CHANGING FOREST-WOODLAND-SAVANNA MOSAICS IN UGANDA:

WITH IMPLICATIONS FOR CONSERVATION

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Thesis

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ABSTRACT

Forest-Woodland-Savanna (FWS) mosaics are complex, highly varied and dynamic landscapes that cover extensive areas of the tropical world. Until recently, these mosaics were, however, considered poor in terms of biodiversity. In addition, most specialists viewed them as either mismanaged forest areas or an intermediate stage in a gradual forest degradation towards savanna. Consequently, only few scientific studies have been done on FWS mosaics and little attention has been paid to their conservation.

In Uganda, several FWS mosaics have been identified as areas of high biodiversity but no specific plans for their conservation have been made. Little, however, is known about the species variation within these mosaics and how they have changed over time. The aim of this study was therefore to assess the spatial and temporal variation in the FWS vegetation and to identify the environmental factors that maintain that variation.

The northern part of Budongo Forest Reserve, located in northwestern Uganda, was selected as the main study site because the forest has high species diversity, has low variation in some environmental variables e.g. soil types and has a fairly well known management history. For a specific focus on the effect of fire on woody plants, an area in the southern part of Murchison Falls National Park, located immediately north of Budongo forest, was selected.

Five vegetation cover classes (VCC) and a burnt area cover class were identified in the Budongo study area and were best classified using Spectral Angle Mapper (SAM) combined with an Expert System (overall accuracy was 94.6%). The VCC were well distinguishable in terms of species composition and vegetation structure. Basal area, in particular, differed strongly between them. Also, for each vegetation cover class (except open woodland) indicator species were identified: *Uvariopsis congensis*, *Funtumia elastica*, all *Celtis* species, *Caloncoba schweinfurthii*, *Holoptelea grandis*, *Diospyros abyssinica* and *Tapura fischeri* for the forest; *Terminalia velutina* and *Albizia grandbracteata* for the closed woodland; *Grewia mollis* and *Combretum molle* for the very open woodland; and *Lonchocarpus laxiflorus*, *Grewia bicolor*, *Combretum binderanum* and *Combretum guenzii* for the wooded grassland.

Many tree species, however, occurred in more than one VCC, and the vegetation, in fact, showed a gradient in species composition. To conserve these wide-ranging species, the variety in VCC needs to be conserved. Other species e.g. *Uvariopsis congensis* showed a very narrow range of distribution. For such species, the specific environment in which they preferentially occur needs to be conserved.

Along a succession gradient, adults and juveniles of most species were found at the same location. Some of the species, however, e.g. *Maesopsis eminii* had their adult trees at a different position along the succession gradient than their saplings and seedlings. To ensure continuity of such species, the succession gradient locations covering the plants' growth stages need to be conserved. For the species whose adults and juveniles occur together, the

environment in the specific location along the succession gradient needs to be maintained. *Uvariopsis congensis*, for example, occurred only at one extreme end of the succession gradient, while *Grewia mollis* occurred at the opposite extreme.

The extent of woodland-savanna vegetation, examined for the period between 1985 and 2002, had increased in 15.1% of the area and decreased in another 14.3%. Whereas most increase occurred between the two forest blocks (Main Budongo and Kaniyo-Pabidi forests) and to the west of Kaniyo-Pabidi forest, most of the decrease was found in the woodland-savanna areas northwest of Main Budongo forest and in the far north of the forest reserve. Most of the areas with vegetation increase were areas jointly managed by the Forest Department (FD) and the Uganda Wildlife Authority (UWA). The areas of vegetation decrease were either managed by the UWA alone, who practice annual burning, or were FD areas where the local people had easy access. The local people also practice annual burning.

Among the environmental variables measured, fire was identified as the major factor influencing woody plant variation over the area. Species composition and indicator species varied between areas with a different fire regime (No fire, Old fire and Recent fire).

Although fire disturbance is essential for the maintenance of some VCC, its excessive use may be detrimental to the existence of the species there in. Three different VCC subjected to a similar fire regime for over 46 years showed a convergence in woody plant composition in a similar direction. Should the fire regime be maintained for a longer period, these VCC will eventually converge. To maintain the existent variation in VCC, fire regimes need to be varied.

The observed variation in vegetation, and species, along the FWS gradient and their interrelationship indicate that each part of the FWS mosaic is essential for the maintenance of the overall diversity within the mosaic. To conserve the variation in composition within the FWS mosaic of Budongo Forest Reserve, the existing variation in vegetation and their spatial and temporal interrelationships need to be conserved. In addition, the variation in environmental factors needs to be maintained. Purposeful fire management is an essential element of this variation. The conservation plans should also provide for maintenance of the varied food resource required by the resident fauna, especially chimpanzees.

SAMENVATTING

De mozaïeken van "bos, boomsavanne en savanne" (FWS, naar 'Forest, woodland, savanna') zijn complexe, zeer gevarieerde and dynamische landschappen, die grote oppervlaktes van de tropen beslaan. Tot voorkort werden deze mozaïeken laag ingeschat wat betreft hun biodiversiteit. Daar kwam nog bij dat veel specialisten ze beschouwden als slecht beheerde bosgebieden of als degradatiefase van bos naar savanne. Daarom hebben slechts weinig studies aandacht besteed aan FWS en hun bescherming.

In Oeganda zijn verscheidene FWS mozaïeken aangemerkt als gebieden met hoge biodiversiteit maar er bestaan geen specifieke plannen voor hun bescherming. Er is echter weinig bekend over de variatie van soorten binnen deze mozaïeken and hoe deze zijn veranderd door de tijd. Het doel van deze studie was derhalve om meer inzicht te krijgen in de ruimtelijke en temporele variatie in de FWS mozaïeken en de omgevingsfactoren die hierbij een rol spelen.

Het noordelijk deel van de 'Budongo Forest Reserve' werd geselecteerd als voornaamste studiegebied omdat dit gebied een hoge diversiteit heeft, met weinig variatie in bodemtypen en een redelijk goed bekende beheersgeschiedenis. Om meer specifiek de rol van brand op houtige planten te bestuderen werd een gebied net ten noorden van Budongo, het zuidelijke deel van "Murchison Falls National Park", uitgezocht.

Met behulp de 'Spectral Angle Mapper (SAM)' gecombineerd met een expert systeem konden vijf vegetatiebedekkingsklassen (VCC, naar Vegetation Cover Class) goed worden geïdentificeerd (de algehele nauwkeurigheid bedroeg 94.6%). Deze VCCs konden goed onderscheiden worden aan de hand van hun soortensamenstelling en vegetatiestructuur. Vooral het grondvlak per ha verschilde sterk tussen de klassen. Voor elke klasse konden indicatorsoorten worden aangewezen: *Uvariopsis congensis*, *Funtumia elastica*, alle *Celtis* soorten, *Caloncoba schweinfurthii*, *Holoptelea grandis*, *Diospyros abyssinica* en *Tapura fischeri* voor het bos; *Terminalia velutina* en *Albizia grandbracteata* voor de gesloten boomsavanne; *Grewia mollis* en *Combretum molle* voor de open boomsavanne; en *Lonchocarpus laxiflorus*, *Grewia bicolor*, *Combretum binderanum* en *Combretum guenzii* voor de zeer open graslanden.

Vele boomsoorten kwamen echter in meer dan een VCC voor en de vegetatie als geheel vertoonde een duidelijke gradiënt in soorten. Om de vele wijdverbreide soorten doelmatig te beschermen moet dan ook de variatie in VCCs in stand worden gehouden. Andere boomsoorten zoals *Uvariopsis congensis* vertoonden een veel nauwere verspreiding. Voor het behoud van dergelijke soorten is vooral het behoud van hun specifieke omgeving gewenst.

Van de meeste soorten treffen we de volwassen en jeugdstadia vaak op dezelfde locaties binnen de gradiënt aan. Van sommige soorten, zoals *Maesospis eminii,* werden de jeugdstadia echter op een andere locatie binnen de gradiënt gevonden. Om deze soorten blijvend te behouden moet dan ook de volledige gradiënt die hun groeistadia beslaat beschermd worden. Voor soorten waarvan de volwassen en jeugdige stadia in dezelfde fase van de successie voorkomen, dient vooral die fase beschermd te worden. *Uvariopsis congensis* komt bijvoorbeeld aan het ene uiterste van de successiereeks voor terwijl *Grewia mollis* juist aan het andere uiterste voorkomt.

Het areaal van de FWS werd onderzocht voor de periode tussen 1985 en 2002. In 15.1% van het oppervlak was sprake van een toename van de bedekking terwijl in 14.3% van het oppervlak sprake was van een afname. De grootste toename had plaats tussen de twee voornaamste bosarealen in het gebied ('Main Budongo' en het 'Kaniyo-Pabidi forest') en ten westen van het 'Kaniyo-Pabidi forest'. De grootste afname vond plaats in de boomsavanne ten noordwesten van het 'Main Budongo forest' en nog verder noordelijk in het reservaat. De meeste gebieden waar een toename van de vegetatiebedekking werd waargenomen werden gezamenlijk door de bosdienst (Forest Department, FD) en de Oegandese Wildautoriteit (Uganda Wildlife Authority, UWA) beheerd. De gebieden waar de vegetatiebedekking was afgenomen waren, werden beheerd door de UWA, welke jaarlijks brandbeheer uitvoert, of waren gebieden die onder verantwoordelijkheid van de FD vielen, maar waar de lokale bevolking gemakkelijk toegang had, en daar jaarlijks vegetatie brandde .

Onder de gemeten omgevingsvariabelen werd brand als de belangrijkste voor het verklaren van de vegetatie gevonden. Er waren dan ook grote verschillen in soortensamenstelling en indicatorsoorten tussen gebieden met verschillend brandregime (geen brand, oude brand, recente brand).

Hoewel brand essentieel is voor het behoud van sommige vegetatieklassen, bleek overmatig gebruik juist schadelijk te zijn voor de soorten die er in voorkomen. Drie verschillende vegetatieklassen, die blootgesteld waren aan eenzelfde brandregime gedurende 46 jaar, vertoonden allen een convergentie in soortensamenstelling. Mocht het huidige brandregime daar gehandhaafd worden, dan zullen deze verschillende klassen uiteindelijk gelijkwaardig in samenstelling worden. Om de huidige variatie in vegetatie te behouden is dan ook een gevarieerd brandbeheer nodig.

De geobserveerde variatie in vegetatie en soorten langs de FWS-gradiënt en hun interactie tonen aan dat ieder deel van de gradiënt belangrijk is voor het behoud van de totale diversiteit binnen het mozaïek. Om de variatie in soortensamenstelling van het FWS-mozaïek, die binnen 'Budongo Forest Reserve' bestaat, te beschermen is het nodig om de huidige variatie in vegetatie met de ruimtelijke en temporele relaties te beschermen. Doelgericht brandmanagement is een essentieel onderdeel van deze variatie. De natuurbeschermingsplannen moeten daarnaast ook ruimte bieden voor het behoud van essentiële voedselbronnen van de lokale fauna, zoals de chimpansee.

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CHAPTER 1

VEGETATION VARIATION IN FOREST-WOODLAND-SAVANNA MOSAICS

1.1. Introduction

Forest-woodland-savanna (FWS) mosaics are an undervalued biodiversity store. Until recently, they were considered poor in terms of biodiversity (Furley, 1999). Their existence as a mixture of vegetation types, however, enables them to hold a unique assemblage of flora (Ratter et al., 1997) and fauna (Skowno and Bond, 2003). Also animals that require more than one vegetation type for their day-to-day survival e.g. breeding in one and feeding in another, often find home in mosaic landscapes. Little is, however, known about how these mosaics have changed over time and, how the vegetation cover and species composition varies over the mosaic.

FWS mosaics did not receive adequate attention because most specialists considered them as either being mismanaged forest areas (Clayton, 1958; Eriksson et al., 2002) or an intermediate stage in a gradual forest degradation towards savanna. As a consequence of the low level of available scientific information, hardly any specific management plans exist for their conservation. In Uganda, for example, undisturbed forest areas have been designated as nature reserves for the conservation of forest species while national parks, where there is regular disturbance, have been designated for conservation of savanna species. This leaves the areas where forest, woodland and savanna coexist not catered for despite the fact that several forest reserves, classified as forest-woodland-savanna mosaics, were identified as areas of high biodiversity value.

Although the vegetation types that occur in mosaics can be stable for millennia, the edges between the vegetation types are often in a state of flux depending on the prevailing environmental conditions (Hopkins, 1992). During periods of drastic changes in the environment, the whole mosaic or big parts of it may change (Favier et al., 2004b). At the same time, management continuity and land use history have been observed to have a strong influence on species richness of mosaic areas (Cousins and Eriksson, 2002; Eriksson and Eriksson, 1997). Apart from the direct effect on colonization and extinction of species, disturbance may over time lead to the creation of a particular environment. For instance, in areas that are often burnt a strong reduction in nutrient levels may occur. In order to develop conservation strategies that will ensure maintenance of the existent species, the species interrelationships, the successional changes and the management systems that have been used over time ought to be understood. In addition, the environmental factors and the disturbances that have contributed to the species' existence and maintenance also need to be understood.

The aim of this study is to assess the vegetation variation and the spatial and temporal changes in FWS mosaics. This will provide the managers of such landscapes with information that is necessary to better plan for their conservation.

1.2. FWS mosaics and the underlying processes

A vegetation mosaic is defined as the occurrence of different plant communities in a specific area (Kent and Coker, 1996). In FWS mosaics the woody plants' composition, canopy cover and vegetation structure are the main differentiating factors. Whereas the forest and woodland vegetation have a near continuous woody plant cover, the savannas have a discontinuous one. On the other hand, the forest has a multilayered canopy and often hosts larger and taller woody plants than the woodland (Hoffman and Franco, 2003). It is also denser than the woodland.

A hypothetical transect through part of the mosaic e.g. from savanna to forest may reveal a pattern that shows several characteristics (Figure 1.1). These include sites ranging from areas of open tree canopy to areas of more closed tree canopy, from shorter and smaller trees with narrow canopies to progressively taller and larger trees with wider canopies, from areas whose ground cover is dominated by grasses to areas where grass cover is minimal or even nonexistent, from plants that are light demanders to those that survive best in shade and species ranging from those that can survive frequent fires to those that are fire intolerant. Although this is the general picture, complex species-to-species as well as species-to-environmental factor interactions occur in mosaic landscapes.

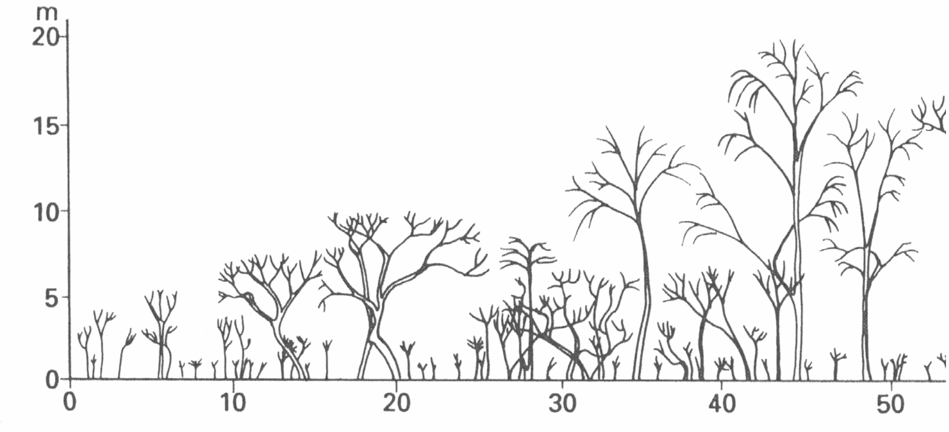

Figure 1.1: Profile diagram of vegetation across the forest-woodland –savanna boundary. Modified from Hopkins (1992)

Although subtle variations in vegetation structure may be evident in some landscapes, the species composition variation is often more complex. In addition to species difference between the different vegetation types of the mosaic, species composition may also vary among areas of a similar vegetation type (Muhlenberg et al., 1990).

The boundaries between vegetation types can be abrupt with a narrow overlap zone (ecotone) that has species from both vegetation types. With a less abrupt boundary, the ecotone is wide and patches from either vegetation type occur in it. In instances where there is no easily distinguishable ecotone, a gradual change in species composition occurs over a distance. This is referred to as a continuum (Forman and Godron, 1986). Even where a continuum occurs the environmental factors may still be patchy.

The causes of the patterns in a landscape can be divided into two categories i.e. environmental variation (e.g. soil quality, water availability and topography) and disturbance (e.g. landslides and hurricanes, which are non-human induced disturbances, and fire and timber harvesting, which are often human induced disturbances) (Bond and van Wilgen, 1996; Corney et al., 2004; Furley, 1999; Whittaker, 1956). These factors are, however, interrelated.

Several studies have shown the effect of soil quality on vegetation (Dezzeo et al., 2004; Jones, 1992; Swaine et al., 1992). Factors ranging from the parent rock qualities to the soil's water holding capacity influence the type of vegetation an area may support.

Fire has been singled out as a key element in determining vegetation structure and floristic composition of mosaic landscapes (Hudak et al., 2004) and it is mostly of anthropogenic origin (Beaty and Taylor, 2001; Gautier and Spichiger, 2004). At the same time, many topographic and climatic factors play a role in the fire-forest structure mosaic (Beaty and Taylor, 2001; Bond and van Wilgen, 1996). In the presence of large topographic variations, fire behavior changes across local topographic gradients because of differences in fuel moisture content, fuel properties and the topographic influence on wind (Wells, 1965). Fire occurrence is also influenced by environmental and compositional gradients, which are partly a result of the history of disturbance (Beaty and Taylor, 2001), the land use, fuel load and fuel flammability (Bekker and Taylor, 2001; Hudak et al., 2004).

Fire affects the spatial pattern of forests by either creating a mosaic of burned and unburned patches (Miller and Urban, 1999) or by burning areas at varying intensities (Parr and Brockett, 1999). The mosaic may further be complicated by variation in time since the area was last burnt and/or change in fire frequency (Paterson, 1991; Tálamo and Caziani, 2003; Wimberly and Spies, 2001). Burning in different seasons (Kauffman and Martin, 1989; Uys et al., 2004) and complete cessation of burning have been noted to produce varying results when carried out on different types of vegetation.

Areas that are regularly disturbed by fire and have developed a species pool adapted to the disturbance will survive for millennia (Eriksson et al., 2002; Forman and Godron, 1986). Most of the existent mosaics have prevailed over long periods of disturbance. The species that occur in them may therefore be more resistant to disturbance than often believed (Eriksson et al., 2002) and so conservation of such landscapes may warrant specific attention.

Whereas fire prevents settlement of forest species in the woodland-savanna areas (Favier et al., 2004a), complete stopping of burning promotes the development of woody vegetation (Everett et al., 2000; Gautier and Spichiger, 2004; Sheil, 1999; Skowno et al., 1999; Uys et al., 2004) and in some areas, the vegetation development is relatively rapid (King et al., 1997; Swaine et al., 1992).

As part of putting into effect her commitment to biodiversity conservation (United Nations Environmental Programme, 1992), the Uganda government has put in place a set of conservation areas (Howard et al., 1998) and has also ensured active management of the already existing ones. In some of these areas local people regularly used fire as a management tool for refreshing grass for both domestic and wild ungulates or for hunting. This is no longer permitted. This has led to vegetation increase but there has been little done to evaluate the vegetation changes and the effect of these changes on the woody species composition and diversity.

1.3. Occurrence of forest-woodland-savanna mosaics

FWS mosaics are prevalent in many areas adjacent to closed forest. They are difficult to isolate and map because of the complex boundaries between them and the adjacent vegetation types; either closed forest or grassland areas. A main difference between woodland, savanna and grassland is in the tree cover. Whereas savannas have trees, grasslands have none. On the other hand, the savanna tree cover is discontinuous while that of the woodland is generally continuous (Belsky and Amundson, 1992). Where FWS mosaics occur and the climate and soil conditions would theoretically be suitable for forest, they are considered relicts of drier periods (Desjardins et al., 1996; Mariotti and Peterschmitt, 1994; Schwartz et al., 1996). In such areas, the mosaic landscapes are maintained through purposeful use of fire (Hopkins, 1992; King et al., 1997; Paterson, 1991).

In areas where there is an environmental factor e.g. soil quality with a pronounced yet irregular gradient, the FWS mosaic pattern can be predicted through the identification of the pattern of the environmental factor (Hovestadt et al., 1999). In other areas, however, the vegetation pattern is less predictable and is mainly determined by the variation in disturbance (Gautier and Spichiger, 2004).

The largest FWS formations in South America occur in Brazil and cover an area equivalent to western Europe (Furley, 1999). Another big mosaic area stretches from Guyana into Brazil (Jansen-Jacobs and ter Steege, 2000).

In Africa FWS mosaics are prevalent in areas surrounding the Congo basin forests, including Uganda. These areas have been defined as transitional zones between the moist tropical forest and the drier savanna landscape typical of much of Africa. On the northern side, the transition occurs at about 8°N with the exception of Togo and Benin and part of Ivory Coast (Gautier and Spichiger, 2004).

Ecologically, Uganda is exceptionally diverse. Of the 18 floristic regions that occur in mainland Africa (White, 1983), seven are represented in Uganda. Hence, the country possesses more species for its size than almost any other country in Africa (Pomeroy, 1993). Many FWS mosaics occur in Uganda because of its location in a zone of overlap between the ecological communities characteristic of the dry East African savannas and the West African rainforests (Howard, 1991). Because of the relatively high amount of rainfall (above 1,000mm a year) received in most parts of the country, the woodland and savanna areas are mainly maintained by fire.

1.4. Selection of study area

Few studies have been carried out that address vegetation variation within the mosaic landscape as a whole (Hovestadt et al., 1999). At the same time, models of species distribution often focus on environmental predictors but other processes e.g. dispersal, succession, fire and grazing need to be incorporated (Austin, 2002). In this study, species succession and fire are of special interest.

In Uganda, forest species distribution, succession and dynamics has been extensively studied (Babaasa et al., 2004; Chapman and Chapman, 2004; Eggeling, 1947; Eilu et al., 2004; Lwanga, 2003; Mwima and McNeilage, 2003; Paul et al., 2004; Sheil and Salim, 2004). Woodland and savanna landscapes have also received considerable attention (Buechner and Dawkins, 1961; Laws et al., 1975; Lock, 1993; Smart et al., 1985). The areas where forest, woodland and savanna vegetation co-occur have, however, hardly been studied resulting in an information gap which is also reflected in the biodiversity conservation planning where there is lack of specific plans of conservation of FWS mosaics. The variation in vegetation types within the FWS mosaics enables them to support a variety of species (Ratter et al., 1997) and so each of the vegetation types contributes differently to the overall diversity of a FWS mosaic area. Assessing the species composition and assemblage of vegetation within a FWS mosaic and how the area has changed over time would provide key information for conserving such areas.

Carrying out this study in Uganda will, therefore, provide valuable information for the Ugandan conservation planners as well as for conservational planners of other areas where FWS mosaics occur. To reduce the number of environmental factors that may have to be considered, an area with low variation in some environmental variables was chosen. The site finally chosen, Budongo Forest Reserve, has a similar soil type in over 90 per cent of its area, has low variation in topography and receives high enough rainfall (above 1200 mm per year) to support forest vegetation. Budongo forest has a sizable forest-woodland-savanna mosaic area and good historical information about its management is available. The forest is of exceptional importance in terms of biodiversity, ranking third in overall importance in the country (Forest Department Uganda, 1999).

To specifically evaluate the effect of annual burning on woody plants, an area with a known fire regime had to be studied. The area selected was in the southern part of Murchison Falls National Park, Uganda, which is located immediately north of Budongo Forest Reserve. Details about this study area will be provided in Chapter 6.

1.5. Budongo Forest Reserve

1.5.1. Location

Budongo Forest Reserve is located in the northwestern part of Uganda and it consists of two forest blocks, Main Budongo (made up of Budongo, Siba, Busaju forests) and Kaniyo-Pabidi forest blocks (Figure 1.2). It is situated in the districts of Masindi and Hoima with the largest part falling in Masindi. It is located between 1° 35′-1° 55′ N and 31° 18′ – 31° 42′ E on the edge of the western rift valley. Budongo forest is classified as a medium altitude, moist semi-deciduous forest (Langdale-Brown et al., 1964).

Budongo Forest Reserve was gazetted as a central forest reserve in 1932. The reserve, which is a mixture of tropical high forest with a large population of mahogany species e.g. *Khaya* spp. and *Entandrophragma* spp., woodlands and savanna grasslands (Hamilton, 1984), covers 82,530 ha, making it Uganda's largest forest reserve. It consists of 53.7% forest and 46.3% "grassland". A woodland-savanna area, interspersed with forest patches, commonly referred to as Kaniyo-Pabidi Woodland, separates the Main Budongo forest block from the Kaniyo-Pabidi forest block.

1.5.2. Climate

Budongo forest is located in a zone described as transitional between the Congo forest and the Uganda savanna climates and is characterized by high temperatures. The minimum temperature is 23 – 29°C during June – July, while the maximum temperature is 29 – 32°C during December to February. The rainfall received varies between 1,397 and 1,524 mm annually on 100 to 150 rainy days. Rainfall is predominantly of the thunderstorm type and occurs mainly in the afternoon. The peaks of the rainy season are during the months of April – May and October – November. The east and south parts of the forest receive more rain compared to the north and north west (Forest Department Uganda, 1997).

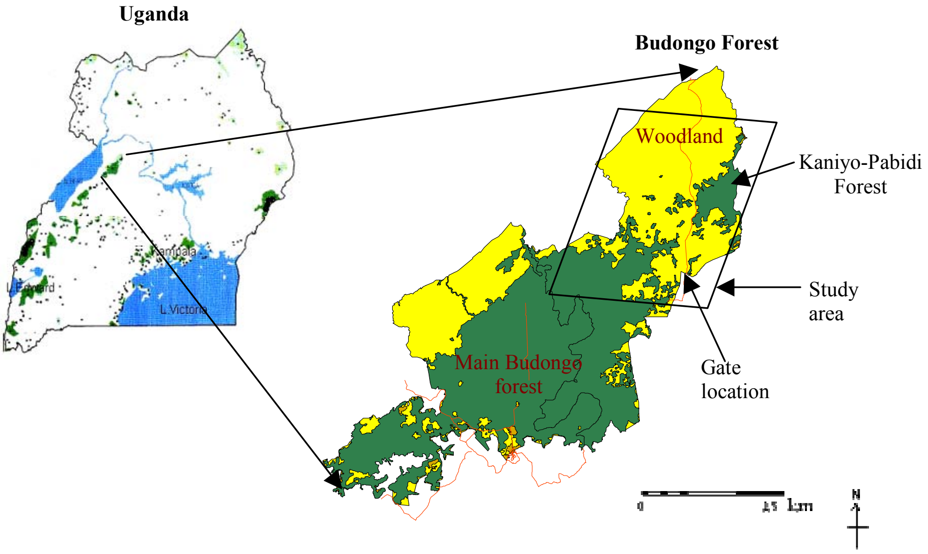

Figure 1.2: Study area map showing the location of the entrance gate to the conservation area since 1985 (gate location). Before 1985, the gate was located at the eascarpment, north of the forest reserve.

1.5.3. Geology and Soils

The underlying geology of the Budongo Forest is of Precambrian origin consisting of high-grade metamorphic rocks of the 2.9 billion year old granulite group (van Straaten, 1976). The soils found over 90% of the study area are orthic Ferralsols: highly weathered, deep well drained soils with low pH. The remaining 10% of the area has soils called Lithosols. These soils are mainly found on hilltop regions and are predominantly underlain by rocks. In river valleys, eutric Fluvisols are found (FAO-UNESCO, 1977).

1.5.4. The local people around the forest

The forest is surrounded by several agro-pastoral ethnic groups. Crop production is the major economic activity. According to Langoya and Long (1977), the local population has changed in composition during the last century. People from other parts of Uganda, Sudan and Congo settled and joined the traditional inhabitants, the Banyoro in the villages surrounding the forest. As a result, the local community today is very heterogeneous in terms of culture, language and nationality.

With the population growth of the community living around Budongo forest, human pressure on the forest has also increased. Some of the immigrant tribes practice game hunting as a means of providing supplementary protein for their families. In a research carried out by Obua et al. (1998) among the communities around Budongo forest, it was recorded that 55.5% of the respondents secured bush meat from the forest. Howard (1991) records the hunting methods commonly used in 9 of the 12 main forests reserves. Budongo Forest Reserve is one of those that lack this information.

1.5.5. Vegetation condition

The species compositional makeup of Budongo forest resembles that of the Congo basin but supports lower species diversity and a rare and significant climax community. It contains two types of climax i.e. the *Cynometra* forest climax and an edaphic climax of the swamp forest. Other stages of the forest, referred to as the colonizers, include the mixed forests, the *Maesopsis* forests and the colonizing forest. The most common genera in the mixed forests are *Chrysophyllum, Cynometra, Khaya* and *Trichilia*. Economically this is the most important component of the forest. The swamp forest covers the smallest part of the forest and it is found on locations that are flooded for part of the year and water logged for the remainder. The *Maesopsis* forest is found on slightly better soils than the colonizing and is dominated by *Maesopsis eminii.* The colonizing forest is often found on the sides of ridges. The colonizing forest types expand into the savanna areas located in the forest and on its fringes. The colonizing process usually starts with *Acanthus arboreus* which is replaced by *Maesopsis eminii* and then a mixed forest. In the absence of *Acanthus* the colonization is much slower (Laws et al., 1975). A natural boundary between a colonizing forest and the tree savanna is usually dominated by *Albizia* and *Caloncoba*. Such areas are most prominent where conditions of soil fertility and water supply favor forest expansion and where fire has not been intense enough to kill off the young trees (Paterson, 1991).

In the woodlands, fire has been prevalent for hundreds of years (Paterson, 1991). The causes of fire include land clearance, verge clearance, lightening strike, hunting and refreshing grass (Wheater, 1971). Pictures taken from the southern and northern end of Kaniyo-Pabidi forest reveal some of the structural differences in vegetation in the reserve. In figure 1.3a, taken from Pabidi hill in the south, the height and greenness differences between the woodland, foreground, and the forest, background, are shown. Figure 1.3b was taken from Igisi hill located north of Kaniyo-Pabidi forest. Except for a small intrusion of the Kaniyo-Pabidi forest at the far left hand corner, the picture shows variation in woodland and savanna vegetation.

(a)

(b)

Figure 1.3: Some of the vegetation variation within the forest (a) Height and greenness differences between the woodland, foreground, and forest, background. The picture was taken from Pabidi hill. (b) variation in vegetation cover in the woodland and savanna areas. An intrusion of the Kaniyo-Pabidi forest is evident in the far left corner. The picture was taken from Igisi hill.

Thus, the hypothesis of this study is that forest, woodland and savanna each contribute significantly to the diversity of the FWS mosaic. To explore this hypothesis, the following questions are answered;

1. What vegetation classes can be identified in the area and what classification method best differentiates them?
2. How does tree species composition and vegetation structure vary over the area?
3. How has the vegetation cover of the area changed over time?
4. What role has management played in influencing vegetation change?
5. How do woody plants from different vegetation cover classes respond to a regular fire regime?
6. What are the conservation implications of the observed vegetation variations?

1.6. Outline of this dissertation

In order to sustainably manage mosaic landscapes, there is need to know what is contained in the mosaic i.e. vegetation types and the species that occur in them, and to understand the changes taking place within the mosaic. Hence, the aim of this dissertation is to assess vegetation variation and the spatial and the temporal changes in FWS mosaics. In chapter 2 we identify and classify the main vegetation cover classes that exist in our area of study. To ensure acquisition of the most accurately classified map, we use several classification methods. This is the quickest way one can obtain an idea of what is contained in the area. The output is used in some of the following chapters.

In Chapter 3 we analyze the species composition of the area and evaluate how much of the variation can be explained by the environmental factors. We check if there are significant differences between the classes identified in Chapter 2 and also check for indicator species for each of the vegetation cover classes. In addition, we analyze differences in species diversity and vegetation structure of the vegetation cover classes. This provides us with an idea of the species interrelationships over the area.

In Chapters 4 and 5 the vegetation changes that took place between 1985 and 2002 in the Kaniyo-Pabidi woodlands are assessed. Chapter 4 gives an evaluation of how the vegetation changes relate to management changes over the years, especially their impact on fire use, or restriction, in the woodland and its eventual influence on the vegetation of the area. In Chapter 5 an evaluation of how the changes relate to the species succession is carried out. This chapter enables us to identify which species are early colonizers and which ones are late colonizers. Whereas in Chapter 4 it was important to ascertain whether vegetation change was taking place in the area and where it was occurring, in Chapter 5 it was important to estimate the change as accurately as possible since the pixel information is combined with plot biophysical data during further analyses.

In Chapter 6 we take a focused look at the vegetation response to regular burning. In Chapters 3, 4 and 5, there is an underlying notion of advocating for fire and in Chapter 6 the underlying question is how far should we go with the use of fire? An area where 3 vegetation classes were identified in 1958 was revisited in 2004 to assess how the species composition had changed.

In Chapter 7 we present a synthesis of the preceding chapters and return to the question; what are the implications of the observed vegetation variations for the conservation of FWS mosaics?

CHAPTER 2

MAPPING VEGETATION COVER OF BUDONGO FOREST - A COMPARISON OF CLASSIFIERS

Abstract

Four classification methods i.e. Maximum Likelihood classifier (MLC), Spectral Angle Mapper (SAM), Maximum Likelihood combined with an Expert System (MaxExpert) and Spectral Angle Mapper combined with an Expert System (SAMExpert) were compared in this study. The combination of conventional classifiers with an Expert System proved to be an effective approach for forest mapping. This was the first time, in fact, the SAMExpert had been used in tropical forest mapping. SAMExpert not only maps with high accuracy but is also fast and easy to use in less developed countries. It can be executed on a standard PC set up for image processing, and the labour cost is low.

