

**Changing woodland ecosystems:
Post-disturbance woody species succession
dynamics and spatial trends**

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By:

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Dedicated
To my Papa
for *our* Budongo adventures

&
To my Mom
With love

Abstract

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

Due to increased fire prevention measures enforced throughout the past two decades, there is a net increase in vegetation with the surrounding forests encroaching into the woodland. The successional development trajectory depicts a species turnover pattern from an open savannah type landscape, dominated by fire resilient tree species, to a tropical high forest condition dominated by fire intolerant and shade loving species. The distance to the forest edge plays an important role in the successional development rate. In general, sites in close vicinity to the forest edge were found at further advanced stages of successional development than those sites far from the forest edge. The NDVI values for the 2002 image proved to explain 32% of the species composition changes through succession. The NDVI changes between image years, also, corroborated the successional index and explained 28% of the variation in compositional changes.

For purposes of maintaining a dynamic landscape, where both the forest and the woodland communities co-exist into the future, it is important that fire disturbance regimes be managed consciously. Sustainable woodland management will require a balance of both fire restriction and fire establishment, to control and shift the ecosystem to suite future management objectives.

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Table of Contents

ABSTRACT	V
ACKNOWLEDGEMENTS	VI
TABLE OF CONTENTS	VII
LIST OF FIGURES	IX
LIST OF TABLES	X
LIST OF TABLES	X
LIST OF APPENDICES	X
ACRONYMS	1
1. INTRODUCTION	2
1.1. BACKGROUND	2
1.2. BUDONGO FOREST RESERVE STUDY AREA	2
1.3. TOPIC RATIONALIZATION AND SUPPORTING ARGUEMENTS.....	3
1.4. RESEARCH OBJECTIVES.....	4
1.4.1. <i>Specific Research Objectives</i>	5
1.5. HYPOTHESIS	5
1.6. RESEARCH QUESTIONS.....	6
2. BACKGROUND CONCEPTS	7
2.1. SPECIES SUCCESSIONAL DEVELOPMENT.....	7
2.2. ORDINATION.....	9
3. METHODS AND MATERIALS	11
3.1. STUDY AREA	11
3.1.1. <i>Location</i>	11
3.1.2. <i>Climate</i>	11
3.1.3. <i>Soils and Geology</i>	12
3.1.4. <i>Kaniyo-Pabidi woodland vegetation</i>	12
3.2. DATA ACQUISITION: IMAGERY AND FIELD DATA	12
3.2.1. <i>Field data collection: sampling design</i>	13
3.2.2. <i>Field data collection: data collection</i>	15
3.3. DATA ANALYSIS: SPATIAL VEGETATION COMMUNITY CHANGES.....	17
3.3.1. <i>Visual interpretation of satellite imagery</i>	17
3.3.2. <i>Temporal image differencing</i>	17
3.4. DATA ANALYSIS: SUCCESSION DYNAMICS POST-FIRE DISTURBANCE	20
3.4.1. <i>Research approach description: DCA gradient analysis</i>	22
3.5. DATA ANALYSIS: FOREST EDGE INFLUENCE ON ECOSYSTEM SUCCESSION	23

3.5.1.	<i>Successional index comparison</i>	23
3.5.2.	<i>NDVI - forest edge comparison</i>	24
4.	RESULTS	25
4.1.	SPATIAL DISTRIBUTION OF VEGETATION CHANGE	25
4.1.1.	<i>Visual interpretation</i>	25
4.1.2.	<i>Temporal image differencing</i>	27
4.2.	SUCCESSION DYNAMICS POST FIRE DISTURBANCE	31
4.2.1.	<i>Established tree DCA</i>	31
4.2.2.	<i>Established tree DCA interpretation</i>	33
4.2.3.	<i>Ecological connotation of DCA axis 1</i>	34
4.2.4.	<i>Species progression DCA</i>	40
4.2.5.	<i>Successional pattern developments and inferences</i>	44
4.2.6.	<i>Canopy density measure for species</i>	46
4.3.	FOREST EDGE INFLUENCE ON ECOSYSTEM SUCCESSION.....	47
5.	DISCUSSION	50
5.1.	SPATIAL EXTENT OF VEGETATION DEVELOPMENT	50
5.1.1.	<i>Comparison of image processing methods</i>	50
5.1.2.	<i>Interpretation of vegetation change patterns</i>	51
5.2.	SUCCESSION DYNAMICS POST FIRE DISTURBANCE	52
5.2.1.	<i>Overstory tree succession dynamics</i>	52
5.2.2.	<i>Size class progression dynamics</i>	54
5.2.3.	<i>Successional development trends</i>	56
5.2.4.	<i>Successional development as explained by NDVI reflectance</i>	56
5.3.	FOREST EDGE EFFECT	57
6.	CONCLUSION AND RECOMMENDATIONS	59
	CONCLUSION	59
	RECOMMENDATIONS	60
	REFERENCES	61
	APPENDICES	64

List of Figures

FIGURE 2.1: INTERMEDIATE DISTURBANCE HYPOTHESIS (IDH) (SOURCE: CONNELL, 1978)	7
FIGURE 2.2: A) SINGLE SPECIES RESPONSE CURVE TO AN ENVIRONMENTAL GRADIENT. B) NUMEROUS SPECIES' RESPONSE TO AN ENVIRONMENTAL GRADIENT (PALMER, 1999).	8
FIGURE 3.1: BUDONGO FOREST RESERVE STUDY AREA LOCATION	11
FIGURE 3.2: PLOT LAYOUT SCHEMATIC	13
FIGURE 3.3: STUDY AREA MAP DEMARCATING WHERE PLOTS WERE LOCATED AND VARIOUS STUDY AREA FEATURES	14
FIGURE 3.4: FIRE ADAPTATION PHOTOS:	16
FIGURE 3.5: NDVI IMAGE DIFFERENCING PROCEDURE	19
FIGURE 3.6: RESEARCH APPROACH TO EVALUATE THE SUCCESSION GRADIENT TREND IN SPECIES COMPOSITION AND STRUCTURE	21
FIGURE 4.1: VISUAL INTERPRETATION OF FOREST ENCROACHMENT	26
FIGURE 4.2: TEMPORAL NDVI DIFFERENCING OF THE 1985 AND 1995 IMAGES. COLORED AREAS INDICATE AREAS OF SIGNIFICANT VEGETATION CHANGE	28
FIGURE 4.3: TEMPORAL NDVI DIFFERENCING OF THE 1995 AND 2002 IMAGES. COLORED AREAS INDICATE AREAS OF SIGNIFICANT VEGETATION CHANGE	29
FIGURE 4.4: TEMPORAL NDVI DIFFERENCING OF THE 1985 AND 2002 IMAGES. COLORED AREAS INDICATE AREAS OF SIGNIFICANT VEGETATION CHANGE	30
FIGURE 4.5: DETRENDED CORRESPONDENCE ANALYSIS: SPECIES SCORES AS EXPLAINED BY AXIS 1 AND 2, FOR 32 SPECIES AT AN ESTABLISHED STAGE OF DEVELOPMENT (≥ 10 CM DBH)	32
FIGURE 4.6: DETRENDED CORRESPONDENCE ANALYSIS BIPLLOT:	33
FIGURE 4.7: SUCCESSIONAL GRADIENT SPECIES TURNOVER: TREE ABUNDANCES FOR ALBIZIA GRANDIBRACTEATA, TERMINALIA VELUTINA AND GREWIA MOLLIS ALONG THE SUCCESSIONAL GRADIENT	36
FIGURE 4.8: RELATIONSHIP BETWEEN 2002 NDVI IMAGE AND DCA AXIS 1	37
FIGURE 4.9: RELATIONSHIP BETWEEN CHANGES IN NDVI REFLECTANCE (BETWEEN 1985 AND 2002) AND THE SUCCESSIONAL INDEX (DCA AXIS 1)	38
FIGURE 4.10: BOXPLOT OF SI SITE SCORE VALUES AGAINST OBSERVED FIRE SCAR EVIDENCE	39
FIGURE 4.11: CANOPY DENSITY CHANGES ALONG THE SUCCESSION GRADIENT	40
FIGURE 4.12: THE SPECIES PROGRESSION DCA AXIS 1 VS. THE ESTABLISHED TREE SUCCESSIONAL INDEX DCA AXIS# 1	41
FIGURE 4.13: SPECIES PROGRESSION THROUGH SUCCESSION	43
FIGURE 4.14: TREE DENSITY ALONG THE SUCCESSIONAL GRADIENT	45
FIGURE 4.15: SPECIES COUNT TESTED AGAINST THE SUCCESSIONAL INDEX	45
FIGURE 4.16: PLOT DISTANCE TO FOREST SEED SOURCE VS. PLOT SUCCESSIONAL INDEX RATING	47
FIGURE 4.17: NDVI WEIGHTED AVERAGES (1985 AND 2002) AT DIFFERENT DISTANCE CLASSES FROM FOREST	48
FIGURE 4.18: NDVI CHANGES BETWEEN 1985 AND 2002 ACCORDING TO DIFFERENT DISTANCE CLASSES FROM FOREST	49

List of Tables

TABLE 3.1: AVAILABLE IMAGERY DATA	12
TABLE 3.2: SITE STRATIFICATION CRITERIA.....	13
TABLE 3.3: FIELD DATA COLLECTED AT EACH PLOT	15
TABLE 4.1: PEARSON CORRELATION SIGNIFICANCE LEVELS WITH DCA AXIS 1 AND DCA AXIS 2.....	34
TABLE 4.2: SUCCESSIONAL INDEX SPECIES SCORES AND THE NUMBER OF RESPECTIVE TREES MEASURED	35
TABLE 4.3: ANALYSIS OF VARIANCE BETWEEN FIRE SCAR AGE ESTIMATES AND SUCCESSIONAL INDEX SCORES.....	39
TABLE 4.4: LSD AND BONFERRONI POST HOC TEST: THE DEGREE OF SIGNIFICANCE BETWEEN FIRE SCAR AGE ESTIMATES	39
TABLE 4.5: OCCURRENCES OF THE DIFFERENT COMBINATIONS OF PROGRESSION PATTERNS	42
TABLE 4.6: SUCCESSIONAL SPECIES SCORES AT CORRESPONDING SIZE CLASSES	44
TABLE 4.7: OPTIMAL CANOPY COVER CONDITION FOR 16 TREE SPECIES AT DIFFERENT SIZE CLASSES	46

List of Appendices

APPENDIX 1: DETRENDED CORRESPONDENCE ANALYSIS OUTPUTS	64
APPENDIX 2: NORMALITY TESTING.....	64
APPENDIX 3: LEAST SQUARES REGRESSION OUTPUTS	68
APPENDIX 4: SUCCESSIONAL INDEX COMPARISON	71

Acronyms

DBH – Diameter at Breast Height
GPS – Global Positioning System
GIS – Geographical Information System
FAO – Food and Agriculture Organization of the United Nations
NIR – Near Infrared
MIR – Middle Infrared
NDVI – Normalized Difference Vegetation Index
DCA – Detrended Correspondence Analysis
PCA – Principle Component Analysis
NMMDS – Nonmetric Multidimensional Scaling
LSR – Least squares regression
SI – Successional Index
UWA – Uganda Wildlife Authority

1. Introduction

1.1. Background

In recent years the concept of biodiversity has become a central consideration in conservation strategies. Despite mounting efforts, biodiversity degradation continues. Natural resources around the world are being degraded by the destruction of natural habitats, over-exploitation, pollution, and the introduction of exotic species (Johnson, 1993).

The concept of 'biodiversity' tries to capture the essence of the complex multi-dimensional interaction of biological elements within an ecosystem. There are numerous proposed definitions. 'Biodiversity' was defined at the 1992 Convention on Biological Diversity in Rio de Janeiro as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes they are part. This includes diversity within species, between species and of ecosystems". Another definition by McNeely *et al.* (1990) states: "Biological diversity encompasses all species of plants, animals, and microorganisms and the ecosystems and ecological processes of which they are parts. It is an umbrella term for the degree of nature's variety, including both the number and frequency of ecosystems, species or genes in a given assemblage". In quantifiable terms, it can measure the number of different species present, the relative abundance of species, the ecological uniqueness of species and their functional role, and the evolutionary distinctiveness of the species present (Holsinger, 2001).

Species biodiversity has been recognized as an integral component for maintaining the health of ecosystems at varying spatial and temporal scales. The variety of organisms present affects the productivity and the functional capacities of ecosystems (Boyle *et al.* 1994). Ecosystem relationships are extremely complex and eliminating or removing key components from an ecosystem can dramatically change its ecological dynamics (Mooney *et al.*, 1995).

Forest ecosystems are rarely if ever at equilibrium. They are in a continuous stage of transition, from their establishment after a destructive disturbance to the late mature forest. For effective, realistic biodiversity management planning it is mandatory to realize the succession stages and the ecological dynamics of an ecosystem. Vegetation communities constantly shift in composition and structure as they grow and are exposed to changing climates, ever altering microsite conditions, microclimates, disturbances and inter-plant competition.

When describing plant community succession patterns, the response variable of time is frequently used to explain changes. Time is however not the agent of change. It is the biophysical site changes that occur over time that drive the changes in ecosystems. Time is a response variable for all the underlying changes driving the success and failure of plant establishment and survival. Such factors include species competition, changing soil conditions, changing microclimate conditions and the random occurrences of nature. When inferences are made regarding succession patterns it is in fact a generalization on how sites have changed and which species can establish and prosper in the respective conditions.

Although it is the species-to-site and species-to-species interactions that determine the degree of species success, there is a similar trend on a larger scale of species progression through time given similar conditions (i.e. soil conditions, climatic conditions and similar seed pools). This is succession.

Woodlands in the Budongo forest reserve, in Uganda, are herein used as a case study for how succession trends after fire develop. This study focuses on the successional development starting from the recently burnt open woodland to the unburnt closed canopy woodland. Various investigative methods will be used to judge how the vegetation composition has shifted over time in the woodland. Aging trees, by counting tree rings can not be used in this study as trees continue to grow year round and do not create distinctive ring formations (Worbes, 2002). Therefore other diagnostic measures were used. First, satellite imagery will be used as historical snapshots to identify burnt areas of different years. Such information was used practically to confirm which areas were burnt in the respective years of the available satellite imagery. Realizing an area burnt in a certain year (e.g. 1985), one knows positively it was burnt in that year and that the fire most likely killed all trees species not adapted to fire or that were too weak to survive. Hence assumptions can be made that any regeneration of fire intolerant species could only have regenerated after that destructive event. This is but the first insight into the greater puzzle of understanding the site history.

Second, this study will utilize the ‘space-for-time’ approach and attempt to capture the dynamics of various successional stages, by analyzing the differences on a broad range of sites at different ages after disturbance. The downfall of this approach is that it fails to consider the influence of shared events each site incurs, such as climatic changes or the introduction of exotic species (Sheil, 1999). However, given the time constraints of this study, such limitations have to be overlooked.

Thirdly, species composition and structural parameters will be carefully analyzed of all experimental sites, to provide insight into the historical structure of past site conditions. The record and dimensions of the existing dead and alive trees act as a historical record of each site, and can be used as yet another clue to understand the stand changes and some of the ecological processes taking place. Sheil (1999) stated “that the vegetation found at any site is the product of local history”.

1.2. Budongo forest reserve study area

The Budongo Forest Reserve (BFR) is located in north-western Uganda between 1°35’ and 1°55’ north and between 31°18’ and 31°42’ east. To the northwest lies the Albertine rift valley escarpment and Lake Albert and to the north and east is the Victoria Nile. The forest reserve is 82,530 hectares in size, of which 53.7% is tropical high forest and 46.3% is woodland. The Budongo forest reserve is a highly diverse ecosystem, hosting approximately 465 types of trees or shrubs, 359 bird species, 289 butterfly species and 130 species of large moths (Nangendo, 2000). This forest has widely been recognized as being a biological hotspot, ranking third in biological diversity in Uganda.

A number of studies have been undertaken to determine biological and successional trends that take place in the Budongo tropical high forests. Eggeling (1947) established a series of permanent sample plots within the Budongo forest with the intention of monitoring ecological succession patterns. These plots now account for some of the oldest permanent sample plot data available for tropical rainforests. He classified the forest reserve into four different forest cover types: colonizing forest, mixed forest, ironwood forest and swamp forest. The swamp forest belongs to an independent sere, while the other forest types are successional related, starting with colonizing forests to mixed to the climax ironwood forest. More recently, Sheil (1999; 2000; 2001) examined how Eggeling’s permanent sample plots changed over a 50 year period and specifically noted quantitative differences in species compositions and stand dynamics.

The woodland / grassland ecosystem constitutes a mosaic of woody plant species found at varying densities and sizes. The woodland is classified as an open forest type. Open forest as defined by FAO constitute a crown cover between 10 and 40 percent, and generally found in association with a continuous grass layer (FAO, 2000).

The Budongo forest woodland ecosystem has been shaped and maintained by frequent animal and human disturbance. In the past elephants were an active source of disturbance, but in recent years they have been exterminated from the area and thus can no longer serve as a disturbance agent in this woodland ecosystem. Fire, on the other hand, is perhaps the most important disturbance factor still affecting the growth and succession of the woodland forests. Fire has been used for thousands of years in the Lake Albert region by cattle herders and hunters as a tool to scare out game and to open up the landscape to improve visibility. Earliest confirmed records of fire in the Budongo Forest have been dated back 600 years (Paterson, 1991), although it is suspected that it has been a prevalent disturbance regime well prior to this date (Beuning *et al.*, 1997).

In the early 20th century the British colonial rule implemented various ordinances to limit and control burning. Burning was only permitted on a limited scale in the early dry season from January to March (Paterson, 1991). The impact of reduced burning practices changed the resulting grassland species composition shifting to support more woody species. In 1903 the “forestry ordinance” was implemented and in 1920 the “careless use of fire” ordinance was invoked. Such measures resulted in increased woody species establishment and, as a negative consequence, increased tsetse fly populations. The tsetse fly acted as a disease vector of Trypanosomiasis, commonly known as sleeping sickness, and was responsible for a dramatic increase in disease among both human and cattle populations. By 1910 the conditions had deteriorated enough to invoke a full scale evacuation of both humans and cattle from the northern and western regions of the forest. It was only in 1928 that people returned to in these regions. Since then, populations have grown significantly as other Ugandan migrants and immigrants from Sudan and Congo have resettled in these parts. Burning practices although not permitted did continue on a smaller scale (Paterson, 1991).

In the early 1990s, the Uganda Wildlife Authority (UWA) assumed a greater responsibility over the northern Budongo forest woodlands and as such enforced anti-poaching measures more diligently. In 1995, the entrance gate to Murchison Falls National Park was relocated further south to the edge of the Kaniyo-Pabidi woodland, therein limiting accessibility and further reducing the poaching induced fires.

1.3. Topic rationalization and supporting arguments

For effective management planning of ecological resources it is critical to make decisions based on accurate and up to date biological inventories, to have a comprehensive understanding of the temporal ecological community changes and to understand the respective species response patterns to change.

The Kaniyo-Pabidi woodlands have in the face of fewer fire disturbances begun to develop along a successional trajectory towards becoming a closed tropical forest. Forest species, formerly excluded from this area due to fire, are now establishing (Sheil, 2001). Forest managers, who previously had little invested interest in the woodlands, now realize the commercial and biodiversity potential associated with an expanding forest. Predicting the trend of woodland composition changes through time is one important criterion necessary for implementing successful management practices in both commercial and conservation strategies.

Ecosystem succession is a temporal phenomenon, organism communities change over time as competitive processes (among other processes) affect which species can establish and maintain themselves within that ecosystem. Measuring and monitoring ecosystem interaction dynamics is usually very difficult due to the lack of detailed baseline historical data on species composition and structure. To make accurate conclusions about the implication of ecosystem change, it is necessary to have reliable information of the initial site condition. In the Budongo forest, succession studies by Sheil (1999) assessed species development dynamics over a 50 year period with the help of detailed permanent sample plot information established and collected by Eggeling in the mid to late 1940's. This allowed Sheil to make definitive conclusions about ecological changes within the forest and among other things comment on how management practices have influenced stand composition. Unlike Sheil's study, the present investigation does not have the detailed historical data on the woodland ecosystem, except brief snapshots in time from various satellite images. Due to the nature of this study, such limitations can be resolved with some investigative studies.

While extensive efforts have been put into understanding the ecological processes defining plant community changes in the forest, little has been studied in the Budongo woodland environment. Eggeling had established one permanent sample plot in a woodland region which has since been re-measured and reported by Sheil (1999), but that is the extent of any woodland research conducted. Considering that the woodland constitutes 46.3% of the reserve and is currently actively changing, it is important to accurately understand the overall succession dynamics.

1.4. Research Objectives

To contribute to a better understanding of the spatial succession patterns within the Budongo forest woodlands and the processes which regulate species distribution and abundance for the intended purpose of improving the Budongo Forest Reserve conservation management plan.

1.4.1. Specific Research Objectives

1. To investigate the implications of recent fire control measures on woodland succession and "forest creep".
2. To determine changes in woodland species composition and structure in the face of less intense fire disturbance regimes
3. To investigate the forest encroachment gradient in terms of species composition and stand structure.

1.5. Hypothesis

Extended periods between fire cycles have altered species composition in the woodland ecosystem. The grasslands are slowly shifting to support greater numbers of woody plant species. There will be an increase in the abundance and relative spatial distribution of woody plants; an increase in the diversity of species; and a species composition gradient in respect to the distance to seed sources, whereby isolated patches of regenerating woodland will regenerate free of competition from forest species and areas close to the forest boundary where there is stiff competition from forest species migrating into these sites.

1.6. Research Questions

1. How has woody plant species abundance and spatial coverage changed during the last 17 years?
2. What effect does fire have on woodland species composition, abundance and stand structure?
3. Is there a compositional and structural gradient present relative to the forest edge?

2. Background concepts

Prior to proceeding with the analysis, it is important to know various background concepts that form the basis for this research. This includes an overview of ecosystem development patterns and how to appropriately analyze species composition data to determine underlying trends.

2.1. Species successional development

Various simple models have been developed that attempt to explain some of the observed biological changes taking place in forest ecosystems. The Intermediate Disturbance Hypothesis (IDH) developed by Connell (1978) predicted that disturbance and succession patterns influenced species diversity.

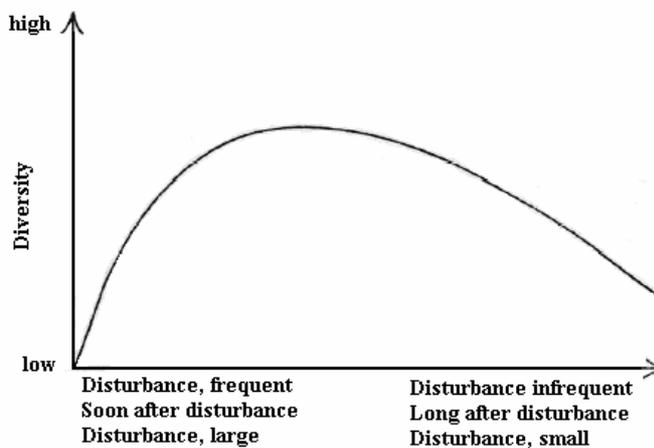


Figure 2.1: Intermediate Disturbance Hypothesis (IDH) (Source: Connell, 1978)

The IDH model, as demonstrated in figure 2.1, predicts a unimodal humpback relationship. The theory behind the model is as follows: species diversity is low on sites exposed to frequent disturbances or at early stages of succession; it reaches maximum levels at intermediate levels of disturbance or after an extended period post disturbance; species diversity drops during the later stages of succession once again as species are competitively displaced. The initial drop in species diversity following a disturbance is due to the inability of species to recover promptly. Natural regeneration requires an element of time for species to become reintroduced and able to re-establish. Given due time species will once again colonize the site and utilize as many of the available resources as the ecosystem carrying capacity can sustain. However, as more plants establish themselves there is an evident increase in the competition for resources and as a result less competitive species are weeded out to those few species with a competitive edge.

