 387-418.

Kates, R.W., Clark, W.C., Norberg-Bohm, V. & Turner, B.L.II. 1990. Human sources of global change: a report on priority research initiatives for 1990-1995. Discussion paper G-90-80. Global Environmental Policy Project, John F. Kennedy School of Government, Harvard University, Cambridge, Massachusetts, USA.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. *Journal of Cleaner Production* 12: 1047-1057.

Kristensen, M. & Lykke, A.M. 2003. Informant-Based Valuation of use and Conservation Preferences of Savanna Trees in Burkina Faso. *Economic Botany* 57(2): 203-217.

Kruger, L.M., Midgley, J.J. & Cowling, R.M.1997. Resprouters versus Reseeders in South African forest trees, a model based on forest canopy height. *Functional Ecology* 11: 101-105.

Langdale-Brown, I., Osmaston, H. A. & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land-use. Entebbe Government Printers, Uganda. pp. 147.

Lawes, M.J., Eeley, H.A.C., Shackleton, C.M. & Geach, B.G.S. (Eds.) 2004. Indigenous forests and woodlands in South Africa: Policy, People and Practice. University of Kwazulu-Natal Press, Scottsville.

Legendre, P., Borcard, D. & Peres-Neto, P.R. 2005. Analysing beta-diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75 (4): 435-450.

Leibold M.A. & McPeek, M.A. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology, 87(6): 1399-1410.

Letsela, T., Witkowski, E.T.F. & Balkwill, K. 2003. Plant Resources Used for Subsistence in Tsehlanyane and Bokong in Lesotho. *Economic Botany* 57(4): 619-639.

Liu, D.S., Iverson, L.R. & Brown, S. 1993. Rates and patterns of deforestation in the Philippines: application of geographic information system analysis. *Forest Ecology and Management* 57: 1-16.

Liu, Q. & Brakenhielm, S. 1996. Variability of plant species diversity in Swedish natural forest and its relation to atmospheric deposition. *Academic Publishers* 125: 63-72.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000. Economic of charcoal production in miombo woodlands of eastern Tanzania. Some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 16:15-30.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land-use. *Forest Ecology and Management* 189: 23-35.

Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell Science Ltd. pp. 1-26.

MEA (Millennium Ecosystem Assessment) 2005a. *Ecosystems and Human Well-Being: Biodiversity Synthesis*: Island Press, World Resources Institute, Washington, DC.

MEA (Millennium Ecosystem Assessment) 2005b. *Ecosystems and Human Well-Being: Desertification Synthesis*: Island Press, World Resources Institute, Washington, DC.

Midgley, J.J. 1996. Why is the world's vegetation not totally dominated by resprouters: an architectural hypothesis. *Ecography* 19: 92-95.

Ministry of Environment and Natural Resources 1994. National Environmental Action Plan. Ministry of Environment and Natural Resources, Lusaka, Zambia. pp. 168

Moyo, S., O'Keefe, P. & Sill. M. 1993. The Southern African Environment: Profiles of the SADC Countries. ETC Foundation/Earthscan Publishers, London. pp. 354

Moyoni, Y. 2001. The role of forests in Uganda's National Economy. Innovation- Special Issue on valuation of Forest Resources in East Africa. pp 10-12.

Murphy, G.P. & Lugo, A.E. 1986. Ecology of Tropical dry forest. *Annual Reviews of Ecology and Systematics* 17: 67-88.

Murphy, P.G., Lugo, A.E., Murphy, A.J. & Nepstand, D.C. 1995. The dry forests of Puerto Rico's south cost. pp.178-209. In: Lugo, A.E. & Lowe, C. (Eds.) Tropical Forests: Management and Ecology. Springer, New York.

Noss, R.F. & Cooperrider, A.Y. 1994. Saving nature's legacy, protecting and restoring biodiversity. Island Press, Washington. pp. 417

Nyström, M. & Folke, C. 2001. Spatial resilience of coral reefs. *Ecosystems* 4: 406-417.

Nyström, M., Folke, C. & Moberg, F. 2000. Coral reef disturbance and resilience in a human dominated environment. *Trends Ecology Evolution* 15: 413-417.

O'Connor, T.G. 2005. Influence of land use on plant community composition and diversity in Highland Sourveld grassland in Southern Drankensberg South Africa. *Journal of Applied Ecology* 42: 975-988.

O'Higgins, R.C. 2007. Savannah Woodland Degradation Assessments in Ghana: integrating ecological indicators with local perceptions. *Earth and Environment* 3: 246-281.

O'Neill, R.V., De Angelis, D.L., Waide, J, B. & Allen, T.F.H. 1986. A Hierarchical Concept of Ecosystems, Princeton University press, Princeton, New Jersey. pp. 254

Osborne, P.L. 2000. Tropical ecosystems and ecological concepts. Cambridge University Press, UK. pp. 238-279.

Paine, R.T., Tegner, M.J. & Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535-545.

Parker, D., Downer, E.R. & Cole, G.E.D. 1967. Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Perlin, J. 1989. A forest journey: the role of wood in the development of civilization. pp. 145-161. Cambridge, London.

Peterson, G.D., Allen, C.R. & Holling, C.S. 1998. Ecological resilience, biodiversity and scale. *Ecosystems* 1: 6-18.

Phillips, O. & Gentry, A. H. 1993. The useful plants of Tambopata. Pem.1: Statistical hypothesis test with a new quantitative technique. *Economic Botany* 47: 15-32.

Pimm, S. L 1984. The complexity and stability of ecosystem. *Nature* 307: 321-326.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Nunez, P., Neill, D.A., Ceron, C.E., Palacios, W.A. & Aulestia, M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82: 2101–2117.

Pivello, V.R. & Norton, G.A. 1996. FIRETOOL: an expert system for the use of prescribed fires in Brazilian savannas. *Journal of Applied Ecology* 33: 348-356.

Purtauf, T., Douber, J. & Wolters, V. 2001. Effects of changes in landscape patterns on carabid diversity and community structure. pp 70-75. In: Mander, U., Printsmann, A. & Palang, H. (Eds.) Development of European landscapes. Publicationes Instituti Geographici Universitis Tartuensis 92, Tartu.

Rennolls, K. & Laumonier, Y. 2000. Species diversity structure analysis at two sites in tropical rain forest of Sumatra. *Journal of Tropical Ecology* 16: 253-270.

Richards, J.F. 1990. Land transformations. pp. 163-178. In: Turner, B.L.II., Clark, W.C., Kates, R.W., Richards, J.F., Matthews, J.T. & Meyer, W.B. (Eds.) The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge University Press, New York, New York, USA.

Riebsame, W.E., Parton, W.J., Galvic, K.A., Burke, K., Bohren, L., Young, R. & Knop, E. 1994. Integrated modelling of land use and cover change. *Bioscience* 44: 350-356.

Ruthenberg, H. 1980. Farming systems in the Tropics. 3rd Edition. Claredon Press, Oxford. 424 pp.

SADC, 1993. Energy Statistics Year Book for 1991. Energy Sector, TAU, Luanda, Angola.

Sagers, C. L. & Lyon, J. 1997. Gradient analysis in a riparian landscape: Contrasts among forest layers. *Forest Ecology and Management* 96: 13-26.

Scholes, R. & Archer, S. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.

Scholes, R.J. & Walker, B.H. 1993. An African Savanna: Synthesis of the Nylsvley Study. Cambridge University Press, Cambridge, UK. pp. 306.

Schulze, E.D., Beck, E. & Müller-Hohenstein. 2002. Plant Ecology. Springer-Verlag Berlin Heidelberg New York. pp 417-423.

Shackleton, C.M. 1993. Fuel wood harvesting and sustainable utilization in a communal grazing land and protected area of the eastern Transvaal Lowveld. *Biological Conservation* 63: 247-254.

Shackleton, C.M. 1997. The prediction of woody productivity in the savanna biome, South Africa. PhD thesis. University of Witwatersrand, Johannesburg, South Africa.

Shackleton, C.M. 2000. Stump size and the number of coppice shoots for selected savanna tree species. *South African Journal of Botany* 66: 124-127.

Shackleton, C.M., Shackleton, S.E., Netshiluvhi, T.R. & Geach, B. 2002. Direct use value of woodland resources in three rural settlements, South Africa. In: Campbell, B.M and Luckert, M.K. (Eds.) Uncovering the hidden harvest. Valuation methods for woodland and forest resources. Earthscan Publications, London, UK.

Skarpe, C. 1992. Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3: 293-300.

Solbrig, O.T., Menault, J.C., Mentis, M., Shugart, H.H., Scott, P. & Wigston, D. (Eds.) 1991. Savanna modelling for global change. *Biology International* 24: 1-47

Solbrig, O.T., van Emden, H.M. & van Oordt, P.G.W.J. (Eds.) 1992. *Biodiversity and global change.* CABI, Wallingford.

Stewart, G.H. & Rose, A.B. 1990. The significance of life history strategies in the development history of mixed beech (Nothofagus) forests, New Zealand. *Vegetatio* 87: 101-114.

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

Tilman, D. & Downing, J.A. 1994. Biodiversity and Stability in Grasslands. *Nature* 367: 363-365.

Tilman, D. 1996. Biodiversity: Population versus Ecosystem Stability. *Ecology* 77: 350-363

Tilman, D., Wedin, D. & Knops, J. 1996. An evolutionary approach to ecosystem functioning. Nature London 379: 718-720.

Tothill, J.C. & Mott, J.J. 1985. Management of the World's savannas. Australia Academic of Science, Canberra, Australia.

Traband, L. & Lepart, J. 1981. Changes in the floristic composition of a *Quercus coccifera* L. *garrigne* in relation to different fire regimes. *Vegetatio* 46: 105-116.

Turner, B.L.II & Meyer, W.B.1994. Global land use and land cover change: an overview. pp 3-10. In: W.B. Meyer and B. L. Turner II, (Eds.). Change in land use and land cover: a global perspective Cambridge University Press, Cambridge UK.

Turner, B.L.II, Clark, W.C., Kates, R.W., Richards, J.F., Matthew, J.T. & Meyer, W.B. (Eds.) 1990. The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge Press, New York, New York, USA.

UBOS (Uganda Bureau of Statistics) 2000. National household census estimates 2000. (http://www.ugandadish.org/nakasongola.doc, retrieved on 17/11/2005).

United States Agency for International Development (USAID) report 2002: On Strategic Assessment of land use options for Uganda.

Van Wyk, B. & Van Wyk, P. 1997. Field guide to trees of Southern Africa. Cape Town: Struik Publishers, Pty Ltd, Cape Town, South Africa. pp. 207

Vanclay, J.K. 1998. Towards more rigorous assessment of biodiversity. pp. 211-232. In: Bachmann, P., Koehl, M. & Paivienen, R. (Eds.) Assessment of biodiversity for improved forest planning. Kluwer Academic Publishers, Dordecht. Forest Science Series 51.

Vavrek, M.C., Fetcher, N., McGraw, J.B., Shaver, G.R., Chapin, F.S. & Bovard, B. 1999. Recovery of productivity and species diversity in Tussock tundra following disturbance. Arctic. Antarctic Alpine. Research 31:254-258.

Vermeulen, S.J. 1996. Cutting of trees by local residents in a communal area of an adjacent state forest in Zimbabwe. *Forest Ecology and Management* 81: 101-111.

Vesk, P.A. & Westoby, M. 2004. Global patterns of sprouting ability: Can all plant species be divided into sprouters and non-sprouters? *Journal of Ecology* 92: 310-320.

Vitousek, P.M. 1994. Beyond global warming: ecology and global change. *Ecology* 75(7): 1861-1876.

Wagner, H.H., Wildi, O. & Ewald, K.C. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* 15: 219-227.

Waldhardt, R. & Otte, A. 2003. Indicators of plant species and community diversity in grasslands. *Agricultural Ecosystems and Environment* 98: 339-351.

Walker, B. & Stefan, W. 1996. Global change and terrestrial ecosystems. Cambridge University Press. Cambridge.

Walker, B., Carpenter, S., Anderies, J., Abel, N., Cumming, G., Janssen, M., Lebel, D., Norberg, J., Peterson, G.D. & Pritchard, R. 2002. Resilience management in social-ecological systems: a working hypothesis for participatory approach. *Conservation Ecology* 6(1): 14 [online] URL: http://www.consecol.org/vol6/iss1/art14.

Walker, B.H. & Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. pp. 83-93. In: Huntley, B.J. & Walker, B.H. (Eds.) Ecology of Tropical Savannas. Springer, Canberra.

Walker, L. R., Zarin, D.J., Fetcher, N., Myster, R.W. & Johnson, A.H. 1996. Ecosystem development and plant succession on land slides in the Caribbean. *Biotropica* 28: 566-576.

Welden, C., Hewerr, W., Hubbell, S.W.S.P. & Foster, R.B. 1991. Sapling survival, growth and recruitment: relationship to canopy height in a Neotropical forest. *Ecology* 72: 5-50.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFET/UNSO vegetation map of Africa. UNESCO Paris.

White, P.S. & Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction.-In: Pickett, S.T.A & White, P.S (Eds.), The ecology of natural disturbance and patch dynamics. pp. 3-13. Academic Press, Orlando, Florida.

Whitmore, T.C. 1989. Tropical forest nutrients, where do we stand? A tour de horizon. pp.1-13. In: Proctor, J. (Ed.) Mineral nutrients in tropical forest and savanna ecosystems. Blackwell, Oxford.

Whitmore, T.C. 1991. Tropical rain forest dynamics and its implications for management. pp. 67-90. In: Gmer-Pompa, A., Whitmore, T.C. & Hadley, M. (Eds.). *Rain Forest Regeneration and Management*, UNESCO, Paris.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon*, 21: 213-251.

William-Linera, G. 2002. Tree species richness complementarity, disturbance and fragmentation in Mexican tropical montane cloud forest. *Biodiversity and Conservation* 11:1825-1843.

Witkowski, E.T.F. & Garner, R.D. 2008. Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive *Solanum mauritianum* in a temperate to subtropical riparian ecosystem. South African Journal of Botany 74: 476-484.

World Bank 1999. World development report. Knowledge for Development, 1998/99, Oxford University Press, New York.

Worm, B., Lotze, H., Hillebrand, H. & Sommer, U. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417: 848-851.

Yarie, J.K., Viereck, K., Van Cleve & Adams, P. 1998. Flooding and ecosystem dynamics along the Tanana River. *BioScience* 48: 690-695.

Yirdaw, E. & Luukkanen, O. 2003. Indigenous woody species diversity in *Eucalyptus globulus* Labill. subsp. *globulus* plantations in the Ethiopian highlands. *Biodiversity and Conservation* 12: 567-582.

CHAPTER 2

Household livelihoods and income from charcoal production in a multiple land use equatorial African savanna woodland, central Uganda

Abstract

This study identifies livelihood strategies and activities adopted by households, as well as the contribution of charcoal production to household income in the savanna woodlands of Nakasongola District, central Uganda. To secure their livelihoods, rural households in this savanna adopt multiple livelihood activities that include charcoal production and generation of money through charcoal and firewood sale, the utilization of woodland areas for subsistence crop cultivation and livestock grazing as well as woody species for medicine and fruits/food. Village respondents listed 24 woody species (including the fruit trees *Mangifera indica* and *Artocarpus heterophyllus*) that are harvested. The composition of species harvested for charcoal production varied significantly among the sub-counties ($Global_{ANOSIM}$ = 0.44, p = 0.001); and harvesting is almost entirely influenced by availability and accessibility of plant species, and not the quality of the charcoal produced. The most common uses of woody plants by households were for charcoal (100%) and firewood extraction (100%), with charcoal production being the major source of income to the rural households, contributing on average US$ US$ 259 ± 46 (S.E.) per household annually. Nakasongola District is estimated to have produced about 149,932 tonnes of charcoal per year in 2006 from 1,499,315 tonnes of wood, with each household harvesting on average 58.7 ± 8.3 (S.E.) tonnes of wood annually. There were significant differences in charcoal production (Kruskal-Wallis: H = 31.42, p < 0.0001), producer sale prices per bag of charcoal (H = 35.62, p < 0.0001), and annual incomes from charcoal production (H = 32.44, p < 0.0001) per households across sub-counties. The best predictors of the amount of charcoal produced per household were cost of production (excluding the cost of logs), gross income, number of households and age of respondents combined (with delta Akaike of 0.0). Although woodland resources contribute highly to rural household incomes and livelihoods, the increasing commercialisation of charcoal production is resulting in non-selective harvesting of multiple land use species, hence, affecting savanna woodland sustainability. This threatens the sustainable livelihoods of rural households who are almost entirely dependent on woodland resources. Therefore, maintenance of savanna woodland resources and other ecosystem services essential for human well-being will require an effective legal framework to prevent over-exploitation and provide incentives for the protection of the fragile savanna woodland vegetation.

Key words: Ecosystem services, human well-being, Millennium Development Goals, sustainable livelihoods, woodland resources

1.0. Introduction

Savanna woodlands are vitally important in providing both ecological (e.g. erosion protection, micro-climate, wildlife habitats, etc.) and economic services (e.g. timber, food, fodder, non-wood products, etc.) that sustain local livelihoods and national economies (Chidumayo, 1988; Scholes & Archer, 1997). For example, in the southern African region, miombo (savanna) woodlands are economically important for the supply of timber, poles, firewood, charcoal, medicines, food, fibre and carvings (Chidumayo, 1988; SADC, 1993; Luoga *et al.,* 2000a). They are the major source of energy (fuelwood) for a high percentage of Sub-Saharan African households (Hofstand, 1996; Luoga *et al.,* 2002; Kituyi, 2004), and serve as sources of food and medicine for many natural resource dependent households. Wild plants from woodlands and other vegetation types are very important to livelihoods in the subsistence sector, both by meeting a wide range of household needs and through the sale of wood for fuel, thereby, generating incomes (Braedt & Standa-Gunda, 2000; Dovie *et al.,* 2003; Letsela *et al.,* 2003; Botha *et al.,* 2004). Various studies (e.g. Luoga *et al.,* 2000a & b; Dovie *et al.,* 2004; Campbell *et al.,* 2002; Shackleton *et al.,* 2002a) indicated that the majority of rural households make use of non-timber forest products (NTFPs) from their immediate environment, and their harvesting and utilization is a livelihood activity in marginalized communities. Indeed, NTFPs, particularly from savanna woodlands have been identified as important to rural livelihoods as alternative land use options as well as in fulfilling an important safety-net function (Paumgarten, 2005). In addition, savanna woodlands provide spiritual and aesthetic values, ecological services such as carbon sequestration and water regulation (Shackleton *et al.,* 2007), and, thus, make a significant contribution to local and national production and economic growth (Shackleton, 1996).

Similar to all developing countries, Uganda's energy sector is characterized by low energy consumption, high dependency on fuelwood (charcoal and firewood) and little use of 'modern' fuels. In 2001, wood fuel supplies accounted for (US$ 6,060,606), ten times the value of both electricity and petroleum (US$ 606,060), each utilized by Uganda's industrial sector (1US$ = UGX 1,650; MEMD, 2001). With rapid population growth (3.4% year^{-1}, USAID, 2005; http://www.usaid.gov/policy/budget/cbj2006/afr/ug.html, accessed on 12/9/2006), expanded commercial charcoal production as well as urban and industrial fuelwood demands are fundamentally altering the woodland resource base (Naughton-Treves *et al.,* 2007). However, similar to other East African woodlands, Uganda's savanna woodlands' contribution to sustainable rural livelihoods and the economy is grossly under-estimated by planners, policy-makers, and resource managers. Rapid deforestation in Uganda (~ 600 km^2 year^{-1}) threatens their sustainable management and conservation (Banana & Gombya-Ssembajjwe, 1996), resulting in unsustainable rural livelihoods. A sustainable livelihood is one that can recover from shocks and maintains and improves its assets without unsustainably impacting the available natural resources base (Paumgarten, 2005). In dry savanna areas, where rural community livelihoods are often vulnerable to adversity, people adopt a range of livelihood strategies (Shackleton *et al.,* 2001). A livelihood strategy is defined as the range and combination of activities and choices that people make and undertake in order to achieve their livelihood goals. A livelihood strategy comprises "capabilities, assets and activities required for a means of living" (DFID, 1999). According to the "Induced Innovation Theory" the types of livelihood strategies and specific options considered, are a response to historical changes in socio-economic conditions (particularly increased population density and market development) which lead to changes in relative input and output prices (Binswanger & Ruttan 1978; Ruthenberg, 1980). While the livelihood approach states that the type of activity undertaken and the amount of income earned by a household is a function of the assets at its disposal (Barrett et al., 2005, Brown et al., 2006). However, households may respond in certain ways when faced with resource scarcity. Hence, assessing livelihood strategies and attaching use values (both direct and indirect) to woodland resources can aid decision making to assess planning and development alternatives, to allocate scarce human and financial resources, reconcile conflicting demands, and determine compensation levels for loss of resources (Shackleton *et al.,* 2002a & b; Luoga *et al.,* 2002; Campbell & Luckert, 2002; Shackleton & Shackleton, 2006).

Although there have been studies on the monetary values of woodland resources as well as their contribution to total livelihoods in southern Africa (e.g. Dovie *et al.,* 2002; Shackleton et al., 2002a & b; Campbell & Luckert, 2002), miombo (savanna) woodland in Tanzania (Luoga *et al.,* 2000b) and rainforests in Uganda (Naughton-Treves *et al.,* 2007), little is known about the equatorial savanna woodlands of Uganda. Studies in East Africa (e.g. Kakudidi, 2004; Liwenga, 2003, 2009) have focused on the contribution of woodland resources to social and cultural aspects of rural households. Moreover, with increasing demand for services from natural resources, decision makers are faced with a variety of impending problems that require informed ecosystem management decisions (Bennett *et al.,* 2005). Case studies that assess the livelihood strategies adopted by rural people in savanna woodlands are necessary to make developmental decisions. Inhabitants of East African woodlands are gradually taking up various income generating activities that involve the use of locally available resources (Liwenga, 2009). More information about the ecological, economic, social and cultural values of natural areas and the synergy between these values are necessary to 'feed the public dialogue' and to internalize these values into policy and decision making (Cavendish, 2002). The role of people as components of integrated social-ecological systems (SES) warrants additional attention, because impacts of human actions on ecological communities are increasing in magnitude and extent (Foley *et al.,* 2005).

This study aimed to identify household livelihood strategies and assess the economic contribution of charcoal production to rural livelihoods in an equatorial savanna woodland of central Uganda. Specifically, the questions asked included: (i) what are the main livelihood strategies adopted by the rural households in this area? (ii) what are the most frequently used woody plant species by the households to meet their livelihood needs? (iii) How much money/income do households earn from charcoal production as a livelihood strategy? (iv) Do households differ in their utilization of woody plants and incomes gained from charcoal production? (v) How does household composition relate to their use of the woodlands? (vi) What are the contributions of subsistence cultivation and livestock grazing to the livelihood of the rural households?

2.0. Material and Methods

2.1. Study area

The study focused on households and the surrounding multiple land use savanna woodlands of Nakasongola District, south of Lake Kyoga, central Uganda ($0^0$40′- $1^0$41 N, $31^0$57’ - $32^0$48’ E). The District covers about 3,424 km^2, most of which is woodland and grassy savanna, with 322 km^2 (10%) of open water and wetlands. It comprises eight sub-counties (administrative sub-divisions), namely Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata (see Chapter 1). Each sub-county has a mean (± S.E.) of 49 (± 22) villages and 3,193 ± 390 households. The mean number of households/village was 82 (± 32), with an average of seven persons/household. The district has a total human population of 128,126 (41 people/km^2) (2000 National Housing Census), with 50.2% males and 49.8% females. About 95.3% of the population are rural and 4.7% urban (Uganda Bureau of Statistics, 2002).

Mean annual rainfall ranges from 500 – 1000 mm and is concentrated into two wet seasons (March to May and August to November), but rainfall amount and reliability is higher in the south and declines gradually to the north. The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C, respectively. The topography of the area undulates between 1,036 m and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al.,* 1967).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964). This is a natural savanna woodland or woodland of mixed deciduous trees (3 to 12 m high) and grasses (0.3 to 1.3 m high) at maturity. However, the cover of the grass layer varies with season, which is often patchy and is subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirki*i subsp. *mildbraedii, A. senegal,* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983).

2.2. Methods

2.2.1. Data collection

Data on household livelihood strategies, woodland resources use, incomes from charcoal production and woody species harvested for charcoal production were collected using semi-structured interviews (hereafter SSI), to profile household livelihoods in the area. The SSI involves the preparation of an interview guide that lists a predetermined set of questions or issues that are to be explored during the interview (Chambers, 1994; Pretty & Vodouhê, 1996). The semi-structured nature enables "key topics to be gathered from all respondents, while allowing the respondents the flexibility to define those topics within their own contextual understanding" (O'Higgins, 2007). The interview guide served as a checklist to ensure that the same questions were asked to a number of people. The advantage of the interview guide approach is that it makes a person interviewing more systematic and comprehensive by delimiting the issues to be taken up in the interview (Chambers, 1994; Inglis, 1992).

2.2.1.1. Household

The three major land uses (i.e. charcoal production, grazing, and cultivation) were determined by field observations, discussions with key informants such as local village leaders and sub-county chiefs (advisors) and existing literature (Byabashaija *et al.,* 2004; Namaalwa *et al.,* 2005); and formed the basis for selection of households to be interviewed. However, people in Nakasongola also keep goats and sheep in small numbers, this study focused on cattle. Within each sub-county 5 to 6 representative households were selected with the help of an adviser from the sub-county aware of the major livelihood activities of a given household. In total, 45 respondents were interviewed from the 8 sub-counties. The 45 households chosen were sufficient and representative of the studied population, because the population of Nakasongola has the same ethnic groups with similar characteristics, within all the sub-counties of the district. In addition, the households within the study area have similar major livelihood strategies (i.e. charcoal production, cattle grazing, subsistence cultivation or a combination), except for minority fishing community on Lake Kyoga. Household interviews were conducted on an individual basis to minimise peer influence and improve the quality of data (Phillips & Gentry, 1993). The interview questions covered broad social and economic perspectives of household livelihood strategies and use of woodland resources. Related information was gathered on: (a) the various woodland resources utilized, (b) plant species commonly harvested/highly utilized for charcoal production, (c) woodland resource availability, accessibility and utilization over the past 10 years, and (d) incomes from charcoal production and costs of production (tools, transport, taxes, etc.). The interviews were uniformly conducted so as to give all the respondents equal exposure to the questions posed (Bernard, 1996). Household level data was also collected on charcoal producer sale price per bag, annual charcoal production, unit cost of charcoal production, and local charcoal and firewood use.

2.2.1.2. Key informants

Key informants, including village leaders (aware of business but not in business) and the government forest employees, namely the District Natural Resource Officer, District Environmental Officer, and District Livestock Officer were interviewed. Information acquired included trends in woodland resource availability and management strategies over the past 10 years; as well as revenues associated with charcoal production. The key informant interviews were intended to provide independent assessments to compare with the households interviews and to provide additional and often synthetic information (e.g. issues that households were not comfortable to reveal, especially about charcoal production) (Luoga *et al.,* 2000a; Shackleton *et al.,* 2002a & b; Dovie *et al.,* 2003). Both the household and key informant interviews were conducted from July to August in 2006.

2.2.2. Data analysis

Composition of species harvested for charcoal production were compared between sub-counties using the ANOSIM (ANalysis Of SIMilarity) permutation test (Seaby *et al.,* 2006), based on a species x respondent data matrix.

The quantities of charcoal and incomes from charcoal production were calculated on a per household per annum basis and, then, extrapolated to sub-county scale. The quantities of charcoal produced by each household per annum were determined by the number of bags of charcoal produced per household multiplied by the number /frequency of production.

The gross and net income from charcoal production was estimated by discounting the direct costs (e.g. costs of tools, logs, and taxes levied), and the opportunity costs (i.e. labour). This was first done for each household, then extrapolated to sub-county level, using the human population data from the National Housing Census of 2002 (Uganda Bureau of Statistics, 2002). In the study area, the opportunity costs are negligible, because the respondents revealed that charcoal production was carried out by household labour, and deduction of opportunity costs of labour in such environments of low earning skills and negligible labour opportunities is perhaps misleading (Gram, 2001; Shackleton & Shackleton, 2006). Household gross income from charcoal production was calculated by multiplying number of bags of charcoal produced by the household with unit price for a bag of charcoal in that particular sub-county. Net-income was determined by discounting both direct and opportunity costs of charcoal production (gross income minus costs of production). Both gross and net income were then extrapolated to sub-county scale, and contrasted. The incomes were computed in Uganda shillings (UGX) and then converted to United States Dollar (US$) at a mean exchange rate of US$ 1= 1,600 UGX at the time of the study in 2006.

Differences in the amount of charcoal produced, charcoal producer sale prices, and income from charcoal production were compared among the eight sub-counties using the Kruskal-Wallis test.

Regression analyses was used to assess the relationship between; (a) charcoal produced per household and population density per sub-county, (b) price of charcoal per bag per sub-county and total number of households per sub-county, (c) total number of households per sub-county and total number of bags of charcoal produced per sub-county, (d) population per sub-county and total number of bags of charcoal produced per sub-county and (e) producer price and available woody plants per plot from the vegetation data (Chapter 4). To identify the predictors that influence charcoal produced per household in Nakasongola, a model was selected based on the Akaike Information Criterion (AIC_c), using the Macroecology package (SAM version 3.1). Given the sample size of this study (n = 45), the second-order Akaike Information Criterion (i.e. n/K < ~ 40) was used to select a model that has the best fit (Burnham & Anderson, 2002). Sixteen models were compared and the model with the lowest AIC_c was considered the "best" model. Delta Akaike (Δ_i) (model comparison) was done by calculating the difference between AICs model *i* and the minimum AIC_c value of the "best" model. As a rule of thumb, a $\Delta_i < 2$ suggests substantial evidence in support of the model; values between 3 and 7 indicate that the model has considerably less support, while a $\Delta_i > 10$ indicates that the model is very unlikely (Burnham & Anderson, 2002). To quantify the plausibility of each model, the Akaike weight (w_i) of each model was calculated to indicate the probability that the model selected is the best and to measure the strength of evidence between the models. In addition, an Akaike weight of the "best" model was compared with the "competing model" (the next "best model") to calculate the evidence ratio to determine to what extent it is better than the other.

The crops cultivated, the fallow period and field sizes of crops (mean ± S.E.) in the sub-counties were also determined. Information on livestock number per sub-county and areas of established ranches was obtained from the District Livestock Officer.

3.0. Results

3.1. Livelihood strategies

The three basic major livelihood activities for the rural households in this savanna dryland based on area coverage and time and effort spent by the households are charcoal production, subsistence crop cultivation and livestock grazing. Overall the predominant livelihood strategy in Nakasongola is a combination of charcoal production, subsistence crop cultivation for both food and cash, and livestock grazing for income generation through selling livestock products such as milk and sometimes the whole animal. The relative emphasis among the three major livelihood activities differs across sub-counties depending on the relative availability of resources. In addition, sometimes, there is replacement of one activity by another and it differs across sub-counties. For instance, in Lwampanga and Lwabiata sub-counties, situated close to Lake Kyoga, fishing is also a major livelihood activity. Fishing may alternate with charcoal production or both activities may be carried out simultaneously. In Wabinyonyi sub-county, people, sometimes, engage in brick making and bee keeping as additional livelihood activities during the dry season. All the respondents were commercial charcoal producers, and they also rely on firewood for cooking (Figure 1). Most of the youth (≤ 20 years old) derive their livelihoods from charcoal production, a small amount of trade, offering labour services, livestock grazing, fishing, bee keeping and earth brick making. Charcoal production, livestock grazing and hunting are carried out particularly by men, whereas, crop cultivation, fire wood collection and collection of medicinal plants and fruits are carried out mainly by women, however, men are also engaged in cultivation but only during rainy season. The major land resources utilized by the households are derived from the savanna woodlands.

3.1.1. Woodland resource utilization by households

The households listed thirteen uses of the woodland resources to meet their daily livelihood needs (Figure 1). The most common uses (particularly for woody plants) were charcoal production, firewood extraction, and harvesting of poles for house construction. The woodlands provided land for subsistence crop cultivation. The majority of households (56%) derive all these resources from natural woodlands, 16% derive all resources from forest plantations, while 31% did not respond. None of the respondents owned a forest plantation or woodlot. According to the respondents and key informants, *mailo* (the registered owner holds the land in perpetuity but is subject to customary and statutory rights of lawful and *bonafide* occupants) and customary land ownership (the system that recognizes both individual, family and community ownership of land) are the two major land tenure systems in the study area. Of the 45 households interviewed, 25 (56%) were under *mailo*, 14 (31%) under customary, 4 (9%) under freehold, and 2 (4%) under leasehold land ownership.

The majority (69%) of respondents concurred that tree biomass within the area they derive their livelihoods had decreased considerably over the past 15 years, threatening the continued availability of the resources. In contrast, 27% thought there was an increase in trees, 2% indicated no change, and 2% did not know. Consequently, the distance travelled to get firewood has increased, with some households having to travel as far as 15 km from their homesteads (Figure 2), because of increasing loss of woodlands and scarcity of firewood around settlements. All respondents concurred that this is attributed to the large number of households in the village, the increasing extent of land used for subsistence crop cultivation, and over-harvesting of woody plants for commercial charcoal production and firewood harvesting. Resource utilization was not only for local residents, 35 (78%) respondents revealed that commercial harvesters from neighbouring (e.g. Luwero, Masindi, etc.) and also distant districts (e.g. Kampala, Lira, Arua, etc.), also utilize the woody plants for charcoal production.

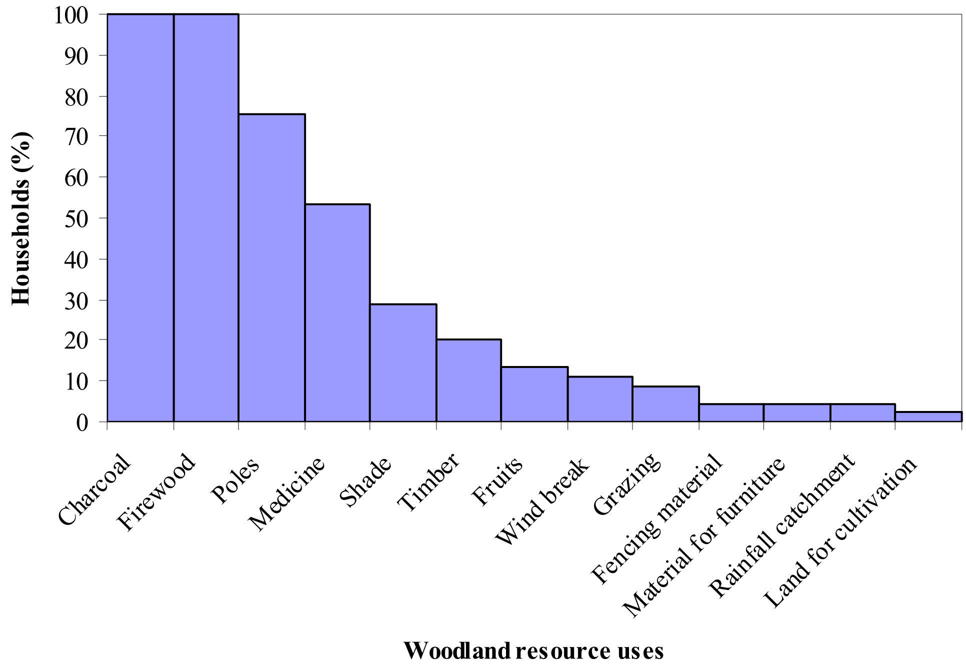

Figure 1. Reported uses of savanna woodland resources (with emphases on wood resources) by households in a multiple land use equatorial African savanna woodland, central Uganda (n = 45 respondents).

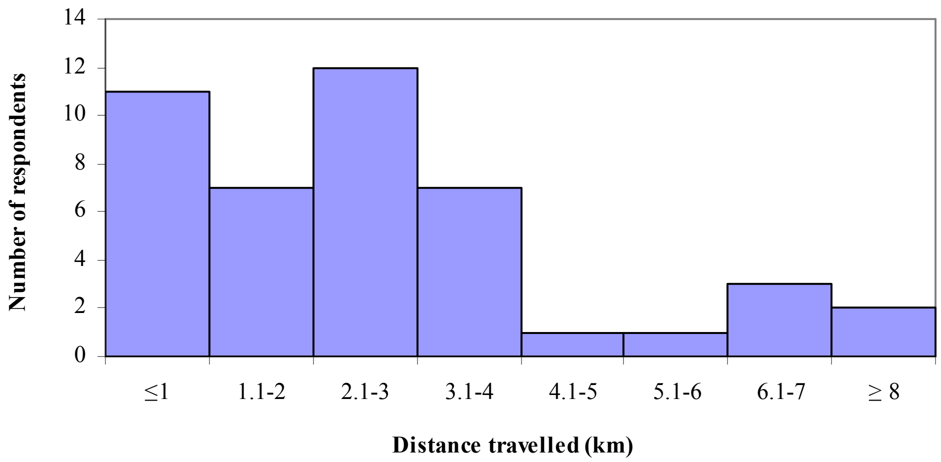

Figure 2**.** Distance travelled by respondents to obtain firewood in a multiple land use equatorial African savanna woodland, central Uganda (n = 45).

3.2. Subsistence crop cultivation

Subsistence crop cultivation is the major food source for local households and sometimes also a source of income. Based on the households interviewed, overall farm sizes ranged from 0.4 to 6.0 ha, with mean ± S.E. of 1 ± 0.2 ha per household. When sub-counties were considered separately, the mean ± S.E. ranged from 0.7 ± 0.2 to 1.7 ± 0.9 ha per household per sub-county (Table 1). Of the 45 households interviewed, 36 (80%) grew both food and cash crops, while 9 (20%) grew only food crops. The major crops include cassava (*Manihot esculenta*), sweet potatoes (*Ipomoea batatas*), beans (*Phaseolus vulgaris*), ground nuts (*Arachis hypogaea*) and maize (*Zea mays*) as both food and cash crops. Crop cultivation is mainly practiced by women. Men only engage in crop cultivation during the rainy season when charcoal production is low because the land is wet and it is difficult to make an earth kiln in wet weather. The land area that has been cultivated in Nakasongola in 2006 was estimated at 28,260 ha (9%) of total land (310,200 ha) and only 8% of overall total area (342,400 ha). In addition, areas (ha) and percentage of area under cultivation in different sub-counties are also presented in (Table 1). The majority of respondents (39 = 87%) concurred that the land available for cultivation per household has decreased over the years as a result of the ever increasing human and animal populations in the district. Three respondents reported that it has remained the same, one that it increased, and one had no idea.

3.3. Livestock grazing

Cattle grazing is the predominant livestock enterprise in Uganda; and pastoralists keep large herds of cattle on rangelands. Nakasongola District is one of the cattle corridor districts in Uganda. Cattle grazing in Nakasongola is important for milk production, meat, hides and skin, social functions, prestige and other cultural functions. According to the District Veterinary Officer (Dr. Bugeza James, pers. comm. 2006), Nakasongola had a cattle population of 163,851 animals, with Nabiswera sub-county having the highest number (43,494) among the eight sub-counties and Lwabiata had the highest stocking rate 122 animals per km^2 (Table 2). There were, however, additional animals from other areas that are temporarily brought into the district for seasonal grazing. Thirty four (about 76%) of the respondents reported an increasing number of people from neighbouring districts, who seasonally move into the area to graze livestock. In Nakasongola, a seasonal movement to lowland or lake shore areas occurs during the dry seasons of December to February and June to July in search of water and grazing, and they move back to where they came from at the start of the rainy seasons in March and August, respectively. The District Veterinary Officer revealed that between 1985 and 2004, six new ranches covering an area of about 23,624 ha were established.

Table 1. Crops cultivated, crop field sizes (area in ha) and fallow periods in eight sub-counties in a multiple land use equatorial African savanna woodland, central Uganda.

Sub-county	Mean ± S.E. field size (ha)	Cultivated area (ha)	Cultivated area (%)	Fallow period (years)	Crops cultivated	
					Food	Cash
Kakooge	1.5 ± 0.5	6,362	13	1 - 2*	Irish potatoes, cassava, sweet potatoes ,beans, maize, ground nuts	Cassava, maize, cotton, sweet potatoes, beans ground nuts, Irish potatoes
Kalongo	0.7 ± 0.2	1,747	5	1*	Cassava, sweet potatoes, ground nuts, millet, bananas	Cassava, sweet potatoes, ground nuts, cotton, coffee, maize, bananas
Wabinyonyi	1.0 ± 0.3	3,993	10	2 *	Sesame, beans, ground nuts, cassava, Irish potatoes, maize, ground nuts	Cassava, Irish potatoes, maize, beans, yams, sweet potatoes, ground nuts
Kalungi	0.7 ± 0.3	2,278	5	1 - 3	Cassava, ground nuts, sweet potatoes, maize, millet, beans, Irish potatoes, mangoes	Cassava, maize, millet, Irish potatoes, rice, beans
Nabiswera	0.8 ± 0.3	2,280	4	0.5 - 2*	Cassava, Irish potatoes, millet, maize, sorghum, beans, sweet potatoes, ground nuts	Cotton, cassava, Irish potatoes, ground nuts, maize
Nakitoma	0.7 ± 0.2	1,219	3	1 *	Cassava, bananas, sweet potatoes, ground nuts, Irish potatoes, maize	Cotton, coffee, maize, ground nuts, cassava, Irish potatoes, maize
Lwampanga	1.7 ± 0.9	8,291	29	0*	Maize, cassava, beans, millet, ground nuts, bananas, sweet potatoes	Maize, cassava, beans, ground nuts, sweet potatoes, bananas, Irish potatoes, millet
Lwabiata	1.0 ± 0.2	2,090	13	0.5 - 1 *	Sweet potatoes, maize, cassava, ground nuts, millet, sorghum, peas, Irish potatoes	Maize, cassava, cotton
Overall Nakasongola	8.1 ± 2.9	28,260	9	0.5 - 3 *	Sweet potatoes, maize, cassava, ground nuts, millet, sorghum, peas, Irish potatoes, bananas, sesame, mangoes	Maize, cassava, cotton, sweet potatoes, beans, ground nuts, Irish potatoes, coffee, bananas, yams, rice, millet

* Crop rotation system; 0 = No fallow.

Table 2. Cattle population and stocking rates in eight sub-counties in a multiple land use equatorial African savanna woodland, central Uganda.

Sub-county	**Cattle population (No. of animals)**	**Land area (km^2)**	**Stocking rate (No. of animals/ km^2)**
Kakooge	24,557	475	52
Kalongo	14,282	352	41
Wabinyonyi	24,514	375	65
Kalungi	7,247	496	15
Nabiswera	43,494	589	74
Nakitoma	30,432	370	82
Lwampanga	9,112	288	32
Lwabiata	19,213	157	122

3.4. Charcoal production

Charcoal production is mainly done by males aged 20 to 40 years, most (91%) of whom have not attained formal education beyond the primary school level. The majority (60%) of the respondents reported to have been engaged in charcoal production in the area for 10 to 27 years, and the rest (40%) for less than 10 years.

3.4.1. Charcoal production process

As elsewhere in East Africa, charcoal is produced by burning logs in oxygen-restricted pyrolytic conditions inside earth mound kilns known as 'heaps'. The earth mound kiln is built by covering a stacked pile of logs on the ground with earth. In this study, the largest earth mound kiln was observed in the Kyalubanga Forest Reserve in Nakayonza Parish (estimated at 15.4 m^3, Figure 3). However, typical earth mound kiln dimensions differ depending on the amount of wood available at the kiln site. Earth kiln volume ranged from 5 - 15.4 m^3, with mean ± S.E. of 7.7 ± 0.5 m^3 (n = 24). Charcoal production is very labour intensive and requires a high degree of manual labour and, hence, is mainly carried out by men, although labour sharing between men and women is common especially in obtaining the wood raw material (felling, crosscutting, stacking of logs, also cutting grass and cutting soil blocks) in preparing the earth kiln. A single earth mound kiln can utilize the man power of 1-6 people, and to prepare an earth kiln takes about 1-2 weeks depending on the number of people and its size. Several tools are used in charcoal production (axe, machete, hoe, shovel, fork and sickle). After felling trees, the logs are crosscut into 3 m long billets, piled into stacks with the big logs at the base and twigs at the top (Figure 3), and, then, thatched with grass before plastering with earth, leaving a small window through which the fire is set. Once the fire has been established, the window is plugged with an earth block to ensure controlled partial combustion (carbonization) of the logs into charcoal; the process takes approximately 1 week. Then, the kiln is unloaded, charcoal spread and then sorted to remove partially burnt pieces, which takes an average of 4 days. Finally, charcoal is, then, packed into large bags (each holding ± 61 kg) ready to be transported to collecting points.

Figure 3. Harvested wood stacked in preparation for charcoal production, using a traditional earth mound kiln, in a multiple land use equatorial African savanna woodland, central Uganda.

3.4.2. Species most frequently harvested for charcoal production

The major uses of woodland woody plants are charcoal production and firewood provision for both domestic and commercial purposes. Of the 99 woody species recorded in the study area, 24 (24%) were listed by respondents as being utilized for charcoal production. Of these, three (*Mangifera indica*, *Artocarpus heterophyllus,* and *Senna siamea*) are non-traditional charcoal production use trees (Table 3). The 24 species are mostly targeted either because they are readily available and easy to access (81% respondents) and/or are known traditional charcoal production species (79% respondents). Harvesting of non-traditional charcoal species and at times even fruit trees (e.g. *Mangifera indica* and *Artocarpus heterophyllus*) has became more prevalent because the common traditional charcoal species are scarce or have been depleted in some of the areas (60% of respondents). However, in this study, 71 species were found to be harvested during field surveys and their stumps identified and recorded (Chapter 6). Of these, 22 were the species listed by respondents as frequently utilized for charcoal production. However, *Artocarpus heterophyllus* and *Mangifera indica* stumps were not recorded. The species listed by respondents was not selected from the list of 71 harvested species recorded in vegetation plots, because vegetation sampling and interviews were carried out concurrently. The number of species listed by respondents ranged from 2 - 8 species per respondent, with a mean (± S.E.) of 5.2 ± 0.2.

The harvested species listed by respondents for charcoal production varied significantly among the sub-counties ($Global_{ANOSIM} = 0.44$, $p < 0.001$), with over 75% of the sub-county pair-wise comparisons being significantly different at $p < 0.05$. This is corroborated by low within sub-county similarities, which ranged between 42.2 and 60.8% (62.5% having similarities < 50%). There were significant differences in the species harvested by charcoal producers even within the same sub-county due to depletion of traditional charcoal species. This further corroborates the respondents answer to "*what determines the choice of the species they harvest for charcoal*?"; it is almost entirely influenced by availability and accessibility; and not necessarily the quality of the charcoal they produce.

The top 16 of the 24 species were considered "highly utilized" (≥ 11% of correspondents using them) for charcoal production (Table 3). The most frequently used were *Combretum molle, Combretum collinum, Vepris nobilis*, *Grewia mollis* and *Terminalia glaucescens* (Table 3). In addition to charcoal production, these woody species were reported to serve over ten other uses, including firewood, poles, medicine, shade, wind breaks, fencing, timber, food/fruits, mortar and pestle making and boat making (Figure 4). All respondents harvested firewood (Figure 4), with 75% using it for domestic purposes only, while 25% used it for both domestic and commercial purposes. Most households (80%) only harvest dead tree/shrub branches for firewood, although some (20%) harvest the whole plant (dead and live plants).

Table 3. The 24 woody species used for charcoal production in a multiple land use equatorial African savanna, central Uganda. Included are the plant family and the percentage of respondents who used a particular species. The top 16 species are referred to as the "highly utilized species".

Species	**Family**	**Respondents (%) (N = 45)**
Combretum molle Engl. & Diels	Combretaceae	67
Combretum collinum Fresen.	Combretaceae	62
Vepris nobilis (Delile) Mziray	Rutaceae	56
Terminalia glaucescens Planch. ex Benth.	Combretaceae	47
Grewia mollis Juss.	Tiliaceae	38
Albizia zygia J. F. Macbr.	Mimosaceae	29
Acacia hockii De Wild.	Mimosaceae	24
Gymnosporia senegalensis Loes.	Celastraceae	20
Albizia coriaria Welw.	Mimosaceae	18
Combretum ghasalense Engl. & Diels	Combretaceae	18
Piliostigma thonningii (Schumach.) Milne-Redh.	Caesalpiniaceae	18
Acacia polyacantha Willd.	Mimosaceae	11
Hymenocardia acida Tul.	Euphorbiaceae	11
Combretum capituliflorum Fenzl ex Schweinf.	Combretaceae	11
Acacia seyal Delile	Mimosaceae	11
Acacia sieberiana DC.	Mimosaceae	11
Zanthoxylum chalybeum Engl.	Rutaceae	7
Ficus natalensis Hochst.	Moraceae	7
Senna siamea (Lamarck) H. S. Irwin & Barneby†	Caesalpiniaceae	7
Trema guineensis (Schum. & Thonn.) Ficalho	Tiliaceae	7
Dichrostachys glomerata Chiov.	Mimosaceae	7
Artocarpus heterophyllus Lam.*	Moraceae	2
Lannea barteri Engl.	Anacardiaceae	2
Mangifera indica L.*	Anacardiaceae	2

*Fruit trees; †Introduced/invasive species

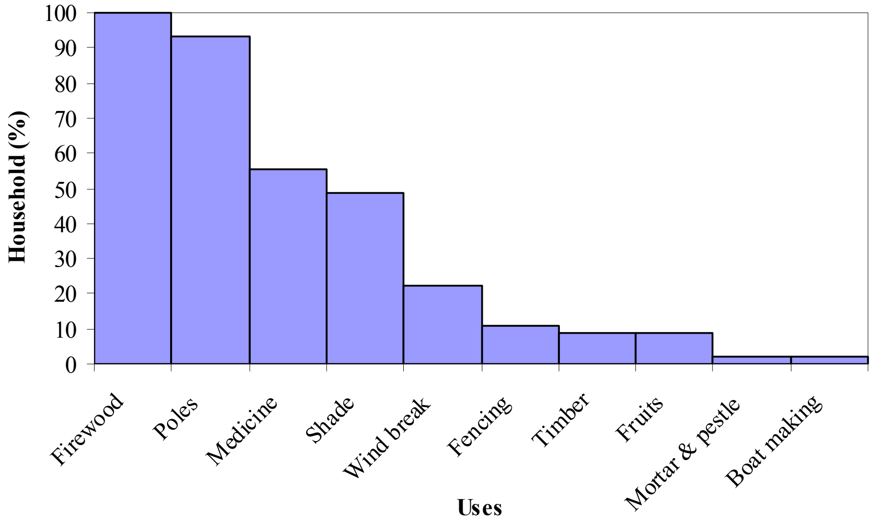

Figure 4. Household responses on other uses of the 16 species highly utilized for charcoal production (Table 3) in a multiple land use equatorial African savanna woodland, central Uganda.

3.4.3. Incomes from charcoal production.

All respondents concurred that charcoal production is a very important household livelihood activity that earns income used to meet various household needs that include; paying school fees for children, medical bills, building homes and buying clothing. All 45 households were engaged in the charcoal production business mainly for commercial purposes. Only 19 (42%) of the respondents use charcoal in the household, but in very small quantities (≈ 13 ± 3 kg per household year^{-1}) for domestic energy requirements, mainly for ironing/pressing clothes. They also concurred that there were too many households engaged in charcoal production compared to ten years ago. A range of 5 to 360 bags of charcoal (with means ± S.E. ranging from 41 ± 10 to 290 ± 33 bags across the sub-counties; n= 45) is produced per household per year (Table 5). Hence, with 1 bag ≈ 61 ± 2 (S.E.) kg (n = 45), household annual charcoal production tonnage ranged from 0.31 to 21.96 tonnes, with a mean (± S.E.) of 5.87 ± 0.8 tonnes, hence, on average, each household harvested 58.7 ± 8.3 (S.E.) tonnes of wood annually. With a charcoal production earth kiln recovery efficiency of only 10% (Kisakye, 2004), based on the assumption that all households in Nakasongola produce charcoal, the district is estimated to have produced about 149,932 tonnes per year in 2006 from 1,499,315 tonnes of wood. Consequently, increasingly smaller woody plants are harvested every year (Figure 3), as there is little time accorded for maturation and biomass accumulation or woodland recovery.

3.4.3.1. Costs incurred in charcoal production

The main costs incurred in charcoal production include the cost of logs, purchase of essential tools for cutting and transportation from production sites to storage or places of sale. The annual cost of the essential basic tools (i.e. axe, machete, hoe, shovel, fork) used in charcoal production is relatively low (≈ US$ 2.7 in 2006) per household; with tools having relatively long life spans of 3 - 15 years (Table 4). Rarely do charcoal producers pay taxes/license fees, however, in this study the respondents mentioned the tax/license fees and it was included in calculating the cost of production per household per year. The taxes/license fees related to how much charcoal they produce differed among the sub-counties, being higher in Kalongo US$ 1.09 compared to other sub-counties. However, in Lwampanga all respondents reported not having to pay any tax/license fee (Table 5). Means of transporting charcoal from production sites by producers included use of bicycles (46.7%), motorcycles (6.7%), humans on foot (15.7%) and motor vehicles (31.1%). Use of bicycles and humans on foot was usually for shorter distances ranging from 0.8 to 9.7 km. Most of the charcoal producers owned bicycles as their main means of transportation, while those who did not, hired them at a cost of ≥ 0.3 US$ per bag of charcoal depending on the distance travelled. Those who hired transport, paid by an equivalent number of bags of charcoal, and not cash (i.e. a barter system). The annual costs of production (US$) incurred per household differed significantly among the sub-counties ($F_{7, 37} = 10.02$, $p < 0.0001$), being highest in Wabinyonyi (492 ± 95) sub-county, followed by Lwabiata (278 ± 106) and lowest in Kalungi (31 ± 6) (Table 5). Similarly, the mean distance travelled from production sites to storage or sale sites differed significantly between sub-counties ($F_{7, 37} = 21.39$, $p < 0.0001$), being longer in Kakooge (41.7 ± 6.5 km), followed by Lwabiata (11.6 ± 2.0 km) and shortest in Nabiswera (1.2 ± 0.4 km) (Table 5). In addition to the direct costs of charcoal production, all respondents mentioned that the charcoal production process was associated with health hazards that include body burns, cuts, and respiratory diseases/symptoms (e.g. cold and sneezing, chest pain, and cough) as a result of inhaling charcoal dust.

Table 4. The tools used in charcoal production, and their life span and costs (in US$) as indicated by respondents in a multiple land use equatorial African savanna woodland, central Uganda.

Tools	Life span	Costs(US$)/HH	Annual costs (US$)/HH
Machete	3	1.9	0.6
Axe	15	3.1	0.2
Hoe	5	2.5	0.5
Shovel	5	1.3	0.3
Fork	3	1.9	0.6
Sickle	15	1.3	0.1
Rake	3	1.3	0.4
Total		**13.3**	**2.7**

At exchange rate 1 US$ = 1600 UGX; HH = household

Charcoal produced per household differed significantly among sub-counties (Kruskal-Wallis H (7, N = 45) = 31.42, $p < 0.0001$). Similarly, the producer sale price for a bag of charcoal differed significantly among sub-counties ($H = 35.62$, $p < 0.0001$), ranging from US$ 0.8 to 4.0 with means (± S.E.) ranging from US$ 1.7 ± 0.1 to 3.6 ± 0.1 (Table 5). The household's annual net income from charcoal production ranged from US$ - 174 ± 71 to 460 ± 66. (Table 5), and was significantly different between sub-counties ($H = 32.44$, $p < 0.0001$). The negative income in Lwabiata sub-county, is due to the relatively high costs of production and yet, low price per bag of charcoal in comparison with other sub-counties. The negative sign indicates that in this case, if they actually did cover all the listed costs of production, then charcoal production will not be profitable, hence clearly they did not meet all these costs. Given that a negative net income is highly unlikely in a subsistence situation, net income excluding the cost of logs (which might not have been paid) is also determined and differed among sub-counties ($H = 31.19$, $p < 0.0001$), ranging from US$ 42 ± 10 to 940 ± 113 (Table 5). The price of charcoal at the production sites was lower (≈ US$ 2 per bag) compared to the market prices in urban centres, with a bag of charcoal selling for US$ 11 to 13 in Kampala city.

Only the positive linear regression relationship between charcoal producer price and available plants was relatively strong (Figure 5). Wabinyonyi sub-county is an outlier in all regression analyses. This can be explained by the location of Wabinyonyi, being the central sub-county; it is closer to the main roads to Kampala and Masindi, the largest markets for charcoal. Being closer to the main roads is an added advantage as some costs are minimized and this translates into profit maximization. Wabinyonyi produces the highest amount of charcoal and generates the highest net income compared to the other sub-counties. Available woody plants per plot in the charcoal production land use also differed significantly among the sub-counties ($F_{7, 16} = 3.3$, $p = 0.02$), being highest in Wabinyonyi (550 ± 116), followed by Kalongo (273 ± 12) and lowest in Lwabiata (87 ± 37) (Table 5; plant data from Chapter 4).

The Akaike Information Criterion (AIC_c) revealed that the cost of production (excluding cost of logs), gross income, number of households and age of respondents (combined) were the most significant predictors (with delta Akaike value of 0.0) of the amount of charcoal produced per household in Nakasongola, as they produced the "best" model (Table 6). The competing model (including overall cost of production) was also significant (with delta Akaike value of 0.5). The two models support the cost of production, gross income, age of respondents and number of households as being the significant predictors of charcoal produced in this district. The next four models in (Table 6) had considerably less support, while the rest of the models were very unlikely. The best model, with an Akaike weight of 0.47, has a 47% chance of being the best model compared to the competing model with a 36% chance. Moreover, the evidence ratio indicates that the best model is only 1.315 more likely than the competing model to be the best given the set of candidate models (Table 6).

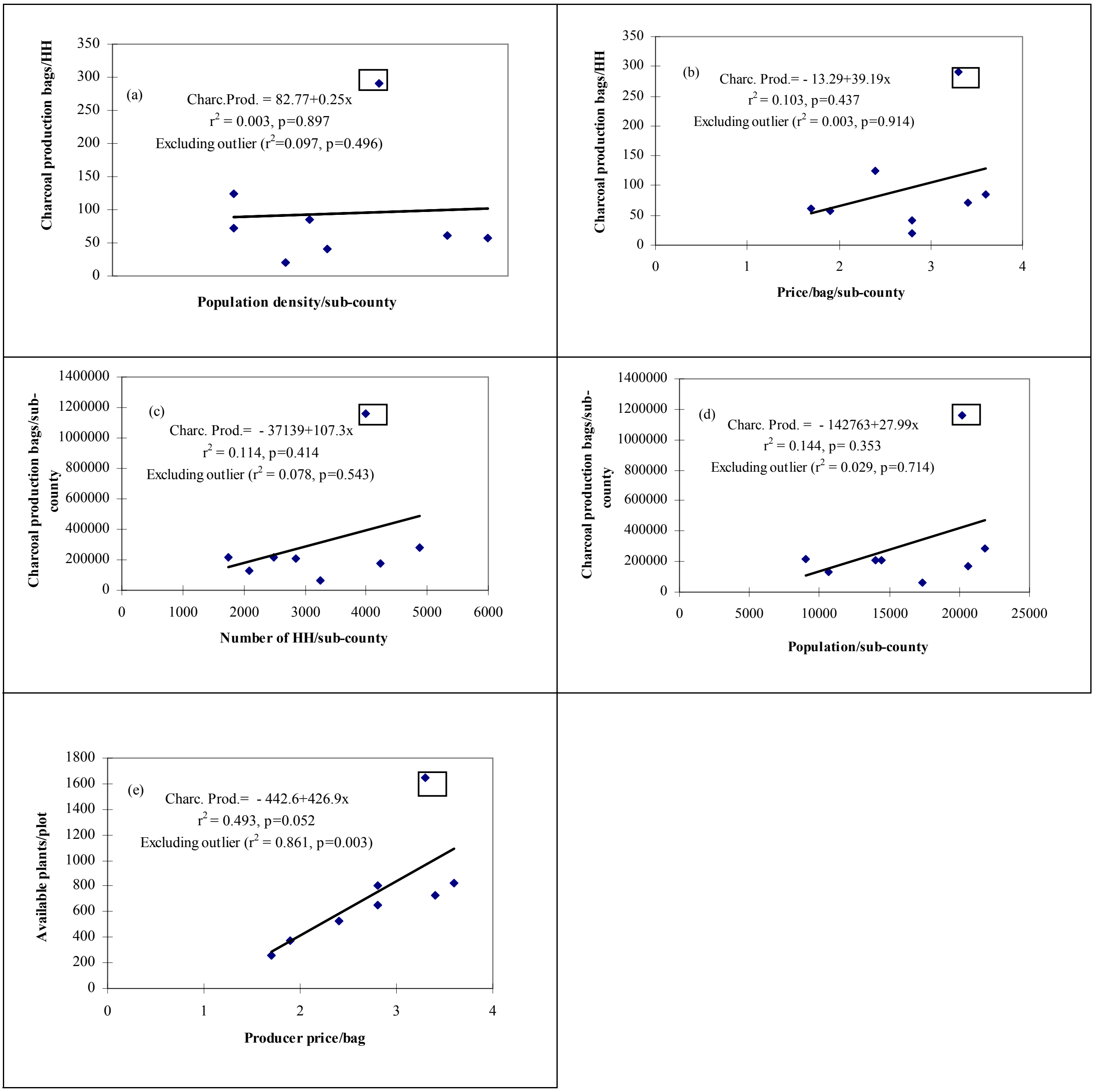

Figure 5. Linear regression analyses of: (a) population density/sub-county versus charcoal production/household, (b) price of charcoal/sub-county versus production/household, (c) households/sub-county versus bags of charcoal/sub-county, (d) population/sub-county versus bags of charcoal/sub-county, and (e) producer price versus available plants /plot in a multiple land use equatorial African savanna woodland, central Uganda. The highlighted outlier in each case is Wabinyonyi sub-county.

Table 5. Population (total population, land area, population density, and number of households) and charcoal production parameters in charcoal production land use type (available plants/ha mean ± S.E.), bags of charcoal produced per household, total production (bags) per sub-county, charcoal price/bag per sub-county, gross income, cost of production (with and without cost of logs), net income (in US$) per household and per sub-county and distance from production sites (km; mean ± S.E.) per sub-county, in a multiple land use equatorial African savanna woodland, central Uganda.

Sub-county	**Kakooge**	**Kalongo**	**Wabinyonyi**	**Kalungi**	**Nabiswera**	**Nakitoma**	**Lwampanga**	**Lwabiata**	**Overall Nakasongola Dist.**
Number of respondents	**5**	**5**	**6**	**6**	**6**	**6**	**6**	**5**	**45**
2002 Population (No. of people)	20,615	13,991	20,211	17,336	14,447	9,063	21,836	10,627	128,126
Land Area (km^2)	475	352	375	496	589	370	288	157	3,102
Population Density (People/km^2)	43	40	54	35	25	24	76	68	41
House holds (HH)	4,241	2,496	3,993	3,254	2,850	1,741	4,877	2,090	25,542
Charcoal production									
Tree & Shrub density (plants/ha) in Charc. Prod.	217 ± 79	273 ± 12	550 ± 116	267 ± 87	243 ± 130	117 ± 24	123 ± 50	87 ± 37	242 ± 36
Bags of charcoal/HH (mean ± S.E.)	41 ± 10	85 ± 12	290 ± 33	20 ± 4	72 ± 16	124 ± 12	58 ± 14	62 ± 21	96 ± 14
Total production/sub-county (No. of bags)	173,033	212,659	1,157,970	65,622	205,200	215,884	282,866	130,416	2,443,650
Total production/sub-county (tonnes/yr)	24,895	14,652	23,439	19,101	16,730	10,220	28,628	12,268	149,932
Wood equivalent /sub-county (tonnes/yr)	248,947	146,515	234,389	191,010	167,295	102,197	286,280	122,683	1,499,315
Costs incurred and income generated (US $)/year									
Charcoal price/bag/sub-county (mean ± S.E.)	2.8 ± 0.2	3.6 ± 0.06	3.3 ± 0.2	2.8 ± 0.1	3.4 ± 0.1	2.4 ± 0.03	1.9 ± 0.4	1.7 ± 0.05	2.7 ± 0.1
Gross Income/HH (mean ± S.E.)	115 ± 31	306 ± 43	957 ± 110	56 ± 11	245 ± 55	298 ± 32	110 ± 49	105 ± 36	259 ± 46
Gross Income/sub-county	593	1541	5728	334	1484	1772	669	533	12,654
Costs of production /HH (mean ± S.E.)	111 ± 21	227 ± 24	495 ± 95	33 ± 6	41 ± 10	163 ± 16	50 ± 19	281 ± 106	173 ± 28
Costs of production /sub-county	553	1135	2968	200	246	979	299	1403	7,782
Costs of production (without costs of logs)/HH	8 ± 3	137 ± 22	16 ± 10	14 ± 4	16 ± 6	8 ± 1	7 ± 5	4 ± 0.3	25 ± 7
Costs of production (without costs of logs)/SC	40	687	95	84.00	96	49	44	20	1,114
Tax/license fee paid by house hold per bag	0.31	1.09	0.35	0.76	0.25	0.38	0	0.19	3
Net Income /HH (mean ± S.E.)	8 ± 15	81 ± 47	460 ± 66	23 ± 8	206 ± 46	132 ± 17	62 ± 31	-174 ± 71	108 ± 29
Net Income/sub-county	40	406	2761	135	1238	793	370	-870	4,873
Net Income (without costs of logs)/HH	110 ± 33	171 ± 60	940 ± 113	42 ± 10	231 ± 52	287 ± 32	104 ± 45	103 ± 35	256 ± 46
Net Income (without costs of logs)/SC	552	855	5,633	251	1,388	1,723	625	513	11,540
Mean distance (km) prod. site to collecting point	42.0 ± 6.5	1.3 ± 0.3	10.0 ± 0.8	10.1 ± 4.5	1.2 ± 0.4	3.6 ± 0.4	2.2 ± 1.2	12.0 ± 2.0	9.7 ± 2

At exchange rate 1US$ = 1600 UGX (2006); Population data source: Uganda Bureau of Statistics, (2002).

Table 6. Akaike's second-order information criterion (AIC_c) of the regression models of the number of bags of charcoal produced per household annually as a response variable and five predictor variables in a multiple land use equatorial African savanna woodland, central Uganda. HH = households. Models order is based on AIC_c values.

Model ID	**AICc value**	**Log likelihood**	**No. of parameters (No. of variables + the intercept)**	**Delta AICc (Δ_i) (AIC_i - min AIC)**	**Relative likelihood ($\sum exp(-0.5\Delta_r)$)**	**Akaike weight (w_i) ($exp(-0.5\Delta_i)$) / ($\sum exp(-0.5 \Delta_r)$)**	**Evidence ratio (w_i/w_i)**
Best model							
Gross income + Number of HH + Age of respondents + cost of prod (excl. logs)	403.98	- 40.52	5	0.00	1.00	0.4737	
Competing model							
Gross income + Number of HH + Age of respondents + Cost or prod. (overall costs)	404.53	- 37 .82	5	0.55	0.76	0.3602	1.315
Model with less support							
Gross income + Age of respondents	407.13	- 37.08	3	3.15	0.21	0.0979	
Gross income + Number of HH + Age of respondents	409.09	- 36.37	4	5.10	0.08	0.0369	
Gross income	410.21	- 43.54	2	6.23	0.04	0.0210	
Gross income + Number of HH	411.68	- 42.27	3	7.70	0.02	0.0101	
Very unlikely models							
Cost of production (overall costs)	486.43	- 33.56	2	82.45	0.00	0.0000	
Cost of prod. (overall costs) + Number of HH	487.05	- 124.07	3	83.07	0.00	0.0000	
Cost of prod. (overall costs) + Age of respondents	487.98	- 123.69	3	84.00	0.00	0.0000	
Cost of prod. (overall costs) + Number of HH + Age of respondents	488.96	- 116.35	4	84.98	0.00	0.0000	
Number of house holds	538.88	- 93.69	2	134.90	0.00	0.0000	
Cost of production (excluding cost of logs)	539.04	- 91.86	2	135.06	0.00	0.0000	
Age of respondents	539.05	- 90.66	2	135.07	0.00	0.0000	
Cost of prod. (excl. cost of logs) + Number of HH	541.29	- 93.70	3	137.31	0.00	0.0000	
Cost of prod. (excl. cost of logs) + Age of respondents	541.45	- 91.15	3	137.47	0.00	0.0000	
Cost of prod. (excl. cost of logs) + Number of HH + Age of respondents	543.82	- 92.49	4	139.84	0.00	0.0000	
Total					**2.11**	**1.00**	

4.0. Discussion

The results of this study revealed various livelihood activities among the households and communities, with the major land use activities being charcoal production, livestock grazing and subsistence crop cultivation. Charcoal production and livestock grazing are done particularly by men, whereas crop cultivation is done by women. Charcoal production is a labour intensive activity, and a major source of income, but the charcoal producer has to provide all the labour to maximise profits. Most of the Ugandan rural population depends on crop cultivation. In the study area households have relatively small crop fields and a small variety of crops cultivated. The small crop fields are the result of the ever decreasing availability of land for cultivation per household over the years, due to ever increasing human and animal populations in the district. However, households are trying to cope with scarcity of land by practicing a crop rotation system where they alternate crops such as cereals with legumes. Crop rotation is commonly practiced in Lwampanga, the most highly populated sub-county. Other sub-counties practice both crop rotation and shifting cultivation, with fallow periods ranging from six months to three years, with the exception of Kalungi sub-county which only practices shifting cultivation. The limited crop cultivation and dependency on a small variety of hardy crops (e.g. cassava and millet) for both food and income are influenced by the low and unreliable rainfall characteristics of most African drylands/savannas. Most of the people in this savanna have low levels of formal education, making them unqualified for formal paid employment, consequently forcing them to rely entirely on the exploitation of natural resources. Indeed, the poorer and more vulnerable households tend to be more dependent on the natural resources base, use a greater diversity of resources, and more of each resource than those households with access to other forms of income (Shackleton *et al.,* 2002b). The importance of land-based livelihoods to rural households is influenced by the characteristics of households and the community at large (Dovie *et al.,* 2005). According to Gunatilake (1998), some households may depend more on woodland resources because of their socio-economic characteristics, while others may depend less. Furthermore, households vary in their access to natural, human, physical and financial capital; they also vary in how endowments of these translate into livelihood strategies (De Sherbinin *et al.,* 2008). In the study area, households differ in their socio-economic characteristics, some are culturally entirely pastoralists and others crop cultivators; and there are also relatively poor and rich households.

