

FLOODPLAIN VEGETATION RESPONSES TO FLOOD REGIME IN THE SEASONAL
OKAVANGO DELTA, BOTSWANA

By

MICHAEL MURRAY-HUDSON

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2009

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To the late Pete Smith, who planted the seed, and to Frances, who helped it grow.

ACKNOWLEDGEMENTS

The research on which this dissertation is based was funded and supported by many and various agencies: The University of Botswana, University of Florida (Adaptive Management: Water, Wetlands and Watersheds program funded by the National Science Foundation), and the Biokavango project (Global Environment Facility). The University of Botswana also provided funding for the costs of studying and living abroad. Their support is gratefully acknowledged. In addition the support of all of the staff at the Harry Oppenheimer Okavango Research Centre was instrumental in facilitating both the field research and the remote sensing components of this work. In particular, Piotr Wolski (who can make computers work *for* him), Cornelis Vanderpost for help with imagery, and Wilfred Kaneguba, Moagisi Diare, Florian Bendsen and Aulter Karumendu for unflagging enthusiasm, willingness to do transects chest deep in crocodile-infested waters, and very fine goat stews in very remote places. Dr Jonathan Timberlake and the staff at the Royal Botanical Gardens in Kew, England, provided invaluable help with identifying stubborn species.

Special thanks are due to Dr Mark Brown, my supervisor, for allowing me great flexibility in achieving my goals, and for the field trips in support of the Integrative Graduate Education and Research Traineeship Program (IGERT) program.

Thanks are also due to the following hunting and photographic safari operators for their cooperation: Harry Charalambous (Johan Calitz Safaris), Horseback Safaris, Elephant Back Safaris, and Rann Hunting Safaris.

Lastly, and most important, my wife Frances not only participated in the field data collection, but also put up with me and my moods throughout the entire process: without her this dissertation would not have been possible.

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Abstract of Dissertation Presented to the Graduate School
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Requirements for the Degree of Doctor of Philosophy

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Michael Murray-Hudson

August 2009

Chair: M. T. Brown

Major: Environmental Engineering Sciences

As the global anthropogenic footprint grows, its effect is perhaps nowhere as profound as on the water cycle. Multiple influences act to change the variability of hydrological regimes: increasing rates of change in climate, a warmer, more carbon-rich biosphere, changes in land cover, and manipulations of river systems for water and energy supply. This increased variability is manifested as change in ecosystem services. Wetlands, which provide many such services, are particularly susceptible to changes in hydrology, and if we are to continue deriving ecosystem services from them, we need to understand the potential effects of hydrological change.

This dissertation describes the development of tools for investigating the effects of hydrological change on floodplain plant communities in the Okavango Delta, a flood-pulsed wetland at the terminus of a river basin shared by three countries. A hierarchical vegetation classification system for floodplains in the seasonally-pulsed Boro and Xudum distributaries was developed based on vegetation survey data from 30 floodplains. Analysis of two time-series of satellite imagery was used to derive flooding history in terms of extent, annual frequency and monthly duration. Correlations were established between hydroperiod parameters and plant species composition; the predictive capacity of remotely-sensed hydroperiod was tested using a 25-site calibration data set and a 5 site validation set. Species assemblages defined through

cluster analysis reflect the influence of hydroperiod in 2 distinct groups: i) assemblages of regularly flooded areas, in which species composition is driven by flood duration; ii) assemblages of infrequently flooded areas, in which species composition follows a typical dry-land succession from herbaceous to woody species between flood pulses. Finally, floodplain classes and species hydroperiod response relationships were used to construct a multi-species distribution models as a layer for a spatial hydrological model.

In the semi-arid environment of the Delta, hydroperiod is clearly a major determinant of floodplain plant ecology. The tools outlined here provide both a simple system for monitoring of floodplain status and trends through time, and a system for testing scenarios of future hydrological change and its potential effects on species distributions. Temporal testing of the models, to improve confidence in their ability to predict species distribution change, and extension of the classification system to include assemblages of perennially inundated floodplains are needed. Better knowledge of species autecology would improve the interpretation of species distributions and consequently the modeling.

CHAPTER 1 INTRODUCTION

Problem Statement

As the global anthropogenic footprint grows, its effect is perhaps nowhere as profound as on the water cycle. Multiple influences act to increase the variability of hydrological regimes: increasing rates of change in climate, a warmer, more carbon-rich biosphere, changes in land cover, and manipulations of river systems for water and energy supply. This increased variability is manifested in the ecology, and consequently as change in ecosystem services. Wetlands, which provide many such services, are particularly susceptible to changes in hydrology. There is an increasingly urgent need for a better understanding of the consequences of change, as pressure on natural resource systems grows.

A key question is how wetland vegetation responds to changes in hydrology. The ability to predict changes in wetland vegetation is fundamental to ensuring the sustained flow of services and benefits we derive from wetlands. This dissertation investigated and quantified the responses of vegetation to different flooding regimes in the Okavango Delta, a large seasonally-pulsed tropical wetland in Botswana, southern Africa.

Hydrology and Wetland Vegetation

Hydrology is probably the single most important determinant of the establishment and maintenance of specific types of wetland and wetland processes (Mitsch and Gosselink 2000). Water inflows to wetlands result from direct precipitation, sheet or river inflows, groundwater seepage, or combinations of any or all of these. The hydrological regime of wetlands may be characterized in terms of frequency (the number of times a wetland is flooded in a given period), duration (the length of time there is standing water), and depth. Many tropical and subtropical wetlands experience an annual flood pulse as a result of pronounced seasonality in rainfall (Junk

2002), while others may experience sporadic or intermittent flooding, particularly in arid areas (Brock and Rogers 1998, Capon 2005), or a predictable daily pulse as occurs in marshes within the range of influence of ocean tides.

The variability of hydrology both between different wetlands, and within specific wetlands, exerts a major controlling influence over the establishment and development of vegetation (Junk and Piedade 1993, Seabloom et al. 2001, Murphy et al. 2003, De Steven and Toner 2004, Porter et al. 2007). Although many wetland species can tolerate long periods of flooding, initial establishment may require specific hydrological conditions. For example, the propagules of many herbaceous marsh species only germinate after one or more drawdowns of water level exposes the wetland substrate (Boutin and Keddy 1993, Ter Heerdt and Drost 1994, Porter et al. 2007). Some species have developed the ability to stagger germination across many successive inundation periods (Brock and Rogers 1998). Once established, or where inundation is perennial or near-perennial, reproduction is often clonal; plants develop extensive systems of rhizomes or stolons which produce new plants, and may also act as energy storage systems to cope with the higher energy demands of the wetland habitat (Blom and Voesenek 1996). Sexual reproduction in wetlands with long durations of flooding usually requires the production of aerial flowers to allow pollination (Cronk and Fennessey 2001). Van der Valk (1981), in a model of freshwater wetland vegetation dynamics, recognized two end-members of wetland species: i) species with long-lived propagules that can become established whenever suitable environmental conditions occur; and ii) species with short-lived propagules, which can only become established if the propagules arrive in a wetland during a period when environmental conditions are suitable. Recruitment and dispersal limitations, and their relationship to hydrology are therefore fundamental factors in determining species distribution and community composition

(“community” is used in the sense of the collection of species found at a specific place and time throughout this document).

In many wetlands, where topography, in combination with hydrology, creates a flooding gradient, this results in zonation, or banding, of plant species according to their different hydrological tolerances (Johnson et al. 1987, Van Der Valk and Welling 1988, Lenssen et al. 1999). Given the dynamic nature of wetland hydrology, however, such zones may not be fixed geographically, but may be mobile along the gradient (Niering 1987). Likewise, the composition of the species which constitute such zones may vary with time and space, depending on starting conditions, species characteristics and specific hydrological conditions.

Other variables (apart from direct manipulation by humans) that may affect wetland vegetation establishment and development include soil chemistry and structure, water quality, and fire. Wetland soils may be categorized as organic or mineral, with organic soils generally having higher porosity and water holding capacity, but lower pH and often lower nutrient availability than mineral soils (Mitsch and Gosselink 2000). During inundation, wetland soils are anaerobic, which affects nutrient availability and cycling, and requires specific adaptations by rooted wetland plants to overcome the low oxygen conditions, such as aerenchyma and various other structural adaptations for increasing within-plant gas flow (Cronk and Fennessy 2001). Where hydrological variability results in periodic drawdowns, nutrient cycling and organic matter turnover tends to be more rapid than in perennially inundated wetlands. Water quality may have profound effects on species composition and distribution, with higher nutrient conditions frequently associated with reduced diversity and increased production, within limits (Bornette et al. 1998, Bedford et al. 1999). Fire is a feature of many tropical and sub-tropical wetlands which experience seasonal fluctuations in flooding. Depending on the frequency and

intensity, it may be considered an acute disturbance or an important part of the normal regime of the wetland (Cronk and Fennessy 2001). Many wetland plant species are adapted in various ways to a regime of recurrent fire: underground storage organs and vegetative propagules are common in wetland plants, as are fire-resistant propagules; fire may stimulate growth, seed release or flower production (Main and Barry 2002)

Wetland plants are the base of the wetland food chain, and so constitute a major conduit for energy flow into the system. They also provide habitat structure for epiphytic microbial communities, macro-invertebrates and fish; they modify water and substrate chemistry, and influence the hydrology and sediment regime of wetland environments (Cronk and Fennessy 2001). They are thus the key to understanding wetland ecology.

The Okavango Delta: A Flood-Pulsed Tropical Wetland

In the Okavango river basin in southern Africa (Figure 1-1), low human population densities of basin states (partly as a result of decades of war in Namibia and Angola) mean that the river system has experienced little of the anthropogenic manipulation that has affected similar large wetland systems in the developed world. However, peace, economic growth and development in the three basin states, in conjunction with global climate change, make hydrologic change inevitable (Ashton and Neal 2003). As the downstream terminus of this endorheic river system, the Okavango Delta, in northern Botswana, is particularly vulnerable to upstream change (Scudder et al. 1993, McCarthy et al. 2000). Land use in the Delta is predicated on wildlife management, and the wildlife resource is inextricably linked with Delta ecology, in particular the flood regime (Patterson 1976). A thorough understanding of vegetation-hydrology relationships is needed to inform policy development and management of both the basin, and the Delta.

The Delta is a 14,000 km² complex of channels and floodplains on a tectonically defined alluvial fan (McCarthy et al. 1997). It receives a regular, highly variable, but essentially unimodal annual flood pulse (Figure 1-2) resulting from seasonal rains falling between October and April in the central plateau of Angola. The pulse takes almost six months to arrive in the distal reaches of the Delta, traveling more than 1000 km across low gradients (Wilson and Dinçer 1976). The increased flow surcharges the main channel, spills through the vegetated banks and spreads across the surface of the Delta through distributary channels and floodplains, reaching its maximum extent between late August and September (Porter and Muzila 1988, Gumbrecht et al. 2004c). Water infiltrates through the floodplain soils, moving laterally towards the islands under a gradient maintained through evapo-transpiration by riparian trees (McCarthy et al. 1993, Wolski and Savenije 2006). Over ninety-five percent of the inflow is lost in this way, outflow constituting 3-5% of the total inflow (Dinçer et al. 1987). Different floodplains are inundated for varying durations each successive year, with the degree and extent depending primarily on the hydrograph characteristics of the incoming flood, but also on antecedent conditions relating to floods from the previous years, and the local rainfall preceding the arrival of the flood pulse. The infiltration rates are such that the movement of water into floodplains is highly uni-directional; there is little evidence of return flows from floodplains to channels during flood recession (Wolski et al. 2006)

The Okavango Delta soils consist primarily of fine, homogeneous fluviually-reworked aeolian quartz sands. Grain size is highly uniform (~0.3 mm), and there is a variable amount of clay-sized material, apparently mainly endogenic in origin (Baert 1986). Soil organic content has been recorded as between 2.2 and 2.6% in one seasonal floodplain in the Boro distributary (Mubyana et al. 2002). The nutrient status of water in the channels is consistently oligo- to

mesotrophic (total nitrogen (TN), 0.9mg l^{-1} and total phosphorous (TP), $44\ \mu\text{g l}^{-1}$ (Cronberg et al. 1996)), although in the seasonal floodplains, higher levels of TN ($1.5\text{-}3.1\ \text{mg l}^{-1}$) and TP ($125\text{-}466\ \mu\text{g l}^{-1}$) have been recorded (Høberg et al. 2002), with highest levels coincident with the arrival of floodwaters, and subsequent sigmoidal declines to approach channel values over a period of about 3 months.

Seasonal floodplains in the Okavango Delta burn more frequently than the surrounding drylands, with a maximum frequency of 10 times in 15 years (Heinl et al. 2006). Fire frequency was maximum at an intermediate flooding frequency of about one year in two. Despite these clear correlations between flooding and fire frequency, Heinl et al (2007) found that no differences in floodplain species composition could be attributed to fire frequency. They concluded that flood frequency and specific annual flood cycles were the determining factors for vegetation on active seasonal floodplains.

Research Questions

In the context of the generally consistent soils and water quality, and the minimal effects of fire on species composition in the seasonal floodplains of the Okavango Delta, the hydrological regime of flood pulsing, with its intra- and inter-annual variability is likely to be the major determinant of the spatial arrangement of floodplain species. This study investigated and quantified the relationships between hydrological variables and seasonal floodplain plant communities in the Boro-Xudum distributaries of the Okavango Delta (Figure 1-3). The following research questions were posed:

1. What different vegetation species groups occur on seasonal floodplains? Given the hydrological and physiographic variability, seasonal floodplains in the Delta are subject to different frequencies and durations of inundation. The identification of groups of species related to these hydrological differences would allow the definition of categories of floodplain.

2. What relationships exist between species groups and flood regimes? Floodplains characterized by different flood regimes should be dominated by species groups with preferences for the prevailing regime. Knowledge of such relationships would allow the prediction of species group based on hydrology.
3. What are the responses of individual species to differences in flooding regime? Plant species in less frequently flooded areas might be expected to be seed-producing opportunists, with short life-cycles , while increasing frequency and duration of flooding should favour clonal perennial species. Information on species response to hydrological variables would permit predictive modeling of species.

Dissertation Structure

This introductory chapter provides an overview and framework for the remainder of the document, which describes the results of different analyses of the data, and is structured as a series of stand-alone papers. Figure 1-4 is a graphic description of the study, showing: i) the parallel processes of collecting and analyzing vegetation data, and deriving a spatial hydrological history from satellite remote sensing; ii) the integration of these two data sets through ordination and regression modeling to develop flood-duration driven spatial species and community distribution models.

Chapter 2 describes the derivation of hydrological histories for floodplains in the Delta by interpretation of remote sensing. Analysis of two time-series of satellite imagery was used to derive flooding history in terms of extent, annual frequency (from an 18-year Landsat Thematic Mapper (TM) series) and monthly duration (from a 8-year Moderate Resolution Imaging Spectroradiometer (MODIS) series). Correlations were established between hydroperiod parameters and plant species composition, and the predictive capacity of remotely-sensed hydroperiod was tested using a 25-site calibration data set and a 5-site validation set.

In Chapter 3, the development of a hierarchical vegetation classification system for floodplains in the seasonally-pulsed Boro and Xudum distributaries is described. The system was based on the ordination and cluster analysis of vegetation survey data from 30 floodplains.

Indicator species analysis was used to determine the most ecologically sound levels of division. The classification system is presented as a dichotomous key using indicator species. It is intended as a simple survey instrument to facilitate monitoring of the Delta for management purposes.

In Chapter 4, the influence of the flood pulse on species and community distribution is investigated and quantified. Eight communities defined through cluster analysis reflect the influence of hydroperiod in 2 distinct groups: i) communities of regularly flooded areas, in which species composition is driven by flood duration; ii) a community of infrequently flooded areas, in which species composition follows a typical dry-land succession from herbaceous to woody species between flood pulses. Generalized linear models of individual species distributions in relation to average flood duration were derived from canonical correspondence analysis and logistic regression, and average duration optima were used to characterize communities of the regularly flooded areas.

Finally, in Chapter 5, generalized linear models of species hydroperiod response relationships were used to construct a multi-species distribution model and an aggregated community model, as layers for a spatial hydrological model. The model is intended for testing hypotheses about the effects of changing inflows (as a result of human development and/or climate change) on floodplain plant distributions. Model output is in the form of raster maps of pixel size 1 km², of individual species distributions and aggregated community distributions. Hydrological input is as monthly inflows; the historical data set may be modified to simulate different development and climate change scenarios.

Chapter 6 provides a summary of the main findings, conclusions and a brief discussion of directions for further work.

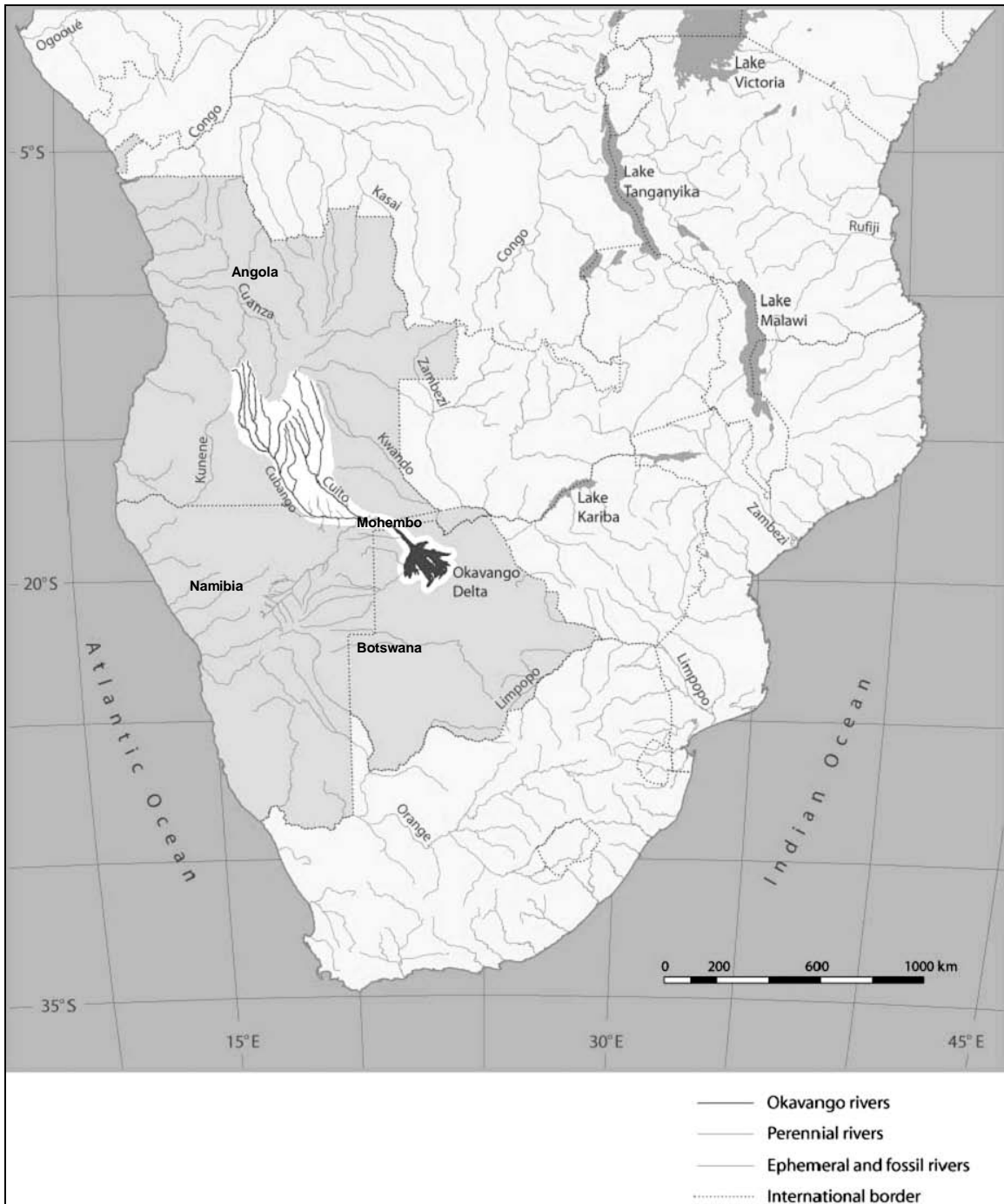


Figure 1-1. Map of southern Africa, showing the Okavango Basin, with the catchment systems (Cubango, Cuito) in Angola, and the Delta in northern Botswana. Moheumbo is where Delta inflow is gauged.

