HUMAN IMPACT, PLANT COMMUNITIES, DIVERSITY AND REGENERATION IN BUDONGO FOREST RESERVE, NORTH-WESTERN UGANDA

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ABSTRACT

Budongo Forest Reserve (BFR) is a flagship reserve for primate conservation due to its abundant chimpanzee (*Pan troglodytes*) population, and its current management policy for multiple economic, conservation and environmental benefits. The identification and better understanding of the structure and dynamics of the forest/plant community types, patterns of species distribution and quantitative properties of their diversity is important to the conservation and sustainable management of tropical rainforests. This study seeks to contribute to a better understanding of the BFR forest community types, species diversity patterns and environmental correlates, as well as natural regeneration processes (i.e. seedling establishment and sprouting). Data on vegetation and environmental variables were collected using rectangular 50 x 100m (0.5 ha) plots, sub-divided into five equal contiguous (20 x 50 m) 0.1 ha sub-plots. Data on land-use/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 study revealed significant land-use/cover changes, with the area under sugarcane cultivation increasing over 17-fold, from 690 ha in 1988 to 12729 ha in 2002, with a concomitant loss of about 4680 ha (8.2% loss) of forest/woodland, mainly in the southern part of BFR. These changes are attributed to agricultural expansion, a rapidly increasing human population, exacerbated by large influxes of refugees, lack of alternative sources of income, conflicts of interest and political interference in the management of BFR, and an unclear land tenure system. The need for more land for agricultural expansion and the loss of woodlands (a source of building materials and fuelwood for the local communities) is leading to the invasion of and encroachment on BFR, which threatens plant and wild animal conservation.

The study revealed that the vegetation of BFR is formed by a mosaic of plant communities, with the major forest types being; *Pseudospondias microcarpa* Swamp Forest, *Funtumia elastica - Pouteria altissima*, *Lasiodiscus mildbraedi - Khaya anthotheca* and *Cynometra alexandri - Rinorea ilicifolia* forest communities. Canonical correspondence analysis (CCA) indicated that soil nutrients (Si, Ca, N, Fe and Li) and anthropogenic disturbances are the main factors controlling forest community patterns. The variances explained as a proportion of total inertia were relatively high (0.53 and 0.56 for basal area and abundance, respectively), showing how well the measured variables explained species composition. These plant communities differed significantly in terms of woody species diversity and richness; being highest in the *Pseudospondias microcarpa* swamp and lowest in the *Cynometra alexandri-Rinorea ilicifolia* forest. However, about 48 species were shared between the forest community types. A total of 269 species representing 171 genera and 51 families was recorded. Fisher's alpha-diversity ranged 4.45-30.59 and 3.07-29.7 for stem diameters ≥2.0 cm and ≥10 cm, respectively, being significantly higher for stem diameters ≥2.0 cm. The use of stem diameters ≥2.0 cm unveiled 53 more species (19.7%), with only 216 species recorded for the standard ≥10 cm dbh minimum size usually applied in tropical forests. A SHE analysis also showed greater richness (ln(S)) and H diversity for the ≥2.0 cm than the ≥10cm stem diameters. Hence, the study reaffirmed that the use of 10 cm as a minimum dbh in woody plant diversity studies in forests, where many tree species rarely exceed 10 cm stem diameter, is highly likely to underestimate diversity and richness, potentially biasing the understanding of diversity patterns. The most speciose families were Euphorbiaceae, Fabaceae, Rubiaceae, Moraceae, Meliaceae, Rutaceae, Annonaceae, and Flacourtiaceae, accounting for 147 species. Families with the highest Familial Importance values (FIV) were; Fabaceae (17.5), followed by Euphorbiaceae (16.3), and Ulmaceae (8.35). The BFR exhibits characteristics intermediate between log-normal and log-series species-abundance distributions, indicating a community with a small number of abundant species and a relatively large proportion of rare species. Both Whittaker's (β_w) and the Morisita-Horn Index measures of β-diversity consistently showed higher β-diversity for logged and arboricide treated areas, followed by logged only, and then nature reserve historical management practice types. β-diversity was relatively high at the total forest community scale, but lower for stem diameter ≥2.0 cm than ≥10.0 cm data. Environmental variables significantly explained 66.5% and 61.9% of the variance in species composition for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively. Hence, the variation in species composition of BFR is characterised by significant spatial patterns, and the patterns in β-diversity are to a great extent associated with environmental heterogeneity (i.e. soil nutrients, topographic and light gradients) and anthropogenic disturbances.

Investigation of natural regeneration showed that sprouting is generally common among the woody species, with both canopy and sub-canopy trees sprouting prolifically. Of the 122 species affected by harvesting, and tree and branch fall disturbances, 199 (97.5%) from 31 families sprouted from the cut stumps, with only *Caloncoba crepiniana* (De Wild. & Th.Dur.) Gilg exhibiting both stem and root sprouting. Stump basal diameter, height, bark-thickness, and height of stump above the ground at which the first sprout emerged, were significant predictors of sprouting ability among individuals. Number of sprouts/stump differed significantly among families, species, and stump size-classes.

Of the 241 seedling species, representing 46 families, about 30.3% were rare (only 2-10 individuals); while 12% were very rare (only 1 individual each). *Cynometra alexandri* C.H. Wright and *Lasiodiscus mildbraedii* Engl. were the most abundant seedlings and also among the most widely distributed species in the forest. Analysis of similarity (ANOSIM) revealed significant differences in seedling composition between transects, but not between topographic positions or historical management practice types. Canonical Correspondence Analysis (CCA) showed that the measured environmental variables significantly explained 59.4% of the variance in seedling species distributions, with the three most important variables being organic matter, titanium and leaf area index (LAI; an indicator of light availability below the canopy). Hence, the important mechanisms influencing regeneration via seedlings in BFR operate through the soil system, and the ground and canopy vegetation characteristics. Nine of the 15 intensively studied multiple-use species, namely *L. mildbraedii*, *Celtis Mildbraedii* Engl., *Pouteria altissima* (A. Chiev.) Aubrev. & Pellegr., *Chrysophyllum albidum* G. Don., *C. alexandri*, *Diospyros abyssinica* (Hiern) F. White, *Funtumia elastica* (Preuss) Stapf., *Chrysophyllum perpulchrum* Hutch. & Dalz, and *Antiaris toxicaria* (Pers.) Lesch. had highly negative size-class distribution (SCD) slopes and substantial seedling regeneration. While *Alstonia boonei* De Wild. and *Cordia millenii* Bak. had weakly negative SCD slopes and pulsed or sporadic regeneration patterns. The wide distribution of seedlings for a variety of species, and with most of the intensively studied species having population structures showing healthy regeneration patterns, suggests that BFR is currently experiencing a continuous regeneration phase. In conclusion, the gradients in the vegetation of BFR are a reflection not only of site conditions as shown by the edaphic and abiotic factors, but also the history of human interventions.

***Key words**: alpha diversity, ANOSIM, beta-diversity, Canonical Correspondence Analysis, cluster analysis, human impact, land-use/ cover change, leaf area index (LAI), logging, plant communities tropical semi-deciduous forest, seedling regeneration, SIMPER, size-class distributions (SCDs), sprouting.*

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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…07th ..day of …*February*….2007

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LIST OF SYMBOLS & ACRONYMS

BFR:	Budongo Forest Reserve
FAO:	Food and Agriculture Organization
MEA:	Millennium Ecosystems Assessment
KSWL:	Kinyara Sugar Works Limited
NGOs:	Non-Government Organizations
CCA:	Canonical Correspondence Analysis
DBH:	Diameter at Breast Height
ANOSIM:	Analysis Of SIMilarity
SIMPER:	SIMilarity PERcentages
Ca:	Calcium
Mg:	Magnesium
Si:	Silicate
N:	Nitrogen
Na:	Sodium
P:	Phosphorous
Ti:	Titanium
Fe:	Iron
Li:	Lithium
OM:	Organic matter
pH:	Alkalinity/ Acidity
H':	Shannon-Weiner Index of Diversity
UFD:	Uganda Forestry Department
ANOVA:	Analysis of Variance
LAI:	Leaf Area Index
BA:	Basal Area
SCDs:	Size-class distributions

GLOSSARY OF FREQUENTLY USED TERMS

(References in Chapter 1: Introduction)

Alpha-diversity: The diversity in woody species at individual sites (e.g. plots, quadrats) 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: Is any event in time that disrupts ecosystems, changes the community or population structure, resource availability or physical environment (White & Pickett 1985, Osborne 2000)

Forest types: Are associations of tree species that occur because of similar ecological requirements.

Gamma diversity: Is the diversity for the whole region of interest for the study (Whittaker 1972). It can be partitioned into two components: local (alpha) diversity and turnover of species between habitats or localities (beta-diversity) (Magurran, 2004, Legendre et al. 2005).

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

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

Leaf Area Index: Leaf Area Index is variously defined in literature. In this study, however, it is defined as the projected area of foliage per unit ground surface area (Parker 1995, Kram, 1998).

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/root crown of a woody plant following damage e.g. from harvesting, tree/branch fall.

Species diversity: Referred to as the variety of life (Osborne 2000, Magurran 2004)

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

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

CHAPTER 1

GENERAL INTRODUCTION: HUMAN IMPACT, PLANT COMMUNITIES, DIVERSITY AND REGENERATION IN BUDONGO FOREST RESERVE, NORTH-WESTERN UGANDA

1.0. INTRODUCTION

1.1. Background

Tropical rainforests have incomparably rich and varied plant and animal species richness, and provide habitat for half or more of the world's known terrestrial plant and animal species (Osborne 2000, MEA 2005a), making them the world's most diverse ecosystems. In addition to having the highest tree diversity on earth (Gentry & Dodson 1987, Richards 1996, Clark *et al*. 1999), they hold 50% of the terrestrial carbon pool (Köhler *et al*. 2001). This biodiversity is essential for the continued health and functioning of forest ecosystems, and it underlies the many ecosystem services that forests provide (MEA 2005a). Uganda's natural forest reserves have for a long time been managed primarily to provide economic (e.g. timber and charcoal) and environmental (e.g. maintenance of soil, water and climate quality that support agriculture and fisheries) benefits (e.g. Moyoni 2001). They are also central to Uganda's national three pillars of sustainable development - the economy, society and environment; and together with savannah woodlands supply well over 90% of the country's energy requirements (NEMA 1998, Moyoni 2001). Similarly, elsewhere in Africa, they are being threatened and lost at a rate of about 13 million ha/year by a combination of factors, including agricultural expansion, commercial harvesting, increased firewood collection and charcoal making, and inappropriate land and tree tenure regimes (GEO-2000 1999, MEA 2005b), resulting in the loss of species, habitats and resources. This is a threat to forest health (Battles & Fahey 2000), yet forestry has immense potential to alter landscapes, and biodiversity conservation within forested landscapes has become a priority (Boutin & Herbert 2002). With the increasing human population in Uganda, the shrinking extent of natural habitats, and the largely agrarian economy (NEMA 1998), it is important to have a good understanding of the condition of the forests. However, according to MEA (2005b), the overall state of knowledge on the condition and trends in coverage of forests/woodlands in many regions of the world, including Uganda, is incomplete.

The ecological and environmental importance of tropical rainforests necessitates their conservation and sustainable management, aided by accurate identification and better understanding the biology of forest species (Sagers & Lyon 1997), and patterns of species distribution and quantitative properties of their diversity (Buzas & Hayek 1996, Eilu *et al.* 2004a). Indeed, ecological management of any area should be based on a sound understanding of the natural resources present (Coetzee *et al*. 1994), and their extent and use for the development of sustainable management practices (Petit *et al.* 2001, Dovie *et al*. 2002). In addition, there is a growing recognition by the scientific community that, principles from the biological, physical and social sciences must be integrated to understand and predict the behaviour of managed systems (Antle *et al*. 2001). Reliable data and information are essential for determining forest conditions and trends and for development of national and international forest policies (MEA 2005a). In this regard studies of human impacts, plant communities, diversity and regeneration in forest vegetation are fundamental.

1.2. Plant community composition, structure, and species diversity and distributions

Several communities may belong to the same vegetation type (i.e. have similar physiognomies), yet they differ in the identity of dominants or other species, leading to vegetation gradients. Plant composition and structure are important elements of any description of the development of a forest stand (Norland & Nix 1996). Central to our understanding of tropical plant and animal species, communities and ecosystems is the concept of diversity (Richter & Babber 1991). Species diversity, referred to as the variety of species (Osborne 2000), integrates two aspects of community structure, i.e. species richness (describes the number of species) and species evenness or equitability (describes relative abundances among the species in the community) (Hsieh & Li 1998, Magurran 2004). The most important characteristics of tropical forests are species richness and diversity (Atyi 1996), which are major criteria in nature conservation (Liu & Bråkenheilm 1996). They are emphasised in biodiversity research and preservation because of their ecological, economic and environmental value (Wickham et al. 1995). Species richness, a core measure of biodiversity (Buzas & Hayek 1996), is important to the functioning of an ecosystem (Burke & Lauenroth 1995). It is also a fundamental measurement of community and regional diversity, and underlies many ecological models (Cornell 1999, Gotelli & Colwell 2001). In this regard measures of species diversity are essential for understanding the mechanisms that control species diversity and the structure and function of ecosystems (Hsieh & Li 1998), playing a central role in ecology and conservation biology (Naveh & Whittaker 1979, Noss & Cooperrider 1994, Cornell 1999, Ricotta *et al*. 2002, Magurran 2004). Furthermore, an understanding of the association of a species with other species further helps to explain the distribution of that species (Thrash 1998), whereas the description of patterns of species distributions is an important step in generating hypotheses (Jonsson & Moen 1998). Hence, the understanding of species diversity and richness patterns is very important in the management of ecosystems of environmental and conservation value, like Budongo Forest Reserve (BFR), since ecosystem management relies on accurately identifying components of the forest landscape.

1.3. Influence of environmental gradients on plant communities

1.3.1. Theoretical considerations

A number of theories and hypotheses have been put forward to explain the mechanisms responsible for the accumulation and maintenance of species diversity in the diverse tropical rainforest plant communities. The mechanisms are diverse, with some based on abiotic processes and others on biotic processes. However, some operate entirely by chance, whereas others depend on deterministic processes (Terborgh *et al.* 2002). For example, the intermediate disturbance hypothesis (IDH; Connell 1978) posits that species diversity of space-limited communities will be low at high and low rates of disturbance and maximal at some intermediate rate. Therefore, under these conditions, species with different life history strategies are able to coexist and, consequently, high levels of species richness are maintained. The IDH, however, requires that in mature forests, some disturbance types can augment local diversity by adding more generally short-lived species (Sheil 1997b). Gleason (1926) perceived plant and animal communities as changing gradually along environment gradients. Thus, they gradually and independently replace one another along a continuum (Osborne 2000). Firstly, environmental conditions (e.g. moisture, soil nutrients and topography) will determine, which species are able to colonise and reproduce within a particular area, and hence, maintain a population there. Secondly, competition with other organisms in the area will act to refine community composition.

On the other hand, the resource limitation theory (Tilman 1982, 1988) states that spatial distribution patterns of species are determined by gradients in resource availability at a broad scale, and that all plants are resource-limited in their natural habitats. Thus, spatial heterogeneity in the availability of limiting nutrients can generate a corresponding mosaic of species composition. This theory depends on the assumption that an individual plant species is a superior competitor for only a small range of resource supply ratios. Work reviewed by Tilman (1982) strongly suggests that resources are a major factor influencing the diversity and species composition of plant communities. According to Sheil (1999), current theories regarding diversity pattern in tropical forests offer restricted insights, although many relevant principles have been identified and characterized. Some of these theories, have in more recent research (e.g. Debski *et al.* 2000, Blundell & Peart 2002, Penfold & Lamb 2002), been used to explain the coexistence of tree species and their distributions. In addition, a review of these theories by Terbogh *et al.* (2002) revealed that some of them (e.g. the intermediate disturbance hypothesis, resource limitation theory) have stood the scrutiny of analyses at multiple scales.

1.3.2. Environmental gradients

Natural forest vegetation gradients may reflect the combined influence of historic human intervention, climatic changes, and relative species performance (Jeník 1990). For instance, the composition and structure of plant communities is affected by many environmental gradients (e.g. edaphic factors, climate and disturbance) (Klug & Cottingham 2001, Terborgh 1992) that vary both on spatial and temporal scales (Kent & Coker 1996, Porembski *et al.* 1995). According to Bongers *et al.* (1999), the actual distribution of tree species is determined by climate, soil conditions, historic events, disturbances (natural and human), interactions with fauna and competition between tree species for space and other resources. Soil physical and chemical characteristics, rainfall, soil moisture regime, light availability and topography influence the distribution, abundance, diversity and growth of plant species within an area (Ben-Shahar 1987). For example, light availability influences many important biological processes such as seed germination, plant growth and succession (Cannell & Grace 1993), as well as tree recruitment below canopies (Denslow *et al.* 1990).

However, plant species differ in their tolerance of, and requirements from, the environment so that their distribution or abundance varies along environmental gradients (Swaine 1996), even though there may be overlaps between distributions of different species. The assumption is that each species maximises its abundance at some value of each environmental property, but is capable of surviving over some range of values (Ehrenfeld *et al.* 1997). The gradients in plant abundance associated with physical gradients may be different for each species, creating a vegetation mosaic of populations integrated across the landscape (Cody 1989, Patten & Robin 1995). Indeed, some of the most obvious patterns in the distribution and abundance of organisms in nature are generated by associations of species with physical habitat variables (Webb & Peart 2000), and with neighbouring species. For instance, the species continua commonly observed along environmental gradients are a result of both negative and positive plant interactions (Choler *et al.* 2001). A number of studies (e.g. Peet & Allards 1993, Witkowski & O'Connor 1996, Sagers & Lyon 1997, Menges &

Hawkes 1998, Gough *et al.* 2000, Grace 2001) have shown how vegetation structure, species diversity and species associations vary across abiotic gradients (i.e. topography, soil pH; soil moisture and nutrient availability). Indeed, local biotic and abiotic ecological interactions (e.g. environmental conditions and competition) have long been a focus to explain the distribution patterns of plant species (Ehrenfeld *et al.* 1997, Verheyen & Hermy 2001). The understanding of spatial scale distributions of plant species requires understanding the distribution of edaphic factors at a meso-scale (1000 m^2) (Clark *et al.* 1999). Such understanding should, preferably, be based on a study of topography, soil texture and soil chemistry for each sampling plot.

Both species diversity and richness vary over spatial and temporal scales. Changes in species richness and diversity may be caused by intrinsic population processes, natural environmental fluctuations or anthropogenic interferences (e.g. logging, cultivation, habitat destruction, etc.), and changes in human activity (Wilson 1994, Chapin *et al.* 1998). Thus, changes in species diversity are often used as indications of natural and anthropogenic disturbance in ecosystems. It has been argued that the present structure, diversity and dynamics of a forest are determined by both physical conditions and chance factors (e.g. Connell 1978, Denslow 1980, Masaki *et al.* 1999). Thus, species diversity seems to be related to the structural complexity of the environment in many different kinds of systems (Bell *et al.* 2000). For example, the current variation in the structure, diversity and dynamics of the temperate broad-leaved forests in Japan is attributed to both the physical conditions (e.g. climate) and chance factors (e.g. disturbance) (Masaki *et al.* 1999). However, current environmental conditions may not be an adequate explanation of local species richness (Sheil 1996).

1.3.3. Forest disturbance

Disturbance can be defined as any event in time that changes community structure, resource availability or physical environment (Osborne 2000). It can be classified as episodic (sudden changes such as intense fires and tree cutting) or more chronic (continuous changes such as herbivory) (Gómez *et al.* 1999). Disturbance can further be classified on the basis of cause as either ecological or anthropogenic (human induced). Ecological disturbances are relatively discrete events in time that disrupt ecosystem, community, or population structure and change resources, substrate availability, or the physical environment (White & Pickett 1985). However, disturbance whether natural or human induced, plays a critical role in shaping vegetation communities (White 1979) by altering structure and composition, consequently, affecting regeneration patterns and the availability of food for animals (Plumptre 2000). Disturbance may influence community patterns by indirectly altering the environmental and resource distributions, creating/defining opportunities for the establishment and persistence of new species; or reducing populations of established species (Menges & Hawkes 1998, Motzkin *et al.* 1999). However, species responses to disturbance are governed primarily by their history, physiological traits and the characteristics of the disturbance (Gómez *et al.* 1999). For instance, extreme disturbance events may strongly influence the structure and functioning of many ecosystems, particularly those in, which large, infrequent events are the defining forces within the region (Moritz 1997). Infrequent landscape-scale disturbances affect such critical characteristics as species composition, ecosystem productivity and nutrient distribution (Vance & Wilson 1990).

The most important aspects of the disturbance regime are its spatial scale, the frequency of disturbance, and the intensity of disturbance (Grace 1997). Variation in the scale (size), frequency, and magnitude of a disturbance causes spatial and temporal heterogeneity in the environment, and affects community structure through the variable responses of the constituent species (e.g. White & Pickett 1985, Masaki *et al.* 1999), while other components of the disturbance regime may also affect successional patterns, landscape dynamics, and species distributions (Sousa 1984, Halpern 1988). However, the level of species richness will be influenced by the rate of disturbance, being greatest at moderate levels of disturbance (Connell 1978, Crawley 1997).

For natural forests to maintain their species diversity, Everard *et al.* (1994) argue that a certain frequency of disturbance must prevail. Studies (e.g. Eggeling 1947, Sheil 1999) in some African tropical forests have presented evidence suggesting an important role for disturbance in maintaining tropical forest tree diversity. Furthermore, Morgenthal & Cilliers (1999) argue that disturbance agents are necessary to prevent a reduction in plant species diversity and the formation of a homogeneous stand of core forest communities. For instance, disturbance of the soil surface and / or destruction of established plants may provide recruitment microsites, which allow the community to be invaded by new species, leading to increased species richness. However, not all disturbance agents may lead to the maintenance of species diversity. For example, tree cutting that tends to fragment forest habitats might have negative consequences for the maintenance of forest species diversity (Boutin & Herbert 2002). For instance, creation of gaps resulting in patchiness of canopy coverage and associated parameters may lead to low or high levels of species diversity at the α, β, and γ scales (Leach & Givnish 1999). Forest disturbance by logging changes vegetation structure and species composition, while other forest practices may result in dynamic landscapes that remain primarily forested while undergoing spatial and temporal changes in composition and age structure (Schmiegelow & Mönkkönen 2002).

1.3.4. Land-use/cover changes

Worldwide, the most potent forces acting on vegetation are the effects of changing land use arising from both the direct effects of an expanding human population (e.g. habitat destruction for agriculture, human settlement, overgrazing, etc.) and indirect effects (e.g. pollution) (Wilson 1994, Grime 1997). Land-use is the manner in, which human beings employ the land and its resources (e.g. for agriculture, grazing, logging, etc.; Brandon 2001). In the event of habitat loss and changes in habitat configuration (patch size and isolation), species presence could be affected (Andrén 1994, Fahrig 1997). Ecological dynamics in human-influenced landscapes are strongly affected by socio-economic factors that influence land-use decision-making (Berry *et al.* 1995). Throughout the world, many shifting land-use patterns that are driven by a variety of social factors, result in land cover changes that affect biodiversity, water and radiation budgets.

1.4. Natural regeneration of woody plant species in forests

In order to maintain biological diversity, especially of the economically important species, sufficient natural regeneration (i.e. through seed rain, soil seed banks, seedling bank, vegetative reproduction and/or resprouting/ coppicing) that involves recruitment, survivorship and growth of plants (Kigenyi 1979) is required. Forest regeneration, defined as the establishment of new tree cohorts, normally occurs during succession, which involves changes in plants, animals, and microbes (Bernier & Ponge 1994). It has also been noted that sustainable resource use hinges on a species ability to continually establish new seedlings while being subjected to repeated and intensive harvesting (Peters 1994). Indeed, this recruitment of new tree individuals into a forest is an important determinant of the state of the forest in the future, given the present circumstances of increased utilisation and human disturbances. With disturbances, individuals of many woody plants have the ability to respond to damage that removed the crown, by producing new branches (resprouts) along the remaining stem. Greig (1993) asserts that stump resprouting of damaged trees in natural light gaps is one mechanism through, which tropical forests regenerate. Resprouting is an important life history characteristic of woody species in moist tropical forests, and those subjected to serious disturbances such as fire and logging (e.g. Bellingham et al. 1995, Guariguata 1998, Kammesheidt 1999, Bond & Midgley 2001). However, the importance of sprouting for population and community dynamics depends on several demographic parameters that include: (a) the rate of physical damage or dieback; (b) the rate of resprouting by damaged individuals; and (c) the subsequent performance (growth, mortality and reproduction) of the individuals (Paciorek *et al.* 2000). On the other hand, the relative allocation to resprouting versus seed production in woody plant communities is dictated by the nature of the disturbance regime, whereas the response to disturbance either by resprouting or seeding is dictated by the site's productivity (e.g. moisture and alkalinity of the soil, Bellingham & Sparrow 2000).

Substantial variability in regeneration has been reported among forest stands due to differences in disturbance history, site conditions, and chance factors that influence the early successional species mix (Lertzman *et al.* 1996). For instance, the gap forming processes in climax forests affects the regeneration dynamics of tree populations (e.g. Arévalo & Fernández-Palacios 1998). Usually a dramatic change in forest light conditions occurs after canopy gap formation, influencing other micro-environmental changes such as air and soil temperatures, and soil moisture below the canopy. The resulting habitat heterogeneity, provides an opportunity for establishment of new individuals and species (Sousa 1984), and favours the coexistence of species with different life histories and ecological requirements, which contribute to the maintenance of community diversity (Barkham 1992). Consequently, a mosaic of regenerating phases of different sizes and ages occurring simultaneously at a site are created (e.g. Martínez-Ramos *et al.* 1985, Rankle & Yetter 1987). In tropical rainforests, it is well known that species differ in the extent of canopy disturbance in, which they successfully regenerate (Denslow 1987, Swaine & Whitmore 1988). Therefore, an understanding of natural regeneration (by seeds and resprouting) processes and the dynamics of tree and shrub species populations have practical applications in sustainable management of vegetation and the restoration of habitats (Peters 1994, Bekele 2000, Vesk *et al.* 2004). Studies on natural regeneration and seedling ecology can provide options for forest development through improvement in recruitment, establishment and growth of the desired seedlings (Denslow 1987, Whitmore 1996, Kyereth *et al*. 1999, Teketay 1997).

1.5 Description of the study area

Location, topography and size

By 1984 BFR was believed to be the most important timber forest in Uganda, supporting 28% of the country's standing timber resources on only about 6% of its forest area (Howard 1991). BFR is an important forest of exceptional biodiversity importance, as it is home to the largest population of between 600 and 800 wild chimpanzees in Uganda (Plumptre & Reynolds 1994). It is also home to over 465 woody species, 366 bird species, 289 butterfly species and 130 species of large moths (Uganda Forest Department 1997). It is located on the top of an escarpment east of Lake Albert on the edge of the western rift valley (Howard 1991) in western Uganda, between Masindi town and Lake Albert. It lies between $1^0$37' and $2^0$03' N and $31^0$22' and $31^0$45' E (Fig. 1). The altitudinal range of the area is 700 - 1270 m, with 0.2 km^2 of the area lying below 750 m, 385 km^2 at 750 - 1000, 408 km^2 at 1000 - 1250 m and 0.1 km^2 above 1250 m (Howard, 1991). Generally, the altitude of most of the area of the reserve is about 1050 m, with hills rising to just over 1200 m. The rocks of the whole area are well weathered, slopes are, with a few exceptions, gradual and the intervening ridges are rounded. In the BFR main block (Fig. 1), the ground is undulating. The valley bottoms are generally soft, and many of the so-called streams are mere trickles through rattan (*Calamus deerratus* Mann & Wendl.) swamps, with no apparent flow in dry weather (Eggeling 1947).

Geology and soils

The underlying rocks are ancient gneisses, schists and granulites of the Basement Complex. The basement complex is an assemblage of schistose and gneissose rocks, which are highly metamorphosed sandstones, shales and limestones (Eggeling 1947). The soils are ferralitic, mainly sandy or sandy clay loams of low to moderate fertility. In BFR main block (Fig. 1), there are two types of soils, a tropical red earth and a murram. The red earth is red in profile and varies from a heavy loam or sandy clay to a very sandy loam characteristic of most parts of the valley bottoms (Eggeling 1947). Murram is abundant in the form of concretions or sheet ironstones. It covers some high ground, especially hill-tops. Generally, the soils are deep with little differentiation into clearly defined horizons and, they possess a fine granular structure moulded into larger weakly coherent clods, which are friable and porous.

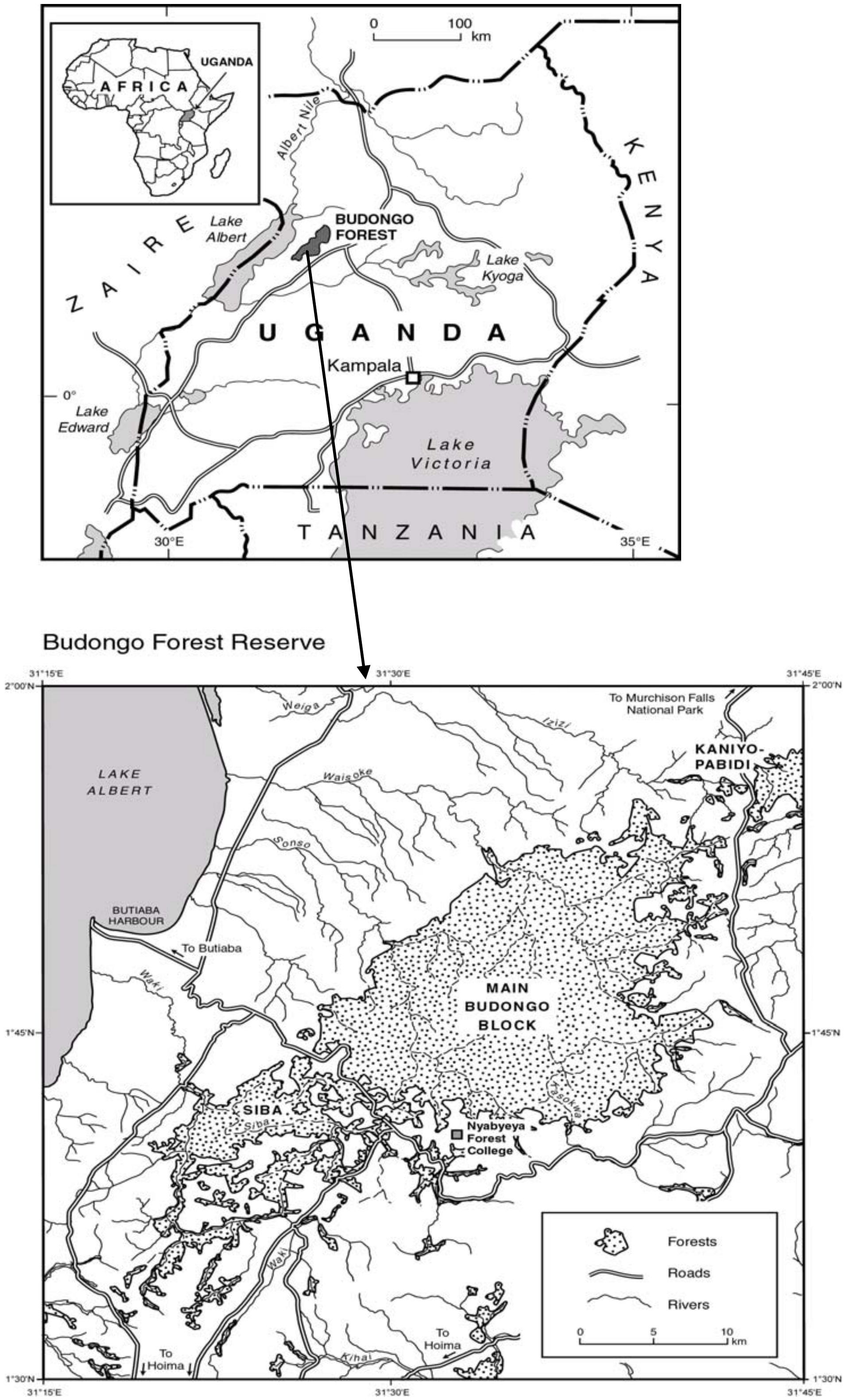

Figure 1: The location map of Budongo Forest Reserve, Masindi District, Uganda.

Climate

BFR occurs in Zone III of Uganda’s climatic zones. This is a narrow zone along the western boundary of Uganda. The climate of this zone is tropical with two rainfall peaks, from March to May and September to

November. The mean annual rainfall in the forest is 1500 mm, with the wet seasons during April - May and September - October, and a dry season during December - February. The number of rainy days usually ranges between 150 and 200 in a year (District Environment Profile 1998). However, the rain in this area is quite variable, so that it is rare to find any two weather stations recording even approximately the same fall on any one day (Eggeling 1947). BFR is affected by incursion of the westerlies that carry masses of rain bearing cumulonimbus, which are responsible for the afternoon thunderstorms. Like all equatorial climates, the zone is characterised by high temperatures with small daily variations. Maximum temperature recorded in a 24-hour period rarely exceeds 32.2^0C, but also occasionally drops below 23.9^0C. The minimum temperatures at night normally lie between 15^0C and 21^0C (District Environment Profile 1998). Generally, the temperatures are relatively uniform throughout the year.

Vegetation

The BFR can be broadly classified as medium altitude semi-deciduous moist tropical rainforest, since several of the dominant species (e.g. *Celtis* spp., *Maesopsis eminii* Engl., *Ficus* spp. etc.) are at least briefly deciduous (Eggeling 1947, Langdale-Brown *et al.* 1964), with a noticeable exception of the wide shade-tolerant *Cynometra alexandri* C.H. Wright (Sheil 1997a). The deciduous habit is noticeable during the dry season that occurs twice each year (June-August and December-February). Leaf shedding, however, is not automatic, but is instead a graded response that depends on the water economy of individual trees, and it is most noticeable on well drained soils. The vegetation is distributed in zones between 670-1500m above sea level. The characteristic vegetation types range from medium-altitude moist semi-deciduous forest to swamps and communities with impeded drainage in the wide and shallow valleys, as well as post-cultivation communities, which are prominent on the hill slopes where intensive cultivation takes place. According to Sheil (1997a), the canopy trees have generally high and emergent stems, occasionally reaching over 60m. Eggeling (1947) classified the vegetation of Budongo Forest into four forest types, namely *Cynometra* forest, mixed forest, colonising woodland, and swamp forest. He argued that the first three types follow an ecological succession, from colonising woodland to mixed forest to *Cynometra* forest, with colonising-mixed and *Cynometra*-mixed ecotones. Generally, the forest is a mosaic of forest types (Reynolds 1992, Plumptre *et al.* 1994), a result of forest dynamics and management history (Eggeling 1947, Plumptre 1996).

Ecology and management history

The BFR is among Uganda's most productive forests, which also include Kibale in the Toro district, Kalinzu in the Ankole district, Mabira in the Lake Victoria region, the forests of Mount Elgon, and the Rwenzori mountains (Byrnes 1992). These are managed as either forest reserves or National Parks. The general ecology, environment, management and history of BFR has been described elsewhere (e.g. Eggeling 1947, Synnott 1985, Howard 1991). Historical management (silvicultral practices) include selective logging and arboricide treatments, enrichment planting and controlled shooting to reduce animal populations in the forest. For example, during the 1940's and early 1950's, logged areas were replanted with African mahoganies (*Khaya anthotheca* (Welw.) C. DC. and *Entandrophragma* spp.) to encourage regeneration of these species. During the 1950's and 1960's, the arboricides trichlorophenoxyacetic acid (2,4,5, T-D) and dichlorophenoxyacetic acid (2,4-D). in 1:2 proportions mixed with diesel, were applied to trees that were assumed to be of no commercial value (so called 'weed' species) to open up the canopy, reduce the extent of monodominant forest stands and encourage the spread of mixed forest (Philip 1964). This treatment ceased in the 1970's when more tree species became marketable and it became difficult to import the chemicals (Synnott 1985). Analysis of the 1951 and 1990 aerial photographs revealed that the extent of *Cynometra* dominated forest had been greatly reduced (loss of 103 km^2 - 24% of the forest), whilst mixed forest expanded (increase of 176 km^2 - 41% of the forest) (Plumptre 2000). In 1991, it was estimated that about 77% of the forest had been cut at least once, and most of the forest has been altered through timber exploitation (Table 1; Howard 1991).

Table 1.Aerial extents (km^2) of different forest types and their condition within Budongo Forest Reserve, based on the 1985 aerial photographs by Gitec Consultants (1985) (Howard 1991).

Condition	**Forest types/ area (%)**				
	Celtis forest	*Khaya* forest	*Senna* forest	*Cynometra* forest	**Total/ (%)**[b]
Undisturbed	3	50	0	40	93 (21.83)
Mechanically. harvested pre-1950	13	27	0	50	90 (21.14)
Mechanically. harvested post-1950	111	52	34	30	227 (53.28)
Pitsawn	0	6	0	10	16 (3.75)
Total (%)[a]	**127 (29.81)**	**135 (31.69)**	**34 (7.98)**	**130 (30.52)**	426 (100)

[a] Percentage contribution of a forest type to the total forested area

[b] Percentage area contribution of a particular forest condition to the total forested area

1.6. Rationale for the study

The importance of BFR has been recognised for both its timber (e.g. Sheil 1996) and wildlife conservation value (e.g. Plumptre & Reynolds 1994, Tweheyo 2003), as well as for local livelihood activities. However, with continued loss of woodlands in surrounding areas and the increasing human utilisation, BFR faces serious challenges from resource utilization that necessitates a strengthening of the ecological basis for its sustainable management (Guariguata 2000). In addition, the long-term survival of the wild animals in BFR requires the development and implementation of management practices/strategies based on the conservation of habitats suitable for a variety of animals. This requires a clear understanding of the structure and dynamics of the forest and its plant community types (Sagers & Lyon 1997). For instance, a detailed knowledge of plant species alpha-diversity of a forest at the landscape level could be one of the first steps in understanding and conserving it (Natta *et al.* 2002). However, for BFR, we do not yet have a full understanding of it, although a number of studies have been carried out. Some of the studies carried out in BFR have addressed issues relating to broad vegetation descriptions (e.g. Eggeling 1947, Langdale-Brown *et al.* 1964), primate ecology (e.g. Plumptre & Reynolds 1994, Tweheyo 2003), seedling regeneration (i.e. regeneration via seedlings) of mahogany species (e.g. Synnott 1975, Babweteera *et al.* 2000, Mwima *et al.* 2001), tree species recruitment in permanent sample plots (Sheil 1996), and species-environmental factor relations for ≥10 cm dbh trees (e.g. Walaga 1994, Sheil 1996, Eilu 2004b). In spite of these studies, a number of questions on: i) causes and patterns of land-use/cover changes around BFR, ii) patterns of woody plant alpha-diversity and richness along a topographic and historical management practice gradient, iii) species-abundance distributions, iv) beta-diversity patterns and their environmental correlates, v) sprouting of woody species, and vi) population structure and regeneration patterns of multiple-use species. In this study, an attempt was made to provide answers to these six questions. Indeed, alpha and beta-diversity patterns for woody species ≥2.0 cm stem diameter in BFR remain largely unanswered. Indeed, Pitman *et al.* (2001) note that although some woody plants with a dbh much lower than 10 cm may be treelets, their contribution to the overall species diversity may be significant, and they influence forest composition and structure. Treelets have been severally classified as woody plants with 5 cm dbh excluding palms, lianas and hemiepiphytes (Galeano *et al.* 1998), or as woody subcanopy plants of 5 - 10 cm dbh (Valencia *et al.* 1994). While shrubs are rooted woody self-supporting plants up to 5 m high, multi-stemmed or single-stemmed and branching at or near the ground level when 2 – 5 m high, or either multi-stemmed or single-stemmed when less than 2 m high (Edwards 1983). In this study, treelets are classified as woody species that are of stem diameter 2.0 - 10 cm excluding shrubs, lianas, palms and hemiepiphytes.

Ever since the failure at enrichment planting attempts in the 1950's (Philip 1964), the forest has relied entirely upon natural regeneration through seeding and resprouting. However, little is known of woody plant sprouting in African tropical forests in general and BFR in particular, even though an understanding of resprouting of damaged stumps is of practical importance for management and conservation of important woody species and ecosystems. It has been noted that, even in forests where large-scale disturbances are infrequent, woody plants still experience significant stem damage from smaller scale disturbances such as pole and sapling harvesting by humans, as well as natural branch and tree fall (e.g. Clark & Clark 1991, Paciorek *et al.* 2000). Therefore, providing clear answers to questions such as: what are the factors that influence plant species diversity in BFR? and how will the diversity patterns be influenced by changes in the environment? is very important (e.g. Walker & Stefan 1996, Sheil 1999). The understanding of diversity patterns aids effective conservation, and land-use planning and management (Fuls *et al.* 1992, Morgenthal & Ciliers 1999). In addition, classification and characterisation of the main forest types enables a better understanding of the driving variables involved in the natural reforestation process and on how the forest regeneration process can be improved (Nansen *et al.* 2001).

1.6.1 Aim of the study

The broad aim of this study was to identify and describe forest community types, patterns of species richness and diversity (alpha and beta), and assess natural regeneration; as well as reveal the links with major environmental factors in order to understand the nature of gradients in the environment and the vegetation of BFR. The historical context of changing management goals in BFR since the 1950's, and the ever increasing influence of the surrounding human population, means that for the aim to be fully dealt with, both the management history and the dynamics of land-use surrounding the forest have to be considered.

1.6.2. Objectives of the study

The studies included in this thesis (Chapters 2-7) had the following specific objectives:

I. To analyse land-use/cover changes within and around BFR with a view to understanding the dynamics of land-use/cover changes especially deforestation and associated agricultural developments from 1988-2004.

II. To classify and describe the main forest community types and to reveal the links between these communities and the major environmental factors using multivariate analysis techniques.

III. To assess the woody plant (i.e. tree and shrub) species α-diversity of BFR, and investigate the nature of diversity and richness in relation to minimum stem diameter sizes, plot size and historical management practices.

IV. To determine and describe tree and shrub species β-diversity patterns and environmental correlates in BFR.

V. To identify the major causes and types of disturbance leading to stem damage and, consequently, sprouting, and to describe the sprouting ability among the woody plant species in BFR.

VI. To describe the size structure of important tree species and the seedling regeneration (i.e. regeneration via seedlings) of woody species in general, as well as the factors responsible for the maintenance of variation in community composition, with a view to improve the understanding of the ecology of natural regeneration in BFR.

1.7 The General approach to the study

In this study, two broad methodologies were used:

i. Collection and analyses of field data

Generation of field data involved vegetation and environmental factor surveys. The surveys focused on the Budongo main block (Fig. 1) covering about 364 km^2 of the total area (825 km^2) of BFR, as it is assumed to be less disturbed by human intervention than the other parts of the forest. The initial sampling was based on stratifying according to the four forest types (i.e. *Khaya*-, *Celtis*-, *Senna*-, and *Cynometra*- dominated) as identified by Howard (1991). Within each forest type, an attempt was made to locate at least three different angulating landscapes (hills) on, which sampling plots were laid following four topographic position categories (i.e. lower slope, mid-slope, upper slope, and flat/ ridge top). Plots were oriented at right angles to topographic gradients with the long side of the plot parallel to the contour. Transects were systematically established to cover as much variation in each community type as possible from valley bottoms to ridge tops. This is recommended where communities are likely to be strongly influenced by environmental gradients (Barbour *et al.* 1987). It is also important to sample various combinations of environmental variables as a means of obtaining a representative sample (Stalmans *et al.* 1999). Sampling a full range of environments ensures that predictive models derived from survey data can be used for interpolation rather than extrapolation (Austin & Heyligers 1989). In vegetation sampling, topography and accessibility are important factors to consider when choosing sites to lay plots. In this study, the availability of the Budongo Forest Project trail system and the demarcation of the forest into management blocks facilitated the location of sampling plots on the ground.

A rectangular 50 x 100 m (0.5 ha) plot (Fig. 2) sub-divided into five equal contiguous 50 x 20 m (0.1 ha) sub-plots to facilitate sampling was employed for vegetation sampling. According to interpretation of the species area relationship curves of the vegetation inventory data from Eggeling (1947), a 50 x 100 m (0.5 ha) plot is appropriate for sampling trees species of ≥10cm (dbh) in Budongo forest. This plot size has also been used in other vegetation studies in Budongo (e.g. Plumptre 1996). On the other hand the 50m x 20m plot size is the standard quadrat area for work on vascular plant species richness (Crawley 1997). Thus, the sample plot size employed for the present study was adequate for sampling woody species diversity in BFR. Given the methods, logistics, and resources, the floristic survey focused on trees and shrubs, leaving out herbs and epiphytes, though they might greatly contribute to the floristic diversity of the forest. Epiphytes are unlikely to show strong correlations with the underlying environmental variables, as they acquire moisture and nutrients aerially.

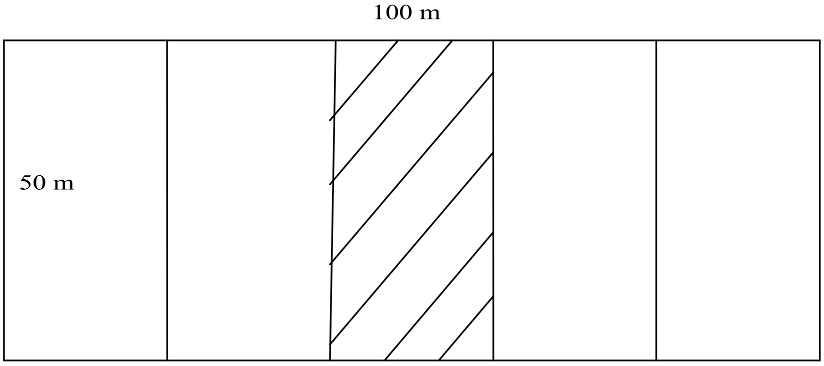

Figure 2. Vegetation sampling plot design

ii. Long-term data

Generation of long-term data involved the use of Landsat images, which were interpreted and complemented with ground surveys to check for land-use/cover changes over the years. Data on land-use practices, land cover changes, relevant associated socio-economic parameters, and the perceptions of the households in villages surrounding BFR were determined through field observations, as well as interviews with local residents and key informants. Households were selected systematically in order to obtain a representative sample in terms of ethnicity, wealth, gender, and age classes. Semi-structured interviews (SSI) and questionnaire interviews were conducted on an individual basis to minimise peer influence and improve the quality of data (Phillips & Gentry 1993). The SSI guide served only as a checklist, delimiting the issues to be considered in the interview to ensure that the same information was obtained from a number of people (Inglis 1992, Chambers 1994). Key informant interviews were also used to obtain information that would assist in clarifying or improving understanding of particular issues or problems that were raised in the household interviews.

1.8. The structure of the thesis

The chapters presented in this thesis are arranged in a thematic progression beginning with an introductory chapter, in which the general background for developing this research and a description of the study area are presented. However, the chapters are autonomous and written in the format of scientific papers to be submitted for publication to peer-reviewed journals, inevitably resulting in repetition of some items (e.g. study area description, methods, and references). Chapter 2 reports on the land-use/cover changes around BFR and their implications for its conservation. In Chapters 3 to 7, plant communities, diversity and natural regeneration in relation to environmental factors, in the vegetation of the BFR are reported. Each of the central chapters has a complete abstract, introduction, methods, results, discussion and conclusion section. In Chapters 3 to 5, plant community patterns and diversity of the woody plant species are described in relation to environmental gradients. In Chapters 6 and 7 the different aspects of natural regeneration (i.e. seeding and resprouting) of a number of multiple use woody species are described. Chapter 8 is a general discussion and synthesis, which serves as the bridge among the different main chapters (i.e. chapters 2-7). It also includes directions for future work and personal thoughts on the implications of this research for the better understanding of forest ecology, influences of humans on forest resources, and hence, the sustainable management of tropical rainforests.

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CHAPTER 2

Land-use/cover changes (1988 – 2002) around Budongo Forest Reserve, NW Uganda: implications for sustainability of the forest/woodland

Abstract

Land-use/cover changes around Budongo Forest Reserve (BFR) were analysed from multi-temporal LandSat images (1988 and 2002) and associated field-based studies in 2003-2004. Three major land-use/cover classes: forest/woodland, sugarcane plantations, and grassland/shifting cultivation/settlements were clearly discriminated. Area under sugarcane cultivation increased over 17-fold, from 690 ha in 1988 to 12729 ha in 2002, with a concomitant loss of about 4680 ha (8.2%) of forest/woodland, mainly in the southern part of BFR. Land-use/cover changes were a result of agricultural expansion, increasing human population, exacerbated by large influxes of refugees, conflicts of interest and political interference in management of BFR, and unclear land tenure. Agriculture is the main land-use practice and source of income to local people, with commercial sugarcane and tobacco as the primary cash crops. Sugarcane plantations covered distances ranging from 30-1440 m along the BFR edge, with no buffer zone, resulting in direct conflicts between farmers and forest wild animals. There is increasing need for more land for agricultural expansion resulting in continued loss of forest/woodland on private/communal lands and encroachment into BFR. This unsustainable agricultural expansion and the local people's perception of BFR as an obstacle to agriculture, threatens the conservation of its wild plants (e.g. *Raphia farinifera* (Gaertn.) Hylander) and endangered chimpanzees. Although legal protection of forests/woodlands on private land has been instituted, the implementation is difficult, either because of conflicts of interest, political interferences or lack of human and financial capacity. Therefore, their sustainable management for development and conservation will require strong and incorruptible institutions that will seek a balance between resource exploitation and conservation.

Keywords: Agricultural practices, change-detection, forest/woodland, forest management, land-tenure, political interference, remote sensing

1.0. INTRODUCTION

In developing countries where a large proportion of the human population depends almost entirely on natural resources for their livelihoods, there are increasing competing demands for utilisation, development and sustainable management of the land resources (e.g. natural vegetation), resulting in land-use/cover 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 and Meyer, 1994; Brandon, 2001). The primary cause of land-cover change worldwide is through changes in the way people use and manage land (Dale et al., 2000; Gobin et al., 2001; MEA 2005a). The most potent forces affecting natural vegetation arises from the direct effects of an expanding human population (e.g. habitat destruction for agriculture, human settlement, land for grazing, etc.) and indirect effects (e.g. pollution) (Grime, 1997; UN/ECE, 2002; MEA, 2005b). Hence, land use directly and indirectly influences environmental conditions, which play a major role in landscape change.

Forests worldwide have been disappearing at an alarming rate, with an estimated 86% of the original forest cover already lost by 1993 (WRI, 1994). Total forest area continues to decrease, with each year about 13 million ha of forest lost due to deforestation, particularly in the tropics, mainly as a result of conversion to agricultural land (FAO, 2005; MEA, 2005b). According to MEA (2005b) forests have completely disappeared in 25 countries and another 29 have lost more than 90% of their forest cover. A crucial link between forests and sustainable development has been recognised in the Millennium Development Goals. The area of forest cover is one of the indicators for the 7th Goal - to "ensure environmental sustainability" (Hoare, 2005). But as humans try to meet their daily needs, they are subjecting forests, woodlands, and grasslands to the highest rates of change that have ever been recorded for large regions (Richards and Flint, 1994; Houghton, 1995; FAO, 1996; MEA, 2005b), and Uganda's forests and other natural vegetation types are no exception. Uganda lies within the region in which at least 30% of the landscape (by area) comes under cultivation in any particular year (MEA, 2005a). However, the disappearance of tropical forests is a result of many pressures, both local and regional, acting in various combinations in different geographical locations (Geist and Lambin, 2002). While it is possible to identify with some certainty the factors underlying tropical deforestation in a general sense, it is very difficult to pinpoint a uniform set of drivers/causes and their relative contributions that apply generally at a global or even regional level (MEA, 2005b). Deforestation is a location specific problem, with the effects and magnitude of each identified factor differing between countries and regions (NRC, 1999). Furthermore, a complicated combination of economic and social development factors, levels of agricultural productivity and urbanization, climatic and geographical peculiarities, and historical factors, together determine the rates of deforestation in any particular place (MEA, 2005b).

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. However, these impacts and changes have not been well documented and quantified, particularly for important natural tropical forests such as Budongo Forest Reserve (BFR), the largest forest reserve in Uganda (Plumptre, 1996). BFR is a semi-deciduous forest in the NW, and of considerable value for both biodiversity conservation (with probably the largest wild chimpanzee population in Africa and several threatened plant species), as well as for local livelihood activities. Forests and woodlands are central to Uganda's three national pillars of sustainable development- the economy, society and environment. But according to MEA (2005b), the overall state of knowledge on the condition and changes of forests/woodlands in many regions of the world is incomplete. With the increasing human population in Uganda, both indigenous and migrant, and the shrinking extent of natural habitats, it is important to evaluate the magnitude, pattern and type of land-use/cover changes that are occurring within and surrounding the BFR. These data will help to project the consequences of these changes on the conservation of natural resources, and with appropriate action, contribute to sustainable management (Petit et al., 2001). Furthermore, the increasing concerns for the consequences of both global environmental change and local development have brought land use/cover research to the forefront of the international agenda (Turner et al*.,* 1994; FAO, 1997; Turner, 1997; WRI, 1997; Dale et al,. 2000). The changes in land-use/cover due to natural and human activities can be observed using current and archived remotely sensed data at very high spatial, spectral and temporal resolutions (Luong, 1993).

Over the years, remote sensing has emerged as the most useful data source for quantitatively measuring land-use/cover changes at the landscape scale (Hudak and Wessman, 1998). Satellite remote sensing in conjunction with GIS has been widely applied, and recognised as a powerful and effective tool in detecting land-use/cover change (Ehlers et al., 1990; Meaille and Wald, 1990; Weng, 2002). It can help decision makers to develop effective land management plans (Mongkolsawat and Thirangoon, 1990). Remote sensing and GIS-based change-detection studies can, therefore, be utilised to provide information on how much, where, and what type of land-use/cover change has occurred. Satellite remote sensing provides cost-effective, multi-spectral and multi-temporal data, and turns them into information valuable for understanding and monitoring land development patterns and processes for building land use/cover data sets (Sunar et al., 1996; Weng, 2002).

In this study, land-use/cover changes within and around BFR, were analysed from multi-temporal images and field based studies, with a view to understanding the dynamics of land-use/cover changes, especially deforestation and associated agricultural developments from 1988 to 2004. Multi-temporal analysis of satellite imagery is effective for change detection because there is a high correlation between spectral variation in the imagery and land cover change (Green et al*.,* 1994). The area studied lies between 31°20'-31°50'E and 1°29'-2°0'N. The main focus was on determining patterns of change within two ecologically important land-use/cover types, namely forest/woodland and commercial sugarcane plantations. The time period investigated encompassed the rehabilitation and expansion of the Kinyara Sugar Works Ltd (KSWL), a sugarcane growing and processing factory. Information on land-use/cover changes and their causes/drivers may provide a better understanding of land utilization, and play a vital role in the formulation of policies and programmes required for development planning at both local and national levels. In addition, understanding the function and structure of landscapes, primarily in terms of human impacts, also requires the integration of biological and socio-economic knowledge. Hence, an assessment of socio-economic conditions that local households face was undertaken through field observations, household interviews and key informants.

2.0 METHODS

2.1. Description of study area

Budongo Forest Reserve (BFR), located in Masindi District, North Western Uganda, is situated on top of the escarpment, east of Lake Albert on the edge of the western rift valley, at $1^0 37'$ - $2^0 03'$N, and $31^0 22'$ - $31^0 45'$E. It was gazetted as a Central Forest Reserve (CFR) in 1932, and covers about 825 km^2. The reserve is contiguous with the Murchison Falls National Park to the North, Bugungu Game Reserve to the Northwest and Karuma Game Reserve to the Northeast. On the southern side, it borders villages, inhabited by subsistence farmers of mixed language, culture and nationality. They are entirely dependent on the land resources for their daily livelihoods and income. In addition, there is the developing Kinyara Sugar Works Ltd (KSWL), fully owned by the Ugandan Government, which engages in commercial sugarcane growing and processing. Its out-growers' scheme had a modest start in the 1980s, but has picked up momentum over the years following the rehabilitation of KSWL in 1995. It is aimed at addressing the problems of the rural poor by making them stakeholders in the sugar industry, by growing and selling sugarcane to the factory. The human population of Masindi District nearly doubled between 1991 and 2002, from 260,796 to 466,204, a mean annual growth rate of 5%. For example, the population of Budongo and Bwijanga sub-counties, the closest to BFR, increased from 44,054 to 76,929 (75% increase; NEMA, 1998, 2001; National Population and Housing Census, http://www.ubos.org/fullreport.html).

2.2. Land-use/cover change analysis

To detect changes in land-use/cover, at least two time-period data sets are required (Jenson, 1986). In this study, land-use/cover changes and forest/woodland loss were assessed using two date ortho-rectified, Landsat 742 RGB combination UTM/WGS84 images, one from 1988 (Landsat TM5), the other from 2002 (Landsat ETM7).

Image classification

The typical approach to developing land-use/cover maps with satellite imagery involves defining spectral classes by clustering the image data and assigning pixels into classes (Hlavka et al., undated: http://geo.arc.nasa.gov/sgez/applitech/autoproc.html; accessed 27th Oct. 2004). ERDAS IMAGINE 8.7 image processing software was used for all image data processing. The *Iterative Self-Organizing DATa Analysis Technique* (ISODATA) algorithm was used to perform an unsupervised classification, with Maximum Iterations set at 99, the Convergence Threshold set at 0.95 and the number of classes set at 36. This initial run revealed spectral confusion in some classes of the classified images. Hence, masking out of these land-use/cover classes was implemented. Known areas (based on other reliable sources) were excluded from automatic processing, then "pasted" in later.

A broad level classification was adopted by mainly focusing on the more clearly defined forest vegetation classes and the commercial sugarcane cultivation area as the areas of interest (AOI), aided by information from field surveys and expert knowledge of the region. By restricting the classification to the AOI, which was manually created as a mask prior to unsupervised classification, classification accuracy was enhanced. For each date, the resultant classified image was recoded to its respective classes. A 3 x 3 majority filter was passed once over the resulting land-use/cover images to eliminate noise and to show only the dominant classification.

Classification accuracy assessment

An accuracy assessment of the derived land-use/cover map was also conducted for the classified imagery based on how well it matched observations at sample points on the ground, by employing the positional accuracy method. Using 42 ground-truthed GPS points (32 inside and 10 outside the BFR boundaries) and relating them to what was classified on the images, a statistical test of the classification accuracy of the whole image was performed using the Kappa Index that accounts for chance agreement.

Change detection

The smoothed classified images were then subjected to a post-classification change-detection process. The post-classification approach to change-detection was deemed suitable since the images were from different sensors, taken on different dates and had been independently classified and labelled. The changes in land-use/cover that were recorded included change from forest/woodland to commercial/subsistence agriculture, shifting cultivation to commercial cultivation, and from grassland/woodland to forest.

2.3. Drivers/causes of land-use/cover change

Data on land-use practices, land cover changes, relevant socio-economic parameters, and the perceptions of the households in villages surrounding BFR were determined through field observations, as well as interviews with local residents and key informants. Thirty-eight (38) households and four key informants, namely the District Environment Officer, Local Government District Forest Officer, KSWL Out-growers Scheme Manager and Central Government District Forest Officer were interviewed. Households were selected systematically in order to obtain a representative sample in terms of ethnicity, wealth, gender, and age classes. Semi-structured interviews (SSI) and questionnaire interviews were conducted on an individual basis to minimise peer influence and improve the quality of data (Phillips and Gentry, 1993). The SSI guide served only as a checklist, delimiting the issues to be considered in the interview to ensure that the same information was obtained from a number of people (Inglis, 1992; Chambers, 1994). Key informant interviews were also used to obtain information that would assist in clarifying or improving understanding of particular issues or problems that were raised in the household interviews. The interviews were conducted between December 2003 and January 2004. Human population data for the adjoining villages were obtained from the 1980 and 2002 national population censuses, and utilised to give an indication of the gender, family size, livelihoods and employment situation in the area. Data from interviews were analysed using both descriptive and inferential statistics. A null hypothesis: "*The benefits of the forest to the local people do not* *outweigh the obstacle it poses to their agricultural production"*, was tested by cross-tabulation using Fisher's Exact test in SPSS Ver.13. Surrounding sugar plantations were identified and their sizes, distances along edge and to the boundary of BFR measured. Differences in their sizes, distances along edge and to the boundary of BFR were compared by one-way ANOVA.