The study also showed that the woodlands have a multitude of uses which vary in importance to households. The savanna woodlands make major contributions to rural household livelihoods. Woodlands play a major role in people's livelihoods by providing various wood and non-wood products, also creating avenues for direct and indirect employment and income from charcoal production. The high dependency on natural resources by households in this savanna is typical of many Sub-Saharan rural communities. In this area there has been a great increase in the number of households per village (Uganda Bureau of Statistics, 2002), subsisting mainly on charcoal production, livestock grazing, and subsistence crop cultivation. Hence, this increase is likely to impact negatively on the resource sustainability and the environment in dryland savannas. Recent analyses suggest that the number of households has a more direct environmental impact than population size *per se* (Dietz & Rosa, 1994; Cramer, 1998; Liu *et al.,* 2003). In the study area, the decrease in resource availability is already evident with people reported to be moving long distances from their homesteads to find and harvest trees/shrubs for firewood and charcoal production. It is also evident in the differences in the distances charcoal producers have to transport their charcoal from production kilns to selling points or homes. High population growth, combined with difficult economic circumstances, often made worse by adverse climatic conditions such as drought (prolonged shortage of rainfall), as is the case for the study area, constrain rural incomes that would have been gained through selling livestock and milk, some of the cash crops and fruits, consequently encouraging rural communities to increase reliance on the woodlands for livelihoods (Chipika & Kowero, 2000). This may lead to the deforestation and/or degradation of the woodlands that are the backbone of rural household livelihood strategies and ecosystem services.

4.1. Species frequently harvested for charcoal production

The number of species (~ 24 species) reported to have been harvested for charcoal production in this study is comparable to what was reported (~ 26 species) for the same purpose in western Uganda (Naughton-Treves *et al.,* 2007). However, the species frequently harvested for charcoal seem to vary among respondents and locations, and their harvesting is largely not determined by the quality of charcoal they give but their availability and accessibility to charcoal producers. This contrasts with areas adjacent to Kibale National Park in western Uganda where old-growth hardwood species were highly targeted for charcoal production because they give high quality charcoal (Naughton-Treves *et al.,* 2007). On the other hand, the ranking of *C. molle*, *C. collinum*, *V. nobilis*, *G. mollis* and *T. glaucescens* as the most highly utilized species for charcoal production is not surprising given the non-selective nature of harvesting and the fact that they characterize most of the savanna woodland vegetation in central Uganda (Langdale-Brown *et al.,* 1964). Furthermore, these species are commonly found in burned and open woodlands in savanna areas (Nangendo *et al.,* 2006), which similarly characterize the studied area.

Among the species preferred for charcoal production are very important multiple land use species utilized for herbal medicine and food (fruits and tubers), which are consequently being non-selectively and unsustainably harvested for charcoal production. For example, *C. collinum*, *V. nobilis* *Piliostigma thonningii*, *Mangifera indica*, *Albizia coriaria*, *C. molle* and *T. glaucescens* are medicinal plants treating a variety of ailments in other parts of Uganda (Wasswa & Deogracious, 2006; Okello & Ssegawa, 2007). In addition all ~ 24 species were also harvested for firewood and poles, and some households were harvesting both dead and live plants. This supports a study by Dovie *et al.* (2004) in a South African village, which revealed that harvesting of fuelwood has gone beyond the simple collection of only dead wood, and encompassed the chopping of live trees. Therefore, their non-selective and unsustainable harvesting for charcoal production, firewood and poles has multiplier effects that may threaten the sustainable livelihoods of rural households in terms of nutrition and health. Forests/woodlands and their products are now well appreciated by several disciplines such as the environmental, conservation, economics and developmental fields for adding value to human well-being and, at times, the very survival of millions of rural poor throughout the world (World Bank, 2002; Kaimowitz, 2003; Sunderlin *et al.,* 2005; MEA, 2005; Shackleton *et al.,* 2007). Similar to the miombo woodlands of Tanzania (Luoga *et al.,* 2000b), the non-specificity and vast extent of harvesting of woody plants for charcoal is resulting in loss of other potential products from woodlands and highlights the possibility of undermining the provision of ecosystem services and goods. This also has implications for the attainment of the Millennium Developmental Goals (1 & 7) in Uganda by 2015, which is aimed at eradicating extreme hunger and poverty and ensuring environmental sustainability, respectively. The dependence of people on plant medicine from natural woodlands is increasingly becoming popular among rural and urban communities due to a number of factors including living costs. This is particularly important in countries like Uganda where most of the population lives on less than one US dollar a day, and natural resource use is crucial in meeting their nutritional and medicinal requirements.

In these savanna woodlands, there is a wealth of wild food (e.g. *Tamarindus indica*, *Vitellaria paradoxa*) and medicinal plants (e.g. *A. coriaria*, *P. thonningii*) that have great potentials for local use as well as commercial development. Moreover, at least 30% of the world's cultivated plants originated from drylands/savannas, and have progenitors and relatives in these areas (MEA, 2005). Some of the wild and under-utilized plants that have a potential for more widespread use and their promotion as new crops could contribute to food security, agricultural diversification, and income generation (Vietmeyer, 1986; Anthony & Haq, 1995). Elsewhere, foods from wild species form an integral part of the daily diets of many poor rural households and are especially important during droughts or famines (e.g. Luoga *et al.,* 2000a; Kaschula, 2008). They are an important source of vitamins, minerals and other nutrients, and also represent ready sources of income for cash-poor households. Wild foods may offer unique benefits to households afflicted by HIV-AIDS, providing a nutritious and freely available food source at minimal labour and financial costs (Velempini *et al.,* 2003; Kaschula, 2008). Indeed, the so-called "safety-net" value of wild foods in times of hardship due to high HIV-AIDS rates has been noted by Shackleton *et al.* (2007) and Hunter *et al.* (2007) in Mpumalanga province of South Africa. Hence, the sustainable management of these savannas is important for the conservation of valuable biodiversity and consequently human well-being.

4.2. Incomes from charcoal production

Generally, charcoal production is the major source of income for the majority of households in this wooded savanna. Similar to other Sub-Saharan African countries such as Mozambique, Malawi, Tanzania, Rwanda and Senegal, the charcoal production sector is a source of income generation for tens of thousands of people especially among the poor (Brouwer & Magane, 1999; Kambewa *et al.,* 2007; World Bank, 2009). However, there were significant differences in the amounts of charcoal produced annually and producer sale prices, translating into differences in annual household incomes. Differences in incomes from charcoal production could be attributed to differences in the availability and access to woody plants, with some areas having open woodlands and others dense woodlands with sufficient wood stocks available for charcoal production. In this savanna woodland area, like in the southern African savannas, there is a significant spatial and temporal variation in the quantities used and values per sample population (Shackleton & Shackleton, 2006). The net incomes from charcoal differed among households and sub-counties because of the differences in cost of production (logs, tax/licensing fees and tools), the differences in proximity to the main road network in the district (a surrogate of proximity to markets) and availability of competing demands from other sources of fuel energy. For example, low charcoal prices and incomes were more common in far off households and those on the Lake Kyoga shores (Lwabiata and Lwampanga sub-counties) where over the years there has been high demand for firewood for fish smoking.

Gross income from charcoal production was US$ 259 ± 46 per household per annum, while net income was only US$ 108 ± 29 per household per annum. However, net income excluding the cost of logs and license fees (as households probably rarely actually pay for these) is much higher at US$ 256 ± 46 per household per annum, probably better represents the actual financial situation for the majority of households. The incomes are comparable to Monela *et al.* (1993), who reported an average household income of US$ 177 per year from charcoal production along the Dar Es Salaam-Morogoro highway, Tanzania. Profit realization from charcoal production is accomplished at the expense of other potential uses of the woodlands (Luoga *et al.,* 2000b). Charcoal production plays a major role in income generation in Nakasongola where the district earns a gross income of US$ 12,654 per year. Considering the US$ 9 - 11 per bag margin between the producer sale price and final buyer price in urban centres, the results of this study suggest that there is relatively low profitability in charcoal production for producer households. However, the probability of making money from charcoal production is much more definite than from cash crops which may fail with drought and crop diseases. This is in accord with findings from western Uganda (Naughton-Treves *et al.,* 2007), and it seems that much higher profits accrue to charcoal transporters and wholesale traders than to producers (Brouwer & Falcao, 2004).

Human actions have both long and short-term effects on ecological systems that in turn influence human well-being (Chapin *et al.,* 2006). Although commercial charcoal production generates most of the household incomes for those dependent on woodland resources, it appears to be mining the woodlands with little regard for sustainability and the environment. Similar patterns have been observed in western Uganda (Naughton-Treves *et al.,* 2007) and Tanzanian miombo woodlands, where commercial harvesting for charcoal overrides ecological impacts from all other harvesting purposes because of the powerful economic incentives to produce charcoal (Luoga *et al.,* 2002a). Commercial use of the resources often leads to depletion of biological resources, which are not increasing in value as fast as the rate of interest paid by banks and revenues put into other markets (Costanza *et al.,* 1997).

The lack of viable alternative sources of income for the rural households, the low capital investment required and the ready and large market for charcoal in urban areas (e.g. Kampala) appear to be the driving forces for commercialisation and production of charcoal in these savanna woodlands. A study by Kisakye (2004) on charcoal consumption in Kampala in 2004 revealed that a total of 96,637 bags of charcoal with an average weight of 60 kg were transported to Kampala market over a period of one week, which means a total of 302,330 tonnes of charcoal per year, mainly from savanna woodlands. Similarly, a study by WWF Tanzania revealed that the amount of charcoal entering Dar Es Salaam city, which is the major charcoal market, was 6,777. 56 kg/bag per day (Malimbwi *et al.,* 2007) or 138,522 tonnes/year. Furthermore, Uganda is facing increased urbanization, yet urbanization increases deforestation by increasing the demand for the production of charcoal, a primary fuel among urban dwellers (Wong *et al.,* 2005). In Uganda, this has not been helped by the high costs of alternative sources of energy (e.g. electricity and kerosene), resulting in high dependences on biomass energy by over 80% of households. Ugandans have witnessed kerosene prices rising from UGX 1,650 (US$ 0.95) in March 2006 to UGX 2,900 (US$1.70) in June 2008. The ever increasing electricity and fossil fuels (e.g. kerosene) tariffs in Uganda makes such energy sources unaffordable to many urban households leading to their increased dependency on the relatively cheaper wood fuel. Hence, a combination of these socio-economic factors has led to increased demand and commercialisation of charcoal, with negative impacts on the sustainability of woodlands and biodiversity in the area.

The increased commercialization of charcoal production and its low capital investment requirement makes it an attractive income generating activity for most rural households and is increasingly attracting immigrants. Such a scenario has similarly been reported from South Africa where the extraction of resources from the woodlands has become much more extensive and intensive as a result of outsiders (i.e. non villagers) harvesting large amounts of resources, particularly those which are wood-based (Dovie *et al.,* 2005). A similar trend was reported in eastern Tanzania, in an active charcoal making area (Gwata area in Morogoro Region), where 60% of charcoal producers were immigrants from other parts of the country (Zahabu, 2001). Indeed, in Uganda, many landless people migrate from the more densely to less populated natural resource endowed areas, particularly forest/woodland areas, to engage in charcoal production and timber pit sawing for sale in urban markets, thus accelerating deforestation (Kanabahita, 2001; Anderson *et al.,* 2004).

5.0. Conclusions

Woodlands in this equatorial savanna are vital components of local rural livelihoods, with the majority of household livelihood strategies dependant on the exploitation of woodland plant resources. In this savanna woodland, charcoal production is the major income source for most of the rural households, enabling them to meet their monetary needs. The low levels of rainfall in the area limit productive arable agriculture. The low levels of formal education and lack of alternative viable economic activities are exacerbating people's high dependence on woodlands for charcoal production. In spite of the income generated from woodland resource exploitation, their unsustainable use contributing to environmental degradation threatens the long term survival of the rural households whose livelihoods are mostly dependent on these woodlands. Indeed, the UN commissioned Millennium Ecosystem Assessment (2005) found that increasing demands on ecosystem services over the past 50 years have been fulfilled at the cost of ecosystem degradation and loss of diversity.

Although households within and around these woodlands cope with surprise and uncertainty in various ways (e.g. charcoal producers also engage in crop cultivation, bee keeping, brick making and fishing in some sub-counties during periods of poor charcoal production), this may in the long-term not be sustainable. The increasing demands for woodland resources are likely to surpass the capacity of these ecosystems to provide goods and services that are essential to rural livelihoods, hence, compromising their socio-ecological resilience and persistence for human well-being. Therefore, sustainable woodland resource conservation will be necessary since its benefits extend far beyond the profits of commercial resource use. Although there have been efforts (including incentives for sustainable selective harvesting and imposing penalties for illegal harvesting) to minimize the impacts of unsustainable harvesting, accruing profits from commercial charcoal production have made it difficult to enforce legislation. Hence, woodland/forest management institutions need to pay more attention to the regularization of charcoal production and selective harvesting of woody plants to ensure sustainable use of the woodland resources in the rural drylands. There is a need to select those tree species that are relevant to the communities in terms of utilization or which meet the real needs of the users, such as fruits, wood fuel, medicines and fodder, and use the opportunity to domesticate these species. Maintenance of savanna woodland resources and other ecosystem services essential for human well-being will require an effective legal framework to prevent over-exploitation and provide incentives for the protection of savanna woodland vegetation. It will also be necessary to investigate the resilience of woody plants to harvesting and assess their regeneration status within the various land uses to guide their management for the sustainability of the woodlands.

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References

Anderson, R.E., Sewakambo, F. & Vandergrift, K. 2004. "Pawns of Politics: Children, Conflict and Peace in Northern Uganda" *Africafocus Bulletin*: Retrieved from http://www.africafocus.org/docs04/ugan0409.php. Accessed on 17/11/2006.

Banana, A.Y. & Gombya-Ssembajjwe, W. 1996. Successful Forest Management: The Importance of Tenure and Rule Enforcement in Ugandan Forests. International Forestry Resources and Institutions Research Program Series, Bloomington, Indiana.

Barrett, C.B., Bezuneh, M., Clay, D.C. & Reardon, T. 2005. Heterogeneous constraints, incentives and income diversification strategies in rural Africa. *Quarterly Journal of International Agriculture* 44(1): 37-60.

Bennett, E.M., Peterson, G.D. & Levitt, E.A. 2005. Looking to the future of ecosystem services. *Ecosystems* 8: 125-132.

Bernard, R.H. 1996. "Qualitative data, quantitative analysis". *The cultural Anthropology Methods Journal* 8 (1): 9-11.

Binswager, H.P. & Ruttan, V. 1978. Induced Innovation. Technology, Institutions and Development: John Hopkins University Press.

Botha, J., Witkowski, E.T.F. & Shackleton, C.M. 2004. Market profiles and trade in medicinal plants in the Lowveld, South Africa. *Environmental Conservation* 31: 38-46.

Braedt, O. & Standa-Gunda, W. 2000. Woodcraft markets in Zimbabwe. *International Tree Crops Journal* 10:367-84.

Brouwer, R & Magane, D. M. 1999. The charcoal commodity chain in Maputo [Mozambique]: Access and Sustainability. *Southern Africa Forestry Journal* 185: 27-34.

Brouwer, R. & Falcao, M.P. 2004. Wood fuel consumption in Maputo, Mozambique. *Bioenergy* 27: 233-245.

Brown, D.R., Stephens, E.C., Ouma, J.O., Murithi, F.M. & Barrett, C.B. 2006. Livelihood stratergies in the rural Kenyanhighlands. *African Journal of Agricultural and Resource Economics* 1(1): 21-36.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretical approach, 2nd edition. Springer-Verlag, New York.

Byabashaija, M.D., Esegu, J.F.O., Kidiya, J.M., Basoga, M. & Odia, R.K. 2004. Traditional uses of indigenous tree species. *Ugandan Journal of Agricultural Sciences* 9: 363-371.

Campbell, B.M. & Luckert, M.K. 2002. Towards understanding the role of forests in rural livelihoods. pp. 1-16. In: Campbell, B.M. & Luckert, M.K. (Eds.) Uncovering the Hidden Harvest: Valuation Methods for Woodland and Forest Resources. CIFOR, Bogor.

Campbell, B.M., Jeffery, S., Kozanayi, W., Luckert, M., Mutamba, M. & Zindi, C. 2002. Household Livelihoods in Semi-Arid Regions: Options and Constraints. CIFOR, Bogor, pp.153.

Cavendish, W. 2002. Quantitative methods for estimating the economic values of resource use to rural households. pp. 17-65. In: Campbell B.M. & Luckert M.K. (Eds.) Uncovering the Hidden-Harvest valuation methods for woodland and forest Resources. Earthscan Publications, London.

Chambers, R. 1994. The origins and practice of participatory rural appraisal. *World Development* 22(7): 953-969.

Chapin III, F. S., Robards, M. D., Huntington, H. P., Johnstone, J. F., Trinor, S. F., Kofinas, G. P., Ruess, R. W., Fresco, N. Natcher, D.C. & Natlor, R. L. 2006. Directional changes in Ecological communities and Social-Ecological Systems: A framework for prediction based on Alaskan examples. *The American Naturalist* 168: 36-49.

Chidumayo, E.N. 1988. Estimating fuelwood production and yield in regrowth dry miombo woodland in Zambia. *Forest Ecology Monograph* 24: 59-66.

Chipika, J.T. & Kowero, G. 2000. Deforestation of woodlands in communal area Zimbabwe: is it due to agricultural policies? *Agriculture, Ecosystems and Environment* 7: 175-185.

Costanza, R., Cumberland, J., Daly, H., Goodland, R., Norgaard, R. (Eds.) 1997. An Introduction to Ecological Economics. ISEE, St. Lucie Press, Florida.

Cramer, J.C. 1998. Population growth and air quality in California. *Demography* 35:45-56.

De Sherbinin, A., VanWey, L.K., McSweeney, K., Aggarwal, R., Barbieri, A., Henry, S., Hunter, L.M., Twine, W. & Walker, R. 2008. Rural household demographics, livelihoods and the environment. *Global Environmental Change* 18: 38-53.

DFID (Department for International Development). 1999. Sustainable livelihoods Guidance sheets. Accessed on 9.04.2009 from http://www.eldis.org/vfile/upload/1/document/0901/sectio2.pdf.

Dietz, T. & Rosa E.A. 1994. Rethinking the environmental impacts of population, affluence and technology. *Human Ecology Review* 1: 277-300.

Dovie, B.K., Shackleton, C.M. & Witkowski, E.T.F. 2002. Direct-use values of woodland resources consumed and traded in a South African village. *International Journal of Sustainable Development and World Ecology* 9: 269-283.

Dovie, D.B.K, Witkowski, E.T.F. & Shackleton, C.M. 2004. The fuelwood crisis in Southern Africa-relating fuelwood use to livelihoods in a rural village. *GeoJournal* 60: 123-133.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2003. Direct-use value of smallholder crop production in semi-arid rural South African village. *Agricultural Systems* 76: 337-357.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2005. Monetary valuation of livelihoods for understanding the composition and complexity of rural households. *Agriculture and Human Values* 22: 87-103.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonnen, G., Carpenter, S.R., Chapin, S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. 2005. Global Consequences of Land Use. *Science* 309: 570-574.

Gram, S. 2001. Economic valuation of special forest products: an assessment of methodological shortcomings. *Ecological Economics* 36: 109–117.

Gunatilake, H.M. 1998. The role of rural development in protecting tropical rainforests: evidence from Sri Lanka. *Journal of Environment Management* 53: 273-292.

Hofstand, O. 1996. Woodland Deforestation by charcoal supply to Dar eEs Salaam. *Journal of Environmental Economics and Management* 33: 17-32.

Hunter, L.M., Twine, W. & Petterson, L. 2007. "Locusts are now our beef": Adult mortality and household dietary use of local environmental resources in rural South Africa. *Scandinavian Journal of Public Health* 35: 165-174.

Inglis, A. 1992. A tale of two approaches: conventional questionnaire surveys versus PRA. The Network, London, 1992.

Kaimowitz, D. 2003. Not by bread alone: forests and rural livelihoods in Sub-Saharan Africa. pp. 45-63. In: Oksanen, T., Pajari, B. & Tuomasjakka, T. (Eds.) Forests in Poverty Reduction Strategies: Capturing the Potential. European Forest Institute, Torikatu, Finland.

Kakudidi, E.K. 2004. Cultural and social uses of plants from and around Kibale National Park, Western Uganda. African *Journal of Ecology* 42: 114-118.

Kambewa, P., Mataya, B., Sichinga, K. & Johnson, T. 2007. Charcoal: the reality-A study of charcoal consumption, trade and production in Malawi, small and medium size enterprise. Series No, 21, IIED, London.

Kanabahita, C. 2001. *Uganda. Forestry outlook studies in Africa (FOSA)* [s.l.] Ministry of Water, Lands, and Environment, Uganda. pp.32.

Kaschula, S.A. 2008. Wild foods and household food security responses to AIDS: evidence from South Africa. *Population and Environment* 29:162-185.

Kisakye, R. 2004. Charcoal consumption in Kampala and its source districts. Unpublished Report on a consultancy survey for the GTZ Energy Advisory Project, Ministry of Energy and Mineral Development, Kampala, Uganda.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. *Journal of Cleaner Production* 12: 1047-1057.

Langdale-Brown, I., Osmaston, H.A., & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land use. Entebbe Government Printers, Uganda. pp.159.

Letsela, T., Witkowski, E.T.F. & Balkwill, K. 2003. Plant resources used for subsistence in Tsehlanyane and Bokong in Lesotho. *Economic Botany* 57(4): 619-639.

Liu, J., Daily, G.C., Ehrlich, P.R. & Luck, G.W. 2003. Effects of households' dynamics on resource consumption and biodiversity. *Nature* 421: 530-33.

Liwenga, E.T. 2003. Food Insecurity and Coping Strategies in Semiarid Areas: the Case of Mvumi in Central Tanzania. Stockholm Studies in Human Geography No. 11. A PhD Dissertation, Department of Human Geography, Stockholm University, Stockholm, Sweden.

Liwenga, E.T. 2009. Livelihood diversification and implications on dryland resources of central Tanzania. *African Journal of Ecology* 47: 142-146.

Luoga, E.J, Witkowski, E.T.F. & Balkwill, K. 2000a. Economic of charcoal production in miombo woodlands of eastern Tanzania. Some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000b. Differential utilization and ethnobotany of trees in Kitulanghalo Forest Reserve and surrounding communal lands, Eastern Tanzania. *Economic Botany* 54(3): 328-343.

Luoga, E.J., Witkowski, E.T.F., Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 16: 15-30.

Malimbwi, R.E., Zahabu, E. & Mchome, B. 2007. Situation analysis of charcoal sector in Dar eEs Salaam. Consultancy report submitted to WWF Tanzania. pp.48.

MEA (Millennium Ecosystem Assessment) 2005. *Ecosystems and Human Well-Being: Biodiversity Synthesis*: Island Press World Resources Institute, Washington, DC.

MEMD (Ministry of Energy and Mineral Development) 2001. *National Biomass Energy Demand Strategy 2001-2010*. Kampala, Uganda. pp. 36.

Monela, G.C., O'kting'ati, A. & Kiwele, P.M. 1993. Socio-economic aspects of charcoal consumption and environmental consequences along the Dar Es Salaam-Morogoro highway, Tanzania. *Forest Ecology and Management* 58: 249-258.

Namaalwa, J., Eid, T. & Sankhayan, P. 2005. A multi-species density-dependent matrix growth model for the dry woodlands of Uganda. *Forest Ecology and Management* 213: 312-327.

Nangendo, G., Steege, H.T. & Bongers, F. 2006. Composition of woody species in a dynamic forest-woodland-savannah mosaic in Uganda: implications for conservation and management. *Biodiversity and Conservation* 15: 1467-1495.

Naughton-Treves, L., Kammen, D.M. & Chapman, C. 2007. Burning biodiversity: Woody biomass use by commercial and subsistence groups in western Uganda's forests. *Biological Conservation* 134: 232-241.

O'Higgins, R.C. 2007. Savannah Woodland Degradation Assessments in Ghana: integrating ecological indicators with local perceptions. *Earth and Environment* 3: 246-281.

Okello J. & Ssegawa, P. 2007. Medicinal plants used by communities of Ngai sub-county, Apac District, northern Uganda. *African Journal of Ecology* 45: 76-83.

Parker, D., Downer, E.R. & Cole, G.E.D. 1967. Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Paumgarten, F. 2005. The role of non-timber forest products as safety-nets: A review of evidence with a focus of South Africa. *GeoJournal* 64: 189-197.

Phillips, O. & Gentry, A.H. 1993. The useful plants of Tambopata. Pem.1: Statistical hypothesis test with a new quantitative technique. *Economic Botany* 47: 15-32.

Pretty, J.N. & Vodouhé, S.D. 1996. Using rapid or participatory rural appraisal. International Institute of Environment and Development (IIED). London, UK.

Ruthenberg, H. 1980. Farming systems in the Tropics, 3rd Edition. Claredon Press, Oxford. 424 pp.

SADC, 1993. Energy Statistics Year Book for 1991. Energy Sector, TAU, Luanda, Angola.

Scholes, R.J. & Archer, S. 1997. Tree-grass interactions in savannas. *Annual Reviews of Ecology and Systematics* 28: 517-544.

Seaby, R.M.H. & Henderson, P.A. 2006. Species Diversity and Richness® Version IV. Pisces Conservation Limited, Lymington, England.

Shackleton, C.M. & Shackleton, S.E. 2006. Household wealth status and natural resource use in the Kat River valley, South Africa. *Ecological Economics* 57: 306-317.

Shackleton, C.M. 1996. Potential Stimulation of Local Rural Economies by Harvesting Secondary Products: A case study from the Transvaal Lowveld, South Africa. *Ambio* 25: 33-38.

Shackleton, C.M., Shackleton, S.E., & Cousins, B. 2001. The role of land-based strategies in rural livelihoods: the contribution of arable production, animal husbandry and natural resources harvesting in communal areas in South Africa. *Development Southern Africa* 18: 581-603.

Shackleton, C.M., Shackleton, S.E., Buiten, E. & Bird, N. 2007. The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa. *Forest Policy and Economics* 9: 558-577.

Shackleton, C.M., Shackleton, S.E., Ntshudu, M. & Ntzebeza, J. 2002a. The role and value of savanna non-timber forest products to rural households in the Kat valley, South Africa. *Journal of Tropical Forest Products* 8: 45-65.

Shackleton, S.E., Shackleton, C.M., Netshuluvhi, T.R., Geach, B.S., Balance, A. & Fairbanks, D.H. 2002b. Use patterns and value of savanna resources in the three rural villages in South Africa. *Economic Botany* 56: 581-604.

Sunderlin, W.D., Angelsen, A., Belcher, B., Burgers, P., Nasi, R., Santos, L. & Wunder, S. 2005. Livelihoods, forests and conservation in developing institutional and policy needs. *Forest Policy and Economics* 2: 333-353.

UBOS (Uganda Bureau of Statistics) 2000. National household census estimates 2000. (Retrieved on 17/11/2005 from http://www.ugandadish.org/nakasongola.doc, accessed on 17/11/2005).

USAID, Uganda 2005. http://www.usaid.gov/policy/budget/cbj2006/afr/ug.html accessed on 12/9/2006).

Velempini, P., Riddoch, I. & Batisani, N. 2003. Seed treatments for enhancing germination of wild Okra (*Corchorus otitorus*). *Exploration Agriculture* 39: 441-447.

Vietmeyer, N.D. 1986. Lesser-Known Plants of Potential Use in Agriculture and Forestry. *Science* 232: 1379-1384.

Wasswa, P. & Deogracious, O. 2006. The in-vitro ascaracidal activity of selected indigenous medicinal plants used in ethno-veterinary practices in Uganda. *African Journal of Complementary and Alternative Medicine* 3(2): 94-103.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFET/UNSO vegetation map of Africa. UNESCO Paris.

Wong, C., Roy, M., & Duraiappah, A.K. 2005. Connecting poverty and Ecosystem services. A series of seven country scoping studies: Focus on Uganda. Published for the United Nations Environment Programme by the International Institute for Sustainable Development (IISD). pp. 1-38.

World Bank, 2002. A Revised Forest Strategy for the World Bank Group. World Bank, Washington, DC. pp. 84.

World Bank, 2009. Environmental crisis or sustainable development opportunity?-transforming the charcoal sector in Tanzania, Policy Note, Sustainable Development, African Region, The World bank, Washington, DC.

Zahabu, E. 2001. Impact of charcoal extraction on the miombo woodlands: the case study of Kitulangalo area, Tanzania. Unpublished MSc. Dissertation, Sokoine University of Agriculture (SUA), Morogoro, Tanzania. pp. 106.

Appendix 1.Questionnaire on resources used by households living around and within a multiple land-use equatorial African savanna woodland, central Uganda.

A. Details of Respondent

1. Name of respondent
2. Sex: Male ( ), Female ( )
3. Age: Below 20 ( ), 20-30 ( ), 30-40 ( ), Above 40 ( )
4. Education level, No school ( ), Primary ( ), Secondary ( ), Above ( )
5. What is the size of your household? Males ( ) Females ( )
6. (i) Were you born in this place? Yes ( ) No ( )
   (ii) If no, which year did you settle in? Reason for settlement?
7. How many people/households were in this village in the past 16 years?
8. How long have you been in the charcoal business?

B. Charcoal Production

9. Preparation for charcoal production

(i) What stem size do you harvest for charcoal burning? ....

(ii) How much in terms of logs do you need to burn one standard bag of charcoal? No. of logs Cubic volume

(iii) What is the current cost of logs in the market? Ug shs.

(iv) How many people do you need to work on a single kiln?

(v) How many hours a day do you need to work on a single kiln? Hours ( ), Days ( )

(vi) What other materials are used in the production process apart from the logs?

(vii) What is the equipment used? (Tick), Panga ( ), Axe ( ), Hoe ( ), Others (specify)

(viii). How many do you own/use? Panga, , axe , hoe .

(ix) When did you buy the equipment?

(x) What were the costs involved? For panga , axe , hoe Ug. Shs.

(xi).Which mode of transport do you use and how far do you travel to collect charcoal from the kiln to the point of sale?

Means	Distance	Costs
By foot		
By bicycle		
By motorcycle		
By vehicle		
Others		

10. How much do you produce (quantities).

(i) Per day	
(ii) Per week	
(iii) Per month	
(iv) How many bags do you get per kiln	
(iii) How many kilograms in a single bag	

C. Consistence in production

11. How frequently do you produce charcoal	Tick	Quantity (bags)
Every day		
Once a week		
Twice a week		
Every second week		
Monthly		
Others		

12. Is the production consistent throughout the year? Yes (   ), No (   )

(i) If no, during which season do you produce more/less charcoal?

(ii) What are the reasons for such fluctuations?

(iii) Does demand and price for charcoal fluctuate with season? Yes (   ), No (   )

(iv) What is the price of an average bag (approx. 60kgs) of charcoal during low/high season? …../…Ug shs.

(v) During the season of low or no production what other income generating activity do you engage in? Any other business (Specify ….).

D. Consumption at household level

13. Do you use charcoal?

(a) If yes for what purposes? Cooking ( ), House heating ( ), other (specify) (   )

(b) What is the source of charcoal you use? I buy ( ), I produce (   )

(c) If you produce charcoal, for what purposes? Commercial (selling) ( ) Domestic use only ( ) or Both ( )?

(d) What is your source of trees/wood? Personal plantation ( ), Nearly woodland ( ), Public land ( )

(e) How much charcoal (weight in kg) is used daily in your household?/or by volume

A big bucket	
A small bucket	
How much did you give away as gift	

E. Income from charcoal production

14. How much do you get from selling a bag of charcoal   Ug Shs.

How many bags do you sell	Quantities
Per day	
Per week	
Per month	

F. Trend in costs

15. How has the price of charcoal changed over the past last five years? Increasing (   ), Decreasing (   )?

(i) If increasing/decreasing what might be the possible reasons for this?

G. Resource assessment

16. What species do you use frequently in charcoal production?

(i)
(ii)
(iii)
(iv)
(v)
(vi)

17. What are the main reasons for using these species? (Tick the appropriate answer)

(i) Easy to access	
(ii) It has always been traditionally used	
(iii) They are close to the village	
(iv) The common ones are depleted	
(v) Easy to cut	

18. Apart from charcoal production what are the other uses of the species mentioned in item 13?

Species	Uses

19.(a) What is your assessment of resource availability for charcoal production between now and the past ten years?

(i) Resource always available	
(ii) Species for good quality charcoal has disappeared	
(iii) Long distances are travelled to get resources	
(iv) Too many households now engaging in charcoal production as the result of scarcity of the resource	
(v) Too many people depending on charcoal in the area	

(b) Resource use: is it only for the residents or are there other commercial harvesters from neighbouring districts?

20. What species were previously used in charcoal production in the past ten years and what is their status?

Species	Present status
(i)	
(ii)	
(iii)	

H. Revenues

21. What are the revenues associated with charcoal business?

22. Do people living within the area (Nakasongola) benefit from charcoal business in terms of benefit gained from tax paid by charcoal business?

23. To what extent does charcoal production contribute to better living standards of local people?

I. Future prospects

24. What are the major opportunities for charcoal business?

25. What are the major threats to the business?

26. Is the charcoal business something worth doing? Yes ( ), No ( )

(i) If yes/no give the reasons

27. Woodland Resources Utilization

(i) General

(i) What type of woodland exists in your village or sub county? Plantation ( ), Traditional woodland ( )

(ii) Which one do you use? Give Reason

(iii) Are there any rules or laws governing the use of these woodlands?

(iv). Do you need a license/permit to utilize the woodland resource? Yes ( ) No ( )

(v) Do you pay for the product you get from the woodland? Yes ( ) No ( ).

If yes, for which product?

How much money do you pay for a particular product? Product……….(…..Ug. shs.)

(vi) Has the size of the woodland decreased ( ), remained the same ( ), Increased ( ) over the past 10, 5 years?

(vii) What uses or benefits does your household get from the woodland? Please list them and rank them according to their importance.

(ii) Specifics

J. Agriculture

a. Does your household practice agriculture? Yes ( ) No ( )

b. If yes, where? Around homestead ( ), Field away from the woodland ( ), In the woodland ( )

c. What type of crops do you cultivate? Cash crops ( ), Food crops ( ), Both ( )

d. If cash, which ones?

e. If food crops which ones?

f. What is the size of your farm? Less than 1acre ( ), About 1 acre ( ), 2 acres ( ), above ( )

g. What is the distance of your crop field from the homestead?

h. How long do you leave the land in fallow after harvest?

i. Do you own land? Yes ( ), No ( )

j. If yes what land tenure system? Mailo ( ), Free hold ( ), Customary ( ), Leasehold ( )

k. If no, why?

l. Where do you get land for expansion of your crop cultivation?

m. Has the amount of land available for crop cultivation, Increased ( ), Same ( ), Decreased ( ), No Idea ( ). Give reasons for your answer and give suggestions.

K. Timber

a. Do you harvest trees for timber? Yes ( ) No ( )

b. If yes, for what purpose? Commercial ( ) Own house construction ( ) Both ( )

c. What is your source of trees/wood for timber? Personal plantation ( ) Woodland ( ), Public land ( )

d. What tree species do you use and why?

Tree species	Rank	Reason for preference
1		
2		
3		
4		
5		

e. What stem diameter do you harvest for

(i) Commercial

(ii) House construction

f. How often do you harvest timber?

g. What distance do you walk to find them?

h. Has the amount or quality of harvestable tree species for commercial timber changed over the years? Increased ( ), Same ( ), Decreased ( ), No Idea ( ). Give reasons and suggestion.

L. Firewood

a. Do you harvest any trees/shrubs for firewood? Yes ( ) No ( )

b. If yes, for what purpose? Commercial ( ) Domestic use ( ) Both ( )

c. What part of the tree/shrub do you harvest?

d. What tree species do you harvest?

e. Can you please rank them in order of preference and give reasons why?

Species name	Part harvested	Rank	Reason for preference
1			
2			
3			
.			
.			
n			

f. What is your source of trees? Personal plantation ( ), Forest reserve ( ), Public land ( )

g. What distance do you walk to find them?

h. Has the amount or quantity change? Increased ( ) Decreased ( ) Remained the same ( ) No Idea ( ) over the past 15 years? Give the reasons and suggestions.

(i)

(ii)

(ii)

M. Management

(i). Which group of people manage the woodland in your village? Local Council [ ], Forest Department [ ], Clan leaders [ ], NGO [ ].

(ii). Are there any rules governing the use of the woodland resources (local council, central government)?

(iii). List all government rules you know regarding the protection of woodlands

(iv). What happens to a person if he/she breaks these rules?……………………

(v). Apart from the government Forest Department, which other institutions in the village have been active in protecting the woodland in your area?

(vi). Are there any people who are not residents of this village cutting trees in the woodlands? Yes [ ] No [ ]

(a) If yes for what purpose? (Timber, charcoal or fuel-wood)

(vii). Are the local people involved in woodland management? Yes [ ] No [ ]

(a) If yes, how?

Thank you for your cooperation.

CHAPTER 3

Land use and land cover changes (1984 – 2001) in a multiple land use equatorial African savanna, central Uganda

Abstract

Land cover changes in an African equatorial savanna were analysed from three Landsat satellite images (1984, 1995 and 2000/1) and associated field-based studies in 2006, with a view to assess the influence of human utilization on the woodland vegetation. Dense woodland cover decreased by 64% from 1984 to 2001, whereas, medium woodland cover increased by 31%, open woodland cover increased by 3%, and areas under cultivation/settlements increased by 80% from 1984 to 2001. This is attributed to significant spatial expansion in agriculture, charcoal production, grazing and settlements. If the landscape change continues to follow these trends of woodland loss and land degradation, woody species will be at higher risk of local extinction. These trends threaten the livelihoods of local communities who are entirely dependent on these natural resources. Therefore, sustainable management of woodlands in the area will require controlled harvesting of wood resources, the use of high recovery charcoal production methods, and creation of alternative sources of income for the local residents.

Key words: Change detection, charcoal production, Landsat imagery, land-tenure, livestock grazing, savanna woodland, subsistence agriculture.

Abbreviations: DEM- Digital elevation models, ISODATA- Iterative self-organizing data analysis, MEA- Millennium Ecosystem Assessment, RMSE-Root mean square error, SRTM-Shuttle radar topography mission, UTM- Universal transverse Mercator, WGS- World geodetic system.

1.0. Introduction

Savanna woodlands serve important ecological functions and provide wood and numerous non-wood products that contribute significantly to human well-being at local, national and global levels (Shackleton *et al.,* 2002; Luoga *et al.,* 2002; Dovie *et al.,* 2004; MEA, 2005a). With a large proportion of the human population in Sub-Saharan Africa depending almost entirely on natural resources (particularly savanna woodlands) for their livelihoods, there are increasing competing demands for their utilization, management and development, resulting in land use and land cover changes (Luoga *et al.,* 2005; Mwavu & Witkowski, 2008). Land use is defined as the manner in which human beings employ the land and its resources (e.g. for agriculture, grazing, logging, etc.), while land cover is the ecological state and physical appearance of the land surface (e.g. closed forests, woodlands or grasslands; Turner & Meyer, 1994; FAO, 1997; Brandon, 2001).

Land cover change is a dynamic, widespread and accelerating process, mainly driven by anthropogenic activities and natural phenomena, which in turn drive changes that impact ecosystems (Agarwal *et al.,* 2002; Liu *et al.,* 2003). Climate change and rapid human population growth are widely recognized proximate causes and driving forces of land degradation, desertification and species loss in many parts of the world (Githinji & Perrings, 1993; Vitousek, 1994; Thomas *et al.,* 2004; Geist & Lambin, 2004; Hulme, 2005; MEA, 2005a). Although the primary causes of land cover change worldwide is the way people use and manage land (Dale *et al.,* 2000; Gobin *et al.,* 2001), the causes of land cover changes cannot be generalized across regions of the world (Mwavu & Witkowski, 2008). For example, deforestation is a location specific problem, with the effects and magnitude of each identified factor differing between countries and regions (NRC, 1999).

Rapid human population growth has resulted in unsustainable use of resources by increasing consumption of natural resources and causing widespread loss of native land cover and ecosystem functioning (McKinney, 2001; Loucks *et al.,* 2008). Accompanying population growth is a dramatic increase in conversion of native vegetation to agricultural land, and this is a primary driver of global habitat loss (Wood *et al.,* 2000; Tilman *et al.,* 2001). Furthermore, economic development, and increasing consumption and production are some of the important indirect drivers of change in ecosystems and ecosystem services (MEA 2005b & c). The changes in land cover due to human and natural activities (Baker, 1992) can be observed and monitored using current and archived remotely sensed data at appropriate spatial, spectral and temporal resolutions (Singh, 1989; Hall *et al.,* 1991; Luong, 1993). Over the years, satellite imagery (including Landsat) has been used for land cover classification (Chuvieco, 1996; Mwavu & Witkowski, 2008), land use monitoring (Zerda, 1998) and assessment of desertification processes (Tucker *et al.,* 1991; González Sánchez & Calvo Herrero, 1994).

Uganda is a developing country with a largely agrarian economy, where over 90% of the human population rely heavily on natural resources for livelihood needs (NEMA, 1998), leading to varying impacts on its forests (Mwavu & Witkowski, 2008). However, little is known of the trends in land cover change and drivers of this change within Uganda's savanna woodlands. Yet, these savanna woodlands play an important role in the country's economy by providing energy, timber and non-timber products, employment, livelihood support, livestock grazing resources, land for subsistence crop cultivation, government revenues and business opportunities (Sankhayan & Hofstand, 2000, Namaalwa *et al.,* 2007). In Uganda, forests and savanna woodlands supply well over 90% of its energy requirements (Moyoni, 2001), with Kampala District alone using over 300,000 tons of charcoal annually (over 50% of the total national consumption; The Monitor, May 10-16, 2005). Most of it originates from savanna woodlands of Nakasongola and Luwero Districts, central Uganda. Although Uganda's savanna woodlands are of environmental and socio-economic importance, they are faced with serious management challenges. Hence, their sustainable management requires an evaluation of the magnitude, pattern, and type of land use/cover changes and the projection of the consequences of these changes to their conservation (Wu & Hobbs, 2002; FAO, 2004; MEA, 2005b). It is also important to precisely describe and classify land cover changes in order to define sustainable land use systems that are best suited for each place (FAO, 1998). Monitoring the locations and distributions of land cover changes is important for establishing links between policy decisions, regulatory actions and subsequent land use activities (Lunetta *et al.,* 2006). In this regard, there is a need to consider both the socio-economic environment (Brandt *et al.,* 1999; Baudry *et al.,* 1999; Lambin *et al.,* 1999; Pfund *et al.,* 2006; Giannecchini *et al.,* 2007; Mwavu & Witkowski, 2008) and other environmental factors. This study analysed land cover change between 1984 and 2000/1 and carried out additional field work to attribute the observed land cover changes to specific land use practices that have changed over time within the savannas of Nakasongola District, central Uganda, to assess the influence of human utilization of the woodland vegetation.

2.0. Methods

2.1. Study area

The study focused on households and the surrounding multiple land use savanna woodlands of Nakasongola District, south of Lake Kyoga, central Uganda ($0^0$40′- $1^0$41′ N, $31^0$57′ - $32^0$48′ E). The District covers about 3,424 km^2, most of which is woodland and grassy savanna, with 322 km^2 (10%) of open water and wetlands. It comprises eight sub-counties (administrative sub-divisions), namely Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata. Each sub-county has a mean (± S.E.) of 49 (± 22) villages and 3,193 ± 390 households. The mean number of households/village was 82 (± 32), with an average of seven persons/household. The district has a total human population of 128,126 (41 people/km^2) (2000 National Housing Census), with 50.2% males and 49.8% females. About 95.3% of the population are rural and 4.7% urban (Uganda Bureau of Statistics, 2002).

Mean annual rainfall ranges from 500 – 1000 mm and is concentrated into two wet seasons (March to May and August to November), but rainfall received and reliability is higher in the south, declining gradually to the north. The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C, respectively. The topography of the area undulates between 1,036 and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al.,* 1967).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964), a natural savanna woodland or woodland of mixed deciduous trees 3 to 12 m high and grasses 0.3 to 1.3 m high at maturity. However, the cover of the grass layer varies with season, is often patchy and subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirki*i subsp. *mildbraedii, A. senegal,* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983).

The major human livelihood activities are charcoal production (engaging about 70 to 80% of the total households), livestock keeping, fishing (close to Lake Kyoga), and subsistence agriculture. Subsistence agriculture accounts for about 85% of household food supply and more than 50% of monetary income (DEP, 2002). Hence, the major land use practices over the whole district are (a) charcoal production (b) cattle grazing and (c) subsistence crop cultivation (Figure 1).

2.2. Land cover classification and change analysis

To detect changes in land cover, at least two time-period data sets are required (Jenson, 1986). Land cover changes, specifically the loss in woodland extent, were assessed using ortho-rectified five multi-temporal Landsat satellite images acquired from three dates (1984, 1995, and 2000/1). The Landsat images were used to map vegetation change in order to understand the spatial variability and trends in land cover change. For each date, two Landsat images from the dry and rainy seasons were acquired in order to classify land cover and to distinguish wet and dry areas, lowland areas, and green areas between different seasons (Table 1).

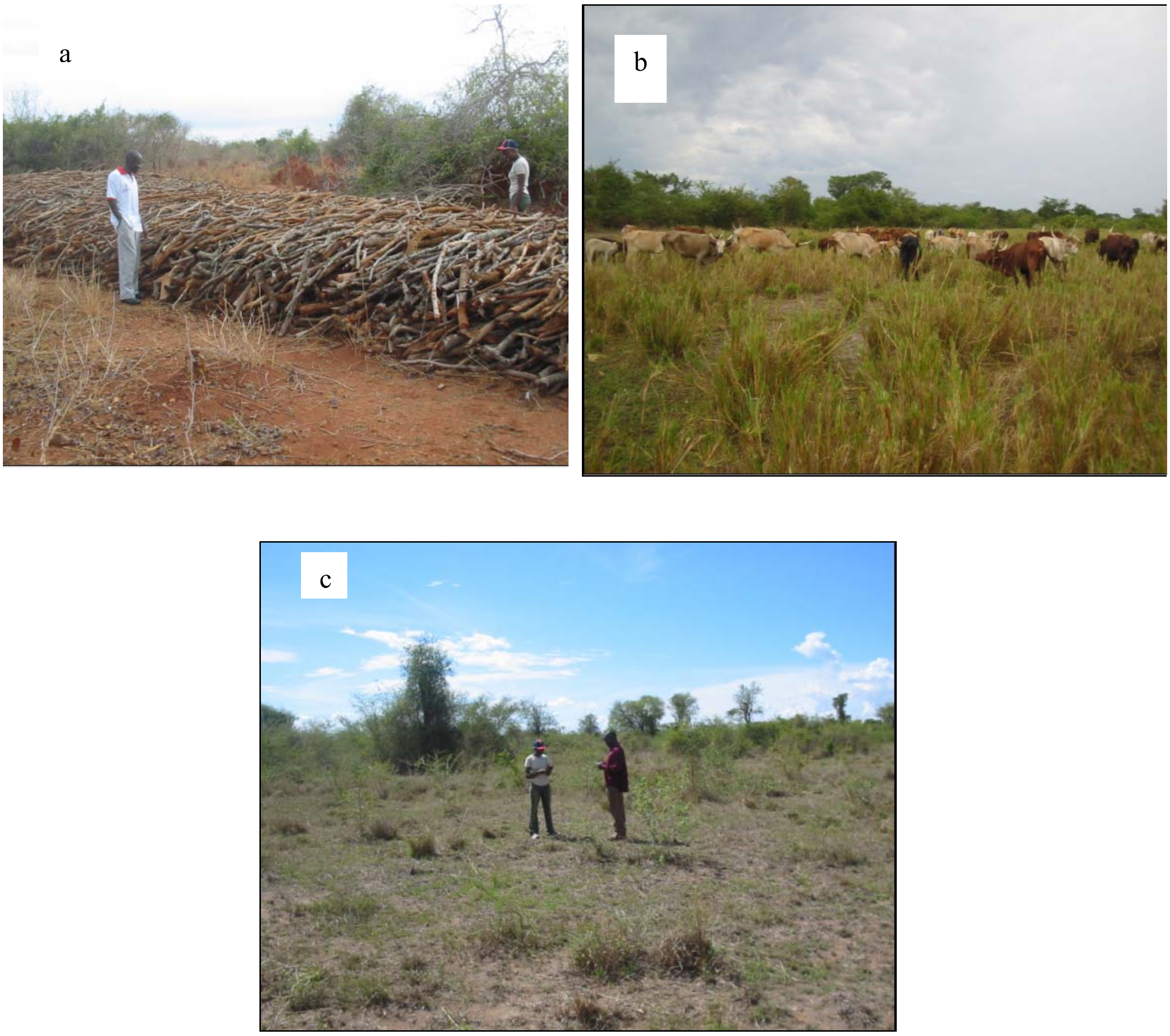


Figure 1. Plates showing the major land use practices: (a) wood stacked in preparation for charcoal production, (b) cattle grazing in a wetland, and (c) cultivation fallow, in a multiple land use equatorial African savanna, central Uganda.

Table 1: List of satellite imagery data used to study the land cover of a multiple land use equatorial African savanna, central Uganda.

Satellite	**Path/row**	**Acquisition date**	**Season**	**RMSE**
EarthSAT US	171-059	27-Nov-01	Dry season	Nil
EarthSAT US	172-059	23-May-00	Rainy season	Nil
USGS data archives	171-059	03-Jan-95	Dry season	0.79
USGS data archives	172-059	27-Feb-95	Rainy season	0.30
USGS data archives	171-059	01-Sep-84	Rainy season	0.72
USGS data archives	172-059	20-Jun-84	Towards dry season	0.38

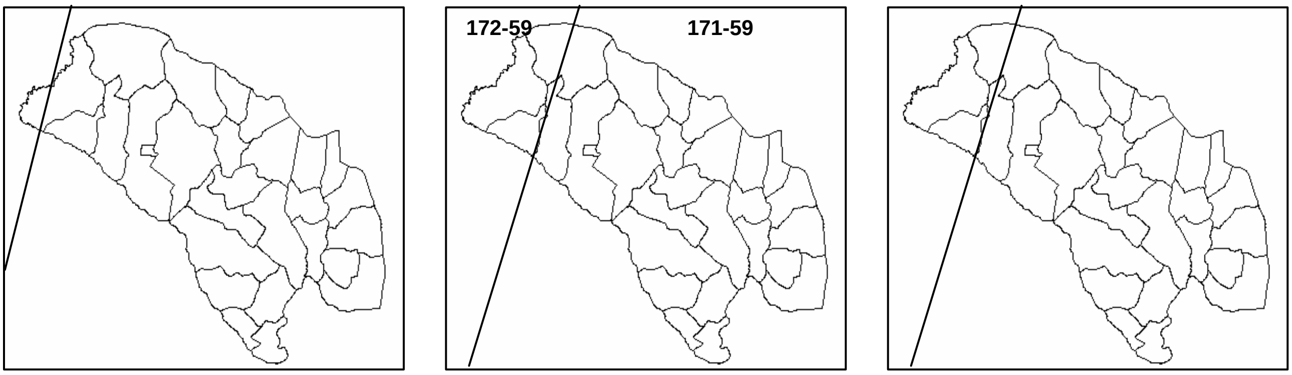
All images were precision ortho-corrected to a sub-pixel accuracy using an image to image ortho-rectification with the 2000/1 EarthSAT ortho-imagery and the Shuttle Radar Topography Mission (SRTM) (90 m, pixel size) digital elevation models (DEM) for geographical reference. Final root mean square errors (RMSE; in pixel units) for each ortho-correction process are shown in Table 1. The final ortho-corrected imagery was input as 28.5 m pixels in UTM (zone 36 North) coordinate system and the WGS1984 global datum.

2.2.1. Image classification

The land cover classification was generated for each assessment period using both standard unsupervised Iterative Self-Organizing Data Analysis Technique (ISODATA) algorithm clustering procedure and supervised classification approach. ISODATA is a standard unsupervised classification procedure in ERDAS-IMAGINE 8.7® remote sensing image processing software. In this procedure, the required land cover type classes were identified and delineated on the basis of amalgamation of suitable spectral classes into the 14 land cover classes which included: (1) cultivated (fallow), settlement and / or disturbed areas (i.e. no or little surface vegetation), (2) cultivated fields with crop cover evident, (3) – (4) exotic timber plantations, (5) open water, (6) wetlands (floating vegetation), (7) hydromorphic grasslands (also know as *vlei grasslands, dambos, fadamas,* etc.), (8) dense woodland, (9) medium woodland, (10) open woodland, (11) grassland (primarily around periphery of wetland grasslands), (12) cloud cover, (13) cloud shadow cover, and (14) natural bare ground (primarily on local hills). All information classes, with the exception of the hydromorphic grassland class, were defined solely on the basis of seasonal spectral characteristics. Delineation of the hydromorphic grasslands was completed by first creating a DEM-defined model of all possible inundation areas to a depth of 2 m. This theoretical 2 m flooding extent was then used as a geographical mask within which an additional iso-clustering classification was undertaken, in order to further exclude any forest/dense woodland areas that were erroneously included due to the generalized nature of the DEM data. The final corrected hydromorphic grassland extent was then used as a standard class-extent mask in all assessment periods, based on the assumption that the effect of these wetlands would be static over time, and would not contain any major woodland resources.

All land-cover mapping was first completed on the larger extent of the 171-59 imagery, and then extrapolated to the outstanding areas within the adjacent 172-59 imagery (Figure 2), using reference landscape features (e.g. key woodland areas) evident in the overlap zone. A similar approach was used to ensure comparable interpretation and delineation of woodland/grass sub-class boundaries between assessment years. Time-dependent stable woodland features, with obvious static boundary characteristics, were matched in terms of class codes and spectral class groupings in all images, whilst allowing for all other areas to be coded according to the extrapolation of such characteristics across the full study area. The specific approach taken was to first map and delineate the dense woodland and open grassland classes, as two extremes of the defined woodland cover gradient, and then "*fill-in*" the remaining areas with the medium woodland and/or open woodland classes according to the interpretation of local conditions. The raster calculator in ARCMAP® version 9.0 (Sawatzky *et al.,*

2004) was used to calculate the changes in woodland cover in the studied area (i.e. areas that persisted with dense, medium, or open woodland throughout 1984, 1995 and 2000/1).



1984 1995 2000/1

Figure 2. Illustrations of the geographical boundaries between two Landsat images (171-59 and 172-59) used to map the land cover at each time period (1984, 1995 and 2000/1).

2.2.2. Classification accuracy assessment

Historical images could not be ground-truthed, but since stable spectral features were used in the classification, we assume that the classification was accurate enough for a reasonable comparison. In this study, 135 points, of which 75 sampling plots were for vegetation assessment (Chapter 4), and 60 ground-truthed GPS points from representative homogenous patches of a specific land cover type [(i.e. (a) cultivated, disturbed and settlement, (b) woodlots, (c) aquatic wetlands, (d) hydromorphic grassland, (e) dense, (f) medium, (g) open woodlands, (h) grassland (wetland periphery) and (i) natural bare ground)] were related to what was classified on the images. The image used in the assessment is the 2000/1 and only nine classes were included in the final assessment (i.e. class 1: cultivated, disturbed and settlements; class 4: woodlots; class 6: aquatic wetlands; class 7: hydromorphic grassland; class 8: dense woodland; class 9: medium woodland; class 10: open woodland; class 11: grassland (wetland periphery); and class 14: natural bare ground). Classes 12: clouds; 13: cloud cover; and 5: water were not included. Finally class 2: cultivated only, and class 3: settlements only, were combined into class 1: cultivated, disturbed and settlements, because on the ground these classes were not exclusively separate, the patches of cropland occurred in close proximity to human settlements.

Of the 135 points, 46 were in cultivated, disturbed and settlement, 3 in woodlots, 3 in aquatic wetlands, 15 in hydromorphic grassland, 3 in dense woodland, 16 in medium woodland, 42 in open woodland, 6 in grassland (wetland periphery) and 1 in natural bare ground. The 60 ground truthing points were selected randomly; but aided by physical accessibility. The 75 vegetation plots were selected based on the major land use types of the study area (charcoal production, cultivation and grazing), 24 plots were assessed in both the charcoal production and cultivation land use types and 27 plots in grazing land use. An accuracy assessment of the land cover was conducted for the classified imagery based on how well the image-based classification matched observations at sample points. An error matrix (contingency table) for the classified image was generated using field data (ground truthing points). Using the error matrix, overall accuracy and conditional Kappa (K_i) were calculated. Classification accuracy of the whole image was determined by using the Kappa index that accounts for chance agreement between the classes represented in the image and on the ground (Foody, 2002). K_i provides an individual measure of agreement for each class represented in the classified image (Hudson & Ramm, 1987). Generally, K_i values greater than 0 indicate better than chance agreement, and values near to 1.0 are approaching perfect agreement. Previous uses of K_i suggested values ≥ 0.4 indicated good to excellent agreement (Fitzgerald & Lees, 1994).

Liu *et al.* (2007) recommended that user's and producer's accuracies and the overall accuracy should be provided as primary accuracy measurements. Therefore, user's and producer's accuracies were determined for the classified images. Producer's accuracy indicates the probability of a reference pixel being correctly classified (Liu *et al.,* 2007), is related to error of Omission because error of Omission occurs when an area is excluded from a category that it does belong to (Congalton, 1991). Therefore, producer's accuracy for different classes is expressed as 100 minus % omission error. The user's accuracy is indicative of the probability that a pixel classified on the map actually represents that category on the ground (Liu *et al.,* 2007). This is related to error of Commission which occurs when an area is included in a category it does not belong to (Congalton, 1991). Therefore, user's accuracy for different classes is expressed as 100 minus % commission error.

2.3. Drivers of land cover change

The history of land use and causes of land cover change in the eight sub-counties within the study area from 1984 to 2006 were obtained through field observations and interviews. For example, observations were made of standing trees and harvested stumps within vegetation sampling plots, and enumerated to give an indication of whether the area was dense, medium or open woodland. Interviews with households and key informants living around and within the woodlands were also conducted. Households interviewed were selected systematically in order to obtain a representative sample in terms of ethnicity, wealth, gender and age classes. Forty five (45) respondents/resource users (charcoal producers, livestock keepers and peasant farmers) from the eight sub-counties (five to six in each) were interviewed. In addition, three key informants (i.e. the District Resource Officer, District Environmental Officer and District Livestock Officer) were interviewed, and all the responses recorded verbatim. Key informant interviews were used to obtain information that would assist in clarifying or improving the understanding of particular issues of concern that were raised in the household interviews. The interviews were carried out on an individual basis to minimise peer influence and improve the quality of data (Phillips & Gentry, 1993). Interview questions generally focused on changes in resource use and availability, causes of woodland loss or change, and income generating activities. Human population data for the surrounding villages were obtained from the

2002 National Household Census (Uganda Bureau of Statistics, 2002) and utilized to give an indication of the gender, family size, livelihoods and employment situation in the district. Data from the interviews were analysed using both descriptive and inferential statistics (Chapter 2).

3.0. Results

3.1. Land cover change

The land cover classification clearly identified mixed woodland, hydromorphic grassland and cropland as the dominant land cover types, although the relative coverage varied between sites and years (Figures 4a, b and c, Table 3). The overall accuracy of the land cover maps was 93% for 1984 and 94% for both 1995 and 2000/1, with the mapping errors of 6 - 7%. The overall accuracy of the classification was 60%, with a Kappa index of 0.5. The conditional Kappa values (K_i) for the individual classes ranged from 0.209 to 1, with woodlot and natural bare ground having perfect agreement, and four classes having greater than 0.4 values indicating excellent agreement, however three classes had < 0.4 but > 0 indicating better than chance agreement (Table 2). Most of the errors in the matrix were due to misclassification of the following classes: (a) medium woodland, (b) aquatic wetlands, (c) dense woodland, (d) open woodland and (e) cultivated, disturbed and settlement (Table 2, Figure 3). The misclassification frequencies ranged from 0.02 to 0.33, most often within (a) woodlands and (b) cultivated, disturbed and settlement classes (Figure 3). Although there were some misclassifications, generally, the results show an acceptable trend as more land is continuously cleared for cultivation, settlements and infrastructure over time. Hence, the change from closed woodland to medium or open and/or to cultivated, disturbed and settlement, or to grassland were expected or acceptable. Generally, most of the misclassifications in this study were due to: (i) difference in time between the last image (2001) used and when the ground truthing was carried out (2006), which accounted for 30 misclassified points, consequently land cover changes over time due to land use practices taking place (ii) edge effects as the ground-truthing points could fall either one pixel away from the classified class, or in two pixels representing two different classes on the Landsat image, and this accounted for 17 misclassified points. Low accuracy in dense woodland was the result of 3 points that were classified as dense woodland, which were observed to be medium and open woodland, the misclassification is due to the difference in time of the image used and the time when ground truthing were carried out. Similarly the low accuracy in medium woodland class was due to this variation in time. Two points were observed as open woodland and 1 point as cultivated, disturbed and settlement, however, they were classified as medium woodland. In addition, 3 points were observed to be dense woodland due to edge effect. Six points classified as open woodland were observed to be cultivated, disturbed and settlement and 1 point as grassland (wetland periphery). The misclassification was due to the difference in time of the image used and the time when ground truthing were carried out. In addition, 1 point classified as open woodland was observed as aquatic wetland, 2 points as hydromorphic grassland, 2 as dense woodland and 11 as medium woodland, and these points were misclassified due to edge effects. Twenty points classified as cultivated, disturbed and settlement were observed as: 2 points as aquatic wetland, 2 as hydromorphic grassland, 10 as medium woodland, 5 as open woodland and 1 as grassland, and the misclassification were all due to edge effect (Table 2, Figure 3).

Table 2. Producer's and user's accuracies and conditional Kappa (K_i) for land cover types in a multiple land use equatorial African savanna, central Uganda, based on Landsat image 2000/2001.

Class	**Accuracy (%)**		**Conditional Kappa (K_i)**	**Class names**
	Producer's	**User's**		
Class 1	57	77	0.642	Cultivated, disturbed and settlement
Class 4	100	100	1	Woodlots
Class 6	67	33	0.318	Aquatic wetlands
Class 7	80	75	0.718	Hydromorphic grassland
Class 8	100	38	0.361	Dense woodland
Class 9	63	30	0.209	Medium woodland
Class 10	45	70	0.568	Open woodland
Class 11	83	71	0.701	Grassland (wetland periphery)
Class 14	100	100	1	Natural bare ground

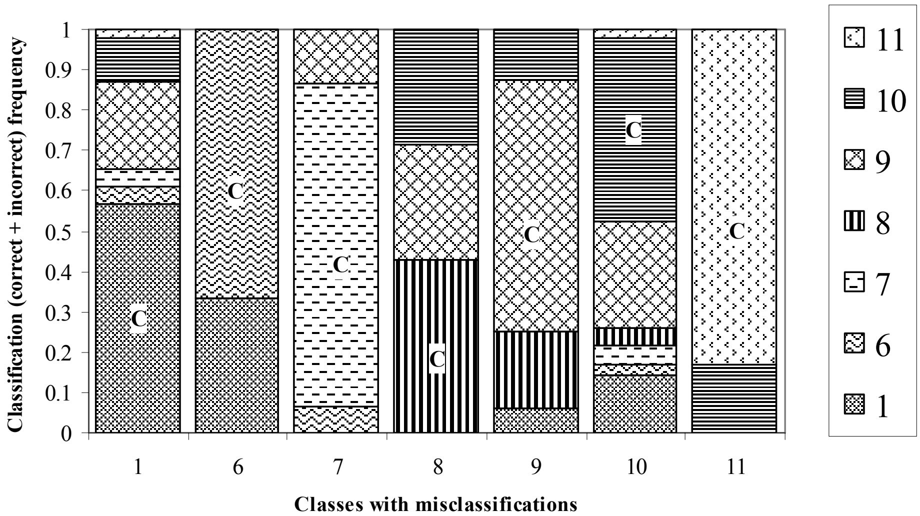


Figure 3: The frequencies of classification (correct + incorrect) of the classes with misclassifications in a multiple land use equatorial African savanna, central Uganda. Classes: 1 = cultivated, disturbed and settlement, 6 = aquatic wetlands, 7 = hydromorphic grassland, 8 = dense, 9 = medium, 10 = open woodlands and 11 = grassland (wetland periphery) (**C**: represents correctly classified frequency of a given class).

Trends in woodland cover change in the study area indicated severe reduction for the study period 1984-2001 (Table 3, Figure 5). Over the years, the dense and medium woodlands, have changed into open woodland and most of them into cultivated, disturbed and settlement areas (Figures 4a,b,c; Figure 5). The area under dense woodland cover decreased from 63,488 ha in 1984, to 30,419 ha in

1995 and to 22,836 ha in 2000/2001 (Table 3, Figure 5), hence a total loss of 64% for the 17 year period. Medium woodland cover decreased from 78,517 ha in 1984 to 75,062 ha in 1995, and increased to 102,540 ha in 2000/1, indicating a 31% overall increase between 1984 and 2000/1 (Table 3). Similarly, open woodland cover increased from 48,876 ha in 1984 to 85,906 ha in 1995, but decreased to 50,237 ha in 2000/2001. Hence, there was an overall 3% increase in open woodland cover between 1984 and 2000/1 (Table 3). There was also a noticeable increase in cultivated, disturbed and settlement land, rising from 21,434 ha in 1984 to 38,478 ha in 2000/1, an 80% increase (Table 3). Mixed open woodland, shrubs and grassland patches occurred in close proximity to patches of cropland and human settlement, indicating that those were patches of high disturbance. Bare ground increased by 232% from 1984 to 2000/2001 (Table 3). The increase in cultivated, disturbed and settlement and bare ground land cover types generally imply a decrease in woodland cover, this was the assumed direction of changes. Based on assumed direction, we would expect to have woodland cover in 1984 decreasing towards 2000/2001.Contrarily, Figure 5 showed the absence of woodland in 1984 and 2000/2001, meaning woodland was only present in 1995, and absence of woodland in 1984 and 1995 woodland only present in 2000/2001. This means that other land covers, for example, cultivated, disturbed and settlements, hydromorphic grassland or open woodland are becoming dense woodland, these changes are the reverse of the assumed/predicted direction; these are mapping errors indicated in Figure 5. With global trend towards tree densification in rangelands and savanna the assumption of open woodland becoming dense woodland would have been possible. In Nakasongola woodland, this assumption is not realistic as the rate of harvesting of trees for charcoal production, firewood and poles exceed the rate of regeneration. The trees are harvested continuously, and there is no enough time for regenerated trees to attain maturity. However, 12,413 ha (20%) of dense woodland, 21,345 ha (27%) of medium and 8,732 ha (17%) of open woodland cover persisted throughout 1984 to 2000/2001 (Table 4), which is quite low compared to the hectares of woodland lost (Figure 5). These are the areas indicated as woodland all years (i.e. closed, medium and open) on the woodland cover change map (Figure 5).

Table 3. Changes in land cover types in a multiple land use equatorial African savanna, central Uganda, over a 17 year period between 1984 and 2000/2001 as determined from Landsat images of 1984, 1995 and 2000/2001.

Land cover class	**Area (ha)**			**Area loss (-) or increase (+) (%)***		
	1984	**1995**	**2000/1**	**1984-1995**	**1995-2000/1**	**1984-2000/1**
Cultivated, disturbed and settlement	21,434	23,785	38,478	11^{+}	62^{+}	80^{+}
Cultivated only	1,961	1,464	2,651	25^{-}	81^{+}	35^{+}
Woodlots	952	1,439	1,126	51^{+}	22^{-}	18^{+}
Hydro-grassland-general	72,787	74,331	73,559	2^{+}	1^{-}	1^{+}
Dense woodland	63,488	30,419	22,836	52.1^{-}	25^{-}	64^{-}
Medium woodland	78,517	75,062	102,540	4.4^{-}	37^{+}	31^{+}
Open woodland	48,876	85,906	50,237	76^{+}	42^{-}	3^{+}
Natural bare ground	130	267	431	105^{+}	61^{+}	232^{+}
Total area (ha)	288,145	292,673	291,858			

*The percent loss or increases are calculated from the previous year.

Table 4. Land cover (ha) that persisted with dense, medium and open woodland cover in a multiple land use equatorial African savanna, central Uganda throughout 1984, 1995 and 2000/2001.