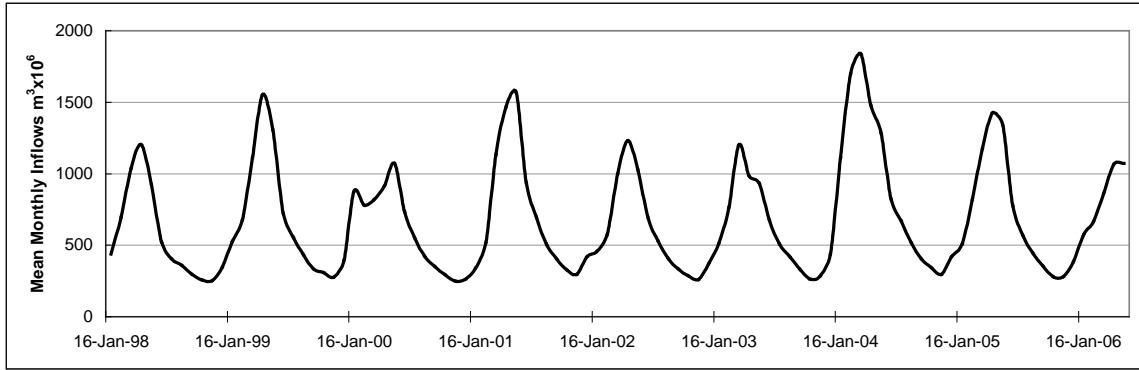


Figure 1-2. Inflow hydrograph for the Okavango Delta at Mohembo (Figure 1-1). The record runs from 1933 to the present. Note highly variable annual maxima and volumes (area under peaks), but consistent base-flow values.

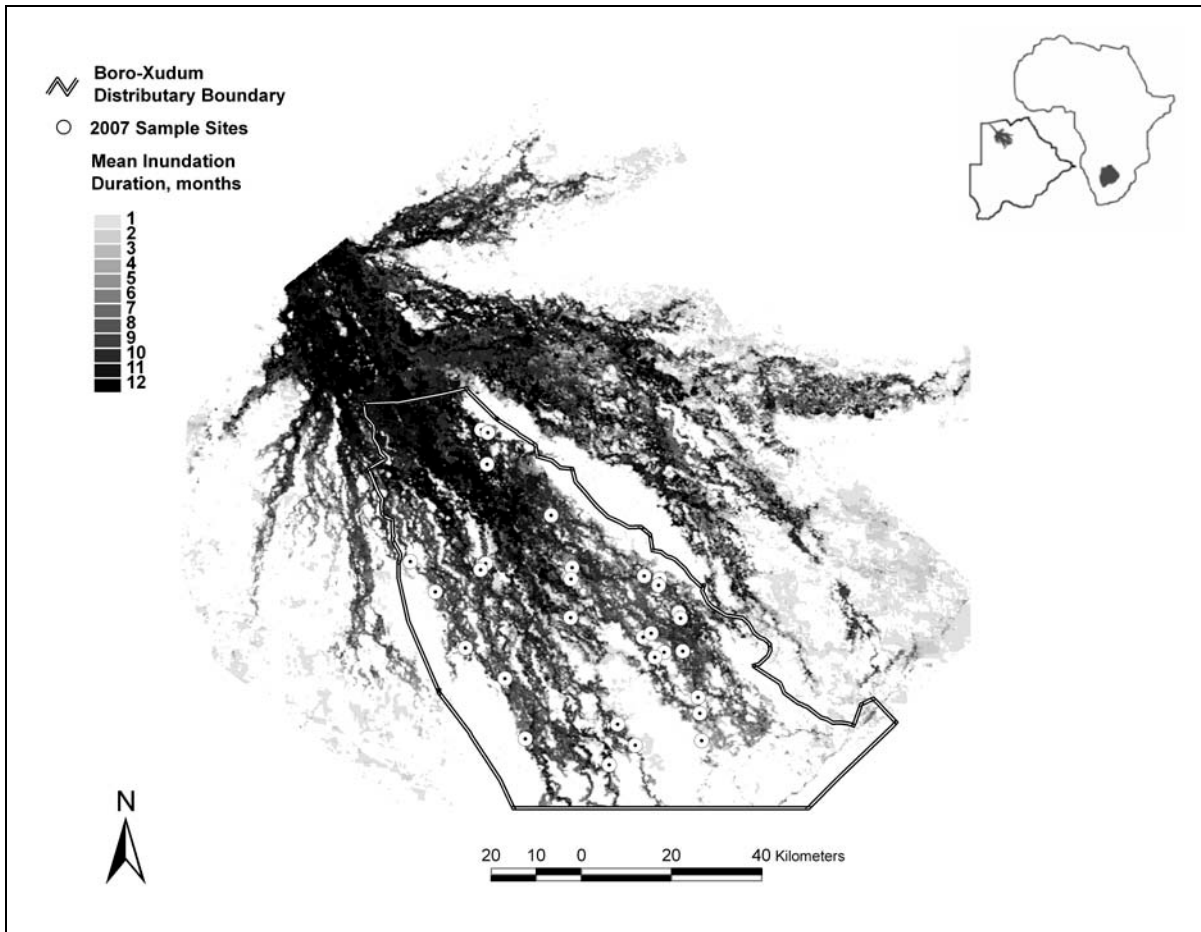


Figure 1-3. The study area, with sample sites and the boundaries of the Boro-Xudum distributary.

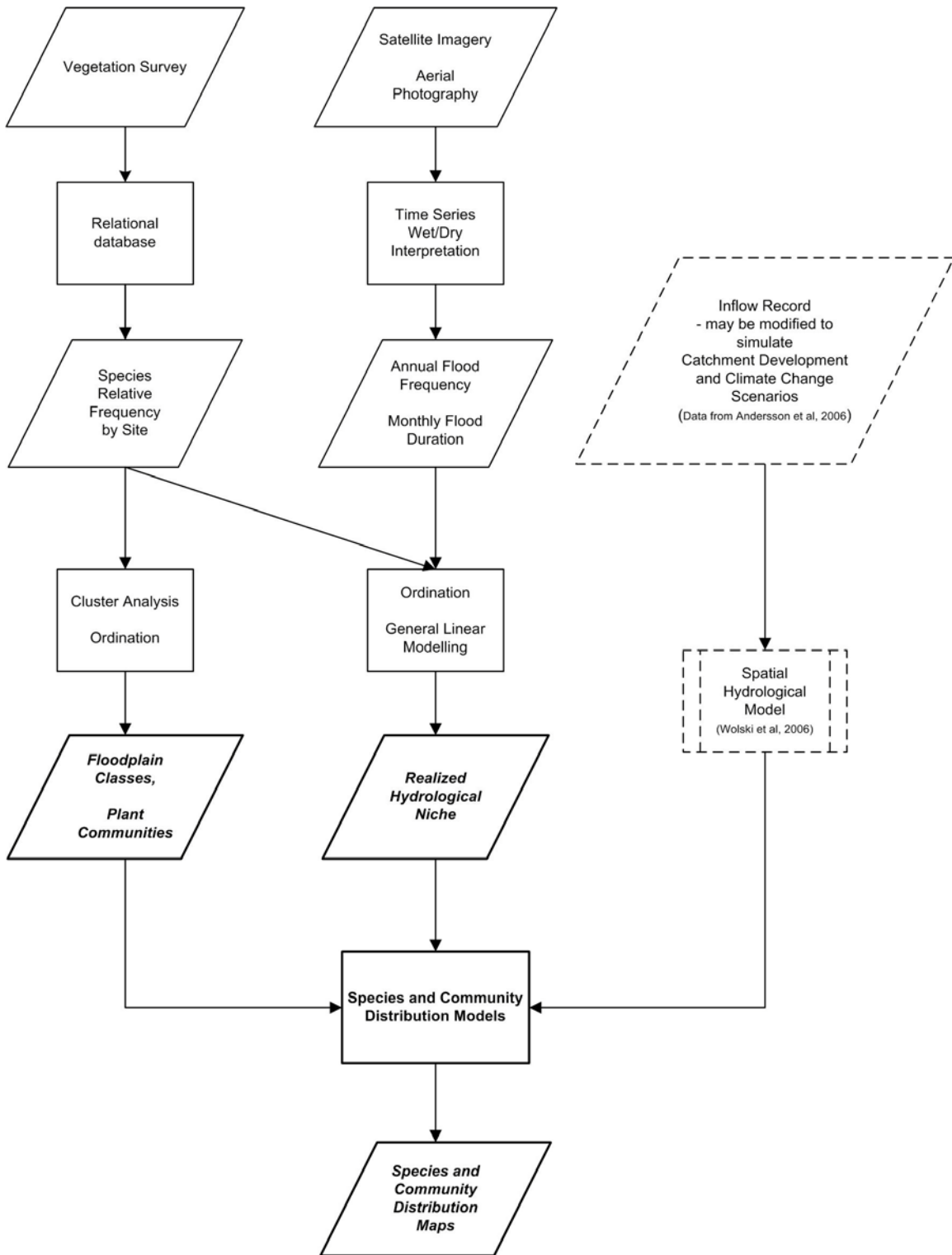


Figure 1-4. Study schematic. Rhomboids represent data (collection ,collation and products), rectangles are processes (analysis, modeling). Objectives of the study are in bold. External data sources and modeling processes are shown with dotted lines along the right of the diagram.

CHAPTER 2
PREDICTING VEGETATION SUCCESSIONAL STAGE IN SEASONAL FLOODPLAINS
FROM REMOTE SENSING-DERIVED HYDROLOGICAL HISTORY

Introduction

The relationships between hydrology and floodplain ecology in Botswana's flood-pulsed Okavango Delta are not quantified, but are critical inputs to national and international policy development, and to management decisions for both the Delta and the whole Okavango basin, which lies predominantly in Angola and passes through Namibia en route to the endorheic Delta (Figure 1-1). Regional climate change and land-use change are inevitable sources of hydrological change in the catchment and the Delta (Ashton and Neal 2003, Andersson et al. 2006), with equally inevitable ecological effects. The various different vegetation communities on the Delta floodplains support very different trophic networks, both terrestrial and aquatic. The arrangement and interdependence of these ecological networks in space and time forms the basis of the low-impact, high-return eco-tourism industry in the Delta. Detailed understanding of the wetland vegetation and how it responds to hydrological change superimposed on the natural variability is an essential step in formulating management strategy.

Remote Sensing (RS) is an increasingly important tool for monitoring and management of wetland environments, particularly in the context of change in climate and catchment characteristics. For large wetlands in developing countries with limited management resources, RS-based assessments are clearly a first-choice approach (Ozesmi and Bauer 2002). The application of RS to wetland management problems, however, is subject to a number of constraints, which significantly include a paucity of continuous historical records, cost, and resolution (spatial, temporal and spectral). In a review of the application of remote sensing techniques to wetlands, Mertes (2002) concluded that observations of channel flow and inundation patterns are one of the most significant potential uses for remote sensing over large

regional scales. Wetland environments, particularly marshes, which present a surface of combined vegetation signature and open water, are often more difficult to differentiate than terrestrial environments (Jensen 2005). Ringrose et al (2003) found in a portion of the distal Okavango Delta that most ecological units (these were defined in terms of major conspicuous species with some description of vegetation structure) could be differentiated on Landsat Thematic Mapper (TM) imagery. They also noted, however, that the riparian woodland which forms a thin perimeter to most islands in the system is of sufficient vigour to saturate the TM sensor array, resulting in overestimates of this unit by up to 30% when interpreting the imagery. In general, they concluded that TM imagery was more suitable for monitoring ecological change than Advanced Very High Resolution Radiometer (AVHRR) imagery because of the higher spatial resolution, but noted that there were separability problems associated with the spectral signatures of some dryland and floodplain associations. In forested wetlands in temperate areas, Landsat TM has been successfully used in conjunction with ground surveys to produce a hierarchical classification system, using multiple images through the year and phenological changes to distinguish communities of deciduous and evergreen tree species (Townsend and Walsh 2001).

More recent work in the Okavango (Wolski and Murray-Hudson 2006) has also shown that where spectral overlap occurs between certain dryland cover signatures and seasonally flooded areas with emergent vegetation, the classic approaches such as Tasseled Cap wetness or the thermal band are ineffective at discriminating land from water. In that study, a classification procedure based on a combination of supervised and unsupervised classification of multi-spectral data and indices and contextual analysis from aerial photography was developed, and applied to

a time series of Landsat TM and TM+ imagery to derive 3 inundation classes and 4 dry land classes in the Delta.

Many practitioners stress the importance of matching the spatial requirements of the prospective use to those of the intended source of data (Johnson and Gage 1997, Jensen 2005). The land forms of interest in the Okavango Delta (floodplains) are in general on the order of hundreds of metres to a few kilometres in extent (Gumbrecht et al. 2004b). In this regard, Landsat TM, which has a general spatial resolution of pixel side length ~30m (although the thermal band is 120m), is more than sufficient for these requirements, while AVHRR imagery, at a resolution of 1100m, generalises the landscape too much to be useful except in small-scale models of flood extent (Gumbrecht et al. 2004c, Wolski et al. 2006). Moderate Resolution Imaging Spectroradiometer (MODIS) 09Q1a 250m imagery is of medium-high spatial resolution, and high temporal resolution, and has been used very effectively in detecting vegetation cover change resulting from flooding in south-east Asia and South America (Zhan et al. 2002). Powell et al (2007) compared Normalized Difference Vegetation Index (NDVI) values from AVHRR and MODIS imagery for modeling wetland response to flooding, and found that over 80% of the variation between the two platforms could be explained by a simple linear regression model. Given the large spatial extent, landscape grain and history of remote sensing application, MODIS appeared to warrant investigation as an alternative, low-cost means of high-temporal medium-spatial resolution monitoring in the Okavango.

Hydrological conditions in the Okavango Delta are determined by the combination of local rains and the magnitude of the annual flood originating from the Okavango River catchment. The seasonal and inter-annual variability of hydrological inputs to the Delta translates into spatial heterogeneity and temporal variability of hydroperiod conditions taking place at various spatial

and temporal scales. We hypothesized that development processes in floodplain vegetation communities in the Delta are primarily driven by the prevalent hydroperiod conditions, and species composition is thus a reflection of the recent past and present hydroperiod dynamics. Could remote sensing-derived hydrological history be used to predict vegetation successional stage?

This paper describes an approach to developing ecological monitoring for a wetland by seeking relationships between various disparate archival RS data and floodplain vegetation community data. The specific objectives of the study were: i) to develop a spatially explicit inundation history for the Boro-Xudum distributary (a portion of the Delta which is subject to large fluctuations of water level and extent from the seasonal flood-pulse) at a spatial resolution appropriate to floodplain vegetation ecology, ii) to find correlations between floodplain vegetation and inundation history, and iii) to assess the potential of this approach for monitoring hydrologically-driven ecological change in the system.

The classical approach to using low spectral resolution RS for assessment of relationships between hydrology and floodplain ecology faces two difficulties in herbaceous wetlands, and in the Delta in particular (Ringrose et al. 1988, Bengert 2007). Firstly, there are spectral resolution problems in discriminating vegetation with subtly different signatures but radically different ecological functions. Secondly, spectral responses are dynamic in time, resulting from superposition of effects arising from emerging and increasingly denser vegetation with those resulting from varying water levels (dry-inundated). These were avoided in this study by limiting RS interpretation to a simple two-class system, wet or dry, and derivation of hydroperiod conditions from time series of RS images at annual and intra-annual scales.

A third more general problem associated with the use of many RS time series is that they are not always complete. Such hiatuses may be filled by extrapolation if, for example, the relationship between inflow and flood extent is well defined. In this case, however, we sought independent data to avoid the tautology implicit in relating interpreted hydrology to the spatial distribution of vegetation. Historical RS records were filled by using data from two different platforms, between which there is sufficient temporal overlap to ensure agreement across platforms.

The work described here was developed against a baseline of previous work described in detail in Wolski and Murray-Hudson (2006). That study developed a routine for discriminating floodplain vegetation from actively growing riparian vegetation, and for distinguishing dry and wet fire scars, through the interpretation of Landsat TM and Enhanced Thematic Mapper (ETM) images of annual maximum flood extent in the year 2002 against a reference set of large-scale aerial photography. This allowed the identification of areas not prone to flooding in the medium to long term (notably riparian woodland), as well as an objective system for mapping annual maximum flood extent in a time-series of Landsat images from 1989 to 2007. A major problem with that time series is 3 gaps: 1991, 2003 and 2004. For the latter two years, full coverage of the Delta is available from MODIS archival imagery, while for 1991 there is Landsat coverage of the western portion of the Delta, on which this study is focused.

Methods

Establishing Historical Hydroperiod

A second time series of flood area was derived from MODIS 8-day composite imagery at 250m resolution for the period of maximum extent for each year between 2000 and 2007. Imagery was clipped using an area-of-interest (aoi) mask to reduce the effects of signatures from non-Delta landscapes and to ensure maximum local contrast (Figure 2-1). Initially, a sequence of

different classification approaches was tested for their ability to reproduce the calibration Landsat interpretation. MODIS 8-day composite images (250m and 500m) from 28th August 2002 were classified and compared to the 2002 Landsat classified image (a mosaic from 31st August and 7th September) as the reference data set, using 6 repetitions of the accuracy assessment routine of ERDAS Imagine 9.1 (Leica-Geosystems 2006) for each approach, from an equalized random sample of each class (n = 256). Classification routines tested included unsupervised (2 clusters, 6 iterations, 0.950 convergence threshold - ISODATA clustering, ERDAS Imagine 9.1), supervised (defining wet and dry area signatures against reference Landsat images, aerial photography and using local knowledge), a ratio of Band 5 to Band 6 (1.24 and 1.64 μm respectively), and lastly a Band 1 (620-670 nm) threshold, derived as follows: pixel values of less than 87% of the distribution minimum in the histogram for each image were classified as wet; higher values were classified as dry (Figure 2-2).

As an independent accuracy check, interpreted images from 2007 were compared with field truth data collected during the vegetation survey of 2007 described below.

Based on this comparison, the simple Band 1 threshold was selected, and used to classify a series of 89 MODIS 250m 8-day composite images selected at as close to 32 day intervals as possible, generating flood extent maps at approximate monthly intervals for the period 2000-2007. These maps were then stacked to produce a flood duration map for each hydrological year. The annual flood frequency (proportion of years in which a given pixel was flooded), and flood duration at a monthly time step, of landscape units at the scale of individual floodplains, was thus established for a continuous 8-year sequence from 2000-2007.

Establishing Extant Floodplain Vegetation State

Two distributaries in the Delta were selected for detailed study: the Boro and neighboring Xudum systems (Figure 1-3). These systems are characterized by pronounced seasonal

fluctuations in response to the annual pulse, and thus exhibit a wide range of hydroperiod variation (Dinçer et al. 1987).

A stratified random set of 30 floodplain vegetation communities across these distributaries was selected to represent the full spectrum of possible flooding frequencies (excluding perennially flooded and dryland areas) from the frequency distribution map, with 6 sites in each of 5 strata of approximately equal area (Table 2-1, Figure 2-3). These were sampled for species composition and cover in March-July (the rising limb of the flood pulse) of 2007, using multiple quadrats 20m apart on transects oriented across the long axis of the floodplains. Hierarchical cluster analysis of these data from a sub-sample of 25 calibration sites (5 sites were withheld as a validation set) was used to identify vegetation communities. Non-metric multidimensional scaling (NMS, Mather (1976), Kruskal (1964)) was used to ordinate the calibration sites in species-space. NMS was also subsequently used to predict ordination scores, and thus class membership, for each site in the validation set. Correlations with hydrological variables were extracted from the ordination matrices, and tested with the multi-response permutation procedure (MRPP) available in PCOrd ordination software (McCune and Mefford 2006).

The relationships identified between hydrological characteristics and vegetation communities were then translated into spatial distribution maps of current vegetation state, and validated using the sites withheld from analysis. Flood frequency and monthly duration by year for each quadrat was generated from spatial analysis, then an estimate of yearly flood parameters for each site was obtained by taking the mean of frequency or duration for all quadrats at that site.

Results And Discussion

Hydrological Variables

Table 2-2 presents an accuracy assessment of classification techniques. The principle of using the strong differential absorption between Near Infrared (NIR) and Mid Infrared (MIR) for

mapping water (Jensen 2005) was tested with a ratio of bands 5 and 6 (1.24 and 1.64 μm respectively; this produced a reasonable threshold-based classification, but did not perform significantly better than the band 1 threshold. Application of the Band 1 threshold classification routine to all years in which there was overlap between Landsat and MODIS coverage showed good correlation between flood extents given by the two platforms (Figure 2-4). A crosscheck of classification accuracy was carried out by matching the flood status of the quadrats surveyed in the first half of 2007 to the classified 8-day composite image closest to the date of sampling: 118 of 1083 quadrats were misclassified (either as dry when they were wet, or wet when they were dry), giving an independently calculated accuracy of 89.1% to the interpretation technique. Misclassification errors may have arisen from problems of timing (date of survey not matching date of image), or from geo-registration errors (pixel centroid did not match floodplain transect centroid).

The relatively large pixel size would be expected to greatly increase the potential for misclassification, as many (up to 17) 20m spaced quadrats may be included in each 250 MODIS pixel, while Landsat TM 30m pixels can be expected to include 2 at most. It appears, however, that while this effect may have been manifest in the ratio techniques, which are based in part on 500m resolution MODIS bands, the grain of floodplain dimensions and pixel size are sufficiently close to reduce this source of error.