3.0. RESULTS

3.1. Land-use/cover changes

The land-use/cover classification clearly discriminated two classes: forest reserve and commercial sugarcane plantations. However, shifting cultivation plots and grassland areas were difficult to clearly discriminate from each other as they had similar spectral classes and were, therefore, recoded into one class. The major land-cover conversions were from forests/woodlands and grasslands to sugarcane plantations, settlements and shifting cultivation. The area under sugarcane increased considerably from 690 ha in 1988 to 12729 ha in 2002, with a concomitant loss of about 4680 ha of forest/woodland (Table 1), all outside the BFR and mostly on the southern part of BFR (Figures 1 and 2). Thus, forest/woodland cover decreased from 57079 ha in 1988 to 52399 ha in 2002, an 8.2% loss in a 14 year period (Table 1). However, the 2002 map shows an increase in forest cover within the northern part of BFR. This increase is probably due to the protection that the nature reserve provides within this area, as well as its greater distance from human settlements. The overall accuracy of the classification was 97.6%, with a Kappa coefficient of 92.7 %.

Table 1. Changes in the major land- use/cover classes around Budongo Forest Reserve between 1988 and 2002.

Land-use / cover type (class)	**Area (ha)**		**Change**	
	1988	**2002**	**Absolute (ha)**	**%**
Forest/woodlands	57079	52399	-4680	8.2
Sugarcane plantations	690	12729	12039	1745
Forest/woodlands loss to cultivation (sugarcane & crops)	-	4680	4680	-

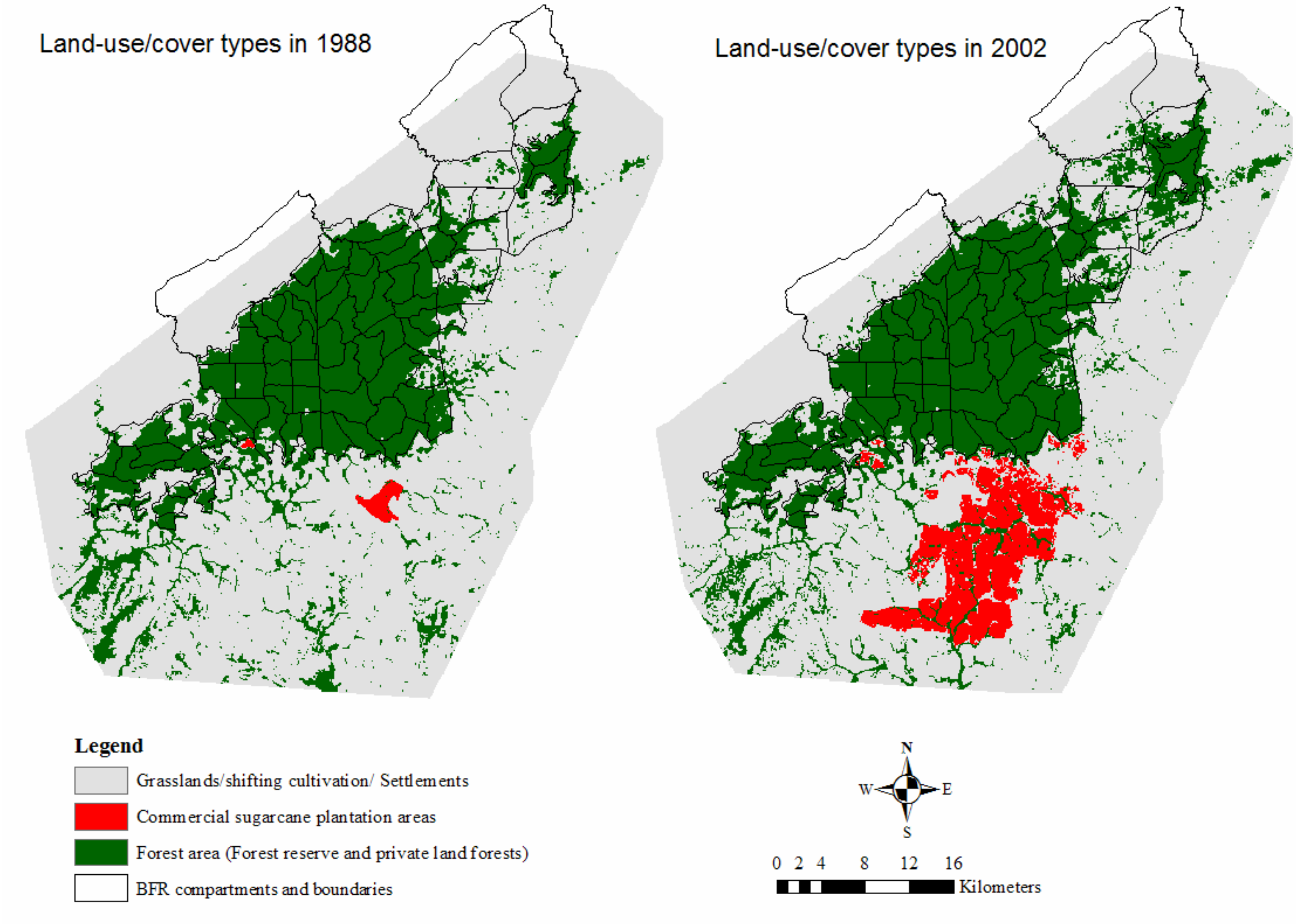

Figure 1. Extent of forest/woodland cover and sugar cane plantations in 1988 and 2002, for the area within, and surrounding Budongo Forest Reserve, NW Uganda

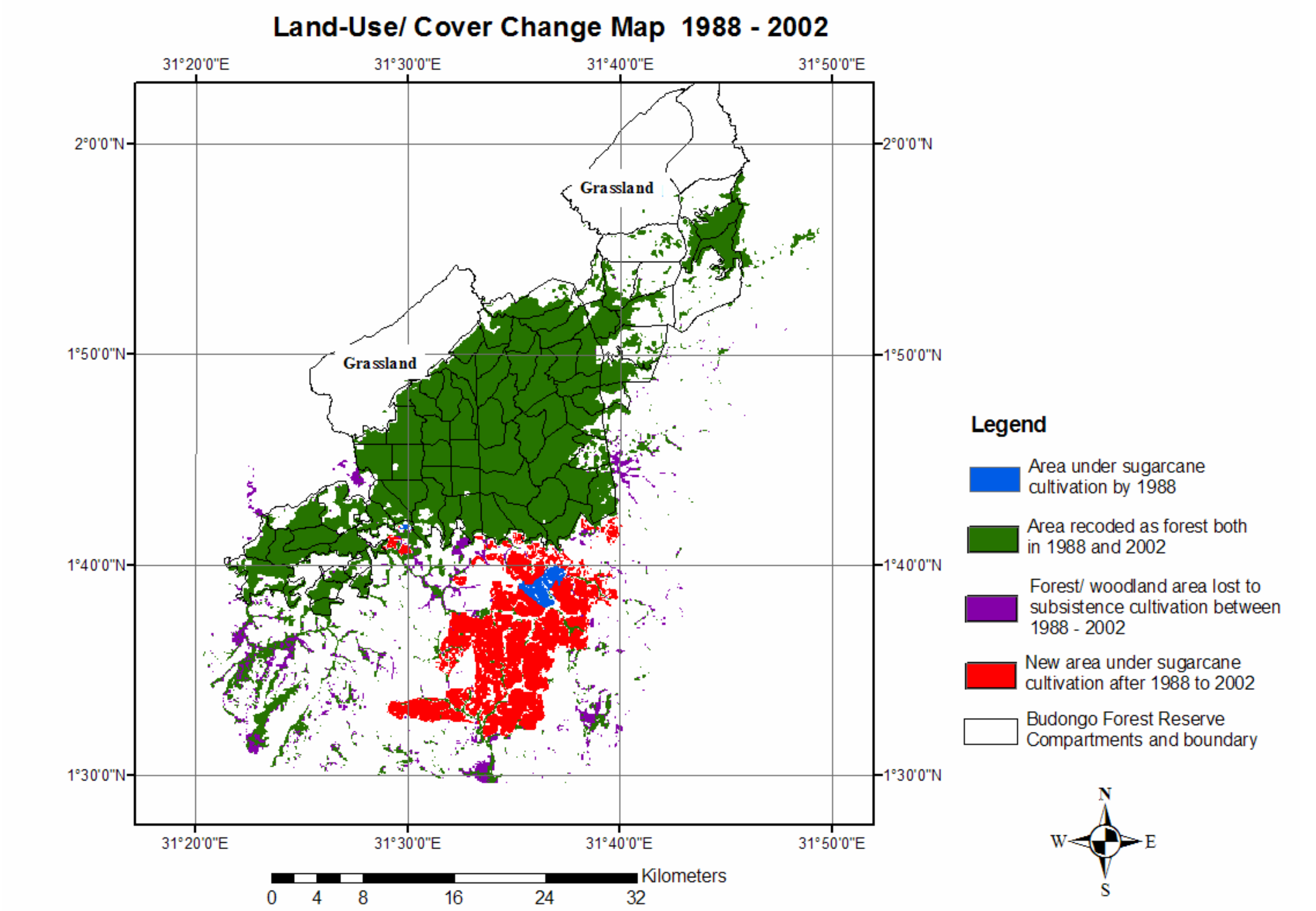

Figure 2. Map of change detection in the major land-use/cover categories surrounding Budongo Forest Reserve, NW Uganda, from 1988-2002.

Field surveys and observations undertaken in 2003-2004 corroborated the image classification analysis results for 2002, and revealed the destruction of woodlands/forests, particularly outside the boundaries of BFR. Records from KSWL showed that sugarcane plantations (including those owned by KSWL and private farmers) on the southern side of BFR increased over 10-fold, from 1368 ha in 1996 to 15347 ha in 2004. In 2004, the out-growers sugarcane plantation area was 5423 ha, about 35% of the total area, further supporting the Landsat analysis results. The out-growers' scheme had a significant expansion between 1995 and 2001, and for example planted about 4560 ha between the 2001/02 and 2003/04 financial years (Figure 3). This increase is due to a strategy adopted by the company to outsource sugarcane production from self-employed farmers (out-growers) having land within a reasonably close distance of 25 km from the factory. No data are available prior to 1996 as a result of national upheaval and the economic decline that resulted in the closure of the factory in 1985, which only returned to production in March 1996. The future expansion of the sugar industry is focussed on the out-growers' scheme. The out-growers state that they each need a minimum of 5-7 ha of cultivated land to make sufficient income to sustain themselves.

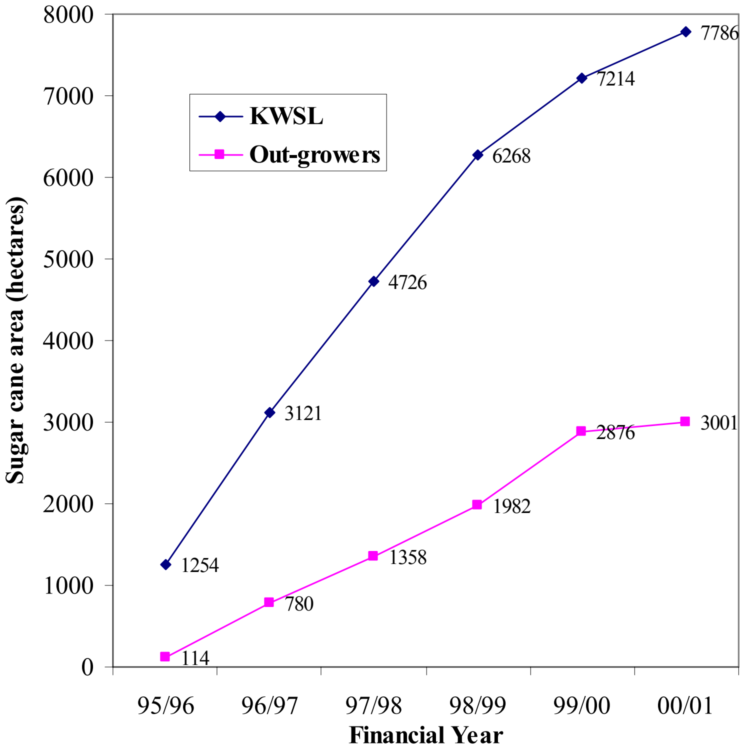

Figure 3: Cumulative sugarcane area planted (ha) by (a) the Kinyara Sugar Works Ltd. (KWSL) and (b) the out-growers scheme, between the 1995/96 and 2000/01 financial years.

Although image analysis for the period 1988-2002 (Figures 1 and 2) showed that the BFR had not been encroached by agriculture, field surveys and observations in 2003-2004 revealed that illegal harvesting of trees for timber was nonetheless, degrading the forest. There were numerous signs of illegal pitsawing, even in the so-called “nature reserve” (no harvesting allowed) part of the forest. In addition, outside the BFR there were encroachments from settlements, as well as sugarcane and tobacco growing at the forest edges.

3.2. Socio-economic issues acting as drivers of land-use/cover changes

Both the local people and key informants were concerned that land-use/cover changes in the area have occurred with the increase in sugarcane plantations and deforestation, threatening the availability of land for further increases in crop cultivation. This change was attributed to a number of factors/drivers, including the rapid human population increase, which is associated with agricultural expansion (e.g. commercial sugarcane and tobacco growing, subsistence crop cultivation), unclear land tenure, and political interference in the management of forests/woodlands on both private and gazetted reserves.

3.2.1. Agricultural expansion

Agriculture is the main land-use practice and the main source of income for the local population and, consequently, for the local governments in terms of tax. According to both the local communities and the key informants, commercial sugarcane and tobacco growing are the primary economic activities, followed by maize cultivation. In 2001, sugarcane farmers recorded a net annual income of about Uganda Shs. 600,000/ha, equivalent to US $351/ha. Field surveys (2003/4) revealed that the out-growers’ sugarcane areas were expanding so fast that plantations were being established close to the BFR boundaries, with little or no buffer zone between the two on the southern part of BFR (Table 2). The expansion of the sugarcane plantation area is primarily due to the introduction and strengthening of the out-growers scheme, with soft loans and ready market incentives. Distances of adjoining plantations from the BFR boundary ranged from -1 (one metre inside the forest) – 30 m, while distance along the boundary ranged from 30-1440 m.

Table 2. Extent and size of sugarcane plantations along the Budongo Forest Reserve (BFR) boundary from a 2003 survey. All the villages surveyed are located on the southern side of the BFR.

Village	*Number of surveyed plots*	*Size (ha) (mean ± SE)**	*Distance (m) from forest boundary (mean ± SE)**	*Distance (m) along forest edge (mean ± SE)**
Kyarugangara	2	4.7±0.7	5.0±0.0	155.0±45.0
Kirema	9	3.4±0.9	4.4±1.8	181.3±38.9
Kiswata	1	9.4	5	300
Kijaikwe	5	5.0 ±0.1	12.0±7.3	274.0±74.7
Kapeka II	6	3.2±0.6	4.0±1.0	215.7±71.8
Kapeka III	7	4.7±2.9	4.3±0.7	188.6±68.8
Wafala	7	1.9±0.1	3.9±0.4	91.4±9.6
Nyabyeya II	2	1.2±0.2	6.0±4.0	110.0±10.0
Kanyege	1	65.3	-1	1440
Total	**40**	**207.8**	**-**	**7960**

**Size of sugarcane plantations, their distance from BFR boundary, and distance along the BFR edge were not significantly different among the villages (ANOVA, p >0.05).*

Of 40 surveyed sugarcane plantations, totalling 208 ha, 9 (30 ha in total, and each with 100 - 550 m of forest edge) were 0 m from, and 2 were 30 m from the boundary, while 2 were 1 m inside the BFR boundary. Generally, many of the sugarcane plots covered long distances along the forest edge, with 32 (80%) being ≥100 m in length along the boundary. However, among the nine villages surveyed, there were no significant differences for the plantation sizes (p = 0.649), their length along the forest edge (p = 0.305) and distance from the BFR boundary (p = 0.572). These results suggest that many of these plots were established within what was previously a buffer zone between the agricultural areas and the BFR. Given the increasing shortage of land in the region, it is likely that all remaining strips of land adjoining the forest will be converted to agriculture. Instead of using fertilizers, tobacco farmers resort to clearing forest/woodland patches every other growing season in the belief that they are more fertile than the already cleared agricultural land and to avoid buying fertilizers. This has resulted in the loss of numerous forest and woodland patches, particularly outside BFR, but also sometimes even within remote parts of BFR. Farmers also destructively cut down whole palm stems (*Raphia farinifera*) in BFR to access branches to peel off the woody material used in the drying of tobacco leaves.

On the question of whether land available for cultivation expansion has been decreasing over the years, about 55% of the 38 respondents were affirmative, concurring with all the key informants, while 24% had no comment. To alleviate land shortage for agriculture expansion, they made a number of recommendations that interestingly included providing part of BFR for agricultural expansion (Table 3). Yet, they recognised that the forest offers them benefits, which they ranked on the basis of importance in the order; rainfall catchment (60.5%), building materials (15.8%), commercial timber (7.9%), and wood-fuel (7.9%) (Figure 4). No respondent ranked water catchments, furniture materials or wild fruits as the most important benefit from the forest. A cross-tabulation (Fisher's exact test) of the forest benefits and responses to the question: whether the presence of a forest near the homestead was a threat to agriculture, revealed that actually the benefits do not outweigh the threats ($p = 0.53$). This suggests that agriculture is more valued than forest conservation, even if it may contribute to rain-fed agricultural productivity.

Table 3. Local people's suggestions/recommendations for alleviating the decreasing land availability for agricultural expansion and settlements.

Suggestions/recommendations	Responses (% of respondents; n=38)
1. Find land elsewhere	15.8
2. Provide part of the Budongo Forest Reserve	10.5
3. Population control (e.g. through family planning)	7.9
4. Employ better methods of farming and modernise agriculture	7.9
5. No comment	50.0

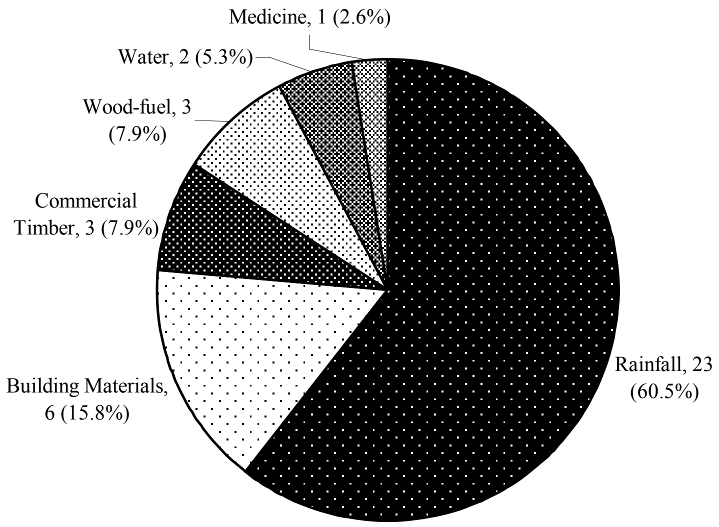

Figure 4. Number of respondents ranking each selected forest benefit as the most important to them (percentage of respondents (n = 38) in parentheses).

3.2.2. Population increases

The 38 households interviewed constituted a total of 305 people, with an average of 8 (±0.81*SE*) and a range of 2-25 people/household, and hence, large families. Local respondents and key informants concurred that the local human population in the area has increased over the years. Comparisons of the 1990 and 2002 census data showed dramatic increases, ranging from 135 to 835% for the villages on the southern part of BFR and within a radius of 25 km from KSWL. The highest increase of 835% was for the villages Bulyango I & II, which are close to the factory, and where most of the casual labourers for the factory live. Of the 38 household heads, 14 (36.8%) had settled in the area between 1988 and as recently as 2001, 7 (18.4%) were already resident prior to 1988, while 17 (44.7%) did not respond. The two major reasons cited for settling were (a) finding fertile land for agriculture (32.4%) and (b) employment (18.4%).

Of the 305 people in the 38 interviewed households, 51.5% were males and 48.5% females, with low levels of education, lack of employment opportunities and all relying mainly on agriculture for subsistence and monetary income to meet their daily needs. Even for the 15.8% of the respondents that had some sort of formal employment (all males), they practiced subsistence agriculture, because their salaries are insufficient to support all their household needs. Among them are primary school teachers, builders and KSWL casual workers, none of whom are paid substantial salaries, lack social benefits and are faced with increasing food prices due to the promotion of sugarcane production instead of traditional food crops. Alternative sources of income were pitsawing (2.6% of the respondents), charcoal burning (5.3%), bee-keeping (2.6%), and formal employment (2.6%). Others were rattan cane and pole harvesters, with BFR being the main source. However, the number obtaining income from pitsawing may be higher than reported as many may be doing it illegally. Hence, there are few alternative sources of monetary income for the local population in the area, and two of those mentioned above are entirely reliant on woodlands and forests.

3.2.3. Land tenure system

On the southern border of BFR, the major land tenure systems are leaseholds and freeholds, with very little customary land, as most of the population is immigrant. The leaseholds are mainly held by Indians, most of whom are absentee landlords. Of the 38 households, 8 (21%) explicitly stated that they were squatters who actually had no legal ownership right over the land. Though the rest of the households claimed ownership of the land they occupied, they were not clear on the type of land tenure they possessed, and indeed, it is also possible that some of them might not actually have legal ownership. It was also noted that the local people did not clearly know the position of the forest reserve boundaries.

3.3.4. Management, regulation and enforcement

Local respondents were aware that rules and regulations pertaining to the use of the forest reserve do indeed exist. Considering whether a permit is required in order to harvest/extract some forest products, 37.7% responded ‘yes’, 48.8% ‘no’, while 13.5% had no comment. Agricultural encroachment, illegal pitsawing, charcoal production, and pole and rattan cane harvesting were cited as the major threats to the conservation of forests and woodlands in the area (Table 4). Interestingly, one respondent cited poverty as the major threat.

Table 4. Local people's perceived threats to the sustainable management of communal forests/woodlands and Budongo Forest Reserve, NW Uganda.

Threats	**Responses (% of respondents; n=38)**
Illegal pitsawing and pole cutting	92.1
Agricultural expansion and encroachment (e.g. tobacco and sugarcane growing)	31.6
Charcoal burning	15.8
Poaching and hunting	10.5
Poverty	5.3
Rattan cane harvesting	5.3
Unsustainable resource harvesting	5.3
Fires on forest edges	2.6
Lack of sensitization to protect forest/woodlands	2.6
Lack of tree planting	2.6

On the major challenges to forest/woodland management, key informants cited the increased immigrant human population as leading to forest encroachment, illegal pitsawing (in BFR), political interference, as well as the limited capacity (manpower and financial resources) to enforce by-laws. Confiscated timber planks were observed in a local leader's house, indicating a lack of collaboration with the Forest Department to help stop illegal activities. Although there are legal instruments, through the local government councils to enact by-laws, no legal protection of woodlands/forests on private/communal lands around BFR occurs. Key informants stated that the best institutional/organizational arrangement for the management of forests in order to benefit both local people and meet conservation requires the involvement of the District Council and the Forest Department, which both have the structure and capacity. For the communal forests/woodlands, it was suggested that NGO's be mandated, as they have the capacity to mobilise the local people.

4.0. DISCUSSION

4.1. Land-use/cover changes

The land-use/cover changes involving a decrease in vegetation cover corresponded to patches of deforestation and sugarcane plantations, and were outside and at the boundaries of BFR. Similarly, studies from other parts of Uganda report that the extent of forest decline is much greater outside permanent forest estates, due to changes in land use/cover from tropical forest or savannah woodlands to cultivated and/or grazed land (Plumptre, 2002). With agricultural expansion being the major driver of deforestation in the area, our findings are similar to those from other parts of the world. Agricultural expansion is by far the leading land-use change associated with deforestation in Asia, Africa and Latin America (Geist and Lambin, 2002, MEA 2005a, b). Based on aerial photographs, Campbell et al. (1993) noted that deforestation in Zimbabwe had been largely a result of clearing land for cultivation. Similarly most of the deforestation in Tanzania stems from activities related to agricultural expansion and harvesting for wood-fuels (Bagachwa et al., 1995). Anthropogenic factors, which favour arable land-use, are reported to be the drivers of change on the South Downs landscape, United Kingdom **(**Burnside et al., 2003).

4.2. Land-use/cover change drivers

Presently, in the study area, sugarcane growing is highly preferred to other traditional crops and forests with a long gestation, as it is profitable and more economically valuable. The valuing of agriculture over forest conservation shows why forests/woodlands, particularly outside the BFR, are being converted into sugarcane plantations. Thus, these land-use/cover changes are the result of landowner decisions and reflect the ranking of possible land-uses in the area. Similarly, studies elsewhere indicate that ecological dynamics in human-influenced landscapes are strongly affected by socio-economic factors that influence land-use decision-making (Berry et al., 1995). Kajembe et al. (2005) noted that people carry out activities that degrade forests/woodlands because of the high economic benefits they obtain from such activities. They often see little immediate economic gain from conserving forest/woodland resources or assuring their sustainable utilization. Increases in prices of agricultural produce (Angelsen et al., 1999; Angelsen and Kaimowitz, 1999; Chipika and Kowero, 2000), fertilizers (Barbier and Burgess, 1996), and export goods (Reed, 1989) may also lead to an increase in areas under cultivation, probably resulting in more deforestation. For example, in Sudan, increased producer prices of export crops encouraged woodland clearing for crop cultivation, resulting in significant deforestation (Stryker et al., 1989).

Although the expansion in sugarcane growing has had some positive impacts for rural development, such as improved road infrastructure and household income, it has also had attendant negative impacts. Plantation sugarcane growing conflicts with other agroforestry practices, as standing trees are usually removed in a plantation. Yet, KSWL does not cover afforestation among its environmental protection and rehabilitation initiatives. Road construction is reported to play a crucial role in deforestation as it provides access to previously inaccessible forest areas (Dudley et al., 1995; Bryant et al., 1997; MEA, 2005b) and in the case of BFR, probably facilitates illegal harvesting of timber and palms for tobacco drying. In a study of the causes of deforestation based on analysis of economic models, Angelsen and Kaimowitz (1999) concluded that more roads, higher agricultural prices, lower wages, and shortages of off-farm employment generally led to more deforestation. Similarly, our study area was characterised by such socio-economic conditions, as alternative sources of income are very few and most of the employment is on farms with low wage returns, that are also important for developed countries. For example, Allison and Hobbs (2004) report that in the Western Australian agricultural region, land-use/cover changes and ensuing natural resource degradation are rooted in the economic, demographic and social changes that link variables in the ecological system to those in the social system.

Increasing human population

The increasing human population in the villages adjoining BFR is also leading to deforestation as both the immigrants and indigenous people seek to expand land for food crops and tobacco cultivation and settlements. It is currently estimated that over 100,000 people, mainly non-indigenous, are living in Uganda's forest reserves, with Masindi District, in which BFR lies being the most affected (The NewVision Newspaper, 19th May, 2005). The occupation of tropical rainforests by large- and small-scale non-indigenous resource users often leads to widespread deforestation and resource depletion, primarily because the productive choices of the people concerned often require replacing the forest/woodland with other land-uses (Sierra, 1999). A study by Place and Otsuka (2000) similarly revealed that population pressure, market access and land tenure are important factors affecting land use and resource management in east-central Uganda. Similarly, deforestation continues to accelerate in tandem with poverty and high levels of population growth in many parts of the developing world (MEA, 2005b).

Land tenure system

The Uganda Constitution of 1995 and the Land Act of 1998 spells out four general legal land tenure systems namely: customary, freehold, mailo and leasehold land. Thus all land is owned, including the trees growing on it, whether government or private land (The Uganda Forestry Policy 2001). This has various management implications for the forest/woodlands depending on the nature of ownership and management goals. Deliberate protection of forests/woodlands on private lands in the study area, particularly those with absentee landlords, has not been seriously addressed due to unclear ownership and lack of secure tenure, resulting in deforestation. Whereas absentee owners tend to use land less intensively and manage tree resources less effectively (Place and Otsuka, 2000), it is widely accepted that the resource-use strategy of recent migrants in tropical rainforests results in extensive deforestation and other negative environmental impacts (Sierra, 1999). In other parts of Uganda, customary land tenure institutions have been found to provide strong rights in agricultural land, but are relatively weak in collective management of other resources, such as woodlands (Place and Otsuka, 2000). They also report that conversion of land for agricultural use is greater under the customary tenure system. Similarly in the Ivory Coast, the lack of a consistent and secure land tenure system contributed to deforestation to a greater extent than the effects of price increases of export goods (Reed, 1989). Studies of land cover change in forest-dominated landscapes in the USA (Spies et al., 1994; Turner et al., 1996) and Brazil (Dale et al., 1993) also demonstrated that land ownership greatly affects landscape dynamics. Thus, land ownership is an important determinant of landscape pattern (Gobin et al., 2001), and security of tenure is important in shaping who uses land resources and how.

Management, regulations and enforcement

Worldwide, societies have rules to protect the collective welfare from harmful actions perpetrated by individual members of society. However, the successful implementation of these rules will depend on an enabling environment, the willingness of all stakeholders to uphold them and reflection of societies' conscious and unconscious ideologies entrenched through history. In Uganda, Environmental Impact Assessment (EIA) is a legal requirement for any large scale development project. However, the establishment of sugarcane plantations in the study area has not been subjected to an EIA. Yet, this type of agricultural practice has serious implications for the environment. This illustrates that despite the presence of strong environmental and supportive policies and legislation (e.g. The National Environment Statute, 1995; The Land Act, 1998), the present land-use pattern in the area is quite haphazard and results in poor management and degradation of the environment. The lack of a buffer zone between the forest reserve (the only alternative in the area for the conservation of wild plants and animals) and sugarcane plantations is resulting in direct conflicts between the local farmers and important forest wild animals, particularly the chimpanzees. One of the habituated chimpanzees was killed in 2003 as it strayed into an adjoining sugarcane plantation in search of food, and a number of them have been injured by snares set by local hunters and farmers (BFP report, 2003). It is, therefore, necessary to establish and maintain a buffer zone- an area around or adjacent to the protected area, where a harmonious relationship between the natural environment and people is promoted (Brown, 1992). Buffer zones have had positive impacts in some parts of the world where they have been implemented. For example, land degradation around forest patches in Maribios, Nicaragua was halted when locally formed co-operatives integrated trees into the land-use system in various ways (Sayer, 1991).

The encroachment into BFR by migrants and illegal timber harvesting is happening with some encouragement by corrupt authorities in the local administrative councils. Similarly, Banana et al. (2004) attributed the decline in forest conditions in Mpigi District between 1994 and 2000, among other factors, to corruption by local government officials, as they allowed powerful individuals from within and outside the community to illegally harvest timber. The mapping of frontier forest according to "risk of mismanagement" from corrupt behaviour places Uganda in the High Corruption Level category (Bryant et al., 1997; Transparency International, 2002). The correlation between corruption and forest crime is believed to be remarkably high in many countries (Contreras-Hermosilla, 2001), and in most parts of Africa, corruption whether petty or grand, is a major force undermining environmental equity and destroying ecosystems (Mock, 2003). For Uganda, corruption in the forest sector seems to have been aided by the central government's retrenchment policy of the 1990's that greatly reduced the Forest Department's manpower (i.e. forest rangers, forest guards, patrol persons, etc.) on the ground to monitor and guard the forest (Muhereza, 2003). Furthermore, in Uganda at present, the need to access resources to alleviate poverty out-weighs the desire to conserve natural resources, while political interests out-weigh the need to follow the approved laws and regulations. This has been a serious impediment to management, particularly where the demand for natural resources to sustain livelihoods is acute, since 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). There is also a misconception among Uganda's politicians that the country needs "development" and cannot afford the luxury of protecting nature's ecological processes. They tend to identify development merely with sectoral growth, ignoring the underdevelopment introduced in related sectors through negative externalities and the related undermining of the productivity of the ecosystem (Shiva, 1991). As a consequence, a number of reserves (e.g. Butamira, Namanve, and Kalangala Islands Forests), which were public land, have been degazzetted by the directives of the President to give way for agricultural expansion by the so-called investors. Thus, in 2001, Butamira Forest Reserve was allocated to Kakira Sugar Works Ltd to grow sugarcane, while in 2002 some of the Kalangala Island forests were also degazzetted and allocated to BIDCO, an edible oil processing company to plant palm oil trees. As recently as 2006, there has also been a push by the Mehta Group and government to degazzette part of Mabira Forest Reserve so that the Mehta Group can grow sugarcane. Such moves are more likely to be a disincentive to local communities and NGO's to actively participate in the sustainable management of Uganda's forests and woodlands, particularly those on public land.

Whereas there have been attempts to decentralize the management of forests/woodlands in various parts of the country, it would not be advisable for BFR with its high biodiversity value. Completely decentralising management of such a forest reserve runs the risk of degradation as local councils are more interested in short-term revenues than biodiversity issues, and are often reluctant to reinvest revenues into forest resource management. For example, significant loss of forest/woodland cover has occurred in local forest reserves that were returned to the Bunyoro-Kitara Kingdom within Uganda, who were more interested in monetary income rather than sustainable harvesting (Muhereza, 2003). In addition, with over 70 of the local communities around BFR coming from elsewhere in the country (mainly Nebbi, Arua, and Lira districts) and the Democratic Republic of Congo (DRC), few consider themselves residents, and many plan to return to their original homes in the future. Hence, they are not interested in the long-term planning and management of the forests/woodlands. In this case the involvement of the Forestry Department, a central government department, to resolve conflicts between forest users who have differing objectives and temporal needs is necessary. In his analysis of forest policies and legislation in Uganda, Banana (2005) revealed that neither the top-down protectionists nor the decentralised co-management approaches have been uniformly effective in averting threats to forest resources. Similarly, case studies on forests in Kenya and Tanzania have reported both success and failure in halting resource degradation under decentralised management. Ongugo and Njuguna (2004), in decentralised forests in Kenya, showed that despite the efforts and good intentions of decentralization in the Forest Department, conditions of many forests continued to be poor. In contrast, Kajembe et al. (2005) revealed that community forest-based management (CBFM) in Duru-Haitemba, Tanzania, had a positive impact on the resource base, while joint forest management (JFM) at Kwaizu Forest Reserve did not as illegal activities were still rampant and deforestation is increasing. They suggested that the success at one site and relative failure at the other was probably linked to the type of ownership of the resource and the law enforcement mechanism.

5.0 CONCLUSIONS

This study provides comparative estimates of land-use/cover types and changes in area adjoining BFR. Land-use/cover was found to have changed significantly, from 1988 - 2002, in particular the areas of woodlands/forests outside the BFR have been decreasing (8.2% loss between 1988 and 2002), while area of sugarcane plantations and subsistence agricultural fields have increased substantially (over 17-fold between 1988 and 2002). A number of socio-economic factors, including human population increases, insecure land tenure, inappropriate economic policies, conflicts of interest, lack of alternative sources of income, and weaknesses in the legal and policy framework, are causes/drivers of land-use/cover changes in the area.

As commercialization of sugarcane and tobacco growing increases in importance, the value of productive land and incentives to increase yields will continue to increase, resulting in further loss of natural vegetation, and reduction of land available for food crop cultivation. This might also have crucial consequences for food security and nutrition for the local population. The continued loss of tree cover on private/communal lands leaves the managed BFR and neighbouring forest reserves as the only places for the conservation of wild plants and animals in the region. However, their conservation is threatened as they are viewed as the only major source of building materials, commercial timber and non-timber products by inhabitants of surrounding villages and areas afar. Yet, the poverty and political interferences are major challenges to the management of woodlands/forests in the area. Therefore, strong institutions that can withstand conflicts of interest and a political will to manage sustainably the forests/woodlands in the area for development and conservation are required. Since Uganda's woodlands/forests continue to be converted to other land-uses (e.g. agriculture and charcoal burning), while socio-economic disparities keep increasing, there is need for a continuation of monitoring BFR and the surrounding areas. Future studies should consider more recent changes and also attempt to assess the changes within the interior of the forest at a finer scale of resolution (given the expected improvements in technology) as it faces increased selective timber and pole harvesting. Research is also required to aid the integration of aspects of the livelihoods of local rural people with both conservation and landscape process planning, particularly because BFR is of prime importance for the conservation of plants and primates, particularly chimpanzees.

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CHAPTER 3

Plant community patterns in a semi-deciduous tropical rainforest, north-western Uganda

Abstract

Forest plant community types were classified and described based on two data sets from the Budongo Forest Reserve (BFR) in Uganda, a semi-deciduous tropical rainforest; and related to soil variables and historical management practice types employing multivariate analytical techniques. The first data set contained information on species basal area, while the other data set featured abundance for woody plants of stem diameter ≥2.0 cm. Four forest community types: *Pseudospondia*s *microcarpa* Swamp Forest, *Funtumia elastica–Pouteria altissima* Forest, *Lasiodiscus mildbraedii–Khaya anthotheca* Forest and *Cynometra alexandri–Rinorea ilicifolia* Forest were distinguished. Groups of species characterise particular forest communities, however a considerable number of species is shared among these communities. The first two forest community types and the last one were clearly distinguished along a soil nutrients (i.e. OM, Na, N, Ca, Mg, and Si) gradient, hence, corroborating the canonical correspondence analysis (CCA) results. For the species basal-area data, Axes 1 and 2 of the CCA, explained 18% in species, and 34% of the variance in species-environment relations. Whereas, for the abundance data the amount of information accounted for by the first two axes was 25% and 44%, in species variance and species-environment relations, respectively. Axis 1 of CCA was strongly correlated with soil nutrients, while Axis 2 was correlated with logging and arboricide treatment. Hence, we interpret axis 1 as an edaphic gradient, while axis 2 is depicting an anthropogenic disturbance gradient. In general CCA of the species composition clearly separated the communities revealed by the cluster analysis. In conclusion, the present pattern of forest community types in BFR is a reflection not only of the site conditions as evidenced by the edaphic and abiotic factors, but also the history of anthropogenic disturbances.

Abbreviations: ANOSIM – Analysis of Similarity, BFR – Budongo Forest Reserve, DRH – diameter at reference height, SIMPER – SIMilarity PERcentage

Key words*: ANOSIM, arboricide treatment, CCA, cluster analysis, logging, SIMPER, species diversity, tropical semi-deciduous forest*

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

1.0. INTRODUCTION

Biological communities are frequently exposed to environmental changes that cause measurable responses in the properties of the community such as composition and structure (KLUG & COTTINGHAM 2001). Plant species differ in their tolerance to and requirements of environmental factors so that their distribution or abundance varies along environmental gradients (SWAINE 1996). The gradients in plant abundance associated with physical gradients may be different for each species, creating a vegetation mosaic of populations integrated across the landscape (PATTEN & ROBIN 1995). Forest plant communities are largely influenced by the dominant species, hence, the largest and the most abundant woody species may serve as a good proxy for understanding the structure and dynamics of a plant community as a whole (EYRE 1980). An understanding of the association of a particular species with other species further helps to explain the distribution of that species (THRASH 1998), whereas the description of patterns of species distributions is an important step in generating hypotheses (JONSSON & MOEN 1998). Such knowledge is therefore very important in the management of ecosystems of high environmental and wild animal conservation value such as the Budongo Forest Reserve (BFR) in north-western Uganda (see TWEHEYO 2003).

However, the long-term survival of the wild animals in BFR requires the development and implementation of management practices (and strategies) based on the conservation of habitats suitable for a variety of animals. This requires a clear understanding of the structure and dynamics of the forest community types (SAGERS & LYON 1997). The knowledge of the BFR forest community types has been, however, limited, relying only on broad and much generalised descriptions (EGGELING 1947, LANGDALE-BROWN et al. 1964, HOWARD 1991). EGGELING (1947) classified the vegetation of BFR into four forest types, the *Cynometra* Forest, the Mixed Forest, the Colonising Woodland, and the Swamp Forest. He classified the first three forest types following a successional gradient. Previous classification schemes did not incorporate an understorey component and relied only on the overstorey dominant tree species (≥10 cm DBH). Yet, some woody plants with a dbh much lower than 10 cm (that may be treelets), may contribute significantly to the overall species diversity, and influence forest composition and structure (PITMAN et al. 2001). Indeed studies that have employed a <10 cm dbh in the sampling of woody plant alpha diversity in tropical forests have shown that forest woody diversity is substantially contributed to by treelets (see VALENCIA et al. 1994, GALEANO et al. 1998, Chapter 4). In addition, whereas some studies have looked at the influence of environmental factors on the distribution of plant species (including WALAGA 1994, SHEIL 1996, and EILU et al. 2004), there has not been consideration of soil nutrients such as for instance silicon.

Over the last three decades BFR has become increasingly affected by rising demands for timber (SHEIL 1996), wood-fuel, building materials, animals, and for other non-timber products such as rattan canes (TURYAREEBA 2000), and land for agriculture (Chapter 2). Much of BFR has also been silviculturally treated by planting some favoured tree species (including *Khaya* and *Entandrophragma*) or poisoning 'unwanted' ones such as *Cynometra alexandri* (SYNNOTT 1985), cutting and control of lianas, creepers and other impeders (e.g. *Ficus* spp.; DAWKINS 1955, SHEIL 1996). It has also been argued that the present structure, diversity and dynamics of a forest are determined by both physical conditions and chance factors

(CONNELL 1978, DENSLOW 1980, MASAKI et al. 1999). Indeed, local biotic and abiotic ecological interactions strongly influence ecological processes and have long been focussed on to explain the distribution patterns of plant species (TURNER 1989, VERHEYEN & HERMY 2001). Therefore, the vegetation classification generated by EGGELING (1947) and LANGDALE-BROWN et al. (1964), representing plant community types defined by a qualitative inventory of dominant tree species rather than by quantitative data from the entire local flora, may not adequately explain the current vegetation of BFR.

The aim of the study was to carry out an exploratory analysis to classify and describe the main forest community types of BFR, and to relate the community types to soil variables and historical management practices types, using multivariate analysis techniques. The relative influence of edaphic and anthropogenic factors on the plant species and plant communities in BFR was targeted. The classification and description of the main forest types enables a better understanding of the driving variables involved in the natural reforestation process (NANSEN et al. 2001). This understanding can contribute to setting an ecological framework to guide utilisation and restoration, and implementation of suitable management strategies for BFR.

2.0. MATERIALS AND METHODS

2.1. Study area

The BFR is an equatorial lowland tropical rainforest, with some areas protected as a nature reserve. The forest is situated between $1^0 37'$ and $2^0 03'$ N and $31^0 22'$ and $31^0 45'$ E, has an area of 825 km^2 and average altitude of 1050 m, and belongs to the lowland rainforest subformation (see Eggeling 1947). It is broadly classified as mid-altitude semi-deciduous moist tropical rainforest, since several of the dominant trees (incl. representatives of the genera *Celtis, Maesopsis* and *Ficus*) are at least briefly deciduous (EGGELING 1947, LANGDALE-BROWN et al. 1964), with a noticeable exception of *Cynometra alexandri* (SHEIL 1996). The deciduous habit is noticeable during the two dry seasons of the year (June–August, December–February). According to SHEIL (1996) the canopy trees are generally high and emergent stems occasionally reach over 60 m. BFR has a generally wet climate, with a monthly mean rainfall of 138.5 ±66.7 mm. It has a relatively constant minimum temperature with a monthly mean of 20.86 ±0.9 °C (TWEHEYO 2003). It is the largest forest reserve in Uganda, covering about 825 km^2, 53% of which is continuous tropical forest, while the remaining area of the reserve comprises grasslands (HOWARD 1991).

Like all Uganda's natural forest reserves, BFR is managed primarily for economic, conservation and environmental benefits. It was planned to be sustainably managed from the start of mechanical logging operations in the 1920's. Consequently, a number of management plans have been carried out. The management operations have included logging (both mechanical and pitsawing) and a refining operation using arboricides (e.g. 2, 4, 5-trichloro-phenoxyacetic acid and 2, 4-dichloro-phenoxyacetic acid) during the 1950's and 1960's aimed at killing trees that were regarded as "weed species" (PLUMPTRE & REYNOLDS 1994). Therefore, most of the forest's compartments have been treated with arboricides, and today some

77% of the forest has been more or less logged at least once, except for a few that from the onset were set aside to be left untouched and managed as nature reserves.

2.2. Field data collection and laboratory analyses

2.2.1 Vegetation data

The forest was stratified into four forest types as identified by HOWARD (1991) and using data on historical management practice types. The forest types are dominated by *Khaya, Celtis, Senna,* and *Cynometra*, respectively. Within each forest type hilly landscapes were located for the establishment of transects. Transects were widely laid to capture all the historical management practice types, and to cover as much variation in each assumed community type as possible from valley bottoms to ridge tops to enable the sampling of various slope and topographic positions. A rectangular 50 m x 100 m (0.5 ha) plot consisting of five contiguous (50 m x 20 m) sub-plots was employed for vegetation sampling. Along each transect at least three 0.5 ha sampling plots were laid, following topographic position categories, such as lower slope (swamp), mid-slope, upper-slope, and flat/ridge top. The sampling plots were oriented at right angles to topographic gradients with the long side parallel to the contour. For each plot the historical management practice type was recorded on a presence/absence (1 or 0) scale. A total of 32 plots, 6 in the nature reserve areas, 19 in logged and arboricide treated, and 7 in logged but not arboricide treated areas were laid. The variation in the number of plots per historical management practice type is related to the corresponding size of the area in the forest.

Within each plot the identity of each woody species, number of individuals with ≥2.0 cm stem diameter (hereafter referred to as DRH: diameter at reference height) were recorded and measured. We adopted DRH instead of the usual diameter at breast height (DBH), because of the differences in growth habit and stem irregularities for most individuals. We used 2.0 cm as the minimum stem-diameter cut-off to include more species, as many of them rarely exceed a 10 cm stem-diameter at maturity. Indeed, woody plant species diversity and richness in BFR is substantially contributed to by treelets (for definition see VALENCIA et al. 1994) and shrubs that rarely attain a stem diameter size of ≥10 cm (Chapter 4). Diameters of all canopy tree and pole stems were measured at breast height (1.3 m above the ground), unless there were irregularities at this height, using a diameter tape. For trees with large buttresses or prop roots, their diameters were measured above these protrusions. Basal area per stem was calculated as $\pi\ (DRH/2)^2$, on the assumption that stem cross-section area is a circle (IBARRA-MANRÍQUEZ & MARTÍNEZ-RAMOS 2002). For each shrub, all stems were counted, the diameter of 3 “average” stems measured and then used to extrapolate the composite DRH value of the whole shrub to enable the computation of its basal area in the same manner as done for the trees. The values of the basal area for each taxon sampled were used in both the classification and ordination analyses. Initial plant species identification was done in the field with reference to plant identification guides (HAMILTON 1991), the Flora of Tropical East Africa (POLHILL 1952 and subsequent volumes), and the help of an expert. Trees were identified using a combination of characters, including general growth form, bark texture, slash colour and smell, occurrence of exudates as well as leaf traits (WHITE 1994). Specimens of shrubs and trees which could not be confidently identified in the field were sampled and subsequently identified in the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda.

2.2.2. Soil variables

Soil cores (samples) were collected with a soil auger (2 cm diameter, 15 cm deep cores) from 10 randomly chosen locations within each of the 0.5 ha samples and placed into polyvinyl bags, then bulked, and sub-sampled, air-dried, cleaned by removing stones and root fragments, and finally passed through 20 mm and 2 mm sieves. The pH of soil was determined in a 1:1 soil-water suspension using the Glass Electrode Method (MCLEAN 1982), while organic matter (%OM) content was indirectly estimated through the determination of the organic carbon (C) content by the Walkley-Black procedure (NELSON & SOMMERS 1982), and total nitrogen (N) was determined by the Kjedahl method (BREMNER & MULVANEY 1982). Analyses for % organic matter, pH, and total N were performed by the Soil Science Department Laboratory, Makerere University, Kampala, Uganda. The major (e.g. Na^+, K^+, Mg^{2+}, and Ca^{2+}) and minor elemental constituents of the soil samples were determined using the X-Ray Fluorescence Spectrometry method (FEATHER & WILLIS 1976, THOMSEN 2002) in the Department of Geology, University of the Witwatersrand, Johannesburg.

2.3. Data analysis

Three data matrices were created, namely (1) the matrix of plots x species featuring basal-area values, (2) matrix of plots x species featuring counts of individuals (abundance), and (3) matrix of plots x environmental factors (soil variables and historical management practice type). The historical management practice type data was treated as a nominal variable. Due to incommensurability of the scales used in measurement and estimation of the environmental factors, major and minor mineral constituents of the soils were log-transformed. Further data incommensurability was addressed by the choice of the appropriate multivariate technique as well as intrinsic transformation involved in the choice of clustering and ordination analyses.

2.3.1. Classification

The species basal area and abundance (i.e. number of individuals of a species in a 0.5 ha plot) data sets were separately classified employing a clustering approach in order to identify forest types (groups of plots similar in species composition). Prior to the cluster analysis the original abundance values were code-replaced into a 0–9 scale (i.e. <5=1, 5–9=2, 10–19=3, 20–49= 4, 50–99= 5, 100–199= 6, 200–299= 7, 300–499= 8, 500+ = 9). The code-replaced abundance values were also used to construct a synoptic table for the communities/clusters. Species which occurred 1–5 times but failed to show any obvious link to one or two communities were discarded. We adopted Incremental Sum of Squares clustering (ISS), known also as Ward's method (see PODANI 2000, 2001). Chord Distance was applied as the resemblance measure in order to remedy for unequal species richness of the classified plots (the Chord Distance employs intrinsic normalization). Basal area data were used as indicators of the importance (dominance) of tree and shrub cover (NELDER & HOWITT 1991, CARATTI et al. 2004). Comparisons between the communities were made using the ANOSIM (ANalysis Of SIMilarity) permutation test sub-routine within the CAP 3.1 software

(Pisces Conservation Ltd. 2004). A significance level of 0.5 (5%) was used to distinguish the communities from one another. Species contributing to the similarities within communities were determined using a SIMilarity PERcentage (SIMPER; CLARKE 1993). Species abundance and basal area per plot data were used separately in the SIMPER test. The SIMPER estimates the contribution of individual taxa to similarity among or within clusters, and it is used to determine the extent to which individual species contribute to the patterns detected by the cluster analyses and ANOSIM. The analysis breaks down the contribution of each species to the observed similarity (or dissimilarity) between samples. The method uses the Bray-Curtis similarity, comparing in turn each sample in Group 1 and Group 2. The species primarily responsible for observed similarity within the clusters (i.e. make up 90% of the similarity within the communities) as revealed in the results of SIMPER analysis were used in describing each cluster. Only species with >2.0% contribution to the similarity within the cluster (in terms of average abundance and average basal area) were considered.

2.3.2. Ordination

Species basal area and abundance data for each 0.5 ha plot together with the corresponding plot x environmental variables data matrix were subject to Canonical Correspondence Analysis (CCA) to reveal the relations between the species composition and environmental variables. The CANOCO version 4.5, software for Canonical Community Ordination was employed (TER BRAAK & ŠMILAUER 2002). The environmental factors included in the CCA featured soil variables (pH, Ca, Mg, Na, P, Li, Si, Ti, Fe, OM and N) and historical management practice types (i.e., nature reserve, logged only, and logged and arboricide treated). The vegetation samples were plotted in an ordination diagram with the soil variables shown by vectors (arrows), while management by filled triangles. The length of the arrows is proportional to their importance and the directions of the arrows show their correlation with the axes. Statistical significance of the relationship between species and the whole set of environmental variables was evaluated using a Monte Carlo randomisation procedure with 999 permutations under reduced model (TER BRAAK & ŠMILAUER 2002). This is a direct test of whether the included environmental variables have significant effect on the species composition. It was calculated firstly for axis 1 and then for all the canonical axes. The CCA generated intra-set correlations (i.e., correlations between environmental variables and ordination axes) were used to infer the relative importance of each environmental variable for prediction of species composition and distribution (TER BRAAK 1995).

3.0. RESULTS

3.1. Numerical classification

A total of 269 species from 171 genera and 51 families were recorded. Based on both the species basal-area and abundance data from 32 half-hectare sampling plots, the cluster analysis yielded four community groups with sub-communities for some. The dendrograms showed several common features such as clearly revealing clusters of the *Cynometra alexandri* - dominated, *Senna spectabilis* and Swamp Forest plots (see Fig. 1 featuring the abundance-data analysis; the clustering of the basal-area data is not shown).

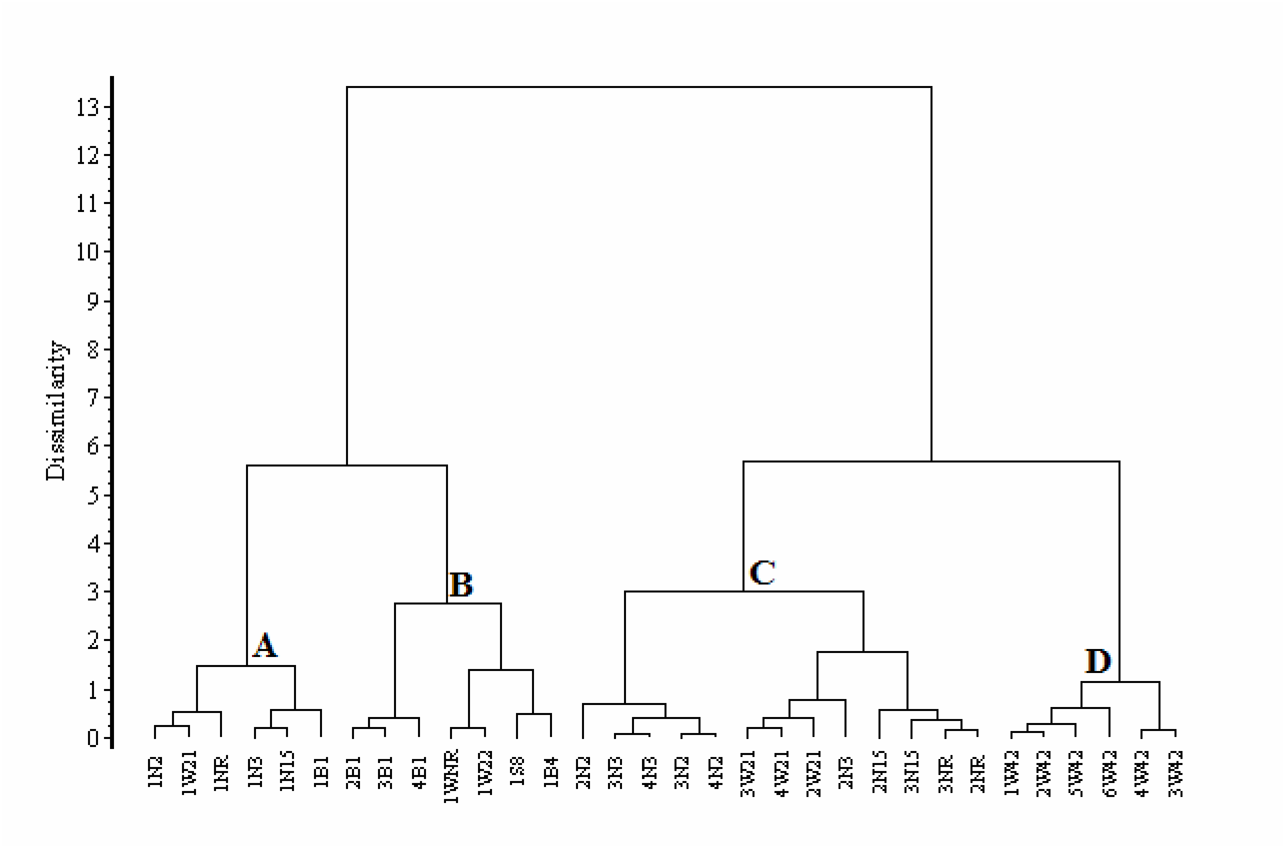

Figure 1. Cluster analysis dendrogram based on code-replaced abundance per species per plot data for woody species of stem diameter ≥2.0 cm from 32, 0.5 ha plots in BFR NW Uganda using Incremental Sum of Squares (ISS) clustering method with the Chord distance. The abbreviations for the plots stand for plot and compartment number in BFR (i.e. 1N2, 2N2 and 3N2 are plots 1, 2 and 3 sampled along the same transect in compartment N2).

The ANOSIM test indicated the separation of plots based on the four communities to be significant ($R_{ANOSIM} = 0.76$, $p = 0.001$; $R_{ANOSIM} = 0.71$, $p = 0.001$ for species abundance and basal area, respectively). However there were visible differences in the clustering of plots for the other communities. The observed differences could be ascribed to the continuous nature of the forest vegetation. In such cases, the fine differentiation between natural clusters (well-defined forest communities) is rather of quantitative than qualitative nature. Hence, any importance values beyond mere abundances would add information leading to clearer cluster definition. Therefore in the sequel the emphasis was on the interpretation of the clustering based on code-replaced abundance data (for a simplified synoptic table see Table 1) and SIMPER analysis results. The following four communities (A–D) were distinguished:

A. ***Pseudospondias microcarpa*** Swamp Forest

The plots clustered within this community were all sampled from seasonally flooded ("swamp") habitats. This community is characterised by *Pseudospondias microcarpa* (A. Rich.) Engl., *Raphia farinifera* (Gaertn.) Hylander, *Euphorbia teke* Schweinf. ex Pax, *Neoboutonia melleri* (Muell. Arg.) Pain, *Leea guineensis* G. Don. and *Baphia wollastonii* Bak. f. (Table 1). The SIMPER analysis showed that there were 26 and 38 (for basal area and abundance data, respectively) species making up 90% of the similarity within this community. The five species contributing most to the similarity (based on abundance data) were *P. microcarpa*, *Cynometra alexandri* C.H. Wright, *Khaya anthotheca* (Welw.) C. DC., *Cleistopholis patens* (Benth.) Engl. & Diels. and *Glyphaea brevis* (Spreng.) Manachino. If basal-area data were considered, the top 5 species included *Lasiodiscus mildbraedii* Engl., *Acalypha neptunica* Muell. Arg., *G. brevis, Mallotus oppositifolius* (Geisel.) Muell. Arg. and *P. microcarpa.* This suggests that generally *P. microcarpa* defines this community. The species richness for this plant community spanned 78–106. However, two sub-communities, characterised by *B. wollastonii* and *L. guineensis,* respectively were distinguished (Table 1).

B. *Funtumia elastica–Pouteria altissima* Forest

This community comprises plots that were sampled from distant locations of the forest (Table 1). The SIMPER analysis identified 24 and 37 species (basal-area and abundance data, respectively) contributing to 90% of the observed similarity. The five species contributing most to similarity on the basis of abundance were *Senna spectabilis* (DC.) Irwin & Barneby, *Funtumia elastica* (Preuss) Stapf., *Acalypha neptunica* Muell. Arg., *Alchornea laxiflora* (Benth.) Pax & K. Hoffm. and *Teclea nobilis* Del.. The most important ones identified by SIMPER on the basis of the basal-area data include *Senna spectabilis*, *Funtumia elastica, Cola gigantea* A. Chiev., *Khaya anthotheca* and *Pouteria altissima* (A. Chiev) Aubrev. & Pellgr. The species richness for this plant community spanned 67–94. Two sub-communities, such as the *Piptadeniastrum africanum* sub-community and *Senna spectabilis* sub-community were identified.

The *Senna spectabilis* Sub-community is characterised by *S. spectabilis* which is both dominant (in terms of basal area) and most frequent. The species richness in the plots classified within this forest type spanned 67–85. The associated upper-storey and understorey varied with location of the plots. Plots from the forest interior included interior forest species such as *L. mildbraedii* and *Argomuellera macrophylla* Paxa Laka*,* while those sampled towards the forest edges were associated with typical savanna woodland species such as *Albizia coriaria* Oliv., *Combretum collinum* Fres., *Combretum molle* G.Don and *Terminalia glaucescens* Benth. (Table 1).

The *Piptadeniastrum africanum* sub-community is characterised by the dominant *K. anthotheca,* followed by *Pouteria altissima*, *Trilepsium madagascariensis* DC.*, C. gigantea* and *Funtumia elastica.* The most frequent species include *Acalypha neptunica*, *Acalypha ornata* Hochst. ex A. Rich.*, Alchornea laxiflora* and *Pouteria altissima*. The plot species richness for this sub-community spanned 83–94. This community has been, presumably, shaped by past anthropogenic activities. The Uganda Forest Department records indicated that *K. anthotheca* dominance here is a result of enrichment planting and its protection from illegal and legal harvesting.