Combining the conventional classifiers (MLC and SAM) with the Expert System significantly improved the classification accuracy. The highest overall accuracy (94.6%) was obtained with SAMExpert. The MaxExpert approach yielded a map with an accuracy of 85.2%, which is also significantly higher than that obtained using the conventional MLC approach.

The SAMExpert classifier accurately mapped individual classes. Interestingly, woodland classes that could not be discriminated accurately when using conventional methods (MLC and SAM), could now be mapped. These classes included a Terminalia woodland that had been identified by ecologists although never previously mapped, and a new wooded grassland cover class.

Key words: Forest classification, conventional classifiers, Expert System, classification accuracy, East Africa

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Based on Grace Nangendo, Henk van Oosten and Andrew K. Skidmore (*Submitted*) Mapping East African tropical forests and woodlands - a comparison of classifiers.

2.1. Introduction

For nearly a century, forest and national park agencies have been engaged in mapping tropical woodlands and forests (Lane and McDonald, 2002) in order to provide managers with information (Achard and Estreguil, 1995; Adriaensen et al., 2003; Bauer et al., 1994; Goor et al., 2003; Hallett et al., 2003; Quinn et al., 2001; Robert and Laques, 2003; Taillefumier and Hervé, 2003) and monitor the condition of ecosystems over time (Achard and Estreguil, 1995; Adriaensen et al., 2003; Bauer et al., 1994; Hallett et al., 2003; Hill, 1999; Mickelson, 1998; Taillefumier and Hervé, 2003; Tole, 2002; Wolter et al., 1995). However, the accuracy of the maps produced using aerial photograph interpretation (API) is low (Kilpeläinen and Tokola, 1999; Schmidt et al., 2004). For 25 years, there have been attempts to improve the accuracy of forest maps of tropical regions, but the accuracy of these products remains poor and the labour costs (the greatest cost component of the work) remain high (Schmidt et al., 2004). In an attempt to evaluate whether it is indeed possible to reduce costs and increase accuracy, a number of classifiers were used to map a tropical forest in Uganda and were compared in terms of accuracy and efficacy.

In forest classification, focus has over time evolved from a concentration on delineation of forests for timber production (Lane and McDonald, 2002) to incorporation of other purposes e.g. biomass estimation, species/genus identification (Hill, 1999; Mickelson, 1998; Wolter et al., 1995). With the focus on forested areas, new methods for identifying forest cover types have been explored over time (Hill, 1999; Horler and Ahern, 1986; Joy et al., 2003; Luckman et al., 2002; Tole, 2002).

Forest classification in Uganda has evolved from the initial identification of forested areas (Dawe, 1906) to the determination of existing forest types (Langdale-Brown et al., 1964). Initially, it was driven by management objectives i.e. to safeguard supplies of timber and other forest products, and to provide environmental services, particularly the protection of fragile mountain catchment areas. Over the years, however, nature conservation, recreation, research and education have presented additional objectives (Forest Department Uganda, 1997). The earliest forest management plan for Budongo forest was written in 1934, and later Eggeling (1947) initiated the first in-depth classification of the same forest. Other ecological studies have subsequently been carried out there (Plumptre, 1996; Sheil et al., 2000). So whereas production managers concentrated on how much timber could be extracted, ecologists focused on the interrelationships among the existing cover types.

Most research in remote sensing applications for forest ecosystems, however, has focused on parameter identification rather than the spatial relations of ecological parameters (Iverson et al., 1989). With the mounting interest in developing species diversity conservation strategies, there is a need to consider the cover variations of the area as a whole (including non-forest parts) in order to understand the spatial interrelationships of the existing cover types and provide a platform for in-depth study of the species within these cover types.

In this study, four classification methods were used, i.e. Maximum Likelihood Classifier (MLC), MLC combined with an Expert System (MaxExpert), Spectral Angle Mapper (SAM) and SAM combined with the same Expert System (SAMExpert). While MLC and SAM make use of the available spectral data, it has been shown that additional data improve classification accuracy (Bolstad and Lillesand, 1992; Iverson et al., 1989; Senoo et al., 1990). MaxExpert and SAMExpert make use of these additional data.

Through using these classification methods, two main objectives were realized, i.e. the identification of the existing vegetation cover classes and the identification of the classification method that best represents the vegetation cover on the ground for the express purpose of managing and monitoring the vegetation of such a dynamic forest-woodland-savanna (FWS) mosaic.

Thus the aim of the study was to develop and use a (combined) Spectral Angle Mapper and Expert System classifier, to compare the accuracy of the SAMExpert classifier with that of three other classifiers, and to evaluate the operational benefits of the classifier.

2.2. Materials and Methods

Fire (most frequently of anthropogenic origin) and elephants, the major modifiers of the forest patterns in Africa, have been active in Uganda, and in Budongo forest in particular, for thousands of years. The coming of the Europeans brought new controls. They suppressed and controlled fires, periodically removed large animals, and managed the forest for timber production (Sheil and Salim, 2004). These conditions have favored the expansion of the forest (Paterson, 1991).

2.2.1. Vegetation cover class recognition

Six major classes were recognized in the study area. In the field, however, data were collected for only five of these classes. The sixth class, burnt area, was no longer identifiable by the time the field data were collected and was therefore identified only on the image. The areas that were burnt could probably belong to any of the classes except forest, which is too moist to burn. Although burnt area is not a vegetation class per se, fire is part and parcel of this landscape and so it was seen fit to leave these burnt areas as an independent class.

In this classification, the woodland classes are named in an incremental way, from “closed woodland” to “very open woodland”, because the whole area is labeled “woodland” as on the current Uganda forestry maps. Here, an attempt is made to differentiate between the different woodland classes, e.g. the *Terminalia* woodland class, which has been named by several researchers, including Eggling (1947) and Sheil (1999). In this study, the *Terminalia* woodland is called open woodland.

The main criteria used for differentiating the cover classes are canopy cover percentage range, main type of woody species making up the canopy, and type and thickness of main undergrowth. The details are shown in table 2.1.

2.2.2. Data preparation

Several types of data were used in this classification, including a Landsat ETM+ image, random point data collected in the field, a digital elevation model (DEM) and percentage canopy cover. A cloud-free Landsat ETM+ image acquired in February 2002 was used. When received, the image had already been resampled to a 30-m square grid. It was then geometrically rectified to scale 1:50,000 topographic maps from the Lands and Survey Department, Uganda. However, the accuracy acquired was not very satisfactory because the maps were old and much of the infrastructure had changed. This meant additional control points had to be collected during the fieldwork period. With these, a good accuracy was obtained.

Table 2.1: Criteria used for identification of cover classes

Cover type	Canopy cover (%)	Canopy woody species	Main undergrowth
Forest	81-100	Typical forest species	Minimum to no undergrowth
Closed Woodland	51-80	Woodland species interspersed with pioneer species	*Papea carpensi* dominant
Open Woodland	31-50	Terminalia dominated woodland	*Panicum maximum* (partial cover)
Very open woodland	11-30	Mixed woodland species	*Panicum maximum* (continuous cover)
Wooded grassland	0-10	Mixed woodland species but smaller, shorter (<5m) & scattered	*Setaria* species (Continuous cover)
Burnt area	NA	NA	NA

Data collected from randomly distributed points in the study area were used as a training data set for the classification. The criteria used in identifying the individual classes in the field are indicated in table 2.1. There were 210 data points in all. These points were identified on the image before going into the field. In the field, however, data could be collected for only 185 points because the remaining 25 points belonged to the burnt area class, which by then was no longer evident in the field. The burnt area points could, however, be confidently identified on the image because of the very high contrast in reflectance between these points and other points that had vegetation cover at the time. A burnt area whose fire front was evident at the time of image acquisition provided further confirmation.

The DEM of the area was obtained from the Biomass Section of the Uganda Forest Department. It was based on 50m interval contours. Using ILWIS software, the individual layers i.e. slope, aspect, terrain position and elevation were then extracted. The topographic data were also resampled to a regular grid of 30 meters.

The percentage canopy cover layer was constructed from data collected in the field. These data (591 points) were collected using a canopy densiometer (Robert E: Lemmon, Forest Densiometers, Oklahoma, U.S.A.) following the provided guidelines. The information obtained from these points was used to create 10 canopy cover classes, each with a range of 10 values i.e. 0-10, 11-20, …., 91-100. These were used to classify the TM image. The burnt areas were considered as an additional class, numbered class 11.

2.2.3. Classification methods

Four classification methods were explored: Maximum Likelihood classifier (MLC), Spectral Angle Mapper (SAM), an Expert System method based on Bayesian theory and combined with Maximum Likelihood (MaxExpert), and the same Expert System combined with SAM (SAMExpert).

Maximum Likelihood classifier (MLC)

The roots of MLC can be traced back to electrical engineering (Nilsson, 1965). It was applied as a standard approach, as indicated in Richards (1986). A specific characteristic to note is that the decision surfaces in MLC are quadratic.

Spectral Angle Mapper

In a multidimensional space, a pixel vector has both magnitude and an angle. Spectral Angle Mapper (SAM) makes use of the angular information. Angular decision boundaries are set up based on the angular information obtained from the training data. This is then used to segment the space into classes (Richards and Jia, 1999). If the angular information for the different classes is well distributed in space, good results are obtained. If, however, magnitude is important for separating the classes, SAM may yield poor results.

Expert System

The Expert System makes use of several layers in a raster database, each layer relating to a type of evidence. For this study, the layers used included a conventional classifier output layer, DEM layers (slope, aspect, terrain position and elevation) and a percentage canopy cover layer.

The Expert System infers the most probable cover class, say $S_{a,}$ that would occur at a given pixel location $x_{i,j}$. This is done by selecting the cover class with the highest probability as the class for the pixel in question. The Expert System uses a probability rule in making this decision;

$$p(H_a|E_b) = \frac{p(E_b|H_a)p(H_a)}{p(E_b)}$$

where $P(E_b|H_a)$ is the class conditional probability. $P(H_a)$ is the probability for the hypothesis (H_a) that class S_a occurs at location $x_{i,j}$. The starting probability is obtained from the probability of the correct classification supplied by the initial classifier used, in this case either MLC or SAM. $P(E_b)$ is the probability of the evidence layer alone. It can be calculated from Bayes' theorem formula:

$$P(E_b) = \sum_{a=1}^{n} P(E_b|H_a)P(H_a)$$

This allows $P(E_b)$ to be continually updated as $P(H_a)$ is updated. Details of this method can be found in Skidmore (1989) and Schmidt et al. (2004).

To ensure that the evidence for an individual layer was treated independently of the other evidence layers, Bayes' theorem was used in the Expert System. This theorem operates on the probability of a class occurring given a single piece of evidence. With each cell, however, the same number of evidence layers was used. This ensured that the relative order of errors was the same (Naylor, 1984). The forward chaining approach was used to determine the order in which the evidence was considered. Here, running out of evidence terminated the search.

Since the rules are based on environmental relationships, which in most instances are a continuum over a landscape, they cannot be expressed with absolute certainty; rather they lie along a continuum between 0 (false) and 1 (true).

Taking a simple example of two layers i.e. the initial classifier layer and one evidence layer, an example is given of how the expert system selects the final class for a given pixel x_{ij}.

Given the class conditional probability $P(E_b|H_a)$ that pixel x_{ij} belongs to class S as,

Class	$P(E_b \mid class_s)$
Forest	0.0559
Closed woodland	0.1326
Open woodland	0.3531
Very open woodland	0.3059
Wooded grassland	0.1040
Burnt area	0.0486

with the probability given by an evidence layer that pixel x_{ij} belongs to class S as:

Class	$P(H_a)$
Forest	0.2669
Closed woodland	0.3329
Open woodland	0.1780
Very open woodland	0.2220
Wooded grassland	0.0001
Burnt area	0.0001

The expert system then uses the forward chaining approach with complete enumeration of the data to search for the class with the highest probability. Here, we are interested in the rank of the conditional probability, so we work with $P(E_b \mid H_a)P(H_a)$. The system classifies for a pixel class S as most likely:

$$\text{If } \forall H : P(H_s \mid E_{b=1} \cdots E_{b=n}) > (H_a, a \neq s \mid E_{b=1} \cdots E_{b=n})$$

In this example, the very open woodland had the highest probability (0.3059*0.2220 = 0.0679), and so it infers that pixel x_{ij} is very open woodland.

2.2.4. Preparation of the expert rule base

The rule base, which is a link between the GIS layers and the knowledge of the vegetation scientists, was generated from statistical analysis of the field plot data. It was then compared with ecological knowledge about vegetation cover in the FWS mosaic. For the relationship between the evidence layers and the cover classes, ancillary data of the field plots were used to produce expert rules. The rules were expressed as the probability of evidence of an item, say forest, occurring at a specific place e.g. slope 10.

The 210 training data points were overlaid on the ancillary data layers to produce a table of attributes for each field plot. Here, for each attribute, the histogram distribution of the field plots was divided into 10 equal percentiles. This defined the boundary layers for the expert system. The frequency per vegetation cover type, of the plots falling in each boundary layer, defined the weight for the expert rule table. These were then taken as input into the Expert System. The probability rule outputs for the layers that were used in the classification are shown in figure 2.1.

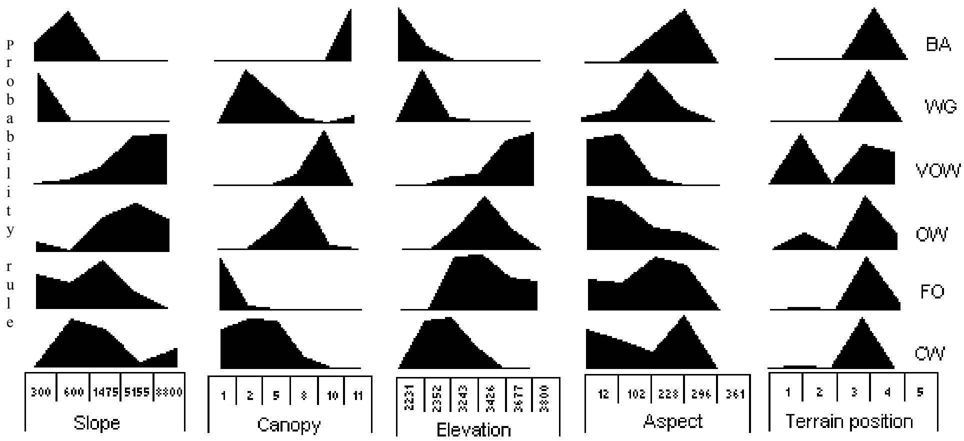

Figure 2.1: The expert rule weights for (a) Slope in cm (b) Canopy, where 1 represents a range of 90 –100%, 10 a range of 0-10% and 11 an independent class for burnt area which was no longer measurable in the field, (c) Elevation above sea level in feet; (d) Aspect, where 0 degrees is north; (e) Terrain position, where 1 = peak, 2 = Ridge, 3 = Pass, 4 = almost flat, 5 = gully. CW= Closed woodland, FO= Forest, OW= Open woodland, VOW= Very open woodland, WG= Wooded grassland and BA= Burnt area. Each interval on the y-axis represents an interval between 0 and 1 for each vegetation cover classes indicated.

2.2.5. Combining the layers within the expert system

Prior to inputting the Expert layer, standard commands of ENVI (the Environment for Visualizing Images) image-processing system are used to combine the pieces of evidence and create a single layer referred to as the "expert layer". In the expert layer, each piece of evidence is represented as an individual band. This layer is then used as the expert layer input into the Expert System. The expert system algorithm programmed using Interactive Data Language (IDL; Research Systems, Inc.) was used to combine the conventional classifier layer with the expert layer. Here, the conventional classifier occupies the position for the initial input probability. The expert layer occupies the other position provided. For the conventional classifier, both the output thematic map and its rules are required.

The programme has provision for adjusting the weight of each data layer. For the expert layer, the weight of each piece of evidence can be adjusted or even made completely inactive, if required. After adjusting the weights, the classification is then carried out. For the expert system to allocate a certain pixel to a class, say S, it combines the probabilities of the pixel being that class from all layers. If this probability is higher than the probability of the pixel being any other class, then the classifier infers that class S is the correct class.

In order to select which layers provide additional information for the classification, all layers were first used with equal strength. The obtained classification accuracy was compared with that of the conventional classifier, since it provides the initial probability. On observing that the accuracy was higher than that of the conventional classifier, it was agreed that the layers provided additional information for the classification. It was necessary, however, to test for the contribution of the individual layers.

2.2.6. Classification accuracy assessment

Accuracy assessment of the classified maps was based on an independent test data set consisting of homogeneous areas. For each class, at least 90 pixels were selected. These were located within the study area but away from where the random points were collected. There was therefore no overlap between the training and test data sets. For further validation, these areas were visited during another stint of field data collection.

Both the overall classification accuracy and the accuracies of the individual classes have been considered. While the overall classification accuracy provides a general picture of how a specific classifier is performing, the accuracies of the individual classes provide details of where misclassification may be occurring. Here, consideration of the user and producer accuracies helps to ascertain whether the classified pixel actually represents that information class on the ground (Tso and Mather, 2001). The user accuracy provides the conditional probability that an area classified as a particular cover class, say “s”, by the map is classified as class “s” by the test data. On the other hand, producer accuracy for cover class “s” provides the conditional probability that the area classified as cover class “s” by the test data is classified as class “s” by the map (Stehman, 1997). A classifier that provides high user and producer accuracies for the class in question would then be the best for classifying that class. To check whether there were significant differences between the outputs of the different classifiers, the matrices were statistically compared using the Z-statistic (Cohen, 1960).

2.3. Results

2.3.1. Classification output maps

Visually, the MaxExpert map shows a greater area covered by wooded grassland than the MLC map does (see Figure 2.2). The classified maps of (a) SAM and (b) SAMExpert are shown in figure 2.3.

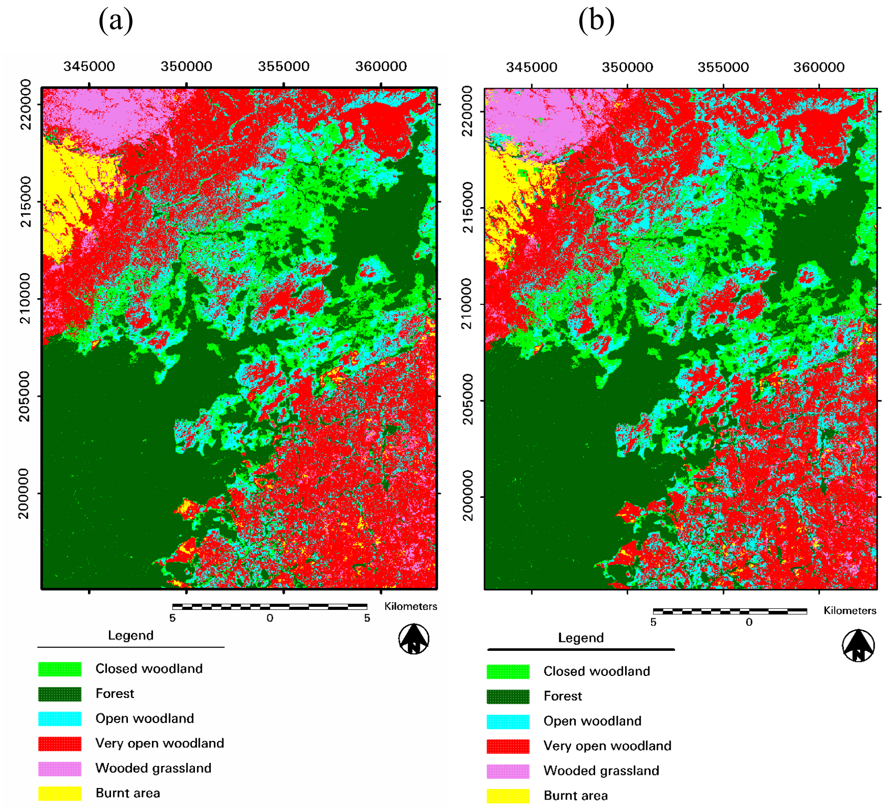

Figure 2.2: Classified maps of (a) MLC and (b) MaxExpert

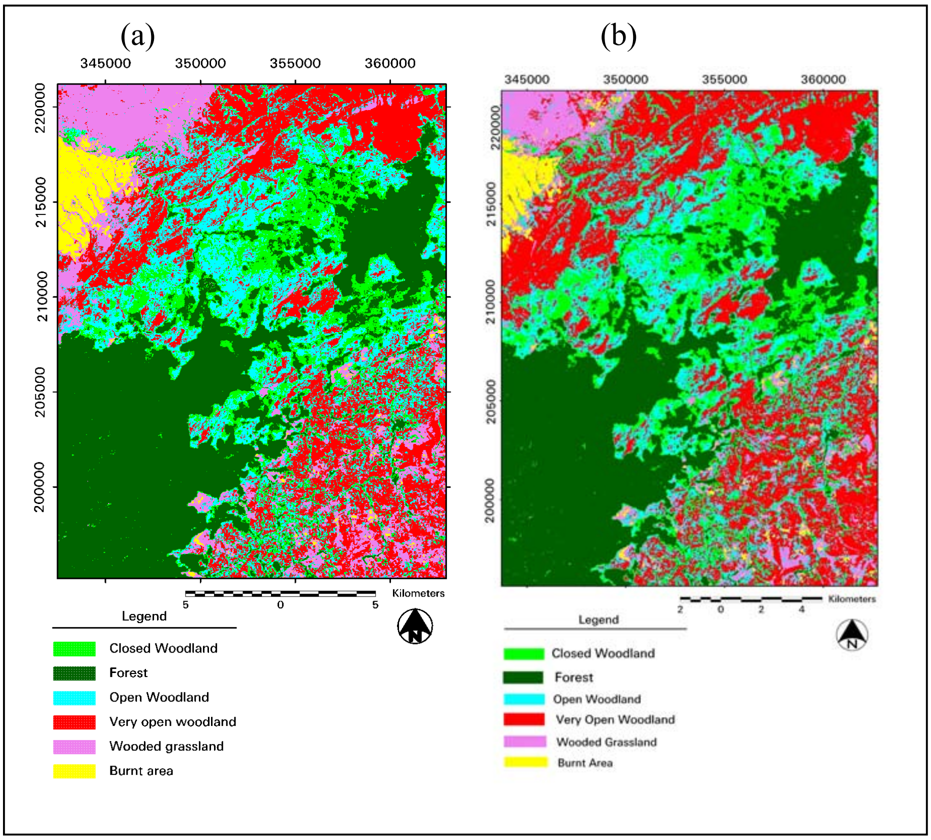

Figure 2.3: Classified maps of (a) SAM and (b) SAMExpert

2.3.2. Classification accuracy

Overall accuracy

Overall accuracy for all methods is generally high (Table 2.2). The highest, however, was obtained when using SAMExpert (94.6%), and the lowest when using MLC (78.3%).

When combining the classifier with the Expert System, not all the available data layers were used. Some layers did not provide any additional discriminatory information. With MaxExpert, slope and aspect contributed positively and with SAMExpert, slope and percentage canopy cover contributed positively.

Class accuracy

Figure 2.4 shows the percentage accuracy comparison between classes for all classification methods.

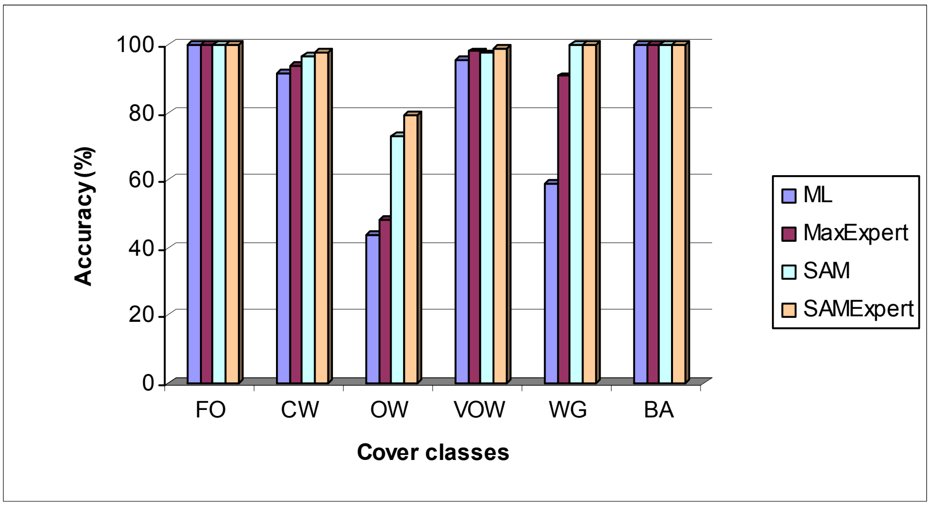

Figure 2.4: Percentage accuracy comparison between classes for all classification methods.

FO=Forest, CW=Closed Woodland, OW=Open Woodland, VOW=Very Open Woodland, WG=Wooded grassland and BA=Burnt Area.

ML=Maximum Likelihood, MaxExpert=maximum likelihood combined with the Expert System, SAM=Spectral Angle Mapper and SAMExpert=Spectral Angle Mapper combined with the Expert System.

The generally high overall accuracy (Table 2.2) is attributed to certain classes that were fully separable in all classification methods (Figure 2.4), namely forest and burnt area classes. The most poorly classified class was open woodland.

Table 2.2: Overall accuracy for the different classification methods and the Kappa statistics value for each classification method.

Classification method	**Overall accuracy (%)**	**Kappa coefficient**
Maximum Likelihood (MLC)	78.3	0.7357
MLCExpert	85.2	0.8207
SAM	92.7	0.9122
SAMExpert	94.6	0.9343

User and producer accuracy comparisons

Figure 2.5 shows comparisons of the producer and user accuracies for the woodland and wooded grassland classes. The forest and burnt area classes are not included because for all the classification methods, both the user and producer accuracies were above 90%.

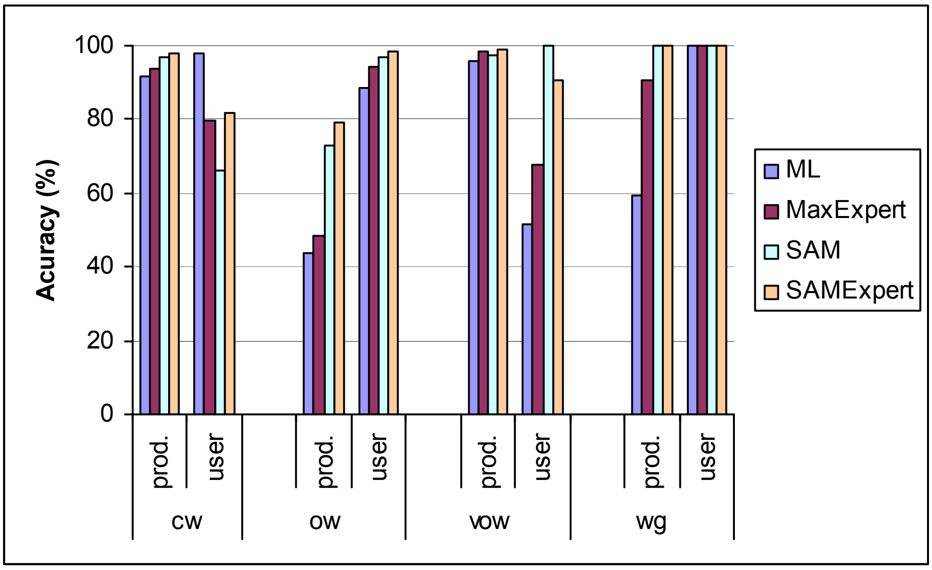

Figure 2.5: Comparisons of the Producer and User accuracies for the woodland and wooded grassland classes. The forest and burnt area are not included because for all the classification methods, both the user and producer accuracy was above 90%.

Examining the user and producer accuracies, it became evident that much of the misclassification occurred in the woodland classes. Although the closed woodland class has high producer accuracy for all classifiers, user accuracy is lower for MaxExpert and SAM. This indicates that some of the pixels classified as closed woodland by these classifiers do not belong to that class. On the other hand, the open woodland class has low producer accuracy while user accuracy is high for all classifiers. So, there is a higher probability that the pixels classified as open woodland actually belong to that class. However, many more pixels belonging to the class were omitted. As regards the very open woodland, all classifiers have high producer accuracy but MLC and MaxExpert have low user accuracy. These two classifiers add many more pixels that belong to other classes to very open woodland. SAM and SAMExpert, however, give a good representation of both the very open woodland and the wooded grassland classes (i.e. both producer and user accuracies are high).

2.4. Discussion

SAMExpert was used here for the first time in tropical forest mapping. Of all the classification methods used, SAMExpert produced the best results. It had the highest overall accuracy (94.6%) as well as the highest Kappa value (0.93), and the highest z statistic (-9.5713) was obtained when comparing SAMExpert with Maximum Likelihood (Table 3) (Dymond et al., 2002; Tso and Mather, 2001).

Table 2.3: KAPPA analysis comparison between error matrices of the classification methods used.

Classification method 1	KAPPA statistic	Classification method 2	KAPPA statistic	Z statistic
Maximum Likelihood	0.7357	MaxExpert	0.8207	-3.5532
Maximum Likelihood	0.7357	SAM	0.9122	-8.2301
Maximum Likelihood	0.7357	SAMExpert	0.9343	-9.5713
MaxExpert	0.8207	SAM	0.9122	-4.7454
MaxExpert	0.8207	SAMExpert	0.9343	-6.1394
SAM	0.9122	SAMExpert	0.9343	-1.4586

Combining each of the conventional classifiers with the expert system resulted in higher accuracies. With MaxExpert, there was an increase of 7%, while with SAMExpert there was an increase of 1.9%. The DEM layers and canopy cover layer used in the Expert System provided extra information that complemented the spectral information. Use of this additional information resulted in better discrimination of the classes that may otherwise have been difficult to classify. Iverson et al (1989), Skidmore (1989), Senoo et al (1990), and Schmidt et al (2004), also observed this advantage of using additional data layers when using an expert system.

Looking at individual classes, MaxExpert allowed an accurate delineation of the wooded grassland class; the accuracy improved from 59.2% to 90.8%. Figure 2.1 shows that the wooded grassland class is quite distinct in the slope layer of the Expert System. SAMExpert, however, produced a negligible improvement on the accuracy of the individual classes. Its main positive effect is noted when one looks at producer versus user accuracy. Here, although SAM had a high producer accuracy (96.88%) for closed woodland, the user accuracy was low (65.96%). When SAMExpert was used, the user accuracy for this class was improved by 16%. In essence, SAMExpert has provided a much more accurate mapping for this class.

With all classification methods, the open woodland class had the lowest classification accuracy. Class accuracy improved when the expert system was combined with the conventional classifiers. When combining the expert system with MLC, the accuracy improved by 4.5%; with SAMExpert the accuracy improved by 6.2%. The almost pure *Terminalia* stand occurs as a narrow strip after which the species is mixed with other species occurring in the closed woodland on one side or the very open woodland on the other side. The additional information, particularly canopy cover, gave extra discriminatory power for this class (Figure 2.1).

It should be noted, however, that while several DEM layers were available, only slope and aspect provided positive information for MaxExpert and only slope provided positive information for SAMExpert. This shows that, although the DEM is the most common additional data used in vegetation classification, it should not be taken for granted that all derived terrain layers are beneficial to every classification.

The high accuracies obtained can be attributed partly to differences in the spectral properties of the cover types and the strengths of Landsat ETM+ MIR bands 5 and 7, which are able to discriminate between vegetation of varying moisture levels (Thenkabail et al., 2003). Differences in moisture level are most pronounced during the dry season, and our image was acquired during the driest time of the year. This greatly contributed to the high accuracy. The existence of a closed canopy, streams and deeper shadows in the forest results in moist canopy conditions. In contrast, the burnt area is completely open and had very low moisture levels.

The spectral properties of the forest are highly correlated with changes in species composition and stand structure (Boyd et al., 1999; Vieira et al., 2003). During data collection, it was observed that there is almost a discrete difference in species composition between forest and other cover types. Within the other cover classes, the variation is gradual but still evident. So, combining the moisture difference and the spectral property differences of the classes resulted in the classes at the extreme ends of the spectral and moisture spectrum (i.e. forest and burnt area) being completely separable (Figure 2.4). This corresponds with the findings of Achard and Estreguil (1995), who pointed out that classification accuracy is related to the unambiguous association between spectral signatures and particular vegetation classes.

The classes that are most mixed are the woodland classes. From the maps, these classes tend to occur next to one another. It was observed in the field that, although each of these classes had certain characteristic species that were most abundant, the three classes shared many species. Bauer et al. (1994), when classifying the forests of Minnesota, also observed that misclassification occurred mostly between related classes.

Five vegetation cover classes and one non-vegetation cover class were identified. The non-vegetation class is a representation of the disturbance factor, fire. Of the five vegetation classes, forest has been studied intensively by earlier researchers (Eggeling, 1947; Plumptre, 1996; Sheil, 1999; Sheil et al., 2000), and the ecologically separable classes within it have been identified. The woodland area has received little attention, however, and its existent classes had never been identified. The woodland area has over time been classified as one entity but, through this study, three classes of woodland plus a wooded grassland class have been identified. The SAMExpert classifier produced the best classification results with an overall accuracy of 94.6%. The identification of the vegetation classes existing in the area and at such high accuracy now provides managers and planners with a resource that can be used for making management plans and for monitoring the impact of management practices through identifying changes in land cover. The obtained maps will also be a useful resource for studying the compositional relationships of the vegetation cover classes, as well as variations within the vegetation cover classes.

CHAPTER 3

TREE COMPOSITION OF A DYNAMIC FOREST-WOODLAND-SAVANNA MOSAIC IN UGANDA: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT.