Flood duration 2000-2007

The band 1 threshold classification routine was applied to the selected 2000-2007 monthly time series. Figure 2-5 shows the interpreted monthly variation in flood extent. The August/September peak and summer minima are clear, as is the magnitude of inter-annual variation in size. In addition, minor short-term peaks occur in mid-late summer as a result of good local rains. The

trough in early 2002 represents the smallest extent of flooded area in the Delta in this period; in general this perennially flooded area varies between 2000 and 3600km². Maximum area of flooding shows a much larger variation, from 4100 km² (2003) –7200 km² (2006), and overall duration of flooding (breadth of annual wave, trough-to-trough distance) varies between 8 and 15 months. What is not immediately apparent from Figure 2-5, however, is the effect of this variation on the flooding status of individual pixels. Figure 2-6 shows flood duration for 2003 (a short-lived low-amplitude flood, and for 2004, a large and long flood. The more extensive short-term flooding of the study area by the larger 2004 flood can clearly be seen, while the perennially flooded “core” appears to be of similar extent in both years. Interpreted extents during the rainy season are not as reliable as those between April and November: cloud cover, growth of emergent floodplain species in response to summer temperatures, and the effects of local rainfall on surface water in the Delta all potentially confound the interpretation. Correlation coefficients from the vegetation analysis (Table 2-3., see discussion below), however, show that replacing the small summer peaks with the yearly minimum in the duration index calculation in fact improves the agreement with species composition, albeit by a small margin.

Vegetation-Hydroperiod relationships

Hierarchical clustering (distance measure Sorensen, flexible beta) of the calibration data set suggested three main groups; ordination of the data showed that these groups were differentiated primarily on axis 1 (Figure 2-7), aligned with change in all the hydrological variables tested. The main indicator species in each class and the approximate range of annual flooding frequency and mean monthly duration are given in Table 2-4. The distinction of corresponding frequency classes is straightforward, with no overlap, while classes from the mean duration of flooding over the past 3 years show overlap of a month across each transition.

Correlations (PCOrd NMS ordination routine, McCune et al (2002)) between ordination axes and hydrological variables are given in Table 2-3. The strongest correlation was with the long-term (18 year Landsat-MODIS combination) frequency ($r = 0.934$, Pearson correlation coefficient); mean duration of flooding preceding the vegetation survey also showed strong correlations, with the highest coefficient being for the most recent 3 years (Pearson $r = 0.859$); noteworthy is the progressive decline in relationship strength with increasing averaging record length. Only the parameters “years since last flood” and “mean 2007 flooding depth” showed any (slight) relationship with axis 2; their relationships with axis 1 were stronger. Proportions of variance represented by each axis (coefficients of determination for the correlations between ordination distances and distances in the original n -dimensional space – r^2 axis 1: 0.742; axis 2: 0.088) support the strong dominance of flood frequency and duration as the primary determinants of species composition.

The positions of the validation sites in the calibration ordination space are shown in Figure 2-7. These positions are based on scores calculated without changing the shape of the calibration ordination (NMS Scores, McCune et al (2002)). The validation sites all met a criterion of $< 5\%$ of total axis length used as a cutoff; that is, their species space scores were within 5% of the maximum variation of the calibration sites. Although not an outlier under the criteria used here, the site MOC shows noticeable separation from the remainder of group 3. From the main species recorded there (3 grasses, 5 aquatic herbs and 5 sedges), it may represent an end-member of both frequency and duration for seasonal flooding. The frequency and duration classifications for the validation sites are given in Table 2-5, with listings of most abundant species and what proportion of the indicator species suite is represented for each class. For sites falling in classes 1 and 2, at least 60% of possible indicator species are present at each site; the class 3 site (MOC)

only has 42% of class 3 indicators, but again, this site is not considered typical of class 3. The TSW site has indicator species from both class 2 and class 3, although the majority is for class 2. This possibly represents an assemblage of species in transition; one of the failings of correlation models of this type is an inescapable assumption that vegetation composition is at equilibrium (Austin 2002). The extreme variability of the Okavango hydrology (Andersson et al. 2003) makes it unlikely that seasonal floodplain communities in this system are ever at equilibrium; it is considered more likely that there is a process of constant adjustment to hydrological conditions at both the seasonal and long-term time (decades) scales. Thus the TSW site presents some characteristic species of a very frequently flooded (class 3) site, but its recent duration history puts it on the boundary between classes 2 and 3, and most of the indicator species found would imply a class 2 site. Such transitional signatures are to be expected, and may provide some information on trends; the TSW site appears to be changing towards a lower frequency of flooding, for example.

The strongest correlation was found between the long-term frequency record and species composition. This may not be not the most useful relationship if the model is intended for management purposes, as the frame of analysis is long and therefore of limited sensitivity to rapid change. Why this relationship is stronger than, say, the mean duration for the most recent 3 years is difficult to determine; it may be due to the overall higher spatial resolution of the (mainly) Landsat-based frequency record, or it may be that the species composition is indeed a strong integrator of long-term flooding patterns. This latter is considered less likely, given the relatively short life-histories of the floodplain species (and the wide variation in hydrology (a long sequence of dry years in the 1990s, followed by increasing wetness after 2000);

compositional change in response to hydrological change can be expected to be relatively rapid in herbaceous tropical and subtropical wetlands (Junk and Piedade 1993, Henry et al. 1996).

Conclusions

By combining independent RS dry-wet interpretation and vegetation survey techniques to identify relationships between vegetation state and hydroperiod in floodplains, the problems of spectral overlap in space and time, which have dogged the application of RS to vegetation mapping in the Okavango Delta floodplains, were avoided. Such relationships are likely to exist in most marsh-dominated wetland systems, where the response of vegetation to hydrological change is expressed in terms of relatively rapid compositional change along succession gradients, and the approach may be found useful in these cases. A strong and quantifiable relationship was identified between hydrological characteristics (frequency and duration) and plant species composition in the seasonal floodplains. This relationship can be used to predict the occurrence of indicator species at a site of known flood duration or frequency.

For management purposes some combination of recent flooding history like the duration means presented here have more potential utility than the long-term frequency. For monitoring purposes, it appears that MODIS 250m imagery can be used very effectively to compare flooding extents, and infer the development state of floodplain vegetation on these seasonal floodplains.

Table 2-1. Areas of flood frequency strata used in sample site selection. Frequency classes were grouped to maximize similarity of area.

Stratum	Number of pixels	Area km ²	Frequency class groups
1	1302836	1058.2	1
2	1063578	863.9	2-3
3	1283557	1042.6	4-6
4	1456122	1182.7	8-12
5	1065975	865.8	13-14

Table 2-2. Comparison of accuracy of different wet-dry classification techniques for MODIS 8 day composite imagery (peak flood, 2002). Overall accuracy (%) and the Kappa statistic (κ) were calculated using the ERDAS Imagine 9.1 assessment routine against the reference classified Landsat TM image; each comparison was run for 6 iterations.

	Unsupervised		Supervised		Band 5:6 Ratio		Band 1 Threshold	
	%	κ	%	κ	%	κ	%	κ
Mean	88.93	0.78	92.45	0.84	85.68	0.71	92.00	0.84
SD	1.23	0.02	1.30	0.03	2.27	0.05	1.43	0.03

Table 2-3. Pearson correlation coefficients, “r”, between ordination axes and remote-sensing derived hydrological variables. Mean depth is for sites that were flooded at the time of the 2007 vegetation survey. Frequency is the proportion of years a pixel was flooded, from an 18 year Landsat time series (n=18) year MODIS time series (n=8).

Hydrological Variable	Axis 1	Axis 2
	r	r
Mean annual flood frequency (n=18)	0.932	0.103
Years since last flood	-0.709	-0.235
Mean flood duration: 3 preceding years	0.854	0.048
4 preceding years	0.845	0.057
7 preceding years	0.828	0.002
*3 preceding years incl. summer peaks	0.825	0.055
Mean depth of water (2007) (n=17)	0.681	0.264

*The correlation of mean flood duration of the 3 preceding years without the summer peaks is higher than when they are included.

Table 2-4. Floodplain classes with major indicator species, and flood frequency and duration range. Only species showing an indicator value of >50% and a p value of <0.05 are listed, in order of indicator value.

Class 1	Class 2	Class 3
1-2 years of 18 (<11%)	5-11 years of 18 (11-60%)	12-18 years of 18 (>60%)
Mean duration 1-3 months	2-8 months	7-10 months
Occasionally flooded savanna	Seasonally flooded grassland	Seasonally flooded sedgeland
<i>Urochloa mossambicensis</i>	<i>Nicolasia costata</i>	<i>Leersia hexandra</i>
<i>Cynodon dactylon</i>	<i>Eragrostis lappula</i>	<i>Nymphoides indica</i>
<i>Ipomea coptica</i>	<i>Panicum repens</i>	<i>Oryza longistaminata</i>
<i>Eragrostis cylindriflora</i>	<i>Setaria sphacelata</i>	<i>Nymphaea nouchali</i>
<i>Chloris virgata</i>	<i>Cyperus sphaerospermus</i>	<i>Acroceras macrum</i>
<i>Melinis repens</i>		<i>Eleocharis dulcis</i>
<i>Pluchea leubnitziae</i>		<i>Cyperus articulatus</i>
<i>Pogonarthria squarrosa</i>		<i>Sacciolepis typhura</i>
<i>Stipagrostis uniplumis</i>		<i>Eleocharis variegata</i>
<i>Tragus berteronianus</i>		<i>Pycneus nitidus</i>
<i>Gisekia africana</i>		<i>Schoenoplectus corymbosus</i>
<i>Bergia pentheriana</i>		<i>Potamogeton thunbergii</i>
<i>Kohautia virgata</i>		
<i>Corchorus tridens</i>		
<i>Aristida meridionalis</i>		
<i>Hermannia quartiniana</i>		
<i>Tephrosia purpurea</i>		

Table 2-5. Validation site flood frequency, duration, main species and representation of indicator species. Flood classes are indicated in parentheses below frequency and duration values.

Site name	Flood Frequency (% of years)	Mean Duration last 3 years	Major Species (occurring in >20% of quadrats, in order of relative abundance)	Proportion of Class Indicator Species (%)
KIR	35 (class 2)	6 months (class 2)	<i>Panicum repens</i> <i>Cyperus denudatus</i> <i>Setaria sphacelata</i> <i>Kyllinga erecta</i> <i>Fimbristylis complanata</i> <i>Pycnus nitidus</i> <i>Schoenoplectus corymbosus</i> <i>Cyperus sphaerospermus</i> <i>Eragrostis inamoena</i> <i>Paspalum scrobiculatum</i> <i>Cynodon dactylon</i> <i>Kohautia virgata</i>	60
KOA	6 (class 1)	1 month (class 1)	<i>Eragrostis cylindriflora</i> <i>Cynodon dactylon</i> <i>Tephrosia purpurea</i> <i>Chloris virgata</i> <i>Eragrostis viscosa</i> <i>Ipomea coptica</i> <i>Aristida meridionalis</i> <i>Kohautia virgata</i> <i>Corchorus tridens</i> <i>Dactyloctenium aegyptium</i> <i>Stipagrostis uniplumis</i> <i>Urochloa mossambicensis</i> <i>Pluchea leubnitziae</i>	65
MOC	95 (class 3)	8months (class 3)	<i>Ludwigia stolonifera</i> <i>Eleocharis dulcis</i> <i>Leersia hexandra</i> <i>Nymphaea nouchali</i> <i>Potamogeton thunbergii</i> <i>Paspalidium obtusifolium</i> <i>Eleocharis acutangula</i> <i>Nymphoides indica</i> <i>Caldesia reniformis</i> <i>Pycnus flavescens</i> <i>Pycnus mundii</i> <i>Fimbristylis complanata</i> <i>Sacciolepis africana</i>	42

Table 2-5 Continued.

Site name	Flood Frequency (% of years)	Mean Duration last 3 years	Major Species (occurring in >20% of quadrats, in order of relative abundance)	Proportion of Class Indicator Species (%)
TSW	77 (class 3)	7 months (class 2)	<i>Panicum repens</i>	60 (class 2)
			<i>Cyperus longus</i>	25 (class 3)
			<i>Fimbristylis complanata</i>	
			<i>Rhynchospora holoschoenoides</i>	
			<i>Cyperus denudatus</i>	
			<i>Cyperus sphaerospermus</i>	
			<i>Cyrtium tubulosum</i>	
			<i>Setaria sphacelata</i>	
			<i>Brachiaria humidicola</i>	
			<i>Eleocharis variegata</i>	
			<i>Sacciolepis typhura</i>	
			<i>Nymphaea nouchali</i>	
			XAN	40 (class 2)
<i>Eragrostis inamoena</i>	8 (class 3)			
<i>Panicum repens</i>				
<i>Trachypogon spicatus</i>				
<i>Cyperus denudatus</i>				
<i>Eragrostis lappula</i>				
<i>Imperata cylindrica</i>				
<i>Schoenoplectus corymbosus</i>				

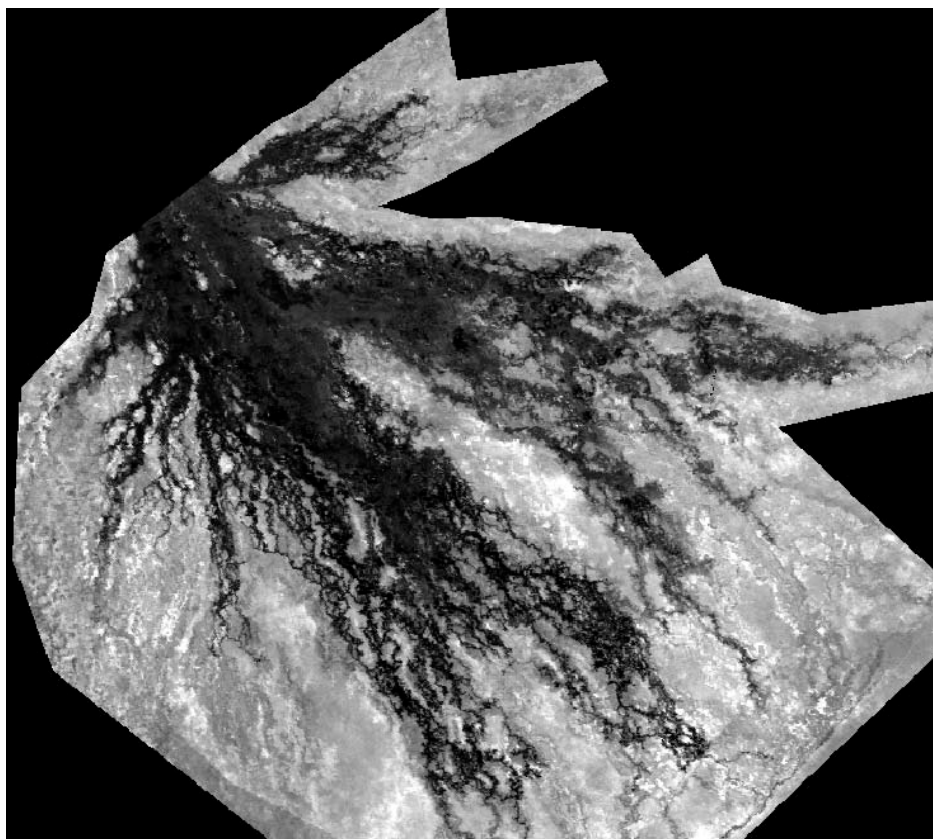


Figure 2-1. Example of MODIS 09Q1A Band 1 (620-670 nm) image (August 2002) clipped to the Okavango Delta area of interest from Tile h20v10. Inundated areas are dark tones, while dry land is lighter, indicating greater reflectance.

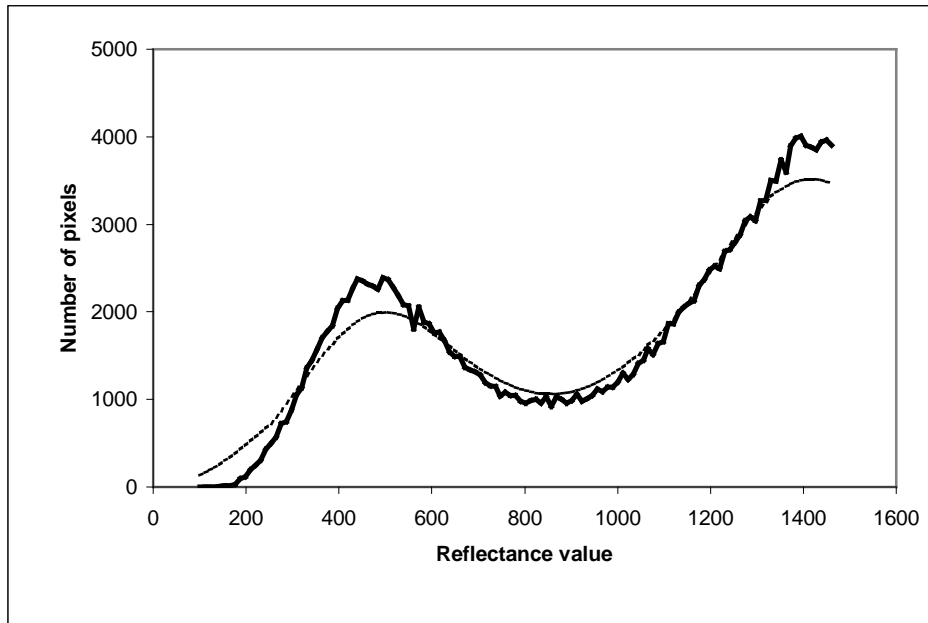


Figure 2-2. Example of histogram from image in Fig. 2-1, of Band 1 pixel values and smoothed distribution curve. Lower reflectance values represent the inundated areas (dark areas in Fig. 2-1). A threshold of 87% of the pixel value at the local minimum (in this case, 755) between the dark and bright peaks produced the closest fit of maximum flood extent with calibration data.

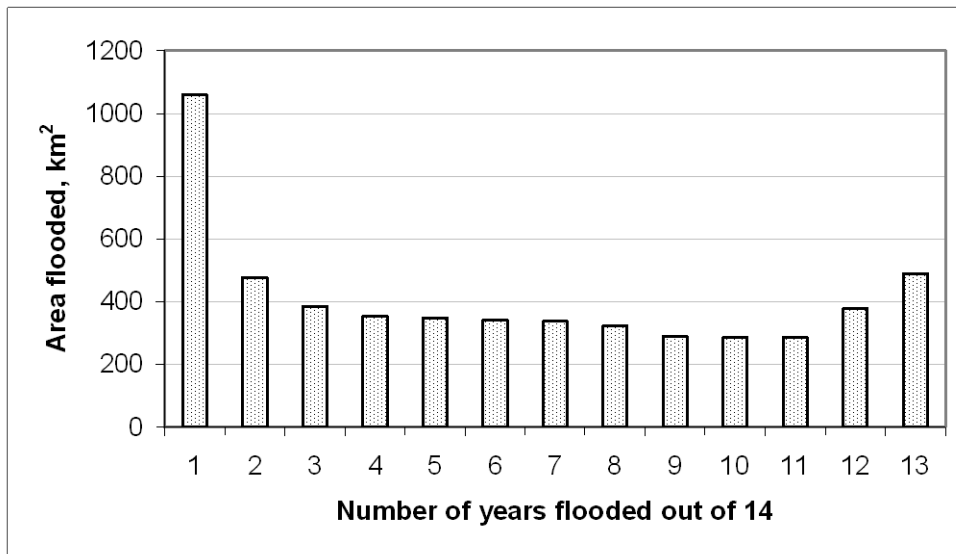


Figure 2-3. Histogram showing areas of flood frequency classes; dryland and perennially flooded areas are excluded.

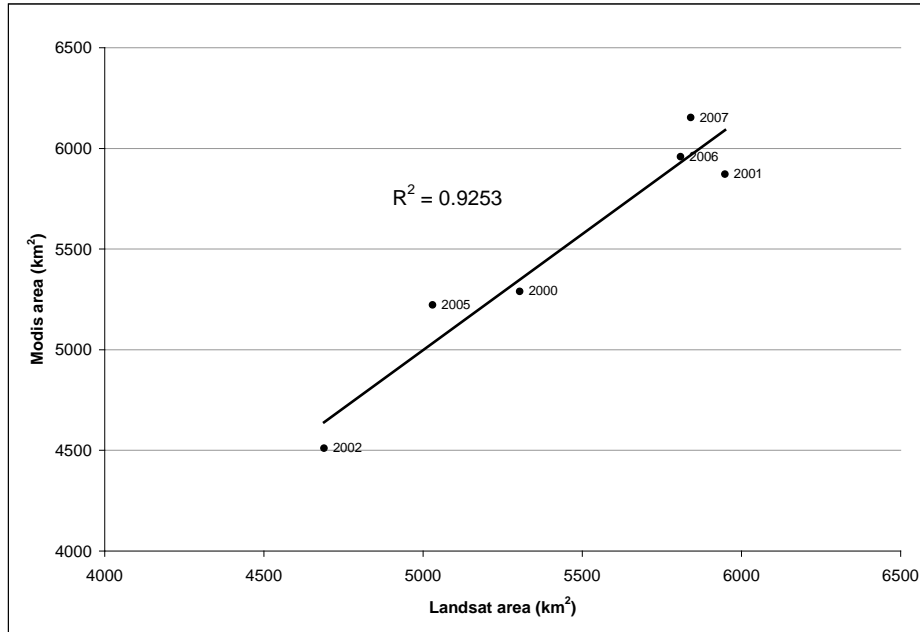


Figure 2-4. Interpreted maximum flood extent from MODIS and Landsat imagery for the period 2000-2007, except 2003 and 2004, for which there are no Landsat data. The classification system for the MODIS imagery produces a close fit with the Landsat maximum extents, with the maximum deviation (5.3%) in 2007.