Competition is a major factor influencing the number of coexisting species that an ecosystem can support. The competitive struggle between plants is generally limited to those of similar functional types (i.e. same feeding guild or plant growth type), as they compete for the same resources and physical space. Under certain environmental conditions, competition between plants can be quite intense. Competitive interactions are also a major factor for plant mortality. If a plant is unable to get

the required resources, for example nutrients, water or light, it will die. Such mortality causing events effectively remove those species incapable of competing (Huston, 1994).

Many models, such as the IDH model by Connell (1978), are an over simplification of reality, and have been criticized for their failure to comply in all circumstances. Sheil (1999) argues that in fact the “environment is a multivariate and a changing complex of variables”, or, in other words, there are numerous interacting variables and event sequences that are responsible for how species composition change over time. Basically, univariate models are incapable of explaining the multidimensional, intricate processes that occurs at so many different scales and the sometimes very thin biological parameter thresholds that often dictate how vegetative communities grow.

Plant community succession is a response to changing environmental conditions and the species' physiological characteristics to grow in certain environmental conditions. For optimal growth, plants require a specific set of conditions in order to grow and reproduce. Generally speaking, plant success follows a unimodal relationship, whereby there is an optimal peak condition in species growth and abundance in relation to a range of environmental variables. Refer to figure 2.2.

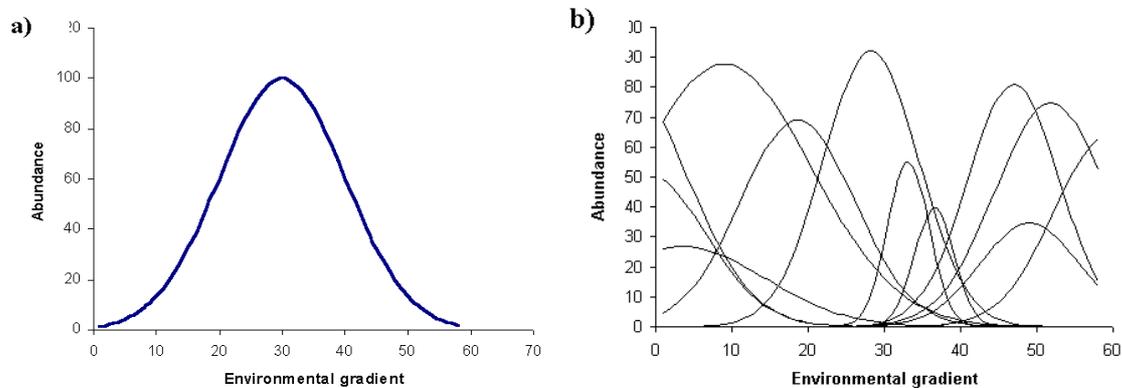


Figure 2.2: a) *Single species response curve to an environmental gradient.* b) *Numerous species' response to an environmental gradient (Palmer, 1999).*

Different species have varying optimal conditions along this gradient, as their physiological requirements differ (figure 2.2b). Species presence and abundance is a function of a series of different plant requirements at varying environmental gradients. To successfully reach maturity and seed bearing age, a plant needs an environment suitable for every stage of its life cycle to succeed or otherwise it will perish. From germination to establishment to reproduction, site factors must be conducive for growth and survival, at bare minimum. Hence, the species compositions of any given site give insight into historical environmental conditions existing during the lifecycle of the vegetation present (Sheil, 1999).

When the succession gradient is described it is the variable of time that is often unwittingly misinterpreted as the explanatory response variable (Huschule & Hironaka, 1980). The floristic succession patterns, however, are driven by a specific dynamic series of species-to-site and species-to-species interactions (Huston, 1994).

In association with floristic competition and interspecies interactions, site condition changes during succession and are in itself a major influence on species development. A closing canopy will decrease the amount of light reaching the woodland floor, which will increase the relative humidity and it can potentially increase the overall moisture condition in the soil. Soil conditions will also change with time after a fire disturbance; pH levels will begin to stabilize, and the amount of avail-

able nutrients may decrease as they become tied up in plant material both alive and dead. (Chandler *et al.*, 1983; Higgins, 2000).

2.2. Ordination

Given the nature of ecological data, interpreting the underlying gradients influencing species community distributions is difficult. However, there is a particular family of mathematics, known as ordination that deals specifically with analyzing and interpreting complex multivariate data types, such as species compositions. These techniques essentially extract the dominant, underlying gradients present in a data set, into a manageable capacity (Jongman *et al.*, 1987; McGarigal *et al.*, 2000; Palmer, 1999). Preliminary species composition data are usually expressed in a tabular format, where species' abundance by plot is recorded (species types expressed in columns, plots in rows).

Ordination techniques essentially exploit and extract information based on various properties exhibited by ecological data. The following list explains several of these characteristics:

- In ecological systems, there are numerous interacting variables, both biotic and abiotic, that determine which species are present and can coexist.
- Generally however, the number of highly influential environmental or ecological agents determining species compositions is small. Hence, the greatest amount of species variability can be explained by only a few variables and as such ecological data is said to have low 'intrinsic dimensionality' (Palmer, 1999).
- There is a great deal of redundant information in composition data matrices. Many plant species have similar response curves to environmental conditions and will grow abundant in harmony to one another.
- Plot composition data matrices contain a lot of noise. The random processes of nature introduce sizeable amounts of variability between plots of even similar vegetation types.

Ordination essentially computes the degree of correspondence or similarity between plots and explains it in various axes. The intention of ordination is to arrange similar entities in close proximity to one another and those that behave very differently, very far apart. The result of an ordination analysis can be represented both in tabular or in graphical forms, whereby different theoretical gradients for sites and species are sequentially defined in various axes. The first axis of the ordination output explains the greatest degree of variation influencing species abundance, and represents the most important gradient influencing species composition. Subsequent axes, also representing different gradients, explain sequentially less (Jongman *et al.*, 1987).

There are 2 types of ordination, direct ordination and indirect ordination. Direct ordination techniques explain the degree which measured environmental factors influence species composition trends. This technique was not used and will not be followed up further. Indirect ordination, does not require extraneous environmental data in its calculation, and is based exclusively on species composition data. This method calculates a theoretical gradient, based on the assumption that there are latent and underlying structures in the data that explain the majority of the variation in species compositions. Subsequently, once analyzed, it is the ecologist's responsibility to infer and determine the factors that explain the variation observed in the ordination outputs (Jongman *et al.*, 1987; McGarigal *et al.*, 2000).

Indirect ordination can prove more insightful than their direct ordination cousin, as the data collection methods are quite straight forward, considering that species are easily distinguishable entities. Direct ordination requires the exhaustive collection of environmental data which only then can

be tested against species composition information. Characterizing and quantifying precise environmental factors often proves both difficult and tedious. The other advantage provided by indirect ordination methods is that it explains the variation regardless of environmental data; on the other hand, if in the direct ordination the critical explanatory environmental data is lacking the overall trend will be misinterpreted (Jongman *et al.*, 1987).

In ecological studies today there are 4 types of indirect ordination techniques commonly used; these include Principle Component Analysis (PCA), Correspondence Analysis (CA) (also known as Reciprocating Average), Detrended Correspondence Analysis (DCA) and Nonmetric Multidimensional Scaling (NMMDS). This study focused particularly on the Detrended Correspondence Analysis DCA, as it is well suited for handling ecological data that are non linear and exhibits a unimodal species response curve (shown in figure 2.2a) (McGarigal *et al.*, 2000). This method has proven to be a robust and well understood approach to develop a 'best fit' representation how species composition changes (Hill & Gauch, 1980; Jongman *et al.*, 1987; Ter Braak, 1985)

This thesis will investigate how species change through time, where time is substituted by sampling a range of successional snapshots. A DCA will be used to explain the species turnover patterns exhibited through succession and, in effect, it is the variable of time that will explain species augmentation patterns.

3. Methods and materials

3.1. Study area

3.1.1. Location

The Budongo Forest Reserve is located in northwestern Uganda (figure 3.1) between 1°35' and 1°55' north and between 31°18' and 31°42' east. To the west is Lake Albert, and the Albertine rift valley escarpment, and to the north and east is the Victoria Nile. The Budongo forest region is situated between 900 and 1000 meters above sea level, on a gently undulating terrain. The Budongo forest is found in Masindi and Hoima districts, and is managed by the Uganda Forestry Department. The forest is comprised of 4 different forest blocks: Budongo, Siba, Busaju, and the Kaniyo-Pabidi forest to the north. The forest reserve is 82,530 hectares in size, of which 53.7% is tropical high forest and 46.3% is woodland. The focus of this study is particularly the woodland ecosystems located to the northern parts of the forest reserve, directly between the Kaniyo-Pabidi forest block and the main Budongo forest. These woodlands known as the Kaniyo-Pabidi woodlands cover an area of 27,280 hectares in size (Forest Department, 1997).

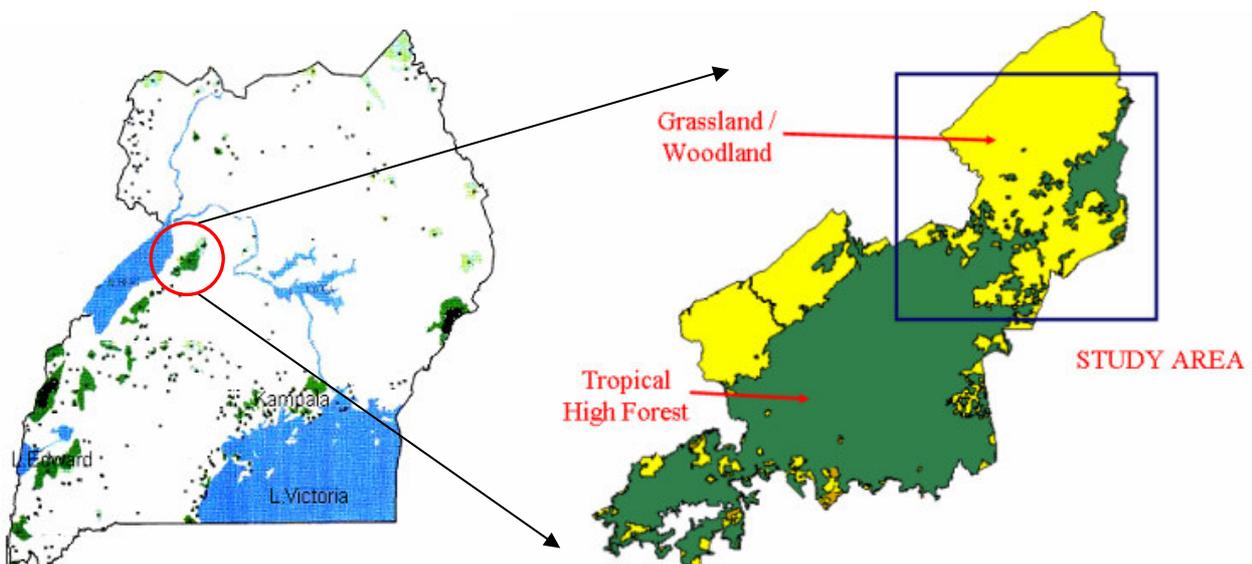


Figure 3.1: Budongo Forest Reserve study area location

3.1.2. Climate

The Budongo forest is located in a transitional zone between the moist climates of the Congo forests and the characteristically drier savannah climates of Uganda. There is an average rainfall of between 1,397 and 1525 mm annually. Highest temperatures are reached during dry seasons, from December to February, with temperatures between 29-32 °C, while minimum temperatures of 23-29 °C are recorded from the wet seasons, between June and July. Relative humidity ranges between 45% and 50% during the dry season, and averages around 75 % during the rainy season.

3.1.3. Soils and Geology

The underlying geology of the Budongo forest is of Precambrian origin, consisting of high grade metamorphic rocks of the 2900 million year old 'Granulite group' (van Straaten, 1976). The geological bedrock material, made up of coarse grained, relatively homogenous granulite rocks, made up of predominantly quartz, plagioclase, K-feldspar, hypersthen, biotite, and garnet, has weathered into light textured, quartz rich, sandy soils.

The soils found over 90 % of the study area are Orthic Ferralsols. They are characteristically highly weathered deep soils, well drained, with a low (acidic) pH. The soils are relatively infertile, as they are characterized by low nutrient concentrations and low water holding capacities. The remaining 10% of the area has typically shallow soils, called Lithosols. These soils are typically found along hilltop regions, and are predominantly underlain by rocks. In river valleys Eutric Fluvisols are found. These soils are characteristically more fertile than surrounding soils, and can at times become flooded.

3.1.4. Kaniyo-Pabidi woodland vegetation

The Kaniyo-Pabidi woodland region is a mosaic of woodlands with interspersed patches of small forest islands. The woodland ecosystem is dominated by plants adapted to relatively frequent fire regimes. The vegetation in this area is heterogeneous as the time post fire disturbance varies. Some areas have been frequently burnt while others have not experienced fire in more than 10 and possibly 20 years. The sites recently exposed to fire disturbance have an open canopy, and are dominated by various grass species and fire tolerant tree species, such as *Grewia mollis*, *Combretum collinum*, *Annona senegalensis* and *Stereospermum kunthianum*. Those sites not recently burnt have an increasingly closed canopy structure and are composed of both fire resilient trees and fire intolerant trees such as *Funtumia elastica*, *Maesopsis eminii*, *Pterygota mildbraedii* and *Khaya anthotheca*.

3.2. Data acquisition: Imagery and field data

Utilizing the remote sensing imagery identified in table 3.1, the spatial extent of vegetation changes has been mapped. The specific steps are outlined in section 3.3. The change detection results were used to study the spatial extent of changes and as a basis for the identification of sample areas.

Table 3.1: Available imagery data

Sensor	Date	Season
Landsat 5 TM	January 14, 1985	Dry season
Landsat 5 TM	January 26, 1995	Dry season
Landsat 7 +ETM	February 6, 2002	Dry season

To capture a range of different succession snapshots, change detection results were used to provide insight into when and where there were significant changes for different areas. Image pixel values, specifically NDVI values, were used as a proxy to objectively identify site changes. Sites were selected as follows:

Table 3.2: Site stratification criteria

	NDVI pixel value changes between image years		
	1985-1995	1995-2002	1985-2002
No changes over 17 year period	no change	no change	no change
Recent changes from 1995-2002	no change	Increase or decrease	Increase or decrease
Changes between 1985-1995	Increase or decrease	no change	Increase or decrease
Gradual changes	no change	no change	Increase or decrease

This stratification formed the basis for plot selection during the fieldwork activity. According to the image, plots were established in areas where vegetation has significantly changed (i.e. areas of high NDVI increases), as it was the interest of this study to monitor vegetation establishment patterns. Transects were, however, also established at sites where there had not been observable changes in image reflectance. Such sites were measured to understand the agents that maintained the structure of the ecosystem through time.

To determine how vegetation communities changed and developed after fire, without baseline data available for each site, a space-for-time sample was taken. Plots were established in many different sites at different snapshots of their transitory development. The change detection products were used to estimate different stages of development.

3.2.1. Field data collection: sampling design

A systematic sample design was utilized during the fieldwork. Nested concentric circular plots of 50 m² and 500 m² were established at an interval of 50 meters apart along transects and then 300 meters apart between transects (figure 3.2).

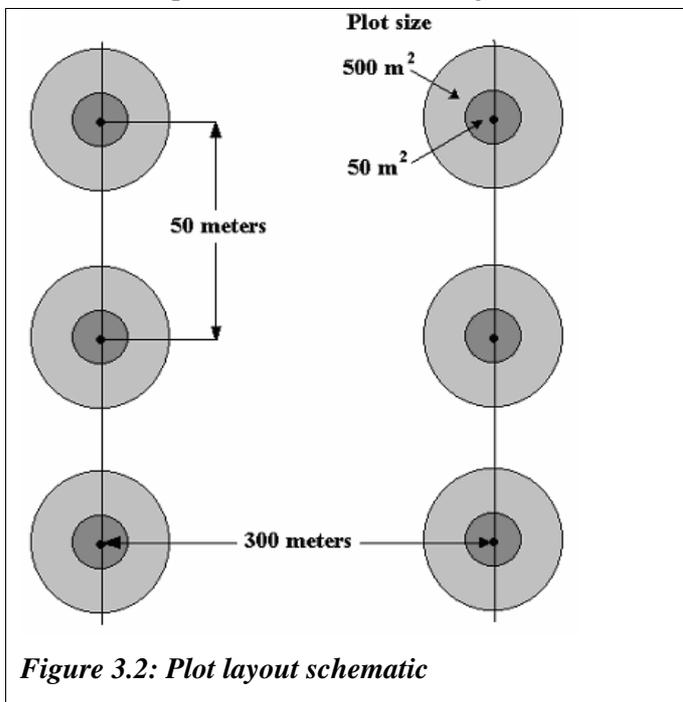


Figure 3.2: Plot layout schematic

A systematic sample was utilized due to the nature of the study and the ease of its implementation. Because of an interest in studying succession gradients relative to the forest edge, plots were staggered at different distances from the forest. Plots were subsequently located perpendicular to the forest edge and extended on average between 700 to 1000 meters into the woodland and approximately 100 to 150 meters into the forest.

Plots were established along the cardinal directions (North – South or East – West), in order to improve transect straightness, for simplicity sake, and to quickly deduce and reduce GPS error.

Figure 3.3 maps the location of the 335 plots established in the study area. Of the plots measured, 268 were located in the woodland and 67 in the forest. The map also delineates the study area boundary, and some other significant features present in the study area.

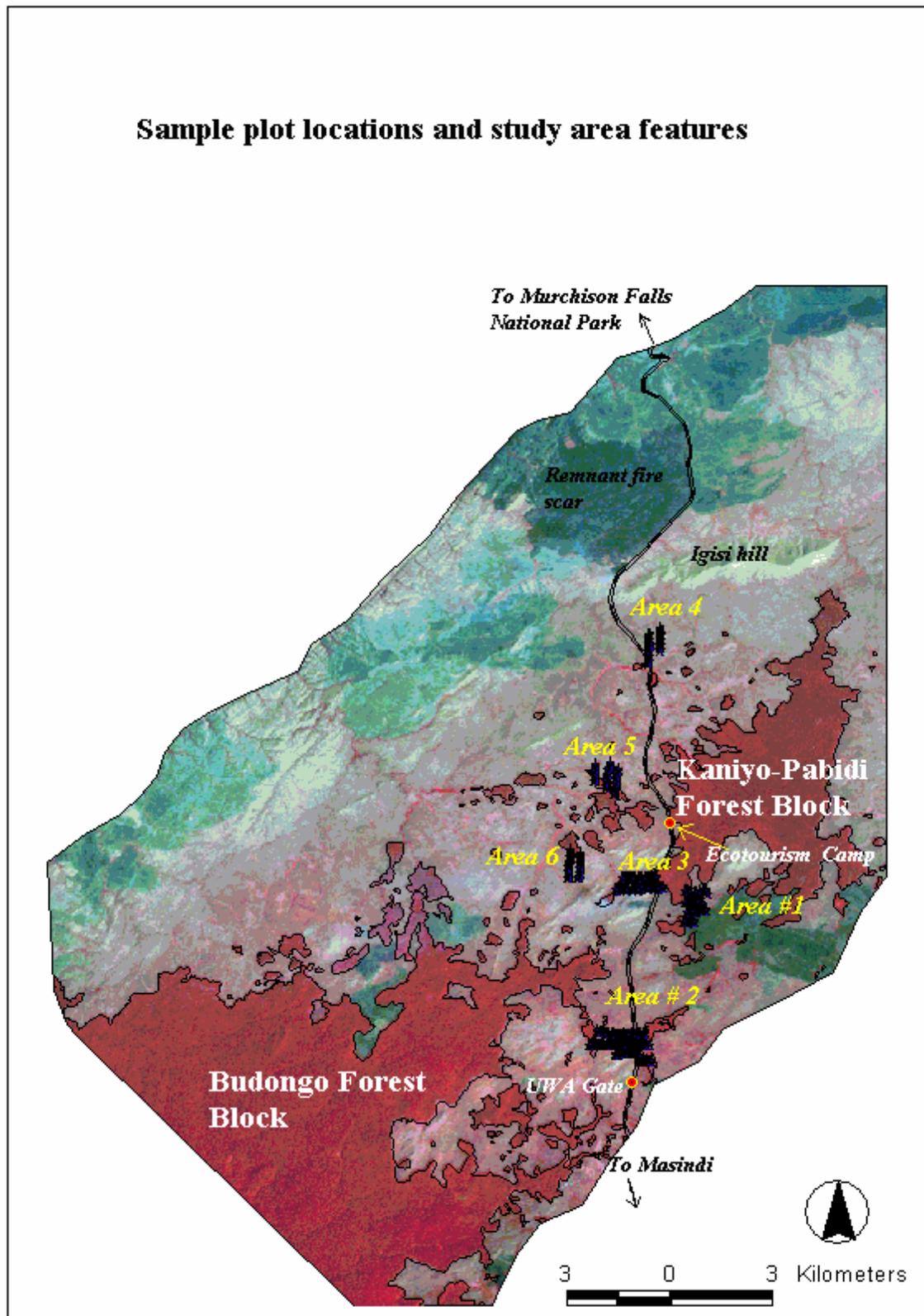


Figure 3.3: Study area map demarcating where plots were located and various study area features

3.2.2. Field data collection: data collection

Field data was collected during the months of September and October 2002. Table 3.3 outlines the variables collected at each plot.

Table 3.3: Field data collected at each plot

General plot information	<ol style="list-style-type: none"> 1) Geographical coordinates using GPS 2) Visible disturbance indicators (i.e. fire scars, ash, logging, etc.) 3) Canopy density measurements (%) using canopy densitometer 4) Slope and aspect
50 m ² plot	<ol style="list-style-type: none"> 1) Recorded species and diameter of all <i>alive</i> trees greater than 2 cm DBH 2) Recorded species and diameter of all <i>dead</i> trees greater than 2 cm DBH 3) Recorded the number of regenerating trees that were less than 2 cm DBH but greater than 50 cm in height
500 m ² plot	<ol style="list-style-type: none"> 1) Recorded species and diameter of all <i>alive</i> trees greater than 10 cm DBH 2) Recorded species and diameter of all <i>dead</i> trees greater than 10 cm DBH

General plot information:

Geographical coordinates: collected using a Global Positioning System (model: Garmin e-Trex Legend).

