Lehrstuhl für Vegetationsökologie
Department für Ökologie
Technische Universität München

Fire Regime and Vegetation Response in the Okavango Delta, Botswana

Michael Heinl

Vollständiger Abdruck der von der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr. rer. nat)

genehmigten Dissertation.

Vorsitzender:		Univ.-Prof. Dr. rer. nat. Ludwig Trepl
Prüfer der Dissertation:	1.	Univ.-Prof. Dr. rer. nat. Jörg Pfadenhauer
	2.	Univ.-Prof. Dr. sc. techn. (ETH Zürich) Johannes Schnyder
	3.	apl. Prof. Dr. rer. nat. habil. Johann Georg Goldammer, Albert-Ludwigs-Universität Freiburg (schriftliche Begutachtung)

Die Dissertation wurde am 06.06.2005 bei der Technischen Universität München eingereicht und durch die Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am 08.08.2005 angenommen.

Heinl, M (2005): Fire Regime and Vegetation Response in the Okavango Delta, Botswana. Dissertation at the Chair of Vegetation Ecology, Technische Universität München, Freising-Weihenstephan, Germany; pp. 134.

Abstract. The scope of the study was to analyse the fire history and the effects of fire on vegetation for the floodplains of the southern Okavango Delta in Botswana. The fire history of the study area was reconstructed by using a series of 98 satellite images from 1989 until 2003 and habitat types based on the flood frequency were separated. Annual extent of fires, main fire season, maximum fire frequency and mean fire frequency related to flood frequency were calculated. The temporal occurrence of fire could be associated to rainfall and flood-events and the interaction of the spatial distribution of fire on different habitat types was discussed. Vegetation response to fire was studied by analysing the relation of vegetation structure and species composition to fire frequency and time-since-fire, as well as by comparing burned and unburned sites. Woody species were shown to be generally negatively affected by frequent fires. Reduced cover values after periods with high fire frequency were also observed for single wetland species. Post-fire succession was shown to be not only driven by the life-history of the occurring species, but also by competition and niche differentiation.

Zusammenfassung. Der Inhalt der Studie war die Untersuchung der Feuergeschichte sowie der Einfluss von Feuer auf die Vegetation der Floodplains im südlichen Okavango Delta in Botswana. Die Feuergeschichte wurde anhand einer Sequenz von 98 Satellitenbildern von 1989 bis 2003 rekonstruiert und Habitattypen wurden anhand von Flutfrequenzen differenziert werden. Das Ausmaß der jährlich gebrannten Fläche, die Hauptfeuersaison, die maximal Feuerfrequenz sowie die mittlere Feuerfrequenz in Relation zur Flutfrequenz wurden ermittelt. Das zeitliche Auftreten der Feuer konnte mit Niederschlag und Überflutungsereignissen in Zusammenhang gebracht werden und das Zusammenspiel der räumlichen Verteilung der Feuer auf verschiedenen Habitattypen wurde diskutiert. Der Einfluss von Feuer auf die Vegetation wurde anhand der Wirkung von Feuerfrequenz und der Zeitspanne seit dem letzten Feuer (time-since-fire) auf die Vegetationsstruktur und Artenzusammensetzung sowie durch den Vergleich von gebrannten und ungebrannten Flächen untersucht. Hohe Feuerfrequenzen wirkten sich prinzipiell negative auf Gehölze aus und auch einzelne Feuchtgebietsarten zeigten verringerte Deckungswerte bei hoher Feuerfrequenz. Die Sukzession nach Feuer erwies sich als nicht nur bestimmt durch die Überlebensdauer der vorkommenden Arten, sondern auch durch Konkurrenz und Nischendifferenzierung.

Preface and Acknowledgements

The present thesis on „Fire Regime and Vegetation Response in the Okavango Delta, Botswana" was worked out within the scope of the international research project *"Effects of different fire regimes on the vegetation in southern African savanna and floodplain ecosystems, Focus area: Okavango Delta, Botswana"* funded by Volkswagen Foundation.

The project was initiated by Dr. Jan Sliva and myself in 2001, and a research collaboration was set up between the Chair of Vegetation Ecology (Technische Universitaet Muenchen, Germany), Harry Oppenheimer Okavango Research Centre (University of Botswana) and Department of Botany (University of Pretoria, South Africa). During the project, other institutions became involved in the research, and especially Conservation International Botswana and the Centre for Space Research at the University of Texas at Austin contributed significantly to the success of the study.

The aim of the research was to gain first insight into the spatial and temporal distribution of vegetation fires in the Okavango Delta wetland and to assess vegetation response to burning regimes. Even though fires are common and widespread in and around the Okavango Delta and are part of ecological processes and historical land-use practices, the fire-issue was so far not discussed politically or scientifically. With assessing major fire regimes for different habitat types and by analysing the vegetation response to that, an important step towards a better understanding of the threats and benefits of these fires was undertaken and results are planned to be incorporated into the Okavango Delta Management Plan, which is currently in progress.

The successful completion of the study is thanks to both the enthusiasm of all people involved and the stable financial support throughout the project.

The project was funded by Volkswagen Foundation, Germany for a three-year period from July 2002 to June 2005 under their *"'Programme of Partnership' - Joint Research Projects in the Natural, Engineering and Economic Sciences with Institutes in Africa, Asia and Latin America"*. The relationship with Volkswagen Foundation was pleasantly uncomplicated and due to minimal bureaucracy, we were able to focus purely on the study. Their flexibility and helpful cooperation was very important for the successful completion of the project in time. Special thanks therefore to Volkswagen Foundation for funding this project and for their excellent cooperation.

The project was further supported financially and logistically by Conservation International Botswana, Okavango Program in Maun. Their financial contribution especially to the process of analysing the satellite images significantly accelerated the progress of the study and made it

possible to keep the schedule for the field campaign in 2004. Their invitation to join the Aquatic Rapid Assessment Program (AquaRAP II) in 2003 allowed for the intense discussion of aspects of fire and vegetation in the Okavango Delta with local and international scientists, which significantly widened the horizon of the study. Many thanks to Conservation International for supporting the study and for offering these opportunities.

Additional financial support was provided by the German Academic Exchange Service (DAAD) in 2003 for a four month visit to the Centre for Space Research at the University of Texas at Austin for satellite image interpretation. This stay allowed for the gain of detailed insights into remote sensing analyses and techniques and also enhanced the quality of the final data products through intense scientific support. Many thanks to DAAD for the chance to get deeper into the world of remote sensing and for the experience of working at an American University.

This financial support from the various sources allowed us to build an extensive international network of people contributing to this project. The contribution and importance of many people changed with the project phases but everyone involved played an important role for the success of this project. I would like to thank all of the people who I met and worked with during those three years very much for your help and support, no matter if you worked with me in the bush or in the lab, if you dug out grasses or Landrovers or if you spent days answering questions about remote sensing or correcting my manuscripts. All of you contributed significantly to getting to the point of finalising this study successfully.

I want to thank all staff of the Harry Oppenheimer Okavango Research Center in Maun, who always gave me a warm welcome and made me feel part of the team. Special thanks go to Prof. Lars Ramberg, the director, Dr. Cornelis Vanderpost, responsible for the project coordination in Botswana, Mike Murray-Hudson, for all kind of discussions and practical hints and Dr. Elmar Veenendaal, now at University of Wageningen, who helped to initiate this project. Happily there was also Budzanani Tacheba, who not only spent all my days in the bush with me but also showed me the local way of life and made this study in Botswana an impressive personal experience.

Conservation International Botswana helped us significantly to run this project financially and logistically and special thanks to Lovemore Sola, Belda Mosepele and Innocent Magole for their excellent teamwork and personal support.

Warm thanks to Prof. George Bredenkamp, University of Pretoria, for joining us during the field campaigns and for assisting us in methodology and plant identification.

The Center for Space Research in Austin, Texas played a very important role for the study and special thanks to Prof. Melba Crawford and Amy Neuenschwander. Amy especially made the stay

in Texas for me a smooth and brilliant experience, not only by assisting me with the satellite images, but also by getting me in touch with the Texan lifestyle and the “Horns”.

Finally, there is the Chair of Vegetation Ecology at the Technische Universitaet Muenchen, where I completed my MSc- and PhD-studies. Some of the staff I know for almost ten years now and they have all become very important to me, scientifically and personally. I thank each of them wholeheartedly for their support and encouragement. Special thanks to Prof. Joerg Pfadenhauer, who offered me a very nice and uncomplicated environment to work in and supported me through all these years of studies. And very special thanks to Dr. Jan Sliva, who not only changed my life by offering me my first trip to the African continent, but who also organised the project and shared with me the bush experience, paperwork and many nights at the camp fire.

Sincere thanks to you, Jan, and again to everyone involved.

Contents

Abstract/Zusammenfassung

Preface and Acknowledgements

Chapter 1 **1**
Introduction

Chapter 2 **17**
Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana
(Heinl M, Sliva J and Tacheba B)

Chapter 3 **37**
Interactions between fire and flooding in a southern African floodplain system
(Okavango Delta, Botswana)
(Heinl M, Neuenschwander A, Sliva J & Vanderpost C)

Chapter 4 **55**
Fire activity on drylands and floodplains in the southern Okavango Delta, Botswana
(Heinl M, Frost P, Vanderpost C & Sliva J)

Chapter 5 **69**
Vegetation response to fire frequency in the Okavango Delta floodplains, Botswana
(Heinl M, Sliva J, Tacheba B & Murray-Hudson M)

Chapter 6 **89**
Changes in plant species diversity and vegetation structure with time-since-fire
on drying floodplains in the Okavango Delta wetland, Botswana
(Heinl M, Sliva J, Murray-Hudson M & Tacheba B)

Chapter 7 **105**
Synthesis - Fire regime and vegetation response in the Okavango Delta

Appendix

Chapter 1

Introduction

Introduction

This introductory section provides an overview on the aspects of fire in southern African savanna ecosystems, including their major characteristics and principle effects on vegetation, and an insight into the ecology of the study area Okavango Delta in Botswana.
Additional, an outline of the thesis and of the main methodology is included into this chapter.

Fire in southern African savanna ecosystems

Besides climatic conditions and herbivores, fire is considered one of the major sculptors of southern African landscapes (Bond 1997). Especially savannas experience fires on a regular basis and roughly 40 % of all savanna areas are expected to burn every year (Bond & van Wilgen 1996). The high fire susceptibility is related to the predominance of productive, easily flammable graminoid species, a distinct seasonality of rainfall with pronounced wet and dry seasons, and the presence of natural and anthropogenic ignition sources (van de Vijver 1999; Bond & van Wilgen 1996).

Savannas can be described as a tree-grass co-dominated, tropical vegetation type, with woody species coverage ranging from about 5 % to 90 %. In southern Africa they spread from about 34° S in the Eastern Cape up to the tropical forests of Central Africa and cover roughly 60 % of sub-saharan Africa (Scholes 1997). Many hypotheses have evolved that try to explain this tree-grass co-existence in savannas (Walter 1971; Bond & van Wilgen 1996; San Jose & Montes 1997; Scholes & Archer 1997; Jeltsch et al. 1999; Higgins et al. 2000;), while two main approaches are established:
Equilibrium theories are based on a competitively driven co-existence of grasses and trees, grounded on the niche differentiation concept, and explain tree-grass coexistence, for example by water acquisition efficiency with respect to root-depth (niche separation by depth) or growth season (niche separation by phenology). Practical observation largely supports these hypotheses, as trees tend to exploit deeper water resources while grass-roots are primarily found in the upper soil-layers, or as trees usually tend to flower earlier than grasses. However, detailed studies revealed that many woody species in savannas are also shallow-rooted and show physiological activities related to moisture availability in upper horizons and that different tree-grass ratios exist in uniform climate and soil conditions (Scholes & Archer 1997). Competition for water or light are therefore today not considered as the only driving forces for the tree-grass coexistence and studies on for

example fire exclusion have shown that disturbance alone can alter the tree-grass balance in favour of trees (Bond & van Wilgen 1996). As these equilibrium theories based on niche differentiation by competition have shown to be not sufficient for explaining the tree-grass coexistence, non-equilibrium or state-and-transition models were developed to explain the vegetation structure of savannas (Scholes 1997). These non-equilibrium theories explain the tree-grass coexistence by effects that refer to the timing of life-history events in relation to disturbance. For example the 'storage effect' is based on the theory that coexistence can be promoted by recruitment fluctuations of long-lived species (e.g. trees), while the reproductive potential is 'stored' between generations (Warner & Chesson 1985; Higgins et al. 2000). Recruitment rates are considered to be dependent on favourable conditions and therefore variable climate and rainfall, typical of savanna regions, leads to fluctuations in the recruitment rates. The average population growth rate is then more strongly influenced by the benefits of the favourable periods than by costs of the unfavourable periods (Higgins et al. 2000). Hence, the importance of the storage effect for the tree-grass coexistence is the promotion of low tree densities by variations in seedling establishment and adult recruitment, based on fluctuations in growth conditions.

The 'Gulliver effect' is in contrast not primarily based on climatic conditions but rather on fire, with 'Gullivers' being typically multi-stemmed shrubs that struggle to emerge from the herbaceous layer, usually dominated by grasses (Bond & van Wilgen 1996). Grasses are extremely effective at suppressing the regeneration of other growth forms because of their rapid growth rates and quick seed production after germination and their high flammability combined with fire-protected growing points. This layer interferes with tree recruitment not only by suppressing seedlings, but also by fuelling frequent fires, which kill or stunt established woody individuals so that they fail to escape the fire danger zone and to grow to larger trees. The situation changes only if the herbaceous layer is reduced or removed, for example by droughts, grazing or fire. The complex dynamics of savannas are nicely described by the phenomenon that although fire, droughts or grazing usually support grasslands and suppress tree establishment, they can for a certain degree also be made responsible for tree establishment in savannas. Alternatively, 'Gullivers' can also escape the grass layer during long inter-fire-intervals, thereby reducing the die-back of the 'Gullivers' (Bond & van Wilgen 1996).

However, an important factor in savanna dynamics is not only a sparse tree establishment, caused by difficulties for woody species to establish in savannas because of regular fires or due to fluctuations in favourable conditions for recruitment, but also a permanent killing of larger trees, which prevents savannas growing to thicker woodlands. Droughts and floods can cause mass mortality of woody species, but tree densities are often also regulated by damages caused by animals, like porcupines, termites or elephants in combination with fire (Yeaton 1988; Bond & van Wilgen 1996).

As could be demonstrated, fire is definitely a key factor for the existence of savannas (Booysen & Tainton 1984; Scholes 1997). The main prerequisites for fire occurrences are drought conditions, adequate fuel loads and sources of ignition.

The climates of southern hemisphere Africa show an aridity gradient with increasing seasonality of rainfall to the south. The largest portion of southern Africa therefore experiences a climate in which there is a prolonged dry period every year during winter (May - September). The atmosphere is warm and dry due to high radiation and fine fuels quickly dry out sufficiently to ignite. The existence of this 'fire climate' plays an essential role in the distribution of savannas in southern Africa and they are largely confined to these summer rainfall regions (van Wilgen & Scholes 1997).

Most of the fuel in savannas is provided by the grass component of the vegetation. Above ground living biomass in savannas range from 500 - 6000 gm^{-2}, but grass fuels account for only 100 - 2000 gm^{-2} (Stocks et al. 1997). Approximately 40 - 50 % of the grass produced in savannas is eaten by herbivores and heavy grazing can limit the fuel load under a minimum of about 50 - 100 gm^{-2} needed to carry a fire (van Wilgen & Scholes 1997). Within burned patches, over 90 % of the grass fuels can be consumed by fire and experiments showed that consumption of the grass sward can range from 29 - 97 %, with a mean of 76 % (Stocks et al. 1997). This fire pattern is for example due to pre-fire fuel moisture and vegetation density or because of topography or changing weather conditions during the fire.

The conditions at the time and at the location of the fire occurrence not only affect the vegetation pattern by leaving burned and unburned patches, but also by determining the characteristics and therefore the severity of a fire. Rate of spread, flame height, fire temperature and fire intensity are considered as the most important parameters of fire behaviour for assessing direct ecological effects of fire-events (Booysen & Tainton 1984; Bond & van Wilgen 1996; Stocks et al. 1997). Spread rates are determined particularly by wind speed and direction. Experimental studies in savannas documented fire spread rates from 2 - 97 m min^{-1}, which are approximately in the same order of magnitude than those for boreal and temperate forest fires. However, intense fires more commonly spread at rates around 30 - 60 m min^{-1} (Stocks et al. 1997). Flame heights can vary extremely during fire-events, dependent on wind and fuel conditions, but seldom exceed the height of the grass layer in savannas and leave branches of trees in general unaffected. However, flame heights are important to consider in terms of damage ('topkill') to small woody species (Morgan 1999; Stocks et al. 1997). Temperature during savanna fires can rise up to 900° C, but usually are in the range of 200 - 400° C (Morgan 1998; Andersen et al. 1998). Soil temperatures during a fire barely change further than 3 cm below the surface. Temperatures higher than 60° C in the upper 3 cm were only observed under extreme conditions of slow moving fires (rate of spread <2 m min^{-1}) and a maximum of 120° C was measured during an experimental burn 0.4 cm below the soil surface (Bradstock & Auld 1995). The absolute soil temperatures are important factors for the post-fire recover, as they determine survival and germination of seedbanks (Bond & van Wilgen 1996). As a general measure to quantify the severity of a vegetation fire, the concept of fire intensity considers the heat yield of the fuel, the mass of the fuel consumed and the rate of spread (Byram 1959; Booysen & Tainton 1984). Fire intensity in savannas is in the range of about 100 to 10 000 kWm^{-1}, with a maximum of about 20 000 kWm^{-1}, and is relatively low compared to observed 50 000 - 100 000 kWm^{-1} in boreal zone wildfires due to comparatively low fuel loads (Bond 1997; Andersen et al. 1998; Stocks et al. 1997).

Besides the described climatic conditions and fuel characteristics supporting a fire, ignition sources are important factors for starting a fire and determine fire season and fire frequency. For southern African savannas, lightning as opposed to rockfall or volcanic eruptions, is the chief cause of natural fires. However, since humans domesticated fire over 100 000 years ago, the majority of vegetation fires are today anthropogenic (Bond 1997; Booysen & Tainton 1984; van Wilgen & Scholes 1997). With increasing population levels the relative importance of humans as source of ignition also increased so that modern fire regimes unaffected by human sources of ignition are today extremely rare (Bond & van Wilgen 1996). Natural vegetation fires occur in southern African savannas in principle early in the rainy season and are lightning-induced during the first thunderstorms around October. But as most fires are human-caused, the actual fire season is often shifted into the dry season because of the susceptibility of the dried-out vegetation to burn and permanently present anthropogenic ignition sources, like camp-fires, cigarettes, etc. or land-use and land-clearing practices (Bond 1997; Booysen & Tainton 1984, Cassidy 2003). Similar to fire season, fire frequency today is in principle also controlled by humans. Although specific fire managements with monitored fire-return-intervals are rarely installed in southern Africa, the anthropogenic ignition of the fires automatically lead to fire frequencies affected by humans. Southern African savannas show a huge variety in fire frequency, dependent on rainfall, herbivory, vegetation or local management practices, but seldom burn more often than every third year and are on average affected by fires every eight to ten years. Nevertheless, the fraction of areas that burn every year is estimated to be 10 % (van Wilgen & Scholes 1997).

Both fire season, fire intensity and fire frequency show typical effects on the vegetation. For example, early spring burns soon after trees have flushed their leaves favour grasses at the expense of trees, whereas fires during or towards the end of the rainy season in principle favour trees at the expense of grasses. During the dry winter season, plants in general survive fire best, as they are dormant (Bond 1997; Booysen & Tainton 1984). Fire intensity or fire temperatures affect the survival of trees and seedbanks and can trigger germination cues (Bond & van Wilgen 1996). Fire frequency basically affects vegetation structure: the more frequent the fire, the greater the herbaceous component and the less frequent the fire, the greater the woody component (Booysen & Tainton 1984). However, despite these principle effects of the fire regime on vegetation, the relative importance of each of these factors as well as their combination is not well understood yet and contradictory results still indicate an insufficient understanding of the effects of fire on vegetation in savannas (Uys et al. 2004; Bond 1997; Andersen et al. 1998; Kennedy & Potgieter 2003; Collins 1992; Walker & Peet 1983; Morrison et al. 1995).

Plant species occurring in savannas are largely adapted to regular fire-events, although specific adaptations to fire are rare and rather general adaptations to regular disturbance-events, like the ability to resprout, thick barks or massive seed production and persistent seedbanks, are common (Scholes 1997; Bond & van Wilgen 1996). Species present pre-fire are in principle also present post-fire (Morgan 1999) and fire in savannas therefore rather affects the dominance of specific species and vegetation structure than species composition. Plant strategies to survive fire are escape in space, for example by inhabiting rocky outcrops or termite mounds, or escape in time, by scheduling phenological phases, especially dormancy, to the main fire-season (Booysen & Tainton 1984). But as today most fires in southern African savannas are anthropogenic and occur almost throughout the year, dormancy appears to be less an adaptation to fire and rather a factor that favours specific species that are fortunately dormant during a fire, and is most likely simply timed with seasonal climate. Fire resistance is mainly observed for woody species, as their bark can protect living buds and the cambium. As the vulnerability to fire and heat is dependent on the thickness of the bark, particularly older trees are well protected against fire and smaller trees or trees with a thin bark are more easily damaged by fire (Bond & van Wilgen 1996). Typical for many savanna trees is also the ability to recover after fire by resprouting from dormant buds. However, repeated basal resprouting leads to a changed plant architecture and results in multi-stemmed shrubs, which brings canopy foliage within reach of stress by herbivores, fire and shading by grasses (Booysen & Tainton 1984; Bond 1997). Although grasses have no bark, they are among the most fire resistant components of plant communities. They survive fires by continuing leaf growth from intercalary meristems and from new tillers growing from protected buds. Grasses are most vulnerable to fire damage if they are burned during active growth periods, as regrowth is then initiated from axillary buds and is much slower than from undamaged intercalary meristems (Bond & van Wilgen 1996; Booysen & Tainton 1984).

Those described adaptations of plants to survive fires are found in many fire-prone environments all over the world. However, Bond and van Wilgen (1996) call it the ‘irony of fire ecology’ that plants with thin bark, canopies consumed by fire and lacking any capacity to resprout often dominate fire-prone vegetation. This is presumably due to an adaptation to the post-fire environment, or in general to a post-disturbance environment; and is hence less related to the survival of individuals but rather on the species-level.

What characterises the post-fire environment is the removed biomass, which offers more open space, less nutrient competition and higher light availability. Water becomes more available because of a decrease in transpiring leaf surface area and the availability of almost all nutrients increases. The result is a nutrient pulse much larger than from rainfall or litterfall for the first few months after a fire (Bond & van Wilgen 1996). The post-fire environment therefore offers perfect conditions for the establishment of seedlings and many plant mechanisms have evolved in order to be just in time with the fire-event and to be able to profit from these conditions. The most common phenomena are fire-stimulated flowering, fire-stimulated seed release and fire-stimulated germination which are connected to specific stimuli, for example ethylene in smoke, threshold temperatures, or melting waxes etc. (Booysen & Tainton 1984; Bond & van Wilgen 1996). However, these fire-related mechanisms are rarely observed in southern African savannas and rather for example in fynbos vegetation. This is most likely due to the fact that fire in savannas is just one of many regular disturbance events, like grazing or trampling (while herbivores are relatively rare in fynbos), and a specific fire-adaptation in savannas might be contra-productive for dealing with other disturbance-events. Hence, the post-fire environment in savannas is not utilised by specifically fire-stimulated plants, but rather by general disturbance tolerant species, which are able to produce seeds in large quantities during inter-fire intervals and seeds that survive the fire and that are able to germinate quickly after the fire. As these species invest their allocation costs basically in growth and reproduction, they are usually short-lived and non-sprouters, and are in most cases not able to survive a fire on the level of the individual. However, as they are able to recruit from the seeds immediately after the fire, they often dominate fire-prone environments especially shortly after the fire-event. Perennial grasses or long-lived, resprouting woody species which survive the fire are then much less represented. This variety of plant species strategies to deal with fire on all kind of levels of intensity, frequency and season leads automatically to a variety in life-forms and this largely contributes to the typical tree/grass co-dominated appearance of the savannas in southern Africa.

The Okavango Delta

Research for this thesis was performed in the Okavango Delta in northern Botswana in southern Africa (Figure 1). The Okavango Delta is an extensive wetland covering approximately 15 000 km^2 and is inclusive of surrounding habitats the largest RAMSAR-site of 68 640 km^2. It consists of a small habitat mosaic of channels, floodplains, seasonal and permanent swamps, dry islands and savanna habitats. The Okavango Delta is situated in the central Kalahari approximately between E22.0° - 24.0° and S18.5° - 20.0° and is supplied by the Okavango River, coming from Angola and through Namibia. The annual rainfall for northern Botswana of ca. 490 mm shows a strong seasonality, and rainfall is limited to the summer period between November and March. Mean annual evaporation rates are about 2200 mm (Lieth 1999; McCarthy et al. 2000). These climatic conditions cause vegetation to dry up quickly during drought periods and especially during the winter months, and make especially grasses and sedges on seasonal floodplains susceptible to fire. Hence, despite being characterised as a wetland, the situation of the Okavango Delta in a typical savanna climate causes regular vegetation fires and the formerly described characteristics of fire in southern African savanna ecosystems are in principle also applicable for the Okavango Delta region.

The Kalahari Basin in which the Okavango Delta is situated was formed with the up-lift of the Great Escarpment on the edges of the southern African continent during the Cretaceous period about 70 Million years ago. Since then the Kalahari Basin was filled by erosive processes and today, sand-layers of up to 200 m are found in the Okavango Delta region (Scudder et al. 1993).
The Okavango Delta is an alluvial fan spreading into this sand-filled basin and is confined by geological fault-lines. The northern section, the so-called ‘Panhandle’, is bordered by north-westerly striking graben structures and forms today a roughly 10 km wide and 100 km long permanent swamp with meandering channels of the Okavango River. With the drop of the confining structures along the river, the water spreads out south- and eastwards and forms the ‘Fan’, which is only limited in the southeast about 150 km away from the ‘Panhandle’ by the Thamalakane Fault (Scudder et al. 1993). The water passing through the Okavango Delta collects at this fault-line and forms the Thamalakane River which, however, carries only about 2 % of the annual input into the Okavango Delta while about another 2 % leaves as ground-water flow and roughly 96 % is lost to the atmosphere by evapotranspiration (McCarthy et al. 1998). The Thamalakane River continues its flow as the Boteti River south-eastwards but dries up completely in the Central Kalahari.

The Okavango Delta shows over its entire extension limited local relief and a very low gradient of about 1:3300, that is a change in altitude of about 75 m over the entire length of ca. 250 km from the northern Panhandle to the Thamalakane River (McCarthy et al. 1997). Therefore, water entering the 'Panhandle' needs months to pass the Okavango Delta and an out-of-phase correlation between rainfall and flooding can be observed. With the catchment of the Okavango River mainly in the highlands of central Angola, the peak inflow in the 'Panhandle' region is around April at the end of the rainy season and not earlier than three months after the main rainfalls. The spreading of the flood across the whole Okavango Delta takes another four to five months and happens during winter in the dry period from roughly April to July. The flood peak reaches the Thamalakane River usually not earlier than August (McCarthy et al. 1998).

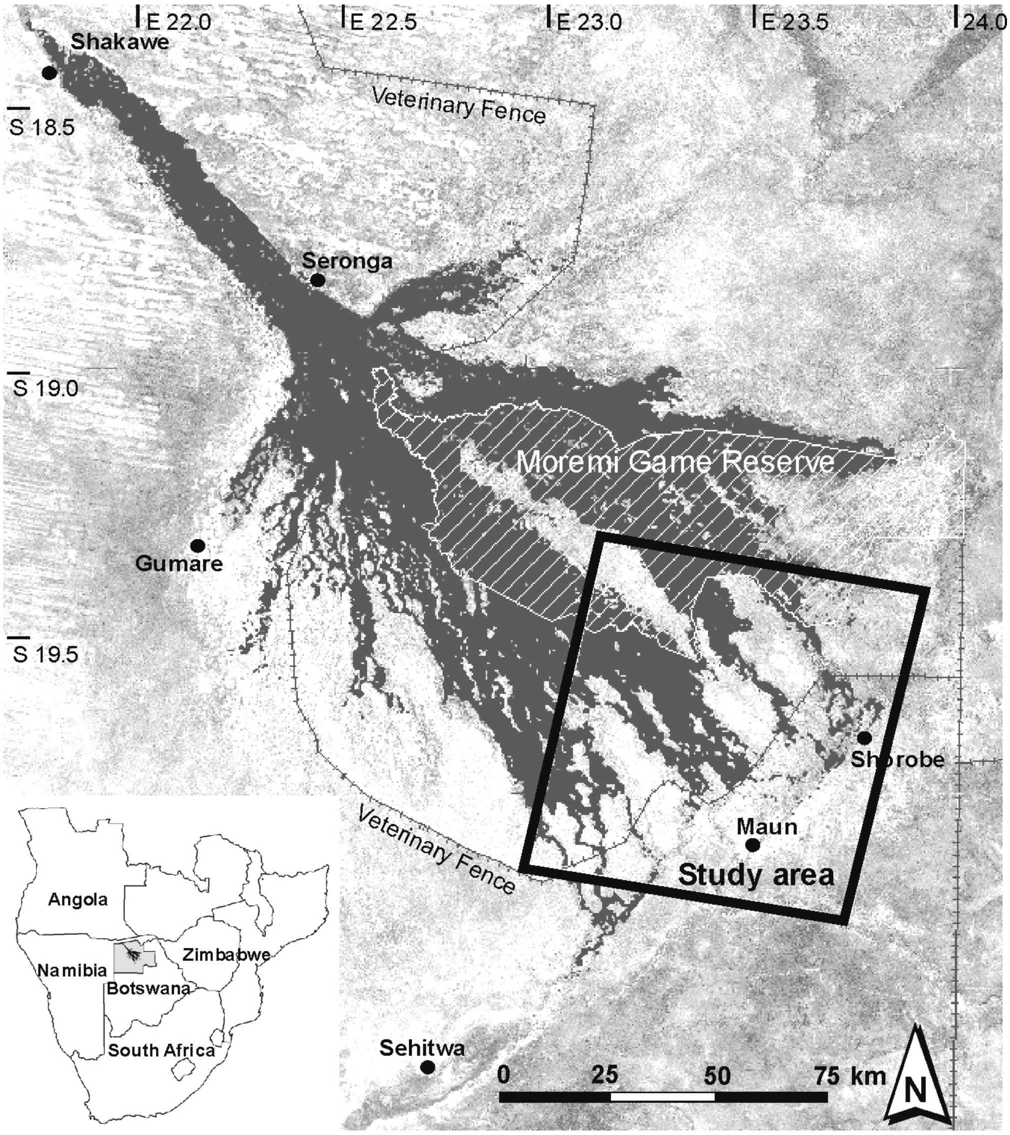


Figure 1. Location of the study area in the southern Okavango Delta. The dark colour indicates the areas usually affected by the flooding.

Due to this seasonal flood pattern and because of changing amounts of annual rainfall, both in the catchment and over the Okavango Delta, the extension of the flooding shows a huge variability during the year and between the years. The ecological consequence is the formation of temporal wetland habitats in almost all parts of the Okavango Delta, depending mainly on rainfall, duration and depth of the flooding (SMEC 1989). The 'Panhandle' receives a rather permanent water supply, but experiences fluctuations in water depth. It is characterised by meandering channels of the Okavango River and is dominated by large *Cyperus papyrus* stands and riverine forests. The 'Fan' rather consists of a small-scale mosaic of channel and floodplain systems and dry islands.

The study area for the present research is located in the southern part of the Okavango Delta and covers basically seasonal floodplains. They are dominated by grasses or sedges and occasionally by woody species, but their specific species composition is highly dependent on the flooding regime. Wetter sections of the floodplains which are subject to longer and deeper floods are usually dominated by the tall sedges *Schoenoplectus corymbosus* and *Cyperus articulatus*, with the grasses *Oryza longistaminata* and *Leersia hexandra* on the floodplain fringes. The occurrence of *Panicum repens* or *Setaria sphacellata* indicates lower flood intensities, and dry floodplain fringes are typically dominated by *Cynodon dactylon*. Occasionally flooded floodplains with single woody species (e.g. *Acacia tortilis*, *Colophospermum mopane*, *Combretum imberbe, Pechuel-loeschea leubnitziae*) are usually dominated by *Urochloa* spec., *Eragrostis* spec. or *Aristida* spec. (Bonyongo et al. 2000; Ellery & Ellery 1997).

Methodology and outline of the thesis

The aim of the investigation is to determine the spatial and temporal distribution of fires and to investigate the effects of fire on vegetation in the Okavango Delta. An important part of the study was therefore to gain insight into the fire history of the study area, which was done by analysing a series of 98 Landsat satellite images (upper left quarter of the Landsat scene 174/074), covering the years from 1989 until 2003 (Appendix 1). These satellite images also determined the specific study area of about 6141.1 km^2, which represents the common region that is covered by all used images (Figure 1).

The results of the analysis of the satellite images were annual fire distribution maps, showing the date and the spatial extent of fires for the study area on 30 m resolution (Appendix 2). A fire frequency map was generated by stacking these images (Appendix 3). Parallel to these analyses,

also the inundated areas were determined for each year and a flood frequency map was generated for the study area.
The gained information on the fire distribution and frequency were treated as own results of the study, but also as variables for the studies on the effects of different fire regimes on vegetation. Flood frequency data was basically used for the separation of habitats related to flooding.

As a preliminary study, prior to the determination of the flood and fire history, vegetation changes after single fire-events were investigated and results are presented in Chapter 2. The idea of this study was to compare species diversity, vegetation structure and biomass on burned and unburned sites and to determine the short-term vegetation response to burning for different habitat types of the Okavango Delta.
Chapter 3 describes the interactions between flooding and fire based on the data derived from the satellite images. Special focus was set on the importance of rainfall and flooding as determining factors for fire occurrences on drylands and floodplains.
Chapter 4 assesses the temporal and spatial distribution of fires. The extent and date of fire occurrences are analysed and the main fire season and areas of high frequency are located.
Chapter 5 investigates the effects of fire frequency on species diversity, vegetation structure and heterogeneity and compares differences of vegetation response to fire frequency dependent on the habitat type.
Chapter 6 determines dominating species and changes in vegetation structure related to time-since-fire on dry savanna habitats of the Okavango Delta. The aim of this study is to draw a picture of a successional pathway after fire for this habitat type.
A final synthesis of the findings of this investigation on fire regime and vegetation response in the Okavango Delta wetland is presented in Chapter 7.

References

Andersen AN, Braithwaite RW, Cook GD, Corbett LK, Williams RJ, Douglas MM, Gill AM, Setterfield SA & Muller WJ (1998): Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. Australian Journal of Ecology 23: 95-110.

Bond WJ (1997): Fire. Cowling RM, Richardson DM, Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge 421-446.

Bond WJ & van Wilgen BW (1996): Fire and Plants. Population and Community Biology Series 14, Chapman & Hall, London, UK.

Bonyongo MC, Bredenkamp GJ & Veenendaal E (2000): Floodplain vegetation in the Nxaraga Lagoon area, Okavango Delta, Botswana. South African Journal of Botany 66: 15-21.

Booysen PdV & Tainton NM (1984): Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48, Springer-Verlag, Berlin.

Bradstock RA & Auld TD (1995): Soil temperatures during experimental burning bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. Journal of Applied Ecology 32: 76-84.

Byram GM (1959): Combustion of forest fuels. In: Davis KP (ed.): Forest Fire control and use, McGraw-Hill, New York, p. 61-89.

Cassidy L (2003): Anthropogenic burning in the Okavango Panhandle of Botswana: Livelihoods and spatial dimensions. Unpublished M.Sc.Thesis, University of Florida.

Collins SL (1992): Heterogeneity of disturbed tallgrass prairie communities. Ecology 73: 2001-2006.

Ellery K & Ellery W (1997): Plants of the Okavango Delta - A Field Guide. Tsaro Publishers, Dalbridge.

Higgins SI, Bond WJ & Trollope WSW (2000): Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88: 213-229.

Jeltsch F, Moloney K & Milton SJ (1999): Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. Oikos 85: 451-466.

Kennedy AD & Potgieter ALF (2003): Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. Plant Ecology 167: 179-192.

Lieth H (1999): Climate and Biosphere. Backhuys Publishers, Leiden.

McCarthy TS, Barry M, Bloem A, Ellery WN, Heister H, Merry CL, Rüther H & Sternberg H (1997): The gradient of the Okavango Fan, Botswana, and its sedimentological and tectonic implications. Journal of African Earth Sciences 24: 65-78.

McCarthy TS, Bloem A & Larkin PA (1998): Observations on the hydrology and geohydrology of the Okavango Delta. South African Journal of Geology 101: 101-117.

McCarthy TS, Cooper GRJ, Tyson RD & Ellery WN (2000): Seasonal flooding in the Okavango Delta, Botswana - recent history and future prospects. South African Journal of Science 96: 25-32.

Morgan JW (1998): Small-scale plant dynamics in temperate *Themeda triandra* grasslands of southeastern Australia. Journal of Vegetation Science 9: 347-360.

Morgan JW (1999): Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology 144: 127-144.

Morrison DA, Cary GJ, Pengelly SM, Ross DG, Mullins BJ, Thomas CR & Anderson TS (1995): Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Inter-fire interval and time-since-fire. Australian Journal of Ecology 20: 239-247.

San Jose JJ & Montes RA (1997): Fire effect on the coexistence of trees and grasses in savannas and the resulting outcome on organic matter budget. Interciencia 22: 289-298.

Scholes RJ (1997): Savanna. In: Cowling RM, Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge, p. 258-277.

Scholes RJ & Archer SR (1997): Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28: 517-544.

Scudder T et al. (1993): The IUCN Review of the Southern Okavango Integrated Water Development Project. IUCN, Gland.

SMEC (1989): Ecological Zoning Okavango Delta, Final Report, Volume I - Main report. Snowy Mountains Engineering Corporation, Cooma NSW Australia.

Stocks BJ, van Wilgen BW & Trollope WSW (1997): Fire Behaviour and the Dynamics of Convection Columns in African savannas. In: van Wilgen BW, Andreae MO, Goldammer JG & Lindsay JA (eds.): Fire in Southern African Savannas, Witwatersrand University Press, Witwatersrand, p. 47-55.

Uys GU, Bond WJ & Everson TM (2004): The effect of different fire regimes on plant diversity in southern African grasslands. Biological Conservation 118: 489-499.

van de Vijver C (1999): Fire and Life in Tarangire: Effects of burning and herbivory on an East African Savanna System. Tropical Resource Management Papers, Wageningen University 27.

van Wilgen BW & Scholes RJ (1997): The Vegetation and Fire Regimes of Southern Hemisphere Africa. In: van Wilgen BW, Andreae MO, Goldammer JG & Lindsay JA (eds.): Fire in Southern African Savannas, Witwatersrand University Press, Witwatersrand, p. 27-46.

Walker J & Peet RK (1983): Composition and species diversity of pine-wiregrass savannas of the Greenswamp. Vegetatio 55: 163-179.

Walter H (1971): Ecology of Tropical and Subtropical Vegetation, Oliver and Boyd, London, UK.

Warner RR & Chesson PL (1985): Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 125: 769-787.

Yeaton RI (1988): Porcupines, fires and the dynamics of the tree layer of *Burkea africana* savanna. Journal of Ecology 67: 1017-1029.

Chapter 2

Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana

Heinl M[1], Sliva J[1] and Tacheba B[2]

[1] Chair of Vegetation Ecology, Technische Universitaet Muenchen (TUM),
Am Hochanger 6, D-85350 Freising-Weihenstephan, Germany
[2] Harry Oppenheimer Okavango Research Centre (HOORC), University of Botswana,
Private Bag 285, Maun, Botswana

(published in South African Journal of Botany 2004, 70 (5): 695-704)

Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana

Abstract. A comparative study on burned and unburned areas has been conducted for the south-eastern floodplains of the Okavango Delta wetland, Botswana to assess differences in vegetation composition and structure after single fire-events. Main findings on plant traits and species occurrences supported the theory of only slight vegetation changes after fire in fire-prone environments. No specific plant trait was found to be favoured by the fire-event and only *Urochloa mosambicensis* showed a highly significant correlation to burning. Main changes were observed in vegetation structure, e.g. height and cover of the herbaceous layer or biomass production. Interestingly, no main trends regarding how vegetation structure is generally affected by fire-events were derivable. Detailed analyses of five habitat types clearly showed different and contradictory responses to burning. This variability of vegetation response to fire-events dependent on the habitat was explained along a productivity gradient from active floodplains to dry Mopane woodlands. While floodplains showed an obvious decrease of standing biomass after the fire-event, an increase of biomass was observed for the Mopane woodlands. The nutrient pulses often described after fire-events, therefore seem to improve nutrient conditions best in poorer habitats, while for more productive sites, the enhanced nutrient availability after burning seem to be minor.