Abstract

Forest-woodland-savanna mosaics are a common feature in the East African landscape. For the conservation of the woody species that occur in such landscapes, the species patterns and the factors that maintain it need to be understood. We studied the woody species distribution in a forest-woodland-savanna mosaic in Budongo Forest Reserve, Uganda. The existing vegetation gradients were analysed using data from a total of 591 plots of 400 or 500m^2 each. Remotely sensed data was used to explore current vegetation cover and the gradients there in for the whole area.

The area shows a clear species gradient ranging from forest, where there is least disturbance, to wooded grassland, where frequent fire disturbance occurs. Most species are not restricted to a specific part of the gradient although many show a maximum abundance at some point along the gradient. Fire and accessibility to the protected area were strongly related to species turnover along the ordination axis with species like *Cynometra alexandri* and *Uvariopsis congensis* occurring at one end of the gradient and *Combretum guenzii* and *Lonchocarpus laxiflorus* at the other. The vegetation cover classes identified in the area were differentiated in terms of diversity, density and, especially, basal area.

All vegetation cover classes, except open woodland, had indicator species with *Diospyros abyssinica, Uvariopsis congensis, Holoptelea grandis* and all *Celtis* species for the forest class, *Terminalia velutina* and *Albizia grandibracteata* for closed woodland, *Grewia mollis* and *Combretum molle* for very open woodland and *Lonchocarpus laxiflorus*, *Grewia bicolor* and *Combretum guenzii* for the wooded grassland class. Eleven of the species occurred in all cover classes and most of the species that occurred in more than one vegetation cover class showed peak abundance in a specific cover class.

For conservation of the full range of the species within the mosaic, all existent vegetation cover classes need to be considered. Burning should be managed in such a way that the different vegetation cover classes of the mosaic are maintained.

Key words: Budongo Forest Reserve, fire disturbance, Forest-woodland-savanna mosaics, Intermediate Disturbance Hypothesis, Tree composition, species gradient

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Based on Grace Nangendo, Hans ter Steege, Frans Bongers (*Submitted)* Tree composition of a dynamic forest-woodland-savanna mosaic in Uganda: implications for conservation and management.

3.1. Introduction

Large areas of East Africa are covered with forest-woodland-savanna (FWS) mosaics. Fire, both of natural and anthropogenic origin, is typical for the woodland-savanna part of the mosaic (Walter, 1985). The fresh grass that re-grows after the fire is advantageous for the many ungulates of East Africa and many of these ecosystems are, therefore, managed mainly for wildlife conservation. Forests, on the other hand, are managed for timber production, for woody species conservation, as water catchment areas and for their aesthetic values e.g. the large trees they host. Consequently the forest and the woodland-savanna areas, even where they occur together as a mosaic, are often treated as independent conservation entities.

Uganda is endowed with large tracts of the FWS mosaics. Several of the FWS mosaics have been enlisted for gazetting as conservation areas because of their high biodiversity value (Forest Department Uganda, 1999), yet surveys in such areas have focused on the forest and have not taken the woodland-savanna areas into account. Although forests are arguably richer in species (Sheil and Burslem, 2003), this does not do justice to the specific flora and fauna found in woodlands and savannas that are adjacent to or within the forests.

In our study area, Budongo Forest Reserve, fire has been used as a management tool in the woodland areas for hundreds of years (Paterson, 1991). The local people, resident on the outskirts of the forest reserve, set most of the fires. Changes in management of the area, which resulted in more active policing of the protected area, and the establishment of a gate entrance to the only access route, have led to less use of fire in the woodland-savanna areas. As a consequence, forest vegetation is now colonizing the woodland-savanna areas (van Straaten, 2003). It is unknown to what extent accessibility to the protected area acts as a controlling factor. As specific floristic information for the area is lacking, it is as yet unknown what the effects of continuing reforestation will be on the tree diversity of Budongo Forest Reserve. In this paper we explore the current status of the forest in terms of species composition and diversity and, how the species are distributed.

Studies that have explored the species interrelationship within FWS mosaics are rare (Hovestadt et al., 1999). Most studies have concentrated on species distribution within the forest (Eggeling, 1947; Eilu et al., 2004; Mwami and McNeilage, 2003; Sheil et al., 2000) or the woodland-savanna (Li et al., 2004; Schwartz and Caro, 2003; Schwilk et al., 1997; Swaine et al., 1992). Previous data of Budongo forest (Eggeling, 1947) stimulated the emergence of the important Intermediate Disturbance Hypothesis (Connell, 1978). At the time when Eggeling carried out his study, much burning was being carried out and had arrested the forest expansion into the woodland. Eggeling's gradient mainly reflects the succession within the forested area. With the increased control of burning over the years, resulting in variation of burning with some areas burnt more often than others, forest expansion into the woodland became possible. Hence, an added component of our study is the extension of a historically important succession gradient, exploring its range into the woodland-savanna areas.

In this study special emphasis will be put on how the existent vegetation types can be characterized in terms of the woody plants they hold and the implication of the observed species patterns to conservation of woody plants in such landscapes. An assumption made here is that all the vegetation types that exist within the study area, and the species they support, are an integral part of a compositional/successional gradient that stretches across the FWS mosaic. We ask the following questions: Is it possible to quantify the gradient? What species are specific for certain areas? How does the species composition vary along the succession gradient? Can the gradient be explained in relation to environmental variables?

A further question we address is whether a satellite image classification of the area can be used to adequately map the vegetation and its composition in the area. For this we made use of discrete vegetation cover classes, obtained from a classification carried out using a combination of spectral information and environmental variables' information (Chapter 2). The vegetation cover classes are considered a proxy of the vegetation types found in the area. Standard vegetation indices (NDVI and Tasseled Cap vegetation index) based on the same image were also compared in their ability to explain the observed gradient. Finally, we discuss the conservation and management implications of the results obtained.

3.2. Materials and methods

In the woodland-savanna areas, fire has been prevalent for hundreds of years (Paterson, 1991). The woodland burning was initially carried out by the local people for purposes of hunting and refreshing grass for both domestic and wild ungulates (Buechner and Dawkins, 1961). With the transfer of the control of the woodlands from the local people (Bunyoro Kingdom) to the central government (Forest Department) in 1968, measures to control burning were put in place (Forest Department Uganda, 1997). These were not very effective, however, until the establishment of the joint management between Forest Department and Uganda Wildlife Authority in the mid 1980s. Fewer, and smaller, areas are now burnt and the burning is also less frequent. The woodland-savanna is therefore heterogeneous and it is made up of vegetation patches at varying stages of recovery since they were last burnt.

3.2.1. Data collection

Data was collected from 591 plots, 265 of which had an area of 400m^2 and 326 with an area of 500m^2. All data was collected during the same period (August to October 2002). Along a transect, perpendicular lines were laid every 300m. Along each perpendicular line, data was collected at every 75 meters. For sites 1 to 5, a plot size of 400m^2 was used (Figure 3.1), while for sites a to e, it was 500m^2. Based on a 2002 satellite image of the study area, sites 1 to 5 were located in areas that showed a similar spectral reflectance whereas sites a to e were located in areas that showed varying spectral reflectance. The variation of the site locations was to ensure that we capture as much as possible of the species variation within the area. In each plot the following data were collected:

- Plot coordinates
- Species names, diameter at breast height (DBH) for all woody plants ≥10 cm DBH, measured at 130cm
- Canopy cover percentage, using a canopy densiometer (Robert E: Lemmon, Forest Densiometers, Oklahoma, U.S.A.), following the provided guidelines. Four measurements were taken in each plot and an average of these measurements was calculated to determine the final canopy cover of the plot.
- A fire indicator value. The fire indicator value was based on several factors (1) the degree of scorching on the woody stems i.e. if it was fresh or old, (2) if there existed remains of burnt grass in the undergrowth and (3) whether fresh ash was found in the area. Plots with fresh fire scorching on the woody stems, remains of burnt grass or ash were recorded as "recent burns" and labelled class 2. Plots with old signs of fire were labelled class 1 (old fires) and plots with no sign of fire were labelled class 0 (no fire).

Species identification was based on Eggeling and Dale (1952) and Hamilton (1991). Samples of the species that could not be clearly identified in the field by the botanist on the team were sent to the Uganda National Herbarium where they were identified.

3.2.2. Data preparation

A Detrended Correspondence Analysis (DCA) (Multi-Variate Statistical Package (MVSP) 3.11, Kovach Computing Services, UK) was run using the two data sets i.e. for the 400m^2 plots and the 500m^2 plots. When the plot scores of DCA axis one and two were plotted together, using a separate symbol for each plot size, the data for the two sets fell within the same range i.e. they showed near to identical results and complemented each other. As the plots also overlap spatially, and in terms of species composition, it was therefore decided to pool the two data sets. Plots with less than 10 individuals were removed from the data. As the larger plots have more individuals and thus capture more species on average than the smaller plots, rare species, defined as those having a total of less than 25 individuals, were also removed from the data set. The final dataset consisted of 491 plots with 45 species.

Expressing density as the number of trees per 1000m^2, the abundance values were calculated for each plot. From the DBH values measured in the field, basal area (BA, m^2 ha^{-1}) was calculated for each plot, including all trees of the actual plot data. Two diversity indices, Fisher's α (Fisher et al., 1943) and

Simpson index (Magurran, 1988) were also calculated. These indices have low sensitivity to plot size difference (Magurran, 1988).

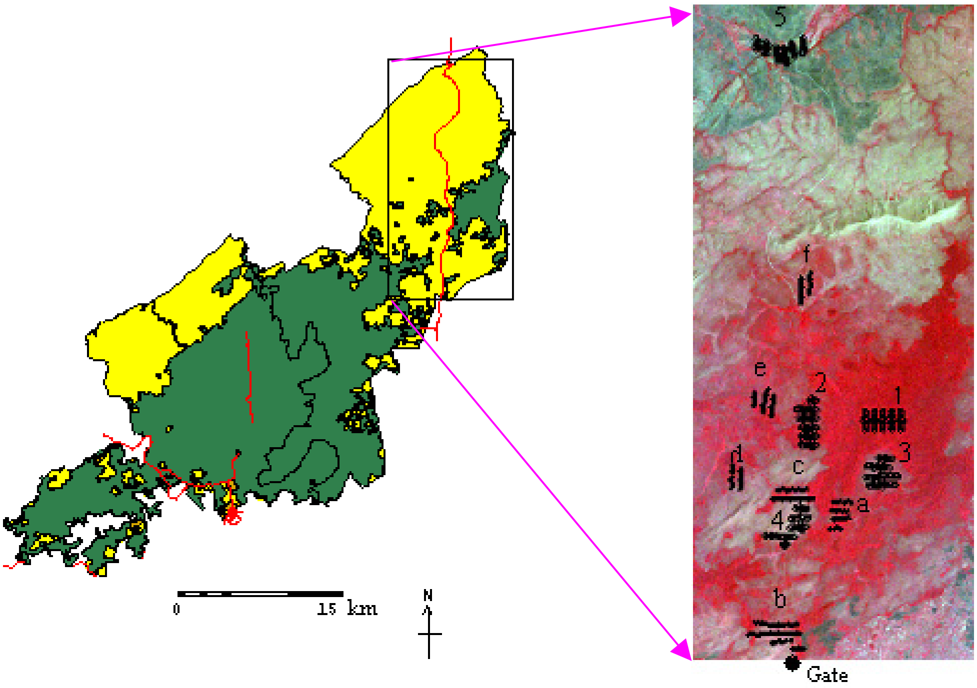

Figure 3.1: The location of the data collection points. 1,2,3,4 and 5 are locations where the plots were 400m² and a, b, c, d, e and f are locations where the plot size was 500m².

3.2.3. Remote sensing data

Values of the Normalized Difference Vegetation Index (NDVI), which is well correlated with vegetation biomass (Tucker, 1979) and Tasseled Cap vegetation index (TC), which has a good correlation with forest stand density (Crist et al., 1986), were extracted for each plot from the respective vegetation index maps calculated using a 2002 Landsat ETM+ satellite image. These values were used for further analyses. Vegetation indices provide values that are indicative of the spectral reflectance of the vegetation at a given place. Depending on the satellite image bands selected and the ratios used, each vegetation index measure will result in a different value for a specific plot. Because there is a high variation in reflectance over a forested area, the resultant pixel values for a given index vary from point to point resulting in continuous values over the forested area.

Vegetation cover class values for each plot were extracted from a vegetation cover map of the area obtained from an earlier classification (Chapter 2) of a Landsat +ETM image using both spectral and environmental information.

3.2.4. Accessibility

We used distance from the southern forest boundary to each plot as a surrogate for accessibility, by the local people, to the sampled areas. The conservation area gate marks the southern boundary between the conservation area and the local people's settlements. From here on, distance will be referred to as "distance from gate".

During fieldwork, it was observed that because of the gate control, the local people entered the protected area at other points along the boundary of the protected area, instead of using the road. Having recorded the coordinate of the gate location, an east-west line was established at this point and distance for each plot was calculated based on this line. This provided the plot distance relative to the conservation area gate.

All 591 plots were separated into the discrete cover classes (forest, closed woodland, open woodland, very open woodland and wooded grassland) based on a classification of the area (Chapter 2). Having used a Landsat satellite image, with a pixel size of 30m, in the classification, the minimum area belonging to a specific cover class is 900m^2. Species composition, diversity and forest structure were analyzed in consideration of the vegetation cover class in which each plot fell with the assumption that these vegetation cover classes were representative of the major vegetation variation within the area.

3.2.5. Analysing the gradient

To explore the species distribution within the study area, we used Detrended Correspondence Analysis (DCA). To determine which variables best explained the gradient in species composition, the plot scores on the DCA axes were related to the environmental variables using stepwise regression.

3.2.6. Linking remote sensing with the gradient

In analysing remote sensing outputs, two approaches were used. First, plot values obtained from vegetation indices (such as TC), which are continuous classifiers, were compared to DCA plot scores. To identify the vegetation index that best explained the gradient, a non-linear regression method was used since the scatter plot of the DCA versus the index values showed a non-linear relationship. Second, discrete classes obtained from an earlier classification (Chapter 2) were analysed for differences in terms of species composition and diversity and, in basal area. Although the same satellite image was used for the classification and for the creation of the vegetation index maps, it needs to be noted that the plots used for the classification are not the same as those used in the analysis in this paper.

3.2.7. Differences in composition

To test for differences in composition between the different vegetation units we used the Multiple-Response Permutation Procedure (MRPP) and Indicator Species Analysis of PC-ORD (McCune et al., 2002; McCune and Mefford, 1999). MRPP is a non-parametric procedure that can be used for testing the hypothesis that no difference exists in composition between two or more groups of plots. For distance in composition between the plots we used Relative Sørensen (Bray-Curtis) (Magurran, 1988), as it takes both composition (presence-absence of species) and abundance into account. For weighting option: $C_I = n_I / \sum n_I$ was used, which is the most widely used and recommended measure. C_I is the weight and is dependent on the number of items in a group, say ${}_I$, and n_I is the number of items in group ${}_I$. The software uses 9999 permutations in the test. Two tests were carried out based on a-priori selection: vegetation cover classes and fire classes. An Indicator Species Analysis was also carried out on the basis of these two classifications.

Diversity of the plots was expressed in two ways: Species dominance, which was calculated with the Simpson Index (SI) (Magurran, 1988) and Fisher's α (Fα), (Fisher et al., 1943). These indices have low sensitivity to plot size differences (Magurran, 1988). Differences between plots in different fire and vegetation cover classes with respect to SI, Fα and BA were tested with ANOVA using SPSS (SPSS 10, SPSS Inc. USA).

3.3. Results

3.3.1. Species distribution

A total of 591 plots were sampled in the field. On these plots we found 26,076 individuals from 121 species, 89 genera and 38 families. The most species-rich family was Moraceae with 11% of all species found (13), followed by Euphorbiaceae and Mimosaceae with 8% each (10). The most species-rich genus was *Ficus* with 5% of all species (6), followed by *Acacia*, *Albizia*, *Celtis* and *Combretum* with 3% each (4). Nine species could not be identified to genus level, this accounted for 7% of all species. A full species list with abundances is given in appendix 3. The most abundant genus, in terms of total individuals encountered, was *Combretum*, with close to 16% of all individuals, followed by *Terminalia* (14%), *Grewia* (13), *Stereospermum* (6%), and *Uvariopsis* (6%).

The DCA analysis ordered the plots mainly along axis 1 (Figure 3.2a). This axis had a relatively high eigenvalue (0.465) suggesting significant woody plant variation along this axis. The eigenvalue for the second axis was 0.172. With 491 plots included, axis 1 explained 11.8% of the variation. There was, however, one outlier plot strongly influencing the second axis. This outlier plot was dominated by *Sapium ellipticum*, a species that hardly occurred elsewhere in the study area. After removing this plot, axis 1 explained 12.5% of the variation and axis 2 an additional 4.6%. This is the actual result presented in Figure 3.2a. Plots with a low axis score (close to 0) are found in the forest area, plots with a high score (> 7) are found in the most open areas. As most of the discussion here on will pertain to axis 1, the main gradient, we will abbreviate 'DCA axis 1 plot scores' to 'DCA scores'.

The species plot (Figure 3.2b) also shows most of the variation along the first axis. The effect of the second axis is only evident close to zero along axis 1, the forest side, where there appear to be two groups (the same can be said for the plot scores). Based on this interpretation the species can be divided into three groups; A, B and C (Figure 3.2b). Groups A and B occur within the forest area and group C, probably starting at the forest edge, stretches through to the woodland-savanna area. Species found in group A include *Cynometra alexandri*, *Diospyros abyssinica* and *Khaya anthotheca*. Group B species include *Uvariopsis congensis, Celtis wightii, Holoptelea grandis* and *Funtumia elastica.* And species found in group C include *Albizia grandibracteata, Terminalia velutina, Grewia mollis, Combretum molle* and *Lonchocarpus laxiflorus*.

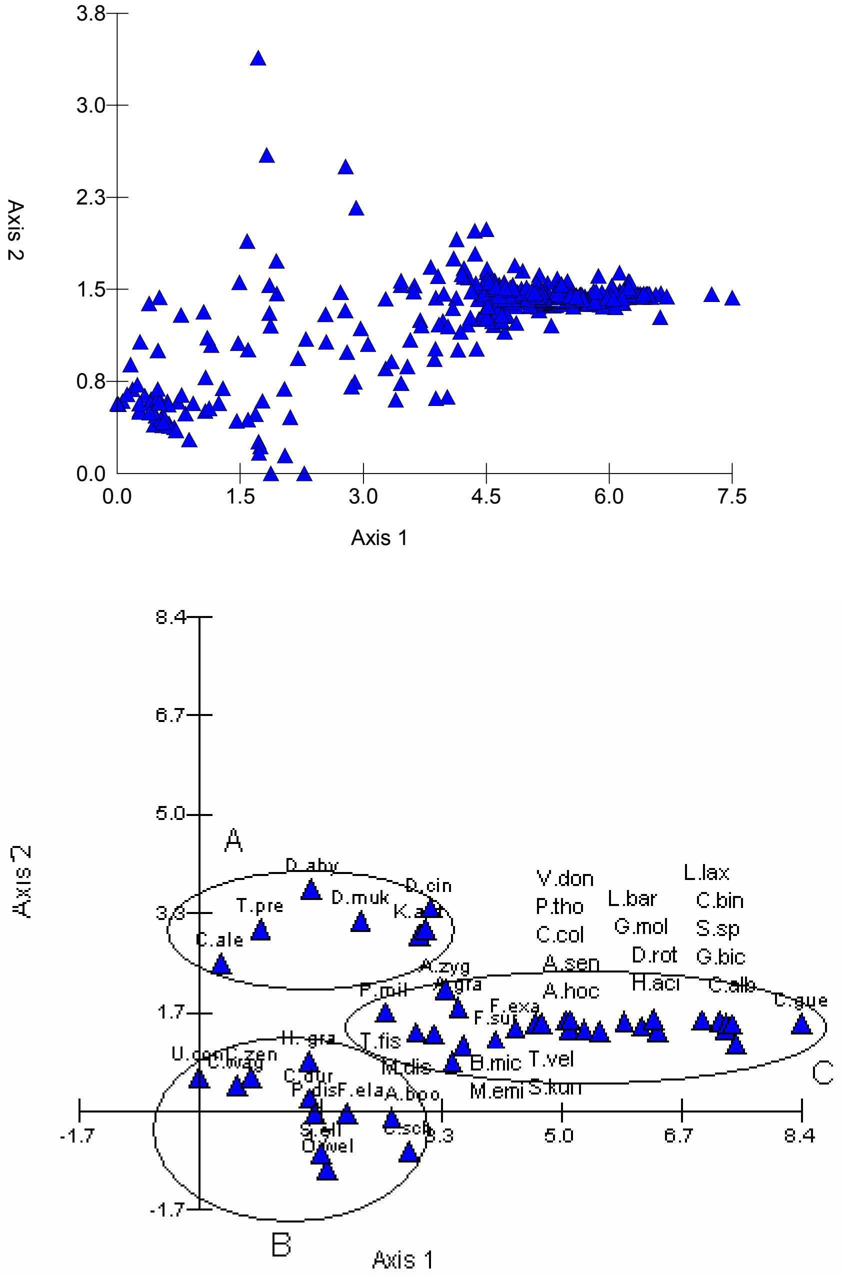

Figure 3.2: DCA graph showing (a) plot composition variation (b) species composition variation along the first two ordination axes. The full names of each of the species in b are listed in appendix 4.

Fire indicator best explained the gradient in species composition followed by slope and then distance from gate (Table 3.1). Vegetation cover class was not significant and so it does not appear in the results table. Relating the site variables individually to DCA (results not shown) showed that whereas all the other variables had a positive correlation with the DCA, distance from gate had a negative correlation.

Table 3.1: Model output for a stepwise regression between DCA axis 1, indicating the major vegetation composition gradient, and the site variables; fire indicator, slope and distance from gate.

Model	R	R Square	Adjusted R Square	Std. Error
1	0.569	0.324	0.323	1.395
2	0.595	0.354	0.351	1.365
3	0.599	0.359	0.355	1.361

1 Predictors: Fire indicator
2 Predictors: Fire indicator, slope
3 Predictors: Fire indicator, Slope, distance from gate

3.3.2. Species composition and vegetation indices

All the vegetation-indices explained well the DCA variation but TC-wetness showed the best relationship with DCA scores (Table 3.2). Its statistic could explain nearly 3 quarters of the variation in the DCA scores.

Table 3.2: R^2 values indicating correlation between DCA axis 1 and the vegetation indices. Having observed that the relationship between DCA and the indices was not linear, a second order polynomial was fitted on each scatter plot and the r^2 was obtained.

Index measures	DCA Axis 1
NDVI	0.64
Tasseled cap (brightness)	0.46
Tasseled cap (greenness)	0.70
Tasseled cap (wetness)	0.73

3.3.3. Species distribution in discrete vegetation cover classes

The classes derived from the analyses of the satellite image differed considerably in their DCA scores (Figure 3.3a,b). Plots of the ‘No-fire’ class had consistently low DCA scores, whereas the plots from the class ‘Recent-fire’ have high DCA scores. Plots from the class ‘Old-fire’ were intermediate. The Fire classes also differed considerably in their TC-greenness values. Consequently a combination of DCA scores and TC-greenness value segregated the fire classes well (Figure 3.3a).

A similar result was found for the cover classes. These classes are segregated both by their DCA scores and TC-greenness values (Figure 3.3b).

Plots of different fire classes also differed significantly in their species composition (MRPP, A = 0.061, p << 0.0001). *Uvariopsis congensis, Celtis wightii, Diospyros abyssinica, Phyllanthus discoideus, Celtis zenkeri, Alstonia boonei, Cynometra alexandri* and *Trichilia prieuriana*, all exclusively occur in the No-fire class i.e. relative abundance (RA) equals 100% for each of the species. The indicator species analysis also identified the above named species as indicators for the No-fire class i.e. significant p values (Appendix 1). Although no species occurred in all plots i.e. had 100% relative frequency in any class, *Terminalia velutina* and *Grewia mollis* had very high relative frequency, 90% and 87%, in Old-fire and Recent-fire classes respectively. For the Old-fire class, species that had significant species indicator values include *Terminalia velutina, Stereospermum kunthianum* and *Piliostigma thoningii*. And for the Recent-fire, species that had significant species indicator values include *Grewia mollis, Annona senegalensis*, *Combretum molle*, *Loncocarpus laxiflorus* and *Grewia bicolor*.

Whereas in the forest some of the species that had the highest relative frequency are part of those that had the highest relative abundance, it is different for the other vegetation cover classes. In the closed woodland, the species with the highest relative abundance were *Bridelia michrantha* (70%), *Albizia grandibracteata* (55%) and *Maesopsis eminii* (55%). In the open woodland there were no species with relative abundance above 50%. The highest was *Ficus exasperata* with 48%. In the very open woodland, *Dombeya rotundifolia, Combretum molle and Securinega virosa* had the highest relative abundance with 75%, 74% and 71% respectively. *Combretum guenzii* exclusively occurred in the wooded grassland. Other species with high relative abundance in the wooded grassland were *Combretum binderanun*, *Grewia bicolor*, *Lonchocarpus laxiflorus* and *Hymenocardia acida* with 78%, 66%, 58% and 50% respectively.

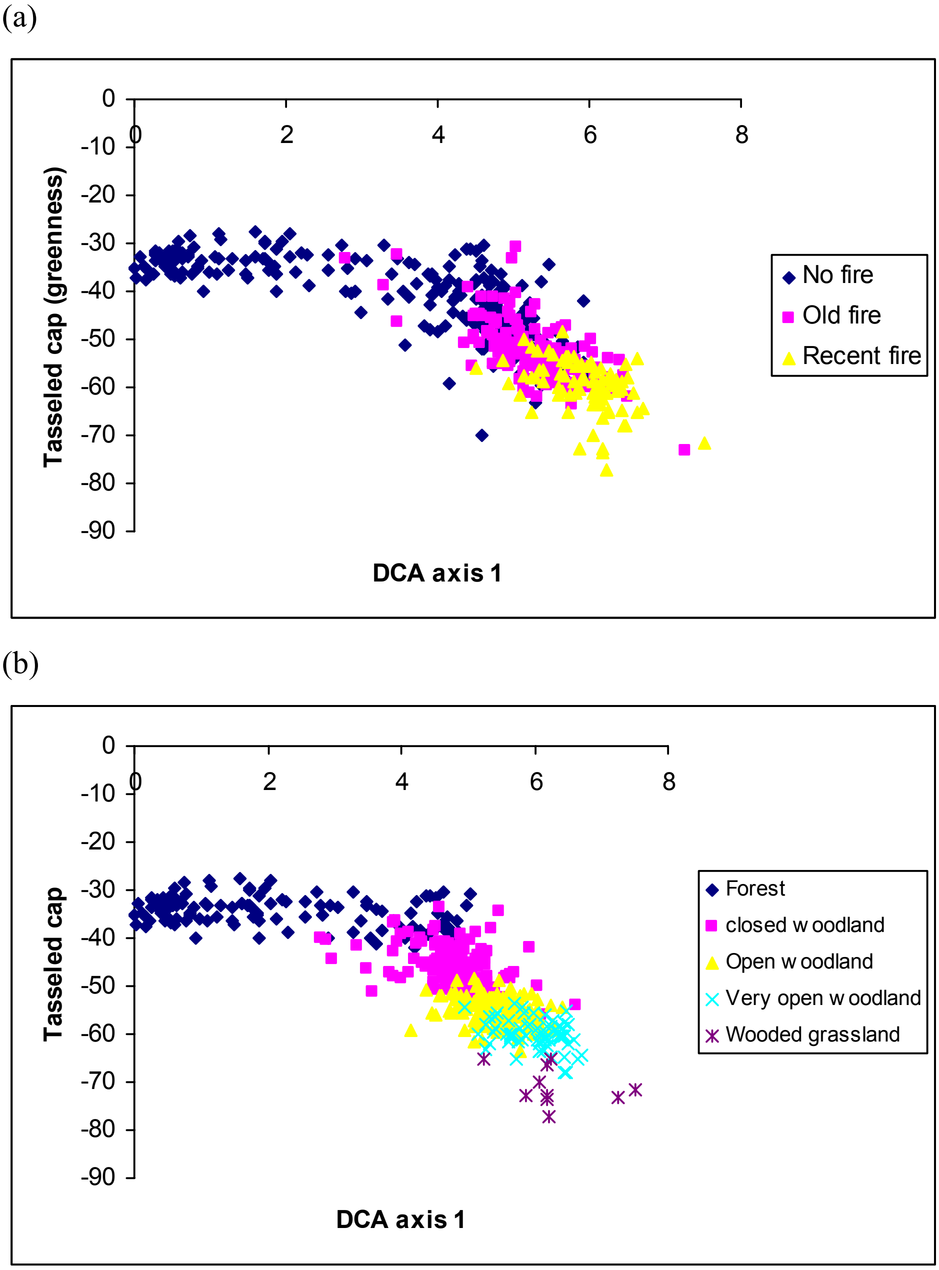

Figure 3.3: DCA axis 1-Tasseled Cap relationship as subdivided by (a) fire regimes and (b) vegetation cover classes

Most of the species identified as belonging to groups A and B e.g. *Cynometra alexandri, Khaya anthotheca, Diospyros abyssinica, Uvariopsis congensis* and *Holoptelea grandis* (Figure 3.2b) were also identified through indicator species analysis as good indicators for the No-fire class. Of these, *Diospyros abyssinica, Uvariopsis congensis, Holoptelea grandis* and all *Celtis* species were also good indicators of the forest class (Appendix 2). The species in group C belonged both to Old-fire and Recent-fire classes. Considering the cover classes, *Terminalia velutina* and *Albizia grandibracteata* were good indicators for closed woodland, *Grewia mollis* and *Combretum molle* for very open woodland and *Lonchocarpus laxiflorus, Grewia bicolor* and *Combretum guenzii* were good indicators for the wooded grassland class. Several of these species e.g. *Uvariopsis congensis, Terminalia velutina* and *Grewia mollis* have distinctively high abundance in specific areas along the gradient (Figure 3.4).

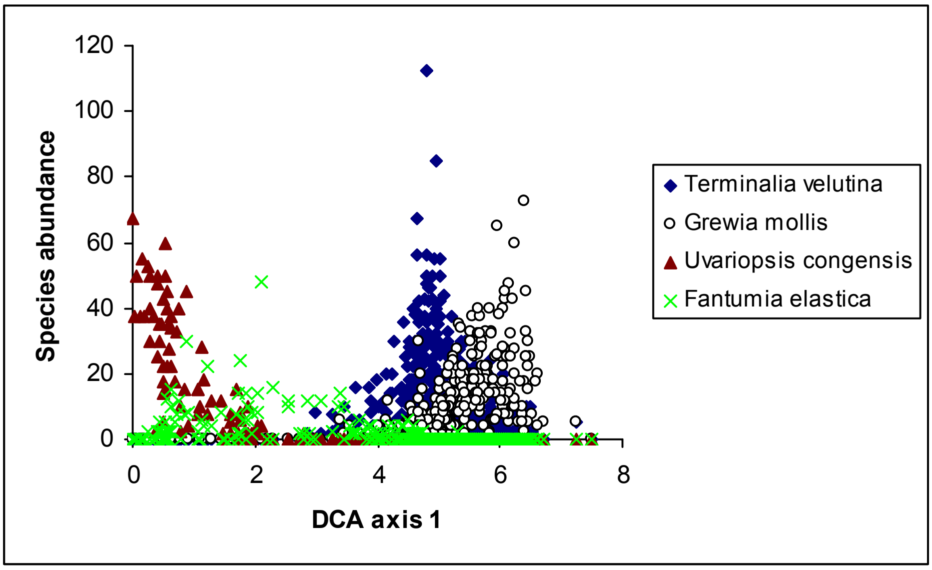

Figure 3.4: Relationship between DCA axis 1 and some of the most abundant species whose maximum abundance occur in different areas along the gradient. The selected species also display a variation in their distribution range.

Although the closed woodland had the largest area sampled followed by the open woodland, the forest had the highest number of species and genera identified (Appendix 3). The lowest number of species and genera was found in the wooded grassland. The highest ratio of species to genera was in very open woodland (1.4) and the lowest in wooded grassland (1.2). 11 species occur in all classes and most the species occur in more than one cover class but their abundance varies greatly between classes. Forest and closed woodland classes had an equal number of families and wooded grassland class had the lowest number of families.

The Simpson index of all vegetation classes differed only slightly except that of wooded grassland (Figure 3.5a). The wooded grassland had the highest value and the highest standard error. The forest class had the highest mean

Fisher's alpha (Figure 3.5b) followed by the closed woodland class. These two classes were significantly different from each other. The open woodland was not significantly different from the wooded grassland. The wooded grassland had the lowest Fisher's alpha.