Visible disturbance indicators: any observable indication of recent or old disturbances: fire scars, ash, logging, animal activity, or other biophysical disturbances (i.e. blow-down) that may effect vegetation regeneration. Where fire evidence was observed, it was carefully analyzed and categorized as either a recent or old fire occurrence. Judgment was based on the degree of fire scorching, how much charcoal had weathering off remnant stems and whether fresh ash was still to be found on the ground. Where and on which tree species fire scorching was noted was also relevant, as some species (e.g. *Grewia mollis*) slough off their bark directly after a disturbance, while other species have robust layers of bark which maintain fire scar evidence for long periods (e.g. *Terminalia velutina*). (figure 3.4)

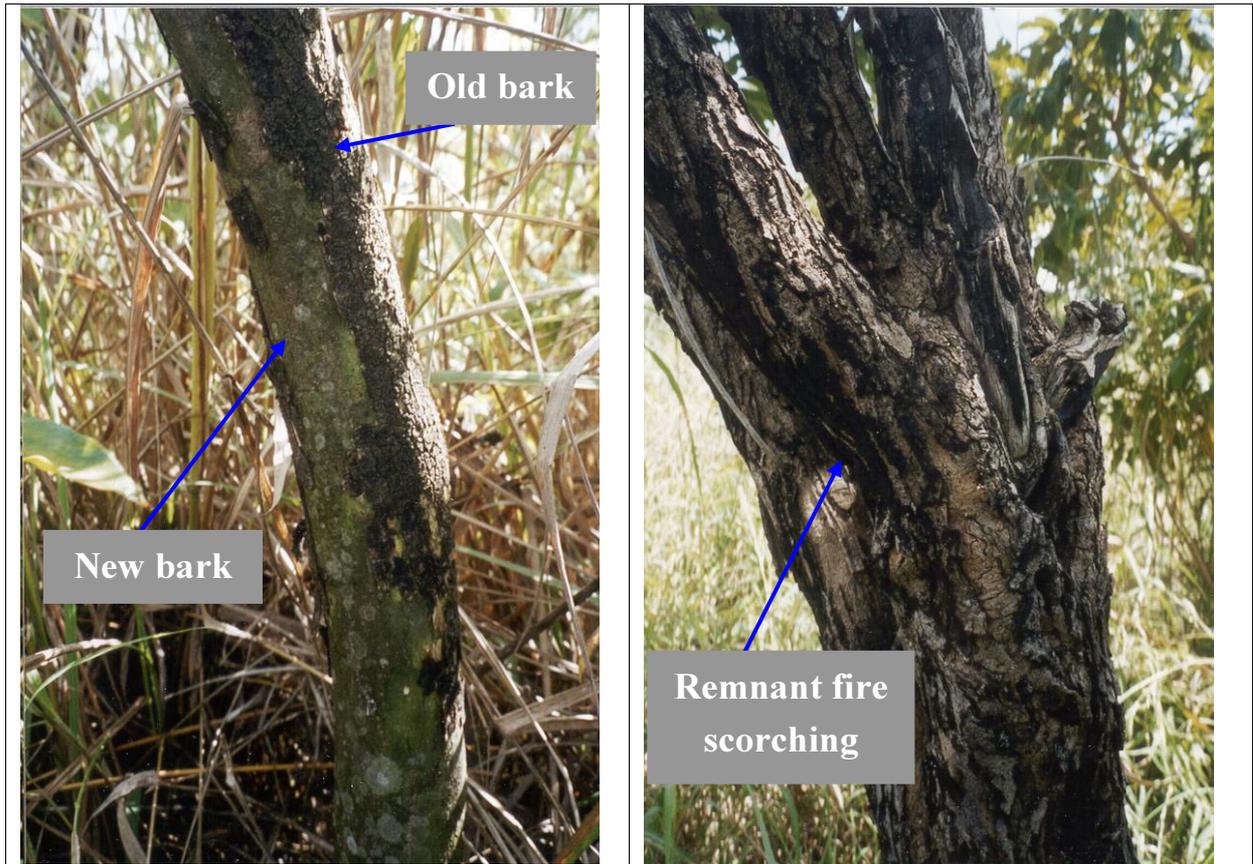


Figure 3.4: Fire adaptation: *Grewia mollis* (left) sheds its bark shortly after a fire disturbance and *Terminalia velutina* has a thick bark capable of surviving fire, on which fire evidence persists.

Canopy density percent: measured using canopy densitometer according to recommended guidelines. Four measurements were taken per plot from different plot quarters and then averaged for an overall canopy density measurement.

Slope and aspect: measured using a clinometer, and compass respectively.

50 m² plot:

DBH of alive trees: Measured the species and DBH of all live trees greater than 2 cm in DBH, to attain information on plant community compositions and structure. Mensuration rules were strictly followed.

DBH of dead trees: Measured the species (where possible) and DBH of all dead trees greater than 2 cm DBH, to give insight into historical site conditions.

500 m² plot:

DBH of alive trees: Measured the species and DBH of all live trees greater than 10 cm in DBH (for the aforementioned reason)

DBH of dead trees: Measured the species (where possible) and DBH of all dead trees greater than 10 cm DBH (for the aforementioned purpose)

3.3. Data analysis: spatial vegetation community changes

3.3.1. Visual interpretation of satellite imagery

Two methods were utilized to locate and determine where spatial vegetation communities had changed significantly. The first method was a visual interpretation of the 1985, 1995 and 2002 satellite images. The images were classified and then compared to determine changed areas. Classification by visual interpretation are useful because the human operator is able to pick up subtle features, correct for illumination differences due to the shading effects of topographic features and smoke and finally can distinguish overall patterns much easier than by an automated process (Lillesand & Kiefer, 2000).

The image interpretation exercise was based on the following:

- Bare dry soil has a high reflectance in the mid-infrared (MIR) as compared with vegetation (Lillesand & Kiefer, 2000).
- Frequently burnt woodlands are dominated by low tree densities and grasses that are not actively growing during in the dry season.
- Tropical high forest has a cooler and moister microclimate that allows most species to continue to grow during the dry season.
- The woodland species also continue to grow, but due to moisture stress they are unable to grow as actively as during wetter periods.
- The canopy of the forested areas is irregular and varies significantly in height, while the woodland canopy is much more uniform and of similar height ranges.

Using a 453 color composite, the different vegetation types were estimated. The various Landsat images, acquired in the dry season, were classified as either forest, regenerating woodland or as open woodland. The areas were classified as follows: Forests were delineated as areas which had a very high reflectance in the NIR and so appeared red in the image. Due to the canopy height variability, the forest had a rough uneven texture. The regenerating woodland also appeared red for the same reason but not to the same intensity as the forest, likely due to the mixed composition of woodland species, dead grasses and actively growing plants. The regenerating woodland had a relatively even texture, further distinguishing it from the forest. Remnant individual or isolated clumps of mature forest trees also had a similar reflection signature as the regenerating woodland. Lastly, the open woodland appeared light brown to greenish in the image with a smooth texture.

Hence, it is presumed that observed increases of NIR reflectance indicate the establishment of actively growing plants. Correspondingly, plots were established in various sites where advanced regeneration woodland had and had not established over the course of the 17 year window. More specifically, sites were selected based on when during this period most of the change had occurred, whether it was during the first 10 years (1985-1995) or during the last 7 years (1995-2002), or a more gradual change.

3.3.2. Temporal image differencing

The second change detection method utilized was temporal image differencing. This technique determines the difference in reflectance values over comparative images from different years, pixel against pixel. Normalized Difference Vegetation Index (NDVI) images from different temporal periods were 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 the changes that have occurred and in which direction. By establishing threshold values, significant cutoff levels of change can be determined. Thresholds of 1 and 2 standard deviations were determined to explicitly express the degree of species change and the highlight the progression of species development.

As outlined in figure 3.5, there are a number of necessary steps to be completed prior to image subtraction. First the images must be geometrically aligned (rectified). All images should overlap so that the pixels for a corresponding area will have the same geographical coordinates in all the images to be compared. Second, the area of interest must be isolated, and so all areas outside the study area are masked out. Third, any area which exhibits a much different spectral signature due to known artifacts in the image such as fire scars, smoke, clouds and cloud shadows are also to be removed. Fourth, images must be radiometrically corrected to ensure they are comparable. A histogram match was used to equilibrate the images and ensure similar values. Consequently, pixel value differences can be attributed to actual changes on the ground instead of difference associated with sensor calibration or illumination conditions. The last step prior to image subtraction involves calculating a vegetation index to accentuate presence and abundance of active plants; for this a Normalized Difference Vegetation Index (NDVI) was used (calculated using equation 3.1).

$$\text{NDVI} = \frac{(\text{NIR band} - \text{Red band})}{(\text{NIR band} + \text{Red band})} \quad \text{equation 3.1}$$

NDVI image pairs are subsequently subtracted producing a continuous map defining the differences between the two images.

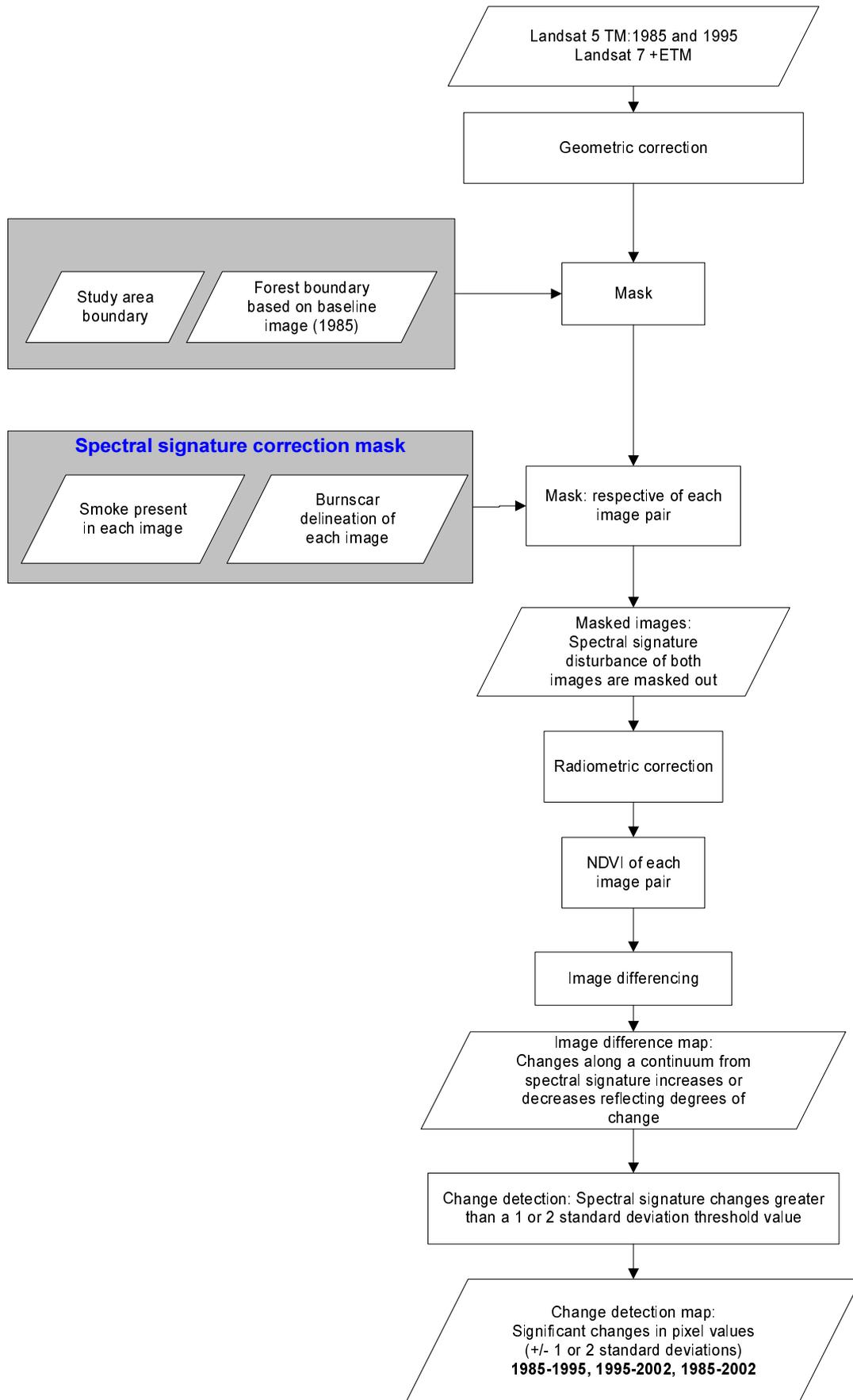


Figure 3.5: NDVI image differencing procedure

3.4. Data analysis: succession dynamics post-fire disturbance

Utilizing field data collected over various succession stages the intention is to come to understand how the vegetation of the Budongo forest woodland is changing in the face of fewer fire disturbances. Plots from various succession snapshots were analyzed to determine the ecological progression patterns. This primarily entails a data exploration exercise to uncover the vegetation gradient shift occurring over time. Many of the analyses will highlight the current vegetation condition of the woodland and relate it to changes observed in the satellite imagery over the 17 year period. When image reflectance values and changed reflectance values from specific plots are related and compared with plot species compositions, the findings can be upscaled to other regions of the study area and conclusions can be inferred about compositional states of previous image years. The second approach to determining the species gradient is to analyze the species compositions of a range of plots. Utilizing a detrended correspondence analysis (DCA) species and plots are arranged according to their similarity, giving a theoretical succession index.

The conceptual diagram described in figure 3.6 outlines the research approach taken to objectively identify species turnover and associated physical changes occurring to sites through succession.

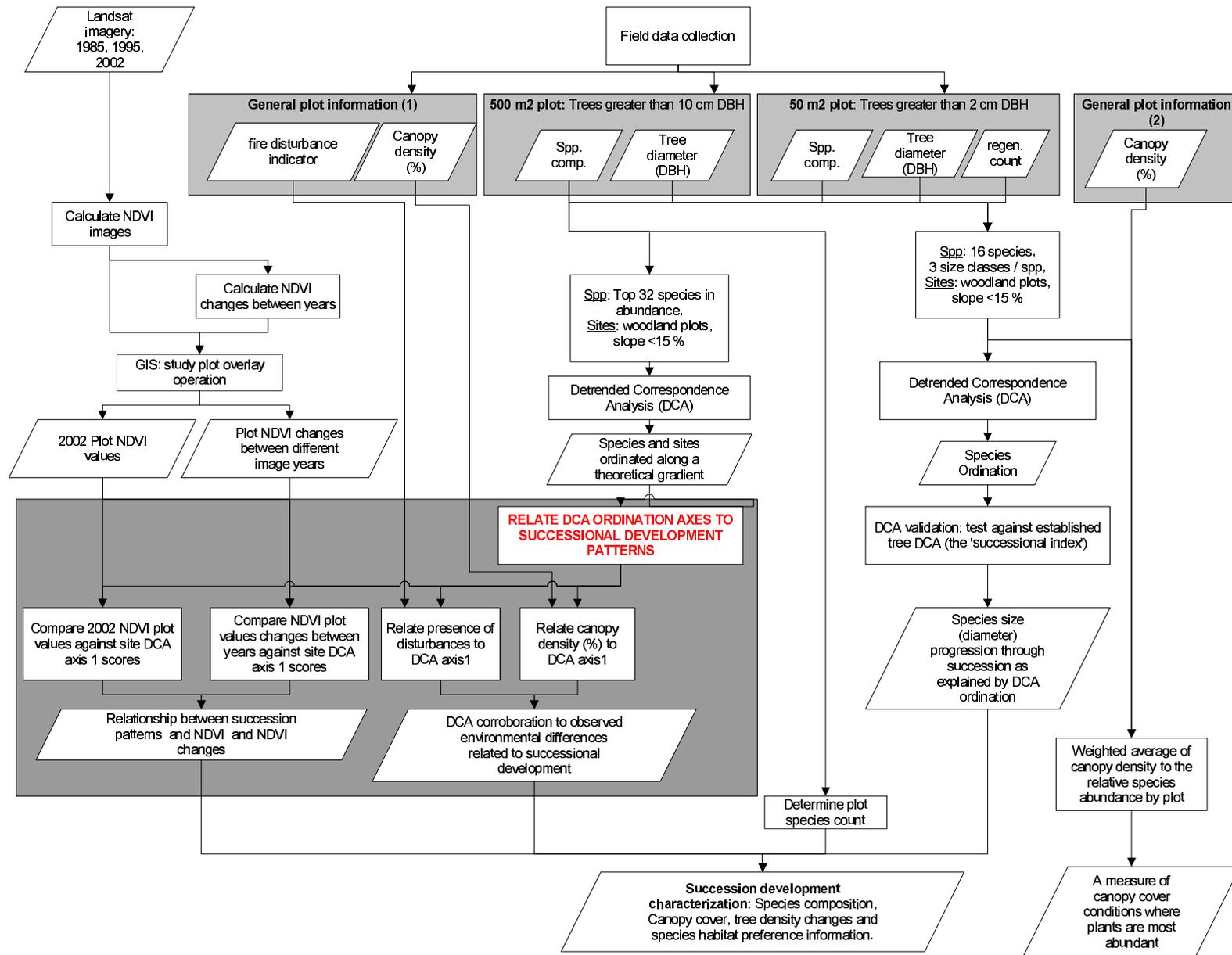


Figure 3.6: Research approach to evaluate the succession gradient trend in species composition and structure

3.4.1. Research approach description: DCA gradient analysis

Species composition and abundances between sites were compared using a detrended correspondence analysis (DCA) to determine the underlying gradients explaining species composition trends. Multivariate ordination analyses were discussed previously in section 2.2.

In this analysis, established trees (trees equal to or exceeding 10 cm in DBH in the 500 m² plot) were used to determine how the overstory species compositions developed through the successional related plots. First, plots which had biologically different site conditions were removed from the analysis. Plots were selected based on the following criteria:

- Plots situated on steep slopes exceeding 15 percent, on bedrock / exposed rock or on saturated soils (i.e. swampy) were screened from the analysis. The remaining plots were situated on similar soils (texture, structure, drainage and moisture) and were exposed to similar climatic influences and theoretically should develop along the same successional gradient.
- Plots established in the forest were disregarded in the analysis as it is the woodland succession dynamics that are of interest and not the forest. Also, there were too few plots established in the forest to determine how the succession patterns of the woodlands related to the forests'.

Once the plots of interest were selected, of which there were 268, the relationship between only the top 32 most abundant species were examined, ensuring at minimum 10 members of each species were recorded. Using the statistical program MVSP (Multivariate Statistical Package), a DCA was calculated on the respective plots and species.

Once calculated, the DCA outputs were interpreted. Validation requires corroboration with different known site factors and site developments, i.e. NDVI, change detection results, disturbance indicator observations and species size class distributions, to explain the gradients expressed for the species and site ordination scores.

To validate against satellite image data, plot NDVI value were determined for all the different image years. A simple overlay operation in a Geographical Information System (GIS), that supports raster capabilities, was used. Once NDVI values for plots of interest were calculated, changes between years were also calculated by subtraction. This plot data can now be tested against DCA axis 1 site scores. The strength and significance of the relationship was tested using a Pearson correlation coefficient and a linear least squares regression.

The second approach to validate the DCA axis 1 site data is to compare it with observed remnant fire disturbance scars. At each plot, a classification of fire scar age was noted (recent, old, or none observed). DCA axis 1 site scores were compared and statistically tested against the classification. An analysis of variance (ANOVA) and a LSD and Bonferroni post hoc tests were used to determine the degree of significance.

The third approach to understanding the succession gradient was to analyze the species size structure progression through ordination. This is done by reorganizing the screened data set and running another detrended correspondence analysis. Sixteen species were analyzed, each repeated at three different size classes. In the analysis each species size class was regarded as an independent species. The size classes were defined as follows:

- Regeneration count (≥ 50 cm in height and < 2 cm DBH),
- Small sized tree count (≥ 2 cm DBH and < 10 cm DBH)
- Established tree count (≥ 10 cm DBH)

The five top most abundant regeneration and small tree species were included into the analysis as were the top 10 most abundant established tree species. This accounted for 16 species in total considering the overlap. A minimum of five individuals per species size class were necessary for the analysis. As the data originated from two different sized plots (50 m² and 500 m²), the established trees had a stronger effect on the DCA in the relation to the abundance per unit area. The establishment or presence of young plants often reflects a degree of randomness and does not actually reflect optimal site conditions. Many to most of these young plants will not live to maturity. By placing greater emphasis on established trees the resulting DCA output will more accurately reflect the actual succession patterns exhibited in the ecosystem.

When the DCA was rerun on the corresponding plots and species, the progression of each species along the first axis were analyzed, to determine at which stage of development a species flourished and if there was a trend how tree sizes developed along this gradient. It is anticipated that there is a dimensional increase in species diameter as a tree progresses through succession. Trees establish and grow through time. As succession is a temporal phenomenon, a trend in increasing diameter should be quantifiable. Species classes were sorted according to the first DCA axis in ascending order, where lower scores reflected an open type of woodland, while higher scores indicate a closed type of woodland. How, and in what order did each species progress through the theoretical DCA axis 1 succession gradient? Was it random or was there a trend? By analyzing the transition path of each plant species through succession, species turnover can be objectively identified and species establishment characteristics charted.

Once the DCA species composition gradient was sufficiently understood, further investigations were executed to trace further successional development patterns. Canopy cover, tree density and species count were compared against the successional development index (the DCA output), which in turn provided further insight into the compositional and structural condition of the woodland.

To understand the relationship present between canopy closure and species abundance, a weighted average was calculated. This analysis was performed for the 16 tree species previously mentioned at the three size classes. This information indicates where and under which light conditions species grow most abundant.

3.5. Data analysis: forest edge influence on ecosystem succession

Two approaches are taken to determine the forest influence on woodland succession dynamics. The first approach entails a comparison of the successional development index against the distance to the forest edge. The second approach determines how NDVI values changed in relation to the distance from the forest edge throughout the entire image.

3.5.1. Successional index comparison

Further analysis requires the calculation of plot distance to forest edge. This was done simply in a GIS, using a distance calculation from forest edge and an overlay operation of plot locations. The forest edge was delineated from the 1985 Landsat satellite image, as the forest's boundary appeared crisp and distinct from the surrounding woodland in this image. Field observations corroborated forest edge locations, whereby a sharp boundary was noted between the woodland's small diameter trees and the mature forest's large diameter trees.

Once plot distances were determined they were plotted against the mature tree successional index for plots.

3.5.2. NDVI - forest edge comparison

To determine successional development on the large scale, NDVI values were used as a proxy for successional change. Assuming this, it is possible to extrapolate successional information to the entire study area using the satellite imagery available. Using the 1985 and 2002 NDVI maps, the corresponding change map, and the distance from forest map (calculated in section 3.5.1), the average changes in NDVI values over distance were calculated for the different years and the changes between years.

4. Results

4.1. Spatial distribution of vegetation change

Two separate change detection methods were investigated to determine the spatial progression of vegetation communities over a 17 year period from 1985 to 2002.

4.1.1. Visual interpretation

Through visual interpretation of Landsat images from 1985, 1995 and 2002, vegetation cover classes were delineated and then compared to determine where changes had occurred in vegetation cover. Figure 4.1 illustrates the visual interpretation results and depicts where changes were observed. The areas highlighted in green (both the solid green and blue with green speckles) represent vegetative changes incurred over the 1985 to 1995 period. The difference between classes is that solid green areas were no longer classified as advanced regeneration in 2002, and have been set back to an earlier stage of vegetative development. The blue with green speckles represents an area delineated as advanced regeneration in both the 1985-1995 period and the 1985 - 2002 period. Finally, the area depicted in solid blue represents what has grown up in the 1995 to 2002 period. This map depicts how the forest is encroaching into the woodland and which areas have not experienced fire for some time.

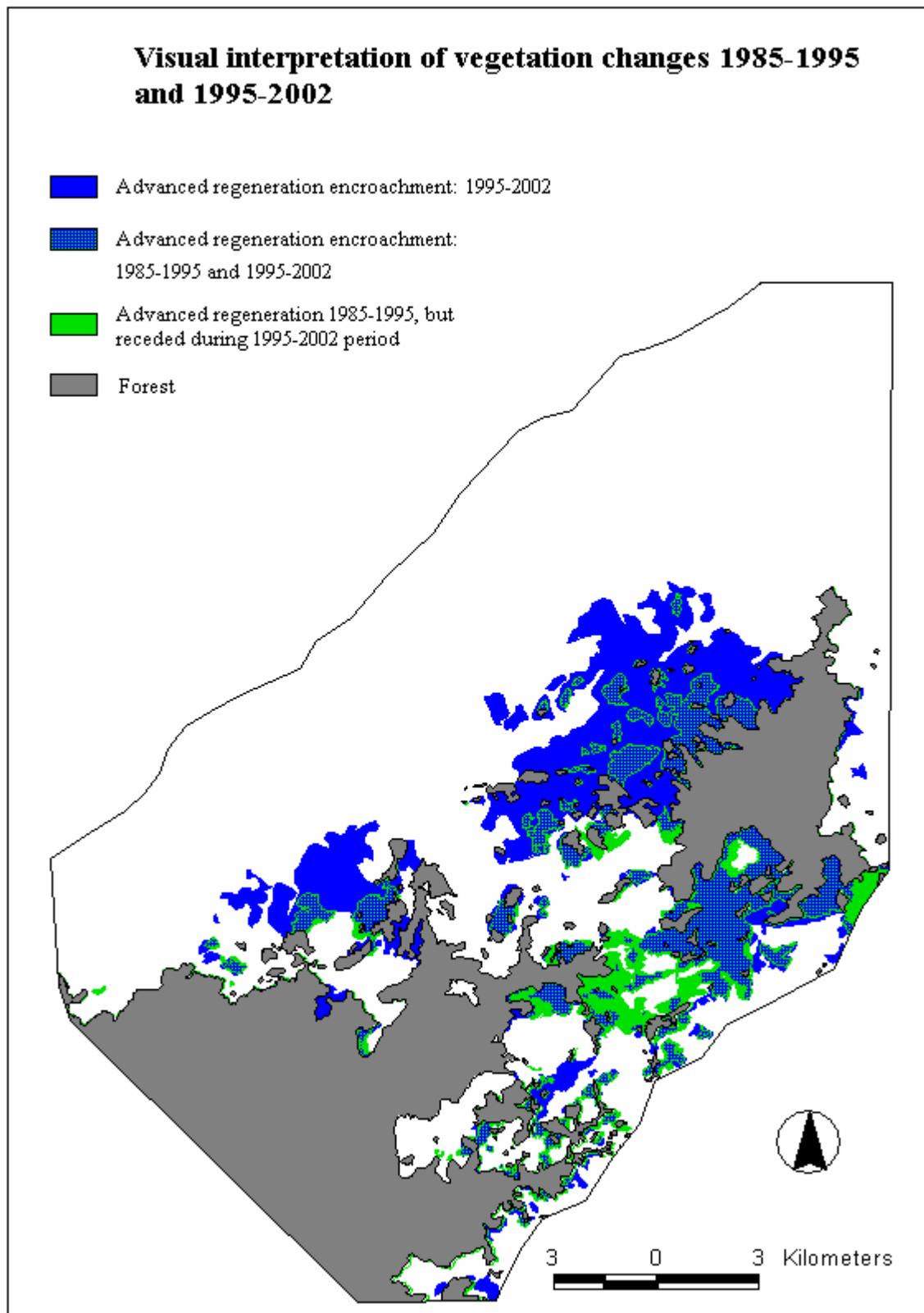


Figure 4.1: Visual interpretation of forest encroachment

4.1.2. Temporal image differencing

The spectral reflectance values, specifically NDVI values, from the 3 different image years were subtracted. Difference values exhibited on a continuous map defined the degree and intensity of change between image pairs. Standard deviations for each difference map were calculated and then used to define threshold values. A change map was produced where all pixels that had increased or decreased, by more than 1 standard deviation and then by more than 2 standard deviations, were highlighted with different shades. This map provided insight into where and by how much NDVI values had actually changed.