Nomenclature: Arnold and de Wet (1993)

Introduction

Fire in southern African savannas is often described as a natural phenomenon. For hundreds of thousands of years fire has played an essential role in determining the savannas in a complex and dynamic interaction with climate, soils, geomorphology and herbivory (Scholes 1997; Bond & van Wilgen 1996). The outcome of the combination of these factors in most of the tropical and subtropical environments of southern Africa is an open mosaic of trees and grasses, where none of the components is dominant. As simple as it is to define savannas roughly as tree-grass co-dominated vegetation types in the tropics (Scholes 1997), it is difficult to explain the reasons for this co-occurrence. Many studies have been published concerning tree-grass interactions in savannas, describing different hypotheses, models or recipes (Higgins et al. 2000; Scholes 1997; Jeltsch et al. 1999; Bond & van Wilgen 1996; Scholes & Archer 1997; San Jose & Montes 1997), but they are often just based on case studies ending with the statement about savannas being notoriously complex and too unpredictable to identify, isolate or quantify the key determinants of savanna structure (Scholes 1997; Bond & van Wilgen 1996). An approach to start untangling this complex web of interactions is to focus on one single factor, e.g. fire.

When fire is described as a natural phenomenon, it becomes part of the ecology of savannas. Species occurring in these fire-prone environments are therefore highly adapted to the fire occurrences and the post-fire environment. Species not escaping the fire in space or time or not being able to resist the fire or to recover or re-grow quickly after the fire are usually rare in savannas as they are out-competed by more fire tolerant species (Booysen & Tainton 1984; Bond & van Wilgen 1996). Fire tolerance does not imply specific adaptations to fire (e.g. fire stimulated flowering, seed-release or germination), which is actually seldom found in savannas (Bond & van Wilgen 1996; Bond 1997), but refers to the general ability to survive this kind of disturbance.

All these findings stress the importance of fire in savannas as an ecological factor, determining the typical plant species composition and vegetation structure through a permanent reoccurring disturbance. Different studies on post-disturbance species compositions have shown that the species assemblage of a community that experienced a certain, regular disturbance regime over a long period of time, does not alter further after disturbance events, as a result of the loss of disturbance intolerant species in the flora (Lavorel et al. 1999; Días et al. 1999). Morgan (1999) even states specifically related to fire that all species present pre-fire are also present post-fire in fire-prone environments.

Nevertheless fire can alter the vegetation, this not only where fire occurrences are rare events but also in the frequently burned savannas. Many findings have been published describing the relation between tree densities and fire frequency (Booysen & Tainton 1984; Trollope et al. 1998; Walker

1985), effects of season of burning on species composition (Walker 1985, Frost et al. 1986) and the varying destructiveness of different fire intensities (Morgan 1999). Although the relative importance of fire frequency, intensity and season to the species composition and vegetation structure is still discussed, it is commonly accepted that for example annually burned sites are different to sites burned every ten years. Hence, effects of fire on vegetation have to be also considered in the long-term, by the so-called fire regime (Bond & van Wilgen 1996).

The status of the fire as a natural phenomenon therefore has to be relativized: considering a single fire-event in general, it can always be seen as part of the ecology of the system, but putting this fire into a concrete broader context of a certain fire history, it can become a quite unusual or unnatural event. Therefore, especially for the assessment of the ecological consequences of fire, it is important not only to consider the immediate ecological settings at the fire-event, but additionally the ecological conditions during the last years. However, to work with the pre-fire history of a site is a big and yet unsolved challenge, both in terms of assessing the fire-events for the past and in terms of handling the fire-occurrences. Fires happen, if not managed, chaotically and show no systematic reoccurring pattern (e.g. every second year in October) as managed systems do, and vary therefore highly in season, intensity and frequency. The combination of these factors, for the past decades, without knowing about the relative importance of each of the factors, leaves an unsolvable puzzle. More studies on the importance of these fire-regime parameters and their combinations should therefore be conducted to be finally able to describe the key factors of the fire history.

Detailed studies on the fire history of the last decades for the study area "Okavango Delta" by using remote sensing techniques are in progress but not applicable yet. Before gathering these long-term fire data, a primary field study was carried out to investigate the immediate effects of fire on vegetation after single fire-events. The study is based on the above stated assumption, that under a regular fire regime no significant species shifts occur after a single fire and that only changes in the regular fire regime will alter the vegetation. As fire-events in the Okavango Delta have been totally uncontrolled for decades, and no regular fire-regimes exist, shifts in species composition should be expected with every single fire-event. Thus, the main aim of this study is to prove the hypothesis that vegetation changes after single fire-events in the Okavango Delta.

The Okavango Delta in Botswana was chosen as a study site, because of rising anthropogenic pressures during the last decade and expected high changes in the spatial and temporal distribution of fires. The present study is part of an international research initiative on fire and ecological consequences for the Okavango Delta region, which should ultimately lead to a better understanding of ecological interactions between fire and vegetation and to new approaches in dealing with fire in this extraordinary valuable landscape.

Study area

The Okavango Delta is situated in north-western Botswana in southern Africa approximately between E 22° - 24° and S 18° - 20° (Figure 1). This vast wetland, protected by the RAMSAR convention lies in the central Kalahari with a mean annual rainfall of about 490 mm, which falls mainly during the rainy season from November to April (McCarthy et al. 2000).

The Okavango Delta is an alluvial fan with a very low gradient (app. 1:3300; (McCarthy et al. 2000)) over the whole extension of roughly 15000 km^2, forming a widespread wetland composed of a pattern of channels, lakes, floodplains and slightly elevated dry islands. It is supplied by the Okavango River, with its catchment in central Angola, and enclosed by different geological fault-lines, which divide the Okavango Delta into two main parts: the northern 'Panhandle', confined by a north-westerly striking graben and the 'Fan', confined by south-westerly striking fault-lines, probably extensions of the Great Rift Valley (Scudder 1993). With the drop of the confining major fault-lines at the south-eastern end of the 'Panhandle', the water spreads out and forms the 'Fan' of the Okavango Delta. In this region, because of the missing confinement, the intensity of the flooding decreases to the distal reaches, where the permanent swamps change to seasonal swamps and irregularly inundated floodplains. The water inflow into the Okavango Delta system through the Okavango River as well as the annual amount of rainfall shows typically high variations. As a consequence of these variable water amounts every year, there are strong annual shifts in the water distribution, hence dry areas become inundated or swamps desiccate regularly as a part of this dynamic.

Fire-use in the Okavango Delta region

The Okavango Delta region, situated in the Kalahari, can be described as semi-arid savanna and is therefore fire-prone, as most parts of southern Africa. Although the extensive flooding is the dominating ecological factor of the Okavango Delta that makes it incomparable to the typical savannas in southern Africa, fire is a common phenomenon for the Okavango Delta as for its surroundings. Most of these fires are man-made (Barbosa et al. 1999) and the majority of savanna fires are lit by people in the context of land clearing, livestock management and protection of property (Andersen et al. 1998). Discussions with local people and scientists confirmed these statements. So today almost all fires in the Okavango Delta region can be characterised as man-made.

The purposes for setting fires are quite varied, but they have not changed that much over the millenniums. For thousands of years people have burned for cultivation, land clearing and to attract game to the palatable, nutritious flush after the burn (Booysen & Tainton 1984). Whereas the latter was used just for hunting in the past, nowadays game is also attracted for tourism and safari activities. Possibly because of this ‘new source’ of fire ignition, local scientists hypothesise that the number of fire occurrences in the Okavango Delta rose during the last decades. Although this could have grave ecological consequences for the whole region, no scientific research or administrative monitoring has been done on this topic yet. This paper therefore provides the first scientific insight into correlations between fire and vegetation for the Okavango Delta.

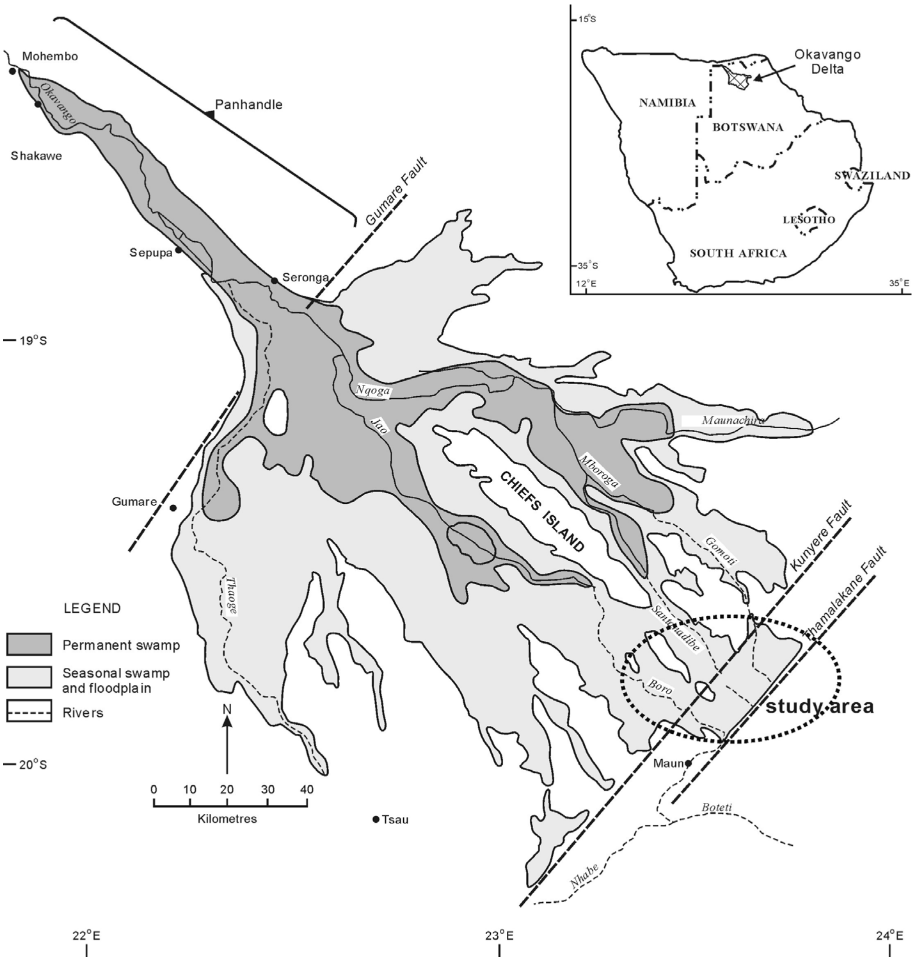


Figure 1. Location of the study area in the southern Okavango Delta (map after Ellery & Tacheba (2003), modified).

Material and methods

The main purpose of the present study aims to compare burned and unburned areas during the fire season 2000/2001, with respect to the effect of fire on vegetation diversity and the vegetation structure. As up to now no appropriate reports or data about fire occurrences in the Okavango Delta exist, LANDSAT 7 satellite images were used to map recent fire scars. Four images between August 2000 and February 2001 (09.08.2000, 25.08.2000, 10.09.2000 and 17.02.2001) were available to document this fire season. Fire scars were detected manually by their colour and shape in combination with personal knowledge of burned areas by local researchers.

The study area was restricted to the south-eastern part of the Okavango Delta, consisting basically of seasonal floodplains and encompassing about 1200 km^2 (see Figure 1). This area was chosen because of regular fire occurrences, a relatively homogenous landscape and the accessibility of the study sites. Within this area, 149 plots of 3 m x 3 m size were selected arbitrarily, knowing that the plot either burned (n_b=77) or did not burn (n_u=72) during the preceding months. The co-ordinates of the plots can be made available on request. All plots were investigated between 15th March and 9th April 2001 at the end of the rainy season.

For each plot, all species were recorded. Each species was described in terms of coverage, phenology, plant type, life form, growth form, hairiness of the plant and leave characters. Phenology was classified in juvenile/sterile, fertile/in flower and ripe/with seeds. The plant type distinguishes grass, sedge, herb, shrub and tree, with trees per definition being woody species higher than 2 metres. Life form was noted following the classification by Raunkiaer (1934), distinguishing phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes. Growth form was described as reptant (creeping), caespitose (tufted) or scapose (single stemmed). Concerning the leaves, their form (entire or compound/lobed) and their size was described in three classes: small (<1 cm^2), medium (1 cm^2 - 25 cm^2) and large (>25 cm^2). Additionally presence or absence of waxes on the leaves and succulence was noted as well as the hairiness of the species, which was described in terms of presence or absence of clearly visible hairs.

Other parameters estimated at each plot were the mean height of the herb layer as well as the cover of living plants, of dry litter and of bare soil. Finally, within a sub-plot of 0.5 m x 0.5 m, the above ground living biomass was clipped at each plot. The biomass was dried for 48 hours at 80°C, weighed and calculated to gram per square meter [g/m^2]. Grazing was assessed subjectively for each plot by looking for presence/absence of bitten-off culms.

Around each plot, a 50 m x 50 m quadrat was laid out to characterise the habitat in which the plot was located to allow a classification into broad habitat types. Within these quadrats only woody species taller than 0.5 m were recorded and their cover was estimated.

For statistical analysis on correlations between the fire-event and the occurrence or failure of certain plant species, plant traits or site characteristics, bivariate analyses (Mann-Whitney test; U-test) using SPSS 11.0 were applied. Multivariate analyses (Detrended Correspondence Analysis (DCA)) using PC-ORD 4.0 was applied to find species assemblages related to the fire-event. For the determination of the habitat types cluster analyses were used.

Data analyses and results

As one of the main purposes of the present study was to find differences in species composition following a single fire-event, in a first step DCA analyses were used to measure the importance of the fire parameter for the species assemblage. For the analysis all 149 plots were included. The results show that the importance of the fire occurrence for the species assemblage regarding the whole data set of 149 plots is quite negligible. The first axis explains only 19.1 % of the variance of the species data (see Figure 2 for r^2-values of the axis) and the maximum correlation of fire is with the third axis on a very low level of $r^2 = 0.015$.

The main factors determining the species assemblage derivable from the data are the cover of the herbaceous species (grasses, sedges and herbs) (correlation with first axis: $r^2 = 0.241$) and the cover of trees and shrubs ($r^2 = 0.109$). Although these parameters are not true “environmental variables”, they were included into the analysis because they indirectly reflect the time since the last flooding and the flood frequency. These parameters could not be considered directly because of missing data, but also could not be neglected because of the most likely superior ecological impact water has on the species distribution in the Okavango Delta. The two negatively correlated parameters as shown in Figure 2 reflect a flooding (moisture) gradient from active floodplains, with typically high cover of herbaceous species (mainly sedges) and no woody species to woodlands, with low cover of herbaceous species. Hence, along this gradient the whole data set can be split into several habitat types based on the cover of the woody species independently of the fire-event, as the cover of the woody species showed no correlation to fire (Figure 2).

Therefore, for the cluster analysis (Relativized Euclidean Distance and Ward’s Method as group linkage method) only cover values of the most dominant woody species of the study area were used, i.e. *Colophospermum mopane*, *Pechuel-loeschea leubnitziae* and *Acacia* species as well as a cumulative class for all other woody species. The cluster analysis split the data set into four groups (Table 1). After the analysis, the treeless Group 0 was separated into two obviously different habitat types floodplains (Group 1) and pans (Group 5) because of their extremely different site conditions and species composition (cf. Figure 2).

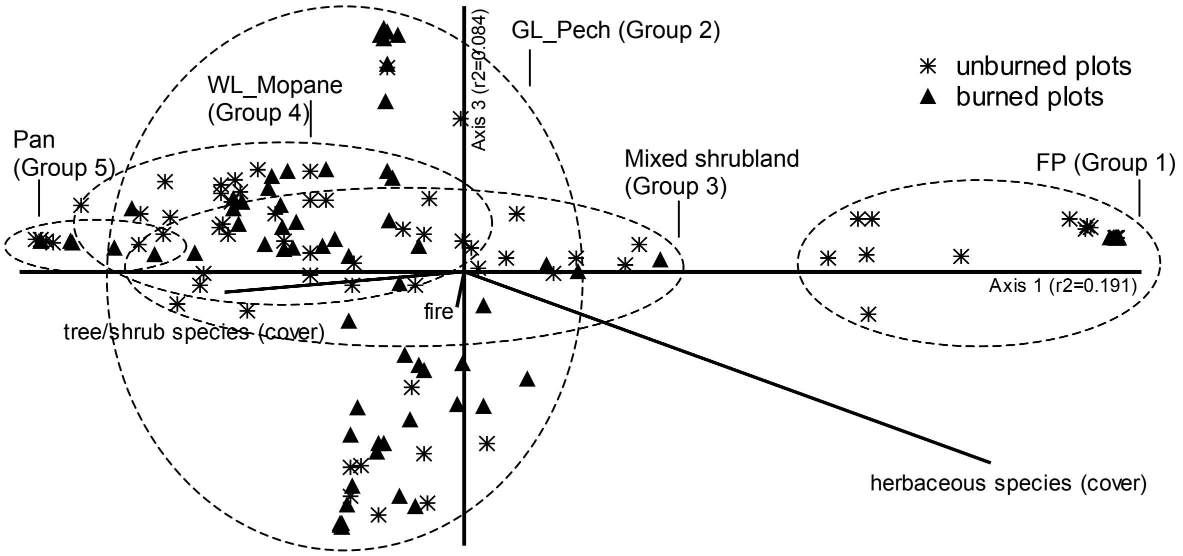


Figure 2. Graph plotted according to Detrended Correspondence Analyses (DCA) showing burned (n_b=77) and unburned (n_u=72) plots based on their similarities in species composition. The dotted ellipses summarise the plots grouped into one habitat type (see text for explanations and abbreviations). Note the clear separation of pans (Group 5) and floodplains (FP; Group 1) along the first axis.

Table 1. Mean cover values and standard deviation (in brackets) for four groups after cluster analyses of the plots (using Relativized Euclidean Distance and Ward's Method as group linkage method). The analysis was based on the cover values of *Colophospermum mopane*, *Pechuel-loeschea leubnitziae*, *Acacia* species and a cumulative class for all other woody species.

	Colophospermum mopane	*Pechuel-loeschea leubnitziae*	*Acacia* spec.	others
Group 0	0.0	0.0	0.0	0.0
Group 2	0.0	16.8 (± 8.0)	0.9 (± 1.5)	1.3 (± 2.3)
Group 3	8.1 (± 2.4)	10.6 (± 3.9)	0.1 (± 0.3)	0.4 (± 0.7)
Group 4	20.6 (± 15.0)	0.3 (± 0.7)	0.0	0.9 (± 1.6)

Following the cluster analyses, the presence/absence of just two main plant species was found sufficient to describe the groups (habitat types) and their position along the described gradient: On the one hand *Colophospermum mopane* (Mopane), typically the dominant tree species on arid sites in the vicinity of the Okavango Delta (Scholes 1997) unaffected by the flooding of the Okavango River, and on the other hand *Pechuel-loeschea leubnitziae*, a suffruticose *Asteraceae* showing pioneer character with high seed production and good resprouting capacities, and highly intolerant of flooding. It is therefore expected that a successional process on drying floodplains is roughly indicated by a reduced cover of sedges and first appearance of *Pechuel-loeschea leubnitziae*, followed by increasing *Colophospermum mopane*.

Finally the derived habitats are therefore (see also Figure 2 and Table 1): (i) active floodplains (FP; n=28), with no woody species, dominated by sedges or *Panicum repens* (Group 1), (ii) Pechuel-loeschea grasslands (GL_Pech; n=61), with *Pechuel-loeschea leubnitziae* and no *Colophospermum mopane* trees and just single other woody species (Group 2), (iii) mixed shrublands with about similar covers of *Pechuel-loeschea leubnitziae* and *Colophospermum mopane* (Mop_Pech; n=24), both having higher cover values than 5 % (Group 3), (iv) Mopane woodlands (WL_Mop; n=27), on sites unaffected by the flooding, with *Colophospermum mopane* as the dominating woody species with just single individuals of other woody species or *Pechuel-loeschea leubnitziae* (Group 4) and (v) pans (Pan; n=9) with no woody species and in contrast to floodplains with totally different dominant species, e.g. *Sporobolus ioclados*, *Sporobolus spicatus* (Group 5).

This division of habitat types primarily based on the cover of woody species was legitimated also by further analyses of vegetation parameters (discussed in detail later, cf. Table 3). Significant differences for burned and unburned plots were only found for the cover of the herb layer (including grasses, sedges and herbs) while no differences were found for the cover of trees and shrubs. This indicates the independence of the tree cover on the single fire-event. On the other hand, tree cover is most likely dependent on flooding and water fluctuations or long-term fire regimes. As these environmental parameters are not applicable but highly determine the habitat conditions and species composition, the tree cover was chosen to substitute these variables.

Also the more detailed DCA for the separate habitat types showed no indications on fire determining the species composition. Thus, the Mann-Whitney-Test (U-test) was used to test the significance of differences in mean values for the measured plant attributes on burned and unburned plots on the bivariate level. Significant differences were found for sedges, grasses, perennial grasses, hemicryptophytes, hairiness of the plant and leave size (Table 2). All other traits investigated showed no significant response to the fire disturbance. Significant differences between burned and unburned areas valid for all plots were only found for hemicryptophytes, which were favoured on unburned plots. All other responses were valid for certain habitat types only (Table 2).

Table 2. Median cover values of selected plant types, life forms and plant traits on burned and unburned plots.
* indicates the significance of the difference of the values (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$); n.s. = no significance; (n_u) = number of unburned plots; (n_b) = number of burned plots.

		all plots	Pan	FP	GL_Pech	Mop_Pech	WL_Mop
		n_u=72	n_u=3	n_u=17	n_u=25	n_u=12	n_u=15
		n_b=77	n_b=6	n_b=11	n_b=36	n_b=12	n_b=12
sedges	unburned	n.s.	4.0 *	n.s.	n.s.	n.s.	n.s.
	burned		0.0				
grasses	unburned	n.s.	38.0	n.s.	61.5 *	n.s.	n.s.
	burned		66.5 *		44.3		
perennial grasses	unburned	n.s.	n.s.	n.s.	58.0 **	n.s.	n.s.
	burned				41.8		
hemicryptophytes	unburned	57.8 *	n.s.	87.5 ***	60.5 **	n.s.	n.s.
	burned	43.5		63.0	43.8		
plant hairy	unburned	n.s.	37.5	n.s.	58.0 *	n.s.	n.s.
	burned		66.0 *		42.0		
leaves <1 cm^2	unburned	n.s.	4.0 *	n.s.	n.s.	n.s.	n.s.
	burned		0.0				
leaves 1-25 cm^2	unburned	n.s.	38.0	87.5 **	n.s.	n.s.	n.s.
	burned		66.5 *	63.0			

Results on structural parameters of the vegetation, grazing evidence and biomass are presented in Table 3. Significant differences were found for height and cover of the herb layer (i.e. cover of grasses, herbs and woody species smaller than 0.5 m), cover of the litter layer and bare soil. Also the evidence of grazing and biomass production showed significant differences on burned and unburned plots. Interestingly, the median values calculated for all plots barely reflect the reaction of single habitat types, which show the variable and also sometimes contradictory response to fire dependent on the habitat. No significant differences were found in tree/shrub cover and height as already mentioned above, and in the mean number of species per plot.

Finally, species cover was analysed to detect certain species favoured or suppressed by the single fire-event (Table 4). Only eight species out of the 109 species recorded showed significant differences in cover on burned and unburned plots. Five of them even showed significant differences not only for certain habitats but also for all plots. This could be interpreted as a general trend on how these species are affected by fire, independent of the habitat type. Nevertheless, *Sporobolus ioclados* showed different response to fire for the habitat types. Obvious dependence ($p < 0.001$) between the cover values and the fire-event was found for *Urochloa mosambicensis*, which seems to be highly favoured after the fire, especially on mixed shrublands (Mop_Pech) and on Mopane woodlands (WL_Mop).

Table 3. Median values for selected vegetation parameters on burned and unburned plots. See text for abbreviations of the habitat types.
* indicates the significance of the difference of the values (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$); n.s. = no significance; (n_u) = number of unburned plots; (n_b) = number of burned plots

		all plots	Pan	FP	GL_Pech	Mop_Pech	WL_Mop
		n_u=72	n_u=3	n_u=17	n_u=25	n_u=12	n_u=15
		n_b=77	n_b=6	n_b=11	n_b=36	n_b=12	n_b=12
herb layer	unburned	n.s.	63.3	80 ***	n.s.	80.0 *	n.s.
(height [cm])	burned		66.7 *	33.3		70.0	
herb layer	unburned	63.3 *	33.3	83.3 ***	63.3 **	51.7 ***	23.3
(cover [%])	burned	50.0	63.3 *	66.7	50.0	46.7	31.7 *
litter layer	unburned	8.1 ***	5.3 *	40.0 ***	5.3 ***	n.s.	n.s.
(cover [%])	burned	1.0	0.2	1.0	0.8		
bare soil	unburned	33.3	66.7 *	13.3	33.3	40.0	n.s.
(cover [%])	burned	50.0 **	36.7	33.3 ***	46.7 **	50.0 ***	
biomass	unburned	418.5 **	262.7	858.3 ***	418.5 **	n.s.	85.3
[g/m^2]	burned	285.2	361.1 *	307.4	324.1		157.3**
grazing	unburned	low	low	low	n.s.	n.s.	high *
evidence	burned	high **	high *	high ***			low

Table 4. Mean cover values of selected plant species on burned and unburned plots. See text for abbreviations of the habitat types.
* indicates the significance of the difference of the values (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$); n.s. = no significance; (n_u) = number of unburned plots; (n_b) = number of burned plots

		all plots	Pan	FP	GL_Pech	Mop_Pech	WL_Mop
		n_u=72	n_u=3	n_u=17	n_u=25	n_u=12	n_u=15
		n_b=77	n_b=6	n_b=11	n_b=36	n_b=12	n_b=12
Aristida congesta	unburned	0.6 **	n.s.	n.s	0.2 *	n.s	n.s
ssp. congesta	burned	0.0			0.0		
Dactyloctenium	unburned	1.1	n.s	n.s	3.2	n.s	n.s
giganteum	burned	2.6 **			5.7 *		
Pogonarthria	unburned	0.6	n.s	n.s	n.s	n.s	1.1
squarrosa	burned	3.0 **					4.8 *
Schoenoplectus	unburned	n.s	n.s	0.0	n.s	n.s	n.s
rowlei	burned			0.6 *			
Sporobolus	unburned	0.1 *	0.5 *	n.s	n.s	n.s	n.s
africanus	burned	0.0	0.0				
Sporobolus	unburned	n.s	37.5	n.s	8.2 *	n.s	n.s
ioclados	burned		62.5 *		1.4		
Tragus	unburned	n.s	n.s	n.s	n.s	0.1	n.s
berterionanus	burned					0.7 *	
Urochloa	unburned	5.3	n.s	n.s	n.s	0.1	0.5
mosambicensis	burned	11.3 ***				17.7 ***	11.0 ***

Discussion

Many of the plant traits recorded and analysed have not been further described in the results. This is not only because of the missing significant difference of these attributes for burned and unburned plots, but also because during the survey several traits appeared less useful for further evaluation. For example phenology of the species varied widely during the three weeks period. Thus, the phenology could not reflect the effect of fire, as this was masked by the strong influence of the fast development of the plants. The hairiness of the plants showed high variability through the individuals of one species, not allowing a clear prediction on the species level. Leaf characteristics, e.g. a waxy surface or succulence, could not be considered because of a too rare occurrence for sound statistical analyses.

As important, the division of the habitat types for analysing the effects of the fire-event on vegetation has to be stressed. The results vary widely dependent on the habitat and show partially contradictory development of the vegetation after fire, e.g. for grass cover on pans or on Pechuel-loeschea grasslands (GL_Pech) (Table 2). But before further interpretations on the traits can be done, the significant differences of certain plant traits related to fire have to be relativized. This is because all plant traits (Table 2) showed the same response to the fire-event as the general cover of the herb layer (Table 3), i.e. if a higher/lower cover of the herb layer was observed on e.g. unburned plots, also the plant traits seem to be favoured/suppressed on unburned plots. (The exception of the habitat type ‘pan’ will be discussed later.) This indicates that the higher values for certain plant traits are just because of the higher vegetation cover values on the plots. Therefore the significant differences between burned and unburned plots for certain traits is most likely not related directly to the fire-event itself, but only to different cover values after the fire-event. These traits are therefore presumably the ones that dominate the vegetation in general, independent of the fire-event both on burned and unburned plots. This was found looking at the example of hemicryptophytes, which account for 91.3 % and 87.0 % of the vegetation cover on unburned and burned plots, respectively, or grasses, which account for 92.4 % and 97.2 % of the vegetation cover on unburned and burned plots, respectively. Recognising this effect, the importance of the species groups or traits was calculated in relation to their relative cover values, i.e. instead of the plot size the total vegetation cover within the plot was set to 100 %. Using this relative value, for example, the significance of differences of hemicryptophytes on burned and unburned plots on floodplains dropped from $p = 0.001$ to $p = 0.796$. To additionally prove these findings the general ratios between grasses and herbs and between annual and perennial species were analysed. Neither for all plots nor for each habitat type were significant differences found for both ratios analysed. All these analyses led finally to the assumption that none of the investigated plant traits was favoured or suppressed specifically by the fire-event. The plant traits present and characterising the burned plots seem to endure for longer periods and seem not to be directly dependent on single fire-events.

As indicated above, the habitat type ‘pan’ represents an exception, as the described parallels between the cover of the herb layer and the cover of the plant traits could not be found. Unfortunately this habitat type is only represented by 9 plots and the contradictory results could also be because of statistical deficits. Nevertheless, the cover of the herb layer showed higher values on burned plots, which is already unusual for the data set, but which will be discussed later. Parallel to these values, grasses also showed significant higher cover values on burned plots (Table 2), following the same trend as described above. But in the case of this habitat type, also the relative cover values for grasses showed significant differences ($p < 0.05$) on burned and unburned plots, indicating a general trend not only to absolutely but also to relatively more grasses on the burned plots. On the other hand sedges showed both significantly higher absolute and relative cover values on unburned plots, even despite a lower herb layer cover on these plots. This implies for the habitat type ‘pan’ that sedges decline immediately after the fire-event and become replaced by grasses, while with time sedges recover and become more abundant relative to grasses. As no such phenomenon could be found for the other habitat types, one cannot expect or derive a general fire-sensitivity of sedges. This trend is probably highly dependent on the specific species found around the pans of the Okavango Delta.

The analysis on the species level led to a much higher variability in response to fire than was found for the traits. This is most likely because the level of detail of the regarded unit is in the case of species much higher than for the traits (e.g. just five categories for life form). So the observed dependence of the absolute cover values of the plant traits on the cover values of the herb layer was not repeated for the species cover values. This implies true responses of the species to the fire-event. However, the observed significant correlations presented in Table 4 have to be relativized. Many of the species show very low mean cover values, as *Aristida congesta spp. congesta*, *Schoenoplectus rowlei*, *Sporobolus africanus* and *Tragus berterionanus* below 1 % and *Dactyloctenium giganteum*, *Pogonarthria squarrosa* just around 5 %. In combination with weak significance values ($p < 0.05$) a clear trend is not derivable for those species. For *Sporobolus ioclados* clearly higher cover values could be recorded for pans on burned plots (Table 4). But the above described phenomenon of the dependence of higher species cover values on higher total vegetation cover can be observed here as well. *Sporobolus ioclados* is the dominant plant species on pan depressions in the Okavango Delta and this most likely independent of the fire-event, as the relative cover values for *Sporobolus ioclados* are 87 % on unburned and 91 % on burned plots ($p>0.05$). Similarly, for Pechuel-loeschea grasslands (GL_Pech), relative cover values showed no significant differences for *Sporobolus ioclados* on burned and unburned plots. The only obvious correlation between the fire-event and one single species was found for *Urochloa mosambicensis*. For all plots surveyed and for mixed shrublands (Mop_Pech) higher cover values of *Urochloa mosambicensis* were found on burned plots at a very high significance level ($p < 0.001$) even against the trend of higher vegetation cover on unburned plots for these habitat types. Though, the higher cover of *Urochloa mosambicensis* on Mopane woodlands (WL_Mop) on burned plots could be again related to the higher vegetation cover after fire, this does not contradict the finding of *Urochloa mosambicensis* being favoured after a fire-event. A good recovery and dominance after fire was also reported for *Urochloa mosambicensis* for northern Australia (Falvey 1979; FAO n.d.). This perennial grass requires relatively high soil fertility on lighter soils and rainfall of more than 600 mm/a over 3 to 4 months and is highly palatable. Under these conditions burning might therefore be a tool to provide good grazing grass, but besides more detailed studies on the positive correlation of *Urochloa mosambicensis* to fire, additional investigations on side effects (e.g. overgrazing, species diversity) are necessary.

The investigations finally give the impression that almost no changes can be found on burned and unburned plots after single fire-events, comparing either all plots or just certain habitat types. Comparable results for fire or other kinds of regular disturbances are cited in the literature (Lavorel et al. 1999; Días et al. 1999; Morgan 1999). Nevertheless all these findings contradict with common disturbance theories or succession models (e.g. Margalef 1968), which describe an initial colonisation of the post-disturbance environment, that is characterised basically by less competition, more light and higher nutrient availability (Bond & van Wilgen 1996), thus by a few annual, fast growing species, with high seed production, which are out-competed during the successional process. But as differences on burned or unburned plots could not be found for the present studies, neither on species composition nor even on herb/grass or annual/perennial ratios, this general successional pathway cannot be supported, despite finding the typical post-fire environment with a reduced litter layer, less vegetation cover and more bare soil on burned plots (Table 3). A theory for this missing linear succession after the fire-event was already developed by Bond and van Wilgen (1996). It describes a fire succession not dependent on a competitive hierarchy but on the timing of life-history events in relation to disturbance, indicating high species numbers after the fire and a successive elimination of species determined by the relative longevity of the species. The dominance of each species is therefore transitory as it ages and dies and re-establishes after the disturbance event. Following this argumentation, the missing differences on burned and unburned plots found for the present investigation would lead to the assumption that for the study area the inter-fire-interval is very low, and allows all species to re-establish in short intervals.

Another explanation of the missing differences on burned and unburned plots could simply be the independence of the species establishment on the fire-event. As in fire-prone environments most species are adapted to the fire-event, one can assume that most perennial species manage to survive the fire, e.g. by protected growing points or resprouting. Annual species will most likely die-off but will not only find good conditions for regrowth immediately after the fire, but also during the inter-fire intervals as light and space are not limited in general for savannas. The low values for the vegetation cover of usually less than 60 % support this theory (Table 3).

Despite the missing differences on burned and unburned plots related to plant traits and species composition, structural changes could be found highly dependent on the habitat type. This was already indicated above, since certain habitat types show higher herb layer cover values for burned plots and others for unburned plots (Table 3). The interesting phenomenon of the habitat types not showing the same response to fire can be explained along a rough productivity gradient of the habitats, described by the measured above ground living biomass on unburned plots. The gradient shown on Figure 3 ranges from highly productive, inundated active floodplains on organic rich soils (FP), to drying floodplains on loamy sands (Mop_Pech, GL_Pech), to pans and Mopane woodlands (WL_Mop) on poor sands. Regarding the biomass on burned plots and the differences in biomass between the burned and unburned plots, a contrary development can be observed, as biomass production increases against the productivity gradient, at least relative to the quantities of biomass on the unburned plots of the same habitat (see trend on Figure 3). The habitat types Pan and Mopane woodlands (WL_Mop) even show higher biomass values on burned than on unburned plots.

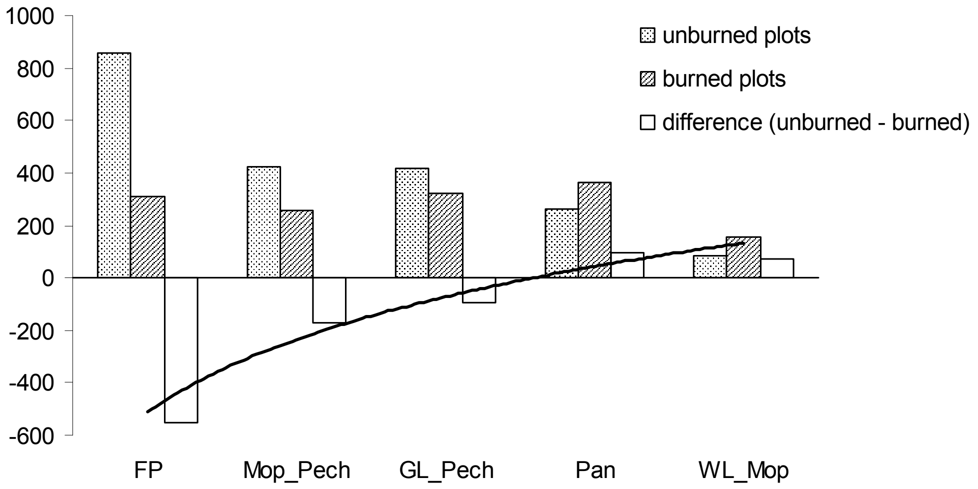


Figure 3. Median values for above-ground living biomass [g/m^2] of the five habitat types differentiated into burned and unburned plots. The trend shows the development of the differences between the biomass on burned and unburned plots along a productivity gradient from floodplains (FP) to Mopane woodlands (WL_Mop).

To explain these trends, the productivity of each habitat type has to be considered separately. The inundated floodplains (FP) experience a permanent nutrient and water supply even throughout the dry-season, as flooding is most intense during the dry period for the Okavango Delta. With a fire, the biomass of a certain site is reduced almost to zero, while the unburned sites remain undisturbed. Due to the high productivity of the habitat, both on the burned and on the unburned plots, there is a steady parallel increase of biomass leaving significant differences between the two treatments shown in Figure 3.

The drying floodplains, i.e. mixed shrubland (Mop_Pech) and Pechuel-loeschea grassland (GL_Pech), in contrast experience the dry season without water supply and all herbs and grasses die off. After a fire that occurs during the dry season, similar conditions exist on burned as well as on unburned sites at the beginning of the rains. Pans and Mopane woodlands (WL_Mop), on sites with poor nutrient conditions, show a very low cover of the herb layer around 30 % on unburned plots and significantly higher values for burned plots (cf. Table 3). They probably experience a nutrient pulse after a fire that can lead in short-term to a higher biomass production than on unburned sites. These nutrient pulses after a fire, also described by DeBano et al. (1998), probably also happen in other habitat types, but the improvement of the nutrient condition is most likely observable best on the poorest sites. Long-term studies would be required to see how often these ‘pulses’ can be repeated before soil depletion takes place.

In the context of variable response of fire for each of the habitat types, the evidence of grazing is also interesting to discuss (cf. Table 3). All habitat types without woody species, i.e. pans and floodplains (FP), were grazed after fire-events, while all unburned plots of these habitats remained ungrazed. In contrast, most of the plots (80 %) with woody species, i.e. on Pechuel-loeschea grasslands (GL_Pech), mixed shrublands (Mop_Pech) and Mopane woodlands (WL_Mop), were ungrazed and this effect is obviously independent of the fire-event, as both grazed and ungrazed ‘woody plots’ were about equally affected by fire. Grazers probably avoid these 'woody areas' in general, as they do not provide open view and terrain to see and escape predators. In contrast, the open grasslands seem to be generally favoured by grazers and burned ones even more preferred, presumably due to the fresh young grasses growing immediately after the fire (Booysen & Tainton 1984, Bond & van Wilgen 1996). This nutrient pulse after the fire is therefore most likely also the reason for the light grazing evidence in the open Mopane woodlands (WL_Mop) (cf. Table 3), where higher biomass production could be described after the fire.

Conclusion

After a single fire-event, the comparison of burned and unburned areas in the Okavango Delta region showed almost no differences on species composition and the cover of specific plant traits. Differences were found in vegetation structure.

Interestingly, the defined habitat types varied considerably in their response to fire. In active floodplains (FP) with the highest observed biomass production and vegetation cover (Table 3), fire opens space in the dense stands with up to 100 % vegetation cover, and most likely enhances the habitat and species diversity slightly due to the reduction of the dominance of a few high competitive species, e.g. *Panicum repens.* Hence, fire on active floodplains should show high effects on vegetation through structural changes by biomass reduction (Figure 3) and should lead to a diversification of the vegetation. For drying floodplains, i.e. Pechuel-loeschea grasslands (GL_Pech) and mixed shrublands (Mop_Pech) in contrast, the effects of single fire-events seem to be weak, as vegetation tends to recover quickly after the fire, getting close to the pre-burn conditions (Figure 3). On pans and Mopane woodlands (WL_Mop) on poor sites with little cover of the herb layer, fires are followed by a short nutrient pulse, which enhances nutrient availability and productivity. These effects are most probably not repeatable in high intervals, as soil-nutrients are limited. Fire in Mopane woodlands (WL_Mop) and pans have hence clear effects on the herbaceous vegetation and should run on low frequencies to avoid soil-depletion.