1984	**1995**	**2000/1**	**Area that persisted (1984-2001)**	
			Area (ha)	**Percentage**
Dense	Dense	Dense	12,413	20
Medium	Medium	Medium	21,345	27
Open	Open	Open	8,732	17

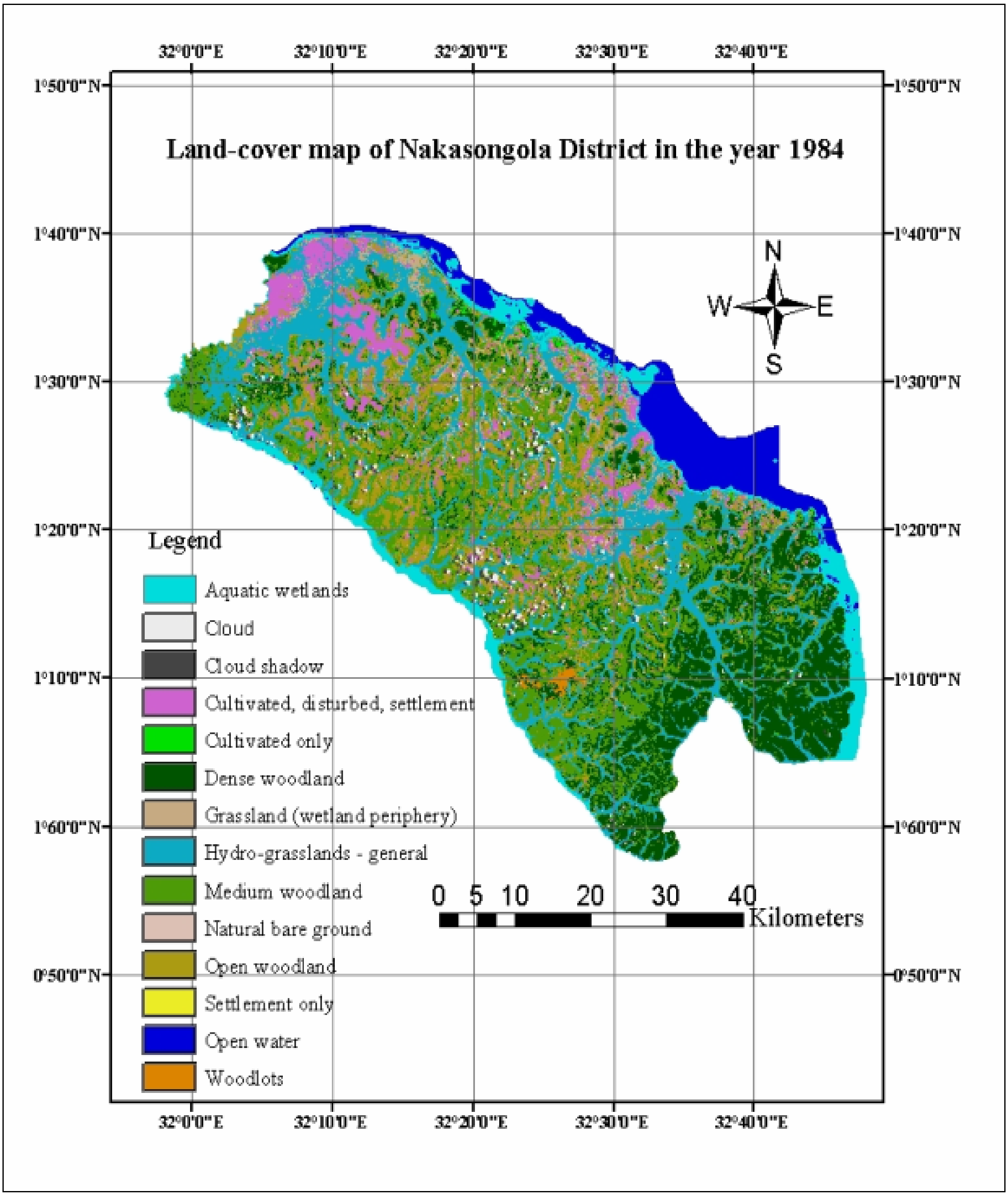


Figure 4a. Land cover types of a multiple land use equatorial African savanna, central Uganda in the year 1984.

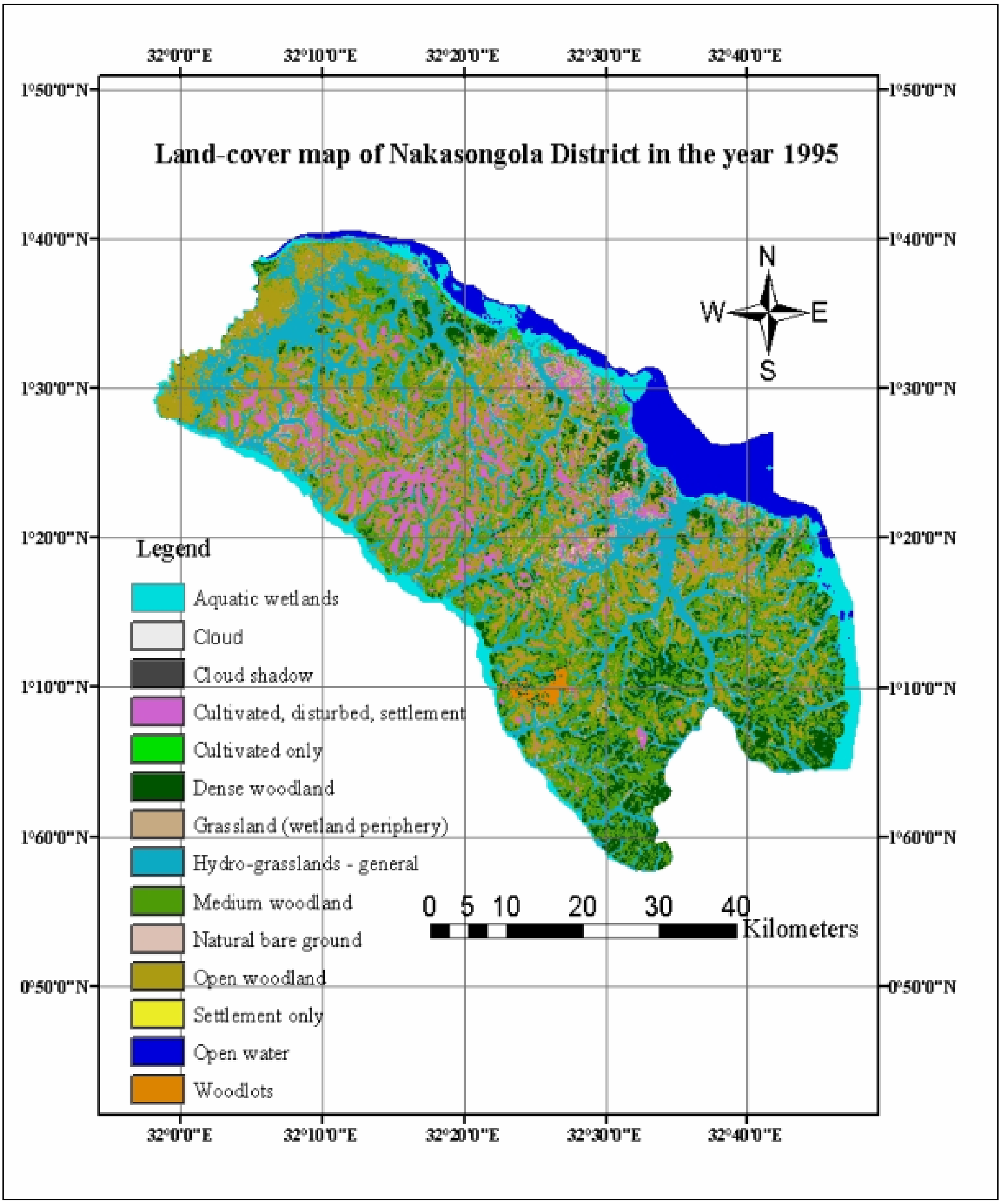


Figure 4b. Land cover types of a multiple land use equatorial African savanna, central Uganda in the year 1995.

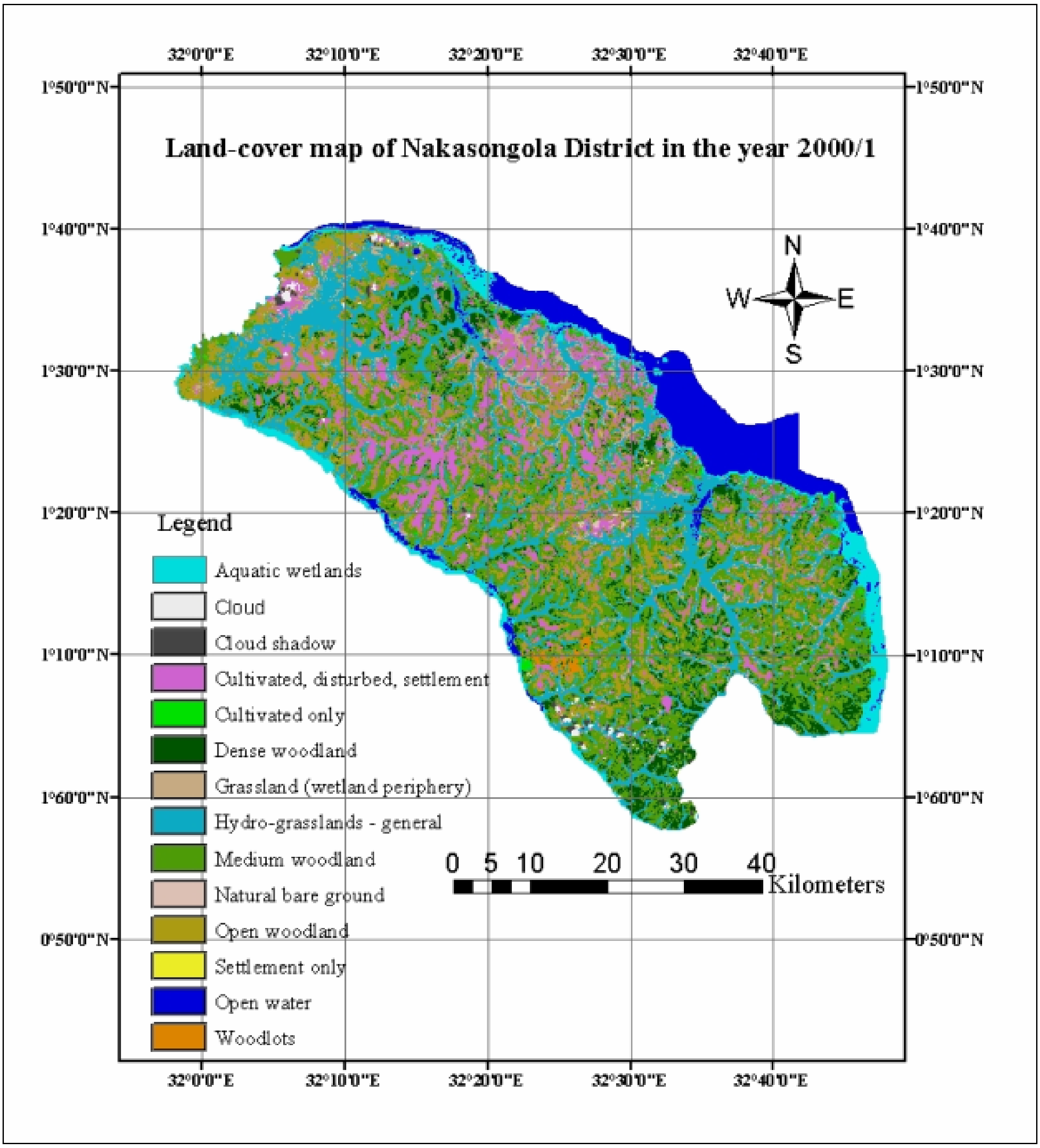


Figure 4c. Land cover types of a multiple land use equatorial African savanna, central Uganda in the year 2000/2001.

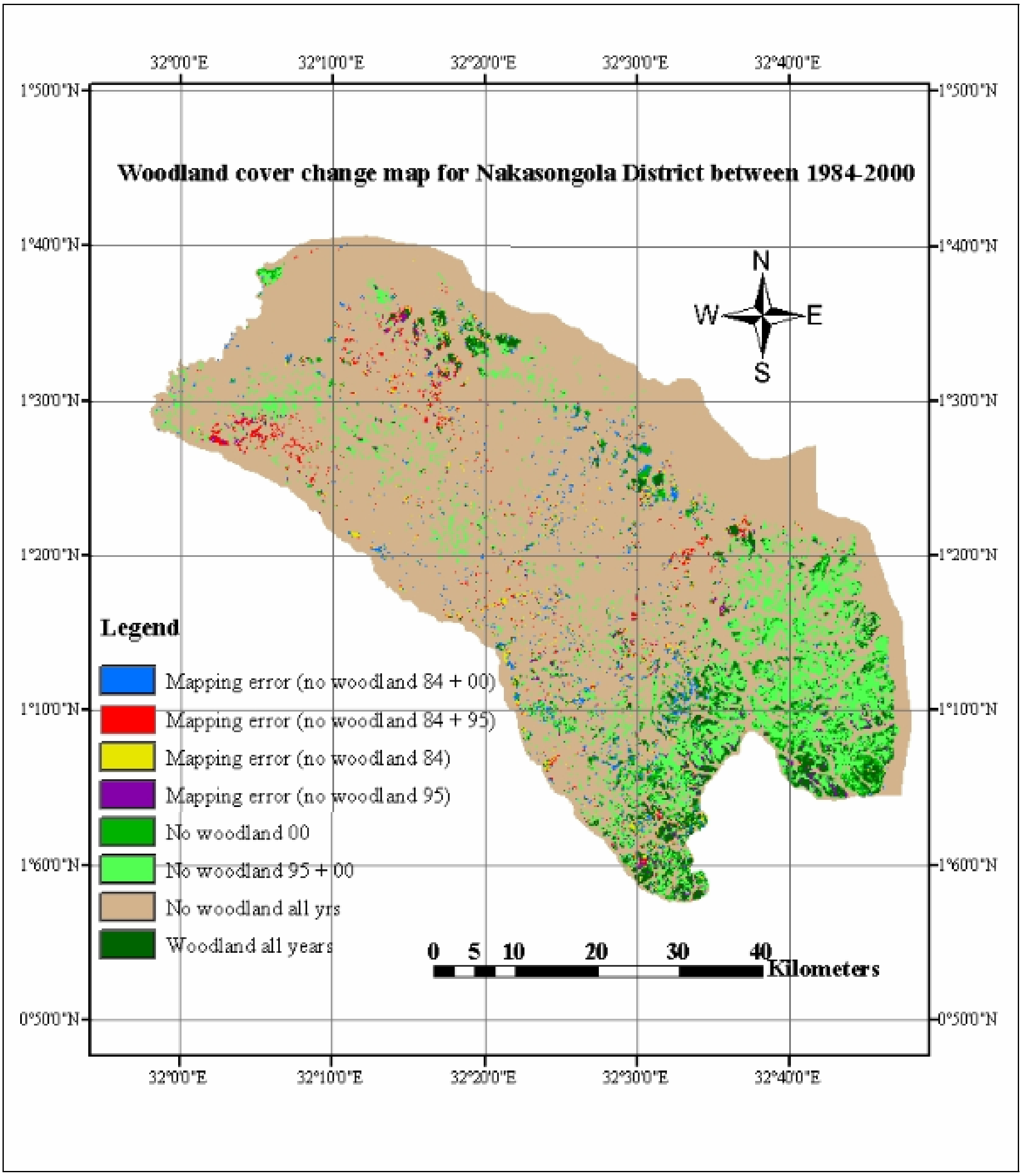


Figure 5. Woodland cover change map for a multiple land use equatorial African savanna, central Uganda over a 17 year period between 1984 and 2000/2001.

3.2. Socio-economic issues acting as drivers/causes of land cover change

Both the households/resource users and Key Informants concurred that the savanna woodlands have been rapidly decreasing in cover and tree density due to unsustainable harvesting. This corroborates the change analysis results (Table 3, Figure 5). All respondents cited uncontrolled harvesting of trees and shrubs for charcoal production, overgrazing and clearing woody vegetation for establishing/rehabilitating farms/ranches, expanding shifting crop cultivation, unplanned seasonal bush fires and insecure land use tenure systems as the major drivers of dense woodland cover loss in the district. The detailed data analysis and results on how each of these driver causes land cover change are fully explained in Chapter 2. The respondents also revealed that prior to 2006, dense and medium woodlands mainly persisted in forest reserves and some other areas that were under the protection of government agencies (e.g. the National Forestry Authority). They further stated that the three major land use practices in the district are charcoal production, shifting crop cultivation and livestock grazing. However, there is a succession of land use change over time, which is typical of areas subject to slash and burn agriculture. Areas used for charcoal production are then used for cultivation, while cultivated areas may subsequently be used for grazing; the difference is in intensity and frequency from one area to another. Moreover, most of the grazing lands occur on hydromorphic grasslands, which are only suitable for grazing.

4.0. Discussion

4.1. Land cover change

The Landsat imagery analyses clearly showed woodland to grassland vegetation transition, with significant losses of dense woodland cover, and increases in open woodland, grassland and settlement land cover types. Although there were some misclassifications in some classes, the classification accuracy of 60%, and with the Kappa Index of > 0.5 recorded in this study, it can be relied upon to predict future trends in land cover changes in the area. A Kappa index of 0.5 is within the acceptable range, indicating that the classification was sufficient for the evaluation of land cover changes (Wulder *et al.,* 2006). The accurate assessment of several recently completed regional-scale land cover mapping projects indicate that producer's accuracies are stabilizing in the 50 to 70% range, independent of level of taxonomic detail or methodological approaches (Edwards *et al.,* 1998; Zhu *et al.,* 2000; Ma *et al.,* 2001; Wulder *et al.,* 2006). In this study, most of the misclassifications were realistic, because most of them followed the hypothesized trend of woodland cover decreasing from dense to medium to open woodland and also to cultivated, disturbed and settlement areas. Furthermore, the misclassification resulted from a mismatch between the ground truthing points of 2006 with the classified Landsat image of 2000/1 used, because of the time differences and the accompanying land cover changes. Individual class accuracies for cultivation, disturbed and settlement, woodlots, hydromorphic grassland, grassland (wetland periphery), open woodland and natural bare ground with conditional Kappa values ranging from 0.56 to 1, were all above 0.4 indicating excellent agreement, i.e. these land cover classes were effectively represented. Aquatic wetland, dense woodland, and medium woodland had low accuracy values with conditional Kappa ranging from 0.209 to 0.318. However, these classes had less than 0.4 and > 0 K_i values, indicating better than chance agreement. The low user's accuracy of 33% in aquatic wetland class compared to 67% producer's accuracy might have been due to edge effect and changes of land use practices over time. In addition, the low accuracy in medium and dense woodlands with user's accuracy of 30 and

38% compared to producer's accuracy of 63 and 100%, respectively, was due to the change that had occurred especially in woodland cover as a result of changes in land use practices taking place over time, especially conversion of woodland into crop fields, clearing land for settlements and infrastructure and harvesting woody plants for charcoal production, firewood and poles (Chapter 2). The 135 points used in this study compare with 132 points used by Waite *et al.* (2009) in evaluating if land cover change within a newly protected area signalled human-driven ecological degradation in Rajasthan, India. However, other land cover change analyses studies (e.g. Mwavu & Witkowski 2008; Kamusoko & Aniya, 2007) used 42 and 40-45 ground truthed GPS points. Many authors recommend 30 to 50 samples per class (e.g. Goodchild *et al.,* 1994; Wulder *et al.,* 2006). In this study, cultivated, disturbed and settlement areas, and open woodland classes attained the recommended sample per class. However, dense and medium woodland, hydromorphic grassland, aquatic wetland, grassland (wetland periphery) and woodlots did not attain the recommended sample per class but they were well represented. This corroborates the conditional Kappa, with the exception of dense and medium woodlands with low conditional Kappa. However, the results were realistic because they followed the predicted trend of reduction in woodland cover and an increase in cultivated, disturbed and settlement areas.

The study area experienced a relatively high loss of woodlands and an increase in land degradation during the 17 year study period. The study period overlapped with the 1990-2005 period when Uganda reportedly lost about 24.7% of its forest and woodland habitat (NEMA, 2007). On the other hand, the 76% increase of open woodland between 1984 and 1995 overlapped with a period of road network development and improvement in the District, probably facilitating settlement establishment and the charcoal production business in previously inaccessible areas. In addition, the district has a reliable road network linking it to various urban centres including Kampala City and Luwero in the south and Masindi in the west, whose residents highly depend on biomass energy. Moreover, road infrastructure plays a crucial role in deforestation by providing access to previously inaccessible forest areas, facilitating illegal harvesting of timber and non-timber products (Bryant *et al.,* 1997; MEA, 2005b; Mwavu & Witkowski, 2008).

The high rates of woodland vegetation loss of about 64% over the 17 year study period suggests a lack of sustainable resource management practices, which is common in many African woodlands (Letsela *et al.,* 2002; Dovie *et al.,* 2004; Luoga *et al.,* 2005; MEA 2005a; Mwavu & Witkowski, 2008). Since 1980, Uganda has witnessed disturbances and pressures on land use and natural resource management institutions, including: (a) the civil war period (1980-1985), (b) the economic recovery from 1986 and then (c) the decentralization system of governance through the enactment of the Local Government Act of 1997. The economic recovery has driven urban population growth and higher demands for timber, fuelwood, charcoal, and food crops; while the decentralized system of governance has transferred the powers for natural resource management to local governments (i.e.

Districts). Yet, at the local level, the need to access resources to alleviate poverty outweighs the desire to sustainably manage and conserve natural resources, while political interests outweigh the need to follow the approved laws and regulations (Mwavu & Witkowski, 2008). For example, in a bid to raise income, the local authorities of Nakasongola District issue licences to people wishing to produce charcoal, without any clear guidelines on where, when and how much woody biomass should be harvested seasonally or annually. When local governments in the past have attempted to influence natural resource conservation, the social and environmental outcomes have not always been positive, due to conflicts of interest among the sectors (Bazaara, 2003) and corruption by local government officials (Banana *et al.,* 2007; Mwavu & Witkowski, 2008). Moreover, in areas like Nakasongola District where demand for natural resources to sustain livelihoods is acute, voting decisions are based on the perceived ability of the aspiring politicians to help local people (voters) access resources to increase their income (Bazaara, 2003) and, thus, exacerbating the problem. Although, there has been increasing decline and loss of woodlands in the study area, some areas with dense woodlands representative of the original vegetation cover still exist. For example, in places under the jurisdiction of the Uganda Military and the National Forestry Authority, where local communities' use is restricted, disturbances have been minimal. This suggests that with restricted access and controlled use, hence minimal disturbance, some of the woodlands in the area can be maintained.

4.2. Socio-economic drivers of land cover changes

The interview results corroborate the Landsat imagery analyses, indicating a decrease in woodland cover attributed to the ever increasing woody plant harvesting, shifting crop cultivation and land clearing for the establishment of ranches, settlements and other infrastructure. Indeed, the major anthropogenic causes of change in land cover include human population growth and associated infrastructure developments, economic factors, technological capacity, political systems (institutions and policies), and social cultural factors (attitudes, preferences and values; Dale *et al.,* 2000; MEA 2005b). In most landscapes, rate of changes in vegetation is directly or indirectly influenced by human activities (Wear *et al.,* 1996), since humans act as disturbance agents and interact with the physical environment (Kennedy & Spies, 2004).

4.2.1. Charcoal production

Charcoal production is now a widespread major economic activity for many households within the study area, affecting even the local and central government managed forest reserves which are supposedly "protected" from unplanned harvesting. Similar to the miombo woodlands (Monela *et al.,* 1993; Luoga *et al.,* 2000a & b), charcoal production is the major factor causing woodland decline/loss in this multiple use equatorial wooded savanna. Results of the present study, however, contrast with the findings of Campbell *et al.* (1993) that showed deforestation in the miombo woodlands of Zimbabwe to be largely a result of clearing of land for cultivation and not tree harvesting. Similarly, in Kenya (Okello *et al.,* 2001) and most Sub-Saharan African countries, there is a high dependency of the majority (over 90%) of urban households on firewood and charcoal for cooking (Arnold *et al.,* 2003; Brouwer & Falcão, 2004). Hence, greatly contributing to the deforestation of savanna woodlands (Chidumayo, 1989; Moyo *et al.,* 1993; Young & Francombe, 1991; Luoga *et al.,* 2005). Ugandans have witnessed kerosene prices rising from UGX 1,650 (US$ 0.95) in March 2006 to UGX 2,900 (US$1.70) in June 2008. The ever increasing electricity and fossil fuels (e.g. kerosene) tariffs in Uganda, makes such energy sources unaffordable to many urban households leading to their increased dependency on the relatively cheaper wood fuel. As a result, by 2001 woodlands were supplying well over 90% of Uganda's energy requirements (Moyoni, 2001; MEMD, 2001). Hence, a combination of these socio-economic factors has led to increased demand and commercialisation of charcoal, with negative impacts on the sustainability of woodlands and biodiversity in the area. Unsustainable harvesting of woody plants and illegal charcoal production is now affecting local government forest reserves, which should essentially be enjoying some protection. By 2003, almost 90% of the charcoal production was taking place illegally on state and co-operative ranches and only 10% from private holdings in the study area (Namaalwa *et al.,* 2007). Consequently, like the miombo woodlands (Chidumayo, 1991; Monela *et al.,* 1993; Luoga *et al.,* 2000a), this is resulting in the degradation and loss of savanna woodlands in Uganda, particularly those near urban centres and those that are unrestricted and easily accessible.

4.2.2. Establishment and development of livestock ranches, livestock grazing and seasonal fires

Livestock grazing is very common and is one of the major land uses and income generating activities in the Nakasongola District. The study period coincides with the period 1986 to 2001 during which Uganda experienced steady economic growth, resulting in an increase in the livestock population, rehabilitation of old ranches and establishment of new ones in the area (Kisamba-Mugerwa, 2001). In the process of developing ranches, woody plant cover was cleared to allow grasses to flourish, consequently reducing woodland cover. In addition, people and their animals from elsewhere continue to migrate into Nakasongola District in search of land for settlement and grazing. The increase in the livestock population and the reduction in open access grazing land as large areas were fenced-off, increased the unsustainable utilization of the savanna-woodland vegetation, resulting in vegetation degradation in common access grazing areas.

The increased loss of woodland vegetation cover in the study area may also be attributed to the interaction between fires and animal grazing that is common in the district. The occurrence of frequent and unplanned anthropogenic seasonal fires in combination with livestock grazing may arrest the development of transition of savanna grassland to woodland vegetation. In tropical savannas, fire and grazing are among the most important anthropogenic disturbances (Scholes & Walker, 1993; Breman & Kessler, 1995; Menaut *et al.,* 1995) that determine vegetation patterns (Kennedy & Potgieter, 2003). In savanna vegetation around Budongo Forest Reserve, Uganda, fire was identified as the major factor influencing woody plant variation, with the extent of woodland savanna vegetation area decreasing in places where annual burning was practiced, while increasing in unburnt areas (Nangendo, 2005). Similarly, when East African savannas of central and northern sections of the Serengeti ecosystem and open savannas in Tsavo National Park were protected against fire and herbivores, a higher density of trees was recorded (Belsky, 1984, van Wijngaardsen, 1985). Elsewhere, studies (e.g. Everett *et al.,* 2000; Gautier & Spichiger, 2004; Uys *et al.,* 2004) have shown that complete cessation of burning promotes the development of woody vegetation in some savannas. Protection against fire can result in the development of a dense woody understory (Bowman *et al.,* 1988), potentially developing into closed woodland under the current climate (Bond *et al.,* 2005).

4.2.3. Increasing human population and expanding shifting crop cultivation

The high increase (over 80%) in land area under crop cultivation and settlements between 1984 and 2001 may be attributed to the increase in the indigenous and immigrant human population requiring more land for crop cultivation and settlement. Local households largely depend on subsistence agriculture, cultivating food crops to meet their food supplies. Human population pressures on woody resources are higher in Uganda (with a human population growth rate of 2.9% between 1969 and 2002) than in other East African countries (with a growth rate of 2.0 - 2.7%; Uganda Bureau of Statistics, 2002). Increasing human population and ongoing demand for land for crop cultivation is leading to shorter fallow periods of less than 2 years, which may not allow the recovery of woody vegetation in the area. In the miombo woodland areas, even 10 year fallow cycles have been reported to result in woodland degradations through a change in vegetation structure (Luoga *et al.,* 2000b). Moreover, shifting crop cultivation is associated with slashing and burning of woody vegetation in preparation of crop fields, thereby, contributing to the loss of woodland cover. Given the fragile nature and low soil fertility of these drylands (NEMA, 2007), usually wooded areas are targeted for agriculture expansion on the assumption that they are more fertile and could give higher crop yields. Shifting cultivation is a potentially important cause of land cover change in many Sub-Saharan African countries. It has been responsible for the modification and transformation of the landscape and deforestation in the miombo woodlands of southern Africa (incl. Tanzania, Zambia and Zimbabwe; Luoga *et al.,* 2000b; Chidumayo & Kwibisa, 2003; Kamusoko & Aniya, 2007) and Ethiopian savanna woodlands (Yirdaw & Luukkanen, 2003). Agricultural expansion has been by far the leading land use change associated with deforestation in Asia, Africa and Latin America (Reid *et al.,* 2000; Geist & Lambin, 2002).

4.2.4. Land tenure systems

Mailo and customary land ownership are the major land tenure systems in Nakasongola District accounting for 87%, whereas customary and leasehold land ownership accounts for 13%. Under The Uganda Constitution of 1995, all the land in the study area is owned, including the trees growing on it according to The Uganda Forestry Policy of 2001. This has management implications for the woodlands and other resources on the various lands and the various land tenure systems. It would have been expected that there would be restricted use of woodlands on *mailo* (the registered owner holds land in perpetuity, but is subject to customary and statutory rights of lawful and *bonafide* occupants), hence, less woodland loss. However, woodland loss in the study area over the 17 year study period occurred and continues to occur mostly in areas under *mailo* and customary land tenure systems, and also on privately owned land, particularly those with absentee landlords. In fact the studied savanna woodlands seem to be de-facto open-access regimes, with no effective institutions and mechanisms to enforce the rules to ensure that they are sustainably managed. These findings compare with those of Hanna *et al.* (1995) who reported that common property regimes are responsible for overexploitation and destruction of natural resources. In many Ugandan communities, customary land is open-access due to weak traditional controls over land allocation and relatively weak institutions in collective management of resources such as woodlands (Place & Otsuka, 2000; Mwase *et al.,* 2007). It is also evident that there is no consistent and secure land tenure system in this savanna, thereby undermining the sustainable utilisation of the plant resources. Lack of a consistent and secure land tenure system, is similarly argued to have to a great extent contributed to deforestation in Ivory Coast (Reed, 1992). Indeed, land cover change studies in woodland/forested landscapes in the USA (Spies *et al.,* 1994; Turner *et al.,* 1996; Cohen *et al.,* 2002; Kennedy & Spies, 2004) and Brazil (Dale *et al.,* 1993) highlight the important role land ownership may play in the spatial distribution and magnitude of change in vegetation patterns.

5.0. Conclusions

Landsat imagery and socio-economic interviews facilitated a better understanding of the dynamics of land cover change and woodland loss in this equatorial savanna. Analysis of Landsat images of 1984, 1995 and 2001 revealed great land cover changes that occurred mainly in the dense and medium woodlands, reflected by the increase in open woodland, grasslands and cultivation/settlement land cover types. Generally, dense woodland areas declined while medium and open woodlands increased between 1984 and 2001. If landscape cover changes continue to follow these trends of woodland loss and land degradation, the cover and persistence of woody species will be increasingly threatened. It is also predicted that charcoal burners, whose decisions are driven by short-term profits, will continue to harvest trees from woodlands for charcoal production as long as there are woodlands left to clear. Such unsustainable management of the woodland vegetation will ultimately result in loss of income, environmental services, food security, fuelwood availability, habitat degradation and biodiversity loss (MEA, 2005a), thereby, threatening local and regional sustainability and livelihood systems (Singh *et al.,* 2001). The baseline land cover change maps, produced from the Landsat imagery, and the woodland loss analyses, provide a valuable tool for planning and implementing sustainable development programmes within the Nakasongola District and other neighbouring districts with similar vegetation cover and land use practices.

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References

Agarwal, C., Green G.M., Grove, J.M., Evan, T.P. & Schweik, C.M. 2002. A review and assessment of land use change models: Dynamics of space, time and human choice. USDA (Forest Services), Technical Report NE-297.

Arnold, M., Kohlin, G., Persson, R. & Shepherd, G. 2003. *Fuel wood revisited: what has changed in the last decade?* CIFOR Occasional Paper Number 39. Center for International Forestry Research (CIFOR), Jakarta, Indonesia.

Baker, W.L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7: 181–194.

Banana, A., Vogt, N.D., Gombya-Ssembajwe, W.S. & Bahati, J. 2007. Decentralised governance and ecological health: why local institutions fail to moderate deforestation in, Mpigi district of Uganda. *Scientific Research and Essay* 2: 434-445.

Baudry, J., Laurent, C., Thenail, C., Denis, D. & Burel, F. 1999. Driving factors of land use diversity and landscape patterns at multiple scales-a case study in Normandy, France. pp. 103–120. In: Kronert, R., Baudry, J., Bowler, I.R. & Reenberg, A. (Eds.) Land use changes and their environmental impact in rural areas in Europe. UNESCO, Paris, France.

Bazaara, N. 2003. Decentralization, politics and environment in Uganda. Environment and Governance in Africa, Working Paper 7. World Resources Institute, Washington DC., USA.

Belsky, A.T. 1984. The role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *Journal of Ecology* 22: 271-279.

Bond, W.J., Woodward, F.T. & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 523-538.

Bowman, D.M., Wilson, B.A. & Hooper, R.J. 1988. Response of Eucalyptus forest and woodland to four fire regimes, Munmarlary, Northern Territory Australia. *Journal of Ecology* 76: 215-232.

Brandon, R.B. 2001. Mapping Rural Land Use & Land Cover Change in Carroll County, Arkansas Utilizing Multi-Temporal Landsat Thematic Mapper Satellite Imagery. Thesis University of Arkansas. http://www.cast.uark.edu/local/brandon_thesis /index.html

Brandt, J., Primdahl, J. & Reenberg, A. 1999. Rural land use and landscape dynamics-analysis of 'driving forces' in space and time. pp. 81-102. In: Kronert, R., Baudry, J., Bowler, I.R., Reenberg, A. (Eds.) Land use changes and their environmental impact in rural areas in Europe. UNESCO, Paris.

Breman, H. & Kessler, J.J. 1995. Woody plants in agro-systems of semi-arid regions, with and emphasis on the Sahelian countries, advanced series. pp. 23–340. Agricultural Sciences, Springer Verlag, Berlin, Germany.

Brouwer, R. & Falcão, M.P. 2004. Wood fuel consumption in Maputo, Mozambique. *Biomass and Bioenergy* 27: 233-245.

Bryant, D., Nielsen, D. & Tangley, L. 1997. *The last frontier forests: Ecosystems and Economies on the edge*. World Resources Institute. Washington DC., USA.

Campbell, B., Grundy, I., Matose, F. 1993. Tree and woodland resources-the technical and practices of small scale farmers. pp. 29-62. In: Bradley, P.N. & MacNamara, K. (Eds.) Living with Trees: Policies for Forestry Management in Zimbabwe. World Bank Technical Paper No. 210, The World Bank, Washington DC.

Chidumayo, E.N. & Kwibisa, L. 2003. Effects of deforestation on grass biomass and soil nutrient status in miombo woodland, Zambia. *Agriculture, Ecosystems and Environment* 96: 97-105.

Chidumayo, E.N. 1989. Land use, deforestation and reforestation in the Zambian copper belt. *Land Degradation and Development* 1: 209–216.

Chidumayo, E.N. 1991. Woody biomass structure and utilization for charcoal production in Zambian miombo woodland. *Bio-Resource Technology* 37: 43–52.

Chuvieco, E. 1996. Fundamentos de Teledetección especial. Tercera edicio´n revisada. pp. 211–221. RIALP, SA, Madrid, Spain.

Cohen, W.B., Spies, T.A., Alig, R.J., Oetter, D.R., Maiersperger T.K. & Fiorella, M. 2002. Characterizing 23 years (1972-1995) of standard replacement disturbance in western Oregon forests with Landsat imagery. *Ecosystems* 5: 125-137.

Congalton, R.G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment* 37: 35-46.

Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.H., Huntley, N., Naiman, R.J., Riebsame, W.E., Turner, M.G. & Valone, T.J. 2000. Ecological Principles and Guidelines for Managing the use of Land. *Ecological Applications* 10(3): 639-670.

Dale, V.H., O'Neill, R.V., Redlowski, M. & Southworth, F. 1993. Causes and effects of land use change in central Rondônia, Brazil. *Photogrammetric Engineering and Remote Sensing* 56: 997-1005.

District Environmental Profile (DEP) 2002. In: Nakasongola District Forest Development Plan*:* Period of plan: 2003-2014, pp. 1-79.

Dovie, D.B.K, Witkowski, E.T.F. & Shackleton, C. M. 2004. The fuelwood crisis in Southern Africa-relating fuelwood use to livelihoods in a rural village. *GeoJournal* 60: 123-133.

Edwards Jr, T.C., Moisen, G.G. & Cutler, D.R. 1998. Assessing map accuracy in a remotely sensed ecoregion-scale cover map. *Remote sensing of Environment* 63: 73-83.

Everett, R.L., Schellhaas, R., Keenum, D., Spurbeck, D. & Ohlson, P. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *Forest Ecology and Management* 129: 207-225.

FAO, 1997. Africover Land Cover Classification. FAO, Rome, Italy.

FAO, 1998. World Reference Base for Soil Resources. FAO, ISRIC and ISSS, Rome, Italy.

FAO, 2004. Land Cover Classification System. Land Cover Topic Centre. Rome, Italy.

Fitzgerald, R.W. & Lees, B.G. 1994. Assessing the classification accuracy of multisource remote sensing data. *Remote Sensing of Environment* 47: 362-368.

Foody, G.M. 2002. Status of land cover classification accuracy assessment. *Remote Sensing of Environment* 80: 185-201.

Gautier, L. & Spichiger, R. 2004. The forest-savanna transition in West Africa. pp. 33-40. In: Poorter, L., Bongers, F., Kouamé, F.N. & Hawthorne, W.D. (Eds.), Biodiversity of West African forests: an ecological atlas of woody plant species. CAB International, Wallingford, UK.

Geist, H.J. & Lambin, E.F. 2002. Proximate causes and underlying driving forces of tropical deforestation. *BioScience* 52: 143-149.

Geist, H.J. & Lambin, E.F. 2004. Dynamic causal patterns of desertification. *Bioscience* 54: 817-829.

Giannecchini, M., Twine, W. & Vogel, C. 2007. Land-cover change and human-environment interactions in a rural cultural landscape in South Africa. *The Geographical Journal* 173(1): 26-42.

Githinji, M. & Perrings, C. 1993. Social and Ecological Sustainability in the Use of Biotic Resources in Sub-Saharan Africa. *Ambio* 22(2-3): 110-116.

Gobin, A., Campling, P. & Feyen, J. 2001. Spatial analysis of rural land ownership. *Landscape and Urban Planning* 55: 185-194.

González Sánchez, E. & Calvo Herrero, R. 1994. Estudio de la desertificacio´n mediante ima´genes LANDSAT. *El Campo* 131: 109–116.

Goodchild, M.F., Biging, G.S., Congalton, R.G., Langley, P.G., Chrisman, N.R. & Davis, F.W. 1994. *Final Report of the Accuracy Assessment Task Force, California Assembly Bill AB1580*, National Center for Geographic Information and Analysis, UCSB, California, USA.

Hall, G.F., Botkin, D.B., Strebel, D.E., Woods, D.E. & Goetz, S.J. 1991. Large-scale patterns of forest succession as determined by remote sensing. *Ecology* 72: 628–640.

Hanna, S., Folke, C. & Maler, K.G. 1995. Property rights and environmental resources. pp 15-29. In: Hanna, S., & Munasinghe, M. (Eds.) Property rights and the environment: Social and ecological issues. The World Bank, Washington DC., USA.

Hudson, W.D. & Ramm, C.W. 1987. Correct formulation of the kappa coefficient of agreement. *Photogrammetric Engineering and Remote Sensing* 53: 421-422.

Hulme, P.E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology* 42: 784-794.

Jensen, J.R. 1986. Introductory Digital Image Processing. Prentice Hall, New Jersey, USA.

Kamusoko, C. & Aniya, M. 2007. Land use/cover change and landscape fragmentation analysis in the Bindura district, Zimbabwe. *Land Degradation and Development* 18: 221-233.

Kennedy, A.D. & Potgieter, A.L.F. 2003. Fire season affects size and architecture of Colophospermum mopane in South African Savannas. *Plant Ecology* 167: 179-92.

Kennedy, R.S.H. & Spies, T.A. 2004. Forest cover changes in the Oregon Coast Range from 1939 to 1993. *Forest Ecology and Management* 200: 129-147.

Kisamba-Mugerwa, W. 2001. Rangelands management policy in Uganda. A paper prepared for the international conference on policy and institutional options for the management of rangelands in dry areas, 7-11 May 2001 Hammamet, Tunisia.

Lambin, E.F., Baulies, X., Bocksteal, N., Fischer, G., Krug, T., Leemans, R., Moran, E.F., Rindfuss, R.R., Sato, Y., Skole, D., Turner II B.L. & Vogel, C. 1999. Land use and land cover change: implementation strategy IGBP Report No. 48 and IHDP Report No. 10 International Geosphere-Biosphere Programme and the Human Dimensions of Global Environmental Change Programme, Stockholm.

Langdale-Brown, I., Osmaston, H.A. & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land use. Entebbe Government Printers, Uganda. pp. 159.

Letsela, T., Witkowski, E.T.F. & Balkwill, K. 2002. Direct use values of communal resources in Bakong and Tsehlanyane in Lesotho. Whither the Commons? *International Journal of Sustainable Development and World Ecology* 9: 351-368.

Liu, C., Frazier, P. & Kumar, L. 2007. Comparative assessment of the measures of thematic classification accuracy. *Remote Sensing of Environment* 107: 606-616.

Liu, J., Daily, G. C., Ehrlich, P, R. & Luck, G. W. 2003. Effects of household dynamics on resource consumption and biodiversity. *Nature* 421: 530–533.

Loucks, C., Ricketts, T.H., Naidoo, R., Lamoreux, J. & Hoekstra, J. 2008. Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural sustainability. *Journal of Biogeography* 35: 1337-1348.

Lunetta, R.S., Knight, J.F., Ediriwickrema, J., Lyon, J.G. & Worthy, L.D. 2006. Land-cover change detection using multi-temporal MODIS NDVI data. *Remote Sensing of Environment* 105: 142-154.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000a. Economics of charcoal production in miombo woodlands of eastern Tanzania: Some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000b. Subsistence use of wood products and shifting cultivation within a miombo woodland of eastern Tanzania, with some notes on commercial uses. *South African Journal of Botany* 66: 72-85.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 16: 15-30.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2005. Land-cover and use changes in relation to the institutional framework and tenure of land and resources in eastern Tanzania miombo woodlands. *Environment, Development and Sustainability* 7: 71-93.

Luong, P.T. 1993. The detection of land use/land cover changes using remote sensing and GIS in Vietnam, Asia pacific. *Journal of Remote Sensing* 5: 63-66.

Ma, Z., Hart, M.M. & Redmond, R.L. 2001. Mapping vegetation across large geographical areas: integration of remote sensing and GIS to classify multi-resource data. *Photogrammetric Engineering and Remote Sensing* 67: 295-307.

McKinney, M.L. 2001. Role of human population size in raising bird and mammal threat among nations. *Animal Conservation* 133: 455-473.

MEA (Millennium Ecosystem Assessment) 2005a. *Ecosystem and Human Well-Being: Biodiversity Synthesis*: Island Press, World Resources Institute, Washington, DC.

MEA (Millennium Ecosystem Assessment) 2005b**.** *Ecosystem and Human Well-Being: Desertification Synthesis*: Island Press, World Resources Institute, Washington, DC.

MEA (Millennium Ecosystem Assessment) 2005c**.** *Ecosystem and Human Well-Being: Forest and Woodland Systems.* Current State and Trends. Volume 1. Island Press, World Resources Institute, Washington, DC.

MEMD (Ministry of Energy and Mineral Development) 2001. *National Biomass Energy Demand Strategy 2001-2010*. Kampala, Uganda. pp.36.

Menaut, J.C., Lepage, M. & Abbadie, L. 1995. Savannas, woodlands and dry forests in Africa. pp. 64-92. In: Bullock, S. H., Mooney, H. A., Medina, E. (Eds.), Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, UK.

Monela, G.C., O'kting'ati, A. & Kiwele, P.M. 1993. Socio-economic aspects of charcoal consumption and environmental consequences along the Dar Es Salaam-Morogoro highway, Tanzania. *Forest ecology and Management* 58: 249-258.

Moyo, S., O'Keefe, P. & Sill, M. 1993. The Southern African Environment: Profiles of the SADC Countries. ETC Foundation/Earthscan Publishers, London, pp. 354.

Moyoni, Y. 2001. The role of forests in Uganda's National Economy. Innovation- Special Issue on valuation of Forest Resources in East Africa. pp. 10-12.

Mwase, W.F., Bjørnstand, Å., Bokosi, J.M., Kwapata, M.B. & Stedje, B. 2007. The role of land tenure in conservation of tree and shrub species diversity in miombo woodlands of Southern Malawi. *New Forests* 33: 297-307.

Mwavu, E.N. & Witkowski, E.T.F. 2008. Land use and cover changes (1988 – 2002), around Budongo Forest Reserve, NW Uganda: Implications for forest and woodland sustainability. *Land Degradation and Development* 19: 606-622.

Namaalwa, J., Sankhayan, P.L. & Hofstand, O. 2007. A dynamic bio-economic model for analyzing deforestation and degradation: An application to woodlands in Uganda. *Forest Policy and Economics* 9: 479-495.

Nangendo, G. 2005. Changing forest-woodland-savanna mosaics in Uganda: with implications for conservations. PhD Thesis. International Institute of Geo-Information Science and Earth Observation, Enschede, The Netherlands (available at http://library.wur.nl/wda/dissertations/dis3765.pdf)

National Research Council (NRC) 1999. Our common journey: A Transition Towards Sustainability. National Academic Press: Washington, DC., USA.

NEMA (National Environment Management Authority) 1998. State of environment report for Uganda. The Republic of Uganda. Kampala, Uganda.

NEMA (National Environment Management Authority) 2007. State of environment report for Uganda. The Republic of Uganda. Kampala, Uganda.

Okello, B.D., O'Connor, T.G. & Young, T.P. 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *Forest Ecology and Management* 142: 143-153.

Parker, D., Downer, E.R. & Cole, G.E.D., 1967. Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Pfund J.-L., O'Connor, T., Koponen, P. & Boffa, J.-M. 2006. Trans-disciplinary research to promote biodiversity conservation and enhanced management of tropical landscape mosaics. IUFRO Landscape Ecology Conference, Sept. 26-29, 2006 – Locorotondo, Bari, Italy.

Phillips, O. & Gentry, A.H. 1993. The useful plants of Tambopata. Pem.1: Statistical hypothesis test with a new quantitative technique. *Economic Botany* 47: 15-32.

Place, F. & Otsuka, K. 2000. Population pressure, land tenure and tree resource management in Uganda. *Land Economics* 76 (2): 233-251.

Reed, D. 1992. 'Structural adjustment and the environment'. In: Munasinghe M. 1996 (Ed.) Environmental Impacts of Macroeconomics and sectoral policies. The International Society for Ecological Economics (ISEE). The World Bank and the United Nations Environmental Programme (UNEP).

Reid, R.S., Kruska, R.L., Muthi, N., Taye, A., Wotton, S., Wilson, C.J. & Mulatu, W. 2000. Land use and land-cover dynamics in response to changes in climatic, biological and socio-political forces: the case of south-western Ethiopia *Landscape Ecology* 15: 339-55.

Sankhayan, P.L. & Hofstand, O. 2000. An economic model for analysing woodland degradation in Sub-Saharan Africa. *Scandinavia Forest Economics* 37: 32-45.

Sawatzky, D.L., Raines, G.L., Bonhan-Carter, G.F. & Looney, C.G. 2004. ARCSDM3: Arc MAP extension of spatial data modelling using weights of evidence, logistic regression, fuzzy logic and neural network analysis. http://www.ige.unicamp.br/sdm/ArcSDM3/.

Scholes, R.J. & Walker, B.H. 1993. An African Savannas: Synthesis of the Nylsvley Study. Cambridge University Press, Cambridge, UK. pp.306.

Shackleton, C.M., Shackleton, S.E., Netshiluvhi, T.R., Geach, B., Balance, A. & Fairbanks, D.H.K 2002. Use Patterns and Value of Savanna Resources in Three Rural Villages in South Africa. *Economic Botany* 56: 130-146.

Singh, A. 1989. Review article-digital change detection techniques using remotely-sensed data. *International Journal of Remote Sensing* 10: 959-964.

Singh, R.B., Fox, J. & Himiyama, Y. (Eds.). 2001. *Land use and land cover change*. Science Publishers, Inc: NH.

Spies, T.A., Ripple, W.J. & Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecological Applications* 4: 55-568.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hanna, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. 2004. Extinction risk from climate change. *Nature* 427: 145-148.

Tilman, D., D'Antonio, C., Dobson, A., Fargione, J., Howarth, R, Schindler, D., Schlesinger, W., Simberloff, D., Swackhammer, D. & Wolff, B. 2001. Forecasting agriculturally driven global environmental change. *Science* 292: 281-284.

Tucker, C.J., Dregne, H.E. & Newcombe, W.W. 1991. Expansion and contraction of the Sahara desert from 1980 to 1990. *Science* 253: 299–301.

Turner, B. L. II & Meyer, W. B.1994. Global land use and land-cover change: an overview. pp. 3-10. In: W.B. Meyer and B. L. Turner II, (Editors). Change in land use and land cover: a global perspective Cambridge University Press, Cambridge UK.

Turner, M.G., Wear, D.N. & Flamm, R.O. 1996. Land ownership and land cover change in the southern Appalachian highlands and the Olympic Peninsula. *Ecological Applications* 6: 1150-1172.

UBOS (Uganda Bureau of Statistics) 2000. National household census estimates 2000. (Retrieved on 17/11/2005 from http://www.ugandadish.org/nakasongola.doc).

Uys, R.G., Bond, W.J. & Everson, T.M., 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118: 489-499.

van Wijngaardsen, W. 1985. Elephants-tree-grass-grazers. ITC Publication No. 4, pp. 159. Enscheda. Netherlands.

Vitousek, P.M. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861-1876.

Waite, T.A., Corey, S.J., Campbell, L.G., Chhangani, A.K., Rice, J. & Robbins, P. 2009. Satellite Sleuthing: does remotely sensed land cover change signal ecological degradation in a protected area? *Diversity and Distributions* 15: 299-309.

Wear, D.N., Turner, M.G. & Flamm, R.O. 1996. Ecosystem management with multiple owners: Landscape dynamics in a southern Appalachian watershed. *Journal of Applied Ecology* 6: 1173-1188.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFET/UNSO vegetation map of Africa. UNESCO, Paris, France.

Wood, S., Sebastian, K. & Scherr, S.J. 2000. Pilot analysis of global ecosystems: agroecosystems. World Resources Institute, Washington DC.

Wu, J.G. & Hobbs, R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecology* 17: 355 – 365.

Wulder, M.A., Franklin, S.E., White, J.C., Linke, J. & Magnussen, S. 2006. An accuracy assessment framework for large-area land cover classification products derived from medium-resolution satellite data. *International Journal of remote Sensing* 27(4): 663-683.

Yirdaw, E. & Luukkanen, O. 2003. Indigenous woody species diversity in *Eucalyptus globules* Labill. ssp. *globules* plantations in the Ethiopian highlands. *Biodiversity and Conservation* 12: 567-582.

Young, T.P. & Francombe, C., 1991. Growth and yield estimates in natural stands of leleshwa (*Tarchonanthus camphoratus*). *Forest Ecology and Management* 41: 309-321.

Zerda, H.R. 1998. Monitoring der Vegetations—und Landnutzungsvera¨nderungen durch Brandrohdung und U¨ bernutzung im Trocken—Chaco Argentiniens mit Satellitenfernerkundung und GIS. Ph.D. dissertation, Universita¨t Go¨ttingen, Germany, Cuvillier Verlag Go¨ttingen, pp.175.

Zhu, Z., Yang, L., Stehman, S.V. & Czaplewski, R.L. 2000. Accuracy assessment from the US Geological Survey Regional Land Cover Mapping Program: New York and New Jersey Region. *Photogrammetric Engineering and Remote Sensing* 66: 1425-1435.

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CHAPTER 4

Diversity and density of woody species in a multiple land use equatorial African savanna, central Uganda

Abstract

Woody plant species diversity and distributions were studied in multiple land use savanna woodlands in central Uganda, using 75 0.1 ha plots. A total of 44,195 woody plants representing 99 species in 67 genera and 31 families were recorded. Woody plant density differed significantly ($F_{2, 72}$ = 6.3, P < 0.0031), being higher under charcoal production (7,131 ± 755 plants/ha) and cultivation (6,612 ± 665) areas compared with the grazing lands (4,152 ± 525). At the plot level, species richness and Fisher's alpha-diversity (α) were relatively low, ranging from 2 - 31 species, and 0.34 – 6.34, respectively. Plot-level species richness and Fisher's alpha diversity (α) were both significantly higher in the charcoal production and cultivation areas compared with the grazing lands. Similarly, cumulative species richness and Fisher's (α) were also higher under charcoal (10.43) and cultivation (10.36) compared with grazing (7.85). Shannon-Wiener diversity index was highest under cultivation (2.1 ± 0.1) and charcoal production (2.0 ± 0.1), and significantly lower under grazing (1.6 ± 0.1). Similarly, the cumulative Shannon-Wiener diversity was higher under cultivation (2.95) and charcoal production (2.93) and lowest under grazing (2.49). Analysis of similarity also showed that community species composition differed significantly (Global R_{ANOSIM} = 0.14, p= 0.001) among land use types. Morisita-Horn values did not differ significantly ($F_{2, 900}$ = 2.43, P = 0.09) among land uses, but charcoal production and grazing areas tended to have higher Morisita-Horn values (0.37 ± 0.02, n = 276; 0.37 ± 0.02, n = 351) than the cultivation land use (0.33 ± 0.02, n = 276). All measures of beta-diversity (spatial "turnover" in species composition) were consistently higher in the grazing lands (β_W = 3.1; β_T = 3.1), followed by cultivation (β_W = 2.8; β_T = 3.0) and lowest for charcoal production (β_W = 2.7; β_T = 2.8). This suggests a more heterogeneous spatial distribution of species in the grazing lands. The beta-diversity results were corroborated by SIMilarity PERcentages (SIMPER) analyses, in that, within each land use, the mean similarities were quite low, ranging from 25 - 31%. However, the mean pair-wise dissimilarities between the land use types were relatively high, ranging from 73 - 81%. This suggests that variations in species composition and diversity are to a great extent influenced by land use type and anthropogenic disturbances in this region. The relatively low woody species diversity and richness in this savanna may be an indicator of woodland degradation, fragmentation and local species loss, a result of unsustainable harvesting for charcoal production, grazing and shifting cultivation. Hence, more sustainable woodland management practices will be necessary to maintain the plant diversity of these woodlands.

Key words: Alpha-diversity, ANOSIM, anthropogenic disturbance, beta-diversity, conservation strategies, land degradation, land use type, SIMPER.

Nomenclature: Polhill (1952 et seq.), Hamilton (1991).

1.0. Introduction

Savanna woodlands make up most of the tropical and subtropical woodland cover, from which rural households throughout Sub-Saharan Africa derive a wide range of products, making a significant contribution to local and national production and economic growth (Dzerefos *et al*., 1999; Letsela *et al.* 2002; Dovie *et al.,* 2002, 2005). They are the major source of energy (firewood and charcoal) for many African households (e.g. Luoga *et al*., 2000a, 2002; Kituyi, 2004; MEA, 2005a) and a livelihood activity in marginalized communities (Luoga *et al.,* 2000b; Dovie *et al.,* 2004). Wild plants from woodlands and other vegetation types are very important in the subsistence sector, both by meeting a wide range of household needs and through increasing commercialization, and hence generating incomes (Braedt & Standa-Gunda, 2000; Dovie *et al.,* 2003; Letsela *et al.,* 2003; Botha *et al.,* 2005). In southern and eastern Africa, miombo woodlands are economically important for the supply of timber, poles, firewood, charcoal, medicines, food, fibre and carvings (e.g. Chidumayo, 1988; Luoga *et al.,* 2000a; Shackleton *et al.,* 2002); meeting both urban and rural peoples' needs (Clarke *et al.,* 1996; Luoga *et al.,* 2000c). For example, in Tanzania, about 24 million people (URT, 1991) live in, and derive their livelihoods, from areas covered or formerly covered by miombo woodlands (Luoga *et al.,* 2004). In Uganda, like elsewhere in Sub-Saharan Africa, woodlands play an important role in the economy of the country by providing firewood and charcoal as well as grazing resources, land for cultivation, and other services (Namaalwa *et al.,* 2005). In Nakasongola District, with a human population density of 41 people/km^2 (2002 National Housing Census; Uganda Bureau of Statistics, 2002), woodlands are the major source of livelihood activities such as charcoal production (engaging about 70 - 80% of the total households), livestock grazing, and subsistence cultivation. Subsistence cultivation accounts for about 85% of the food supply for households and more than 50% of their monetary income. Hence, the major land use practices are cattle grazing, charcoal production and crop cultivation.

There is widespread concern that savanna woodland ecosystems with unique and valuable biodiversity resources are being lost (Rennolls & Laumonier, 2000) as a result of both natural and anthropogenic disturbances and mismanagement (O'Connor, 2005; Luoga *et al.,* 2005). They are rapidly undergoing severe large-scale changes, through harvesting, burning or conversion to other land use and cover types (Gerhardt & Hytteborn, 1992; Rennolls & Laumonier, 2000; MEA, 2005a & b). Consequently, the conservation of savannas and their species, particularly the woody component, has become increasingly important for the development of sustainable land use systems. Climate change, increasing demands for the conservation and improvement of dryland woodlands, and desertification concerns, necessitate a sound understanding of the nature, dynamics and production potential of savanna woodland systems, particularly the woody plant species component. Therefore, an understanding of the patterns of woody plant species diversity within the prevailing land uses and how they might be influenced by changes in the environment is essential for long-term sustainability

(Solbrig *et al.*, 1992; Walker & Stefan, 1996). In addition, to best conserve biodiversity, we must know where species richness is highest and how species assemblages change in space (Belbin, 1995; Faith & Walker, 1996; Vanclay, 1998; Plotkin & Muller-Landau, 2002). Hence, studies on woody plant diversity in savanna ecosystems are very important as they aid in decisions about conservation priorities, as well as helping to integrate priorities for monitoring and restoration programs (William-Linera, 2002; Folke *et al.,* 2004). Diversity measures can be used to evaluate the intensity of resource use by human populations (Begossi, 1996; Williams *et al.,* 2005). They also have potential application in conservation management (Magurran, 2004). However, little is known of the diversity and richness of woody plants in savanna woodlands outside the miombo eco-region and southern Africa, this is particularly the case in Uganda. Most diversity studies on woody plants in Uganda have focused on tropical forests (e.g. Sheil, 1996; Eilu *et al.,* 2004; Mwavu *et al.,* 2008), with little attention to savanna woodlands. Studies on savanna woodlands in Uganda have mainly focused on biomass and bio-energy, management of ranching schemes (e.g. Akankwasa & Tromborg, 2001; Kisamba-Mugerwa, 2001; NEMA, 2002), as well as growth, use and management of woodland resources (e.g. Namaalwa *et al.,* 2005). The present study aims to assess species diversity (richness, alpha, and beta diversity) and distributions of woody plants (trees and shrubs) in relation to the three main land use types in the savanna woodlands of Nakasongola District, central Uganda. The following questions were explored: (i) What is the overall woody species diversity in the wooded savanna? and (ii) Does woody species diversity vary between the major land use types (grazing, cultivation and charcoal production)?

2.0. Material and Methods

2.1. Study area

The study focused on multiple land use savanna woodlands of Nakasongola District, south of Lake Kyoga, central Uganda ($0^0$40′- $1^0$41′ N, $31^0$57′ - $32^0$48′ E). The District covers about 3,424 km^2, most of which is woodland and grassy savanna, with 322 km^2 (10%) of open water and wetlands. It comprises eight sub-counties (administrative sub-divisions), namely Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata. Each sub-county has a mean (± S.E.) of 49 (± 22) villages and 3,193 ± 390 households. The mean number of households/village was 82 (± 32), with an average of seven persons/household. The district has a total human population of 128,126 (41 people/km^2) (2000 National Housing Census), with 50.2% males and 49.8% females. About 95.3% of the population are rural and 4.7% urban (Uganda Bureau of Statistics, 2002).

Mean annual rainfall ranges from 500 – 1000 mm, and is concentrated into two wet seasons (March to May and August to November), but rainfall received and reliability is higher in the south, declining gradually to the north. The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C respectively. The topography of the area undulates between 1,036 and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al*., 1967).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964), a natural savanna woodland or woodland of mixed deciduous trees 3 to 12 m high and grasses 0.3 to 1.3 m high at maturity. However, the cover of the grass layer varies with season, is often patchy and subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirki*i subsp. *mildbraedii, A. senegal* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983). The major land use practices in this savanna are livestock grazing, subsistence crop cultivation, and charcoal production (Chapter 2).

2.2. Sampling design

There is a succession of change in land use over time which is typical of areas subject to slash and burn agriculture. Areas used for charcoal production are, then, used for cultivation, while cultivated areas may subsequently be used for grazing. However most of the grazing lands occur on hydromorphic grasslands which are only suitable for grazing. The current land use was identified for the purposes of this study. Representative villages (areas) in each of the eight sub-counties were selected (with the help of local leaders and officials from the Department of Natural Resource and Environment) for woody vegetation sampling in March 2006. In each sub-county at least three transects were laid, each representing one of the three major land uses, with the exception of Nabiswera which had four transects. The locations of the transects were selected randomly, but taking into consideration, the homogeneous nature of the area for a particular land use and being sufficiently large in extent to accommodate at least three 20 x 50 m (0.1 ha) plots, with a minimum separation distance of 200 m. The 20 x 50 m plot size is the standard area for work on vascular plant species richness (Crawley, 1997). It has been widely used in studies of the vegetation of grasslands, tropical savannas, woodlands, and forests (e.g. Luoga *et al.,* 2000a & b; Dupré, 2001; Duque *et al.,* 2002; Witkowski & Garner, 2008). Transects were laid radiating away from the source of disturbance, because in villages where subsistence activities are paramount, there may be gradients of increasing resource availability, with increasing distance from the source of disturbance. In total, 25 transects representing 75, 0.1 ha, plots were laid across the study area. Twenty four plots were sampled in each land use type, except for "grazing" which had 27 plots. The geographical location of each transect was recorded using a GPS, and then mapped with ARCMAP version 9.0 (Sawatzky *et al.,* 2004; Figure 1).

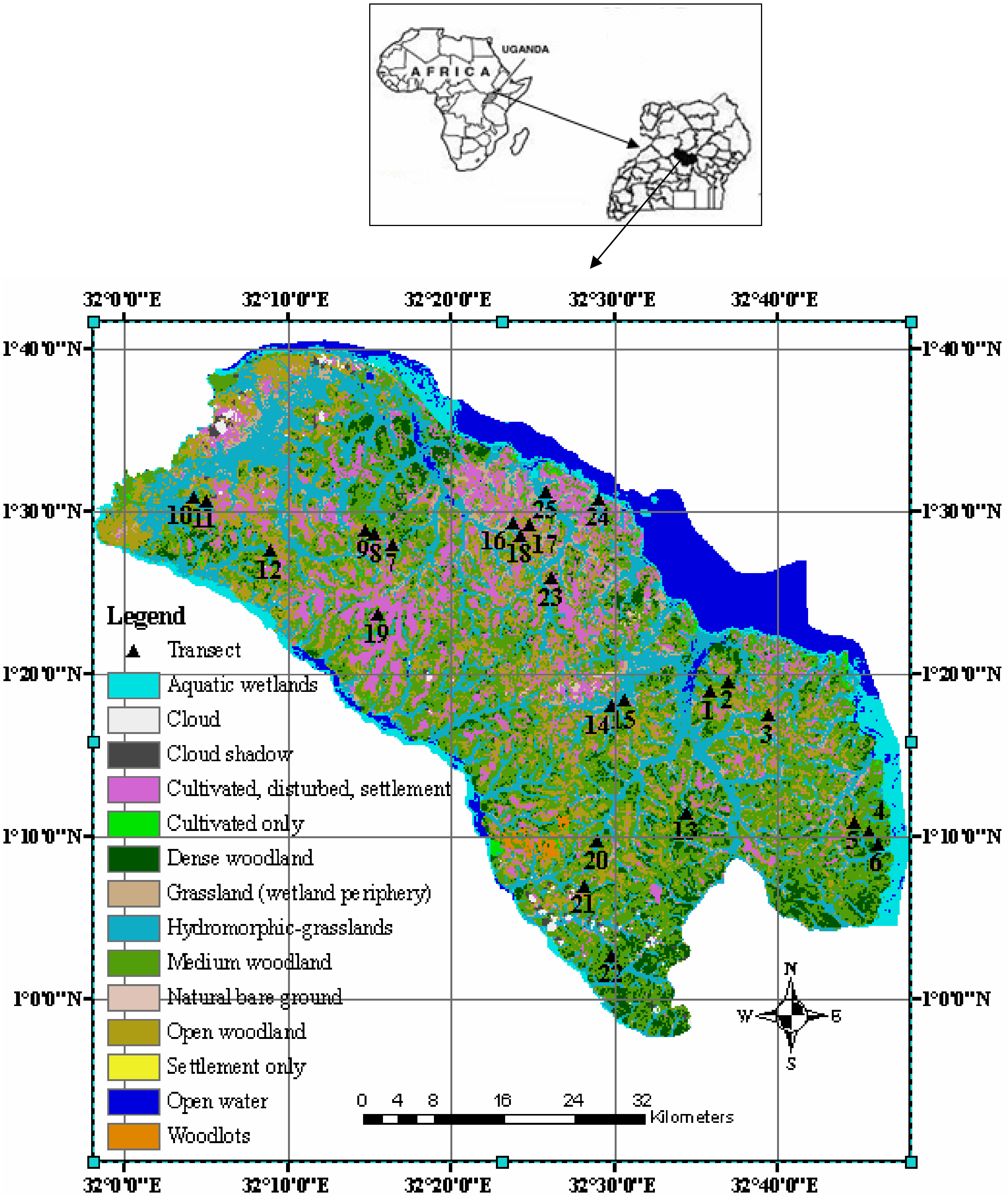


Figure 1: Map of Nakasongola District showing the location of the sampled transects within the three major land use types. Transects 2, 4, 7, 11, 15, 16, 22, and 25 – cultivation; Transects 3, 5, 9, 12, 13, 18, 20, and 23 – charcoal production; and Transects 1, 6, 8, 10, 14, 17, 19, 21, and 24 – grazing.

2.3. Data collection

Within each 0.1 ha plot, the identity of all the woody plants, the number of individuals, height and stem diameter at diameter at breast height (1.3 m) of each individual (except for seedlings), were recorded. Based on stem diameter and height, woody plants were categorized as trees or shrubs. A tree usually has one or more perennial stems at least 7 cm dbh, a more or less definitely formed crown of foliage and a height of at least 5 m at maturity (USDA Forest Service, 1989). A shrub has persistent woody stems and a relatively low growth habit, and generally produces several basal shoots instead of a single bole. Hence a shrub differs from a tree by its low stature and non-arborescent form, and is usually less than 5 m tall. A sapling was defined as a juvenile tree with > 0.5 to 5 cm dbh and > 1 m in height. Seedlings had a single stem with stem diameter ≤ 0.5 cm and ≤ 1 m height and had never resprouted. Initial plant species identification was done in the field using identification guides, mainly based on the Flora of Tropical East Africa (Polhill, 1952 & subsequent volumes), Hamilton (1991) and Katende *et al.* (1995), as well as the help of a botanist familiar with the flora. Voucher specimens were subsequently identified in the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda.

2.4. Data analysis

2.4.1. Alpha-diversity

Fisher's alpha (α) and Shannon-Wiener (H') diversity indices were employed to quantify alpha-diversity at the 0.1 ha scale, while rarefaction was used to estimate the number of species expected (E(Sn)) to be present in a random sample of individuals taken from any given collection, and provides confidence limits of species richness (Hsieh & Li, 1998). The cumulative number of species is plotted against some measure of the effort it took to obtain the sample of species (Hayek & Buzas, 1997). Plotting the curves facilitates improved interpretation of species richness results for samples of varying size and from different communities (Gotelli & Colwell, 2001; Williams *et al.,* 2005). The samples were randomized 100 times to compute the mean estimator and expected species richness for each sample accumulation level. The species accumulation curves were constructed from variables computed in EstimateS (Colwell, 2006).

H' combines species richness with relative abundance and was calculated using the formula:

$$H' = -\sum_{i=1}^{S}(p_i)(\ln p_i)$$

where; **s** = the number of species; $\boldsymbol{p_i}$ = the proportion of individuals or abundance of the i^{th} species.