During the image pre-processing, burnt areas and areas covered by either smoke or cloud were masked out of the respective image pairs. The unfortunate implication is that this excludes certain areas from the study area. Due to a large fire in 1995, which was burning along the western perimeter of the study area, a sizable portion of the image was obscured by smoke. Subsequently, any comparisons made with the 1995 image required the removal of this particular anomaly from both image pairs.

Many fires were noted to have occurred along the western edge of the study area in the vicinity of the rift escarpment in all three images. The fire regimes in this area seem not to have changed during this period. NDVI differencing indicated that much of the western portion of the study area either decreased or remained relatively unchanged over the 17 year period.

Change maps produced for the 1985 -1995, 1995-2002, and the 1985 -2002 time periods are shown in figures 4.2, 4.3 and 4.4 repetitively. The overall vegetation cover change map (1985-2002), figure 4.4, provides an overview of how vegetation changed during the last 17 year period, while the other two change maps illustrate when in which time window those changes occurred.

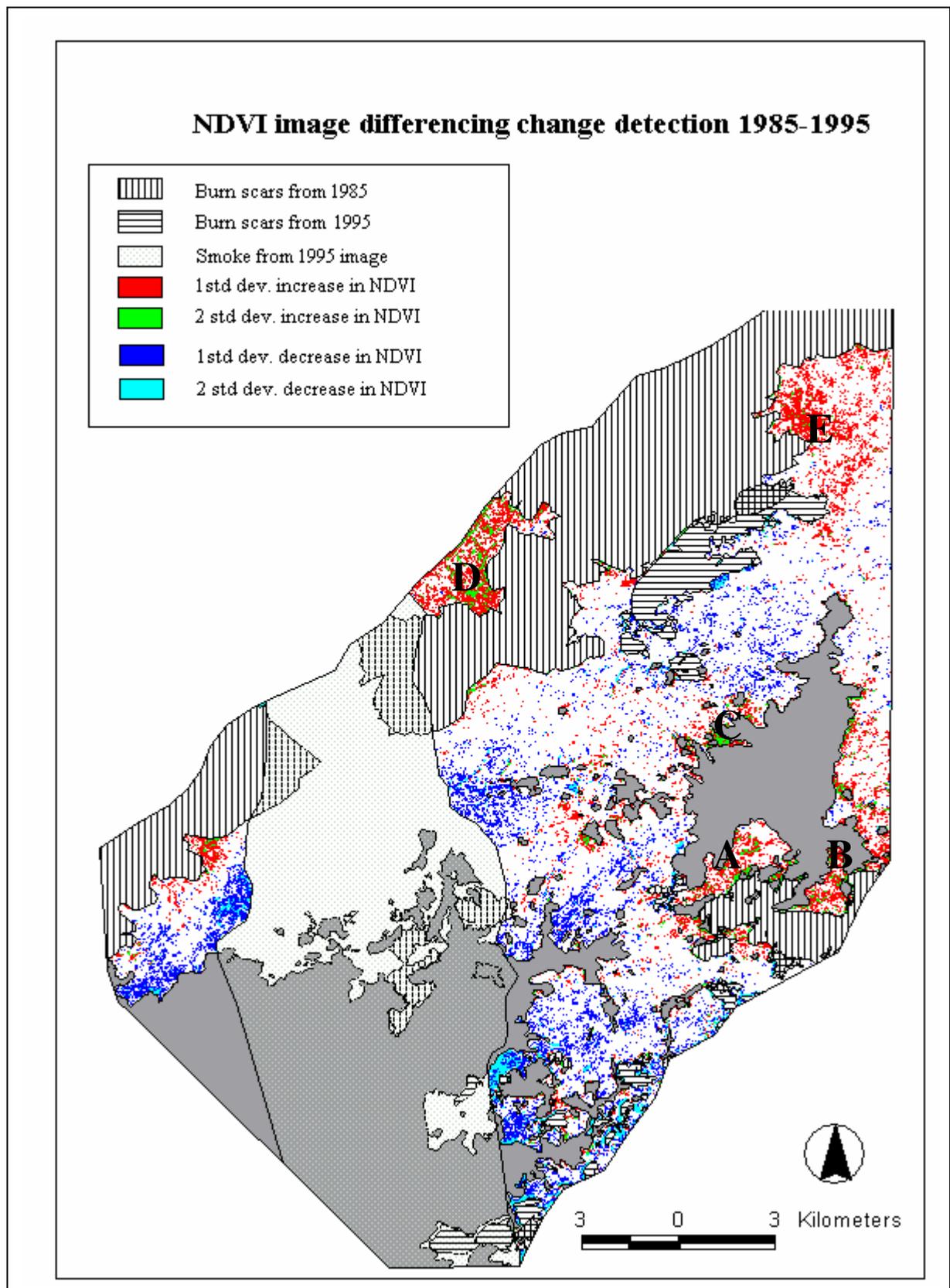


Figure 4.2: Temporal NDVI differencing of the 1985 and 1995 images. Colored areas indicate areas of significant vegetation change

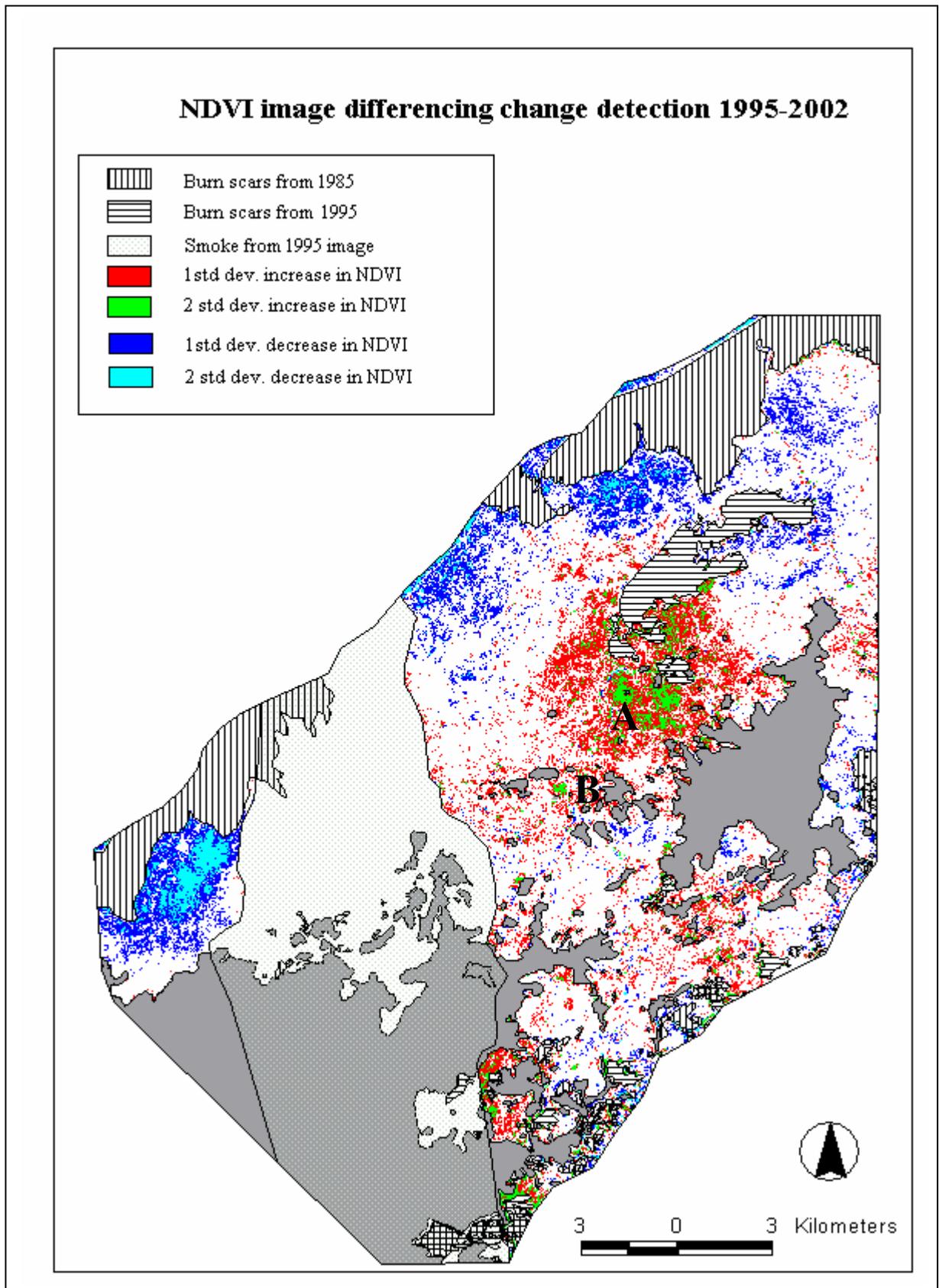


Figure 4.3: Temporal NDVI differencing of the 1995 and 2002 images. Colored areas indicate areas of significant vegetation change

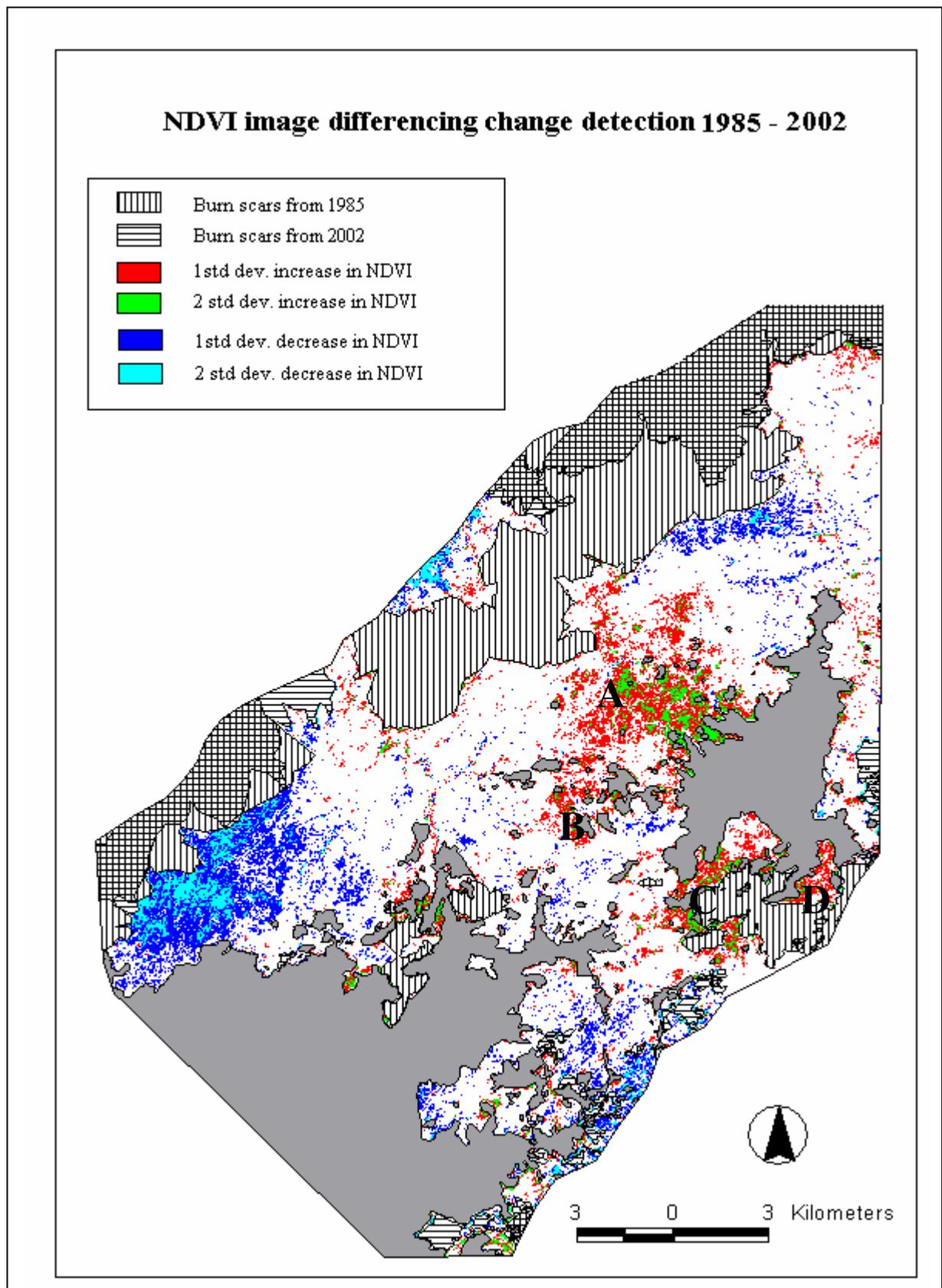


Figure 4.4: Temporal NDVI differencing of the 1985 and 2002 images. Colored areas indicate areas of significant vegetation change

According to the satellite imagery, the areas in close proximity to the forest exhibited fewer fire disturbances in recent years. These areas also exhibited an overall increase in the NDVI reflectance, indicating a change in the vegetation community structure and species compositions. On all maps, areas which had *increased* by more than *one* standard deviation are colored red, areas which *increased* by more than *two* standard deviations are colored green; and those areas that had *decreased* by *one* standard deviation are dark blue and by *two* standard deviations are cyan.

The 1985-1995 change image as shown in figure 4.2, depicts changes which occurred early on in the study period. In this image it is apparent that there are certain regions which have undergone dramatic changes, these are specifically indicated by the letters A, B, C, D and E.

The 1995 – 2002 change image as shown in figure 4.3, depicts more recent vegetation changes. Using the same color shading, it again becomes apparent that there are certain regions which have changed significantly. During this period, most notably is a large area directly northwest of the Kaniyo Pabidi forest increased in NDVI (depicted by letters A and B).

Figure 4.4, highlights where overall changes had occurred during the 17 year time window. Specific areas where significant vegetation development increases were noted are depicted by the letters A, B, C and D.

4.2. Succession dynamics post fire disturbance

Using field data collected in September to October 2002, successional trends were evaluated. A total of 268 plots were established in the woodlands in a range of sites at different stages of successional development (refer to figure 3.3). During the field survey a total of 79 different established tree species were encountered, and a total of 5,584 established trees were measured.

4.2.1. Established tree DCA

Using abundance counts per plot of trees 10 cm in DBH or greater, a species compositional gradient was determined using a DCA ordination. Figure 4.5, graphs the DCA species scores according to the first two axes, the two theoretical variables that explain the greatest variation.

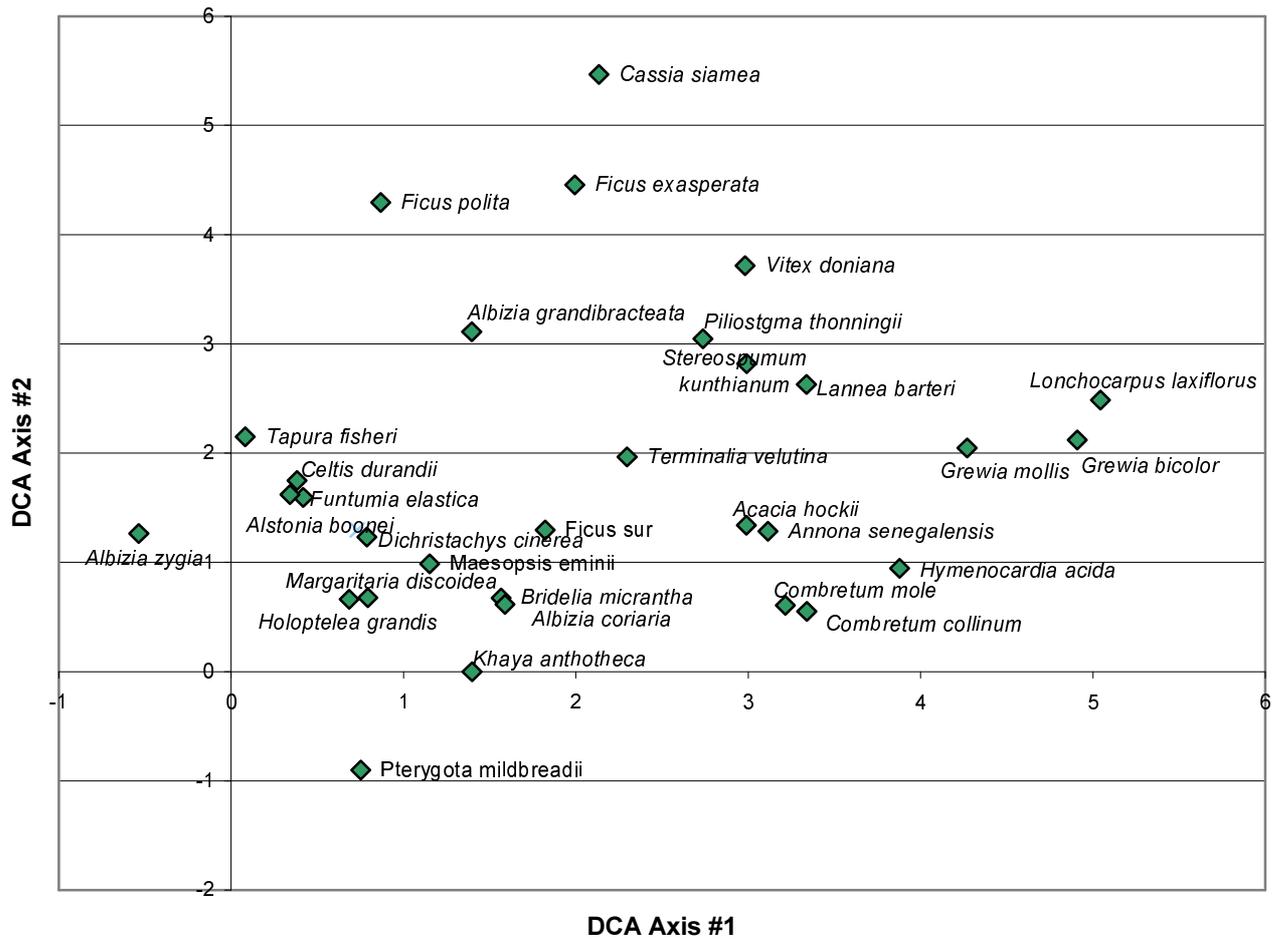


Figure 4.5: Detrended Correspondence Analysis: Species scores as explained by axis 1 and 2, for 32 species at an established stage of development (≥ 10 cm DBH)

The first axis of the DCA explained the most variation, with eigenvector values of 0.472, explaining 12.2% of the variation. The second axis of the DCA exhibited a weaker eigenvector value of 0.242, and explained a cumulative of 18.6% of the species composition variation. The DCA axis values represent the standard deviation of species turnover, or units of beta diversity (Palmer, 1999).

At the first glance of this ordination graph it becomes apparent that the species which were found in abundance in the open woodland, like *Grewia mollis* and *Lonchocarpus laxiflorus*, had high species scores along the first axis of the DCA, while species characteristic of a closed woodland, like *Albizia grandibracteata*, *Maesopsis eminii*, and *Holoptelea grandis* had lower DCA axis 1 scores. Basic knowledge could not identify the differences exhibited in the second axis of the DCA.

Figure 4.6 demonstrates the corresponding site scores per plot on the first 2 axes of the DCA.

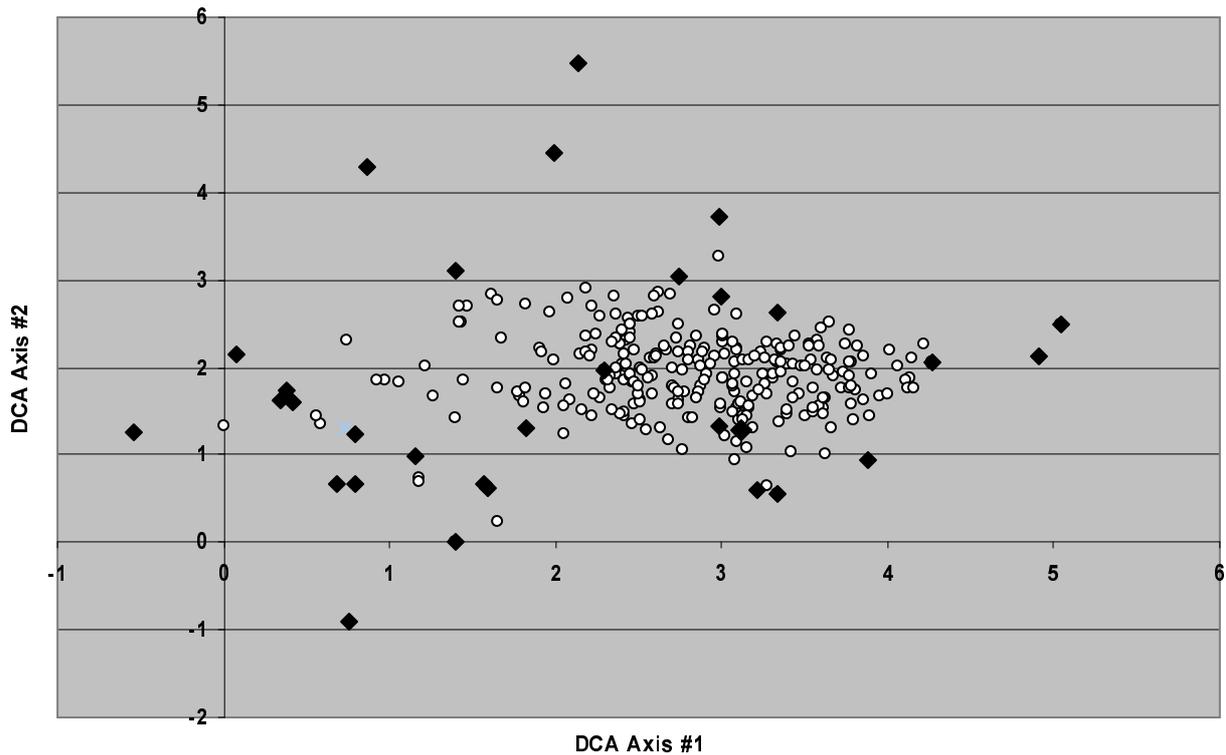


Figure 4.6: Detrended Correspondence Analysis biplot: Plot site scores (white) and species scores (black) as explained by axis 1 and 2, for 32 species at an established stage of development (≥ 10 cm DBH)

In this representation, the relationship between plant scores and corresponding plot site scores are noted. Species names are shown above in figure 4.5. Plot scores are a weighted species score average, where relative plant abundances per plot impact the output site score (Jongman *et al.*, 1987). Based on initial impressions it appears that the first axis of the DCA strongly relates to visual trends recognized in the field. Plots found in open woodland had higher DCA scores, and closed woodland plots had low DCA scores.