The assessment of effects of single fire-events on vegetation could only give an insight into what happens immediately after the fire and most of the slight changes are not expected to be still observable for the following vegetation period after the next drought. Long-term assessment of fires, i.e. working with the fire-regime of the area, would most likely provide more detailed results and a better understanding of the ecological processes determining the vegetation of the Okavango Delta.

Acknowledgement

The presented study was kindly supported by the German Foundation “Stifterverband für die Deutsche Wissenschaft”, the German Academic Exchange Service (DAAD) and Volkswagen Foundation.

References

Arnold TH & De Wet BC (1993): Plants of Southern Africa: Names and Distribution. Memories of the Botanical Survey of South Africa No. 62; Botanical Research Institute, Pretoria.

Andersen AN, Braithwaite RW, Cook GD, Corbett LK, Williams RJ, Douglas MM, Gill AM, Setterfield SA & Muller WJ (1998): Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. Australian Journal of Ecology 23: 95-110.

Barbosa PM, Stroppiana D, Gregoire J-M & Pereira JMC (1999): An assessment of vegetation fire in Africa (1981-1991): Burned areas, burned biomass, and atmospheric emissions. Global Biogeochemical Cycles 13: 933-950.

Bond WJ (1997): Fire. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge 421-446.

Bond WJ & van Wilgen BW (1996): Fire and Plants. Population and Community Biology Series 14, Chapman & Hall, London, UK.

Booysen PdV & Tainton NM (1984): Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48, Springer-Verlag, Berlin.

DeBano LF, Neary DG & Folliott PF (1998): Fire's Effects on Ecosystems. Wiley and Sons, Inc., New York.

Días S, Cabido M, Zak M, Martínez Carretero E & Araníbar J (1999): Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. Journal of Vegetation Science 10: 651-660.

Ellery WN & Tacheba B (2003): Floristic Diversity of the Okavango Delta, Botswana. In: Alonso LE, Nordin LA (eds): A rapid Biological Assessment of the Aquatic Ecosystems of the Okavango Delta, Botswana: High Water Survey. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, DC, p. 69-96.

Falvey L (1979): Establishment of two Stylosanthes species in a *Urochloa mosambicensis*-dominated sward in the Daly River basin. Journal of the Australian Institute of Agricultural Science 45: 69-71.

Frost P, Medina E, Menaut J-C, Solbrig O, Swift M & Walker B (1986): Responses of savannas to stress and disturbance. Biology International, Special Issue 10,

Higgins SI, Bond WJ & Trollope WSW (2000): Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88: 213-229.

Jeltsch F, Moloney K & Milton SJ (1999): Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. Oikos 85: 451-466.

Lavorel S, McIntyre S & Grigulis K (1999): Plant response to disturbance in a Mediterranean grassland: How many functional groups? Journal of Vegetation Science 10: 661-672.

Margalef F (1968): Perspectives in ecological theory. University of Chicago Press, Chicago, Illinois.

McCarthy TS, Cooper GRJ, Tyson RD & Ellery WN (2000): Seasonal flooding in the Okanvango Delta, Botswana - recent history and future prospects. South African Journal of Science 96: 25-32.

Morgan JW (1999): Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology 144: 127-144.

Raunkiaer C (1934): The life forms of plants. Oxford University Press.

San Jose JJ & Montes RA (1997): Fire effect on the coexistence of trees and grasses in savannas and the resulting outcome on organic matter budget. Interciencia 22: 289-298.

Scholes RJ (1997): Savanna. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge, p. 258-277.

Scholes RJ & Archer SR (1997): Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28: 517-544.

Scudder T et al. (1993): The IUCN Review of the Southern Okavango Integrated Water Development Project. IUCN, Gland.

Trollope WSW, Trollope LA, Biggs HC, Pienaar D & Potgieter ALF (1998): Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. Koedoe 41: 103-112.

Walker BH (1985): Determinants of Tropical Savannas. IRL Press Limited, Oxford.

Chapter 3

Interactions between fire and flooding in a southern African floodplain system (Okavango Delta, Botswana)

Heinl M[1], Neuenschwander A[2], Sliva J[1] & Vanderpost C[3]

[1] Chair of Vegetation Ecology, Technische Universitaet Muenchen (TUM),
Am Hochanger 6, D-85350 Freising-Weihenstephan, Germany
[2] Center for Space Research, University of Texas at Austin
3925 W. Braker Lane, Suite 200, Austin, TX 78759
[3] Harry Oppenheimer Okavango Research Centre (HOORC), University of Botswana,
Private Bag 285, Maun, Botswana

(accepted for publication by Landscape Ecology)

Interactions between fire and flooding in a southern African floodplain system (Okavango Delta, Botswana)

Abstract. A series of 98 satellite images was analysed to reconstruct the fire and flood history of a floodplain system in southern Africa (Okavango Delta) to investigate interactions between fire and flooding and to determine the relevance of rainfall versus flood-events for fire occurrences on floodplains and on drylands. The aims of the study are to (1) analyse and compare the fire frequency on floodplains and on adjacent drylands, (2) investigate the influence of rainfall and flooding on the fire occurrence on floodplains and drylands and to (3) determine correlations between fire frequency and flood frequency. The analyses show higher fire frequencies on floodplains than on drylands, because of higher biomass production and fuel loads. While the fire occurrence on drylands depends on annual rainfall events, the fire frequency on floodplains is in principle determined by the flood frequency. Like the variation in rainfall determines the fire occurrences on the drylands, the variation in the flood frequency determines the fire frequency on the floodplains. Clear differences among the floodplains where shown by analysing the flood frequency versus the fire frequency. Here, the highest potential to burn was found for areas with a medium flood frequency, that is areas that get flooded about every second year. Calculated mean fire return intervals for different floodplain types, characterised by flood frequencies, specify the potential to burn of each floodplain type and allow to evaluate the fire frequencies of specific floodplains in terms of their averageness.

Introduction

Vegetation fires are important ecological factors in many parts of the world and can, in principle, occur under most climate regimes (Bond & van Wilgen 1996). But global observations have shown that most biomass burning occurs in the tropics and subtropics, especially in savannas (van de Vijver 1999). Typical for this biome are a hot wet season of four to eight months and a warm dry season for the rest of the year (Nix 1983). These climatic conditions are often responsible for extensive and regular fires common to savannas (Scholes 1997; van Wilgen & Scholes 1997): During the rainy season, vegetation grows rapidly and accumulates fuel loads that are susceptible to burning during the dry season.

While the dry season in savanna regions is simply the period of potential burning, the amount of water available during the wet growing season strongly determines the biomass accumulation and therefore affects the chance of fire. Direct dependencies between rainfall, as prerequisite for fuel accumulation, and fire was found by van Wilgen and Scholes (1997), who describe a positive relationship between rainfall, biomass production and fire frequency. Similar trends are described by Du Plessis (1997) or van Wilgen et al. (2003). Also for Bond (1997), fire frequency in southern Africa follows a productivity gradient, which is determined by a rainfall gradient.

However, all these studies use rainfall just as a surrogate for fuel accumulation. Despite the accepted applicability of this approach for most savanna regions, other factors or even other sources of moisture, besides rainfall, have to be considered for fuel accumulation where relevant. Following the approach of using water availability for fuel load estimations, especially seasonal floodplain systems deserve special consideration. They usually show a clear difference to adjacent non-flooded areas in terms of the amount of water available, the season of water availability and soil properties. In addition, the associated floodplain vegetation differs clearly from non-flooded areas and often consists of unpalatable sedges. This reduces biomass off-take by herbivores and leads combined with the usually higher rates of biomass production on floodplains to higher fuel loads, which in turn should lead to higher fire frequencies and different fire regimes compared to non-flooded areas.

The aims of the present study are therefore

1) comparing the fire frequency on floodplains and on adjacent drylands. It is hypothesised, that the fire frequency on floodplains is significantly different to the fire frequency on adjacent drylands despite the same amount of rainfall;

2) investigating the influence of rainfall and flooding on the fire occurrence on floodplains and drylands, hypothesising that on drylands fire occurrences are positively correlated with the amount

of rainfall, and on floodplains fire occurrences are positively correlated with the extent of the flooding;

3) determining correlations between fire frequency and flood frequency independent of rainfall.

These analyses should lead towards refining the present approach on estimating fire frequencies - but also towards improving the knowledge about biomass burning, especially for wetlands. Although floodplain systems or temporal wetlands in general might be a minority in savanna areas, they are of significant importance for the ecology of arid or semi-arid environments (e.g. Okavango Delta (Botswana), Kafue Flats (Zambia), Kakadu National Park (Australia)). They therefore deserve attention and a separate consideration in burning assessments. Scholes et al. (1996) have already indicated the differences of fire regimes on wetlands and drylands, but only single studies (e.g. Russell-Smith et al. (1997)) are available on fire regimes, specific to floodplains or temporal wetlands. With a more detailed understanding of specific fire regimes, not only certain wetlands can be protected and managed more effectively, but also global estimations on biomass burning might be more precise, as wetlands contribute a significant part to the total biomass consumed by fire (Scholes et al. 1996).

For the present study, the Okavango Delta in Botswana was chosen as the study area. This large wetland in southern Africa experiences many fires every year and provides a mosaic of seasonal floodplains that allow comparative studies of areas with different flood and fire frequencies. Besides its suitability for the aims of the study, the Okavango Delta itself acts as own important study object. Ecological research in the Okavango Delta has mainly focused on the hydrology of the wetland system (e.g. McCarthy et al. 1998, Ellery et al. 1993) and scientific knowledge about frequency and distribution of vegetation fires are currently not available. The present study therefore provides initial insights into the relationship between the fire frequency and the flood regime, so that mean fire return intervals for the floodplains of the Okavango Delta can be derived. This should lead to a better understanding of the driving ecological forces in the Okavango Delta and help to manage and protect this unique wetland system in times of rising anthropogenic pressure.

Study area

The Okavango Delta is situated in northern Botswana (Ngamiland District) in southern Africa approximately between E22.0° - E24.0° and S18.5° - S20.5° (Figure 1). The vast tropical wetland in the central Kalahari is supplied by the Okavango River, which has its catchment in central

Angola. The mean annual rainfall is 490 mm, and the season of rainfall is typically from November to March (McCarthy et al. 2000).

The Okavango Delta is an alluvial fan with a very low elevation gradient (app. 1:3300; (McCarthy et al. 2000)) over the whole extension of roughly 15000 km^2, forming a wetland composed of an intricate system of channels, lakes, floodplains and elevated dry islands. The water inflow into the Okavango Delta system through the Okavango River as well as the annual amount of rainfall is highly variable. As a consequence, there are strong annual shifts in the water distribution, with dry areas becoming inundated and swamps being desiccated regularly. At the distal reaches of the permanently flooded areas the intensity and duration of the flooding decreases and the permanent swamps change to seasonal swamps and irregularly inundated floodplains (Ellery et al. 2003). These floodplains in the southern, drier section of the Okavango Delta are primarily the focus area of the present study (Figure 1). The habitats range from small permanently flooded swamps and channels, dominated by *Phragmites ssp.* and aquatic herbs (e.g. *Nymphaea* ssp., *Potamogeton thunbergii*) to regularly inundated floodplains, dominated by sedges (e.g. *Cyperus articulatus*, *Schoenoplectus corymbosus*) and old floodplains that have not been flooded for years, dominated by grasses (e.g. *Eragrostis* ssp., *Panicum* spp., *Stipagrostis uniplumis*) with scattered shrubs and trees (e.g. *Pechuel-loeschea leubnitziae, Acacia* spp.). Besides these Okavango floodplains, a large portion of the study area is covered by typical savanna vegetation, with *Acacia spp.* or *Colophospermum mopane*, unaffected by the floodwaters from the Okavango River.

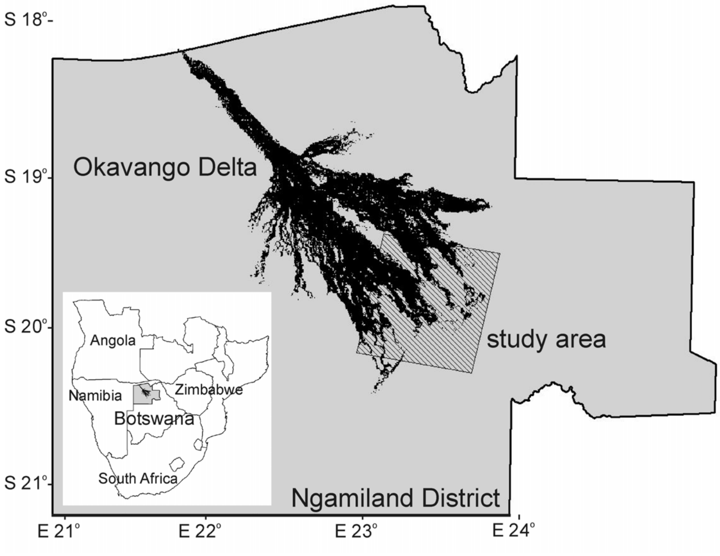


Figure 1. Location of the study area. The central quadrate indicates the study area in the southern part of the Okavango Delta fan in northern Botswana (Ngamiland District), southern Africa.

Fires are common phenomena throughout the entire study area. Main fire season is from the middle to the end of the dry season, i.e. roughly from June to September. The fires are almost exclusively surface fires, supported by grasses and small shrubs and trees. Natural ignition is rare and most fires are of anthropogenic origin, as access to natural resources in this area is often dependent on burning, e.g. fishing, hunting, etc. (Cassidy 2003). Burning is usually just applied to small areas and the fires then spread uncontrolled, where they are supported by vegetation. Due to a general burning prohibition, fires are usually considered as accidental.

The study area in the Okavango Delta provides a regime of infrequent flooding and uncontrolled burning, which leads to a fine-scaled mosaic of areas with different flood and fire frequencies and therefore offers excellent opportunities to investigate the relationships between burning and flooding.

Material and methods

The analysis of the temporal and spatial distribution of fires as well as the calculation of fire and flood frequencies require a detailed knowledge about the fire and flood history of the study area. Since no comprehensive documentation is available for fires in the Okavango Delta region, the fire and flood history was reconstructed using remotely sensed data.

A series of 98 satellite images (91 Landsat Thematic Mapper (TM, ETM+) and 7 EO-1 Advanced Land Imager (ALI) scenes) with a spatial resolution (pixel size) of 30 x 30 meters were used to determine the extent of flooded and burned areas for a 15-year period from 1989 through 2003. The study area is represented by the upper left quarter of the Landsat scene 174/074 with an extent of approximately 6141.1 km^2. The images were primarily selected based on availability and cloud cover. As preliminary studies showed, the ideal temporal resolution for conducting the fire history studies is six to eight weeks. Fire scars in this region are almost undetectable after an eight weeks period both on the ground and in the imagery. Due to cloud cover and technical restraints, this temporal resolution was not achievable for every year. However, for all years at least five images, spread evenly over each year, were available. Detection of burned and flooded areas was extracted from a 40-class unsupervised classification (ISODATA) of the georeferenced satellite images. Three bands, representing the mid-, near- and thermal infrared wavelengths (Landsat TM bands 4, 7 and 6, respectively) were included into the classifier, which showed the best approximation on preliminary assessments of burned and flooded areas in 2001. Annual fire and flood distribution maps were generated from the image analyses using ArcView 3.2 software. The fire distribution maps contain information about the spatial extent and the date of each fire, while the flood distribution maps show all areas inundated for the particular year. Fire frequency and flood frequency maps were generated by summarizing recoded annual fire and flood distribution maps, using ENVI 3.4 software. Areas (pixels) identified with similar fire or flood frequency were grouped into frequency classes according to their number of burns or floods, respectively. The number of the class represents the number of burns or floods during the 15-year period. Hence, areas burned for example seven times in the 15-year period are named as fire frequency class 7 and areas flooded twelve times are described as flood frequency class 12. Rainfall data were provided by the Harry Oppenheimer Okavango Research Centre in Maun, Botswana. Mean annual rainfall over the study area was approximated by the average of the Maun and Shakawe records as suggested by McCarthy et al. (2000). For statistical analyses, SPSS 11.0 software was used.

Results and discussion

Distribution of fire and flood frequencies

The analyses of the distribution of the flood frequency classes over the entire study area (6141.1 km^2) showed that areas never flooded (flood frequency class 0) during the 15-year period (1989-2003) account for 75.4 % (Figure 2). The flood frequency class 1 accounts for 7.5 %. The areas flooded 2 times or more (classes 2 to 15) show almost similar cover values between 2.7 % and 0.6 % of the study area. Responsible for the higher values of class 1 is one extensive flood event in 1989, which inundated areas that were never recorded as flooded again until 2003. Flood frequency class 15 covers basically permanent channels and lakes. Also included in this class are floodplains that are inundated regularly every year, but are not permanently flooded. These floodplains are mainly located adjacent to channels or lakes.

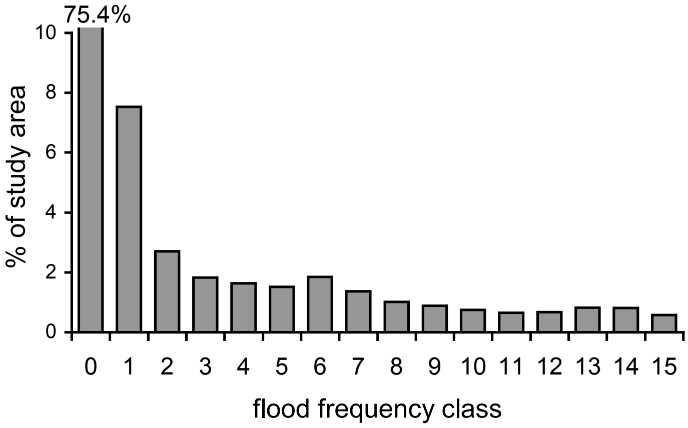


Figure 2. Distribution of the flood frequency classes within the study area. The flood frequency classes represent the number of floods during the 15-year study period.

For analysing the dependence of fire occurrences on the water availability, the flood frequency was used to divide the study area into two basic landscape units, that is drylands and floodplains. Drylands were defined as areas that were never flooded during the study period and are represented by the flood frequency class 0 (75.4 % of the study area). Floodplains were defined as all areas for which at least one flood-event was recorded in the 15-year period. Therefore, they are represented by the flood frequency classes 1 to 15 and account for 24.6 % of the study area.

Analysing the distribution of the fire frequency classes revealed no fire activity for almost half of the study area (Figure 3). The maximum number of burns for a single area during the 15-year study period was 10, so the fire frequency classes range from 0 to 10, only. The fire frequency classes 5 to 10 account for less than 5.0 % of the study area, with the fire frequency classes 7 to 10 even covering less than 1.0 %. However, with a study area of more than 6000 km^2 these classes still constitute more than 60 km^2 and are therefore still considerable. The distribution of floodplains and drylands within each fire frequency class differed significantly (Figure 3; secondary axis). The fire frequency classes 0 and 1 show a clear trend of being represented by drylands, which account for more than 80 % (90.1 % and 81.2 %, respectively) of each of the fire frequency classes. In contrast, floodplains dominate the fire frequency classes 5 to 10, accounting also for more than 80 % of each class (83.9 %, 92.8 %, 94.3 %, 97.9 %, 94.2 % and 100 %, respectively). Areas with the maximum frequency of 10 fire records during the study period were solely found on floodplains.

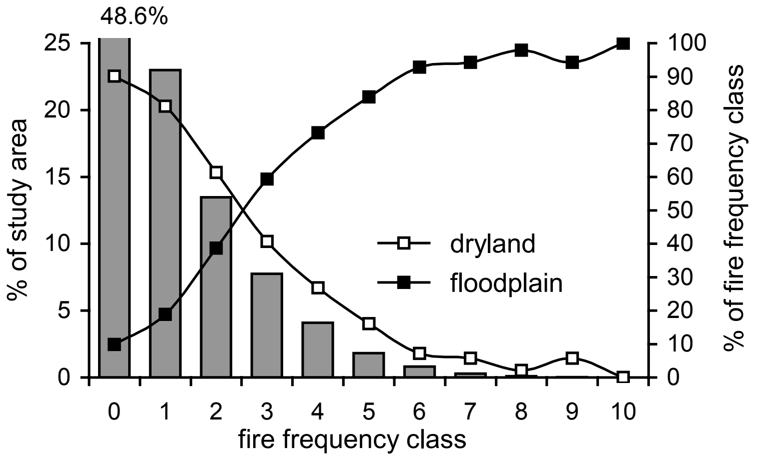


Figure 3. The distribution of the fire frequency classes within the study area (grey bars on primary axis). The lines with markers, corresponding to the secondary axis, show the portion of floodplains and drylands within each fire frequency class. The fire frequency classes represent the number of burns during the 15-year study period.

This analysis shows that areas with a low fire frequency are mainly covered by drylands and areas with a high fire frequency are basically located within floodplains. Therefore, as hypothesised, a significant difference in the fire frequency of floodplains and drylands exist and a trend towards higher fire frequencies on floodplains can be derived, despite the same amount of rainfall on both floodplains and drylands.

Fire frequency versus rainfall and flooding

The preceding analysis showed the differences of floodplains and drylands in terms of fire frequency, despite a similar rainfall. However it cannot be concluded, that rainfall has no effects on the fire occurrence and that flooding is automatically the determining factor for the fire frequency. Therefore, to investigate the influence of rainfall and the extent of flooding directly on the fire occurrence on floodplains and on drylands, the burned area is set into relation to the extent of flooding and rainfall on a yearly basis (Figure 4). Rainfall shows a significant positive correlation to the area burned on drylands (r_S= 0.54; p= 0.04) and no correlation to the burned area on floodplains. No significant correlation was found between the extent of the flooding and the area burned on floodplains or on drylands.

Hence, as hypothesised, a direct effect of rainfall on the extent of the annual burns on drylands can be observed, whereas on floodplains, the extent of the fire is not directly dependent on the rainfall. But, for floodplains, also the extent of the flooding showed no correlation to the annual extent of burned areas. The formerly stated relation of high fire frequencies on floodplains, indicating a general trend towards wetter areas burning more often, was therefore not observed on a yearly basis. Areas, that get flooded during a particular year, do not necessarily show a high probability to burn in this particular year.

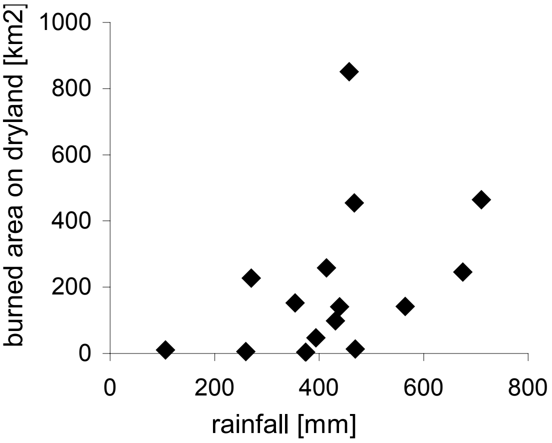


Figure 4. Relationship between the extent of the burned area on drylands and the amount of rainfall for the years 1989 to 2003.

Comparing fire on drylands and floodplains

The comparison of drylands and floodplains, as defined for the present study, revealed clear differences in their susceptibility to burning, and this susceptibility seems to be dependent on the time-scale considered.

On drylands, burning seems to be directly affected by the amount of rainfall for a particular year (Figure 4). The amount of rainfall, falling typically at the beginning of the year, affects immediately the biomass production and determines biomass growth and accumulation. For years with high rainfall, high fuel loads are present after the growing season, supporting fires during the dry fire season. Responsible for the immediate effects on the fire occurrences are probably fast growing and productive grass species (e.g. *Urochloa mosambicensis*), which are able to grow and seed quickly after rainy periods. In 2004, a year with exceptionally high rainfall and several separated wet periods during the rainy season, even the development of several plant generations, which multiplied fuel loads, could be observed (pers. obs. MH). For floodplains, no such direct dependence of the extent of the burned area on the amount of rainfall was observed. Also the extent of the flooded area did not correspond with the burned area for the particular years. Nevertheless, higher fire frequencies were observed on floodplains than on drylands. Therefore, it is expected that burning on floodplains does not immediately respond to a sudden availability of fuel loads (as it was observed for drylands), but is rather following a trend dependent on mean fuel loads in the long run.

In contrast to the drylands, most floodplains of the Okavango Delta do not experience a distinctive dry period and hence, large fluctuations in water availability throughout the years are small. Thus, there are no significant changes in standing biomass for particular floodplains observed over the years. However, the variety of floodplain types is high. The broad class of floodplains, as defined for this study, ranges from irregularly inundated grasslands with scattered shrubs to annually flooded wetlands, dominated by tall sedges or reeds. And these differences are not due to the annual flood or rainfall events, but are determined by the long-term water supply of these habitats. The fire frequency on floodplains should therefore be dependent on the flood frequency, as water availability is the factor that, in principle, determines the vegetation on floodplains and that is also responsible for the variety in the amount of fuel load.

Comparing drylands and floodplains showed a trend of higher fire frequencies on the floodplains. But, do the floodplains themselves follow this trend of the wetter areas burning more often, that is, is there a linear positive correlation between the flood frequency and the fire frequency on floodplains? Theoretically, permanently flooded areas should then show the highest fire frequencies – but this is unlikely. To investigate this correlation between flooding and burning, the floodplains are analysed more detailed and subdivided according to their flood frequency.

Interdependence between flood frequency and fire frequency

For comparative analyses of flood and fire frequency, the study area was divided into regions with different flood frequencies. For each of these flood frequency classes, the mean number of burns was calculated to show how often an area with a certain flood frequency burned on average (Figure 5A). The fire frequency shows an obvious correlation to the flood frequency. The results indicate a trend towards lower fire frequencies for the lowest and highest flood frequency classes, with the highest fire frequencies occurring at intermediate flood frequencies, i.e. areas that are flooded about every second year. Therefore, there is no linear correlation between the fire and flood frequency, and hence the general trend of wetter areas burning more often is not supported. However, the drier sections (flood frequency classes 0 to 7) show a steady rise of the fire frequency with the wetness of the classes. There, flooding supports burning, most likely since more fuel load is available in areas with higher flood frequencies. In contrast, for the areas that get flooded more than every second year (flood frequency classes 8 to 15), the flooding already seems to suppress the fires. As a decline in biomass production on these sites cannot be expected, the areas are simply to wet to burn regularly, as the inter-flood intervals get shorter.

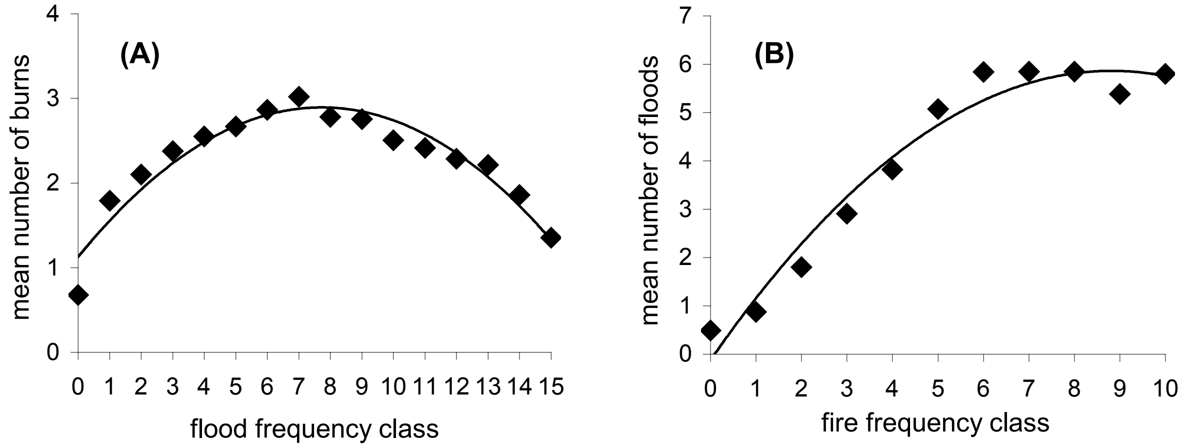


Figure 5. The calculated mean number of burns for each flood frequency class (A) and the calculated mean number of floods for each fire frequency class (B). 30 x 30 m pixels were used as sample units (N=9498560). The black line shows the regression curve (r^2_A=0.913; r^2_B=0.989).

Similar to the flood frequency classes, the fire frequency classes were analysed to show how often an area with a certain fire frequency was flooded on average (Figure 5B). Fire frequency and mean flood frequency show an almost linear relation (r^2=0.989) for the areas 0 to 6 times burned (fire frequency classes 0 to 6), with the more often an area was burned, the higher the mean number of floods. Since these fire frequency classes account for more than 99 % of the study area, they reflect a clear trend towards areas with higher fire frequencies being represented by high flood frequency classes. Nevertheless, the fire frequency classes 7 to 10 should not be neglected. Interestingly, for all these classes, about the same mean number of floods between 5.3 and 5.8 were calculated, not following the just described trend of rising flood frequency with fire frequency. Moreover, these fire frequencies seem to be independent of the flood frequency and thus, other factors than the accumulated biomass, which is dependent on the flooding, have to be made responsible for these high fire frequencies. It can only be hypothesised, that these areas that were burned seven times or more are the centres of anthropogenic ignition sources and the points from which most of the fires spread.

An estimate on the general burning capacity of the floodplains can be drawn by summarizing these findings: The areas flooded about every second year (flood frequency class 7) show the potential to support the most fires, and the maximum number of fires that is supported by this vegetation type is six. Hence, areas that burned more often than six times during the 15-year study period were most likely forced to burn.

To specify these findings, a matrix was generated, that describes the distribution of the fire frequency classes within each flood frequency class. Following these analyses, the fire frequency classes can be grouped into three categories (low, mid and high fire frequency), with each category showing a typical distribution over the flood frequency classes (Figure 6). Low fire frequencies, i.e. the fire frequency classes 0 and 1 (Figure 6A), are basically located in the “extremes” of the flood frequency, that is the dry section (classes 0 and 1) and the wet section (classes 12 to 15). These two fire frequency classes summarized (classes 0 and 1), account for more than 40 % of each of these “extreme” flood frequencies. In contrast, for the intermediate flood frequency classes 6 to 8, the portion of the fire frequency classes 0 and 1 are lowest. Hence, simplified, in the extremely dry and wet parts of the study area, fire is rare whereas in intermediately flooded parts, a low fire frequency is the most unlikely.

Medium fire frequencies, i.e. fire frequency classes 2 and 3 (Figure 6B) are almost equally distributed over the different flood frequency classes, together covering about 40 % of each of the flood frequency classes. In this case, fire shows no clear relation to the flooding and areas with medium fire frequencies are likely to be found over the entire study area. Exceptions are the extremely high and low flood frequency classes (classes 0, 14 and 15). They clearly have a lower portion of the mid fire frequencies, basically because of the already high portion of areas unburned or burned just once (fire frequency classes 0 and 1) as described above (Figure 6A).

The high fire frequencies, i.e. the fire frequency classes 4 to 10 (Figure 6C), show a totally different distribution over the flood frequency classes, compared to the low and mid fire frequencies. Although these high fire frequency classes are comparatively rare in the study area (Figure 3), they still account for more than 25 % of each of the flood frequency classes 4 to 12.

High fire frequencies are therefore basically found on the intermediately flooded areas, with the highest fire frequency in the flood frequency class 7. The drier and wetter areas show, as expected after the previous results, just minor areas with a high fire frequency.

Summarised, low fire frequencies have their maximum in the “extremes”, i.e. in the driest and the wettest parts and their minimum in the intermediate flood frequencies. High fire frequencies are in contrast basically found in the intermediate flood frequencies and are rare in the “extremes” of the flooding. Mid fire frequencies are found about equally in all flood frequency classes.

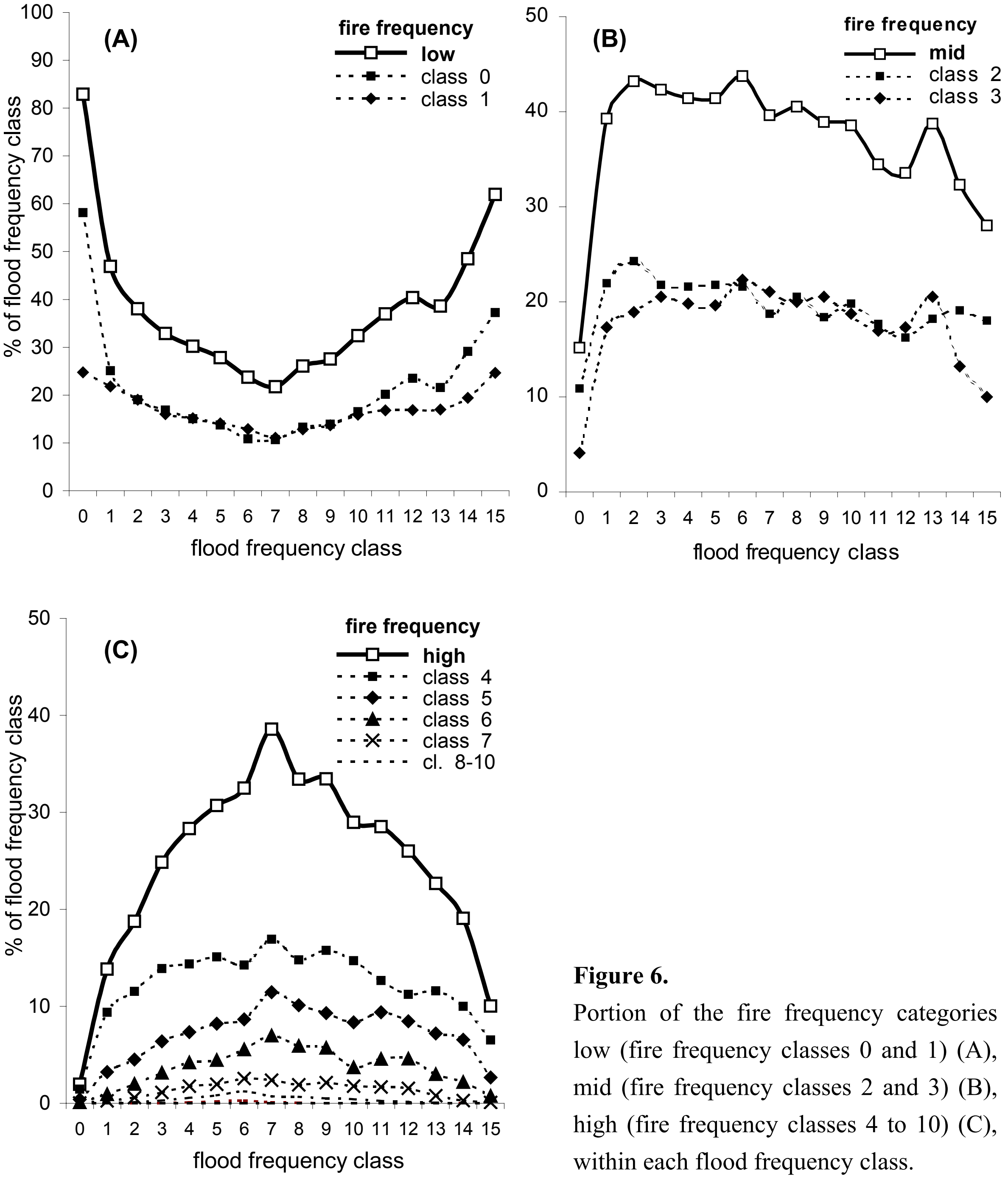


Figure 6.
Portion of the fire frequency categories low (fire frequency classes 0 and 1) (A), mid (fire frequency classes 2 and 3) (B), high (fire frequency classes 4 to 10) (C), within each flood frequency class.

Mean fire return intervals

By determining the proportion of the fire frequencies within each flood frequency class, a mean fire-return-interval (MFRI) can be calculated. For each flood frequency class, the MFRI was calculated by using the following equations:

$$MNB = \sum [(Afc_i / At) * NB_i]$$

$$MFRI = 15 / MNB$$

Here, MNB is the mean number of burns during the 15-year period, At is the total extent of the flood frequency class, Afc is the extent of a single fire frequency class within At, and NB is the number of burns. As expected, the intermediate flood frequency classes (classes 5 to 9) show the lowest MFRI, all with values below six years and the absolute minimum for class 7 with 5.1 years (Figure 7). The highest MFRI were recorded for the flood frequency classes 15, 1 and 14, all with a MFRI over eight years, with values of 11.1, 8.4 and 8.1 years, respectively. For the flood frequency class 0, a theoretical MFRI of 22.2 years was calculated, but this value was not considered as reasonable due to the study period of only 15 years.

These data now allow, in combination with the previously gained results, an estimation of fire return intervals and fire frequencies for specific floodplains. And these estimations are, as intended, not based on rainfall data, which proved to be inadequate to estimate fire frequencies on floodplains, but rather based on the flood frequencies.

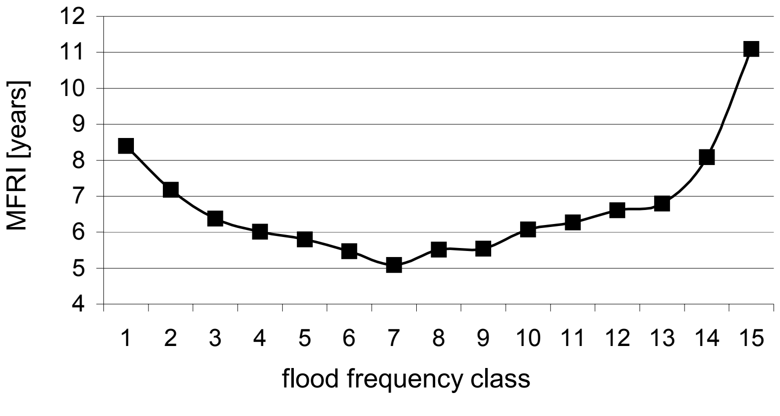


Figure 7. Mean fire return interval (MFRI) in years for each of the flood frequency classes. Flood frequency class 0 is not considered.

Conclusion

Relevance of the results

For the analyses of the fire frequency classes, mean values were used to describe the relation between fire and flooding (Figure 5). Sound trends and significant regression curves could be derived. However, each flood frequency class shows a high range of fire frequencies. For almost every flood frequency class, fire frequency shows the maximum possible range from 0 to 10, so that for all floodplain types all kind of fire frequencies were recorded. Drylands were recorded as burned up to nine times and floodplains were recorded as unburned during the 15-year study period. Although these areas are small, no significant cause-and-effect relation between flooding and burning can be derived from the results and fire-events or fire recurrences for specific floodplains cannot be predicted accurately. Although areas with the highest fire frequencies had their principle distribution on floodplains that were flooded about every second year, not all of these floodplains show necessarily high fire frequencies. In fact, only 40 % of the flood frequency class 7 show high fire frequencies and still about 25 % show low fire frequencies (Figure 6). But the point is that flood frequency class 7 shows the highest portion of high fire frequencies and that these floodplains therefore show the highest potential to burn. The results of this study can therefore be used to estimate the main distribution of fires and the probability of an area to support a fire.

Interpretation and application of the results

Comparable studies on fire frequencies in floodplain systems are rarely published. Available data on fire occurrences are often just describing the results of an applied fire management (Du Plessis 1997, van Wilgen et al. 2000) and documentations of natural or uncontrolled burning regimes are extremely rare (Russel-Smith et al. 1997). Studies considering fire regimes specifically on wetlands were not found at all. Fire frequency estimations for wetlands are therefore mostly just anecdotal or based on subjective ground observations. Scholes et al. (1996) argue, that these kind of observations usually overestimate the fire frequency for a specific landscape type, as they focus only on the burned areas, eventually with high fire frequencies, and ignore unburned sections of the same landscape type. The estimation is therefore only applicable to specific investigated areas. Also for the present study, the calculated fire frequencies for floodplains are much lower than estimated frequencies by local scientists, who expected floodplains to burn at least every second year. The fire frequencies are in contrast much more in line with studies following similar remote sensing techniques, which show mean fire return intervals for floodplains of roughly about 4 to 10 years (Scholes et al. 1996, Russel-Smith et al. 1997, Du Plessis 1997). On the other hand, the anecdotes about high fire frequencies from on the ground observations should not be neglected, as they are also in line with the presented results. The analyses of the distribution of the fire frequency classes revealed areas with seven to ten burns during the 15-year study period. Hence, there are areas that show the observed fire frequencies, although they might be small and can be considered as not representative for a specific floodplain type.