Fisher's α-diversity Index is defined implicitly by the formula:

$$S = a^* \ln\left(1 + \frac{N}{a}\right)$$

where, 'S' is the number of taxa, 'N' is the number of individuals, and 'a' is Fisher's alpha (Fisher *et al.,* 1943; Harper, 1999). Fisher's α-diversity index is not influenced by the size of the sampling area and is less affected by the abundance of the rarest or commonest species than other diversity measures (Magurran, 2004). It depends more on the number of species of intermediate abundance (Williams *et al.,* 2005). However, Fisher's alpha cannot be calculated when N/S ≤ 1.44 (Hayek & Buzas, 1997). Calculation of the diversity indices was done using Species Diversity and Richness® version IV software (Seaby & Henderson, 2006) and EsimateS version 8.0 (Colwell, 2006). The samples were randomized 100 times in EstimateS to compute the cumulative H' and Fisher's alpha diversity values and to construct the curves. Differences in tree and shrub species richness and diversity between the three land use types were compared using one-way ANOVA, followed by Tukey HSD for unequal sample sizes (Zar, 1990; Dytham, 2003).

2.4.2. Beta-diversity

Beta-diversity at the plot level was assessed using Whittaker's β-diversity Index (β_W; Whittaker, 1960, 1972), and Wilson and Shmida (β_T) and the modified Morisita-Horn (Wolda, 1983) Indices of similarity. The Morisita-Horn Index assesses similarity in species composition between plots (Colwell *et al.,* 2004; Magurran, 2004), and is a quantitative similarity index that is not strongly influenced by species richness and sample size.

β_W -diversity was calculated based on the formula:

$$\beta_W = S / \bar{\alpha} - 1$$

where S = the total number of species in a set of samples, and $\bar{\alpha}$ = the average species richness of the samples.

Whereas, β_T was calculated as:

$$\beta_T = \frac{[g(H) \pm l(H)]}{2\alpha}$$

where g(H) = the number of species gained, l(H) = the number lost moving along the transect, and α = the average species richness of the sample.

The modified Morisita-Horn Index (C_{MH}) for all 0.1 ha plot pairs was calculated based on the formula:

$$C_{MH} = \frac{2\sum(a_i . b_i)}{(d_a + d_b) * (N_a * N_b)}$$

Where N_a = the total number of individuals at plot/site A; N_b = the total number of individuals at plot/site B; a_i = the number of individuals in the i^{th} species in A; b_i = the number of individuals in the i^{th} species in B; and d_a (and d_b) are calculated as follows:

$$d_a = \frac{\sum a_i^2}{N_a^2}$$

For each land use type, C_{MH} was calculated by averaging all the plot pair-wise values for that particular land use. The Morisita-Horn Index varies from 1 (complete similarity) to 0 (complete dissimilarity) in species abundance (William-Linera, 2002).

Furthermore, sample plots were grouped according to land use type and their variation in community species composition tested by employing the ANalysis Of SIMilarity (ANOSIM), a permutation test (Clarke, 1993) in CAP® 3.1 (Seaby *et al.,* 2006). ANOSIM computes a test statistic (R_{ANOSIM}) reflecting the observed differences among replicates between sites, contrasted with differences among replicates within sites (Clarke, 1993; Pandolfi & Greenstein, 1997). A zero (0) occurs if the high and low similarities are perfectly mixed and bear no relationship to the group. A value of minus one (- 1) indicates that the most similar samples are all outside of the group. A value of positive one (+ 1) indicates that the most similar samples are within the same group (Seaby *et al.,* 2006; Clarke 1993). The percentage of similarity among land uses was also analysed by SIMilarity PERcentages (SIMPER) techniques in CAP® 3.1. SIMPER analysis breaks down the contribution of each species to the observed similarity (or dissimilarity) between samples. It allows the user to identify the species that are most important in creating the observed pattern of similarity. The method uses the Bray-Curtis measure of similarity, comparing, in turn, each sample in Group 1 with each sample in Group 2. The Bray-Curtis method operates at the species level and therefore the mean similarity between group 1 and 2 can be obtained for each species (Clarke, 1993).

3.0. Results

3.1. Composition and structure of woody species

A total of 44,195 woody plants representing 99 species from 67 genera and 31 families were recorded from the 75, 0.1 ha, plots. The most species rich families were Mimosaceae (13), Rubiaceae (9), Moraceae (7), Euphorbiaceae (7), Anacardiaceae (6), Combretaceae (5) and Verbenaceae (5) (Appendix 1), and fifteen other families were represented by two to four species. Nine families were represented by one species each (Appendix 1). The most species-rich genera were *Acacia* (8 species) followed by *Combretum* (4), *Ficus* (4), *Albizia* (3), *Pavetta* (3) and *Tricalysia* (3), with the rest being represented by one to two species (Appendix 1). Four species were introduced, namely *Calliandra* sp., *Artocarpus heterophyllus, Senna siamea* and *Lantana camara,* which is also invasive (Appendix 4). The species accumulation curves for the total 75 plots, and for each land use type reached asymptotes, showing that almost all species were accounted for in this woodland (Figure 2). In addition, the species accumulation curve was below the rarefaction curve, suggesting heterogeneity among samples.

,Density of all woody species across all land use types was 5,893 ± 399 plants/ha. Density of woody species differed significantly ($F_{2, 72} = 6.3$, $P < 0.0031$) among the three land use types. Charcoal production areas had the highest (7,131 ± 755 plants/ha), followed by cultivation (6612 ± 665 plants/ha) and grazing land uses (4,152 ± 525 plant/ha, Table 1). ANOSIM showed that community species composition was significantly different among the land uses (Global $R_{ANOSIM} = 0.14$, $p = 0.001$). Pair-wise comparisons showed significant differences in community species composition between cultivation and grazing, as well as grazing and charcoal production, but not between cultivation and charcoal production (Table 2).

Table 1: Woody plant density (plants ha^{-1}), species diversity and richness (at the plot level 0.1 ha; means ± S.E.) in a multiple land use equatorial African savanna, central Uganda. H' – Shannon-Wiener Index, S - Richness, β_W – Whittaker's β-diversity, β_T – Wilson & Shmida Index of Similarity, C_{MH} -Morisita-Horn Index of Similarity.

Land use types	**No. of plots**	**Density (plants ha^{-1})**	**Diversity indices**					
			S	**H'**	**Fisher's α**	**β_w**	**β_T**	**C_{MH}**
Grazing	27	4,152 ± 525^a	14 ± 1.1^a	1.2 ± 0.1^a	3.0 ± 0.3^a	3.1	3.1	0.37 ± 0.02^a
Cultivation	24	6,612 ± 665^b	20 ± 1.2^b	2.1 ± 0.1^b	4.1 ± 0.2^b	2.8	3.0	0.33 ± 0.02^a
Charcoal production	24	7,131 ± 755^b	21 ± 1.1^b	2.0 ± 0.1^b	4.1 ± 0.2^b	2.7	2.8	0.37 ± 0.02^a

Values in the same column accompanied by the same superscript do not differ significantly (Tukey's HST: P < 0.05).

Table 2. Analysis of similarity in community species composition among the different land use types in a multiple land use equatorial African savanna, central Uganda. The ANOSIM sample statistic (R_{ANOSIM}) is reported with significance level (p-value) in parentheses.

Land –use type	**Charcoal production**	**Grazing**
Cultivation	0.04 (0.063)	0.21 (0.001)
Grazing	0.15 (0.001)	

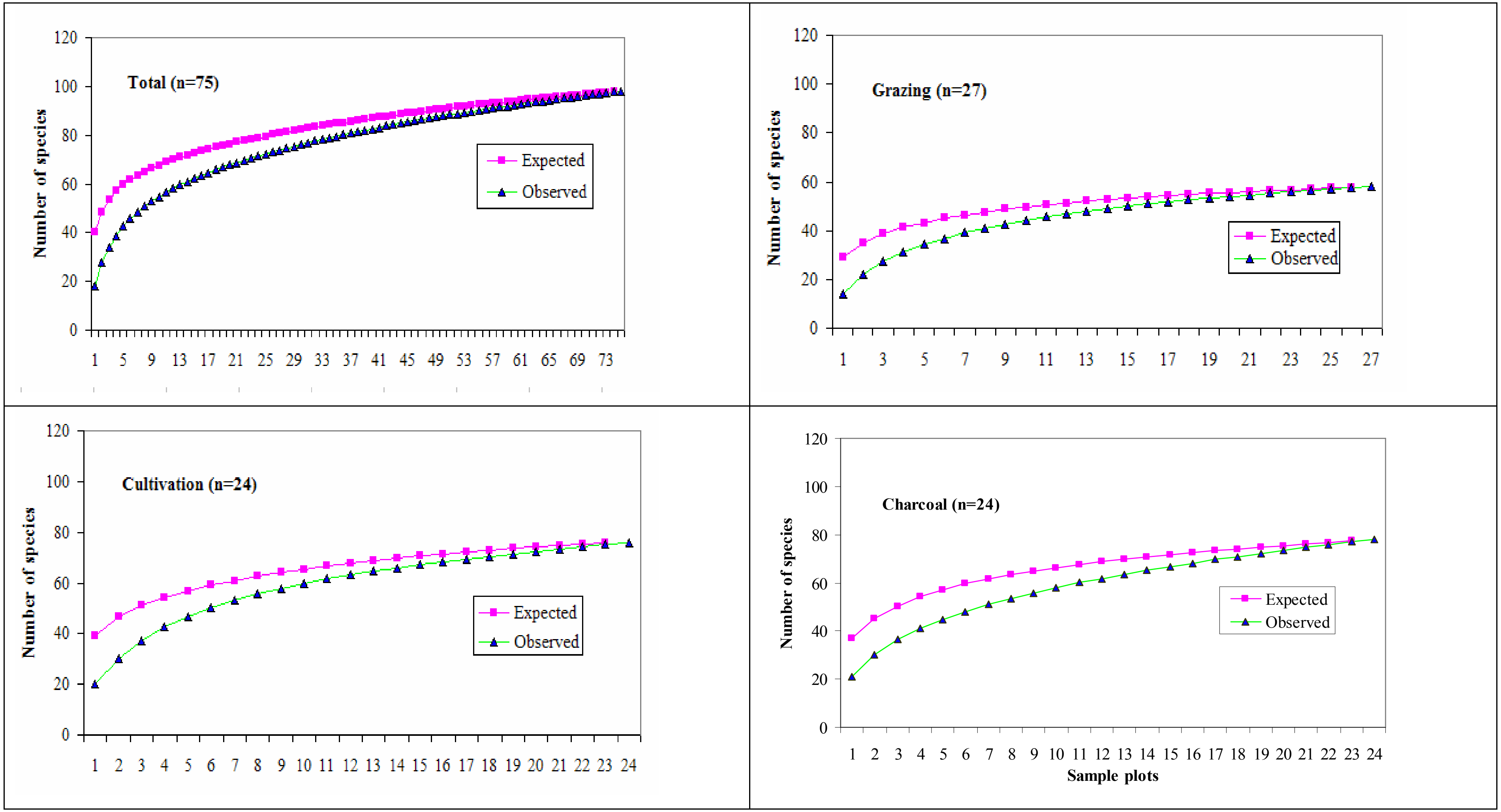


Figure 2: Rarefaction (expected) and species accumulation (observed) curves for all woody species recorded in the 0.1 ha plots throughout the area (total), and for the grazing, cultivation and charcoal production land use types, within a multiple land use equatorial African savanna, central Uganda.

3.2. Species richness and alpha-diversity of woody species

At plot level, total woody plant species richness differed significantly ($F_{2,72} = 10.7$, $P<0.0001$) among the three land uses, with charcoal production and cultivation areas being significantly higher than the grazing land use (Table 1). Similarly, the cumulative species richness was higher for the charcoal production and cultivation areas and lower for grazing land use (Figure 3). These results corroborate the Analysis of Similarity (ANOSIM) that showed that community species composition was significantly different among the land use types.

Across all the plots, woody plant alpha-diversity ranged from 0.34 to 6.34 and from 0.14 to 2.64 for Fisher's Alpha and Shannon-Wiener (H') Indices, respectively. Both H' and α diversity indices were significantly different (H': $F_{2, 72} = 7.31$, $P = 0.001$: α: $F_{2, 72} = 7.29$, $P = 0.001$) among the land use types (Table 1). H' diversity was significantly highest under cultivation and charcoal production and significantly lower under grazing land uses. Similarly, the cumulative H' values followed the same trend, being higher for cultivation (2.95) and charcoal production (2.93) areas with the grazing land use having the lowest value (2.49, Figure 4a). Fisher's α-diversity index was higher for cultivation and charcoal production areas, but lower for the grazing land use (Table 2). The cumulative α-diversity was also higher for charcoal production (10.43) and cultivation (10. 36) areas, and lower under grazing land use (7.85, Figure 4b).

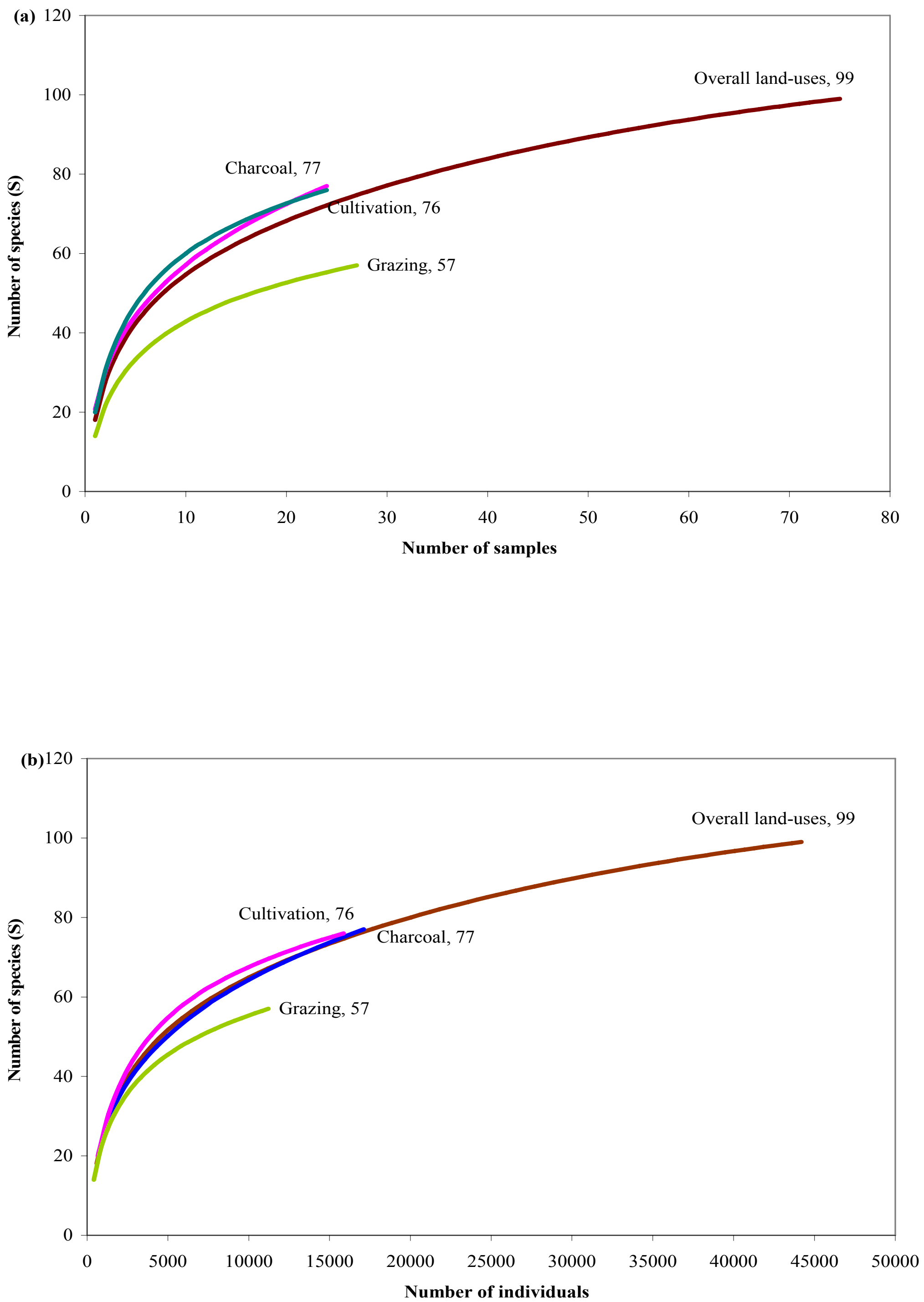
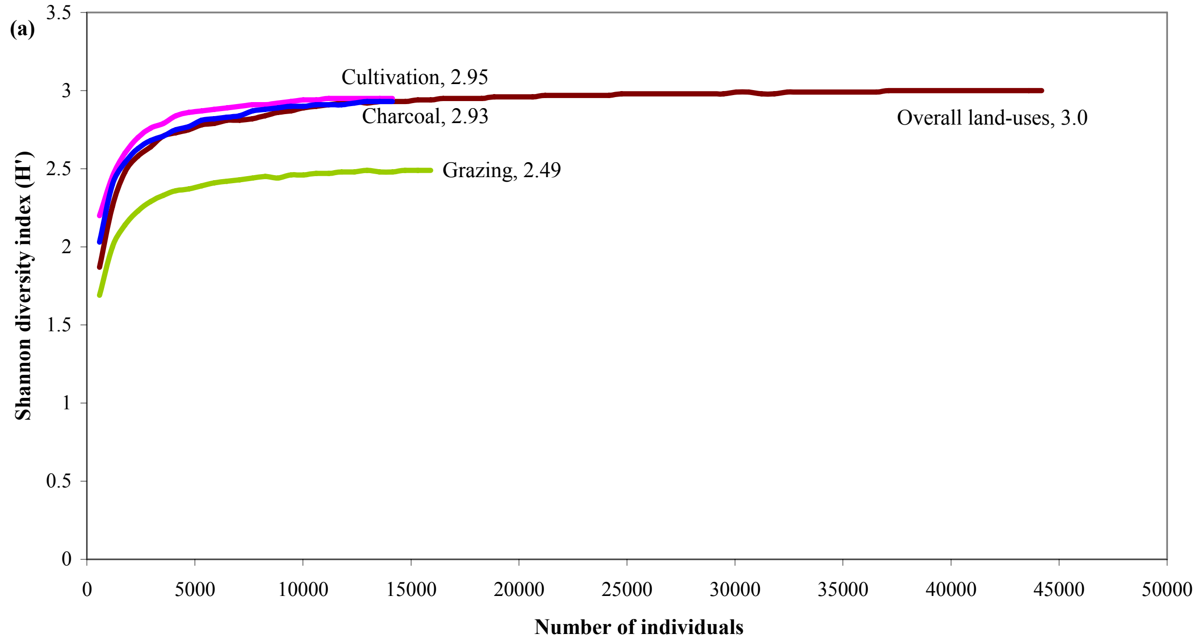


Figure 3: The cumulative species richness curves for all woody species based on: (a) sample plots and (b) number of individuals for all land uses combined (overall), and the grazing, cultivation and charcoal production land use types within a multiple land use equatorial African savanna, central Uganda.



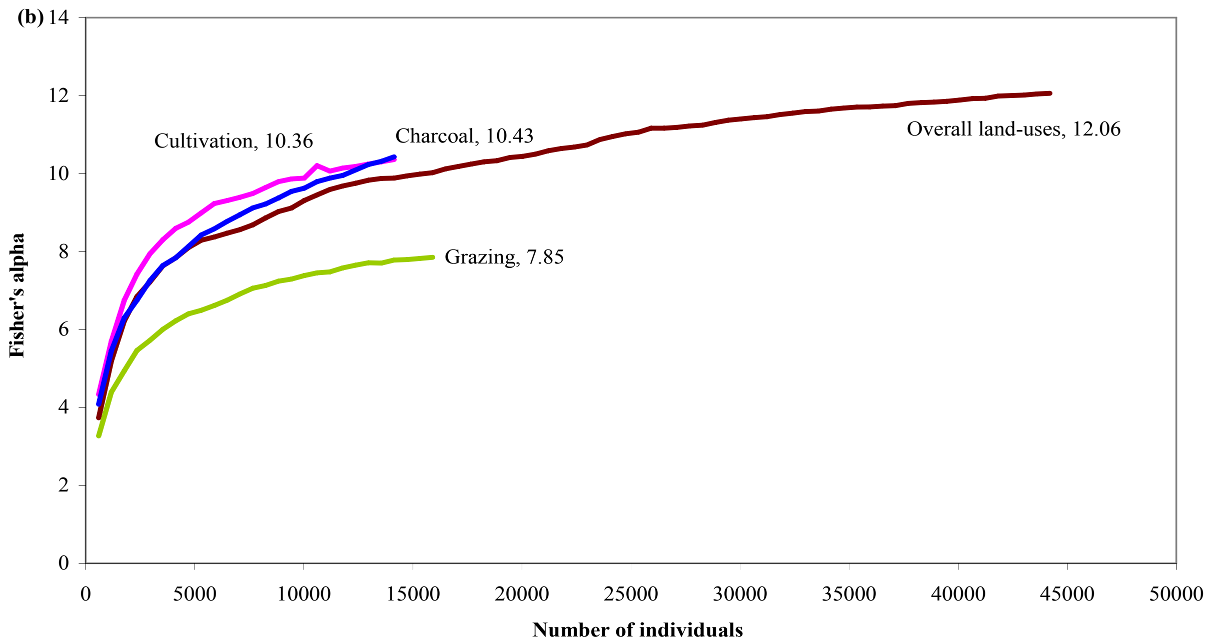


Figure 4: The cumulative diversity curves plotted against number of individuals for: (a) Shannon-Wiener diversity index and (b) Fisher's alpha diversity for all woody species for all land uses combined (overall), and the grazing, cultivation and charcoal production land use types within multiple land use equatorial African savanna, central Uganda.

3.2.1. Species richness and alpha-diversity of trees

Tree species richness differed significantly among the land use types ($F_{2, 72} = 16.6$, $P < 0.0001$), being higher in the cultivation and charcoal production land uses and lower in grazing land use (Table 3). Overall, the most abundant tree species were *Acacia hockii* (120 plants), *Combretum ghasalense* (116), *Combretum molle* (116), *Combretum collinum* (92) and *Piliostigma thonningii* (89), whereas, the most frequent were *C. molle* (45% of plots), *C. ghasalense* (44%), *C. collinum* (43%), *A. hockii* (40%), *G. mollis* (36%) and *P. thonningii* (32%). *Acacia seyal*, *Commiphora africana* and *Commiphora dawei* were only encountered in the grazing areas; *Albizia coriaria* and *Albizia malacophylla* were recorded only in the cultivation land use, while *Pavetta crassipes* and *Zanthoxylum rubescens* were only recorded within the charcoal production land use.

Tree species H' diversity ranged from 0.0 to 2.6, and differed significantly among the land use types ($F_{2, 72} = 15.9$, $P < 0.0001$), being highest for both cultivation and charcoal production and significantly lower for the grazing areas (Table 3). Fisher's alpha for both trees and shrubs could not be calculated due to the high number of singletons in the data sets, which resulted in both tree and shrub number of individuals (N) divided by number of species (S) being ≤ 1.44.

3.2.2. Species richness and alpha-diversity shrubs

Shrub species richness differed significantly among land use types ($F_{2, 72} = 8.28$, $P = 0.0006$), being highest in the cultivation areas (3.4 ± 0.5) followed by charcoal production land use (2.7 ± 0.4) and lowest in the grazing land use (1.3 ± 0.3; Table 3). Overall, the most abundant shared shrub species among the three land use types were *Harrisonia abyssinica* (103 plants), *Rhus natalensis* (87) *Albizia zygia* (75), *Annona senegalensis* (62) and *Lantana camara* (43). The most frequent shrubs were *R. natalensis* (53% of plots), *H. abyssinica* (51%), *A. zygia* (32%), *A. senegalensis* (27%) and *L. camara* (13%). *Clerodendrum cordifolia*, *Flueggea virosa*, *Microglossa pyrifolia* and *Phyllanthus ovalifolius* were recorded only in the grazing areas, while *Zanthoxylum chalybeum* and *Erythrina abyssinica* were recorded only in cultivation and *Dombeya dawei* only in charcoal production areas. Shrub H - diversity ranged from 0.0 to 2.0, and differed significantly among land uses ($F_{2,72} = 7.08$, $P = 0.002$), being highest for cultivation, followed by charcoal production, and lowest for grazing land use (Table 3).

Table 3. Diversity and richness (mean ± S.E.) of tree and shrub species at the 0.1 ha plot level in the different land use types in a multiple land use equatorial African savanna, central Uganda. S - Species richness and H'– Shannon-Wiener diversity index.

Land use type	No. of plots	Species richness and Diversity			
		Tree		Shrub	
		S	H'	S	H'
Grazing	27	3.6±0.3[a]	1.0±0.1[a]	1.3±0.3[a]	0.3±0.1[a]
Cultivation	24	7.8±0.7[b]	1.7±0.1[b]	3.4±0.5[b]	0.9±0.1[b]
Charcoal production	24	7.5±0.7[b]	1.7±0.1[b]	2.7±0.4[b]	0.7±0.1[b]

Values in the same column accompanied by the same superscript do not differ significantly (Tukey, P < 0.05).

3.3. Beta diversity of woody species

The plot-level pair-wise C_{MH} values ranged from 0 – 0.979 for the grazing, 0.005 – 0.972 for charcoal production and 0.001 – 0.961 for cultivation areas. Mean Morisita-Horn (C_{MH}) did not differ significantly ($F_{2,900} = 2.43$, P = 0.09) among the land uses. However, charcoal production and grazing land uses tended to be higher (0.37 ± 0.02, n = 276; 0.37 ± 0.02, n = 351, respectively) than cultivation land use (0.33 ± 0.02, n = 276). Similarly, β_W and β_T were highest for the grazing land use (β_W = 3.1; β_T = 3.1), followed by cultivation (β_W = 2.8; β_T = 3.0) and lowest for charcoal production (β_W = 2.7; β_T = 2.8; Table 3). Hence, the β_W, β_T and C_{MH} values suggest higher β-diversity for the grazing land use type compared to the others. Furthermore, these results are corroborated by the very low within land use SIMPER similarities, and very high between land use dissimilarities. The within land use type similarities were quite low, ranging from 25.3 to 30.5%; being highest for charcoal production (30.5%), followed by grazing (25.4%), and lowest for cultivation (25.3%; Appendix 2). Furthermore, SIMPER analysis showed relatively high mean pair-wise dissimilarities between land use types, ranging between 73.2 and 81.2%. The highest mean dissimilarity was for cultivation versus grazing (81.2%), followed by charcoal versus grazing (76.7%) and lowest for charcoal versus cultivation (73.2%, Appendix 3).

These results are corroborated by lower similarity percentages within land use types. Indeed, SIMPER showed that the number of species making up 90% of the observed similarity within each land use type was 12 for cultivation and charcoal production and 9 for grazing (Appendix 3). The top two species contributing most to the percentage similarity in community species composition within cultivation and charcoal production were *Combretum collinum* and *Combretum molle*. However, for grazing, the second species was *Piliostigma thonningii* (Appendix 3). SIMPER analysis indicated that 24 species between charcoal production and cultivation, 22 species between charcoal and grazing and 23 species between cultivation and grazing contributed most to the dissimilarity between land uses, reflecting the overall differences in community composition, especially between cultivation and grazing (81.2% of dissimilarity; Appendix 3).

4.0. Discussion

4.1. Floristic composition of woody species

Woody plant species accumulation and rarefaction curves reached near asymptote in all land use types, indicating that the sampling effort was sufficient (Figure 2) and that most of the species in the savanna woodlands of Nakasongola had been accounted for. The species-accumulation curves were below the rarefaction curves, suggesting heterogeneity among the samples. This corroborated the species richness results that differed significantly among land use types, being highest for charcoal production and cultivation, and significantly lower for grazing. Of the 99 species recorded in the study area, none has a restricted range in distribution; they all occurred in more than one of the four floral regions of Uganda as per Flora of Tropical East Africa (Polhill, 1952 and more recent). However, *Milicia excelsa* and *Pouteria* sp., both recorded in the study area, are near threatened based on IUCN classification (Pomeroy *et al.,* 2002).

Generally, *Acacia hockii*, *Combretum ghasalense*, *Combretum collinum*, *Combretum molle* and *Piliostigma thonningii* were the most abundant and frequent species across all land use types in the study area. This compares well with the findings of Nangendo *et al.* (2006) that *Combretum molle, Grewia mollis, Annona senegalensis* and *Grewia bicolor* are commonly found in burned areas and in extremely open woodlands. Fire is important for the maintenance and conservation of African savannas ecosystems (Bond & Van Wilgen, 1996; Anderson *et al.,* 2003; Govender *et al.,* 2006). About 20-50% of the grazing areas in Nakasongola are seasonally burned towards the end of the dry seasons before the onset of rainfall (February and July), to allow fresh pastures and kill ticks. People also burn before the rains to clear land for new farms. In addition, large tracks of woodlands are set on fire during dry periods for "calling rainfall", a customary practice commonly undertaken in Nabiswera, Lwampanga, Wabinyonyi and Kalungi sub-counties (Nakasongola District Resource Officer Mbaziira Josephat, pers. comm. 2006). Accidental fires also occur during charcoal production, and fire is used to flush out wild animals during hunting, while arson also occurs. Morris (1995) also observed that people in the miombo woodlands of Malawi burn the bush for preparing their gardens for planting, hunting and calling the rains. Since fires occur at more than one time of the year, and for different purposes, this might result into some patches being burnt twice or more in a year, some specific patches of land may be burnt more than once a year. These numerous fires result in relatively low fire intensities because fuel does not accumulate and fire maintains much of the woodlands as a shrub transition.

The vegetation in Nakasongola District is mainly open woodland in transition to thickets/shrubland, as woodland cover has decreased, while areas under cultivation/settlements have greatly increased since 1984 (Chapter 2). The high number of *Acacia* spp. and density encountered may be due to seed dispersal by ruminants' and they find favourable germination beds within animal faeces (Schultka &

Cornelius, 1997). In addition, the formation of a soil seed bank is also a common survival strategy of *Acacia* spp., which may accumulate viable but dormant seeds in the soil (Sabiiti & Wein 1987; Witkowski & Garner, 2000). Seasonal bush burning may be a contributory factor, since germination of *Acacia* spp. is in general enhanced when subjected to the heat of fire (Teketay, 1996, 1997; Eriksson *et al.,* 2003).

Some of the species encountered were restricted to particular land use types, suggesting the influence of land use practices in the distribution of woody plants. For example, the higher abundance of *Piliostigma thonningii* and *Acacia seyal* in the livestock grazing areas than in cultivation and charcoal production areas, may be attributed to the preference of herbivores to palatable species (Anderson *et al.,* 2007), high resprouting ability (Chapter 6) and dependence on animals for seed dispersal. On the other hand, the presence of *Acacia mellifera*, *Harrisonia abyssinica, Lantana camara, Rhus natalensis and Carissa edulis,* which are encroacher species in disturbed vegetation, is not surprising (Van Vegten, 1981, 1983). Selective predation of preferred seedling species by herbivores has far-reaching consequences for plant community development (Hanley, 1998). Anthropogenic factors (charcoal production and shifting cultivation) have similarly been reported to be causative agents of degradation in the central Ethiopian highlands (Yirdaw & Luukkanen, 2003). However, the differences among land use types may be the result of the extent (intensity and frequency) and duration of anthropogenic disturbances and particular land use practices taking place in a given area. Changes in land use practice may result in continuously or more abruptly deteriorating environmental conditions for some plant species, causing their decline in abundance and distribution.

The chopping down of trees for charcoal production on a short rotation has clearly resulted in local species loss. Some of the highly utilized species for charcoal production, firewood and harvested as poles for building fences and houses are *Acacia hockii, A. polyacantha, A. seyal, A. sieberiana, Albizia coriaria, A. zygia, Combretum capituliflorum, C. collinum, C. ghasalense, C. molle, Grewia mollis, Hymenocardia acida, Gymnosporia senegalensis, Piliostigma thonningii, Terminalia glaucescens* and *Vepris nobilis.* This list is based on the responses of people interviewed (Chapter 2), and existing literature (Namaalwa *et al.,* 2005; Byabashaija *et al.,* 2004; Kisakye, 2004). However, the most adversely affected were species of *Albizia* and *Terminalia* because of relatively poor regenerative capacities (few resprouting stumps and relatively low recruitment; Chapter 6 & 7). While, resource users also mentioned they were decreasing in abundance (Chapter 7).

4.2. Species richness

Total woody species richness differed significantly among land uses with areas of charcoal production and cultivation having higher species richness than grazing. Differences in species richness between land uses may be the result of the different land use practices *per se*, or because of differences in the number of individuals counted (Gotelli & Colwell, 2001). Charcoal production and cultivation were equally well sampled (24 plots each) and had an almost equal number of species (77 versus 76 respectively), while grazing with 27 plots had only 57 species. The number of individuals recorded in charcoal production was higher than cultivation (17,117 versus 15,869, respectively; Figure 3b), but there were only 11,211 individuals under grazing. Major disturbances can remove some species directly without affecting the dominance relations of those remaining (Clinton *et al.,* 1993). Forest/woodland conversion to farmland, selective harvesting of woody plants for firewood and charcoal production, seasonal fires, livestock grazing and hunting of native herbivores are major mechanisms of forest/woodland degradation, habitat change and biodiversity loss (Ramirez-Marcial *et al.,* 2001; Reyers, 2004; Banda *et al.,* 2006).

Species richness of woody species in a miombo woodland was different between shifting cultivation and more permanently cultivated areas (Luoga *et al.,* 2005). The patchwork in the landscape after abandonment of the land provides opportunities for different functional groups of species without the disappearance of the original species (Luoga *et al.,* 2002, 2004). Indeed, richness and diversity increases with an increase in heterogeneity within a range of patch sizes (Cabral *et al.,* 2003). However, the ever expanding shifting cultivation, leading to fragmentation of the remaining natural habitats may result in the local extinction of small fragmented and isolated populations (Robinson & Southerland, 2002; Tilman *et al.,* 2002; Benton *et al.,* 2003). Thus, shifting cultivation can play either a positive or a negative role, depending on how it is managed. Variability in species richness between land uses may also be explained by a variety of factors that include habitat quality (Dauber & Wolters, 2000), spatial-temporal dynamics (Purtauf *et al.,* 2001; Waldhardt & Otte, 2003), boundary characteristics (Fagan *et al.,* 1999) and neighbourhood effects (Tilman & Downing, 1994). These interact to define species richness in a landscape.

Species richness of all woody species in Nakasongola (99 species, 31 families within 75 0.1 ha plots) is lower than the forest-woodland-savanna mosaic of northern Budongo Forest Reserve, NW Uganda (121 species, 38 families, using 594 0.05 ha plots; Nangendo *et al.,* 2006). Although both occur within the same ecological zone, the latter is a reserve, where human disturbances are restricted. The woody species richness of Nakasongola is also lower than that of the woodlands of Katavi-Rukwa ecosystem in western Tanzania (229 species, 45 families, within 50 0.1 ha plots; Banda *et al.,* 2008), the Kitulangalo Forest Reserve and surrounding communal lands of Tanzania (133 species, 31 families, within 64 0.1 ha plots; Luoga *et al.,* 2000b), and communal savanna woodlands in three South African provinces (135 species, 42 families, within 90 0.1 ha plots; Dovie *et al.,* 2008). These comparisons suggest loss of species from Nakasongola through habitat degradation. The richness of 2 - 31 species per 0.1 ha in Nakasongola is low relative to those reported elsewhere. However, Nakasongola is similar to the 1 – 28 species per 0.1 ha in the woodlands of western Tanzania (Banda *et al.,* 2008).

4.3. Alpha-diversity

Alpha-diversity (H' and Fisher's) of woody species was significantly higher in cultivation and charcoal compared with grazing, which may be a consequence of the lower species richness under grazing (Figure 4a). Similarly, cumulative Fisher's alpha was higher under charcoal and cultivation than under grazing (Figure 4b). These results are consistent with the suggestion of Hayek & Buzas' (1997) that the more species present and the more evenly the individuals are spread across the species, the higher H'. Fisher's alpha diversity was low when the number of species is low (Figure 4a & b). The low species diversity in the grazing lands may be a consequence of greater herbivory and extent of bush fires than in the other land uses. Both fire and herbivory prevent establishment of seedlings. Other studies in grazing ecosystems (e.g. Milchunas & Lauenroth, 1993; Huston, 1994; Noy-Meir, 1995; Proulx & Mazunder, 1998; Osem *et al.,* 2002) have shown that primary productivity, evolutionary history and resulting vegetation physiognomy and plant life form can interact with grazing in determining plant community structure and diversity. Tree density at a site may change rapidly with changes in the frequency or intensity of herbivory and fire (Bond & Van Wilgen, 1996; Scholes & Archer, 1997). Such changes can be extensive, influencing vegetation at a landscape scale (Dublin *et al.,* 1990; Sinclair, 1995; Dublin, 1995). In some places where livestock grazing and termite damage are heavy, bare patches were common.

Compared to other African savannas, H' diversity (0.41 - 2.64) in Nakasongola tended to be higher than that of southern Malawi miombo woodlands (0.55 - 1.26; Mwase *et al.,* 2007), but lower than that of the Kitulangalo miombo woodland of Tanzania (2.9 - 3.13; Malimbwi *et al.,* 1994), and the South African communal savannas (2.5 – 3.9; Dovie *et al.,* 2008).

4.4. Beta-diversity

ANOSIM revealed no significant difference in species richness between cultivation and charcoal production areas. However, the Morisita-Horn results indicated higher mean values (higher similarities) in species richness of both charcoal production and grazing lands than for cultivated lands. The general absence of significant differences in species richness between charcoal production and cultivation areas could, probably, be due to the cyclic succession of land use over time. The cleared woodlands are burnt after charcoal production and then used for cultivation. Within much of the grazing lands, hydromorphic grasslands, aquatic wetlands and the grassland (wetland periphery) are permanently used for communal grazing. They are dominated by grasses with few trees and are seasonally flooded. These areas are not used for cultivation as they typically have poor soils. In contrast, cultivated land that is left fallow inevitably supports grasses and forbs that are used for grazing for a relatively short time period.

Generally, and despite the low alpha diversity, these results suggest that Nakasongola has relatively high β-diversity. The spatial distribution within the grazing lands was more heterogeneous than for cultivation and charcoal production, and was consistent with the fact that grazing occurs in both hydromorphic grasslands and more temporary grazing areas within the cultivation / charcoal production mosaic. In contrast, for the cultivation and charcoal production land uses, species were more evenly distributed. The high β-diversity in the grazing areas might also be due to varying levels and intensities of grazing (stocking rates) in different areas. Livestock grazing impacts are typically not uniform across a landscape because herbivores are highly selective of areas with higher soil fertility (soil type) and landscape position (Bell, 1982; Senft *et al.,* 1987), and also favour new grass growth from burnt areas. Grazing increases the heterogeneity in resource distribution (de Bello *et al.,* 2006), thereby, promoting coexistence of species with dissimilar resource acquisition strategies (Pugnaire *et al.,* 2004; Stubbs & Wilson, 2004).

SIMPER analysis showed that *Combretum collinum, C. molle* and *C. ghasalense* contributed highly to the similarity in species composition among plots under charcoal production, and yet they are the most utilized species for charcoal production. Similarly, Luoga *et al.,* (2002) found relatively large standing volumes of *Julbernardia globiflora* and *Combretum molle,* despite their high levels of utilization. In both cases these highly important resource species recover well after harvesting through resprouting (Chapter 6; Luoga *et al.,* 2004). Similar results were also noted by Shackleton *et al.* (1994) in communally managed South African savannas.

5.0. Conclusions

Woody species density, and species richness and diversity were significantly higher in both cultivation and charcoal production relative to grazing. These different land uses have altered natural disturbance patterns and have resulted in changes in species abundance and distribution, community composition and ecosystem function. The relatively low woody species alpha diversity and richness in the savanna woodlands of Nakasongola may be an indicator of woodland degradation, fragmentation and local species loss; a result of unsustainable woody plant harvesting for charcoal production, and possibly the relatively short-term cycle of shifting cultivation. Over the long term, charcoal production and grazing (including associated burning practices) have resulted in loss of tree cover, and probably reductions in woody species richness and diversity. More sustainable harvesting practices are needed in order to halt and reverse the loss of tree cover and diversity.

Maintenance of biodiversity and ecosystem functioning requires closer collaboration between farmers and foresters (Jackson & Jackson, 2002). Securing the long-term survival of plant diversity and richness in these savanna woodlands will require appropriate policies to guide changes in land use practices that accommodate the requirements of land users and conservation efforts. However, current market forces, such as demand for charcoal and firewood are likely to result in a rapid attrition of these natural assets if effective and efficient management is not implemented. Although we have gained a good understanding of diversity patterns in relation to anthropogenic factors in the woodland of Nakasongola, a detailed study of the influence of other environmental factors, particularly topo-edaphic factors (e.g. Witkowski & O'Connor, 1996) would provide a more complete understanding of species distribution patterns.

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References

Akankwasa, D. & Tromborg, E. 2001. Challenges and strategies in the biomass energy sector-Working paper: revision of the Tax and Fee system in the Forest Sector, Uganda.

Anderson, A.N., Cook, G.D. & Williams, R.J. 2003. *Fire in Tropical Savannas*. Springer, New York.

Anderson, T.M., Ritchie, M.E. & Mc Naughton, S.J. 2007. Rainfall and soils modify plant community response to grazing in Serengeti National Park. *Ecology* 88: 1191-1201.

Banda, T., Mwangulango N, Meyer B, Schwartz MK, Mbago F., Sungula M. & Caro T. (2008) The woodland vegetation of Katavi-Rukwa ecosystem in western Tanzania. *Forest Ecology and Management* 255: 3382-3395.

Banda, T., Schwartz, M.W. & Caro, T. 2006. Woody vegetation and composition along a protection gradient in a miombo ecosystem of western Tanzania. *Forest Ecology and Management* 230: 179-185.

Begossi, A. 1996. Use of ecological methods in ethnobotany. *Economic Botany* 50: 280-289.

Belbin, L. 1995. A multivariate approach to the selection of biological reserves. *Biodiversity and Conservation* 9: 951-963.

Bell, R.H.V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. pp 193-216. In: Huntley, B.J. & Walker, B.H. (Eds.) Ecology of Tropical Savannas. Springer-Verlag, Berlin, Germany.

Benton, T. G., Vickery, J. A. & Wilson, J. D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and. Evolution* 18: 182-188.

Bond, W.J. & van Wilgen, B.W. 1996. Fire and plants. pp. 38-42. Chapman and Hall, London, UK.

Botha, J., Witkowski, E.T.F. & Cock, J. 2005. A review of nurseries as conservation or social forestry outreach tools. *International Journal of Biodiversity Science and management* 1: 33-51.

Braedt, O. & Standa-Gunda, W. 2000. Woodcraft markets in Zimbabwe. *International Tree Crops Journal* 10: 367-84.

Byabashaija, M.D., Esegu, J.F.O., Kidiya, J.M., Basoga, M. & Odia, R.K. 2004. Traditional uses of indigenous tree species. *Ugandan Journal of Agricultural Sciences* 9: 363-371.

Cabral, A.C., De Miguel, J.M., Rescia, A.J., Schmitz, M.F. & Pineda, F.D. 2003. Shrub encroachment in Argentinean savannas. *Journal of Vegetation Science* 14: 145-152.

Chidumayo, E. N. 1988. Estimating fuelwood production and yield in regrowth dry miombo woodland in Zambia. *Forest Ecology and Management* 24: 59-66.

Clarke, J.M., Cavendish, W. & Coote, C. 1996. Rural household and miombo woodlands: use, value, and management. pp. 101-135. In: Campbell, B.M. (Ed.) The Miombo in Transition: Woodlands and Welfare in Africa. Centre for International Forestry Research (CIFOR*)*, Bangor, Indonesia.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143.

Clinton, B.D., Boring, L.R. & Swank, W.T. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology* 74: 1551-1558.

Colwell, R.K. 2006. EstimateS: Statistical Estimation of Species Richness and Shared Species from samples. Version 8.0. Persistent URL<purl.oclc.org/estimates>

Colwell, R.K., Mao C.X. & Chang, J. 2004. Interpolating, extrapolating and comparing incidence-based species accumulation curves. *Ecology* 85: 2717-2727.

Crawley, J.M. 1997. The structure of plant communities**.** pp. 475-531. In Crawley M.J (Ed) Plant Ecology. Blackwell Science, Oxford, UK.

Dauber, J. & Wolters, V. 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biology and Biochemistry* 32: 93-99.

De Bello, F., Lepš, J. & Sebastià, M. T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* 29: 801-810.

Dovie, D.B.K, Witkowski, E.T.F. & Shackleton, C.M. 2004. The fuelwood crisis in Southern Africa-relating fuelwood use to livelihoods in a rural village. *GeoJournal* 60: 123-133.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2008. Knowledge of plant resource use based on location, gender and generation. *Applied Geography* 28: 311-322.

Dovie, D.B.K., Shackleton, C.M. & Witkowski, E.T.F. 2002. Direct-use values of woodland resources consumed and traded in a South African village. *International Journal of Sustainable Development and World Ecology* 9: 269-283.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2003. Direct-use value of smallholder crop production in semi-arid rural South African village. *Agricultural Systems* 76: 337-357.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2005. Monetary valuation of livelihoods for understanding the composition and complexity of rural households. *Agriculture and Human Values* 22: 87-103.

Dublin, H. 1995. Vegetation dynamics in the Serengeti Mara ecosystem: the role of elephants, fire and other factors. pp. 71-90. In: Sinclair, A & Arcese, P. (Eds.) Serengeti II: dynamics, management, and conservation of an ecosystem. Chicago University Press, Chicago.

Dublin, H.T., Sinclair, A.R.E. & McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59: 1147-1164.

Dupré, C. 2001. Regional and local variation in plant species richness. Acta Universitatis Upsaliensis. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 641. Uppsala, ISBN 91-554-5064-4, pp.32.

Duque, A., Sanchez, M., Cavelier, J. & Duivenvoorden, J.F. 2002. Different floristic patterns of woody under storey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology* 18: 499-525.

Dytham, C. 2003. Choosing and using statistics: a Biologist's Guide. 2nd edition, pp. 77-150. Blackwell Science, Oxford, UK.

Dzerefos, C.M., Shackleton, C.M. & Witkowski, E.T. 1999. Sustainable utilisation of woodrose-producing mistletoes (Loranthaceae) in South Africa. *Economic Botany* 53: 439-447.

Eilu, G., Hafashimana, D.L.N. & Kasenene, J.M. 2004. Density and species diversity of trees in four tropical forest of the Albertine Rift, Western Uganda. *Diversity and Distributions* 10: 303-312.

Eriksson, I., Teketay, D. & Granström, A. 2003. Response of plant communities to fire in an Acacia woodland and a dry Afromontane forest, southern Ethiopia. *Forest Ecology and Management* 177: 39-50.

Fagan, W.F., Cantrell, R.S. & Cosner, C. 1999. How habitat edges change species interactions. *Journal of American Nature* 153: 165-183.

Faith, D.P. & Walker, P.A. 1996. Environmental diversity: on the best possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation* 5: 399-415.

Fisher, R.A., Corbet, A.S. & Williams, C.B. 1943. The relation between the number of species and the number of individuals in a Random sample of an animal population. *The Journal of Animal Ecology* 12: 42 – 58.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Reviews of Ecology and Systematics* 35: 557-581.

Gerhardt, K. & Hytteborn, H. 1992. Natural dynamics and regeneration methods in tropical dry forests-an introduction. *Journal of Vegetation Science* 4: 95-102.

Gotelli, J.N. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391.

Govender, N., Trollope, W.S.W., & Van Wilgen, B.W. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748-758.

Hamilton, A.C. 1991. A Field Guide to Uganda Forest Trees. Makerere University, Kampala, Uganda.

Hanley, M.E. 1998. Seedling herbivory, community composition and plant life history traits: *Perspectives in Plant Ecology*. *Evolution and Systematics* 1: 191-205.

Harper, D.A.T. (Ed.) 1999. Numerical Palaebiology. Computer-based modeling and analysis of fossil and their distributions. John Wiley and Sons, Chichester, New York. pp.468.

Hayek, L.C. & Buzas, M.A. 1997. *Surveying Natural Populations*. Columbia University Press, New York, pp. 563

Hsieh, H.L. & Li, L.A. 1998. Rarefaction Diversity: a Case Study of Polychaete Communities Using an Amended FOTRAN Program. *Zoological Studies* 37: 13-21.

Huston, M.A. 1994. Non-equilibrium processes and the maintenance of local species diversity. pp. 110-155. In: Huston MA (Ed.) Biological diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Jackson, D.D.L. & Jackson, L.J. 2002. The farm as Natural Habitat Reconnecting Food Systems with Ecosystems. Island Press, Washington, DC, USA. pp. 250.

Katende, A.B., Birnie, A. & Tengnas, B. 1995. Useful trees and shrubs for Uganda. Identification, propagation and management for agricultural and pastoral communities. Technical Handbook No. 10. Regional Soil Conservation Unit, RSCU/SIDA, Nairobi, Kenya.

Kisakye, R. 2004. Charcoal consumption in Kampala and its source districts. Unpublished Report on a consultancy survey for the GTZ Energy Advisory Project, Ministry of Energy and Mineral Development, Kampala, Uganda.

Kisamba-Mugerwa, W. 2001. Rangelands management policy in Uganda. A paper prepared for the international conference on policy and institutional options for the management of rangelands in dry areas, 7-11 May 2001 Hammamet, Tunisia.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. *Journal of Cleaner Production* 12: 1047-1057.

Langdale-Brown, I., Osmaston, H.A. & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land use. Entebbe Government Printers, Uganda. pp. 159.

Letsela, T., Witkowski, E.T.F & Balkwill, K. 2002. Direct use values of communal resources in Bokong and Tsehlanyane in Lesotho: whither the commons? *International Journal of Sustainable Development and World Ecology* 9: 351-368.

Letsela, T., Witkowski, E.T.F. & Balkwill, K. 2003. Plant resources used for subsistence in Tsehlanyane and Bokong in Lesotho. *Economic Botany* 57(4): 619-639.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2005. Land-cover and use changes in relation to the institutional framework and tenure of land and resources in eastern Tanzania miombo woodlands. *Environment, Development and Sustainability* 7: 71-93.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000a. Economic of charcoal production in miombo woodlands of eastern Tanzania: some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000b. Differential utilisation and ethnobotany of trees in Kitulangalo Forest Reserve and surrounding communal lands, eastern Tanzania. *Economics Botany* 54: 328-343.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000c. Subsistence use of wood products and shifting cultivation within a miombo woodlands of eastern Tanzania, with some notes on commercial uses. *South African Journal of Botany* 66: 72-85.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 16: 15-30.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forest Ecology and Management* 189: 23-35.

Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell Science Ltd, USA. pp. 256.

Malimbwi, R.E., Misana, S., Monela, G.C., Jambiya, G. & Zahabu, E. 1994. Impact of charcoal extraction to the forest resources of Tanzania. Charcoal Potential in Southern Africa (CHAPOSA).

MEA (Millennium Ecosystem Assessment) 2005a. *Ecosystem and Human Well-Being: Biodiversity Synthesis*: Island Press World Resources Institute, Washington, DC.

MEA (Millennium Ecosystem Assessment) 2005b. *Ecosystem and Human Well-Being: Desertification Synthesis*: Island Press World Resources Institute, Washington, DC.

Milchunas, D.G. & Lauenroth, W. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 6: 327-366.

Mwase, W.F., Bjornstand, A., Bokosi, J.M., Kwapata, M.B. & Stedje, B. 2007. The role of land tenure in conservation of tree and shrub species diversity in miombo woodlands of southern Malawi. *New Forests* 33: 297 – 307.

Mwavu, E.N., Witkowski, E.T.F. & Mucina, L. 2008. Plant communities of a semi-deciduous tropical rainforest in north-western Uganda: role of soil and anthropogenic factors. *Phytocoenologia* 38: 193-211.

Namaalwa, J., Eid, T. & Sankhayan, P. 2005. A multi-species density-dependent matrix growth model for the dry woodlands of Uganda. *Forest Ecology and Management* 213: 312-327.

Nangendo, G., Steege, H.T. & Bongers, F. 2006. Composition of woody species in a dynamic forest-woodland-savannah mosaic in Uganda: implications for conservation and management. *Biodiversity and Conservation* 15: 1467-1495.

National Environment Management Authority (NEMA), 2002. State of environment report for Uganda. National Environment Information Centre, Kampala.

Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science* 6: 701-710.

O'Connor, T.G. 2005. Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the Southern Drakensberg, South Africa. *Journal of Applied Ecology* 42: 975-988.

Osem, Y., Perevolotsky, A. & Kigel, J. 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology* 90: 936-946.

Pandolfi, J.M. & Greenstein, B.J. 1997. Preservation of community structure in depth assemblages of deep water Caribbean reef corals. *Limnology and Oceanography* 47: 1505-1516.

Parker, D., Downer, E.R. & Cole, G.E.D. 1967. Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Plotkin, J.B. & Muller-Landau, H.C. 2002. Sampling the species composition of a landscape. *Ecology* 83: 3344-3356.

Polhill, R.M (Ed.) (1952 et Seq.): Flora of Tropical East Africa (FTEA). Royal Botanic Gardens, Kew.

Pomeroy, D., Tushabe, H., Mwima, P & Kasoma, P. 2002. Uganda Ecosystem and Protected Area Characterisation: A contribution to Strategic Criteria for Rural Investments in Productivity (SCRIP). Program of the USAID Uganda Mission. pp. 1-55.

Proulx, M. & Mazumder, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor versus nutrient-rich ecosystems. *Ecology* 79: 2581-2592.

Pugnaire, F.I., Armas, C. & Valladares, F. 2004. Soil as a mediator in plant-plant interactions in semi-arid community. *Journal of Vegetation Science* 15: 85-92.

Purtauf, T., Dauber, J. & Wolters, V. 2001. Effects of changes in landscape patterns on carabid diversity and community structure. pp. 70-75. In: Mander, U., Printsmann, A. & Palang, H. (Eds.) Development of European landscapes. Publicationes Instituti Geographici Universitis Tartuensis 92, Tartu.

Ramírez-Marcial, N., González-Esponosa, M. & William-Linera, G. 2001. Anthropogenic disturbance and tree diversity in montane rainforest in Chiapas, Mexico. *Forest Ecology and Management* 154: 311-326.

Rennolls, K. & Laumonier, Y. 2000. Species diversity structure analysis at two sites in tropical rain forest of Sumatra. *Journal of Tropical Ecology* 16: 253-270.

Reyers, B. 2004. Incorporating anthropogenic threats into evaluations of regional biodiversity and prioritization of conservation areas in the Limpopo South Africa. *Biological Conservation* 118: 521-531.

Robinson, R.A. & Southerland, W.J. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39: 157-176.

Sabiiti, E.N. & Wein, R.W. 1987. Fire and acacia seeds: a hypothesis of colonization success. *Journal of Ecology* 74: 937-946.

Sawatzky, D.L., Raines, G.L., Bonhan-Carter, G.F. & Looney, C.G. 2004. ARCSDM3: Arc MAP extension of spatial data modelling using weights of evidence, logistic regression, fuzzy logic and neural network analysis. http://www.ige.unicamp.br/sdm/ArcSDM3/.

Scholes, R.J. & Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Reviews of Ecology and Systematics* 28: 517-544.

Schultka, W. & Cornelius, R. 1997. Vegetation structure of a heavily grazed range in northern Kenya: tree and shrub canopy. *Journal of Arid Environments* 36: 291-306.

Seaby, R.M.H & Henderson, P.A. 2006. Species Diversity and Richness® Version IV. Pisces Conservation Limited, Lymington, England.

Seaby, R.M.H., Henderson, P.A., Prendergest, J.R., 2006. Community Analysis® Version 3.1. Pisces Conservation Limited, Lymington, England.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *Bioscience* 37: 789-799.

Shackleton, C.M., Griffin, N.J., Banks, D.I., Mavrandonis, J.M. & Shackleton, S.E. 1994. Community structure and species composition along a disturbance gradient in a communally managed South African savanna. *Vegetatio* 115: 157-167.

Shackleton, S.E., Shackleton, C.M., Cunningham, A.B., Lombard, C., Sullivan, C.A. & Netshiluvhi, T. R. 2002. Knowledge on *Sclerocarya birrea* subsp. c*affra* with emphasis on its importance as non-timber forest product in South and southern Africa: a summary. Part 1: Taxonomy, ecology and role in rural livelihoods. *Southern African Forestry Journal* 194: 27- 42.

Sheil, D. 1996. Species richness, tropical forest dynamics and sampling: questioning cause and effect. *Oikos* 26: 587-590.

Sinclair, A.R.E. 1995. Serengeti past and present. pp. 3-30. In: Sinclair, A.R.E. & Arcese, P. (Eds.) Serengeti II: Dynamics, Management and Conservation of an Ecosystem. University of Chicago Press, Chicago.

Solbrig, O.T., Goldestein, G., Medina, E., Sarmiento, G. & Silva, J. 1992. Responses of savannas to stress and disturbance: a research approach. pp. 63-73. In: Wali, M.K. (Ed.) Environmental rehabilitation, volume 2. SPB Academic Publications, The Hague.

Stubbs, W.J. & Wilson, J.B. 2004. Evidence for limiting similarity in a sand dune community. *Journal of Ecology* 92: 557-587.

Teketay, D. 1996. Germination ecology of twelve indigenous and eight exotic multipurpose leguminous species from Ethiopia. *Forest Ecology and Management* 80: 209-223.

Teketay, D. 1997. Germination ecology of *Acacia negrii*, an endemic multipurpose tree from Ethiopia. *Tropical Ecology* 38: 39-46.

Tilman, D. & Downing, J.A. 1994. Biodiversity and Stability in Grasslands. *Nature* 367: 363-365.

Tilman, D., Cossman, K.G., Matson, P.A., Naylor, R. & Polasky, S. 2002. Agricultural sustainability and intensive production practices. *Nature* 418: 671-677.

UBOS (Uganda Bureau of Statistics) 2000. National household census estimates 2000. (Retrieved on 17/11/2005 from http://www.ugandadish.org/nakasongola.doc).

URT, 1991. Population census national profile Bureau of statistics, President's office planning commission, Dar Es Salaam, Tanzania.

USDA Forest Service, 1989. Interim Resource Inventory Glossary. Department of Agriculture, Forest Service, Washington DC, U.S.A. pp. 96

Van Vegten, J.A. 1981. Man made vegetation changes: an example from Botswana's savanna. Working paper No. 40. Botswana. National Institute of Development and Cultural Research (NIR), Botswana.

Van Vegten, J.A. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56: 3-7.

Vanclay, J.K. 1998. Towards more rigorous assessment of biodiversity. pp. 211-232. In: Bachmann, P., Koehl, M. & Paivienen, R. (Eds.) Assessment of biodiversity for improved forest planning. Forest Science Series 51, Kluwer Academic Publishers, Dordecht.

Waldhardt, R. & Otte, A. 2003. Indicators of plant species and community diversity in grasslands. *Agricultural Ecosystems and Environment* 98: 339-351.

Walker, B. & Stefan, W. 1996. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAET/UNSO vegetation map of Africa. UNESCO, Paris, France.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.

William-Linera, G. 2002. Tree species richness complementarity, disturbance and fragmentation in Mexican tropical montane cloud forest. *Biodiversity and Conservation* 11: 1825-1843.

Williams, V.L., Witkowski, E.T.F. & Balkwill, K. 2005. Application of diversity indices to appraise plant availability in the traditional medicinal markets of Johannesburg, South Africa. *Biodiversity and Conservation* 14: 2971-3001.

Witkowski E.T.F. & O'Connor, T.G. 1996. Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. *Vegetatio* 124: 9-23.

Witkowski, E.T.F. & Garner, R.D. 2000. Spatial distribution of soil seed banks of three African savanna woody species at contrasting sites. *Plant Ecology* 149: 91–106.

Witkowski, E.T.F. & Garner, R.D. 2008. Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive *Solanum mauritianum* in a temperate to subtropical riparian ecosystem. *South African Journal of Botany* 74: 476-484.

Wolda, H. 1983. Diversity, diversity incidences and tropical cockroaches. *Oecologia* 58: 290-298.

Yirdaw, E. & Luukkanen, O. 2003. Indigenous woody species diversity in *Eucalyptus globules* Labill. ssp. *globules* plantations in the Ethiopian highlands. *Biodiversity and Conservation* 12: 567-582.

Zar, J.H. 1990. Biostatistical Analysis. Prentice-Hall, Englewood Cliff. NJ.

Appendix 1: Species list arranged alphabetically by families for woody species recorded in 75, 0.1 ha plots within a multiple land use equatorial African savanna, central Uganda. The total number of individuals and frequencies within plots (number of times present within the 75 plots) are included.

Families	**Species**	**Number of individuals**	**Frequency within plots**
ACANTHACEAE	*Acanthus* sp. L.	4	1
ANACARDIACEAE	*Lannea barteri* Engl.	397	21
	Lannea schweinfurthii Engl.	4	1
	Oncoba spinosa Forssk.	1	1
	Ozoroa insignis Delile	42	3
	Rhus natalensis Bernh. ex Krauss	1,445	68
	Rhus vulgaris Meikle	232	26
ANNONACEAE	*Annona senegalensis* Pers.	791	43
	Monanthotaxis ferruginea (Oliv.) Verdc.	2	2
APOCYNACEAE	*Alstonia boonei* De Wild.	34	12
	Carissa edulis Vahl	219	32
ARALIACEAE	*Cussonia arborea* Hochst. ex A. Rich.	17	4
ASTERACEAE	*Microglossa pyrifolia* Kuntze	1	1
BIGNONIACEAE	*Kigelia africana* (Lam.) Benth.	76	15
	Markhamia lutea K. Schum.	15	3
	Stereospermum kunthianum Cham.	105	16
BURSERACEAE	*Commiphora africana* (A. Rich.) Engl.	45	10
	Commiphora dalzielii Hutch.	50	2
CAESALPINIACEAE	*Piliostigma thonningii* (Schumach.) Milne-Redh.	2,275	43
	Senna siamea (Lamarck) H. S. Irwin & Barneby**	6	2
CAPPARIDACEAE	*Capparis fascicularis* DC.	361	3
	Crateva adansonii DC.	4	1
	Maerua triphylla A. Rich.	2	2
CELASTRACEAE	*Mystroxylon aethiopicum* (Thunb.) Loes.	11	2
	Gymnosporia senegalensis Loes.	418	30
COMBRETACEAE	*Combretum capituliflorum* Fenzl ex Schweinf.	1,801	22
	Combretum collinum Fresen.	9,241	63
	Combretum ghasalense Engl. & Diels	4,725	59
	Combretum molle Engl. & Diels	5,814	60
	Terminalia glaucescens Planch. ex Benth.	521	32
EBENACEAE	*Euclea latidens* Stapf	252	31
EUPHORBIACEAE	*Bridelia scleroneura* Müll. Arg.	87	12
	Euphorbia candelabrum Tremaut ex Kotschy	29	11
	Flueggea virosa Buch. –Ham. ex Wall.	1	1
	Hymenocardia acida Tul.	2,191	40
	Phyllanthus ovalifolius Forssk.	3	1
	Securinega sp. Comm. ex Juss.	1	1
	Securinega virosa (Willd.) Baill.	62	15
HYPERICACEAE	*Psorospermum febrifugum* Spach	1	1
LAMIACEAE	*Clerodendrum cordifolium* A. Rich.	1	1
	Vitex doniana Sweet	365	7
	Vitex ferruginea Schumach.	510	21
	Vitex fischeri Gürke	26	2
LOGANIACEAE	*Strychnos innocua* Delile	455	30
MELIACEAE	*Ekebergia capensis* Sparrm.	33	3
	Pseudocedrela kotschyi Harms	186	16
	Trichilia dregeana Harv. & Sond.	1	1

	Trichilia emetica Vahl	2	2
MIMOSACEAE	*Acacia hamulosa* Benth.	74	15
	Acacia hockii De Wild.	1,708	49
	Acacia malacocephala Harms	7	2
	Acacia mellifera Benth.	2	1
	Acacia polyacantha Willd.	894	47
	Acacia senegal Willd.	113	8
	Acacia seyal Delile	139	4
	Acacia sieberiana DC.	384	36
	Albizia coriaria Welw.	106	14
	Albizia malacophylla Walp.	64	7
	Albizia zygia J.F. Macbr.	1,738	38
	Calliandra sp. Benth.**	32	2
	Dichrostachys glomerata Chiov.	179	15
MORACEAE	*Antiaris toxicaria* Lesch.	62	10
	Artocarpus heterophyllus Lam.**	2	1
	Ficus dicranostyla Mildbr.	1	1
	Ficus natalensis Hochst.	29	8
	Ficus ovata Vahl	1	1
	Ficus sp. L.	33	2
	Milicia excelsa (Welw.) C.C. Berg****	91	5
OLACACEAE	*Ximenia aegyptiaca* L.	4	1
	Ximenia americana L	9	2
PAPILIONACEAE	*Erythrina abyssinica* Lam.	6	3
	Lonchocarpus laxiflorus Guill. & Perr.	3	2
RHAMNACEAE	*Ziziphus mauritiana* Lam.	56	3
RUBIACEAE	*Canthium vulgare* (K. Schum.) Bullock	2	1
	Gardenia ternifolia Schumach.	380	46
	Pavetta crassipes K. Schum.	22	4
	Pavetta gardeniifolia Hochst. ex A. Rich.	56	4
	Pavetta insignis Bremek.	6	1
	Tricalysia bagshawei S. Moore	4	2
	Tricalysia niamniamensis Schweinf. ex. Hiern	1	1
	Vangueria apiculata K. Schum.	23	3
	Vangueria tomentosa Hochst.	18	1
RUTACEAE	*Vepris nobilis (*Delile) Mziray	1,320	24
	Zanthoxylum chalybeum Engl.	88	9
	Zanthoxylum rubescens Planch. ex Hook.	33	5
SAPINDACEAE	*Allophylus abyssinicus* Radlk.	1	1
	Allophylus africanus P. Beauv.	137	23
SAPOTACEAE	*Manilkara dawei* (Stapf) Chiov.	140	16
	Pouteria sp. Aubl.****	1	1
SIMAROUBACEAE	*Balanites aegyptiacus* Delile	17	4
	Harrisonia abyssinica Oliv.	1,675	65
STERCULIACEAE	*Dombeya dawei* Sprague	40	2
TILIACEAE	*Grewia mollis* Juss.	1,142	53
	Grewia trichocarpa Hochst. ex A. Rich.	4	2
	*Trema guineense (*Schumach. & Thonn.) Ficalho	74	11
UMBELLIFERAE	*Steganotaenia araliacea* Hochst.	12	4
VERBENACEAE	*Lantana camara* L.***	368	18
UNIDENTIFIED	*Enseka**	24	2
	*Kiondo**	5	1

* Local vernacular name; ** Introduced species; *** Introduced and invasive alien

****Near Threatened

Appendix 2: Contribution of individual species to the overall similarity within land use types (grazing, cultivation and charcoal production). Species are ranked according to their percentage contribution to the similarity within each land use. Average similarity and percentage cumulative similarity are also given.

Species	Mean Abundance	Mean Similarity	Percentage Contribution	Cumulative Percentage
Charcoal (mean similarity = 30.5)				
Combretum collinum	129.9	7.4	24.1	24.1
Combretum molle	104.8	4.8	15.9	40.0
Combretum ghasalense	70.2	4.7	15.4	55.4
Rhus natalensis	30.2	3.2	10.4	65.8
Hymenocardia acida	43.0	1.8	6.0	71.8
Harrisonia abyssinica	23.3	1.6	5.3	77.1
Combretum capituliflorum	50.6	0.9	2.8	79.9
Grewia mollis	19.5	0.8	2.7	82.6
Annona senegalensis	15.4	0.7	2.2	84.8
Acacia hockii	21.7	0.7	2.2	87.1
Albizia zygia	13.5	0.6	1.9	89.0
Vepris nobilis	47.2	0.5	1.6	90.6
Cultivation (mean similarity = 25.3)				
Combretum collinum	135.7	6.5	25.6	25.6
Combretum molle	102.5	4.2	16.5	42.1
Albizia zygia	58.5	2.6	10.2	52.4
Acacia hockii	42.5	2.2	8.5	60.9
Harrisonia abyssinica	33.4	1.9	7.6	68.5
Combretum ghasalense	31.4	1.5	5.8	74.3
Rhus natalensis	17.7	1.2	4.8	79.1
Grewia mollis	21.3	1.1	4.2	83.4
Acacia polyacantha	20.3	0.6	2.5	85.9
Hymenocardia acida	28.2	0.5	1.9	87.8
Strychnos innocua	14.1	0.4	1.8	89.6
Combretum capituliflorum	23.6	0.4	1.5	91.0
Grazing (mean similarity = 25.4)				
Combretum collinum	106.2	7.3	28.7	28.7
Piliostigma thonningii	64.4	7.0	27.7	56.3
Combretum ghasalense	84.7	4.5	17.6	74.0
Combretum molle	31.1	1.8	7.0	81.0
Rhus natalensis	11.0	0.8	3.3	84.3
Harrisonia abyssinica	11.7	0.6	2.2	86.5
Acacia polyacantha	5.8	0.5	1.8	88.3
Hymenocardia acida	17.9	0.4	1.7	90.0
Gardenia ternifolia	6.6	0.4	1.6	91.5

Appendix 3: Results of SIMPER analysis highlighting the species contributing most to the dissimilarity between land uses types. Species are ranked according to their percentage contribution to the dissimilarity between land use types and only those with > 2% contribution are shown. Dissimilarity and percentage cumulative dissimilarity are also given.