4.2.2. Established tree DCA interpretation

Detrended correspondence analysis is an indirect ordination technique, as it calculates a theoretical gradient based on species composition data with no explanatory environmental data. Interpretation of the ordination output requires corroboration with extraneous environmental data. Correlation coefficients between ordination gradients and environmental data are adequate to summarize the relationship exhibited between the two factors (Jongman *et al.*, 1987).

To test the ordination output, the first 2 DCA site score axes were evaluated against the following known plot characteristics indicative of successional development:

- plot NDVI values from 2002 image, indicative of current vegetation status
- the NDVI changes between 1985 and 2002, indicative of the degree of vegetation change
- fire scar age estimates, indicative of time post disturbance
- overall tree densities, indicative of degree of vegetation establishment
- and canopy density, indicative of canopy closure

Hence, when the first DCA axis was analyzed using a Pearson’s correlation, a significant negative correlation emerged in all but the tree density measure (table 4.1). The remainder, the 2002 plot NDVI, the 1985 – 2002 plot NDVI change, the fire scar age estimate, and the canopy density, were all highly significant ($p < 0.001$). Hence, it was inferred that the gradient exhibited in the first DCA axis reflects successional changes. This axis will hereon be termed the “successional index” (SI). The relationships exhibited with this axis will be further examined to determine some of the related changes occurring during succession.

Table 4.1: Pearson correlation significance levels with DCA axis 1 and DCA axis 2

Plot characteristics	DCA axis 1		DCA axis 2	
	Pearson correlation	Sig. (2-tailed)	Pearson correlation	Sig. (2-tailed)
2002 NDVI values	-0.5640	0.000	-0.0225	0.725
NDVI change between 1985 and 2002	-0.5281	0.000	0.0146	0.820
Fire scar age estimate	-0.5896	0.000	-0.0601	0.321
Canopy density	-0.5090	0.000	0.1165	0.056
Overall tree density	-0.0447	0.466	-0.0617	0.313

The same plot information was again tested against the second DCA axis, and did not demonstrate any significant relationship. The variation in this axis could not be corroborated or explained by any of the data that was collected in the field; therefore this axis will be omitted from further analysis and interpreted as noise.

It should be noted that the direction of the ordination output is arbitrary, and should not influence how it is interpreted (Palmer, 1999). In this case it appears contradictory to logic, but it is not. Here, the early successional stages are found far along the axis while the late succession stages are at or approaching the origin.

4.2.3. Ecological connotation of DCA axis 1

Based on the conclusion that the first DCA axis explains successional development, it is now possible to scrutinize and explore some successional trends in greater detail. Table 4.2 lists the 32 species and the corresponding “successional index” values in descending order, from the characteristically open type woodland to the closed woodland / forest condition.

Table 4.2: Successional index species scores and the number of respective trees measured

Species	SI	Number of trees sampled	Species	SI	Number of trees sampled
1. <i>Lonchocarpus laxiflorus</i>	5.043	129	17. <i>Albizia coriaria</i>	1.587	11
2. <i>Grewia bicolor</i>	4.909	24	18. <i>Bridelia micrantha</i>	1.565	64
3. <i>Grewia mollis</i>	4.269	921	19. <i>Khaya anthotheca</i>	1.397	27
4. <i>Hymenocardia acida</i>	3.878	16	20. <i>Albizia grandibracteata</i>	1.395	349
5. <i>Combretum collinum</i>	3.339	682	21. <i>Maesopsis eminii</i>	1.152	58
6. <i>Lannea barteri</i>	3.337	134	22. <i>Ficus polita</i>	0.867	11
7. <i>Combretum mole</i>	3.216	18	23. <i>Margaritaria discoidea</i>	0.792	34
8. <i>Annona senegalensis</i>	3.114	326	24. <i>Dichrostachys cinerea</i>	0.787	13
9. <i>Stereospermum kunthianum</i>	2.991	251	25. <i>Pterygota mildbreadii</i>	0.751	14
10. <i>Acacia hockii</i>	2.989	140	26. <i>Caloncoba schweinfurthii</i>	0.73	63
11. <i>Vitex doniana</i>	2.982	199	27. <i>Holoptelea grandis</i>	0.684	14
12. <i>Piliostigma thonningii</i>	2.737	95	28. <i>Funtumia elastica</i>	0.418	68
13. <i>Terminalia velutina</i>	2.297	1612	29. <i>Celtis durandii</i>	0.382	12
14. <i>Cassia siamea</i>	2.135	13	30. <i>Alstonia boonei</i>	0.341	14
15. <i>Ficus exasperata</i>	1.993	12	31. <i>Tapura fisheri</i>	0.082	11
16. <i>Ficus sur</i>	1.822	56	32. <i>Albizia zygia</i>	-0.536	38

The corresponding SI score indicates where along the successional gradient a particular species maximizes in abundance. Species like *Lonchocarpus laxiflorus*, *Grewia bicolor*, and *Grewia mollis*, for instance, reach optimal growth early in the succession gradient, while species at the other end of the SI, like *Holoptelea grandis*, *Funtumia elastica* and *Celtis durandii*, reach optimal conditions at the latter stages of woodland succession.

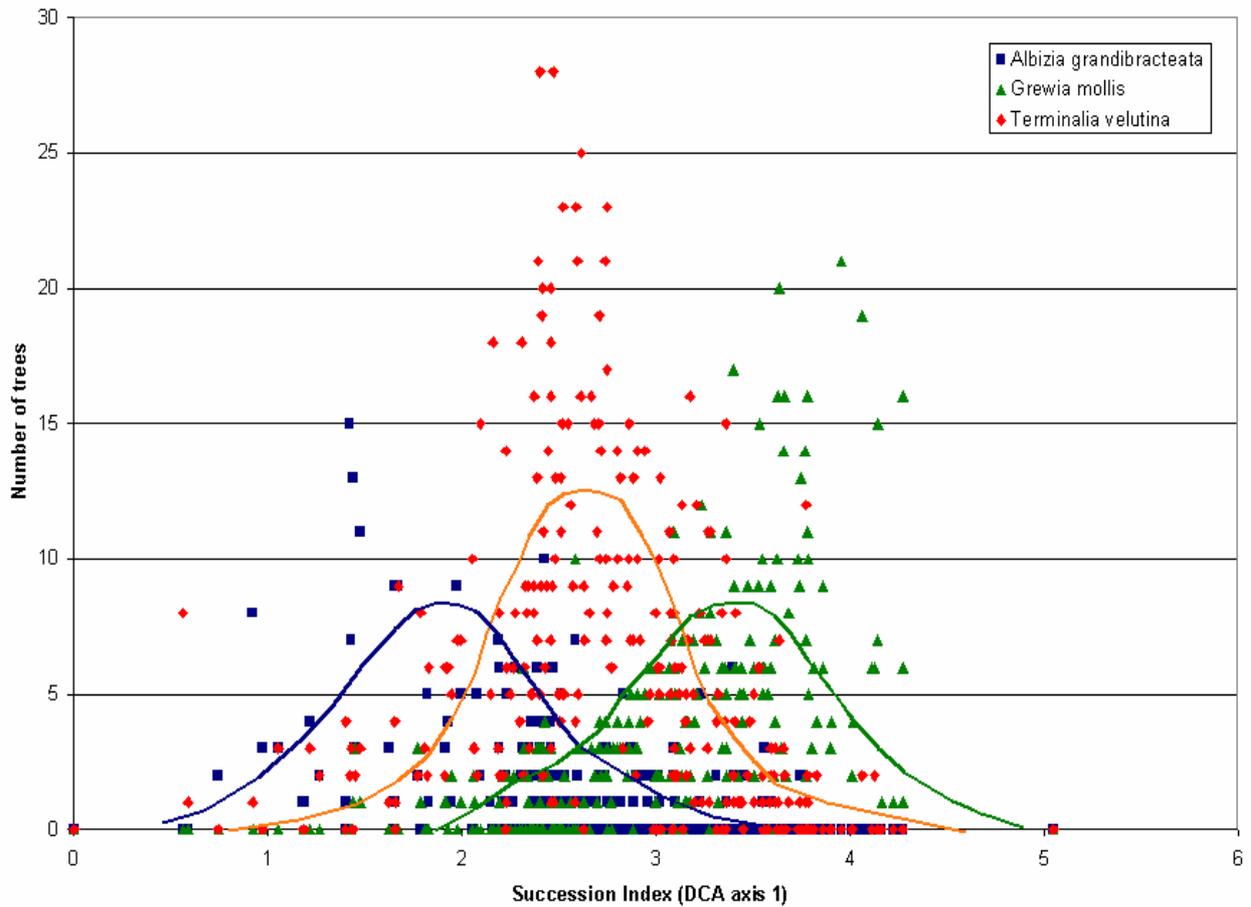


Figure 4.7: Successional gradient species turnover: Tree abundances for *Albizia grandibracteata*, *Terminalia velutina* and *Grewia mollis* along the successional gradient

Plant abundance follows a bell shaped development pattern, whereby species reach maximum abundance at a certain stage and thereafter decline. Figure 4.7 shows that top tree abundances of three common species (*Albizia grandibracteata*, *Terminalia velutina*, and *Grewia mollis*), plotted against the plot succession index rating. These species grow optimally in different successional stage environments. It is this optimal peak environment that is indicated for each of the different species listed in table 4.2.

The 2002 plot NDVI values were compared to the plot successional index. As is apparent in figure 4.8, there is an observable trend where increases in the successional index, correspond to NDVI decreases.

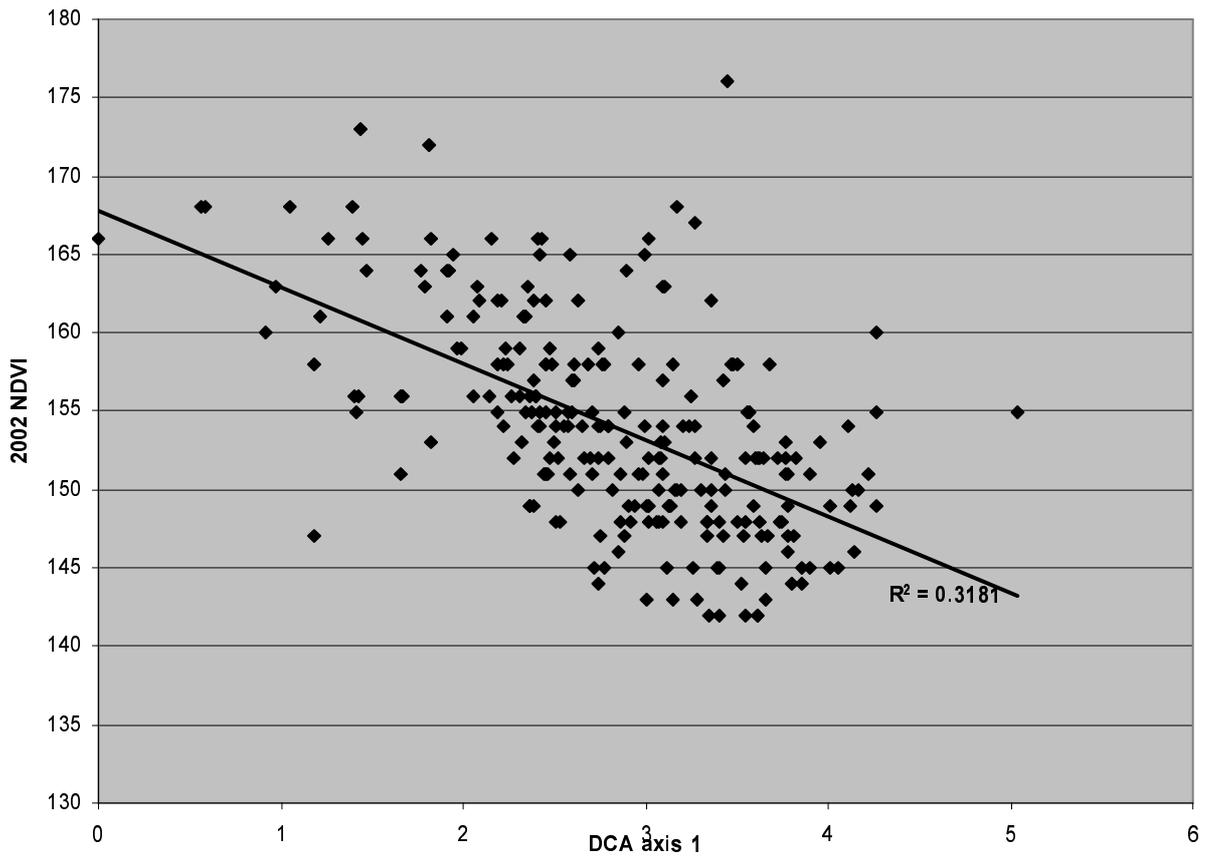


Figure 4.8: Relationship between 2002 NDVI image and DCA Axis 1

This indicates that areas having lower NDVI values relate to early successional species compositions, while high NDVI values corroborate with latter succession vegetation communities. After testing and confirming normality of both the NDVI plot values and the DCA site score, with a histogram, a Q-Q plot, and a Kolmogorov-Smirnov normality test, a linear least squares regression analysis was run. The regression output indicated the degree by which NDVI values explained the successional index plot scores. In this analysis 31.82 percent of the variation in NDVI values was explained by the successional index (LSR, $R^2 = 0.3182$, $p < 0.01$).

The change in NDVI plot values between 2002 and 1985 were also examined against the SI site score values. Figure 4.9 demonstrates the relationship exhibited between the NDVI changes and the SI scores for corresponding plot locations. Areas of positive change indicated areas that had increased in NDVI in 2002.

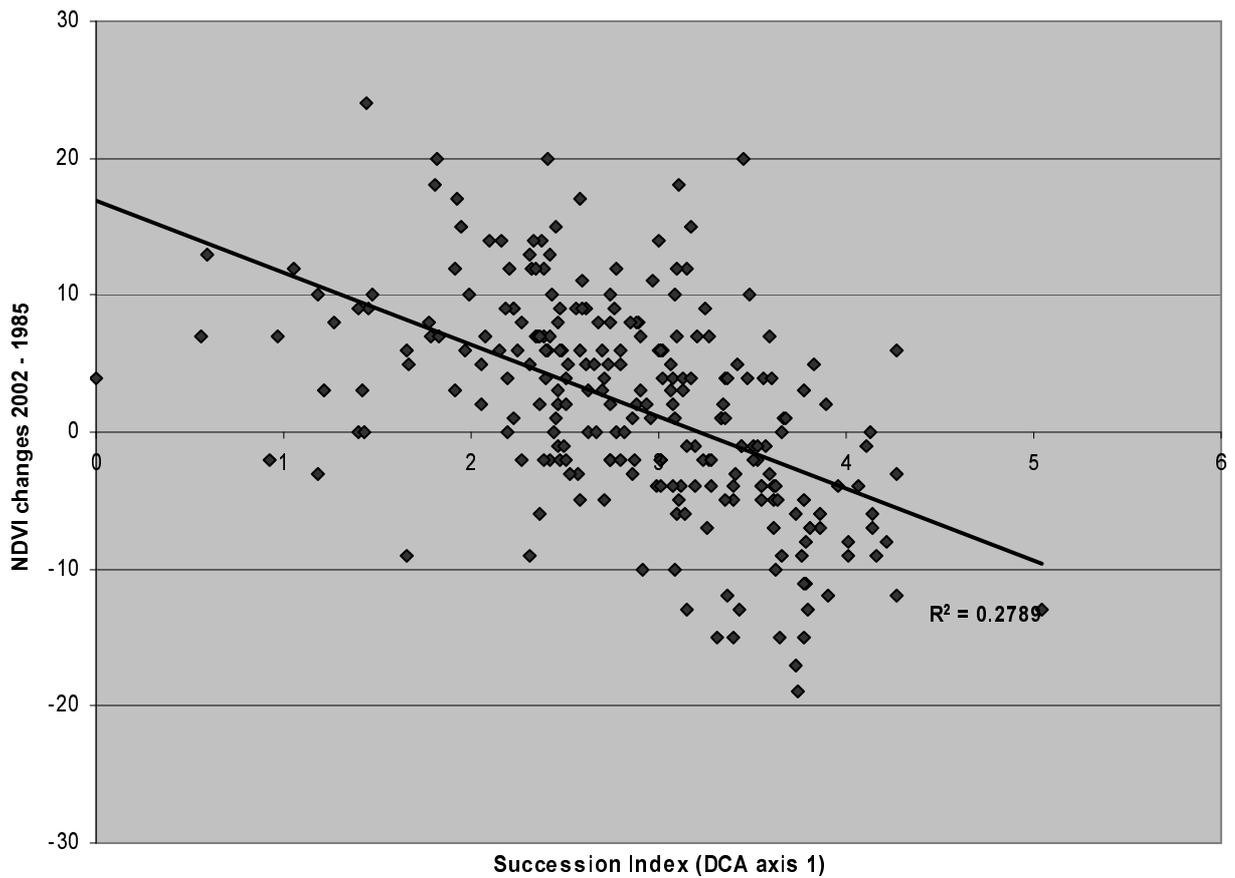


Figure 4.9: Relationship between changes in NDVI reflectance (between 1985 and 2002) and the successional index (DCA axis 1)

The graph depicts a negative relationship between NDVI and the SI scores. Sites that decreased in NDVI generally were at earlier stages of succession, while sites which increased in NDVI generally were at advanced stages of succession. Again, once normality was tested and confirmed for NDVI changes, another regression analysis was run. In this case, NDVI changes explained 27.89 percent of the variation exhibited in the SI plot scores (LSR, $R^2 = 0.2789$, $p < 0.01$).

Third, succession index site scores were compared to observed fire scar evidence, whereby the relative age of the fire scars were classified as recent, old or not observed. Figure 4.10 displays a box plot, for the succession index distribution range of the different fire scar age classifications

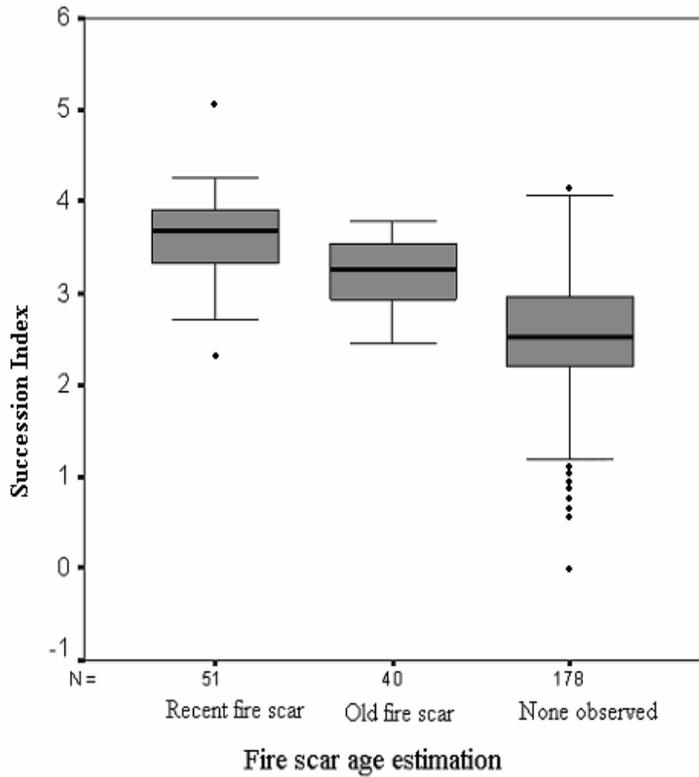


Figure 4.10: Boxplot of SI site score values against observed fire scar evidence

It is apparent that sites where recent fire scar evidence was observed were found at sites in early stages of succession (high SI); old fire scars were found at sites located at intermediate phases of development (mid-range SI); and lastly where no fire evidence was observed these sites were located in respectively closed woodlands (low SI). Statistically, differences between the 3 different classes were significant, both overall (ANOVA, d.f.= 268, $p < 0.01$) and between all classes (Bonferroni and LSD post hoc tests). (Table 4.3 and 4.4, respectively)

Table 4.3: Analysis of variance between fire scar age estimates and successional index scores

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	55.589	2	27.795	71.573	.000
Within Groups	103.298	266	.388		
Total	158.887	268			

Table 4.4: LSD and Bonferroni Post hoc test: the degree of significance between fire scar age estimates

Disturbance code	Disturbance code	LSD Sig.	Bonferroni Sig.
none	Old fire	.000	.000
	Recent fire	.000	.000
Old fire	None	.000	.000
	Recent fire	.001	.002
Recent fire	None	.000	.000
	Old fire	.001	.002

The forest canopy was subsequently compared to the successional index to determine how the canopy structure of the woodland changed through successional development (Figure 4.11)

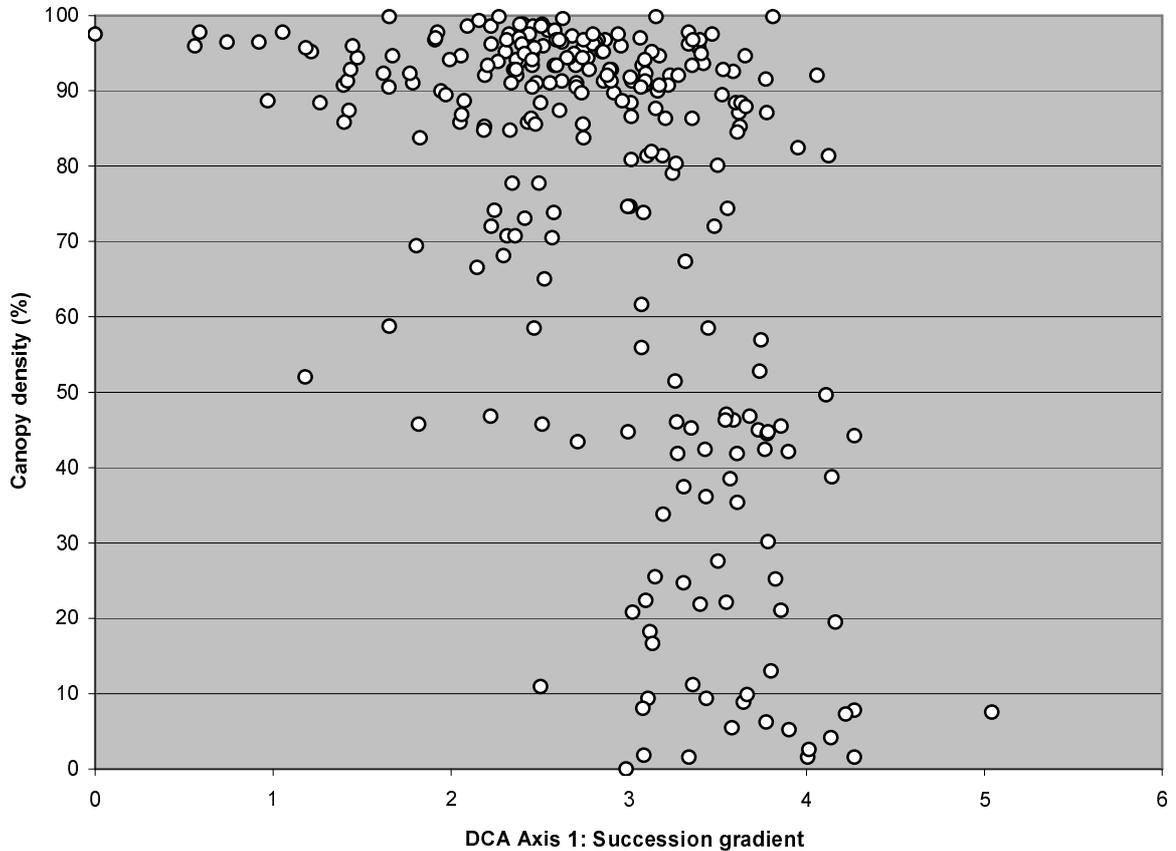


Figure 4.11: Canopy density changes along the succession gradient

It is apparent that during early stages of establishment post-fire, canopy density can be quite open, but closes quite abruptly and remains closed through latter stages of succession.