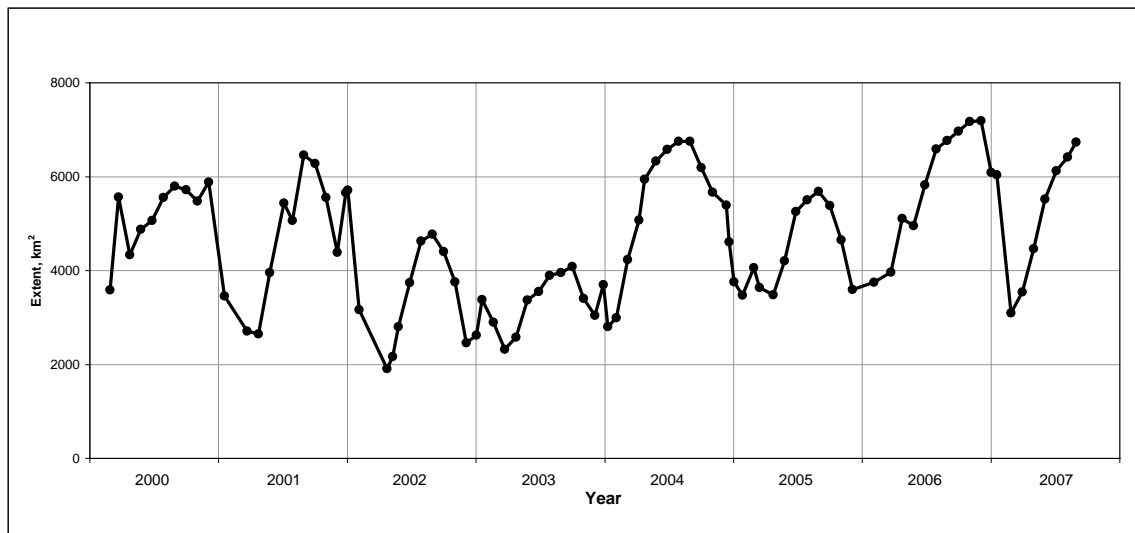


Figure 2-5. Inundation area as interpreted from MODIS imagery for the period 2000 to 2007. Major peaks in the middle of each calendar year result from the inflow to the Delta from Angola; minor peaks at the beginnings and ends of calendar years result from rain falling directly on the Delta.

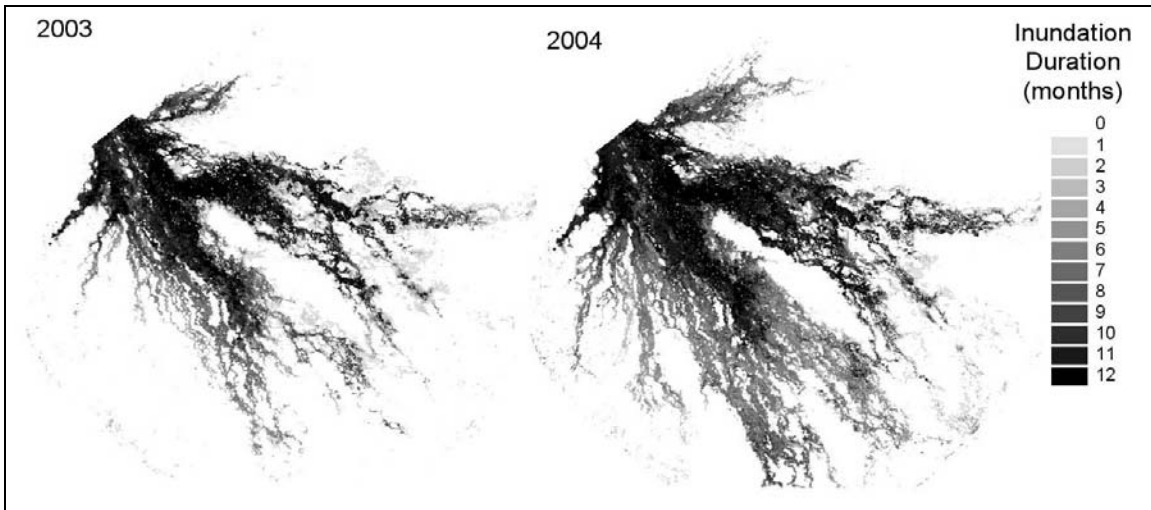


Figure 2-6. Flood duration in months for 2003 and 2004. Differences in duration are particularly evident in the more extensively flooded seasonal Boro and Xudum systems in the south of the Delta, while the core perennially flooded (darkest) portion is less dramatically affected by the larger 2004 flood.

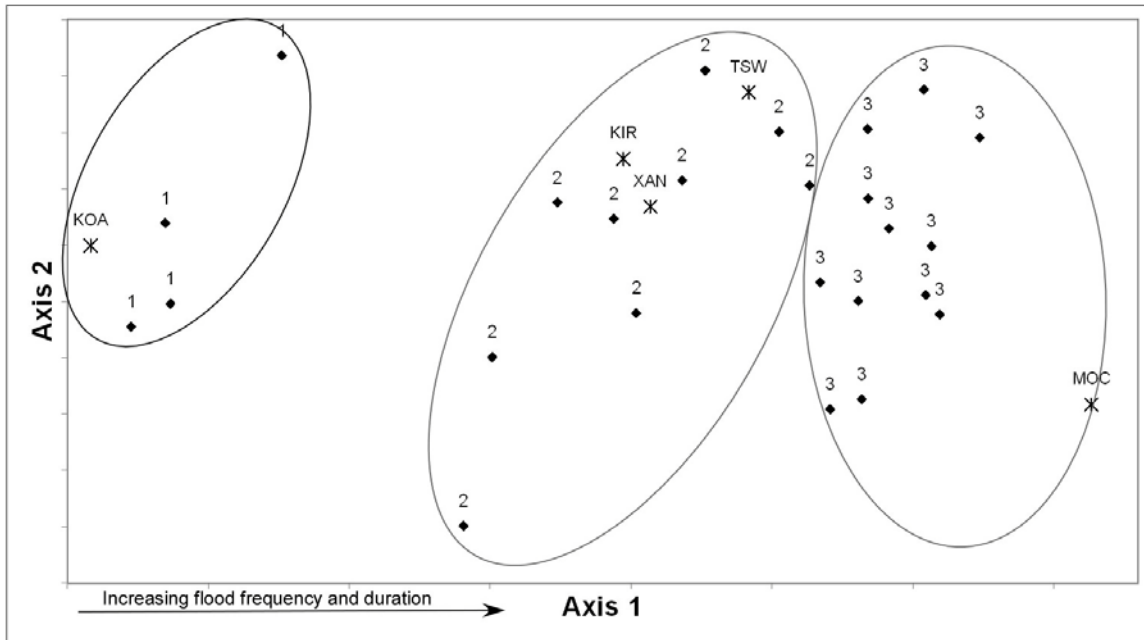


Figure 2-7. Ordination of floodplain sites in 2-dimensional species space. Flood frequency and duration parallel axis 1. Oval envelopes are vegetation classes from hierarchical cluster analysis (also indicated by numeric labels on the calibration data points, e.g., ♦ 2). Predicted positions (NMS Scores, McCune et al 2002) of validation points (e.g., * MOC) are labeled with their site name.

CHAPTER 3
A VEGETATION-BASED HIERARCHICAL CLASSIFICATION FOR SEASONALLY
PULSED FLOODPLAINS IN THE OKAVANGO DELTA

Introduction

Wetlands provide a significant array of ecosystem services (Wilson and Carpenter 1999, Mitsch and Gosselink 2000), and in developing countries they are relied on for the provision of direct services such as food, building materials, and medicines, in addition to the “hidden” hydrological and biophysical services, such as flood amelioration and water quality improvement (Barbier 1994, Acharya 2000, National Conservation Strategy Agency 2000). The continued survival of wetlands is dependent in large part on maintenance of the hydrologic regime, and this is increasingly under threat globally, as a result not only of climate change but also of local changes such as surrounding land use, water abstraction, or changes to flow regimes as a result of damming for water and power supply. Sub-Saharan Africa is projected to be particularly affected by water stress resulting from climate change by 2025 (Postel 2000). Most southern African countries have a positive population growth rate, and many have newly emerging economies, yet little is known about how climate changes will affect freshwater ecosystems, and the flow of benefits from them.

Tropical wetlands are often subject to one or more distinct pulses in water supply as a result of rainfall seasonality, and are ecologically adapted to this varying hydrology (Junk and Piedade 1993, Bayley 1995, Junk 2000). Changes to rainfall, evapo-transpiration and river flows may affect the flood-pulse in terms of timing, amplitude and duration, and consequently affect ecosystem properties. Understanding such changes and their likely effects is of critical relevance to land-use planning and management. Botswana’s Okavango Delta is a large (16,000 km²), open wetland ecosystem which has so far escaped major anthropogenic impact. Hydrological change resulting from development in the catchment and climate change is considered inevitable

(Ashton and Neal 2003, Andersson et al. 2006). Knowledge of the baseline state and functioning of the system has, however, been limited largely due to its sheer size and inaccessibility. Consequently the potential for monitoring the effects of hydrologic change on vegetation has been mainly restricted to remote sensing methods. Historically these have been either of insufficient spectral resolution to distinguish differences between major floodplain vegetation types, or too expensive (Ringrose et al. 1988, Wolski and Murray-Hudson 2006) to apply in this large and dynamic wetland at high temporal resolution.

The Okavango Delta falls into to the Zambebian Flooded Grasslands biome, characterized by low levels of endemism, but locally very high species richness, both in flora and fauna, including a number of endangered bird species (Junk et al. 2006, Ramberg et al. 2006, McGinley 2008). The richness per area of the Okavango flora is about one order of magnitude higher than the background value for Botswana as a whole – the species-area ratio for the delta is about 0.054/km², higher than all other biomes in the southern African subcontinent, with the exception of the Fynbos biome of the western Cape of South Africa (Snowy Mountains Engineering Corporation 1989), due in large part to the significant extent of perennially flooded areas. The Delta is a declared wetland of international importance - a RAMSAR site - and commitments to the “wise use” principle embodied in the convention, and the national Wetlands Policy and Strategy (National Conservation Strategy Agency 2000) require that management ensure the maintenance of ecosystem functioning and biodiversity (Jansen 2002b). Adaptive management would be a logical framework to apply to the Delta and its development, but our basic understanding of the ecological organization, and the drivers of that organization is incomplete. A first step towards addressing this gap is gathering baseline ecological information, such as the distribution of different ecological communities (flora and fauna), and monitoring change.

Historically the vegetation of the Delta has been qualitatively described by various authors (Snowy Mountains Engineering Corporation 1989, Ellery and Ellery 1997), with some more quantitative but localized work in the perennially flooded areas (Ellery et al. 1990, Ellery et al. 2003), in the Xudum-Xwaapa system (Heemstra 1976), and on Chief's Island (Biggs 1979). Bonyongo et al (2000) carried out a detailed phytosociological survey of a single floodplain in the middle Boro and recommended extension of the approach. The qualitative ecological zoning system developed by Snowy Mountains Engineering Corporation (1989) for the Delta as a whole was based on the author's personal experience and observation of Delta floodplains. It provides the first full compilation of plant species, and some floristic and life form analysis of Delta plants by habitat, but had no quantitative basis. The checklist developed for that project has subsequently been updated and augmented by two consecutive rapid assessment studies carried out by Conservation International (2003), who also developed an overview of main vegetation groups from ordination of data from 4 sites in the Panhandle, western, central and northern Delta (Sliva et al. 2004). All of these studies are limited either in their geographic scope or their quantitative basis, effectively reducing their replicability.

This study describes the derivation of a simple hierarchical classification system for seasonally-pulsed floodplains in the Delta. The vegetation in different floodplains of the Boro-Xudum distributary was sampled in order to: i) test for the presence of distinct species assemblages which could provide a classification system for floodplains; ii) identify indicator species or groups of species which could be used to characterize such a system. A system of classification which is broadly applicable can be used to establish a baseline of floodplain vegetation distribution, and subsequently to monitor change with time. These data may then be used to inform management decisions in an adaptive management framework.

Methods

The study area is shown in Figure 1-3; the Boro-Xudum distributary is approximately 6000 km² in extent; accession of flood water to the system is by over-bank flow from the main Okavango channel, after which flow converges and heads south-east through multiple floodplains and channels.

Floodplains were divided into 5 strata of approximately equal area based on historic flood frequency reconstructed from a time series of satellite imagery (Wolski and Murray-Hudson 2006), and 6 sites were randomly selected within each stratum. Sites were surveyed between March and June 2007; a synopsis of sites is given in Appendix 1, including acronyms used here. Species composition and relative abundance was sampled along transects oriented orthogonally to the long axis of the floodplain, using 1m² quadrats spaced 20m apart; geographic coordinates for each quadrat were recorded in the field. Species area-curves from a preliminary survey (Murray-Hudson 2006 unpublished data) were used to determine the required sample area as $\geq 25\text{m}^2$; a minimum of 30 quadrats per site were surveyed. Species were identified in the field where possible; samples were taken of unknowns and pressed in the field; those which could not be identified from the Peter Smith Herbarium collection at the Okavango Research Centre were sent to Kew Botanical Gardens, London, United Kingdom for identification. Nomenclature followed Germishuizen and Meyer (2007). The field sampling campaign was timed to maximize availability of inflorescences to facilitate identification. This resulted in sampling on the rising limb of the hydrograph; many sites were about to receive or had just received floodwater from the 2006-2007 inflow.

Multivariate data analyses were carried out with routines in PCOrd 5.1 (McCune and Mefford 2006), and EstimateS (Colwell 2006) was used for analysis of richness and diversity parameters. For analysis at the site level, species abundances were calculated from their

proportional presence in quadrats (frequency). In order to avoid confounding effects from higher elevation (and therefore less flooded) margins of floodplains, these data excluded quadrats within 40m of islands. Hierarchical cluster analysis (flexible β linkage, $\beta = -0.25$, Sorensen distance) of sites was carried out on a data set comprising only species which occurred at more than 3 sites, based on their frequency distribution among quadrats. To test the hypothesis of no differences between clusters, a multi-response permutation procedure (MRPP) statistical test included in PCOrd was carried out using Sorensen distance and rank-transformed data. MRPP is a data-dependent routine which requires no assumptions about the underlying distribution structure of the population (Biondini et al. 1988). The weighted mean within group distance ($\delta = \sum_{i=1}^g C_i x_i$ for g groups where x_i is the average within-group distance, C is a weight derived from the number of species in the groups, and smaller values of δ indicate tighter clustering within groups), is calculated. The probability p of δ being less than or equal to this calculated value is estimated against a Pearson type III distribution (which accommodates the potential skewness of the underlying permutation distribution); this gives the probability of a type I error under the null hypothesis of no difference between groups. The test statistic $T = (\delta_{\text{obs}} - \delta_{\text{expected}}) / \sigma_{\delta}$ describes the separation between groups, with more negative values indicating stronger separation. Effect size is provided by the chance-corrected within-group agreement $A = 1 - (\delta_{\text{obs}} / \delta_{\text{expected}})$; this describes within-group homogeneity.

Indicator species analysis (ISA, Dufrêne and Legendre (1997)) was used to identify levels for defining classes. This routine calculates indicator values (IVs) for species based on fidelity and relative abundance in *a priori* defined groups, and evaluates the statistical significance of the IVs by comparison with IVs generated by Monte Carlo randomization of the data set.

Ecologically meaningful levels for defining classes were determined by applying indicator

species analysis iteratively to an increasing number of divisions (Figure 3-1) and plotting the overall number of species identified as significant (at $p < 0.05$) indicators, and the overall average p-value at each level of division. Where the mean p-value is minimized or number of significant indicator species is maximized represents a maximum of ecological information.

Non-metric multi-dimensional scaling (NMS)(Kruskal 1964, Mather 1976) was used to ordinate the sites-species matrix (Sorensen distance, random starting configuration, 250 runs real and randomized, final selection of 2-dimensional representation based on stress < 10), to investigate inter-site and environmental relationships. Species characteristic of clusters were determined by ISA.

Results

A total of 166 positively identified species were recorded in the seasonal floodplains sampled, including 53 grasses, 31 sedges and 33 aquatic herbs. Adjusted jackknife 1 & 2 estimates (Colwell 2006) of potential total richness were 227 and 269 respectively. The dataset used for ordination and clustering was reduced to 53 by excluding species which occurred at less than 3 sites.

There is a coincident minimum of ISA p-value and maximum of number of significant indicator species at 4 divisions, with the full set of sites. At 6 divisions, the first single site class appears (MOC), and a second appears at 7 divisions (XHA). A further indicator species maximum occurs at 8 divisions and a p-value minimum at 9, so these represent possible levels for sub-classes. The four ecological classes are designated Dry Floodplain Grassland (DFG), Seasonally Flooded Grassland (SFG), Seasonally Flooded Sedgeland (SFS), and Seasonal Aquatic Communities (SAC).

The ordinated sites (Figure 3-2) fall into discreet clusters; envelopes correspond to the 4 classes defined in Figure 3-3. One major gradient captured most of the variance in the floodplain

communities, the first dimension containing 82.8% and the second 6.7% of the information in the data set (cumulative = 89.5%). This major gradient is parallel to historic flood frequency; which increases from left to right in the diagram. Here the relationship of the sites MOC and XHA to the other members of their class (which causes them to fall out as single site classes at higher cluster levels) can be seen. Despite the apparent large distances between these sites and their cluster centroids, all sites are within 2 standard deviations of the mean of ordination distance, and consequently did not meet the criterion used to identify outliers. MRPP tests of the 4 class division showed a chance-corrected within-group agreement $A = 0.541$, with the probability of a smaller or equal δ (the weighted mean within-group distance) $p < 1E-8$; that is, the hypothesis of no difference between groups can be rejected. Pairwise comparisons between clusters likewise all resulted in p -values < 0.001 (Table 3-1).

Further sub-division into 8 classes, as mentioned above, results in the appearance of 2 single site classes. Once these are excluded, 2 of the remaining classes can be meaningfully subdivided, specifically the larger groups of seasonally flooded grasslands and sedgeland. MRPP of these subdivisions also showed a strong within-group agreement ($A=0.675$, $p < 1E-8$), implying classes are different.

Ratios of annual to perennial plants (A:P), sedge:grass (Cyp:Gram) ratios and Shannon diversity indices (calculated from the full dataset) are given in Table 3-2. A:P ratios are lowest in the Seasonal Aquatic Communities, increasing through the 2 intermediate classes and reach a maximum in the Dry Floodplain Grasslands, the inverse of the pattern followed by the sedge:grass species ratio. Mean diversity indices (richness, evenness, Shannon and Simpson) were lowest in the DFG class, intermediate in SFG and SAC, and highest in the SFS class, but nowhere are these differences statistically significant.

An annotated dendrogram (Figure 3-3) is structured as a dichotomous key; major indicator species are included to allow identification of the 8 floodplain sub-classes. Table 3-3 lists the major indicator species of the four primary classes, their indicator values, p-values and their life-cycle and growth form.

Discussion

The vegetation of the floodplains in general is characterized by short-lived herbaceous plants. Where long-term environmental changes are most pronounced (Dry Floodplain Grasslands), these are more likely to be opportunistic, fast-growing annuals, while in areas which are regularly flooded, perennial species and those with vegetative reproductive strategies are likely to dominate.

The overall results of this classification exercise correspond in a broad sense with the qualitative categorization of Snowy Mountains Engineering Corporation (1989). There is also close correspondence with two of the main vegetation groups identified in the slightly more quantitative assessment of Sliva et al (2004): SFS being equivalent to the *Schoenoplectus corymbosus-Cyperus articulatus* communities, and DFG to the *Urochloa mosambicensis-Pechuel-Loeschia leubnitziae* communities. SFG falls into their category “communities of the aquatic-terrestrial transition zone” and corresponds roughly to “*Panicum repens* grassland communities”. Although based on cluster analysis, that study was not designed to develop a classification system, and consequently no quantitative basis for selecting indicator species is given. In this study, for example, we found that the two species used for characterizing the seasonal sedgeland in most previous work (Snowy Mountains Engineering Corporation 1989, Bonyongo et al. 2000, Sliva et al. 2004), *Schoenoplectus corymbosus* and *Cyperus articulatus*, seldom actually occur as co-dominants. Although both are recognized as significant indicators for this class in our analysis, *C. articulatus* in fact only emerges as a primary indicator (with the

highest IV) at the 8th level of division. These species are both conspicuous, tall, emergent sedges which tend to visually mask their diminutive but more statistically important neighbors, such as *Leersia hexandra* or *Eleocharis dulcis*. The SFG and SFS classes are better represented in the survey dataset (n = 9 and n = 10, respectively) and there are good indications (Figures 3-1 and 3-3) that these classes can profitably be subdivided. It is also in these classes that most of the species diversity is concentrated.

The single site classes MOC and XHA are clearly defined by small suites of species not found at other sites. In the case of MOC, these species are primarily aquatic herbs, and it seems likely that this site represents an end-member of seasonal flooding, in which both frequency and duration are close to 100%. XHA is a dry floodplain grassland site, but the presence of *Cyperus longus* suggests that the flooding regime is slightly longer or more frequent. This possibility is corroborated by the position of XHA within its envelope in ordination space (Figure 3-2), where flood frequency and depth parallel axis 1.