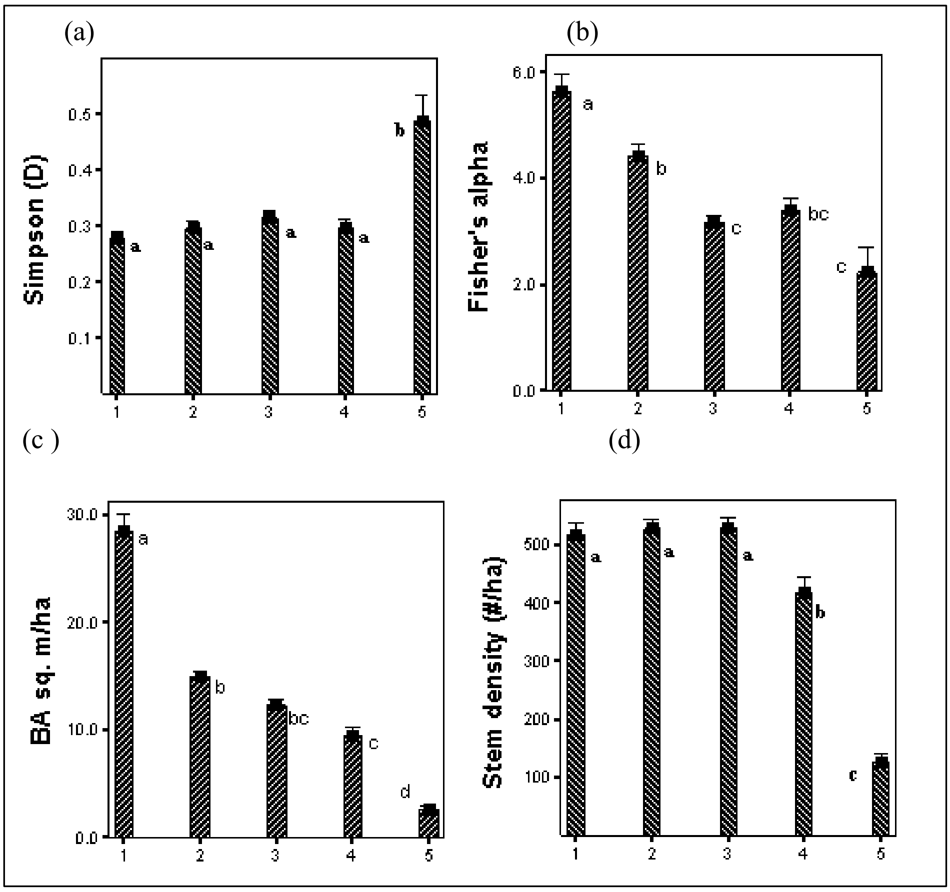

Figure 3.5: Comparison of cover class mean and standard deviation for (a) Simpson index, (b) Fisher's alpha, (c) basal area and (d) stem density. The class numbers consistently represent 1=forest, 2=closed woodland, 3=open woodland, 4=very open woodland and 5=wooded grassland. The letters beside each bar indicate significance differences. Bars, for a specific variable, which have the same letter mean that they are not significantly different. (ANOVA: p=0.05)

The basal area (Figure 3.5c) decreased from the forest, which had the highest value, to the wooded grassland, which had the lowest. The forest also showed the highest variation. All cover classes were significantly different from each other. The mean stem density values for the forest, closed woodland and open woodland were very close (Figure 3.5d) and there was no significant difference between them. The very open woodland also had a high mean value although slightly lower than the other 3. The wooded grassland is much lower than all others. The very open woodland and the wooded grassland are each significantly different from all others. So while many individual trees may be found in each cover type, they vary in size with the forest having larger diameter trees than any of the other cover classes. Details of the species occurring in each cover type and their abundance are given in Appendix 3.

3.4. Discussion

Although the existence of a forest-woodland-savanna (FWS) gradient is well documented (Huston, 1994a) studies have overtime explored species variation on parts of the gradient only. Information exploring the interrelationship of the species along the whole gradient is lacking. Our analysis confirmed the existence of a clear gradient along which all plots were systematically aligned. Despite the gradient being visibly evident, the percentage of explained variation is not very high. This is mainly because the gradient is a continuum (Balvanera et al., 2002) and the species composition gradually changes along the gradient i.e. there is no separation of groups along the gradient. Most of the species are found in several cover classes but their relative abundances differ.

3.4.1. Variation in species composition along the gradient

The species composition along the gradient gradually changes from species that attain maximum abundance in areas of minimum disturbance e.g. *Cynometra alexandri* and *Uvariopsis congensis* to species that attain maximum abundance in areas with frequent disturbance e.g. *Grewia mollis*. On the other hand, species like *Terminalia velutina* attain maximum abundance in the moderately disturbed areas (Smart et al., 1985). Many species, as evidenced by the species abundance plot (Figure 3.4), are wide ranging although they have a clear optimum (Huston, 1994a), which occurs at species specific locations along the gradient. Identification of a vegetation class should, therefore, be based on species abundance proportions other than species incidence alone. This variation in species tolerance range has also been observed in a Mexican dry forest (Balvanera et al., 2002). In another study (Chapter 5), it was observed that the wide-ranging species often have their different development sizes (seedlings, saplings and trees) in species specific locations along the gradient.

3.4.2. Relationship between environmental variables and the observed gradient

Of the environmental variables recorded, fire best explained the gradient. This is evidenced by the high correlation between DCA and fire (Table 3.1) and the fact that the compositional gradient was divided using the fire regime (Figure 3.3a). Areas that had recent fires, and are probably most frequently burnt, had species that characteristically display fire resistant traits e.g. a thick bark, peeling off of the old bark (Figure 3.7) and good sprouting ability after a fire (Gashaw et al., 2002; Saha and Howe, 2003; Vesk and Westoby, 2004). The occurrence of some species is thus influenced by their fire-tolerance level (Cauldwell and Zieger, 2000) with increasingly more of the less fire resistant species in the Old-fire class. Here, seed dispersal, a factor not explored in this study, may have an important role. A number of the species that occurred in the Old-fire class were most abundant in the No-fire class. Their seeds were probably dispersed into the Old-fire class areas e.g. by wind and, when conditions became favorable, they got established. Hence we suggest that the existent fire regime influences their low occurrence (Huston, 1994a).

Although water is often a limiting factor for plant survival (Favier et al., 2004a), in humid FWS mosaics, water distribution is not a critical controlling factor. Despite the variation in rainfall over Budongo Forest Reserve, with the northern part receiving less rain than the south (Plumptre, 1996), the north still receives over 1200mm a year (Forest Department Uganda, 1997) which is sufficient for forest maintenance. Also elephants that previously restricted forest expansion (Laws et al., 1975) no longer exist. The species turnover could possibly be explained by an additive effect of the environmental variables considered in this study, the historical impact by elephants and probably others that were not considered in this study e.g. seed dispersal mechanisms, which have been shown to favor establishment of species with higher dispersal ability in the post disturbance period (Hovestadt et al., 1999; Ohsawa et al., 2002). However, just like in other studies where FWS occur (Elliott et al., 1999; Hovestadt et al., 1999), fire plays a major role in controlling species distribution pattern but it does not explain all the variation (Weiher, 2003). Accessibility to a protected areas, where local people mainly utilize areas closest to them (Acharya, 1999; Obiri et al., 2002), also showed a significant relationship with the species composition gradient.

3.4.3. Vegetation variation and composition as mapped using satellite image classification

The image classification provided a good representation of the vegetation cover classes. Each cover class had significant indicator species and there existed structural and species diversity differences between the cover classes (Figure 3.5). Although the best differentiating factor was the basal area, where each cover class was significantly different from the others, indicator species have also been shown (Cousins and Lindborg, 2004) to correspond well with the succession gradient. Classification of mosaic areas using remotely sensed data could therefore be a good start for identification of the vegetation types that exist within them. This would require less time (Schmidt et al., 2004) as compared to when only field surveys would have been used.

From field observation, the forest area looks outstandingly different from the woodland area. This may probably be the reason why it is often treated as an independent entity. This study has, however, shown that although the values for the forest, especially basal area, were often much higher, the systematic decrease in basal area from forest to wooded grassland cannot be ignored (Figure 3.5). A major gradient stretching from the forest to the wooded grassland is evident (Dezzeo et al., 2004) and species composition and forest structure vary along this gradient. Most of the areas sampled by Eggeling (1947) and followed up in Sheil (2000) had not had disturbance for a long time. Areas sampled in this study, however, cover both areas with ranging times since last disturbance and areas that are still experiencing frequent disturbance. Thus, in this study we observe a wider range of vegetation variation.

3.4.4. The effect of continuing reforestation on the biodiversity of Budongo

Eggeling (1947), also followed up in Sheil (1999), identified successional stages within the forest, with ironwood (*Cynometra alexandri*) at the climax end of the spectrum and the colonizing (woodland) forest as the starting point. In their study, the lowest diversity occurred in the ironwood forest. In this study, although diversity is low at the ironwood end of the gradient (Eggeling, 1947), it is even lower on the wooded grassland side of the gradient, as observed from this study (plot level values not shown) indicating a drop on either end of the gradient. The highest diversity is within the forest area and it gradually reduces until the lowest level, which occurs in the wooded grassland. The colonizing forest, identified by Eggeling as the starting point of the succession, occurs somewhere towards the middle of the current gradient. The current study has, therefore, extended the succession gradient to further into the wooded grassland and yet still conforms with the Intermediate Disturbance Hypothesis (IDH) (Connell, 1978).

Another DCA run, after combining a resampled set of Eggeling's data with data used in this study, revealed more of the similarities between the two gradients. It, additionally, emphasized the existence of more than one succession path in the forest (Eggeling, 1947; Sheil et al., 2000) and the variation within the forest (Plumptre, 1996). To incorporate Eggeling's data, resampling from the original data set was carried out. Having known the plot size and the number of individuals collected from each of his plots, the number of individuals expected to occur in a 500m^2 plot was calculated. The calculated number of individuals was then randomly sampled from the original individuals of the respective plot. The abundance of each species in each plot was then raised to that which would occur in an 1000m^2 plot. After crosschecking the species names for possible changes in naming, the data was combined with the rest of the tree data used in this study and a DCA was carried out. All Eggeling's plots, considering the first axis, occurred at one end of the gradient but in line with the rest of the plots (Figure 3.6). Eggeling's observation of compositional convergence (Eggeling, 1947) is still evident in his plots (see dotted lines in Figure 3.6).

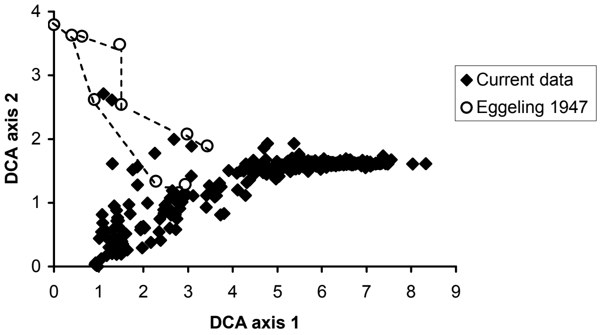

Figure 3.6: DCA graph obtained after combining a resampled set of Eggeling's data (Eggeling, 1947) to the data used in this paper. Axis 1 had an eigenvalue of 0.38 and explained 9.8% of the variation. The second axis had an eigenvalue of 0.19 and explained 4.9%. The dotted lines connecting Eggeling's data points indicate his two succession trends, which converge into a *Cynometra* climax.

Plumptre (1996) identified a north-south compositional gradient. In our study the variation along the second DCA axis of Figure 3.6 is an indicator of this gradient. Eggelling's plots collected from the southern part of the forest occur separate from most of our plots, which were collected from the northern part of the forest.

Succession always starts with very few species, then progresses a while along one line with more species coming in as conditions become more favorable (Huston, 1994a). In our study, few species were observed in the wooded grassland end of the gradient and species numbers increased as one moved towards the forest (Figure 3.2b). Although the forest side of the gradient had more species, other species occur away from the forest environment. The diversity of an area is influenced by the type, frequency and intensity of the disturbance (Petraitis et al., 1989). Hence, if the whole succession gradient occurs in an area, there would be more species (Connell, 1978; Huston, 1994a) than if one or a few stages of the succession gradient were conserved. So while the areas that have high species numbers e.g. forest ought to be preserved (Sheil and Burslem, 2003), the woodland areas should not all be allowed to become forest since that would mean loosing the woodland dependant species. And the highest number of species can only be conserved when complementary areas are included in the conservation plan (Howard et al., 1998). The maintenance of the high diversity of Budongo, being an isolated forest with no immediate source of additional forest species, may be more attributed to the existence of all stages of the succession gradient (Richardson-Kageler, 2004; Shea et al., 2004) than acquisition of more forest species from elsewhere, which, additionally, often takes a long time (Chapman et al., 1997). Hence, if reforestation of Budongo Forest Reserve would continue to the extent that the woodland-savanna areas would be lost, the biodiversity of the reserve would probably decrease. For purposes of conserving woody plants in a dynamic landscape, it is thus important that each vegetation class represented is included and maintained within the conservation area (Bengtsson et al., 2003). In the area under study, fire disturbance is a requirement for species coexistence (Shea et al., 2004).

In areas where fire may be applied, the vegetation type and its development stage may affect the potential for ignition and spread of the fire (Everett et al., 2000). Although no evidence exists of fires having destroyed tropical rain forests in Uganda, it has been observed elsewhere that tropical forests can burn (Cochrane and Laurance, 2002; Cochrane and Schuize, 1999; Laurence, 2003). This, however, mainly occurs in presence of very dry conditions, in fragmented forest landscapes and when fire is carelessly applied in or adjacent to logged over areas. Fire also remains a highly debated conservation management tool (Mentis and Bailey, 1990; Trollope et al., 1995; van Wilgen et al., 1998). It is therefore important that fire be used cautiously and, probably learning and using burning methods that have been used in the past (Goma et al., 2001) will be a prerequisite. In this respect, conservationists need to put more attention to current vegetation management practices of the local people surrounding conservation areas (Leone and Lovreglio, 2004) since, in addition to possessing valuable fire management knowledge, they have been noted to also use fire destructively (Condit et al., 1998; Wheater, 1971).

We conclude that areas with a dynamic FWS mosaic need a purposeful management that takes into account the relationship between the observed vegetation pattern and how this has been generated over time (Alados et al., 2004). A well balanced management, including a controlled fire management system that will prevent forest from colonizing the whole area, or vise versa, yet allowing the existence of varying disturbance regimes is a prerequisite (Crow and Perera, 2004) for species and species diversity maintenance.

Figure 3.7: Fire resistance traits evidenced by the tree bark of (a) a young *Terminalia velutina* with a thick bark and (b) a *Combretum* species whose old bark was peeling off. The lower part of the *Terminalia velutina* is still scarred from the last fire.

CHAPTER 4

BIODIVERSITY CONSERVATION THROUGH BURNING: A CASE STUDY OF WOODLANDS IN BUDONGO FOREST RESERVE, NW UGANDA

In order to determine suitable areas for conservation, it is important that the spatial dynamics and the forces fostering that dynamic change are understood. In East Africa most woodland and savanna landscapes are shaped by fire (Eckhardt *et al., 2000).* In these ecosystems, fire is deterministic in forming a sub-climax vegetation community. Changes in the fire regime will therefore result in a change in vegetation cover and composition. In this chapter, the woodlands located in the northern part of Budongo Forest Reserve in north-west Uganda were used for a case study to analyze changes in vegetation cover over time (a 17 year period). Here we present the findings of this study and their implications for the management of the Budongo Forest Reserve woodland-savanna areas.

Based on Grace Nangendo, Oliver van Straaten, Alfred De Gier (2005) Biodiversity Conservation through Burning: A Case Study of Woodlands in Budongo Forest Reserve, NW Uganda. In *Linking global conservation objectives and local livellihood needs: lessons from Africa*. M. A. F. Ros-Tonen, T. Dietz (Eds). Mellen Press. pp 113-128

Chapter 4

4.1. The Budongo Forest Reserve

The Budongo Forest Reserve, located in north-western Uganda (Figure 1.2). has been identified as one of the nation's richest forests in terms of its biodiversity value. Currently, research and management plans are being drafted to delineate areas suitable for conservation.

The forest reserve consists of *53.7* per cent tropical high forest and *46.3* per cent woodland (Forest Department Uganda, 1997). In the woodland areas, local inhabitants have utilized fire for hundreds of years (Beuning et al., 1997; Buechner and Dawkins, 1961; Paterson, 1991).

Many ecosystems that experience frequent fire disturbances over long periods consequently develop a unique species pool adapted to fire. However, in absence of such disturbances, various ecological changes occur within the ecosystems (Chandler et al., 1983).

Before attempting to understand the ecological changes it is, however, important to establish the existence of physical change in vegetation cover and the possible causes of such a change. The aim of this study was therefore to analyze the vegetation cover changes in the woodland areas, following changes in fire frequency and analyze the implications this has for the management of the Budongo Forest Reserve. The research was carried out using remote sensing and participatory rural appraisal (PRA).

4.2. The management history of Budongo forest

The value of Budongo forest was first noted by outsiders as early as 1905 (Paterson, 1991), when it was observed that the forest had larger and better quality trees and contained almost all of the most valuable timber stands in Uganda. Timber harvesting began shortly thereafter (around 1910) with small quantities being extracted by government departments. Systematic harvesting of much of Main Budongo was, however, carried out between 1936 and 1984 (Forest Department Uganda, 1997).

Budongo forest was first gazetted as a game reserve in 1906 but this was repealed in 1913. In 1932, the forest was re-gazetted as a Crown Forest Reserve and then in 1948 it was changed from a Crown to a Central Forest Reserve. Since then, Budongo forest has been managed by the central government, specifically by the Forest Department. Part of the current Budongo Forest Reserve, namely the Busaju and Kaniyo-Pabidi blocks, were originally Local Forest Reserves managed by the Bunyoro Kingdom government. These blocks were finally transferred to the central government in 1968 (Forest Department Uganda, 1997).

In the mid 1980s, Uganda National Parks (which later became the Uganda Wildlife Authority (UWA) in 1996) joined forces with the Forest Department in the management of a part of the Budongo Forest Reserve. With the establishment of the joint management, the entrance gate to the conservation area was moved from the north, way past the boundary of Budongo Forest Reserve, to the southern boundary of the forest along the only access road through the forest area. The UWA is currently also responsible for establishing entrance control to the conservation area. With the UWA now actively involved in the management of much of the woodland-savanna area, access by the local people to the forest has become severely restricted.

4.2.1. The current management of the Kaniyo-Pabidi woodland-savanna area

There are three main players involved in the management of this area, namely the Forest Department, the UWA and the local people. Since the gazetting of the forest area as a Central Forest Reserve, the woodland-savanna area has been under the management of the Forest Department. Under the management system that prevailed at the time, early burning was recommended. However, the Forest Department officials never carried out this action themselves but instead relied on the local people to do the burning.

Currently, due to increased patrol of the jointly managed area, local people are afraid to set the fires. At the same time, there is limited communication between the UWA and Forest Department concerning fire management in these areas. The UWA readily admits that there is no clear understanding among the UWA field staff as to the location of the boundary of the Budongo Forest Reserve area that is jointly managed by UWA and the Forest Department and the area strictly controlled by the Forest Department alone. The UWA officials are also unaware of the general Forest Department conservation/utilization policy for the areas that are jointly managed (Uganda Wildlife Authority, 2001). This lack of communication is two-way in that the Forest Department is also unaware of UWA's conservation strategies. At the same time, under the decentralization policy, the local government (at district level) has gained a larger stake in the natural resources under their jurisdiction. Setting up a workable management scheme that would involve and effectively utilize the potentials of all players is still a challenge.

4.3. Materials and methods

4.3.1. The study area

We selected the woodland-savanna area located in the northern region of Budongo Forest Reserve as our study area (Figure 1.2). This woodland-savanna region is located between the Kaniyo-Pabidi forest block and the Main Budongo forest and it is commonly referred to as Kaniyo-Pabidi woodland. The woodland-savanna is interspersed with forest patches. The woodland-savanna area is quite heterogeneous and is made up of sites of varying fire regimes ranging from areas that have not been exposed to fire for a long time to areas that have been burnt recently, and probably, at frequent intervals. As a result, some sites have an open canopy, predominated by grasses and consisting of fire-tolerant woody plants, while other sites have an increasingly closed canopy structure and are often composed of both fire-resilient woody plants and fire-intolerant woody plants.

4.3.2. Vegetation cover change detection

Landsat Thematic Mapper ™ images of 1985 and 2002 were used for the study. The change detection method used was temporal image differencing using calculated Normalized Difference Vegetation Index (NDVI) values. This technique determines the difference in reflectance values over comparative images from different years, pixel by pixel. Selected bands from the two temporal periods are subtracted from each other and the resulting image displays a continuous field of change values. The areas which have not changed will have values close to zero, while areas that have changed will respectively have larger positive or negative values based on the direction of change. As the output image displays a continuous field of difference values, one can evaluate the intensity of change by establishing threshold values for the different levels of change. Thresholds of one and two standard deviations (std) were determined to express explicitly the degree of vegetation cover change and to highlight the progression of vegetation development.

Nelson (1983) observed that vegetative index difference more accurately delineated forest canopy change than other change detection methods and Singh (1989), in his review of forest-change detection methods, observed that image differencing produced one of the highest accuracies.

4.3.3. Assumptions

The first assumption made was that areas which had increased significantly in NDVI between the image years, had not experienced extensive fire disturbance within that time, whereas areas that did not change or that decreased in NDVI were assumed to have experienced some fire disturbance.

Second, the scaling of change intensity provided a clearer picture of how the forest was changing. The areas that had changed by at least 1 std but less than 2 std had theoretically experienced a slight change in their vegetative condition, while those areas that changed by two or more standard deviations had encountered more dramatic shifts. This representation highlights the intensity of change and forecasts the spatial development in future years, as those sites with marginal increases (1 std) are likely to follow a change trajectory similar to that of the sites which have increased more dramatically.

4.3.4. Local people’s management of the woodland areas

Participatory Rural Appraisal (PRA) methods were used to collect information on how the local people carry out the burning activities in the woodland-savanna areas. We used semi-structured interviews and group discussions. Since the woodland-savanna has been shaped by fire and is frequently utilized by local people for hunting, it was regarded as appropriate to select the hunters as the target group for the discussions. For the purpose of acquiring more accurate information, a hunting group operating outside the jointly managed area, but within the gazetted forest area, was selected because those hunting within the jointly managed area are too afraid even to admit that they hunt lest they get arrested. Since hunting is considered illegal, it was necessary to identify one of the hunters who could convince the others to join the discussions. An elderly man who has been hunting for over 50 years was used as a key informant. Being respected among the hunting community, the key informant was helpful because he assured the other hunters that we were not disguised Forest Department or UWA officials. The initial information concerning hunting that he provided enabled us to engage in more fruitful discussions with the bigger group.

During later stages of the PRA, up to 31 hunters became involved in the discussions. These people lived close to a woodland-savanna area enclosed by the forest and much of the discussion focused on their activities in this woodland-savanna area. The information gathered was on when and how they carry out the burning and which animals they were interested in. Information was also sought on their views about vegetation cover status. A transect walk through the woodland-savanna was carried out with two of the hunters to verify the information gathered during the discussion. During the walk, the hunters identified recently burnt areas and pointed out the different types of traps utilized to catch game in the woodland-savanna area.

4.4. Results

4.4.1. Changes in vegetation cover between 1985 and 2002

Upon subtraction of the NDVI values of the two images, difference values produced a continuous map that defined the degree and intensity of change between the image pair. Standard deviations for the difference map were calculated and then used to define threshold values. A change map (Figure 4.1) was produced where all pixels that had increased or decreased by more than 1 std and then by more than 2 std were highlighted with different shades to illustrate the trend and the rate of change of vegetation expansion or reduction.

NDVI differencing indicated that much of the western portion of the study area either decreased or remained relatively unchanged over the 17-year period. A total decrease in vegetation cover of 13 per cent was registered over the woodland-savanna areas. The NDVI reflectance of most of the areas in close proximity to the forest increased.

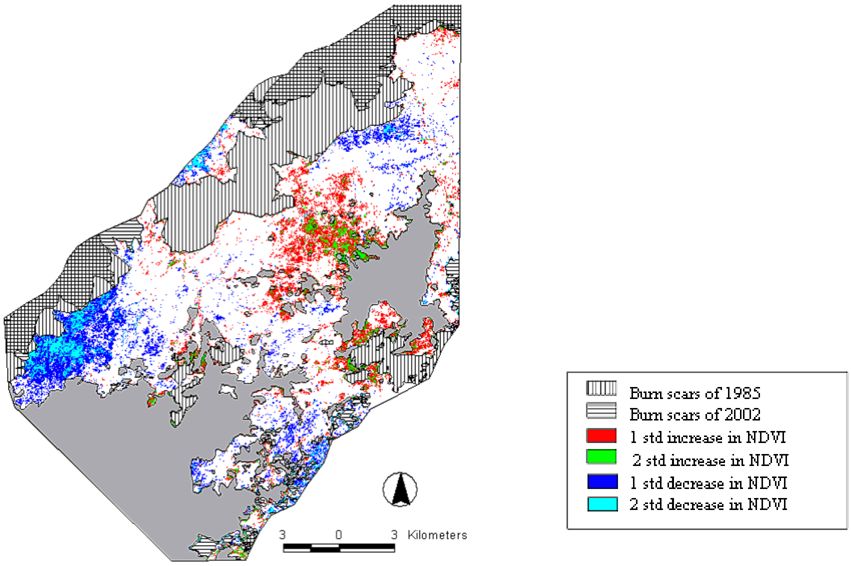

Figure 4.1: Vegetation change map (1985-2002)

Note: The two large grey areas represent the masked out 1985 forest and the double-checked areas indicate the sites that were burnt in both image years (1985 and 2002). All changes are presented as dots (pixels) and the areas that did not change are represented as white space.

Overall, vegetation cover increased by 14 per cent. Figure 4.1 highlights areas where specific changes occurred. During the image pre-processing, burnt areas were masked out of the respective image pairs. The unfortunate implication is that this excludes a considerable area from the study area. These masked areas are indicated in Figure 4.1 as burn scars for the respective years.

4.4.2. Local people's burning practices

Burning is mainly carried out in the driest season (December to February). In the area of interest, the burning is carried out systematically (Figure 4.2). Adjacent areas are never burnt in consecutive weeks. Instead, if an area on the lower part of the woodland-savanna is burnt one week, the next week's burning would be on the upper part of the woodland-savanna. At the same time, the hunters exercise a two-year burning cycle. If an area is burnt this year it will not be burnt again the following year (Goma *et al.,* 2001).

On the day of burning, a line is cut close to the forest on the lower side of the slope and a series of nets set up along this line. Fire lines are cut to separate the area to be burnt from the rest of the woodland-savanna to ensure that the fire is contained within the targeted area. When ready, the fire will be started on the upper side of the slope.

According to the hunters, there has been more regeneration of woody vegetation in the woodland-savanna areas. During the transect walk, hunters pointed out some of the woody vegetation regeneration, especially on termite mounds. They also pointed out indicators of recent burning. These included burnt grass (especially *Pennisetum purpureum* and *Imperata cylindrica* grasses), regenerating trees and mature trees with a thick cover of charred tree bark. Hunters could easily differentiate between areas burnt that year and the year before, based on the grass remains. Areas identified in the field as burnt that year were also found to have fire scars on the respective satellite images. On bringing up the issue of the current management system, the hunters specifically identified the UWA officials (especially the rangers) as being more vigilant than the Forest Department officials and that it was now much harder for them to carry out the hunting, which is often accompanied by burning.

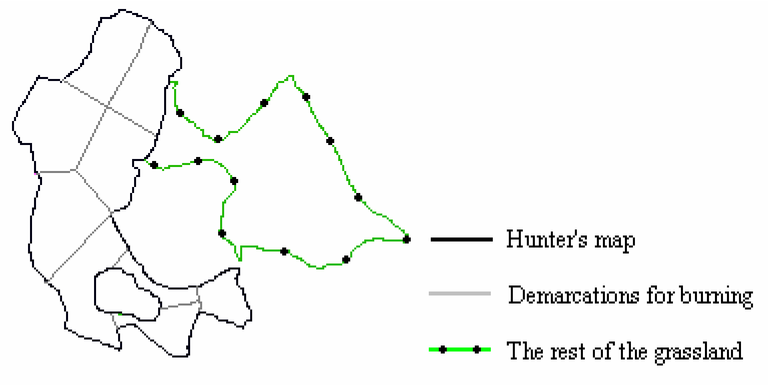

Figure 4.2: The hunters' map in relation to the actual woodland-savanna map

Note: The hunters drew this map during one of the group discussion sessions to illustrate the way they divide the area for burning (Goma et al., 2001).

4.5. Discussion

4.5.1. Local people and the forest

Typically, the presence of indigenous people close to any forest has, in the eyes of a forester, been a threat to the survival of the forest. Throughout history, fire is one of the tools utilized by local people for activities such as clearing and fertilizing the land, recharging pastures, purging fields of pests and disease, protecting lands against later wildfire and for hunting (Pyne, 1996).

In this study, several participatory approaches were used to understand which forest resources the local community valued, how they use the forest and what their view was of the state of the forest. Discussions revealed that the woodland-savanna areas within and adjacent to the forest were of great importance to them as a main source of animal protein and a source of other supplies such as medicinal plants.

Although most woodland-savanna areas are located inside the gazetted forest, hunters still utilize these areas at the risk of facing prosecution charges for illegal hunting. This is a clear indication that the local people are still attached to the forest resource for their livelihood. Obua et al. (1998) found that 55 per cent of the local people around Budongo secured bush meat from the woodland-savanna areas and Howard (1991) recorded hunting activities in all the large forests in Uganda, including Budongo. Their findings corroborate this study.

Hunting is often accompanied by burning and it is the burning that has been condemned by the forest managers. Their concern is that the forest areas are being converted to woodland due to fires. With the burning mechanism used here, the fire lines cut at the edge of the forest prevent fire from entering the forest. At the same time, the debris in the forest is in most cases too moist to burn. The areas burnt at each time are also small and scattered (see the southern part of Figure 4.1). This in some way prevents major losses in terms of flora, and probably fauna. Their rotation type of burning also ensures that no area is left unburnt for long periods.

Concerning the vegetation status, the local people observed that the forest was encroaching into the woodland-savanna areas and forest species can now be found in many parts of the woodland. They also indicated that much of the area used to be covered by grass but now there are evident patches of large trees.

4.5.2. Vegetation cover changes

Historically, fire has had a profound influence on the Budongo forest's woodland-savanna ecosystem (Paterson, 1991). In recent years, a decline in fire frequency and extent has changed the ecological balance formerly maintained by this disturbance agent. Fire-resilience adaptations are no longer a prerequisite for survival in most of the woodland-savanna areas. This is corroborated by Jacobs and Schloeder (2002) who state that species that can tolerate the existent fire regime are the ones that often persist. During the 17-year time lapse, the forest cover in a large area to the south of the Kaniyo-Pabidi forest block increased significantly, as did areas adjacent to the northwest region of the forest block and, in particular, woodland intrusion areas into the forest. It is speculated that these areas were left undisturbed during this period. The areas of intensive change seem to be located closer to the forest and in clustered patches. Field observations recorded the existence of fire scars, but all observed fire scars were old and weathering away. It can be deduced that such areas would quickly develop into forest in the absence of fire, since conditions are ideal for forest tree establishment and there is no shortage of available seeds. In areas where there were no dramatic changes in vegetation according to the satellite imagery, plot evidence most frequently noted signs of recent fire scars and ash.

Should current fire prevention measures persist, it can be anticipated that the vegetation in this woodland-savanna region will continue to develop towards a closed forest condition. The UWA, having joined forces as regards the management of this part of the Budongo Forest Reserve, has created a stricter format of control of local people's forest use. It has also been stipulated that movement of the UWA gate closer to the local people, along the only access road into the woodland-savanna area, has also created an extra check point for the local people who wish to enter the forest. The access limitations enforced by UWA make it increasingly difficult for local people who live to the south of the woodland-savanna area, to enter the forest and set fires. The few fires, which were set in the woodland-savanna, were located relatively close to the southern boundary or were sometimes, but infrequently, established inside the woodland areas well away from the UWA officials' reach. Furthermore, in 1994 the Kaniyo-Pabidi forest ecotourism site was established along the western border of the Kaniyo-Pabidi forest block to attract tourists to visit resident chimpanzee populations in the forest. In effect, this further discouraged illegal hunters from accessing the surrounding woodland-savanna areas and may provide some explanation as to why there were dramatic changes in vegetation cover directly to the north of the ecotourism site.

Areas invaded by fire-intolerant species will continue to develop unchecked unless a fire disturbance from other regions encroaches and sets back the successional clock. Field staff indicated that, in time, fire will eventually be unable to burn into the closed woodland, as the ecosystem will have become too moist for fire to burn efficiently. At this point, the woodland can develop unchecked through succession, barring any human intervention. At the other end of the study area, along the north-western edge, frequent fire disturbances still persist. These fires are believed to originate mainly from areas further west in the Bukumi-Bugungu hunting area or from Murchison Falls National Park prescribed fires. These fires have maintained a vegetation community adapted to frequent fire disturbance. The areas where a significant NDVI decrease was noted can be related to fire disturbances which have set back successional development.

Predicting precisely where the advancing forest will move is as yet impossible. However, if current trends in fire disturbance persist, with fewer fires occurring in the south-eastern regions (between the UWA gate and the Kaniyo-Pabidi forest block) and relatively regular fires regimes to the north and west, there is a possibility that a forest corridor will form between the Kaniyo-Pabidi forest block and the Main Budongo forest block. Such changes may have widespread ecological implications for flora, and also fauna, and for the human communities that rely on these regions for their livelihood.

For purposes of maximizing woody plants conservation in this forest, a heterogeneous landscape is more advantageous. The fire-intolerant species are already provided for within the existing forest. The woodland-savanna area would provide a safe heaven for the species that require varying fire disturbance regimes. With this in place, combining the species conserved within the forest area with those in the woodland-savanna would result in a higher overall number of species being conserved.

4.5.3. The need for balanced fire management

To encourage the local people to stay away from the protected area, revenue sharing programmes and income-generating projects have been set up. The children in the surrounding schools are also being taught about the value of conservation. While this may succeed, one problem still remains: by whom and when are the fires in the woodland-savanna areas to be set? Is the management willing to learn from the local people who have maintained the woodland-savanna layout of this area for hundreds of years? Are we, foresters, willing to come down and admit, especially to the local people, that fire is not always an evil to be avoided and that it is even beneficial to certain ecosystems such as the woodland-savanna areas?

For the purpose of maintaining a dynamic landscape, where both the forest and the woodland-savanna communities co-exist in the future, it is important that fire disturbance regimes are managed consciously. Sustainable wood*l*and-savanna management would require a balance between fire restriction and fire establishment, to control and shift the ecosystem to suit future management objectives.