C. *Lasiodiscus mildbraedii–Khaya anthotheca* Forest

This community comprises up-slope plots from forest compartments of various management practice history, including mechanical logging, arboricide treatment, and pitsawing (between 1995 and 1997). It also contains plots from protected parts of the forest which have not experienced arboricide treatment, legal logging, or pitsawing. The latter plots form a sub-cluster (Fig. 1). The sub-units within this community (see Fig. 1, Table 1) are considered only as variants and not sub-communities because their differentiation is more quantitative (in terms of abundance of the species involved) than qualitative (presence of species or species groups). The SIMPER analysis identified 19 and 23 species (basal area and abundance data, respectively) making up 90% of the observed similarity within this community. The top five species contributing most to similarity on the basis of abundance were *L. mildbraedii*, *Celtis mildbraedii* Engl., *A. neptunica, A. ornata* and *Rinorea ardisiiflora* Ktze*,* while those on the basis of basal area include *Cynometra alexandri*, *C. mildbraedii*, *Funtumia elastica, Alstonia boonei* De Wild*, Celtis zenkeri* Engl. and *K. anthotheca.* The species richness patterns are highly variable spanning 59–111. In some places, the forest floor is densely covered with *Leptaspis zeylanica*, a species characteristic of closed (including old mixed) forests, but not of the unlogged *Cynometra* Forest (SYNNOTT 1985).

D. ***Cynometra alexandri–Rinorea ilicifolia*** Forest

This community comprises plots that are all from an area with no history of arboricide treatment and mechanical logging, except for pitsawing. The sub-units within this community (Fig. 1, Table 1) are considered only as variants and not sub-communities because their differentiation is more quantitative (in terms of abundance of the species involved) than qualitative (presence of species or species groups). The SIMPER analysis showed that species making up 90% of the similarity within this community were 4 and 11 for the basal area and abundance data respectively. The three species were *Cynometra alexandri*, *Celtis mildbraedii* and *Lasiodiscus mildbraedii*. On the basis of abundance, the five species contributing most to the similarity were; *Thecacoris lucida* (Pax) Hutch.*, A. ornata, A. neptunica, L. mildbraedii* and *Argomuellera macrophylla*. In areas where *Cynometra alexandri* formed a closed upper-storey canopy, the forest floor was devoid of a herbaceous layer, and the understorey was dominated by *T. lucida*. In habitats where recent human disturbance was evident, the understorey was dominated by shrubs such as *A. neptunica*, *A. ornata*, and *A. macrophylla*. Species richness of this community spanned 24–59.

Table 1. Synoptic table of the studied forest communities. The Plot Code carries the identity of each sample plot. The "Cluster No." corresponds to the clusters identified by the clustering analysis (see Fig. 1). The values in the body of the table are the code-replaced abundance values (see section on Materials and methods for the code replacement rules). The meaning of the diagnostic (Diag.) codes: G: general taxon (occurring in all 4 communities); Example 1: “G, B1, D1” means that the taxon occurs in all 4 communities, but it appears as differentiating also among sub-communities within Community B and D. Example 2: “G, C1-2” means that the taxon is a general one (see above), but it discriminates between sub-communities C1 and 2 against sub-community C3. Example 3: “AB,A1” taxon occurs in both communities A and B and is (at the same time) discriminating sub-communities within the community A. Example 4: “B” means that the taxon is characteristic of the community B. Example 5: “B1” means that the taxon is characteristic of the community B and is (at the same time) discriminating between sub-communities within the community B. Example 6: “ABC,(A),C1-2” means that the taxon occurs in 3 communities (A,B,C), while it show preference to community A and is also discriminating sub-communities C1 and C2 against C3. The taxa indicated by asterisk are alien to the region.

A: *Pseudospondias microcarpa* Swamp Forest
  A1: *Baphia wollastonii* Sub-Community
  A2: *Leea guineensis* Sub-Community
B: *Funtumia elastica–Pouteria altissima* Forest
  B1: *Piptadeniastrum africanum* Sub-Community
  B2: *Senna spectabilis* Sub-Community
C: *Lasiodiscus mildbraedii–Khaya anthotheca* Forest
  C1: *Ficus exasperata* Variant
  C2: *Glyphaea brevis* Variant
  C3: *Rothmannia urcelliformis* Variant
D: *Cynometra alexandri–Rinorea ilicifolia* Forest
  D1: *Rothmannia urcelliformis* Variant
  D2: *Ochna holstii* Variant

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WN**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Acalypha neptunica	**G**	4	5	5	5	4	5	6	5	7	5	5	2	1	5	6	6	6	7	6	5	5	6	7	7	4	4	5	4	6	6	6	5
Acalypha ornata	**G**	4	3	3	3	2	4	5	4	6	3	4	.	.	4	8	7	6	7	6	5	4	6	5	5	5	4	7	6	8	5	5	6
Alchornea laxiflora	**G**	3	6	3	6	3	4	4	5	6	5	6	1	4	1	2		4	2	4	5	4	4	2	4	1		1	.	2	6	4	3
Celtis mildbreadii	**G**	1	.	5	2	3	2	1	3	5	4	4	.	.	4	6	7	5	5	5	6	6	7	6	6	7	7	4	3	4	1	4	7
Funtumia elastica	**G**	3	3	3	5	3	3	4	4	5	6	6	5	2	6	6	6	6	5	6	5	5	6	2	3	3	4	1	.	3	1	.	3
Antiaris toxicaria	**G**	1	1	1	1	2	2	5	3	3	1	1	1	1	3	3	3	4	3	.	3	3	4	1	2	1	1	.	.	3	1	1	.
Celtis zenkeri	**G**	.	1	2	2	1	2	3	5	3	3	3	1	.	3	4	4	4	4	3	4	4	3	3	2	4	3	4	4	2	2	2	4
Chrysophyllum albidum	**G**	1	2	2	2	.	1	2	3	2	4	2	1	1	2	1	3	1	1	2	2	2	1	2	1	2	2	1	1	1	.	1	3

Table 1 contd.

Plot Code	Diag.	1N2	1W2	1NR	1N3	1N15	1B1	2B1	3B1	4B1	1WN	1W2	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W2	4W2	2W2	2N3	2N15	3N15	3NR	2NR	1W4	2W4	5W4	6W4	4W4	3W4
Cluster No.		A1	A1	A1	A2	A2	A2	B1	B1	B1	B2	B2	B2	B2	C1	C1	C1	C1	C1	C2	C2	C2	C2	C3	C3	C3	C3	D1	D1	D1	D1	D2	D2
Cynometra alexandri	**G**	3	4	4	3	2	4	.	.	2	4	5	.	.	5	5	4	5	4	4	5	3	4	4	4	4	3	4	4	4	4	4	5
Lychnodiscus cerospermus	**G**	3	1	3	1	2	2	3	4	3	.	1	1	1	1	4	3	1	2	3	2	3	3	3	2	3	4	.	.	1	.	1	1
Tapura fischeri	**G**	1	2	1	1	.	1	3	3	1	3	2	2	1	3	1	3	2	2	3	4	3	3	2	1	1	.	4	2	2	1	2	1
Teclea nobilis	**G**	2	1	1	3	.	1	4	5	3	2	2	3	4	1	2	1	3	2	2	2	3	2	2	1	.	1	1	1	3	3	2	4
Rinorea ardisiflora	**G**	2	1	5	1	.	.	1	.	5	3	3	.	.	4	7	8	7	5	4	4	2	6	5	4	5	6	5	4	2	.	2	1
Trichilia prieureana	**G**	3	1	2	1	1	.	3	5	3	2	1	.	3	2	.	.	.	.	2	3	3	1	4	4	3	3	1	.	2	1	1	1
Celtis wightii	**G**	2	4	1	.	1	.	1	1	.	3	1	.	4	1	.	.	1	.	1	2	2	.	1	4	1	1	3	2	1	4	1	5
Vitex amboniensis	**G**	1	1	1	1	1	1	.	1	.	.	1	.	.	.	1	1	1	.	.	1	1	1	.	.	.	1	1	.	.	1	.	.
Melanodiscus sp.	**G**	1	.	1	1	1	1	3	4	3	1	1	1	2	.	1	1	1	.	1	1	.	1	2	1	.	1	.	.	1	.	1	1
Albizia zygia	**G**	1	.	.	.	.	1	2	1	1	1	1	1	2	1	1	.	.	1	1	.	.	.	1	.	.	.	.	.	1	2	.	.
Bridelia micrantha	**G**	1	.	1	1	1	1	1	1	.	1	.	3	1	1	.	.	.	.	2	.	.	1	.	.	.	.	.	.	1	.	1	.
Chaetacme aristata	**G**	1	2	.	.	.	1	1	2	.	.	.	.	1	1	.	.	.	.	1	.	.	.	1	.	.	.	.	.	1	3	2	3
Citropsis articulata	**G**	2	.	1	.	.	1	.	.	1	1	1	.	.	.	1	2	.	1	1	.	1	1	.	1	.	1	.	.	1	1	.	.
Coffea euginoides	**G**	2	1	.	1	.	.	1	2	1	2	.	.	1	.	.	.	.	.	.	1	.	.	1	1	1	.	.	.	1	1	.	2
Ehretia cymosa	**G**	1	1	1	1	.	.	1	.	1	1	1	.	.	.	1	1	.	.	1	2	.	1	1	.	.	.	.	.	1	1	.	.
Monodora angolense	**G**	1	.	.	.	.	.	1	2	1	1	.	1	1	1	1	1	1	.	1	.	1	.	.	.	.	1	.	.	1	.	.	2
Vangueria apiculata	**G**	.	.	.	2	.	1	.	.	.	.	.	.	4	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Aeglopsis eggelingi	**G**	.	.	1	1	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.
Dictyandra arborescens	**G**	.	.	1	1	.	1	.	2	.	1	.	.	.	1	1	1	1	1	1	.	1	1	1	.	.	.	1	.	3	.	.	.
Drypetes ugandensis	**G**	.	.	3	.	1	1	2	4	3	.	.	1	1	1	3	2	.	1	1	1	1	1	1	2	.	1	1	.	.	.	1	.
Pavetta molundensis	**G**	1	1	.	4	.	1	1	2	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Diospyros abyssinica	**G, A1**	1	1	.	.	.	.	.	.	.	1	.	.	4	1	.	.	.	.	1	3	1	1	.	.	3	1	.	.	.	.	1	4
Tetrapleura tetraptera	**G, B1, D1**	1	1	.	.	1	1	2	1	1	.	.	.	.	.	1	2	1	1	1	1	1	2	1	1	.	1	1	.	1	.	.	.
Rinorea brachypetala	**G, B1, D1**	3	5	5	1	1	4	.	4	4	.	.	.	.	1	4	5	2	3	1	.	4	3	2	7	4	5	2	3	.	4	.	.
Mimusops bagshawei	**G, B1**	2	.	.	1	1	3	3	3	3	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	.	1	.	.	.	1	1	1
Holoptelea grandis	**G, B1**	1	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.	1	1	1	.	.	.	1	.	.	.	.	1
Lasiodiscus mildbraedii	**G, B2**	7	8	6	5	4	1	.	.	.	4	5	.	.	6	8	7	7	6	5	7	6	8	8	6	8	6	6	6	6	9	3	5
Argomuellera macrophylla	**G, B2**	2	1	1	2	2	3	.	.	.	3	3	.	.	2	3	4	1	.	2	4	4	4	.	5	4	3	4	5	5	5	6	5
Celtis gomphophylla	**G,C1-2**	1	1	1	1	1	.	.	.	1	3	2	1	.	5	3	4	2	.	2	4	3	3	.	.	1	1	.	.	2	.	.	.
Grewia sp.	**G,C1-2**	2	1	1	2	1	.	1	3	1	.	.	1	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	1	1

Table 1 contd.

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WNR**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Margaritaria discoidea	**G,C1-2**	.	1	1	1	2	.	1	.	1	2	1	1	1	1	1	1	.	1	1	3	.	3	.	.	.	.	.	.	1	.	.	2
Markhamia lutea	**G,C1-2**	2	2	.	2	3	1	1	.	.	1	2	3	.	1	1	.	.	.	1	1	.	.	.	.	.	.	1	.	1	.	1	2
Oncoba spinosa	**G, C1-2, D1**	.	2	.	1	.	1	.	1	.	1	1	.	.	.	1	.	1	.	1	.	.	1	.	.	.	.	.	.	1	1	.	.
Ochna holstii	**G, C2, D2**	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	3
Khaya anthotheca	**G, D1**	4	4	3	2	2	4	5	4	4	2	.	4	1	3	4	4	4	2	4	3	4	2	2	2	1	3	1	.	1	1	.	.
Blighia unijugata	**G, D1**	2	1	.	2	1	2	4	2	1	1	1	2	.	3	3	2	3	4	1	.	1	2	1	1	.	1	1	1	1	.	.	.
Morus mesozygium	**G, D1**	1	.	1	1	1	1	3	2	2	1	.	2	.	1	1	1	1	1	.	1	.	1	2	2	1	1	.	1	1	.	.	.
Albizia glaberrima	**G, D1**	1	.	.	2	1	1	1	.	.	1	1	1	.	1	1	.	1	1	1	1	1	2	.	.	1	.	1	.	.	1	.	.
Ricinodendron heudelotii	**G, D1**	.	.	1	.	1	1	.	1	.	.	1	.	.	1	1	1	.	.	1	.	1	1	.	.	.	.	.	.	1	1	.	.
Rothmannia urcelliformis	**G, D1**	.	1	.	.	1	.	1	2	2	1	1	.	1	1	.	.	.	.	.	.	.	1	1	2	2	1	1	1	1	1	.	.
Treculia africana	**A, C2**	2	.	2	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.
Neoboutonia melleri	**A**	2	.	3	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eurphobia teke	**A**	3	1	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Raphia farinifera	**A**	4	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Baphia wallastonii	**A1**	.	3	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mitragyna stipulosa	**A1**	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spondianthus preussii	**A1**	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pleiocarpa pycnantha	**A1**	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leea guineensis	**A2**	1	.	.	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Zanthoxylum gillettii	**A2**	1	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Syzygium cordatum	**A2**	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dovyalis macrocalyx	**AB,A1**	1	.	1	.	.	.	.	1	.	2	.	1	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Parkia filicoidea	**AB,A1**	1	.	2	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linociera johnsoni	**AB**	1	3	.	1	1	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Syzygium guineensis	**AB**	1	1	.	1	.	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sapium ellipticum	**AB**	1	1	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spathodea campanulata	**AB,B2**	.	1	.	1	.	1	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Olea welwitschii	**AB,B2**	.	2	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 1 contd.

Plot Code	Diag.	1N2	1W21	1NR	1N3	1N15	1B1	2B1	3B1	4B1	1WNR	1W22	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W21	4W21	2W21	2N3	2N15	3N15	3NR	2NR	1W42	2W42	5W42	6W42	4W42	3W42
Cluster No.		A1	A1	A1	A2	A2	A2	B1	B1	B1	B2	B2	B2	B2	C1	C1	C1	C1	C1	C2	C2	C2	C2	C3	C3	C3	C3	D1	D1	D1	D1	D2	D2
Senna spectabilis	**B**	.	.	.	.	.	.	1	.	2	8	9	7	8	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Pachystela brevipes	**B**	.	.	1	.	.	.	3	2	2	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Rytigynia usambarensis	**B**	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Piptadeniastrum africanum	**B1**	.	.	.	.	.	1	1	2	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
*Citrus citrus**	**B1**	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Albizia coriaria	**B2**	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Rytigynia sp.	**B2**	.	.	1	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Psidium guajava**	**B2**	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Mangifera indica**	**B2**	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Combretum collinum	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antidesma membranaceum	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Combretum molle	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Maytenus gracilipes	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tabernaemontana holstii	**ABC**	3	2	4	4	4	2	4	1	2	3	1	2	1	4	4	3	3	2	4	2	4	4	3	1	2	3	.	.	.	.	.	.
Aningeria altissima	**ABC**	1	1	1	1	1	2	4	6	4	2	1	4	2	1	1	2	1	1	4	3	2	3	1	3	2	1	.	.	.	.	.	.
Trichilia rubescens	**ABC**	2	2	4	4	5	3	1	1	3	5	1	3	.	5	4	2	2	1	3	3	2	4	2	1	1	3	.	.	.	.	.	.
Trilepisium madagascariensis	**ABC**	1	1	2	2	2	3	1	3	4	1	.	1	1	2	2	2	1	1	2	2	2	3	3	2	1	2	.	.	.	.	.	.
Entandrophragma utile	**ABC**	1	1	1	1	1	1	2	3	1	1	.	.	.	1	1	1	1	1	2	.	1	1	.	1	1	1	.	.	1	.	.	.
Trichilia dregeana	**ABC**	1	1	1	.	1	2	2	1	2	1	.	.	.	4	3	4	4	4	1	1	.	3	1	2	1	1	.	.	.	.	.	.
Bequaertiodendron oblanceolatum	**ABC**	1	.	1	1	2	1	4	4	2	1	.	.	1	1	1	1	2	2	1	2	1	1	1	.	1	1	.	.	.	.	.	1
Chysophyllum perpulchrum	**ABC**	1	1	3	1	.	2	1	3	3	1	.	.	.	4	2	3	3	1	1	1	1	2	2	2	3	3	.	.	.	.	.	.
Myrianthus holstii	**ABC**	1	1	4	4	4	4	2	3	3	.	.	4	.	4	4	1	1	1	2	1	2	3	2	1	1	1	.	.	.	.	.	.
Belonophora hypoglauca	**ABC**	2	1	3	1	.	1	1	2	2	1	1	.	1	1	.	.	.	1	1	2	3	1	3	3	3	4	.	.	.	.	.	.
Guarea cedrata	**ABC**	.	1	3	1	1	.	.	2	1	1	1	.	.	3	1	1	2	1	2	1	1	3	1	1	1	2	1	.	.	.	.	.
Coffea canephora	**ABC**	.	3	1	1	.	.	1	4	3	1	.	2	1	1	1	1	1	1	1	1	2	1	1	.	.	.	.	.	1	.	.	.
Greenwayodendron suaveolens	**ABC**	.	.	1	1	1	.	.	1	2	.	.	.	1	1	2	2	1	.	1	1	1	4	1	1	2	1	1	.	.	.	.	.
Erythrophleum suaveolens	**ABC**	1	1	1	1	.	.	.	3	1	1	1	.	1	1	.	1	1	1	1	1	1	1	1	.	1	.	.	.	.	.	.	.
Entandrophragma angolense	**ABC**	1	1	1	1	.	1	2	1	.	.	.	.	1	1	.	.	1	1	1	.	1	1	1	.	1	.	.	.	.	.	.	.
Maesopsis eminii	**ABC**	.	.	1	.	.	.	1	.	1	.	1	1	.	1	1	3	1	.	1	2	2	1	1	1	1	1	.	.	1	.	.	.
Cordia millenii	**ABC**	1	1	1	.	.	1	.	1	1	1	.	.	.	1	1	.	1	.	2	1	3	1	1	.	1	.	.	.	.	.	.	.

Table 1 contd.

Plot Code	Diag.	1N2	1W21	1NR	1N3	1N15	1B1	2B1	3B1	4B1	1WNR	1W22	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W21	4W21	2W21	2N3	2N15	3N15	3NR	2NR	1W42	2W42	5W42	6W42	4W42	3W42
Cluster No.		A1	A1	A1	A2	A2	A2	B1	B1	B1	B2	B2	B2	B2	C1	C1	C1	C1	C1	C2	C2	C2	C2	C3	C3	C3	C3	D1	D1	D1	D1	D2	D2
Oxyanthus speciosus	**ABC**	1	2	1	1	2	.	.	1	2	1	.	2	.	2	.	1	1	.	1	.	1	.	1	1	.	.	.	.	.	.	.	.
Memecylon jasminiodes	**ABC**	1	.	1	1	1	.	1	4	.	1	.	.	1	1	.	.	1	.	.	.	.	1	1	1	1	1	1	.	.	.	.	.
Mammea africana	**ABC**	.	1	1	1	1	3	.	.	.	1	.	.	.	4	3	1	1	1	2	.	1	2	.	.	2	.	.	.	.	.	.	.
Kigelia africana	**ABC**	2	3	1	4	2	2	1	1	1	2	.	.	1	.	2	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.
Ficus sur	**ABC**	1	1	.	.	.	.	1	.	1	.	2	1	.	1	1	1	1	.	1	1	1	4	1	.	.	.	.	.	.	.	.	.
Caloncoba crepiniana	**ABC**	2	.	1	.	.	1	.	.	1	.	1	5	3	4	1	.	2	.	1	4	.	1	1	.	.	.	.	.	.	.	.	1
Lannea welwitschii	**ABC**	1	.	1	.	.	1	.	1	1	.	1	1	1	.	.	.	.	.	4	.	1	1	1	.	.	.	.	.	.	.	.	.
Mildbraediodendron excelsum	**ABC**	1	.	1	.	.	.	1	1	.	1	.	.	.	1	.	1	1	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.
Pycnanthus angolensis	**ABC**	1	2	2	.	1	2	1	.	1	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Klainedoxa gabonensis	**ABC**	1	.	1	.	.	1	1	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Xylopia parviflora	**ABC**	.	.	.	1	1	.	.	1	.	.	.	.	1	.	.	1	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Strombosia scheffleri	**ABC**	1	.	.	.	.	.	.	.	1	1	.	.	.	1	.	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.
Mallotus oppositifolius	**ABC,(A),C2-3**	5	6	4	4	5	5	.	.	.	1	.	.	.	.	.	.	.	.	4	.	1	1	1	2	2	2	.	.	.	1	.	.
Ouratea densiflora	**ABC,(A)**	4	3	4	6	3	1	1	3	2	1	.	.	.	3	3	.	.	.	.	.	2	1	1	1	.	.	.	.	.	.	.	1
Pseudospondias microcarpa	**ABC,(A)**	4	4	3	4	4	4	2	.	.	1	.	1	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Glyphaea brevis	**ABC,(A),C2-3**	4	6	4	5	6	6	2	2	3	.	.	.	1	.	.	.	.	1	3	2	1	2	.	.	.	.	.	.	.	.	.	.
Desplatsia dewevrei	**ABC,B1**	1	1	2	3	1	.	.	1	1	.	.	.	.	3	1	.	3	.	.	1	2	3	1	.	1	.	.	.	.	.	.	.
Entandrophragma cylindricum	**ABC,B1**	.	.	2	.	.	1	1	3	3	.	.	.	.	1	1	1	2	1	1	.	.	2	1	1	2	1	1	.	.	.	.	.
Alstonia boonei	**ABC,B2**	2	.	2	1	1	1	.	.	.	2	1	1	.	3	1	2	1	.	1	2	2	2	1	.	1	1	.	.	1	.	.	.
Clausena anisata	**ABC,C1**	1	.	1	1	.	.	1	.	1	1	1	.	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cola gigantea	**ABC,C1-2**	1	1	.	1	1	1	3	3	1	1	.	1	4	1	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.
Cleistopholis patens	**ABC,C1-2**	5	2	4	1	2	.	.	1	.	3	1	.	.	1	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.
Rauvolfia vomitoria	**ABC,C1-2**	1	.	1	.	.	1	.	.	1	.	1	3	.	1	1	1	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.
Croton macrostachyus	**ABC,C1-2**	.	.	.	.	.	2	1	.	1	.	.	3	2	3	1	2	3	3	.	.	1	2	.	.	.	.	1	.	.	.	.	.
Lovoa swynnertonii	**ABC,C1-2**	1	.	.	.	1	.	2	2	1	.	.	.	1	.	1	1	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.
Canarium schweinfurthii	**ABC,C1-2**	.	.	.	.	1	.	.	.	1	.	1	1	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.
Rothmannia whitfieldii	**ABC,C1-2**	1	.	.	.	.	2	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Croton sylvaticus	**ABC,C2-3**	.	.	1	1	1	.	1	1	1	3	3	.	1	.	.	.	.	.	1	1	3	1	.	1	1	1	.	.	.	.	.	.
Leptonychia mildbreadii	**ABC,C2-3**	1	1	1	1	.	1	2	3	1	1	1	1	.	.	.	.	.	.	2	1	2	.	.	.	1	.	.	.	.	.	.	.

Table 1 contd.

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WNR**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Teclea grandifolia	**ABC,C2-3**	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.
Zahna golungensis	**ABC,C2-3**	1	1	.	.	.	.	1	3	2	.	1	.	1	.	.	.	.	.	.	1	.	.	1	1	.	1	.	.	.	.	.	.
Lindackeria schweinfurthii	**ABC,C2-3**	1	.	2	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	1	1	1	.	1	.	.	.	.	.	.	.	.	.
Trema orientalis	**ABC,C2-3**	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	2	.	2	.	.	.	.	.	.	.	.	.
Chrysophyllum muerense	**ABC,B1**	.	1	.	.	.	2	2	6	2	.	.	1	.	1	1	.	.	.	.	2	.	.	.	2	.	1	.	.	.	.	.	.
Alchornea floribunda	**ABC,B1,C3**	.	.	.	2	.	.	4	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.
Dracaena fragrans	**ABC,C2**	1	1	1	1	.	.	.	.	.	1	1	.	.	.	.	.	.	.	1	2	1	1	.	.	.	.	1	.	.	.	.	.
Antidesma laciniatum	**ABC,C2**	2	.	2	3	2	.	1	1	2	.	.	3	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
Rinorea oblongifolia	**AC,A1,C2-3**	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	5	4	.	.	.	.	6	.	.	.	.	.	.
Staudtia kamerunensis	**AC.A1**	1	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.
Ficus orttonofolia	**AC,A1 ,C2**	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	1	.	.
Allophyllus dummeri	**AC,C2**	1	1	.	2	1	1	.	.	1	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.
Sterculia dawei	**AC,C2-3**	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.
Zanthoxylum rubescens	**AC**	1	.	1	2	1	.	.	.	.	.	.	1	.	.	1	1	.	1	.	1	1	.	1	.	.	.	1	.	.	.	.	.
Erythrina excelsum	**AC**	1	.	1	1	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.
Claoxylon hexandrum	**AC**	.	.	1	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	.	.	.	.	1	.	.	.	.	.	.
Macaranga pynaertii	**AC**	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.
Alangium chinense	**AC**	.	.	1	1	4	3	.	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.
Picralima nitida	**AC,A2**	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Desplatsia chrysochlamys	**AC,A2,C1-2**	.	.	.	2	1	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Monodora myristica	**AC,A2,C1-2**	.	.	.	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
Ochna membranacea	**C,C1-2**	.	.	1	.	.	.	.	.	.	.	.	.	.	3	1	.	1	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.
Ficus asperifolia	**C,C1-2**	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Randia longiflora	**C,C1-2**	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Majidea fosteri	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	1	1	.	1	.	.	.	.	.
Lindackeria ruwenzoriensis	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Croton megalocarpus	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Coffea spathycalyx	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.

Table 1 contd.

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WNR**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Cedrella cedrata	**C,C2**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.
Alchornea hirtella	**C,C2-3**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.
Gardenia vogelli	**C,C2-3**	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.
Englerophytum natalense	**BC,B2**	.	.	.	.	.	.	.	.	.	1	.	2	2	3	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Fagaropsis angolensis	**BC,C1**	.	.	.	.	.	.	1	1	.	4	.	2	2	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Ficus exasperata	**BC,C1-2**	.	.	.	.	.	.	1	.	1	.	.	1	.	4	1	1	2	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Pancovia turbinata	**BC,C1-2**	.	.	.	.	.	1	.	2	1	.	.	.	.	2	1	1	1	1	.	.	.	2	.	.	.	.	.	.	.	.	1	.
Uvariopsis sp.	**BC,C1-2**	.	.	.	.	.	1	.	.	.	.	1	.	1	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Ficus mucuso	**BC,C1-2**	.	.	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.
Aphania senegalensis	**BC**	.	1	.	.	.	.	.	1	1	1	1	1	1	.	.	1	1	1	1	.	.	.	.	1	2	.	.	.	.	.	.	1
Milicia excelsa	**BC**	.	.	.	.	.	.	1	.	.	1	.	1	1	1	.	1	.	1	.	1	.	.	.	1	.	.	.	.	1	.	.	.
Zanthoxylum leprieurii	**BC**	.	.	1	.	.	.	.	.	1	.	1	.	1	2	.	1	.	.	1	.	1	1	.	.	.	1	.	.	.	.	.	.
Tetrorchidium didymostemon	**BC**	.	.	.	1	.	.	.	.	1	1	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
Antidesma venosum	**BC**	.	.	.	.	.	.	.	.	.	.	.	.	4	2	3	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Uvariopsis congensis	**BCD**	.	.	.	.	.	.	1	1	.	1	4	.	.	1	.	.	1	.	.	4	.	.	.	1	.	.	.	1	.	.	.	1
Drypetes gerrardii	**BCD**	.	.	.	.	.	.	1	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	3	5
Maerua duchesnei	**BCD**	.	.	.	.	.	.	.	1	1	3	1	.	.	1	1	.	1	2	1	1	1	.	1	4	1	.	1	3	3	3	5	6
Rawsonia lucida	**BCD**	1	.	.	.	.	.	1	1	.	.	1	.	.	1	4	1	.	.	.	.	.	1	1	3	.	.	3	3	3	4	1	6
Lovoa trichilioides	**BCD,B1,D1**	1	.	.	.	.	.	2	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	1	.	.	.
Suregada procera	**BCD,C3**	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	2	.	1
Thecacoris lucida	**CD**	.	.	1	7	.	.	.	.	.	.	1	.	.	1	.	.	5	6	.	.	5	3	3	5	4	3	8	8	7	5	3	6
Whitfieldia elongata	**CD,C2-3**	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	1	.	3	1	4	1	3	1
		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 1 contd.

Plot Code	Diag.	1N2	1W2	1NR	1N3	1N1	1B1	2B1	3B1	4B1	1W	1W2	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W2	4W2	2W2	2N3	2N1	3N1	3NR	2NR	1W4	2W4	5W4	6W4	4W4	3W4
Cluster No.		A1	A1	A1	A2	A2	A2	B1	B1	B1	B2	B2	B2	B2	C1	C1	C1	C1	C1	C2	C2	C2	C2	C3	C3	C3	C3	D1	D1	D1	D1	D2	D2
Strychnos mitis	**D**	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	1	2	.	.	1	5
Maytenus undata	**D**	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	2
Dialium excelsum	**D**	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	1	1	1
Rinorea ilicifolia	**D**	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	4	1	7	1	.
Balsamocitrus dawei	**D**	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	3
Manilkara dawei	**D**	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	4	.	.	.	1	1
Dombeya mukole	**D**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2	2
Ficus pseudomangifera	**D,D1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.

Results of the analyses of SIMilarity PERcentages (SIMPER procedure from CAP 3.1) for the identified communities showed that species making up 90% of the observed similarity within each community spanned 4–26, and 11–38 for the basal area and abundance data, respectively. In both cases community D had the lowest, while community A had the highest number of species. This suggests that community A (swamp forest) is characterised by high species richness, while the community D (*Cynometra alexandri* dominated) and *Senna spectabilis* sub-community are characterised by low species richness. These results corroborate the CCA results as revealed by the location of the above communities in relation to the number of species isolines (Figs. 2a & b). Separation of species composition among clusters is evident but considerable overlap is also evident, with over 48 species present in all four communities (A–D; Table 1). Notable among the 48 species are *A. neptunica*, *A. ornata, C. mildbraedii* and *F. elastica* that were relatively frequent in all the 4 communities and could be regarded as generalists (Table 1). A few species however, were exclusively associated with particular plots because of their unique environmental conditions. For example, *Pseudospondias microcarpa*, *Raphia farinifera*, *Euphorbia teke*, and *Neoboutonia melleri* were exclusively associated with the Swamp Forest community.

3.2. Ordination

The relative influence of the measured environmental variables on species variance can be inferred from the CCA ordination diagram (Figs. 2a & 2b), and the intra-set correlations (Table 2). In relation to soil variables, the following trends can be observed in Fig. 2. For both data sets Fe, Si, and OM are the most important soil variables determining variation in species composition along axis 1. Ca, N, and to lesser extent P, also contribute to this variation. On the other hand, Mg and Ti are the most important soil variables determining variation in species composition along axis 2. Na also contributes to this variation. Although the overall correlations of environmental variables were more similar among the species data sets, their relative importance as controlling factors of community species composition vary. For example, pH is strongly correlated with Axis 1 in the abundance data than in the basal-area data (Table 2). The logged only, and logged and arboricide treatment historical management practice types historical management practice type was strongly correlated with axis 2 (Table 2, Fig. 2). Thus Axis 1 can be seen as representing an edaphic gradient, while Axis 2 can be interpreted as an anthropogenic disturbance gradient.

Reasonably high amounts of variance in the species data and the variance in species-environmental factor relations were explained by Axes 1 and 2 of the CCA for both data sets, although higher for the abundance than for the basal area (Table 3). For both data sets, the variance in species-environmental factors relation was higher than 50%, suggesting a relatively great influence of environmental factors on species composition and distributions. In addition, the variances explained (sum of all canonical eigenvalues) as a portion of the total inertia were relatively high (0.53 and 0.56 for basal area and abundance, respectively), suggesting how well the measured variables explained species composition. The summary of the Monte Carlo permutation test results showed significance for the first canonical axis ($F = 1.71$, $p = 0.028$) and all the canonical axes (F = 1.53, p = 0.002) for the ordination of the species presence/absence data. The ordination of the species basal area data did not show significance for Axis 1 (F = 1.71, p = 0.116), but a significance for all the canonical axes (F = 1.35, p = 0.001).

Table 2. Intra-set correlations between environmental variables (i.e., soil variables and historical management practices) and the first four first axes of CCA. OM: Organic matter; Li: Lithium; Log.arbt: Logged and arboricide treated (see Materials and Methods section).

Variable	**Basal area data CCA Axes**				**Abundance data CCA Axes**			
	1	2	3	4	1	2	3	4
pH	0.418	-0.063	0.049	-0.157	0.587	-0.132	-0.132	-0.231
Si	-0.685	0.116	0.287	-0.080	-0.696	0.051	0.276	-0.154
Ti	0.202	0.234	-0.439	-0.226	-0.053	-0.454	-0.522	0.200
Fe	0.593	-0.307	-0.473	-0.004	0.642	0.125	-0.542	0.099
Mg	0.073	-0.307	0.339	0.178	0.252	0.480	0.391	-0.066
Ca	0.603	0.161	0.142	0.018	0.669	-0.085	0.203	0.006
Na	-0.156	0.497	0.714	0.247	-0.113	-0.340	0.804	0.070
P	0.327	-0.523	-0.168	0.008	0.453	0.424	-0.216	-0.143
Li	0.603	-0.159	-0.155	0.180	0.636	0.171	-0.082	0.179
OM	0.559	0.109	0.326	0.586	0.637	-0.048	0.403	0.483
N	0.654	0.215	0.086	-0.017	0.636	-0.130	0.254	0.003
Logged only	0.290	0.224	-0.106	0.219	0.266	0.062	0.130	0.068
Log.arbt	0.178	0.685	-0.430	0.071	0.136	-0.589	-0.223	0.084

Table 3. Summary table of CCA of 32 plots distributed over the major areas of the different management practices history in the Budongo Forest Reserve (for details see Materials and Methods section).

Axes	1	2	3	4	Total Inertia
a) Basal area data					
Eigenvalues	0.437	0.42	0.329	0.226	4.785
Species-environmental correlations	0.9	0.943	0.949	0.943	
Cumulative percentage variance					
of species data:	9.1	17.9	24.8	29.5	
of species-environment relation:	17.3	33.9	47	55.9	
Sum of all eigenvalues					4.785
Sum of all canonical eigenvalues					2.523
b) Abundance data					
Eigenvalues	0.422	0.333	0.225	0.151	3.085
Species-environmental correlations	0.923	0.909	0.929	0.899	
Cumulative percentage variance					
of species data:	13.7	24.5	31.8	36.7	
of species-environment relation:	24.5	43.9	57	65.8	
Sum of all eigenvalues					3.085
Sum of all canonical eigenvalues					1.72

The CCA of the species abundance and basal area data sets to a great extent reflected the categorization of plant community clusters identified in the hierarchical cluster analysis for the respective data sets (Fig. 2). Although the sample plots were relatively highly dispersed in the ordination space, those that comprised communities A, D and the *Senna spectabilis* Sub-community (plots on the far right) were distinctly delineated (Figs. 2a & b). Along CCA axis 1 forest community types A and B are generally clearly differentiated from the others, while along axis 2 it is forest community type D. Generally, forest community A is associated with high levels of Na and Si; while community B is associated with high levels of OM, Ca and N; and community D with high levels of Mg. The relatively high dispersion of plots in some clusters in the ordination space corroborates the cluster analysis (Fig.1), and the SIMPER results that showed that the within community average similarity was fairly low and spanned 33–55%.

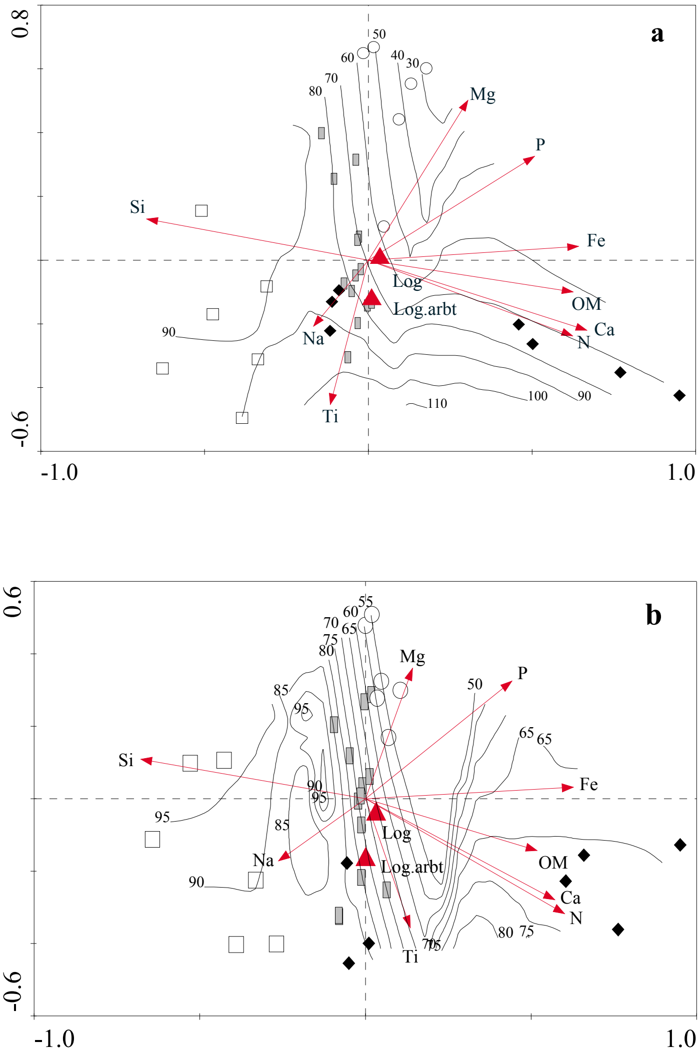

Figure 2. CCA ordination diagram with soil variables (arrows), historical management practice types nominal variables (▲) and sampling plots grouped into 4 communities (A-D) using species (a) abundance, (b) basal area data; first axis is horizontal, second axis vertical. The isolines of number of species are also plotted in the CCA ordination diagram. A= empty square, B= diamond, C= filled box, and D= empty circle. Sample labels and environmental variables pH and Li have been suppressed for clarity.

4.0. DISCUSSION

The classification of the vegetation of BFR showed that the forest is formed by overlapping plant communities, which were identified both by the cluster analysis and CCA ordination, and scrutinised by ANOSIM and SIMPER analyses. However, there were some differences in the grouping of samples into clusters for the abundance and basal area data sets. The relatively poor agreement between the clusters for the two data sets is not surprising. Several communities may show similarity in physiognomy (resulting from sharing dominant species), and differ in abundance of other species. The dominant species were not necessarily the most abundant and frequent ones in the communities, except for the *Senna spectabilis* sub-community. Thus, it might be misleading to classify woody plant communities using basal area alone, particularly in environments where relatively small stature plant species are frequent and anthropogenic disturbance is pronounced. A few large trees (e.g. *Alstonia boonei, Cynometra alexandri*) may contribute enormously to the total basal area of a plant community, yet they may be rare or scattered (hence, less important in terms of frequency). The high degree of dispersion of plots within communities as featured in the dendrogram (Fig. 1) and ordination diagram (Fig. 2) is usually indicative of internal heterogeneity of the cluster (MIRANDA et al. 2002).

The relatively high number of shared species among the communities is not surprising, because of the patchy and heterogeneous nature of the environment within the communities as a result of opening of canopy gaps due to natural and human disturbance (Chapter 2). The opening of canopy gaps as found in BFR is a recurring source of environmental heterogeneity in forest habitats that favours the coexistence of species with different life histories, contributing to the maintenance of community diversity (BARKHAM 1992, VALVERDE & SILVERTOWN 1998). Indeed, some of the species, (e.g. *Cynometra alexandri*, *Celtis mildbraedii*, and *Lasiodiscus mildbraedii)* all highly abundant and occurring in all four communities have been classified by WALAGA (1994) as 'generalists' with respect to the soil variation in BFR. Similarly, TERBORGH & ANDERSEN (1998) in their study of the distribution of tree species in a variety of habitats, found about 15% of the species to have been habitat specialists, while the majority were generalists. On the other hand, many canopy trees shed their leaves during the dry season, consequently increasing light availability. This allows the germination of seeds and growth of many light demanding species, even in areas of dense upper-canopy that would otherwise not have been possible.

The cluster analysis results are corroborated by the CCA biplots, which demonstrate that plant communities in this forest inter-grade and are not highly discrete, probably due to the individualistic nature of species responses to environmental factors. However, clear separation of *Pseudospondias microcarpa* Swamp Forest as well as the *Senna spectabilis* and the *Cynometra alexandri* dominated forest communities, compares to some extent with the findings of EGGELING (1947) and HOWARD (1991). These three communities were identified by EGGELING (1947) on the basis of a successional gradient, while HOWARD (1991) also distinguished the *Senna spectabilis* Forest Community. Results of the present study, however, contrast with earlier classifications in that the *Maesopsis eminii* Forest described by EGGELING (1947) was not identified. *Maesopsis eminii* Engl. is an early successional species that has been ascribed to a period when Budongo Forest was spreading unhindered, except for being contained by natural factors such as unfavourable soils or elephant herbivory (e.g. LAWS et al. 1975, WALAGA 1994). However, in the last two decades, large herbivores such as elephants, have disappeared from the interior of the forest (LAWS et al. 1975, SHEIL & SALIM 2004). Nonetheless, increasing anthropogenic disturbances, including mainly timber (targeting mahogany species and *Maesopsis eminii*) and pole harvesting, have become more common phenomenona in most parts of the forest, except in some patches in the nature reserve area (Chapter 2 & 6). Consequently, the successional pathways postulated by EGGELING (1947) have been disrupted. Shifts in relative densities of various woody species have also been observed, with some previously absent species now ranked as widespread (SHEIL et al. 2000). Indeed, disturbances, both human-induced and natural, are known to shape forest communities by influencing their composition, structure, and functional processes (DALE et al. 2001, van GERMERDEN et al. 2003). However, different levels and types of disturbance have differential impact on forest communities (HALPERN & SPIES 1995). The occurrence of *S. spectabilis* in the BFR interior and on its edges, and the dominance of *C. alexandri* (even in areas where it was treated with arboricides over 40 years ago) are, to a great extent, directly or indirectly results of human interventions. *Senna spectabilis* was commonly planted as an ornamental (SYNNOTT 1985), and is now naturalised widely in colonising forest and forest edges. The dominance of *C. alexandri* may be attributed to it having not been targeted for timber harvesting, hence, enjoying a competitive advantage over other species that have been constantly targeted for timber over the years.

The CCA ordination, to a great extent, illustrates the position of the forest communities and the link between the community species composition and the measured environmental variables operating in BFR. The CCA Axes 1 and 2 for both data sets had eigenvalues >0.33, which denotes a fair separation of species along both axes (TER BRAAK 1987). As a rule of thumb, an eigenvalue >0.30 indicates a strong gradient (TER BRAAK 1995). The relatively strong bias in the spatial distribution of tree species in relation to edaphic variation, as observed in BFR, has similarly been widely reported for tropical forest trees in Ghana (SWAINE 1996), neotropical rainforests (CLARK et al. 1998, SVENNING 2001) and the mixed dipterocarp forest in Malaysia (LEE et al. 2002). Soil characteristics such as texture, nutrient status, depth, and soil moisture regime are important factors that determine competitive relationships and growth rates of plants in a wide variety of environments, consequently, determining spatial or temporal species distribution (TILMAN 1982) and composition of a community (BARBOUR et al. 1987). A number of studies (e.g. DUIVENVOORDEN 1995, SWAINE 1996, CLARK et al. 1998, SHEIL et al. 2000, SVENNING 2001) demonstrated that species distributions were also strongly aggregated with respect to variation in topography, soil water, and soil nutrient status. In BFR, some of the soil nutrients (e.g. Si, Na, Mg, N and Ca) are clearly correlated with distinct forest communities. A study by WALAGA (1994) on the development of climax vegetation on BFR similarly reported significant correlations between local patterns of tree species distribution and soil variables (K, N, Mg, Ca and silt content). The fact that in the present study, apart from soil nutrients, no other measured environmental variable was strongly correlated with Axis 1 of the CCA, suggests the strong influence of soil nutrients on the species distributions in BFR. For instance, *Pseudospondias microcarpa*, *Eurphorbia teke* and *Neoboutonia melleri,* characteristic of the swamp forest, are spatially aggregated on silicon-rich soils in the seasonally flooded lower-slope areas. However, clear correlation between forest vegetation and Si, Fe, Ti, and Li as shown in BFR was not previously well known. Nevertheless, it is reported that plants lacking in silica (Si) are more susceptible to biotic and abiotic stresses, can exhibit abnormal growth, and are structurally weak (EPSTEIN 1994, MARSCHNER 1995). This suggests that plants growing on silica rich soils are more likely to survive and contribute to the high species richness of the forest community as shown for the *Pseudospondias microcarpa* Swamp Forest in BFR. It has been suggested for Borneo's mixed dipterocarp forests that availability of soil nutrients, particularly phosphorus and magnesium, directly influences species distributions and community composition (BAILLIE et al. 1987, POTTS et al. 2002). Phosphorus is widely reported to be the principal nutrient limiting factor for tree growth and productivity in tropical forests (SOLLINS 1998, TIESSEN 1998, CLEVELAND et al. 2002). Other studies (including LICHTER 1998 and FRELICH et al. 2003) have similarly reported on the influence of soil nitrogen on the structure of forests (especially their understorey component). While according to SOLLINS (1998) phosphorus availability, aluminium toxicity, drainage, water holding capacity, and availability of K, Ca, Mg, N and micronutrients such as B and Zn are reportedly the soil properties most likely to influence species composition and structure of lowland tropical rainforests.

The distribution of plant communities along edaphic gradients, as shown in BFR, supports the individualistic hypothesis of community organization (GLEASON 1926). Similarly, this study suggests that small spatial scale variability in soil nutrients (at the scale of hundreds of meters) structures the plant communities of BFR. Indeed, elsewhere it has been reported that species composition and forest structure can vary quite dramatically with small scale edaphic and topographic gradients (NEWBERRY & PROCTOR 1984, BAILLIE et al. 1987, DAVIES & BECKER 1996). On the other hand, the wide and abundant occurrence of *Cynometra alexandri* across a variety of soil types and nutrient status contradicts OSMASTON's (1959) characterisation of *Cynometra* consociation as an edaphic climax. However, it confirms Walaga's (1994) suggestion that *Cynometra alexandri* is a generalist with no soil preferences, and therefore OSMASTON's (1959) theory, as regards its dominance only under certain soil conditions, is not operational in BFR.

Although there is strong evidence that soil nutrients and anthropogenic gradients influence the composition and structure of plant communities in BFR, there may be other abiotic and biotic factors whose influence cannot be disentangled in this study. For instance the plots of the Swamp Forest community, although located far apart, in terms of species composition resembled each other more than the adjacent up-slope plots along the same transect, suggesting a strong relationship between the habitat and floristic composition (see also TERBORGH et al. 1996). It appears that *Pseudospondias microcarpa* and *Senna spectabilis* show a degree of habitat specialization, suggesting that the *Pseudospondias microcarpa* Forest and *Senna spectabilis* Forest are organised by niche-assembly processes (CLARK et al. 1999, HUBBELL 2001). Species neighbourhood effects may also contribute to the differences in species community composition found in BFR. For instance, the *Cynometra alexandri* Forest had the lowest species richness, followed by the *Senna spectabilis* Sub-community. A secondary effect of the closed canopy of these forest types is that it limits the understorey development leading to a simplified forest structure and lower diversity of plants (FRANKLIN et al. 1993).

5.0. CONCLUSIONS

The numerical classification-multivariate analysis approach followed in this study has proven to be effective in the description of the forest communities and forest community-environment relationships in this semi-deciduous tropical rainforest. Although the cluster analysis clearly shows the existence of four plant community groups, the present BFR is more of a mosaic of community types with varying dominant and abundant species, because of the considerable overlap in species composition and local environment. The CCA ordination points to the importance of soil nutrients (i.e. OM, Na, N, Ca, Mg, Si, and Ti) and anthropogenic disturbances as controlling factors of forest community type patterns in BFR. Hence, there is evidence supporting the hypothesis that edaphic, habitat variation and anthropogenic factors that interrupt environmental vegetation gradation, directly contribute to the diversity and heterogeneous nature of the BFR plant communities. The impacts of human activities may play an important role in the conservation of the natural vegetation of this forest; hence, adequate management plans are urgently required for BFR. It will also be important to ensure adequate conservation of the various forest community types identified, to preserve its woody species diversity.

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CHAPTER 4

Alpha-diversity and species-abundance distributions of woody plants in a semi-deciduous tropical rainforest, NW Uganda

Abstract

Alpha-diversity, species-abundance distributions and ecological importance of tree and shrub species and families were examined based on stem diameter ≥2.0 cm in the semi-deciduous Budongo Forest Reserve (BFR), north-western Uganda. Thirty-two 0.5 ha plots were sampled, capturing the main forest communities, historical management practice types and topographic gradients in the forest. Fisher's alpha (α) and Shannon-Wiener (H') diversity indices were employed to quantify alpha-diversity, while a SHE Analysis was employed to characterise species-abundance distributions. A total of 36468 individuals, representing 269 species in 171 genera and 51 families were recorded. The use of stem diameters of ≥2.0 cm revealed 53 more species (19.7%), with only 216 species recorded for the standard ≥10 cm dbh minimum size usually applied in tropical forests. The most speciose families were Euphorbiaceae, Fabaceae, Rubiaceae, Moraceae, Meliaceae, Rutaceae, Annonaceae, and Flacourtiaceae, accounting for 147 (54.6% of 269) species. The families with the highest familial importance values (FIV; based on relative dominance, density, and diversity) were Fabaceae (17.5), Euphorbiaceae (16.3) and Ulmaceae (8.35). The species with the highest importance value index (IVI; relative density and basal area) were C*ynometra alexandri* C.H. Wright (14.17)*, Lasiodiscus mildbraedii* Engl. (7.74) and *Celtis mildbraedii* Engl. (6.37). Fisher's alpha-diversity ranged 4.45 - 30.59 and 3.07 - 29.7 for species with stem diameters ≥2.0 cm and ≥10 cm, respectively, with a paired t-test indicating that they are significantly different ($t_{(31)} = 6.54$, $p<0.001$). Alpha-diversity and richness were highest in the logged and arboricide treated sites (H' = 3.17±0.10, α = 21.43±1.10, S = 84.68±2.95), being lowest in logged only sites (H' = 3.05±0.19, α = 19.66±2.68, S = 76.50±6.63), with the nature reserve sites intermediate (H' = 2.57±0.12, α = 11.19±1.51, S = 49.43±5.20). Diversity and richness were highest in the *Pseudospondias microcarpa* Swamp Forest, followed by *Funtumia elastica-Pouteria altissima*, *Lasiodiscus mildbraedii-Khaya anthotheca* and lowest in *Cynometra alexandri-Rinorea ilicifolia* forest community. A SHE analysis showed greater richness (ln(S)) and H diversity for the ≥2.0 cm than the ≥10cm stem diameters. BFR exhibits characteristics intermediate between log-normal and log-series species-abundance distributions, indicating a community with a small number of abundant species and a relatively large proportion of rare species. This study shows that it is better to characterize woody species richness of a forest using >2 cm rather than ≥10 cm dbh, particularly if many woody species rarely exceed 10 cm dbh, which is quite prevalent in semi-deciduous forests. Although BFR has a similar suite of woody plant families to other Albertine Rift, Guineo-Congolese and Amazonian forests, its species diversity and richness is low compared to Amazonia and other high rainfall tropical forests.

***Keywords*:**, Alpha-diversity, dbh cut-offs, Ecological importance, Importance Values; Management practices, Rarefaction diversity, Semi-deciduous forests, SHE Analysis, Species-abundance distributions, Threatened species.

1.0. INTRODUCTION

Tropical rainforests are regarded as the most speciose biome of the world, and yet they are under serious threat of degradation and biodiversity loss. The ecological and environmental importance of these forests necessitates their conservation and sustainable management, aided by accurate identification and better understanding of the biology of forest species (Sagers and Lyon 1997), patterns of species distribution and quantitative properties of diversity (Buzas and Hayek 1996). The important characteristics of tropical forests are plant species richness and diversity, which are major criteria in nature conservation and ecology (e.g. Liu and Bråkenheilm 1996, Ricotta *et al*. 2002), and emphasised in biodiversity research and preservation because of their ecological, economic and environmental values (Wickham *et al.* 1995). Hence, under the present circumstances of increased anthropogenic disturbances and climate change, reliable information about plant species diversity patterns and distributions has become critical in order to protect and conserve the remaining species efficiently and effectively (e.g. Valencia *et al.* 1994, Myers *et al.* 2000, Cadotte *et al.* 2002, Natta *et al.* 2002, Eilu *et al.* 2004). Indeed, measures of diversity at local and regional scales have often been related to species alpha-diversity and richness, which are important to the functioning of an ecosystem (Burke and Lauenroth 1995). Species diversity and richness underlies many ecological models (e.g. Gotelli and Colwell 2001).

Although Budongo Forest Reserve (BFR) in Uganda is of high conservation values with an abundant population of chimpanzee (*Pan troglodytes*), as well as African mahogany trees, we do not yet have a full understanding of its woody species diversity. Previous studies in BFR related to woody plant species diversity have looked at tree species richness, diversity and turnover (e.g. Sheil 1996, Plumptre 1996, Eilu *et al.* 2004), broad vegetation descriptions (e.g. Eggeling 1947, Synnott 1985), and patterns of tree species richness in terms of a successional series (Eggeling 1947, Connell 1978). Sheil (1996) investigated species diversity and community structure using Eggeling's permanent sample plots and found species richness to have increased over a 30 year period, and reflecting community level differences. He found that tree diversity in BFR may markedly increase following disturbances that occurred three decades previously. Both Eggeling (1947) and Connell (1978), using Eggeling's data, argued that species number increases during the initial development from colonising to mixed forest and declines again during the progression to a *Cynometra alexandri* C.H. Wright dominated community. Plumptre (1996), using ordination of basal areas of common tree species, showed that the geographical position of a forest compartment explained more of the variation in species distribution than the variation between adjacent logged and unlogged compartments.All previous studies focused only on trees of dbh ≥10 cm, although in BFR a number of woody species such as *Coffea euginioides* S. Moore and *Rinorea oblongiflora* C. Marquand that flower at a dbh of <2.5 cm and others that rarely attain a ≥10 cm dbh at maturity occur (EN. Mwavu, personal observations). Studies (e.g. Valencia *et al.* 1994, Killeen *et al.* 1998, Galeano *et al.* 1998) that have employed a <10 cm dbh in the sampling of alpha diversity of woody plants in tropical forests have shown that forest woody diversity is substantially contributed to by treelets. Treelets have been classified as woody plants 5 cm dbh excluding palms, lianas and hemiepiphytes (Galeano *et al.* 1998), or as woody sub-canopy plants of 5 - 10 cm dbh (Valencia *et al.* 1994). Shrubs are rooted, woody, self-supporting plants up to 5 m high, multi-stemmed or single-stemmed and branching at or near the ground level when 2 - 5 m high, or either multi-stemmed or single-stemmed when less than 2 m high (Edwards 1983). In this study, treelets are classified as woody species that have stem diameter of 2.0 - 10 cm, excluding shrubs, lianas, palms and hemiepiphytes. Although some woody plants with a dbh much lower than 10 cm may be treelets, their contribution to the overall species diversity may be significant, and influence forest composition and structure (Pitman *et al.* 2001). It is also worthy of noting that tree species ≥10.0 cm dbh constitute only 15-20% of the complete floras of many neotropical sites (Gentry and Dodson 1987), while in many Amazonian forests where tree species prevail they scarcely account for 10 - 30% of the total number of species (Duivenvoorden 1994). Hence, the use of a lower than 10 cm stem diameter size cut-off results in the sampling of a larger proportion of the forest flora (Phillip *et al.* 2003).

Furthermore, no reported study has yet attempted to separate the effects of richness and evenness on woody species diversity (H') and determine the underlying species-abundance distributions in BFR. In addition, the relative ecological importance of each plant family or species, and their relative contribution to the entire forest plant community composition has not been determined so far. Over the years, silvicultural treatments have changed, large herbivores, notably elephants (*Loxodonta Africana*), have disappeared from the forest interior (e.g. Laws *et al.* 1975, Dawkins and Phillip 1998, Sheil and Salim 2004), and anthropogenic disturbances have increased, leading to significant environmental changes in BFR. Changes in environmental and ecological processes may contribute to both accumulation and erosion of species diversity and richness at all spatial and temporal scales (e.g. Sheil 1999, Peltzer *et al.* 2000, Cadotte *et al.* 2002, Tálamo and Caziani 2003).

In spite of these studies, a number of questions on; i) patterns of alpha-diversity of woody plants along a topographic and historical management practice gradient, ii) diversity in relation to minimum stem diameter, and iii) effects of richness and evenness on diversity (H') in BFR remain largely unanswered. This study aimed at assessing alpha-diversity of woody plants (i.e. trees, treelets and shrubs excluding lianas) in BFR, and investigating the nature of species diversity in relation to minimum stem diameter size (2 cm versus 10 cm), and historical management practice types. Unlike previous studies, the effects of richness and evenness on H' were separated, and the species-abundance distributions within the plant communities determined. In order to achieve the stated aim, the following questions were posed: 1. Are species diversity for the ≥2.0 cm and ≥10 cm stem dbh cut-offs different? If so, does the traditional use of only ≥10 cm dbh underestimate the diversity of BFR? 2. Which are the most ecologically important and speciose woody plant families? 3. What species-abundance distributions types do the forest plant communities exhibit? 4. How do the alpha-diversity and plant family composition of BFR compare with other tropical rainforests?

2.0 MATERIALS AND METHODS

2.1. Study area

The BFR is located at the top of the escarpment east of Lake Albert on the edge of the western rift valley (Howard 1991) in north-western Uganda, between Masindi town and Lake Albert. It has an area of 793 km^2 and lies between $1^{0}37'$ and $2^{0}03'$ N and $31^{0}22'$ and $31^{0}45'$ E (Figure 1). The altitudinal range is 700-1270 m above sea level with a mean of 1050 m. It is part of the Albertine Rift Ecoregion, which consists of several forests, and believed to be one of Africa's most speciose and highly endemic regions. It is now also one of Africa's most important sites for biodiversity conservation as these forest habitats contain nine primate and numerous endemic bird species (Struhsaker 1981, Plumptre *et al.* 2007). Furthermore, BFR is probably the most important of these forests for conservation as it has five diurnal primate species (Tweheyo 2003), with probably the largest population of chimpanzees in Uganda, as well as populations of African mahogany trees (e.g. *Khaya anthotheca* (Welw.) C.DC. and *Entandrophragma* spp.).