The estimates of overall species richness of these seasonal floodplains agrees closely with the Snowy Mountains Engineering Corporation 1989 estimate of 240. It appears that only a small subset of these species are widely distributed enough to make useful indicators. Between-group differences in annual:perennial and sedge:grass ratios are a good reflection of differences in hydroperiod between sites. The DFG class of floodplain is characterized by annual grasses and herbs adapted for rapid seasonal growth and seed production during the short rainy season; there are also 3 woody species, one of which (*Acacia erioloba*) emerged with an IV of 60 for this group. This may be interpreted as follows: the low frequency of flooding in these sites results in flood events becoming major disturbances, and between such events, successional processes are those operating in the surrounding savanna woodlands: an initial burst of weedy species followed

by a slow intrusion of woody species. SFG floodplains are characterized by perennial grasses; some sedges and herbs are annual, and may be related to rainy season growth. The decline in the proportion of annual species with increasing hydroperiod in the SFS and SAC classes may simply be attributable to the lack of a sufficiently long window for germination and growth.

Most of the floodplains sampled in this study exhibited zonation of vegetation along the topographic gradient from upland to thalweg; to remove noise from ecotones, only quadrats more than 40m from upland areas were used in the analysis, this representing approximately 68% of the data collected. There is evidence from other studies that species assemblages may be replicated in such zones within single floodplain sites. Bonyongo et al (2000) studied floodplain vegetation in a single floodplain in the Boro system and described 3 vegetation types which were further divided into a total of 8 communities. From their data, under the classification proposed here, the overall designation of this floodplain would be SFS, while the fringe type “*Setaria sphacelata-Eragrostis inamoena*” corresponds to class SFG. These communities should be considered as mobile assemblages, and their distribution reflects the conditions of the current year. Timing of sampling in relation to plant phenology was also a factor in our survey work: several herbaceous species (eg, *Abildgaardia hispidula*, *Nicolasia costata*) apparently take advantage of space opened by the die-back of hydrophytes as the flood retreats, and grow rapidly in response to day-length and rainfall. These opportunists do not survive prolonged inundation, but are found (up to 20% of cover in some quadrats) in regularly flooded areas immediately prior to and during the early stages of the rising flood. If sampling were carried out after the flood peak, no evidence of their presence would remain. Such effects are characteristic of the bimodal nature of ecological production in this asynchronous system. Bonyongo et al (2000) note that grazing by large mammals was most prevalent in the *Paspalidium obtusifolium-Panicum*

repens community in the floodplain they studied, in both wet and dry seasons, as *P. repens* responds to the advent of both local (summer) rain and winter floods.

Perhaps the most difficult obstacle to overcome with regard to vegetation distribution in large wetlands is accommodating the dynamics of composition. Remote sensing is often the approach of choice for mapping vegetation, given the constraints of access and size, but is itself constrained by cost, temporal, spatial and spectral limitations. McCarthy et al (2004) identified 12 eco-region classes in the Delta based on remote sensing of seasonally flooded wetland. They defined these in terms of gross vegetation structure, although they identified examples of key species. This classification was done at a pixel resolution of 28.5m, well suited to the grain of spatial variation in vegetation. They noted, however, that the class definitions were ambiguous, “even if distinct species composition is suggested by Ellery and Ellery (1997) for example”. This ambiguity arises because there is constant adjustment to hydrological variation; vegetation communities (and therefore ecoregions in the strict sense) in wetlands are never spatially static. Unless such ecoregion maps are produced on an annual basis from new data, they remain snapshots of a particular instant in the successional history of the vegetation, and are essentially maps of physiography, or “potential habitat”. Correlations must be sought between physiography, hydrological variation and floodplain species assemblages to accommodate the dynamic interactions between species composition and its drivers in order to maximize the utility of such remote sensing approaches. Monitoring floodplain species composition through simplified ground survey requires only that a common classification system is employed. Describing and defining such classes is a vital step in mapping and monitoring change in the Okavango Delta, where national policies and international conventions mandate ecological monitoring, but the country lacks the capacity to do it (Jansen 2002a). The knowledge required

to recognize the few indicator species involved in classification is easily acquired; the field assistants involved in this field study were adept at sampling methodology and identification of the most common species within 2 weeks of training. It is likely that a more economic method of sampling could be used, such as one large fixed quadrat, and repeated measures taken to observe trends.

Conclusions

This study has made possible a repeatable and relatively simple classification of floodplains based on the detection of different suites of indicator species and a dichotomous key. Floodplain classes identified from quantitative analysis of frequency of occurrence data for herbaceous species correspond to some extent with earlier qualitative classifications, although indicator species identified in this study did not necessarily correspond with the dominant or conspicuous species used to define classes in earlier studies.

Analyzing change in the strength of species indicator value and significance with changing number of classes provided a robust method for identifying an ecologically optimum number of classes, and where to make further subdivisions.

Table 3-1. MRPP pairwise-comparison of between-cluster differences. t = test statistic, A = chance-corrected within-group agreement, p = probability of a smaller or equal δ . Note: p is not corrected for multiple comparisons.

Classes	t	A	p
SFG vs SAC	-7.847	0.361	0.00005
SFG vs DFG	-7.416	0.416	0.00016
SFG vs SFS	-9.397	0.328	0.00001
SAC vs DFG	-6.090	0.454	0.00092
SAC vs SFS	-6.029	0.228	0.00007
DFG vs SFS	-8.235	0.398	0.00005

Table 3-2. Class life-cycle characteristics and Shannon diversity.

Class	Annual:Perennial	Sedge:Grass	# Herb spp	Mean H'
DFG	1.2	0	7	2.76
SFG	0.27	0.36	4	2.81
SFS	0.14	0.57	5	2.98
SAC	0.045	2.0	6	2.80

Table 3-3. Indicator species parameters for the 4 class division. Indicator values and their p-values are derived from ISA (Dufrêne and Legendre, 1997); lifecycle and growth form data are from Germishuizen and Meyer (2007).

Primary Class	Indicator			
	Value	p-value	Lifecycle*	Growth Form
Dry Floodplain Grasslands				
<i>Urochloa mosambicensis</i> (Hack.) Dandy	99.1	0.0002	P	Graminoid
<i>Ipomoea coptica</i> (L.) Roth ex Roem. & Schult.	90.8	0.0002	A	Herb
<i>Chloris virgata</i> Sw.	80.0	0.0004	A (p)	Graminoid
<i>Pechuel-Loeschea leubnitziae</i> (Kuntze) O.Hoffm.	80.0	0.0004	P	Shrub
<i>Pogonarthria squarrosa</i> (Roem. & Schult.) Pilg.	80.0	0.0004	P (a)	Graminoid
<i>Tragus berteronianus</i> Schult.	80.0	0.0004	A	Graminoid
<i>Stipagrostis uniplumis</i> (Licht.) De Winter	79.4	0.001	P (a)	Graminoid
<i>Gisekia africana</i> (Lour.) Kuntze	73.4	0.0018	A (p)	Herb
<i>Eragrostis cylindriflora</i> Hochst.	73.0	0.0008	A	Graminoid
<i>Cynodon dactylon</i> (L.) Pers.	72.7	0.0002	P	Graminoid
<i>Bergia pentheriana</i> Keissl.	67.3	0.0008	P	Herb
<i>Melinis repens</i> (Willd.) Zizka	60.0	0.0026	A (p)	Graminoid
<i>Acacia erioloba</i> E.Mey.	60.0	0.0028	P	Shrub, Tree
<i>Corchorus tridens</i> L.	60.0	0.0028	A	Herb
<i>Eragrostis viscosa</i> (Retz.) Trin.	60.0	0.0028	A	Graminoid
<i>Aristida meridionalis</i> Henrard	60.0	0.004	P	Graminoid
<i>Hermannia quartiniana</i> A.Rich.	60.0	0.004	P	Herb
<i>Tephrosia purpurea</i> (L.) Pers.	60.0	0.004	A (p)	Herb
<i>Sporobolus ioclados</i> (Trin.) Nees	54.5	0.006	P	Graminoid
<i>Kohautia virgata</i> (Willd.) Bremek.	52.3	0.016	A (p)	Herb
<i>Combretum imberbe</i> Wawra	34.5	0.0398	P	Shrub, Tree
<i>Acacia nigrescens</i> Oliv.	26.0	0.0824	P	Tree
<i>Digitaria debilis</i> (Desf.) Willd.	14.3	0.6373	A	Graminoid
<i>Gomphocarpus fruticosus</i> (L.) Aiton f.	8.9	0.7586	A (p)	Herb, Shrub

Table 3-3 Continued.

Seasonally Flooded Grasslands				
<i>Nicolasia costata</i> (Klatt) Thell.	74.3	0.002	P	Herb
<i>Eragrostis lappula</i> Nees	71.8	0.001	P	Graminoid
<i>Setaria sphacelata</i> (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss	62.3	0.0002	P	Graminoid
<i>Cyperus sphaerospermus</i> Schrad.	60.6	0.0058	P	Cyperoid
<i>Nidorella resedifolia</i> DC.	51.6	0.006	A	Herb
<i>Vernonia glabra</i> (Steetz) Vatke	42.9	0.1034	P	Herb
<i>Panicum repens</i> L.	42.3	0.0352	P	Graminoid
<i>Abildgaardia hispidula</i> (Vahl) Lye	38.9	0.1886	A	Cyperoid
<i>Trachypogon spicatus</i> (L.f.) Kuntze	35.5	0.1188	P	Graminoid
<i>Panicum coloratum</i> L.	33.3	0.0428	P	Graminoid
<i>Aristida junciformis</i> Trin. & Rupr.	33.3	0.0648	P	Graminoid
<i>Schoenoplectus erectus</i> (Poir.) Palla ex J.Raynal	33.3	0.0694	A	Cyperoid
<i>Sorghastrum friesii</i> (Pilg.) Pilg.	33.3	0.1026	P	Graminoid
<i>Paspalum scrobiculatum</i> L.	28.2	0.2653	P	Graminoid
<i>Digitaria eriantha</i> Steud.	23.8	0.2088	P	Graminoid
<i>Kohautia caespitosa</i> Schnizl.	21.5	0.1882	A (p)	Herb
<i>Eleocharis acutangula</i> (Roxb.) Schult.	21.5	0.6791	P	Cyperoid
<i>Sporobolus spicatus</i> (Vahl) Kunth	16.4	0.5205	P	Graminoid
<i>Cenchrus ciliaris</i> L.	13.4	0.3761	P	Graminoid

Table 3-3 Continued.

Seasonally Flooded Sedgeland				
<i>Leersia hexandra</i> Sw.	71.2	0.0002	P	Graminoid
<i>Eleocharis dulcis</i> (Burm.f.) Trin. ex Hensch.	71.2	0.003	P	Cyperoid
<i>Oryza longistaminata</i> A.Chev. & Roehr.	67.5	0.0004	P	Graminoid
<i>Cyperus articulatus</i> L.	64.1	0.0022	P	Cyperoid
<i>Ludwigia stolonifera</i> (Guill. & Perr.) P.H.Raven	61.6	0.0066	A (p)	Herb
<i>Acroceras macrum</i> Stapf	53.3	0.0068	P	Graminoid
<i>Cyperus dives</i> Delile	50.0	0.0076	P	Cyperoid
<i>Persicaria limbata</i> (Meisn.) H.Hara	47.8	0.0094	P	Herb
<i>Paspalidium obtusifolium</i> (Delile) N.D.Simpson	44.1	0.042	P	Graminoid
<i>Vossia cuspidata</i> (Roxb.) Griff.	41.2	0.0236	P	Graminoid
<i>Schoenoplectus corymbosus</i> (Roth ex Roem. & Schult.) J.Raynal	41.1	0.0168	P	Cyperoid
<i>Potamogeton thunbergii</i> Cham. & Schldl.	39.0	0.0876	P	Herb
<i>Brachiaria humidicola</i> (Rendle) Schweick.	31.8	0.2288	P	Graminoid
<i>Phragmites australis</i> (Cav.) Steud.	29.9	0.1046	P	Graminoid
<i>Sesbania microphylla</i> Harms	27.0	0.1274	A	Herb
<i>Nesaea radicans</i> Guill. & Perr.	7.7	0.8712	P	Herb

Table 3-3 Continued.

Seasonal Aquatic Communities				
<i>Sacciolepis typhura</i> (Stapf) Stapf	80.5	0.0002	P	Graminoid
<i>Eleocharis variegata</i> (Poir.) C.Presl	75.2	0.0002	P	Cyperoid
<i>Fuirena pubescens</i> (Poir.) Kunth	66.7	0.0008	P	Cyperoid
<i>Burnatia enneandra</i> P.Micheli	64.8	0.0026	P	Herb
<i>Cygnium tubulosum</i> (L.f.) Engl.	62.7	0.0028	P	Herb
<i>Fimbristylis complanata</i> (Retz.) Link	56.2	0.0006	P	Cyperoid
<i>Nymphoides indica</i> (L.) Kuntze	46.8	0.0422	P	Herb
<i>Eragrostis inamoena</i> K.Schum.	45.7	0.034	P	Graminoid
<i>Miscanthus junceus</i> (Stapf) Pilg.	43.8	0.0262	P	Graminoid
<i>Cyperus denudatus</i> L.f.	43.3	0.044	P	Cyperoid
<i>Utricularia stellaris</i> L.f.	41.6	0.0344	P (a)	Herb
<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	38.1	0.1082	P	Cyperoid
<i>Pycneus nitidus</i> (Lam.) J.Raynal	36.9	0.0886	P	Cyperoid
<i>Nymphaea nouchali</i> Burm.f.	36.2	0.1204	P (a)	Herb
<i>Scleria dregeana</i> Kunth	35.4	0.0626	P	Cyperoid
<i>Sphaeranthus flexuosus</i> O.Hoffm.	33.8	0.133	A (a)	Herb
<i>Scleria distans</i> Poir.	30.0	0.0902	P	Cyperoid
<i>Andropogon huillensis</i> Rendle	30.0	0.0962	P	Graminoid
<i>Imperata cylindrica</i> (L.) Raeusch.	27.3	0.4787	P	Graminoid
<i>Cyperus longus</i> L. var. <i>longus</i>	26.4	0.6199	P	Cyperoid
<i>Fuirena umbellata</i> Rottb.	23.5	0.4893	P	Cyperoid
<i>Digitaria eylesii</i> C.E.Hubb.	16.3	0.4753	P	Graminoid
<i>Kyllinga erecta</i> Schumach.	15.4	0.4477	P	Cyperoid
<i>Kyllinga intricata</i> Cherm.	14.7	0.4137	P	Cyperoid
<i>Sopubia mannii</i> Skan	8.0	0.7958	P	Herb

*P = perennial, A = annual, (a) or (p) = occasionally annual or perennial.

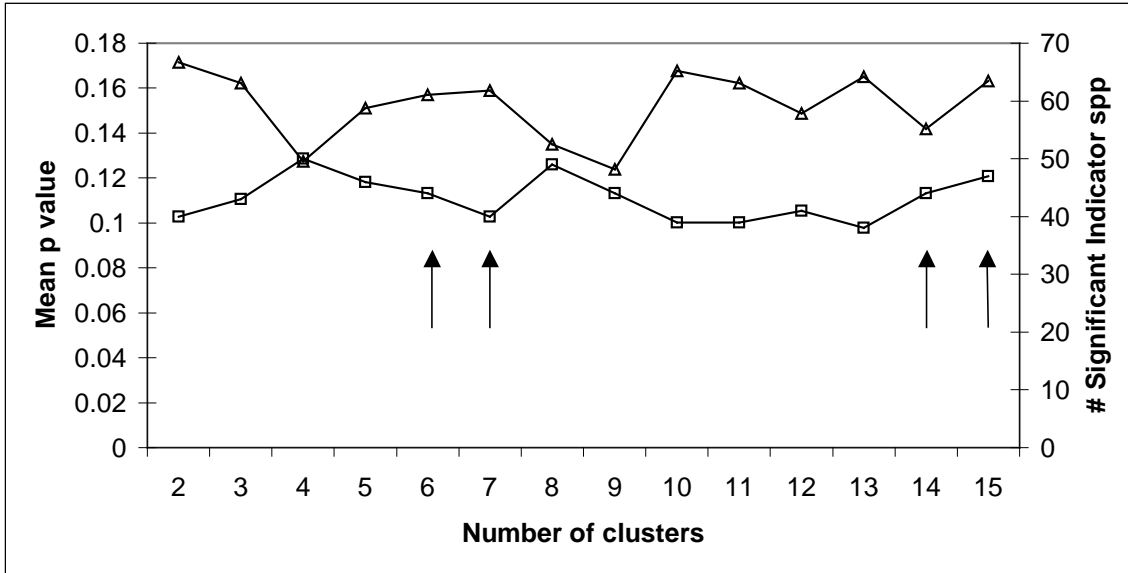


Figure 3-1. Changes in mean p-value (Δ) and number of significant indicator species (□, $p < 0.05$) from ISA, with increasing number of clusters. Arrows indicate points at which single site classes occur. Minima in mean p-value occur at 4 and 9, and maxima in number of indicators at 4 and 8 clusters respectively.

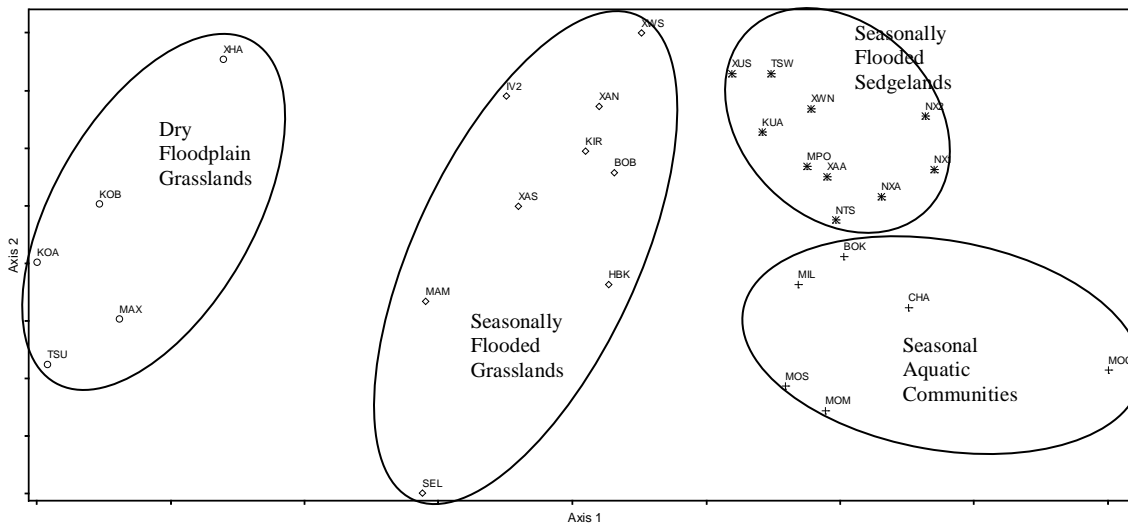


Figure 3-2. Non-metric multidimensional scaling ordination of sites by species. Envelope groupings correspond to the classes shown in Fig. 1. Axis 1 is correlated with hydrological variables such as flood frequency (Pearson $r^2 = 0.885$) and mean duration over the last three years ($r^2 = 0.796$). Axis 2 showed no strong correlations with any of the other environmental variables measured.