4.6. Conclusions

The woodland-savanna vegetation is changing. The vegetation increase (14 per cent) occurred mainly in the woodland-savanna area between the Main Budongo and Kaniyo-Pabidi forest blocks and to the west of Kaniyo-Pabidi forest. The decrease (13 per cent) occurred mainly to the north and the northwest of the forest area. Most areas that experienced significant vegetation cover increase were located within the area jointly managed by the Forest Department and the Uganda Wildlife Authority (UWA). It is believed that recent changes in management strategies by UWA and Forest Department, which greatly restrict local people's access to the woodland-savanna area and therefore the opportunities to light fires, have led to the reduction in fire use and have resulted in an increase in vegetation cover. These management changes also deny people access to much-needed animal protein sources (wild game).

Vegetation increase means more of the woodland and savanna species are likely to be replaced by forest species which are already well represented in the forested area. This will eventually lead to a reduction in the overall number of species found in the area. The woodland-savanna vegetation loss also implies a reduction in grass and herbs, which form the main food source for herbivores. Sustainable woodland-savanna management will require a balance between fire restriction and fire establishment and the development of alternatives to meet local people's animal protein needs.

CHAPTER 5

RELATIONSHIP BETWEEN VEGETATION COVER CHANGE AND SPECIES DISTRIBUTION DYNAMICS

Abstract

Many woodland-savanna ecosystems in sub-Saharan Africa have been formed and maintained by recurrent fires. In the absence of such disturbances, various ecological changes occur within the ecosystem. The woodland-savanna areas found in the north of Budongo Forest Reserve, western Uganda, were used as a case study to determine spatial and species composition changes in the event of fire regime changes. The spatial extent of vegetation changes was mapped using satellite imagery over a 17-year period from 1985 to 2002. Temporal image differencing technique was used to determine areas of vegetation change. Successional vegetation development trends were quantifiably determined using multivariate ordination tools, and specifically Detrended Correspondence Analysis.

Woodland-savanna vegetation cover increased with 15.1% during the last 17 years of which most occurred in the relatively open area between the two forest blocks (Main Budongo and Kaniyo-Pabidi forests). And a decrease of 14.3% was recorded but most of it occurred to the northwest of Main Budongo forest. The successional development trajectory depicts a species turnover pattern from an open savanna type landscape, dominated by fire resilient tree species, to a tropical high forest condition dominated by fire intolerant and shade loving species. Fire resilient species e.g. *Lonchocarpus laxiflorus* and *Grewia mollis* occurred early while fire intolerant species e.g. *Funtumia elastica* and *Pterygota mildbreadii* occurred later along the succession gradient. Others like *Maesopsis eminii* had seedlings (dbh < 2cm) early along the succession gradient and the big trees (dbh > 10 cm) late along the succession gradient. For purposes of maintaining a dynamic landscape, where both the forest and the woodland-savanna communities co-exist into the future, it is important that fire disturbance regimes be managed consciously. Sustainable woodland-savanna management will require a balance of both fire restriction and fire establishment.

Based on Grace Nangendo, Oliver van Straaten, Hans ter Steege, Alfred de Gier and Frans Bongers *(Submitted).* Relationship between vegetation cover change and species distribution dynamics.

5.1. Introduction

Most studies in disturbed forest landscapes focus on the threat of conversion of the forest to other vegetation types e.g. woodland and farmland (Gerwing, 2002; Hayes et al., 2002; Humphries, 1998; Laurence, 2003). The reverse is, however, also happening. In areas where forest, woodland and savanna have coexisted for hundreds of years, most of the woodland-savanna areas have been maintained by fire. Such mosaic landscapes have a unique species pool, which ought to be preserved (Eriksson et al., 2002; Furley, 1999). Unfortunately, policies that foster forest expansion have often been applied indiscriminately to protected forest areas. The elimination of fire disturbance, in particular, has lead to the expansion of forest at the expense of the woodland and savanna areas (Brown and Archer, 1989; Skowno et al., 1999; Uys et al., 2004). Little attention has been paid to assessment of changes in woodland-savanna areas and to understanding the relationship between these vegetation changes and the associated species dynamics (Bond and van Wilgen, 1996; Schmidt and Vlok, 2002).

Budongo Forest Reserve (BFR), Uganda, has been managed by the central government since 1932. Part of the current Budongo Forest Reserve i.e. Busaju and Kaniyo-Pabidi blocks were, however, Local Forest Reserves managed by the Bunyoro Kingdom government until 1968. Upon their transfer to the central government in 1968, the burning restrictions exercised in government forest reserves were enforced (Forest Department Uganda, 1997). Further restrictions were implemented in the mid 1980s when the Uganda National Park management (now Uganda Wildlife Authorities) joined hands with Forest Department in the management of the northern part of Budongo Forest Reserve (Chapter 4). These changes in management have over time resulted in reduction of the area burned and frequency of fire applied in woodland-savanna areas. The consequence of this is that the woodland-savanna is slowly developing into forest.

In areas where fire is predominant, a woodland-savanna sub climax is often created (Eriksson et al., 2002). Burning opens up the area for seed germination and also releases seeds of fire dependant species (Gashaw and Michelsen, 2002). The survival and growth of the regeneration is, however, dependant on the prevailing environmental conditions and the individual species' survival characteristics (Hoffman and Franco, 2003). BFR receives over 1300mm of rain annually and so water availability may not be a limiting factor (Bongers et al., 2004) for tree growth for most of the year. When elephants and fire existed in BFR, they controlled tree growth but the elephants were finally eliminated in the late 1960s. Fire then remained as the major disturbance agent maintaining the woodland-savanna vegetation. In the event of less frequent fires, the woodland-savanna areas in BFR provide a good environment for forest colonization (Eggeling, 1947).

Succession studies carried out by Sheil (1999) assessed species development dynamics of Budongo forest over a 50-year period through resampling permanent sample plots established and collected by Eggeling

(Eggeling, 1947). All plots except one were established in the forest. The study revealed that in absence of disturbance the forest advanced in succession from a mixed forest towards a *Cynometra* climax. The woodland plot also showed an increase in forest species (Sheil, 1999). Considering the fact that the woodland-savanna constitutes 46.3% of the forest reserve (Forest Department Uganda, 1997) and that its management system has changed over time, it is important that the succession dynamics of the woodland-savanna areas be assessed in order to carry out better-informed management planning for these woodland-savanna areas and, for Budongo forest in general. Studies focusing on changes in woodland-savanna areas at sites where forests, woodland and savanna coexist are rare and no study so far has analyzed the successional pattern of the woodland-savanna areas found in BFR. Hence, the main objective of this study is to analyze the vegetation cover changes and the associated succession patterns of the woodland-savanna areas. Specifically, in this paper we evaluate vegetation changes over a 17-year period and use a chronosequence approach to analyze the related vegetation composition changes.

5.2. Methods and materials

This study focuses on the woodland-savanna ecosystems located in the northern part of the forest reserve, between the Kaniyo-Pabidi forest block and the Main Budongo forest (Figure 1.2). These woodland-savannas, known as the Kaniyo-Pabidi woodlands, cover an area of 27,280 hectares (Forest Department Uganda, 1997) . Before being gazetted, the local people used the woodland-savannas as grazing and hunting grounds and fire was an essential tool for refreshing grass and creating an open landscape for easier hunting (see figure 5.5 for grass height).

5.2.1. Satellite imagery

Cloud-free Landasat 5 TM for 1985 and 1995, and Landsat 7 ETM+ of 2002 images were used for this study. All the images were acquired during the driest months (January–February) of the respective years. The images when received were already resampled to a 30-m pixel size.

There were a number of necessary steps to be completed prior to image subtraction. First the images were geometrically aligned (rectified) so that the pixels for a corresponding area had the same geographical coordinates in all the images to be compared. Second, the area of interest was isolated, and so all areas outside the study area were masked out. Third, the areas that exhibited a contrasting spectral signature due to known artifacts in the image such as recent fire scars and smoke covered areas were also removed. Fourth, the images were radiometrically corrected to ensure they were comparable. A histogram match was used to equilibrate the images and ensure similar values. Pixel value differences could now be attributed to actual changes on the ground instead of difference associated with geometrical alignment differences, sensor calibration or illumination conditions.

5.2.2. Sampling design and data collection

A systematic sampling design was utilized for data collection. Nested circular plots of 50m^2 and 500m^2 were established at an interval of 50 meters apart along transects and then 300 meters apart between transects. The transects were located perpendicular to the forest edge and extended on average between 700 to 1000 meters into the woodland-savanna and approximately 100 to 150 meters into the forest. A total of 335 plots were collected. Of these, 268 were located in the woodland and 67 in the forest. Data collected at each plot consisted of a geographical coordinate, percentage canopy density measurement and fire scar age (recent, old, or none observed). In the 50m^2 plots, abundance and names of individual species, for woody plants less than 2cm diameter at breast height (DBH) and > 50cm in height, was recorded. In the 500m^2 plot, species names and DBH for all woody plants with diameter ≥ 2cm were recorded.

Canopy cover percentage was measured using a canopy densiometer (Forest densiometers, Bartlesville, Oklahoma, U.S.A.), following the provided guidelines. Four measurements were taken in each plot and an average of these measurements was calculated to determine the final canopy cover of the plot.

The fire indicator value was based on several factors (1) the degree of scorching on the woody stems i.e. if it was fresh or old, (2) if there existed remains of burnt grass in the undergrowth and (3) whether fresh ash was found in the plot area. Plots with fresh fire scorching on the woody stems, remains of burnt grass or ash were recorded as “recent fire” and labeled class 2. Plots with old signs of fire were labeled class 1 (old fire) and plots with no sign of fire were labeled class 0 (no fire).

Species identification was based on Eggeling and Dale (1952) and Hamilton (1991). Samples of the species that could not be clearly identified in the field by the botanist on the team were sent to the Uganda National Herbarium where they were identified.

5.2.3. Data analysis

Detecting vegetation changes between image years

Temporal image differencing was utilized for analyzing spatial vegetation change between the image years. Image differencing was chosen as it is the most widely used technique (Nelson, 1983; Singh, 1989; Weismiller et al., 1977) and has been found to perform better than other techniques (Jenson and Toll, 1982). A further advantage of image differencing is incremental display of change intensity, prior to thresholding, so that the obtained values can subsequently be correlated to other field data. The existing maps of the study area had two main vegetation classes represented i.e. forest and grassland/woodland. There were no old maps or digital data, with woodland classes, against which change could be estimated. A method that explored pixel-to-pixel comparisons was therefore essential. Temporal image differencing technique determines the difference in reflectance values over comparative images from different years, pixel by pixel. Difference values exhibited on a continuous map defined the direction and intensity of change between image pairs. The areas which have had minor changes will have values close to zero while areas that have dramatically changed will respectively have larger positive or negative values based on the direction of change. By establishing threshold values, significant cut-off levels of change can be determined.

The threshold values for the change images, all of which had normal distributions, were determined as threshold levels of 1 and 2 standard deviations from the mean (Rosin, 2002) to explicitly express the degree of vegetation change. The areas that had changed by more than one standard deviation but less than two standard deviations had theoretically experienced a slight change in their vegetative condition while those areas that changed by more than 2 standard deviations had encountered more dramatic shifts.

Removing the burnt areas and areas covered by either smoke or cloud unfortunately results in exclusion of certain parts from the study area. Due to a large fire in 1995, which was still burning along the western perimeter of the study area at the time of image acquisition, a sizable portion of the image was obscured by smoke. Subsequently, any comparisons made with the 1995 image required the removal of the area with this particular anomaly.

Prior to image subtraction, vegetation indices were calculated to accentuate presence and abundance of actively growing vegetation. The Normalized Difference Vegetation Index (NDVI) and the Modified Soil-Adjusted Vegetation Index (MSAVI) were calculated. MSAVI is modified NDVI where the soil effect on the reflectance has been minimized (Qi et al., 1994). These methods use the red and near-infrared (NIR) bands of a satellite image. The equations for the two indices are:

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

$$MSAVI = \frac{2NIR + 1 - \sqrt{(2NIR + 1)^2 - 8(NIR - RED)}}{2}$$

Image pairs of the same vegetation index, for subsequent years, were subtracted producing continuous maps indicating areas of change.

Two change maps i.e. one for NDVI and another one for MSAVI resulted after the above analysis. Statistical analysis was carried out to see if there is a correlation between the two sets of output. NDVI and MSAVI pixel values were extracted for the 2002 image and compared statistically.

When each vegetation index's plot values for the 2002 image were tested against other known plot variables, MSAVI consistently gave slightly stronger correlations. Hence, MSAVI output maps are presented and the MSAVI pixel values were used in the rest of the analysis.

Since the vegetation change periods we compare are unequal (1985-1995, 1995-2002, 1985-2002), it was important to ascertain that there was no significant difference between the standard deviation values of the different periods. This was done using Bartlett's test for homogeneity of population standard deviations, which is defined as:

H$_0$: $\sigma_1 = \sigma_2 = \cdots = \sigma_k$
H$_a$: $\sigma_i \neq \sigma_j$ for at least one $i \neq j$

If $T > \chi^2(\alpha, k-1)$, the hypothesis of equal standard deviations is rejected. *T* is Bartlett's test value, and $\chi^2(\alpha, k-1)$ is the upper critical value of the chi-square at an α level of significance with $k-1$ degrees of freedom. With the results obtained ($T = 1.08$; $\chi^2(0.05,2) = 5.99$), we failed to reject the null hypothesis at the 5% level of significance and 2 degrees of freedom. The p-value for the test is 0.58. So it was acceptable to use the standard deviation values obtained for reach period. The outputs would be comparable.

Biophysical data analysis

Detrended Correspondence Analysis (DCA) was used for the analysis of species turnover along gradients because it is a robust and well understood method for developing a best-fit representation describing species composition differences (Hill and Gauch, 1980; Ter Braak, 1985).

First, data of established trees (trees ≥10 cm DBH) were used in the analysis. To prepare the data, plots situated on bedrock / exposed rock or on saturated soils (i.e. swampy) were removed from the analysis. The remaining plots were situated on similar soils, which are orthic Ferralsols.

Whereas the woodland-savanna can be burnt at any time, the forest, under normal circumstances, is too moist to burn. Succession within the forested areas would therefore be influenced by factors other than fire, but in the woodland-savanna areas fire is considered a major disturbance factor. Hence, the plots established in the forest, boundary of which was based on the 1985 image, were also removed from the data set.

Focus was then on the most abundant species because they make up the largest part of the canopy. All species that registered a total of at least ten individuals were included in the data set. This resulted in 32 species for the total of 268 woodland-savanna plots. A DCA was performed on the respective plots and species using the Multivariate Statistical Package (MVSP). Different known site factors and site developments, i.e. MSAVI changes between 1985 and 2002 (indicative of the degree of vegetation change), fire scar age estimates (indicative of time post disturbance), tree density (indicative of degree of vegetation establishment) and percentage canopy cover (indicative of canopy closure) were then used to interpret the DCA scores. The strength and significance of the relationship was determined using the Pearson correlation coefficient.

For analyzing the relationship between woody plants composition and vegetation change, the vegetation change that had occurred within the woodland-savanna areas over the 17-year period (1985 to 2002) was used. Trees grow slowly and examining their change at short intervals may not yield significant relationships. At the same time, some of the areas where data was collected had been masked out of the 1995 image due to fire and a large smoke cloud. Vegetation change values between 1985 and 2002 were obtained by subtraction of MSAVI values of the respective years.

An analysis of variance (ANOVA) was used to determine the degree of significance of the relationship between DCA axis 1 and other plot factors. Graphs of the relationship between DCA axis 1 and vegetation change (1985 to 2002), and between DCA axis 1 and fire scar age estimate values were also plotted.

Size class distributions have over time been used as indicators of species composition change and succession trends (Barnes, 1985; Jones, 1956; Lawson et al., 1968; Lykke, 1998; Murphy and Lugo, 1986; Swaine et al., 1990; Walker et al., 1986). More understanding of the vegetation changes taking place in the area was sought through analyzing the species size structure progression (Sheil, 1999). A new data set was extracted by considering three diameter classes (DBH≥ 10cm, 2cm ≤ DBH < 10cm and, DBH<2cm and ≥50cm in height). Species that had individuals in all three groups were identified and of these, species that had at least 5 individuals per size class were selected. This resulted in 16 species. For each species, individuals in each species size class were treated independently i.e. as a pseudo-species with its abundance indicated in each plot. The analysis outcome would then reflect the species' DBH class location along the succession gradient.

A DCA was then run on the corresponding plots and species, the progression of each species along the first axis was analyzed to determine how species recruitment and progression varied over the gradient. When the DBH classes were considered as proxies for the species growth stages, mapping a species according to its diameter classes should thus reveal where, along the gradient, each species size class attains maximum abundance and how the species progresses through succession. The results, therefore, demonstrated where and in which succession stage the size class for a particular species grows best.

5.3. Results

5.3.1. Vegetation change (1985-1995-2002)

Between 1985 and 1995, areas northwest and south of Kaniyo-Pabidi[*] forest and in the far north of the forested area showed a high degree of vegetation increase (two standard deviations) while areas around Main Budongo had a high degree of vegetation decrease (Figure 5.1a). Between 1995 and 2002, a large area directly northwest of the Kaniyo-Pabidi forest had the highest vegetation increase (Figure 5.1b). Areas on the fringes of Main

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[*] Kaniyo-Pabidi and Main Budongo forest blocks are indicated in figure 1.2.

Budongo, which had showed a high decrease in vegetation cover in the 1985 to 1995 period, showed vegetation increase in the 1995 to 2002 period.

Whereas the 1985-1995 period registered more vegetation cover increase (19.4%) than decrease (18%), the 1995-2002 period had more vegetation cover decrease (14.8%) as compared to the 13.8% decrease (Table 5.1). Most of the changes in the two periods are at the one standard deviation level.

Table 5.1: Change in vegetation cover between image years (1985-1995, 1995-2002 and 1985-2002) in Budongo Forest Reserve. Change is indicated relative to the standard deviation (STD) e.g. increased 2*STD indicates the percentage of the woodland area that increased by two standard deviations.

		Image years		
		1985-1995	**1995-2002**	**1985-2002**
Increase	1*STD	13.9	11.8	12.3
	2*STD	5.5	2.0	2.8
Decrease	1*STD	13.3	12.2	12.5
	2*STD	4.7	2.6	1.8
Total increase		19.4	13.8	15.1
Total decrease		18.0	14.8	14.3
Burn & smoke		31.6	19.2	20.7
No change		31.0	52.2	49.9

Considering the whole 17-year period (1985 to 2002), there was a total vegetation increase of 15.1% and a decrease of 14.3% (Table 5.1). Although the percentage vegetation increase and vegetation decrease almost balance out, the two types of vegetation change occurred in distinctively separate areas. Vegetation increase is mainly between the two forest blocks and on the western side of Kaniyo-Pabidi forest while the decrease is mainly on the northwestern edge of Main Budongo forest (Figure 5.1c).

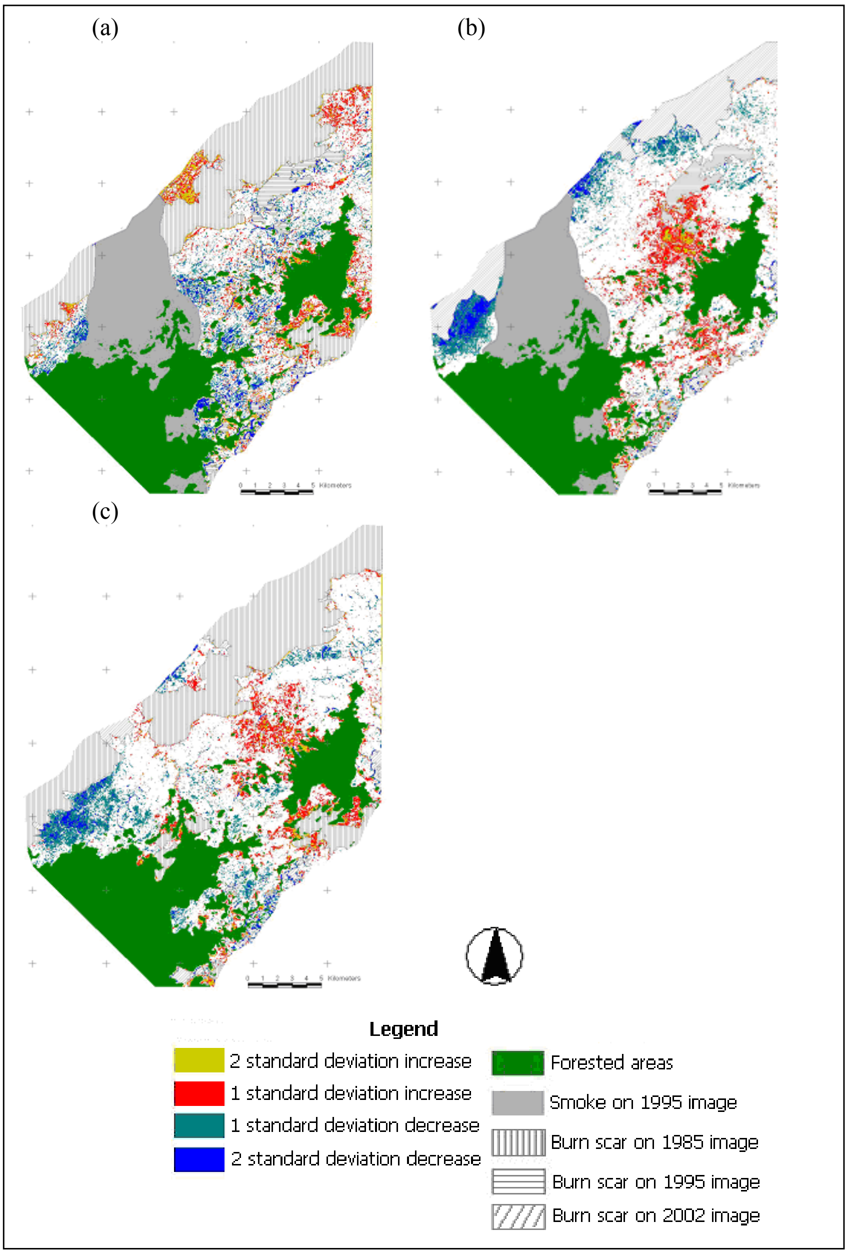

Figure 5.1: Vegetation change maps for (a) 1985 to 1995, (b) 1995 to 2002 and (c) 1985 to 2002

All three images indicated the occurrence of fires along the western edge of the study area, in the vicinity of the rift valley escarpment. The fire regime in this area appears not to have changed during this period. MSAVI differencing indicated that much of the western portion of the study area either decreased in vegetation cover or remained relatively unchanged over the 17-year period.

Comparing areas where vegetation cover had increased by one standard deviation but less than two standard deviations in the 1985 to 1995 period to areas that had increased by more than two standard deviations in the 1995 to 2002 period resulted in a high correlation (results not shown). This correlation forecasts the future spatial development i.e. areas currently with marginal increases (one standard deviation) may follow a similar change trajectory.

5.3.2. Succession dynamics

The first axis of the DCA gradient determined using abundance counts per plot of trees ≥ 10 cm dbh had an eigenvalue of 0.472 and explained 12.2% of the variation (Figure 5.2). The second axis exhibited a weaker eigenvector value of 0.242, and explained an additional 6.4% of the species composition variation. Together, axis 1 and 2 explained a cumulative total of 18.6%.

The first axis scores indicate where along the gradient a particular species obtains optimal growth. Species like *Lonchocarpus laxiflorus*, *Grewia bicolor* and *Grewia mollis* reach optimal growth early along the gradient while species like *Holoptelea grandis*, *Funtumia elastica* and *Celtis durandii* reach optimal growth conditions at later stages of woodland-savanna succession. This axis is, therefore, an indicator of the succession trend within the area. It will from hereon be termed the "successional index" (SI).

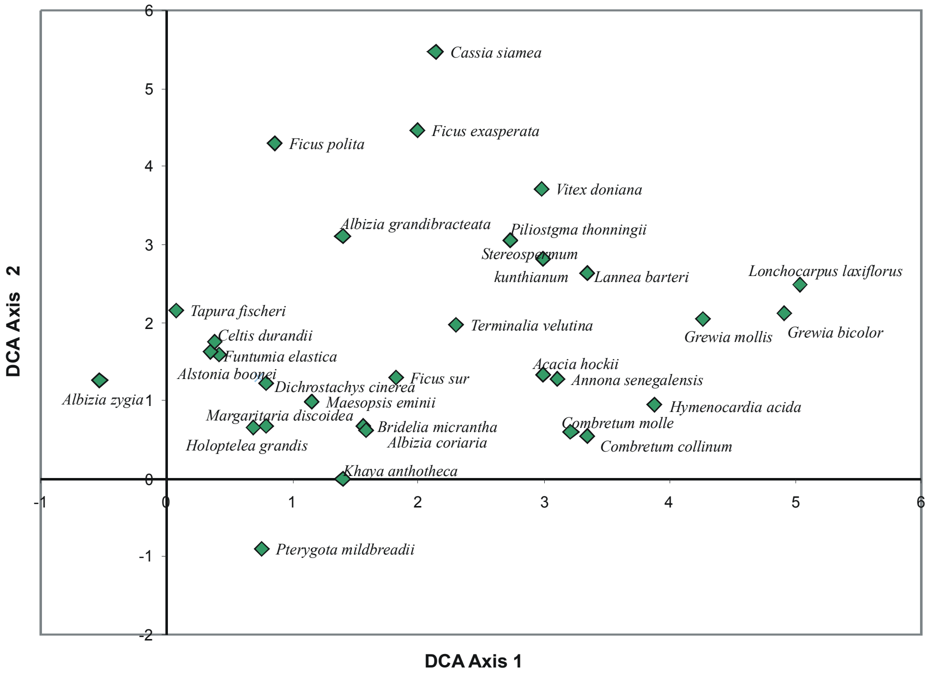

Figure 5.2: Species scores as explained by axis 1 and 2, for 32 species at an established stage of development (≥10 cm DBH)

The two major axes of variation in plot composition were related to fire scar age estimates, stem density, canopy cover and MSAVI change values (1985-2002). All but the tree density measure showed significant negative correlations for the relationship between DCA axis 1 and the plot factors (Table 5.2). For the second DCA axis, there was no significant relationship demonstrated.

Table 5.2: Pearson correlation significance levels of plot characteristics with DCA Axis 1

	DCA axis 1	
Plot characteristics	***Pearson correlation***	***P=0.01***
MSAVI change between 1985 and 2002	-0.587	0.001
Fire scar age estimate	-0.589	0.001
Canopy cover	-0.509	0.001
Overall tree density	-0.045	0.466

Trees adapted to fire e.g. *Lonchocarpus luxiflorus* and *Grewia mollis* were found in areas of recent, and probably regular, fire. Here succession is maintained at its lowest level. Trees less adapted to fire e.g. *Bridelia micrantha* and *Funtumia elastica* were found in areas with old and no fires These trends were confirmed by the high correlation (-0.587) between plot values for the species turnover (DCA axis 1) and the vegetation changes (1985-2002).

Plotting the MSAVI plot values for the vegetational change between 1985 and 2002 against the SI site score values revealed that sites that decreased in MSAVI were generally at earlier stages of succession, while sites that increased in MSAVI were generally at advanced stages of succession.

Comparing the succession index plot scores to fire scar age estimate values showed where, along the gradient, each fire scar age group occurred (Figure 5.3). Plots with recent fire scar evidence were in early stages of succession (high SI), plots with old fire scars were at intermediate phases of development (mid-range SI) and plots with no fire evidence were located at late stages of development (low SI). Statistically, differences between three classes were significant (ANOVA, F=71.57, d.f.= 268, $p<0.001$).

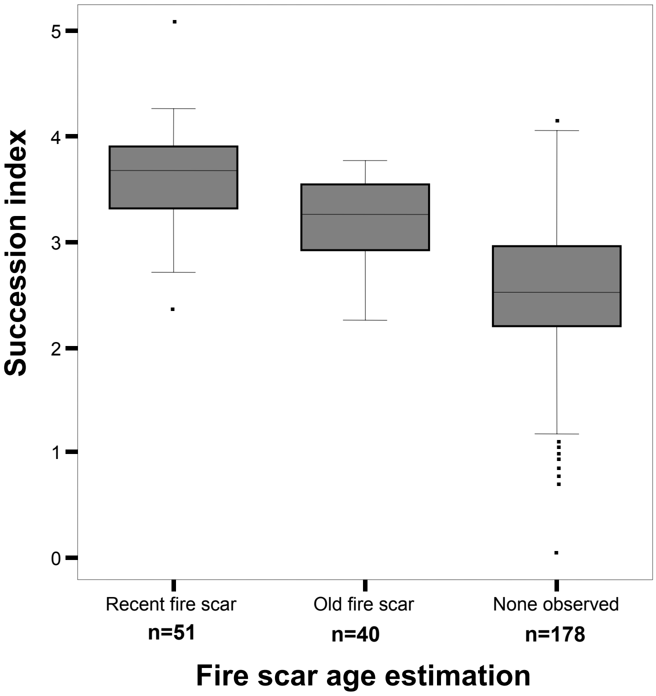

Figure 5.3: Box-plot of SI site score values against observed fire scar evidence. The x-axis figures indicate the number of plots in each of the fire classes

5.3.3. Species progression

For the "species progression" a DCA was run using 16 species, the first axis explained 10.5% of the variation and the second axis explained an additional 6.9%. Two types of establishment patterns were observed. Some species e.g. *Grewia mollis, Terminalia velutina* and *Lonchocarpus laxiflorus* establish seedlings (DBH < 2cm and ≥ 50cm in height) early in the succession development and others e.g. *Pterygota mildbraedii and Khaya anthotheca* establish seedlings (DBH < 2cm and ≥ 50cm in height) at later succession stages. The majority of the species follow a defined progression trend i.e.

1. The regeneration occurs late in succession e.g. *Bridelia micrantha* and *Khaya anthotheca* and they grow to maturity only in the late succession (Figure 5.4).
2. The regeneration occurs earlier in succession followed by small trees (2cm ≤ DBH < 10cm), and then by established trees (DBH≥ 10cm). The species that establish early in succession also follow one of several growth patterns.

Some species such as *Grewia mollis, Annona senegalensis* and *Lonchocarpus laxiflorus* establish early and remain prevalent only in the early succession stages (Figure 5.4). Other species e.g *Maesopsis eminii* and *Terminalia velutina* establish early and progress into later stages of succession.

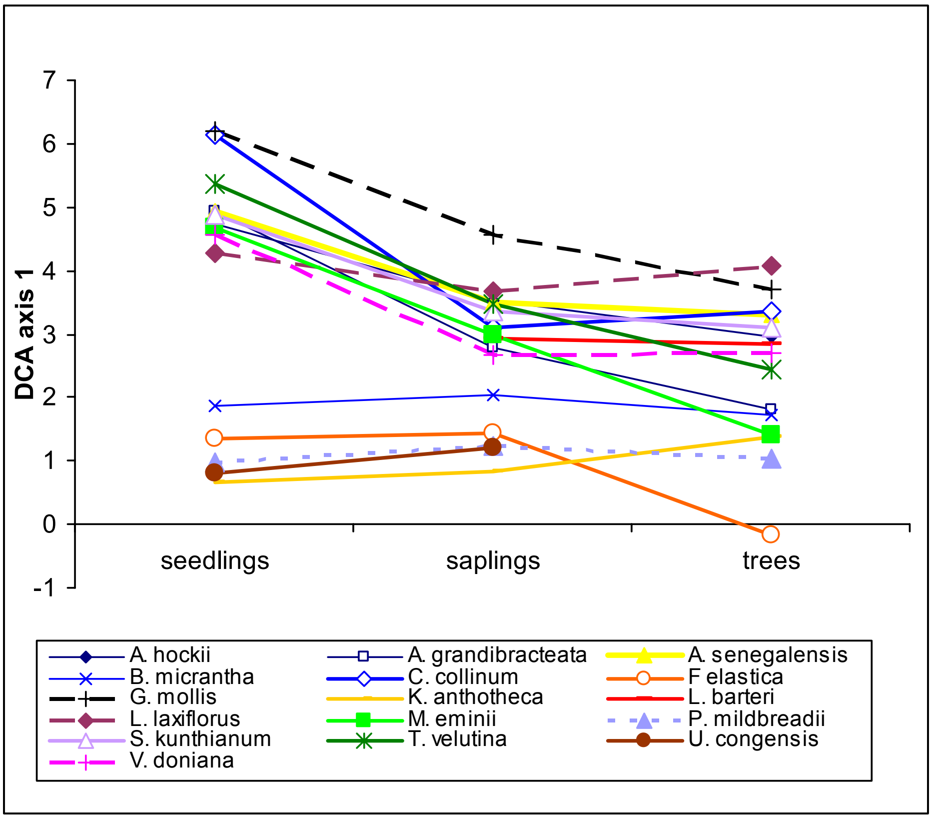

Figure 5.4: DCA graph for the three size classes (< 2cm dbh and > 50cm height, ≥ 2cm dbh<10cm and, ≥ 10cm dbh) for each species. The lines indicate how each species progresses through succession

5.4. Discussion

5.4.1. Vegetation change patterns

There is a general increase in vegetation cover in the northwest and south of Kaniyo-Pabidi forest. Many of the woodland intrusions into the forest also increased in vegetation cover. It can be inferred that such areas would quickly develop in the absence of fire, since conditions would be ideal for forest tree establishment, and there is sufficient supply of seed from the surrounding forest. During fieldwork, little fire scorching or fire evidence was found at these sites, and vegetation changes can be attributed to successional species establishment in the absence of fire.