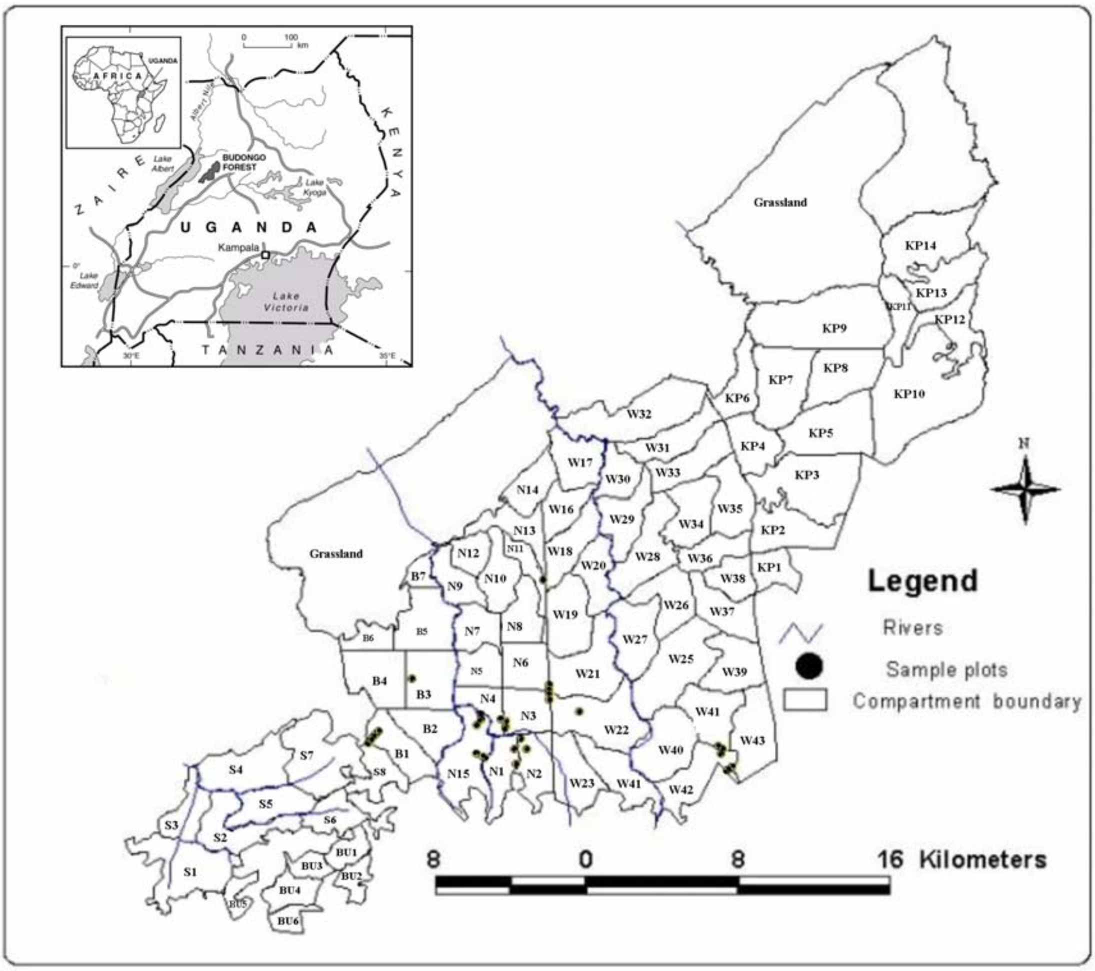

Figure 1. Location and map of Budongo Forest Reserve, Masindi District, Uganda, showing all the management compartments. N= Nyakafunjo, S= Siba, B= Biiso, W= Waibira, KP= Kaniyo Pabidi are the constituent blocks that have further been sub-divided and numbered (e.g. N1-N15).

The general ecology, environment, management and history of BFR have been described by Eggeling (1947), Synnott (1985) and Howard (1991). BFR is broadly classified as medium altitude semi-deciduous moist tropical rainforest, because several of the dominant species (e.g. *Celtis* spp., *Maesopsis eminii* Engl., *Ficus* spp. etc) are at least briefly deciduous (Eggeling 1947, Langdale-Brown 1964), with the notable exception of the shade-tolerant *Cynometra alexandri* C.H. Wright (Sheil 1997). Eggeling (1947) classified the vegetation of BFR into four broad forest types; *Cynometra*, mixed, colonising woodland and swamp forest, following a successional gradient. However, a recent numerical classification (Chapter 3) revealed four forest community types namely; (i) *Pseudospondias microcarpa* Swamp forest, (ii) *Funtumia elastica-Pouteria altissima* Secondary Dry forest, (iii) *Celtis mildbraedii-Lasiodiscus mildbraedii* mixed forest, and (iv) *Cynometra alexandri- Rinorea ilicifolia* forest. Generally, however, there is a mosaic of forest types, resulting from forest dynamics and management history and position on slope? (Plumptre 1996, Chapter 3). Over the years, BFR has been managed for economic, conservation and environmental benefits, and a number of management plans have been implemented (Plumptre 1996, UFD 1997). Most of the forest's compartments have been treated with arboricides and logged at least once, except for a few that have been set aside as "nature reserves" since 1932 (UFD 1997).

The whole area is well weathered, slopes are with a few exceptions gradual and the intervening ridges are rounded. The valley bottoms are generally, well weathered, and many of the streams are trickles through rattan (*Calamus deerratus* Mann & Wendl.) swamps, with no apparent flow during the dry months (Eggeling 1947). There are two types of soils, a tropical red earth and a murram. The red earth, in profile varies from a heavy loam or sandy clay to a very sandy loam characteristic of many of the valley bottoms (Eggeling, 1947). Generally, the soils are deep with little differentiation into clearly defined horizons and possess a fine granular structure moulded into larger weakly coherent clods, which are friable and porous. The climate is tropical, with two rainfall peaks, from March-May and September-November, and a dry season from December to February. Mean annual rainfall is 1500 mm. Like all equatorial climates, BFR is characterised by high temperatures with low daily variation. Maximum temperature recorded in a 24-hour period rarely exceeds 32^0C and only occasionally drops below 24^0C.

2.2. Sampling and data collection

The forest has been divided for administrative and descriptive purposes into five large blocks (named after local villages), namely Biiso (B), Nyakafunjo (N), Siba (S), Waibira (W) and Kaniyo-Pabidi (KP). For management purposes the blocks have been further sub-divided into numbered compartments (e.g. N1, N15, W21, etc; Figure 1). There are three general historical management practice types, namely (a) logging and arboricide treatment, (b) logging without arboricide treatment, and (c) no logging and no arboricide treatment (nature reserve), which formed the basis for stratifying the forest and the choice of sites for vegetation sampling (Table 1). An attempt was made to capture the main forest types and the environmental variations as much as possible within the sampled compartments. In each compartment and following a topographic gradient, transects were established, along which 50 x 100 m (0.5 ha) plots consisting of five (50 x 20 m (0.1 ha)) contiguous sub-plots were laid for vegetation sampling. Along each transect, at least three 0.5 ha plots were laid following topographic position categories (lower slope (swamp), mid-slope, upper-slope, flat/ridge top), and oriented at right angles to this gradient, with the long side of the plot parallel to the contour.

Table 1. Compartments in Budongo Forest Reserve, with historical management practice types where study plots were situated. The compartments are designated by the block name initial and numeral (e.g. S8 means compartment number 8 of Siba block).

Block	**Compartment**	**Management practices/history**		
		Mechanical logging	**Pitsawn**	**Arboricide(butyl esters) treatment**
Nyakafunjo	N15 (Nature Reserve)	None	None	None
	N2	1945-47	None	Treated*
	N3	1947-52	None	Treated, 1960-61
Waibira	W21	1963-64	1995-97	Treated*
	W22	1965-1966	None	Treated*
	W42	None	1977-81	None
	W43	None	1977-81	None
Biiso	B1	1935, 1982-86	None	Treated, 1958
	B4	1941-42	None	Treated*
Siba	S8	1930-35	None	None

* Arboricide treatment years are unknown

Counting stems, measuring stem diameter and preliminary identification of all trees and shrubs (hereafter referred to as woody plants) with ≥2.0 cm stem diameter was done systematically, with stems being blazed to prevent accidental re-measurement. 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 buttresses or other stem irregularities at breast height, stem diameter was measured above the buttresses. For each shrub, all stems were counted, the diameter of three "average" stems measured, and then the composite dbh of the whole shrub was calculated to enable the computation of its basal area in the manner used for the trees. Species identification in the field was done using identification guides, but mainly based on the Flora of Tropical East Africa (FTEA) (Polhill 1952 and subsequent volumes), and the help of a botanist familiar with the flora. For species that could not be confidently identified in the field, vegetative structures and if available, flowering or fruiting samples were collected, pressed and vouchers subsequently identified at the Botany Department Herbarium (MHU), Makerere University, Kampala, Uganda.

2.3. Data analysis

The total number of species recorded in the sampling plots (species richness), rarefaction measure as well as Shannon-Wiener diversity Index (H'), Fisher's alpha diversity and SHE Analysis, were employed to quantify and characterise species diversity and species-abundance distributions of the plant communities. Rarefaction diversity ($E(S_n)$) was also computed from the floristic data in order to compare species numbers from samples of different sizes among the community types. It is used to estimate the number of species expected ($E(S_n)$) to be present in a random sample of individuals taken from any given collection, and provides confidence limits of species richness (Hsieh and Li 1998). It also allows for a meaningful standardisation and comparison of datasets from different communities (Gotelli and Colwell 2001). The generation of rarefaction curves (Hsieh and Li 1998). $E(S_n)$ is expressed as:

$$E(S_n) = 1 - \frac{(N - N_i)/n}{N/n}$$

where **N** is the total number of individuals in the sample; and **N***ᵢ* the number of individuals belonging to the i^{th} species (Tokeshi 1999).

Importance value index (IVI), the relative ecological importance of each plant family or species to the entire forest community (Curtis and McIntosh 1951), was used to compare the relative contribution of each family and species to forest woody plant composition. Using all measured individuals of ≥2.0 cm diameter, IVI for each species was determined for the total forest community, and calculated as:

$$\text{IVI} = \frac{(\text{Re}\mathit{lative\ density} + \text{Re}\mathit{lative\ basal\ area})}{2}$$

While Family Importance Value (FIV) was calculated as the average of the values of relative dominance (RDo), relative density (RDe), and relative diversity (RDi) i.e.

$$\frac{RDo + RDe + RDi}{3},$$

where

$$\text{- } RDo = \frac{Basal\ area\ of\ Family}{Total\ basal\ area} \times 100$$

$$\text{- } RDe = \frac{Number\ of\ individuals\ in\ a\ Family}{Total\ number\ of\ woody\ individuals} \times 100$$

$$\text{- } RDi = \frac{Number\ of\ Species\ in\ Family}{Total\ number\ of\ Species} \times 100$$

Alpha-diversity for both ≥2.0 cm and ≥10 cm stem diameter data at the 0.5 ha scale were quantified using Fisher's alpha (α) and Shannon-Wiener (H') diversity indices, using all individuals and species per plot. The α-diversity index is relatively insensitive to sample size and performs very well on data within forest plots (Condit *et al.* 1998), and if abundance of plants varies considerably among plots (Laurance *et al.* 2001). In contrast, H' incorporates evenness and, therefore, describes the distribution of individuals among the species in addition, to number of species in a plot (Magurran 2004), 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.

The decomposition of diversity using the equation H=lnS+lnE, to enable separation of the effects of richness (S) and evenness (E), is what is referred to as SHE analysis (Hayek and Buzas 1998). In SHE analysis the values of lnS and lnE were calculated as well because the pattern of H', lnS, lnE, and lnE/lnS during the accumulation of individuals is characteristic of the underlying species abundance distributions (Hayek and Buzas 1998, Magurran 2004). The pattern of H', lnS, lnE, and lnE/lnS in relation to the number of samples was graphically displayed and examined for the specific species-abundance distribution (e.g. log series, log normal, broken stick, etc.). With the broken stick distribution, both lnS and H' increase while lnE remains constant; for log normal, lnS and H' increase while lnE/lnS remains constant; and for the log series lnS increases and lnE decreases while H' remains constant (e.g. Hayek and Buzas 1998, Magurran 2004).

The richness, alpha-diversity indices, rarefaction and SHE analyses were performed using the Species Diversity and Richness III Programme (Pisces Conservation Ltd. 2003). Differences in species richness and diversity between sample plots, historical management practice types, and forest community types were compared by one-way ANOVA and Tukey HSD for unequal sample sizes. A paired t-test was also performed to determine whether species diversity values from the ≥2.0 cm and ≥10 cm stem-diameter data sets stastically differ.

3.0. RESULTS

3.1. Species composition and richness

Community composition

A total of 36,468 stems of woody plants with a diameter of ≥2.0 cm, representing 269 species in 171 genera and 51 families, were recorded from the 32, 0.5 ha plots. This compares with 216 species for ≥10 cm dbh cut-off, thus excluding 53 (19.7%) species from the species pool. The 53 species represented shrubs and treelets, of which 20 were distinctly shrubs in their growth form regardless of where they were found growing in the forest (either forest edge or interior). Of the 269 species, 15 were among the 46 threatened plant species on the 2000 IUCN Plant RedList for Uganda, of which two are endangered and eight vulnerable (Table 2) (IUCN 2000). However, additional RedList species may be present among the unsampled herbaceous, epiphyte and liana species. The species-accumulation curves for the ≥2.0 cm and ≥10 cm stem diameter data, at both 0.1 ha and 0.5 ha plot sizes, all reached an asymptote, showing that species richness was not far from being completely recorded for this forest (Fig. 2). In addition, the species-accumulation curves were below the rarefaction curves, suggesting heterogeneity among the samples (patchiness).

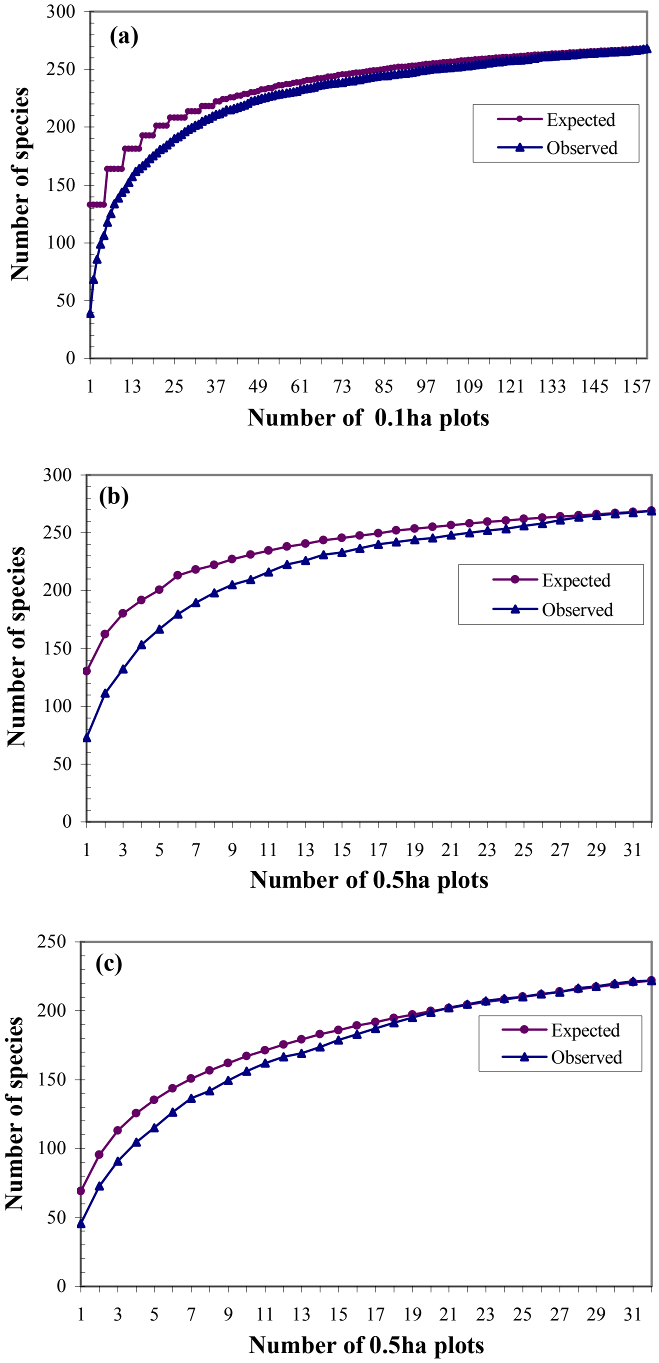

Figure 2. Rarefaction (expected) and species-accumulation (observed) curves for woody species of (a) stem diameter ≥2.0 cm, measured in 160, 0.1ha plots, and (b) ≥2.0 cm and (c) ≥10 cm dbh, measured in 32, 0.5ha plots in Budongo Forest Reserve, north-western Uganda. The finite version of the rarefaction was used where resampling was done without replacement.

By default the following points refer to the ≥2.0 cm stem diameter scale unless stated otherwise. The nine families with the highest number of genera were Euphorbiaceae (22 genera), Fabaceae (18 genera), Rubiaceae (16 genera), Rutaceae (8 genera), Sapindiaceae (8 genera), Meliaceae (8 genera), Annonaceae (7 genera), Moraceae (7 genera) and Flacourtiaceae (7 genera). Of the remaining 42 families, 16 were represented by only one genus each. The most speciose genera were *Ficus* (12 species), *Celtis* (5), *Rinorea*

(5) and *Albizia* (5). The eight most speciose families were Euphorbiaceae (34 species), Fabaceae (24 species), Rubiaceae (24 species), Moraceae (18 species), Meliaceae (17 species), Rutaceae (12 species), Annonaceae (10 species) and Flacourtiaceae (10 species), accounting for 147 (54.6%) of woody species (Appendix 1). The remaining 43 families had low representation, with 19 of them having only one species each.

Table 2. Threatened species encountered, and their abundances from the 32, 0.5ha plots in the semi-deciduous tropical Budongo Forest Reserve, north-western Uganda.

Species	***Total Number of Individuals***	***Number of plots***	***Conservation status****
Albizia ferruginea (Gull. & Perr.) Benth	5	4	Vulnerable
Cordia millenii Bak.	45	16	Lower risk/ least concern
Dialium excelsum J. Louis ex Steyaert	11	8	Endangered
Entandrophragma angolense (Welw.) C.DC.	39	16	Vulnerable
Entandrophragma cylindricum (Sprague) Sprague	78	17	Vulnerable
Entandrophragma excelsum Sprague	4	2	Lower risk
Entandrophragma utile (Dawe & Sprague) Sprague	66	22	Vulnerable
Guarea cedrata (A. Chiev.) Pellegr.	100	22	Vulnerable
Irvingia gabonensis (Aubry-Lecomte O'Rorke) Baill	4	4	Lower risk/ near threatened
Khaya anthotheca (Welw.) C.DC.	489	28	Vulnerable
Lovoa swynnertonii Bak. F.	24	10	Endangered
Lovoa trichilioides Harms	30	7	Vulnerable
Milicia excelsa (Welw.) C.C.Berg	16	10	Lower risk/ near threatened
Pouteria altissima (A. Chiev.) Aubrev. & Pellegr.	357	26	Lower risk
Prunus africana (Hook. F.) Kalkman	1	1	Vulnerable

**Data sources: Oldefield et al. (1998), Hamilton (1991) and IUCN Red List of Threatened species (2000).*

One hundred and one (101) species were represented by <10 individuals, of which 28 species were each represented by a single individual. The nine species with the highest number of individuals were *Lasiodiscus mildbraedii* Engl., *Acalypha neptunica* Muell. Arg, *Acalypha ornata* Hochst.ex A., *Celtis mildbreadii* Engl., *Senna spectabilis* (DC.) Irwin & Barneby, *Funtumia elastica* (Preuss) Stapf., *Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze, *Thecacoris lucida* (Pax.) Hutch and *Cynometra alexandri* C.H. Wright, accounting for 20647 (56.6%) of the individuals in the 32 plots. These species combined high abundance with high frequency, except for *S. spectabilis*.

The ecologically most important families were Fabaceae, Eurphobiaceae, Ulmaceae, Meliaceae, Rhamanaceae and Apocynaceae, with FIV of 17.5, 16.33, 8.35, 6.57, 6.11, and 5.49, respectively (Table 3). Fabaceae, Eurphobiaceae and Rubiaceae had both high generic and species representation. The most important species were *C. alexandri, L. mildbraedii, Celtis mildbreadii* Engl., *S. spectabilis, A. neptunica, A. ornata* and *F. elastica* (Table 4).

Table 3. Families with the highest Familial Importance Values (FIV) (i.e. FIV≥3.0) for woody plants with stem diameter ≥2.0 cm measured in thirty-two 0.5 ha plots in Budongo Forest Reserve, north-western Uganda.

Family	***No. of Genera***	***No of Spp.***	***FIV***
Fabaceae	18	24	*17.50*
Euphorbiaceae	22	33	*16.33*
Ulmaceae	4	8	*8.35*
Meliaceae	8	17	*6.57*
Rhamnaceae	2	2	*6.11*
Apocynaceae	6	7	*5.49*
Moraceae	7	18	*4.98*
Rubiaceae	16	28	*3.69*
Violaceae	1	5	*3.61*
Sapotaceae	6	9	3.04
		Total	75.67%
		Remaining families	41 (24.33%)

Table 4. The 18 species with the highest Importance Value (IV) (i.e. IV≥1.0) for woody plants with stem diameter ≥2.0 cm measured in thirty-two 0.5 ha plots in Budongo Forest Reserve, north-western Uganda.

Family	***Species***	***Species IV***
Fabaceae	*Cynometra alexandri* C.H. Wright	14.17
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	7.74
Ulmaceae	*Celtis mildbreadii* Engl.	6.37
Fabaceae	*Senna spectabilis* (DC.) Irwin & Barneby	4.89
Euphorbiaceae	*Acalypha neptunica* Muell. Arg.	4.64
Euphorbiaceae	*Acalypha ornata* Hochst ex. A.	4.12
Apocynaceae	*Funtumia elastica* (Preuss) Stapf	4.09
Meliaceae	*Khaya anthotheca* (Welw.) C.DC.	2.92
Violaceae	*Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze	2.57
Euphorbiaceae	*Thecacoris lucida* (Pax.) Hutch	2.45
Ulmaceae	*Celtis zenkeri* Engl.	2.33
Euphorbiaceae	*Alchornea laxiflora* (Bench) Pax & K. Hoffm	2.01
Apocynaceae	*Alstonia boonei* De Wild.	1.85
Anacardiaceae	*Pseudospondias microcarpa* (A. Rich.) Engl.	1.51
Ulmaceae	*Celtis gomphophylla* Baker	1.32
Tiliaceae	*Glyphaea brevis* (Spreng.) Manachino	1.12
Violaceae	*Rinorea brachypetala* (Turcz.) O. Ktze	1.10
Rhamnaceae	*Maesopsis eminii* Engl.	1.05
	Total	66.25%
	Remaining species.	251 (33.75%)

Species richness

Species richness at the 0.5 ha level varied with topographic position and historical management practice type, ranging from 24-111 for ≥2.0 cm and 12-61 for ≥10 cm stem diameter (Table 5), but was clearly much lower when using stem diameter ≥10.0 cm. A paired t-test indicated that there were significant differences ($t_{(31)} = 20.16$, $p<0.001$) in species richness values from the ≥2.0 cm and ≥10 cm stem diameter size data. At the 0.5 ha level, species richness was highest in plots that were both logged and arboricide treated, and lowest in those with higher densities of large *C. alexandri* and *S. spectabilis* trees. Lower-slope plots, which are seasonally flooded, and from sites with a history of logging and arboricide treatment, but that have been under protection from both legal and illegal pitsawing for the past 15 years, and those from the nature reserve were the most species rich, compared to other plots on the same topographic category. Species richness was significantly different between the historical management practices for both the ≥2.0 cm (ANOVA, $F_{2,29}$ = 16.98, p <0.0001) and ≥10 cm stemdiameter data (ANOVA, $F_{2,29}$ = 37.27, p <0.0001). Species richness also varied significantly (ANOVA, $F_{3,28}$ = 13.3, p <0.0001) between forest communities, with the *Pseudospondias microcarpa* swamp forest having the highest, followed by *Funtumia elastica-Pouteria altissima*, *Lasiodiscus mildbraedii-Khaya anthotheca* and lowest in *Cynometra alexandri-Rinorea ilicifolia* forest community (Table 6).

3.2. Alpha-diversity and species-abundance distributions

3.2.1. Alpha-diversity

The ranges for α-diversity values were relatively low, from 4.45 - 30.59 for stem diameter ≥2.0 cm, and 3.07 - 29.7 for the ≥10 cm dbh data (Table 5). Using ≥2.0 cm stem diameter data resulted in higher Fisher's alpha values for 28 plots (or 87.5%), compared with ≥10 cm dbh data. However, this was not the case for H' values as some plots that had higher α-diversity values, did not similarly have higher H' values (Table 5). Generally, α-diversity was significantly higher for the ≥2.0 cm than for the ≥10 cm stem diameter data (p = 0.0239), while the H' was not (p = 0.075).

On the basis of ≥2.0 cm diameter data, plots within previously logged and arboricide treated compartments, had the highest α- diversity and H' values, followed by plots from the Nature Reserve, *S. spectabilis* dominated plots, and lastly *C. alexandri* dominated plots. Both α-diversity and H' were significantly higher for the previously logged and arboricide treated areas, followed by nature reserve and lowest for the logged only, for both ≥2.0 cm (α; p = 0.00032, H'; p = 0.0134) and ≥10 cm (α; p <0.0001, H'; p <0.0001) stem diameter data (Table 6). Forest communities also differed significantly (p <0.01) in alpha-diversity for both stem diameter ≥2.0 cm and ≥10 cm. Generally, species alpha-diversity was highest in *Pseudospondias microcarpa* swamp forest, followed by *Funtumia elastica-Pouteria altissima*, *Lasiodiscus mildbraedii-Khaya anthotheca* and lowest in *Cynometra alexandri-Rinorea ilicifolia* forest community (Table 6).

3.2.2. Species-abundance distributions

The SHE Analysis also showed greater richness (ln(S)) and higher H' diversity for the stem diameter ≥2.0 cm than ≥10 cm data (Figure 3). A graphical presentation of evenness and richness data shows that decreases in evenness are accompanied by increases in species richness for both stem diameter ≥2.0 cm and ≥10 cm data. SHE analysis further showed that the relatively greater H' for the ≥2.0 cm data resulted from greater richness (higher ln(S) curve) rather than evenness (ln(E)). Cumulative ln(E)/ln(S) remained relatively constant for both stem diameter size data sets, indicating that these data are best fitted by a log normal species-abundance distribution. However, a further look at the cumulative H' for both stem diameter sizes, revealed that H' becomes relatively constant with an increasing number of samples (N), which is characteristic of a log series distribution. In addition, for both data sets cumulative ln(E) decreased, although only slightly, which is characteristic of both the log normal and log series distributions. Thus, these data fit between the log normal and log series species-abundance distributions.

Table 5. Tree and shrub species richness and diversity in 32, 0.5 ha plots for the (a) ≥2.0 cm and (b) ≥10 cm minimum stem diameter data from Budongo Forest Reserve, north–western Uganda. Sample plot number, historical management practice types and forest community types (A-D) are included. A: *Pseudospondias microcarpa* Swamp; B: *Funtumia elastica-Pouteria altissima*, C: *Lasiodiscus mildbraedii-Khaya anthotheca*, and D: *Cynometra alexandri-Rinorea ilicifolia* Forest.

Historical management practice types	***Sample plot***	***Forest community type***	***≥2.0 cm stem diameter data***			***≥10.0 cm dbh data***		
			Species richness	***Fisher's alpha (α)***	***Shannon-Wiener (H')***	***Species richness***	***Fisher's alpha (α)***	***Shannon-Wiener (H')***
Logging and arboricide treatment	1	A	*106*	**30.59†**	*3.49*	**61†**	**29.27†**	**3.51†**
	2	C	**111†**	*29.90*	**3.65†**	*55*	*21.55*	*3.22*
"	3	C	*71*	*15.85*	*2.97*	*42*	*14.92*	*2.87*
"	4	C	*64*	*14.56*	*2.75*	*46*	*17.58*	*3.13*
"	5	A	*94*	*25.92*	*3.61*	*45*	*22.71*	*3.33*
"	6	C	*98*	*23.15*	*3.14*	*54*	*18.75*	*3.30*
"	7	C	*77*	*16.27*	*2.85*	*45*	*16.24*	*3.09*
"	8	C	*72*	*15.12*	*2.81*	*43*	*14.02*	*2.88*
"	15	B	*85*	*20.59*	*2.75*	*40*	*14.14*	*2.53*
"	17	B	*71*	*19.34*	*2.72*	*42*	*14.03*	*2.69*
"	18	B	*71*	*14.66*	**2.00†**	*38*	*11.65*	*2.14*
"	19	A	*83*	*21.41*	*3.00*	*49*	*21.61*	*3.23*
"	20	C	*91*	*23.68*	*3.53*	*56*	*23.51*	*3.37*
"	21	C	*92*	*24.71*	*3.38*	*55*	*24.89*	*3.27*
"	22	C	*76*	*18.23*	*3.24*	*46*	*15.44*	*3.11*
"	29	A	*78*	*22.59*	*3.61*	*46*	*20.65*	*3.22*
"	30	B	*83*	*22.35*	*3.47*	*50*	*17.81*	*3.26*
"	31	B	*92*	*23.40*	*3.77*	*52*	*17.35*	*3.19*
"	32	B	*94*	*24.77*	*3.51*	*57*	*22.64*	*3.38*
Nature Reserve	9	A	*87*	*27.21*	*3.53*	*42*	*16.85*	*2.99*
"	10	C	*77*	*18.71*	*2.74*	*43*	*13.51*	*2.35*
"	11	C	*67*	*14.97*	*2.91*	*34*	*10.19*	*2.50*
"	12	A	*103*	*28.43*	*3.71*	*48*	*19.85*	*3.18*
"	13	C	*66*	*15.36*	*2.80*	*33*	*9.72*	*2.30*
"	14	C	*59*	*13.26*	*2.59*	*24*	*6.08*	*1.98*
Logging	16	B	*67*	*17.83*	*2.79*	*22*	*7.08*	**1.61†**
"	23*	D	*47*	*10.02*	*2.34*	*18*	*4.90*	*2.00*
"	24*	D	**24†**	**4.45†**	*2.14*	**12†**	**3.07†**	*1.83*
"	25*	D	*56*	*11.61*	*3.05*	*31*	*9.70*	*2.81*
"	26*	D	*50*	*10.50*	*2.37*	*29*	*8.89*	*2.18*
"	27*	D	*59*	*13.14*	*2.48*	*26*	*10.07*	*2.50*
"	28*	D	*43*	*10.80*	*2.82*	*17*	*5.26*	*2.23*
	Overall	$\overline{X}$	**75.44**	**18.86**	**3.02**	**40.66**	**15.12**	**2.79**
		SD	**19.51**	**6.40**	**0.48**	**12.77**	**6.50**	**0.53**

* Indicates *Cynometra alexandri* dominated plots; † indicates the highest and lowest species number and diversity values.

Table 6. Fisher's alpha (α) and Shannon-Wiener (H') diversity indices and species richness (mean ± S.E.) calculated separately for sites with different historical management practice types using the ≥2.0 cm and ≥10 cm minimum stem diameter woody species data at a 0.5 ha plot scale. The diversity values are means of the plot values for each site.

Grouping	***No. of plots***	***≥ 2.0 cm stem diameter data***			***≥ 10.0 cm dbh data***		
		S	***α***	**H'**	**S**	***α***	**H'**
A). Historical management practice type							
Logging and arboricide treatment	19	84.68±2.95**a**	21.43±1.10**a**	3.17±0.10**a**	48.53±1.48**a**	18.88±1.04**a**	3.09±0.08**a**
Nature Reserve	6	76.50±6.63**a**	19.66±2.68**a**	3.05±0.19**ab**	37.33±3.53**b**	12.70±2.06**b**	2.55±0.18**b**
Logging	7	49.43±5.2**b**	11.19±1.51**b**	2.57±0.12**b**	22.14±2.61**c**	6.99±1.01**c**	2.17±0.15**b**
B). Forest community type							
Pseudospondias microcarpa Swamp	6	91.8±4.56c	26.03±1.43c	3.49±0.10c	48.5±2.69c	21.82±1.70c	3.24±0.07c
Funtumia elastica-Pouteria altissima	7	80.4±4.09c	20.42±1.31cd	3.00±0.23cd	43.0±4.37c	14.96±1.87c	2.69±0.25cd
Lasiodiscus mildbraedii-Khaya anthotheca	13	78.5±4.21c	18.75±1.40d	3.03±0.09cd	44.3±2.68c	15.88±1.52c	2.88±0.12c
Cynometra alexandri-Rinorea ilicifolia	6	46.5±5.09d	10.09±1.21e	2.53±0.14d	22.2±3.09d	6.98±1.20d	2.26±0.14d

Species richness and diversity values in same column under each grouping and dbh size data, accompanied by the same superscript do not differ significantly (Tukey, P<0.05).

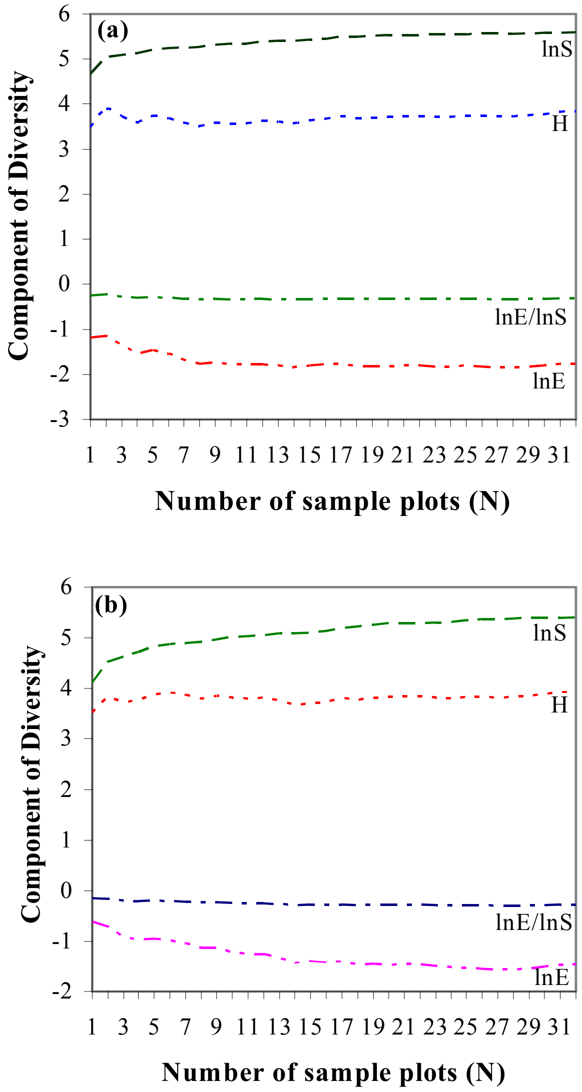

Figure 3. Plot of H, lnS, lnE, and lnE/lnS (SHE analysis) with increasing number of sampling plots (N) for stem diameter (a) ≥2.0 cm and (b) ≥10 cm tree and shrub data from 32, 0.5 ha plots in Budongo Forest Reserve, north-western Uganda.

The widely distributed species (present in ≥30 of the 0.5 ha plots) were *A. neptunica*, *A. ornata*, *F. elastica*, *C. zenkeri*, *Chrysophyllum albidum* G. Don., *Teclea nobilis* Del. and *Tapura fischeri* (Engl.) Engl., with only *A. neptunica* present in all 32 plots. In contrast, 171 (63.6%) species were each recorded in <10 plots, of which 51 were recorded in only one plot (Appendix 1). Thus, many of the species in BFR are sparsely distributed, with some of them having restricted habitats. For example, *P. microcarpa*, *Alangium chinense* (Lour.) Harms, *Glyphaea brevis*, *Cleistophilis patens* (Benth.) Engl. & Diels and *Neoboutonia melleri* (Muell. Arg.) Pain had >80% of individuals on the lower-slope, while *Neoboutonia melleri*, *Raphia farinifera* (Gaertn.) Hylander, *Euphorbia teke* Schweinf. ex Pax and *Leea guineensis* G. Don. were only recorded in the lower-slope seasonally flooded plots.

4.0. DISCUSSION

4.1. Species diversity and richness patterns

Species-accumulation and rarefaction curves for all the minimum diameter size cut-offs and plot sizes reached an asymptote, indicating that most of the species in the BFR community had been accounted for. This suggests that the sampling design chosen may successfully be applied to unveil the woody species diversity of lowland semi-deciduous tropical forests, like BFR. A ≥2.0 cm stem diameter size and 0.5 ha plots are suitable as most of the ecologically important species (e.g. *A. ornata*, *A. neptunica*, *R. ardiisiflora*, and *R. oblongifloria*) rarely exceed the more commonly employed ≥10 cm stem diameter. Using a stem diameter ≥2.0 cm unveiled 53 more species (19.7% of the total species richness), than with the ≥10 cm dbh. Similarly other tropical forest studies (e.g. Gentry and Dodson 1987, Valencia *et al.* 1994, Galeano *et al.* 1998, Neider *et al.* 2000) have shown that non-tree woody species can also exhibit high levels of species richness. Tree species ≥10.0 cm dbh constituted only 15-20% of the complete floras of many neotropical sites (Gentry & Dodson 1987), while in many Amazonian forests where tree species prevail they scarcely account for 10-30% of the total number of species (Duivenvoorden 1994). Furthermore, Pitman *et al.* (2001) noted that although some woody plants with a dbh much lower than 10 cm may be treelets, their contribution to the overall species diversity may be significant, and influence forest composition and structure, as revealed in this study. Therefore, it is a shortcoming to only characterize tropical forests by tree species based on ≥10 cm dbh alone, particularly in places where treelets, shrubs and non-tree woody plants might exhibit high levels of species richness (Gentry and Dodson 1987). Hence, inventories attempting to assess woody species alpha-diversity for conservation goals should consider growth forms other than large trees, as this will ensure that the greatest part of species richness is taken care of (Galeano *et al.* 1998).

Woody plant species diversity and richness of BFR, although relatively higher than for other Albertine Rift forests (e.g. Kasyoha, S=12, α=12.3; Eilu et al. 2004), appears to be relatively lower than that of forests receiving higher rainfall like those in Amazonia. In the present study, species richness ranged from about 12 - 61 per 0.5 ha (i.e. 24 - 122 ha^{-1}) for trees with ≥10 cm dbh, whereas Richards (1939) recorded 23, 28 and 47 species in Omo forest Nigeria, Hall and Swaine (1981) indicated 85 ha^{-1} in Kade Ghana, and Davies (1987) reported up to 76 species ha^{-1} in Sierra Leone. Elsewhere, using ninety-five, 0.1 ha plots, Duivenvoorden (1995) recorded a total of 1077 tree species, classified into 271 genera and 60 families from a Colombian rainforest, in NW Amazonia, while Valencia *et al.* (1994) recorded 473 species, 187 genera and 54 families using ≥5.0 cm dbh tree data from a 1 ha plot in Amazonian Ecuador. Higher Fisher's alpha diversity values than those for BFR have been found, for example >200 for the Amazonian forests, employing ≥10 cm dbh and a 1 ha plot (ter Steege *et al.* 2000). Indeed, in discussing the patterns and trends of tree diversity on six continents, Gentry (1988) showed that the highest alpha-diversity of trees in the world occurs in upper Amazonia, with record diversities of 275-283 tree species (dbh: ≥10 cm) per hectare. However, comparisons among the various studies are complicated by the fact that different plot sizes were used and the subjectivity used to achieve the various values is unclear.

This study showed that BFR has a number of very diverse woody plant communities, from relatively species rich *Pseudospondias microcarpa* Swamp communities to almost monodominant tracts of *C. alexandri* and *S. spectabilis*. Although not based on long-term data, these results compare with Sheil's (2001) findings that the almost monodominant *C. alexandri* forests have low species richness and densities of other tree species, compared to disturbed forests. The relatively high degree of variation in species richness and diversity between plots, even for plots from within the same management practice type or forest community type, suggests the heterogeneous nature of the BFR vegetation and environmental conditions. The differences in alpha-diversity, species composition and richness, and species distributions in BFR may also be a result of edaphic and light gradients, and stand age, as well as anthropogenic disturbances and historical management practices. The overall sizes of areas for the three historical management practice types within the forest main block differ greatly, with over 30 compartments having been logged and arboricide treated, 15 logged only, and only two are nature reserves (UFD 1997). Nevertheless, results for stem diameter ≥2.0 cm data at the 0.5 ha plot scale indicated that most (>47%, Table 5) of logged and arboricide treated plots had higher species richness and diversity compared with either nature reserve or logged only. In addition, all logged only plots had lower species richness and diversity than any of the logged and arboricide treated plots for the ≥10.0 cm dbh data. Hence, the difference in species richness and diversity between historical management practice types is not a result of the differences in the size of area *per se*. Furthermore, the higher species diversity and richness for lower-slope *Pseudospondias microcarpa* swamp forest, experiencing longer periods of soil moisture availability than for the drier upper-slope communities, suggests the influence of water availability. While the variation in species richness and diversity along a topographic gradient in BFR, has similarly been observed in the montane forests of Jamaica where species diversity increases from the ridges to the valley bottoms (Tanner 1977).

Results of this study, however, contrast with those of Chittibabu and Parthasarathy (2000), who recorded reduced diversity and altered species composition in disturbed plots, relative to undisturbed plots in a tropical evergreen forest in Ghats, India. The contrasts in species diversity between the BFR and Ghat forests may be attributed to differences in severity of disturbance experienced by the two forests. Presently BFR appears to be experiencing less severe and patchy anthropogenic disturbances. According to the Intermediate Disturbance Hypothesis (IDH; Connell 1978) species diversity of space-limited communities will be low at high and low rates of disturbance and maximal at some intermediate rate. Therefore, under conditions of periodic or recurrent anthropogenic disturbance at the intermediate level, species with different life history strategies (e.g. pioneer and primary species) are able to coexist and, consequently, high levels of species richness are maintained. Studies (e.g. Eggeling 1947, Sheil 1999) in BFR have presented evidence from limited data suggesting an important role for disturbance in maintaining tropical forest tree diversity. However, not all disturbance agents maintain species diversity in tropical forests, since species differ in the extent of canopy disturbance to which they can successfully regenerate (e.g. Swaine and Whitmore 1988). For instance, creation of gaps resulting in patchiness of canopy coverage and associated parameters may lead to low or high levels of species diversity at α, β, and γ scales (Leach and Givnish 1999). Whereas a closed canopy limits the understorey development leading to a simplified forest structure and lower diversity of plants (Franklin *et al.* 1993). This may explain the low species richness and diversity in the *C. alexandri-Rinorea ilicifolia* forest of BFR, which maintains an almost closed canopy throughout the year. This suggests that increased area coverage and densities of *C. alexandri* in BFR are more likely to adversely affect species richness and diversity of the forest than anthropogenic disturbance *per se*.

4.2. Familial importance

The relative ecological importance of the most important families is attributed to mainly high species richness and abundances of the constituent species. For example, Euphorbiaceae's inclusion among the most important families, is because of its being the most speciose (33 species, Table 3), and the constituent species are of high frequency in BFR. On the other hand, Rhamnaceae's inclusion among the most important families, although only represented by two species, is because of the combined high abundance and frequency of its constituent species. In BFR, like the forests of Peru and Ecuador, a small number of common species dominated the tree community, accounting for over 50% of individuals. Similarly Pitman *et al.* (2001) postulated that in regions where the tree flora was distinct from the Amazon, a small portion of the taxa occurred with high frequency and high local abundance across the landscape.

Comparison of BFR with other Albertine Rift and tropical forests, revealed important similarities in terms of the most ecologically important and speciose woody plant families, although the other studies employed different plot and minimum stem diameter sizes. For example, Fabaceae, Rubiaceae, Euphorbiaceae, Sapotaceae, Apocynaceae among the ten most important families in BFR, have similarly been recorded among the ten most important in the dry tropical forests of Madagascar (Cadotte *et al.* 2002). Similar to BFR, the families Euphorbiaceae, Meliaceae and Rubiaceae are the most speciose in other Albertine Rift forests of Uganda (Eilu *et al.* 2004), while Fabaceae and Sapotaceae were also reported among the top three most speciose in Amazonian Ecuador forests (Valencia *et al.* 1994). In a study of the forests of New Caledonia, Gillespie and Jaffré (2003) recorded Euphorbiaceae and Rubiaceae among the five most speciose families. In addition, Terborgh and Andresen (1998) reported Moraceae and Euphorbiaceae to be among the seven most abundant families in Amazonia. The ranking of Fabaceae as second in terms of its high number of genera and species in BFR, closely agrees with findings of Gentry and Ortiz (1993) and Valencia *et al.* (1994), in that Fabaceae is the most diverse family of trees in lowland primary forests. However, different stem diameter sizes might have been employed in these studies. Some families such as Euphorbiaceae, Meliaceae, Moraceae and Sapotaceae, probably very ancient families, are as well represented in BFR as in South America.

4.3. Species-abundance distributions

The SHE analyses showed woody species evenness to generally decrease with increasing sample size. Such changes in evenness with increasing sample size may better reflect changes in species diversity and abundance patterns (Small and McCarthy 2002). While the small change in H' diversity with increasing sample size as shown in the SHE analysis may be attributed to decreases in evenness that parallel increases in species richness. This suggests that the added species tend to be relatively uncommon or rare (Small and McCarthy 2002, Magurran 2004), further confirming the results of the rarefaction curves for the present study. The log-normal species-abundance distribution revealed for both stem diameter cut-offs (≥2.0 and ≥10cm), also indicates that some of BFR's forest communities are mature and diverse, with a high proportion of rare species (Hayek and Buzas 1998, Small and McCarthy 2002, Magurran 2004). BFR has historically experienced silvicultural treatments and intrinsic disturbances resulting in the creation of a mosaic of forest types at different seral stages, with the nature reserve area presumed to be the only representative of a mature forest. Characteristics intermediate between log-normal and log-series distributions exhibited by BFR woody plant community are expected of a community with a small number of abundant species and a relatively large proportion of rare species (Magurran 2004). Indeed, the BFR woody plant community is characterised by a small number of abundant species and a relatively large proportion of rare species.

5.0. CONCLUSIONS

Woody species diversity and richness in BFR is substantially contributed to by treelets and shrubs that rarely attain a stem diameter size of ≥10 cm. The use of 10 cm as a minimum dbh in woody plant diversity studies in forests, where many tree species rarely exceed 10 cm in diameter, tends to to underestimate woody plant diversity, potentially biasing the understanding of diversity patterns. Plant diversity in BFR is low compared to Amazonian and other high rainfall tropical forests. The present study shows that BFR's woody plant communities have a similar suite of plant families to other tropical forests of Africa and the Amazon. Most of the families are represented by a very small number of genera and species. They are also characterised by a small number of abundant species and a relatively large proportion of infrequent species. SHE analysis and rarefaction curves highlight the heterogeneous nature of the forest communities that may be attributed to influences of local environmental conditions and anthropogenic disturbances.

Although BFR has similar species richness and qualitative characteristics with other Albertine Rift forests, its harbouring of at least 15 threatened plant species and a viable chimpanzee population makes it a conservation priority in Uganda in the face of the increasing human population. However, the status of the threatened plant species including herbs, epiphytes and lianas should be examined using quantitative methods, given the increasing human population pressure surrounding the forest and increased loss of adjoining woodlands (Chapter 2). In addition to the nature reserve compartments, conservation efforts/priorities need to be mindful of the logged and arboricide treated areas, not only because of their high species diversity, but also as an important habitat for chimpanzees, providing them with a variety of plant species (particularly from the Family Moraceae) as sources of food (Tweheyo 2003). Disturbance events that lead to a great loss of seed trees and tend to fragment forest habitats should be avoided as they might have negative consequences for the maintenance of forest plant species diversity (Boutin and Herbert 2002), and survival of forest wild animals, particularly the chimpanzees.

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Appendix 1. Species list arranged alphabetically by family for tree and shrub species of ≥2.0 cm in diameter at reference height, recorded in 32, 0.5 ha plots within the semi-deciduous Budongo Forest Reserve, Uganda. The number of individuals, frequencies within plots and basal area for each species are included.

Family	***Species***	***Number of Individuals***	***Number of plots***	***Basal area***
Acanthaceae	*Brillintaisia cicatricose*	*2*	*1*	*0.0015*
	Whitfieldia elongata (Beauv.) C.B.Cl.	*84*	*12*	*0.048*
Alangiaceae	*Alangium chinense* (Lour.) Harms	*51*	*8*	*2.064*
Anacardiaceae	*Lannea africana*	*3*	*3*	*0.5795*
	Lannea barteri (Oliv.) Engl.	*1*	*1*	*0.1176*
	Lannea welwitschii (Hiern) Engl.	*45*	*11*	*1.4313*
	Mangifera indica L.	*6*	*1*	*0.3603*
	Pseudospondias microcarpa (A. Rich.) Engl.	*187*	*11*	*15.58*
Annonaceae	*Artabotrys likimensis* De Wild.	*2*	*1*	*0.075*
	Cleistopholis patens (Benth.) Engl. & Diels.	*146*	*13*	*7.4183*
	Greenwayodendron suaveolens (Engl. & Diels) Verdcourt	*73*	*19*	*0.1601*
	Monodora angolense Welw.	*36*	*16*	*0.2316*
	Monodora myristica (Gaertn.) Dunal	*6*	*5*	*0.8261*
	Uvaria welwitschii Engl & Diels	*1*	*1*	*0.0024*
	Uvariopsis congensis Robyns & Ghesquiere	*66*	*10*	*0.1524*
	Uvariopsis sp.	*11*	*6*	*0.256*
	Xylopia parviflora (A. Rich.) Benth.	*12*	*7*	*0.02*
	Xylopia staudtii Engl.	*4*	*2*	*0.0414*
Apocynaceae	*Alstonia boonei* De Wild.	*86*	*20*	*21.544*
	Funtumia africana (Benth.) Sprague	*1*	*1*	*3.008*
	Funtumia elastica (Preuss) Stapf.	*1860*	*30*	*20.628*
	Picralima nitida (Stapf) Th. & Hel. Dur.	*4*	*4*	*0.0131*
	Pleiocarpa pycnantha (K. Schum.) Stapf.	*5*	*1*	*0.009*
	Rauvolfia vomitoria Afzel.	*28*	*12*	*0.1353*
	Tabernaemontana holstii K. Schum.	*413*	*26*	*1.482*
Balanitaceae	*Balanites wilsoniana* Dawe & Sprague	*3*	*3*	*0.0336*
Bignoniaceae	*Kigelia africana* (Lam.) Benth.	*89*	*15*	*0.453*
	Markhamia lutea K. Schum.	*80*	*17*	*0.47*
	Spathodea campanulata P.Beauv.	*10*	*5*	*1.075*
Boraginaceae	*Cordia africana* Lam.	*1*	*1*	*1.003*
	Cordia millenii Bak.	*45*	*16*	*5.793*
	Ehretia cymosa Thonn.	*38*	*16*	*1.28*
Burseraceae	*Canarium schweinfurthii* Engl.	*10*	*7*	*0.4671*
Capparidaceae	*Maerua duchesnei* (De Wild.) F. White	*244*	*20*	*2.59*
	Ritchiea albersii Gilg	*36*	*6*	*0.194*
Celastraceae	*Cassine aethiopica* Thunb.	*7*	*4*	*0.018*
	Maytenus gracilipes (Welw.ex Oliv.) Exell.	*5*	*1*	*0.0006*
	Maytenus undatum (Thunb.) Blakelock	*18*	*5*	*0.1407*
Chailletiaceae	*Tapura fischeri (*Engl.) Engl.	*230*	*30*	*2.8634*
Clusiaceae	*Harungana madagascariensis* Poir.	*4*	*4*	*0.065*
	Mammea africana Sabine	*84*	*15*	*0.1144*
	Symphonia globulifera L.f.	*2*	*1*	*0.0034*
Combretaceae	*Combretum collinum* Fres.	*20*	*1*	*0.1975*
	Combretum molle G. Don	*15*	*1*	*0.1361*
	Terminalia glaucescens Benth	*2*	*1*	*0.1156*
Connaraceae	*Cnestis ugandensis* Schellenb.	*9*	*5*	*0.012*
Dracaenaceae	*Dracaena fragrans* Ker-Gawl.	*23*	*11*	*0.024*
Ebenaceae	*Diospyros abyssinica* (Hiern) F. White	*125*	*13*	*1.430*
Euphorbiaceae	*Acalypha neptunica* Muell. Arg.	*2691*	*32*	*4.308*
	Acalypha ornata Hochst.ex A. Rich.	*2587*	*30*	*3.225*

Family	***Species***	***Number of Individuals***	***Number of plots***	***Basal area***
	Alchornea floribunda Muell. Arg.	*115*	*5*	*0.119*
	Alchornea hirtella Muell. Arg.	*3*	*3*	*0.001*
	Alchornea laxiflora (Benth.) Pax & K. Hoffm.	*839*	*29*	*5.490*
	Alchornea laxissima	*2*	*1*	*0.003*
	Antidesma laciniatum Muell. Arg.	*60*	*10*	*0.162*
	Antidesma membranaceum Muell. Arg.	*14*	*1*	*0.466*
	Antidesma venosum E. Mey. ex Tul.	*45*	*5*	*0.781*
	Argomuellera macrophylla Pax Laka	*739*	*25*	*0.433*
	Bridelia micrantha (Hochst) Baill.	*44*	*15*	*0.599*
	Claoxylon hexandrum Muell. Arg.	*7*	*6*	*0.035*
	Cleistanthus polystachyus Hook. f. ex Planch.	*3*	*1*	*0.011*
	Croton macrostachyus Hochst. ex Del.	*84*	*13*	*6.334*
	Croton megalocarpus Hutch.	*4*	*2*	*0.181*
	Croton sylvaticus Hochst. ex Krauss	*65*	*15*	*2..238*
	Drypetes gerrardii Hutch. var. *grandifolia*	*87*	*8*	*0.290*
	Drypetes ugandensis (Rendle) Hutch.	*100*	*21*	*0.677*
	Erythrococca atrovirens Prain	*1*	*1*	*0.0005*
	Erythrococca stolziana Pax & K. Hoffn	*4*	*2*	*0.002*
	Eurphobia teke Schweinf. ex Pax	*44*	*3*	*0.270*
	Macaranga pynaertii De Wild.	*29*	*3*	*0.2422*
	Macaranga schweinfurthii Pax	*1*	*1*	*0.007*
	Mallotus oppositifolius (Geisel.) Muell. Arg.	*295*	*15*	*1.346*
	Margaritaria discoidea (Baill.) Webster	*63*	*19*	*5.07*
	Neoboutonia melleri (Muell. Arg.) Prain	*94*	*4*	*1.2105*
	Phyllanthus inflatus Hutch.	*1*	*1*	*0.0004*
	Ricinodendron heudelotii (Baill.) Pierre ex Pax	*17*	*12*	*6.055*
	Sapium ellipticum (Hochst. ex Krauss) Pax	*7*	*4*	*0.3372*
	Spondianthus preussii Engl.	*17*	*1*	*0.2594*
	Suregada procera (Prain) Croizat	*38*	*5*	*0.1583*
	Tetrorchidium didymostemon (Baill.) Pax & K. Hoffm.	*7*	*6*	*0.453*
	Thecacoris lucida (Pax.) Hutch.	*1652*	*18*	*3.743*
Fabaceae	*Acacia sieberiana* DC.	*1*	*1*	*0.176*
	Albizia coriaria Oliv.	*6*	*5*	*0.764*
	Albizia ferruginea (Guill. & Perr.) Benth.	*5*	*4*	*0.915*
	Albizia glaberrima (Schumach. & Thonn.) Benth.	*50*	*19*	*6.101*
	Albizia grandibracteata Taub	*24*	*5*	*0.364*
	Albizia zygia (DC.) Macbr.	*43*	*16*	*2.407*
	Baikiaea insignis Benth	*3*	*1*	*0.483*
	Baphia wallastonii Bak. f.	*32*	*3*	*0.603*
	Caesalpina bondue	*1*	*1*	*0.0005*
	Craibia brownii Dunn	*7*	*1*	*0*
	Cynometra alexandri C.H. Wright	*1031*	*28*	*158.594*
	Dialium excelsum J. Louis ex Steyaert	*11*	*8*	*0.067*
	Dichrostachys cinerea (L.) Wight & Arn	*4*	*3*	*0.133*
	Erythrina excelsum Bak.	*18*	*8*	*0.649*
	Erythrina sp.	*1*	*1*	*0.073*
	Erythrophleum guinieense	*1*	*1*	*0.182*
	Erythrophleum suaveolens (Guill. & Perr.) Brenan	*45*	*19*	*7.285*
	Mildbraediodendron excelsum Harms	*20*	*11*	*3.9441*
	Milletia dura Dunn	*1*	*1*	*0.0016*
	Newtonia buchananii (Baker) Gilb. & Bout..	*3*	*3*	*0.0104*
	Parkia filicoidea Welw.ex Oliv.	*14*	*4*	*1.016*
	Piptadeniastrum africanum (Hook. F.) Brenan	*15*	*6*	*0.1321*
	Senna spectabilis (DC.) Irwin & Barneby	*2140*	*7*	*26.007*
	Tetrapleura tetraptera (Schumach. &Thonn.) Taub.	*53*	*20*	*1.7383*
Flacourtiaceae	*Caloncoba crepiniana* (De Wild. & Th. Dur.) Gilg	*119*	*15*	*2.511*

Family	*Species*	*Number of Individuals*	*Number of plots*	*Basal area*
	Casearia runssorica Gilg	*1*	*1*	*0.010*
	Dasylepis eggelingii J.B. Gillett	*1*	*1*	*0.0003*
	Dovyalis macrocalyx Warb	*23*	*8*	*0.041*
	Lindackeria bukobensis Gilg	*2*	*1*	*0.0041*
	Lindackeria mildbraedii De Wild.	*10*	*4*	*0.086*
	Lindackeria ruwenzoriensis	*4*	*2*	*0.001*
	Lindackeria schweinfurthii Gilg	*27*	*8*	*0.056*
	Oncoba spinosa Forssk.	*31*	*12*	*0.2034*
	Rawsonia lucida Harv. & Sond.	*245*	*16*	*0.623*
Icacinaceae	*Apodites dimidiata* Arn	*9*	*3*	*0.464*
	Leptaulus daphnoides Benth.	*3*	*2*	*0.0115*
Loganiaceae	*Strychnos mitis* S. Moore	*104*	*8*	*0.7043*
Malvaceae	*Hibiscus vitifolius* L.	*3*	*3*	*0.0028*
Melastomataceae	*Memecylon jasminiodes* Gilg	*44*	*16*	*0.041*
Meliaceae	*Ekebergia capensis* Sparrm.	*1*	*1*	*0.0014*
	Entandrophragma angolense (Welw.) C.DC.	*39*	*16*	*0.8322*
	Entandrophragma cylindricum (Sprague) Sprague.	*78*	*17*	*6.820*
	Entandrophragma excelsum Sprague	*4*	*2*	*0.007*
	Entandrophragma utile (Dawe & Sprague) Sprague	*66*	*22*	*7.360*
	Guarea cedrata (A. Chiev.) Pellegr	*100*	*22*	*0.369*
	Khaya anthotheca (Welw.) C. DC.	*489*	*28*	*28.230*
	Lovoa brownii Sprague	*3*	*3*	*0.0132*
	Lovoa swynnertonii Bak. F.	*24*	*10*	*0.370*
	Lovoa trichilioides Harms	*30*	*7*	*1.283*
	Trichilia drageana Sond.	*187*	*21*	*1.686*
	Trichilia prieureana A. Juss	*293*	*25*	*3.660*
	Trichilia rubescens Oliv.	*400*	*25*	*5.476*
	Turraea floribunda Hochst.	*10*	*4*	*0.019*
	Turraea robusta Guerke	*7*	*4*	*0.211*
	Turraea vogelioides Bagshawe & Bak.f.	*13*	*2*	*0.155*
Melianthaceae	*Bersama abyssinica* Fresen	*6*	*1*	*0.094*
Moraceae	*Antiaris toxicaria* (Pers.) Lesch.	*262*	*28*	*4.595*
	Ficus asperifolia Miq.	*12*	*6*	*0.665*
	Ficus exasperata Vahl	*61*	*9*	*6.113*
	Ficus mucuso Welw. ex Ficalho	*8*	*5*	*0.2296*
	Ficus natelensis Hochst.	*2*	*2*	*0.0181*
	Ficus ottoniifolia C.C. Berg	*13*	*5*	*0.2600*
	Ficus polita Vahl.	*3*	*3*	*0.0162*
	Ficus pseudomangifera Warb.	*2*	*2*	*0.0165*
	Ficus sansibarica Warb.	*1*	*1*	*0.002*
	Ficus saussureana DC.	*3*	*2*	*0.0081*
	Ficus sur Forssk.	*57*	*15*	*5.056*
	Ficus vallis-choudae Del.	*2*	*2*	*0*
	Ficus variiforia Warb.	*3*	*3*	*0.136*
	Milicia excelsa (Welw.) C.C.Berg	*16*	*10*	*3.108*
	Morus mesozygium Stapf.	*81*	*23*	*1.796*
	Myrianthus holstii Engl.	*303*	*23*	*4.507*
	Treculia africana Decne	*31*	*7*	*0.497*
	Trilepisium madagascariense DC.	*203*	*25*	*6.400*
Myristicaceae	*Pycnanthus angolensis* (Welw.) Warb.	*35*	*9*	*0.4413*
	Staudtia kamerunensis Warb	*10*	*7*	*0.066*
Myrtaceae	*Psidium guajava* L.	*25*	*1*	*0.2132*
	Syzygium cordatum Hochst ex C. Krauss	*6*	*2*	*0.0265*
	Syzygium guineense (Willd.) DC	*12*	*6*	*2.255*
	Syzygium meriancea	*1*	*1*	*0.4693*
Ochnaceae	*Ochna hiernii* (Van Tiegh.) Exell	*1*	*1*	*0.009*