4.2.4. Species progression DCA

To monitor species progression along the succession gradient, a second DCA was run, hereon out called the “species progression” DCA. The 16 most abundant species were analyzed each at three different size classes. Each species size class was treated independently, and treated as individual species for the analysis. Subsequently, species scores were examined and species trends were noted. The analysis output indicated that the first axis clearly explained the majority of the variation, having a strong eigenvector value of 0.501; the second axis was weaker and had an eigenvector of 0.3236.

To interpret the species progression DCA, the previous successional index DCA for overstorey trees was used to corroborate trends exhibited. Figure 4.12 plots the relationship between the two ordination results.

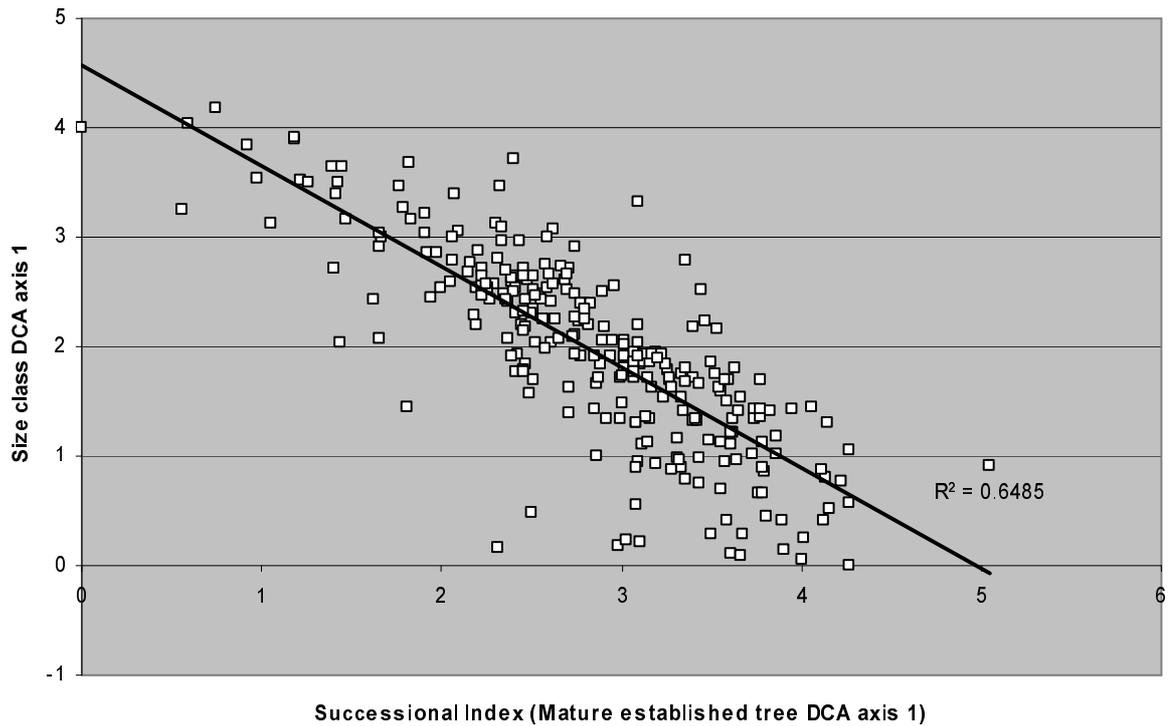


Figure 4.12: The species progression DCA axis 1 vs. the established tree successional index DCA axis 1

An inverse relationship was exhibited between the two DCA axes, of which the established tree successional index DCA explained 64.85 % of the variation in the species progression DCA (LSR, $R^2 = 0.6485$ $p < 0.001$). This irrefutably implies that the first axis of the species progression DCA also explains successional development patterns.

Furthermore, the trend in species scores was examined, where the order and degree of species progression through succession was measured. As is demonstrated in table 4.5, the majority of species follow a defined progression trend, whereby successional index scores increase with increasing diameter. The regenerating tree seedlings are found earlier in the hypothetical succession gradient further proceeded by small trees, and then by established trees.

Table 4.5: Occurrences of the different combinations of progression patterns

Species progression over DCA Axis #1	No. of occurrences	Species
Regenerating – Small – Established (R-S-E)	7	<i>A. grandibracteata</i> <i>A. hockii</i> <i>A. senegalensis</i> <i>G. mollis</i> <i>M. eminii</i> <i>T. velutina</i> <i>S. kunthianum</i>
Regenerating – Established – Small (R-E-S)	3	<i>C. collinum</i> <i>L. laxiflorus</i> <i>V. doniana</i>
Small – Regenerating – Established (S-R-E)	2	<i>B. micrantha</i> <i>F. elastica</i>
Established – Small – Regenerating (E-S-R)	1	<i>K. anthotheca</i>
Small – Established – Regenerating (S-E-R)	1	<i>P. mildbreadii</i>

The DCA species scores for the different plant size classes are demonstrated in figure 4.13. This chart basically demonstrates where and in which succession stage, the size class for a particular species grows best, i.e. where and in which environment species establish as regenerators, and where they grow at progressively larger sizes.

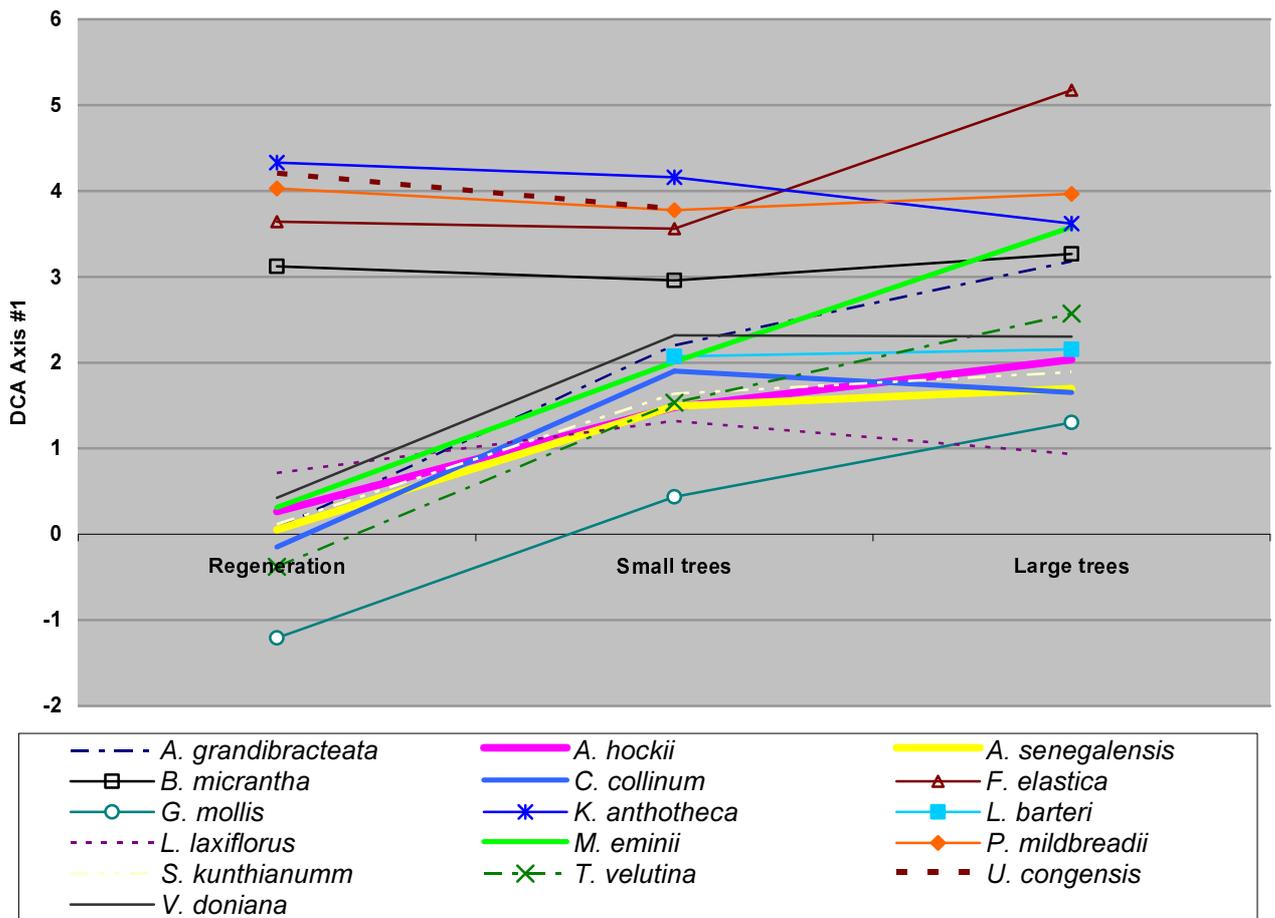


Figure 4.13: Species progression through succession

This further corroborates and reconfirms the successional development trend already previously noted. As such, lower scores relate to early development stages post fire and higher values correspondingly relate to a latter phase of successional development. Hence, when the graph is regarded it is the species, *Grewia mollis*, *Terminalia velutina*, *Albizia grandibracteata*, *Combretum collinum*, *Lonchocarpus laxiflorus*, *Maesopsis eminii*, *Stereospermum kunthianum*, *Vitex doniana*, *Acacia hockii* and *Annona senegalensis* that establish themselves in the open woodland, while *Pterygota mildbraedii*, *Bridelia micrantha*, *Uvariopsis congensis*, *Khaya anthotheca*, and *Funtumia elastica* regenerate in more of a closed woodland condition. This graph subsequently shows where and how these species progress along the succession gradient. Some species for instance, *Maesopsis eminii* or *Albizia grandibracteata* will establish in an open woodland but finally achieve maximum abundance in a closed canopy woodland / colonizing forest environment. Other species such as *Grewia mollis* or *Lonchocarpus laxiflorus* react differently and establish in the open woodland, but remain prevalent only here, dying out when the environment becomes inhospitable at latter stages of succession. The species scores are specifically listed below in table 4.6.

Table 4.6: Successional species scores at corresponding size classes

	Species	Regenerating trees	Small trees	Large trees
1	<i>Lonchocarpus laxiflorus</i>	0.7138	1.3218	0.9341
2	<i>Grewia mollis</i>	-1.2067	0.4362	1.3021
3	<i>Combretum collinum</i>	-0.1462	1.9019	1.6531
4	<i>Annona senegalensis</i>	0.0528	1.4929	1.6954
5	<i>Stereospermum kunthianum</i>	0.1147	1.6364	1.8913
6	<i>Acacia hockii</i>	0.2646	1.4818	2.0355
7	<i>Lannea barteri</i>	-	2.0724	2.1558
8	<i>Vitex doniana</i>	0.4238	2.3163	2.3016
9	<i>Terminalia velutina</i>	-0.3781	1.5319	2.5715
10	<i>Albizia grandibracteata</i>	0.0739	2.2022	3.1802
11	<i>Bridelia micrantha</i>	3.121	2.9564	3.2666
12	<i>Maesopsis eminii</i>	0.3117	2.0086	3.5772
13	<i>Khaya anthotheca</i>	4.3316	4.1594	3.6181
14	<i>Pterygota mildbreadii</i>	4.0282	3.7743	3.9659
15	<i>Funtumia elastica</i>	3.6403	3.5615	5.1734
16	<i>Uvariopsis congensis</i>	4.2061	3.7925	-

4.2.5. Successional pattern developments and inferences

Sections 4.2.1 and 4.2.2 highlighted and provided evidence that the first DCA axes for both analyses corroborated with successional patterns. To further characterize successional development patterns, the “successional index” for the mature trees (section 4.2.1: DCA axis 1 for trees greater or equal to 10 cm) was tested against tree density and plot species count. Figure 4.14 illustrates the relationship between succession and tree density.

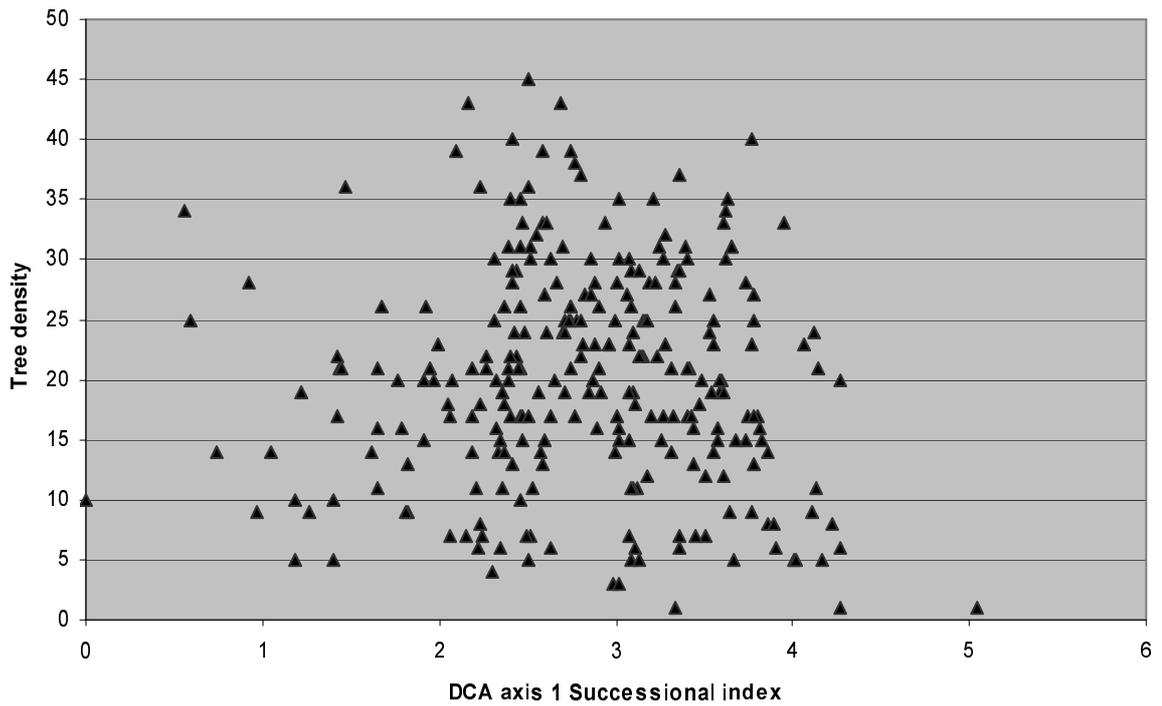


Figure 4.14: Tree density along the successional gradient

There is no apparent trend visible between tree density and successional progression.

Figure 4.15, demonstrates how species diversity changes over time through successional development.

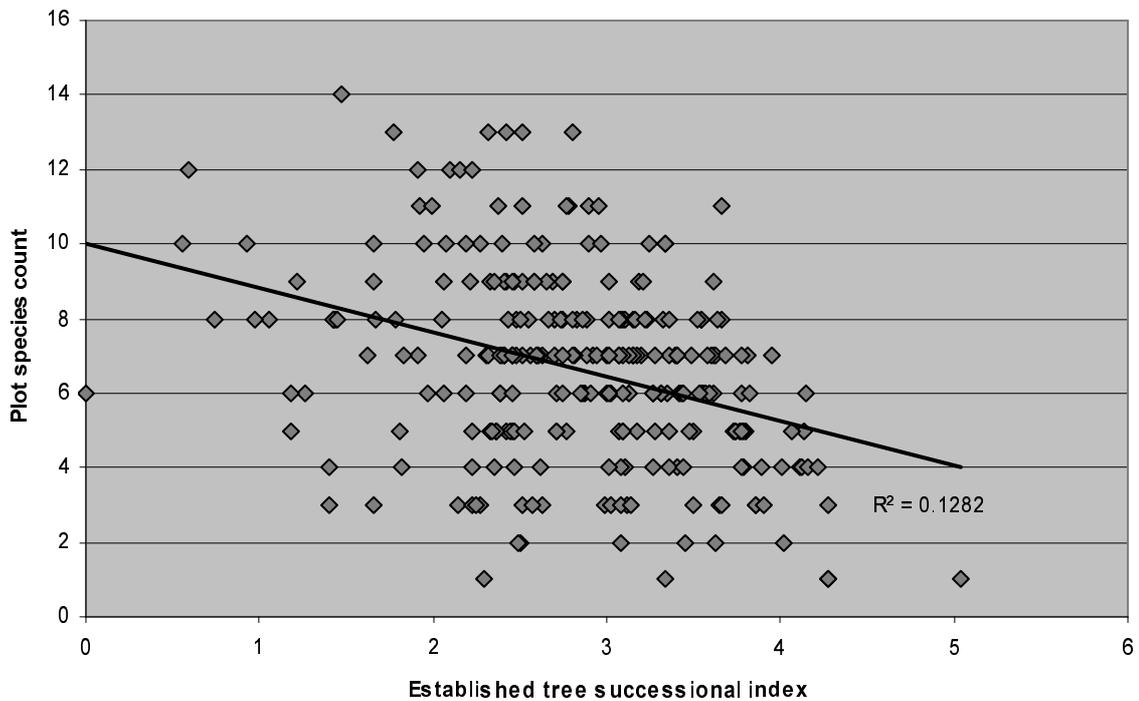


Figure 4.15: Species count tested against the successional index

Although this relationship is weak, there is a trend indicating that the numbers of species present per unit area increases with time after disturbance. A least squares regression analysis determined that 12.82 % of the variation in species count could be explained by the stage of successional development (LSR, $R^2 = 0.1282$, $p < 0.01$).

4.2.6. Canopy density measure for species

To determine under which canopy density conditions species are most prevalent, a weighted canopy density average for different species was calculated, where plant abundance counts were used as weight. Below in table 4.7, the weighted canopy density for different species at the three different size classes is indicated. Note there is a similar pattern in species establishment and progression through succession as was demonstrated in the species progression detrended correspondence analysis (section 4.2.4).

Table 4.7: Optimal canopy cover (%) condition for 16 tree species at different size classes

	Species	Regenerating trees	Small trees	Large trees
1	<i>Acacia hockii</i>	57.8	72.7	81.6
2	<i>Albizia grandibracteata</i>	55.2	73.8	89.4
3	<i>Annona senegalensis</i>	53.0	80.5	73.5
4	<i>Bridelia micrantha</i>	91.2	91.0	93.4
5	<i>Combretum collinum</i>	52.9	78.2	77.4
6	<i>Funtumia elastica</i>	94.6	93.9	95.4
7	<i>Grewia mollis</i>	33.2	55.3	72.8
8	<i>Khaya anthothea</i>	89.7	93.1	84.9
9	<i>Lannea barteri</i>	-	80.9	85.4
10	<i>Lonchocarpus laxiflorus</i>	43.4	84.1	71.2
11	<i>Maesopsis eminii</i>	68.9	94.1	93.4
12	<i>Pterygota mildbreadii</i>	95.8	94.3	82.6
13	<i>Stereospermum kunthianum</i>	64.4	76.6	72.9
14	<i>Terminalia velutina</i>	42.6	67.6	89.0
15	<i>Uvariopsis congensis</i>	94.1	90.9	-
16	<i>Vitex doniana</i>	60.7	74.4	87.5

4.3. Forest edge influence on ecosystem succession

The forest acts as a seed source and implicitly speeds or enhances the rate of succession development. Figure 4.16 demonstrates the relationship between distance to the forest and the successional index calculated for mature trees (section 4.2.1).

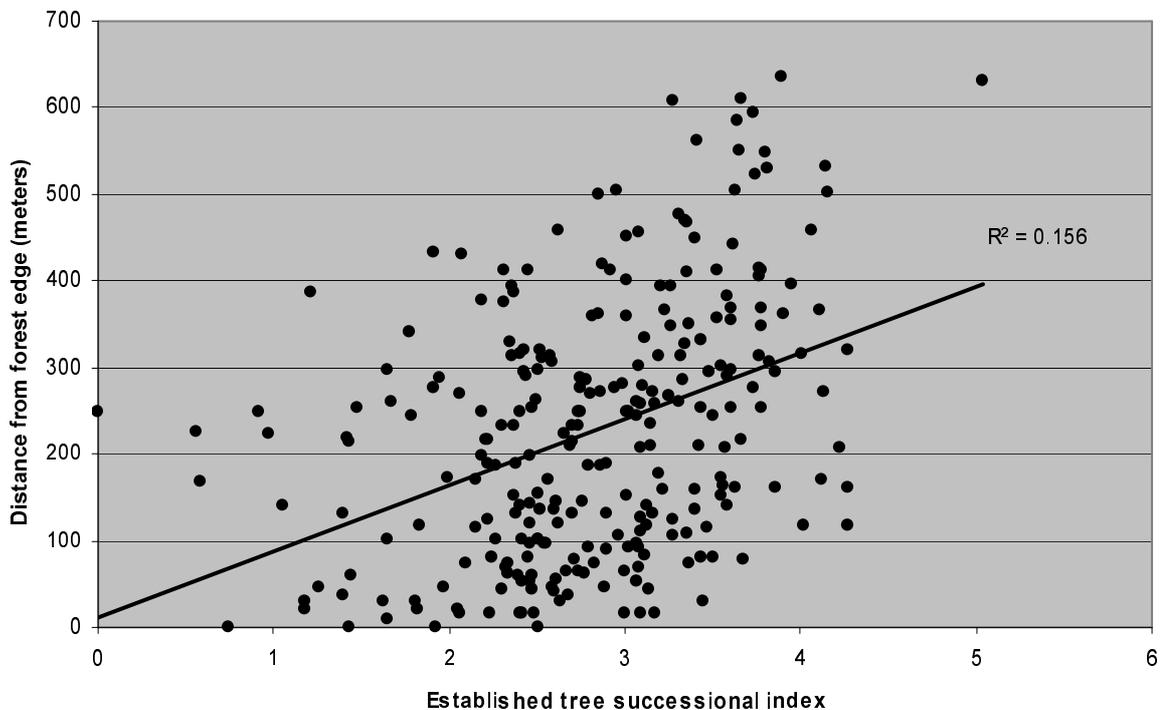


Figure 4.16: Plot distance to forest edge vs. plot successional index rating

This figure shows there may be an underlying relationship present, but still contains too much noise to make definitive proof. A least squares regression analysis was used, once normality was tested and proven, to test the strength of the relationship, and subsequently proved that 15.6 percent of the variation in the successional index was explained by distance alone (LSR, $R^2 = 0.156$). This graph hints that sites far from the forest have higher successional index scores (open woodland), while those closer to the forest have lower site scores (closed woodland)

To determine the forest's sphere of influence on woodland succession development patterns, a holistic landscape approach was used. NDVI values were assumed explanatory variables for succession (Figures 4.8 and 4.9).