Much of the vegetation cover increase is not an advancement of the forest edge but increase in vegetation cover within the woodland-savanna area. Factors that may have contributed to this increase, in addition to regeneration of seeds of the already existing trees include the existing trees acting as perch sites for birds that bring in seed of early invaders (Archer et al., 1988) and the release of 'Gullivers', a word coined by Bond and Van Wilgen (1996) for individuals held in the grass layer by heavy grazing or regular fires.

Should current fire prevention measures persist, it can be anticipated that the vegetation in this woodland-savanna region will continue to develop towards a closed forest condition (Lwanga, 2003). The access limitations enforced by the Uganda Wildlife Authority (UWA) and Forest Department make it increasingly difficult for local people, who live to the south of the woodland-savanna area, to enter and set fires (Chapter 4). Furthermore, in 1994 the Kaniyo-Pabidi ecotourism site was established on the western edge of Kaniyo-Pabidi forest to attract tourists to visit resident chimpanzee populations. This further discouraged local people from accessing surrounding woodland-savannas and can possibly provide some explanation why, between 1995 and 2002, there was dramatic vegetation increase north of the ecotourism site. It was indicated by field staff that in due time, fire will be unable to burn into the closed woodland, as the environment would have become too moist for fire to burn efficiently.

Fire disturbance regimes along the western and northern edge of the study area do not appear to have changed over the 17 years. The few areas that exhibited increased vegetation cover during the 1985 to 1995 time period were subsequently reclaimed by fire in the 1995 to 2002 time period. The areas, which significantly decreased in vegetation cover, can be related to more frequent fire disturbances, which have set back successional development. These fires mainly originated, and spread uncontrolled into the study area, from areas further west in the Bukumi-Bugungu hunting area or from prescribed fires set in Murchison Falls National Park to the northwest.

If the current trends in fire disturbance persist, whereby certain regions are frequently burnt while others are not, the northern peripheries of the Budongo forest block and the southern parts of the Kaniyo-Pabidi forest block will encroach towards one another eventually forming a forested corridor. Such changes will have widespread ecological implications for flora, as this study examines, but also on fauna and on the human communities that rely on these regions for their livelihood. The areas further north will remain unchanged or reduce in vegetation cover due to the frequent fires.

5.4.2. Species succession dynamics

The floristic transition is gradual as species compositions change to suit the changing environment. In the absence of fire or change in fire regime, the growing conditions change. While becoming increasingly inhospitable to some species, they become suitable for others (Huston, 1994b). The variety of species observed at different succession stages within the study area is an indicator of the species response to the changing environment (van Wilgen et al., 1998). With changes in fire disturbance regime, species less adapted to fire disturbance replace the fire resilient species. This trend was also observed in the lower part of Budongo forest where species like *Grewia mollis* no longer existed and others e.g. *Maesopsis eminii* were on the decrease while others e.g. *Alstonia sp.* and *Khaya sp*. had gotten established in an originally woodland plot (Sheil et al., 2000), in Kibale forest (Lwanga, 2003) and in parts of Hluhluwe Game Reserve where frequency of intense fires had decreased (Skowno et al., 1999). This is further proof that if fire is eliminated from the landscape, the woodland-savanna areas would be overtaken by forest species.

5.4.3. Species progression along the succession gradient

Immediately following a fire disturbance, there is increased availability of soil nutrient concentrations but this is short lived (Van de Vijver et al., 1999a). The existing and surrounding trees provide seed to the newly formed fertile seedbed (Acharya, 1999; Wilson and Witkowski, 2003; Witkowski and Garner, 2000). The success of the seedling establishment, however, depends, among others, on the characteristics the individual species possess. With recurring fires, the forest species, which are less adapted to fire (Hoffman and Franco, 2003), are eliminated from such areas. Species observed in the early succession stage, apart from *Maesopsis eminii,* have fire resistant adaptations that allow them to survive the fire disturbance. For *Maesopsis eminii* whose seeds are dispersed mainly by birds, particularly hornbills, there is regular reseeding of the disturbed sites (Cordeiro et al., 2004).

Most of the seedlings that survive then develop into the sapling class ($2cm \leq DBH < 10cm$) whose peak abundance is found further along the successional gradient. Where and at what phase of succession the sapling population exists mainly depends on the vital attributes e.g. growth rate of the species (Noble and Slatyer, 1980). Hence, either, a slow growing species will have stayed in the sapling size class for a longer period of time and, as an effect, the surrounding environment shifted further along the succession gradient. Or the fast growing tree species e.g. *Maesopsis eminii* quickly increased in dbh (Alder et al., 2002).

The development from sapling to tree class ($dbh > 10cm$) highlights the characteristics of the individual species. For the first growing species e.g. *Maesopsis eminii*, there was a drastic increase in diameter. For species that characteristically exhibit small diameters even at maturity e.g. *Combretum collinum* (Eggeling and Dale, 1952; Hoffman and Franco, 2003), there was marginal increase in diameter. Thus their shift along the progression gradient was marginal compared to fast growing species.

As succession proceeds, it has influence on the soil properties, which in turn may have notable feedback on the vegetation (Miles et al., 2001). With the advancement of the early succession species to tree size, the canopy closes and the environment becomes moister. This then favors establishment and development of the late succession species (Franco-Pizana et al., 1996; Smith and Goodman, 1986; Vetaas, 1992), which, on our gradient, occur after the early succession species (Figure 5.4).

The late succession species did not exhibit a strong progression trend but instead indicated that all three size classes are found at similar sites. Vegetation change is driven by, but always lags behind, environmental change (Sheil, 1999). It is suspected that regeneration of these species is not a sudden occurrence but instead it occurs over a prolonged period after the canopy has closed and conditions have gradually become more suitable. With the low growth rate of most tropical forest species (Ernst, 1988; Worbes et al., 2003), the sampled areas probably did not cover the full range of successional phases exhibited by these late succession species. The plots considered in this analysis were determined based on woodland-forest delineation made on the 1985 satellite image and as such will only represent a woodland-savanna successional development of approximately two decades. It is suspected that these species did not have sufficient time to grow to larger diameters in the areas that were sampled. If, however, fire does not occur in these areas for the next few years, the established species will grow to overtake the early succession species (Skowno et al., 1999) and the reversion to the previous vegetation states will be almost impossible (Archer, 1990; Hudak et al., 2004).

5.5. Conclusion

With frequent disturbance, only fire resilient species may survive. Complete elimination of fire will provide opportunity for the forest species to get established and probably take over the area. Fire survival characteristics may no longer be necessary. Instead, better ability to compete for the available resources may play a role. In between these extremes, many vegetation types can exist and even be stable (Miles et al., 2001) although succession may still occur but following varied pathways (Bongers and Blokland, 2004).

In the interest of maintaining a dynamic ecosystem, it is critical to manage a diverse landscape encompassing all the successional stages of development. Should extreme protection restrictions be maintained, there is a risk of losing many of the species found in the woodland-savanna areas. However, on the same note, should intensive fire regimes be reinstituted, any successional development present in the woodland-savannas will be halted, and very little early successional forest will form. Therefore, a balance between the two scenarios may have to be identified and implemented.

It needs to be recognized that vegetation changes have implications at other levels also. Local communities who utilize these woodlands for various products may in the future be unable to obtain these products. Furthermore, resident woodland-savanna fauna populations may change due to habitat changes. Future studies ought to explore how the ecological changes in the woodland-savanna areas are impacting local communities and the fauna populations, especially the chimpanzees.

Figure 5.5: Vegetation in the very open woodland. Some of the grass grows to almost 2m, which would result in poor visibility during hunting.

CHAPTER 6

RESPONSE OF DIFFERENT VEGETATION TYPES TO A SIMILAR FIRE REGIME: A COMPARISON OF VEGETATION TYPES AFTER 46 YEARS OF BURNING

Abstract

The effect of regular burning of woodland vegetation in Africa over an extended period (46 years) was studied in the Murchison Falls National Park, Uganda. Areas identified as having different vegetation types in 1958 were revisited to analyse vegetation changes and to test the prediction that convergence would occur as a result of the regular fire. In each of the three vegetation cover classes, a transect was analysed.

Results show that the vegetation cover classes have changed and there is evidence of vegetation convergence. A Detrended Correspondence Analysis (DCA) and a Morisita similarity index analysis showed a good separation between the 1958 and 2004 transects for each of the vegetation cover classes. The DCA also showed that the three 2004 transects were compositionally closer to each other than the 1958 transects. The 2004 transects had also shifted away from the 1958 transects. Whereas in 1958 compositional similarity was highest between the *Terminalia glaucescens* conversion transect (T2) and the wooded grassland conversion transect (T3) (0.86), in 2004 it was most similar between the transects closest to Wairingo river (T1 and T2, correlation coefficient of 0.80). T1 was referred to as the *Terminalia* woodland transect. Comparing the 2004 transects to the 1958 transects, a low compositional similarity was observed. The highest was between T3-1958 and T3-2004 (0.62). Additionally, fewer indicator species (species specific for one transect) were identified in 2004 than in 1958 and, the transects shared more species in 2004 than in 1958. All the big trees (dbh ≥ 30cm) that existed along T1 in 1958 died off. Clustering of individual woody plants, a protective mechanism used by plants in presence of fire, was identified in each of the plots analysed.

To counterbalance the unifying effect of fire for the vegetation in the area and to maintain diverse vegetation, a variety of fire management regimes are needed.

Based on Grace Nangendo, Alfred Stein, Hans ter Steege and Frans Bongers (*submitted*). Response of different vegetation types to a similar fire regime: a comparison of vegetation types after 46 years of burning.

Chapter 6

6.1. Introduction

The effect of fire and elephant disturbance to woodland vegetation in Africa is well documented (Dublin et al., 1990; Eckhardt et al., 2000; Laws, 1970; Leuthold, 1977; Spence and Angus, 1971). With high numbers of elephants, their intensive grazing, browsing and rubbing on the boles of woody vegetation work together to reduce or deter growth of these plants (Ben-Shahar, 1993; Laws, 1970; Sheil and Salim, 2004; Smart et al., 1985; Van Wijngaarden, 1985). Fires reduce or prevent settlement of forest species in the savannas (Favier et al., 2004a) while promoting the survival of the fire resistant species (Smart et al., 1985). Fire and elephants being jointly active as disturbance agents have an intertwined effect: elephants open up thickets which in turn allow encroachment of more combustible grass thus creating conditions for easier spread of fire. Debarking of trees by elephants also makes the trees more susceptible to fire destruction (Buechner and Dawkins, 1961; Tafangenyasha, 2001; Yeaton, 1988).

Many studies were carried out during a period in which both elephants and fire were active disturbance agents and most of these emphasized the negative effect of high densities of elephants on large trees (Barnes, 1983; Laws, 1970; Lewis, 1986). This led to enforcing management policies, such as culling, which, coupled with poaching, almost led to extermination of elephants (Western and Maitumo, 2004) from many protected areas. After the reduction of elephants, little attention was paid to the effect of fire on the vegetation despite the continued debate on fire use as a management option in conservation areas (Trollope, 1993; van Wilgen et al., 1998). Monitoring studies on vegetation changes after elephant elimination were also rare and most were carried out soon after the elephants were reduced (Smart et al., 1985). In view of the ongoing use of fire as a management tool in conservation areas, a better understanding of the effects of fire on woody vegetation is needed (Sheil and Salim, 2004; Wheater, 1971), especially with respect to the determination of acceptable limits of change (Eckhardt et al., 2000).

The season of fire, fire frequency and fire intensity are major factors that influence tree survival (Gautier and Spichiger, 2004). The effect of these factors is, however, intertwined. The season of fire affects the species' reproductive ability and influences fire intensity, which in turn determines the species that survive after a fire. Fire intensity also increases in presence of a high fuel load (Leuthold, 1996; McShane, 1987; Sabiti and Wein, 1988; Salvatori et al., 2001), which would be the case after the elimination of the elephants (Smart et al., 1985). The frequency of fire relative to the life cycle of a plant and subsequent opportunities for seed formation will have great influence in determining the species that exist in an area (Chandler et al., 1983). Regeneration patterns are, however, determined by interactions between the disturbance regime and the species' biology (Kennard et al., 2002; Pickett and White, 1985; Sagar et al., 2003).

The spatial arrangement of woody plants in an area is in part determined by the species present, the life history survival strategy of the species (Leps et al., 2001) and the disturbance history of the stand (Wells and Getis, 1999). When the fire regime is an important disturbance factor, it controls the size of clusters of woody plants (Favier et al., 2004a). Clustering, on the other hand, reduces fire impact on the woody plants (Witkowski and Garner, 2000). Hence analysis of woody plants patterns would further our understanding of the plants' survival mechanisms in the prevailing conditions.

In the present study we evaluate changes in woody plants composition that have occurred over the last 46 years in 3 areas in Murchison Falls National Park. These areas were studied in 1958 and were then identified as belonging to different vegetation classes. Before 1958 the area was always burnt once a year during the hottest season (December to February) (Buechner and Dawkins, 1961). Despite recommendations made on fire regime variation for the different vegetation classes (Spence and Angus, 1971), a regular (annual) fire regime has been used for the last 46 years (Lock, 1977; Smart et al., 1985; Uganda Wildlife Authority, 2001). The questions addressed in this study therefore are; are plants spatially clustered along each transect? How did the vegetation change in the last 46 years? Is the change a convergent one? And, which could be the role of the fire regime in these changes?

6.2. Materials and methods

6.2.1. Study area

The study area is located in Murchison Falls National park, northwestern Uganda (Figure 6.1). The Park has an average elevation of 800m. The rainfall varies between 1,000 and 1,500mm annually and it falls mainly during the "long rains" from mid-March to June and the "short rains" in September and November. Wairingo area, the location of our study site, receives an average of 1270 mm of rain annually and has an annual average of 117 rain days (Laws et al., 1975). The main dry season is from mid December to mid February.

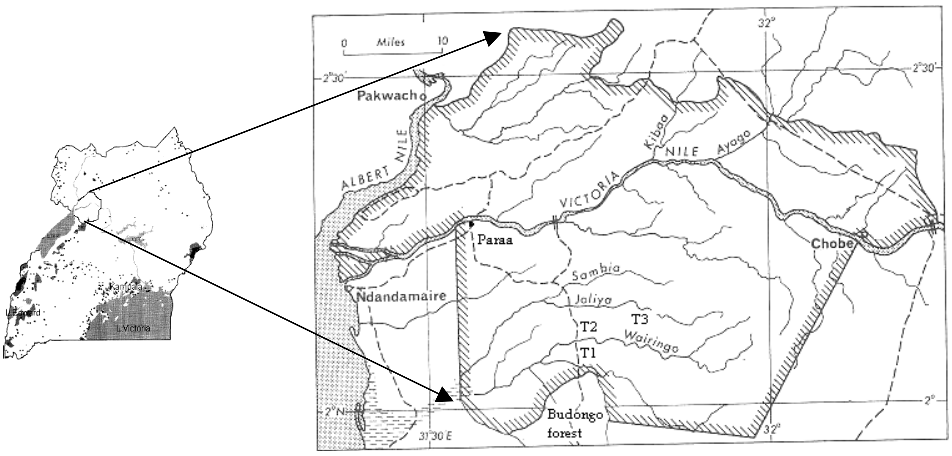

Figure 6.1: The map of Murchison Falls National Park showing the data collection sites (T1, T2 and T3) close to Wairingo river.

The park has a long history of disturbance, especially caused by elephants and fire use (Buechner and Dawkins, 1961; Hatton and Smart, 1984; Laws, 1970). Several short-term studies carried out on the effect of the disturbances on vegetation in the 1960s and early 1970s showed that with elimination of fire and/or elephants, there was higher vegetation regeneration (Lock, 1977; Spence and Angus, 1971). At that time inference to the previous vegetation states was based on circumstantial evidence e.g. vegetation relics. In 1958 Buechner and Dawkins had carried out a study in which they described the vegetation of Murchison Falls National Park. Part of the data was collected from the area close to Waringo ranger post. Here, the authors identified three vegetation classes i.e. a *Terminalia* woodland, a *Terminalia glaucescens* conversion and a wooded grassland conversion. The naming of the vegetation classes could have, probably, been prompted by what the authors observed in the field because they record that the woody plants within the area were being destroyed by a combined influence of the elephants (*Loxodonta africana*) and fire thus converting the woodlands into grassland areas. Within each of the vegetation classes, they collected data along a single transect. These same transects were revisited in the current study.

Although the stakeholders that carry out the burning have changed over time, the time and frequency of burning has not changed. At the time of Buechner and Dawkins' research, the local people set fires between December and February until the entire area was burnt (Buechner and Dawkins, 1961). This was done to provide grassy vegetation for wild as well as domestic ungulates and to ease the hunting activity by providing better visibility. Currently, the park authorities set the fire but local people also set fires at the fringes of the conservation area, which occasionally spread into the park. Each part is burnt once every year during the hottest season (December to February).

The park authority burns to provide fresh grass for the herbivores as well as to counteract the local people's burning, which aims at attracting animals to outside of the conservation area (Uganda Wildlife Authority, 2001).

6.2.2. Data collection

To be able to describe the vegetation changes in the last 46 years, we collected the same type of data and used the same methods as had been done earlier by Buechner and Dawkins (1961). They collected vegetation data along transects in areas of the different vegetation classes. Rectangular plots of 20 by 50m were randomly established at intervals ranging from 200m to 300m along transects running in the west-east direction. Buechner and Dawkins established three transects and data for this study was collected along these same transects. The first transect (T1) was located 500m south of the survey Marker (elevation 764m) at Wairingo ranger post, the second transect (T2) was located 1000m north of Wairingo ranger post and the third transect (T3) was located 10km northeast of the Wairingo ranger post. Along T1, T2 and T3, we established 10, 5 and 5 plots respectively, the same number of plots that was established by Buechner and Dawkins in 1958.

For each plot, we recorded plot coordinates and for all woody plants with dbh ≥ 2cm diameter at breast height (dbh) we recorded the dbh and species name, for woody plants of dbh < 2cm and height > 50cm, the species name and abundance of individuals was recorded. For one randomly selected plot on each of the transects T1, T2 and T3, coordinates were recorded for each woody individual (dbh ≥ 2cm) to allow for a more detailed analysis of woody plant distribution. These three plots are denoted P_1, P_2, and P_3 respectively.

Species identification was based on Eggeling and Dale (1952) and Hamilton (1991). Samples of the species that could not be clearly identified in the field by the botanist on the team were sent to the Uganda National Herbarium where they were identified. The 1958 species list was also checked for changes in species nomenclature.

6.2.3. Data analysis

The data set of 2004 was separated into 3 groups; trees (dbh ≥ 10cm), saplings (dbh ≥ 2cm <10), and seedlings (dbh < 2cm and height ≥ 50cm). Comparison of species abundance between the transects was carried out based on the three groups.

Distribution of woody individual ≥ 2cm dbh in 2004

To explore woody plants distribution at plot level, the positions of all individuals dbh ≥ 2 cm at a single plot along each 2004 transect were analyzed using a spatial point pattern analysis. Clustering is conceived as an adaptation of fire (Favier et al., 2004a) and the more extreme the clustering in an area, the more adapted the individuals are to fire disturbance. The spatial point pattern analysis used here relates the observed set of coordinates to that obtained by a pattern of the same intensity but observed from a completely spatial random (CSR) distribution of individuals. The latter is based on the assumption that the number of individuals in an area $|A|$ of site A follows a Poisson distribution with mean $\lambda|A|$ (Diggle, 2003).

The *K(h)*-function was chosen to model pattern in this study. It is estimated as

$$\hat{K}(h) = A/N^2 \sum_i \sum_j u_{ij}^{-1} I_h(h_{ij} \leq h) \quad i \neq j$$

where N is the number of individuals in A, h_{ij} is the distance between the i^{th} and the j^{th} individuals and $I_h(h_{ij} \leq h)$ is an indicator function which is 1 if h_{ij} is less than or equal to distance *h* and 0 otherwise. When *i* is the individual at a center of a circle passing through event *j*, u_{ij} is the proportion of the circle that lies within A.

To evaluate the significance of the distribution pattern displayed, i.e. if individuals occur in clusters or at regular intervals, simulation envelopes and averages of the plot were also calculated based on 999 simulations. The average of the simulation provides a reference line, and the maximum and minimum provide the 99% simulation envelopes. If $\hat{K}(h)$ falls outside the simulation envelope, there is evidence against complete spatial randomness (CSR). $\hat{K}(h)$ also takes care of the edge effect making it an unbiased estimator of *K(h)*.

1958-2004 vegetation changes

Before starting the detailed comparisons, a Paired Samples T-test was carried out to compare the population means, 1958 and 2004, for each transect. Abundance of individuals and number of species per transect were analyzed.

For the abundance of individuals, a significant difference of the means was obtained for all transects (Table 6.1). And for the number of species, a significant difference of the means was obtained for T2 and T3. It was now possible to proceed to the more rigorous comparisons.

Table 6.1: Comparison of the population mean for species abundance and number of species between the 1958 and 2004 data sets for each transect using Paired Samples T-test. N = number of individuals and S = number of species.

Transect	Variable		t	df	*p* = 0.05
T1	N	Equal variance assumed	-4.8	18	0.001
		Equal variance not assumed	-4.8	10.8	0.001
	S	Equal variance assumed	-1.1	18	0.29
		Equal variance not assumed	-1.1	16.6	0.29
T2	N	Equal variance assumed	3.2	8	0.013
		Equal variance not assumed	3.2	7.9	0.013
	S	Equal variance assumed	2.3	8	0.05
		Equal variance not assumed	2.3	5.2	0.067
T3	N	Equal variance assumed	3.8	8	0.05
		Equal variance not assumed	3.8	7.8	0.05
	S	Equal variance assumed	2.4	8	0.041
		Equal variance not assumed	2.4	6.6	0.047

To identify changes that had occurred between 1958 and 2004 along the transects, several methods were used. First we calculated the similarity coefficient (r) among the transects using the Sørensen similarity measure (Janson and Vegelius, 1981). Comparisons were made among the 1958 transects, among the 2004 transects and between the 1958 and 2004 transects.

Comparison between transects in terms of species composition was made using species relative abundance values for each transect in the respective year (1958 and 2004). Detrended correspondence analysis (DCA) was used to explore these differences. The proximity of transects to each other along the resulting DCA gradient space reveals similarity in species composition. Relative abundance values calculated as

$$\text{Relative abundance of a species} = \frac{\text{Abundance of a species}}{\text{Abundance of all species}} \text{ X } 100$$

To check for compositional similarity at plot level, the Modified Morisita similarity index, which is less sensitive to the abundance of the most abundant species than the unmodified one, was used (Wolda, 1983).

Species composition

To further test for differences in species composition between the transects we used the Multiple-Response Permutation Procedure (MRPP) and the Indicator Species Analysis of PC-ORD (McCune et al., 2002; McCune and Mefford, 1999).

MRPP is a non-parametric procedure used to test the hypothesis that no difference exists in composition between two or more groups of plots. As a distance measure between compositions of the plots we used the relative Sørensen distance, as it takes both composition (presence-absence of species) and abundance into account. A weighting option: $C_I = n_I / \sum n_I$ was used, which is the most widely used and recommend measure (Mielke, 1984). C_I is the weight and is dependent on the number of items in a group, say $_I$, and n_I is the number of items in group $_I$. We used 9999 permutations to statistically test if the within-group homogeneity is different from that expected by chance (random expectation). Both the MRPP and the indicator species analysis were calculated basing on prior identified vegetation cover classes for T1, T2 and T3.

Species identified as indicator species mainly occur in one group (transect) and, occur in most of the plots in that group. We predict that if there is significant difference between the 1958 and 2004 data sets, the species identified as indicator species in the 1958 data set will be different from those identified in the 2004 data set. And if the transects are converging, there will be fewer indicator species in 2004 as compared to 1958 since there will be more species shared among the transects of 2004.

For the Indicator Species Analysis, the output values of interest are the relative abundance (RA), relative frequency (RF), the highest indicator value (IV), a statistical significance of the indicator value (P) and the vegetation cover class in which a particular species had the highest indicator value. RA is the concentration of each species in each cover class and is expressed as a proportion of a particular species in a particular class relative to its abundance in other classes. And RF is the faithfulness of occurrence of the species in that cover class and is expressed as the percentage of sample units in a class that contain that species.

We also explored changes in the abundance of large trees (dbh ≥ 30cm) along T1. In 1958, large trees could mainly be found along T1. So, an independent table is presented for woody plants with dbh ≥ 30cm for only T1. Hence, to evaluate if there is still a good representation of the large trees along T1, the 2004 large trees were recorded against those identified in 1958 and the table was visually surveyed for differences.

6.3. Results

With the three transects combined, in 1958 a total of 25 species belonging to 17 families were identified and in 2004, 36 species belonging to 22 families. The three most abundant species in 1958 were *Terminalia velutina*, *Lonchocarpus laxiflorus* and *Combretum binderanum* and in 2004 they were *Combretum molle*, *Combretum collinum* and *Combretum binderanum*. Species that existed in 1958 but not encountered in 2004 were *Afzelia Africana, Albizia coriaria, Combretum guenzii, Crataeva adansonii, Dombeya rotundifolia, Harrisonia abyssinica, Pseudocedrela kotschyi, Securinega virosa and Strychnos innoccua* and the ones only occurring in the 2004 data set were *Albizia grandibracteata, Caloncoba schweinfurthii, Combretum collinum, Combretum molle, Dombeya mukole, Ficus sur,* *Grewia bicolor, Lannea barteri, Lannea schweinfurthii, Maytenus undata, Pappea capensis, Rothmannia urcelliformis, Strychnos cocculoides, Syzigium sp, Teclea nobilis* and *Vitex doniana.*

Considering the 3 size classes (trees, saplings and seedlings) along each transect, for the 2004 data the trees on T3 had the lowest number of species (10) and the trees on T1 had the highest (23) (Table 6.2). T3 also had the lowest mean values and, the lowest and the highest standard deviation, hence showing the largest variation. The median and the mean were almost equal for all groups at T1 and, for saplings and seedlings at T2 indicating a symmetric distribution for these groups. Overall, T2 had a higher mean number of species.

Table 6.2: Comparison of the 2004 number of species identified along the transects (T1, T2 and T3) located in the vicinity of Wairingo river in Murchison Falls National park, Uganda.

Transect number	**Number of plots**	**Groups**	**Number of species along transect**	**Range**	**Median**	**Mean**
T1	10	Trees	23	7-13	10	10
		Saplings	23	7-14	12	11
		Seedlings	19	7-14	10	11
		Total	29	14-16	14	15
T2	5	Trees	14	4-10	8	7
		Saplings	19	9-14	11	11
		Seedlings	20	8-15	12	12
		Total	26	14-17	16	16
T3	5	Trees	10	3-6	3	4
		Saplings	14	2-13	5	6
		Seedlings	22	4-13	11	9
		Total	24	12-15	14	14

6.3.1. Distribution of woody individuals $\geq$ 2cm dbh in 2004

P_1 had the highest number of individuals (160) followed by P_2 (115) and P3 had the lowest number of individuals (31). In the $\hat{K}(h)$ graphs (Figure 6.2), if the data points (circles) fall directly over the central line, it indicates that the distribution is completely random. If, however, points fall above or below the central line, it indicates that there is recognizable clustering of individuals at the distance indicated, or, respectively, that a regular pattern of distribution is found. The $\hat{K}(h)$ graph for P_2 shows a highly significant departure from CSR.

For distances less than 10m, P_2 shows a clustered pattern and for distances between 10 and 20m, it shows a regular pattern of distribution (Figure 6.2-P_2). This indicates that individual woody plants occur together in clumps that are less than 10m wide and these clumps are more or less spaced regularly at distances of 10 to 20 meters from each other. P_1 and P_3 also show a departure from CSR at short distances but this is far less significant than for P_2. P_1 clusters are up to 8m wide while P_3 clusters are up to 6m wide (Figure 6.2-P_1 & P_3).

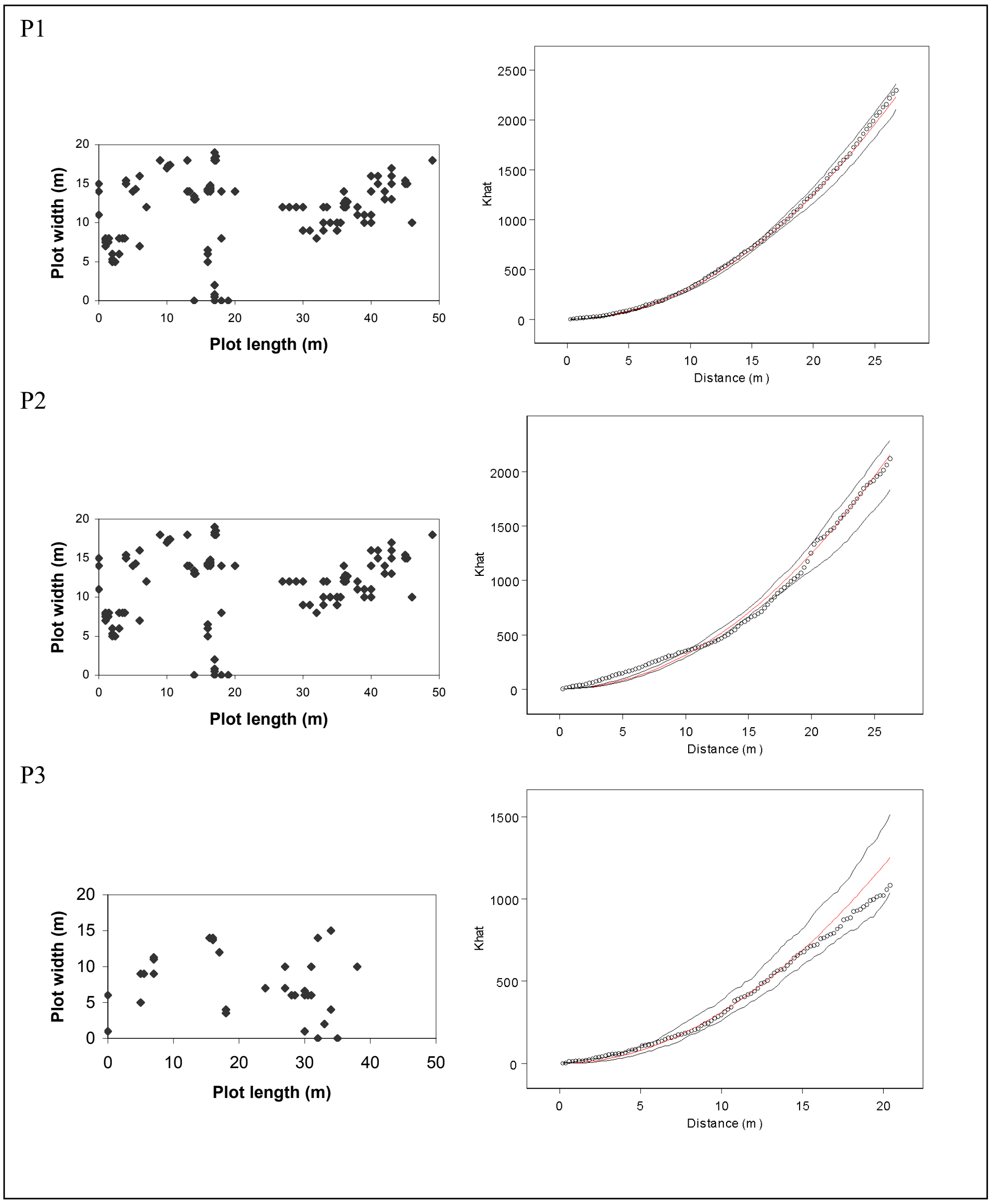

Figure 6.2: Woody plants distribution of an individual plot along each transect (T1, T2 and T3) shown both as a scatter plot and a K-function with the 99% confidence envelopes.

6.3.2. Vegetation change

Large changes over time occurred in the relative abundance of species found along each of the three transects. A comparison of species composition using the Sørensen similarity measure showed that in 2004, T1 and T2 had the highest compositional similarity (r = 0.80) (Table 6.3). In 1958, the highest compositional similarity was between T2 and T3 (r = 0.86). Comparison of the 2004 transects with their respective 1958 transects resulted in low coefficient values. The highest was between T3-1958 and T3-2004 (r = 0.62).

Table 6.3: Between transects comparison of species composition similarity using Sørensen similarity index. T1-58, T2-58 and T3-58 are the transects in 1958 and T1-04, T2-04 and T3-04 are the transects in 2004

Transect	**T1-04**	**T2-04**	**T3-04**	**T1-58**	**T2-58**
T2-04	0.80				
T3-04	0.78	0.72			
T1-58	0.51	0.51	0.54		
T2-58	0.46	0.50	0.49	0.83	
T3-58	0.53	0.59	0.62	0.81	0.86

The trees with dbh ≥ 30cm that existed along T1 in 1958 have all died off (Table 6.4). Only one large *Terminalia velutina* (dbh = 33.5 cm) was encountered and 2 dead ones could also be identified as a *Terminalia velutina* and a *Stereospermum kunthianum*. A few other dead ones were also encountered but they could not be identified because they had partly disintegrated. However, a new generation of trees (10cm ≥ dbh < 25cm) with large numbers of *Terminalia velutina* individuals now exists. A further check also revealed that Terminalia velutina had very low abundance of seedlings (DBH < 2cm and height ≥ 50cm).

Table 6.4: Comparison of 1958 and 2004 trees composing the *Terminalia velutina* woodland transect (T1) at Wairingo Ranger Post. **Plot No.** indicates the field plot at which the trees were identified. Woody plants of dbh ≥ 30 were recorded in 1958 and the same size limit was used in 2004. They are referred to as large trees.