Showing this existence of a representative fire frequency for certain floodplain types, which are definable by flood frequencies, is the major finding of the present study. Although the overall fire frequency of the floodplains might be in line with other studies, the detailed investigations showed clear variations of the mean fire return interval (MFRI) within the floodplains. These calculated mean fire return intervals specify the potential to burn for each flood frequency class and the absolute values provide the possibility to assess the fire frequency on specific floodplains in terms of their averageness. Hence, areas with fire frequencies above average can be determined and causes and ecological consequences can be analysed, as it is in progress for the presented study area.

Acknowledgements

The present study is embedded into the project “Fire regime and vegetation response in the Okavango Delta, Botswana” funded by the Volkswagen Foundation, Germany and in collaboration with the Harry Oppenheimer Okavango Research Centre (HOORC, University of Botswana) and University of Pretoria, South Africa. Special thanks for financial support to Conservation International Botswana and the German Academic Exchange Service (DAAD). For all other inspirative support and comments we thank Lars Ramberg (HOORC), Melba Crawford (Center for Space Research), Joerg Pfadenhauer and Steven Higgins (both TU Muenchen). EO-1 and recent Landsat ETM+ data were made available by the NASA EO-1 Scientific calibration program and the NASA Safari 2000 program.

References

Bond WJ (1997): Fire. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge 421-446.

Bond WJ & van Wilgen BW (1996): Fire and Plants. Population and Community Biology Series 14, Chapman & Hall, London, UK.

Cassidy L (2003): Anthropogenic burning in the Okavango Panhandle of Botswana: Livelihoods and spatial dimensions. Unpublished M.Sc.Thesis, University of Florida.

Du Plessis WP (1997): Refinements to the burning strategy in the Etosha National Park, Namibia. Koedoe 40: 63-76.

Ellery WN, Ellery K, Rogers KH, McCarthy TS & Walker BH (1993): Vegetation, hydrology and sedimentation processes as determinants of channel form and dynamics in the northeastern Okavango Delta, Botswana. African Journal of Ecology 31: 10-25.

Ellery WN, McCarthy TS & Smith ND (2003): Vegetation, hydrology and sedimentation patterns on the major distributary system of the Okavango Fan, Botswana. Wetlands 23 (2): 357-375.

McCarthy TS, Cooper GRJ, Tyson RD & Ellery WN (2000): Seasonal flooding in the Okavango Delta, Botswana - recent history and future prospects. South African Journal of Science 96: 25-32.

McCarthy TS, Ellery WN & Bloem A (1998): Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius L.*) in the Okavango Delta, Botswana. African Journal of Ecology 36: 44-56.

Nix HA (1983): Climate of tropical savannas. In: Bourliere F (ed): Tropical savannas, Ecosystems of the World, Elsevier, Amsterdam 13: 37-62.

Russel-Smith J, Ryan PG & Durieu R (1997): A LANDSAT MSS-derived fire history of Kakadu National Park, monsoonal northern Australia, 1980-94: seasonal extent, frequency and patchiness. Journal of Applied Ecology 34: 748-766.

Scholes RJ (1997): Savanna. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge, p. 258-277.

Scholes RJ, Kendall J & Justice CO (1996): The quantity of biomass burned in southern Africa. Journal of Geophysical Research 101: 23667-23676.

van de Vijver C (1999): Fire and Life in Tarangire: Effects of burning and herbivory on an East African Savanna System. Tropical Resource Management Papers, Wageningen University 27.

van Wilgen BW, Biggs HC, O'Regan S & Mare N (2000): A fire history of the savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. South African Journal of Science 96: 167-178.

van Wilgen BW & Scholes RJ (1997): The Vegetation and Fire Regimes of Southern Hemisphere Africa. In: van Wilgen BW & Andreae MO & Goldammer JG & Lindsay JA (eds.): Fire in Southern African Savannas, Witwatersrand University Press, Witwatersrand 27-46.

van Wilgen BW, Trollope LA, Biggs HC, Potgieter ALF & Brockett BH (2003): Fire as a Driver of Ecosystem Variability. In: du Toit J & Biggs H and Rogers K (eds): The Kruger Experience: ecology and management of savanna heterogenity, Island Press, Washington 149-170.

Chapter 4

Fire activity on drylands and floodplains in the southern Okavango Delta, Botswana

Heinl M[1], Frost P[2], Vanderpost C[3] & Sliva J[1]

[1] Chair of Vegetation Ecology, Technische Universitaet Muenchen (TUM),
Am Hochanger 6, D-85350 Freising-Weihenstephan, Germany
[2] Institute of Environmental Studies, University of Zimbabwe,
P.O. Box MP 167, Mt Pleasant, Harare, Zimbabwe
[3] Harry Oppenheimer Okavango Research Centre (HOORC), University of Botswana,
Private Bag 285, Maun, Botswana

(accepted for publication by Journal of Arid Environments)

Fire activity on drylands and floodplains in the southern Okavango Delta, Botswana

Abstract. Satellite image derived fire history data for the southern Okavango Delta from 1989 to 2003 were used to analyse fire activity on floodplains and drylands. Maximum fire activity was encountered for 1997 with 24.1 % of the study area burned. On floodplains higher fire frequency was observed compared to drylands, but no increase in fire activity was detected over the study period on both floodplains and drylands. The main fire activity on drylands is in September at the end of the dry season, while most floodplains burn earlier in the year. Both burning of floodplains and drylands appear to peak prior to floods and rainfall-events, respectively. The annual extent of burned areas fluctuated considerably, but there appeared to be a regular six-year-oscillation apparently induced by floodplain fires. Areas with highest fire frequency were outlined and spatial analyses showed that fires on the drylands are largely due to burning of adjacent floodplains. The floodplains were therefore identified as the centres of fire activity, being the regions with the highest fire frequency and serving as source of fires spreading into drylands.

Introduction

Fire is a natural process that has been part of the functioning of many ecosystems for millennia, particularly in southern Africa. Even fires started by people must be considered as part of the process, given the antiquity of human existence in Africa. Evidence for the use of fire by Stone-Age people in Zambia goes back as far as 55 000 years ago (Clark & van Zinderen; Bakker 1964), pre-dating present plant communities. Brain & Sillen (1988) report signs of even earlier use of fire by hominids at the Swartkrans Cave, South Africa, dated at about 1.2 million years BP.

Today, fire is a widespread phenomenon throughout tropical and subtropical southern Africa, occurring mostly during the annual dry season (May to October in southern Africa) when the herbaceous vegetation is either dormant or, in the case of annual grasslands, dead, and when deciduous trees have shed their leaves (Frost 1999). These conditions contribute to an accumulation of dry, easily combustible, fine fuels. Fire is generally less frequent in drier regions where low rainfall limits the production of biomass fuels (grass, shrubs, litter and dead wood) (van Wilgen & Scholes 1997; Bond 1997). In these areas, several years of fuel accumulation, or an exceptionally wet preceding growing season, are needed to produce sufficient fuel to support a spreading fire.

The Okavango Delta is unique in that it is an extensive wetland ecosystem within an otherwise arid environment. Plant production and, in turn, the output of potential fuel for fire, depends more on the extent, level and duration of flooding, particularly in the seasonal swamps and floodplains of the southern Delta, than on the level of incident rainfall (Heinl et al. 2005). Towards the southern parts of the Delta, where flooding is more seasonal and there is more woody vegetation, fires occur across all landscape units, though they are most extensive in the seasonally flooded grasslands (Heinl et al. 2005). Burning within the woodlands is limited largely by the amount of fuel present to maintain a fire, itself inversely proportional to tree canopy cover (Frost 1996). Generally, fuel loads in the area are relatively low, because of the herbaceous production is limited by low incident rainfall, infertile sandy soils, and high levels of herbivory. When fires do occur, they are usually surface fires of low intensity.

Fires in the Okavango Delta have basically two main sources of ignition: lightning strikes, especially during the 'dry' thunderstorms that are common at the start of the rainy season (October-November), and fires set by people for various purposes, potentially at any time of the year. Reasons for burning include efforts to induce higher quality grass regrowth for grazing animals or to attract wildlife for hunting, to clear land for cultivation close to or in floodplains where flood-recession (or molapo) farming is practiced or to clear channels on the floodplains to improve access to fishing grounds. Accidental fires are caused by campfires, fish-smoking or collecting honey

(Cassidy 2003). Although most fires are considered to have an anthropogenic origin, they usually spread uncontrolled and can extent over many square kilometres, if fuel loads are sufficient.

In recent years, concerns have been expressed by local organisations that fire regimes have changed significantly in recent times as human population densities, and therefore the number of potential ignition sources, have risen (OWLS 1998; Cassidy 2003). Fires are said to be more frequent than in the past and, in aggregate, to burn a greater portion of the landscape, resulting in increasing adverse impacts on plant and animal communities and on ecosystem functioning. Though quantitative data are lacking. To address these concerns and the lack of data, a series of satellite images covering a 15-year period were analysed to reconstruct the spatial and temporal distribution of fires for the southern floodplains of the Okavango Delta (Heinl et al. 2005).

Study area

The Okavango Delta in northern Botswana (southern Africa) is situated approximately between E22.0° - E24.0° and S18.5° - S20.5° (Figure 1). The vast tropical wetland in the Kalahari Desert is supplied by the Okavango River, which has its catchment in central Angola. The mean annual rainfall over the Okavango Delta is about 490 mm, and the season of rainfall is typically from November to March (McCarthy et al. 2000).

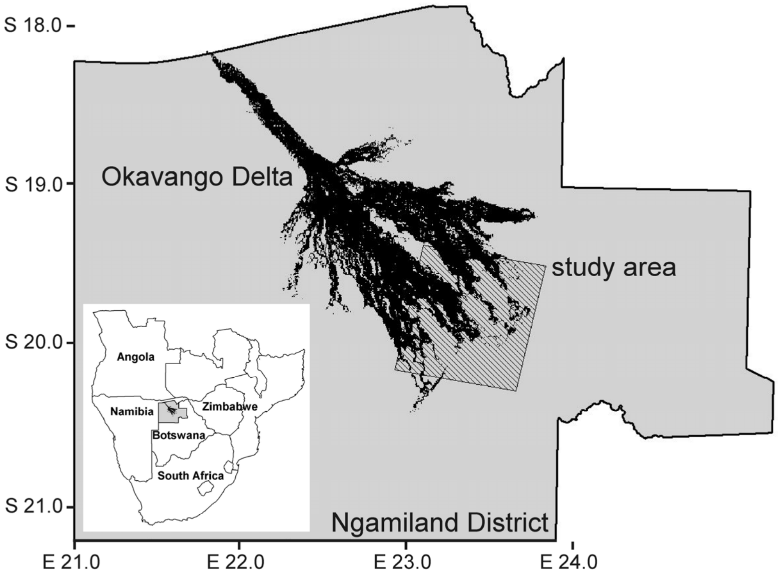


Figure 1. Location of the study area. The quadrate indicates the study area in the southern part of the Okavango Delta Fan in northern Botswana (Ngamiland District), represented by the upper left quarter of the Landsat scene 174/074.

The Okavango Delta is an alluvial fan with a very low elevation gradient of approximately 1:3300 (McCarthy et al. 2000) over the whole extension of roughly 15000 km^2, forming a wetland composed of an intricate system of channels, lakes, active floodplains, drying floodplains and slightly elevated dry islands.

The water inflow into the system through the Okavango River as well as the annual amount of rainfall is highly variable. As a consequence, there are marked annual shifts in water distribution, with dry areas becoming inundated and swamps being desiccated regularly. At the distal reaches of the permanently flooded areas the intensity and duration of the flooding decreases and the permanent swamps change to seasonal swamps and irregularly inundated floodplains (Ellery et al. 2003).

These floodplains in the southern, drier section of the Okavango Delta are primarily the focus of the present study (Figure 1). The habitats in this section of the Okavango Delta range from small permanently flooded swamps and channels, dominated by *Phragmites ssp.* and aquatic herbs (e.g. *Nymphaea ssp.*, *Potamogeton thunbergii*) to regularly inundated floodplains, dominated by tall sedges (e.g. *Cyperus articulatus*, *Schoenoplectus corymbosus*) and old floodplains that have not been flooded for years, dominated by grasses (e.g. *Eragrostis ssp.*, *Panicum spp.*, *Stipagrostis uniplumis*) with scattered shrubs and trees (e.g. *Pechuel-loeschea leubnitziae, Acacia spp.*). Besides these Okavango floodplains, a large portion of the study area is covered by typical savanna vegetation, with *Acacia spp.* or *Colophospermum mopane*, unaffected by the floodwaters from the Okavango River.

Materials and methods

A series of 98 satellite images (91 Landsat Thematic Mapper (TM, ETM+) and 7 EO-1 Advanced Land Imager (ALI) scenes) with a spatial resolution (pixel size) of 30 x 30 meters were used to obtain information about flooded and burned areas for a 15-year period from 1989 through 2003 (Heinl et al. 2005). The investigated area is represented by the upper left quarter of the Landsat scene 174/074 with an extent of approximately 6141.1 km^2 (cf. Figure 1).

Annual fire and flood distribution maps were generated from the image analysis. The fire distribution maps contain information about the spatial extent and the date of each fire, while the flood distribution maps show all areas inundated for a particular year. Fire frequency and flood frequency maps for the 15-year study period were generated by summarizing the annual fire and flood distribution data.

The study area was divided into floodplains and drylands, following Heinl et al. (2005), with floodplains defined as areas inundated at least once during the study period from 1989 to 2003 and drylands as areas that never flooded during that period. Drylands and floodplains account for approximately 75 % and 25 % of the study area, respectively.

Results

Annual fire activity

The analyses of the temporal fire distribution showed a high variability of the extent of the area burned annually over the 15-year study period. The highest level of fire activity in the study area was recorded for 1997 with 1479.0 km^2 burned, covering 24.1 % of the study area. The minimum area burned was recorded for 1998 with 56.2 km^2 (0.9 %). The mean annual extent of the burned area between 1989 and 2003 is of 435.9 km^2 (7.1 %).

For floodplains, the greatest fire activity was observed for 1997 with 41.6 % of all floodplains in the study area burned (Figure 2). The lowest fire activity on floodplains was in 1989, when during an exceptionally high flood (cf. Figure 2) most floodplains remained inundated and only 0.3 % of the floodplains burned. In the mean, 15.1 % of the floodplains burned every year.

For drylands, maximum fire activity was also calculated for 1997 with 18.4 % of the drylands burned, while the minimum fire activity was in the following year 1998 with only 0.1 % (Figure 2). The mean portion of drylands burned per year is 4.5 %.

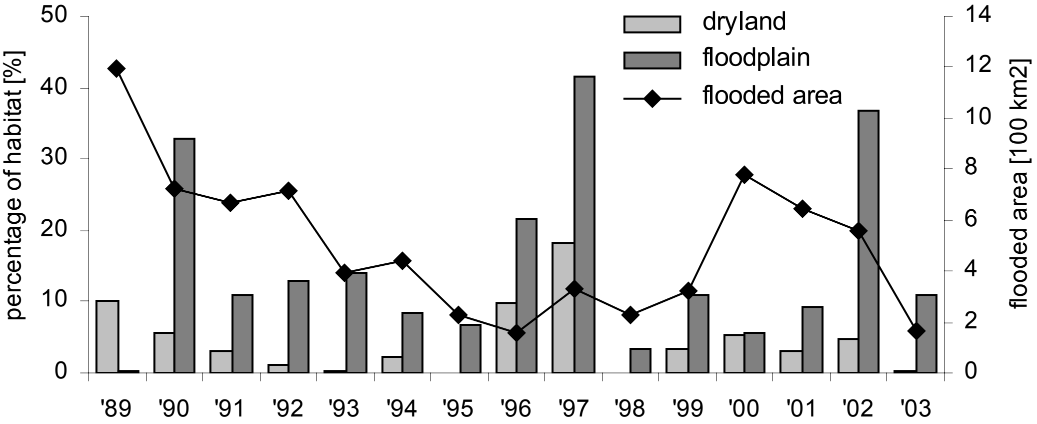


Figure 2. Burned area on drylands and floodplains per year from 1989 to 2003, relative to the extent of the habitat (dryland, floodplain). The line with markers refers to the second axis and shows the extent of the flooded area.

Fire season

The time of the year with the main fire activity (the fire season) was determined by calculating the mean area burned for each month on drylands and floodplains. Most drylands burned during the dry period, with a steady rise of the fire activity from May to a peak in September (Figure 3A). From December to April, during the wettest part of the rainy season, fires on the drylands were extremely rare. As lighting, the only natural ignition source in this region does not occur between May and August, most of these dryland fires must have had an anthropogenic origin. The incidence of lightning increases from September to November, in advance of the coming rainy season, so that fires can then also be ignited by lightning. September is typically the period with the most and largest fires, as the biomass has dried out completely and strong winds and frequent lighting strikes occur, often without any following rainfall, allowing the fires to spread extensively.

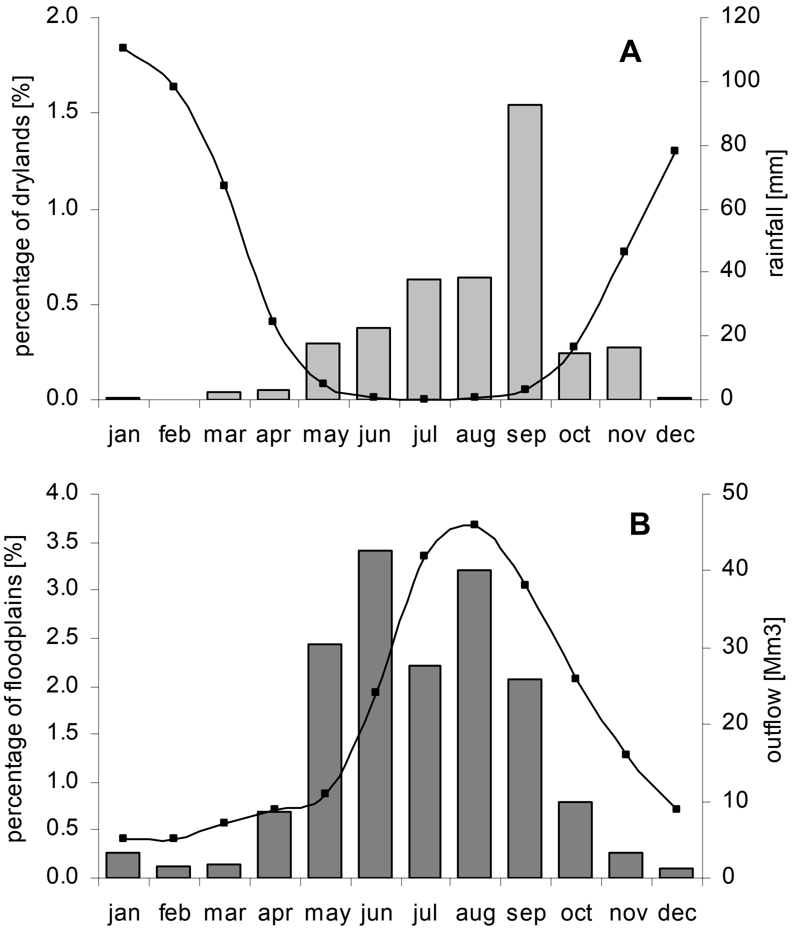


Figure 3. Mean area burned on drylands (A) and floodplains (B) per year, relative to the total extent of the habitat (dryland, floodplain) for each month. The lines with markers refer to the second axis. Mean monthly rainfall data were obtained at Maun. The outflow data, measured for the Thamalakane River at Maun are used to represent the extent of the flooding for the study area in the specific months (derived from McCarthy et al. 1998).

Fire on the floodplains showed a similar pattern, occurring mainly during the dry period from May to September (Figure 3B). However, the fire activity was distributed more evenly over the fire season, as for each of the months an almost similar extent of the burned area was recorded. With most fires on floodplains being during the dry season and clearly before the beginning of the rainy season and first lightning strikes, natural ignition sources are most likely of marginal importance for floodplains. However, burning floodplains were also recorded during the rainy season, although the extent was relatively small.

Comparing the temporal distribution of fires in the two habitats showed that floodplains tend to burn earlier during the year than drylands (Figure 3). But for both habitats fire activity peaked shortly before water became available to the system: the highest fire activity on drylands was observed in September, before the beginning of the rainy season (Figure 3A), while the floodplains in the study area showed their peak in fire activity immediately before the flooding (Figure 3B). This supports the assumption of fires being basically man-made. Apparently, people used fire as a tool to clear land and to remove dead biomass in order to optimise conditions for cultivation and harvesting in the new growing season (Cassidy 2003). Similar shifts of the fire activity towards the dry season earlier in the year due to anthropogenic burning has also been reported by Bond (1997).

Spatial distribution of the fire activity

The areas with most fire activity in the study area showed fire frequencies of up to 10 burns during the 15-year study period (Heinl et al. 2005). About 60 % of the drylands were never recorded as burned during the study period, while only 20 % of the floodplains remained unburned from 1989 until 2003 (Figure 4). Highest fire frequencies were recorded for floodplains, and drylands rarely burned more often than three times during the study period.

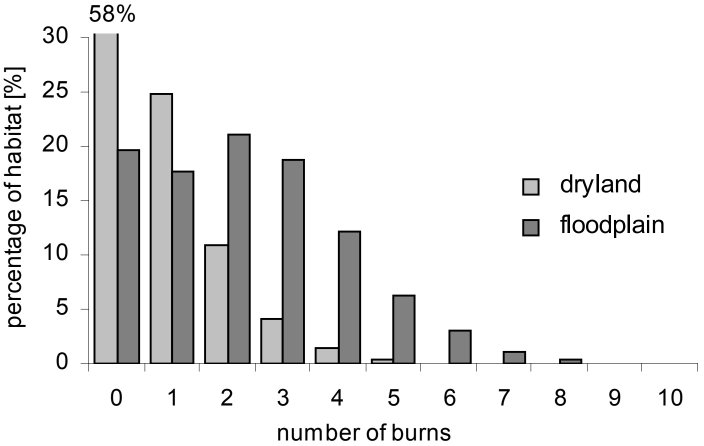


Figure 4. The area covered by fire frequency classes (number of burns between 1989 and 2003), relative to the extent of the habitat (dryland, floodplain).

Based on these findings, thresholds for defining high fire frequency were set to determine the spatial distribution of areas with extremely high fire activity and to investigate the interaction between the fire activity on floodplains and drylands. Only the 10 % of each habitat type with the highest fire frequency were taken into account in the following analyses, i.e. for drylands areas that burned three times or more and for floodplains areas that burned five times or more (cf. Figure 4). The analyses of the spatial distribution of these areas with high fire frequency revealed the highest fire activity for the floodplain systems that are connected to the main distributary channels. Highest fire activity was found for the south-eastern Boro River system, with floodplains showing high fire frequency spreading all over this section (Figure 5).

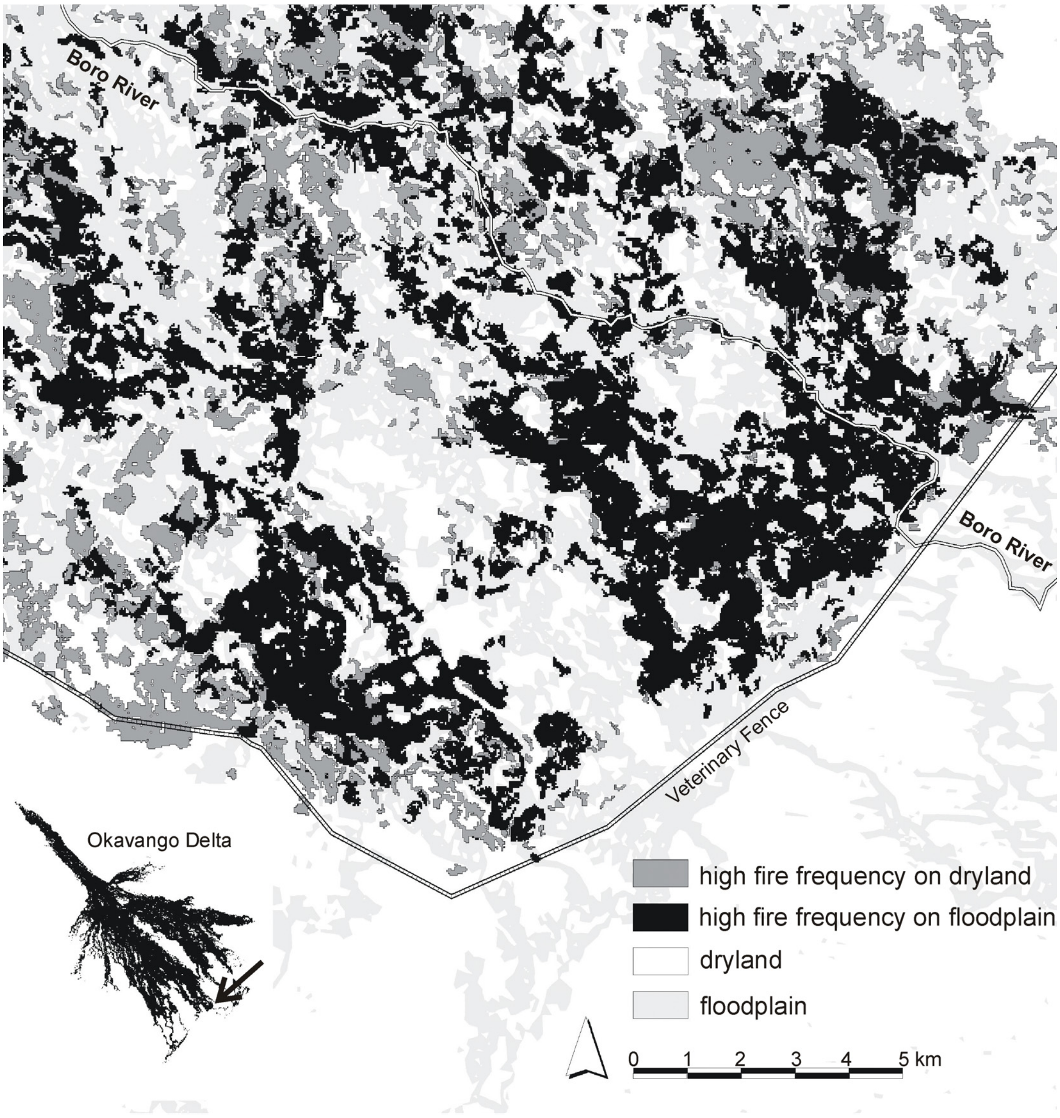


Figure 5. Areas with high fire frequency on drylands and floodplains along the Boro River in the southern floodplains of the Okavango Delta. As high fire frequency are considered three or more burns for drylands and five or more burns for floodplains during the 15-year study period.

Interestingly, the areas with high fire activity on drylands are not that evenly distributed, but rather seem to be concentrated along or close to floodplains. Drylands outside the floodplain system show the typically low fire activity.

The veterinary fence obviously acts as fire break because of cleared tracks and reduced fuel loads due to intensive livestock grazing on the southern side of the fence.

Temporal development of the fire activity

Analyses of the burned area for the particular years during the study period showed a high variation in the fire activity between the years, without any trends that could indicate rising or declining fire activities (cf. Figure 2). For analysing the temporal development of the fire activity, special attention was therefore paid to areas with high fire frequency as defined previously, as these areas are expected to show the clearest trend in the development of fire activity due to the most fire records. The analyses revealed an almost linear development of the cumulative area burned, therefore showing no rising or declining average fire activity for the study area during the 15-year period both for floodplains and for drylands (Figure 6). Increasing fire frequency on dryland appeared to be indicated by the steep rise of the burned area between 1995 and 1997, but this trend was not continued for the years after 1997. These changes in fire activity were therefore just due to an extraordinary high fire activity in particular years and did not indicate a general change in average fire activity.

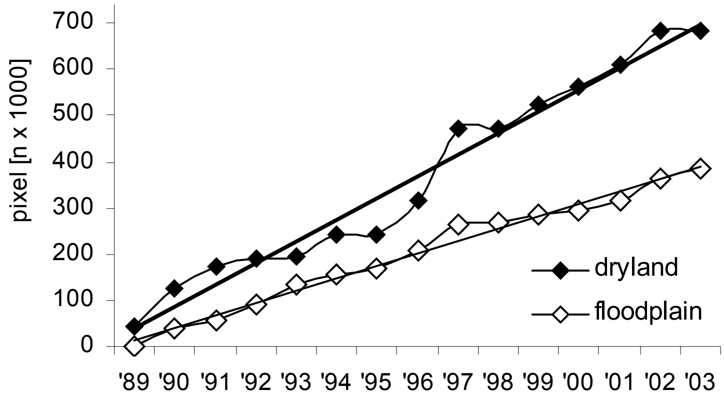


Figure 6. Cumulative number of pixels with a fire record for drylands and floodplains for the study period from 1989 to 2003. The linear regression curves show a regression coefficient for drylands and floodplains of R^2= 0.97 and R^2= 0.99, respectively. Considered for the analyses were only pixel clusters (consisting of more than 10 pixels) with high fire frequency, that is for drylands areas burned three times or more (N_D = 197017) and for floodplains areas burned five times or more (N_F = 63256).

Discussion

The analyses of the extent of the annual fires and of the temporal development of fire occurrences revealed no significant changes in fire activity over the 15-year study period. Hence, particular areas with high fire frequency are not expected to result from high fire activities during the last few years only, but rather reflect a regular high fire activity during the whole 15-year study period.

But the extent of the burned area was not similar for each year and this variability indicates that the probability of a fire is not equal for all years. The analysis of the annual fire activity revealed a maximum burned area for 1997 and a minimum burned area for 1998. Thus, these two extremes in fire activity were found for two consecutive years, indicating a low fire activity due to reduced fuel loads after a year with high fire activity. Similar relations were found for the peaks in 1990 and 2002 (Figure 2). This pattern of reoccurring years with high fire activity separated by a sequence of years with a relatively constant extent of the burned area on a significantly lower level, suggests an oscillation in fire activity that peaks roughly every six years. However, this oscillation cannot be projected to predict main fire-events, as the peaks in fire activity rather depend on inter-fire conditions than simply on the inter-fire interval. The oscillation of the fire-activity might for instance be influenced by changes in the extent of the flooding during the pre-fire period, as for the study area, the highest fire activities can be observed after declining flood-events (Figure 2). The flooded areas usually build up much biomass and thus, high fuel loads are available when these areas are exposed and dry for consecutive years. But even if this mechanism determines the fire occurrence for the study period, there is still no evidence for a regular six-year-oscillation of flooding and desiccation that would account for the observed fire oscillation.

This explanation of the fire activity based on regular inundation and exposure applies to floodplains only. For drylands a different burning regime was determined, that is rather dependent on rainfall than on flooding (Heinl et al. 2005). Nevertheless, the separate analyses of floodplains and drylands showed for both habitat types a slight six-year-oscillation of the fire activity with peaks in 1989/1990, 1996/1997 and 2002 (Figure 2). However, this oscillation is much more pronounced for floodplains than for drylands.

The mean portion burned for the two habitat types differ substantially, with about 15.1 % of the floodplains and only 4.5 % of the drylands burned per year on average. This implies a mean fire return interval for floodplains of 6.6 years and for drylands of 22.2 years (Heinl et al. 2005). Hence, the observed six-year-oscillation of the fire activity in the study area is most likely induced and dominated by the fire activity on the floodplains, while the peaks in fire activity on the drylands have much wider phases, not detectable by a 15-year data set. The observed slight six-year-oscillation of the fire activity on the drylands might therefore be linked to fires started on the floodplains, affecting fire activity in adjacent drier sections. This could be caused by the more frequent fires on floodplains simply spreading into drylands. As fuel loads in the drylands are limited, these dryland fires usually stay small and of low intensity. The drylands adjacent to floodplains might also differ from the ones further away from the wet areas. Although they are both not inundated, more water is supplied close to the floodplains due to lateral movement of water through the soil from the floodplains, increasing grass production, making more fuel load available and creating conditions that support higher fire frequencies. Probably both the proximity to floodplains and a better water supply and hence more biomass play an important role in determining the fire frequency on these drylands, with the first factor affecting the time of ignition, as floodplains burn more often than drylands and floodplain fires simply spread into adjacent drylands, and the latter determining the conditions influencing the extent of the fire.

This suggests that fires on drylands are partially due to the fire activity on floodplains, given their spatial proximity and the fact that the floodplains show significantly higher fire frequency than drylands because of their higher fuel loads (Heinl et al. 2005). Areas with high fire frequency on floodplains therefore deserve special consideration, as they are not only the regions of outstanding high fire activity but also the sources of fires on adjacent drylands and transition zones.

Areas with high fire frequency are currently of limited extent in the southern parts of the Okavango Delta and the mean fire frequency both on floodplains and drylands are overall in line with other studies (Scholes et al. 1996; Russel-Smith et al. 1997; Du Plessis 1997). However the reasons for localized high fire frequency need to be identified and understood. If human activities are connected to these high fire frequencies, rising anthropogenic impacts on the Okavango Delta can lead to more areas experiencing high fire activity in the future. Rather than changing significantly the overall extent of burning, the increase in human impact is more likely to result in specific areas being affected more frequently, especially where fire is used intentionally as a tool to manage certain resources. The consequences of such frequent burning can only be hypothesized at this stage, as specific studies on ecosystem resilience and ecological effects of different fire regimes are still missing.

Acknowledgements

The present study is part of the project “Fire regime and vegetation response in the Okavango Delta, Botswana” funded by Volkswagen Foundation, Germany and carried out in collaboration with the Harry Oppenheimer Okavango Research Centre (HOORC, University of Botswana) and University of Pretoria, South Africa. Special thanks for financial support to Conservation

International Botswana and the German Academic Exchange Service (DAAD). For all other inspirative support and comments we thank Lars Ramberg (HOORC), Melba Crawford (Center for Space Research, Texas) and Joerg Pfadenhauer (TU Muenchen).

References

Bond WJ (1997): Fire. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge, p. 421-446.

Brain CK & Sillen A (1988): Evidence from the Swartkrans cave for the earliest use of fire. Nature 336: 464-466.

Cassidy L (2003): Anthropogenic burning in the Okavango Panhandle of Botswana: Livelihoods and spatial dimensions. Unpublished M.Sc.Thesis, University of Florida

Clark JD & van Zinderen Bakker EM (1964): Prehistoric culture and Pleistocene vegetation at Kalambo Falls, Northern Rhodesia. Nature 201: 971-975.

Du Plessis WP (1997): Refinements to the burning strategy in the Etosha National Park, Namibia. Koedoe 40: 63-76.

Ellery WN, McCarthy TS & Smith ND (2003): Vegetation, hydrology and sedimentation patterns on the major distributary system of the Okavango Fan, Botswana. Wetlands 23 (2): 357-375.

Frost P (1996): The ecology of miombo woodlands. In: Campbell (ed.): The Miombo in Transition: Woodlands and Welfare in Africa, Centre for International Forestry Research, Bogor, Indonesia, p.11-57.

Frost PGH (1999): Fire in southern African woodlands: origins, impacts, effects, and control. Proceedings of an FAO Meeting on Public Policies Affecting Forest Fires, FAO Forestry Paper 138: 341-351.

Heinl M, Neuenschwander A, Sliva J & Vanderpost C (2005): Interactions between fire and flooding in the Okavango Delta floodplains, Botswana (accepted for publication by Landscape Ecology; *Chapter 3).*

McCarthy TS, Bloem A & Larkin PA (1998): Observations on the hydrology and geohydrology of the Okavango Delta. South African Journal of Geology 101: 101-117.

McCarthy TS, Cooper GRJ, Tyson RD & Ellery WN (2000): Seasonal flooding in the Okavango Delta, Botswana - recent history and future prospects. South African Journal of Science 96: 25-32.

OWLS (1998): Newsletter 1998/1. Okavango Wildlife Society, Maun, Botswana (online at http://www.stud.ntnu.no/~skjetnep/owls/newsletter/owls_news98_1.html#ch5

Russel-Smith J, Ryan PG & Durieu R (1997): A LANDSAT MSS-derived fire history of Kakadu National Park, monsoonal northern Australia, 1980-94: seasonal extent, frequency and patchiness. Journal of Applied Ecology 34: 748-766.

Scholes RJ, Kendall J & Justice CO (1996): The quantity of biomass burned in southern Africa. Journal of Geophysical Research 101: 23667-23676.

van Wilgen BW & Scholes RJ (1997): The Vegetation and Fire Regimes of Southern Hemisphere Africa. In: van Wilgen BW & Andreae MO & Goldammer JG & Lindsay JA (eds.): Fire in Southern African Savannas, Witwatersrand University Press, Witwatersrand, p. 27-46.

Chapter 5

Vegetation response to fire frequency in the Okavango Delta floodplains, Botswana

Heinl M[1], Sliva J[1], Tacheba B[2] & Murray-Hudson M[2]

[1] Chair of Vegetation Ecology, Technische Universitaet Muenchen (TUM),
Am Hochanger 6, D-85350 Freising-Weihenstephan, Germany
[2] Harry Oppenheimer Okavango Research Centre (HOORC), University of Botswana,
Private Bag 285, Maun, Botswana

(submitted to Journal of Tropical Ecology)

Vegetation response to fire frequency in the Okavango Delta floodplains, Botswana

Abstract. The aim of this study was to investigate how fire frequency affect (i) plant species composition and species richness, (ii) plant diversity and evenness on different spatial scales, (iii) vegetation structure and tree density on floodplains of the Okavango Delta wetland in Botswana, southern Africa. Based on flood and fire frequency data derived from a series of satellite images, active and drying floodplains were separated and study plots were selected with fire frequencies up to ten burns between 1989 and 2003. Both for drying and active floodplains no typical species assemblage could be associated to fire frequency and no variation in vegetation heterogeneity according to fire frequency could be determined. However, on active floodplains more plant species were encountered to be affected by fire frequency compared to drying floodplains. On drying floodplains, significantly lower values for cover and abundance of large trees were found on high fire frequency. It was therefore concluded that active and drying floodplains show clear differences in response to fire frequency. While active floodplains show no structural response, many species are affected by fire frequency and changes are in the dominance of certain species. On drying floodplains fire frequency shows no effect on species composition, but rather vegetation structure is affected by the burning.

Nomenclature: Arnold & De Wet (1993)

Introduction

Vegetation fires are considered natural phenomena in many parts of the world and are shaping the landscape for millennia across entire continents (Bond & van Wilgen 1996). Fire is hence a determinant of plant diversity and vegetation structure (Bond 1997; DeBano et al. 1998). As today anthropogenic burning became the leading ignition source (DeBano et al. 1998; Frost & Robertson 1985), the ecological impact of certain fire regimes is subject of intense discussions. Nevertheless, relatively few studies try to identify the effects of certain fire regimes on vegetation (e.g. Russell-Smith et al. 1998; Watson & Wardell-Johnson 2004; Uys et al. 2004) and many of these studies show conflicting results because of the variety of the investigated vegetation types and fire regimes. Therefore, given the interaction between people, fire and vegetation in most parts of the world, studies considering local fire regimes on certain vegetation types are required to fully understand the ecological implications of a specific burning regime (Uys et al. 2004; Bond & van Wilgen 1996).

The focus of the present study is on the effects of fire frequency on floodplains in the Okavango Delta wetland in Botswana in southern Africa. By taking this focus, interval-dependent effects on the vegetation were studied and event-dependent mechanisms related to fire season or fire intensity were ignored. Analyses by Heinl et al. (2005a), however, showed that most fires occur during the dry season, and low variance in the fire intensity is expected when regarding a single vegetation type only, e.g. floodplains. Thus, within the fire regime parameters of the study area, fire frequency was considered as the most relevant to the ecology of the study area.

Recent studies of grasslands in southern Africa and Australia have shown only minor effects of fire frequency on species composition due to the general dominance of fire-tolerant species and the loss of disturbance-intolerant species in the flora (Morgan 1999; Uys et al. 2004). This trend towards a disturbance-adapted vegetation can be expected for the fire-prone floodplains of the Okavango Delta, but studies on the vulnerability of wetland plants in particular to fire are sparse as the fire issue in wetlands has been largely ignored so far. Although these studies documented no difference in the overall species composition related to fire frequency, the patchiness of the spatial plant distribution or heterogeneity could be correlated to this parameter (Collins 1992; Walker & Peet 1983). Sites with low fire frequency and long inter-fire-intervals were found to be more heterogeneous than annually burnt sites and the effect of high fire frequency was to favour few dominant species with many accompanying species, leading to a more homogenous appearance of the sites (Bond & van Wilgen 1996).