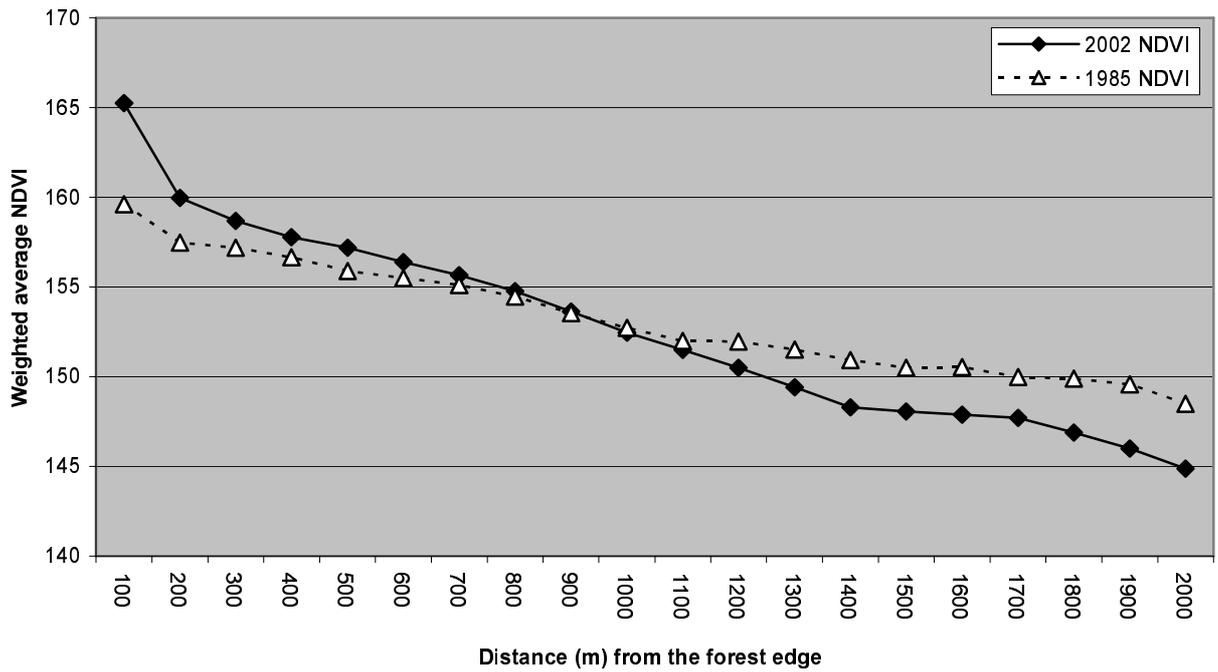


Figure 4.17: NDVI weighted averages (1985 and 2002) at different distance classes from forest

Figure 4.17 depicts weighted average NDVI values for each 100 meter interval for both the 1985 and 2002 images. As is apparent in the graph, the areas close to the forest had higher NDVI reflectance which suggests an advanced state of succession compared to surrounding regions.

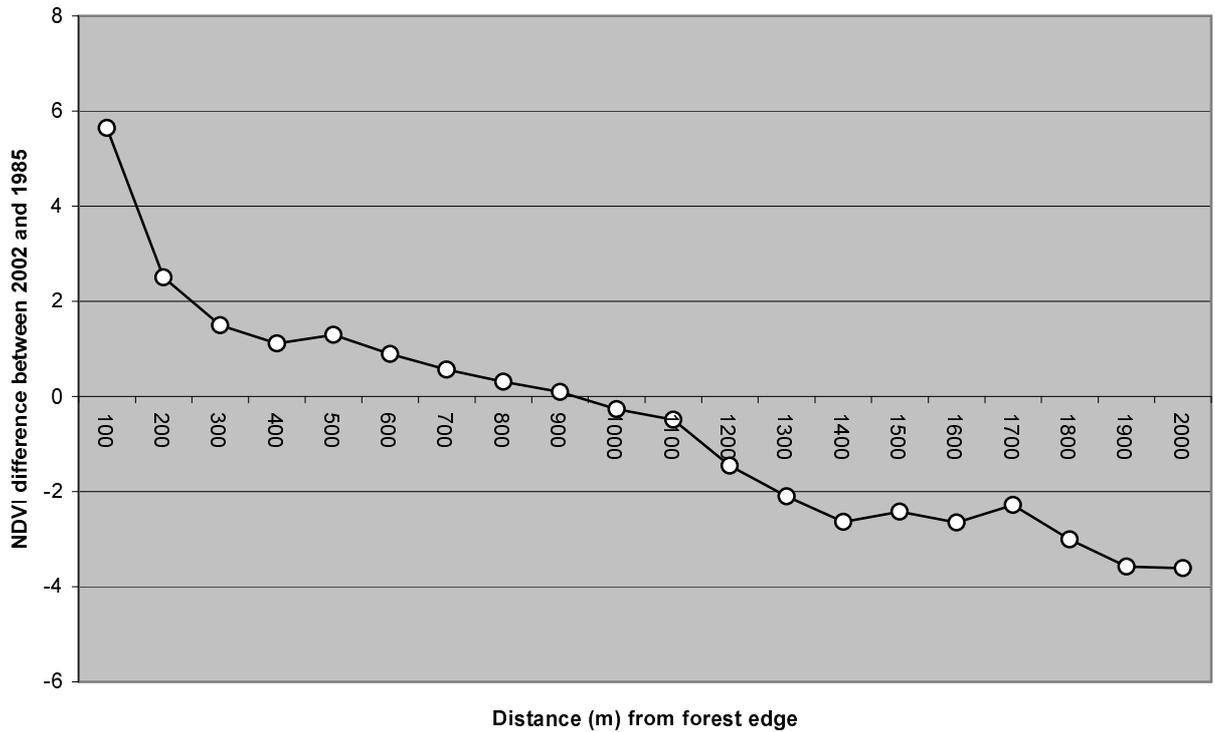


Figure 4.18: NDVI changes between 1985 and 2002 according to different distance classes from forest

When the 1985 and 2002 NDVI graphs were compared in figure 4.18, it is apparent that NDVI values have increased in areas directly adjacent to the forest while areas further from the forest have actually decreased in NDVI reflectance. Those areas quite distant from the forest have decreased in NDVI largely because that particular area even today experiences frequent fire disturbances.

5. Discussion

Historically, fire has had a profound influence on the Budongo forest woodland ecosystem. In recent years, a decline in fire frequency and extent has changed the ecological balance formerly maintained by this disturbance agent (Paterson, 1991).

This thesis seeks to gain deeper insights into the complex topic of successional progression dynamics after fire. As succession is a temporal phenomenon, it is vegetation turnover patterns through time which are the essence of this research. However, data and time constraints limited the possibility of monitoring any specific site through its actual development history to the current vegetation condition. There were little to no baseline data available which could provide detailed accounts of site histories. To potentially overcome this constraint, available satellite imagery were used to identify fire scars of image years. Yet, the temporal resolution of this information is inadequate, as fires of non-image years remain unknown. These constraints proved to be a challenge, and various assumptions were required.

The first assumption made was that areas which had increased significantly in the NDVI between image years, had not experienced extensive disturbance (i.e. fire) within that time; whereas, areas that did not change or decreased in NDVI were assumed to have experienced some destructive disturbance. The second assumption made was that inter species diameter differences can reflect the stage of its successional establishment. Smaller trees establish at early stages of succession and progressively grow in diameter through succession, till mortality.

5.1. Spatial extent of vegetation development

5.1.1. Comparison of image processing methods

During preliminary analysis, satellite images were carefully analyzed to identify areas that had increased in spectral signature indicative of vegetative abundance. This was done in two ways, a visual interpretation, and a temporal NDVI differencing. The visual interpretation results indicated a much greater area of change. While the areas outlined in the NDVI differencing did for the most part correspond, the area indicative of vegetation change was much smaller. The difference in output can be attributed to the visual interpretation exercise, where visual difference discrimination thresholds were based on intuitive visual differences as compared to the systematic approach using NDVI where comparisons are at pixel level. The visual interpretation results may reflect the subtle differences present in the image from previous fire boundaries, whereby there were respectively differing vegetation types. The intuitive method of delineation can prove useful in this context because fires which are the primary disturbance agent, generally constitute large scale disturbances (Chandler et al., 1983). This theory could not be quantitatively substantiated however, and was not applied in the scope of this study.

The temporal NDVI differencing displayed maps indicating the intensity of change in reflectance at two threshold levels. This scaling of change intensity provided insight into how the forest was encroaching and expanding through time. The areas that had changed by more than 1 standard devia-

tion but less than 2 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. This representation highlights the intensity of change and forecasts the spatial development in future years, as those sites with marginal increases (1 standard deviation) will likely follow a similar change trajectory as the sites which have increased more dramatically. This is proven when areas that had changed by 1 standard deviation but less than 2 standard deviations, in the 1985 to 1995 period were compared to areas that had increased by more than 2 standard deviations in the 1985 to 2002 period. Here a high correlation was observed.

In essence, the NDVI differencing exercise remains a more credible measure of vegetation change as it can be repeated numerous times by different persons. The visual interpretation method is more ambiguous in its delineation, and can be interpreted differently by different people. The visual interpretation method still holds merit, however because it provides a general context of vegetation boundaries and can correct for visible known image anomalies. The further advantage offered by NDVI differencing is that difference values, prior to thresholding, incrementally display the intensity of change and can subsequently be correlated to observed vegetation differences noted in the field.

5.1.2. Interpretation of vegetation change patterns

During the 17 year time lapse, vegetation changes were noted for different regions during different time windows. During the 1985 to 1995 period a large area to the south of the Kaniyo Pabidi forest block exhibited significant increases in forest cover (demarcated as 'A' and 'B' on figure 4.2), as did areas adjacent to the northwest region of the forest block, and in particular woodland intrusion areas into the forest (marked 'C'). It can be fathomed that such areas would quickly develop in the absence of fire, conditions would be ideal for forest tree establishment, and there would be no shortage of available seeds. During the fieldwork exercise, little fire scar scorching or fire evidence could be found at these sites, and vegetation changes are attributed to successional species establishment in the absence of fire. At Area #1, a site which had experienced significant vegetation changes, five plots were located in an area burnt in 1985, according to satellite imagery. Field observations here however found fire evidence only very sporadically and if present at a very weathered condition.

During the 1995 to 2002 time period different regions again displayed significant increases in vegetation cover. Very large areas to the northwest of the Kaniyo – Pabidi forest block exhibited significant increases in vegetation (indicated by 'A' and 'B' on figure 4.3). It is speculated that this area was left undisturbed during this period and possibly even slightly prior to the 1995 image acquisition date. The areas of intensive change apparently appear closer to the forest and in clustered patches. As the forest acts as a major seed source for woodland regeneration, it is expected that it will hasten vegetation establishment in the woodland after fire and accelerate vegetation succession. Field observations in this area noted that there were more frequent occurrences of fire scars, but all the observed fire scars found were old and weathering away.

In areas where no dramatic changes in vegetation were indicated in the vegetation change analysis, fire evidence was quite frequently observed. Recent fire scars and ash could be still found.

Should current fire prevention measures persist, it can be anticipated that the vegetation in this woodland region will continue to develop towards a closed forest condition. The access limitations enforced by the Uganda Wildlife Authority (UWA) make it increasingly difficult for local people, who live to the south of the woodland, to enter and set fires. The few fires which were set in the woodland were generally located at relative close proximity to the southern boundary, or infrequently established inside the woodland areas well away from the road and UWA gate. Furthermore, in 1994

the Kaniyo Pabidi forest ecotourism site was established along the western border of the forest to attract tourists to visit resident chimpanzee populations in the forest (see map on figure 3.3). In effect this further discouraged hunters from accessing surrounding woodlands and can possibly provide some explanation why, between 1995 and 2002, there were dramatic changes evident in vegetation cover directly north of the ecotourism site.

Areas encroached upon by forest species will continue to progress to latter phases of succession unchecked unless a fire disturbance from other regions encroach and set back the successional clock. It was indicated by field staff that given due time, fire will eventually be unable to burn into the closed woodland, as the ecosystem has become too moist for fire to burn efficiently. At such a point, the forest would develop unchecked through succession.

Fire disturbance regimes along the western edge of the study area do not appear to have changed significantly over the 17 year time frame. A few areas were exhibited to have increased dramatically during the 1985 – 1995 time period (marked 'D' and 'E' on figure 4.2), but these areas were subsequently reclaimed by fire in the 1995 to 2002 time period (figure 4.3).

The fires occurring in this region are believed to have 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. This fire regime has maintained a vegetation species community adapted to frequent fire disturbances and has slowed the establishment of fire intolerant tree species. The areas where significant NDVI decreases were noted can be related to destructive disturbances which have set back successional development.

Predicting precisely where the advancing forest will move is impossible. If current trends in fire disturbance persist, whereby certain regions are frequently burnt while others are not, a rudimentary forecast may be made. In the context of this situation, it is entirely feasible that 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 which rely on these regions for their livelihood.

5.2. Succession dynamics post fire disturbance

Vegetation community development patterns have been proven to follow defined transition patterns. The occurrence of particular tree species is a product of time and the historical environmental conditions present at a site (Sheil, 1999). In the Budongo forest context, Eggeling (1947) has characterized the forest to have two independent seral communities, the swamp forest and the tropical high forest.

Soil, climate and general physiological growing conditions are relatively homogeneous throughout both the Budongo forest and the woodland areas (Eggeling, 1947; Forest-Department, 1997). This means that in the absence of active succession suppression disturbances (i.e. fire) the woodland will eventually develop to a mature forest.

5.2.1. Overstory tree succession dynamics

The species turnover model that was developed using a DCA exhibited species composition changes through time after fire disturbance. The floristic transition, as proven by the DCA analysis, is gradual as species compositions change to suit the changing environment. This is in agreement with

Sheil (1999) who explained that “vegetation change is driven by, but always lags behind, environmental change”.

It needs to be recognized however that when fire resistant woodland tree populations are evaluated with a DCA there is a relative degree of noise introduced into the analysis. The woodland trees, which have survived the last fire regime, will be present at all stages of succession to the point where the environment becomes inhospitable. However, when both the new generation of woodland trees and those from the previous generation, which survived the fire are counted, a degree of noise is introduced into the analysis that actually underestimates at which phase of succession these species grow optimally. The species response curve is skewed and does not follow a perfect bell shaped pattern as there may be many remnant trees from earlier stages of succession. It is the relic trees present from a previous era that are contributing to a considerable portion of the noise. This may explain why the successional index (DCA axis 1) eigen value of 0.472 was slightly lower than those statistically recommended for a strong relationship (Jongman *et al.*, 1987). The establishment of fire intolerant trees, on the other hand, will not exhibit this noise as all trees are part of one successional cohort.

Regardless of this artifact, the model provides important insights into species successional development. According to the DCA output (table 4.2), species scores explain species turnover patterns along the hypothetical succession gradient. Results indicated that the established trees with high SI scores such as *Lonchocarpus laxiflorus* (SI = 5.043), *Grewia mollis* (SI = 4.269), *Combretum colinum* (SI = 3.339), and *Lannea barteri* (SI = 3.337) achieved optimal abundances at early periods following fire disturbances. These species all exhibited physiological characteristics which enabled them to tolerate fire disturbances (figure 3.4), and allowed them to utilize the liberated space and nutrient resources. Given time in the absence of fire, however, their relative abundances began to drop off as conditions become inhospitable for survival, due to increased competition and changing environments.

During successional development, the species composition continues to adjust to changing conditions. *Terminalia velutina* (SI = 2.297) was a very prominent species during intermediate phases, but was subsequently replaced, and species such as *Albizia grandibracteata* become more prominent. The ecological system is still not yet in a state of equilibrium however, and different colonizing forest species begin to establish and dominate the overstory. Species such as *Maesopsis eminii* (SI = 1.152), *Pterygota mildbraedii* (SI = 0.751), *Holoptelea grandis* (SI = 0.684) and *Funtumia elastica* (SI = 0.481) now find the environment in the closed woodland ideal for growth.

The general pattern depicted in this successional index shows a gradual species turnover progression from the fire disturbed woodland to the closed canopy forest condition. Over the course of the successional gradient, species face a myriad of complex interrelationships which dictate the plant's success. In the absence of fire the growing conditions change, while becoming increasingly inhospitable for some species they become suitable for others. Those species not adapted to either the increased competition for nutrients, space, or water, or adapted to the change in microsite conditions, will either perish or stagnate in growth until conditions improve (Huston, 1994). Regardless of the precise cause there appear to be deterministic factors which act as thresholds to limit the persistence of some of these woodland species. For instance *Grewia mollis* is found at highest abundance during early stages of ecosystem development, but during later stages, they are virtually wiped out (figure 4.7). Apparently somewhere along the successional gradient conditions became too hostile for such species, and subsequently they disappear. Similarly, at some point the environment reached an undefined threshold where the woodland became suitable to support forest species. This threshold may

have been related to the time necessary for a forest tree species to deliver a seed to a site or related to specific microsite condition requirements. According to Sheil (1996), the proportion of shade tolerant species increases through successional development.

Through succession, the native woodland species were slowly phased out and replaced by species characteristic of a colonizing forest. At late stages of woodland succession, field observations noted that the environment became moister reducing the possibility of future fire disturbances. As such, woodland trees which are light demanding and previously depended on their physical fire adaptations for survival now had to compete in an environment they were not adapted to. Regardless, there are some woodland species that are more capable of living in the closed forest environments than others. Species like *Albizia grandibracteata* and *Albizia zygia* can occasionally be found to grow within the established forest (Hamilton, 1991). Their relative abundances further along the successional index however were limited to only a few individuals.

When species successional trends for the Budongo forest woodland were described by Sheil (2000), and by Eggeling (1947), findings indicate similar species succession gradients. One permanent sample plot in a closing woodland, located at the southern part of the Budongo Forest, provided temporal species composition changes between 1944, 1950 and 1992. When measured in 1944 the plot had a species compositions dominated by woodland species such as *Terminalia*, *Albizia* spp. with an understory of *Grewia*, *Piliostigma*, *Erythrina* and *Acacia* (Eggeling, 1947). When re-measured in 1992, there were many more large stemmed species present. Species present in 1992 included *Maesopsis eminii*, which was in decline, but also *Alstonia*, *Prunus*, *Khaya*, *Milicia* and *Albizia* spp. (Sheil, 2000).

In fact, when a comparison was made to Sheil's "successional index" an almost perfect correlation was revealed, apart from a few outlying species for which the reason is not fully understood (Appendix 4).

5.2.2. Size class progression dynamics

When a second DCA was tested on 16 tree species using the three size classes, the lifecycle characteristics of different trees was further explained. This ordination scoring technique verified many of the conclusions previously reached about where and in what type of ecosystem the established trees of a particular species grows best. This technique also contributed to a better comprehension of how those established species developed to where they are now. When the graph in figure 4.13, was carefully examined it was clear there were two types of establishment patterns for the 16 listed species; there were those species which established seedlings immediately after a fire disturbance (*Grewia mollis*, *Terminalia velutina*, *Stereospermum kunthianum*, *Maesopsis eminii*, *Lonchocarpus laxiflorus*, *Combretum collinum*, *Annona senegalensis*, *Acacia hockii*, *Albizia grandibracteata* and *Vitex doniana*) and those species that established seedlings at latter succession stages (*Bridelia micrantha*, *Funtumia elastica*, *Pterygota mildbreadii*, *Uvariopsis congensis* and *Khaya anthotheca*).

After a fire disturbance, the existing and surrounding trees will provide seed to the newly formed fertile seedbed and establish a new crop of seedlings (Acharya, 1999). The success of species seedling establishment depends on individual species. All of these species apart from *Maesopsis eminii* have fire resistant adaptations which allow them to survive the fire disturbance and subsequently reseed the surrounding areas quickly. *Maesopsis eminii* seeds are dispersed by birds and particularly hornbills and as such find their way quickly to the newly disturbed site (Binggeli, 1997). Given time the seedlings that have established will grow into a harsh reality and need to compete with

other species for available resources and adjust to changing site conditions. This is in agreement with Van de Vijver (1999), who indicated that available soil macronutrient concentrations in east African savannas are higher immediately following a fire disturbance, but the effects are short lived.

At a small diameter (>2cm and <10 cm dbh) the peak abundance for these species is found further along the successional continuum. Where and at what phase of succession the small tree population exists is indicative of two possibilities. Either, a slow growing species will have stayed in the “small tree” size class for a longer period of time and, as an effect, the surrounding environment shifted further along the succession gradient. This would be in contrast to a fast growing tree which reach a greater diameter very quickly and so effectively remain in the “small tree” diameter class size for a shorter period of time. The second possibility is that species have reached maximum abundance at a certain threshold level in succession due to the physical inability to survive the changing environmental conditions in later stages (Sheil, 1999).

Beyond this point, when large trees were examined, the exhibited species progression showed two trends; either species continued to develop along to latter successional stages or they remained relatively stable. The degree of increase along the successional scale may be attributed to a number of factors. First, the physical threshold of growth is reached; plants have reached their optimal site condition and future site changes become increasingly hostile towards continued growth. Second, certain tree species characteristically grow slowly and will exhibit small diameters even at maturity. Trees like *Grewia mollis* for instance will remain relatively small and only reach a maximum height of 7 meters (Eggeling, 1951). Thus when these species are considered in the “large tree” size class they are already nearing their mortality and the exhibited increase in successional development may be negligible compared to the small tree size class. Third, remnant woodland trees which survived the fire disturbance and are not a part of the new successional development, contribute noise to the successional progression model, by repressing the succession score. The maximum successional score for these species will likely be higher than actually represented on the graph. The degree of error depends entirely on the number of species which survived the fire disturbance and prevailed during the early phases of succession.

The late establishing species did not exhibit a strong progression trend but instead indicated that all three size classes are found at similar sites. It is suspected that regeneration of these species is not a sudden occurrence, as it is after a fire disturbance, but instead it occurs over a prolonged period when the canopy closes and conditions gradually become more suitable. The large trees originated earlier when conditions first became suitable for seedling establishment, and these trees have now reached a point of optimal growth. The “small” trees, of the same species, established slightly later than the “big” trees but have now grown into the same conditions as the larger trees. The seedlings too were found to grow at highest abundance in association with the established trees. The peak score noted in this case reflects an artifact, as the actual seedlings that succeed into growing to large sizes establish at much earlier stages of development. The high score presented here is a reflection of seedlings that are distributed by the established mother trees. It can be predicted by the trend observed in the small and large trees species score that these seedlings will either die or remain in the understory till an opening in the canopy occurs. In this case, where the peak abundance of seedlings occurred is not related to the successional development trend. The alternative possibility is that established plots did not attain the full range of successional phases exhibited by these forest species, and the optimal conditions in which they thrive occur later. The plots considered in this analysis were determined based on woodland-forest delineation made on the 1985 satellite image and as such will only repre-

sent a woodland successional development of approximately two decades. This could be the case for *Uvariopsis congensis* which though found in relatively high numbers, was not found to grow beyond 10 cm in any the plots established. It is suspected that it had insufficient time to grow to mature sizes in the areas that were measured.

5.2.3. Successional development trends

Canopy Density

When field data were analyzed it was observed that canopy density closed quickly during successional development, and apart from the occasional canopy gap the woodland continued to develop under a closed canopy cover, exceeding 80% canopy density (figure 4.11). It is anticipated that the conditions associated with a closed canopy likely play an important role in determining which species could establish and grow. When a weighted average was calculated for species abundance at different canopy densities (table 4.7), it became clear that that some species, e.g. *Grewia mollis* established most abundantly under well lit site conditions (33.2 % canopy density) and even at maturity they remained most prevalent where site conditions remained quite open (72.8%). Other species (e.g. *Terminalia velutina*) also established under an open canopy (42.6 %) but continued to grow unimpeded when the canopy closed (89.0 %), strongly suggesting that it was relatively unaffected by the changes incurred as a direct result of canopy closure. Lastly, there was a group of species which established as seedlings under a closed canopy and through their life cycle grew up under such conditions (e.g. *Funtumia elastica*: seedling - 94.6 % and mature tree – 95.4 %).

Tree density

When overall tree density was further analyzed it was anticipated that there would be an increase in the tree stem count over time to a certain quantity and there after level off. This however was not the case, as no strong correlation between tree density and successional development was observed in the plots analyzed (figure 4.14). This may be attributed to two possibilities. One, the occupation of space by trees occurred very quickly and the scale of successional development observed in this study was too coarse to capture the increase in density, Or two, the noise to signal ratio was too high to give a precise measure of the degree of change. The relic fire surviving trees still occurred at varying densities regardless whether it had occurred directly after a fire or not.

Species count

As an approximate measure of species diversity, a species count was made of each plot. Although the relationship exhibited in figure 4.15 did not indicate a strong relationship with an R^2 value 0.1282, there was evidence of an upward trend in species numbers over time. This trend is conceivably related to the establishment of forest species into the woodland.

5.2.4. Successional development as explained by NDVI reflectance

To determine the extent how the NDVI and NDVI changes reflect actual succession patterns, respective values for corresponding plot locations were related to the successional development index rating (figure 4.8 and 4.9). The relationship for the 2002 NDVI exhibited a clear correlation between the two variables. The relationship when tested with a least squares regression analysis indicated that 32 percent of the variability in the plot NDVI values could be explained by the successional index scores.