		Living				Dead standing			
		1958	dbh ≥ 30cm	2004 dbh ≥ 30cm		1958 dbh≥ 30cm		2004 dbh≥ 30cm	
Species	Plot No.	No. of trees	Mean dbh (cm)	No. of trees	dbh (cm)	No. of trees	dbh (cm)	No. of trees	dbh (cm)
Combretum guenzii	8	2	43(40-45)						
Ficus dicranostyla	1	2	75(60-90)						
Ficus sp	7	1	90						
Stereospermum kunthianum	7							1	43.9
Terminalia velutina	1	2	40(30-50)						
	2	5	35(30-55)			2	25,25		
	3	5	35(30-45)						
	4	2	55(45-50)						
	5	5	40(30-50)					1	40.2
	6	3	50(35-65)			1	35		
	7	6	45(35-50)	1	33.5	2	25,70		
	8	9	40(30-45)			1	35		
	9	6	4.5(35-65)			2	10,25		
	10	5	45(40-50)						

Axis 1 of the DCA explained 42% of the variation and axis 2 explained an additional 12.8%. Along DCA axis 1 the 2004 transects are all far from the 1958 transects (Figure 6.3). The major variation in the data is thus explained by time. In 1958, T1 was very different from T2 and T3 (as shown by the difference along axis 2) but has become very similar with the other plots in 2004 (Figure 6.3). In 1958 transect T2 and T3 were very close and thus their composition was very similar. Transect T1 was different. In 2004 transects T1 and T2 are very close and both are further from T3. Changes in relative position among the transects between 1958 and 2004 show that both convergent and divergent processes are playing a role, as some transect combinations get closer while others get further apart. The location of the 2004 set of transects in the graph as compared to the 1958 transect, in that the transect sets are far apart, indicates that a shift in species composition of the whole set away from the 1958 species composition has occurred and all transects are moving in the same direction with respect to axis 1.

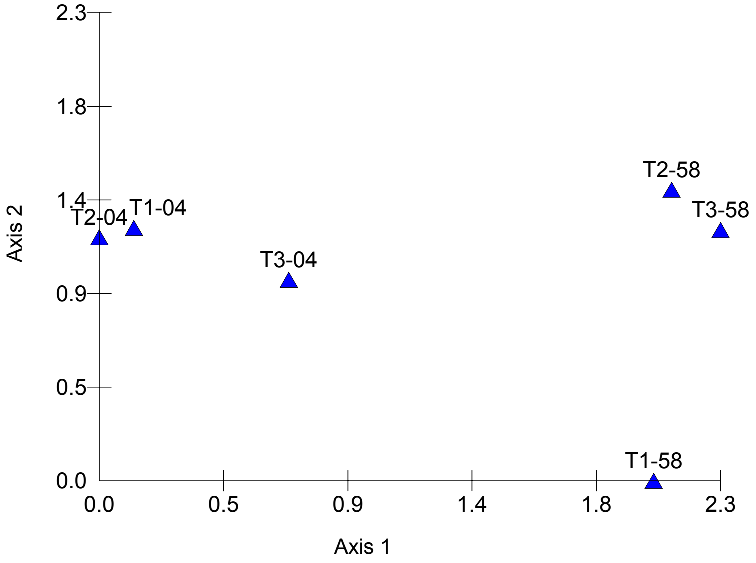

Figure 6.3: DCA graph indicating relationship between the transects in terms of their species composition. T1-58, T2-58 and T3-58 are the three transects in 1958 and, T1-04, T2-04 and T3-04 are the respective transects in 2004.

In 1958, T1 and T2 had *Terminalia velutina* as the most abundant species (with a relative abundance of 33.8% and 24.2% respectively). T1, additionally, had a high abundance of *Harrisonia abyssinica* (10.4%) and *Stereospermum kunthianum* (18.5%). T2 and T3 shared *Combretum binderanum* with a relative abundance of 21.8% and 11.9% respectively. T3 also had a high abundance of *Carpolobia alba* (27.7%).

In 2004, T1 and T2 shared *Combretum collinum* and *Combretum molle*, which did not exist in 1958, as the most abundant species with 15.9 and 17% respectively for T1 and 14.3% and 15.2% respectively for T2. *Combretum binderanum*, which was more abundant along T2 and T3 in 1958, is most abundant along T1 in 2004. Along T2, *Gardenia jovis-tonantis* and *Hymenocardia acida* are also highly abundant with 10.1% and 17.5% respectively. Along T3, *Stereospermum kunthianum* (20.9%) is the most abundant species.

Morisita similarity index also separates well the 1958 transects from the 2004 transects (Figure 6.4). Whereas the plots along each transect occur almost exclusively together in 1958, plots from the three transects are mixed in 2004 thus indicating compositional convergence of the plots in 2004.

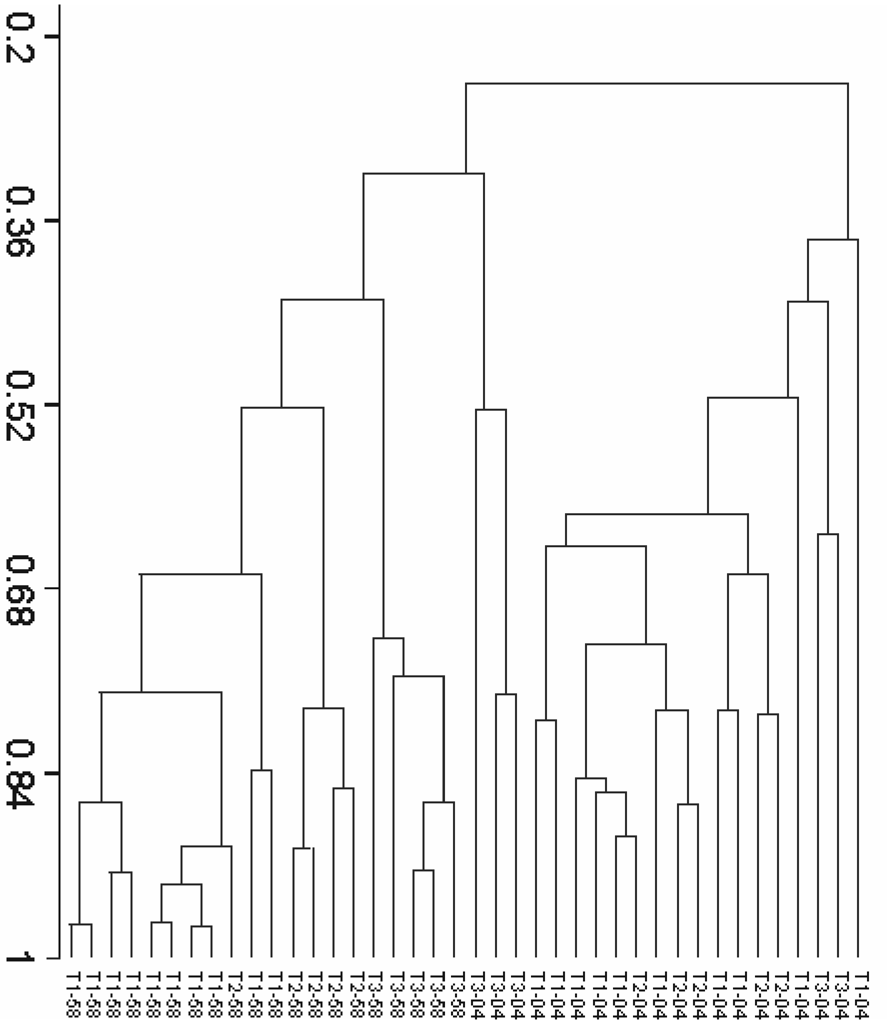

Figure 6.4: A dendrogram indicating species composition similarity between plots along both the 1958 and the 2004 transects analyzed using Morisita similarity index. T1-58, T2-58 and T3-58 are the three transects in 1958 and, T1-04, T2-04 and T3-04 are the respective transects in 2004.

6.3.3. Species composition

With MRPP, a significant difference in species composition between the transects was observed in both years with A=0.29 ($p=2*10^{-8}$) for 1958 and A=0.15 ($p=3.7*10^{-6}$) for 2004. Considering the p values for the two years, the 1958 transects were more dissimilar than the 2004.

The Indicator Species Analysis revealed that although there was a higher number of species in 2004 (36) as compared to 25 in 1958, there were fewer indicator species identified in 2004 (Table 6.5a & b). In 1958, 8 species had p values lower than 0.01 as compared to 2 in 2004. In this study, p is considered significant at 0.05. Hence in 1958 T1 had *Albizia coriaria* as a significant indicator species, T2 had *Albizia zygia*, *Bridelia schleroneuroides*, *Combretum binderanum*, *Combretum guenzii*, *Hymenocardia acida*, *Securinega virosa*, *Strychnos innocua* and *Terminalia velutina* and, T3 had *Gardenia jovis-tonantis* and *Securidaca abyssinicus*. In 2004, significant indicator species for T1 were *Albizia grandibracteata*, *Combretum collinum* and *Grewia bicolor*. For T2 they were *Gardenia jovis-tonantis* and *Hymenocardia acida* and, for T3 they were *Dombeya mukole* and *Maytenus undata*.

Table 6.5: Indicator Species Analysis output for (a) 1958 and (b) 2004. It indicates the concentration of each species along each transect (Relative abundance=RA), the faithfulness of occurrence of the species along that transect (Relative frequency=RF), the highest species indicator value across the transects (IV), the statistical significance of the indicator value (P) and the transect along which the highest indicator value of the species occurred.

(a)

Species	**RA-T1**	**RF-T1**	**RA-T2**	**RF-T2**	**RA-T3**	**RF-T3**	**IV**	**P**	**Classes**
Albizia coriaria	79	80	21	20	0	0	63.4	0.013	T1
Albizia zygia	5	30	60	100	35	60	60	0.021	T2
Bridelia schleroneuroides	7	40	73	100	20	80	72.9	0.005	T2
Combretum binderanum	1	20	78	100	21	100	77.7	0.004	T2
Combretum guenzii	2	40	77	100	21	80	77.2	0.003	T2
Gardenia jovis-tonantis	16	30	0	0	84	80	67.4	0.016	T3
Hymenocardia acida	1	10	88	100	11	80	87.9	0.001	T2
Securidaca abyssinicus	1	30	8	60	91	100	90.8	0.001	T3
Securinega virosa	2	10	76	100	22	40	75.6	0.004	T2
Strychnos innocua	8	60	81	100	11	40	80.6	0.001	T2
Terminalia velutina	28	100	65	100	6	80	65.5	0.001	T2

(b)

Species	RA-T1	RF-T1	RA-T2	RF-T2	RA-T3	RF-T3	IV	P	Classes
Albizia grandibracteata	85	80	7	60	7	20	68.4	0.018	T1
Combretum collinum	55	100	45	100	0	0	54.7	0.036	T1
Dombeya mukole	0	0	0	0	100	60	60	0.025	T3
Gardenia jovia-tonantis	33	80	66	100	1	40	65.6	0.028	T2
Grewia bicolor	60	100	36	100	4	80	59.7	0.021	T1
Hymenocardia acida	27	90	72	100	1	20	71.6	0.007	T2
Maytenus undata	0	0	4	20	96	80	76.6	0.002	T3

T1= *Terminalia* woodland, T2= *Terminalia glaucescens* conversion and T3= Wooded grassland conversion. P is significant at p = 0.05

6.4. Discussion

Many changes have occurred in the vegetation cover of the whole area during these 46 years. The species composition similarity values between the respective (1958 and 2004) transects (Table 6.3) and the disappearance of almost all the large trees along T1 (Table 6.4) are evidence of the changes that have taken place. Elephants may have played a role in the reduction of the large trees (Buechner and Dawkins, 1961) but there was evidence of elephant disturbance tolerance (Sheil and Salim, 2004) on some of the dead large trees encountered (e.g. Figure 6.5a). Although the tree was highly scarred, it grew back to cover the damaged area. Such trees probably died later when they could no longer withstand the impact of the fires. Many of the living individuals also had old scars that were the result of previous elephant gouging. Within plot 5 along T1, there were as many as 5 dead trees dbh >30cm and several others in its vicinity. Unfortunately, most of them could not be identified. These were most likely not killed during the time when elephants were abundant (in the 1960s) but must have died recently. Hence, we conclude that the fire regime that has remained unchanged for such a long time has contributed to the loss of the large trees that did survive destruction by elephants. This is in line with the findings of Ben-Shahar (1998) who indicates that fire precipitates the decline of mature trees in woodlands.

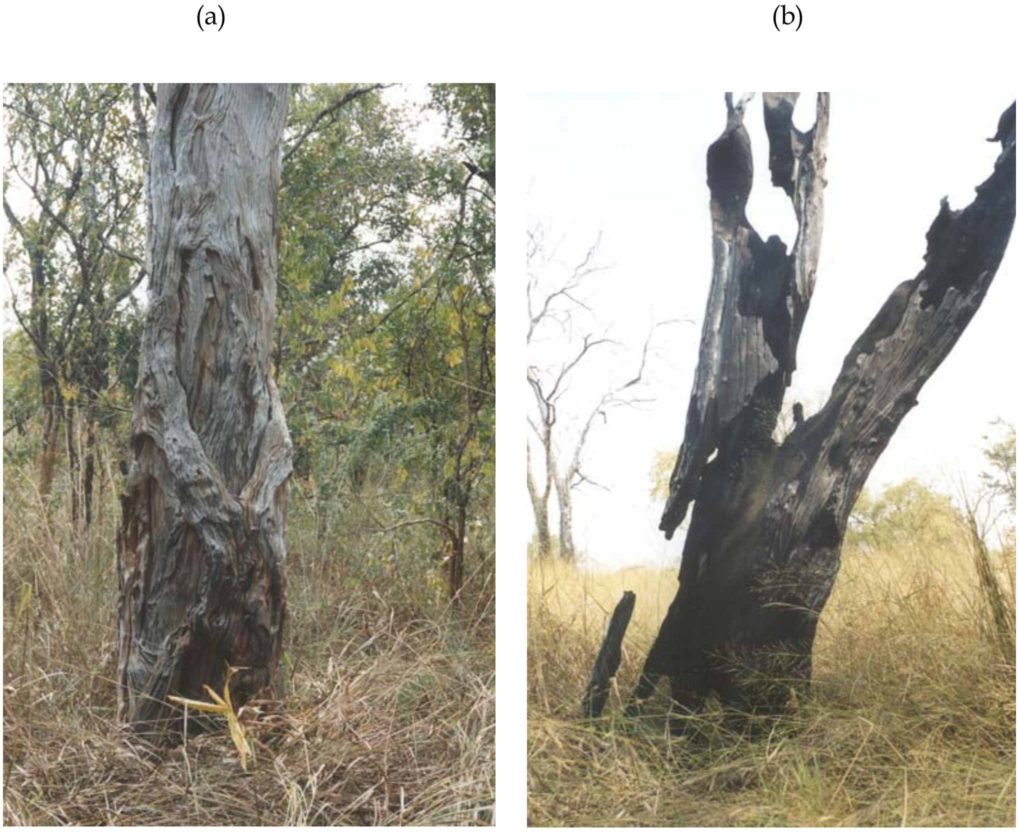

Figure 6.5: Photographs of some of the dead trees with dbh > 30cm encountered along T1. The pattern on (a) shows parts that had been gouged by elephants but has eventually recovered and the tree continued growing. The constant fires have slowly eaten away on the tree in (b). Two other trees, in the background, were also dead.

Although the transects differ significantly in both 1958 and 2004, there is evidence that the transect vegetations have greatly changed, especially that of T1. The closeness in location of T1-2004 to the other 2004 transects on the ordination graph (Figure 6.3), the higher compositional similarity, at plot level, between transects in 2004 as compared to the 1958 plots (Figure 6.4) and the identification of fewer indicator species in 2004 as compared to 1958 (Table 6.5a & b) are all indicators of convergence of the vegetation classes represented by the transects. The shift in location of all 2004 transects, away from the 1958 transects, and their being compositionally close (Figure 6.3) is an indicator that the vegetation is adjusting to suit the existing fire regime (van Wilgen et al., 1998) and as a result the area may become more homogeneous. If the current fire regime is maintained into the future, a homogeneous vegetation class that is compositionally different from any of the 1958 transects may emerge. To maintain the varied landscape, a variation in burning frequency is needed with a reduction of fire in some vegetation classes (Skowno et al., 1999) especially the *Terminalia* woodland (Spence and Angus, 1971).

Terminalia velutina had the highest relative abundance along T1 and T2 in 1958 but in 2004, *Combretum collinum* and *Combretum molle*, which are more adapted to frequent fire disturbance, had become most abundant. Taking tree size (dbh) as a proxy for age (Wells and Getis, 1999), we argue that most of the *Terminalia* trees on T1 regenerated around the same time since most of them occur within a narrow dbh range (10cm > dbh < 25cm, data details not shown). The 1958 large *Terminalia* trees supplied seed, which resulted into the current individuals with dbh > 10cm, and as the large trees died off, there were hardly any mature trees to produce new seed and thus the lower *Terminalia velutina* relative abundance in 2004. The death of the parent trees, however, opened up the canopy and also left behind a nutrient rich environment (Ludwig et al., 2004) which enabled the regenerated plants to thrive.

Whereas high numbers of herbivores, especially elephants, have been associated with destruction of woody vegetation (Laws, 1970; Lewis, 1986), their elimination often leads to increase in vegetation cover but with lower diversity of both grasses and woody species (Smart et al., 1985). Increase in grass cover in turn leads to more intense fires (Huston, 1994a; Salvatori et al., 2001) and since burning has gone on for a long time, the areas have started to respond to the disturbance in a similar fashion (Shackleton et al., 1994).

Analysis of distribution patterns revealed clustering of individuals, which has often been identified as a fire survival mechanism (Favier et al., 2004a). The pattern displayed by the P_2 plot (Figure 6.2) is probably an indicator of a survival mechanism of some of the dominant species, *Gardenia jovis-tonantis* and *Hymenocardia acida,* which were often encountered in clusters. Elsewhere, other species e.g. *Pinus torreyana* have been observed to display similar patterns in presence of regular burning (Wells and Getis, 1999). The clustering reduces fire penetration by reducing grass cover within the cluster and the young trees also protect the parent tree from subsequent fires (Favier et al., 2004a; Witkowski and Garner, 2000). Clustering also ensures survival of most seedlings which often occur below the parent plant (Acharya, 1999; Wilson and Witkowski, 2003) where the fuel load is often lower due to the shade of the crowns of the parent trees (Gautier and Spichiger, 2004). Although the distribution pattern was more evident in P_2, all three transects displayed some level of clustering (Figure 6.2). We suggest that woody plants in these vegetation classes use clustering as a mechanism to protect themselves against the existing fire disturbance regime.

The park authorities aim at creating a landscape with diverse habitats (Spence and Angus, 1971; Wheater, 1971) and variation of fire use has been recommended for this purpose (Uganda Wildlife Authority, 2001). However, efforts made over the years to vary the fire regimes in the park (Wheater, 1971) have had little success because of the increase in human settlement in the vicinity of the park and the low financial and human resource to implement the plans. The annual fires (e.g. Figure 6.6) have in turn destroyed almost all the big trees. And since these are the main seed source, the consequence has been a reduction in the abundance of some of the species, especially *Terminalia velutina* in the regeneration (dbh < 2cm). Increase in grass cover due to fewer grazers and death of the large woody plants also fostered the occurrence of hotter fires, which in turn favored more fire adapted woody species. An example is the replacement of *Terminalia velutina* along T1 and T2, as the most abundant species, by *Combretum* species.

All sampled areas in this study have changed in woody plants cover and composition, and there is ample evidence that the vegetations are converging. To counterbalance this unifying effect, and since one of the aims of the park is to create a diverse habitat, fire regimes need to be varied over the area.

For future management support, permanent plots for vegetation monitoring in the park need to be (re) established and maintained. Thresholds of vegetation change need to be set which, if reached, should trigger an assessment of the causes of the change and which should lead to possibly corrective actions. Additional data sets from other parts of the conservation area, e.g. Pandera woodlands, Rabongo forest and the banks of River Nile ought to be analyzed and interpreted to substantiate the observed trend.

Figure 6.6: *Terminalia* woodland area. The area was burnt a day after we finished collecting the data along the transect (T_1).

CHAPTER 7

CHANGING FOREST-WOODLAND-SAVANNA MOSAICS: SYNTHESIS AND IMPLICATIONS FOR CONSERVATION

7.1. Introduction

The theme of this dissertation is how woody plant vegetation in forest-woodland-savanna (FWS) mosaics varies in terms of species composition and how it has changed over time. FWS mosaics cover extensive areas of the tropical world. The need for their conservation, because of the high plant and animal species diversity they host, has recently been recognized (Furley, 1999). To conserve the woody species in the mosaics, there is need to know what flora exists within the area, how it is distributed and the mechanisms that have maintained it. This would then provide forest and park managers of such areas with a baseline on which to build better-informed conservation plans. Hence the aim of this study is to assess the vegetation variation and the spatial and temporal changes in FWS mosaics. The hypothesis is that the forest, woodland and savanna each contribute significantly to the diversity of FWS mosaics.

In the Introduction a number of research questions were asked. The first two questions concern the variation within the Budongo Forest Reserve.

1. What vegetation classes can be identified in the area and what classification method best differentiates them?
2. How does tree species composition and vegetation structure vary over the area?

We then investigated if there was temporal change taking place in the area and the factors that might be influencing such a change, focusing on the questions:

3. How has the vegetation cover of the area changed over time?
4. What role has management played in influencing vegetation change?

Since it is very hard to point to fire as a major factor causing change without experimentally testing it, a different area with a known, long term (over 40 years), fire regime was studied to assess the effect of fire on woody vegetation. The main research question was;

5. How do woody plants in the different vegetation cover classes respond to a regular fire regime?

The obtained information from this study will enable managers to better plan the conservation of FWS mosaics. In the last part of this chapter I, therefore, discuss the implications of the research results for the conservation of FWS mosaics in Uganda.

In the following sections a synthesis of the study is presented starting with vegetation variation, followed by vegetation changes and the implicated causes of change. One management aspect, fire, is discussed thereafter. Finally, the implications of the research findings to conservation of FWS mosaics are presented.

7.2. Vegetation cover and woody plant variation within the mosaic

The vegetation of the northern part of Budongo Forest Reserve can be separated into discrete vegetation cover classes (Chapter 2). The vegetation cover classes identified are Forest, Closed woodland, Open woodland, Very open woodland and Wooded grassland (Figures 2.2 & 2.3). They were best identified using SAMExpert, a combination of Spectral Angle Mapper (SAM) classifier and an Expert System achieving a 94.6% overall classification accuracy. In this method satellite image information and plot information e.g. slope and canopy cover were combined using a geographic information system (GIS). Conventional classification methods i.e. Maximum Likelihood and SAM, when applied alone, gave consistently lower classification accuracy than when they were combined with the Expert System (Table 2.2.). Since each FWS mosaic is unique, combining satellite image information with site-specific factors, e.g. slope or soil characteristics, may hold the key to acquiring high accuracy maps of mosaic landscapes.

The vegetation cover classes identified were separable in terms of species composition and vegetation structure (Chapter 3). The differences in vegetation structure between cover classes were most evident in basal area (Figure 3.5c). Each cover class also had indicator species that could be used to identify it. Analyzing the species turnover along a compositional gradient revealed that the species occurred in a continuum (Figure 3.2). Many species, as evidenced by the species abundance plot (Figure 3.4), are wide ranging though they may have a clear optimum, which occurs at species-specific locations along the gradient. Hence, although vegetation cover classes are evident, the species composition of the classes overlaps.

Tasseled Cap (TC), a continuous classifier i.e. no descrete classes, ordered well the species composition of the area. This was evidenced by its high correlation with the species composition gradient (Table 3.2). The vegetation cover classes also occurred in a sequence (from forest to wooded grassland) along the continuous distribution (Figure 3.3b). TC differentiates well areas of varying vegetation structure (Cohen and Spies, 1992) and this feature was especially evident in the study area. TC would, therefore, be a very useful means of obtaining a quick overview of vegetation variation of a FWS mosaic.

The area studied had low variation in several environmental factors e.g. parent rock, soil, rainfall and topography, which led to the identification of fire as a major cause of variation in vegetation. Variation in fire disturbance has been isolated in other studies as a major cause in woody plant variation (Dezzeo et al., 2004; Grant, 2003). This was also true for our study in that the species gradient observed had a high correlation with the fire regime. Plots belonging to the different fire regimes i.e. areas of no fire, old fire and recent fire were also separable in terms of species composition (Figure 3.3a). Accessibility to a protected area, as observed elsewhere (Acharya, 1999; Obiri et al., 2002), also had a significant correlation with species turnover. Although not investigated, seed dispersal mechanisms may play a role in the colonization process in the FWS mosaic since this has been observed to influence species composition of disturbed areas elsewhere (Belsky and Amundson, 1992; Brunet et al., 2000; Hovestadt et al., 1999; Ohsawa et al., 2002).

Using a combination of the vegetation cover class information for each plot and other plot information in a GIS environment proved crucial for analyzing the characteristics of the FWS mosaic vegetation cover classes. If various FWS mosaics would be analyzed in a comparative way, considering factors that are highly distinguishable between classes e.g. basal area and species composition, standardized classes with specific ranges could be established for the identified characteristics. These could then be used to monitor changes in the vegetation classes. Knowledge on extreme changes (changes exceeding or falling below accepted limits for a specific vegetation cover class) could direct intervention measures.

Species diversity showed a decrease at either end of the vegetation composition gradient. When our data was combined with Eggeling's (Eggeling, 1947) data (Figure 3.6), the compositional convergence, at the *Cynometra* end of the forest, were more evident. Eggeling's data also fitted well with the rest of the data indicating that both the north and south of Budongo Forest Reserve belong to the same compositional gradient. Eggeling set up and collected data from forest plots, which are now some of the oldest permanent forest plots in Africa. His work showed that species richness, in addition to declining at the colonizing end of the forest, also declined in late succession. Connell later adopted Eggeling's account of forest succession as the main illustration for his Intermediate Disturbance Hypothesis (IDH) model (Connell, 1978). Our data fitting well with Eggeling's data is a fine extension of this model.

The species diversity generally decreased from forest to wooded grassland. The open woodland, however, showed a greater decrease creating a slump in the downward trend (Figure 3.5b). Using a simplified division, the species could be divided into forest and savanna species. It is, however, important to keep in mind the fact that the peak abundance for a species may have been in the savanna, forest or the woodland area. Whereas the closed woodland had a high number of forest species in addition to the savanna species, the open woodland mainly had savanna species. It is also only within the open woodland areas that an almost monodominance of *Terminalia velutina* was found. The environment in the open woodland seems hospitable to very few woody species. The species numbers increase in the very open woodland where the canopy is more open and fires are probably more frequent then they drastically decrease in the wooded grassland. Most of the individuals encountered in such areas had recent fire scars and displayed fire resistance traits e.g. a thick bark, peeling off of the old bark and good sprouting ability after a fire (Gashaw et al., 2002; Saha and Howe, 2003; Vesk and Westoby, 2004).

The vegetation variation within the forest area (Eggeling, 1947; Plumptre, 1996; Sheil et al., 2000) and that within the woodland and savanna areas, has resulted in the occurrence of a high variety of species in Budongo Forest Reserve. Combining the species identified in the woodland and wooded grassland areas with those that occur in the forest would therefore result in a higher number of species for the reserve than if some of the vegetation cover classes were eliminated. Some of the species observed in the forest had most of their seedlings in the woodland and vise versa. These vegetation cover classes, therefore, complement each other as far as species composition is concerned.

7.3. Changes in vegetation cover and its relationship with species composition and management

Vegetation change for the woodland areas was evaluated over a 17-year period using satellite image differencing where pixel-by-pixel subtraction is applied. Changes in vegetation cover were therefore interpreted as vegetation increase or decrease. Between 1985 and 2002 both decrease (14.3% of the area studied) and increase (in 15.1%) in vegetation cover were observed. Most of the increase in vegetation occurred between the two forest blocks (Main Budongo and Kaniyo-Pabidi forests) and west of Kaniyo-Pabidi forest (Figure 5.1). On the other hand, vegetation cover decreased in the northwest of Main Budongo and the northern part of the study area.

Species like *Lonchocarpus laxiflorus*, *Grewia mollis* and *Combretum collinum* occurred at one end of the gradient (early succession) and others e.g. *Albizia zygia*, *Celtis durandii* and *Alstonia boonei* occurred at the other end (late succession) (Figure 5.2). Vegetation change values (1985-2004) explained a significant portion of the variation in species composition along the gradient, when analyzed with multivariate techniques (Chapter 5).

The differences in vegetation change relate to differences in management. Whereas in the areas jointly managed by the Forest Department (FD) and the Uganda Wildlife Authority (UWA), vegetation cover generally increased, in areas independently managed by either the UWA or the FD, a decrease in vegetation cover was found. This difference is strongly related to the differences in fire management: in the areas under joint management fire use and the local peoples' access is strongly restricted. In the areas managed by the UWA only, fire is set mainly once a year in the hottest season by either UWA staff, road maintenance personnel or poachers (Uganda Wildlife Authority, 2001; Wheater, 1971). For areas managed by FD and are easily accessed by the local people, local people set fire annually in the hottest season of each year.

Whereas some species e.g. *Combretum collinum*, *Grewia mollis* and *Lonchocarpus laxiflorus* regenerated and also attained larger diameters (dbh ≥ 10cm) in the early part of the species succession gradient (Figure 5.4), others e.g. *Maesopsis eminii* regenerated in the early part but only attained larger size in the late part of the species succession gradient. Still others e.g. *Uvariopsis congensis*, *Cynometra alexandri* and *Pterygota mildbreadii* regenerated in late part and also attained larger sizes in the late succession part.

Although not fully explored in this dissertation, based on field observations and dbh measurements, some species e.g. *Albizia grandibracteata* had most individuals with dbh ≥ 10cm in areas of less frequent disturbance but individuals occurred in the whole range from forest to wooded grassland. Other species e.g. *Funtumia elastica* had individuals with dbh ≥ 10cm in the forest but smaller size individuals mainly occurred in areas of less frequent burning i.e. closed woodland and open woodland.

In this study, the aspect of the origin of the FWS mosaic has not been addressed but studies carried out in the Albertine rift valley, to which this forest reserve is adjacent, indicate that savannas existed in these areas thousands of years ago (Beuning et al., 1997). It has also been suggested that savanna vegetation in much of East Africa is maintained by fire (Hopkins, 1992; Paterson, 1991). In the absence of fire, the vegetation develops to more closed woody vegetation.

High numbers of elephants have also been observed to be a major cause of changes in vegetation cover (Barnes, 1983; Buechner and Dawkins, 1961; Eckhardt et al., 2000; Laws, 1970; Lewis, 1986). These animals either destroy trees or debark them so that they are susceptible to fire (Buechner and Dawkins, 1961; Tafangenyasha, 2001; Yeaton, 1988) and, they browse on the seedlings as well. The tree composition of such an area is therefore determined by the survival traits (e.g. having a spiny or toxic bark), sensitivities and response to disturbance of the existing woody plants (Sheil and Salim, 2004)). Van de Vijver (1999b), on the other hand, found that in Tarangire National Park, Tanzania, the elephants did not kill the trees but reduced them to lower height classes. At the time of high abundance of elephants in Budongo Forest Reserve and Murchison National Park, Uganda, Laws (1975) observed that the forest edge woody plants e.g. *Acanthus pubescens*, which prevented the fire from penetrating into the forest, were often destroyed by elephants. This created the starting point for grass encroachment into the forest and thus fire destruction of forest edges. At the time of the current study, no more elephants existed in the Budongo Forest Reserve. As a result, the whole range of species including the mid successional species, which were found to be missing in Rabongo forest (Sheil and Salim, 2004), were well represented.

7.4. Impact of regular fire on woody plant survival

Three transects, located in Murchison Falls National Park, that differed in vegetation cover were evaluated in terms of woody plant composition change. All transects had changed drastically after a period of 46 years. The species composition of all three transects shifted in the same direction (Figure 6.3). The Sørensen similarity coefficients for the transects in 1958 and in 2004 were high but a comparison between the 1958 and the corresponding 2004 transects resulted in low similarity coefficients (Table 6.3). A large number of the species that existed in 1958 (Chapter 6) were encountered no more in 2004 but some new species had become very abundant. Among the newly established species, the genus *Combretum* was the most abundant on all the transects.

Large *Terminalia velutina* individuals that existed in high numbers in 1958 along the *Terminalia* woodland transect (T1) were not encountered in 2004. In 2004, there were also very few *Terminalia velutina* seedlings along T1 yet it was the most abundant species along this transect in 1958. Since seedlings mirror the future forest (Sheil, 1999), it can be argued that the *Terminalia* woodland that once existed in this area is in a process of disappearing unless drastic measures are taken to reactivate seedling establishment. The vegetation most probably is changing to suit the existing fire regime, as has been observed else where (Shackleton et al., 1994). In figure 6.3, the 2004 transects are more clustered than the 1958 transects and they are away from the 1958 transects. At the same time, there were fewer indicator species in 2004 than in 1958 (Table 6.5a & b) and species composition at plot level, for the three transects, was more similar in 2004 than 1958 (Figure 6.4). This indicates convergence.

7.5. Fire, species composition and vegetation structure interrelationship in the study area

The events that occur in a dynamic FWS mosaic are interrelated. Whereas the vegetation cover of an area is a reflection of the species composition and vegetation structure, the species composition and vegetation structure are a result of the change processes. The vegetation changes are, in part, driven by the variation in the fire regime over the area. Fire presence or absence and its frequency, influence the level of canopy closure and the species that can regenerate and grow in an area.

Based on what was observed elsewhere, through the study of permanent forest plots (Verburg et al., 2003), an attempt can be made to explain the trends that occur in a FWS mosaic. After a fire, seeds of existing trees, which are often fire resistant, and other species (pioneer species) that have good dispersal ability get established (Acharya, 1999; Hovestadt et al., 1999; Wilson and Witkowski, 2003). If no fire occurs again, these grow to close up the canopy creating conditions suitable for forest species establishment. If the time after the fire is long enough, the forest species regenerate and grow to replace the fire resistant and the pioneer species. If, however, a fire re-occurs, the fire resistant species will persist and pioneer species will again regenerate. If the fire occurs often enough, even the pioneer species may be eliminated leaving only those species that are adapted to fire disturbance. These differences in the fire regime i.e. frequent fire areas and less frequent fire areas plus the no fire areas create the FWS variation in species composition and structure.