Land use types	**Species**	**Mean Abundance**		**Mean Dissimilarity**	**Percentage Contribution**
		Charcoal	**Cultivation**		
Charcoal versus Cultivation (*mean dissimilarity = 73.2%*)	*Combretum collinum*	129.9	135.7	11.5	15.8
	Combretum molle	104.8	102.5	9.0	12.3
	Combretum ghasalense	70.2	31.4	5.8	8.0
	Hymenocardia acida	43.0	28.2	4.3	5.9
	Combretum capituliflorum	50.6	23.6	4.0	5.5
	Acacia hockii	21.7	42.5	3.9	5.4
	Albizia zygia	13.5	58.5	3.7	5.0
	Vepris nobilis	47.2	7.8	3.2	4.4
	Harrisonia abyssinica	23.3	33.4	2.4	3.3
	Acacia polyacantha	10.5	20.3	2.3	3.1
	Rhus natalensis	30.2	17.7	2.2	3.0
	Grewia mollis	19.5	21.3	2.0	2.7
	Annona senegalensis	15.4	10.9	1.7	2.4
	Piliostigma thonningii	17.3	5.0	1.6	2.2
	Vitex doniana	0.0	15.2	1.3	1.8
	Strychnos innocua	3.9	14.1	1.1	1.5
	Vitex ferruginea	11.0	9.3	1.1	1.5
	Terminalia glaucescens	8.9	6.5	0.9	1.3
	Lannea barteri	12.5	2.0	0.9	1.2
	Capparis fascicularis	15.0	0.0	0.8	1.1
	Lantana camara	1.1	9.8	0.8	1.0
	Acacia sieberiana	7.7	3.7	0.7	1.0
	Dichrostachy glomerata	0.4	5.3	0.5	0.7
	Carissa edulis	3.3	4.3	0.5	0.6

		Charcoal	**Grazing**		
Charcoal versus grazing *(mean dissimilarity =76.7%)*	*Combretum collinum*	129.9	106.2	12.6	16.4
	Combretum ghasalense	70.2	84.7	9.5	12.4
	Combretum molle	104.8	31.1	8.1	10.6
	Piliostigma thonningii	17.3	64.4	6.2	8.1
	Hymenocardia acida	43.0	17.9	4.9	6.4
	Combretum capituliflorum	50.6	0.7	3.6	4.7
	Vepris nobilis	47.2	0.0	3.3	4.3
	Rhus natalensis	30.2	11.0	3.1	4.0
	Acacia hockii	21.7	6.2	2.3	3.0
	Harrisonia abyssinica	23.3	11.7	2.2	2.9
	Annona senegalensis	15.4	5.9	1.9	2.5
	Grewia mollis	19.5	6.1	1.8	2.4
	Acacia polyacantha	10.5	5.8	1.4	1.8
	Albizia zygia	13.5	0.3	1.4	1.8
	Gymnosporia senegalensis	4.6	9.6	1.1	1.4
	Terminalia glaucescens	8.9	5.6	1.0	1.4
	Lannea barteri	12.5	1.8	1.0	1.3
	Acacia sieberiana	7.7	4.1	0.9	1.2
	Vitex ferruginea	11.0	0.9	0.9	1.2
	Capparis fascicularis	15.0	0.0	0.9	1.2
	Acacia seyal	0.0	5.1	0.8	1.0

	Gardenia ternifolia	5.0	6.6	0.8	1.0
		Cultivation	**Grazing**		
Cultivation versus grazing ***(mean dissimilarity = 81.2%)***	*Combretum collinum*	135.7	106.2	14.3	17.6
	Combretum molle	102.5	31.1	8.3	10.2
	Combretum ghasalense	31.4	84.7	8.0	9.8
	Piliostigma thonningii	5.0	64.4	6.6	8.2
	Albizia zygia	58.5	0.3	4.7	5.8
	Acacia hockii	42.5	6.2	4.6	5.7
	Hymenocardia acida	28.2	17.9	3.4	4.1
	Harrisonia abyssinica	33.4	11.7	3.1	3.8
	Acacia polyacantha	20.3	5.8	2.6	3.2
	Grewia mollis	21.3	6.1	2.1	2.6
	Combretum capituliflorum	23.6	0.7	1.9	2.4
	Rhus natalensis	17.7	11.0	1.8	2.2
	Vitex doniana	15.2	0.0	1.7	2.1
	Annona senegalensis	10.9	5.9	1.5	1.8
	Strychnos innocua	14.1	0.9	1.3	1.6
	Lantana camara	9.8	3.9	1.2	1.5
	Acacia seyal	0.0	5.1	1.0	1.2
	Gymnosporia senegalensis	2.1	9.6	1.0	1.2
	Terminalia glaucescens	6.5	5.6	1.0	1.2
	Gardenia ternifolia	3.4	6.6	0.8	1.0
	Vepris nobilis	7.8	0.0	0.8	1.0
	Dichrostachys glomerata	5.3	1.5	0.8	0.9
	Vitex ferruginea	9.3	0.9	0.7	0.9

CHAPTER 5

Variations in woody species composition in relation to environmental gradients in a multiple land use equatorial African savanna, central Uganda

Abstract

Different components of a plant community may vary independently of each other along environmental gradients. In this study the interrelations between the woody species composition and the corresponding site environmental (soil chemical and physical properties), and anthropogenic factors were described for a multiple land use equatorial wooded savanna in central Uganda. A total of 44,195 woody plants, representing 99 species in 67 genera and 31 families were recorded within 75, 0.1 ha, plots. Woody plant basal area and density differed significantly ($F_{2,72} = 12$, $P < 0.0001$; $F_{2,72} = 6.3$, $P = 0.003$, respectively) among land use types, being higher under cultivation and charcoal production than under grazing land uses. The Detrended Correspondence Analysis (DCA) revealed a gradient in species composition and distributions for all woody plant density. For both basal area and abundance of all woody species, the total variance in species-environmental factor relations (for the combined first four canonical axes) was higher than 50%, suggesting a relatively strong influence of the measured environment variables on species composition and distributions. For the 16 highly utilized species, CCA axes 1 and 2 explained 18.1% of the variance in their abundance, and 49.9% in species-environment relations, while for basal area the first two axes explained 22.4 and 57.8%, respectively. For both all woody species and the 16 highly utilized species, the 1st canonical axis was more highly correlated with exchangeable cations, and the 2nd axis was highly associated with the grazing land use. Hence, canonical axis 1 may be interpreted as an edaphic gradient, and axis 2 as a grazing land use gradient. The CCA revealed a significant ($P < 0.05$) influence of soil Ca^{2+} and Mg^{2+} associated with grazing on the woody species composition and structure in this savanna. Therefore, human activities carried out within the savanna woodlands should aim at sustainable utilization of the wood resources. In addition, an appropriate savanna woodland management policy will be required to guide changes in land use that accommodate the requirements of land users aided by targeted conservation efforts.

Abbreviations: CCA-Canonical Correspondence Analysis, DCA-Detrended Correspondence Analysis

Key words: CCA ordination, degradation, land use types, variance partitioning

Nomenclature: Polhill (1952 et seq.), Hamilton (1991).

1.0. Introduction

Savannas cover about 40% of the land surface of Africa (Huntley & Walker, 1982) and are vitally important in providing both ecological (e.g. erosion protection, micro-climate amelioration, etc.) and economic services (e.g. timber, food, fodder, medicine, non-wood products, and wild-life habitats) that sustain local livelihoods and national economies (e.g. Luoga *et al.,* 2000; Shackleton *et al.,* 2002; Kristensen & Lykke, 2003; Kituyi, 2004; Dovie *et al.,* 2005; Pote *et al.,* 2006). In spite of their importance in many parts of Africa, little is known about their plant species and communities responses to gradients in environmental (e.g. edaphic) and spatial factors. Understanding how plant species and communities respond to gradients in environmental variables and land use practices may aid in their conservation and management. Local biotic and abiotic ecological interactions have long been a focus to explain the distribution patterns of plant species in communities and ecosystems (Ehrenfeld *et al.,* 1997; Verheyen & Hermy, 2001). Indeed, a number of ecological studies (e.g. Witkowski & O'Connor, 1996; Grace, 2001; Eilu *et al.,* 2004; Mwavu *et al.,* 2008) have shown how vegetation structure, species diversity and species association vary across abiotic gradients (i.e. topography, soil pH, soil moisture and nutrient availability). Edaphic conditions are among the abiotic factors that play a significant role in dictating vegetation structure and dynamics in savanna ecosystems (Scholes & Walker, 1993) and plant distributions (Brown, 1988). For instance, soil characteristics such as clay content influence infiltration rates and the ability of plants to take up water (Patten & Ellis, 1995), and consequently, the type of plants that grow in a particular soil type. In totality, precipitation, soil texture, topographic relief and anthropogenic activities are some of the key factors that may affect the overall vegetation pattern in dryland areas (Patten & Ellis, 1995). Therefore, an understanding of spatial distribution of plant species requires an understanding of their relationship with edaphic factors. In addition, a predictive knowledge of the relationships between land use practices, the composition, structure and function of vegetation, and the supply of ecosystem services is required (Higgins *et al.,* 1999).

In 2005 Uganda had about 2.72 million hectares of woodlands compared to the 3.974 million hectares in 1990; hence a loss of about 32% of woodland area over the period 1990 - 2005 (NFA, 2008). The savanna woodlands of Uganda are highly utilized by subsistence farmers and in many regions cultivation, charcoal production and grazing are undertaken. Similarly, the multiple land use woodlands of Nakasongola District, central Uganda (the focus of this study) were by 2002 supporting a human population density of 41 people/km^2 (Uganda Bureau of Statistics, 2002). This is mainly through charcoal production (engaging 70-80% of the total households), livestock grazing, and subsistence crop cultivation. Subsistence crop cultivation accounts for about 85% of the food supply for households and more than 50% of their monetary income (DEP, 2002). In Uganda, studies have been undertaken relating biomass to bio-energy, on ranching schemes and their management (e.g.

Akankwasa & Tromborg, 2001; Kisamba-Mugerwa, 2001; NEMA, 2002) as well as growth, use and management of woodland resources (Namaalwa *et al.,* 2005). Hence, the limited information on the ecological diversity and spatial distribution of only a few important woody plant species, particularly those highly utilized for charcoal production (Chapter 2), is insufficient to inform their conservation and sustainable management. Knowing the environmental variables that determine woody plant species abundance and distribution will be of significance in developing management strategies as they are vital in supporting the livelihoods of local people.

This study assessed the variation in woody plant abundance and basal area across land uses, and the relative role of edaphic factors as controls of woody species composition in a multiple use equatorial savanna, central Uganda. The following questions were explored; (i) Do abundance and basal area of woody species differ across land use types? (ii) Which species are most abundant and with the highest basal area in each land use type? and (iii) To what degree do the soil and environmental variables as well as land use types, explain the variation in species distributions in the savanna woodlands?

2.0. Materials and Methods

2.1. Study area

The study focused on multiple land use savanna woodlands of Nakasongola District, south of Lake Kyoga, central Uganda ($0^{0}40'$- $1^{0}41'$ N, $31^{0}57'$ - $32^{0}48'$ E). The District covers about 3,424 km^2, most of which is woodland and grassy savanna, with 322 km^2 (10%) of open water and wetlands. It comprises eight sub-counties (administrative sub-divisions), namely Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata. Each sub-county has a mean (± S.E.) of 49 (± 22) villages and 3,193 ± 390 households. The mean number of households/village was 82 (± 32), with an average of seven persons/household. The district has a total human population of 128,126 (41 people/km^2) (2000 National Housing Census), with 50.2% males and 49.8% females. About 95.3% of the population are rural and 4.7% urban (Uganda Bureau of Statistics, 2002).

The only available rainfall records for the period 1993-2003 showed that the mean annual rainfall ranged from 500 – 1000 mm and is concentrated into two wet seasons (March to May and August to November), but rainfall received and reliability is higher in the south, declining gradually to the north. The mean monthly rainfall ranges from 22.8 to 127.8 mm, being lowest from December to February (Figure 1). The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C, respectively. The topography of the area undulates between 1,036 and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al.,* 1967).

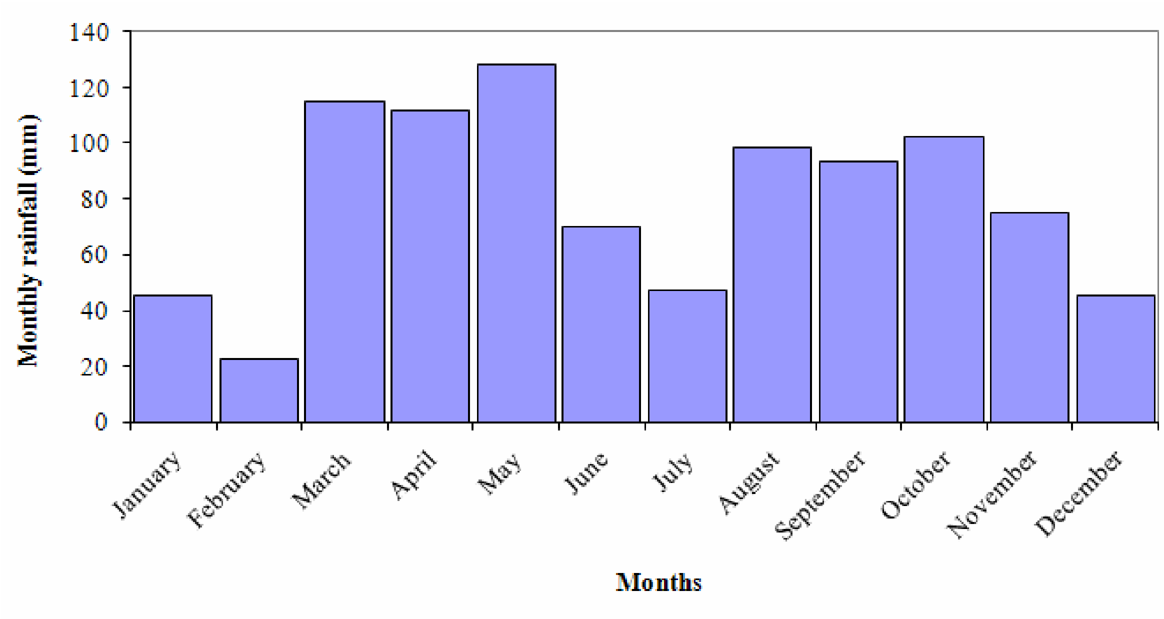

Figure 1: Mean annual rainfall for the past ten years (1993-2003) in Nakasongola District, central Uganda. (Data source: Mr. Senkaali Sammy, pers. comm. 2006, Katuugo weather station).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964), a natural savanna woodland or woodland of mixed deciduous trees 3 m to 12 m high and grasses 0.3 m to 1.3 m high at maturity. However, the cover of the grass layer varies with season, is often patchy and subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirk*ii ssp. *mildbraedii, A. senegal* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983). The major land use practices in this savanna are livestock grazing, subsistence crop cultivation, and charcoal production (Chapter 2). There is a succession of land use change over time which is typical of areas subject to slash and burn agriculture. Areas used for charcoal production are then used for cultivation, while cultivated areas may subsequently be used for grazing. However most of the grazing lands occur on hydromorphic grasslands which are only suitable for grazing.

2.2. Sampling design

The present main land use types (i.e. cultivation, grazing and charcoal production) were identified and selected for the purposes of this study. Representative villages (areas) in each of the eight sub-counties were selected (with the help of local leaders and officials from the Department of Natural Resource and Environment) for woody vegetation sampling in March 2006. In each sub-county, at least three transects were laid, each representing one of the three major land uses, with the exception of one sub-county which had 4 transects. The locations of the transects were selected randomly, but taking into consideration, the homogeneous nature of the area for a particular land use type and being sufficiently large in extent to accommodate at least three 20 m x 50 m (0.1 ha) plots, with a minimum separation distance of 200 m. Transects were laid radiating away from the source of disturbance, because in villages where subsistence activities are paramount, there may be gradients of increasing resource availability, with increasing distance from the source of disturbance. In total, 25 transects representing 75, 0.1 ha plots were laid across the study area. Twenty four plots were sampled in each land use type, except for "grazing" which had 27 plots. The geographical location of each transect was recorded using a GPS, and then mapped with ARCMAP version 9.0 (Sawatzky *et al.,* 2004; Chapter 4).

2.3. Data collection

Within each 0.1 ha plot, the identity of all the woody (i.e. trees and shrubs) species, the number of individuals as well as height and stem diameter of each individual (except for seedlings), were recorded. A tree usually has one or more perennial stems at least 7 cm dbh, a more or less definitely formed crown of foliage and a height of at least 5 m at maturity (USDA Forest Service 1989). A shrub has persistent woody stems and a relatively low growth habit, and generally produces several basal shoots instead of a single bole. Hence a shrub differs from a tree by its low stature and non-arborescent form, and is usually less than 5 m tall. Stem basal diameter of all woody plants was measured at 1.3 m height (DBH) for trees and at reference height (DRH) for shrubs. For multi-stemmed plants, all stems were counted, and the diameter of three average stems was measured. Sampling for shrubs and seedlings was also done in the whole 0.1 ha plot to avoid under representation, since shrub density was relatively low. Initial plant species identification was done in the field using identification guides, mainly based on the Flora of Tropical East Africa (Polhill, 1952 et seq.) and Hamilton (1991), and the help of a botanist familiar with the flora of the area. Unidentified species were collected and vouchers subsequently identified in the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda. In addition, data on numbers of livestock per sub-county were obtained from the District Veterinary Officer (Dr. Bugeza James, pers. comm. 2006).

2.3.1. Selection of the 16 species highly utilized for charcoal production

The 16 species highly utilized for charcoal production were determined through interviews with 45 respondents that included at least 5 to 6 resource users (i.e. charcoal producers and peasant farmers) from each sub-county, from key informants (Chapter 2) and existing literature (e.g. Byabashaija *et al.,* 2004, Kisakye, 2004; Namaalwa *et al.,* 2005). In addition, the respondents were interviewed on the present status of these species, and whether their numbers were increasing or decreasing.

2.4. Soil variables

Soil samples (0 to15 cm depth) from 5 random locations within the 0.1 ha plot were collected with a soil auger (2 cm diameter, 15 cm deep cores). Samples were bulked, air-dried, cleaned (by removing stones and charcoal fragments) and thoroughly mixed. The composite samples for each sampling plot were passed through 20 and 2 mm sieves and sub-sampled. Soil texture, pH, organic matter and elemental content were then determined. Texture analysis was conducted to determine clay (particles < 0.002 mm diameter), silt (0.002 - 0.05 mm), and sand (0.05 - 2 mm) fractions using the pipette method (Bouyoucos, 1936). The soil pH was determined in a distilled water (1:1 v/w) soil suspension using the McLean (1982) Glass Electrode Method, while organic matter (OM) content was indirectly estimated through the determination of organic carbon (C) content by the Walkley-Black procedure (Nelson & Sommers, 1982). Total nitrogen (N) was determined by the Kjedahl method (Bremner & Mulvaney, 1982). Exchangeable cations (Na^+, K^+, Mg^{2+}, and Ca^{2+}) were leached from 10 g soil with 200 ml of buffered normal ammonium acetate (pH 7) and concentrations in the leachate determined by Atomic Absorption Spectrophotometry. Available phosphorus was determined by digestion in HNO_3, $HClO_4$, and HF (Lim & Jackson, 1982) and determined colorimetrically using molybdenum blue (Allen *et al.,* 1989). All soil analysis was performed by the Soil Science Department Laboratory, Makerere University, Kampala, Uganda.

2.5. Data analysis

2.5.1. Community structure

For each woody species, density (plants/ha) and basal area (m^2/ha) per plot, as well as overall frequency (number of plots in which it was recorded) were determined. Basal area of each individual was obtained using the formula: $BA = \pi\ (DBH/2)^2$, on the assumption that stem cross-sectional area is based on a circular stem (Ibarra-Manríquez & Martínez-Ramos, 2002). To obtain the overall basal area for a shrub individual, the mean basal-area for three average stems was calculated and then multiplied by the total number of stems encountered. Differences in species basal area and density among land use types for both total woody species and the 16 highly utilized species were tested using one-way ANOVA, followed by Tukey's HSD test. Similar tests were performed for soil chemical and physical parameters.

2.5.2. Ordinations

Patterns of woody species composition were analysed using both the unconstrained (i.e. DCA) and constrained (i.e. CCA) ordinations. The Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980) with 26 segments was used to test if there was a gradient in species composition. A DCA is one of the most powerful multivariate tools for representing pattern in communities composed of species that vary unimodally along underlying compositional gradients (Gauch, 1982).

The DCA was then followed by variance partitioning ordinations to separate the effects of soil variables, land use types, and position (i.e. degrees East and North) explanatory variables on woody species composition and distribution in the studied savanna. Two sets of partial ordinations were carried out between overall woody plant abundance and the environmental variables. Explanatory variables included in the first partial ordination were grouped into: (i) Soil variables (i.e. silt, clay, sand, pH, organic matter, available phosphorus, total nitrogen, Na^+, K^+, Mg^{2+}, and Ca^{2+}), (ii) anthropogenic variables (grazing, cultivation and charcoal production) and (iii) geographic position. The second partial ordination only included soil variables that were sub-grouped into; (i) texture (silt, clay and sand), (ii) exchangeable cations (i.e. Na^+, K^+, Mg^{2+}, and Ca^{2+}), and (iii) others (organic matter, pH, Available phosphorus). Total exchangeable cations (S) were calculated as a sum of Na^+, K^+, Mg^{2+}, and Ca^{2+}.

Canonical Correspondence Analysis (CCA) was employed to relate species composition data to edaphic and anthropogenic variables (i.e. land use types), using CANOCO version 4 (ter Braak & Šmilauer, 2003). Included in the CCA were plot species data (i.e. basal area and abundance) and corresponding edaphic variables (i.e. texture, organic matter, pH, and exchangeable cations 'S'), land use type (i.e. cultivation, grazing, and charcoal production), number of livestock, human population, and geographic position to account for potential spatial differences. CCA ordinations were performed separately for: (a) the total woody species data set, (b) total woody species > 1 m height, (c) the 16 species highly utilized for charcoal production and (d) the 16 species with > 1 m height and highly utilized for charcoal production, using the same data categorisation employed for the community structure analysis. When two variables showed collinearity, only one of them was included in further analysis. The Monte Carlo Re-Randomisation Permutation Test was used to evaluate the statistical significance of the relationship between species and the measured environmental variables. This is a direct test of whether the included environmental variables have a significant effect on variation in community species composition. It was calculated for the first canonical axis and then for the combination of the first four canonical axes, under a reduced model using 499 permutations. The intra-set correlations and the length of the arrows were used to infer the relative importance of each environmental variable for the prediction of species composition and distribution (ter Braak & Verdonschot, 1995).

3.0. Results

3.1. Densities, basal areas and frequencies of woody species

A total of 44,195 woody plants, representing 99 species in 67 genera and 31 families were recorded from the 75, 0.1 ha, plots. Of the 99 species, only 45 (45.5%) were recorded in all the three land uses (Appendix 1).

Basal area of woody species differed significantly ($F_{2, 72} = 12.0$, $P < 0.0001$) among the land use types, being highest in cultivation, followed by charcoal production and lowest in grazing (Table 1). However, the cultivation and charcoal production land use types did not differ significantly in terms of plant basal area. On the other hand, woody species density was significantly different ($F_{2,72} = 6.3$, P

= 0.003) across land uses, with charcoal production having the highest density, followed by cultivation and then grazing (Table 1). However, cultivation and charcoal production were not significantly different in terms of their density of woody species.

The species that contributed most to both basal areas and densities across all the land use types were *Combretum collinum* and *Combretum molle* (Appendix 1). However, there were different species which contributed the next most, *Piliostigma thonningii* in grazing; *Albizia zygia* and *Harrisonia abyssinica* in cultivation; and *Vepris nobilis* in charcoal production areas.

Table 1: Basal areas and densities (mean ± S.E.) of all woody and highly utilized (for charcoal production) species in the land use types in a multiple land use equatorial African savanna, central Uganda.

Land use types	No. of plots	All woody species		Highly utilized species	
		Basal area (m^2ha^{-1})	Density (plants ha^{-1})	Basal area (m^2ha^{-1})	Density (plants ha^{-1})
Grazing	27	62 ± 6.6^{a}	$4,152 \pm 525^{a}$	42 ± 4.7^{a}	$3,485 \pm 463^{a}$
Cultivation	24	124 ± 11.7^{b}	$6,612 \pm 665^{b}$	76 ± 9.1^{b}	$4,905 \pm 573^{b}$
Charcoal prod.	24	112 ± 10.7^{b}	$7,131 \pm 755^{b}$	68 ± 5.4^{b}	$5,496 \pm 623^{b}$

Values in the same column accompanied by the same superscript do not differ significantly (Tukey's HSD Test, P < 0.05).

3.1.1. Species highly utilized for charcoal production

For the 16 highly utilized species, woody basal area differed significantly ($F_{2,\ 72} = 7.5$, $p = 0.001$) among the land uses, being highest for cultivation and charcoal production and lower for grazing (Table 1). Woody species densities also differed significantly ($F_{2,\ 72} = 3.6$, $p = 0.032$) across the land use types, being highest for charcoal production, and cultivation and lowest for grazing (Table 1).

3.1.2. Variation in soil variables among different land use types

In terms of the measured soil variables, only Na^{+} and Mg^{2+} differed significantly ($p < 0.05$; Table 2) among the land use. Soil pH was relatively consistent in the three land uses and did not differ significantly (Table 2). Organic matter, total nitrogen, available phosphorus, potassium, calcium and percentage sand did not differ significantly among the land use types. Sodium concentration was significantly higher ($F_{2,72} = 10.68$, $p < 0.0001$) in the grazing land use than in cultivation and charcoal production (Table 2). Similarly, Mg^{2+} also differed significantly ($F_{2,72} = 5.49$, $p < 0.006$) between grazing and charcoal, being highest under grazing (Table 2). Both percentage clay and silt differed significantly between the grazing and cultivation land use types. The highest percentage of clay occurred in the cultivation land use, whereas, the grazing land use had the highest percentage of silt (Table 2).

Table 2: Variation in soil chemical and physical parameters (mean ± S.E.) among the different land use types in a multiple land use equatorial African savanna, central Uganda.

Variables	**Land uses**			**Statistical parameters**	
	Grazing (n = 27) (Mean ± S.E.)	**Cultivation (n = 24) (Mean ± S.E.)**	**Charcoal (n = 24) (Mean ± S.E.)**	$F_{2,72}$	**P**
pH	5.6 ± 0.2[a]	5.7 ± 0.1[a]	5.7 ± 0.1[a]	0.08	0.93
Organic matter (%)	2.0 ± 0.2[a]	1.9 ± 0.2[a]	1.5 ± 0.1[a]	1.4	0.3
N (%)	0.08 ± 0.01[a]	0.09 ± 0.005[a]	0.08 ± 0.008[a]	0.71	0.49
Av. P (mg/kg)	11.8 ± 1.34[a]	13.3 ± 1.1[a]	13.2 ± 1.1[a]	0.55	0.58
K (C. moles/kg)	0.5 ± 0.04[a]	0.5 ± 0.05[a]	0.4 ± 0.03[a]	1.29	0.3
Na (C. moles/kg)	0.1 ± 0.01[a]	0.04 ± 0.004[b]	0.03 ± 0.003[b]	10.68	<0.0001
Ca (C. moles/kg)	3.8 ± 1.04[a]	2.8 ± 0.6[a]	1.5 ± 0.8[a]	2.51	0.09
Mg (C. moles/kg)	1.2 ± 0.2[a]	0.8 ± 0.2[ab]	0.5 ± 0.1[b]	5.49	0.006
Sand (%)	69.9 ± 2.2[a]	69.7 ± 1.6[a]	70.7 ± 1.8[a]	0.47	0.63
Clay (%)	14.7 ± 1.4[a]	20.8 ± 1.3[b]	18.2 ± 1.7[ab]	5.7	0.005
Silt (%)	15.5 ± 1.4[a]	9.6 ± 0.9[b]	11.2 ± 1.5[ab]	4.3	0.02

Values in the same column accompanied by the same superscript do not differ significantly (Tukey, $P < 0.05$).

3.2 .Woody species composition in relation to environmental gradients

3.2.1. Unconstrained ordination

3.2.1.1. Detrended Correspondence Analysis (DCA)

The DCA of the total woody species density showed evidence of a strong gradient in species composition and distribution, with an axis length of 2.72 for 1st axis (Table 3).

Table 3: Statistics from the Detrended Correspondence Analysis (DCA) of woody species distribution in a multiple use equatorial African savanna, central Uganda.

Axes	**DCA1**	**DCA2**	**DCA3**	**DCA4**
Eigenvalues	0.2404	0.1524	0.1631	0.1256
Decorana values	0.3419	0.2058	0.1722	0.1236
Axis lengths	2.7193	2.7127	2.2561	2.2947

Furthermore, the DCA showed a clear gradient in the distribution of woody species (Figure 2).

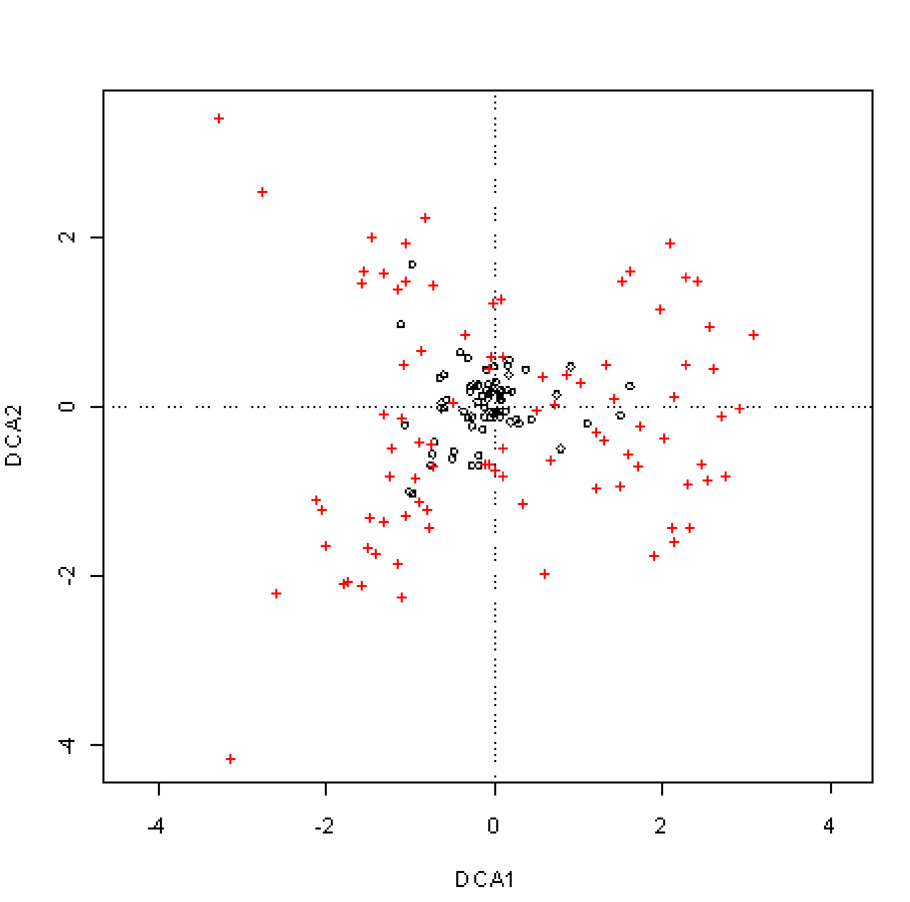

Figure 2. Detrended Correspondence Analysis ordination showing the species distribution (+) and sample plots (**o**) in a multiple use equatorial African savanna, central Uganda.

3.2.2. Constrained ordination

3.2.2.1. Variance partitioning

In the first variance partitioning ordination the explanatory variables (i.e. soils, space, anthropogenic factors), jointly explained 33% of the variation in species composition (Figure 3). Of the explained variance accounted for, soils, position (degrees East and North) and anthropogenic variables explained 18.3, 6.5 and position 3.8%, respectively. Hence, edaphic factors seem to be the most important explanatory variables for the variation in species composition in this savanna. Among the soil variables, exchangeable cations accounted for most of the explained variance in species composition, with soil texture explaining the least (Figure 4).

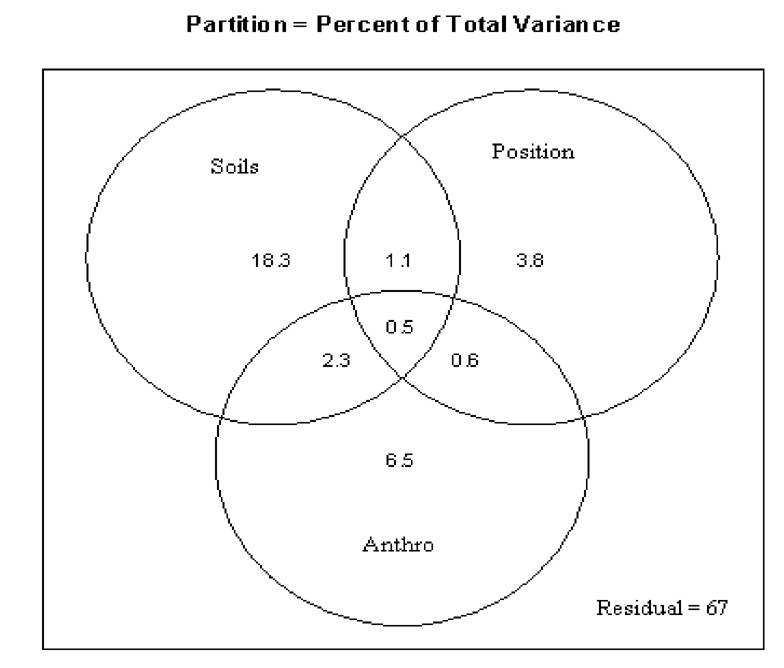

Figure 3: Set diagram of percent of total variance in woody species composition explained by soils, anthropogenic factors (anthro) and geographic position (position) variables in a multiple land use equatorial African savanna, central Uganda.

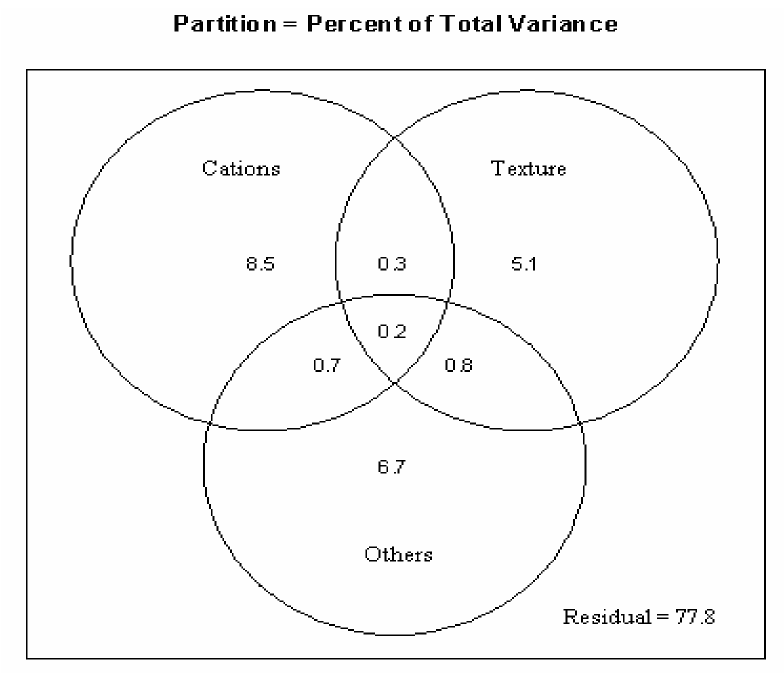

Figure 4: Set diagram of percent of total variance in woody species composition explained by only soil variables [(i.e. exchangeable cations, texture and others (organic matter, pH and Av. phosphorus)], in a multiple land use equatorial African savanna, central Uganda.

3.2.2.2. Canonical Correspondence Analysis ordination

The CCA ordination results did not show clear separation between the cultivation and charcoal production land use types. However, when environmental variables were included the CCA triplot showed separation of the grazing land use from both the cultivation and charcoal production land uses. In the study area, the grazing areas were mostly spatially separate from the others as they were largely found in the hydromorphic grassland with seasonal inundation, although some grazing areas occur on fallow lands. Cultivation and charcoal production land uses seem to overlap, indicating that these land use types take place on similar lands. It appears to be only the intensity of use that separates these two specific land uses at a given time and place (Figure 5).

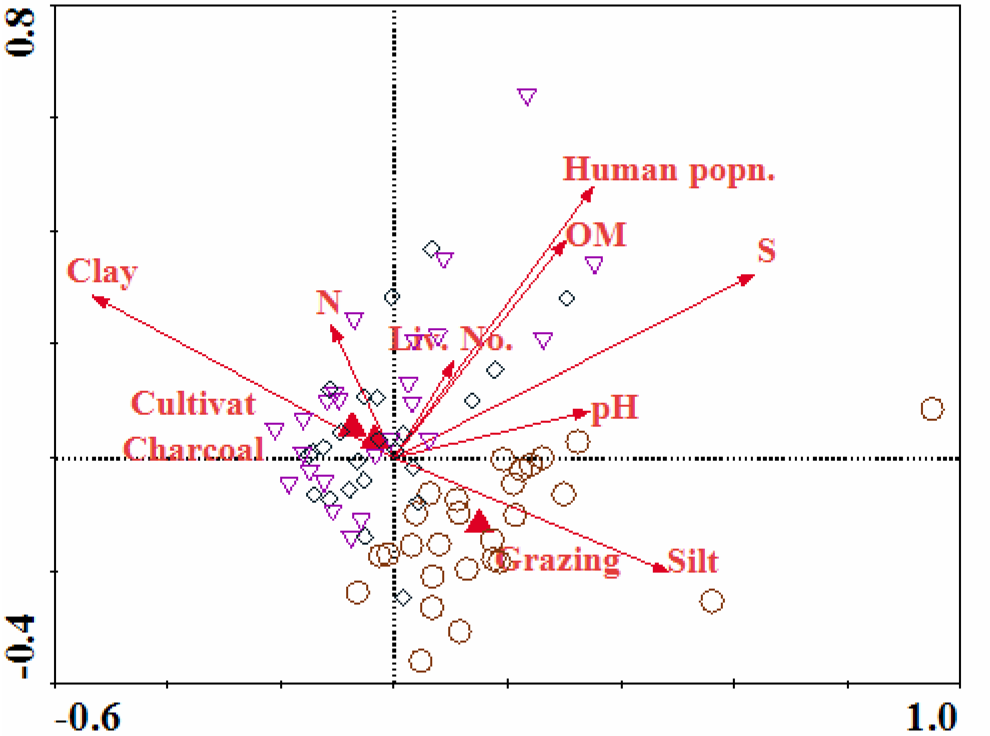

Figure 5. Canonical Correspondence Analysis ordination based on total woody species abundance (99 species) recorded in 75 0.1 ha plots, showing the distribution of plots in relation to the environmental variables in a multiple land use equatorial African savanna, central Uganda. S = (K + Mg + Ca + Na). Some of the environmental variables with short arrows such as Minutes E, Minutes N, sand and Available Phosphorous were suppressed to increase clarity. O = grazing ▽ = cultivation, ◊ = charcoal plots.

3.2.3. Total woody species composition in relation to environmental factors

The CCA ordination using only woody plant species with individuals of > 1 m in height is not presented in this section because the results were not different from those obtained using the total woody species data. Therefore, only the ordination of total woody plant composition and environmental factors are presented. The CCA ordination of data from all woody species based on abundance showed that canonical axes 1 and 2 (with eigenvalues 0.271 and 0.219 respectively) explained 11.8% of the variance in species, and 39.1% of species-environmental relations (Table 4). For the basal area data, the first two canonical axes explained 9.4 and 35.8% of the variance of species and species-environmental relations (Table 4). The Monte-Carlo Permutation Test for the abundance data was significant for both the first canonical axis ($F = 4.21$; $p = 0.048$) and the combination of the first four axes ($F = 1.857$; $p = 0.002$), indicating that the first four canonical axes significantly explained the species–environment relations. However, for the basal area, only the combination of the first four canonical axes was significant. ($F = 1.52$; $p = 0.002$).

Table 4. Summary of Canonical Correspondence Analysis results for total woody species composition based on: (a) abundance, and (b) basal area in a multiple land use equatorial African savanna, central Uganda.

Data			**Axes**		**Total inertia**
	1	**2**	**3**	**4**	
a) Abundance					
Eigenvalues	0.271	0.219	0.208	0.138	4.144
Species-environment correlations	0.808	0.821	0.712	0.665	
Cumulative percentage variance					
Of species data	6.5	11.8	16.9	20.2	
Of species-environment relation:	21.7	39.1	55.8	66.7	
Sum of all eigenvalues					4.144
Sum of all canonical eigenvalues					1.253
b) Basal area					
Eigenvalues	0.234	0.224	0.174	0.132	4.889
Species-environment correlations	0.851	0.822	0.678	0.687	
Cumulative percentage variance					
of species data	4.8	9.4	12.9	15.6	
of species-environment relation:	18.3	35.8	49.4	59.8	
Sum of all eigenvalues					4.889
Sum of all canonical eigenvalues					1.279

For the abundance data, total exchangeable cations (S) was strongly correlated with axis 1 ($r = 0.51$), while axis 2 was negatively correlated with grazing ($r = -0.41$). In contrast, for the basal area data, axis 1 was negatively correlated with grazing ($r = -0.48$), while axis 2 was correlated with human population size ($r = 0.42$).

For both data sets some species showed a clear association with particular soil variables or land use types. For example, *Piliostigma thonningii* was associated with the grazing land use, *Acacia seyal* with increasing exchangeable cation concentrations, and *Albizia zygia* and *Harrisonia abyssinica* with the cultivation and charcoal production land uses (Figure 6 a & b).

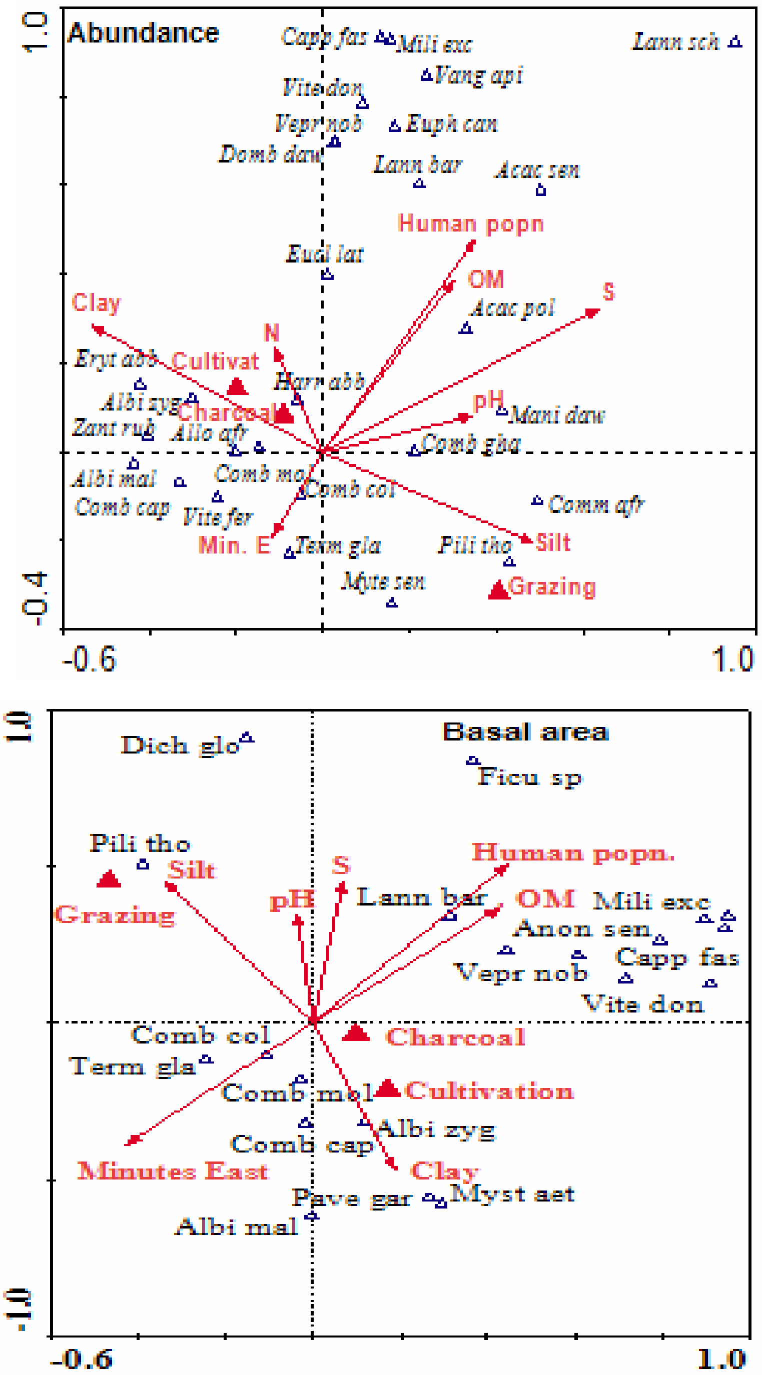

Figure 6. Canonical Correspondence Analysis ordinations based on total woody species: (a) abundance, and (b) basal area, showing environmental variables (arrows), land use types (▲), and species (Δ) in a multiple use equatorial African savanna, central Uganda, with a species fit range of 8-100%. Some of the species in the centre and soil variables with shorter arrows are suppressed in the ordination space for clarity in the ordination diagram. S = (K + Mg + Ca + Na) OM: Organic matter, N: total nitrogen, Av. P: Available phosphorus, Liv. No: Livestock number, Human pop: human population, Min. E.: Minutes East, Acac hoc: *Acacia hockii*, Acac sie: *Acacia sieberiana*, Acac sey: *Acacia seyal*, Albi mal: *Albizia malacophylla*, Albi zyg: *Albizia zygia*, Allo afr: *Allophylus africanus*, Bala aeg: *Balanites aegyptiacus* Comb cap: *Combretum capituliflorum*, Comb col: *Combretum collinum*, Comb gha: *Combretum ghasalense*,

Comb mol: *Combretum molle* , Capp fas: *Capparis fascicularis,* Carr edu: *Carissa edulis,* Eryt aby: *Erythrina abyssinica,* Euph can: *Euphorbia candelabrum,* Ficu sp: *Ficus* sp.*,* Harr aby: *Harrisonia abyssinica,* Kige afr: *Kigelia africana,* Lann bar: *Lannea barteri* , Lann sch: *Lannea schweinfurthii,* Mani daw: *Manilkara dawei, Myte* sen: *Gymnosporia senegalensis,* Mili exc: *Milicia excelsa,* Pave gar: *Pavetta gardeniifolia,* Pili tho: *Piliostigma thonningii,* Pout sp: *Pouteria* sp.*,* Stry inn: *Strychnos innocua,* Tric dre: *Trichilia dregeana,* Vang tom: *Vangueria tomentosa,* Vite don: *Vitex doniana* and Vepr nob: *Vepris nobilis*.

3.2.4. The 16 highly utilized species in relation to environmental factors

The relative influence of the measured soil variables and land use types on the distribution and abundance of the 16 highly utilized woody species based on abundance and basal area can be inferred from the CCA ordination diagrams (Figure 7). The CCA ordination using highly utilized species with only individuals of > 1 m in height is not presented because the results were not different from those obtained using all individuals.

The CCA ordination based on the abundance of the total highly utilized plants (i.e. seedlings, juveniles and adults of both trees and shrubs), showed that canonical axes 1 and 2 explained 18.1% of the variance in species, and 49.9% of species-environment relations (Table 5). For the basal area, the first two canonical axes explained 22.4 and 59.8% of the variance of species and species-environmental relations, respectively (Table 5). The Monte-Carlo Permutation Test for abundance was significant for both the first canonical axis ($F = 7.22$; $p = 0.03$), and the combination of the first four axes ($F = 2.44$; $p = 0.002$) .Similarly, for the basal area, both the first canonical axis ($F = 11.24$; $p = 0.008$), and the combination of the first four axes ($F = 2.73$; $p = 0.002$) were significant.

For the abundance CCA ordination, the environmental variables that were strongly correlated with the 1st canonical axis were total exchangeable cations (S; $r = 0.63$), while the 2nd axis was positively correlated with grazing ($r = 0.56$), and negatively correlated with clay content ($r = - 0.52$). Similarly, for the basal area data, the 1st axis was strongly correlated with exchangeable cations ($r = 0.71$), while the 2nd axis was positively correlated with grazing ($r = 0.56$), and negatively correlated with clay content ($r = - 0.49$). For both data sets, some species showed clear associations with particular soil variables or land use types (Figure 7a & b). For example, *Piliostigma thonningii* was clearly associated with the grazing land use type, *Acacia seyal* with high concentrations of Ca^{2+}, while *Acacia hockii*, *Combretum capituliflorum*, and *Vepris nobilis* were clearly associated with both the cultivation and charcoal production land uses. Furthermore, it can be interpreted that *Acacia sieberiana* prefers soils with low exchangeable cations concentrations whereas *Acacia seyal* prefers soils with higher levels of exchangeable cations, specifically Ca^{2+}.

Table 5. Summary of Canonical Correspondence Analysis results for the composition of woody species highly utilized for charcoal production based on: (a) abundance and (b) basal area in a multiple land use equatorial African savanna, central Uganda.

Data	**Axes**				**Total inertia**
	1	**2**	**3**	**4**	
a) Abundance					
Eigenvalues	0.392	0.268	0.243	0.157	3.647
Species-environment correlations	0.723	0.764	0.719	0.692	
Cumulative percentage variance					
Of species data	10.7	18.1	24.7	29.1	
Of species-environment relation	29.6	49.9	68.3	80.2	
Sum of all eigenvalues					3.647
Sum of all canonical eigenvalues					1.321
b) Basal area					
Eigenvalues	0.554	0.234	0.209	0.142	3.511
Species-environment correlations	0.778	0.789	0.666	0.739	
Cumulative percentage variance					
of species data	15.8	22.4	28.4	32.5	
of species-environment relation	40.6	57.8	73.1	83.5	
Sum of all eigenvalues					3.511
Sum of all canonical eigenvalues					1.365

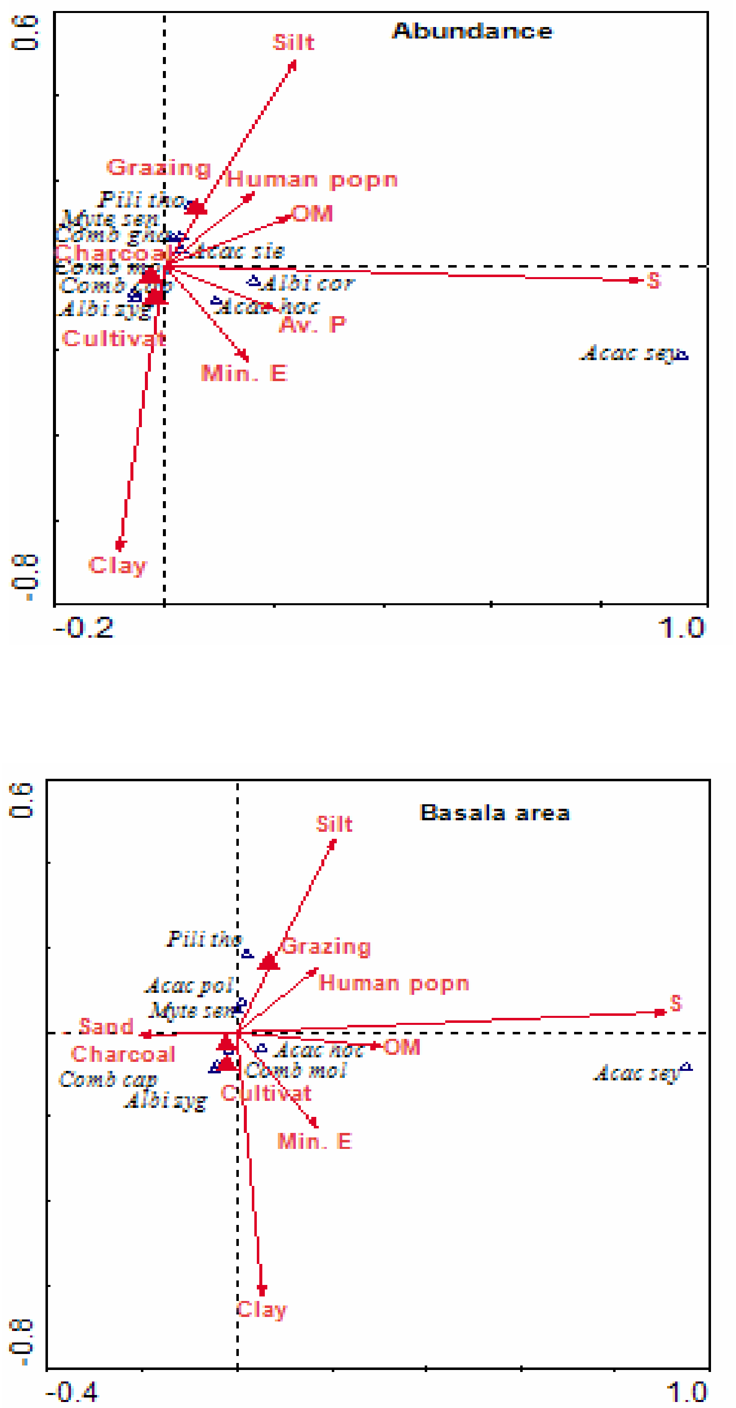

Figure 7. Canonical Correspondence Analysis ordination based on the 16 highly utilized species for charcoal production (all individuals including seedlings, juveniles, shrubs and trees): (a) abundance, and (b) basal area data, showing environmental variables (arrows), land use type (▲) and species (Δ) in a multiple use equatorial African savanna, central Uganda, with a species fit range of 3 - 100%. Some of the species in the centre and soil variables with shorter arrows are suppressed in the ordination space for clarity in the ordination diagram. S = (K + Mg + Ca + Na), OM: Organic matter, N: total nitrogen, Av.P: Available phosphorus, Liv. No: Livestock number, Human popn: Human population, Min. E: Minutes East, Min. N: Minutes North, Acac hoc: *Acacia hockii*, Acac sie: *Acacia sieberiana*, Acac sey: *Acacia seyal*, Acac pol: *Acacia polyacantha*, Albi cor: *Albizia coriaria*, Albi zyg: *Albizia zygia*, Comb cap:

Combretum capituliflorum, Comb col: *Combretum collinum*, Comb gha: *Combretum ghasalense*, Comb mol: *Combretum molle*, Myte sen: *Gymnosporia senegalensis*, Pili tho: *Piliostigma thonningii* and Vepr nob: *Vepris nobilis.*

4.0 Discussion

4.1. Community structure

The land uses studied differed significantly in terms of woody species abundance and basal area. Woody species abundance and basal area were related to edaphic and land use (grazing) in a multiple use equatorial African savanna, central Uganda. The high basal area in the cultivated land use offers an opportunity for the conservation of some valuable woody plants in the study area. For the highly utilized species, cultivation had the highest basal area and charcoal production had the highest abundance, whereas grazing had the lowest basal area and abundance. These anthropogenic disturbances as dynamic factors frequently alter floristic composition and vegetation structure (Pickett & White, 1985; Skarpe, 1990). Throughout the savanna woodland, woody plants are harvested for charcoal production, fuelwood, and poles, thereby influencing species diversity in the different land use types. For example, it is reported that the harvesting of medicinal plants in the communal rangelands of Kwazulu-Natal resulted in the local extirpation of some species (O'Connor, 2004). The high density of woody species and low basal area in the charcoal production area is attributed to the fact that charcoal production takes place in areas with woody species having the sizes required for making good charcoal. In contrast, the lower woody abundance associated with the cultivation land use was a result of tree removal during preparation for new crop land, which involve tree cutting and burning. However, a few trees are left in order to provide shade for crops. The lower abundance of woody species in the grazing lands was due to predominantly hydromorphic grasslands dominated by grasses with few trees, which are seasonally flooded. The lower woody species abundance in the cultivation and grazing land uses represent a loss of goods and services to local households within these areas (Higgins *et al.,* 1999). For example, most of the *Combretum* spp., *Acacia* spp., and *Piliostigma thonningii* provide resources such as fuelwood, construction timber, medicine, and forage for bees that are important in honey production.

The dominant species (best represented by basal area) were not necessarily the most abundant and frequent species in the different land use types, with the exception of *Combretum collinum* that had both the highest basal area and density across all land use types. This is not surprising since several communities may show similarity in physiognomy (resulting from sharing dominant species) and differ in abundance of other species (Mwavu *et al.,* 2008). In environments where relatively small stature plant species are frequent and anthropogenic disturbances are pronounced, the use of both basal area and abundance in woody plant community studies is recommended, because the use of either one only might not provide a complete picture. In this study, 45 species were shared among the three land uses though they differed in density, basal area and frequency. Most of the shared species are the dominant species. The pattern of dominance of the woody species observed in the study area supports the broad pattern, which had previously been proposed for the savanna woodlands of central Uganda (Langdale-Brown *et al.,* 1964; White, 1983). The dominance of *Combretum* spp. in terms of abundance and basal areas among the land uses may be attributed to their prolific resprouting in the study area (Chapter 6). The high abundance of *Rhus natalensis, Harrisonia abyssinica* and *Acacia hockii* in all land uses is because of their ability to colonize and grow in areas where indigenous species have been over-harvested.

4.2. Woody species diversity and distribution in relation to environmental gradients

The DCA for overall abundance revealed that there is a gradient in species distribution. The variance partitioning showed that species distribution mainly followed an edaphic or soil gradient, which was dominated by soil cation. Anthropogenic factors also governed species distribution, whereas the altitudinal range had little impact on distribution. These results are corroborated by the CCA ordination that showed a fair separation of the grazing land use from the other two land uses. However, cultivation and charcoal production overlapped, because areas formally used for charcoal production can, then, be used for cultivation and, later on, for grazing. The separation of grazing from the other land uses is mainly due to permanent grazing areas in the study area, i.e. the hydromorphic grasslands, aquatic wetlands and the grassland wetland periphery. However, grazing also take place in open woodlands and fallow lands. The results also showed an overlap of species among the land use practices, indicating that most of the species are not particularly influenced by land use type Hence the effect of current and past land use on the structure of the woody vegetation in the study area cannot clearly be elucidated owing to the complex, interactive and heterogeneous nature of the land uses. Indeed the nature of land use is not constant in time and space (McGregor, 1994).

Of the 99 species included in the CCA, relatively few were shown to be significantly associated with a particular soil variable or land use type. Plotting these species on the ordination axes showed that most species are clustered around the centre of the axes, showing that they are widely distributed in the study area. Species that are not related to the ordination axes are placed in the centre of the diagrams by the CCA algorithm. Thus, it may be difficult to distinguish them from those which have a true optimum at the centre (ter Braak, 1986; Glavac, 1996).

For all data sets [(i.e. abundance and basal area for: (i) total woody plants and (ii) the highly utilized species for charcoal production (including seedlings, saplings, shrubs and trees for both sets)], the total (for the first four axes) variance in species-environmental factors relations was higher than 50%, suggesting a relatively strong influence of the environmental factors on species composition and distribution. However, it was far higher for the 16 species highly utilized for charcoal production, than for the total woody species data. Furthermore, apart from the total woody species, the CCA axis 1 had eigenvalues > 0.33 for the rest of the data sets, which denotes a fair separation of species along this axes (ter Braak, 1987). As a rule of thumb, an eigenvalue > 0.30 indicates a strong gradient (ter Braak, 1995).

The strong correlation between CCA axis 1 with exchangeable cations (S), particularly Ca^{2+} and Mg^{2+}, suggests an edaphic gradient, while that between canonical axis 2 and the grazing land use may be interpreted as a grazing gradient. These results are not surprising, since environmental factors like substrate, topography or soil characteristics are important in determining plant species distribution at smaller spatial scales (Wiens, 1989). The relatively strong assertion in the spatial distribution of woody plants in relation to edaphic factors and with grazing as observed in this savanna woodland has similarly been reported from other savanna woodlands. Soil moisture, soil nutrients, and disturbances such as fire and herbivory, are some of the major determinants of tropical savanna pattern, structure and function (Walker & Noy-Meir, 1982; Tothil & Mott, 1985; Frost *et al.,* 1985; Higgins *et al.,* 2000; Sankaran *et al.,* 2005; Bond *et al.,* 2005). In the South American savannas fire, herbivory and human disturbances have been considered important factors in the determination of the floristic heterogeneity (Durigan *et al.,* 1994; Hoffmann, 1996). Similarly, in the semi-arid woodland savannas of South Africa, plant communities are influenced by soil factors and various levels of defoliation of the grasses and trees (Stuart-Hill & Tainton, 1989). A number of studies (e.g. Duivenvoorden, 1995; Swaine, 1996; Witkowski & O'Connor, 1996; Clark *et al.,* 1998; Svenning, 2001) demonstrated that species distributions were also strongly aggregated with respect to variations in topography as well as soil water and nutrient status.

Grazing, fire and selective tree harvesting are major disturbances shaping species diversity and productivity in Sudanian savanna-woodland ecosystems (Savadogo, 2007), in dry tropical forests in southern India (Mehta *et al.,* 2008), and patterns of plant distribution in southern African savannas (Scholes & Walker, 1993). Grazing is a predictable selective form of disturbance with animal behaviour through browse choice playing a significant role in determining which species are impacted (Whelan, 2001). Grazing pressure may also play a significant role in determining plant community structure and composition by facilitating bush encroachment in frequently grazed areas (Witkowski & O'Connor, 1996). Fire is much less selective in the removal of biomass. However, the length, intensity and recurrence intervals of fire events are partly dependent on the accumulation of fuel and, therefore, the time elapsed since the last fire (Whelan, 2001). Interactions between grazing and fire have been shown to be important for a number of ecosystem functions (Hobbs *et al.,* 1991; Wedin, 1995; de Mazancourt *et al.,* 1999; Kochy & Wilson, 2005; Holdo *et al.,* 2007), and community structure and composition (Collins *et al.,* 1998). The combined effects of grazing, fuelwood/fodder extraction and fire, have a negative effect on soil nutrient availability through the reduction in clay content and soil organic matter of surface soils (Mehta *et al.,* 2008). Nutrients are depleted immediately by volatilization and subsequently by leaching of the elements from ash beds by rain. However, the degree of depletion of various nutrients depends on the intensity of the fire (Orians & Milewski, 2007). An ecological study in Australia revealed that the more intense the fire, the higher the proportions of N and S that are likely to be lost from the ecosystem (Orians & Milewski, 2007). Another study in a miombo woodland in Zambia (Chidumayo & Kwibisa, 2003) revealed that irregular burning and deforestation followed by shifting cultivation, had significant impact on soil nutrients, since they significantly reduce organic matter and N content in top soils. The grazing land use in savanna woodlands of Nakasongola had a significantly lower percentage of clay compared to cultivation and charcoal production land uses. Other studies in savanna areas have concluded that differences in land use are secondary correlates of vegetation pattern (e.g. Coughenour & Ellis, 1993; Higgins *et al.,* 1999).

In this study, some plant species were highly associated with certain environmental variables. *Acacia seyal* was highly associated with magnesium and calcium. *Acacia seyal* is considered a farmers' indicator of poor soils for traditional land uses of the Mbe region, Cameroon, and, indeed, its nitrogen supply is negligible (Ibrahima *et al.,* 2007; Breman & Kessler, 1995). In all the CCA ordinations, *Piliostigma thonningii* was relatively more responsive by increasing in abundance at the grazing gradient. This may be attributed to seasonal fires and animal defoliation being more common in grazing areas. Studies elsewhere have shown that both manual and fire induced defoliation in the dry season advanced bud break and leaf flush in *Piliostigma thonningii* (Chidumayo, 2007; Fatubarin, 1985). This might be contributing to its resilience in the areas where grazing takes place. According to Trollope (1980), browsing and grazing by animals often controls the recruitment of woody species to the adult stage. Grazing reduces grass biomass and can, thus, directly reduce the competition faced by woody seedling, favouring shrubs and trees (Harrington, 1991; Watson *et al.,* 2009). Indirectly grazing encourages tree and shrub establishment by limiting grass fuel, and, thus, reducing the frequency and intensity of fires that might otherwise kill young trees and shrubs, or prevent juveniles reaching adult size (Hodgkinson & Harrington, 1985; Scholes & Archer, 1997).

Although there is strong evidence that soil nutrients and grazing influence the composition and structure of woody plant communities in this savanna woodland, there may be other abiotic and biotic factors whose influence could not be disentangled in this study. For instance, the low eigenvalues recorded for the total woody plant data, as compared to that excluding seedlings and resprouts, may be attributable to other factors. A variety of factors including climate, precipitation, soils and disturbance, modified by land use practices (Skarpe, 1991), interact to determine the relative abundance of trees, shrubs and grasses in dryland ecosystems (Walker, 1987; Scholes & Archer, 1997). Plant community structure is considered a product not only of local physical conditions and interactions among species, but also regional constraints such as climate, and of historical processes such as dispersal, speciation, migration and extinction (Menge & Olson, 1990). Hence, the array of environmental factors that influence plant abundance, distribution and community patterns is often complex and difficult to ascertain (Ben-Shahar, 1993).

5.0. Conclusions

Edaphic factors and land use practices interact to determine the structure and composition of the woody plant community in the study area. The most important environmental factors are exchangeable cations, particularly Ca^{2+}, Mg^{2+}, and grazing. The study revealed that the cultivation and charcoal production land uses seem to overlap. The two land use types take place on a similar land, and it is only the intensity of use that separates them at a given time and place. However, the grazing land use is separate from the other two. The reason is that most of the grazing occurs within hydromorphic grasslands, aquatic wetlands and the wetland periphery of the grassland with little or no trees.

The woody plant structure of this savanna woodland follows an edaphic and grazing land use disturbances. The CCA showed a weaker influence of the included environmental variables for the total woody species (including seedlings and resprouts) than that in which seedlings and resprouts had been excluded. This suggests that some other environmental factors that could better explain variations in the distribution of seedlings and resprouts have not been included. Therefore, it will be important to include more environmental variables like fire and soil moisture if all the variations have to be properly explained in the distribution of woody species in this savanna woodland. A consistent feature of the CCA was the response of *Acacia seya*l with increased concentration of Ca^{2+} and increase of *Piliostigma thonningii* along the grazing gradient. In general, the important environmental variables influencing woody species composition and structure were calcium, magnesium and grazing.

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References

Akankwasa, D. & Tromborg, E. 2001 Challenges and strategies in the biomass energy sector-Working paper.

Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. 1989. Chemical analysis of Ecological Materials, 2nd Ed. Blackwell Scientific Publications, Oxford, UK.

Ben-Shahar, R. 1993. Patterns of nutrient content in grasses of semi-arid savanna. *African Journal of Ecology* 31: 343-347.

Bond, W.J., Woodward, F.I. & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165, 525-537.

Bouyoucos, G.J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. *Soil Science* 42: 225-229.

Breman, H. & Kessler, J.J. 1995. Woody plants in agro-systems of semi-arid regions, with and emphasis on the Sahelian countries, advanced series, pp. 23 – 340. Agricultural Sciences, Springer Verlag, Berlin.

Bremner, J.M. & Mulvaney, C.S. 1982. Total Nitrogen and total Phosphorus. In: Page, A.L., Miller, R.H. & Keaney, D.R. (Eds.) Methods of soil Analysis, Part 2- Chemical and Microbiological Properties, 2nd Edition, pp. 595-599. American Society of Agronomy, Madison, WI, USA.

Brown, J.H. 1988. Species diversity. pp. 57-90. In: Myers, A.A. & Giller, P.S (Eds.) Analytical Biogeography, Chapman and Hall, New York, USA.

Byabashaija, M.D., Esegu, J.F.O., Kidiya, J.M., Basoga, M., and Odia, R.K. 2004. Traditional uses of indigenous tree species. *Ugandan Journal of Agricultural Sciences* 9: 363-371.

Chidumayo, E.N. 2007. Growth responses of an African savanna tree, *Bauhinia thonningii* Schumaacher to defoliation, fire and climate. *Trees* 21: 231-238.

Chidumayo, E.N. & Kwibisa, L. 2003. Effects of deforestation on grass biomass and soil nutrient status in miombo woodland, Zambia. *Agriculture, Ecosystem and Environment* 96: 97-105.

Clark, D.B., Clark, D.A. & Read, J.M. 1998. Edaphic variation and the mesoscale distribution of tree species in a Neotropical rainforest. *Journal of Ecology* 86: 101-112.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tall grass prairie. *Science* 280: 745-747.

Coughenour, M.B. & Ellis, J.E. 1993. Landscape and climatic control of woody vegetation in a dry tropical ecosystem Turkana district, Kenya. *Journal of Biogeography* 20: 383-398.

De Mazancourt, C., Loreau, M. & Abbadie, L. 1999. Grazing optimization and nutrient cycling: potential impact of large herbivores in a savanna system. *Ecological Applications* 9: 784-797.

District Environmental Profile (DEP) 2002. *In* Nakasongola District Forest Development Plan*:* Period of plan: 2003-2014.

Dovie, D.B.K., Witkowski, E.T.F. & Shackleton, C.M. 2005. Monetary valuation of livelihoods for understanding the composition and complexity of rural households. *Agriculture and Human Values* 22: 87-103.

Duivenvoorden, J.F. 1995. Tree species composition and rainforest-environment relationships in the middle Caquetá area, Colombia, NW Amazonia. *Vegetatio* 120: 91-113.

Durigan, G., Leitão Filho, H.F. & Rodrigues, R.R. 1994 Phytosociology and structure of a frequently burnt cerrado vegetation in SE-Brazil. *Flora* 189: 153-160.

Ehrenfeld, J.G., Hna, X., Parsons, W.F.J. & Zhu, W. 1997. On the nature of environmental gradients: temporal and spatial variability of soils and vegetation in the New Jersey Pinelands. *Journal of Ecology* 85: 785-798.