The generally accepted trend of the structural response of vegetation to fire frequency is that the more frequent the fire, the greater the herbaceous component, and the less frequent the fire, the more abundant the woody component (Booysen & Tainton 1984). The suppression of woody species by high fire frequency is also described as the Gulliver effect (Higgins et al. 2000; Bond & van Wilgen 1996), with Gullivers being stunted multi-stemmed shrubs, which could come to dominance as adults but struggle to emerge from the herbaceous layer as juveniles because of regular fire-events in this layer. However, high fire frequency can also reduce the mortality of large trees due to lower fire intensity and therefore flame heights, because of lower amounts of accumulated fuel loads (Trollope 1980). According to these models, high fire frequency should lead to the occurrence of many small shrubs and few large and intermediate sized trees above the flame height. The present study investigates the vegetation response specifically to fire frequency and considers (i) species composition and species richness, (ii) plant diversity and evenness on different spatial scales, (iii) vegetation structure and tree density for drying and active floodplains of the Okavango Delta in Botswana.

Study area

The Okavango Delta in north-western Botswana, southern Africa, is a vast tropical wetland located in the centre of the Kalahari region. The wetlands of the world's largest RAMSAR site are supplied by the Okavango River, which has its catchment in the highlands of Angola. They form a mosaic of temporal, seasonal and permanent wetland habitats and drylands over an area of approximately 15000 km^2. The Okavango Delta is an alluvial fan with a very low gradient of roughly 1:3300 (McCarthy et al. 2000) divided by geological fault-lines into the northern Panhandle and the unconfined Fan in the southeast (Figure 1).

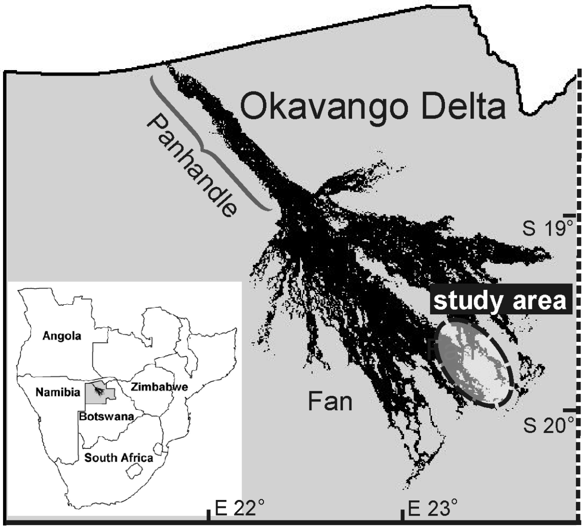


Figure 1. Location of the study area in the southern floodplains of the Okavango Delta wetland in northern Botswana.

The Panhandle region can be described as a permanent swamp, bounded by south-easterly striking fault lines, with water supply throughout the year. It is characterised by extensive mono-dominant *Cyperus papyrus* stands. With the drop of the confining fault-lines, the water of the Okavango River spreads and forms the Fan of the Okavango Delta. Because of the missing confinement, the intensity of the flooding decreases to the distal reaches, so that permanent swamps are replaced by seasonal swamps and floodplains.

The extent and duration of the flooding in the Okavango Delta show typically strong fluctuations. They are caused by variations in inflow of the Okavango River (app. 10^{10} m^3 mean annual inflow), which are related to rainfall patterns in the catchment and by the periodic summer rainfall over the Okavango Delta, occurring typically from October to April (app. 490 mm mean annual rainfall) (McCarthy et al. 2000). With the catchment of the Okavango River situated in Angola and a delayed inflow of these rainfalls of about three months, there is an out-of-phase correlation between inflow and precipitation for the Okavango Delta region. As both inflow and rainfall show high variability and seasonality, the Okavango Delta experiences extreme variations in the local water supply throughout the year, especially in the seasonally flooded areas. The consequence of these shifts in the annual water distribution is a small-scale pattern of temporal habitats and vegetation types, highly dependent on the flooding regime.

An extensive ecological zoning based on the flooding pattern of the Okavango Delta was done by SMEC (1989). According to the classification of this study, the focus area of the present research is comprised of floodplains characterised by being subject to inundation on a seasonal basis in some years, but not in most years or only during higher floods. These floodplains are basically dominated by grasses, with some sedges and occasionally woody species, but the specific species composition is highly dependent on the flooding regime inside the floodplain category. Wetter sections of the floodplains subject to longer and deeper floods are dominated by the tall sedges *Schoenoplectus corymbosus* and *Cyperus articulatus*, with the grasses *Oryza longistaminata* and *Leersia hexandra* on the floodplain fringes (Bonyongo et al. 2000). The occurrence of *Panicum repens* or *Setaria sphacellata* indicates lower flood intensities, and dry floodplain fringes are typically dominated by *Cynodon dactylon*. Occasionally flooded floodplains with single woody species (e.g. *Acacia* spec., *Combretum imberbe, Pechuel-loeschea leubnitziae*) are usually dominated by *Urochloa* spec., *Eragrostis* spec. or *Aristida* spec. (Ellery & Ellery 1997).

All these floodplains are subject to inundation on a seasonal basis and therefore also experience periods when they are dry and not inundated. These are the periods when the floodplains are most susceptible to fire. Recent studies showed a high correlation between flood frequency and fire frequency. Floodplains that get inundated about every second year show the highest fire frequency and a mean fire return interval of about five years, while both drier and wetter sections of the floodplains showed mean fire return intervals of about seven to eight years (Heinl et al. 2005b). Most of the fires in the Okavango Delta are thought to have an anthropogenic origin today (Cassidy 2003; Heinl et al. 2005a). The reasons for burning are various and include land clearing for cultivation, stimulating grass growth for grazing animals and hunting or to improve access to fishing grounds. Accidental fires may for example be caused by camp fires or fish-smoking. As these fires spread uncontrolled over the floodplains, they usually extend over many square kilometres.

The specific study sites for this research are situated in the southern floodplains of the Okavango Delta (Figure 1) in Wildlife Management Areas with no agricultural land use or livestock grazing. The study sites were chosen based on their flooding and fire regime.

Methods

The selection of specific study sites was based on the findings by Heinl et al. (2005b). Analyses of a series of 98 satellite images from 1989 until 2003 provided data on fire occurrences and inundated areas for the southern floodplains of the Okavango Delta. These data were used to identify target areas according to their fire and flood history.

The focus of the present research was on the effects of fire frequency on the floodplain vegetation. Therefore areas with a specific fire frequency needed to be determined and floodplains needed to be specified. For the present study, all areas that were recorded as flooded at least once during the investigated period from 1989 until 2003 were considered as floodplains (Heinl et al. 2005b). This definition is in line with SMEC (1989), characterising floodplains as subject to inundation on a seasonal basis or only during higher floods. However, the category still consists of a high variety of habitats dependent on a flood frequency gradient, and includes almost permanently inundated regions as well as areas that were not flooded for more than 10 years. To accommodate this gradient, the study sites were further subdivided into drying floodplains and active floodplains based on flood frequency data.

For the selection of specific sites, in addition to the flood frequency, the time elapsed since the last flood and since the last fire were considered. This led to the identification of comparable study sites and allowed to assign differences in the vegetation more clearly to the fire frequency.

Based on these criteria, study sites were selected on drying and active floodplains according to the following characteristics:

- sites on drying floodplains – floodplains not inundated after 1992, but flooded at least once between 1989 and 1992 (drying floodplains); burned in 2000, but not after 2000;

- sites on active floodplains – floodplains flooded at least every second year (active floodplains); flooded and burned in 2003, but not after 2003.

The specific threshold values (years) for the criteria were needed to establish a set of study sites with exactly the same flood history and time since last fire for each floodplain type, while covering a wide range of fire frequencies. Both the sites on drying and on active floodplains include areas with fire frequencies from 0 to 10 burns between 1989 and 2003. For comparative vegetation analyses, the fire frequency was grouped into three fire frequency classes, with low fire frequency (0-2 burns between 1989 and 2003), mid fire frequency (3-5 burns between 1989 and 2003) and high fire frequency (6-10 burns between 1989 and 2003).

The vegetation survey was performed in February 2004. A total number of 169 plots at 29 study sites were investigated, with at least 4 sample plots on each site. The sample plots were selected randomly within the study sites of about 2 ha each. On active floodplains, in total 95 plots (at 14 sites) were sampled, with 33 plots (5 sites) in high fire frequency areas, 16 plots (3 sites) in mid fire frequency and 46 plots (6 sites) in low fire frequency. On drying floodplains, 74 plots (15 sites) were sampled, with 25 plots (5 sites) in high fire frequency, 24 plots (5 sites) in mid fire frequency and 25 plots (5 sites) in low fire frequency areas.

For each plot (10 m x 20 m; longer side set parallel to the contour line) cover and abundance were measured for each woody species as well as for three height layers: tree layer S (all woody species <1.5 m), tree layer M (1.5 m – 3.0 m), tree layer L (> 3.0 m).

In one corner of each plot, a quadratic 4 m^2 subplot was investigated, for which all species and their cover after Londo (1984) were recorded. Biomass data for the investigated subplots were provided by Rutz (2004).

Statistical analyses were done using PC-Ord 4.26, SPSS 12.0 and R (R, 2004). The nonparametric Mann-Whitney-Test (U-test) and additional Generalised Linear Models (GLM) were used for assessing the significance of differences in the investigated parameters (e.g. species number) related to fire frequency.

Results

Fire frequency and species assemblage

The separation of the study area into active and drying floodplains and the selection of the study sites was based solely on flood and fire frequency data derived from satellite images, with the intention of subdividing the broad class ‘floodplain’ into two more homogenous habitats. The utility of this a priori approach was tested by using detrended correspondence analysis (DCA).

Additionally, the importance of flood and fire frequency as environmental variables for the species assemblage, and hence the relevance of the subdivision of 'floodplains' on this basis, was investigated. Only the data on species cover collected on the subplots were used for the analyses. The DCA showed a clear separation of the subplots on active and drying floodplains according to the species cover values (Figure 2). The investigated subplots were grouped along a flood frequency gradient (first axis) with no overlap. Compared to the flooding, the fire frequency played a marginal role for the species assemblage. The separation of the floodplains into active and drying habitats was shown to be useful and relevant to the posed research question.

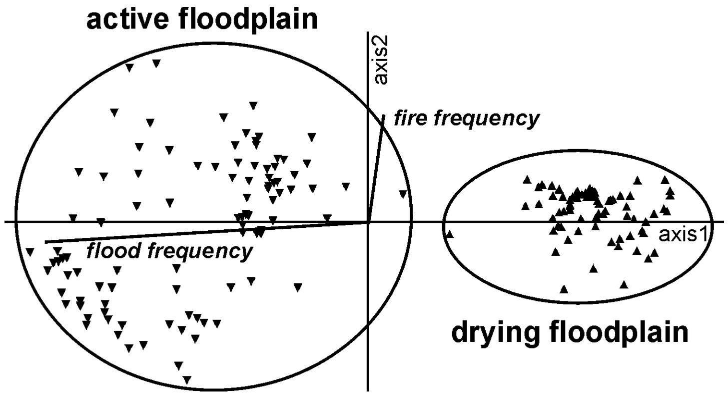


Figure 2. Detrended Correspondence Analysis (DCA-biplot) of the investigated plots on active and drying floodplains. The flood frequency shows a high correlation with the first axis (r^2=0.902), with the first axis explaining 42.0 % of the variance in the data. Fire frequency shows only a weak correlation to the second axis (r^2=0.215), with the second axis explaining only 4.4 % of the variance in the data.

Further DCA were carried out separately for the study subplots on drying and active floodplains to investigate the relevance of fire and flood frequency for the species assemblage. For drying floodplains neither the flood frequency nor the fire frequency showed a significant effect on the species assemblage (Figure 3). The gradient that is represented by the species grouped along the first axis is therefore difficult to assess, especially without further secondary environmental variables. But information from literature on the ecology of the species (Gibbs-Russell et al. 1990, Oudtshoorn 1999) indicate that most likely soil texture and soil moisture are responsible for the species assemblage, with *Eragrostis rigidior*, *Panicum repens* or *Cyperus esculentus* representing species on moist, loamy sites (left side on Figure 3) and *Chloris virgata*, *Melinis repens* or *Eragrostis viscosa* representing species on dry sandy soils (right side on Figure 3).

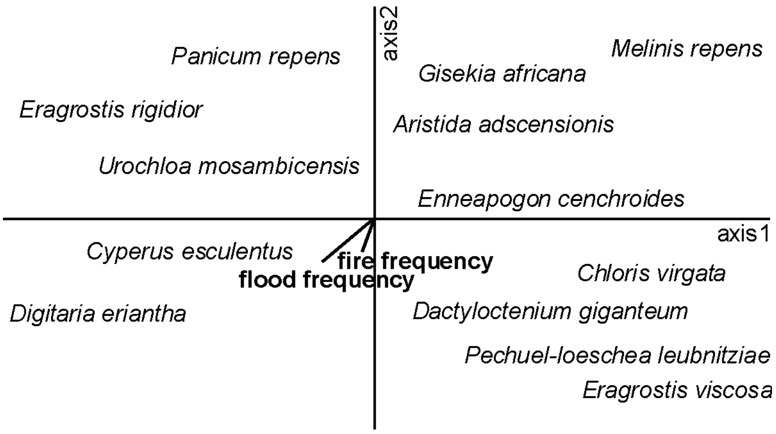


Figure 3. Detrended Correspondence Analysis (DCA-biplot) showing the distribution of selected species on drying floodplains. The flood frequency and the fire frequency show a very low correlation with the axes (r^2=0.085 and r^2=0.067, respectively), with the first axis explaining 41.8 % and the second axis 12.0 % of the variance in the data.

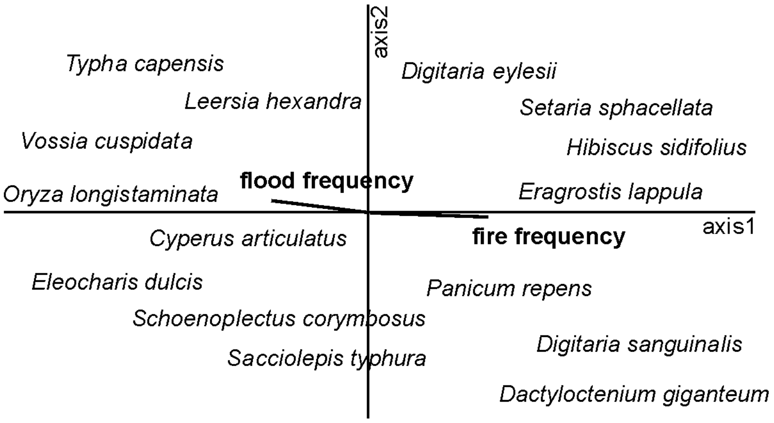


Figure 4. Detrended Correspondence Analysis (DCA-biplot) showing the distribution of selected species on active floodplains. The flood frequency and the fire frequency show a slight correlation with the first axis (r^2=0.282 and r^2=0.341, respectively), with the first axis explaining 50.4 % and the second axis 10.5 % of the variance in the data.

On active floodplains, the species were grouped both along a flood frequency and a fire frequency gradient on the first axis (Figure 4). The negative correlation found between fire frequency and flood frequency on active floodplains, which is due to fire suppression by the flooding, has been documented in previous studies (Heinl et al. 2005b).

Therefore, the effects of fire frequency on the species assemblage on active floodplains cannot clearly be separated from the effects of the flood frequency. But when analysing the species representing this gradient and their ecology, an obvious separation of species from drier and wetter habitats can be determined, with for example *Typha capensis*, *Vossia cuspidata* or *Oryza longistaminata* representing the wet wing (left side on Figure 4) and *Eragrostis lehmanniana*, *Hibiscus sidifolius* or *Dactyloctenium giganteum* representing the dry wing (right side on Figure 4). The species assemblage on active floodplains is therefore obviously determined by the flood frequency, while the fire frequency is in principle simply negatively correlated to the flood frequency.

According to the DCA, no typical species assemblages could be associated with fire frequency, either for drying or for active floodplains. The major environmental variable that determines the vegetation of the floodplains is most likely the water availability, while the fire frequency is expected to rather affect individual species or vegetation structure.

Fire frequency and species composition

Within the investigated subplots, a total number of 112 plant species were recorded, of which 82 could be identified. On drying floodplains 50 species were recorded, while on active floodplains 79 species were encountered. The active floodplains therefore showed higher plant species numbers than drying floodplains, however more sample plots were considered for active (95) compared to drying floodplains (74). Species numbers per plot were not significantly different for active and drying floodplains and the mean number of species was 7.5 and 6.9, respectively.

The species composition occurring on drying floodplains differed clearly from that on active floodplains. Indicator values for each species were determined by calculating the difference between the number of plots with a species record on active and drying floodplains, to show their principle occurrence on the floodplain habitats and to document their abundance (Table 1). Almost all species were clearly assignable either to drying or to active floodplains, and only few species like *Panicum repens* or *Digitaria eriantha* occurred significantly on both floodplain habitats. Most abundant species on drying floodplains, found on more than every third plot, were *Urochloa mosambicensis*, *Tragus berterionanus*, *Gisekia africana*, *Enneapogon cenchroides*, *Vernonia glabra*, *Chloris virgata* and *Melinis repens*. Species most abundant on active floodplains were *Schoenoplectus corymbosus*, *Eragrostis lappula*, *Panicum repens*, *Cyperus articulatus*, *Leersia hexandra*, *Cyperus denudatus* and *Setaria sphacellata*. The species composition found on active and drying floodplains can therefore be used to characterise the two habitats as significantly different and require separate analyses of these floodplain habitats.

Table 1. Identified species with the number of records on drying floodplains (FQd) and active floodplains (FQa), sorted by indicator value. The indicator value is calculated as the difference between the number of plots on which the species occurred on FQa and FQd. Negative indicator values document a principle occurrence on active floodplains, positive values document the occurrence on drying floodplains. The response to high fire frequency is indicated as positive (+) or negative (-) with the significance (* p<0.05; ** p<0.005; *** p<0.001; n.s. not significant). Superscript letters indicate either fire frequency (^{F}) or flood frequency (^{W}) as the expected determining environmental parameter for the species cover on active floodplains after GLM.

species	number of records for FQd	number of records for FQa	indicator value	response to high fire frequency
Schoenoplectus corymbosus	0	68	-68	n.s.
Eragrostis lappula^{F}	0	51	-51	+ ***
Panicum repens^{W}	7	55	-48	+ ***
Cyperus articulatus^{F}	0	45	-45	- ***
Leersia hexandra^{W}	0	45	-45	- ***
Cyperus denudatus^{F}	0	42	-42	+ ***
Setaria sphacellata^{F}	0	33	-33	+ ***
Sacciolepis typhura	0	29	-29	n.s.
Oryza longistaminata^{W}	0	26	-26	- ***
Acroceras macrum	0	25	-25	n.s.
Eleocharis dulcis^{W}	0	23	-23	- ***
Oldenlandia corymbosa^{F}	0	21	-21	- **
Rhynchospora holoschoenoides	0	19	-19	n.s.
Eclipta prostrata^{F}	0	18	-18	- ***
Ludwigia stolonifera^{W}	0	18	-18	- ***
Fymbristylis complanata	0	16	-16	n.s.
Miscanthus junceus	0	12	-12	n.s.
Althernanthera sessilis^{W}	0	11	-11	- **
Kyllinga erecta^{F}	0	9	-9	- *
Digitaria eylesii	0	8	-8	n.s.
Echinochloa jubata	0	8	-8	n.s.
Sphaeranthus flexuosus	0	6	-6	n.s.
Paspalum scrobiculatum^{W}	0	5	-5	+ *
Persicaria limbatum	0	5	-5	n.s.
Potamogeton thunbergii	0	5	-5	n.s.
Sida cordifolia	0	5	-5	n.s.
Sopubia mannii^{F}	0	5	-5	+ *
Crotolaria spec	1	5	-4	n.s.
Nymphoides indica	0	4	-4	n.s.
Crotolaria sphaerocarpa	0	3	-3	n.s.
Cyperus esculentus	2	5	-3	n.s.
Hibiscus sidiformis	0	3	-3	n.s.
Amaranthus thunbergii	0	2	-2	n.s.
Cyperus longus	0	2	-2	n.s.
Digitaria sanguinalis	0	2	-2	n.s.
Echinochloa stagnina	0	2	-2	n.s.
Fuirena stricta	0	2	-2	n.s.
Heliotropium ovalifolium	0	2	-2	n.s.
Ludwigia leptocarpa	0	2	-2	n.s.
Typha capensis	0	2	-2	n.s.
Zygnium tubulosum	0	2	-2	n.s.
Species (cont.)				
Eragrostis lehmanniana	0	1	-1	n.s.
Evolvolus alsanoides	0	1	-1	n.s.
Fuirena phylliformis	0	1	-1	n.s.
Gomphocarpus fruticosus	0	1	-1	n.s.
Sesbania microphylla	0	1	-1	n.s.
Sesbania sesban	0	1	-1	n.s.
Thephrosia spec.	0	1	-1	n.s.
Vossia cuspidata	0	1	-1	n.s.
Acacia erioloba	1	1	0	n.s.
Eragrostis viscosa	1	0	1	n.s.
Lonchocarpus capassa	1	0	1	n.s.
Nidorella residifolia	2	1	1	n.s.
Schmidtia pappophoroides	1	0	1	n.s.
Cholophospermum mopane	3	1	2	n.s.
Digitaria eriantha	15	13	2	- *
Pogonarthria squarrosa	2	0	2	n.s.
Sesamum triphyllum	3	1	2	n.s.
Combretum imberbe	3	0	3	n.s.
Dactyloctenium aegyptium	3	0	3	n.s.
Eragrostis cilianensis	3	0	3	n.s.
Cenchrus ciliaris	4	0	4	n.s.
Hibiscus calyphyllos	5	0	5	n.s.
Aristida adscensionis	7	0	7	n.s.
Aristida stipitata	7	0	7	n.s.
Ipomea coptica	8	1	7	+ *
Corchorus triocularis	16	7	9	n.s.
Eragrostis rigidior	9	0	9	n.s.
Eragrostis trichophora	10	0	10	n.s.
Aristida stipoides	13	0	13	n.s.
Cynodon dactylon	16	1	15	- ***
Dactyloctenium giganteum	17	1	16	+ *
Indigofera tinctoria/spec.	20	2	18	n.s.
Stipagrostis uniplumis	18	0	18	n.s.
Pechuel-loeschea leubnitziae	19	0	19	n.s.
Melinis repens	25	0	25	n.s.
Chloris virgata	27	0	27	n.s.
Vernonia glabra	31	2	29	n.s.
Enneapogon cenchroides	30	0	30	n.s.
Gisekia africana	33	1	32	+ *
Tragus berterionanus	57	1	56	n.s.
Urochloa mosambicensis	66	1	65	n.s.

The statistical analyses (U-test) on species cover in relation to fire frequency revealed a significant response to the burning for certain species (Table 1). On active floodplains more species were found to be significantly affected by fire frequency than on drying floodplains, both positively and negatively, indicating a higher sensitivity to burning of species occurring on the active floodplains (Table 2). For drying floodplains *Cynodon dactylon* showed significantly lower cover values with high fire frequency. On active floodplains *Eclipta prostrata*, *Eleocharis dulcis* and *Ludwigia stolonifera* were only found on low and mid fire frequency and *Leersia hexandra, Cyperus articulatus* and *Oryza longistaminata* similarly showed extremely low cover and abundance values on plots with high fire frequency. Species with higher cover values on high fire frequency were *Cyperus denudatus*, *Eragrostis lappula*, *Panicum repens* and *Setaria sphacellata*. As for active floodplains a negative correlation between fire and flood frequency was encountered, these significant differences in species cover could not be clearly assigned to fire frequency. Therefore, a generalised linear model (GLM) with Poisson errors was used for these species to test further whether fire or flood frequency explains more variance in the data. The results indicate that for *Cyperus articulatus, Eclipta prostrata, Cyperus denudatus, Eragrostis lappula* and *Setaria sphacellata*, fire frequency rather than flood frequency is the determining factor for the cover values of these species.

Table 2. Mean cover values and number of occurrences in plots of selected species with highly significant response ($P<0.001$) to fire frequency. The superscript letters indicate either fire frequency (^{F}) or flood frequency (^{W}) as the expected determining environmental parameter for the species cover on active floodplains after generalised linear models (GLM).

	mean cover value (number of plots) at		
	low	mid	high
		fire frequency	
drying floodplains			
Cynodon dactylon	4.5 (11)	1.5 (4)	0.2 (1)
active floodplains			
Cyperus articulatus ^{F}	7.9 (30)	3.3 (10)	0.3 (5)
Eclipta prostrata ^{F}	3.0 (15)	0.3 (3)	- (0)
Eleocharis dulcis ^{W}	5.0 (17)	2.2 (6)	- (0)
Leersia hexandra ^{W}	17.0 (29)	16.4 (13)	1.3 (3)
Ludwigia stolonifera ^{W}	1.5 (17)	0.3 (1)	- (0)
Oryza longistaminata ^{W}	11.4 (18)	4.6 (7)	0.3 (1)
Cyperus denudatus ^{F}	0.6 (8)	1.2 (8)	3.3 (26)
Eragrostis lappula ^{F}	5.7 (14)	3.0 (7)	14.4 (30)
Panicum repens ^{W}	5.5 (17)	8.3 (9)	11.0 (29)
Setaria sphacellata ^{F}	1.4 (8)	0.3 (1)	7.5 (24)

Comparing absolute cover values, species favoured at high fire frequency (e.g. *Cyperus denudatus*, *Eragrostis lappula*) did not show the extremely low cover values at low fire frequency as were found for e.g. *Eclipta prostrata* or *Cyperus articulatus* at high fire frequency. Low and mid fire frequency on active floodplains therefore seem to support more species than high fire frequency, as individual species seem to get suppressed or drop out with too frequent burning. However, statistical analyses of the species numbers both on active and drying floodplains showed no significant differences for low and high fire frequency.

Fire frequency and vegetation heterogeneity

To assess differences in the spatial heterogeneity and species diversity related to the fire frequency, the Shannon-Weaver index of diversity and evenness were calculated (Shannon & Weaver 1949; Ludwig & Reynolds 1988). The indices were calculated for all subplots on drying and active floodplains. Additionally, to investigate the diversity and heterogeneity on a larger scale, the mean values of species found for all subplots on one site were used to characterise the sites according to diversity and evenness.

The statistical analyses (U-test) for comparing high and low fire frequency both on plots and sites for drying and active floodplains showed no significant differences in either diversity or evenness. Therefore, no variation in the vegetation heterogeneity according to fire frequency could be determined.

Fire frequency and vegetation structure

On active floodplains, only the structural response of the herbaceous layer was investigated, as no woody species occurred on plots on active floodplains because of frequent flood events. The active floodplains showed significantly higher mean cover values of the herbaceous vegetation for low fire frequency and also higher aboveground biomass values, both for living and dead material. This indicates a negative impact of high fire frequency on the biomass production and vegetation cover. However, as fire frequency and flood frequency were shown to be negatively correlated to each other for active floodplains, it is expected that higher cover and biomass values are due to high flood frequency instead of low fire frequency. These findings were supported by results of GLM analyses. A clear trend towards a negative impact of high fire frequency on vegetation structure could therefore not be derived for the active floodplains.

On drying floodplains, significant response of the vegetation structure to fire frequency was found for woody species. At high fire frequency a significantly lower number of woody species were found, as well as lower cover and abundance values for large trees (tree layer L). Cover values of *Combretum imberbe* also showed a significant negative response to high fire frequency. The data therefore imply a negative impact of high fire frequency on the occurrence of larger trees on drying floodplains.

Discussion

Vegetation response to fire frequency on active floodplains

Detrended correspondence analysis (DCA) of the study plots on active floodplains based on the species cover indicated a gradient for both the flood and the fire frequency along the first axis (cf. Figure 4). Since the flood frequency was shown to determine the species assemblage on active floodplains, the vegetation structure is also expected to be influenced primarily by the flood frequency. The higher biomass production and vegetation cover found on plots with low fire frequency is therefore more likely due to the associated high flood frequency. The better and more regular water supply on these high flood frequency sites simply supports more vegetation growth (Rutz 2004). Hence, it can be concluded that species assemblage and vegetation structure on active floodplains are in principle determined by the flood frequency. Due to an observed negative correlation between fire- and flood frequency, also the fire frequency can be correlated with the species assemblage and structure, but is most likely not affecting them significantly.

However, analyses of the cover values revealed for some species a highly significant decline on high or low fire frequency, indicating an impact of fire frequency on specific species (Table 2). While species like *Cyperus articulatus* or *Eclipta prostrata* have highest cover and abundance values at low fire frequency and are almost not present at high fire frequency, *Setaria sphacellata*, *Eragrostis lappula* or *Cyperus denudatus* show higher cover values at high fire frequency. This suggests that certain species are suppressed and others are favoured by high fire frequency. But it is noteworthy that the species favoured by high fire frequency still exhibit high cover and abundance values at low fire frequency, while the species favoured by low fire frequency are almost not present at high fire frequency. Low fire frequency therefore seems to support more species with more even cover values, while at high fire frequency certain fire-sensitive species are suppressed and other species are favoured and achieve higher cover values. High fire frequency should therefore lead to more homogenous sites with few dominant species, like *Setaria sphacellata* or *Eragrostis lappula*, accompanied by other species with low cover values, while low fire frequency results in more heterogeneous sites with medium cover values for most occurring species. Recent studies elsewhere support these findings (Collins 1992; Walker & Peet 1983; Bond & van Wilgen 1996).

As the number of species significantly affected by fire frequency on active floodplains is low (Table 2) and as almost none of the species appear at low or high frequency only, no shifts in the species composition are observable and also no significant difference in diversity or evenness can be ascribed to fire frequency. The main effect of high fire frequency on active floodplains is therefore a shift in the dominance of a few specific species and a slight reduction in heterogeneity.

Vegetation response to fire frequency on drying floodplains

In contrast to active floodplains, the DCA of the study plots on drying floodplains based on the species cover indicates neither a flood nor a fire frequency gradient in the data (cf. Figure 3). Hence, no significant effect of fire frequency on the species assemblage could be detected. The overall missing effect of fire frequency on species cover on drying floodplains is most likely due to their adaptation to frequent fires as typical savanna species.

Significant effects of fire frequency on individual species could only be determined for *Cynodon dactylon* on drying floodplains, with higher cover values on low fire frequency (Table 2). Although the ability of *Cynodon dactylon* to reproduce from rhizomes generally enables it to survive most fires, the response to burning is documented to vary with moisture conditions and nutrient levels (Carey 1995). Since *Cynodon dactylon* requires a minimum of 410 mm of rainfall or surface water, the specific negative response of *Cynodon dactylon* to high fire frequency might be influenced by water stress on drying floodplains in combination with relatively low rainfall and high evapotranspiration rates.

The main response of drying floodplains to fire frequency was found for cover and abundance of woody species. Generally, the abundance of woody species reflects a high tree mortality for all fire frequency classes with time (Figure 5). Large trees (tree layer L) account for only about one tenth of the abundance of small trees (tree layer S), independent of fire frequency. However, significantly lower abundance values for larger trees under high fire frequency compared to low fire frequency suggest a higher tree mortality on high fire frequency.

In contrast to the almost parallel decline of the abundance of woody species with size through all fire frequency classes, the cover values differ clearly between high fire frequency and the other fire frequency classes (Figure 5). For small trees (tree layer S) higher cover values are observed at high fire frequency compared to mid and low fire frequency. As abundance values are almost similar through all fire frequency classes, small woody species at high fire frequency tend to have higher cover values per individual than at other fire frequency. This wider growth of small woody species under high fire frequency is most likely due to lateral, basal regrowth after frequent disturbance events like fire. The ability of basal resprouting can be observed frequently in the study area, in particular for *Colophospermum mopane* and *Pechuel-loeschea leubnitziae*, the most common woody species in the study area (Heinl, pers. obs.). In contrast to small woody species, larger trees (tree layer L) show comparatively low cover values at high fire frequency (Figure 5). In combination with the low abundance values for larger trees at high fire frequency, an overall negative impact of high fire frequency on large trees is indicated. However, it is suggested that high fire frequency is not responsible for killing large trees, as flame heights of a burning grass layer are usually too small, but rather suppresses the recruitment of small individuals to the canopy layer.

These findings are very much in line with the phenomenon described as the Gulliver effect (Higgins et al. 2000; Bond & van Wilgen 1996). Regular fires in the grass layer lead to a constant defoliation of small trees inside the grass layer and induce a lateral, basal regrowth that is responsible for higher cover values of these trees. The higher the fire frequency, the more difficult it is then for these woody species to emerge and to escape from the fire. Therefore large trees are scarce under high fire frequency.

In addition to these findings of a negative impact of high fire frequency on larger trees, significantly fewer woody species numbers were recorded at high fire frequency and a significant decline of *Combretum imberbe* was observed. The high fire frequency, with fires occurring more than every third year, is therefore considered as too high to sustain a diverse savanna structure on drying floodplains in the Okavango Delta.

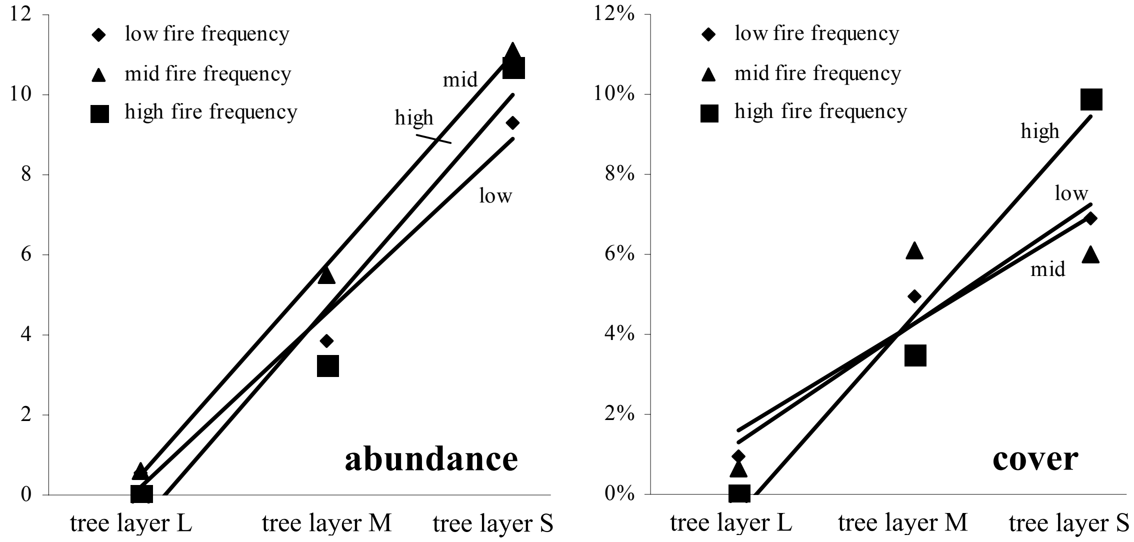


Figure 5. Mean abundance and cover values of the investigated tree layers S (small), M (medium) and L (large) on drying floodplains.

Conclusion

The results presented show clear differences between active and drying floodplain vegetation in response to fire frequency. While the vegetation on active floodplains showed no structural response, many species seem to be affected by fire frequency and changes in the dominance for certain species could be detected. Further studies and analyses on the effects of fire specifically on wetland plants are required to assess comprehensively their response to fire and to be able to evaluate certain fire regimes in the scope of wetland conservation and management.

On drying floodplains, the effects of fire frequency on species composition seem to be marginal and instead, vegetation structure is affected by burning. As especially large trees are negatively affected by high fire frequency, fire regimes should be reconceived in some areas to secure these valuable resources for humans and wildlife.

Acknowledgement

The studies were conducted in the scope of the project “Fire regime and vegetation response in the Okavango Delta, Botswana” financed by Volkswagen Foundation, Germany with support from Conservation International Botswana, Okavango Program. Special thanks to all staff from the Harry Oppenheimer Okavango Research Centre in Maun and to Prof. George Bredenkamp (University of Pretoria), Prof. Joerg Pfadenhauer and Dr. Steven Higgins (both Technische Universitaet Muenchen) for scientific support.

References

Arnold TH & De Wet BC (1993): Plants of Southern Africa: Names and Distribution. Memories of the Botanical Survey of South Africa No. 62; Botanical Research Institute, Pretoria.

Bond WJ (1997): Fire. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge, p. 421-446.

Bond WJ & van Wilgen BW (1996): Fire and Plants. Population and Community Biology Series 14, Chapman & Hall, London, UK.

Bonyongo MC, Bredenkamp GJ & Veenendaal E (2000): Floodplain vegetation in the Nxaraga Lagoon area, Okavango Delta, Botswana. South African Journal of Botany 66: 15-21.

Booysen PdV & Tainton NM (1984): Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48, Springer-Verlag, Berlin.

Carey JH (1995): Cynodon dactylon. In: Fire Effects Information System, [Online], U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2004, December 30].

Cassidy L (2003): Anthropogenic burning in the Okavango Panhandle of Botswana: Livelihoods and spatial dimensions. Unpublished M.Sc.Thesis, University of Florida

Collins SL (1992): Heterogeneity of disturbed tallgrass prairie communities. Ecology 73: 2001-2006.

DeBano LF, Neary DG & Folliott PF (1998): Fire's Effects on Ecosystems. Wiley and Sons, Inc., New York.

Ellery K & Ellery W (1997): Plants of the Okavango Delta - A Field Guide. Tsaro Publishers, Dalbridge.

Frost PGH & Robertson F (1985): The ecological effects of fire in savannas. In: Walker B (ed.) *Determinants of Tropical Savannas*, IRL Press Limited, Oxford, UK. Oxford, p. 93-140.

Gibbs-Russell GE, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM & Dallwitz MJ (1990): Grasses of Southern Africa. Memoirs of the Botanical Survey of South Africa, No. 58, National Botanical Institute, Pretoria.

Heinl M, Frost P, Vanderpost C & Sliva J (2005a): Fire activity on floodplains and drylands in the Okavango Delta, Botswana (accepted for publication by Journal of Arid Environments; *Chapter 4*).

Heinl M, Neuenschwander A, Sliva J & Vanderpost C (2005b): Interactions between fire and flooding in the Okavango Delta floodplains, Botswana (accepted for publication by Landscape Ecology; *Chapter 3)*.

Higgins SI, Bond WJ & Trollope WSW (2000): Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88: 213-229.

Londo G (1984): The decimal scale for relevés of permanent quadrats. In: Knapp R (ed.): Sampling methods and taxon analysis in vegetation science, Handbook of Vegetation Science (4), Junk Publishers, The Hague, p. 45-49.

Ludwig JA & Reynolds JF (1988): Statistical ecology. Wiley-Interscience Publication, New York

McCarthy TS, Cooper GRJ, Tyson RD & Ellery WN (2000): Seasonal flooding in the Okavango Delta, Botswana - recent history and future prospects. South African Journal of Science 96: 25-32.

Morgan JW (1999): Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology 144: 127-144.

Oudtshoorn Fv (1999): Guide to Grasses of Southern Africa, Briza Publications.

Russell-Smith J, Ryan PG, Klessa D, Waight G & Harwood R (1998): Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. Journal of Applied Ecology 35: 829-846.

Rutz D (2004): The influence of fire on site productivity in southern Africa (Study site: Okavango Delta, Botswana). MSc-Thesis at Chair of Vegetation Ecology, Technische Universitaet Muenchen (unpubl.).

Shannon CE & Weaver W (1949): The mathematical theory of communication. University Illinios Press, Urbana, IL.

SMEC (1989): Ecological Zoning Okavango Delta, Final Report, Volume I - Main report. Snowy Mountains Engineering Corporation, Cooma NSW Australia.

Trollope LA (1980): Controlling bush encroachment with fire in the savanna area of South Africa. Proceedings of the Grassland Society of South Africa 15: 173-177.

Uys GU, Bond WJ & Everson TM (2004): The effect of different fire regimes on plant diversity in southern African grassalnds. Biological Conservation 118: 489-499.

Walker J & Peet RK (1983): Composition and species diversity of pine-wiregrass savannas of the Greenswamp. Vegetatio 55: 163-179.

Watson P & Wardell-Johnson G (2004): Fire frequency and time-since-fire effects on the open-forest and woodland of Girraween National Park, south-east Queensland, Australia. Australian Journal of Ecology 29: 225-236.