Family	*Species*	*Number of Individuals*	*Number of plots*	*Basal area*
	Ochna holstii Oliv.	*24*	*6*	*0.052*
	Ochna membranacea Oliv.	*32*	*6*	*0.036*
	Ouratea densiflora De Wild. & Th.Dur.	*258*	*17*	*0.313*
	Ouratea hiernii Exell	*11*	*4*	*0.0321*
Olacaceae	*Strombosia scheffleri* Engl.	*8*	*7*	*0.2115*
Oleaceae	*Linociera johnsoni* Baker	*31*	*6*	*0.0614*
	Olea africana L.	*1*	*1*	*0.0005*
	Olea senegalensis	*3*	*1*	*0.0044*
	Olea welwitschii (Knobl.) Gilg & Schellenb.	*13*	*3*	*1.61*
	Schrebera arborea A. Chev.	*2*	*2*	*0.386*
Palmae	*Raphia farinifera* (Gaertn.) Hylander	*29*	*2*	*3.1337*
Passifloraceae	*Paropsia guineensis* Oliv.	*4*	*3*	*0.1994*
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	*4548*	*27*	*22.544*
	Maesopsis eminii Engl.	*49*	*18*	*12.134*
Rhizophoraceae	*Cassipourea congensis* DC.	*17*	*4*	*0.096*
Rosaceae	*Prunus africana* (Hook. F.) Kalkman	*1*	*1*	*0.0935*
Rubiaceae	*Belonophora hypoglauca* (welw. Ex Hiern) A. Chiev	*149*	*21*	*0.662*
	Canthium vulgare (K.Schum.) Bullock	*11*	*4*	*0.0473*
	Coffea canephora Pierre ex Froehn	*100*	*20*	*0.1913*
	Coffea euginoides S. Moore	*39*	*15*	*0.0227*
	Coffea spathycalyx	*2*	*2*	*0.2254*
	Cola abyssinica	*3*	*3*	*0.3297*
	Dictyandra arborescens Welw.ex Benth. & Hook. F.	*40*	*16*	*0.1900*
	Galiniera saxifraga Del.	*4*	*1*	*0.7884*
	Gardenia vogelli Planch.	*6*	*4*	*0.0057*
	Hallea rubrostupulata (K. Schum) Leroy	*1*	*1*	*0.1392*
	Mitragyna stipulosa (DC.) O. Ktze.	*3*	*2*	*0.056*
	Oxyanthus speciosus Hook. F.	*61*	*16*	*0.2383*
	Pavetta molundensis K. Krausse	*49*	*11*	*0.0930*
	Psydrax parviflora (Afzel.) Bridson	*4*	*1*	*0.0257*
	Randia longiflora Durand & Schinz	*5*	*4*	*0.0134*
	Rothmannia longiflora Salisb.	*3*	*2*	*0.0048*
	Rothmannia urcelliformis (Hiern) Bullock ex Robyns	*45*	*18*	*0.097*
	Rothmannia whitfieldii (Lindl.) Dandy	*10*	*5*	*0.012*
	Rytigynia amaniensis K. Krausse	*1*	*1*	*0.0008*
	*Rytigynia beniensis (*De Wild.)Robyns	*4*	*2*	*0.0007*
	Rytigynia butaguensis (Robyns)	*13*	*3*	*0.1959*
	Rytigynia sp.	*12*	*3*	*0.0160*
	Rytigynia usambarensis	*4*	*2*	*0.0034*
	Vangueria apiculata K. Schum.	*36*	*7*	*0.2622*
Rutaceae	*Aeglopsis eggelingi* M.R.F. Taylor	*7*	*6*	*0.0139*
	Balsamocitrus dawei Stapf	*15*	*4*	*0.0695*
	Citropsis articulata (Sprengel) Swingle & Kellerman	*35*	*16*	*0.0293*
	Citrus citrus	*2*	*2*	*0.0012*
	Clausena anisata (Willd.) Benth.	*19*	*10*	*0.0843*
	Fagaropsis angolensis (Engl.) Dale	*46*	*9*	*0.5551*
	Teclea grandifolia Engl.	*10*	*5*	*0.0067*
	Teclea nobilis Del.	*294*	*30*	*1.336*
	Zanthoxylum gillettii (De Wild.) Waterm	*11*	*4*	*0.0573*
	Zanthoxylum leprieurii Guill. & Perr.	*29*	*10*	*1.035*
	Zanthoxylum rubescens Hook. f.	*25*	*12*	*0.191*
	Zanthoxylum sp.	*6*	*5*	*0.3535*
Sapindaceae	*Allophyllus dummeri* Bak. f.	*21*	*8*	*0.0804*
	Aphania senegalensis (Juss. ex Pior.) Radlk.	*27*	*14*	*0.177*
	Blighia unijugata Bak.	*187*	*25*	*0.6733*
	Lychnodiscus cerospermus Radlk.	*251*	*28*	*1.0111*

Family	*Species*	*Number of Individuals*	*Number of plots*	*Basal area*
	Majidea fosteri (Sprague) Radlk.	*6*	*5*	*0.3832*
	Melanodiscus sp.	*113*	*24*	*1.430*
	Pancovia turbinata Radlk.	*36*	*10*	*0.085*
	Zanha golungensis Hiern	*38*	*11*	*0.303*
Sapotaceae	*Bequaertiodendron natelense* (Sond.) Hiene & J.H. Hemsl.	*24*	*5*	*0.2611*
	Bequaertiodendron oblanceolatum (S. Moore) Hiene & J.H. Hemsl.	*133*	*23*	*0.5215*
	Chrysophyllum albidum G. Don.	*311*	*30*	*5.074*
	Chrysophyllum muerense Engl.	*23*	*11*	*0.208*
	Chrysophyllum perpulchrum Hutch. & Dalz	*162*	*22*	*3.876*
	Manilkara dawei (Stapf) Chiov.	*33*	*5*	*0.2095*
	Mimusops bagshawei S. Moore	*72*	*15*	*0.946*
	Pachystela brevipes (Baker) Engl.	*36*	*6*	*0.1332*
	Pouteria altissima (A. Chiev.) Aubrev.&Pellegr.	*357*	*26*	*5.626*
Simaroubaceae	*Irvingia gabonensis* (Aubry- Lecomte O'Rorke) Baill.	*4*	*4*	*0.018*
	Klainedoxa gabonensis Pierre ex Engl.	*16*	*8*	*0.360*
Solanaceae	*Solana wrightii* Benth	*4*	*2*	*0.1121*
	Solanum sp.	*2*	*1*	*0.0111*
Sterculiaceae	*Cola gigantea* A. Chev.	*106*	*16*	*3.8581*
	Dombeya mukole Sprague	*16*	*4*	*1.238*
	Leptonychia mildbreadii Engl.	*52*	*15*	*0.4813*
	Pterygota mildbraedii Engl.	*5*	*2*	*3.821*
	Sterculia dawei Sprague	*11*	*7*	*1.94*
Thymelaeaceae	*Craterosiphon louisii* R. Wilczek ex A. Robyns	*1*	*1*	*0.0005*
	Dicranolepis buchholzii Engl. et Gilg	*3*	*2*	*0.0016*
	Dicranolepis glomerata	*1*	*1*	*0.3318*
	Peddia africana Engl.	*4*	*1*	*0.0041*
Tiliaceae	*Desplatsia chrysochlamys* (Mildbr. & Burret) Mildbr. & Burret	*21*	*5*	*0.109*
	Desplatsia dewevrei (De Wild. & T.Dur.) Burret	*79*	*15*	*0.7016*
	Glyphaea brevis (Spreng.) Manachino	*346*	*14*	*2.3313*
	Grewia sp.	*46*	*14*	*0.1517*
Ulmaceae	*Cedrella cedrata*	*9*	*2*	*0.6673*
	Celtis africana Burm. f.	*7*	*2*	*0.355*
	Celtis gomphophylla Baker	*216*	*20*	*12.86*
	Celtis mildbreadii Engl.	*2472*	*29*	*39.03*
	Celtis wightii Planch.	*237*	*24*	*2.009*
	Celtis zenkeri Engl.	*549*	*30*	*19.945*
	Chaetacme aristata Planch.	*56*	*13*	*0.793*
	Holoptelea grandis (Hutch.) Mildbr.	*19*	*9*	*2.91*
	Trema orientalis (L.) Bl.	*16*	*5*	*0.7136*
Urticaceae	*Boehmeria macrophylla* Hornem	*1*	*1*	*0.0018*
Verbenaceae	*Lantana camara* L.	*1*	*1*	*0.0033*
	Premna angolensis Guerke	*2*	*2*	*0.0255*
	Vitex amboniensis Guerke	*39*	*17*	*0.522*
	Vitex doniana Sweet	*1*	*1*	*0.0003*
Violaceae	*Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze	*1666*	*26*	*4.938*
	Rinorea brachypetala (Turcz.) O. Ktze.	*802*	*23*	*0.7546*
	Rinorea dentata (P. Beauv.) O. Ktze.	*26*	*3*	*0.0235*
	Rinorea ilicifolia (Oliv) O. Ktze.	*259*	*7*	*0.1316*
	Rinorea oblongifolia C. Marquand	*298*	*6*	*0.429*
Vitaceae	*Leea guineensis* G. Don	*59*	*3*	*0.0446*
N/A	*Diasferonia* sp.	*1*	*1*	

CHAPTER 5

Beta-diversity of the woody flora of a managed semi-deciduous tropical rainforest, north-western Uganda

Abstract

Patterns of β-diversity for tree and shrub species in Budongo Forest Reserve (BFR), Uganda, were described and determined in relation to environmental heterogeneity and minimum stem diameter size. There were relatively high shared species and similarities, and low complementarities among the 0.5 ha plots, transects and historical management practice type pairs for both stem diameter ≥2.0 cm and ≥10.0 cm data. Shared species for plot pairs ranged from 6 - 73 and 1 - 35 for stem diameter ≥2.0 cm and ≥10.0 cm, respectively. Both β_w and Morisita-Horn Index measures of β-diversity were higher along topographic gradient transects for dbh ≥10.0 cm data, ranging from 0.8 - 1.2 and 0.32±0.19 - 0.71±0.11, than for ≥2.0 cm data, which ranged from 0.63 - 0.92 and 0.41±0.12 - 0.66±0.11, respectively. Comparisons of similarity values among plots and transects indicated that floristic changes are related to topographic gradients and habitat types. However, on the basis of topographic position groupings, all up-slope (i.e. mid-slope, upper-slope, and crest) plot groups were significantly different ($R_{ANOSIM} > 0.2$, $p < 0.05$) from the lower slope (swampy) plots in terms of species composition. However, up-slope plot groups did not differ significantly among themselves. The lack of significant differences is possibly due to BFR having a more or less uniform altitude, with generally flat to rolling plateaus, while other major sources of spatial heterogeneity (e.g. through selective timber and pole harvesting) are independent of elevation. β_w and Morisita-Horn consistently showed higher β-diversity for logged and arboricide treated, followed by logged only, and then nature reserve areas. β-diversity was relatively high at the total forest community scale, but lower for stem diameter ≥2.0 cm than ≥10.0 cm data. Environmental variables significantly explained 66.5% and 61.9% of the variance in species composition for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively. The CCA ordination axis 1 strongly correlated with calcium, nitrogen and organic matter. Thus, the variation in species composition in BFR is characterised by significant spatial patterns, and the patterns in β-diversity are to a great extent associated with environmental heterogeneity (i.e. soil nutrients, topographic and light gradients).

Abbreviations: dbh - diameter at breast height, β_w - Whittaker's beta-diversity, BFR – Budongo Forest Reserve, CCA - canonical correspondence analysis.

Keywords**:** ANOSIM, Anthropogenic disturbances, arboricides, canonical correspondence analysis, complementarity, logging, shared species, similarity indices, topographic gradient.

1.0. INTRODUCTION

The ever increasing human use pressure on tropical rainforests makes information on their patterns of plant species diversity (alpha and beta) and distributions more critical today than ever before in order to protect and conserve the remaining species effectively and efficiently (e.g. Myers et al. 2000, Cadotte et al. 2002, Zapfack et al. 2002, Natta et al. 2002). Beta-diversity (i.e., variability in species composition among sampling units) is central to concepts dealing with controls of diversity in ecological communities and is as important as alpha-diversity for conservation, because it influences diversity at large spatial scales (Condit et al. 2002). It also indicates the degree to which habitats have been partitioned by species (e.g. Balvanera et al. 2002), and accounts for changes in species composition across space in response to environmental heterogeneity (Whittaker 1972, Magurran 2004). Beta-diversity for a given area can reflect deterministic processes, such as species' adaptations to micro-climates or substrates, or it can result from limited dispersal coupled with speciation, or even a delayed response to climatic change, or other historical effects (Sheil 1996, Condit et al. 2002).

Although an understanding of species diversity and distributions in tropical rainforests has been a major focus for many ecological studies, these have often mainly concentrated on alpha-diversity (e.g. Huang et al. 2003). Many of the published studies on β-diversity are from Amazonia (e.g. Duivenvoorden et al. 2002, Condit et al. 2002, Ruokolainen and Tuomisto 2002), and the tropical dry forests of Mexico (Balvanera et al. 2002), and have only included woody plants with stems of dbh ≥10 cm. This study focuses on β-diversity in Budongo Forest Reserve (BFR), a semi-deciduous tropical rainforest of NW Uganda in Africa, which is of considerable conservation importance. Previous studies in BFR have related variability in species composition to successional gradients (e.g. Eggeling 1947, Connell 1978, Sheil 1996), the geographical position (east to west) of management compartments and silvicultural treatments (e.g. Plumptre 1996), elephant herbivory (e.g. Laws et al. 1975, Sheil and Salim 2004) and variability in soils (e.g. Walaga 1994, Eilu et al. 2004). According to Langdale-Brown et al. (1964) and Hamilton (1976), past and present climate is a major factor responsible for the nature and distribution of plant species in Uganda. Both Eggeling (1947) and Connell (1978), using Eggeling's data, argued that species number increases during the initial development from colonising to mixed forest and declines again during the progression to a *Cynometra alexandri* C.H. Wright dominated community. Plumptre (1996), using ordination of basal areas of common tree species, showed that the geographical position of a forest compartment explained more of the variation in species distribution than the variation between adjacent logged and unlogged compartments. In addition, when assessing alpha-diversity in Chapter 4, the use of stem diameters of ≥2.0 cm unveiled 53 more woody species (an increase of 19.7%), compared with the standard ≥10 cm dbh minimum size usually applied in tropical forests.

In spite of the previous, patterns of beta-diversity or how species composition changes with distance or along environmental gradients, particularly at the plot level, are not well understood in BFR Over the years, many changes have occurred in the BFR interior in terms of silvicultural treatments and the disappearance of elephant herbivory (e.g. Laws et al. 1975, Sheil and Salim 2004), as well as the ever increasing anthropogenic disturbances through subsistence exploitation from surrounding villagers (Chapter 2). There is unlikely to be a single factor explanation for changing patterns in species diversity and richness in an area, since even local changes are multivariate in nature. Various studies (e.g. Clark et al. 1998, Rennolls and Laumonier 2000, Hanba et al. 2000, Takyu et al. 2002) point to topographic heterogeneity as an important factor that governs diversity in tropical forests, but its influence in BFR is yet to be clearly understood.

This study, aimed at determining and describing β-diversity patterns of tree and shrub species and their environmental correlates in BFR. To explain patterns of beta-diversity, the following questions were addressed; 1. Is species composition uniform or variable across the forest? 2. Do environmental variables (i.e. soil nutrient status, topographic and light gradients) explain a significant proportion of the variation in community species composition? 3. From a methodological viewpoint, do patterns of beta-diversity significantly change when using a minimum stem diameter size of $\geq$2 cm, compared with the standard $\geq$10 cm dbh. Approaches to beta-diversity assessment include the degree to which the species composition of sample plots or sites in the same biogeographic realm differ, and how species diversity changes along environmental gradients (e.g. Colwell and Coddington 1994, Ricotta et al. 2002).

2.0. MATERIALS AND METHODS

2.1. Study area

Budongo Forest Reserve (BFR) is located on the escarpment east of Lake Albert and on the edge of the western rift valley (Howard, 1991) in North-western Uganda, between Masindi town and Lake Albert. It is part of the Albertine Rift Ecoregion, which consists of several forests, and believed to be one of Africa's most speciose and highly endemic regions (Cordeiro et al. 2007, Plumptre et al. 2007). It has an area of about 793 km^2 and lies between 1^{0}37' and 2^{0}03' N and 31^{0}22' and 31^{0}45' E. The altitudinal range is 700 - 1270 m averaging at 1050 m, with a gentle undulating terrain. The slopes are generally gradual and the intervening ridges rounded. The valley bottoms are generally well weathered, and many of the streams are trickles through rattan (*Calamus deerratus* Mann & Wendl.) swamps, with no apparent flow of water during dry months (Eggeling 1947). It is managed primarily for economic, conservation and environmental benefits. Management practices have included selective logging (both mechanical and pitsawing) and arboricide treatments during the 1950's and 1960's, aimed at killing trees that were regarded at that time as "weed species" (Plumptre and Reynolds 1994), enrichment planting and controlled shooting to reduce animal populations (e.g. Synnott 1985, Howard 1991). Most of the forest's compartments have been treated with arboricides and logged at least once, except for a few that have been set aside as "nature reserves" since 1932 (UFD 1997).

2.2. Sampling

The areas chosen for woody plant species and soil sampling represented the major management practices that have taken place in this forest and are categorised as: (i) no logging and no arboricide treatment (nature reserve); (ii) logging and arboricide treatment; and, (iii) logging only. In each management practice category area, at least 2 transects were established along topographic gradients, each providing at least three topographic positions (i.e. lower-slope (swampy/riparian), mid-slope, upper-slope, and flat/ridge-top). In each topographic position, with a separation distance of not less than 150 m, a 100 x 50 m (0.5 ha) plot divided into five 20 x 50 m contiguous sub-plots was sampled for tree and shrub individuals of stem diameter ≥2.0 cm (Figure 1). Soil samples were collected at a depth of 0 - 15 cm from 10 randomly chosen locations within each of the 0.5 ha plots. A total of 32 plots, 6 in the Nature Reserve areas, 19 in logged and arboricide treated, and 7 in logged only were laid. The number of plots per historical management practice type is related to the corresponding size of the area in the forest. Identification of plant species was based on the Flora of Tropical East Africa (FTEA) (Polhill 1952 et seq) and Hamilton's (1991) plant identification guide.

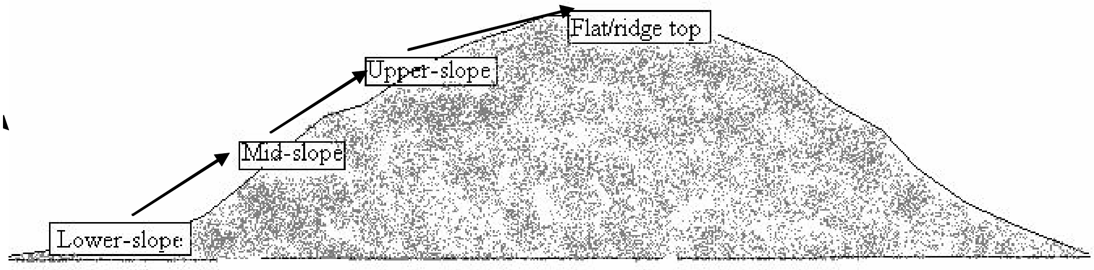

Figure 1. Schematic representation of sample plots positioned along a transect, following a topographic gradient within various historical management practice type compartments in Budongo Forest Reserve, north-western Uganda.

2.3. Environmental factors

The environmental factors considered were; (i) soil elemental constituents (total Ca, Mg, Na, P, Li, Si, Ti, Fe and N), (ii) soil pH, (iii) soil organic matter (OM), (iv) historical management practice type, and (v) topographic and light gradients. Soil OM, pH and total N were determined using the standard methods in Nelson and Sommers (1982), McLean (1982), and Bremner and Mulvaney (1982), respectively. The elemental constituents, except for total N, were determined using X-Ray Fluorescence Spectrometry (XRF; Thomsen, 2002) in the Department of Geology, University of the Witwatersrand, South Africa. Light availability under the canopy was indirectly measured as leaf area index (LAI) using a LAI-2000 Plant Canopy Analyser (Li-Cor Lincoln Nebraska, USA) at 1.0 m above the ground level at 5 random points in each 0.5 ha plot. The extinction of light as it travels through a vegetation canopy depends on the total LAI (area of foliage projected on a unit area of ground surface) (Barbour et al. 1987). Thus, LAI describes a fundamental property of the plant canopy in its interaction with the atmosphere, especially concerning radiation, energy, water and gas (e.g. CO_2) exchange at forest stand scale (Monteith and Unsworth 1990, Cournac et al. 2002).

2.4. Data analysis

Beta-diversity was analysed at the sampling point (0.5 ha plot), transect, historical management practice type, and total forest community scales, employing separately both the ≥2.0 cm and ≥10.0 cm stem diameter data. Thus, shared species, β-diversity and similarity indices were separately computed between the 496 plot-pairs, 8 transects and 3 management practice types.

2.4.1. Measures of β-diversity

From the available beta-diversity measures, Whittaker's (β_W) Index (Whittaker 1972) and the Morisita-Horn Index of similarity, as modified by Wolda (1983), were used to determine beta-diversity. β_W explicitly relates the components of diversity, α and β, to overall diversity, S, and is considered a measure of choice when samples cannot be arranged along a single gradient (Wilson and Shmida 1984). β_W-diversity was calculated as:

$$\beta_W = S / \alpha - 1$$

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

The Morisita-Horn Index assesses similarity in species composition between plots (e.g. Colwell 2004, Magurran 2004), and is a quantitative similarity index that is not strongly influenced by species richness and sample size. For all pairs it was calculated as:

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

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 ith species in B; and d_a (and d_b) is calculated as follows:

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

For each historical management practice type, C_{MH} was calculated by averaging all the plot pair-wise values for that particular practice.

Similarity

Similarity was measured using both Sørensen's and Jaccard's Index for presence-absence data. Sørensen's Similarity Index was also used to explore whether species distributions conformed to the vegetation or ecological continuum hypothesis, and was calculated as:

$$\mathrm{S} = \frac{2W}{[a+b]};$$

where '***a***' and '***b***' are species richness in two site samples, and '***W***' is the number of species in common (or shared species between two plots or sites). This index gives strong importance to the shared species and relates them to the mean species number of the pair (Zapfack et al. 2002).

Jaccard's Similarity Index was used to quantify the species composition overlap (shared species), and was calculated as:

$$\mathrm{J} = \mathrm{A}/(\mathrm{A}+\mathrm{B}+\mathrm{C});$$

where A = the number of species found in both of the plots or sites, B= species in location I but not in location II, and C= species in location II but not in location I (Magurran 2004). Ideally Jaccard's Index is the proportion of shared species to the total for a plot or site pair.

Complementarity was measured using the Marczewski-Steinhaus (M-S) distance measure, a complement to the Jaccard Similarity Index (Colwell and Coddington 1994, Magurran 2004). This measure was calculated as:

$$\mathrm{C}_{\mathrm{M\text{-}S}} = 1 - \frac{a}{a+b+c}\text{ ; where, } \frac{a}{a+b+c} \text{ is Jaccard's index}$$

Computations of β_w-diversity were performed using the Species Diversity and Richness III Programme (Pisces Conservation Ltd 2003), while Sørensen's and Jaccard's similarity indices, the Morisita-Horn Index, complementarity and shared species were computed using Estimate*S* Version 7.5 (Colwell 2004).

2.4.2. Tests for variation in β-diversity

The sample plots were also grouped in three different ways: (i) transects, (ii) topographic positions, and (iii) historical management practice type. Variation in community species composition among these groupings was subsequently tested for significance with ANOSIM (ANalysis Of SIMilarity) permutation tests (Clarke 1993) using CAP 3.1 (Pisces Conservation 2005). ANOSIM is simply a form of the Mantel test (Legendre and Legendre 1998), and tests *a priori* defined groups against random groups in ordinate space. The Mantel approach is appropriate for testing the variation in beta-diversity among groups of sites (Legendre et al. 2005). ANOSIM computes a test statistic (R_{ANOSIM}) reflecting the observed differences among replicates between sites, contrasted with differences among replicates within sites (Pandolfi and Greenstein 1997). The R_{ANOSIM} statistic values generated by CAP 3.1 are relative measures of separation of the *a priori* defined groups. An outcome value of zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples within groups are more similar to one another than any samples from different groups. The relationship between beta-diversity and variability in environmental factors was explored with Canonical Correspondence Analysis (CCA) using CANOCO version 4.5 (ter Braak and Šmilauer 2002). According to Legendre et al. (2005), canonical partitioning is the proper statistical procedure for partitioning the spatial components and for testing hypotheses about the origin and maintenance of variation in community composition among sites. Canonical Analyses of species abundance data can provide more powerful tests of significance than analyses based on distance matrices. The amount of species data variance explained by, and the intra-set correlations derived from, CCA were used to infer the relative importance of each environmental variable for prediction of community species composition variability (ter Braak 1995). A Monte Carlo permutation test (with 499 permutations) was used to test the significance of the canonical axes.

3.0. RESULTS

3.1. Species composition

A total of 269 woody species of stem diameter ≥2.0 cm were recorded from the thirty-two, 0.5 ha plots. The number of species per plot ranged from 24 - 111 (for stem diameter ≥2.0 cm data) and 12 - 61 (for dbh ≥10.0 cm data). Shared species for plot pairs ranged from 6 - 73 and 1-35 for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively. Generally, plot-pairs from areas that were logged and arboricide treated had the highest number of shared species regardless of the physical distance between them.

On the basis of historical management practice type, the logged and arboricide treated forest areas had the highest species richness (247, 195), followed by Nature Reserve (166, 100), and logged only (141, 80) for the ≥2.0 cm and ≥10.0 cm dbh data, respectively. The proportion of species that each of the three management practices shared with the total woody flora (269 species) varied from 141 (52.4%) in logged, 166 (61.7%) in Nature Reserve, to 247 (91.8%) in logged and arboricide treated. Shared species among the three historical management practice types ranged from 101 - 153 and 40 - 88 for the stem-diameter ≥2.0 cm and ≥10.0 cm data, respectively. However, only 97 and 38 species were shared among all three historical management practices for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively (Fig. 2). Logging and arboricide treated plots had the highest number of species restricted to them, for both stem diameter ≥2.0 cm (63 species) and ≥10.0 cm data (83 species). Stem diameter size cut-off did not, however, greatly affect the number of species recorded only in the Nature Reserve, as 9 and 10 species were revealed for stem diameter ≥2.0 cm and ≥10.0 cm, respectively.

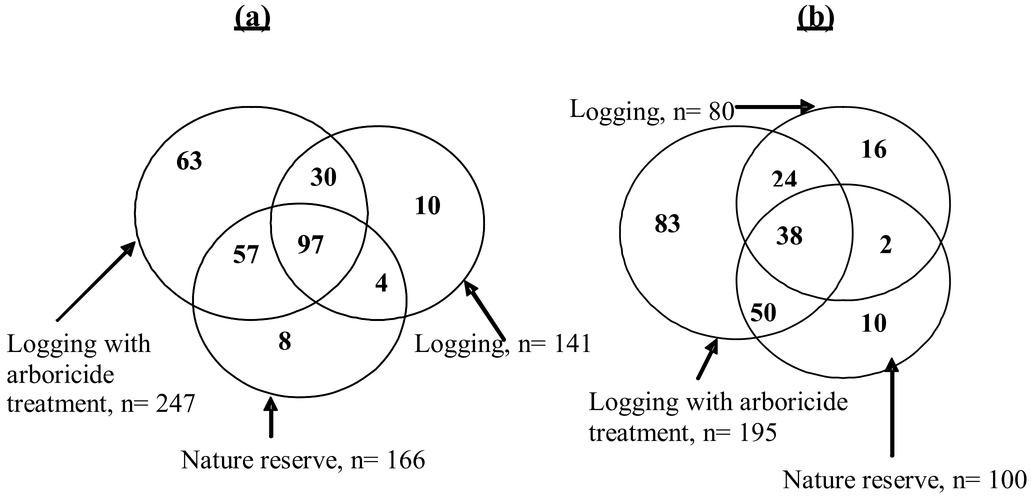

Figure 2. Set diagram of numbers of shared species among the three historical management practice types in Budongo Forest Reserve, for (a) ≥2.0 cm and (b) ≥10.0 cm dbh tree and shrub species data (n= total number of species recorded in a particular historical management practice type).

When lower-slope (“swamp”) plots were compared with adjacent plots along the same transect, shared species as a proportion of the total for a plot pair decreased markedly up the topographic gradient for transects 1, 2 and 6 for stem diameter ≥2.0 cm data, and transects 1, 3, 4, 6 and 8 for dbh ≥10 cm data (Figure 3). There was also a noticeable decrease in similarity between the lower slope and adjacent plots with increasing distance up the slope for transects 1, 2, 3 and 4. Generally, the closer the plots are along the topographic gradient, the more similar they are, and the further they are the more dissimilar.

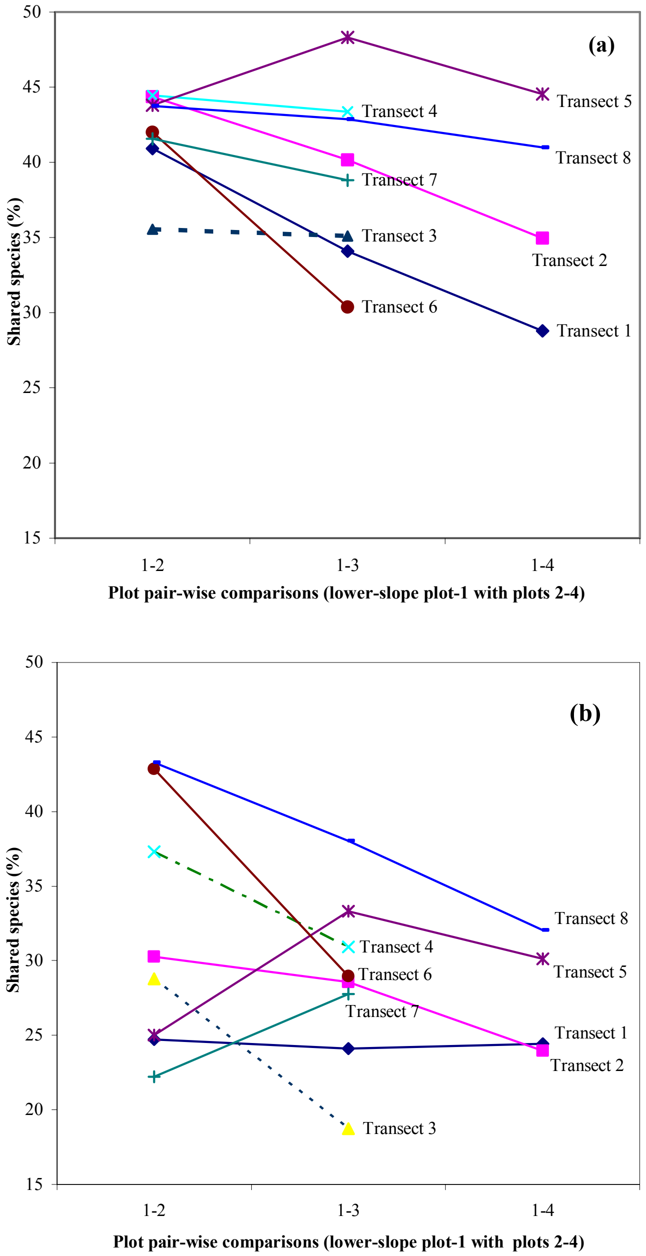

Figure 3. Variation in the proportion of shared species for lower-slope (plot = 1) and adjacent plot pairs up the topographic (plots 2 - 4) gradient using (a) ≥2.0 cm and (b) ≥10 cm dbh data for the 8 transects in Budongo Forest Reserve. Shared species are expressed as a percentage of the total species number for each plot pair. Transects 6-7, from logged only; Transects 3 – 4 from nature reserve, Transects 1, 2, 5 and 8 from logged and arboricide treated areas.

Similarity

At the plot level, Sørensen’s similarity (S) ranged from 0.13 - 0.75 (278 plot pairs were ≥0.5) and 0.04 - 0.71 (95 plot pairs were ≥0.5) for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively (full matrix of plot pair-wise values are not presented). While the Jaccard’s Index (J) ranged from 0.07 - 0.60 for stem diameter ≥2.0 cm, and 0.02 - 0.55 for dbh ≥10.0 cm data. The plot pairs with the highest similarities were different for stem diameter ≥2.0 cm (S = 0.75, J = 0.60) and ≥10.0 cm data (S = 0.71, J = 0.55), although both were up-slope plots from a transect in a logged and arboricide treated area. Generally, the Sorensen and Jaccard's similarity indices gave consistently similar plot pair results for both stem diameter ≥2.0 cm and ≥10.0 cm data. At the historical management practice type level, highest similarity was recorded between the logged and arboricide treated, and Nature Reserve areas for both stem diameter ≥2.0 cm and ≥10.0 cm data (Table 1).

Table 1. Sørensen's and Jaccard's Similarity Indices, and percent shared species (in parentheses) between pairs of historical management practice types in Budongo Forest Reserve, NW Uganda, employing both stem diameter (a) ≥2.0 cm and (b) ≥10.0 cm tree and shrub species data.

	Sørensen		**Jaccard**	
Management practice type	Logged only	Nature Reserve	Logged only	Nature Reserve
a). ≥ 2.0 cm data				
Logged & arboricide treated	0.66	0.74	0.49(49.23)	0.59(58.85)
Logged only		0.66		0.49(49.03)
b). ≥ 10.0 cm data				
Logged & arboricide treated	0.45	0.60	0.29(29.11)	0.43(42.51)
Logged only		0.44		0.29(28.57)

3.2. Beta-diversity at the transect, historical management practice type, and total forest level

Plot level

Plot pair-wise Morisita- Horn values ranged (i) 0.24 - 0.89 and 0.1 - 0.92 for Nature Reserve, (ii) 0.01 - 0.95 and 0.0 - 0.96 for logged and arboricide treated, and (iii) 0.0 - 0.95 and 0.0 - 0.89 for logged only, for stem diameter ≥ 2.0 cm and ≥10.0 cm data, respectively. The plot level pair-wise percent complementarity (C_{MS}) values were (i) 40 - 93% for ≥2.0 cm, and (ii) 45 - 98% for dbh ≥10.0 cm data. However, plot pairs with the highest complementarities were different for stem diameter ≥2.0 cm ($C_{MS=}$ 40%) and the ≥10.0 cm data ($C_{MS=}$ 45%), although both were up-slope plots from transect 2 (logged and arboricide treated).

Transect level

β_W -diversity along transects was generally low, ranging from 0.69 - 0.92, and 0.80 - 1.20 for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively (Table 2). Hence, it was higher for stem diameter ≥10.0 cm than for ≥2.0 cm, with 6 of the 8 transects having values greater than 0.92. This suggests a higher spatial variability in community species composition for tree and shrub species ≥10.0 cm compared to ≥2.0 cm stem diameter across the forest.

Table 2. Whittaker's beta-diversity (β_W) and Morisita-Horn Index for the 8 transects and other groupings of plots using stem diameter ≥2.0 cm and ≥10.0 cm tree and shrub species data at the 0.5 ha plot scale in Budongo Forest Reserve, NW Uganda.

Management practices or other groupings	**Transect number (plots)**	β_W		***Morisita-Horn* (mean ± SE)**	
		≥2.0 cm	**≥10 cm**	**≥2.0 cm**	**≥10 cm**
Logged & arboricide treated	1 (1-4)	0.92	1.20	0.623±0.05	0.428±0.11
"	2 (5-8)	0.75	0.93	0.663±0.11	0.687±0.06
"	5 (19-22)	0.71	1.00	0.657±0.07	0.540±0.11
"	8 (29-32)	0.69	0.87	0.562±0.06	0.435±0.04
Nature Reserve	3 (9-11)	0.75	1.02	0.407±0.12	0.320±0.19
"	4 (12-14	0.63	0.80	0.737±0.08	0.710±0.11
Logged only	6 (23-25	0.89	0.97	0.647±0.15	0.643±0.12
"	7 (26-28)	0.70	1.08	0.513±0.08	0.590±0.06
Riparian plots	(1, 5, 9,12,19, 23, 26 & 29)	1.06	1.58	0.535±0.04.	0.379±0.04
Senna spectabilis plots	(15-18)	1.08	1.51	0.913±0.01	0.890±0.02
All plots	(1-32)	2.57	4.49	0.398±0.01	0.318±0.01

The Morisita-Horn values are means for pair-wise plot values for each historical management practice type. The lower the Morisita-Horn value, the higher the beta-diversity.

Historical management practice type level

β_W and mean Morisita-Horn consistently showed higher β-diversity for the logged only, followed by logged and arboricide treated, and Nature Reserve areas for the ≥2.0 cm stem diameter data(Table 3). The lower the Morisita-Horn values the higher the β-diversity. The mean Morisita-Horn values for plot-pairs in the Nature Reserve were the same for stem diameter ≥2.0 cm and ≥10.0 cm dbh data, while for the logged and arboricide treated it was higher for the ≥2.0 cm; and for logged only it was higher for stem diameter ≥10.0 cm data (Table 3). The matrix of Morisita-Horn Index similarities between management practice types yielded values between 0.64 - 0.78 and 0.39 - 0.76 for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively (Table 4). The management practice types also yielded complementarities between 41-51% and 51 - 71% for stem diameter ≥2.0 cm and ≥10.0 cm data, respectively (Table 4).

Table 3. Whittaker's (β_W) and Morisita-Horn β-diversity Indices calculated separately within each historical management practice type, using stem diameter (a) ≥2.0 cm and (b) ≥10.0 cm tree and shrub species data at a 0.5 ha plot scale. Number of plot pairs and species recorded in each management practice type is included.

Management practice type	**No. of plot pairs**	**No. of species**	**Beta-diversity Index**	
			β_W	***Morisita-Horn*** (mean±SE)
a) ≥2.0 cm data				
Nature Reserve	15	166	1.17	0.56±0.05
Logged & arboricide treated	171	247	1.85	0.42±0.02
Logged only	21	141	1.92	0.41±0.07
b) ≥10.0 cm data				
Nature Reserve	15	100	1.68	0.56±0.08
Logged & arboricide treated	171	195	2.61	0.39±0.02
Logged only	21	80	3.02	0.46±0.07

The Morisita-Horn varies from 1, which is complete similarity, to 0, which is complete dissimilarity in species abundance; and the lower the Morisita-Horn value the higher the beta-diversity.

Table 4. Morisita-Horn index of similarity and shared species (in parentheses), and complementarities between historical management practice types in Budongo Forest Reserve for stem diameter (a) ≥2.0 cm and (b) ≥10.0 cm tree and shrub species data.

	Morisita-Horn Index		**Percentage complementarity ($C_{M\text{-}S}$)**	
Management practice type	Logged only	Nature Reserve	Logged only	Nature Reserve
a) ≥2.0 cm data				
Logged & arboricide treated	0.67 (128)	0.78 (153)	51	41
Logged only		0.64 (101)		51
b) ≥10.0 cm data				
Logged & arboricide treated	0.42 (62)	0.39 (88)	71	57
Logged only		0.76 (40)		71

The Morisita-Horn varies from 1, which is complete similarity, to 0, which is complete dissimilarity in species abundance. Complementarity varies from 0 (when the lists are identical) to unity (when the lists are completely distinct).

Total forest community level

Both the β_W and Morisita-Horn Index consistently showed that total forest community beta-diversity values were higher for stem diameter ≥10.0 cm than ≥2.0 cm (Table 2). The use of a 10.0 cm dbh cut-off gave higher β_W -diversity values at the transect, management practice type, and whole forest community levels.

3.3. Variability in species composition and environmental correlates

Overall, the ANOSIM test showed that plant community species composition differed significantly ($p<0.05$) for all comparisons, whether at transect, topographic position or management practice type level (Table 5) for both stem diameter ≥2.0 cm and ≥10.0 cm data. Thus, the within group similarities are much higher than the between group similarities.

Table 5. Analysis of similarity of community composition between transects, topographic position categories and historical management practice types. The ANOSIM sample statistic (R_{ANOSIM}) is reported with significance level (p-value) in parentheses.

	Stem diameter size cut-off	
Grouping	≥2.0 cm	≥10 cm
Transect	0.35 (0.001)	0.45 (0.001)
Topographic position	0.10 (0.038)	0.13 (0.014)
Management practice	0.30 (0.016)	0.53 (0.001)

On the basis of topographic position grouping, all up-slope plots were significantly different ($R_{ANOSIM} >0.2$, $p <0.05$) from the lower-slope ("swamp") plots in terms of species composition. However, the up-slope plot groups did not differ significantly from each other, with pairwise comparisons having an $R_{ANOSIM} <0.01$ and p-values >0.4. For the management practice categorisation, although the global test was significant ($R_{ANOSIM} = 0.3$, $p = 0.016$), the pairwise test for logged and arboricide treated versus Nature

Reserve was not ($R_{ANOSIM} = 0.05$, $p = 0.31$). These results were also corroborated by the CCA ordination as some of the nature reserve plots are closer to some of the logged and arboricide treated plots.

The CCA illustrates a clear separation of the lower-slope ("swamp") and *Senna spectabilis* dominated plots (on the far right of the figure), from the rest (Fig. 4), and this clearly corroborates the ANOSIM results. The first four CCA canonical axes individually explained 14.5, 11, 6.7 and 4.9% of the total variance in species composition, respectively (Table 6). A Monte-Carlo Permutation test showed that both the first canonical axis ($F = 2.87$; $p = 0.014$) and the combined four axes ($F = 1.53$; $p = 0.002$) were significant for stem diameter ≥2.0 cm data. Similarly for dbh ≥10.0 cm data, the four axes individually explained 12.1, 10.3, 7.5 and 4.9% of the total variance in species composition, respectively. The first canonical axis ($F = 2.35$; $p = 0.002$) and the combined four axes ($F = 1.56$; $p = 0.002$) were significant.

Table 6. Summary table of Canonical Correspondence Analysis (CCA) of 32, 0.5 ha plots distributed over the major areas of the different historical management practice types in Budongo Forest Reserve, NW Uganda

Axes	1	2	3	4	Total Inertia
a) ≥2 cm data					
Eigenvalues	0.450	0.344	0.208	0.153	3.116
Species-environmental correlations	0.910	0.964	0.924	0.937	
Cumulative percentage variance					
of species data:	14.5	25.5	32.2	37.1	
of species-environment relation:	25.9	45.8	57.7	66.5	
Sum of all eigenvalues					3.116
Sum of all canonical eigenvalues					1.736
b) ≥10 cm data					
Eigenvalues	0.527	0.444	0.328	0.213	4.339
Species-environmental correlations	0.939	0.972	0.958	0.967	
Cumulative percentage variance					
of species data:	12.1	22.4	29.9	34.8	
of species-environment relation:	21.6	39.8	53.2	61.9	
Sum of all eigenvalues					4.339
Sum of all canonical eigenvalues					2.441

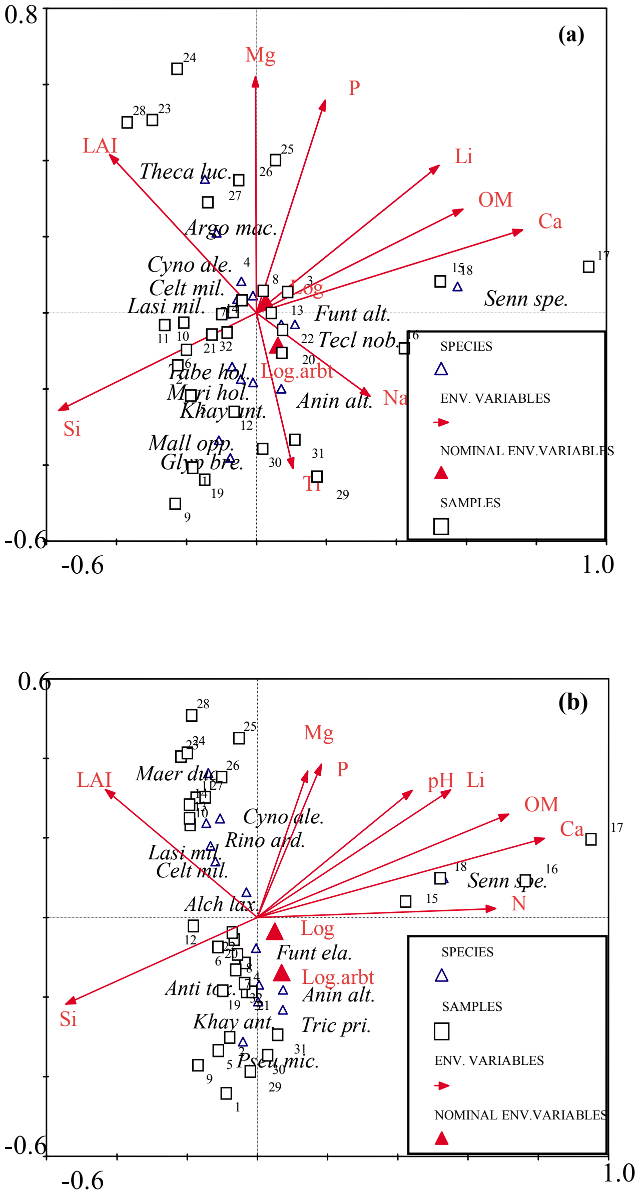

Figure 4. Triplot of CCA results from an analysis of variation in woody species composition among 0.5 ha plots for stem diameter (a) ≥2.0 cm and (b) ≥10 cm, showing environmental variable vectors, plots and species with a species weight range 10 - 100%. Some of the species in the centre of the plot and environmental variables with shorter arrows have been suppressed for clarity. Si: Silicate Ti: Titanium; Mg: Magnesium; Ca: Calcium; Li: Lithium; OM: Organic matter; N: Nitrogen; P: Phosporus; LAI: Leaf Area Index; Log.arbt: logged and arboricide treated; Log.: logged only.

For stem diameter ≥2.0 cm data, intra-set correlations showed that CCA axis 1 was most strongly correlated with Ca (r = 0.76), followed by N (r = 0.59), OM (r = 0.58) and Si (r = 0.56). While CCA axis 2 was strongly correlated with Mg (r = 0.62) and P (r = 0.560. Similarly, for dbh ≥10.0 cm data, the 1st axis was most strongly correlated with Ca (r = 0.82), followed by OM (r = 0.72) and N (r = 0.68). The 2nd axis was most strongly negatively correlated with the logging and arboricide (r = -0.74) management practice.

Thus, Ca, OM and N dominate axis 1 of the CCA biplot for both stem diameter cut-off data sets (Table 7, Fig. 4a & b), but the relative importance of the other environmental variables vary. Overall, correlations of environmental variables with the first two CCA axes are more similar among the species data sets.

Table 7. Canonical Correspondence Analysis (CCA) intra-set correlations of environmental variables with the four first CCA axes. OM: Organic matter; LAI (leaf area index; indirect measure of light availability under canopy); Li: Lithium (see Materials and Methods).

Variable	**Stem diameter≥2.0 cm data**				**Stem diameter ≥10.0 cm data**			
	CCA Axes				**CCA Axes**			
	1	2	3	4	1	2	3	4
Ph	0.53	0.16	-0.29	-0.07	0.44	0.32	-0.16	0.01
Si	-0.56	-0.26	0.46	-0.15	-0.55	-0.22	0.52	-0.11
Ti	0.10	-0.41	-0.47	0.06	0.06	-0.18	-0.35	-0.06
Fe	0.50	0.20	-0.54	-0.09	0.39	0.14	-0.60	-0.10
Mg	0.00	0.62	0.36	0.07	0.14	0.37	0.10	0.10
Ca	0.76	0.22	0.09	0.19	0.82	0.20	0.01	0.18
Na	0.32	-0.22	0.67	0.45	0.53	0.00	0.67	0.47
P	0.20	0.56	-0.26	-0.12	0.18	0.38	-0.42	-0.14
Li	0.52	0.39	-0.19	0.15	0.55	0.32	-0.32	0.07
OM	0.59	0.27	0.22	0.63	0.72	0.26	0.12	0.55
N	0.59	0.20	0.15	-0.02	0.68	0.02	-0.10	-0.07
Logged only	0.23	0.18	0.06	-0.02	0.38	-0.31	-0.25	-0.02
Logged & arboricide treated	0.31	-0.46	-0.31	0.05	0.35	-0.74	-0.32	0.16
LAI	-0.42	0.42	-0.16	0.11	-0.43	0.32	-0.21	0.26

4.0. DISCUSSION

4.1. The magnitude of β-diversity

Overall, relatively high shared species were shown by Sørensen's, Jaccard's and Morisita-Horn similarity values, and consequently low complementarities among plots, transects and historical management practice type pairs, particularly for the stem diameter ≥2.0 cm data. This provides evidence for low β-diversity, as the lower the Morisita-Horn and the higher the complementarity, the higher is the *β*-diversity. Although the various methods yielded slightly different results, they consistently highlighted low *β*-diversity in BFR. *β*-diversity was however, higher for the total forest community than for the management practice type, transect or plot levels. The higher *β*-diversity at the total forest community level is in agreement with Gentry (1988) and Campbell (1994), that tropical rainforests undergo high spatial turnover rates in species composition. Even at this level, it was lower for the 2.0 cm than for the 10.0 cm stem diameter cut-off. The high plot pair-wise similarities and relatively low complementarities between management practice type pairs, ranging from 41 - 51% for stem diameter ≥2.0 cm data suggests lower *β*-diversity for this diameter size cut-off. This is probably because most of the species that usually have a stem diameter <10 cm (e.g. *Acalypha neptunica*, *Acalypha ornata*, *Lasiodiscus mildbraedii* and *Rinorea ardiisiflora*) are sub-canopy species, which are widely distributed in the forest, as well as along the topographic gradient from the lower-slope to the drier upper-slope areas (Chapter 3 and 4).

4.2. Environmental correlates of β-diversity

The higher *β*-diversity for both β_W- and Morisita-Horn Index, using dbh ≥10.0 cm data at the total forest community level reflects the greater environmental and silvicultural treatment variability. At the whole forest community level, habitat heterogeneity increases, since logged and arboricide treated, logged only and nature reserve plots are pooled and considered as a single unit. In addition, the areas of different historical management practices are in different places and probably at different successional stages resulting in greater habitat variation. Similarly, the higher *β*-diversity reported in Panama than western Amazonia has been attributed to the greater habitat variation among the study plots (Condit et al. 2002). The changes in environmental conditions that accompany habitat variation may favour particular species, thus greatly affecting variability in species composition in the forest. However, Plumptre (1996) found that differences in geographical location (East–West) of compartments in BFR explained more of the variation in species distribution than the variation between adjacent logged and unlogged compartments. The influence of position of each plot along an east-west gradient, however, requires further testing. Indeed, in the present study the nature reserve and the logged and arboricide treated areas that were closer to each other in terms of separation distance were not significantly different in their community species composition. Similarly *β*-diversity in a Mexican tropical dry forest increased with distance between sites (Balvanera et al. 2002). Furthermore, in the same study, habitat, environmental heterogeneity and distance contributed differentially to β-diversity, but the differences were mainly associated with environmental heterogeneity.

Similar to BFR, studies of Kibale Forest in Uganda also showed that even within the same forest, considerable spatial heterogeneity in tree community structure and composition exists (Butynski 1990, Chapman et al. 1997). For example, in their comparison of four sites at Kibale, Chapman et al. (1997) found that occurrences and densities of many tree species varied widely between sites, as they do in Budongo (Chapter 3). They concluded that causes for this spatial variability were potentially manifold, ranging from small differences in elevation and rainfall to past differences in habitat alterations by elephants and humans. BFR similarly has a disturbance history involving silvicultural treatments (e.g. selective logging and arboricide treatment), anthropogenic disturbances and elephant herbivory (e.g. Laws 1978, Dawkins and Philip 1998), which have been patchy and had differing influences on community species composition (e.g. Plumptre 1996). Such intrinsic disturbances may lead to abrupt changes in habitat in the form of canopy gaps, consequently, greatly contributing to heterogeneity in the forest environment and reversal or delay of the successional stages. Abrupt changes in site conditions that are accompanied by changes in the physical and chemical nature of the soil, nutrient dynamics, and microclimate may influence species diversity patterns in plant communities, particularly β-diversity (Pitman et al. 1999, Grace 2001). The creation of gaps that results in patchy canopy coverage and associated parameters may lead to low or high levels of diversity at the *α*, *β*, and *γ* scales (Leach and Givnish 1999). At the management practice type level, β_w-diversity was lowest for the Nature Reserve for both minimum stem diameter sizes, suggesting that higher beta-diversity within BFR is to a large extent promoted by anthropogenic disturbances. However, more information is required on species-specific responses to particular anthropogenic disturbances (e.g. logging, pitsawing and pole cutting) in BFR. The high similarity between logged only and Nature Reserve areas for the dbh ≥10.0 cm data can be attributed to the presence of high densities of *C. alexandri* in both.

In this study, comparisons of similarities among sampling plots and transects, and corroborated by ANOSIM provided evidence of floristic changes in relation to topographic position and habitat. This highlights the relative influence of the topographic gradient on spatial variability in species composition in BFR. The lower-slope plots are relatively unique within BFR in their edaphic properties (e.g. higher soil moisture) since they are seasonally flooded, favouring a different suite of plant species compared with the drier up-slope plots. However, apart from the lower-slope plots, ANOSIM revealed no significant variability in species composition among up-slope (i.e. mid-slope, upper-slope, and crest) topographic position groupings. The lack of significant differences between the up-slope plot groupings is probably because BFR is of more or less uniform altitude (Walaga 1994), eliminating the influence of local climatic regimes that occur in forests spanning a wide altitudinal range. Local topography provides habitat diversity for plant communities (Takyu et al. 2002), and influences species distributions and abundance patterns at small spatial scales (Pitman et al. 1999, Hanba et al. 2000). Indeed, areas of greater topographic or environmental variability tend to have more species than more uniform areas (Rosenzweig 1995), because the growth and survival of a variety of species with different functional traits are diversified by environmental conditions along topographic positions (Kubota et al. 2004). Nevertheless, the variation in species abundances and forest structure along the topographic gradient is not always uniform, because some sources of spatial heterogeneity (e.g. tree falls) are independent of elevation (e.g. Ross et al. 1986, Legendre et al. 2005).

The clear separation of the lower-slope plus *Senna spectabilis* dominated plots from the upper-slope plots in the CCA (Fig. 4) corroborates the ANOSIM results based on topographic position groupings. This shows that variation in species composition in BFR is characterised by significant spatial patterns. In addition, the significance of the 1st and the combined four axes of the CCA for both stem diameter ≥2.0 cm and ≥10 cm data sets shows that beta-diversity in BFR is to a great extent associated with environment heterogeneity (i.e. edaphic and light gradients). The light gradient may also to an extent be a surrogate for disturbance, since the opening of the canopy through logging results in high light levels at the forest floor. Results of the present study suggest that small spatial scale (in the order of hundreds of meters) variability in soil nutrients influences plant community species composition in BFR. Similarly, other studies (e.g. Newberry and Proctor 1984, Baillie et al. 1987, Davies and Becker 1996) report that species composition and forest structure can vary quite dramatically with small scale edaphic and topographic gradients. The significant correlations between local patterns of woody species distributions and soil variables K, N and total P in BFR have similarly previously been reported by Walaga (1994) and in the Albertine Rift forests by Eilu et al. (2004). In the present study for instance, *Pseudospondias microcarpa*, *Eurphorbia teke* and

Neoboutonia melleri were spatially aggregated on silica rich soils in the seasonally flooded lower-slope ("swamp") areas, while *Thecacoris lucida*, *Rinorea ilicifolia* and *Maerua duchesnei* were aggregated in areas of low light availability (high LAI). However, clear correlations between forest species distributions and silica (Si) as shown in BFR, are not previously well known in tropical rainforests. Elsewhere, in Borneo mixed Dipterocarp forests, it has been suggested that soil nutrient availability, particularly P and Mg, directly influenced species distributions and community composition (Baillie et al. 1987; Potts et al. 2002). In a review of 18 studies across the world (including Latin America, Asia and Africa), Sollins (1998) showed that phosphorus availability, aluminium toxicity, drainage, water holding capacity, and availability of K, Ca, Mg and N, micronutrients (e.g. B, Zn) are the soil properties most likely to influence lowland tropical rainforest species composition and structure. Furthermore, recent evidence suggests that diverse site environmental conditions contribute to the maintenance of species richness (e.g. Clark et al. 1999, Pitman et al. 1999, Harms et al. 2001, Toumisto et al. 2003), although the degree of specialization may differ between forests (Kubota et al. 2004).

5.0. CONCLUSIONS

The *β*-diversity of the tree and shrub species in BFR is generally low compared to the tropical montane cloud forests of Mexico and tropical forests of Peru and Ecuador. However, no comparable data is available from similar African tropical forests. Our results also show that the *β*-diversity of woody plant species for the same forest is likely to vary depending on the minimum stem diameter size adopted. However, the use of 2.0 cm as stem diameter cut-off would be more appropriate as it captures more of the species richness; and since one of the approaches to *β*-diversity assessment includes the degree to, which species composition of sample plots or sites in the same biogeographic realm differs (e.g. Colwell and Coddington 1994, Ricotta et al. 2002). With plant species community composition differing significantly for all comparisons, whether at the transect, topographic position or historical management practice type level, conservation approaches that tend to capture as much of the habitat and environmental heterogeneity will be the most appropriate for both plant and primate conservation. Collectively, the *β*-diversity patterns in BFR are to a great extent explained by local variability in soil nutrients, topography, light availability and anthropogenic disturbances.

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CHAPTER 6

Sprouting of woody species following cutting and tree-fall in a lowland semi-deciduous tropical rainforest, North-Western Uganda

Abstract

Effective management, conservation and restoration of tropical forests require an understanding of responses to disturbance events. Sprouting among woody plants within Budongo Forest Reserve (BFR) in response to harvesting for poles and saplings, and disturbance from tree and branch fall was examined. A total of 835 woody stumps representing 122 species were recorded. Human harvesting accounted for 83% of 835 damaged stumps. Both canopy and sub-canopy trees sprouted prolifically. Of the 122 affected species, 119 (97.5%) from 31 families sprouted from stem stumps, with only *Caloncoba crepiniana* exhibiting stem and root sprouting. Only *Maesopsis eminii, Cordia milleni* and *Raphia farinifera* did not resprout. Sprouts per stump ranged from 16.3±1.8 (SE) for *Rawsonia lucida*, to 1 for ten species. Number of sprouts/stump differed significantly among families (Kruskal-Wallis H = 182.63, P <0.0001), species (H = 256.26, P <0.0001) and stump size-classes (H = 73.18, P <0.0001). Mean sprouts per stump was significantly higher for intermediate sized stems of basal diameter (BD) 5.1 - 20.0 cm. Dead sprouts occurred on 26 species. There were species-specific significant differences in height (H = 39.92, P = 0.0297) and BD (H = 52.34, P = 0.0011) of the leading sprout. Stump BD (χ^2_1 = 6.62, P = 0.0101), height (χ^2_1 = 38.52, P <0.0001), bark-thickness (χ^2_1 = 14.56, P <0.0001) and height of stump above ground at, which the first sprout emerged (χ^2_1 = 74.42, P <0.0001) were significant predictors of sprouting ability among individuals. Hence, this semi-deciduous tropical rainforest has a high proportion of sprouting species and incidence of sprouting stems. Sprouting of small and relatively large stumps, and the survival and growth of sprouts, suggests that sprouting plays an important role in forest resilience to selective timber, pole and sapling harvesting.

***Key words**: Bark-thickness, coppicing, harvesting, root suckering, resilience, resprouting, stumps.*

1.0. INTRODUCTION

In tropical forests and woodlands, woody plants are subjected to various types of physical disturbance (e.g. timber harvesting, fires, storms, hurricanes, and tree and branch fall), resulting in loss of foliage or stems. In response to these disturbances, plants either resprout/coppice (henceforth referred to as sprouting) along the remaining stem, from the root-stock or die (Kammesheidt 1998, Paciorek *et al.* 2000, Bond & Midgley 2001). Sprouting in woody plants, which results in the production of secondary trunks usually from suppressed buds on the stem or roots of a plant is an induced response to injury or to a dramatic change in surrounding environmental conditions (Del Tredici 2001). The ability of a plant to resprout after its above-ground parts are killed (top-kill) is a typical feature of many plant species from disturbance-prone, terrestrial ecosystems (Cruz *et al.* 2003). However, the potential of a species to establish and persist following disturbance differs among species. It is governed primarily by life-history and physiological traits and by the characteristics of the disturbance event (Gómez Sal *et al.* 1999).