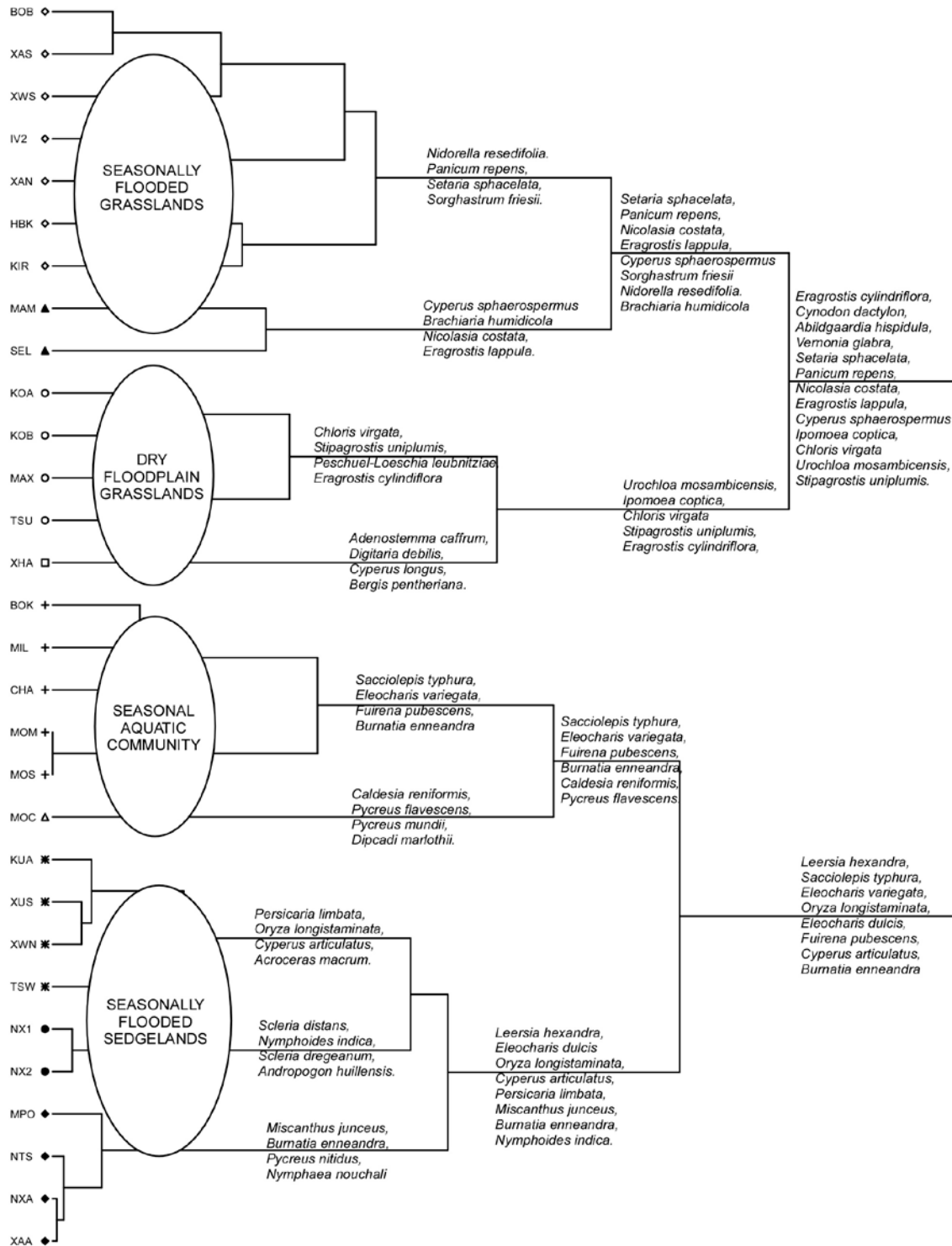


Figure 3-3. Dendrogram of sites clustered by species (flexible β linkage, $\beta = -0.25$, Sorensen distance). Four primary classes (envelopes) and nine sub-classes of sites are shown (\diamond , \blacktriangle , \circ , \triangle , $+$, $*$, \bullet , \square , and \blacklozenge), based on analysis of changes in indicator strength. At levels 6 and 7 of division, single site classes are generated, MOC \triangle , and XHA \square , respectively. Site codes are elaborated in Appendix 1.

CHAPTER 4
AN ANNUAL FLOOD PULSE AS THE PRIMARY DRIVER OF PLANT SPECIES
DISTRIBUTION IN SEASONAL FLOODPLAINS OF THE OKAVANGO DELTA,
BOTSWANA

Introduction

Junk (2000) defines floodplains as complex dynamic systems of ecotones of different spatial and temporal scales, periodically crossed by a mobile ecotone, the moving littoral zone (the land-water boundary). The periodic inundations which occur in most tropical and subtropical wetlands are often unimodal, of long duration and high amplitude, although in arid areas, many wetlands are ephemeral, and exhibit very large ranges of hydrologic variation (Capon 2005). The flood regime in these systems, however, is frequently the strongest factor affecting species richness, cover, and community composition (Bayley 1991, Lenssen et al. 1999, Robertson et al. 2001, Capon 2005). There is evidence that flood-pulsing is linked to high productivity and diversity (Brinson et al. 1981, Junk and Piedade 1993, Murphy et al. 2003), and that tropical wetland systems are well adapted to large variations as a result of the reproductive strategies and physiognomic characteristics of the plant species. Persistent, flood tolerant seed banks, the ability to reproduce both clonally and by seed, and to produce structure rapidly, typify tropical wetland plant communities (Henry et al. 1996, Brock and Rogers 1998, Alexander et al. 2008). Responses to hydrologic variation are usually relatively rapid, since many plants are herbaceous with short life-cycles, and as a result, the species composition is in a state of constant flux (Junk and Piedade 1993). Topographic gradients in wetlands often exhibit vegetation zoning or banding, which is the response of the species pool to changing hydrology; Niering (1987) suggests the term vegetative development for such compositional change, rather than succession. We suggest that in hydrologically dynamic systems, vegetative adjustment may be a more appropriate term, lacking the directional implications of succession or development.

The floodplains of the Okavango Delta in northern Botswana (19°S, 23°E, Figure 1-1) receive a large, essentially unimodal annual flood pulse, which arrives during the dry season (March-May), and takes 3-4 months to traverse the system. The pulse surcharges the main channel and spreads out over a large alluvial fan which is a mosaic of islands and approximately 12,800 km² of wetlands, of which 10,000 km² are seasonally inundated to varying degrees (Gumbricht et al. 2004a). The primary form of land use in the Delta is wildlife conservation, which supports a lucrative ecotourism industry. The aphasical relationship between the flood pulse and the local rains results in extraordinary concentrations of large mammals which move in to the Delta from the surrounding semi-desert during the dry winter (Patterson 1976). Floodplain primary production is the energy source for both this terrestrial ecosystem, and the aquatic system, which supports not only aquatic life, but also large populations of wetland birds (Ramberg et al. 2006). The Delta thus far has not been affected by major anthropogenic impacts, and represents one of few large open wetland ecosystems which is relatively unperturbed. Seasonal floodplains in the Delta exhibit conspicuous zoning, and obvious compositional changes with lateral and downstream distance from water sources. While the hydrology is relatively well understood (Bauer et al. 2003, Wolski and Savenije 2006, Wolski et al. 2006), the relationships between plant species composition and hydrology have not previously been quantified, although some qualitative descriptions have been made (Smith 1976). This is considered essential information for the development of management tools, and also policy development for the Delta and other wetlands in Botswana (National Conservation Strategy Agency 2000). The need for such tools, and for science to guide policy in this system is becoming increasingly urgent, as development pressures increase in the Okavango basin, which links three sovereign states, two of which (Namibia and Botswana) have very limited water

sources (Ashton and Neal 2003). This study investigated plant species distribution in relation to hydrological parameters in the Boro-Xudum distributary floodplains, where the effects of pulsing are most strongly manifested, (Figure 1-3), based on a field survey, and remote-sensing derived hydrological history.

Methods

Hydrological Variables

Flood duration in months was derived from an 8 year time series of MODIS imagery (spatial resolution 250m), while annual frequency and elapsed time since last flood were derived from an 18 year record of Landsat TM imagery (spatial resolution 28.5m) (see Chapter 2).

Vegetation Sampling

Floodplains in the Boro-Xudum distributary (Figure 1-3) were divided into 5 strata, based on historic flood frequency (Wolski and Murray-Hudson 2006), and 6 sites were randomly selected within each stratum. Sites were surveyed between March and June 2007. Species composition and relative abundance was sampled along transects oriented orthogonally to the long axis of the floodplain, using 1m² quadrats spaced 20m apart; geographic coordinates for each quadrat were recorded in the field. Species area-curves from a preliminary survey (Murray-Hudson 2006, unpublished data) were used to determine the required sample area as $\geq 25\text{m}^2$. Water depth at the time of survey (if wet), categorical data on soil type (if dry), and evidence of recent fire were recorded for each quadrat (presence/absence). At flooded sites, depth of inundation was measured for each wet quadrat during the field survey, between 1 and 4 months prior to flood peak. Species were identified in the field where possible; samples of unidentifiable plants were pressed in the field; those which could not be identified from the Peter Smith Herbarium collection at the Okavango Research Centre were sent to Kew Botanical Gardens, England for identification. Nomenclature follows Germishuizen and Meyer (2007). Species life-

cycle attributes (life-span, growth form, reproductive strategy) were derived from the literature, primarily Snowy Mountains Engineering Corporation (1989), Conservation International (2003), Germishuizen and Meyer (2007), and the FAO Grassland Species database (1977).

Analysis

Species data were summarized for each sample site by the proportion of quadrats in which they were present to the total number of quadrats for each site; this measure is the relative frequency, and values were not transformed. Within-group relationships were investigated using agglomerative cluster analysis to define communities (used here in the sense of the collection of plant species occurring in one place at one time), based on species occurring in more than 5 sites. Within-group and pairwise similarities for communities identified were tested with the multi-response permutation procedure (MRPP) in PCOrd software (McCune and Mefford 2006). To investigate patterns of species distribution in relation to flooding parameters, two separate approaches to ordination were carried out. The primary matrix was 53 species by 30 site matrix, using only quadrats which were more than 40m from island margins, while the environmental matrix was 30 sites with average flood frequency, mean flood duration of 3 preceding years, years since last flood, average water depth in 2007 in flooded quadrats, number of burnt quadrats, and average clay content in quadrats not flooded at the time of sampling.

- a) The first approach used non-metric multidimensional scaling (NMS)(Kruskal 1964, Mather 1976, McCune and Mefford 2006), which makes no assumptions of linear relationships among variables, but tends to linearize relationships between species space and environmental space. Sorensen distance was used with random starting configurations, and 250 runs each of real and randomized data; a 2 dimensional solution was selected from the rate of change in stress. This technique was used to investigate relationships between species and sites;

b) The second approach used canonical correspondence analysis (CCA) on the same data set; this procedure constrains the ordination by a multiple regression on environmental variables. The ordination was centered with unit variance to allow interpretation of fitted species abundances, with scaling to optimize species distances, and site scores derived from species (to get the best approximation of chi-squared inter-species differences). CCA was used to investigate the relationship of community structure and species distribution to a reduced set of hydrological variables. The strength of this relationship was tested against a multiple (Monte Carlo) randomization of the full dataset. Individual species distribution relationships with frequency and duration were derived subsequently from CCA ordination against these two variables separately. Probabilistic species distribution parameters along these hydrological gradients were estimated using generalized linear models (GLMs) based on Gaussian logistic regression (Ter Braak and Looman 1986). This approach assumes a unimodal bell-shaped response curve, and allows the derivation of species optimum values (the value of the environmental variable at which the probability of occurrence is highest), tolerance (a measure of ecological amplitude, related to the breadth of the bell), and the maximum probability of occurrence. Distribution curves were generated from CANOCO (Ter Braak and Smilauer 2006). One of the drawbacks with this method is that species whose optima lie outside the sampled range of the independent variable are not well modeled. In this study, species whose modeled flood duration optima were estimated at greater than 12 months were set to 12 months, and those (dryland species) whose optima were less than 0 (that is, negative) were set to 0; similar thresholds were set for distributions with annual flood frequency at 0 and 18.

To investigate responses to hydrological variation and species distribution in more detail, ordination and cluster analysis was carried out on the intermediate frequency and duration

groups, (seasonally flooded grassland, SFG and seasonally flooded sedgeland, SFS), separately but based on the full complement of quadrats (i.e., including those quadrats within 40m of island margins).

Results

General Floristics

A total of 166 species (124 genera) were recorded, in 44 families of which 36 are dicotyledonous and 8 monocotyledonous. By far the largest numbers of *species*, however, are monocots, the bulk of these being Poaceae (55) and Cyperaceae (29) making up almost half of the total; the next largest group are the Asteraceae (10), a large group of primarily annual herbs. The overall ratio of annual to perennial species is 1:2 (55:111); about half of the annual species recorded are opportunistically perennial, while 7 perennial species exhibit the opposite trait. Half of the species recorded are wetland plants (riverine, lacustrine, palustrine or flooded grassland habitats), and half are terrestrial (84:82), according to the Snowy Mountains Engineering Corporation (1989) classification. It should be noted here that many species occurred at relatively few sites: removal of species occurring at less than 4 sites reduces the number of species to 53. A summary of growth forms for species found in more than one site is given in Table 4-1. Grass-like and herbaceous plants are the most numerous; there are numerous forms of aquatic plants, while trees and shrubs are poorly represented.

Hydrology

As may be expected (Table 4-2) the hydrological variables are themselves strongly co-linear. Thus floodplains which are more frequently flooded tend to be flooded for longer; the converse is also true. Average depth here is the average derived from multiple quadrats at each flooded site (17 of the 30 sites were flooded at the time of sampling). It does not represent the

realized long term average or potential maximum depth, as the field campaign was carried out while the flood was rising.

Hydrology-Vegetation Relationships

NMS ordination of the data (Figure 4-1) shows that there are strong relationships (Table 4-3) between species composition and three hydrological variables: 18-year average frequency (the average of the proportion of 18 years that each quadrat at a site was inundated), 3-year average monthly duration (the average number of months of inundation over the preceding 3 years for all quadrats at a site), and the number of years since last flood. Since the survey was undertaken prior to the flood peak, while flood waters were still rising and expanding horizontally, this measure does not robust for between-site comparisons. That notwithstanding, there is a detectable relationship between ordination space and site average depth (as may be expected, given the co-linear relationship of depth and duration). Correlations with mean durations for different lengths (3, 4 and 7 years) of duration record were 0.74, 0.69 and 0.67 respectively. Long-term flooding frequency is the strongest predictor of species composition for the full dataset.

The classes of sites in Figure 4-1 are derived from agglomerative cluster analysis of sites in species space. The class on the far left (○) is strongly separated from the other sites, and is comprised of floodplains which have only received water in the highest floods of the last 2 decades (i.e., less than one year in ten). Axis 1 explains 71% of the variance in the data, while axis 2 explains 11%. Pearson correlations between NMS ordination axes and hydrological variables are given in Table 4-3. All variables are correlated with axis 1; none are significantly correlated with axis 2, except Years since last flood (0.197), and no alternative explanation is immediately apparent for the variation in this dimension. No relationships were found with

number of quadrats burnt; clay content has a weak relationship with axis 1 (Kendall's Tau = 0.352).

The effects of the time elapsed since flooding on species-distance relationships between sites is more evident when the data are subjected to CCA, which constrains the ordination with the environmental variables (Figure 4-2a), and indicates two distinct drivers: duration/frequency, and time-since-last flood. Note the near-orthogonal relationship between the labeled sites (which have not been flooded for at least 2 years) and the remainder. Removing sites with long elapsed time since flooding profoundly affects the arrangement of sites in ordination space (Figure 4-2b). The change in the correlations between ordination space and environmental variable (Table 4-4) is also marked; the simplified structure of ordination space results in a stronger primary relationship with frequency, and the co-linear relationship between frequency and duration is also clear. Table 4-5 gives the strength of the relationship between species and environmental matrices (H_0 : no linear relationship).

A dendrogram of major communities is given in Figure 4-3; the average duration optima for the different groups are shown on each major branch. MRPP tests (Sorensen distance, flexible $\beta=0.25$) on all cluster-defined communities showed significant differences ($p<1E-8$); pairwise testing for difference between these 8 communities was also significant ($p<0.05$). Descriptive names (ellipses) on the dendrogram branches represent interpreted information on habitat preference for the 8 communities.

Table 4-6 lists all species found in more than 4 sites, their main life-cycle characteristics and lists the hydrological parameters estimated from generalized linear models for each. Half of the species found in drier floodplains (frequency < 20%, duration < 2 months) are annuals which propagate by seed; growth form is half graminoid, half herb. As flood frequency and duration

rises, the proportion of clonal perennials rises, as does the proportion of graminoid species, until frequency reaches about 80%, when perennial aquatic herbs start to appear. An exception here is the perennial herb *Cyrtium tubulosum*, which is a conspicuous component of the sedge meadow community (Figure 4-3).

Average duration optima for communities were different ($p < 0.05$) at all levels tested, as were frequency optima. Among the 8 communities, average duration tolerance (as determined from the GLMs) margins were different at $p = 0.08$, indicating that the breadth of tolerance ranges is not very different between these communities. The lowest tolerance was in the Dry Floodplain Grassland (DFG) community, and this contributes most of the difference between communities at this level of clustering; exclusion of this group reduces the probability of significance to $p = 0.24$. Duration optima are not uniformly distributed (Figure 4-4): peaks occur at 1, 4 and 8-9 months. Few species appear to be specifically adapted to the intermediate ranges 2-3 and 6-7 months. There are 16 species with duration tolerance ranges greater than 4 months, constituting about a third of the most common species. These species occur mostly in communities in the intermediate to high ranges of duration. A notable exception is *Cynodon dactylon* (tolerance ~5 months), which Junk and Piedade (1993) also found to be very tolerant of flooding in the Amazon.

Analyzing classes separately provides some insight into composition variation and overlap. Within the larger groups of intermediate floodplains (Seasonally Flooded Grassland, SFG, and Seasonally Flooded Sedgeland, SFS), analysis of full transect data (i.e., including quadrats within 40 m of island margins) indicates (Figures 4-5, 4-6 and 4-7, and Table 4-7) that there are distinct communities of species which occupy the floodplain margins in proximity to islands (higher elevations). In floodplains dominated by SFG communities, this marginal community has

species in common with DFG communities. The marginal community in floodplains which are dominated by SFS communities has a broad composition, with few flood-intolerant species; it contains many sedges and grass species which have a preference for short duration flooding. It is similar in composition to the sedge meadow community and the seasonally flooded grassland margins community (Figure 4-3). Both marginal communities also have a number (9 in the SFS and 5 in the SFG) of woody species, as shrubs.

Discussion

The co-linearity between hydrological variables simply reflects the hydro-geomorphological character of the Delta, in which topographic gradient is sufficiently low that water surface gradient is effectively the same, and local floodplain-dryland relief differences are seldom greater than 2 m (Gumbricht et al. 2004b). The strong correlations found between these variables and species distributions indicate that hydrological variation exerts a powerful and somewhat predictable influence on plants in the seasonal floodplains.

In seasonally pulsed floodplains of the Amazon near Manaus, Junk and Piedade (1993) found that grasses (Poaceae) were the dominant family, followed by the Cyperaceae; in general the proportions of herbaceous species were very similar to those found in this study, although overall richness was lower in the Okavango. They noted that pulse-adapted floodplain species had characteristically short reproductive cycles and high reproductive rates. These traits are common in communities in those Okavango floodplains where average flood duration is less than 4.8 months; that is, the flooded grassland communities (top main branch in Figure 4-3). Here, grasses are annual or short-lived tuft-forming perennials. A critical difference between the two studies may be that the Amazon data were compiled over several years, and covered both high and low water stages. Our study was essentially a snapshot of floodplain vegetation during the rising stage only, and a mixture of low-water grown species (terrestrial) and wetland species

was recorded. They found many species which showed great morphological and physiological plasticity, noting the ability of many aquatic species to survive the terrestrial phase by reducing leaf size or water content, or by aestivating as rhizomes in the sediments. These characteristics are found particularly in the wetter communities (mean duration >4.8 months, lower main branch in Figure 4-3) of the Boro-Xudum system. These communities are dominated by clonal perennials, and many of the sedges use rhizomes and corms as storage organs. This not only allows them to survive short drawdown periods, but also the frequent fires that occur on seasonal floodplains in the Delta.

This study found a clear distinction between communities of floodplains which had not been inundated for several years, and those which receive regular flooding under present hydrological circumstances, a finding corroborating that of Heintz *et al* (2007). Once flooding drops below a threshold frequency (estimated as 20%, or longer than 3 years, from Table 4-6), soil moisture is insufficient to support wetland plants, and a successional trend is started towards open savanna woodland. The early stages of this succession are characterized by pioneer species such as *Pechuel-Loeschia leubnitziae*, *Pogonarthria squarrosa* and *Urochloa mosambicensis*. If re-flooding does not occur within 7 years (the shortest time since last flood that was more than 2, recorded at KOB), shrub and shrub/tree species become established (*Acacia erioloba*, *Combretum imberbe*); in this study these species occurred at the drier sites (KOA, KOB, MAX, TSU, Fig. 4-1). Under renewed flooding, these opportunists are effectively forced out, and a seasonally flooded grassland develops. In this context, the flood pulse represents a major disturbance, and resets the dryland succession each time it occurs, opening them up to re-invasion by dryland species. The species pool does not contain propagules of flood-tolerant trees, and re-flooding (for sufficient duration) kills the woody species. The longevity of Delta wetland

species propagules under prolonged dry conditions is unknown, although seed bank experiments in South Africa (Brock and Rogers 1998) have shown staggered germination of wetland species from an ephemeral wetland after a 5 year dry period in response to 2 wetting cycles; longer survival than this is considered likely for both seed and clonal plants. In addition, rising floodwater is likely to carry with it seeds from upstream plants, so recruitment of water-adapted plants is likely to be relatively rapid.

Effects of the flood pulse at sites of intermediate levels of frequency and duration are not as distinct, although there are clear differences in species composition, and in growth form and life-cycle characteristics. The majority of species are grasses or sedges - emergent flood-tolerant (to varying degrees) plants. Most of the grasses in the seasonally flooded grassland communities (mean duration >3.8 months) are tuft-forming perennials; these rely predominantly on seed for dispersal, although individual plants may live for several years (Germishuizen and Meyer 2007). In the seasonally flooded sedgeland, where mean duration is between 4 and 9 months, all the main species are rhizomatous perennials (although most produce seeds as well). Few species have duration optima between 6 and 7 months; those that do tend to have broad tolerance ranges (e.g., *Brachiaria humidicola*, *Panicum repens*); instead these intermediate communities are characterized by an admixture of flood-intolerant species, which are found on the ecotones between the floodplain core and island dryland communities, and flood-tolerant species which inhabit the core zone itself.