Eilu, G., Hafashimana, D.L.N. & Kasenene, J.M. 2004. Density and species diversity of trees in four tropical forest of the Albertine Rift, Western Uganda. *Diversity and Distributions* 10: 303-312.

Fatubarin, A. 1985. Observations on the phenology of the woody plants and grasses in a savanna ecosystem in Nigeria. *Tropical Ecology* 26: 32-42.

Frost, P., Menaut, J.C., Walker, B., Medina, E., Solbrig, O. & Swift, M. 1985. Responses of savannas to stress and disturbance: a proposal for a collaborative programme of research. Report of a meeting of an IUBS Working Group. *Biology International* (Spec. Issue). 10: 1- 82.

Gauch, H.G. Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.

Glavac, V. 1996. Vegetationsökologie. Grundfragen, Aufgaben, Methoden. Gustav Fischer, Jena. pp. 358.

Grace, J.B. 2001. The roles of community biomass and species pools in the regulation of plant diversity. *Oikos* 92: 193-207.

Hamilton, A.C. 1991. A Field Guide to Uganda Forest Trees. Makerere University, Kampala, Uganda.

Harrington, G.N. 1991. Effect of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72, 1138-1149.

Higgins, S.I., Bond, W.J. & Trollope, W.S. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savannas. *Journal of Ecology* 88: 213-229.

Higgins, S.I., Shackleton, C.M. & Robinson, E.R. 1999. Changes in woody community structure and composition under contrasting land use systems in a semi-arid savanna, South Africa. *Journal of Biogeography* 26: 619-627.

Hill, M.O. & Gauch, H.G. Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.

Hobbs, N.T., Schimel, D.S., Owensby, C.E., & Ojima, D.S. 1991. Fire and grazing in the tall grass prairie-contingent effects on nitrogen budgets. *Ecology*: 72: 1374-1382.

Hodgkinson, K.C. & Harrington, G.N. 1985. The case of prescribed burning to control shrubs in eastern semi-arid woodlands. *Australian Rangeland Journal* 7: 64-74.

Hoffmann, W.A. 1996. The effects of fire and cover on seedling establishment in a Neotropical savannah. *Journal of Ecology* 84: 383-393.

Holdo, R.M., Holt, R.D., Coughenour, M.B. & Ritchie, M.E. 2007. Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. *Journal of Ecology* 95: 115-128.

Huntley, B. & Walker, B.H. 1982. Ecology of Tropical Savannas. Springer, Berlin. pp. 671.

Ibarra-Manriques, G. & Martinez-Ramos, M. 2002. Landscape variation of liana communities in a Neotropical rainforest. *Plant Ecology* 160: 91-112.

Ibrahima, A., Nguetnkam, J.P., Pabame, P., Beunon, T. & Guidawa, G. 2007. Soil degradation in the Sudano-Guinea savannas of Mbe, Cameroon: Farmers' perception, indicators and soil fertility management strategies. *Research Journal of Agriculture and Biological Science* 3: 907–916.

Kisakye, R. 2004. Charcoal consumption in Kampala and its source districts. Unpublished Report on a consultancy survey for the GTZ Energy Advisory Project, Ministry of Energy and Mineral Development, Kampala, Uganda.

Kisamba-Mugerwa, W. 2001. Rangelands management policy in Uganda. A paper prepared for the international conference on policy and institutional options for the management of rangelands in dry areas, 7-11 May 2001, Hammamet, Tunisia.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. *Journal of Cleaner Production* 12: 1047-1057.

Kochy, M. & Wilson, S.D. 2005. Variation in nitrogen deposition and available soil nitrogen in a forest-grassland ecotone in Canada. *Landscape Ecology* 20: 191-202.

Kristensen, M. & Lykke, A.M. 2003. Informant-Based Valuation of use and Conservation Preferences of Savanna Trees in Burkina Faso. *Economic Botany* 57: 203-217.

Langdale-Brown, I., Osmaston, H.A. & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land use. Entebbe Government Printers, Uganda. pp 159.

Lim, C. H. & Jackson, M. L. 1982. Dissolution for total elemental analysis. In: Page, A.L., Miller, R.H. & Keaney, D.R. (Eds.) Methods of soil Analysis, Part 2- Chemical and Microbiological Properties, 2^{nd} Edition, pp. 1-12. American Society of Agronomy, Madison, WI, USA.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000. Differential utilisation and ethnobotany of trees in Kitulangalo Forest Reserve and surrounding communal lands, eastern Tanzania. *Economics Botany* 54: 328-343.

McGregor, J. 1994. Woodland pattern and structure in a peasant farming area of Zimbabwe: ecological determinants and present and past use. *Forest Ecology and Management* 63: 97-133.

McLean, E.O. 1982. Soil pH and lime requirements. In: Page, A.L., Miller, R.H. & Keaney, D.R. (Eds.) Methods of soil Analysis, Part 2- Chemical and Microbiological Properties, 2nd Edition, pp. 199-224. American Society of Agronomy, Madison, WI, USA.

Mehta, V.K., Sullivan, P.J., Walter, M.T., Krishnaswamy, J. & de Gloria, S.D. 2008. Impacts of disturbance on soil properties in a dry tropical forest in southern India. *Eco-hydrology* 1: 161-175.

Menge, B.A. & Olson, A.M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends Ecology Evolution* 5: 52-57.

Mwavu, E.N., Witkowski, E.T.F. & Mucina, L. 2008. Plant communities of a semi-deciduous tropical rainforest in north-western Uganda: role of soil and anthropogenic factors. *Phytocoenologia* 38: 193-211.

Namaalwa, J., Eid, T. & Sankhayan, P. 2005. A multi-species density-dependent matrix growth model for the dry woodlands of Uganda. *Forest Ecology and Management* 213: 312-327.

Nelson, D.W. & Sommers, L.E. 1982. Total Carbon, organic matter, and organic carbon. In: Page, A.L., Miller, R.H. & Keaney, D.R. (Eds.) Methods of soil Analysis, Part 2- Chemical and Microbiological Properties, 2nd Edition, pp. 539-575. American Society of Agronomy, Madison, WI, USA.

NEMA (National Environment Management Authority) 2002. State of environment report for Uganda. National Environment Information Centre, Kampala.

National Forestry Authority (2008) Strategic action plan for the period 2008 ⁄ 9 to 2012 ⁄ 13 with priorities for the first five years. Government of Uganda, Kampala.

O'Connor, T.G. 2004. Influence of land tenure on populations of the medicinal plant *Alepidia amatymbica* in the southern Drakensberg. *South African Journal of Botany* 70: 319-322.

Orians, G.H. & Milewski, A.V. 2007. Ecology of Australia: the effect of nutrient-poor soils and intense fires. *Biological Reviews* 82: 393-423.

Parker, D., Downer, E.R. & Cole, G.E.D. 1967. Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Patten, R.S. & Ellis, J.E. 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. *Vegetatio* 117: 69-79.

Pickett, S.T.A. & White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, CA.

Polhill, R.M. (ed.) 1952 et seq. Flora of Tropical East Africa (FTEA). Royal Botanic Gardens, Kew, UK.

Pote, J., Shackleton, C., Cocks, M. & Lubke, R. 2006. Fuel wood harvesting and selection in valley thicket, South Africa. *Journal of Arid Environments* 67: 270-287.

Sankaran, M., Hanan, N.P. & Scholes, R.J. 2005. Determinants of woody cover in African savanna. *Nature* 438: 846-9.

Savadogo, P. 2007. Dynamics of Sudanian savanna-woodland ecosystems in response to disturbances. A Doctoral thesis. Swedish University of Agricultural Sciences, Umeå, Sweden.

Sawatzky, D.L., Raines, G.L., Bonhan-Carter, G.F. & Looney, C.G. 2004. ARCSDM3: Arc MAP extension of spatial data modelling using weights of evidence, logistic regression, fuzzy logic and neural network analysis. http://www.ige.unicamp.br/sdm/ArcSDM3/.

Scholes, R. & Archer, S. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.

Scholes, R.J. & Walker, B.H. 1993. An African savanna: Synthesis of the Nylsvley study. Cambridge University Press, Cambridge, UK.

Shackleton, C.M., Netshiluvhi, T.R., Shackleton, S.E., Geach, B.S., Balance, A. & Fairbanks, D.F.K. 2002. Direct use values of woodland resources from three rural villages. *Economic Botany* 56: 130-146.

Skarpe, C. 1990. Structure of woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Vegetatio* 87: 11-18.

Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science* 2: 565-572.

Stuart-Hill, G.C. & Tainton, N.M. 1989. The competitive interaction between *Acacia karoo* and the herbaceous layer and how this is influenced by defoliation. *Journal of Applied Ecology* 26: 285-298.

Svenning, J.C. 2001. On the role of micro environmental heterogeneity in the ecology and diversification of Neotropical rainforest palms (Arecaceae). *Botany Review*, 67: 1-53.

Swaine, M.D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* 84: 419-428.

ter Braak C.J.F. 1995. Ordination. pp.91-173. In: Jongman R.H.G., ter Braak C.J.F. & van Tongeren O.F.R. (Eds.) Data analysis in community and landscape ecology, new edition, Cambridge University Press, Cambridge, UK.

ter Braak, C.F.J. 1987. The analysis of vegetation-environment relationships by Canonical Correspondence Analysis *Vegetatio* 69: 69-77.

ter Braak, C.J.F. & Šmilauer, P. 2003. CANOCO reference manual and Cano Draw for windows. Users guide: software for canonical community ordination. Version 4.5.1. Microcomputer power, Ithaca, New York, USA.

ter Braak, C.J.F. & Verdonschot, P.F.M. 1995. Canonical correspondence analysis and multivariate methods in aquatic ecology. *Aquatic Sciences* 57: 255-289.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

Tothil, J.C. & Mott, J.J. 1985. Management of the World's savannas. Australia Academic of Science, Canberra, Australia.

Trollope, W.S.W. 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. *Proceedings of the Grassland Society of Southern Africa* 15: 173-177.

UBOS (Uganda Bureau of Statistics) 2000. National household census estimates 2000. (Retrieved on 17/11/2005 from http://www.ugandadish.org/nakasongola.doc).

USDA Forest Service 1989. Interim Resource Inventory Glossary. Department of Agriculture, Forest Service, Washington DC., U.S.A. pp. 96.

Verheyen, K. & Hermy, M. 2001. The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology* 89: 829-840.

Walker, B. & Noy-Meir, I. 1982. Aspect of the stability and resilience of savanna ecosystem. pp.556-590. In: Huntley, B. & Walker, B. (Eds.), Ecology of Tropical savannas, Springer, Berlin.

Walker, B.H. 1987. A general model of savanna structure and function. pp. 1-12. In: Walker, B.H. (Ed.) Determinants of tropical savannas, IRL Press Limited, Oxford, UK.

Watson, P.J., Bradstock, R.A. & Morris, C. 2009. Fire frequency influences composition and structure of the shrub layer in Australian sub-coastal temperate grassy woodland. *Austral Ecology* 34: 218-232.

Wedin, D.A. 1995. Species nitrogen and grassland dynamics: the constraints of stuff. pp 253-262. In: Jones, C.G & Lawton, J.H. (Eds.), Linking species and ecosystems, Chapman and Hall, New York, USA.

Whelan, R.J. 2001. The Ecology of Fire: Cambridge University Press, Cambridge. 346 pp.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFET/UNSO vegetation map of Africa. UNESCO, Paris, France.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Witkowski, E.T.F. & O'Connor, T.G. 1996. Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. *Vegetatio* 124: 9-23.

Appendix 1: Shared species in three land use types with densities (plants/ha) and frequencies (number of plots in which the species were recorded), in a multiple land use equatorial African savanna, central Uganda.

Species	**Grazing (n=27)**		**Cultivation (n=24)**		**Charcoal (n=24)**	
	Density	**Frequency**	**Density**	**Frequency**	**Density**	**Frequency**
Acacia hamulosa Benth.	10	5	7	4	13	6
Acacia hockii De Wild.	62	15	425	19	217	15
Acacia polyacantha Willd.	58	19	203	15	105	15
Acacia senegal Willd.	1	2	8	2	38	4
Acacia sieberiana DC.	41	13	37	13	77	10
Albizia coriaria Welw.	7	2	34	9	2	3
Albizia zygia J.F. Macbr.	3	2	585	22	135	14
Alstonia boonei De Wild.	6	4	1	3	7	5
Allophylus africanus Radlk.	2	4	28	8	28	11
Annona senegalensis Pers.	59	12	109	14	154	17
Antiaris toxicaria Lesch.	1	1	8	5	17	4
Balanites aegyptiacus Delile	3	2	2	1	1	1
Bridelia scleroneura Stapf Müll. Arg.	8	4	19	5	8	3
Carissa edulis Vahl	14	7	43	11	33	14
Combretum capituliflorum Fenzl ex Schweinf.	7	2	236	10	506	10
Combretum collinum Fresen.	1,062	23	1,357	18	1,299	22
Combretum ghasalense Engl. & Diels	847	21	314	16	702	22
Combretum molle Engl. & Diels	311	17	1,025	20	1,048	23
Dichrostachys glomerata Chiov.	15	7	53	6	4	2
Euclea latidens Stapf	12	8	33	11	58	12
Euphorbia candelabrum Tremaut ex Kotschy	1	2	4	4	7	5
Ficus natalensis Hochst.	4	1	3	4	5	3
Gardenia ternifolia Shumach.	66	15	34	11	50	20
Grewia mollis Juss.	61	13	213	20	195	20
Harrisonia abyssinica Oliv.	117	19	334	22	233	24
Hymenocardia acida Tul.	179	14	282	11	430	15
Kigelia Africana (Lam.) Benth.	7	5	13	5	12	5
Lannea barteri Engl.	18	5	20	7	125	9
*Lantana camara**L.	39	6	98	9	11	3
Manilkara dawei (Stapf) Chiov.	36	6	10	4	9	6
Gymnosporia senegalensis Loes.	96	12	21	7	46	11
*Piliostigma thonningii (*Schumach.) Milne-Redh.	644	21	50	10	173	11
Pseudocedrela kotschyi Harms.	33	7	30	5	10	3
Rhus natalensis Bernh. ex Krauss	110	23	177	23	302	23
Rhus vulgaris Meikle	33	11	24	6	35	9
Securinega virosa (Willd.) Baill.	2	3	17	5	7	7
Steganotaenia araliacea Hochst.	0.4	1	4	2	0.4	1
Stereospermum kunthianum Cham.	8	4	25	9	10	3
Strychnos innocua Delile	9	4	141	14	39	12

Terminalia glaucescens Planch. ex Benth.	56	10	65	7	89	15
Trema guineense (Schumach. & Thonn.) Ficalho	5	3	20	4	6	4
Vangueria apiculata K. Schum.	1	2	6	1	3	1
Vitex ferruginea Schumach.	9	3	93	7	110	11
Zanthoxylum chalybeum Engl.	1	1	12	5	24	3
Zanthoxylum rubescens Planch. ex Hook.	0.4	1	8	2	5	2

*Alien invasive species

CHAPTER 6

Resilience to anthropogenic disturbances through resprouting of woody species in a multiple land use equatorial African savanna, central Uganda

Abstract

Savanna vegetation is reported to be resilient to human disturbances, with individual plant species, communities and vegetation formations re-establishing themselves through regeneration, despite harvesting impacts. Resprouting of woody plants after anthropogenic disturbances in an equatorial multiple land use wooded savanna of central Uganda was examined. A total of 2,595 stumps, representing 74 species in 31 families were recorded from seventy five, 0.1 ha, plots. Of the 2,595 stumps, 98.3% resprouted and were identified to species level. Resprouting stump density differed significantly ($F_{2, 72} = 3.2$, $P = 0.047$) among land use types, being highest under charcoal production, followed by cultivation and lowest under grazing. A total of 22,207 stump resprouts (shoots) and 285 root suckers were recorded. At the species level, the number of resprouts per stump ranged from 1 to 30, while root suckers per stump ranged from 1 to 21. Mean densities of root sucker did not differ significantly ($F_{2, 72} = 0.25$, $p = 0.78$) among land use types. The basal diameter (BD) and height of the leading resprout was weakly but significantly negatively related to number of resprouts per stump ($r^2 = 0.123$, $p < 0.0001$; $r^2 = 0.068$, $p < 0.0001$, respectively). For the 16 most species highly utilized for charcoal production, both the number of resprouts and suckers per stump differed significantly among species. Mean resprouts per stump was higher for intermediate sized stems (BD size-class = 5 - 30 cm), and stump height of 0.31-0.40 m. Although most of the woody species were resilience to harvesting through sprouting via the stumps and roots, their continued unsustainable harvesting will further deplete populations and availability of useful plant products. Consequently, these compromises the goods and services provided by the woodland ecosystems in this savanna. This has serious implications for the well-being of households whose livelihoods are almost entirely dependent on availability of woody resources. Therefore, sustainable management/harvesting of the already highly utilized species and those that are not, is necessary in all the land use types.

Keywords: Charcoal production, human well-being, land use, livelihood strategies, root suckering, stumps

Nomenclature: Polhill (1952 et seq.), Hamilton (1991).

1.0. Introduction

Savanna woodlands throughout Sub-Saharan Africa contribute considerably to household livelihoods by providing fuel, fodder and food security, and potentially supplementing incomes (Shackleton, 1997; Luoga *et al.,* 2000; Dovie *et al.,* 2002). With the ever increasing human population and rural households, continued reliance on fuelwood as the primary energy source, utilization of savanna woodlands is high and, therefore, these resources are increasingly threatened (Geldenhuys, 1997; Luoga *et al.,* 2004). Indeed, a number of major livelihood activities that involve harvesting of woody plants for charcoal production, firewood and other subsistence uses are common and can influence the dynamics of savanna vegetation. In response to harvesting and fire disturbances, depending on plant size, woody plants either resprout from roots and stumps or die. The ability to resprout, which refers to the production of vegetative shoots (van Wyk & van Wyk, 1997), is an efficient means by which woody plants regain biomass lost during disturbances such as frequent fires (Bellingham, 2000). In savanna communities, resprouting plays a major role in the process of post-fire succession, and is a key component of regeneration after harvesting in miombo woodlands of southern and eastern Africa (Luoga *et al.,* 2004). Resprouting is regarded as a key attribute to the resilience and productivity of South African savannas (Shackleton, 2000).

Apart from the miombo woodlands of eastern and southern Africa, little is known of the resilience of equatorial savanna woody plants to harvesting through resprouting (e.g. Luoga *et al.,* 2004; Shackleton, 2000; Kaschula *et al.,* 2005; Neke *et al.,* 2006). To date, studies on Ugandan savanna woodlands (e.g. Akankwasa & Tromborg, 2001; NEMA, 2002; Namaalwa *et al.,* 2005) have not addressed the responses of woody plants to human harvesting through resprouting, while those that have addressed woody plant resprouting have focused on tropical rainforest habitats (e.g. Mwavu & Witkowski, 2008). Yet, in Uganda, like elsewhere in Sub-Saharan Africa, human-use pressure on savanna woodlands is high as they are used for many purposes, including cattle grazing, firewood extraction and charcoal production (NEMA, 2002; Namaalwa *et al.,* 2005), resulting in degradation and loss of ecosystem goods and services.

Similar to elsewhere in Sub-Saharan Africa, the sustainable management and conservation of woodlands in Uganda, in the face of increased commercialization of charcoal production and dependence on biomass energy, requires a consideration of the responses/resilience to anthropogenic disturbances of the constituent woody species (e.g. Kennedy, 1998; Shackleton, 2000; Kaschula *et al.,* 2005). Furthermore, understanding the resprouting of woody plants and the factors affecting resprout/coppice growth of a species, such as environmental conditions and harvesting techniques, is vital for developing models for sustainable fuel use (Kaschula *et al.,* 2005), and management of woodland resources (Shackleton, 1993, 2000). The objective of this study was, therefore, to assess the level of human harvesting of woody species and their responses to harvesting and other forms of anthropogenic disturbances through resprouting. The following questions were explored: i) What proportion of the woody species resprout? ii) How does the resprouting ability of woody species relate to land use practices and level of harvesting? iii) How does resprouting ability of woody plants relate to stump characteristics (i.e. stump basal diameter and height)? and iv) How does the basal diameter and length of the leading resprout relate to the number of resprouts produced on a stump?

2.0. Materials and Methods

2. 1. Study area

The study focused on multiple land use savanna woodlands of Nakasongola District, south of Lake Kyoga, central Uganda ($0^0$40′- $1^0$41′ N, $31^0$57′ - $32^0$48′ E). The District covers about 3,424 km^2, most of which is woodland and grassy savanna, with 322 km^2 (10%) of open water and wetlands. It comprises eight sub-counties (administrative sub-divisions), namely Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata. Each sub-county has a mean (± S.E.) of 49 (± 22) villages and 3,193 ± 390 households. The mean number of households/village was 82 (± 32), with an average of seven persons/household. The district has a total human population of 128,126 (41 people/km^2) (2000 National Housing Census), with 50.2% males and 49.8% females. About 95.3% of the population are rural and 4.7% urban (Uganda Bureau of Statistics, 2002).

Mean annual rainfall ranges from 500 – 1000 mm and is concentrated into two wet seasons (March to May and August to November), but rainfall received and reliability is higher in the south, declining gradually to the north. The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C. The topography of the area undulates between 1,036 and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al.,* 1967).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964), a natural savanna woodland or woodland of mixed deciduous trees 3 to 12 m high and grasses 0.3 to 1.3 m high at maturity. However, the cover of the grass layer varies with season, is often patchy and subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirki*i subsp. *mildbraedii, A. senegal* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983). The major land use practices in this savanna are livestock grazing, subsistence crop cultivation, and charcoal production (Chapter 2). There is a succession of land use change over time which is typical of areas subject to slash and burn agriculture. Areas used for charcoal production are then used for cultivation, while cultivated areas may subsequently be used for grazing. However most of the grazing lands occur on hydromorphic grasslands which are only suitable for grazing.

2.2. Sampling design

The present main land use types (cultivation, grazing, charcoal production) were identified and selected for the purposes of this study (Chapter 2). Representative villages (areas) in each of the eight sub-counties were selected (with the help of local leaders and officials from the Department of Natural Resources and Environment) for woody vegetation sampling in March 2006. In each sub-county at least three transects were laid, each representing one of the three major land uses, with the exception of one sub-county which had 4 transects. The locations of the transects were selected randomly, but taking into consideration the homogeneous nature of the area for a particular land use type and being sufficiently large in extent to accommodate at least three 20 x 50 m (0.1 ha) plots, with a minimum separation distance of 200 m. Transects were laid radiating away from the source of disturbance, because in villages where subsistence activities are paramount, there may be gradients of increasing resource availability, with increasing distance from the source of disturbance. In total, 25 transects representing seventy five, 0.1 ha plots were laid across the study area. Twenty four plots were sampled in each land use type, except for "grazing" which had 27 plots. The geographical location of each transect was recorded using a GPS, and then mapped with ARCMAP version 9.0 (Sawatzky *et al.,* 2004; Chapter 4).

2.3. Vegetation sampling

Within each 0.1 ha plot, all stumps (both resprouting and non-resprouting) were enumerated and the species identified. The basal diameter (BD) and height of only the intact and measurable stumps were measured. For each measurable stump the BD and height were measured just above the basal swelling. For each resprouting stump the number of live resprouts was enumerated. The leading resprout (largest diameter and tallest) on each stump was measured for both height and BD. However, many resprouting stumps could not be measured for stump BD and height, because they had either been chopped very close to the ground level, severely burnt or damaged by termites (Figure 1). Depending on their origin, resprouts were classified as either stump resprouts (emerging from the remaining stump above or below ground) or root suckers (emerging from the roots). For the root suckers, soil around their point of emergence was removed to ascertain that they originated from roots and to eliminate any chance of confusing root suckers with seedlings.

Similar to Luoga *et al.* (2004), the identification of resprouting stumps to species level was based on the shoots of resprouts, wood and bark characteristics of the stumps, as well as bark smell. Initial plant species identification was done in the field using identification guides; mainly the Flora of Tropical East Africa (Polhill, *et al.,* 1952 *et seq.*), Hamilton (1991), Katende *et al.* (1995) and the help of a botanist familiar with the flora. Species which could not be identified in the field were collected and vouchers subsequently identified in the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda.

(a) **(b)**

Figure 1. Woody stumps affected by termites (a & b), resulting in various irregularities, making it difficult to obtain stump height and basal diameter measurements, in a multiple land use equatorial African savanna, central Uganda.

2.4. Data analyses

2.4.1. Responses of woody species to harvesting and resprouting

The frequency with which harvesters had selected particular woody species and stem diameter sizes (hereafter 'harvester's preference') was determined based on the enumerated harvested stumps. Harvested stumps were tallied into various diameter size-classes to examine the frequency of harvesting for particular stem diameter sizes for all species data pooled, and separately for the 16 species that interviews indicated were the most highly utilized for charcoal production in Nakasongola (Chapter 2). Variations in stump densities among the three land use types were compared using an ANOVA, followed by a Tukey HSD test when significant differences were detected (Zar, 1990). Analyses were carried out separately on: (i) total pooled species data, and (ii) the 16 highly utilized species.

2.4.2. Resprouting ability/effectiveness

Resprouting effectiveness was calculated as the mean number of resprouts/number of stumps of each species, and comparisons were made among the land use types using an ANOVA, followed by the

Tukey HSD Test when significant differences were detected (Zar, 1990). The stump inventory data for the 483 measured stumps were pooled and tallied into basal diameter (BD) size-classes of 1 – 5, 6 – 10, 11 – 15, …….., 36 – 40 and ≥ 41 cm, and related to the number of resprouts per stump. Stump BD size-class categorizations follow those used by Luoga *et al.* (2002) and Neke *et al.* (2006).

Species-specific linear regression analyses were performed to relate resprouting effectiveness (number of resprouts/stump) to stump characteristics (BD and height) for the 16 highly utilized species. In addition, the BD and height of the leading resprout were related to the number of resprouts/stump using the pooled species data.

3.0. Results

3.1. Harvesting of woody species and density of stumps

A total of 2,595 harvested woody plant stumps were recorded in the study area. Of the 2,595 stumps 2550 (98.3%) resprouted and 45 (1.7%) did not resprout because they were dead. Over the whole study area, these represented 74 species in 31 families. Of the 2,550 stumps that resprouted, only 483 (19%) stumps were measured for both BD and height. The other 81% were too difficult to measure, because they had been severely burnt, chopped very close to the ground and/or damaged by termites (Figure 1). Analysis of the 483 measured stumps in all the land use types revealed that 78% of harvested stumps were of BD ≤ 15 cm, and a few (22%) were ≥ 16 cm (Figure 2a). Hence, the number of stumps harvested decreased with increasing stem size (Figure 2). This was mainly because there were few trees with larger stems. Both stump and total resprout densities differed significantly ($p < 0.05$) among the land use types, being higher in charcoal production, than the grazing and cultivation land use types (Table 1).

Table 1. Variations in densities of stumps as well as all resprouting shoots and root suckers among land use types within an equatorial multiple land use African savanna woodland of Nakasongola District, central Uganda.

Stumps and sprout density (ind. ha^{-1})	**Land use types**			**Statistical parameters**	
	Grazing (N=27) (Mean ± S.E.)	**Cultivation (N=24) (Mean ± S.E.)**	**Charcoal prod. (N=24) (Mean ± S.E.)**	**$F_{2,72}$**	**p**
Stumps	266 ± 42^{a}	348 ± 43^{ab}	416 ± 42^{b}	3.2	0.047
All resprouts	2,087 ± 401^{a}	2,762 ± 390^{ab}	4,143 ± 591^{b}	5.1	0.009
Root suckers	37 ± 11^{a}	46 ± 22^{a}	31 ± 10^{a}	0.25	0.78
Leading resprouts	206 ± 34^{a}	274± 35^{a}	293 ± 35^{a}	1.84	0.17

Values in the same row accompanied by the same superscript do not differ significantly (Tukey HSD Test, $P< 0.05$).

3.1.1. Most utilized size-classes and harvesters' preferences

At the land use level, and for the 16 highly utilized species, the most harvested stem size-classes were the 6-10 cm followed by the 1-5 cm (Figure 2a, b, c, d). At the species level, for *Acacia polyacantha, A. seyal, Albizia zygia, Combretum capituliflorum, Vepris nobilis* and *Terminalia glaucescens,* the most frequently harvested stems were the 1-5 cm diameter size class. For stems of 6-10 cm diameter size class, the most harvested species were *Acacia hockii, A. sieberiana, C. collinum, C. molle, Hymenocardia acida, Gymnosporia senegalensis* and *Piliostigma thonningii*. For stems of the 11-15 and ≥ 16 cm diameter size-classes, the most harvested species were *Albizia coriaria, Grewia mollis* and *C. ghasalense* (Table 2). From the available plants, harvesters preferred plants in the 11-15 and ≥16 cm diameter size classes (Table 2).

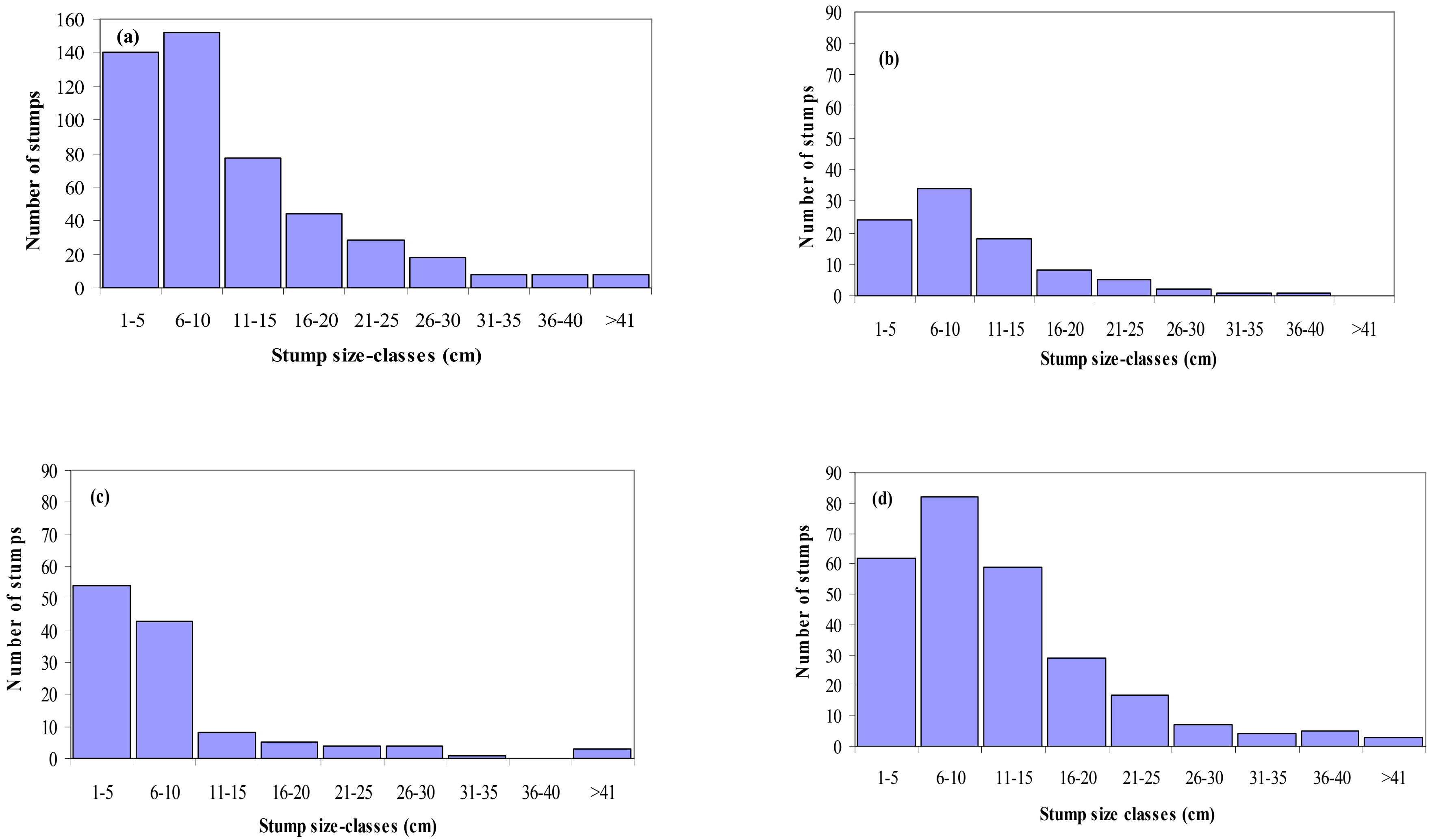


Figure 2. Variations in the number of stumps according to stem diameter size-classes of harvested individuals recorded for the; (a) overall savanna area (n = 483); and in the (b) grazing (n = 93), (c) cultivation (n = 122), and (d) charcoal production (n = 268) land–use types, in a multiple-use equatorial African savanna, central Uganda. (Note the different Y axis scale for Figure 2a).

Table 2. Percentage of harvested stumps in relation to the total available trees for the four major stem size-classes of the 16 species highly utilized for charcoal production within a multiple land use equatorial African savanna, central Uganda

Species	Diameter size-class (cm)	Unharvested trees (trees in 7.5 ha)	Harvested trees (stumps in 7.5 ha) (B)	Proportion of harvested trees (%))
Acacia hockii De Wild.	1-5	758	9	1.2
	6-10	26	14	35.0
	11-15	2	0	0.0
	≥ 16	1	2	66.7
Acacia polyacantha Willd.	1-5	665	4	0.6
	6-10	20	3	13.0
	11-15	0	1	100.0
	≥ 16	0	0	-
Acacia seyal Delile	1-5	98	1	1.0
	6-10	7	1	12.5
	11-15	0	0	-
	≥ 16	0	0	-
Acacia sieberiana DC.	1-5	214	1	0.5
	6-10	20	2	9.1
	11-15	0	0	-
	≥ 16	0	0	-
Albizia coriaria Welw.	1-5	80	0	0.0
	6-10	4	0	0.0
	11-15	0	0	-
	≥ 16	2	1	33.3
Albizia zygia J. F. Macbr.	1-5	1462	2	0.1
	6-10	17	0	0.0
	11-15	5	2	28.6
	≥ 16	2	1	33.3
Combretum capituliflorum Fenzl ex Schweinf.	1-5	386	15	3.7
	6-10	14	8	36.4
	11-15	2	3	60.0
	≥ 16	1	1	50.0
Combretum collinum Fresen.	1-5	3895	15	0.4
	6-10	32	18	36.0
	11-15	4	16	80.0
	≥ 16	4	8	66.7
Combretum ghasalense Engl. & Diels	1-5	1149	15	1.3
	6-10	52	16	23.5
	11-15	3	10	76.9
	≥ 16	5	25	83.3
Combretum molle Engl. & Diels	1-5	2243	17	0.8
	6-10	52	27	34.2
	11-15	4	21	84.0
	≥ 16	3	14	82.4
Grewia mollis Juss.	1-5	260	3	1.1
	6-10	23	2	8.0
	11-15	1	3	75.0
	≥ 16	2	3	60.0
Hymenocardia acida Tul.	1-5	740	2	0.3
	6-10	12	7	36.8
	11-15	0	3	100.0

	≥ 16	3	4	57.1
Gymnosporia senegalensis Loes.	1-5	235	1	0.4
	6-10	7	4	36.4
	11-15	0	0	-
	≥ 16	0	0	-
Piliostigma thonningii (Schumach.) Milne-Redh.	1-5	846	6	0.7
	6-10	37	14	27.5
	11-15	0	2	100.0
	≥ 16	2	1	33.3
Terminalia glaucascense Planch. ex Benth.	1-5	205	23	10.1
	6-10	17	5	22.7
	11-15	0	1	100.0
	≥ 16	3	4	57.1
Vepris nobilis (Delile) Mziray	1-5	728	19	2.5
	6-10	12	4	25.0
	11-15	4	4	50.0
	≥ 16	2	4	66.7

3.2. Resprouting of harvested stumps

Woody species exhibited both stump resprouting and root suckering modes of regeneration following anthropogenic disturbances (harvesting and burning). But, stump resprouting was by far the most common mode among the woody species in this savanna. Of the 2,595 stumps encountered, 98.3% (n = 2,550 stumps) resprouted, with an average of 9 ± 0.3 resprouts per stump. At the savanna woodland scale, a total of 22,492 resprouts were recorded, of which the vast majority of 22,207 (98.7%) were stump resprouts and the rest (285 = 1.3%) were root suckers. Among the resprouting species, 55% occurred only as stump resprouters, 41% occurred both as stump resprouters and root suckers and 4% occurred only as root suckers. Hence, species exhibiting both modes of resprouting were common in this savanna.

The species with the highest resprouting effectiveness in all area (7.5 ha) were *Capparis fascicularis* (27 ± 7 resprouts/stump, n = 5) and *Vepris nobilis* (24 ± 12 resprouts/stump, n = 42), while *Gardenia ternifolia* had the lowest resprouting effectiveness (2 ± 1 resprouts/stump, n = 3). At the land uses scale, of the stumps recorded within each land use, the number of stumps with resprouts was highest under cultivation (n = 838; 99.5%), followed by grazing (n = 717; 97.5%), and lowest under charcoal production (n = 995; 96.8%).

Overall, resprout densities (total resprout shoots from all resprouted stumps for all woody species per ha) differed significantly ($F_{2, 72} = 5.1$, P = 0.009) among the three land use types, and the highest density was recorded in the charcoal production land use, followed by cultivation, and grazing land uses (Table 1). On the other hand, root sucker densities did not differ significantly ($F_{2, 72} = 0.25$, P = 0.78) among the land use types (Table 1). At the species level, the number of root suckers ranged from 21 (for *Vitex doniana*) to 1 (for three species, namely *Pseudocedrela kotschyi*, *Zanthoxylum chalybeum* and *Grewia trichocarpa*; Appendix 1).

3.2.1. Number of resprouts per stump in relation to land use type

Mean resprouts per stump for all woody species differed significantly among land uses ($F_{2, 456} = 7.75$, $p = 0.0005$), being highest in charcoal production land use (mean ± S.E.: 14 ± 1), followed by cultivation (13 ± 1) and grazing land uses (10 ± 1).

For the 16 highly utilized species, resprouts per stump differed significantly ($F_{2, 387} = 6.38$, $p = 0.002$) among land use types, and the highest was recorded in the charcoal production land use (mean ± SE: 13 ± 1), followed by cultivation (12 ± 1), and grazing land uses (9 ± 1). Of the 16 highly utilized species, 14 resprouted via both stumps and root suckering, while *Acacia seyal* and *Albizia coriaria* resprouted only via the stumps. For these species, root suckers/stump ranged between 3 ± 1 (*Combretum capituliflorum)* and 14 ± 1 (*Vepris nobilis)* and resprouts/stump ranged between 3 ± 0.2 (*Acacia seyal*) and 24 ± 12 (*Vepris nobilis*; Appendix 1). Hence, *Vepris nobilis* had both the highest mean resprouts/stump and root suckers/stump. Of the 16 species, only 3 (*V. nobilis, C. capituliflorum* and *C. collinum*) had more than 10 resprouts/stump.

3.3. Relationship between resprouting ability and stump characteristics

Based on data from all woody species, resprouting stumps ranged from 3.0 (*Combretum molle*) to 55.5 cm (*Ficus* sp.) in basal diameter sizes. Stumps heights also ranged from 1 (*Acacia hockii*) to 130 cm (*C. collinum*). Most (87.5%) of the sampled stumps were ≤ 20 cm BD, with only 12.5% being ≥ 21 cm (Figure 2). Generally, the mean number of resprouts per stump increased with increasing stump BD (Figure 3); being highest for BD size class > 41 cm, except in the grazing land use where that size-class was absent. However, for this size-class, there were very few individuals. Similarly for the 16 species highly utilized for charcoal production, generally, the number of resprouts/stump increased with increasing stump BD (Figure 4). In relation to stump height, the highest resprouts/stump was found in stumps with heights of 0.31-0.40 m (Figure 5). Based on individual species, the number of resprouts/stump ranged between 30 (*Ficus* sp.) and 1 (six species, namely *Senna siamea*, *Balanites aegyptiaca*, *X. americana*, *Pavetta insignis*, *Vangueria tomentonsa* and *Grewia trichocarpa*) (Appendix 1).

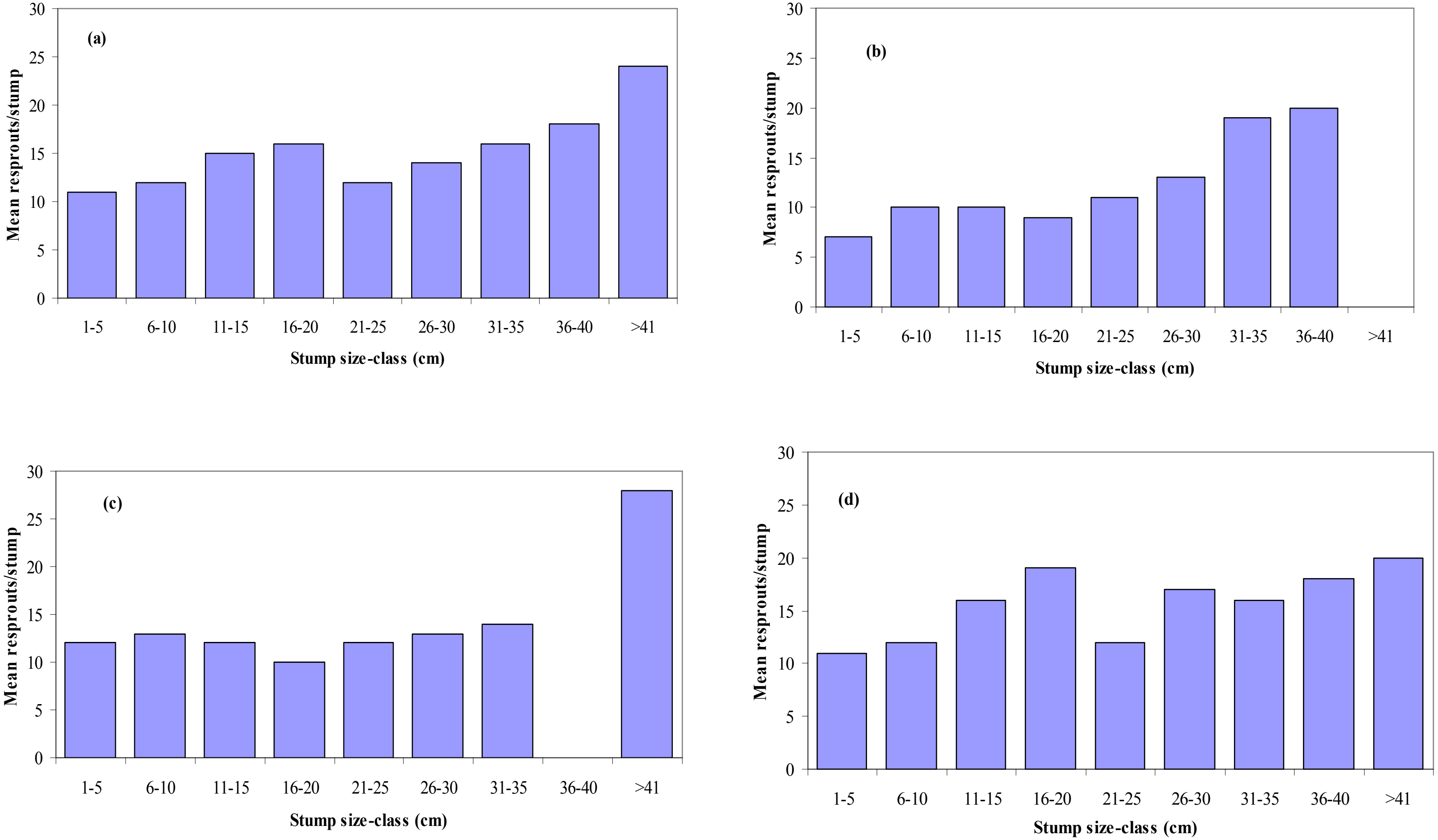


Figure 3. Variations in mean resprouts/stump in relation to stump basal diameter size-classes of harvested woody individuals recorded for: (a) the overall savanna; (b) grazing, (c) cultivation, and (d) charcoal production land use types, in a multiple land use equatorial African savanna, central Uganda.

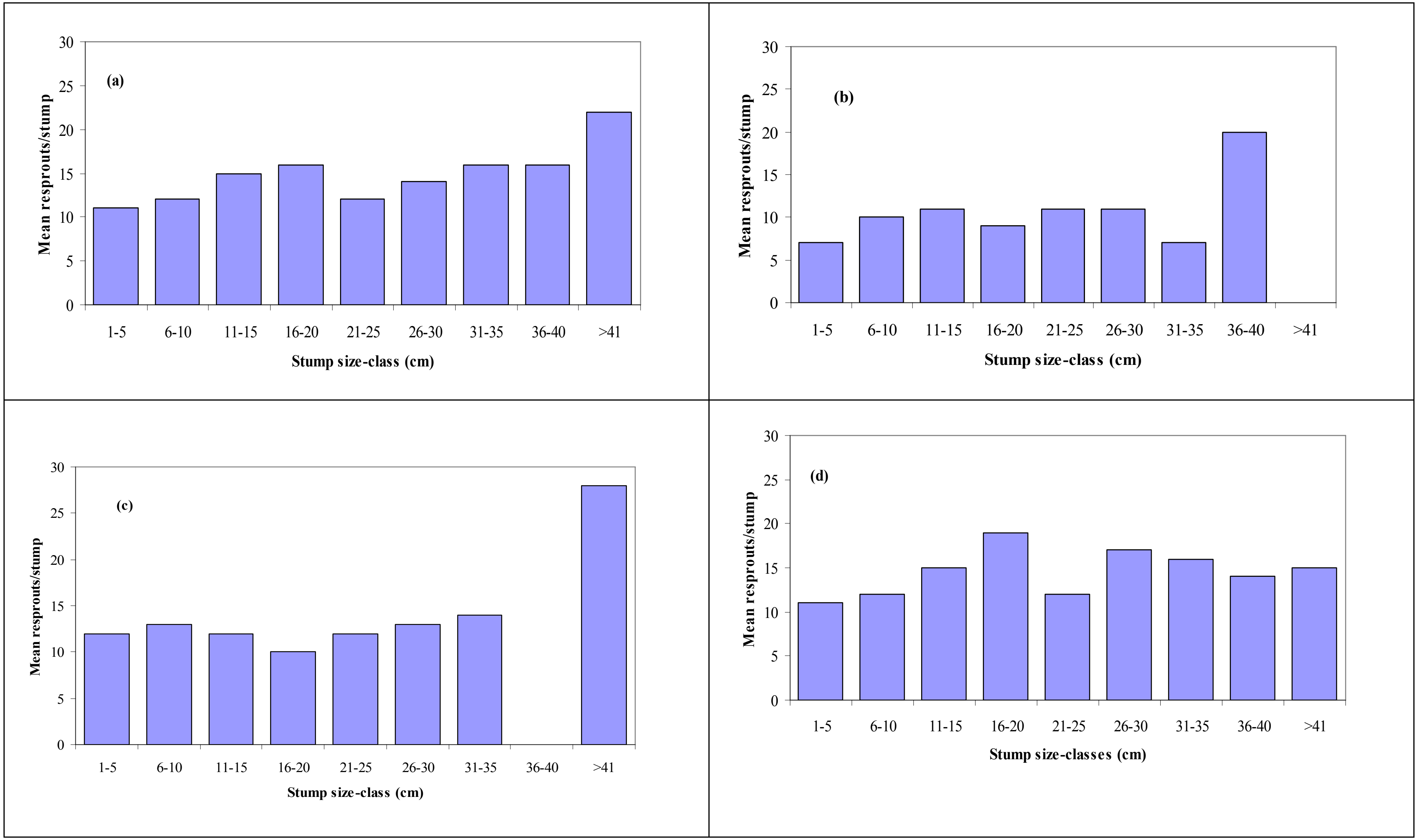


Figure 4: Variations in mean resprouts/stump in relation to stump basal diameter size-classes of harvested individuals recorded for the 16 species highly utilized for charcoal production recorded for (a) the overall savanna; and the (b) grazing, (c) cultivation, and (d) charcoal production land use types, in a multiple land use equatorial African savanna, central Uganda.

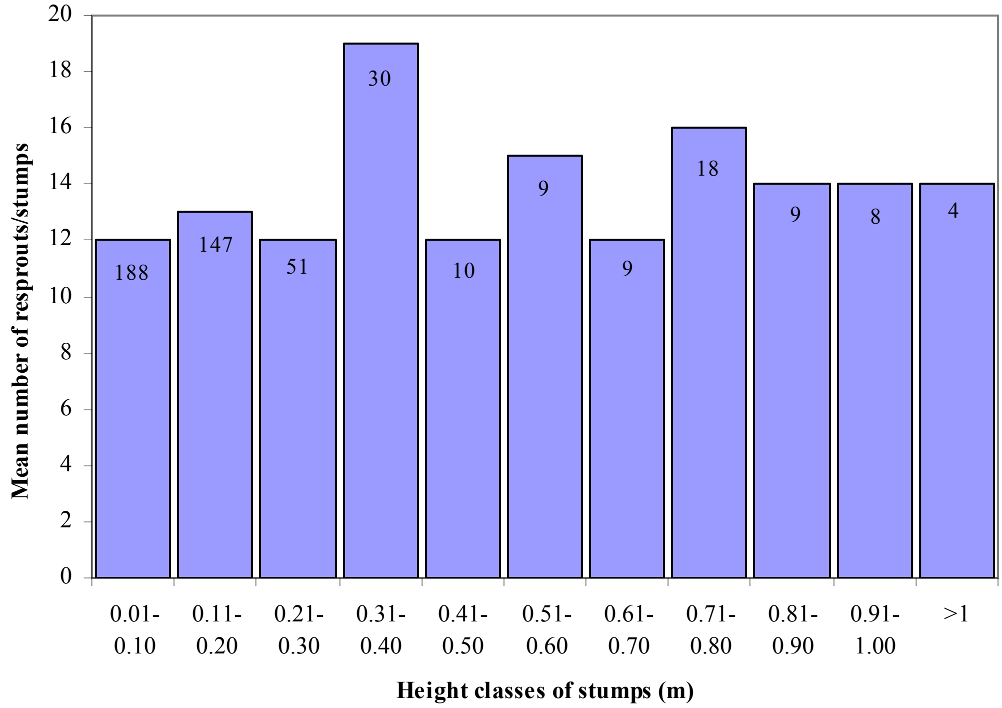


Figure 5: Variations in mean resprouts/stump in relation to stump height size-classes for all harvested woody species (only the measurable ones) in a multiple land use equatorial African savanna, central Uganda (The figures inside the bars are the number of individuals that formed a particular class).

For the 16 species highly utilised for charcoal production, at species level, species-specific linear regression analyses showed significant but weak positive relationship between stump BD and the number of resprouts/stump for only *Combretum ghasalense* (r^2 = 0.094, p = 0.02; Figure 6a) and *Vepris nobilis* (r^2 = 0.128, p = 0.052; Figure 6b). Similarly, there was a significant positive relationship between stump height and number of resprouts/stump for only *Piliostigma thonningi* (r^2 = 0.369, p=0.002; Figure 6c).

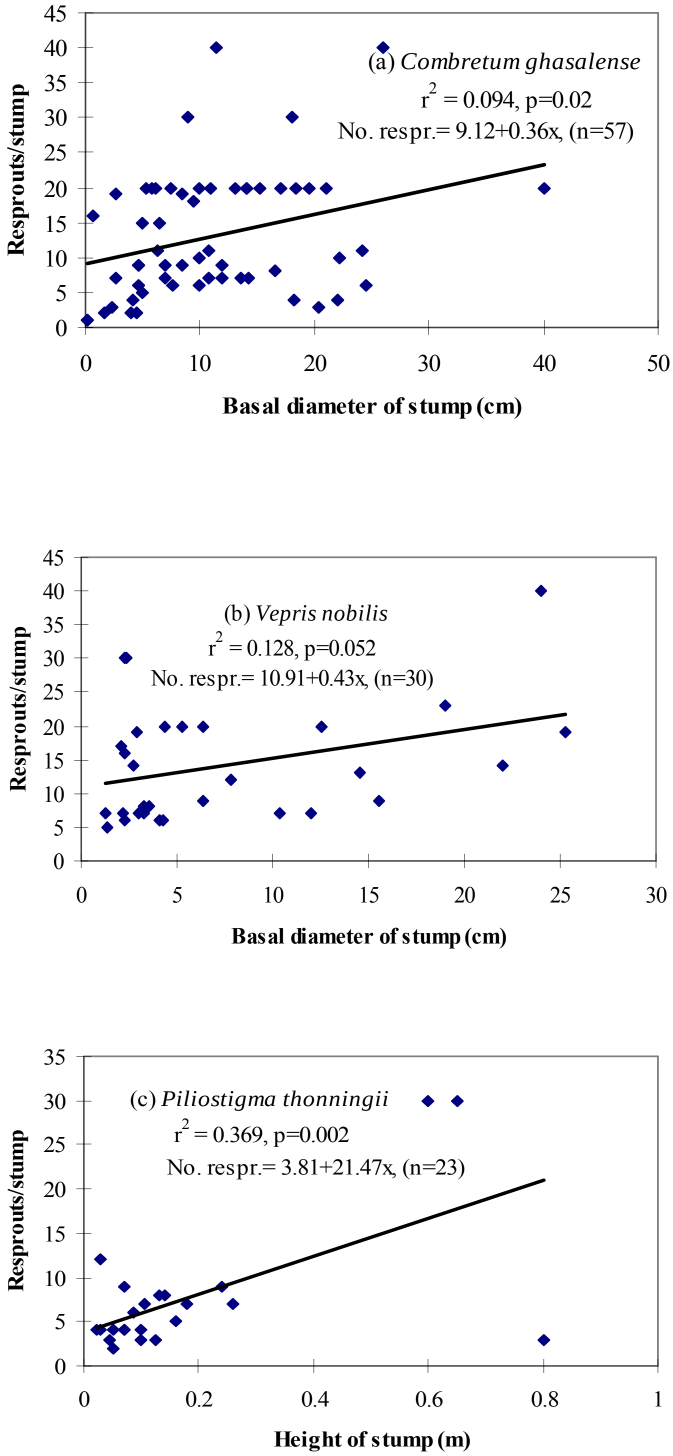
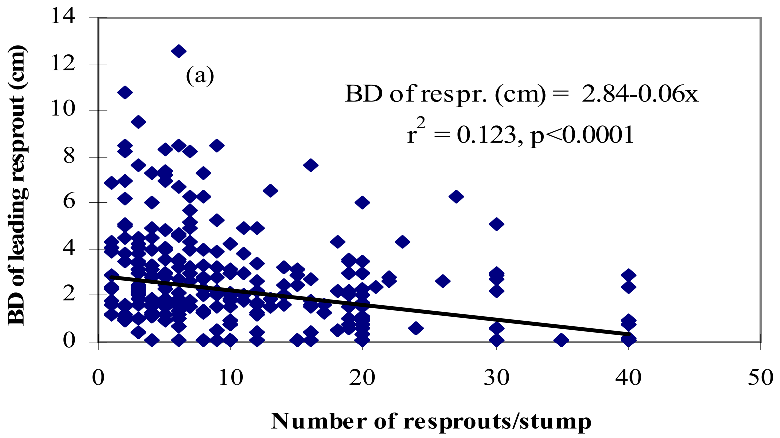


Figure 6. Regression analyses of stump basal diameter (a & b) and stump height (c) on the number of resprouts/stump produced (with statistically significant relationships) for only 3 of the 16 species highly utilized for charcoal production in a multiple land use equatorial African savanna, central Uganda.

3.4. Relationship between leading sprout characteristics and the number of resprouts/stump

For all the woody species, regression analyses showed weak but significant negative relationships between BD of leading resprout and number of resprouts/stump ($r^2 = 0.123$, $p < 0.0001$; Figure 7a), and between height of leading resprout and number of resprouts/stump ($r^2 = 0.068$ $p < 0.0001$; Figure 7b). *Albizia coriaria* had the thickest leading resprout (BD = 12.6 cm) and *Gymnosporia senegalensis* had the tallest leading resprout (Height = 7.5 m).



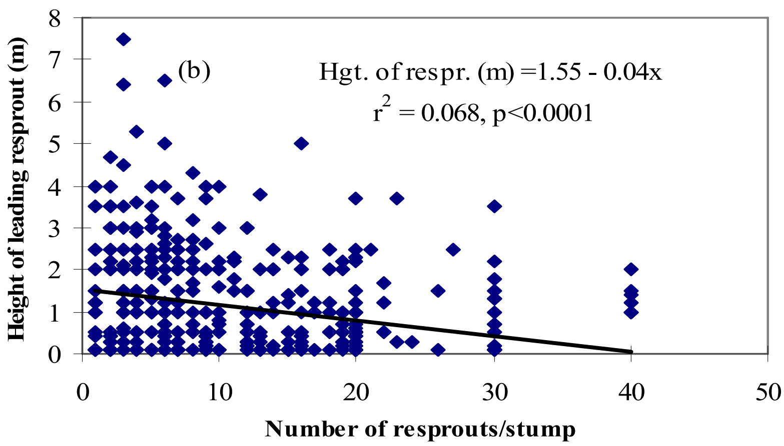


Figure 7. Regression analyses of the number of resprouts/stump in relation to: (a) basal diameter (n = 483), and (b) height of leading resprout (n = 483) for stumps of all woody species in a multiple land use equatorial African savanna, central Uganda.

4.0 Discussion

4.1. Harvesting intensity and the most frequently utilized diameter classes

Human harvesting of woody plants particularly for charcoal production, fuelwood and poles is the major form of disturbance leading to damage of woody plants, contributing greatly to stump creation in this wooded savanna. Indeed, all households in the area are dependent on woody plants for subsistence and commercial use (Chapter 2).

Generally, the most frequently harvested woody plants are the small diameter sized trees ≤ 20 cm BD. These include saplings and poles. In the savanna environment almost all of these species can grow much larger. However, they rarely attain larger sizes because they are continuously harvested. The harvesting of saplings and poles has similarly been reported as the major cause of stem damage in areas, which are more accessible and nearer to human settlements, in Budongo Forest Reserve, Uganda (Mwavu & Witkowski, 2008). Furthermore, Hall & Rodgers (1986) found pole cutting intensity to have accounted for the removal of half or more of the available stems in Tanzanian forests, affecting both lower storey and emergent species.

The harvesting of mainly pole and sapling sized individuals may be attributed to the declining woodland cover (Chapter 3) and, consequently, the low availability of large sized trees (Table 2) or harvesters' preference for the small sized stems that may be easy to cut and carry away. It is also possible that availability of larger sized trees is fast declining because of frequent harvesting for charcoal production that targets large sized woody individuals. Usually, in rural communities, small sized woody plants are harvested for firewood and poles for house construction, which may change woodland size class distribution. For example, Abbort & Homewood (1999) found small sized trees (BD = 5 - 15 cm) to be the most preferred for poles and fuelwood in a miombo woodland in Malawi. Women are the major firewood collectors, and they avoided large logs, which are heavy to carry. In Ongoye Forest Reserve (coastal scarp forest) in South Africa, small pole-size trees (BD <10cm) were the most harvested for firewood, building materials, fencing and for the curio trade (Boudreau *et al.,* 2005). Similar trends in stem size-class harvesting selectivity have been recorded in the Gendagenda, Litipo and Kimboza forests of Tanzania, where trees with a BD < 10 cm constituted the main fraction of the harvested stems (Burgess *et al.,* 2000).

4.2. Resprouting ability/effectiveness of woody species

The ability of woody plants to resprout after stem damage (mainly from harvesting) is common in this equatorial multiple use African savanna, with many of the species exhibiting both stump resprouting and root suckering. The resprouting of woody plants through stump and root suckering, following damage to the stem or disturbance has similarly been reported for the miombo woodlands of Tanzania (Luoga *et al.,* 2004), and the semi-evergreen rainforest in Queensland, Australia (Stocker, 1981). The high percentage of resprouting stumps observed in this study has similarly been reported in various studies (e.g. Shackleton, 2000, 2001; McLaren & McDonald, 2003; Luoga *et al.,* 2004; Kaschula *et al.,* 2005; Neke *et al.,* 2006) on woody plants resprouting in similar savanna ecosystems. Indeed, resprouting is a key attribute to the resilience and productivity of savannas, as well as a well known phenomenon in disturbance-prone environments (Kruger *et al.,* 1997; Shackleton, 2001). The number of resprouting species (98.3%) of the total 74 woody species recorded in this study is higher than the 83% of the 30 harvested woody species in the forest reserve and 90% of the 39 woody species harvested in public land recorded by Luoga *et al.* (2004) in the miombo woodlands of Tanzania. Similarly, it is higher than 94% of the 51 woody species studied by McLaren & McDonald (2003) in a tropical dry limestone forest in Jamaica.

The number of resprouting stumps differed significantly among the land use types. The higher number of resprouting stumps was recorded in the charcoal production land use type than in the cultivation and grazing land uses, suggesting that species behave differently to various environmental and disturbance factors (e.g. harvesting, fire, and grazing; McLaren & McDonald, 2003). Moreover, the land use types in the studied savanna differed in terms of disturbance frequency, which is an important determinant of the relative frequency of resprouting at the community level (White & Picket, 1985; Midgley, 1996; Kruger *et al.,* 1997).

The mean resprouts/stump of all woody species differed significantly among land uses, being highest in the charcoal production land use. The high number of resprouts in the charcoal production land use may be because of the greater number of trees that are harvested. It is in these areas that there is still a dense woodland cover that is exploited for both firewood and charcoal production. The low numbers of resprouts in the cultivation land use might be due to the low density of trees available to be harvested. Moreover, such areas might already have had trees extracted for charcoal production before they were turned into cultivation areas. The low number of resprouts in the grazing areas might be due to the nature of these grazing areas being mainly hydromorphic grasslands with few trees. In addition, the grazing animals also contribute to reduction of number of resprouts by grazing on them. In the cultivation and grazing land uses, fire is a common phenomenon as it is used as a management tool. Yet, fire is a major consumer of plant biomass (Bond & Keeley, 2005; Bond & van Wilgen, 1996; Levick *et al.,* 2009), which may consequently kill the meristematic tissues or the whole plant. Although burning tends to increase the importance of vegetative reproduction relative to sexual reproduction, frequent and more severe fires may also adversely affect sprouting regeneration mechanisms (Hoffman, 1998, 2002), as they may kill both stumps and roots.

Woody species in the present study area varied widely in their mean number of resprouts/stump with some (e.g. *Lannea barteri, Capparis fascicularis, Vitex ferruginea, Harrisonia abyssinica, Pavetta* *grandifolia*, *V. nobilis, C. capituliflorum* and *C. collinum*) producing more than ten resprouts/stump, while a few (e.g. *Senna siamea*, *Balanites aegyptiaca*, *X. americana*, *Pavetta insignis*, *Vangueria tomentonsa*, and *Grewia trichocarpa*) produced only one sprout/stump. Number of resprouts/stump varied among the woody species with some consistently having higher or lower numbers of resprouts/stump across all the land uses studied. For example, despite being frequently harvested for subsistence and commercial use, the regenerative potential of *C. molle, C. ghasalense, C. collinum, A. hockii, A. zygia* and *P. thonningii* was considerable because of effective stump resprouting and root suckering. Similarly, *Combretum molle* has been reported among the vigorous resprouting species after cutting in the miombo woodlands of Tanzania (Luoga *et al.,* 2004). Indeed, the effectiveness of stump resprouting varies with species, plant size/age at time of cutting, stump height and percentage of the stand removed (Shackleton, 2000; Luoga *et al.,* 2002; Mwavu & Witkowski, 2008).

4.3. Relationship between resprouting ability and stump characteristics

Species responses to disturbances are governed primarily by their life history and physiological traits; and by the characteristics of the disturbance (Gomez *et al.,* 1999). Species traits are especially important in determining the potential of species to establish and to persist following disturbance (Chambers, 1995). In this study, resprouting ability was higher in smaller stump basal diameter size-classes than larger size-classes. The increasing number of resprouts/stump with increasing stem size has also been reported elsewhere for savanna and semi- arid plants (Shackleton, 2001; Vesk *et al.,* 2004). This is probably a result of the greater surface area per stump, and greater root/shoot ratio (Shackleton, 2001), offered by larger sized stumps. On the other hand, the significantly higher resprouts/stump for the BD 5-30 cm stump size-class compared to < 5 cm stump size class found in this study, closely compares with results from other studies (e.g. Ickes *et al.,* 2003; Luoga *et al.,* 2004; Mwavu & Witkowski, 2008). The significant but weak positive relationship between stump BD and resprouts/stump for only two of the woody species highly utilized for charcoal production in the Nakasongola woodland was low compared with the seven woody species recorded in a disturbed tropical dry forest in Jamaica (McLaren & McDonald, 2003).

In the present study, of the 16 highly utilized species, only one species (*Piliostigma thonningii*) showed a significant positive relationship between the number of resprouts/stump and the height of the stump, although stump height is among the factors that have been shown to influence the survival of the cut stem and growth rate of the resultant coppice shoots in southern African savannas (Shackleton, 1997; Kaschula *et al.,* 2005). Stump height increases resprout survival because the greater the cutting height the lower the potential impact of browsers and fire (Shackleton, 2001). However, cutting too high may result in loss of sprouting vigour and poor shoot growth (Pawlick, 1989), while cutting too low on the stem of the tree may encourage fungal infections because of moisture from the ground or decay of the stump. The variation in the number of resprouts/stump among woody species may also be attributed to differences in plant size/age at the time of cutting (Shackleton, 2000; Luoga *et al.,* 2004). In the present study, the resprouting stumps found were mainly the small sized stumps (BD ≤ 20 cm; n = 87.5%), and only a few big sized ones (BD ≥ 21 cm; n = 12.5%).

The BD and height of the leading resprout were weakly but significantly negatively related to the number of resprouts per stump. A similar relationship was observed by McLaren & McDonald (2003) for some trees in a tropical dry limestone forest in Jamaica. The average basal diameter and height of resprouts have been shown to be a function of the number of resprouts on a stump; decreasing with increasing number of resprouts on a stump (Mwavu & Witkowski, 2008; McLaren & McDonald, 2003). This may be because a high number of resprouts on a stump would result in increased competition among the resprouts for the available resources. Therefore, a high number of resprouts on a stump may not be an indication of successful vegetative regeneration, as they may result in a significantly lower biomass recovery, although they may act as an insurance against the death of one or a few of the resprouts (McLaren & McDonald, 2003).

5.0. Conclusions

This study shows that human dependence on woodland resources for their livelihoods is the major cause of damage and removal of woody species in this equatorial multiple land use savanna. However, the woodlands appear to be resilient to harvesting as the woody species effectively resprout via stumps and root suckers. This clearly shows considerable resilience of woody species to anthropogenic disturbances in this savanna where seedling recruitment is constrained by unreliable rainfall seasonality. Although the woody species are effectively resprouting, their unsustainable harvesting due to increasing commercialization of charcoal production may result in a reduced range and amounts of useful plant products, with serious implications for the environment and local livelihoods. Over-harvesting of woody species may result in severe resource depletion and possibly irreversible degradation, even for the most abundant and resilient resources (e.g. Struhsaker, 1997; Obiri *et al.*, 2002). In order to achieve sustainable management of highly utilized species, silvicultural treatments such as not cutting trees too high or too low should be practiced. In addition manual thinning could be very important to reduce the number of resprouts on the stumps to encourage the faster development of resprouts into taller and thicker sized individuals as competition between resprouts for resources will be reduced.

Although basal diameters and heights of the stumps were significantly related to resprouting ability, additional experimental studies will be required to determine more precisely their relationship. In addition, long term studies relating woody species resprouting effectiveness to edaphic factors, frequency of burning, rainfall and frequency and timing of harvesting may be necessary for a more complete understanding of species resprouting responses to disturbances in this equatorial multiple land use wooded savanna. Sustainable harvesting of highly utilized species and those that are not, is necessary for all the land uses types.

Acknowledgements

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References

Abbort, J.I.O. & Homewood, K. 1999. A history of change: causes of miombo woodland decline in a protected area in Malawi. *Journal of Applied Ecology* 36: 422-433.

Akankwasa, D. & Tromborg, E. 2001. Challenges and strategies in the biomass energy sector- Working paper: revision of the Tax and Fee system in the Forest Sector, Uganda.

Bellingham, P.J. & Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409-416.

Bond, W.J. & Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387-394.

Bond, W.J. & van Wilgen, B.W. 1996. Fire and plants. Chapman & Hall, London, UK.

Boudreau, S., Lawes, M.J., Piper, S.E. & Phadima, L.J. 2005. Subsistence harvesting of pole-size understorey species from Ongoye forest reserve, South Africa: species preference, harvesting intensity and implications for understorey tree dynamics. *Forest Ecology and Management* 216: 149-165.

Burgess, N.D., Matthews, P., Evers, Y., Woodcock, K. 2000. Non-timber uses, threats and local attitudes. pp 281-302. In: Burgess, N.D. & Clarke, G.P. (Eds.), Coastal Forests of Eastern Africa. IUCN, Cambridge, UK.

Chambers, J.C. 1995. Disturbance, life history strategies, and seed fates in alpine herb field communities. *American Journal of Botany* 82: 421-433.

Dovie, D.B.K., Shackleton, C.M. & Witkowski, E.T.F. 2002. Direct-use values of woodland resources consumed and traded in a South African village. *International Journal of Sustainable Development and World Ecology* 9: 269-283.

Geldenhuys, C.J. 1997. Sustainable harvesting of timber from woodlands in southern Africa: challenges for the future. *South African Forest Journal* 178: 59–72.

Gomez Sal, A., Rey Benayas, J.M., Lopez-Pintor, A. & Rebollo, S. 1999. Role of disturbance in maintaining a savanna-like pattern in Mediterranean Retama sphaerocarpa shrub land. *Journal of Vegetation Science* 10: 365-370.