7.6. Conservation implications

This study has shown that an interesting variation in vegetation exists over the Budongo Forest Reserve. The vegetation cover classes identified are compositionally separable. Each vegetation cover class has indicator species that can typify it. These then are unique vegetation cover classes and need to be treated as important entities of the FWS mosaic when planning for conservation - a portion of each of the vegetation cover classes needs to be conserved to ensure a comprehensive species diversity coverage.

Knowledge of the compositional dynamics is central to understanding the ecological processes (Sheil et al., 2000). The species occur as a continuum along a compositional gradient. Some of the species e.g. *Uvariopsis congensis* have a restricted distribution and occur at one end of the compositional gradient. Others e.g. *Combretum collinum* occur at the other end of the gradient. Yet others e.g. *Funtumia elastica* occur over a wide range but have a peak abundance in a specific location along the gradient. To conserve the variation in species observed in this study, a representative portion of each part of the gradient will have to be maintained.

A large number of species identified in this study are wide ranging i.e. they occur in more than one vegetation cover class. This means the species composition of a particular vegetation cover class is not confined to that vegetation cover class and the species diversity found in a specific vegetation cover class is dependant on other vegetation cover classes for its maintenance. To conserve the diversity of such a vegetation cover class would require conservation of the adjacent vegetation cover classes, which it shares species with. And identification of a vegetation cover class should not be based on species occurrence alone but also on their proportional abundance since many species occur in more than one vegetation cover class.

The forest edge provides for species that do not occur in extremely closed forest environments, species whose juveniles occur along the forest edge but whose big trees occur inside the forest, and movement of the forest edge front (Favier et al., 2004b). Laws (1975) observed, during the period of high disturbance of the woodland areas in Budongo forest, that *Cynometra alexandri*, a climax species (Eggeling, 1947), occurred at the forest edge. This indicates that, at the time, there was limited regeneration of forest edge species (or that the edge changed during the lifetime of this species). Also the species mixture (forest and savanna species) that was encountered in the closed woodland during the current study did not exist at the time (late 1960s). In order to maintain the varied range of species that occur along the forest edge, there is need to vary its disturbance levels thus providing for forest progression in some areas while also keeping a relatively open canopy environment in others.

The relatively high correlation coefficient ($r = -0.59$) observed between change in vegetation cover (1985-2002) and the gradient in species composition in the woodland areas, suggests that the gradient in species composition also reflects the changes in vegetation taking place in the area. The gradient in species composition also showed a high correlation with the fire regime. The changes in vegetation taking place, as a result of changes in fire management in the area, therefore in part determine the species composition. To maintain the current species composition, the forces that drive change will have to be controlled.

It was also shown that whereas some species only occur in the early part of the species succession gradient (Figure 5.4), others occur in the late succession part. For another group of species, the different size classes (DBH ≥ 10cm, 2cm ≤ DBH < 10cm and, DBH < 2cm and ≥ 50cm in height) occupy different positions along the succession gradient. Whereas for the early and late succession species, the specific environment in which they occur needs to be conserved, for the ones whose diameter classes are more spread along the successional gradient, their continuity will depend on conserving all succession stages that accommodate these diameter classes.

A combination of local people's burning practices, where small areas may be burnt in several sites, and the FD and the UWA restrictions have complemented each other to create a more complex mosaic in this area. This has facilitated the establishment and maintenance of a variety of species. On the other hand, it is evident from this study (Chapter 4) and work done elsewhere in Uganda (Lwanga, 2003) that in absence of fire the forest takes over the woodland and savanna areas. Eggeling (1947) also argued that the woodland and savanna areas provided areas for forest expansion and that this maintained the succession of the forest communities. In order to maintain the mosaic landscape, there is need to establish a balance between forest establishment and, woodland and savanna maintenance. This will require identification and implementation of a balance between fire establishment and fire restriction. There is also need to control the extent of areas burnt at any single burning event.

Fire is vital for the control of bush encroachment. For Budongo forest, as for many other forests in Uganda, early burning is recommended (Forest Department Uganda, 1997) but it is hardly practiced by the Forest Department staff. This is due to inadequate staffing at the forest station (Forest Department Uganda, 1999) and lack of explicit fire management plans yet the forest officers have no training in the aspects of fire management. There are also no funds allocated for this activity yet active fire management is an expensive venture (Skowno and Bond, 2003).

The above issues may need to be addressed at policy level where the financial implications are considered. There is need for the policy makers e.g. at the ministry level and the institutional (National Forest Authority[*]) level to recognize the value of FWS mosaics. This will then allow for planning for such landscapes, including allocation of funds and personnel. Forest officers in charge of such areas also need special training on fire management.

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[*] As of 2004, the National Forest Authority took over from Forest Department, Uganda the stewardship of all Central Forest Reserves.

According to the Forestry Nature Conservation Master Plan (1999), the part of Budongo forest used in this study includes a recreation area (Kaniyo-Pabidi forest), a nature reserve (north of Kaniyo-Pabidi forest) and a buffer zone (south and west of Kaniyo-Pabidi forest). In this study, a lot of vegetation variation, which is of conservation value, was observed in the nature reserve and the buffer zone. If the "hands off" type of management currently practiced in much of this area is left to continue, the vegetation variation will be lost through bush encroachment. To maintain the conservation values for which these areas were set aside, active management of the area, where fire use is employed, will have to be revived.

The use of fire is beneficial to certain vegetation cover classes but when used in excess, it may destroy the very vegetation it was meant to conserve. Whereas a vegetation cover class like the *Terminalia* woodland requires fire, which prevents establishment of forest species (Favier et al., 2004a), annual burning carried out for 46 years has drastically reduced the abundance of *Terminalia velutina*, which was previously the most abundant species in that area (Chapter 6). Considering the observations made in Chapter 6 concerning the *Terminalia* woodland, the areas that currently host abundant *Terminalia velutina* i.e. the closed woodland and the open woodland (Chapter 3) require less frequent fires (3 to 5 year intervals[*1] and preferably early burning) for their maintenance. The forest requires no fire disturbance (in fact it would not tolerate it). The very open woodland and wooded grassland require frequent fire disturbance (2 to 3 year interval for the very open woodland and one to two year interval for the wooded grassland and preferably late season burning[*2]). For the conservation of a landscape that varies in vegetation cover, there is, therefore, need to vary the fire regimes. Our findings corroborate earlier experimental work carried out in Uganda (Spence and Angus, 1971).

Although it is not the main focus of this study, it needs to be noted that the animals resident in the mosaic areas may also be affected if the forest colonizes most of the area. Bird species vary with vegetation structure (Skowno and Bond, 2003). Animals that seasonally vary their feeding sites i.e. using the forest in the wet season and, the woodland and savanna in the dry season, or vise versa, may have a problem in finding their food if some of the necessary vegetation types are lost. Taking an example of the Chimpanzees resident in Kaniyo-Pabidi forest, under normal circumstances, they nest in the forest and feed on forest resources (especially fruits) for most of the year but, mainly in the months of September and October, cross over daily to the woodland-savanna areas for fruits of *Vitex doniana* and *Grewia mollis*.

[*1] The burning intervals suggested are estimates based on field observation and discussions with field staff. These fire regimes should be refined basing on experimental studies.

[*2] The grass, in addition to recovering fast after a fire, grows tall and thick and would not easily burn with early season fires.

The tour guides at the ecotourism camp, which is located on the western edge of Kaniyo-Pabidi forest, reported that it was becoming increasingly difficult to track the chimpanzees. The animals were now moving long distances to find their woodland-savanna food sources and sometimes they would nest away from the forest, which used not to be the case in the 1990s and before. This would be defeating the very purpose which the ecotourism project serves i.e. provide jobs for local people and also generate income from chimpanzee tracking by tourists. Part of the income is set aside for the local people's income generating projects. This is intended to enable local people appreciate the resource and also prevent them from destructively using the conservation area's natural resources. It is therefore crucial that the varied feeding grounds for the animals are conserved. When planning for biodiversity conservation in other mosaic landscapes, in addition to woody plant conservation, the other values e.g. ecotourism and water catchment that the area serves need to be considered as well.

7.7. Conclusions

- The FWS mosaic has distinct vegetation cover classes, which are sequentially organized (from forest to wooded grassland) in terms of species composition.
- To conserve the biodiversity in the FWS mosaic, a part of each vegetation cover class needs to be conserved. Preferably, an area where all cover classes occur should be selected for conservation since the cover classes complement each other in terms of species composition.
- Areas that have been more protected from fire increased in vegetation cover. If the fire prevention continues, these areas may be fully colonized by forest. A forest corridor may be formed between Kaniyo-Pabidi and Main Budongo forest blocks.
- Vegetation classes that differ in species composition, when subjected to a similar (annual) fire regime for a long time, over 40 years, experience a species composition convergence towards species that are more adapted to the existing fire regime.
- Fire is essential for conserving FWS mosaics. There is, however, need for well-balanced fire management system that will provide for a controlled forest expansion yet allowing the existence of varying fire disturbance regimes.

7.8. Areas of further research

This study used a modified chronosequence approach and limited time studies to evaluate the changes taking place in a FWS mosaic in Uganda. Dynamical changes were not explicitly observed. To further our understanding of the processes of change taking place, more detailed studies into the establishment of many of the species should be carried out.

To gain a more long-term view of the changes taking place in the FWS system, a system of permanent sample plots needs to be set up to monitor such changes. These plots are also ideally suited for the aforementioned dynamical studies and studies of growth rates of trees in FWS mosaics. Linking tree growth and occurrence of species to particular life history characteristics, such as bark thickness, leaf characteristics, wood density, seed size and dispersal should also widen our understanding and make the results of this study applicable further outside the study area.

Further research is also needed to gain a deeper understanding of how the local people manage the fire, especially how they control its spread and intensity, how they determine their timing for setting the fires and how this affects the fauna in the area.

To explicitly determine the burning intervals suitable for the different vegetation classes, experimental studies evaluating the effect of different burning intervals and the seasons of burning while monitoring the fire intensity under the different conditions needs to be carried out.

Variation in the compositional as well as structural characteristics of the vegetation cover classes ought to be assessed in other FWS mosaics so as to develop standardized ranges for the vegetation cover classes. These will enable conservationists to better monitor changes that take place in the mosaics and take timely action.

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APPENDICES

Appendix 1: The Indicator Species Analysis output based on fire indicator classes. It indicates the concentration of each species in each class (Relative abundance=RA), the faithfulness of occurrence of the species in that class (Relative frequency=RF), the highest species indicator value across the classes (IV) the statistical significance of the indicator value (P) and the class in which a particular species had the highest indicator value. RA is expressed as a proportion of a particular species in a particular class relative to its abundance in other classes. RF is expressed as the percentage of sample units in a class that contain that species.

0=no fire, 1=old fire and 3=recent fire. P is significant at 0.01

Species names	**RA-0**	**RF-0**	**RA-1**	**RF-1**	**RA-2**	**RF-2**	**IV**	**P**	**Fire class**
Terminalia velutina	39	66	52	90	9	47	46.7	0.001	1
Grewia mollis	14	47	37	80	49	87	42.4	0.001	2
Combretum collinum	23	37	39	56	38	49	21.7	0.046	
Uvariopsis congensis	100	26	0	1	0	0	25.7	0.001	0
Annona senegalensis	18	33	35	59	47	55	25.7	0.005	2
Albizia grandibracteata	64	41	31	22	5	6	26.2	0.001	0
Stereospermum kunthianum	22	28	44	50	34	47	21.9	0.003	1
Combretum molle	1	5	31	24	68	49	33.7	0.001	2
Lonchocarpus laxiflorus	10	12	19	22	71	45	31.7	0.001	2
Vitex doniana	38	33	36	36	26	25	12.8	0.585	
Funtumia elastica	94	31	6	3	0	0	28.9	0.001	0
Lannea barteri	27	25	41	32	32	29	13.1	0.174	
Celtis wightii	100	24	0	0	0	0	24.2	0.001	0
Acacia hockii	22	19	46	29	32	23	13.4	0.033	
Piliostgma thonningii	25	18	53	31	23	15	16.2	0.004	1
Caloncoba schweinfurthii	86	23	14	6	0	0	20.2	0.001	0
Holoptelea grandis	99	22	1	1	0	0	21.6	0.001	0
Maesopsis eminii	62	21	38	12	0	0	12.8	0.003	0
Diospyros abyssinica	100	10	0	0	0	0	9.6	0.001	0
Ficus sur	43	15	48	15	9	3	7.1	0.245	
Grewia bicolor	8	5	23	9	69	18	12.8	0.001	2
Khaya anthotheca	86	15	14	2	0	0	12.6	0.001	0
Dombeya mukole	79	8	17	3	5	1	6.4	0.013	0
Bridelia micrantha	87	12	9	1	4	1	10.7	0.001	0
Celtis durandii	86	12	14	2	0	0	9.9	0.003	0
Combretum binderanum	2	0	37	6	61	9	5.6	0.012	2
Margaritaria discoidea	71	11	29	2	0	0	7.6	0.004	0
Phyllanthus discoideus	100	10	0	0	0	0	9.6	0.001	0
Albizia zygia	56	2	20	2	24	3	1.3	0.829	

Celtis zenkeri	100	10	0	0	0	0	10.4	0.001	0
Pterygota mildbreadii	70	5	30	1	0	0	3.8	0.059	
Hymenocardia acida	11	3	27	5	62	9	5.7	0.008	2
Olea welwitschii	95	9	5	1	0	0	8.8	0.001	0
Oncoba spinosa	37	5	14	1	49	6	2.8	0.326	
Tapura fischeri	80	9	20	2	0	0	7.1	0.009	0
Securinega virosa	0	0	38	5	62	10	6.4	0.004	2
Dichrostachys cinerea	73	5	27	1	0	0	3.9	0.064	
Alstonia boonei	100	9	0	0	0	0	8.8	0.001	0
Cynometra alexandri	100	5	0	0	0	0	5	0.007	0
Ficus exasperata	37	3	63	3	0	0	2.2	0.272	
Combretum guenzii	0	0	73	1	27	1	0.5	0.749	
Sapium ellipticum	81	2	19	1	0	0	1.2	0.403	
Carpololobia alba	0	0	21	3	79	6	4.5	0.006	2
Dombeya rotundifolia	8	2	25	5	67	8	5.4	0.012	2
Trichilia prieuriana	100	5	0	0	0	0	5.4	0.007	0

Appendix 2: The Indicator Species Analysis output based on vegetation cover classes. It indicates the concentration of each species in each class (Relative abundance=RA), the faithfulness of occurrence of the species in that class (Relative frequency=RF), the highest species indicator value across the classes (IV) the statistical significance of the indicator value (P) and the class in which a particular species had the highest indicator value. RA is expressed as a proportion of a particular species in a particular class relative to its abundance in other classes. RF is expressed as the percentage of sample units in a class that contain that species.

1=forest, 2=closed woodland, 3=open woodland, 4=very open woodland and 5=wooded grassland. P is significant at 0.01.

Species	**RA-1**	**RF-1**	**RA-2**	**RF-2**	**RA-3**	**RF-3**	**RA-4**	**RF-4**	**RA-5**	**RF-5**	**IV**	**P**	**Cover cord**
Terminalia velutina	12	30	44	97	31	85	8	57	5	44	42.8	0.001	2
Grewia mollis	2	16	16	70	32	88	48	99	1	11	47	0.001	4
Combretum collinum	11	18	20	52	38	64	22	43	10	22	24.3	0.042	
Uvariopsis congensis	100	54	0	0	0	0	0	0	0	0	54.4	0.001	1
Annona senegalensis	6	14	23	52	30	58	42	64	0	0	26.9	0.02	
Albizia grandibracteata	28	26	55	60	14	15	3	3	0	0	32.9	0.002	2
Stereospermum kunthianum	7	11	26	51	22	45	17	39	29	67	19.2	0.063	
Combretum molle	0	2	2	6	15	23	74	66	8	22	48.4	0.001	4
Lonchocarpus laxiflorus	0	0	2	10	14	36	26	47	58	56	32	0.001	5
Vitex doniana	5	11	33	51	23	36	16	24	23	22	16.8	0.095	
Funtumia elastica	89	55	11	11	0	0	0	0	0	0	49.4	0.001	1
Lannea barteri	2	3	23	30	35	40	34	43	6	11	14.7	0.095	
Celtis wightii	100	50	0	1	0	0	0	0	0	0	49.4	0.001	1
Acacia hockii	7	10	16	22	31	37	17	21	29	11	11.6	0.15	
Piliostgma thonningii	5	8	18	24	22	31	10	16	45	44	19.8	0.024	
Caloncoba schweinfurthii	74	38	24	13	2	2	0	0	0	0	27.9	0.005	1
Holoptelea grandis	94	42	6	3	0	0	0	0	0	0	39.8	0.001	1
Maesopsis eminii	45	23	55	28	0	0	0	0	0	0	15.7	0.033	
Diospyros abyssinica	96	18	3	1	1	1	0	0	0	0	17.7	0.005	1
Ficus sur	18	10	43	20	31	14	8	4	0	0	8.8	0.133	
Grewia bicolor	0	0	3	3	11	13	20	20	66	56	36.9	0.001	5
Khaya anthotheca	71	20	23	10	6	1	0	0	0	0	14.2	0.03	
Dombeya mukole	82	14	5	2	11	4	3	1	0	0	11.1	0.04	
Bridelia micrantha	26	7	70	16	2	1	3	1	0	0	11.3	0.046	
Celtis durandii	93	23	7	3	0	0	0	0	0	0	21.5	0.005	1
Combretum binderanum	0	0	1	1	9	5	11	10	78	22	17.4	0.005	5
Margaritaria discoidea	61	14	39	9	0	0	0	0	0	0	8.3	0.078	
Phyllanthus discoideus	97	18	3	1	0	0	0	0	0	0	17.8	0.011	1
Albizia zygia	67	3	12	2	7	1	15	4	0	0	2.1	0.469	
Celtis zenkeri	100	22	0	0	0	0	0	0	0	0	21.6	0.006	1
Pterygota mildbreadii	100	13	0	0	0	0	0	0	0	0	12.8	0.025	
Hymenocardia acida	0	0	3	2	20	9	27	7	50	22	11.2	0.045	

Olea welwitschii	92	17	8	3	0	0	0	0	0	0	15.4	0.016	
Oncoba spinosa	48	9	6	1	12	3	33	6	0	0	4.2	0.166	
Tapura fischeri	90	18	10	2	0	0	0	0	0	0	16.6	0.014	1
Securinega virosa	0	0	8	1	21	3	71	14	0	0	10.1	0.03	
Dichrostachys cinerea	63	6	18	4	12	1	8	1	0	0	4	0.138	
Alstonia boonei	86	14	14	3	0	0	0	0	0	0	12.4	0.033	
Cynometra alexandri	100	10	0	0	0	0	0	0	0	0	10.4	0.022	
Ficus exasperata	6	1	46	5	48	4	0	0	0	0	2.2	0.454	
Combretum guenzii	0	0	0	0	0	0	0	0	100	22	22.2	0.001	5
Sapium ellipticum	82	2	18	1	0	0	0	0	0	0	2	0.174	
Carpololobia alba	0	0	32	1	38	4	30	4	0	0	1.4	0.607	
Dombeya rotundifolia	0	0	8	2	17	4	75	13	0	0	9.7	0.04	
Trichilia prieuriana	100	11	0	0	0	0	0	0	0	0	11.2	0.03	

Appendix 3: The 121 species identified in the field, their abundance per class. At the end of the table, the total abundance, occurrence and total sampled area for each cover class are indicated. Fo=forest, Cw=closed woodland, Ow=open woodland, Vow=very open woodland and Wg=wooded grassland

		Number of individuals				
Family	**Species**	**Fo**	**cw**	**Ow**	**Vow**	**Wg**
Mimosaceae	*Acacia hockii* De Wild.	20	55	97	25	7
Mimosaceae	*Acacia seyal* Delile	.	.	.	1	.
Mimosaceae	*Acacia sieberiana* *1	1	6	.	3	.
Mimosaceae	*Acacia* spp	2	.	.	.	.
Euphorbiaceae	*Acalypha neptunica* Müll. Arg. Var.	9	.	.	.	.
Mimosaceae	*Albizia coriaria* Oliver	9	8	2	.	.
Mimosaceae	*Albizia grandibracteata* Taub.	120	257	57	7	.
Mimosaceae	*Albizia* spp	.	.	1	.	.
Mimosaceae	*Albizia zygia* (DC.) Macbr.	33	5	3	3	.
Apocynaceae	*Alstonia boonei* de Wild	24	5	.	.	.
Sapotaceae	*Aningeria altissima* *2	15	2	1	2	.
Annonaceae	*Annona senegalensis* Pers.	35	157	194	129	1
Balanitaceae	*Balanites* spp	1	.	.	.	.
Rubiaceae	*Belonophora glomerata*	2	1	.	.	.
Sapindaceae	*Blighia unijugata* Baker	2	6	.	.	.
Euphorbiaceae	*Bridelia micrantha* (Hochst.) Baill.	15	49	1	1	.
Euphorbiaceae	*Bridelia scleroneuroides* Pax.	.	2	5	2	.
Elacourtiacea	*Caloncoba schweinfurthii* Glig.	107	42	3	.	.
Polygalaceae	*Carpololobia alba* G. Don	.	9	12	4	.
Caesalpinioideae	*Cassia siamea* Lam.	2	13	.	.	.
Caesalpinioideae	*Cassia* spp.	.	1	.	.	.
Ulmaceae	*Celtis durandii* Engl.	59	6	.	.	.
Ulmaceae	*Celtis mildbraedii* Engl.	7	.	.	.	.
Ulmaceae	*Celtis wightii* Planch.	204	1	.	.	.
Ulmaceae	*Celtis zenkeri* Engl.	43	.	.	.	.
Moraceae	*Chlorophora excelsa* (Welw.) Benth	.	3	.	.	.
Sapotaceae	*Chrysophyllum albidum* G. Don	6	.	.	.	.
Rutaceae	*Citropsis articulata* *3	1	.	.	.	.
Annonaceae	*Cleistopholis patens* (Beth.) Engl. & Diels	1	.	.	.	.
Arecaceae	*Chrysophila* spp	1	.	.	.	.
Rubiaceae	*Coffea canephora* Pierre ex Froechner.	5	.	.	.	.
Rubiaceae	*Coffea euginioides* S. moore	5	.	.	.	.
Sterculiaceae	*Cola gigantea* A. Chev.	13	.	.	.	.
Combretaceae	*Combretum binderanum* Kotschy	.	3	16	14	17
Combretaceae	*Combretum collinum* Fresen.	107	240	431	137	12
Combretaceae	*Combretum guenzii* Sond.	.	.	2	.	21
Combretaceae	*Combretum molle* R. Br. Ex G. Don	4	18	92	243	6
Boraginaceae	*Cordia millenii* Baker	7	7	.	.	.
Aralliaceae	*Cussonia arborea* Hochst. Ex A. Rich.	.	1	4	12	.
Caesalpiniaceae	*Cynometra alexandri* CH Wright	29	.	.	.	.
Mimosaceae	*Dichrostachys cinerea* (L.) Wright & Arn	19	8	3	1	.
Ebenaceae	*Diospyros abyssinica* (Hiern) F. White	90	3	1	.	.
Sterculiaceae	*Dombeya mukole* Sprague	56	3	6	1	.

Sterculiaceae	*Dombeya rotundifolia* (Hochst.) Planch.	2	3	6	12	.
Mimosaceae	*Entada abyssinica* Steud. Ex A. Rich	.	.	1	.	.
Meliaceae	*Entandrophragma angolense* (Welw.) C. DC.	3	.	.	.	.
Meliaceae	*Entandrophragma cylindricum* *4	1	.	.	.	.
Papilionaceae	*Erythrina abyssinica* Lam. Ex DC	1	4	1	3	.
Leguminosae	*Erythrophleum suaveolens* *5	8	.	.	.	.
Rutaceae	*Fagaropsis angolensis* (Engl.) HM. Gardner	5	1	.	.	.
Moraceae	*Ficus capensis* Thunb	1	1	.	.	.
Moraceae	*Ficus casuarina*	.	1	.	.	.
Moraceae	*Ficus exasperata* Vahl	1	10	8	.	5
Moraceae	*Ficus mucuso* Welw ex Ficalho	1	5	1	.	.
Moraceae	*Ficus polita* Vahl	9	5	1	.	.
Moraceae	*Ficus saussureana* DC.	.	1	.	.	.
Moraceae	*Ficus* spp.	1	.	.	.	.
Moraceae	*Ficus sansibarica* Warb.	1	.	.	.	.
Moraceae	*Ficus sur* Forssk	17	41	26	3	.
Apocynaceae	*Funtumia elastica* (Preuss) Stapf	227	32	.	.	.
Rubiaceae	*Gardenia jovis-tonantis* (Welw.) Hiern.	.	1	1	1	.
Tiliaceae	*Grewia bicolor* Juss.	.	10	27	26	17
Tiliaceae	*Grewia mollis* Juss.	58	424	761	531	6
Simaroubaceae	*Harrisonia abyssinica* Oliv.	.	1	.	.	.
Ulmaceae	*Holoptelea grandis* (Hutch.) Mildbr.	99	10	.	.	.
Euphorbiaceae	*Hymenocardia acida* Tul.	3	3	22	15	3
Meliaceae	*Khaya anthotheca* (Welw.) C. DC.	50	16	4	.	.
Meliaceae	*Khaya grandifolia* C. DC.	1	.	.	.	.
Bignoniaceae	*Kigeria africana* (Lam.) Benth	.	.	5	1	.
Anacardiaceae	*Lannea barteri* (Oliv.) Engl.	5	78	107	48	2
Anacardiaceae	*Lannea welwitschii* (Hiern.) Engl.	.	3	.	1	.
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	1	.	.	.	.
Sapindaceae	*Lepisanthes senegalensis* (Juss. Ex Poir.)	6	5	.	.	.
Papilionaceae	*Lonchocarpus laxiflorus* Guill. & Perr.	.	20	116	108	34
Capparidaceae	*Maerua duchesnei* (De Wild) F. White	12	.	.	.	.
Rhamnaceae	*Maesopsis eminii* Engl.	47	61	.	.	.
Meliaceae	Mahogany spp	8	.	.	.	.
Euphorbiaceae	*Margaritaria discoidea* (Baill.) Webster	29	21	.	.	.
Rignoniaceae	*Markhamia platycalyx* (Baker) Sprague	2	1	.	.	.
Celastraceae	*Maytenus undata* (Thunb.) Blakelock	.	1	4	7	4
Papilionaceae	*Mildbraediodendron excelsum* (Harms)	3	.	.	.	.
Moraceae	*Milicia excelsa* (Welw.) CC Berg	2	2	.	.	.
Rubiaceae	*Mitragyna stipulosa* (DC.) O. Ktze	1	.	.	.	.
Moraceae	*Morus lactea* (Sim) Mildbr.	.	1	.	.	.
Moraceae	*Myrianthus holstii* Engl.	4	.	.	.	.
Oleaceae	*Olea welwitschii* (Knobl.) Gilg & Schellenb.	36	4	.	.	.
Flacourtiaceae	*Oncoba spinosa* Forsk.	24	3	5	8	.
Palmae	*Phoenix reclinata* Jacq.	12	.	.	.	.
Euphorbiaceae	*Phyllanthus discoideus* Muell.	46	2	.	.	.
Caesalpiniaceae	*Piliostgma thonningii* (Schum.)	21	66	75	18	12
Verbenaceae	*Premna angolensis* Guerke	18	2	.	.	.
Proteaceae	*Protea madiensis* Oliv.	.	.	.	9	.
Anacardiaceae	*Pseudospondias microcarpa* (A. Rich.) Engl.	4	2	.	.	.

Sterculiaceae	*Pterygota mildbraedii* Engl.	40	2	.	.	.
Euphorbiaceae	*Ricinodendron haudolotii* *6	8	2	.	.	.
Violaceae	*Rinorea dentata* (P. Beauv.) Kuntze	1	.	.	.	.
Violaceae	*Rinorea ilicifolia* (Welw. Ex Oliv.)	13	.	.	.	.
Capparidaceae	*Ritchiea albersii* Gilg	1	.	.	.	.
Rubiaceae	*Rothmannia urcelliformis* *7	.	.	4	5	6
Celestraceae	*Salacia elegans* Welw. Ex Oliv.	.	.	3	2	5
Euphorbiaceae	*Sapium ellipticum* Pax.	20	1	.	.	.
Oleaceae	*Schrebera arborea* A. Chev.	9	.	.	.	.
Polygalaceae	*Securidaca* spp	.	4	10	19	.
Euphorbiaceae	*Securinega virosa* (Roxb. Ex Willd.) Baill	2	3	5	.	.
Bignoniaceae	*Spathodea campanulata* P. Beauv.	4	12	.	.	.
Umbelliferae	*Steganotaenia araliacea* Hochst.	2	2	2	9	.
Bignoniaceae	*Stereospermum kunthianum* Cham.	41	162	126	55	18
Apocynaceae	*Tabernaemontana holstii* K. Schum	13	1	.	.	.
Chailletiaceae	*Tapura fischeri* (Engl.) Engl.	32	6	.	.	.
Rutaceae	*Teclea nobilis* Del.	11	10	2	.	.
Combretaceae	*Terminalia velutina* Rolfe	308	1288	824	103	14
Euphorbiaceae	*Thecacoris lucida*	.	.	.	4	.
Ulmaceae	*Trema orientalis* (L.) Blume	1	2	.	.	.
Meliaceae	*Trichilia prieuriana* A. Juss	23	.	.	.	.
Meliaceae	*Trichilia* spp	3	.	.	.	.
Meliaceae	*Turraea floribunda* Hochst	1	.	1	.	.
Annonaceae	*Uvariopsis congensis* Robyns & Ghesq.	663	.	.	.	.
Rubiaceae	*Vangueria apiculata* K. Schum	.	2	.	.	.
Compositae	*Vernonia amygdalina* Delile	1	2	.	.	.
Verbenaceae	*Vitex doniana* Sweet.	20	143	92	29	6
Rhamnaceae	*Zizyphus abyssinica* Hochst. Ex A. Rich	1	.	1	.	.
Total individuals		3042	3394	3172	1602	196
Total species		95	77	48	39	18
Total genera		73	60	35	28	15
Total families		33	33	23	19	13
Total area (sq. m)		65300	71000	65500	42100	16500

*1Dc. Var. woodii (Burtt Davy) Keay & Brenan
*2 (A. Chev.) Aubr. & Pellegr.
*3 (Wild. Ex Spreng) Swingle & M. Kellerm
*4 (Sprague) Sprague
*5 (Guill. & Perr.) Brenan
*6 (Baill.) Pierre ex Pax
*7 (Hiern) Bullock ex Robyns

Appendix 4: Full names of the species in graph 3.2 b

Graph name	**Full name**
A. hoc	*Acacia hockii*
A. gra	*Albizia grandibracteata*
A. zyg	*Albizia zygia*
A. boo	*Alstonia boonei*
A. sen	*Annona senegalensis*
B. mic	*Bridelia micrantha*
C. sch	*Caloncoba schweinfurthii*
C. alb	*Carpololobia alba*
C. dur	*Celtis durandii*
C. wag	*Celtis waghtii*
C. zen	*Celtis zenkeri*
C. bin	*Combretum binderanum*
C. col	*Combretum collinum*
C. gue	*Combretum guenzii*
C. mol	*Combretum molle*
C. ale	*Cynometra alexandri*
D. cin	*Dichrostachys cinerea*
D. aby	*Diospyros abyssinica*
D. muk	*Dombeya mukole*
D. rot	*Dombeya rotundifolia*
F. ela	*Funtumia elastica*
F. exa	*Ficus exasperata*
F. sur	*Ficus sur*

Graph name	**Full name**
G. bic	*Grewia bicolor*
G. mol	*Grewia mollis*
H. gra	*Holoptelea grandis*
H. aci	*Hymenocardia acida*
K. ant	*Khaya anthotheca*
L. bar	*Lannea barteri*
L. lax	*Lonchocarpus laxiflorus*
M. emi	*Maesopsis eminii*
M. dis	*Margaritaria discoidea*
O. wel	*Olea welwitschii*
O. spi	*Oncoba spinosa*
P. dis	*Phyllanthus discoideus*
P. tho	*Piliostgma thonningii*
P. mil	*Pterygota mildbreadii*
S. ell	*Sapium ellipticum*
S. spp	*Securidaka spp*
S. kun	*Stereospermum kunthianum*
T. fis	*Tapura fischeri*
T. vel	*Terminalia velutina*
T. pre	*Trichillia preiureana*
U. con	*Uvariopsis congensis*
V. don	*Vitex doniana*

Resumé

Grace Nangendo was born on 28th September 1966 in Mpigi district, Uganda. She had her 'O' and 'A' level education at Mt. St. Mary's College, Namagunga. She proceeded to Makerere University where she graduated with a BSc in Forestry. Between 1989 and 1998, she worked with Compassion International, Uganda office, where she served in several positions. In 1998 she obtained a scholarship from the Netherlands fellowship program to study for an MSc in Forestry for Sustainable development. She graduated in 2000, with distinction. She then joined the PhD program at ITC and Wageningen University in October 2001 with a fellowship from the ITC which resulted in this thesis.

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ITC Dissertation List

1. **Akinyede** (1990), Highway cost modelling and route selection using a geotechnical information system
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3. **Bocco Verdinelli, G.** (1990), Gully erosion analysis using remote sensing and geographic information systems: a case study in Central Mexico
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