Sprouting is an important life history characteristic of woody species in moist tropical forests, and those subjected to large-scale disturbance events such as hurricanes, logging (e.g. Bellingham & Sparrow 2000, Del Tredici 2001) and slash-and-burn agriculture (e.g. de Rouw 1993). In these places plants of all sizes survive and resprout after being damaged (e.g. Bellingham *et al.* 1995, McLaren & McDonald 2003). Even in forests where large-scale disturbances are infrequent, woody plants still experience significant stem damage from smaller scale disturbances such as pole and sapling harvesting by humans as well as branch and tree fall (e.g. Clark & Clark 1991, Paciorek *et al.* 2000). Although the frequency of branch and tree fall is probably similar among rainforests sites, additional causes of stem damage are site specific (Ickes *et al.* 2003). Consequently, the ability of woody plants to resprout should also be a common plant characteristic in areas that only experience relatively minor disturbances. However, little is known of woody plant sprouting in African tropical forests, including Budongo Forest Reserve (BFR) in Uganda. Understanding the natural regeneration processes and plant responses to disturbances have practical applications in the restoration and management of forest vegetation (Vesk *et al.* 2004), particularly for economic, conservation and environmental benefits. BFR is an important natural forest for biodiversity conservation in Uganda as it contains threatened mammals (e.g. Chimpanzees) and plant species (Plumptre 1996). It is a prime example of a natural forest where no major natural disturbances such as hurricanes, droughts or fires have been recorded in its history. However, BFR is bordered on the southern side by villages inhabited by subsistence farmers with livelihoods that are entirely dependent on the exploitation of land resources (Chapter 2). This study aimed at identifying the major causes and types of disturbances leading to stem damage and, consequently, sprouting, and to describe sprouting ability among woody plant species and families. To achieve this aim, the following questions were posed; 1. What are the major causes and types of stem damage, and the level of harvesting of the woody species? 2. Are stump characteristics (i.e., basal diameter, height and bark-thickness) predictors of sprouting ability among individuals and species? 3. Does sprouting ability differ between basal diameter size-classes, species, canopy and sub-canopy species and families? 4. What is the relationship between the leading sprout's height and basal diameter, and number of sprouts/stump? Sprouting ability is considered as the number of sprouts per stump.

2.0. MATERIALS AND METHODS

2.1. Study area

Budongo Forest Reserve (BFR) is located at the top of the escarpment, east of Lake Albert, on the edge of the western rift valley in north-western Uganda, between Masindi town and Lake Albert. It has an area of 793 km^2 and lies between $1^0 37'$ and $2^0 03'$ N and $31^0 22'$ and $31^0 45'$ E. The altitudinal range is 700 - 1270 m above sea level, with a mean of 1050 m. This forest has been broadly classified as medium altitude semi-deciduous moist tropical rainforest, because several of the dominant species (e.g. *Celtis* spp., *Maesopsis eminii* Engl., *Ficus* spp. etc) are at least briefly deciduous (Eggeling 1947), with the notable exception of the shade-tolerant *Cynometra alexandri* C.H. Wright (Sheil 1997)**.** Generally, it is a mosaic of forest types, a result of forest dynamics and management history (Plumptre 1996, Chapter 3). The general ecology, environment, management and history of BFR have been described by Eggeling (1947) and Synnott (1985).

The forest reserve is contiguous with the Murchison Falls National Park to the North, Bugungu Game Reserve to the Northwest and Karuma Game Reserve to the Northeast. However, apart from the common primates (e.g. baboons, chimpanzees, white and red-colobus monkeys), there are currently no large herbivores, such as elephants and buffalos, residing in the forest reserve. The elephant populations inside BFR were eliminated in the 1970's (Laws *et al.* 1975, Sheil & Salim 2004). On the eastern, southern, and south-western sides it borders villages whose inhabitants are subsistence farmers of mixed language, culture and nationality. They are entirely dependent on the land resources for their livelihoods, and use woody plant resources for fuel energy and as raw materials for house construction. The climate is tropical, with two rainfall peaks, March-May and September-November, and a dry season December-February. The mean annual rainfall is 1500 mm. Maximum temperature rarely exceeds 32 ^{0}C and only occasionally drops below 24 ^{0}C, with low daily variation. This climate supports a regular rain-fed shifting agriculture, with the main crops being sugarcane, maize, sorghum, beans and tobacco.

2.2. Sampling design and sample size

Thirty two 100 x 50 m (0.5 ha) plots were established in forest compartments, including those that have historically been managed as (a) "nature reserves" (with little or no anthropogenic disturbance), (b) previously selectively logged about 15 years ago (~1990), and those that were (c) mechanically logged and arboricide treated in the 1950s. Some of these areas are close and accessible to surrounding local communities. BFR has a history of intrinsic disturbances such as tree fall, elephant damage, patchy selective logging (both legal and illegal) and pole cutting of specific tree species. In each 0.5ha plot, all stumps, and the number of sprouts (live and dead) from each stump were enumerated, but only live ones were measured for height and basal diameter. Stump height above ground and diameter above the basal swelling were measured. Species were identified from the stumps using the leaves of sprouts, wood and bark characteristics such as colour, smell and texture (Luoga *et al.* 2004), with reference to plant identification guides (e.g. Hamilton 1991), and the Flora of Tropical East Africa (Polhill 1952 *et seq*.). Basal diameter (BD) was measured since most of the stumps were not tall enough to measure at breast height (1.3m). Diameter and height of the largest sprout of each stump was measured, and the number of live and dead sprouts per stump enumerated. Height above the ground at, which the first sprout appeared on the stump (height at first sprout) and bark-thickness of the stump, using a bark-gauge (HAGLOF Barktax), were also measured. An attempt was also made to identify root sprouting among the plants. The type of disturbance associated with the formation of the stump was established, and if it was anthropogenic, then the purpose for removal assessed with the aid of a local elder and a persistent resource user well acquainted with local ethnobotany and regional forest utilization.

2.3. Data analysis

The total number of stumps for each species was counted, and the number and percentage that sprouted was determined, and compared between species and families. This was not, however, done for the three historical management practice types as it was apparent that tree and pole harvesting patterns were not dependent on management practice, but on accessibility to and convenience of the harvesters. The level of harvesting for each species was also determined as a fraction (percentage) of stumps of the present standing stock. Sprouting ability was calculated as the mean number of sprouts per stump for each harvested species, and comparisons among species and families were undertaken using a Kruskal-Wallis test (H-test) (Sokal & Rohlf 1995). This test was found suitable for these data although the stumps might have been of different ages and probably cut in different seasons. Because of the wide range of sites, localities and stump sizes, variance due to time since cutting or breakage would be small in comparison to all the other sources (Shackleton 2000). The stump inventory data were also pooled and tallied into BD size-classes of 0 - 5, 5.1 - 10, 10.1 - 15, …….., 35.1 - 40, and >40 cm and related to mean sprouts/stump and number of stumps. Statistical differences in sprouts/stump among these size-classes was tested by Kruskal-Wallis test with a Bonferroni multiple comparisons procedure. Each species was classified as canopy or sub-canopy based on Synnott's (1985) and Hamilton's (1991) classifications, and its overall mean sprouts/stump calculated. To test for differences in sprouting ability between canopy and sub-canopy species, a Mann-Whitney U test was used. Each species was counted as a single data point in the analyses so that abundant species did not dominate the results.

The number of sprouts/stump was related to stump BD, height and bark-thickness using log linear regression models [PROC GENMOD, based on a negative binomial (*NB*) distribution and a log link function] utilizing SAS version 8.0 (SAS Institute Inc. 2004). The *NB* distribution provides one way of modelling heterogeneity in a population in that it naturally accounts for over-dispersion better than the Poisson distribution. Only species with ≥4 stumps were included in the analyses. The model fit was adequate for the data since values of Pearson Chi-square (=201.6) and deviance (=213.9) divided by the number of degrees of freedom (=210) were close to 1. Species-specific linear regression analyses were also performed to relate sprouting ability (number of sprouts/stump) to stump characteristics (i.e., height, BD, bark-thickness), and height of stump above ground at, which the first sprout emerged. In addition, using pooled stump data, linear regression analyses were performed to relate number of sprouts/stump to the basal diameter and height of the leading sprout. Species-specific differences in the height and BD of the leading sprout were also tested using a Kruskal-Wallis test.

3.0. RESULTS

3.1. Causes and levels of stem damage, and types and levels of sprouting

A total of 835 woody stumps representing 122 species, both cut and broken, were investigated for sprouting, of which 814 (97.5%) from 119 species (within 31 plant families) sprouted (Appendix). Only three species, *Maesopsis eminii, Cordia milleni* Bak. (both canopy species) and *Raphia farinifera* (Gaertn.) Hylander (a palm) did not resprout from the stumps. The first two species are highly sought after for timber, while the latter is of high conservation importance as it is classified as vulnerable. The most harvested and frequently sprouting species were *Celtis mildbraedii* Engl. (104 stumps), *Funtumia elastica* (Preuss) Stapf. (93), *Lasiodiscus mildbraedii* Engl. (81) and *Cynometra alexandri* (46), making up 39.8% of the total stumps sampled. These are the preferred woody species for house construction due to their superior woody quality, pole straightness and high abundance in the forest. Overall, harvesting was low since none of the species had more than 5% of the stem standing stock harvested. Of the 119 sprouting species, only *Caloncoba crepiniana* (De Wild. & Th. Dur.) Gilg sprouted from both the stem stump and roots (root suckering). Although there are many types of disturbances leading to stem damage in a forest, the most frequently recorded in BFR was human harvesting (83% of the stumps), targeting mainly saplings and poles, and tree and branch fall breakage (17%). Saplings and poles were mostly harvested for building purposes, while large trees were harvested for timber or as bed-supports for pitsawing. No stem damage from animals was observed despite the fact that this forest is rich in primates and wild pigs.

3.2. Sprouting ability of species and family

The number of sprouts/stump differed significantly between the plant families sampled (Kruskal-Wallis H= 182.63, P<0.0001). Among the families represented by ≥3 species, the families with highest mean (±*SE*) sprouts/stump were Ulmaceae (8.99±0.55), Flacourtiaceae (7.54±1.61), and Violaceae (7.37±0.62); while those with the lowest were Annonaceae (3.25±0.88), Sapindaceae (3.20±0.43) and Meliaceae (3.08±0.29). There were also significant species-specific differences observed for number of sprouts/stump (Kruskal-Wallis H= 256.26, P<0.0001), and for height (H= 39.92, P= 0.0297) and BD of the leading sprout (H= 52.34, P= 0.0011). At the species level, the number of sprouts/stump ranged between 35 for *C. mildbraedii* and one for ten (10) species, with the latter being quite common (8 of 17 stumps) in *Tabernaemontana holstii* K. Schum. About 38.4% of the *C. mildbraedii* stumps had ≥10 sprouts and only 10.9% had ≤2 sprouts/stump, while those of *T. holstii* mainly had 1 and rarely exceeded 2 sprouts/stump. The highest mean sprouts/stump was 16.3±1.8 (n=3) for *Rawsonia lucida* Harv. & Sond., while the lowest was 1.9±0.3 (n=17) for *T. holstii* (Appendix 1). The 13 species with the highest mean number (≥8.0) of sprouts/stump were from 12 families, which included 7 sub-canopy (i.e. *R. lucida*, *Maerua duchesnei* (De Wild.) F. White , *Alchornea laxiflora* (Benth.) Pax & K. Hoffm., *Tapura fischeri* (Engl.) Engl., *Thecacoris lucida* (Pax.) Hutch., *Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze. and *Lasiodiscus mildbraedii*) and 6 canopy species (i.e. *Strychnos mitis* Moore, *C. mildbraedii, C. zenkeri, Diospyros abyssinica* (Hiern) F. White*, Pouteria altissima* (A. Chiev.) Aubrev. & Pellegr.*,* and *Cynometra alexandri*). Of these species, only 5 (i.e. *C. mildbraedii, C. zenkeri*, *D. abyssinica*, *P. altissima*, *and S. mitis*) are regarded as timber species (MNR, 1997), while the rest are harvested for subsistence uses. There was no overall statistically significant difference (U = 1630.5, p = 0.61, n = 119) in sprouting ability (i.e. mean sprouts/stump) between the sub-canopy and canopy species.

There were relatively few dead sprouts on sprouting stumps, with only 26 species (21.8% of 119 species) having any dead sprouts. Dead sprouts/stump ranged from 7.7% (1 of 13 sprouts) in *R. lucida* to 83% (5 of 6 sprouts) in *Senna spectabilis* (DC.) Irwin & Barneby. *Senna spectabilis* had the highest mean (±SE) dead sprouts/stump (4.0±0.6, n = 15), followed by *F. elastica* (2.3±0.3, n = 12) and *C. mildbraedii* (2.5±0.6, n = 6).

3.3. Relationships between stump characteristics and sprouting ability

Sprouting stumps were of varying BD sizes, ranging from 0.32 cm for *Trichilia drageana* Sond. to 130 cm for *Mildbraediodendron excelsum* Harms. However, about 93% of the sampled stumps were ≤16 cm in BD, with only 1.2% being ≥29.0 cm (Fig. 1a). The relationship between stump size-classes and mean sprouts/stump exhibited a hump-shaped curve, with sprouts/stump rising with increasing size-class and declining beyond the ≥30 cm BD size-class (Fig. 1b). Among the stumps of harvestable size for timber (BD >60.0 cm), *Chrysophyllum albidum* G. Don. (66.5 cm) and *M. excelsum* (130 cm) sprouted, while *Entandrophragma utile* (Dawe & Sprague) Sprague (70.8 cm) and *M. eminii* (75.0 cm) did not. The mean sprouts/stump differed significantly (H = 73.18, P <0.0001) among the stump size-classes. However, pair-wise comparisons with Bonferroni correction only revealed statistically significant differences between the 0 - 5 cm size-class and the 5.1 - 10 (P <0.0001), 10.1 - 15.0 (P <0.0001), and 15.1 - 20 cm (P = 0.002) size-classes. Stumps of BD 5.1 - 20.0 cm on average had higher sprouts/stump than any other size-class.

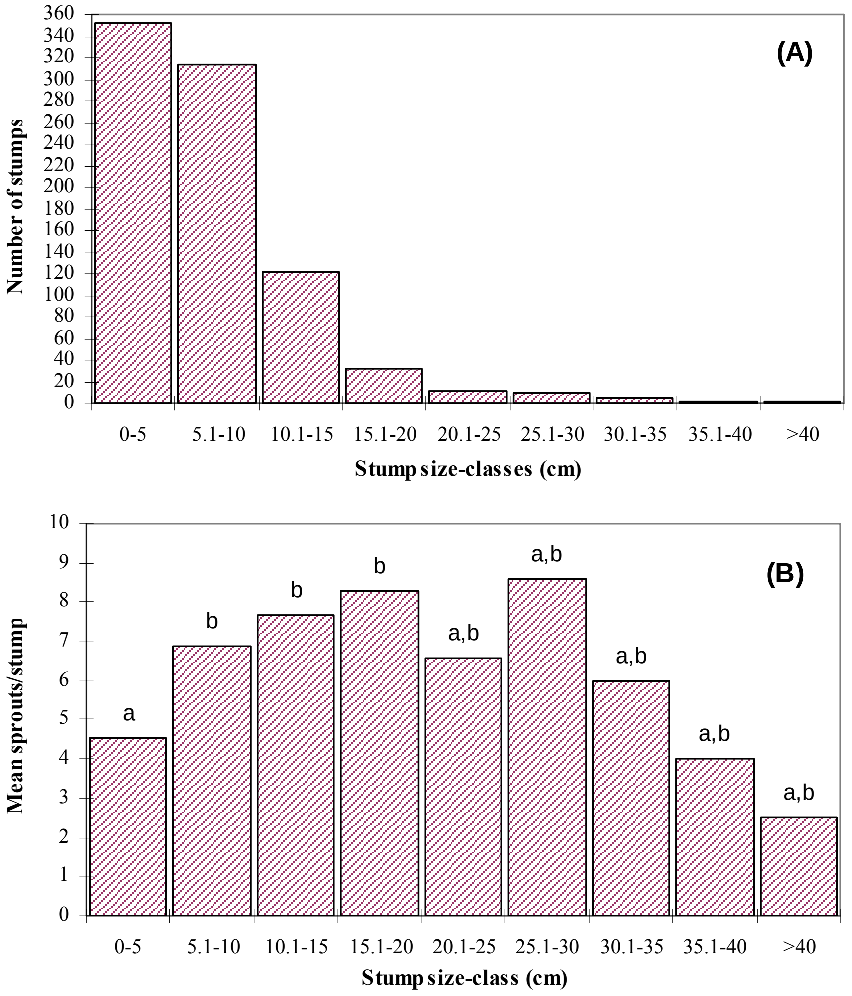

Figure 1. Relationship between stump basal diameter (BD) size-classes and (a) number of stumps, and (b) mean sprouts/stump for damaged woody species in Budongo Forest Reserve, NW, Uganda. Size classes accompanied by the same superscript do not differ significantly ($p < 0.05$).

Stump characteristics (bark-thickness, BD, height and height at first sprout) significantly influenced the number of sprouts/stump. The negative binomial distribution regression model showed that stump bark-thickness (χ_1^2 = 14.56, $P < 0.0001$), BD (χ_1^2 = 6.62, $P = 0.0101$), height (χ_1^2 = 38.52, $P < 0.0001$) and height on stump above the ground at, which the first sprout emerged (χ_1^2 = 74.42, $P < 0.0001$) were significant predictors of sprouting ability of the plants when the species data are pooled. On the other hand, species-specific linear regressions detected significant relationships between stump height and number of sprouts for 4 species (3 positive and 1 negative; Fig. 2), and BD and number of sprouts/stump for 5 species (Fig. 3). Furthermore, it detected significant negative relationships for height on stump above the ground at, which the first sprout emerged with number of sprouts/stump for 5 species (Fig. 4). There were, however, no significant relationships between bark-thickness and number of sprouts/stump.

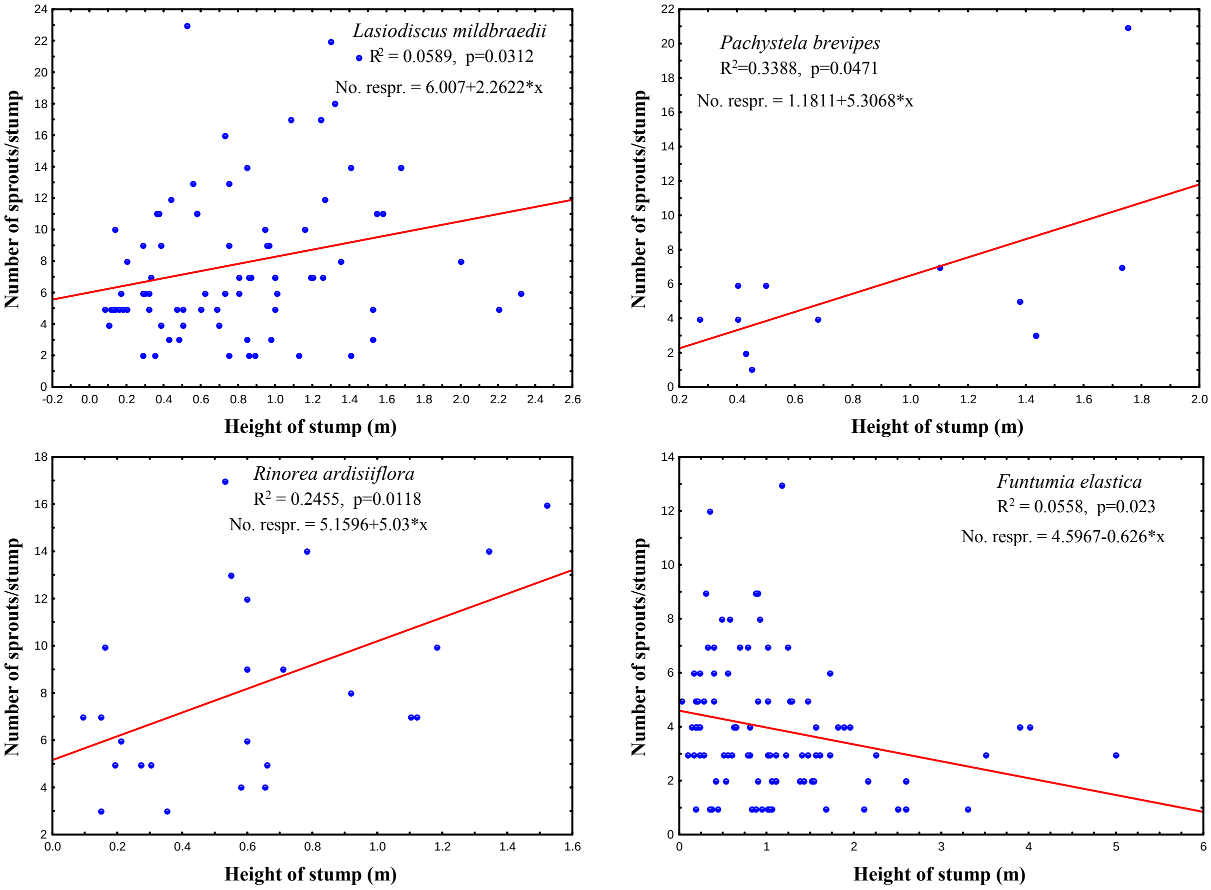

Figure 2. Regression analyses of height of stump on the number of sprouts/stump produced for four species (which showed significant relationships) following cutting, and tree and branch fall disturbances in Budongo Forest Reserve, NW Uganda.

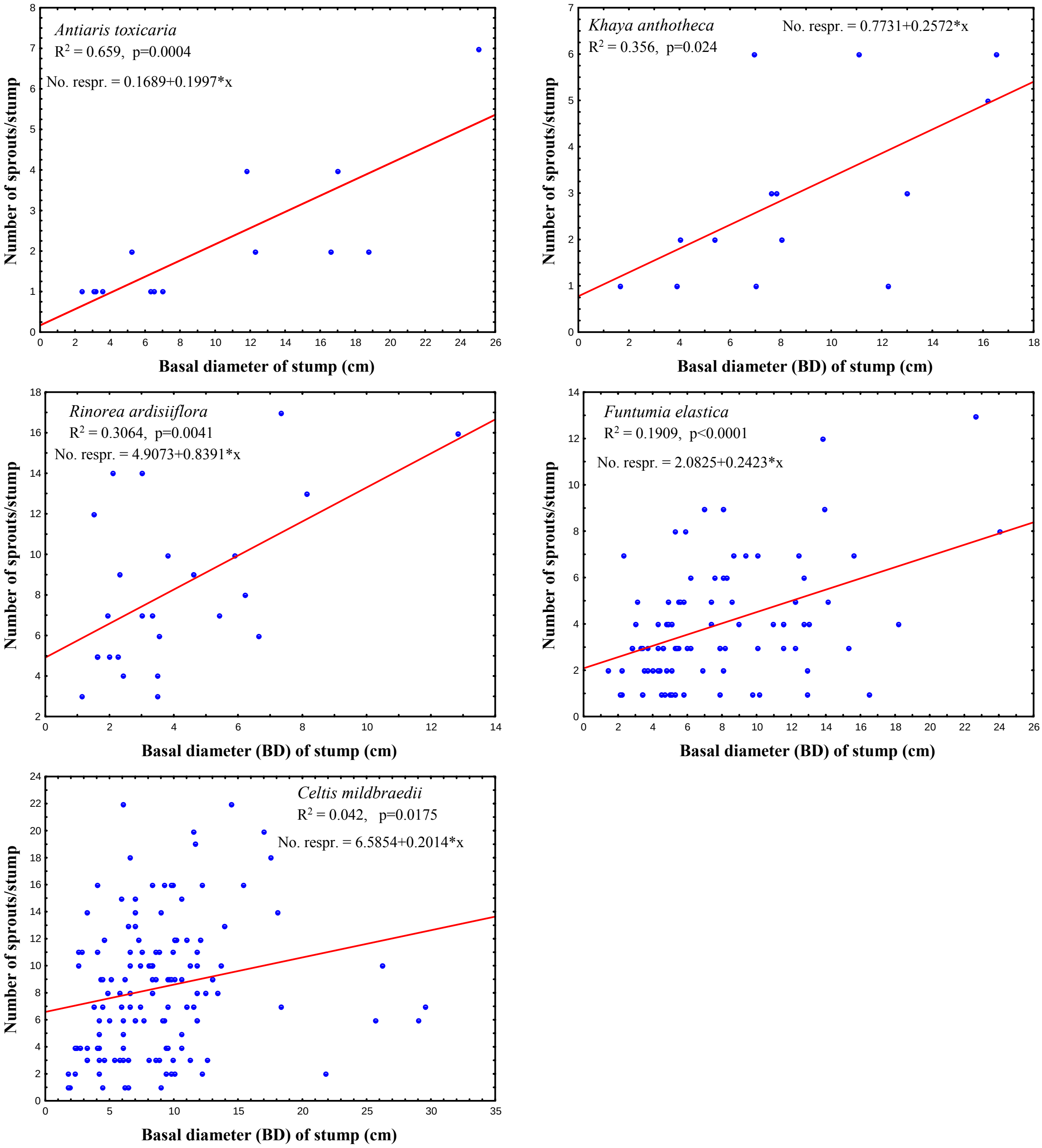

Figure 3. Regression analyses of basal diameter of stump on the number of sprouts/stump produced for five species (which showed significant relationships) following cutting, and tree and branch fall disturbances in Budongo Forest Reserve, NW Uganda.

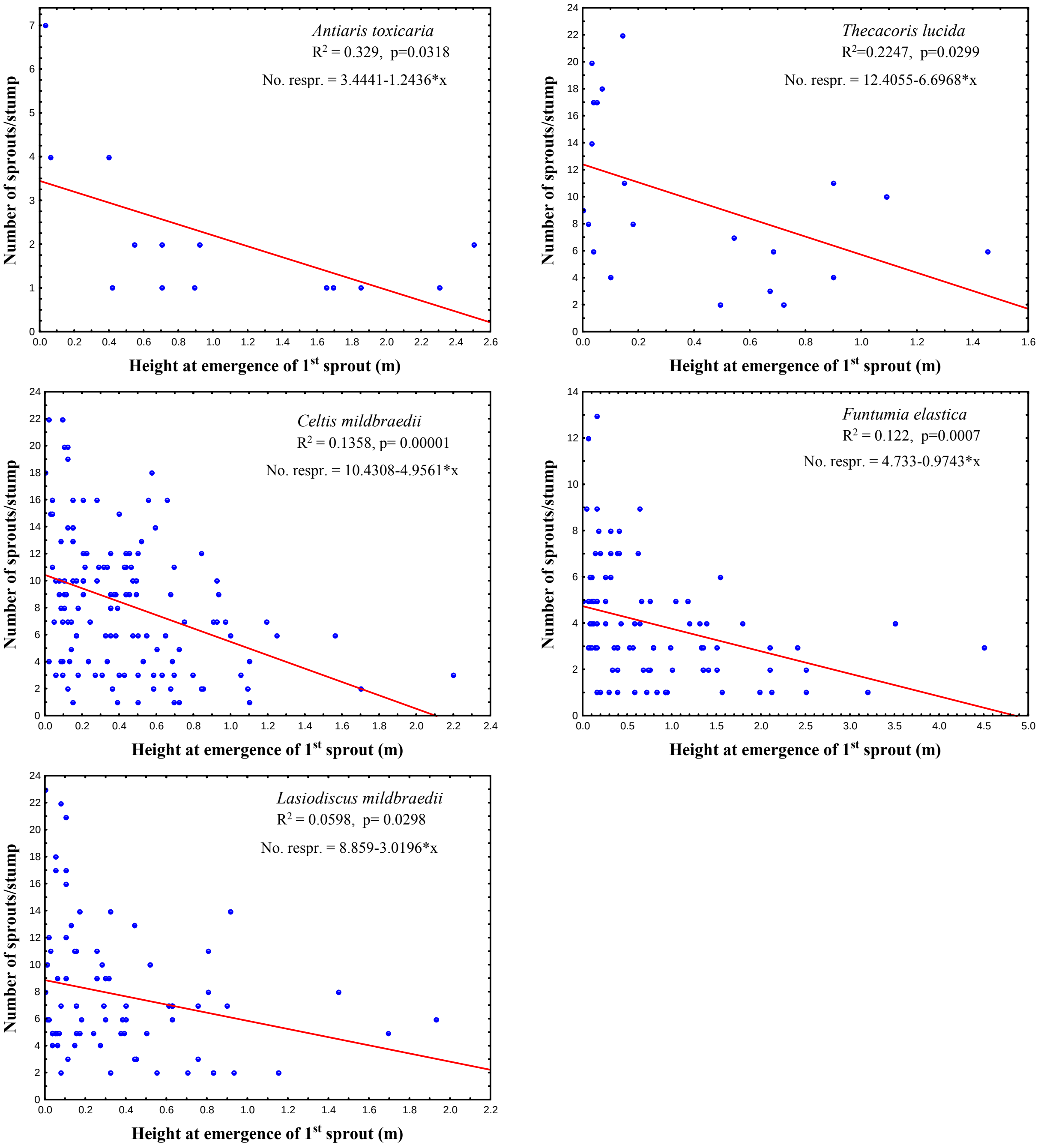

Figure 4. Regression analyses of height of stump above the ground at, which the first sprout emerged on the number of sprouts produced for five species (which showed significant relationships) following cutting, and tree and branch fall disturbances in Budongo Forest Reserve, NW Uganda.

3.4. Relationship between leading sprout BD and height, and number of sprouts/stump

The number of sprouts/stump was a significant negative predictor for both BD ($\chi_1^2 = 26.17$, $P < 0.0001$) and height ($\chi_1^2 = 20.34$, $P < 0.0001$) of the leading sprout for pooled data (Fig. 5). Thus, stumps found with fewer sprouts were expected to have their leading sprouts attaining larger BD and taller sizes, than those densely covered with sprouts. For species having stumps with multiple sprouts, *F. elastica* had both the tallest (15.3 m) and thickest (BD = 8.0 cm) leading sprout, suggesting that it probably has the greatest potential for coppice regrowth and biomass replacement. However, a sawn stump of *M. excelsum* (BD = 130.0 cm) had a single sprout of height 10.0 m and BD of 33.4 cm. This further strengthens the argument that densely sprouting stumps are probably slower at producing tall and thick leading sprouts (Fig. 5).

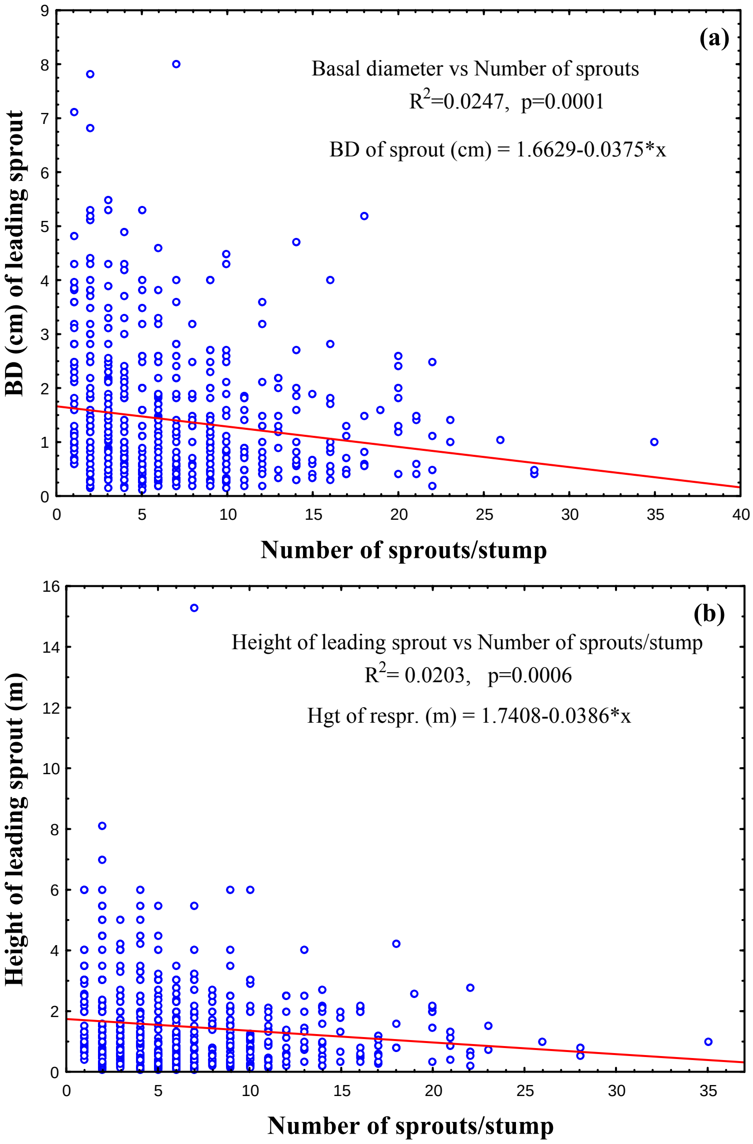

Figure 5. Regression analyses of the number of sprouts/stump on the (a) basal diameter and (b) height of leading sprout for pooled species stump data in Budongo Forest Reserve, NW Uganda.

3.5. Vertical distribution of sprouts on stump

Differences in the vertical distribution of sprouts on the stump were observed among the species. Generally, species that had less than 8 sprouts on a stump (e.g. *F. elastica*, *Myrianthus holstii* Engl., and *C. albidum*), tended to have an almost uniform vertical distribution, while those with many sprouts (e.g. *C. mildbraedii*, *D. abyssinica*, *L. mildbraedii*, and *C. alexandri*) had most sprouts on the upper part close to the cut. It was also observed that those species with an almost uniform distribution of sprouts along the stump had almost uniform sized (BD and height) sprouts. For those with a more concentrated distribution of sprouts on the upper part of stump, the leading (tallest and thickest) sprout was always found among the top-most sprouts, for example in *Celtis mildbraedii* (Fig. 6).

Figure 6. The distribution of sprouts along stumps and the location of the leading sprout (LS) relative to other sprouts on the stump for four selected species, namely *Celtis mildbraedii*, *Lasiodiscus mildbraedii*, *Chrysophyllum albidum* and *Funtumia elastica*.

4.0. DISCUSSION

Human harvesting of saplings and poles is presently the major cause of stem damage and seems to be also more common in areas, which are more accessible and nearer to human settlements. This is probably because BFR is the main source of wood-based products (e.g. poles, saplings, and fuel-wood) to the local human population as most woodlands outside BFR have been cleared for agriculture expansion (Chapter 2), and possibly the absence of elephants. Only one species exhibited root suckering, suggesting that it is not a common type of sprouting in BFR under the present environment conditions, characterised by lack of fires, a closed canopy in almost all parts, and an absence of both heavy logging and large herbivores in the interior (e.g. elephants; Sheil and Salim 2004). Shady conditions under a closed canopy as encountered in most parts of BFR, suppress root sucker production among temperate forest trees (Del Tredici 2001). In tropical rainforests, root suckering is a common mode of regeneration among species in deforested and fire-degraded sites (e.g. Stocker 1981, Kauffman 1991) and forests prone to slash-and-burn agriculture and logging (e.g. Kammesheidt 1999, Marrinan *et al*. 2005).

The number of sprouting species (119 = 97.5% of 122) recorded in BFR is higher than reported from other tropical forests. For example, in the semi-evergreen rainforest in Queensland, of the 82 species that reappeared after the felling and burning of a forest, 74 (90.2%) coppiced from stumps (Stocker 1981).

Similarly, 48 (94%) of 51 species sampled in a tropical dry limestone forest in Jamaica (MacLaren & McDonald 2003) and 35 (60.3%) of 58 species from a moist tropical forest in Eastern Paraguay (Kammesheidt 1998) coppiced from stumps. Furthermore, in Jamaica, Puerto Rico and Nicaragua, 54-87% of trees of various size classes sprouted after hurricane damage (e.g. Zimmerman *et al.* 1994, Bellingham *et al.* 1995). Plant species respond differently to disturbances and gradients in environmental variables, resulting in different sprouting abilities among them. For example, humid forests and tropical sites have been identified with higher community-wide sprouting ability than the temperate forests (Everham & Brokaw 1996).

Results from this study showed that the ability to sprout following stem damage is to some degree common among the woody species of BFR, with both sub-canopy and canopy species showing prolific sprouting. The ability of both sub-canopy and canopy woody species to sprout has also been reported in Jamaican montane forest trees (Bellingham *et al.* 1994), the Pasoh Forest Reserve in Malaysia (Ickes *et al.* 2003) and Barro Colorado Island of Panama (Paciorek *et al.* 2000). The lack of statistically significant differences in sprouting ability (sprouts/stump) between sub-canopy and canopy species in BFR has similarly been reported for moist tropical forest species in Panama (Paciorek *et al.* 2000). Although sprouting is common among the woody plants of BFR, some species (i.e. *Maesopsis eminii*, *Cordia millenii* and *Raphia farinifera*) did not sprout. The canopy species, *M. eminii* and *C. millenii,* did not have any smaller-sized stumps (<30 cm BD), which generally, show high sprouting ability. Although there was sprouting among all the size-classes analysed, mean sprouts/stump was significantly higher in stems of 5.1 - 20.0 cm BD. This closely compares with results from other studies (e.g. Putz *et al.* 1983, MacDonald & Powell 1983, Tworkoshi *et al.* 1990), which reported higher sprouting ability among woody stumps of ≤16 cm and lower for ≥30.0 cm BD. Furthermore, if stumps of 5.1 - 20.0 cm BD are regarded as juveniles (which is reasonable to assume for canopy species), these findings also compare with other studies (e.g. Everham & Brokaw 1996, Bellingham & Sparrow 2000, Paciorek *et al.* 2000) in that many forest tree species sprout as juveniles and then lose the ability to sprout as adults.

Species differences in sprouting ability revealed in BFR is well known in other ecosystems where both strongly and weakly sprouting species occur (e.g. Everham & Brokaw 1996, McLaren & McDonald 2003). However, the relatively high number of woody species sprouting in BFR may be attributable to most of the tree species being hardwoods (G. Eilu, pers. com.). Indeed, in Madagascar, some hardwood trees of the family Leguminoseae (Fabaceae) are able to sprout after being cut (Cunningham *et al.* 2005). The stump characteristics, which were found to be significant predictors for number of sprouts/stump in BFR have also been reported for woody species from other ecosystems (e.g. Weigel & Peng 2002). The significant positive relationship between stump BD and sprouts/stump for 5 species in BFR, was also reported for 7 woody species in a disturbed tropical dry forest in Jamaica (McLaren & McDonald 2003), where some species also had significant negative relationships between stem diameter and average height of the leading sprout.

The significant differences in the number of sprouts/stump among families and species in BFR, has also been reported among savanna woody species, and further attributed to plant size/age at the time of cutting and stump height (Shackleton 2000, Luoga *et al.* 2004). In the present study, all (98.8% of total) smaller sized stumps (BD <30 cm) sprouted, while for larger ones (size suitable for timber harvest >30cm), only 8 of 12 sprouted. This agrees with Lamson (1988), who stated that for most species with small stems, usually <30 cm dbh, had a better sprouting potential than larger stems. However, it is probable that small dead stumps were under-sampled as they would presumably be more easily missed than larger ones, since they decompose quicker than larger stumps. Sprouting ability differences among the >30 cm BD stumps in BFR, suggesting that apart from individual stump physical characteristics, other species-specific characteristics (e.g. stem water status, root allocation and stored starch) may play a role. Plant species may also differ in their ability to resprout as a consequence of differences in other factors such as meristematic capacity (numbers of available buds), root-shoot partitioning, stored carbohydrate and nutrient reserves (e.g. Zimmerman *et al.* 1994). Although sprout survival in BFR is not clearly known, as this is a single observational study, the attainment of tall and large leading sprouts, even for those with a high number of sprouts/stump, suggests that at least one of the sprouts will survive and grow to replace the lost stem. It further shows that sprouts can survive to play an important role in the persistence of the damaged plants and in this respect sprouting is important in the regeneration process and the future state of BFR in the face of increased human utilization. On the other hand, the death of some sprouts on stumps suggests self-thinning among sprouts. In temperate forests self-thinning occurs among sprouts as they increase in size (e.g. Rentena *et al*. 1992).

The tendency of most woody species in BFR to produce sprouts close to the cut end or point of breakage has also been encountered in woody species of Panamian forests, where most sprouts emerged near the top of broken snags (Putz *et al.* 1983). Hence, these results reaffirm the Cannell (1983) principle that distal buds, near the cut ends, are stimulated to grow more than basal buds (‘acrotony’). Trees respond to damage with the sprouting of suppressed buds immediately below the point of damage and, regardless of the height of the damaged stump, some species have a strong tendency to sprout from the top of the stump or near the edge of the cut (Burns & Honkala 1990, Smith *et al.* 1997). In BFR, it was also noticed that the largest and tallest sprout on the stumps of most species was among those emerging closest to the top of the stump. Similarly, Burns & Honkala (1990) pointed out that, generally, buds closest to the point of damage, whether on branches or the trunk show the most vigorous growth. On the other hand, despite producing a lower than average number of sprouts/stump, the growth of the tallest and largest sprout by *Funtumia elastica*, is in keeping with the observation that stumps with low sprout densities achieve relatively larger sprouts.

5.0. CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

Human harvesting for poles and saplings for building purposes and tree and branch fall are the major causes of woody stem damage in BFR. This study showed that semi-deciduous tropical rainforests have both a high proportion of sprouting species and incidence of sprouting stems (both small and relatively large diameter sized). The 119 (97.5%) stem sprouting species in BFR is higher than reported from other tropical forests outside the African continent. However, there are no published data for comparison from other African tropical rainforests. There appears to be a high chance of sprout survival and growth to replace the lost stem, making sprouting a key trait in the persistence of woody plant individuals, populations and communities in BFR. Even the sprouting of large stumps of ≥29.0 cm BD (e.g. *Chrysophyllum albidum, C. mildbraedii* etc.), and the survival and growth of sprouts suggests that sprouting may play an important role in the resilience of the forest following selective timber, pole and sapling harvesting. However, the lack of sprouting of stumps ≥60 cm BD for some important timber species threatens their survival, unless they have sufficient seedling banks to replace the lost mature seed trees. Silvicultural interventions for management of sprouts in BFR should involve cutting as low to the ground as possible in order to stimulate the growth of buds from the collar instead of the trunk, and to prevent sprouts from suffering heart rot (Del Tredici 2001). It is predicted that densely sprouted stumps will be slower at producing tall and thick leading sprouts than sparsely sprouting ones, regardless of the species. Therefore, manual thinning could be important to reduce the number of sprouts on the stump and encourage the faster development of taller and larger sized sprouts in forest areas where timber and pole harvesting is allowed. Although BD, height and bark-thickness of stump, and height at first sprout were found to be good predictors of sprouting ability, additional experimental studies will be required to determine these relationships more precisely. In addition, long term studies and those relating sprouting to edaphic factors and the frequency and seasonal timing of harvesting will be necessary for a more complete understanding of species sprouting responses, particularly for those frequently harvested and of silvicultural importance.

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Appendix 1. Sprouting woody species, listed alphabetically by family, indicating the number of sprouting stumps (=number of damaged plants), mean number of sprouts/stump and the overall number of undamaged plants encountered in 32, 0.5 ha plots within the semi-deciduous Budongo Forest Reserve, NW Uganda. SC: sub-canopy species, <25 m tall; C: canopy species, >25 m tall; Ss: shrub.

Family	***Species***	*No. of Stumps (=No. of damaged plants)*	*No. of sprouts/stump Mean (±SE).*	*No. of undamaged plants*	*Growth form*
Anacardiaceae	*Pseudospondias microcarpa (A. Rich.) Engl.*	5	4.40±1.40	187	C
	Lannea welwitschii (Hiern) Engl.	1	3	45	C
Annonaceae	*Cleistopholis patens (Benth.) Engl. & Diels.*	3	2.00±0.58	146	C
	Greenwayodendron suaveolens (Engl. & Diels) Verdc.	2	3.50±0.50	73	C
	Monodora angolense Welw.	1	2	36	SC
	Monodora myristica (Gaertn.) Dunal	1	2	6	C
	Xylopia staudtii Engl.	1	9	4	
Apocynaceae	*Funtumia elastica* (Preuss) Stapf	93	3.90±0.25	1860	C
	Tabernaemontana holstii K. Schum.	17	1.88±0.25	413	SC
	Alstonia boonei De Wild.	1	3	86	C
	Rauvolfia vomitoria Afzel.	1	4	28	SC
Bignoniaceae	*Markhamia lutea* K. Schum.	5	4.80±1.28	80	SC
	Kigelia africana (Lam.) Benth.	3	3.30±1.33	89	SC
Burseraceae	*Canarium schweinfurthii* Engl.	2	2.50±1.50	10	C
Capparidaceae	*Maerua duchesnei* (De Wild.) F. White	3	11.33±1.20	244	SC
Chailletiaceae	*Tapura fischeri* (Engl.) Engl.	5	12.20±3.29	230	SC
Clusiaceae	*Mammea africana* Sabine	4	1.75±0.25	84	SC
	Symphonia globulifera L.f.	3	8.00±1.15	2	C
Ebenaceae	*Diospyros abyssinica* (Hiern) F. White	9	10.56±2.18	125	C
Eurphorbiaceae	*Thecacoris lucida* (Pax.) Hutch.	22	10.50±1.46	1652	SC
	Argomuellera macrophylla Pax Laka	10	4.00±0.47	739	Ss
	Acalypha ornata Hochst. ex A. Rich.	9	4.55±1.07	2587	Ss
	Acalypha neptunica Muell. Arg.	8	6.75±1.19	2691	Ss
	Alchornea laxiflora (Benth.) Pax & K. Hoffm.	7	12.29±3.10	839	SC
	Drypetes ugandensis (Rendle) Hutch.	4	3.25±0.63	100	SC
	Mallotus oppositifolius (Geisel.) Muell. Arg.	4	5.25±1.11	295	SC
	Drypetes gerrardii Hutch. var. grandifolia	3	6.00±1.00	87	C
	Euphorbia teke Schweinf. ex Pax	2	3.50±0.50	44	SC
	Antidesma laciniatum Muell. Arg.	1	2	60	SC
	Antidesma venosum E. Mey. ex Tul.	1	5	45	SC
	Bridelia micrantha (Hochst) Baill.	1	2	44	SC
	Claoxylon hexandrum Muell. Arg.	1	5	7	SC
	Croton macrostachyus Hochst. ex Del.	1	4	84	SC
	Croton sylvaticus Hochst. ex Krauss.	1	4	65	SC
	Margaritaria discoidea (Baill.) Webster	1	5	63	SC
	Ricinodendron heudelotii (Baill.) Pierre ex Pax	1	1	17	C
Fabaceae	*Cynometra alexandri* C.H. Wright	46	8.35±0.83	1031	C
	Senna spectabilis (DC.) Irwin & Barneby	29	5.28±0.62	2140	C
	Tetrapleura tetraptera (Schumach & Thonn.) Taub	5	2.80±0.49	53	C
	Albizia glaberrima (Schumach. & Thonn.) Benth.	4	3.00±1.22	50	SC
	Mildbraediodendron excelsum Harms	3	1	20	C
	Dialium excelsum J. Louis ex Steyaert	2	3.00±1.00	11	C
	Albizia grandibracteata Taub	1	3	24	C
	Albizia zygia (DC.) Macbr.	1	2	43	C
	Erythrophleum suaveolens (Guill. & Perr.) Brenan	1	4	45	C
	Piptadeniastrum africanum (Hook. F.) Brenan	1	1	15	C

Flacourtiaceae	*Caloncoba crepiniana* (De Wild. & Th. Dur.) Gilg	7	6.14±1.03	119	SC
	Rawsonia lucida Harv. & Sond.	3	16.33±1.76	245	SC
	Oncoba spinosa Forssk.	2	2.50±0.50	31	SC
	Lindackeria mildbraedii De Wild.	1	1	10	SC
Icacinaceae	*Leptaulus daphanoides* Benth	1	3	3	SC
Loganiaceae	*Strychnos mitis* S. Moore	3	15.67±7.88	104	C
Melastomataceae	*Memecylon jasmonoides* Gilg.	5	3.60±0.87	44	SC
Meliaceae	*Khaya anthotheca* (Welw.) C.DC.	13	2.77±0.50	489	C
	Trichilia drageana Sond.	12	2.17±0.20	187	C
	Trichilia prieureana A. Juss	7	3.71±0.68	293	SC
	Trichilia rubescens Oliv.	6	5.17±0.75	400	SC
	Guerea cedrata (A. Chiev.) Pellegr.	5	2.40±0.68	100	C
	Entandrophragma angolense (Welw.) C.DC.	2	1	39	C
	Entandrophragma utile (Dawe & Sprague) Sprague	2	2.00±1.00	66	C
	Entandrophragma cylindricum (Sprague) Sprague.	1	2	78	C
	Lovoa schweinfurthii	1	3	3	
	Lovoa sywnnertonii Bak. F.	1	2	24	SC
	Lovoa trichilioides Harms	1	11	30	C
Moraceae	*Antiaris toxicaria* (Pers.) Lesch.	14	2.14±0.47	262	C
	Myrianthus holstii Engl.	6	4.17±0.70	303	SC
	Morus mesozygium Stapf	5	5.80±2.65	81	C
	Ficus exasperata Vahl	4	4.50±1.04	61	C
	Trilepisium madagascariense DC.	3	4.00±0.58	203	C
	Ficus asperifolia Miq.	2	2.50±1.50	12	SC
	Ficus sur Forssk.	2	6.50±1.50	57	C
	Ficus variifolia Warb.	1	1	3	C
Myrtaceae	*Pycnanthus angolensis* (Welw.) Warb.	1	3	35	C
Ochnaceae	*Ouratea densiflora* De Wild. & Th. Dur.	5	1.80±0.20	258	SC
	Ochna holstii Oliv.	4	3.75±0.48	24	SC
Oleaceae	*Linociera johnsoni* Baker	1	4	31	SC
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	81	8.02±0.58	4548	SC
Rhizophoraceae	*Cassipourea congensis* DC.	1	5	17	SC
Rubiaceae	*Coffea canephora* Pierre ex Froehn	4	4.75±1.55	100	SC
	Belonophora hypoglauca (welw. Ex Hiern) A. Chiev	2	1	149	SC
	Coffea euginoides S. Moore	1	2	39	SC
	Dictyandra arborescens Welw. ex Benth. & Hook. F.	1	7	40	SC
	Galiniera saxifraga Del.	1	2	4	SC
	Pavetta molundensis K. Krausse	1	3	49	SC
	Rothmannia whitfieldii (Lindl.) Dandy	1	1	10	SC
Rutaceae	*Teclea nobilis Del.*	8	7.25±1.26	294	SC
	Zanthoxylum rubescens Hook. F.	2	2.00±1.00	25	SC
	Balsamocitrus dawei Stapf.	1	4	15	SC
	Teclea grandifolia Engl.	1	4	10	SC
Sapindaceae	*Blighia unijugata* Bak.	7	2.43±1.27	187	SC
	Aphania senegalensis (Juss. ex Pior.) Radlk	6	3.00±0.44	27	SC
	Melanodiscus sp.	4	4.25±0.85	113	SC
	Lychnodiscus cerospermus Radlk.	3	4.33±1.20	251	SC
	Pancovia turbinata Radlk.	2	3.50±1.50	36	SC
	Allophyllus dummeri Bak. F.	1	3	21	SC
	Zahna golungensis Hiern	1	2	38	SC
Sapotaceae	*Pouteria altissima* (A. Chiev.) Aubrev. & Pellegr.	14	8.43±1.39	357	C
	Pachystela brevipes (Baker) Engl.	12	5.83±1.48	36	SC
	Chrysophyllum albidum G. Don	10	4.90±0.82	311	C
	Chrysophyllum perpulchrum Hutch. & Dalz	8	5.00±1.07	162	C
	Bequaertiodendron oblanceolatum (S. Moore) Hiene & J.H. Hemsl	7	6.86±1.64	133	SC
	Mimusops bagshawei S. Moore	4	4.50±1.50	72	C
	Manilkara dawei (Stapf.) Chiov.	3	3.00±0.58	33	C

	Bequeartiodendron natelense (Sond.) Hiene & J.H. Hemsl	1	2	24	SC
	Chrysophyllum muerense Engl.	1	8	23	C
Simaroubaceae	*Klainedoxa gabonensis* Pierre ex Engl.	5	7.40±2.04	16	C
	Irvingia gabonensis (Aubry-Lecomte O'Rorke) Baill.	2	4.50±0.50	4	C
Sterculiaceae	*Cola gigantea* A. Chev.	5	2.20±0.58	106	C
Sterculiaceae	*Leptonychia mildbraedii* Engl.	3	5.00±0.58	52	SC
	Sterculia dawei Sprague	1	1	11	C
Tiliaceae	*Desplatsia dawevrei* (De Wild. & T. Dur.) Burret	4	2.75±0.25	79	SC
	Glyphaea brevis (Spreng.) Manachino	1	2	3	SC
Ulmaceae	*Celtis mildbraedii* Engl.	104	8.68±0.55	2472	C
	Celtis zenkeri Engl.	7	14.14±2.44	549	C
	Celtis gomphophylla Baker	1	5	216	C
Violaceae	*Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze.	25	8.24±0.81	1666	SC
	Rinorea brachypetala (Turcz.) O. Ktze.	10	4.80±0.66	802	SC
	Rinorea dentata (P. Beauv.) O. Ktze.	2	9.00±3.00	26	SC
	Rinorea oblongifolia C. Marquand	1	8	298	SC

CHAPTER 7

Seedling regeneration and population structure of woody species in a semi-deciduous tropical rainforest, Budongo Forest Reserve, north-western Uganda

Abstract

Increased loss of woodlands outside Budongo Forest Reserve (BFR) and diminishing stocks of mahoganies is resulting in many forest tree species, including primate food sources to be used increasingly for timber and other domestic needs. Seedling regeneration (i.e. regeneration via seedlings) patterns in relation to environmental factors in BFR, were studied using 32, 0.5 ha plots divided into five 0.1 ha contiguous sub-plots laid along a topographic gradient. The population structure of 15 multiple-use woody species was explored with a view to assess regeneration status and implications for their sustainable management. A total of 85624 seedlings representing 237 species and 46 families were recorded, with *Cynometra alexandri* C.H. Wright and *Lasiodiscus mildbraedii* Engl. being the most abundant and also among the most widely distributed in the forest. About 30.3% of the species were rare (only 2-10 individuals), while 12% were very rare (only 1 individual each). Only mean seedling density was significantly (ANOVA; $F_{2,25} = 4.17$, $p = 0.027$) different between the historical management practice types; highest (8884±2027 individuals ha^{-1}) for the logged only, followed logged and arboricide treated (5034±718 individuals ha^{-1}), and lowest (3925 ±651 individuals ha^{-1}) for the nature reserve area. Analysis of similarity (ANOSIM) revealed significant differences in seedling composition between transects, but not between topographic positions or historical management practice types. Canonical Correspondence Analysis (CCA) showed that the measured environmental variables significantly explained 59.4% of the variance in seedling species distributions. The three most important environmental variables in the CCA were organic matter, titanium and leaf area index (LAI; an indicator of light availability below the canopy). Thus, presently the important mechanisms that influence regeneration via seedlings in BFR operate through the soil system, and the ground and canopy vegetation characteristics. Nine of the 15 species that are as both major timber and primate food sources, namely *L. mildbraedii*, *Celtis mildbraedii* Engl., *Pouteria altissima* (A. Chiev) Aubrev. & Pellgr., *Chrysophyllum albidum* G. Don, *C. alexandri*, *Diospyros abyssinica* (Hiern) F. White, *Funtumia elastica* (Preuss) Stapf., *Chrysophyllum perpulchrum* Hutch. & Dalz, and *Antiaris toxicaria* (Pers.) Lesch. had highly negative size-class distribution (SCD) slopes and vigorous regeneration. While *Alstonia boonei* De Wild and *Cordia millenii* Bak. had a weakly negative SCD slope and pulsed or sporadic regeneration pattern. Seedlings for a variety of species were widely distributed, and most of the selected species have population structures showing vigorous regeneration patterns, suggesting that BFR is currently experiencing a continuous regeneration phase. However, there is a need to develop and implement management plans that will enhance and facilitate a vigorous regeneration of the already vigorous and poor species, to ensure sustainable forest development. Leaving behind standing mature fruiting trees in logged areas would be of great benefit to both long-term sustainable timber production and wild animal conservation as the fruit trees will provide food for primates and birds, which will, consequently, disperse the seeds to other areas.

Key Words: Ecological resilience, leaf area index (LAI), natural regeneration, population structure, primate food trees, size-class distributions.

1.0. INTRODUCTION

The importance of Budongo Forest Reserve (BFR) has been recognised for both its timber (e.g. Sheil 1996) and wildlife conservation values (e.g. Plumptre and Reynolds 1994, Howard *et al.* 1997, Tweheyo 2003). However, with the increasing human utilisation and degradation it faces (Chapter 2), necessitates a strengthening of the ecological basis for its sustainable management (Guariguata 2000). Sustainable resource use hinges on a species ability to continually establish new seedlings while being subjected to repeated and intensive harvesting (Peters 1994). Over the years the sustainable management of BFR for timber has relied on the natural regeneration of timber species, with enrichment plantings attempted with little success, and thus, stopped in the 1950's due to the poor survival of seedlings and high costs (Philip 1965). Ever since, the forest has relied upon natural regeneration through seeding and resprouting, and therefore, an understanding of its woody species regeneration via seedlings (hereafter referred to as seedling regeneration) is vital for the conservation of important constituent woody species and ecosystems. Understanding the natural regeneration (by seeds and resprouting) processes and the dynamics of tree and shrub species populations have practical applications in sustainable management and the restoration of habitats (Peters 1994, Bekele 2000). Studies on seedling regeneration can provide options to forest development through improvement in recruitment, establishment and growth of the desired seedlings (e.g. Whitmore 1996, Teketay 1997a, Kyereth *et al.* 1999). Natural regeneration is not only dependent on seeds or resprouts but also on environmental factors, such as light, temperature, and disturbance regimes (e.g. Herrera *et al.* 1994, Barnes *et al.* 1998, Mwima *et al.* 2001). For example, the amount of light that reaches the lower canopy layers influences conditions for plant recruitment, growth and reproduction, thus affecting community composition (Kotowski and van Diggelen 2004).

Over the years several studies have been undertaken on seedling regeneration of various tree species in BFR, with most focusing on the mahoganies, the key traditional timber species (e.g. Synnott 1975, Mwima *et al.* 2001, Bahati 2005), as well as recruitment of tree species in permanent plots (Sheil 1996). There have also been studies on the phenology of some timber and primate food trees (e.g. Plumptre 1995, Tweheyo 2003). Despite these studies, little is known about seedling establishment of a wide range of other important multiple-use woody species. Yet, with increasing human population coupled with increasing demand for wood products, loss of woodlands outside BFR, and diminishing stocks of mahoganies, many tree species in BFR are increasingly being exploited for timber and other domestic needs. In addition, some of the timber species (e.g. *Antiaris toxicaria* (Pers.) Lesch., *Chrysophyllum* spp) produce fruits that are eaten by primates, an important component of the BFR wild animals, while some primate food trees (e.g. *Pouteria altissima* (A. Chiev) Aubrev. & Pellgr., *Celtis mildbraedii* Engl.) are also increasingly being used as timber (Plumptre 1995, Tweheyo 2003). Thus, there are a number of woody species of multiple-use value, which are harvested by local people for house construction, fuel wood, and timber and at the same time serve as primate food trees. In the absence of long term data, forest dynamics (e.g. change of species composition and regeneration) are most often inferred from a single survey and the analysis of static forest inventory data by constructing species population size-class distributions (SCDs) (e.g. Poorter *et al.* 1996, Sano 1997, Lykke 1998, West *et al.* 2000, Obiri *et al.* 2002, McLaren *et al.* 2005). Some of these studies have described SCDs of trees and used them as indicators of species composition change and rejuvenation. Characterisation of size-class distribution serves as a means of projecting population trend, and to some extent past trends (Harper 1977), and its interpretation has been useful in assessing the state of populations for a variety of management purposes (e.g. Witkowski *et al.* 1994, Obiri *et al.* 2002, McLaren *et al.* 2005, Wangda and Ohsawa 2006). Lykke (1998) demonstrated in savannas and dry tropical forest systems that SCDs give good indications of the impact of disturbance and of successional trends.