Hall, J.B. & Rodgers, W.A. 1986. Pole cutting pressure in Tanzanian forests. *Forest Ecology and Management* 14: 133-140.

Hamilton A.C. 1991. A Field Guide to Uganda Forest Trees. Makerere University, Kampala, Uganda.

Hoffmann, W.A. 1998. Post-burn reproduction of woody plants in Neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* 35: 422-433.

Hoffmann, W.A. 2002. Direct and indirect effects of fire on radial growth of cerrado savanna trees. *Journal of Tropical Ecology* 18: 137-142.

Ickes, K., Dewalt, S.J. & Thomas, S.C. 2003. Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology* 91: 222-233.

Kaschula, S.A., Twine, W.C. & Scholes, M.C. 2005. The effect of catena position and stump characteristics on the coppice response of three savanna fuelwood species. *Environmental Conservation* 32: 76-84.

Katende, A.B., Birnie, A. & Tengnas, B. 1995. Useful trees and shrubs for Uganda. Identification, propagation and management for agricultural and pastoral communities. Technical Handbook No. 10. Regional Soil Conservation Unit, RSCU/SIDA, Nairobi, Kenya.

Kennedy, A.D. 1998. Coppicing of *Tarchonanthus camphorates* (Compositae) as a source of sustainable fuelwood production: an example from the Laikipia Plateau Kenya. *African Journal of Ecology* 36: 148-158.

Kruger, L.M., Midgley, J.J. & Cowling, R.M. 1997. Resprouters versus Reseeders in South African forest trees, a model based on forest canopy height. *Functional Ecology* 11: 101-105.

Langdale-Brown, I., Osmaston, H.A. & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land use. Entebbe Government Printers, Uganda. 147 pp.

Levick, S.R., Asner, G.P., Kennedy-Browdoin, T. & Knapp, D.E. 2009. The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation* 142: 1693-1700.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000. Economics of charcoal production in miombo woodlands of eastern Tanzania: Some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 16: 15-30.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forest Ecology and Management* 189: 23-35.

McLaren, K.P. & McDonald, M.A. 2003. Coppice regrowth in a disturbed tropical dry limestone forest in Jamaica. *Forest Ecology and Management* 180: 99-111.

Midgley, J.J. 1996. Why is the world's vegetation not totally dominated by resprouters: an architectural hypothesis? *Ecography* 19: 92-95.

Mwavu, N.E. & Witkowski, E.T.F. 2008. Sprouting of woody species following cutting and tree-fall in a lowland semi-deciduous tropical rainforest, North-Western Uganda. *Forest Ecology and Management* 255: 982-992.

Namaalwa, J., Eid, T. & Sankhayan, P. 2005. A multi-species density-dependent matrix growth model for the dry woodlands of Uganda. *Forest Ecology and Management* 213: 312-327.

National Environment Management Authority (NEMA), 2002. State of environment report for Uganda. National Environment Information Centre, Kampala.

Neke, K.S., Owen-Smith, N. & Witkowski, E.T.F. 2006. Comparative resprouting response of Savanna woody plant species following harvesting: the value of persistence. *Forest Ecology and Management* 232: 114-123.

Obiri, J., Lawes, M. & Mulokwe, M. 2002. The dynamic and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management* 166: 131-148.

Parker, D., Downer, E.R. & Cole, G.E.D. 1967. Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Pawlick, T. 1989. Coppice with care. *Agroforestry Today* 1: 15–17.

Polhill, R.M. (Ed.). 1952 et seq. Flora of Tropical East Africa (FTEA). Royal Botanic Gardens, Kew, UK.

Sawatzky, D.L., Raines, G.L., Bonhan-Carter, G.F. & Looney, C.G. 2004. ARCSDM3: Arc MAP extension of spatial data modelling using weights of evidence, logistic regression, fuzzy logic and neural network analysis. http://www.ige.unicamp.br/sdm/ArcSDM3/.

Shackleton, C.M. 1993. Fuel wood harvesting and sustainable utilization in a communal grazing land and protected area of the eastern Transvaal Lowveld. *Biological Conservation* 63: 247-254.

Shackleton, C.M. 1997. The prediction of woody productivity in the savanna biome, South Africa. A PhD thesis. University of Witwatersrand, Johannesburg, South Africa.

Shackleton, C.M. 2000. Stump size and the number of coppice shoots for selected Savanna tree species. *South Africa Journal of Botany* 66: 124–127.

Shackleton, C.M. 2001. Managing regrowth of an indigenous Savanna tree species (*Terminalia sericea*) for fuelwood: the influence of stump dimensions and post-harvest coppice pruning. *Biomass and Bioenergy* 20: 261–270.

Stocker, G.C. 1981. Regeneration of North Queensland rain forest following felling and burning. *Biotropica* 13: 86-92.

Struhsaker, T.T. 1997. Ecology of an African rainforest: Logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville, FL. pp. 434

UBOS (Uganda Bureau of Statistics), 2002. Uganda Population and Housing Census, Kampala, Uganda.

Van Wyk, B. & Van Wyk, P. 1997. *Field guide to trees of Southern Africa*. Cape Town: Struik, Cape Town. South Africa.

Vesk, P.A., Warton, D.I. & Westoby, M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* 107: 72-89.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFET/UNSO vegetation map of Africa. UNESCO, Paris.

White, P.S. & Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. pp. 3-13. In: Pickett, S.T.A & White, P.S (Eds.) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall Inc, Englewood Cliffs, NJ, USA.

Appendix 1. Resprouting and root suckering woody species, listed alphabetically by family, indicating the number of resprouting stumps, mean number of resprouts/stump, number of plants with root suckers and mean number of suckers/plant encountered in 75, 0.1 ha, plots within a multiple land use equatorial African savanna, central Uganda (Unmeasurable stumps = resprouting stumps minus measurable stumps).

		Resprouting stumps			**Root suckers**	
Families	**Species**	**Total no. of resprouted stumps**	**No. of measurable stumps**	**No. of shoots/stump (mean ± S.E.)**	**Total root suckers**	**No. of root suckers/stump (mean ± S.E.)**
ACANTHACEAE	*Acanthus pubescens* Engl.	1	1	3		
ANACARDIACEAE	*Lannea barteri* Engl.	18	11	15.2 ± 3.5		
	Ozoroa insignis Delile	3	1	6 ± 4		
	Rhus natalensis Bernh. ex Krauss	94	7	8.0 ± 0.8	17	5 ± 1.2
	Rhus vulgaris Meikle	11	0	8.1 ± 1.3		
ANNONACEAE	*Annona senegalensis* Pers.	66	8	6.8 ± 0.6	10	5 ± 0.8
APOCYNACEAE	*Alstonia boonei* De Wild.	5	3	3.3 ± 0.9		
	Carrisa edulis Vahl	9	0	6.3 ± 1.9		
ARALIACEAE	*Cusonia arborea* Hochst. ex A. Rich.	2	2	3		
BIGNONIACEAE	*Kigelia africana* (Lam.) Benth.	4	1	4.3 ± 1.9		
	Stereospermum kunthianum Cham.	9	2	6.6 ± 2.2		
BURSERACEAE	*Commiphora dalzielii* Hutch.	2	1	2		
CAESALPINIACEAE	*Piliostigma thonningii* (Schumach.) Milne-Redh.	195	23	5.8 ± 0.3	32	3.4 ± 0.4
	Senna siamea (Lamarck) H. S. Irwin & Berneby	1	0	1		
CAPPARIDACEAE	*Capparis fascicularis* DC.	5	5	26.7 ± 6.7	1	5
	Crateva adansonii DC.	1	0	2		
CELASTRACEAE	*Mystroxylon aethiopicum* (Thunb.) Loes.	2	0	2		
	Gymnosporia senegalensis Loes.	22	5	6.9 ± 1.5	7	3.2 ± 0.5
COMBRETACEAE	*Combretum capituliflorum* Fenzl ex Schweinf.	108	32	11.9 ± 0.9	11	2.9 ± 0.6
	Combretum collinum Fresen.	449	75	11.5 ± 0.5	48	8.4 ± 1.2
	Combretum ghasalense Engl. & Diels	342	57	9.2 ± 0.4	17	6.9 ± 1.5
	Combretum molle Engl. & diels	365	87	8.6 ± 0.4	57	4.7 ± 0.5
	Terminalia glaucescens Planch. ex Benth.	52	12	4.6 ± 0.7	4	5.3 ± 2.5
EBENACEAE	*Euclea latidens* Stapf	14	2	8.9 ± 1.9	2	17
EUPHORBIACEAE	*Bridelia scleuroneura* Stapf Müll. Arg.	11	1	2.8 ± 0.6		
	Hymenocardia acida Tul.	137	16	9.4 ± 0.6	16	4.1 ± 0.4

	Securinega virosa (Willd.) Baill	2	0	2		
LAMIACEAE	*Vitex doniana* Sweet	21	1	7.6 ± 1.2	1	21
	Vitex ferruginea Schumach.	30	1	11.5 ± 1.6		
	Vitex fischeri Gurke	2	0	5		
LOGANIACEAE	*Strychnos innocua* Delile	25	3	7.1 ± 1.2		
MELIACEAE	*Ekebergia capensis* Sparrm.	3	0	8.5 ± 6.5		
	Pseudocedrela kotschyi Harms	12	4	6.5 ± 1.8	1	1
MIMOSACEAE	*Acacia hamulosa* Benth.	8	3	3 ± 0.4	1	2
	Acacia hockii De Wild.	120	25	6.5 ±0.6	10	4 ± 0.5
	Acacia polyacantha Willd.	33	8	5 ± 0.9	2	4
	Acacia senegal Willd.	6	3	6 ± 1.5	1	7
	Acacia seyal Delile	6	2	3.4 ± 0.2		
	Acacia sieberiana DC..	18	3	7.2 ± 1.8	3	3 ±1
	Albizia coriaria Welw.	8	4	3.7 ± 0.7		
	Albizia sp.	5	2	3.2± 0.2		
	Albizia malacophylla Walp.	3	3	3.5 ± 1.5	3	2.5 ± 0.5
	Albizia zygia J. F. Macbr.	38	8	5.2 ± 0.6	6	3.4 ± 2.4
	Calliandra sp Benth.	5	1	19		
	Dichrostachys glomerata Chiov.	1	0	8		
MORACEAE	*Antiaris toxicaria* Lesch.	9	0	2.4 ± 0.6		
	Ficus natalensis Hochst.	5	0	6 ± 2.7	1	9
	Ficus sp. L.	1	1	30	1	7
	Milicia excelsa (Welw.) C.C. Berg	3	2	8.5 ± 6.5		
OLACACEAE	*Ximenia africana* L.	1	0	1		
	Ximenia americana L.	1	0	1		
PAPILIONACEAE	*Erythrina abyssinica* Lam.	1	0	3	1	6
RUBIACEAE	*Gardenia ternifolia* Schumach & Thonn.	3	1	1.5 ± 0.5		
	Pavetta crassipes Schumach.				1	2
	Pavetta gardeniifolia Hochst. ex A. Rich.	3	0	15.5 ± 7.5		
	Pavetta grandifolia Korth.	1	0	10		
	Pavetta insignis Bremek.	2	1	1		
	Tricalysia niamniamensis Schweinf. ex Hiern				1	8
	Vangueria apiculata K. Schum.	2	1	9.5 ± 5.5		
	Vangueria tomentosa Hochst.	1	1	1		
RUTACEAE	*Vepris nobilis* (Delile) Mziray	42	30	24 ± 12	2	14 ± 1

	Zanthoxylum chalybeum Engl.	7	3	9 ± 6.3	1	1
	Zanthoxylum rubescens Planch. ex Hook.	3	0	8 ± 7		
SAPINDACEAE	*Allophylus africanus* P. Beauv.	11	1	7.1 ± 1.2	1	20
SAPOTACEAE	*Manilkara dawei* (Stapf) Chiov.	6	3	3.2 ± 1.2		
	Pouteria sp. Aubl.				6	7.8 ± 1.2
SIMAROUBACEAE	*Balanites aegyptiacus* Delile	1	0	2		
	Harrisonia abyssinica Oliv.	59	3	10.3 ± 1.4	11	6.5 ± 1
STECULIACEAE	*Dombeya dawei* Sprague	2	1	9		
TILIACEAE	*Grewia mollis* Juss.	103	10	6.9 ± 0.7	8	6 ± 2.5
	Grewia trichocarpa Hochst. ex A. Rich.	1	0	1	1	1
ULMACEAE	*Trema guineense* (Schumach. & Thonn.) Ficalho	6	0	7.4 ± 2.8		
UMBELLIFERAE	*Steganotaenia araliacea* Hochst.	1	1	3		
VERBENACEAE	*Lantana camara* L.	1	1	5		
SUB - TOTAL		**2,550**	**483**		**285**	
	Dead unidentified stumps	45				
OVERALL TOTAL		**2,595**	**483**		**285**	

CHAPTER 7

Population structure and regeneration of woody species in a multiple land use equatorial African savanna, central Uganda: implications for woodland management

Abstract

A better understanding of woody species regeneration and population dynamics is vital for conservation, sustainable management and restoration of savanna woodlands. The seedling recruitment and population structure of woody species in relation to anthropogenic and edaphic gradients were studied in a multiple land use equatorial African savanna woodland in central Uganda. A total of 17,785 seedlings representing 73 species in 31 families were recorded from seventy five, 0.1 ha, plots. Of the 17,785 individuals, 76% were from the selected 16 woody species highly utilized for charcoal production. Overall mean seedling densities differed among land use types (ANOVA: $F_{2, 72} = 5.9$, $p = 0.004$), being highest for cultivation (3,162 ± 440 individuals ha^{-1}) and charcoal production (2,416 ± 295 ha^{-1}) and lowest in grazing (1,629 ± 205 ha^{-1}). However, significant difference in mean seedling density was found only between the grazing and cultivation land uses. Similarly, for the 16 highly utilized species, seedling densities differed significantly among land uses ($F_{2, 72} = 4.39$, $P = 0.02$), being highest in the cultivation land use (2,408 ± 404 individuals ha^{-1}) followed by charcoal production (1,815 ± 240 ha^{-1}) and grazing land uses (1,224 ± 187 ha^{-1}). Significant differences were found only between grazing and cultivation land uses. Species composition of seedlings differed significantly among land use types (Global $R_{ANOSIM} = 0.119$, $p < 0.001$). Pair-wise comparisons showed significant differences between charcoal production and cultivation land uses ($R_{ANOSIM} = 0.14$, $p < 0.001$), charcoal and grazing land uses ($R_{ANOSIM} = 0.148$, $p < 0.002$) and cultivation and grazing land uses ($R_{ANOSIM} = 0.187$, $p < 0.001$). SIMPER analysis revealed that the species responsible for most of the within land use similarity differed among land uses. SIMPER pair-wise comparisons showed relatively high average dissimilarities in species composition of seedlings among land uses, being highest for cultivation versus grazing (84.6%) followed by charcoal versus grazing (80.2%), and charcoal versus cultivation land uses (79.6%). The first two Canonical Correspondence Analysis (CCA) axes explained 41.9% of the variance in species – environmental relations and were a reflection of edaphic (Ca^{2+}, Mg^{2+}, K and organic matter) and land use gradients. For the selected 16 species, stem diameter size-class distribution (DSCD) slopes ranged from -0.77 (*A. seyal*) to -0.43 (*C. collinum*), and juvenile:adult tree ratios from 9.7 to 99.9. Juvenile:adult tree ratios >>1 and negative DSCD slopes indicate good recruitment and successful regeneration. Based on comparisons of DSCD slopes with information provided by respondents, it is concluded that the species with intermediate and weakly DSCD analyzed are the effects of declining population sizes caused by human harvesting. Although most of the species are successfully recruiting, the continued uncontrolled use of even the most abundant and resilient species may in the long run negatively affect regeneration, resulting in severe resource depletion and possibly irreversible degradation.

Key words: ANOSIM, Canonical Correspondence Analysis (CCA), Edaphic factors, Highly utilized species, Land uses, Resilience, SIMPER, Diameter Size-class distribution (DSCD).

1.0. Introduction

Savanna woodlands, particularly those of Sub-Saharan Africa are very important natural resources for the livelihoods of both the urban and rural human populations in most developing African countries (Luoga *et al.,* 2000; Dovie *et al.,* 2004; Kituyi, 2004; MEA, 2005). However, they are widely affected by various forms of human activities that include grazing and subsistence harvesting of woody plants, which are not effectively and sustainably managed (Oates, 1999). In these areas typical unsustainable harvesting rates are defined by the short-term needs of consumers, the power of traditional and formal authorities, size of consumer communities, availability of suitable tree stem diameter sizes and forest/woodland size and accessibility (Burgess *et al.,* 2000; Boudreau *et al.,* 2005). This is resulting in the degradation of savanna woodlands with serious implications for food security and livelihoods particularly for local communities living in these areas. In this regard, there is an urgent need for conservation measures and adoption of sustainable use methods throughout Africa to avoid further degradation of these resources (Sayer *et al.*, 1992; Myers, 1994; Lykke, 1998). However, the sustainable use and conservation of woodland resources requires management systems that focus on balancing the needs (rate of resource use) of users against the regeneration ecology and growth of the resource (McGregor, 1994; Hartshorn, 1995). Like elsewhere in Sub-Saharan Africa, the sustainable management and conservation of woodlands in Uganda, requires consideration of tree population dynamics and resilience to anthropogenic disturbances. It is also important to identify species susceptible to local extinction and to reveal compositional changes in the vegetation (Lykke, 1998). This necessitates an understanding of regeneration and tree population structure in relation to environmental and anthropogenic factors.

Most seedling recruitment studies on woody plants in Uganda have focused on tropical forests (e.g. Sheil, 1996; Mwima *et al.,* 2001; Mwavu & Witkowski, 2009a), with little attention to savanna woodlands. Previous studies on these savanna woodlands have mainly focused on biomass and bio-energy, and ranching (e.g. Akankwasa & Tromborg, 2001; Kisamba-Mugerwa, 2001; NEMA, 2002), as well as growth, use and management of woodland resources (e.g. Namaalwa *et al.,* 2005). Similar to other Sub-Saharan Africa woodlands, little is known about natural regeneration and seedling establishment of a wide range of woody species highly utilized for subsistence and commercial charcoal production in Uganda. Yet, there is an increasing need for a scientific basis for the sustainable utilization and conservation of the savanna woodlands of Uganda. Therefore, an understanding of woody species regeneration via seedlings is vital for the conservation of important constituent woody species and ecosystems (Mwavu & Witkowski, 2009b). In addition, understanding the natural regeneration process and the dynamics of tree and shrub species populations have practical applications in the management and restoration of habitats (Peters, 1994). Information on plant population dynamics under the current disturbance regime is needed to foresee the trends of community changes in the future. In this regard, ecologists have, often, used stem diameter size-class distributions (DSCD) to indicate the health of a population (Condit *et al.,* 1998). In savannas and dry tropical forest systems, DSCD give a good indication of the impacts of disturbance and successional trends (Lykke, 1998). The characterization of DSCD of harvested woody species is a useful tool for monitoring forest/woodland stands in which harvesting takes place (Luoga *et al.,* 2002; Botha *et al.,* 2004).

This study describes seedling regeneration in relation to environmental factors and the population structure of woody species, with a view to determining resilience to harvesting and other anthropogenic disturbances. The following questions were explored: (i) How do the densities and distributions of seedlings of all woody species vary among land uses? (ii) How are densities and distributions of seedlings related to environmental factors (i.e. soil nutrients, texture and land uses)? and (iii) What is the pattern of population structure and regeneration status of the 16 species highly utilized for charcoal production? In the absence of long term data, forest/woodland dynamics (e.g. change of species composition and regeneration) are most often inferred from a single survey and the analysis of static forest/woodland inventory data by constructing species population DSCD (e.g. Lykke, 1998; Obiri *et al.,* 2002; McLaren *et al.,* 2005). DSCD also serve as a means of projecting population trends and is useful in assessing the state of populations for a variety of management purposes (e.g. Witkowski *et al.,* 1994; Obiri *et al., 2*002; McLaren *et al.,* 2005).

2.0. Materials and Methods

2.1. Study area

The study focused on households and the surrounding multiple land use savanna woodlands of Nakasongola District, south of Lake Kyoga, central Uganda ($0^0$40′- $1^0$41′ N, $31^0$57′ - $32^0$48′ E). The District covers about 3,424 km^2, most of which is woodland and grassy savanna, with 322 km^2 (10%) of open water and wetlands. It comprises eight sub-counties (administrative sub-divisions), namely Kakooge, Kalongo, Wabinyonyi, Kalungi, Nabiswera, Nakitoma, Lwampanga and Lwabiata. Each sub-county has a mean (± S.E.) of 49 (± 22) villages and 3,193 ± 390 households. The mean number of households/village was 82 (± 32), with an average of seven persons/household. The district has a total human population of 128,126 (41 people/km^2) (2000 National Housing Census), with 50.2% males and 49.8% females. About 95.3% of the population are rural and 4.7% urban (Uganda Bureau of Statistics, 2002).

Mean annual rainfall ranges from 500 – 1000 mm and is concentrated into two wet seasons (March to May and August to November), but rainfall received and reliability is higher in the south, declining gradually to the north. The mean monthly maximum and minimum temperatures range from 25 to 35 ^{0}C and 18 to 21 ^{0}C, respectively. The topography of the area undulates between 1,036 and 1,160 m above sea level. The major geological formations are characterized by the presence of young intrusive rocks, mostly acidic and less commonly basic. The youngest formations date from the Pleistocene era and are represented by sands, quartz and clays of alluvial or lacustrine origin (Parker *et al.,* 1967).

The vegetation of the area is classified as *Albizia-Combretum* woodland (Langdale-Brown *et al.,* 1964), a natural savanna woodland or woodland of mixed deciduous trees 3 to 12 m high and grasses 0.3 to 1.3 m high at maturity. However, the cover of the grass layer varies with season, is often patchy and subordinate to the tree layer. There are also thicket patches dominated by *Acacia hockii, A. gerrardii, A. kirki*i subsp. *mildbraedii, A. senegal* and *Euphorbia candelabrum* established in secondary wooded grasslands as a consequence of anthropogenic disturbances (White, 1983). The major land use practices in this savanna are livestock grazing, subsistence crop cultivation, and charcoal production (Chapter 2). There is a succession of land use change over time which is typical of areas subject to slash and burn agriculture. Areas used for charcoal production are then used for cultivation, while cultivated areas may subsequently be used for grazing. However most of the grazing lands occur on hydromorphic grasslands which are only suitable for grazing.

2.2. Sampling design

The present main land use types (cultivation, grazing, charcoal production) were the main focus of this study. Representative villages (areas) in each of the eight sub-counties were selected (with the help of local leaders and officials from the Department of Natural Resource and Environment) for woody vegetation sampling in March 2006. In each sub-county at least three transects were laid, each representing one of the three major land uses, with the exception of one sub-county which had 4 transects. The location of transects were selected randomly, but taking into consideration the homogeneous nature of the area for a particular land use type and being sufficiently large in extent to accommodate at least three 20 x 50 m (0.1 ha) plots, with a minimum separation distance of 200 m. Transects were laid radiating away from the source of disturbance, because in villages where subsistence activities are paramount, there may be gradients of increasing resource availability, with increasing distance from the source of disturbance. In total, 25 transects representing 75, 0.1 ha, plots were laid across the study area. Twenty four plots were sampled in each land use, except for "grazing", which had 27 plots. The geographical location of each transect was recorded using a GPS, and then mapped with ARCMAP version 9.0 (Sawatzky *et al.,* 2004; Chapter 4).

2.3. Vegetation sampling

Within each 0.1 ha plot, trees and shrubs were sampled. Stem diameters were measured using a diameter tape at breast height (1.3 m), unless there were irregularities at this height or trees were shorter. For individuals with multi-stems or other stem irregularities at breast height, stem diameter was measured below breast height. Each 0.1 ha plot was also systematically searched for woody plant seedlings (i.e. single stem of diameter ≤ 0.5 cm, height ≤ 1 m; and had never resprouted). Initial plant species identification was done in the field using identification guides, mainly based on the Flora of Tropical East Africa (Polhill, 1952 et seq.) and Hamilton (1991), and the help of a botanist familiar with the flora of the area. Unidentified species were collected and voucher specimens subsequently identified in the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda.

2.3.1. Selection of the 16 species highly utilized for charcoal production

The 16 highly utilized charcoal production species (Table 5) were determined through interviews with 45 respondents that included 5 to 6 resource users (charcoal producers and peasant farmers) from each sub-county, from key informants (Chapter 2) and existing literature (e.g. Byabashaija *et al.,* 2004, Kisakye, 2004; Namaalwa *et al.,* 2005). In addition the respondents were interviewed on the present status of these highly utilized species, and whether their numbers were increasing or decreasing.

2.4. Soil variables

Soil sample collection, preparation and analyses follow the same procedures as mentioned in Chapter 5. All soil analysis was performed by the Soil Science Department Laboratory, Makerere University, Kampala, Uganda.

2.5. Data analyses

2.5.1. Species richness and diversity of seedlings

Species richness (S) and the Shannon-Wiener Index of diversity (H') were computed to quantify and characterize seedling diversity patterns (Magurran, 2004) among land uses at the 0.1 ha scale, using the Species Diversity and Richness® version IV Programme (Seaby & Henderson, 2006). Differences in seedling densities and diversity for: (a) total woody plants, and (b) the 16 highly utilized species among land uses were compared by ANOVA, followed by a Tukey HSD Test when significant differences were revealed. Variation in seedling species composition was compared between land uses employing the ANalysis Of SIMilarity (ANOSIM; Clarke, 1993) in Community Analysis Package (CAP)® 3.1 (Seaby *et al.,* 2006). ANOSIM computes a test statistic (R_{ANOSIM}) reflecting the observed differences among replicates between sites, contrasted with differences among replicates within sites (Clarke, 1993; Pandolfi & Greenstein, 1997). A zero (0) occurs if the high and low similarities are perfectly mixed and bear no relationship to the group. A value of minus one (-1) indicates that the most similar samples are all outside of the group. While, a value of positive one (+1) indicates that the most similar samples are within the same group (Clarke, 1993; Seaby *et al.,* 2006). When a significant difference ($p < 0.05$) was detected, a SIMilarity PERcentage (SIMPER, Clarke, 1993) breakdown was conducted to determine which species were primarily responsible (make up 90% of the difference or similarity between or within groupings) for observed difference or similarity. The percentage similarity among land uses was also analysed by SIMPER (Seaby *et al.,* 2006). In SIMPER, a randomization process is used to find the probability of gaining particular values (R_{ANOSIM}) by chance. The method uses the Bray-Curtis measure of similarity, comparing in turn, each sample in group 1 with each sample in group 2. The Bray-Curtis method operates at the species level and therefore the mean similarity between group 1 and 2 can be obtained for each species (Clarke, 1993).

2.5.2. Species composition and distributions of seedlings in relation to environmental gradients

To examine variations in species composition and distributions of seedlings along environmental gradients in plots, a Canonical Correspondence Analysis (CCA) constrained ordination was performed using CANOCO® version 4 (ter Braak & Šmilauer, 2003). The environmental variables included in the CCA ordination were soil parameters (Na^+, K^+, Mg^{2+}, Ca^{2+}, P, K, pH, and % organic matter), soil texture (i.e. silt, sand, and clay), and the land uses. A Monte Carlo Re-Randomisation Procedure with 499 permutations under the reduced model was used to test the significance of the 1st canonical axis, and the combination of the first four canonical axes. This is a direct test of whether the included environmental variables have a significant effect on variation in community species composition. The intra-set correlations were used to infer the relative importance of each environmental variable for prediction of species composition (ter Braak & Verdonschot, 1995).

2.5.3. Population structure of the 16 species highly utilized for charcoal production

The stem diameter size-class distributions (DSCD) of each of the selected species were calculated and the proportion of each size class harvested in the corresponding land use determined. The DSCD were analysed using the method proposed by Condit *et al.* (1998) and Lykke (1998)and used by Obiri *et al.* (2002), McLaren *et al.,* (2005), and Mwavu & Witkowski (2009b). For the analysis, stem diameter size-classes were defined so that they accommodate more individuals with increasing size (Lykke, 1998). This balances the samples across diameter size classes, because the number of individuals generally declines with increasing diameter stem size (Condit *et al.,* 1998). In this regard, the inventory data were tallied into the following stem diameter size-classes 0-1, 1-2, 3-4, 5-6, 7-8, 9-10, 11-13, 14-16, 17-19, 20-23, 24-27, 28-31, 32-35, 36-39, and 40-43 cm. Finer divisions like these allow distributions to be calculated for the smallest species in savanna woodlands (Lykke, 1998; Mwavu & Witkowski, 2009b). For each species, a least-squares linear regression was performed with the diameter size-class midpoint as the independent variable and the mean number of individuals in that class (N_i) as the dependent variable. To derive N_i the number of individuals in each diameter size class is divided by the width of the class (Lykke, 1998). The size-class mid-points were not transformed. However, in order to derive straight-line plots of the DSCD, the average number of individuals (N_i) in each size class was transformed by $\ln(N_i + 1)$ because some classes had zero individuals (Lykke, 1998; Obiri *et al.,* 2002; McLaren *et al.,* 2005). The slopes of these regressions are referred to as DSCD slopes and were used as an indicator of status of population structure (Lykke, 1998; Obiri *et al.,* 2002; McLaren *et al.,* 2005). For each species, the DSCD slopes were calculated at the: (i) total savanna woodland (i.e. combined land uses), and (ii) individual land use type levels. The slope values were, then, used to summarize the shape of the DSCD for a species in a single number.

The interpretation of DSCD slopes was based on the four types of DSCD described in Everard *et al.* (1995). Slopes are usually negative, since larger size classes have fewer individuals, and indicate recruitment. Flat distributions with a slope of zero indicate equal numbers of smaller and mature individuals (Obiri *et al.,* 2002). Positive slopes are sometimes referred to as unimodal since they are typically characterised by relatively many but not regenerating canopy individuals (Shackleton, 1993; Everard *et al.,* 1995). The DSCD were also analysed by assessing the ratio of juvenile (seedlings + saplings: < 5 cm DBH) to adult trees (≥5 cm DBH), at the total savanna woodland level. One would expect juvenile:adult tree stem ratios to be > 1 for species that are successfully recruiting. Ratios of << 1 would indicate species with low recruitment and, hence, low representation in the juvenile size classes (West *et al.,* 2000). In this study, seedlings are individuals with a single stem of diameter of ≤ 0.5 cm, ≤ 1 m height and had never resprouted. A sapling is a young tree with 0.5 to < 5 cm dbh and more than 1.5 metres height, whereas an adult tree is one with ≥ 5 cm DBH. These classes were designed with reference to the structural composition of the woodland (Luoga *et al.,* 2002, 2004), and for particular use categories. In this study, it was found that adult trees were mostly used for charcoal production, firewood and building poles (Chapter 2).

3.0. Results

3.1. Diversity and distribution patterns of seedlings of woody species

3.1.1. All woody species

A total of 17,785 seedlings representing 73 woody species in 54 genera and 31 families were recorded from seventy five, 0.1 ha, plots. Of these, 76% (13,440) represented the 16 species highly utilized for charcoal production. The most species rich families were Mimosaceae (13 species), Rubiaceae (9), Euphorbiaceae (7), Moraceae (7), Anacardiaceae (6), Combretaceae (5) and Verbenaceae (5). Both richness (S) and diversity (H’) did not differ significantly (Table 1) among land uses (ANOVA: $F_{2, 72}$ = 1.81, p = 0.17; $F_{2, 72}$ = 0.41, p = 0.67, respectively). Total seedling density differed among land uses (ANOVA; $F_{2, 72}$ = 5.9, p = 0.004), being highest in cultivation land use followed by charcoal production and grazing land uses (Table 1).

3.1.2. The 16 species highly utilized for charcoal production

For the 16 highly utilized species, seedling densities differed significantly among land uses (ANOVA; $F_{2,72}$ = 4.39, p = 0.02), being highest in cultivation, followed by charcoal production and lowest under grazing (Table 1). The most abundant species also differed among land uses. In the grazing land use the most abundant seedling species were *C. collinum* (1,170 individuals), *Piliostigma thonningii* (626) and *C. molle* (354). In the cultivation land use, they were *C. collinum* (1,424 individuals), *C. molle*

(1,289), and *Albizia zygia* (1,185), whereas *C. collinum* (1,251 individuals), *C. ghasalense* (572) and *Vepris nobilis* (536) were most abundant in the charcoal production land use.

Table 1. Species richness (S), diversity (H') and density (means ± S.E.) of seedlings of all woody species at the 0.1 ha scale and the 16 species highly utilized for charcoal production in the main land uses in an equatorial multiple land use African savanna, central Uganda.

Seedling parameter	**Land uses**		
	Grazing (n = 27)	**Cultivation (n = 24)**	**Charcoal prod. (n = 24)**
S	11.3 ± 1.02^{a}	13.3 ± 0.95^{a}	14.0 ± 1.10^{a}
Range	1 - 22	4 - 22	0 - 21
H'	1.65 ± 0.13^{a}	1.79 ± 0.10^{a}	1.75 ± 0.12^{a}
Range	0 - 2.476	1.24 - 2.43	0 - 2.42
Density (ind. ha^{-1})			
All woody species	$1,629 \pm 205^{a}$	$3,163 \pm 440^{b}$	$2,415 \pm 292^{ab}$
Range	50 - 4120	120 - 8500	0 - 5460
Highly utilized species	$1,224 \pm 187^{a}$	$2,408 \pm 404^{b}$	$1,815 \pm 240^{ab}$

Values in the same row accompanied by the same superscript do not differ significantly (Tukey HSD Test, P < 0.05).

3.1.3. Species composition of seedlings

Total woody seedling species composition differed between land use types (Global $R_{ANOSIM} = 0.119$, $p < 0.001$). Pair-wise comparisons were significantly different between charcoal and cultivation ($R_{ANOSIM} = 0.14$, $p < 0.001$), charcoal and grazing ($R_{ANOSIM} = 0.148$, $p < 0.002$), and cultivation and grazing ($R_{ANOSIM} = 0.187$, $p < 0.001$) land uses.

Based on SIMPER, within land use similarities were relatively low, although tending to be higher for charcoal production (22.0%), than cultivation (21.2%), and grazing (20.5%; Table 2). The number of species making up 90% of the observed similarity within each land use was highest for charcoal production (12 species), followed by grazing (11) and cultivation (10). A comparison of individual species contributing most to overall similarity within each land use revealed that the top three species in each land use included *C. collinum* (Table 2). This species was the top for charcoal production and cultivation, but *Piliostigma thonningii* was the top for grazing. Seven species, namely *C. collinum*, *C. molle*, *C. ghasalense*, *Rhus natalensis*, *Harrisonia abyssinica, Acacia polyacantha* and *Acacia hockii* occurred in all land uses, and were among the species contributing to the 90% overall similarity within each land use (Table 2). SIMPER showed high average dissimilarities for pair-wise comparisons between land uses, ranging from 79.6 - 84.6%. The highest average dissimilarity was for cultivation versus grazing (84.6%), followed by charcoal versus grazing (80.2%), and lowest for charcoal versus cultivation (79.6%; Appendix 1). Hence, these results corroborate the ANOSIM pair-wise comparisons.

Table 2. Similarity percentage (SIMPER) analysis highlighting the contribution of individual species to the overall similarity within each land use type (grazing, cultivation and charcoal production) in an equatorial multiple land use African savanna, central Uganda. Species are ranked according to their percentage contribution to the overall similarity within each land use. Average similarity and cumulative percentage similarity are also indicated. The term "average abundance" represents the average abundance (density) of each species in a group or area, while "average similarity" values identify species (ranked by importance) that are found consistently in the group.

Seedling Species	Average Abundance	Average Similarities	Contribution (%)	Cumulative (%)
Charcoal land use (mean similarity = 22.0%)				
Combretum collinum	52.1	5.2	23.4	23.4
Combretum ghasalense	23.8	3.9	17.8	41.2
Harrisonia abyssinica	12.6	2.6	11.9	53.0
Combretum molle	22.3	1.9	8.8	61.8
Rhus natalensis	9.9	1.5	6.6	68.4
Vepris nobilis	22.4	0.8	3.7	72.1
Albizia zygia	9.4	0.8	3.5	75.6
Acacia polyacantha	7.2	0.7	3.3	78.9
Gardenia ternifolia	4.5	0.7	3.2	82.1
Hymenocardia acida	8.9	0.7	3.2	85.2
Acacia hockii	6.3	0.7	3.1	88.4
Anona senegalensis	3.0	0.5	2.1	90.5
Cultivation land use (mean similarity = 21.2%)				
Combretum collinum	59.3	4.7	22.2	22.2
Combretum molle	53.7	3.6	16.7	38.9
Albizia zygia	49.4	3.5	16.3	55.3
Harrisonia abyssinica	14.6	2.3	10.7	65.9
Acacia hockii	18.0	2.2	10.2	76.1
Rhus natalensis	5.2	0.9	4.3	80.4
Acacia polyacantha	14.8	0.8	3.7	84.1
Grewia mollis	4.8	0.6	2.8	86.9
Combretum ghasalense	8.9	0.4	2.0	88.9
Vitex doniana	10.1	0.3	1.6	90.4
Grazing land use (mean similarity = 20.6%)				
Piliostigma thonningii	23.2	5.3	25.7	25.7
Combretum collinum	43.3	4.7	22.8	48.5
Combretum ghasalense	11.2	2.1	10.1	58.6
Combretum molle	13.1	1.5	7.1	65.6
Rhus natalensis	4.6	0.9	4.7	70.3
Gymnosporia senegalensis	6.2	0.9	4.2	74.5
Harrisonia abyssinica	7.3	0.8	3.8	78.3
Gardenia ternifolia	6.4	0.7	3.6	81.9
Acacia polyacantha	3.8	0.7	3.4	85.4
Acacia hockii	3.6	0.6	2.9	88.2
Acacia sieberiana	3.3	0.4	1.8	90.0

3.2. Environmental relationships of seedlings

The relative influence of the measured soil variables and land uses on species variation of seedlings can be inferred from the CCA ordination diagram (Figure 1) and the intra-set correlations (Table 3). The environmental variables that were most correlated with canonical axis 1 were Ca^{2+} (r = 0.69) and Mg^{2+} (r = 0.30), while for axis 2 they were organic matter (r = 0.50), K^{+} (r = 0.41) and charcoal production (r = 0.40, Table 3). Hence, both canonical axes may be regarded as edaphic gradients.

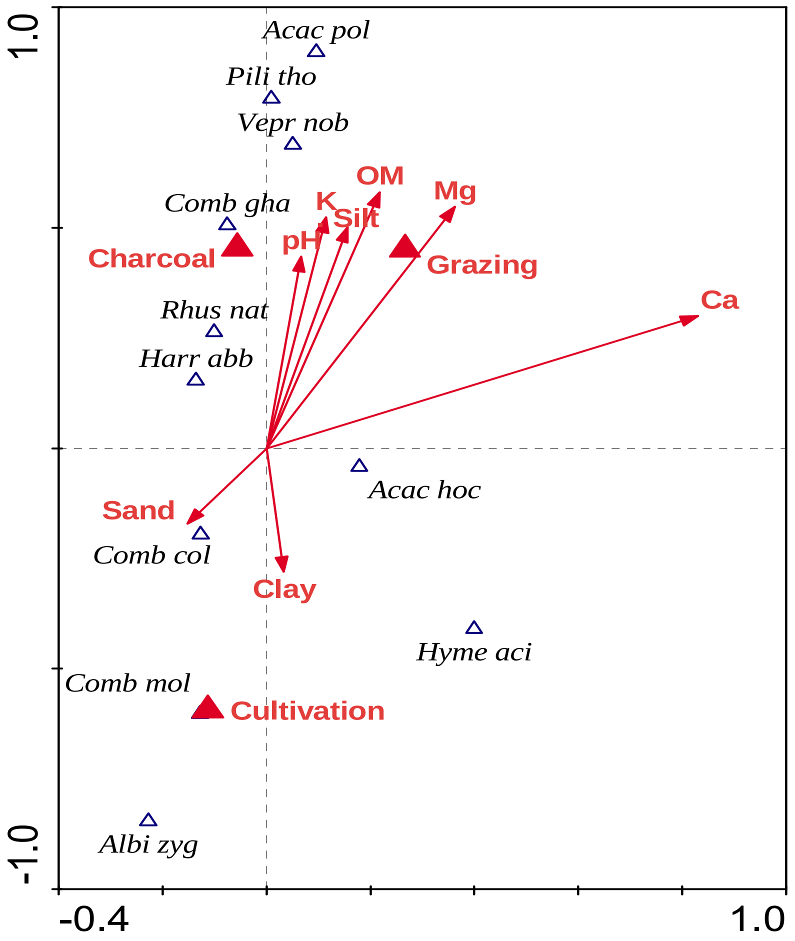

Figure 1. Triplot of Canonical Correspondence Analysis ordination showing soil variables (arrows), land uses (▲), and species of seedling (Δ) with a species weight range of 15- 100%, in an equatorial multiple use African savanna, central Uganda. Some of the species in the centre of the plot and soil variables with shorter arrows are suppressed for more clarity in the ordination diagram. OM: Organic matter, Acac hoc: *Acacia hockii*, Acac pol: *Acacia polyacantha*, Albi zyg: *Albizia zygia*, Comb col: *Combretum collinum*, Comb gha: *Combretum ghasalense*, Comb mol: *Combretum molle*, Harr aby: *Harrisonia abyssinica*, Hyme aci: *Hymenocardia acida,* Rhus nat: *Rhus natalensis*, Pili tho: *Piliostigma thonningii*, and Vepr nob: *Vepris nobilis.*

Table 3. Canonical Correspondence Analysis (CCA) of intra-set correlations of soil variables and land uses with the first four canonical axes in an equatorial multiple land use African savanna, central Uganda.

	CCA Axes			
Variable	**1**	**2**	**3**	**4**
pH	0.067	0.069	0.414	0.128
Organic matter	0.161	0.495	0.11	0.014
N	-0.063	0.227	-0.076	0.076
Available phosphorus	-0.243	-0.059	-0.014	-0.165
K	0.075	0.412	0.173	0.018
Na	0.165	0.009	0.323	-0.219
Ca	0.685	0.179	0.183	0.159
Mg	0.298	0.295	0.333	0.102
Sand	-0.119	-0.031	-0.159	-0.123
Clay	0.009	0.033	-0.352	0.223
Silt	0.139	-0.005	0.513	-0.165
Grazing	0.152	-0.1	0.386	-0.475
Cultivation	-0.082	-0.288	-0.22	0.537
Charcoal	-0.053	0.396	-0.123	-0.129

CCA showed that canonical axes 1 and 2 (eigenvalues 0.590 and 0.357, respectively) explained 14.3% of the variance in the species data, and 41.9% of the species-environmental relations (Table 4). Overall the first four canonical axes explained 22.9% of variance in the species data, and 67.2% of the variance in species-environment relations (Table 4). This suggests a strong relationship between species composition of seedling and the measured environmental variables. The Monte-Carlo permutation test showed that the 1st canonical axis ($F = 5.85$, $p = 0.006$) and the combination of the first four axes ($F = 2.38$, $p = 0.002$) were significant, indicating that the first four canonical axes significantly explained the species-environment relations.

Table 4. Summary table of results from the Canonical Correspondence Analysis of seedlings and environmental factors (soil variables and land uses) from 75, 0.1 ha, plots in an equatorial multiple land use African savanna, central Uganda.

Axes	1	2	3	4	Total Inertia
Eigenvalues	0.59	0.357	0.328	0.243	6.646
Species-environmental correlations	0.841	0.761	0.809	0.815	
Cumulative percentage variance					
of species data:	8.9	14.3	19.2	22.9	
of species-environment relation:	26.1	41.9	56.5	67.2	
Sum of all eigenvalues					6.646
Sum of all canonical eigenvalues					2.26

Although many of the seedlings did not show strong correlations with any of the measured environmental variables, some of them showed preference for certain environmental variables (Figure 1). For example, the distribution of *Acacia hockii* seedlings was clearly associated with low Ca^{2+}

concentrations, *Combretum ghasalense* with charcoal production, *Combretum molle* with cultivation and *Combretum collinum* with sandy soils (Figure 1).

3.3. Population structure of the 16 species highly utilized for charcoal production.

At the savanna woodland level, DSCD slopes of the species ranged from - 0.77 (*A. seyal*) to - 0.43 (*C. collinum*) indicating high numbers of individuals in the lowest diameter size class and a gradual decline in the middle and larger diameter classes (Table 5). However, at the land use level some species had dash (-) DSCD slopes, meaning these species were absent in that particular land use. These included *Albizia coriaria* and *Vepris nobilis* in the grazing land use, and *A. seyal* in both cultivation and charcoal production land uses (Table 5). *Acacia seyal* was similarly reported by respondents to be decreasing in population abundance (Table 5). In addition, all the 16 highly utilized species had juvenile:adult tree ratios ranging from 9.7 (*A. sieberiana*) to 99.9 (*C. collinum*, Table 5). A juvenile:adult tree ratio > 1 suggests that all 16 species have healthy regeneration and are successfully recruiting. For species present in each land use type, the DSCD slopes spanned - 1.19 to - 0.42 for grazing, - 1.16 to - 0.42 for cultivation and -2.38 to - 0.43 for the charcoal production land uses (Table 5). Generally, most species had higher DSCD slopes under charcoal production land use.

The population structures of the 16 highly utilized species exhibited three types of DSCD curves (‘inverse-J’, intermediate and ‘weakly inverse-J’). The first group exhibiting good ‘inverse J’ DSCD comprises *A. hockii, P. thonningii, V. nobilis* and *Grewia mollis,* with DSCD slopes ranging from - 0.66 to - 0.54, and juvenile:adult ratios ranging from 10.8 - 40.4 (Table 5). These species had no size-classes without individuals, and high densities of juveniles (< 5 cm DBH; Figure 2). Given the highly negative DSCD slopes and relatively high juvenile:adult ratios, these species are successfully regenerating. However, according to resource users only *A. hockii* and *V. nobilis* are experiencing an increase in population abundance, whereas *P. thonningii* and *G. mollis* are declining.

The second group consists of *A. polyacantha, C. capituliflorum, C. collinum, C. ghasalense, C. molle, H. acida* and *T. glaucescens* with DSCD slopes ranging from - 0.69 to - 0.43, and juvenile:adult ratios ranging between 11.4 (*T. glaucescens*) and 99.9 (*C. collinum*; Table 5). This group consists of the common species which characterise the vegetation of the area. It is in this group that some of the species had individuals in the largest size-classes (35 - 43 cm; Figure 2), also with several intermediate size-classes without individuals. Four species in this group, all *Combretum* spp., were reported by respondents to be increasing in population abundance.

The third group comprises *Albizia zygia*, *Albizia coriaria*, *A. seyal*, *A. sieberiana* and *G. senegalensis* with DSCD slopes ranging from - 0.77 to - 0.49, and juvenile:adult ratios ranging from 9.7 - 66.5 (Table 5). Although having a relatively high number of individuals in the seedling class, these species exhibited sporadic regeneration, with irregular declines in numbers within the larger size classes (Figure 2). Only *A. sieberiana* and *A. zygia* had individuals above the 9–10 cm size-class. Hence, they were largely represented by juveniles. Indeed, apart from *A. coriaria,* all the species in this group were reported by respondents to be decreasing in abundance. However, the DSCD analyses revealed that *A. coriaria* lacked individuals in the 1-2 cm size-class. *G. senegalensis* was also under-represented in the 1-2 cm size-class compared to the preceding and following size-classes. The strong peak in the seedling size class followed by absence of saplings indicates poor regeneration.

Generally, all the species, except *Albizia coriaria* and *Combretum capituliflorum,* were reported to be increasing in abundance by respondents (Table 5), and also well-represented in both the juvenile and adult classes (Figure 2), with gradually declining number of individuals with increasing stem size-class. This indicates that most of these species have high regeneration potential. For the species cited as decreasing in abundance/availability by respondents, the DSCD revealed that most had some size-classes lacking individuals, with an irregular decline in number of individuals with increasing size-class. Thus, they had a few stem size-classes with individuals (*Albizia zygia* and *A. sieberiana*; Figure 2). These results suggest general agreement between the ecological DSCD and the local peoples' assessment of the population status of these highly utilized woody species.

Table 5. Juveniles:adult trees ratio and DSCD parameters (i.e. slope, t, and r^2 values), uses and population trends for the 16 highly utilized species in an equatorial multiple land use African savanna, central Uganda. The DSCD parameters were calculated based on the combined (including seedlings, juveniles and adults) data for each species.

		All land uses			Grazing			Cultivation			Charcoal prod.				
Species	Ratio	Slope	t	r^2	Slope	t	r^2	Slope	t	r^2	slope	t	r^2	Uses	Spp incr/decr**
Acacia hockii	27.1	- 0.55	9.57	0.88	- 0.72	4.56	0.62	- 0.59	8.54	0.85	- 0.72	7.46	0.81	F, Fe ,Fi, M	Increasing
Acacia polyacantha	30.2	- 0.57	7.37	0.81	- 0.73	4.42	0.60	- 0.62	6.18	0.75	- 0.69	5.43	0.69	F, Fe, Fi	Decreasing
Acacia seyal	14.0	- 0.77	6.48	0.76	- 0.77	6.48	0.76	–	–	– –	–	–	–	F, Fe, Fi	Decreasing
Acacia sieberiana	9.7	- 0.68	6.37	0.76	- 0.77	5.16	0.67	- 1.16	7.11	0.79	- 0.6	2.88	0.39	F, Fe ,Fi	Decreasing
Albizia coriaria	20.0	- 0.69	3.48	0.48	–	–	–	- 0.77	4.31	0.59	- 2.38	2.71	0.36	S, P, T, Fi	Increasing
Albizia zygia	66.5	- 0.49	6.49	0.76	- 1.19	2.72	0.36	- 0.51	6.09	0.74	- 0.64	5.13	0.67	S, P, T, Fi	Decreasing
Combretum capituliflorum	24.1	- 0.61	6.46	0.76	_	–	–	- 1.05	6.96	0.79	- 0.57	4.44	0.60	P, Fi, T	Increasing
Combretum collinum	99.9	- 0.43	6.70	0.78	- 0.42	4.92	0.65	- 0.42	4.72	0.63	- 0.43	4.81	0.64	P, Fi, T	Increasing
Combretum ghasalense	20.5	- 0.53	8.86	0.86	- 0.62	6.56	0.77	- 0.69	7.19	0.79	- 0.55	5.69	0.71	P, Fi, T	Increasing
Combretum molle	42.3	- 0.49	7.98	0.83	- 0.53	3.78	0.52	- 0.51	6.78	0.78	- 0.58	6.16	0.75	P, Fi, T, M	Increasing
Grewia mollis	10.8	- 0.66	8.68	0.85	- 0.73	3.66	0.51	- 0.75	7.26	0.8	- 0.91	6.92	0.79	P, Fi	Decreasing
Hymenocardia acida	53.9	- 0.54	5.38	0.69	- 0.54	3.22	0.44	- 0.58	4.08	0.56	- 0.62	4.66	0.63	P, Fi, M	Decreasing
Gymnosporia senegalensis	33.6	- 0.61	4.30	0.59	- 0.56	3.21	0.44	- 0.98	3.83	0.53	- 0.8	3.30	0.46	Fi, Fe, M	Decreasing
Piliostigma thonningii	22.9	- 0.54	7.15	0.79	- 0.56	7.27	0.80	- 0.78	4.38	0.59	- 0.65	3.69	0.51	Fi, T, M	Decreasing
Terminalia glaucescens	11.4	- 0.69	6.38	0.76	- 0.86	4.10	0.56	- 0.72	4.57	0.62	- 0.77	3.64	0.51	T, P, Fi, M	Decreasing
Vepris nobilis	40.4	- 0.57	7.34	0.81	–	–	–	- 0.65	4.25	0.58	- 0.59	7.15	0.79	P, Fi, M	Increasing

_ = Absence of specie from a particular land use

F = Feed; Fe = Fence; Fi = Firewood; M = Medicinal; P = Poles; S = Shade; T = Timber

**Species increase/decrease were the responses of people (n= 45) interviewed in 8 sub-counties in Nakasongola District, central Uganda.

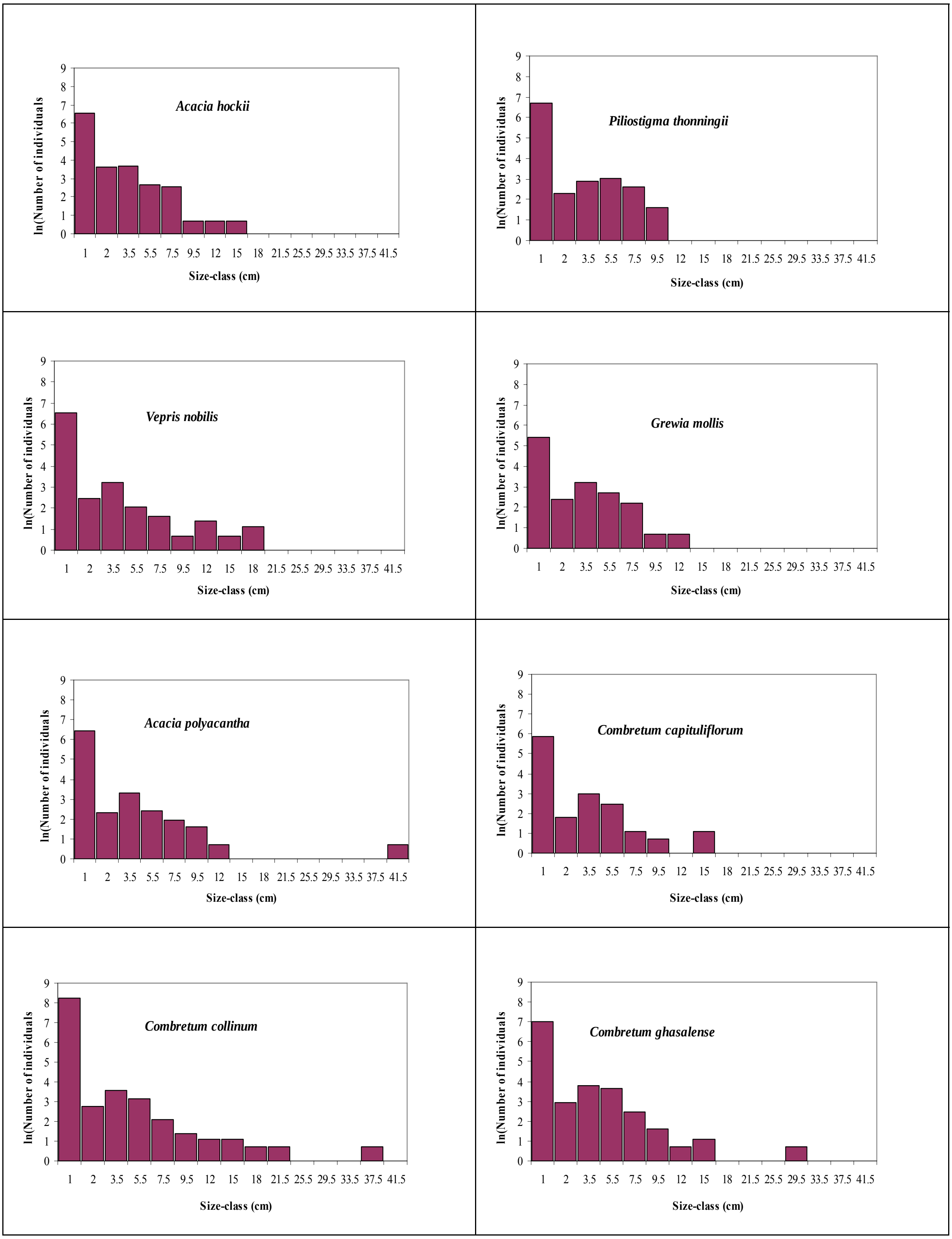

Figure 2. Diameter stem size-class distributions (DSCD) exhibited by the 16 woody species highly utilized for charcoal production in an equatorial multiple land use African savanna, central Uganda, arranged according to the shape of DSCD curves. Mid-points of the diameter size-classes are plotted (with exception of classes 0-1 cm and 1-2 cm rounded whole numbers are plotted). For *Acacia polyacantha* all individuals > 39 cm DBH have been grouped together.

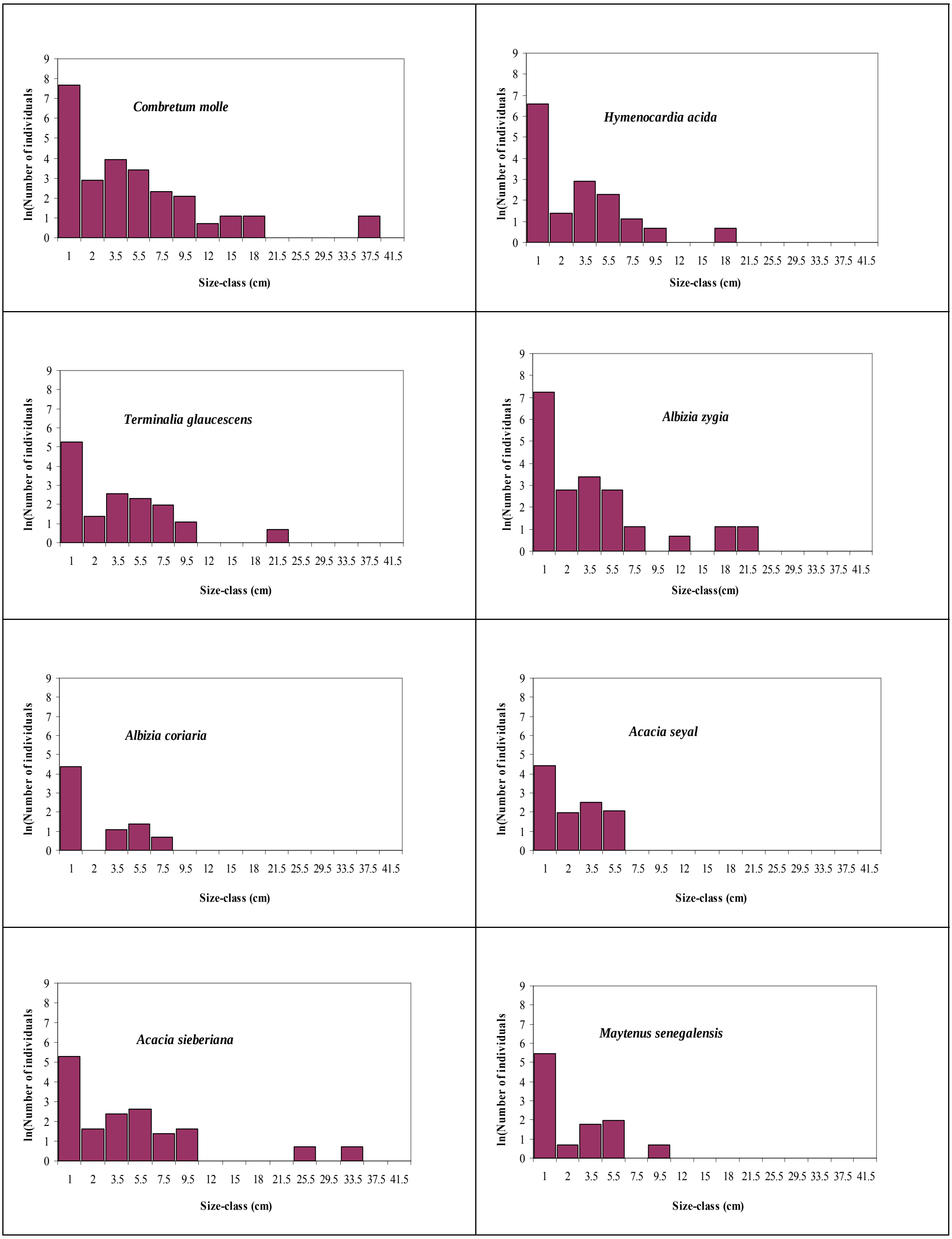

Figure 2: (Continued)

4.0. Discussion

4.1. Diversity and distribution patterns of seedlings

Species composition of seedlings varied significantly among the land uses. Therefore, management interventions to ensure successful regeneration and persistence of these species will have to consider the influence of prevailing land use practices. Results for both seedlings of all species and those of the 16 highly utilized species showed higher seedling density in the cultivation land use followed by charcoal production and grazing land uses. The higher seedling density in cultivated may be attributed to the patchiness of the vegetation as a result of tree removal, and improvement in soil conditions from soil tilling. Thus cultivation enhances the recruitment process by reducing competition for water and nutrients, opening up more growing space and by increasing the availability of light for seed germination and seedling growth (Montgomery & Chazdon, 2002; Hutchison *et al.,* 2005; Zida *et al.,* 2007). Similarly, Harms *et al.* (2004) and Wright *et al.* (2005) observed higher seedling density in seasonal sites, that they attributed to a higher availability of resources (e.g. free space and light), on the forest floor and reduced asymmetric competition with saplings and adults. The low density of seedlings in charcoal production compared to cultivation may be attributed to the high level of tree and shrub cover, and at times the thick grass layer in this land use type. A heavy grass layer shades the establishing woody seedlings, while both grass and tree seedlings compete for water and nutrients (Skarpe, 1992; Scholes & Archer, 1997; Bond *et al.,* 2001).

The low seedling densities and diversity in the grazing land use may be attributed to the effects of herbivory and soil trampling by cattle, and the accompanying bush burning which is common in this savanna. Woody plant regeneration failures due to grazing impacts have been documented in other wooded savanna environments and forests (e.g. Tilghman, 1989; West *et al.,* 2000). Although woody species are affected differently by grazing disturbances, resulting in the loss of some and survival of those species that can resist/withstand grazing pressures, altered species composition and decreased species richness in such areas is possible (Higgins *et al.,* 1999). However, the effects of grazing by livestock on tree regeneration and subsequent growth is generally related to spatial and temporal variations in grazing intensity, stocking rate and feeding behaviour, as well as plant phenophase and differential responses of species to browsing and trampling (e.g. Braithwaite & Mayhead, 1996; O'Connor, 1996; Drexhage & Colin, 2003).

Similar to other African savannas, the grazing areas in this study are seasonally subjected to bush burning that constrains regeneration of the fire sensitive species, as a large proportion of the seedlings and juveniles are killed (Swaine *et al.,* 1976; Frost & Robertson, 1987). Moreover, the presence of herbivores exacerbates the effects of fire by keeping a large percentage of the plant population in the fire-trap (Pellew, 1983; Dublin *et al.,* 1990). These negative effects of fire on woody plant density and seedling regeneration have been reported in a number of studies elsewhere (e.g. Higgins *et al.,* 2000; Hoffmann & Solbrig, 2003; Gambiza *et al.,* 2005; Hutchison *et al.,* 2005; Albrecht & McCarthy, 2006). Furthermore, frequent fires are known to disadvantage the sexual reproduction of most common tree species in savannas, because both seed supply and the number of microsites are reduced (Setterfield, 2002). This might also be the case for the savannas of central Uganda.

4.2. Abundances and distributions of seedlings in relation to environmental factors

Results of the present study show that the distributions and densities of some seedlings species may be explained by gradients in environmental variables, with soil nutrients (i.e. Ca^{2+}, Mg^{2+}, K^{+} and organic matter), and charcoal production being the most important. CCA axes 1 and 2 (with eigenvalues of 0.59 and 0.36 respectively) explained significant variations in species and species-environment factor relationships. Eigenvalues closer to 0.5 denote a fair separation of species along the axes, and indicate a strong gradient for the axes (ter Braak, 1987). As a rule of thumb, eigenvalues > 0.3 indicate strong gradients (ter Braak & Verdonschot, 1995). Hence, seedling abundances and distributions of many woody species in this equatorial multiple use African savanna are substantially influenced by soil nutrients and the charcoal production land use. In areas where charcoal production takes place there is a higher presence of larger/mature trees which will act as seed source, hence influencing variation in seedling regeneration.

Although anthropogenic disturbances seem to be common and widespread in this savanna, seedling regeneration is influenced by soil nutrients (edaphic gradients), which characterise the 1st canonical axis. Similarly, Larpkern *et al.* (2009) found that environmental variables were more important than human disturbance variables in explaining the variation in species richness and diversity. Indeed, edaphic factors appear to be more important at the early stage of tree development than at later life stages (Vargas-Rodriguez *et al.,* 2005). Seedling growth rates can also differ significantly among soil types and along fertility and moisture gradients, which can vary over relatively short distances (Hall *et al.,* 2003; Palmiotto *et al.,* 2004). Because of their small size, seedlings are more susceptible to small-scale variation in environmental conditions such as fertility (Larpkern *et al.,* 2009), resulting in variations in their distributions and densities over short environmental gradient distances. Moreover, successful germination and seedling recruitment, as well as subsequent growth and mortality rates are affected by spatial variation in abiotic resources and interactions with local biotic neighbourhood (Metz *et al.,* 2008).

4.3. Population structure of the species highly utilized for charcoal production

A population size structure is simultaneously the outcome of past demographic events and an indicator of its demographic future (Bullock *et al*., 1996; Wilson & Witkowski, 2003). All the studied species showed a relatively gradual decline in the number of individuals in each diameter size-class with increasing size-classes, and highly negative DSCD slopes, and juvenile:adult tree ratios >> 1, indicating a higher number of juveniles (seedlings and saplings) compared to adult trees/shrubs. This indicates that these species are presently experiencing successful regeneration and recruitment (West *et al.,* 2000), as a lost mature individual is more likely to be replaced by a new individual from the lower size-classes. Larger numbers of smaller individuals would be tolerant of low-intensity disturbance, and have good potential to replace the individuals lost through the "release" of the growth of these small individuals in the "sapling bank" (McLaren *et al.,* 2005). Hence, these species, despite being highly targeted for charcoal production and other subsistence uses resulting in stem damage and loss, appear to be resilient to those anthropogenic disturbances. However, this may be short-lived as there has been increased harvesting of even juvenile woody plants as a result of increased commercialization for charcoal production. The loss of individuals particularly in the juvenile classes with potential to grow to mature reproductive tree for most species may negatively affect their persistence and regeneration potential through seedlings, hence, threatening ecosystem functions and services, and, consequently, human well-being. Sustainable resource use hinges on the ability a species to continually establish new seedlings while being subjected to repeated intensive harvesting (Peters, 1994; Mwavu & Witkowski, 2009a).

Most species (e.g. *A. sieberiana, Albizia coriaria A. zygia* and *M. senegalensis* (now *G. senegalensis*) exhibited truncated population structures within certain size classes (e.g. 1-2, 6-10 cm BD) either missing or under represented. The under-representation or complete absence of individuals in some of the size classes, particularly the smaller size classes, indicates discontinuous regeneration (Poorter *et al.,* 1996). Furthermore, most of the species that exhibited intermediate and sporadic regeneration patterns or had truncated population structures, were also mentioned by respondents to be declining in population abundance. Based on these comparisons, it is concluded that most of the intermediate DSCD analysed are the effects of declining population sizes caused by anthropogenic disturbances (including harvesting by humans). Anthropogenic disturbances, such as harvesting of trees for fuelwood, building materials, and charcoal production are common in this wooded savanna (Chapter 2). These disturbances can change size class distributions of the target species as they may increase trunk mortality, although many savanna woody plants may resprout vigorously after cutting (Negreros-Castillo & Hall, 2000; Rydberg, 2000; McLaren & McDonald, 2003; Luoga *et al.,* 2004). Indeed, the absence of juveniles may not necessarily mean that a tree species will suffer an immediate decline after disturbance because of the importance of vegetative regrowth (McLaren *et al.,* 2005) in most savanna environments.

The lack of individuals in the size-classes ≥ 30 cm DBH for some species (e.g. *A. seyal, G. mollis* and *V. nobilis*), with a potential to grow above this stem size, is further evidence of increased loss of the more mature seed producing trees due to human harvesting for charcoal production (Chapter 2). The loss of individuals within these size-classes, with a reproductive potential, may negatively affect species persistence and regeneration potential through lack of seedlings. Silvertown (1991) suggests that most perennial plants must reach a minimum size before they reproduce. In the life history of a tree, the seed and seedling stages are most important as changes within these stages can result in drastic changes in populations (Harcombe, 1987; Marod *et al.,* 2002).

Harvesting of woody plants for both subsistence and commercial use, such as charcoal production, firewood collection, and pole cutting, are a common phenomenon and widespread in this savanna. Therefore, absence of certain diameter size-classes particularly the pole sized class (6-10 cm DBH), and small reproductive trees (11-15 cm DBH) may be attributed to their preference by local harvesters. Such sizes are easy to cut, large enough for most domestic uses in the area, and easy to carry away manually by the harvesters. Elsewhere, Abbort & Homewood (1999) similarly found that small-sized trees were preferred for fire wood; with women avoiding large logs because they are too heavy to carry manually. In addition, the local people in Malawi preferred smaller size classes from ≥ 5 to 15 cm DBH for firewood, poles for house construction, fencing and roofing purposes. In another study Boudreau *et al.* (2005) found that small pole-size trees (< 10 cm DBH) were harvested from Ongoye Forest Reserve in South Africa and used as building material for huts and fences as well as fuelwood. Similar, trends in size-class selectivity have been recorded in three Tanzanian forests (Gendagenda, Litipo and Kimboza) where trees with < 10 cm DBH constituted the main fraction of the harvested stems (Burgess *et al.,* 2000).

5.0. Conclusions and Recommendations

Savanna plant species are capable of regenerating both sexually and asexually. However, the importance of each regeneration mechanism depends on the species as well as the type and intensity of disturbance. Although this study represents a short-term study of seedling diversity and distribution, and population structure of woody species, the results point out to the importance of soil nutrients and land use practices in structuring the seedling diversity and distribution of woody species in this multiple land use equatorial savanna. There is substantial variability in seedling regeneration among species along gradients of soil variables and land use types, with seedlings establishing better in the cultivation and poorly in the grazing land use types as is the case for many of the world's savannas.