Chapter 6

Changes in plant species diversity and vegetation structure with time-since-fire on drying floodplains in the Okavango Delta wetland, Botswana

Heinl M[1], Sliva J[1], Murray-Hudson M[2] & Tacheba B[2]

[1] Chair of Vegetation Ecology, Technische Universitaet Muenchen (TUM),
Am Hochanger 6, D-85350 Freising-Weihenstephan, Germany
[2] Harry Oppenheimer Okavango Research Centre (HOORC), University of Botswana,
Private Bag 285, Maun, Botswana

(submitted to Basic and Applied Ecology)

Changes in plant species diversity and vegetation structure with time-since-fire on drying floodplains in the Okavango Delta wetland, Botswana

Abstract. Drying floodplains that were not inundated for more than 10 years were investigated to determine changes in plant species diversity and vegetation structure with time-since-fire for the southern Okavango Delta wetland in Botswana. The study sites were chosen to represent areas with 2, 4, 6, 8, 10 and 12 years without a fire. Maximum species diversity was found 4 years and 12 years after the fire-event, while species numbers were lowest 6 and 8 years after the fire. These changes in species numbers with time-since-fire could be associated firstly with the conditions of a post-fire environment, which usually supports high species numbers due to open space and little competition, secondly with the dominance of competitive perennial grasses, especially *Urochloa mosambicensis*, which suppresses the occurrence of other species after 6 to 8 years and thirdly with the enhanced establishment of woody species after about 10 years, creating new habitats for species growing in the vicinity of these shrubs. As highest species numbers were found for short and for long inter-fire-intervals, and different species occurred shortly after the fire-event and at late stages of the post-fire succession, a variety of different inter-fire-intervals is expected to be important for sustaining plant species diversity on drying floodplains in the Okavango Delta.

Nomenclature: Arnold & De Wet (1993)

Introduction

Vegetation fires are common phenomena in almost all parts of southern Africa and are considered determinants of vegetation structure and plant diversity in a multitude of different landscapes (Bond & van Wilgen 1996; DeBano et al. 1998). The specific impact of fire varies with the fire regime and the vegetation type affected.

A combination of fire frequency, fire intensity and the season of the occurrence of the fire are usually considered as constituting fire regime. These fire parameters describe in principle how hard the vegetation is 'hit' by the fire. The maximum temperatures reached and their duration during the fire, state of dormancy of grasses or foliation of trees and the stage of the plant species in their life-history very much determine the severity of the impact on the vegetation by the fire (Booysen & Tainton 1984; Bond & van Wilgen 1996; Andersen et al. 1998; Bond 1997). This approach can in principle be used to predict the state of the vegetation immediately after the fire occurrence, assessing survival and mortality of specific plants by the fire parameters. Succession after fire is very much determined by the survival of the fire-event by specific species and the post-fire condition. They determine the 'starting point' after the disturbance event. But the influence of the fire intensity, fire season (event-dependent effects) and fire frequency (interval-dependent effects) on vegetation become less pronounced with increasing elapsed time since the last fire and the determinants of successional pathways should change from fire-event-dependent or fire-interval-dependent to density-dependent with time (Bond & van Wilgen 1996).

Assessing vegetation changes in a time-since-fire framework investigates the successional development after the fire, but does not consider either the fire-event or the length of the inter-fire interval (Morrison et al. 1995). The changes in the vegetation during the years are therefore expected to reflect a typical development between two fire-events for the investigated vegetation type. Therefore, while working with fire regimes produces a rather static picture of the vegetation according to a recurring disturbance regime, assessing vegetation response to time-since-fire analyses the changes and development between these disturbance-events.

Post-fire succession is determined not only by the fire regime but is complicated by numerous other factors, such as pre-fire species composition and vegetation structure, weather patterns or herbivory. The specific change of certain communities with time-since-fire is therefore not predictable and differs clearly from site to site. The present study therefore focuses on the determination of general trends in the succession after fire, related to vegetation structure and species attributes rather than on species assemblages and plant communities. The aim of this study is therefore not only to enhance the understanding of the post-fire succession on drylands in the

Okavango Delta, but also to provide general insight into successional pathways for savanna habitats in southern Africa after fire.

Study area

The Okavango Delta in northern Botswana is a large tropical wetland located in the centre of the Kalahari region. The world's largest RAMSAR site is supplied by the Okavango River and consists of a mosaic of temporary, seasonal and permanent wetland habitats and drylands over an area of approximately 15000 km^2. The Okavango Delta is an alluvial fan with a very low gradient of roughly 1:3300 (McCarthy et al. 2000) divided by geological fault-lines into the northern Panhandle and the unconfined Fan in the southeast (Figure 1). The Panhandle region can be described as a permanent swamp, with water supply throughout the year. It is characterised by extensive mono-dominant *Cyperus papyrus* stands. With the drop of confining fault-lines, the water of the Okavango River spreads and forms the Fan of the Okavango Delta. The intensity of the flooding decreases towards the distal reaches of the Fan, so that this area is characterised by seasonal swamps, floodplains and drylands.

The focus of the present study is on drying floodplains of the Okavango Delta, which are today basically unaffected by floodwaters or only inundated during years with extremely high floods. While active floodplains are in principle dominated by sedges like *Schoenoplectus corymbosus* and *Cyperus articulatus*, these drier habitats are usually characterised by grasses, mainly *Urochloa* spec., *Eragrostis* spec. or *Aristida* spec. The irregular flooding allows also woody species to establish (e.g. *Acacia* spec., *Combretum imberbe*, *Pechuel-loeschea leubnitziae, Colophospermum mopane*) (Ellery & Ellery 1997).

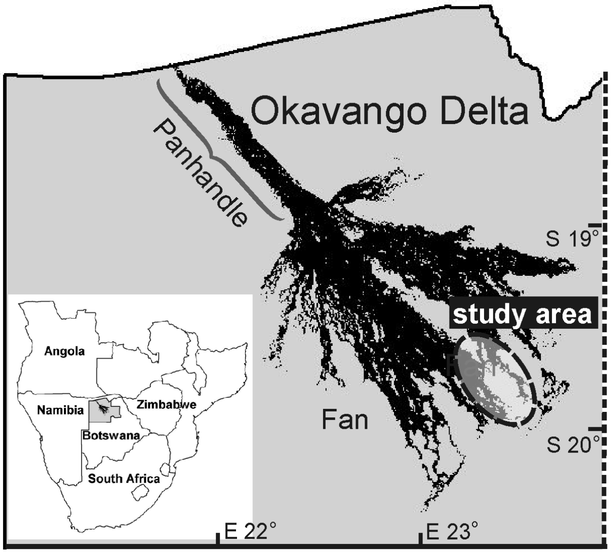


Figure 1. Location of the study area in the southern floodplains of the Okavango Delta wetland in northern Botswana.

All these habitats are susceptible to fire, especially during the dry season with the highest fire activity around September (Heinl et al. 2005a). Recent studies have shown mean fire return intervals for drying floodplains of about seven to eight years (Heinl et al. 2005b). Most of the fires in the Okavango Delta are thought to have an anthropogenic origin today (Cassidy 2003). The reasons for burning are various and include land clearing for cultivation, stimulating grass growth for grazing animals and hunting or to improve access to fishing grounds. Accidental fires are for example caused by camp fires or fish-smoking.

The specific study sites for this research are situated on typical savanna habitats in drying floodplains of the southern Okavango Delta (Figure 1) in Wildlife Management Areas with no agricultural land use or livestock grazing. The study sites were chosen based on their flood history and the elapsed time since the last fire.

Methods

The selection of specific study sites was based on previous studies on the fire and flood history of the southern Okavango Delta (Heinl et al. 2005a; Heinl et al. 2005b). Analyses of a series of 98 satellite images from 1989 until 2003 provided data on fire occurrences and inundated areas, which were used to identify target sites according to flood history and time-since-fire.

All areas investigated were recorded as flooded at least once between 1989 and 2003, and were accordingly called floodplains, but were not flooded after 1993, which characterised them as drying floodplains for the present study. For these drying floodplains, study plots were selected representing 2 years since the last fire (15 sites), 4 years (74 sites), 6 years (6 sites), 8 years (20 sites), 10 years (20 sites) and 12 years (17 sites) since the last fire (space-for-time substitution). The variation in plot numbers was due to inaccessibility of relevant study areas. The number of years since the last fire is consistent with the number of growing seasons that have passed since the last fire. Hence, the plots with two years since the last fire were burned in 2002 and vegetation growth was in early 2003 and 2004.

The vegetation survey was performed in February 2004 and 153 study sites were investigated. On each site with the size of 10 m x 20 m, abundance and cover values after Londo (1984) were measured for each woody species. In one corner of each site, a quadratic 4 m^2 plot was investigated, where all species and their cover were recorded. Biomass data for the investigated plots were provided by Rutz (2004).

Results

The relation of the herbaceous layer to time-since-fire

Analyses of the herbaceous layer showed for both vegetation cover and aboveground living biomass an increase with time-since-fire and significantly higher mean values after 12 years since fire compared to shortly after the fire-event (Figure 2). The absolute mean values indicate a slow recovery immediately after the fire with only 27.3 % vegetation cover and 112.6 gm^{-2} aboveground living biomass after two years, rising to more than 60 % cover and 226.6 gm^{-2} biomass after 12 years without fire. The mean number of species per plot was about 6 species in the second year and declined with time-since-fire to only 3.6 species per plot after eight years without fire (Figure 2). Highest mean species numbers were found after 12 years without fire with 8.6 species per plot.

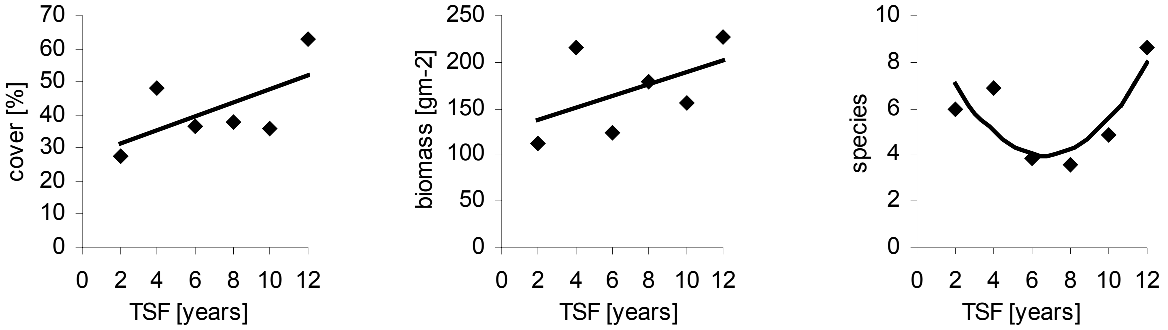


Figure 2. Mean vegetation cover, aboveground living biomass and number of species per plot for time-since-fire (TSF).

For analysing the development of cover values of single species in relation to time-since-fire, the ten most abundant species were selected, each recorded for at least 30 plots. The species could be visually classified into four groups according to the development of their cover with time-since-fire (Figure 3). Species of Group A show highest cover values in the first years after the fire-event and significantly declining cover values with time-since-fire. Species of Group B show low cover values immediately after the fire, but highest cover values after four years and then declining values with time-since-fire. For species of Group C a significant rise in the cover values with-time-since-fire was observed, with the peak in the mean cover value after 12 years without fire. Similarily for the species of Group D an initial rise in cover value with time-since-fire was observable, but with the peak value after eight years without fire and declining cover values on plots with longer fire-free periods.

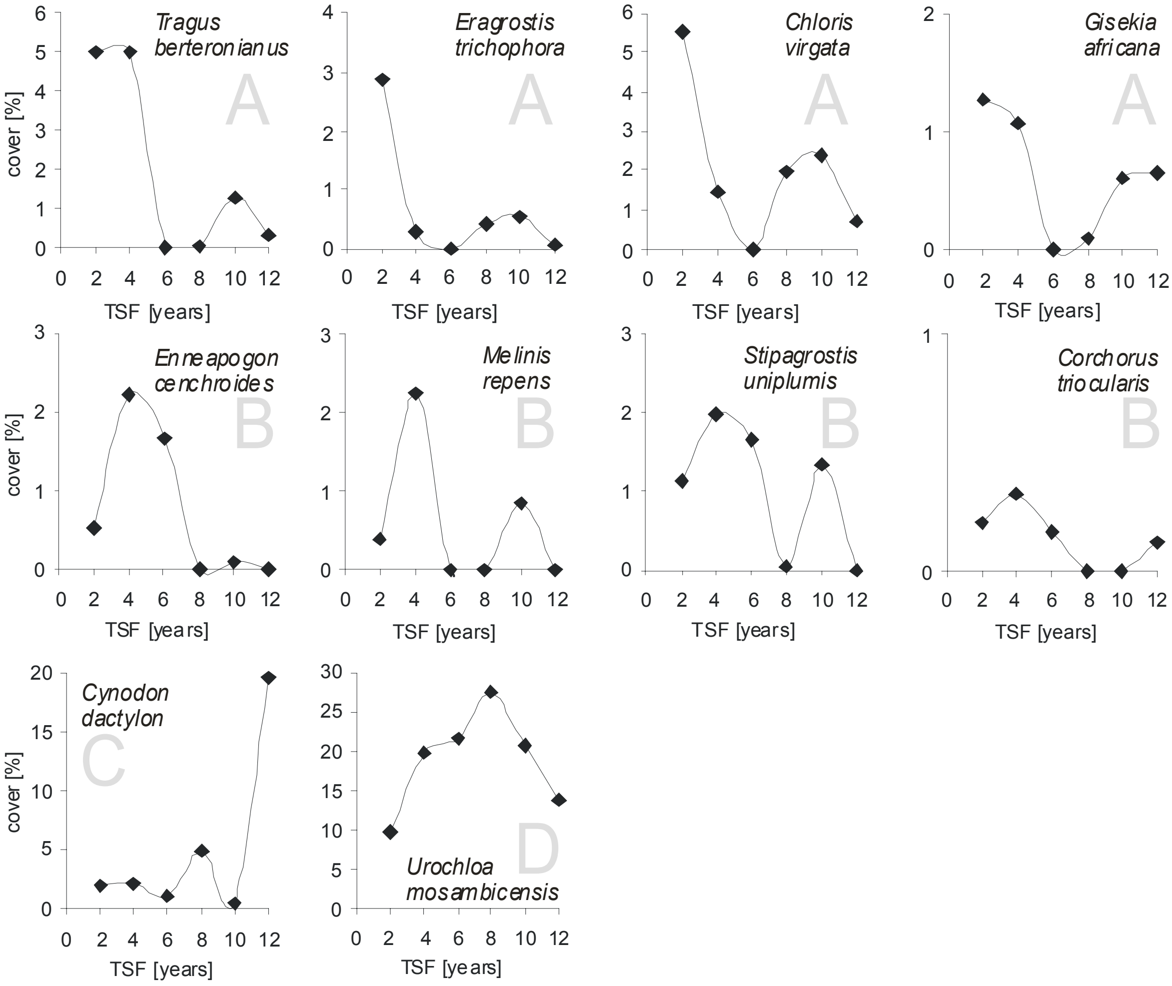


Figure 3. Mean cover values of most the common species in the study plots for time-since-fire (TSF). The species are grouped according to their life-history and the groups are indicated by the letters A, B, C and D (see text for details).

Assessing plant traits of these selected species allowed the assignment of species' life history to the specific groups (RBG Kew 2004; Gibbs-Russell et al. 1990; Oudtshoorn 1999). Group A is represented by annual and typical pioneer species that establish quickly in disturbed places. *Tragus berteronianus* and *Eragrostis trichophora* have highest cover values immediately after the fire-event and low cover values on plots with more than 4 years since the last fire. They thus show an obvious dependence on disturbance-events. Similar effects are observable for *Chloris virgata* and *Gisekia africana*, but less pronounced. Species in Group B are in principle short-lived perennials, although *Enneapogon cenchroides* and *Melinis repens* are also described as annual and *Stipagrostis uniplumis* as subperennial. However, their life-history under prevailing conditions seems to be longer than that of species in Group A and the pioneer character of these species is less pronounced, as they are almost absent in the first years after the fire-event. Group C is represented by *Cynodon dactylon*, typically perennial with rhizomes. The data suggest that more than ten years without fire are needed for *Cynodon dactylon* to spread extensively, although a clear trend towards a steady increase with time-since-fire cannot be derived for this species. Group D is represented by *Urochloa mosambicensis*, also typically perennial, and shows maximum cover values about 8 years after the fire-event.

The analyses of the life history of the most common species revealed a general trend of more annual and short-lived species shortly after the fire and in principle a decline of these species with time-since-fire. However, as these are the most common species, they are present for almost all time-since-fire categories and do not contribute to the observed changes in the species numbers with time-since-fire (cf. Figure 2). To analyse these changes, the mean vegetation cover and total species numbers were calculated for all time-since-fire categories. They were divided into species present in the second year after the fire (reference species) and all other species (supplementary species). This allowed a separate assessment of the development of the species-pool present shortly after the fire-event (reference species) and the fluctuations in number and cover of the supplementary species with time-since-fire (Figure 4).

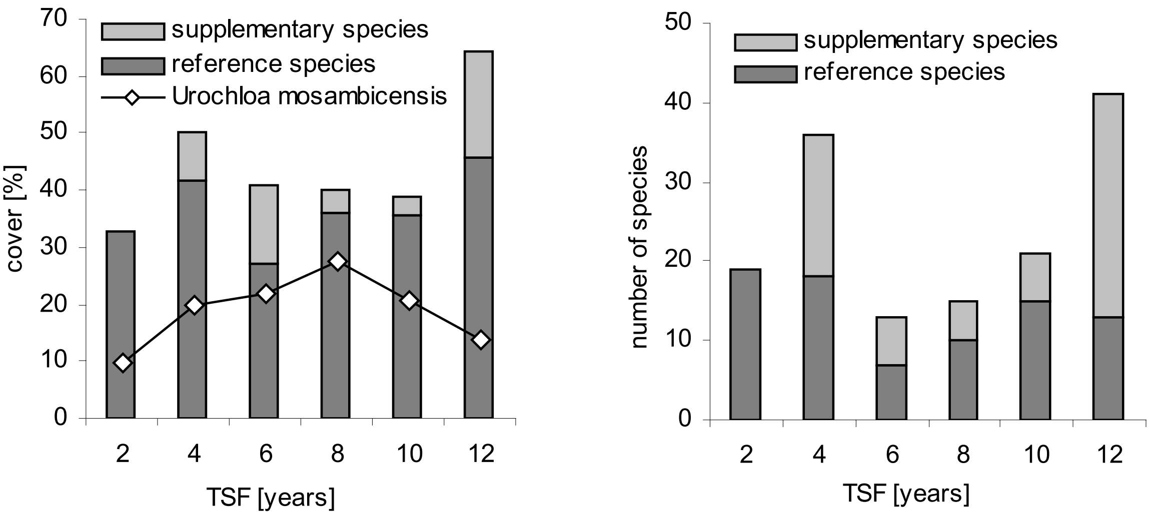


Figure 4. Mean cover values and total number of species for time-since-fire (TSF). Reference species are all species recorded two years since the last fire. Supplementary species are all other species, which were not present two years after the fire-event.

For all plots representing the stage two years after the fire-event, a total number of 19 reference species were encountered and a mean vegetation cover of 32.9 % was calculated. On the plots 4 years after the fire-event, 18 of the 19 reference species were also present, but 18 supplementary species were recorded. As the number of investigated plots for this time-since-fire category is high (75), the absolute species number is not comparable to other categories. However, despite the high number of supplementary species found on plots four years after the fire, the cover value of these species was relatively low (8.3 %), while the cover of the reference species increased relative to the previous years. In contrast, on the plots six years after the fire-event, cover and species number of the reference species decreased and the supplementary species increased in cover, but total species numbers declined significantly. On plots with eight and ten years after the fire, the cover values of the reference species stabilised at a high level and only few supplementary species with low cover values were present. On plots 12 years after the fire, the highest species numbers were encountered in total (41) and for supplementary species (28), of which 15 species were only found on these plots. Mean total vegetation cover was highest with more than 60 %.

The relation of the woody layer to time-since-fire

The analyses of the data derived from the study sites in relation to the woody species generally showed no significant differences in the number (abundance) of woody species with time-since-fire. However, a significant increase in the cover of woody species was observed with the time since the last fire. Highest cover values were found for ten and 12 years since-fire with 22.1 % and 21.0 % mean cover, respectively, compared to 8.6 % cover of woody species on sites two years after a fire-event.

The cover and abundance values of the woody component of the study sites are in principle determined by *Acacia erioloba*, *Colophospermum mopane*, *Combretum imberbe* and *Pechuel-loeschea leubnitziae*, which account for 98 % of the abundance (2631 individuals). *Combretum imberbe* showed no significant response to time-since-fire. For *Acacia erioloba* mean abundance values were significantly higher with the longer the time since the last fire and highest after 12 years without fire (Figure 5). As cover values for *Acacia erioloba* showed relatively little response to time-since-fire, the higher abundance values reflect a trend towards higher numbers of small *Acacia erioloba* individuals with time-since-fire. Abundance values of *Colophospermum mopane* showed a significant decrease with time-since-fire (Figure 5). Cover and abundance values were low on sites with four and more years since the last fire, but high values were recorded for the second year after the fire. The calculated ratio between cover and abundance revealed for *Colophospermum mopane* a linear increase of the area covered per individual with time-since-fire, indicating many small individuals shortly after the fire and significantly fewer, but larger individuals with time-since-fire. For *Pechuel-loeschea leubnitziae* a significant increase in abundance was found with time-since-fire (Figure 5). The sites with 12 years since-fire showed maximum mean cover and abundance values. However, mean abundance values were found on two and four years after the fire and lowest values were recorded for six and eight years after the fire. Cover values show similar trends as the abundance values.

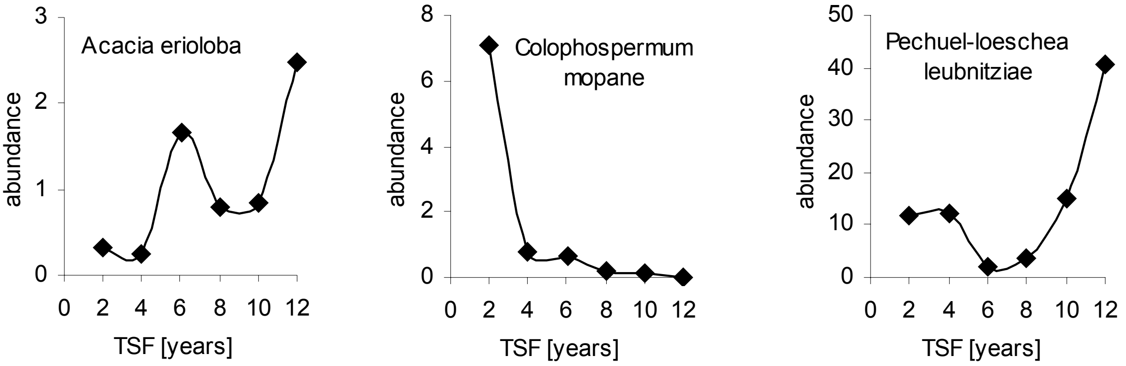


Figure 5. Mean abundance values (mean number of individuals per site) for *Acacia erioloba*, *Colophospermum mopane* and *Pechuel-loeschea leubnitziae* in relation to time-since-fire (TSF).

Discussion

The approach of analysing species composition and vegetation structure on sites with different time-since-fire can be compared to long-term post-fire monitoring. Although it cannot provide a detailed description of a 'real' development on specific sites, the big advantage of this space-for-time substitution is the possibility of comparative analysis of successional stages after the fire-event in a very short time period.

Post-fire succession is described as different from linear and competitively driven replacement sequences (Bond & van Wilgen 1996). Post-fire succession is rather cyclical and leads to reoccurring vegetation patterns under a specific fire regime. Species richness is expected to be highest soon after the fire (Morrison et al. 1995) and the succession proceeds by successive elimination of species, with the order of elimination determined by the relative longevity of the species. The successional change is thus driven by the life histories of the species rather than by their position in the competitive hierarchy (Bond & van Wilgen 1996). The results of this study only partially support this theory: typical fire succession was only observed for the first few years after fire, with competition becoming more relevant for the successional pathway with increasing time-since-fire.

The successional pathway after fire

In line with the post-fire succession model, the results of this study show that many species are present in the second year shortly after the fire (referred to as reference species, in contrast to supplementary species). Those reference species either survive the fire, for instance due to protected buds or as seeds, or have the ability to quickly colonise new habitats. Annual species in particular show relatively high cover values shortly after the fire-event.

Mean total vegetation cover two years after the fire is ca. 30 % and lower than in the following years (ca. 40 %), and predictably also lower than pre-fire (Heinl et al. 2004). After four years without fire, species numbers are relatively high and mean total vegetation cover rises to 40 %. This rise in vegetation cover is primarily because of an increase of the reference species and indicates an ongoing recover of these most common species. However, there is a parallel establishment of new, supplementary species.

In subsequent years, species numbers decline (Figure 2). This is in principle ascribable to the decline of the annual and short-lived species, which are present in the first years after the fire-event (Figure 3) and accordingly cover and species numbers for the reference species decline (Figure 4). Finding high species numbers shortly after the fire-event followed by a steady decrease of species numbers, which is partially ascribable to the life-history of the reference species, strongly supports the concept of the post-fire succession model described above.

Six years after the fire, species numbers are low and also the cover values of reference species, now most likely represented by just a few perennial species, are low. Fewer supplementary species are present, although they show increasing cover values. Most likely only some of the supplementary species, which were present four years after the fire, could establish themselves and now these species compete with the reference species, reducing their cover and abundance values. However, eight years after the fire, cover values of the reference species are high again and the values of the supplementary species are reduced. *Urochloa mosambicensis* in particular shows rising cover values during the first eight years after fire and occupies an increasing portion among reference species (Figure 4). It is therefore expected that with increasing time since the last fire, a few specific highly competitive species come to dominance. Most of these dominant species are reference species, which survive fires, but obviously also some fire-sensitive supplementary species are permanently present. After eight years without fire, mean species numbers are lowest (Figure 2), supplementary species decline significantly in cover and abundance and reference species are in principle represented by dominant perennial species, especially *Urochloa mosambicensis* (Figure 4).

With ten years-since-fire, woody species become more abundant. The long fire-free interval allows especially *Pechuel-loeschea leubnitziae* and *Acacia erioloba* to establish and to grow, as new seedlings and young plants are not suppressed by frequent fires (Higgins et al. 2000; Heinl et al. 2005c; Bond & van Wilgen 1996). For *Acacia erioloba* in particular a relatively high abundance was found after long periods without fire, which is in line with the documented fire-sensitivity of *Acacia erioloba* (Skarpe 1991; Barnes 2001). For *Colophospermum mopane* generally low cover values were observed, except for two years after the fire-event (Figure 5). These high cover values shortly after the fire might be due to an initial lack of browsing pressure from elephants. Although *Colophospermum mopane* is usually heavily browsed, a significant decrease in browsing activity by elephants after fire has been reported (Kennedy 2000; Ben-Shahar 1993). A short period without elephant browsing after fire would therefore allow the fast-growing shrub to recover and to spread extensively. However, no comparative analyses exist of the severity of the impact of fire compared to the impact of elephants on *Colophospermum mopane*, which would be necessary to clearly assign the higher cover values to the suppression of elephant browsing by fire. *Pechuel-loeschea leubnitziae* shows a similar trend to *Acacia erioloba* and an increase in cover and abundance with time-since-fire, especially after more than eight years without fire.

As *Pechuel-loeschea leubnitziae* accounts for by far for the highest cover and abundance values among the woody species (Figure 5), changes in cover and abundance values of this species are expected to have the most significant influence on herbaceous plants. Especially *Urochloa mosambicensis* declines significantly with rising cover and abundance values of *Pechuel-loeschea leubnitziae* (Figure 4), most likely due to competition between these two species. Hence, after 12 years without fire, cover and abundance values of *Acacia erioloba* and *Pechuel-loeschea leubnitziae* are highest, while *Urochloa mosambicensis* shows relatively low values. Interestingly, mean species cover and total species numbers are also highest 12 years after the fire-event, and many new species are found that were not recorded as supplementary species before. The occurrence of new species, which are neither present immediately after the fire nor during the post-fire development, but now appear with the higher cover and abundance of woody species, indicates the creation of new habitats in the vicinity of the established shrubs. Probably by providing shade and protection, new ecological niches are created that are occupied by species which are not typical of floodplains and rather origin from nearby woodland fringes.

The principle successional pathway after fire for the study area can now be simplified by dividing the succession into two main phases: The first eight years show the typical fire succession described by Bond & van Wilgen (1996). About four years, however, are required to reach maximum species numbers and vegetation cover after fire. With the species decline in the following years, a few perennial species, like *Urochloa mosambicensis*, become more abundant and dominant. After more than eight years, mean species numbers increase, as woody species become more abundant. Succession is now driven by competition and niche differentiation rather than by life-history. The decline of *Urochloa mosambicensis* in combination with the rise of *Pechuel-loeschea leubnitziae* indicates a change towards a linear successional pathway independent of the fire-event.

The development of species richness with time-since-fire

Species richness was found to be highest soon after the fire-event and again 12 years after the fire. For the cover values of *Pechuel-loeschea leubnitziae* a similar development was encountered, while for *Urochloa mosambicensis* converse trends were derived.

In order to assess the correlation of *Pechuel-loeschea leubnitziae*, *Urochloa mosambicensis* and mean species numbers on the study plots, Spearman-Rank-Correlation was calculated for these three parameters. Species numbers show a significant positive correlation with the cover of *Pechuel-loeschea leubnitziae* ($p<0.001$; $r^2= 0.33$) and a significant negative correlation with cover values of *Urochloa mosambicensis* ($p<0.001$; $r^2= -0.39$).

The high species numbers found shortly after the fire therefore decline with increasing cover of *Urochloa mosambicensis*. With time-since-fire, *Pechuel-loeschea leubnitziae* becomes more abundant and competes with the dominant grass species. Declining cover values of *Urochloa mosambicensis*, in combination with higher cover values of *Pechuel-loeschea leubnitziae* again lead to higher species numbers.

However, the changes in species numbers may not be specifically connected to the development of these two species, but rather to the general decline of dominating stoloniferous perennial grass species and to the establishment of new habitats with the increase of woody species. It is therefore expected, that a similar increase in cover values of for example *Colophospermum mopane* would have a comparable positive effect on the species numbers of the drying floodplains of the Okavango Delta.

Synthesis

In the context of a fire succession model based on the life-history of the plants (Bond & van Wilgen 1996), species composition and vegetation structure change with the length of the inter-fire-interval. However the present study has shown that the successional pathway after fire is also partially competitively driven, especially with longer elapsed time since the last fire. A synthesis of the presented findings can be drawn by formulating fire succession scenarios regarding different inter-fire-intervals:

Annual or biennial burning leads to relatively low vegetation cover around 30 %, significantly lower than the total cover that can be reached during longer inter-fire-intervals (ca. 40 %). Species numbers are relatively high, because of most species surviving the fire-event, either through protection or as seeds. Woody species, however, are suppressed.

Short inter-fire-intervals (3-4 years) lead to even higher species numbers, as new species are able to establish because of relatively low vegetation cover and hence little competition. However, mainly the same species, typically open savanna or grassland species, are expected to establish after each single fire-event.

Mid inter-fire-intervals (5-8 years) allow perennial, highly competitive species to dominate and lead to low species numbers.

Long inter-fire-intervals (>9 years) facilitate the establishment of woody species and of associated herbaceous plants. High species numbers are found in long inter-fire-intervals. However, to secure the diversity and structure on these sites, reoccurring fire-events are necessary to avoid the dominance of woody species and to keep the typical fire-determined savanna structure.

Highest species numbers were found for short and for long inter-fire-intervals, and different species occurred shortly after the fire-event and at late stages of the post-fire succession. A variety of different inter-fire-intervals is therefore important to sustain the diversity of the drying floodplain habitats in the Okavango Delta wetland.

Acknowledgments

The studies were conducted in the scope of the project “Fire regime and vegetation response in the Okavango Delta, Botswana” funded by Volkswagen Foundation, Germany with support from Conservation International Botswana, Okavango Program. Special thanks to all staff of the Harry Oppenheimer Okavango Research Centre in Maun, to Prof. George Bredenkamp (University of Pretoria, South Africa) and to Prof. Joerg Pfadenhauer (Technische Universitaet Muenchen, Germany) for scientific support.

References

Andersen AN, Braithwaite RW, Cook GD, Corbett LK, Williams RJ, Douglas MM, Gill AM, Setterfield SA & Muller WJ (1998): Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. Australian Journal of Ecology 23: 95-110.

Arnold TH & De Wet BC (1993): Plants of Southern Africa: Names and Distribution. Memories of the Botanical Survey of South Africa No. 62; Botanical Research Institute, Pretoria.

Barnes ME (2001): Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. African Journal of Ecology 39: 340-350.

Ben-Shahar R (1993): Patterns of elephant damage to vegetation in northern Botswana. Biological Conservation 65: 249-256.

Bond WJ (1997): Fire. In: Cowling RM & Richardson DM & Pierce SM (eds.): Vegetation of Southern Africa, Cambridge University Press, Cambridge 421-446.

Bond WJ & van Wilgen BW (1996): Fire and Plants. Population and Community Biology Series 14, Chapman & Hall, London, UK.

Booysen PdV & Tainton NM (1984): Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48, Springer-Verlag, Berlin.

Cassidy L (2003): Anthropogenic burning in the Okavango Panhandle of Botswana: Livelihoods and spatial dimensions. Unpublished M.Sc.Thesis, University of Florida.

DeBano LF, Neary DG & Folliott PF (1998): Fire's Effects on Ecosystems. Wiley and Sons, Inc., New York.

Ellery K & Ellery W (1997): Plants of the Okavango Delta - A Field Guide. Tsaro Publishers, Dalbridge.

Gibbs-Russell GE, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM & Dallwitz MJ (1990): Grasses of Southern Africa. Memoirs of the Botanical Survey of South Africa, No. 58, National Botanical Institute, Pretoria.

Heinl M, Frost P, Vanderpost C & Sliva J (2005a): Fire activity on floodplains and drylands in the Okavango Delta, Botswana (accepted for publication by Journal of Arid Environments; *Chapter 4*).

Heinl M, Neuenschwander A, Sliva J & Vanderpost C (2005b): Interactions between fire and flooding in the Okavango Delta floodplains, Botswana (accepted for publication by Landscape Ecology; *Chapter 3)*.

Heinl M, Sliva J & Tacheba B (2004): Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana. South African Journal of Botany 70 (5): 695-704 (*Chapter 2*).

Heinl M, Sliva J, Tacheba B & Murray-Hudson M (2005c):Vegetation response to fire frequency in the Okavango Delta floodplains, Botswana (submitted to Journal of Tropical Ecology; *Chapter 5*).

Higgins SI, Bond WJ & Trollope WSW (2000): Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88: 213-229.

Kennedy AD (2000): Notes and Records - Wildfire reduces elephant herbivory on *Colophospermum mopane* (Fabaceae). African Journal of Ecology 38 (2): 175-177.

Kew R (2004): Flora Zambesiaca, Royal Botanical Gardens, Kew. online at http://www.kew.org/floras/fz/intro.html.

Londo G (1984): The decimal scale for relevés of permanent quadrats. In: Knapp R (ed.): Sampling methods and taxon analysis in vegetation science, Handbook of Vegetation Science (4), Junk Publishers, The Hague 45-49.

McCarthy TS, Cooper GRJ, Tyson RD & Ellery WN (2000): Seasonal flooding in the Okavango Delta, Botswana - recent history and future prospects. South African Journal of Science 96: 25-32.

Morrison DA, Cary GJ, Pengelly SM, Ross DG, Mullins BJ, Thomas CR & Anderson TS (1995): Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Inter-fire interval and time-since-fire. Australian Journal of Ecology 20: 239-247.

Oudtshoorn Fv (1999): Guide to Grasses of Southern Africa, Briza Publications.

Rutz D (2004): The influence of fire on site productivity in southern Africa (Study site: Okavango Delta, Botswana). MSc-Thesis at Chair of Vegetation Ecology, Technische Universitaet Muenchen (unpubl.)

Skarpe C (1991): Spatial patterns and dynamics of woody vegetation in an arid savanna. Journal of Vegetation Science 2: 565-572.

Chapter 7

Synthesis -
Fire regime and vegetation response in the Okavango Delta

Synthesis -
Fire regime and vegetation response in the Okavango Delta, Botswana

The aim of this investigation was to determine the spatial and temporal distribution of fires and to investigate how these fires affect the vegetation in the Okavango Delta, Botswana. The analyses of the fire distribution using a series of Landsat satellite images between 1989 and 2003 provided insight into when and how often fires occur, and also acted as baseline data for the studies on vegetation response to specific fire regimes. In the following section, the findings of the study are recapitulated and summarised in separate paragraphs and a final conclusion on the significance of the study is presented.

The fire activity in the southern Okavango Delta

The reconstruction of the fire history for the southern Okavango Delta revealed a high variability of fire activity in the study area, both in the extent of the burned area per year and in the susceptibility of habitats.

For the study period, the area affected by fires ranged from less than 1 % in 1998 to almost 25 % of the study area in 1997. A low fire activity, as observed in 1998, was explained by high fire activities in previous years, as in 1997, leaving little biomass as fuel to burn (Chapter 4). Indeed, the studies including biomass estimations showed significantly less fuel load after fire on burned areas, with mean values of about 285 gm^{-2} compared to about 420 gm^{-2} on unburned sites (2). Periods of high fire activity were explained differently for floodplains and drylands, which are unaffected by the flooding. While for drylands the amount of rainfall prior to the fire-event has shown to be a significant determinant of fire occurrences due to the accumulation of fuel loads (3), the floodplains rather tend to burn after receding floods and the exposure of previously flooded areas (4). However, the probability and extent of a fire is not only influenced by the time since the last fire, rainfall or receding floods, but is additionally determined by for example pre-fire grazing intensity, which also reduces fuel loads, or by weather conditions during the fire (1). Adding the anthropogenic factor as ignition source (2) makes a specific fire occurrence in principle unpredictable, both in time and in space. But the knowledge about the fire history of the study area can assist to assess the probability and potential of a specific area to burn by calculating typical fire seasons, mean fire frequencies or mean fire return intervals for specific habitat types.

Floodplains clearly show a higher fire activity than drylands (3 & 4). This difference is explainable by higher fuel loads on floodplains, due to higher biomass production and little off-take by herbivores because of less palatable grasses and sedges and due to local land use practices, like burning floodplains before they become inundated (2). Mean fire return intervals for floodplains and drylands were calculated at 6.6 and 22.2 years, respectively (4). The highest fire frequency was observed for floodplains that are inundated about every second year, showing a mean fire return interval of about 5 years (3). Drylands in general rarely burn and for about 60 % of all drylands in the study area no fire occurrence was recorded (4). However, fire frequency varied extremely for the different habitat types and even drylands that were burned more than every second year were detected. As the fire frequency is generally higher on floodplains and as the drylands with high fire frequency are located close to floodplains, a spatial connectivity between the relatively high fire frequency on drylands and the fire activity on floodplains is expected by fires spreading from floodplains into drylands (4).

The main fire season for both drylands and floodplains is the dry period of the year, roughly between May and October. However, floodplains tend to burn earlier in the year and the fire activity peaks around June, while drylands usually burn at the end of the dry season in September (4). This difference in the timing of the fire-events can be explained by the temporal correlation of floodplain-fires with the arrival of the flood in July and of dryland-fires with the start of the rainy season in October. Hence, most burning takes place immediately before water becomes available, either as floodwater or rainfall. These coincidences indicate an anthropogenic origin of most fires, as burning is a common practice for preparing fields and fishing grounds and as natural ignition sources, like lightning, are extremely rare during the dry season (4).

The fire season indicates an anthropogenic rather than a natural fire regime for the Okavango Delta. Although today most vegetation fires can be considered as human-caused in southern African savannas, local scientists and initiatives in Botswana are especially concerned about extremely high fire frequencies and a negative ecological impact due to rising anthropogenic pressure (4). Indeed, the analyses of the satellite images showed areas with very high fire frequency, clearly above average, both for drylands and floodplains. The area with the maximum fire frequency even burned ten times during the last 15 years. However, these areas are small and the proportion of floodplains that burned six times or more is less then 5 % (4). The extent of the area affected by fire shows for the different years a high variability, indicating no large regulating or homogenising factor. The overall fire frequency is, with most of the areas burning less than every third year, in the range of the fire frequency observed for other savanna or grassland systems in southern Africa (4). A general negative impact on the ecology of the southern Okavango Delta, in form of habitat destruction or species loss, is therefore not expected at the present fire-regime (5). However, the existence of and reasons for the observable high fire frequencies should not be ignored. Since most likely human activities are connected to these high fire frequencies, rising anthropogenic impact on the Okavango Delta could also lead to more areas experiencing high fire activity in the near future. Most likely this will not change significantly the extent of the fires per year, but rather affect specific areas, where fire is used intentionally and frequently as a tool to provide certain resources, like fresh grasses for game and cattle, open view for safari-tourism or around properties. As the ecological consequences of frequent burning cannot be generalised and are not readily evident for the Okavango Delta region, the effects of fire on vegetation in the Okavango Delta were investigated in the scope of this study and the findings are summarised in the following paragraph.