This study, therefore, aimed at describing seedling regeneration of woody species and the factors responsible for the maintenance of variation in community composition, with a view to improve the understanding of the ecology of natural regeneration in BFR. To fulfil this objective the following questions were explored: 1. What is the seedling species diversity, richness and density across the sampling plots, transects, topographic positions and historical management practice types? 2. Are the distributions of species seedling' related to environmental factors (e.g. light availability, soil nutrients, and management history) or by chance only? 3. What is the regeneration status (i.e. vigorous or poor) of the selected multiple-use woody species (i.e. that serve as both timber and primate food sources)? 4. What are the management implications for these species? To answer questions 1 and 2, the number of seedlings (i.e. individuals with stem diameters <2.0 cm), saplings (diameter = 2.0 - 10.0 cm) and adult trees (DBH >10.0 cm), was quantified using 32, 0.5 ha plots (see materials and methods). To answer question 3, the population structure (stem-size class distributions; SCDs) of a selection of 15 multiple-use woody species that have been documented by Plumptre (1995) and Tweheyo (2003) as being both timber and primate food sources was examined. Finding clear answers to these questions is very important for the sustainable management of BFR, since its management policy is for multiple products- economic, conservation and environmental benefits.

2.0. MATERIALS AND METHODS

2.1. Study area

Budongo Forest Reserve (BFR) is located on the escarpment east of Lake Albert on the edge of the western rift valley (Howard 1991) in North-western Uganda, between Masindi town and Lake Albert. It has an area of about 793 km^2 and lies between 1^{0}37' and 2^{0}03' N and 31^{0}22' and 31^{0}45' E. The altitudinal range of the area is 700 - 1270 m above sea level with a mean of about 1050 m, a gently undulating terrain. The slopes are with a few exceptions gradual and the intervening ridges are rounded. The valley bottoms are generally, well weathered, and many of the streams are trickles through rattan (*Calamus deerratus* Mann & Wendl.) swamps, with no apparent flow during dry months (Eggeling 1947).

Previous management practices have included selective logging (both mechanical and pitsawing) and arboricide treatments during the 1950's and 1960's, aimed at killing trees that were regarded as "weed species" (Plumptre and Reynolds 1994), enrichment planting and controlled shooting to reduce animal populations (e.g. Eggeling 1947, Synnott 1985, Howard 1991). Thus, most of the forest's compartments have been treated with arboricides and logged at least once, except for a few that from the onset were set aside to be left untouched and managed as Nature Reserves. In terms of vegetation characteristics, BFR has been broadly classified as a medium altitude semi-deciduous moist tropical rainforest, because several of the dominant species (e.g. *Celtis* spp., *Maesopsis eminii* Engl., *Ficus* spp. etc) are at least briefly deciduous (Eggeling 1947, Langdale-Brown *et al.* 1964), with the exception of the shade-tolerant *Cynometra alexandri* C.H. Wright (Sheil 1997). Generally, the forest is a mosaic of forest types (Plumptre *et al.* 1994), a result of forest dynamics and management history (Eggeling 1947, Plumptre 1996). The general ecology, environment, management and history of Budongo Forest has been described by Eggeling (1947), Synnott (1985) and Howard (1991). Generally, the soils are deep with little differentiation into clearly defined horizons and possess a fine granular structure moulded into larger weakly coherent clods, which are friable and porous.

2.2. Sampling procedure and data collection

Within the forest we identified areas that have been subjected to logging and arboricide treatment, logging alone, and those without logging or arboricide treatment (Nature Reserve); representing the major management practices that have taken place in this forest. In each historical management practice type at least 2 transects were established along topographic gradients, each providing at least three topographic positions (i.e. lower-slope (swamp/riparian), mid-slope, upper-slope, and flat/ridge-top). In each topographic position, with a separation distance of not less than 150 m, a 100 x 50 m (0.5 ha) plot (the 100 m axis along the contour) divided into five 20 x 50 m contiguous sub-plots was sampled for tree and shrub individuals of >2.0 cm stem diameter. 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 buttresses or other stem irregularities at breast height, DBH was measured above the buttresses. Each 20 x 50 m plot was also systematically searched for seedlings (i.e. woody individuals of <2.0 cm stem diameter and ≤1.0 m height) in addition to the >2.0 cm diameter stems. A total of 32, 0.5 ha plots; 6 in the Nature Reserve areas, 19 in logged and arboricide treated, and 7 in logged only (but not arboricide treated) were laid. The number of plots per management practice type is related to the corresponding size of the area in the forest.

Initial plant species identification was done in the field with reference to plant identification guides and the help of a botanist familiar with the flora. For species that could not be confidently identified in the field, vegetative material and if available, flowering or fruiting samples were collected, pressed and vouchers subsequently identified at the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda. Identification of plant species was based on the Flora of Tropical East Africa (Polhill, 1952 et seq) and a field plant identification guide by Hamilton (1991).

2.3. Measurements of Environmental variables

2.3.1. Soil nutrient status

Soil cores (samples) for determination of soil nutrient status were collected at a depth of 0 - 15 cm with a soil auger (2 cm diameter, 15 cm deep cores) from 10 randomly chosen locations within each of the 0.5 ha plots. Samples were collected into polyvinyl bags, and then bulked, thoroughly mixed, sub-sampled, air-dried, cleaned by removing stones and roots fragments, and then passed through 20 and 2 mm sieves. The soil pH in a distilled water (1:1 v/w) soil suspension was determined using the McLean (1982) Glass Electrode Method, while organic matter (OM) content was indirectly estimated through the determination of the organic carbon (C) content by the Walkley-Black procedure (Nelson and Sommers 1982). The elemental constituents (i.e., Ca, Mg, Na, P, Li, Si, Ti, Fe) were determined using X-Ray Fluorescence Spectrometry (XRF; Feather and Willis 1976, Thomsen 2002) in the Department of Geology, University of the Witwatersrand, Johannesburg.

2.3.2. Light availability under the tree canopy

Light availability under the canopy was indirectly measured as leaf area index (LAI) using the LAI-2000 Plant Canopy Analyser (Li-Cor Lincoln Nebraska, USA) at 1.0 m above the ground level at 5 random points in each 0.5 ha plot. The extinction of light as it travels through a vegetation canopy depends on the total LAI (area of foliage projected on a unit area of ground surface) (Barbour *et al.* 1987). Thus, LAI describes a fundamental property of the plant canopy in its interaction with the atmosphere, especially concerning radiation, energy, water and gas (e.g. carbon-dioxide) exchange at forest stand scale (Monteith and Unsworth 1990, Cournac *et al.* 2002).

2.4. Data analysis

2.4.1. Seedling species diversity patterns and distributions

Species richness (S) and the Shannon-Wiener Index of diversity (H') were computed to quantify and characterise seedling species diversity patterns (Magurran 2004) of the plant communities at the 0.5ha scale. Both diversity metrics were calculated using the Species Diversity and Richness IV Programme, a Pisces Software (Pisces Conservation Ltd, 2004). Differences in seedling densities and diversity between historical management practice types were compared by one-way ANOVA and Tukey HSD for unequal sample sizes. The sample plots were grouped in three different ways, i.e. according firstly to transect, secondly topographic position and then historical management practice type. To test whether there were significant variations in seedling species composition between *a priori* groupings of plots, ANOSIM (ANalysis Of SIMilarity), a randomization permutation test in CAP 3.1 (Pisces Conservation, 2004) was employed. ANOSIM, a form of the Mantel test (Legendre and Legendre 1998), is used for detecting and measuring the similarity in species complement within and between groups. 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 and Greenstein 1997). The R_{ANOSIM} statistic values generated by CAP 3.1 are relative measures of separation of *a priori* defined groups. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples within groups are more similar to one another than any of the samples from other groups. A randomization process is used to find the probability of gaining particular values of R_{ANOSIM} by chance. 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 method uses the Bray-Curtis measure of similarity, comparing in turn each sample in the group.

Ordination

To examine seedling densities and their distribution along environmental gradients, a Canonical correspondence analysis (CCA) ordination, using CANOCO version 4.5 (ter Braak 2003) was used. Soil elemental concentration data were log-transformed prior to inclusion in the CCA. The environmental variables included were soil nutrient status (pH, Ca, Mg, Na, P, Li, Si, Ti, Fe, OM, N), historical management practice type (i.e. logged and arboricide treated, and logged only) and LAI. A Monte Carlo re-randomisation procedure, with 499 permutations under the reduced model was used to test for significance of the canonical axes. This is a direct test of whether the included environmental variables have a significant effect on variation in community species composition. It was first calculated for the 1st axis and then for the combination of the first four canonical axes. The intra-set correlations were used to infer the relative importance of each environmental variable for prediction of species composition (ter Braak 1995).

2.4.2. Population structure of a selection of 15 multiple-use woody species

The inventory data set (seedlings, saplings and adults) for each of the 15 selected multiple-use woody species (Table 1) was tallied into stem diameter size classes as follows; 1, 2 - 5, 6 - 10, 11 - 15, 16 - 20, 21 - 25, 26 - 30,……. 56 - 60 cm. Individuals >60 cm DBH were grouped in 10 cm wide classes. This classification was used to balance the samples across size classes, because the number of individuals declines with size (Condit *et al.* 1998, Lykke 1998). SCDs were analysed using the method proposed by Condit *et al.* (1998) and Lykke (1998), and used by Obiri *et al.* (2002) and McLaren *et al.* (2005). For each of the 15 species a least-squares linear regression was calculated with size-class midpoint as the independent variable and the average number of individuals in that class (N_i) as the dependent variable (Obiri *et al.* 2002, McLaren *et al.* 2005). To derive N_i the number of individuals in each size class is divided by the width of the class (Lykke 1998). The size-classes are a linear increment of the dbh and were not transformed, however, in order to derive straight-line plots of the size-class distribution, the N_i for 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 SCD slopes, and were used as indicators of population structure (Lykke 1998, Obiri *et al.* 2002, McLaren *et al.* 2005). The slope values were used to summarise, in a single number, the shape of the size distribution for a species.

The interpretation of the SCD slopes was based on the four types of SCD described in Everard *et al.* (1994). 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 regenerating trees and mature individuals. Positive slopes are sometimes referred to as unimodal since they are typically characterised by relatively many canopy individuals but no regeneration (Shackleton 1993, Everard *et al.* 1994). SCDs were further analysed following a method used by West *et al.* (2000). A ratio of small stems (<10 cm DBH; juveniles) to large stems (>10 cm DBH; adults) was calculated for each of the selected 15 species. Species, which are successfully recruiting are expected to have small stem:large stem ratios of >1. While ratios of <<1 would indicate species with low recruitment, and hence, low representation in juvenile classes.

3.0. RESULTS

3.1. Seedling species diversity patterns and distributions

A total of 85624 seedlings representing 237 species and 46 families were recorded from the 32, 0.5 ha plots. The most speciose families were Euphorbiaceae (24), Fabaceae (21), Rubiaceae (19), Meliaceae (17), Moraceae (15) and Rutaceae (14). Plots varied in terms of seedling species richness (S; ranging from 26 to 88), Shannon-Weiner species diversity (H'; ranging from 1.46-3.54), density (ranging from 824 to 18710 individuals ha^{-1}). However, the plot with the highest seedling density was not the one with the highest species richness and diversity, the plot with lowest diversity also had the lowest density. The plot with the lowest seedling species diversity and density was located on a hill top with shallow soils underlain with rocks, and the forest canopy was dominated by *Senna spectabilis* (DC.) Irwin & Barneby. At the total forest level, the seedling population was dominated by *Cynometra alexandri* (14961 individuals sampled) and *Lasiodiscus mildbraedii* (12623 individuals). However, of the 237 seedling species, 70 (29.6%) were rare (only 2-10 individuals), while 28 species (11.9%) were very rare with each having only 1 individual. Of the 236 seedling species, the 45 species with hundreds of individuals were each encountered in more than 20 plots (Appendix 1). *Chrysophyllum albidum* G. Don. (32 plots), *Celtis zenkeri* Engl. (30 plots), *C. alexandri* (29 plots), *Acalypha neptunica* Muell. Arg. (29 plots), and *Teclea nobilis* Del. (29 plots) were the most frequent. This suggests that these species can exploit a wide range of habitats. Some species e.g. *L. mildbraedii* and *Raphia farinifera* (Gaertn.) Hylander had their seedlings predominantly clumped around the adult tree, suggesting that they disperse their seeds over very short distances.

A one way ANOVA showed that mean seedling density was significantly ($F_{2,25}$ = 4.17, p = 0.027) different between the historical management practice types, being highest (8884±2027 individuals ha^{-1}) for the logged only, followed by logged and arboricide treated (5034±718 individuals ha^{-1}) and lowest (3925

±651 individuals ha^{-1}) for the nature reserve area. Pairwise comparisons (Tukey-test) showed significant differences ($\alpha = 0.05$) between logged only and logged and arboricide treated, as well as Nature Reserve and logged only in their seedling densities. In contrast, species diversity ($F_{2,25} = 0.75$, $p = 0.49$) and richness ($F_{2,25} = 0.41$, $p = 0.67$) were not significantly different between the historical management practice types.

A global ANOSIM showed a significant difference (Global $R_{ANOSIM} = 0.284$, $p = 0.001$) in seedling species composition between transects, that were reflected in pairwise tests, suggesting that samples within the groups were more similar than would be expected by chance. Of the 36 pairwise ANOSIM comparisons, 19 were significant with each pair having a $R_{ANOSIM} > 0.33$ and a $p < 0.05$. However, differences were more marked ($R_{ANOSIM} = 1$, $p = 0.029$, average dissimilarity >85.0) for pairwise tests between the two transects from a *Cynometra alexandri* Forest type (logged only) and those three from *Khaya anthotheca* (Welw.) C. DC. dominated forest community. The two forest community types were the furthest apart in terms of distance, with one on the far eastern and other on the western part of BFR. There were however, no significant differences in seedling species composition between topographic positions (Global $R_{ANOSIM} = -0.02$, $p = 0.602$). Comparing historical management practice types, the overall ANOSIM showed no significant difference in seedling species composition between the groups (Global $R_{ANOSIM} = 0.004$, $p = 0.46$), but the pairwise comparison between logged only and Nature Reserve sites showed significant difference ($R_{ANOSIM} = 0.354$, $p = 0.001$, Average dissimilarity = 64.2%).

Based on the analyses of SIMilarity PERcentages (SIMPER procedure from CAP 3.1), the species making up 90% of the observed similarity within each historical management practice type were 22 for the logged and arboricide treated, 11 for Nature Reserve, and 21 for the logged only. A comparison of the dominant species (Table 1), revealed the absence of *Thecacoris lucida* (Pax) Hutch. in the Nature Reserve and the logged and arboricide treated management practice type. SIMPER results further reveal that the top three species in each historical management practice type (Table 1) included *L. mildbraedii*, *C. alexandri* and *Argomuellera macrophylla* Paxa Laka indicating that these species are widely distributed in the forest, although with varying abundances (Table 1 and 2). SIMPER analysis of dissimilarity between logged only and Nature Reserve sites that showed significant difference in ANOSIM, showed that 20 families, represented by 38 species made up 90.3% of the observed differences in communities among these sites (Table 2).

Table 1. Contribution of individual species to the overall similarity within the historical management practice types (i.e. Nature Reserve, logged only, and logged and arboricide treated). Species are ranked according to their percentage contribution to the similarity within the management practice types and only those with contributions >2% are shown. Average similarity and percentage of cumulative similarity are also given.

Species	**Average Abundance**	**Average Similarity**	**% Contribution**	**Cumulative %**
Logged and arboricide treated (Average Sim= 32.97)				
Lasiodiscus mildbraedii Engl.	408.88	6.38	19.34	19.34
Cynometra alexandri C.H. Wright	411.63	5.12	15.52	34.86
Argomuellera macrophylla Paxa Laka	228.31	3.07	9.31	44.17
Acalypha neptunica Muell. Arg.	160.25	2.96	8.99	53.16
Rinorea ardiisiflora (Welw. ex Oliv.) Kuntze	285.44	2.36	7.16	60.32
Tabernaemontana holstii K.Schum.	63.38	1.77	5.38	65.69
Acalypha ornata Hochst. ex. A. Rich.	108.94	1.30	3.94	69.63
Logged only (Average Sim= 52.24)				
Lasiodiscus mildbraedii Engl.	970.50	11.20	21.45	21.45
Argomuellera macrophylla Paxa Laka	564.00	10.89	20.85	42.30
Cynometra alexandri C.H. Wright	560.83	10.02	19.19	61.49
Rinorea ardiisiflora (Welw. ex Oliv.) Kuntze	320.50	3.94	7.55	69.04
Celtis mildbraedii Engl.	196.50	3.07	5.88	74.92
Acalypha ornata Hochst. ex. A. Rich.	106.83	2.18	4.17	79.09
Thecacoris lucida (Pax) Hutch.	229.17	2.03	3.88	82.97
Acalypha neptunica Muell. Arg.	78.00	1.39	2.65	85.62
Nature Reserve (Average Sim= 39.85)				
Cynometra alexandri C.H. Wright	397.83	9.98	25.05	25.05
Lasiodiscus mildbraedii Engl.	358.17	7.63	19.16	44.20
Argomuellera macrophylla Paxa Laka	147.33	3.20	8.03	52.23
Acalypha neptunica Muell. Arg.	84.67	2.65	6.66	58.89
Rinorea ardiisiflora (Welw. ex Oliv.) Kuntze	160.00	1.82	4.56	63.45
Tabernaemontana holstii K.Schum.	64.17	1.75	4.40	67.85
Belonophora hypoglauca (Welw. ex Hiern) A. Chier.	37.83	1.33	3.33	71.18
Acalypha ornata Hochst. ex. A. Rich.	56.67	1.07	2.69	73.88
Bequeartiodendron oblanceolatum (S. Moore) Hiene	36.83	0.86	2.17	76.04

Table 2. Results of SIMPER analysis, highlighting the species contributing most to the dissimilarity between the historical management practice type pairs. Species are ranked according to their percentage contribution to the dissimilarity between types and only those with contributions >1% are shown. The values of average dissimilarity and the percentage of cumulative dissimilarity are also given.

	Average Abundance				
Species	***Logged only***	***Nature Reserve***	***Ave. Dissim%***	***% Contribution***	***Cumulative%***
Lasiodiscus mildbraedii Engl.	*970.50*	*358.17*	*10.01*	*15.58*	*15.58*
Argomuellera macrophylla Paxa Laka	*564.00*	*147.33*	*6.86*	*10.68*	*26.26*
Cynometra alexandri C.H. Wright	*560.83*	*397.83*	*5.67*	*8.83*	*35.09*
Rinorea ardiisiflora (Welw. ex Oliv.) Kuntze	*320.50*	*160.00*	*5.06*	*7.88*	*42.96*
Rinorea ilicifolia (Oliv.) O. Ktze	*524.00*	*9.83*	*5.00*	*7.78*	*50.75*
Thecacoris lucida (Pax) Hutch	*229.17*	*13.17*	*3.39*	*5.27*	*56.02*
Celtis mildbraedii Engl.	*196.50*	*13.67*	*3.24*	*5.04*	*61.06*
Blighia unijugata Bak	*73.33*	*8.00*	*1.66*	*2.58*	*63.64*
Rawsonia lucida Harv. & Sond.	*111.33*	*4.00*	*1.48*	*2.31*	*65.95*
Teclea nobilis Del.	*96.50*	*5.33*	*1.47*	*2.29*	*68.24*
Acalypha ornata Hochst. ex. A. Rich	*106.83*	*56.67*	*1.14*	*1.77*	*70.01*
Rinorea brachyptela (Turcz) O. Ktze	*66.83*	*44.83*	*1.08*	*1.69*	*71.70*
Tabernaemontana holstii K.Schum.	*0.00*	*64.17*	*1.05*	*1.63*	*73.33*

3.2. Seedling species relationships with environmental factors

The relative influence of the environmental variables on seedling species variance is inferred from the CCA ordination diagram (Fig. 1), and the intra-set correlations (Table 3). Some of the environmental variables with shorter arrows are suppressed in the ordination space for more clarity in the ordination diagram. The 1st environmental axis was mainly strongly correlated with Ti, Mg, OM and N, while the 2nd axis was strongly correlated with pH, Si, and Ca (Table 3, Fig. 1). The CCA plot showed that the supplementary environmental variable- species diversity was strongly correlated with axis 2 (Fig. 1). However, the relative importance of each environmental variable along each axis is shown graphically as vectors in the biplot of the CCA ordination diagram (Fig. 1). Overall, the best three environmental variables were OM, Ti and LAI that was highly correlated with the 1st axis. The contours/ isolines depicting seedling species diversity (Fig. 1) tend to increase in magnitude in the direction of the arrow for the supplementary environmental variable- species diversity, suggesting a positive relationship. The CCA (results not shown) further revealed that seedlings of *Rinorea ilicifolia*, *Thecacoris lucida*, *Rawsonia lucida* Harv. & Sond. and *Argomuellera macrophylla* were associated mainly with high LAI values. Seedlings of other species were exclusively associated with particular plots because of their unique environmental conditions. For example, *Raphia farinifera*, *Pseudospondias microcarpa* (A. Rich.) Engl., *Cleistopholis patens* (Benth.) Engl. & Diels. and *Glyphaea brevis* (Spreng.) Manachino were exclusively associated with the swamp forest community; while *Senna spectabilis* was exclusively associated with the *Senna spectabilis* dominated forest community suggesting its limited dispersal.

Table 3: The CCA inter-set and intra-set correlations of environmental variables with the first four axes for data from Budongo Forest Reserve, NW Uganda. pH: soil alkalinity/acidity; Si: Silicon; Ti: Titanium; Fe: Iron; Mg: Magnesium; Ca: Calcium; Na: Sodium; P: phosphorous Li: Lithium; OM: Organic matter; N: Nitrogen; LAI: leaf area index; Log.arbt: logged and arboricide treated.

Variable	**Inter-set correlations**				**Intra-set correlations**			
	CCA Axes				**CCA Axes**			
	1	2	3	4	1	2	3	4
pH	-0.1567	0.4819	-0.3892	-0.1617	-0.1659	0.5247	-0.4345	-0.1893
Si	-0.0636	-0.4648	0.1187	-0.2001	-0.0673	-0.5061	0.1325	-0.2344
Ti	-0.7032	0.2230	-0.0400	0.0788	-0.7442	0.2429	-0.0446	0.0923
Fe	-0.1280	0.4186	-0.3820	0.1753	-0.1354	0.4558	-0.4264	0.2054
Mg	0.5846	-0.0908	0.0116	0.0425	0.6187	-0.0989	0.0130	0.0498
Ca	0.3038	0.4839	-0.0102	0.1213	0.3216	0.5269	-0.0114	0.1420
Na	0.2211	0.0040	0.3857	-0.4025	0.2340	0.0044	0.4305	-0.4715
P	0.2774	0.1441	-0.3591	0.0951	0.2936	0.1569	-0.4009	0.1114
Li	0.4129	0.2975	-0.0226	0.3920	0.4369	0.3239	-0.0253	0.4591
OM	0.5441	0.5656	0.0715	-0.0782	0.5758	0.6159	0.0798	-0.0916
N	0.5501	0.2927	0.2722	0.0708	0.5822	0.3187	0.3039	0.0829
Logged only	0.1891	0.0997	0.0606	0.1064	0.2001	0.1085	0.0677	0.1247
Log.arbt	-0.4889	0.2646	-0.0429	-0.2897	-0.5174	0.2881	-0.0479	-0.3393
LAI	0.4650	-0.1392	-0.3261	0.2219	0.4921	-0.1515	-0.3640	0.2599

The 1st and 2nd axes of the CCA (eigenvalues 0.323 and 0.285, respectively), explained 18.5% of the species, and 34.4% of the species-environment factor variation (Table 4). Overall, the first four axes explained 31.9% of the variance in species data, and 59.4% of the variance in species-environmental factors relation. The Monte Carlo permutation test was significant for both the first canonical axis (F= 1.851, p=0.02) and the combination of the four axes (F= 1.412, p=0.002), indicating that the first four CCA axes significantly explain the species-environmental factor relations.

Table 4. Summary table of CCA results for 32, 0.5 ha plots from Budongo Forest Reserve, NW Uganda

Axes	**1**	**2**	**3**	**4**	**Total Inertia**
Eigenvalues	0.323	0.285	0.243	0.199	3.288
Species-environmental correlations	0.945	0.918	0.896	0.854	
Cumulative percentage variance					
of species data:	9.8	18.5	25.9	31.9	
of species-environment relation:	18.3	34.4	48.1	59.4	
Sum of all eigenvalues					3.288
Sum of all canonical eigenvalues					1.767

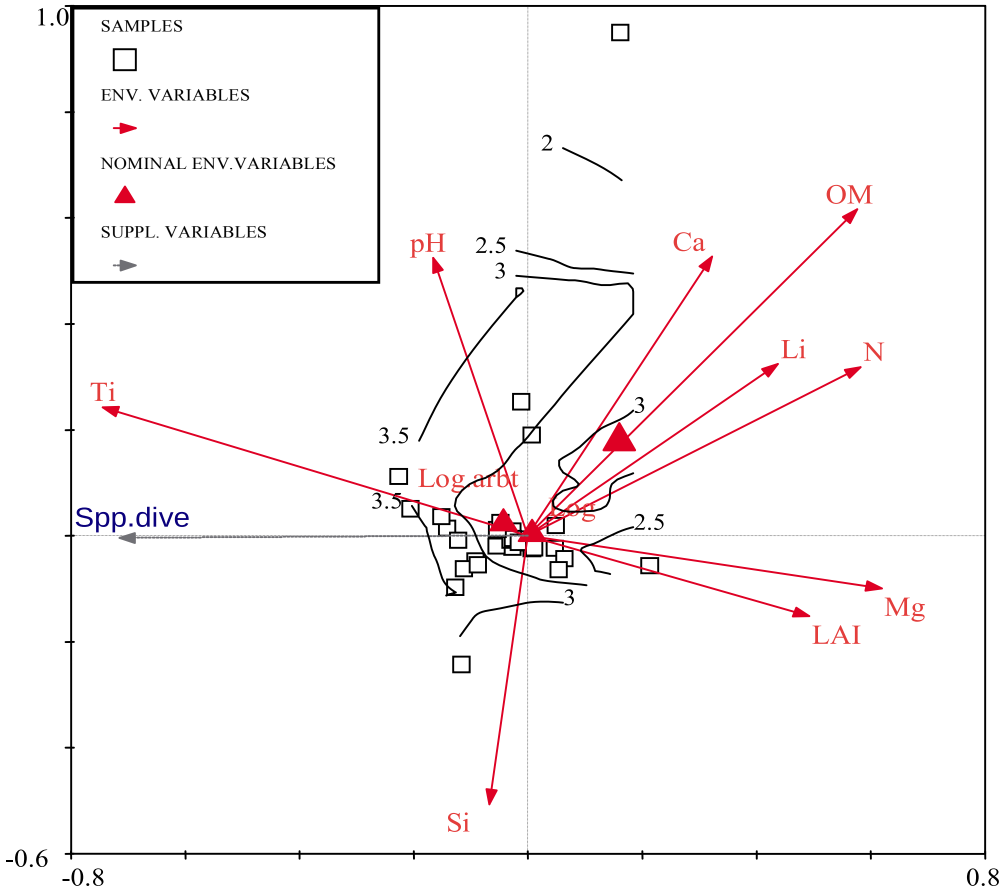

Figure 1. CCA ordination diagram with environmental variables (arrows), historical management practice type (▲) and sampling plots. Species density data were used; first axis is horizontal, second axis vertical. Spp.dive: species diversity (Fisher's α-diversity) for the >2.0 cm DBH individuals (i.e. saplings, poles and trees) data. The isolines show the seedling species diversity (Shannon's diversity) of sample plots. Si: Silicon; Ti: Titanium; Mg: Magnesium; Ca: Calcium; Li: Lithium; OM: Organic matter; N: Nitrogen; LAI: Leaf Area Index; Log.arbt: logged and arboricide treated; Log.: logged only.

3.3. Population structure of a selection of 15 multiple-use woody species

Of the 15 selected species, 10 were each recorded in more than 20 sampling plots, with *C. albidum*, *Celtis mildbraedii*, *C. alexandri*, *F. elastica* and *L. mildbraedii* being the most frequent. *C. alexandri* (14961 individuals) and *L. mildbraedii* (12623 individuals) were the most abundant and widely distributed, with occurrences in 29 and 28, of the 32 plots, respectively. In contrast, *Alstonia boonei* and *Cordia millenii* were the rarest species, with only 1 and 2 individuals each recorded, respectively. On the other hand *R. farinifera* was restricted to only seasonally flooded areas. The 15 multiple-use woody species (Table 5), represented 9 families (Apocynaceae- 2, Boraginaceae- 1, Ebenaceae- 1, Fabaceae- 4, Moraceae- 1, Palmae- 1, Rhamnaceae- 1, Sapotaceae- 3 and Ulmaceae- 1). Apart from *F. elastica*, *Antiaris toxicaria*, *C. millenii*, and *A. boonei*, the other 11 woody species had higher numbers of seedlings (individuals <2 cm stem diameter) than saplings (individuals 2.0 - 10.0 cm DBH) (Table 5, Fig. 2). No saplings were recorded for *Raphia farinifera*. Considering stems with a >50 cm DBH, *C. alexandri* had the highest number (189 individuals), while *R. farinifera*, *Albizia grandibracteata* Taub., *Albizia glaberrima* (Schumach. & Thonn.) Benth., and *L. mildbraedii* had none. Generally, for each species, stem abundances declined with increasing size as shown by the negative SCD slopes (Table 5). The higher number of seedling relative to saplings for 9 of the 15 species (Table 5) indicates that they have a better regeneration potential.

The SCD slopes ranged from -2.47 (for *L. mildbraedii*) to -0.25 (*A. boonei*) indicating high numbers of individuals in the lowest diameter classes and a gradual decline in the middle and larger diameter classes. The ratios of juvenile: adult stems (<10cm DBH/>10cm DBH) range from 34.24 (for *C. alexandri*) to 0.33 (for *A. boonei*) (Table 5). The selected species showed three major patterns of stem diameter size-class distributions (Fig. 2). The first group comprises nine species; *L. mildbraedii*, *C. mildbraedii*, *Pouteria altissima*, *C. albidum*, *C. alexandri*, *D. abyssinica*, *F. elastica, C. perpulchrum*, and *Antiaris toxicaria* (Fig.2), with SCD slopes values ranging from -2.47 to -1.1, and juvenile:adult ratio ranging from 34.24 to 2.53. They show high numbers of individuals in the lowest diameter classes, mainly seedlings, and a gradual decline in the middle and larger diameter classes, and clearly exhibit an 'inverse J' type curve. This shows a continuous representation of individuals in all diameter classes, suggesting a healthy regeneration. The second group, consisting of *R. farinifera*, *A. zygia, A. glaberrima* and *A. grandibracteata* exhibited a nearly 'inverse J' size class distribution. Although *R. farinifera* juvenile/adult ratio was >>1, it was not represented in the sapling class. The strong peak in the seedling size-class followed by an absence of saplings in *R. farinifera* indicates that its regeneration is poor. The third group comprises *A. boonei* and *C. millenii* with weakly negative SCD slopes of -0.25 for both, and juvenile:adult ratios of 0.33 and 0.77, respectively, indicating low recruitment. They are also characterised by stem size-class distribution curves that deviate from the classic 'inverse J' and show evidence of pulsed or sporadic regeneration patterns as a result of under-representation in the seedling and the medium size classes (Fig. 2).

Table 5. A list of the 15 multiple use woody species, indicating family, total number of seedling individuals and their frequency (number of plots in, which they were recorded out of 32, 0.5 ha plots), number of saplings, adults and total plants; seedling: sapling ratio, juvenile (<10 cm DBH): adults (>10 cm DBH) ratio; size-class distributions (SCDs) parameters, stem sprouting following damage, and use.

		Seedling			**Total number of .**		**Ratios**		**SCDs**				
Species	**Family**	*Total no.*	*Freq.*	*Saplings*	*Adults (>10 cm DBH)*	*Plants*	*Seedling:Sapling*	*juveniles (<10 cm DBH):Adults*	*Slope*	*t*	*r^2 (%)*	**Stem sprouting ability†**	**Use***
Lasiodiscus mildbraedii Engl.	*Rhamnaceae*	14961	28	3742	701	19404	4.00	26.68	-2.47	16	97	Y	S, PF
Celtis mildbraedii Engl.	*Ulmaceae*	1621	29	1852	613	4086	0.88	5.67	-1.69	22.21	96	Y	T,S, PF
Pouteria altissima (A. Chiev.) Aubrev. & Pellgr.	*Sapotaceae*	299	22	255	91	655	1.17	6.09	-1.41	20.2	97	Y	T, PF
Chrysophyllum albidum G. Don	*Sapotaceae*	825	32	120	54	999	6.88	17.5	-1.37	10.45	89	Y	T,S, PF
Cynometra alexandri C.H. Wright	*Fabaceae*	12623	29	628	387	13638	20.1	34.24	-1.35	12.4	86	Y	S, PF
Diospyros abyssinica (Hiern) F. White	*Ebenaceae*	303	16	93	30	426	3.26	13.2	-1.32	13.8	95	Y	S
Funtumia elastica (Preuss) Stapf	*Apocynaceae*	285	28	1243	605	2133	0.23	2.53	-1.29	6.35	83	Y	S, PF
Chrysophyllum perpulchrum Hutch. & Dalz	*Sapotaceae*	192	23	121	34	347	1.59	9.21	-1.11	12.42	91	Y	T,S
Antiaris toxicaria (Pers.) Lesch.	*Moraceae*	155	26	182	90	427	0.85	3.74	-1.1	16.55	94	Y	T,S, PF
Raphia farinifera (Gaertn.) Hylander	*Palmae*	528	3	0	19	547	528/0	27.79	-1.07	3	50	N	S, PF
Albizia zygia (D.C.) Macbr.	*Fabaceae*	312	20	12	31	355	26	10.45	-1.06	4.18	66	Y	T
Albizia glaberrima (Schumach. & Thonn.) Benth.	*Fabaceae*	883	26	18	30	931	49.06	30.03	-1.01	5.26	63	Y	T, S
Albizia grandibracteata Taub	*Fabaceae*	71	2	15	7	93	4.73	12.29	-0.99	6.14	82	Y	T, S
Alstonia boonei De Wild.	*Apocynaceae*	1	1	20	64	85	0.05	0.33	-0.25	4.55	48	Y	T
Cordia millenii Bak.	*Boraginaceae*	2	1	18	26	46	0.11	0.77	-0.25	6.47	72	N	T, PF

Source: †Chapter 6; *Plumptre (1995) & Tweheyo (2003); BFR Management Plan:1997-2007 (MNR, 1997); Y- sprouts, N- no sprouting; T- timber, S- subsistence use (e.g. poles for house construction, fuel-wood etc.), PF- Primate food (either leaves, fruits or wood)

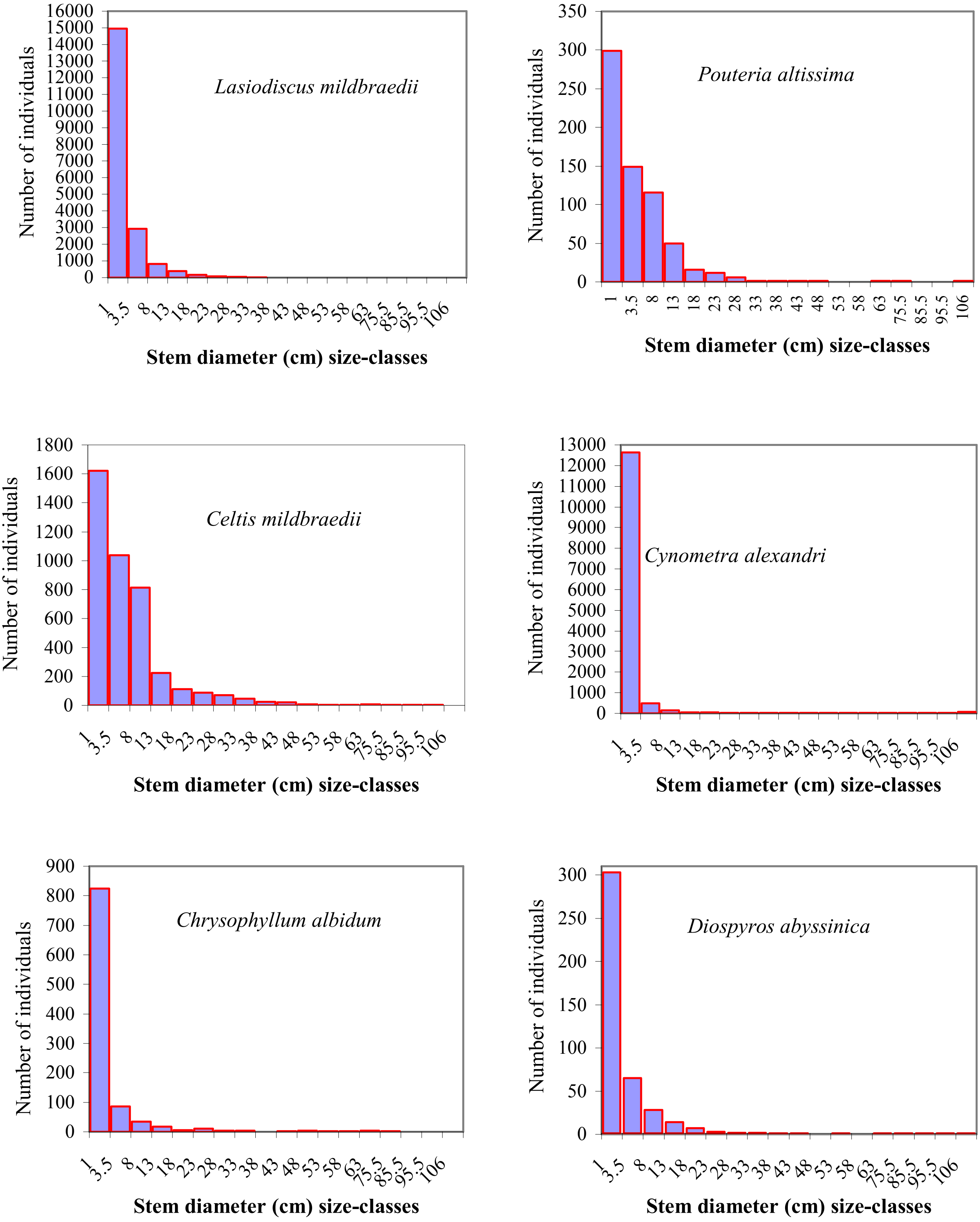

Figure 2. Stem size-class distributions exhibited by 15 selected multiple-use woody species in Budongo Forest Reserve, Uganda, arranged according to SCD slope values. Mid-points of the classes are plotted. For *Celtis mildbraedii*, *Pouteria altissima*, *Cynometra alexandri*, *Antiaris toxicaria* and *Alstonia boonei* all individuals >100 cm DBH have been grouped for graphing. Note: Y axis scales differ.

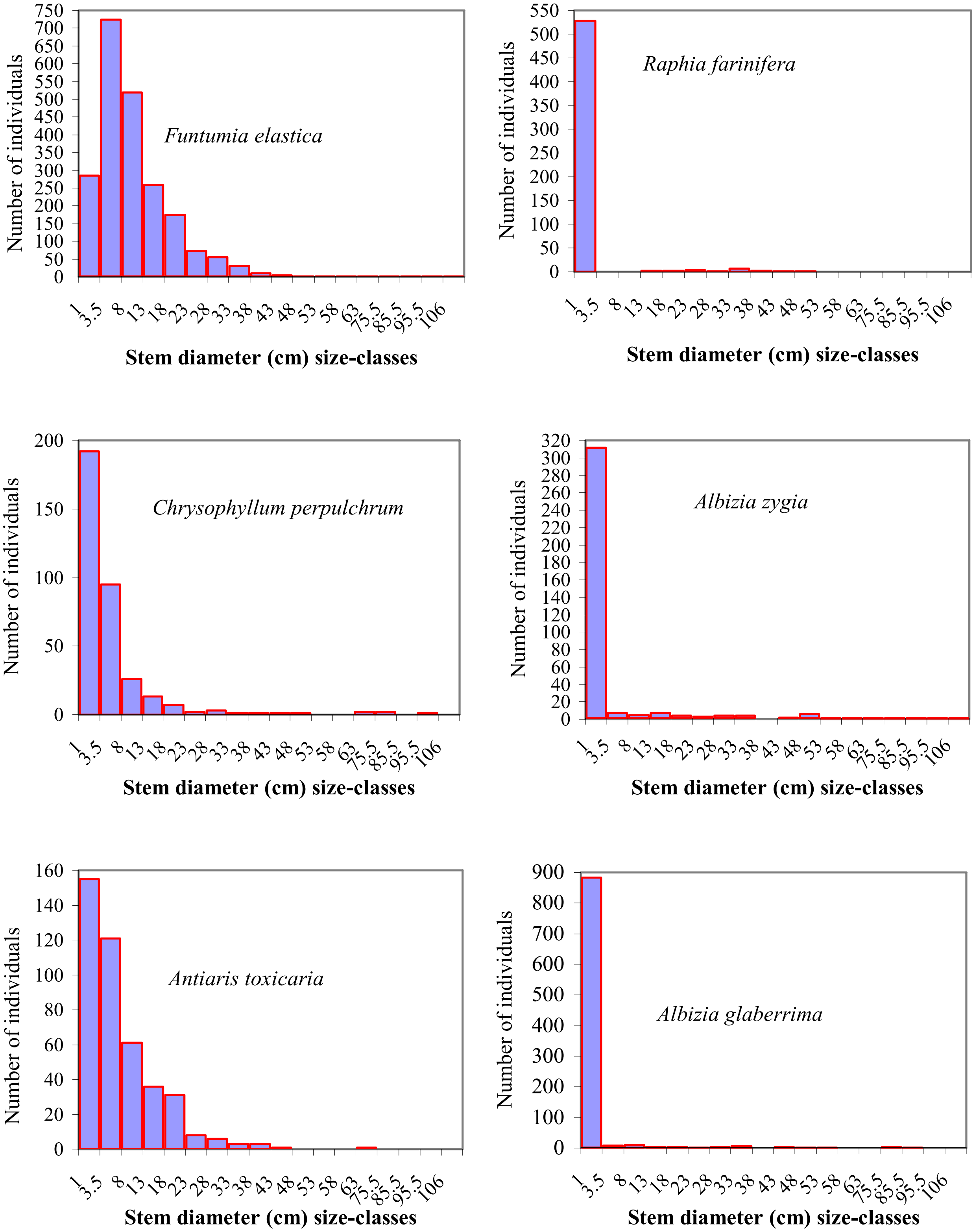

Fig. 2. Stem size-class distributions exhibited by 15 selected multiple-use woody species in Budongo Forest Reserve, Uganda, arranged according to SCD slope values (continued). Note: Y axis scales differ.

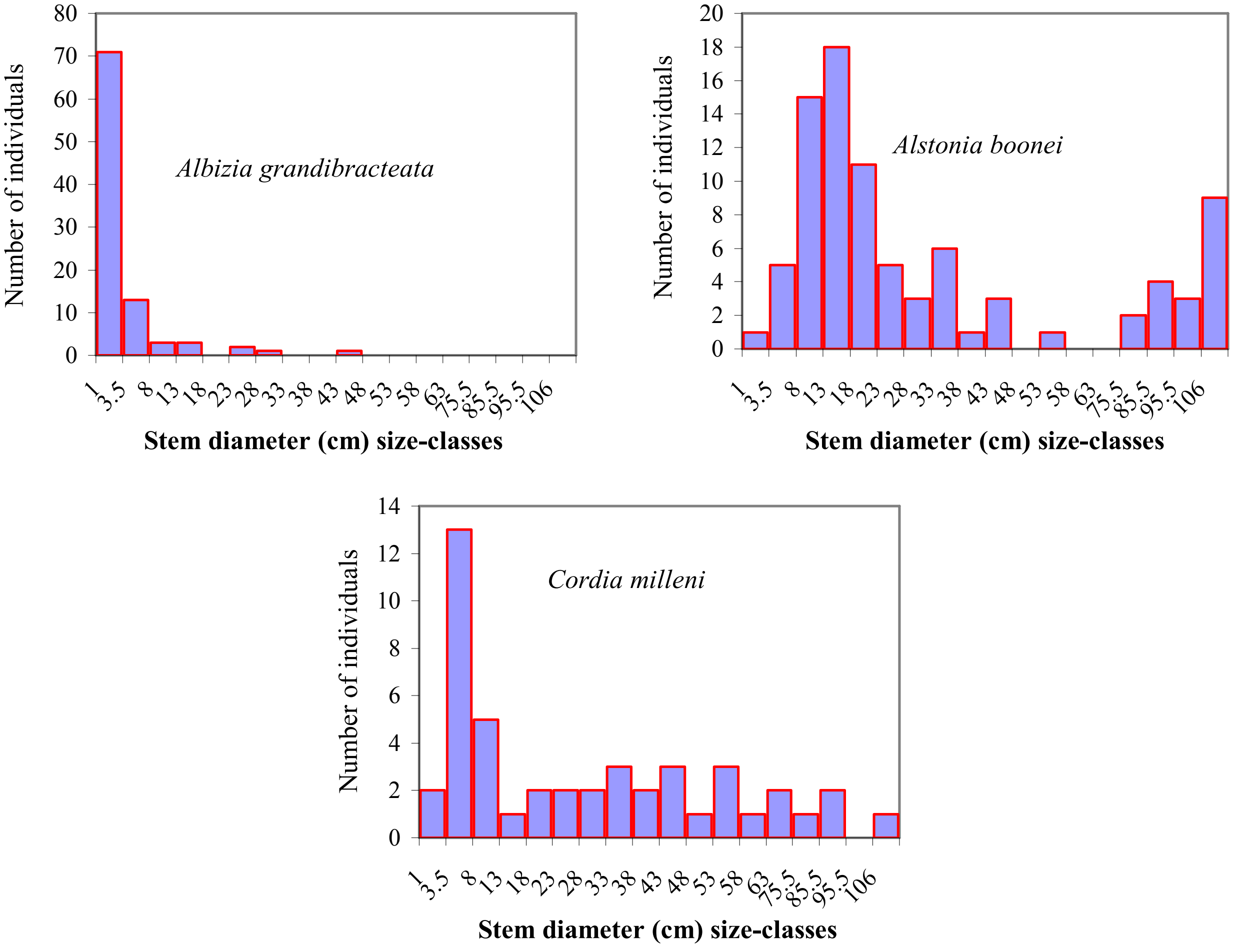

Fig. 2. Stem size-class distributions exhibited by 15 selected multiple-use woody species in Budongo Forest Reserve, Uganda, arranged according to SCD slope values (continued). Note: Y axis scales differ.

4.0. DISCUSSION

4.1. Seedling diversity and richness

Results of this study revealed substantial variability in seedling regeneration in BFR at the plot level in terms of species diversity, abundances and distributions, with some species widely distributed and others restricted to particular habitats and site conditions. A seven year study focusing on 40 chimpanzee food tree species by Tweheyo and Babweteera (2007) showed that fruit quantity varied significantly between the seven years, species, and seasons. They also showed that the interaction between fruit quantities and tree was significant. The substantial variability in seedling regeneration observed in BFR has been similarly, reported among other forest stands due to differences in disturbance history, site conditions, and chance factors that influence the early successional species mix (Lertzman *et al*. 1996). The clumping of seedlings, particularly those of *Lasiodiscus mildbraedii* and *Raphia farinifera* around adult trees is probably because seeds of many tropical tree species are dispersed over short distances, resulting in clumped distributions of seedlings around the adult trees (Zagt and Werger 1997, Guariguata and Pinard 1998, Dalling *et al.* 2002). Indeed, the seeds of *Raphia farinifera* have a very hard coat and seem not to attract frugivores that would disperse them into other habitats thereby offering them a chance to establish there. The flux of propagules (or seeds) is fundamental in determining the potential population of a particular habitat (Harper 1977), and the lack of seed dispersal is a limiting factor in forest regeneration (Holl 1999).

The occurrence of over 45 species with hundreds of seedlings in more than 20 sampling plots of varying LAI suggests that most species in BFR are widely distributed, exploiting a diversity of habitats within the forest. For example the widespread distribution and high abundances of *Cynometra alexandri* seedlings in BFR may be attributed to it being a soil generalist and being able to establish and survive under all soil conditions except in areas of permanent swamp (Walaga 1994). Similarly, it has been reported to occupy most of the forest canopy in the oldest parts of BFR with abundant regeneration and understorey trees of all sizes (Synnott 1985). Although a number of species were widely distributed, some species notably *Raphia farinifera*, *Rinorea ilicifolia*, *Glyphaea brevis*, *Neoboutonia melleri, Rawsonia lucida* and *Thecacoris lucida* were restricted to particular environments in their distribution. *Rinorea ilicifolia*, *Rawsonia lucida* and *Thecacoris lucida* were mostly encountered in areas with high LAI and the upper canopy dominated by *Cynometra alexandri,* which is not deciduous. These areas were also characterised by low seedling species richness and diversity. In closed forests, low (poor) advance regeneration is attributed to poor illumination in the lower levels of the forest, which prevents the seeds from germinating or soon kills those that do (Richards 1996).

The restricted distribution and range of occurrence for some of the species in this study can be explained by the presence of steep ecological gradients in terms of soil moisture, organic matter and pH (Nigatu and Tadese 1989). Indeed, results of the present study show that the distributions of seedlings of some species are related to environmental conditions within the forest. CCA axes 1 and 2 explained 18.5% in species, and 34.4% in species-environment factor relationship (Table 3), with the first Canonical axis and the combination of the four canonical axes being statistically significant. Eigenvalues closer to 0.5 denote a fair separation of species along the axes, and indicates a strong gradient for the axes (ter Braak 1987). As a rule of thumb, eigenvalues >0.30 indicate strong gradients (ter Braak 1995). Thus, in our study the measured environmental variables substantially influenced the observed seedling distributions, abundances, diversity and richness, with organic matter, titanium, and LAI being the most important. This suggests that the important mechanisms that influence the forest regeneration operate through the soil system (soil nutrients) and the ground and canopy vegetation because of the influence of LAI on light availability below the canopy. This is corroborated by the significant ANOSIM results for transect grouping comparisons that suggested that samples within the groups are more similar than would be expected by random chance.

The wide distribution of seedlings of some species could also be attributed to changes in light conditions during the year even in areas where wet season LAI is high, since nearly all larger canopy species, except

Cynometra alexandri are distinctly deciduous (Sheil 1996). The seasonal changes in light conditions under the canopy, consequently, influence other micro-environmental changes such as air and soil temperatures, and soil moisture. The resulting habitat heterogeneity, therefore, provides opportunities for establishment of new individuals and species (Sousa 1984), and favours the coexistence of species with different life histories and ecological requirements, which contributes to the maintenance of community diversity (Barkham 1992). Indeed, in tropical rainforests, high light availability in gaps promotes seed germination and growth of seedlings of most, canopy and understorey species (e.g. Denslow *et al.* 1998, Iriarte and Chazdon 2006), and the recruitment of seedlings to saplings (Dupuy and Chazdon 2006). Seedlings of some tree species trade-off high tolerance of direct sunlight against tolerance of varying degrees of shade. Recent studies clearly indicate the potential for niche partitioning among tropical forest tree seedlings along gradients of light availability (Montgomery and Chazdon 2002, Poorter and Arets 2003, Iriarte and Chazdon 2006). In the present study, apart from *Cynometra alexandri* and *Celtis mildbraedii*, the species contributing >2% to the overall similarity within each historical management practice type were understorey.

The SIMPER analyses indicated that different species contributed most to the dissimilarity between each pair of groups reflecting the overall differences in community composition among the sites. SIMPER results also showed that some seedling species (e.g. *Lasiodiscus mildbraedii*, *Cynometra alexandri*, and *Argomuellera macrophylla*) exhibited a high degree of overlap between the historical management practice types. However, logging does appear to have an impact on forest structure as mean seedling densities were significantly higher in the "logged only" compared with the Nature Reserve management type. The high density of seedlings in the "logged only" areas (dominated by a *Cynometra alexandri* upper-canopy) in BFR, has similarly been reported for sheltered well-shaded sites compared to exposed open sites in a tropical dry forest in Ghana (Lieberman and Li 1992). *C. alexandri* does not loose its leaves during the dry season when most tree species in BFR loose their leaves, providing continuous seasonal shade to the understorey. Shading is reported to improve dry-season survival (McLaren and McDonald 2003) as it cuts down on irradiance that in the absence of moisture exacerbates desiccation in seedlings, and hence, higher rates of mortality (e.g. Gerhardt 1996). Although the cause of seedling mortality in BFR cannot be disentangled in this study, soil moisture stress seems to be an important factor in the survival of seedlings in this forest. For instance, during the wet season, recently germinated seedlings of *Chrysophyllum albidum* were observed around a parent tree, but a few weeks after the onset of the dry season there were no visible seedlings. Through differential effects on seedlings of different species and sizes, drought may affect species population densities and stand structure of the seedling bank in a forest (Delissio and Primack 2003). Similarly, in a study of seedling dynamics in disturbed dry-limestone forest in Jamaica, McLaren and McDonald (2003) showed that the density of some species was affected by the environmental conditions created by partial and clear cutting, and seasonal effects being more pronounced after disturbance. It is also reported that cyclical perturbation due to the pronounced seasonality in the tropical dry forest allows seasonal germination and establishment with different consequences for size-age population distribution and community structure (Rincon and Huante 1993). Pronounced seasonality as experienced in BFR, affects patterns of seed production, germination, survival and seedling development (Khurana and Singh 2000), consequently, influencing the population structure of some woody species.

Although some of the plots with high light availability (low LAI) were expected to have high numbers of seedlings, some of them did not. These plots with low numbers of seedlings were generally characterised by a thick herbaceous layer and ground vegetation that might have suppressed the regeneration of seedlings through competition for space, water and light. In contrast, Lawes *et al.* (2005) found seedling density to be greater at lower levels of disturbance (i.e., with increasing herbaceous cover) in old Afromontane forest fragments in South Africa. However, in a study of the effects of vegetation cover on seedling and sapling dynamics in a tropical wet forest in Costa Rica, Dupuy and Chazdon (2006) suggested that competition with herbaceous species could be a significant factor leading to increased mortality in large gaps. Similarly George and Bazzaz (1999) reported increased mortality and decreased growth of tree seedlings beneath dense herbaceous fern cover in temperate forests and attributed this effect to competition for light.

Generally, most of the woody species in BFR had several thousand seedlings per ha in the understorey, implying that a dense 'seedling bank' (Whitmore 1996) is their major route of regeneration. In addition, some of the species have also been observed to be strong resprouters (Table 5, Chapter Six), thus they have both sexual (seed) and asexual (sprouting) means of regeneration. The ability to resprout may allow advanced regeneration to persist in the understorey, survive damage during gap creation and quickly exploit the resulting gap (Paciorek *et al.* 2000). Thus, BFR is likely to be ecologically resilient following less severe natural and anthropogenic disturbances. In African wooded savannas, the ability of trees to resprout from the remaining stems following disturbance has been regarded as a key attribute to their resilience and productivity (Shackleton 2000, Neke *et al*. 2006).

4.2. Population structure of selected species

Nine of the 15 selected species had highly negative SCD slopes, exhibiting near-perfect 'inverse J' curves (Fig.1). It is, therefore, encouraging that, despite being targeted for timber and subsistence use, these species appear to be resilient to these disturbances and have healthy regeneration. Additionally, these species have also been shown to resprout following stem damage in this forest (Chapter 6). The classic 'inverse J' curve is expected for populations that recruit fairly regularly over time (e.g. Oliver and Larson 1990), and hence, have a stable size class structure (Silvertown 1982). This is the case for 13 of the 15 species analysed, as they had small stem:large stem ratios >>1, ratios expected of species that are successfully recruiting (West *et al*. 2000). Given that *Celtis mildbraedii* and *Cynometra alexandri* are not greatly targeted for timber harvesting, their rather truncated size class distributions need not necessarily be of concern at present in terms of population persistence. Thus, the death of an adult tree will, at some point be replaced by one or more individuals growing up from the smaller size classes.

However, the rainfall distribution across BFR varies from year to year, with the main rainfall coming either in the first or second half of the year (Tweheyo 2003). This may lead to climate forced deviations in the length of the growing period and competition among species, and may alter the resource use patterns in different species. The change in resource use patterns may adversely affect flowering and fruit set, consequently, affecting the seed bank and advance regeneration. It is, therefore, important that seed production rates by local populations is monitored in order to know, which tree species warrant silvicultural intervention fostering seedling establishment. For example, variations in fruiting responses of trees in Kibale National Park, Uganda, both at species and community levels over a three decade period, have been attributed to climate change (Chapman *et al.* 2005). In a study in the dry tropical forests of Costa Rica, Borchert (1994) suggested seasonal variation in water status to be the principle determinant of both phenology and distribution of tree species. In BFR, water status of plants is more likely to be different among the species as they are reportedly of varying wood densities (Kityo and Plumptre 1997). Wood density in interaction with soil water availability and stem water status (SWS), strongly affect phenology and species distributions (Singh and Kushwaha 2005). In tropical forests, the seasonal patterns of fruiting define the temporal variation in the flux of propagules to a determined area during the year and between different years (e.g. White 1994) that may influence the course of succession (Young *et al.* 1987).

The higher number of saplings compared to seedlings in *Antiaris toxicaria*, *Funtumia elastica*, *Celtis mildbraedii, Cordia millenii* and *Alstonia boonei* (Table 5) may be attributed to differences in species phenologies and their responses to seasonal soil moisture variation. A seven year study on 40 tree species that serve as chimpanzee foods showed that the number of tree species in fruit correlated positively with rainfall and was higher during the rainy season than the dry season (Tweheyo and Babwetera 2007). In addition tree phenology studies in BFR (Plumptre 1995, Tweheyo 2003, Tweheyo and Babwetera 2007) have found fruit production in woody species to vary from year to year, with some trees not producing fruits in some years. After periods of low fruit production it is more likely to find low numbers of seedlings within the forest community, a situation that may further be exacerbated by seedling mortality. Seven species showed seedling/sapling ratios of >2.0, suggesting that some species in BFR experience high seedling mortality as a result of the dry season that is followed by loss of leaves for most species leading to increased light availability, temperatures and moisture stress at the ground. However, shade, competition for resources among seedlings, insect herbivory and disease (Augspurger 1984, Teketay 1997b) may be other factors responsible for low recruitment to saplings. Seedling recruitment processes (i.e. growth, survival and establishments) and mortality influence plant populations, and are important in determining the course of succession in tropical forests (Osunkoya *et al.* 1992, Capers *et al.* 2005). However, these recruitment processes of seedlings vary with species, light intensity and other habitat characteristics (Clark 1990, Bazzaz 1991, Teketay 1996). Furthermore, the low numbers of seedlings for a particular species may also depend on whether it has a sufficient seed bank. Grombone-Guarotini and Rodrigues (2002) emphasise the importance of the seed bank and seed rain as potential sources of new individuals and species recruitment in a seasonal semi-deciduous forest in south-eastern Brazil. Seasonal and annual fluctuations in seed production may also partially influence the soil seed density (Putz and Appanah 1987, Dalling *et al.* 1997).

The under-representation or a complete absence of individuals in some diameter size-classes, particularly the middle size-classes for some of the selected species (e.g. *A. zygia, A. grandibracteata, A. glaberrima, Raphia farinifera, Cordia millenii* and *Alstonia boonei*), indicates discontinuous regeneration (Poorter *et al.* 1996). Although the negative SCD slopes indicate recruiting species, the lack of individuals in the sapling class for *R. farinifera* and the under-representation of *Cordia millenii* and *Alstonia boonei* in the seedling size-class (Fig 2) is marked enough to raise questions concerning their long term population persistence. Few seedling and sapling individuals make it unlikely that species populations can be maintained at the present level because for a species to maintain a relatively constant population more individuals are required in the smaller classes than in the larger ones (Lykke 1998). The size-class distributions exhibited by *R. farinifera*, *A. boonei* and *C. millenii* may reflect populations where regeneration has been temporarily interrupted through excessive harvesting of fruits or seeds, direct physical damage to seedlings, or lack of pollinators or dispersal agents (Peters 1994). In BFR it was observed that a number of *R. farinifera* seedlings had been uprooted and the germinated seed remnants eaten (E.N. Mwavu, pers. obs.), while mature stems had been reportedly cut down by tobacco farmers to harvest leaves and leaf stalks. The cutting of mature *R. farinifera* plants effectively removes most of the seed sources for subsequent seed crops, the only source of natural regeneration for this species since it does not resprout from damaged stems (Chapter Six). In addition, the destruction of *R. farinifera* seedlings by baboons (Gerald Eilu, pers. comm.) has also been observed to reduce the number of potential sapling recruits. Although for *R. farinifera* the small stem:large stem ratio and the SCD slope show a recruiting species, the lack of individuals in the sapling class suggests that it could be eliminated from the area if there is continued harvesting of the mature stems. A similar fate could face *Cordia millenii,* which is targeted by illegal pitsawyers, who cut it for canoes for Lake Albert fishermen and traders (Sheil 1996), potentially removing its seed source. Therefore, the presence of species with a hampered (poor) regeneration pattern suggests the need to develop and implement forest management activities in order to reverse their declining population trend and facilitate a healthy regeneration.