It is theorized that the increase in NDVI reflectance through succession is related to a combination of factors. First, the NIR reflectance differs by species. When species compositions change, the

respective NIR reflectance will also change (Lillesand & Kiefer, 2000). Second, the amount of NIR reflected is affected by tree canopy structure, whereby multiple layers of leaves increase the transmittance and reflectance of NIR wavelengths (Lillesand & Kiefer, 2000). During the course of succession, the canopy structure becomes increasingly variable, as plants of varying heights and stages of establishment are present. As such, NIR reflectance will rise with increased canopy structure layers. Third, environmental conditions influence plant vigor, which in turn affect chlorophyll activity and the reflectance of NIR wavelengths (Lillesand & Kiefer, 2000). For example, plants experiencing drought stress in the recently burnt open woodland will have lower NIR reflectance than unstressed trees in the moist closed woodland / colonizing forest.

The unexplained variation in the successional index to NDVI relationship may be due to noise introduced by other plants, not considered in the analysis. This includes grasses which were predominant immediately following fire disturbances in open areas and vines which are present at late stages of succession and overtop many established trees. The presence of these plants significantly contributes to the spectral reflectance and introduces an element of noise. Furthermore, the reflectance of areas outside of the plot, but still within the pixel, will contribute to the reflectance assigned to the pixel value.

When the NDVI change between 1985 and 2002 were related to the successional index using a least squares regression, 28 percent of the variation in the NDVI was explained by the successional index (figure 4.9). This would strongly imply that areas of high NDVI increase were related to late successional changes and those plots where NDVI remained relatively stable or decreased were at early successional phases. Again the unexplained variation can be related to the same two reasons previously mentioned, but now related to two different images.

5.3. Forest edge effect

The woodland successional development is influenced primarily by many *in situ* factors, but extraneous elements such as seed source availability also act as a major factor driving the rate and type of seedling community established. The forest encroachment rate is dependent on a host of factors including the species seed dissemination vector, the species seed characteristics and the establishing environment (Duncan & Duncan, 2000).

When distance from the forest edge was compared with the successional index rating, a weak relationship was revealed, whereby 16 percent of the variation in the successional index could be explained by distance (figure 4.16). This weak relationship is not a surprise however, as the successional history of the plots is not well known. There is a degree of noise introduced into the analysis when different sites with different site histories are considered. The effect the forest has on regeneration will only be noticeable when sites which experienced disturbances during the same time frame are measured. The current analysis compared numerous different sites from many different stages of development regardless of fire history.

Therefore to develop a landscape level overview of the general encroachment trends, NDVI changes over distance were calculated. As indicated in section 4.2.3, NDVI values can be used as a proxy to explain successional development. When examined there was a clear decline in the successional phase of vegetation with distance. The areas close to the forest had higher NDVI values as compared to sites found at a distance (figure 4.17). Even when compared to the NDVI changes incurred between 1985 and 2002, the vegetation development clearly increased most at areas along the forest edge (figure 4.18). This trend is unmistakably the influence of the encroaching forest ecosys-

tem. This is in agreement with Duncan and Duncan (2000), who indicated that environmental conditions closer to the forest edge were lower in temperature and had higher relative humidity. Furthermore, they indicated that seed dissemination was highest within 30 meters of the forest edge.

Areas found at distances greater than 1000 meters exhibited NDVI decreases. This decline is attributed to the large areas of very open woodland which up to today face frequently fire disturbances.

Clearly, the forest plays a major role in the successional development of the woodland in the absence of fire. The forest provides seeds for regeneration and also provides a suitable microclimate for seedling establishment.

6. Conclusion and Recommendations

Conclusion

1. Spatial vegetation changes

- Overall, there has been more vegetation increase than decrease in the Kaniyo Pabidi woodlands. Between 1985 and 1995 the increase was mainly in areas directly south of the Kaniyo Pabidi forest block, and in various small forest intrusions. During the 1995 to 2002 period, increases were found in close vicinity of the Kaniyo Pabidi forest block, and most notably, a large area to the western regions of the forest. Vegetation decrease mainly occurred in the northern and western part of the study area.
- The spatial arrangement and timing of vegetation increase coincided with both the establishment of the Uganda Wildlife Authority gate at the entrance to the woodlands and the institution of the Kaniyo Pabidi ecotourism site. In each case it is suspect that hunters avoided areas close to these two centers of authority and ignited fires elsewhere, leaving the surrounding vegetation to develop unchecked.

2. Effect of fire on woodland species composition, abundance and stand structure

- Woodland succession dynamics, in the absence of fire, follow a defined successional development trend. Species composition continually adjusts to changing environmental conditions. In the presence of frequent fire disturbance only species adapted to such an environment survive to maturity. As such, during early phases of successional development the overstory is dominated by fire resilient species. After a fire disturbance, heliophilic species, which are already in the area, and opportunistic tree species provide seed for early establishment. Given time, in the absence of fire disturbances, more species get established in the area. Forest species are also now found to establish in the woodland ecosystem, as the conditions have become suitable for establishment. This is mainly due to the gradual change in site conditions e.g. the canopy closes, inter-plant competition increases, soil conditions change, and relative humidity increases.
- Species abundance follows a monotonic response curve and it reaches its maximum abundance at a certain condition/point along the successional gradient. In general, for woodland species this is the deterministic threshold limiting development to further successional stages, and for forest species this is the deterministic factor influencing the seedling establishment.
- This study found that NDVI values and NDVI change values were determined to sufficiently describe the successional development gradient.

3. Forest edge influence on woodland successional development

- The proximity of a site relative to the forest plays an important role in the rate of successional development; the forest acts as a seed source, and also affects the microcli-

matic conditions present at a site. The woodland's successional development was found to be further advanced at areas in close vicinity to the forest.

Recommendations

- In the interest of maintaining a healthy and viable ecosystem, it is critical to manage for a diverse landscape encompassing all the successional stages of development. Should harsh protection restrictions be maintained, there is a risk of losing the species native to the woodland areas. However, on the same note, should intensive fire regimes be reinstated, any successional development present in the woodlands will be halted, and very little early successional forest will form. Therefore, a balance between the two scenarios ought to be identified and implemented.
- It needs to be recognized that vegetation changes have implications at other levels also. Local communities who utilized these woodlands for various products may in the future be unable to attain them in this changed woodland ecosystem. Furthermore, resident woodland fauna populations will change due to habitat changes.
- Future studies may further explore how the ecological changes in the woodland are impacting local communities and develop management strategies which will adequately satisfy all stakeholders.

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Appendices

Appendix 1: Detrended Correspondence Analysis outputs

Variability explained by the “Established tree” DCA analysis

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.472	0.242	0.194	0.149
Percentage	12.2	6.3	5.0	3.9
Cum. Percentage	12.2	18.5	23.5	27.4

Variability explained by the “Species progression” DCA analysis

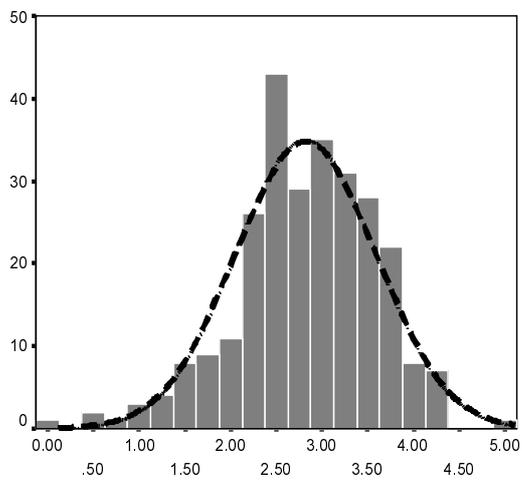
	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.501	0.324	0.270	0.158
Percentage	10.5	6.9	5.6	3.4
Cum. Percentage	10.5	17.4	23.0	26.4

Appendix 2: Normality Testing

Normality was tested by using a histogram, a Q-Q plot, and the One-Sample Kolmogorov-Smirnov Test, for 6 variables: 1) ‘Successional Index’ for overstory trees (DCA)

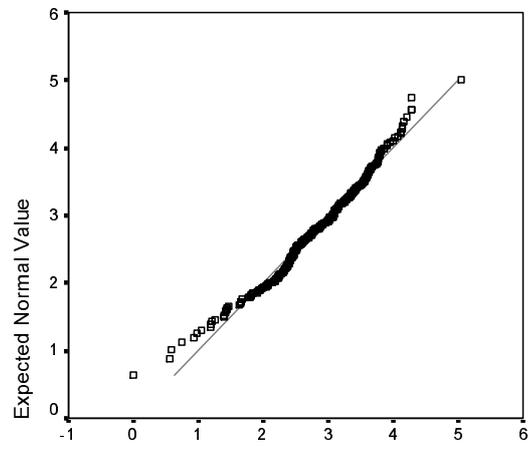
- 2) ‘Species progression’ DCA
- 3) Plot NDVI values for 2002 image
- 4) Plot NDVI change values between 1985 and 2002
- 5) Distance to the forest edge
- 6) Number of species per plot

“Succession Index” Overstory DCA



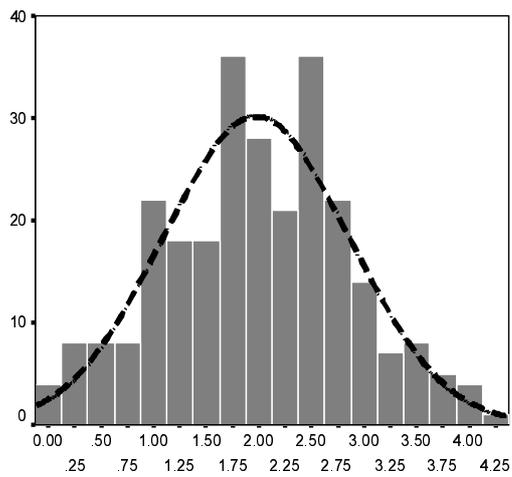
Overstory "successional index" DCA axis 1

Normal Q-Q Plot



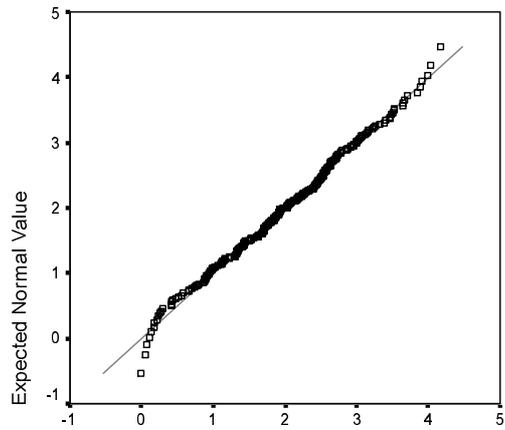
Observed Value

“Species Progression” DCA



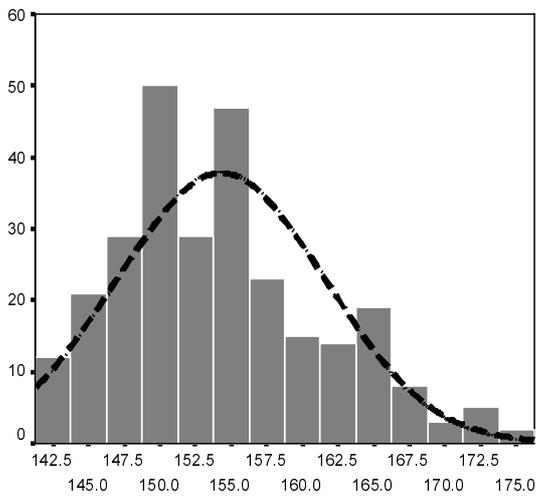
'Species progression' DCA

Normal Q-Q Plot



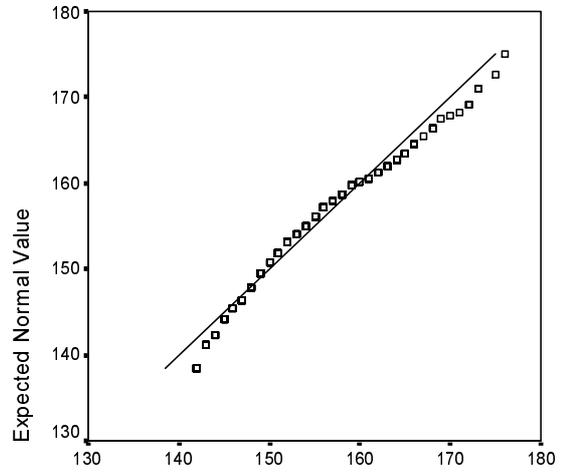
Observed Value

2002 plot NDVI values



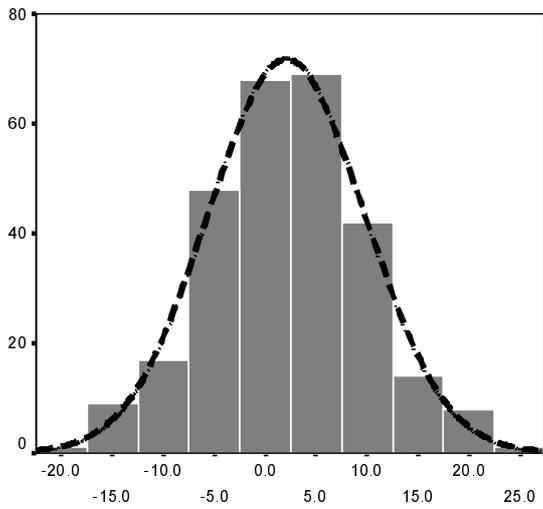
NDVI2002

Normal Q-Q Plot



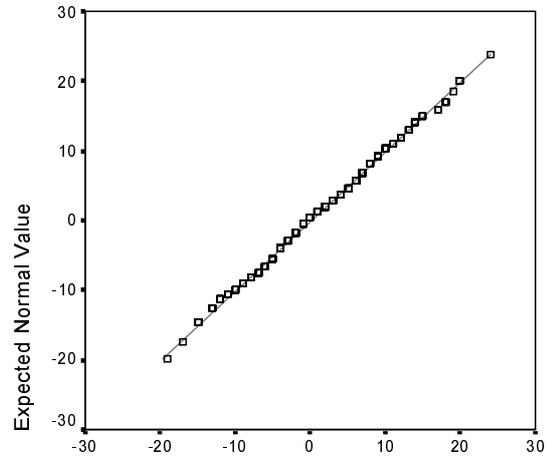
Observed Value

2002 plot NDVI value changes between 1985 and 2002



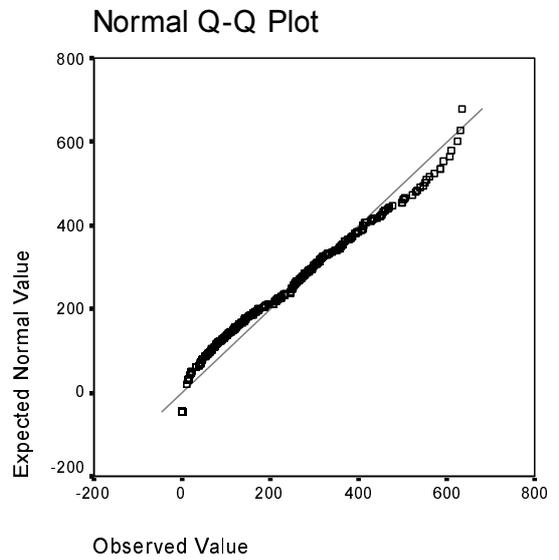
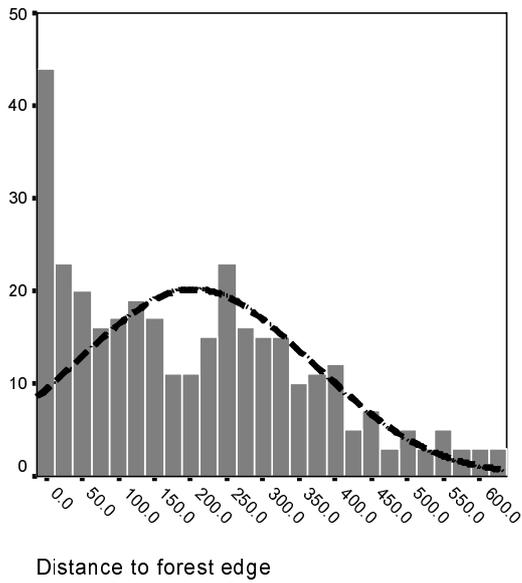
NDVI change between 1985 and 2002

Normal Q-Q Plot

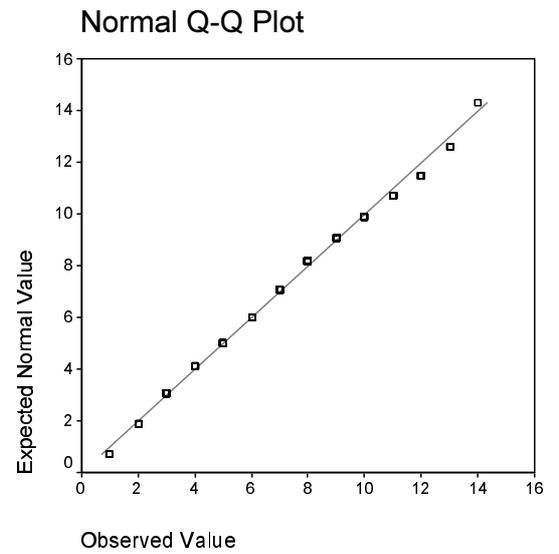
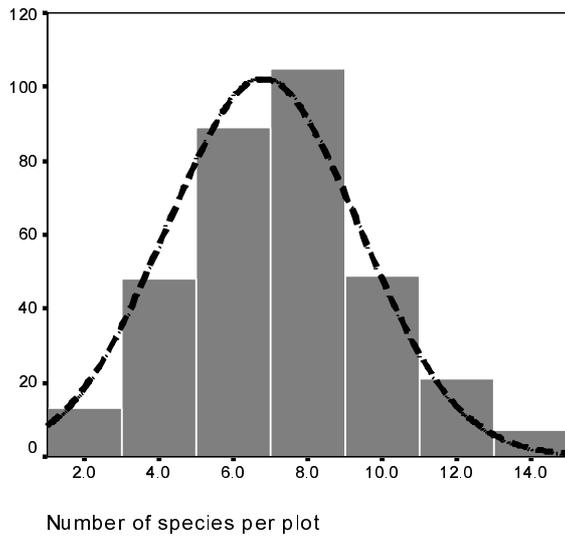


Observed Value

Distance to forest edge



Number of species per plot



One-Sample Kolmogorov-Smirnov Normality Test			
	Kolmogorov-Smirnov Z	Asymp. Sig. (2-tailed)	Normality
Overstory "successional index" DCA	.918	.369	Normal
Species progression DCA	0.732	0.658	Normal
NDVI 2002	1.657	0.008	Normal
NDVI change: 1985 to 2002	0.867	0.440	Normal
Forest edge distance	1.941	0.001	Normal
Number of species per plot	1.849	0.002	Normal

Appendix 3: Least Squares Regression Outputs

Regression output: 2002 NDVI values vs. DCA site scores						
<i>Model Summary</i>						
R	R Square	Adjusted R Square	Std. Error of the Estimate			
.564	.318	.315	.6424			
<i>Analysis of Variance</i>						
	Sum of Squares	d.f.	Mean Square	F	Sig.	
Regression	47.168	1	47.168	114.291	.000	
Residual	101.111	245	.413			
Total	148.279	246				
<i>Coefficients</i>						
	Unstandardized Coefficients		Standardized Coefficients		t	Sig.
	B	Std. Error	Beta			
(Constant)	12.950	.946			13.683	.000
NDVI 2002	-6.566E-02	.006	-.564		-10.691	.000

Regression output: NDVI change vs. DCA Axis 1

Model Summary

R	R Square	Adjusted R Square	Std. Error of the Estimate
.528	.279	.276	.6606368

Analysis of Variance

	Sum of Squares	d.f.	Mean Square	F	Sig.
Regression	41.351	1	41.351	94.745	.000
Residual	106.928	245	.436		
Total	148.279	246			

Coefficients

	Unstandardized Coefficients		Standardized Coefficients	t	Sig.
	B	Std. Error	Beta		
(Constant)	2.948	.043		67.872	.000
NDVI change 85-02	-5.303E-02	.005	-.528	-9.734	.000

Regression output: Number of species per plot vs. DCA Axis 1

Model Summary

R	R Square	Adjusted R Square	Std. Error of the Estimate
.358	.128	.125	.72026

Analysis of Variance

	Sum of Squares	d.f.	Mean Square	F	Sig.
Regression	20.376	1	20.376	39.278	.000
Residual	138.511	267	.519		
Total	158.887	268			

Coefficients

	Unstandardized Coefficients		Standardized Coefficients	t	Sig.
	B	Std. Error	Beta		
(Constant)	3.539	.123		28.781	.000
Number of spp./plot	-.108	.017	-.358	-6.267	.000

Regression output: Distance from forest vs. DCA Axis 1

Model Summary

R	R Square	Adjusted R Square	Std. Error of the Estimate
.395	.156	.153	0.7087088

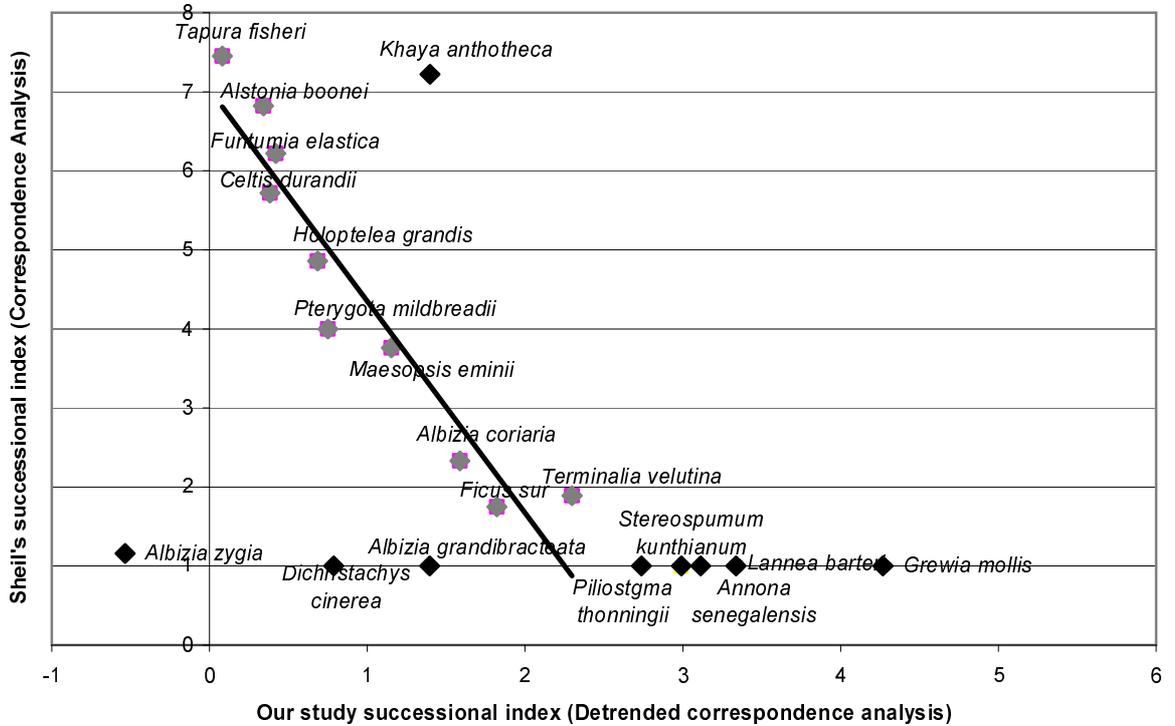
Analysis of Variance

	Sum of Squares	d.f.	Mean Square	F	Sig.
Regression	24.781	1	24.781	49.339	.000
Residual	134.106	267	.502		
Total	158.887	268			

Coefficients

	Unstandardized Coefficients		Standardized Coefficients		t	Sig.
	B	Std. Error	Beta			
(Constant)	2.354	.079			29.781	.000
Distance to forest edge	2.047E-03	.000	.395		7.024	.000

Appendix 4: Successional Index comparison



Successional index species scores from this study were related to successional index species scores determined by Sheil (2000). A close correlation was determined for many of the species (shaded in grey) while others seemed to differ (black). The explanation for species score deviations was not fully explored.