Vegetation response to fire in the Okavango Delta

In theory, only minor changes in plant species composition are expected to occur after fire in fire-prone environments, as the occurring vegetation is usually already a result of regular fire-events and most species are able to survive a fire (Chapter 1, 2 & 5). For the present study, no typical plant species composition could be associated with a specific fire frequency (5) or with the post-fire condition (6) and no specific plant traits were found to be distinctive for the survival of plants after a fire-event (2). Hence, the occurring vegetation in the Okavango Delta appears to be highly adapted to regular fire-events.

However, the simple equation of species that are present pre-fire are also present post-fire stated by Morgan (1999; 1) cannot be supported by the findings of this study on the post-fire succession, as changes in the species composition could be associated with time-since-fire (6). For example drying floodplains that did not burn for more than ten years show a different species composition from sites two years after a fire and hence the fire-event will clearly lead to a change in occurring species on specific sites (6). This argumentation of vegetation changes with the fire-event is also supported by lower values for biomass and vegetation cover found on sites shortly after a fire compared to longer fire-free intervals (2 & 6). The studies indicate a recovery period of more than two years to gain mean vegetation cover values of about 40 % (6).

The results of the investigation of vegetation changes after single-fire events (2), however, seem to contradict this conclusion as no significant changes after the fire-event, especially for species cover, could be found. But for this specific study, simply burned and unburned sites were compared to find characteristics of burned areas, while pre-fire conditions were not considered, as they were unknown at the point of the study. Therefore, both burned and unburned sites covered a huge variety of different successional stages and the changes that are expected to be observable by comparing pre- and post fire vegetation on one specific site might have been blurred by this variety.

Fire-events are expected to cause some kind of reset of the vegetation development to an earlier successional stage. The most common species are expected to be still present after a fire-event, however with lower cover values, while certain species reappear a few years after the fire (6). As the post-fire species composition is highly dependent on the species and their dominance prior to the fire, neither a typical species assemblage nor specific plant traits can be associated with a fire-event, even for similar habitats.

The studies on the effects of single fire-events on the vegetation showed clear differences in vegetation response to fire dependent on the habitat type (2). Thus, the consideration of different habitats proved to be crucial for assessing the vegetation response to fire in the Okavango Delta precisely. However, for the Okavango Delta no consistent definition of habitat or vegetation types is available and the wetland is basically categorised roughly by estimated flooding regimes (2 & 5). A clear definition of habitat types, considering flood parameters, like water depth, flood duration or frequency for habitat differentiation and using derived typical vegetation as visual indicator, is therefore critically important for future ecological studies.

For the studies in the present thesis, two different approaches were used for habitat definition, one based on the cover of woody species (2) and the other based on flood frequency (5 & 6). However, practically, both approaches considered the flooding as the differentiating environmental factor, as also the occurrence and density of woody species in the study area is basically determined by inundation, and hence both approaches led to similar habitat categories.

Detrended correspondence analyses (DCA) on species composition of a variety of investigated study plots revealed five habitat types in the study area, which could later be separated basically by the cover of woody species: active floodplains, Pechuel-loeschea grasslands, mixed Mopane-Pechuel-grasslands, Mopane woodlands and pans (2). Using the spatial flood frequency distribution derived from satellite images distinguished basically active and drying floodplains and drylands (5). As not all habitat types could be investigated comprehensively, the main focus of the study was set on floodplains as the typical habitat type in the study area and the habitat most affected by fires (4). The effects of fire on vegetation are therefore in more detail discussed for (i) active floodplains, which are treeless and in principle dominated by *Panicum repens* or the tall sedges *Schoenoplectus corymbosus* and *Cyperus articulatus* and for (ii) drying floodplains, including Pechuel-loeschea grasslands and mixed Mopane-Pechuel-grasslands as defined in Chapter 2, dominated by the grasses *Urochloa* spec., *Aristida* spec. and *Eragrostis* spec. with single woody species like *Acacia* spec., *Colophospermum mopane*, *Combretum imberbe* or *Pechuel-loeschea leubnitziae*.

Active floodplains are inundated on a regular basis and are defined for that study as flooded at least every second year (5). The analysis of fire occurrences for active floodplains revealed a negative correlation between fire and flood frequency, so that the more often these floodplains become inundated the less frequent they burn. This coincidence was explained by fire suppression with more regular flooding and shorter inter-flood intervals (3). A negative correlation between fire and flood frequency on active floodplains was also supported by Detrended Correspondence Analyses (DCA) of the investigated study plots (5). Vegetation response to fire therefore became difficult to separate clearly from the response to flooding. But as flooding is undoubtedly the major ecological factor in the Okavango Delta, it could be made responsible for most of the observed differences in vegetation. Hence, despite correlating with fire frequency, species assemblage and vegetation structure was shown to be in principle determined by the flood frequency.

Investigating the specific occurrence of species at different fire frequencies, however, revealed for some species a significant difference in cover related to fire frequency. Especially *Cyperus denudatus*, *Eragrostis lappula* and *Setaria sphacellata* showed significantly higher cover values at high fire frequencies, while *Cyperus articulatus* and *Eclipta prostrata* were in principle found at low fire frequency (5). As the species at high fire frequency also show relatively high cover values at low fire frequency and the species occurring mainly at low fire frequency were absent at high fire frequency, some species are expected not to tolerate frequent fire events. However differences in plant species diversity could neither be associated with fire frequency nor with a single fire-event on active floodplains (2 & 5).

The missing significant response to fire for active floodplains could be explained by adaptation of the established plant species to high frequent fire-events or in general to disturbance-events. However, due to missing research especially on the ecological effects of fire in wetlands, a scenario for the Okavango Delta floodplains on the effects of fire on vegetation has to remain speculative:

The active floodplains in the Okavango Delta experience a short draught period in most of the years after the rainfalls in February/March, followed by the flooding, and then the period of a receding flood shortly before the next rainfalls. Fires usually occur during the drought period between the season of rainfall and the flooding (4). Most of the present plants, usually tall perennial sedges or grasses, are therefore dormant during the fire season. They are generally able to spread and regrow by rhizomes, like *Cyperus articulatus*, *Schoenoplectus corymbosus*, *Oryza longistaminata* or *Panicum repens* and these rhizomes are usually covered under a layer of dry accumulated biomass during this period. This thick organic layer of dead leaves and stems is not utilised by herbivores or termites because of the unpalatability and remains wet long after the rainfall, especially in combination with the high water holding capacity of the upper organic layer in the soils of the floodplains. Fire temperatures are hence expected to be significantly reduced by the moisture in the fuel. As therefore the pre-fire vegetation appears to be well protected against fire, changes in plant species composition with fire-events are only likely to happen if space and time is provided for new species to establish. Although the fire-event might provide open space by removing most of the vegetation and litter, the time-span for the establishment of new, e.g. pioneer species, is extremely short because of the next coming flood. Water levels usually rise quickly and small species not capable of surviving under water are expected to drown. In combination with the fast recovery of the highly competitive established species in the active floodplains, the survival of new species after a fire-event in the active floodplains and hence a change in species composition related to fire is therefore expected to be difficult and unlikely.

The drying floodplains, defined for this study as floodplains not inundated since at least 1993, show, unlike active floodplains, also a woody layer due to a long period without inundation (2). Although herbaceous and woody species are interacting (6), the layers are at first regarded separately in order to show typical trends in vegetation response to fire.

The results of the study indicate a rather negative impact of fire on woody species, especially on the establishment of larger trees (5). Study sites with high fire frequency (6-10 burns during the 15-year study period) showed fewer large trees and a broader growth of small woody species compared to low fire frequency (0-2 burns during the 15-years study period). The regular disturbance by fire-events permanently initiates a basal resprouting of the woody species and inhibits small individuals from escaping from the grass layer affected by the fires. High fire frequency can therefore not be made responsible for killing large trees, but rather for suppressing the recruitment of small individuals to the canopy layer. In line with higher cover and abundance values for woody species on low fire frequency are the findings on a significantly increasing cover of woody species with the time since the last fire. During a fire-free period of more than 10 years the mean cover values for woody species more than doubled from 8.6 % to 22.1 % (6).

In contrast to a negative impact of fire on woody species, many herbaceous species on drying floodplains show high cover values that can be related to fire, especially to the period shortly after a fire-event (6). However, lower mean total cover values of the herbaceous layer were recorded after fire (2) and especially short-lived species were found to use the provided space of the post-fire environment to colonise new gaps created by the fire. With progressing time-since-fire, however, the relative high cover values of annual species decline shortly after the fire and semi-perennial and later perennial species become more abundant (6). Hence, most of the species dominating the early post-fire environment are also present in later successional stages after the fire, albeit with lower cover values (6).

The most dominant species for almost all successional stages after fire were found to be the stoloniferous perennial grass *Urochloa mosambicensis* and the shrub *Pechuel-loeschea leubnitziae* (6). The studies suggest a competitively driven negative correlation of the cover values of these species, especially during late post-fire successional stages. Maximum cover values for *Urochloa mosambicensis* were found about eight years after the fire-event, but declined for longer fire-free periods with rising cover values of *Pechuel-loeschea leubnitziae.* Mean species numbers significantly increased with higher cover values for *Pechuel-loeschea leubnitziae* and showed a negative correlation to *Urochloa mosambicensis*. Species numbers are however not expected to be connected specifically to these species, but rather to a general decline of a dominating stoloniferous perennial grass by competition with woody species and to the establishment of new habitats in the vicinity of these woody species (6). As these habitats are comparable to woodland fringes, the associated herbaceous species most likely invade into the floodplains from adjacent woodlands, which hence act as stable sources of species diversity on the drying floodplains of the Okavango Delta during long fire-free intervals.

Concluding, the vegetation response to fire for the drylands of the Okavango Delta is similar to typical savanna dynamics described in theory (2, 5 & 6). Especially the response of the woody layer shows the stated positive effect of reduced fire activity on tree cover. However, the models on post-fire succession could only be partially supported, as succession was shown to be not only driven by the life-history of the occurring species, but also by competition and niche differentiation (6). Vegetation response to fire for floodplains was shown to be hard to assess, basically due to a correlation between fire and flooding and hence, the effects of flooding are difficult to separate from the effects of fire (3 & 5). But obviously only few wetland plants seem to get affected by even regular fires, although detailed insights into ecological effects of fire on wetlands are still missing.

Significance of the study

The relevance of fire as important factor for the ecology of the area and the utilisation of fire in traditional land-use practices is scientifically and politically recognised in Botswana. However, the the fire issue has so far been widely ignored for the Okavango Delta. The present study was therefore designed to give first insight into fire occurrences and ecological effects of fire on the vegetation of the Okavango Delta in order to be able to evaluate trends in fire usage and their ecological consequences.

The method of analysing a series of satellite images proved to be a useful tool for gaining knowledge on the distribution of fire- and flood-events. The level of detail of the images was precise enough to carry out ecological studies on the plant species level and further research should be encouraged using this approach.

Essential for the precise assessment and evaluation of fire occurrences and their ecological effects was the differentiation of habitat types, especially the distinction of active and drying floodplains, and their separate analysis. However, the analyses of the active floodplains regarding vegetation response to fire showed difficulties due to the correlation between fire and flooding. An even more detailed habitat separation considering different classes of active floodplains, dependent on flood frequency, duration or depth, might provide deeper insight into vegetation response to fire on the active floodplains. However, a comprehensive approach for classifying habitat types on floodplains of the Okavango Delta is still missing.

The limitation of the study area to the southern Okavango Delta was necessary because of accessibility and technical and financial restrictions. The results of the study are presumably transferable to ecologically similar floodplain settings in the Okavango Delta, but are most likely not representative for the whole Okavango Delta region, especially due to different habitats and land use practices in the northern sections. Additional studies would therefore be necessary for a complete picture of the fire regime and vegetation response for the entire Okavango Delta.

As initial research, the present study searched for basic trends in vegetation response to fire. Unfortunately, supposed associated ecological effects of fire on the vegetation, like enhanced grazing of herbivores on recent fire scars or the avoidance of freshly burned Mopane leaves by elephants could not be considered. This limitation of the study was not only due to restrictions in time and capacity but also simply because of the unknown relevance of these aspects. The results of the present study now suggest that especially a combined study of effects of fire and herbivory on the vegetation would provide a much more detailed picture on the aspects that determine the vegetation of the Okavango Delta habitats as can be provided with the present approach.

Both fire frequency and time-since-fire were used to assess the effects of fire on vegetation. Although both approaches could not reveal distinctive species assemblages associated with the fire regime, studying vegetation response to time-since-fire allowed a more detailed picture of the effects of fire on vegetation to be drawn than the study on fire frequency. While the latter provided insight into the long-term response of the woody layer on drying floodplains and single wetland plants on active floodplains, using time-since-fire offered a detailed perspective on successional pathways after fire-events, supporting in principle also the results of the study on fire frequency.

Especially by regarding areas with high disturbance frequency and a high potential for recovery after these disturbance events, such as savannas or floodplains, the time for development after the reset by the disturbance is, following these studies, likely to be more important for species composition and vegetation structure than the frequency of the disturbance. The vegetation is therefore expected to be determined rather by specific lengths of fire-free periods than simply by the mean interval between fire occurrences.

The gained scientific knowledge on the distribution of fires and the principle response of floodplain vegetation to fire as well as the insights into the applicability and limitations of the used methods and approaches, qualifies the present study to be applied in management and conservation of the Okavango Delta. Currently the preparation of a Management Plan is in progress for the Okavango Delta region, also considering fire and vegetation issues, and the integration of the results of this thesis into the Okavango Delta Management Plan is highly welcomed, in order not only to participate in the scientific discussion on the fire issue and the ecology of the area but also to contribute with this study to the protection and future sustainable use of the Okavango Delta.

Appendix

Appendix 1

List of dates of the satellite images used for the present study

TM5: Landsat 5, TM sensor; TM7: Landsat 7, ETM+ sensor; ALI: EO-1, Advanced Land Imager

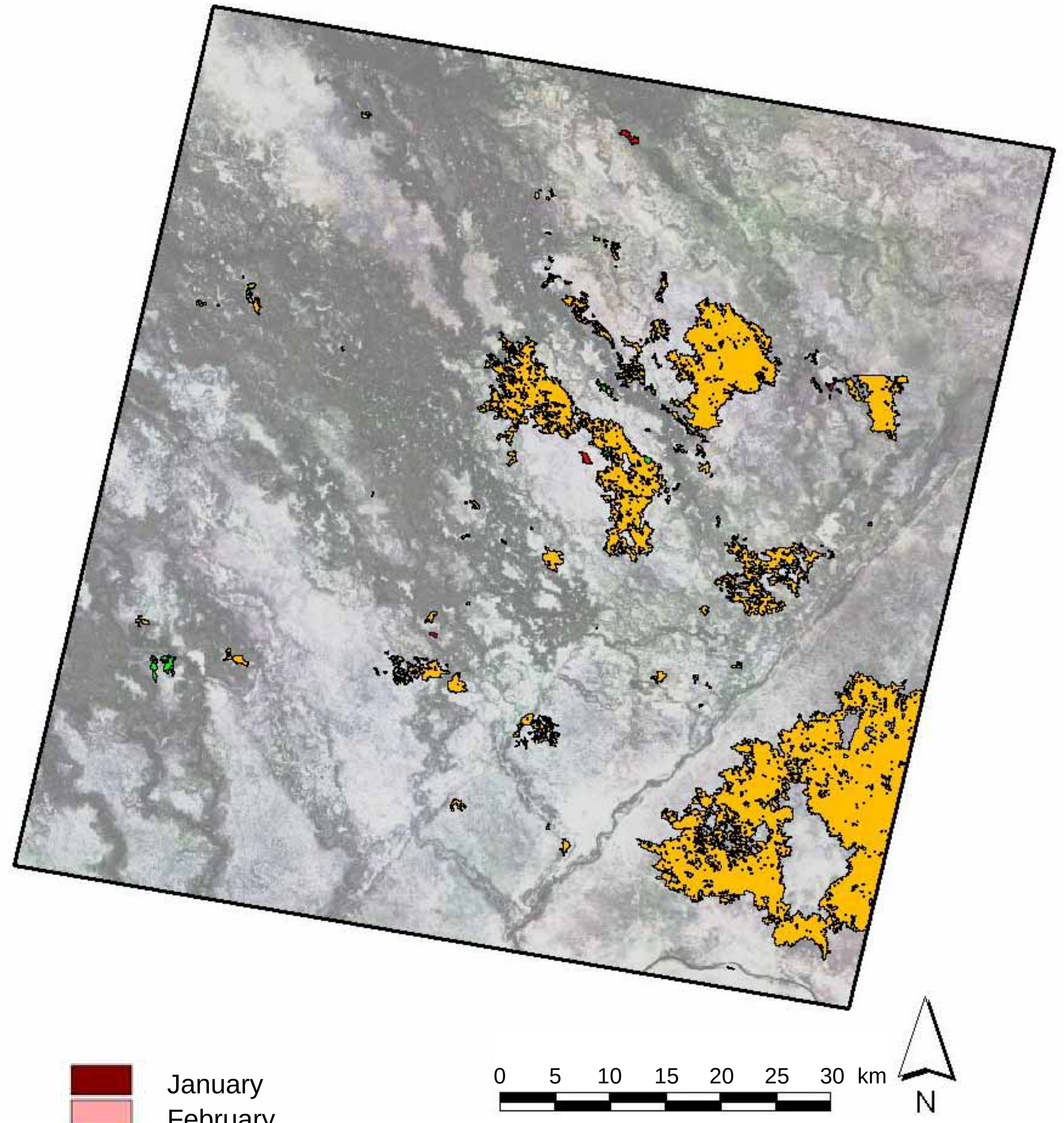
1	29.04.89	(TM5)
2	16.06.89	(TM5)
3	18.07.89	(TM5)
4	04.09.89	(TM5)
5	27.02.90	(TM5)
6	16.04.90	(TM5)
7	03.06.90	(TM5)
8	21.07.90	(TM5)
9	22.08.90	(TM5)
10	23.09.90	(TM5)
11	12.12.90	(TM5)
12	02.03.91	(TM5)
13	03.04.91	(TM5)
14	22.06.91	(TM5)
15	24.07.91	(TM5)
16	09.08.91	(TM5)
17	29.11.91	(TM5)
18	21.04.92	(TM5)
19	08.06.92	(TM5)
20	11.08.92	(TM5)
21	12.09.92	(TM5)
22	14.10.92	(TM5)
23	15.11.92	(TM5)
24	18.01.93	(TM5)
25	07.03.93	(TM5)
26	11.06.93	(TM5)
27	29.07.93	(TM5)
28	30.08.93	(TM5)
29	20.12.93	(TM5)
30	26.03.94	(TM5)
31	13.05.94	(TM5)
32	01.08.94	(TM5)
33	02.09.94	(TM5)
34	04.10.94	(TM5)
35	05.11.94	(TM5)
36	07.12.94	(TM5)
37	24.01.95	(TM5)
38	13.03.95	(TM5)
39	14.04.95	(TM5)
40	01.06.95	(TM5)
41	19.07.95	(TM5)
42	20.08.95	(TM5)
43	21.09.95	(TM5)
44	23.10.95	(TM5)
45	26.12.95	(TM5)
46	16.04.96	(TM5)
47	19.06.96	(TM5)
48	05.07.96	(TM5)
49	22.08.96	(TM5)
50	23.09.96	(TM5)
51	12.12.96	(TM5)
52	21.05.97	(TM5)
53	06.06.97	(TM5)
54	24.07.97	(TM5)
55	09.08.97	(TM5)
56	26.09.97	(TM5)
57	12.10.97	(TM5)
58	15.12.97	(TM5)
59	05.03.98	(TM5)
60	25.06.98	(TM5)
61	27.07.98	(TM5)
62	13.09.98	(TM5)
63	19.01.99	(TM5)
64	09.04.99	(TM5)
65	11.05.99	(TM5)
66	12.06.99	(TM5)
67	10.10.99	(TM7)
68	30.01.00	(TM7)
69	03.04.00	(TM7)
70	29.05.00	(TM5)
71	14.06.00	(TM5)
72	09.08.00	(TM7)
73	25.08.00	(TM7)
74	10.09.00	(TM7)
75	05.11.00	(TM5)
76	08.01.01	(TM5)
77	17.02.01	(TM5)
78	16.05.01	(TM5)
79	17.06.01	(TM5)
80	19.07.01	(TM5)
81	12.08.01	(TM7)
82	13.09.01	(TM7)
83	15.10.01	(TM7)
84	03.01.02	(TM7)
85	24.03.02	(TM7)
86	09.04.02	(TM7)
87	11.05.02	(TM7)
88	14.07.02	(TM7)
89	31.08.02	(TM7)
90	02.10.02	(TM7)
91	27.03.03	(TM7)
92	19.04.03	(ALI)
93	05.05.03	(ALI)
94	21.05.03	(ALI)
95	30.05.03	(ALI)
96	15.06.03	(ALI)
97	09.08.03	(ALI)
98	26.09.03	(ALI)

Appendix 2

Annual fire distribution maps

(see Chapter 2 for location of the study area)

Fire distribution map 1989

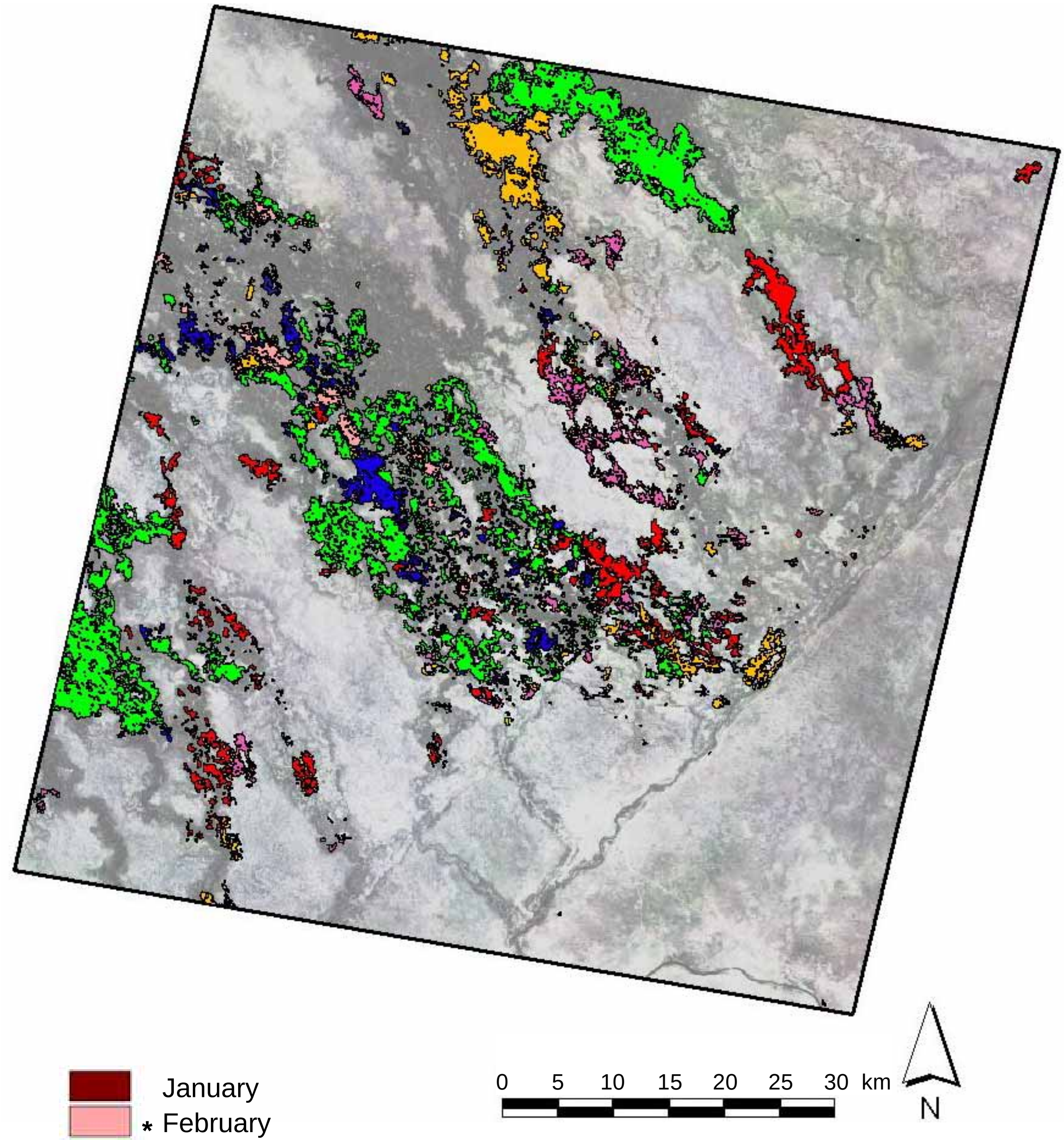


Fire distribution map 1989
Location, extent and date of fires in 1989.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1990



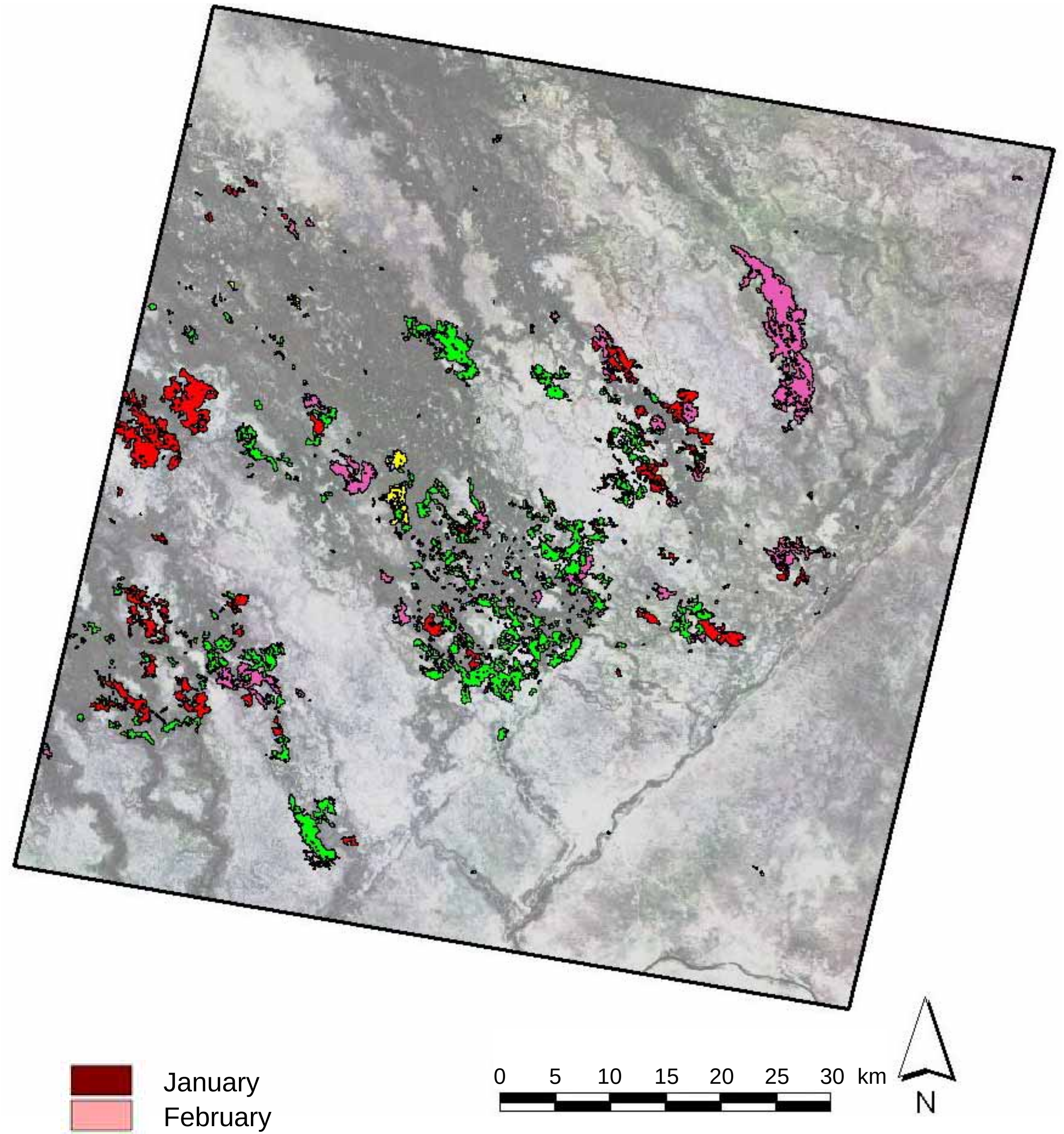
🟫 January
🟥 * February
🟩 March
🟦 * April
🟦 May
🟩 * June
🟥 * July
🟪 * August
🟧 * September
🟦 October
🟨 November
🟦 * December

Fire distribution map 1990
Location, extent and date of fires in 1990.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1991



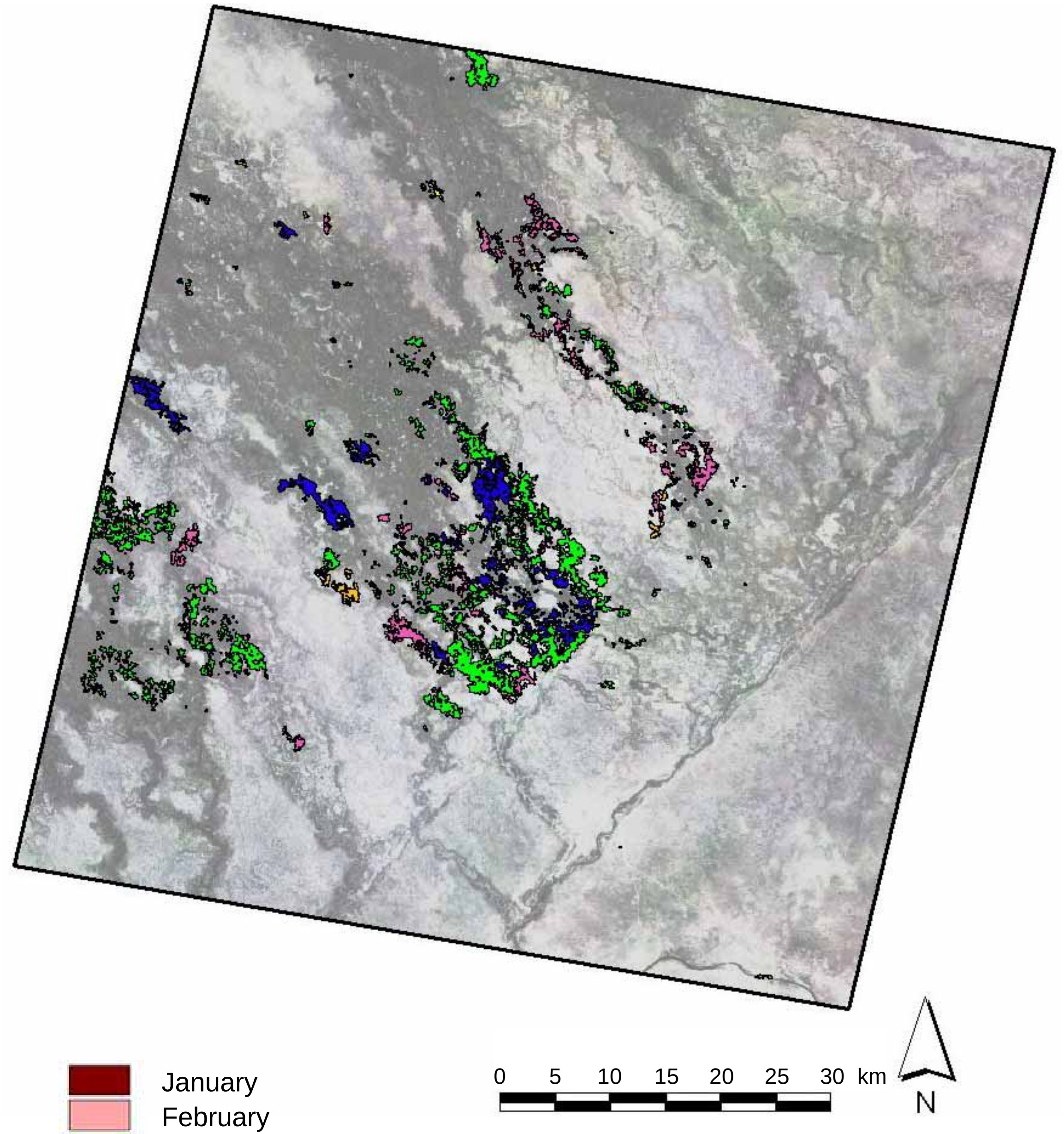
🟫 January
🟥 February
🟩 March
🟦 April
🟦 May
🟩 * June
🟥 * July
🟪 * August
🟧 September
🟦 October
🟨 * November
🟦 December

Fire distribution map 1991
Location, extent and date of fires in 1991.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1992



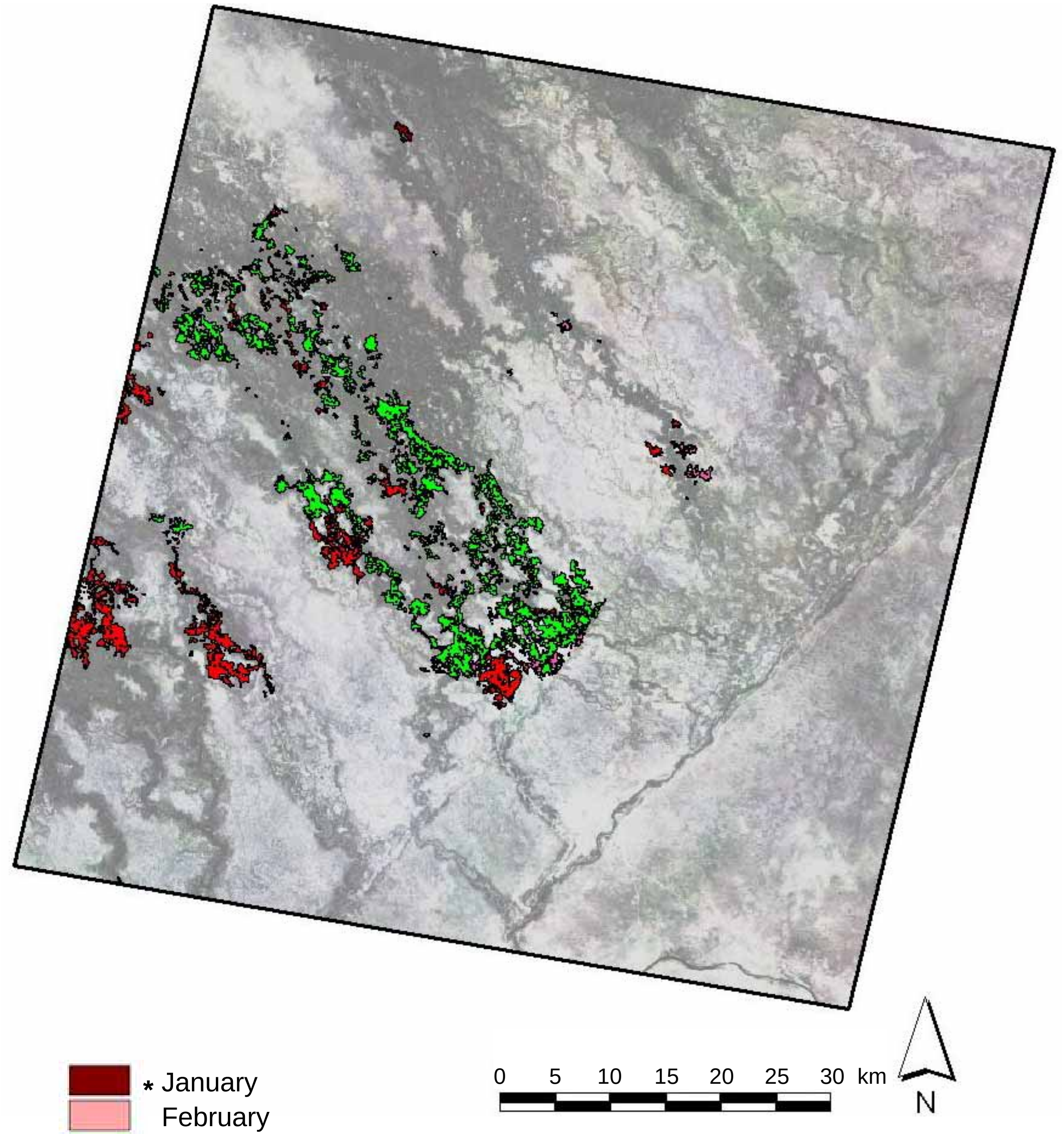
🟫 January
🟥 February
🟩 March
🟦 * April
🟦 May
🟩 * June
🟥 July
🟪 * August
🟧 * September
🟦 October
🟨 * November
🟦 December

Fire distribution map 1992
Location, extent and date of fires in 1992.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1993



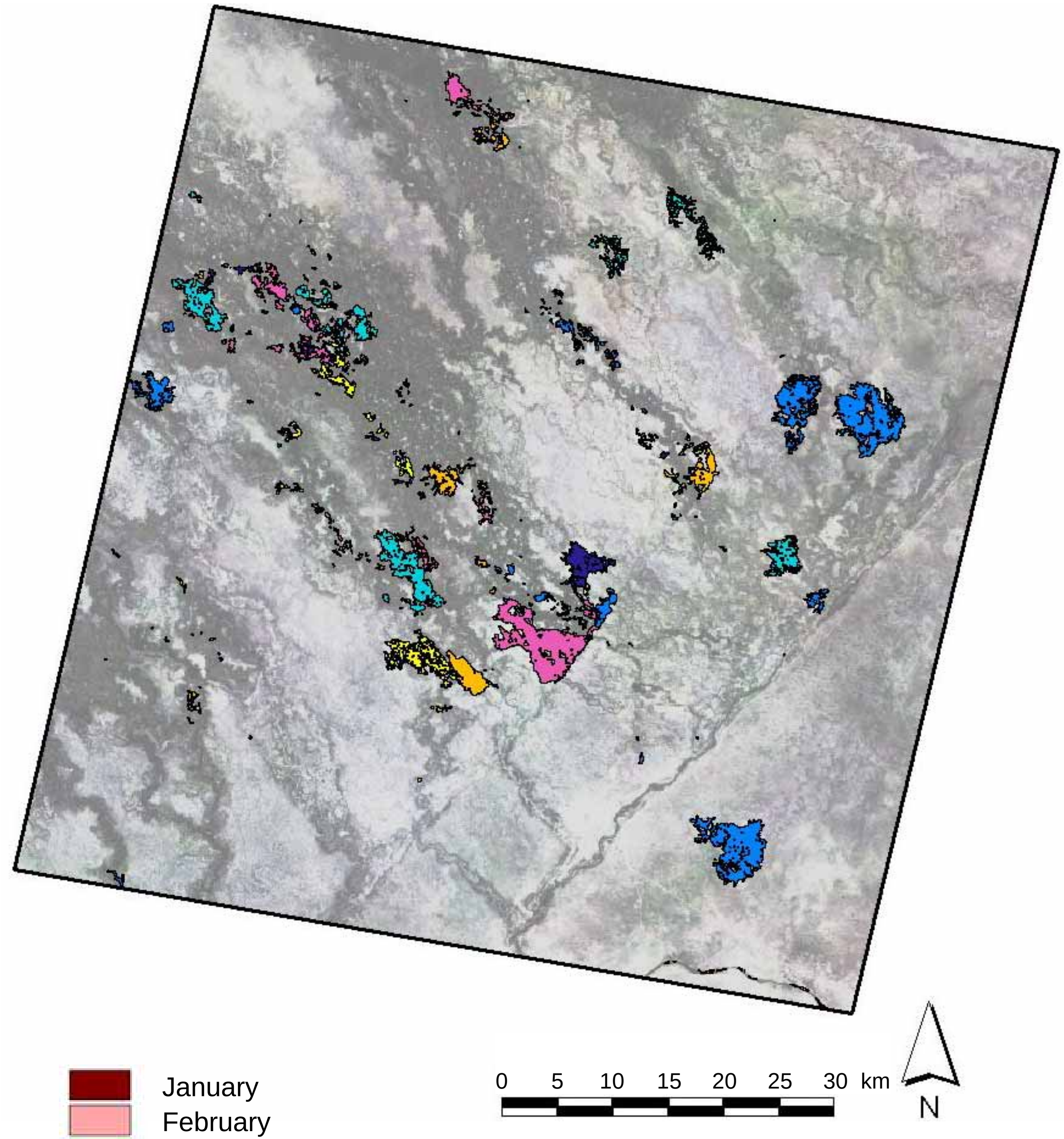
- 🟥 * January
- 🟪 February
- 🟩 * March
- 🟦 April
- 🟦 May
- 🟩 * June
- 🟥 * July
- 🟪 * August
- 🟧 September
- 🟦 October
- 🟨 November
- 🟦 December