The high number of stems in the ≥50 cm diameter class for *Cynometra alexandri* compared to the other selected species may be attributed to human harvesting preferences and species specific growth habits. *C. alexandri* is known to grow very large stems, but these are not harvested for timber, whereas the other species except *R. farinifera*, *L. mildbraedi* and *F. elastica* are harvested by both legal and illegal pitsawyers. The impact of harvesting woody species for poles and timber, although minimal at present for a number of species, may increase in future and impact on regeneration pattern. According to the BFR Forest Management Plan (1997-2007), the recommended minimum felling DBH for most timber species is 50 cm, which is in fact even lower than for previous management plans. So, whereas some of the timber species may be currently having a healthy regeneration, the continued harvesting of trees of ≥50 cm for timber as recommended in the management plan, may in the long run adversely affect their population-structure and regeneration. A study by Plumptre (1995) showed that for most timber tree species in BFR, fruit production was highest at a ≥50 cm DBH, and the density of seedlings rises exponentially with an increase in the number of trees over 50 cm DBH. Yet, there seems to be no deliberate management efforts to ensure that mature trees that are potential sources of seeds are left, even in areas where legal timber harvesting takes place. Leaving behind standing mature trees in logged areas would be of great importance to both timber and wild animals conservation as the fruit trees will provide food for primates and birds, which will, consequently, disperse the seeds to other areas. In tropical forests frugivores play important functions in dispersal and regeneration (van Schaik *et al.* 1993, Wrangham *et al.* 1994).

5.0. CONCLUSIONS

Seedlings of many species were widely distributed under the forest canopy, though a few were restricted to particular habitats. The presence of a variety of seedlings even under canopies of high LAI may be attributed to the deciduous nature of many of the tree species in BFR, which results in a seasonal increase in light availability, facilitating the germination of light requiring seeds. The CCA ordination points to the importance of soil nutrients and LAI (or light availability in the understorey) in maintaining seedling species variation in BFR. With organic matter, titanium and LAI being the most important environmental variables to explain the variance in seedling species data, it can be concluded that the important mechanisms influencing forest renewal in BFR operate through the soil system, above ground and sub-canopy and canopy vegetation. The wide distribution of seedlings for a variety of species, and the vigorous regeneration patterns for most of the selected multi-purpose use trees species suggests that BFR is currently experiencing a continuous regeneration phase. Continuous regeneration refers to the growth of shade tolerant seedlings and saplings beneath canopies lacking obvious gaps so that there is continuous replacement of the older trees (Veblen and Stewart 1980).

Logging of trees for timber by local people (both legally and illegally) to earn an income also seems to affect the SCDs of *Cordia millenii* and *Alstonia boonei*. Under the current circumstances, it will be important for the BFR management to plan and implement practices that would enhance the regeneration of these species, as well as *Raphia farinifera,* as they are already showing poor regeneration. *Raphia farinifera,* with a low population density and restricted habitat preferences, and which only regenerates through seedlings, may not be able to persist for long if effective conservation measures are not taken in time. However, this should not only apply to species with poor regeneration, but also those presently with a healthy regeneration pattern, in order to ensure sustainable forest management and development. Further studies are also required on seed banks, temporal patterns of seed rain, and factors influencing seedling survival and recruitment, as such information is important for conservation and management planning of these species. Furthermore, before assigning trees for timber extraction, it will be necessary to check their seed production. A sudden removal of nearly all reproductive adults of the multi-use woody species will be catastrophic for their future population structures.

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Appendix 1. Species list arranged alphabetically by family for woody seedlings recorded in 32, 0.5ha plots within Budongo Frest Reserve, Uganda. Plot frequencies and overall density for each species are included.

Family	**Species**	**Plot frequency**	**Overall Density**
Acanthaceae	*Thubergia erecta* (Benth.) Hook.	3	84
	Whitfieldia elongata (Beauv.) C.B.Cl.	15	455
Anacardiaceae	*Lannea barteri* (Oliv.) Engl.	1	2
	Lannea welwitschii (Hiern) Engl.	4	6
	Pseudospondias microcarpa (A. Rich.) Engl.	9	79
Annonaceae	*Cleistopholis patens* (Benth.) Engl. & Diels.	8	158
	Greenwayodendron suaveolens (Engl.& Diels)Verdourt	27	309
	Isolana congolana Engl. & Diels	1	3
	Monodora angolense Welw.	21	76
	Monodora myristica (Gaertn.) Dunal	12	46
	Uvaria congensis Robyns & Ghesquire	5	134
	Uvaria welwitschii Engl. & Diels	3	10
Apocynaceae	*Alstonia boonei* De Wild.	1	1
	Funtumia elastica (Preuss) Stapf	28	285
	Picralima nitida (Stapf) Th. & Hel. Dur.	2	1
	Pleiocarpa pycnantha (K.Schum.) Stapf	1	4
	Rauvolfia vomitaria Afzel.	5	36
	Tabernaemontana holstii K.Schum.	26	1511
Bignoniaceae	*Kigelia africana* (Lam.) Benth.	16	106
	Markhamia lutea K. Schum.	15	77
Boraginaceae	*Cordia millenii* Bak.	1	2
	Ehretia cymosa Thonn.	3	4
Burseraceae	*Canarium schweinfurthii* Engl.	2	4
Capparidaceae	*Euadenia eminens* Hook. F.	2	2
	Maerua duchesnei (De Wild.) F. White	10	41
	Ritchiea albersii Gilg.	6	52
Celastraceae	*Maytenus undatum* (Thunb.) Blakelock	2	4
Chailletiaceae	*Tapura fischeri* (Engl.) Engl.	25	141
Clusiaceae	*Mammea africana* Sabine	13	180
	Symphonia globulifera L.F.	1	2
Connaraceae	*Cnestis ugandensis* Schellenb.	6	9
Dracaenaceae	*Dracaena fragrans* Ker-Gawl.	23	855
Ebenaceae	*Diospyros abyssinica* (Hiern) F. White	16	303
Euphorbiaceae	*Acalypha neptunica* Muell. Arg.	29	4268
	Acalypha ornata Hochst.ex A.Rich.	3	3018
	Alchornea floribunda Muell. Arg.	1	55
	Alchornea laxiflora (Benth.) Pax & K.Hoffm.	21	336
	Antidesma laciniatum Muell. Arg.	9	80
	Antidesma membranaceum Muell. Arg.	1	4
	Antidesma venosum E. Mey.ex Tul.	3	15
	Argomuellera macrophylla Pax Laka	28	8458
	Bridelia micrantha (Hochst) Baill.	7	12
	Claoxylon hexandrum Muell. Arg.	2	6
	Croton macrostachyus Hochst. ex Del.	3	8
	Croton sylvaticus Hoshst. ex Krauss	11	59
	Drypetes gerrardii Hutch. var. grandifolia	5	248
	Drypetes ugandensis (Rendle) Hutch.	13	32
	Euphorbia teke Schweinf. ex Pax	4	20
	Macaranga pynaertii De Wild.	1	2
	Mallotus oppositifolius (Geisel.) Muell. Arg.	11	179
	Margaritaria discoidea (Baill.) Webster	4	12
	Neoboutonia melleri (Muell. Arg.) Prain	3	13

	Securinega virosa (Roxb. ex Willd.) Baill.	1	1
	Spondianthus preussi Engl. var. glaber (Engl.) Engl.	1	6
	Suregada procera (Prain) Croizat	4	36
	Tetrorchidium didymostemon (Baill.) Pax & K. Hoffn	3	3
	Thecacoris lucida (Pax.) Hutch.	18	2116
Fabaceae	*Albizia ferruginea* (Guill. & Perr.) Benth.	2	2
	Albizia glaberrima (Schumach. & Thonn.) Benth.	26	883
	Albizia grandibracteata Taub	2	71
	Albizia coriaria Oliv.	1	1
	Albizia sp.	1	8
	Albizia zygia (DC.) Macbr.	20	312
	Baikiaea insignis Benth	1	1
	Baphia wollastonii Bak. F.	5	23
	Craibia brownii Dunn	2	3
	Cynometra alexandri C.H. Wright	29	12623
	Dialium excelsum J. Louis ex Steyaert	6	23
	Erythrina excelsum Bak.	1	1
	Erythrophleum guinieense	1	1
	Erythrophleum suaveolens (Guill. & Perr.) Brenan	10	22
	Mildbraediodendron excelsum Harms	6	14
	Milletia dura Dunn	1	1
	Newtonia buchananii (Baker) Gilb. & Bout	3	3
	Parkia filicoidea Welw. ex Oliv.	5	20
	Piptadeniastrum africanum (Hook.F.) Brenan	12	166
	Senna spectabilis (DC.) Irwin&Barneby	5	973
	Tetrapleura tetraptera (Schumach. & Thonn.) Taub.	10	12
Flacourtiaceae	*Caloncoba crepiniana* (De Wild. & Th.Dur.) Gilg	4	66
	Dasylepis eggelengii J.B. Gillet	1	3
	Dovyalis microcalyx Warb	14	125
	Lindackeria bukobensis Gilg.	1	1
	Lindackeria mildbraedii De Wild.	6	29
	Lindackeria schweinfurthii Gilg.	5	11
	Oncoba spinosa Forssk.	9	13
	Rawsonia lucida Harv. & Sond.	16	772
Icacinaceae	*Leptaulus daphnoides* Benth	2	2
Labiatae	*Hoslundia opposita* Vahl	1	1
Loganiaceae	*Strychnos mitis* Moore	13	313
	Strychnos sp.	1	1
Malvaceae	*Hibiscus* sp.	2	4
	Hibiscus vitifolius L.	2	8
	Sida rhombifolia L.	1	1
Melastomataceae	*Memecylon jasminoides* Gilg.	20	123
Meliaceae	*Entandrophragma angolense* (Welw.) C.D.C.	9	17
	Entandrophragma cylindricum (Sprague) Sprague.	3	4
	Entandrophragma excelsum Sprague	1	1
	Entandrophragma utile (Dawe & Sprague) Sprague	15	35
	Guarea cedrata (A. Chiev.) Pellegr.	25	444
	Khaya anthotheca (Welw.) C.DC.	27	451
	Lovoa sp.	1	1
	Lovoa swynnertonii Bak. F.	2	3
	Lovoa trichiliodes Harms	2	4
	Trichilia drageana Sond.	29	400
	Trichilia prieuriana A.Juss.	28	801
	Trichilia rubescens Oliv.	24	415
	Turrea floribunda Hochst.	5	7
	Turrea robusta Guerke	4	42
	Turrea vogelli	1	12

	Turrea sp.	1	1
	Turrea vogelioides Bgshawe & Bak. F.	1	1
Melianthaceae	*Barsama abyssinica* Fresen	4	31
Moraceae	*Antiaris toxicaria* (Pers.) Lesch.	26	155
	Craterogyne kameruniana (Engl.) Lanjouw	4	32
	Ficus asperifolia Miq.	4	51
	Ficus exasperata Vahl	4	12
	Ficus mucoso Ficalho	2	2
	Ficus ottoniifolia C.C. Berg	0	3
	Ficus polita Vahl.	1	2
	Ficus sur Forssk.	11	31
	Ficus urceolaris Welw. ex Hiern	12	73
	Ficus variiforia Warb	3	5
	Milicia excelsa (Welw.) C.C. Berg	3	3
	Morus mesozygium Stapf	19	75
	Myrianthus holstii Engl.	24	608
	Treculia africana Decne	1	1
	Trilepisium madagascariense DC.	25	157
Myristicaceae	*Pycnanthus angolensis* (Welw.) Warb.	2	2
Myrtaceae	*Psidium guajava* L.	1	8
	Syzygium cordatum Hochst ex C. Krauss	2	9
	Syzygium sp.	1	4
Ochnaceae	Ochna bracteosa	2	8
	Ochna hierni (Van Tiegh.) Exell	4	8
	Ochna holstii Oliv.	12	148
	Ochna membranacea Oliv.	5	14
	Ochna sp.	4	13
	Ouratea densiflora De Wild. & Th.Dur.	22	501
	Ouratea hiernii Exell	7	57
Olacaceae	*Linociera johnsonii* Baker	11	150
	Strombosia scheffleri Engl.	5	7
	Olax sp.	1	1
Oleaceae	*Linociera africana* (Knobl.) Knobl.	1	5
	Linociera latipetala M.R.F. Taylor	1	3
	Olea capensis L.	1	1
	Olea welwitschii (Knobl.) Gilg & Schellenb.	4	4
	Schrebera arborea A. Chev.	2	5
Palmae	Raphia farinifera (Gaertn.) Hylander	3	528
	Calamus deerratus Mann & Wendl.	1	66
	Phoenix reclinata Jacq.	3	7
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	28	14783
	Maesopsis eminii Engl.	2	5
Rhizophoraceae	*Cassipourea congensis* DC.	1	17
	Cassipourea gummiflua Tul.	2	6
	Cassipourea sp.	1	3
Rubiaceae	*Belonophora hypoglauca* (Welw. ex Hiern)A.Chiev	21	398
	Canthium vulgare (K. Schum.) Bullock	2	4
	Coffea canephora Pierre ex Froehn	18	259
	Coffea euganoides S.Moore	21	167
	Dictyandra arborescens Welw. ex Benth. & Hook. f.	4	10
	Gardenia sp.	2	2
	Gardenia vogelli Planch.	1	4
	Oxyanthus sp.	18	75
	Oxyanthus speciosus	8	26
	Pavetta molundensis K. Krause	1	1
	Psychotria sp.	2	6
	Rothmannia sp.	1	1

	Rothmannia urcelliformis (Hiern) Bullock ex Robyns	9	17
	Rothmannia whitfieldii (Linndl.) Dandy	2	5
	Rytigynia beniensis (De Wild.) Robyns	1	1
	Rytigynia butaguensis (Robyns)	1	1
	Rytigynia sp.	6	13
	Rytigynia usambarensis	1	1
	Vangueria sp.	2	5
Rutaceae	*Aeglopsis eggelingi* M.R.F. Taylor	2	10
	Balsamocitrus dawei Stapf	1	1
	Citropsis articulata (Sprengel) Swingle & Kellerman	26	271
	Clausena anisata (Willd.) Benth.	24	266
	Fagaropsis angolensis (Engl.) Dale	8	33
	Fagaropsis sp.	5	11
	Teclea grandifolia Engl.	5	8
	Teclea nobilis Del.	29	1698
	Teclea sp.	1	31
	Zanthoxyllum leprieurii Guill. & Perr.	4	7
	Zanthoxylum gilletii (De Wild.) Waterm.	1	3
	Zanthoxylum rubescens Hook. f.	7	15
	Zanthoxylum sp.	2	4
Sapindaceae	*Allophyllus dummeri* Bak. f.	19	97
	Allophyllus sp.	4	448
	Allophyllus sp.	6	45
	Aphania senagalensis (Juss. ex Pior.) Radlk	16	71
	Blighia unijugata Bak.	23	630
	Lychnodiscus cerospermus Radlk.	26	440
	Majidea fosteri (Sprague) Radlk.	1	1
	Melanodiscus sp.	22	103
	Pancovia turbinata Radlk.	12	52
	Zahna golungensis Hiern	17	86
Sapotaceae	Chrysophyllum albidum G.Don	32	825
	Bequaertiodendron natelense (Sond.) Hiene & J.H. Hemsl.	3	121
	Bequaertiodendron oblanceolatum (S.Moore) Hiene & J.H. Hemsl.	24	662
	Chrysophyllum muerense Engl.	12	119
	Chrysophyllum perpulchrum Hutch. & Dalz	23	192
	Manilkara dawei (Stapf) Chiov.	6	187
	Mimusopis bagshawei S. Moore	13	83
	Pachystela brevipes (Baker) Engl.	5	108
	Pouteria altissima (A.Chiev.) Aubrev. & Pellegr.	22	299
Simaroubaceae	*Irvingia gabonensis* (Aubry-Lecomte O'Rorke) Baill.	1	1
	Klainedoxa gabonensis Pierre ex Engl.	2	2
Sterculiaceae	*Cola gigantea* A. Chev.	21	189
	Dombeya mukole Sprague	2	6
	Leptonychia mildbraedii Engl.	5	11
	Pterygota mildbraedii Engl.	4	33
	Sterculia dawei Sprague	1	3
Thymelaeaceae	Dicranolepsis buchholzii Engl. et Gilg	1	49
	Dicranolepis incisa A. Robyns	2	2
Tiliaceae	Grewia sp.	24	289
	Desplatsia dawevrei (De Wild. & T.Dur.) Burret	12	33
	Glyphea brevis (Spreng.) Manachino	4	11
Ulmaceae	*Celtis africana* Burm. F.	3	14
	Celtis gomphophylla Baker	20	112
	Celtis mildbraedii Engl.	29	1621
	Celtis wightii Planch.	19	249
	Celtis zenkeri Engl.	30	1048

	Chaetecme aristata Planch.	15	146
	Holoptelea grandis (Hutch.) Mildbr.	2	2
	Trema orientalis (L.) Bl.	1	2
Urticaceae	*Boehmeria macrophylla* Hornem	1	13
Verbenaceae	*Lantana camara* L.	2	8
	Vitex amboniensis Guerke	10	27
	Vitex sp.	1	1
Violaceae	*Rinorea affinis* Robyns & Lawalree	1	2
	Rinorea ardiisiflora (Welw. Ex Oliv.) Kuntze	27	7936
	Rinorea dentata Ktze	4	41
	Rinorea brachypetala (Turcz.) O.Ktze	24	1245
	Rinorea ilicifolia (Oliv) O.Ktze	10	3211
	Rinorea oblongofolia C. Marquand	6	410
Vitaceae	*Leea guineensis* G.Don	14	131

CHAPTER 8

GENERAL DISCUSSION AND SYNTHESIS: Human Impact, Plant Communities, Diversity and Regeneration in Budongo Forest Reserve, North-Western Uganda

1.0. INTRODUCTION

Natural forest vegetation gradients (e.g. plant community types, species composition, diversity and tree recruitment) may reflect the combined influence of environmental gradients (e.g. edaphic factors, climate and disturbance) (Klug & Cottingham 2001, Terborgh 1992), human interventions, climatic change, and relative species performance (Jeník 1990). These factors, however, vary both on spatial and temporal scales (Kent & Coker 1996, Porembski et al. 1995). The relationship between human activity and the environment has created ecological, socio-economic, and cultural patterns and feed back mechanisms that govern the presence, distribution and abundance of species assemblages (Farina 2000). Aimed at improving the understanding of the gradients in the vegetation of Budongo Forest Reserve (BFR), the following studies were carried out; i) land-use/land cover changes around BFR, ii) a numerical classification of the vegetation, iii) analysis of species distributions, richness and diversity, vegetation-environmental factor relationships, and iv) assessment of natural regeneration patterns among the woody species. The world over, increasing human populations and per capita resource consumption have engendered pressing problems that threaten ecosystem function and services, the sustainability of production, and the health and well-being of human populations (Eigenbrode et al. 2007). These influences are even more critical in areas such as tropical rainforests where most human livelihoods are heavily dependent on natural resource exploitation. Therefore, finding ways to improve sustainability of use and biodiversity conservation of tropical rainforests requires integrated research that involves ecology, agriculture, sociology and economics (Palmer et al. 2005). This study revealed that BFR is a mosaic of forest community types that differ in their dominants, species diversity and richness. The forest community patterns are not only a reflection of site conditions (edaphic and abiotic factors) but also the history of human interventions. An understanding of the patterns of forest community types, their species distributions and diversity (alpha and beta), and natural regeneration patterns and environmental correlates, as well as land-use/cover changes, will aid in effective conservation, land-use planning and management (e.g. Peters 1994, Whitmore 1996, Sagers & Lyon 1998, Sheil 1999b, Guariguata 2000, Natta et al. 2002, Eilu et al. 2004a).

2.0. SYNERGIES BETWEEN THE STUDY OBJECTIVES

This section serves as a bridge between the different parts of the study, which are presented in an integrative, conceptual model (Figure 1). The human population in the villages adjoining BFR are heavily dependent on natural resources for their livelihood needs, and agriculture is their main source of income. The need to increase their incomes, mainly through subsistence agriculture, as well as the ever increasing human population in the area, has lead to the loss of nearly all the local woodlands outside BFR (Chapter 2). This leaves BFR as the only remaining major source of timber and non-timber products to the local population. Hence, there is little alternative but to undertake selective logging and harvesting of poles in BFR. Harvesting results in small scale disturbances to the forest plants and the habitats of forest animals. Woody plants may respond to these disturbance events by either dying or resprouting via the remaining stump or root suckers. In BFR, almost all damaged stems (119 of 122; 97.5%) sprouted, except those of only three species (Chapter 6). Depending on how the plant species respond to the disturbance events, the population structure and regeneration patterns of the affected plants will be either positively or negatively influenced. In the present study, of the 15 studied species, nine namely: *L. mildbraedii*, *C. mildbraedii*, *Pouteria altissima*, *C. albidum*, *C. alexandri*, *D. abyssinica*, *F. elastica, C. perpulchrum*, and *Antiaris toxicaria* had highly negative size-class distribution (SCD) slopes and juvenile:adult ratios >>1 and hence, adequate/successful regeneration (Chapter 7). The adequate/successful regeneration, consequently, influences plant community patterns (Chapter 3). According to Hubbell et al. (1999), disturbance stimulates regeneration and recruitment but pioneer and light-demanding species are not necessarily favoured. In BFR, species with the highest density of seedling per hectare were also among the top five most vigorous resprouting species. Changes in the population structure and regeneration patterns of plant species within a community will reverse or even change the successional pathways/stages of the plant communities, thereby leading to the formation of an even more diverse mosaic of communities within the forest (Chapter 3). Changes in species richness and diversity (Chapters 3 & 4) may be caused by intrinsic population processes, natural environmental gradients or anthropogenic interferences such as logging and subsistence harvesting of poles (Chapter 2). Many environmental changes and ecological processes contribute to both the accumulation and erosion of diversity at all spatial and temporal scales (Sheil 1999).

The cutting of reproductively mature trees may remove a large proportion of the seed source for future regeneration, which is the only source of natural regeneration for species which do not resprout from damaged stems, as was the case for three species in BFR (Chapter 6). However, the removal of established plants through logging for timber (Chapters 2 & 6) also provides recruitment microsites, which allows the community to be invaded by additional species, leading to increased species richness (Chapter 4). This is because of increased light availability and other changes in the microclimate of the canopy gaps that allows the germination and growth of light demanding species. In addition, the deciduous nature of most of the canopy tree species in BFR results in seasonal increases in light availability under the canopy. This favours the growth of light demanding species under the canopy, where it would have not been otherwise possible. According to Iriarte and Chazdon (2005), high light availability in canopy gaps generally enhances tree seedling growth, compared to low levels beneath a closed canopy. Indeed, canopy gaps are presumed to provide an environment in which tree species of differing competitive abilities partition heterogeneous resources (Schnitzer & Carson 2001). The measurement of light (using LAI in this study) may provide a surrogate or indirect way of determining long-term patterns of disturbance, since the opening of the canopy through logging results in high light levels at the forest floor. The patchy and heterogeneous nature of the environment within the communities, as experienced in BFR, favours the coexistence of species with different life histories, contributing to the maintenance of community diversity (Chapters 3, 4 & 5). It is therefore not surprising that there is a relatively high number of shared species among the forest communities of BFR (Chapter 3).

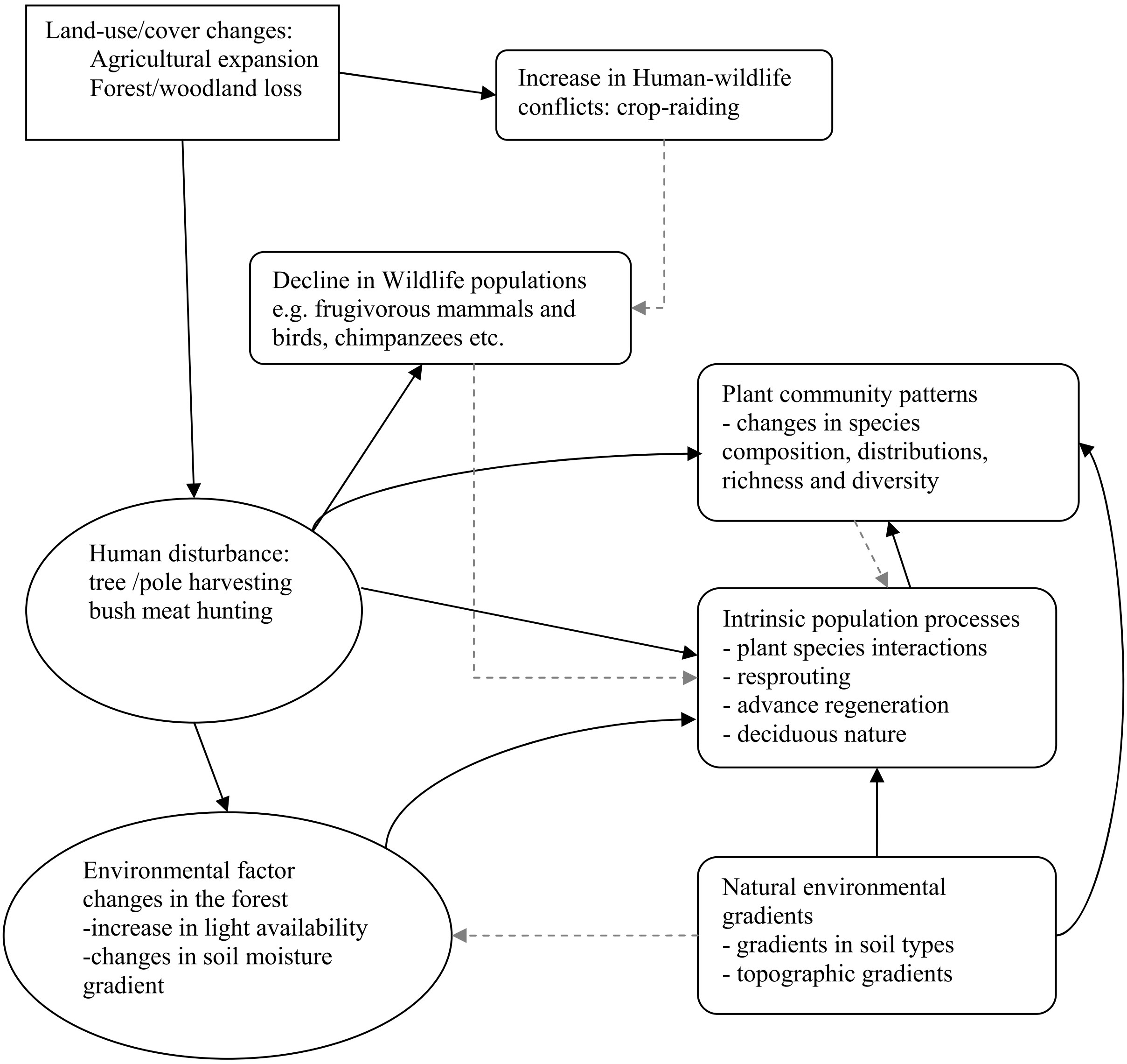

Figure 1. Flow diagram of the inter-relationships between vegetation gradients, human influences and environmental factors in Budongo Forest Reserve, north-western Uganda. Solid lines indicate direct influences, while dashed lines indicate indirect influences.

When disturbance interacts with biotic factors, it may also result in variations in alpha and beta-diversity across forest communities (Chapters 4 & 5). Thus, disturbance, both human-induced (e.g. harvesting of trees for timber and subsistence use; Chapter 6) and natural (e.g. branch and tree fall; Chapter 6), interact to shape forest communities by influencing species composition and diversity patterns (Chapters 3, 4 & 5), as well as population structure and regeneration patterns (Chapters 6 & 7). Indeed, gradients in edaphic and anthropogenic disturbance constitute the major factors that influence plant community patterns, species composition, beta-diversity and regeneration via seedlings in BFR (Chapters 3, 4, 5 & 7). Plant community patterns may also indirectly influence intrinsic population processes (e.g. stand-level regeneration patterns) because of the accompanying variation in forest canopy structure that influences both light availability and its spatial distribution (e.g. Bradshaw & Spies 1992, Brown & Parker 1994). Light availability is a major environmental factor limiting growth and survival of many forest species (e.g.

Whitmore 1996) and its distribution may affect stand-level regeneration patterns of woody species (e.g. Clark et al. 1996, Nicotra et al. 1999).

3.0. WOODY PLANT COMMUNITIES, SPECIES DIVERSITY, NATURAL REGENERATION AND ENVIRONMENTAL GRADIENTS

Understanding forest plant community patterns, species diversity, natural regeneration and environmental gradients is very important in the management of ecosystems of environmental and conservation value, like Budongo Forest Reserve (BFR), since ecosystem management relies on accurately identifying components of the forest landscape. However, in developing countries like Uganda, where human population growth and market demands remain major driving forces of land-use change, sustainable management of forests of prime conservation importance will require an integrated understanding from a range of disciplines (Pfund et al. 2006).

3.1. Land-use/cover changes

The most potent forces affecting natural vegetation arise from the direct effects of an expanding human population (e.g. habitat destruction for agriculture, human settlement, land for grazing, etc.), climate change and indirect effects (e.g. pollution) (Grime 1997, Chapman et al. 2005, MEA 2005b). This study shows that the major land-cover conversions around BFR were from forests/woodlands and grasslands to sugarcane plantations, settlements and cropland through shifting cultivation. The considerable increase in sugarcane plantations, with a concomitant loss of forest/woodland, reflects the importance of commercial agriculture compared to forest/woodland conservation in meeting the immediate livelihood needs of the human population. Agricultural expansion is by far the leading land-use change associated with deforestation in Asia, Africa and Latin America (Geist & Lambin 2002, MEA 2005a, b). The results from this study reinforce the understanding that land-use/cover changes are the result of landowner decisions and reflect the ranking of preferred land-uses in the area (Kajembe et al. 2005, Berry et al. 1995). It is also important to note that 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. Indeed, around BFR, forest / woodland areas that have no clear ownership are the most threatened with degradation and conversion to agriculture. This is yet another example of problems associated with open access regimes and the resultant “tragedy of the commons” (Hardin 1968, Ostrom et al. 1999). The ever increasing extent of land converted for crop cultivation near the forest edge is leading to increased crop-raiding by primates and non-primates from BFR, an already significant source of people-forest conflict (Hill 2000, Tweheyo et al. 2005). Agriculture is the major source of income and livelihood to the local human population in villages adjoining BFR (Chapter 2). Hence, the loss of crops to wild animals undermines local support for conservation efforts in the area. Interviews of local villagers showed that agriculture was considered more valuable than forest conservation, a not unexpected result considering their relatively low income levels (Chapter 2). It indicates that the forest management and researchers working in the forest should place some effort into communicating with the local people and help to inform them of the value of the forest. Improved economic benefits from tourism for example would certainly contribute towards a more favourable attitude in terms of the value of the forest to the locals. Furthermore, the intrusion of humans in the interior of the forest (Chapter 6) and the hunting of mammals (Tweheyo 2003) is likely to affect the behaviour of animal seed dispersers, which may have a knock-on-effect on plant recruitment (Corlett 1998). With increased agricultural expansion and loss of woodlands outside BFR, it will be necessary to establish and maintain a buffer zone. A buffer zone is an area around or adjacent to the protected area, where a harmonious relationship between the natural environment and people is promoted (Brown 1992). For example, buffer zones have had positive impacts, halting land degradation around forest patches in Maribios, Nicaragua (Sayer 1991). However, the establishment and implementation of buffer-zones in areas where people have already settled is a serious socio-economic and political challenge for a developing country like Uganda. In Uganda, the need to access natural resources to alleviate poverty outweighs the desire to conserve the resources, while political interests out-weigh the need to follow the approved laws and regulations. There is also a misconception among Ugandan politicians that the country needs "any type of economic development, despite some having serious environmental costs and negetative repercussions to ecosystem services," and cannot afford the luxury of protecting natural ecological processes.

3.2. Woody plant communities, species diversity and environmental gradients

3.2.1. Woody plant communities

The classification of the vegetation of BFR showed that the forest comprises a mosaic of plant communities, which were revealed to be identified both by the cluster analysis and CCA ordination, and then further scrutinised by ANOSIM and SIMPER analyses. Although groups of species characterise particular forest communities, a considerable number of species are shared between the communities. The relatively high number of shared species among the communities is not surprising, because of the patchy and heterogeneous nature of the environment within the communities as a result of the opening of canopy gaps due to natural and human disturbances (Chapters 2 & 6). The opening of canopy gaps is a recurring source of environmental heterogeneity in forest habitats that favours the coexistence of species with different life histories, contributing to the maintenance of community diversity (Barkham 1992, Valverde & Silvertown 1998). This study also revealed that the use of either qualitative or quantitative data is likely to yield relatively different numerical classification results. Nonetheless, it showed that use of either species abundance (density) or basal area, may successfully be applied in classifying plant communities and in detecting species-environment relationships in semi-deciduous forests. However, it might be misleading to classify woody plant communities using basal area alone, particularly in environments where relatively small stature plant species are frequent and anthropogenic disturbance is pronounced. On the other hand, classifications based on plant density alone are likely to be biased towards the smaller sized plant species that are often very numerous in the forest. Hence, the two-pronged approach of using both measures, basal area/ha and plants/ha to elucidate vegetation – environmental patterns, as used in this study, is a prudent approach.

The study showed relatively strong relationships between the spatial distribution of tree species and edaphic variation. These have similarly been widely reported for tropical forest trees in Ghana (Swaine 1996), neotropical rainforests (e.g. Clark et al. 1998, Svenning 2001), mixed dipterocarp forests (MDF) in Malaysia (Lee et al. 2002) and also widely in savannas (Witkowski & O'Connor 1996). The present study further suggests that small spatial scale (in the order of hundreds of meters) variability in soil nutrients also structures the plant communities in BFR. Hence, there is evidence supporting the hypothesis that edaphic, habitat variation and anthropogenic factors that interrupt environmental vegetation gradation directly contribute to the diversity and heterogeneous nature of the BFR plant communities. It is predicted that anthropogenic disturbance frequency will have greater effects on species composition and community structure than edaphic factors in BFR. Anthropogenic disturbances may lower the abundance and diversity of seed dispersal agents and may indirectly alter plant regeneration (Khan et al. 2005). In addition, Tweheyo et al. (2004) showed that logged areas and forest edges provided 76% of the chimpanzee's food, but these are also the habitats with the highest human interference, e.g. from logging, collecting non-timber forest products (NTFP) and agricultural encroachment. Furthermore, with plant species community composition differing significantly for all comparisons, whether at the transect, topographic position or historical management practice type level, conservation approaches that tend to capture as much of the community types, habitats and environmental heterogeneity as possible will be the most appropriate. In the case of the already designated nature reserves, appropriate management practices that can balance the needs of economic development, environmental integrity and conservation values will be important.

The impacts of human activities play a central role in the future conservation of the natural vegetation and important primates (e.g. chimpanzees); hence, a practical and adaptive management plan is urgently needed for BFR. The development of this plan needs to take cognisance of the multi-use nature of the forest, but at the same time needs to always be mindful of the primary importance of the chimpanzees, the threatened plants and other key components of biodiversity in the forest. The fact that the vast majority of the tree species studied resprout, means that the forest is indeed, very resilient to harvesting and present levels of harvesting appear sustainable, except for a few tree species (see below). However, clear-felling and excessive harvesting (sustainable harvesting levels still need to be determined for each utilized tree species) are not sustainable. More detailed studies on the regeneration ecology, growth and response to harvesting, of multi-use tree species, as well as examples of species that represent various tree growth forms, even those not being used, should be undertaken with the goal of informing and helping to improve the adaptive management plan. Forest research, the monitoring of key features in the forest, and an annual adjustment of the forest management plan, needs to be closely integrated in order to facilitate the long-term conservation and sustainable utilization (economic and environmental goals) of BFR. All stakeholders in the forest need to be part of the team that develop and work on the management plan. This will help to ensure compliance, particularly when some sectors may be faced with the loss of some resources they may have obtained from the forest, but which have not been sustainably utilized. However, the development of such a plan will not be easy.

3.2.2. Species alpha-diversity

Detailed knowledge of species diversity and factors influencing the diversity patterns in African tropical forests is an important step in understanding and conserving them (Natta et al. 2002). This study showed that the diversity of woody species in BFR is substantially contributed to by small stature trees and shrubs that rarely attain a stem diameter size of ≥10 cm. Similarly other tropical forest studies (e.g. Gentry & Dodson 1987, Valencia et al. 1994, Galeano et al. 1998, Neider et al. 2000) have shown that non-tree woody species can also exhibit high levels of species richness. The contribution of such small statured woody species to the overall species diversity may be significant, and influence forest composition and structure (Pitman et al. 2001), as shown in this study. The use of 10 cm as a minimum dbh in woody plant diversity studies in forests, where many tree species rarely exceed 10 cm in diameter, is highly likely to underestimate woody plant alpha-diversity, potentially biasing the understanding of diversity patterns. Therefore, inventories attempting to assess woody species alpha-diversity for conservation goals should consider growth forms other than large trees, as this will ensure that the greatest part of species richness is taken care of (Galeano et al. 1998). The BFR's woody plant species diversity is low compared to tropical forests that receive higher rainfall in Africa and elsewhere, and the Amazon forest in particular, where very high Fisher's alpha diversity values of >200 for trees ≥10 cm dbh were determined (ter Steege et al. 2000). However, the BFR plant communities have a similar suite of plant families to other tropical forests of Africa and the Amazon. Some of the families such as Euphorbiaceae, Meliaceae, Moraceae and Sapotaceae, are nearly as well represented in BFR as in other African (e.g. Cadotte et al. 2002, Eilu et al. 2004) and South America forests (e.g. Valencia et al. 1994, Terborgh & Andresen 1998, Gillespie & Jaffré 2003). Most of the families are represented by a very small number of genera and species. This study showed great variability in species richness and diversity, even for plots from within the same historical management practice type or forest community type, suggesting a patchy and heterogeneous nature of the vegetation community and environmental conditions. Indeed, a SHE analysis and rarefaction curves highlighted the heterogeneous nature of the forest communities that may be attributed to influences of local environment conditions and anthropogenic disturbances (Chapter 3). Recent evidence suggests that diverse site environmental conditions contribute to the maintenance of species richness (e.g. Clark et al. 1999, Pitman et al. 1999, Harms et al. 2001, Toumisto et al. 2003), although the degree of specialization may differ between forests (Kubota et al. 2004). Furthermore, according to the intermediate disturbance hypothesis (IDH; Connell 1978), species diversity of space-limited communities will be low at high and low rates of disturbance and maximal at some intermediate rate. Therefore, under conditions of periodic or recurrent anthropogenic disturbances at intermediate levels, species with different life history strategies are able to coexist and, consequently, high levels of species richness are maintained. Studies (e.g. Eggeling 1947, Sheil 1999) in BFR have presented evidence suggesting an important role for disturbance in maintaining tropical forest tree diversity. The IDH, however, requires that in mature forests some disturbance types can augment local diversity by adding more generally short-lived species (Sheil 1997).

This study shows that BFR has a number of very different woody plant communities in terms of plant diversity, from relatively species rich *Pseudospondias microcarpa* Swamp communities to almost monodominant tracts of *Cynometra alexandri* and *Senna spectabilis*. The BFR woody plant communities exhibit characteristics intermediate between log-normal and log-series distributions, as expected of a community with a small number of abundant species and a relatively large proportion of rare species (Magurran 2004). Indeed, BFR is a mosaic of forest types at different seral stages, and its plant communities are characterised by a small number of abundant species and a relatively large proportion of rare species.

3.2.3. Beta diversity

Information about tropical forest plant species diversity (alpha and beta) patterns and distributions need to be captured to form the basis for the effective and efficient protection and conservation of the remaining species. This study shows that beta-diversity was higher at the total forest community level than at either historical management practice type, transect or plot level, but lower for stem diameter ≥2.0 cm than ≥10.0 cm data. This compared with the propositions by Gentry (1988) and Campbell (1994) that tropical rainforests undergo high spatial turnover rates in species composition. From a methodological view point, this study showed that beta-diversity patterns change significantly when using a minimum stem diameter of 2.0 cm, compared with the standard 10.0 cm dbh. Hence, *β*-diversity of woody plant species for the same forest is likely to vary depending on the minimum stem diameter size adopted. The use of 2.0 cm will be more appropriate as it captures most of the species; and since one of the approaches to *β*-diversity assessment includes the degree to which species composition of sample plots or sites in the same biogeographic realm differ (e.g. Colwell & Coddington 1995, Ricotta et al. 2002). However, there is no evidence that the use of <10 cm dbh sampling obscures beta-diversity patterns. Most inventories in tropical forests continue to include only individuals ≥10.0 cm dbh, because total sampling of vascular alpha and beta-diversity faces the difficulty of collecting within the forest canopy and of identifying sterile material (Whitmore et al. 1985, Galeano et al. 1998). Tree species ≥10.0 cm dbh constitute only 15 - 20% of the complete floras of many neotropical sites (Gentry & Dodson 1987), and in many Amazonian forests where tree species prevail, they scarcely account for 10 - 30% of the total number of species (Duivenvoorden 1994). This study showed that variation in species composition of BFR is characterised by significant spatial patterns, and the patterns in β-diversity are to a great extent associated with environmental heterogeneity (i.e. soil nutrients, topographic and light gradients) and anthropogenic disturbances. The significant correlations observed between local patterns of species distributions and soil variables (i.e. N, Ca, organic matter, Si, K and Mg) in BFR, are similar to what has been reported for other Albertine Rift forests (e.g. Eilu et al. 2004) and Bornean mixed dipterocarp forests (e.g. Potts et al. 2002).

However, clear correlations between forest community patterns and silicon (Si) as shown for BFR are not previously well known.

3.3. Resprouting and seedling regeneration

3.3.1. Resprouting

Little is known of woody species sprouting in African tropical rainforests when natural and anthropogenic disturbances are less severe, e.g. selective felling rather than clear-felling. Yet, effective management, conservation and restoration of forest vegetation requires an understanding of the natural regeneration patterns and responses to disturbance events of its woody species (e.g. Whitmore 1996, Teketay 1997, Peters 1994, Bekele 2000). This study showed that human harvesting of saplings and poles is the major cause of stem damage at present and also seems to be more common in more accessible areas, which are nearer to human settlements. This is probably because BFR is the main source of wood-based products (e.g. poles, saplings, and fuel-wood) to the local human population as most other woodlands outside BFR have been cleared for agricultural expansion (Chapter 2). This study has also shown that BFR, which is a semi-deciduous tropical rainforest, has both a high proportion of sprouting species and incidence of sprouting stems; with both canopy and sub-canopy trees sprouting prolifically. It also shows that species differ in their sprouting ability, a situation, which is well known in other ecosystems where both strongly and weakly sprouting species occur (e.g. Everham & Brokaw 1996, McLaren & McDonald 2003). The significant differences in sprouting ability shown between families and species in BFR, compares with what has been reported among savanna woody species, and further attributed to specific plant size/age at the time of cutting as well as stump height (Shackleton 2000, Luoga et al. 2004, Neke et al. 2006). Plant species may differ in their ability to resprout as a consequence of differences in morphological and eco-physiological traits, such as meristematic capacity (numbers of available buds), root-shoot partitioning, and stored carbohydrate and nutrient reserves (e.g. Zimmerman et al. 1994). In BFR, sprouts emerged mainly from the cut stump, with only one species showing root sprouting (suckering). In tropical rainforests, root suckering as a mode of regeneration has been more commonly reported among species in deforested and fire-degraded sites (e.g. Stocker 1981, Kauffman 1991), and forests disturbed by slash-and-burn agriculture and extensive logging (e.g. Kammesheidt 1999, Marrinan et al. 2005). These conditions were, however, not common in the interior of BFR, which is characterised by a lack of fires, a closed canopy in most parts, and the absence of both heavy logging, as well as presently an absence of large herbivores (e.g. elephants; Sheil & Salim 2004; although these were previously present). The ability of both small and relatively large sized stumps to sprout, and the survival and growth of sprouts, suggests that sprouting plays a very important role in the resilience of BFR to anthropogenic disturbances such as selective timber, and pole and sapling harvesting.

3.3.2. Seedling regeneration

The understanding of seedling regeneration (i.e. regeneration via seedlings) in tropical rainforests is vital in strengthening the ecological basis for their sustainable management for timber and wildlife conservation. The reason is that where enrichment planting is impractical, sustainable forest management relies upon natural regeneration through seedling establishment and resprouting. In addition, studies on natural regeneration and seedling ecology can provide options to forest development through improvement in recruitment, establishment and growth of the seedlings of the desired species (e.g. Whitmore 1996, Teketay 1997). In this study it has been shown that substantial variability in seedling regeneration in terms of species diversity, abundances and distributions exist, even at the plot level. Some of the species are widely distributed, while others are restricted to particular habitats and site conditions (Chapter 7); a pattern that has similarly been observed in other disturbed forests (Lertzman et al. 1996). The observed patterns were a result of the patchy and heterogeneous nature of the environment in this forest. The measured environmental variables substantially influenced seedling distribution, abundance, diversity and richness, with organic matter, titanium, and LAI being the most important environmental factors. These results suggest that an important mechanism that influences forest tree regeneration operates through the soil system (soil nutrients), and forest floor herbaceous layer and forest canopy structure. Variations in LAI as a result of differences in canopy structure and plant responses to soil-moisture stress influences understorey light availability and its spatial distribution (Chapters 3 and 6). It was also observed that most of the woody species had several thousand seedlings per ha in the understorey, implying that a ‘seedling bank’ (Whitmore 1996) is their major route of regeneration. However, most of these species are also strong resprouters (Chapter 6), thus, they have both seedling and sprouting regeneration/recovery from tree harvesting. This suggests that BFR is ecologically resilient to less severe natural and anthropogenic disturbances, since the ability to resprout may allow advanced regeneration to persist in the understorey, survive damage during gap creation and quickly exploit the resulting gap (Paciorek et al. 2000).

3.3.3. Population structure

This study showed that most of the selected multiple-use tree species had a classic ‘inverse J’ curve population structure and small stem: large stem ratios >>1, which are expected of populations that recruit successfully and continuously over time (e.g. Oliver & Larsson 1990, West et al. 2000). The classic inverse J-curve is also expected of a species population with a more stable size structure (Silvertown 1982). Despite being targeted for timber and subsistence use, these species appear to be resilient to the harvesting disturbances as they are able to sprout and exhibit adequate/successful regeneration. Although not investigated, the soil seed banks may be one possible root of regeneration for some of the species in BFR. The ability to sprout and produce seedlings ensures their persistence in this forest under the present scenario of less severe disturbance events. However, some species were under-represented or completely lacked individuals in some size-classes (particularly seedlings and saplings), indicating a discontinuous regeneration pattern (Poorter et al. 1996). A discontinuous regeneration pattern reflects populations where regeneration has been temporarily interrupted through excessive harvesting of fruits or seeds, direct physical damage to seedlings, or lack of pollinators or dispersal agents (Peters 1994). Indeed, in BFR some tree species are unsustainably harvested for timber (e.g. *Cordia millenii*, *Maesopsis eminii,* etc.) and non-timber products (*Raphia farinifera* and *Calamus deerratus* Mann & Wendl.), potentially eliminating seed sources for future generations since some of them appear not to resprout from the cut stump. The presence of species with poor regeneration suggests the need for the BFR management to develop and implement forest management plans/activities that will enhance and facilitate both vigorous and poorly regenerating species, to ensure sustainable forest development. For example, leaving behind standing mature fruiting trees in logged areas would be of great importance to both timber and wild animal conservation as the fruit trees will provide food for primates and birds, which will, consequently, disperse the seeds to other areas. These, however, should be of sufficient population size, and the members of the population should not be too far apart. Plant population-size and spacing is an important factor in the determination of the reproductive output of many species, ranging from annual herbs to large tropical trees (Ghazoul 2005). Ghazoul (2005) also stated that increased spacing among flowering conspecifics, be it through harvesting or habitat fragmentation, may reduce seed set through lower pollinator visitation or pollen quality. If this occurs, then the BFR woody plant community will be greatly affected since the seedling bank is presently its major mode of regeneration. Small populations are likely to be less attractive or less apparent to pollinators than large populations (Ägren 1996, Jennersten & Nilsson 1993, Sih & Bultus 1987), leading not only to a decline in pollinator visits but also poor pollen quality (Silander 1978, Ghazoul 2005).

In this study the woody species *Lasiodiscus mildbraedii* and *Cynometra alexandri* were among the five with the highest sprouting ability (Chapter 6) and also with the highest overall seedling densities (Chapter 7). This is in contrast with the evidence from a Jamaican forest (Bellingham et al. 1994), South African thickets (Midgley & Cowling 1993, Kruger et al. 1997) and in fire prone shrublands (Le Maitre & Midgley 1992), showing that resprouters usually produce fewer seedlings than reseeders. For BFR, anthropogenic disturbances are patchy and less severe, and fires have not been recorded in the interior, at least for the past three decades, which is not the case with South African savannas where fires are more frequent. However, it should be noted that the relative allocation to resprouting versus seedling regeneration in woody plant communities is dictated by the nature of disturbance regimes (Bellingham & Sparrow 2000), and hence, may explain these different patterns.

3.4. Lessons learnt and future challenges

The multi-disciplinary approach, based on remote sensing, socio-economic and ecological science adopted in this study led to a clear understanding of the gradients in the vegetation of BFR. Nonetheless, there are relative strengths and weaknesses in the study, and possible improvements that require discussing. Indeed, integrated research across disciplines is required to address many of the pressing environment problems facing human societies (Eigenbrode et al. 2007). Furthermore, Palmer et al. (2005) stated that research to improve sustainability and biodiversity conservation should involve ecology, sociology, soil science, hydrology, and economics. This study has shown that the anthropogenic disturbances occurring in the forest and that influence plant community patterns within BFR are guided locally by livelihood concerns and social organization, and externally by policy decisions by various sectors of the government and national economy. This study has also shown that it is better to characterize forest woody plant species diversity using >2 cm rather than ≥10 cm dbh, particularly if many woody species rarely exceed 10 cm dbh, which are quite prevalent in semi-deciduous forests. The use of 10 cm as a minimum dbh in woody plant diversity studies in such forests is highly likely to underestimate woody plant diversity, potentially biasing understanding of diversity patterns (Phillip et al. 2003). Therefore, serious consideration has to be given to the dbh classes in deciding on the minimum stem diameter to employ in a diversity study, particularly for forests of prime conservation importance like BFR, which is a mosaic of forest types.

Land-use/cover changes

Uganda's woodlands/forests continue to be converted to other land-uses (e.g. agriculture and charcoal burning), while socio-economic disparities keep increasing. Hence, more recent (up to 2006) land-use/cover changes would have been valuable to assess, but it was not possible because of lack of Landsat images for those dates. However, the available Landsat images, complemented with ground-truthing data and interviews, were sufficient to project future changes in land-use/cover around BFR and the implications for forest conservation (Chapter 2). Future studies should consider more recent changes and also attempt to assess the changes within the interior of the forest at a finer scale of resolution (given the expected improvements in technology) as it faces increased selective timber and pole harvesting. Research is also required to aid the integration of aspects of the livelihoods of local rural people with both conservation and landscape process planning, particularly because BFR is of prime importance for the conservation of plants and primates, particularly chimpanzees. More insight is needed on the effects of human land-use activities on forest composition and especially conservation values to evaluate the role of secondary forests for biodiversity conservation (van Gemerden et al. 2003).

Vegetation sampling

Adequate measurement of species diversity and quantification of species richness, which are essential for understanding the mechanisms of how species diversity is maintained and the structure and functioning of ecosystems requires use of standard methods and plot sizes for comparability of data. Various authors have used a diversity of plot sizes, all influenced by the environment in which they have worked. A good number of studies (e.g. Gentry & Dodson 1987, Duivenvoorden 1996, Vásquez & Givnish 1998, Duque et al. 2002) on vascular plant species diversity in tropical woodlands and forests have employed a 0.1ha (50 x 20m) plot. Although a 0.1ha plot size is the standard area for work on vascular plant species richness (Crawley 1997), a 0.5ha (100 x 50) plot was found to be more appropriate for this study. Analysis of species area relationship curves for species data for the different forest types of BFR by Eggeling (1947) showed that three of the four curves flatten off at about 0.5ha, a point considered adequate for sampling vegetation in this forest. Only the swamp forest community's curve continued upwards.

Plant community patterns

The classification of the vegetation of BFR showed that the forest is formed by a mosaic of plant communities, which were identified by both the cluster analysis and CCA ordination, and then further scrutinised by ANOSIM and SIMPER analyses. Nevertheless, it must be pointed out that further studies are needed to confirm or improve the findings of the present study. Plant communities are dynamic and are influenced by climate change (Chapman et al. 2005) and the seemingly more prevalent human disturbances, which interrupt the successional pathways in BFR. For instance, Eggeling's (1947) and Howard's (1991) classifications also identified a *Maesopsis eminii* Forest community, which was not identified in this study, probably because *Maesopsis eminii* has been constantly harvested for timber over the years. In addition, this study focused only on the Budongo main block (see study site description in Chapter 1) and not the other smaller and more disturbed blocks. In addition, previous classification schemes relied only on broad and much more generalised descriptions, and did not incorporate an understorey component, but relied only on the overstorey dominant tree species (≥10 cm DBH).

Water availability is one of the most important factors that determine tree species distribution in tropical forests (Swaine 1998), and gradients in soil-water are of prime importance in explaining differences in tree growth (Nilsson et al. 1996, Yeh & Eltahir 1998). Although soil moisture data would have been of great value in explaining variations in community species composition and diversity (Chapters 3 & 4), it was not measured because of complexities in local rainfall patterns, variations in rooting pattern and large seasonal differences. The rainfall in BFR is so variable that in a particular day not all the compartments will experience or receive the same amount of rainfall. The soil-moisture measuring equipment that was available could not concurrently measure water in all the 32 plots, which would be necessary in order to avoid variation due to measurements done at different times. In addition, it would require an integrated measure of soil moisture over the whole year, and then also related to rooting depths of the trees. Overall, it would have been a huge task to have it to a sufficient standard, and hence was not practical within the limited time period of a PhD study.

In clearly understanding the influence of light availability under the forest canopy on the variation in plant community species composition (Chapters 3, 5 & 6), seasonal measurements would have been valuable, but time was a major constraint, and hence, LAI was only measured once, under full canopy conditions, which represents the situation over most of the year. However, the single season measurements that were made at the time of active leaf growth for the majority of canopy plants was most important, since during this season soil moisture is not a limiting factor. In addition, not much of the biological historical events (e.g. succession as demonstrated by gap-phase dynamic studies (e.g. Swaine & Hall 1988, Hartshorn 1990) were considered in explaining the species distribution patterns in BFR. With resources and time allowing, it may be important in future studies to consider the influence of biological historical events on species distribution patterns.

Population structure and regeneration patterns

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 important utilized species in BFR (Chapter 7), this was not possible because of lack of data. Collecting meaningful long-term data would probably require a lengthy period of time, which is greater than normally allowed for a PhD study. However, in the absence of long term data, forest dynamics have most often been inferred from single surveys and analysis of static forest inventory data by constructing species' population SCDs (e.g. Lykke 1998, Poorter et al. 1996, Wangda & Ohsawa 2006). Nonetheless, it will be valuable to collect long-term data in permanent monitoring plots, particularly for the important multiple-use tree species, to have a clearer understanding of vegetation change in BFR.

Even though this study has shown that most species have high seedling densities and frequencies, metapopulation 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. As more species are added onto the timber species list, studies are also required on seed banks, temporal patterns of seed rain, seedling survival and recruitment, as this information is important for conservation and management planning for these species. Furthermore, although forest ecologists have collected considerable data on aspects of tree reproductive biology, such as phenology and dispersal and seedling gap requirements in BFR (e.g. Synnott 1975, Plumptre et al. 1994, Plumptre 1995, Mwima et al. 2001, Tweheyo 2003), apart from this study, there is very little information available on the importance of resprouting. Therefore, the relative contribution of resprouting versus seedling establishment in the regeneration of forest trees needs more attention.

4.0. CONCLUSIONS

The new insights into the gradients in the vegetation and regeneration patterns in Budongo Forest Reserve in NW Uganda presented here should help decision makers and researchers to focus their research and conservation strategies on some crucial points that deserve special attention. The results of this study suggest that there is a high likelihood that commercialization of sugarcane and tobacco growing will continue to increase in importance. Hence, the value of productive land and incentives to increase yields will continue, resulting in further loss of natural vegetation, and reduction of land available for other (and particularly local subsistence) food crop cultivation. The continued loss of tree cover on private/communal lands will leave the managed BFR and neighbouring forest reserves, as the only sources for commercial timber and non-timber products for local livelihoods and as the only places for the conservation of wild plants and animals in the region. It may also result in increased agricultural encroachment into the forest, particularly in the more remote parts where forest guard patrols are not common.

The study revealed that the vegetation of BFR is formed of a mosaic of plant communities, that differ significantly in terms of woody species diversity and richness; being most diverse in the *Pseudospondias microcarpa* Swamp and least in the *Cynometra alexandri-Rinorea ilicifolia* forest. The woody plant species diversity and richness in BFR is substantially contributed to by treelets and shrubs that rarely attain a stem diameter size of ≥10 cm. The use of a minimum stem diameter of 2.0 cm in woody species sampling in BFR and similar tropical rainforests, where the richest part of the plant community is the understorey, will be more appropriate as it captures the greatest part of the overall species richness. Indeed, conservation evaluations should be based on as many growth forms, functional types and taxonomic groups as possible (Lawton et al. 1998). Plant diversity in BFR is relatively low compared to Amazonian and other high rainfall tropical forests. However, the woody plant community of BFR have a similar suite of plant families to other tropical forests of Africa and the Amazon. Most of the families are represented by a very small number of genera and species. The variation in species composition of BFR is characterised by significant spatial pattern, and the patterns in β-diversity are to a great extent associated with local environmental heterogeneity (i.e. soil nutrients, topographic and light gradients) and anthropogenic disturbances.

The study showed that semi-deciduous tropical rainforests have both a very high proportion of sprouting species and incidence of sprouting stems (both small and relatively large diameter sizes). There appears to be a high chance of sprout survival and growth to replace the lost stem, making sprouting a key trait in the persistence of woody plant individuals, populations and communities in BFR. Hence, sprouting may play an important role in the resilience of the forest following selective timber, pole and sapling harvesting. Seedling density significantly differs between the historical management practice types, being highest (in the order of several thousand individuals ha^{-1}) for the logged only and lowest for the nature reserve area. However, except between transects, there were no significant differences in seedling composition between topographic positions or historical management practice types. Seedlings for a variety of species were widely distributed, and most of the selected species had population structures showing considerable seedling regeneration, suggesting that BFR is currently experiencing a continuous regeneration phase. However, logging of trees for timber by local people (both legally and illegally) to earn an income may be affecting the SCDs of tree species such as *Cordia millenii* and *Alstonia boonei*.

The present vegetation of BFR is a reflection not only of the site conditions as evidenced by the edaphic and other abiotic factors, but also the history of human interventions. Although natural and anthropogenic disturbances (e.g. logging and arboricide treatment) are important for the maintenance of species richness and diversity within the forest communities, high intensity and frequent disturbances may result in species richness and diversity declines, forest degradation and loss of wildlife. According to the intermediate disturbance hypothesis (IDH; Connell 1978), species diversity of space-limited communities will be low at high and low rates of disturbance and maximal at some intermediate rate. Therefore, disturbance events that lead to a great loss of seed trees and tend to fragment plant populations and forest habitats should be avoided as they are likely to have negative consequences for the maintenance of forest plant species diversity (Boutin & Herbert 2002), and survival of forest wild animals, particularly the chimpanzees (Tweheyo et al. 2004). It is also important to acknowledge the challenges to sustainable management of BFR, which is situated in an area where; i) agriculture is more valued by local people than forest conservation, and ii) 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, strong institutions that can withstand conflicts of interest and a political will to sustainably manage the forests/woodlands in the area for development and conservation will be required.

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