When analyzed as classes of sites, separately, some discrimination of main effects appears to be possible; in SFG, SFS and SAC sites, the overriding strength of frequency is replaced by an apparently stronger response to duration (SFG and SAC), and depth (SFS). These latter variables function at the level of individual plant ecology, while long-term frequency is considered a

reflection of the hydro-geomorphic character of each floodplain, and the Delta itself. Figures 4-5 and 4-7 show that there is overlap in species composition between drier zones (margins, more elevated sections) of SFS floodplains, and SFG core communities; similar overlap occurs between SAC margins and SFS core communities. These results suggest that in all floodplains with intermediate flooding, similar collections of species will be found, with relative proportions reflecting the current hydroperiod of the particular elevation zone within the floodplain. Proportions change as duration and depth change, and different optima are reached or tolerances exceeded. The time-scale for such adjustment will depend on the relative growth rates of the species, but the fact that an average of the duration of 3 preceding years provided the best hydrological fit in the main regularly inundated floodplain classes suggests that many species will be perennial, with some form of vegetative reproduction, and capable of reaching maximum abundance in 3 years. The aquatic communities are also comprised of many species whose optima (probably) lie outside of the range sampled; that is, they are aquatic species capable of tolerating short draw-down periods.

It is clear that better knowledge of the seed-bank, and responses to draw-down and lengths of dry period would provide great insight into the development and maintenance of communities in these floodplains. Unfortunately many studies of wetland seed-banks appear to have been based on hydroperiods which have either been artificially modified (Ter Heerd and Drost 1994, Lenssen et al. 1999) or sporadic, with dry intervals spanning years (Brock and Rogers 1998, Alexander et al. 2008). ter Heerd and Drost found that in marshes in Holland which had lost much of their emergent cover as a result of prolonged inundation, several different communities developed after a draw-down, from seed-banks which did not differ in species composition. Alexander et al similarly found, in a series of wetlands isolated from the main river channel in

the Central Murray region of Australia, that individual wetlands developed individual plant communities despite initial similarities. It appears that the floodplain soils of the Okavango (with the possible exception of those which are flooded in less than 11% of years) are equipped with both a robust, diverse seed-bank, and the perennating organs (rhizomes, stolons, corms, bulbs) of clonal species, which results in common communities developing under equivalent flood regimes. Both types of propagules must be capable of withstanding not only extended periods of draw-down (or conversely, inundation), but also relatively frequent fire. Heinl et al (2007) found that no differences in species composition on seasonal Okavango floodplains could be ascribed to fire frequency. Clearly, the high degree of interconnection of floodplains in this system must play a role in ensuring a diverse seed-bank, probably as a result of rising flood waters carrying seeds with them each year. In this respect, too, the arrival of the flood at the end of the rainy season means that many flowering species have seed set and ready for dispersal.

Better knowledge of life-histories would also enable the development of a more detailed model for community development in Delta floodplains. van der Valk (1981) posited a model for allogenic succession in wetlands based on life-span, propagule longevity, and propagule establishment requirements. Such a model for the Delta would greatly improve the empirical relationships established in this study, but such life-history data are scarce and widely dispersed. As Austin (2007) points out, there is a need for statistical models to be interpreted within an ecological context; more life-history and reproductive strategy information would improve our ability to interpret these findings.

Drawbacks to the Gaussian logistic regression model include the truncation problem, where optima outside the sampled range are poorly estimated. Better resolution of floodplain communities in the higher end of the hydroperiod gradients (frequency > 90%, duration > 9

months) would improve data on those species which straddle the divide between perennial floodplains and seasonal floodplains. Here, too, the effects of depth, which were not well represented in this study, need further work. The assumptions of unimodality and, more importantly, symmetry in species response to hydrological gradients may not always apply. Huisman et al (1993) proposed a series of hierarchical equations which permit both asymmetry and “S” shaped logistic curves in modeling species distributions with environmental variables. Applications of these equations might improve fits and predictive abilities of modeled distributions.

Conclusions

The hydrological variables annual flood frequency, duration and depth vary co-linearly in the Okavango Delta seasonal floodplains. As the ordination and cluster analyses show, distributions of herbaceous plant species are strongly correlated with all three of these variables. At the scale of the distributary (based on all sites sampled), the strongest correlate is frequency, while duration and depth are more important for seasonally flooded grassland, seasonal aquatic, and seasonal sedge communities respectively. Elevation differences within individual floodplains give rise to distinct within-floodplain communities. The considerable compositional overlap suggests that species composition is simply related to extant hydrological conditions at both the distributary scale and the scale of the individual floodplain. It seems likely that there are sufficient propagules either in the soil of existing floodplains, or produced by plants in neighboring floodplains to ensure that similar communities will develop under similar conditions anywhere in the distributary studied, but this aspect of community ecology needs further study in the Okavango. General linear modeling of species distributions in relation to a 3-year average of flood duration shows that species tend to be adapted either to short periods of inundation with long dry periods, or to be adapted to long-term inundation, but be capable of tolerating short dry

periods; there were relatively few species whose flood-duration optima were estimated at 6-7 months (Figure 4-4).

Table 4-1. Summary of growth forms of seasonal floodplain plants found at more than 2 sites.

Growth form	Number of spp
Aquatic emergent.	14
Aquatic emergent & submerged	1
Aquatic free-floating	3
Aquatic free-floating submerged	1
Aquatic floating leaved	5
Aquatic floating stem	2
Aquatic submerged	5
Graminoid (includes sedges)	83
Ground Creeper	4
Geophytic Herb	1
Herb	29
Wetland Herb	2
Herbaceous Climber	3
Shrub	4
Shrublet.	1
Tree	7
Woody Herb	1

Table 4-2. Correlations (r-values) between hydrological variables

Variable	Average frequency	Average Duration	Years since last flood	Average depth
Average frequency	1			
Average Duration	0.909	1		
Years since last flood	-0.617	-0.706	1	
Average depth	0.727	0.609	-0.335	1

Table 4-3. Pearson correlation coefficients between NMS ordination axes and hydrological variables. The ordination was carried out on a 30 site by 53 species matrix.

Hydrological variable	Axis:	
	1	2
	r ²	r ²
18-year Frequency	0.829	0.02
3-year Average Duration	0.736	0.023
Years since last flood	0.589	0.197
Average depth of wet quadrats	0.46	0.002

Table 4-4. Comparison of Pearson correlation coefficients between site hydrological variables and CCA ordination axes for all sites (N = 30) and for regularly flooded sites with < 2 years since last flood (N = 25).

		Axis:		
		1	2	3
Data set	Hydrological Variable	r ²	r ²	r ²
N = 30	Frequency	0.743	0.192	0
	Duration	0.738	0.061	0.094
	Years since last flood	0.791	0.148	0
N = 25	Frequency	0.998	0	0.003
	Duration	0.735	0.320	0

Table 4-5. Monte Carlo test results: CCA species-environment correlations for regularly flooded sites (N = 25). Environmental variables are 18 year mean flood frequency and 3 year average flood duration.

Real Data		Randomized Data, 998 runs			
Axis	R ²	Mean	Min	Max	p ¹
1	0.910	0.687	0.492	0.874	0.001
2	0.739	0.652	0.427	0.892	

1: p = proportion of randomized runs with species-environment correlation greater than or equal to the observed species-environment correlation: i.e., $p = (1 + \text{no. permutations} \geq \text{observed}) / (1 + \text{no. permutations})$; p is not reported for axis 2 because using a simple randomization test for this axis may bias the p values.

Table 4-6. Life cycle characteristics and hydrological controls of species occurring in more than 4 sites. Max. Probability is the calculated probability of occurrence at the optimum duration (*sensu* ter Braak, 1986).

Code	Species	Life span ¹	Growth Form ¹	Reproduction ¹	Optimum Frequency (% of years)	Optimum Duration (months)	Tolerance (months)	Max. Probability
Kohvir	<i>Kohautia virgata</i> (Willd.) Bremek.	A (p)	H	Seed	0.0	0	6.5	0.34
Eracyl	<i>Eragrostis cylindriflora</i> Hochst.	A	G	Seed	1.1	1	3.6	0.58
Uromos	<i>Urochloa mosambicensis</i> (Hack.) Dandy	P	G	Seed/Clonal	5.8	0	2.1	0.51
Ipocop	<i>Ipomoea coptica</i> (L.) Roth ex Roem. & Schult.	A	H	Seed	7.3	0	3.2	0.39
Stiuni	<i>Stipagrostis uniplumis</i> (Licht.) De Winter	P (a)	G	Seed/Clonal	7.5	0	2.1	0.55
Gisafr	<i>Gisekia africana</i> (Lour.) Kuntze	A (p)	H	Seed	7.9	0	2.3	0.33
Vergla	<i>Vernonia glabra</i> (Steetz) Vatke	P	H	Seed	9.1	3	4.2	0.32
Cyndac	<i>Cynodon dactylon</i> (L.) Pers.	P	G	Clonal/Seed	12.0	1	4.7	0.59
Berpen	<i>Bergia pentheriana</i> Keissl.	P	H	Seed	13.9	1	2.7	0.36
Digdeb	<i>Digitaria debilis</i> (Desf.) Willd.	A	G	Seed	18.9	1	2.8	0.22
Abihis	<i>Abildgaardia hispidula</i> (Vahl) Lye	A	G	Seed	36.1	3	8	0.43
Cyplon	<i>Cyperus longus</i> L.	P	G	Clonal/Seed	37.5	6	5.4	0.31
Digeri	<i>Digitaria eriantha</i> Steud.	P	G	Seed	37.7	4	3	0.16
Eralap	<i>Eragrostis lappula</i> Nees	P	G	Seed	39.2	3	2.6	0.40
Niccos	<i>Nicolasia costata</i> (Klatt) Thell.	P	H	Seed	39.2	3	2.4	0.48
Cypsph	<i>Cyperus sphaerospermus</i> Schrad.	P	G	Clonal/Seed	41.1	3	3	0.46
Sorfri	<i>Sorghastrum friesii</i> (Pilg.) Pilg.	P	G	Clonal/Seed	44.8	4	2.7	0.24
Traspi	<i>Trachypogon spicatus</i> (L.f.) Kuntze	P	G	Seed	46.0	4	2.9	0.34
Nidres	<i>Nidorella resedifolia</i> DC.	A	H	Seed	48.2	4	2.5	0.09
Spospi	<i>Sporobolus spicatus</i> (Vahl) Kunth	P	G	Clonal/Seed	50.0	4	6.8	0.04
Impcyl	<i>Imperata cylindrica</i> (L.) Raeusch.	P	G	Clonal/Seed	50.0	8	5.7	0.24
Brahum	<i>Brachiaria humidicola</i> (Rendle) Schweick. <i>Setaria sphacelata</i> (Schumach.) Stapf & C.E.Hubb. Ex	P	G	Clonal/Seed	50.7	4	4.9	0.46
Setsph	M.B.Moss	P	G	Clonal/Seed	53.1	5	3.6	0.51
Passcr	<i>Paspalum scrobiculatum</i> L.	P	G	Clonal/Seed	54.1	5	2.9	0.19
Panrep	<i>Panicum repens</i> L.	P	G	Clonal/Seed	63.6	6	3.8	0.60
Eraina	<i>Eragrostis inamoena</i> K.Schum.	P	G	Seed/Clonal	73.5	8	4.4	0.52
Cypden	<i>Cyperus denudatus</i> L.f.	P	G	Clonal/Seed	74.3	7	4	0.55

Table 4-6 Continued.

Code	Species	Life span ¹	Growth Form ¹	Reproduction ¹	Optimum Frequency (% of years)	Optimum Duration (months)	Tolerance (months)	Max. Probability
Fuiumb	<i>Fuirena umbellata</i> Rottb.	P	G	Clonal/Seed	77.2	7	3.2	0.20
Fimcom	<i>Fimbristylis complanata</i> (Retz.) Link	P	G	Clonal/Seed	77.2	8	4.1	0.43
Cyctub	<i>Cyrtium tubulosum</i> (L.f.) Engl.	P	H	Seed	79.2	8	3.3	0.34
Cypart	<i>Cyperus articulatus</i> L.	P	G	Clonal/Seed	79.5	8	3.2	0.48
Rhyhol	<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	P	G	Clonal/Seed	79.5	8	4.1	0.46
Pycnit	<i>Pycreus nitidus</i> (Lam.) J.Raynal	P	G	Clonal/Seed	80.1	8	3.3	0.46
Fuipub	<i>Fuirena pubescens</i> (Poir.) Kunth	P	G	Clonal/Seed	80.5	7	3.7	0.24
Misjun	<i>Miscanthus junceus</i> (Stapf) Pilg.	P	G	Seed	83.0	8	3	0.38
Leehex	<i>Leersia hexandra</i> Sw.	P	G	Clonal/Seed	83.9	8	3.1	0.57
Digeyl	<i>Digitaria eylesii</i> C.E.Hubb.	P	G	Clonal/Seed	85.7	9	3.7	0.24
Burenn	<i>Burnatia enneandra</i> P.Micheli	P	H	Clonal/Seed	85.7	9	3	0.18
Scldre	<i>Scleria dregeana</i> Kunth	P	G	Clonal/Seed	85.7	9	3.1	0.15
Acrmac	<i>Acroceras macrum</i> Stapf	P	G	Clonal/Seed	86.6	8	3.3	0.50
	<i>Schoenoplectus corymbosus</i> (Roth ex Roem. & Schult.)							
Schcor	J.Raynal	P	G	Clonal/Seed	88.5	8	4.6	0.57
Utricsp	<i>Utricularia</i> sp.	P (a)	H	Clonal/Seed	88.6	9	3.1	0.35
Orylon	<i>Oryza longistaminata</i> A.Chev. & Roehr.	P	G	Clonal/Seed	89.2	8	3.6	0.52
Elevar	<i>Eleocharis variegata</i> (Poir.) C.Presl	P	G	Clonal/Seed	91.2	8	3.2	0.53
Nymnou	<i>Nymphaea nouchali</i> Burm.f.	P (a)	H	Clonal/Seed	91.6	9	3.2	0.54
Sactyp	<i>Sacciolepis typhura</i> (Stapf) Stapf	P	G	Clonal/Seed	91.9	9	3.3	0.53
Ludsto	<i>Ludwigia stolonifera</i> (Guill. & Perr.) P.H.Raven	A (p)	H	Seed/Clonal	100.0	9	9.3	0.32
Nymind	<i>Nymphoides indica</i> (L.) Kuntze	P	H	Clonal/Seed	100.0	10	3.2	0.49
Potthu	<i>Potamogeton thunbergii</i> Cham. & Schtdl.	P	H	Clonal/Seed	100.0	11	4.3	0.44
Pasobt	<i>Paspalidium obtusifolium</i> (Delile) N.D.Simpson	P	G	Clonal/Seed	100.0	12	4.2	0.47
Eleacu	<i>Eleocharis acutangula</i> (Roxb.) Schult.	P	G	Clonal/Seed	100.0	8	3.9	0.35
Eledul	<i>Eleocharis dulcis</i> (Burm.f.) Trin. ex Hensch.	P	G	Clonal/Seed	100.0	12	4.4	0.54

1: Data source: Germishuizen and Meyer, 2007. A = annual; P = perennial, A(p) = annual, sometimes perennial, P(a) = perennial, sometimes annual; G = graminoid (includes sedges), H = herb..

Table 4-7. NMS Pearson correlations with hydrological variables for a) seasonally flooded sedge land sites; b) seasonally flooded grasslands; c) seasonal aquatic communities. In a) and b), 2 ordination dimensions produced least stress in the data; 3 were required in c).

	Axis:		
	1	2	3
Hydrological variable	r ²	r ²	r ²
a) Seasonally flooded grassland (9 sites, 43 spp)			
3-year Average Duration	0.358	0.077	-
Years since last flood	0.04	0.067	-
18-year Frequency	0.0004	0.005	-
b) Seasonally flooded sedge lands (10 sites, 53 spp)			
Average depth of wet quadrats	0.834	0.009	-
3-year Average Duration	0.307	0.408	-
18-year Frequency	0.037	0.342	-
c) Seasonal aquatic communities (6 sites, 32 spp)			
3-year Average Duration	0.267	0.546	0.009
18-year Frequency	0.066	0.461	0.006
Average depth of wet quadrats	0.024	0.396	0.016

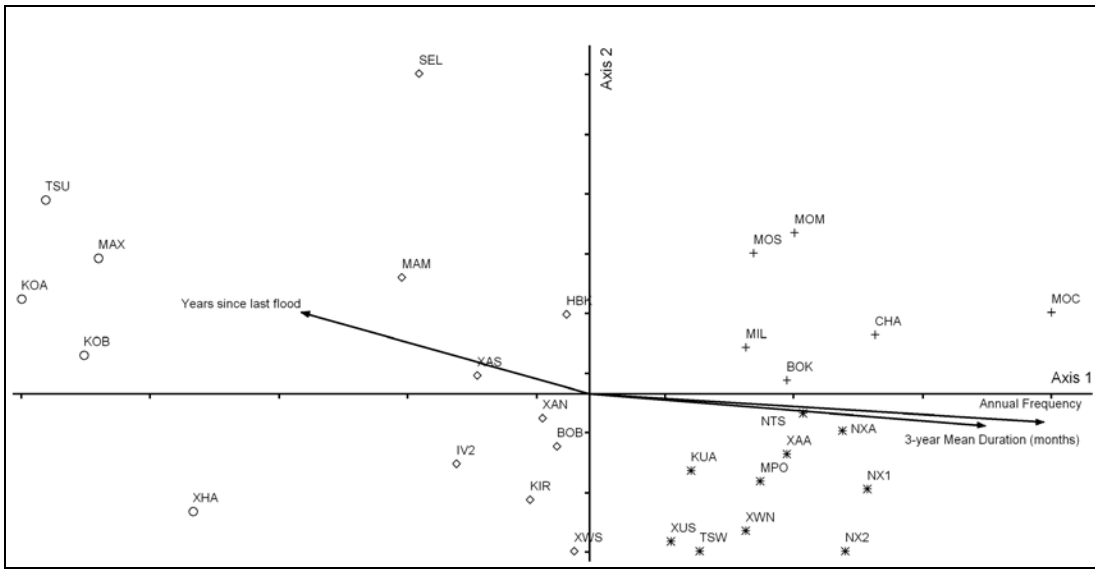


Figure 4-1. Non-metric multi-dimensional scaling (NMS) ordination biplot of 30 sites and 84 species (species occurring in >3sites only), showing 4 major site classes (○, *, +, and ◇) with an overlay of long-term flood frequency, mean flood duration and time since last flood. Hydrological variables are indicated by arrows in the direction of increase.

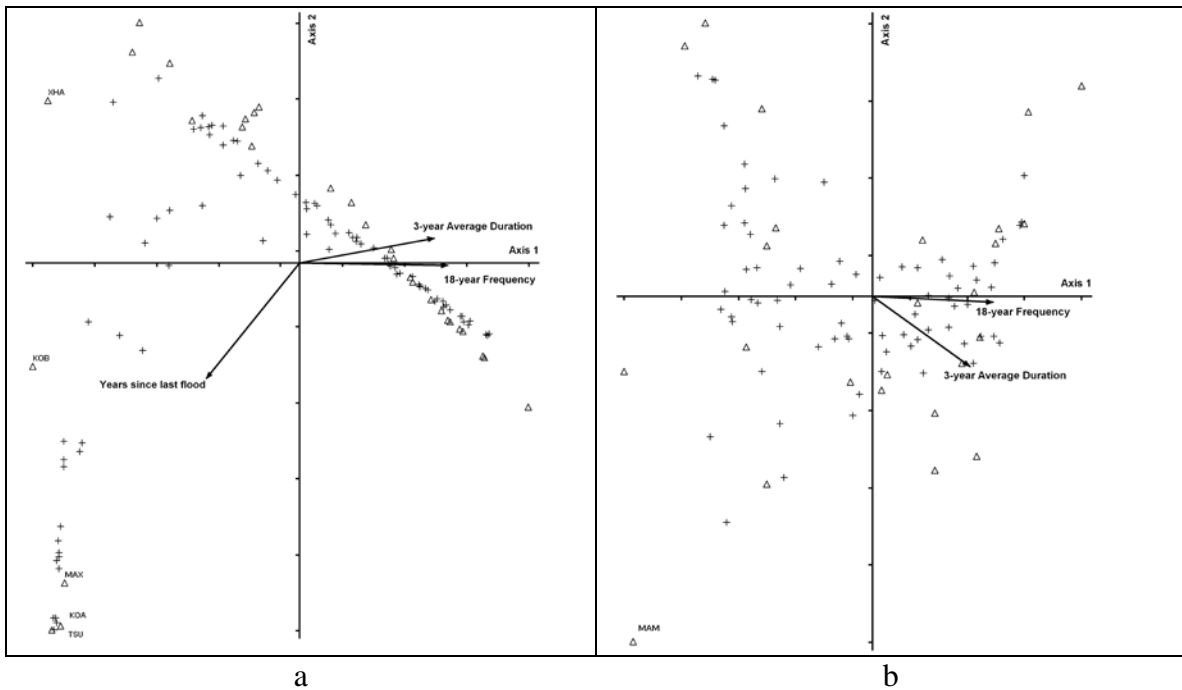


Figure 4-2. CCA ordination biplots of : a) 30 sites and 84 species (species occurring in >3sites only). Hydrological variables are indicated as arrows, sites as Δ , and species as +. A clear distinction exists between regularly flooded sites (unlabelled) and sites in which dryland succession is occurring (labeled, along the left side of the plot). b) 25 sites, with dryland succession sites removed. Note the increased spread of sites in ordination space, and the increased discrimination between frequency and duration.