Fire distribution map 1993
Location, extent and date of fires in 1993.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1994

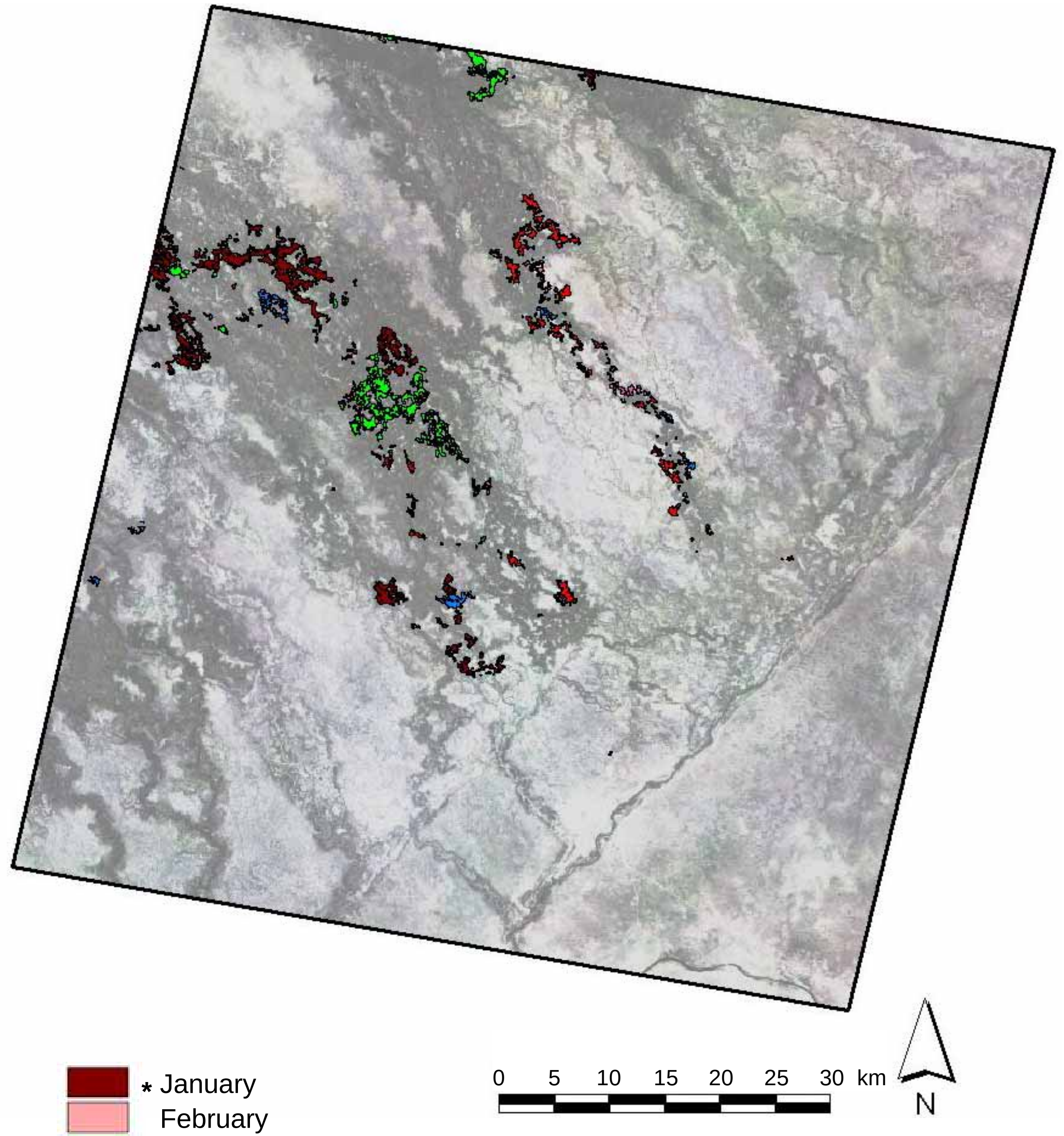


Fire distribution map 1994
Location, extent and date of fires in 1994.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1995



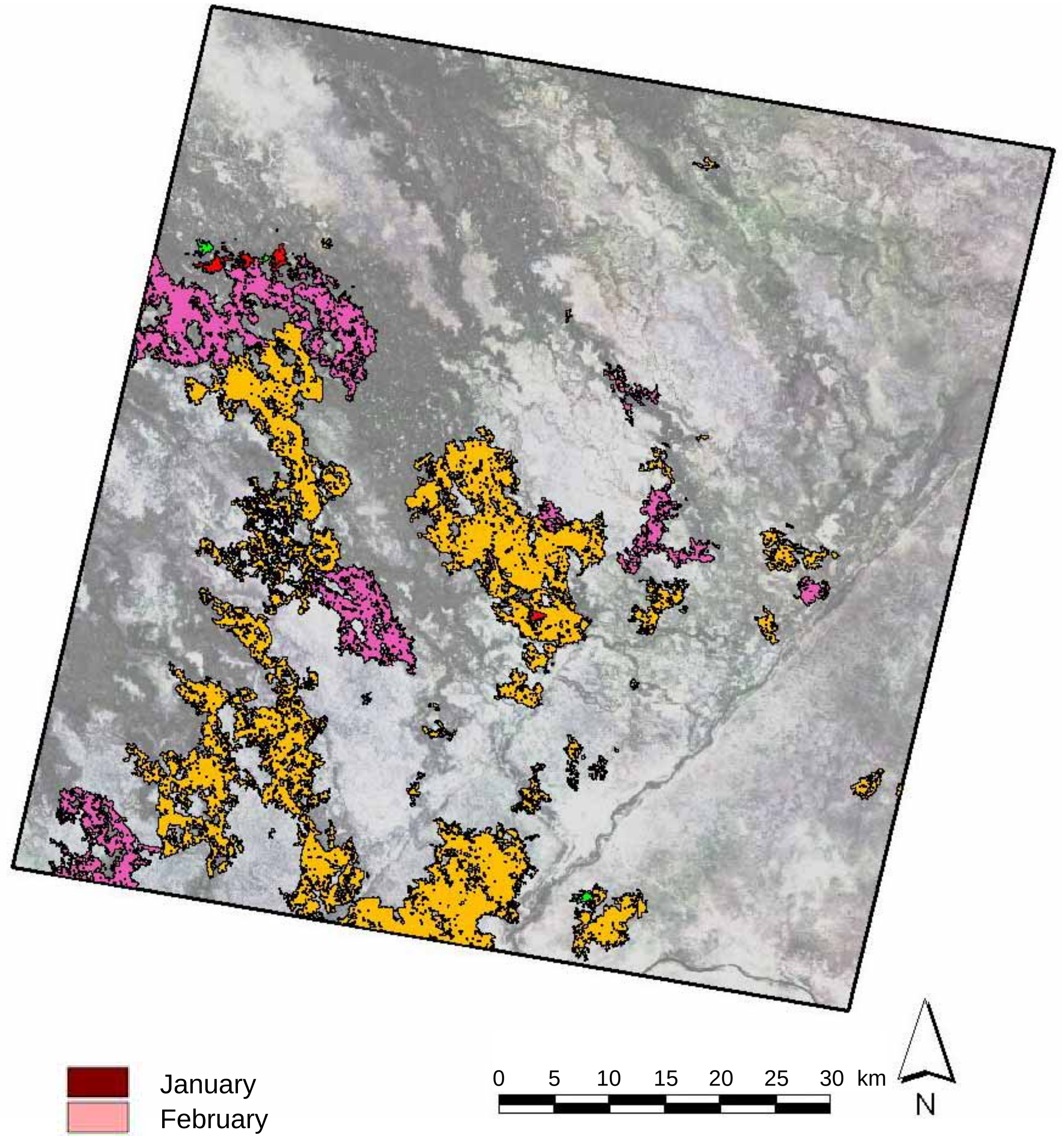
🟫 * January
🟪 February
🟩 March
🟦 April
🟦 May
🟩 * June
🟥 * July
🟪 * August
🟧 September
🟦 * October
🟨 November
🟦 December

Fire distribution map 1995
Location, extent and date of fires in 1995.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1996



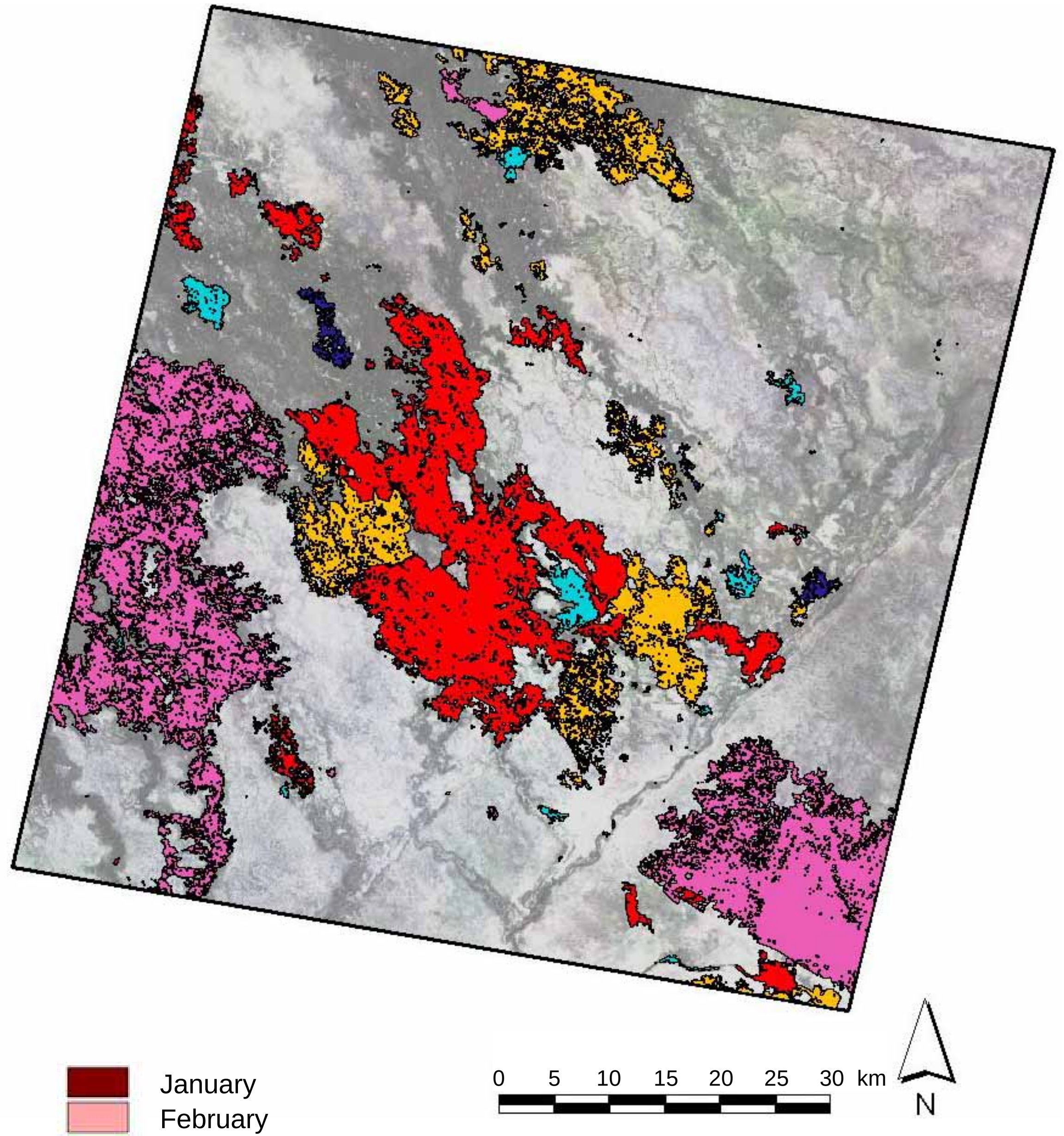
🟥 January
🟥 February
🟩 March
🟦 April
🟦 May
🟩 * June
🟥 * July
🟪 * August
🟧 * September
🟦 October
🟨 November
🟦 December

Fire distribution map 1996
Location, extent and date of fires in 1996.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1997



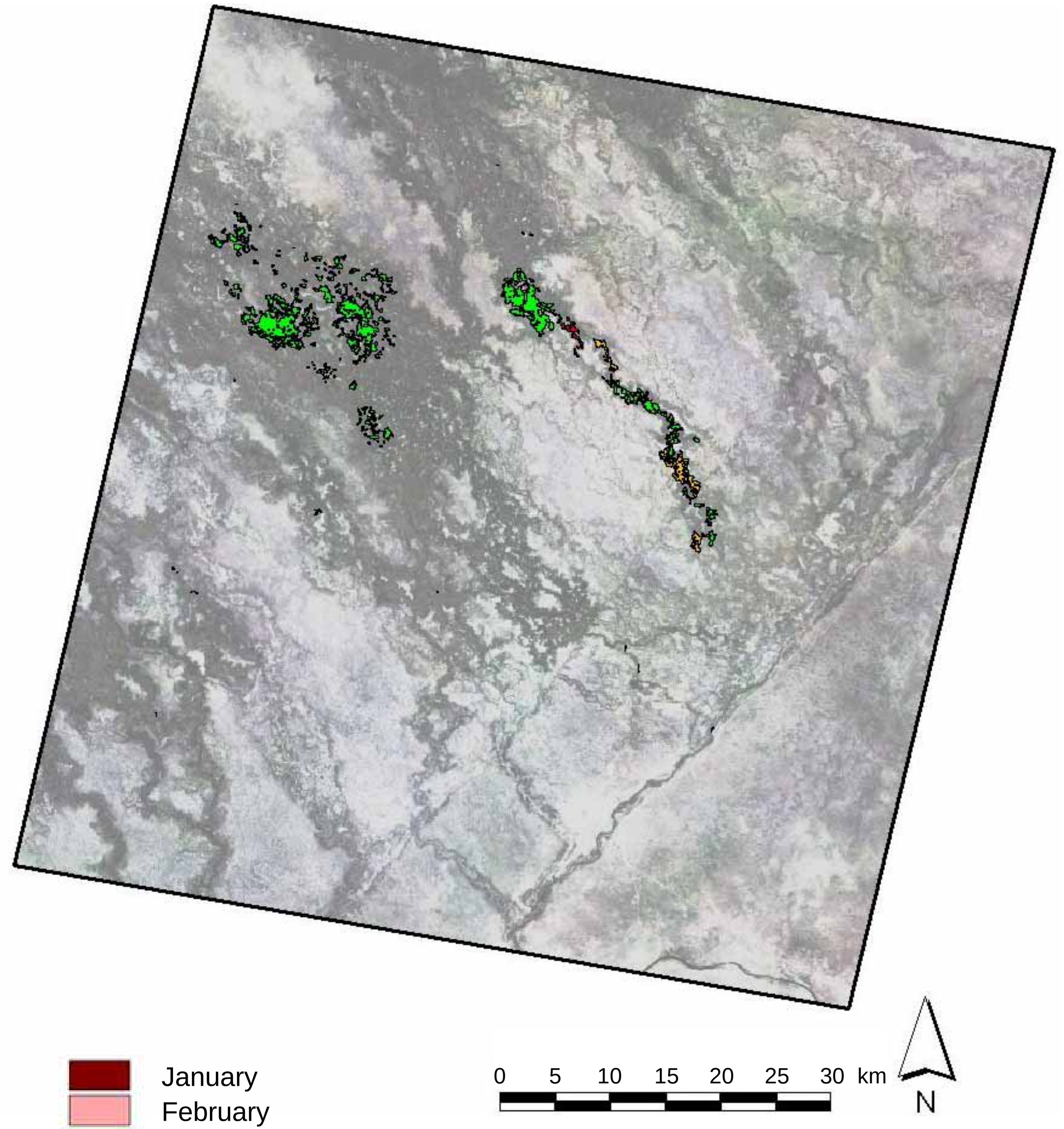
- 🟥 January
- 🟥 February
- 🟩 March
- 🟦 April
- 🟦 * May
- 🟩 June
- 🟥 * July
- 🟪 * August
- 🟧 * September
- 🟦 October
- 🟨 November
- 🟦 * December

Fire distribution map 1997
Location, extent and date of fires in 1997.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1998



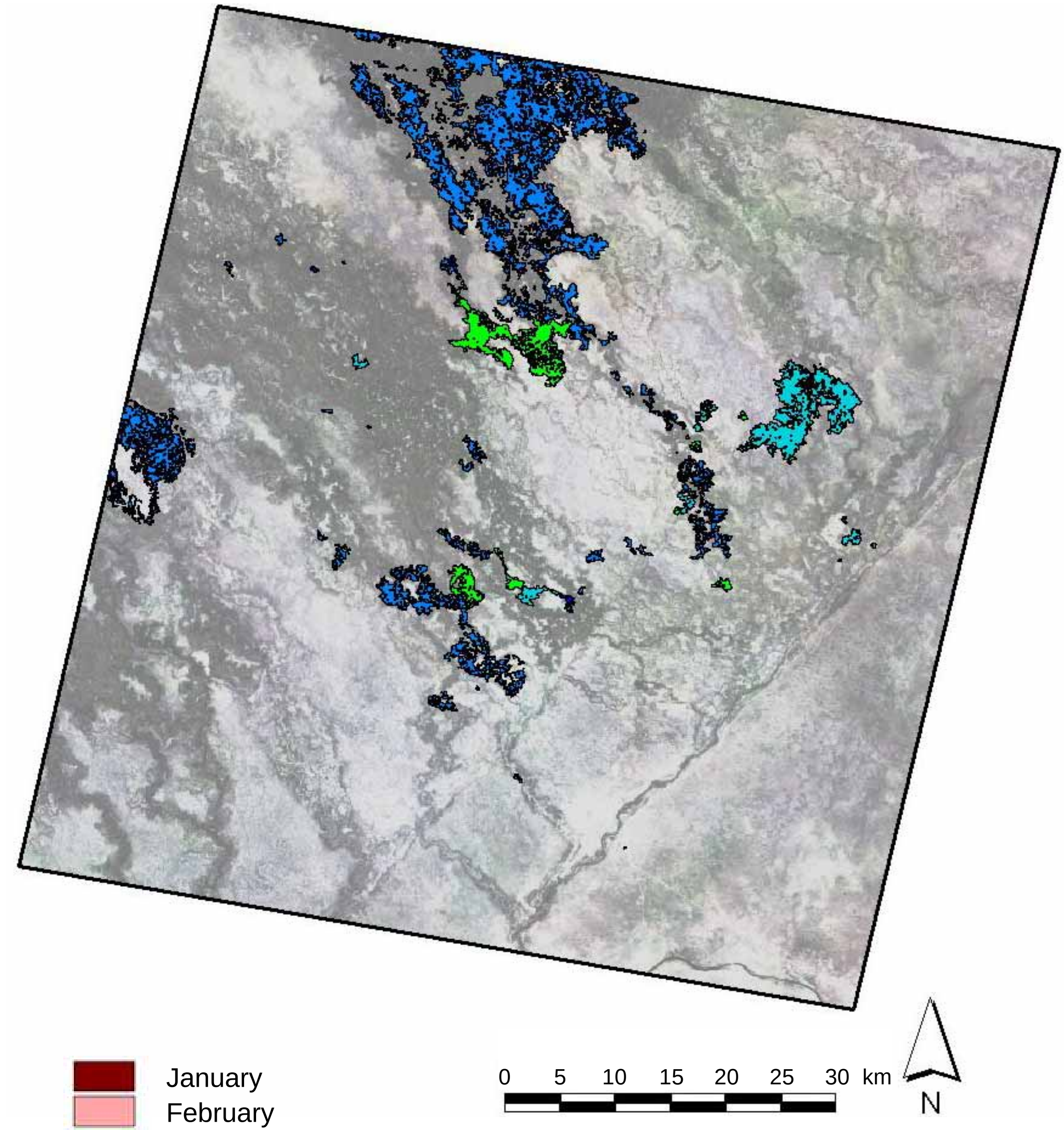
🟥 January
🟥 February
🟩 March
🟦 April
🟦 May
🟩 * June
🟥 * July
🟪 August
🟧 * September
🟦 October
🟨 November
🟦 December

Fire distribution map 1998
Location, extent and date of fires in 1998.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 1999



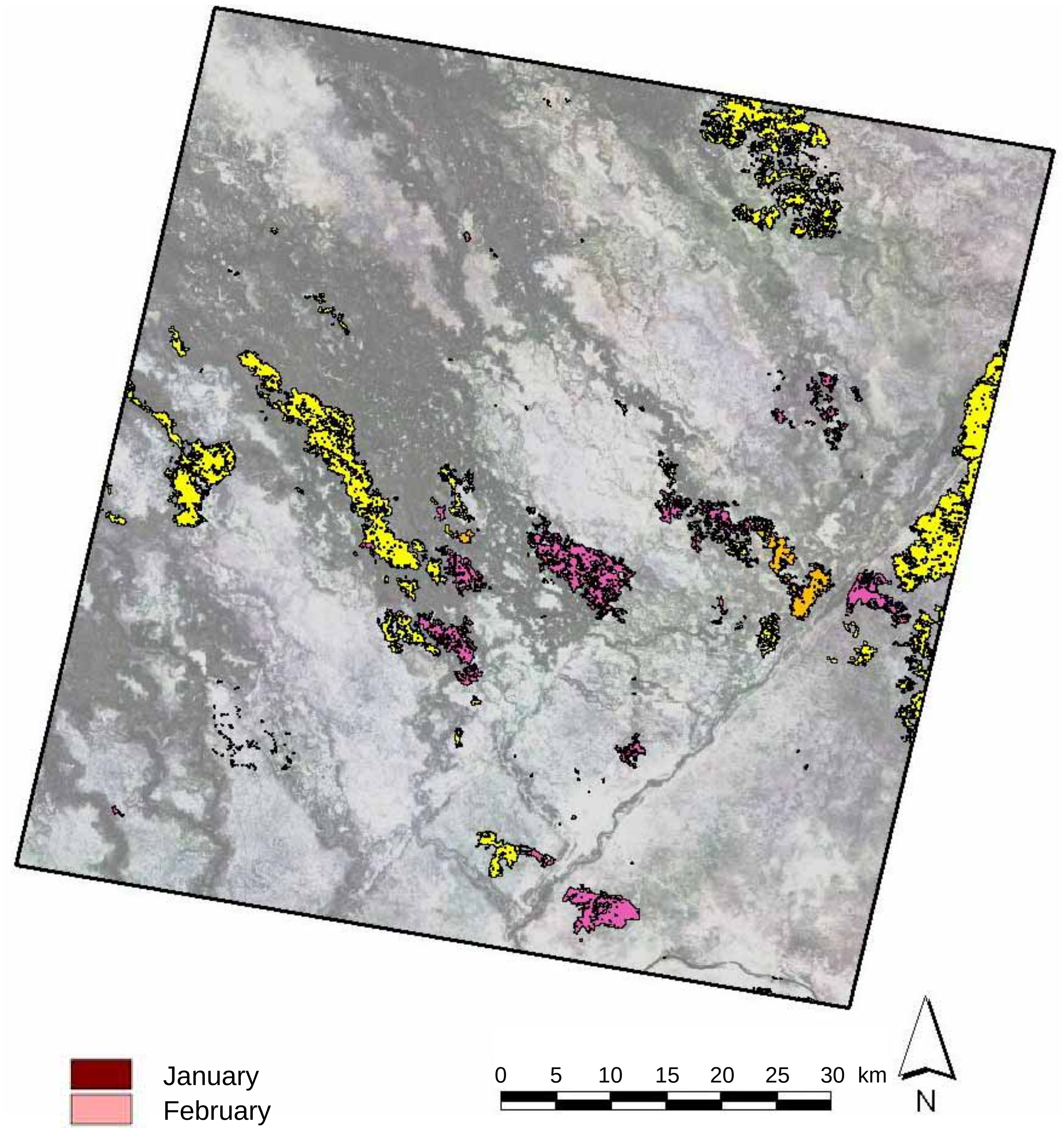
🟫 January
🟥 February
🟩 March
🟦 * April
🟦 * May
🟩 * June
🟥 July
🟪 August
🟧 September
🟦 * October
🟨 November
🟦 December

Fire distribution map 1999
Location, extent and date of fires in 1999.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 2000



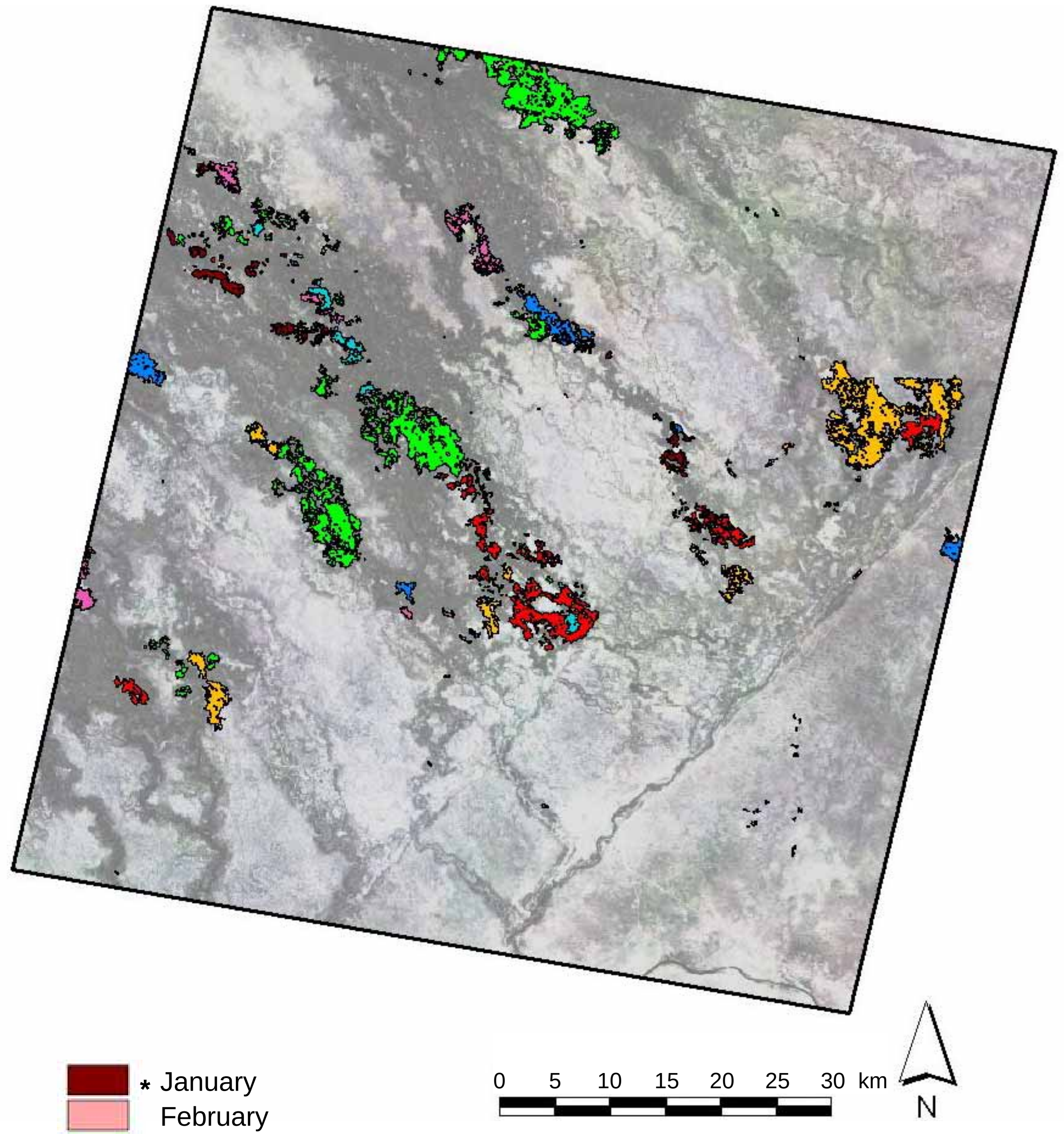
🟫 January
🟥 February
🟩 March
🟦 April
🟦 May
🟩 June
🟥 July
🟪 * August
🟧 * September
🟦 October
🟨 * November
🟦 December

Fire distribution map 2000
Location, extent and date of fires in 2000.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 2001



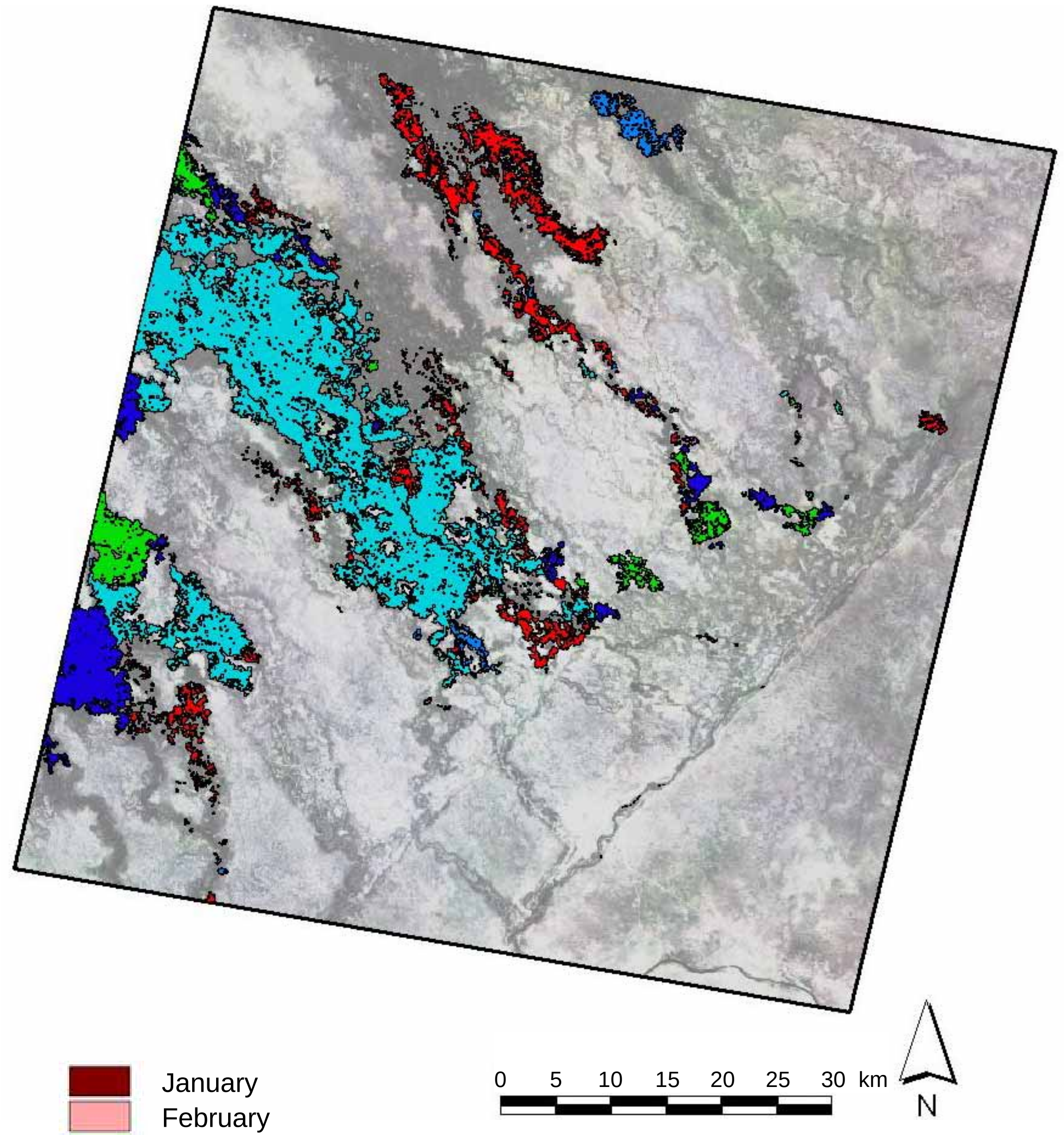
- 🟥 * January
- 🟥 February
- 🟩 March
- 🟦 April
- 🟦 * May
- 🟩 * June
- 🟥 * July
- 🟪 * August
- 🟧 * September
- 🟦 * October
- 🟨 November
- 🟦 December

Fire distribution map 2001
Location, extent and date of fires in 2001.

Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Fire distribution map 2002

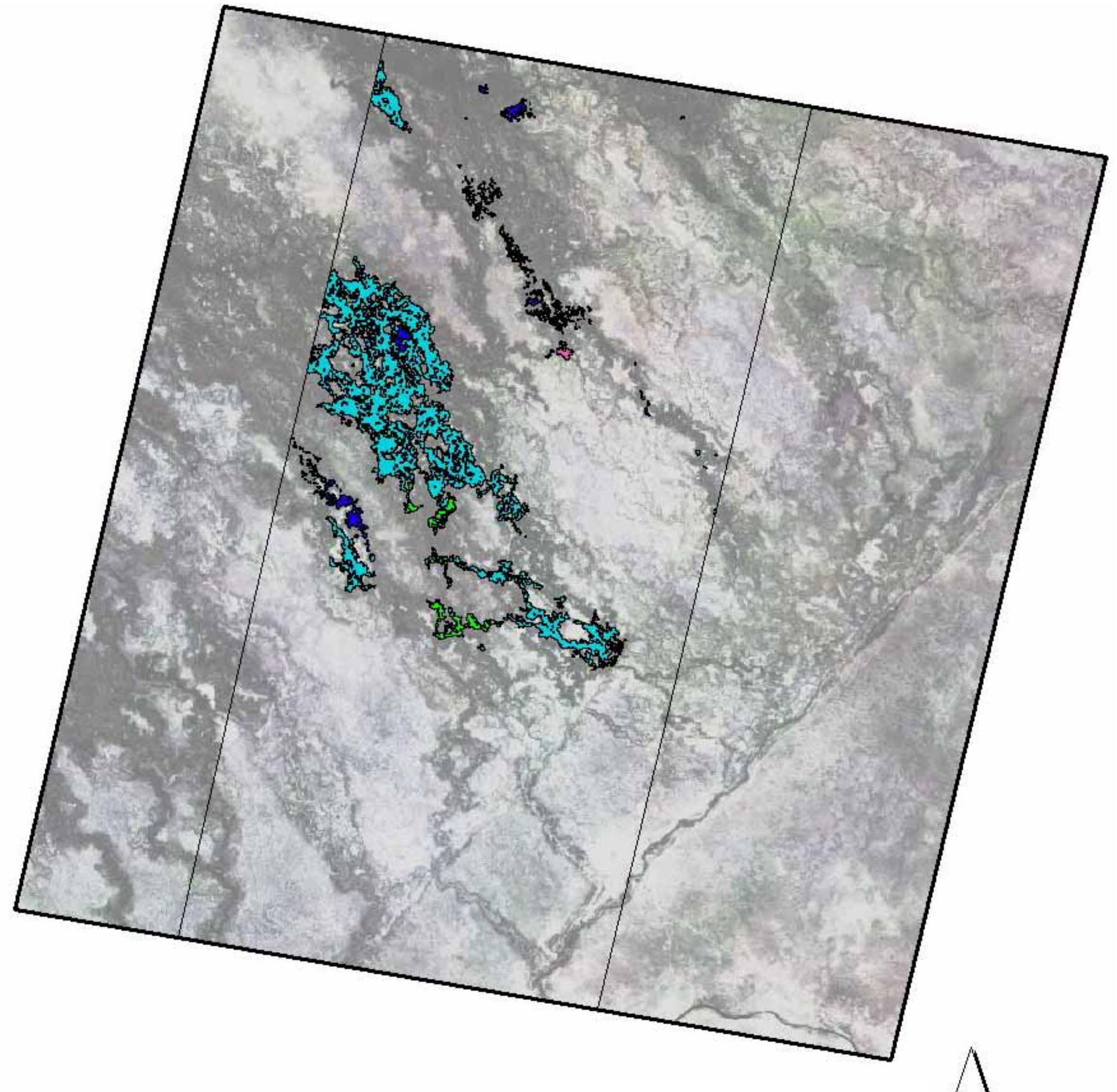


■ January
■ February
■ * March
■ * April
■ * May
■ June
■ * July
■ * August
■ September
■ * October
■ November
■ December

Fire distribution map 2002
Location, extent and date of fires in 2002.

Background image: 03-Jan-2002
(true colour composite)
The asterisks indicate the months for which a fire was recorded.

Fire distribution map 2003



- 🟥 January
- 🟥 February
- 🟩 * March
- 🟦 * April
- 🟦 * May
- 🟩 * June
- 🟥 July
- 🟪 * August
- 🟧 * September
- 🟦 October
- 🟨 November
- 🟦 December

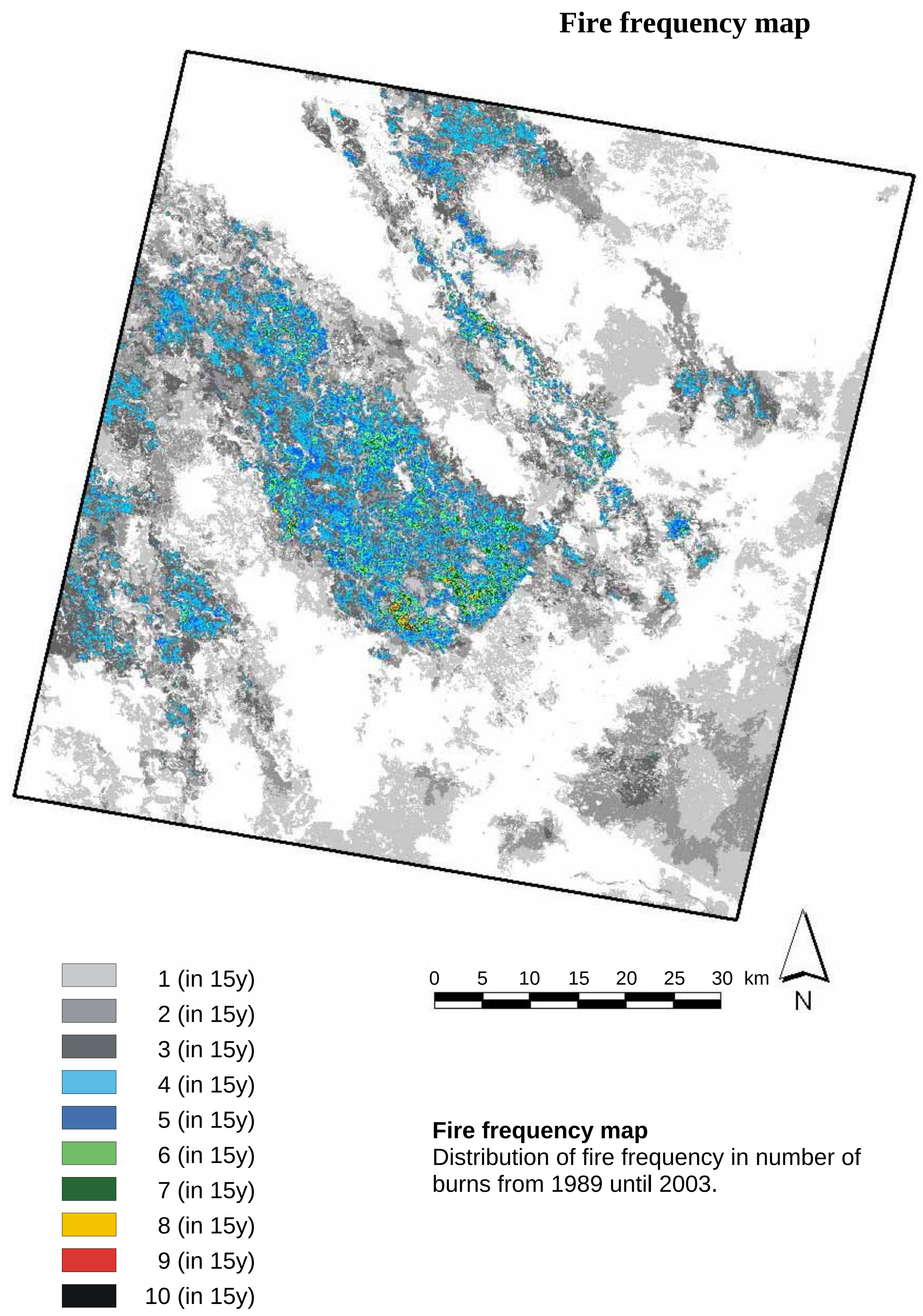
Fire distribution map 2003
Location, extent and date of fires in 2003.

The study area for 2003 was limited to the central part because of reduced spatial coverage of ALI scenes.
Background image: 03-Jan-2002
(true colour composite)

The asterisks indicate the months for which a fire was recorded.

Appendix 3

Fire frequency map



Fire frequency map
Distribution of fire frequency in number of burns from 1989 until 2003.