This study showed that most of the highly utilized species for charcoal production had good or intermediate 'inverse J' population structure curves and juvenile:adult tree ratios >> 1, indicating that they are presently experiencing successful regeneration and recruitment. The large number of individuals in smaller size-classes for most of the species suggests that their populations can be maintained to the adult level, because for species to maintain a relative constant population, more individuals are required in the smaller than larger classes (Obiri *et al.,* 2002). However, some species completely lacked individuals in some size classes, particular sapling and adult trees, indicating a discontinuous regeneration pattern, reflecting populations where regeneration has been temporarily interrupted through excessive harvesting for charcoal production, firewood and poles and direct physical damage of seedlings and saplings through cattle grazing, trampling and burning. The absence of some classes and increased harvesting of small-sized woody plants, threatens the future seedling regeneration since juveniles and adults, future seed sources, are targeted. Based on comparisons of DSCD with local information on the trends in species population changes, it is concluded that most of the intermediate and truncated DSCD observed are the effects of declining population sizes caused by human utilization.

Although the species appear to be presently successfully regenerating and resilient to anthropogenic disturbances, the continued unsustainable harvesting of individuals in the reproductive size-classes, may result in a significant reduction in seedling recruitment, severe resource depletion and possibly irreversible degradation (e.g. Struhsaker, 1997; Obiri *et al.,* 2002). It will, therefore, be important to consider sustainable management of the woodland resources by limiting the harvesting of reproductive individuals that are potential seed sources for the next generation. Sustainable management of the woodlands will require the establishment of suitable integrated community-based institutions and management practices, with support from all key stakeholders, i.e. National Forest Authority (NFA) and local communities.

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References

Abbort, J.I.O. & Homewood, K. 1999. A history of change: causes of miombo woodland decline in a protected area in Malawi. *Journal of Applied Ecology* 36: 422-433.

Akankwasa, D. & Tromborg, E. 2001. Challenges and strategies in the biomass energy sector-Working paper: revision of the Tax and Fee system in the Forest Sector, Kampala, Uganda.

Albrecht, M.A. & McCarthy, B.C. 2006. Effect of prescribed fire and thinning on tree recruitment patterns central hardwood forests. *Forest Ecology and Management* 226: 88-103.

Bond, W.J., Smythe, K-A. & Balfour, D.A. 2001. Acacia species turnover in space and time in an African Savanna. *Journal of Biogeography* 28: 117-128.

Botha, J., Witkowski, E.T.F. & Shackleton, C.M. 2004. The impact of harvesting on *Warburgia salutaris* (pepper-back tree) in Mpumalanga, South Africa. *Biodiversity Conservation* 13: 1675-1698.

Boudreau, S., Lawes, M.J., Piper, S.E. & Phadima, L.J. 2005. Subsistence harvesting of pole-size understorey species from Ongoye forest reserve, South Africa: species preference, harvesting intensity and implications for understorey tree dynamics. *Forest Ecology and Management* 216: 149-165.

Braithwaite, T.W. & Mayhead, G.J. 1996. The effect of simulated browsing on the growth of sessile oak *Quercus petraea* (Matt.) Lieblein. *Arboricultural-Journal* 20: 59-64.

Bullock, J.M., Silverton, J. & Clear Hill, B. 1996. Plant demographic responses to environmental variation: distinguishing between effects on age structure and effects on age-specific vital rates. *Journal of Ecology* 84: 733-743.

Burgess, N.D., Matthews, P., Evers, Y. & Woodcock, K. 2000. Non-timber uses, threats and local attitudes. pp 281-302. In: Burgess, N.D. & Clarke, G.P (Eds.), Coastal Forests of Eastern Africa. IUCN, Cambridge, UK.

Byabashaija, M.D., Esegu, J.F.O., Kidiya, J.M., Basoga, M., and Odia, R.K. 2004. Traditional uses of indigenous tree species. *Ugandan Journal of Agricultural Sciences* 9: 363-371.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecol*ogy 18: 117-143.

Condit, R., Sukumar, R., Hubbell, S.P. & Foster, R.B. 1998. Predicting population trend from size distributions: a direct test in a tropical tree community. *American Naturalist* 152: 495-509.

Dovie, D.B.K, Witkowski, E.T.F. & Shackleton, C.M. 2004. The fuelwood crisis in Southern Africa-relating fuelwood use to livelihoods in a rural village. *GeoJournal* 60: 123-133.

Drexhage, M. & Colin, F. 2003. Effects of browsing on shoots and roots of naturally regenerated sessile oak seedlings. *Annals of Forest Science* 60: 173-178.

Dublin, H.T., Sinclair, A.R.E. & McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59: 1147-1164.

Everard, D.A., Midgley, J.J. & van Wyk, G.F. 1995**.** Dynamics of some forests in KwaZulu-Natal, South Africa, based on ordinations and size-class distributions. *South African Journal of Botany* 61: 283-292.

Frost, P. & Robertson, F. 1987. Fire-the ecological effects of fire in savannas. pp. 93-140. In: Walker, B.H. (Ed.), Determinants of Tropical savannas. IUBS, Oxford, UK.

Gambiza, J., Campbell, B.M., Moe, S.R. & Frost, P.G.H. 2005. Fire behaviour in a semi-arid *Baikiaea plurijuga* savanna woodland on Kalahari sands in western Zimbabwe, South Africa. *South African Journal of Science* 101: 239-244.

Hall, J.S., Ashton, M.S. & Berlyn, G.P. 2003. Seedling performance of four sympatric Entandrophragma species (Meliaceae) under simulated fertility and moisture regimes of a central African rain forest. *Journal of Tropical Ecology* 19: 55-66.

Hamilton, A.C. 1991. A Field Guide to Uganda Forest Trees. Makerere University, Kampala, Uganda.

Harcombe, P.A. 1987. Tree life tables: simple birth, growth and death data encapsulate life histories and ecological roles. *BioScience* 37: 557-568.

Harms, K.E., Powers, J.S. & Montgomery, R.A. 2004. Variation in small sapling density, understory cover, and resource availability in four Neotropical forests. *Biotropica* 36: 40-51.

Hartshorn, G.S. 1995. Ecological basis for sustainable development in tropical forests. *Annual Review of Ecology and Systematics* 26: 155-175.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree co-existence in savanna. *Journal of Ecology* 88: 213-229.

Higgins, S.I., Shackleton, C.M. & Robinson, E.R. 1999. Changes in woody communities and composition under contrasting land use systems in a semi arid savannah, South Africa. *Journal of Biogeography* 26: 619-627.

Hoffmann, W.A. & Solbrig, O.T. 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180: 273-286.

Hutchison, T.F., Sutherland, E.K. & Yaussy, D.A. 2005. Effect of repeated prescribed fires on the structure, composition and regeneration of mixed-oak forests in Ohio. *Forest Ecology and Management* 218: 210-228.

Kisakye, R. 2004. Charcoal consumption in Kampala and its source districts. Unpublished Report on a consultancy survey for the GTZ Energy Advisory Project. Ministry of Energy and Mineral Development, Kampala, Uganda .

Kisamba-Mugerwa, W. 2001. Rangelands management policy in Uganda. A paper prepared for the international conference on policy and institutional options for the management of rangelands in dry areas, 7-11 May 2001 Hammamet, Tunisia.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. *Journal of Cleaner Production* 12: 1047-1057.

Langdale-Brown, I., Osmaston, H.A. & Wilson, J.G. 1964. The vegetation of Uganda and its bearing to land use. Government Printers, Entebbe, Uganda. pp.159.

Larpkern, P., Moe, S.R. & Totland, Ø. 2009. The effect of environmental variables and human disturbance on woody species richness and diversity in a bamboo-deciduous forest in northeastern Thailand. *Ecological Research* 24:147-156.

Luoga, E.J, Witkowski, E.T.F. & Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forest Ecology and Management* 189: 23-35.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000. Economic of charcoal production in miombo woodlands of eastern Tanzania. Some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 164: 15-30.

Lykke, A.M. 1998. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiversity and Conservation* 7: 1261-1275.

Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell Science Ltd. Blackwell Publishing Company, Oxford, UK. pp. 1-256.

Marod, D., Kutintara, U., Tanaka, H. & Nakashizuka, T. 2002. The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology* 161: 41-57.

McGregor, J. 1994. Woodland pattern and structure in a peasant farming area of Zimbabwe: ecological determinants, present and past use. *Forest Ecology and Management* 63: 97-133.

McLaren, K.P. & McDonald, M.A. 2003. Coppice regrowth in a disturbed tropical dry limestone forest in Jamaica. *Forest Ecology and Management* 180: 99-111.

McLaren, K.P., McDonald, M.A., Hall, J.B. & Healey, J.R. 2005. Predicting species response to disturbance from size class distributions of adults and saplings in a Jamaican tropical dry forest. *Plant Ecology* 181: 69-84.

MEA (Millennium Ecosystem Assessment) 2005. *Ecosystem and Human Well-Being: Biodiversity Synthesis*: Island Press World Resources Institute, Washington, DC.

Metz, M.R., Comita, L.S., Chen, Y-Y., Norden, N., Condit, R., Humbell, S., Sun, I-F., Noor$, N.S. & Wright, S.J. 2008. Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. *Journal of Tropical Ecology* 24: 9-18.

Montgomery, R.A. & Chazdon, R.I. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131: 165-174.

Mwavu, E.N. & Witkowski, E.T.F. 2009a. Seedling regeneration, environment and management in a semi-deciduous African tropical rainforest. *Journal of Vegetation Science* 20: 791-804.

Mwavu, E.N. & Witkowski, E.T.F. 2009b. Population structure and regeneration of multiple use tree species in a semi-deciduous African tropical rainforest: Implications for primate conservation. *Forest Ecology and Management* 258: 840-849.

Mwima, P.M., Obua, J. & Oryem-Origa, H. 2001. Effect of logging and natural regeneration of *Khaya anthotheca* in Budongo Forest Reserve, Uganda. *International Forestry Review* 3: 131-135.

Myers, P. 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. *Chemical Geology* 114: 289-302.

Namaalwa, J., Eid, T. & Sankhayan, P. 2005. A multi-species density-dependent matrix growth model for the dry woodlands of Uganda. *Forest Ecology and Management* 213: 312-327.

Negreros-Castillo, P. & Hall, R.B. 2000. Sprouting capacity of 17 tropical tree species after overstorey removal in Quintana Roo, Mexico. *Forest Ecology and Management* 126: 399-403.

NEMA (National Environment Management Authority) 2002. State of environment report for Uganda. Ministry of Environment and Natural Resources, The Republic of Uganda, Kampala, Uganda.

O'Connor, T.G. 1996. Individual, population and community response of woody plants to browsing in Africa savannas. *Bulletin of the Grassland Society of Southern Africa* 7: 14-18.

Oates, J.F. 1999. Myth and reality in the rain forest: how conservation strategies are failing in West Africa. University of California Press, Berkley, USA.

Obiri, J., Lawes, M. & Mulokwe, M. 2002. The dynamic and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management* 66: 131-148.

Palmiotto, P.A., Davies, S.J., Vogt, K.A., Ashton, M.S., Vogt, D.J. & Ashton, P.S. 2004. Soil-related habitat specialization in depterocarp rain forest tree species in Borneo. *Journal of Ecology* 92: 609-623.

Pandolfi, J.M. & Greenstein, B.J. 1997. Preservation of community structure in death assemblages of deep-water Caribbean reef Corals. *Limnology and Oceanography* 42: 1505-1516.

Parker, D., Downer, E. R., Cole, G. E. D. (1967) Atlas of Uganda. Department of Lands and Survey. Government Printers, Entebbe.

Pellew, R.A. 1983. The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology* 22: 73-75.

Peters, C.M. 1994. Sustainable Harvest of Non-Timber Plant Resources in Tropical moist forests: An Ecological Primer. Biodiversity Support Programme, World Wildlife Fund, Washington DC, USA.

Polhill, R.M. (Ed.). 1952 et seq. Flora of Tropical East Africa (FTEA). Royal Botanic Gardens, Kew, UK.

Poorter, L., Bongers, F., van Rompaey, R.S.A.R & de Klerk, M. 1996. Regeneration of canopy tree species at five sites in West African moist forest. *Forest Ecology and Management* 84: 61-69.

Rydberg, D. 2000. Initial sprouting, growth and mortality of European aspen and birch after selective coppicing in central Sweden. *Forest Ecology and Management* 130: 27-35.

Sawatzky, D.L., Raines, G.L., Bonhan-Carter, G.F. & Looney, C.G. 2004. ARCSDM3: Arc MAP extension of spatial data modelling using weights of evidence, logistic regression, fuzzy logic and neural network analysis. http://www.ige.unicamp.br/sdm/ArcSDM3/.

Sayer, J.A., Harcourt, C.S. & Collins, N.M. (Eds.). 1992. The conservation atlas of tropical forests. Africa - IUCN, London, UK.

Scholes, R. J. & Archer, S. R. 1997. Tree-grass interactions in Savannas. *Annual Reviews of Ecology and Systematics* 28: 517-544.

Seaby, R.M.H. & Henderson, P.A. 2006. Species diversity and Richness® Version IV (SDR 4.0). Pisces Conservation Ltd., Lymington, England.

Seaby, R.M.H., Henderson, P.A. & Prendergast, J.R. 2006. Community Analysis Package® Version 3.1 (CAP 3.1). Pisces Conservation Ltd., Lymington, England.

Setterfield, S.A. 2002. Seedling establishment in an Australian savanna: effects of seed supply, soil disturbance and fire. *Journal of Applied Ecology* 39: 949-959.

Shackleton, C.M. 1993. Demography and dynamics of the dominant woody species in a communal and protected area of the eastern Transvaal Lowveld. *South African Journal of Botany* 59: 569-574.

Sheil, D. 1996. Species richness, tropical forest dynamics and sampling: questioning cause and effect. *Oikos* 26: 587-590.

Silvertown, J. 1991. Modularity, reproductive thresholds and plant population dynamics. *Functional Ecology* 5: 577-580.

Skarpe, C. 1992. Dynamics of savanna systems. *Journal of Vegetation Science* 3: 293-300.

Struhsaker, T.T. 1997. Ecology of an African rainforest: Logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville, FL, pp. 434.

Swaine, M.D., Hall, J.B. & Lock, J.M. 1976. The forest-savanna boundary in west-central Ghana. *Ghana Journal of Science* 16: 35-52.

ter Braak, C.J.F. & Šmilauer, P. 2003. CANOCO® for Windows Version 4.5. Centre for Biometry, Wageningen, The Netherlands.

ter Braak, C.J.F. & Verdonschot, P.F.M. 1995**.** Canonical correspondence analysis and multivariate methods in aquatic ecology. *Aquatic Sciences* 57: 255-289

ter Braak, C.J.F. 1987**.** The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-77.

Tilghman, N.G. 1989**.** Impacts of white-tailed deer on forest regeneration in north western Pennsylvania. *Journal of Wildlife Management* 53: 524-532**.**

UBOS (Uganda Bureau of Statistics) 2000. National household census estimates 2000. (Retrieved on 17/11/2005 from http://www.ugandadish.org/nakasongola.doc).

Vargas-Rodriguez, Y.C., Vázquez-Garcia, J.A. & William, G.E. 2005. Environmental correlates of tree and seedling-sapling distributions in a Mexican Tropical Dry Forest. *Plant Ecology* 180: 117-134.

West, A.G., Midgley, J.J. & Bond, W.J. 2000. Regeneration failure and the potential importance of human disturbance in a subtropical forest. *Applied Vegetation Science* 3: 223-232.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFET/UNSO vegetation map of Africa. UNESCO, Paris, France.

Wilson, B.G. & Witkowski, E.T.F. 2003. Seed banks, bark thickness and change in age and size structure (1997-1999) of the African savanna tree, *Burkea africana. Plant Ecology* 167: 151-162.

Witkowski, E.T.F., Lamont, B.B. & Obbens, F.J. 1994. Commercial picking of *Banksia hookeriana* in the wild reduces subsequent shoot, flower and seed production. *Journal of Applied Ecology* 31: 508-520.

Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. 2005. Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. *Ecology* 86: 848-860.

Zida, D., Savadogo, L., Tigabu, M., Tiveau, D. & Oden, P.C. 2007. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. *Forest Ecology and Management* 243: 102-115.

Appendix 1. Results of SIMPER analysis highlighting the species contributing most to the dissimilarity among land uses. Species are ranked according to their percentage contribution to the dissimilarity among land uses and those with > 2% contribution are shown. The values of mean dissimilarity and percentage cumulative dissimilarity are also given.

Land use type	Species	Mean Abundance		Mean dissimillarity	Percentage Contribution	Cummulative percentage
		Charcoal	Cultivation			
Cultivation versus grazing	*Combretum collinum*	54.39	59.33	13.26	16.67	16.67
(mean dissimilarity = 79.6)	*Combretum molle*	23.22	53.71	8.91	11.2	27.87
	Albizia zygia	9.83	49.38	6.84	8.59	36.46
	Combretum ghasalense	24.87	8.88	5.98	7.52	43.98
	Vepris nobilis	23.35	6.54	4.31	5.42	49.4
	Acacia hockii	6.61	18.04	4.14	5.21	54.61
	Acacia polyacantha	7.48	14.75	3.68	4.62	59.23
	Hymenocardia acida	9.26	12.29	3.14	3.95	63.18
	Harrisonia abyssinica	13.13	14.58	2.96	3.72	66.89
	Combretum capituliflorum	14.96	0.75	2.4	3.01	69.9
	Rhus natalensis	10.39	5.17	2.13	2.68	72.59
	Piliostigma thonningii	5.3	3	2.04	2.56	75.15
	Vitex doniana	1.61	10.08	1.9	2.39	77.53
	Capparis fascicularis	10.96	0	1.43	1.8	79.33
	Strychnos innocua	0.83	6.54	1.17	1.47	80.81
	Grewia mollis	2.13	4.75	1.14	1.43	82.24
	Gardenia ternifolia	4.74	3.33	1.12	1.41	83.64
	Anona senegalensis	3.17	3.42	1.12	1.4	85.04
	Lantana camara	0.13	3.13	1.04	1.31	86.36
	Terminalia glaucescens	2.3	4.33	0.95	1.19	87.55
	Acacia sieberiana	4	0.83	0.93	1.17	88.71
	Lannea barteri	0.43	6.38	0.85	1.07	89.79
	Carissa edulis	2	3.13	0.85	1.06	90.85
		Charcoal	**Grazing**			
Charcoal versus grazing	*Combretum collinum*	54.39	43.33	14.68	18.31	18.31
(*mean dissimilarities = 80.2*)	*Combretum ghasalense*	24.87	11.22	7.34	9.15	27.46
	Combretum molle	23.22	13.11	6.4	7.98	35.44
	Piliostigma thonningii	5.3	23.19	6.08	7.59	43.03
	Vepris nobilis	23.35	0	4.22	5.26	48.29
	Harrisonia abyssinica	13.13	7.33	3.85	4.8	53.09
	Hymenocardia acida	9.26	7.85	3.6	4.49	57.58
	Acacia polyacantha	7.48	3.81	2.86	3.57	61.15
	Rhus natalensis	10.39	4.59	2.86	3.56	64.71
	Combretum capituliflorum	14.96	0	2.82	3.52	68.24
	Albizia zygia	9.83	0.3	2.29	2.85	71.09
	Acacia hockii	6.61	3.59	2.19	2.74	73.83
	Gardenia ternifolia	4.74	6.37	2.07	2.58	76.41
	Gymnosporia senegalensis	1.65	6.19	1.9	2.36	78.78
	Capparis fascicularis	10.96	0	1.7	2.13	80.9
	Acacia sieberiana	4	3.26	1.56	1.95	82.85
	Lantana camara	0.13	3.78	1.43	1.79	84.64
	Acacia seyal	0	3	1.15	1.44	86.08
	Anona senegalensis	3.17	1.52	1.02	1.27	87.35
	Manilkara dawei	0.61	2.56	0.93	1.16	88.51

	Grewia mollis	2.13	2.33	0.84	1.05	89.56
	Rhus vulgaris	2	2.07	0.84	1.05	90.61
		Cultivation	**Grazing**			
Cultivation versus grazing	*Combretum collinum*	59.33	43.33	14.82	17.51	17.51
(*mean dissimilarity = 84.6)*	*Combretum molle*	53.71	13.11	9.24	10.92	28.43
	Albizia zygia	49.38	0.3	7.75	9.16	37.59
	Piliostigma thonningii	3	23.19	5.49	6.49	44.08
	Acacia hockii	18.04	3.59	5	5.91	49.99
	Harrisonia abyssinica	14.58	7.33	3.72	4.4	54.39
	Combretum ghasalense	8.88	11.22	3.7	4.38	58.77
	Acacia polyacantha	14.75	3.81	3.49	4.13	62.89
	Hymenocardia acida	12.29	7.85	3.3	3.91	66.8
	Vitex doniana	10.08	0.3	2.12	2.5	69.3
	Gardenia ternifolia	3.33	6.37	1.79	2.12	71.42
	Vepris nobilis	6.54	0	1.75	2.07	73.49
	Gymnosporia senegalensis	1	6.19	1.73	2.04	75.53
	Lantana camara	3.13	3.78	1.58	1.87	77.4
	Strychnos innocua	6.54	0.85	1.55	1.83	79.23
	Grewia mollis	4.75	2.33	1.51	1.78	81.01
	Rhus natalensis	5.17	4.59	1.42	1.67	82.69
	Acacia seyal	0	3	1.29	1.53	84.21
	Dichrostachys glomerata	4.33	1.15	1.05	1.24	85.45
	Anona senegalensis	3.42	1.52	0.98	1.16	86.62
	Terminalia glaucescens	4.33	1.22	0.93	1.1	87.71
	Acacia sieberiana	0.83	3.26	0.9	1.06	88.78
	Lannea barteri	6.38	0.04	0.89	1.05	89.83
	Carissa edulis	3.13	0.37	0.82	0.97	90.79

CHAPTER 8

General discussion, synthesis and summary

1.0. INTRODUCTION

In Africa, savannas make up most of the tropical woodland cover from which many natural resource dependent rural households throughout Sub-Saharan Africa derive a wide range of products that include both timber and non-timber woodland products (e.g. Hofstand, 1996; Luoga *et al.,* 2000a; Shackleton *et al.,* 2002a & b; Kituyi, 2004). Hence, they support a wide range of subsistence and income generating rural household livelihood strategies. Savanna woodlands are endowed with high species diversity (species richness) and high levels of endemism (Homewood & Brockington, 1999). However, species diversity is connected to ecosystem dynamics and environmental quality, and a change in species diversity is often used as an indicator of high levels of anthropogenic or natural disturbances in an ecosystem (Liu & Brakenhielm, 1996). In addition, measures of species diversity play a central role in ecology and conservation biology (Noss & Cooperrider, 1994; Magurran, 2004). To support species diversity within an ecosystem and the continued provision of ecosystems services and goods for human well-being, it is important that they are managed sustainably. However, for sustainable management of important savanna resources, it is important to evaluate the magnitude, pattern, and type of land cover changes and to project the consequences of such change to their conservation (FAO, 2004; MEA, 2005a).

The ever increasing demands on the goods and services from savanna woodland resources, and the need for their sustainable management, require that the ecological, economic, social and cultural values of these resources be explored and brought to the attention of decision makers and the general public (Cavendish, 2002). Therefore, finding ways to improve sustainability of use and biodiversity conservation of savanna woodlands requires integrated research that involves ecology, agriculture, sociology and economics (Palmer *et al.,* 2005). In the present study, an assessment was made on the diversity, distribution, use and resilience to harvesting of woody species in a multiple land use equatorial African savanna, Uganda. The following studies were carried out: (i) Household livelihoods and income from charcoal production (Chapter 2), (ii) Land use and land cover changes (1984 – 2001) (Chapter 3), (iii) Diversity and density of woody species (Chapter 4), (iv) Variations in woody species composition in relation to environmental gradients (Chapter 5), (v) Resilience to anthropogenic disturbances through resprouting of woody species (Chapter 6) and (vi) Population structure and regeneration of tree species through seedling recruitment (Chapter 7) in an equatorial multiple land use African savanna: implications for woodland management.

2.0. SYNTHESIS OF THE DIFFERENT STUDIES

The various studies within this thesis can be displayed in an integrative conceptual model (Figure 1). The human populations in the villages around and within the studied savanna are heavily dependant on its natural resources for livelihood needs. The savanna ecosystem resources are exploited for both subsistence and income generation needs (i.e. wood for both firewood and commercial charcoal production, poles for constructions, crop cultivation and livestock grazing; Chapters 2 & 3). With the increasing human population, there is increased need for sources of income and land for agriculture leading to substantial loss of woodland cover in the area (Chapter 3). Most of the woodland loss in the studied savanna has been attributed to unsustainable harvesting of woody plants as charcoal production is increasingly commercialised. The loss of woodland cover has implications for plant density and species richness and diversity, and, consequently, ecosystem goods and services essential for human well-being. Furthermore, the relatively low woody species diversity and richness in this savanna (Chapter 4) may be an indicator of woodland degradation, fragmentation and local species loss, a result of unsustainable harvesting for charcoal production, grazing and shifting cultivation (i.e. anthropogenic disturbances; Chapter 4). However, variation in species diversity and distributions (Chapters 4 & 5) may also be caused by intrinsic population processes and gradients in natural environmental factors (i.e. soil nutrient content; Chapter 5). Indeed, many environmental changes and ecological processes contribute to both the accumulation and erosion of diversity at all spatial and temporal scales (Sheil, 1999). In multiple use and other savanna ecosystems, woody plants may respond to anthropogenic disturbance events (i.e. fires and cutting/harvesting of stems) by either dying or resprouting via the remaining stump or by root suckers. In addition, the open space may allow new seedlings to establish. In this savanna woodland, woody plants responded to anthropogenic disturbances by resprouting effectively (98.3 % of the harvested stumps; Chapter 6) and regenerating via seedlings (Chapter 7). Moreover, even all the 16 woody species highly utilized for charcoal production (e.g. *Acacia hockii, A. polyacantha, A. seyal, A. sieberiana, Albizia coriaria, A. zygia, Combretum capituliflorum, C. collinum, C. ghasalense, C. molle, Grewia mollis, Hymenocardia acida*, *Gymnosporia senegalensis, Piliostigma thonningii, Terminalia glaucescens* and *Vepris nobilis*) had highly negative DSCDs slopes >> 1, indicating successful regeneration (Chapter 7).

Basal area and abundances of woody species varied across land use types, strongly suggesting the influence of anthropogenic factors (i.e. harvesting). Although species composition differed significantly among the land use types, a relatively high number of woody species (45 species) were common across all land use types, suggesting that those species are environmental generalists. As dynamic factors, anthropogenic disturbances frequently alter floristic composition and vegetation structure of natural ecosystems (Pickett & White, 1985; Skarpe, 1990). There is probably cyclic succession of land use over time (Chapter 5); with areas used for charcoal production, later being used for subsistence crop cultivation, while cultivated land is left fallow and, then, used for livestock grazing. Hence, the effects of current and past land uses on the structure and composition of woody vegetation in the area cannot clearly be elucidated owing to the complex, interactive and heterogeneous nature of the land uses (Chapter 5). Indeed, the nature of land use is not constant in time and space (McGregor, 1994). Thus, anthropogenic disturbances (e.g. human harvesting of trees for charcoal production and fuelwood; Chapter 2) and environmental factors (Chapter 5) interact to shape woodland communities by influencing species composition and diversity patterns (Chapter 4 &

5), as well as population structure and regeneration patterns (Chapter 6 & 7). In this multiple use savanna, gradients in edaphic factors and anthropogenic disturbances constitute the major factors that influence species diversity, composition and distribution and regeneration (Chapter 4, 5 & 7).

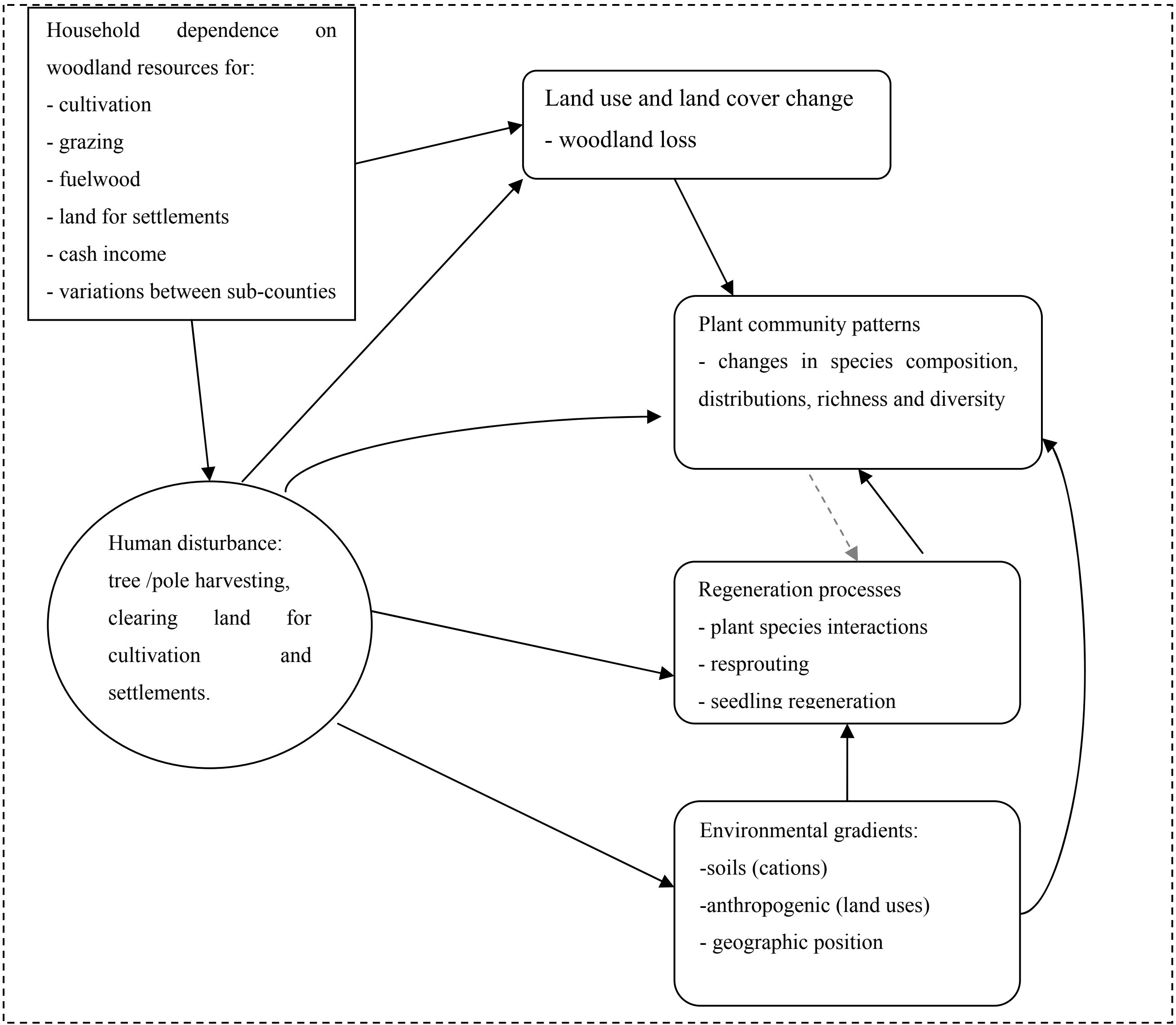

Figure 1. A simplified overview of the relationships among woody species diversity, distributions, regeneration, woodland resources, land use and land cover changes and human livelihood activities. Solid lines indicate direct influences, while dashed lines indicate indirect influences.

3.0. DIVERSITY, USE, AND MANAGEMENT OF RESILIENCE OF WOODY SPECIES

Savanna woodland in Sub-Saharan Africa make a significant contribution to local and national production and economic growth as cash incomes are generated from the sale of wood fuel (Shackleton, 1996). However, they are rapidly undergoing severe large-scale changes, through harvesting, burning or conversion to other land use and land cover types (Gerhardt & Hytteborn, 1992; Rennolls & Laumonier, 2000; MEA, 2005a & b). Consequently, the conservation of savannas and their species, particularly the woody component, has become increasingly important for the development of sustainable land use systems. However, in developing countries like Uganda where demographic growth and market demands remain major driving forces of land uses, sustainable management of these woodlands will require an integrated understanding from a range of disciplines (Pfund *et al.,* 2006). Furthermore, a better understanding of biological diversity and ecosystem resilience is important in the active adaptive management and governance of resilience, required to sustain or create desired ecosystems states (Folke *et al.,* 2004). It is, therefore, important that socio-ecological and socio-economic information on natural resources, particularly woodlands in marginal lands, like the equatorial savannas, be explored to guide decision making for their management. More information about the ecological, economic, social and cultural values of natural areas and the synergy among these values are necessary to feed the public dialogue and to internalize these values into policy and decision making (Cavendish, 2002).

3.1. Household livelihoods and income from charcoal production

Results from the present study revealed that rural households had 13 uses (including charcoal production and grazing) of savanna woodland resources to meet their daily livelihood needs. This suggests a significant contribution of woodland resources (both timber and non-timber products) to rural household livelihoods. Although they make multiple uses of the natural savanna woodlands, local households are yet to invest in establishing their own woodlands/forests. Moreover, the woodland areas where they derive their livelihoods have been gradually decreasing over the past 15 years, threatening the continued availability of the resources (Chapter 3). The decreasing woodland cover and availability of plant resources is attributed to the large number of households in the villages, clearing land for subsistence agriculture, and over harvesting of woody plants for commercial charcoal production and fire wood (Chapter 3). The high dependency on natural resources by households in this savanna is typical of many Sub-Saharan rural communities. High population growth combined with difficult economic circumstances, often made worse by adverse climatic conditions such as drought (prolonged shortage of rainfall) as is the case for the study area, constrain rural incomes that would have been gained through selling livestock and milk, some of the cash crops and fruits, consequently encouraging rural communities to increase reliance on the woodlands for livelihoods (Chipika & Kowero, 2000). Nakasongola exhibits serious land and resource degradation driven by overharvesting of woody resources, shifting cultivation and overgrazing (NEMA, 2007). The overall impact of this degradation has been the disruption of ecosystem services, particularly provisioning services due to habitat fragmentation that reduces complexity and diversity; soil erosion with consequent declining fertility and declining productivity; and invasion by termites. This may lead to the deforestation and/or degradation of the woodlands that are the backbone to rural household livelihood strategies and ecosystem services.

Although commercial charcoal production is the major source of income for the majority of households in the area, in reality it appears to be mining the woodlands with little regard for sustainability and the environment. Similar patterns have been observed in western Uganda (Naughton-Treves *et al.,* 2007), and Tanzanian miombo woodlands, where commercial harvesting for charcoal overrides ecological impacts from all other harvesting purposes because of the powerful economic incentives to produce charcoal (Luoga *et al.,* 2002). Commercial use of the resources often leads to depletion of biological resources, which are not increasing in value as fast as the rate of interest normally exploited and revenues put into other markets (Costanza *et al.,* 1997). In spite of the difficult economic circumstances facing them, people of this equatorial savanna seem to have a resilient social ecological system, i.e. adjusting to various local limitations and changes in order to sustain their livelihoods. For example, during the dry season, they engage in charcoal production, while during the rain season they engage in subsistence crop agriculture.

3.2. Land use and land cover changes

Land cover change is a dynamic, widespread and accelerating process, mainly driven by anthropogenic activities and natural phenomena, which, in turn, drive changes that impact ecosystems (McKinney, 2001; Agarwal *et al.,* 2002; Liu *et al.,* 2003; Loucks *et al.,* 2008). In the present study, the analysis of Landsat images, revealed significant land cover changes from dense woodlands to open woodlands and agricultural fields over a 17 year period (1984-2001). Over the years, the dense and medium woodlands have changed into open woodland and into cultivated, disturbed and settlement areas. This has been attributed to increased unsustainable harvesting of woody plants for charcoal production, overgrazing and clearing woody vegetation for establishing/rehabilitating farms/ranches, expanding cultivation of land, unplanned seasonal bush fires and the types of land tenure systems as the major drivers of dense woodland cover loss in the district (Chapter 2). Indeed, the primary causes of land cover change worldwide is the way people use and manage land (Dale *et al.,* 2000; Gobin *et al.,* 2001), although the specific factors may vary from one society to another. Climate change and rapid human population growth are widely recognized proximate causes and driving forces of land degradation, desertification and species loss in many parts of the world (Githinji & Perrings 1993; Vitousek, 1994; Thomas *et al.,* 2004; Geist & Lambin, 2004; MEA, 2005a; Hulme, 2005). In Uganda, as for the rest of the world, there are likely to be changes in frequency or severity of extreme climate events, such as heat waves, drought, floods and storms due to climate change. Human induced climate change is likely to increase average temperatures in Uganda by up to 1.5 ˚C in the next 20 years and by up to 4.3 ˚C by the 2080s if global greenhouse gas emissions remain high (Hepworth & Goulden, 2008). Climate change is likely to increase food insecurity, shifts in the spread of diseases like malaria, soil erosion and land degradation, flood damage to infrastructure and settlements, and shifts in productivity of agricultural and natural resources (Orindi & Eriksen, 2005). Therefore, Uganda is highly vulnerable to climate change variability because its economy and the well being of its people are tightly bound to climate (Hepworth & Goulden, 2008).

Land ownership is an important determinant of landscape dynamics and pattern (Dale *et al.,* 1993; Turner *et al.,* 1996; Gobin *et al.,* 2001), while security of tenure is also important in shaping who uses land resources and how. Woodland loss in the study area over the 17 year study period occurred and continues to occur mostly in areas under *mailo* and customary land tenure systems, and also on privately owned land, particularly those with absentee landlords. In fact the studied savanna woodlands seem to be *defacto* open-access regimes, with no effective institutions and mechanisms to enforce the rules to ensure that they are sustainably managed. Similarly, Hanna *et al.* (1995) reported that common property regimes are responsible for the overexploitation and destruction of natural resources in most countries. In many Ugandan communities, customary land is open-access due to weak traditional controls over land allocation and relatively weak institutions in collective management of other resources such as woodlands (Place & Otsuka, 2000; Mwase *et al.,* 2007). Furthermore, at the local level, the need to access resources to alleviate poverty outweighs the desire to sustainably manage and conserve natural resources, while political interests outweigh the need to follow the approved laws and regulations (Mwavu & Witkowski, 2008).

3.3. Diversity and distribution of woody species along the environmental gradients

3.3.1. Diversity and distribution of woody species

There is widespread concern that savanna woodland ecosystems with unique and valuable biodiversity resources are being lost (Rennolls & Laumonier, 2000) as a result of both natural and anthropogenic disturbances and mismanagement (O'Connor, 2005; Luoga *et al.,* 2005). In this study woody plant density and diversity (alpha and beta-diversity) were significantly higher under (cultivation and charcoal production) than in the grazing land use type due to different types in disturbance regimes. The grazing lands in the area experience greater herbivory and seasonal bush fires that may inhibit seedling establishment and recruitment. In grazing ecosystems, primary productivity, evolutionary history and resulting vegetation physiognomy and plant life form, can interact with grazing in determining plant community structure and diversity (e.g. Milchunas & Lauenroth, 1993; Huston, 1994; Noy-Meir, 1995; Proulx & Mazunder, 1998; Osem *et al.,* 2002). Differences in species richness between land uses may be the result of the different land use practices *per se*, or because of differences in the number of individuals counted (Gotelli & Colwell, 2001). The relatively higher β-diversity in grazing areas compared to those of cultivation and charcoal production areas suggests a more heterogeneous spatial distribution of plants. Within the grazing areas, the levels and intensities of grazing (stocking rates) vary from one location to another. Hence, land use changes that alter natural disturbance patterns are likely to result in changes in species abundance and distribution, community composition and ecosystem function.

3.3.2. Composition and structure of woody species along environmental gradients

Understanding the role of environmental factors in controlling vegetation structure and function has been a central theme of ecological research for decades (Kyle & Leishman, 2009). Environmental factors (particularly soil nutrients and moisture) have often been used to explain variation in species composition and diversity among vegetation communities. In this multiple land use savanna, woody species abundances differed significantly among the various land use types. Cultivation and grazing areas had lower abundances compared to charcoal production areas, which still have higher densities of woody species. The dominant species (represented by basal area) were not necessarily the most abundant and frequent ones in the different land use types, with the exception of *Combretum collinum* that had both the highest basal area and density for overall woody species across all land uses. The dominance of *Combretum* spp. in terms of abundance and basal area among the land uses may be attributed to the fact that they resprout prolifically in the study area (Chapter 6), suggesting that they are environmental generalists.

Generally the variance in species-environmental factor relations based on Canonical Correspondence Analysis (CCA) was higher than 50%, suggesting a relatively strong influence of the environmental factors on species composition and distribution. Thus, the CCA revealed the strong influence of edaphic factors (i.e. Ca^{2+} and Mg^{2+}) and the grazing land use practice on woody species composition and distribution within the studied savanna. These results were not surprising, since environmental factors like substrate, topography or soil characteristics are important in determining plant species distribution at smaller spatial scales (Wiens, 1989). Although there is strong evidence that soil nutrients and the grazing land use strongly influence woody species community composition and structure in this savanna, there may be other abiotic and biotic factors like fire and moisture whose influence cannot be disentangled in the present study.

3.4. Regeneration through resprouting and seedling recruitment

3.4.1. Resprouting

Sustainable management of multiple use savanna woodlands requires an understanding of how the constituent woody plant species respond to harvesting and other disturbances through resprouting (Kennedy, 1998; Shackleton, 2000; Kaschula *et al.,* 2005). In the study area, the major disturbance causing damage to woody plants is human harvesting resulting in the removal of large amounts of wood for charcoal. Many of the woody species responded to this disturbance by effectively resprouting via the stump (stem resprouting) and roots (root suckering). However, resprouting ability (i.e. number of resprouts/stump) varied among the woody plant species with some consistently having higher or lower numbers of resprouts/stump across all the land use types studied. For example, despite being frequently harvested for subsistence and commercial use, the regenerative potential of *C. molle, C. ghasalense, C. collinum, A. hockii, A. zygia, P. thonningii* and *Vepris nobilis* is considerable because of effective stump resprouting and root suckering. The resprouting ability of species differed with plant stem basal diameter and among land use types. Larger size-classes had higher resprouting ability than the smaller size classes, while the charcoal production areas had a higher number of resprouts than the cultivation and grazing land uses (Table 1). Indeed, the effectiveness of stump resprouting varies with species, plant size/age at time of cutting, stump height and percentage of the stand removed (Shackleton, 2000; Luoga *et al.,* 2002; Mwavu & Witkowski, 2008), as well as type of disturbance (Gomez *et al.,* 1999). The high number of resprouts in the charcoal production land use may be because of the high number of available trees that are harvested. In this multiple use savanna, resprouting is the more common mode of regeneration, as juveniles of most species were encountered as resprouts than as seedlings particularly in the charcoal production and grazing land uses.

Table 1. Densities (individuals ha^{-1}) of all woody species and the 16 species highly utilized for charcoal production in the three land uses in an equatorial multiple land use African savanna woodland, central Uganda.

Land use	Regeneration			
	All wood plants		Highly utilized species	
	Seedlings	Total resprout shoots	Seedlings	Total resprout shoots
Grazing (N = 27)	1,629 ± 205[a]	2,087 ± 401[a]	1,224 ± 187[a]	1,895 ± 378[a]
Cultivation (N = 24)	3,163 ± 440[b]	2,762 ±3 90[ab]	2,408 ± 404[b]	2,053 ± 323[ab]
Charcoal production (N = 24)	2,415 ± 295[ab]	4,143 ± 591[b]	1,815 ± 240[ab]	3,339 ± 522[b]

Values in the same column accompanied by the same superscript do not differ significantly (Tukey's HSD Test, P <0.05).

3.4.2. Seedling recruitment

Understanding the natural regeneration process and the dynamics of populations of tree and shrub species populations have practical applications in management and the restoration of habitats (Peters, 1994). While an understanding of woody species seedling recruitment in relation to environmental factors, population structure, and their resilience to anthropogenic disturbances is key to sustainable management. Information on plant population dynamics under the current disturbance regimes is needed to foresee the trends of community changes in the future. In this regard, ecologists have often used stem diameter size-class distributions (DSCD) to indicate the health of a population (Condit *et al.,* 1998). In savannas and dry tropical forest systems, stem diameter size-class distributions (DSCD) give a good indication of the impact of disturbance and of successional trends of harvested woody species (Lykke, 1998).

There was substantial variability in seedling recruitment in terms of species density, composition and distribution among the land uses in the studied savanna. Some of the species were widely distributed, while others are restricted to particular land use and site conditions (Chapter 5). The distributions and densities of some seedlings are to a great extent explained by gradients in environmental variables, with soil nutrients (i.e. Ca^{2+}, Mg^{2+}, K^{+} and organic matter), and the charcoal production land use type being the most important. According to Vargas-Rodriguez *et al.* (2005), edaphic factors appear to be more important at the early stage of tree development than at later life stages. The higher seedling density in the cultivated land use may be attributed to the patchiness of the vegetation as a result of tree cover removal, and improvement in soil conditions as a result of soil tilling. Thus, cultivation enhances the recruitment process by reducing competition for water and nutrients, opening up more growing space and by increasing the availability of light (Montgomery & Chazdon, 2002; Hutchison *et al.,* 2005; Zida *et al.,* 2007) for seed germination and seedling growth.

The DSCD analyses showed that all the species had highly negative DSCD slopes (>> 1) indicating that they are presently experiencing successful regeneration and recruitment. Hence, despite being targeted for charcoal production and other subsistence use resulting in stem damage and loss, these species appear to be resilient to those anthropogenic disturbances. However, this may be short lived as there is increased harvesting of even juvenile woody plants as a result of increased commercialization of charcoal production. Hence, sustainable management interventions to ensure successful regeneration and persistence of these species have to consider the influence of prevailing land use practices.

3.5. Lessons and future challenges

Integrated research across disciplines is required to address many of the pressing environmental problems facing human societies (Eigenbrode *et al.,* 2007). Furthermore, research to improve sustainability and biodiversity conservation should involve ecology, sociology, soil science, hydrology and economics (Palmer *et al.,* 2005). The multi-disciplinary approach, based on remote sensing, socio-economic and ecological science adopted in this study led to a clearer understanding of the diversity, use and resilience of woody plants in an equatorial multiple use savanna in Nakasongola District, central Uganda. However, there are lessons to learn for future studies and sustainable management of similar ecosystems. The anthropogenic disturbances occurring and influencing woody plant community patterns within this savanna are driven by livelihood needs and social organization, and externally by policy decisions made by various sectors of the government and national economy. However, there may be explanatory variables responsible for the variation in species composition and other dependent factors across the savanna that were not captured in this study and included in the analysis. Therefore, another study should include other factors such as fire and soil moisture.

3.5.1. Household livelihoods and income from charcoal production

Socio-ecological and socio-economic information on natural resources, particularly woodlands in marginal lands, such as the studied equatorial multiple use African savanna, need to be explored to guide decision making for their management. Moreover, information about the ecological, economic, social and cultural values of natural areas and the synergy between these values are necessary to feed the public dialogue and to internalize these values into policy and decision making (Cavendish, 2002). In this study, the focus was on determining income generated from charcoal production; revealing that charcoal production is the major source of income to the local households and local government. However, a clearer understanding of the economics of charcoal production in this area may require a more detailed exploration of the costs of labour, time, as well as opportunity costs for engaging in charcoal production. There may be other savanna woodland resources/products that may require economic evaluation to determine their contribution to local livelihoods and also aid in decision making for conservation of the savanna in this district and other areas of Uganda.

3.5.2. Land use and land cover changes

Analysis of a set of multi-date landsat images complemented with ground truthing and interview data, revealed clearly the declining dense-woodland cover (Chapter 3); clearly highlighting the negative impacts of human use on woody plant dynamics. However, availability of more recent Landsat images (beyond 2006) would have shown updated trends in woodland cover and other land cover types in the area. Future studies should consider more recent changes and also attempt to assess the changes within areas where community utilization is restricted; this will serve as control sites as it will give a clear picture of what the vegetation would be if left without anthropogenic disturbances. This will shed light on how many species are lost or replaced by colonisers or alien invasive species. More insight is needed into the effects of human land use activities on savanna woodland composition and conservation values to evaluate the role of savanna woodlands for biodiversity conservation (van Gemerden *et al.,* 2003).

3.5.3. Vegetation sampling

Adequate measurement and quantification of species diversity, which are essential for understanding the maintenance of species diversity and the structure and functioning of ecosystems, requires use of standard methods and plot size for comparability of data. The 0.1 ha plot size used in this study, is the standard area for work on vascular plant species richness (Crawley, 1997). While the number of plots (i.e. 75 plots) sampled was adequate as the cumulative curves reached an asymptote showing that most of the woody species within the savanna woodland had been accounted for. A number of studies (e.g. Luoga *et al.,* 2000a & b; Duque *et al.,* 2002; Witkowski & Garner, 2008), have employed a 0.1 ha plot for vascular plant species diversity studies of grasslands, tropical savannas, woodlands, and forest vegetation.

3.5.4. Composition and structure of woody species along environmental gradients

The variance partitioning of the woody species composition data showed that the measured edaphic (i.e. soil Ca^{2+} and Mg^{2+}) and anthropogenic (i.e. grazing) factors explained a significant proportion of the variation in species composition among the plots and land uses in this savanna. Hence, plant community composition and distribution are influenced by gradients in edaphic factors and grazing. However, there was a relatively substantial proportion of unexplained variance, suggesting that there may be other factors influencing woody species composition and distributions within this savanna.

Plant communities are dynamic and are influenced by soil moisture, soil nutrients, and disturbances such as fire and herbivory and human harvesting. These are some of the major determinants of tropical savanna pattern, structure and function (Walker & Noy-Meir 1982; Tothil & Mott 1985; Frost *et al.,* 1985; Higgins *et al.,* 2000; Sankaran *et al.,* 2005; Bond *et al.,* 2005). Since data on some of these factors could not be collected within the limited time of the PhD study, it may be useful for future long-term studies to include them. Inclusion of data on water availability, fire and herbivory frequencies and intensities would have been valuable since these factors directly influence plant growth and recruitment. Fire is a major determinant of composition and distribution of plants in savanna. In addition, a detailed study on herbivory and its effect on woody plant composition and distribution as well as details on the number of animals per households, stocking rates, information on how many pastoralists move in and out and the number of livestock moving in per year in the study area is essential.

3.5.5. Population structure and regeneration patterns

Based on the one time data set, the results of this study clearly showed that many of the woody species are presently successfully regenerating both through resprouting and seedling recruiting. Although analyses of long-term data sets would have been of great value and interest in assessing the population structure and regeneration patterns of the highly utilized woody species for charcoal production in Nakasongola woodland (Chapter 7), this was not possible because of a lack of long-term data and the length of time normally allowed for a PhD study. However, in the absence of long term data, forest/savanna woodlands dynamics have most often been inferred from single surveys and analysis of static plant inventory data by constructing the DSCD of species population (e.g. Lykke, 1998; Obiri *et al.,* 2002; McLaren *et al.,* 2005). Perhaps, establishment of permanent sample plots in the area in the future would help to provide long-term data for monitoring woody plant dynamics over time and space.

Although most of the woody species (including those utilised for charcoal production) have high resprout and seedling densities and frequencies, meta-population dynamics suggests that even once-common species are not immune to the effects of widespread habitat alteration or fragmentation. Therefore, it will be important to determine which kinds of species are most vulnerable to local extinction following continued harvesting, and which land uses are likely to have more effects on plant species composition and persistence. Recovery from resprouts was a more common mode of regeneration after harvesting and grazing (Chapter 6). Since the major land uses (i.e. charcoal production and cultivation) in this savanna involve the harvesting of woody plants, there is a need for detailed study on the factors affecting resprout survival and recruitment.

4.0. CONCLUSIONS AND RECOMMENDATIONS

The results of this study revealed large land cover (i.e. woodland cover) changes occurring mainly in the dense and medium woodlands, reflected by the increase in open woodland, grasslands and cultivation areas and settlements. A continued loss of woodland cover and land degradation will increasingly threaten woody plant cover and persistence and, hence, the provision of ecosystem services and goods essential for rural household livelihoods and human well-being. This will ultimately result in loss of income, environmental services, food security, fuelwood availability, habitat degradation and biodiversity loss (MEA, 2005a), thereby threatening local and regional sustainability and livelihood systems (Singh *et al.,* 2001). The relatively low woody species alpha diversity and richness in the studied savanna woodlands may be an indicator of woodland degradation, fragmentation and local species loss; a result of unsustainable woody plant harvesting and anthropogenic disturbances that are common in this area. The relatively high beta-diversity suggests the heterogeneity of species in this multiple land use savanna. The diversity of land use practices creates gradients in habitat environments.

The studied multiple land use savanna ecosystem appears to be resilient to anthropogenic disturbances as most of the utilised woody species successfully regenerate and recruit by both resprouting and seedlings. However, the continued unsustainable harvesting of individuals in the reproductive size-classes, may result in a significant reduction of seedling recruitment, severe resource depletion and possibly irreversible degradation, even for the most abundant and resilient species (e.g. Struhsaker, 1997; Obiri *et al.,* 2002). This may result in a reduced range and amounts of useful plant products with serious implications for the environment and local livelihoods. A combination of edaphic (i.e. Ca^{2+}, and Mg^{2+}) and anthropogenic disturbances (i.e. human harvesting and grazing) factors influence the dynamics of woody plants (i.e. diversity, regeneration, distributions, population structure) within this multiple use savanna ecosystem. Since anthropogenic factors play an important role in species distributions, human activities carried out within the savanna woodlands should aim at sustainable utilization of the wood resources. Hence, adequate management plans are urgently required for these woodlands. An appropriate savanna woodland management policy is required to guide changes in land use that accommodate the requirements of land users, aided by targeted conservation efforts for all woody species and, particularly, for the species highly utilized for charcoal production and the multipurpose species.

Increasing demands for woodland resources are likely to surpass the capacity of these ecosystems to provide goods and services that are essential to rural human livelihoods, hence, compromising the resilience of the socio-ecological system and human well-being. It will, therefore, be important that the community considers sustainable management of woody plants by limiting the harvesting of reproductive individuals that are potential seed sources for the next generation. Therefore, there is urgent need to build local capacity for improved harvesting and utilization of these tree species. This can be achieved through equipping local users with up-to-date information and observing the existing skills. Knowledge, such as how to propagate indigenous tree species and produce them in large quantities, will reduce total dependency on the woodland. It is important that local people are encouraged to establish woodlots to meet their subsistence needs, so that they relieve the over-use pressure on natural woodlands. Therefore, the establishment of suitable integrated community-based institutions and management practices are required for the sustainable management of these woodlands. A joint woodland management system steered by local chiefs, representatives of rural councils and resource managers from the National Forestry Authority would appear to be the most effective way forward. In addition, the households should be encouraged to engage in other income generating activities (alternative source of income) such as fishing, bee keeping, brick making and establishment of tree nurseries to minimise total dependency on charcoal production as the major income generating activity as well as to reduce total dependence on these woodlands. Households in rural and urban areas should adapt to alternative means of cooking such as using biogas, solar energy, crop residues and sawdust in order to reduce total dependency on charcoal and firewood. It is also important to acknowledge the challenges to sustainable management of woodlands of Nakasongola, which is situated in an area where: (i) charcoal production is more valued by households than woodland conservation, (ii) the household livelihoods depend almost entirely on woodland resources and (iii) there is a political climate in which struggles for economic development overshadow the need to set a balance between natural resource exploitation and conservation. Therefore, sustainable management of woodlands will require balancing various developmental objectives in the decision making process. Maintenance of savanna woodland resources and other ecosystem services essential for human well-being will require an effective legal framework to prevent over-exploitation and give incentives for the protection of the fragile savanna woodland vegetation.

References

Agarwal, C., Green G.M., Grove, J.M., Evan, T.P. & Schweik, C.M. 2002. A review and assessment of land use change models: Dynamics of space, time and human choice. USDA (Forest Services), Technical Report NE-297.

Bond, W.J., Woodward, F.I. & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525-537.

Cavendish, W. 2002. Quantitative methods for estimating the economic values of resource use to rural households. pp. 17-65. In: Campbell B.M. & Luckert M.K. (Eds.) Uncovering the Hidden-Harvest valuation methods for woodland and forest Resources. Earthscan Publications, London.

Chipika, J.T. & Kowero, G. 2000. Deforestation of woodlands in communal areas in Zimbabwe: is it due to agricultural policies? *Agriculture, Ecosystems and Environment* 7: 175-185.

Condit, R., Sukumar, R., Hubbell, S.P. & Foster, R.B. 1998. Predicting population trend from size distributions: a direct test in a tropical tree community. *American Naturalist* 152: 495-509.

Costanza, R., Cumberland, J., Daly, H., Goodland, R. & Norgaard, R. (Eds.) 1997. An Introduction to Ecological Economics. ISEE, St. Lucie Press, Florida.

Crawley, J.M. 1997. The structure of plant communities**.** pp. 475-531. In: Crawley M.J. (Ed) Plant Ecology. Blackwell Science, Oxford, UK.

Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.H., Huntley, N., Naiman, R.J., Riebsame, W.E., Turner, M.G. & Valone, T.J. 2000. Ecological Principles and Guidelines for Managing the use of Land. *Ecological Applications* 10(3): 639-670.

Dale, V.H., O'Neill, R.V., Redlowski, M. & Southworth, F. 1993. Causes and effects of land use change in central Rondônia, Brazil. *Photogrammetric Engineering and Remote Sensing* 56: 997-1005.

Duque, A., Sanchez, M., Cavelier, J. & Duivenvoorden, J.F. 2002. Different floristic patterns of woody under storey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology* 18: 499-525.

Eigenbrode, S.D., O'Rourke, M., Wulfhorst, J.D., Althoff, D.M., Goldberg, C.S., Merrill, K., Morse, W., Nielsen-Pincus, M., Stephens, J., Winowiecki, L. & Bosque-Pérez, N.A. 2007. Employing philosophical dialogue in collaborative science. *BioScience* 57: 55-64.

FAO, 2004. Land Cover Classification System. Land Cover Topic Centre. Rome, Italy.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology and Systematics* 35: 557-581.

Frost, P., Menaut, J.C., Walker, B., Medina, E., Solbrig, O. & Swift, M. 1985. Responses of savannas to stress and disturbance: a proposal for a collaborative programme of research. Report of a meeting of an IUBS Working Group. Biol. Int. (Spec. Issue). 10: 1- 82.

Geist, H.J. & Lambin, E.F. 2004. Dynamic causal patterns of desertification. *Bioscience* 54: 817-829.

Gerhardt, K. & Hytteborn, H. 1992. Natural dynamics and regeneration methods in tropical dry forests-an introduction. *Journal of Vegetation Science* 4: 95-102.

Githinji, M. & Perrings, C. 1993. Social and Ecological Sustainability in the Use of Biotic Resources in Sub-Saharan Africa. *Ambio* 22(2-3): 110-116.

Gobin, A., Campling, P. & Feyen, J. 2001. Spatial analysis of rural land ownership. *Landscape and Urban Planning* 55: 185-194.

Gomez Sal, A., Rey Benayas, J.M., Lopez-Pintor, A. & Rebollo, S. 1999. Role of disturbance in maintaining a savanna-like pattern in Mediterranean Retama sphaerocarpa shrub land. *Journal of Vegetation Science* 10: 365-370.

Gotelli, J.N. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391.

Hanna, S., Folke, C. & Maler, K.G. 1995. Property rights and environmental resources. pp 15-29. In: Hanna, S. & Munasinghe, M. (Eds.), Property rights and the environment: Social and ecological issues. The World Bank, Washington DC., USA.

Hepworth, N. & Goulden, M. 2008. Climate change in Uganda: understanding the implications and appraising the response. LTS International, Edinburg. pp. 1-48.

Higgins, S.I., Bond, W.J. & Trollope, W.S. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savannas. *Journal of Ecology* 88: 213-229**.**

Hofstand, O. 1996. Woodland Deforestation by charcoal supply to Dar-Es-Salaam. *Journal of Environmental Economics and Management* 33: 17-32.

Homewood, K. & Brockington, D. 1999. Biodiversity, Conservation and development in Mkomazi Game Reserve, Tanzania. *Global Ecology and Biogeography* 8: 301-313.

Hulme, P.E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology* 42: 784-794.

Huston, M.A. 1994. Non-equilibrium processes and the maintenance of local species diversity. pp. 110-155. In: Huston MA (Ed.) Biological diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Hutchison, T.F., Sutherland, E.K. & Yaussy, D.A. 2005. Effect of repeated prescribed fires on the structure, composition and regeneration of mixed-oak forests in Ohio. *Forest Ecology and Management* 218: 210-228.

Kaschula, S.A., Twine, W.C. & Scholes, M.C. 2005. The effect of catena position and stump characteristics on the coppice response of three savanna fuelwood species. *Environmental Conservation* 32: 76-84.

Kennedy, A.D. 1998. Coppicing of *Tarchonanthus camphorates* (Compositae) as a source of sustainable fuelwood production: an example from the Laikipia Plateau Kenya. *African Journal of Ecology* 36: 148-158.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. *Journal of Cleaner Production* 12: 1047-1057.

Kyle, G. & Leishman, M.R. 2009. Plant functional trait variation in relation to riparian geomorphology: The importance of disturbance. *Austral Ecology* 34: 793-804.

Liu Q. & Brakenhielm S. 1996. Variability of plant species diversity in Swedish natural forest and its relation to atmospheric deposition. *Academic Publishers* 125: 63-72.

Liu, J., Daily, G.C., Ehrlich, P.R. & Luck, G.W. 2003. Effects of households' dynamics on resource consumption and biodiversity. *Nature* 421: 530-33.

Loucks, C., Ricketts, T.H., Naidoo, R., Lamoreux, J. & Hoekstra, J. 2008. Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural sustainability. *Journal of Biogeography* 35: 1337-1348.

Luoga, E.J, Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 16:15-30.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000a. Subsistence use of wood products and shifting cultivation within miombo woodlands of eastern Tanzania, with some notes on commercial uses. *South African Journal of Botany* 66: 72-85.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2000b. Economic of charcoal production in miombo woodlands of eastern Tanzania: some hidden costs associated with commercialization of the resources. *Ecological Economics* 35: 243-257.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2005. Land-cover and use changes in relation to the institutional framework and tenure of land and resources in eastern Tanzania miombo woodlands. *Environment, Development and Sustainability* 7: 71-93.

Lykke, A.M. 1998. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiversity and Conservation* 7: 1261-1275.

Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell Science Ltd, USA. pp. 1-256.

McGregor, J. 1994. Woodland pattern and structure in a peasant farming area of Zimbabwe: ecological determinants and the present and past use. *Forest Ecology and Management* 63: 97-133.

McKinney, M.L. 2001. Role of human population size in raising bird and mammal threat among nations. *Animal Conservation* 133: 455-473.

McLaren, K.P., McDonald, M.A., Hall, J.B. & Healey, J.R. 2005. Predicting species response to disturbance from size class distributions of adults and saplings in a Jamaican tropical dry forest. *Plant Ecology* 181: 69-84.

MEA (Millennium Ecosystem Assessment) 2005a**.** *Ecosystem and Human Well-Being: Desertification Synthesis*: Island Press, World Resources Institute, Washington, DC, USA.

MEA (Millennium Ecosystem Assessment) 2005b. *Ecosystem and Human Well-Being: Biodiversity Synthesis*: Island Press, World Resources Institute, Washington, DC., USA.

Milchunas, D.G. & Lauenroth, W. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 6: 327-366.

Montgomery, R.A. & Chazdon, R.I. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131: 165-174.

Mwase, W.F., Bjørnstand, Å., Bokosi, J.M., Kwapata, M.B. & Stedje, B. 2007. The role of land tenure in conservation of tree and shrub species diversity in miombo woodlands of Southern Malawi. *New Forests* 33: 297-307.

Mwavu, N.E. & Witkowski, E.T.F. 2008. Sprouting of woody species following cutting and tree-fall in a lowland semi-deciduous tropical rainforest, North-Western Uganda. *Forest Ecology and Management* 255: 982-992.

Naughton-Treves, L., Kammen, D.M. & Chapman, C. 2007. Burning biodiversity: Woody biomass use by commercial and subsistence groups in western Uganda's forests. *Biological Conservation* 134: 232-241.

NEMA (National Environment Management Authority) 2007. State of environment report for Uganda. The Republic of Uganda, Kampala, Uganda.

Noss, F. & Cooperride, A.Y. 1994. Saving nature's legacy, protecting and restoring biodiversity-Island Press, Washington, DC.

Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science* 6: 701-710.

O'Connor, T.G. 2005. Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the Southern Drakensberg, South Africa. *Journal of Applied Ecology* 42: 975-988.

Obiri, J., Lawes, M. & Mulokwe, M. 2002. The dynamic and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management* 166: 131-148.

Orindi, V.A. & Eriksen, S. 2005. Mainstreaming adaptation to climate change in the development process in Uganda. African Centre for Technology Studies (ACTS). *Ecopolicy Series* no. 15.

Osem, Y., Perevolotsky, A. & Kigel, J. 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology* 90: 936-946.

Palmer, M., Bernhardt, E., Chornesky, E., Collins, S., Dobson, A., Duke, C., Gold, B., Jacobson, R., Kingsland, S., Kranz, R., Mappin, M., Martinez, M., Micheli, F., Morse, J., Pace, M., Pascual, M., Palumbi, S., Reichman, O., Townsend, A. & Turner, M. 2005. Ecological science and sustainability for the 21st century. *Frontiers in Ecology* 3: 4-11.

Peters, C.M. 1994. Sustainable Harvest of Non-Timber Plant Resources in Tropical moist forests: An Ecological Primer. Biodiversity Support Programme, World Wildlife Fund, Washington DC, USA.

Pfund, J.-L., O'Connor, T., Koponen, P. & Boffa, J.-M. 2006. Trans-disciplinary research to promote biodiversity conservation and enhanced management of tropical landscape mosaics. IUFRO Landscape Ecology Conference, Sept. 26-29, 2006 – Locorotondo, Bari, Italy.

Pickett, S.T.A. & White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, CA.

Place, F. & Otsuka, K. 2000. Population pressure, land tenure and tree resource management in Uganda. *Land Economics* 76 (2): 233-251.

Proulx, M. & Mazumder, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor versus nutrient-rich ecosystems. *Ecology* 79: 2581-2592.

Rennolls, K. & Laumonier, Y. 2000. Species diversity structure analysis at two sites in tropical rain forest of Sumatra. *Journal of Tropical Ecology* 16: 253-270.

Sankaran, M., Hanan, N.P. & Scholes, R.J. 2005. Determinants of woody cover in African savanna. *Nature* 438: 846-9.

Shackleton, C.M. 1996. Potential Stimulation of Local Rural Economies by Harvesting Secondary Products: A case study from the Transvaal Lowveld, South Africa. *Ambio* 25: 33-38.

Shackleton, C.M. 2000. Stump size and the number of coppice shoots for selected Savanna tree species. *South Africa Journal of Botany* 66: 124–127.

Shackleton, C.M., Shackleton, S.E., Ntshudu, M. & Ntzebeza, J. 2002a. The role and value of savanna non-timber forest products to rural households in the Kat valley, South Africa. *Journal of Tropical Forest Products* 8: 45-65.

Shackleton, S.E., Shackleton, C.M., Netshuluvhi, T.R., Geach, B.S., Balance, A. & Fairbanks, D.H. 2002b. Use patterns and value of savanna resources in the three rural villages in South Africa. *Economic Botany* 56: 581-604.

Sheil, D. 1999. Tropical forest diversity, environmental change and species augmentation: After the intermediate disturbance hypothesis. Journal of Vegetation Science 10: 851-860.

Singh, R.B., Fox, J. & Himiyama, Y. (Eds.). 2001. *Land use and land cover change*. Science Publishers, Inc: NH.

Skarpe, C. 1990. Structure of woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Vegetatio* 87: 11-18.

Struhsaker, T.T. 1997. Ecology of an African rainforest: Logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville, FL. pp. 434.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hanna, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. 2004. Extinction risk from climate change. *Nature* 427: 145-148.

Tothill, J.C. & Mott, J.J. 1985. Management of the World's savannas. Australia Academic of Science, Canberra, Australia.

Turner, M.G., Wear, D.N. & Flamm, R.O. 1996. Land ownership and land cover change in the southern Appalachian highlands and the Olympic Peninsula. *Ecological Applications* 6: 1150-1172.

Van Gemerden, B.S., Olff, H., Parren, M.P.E. & Bongers, F. 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. Journal of Biogeography 30: 1381-1390.

Vargas-Rodriguez, Y.C., Vázquez-Garcia, J.A. & William, G.E. 2005. Environmental correlates of tree and seedling-sapling distributions in a Mexican Tropical Dry Forest. *Plant Ecology* 180: 117-134.

Vitousek, P.M. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861-1876.

Walker, B. & Noy-Meir, I. 1982. Aspect of the stability and resilience of savanna ecosystem. pp. 556-590. In: Huntley, B. & Walker, B. (Eds.) Ecology of Tropical savannas. Springer, Berlin.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Witkowski, E.T.F. & Garner, R.D., 2008. Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive *Solanum mauritianum* in a temperate to subtropical riparian ecosystem. *South African Journal of Botany* 74: 476-484.

Zida, D., Savadogo, L., Tigabu, M., Tiveau, D. & Oden, P.C. 2007. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. *Forest Ecology and Management* 243: 102-115.