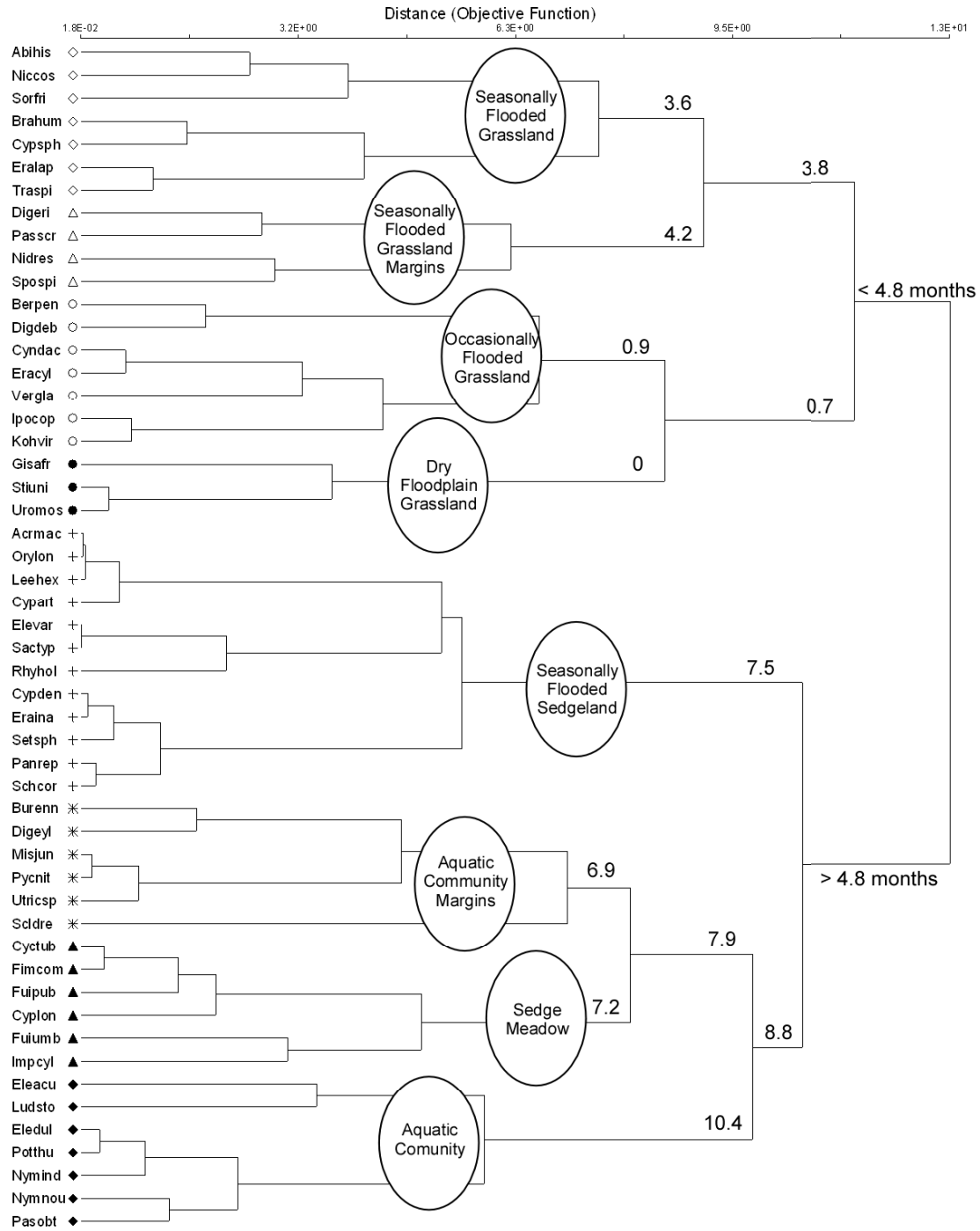


Figure 4-3. Dendrogram of species assemblages based on those species occurring in more than 5 sites. Mean flood duration optima (numbers on branches - months) characterize 8 distinct assemblages. 6-letter species codes are used for brevity; full species names, optima and tolerance ranges, and life cycle data are given in Table 4-6.

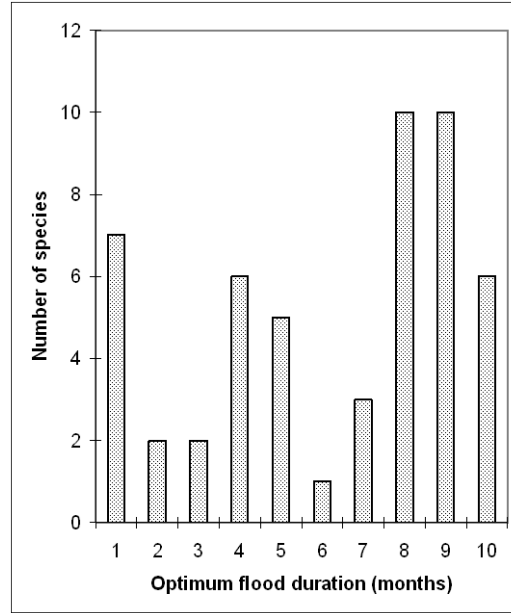


Figure 4-4. Histogram of estimated optimum flood duration for 53 most common species.

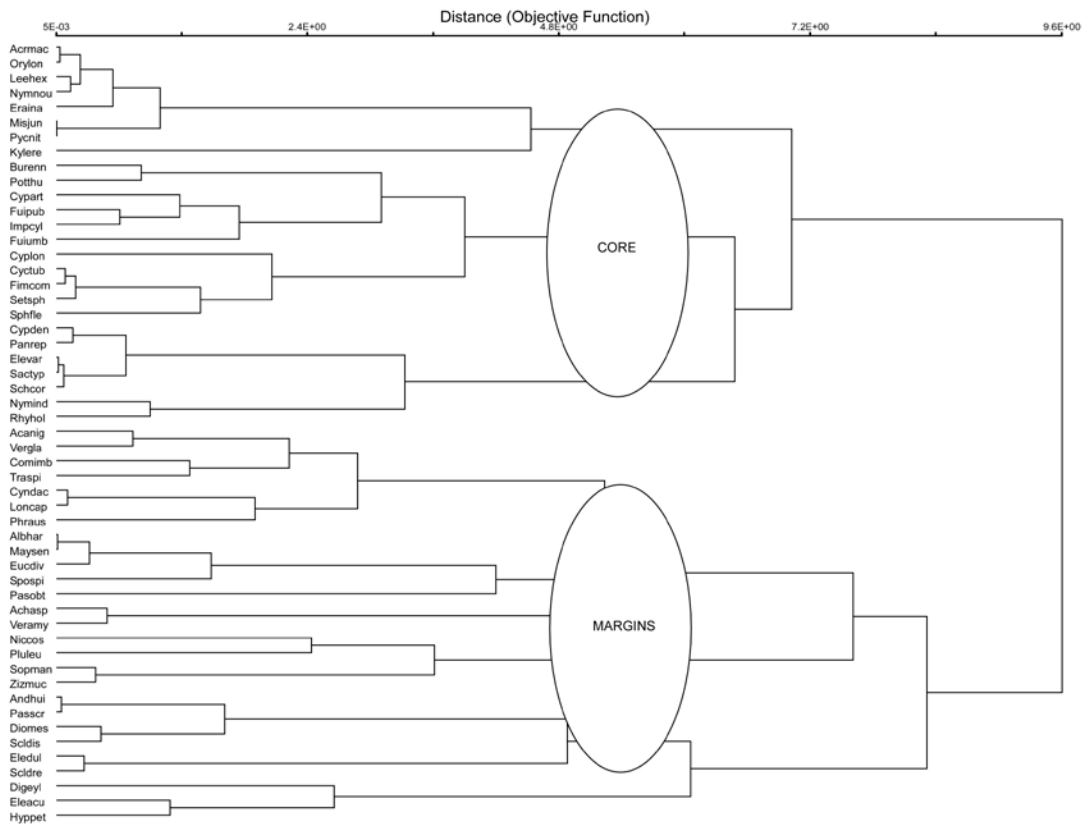


Figure 4-5. Dendrogram showing species groupings from entire transects in seasonally flooded sedge floodplains (N=10). Core species are those that occur in the main body of the floodplain, >40m from island perimeters, and margin species are those that occur in the 40m zone between island perimeters and the core.

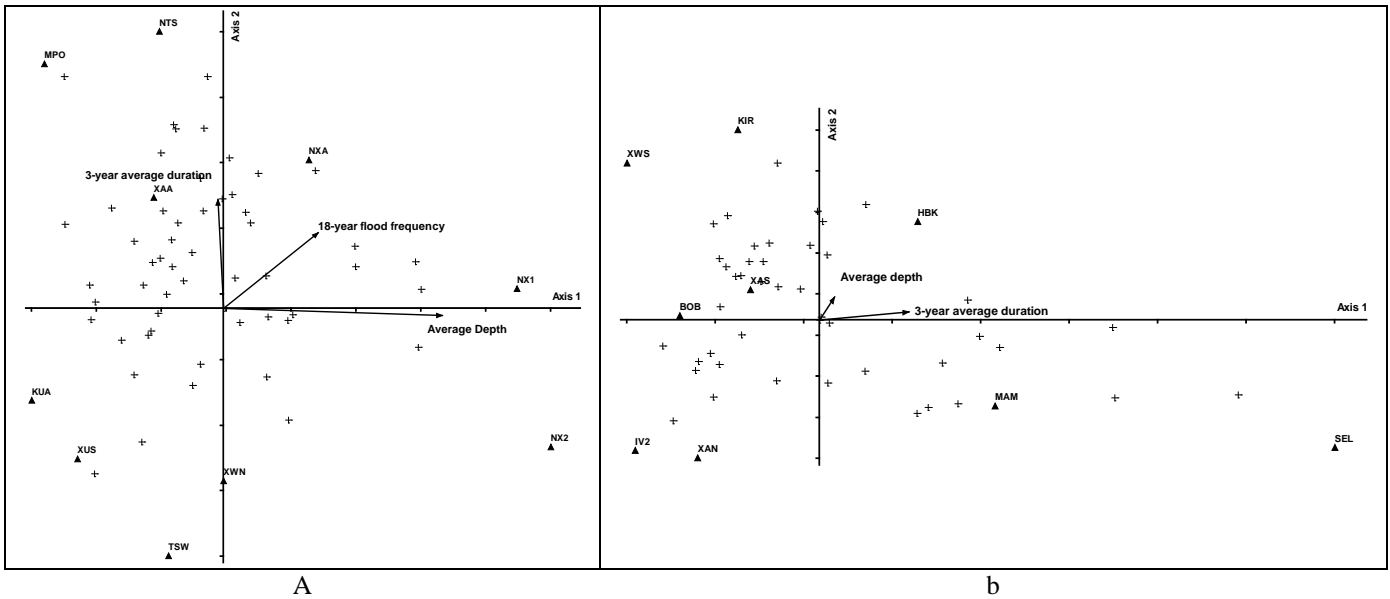


Figure 4-6. NMS ordination biplot of sites classified as: a): seasonally flooded sedgeland (10 sites by 53 species); b) seasonally flooded grassland (9 sites by 43 species). Environmental variables increase in the direction of the arrow. Sedgeland ordination space is most closely correlated with depth, while in grasslands duration is the strongest (Table 4-7).

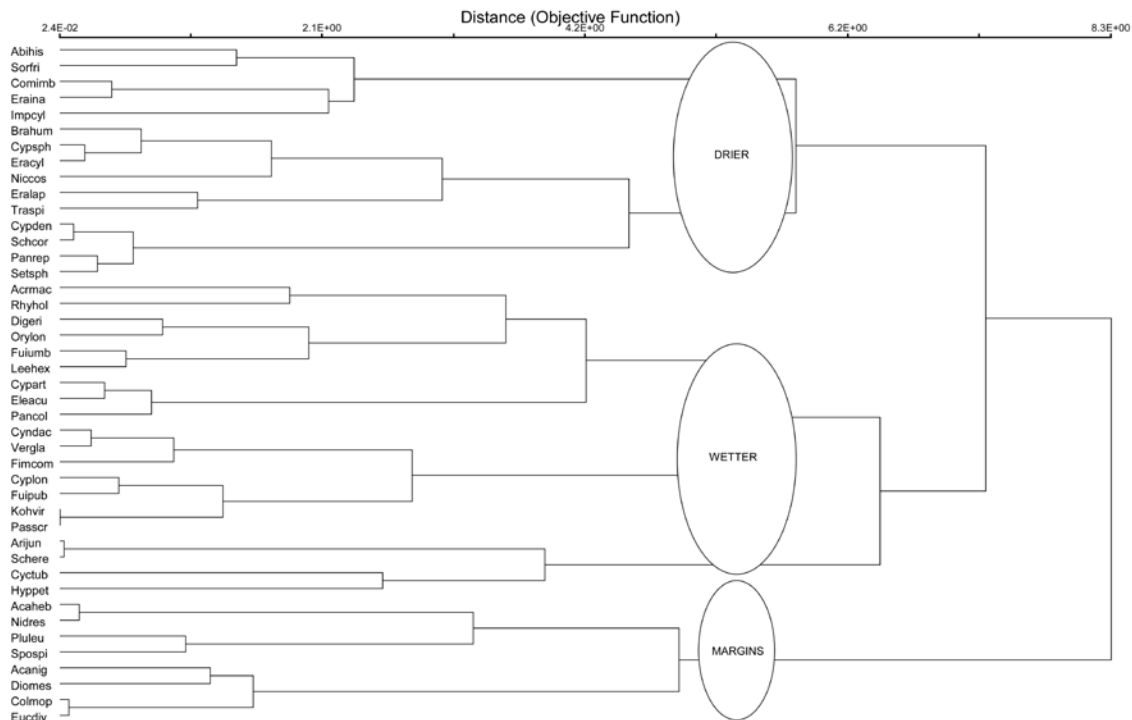


Figure 4-7. Dendrogram showing species groupings from entire transects in seasonally flooded grass floodplains (N=9). Margin and core groups are separated at the first division, while there is a pronounced division between wetter and drier communities at the second level of division.

CHAPTER 5
A SPECIES-DISTRIBUTION MODEL FOR INVESTIGATING HYDROLOGICALLY-
INDUCED CHANGES IN FLOODPLAIN VEGETATION IN LARGE FLOOD-PULSED
TROPICAL WETLANDS.

Introduction

Spatially explicit ecological models are increasingly being used to contribute to the design and evaluation of management and monitoring schemes, often as part of integrated management strategies such as adaptive management (Perry and Enright 2006). The development of ecological modeling is converging in one general direction: the integration of temporal and spatial effects (Sklar and Hunsaker 2001). While many spatial models exist of wetland ecosystems, they are often of limited geographic scale, or of areas which are data-rich because of their location in highly developed countries such as the United States of America and the Netherlands (Poiani and Johnson 1993, Van Horssen et al. 1999). Spatial ecological models of large wetland systems are relatively few, as a result perhaps of the difficulties involved in gathering, collating and analyzing the data required, and the computational resources needed to deal with such data (Costanza and Sklar 1985). Notable exceptions to this are the Mississippi Delta (Barataria-Terrebonne Estuarine Landscape Spatial Simulation, BTELSS) model (Reyes et al. 2000), and the Everglades Landscape Model (ELM, including the Across Trophic Level Systems Simulation, ATLSS)(Fitz et al. 2004). The ELM, like many models used to assist planning and management, undergoes a cycle of continuous assessment and refinement, but has already become an accepted tool in evaluating scenarios of potential restoration of the natural system (Wetzel 2001, Fitz et al. 2004). The general ecological model (GEM) that is the basis of the ELM is a process model designed to produce ecological responses (production, community shifts) to varying environmental conditions (Fitz et al. 1996).

The utility of such models, in allowing hypotheses (including potential management actions) concerning ecological behaviour to be developed, investigated and visualized for very extensive geographic areas, is immediately apparent. One common characteristic of the Mississippi and Everglades systems is that both have been extensively affected by human activities to their detriment, and a major part of the stimulus to develop spatial ecological models has been the perceived necessity to address (and redress) these impacts. In the 14,000 km² Okavango Delta in northern Botswana (Figure 1-1), anthropogenic disturbance on such a scale has not yet occurred. It is, however, inevitable that progressive development of water resources in the catchment in Angola, and the river course in Namibia will occur as both these upstream states grow and develop after years of war (Ashton and Neal 2003, Andersson et al. 2006). The region is one in which the projected effects of climate change are highly uncertain (Andersson et al. 2006, Wolski and Murray-Hudson 2008). The Delta is the distal end of the endorheic Okavango system, with less than 3% of the inflow leaving the Delta as surface flow, the bulk being lost through evapo-transpiration (Wilson and Dinçer 1976, Wolski and Savenije 2003), and consequently is very sensitive to any changes in upstream hydrology. Land use in the Delta is predicated on sustainable use of the wildlife resource; it is a declared RAMSAR site (a wetland of international importance for waterfowl), and a gazetted wildlife management area (WMA) (National Conservation Strategy Agency 2000). As a result of these commitments, the Botswana government is required to design and implement a plan for development and management that will ensure sustainability of current levels of ecosystem services (National Conservation Strategy Coordinating Agency 2005). Such a plan should pre-empt the adverse consequences that manipulation for short-term gain has had in other large wetlands. A spatial ecological model is clearly an important tool for such an undertaking.

Hydrological modeling in the Delta was initiated for the purposes of assessing the potential for water supply downstream through various possible manipulations of channel-floodplain relationships (Dinçer et al. 1987, Snowy Mountains Engineering Corporation 1989, 1990, Scudder et al. 1993). These models provided the basis for subsequent attempts to assess potential change in the Delta due to upstream or climate change. These models were all reservoir-based, with no explicit spatial function, and represent a series of improvements and refinements to the earliest (1987) model. More recently, new initiatives by various authors have attempted to create semi-, or fully spatially distributed hydrological models of the Delta (Wolski et al. 2002, Bauer et al. 2003, Gumbricht et al. 2004c). Such models provided additional information on the extent of inundation in the floodplains, and constituted a significant step forward in understanding the mechanics of water distribution across the face of the alluvial fan. Andersson et al (2006) undertook an extensive analysis of hydrological and rainfall records in the basin to assess the impacts of human development and climate change in the basin on Okavango river flows. All of these models, however, were designed for investigating water budgets for the Delta, and did not consider potential ecological effects of hydrological change. A heuristic rule-based ecotope model was developed by Murray-Hudson and Wolski (2006, 2008) to investigate the feasibility of using a spatial hydrological model as the basis for a vegetation ecological model for Delta floodplains. The approach showed promise: where previous models expressed change simply in terms of loss of flooded area, simulated outputs indicated in quantitative terms that different ecotopes would be affected by varying degrees by hydrological change.

This study presents an approach using empirically determined hydro-period species distribution models (SDMs) (Guisan and Thuiller 2005) to simulate change in floodplain communities in response to hydrological change, in the seasonally pulsed Boro-Xudum

distributary of the Okavango Delta. The approach is based on the determination of species distributions, along a gradient of inundation duration, through canonical correspondence analysis of species frequency data, and generation of generalized linear models (GLMs) of these distributions. The GLM coefficients are then used as predictors driven by inundation duration data from a spatial hydrological model.

Methods

Vegetation Species Composition

Plant species composition was surveyed in 30 floodplain sites (Figure 1-3) over the period March to June 2007; this period was selected to maximize the chances of finding inflorescences, to aid in species identification. Five strata of equal area were defined from a flood-frequency map derived from an 18-year time series of Landsat TM imagery, and six sites randomly selected from each stratum. At each site, approximately 30 1 m² quadrats were placed at 20m intervals along transects orthogonal to the long axis of the floodplain. All plant species were recorded in each quadrat, and species frequencies expressed as the proportion of quadrats with presence to total quadrats for each site. Species were identified as far as possible in the field or the Peter Smith Herbarium at the University of Botswana; where this identification proved impossible, or confirmation was required, specimens were sent to Kew Botanical Gardens in England for identification. Nomenclature follows Germishuizen and Meyer (2007).

Hydrological Variables For GLM Development

Previous analysis (Chapter 4) had shown that long term flood frequency and average duration of inundation in months for the 3 preceding years provided the strongest correlations with species distribution. Since a 3-year average of monthly duration is closer in scale to the mean life-span of most of the plant species found in the floodplains (Germishuizen and Meyer 2007) than an 18-year average frequency, this variable was selected as the independent variable

for model development. Inundation duration for the years 2000-2007 was derived from interpretation of a monthly time series of 89 MODIS images (spatial resolution 250m) (see Chapter 2). This time series was calibrated against a set of flood extents interpreted from Landsat TM images for the years 2000, 2001, 2002, 2005 and 2006, and also tested for accuracy using actual flood data recorded from the 2007 vegetation survey sites. Inundation duration in months was thus available for each 250m pixel for each year.

Species Distribution Model Derivation

A data set (110 species) was generated from a subset of 25 sites for model calibration; 5 sites were held back for assessing model performance. The site-species matrix was then ordinated using canonical correspondence analysis (CCA); this procedure constrains the ordination by a multiple regression on a second site-flood duration matrix. The ordination was centered with unit variance to allow interpretation of fitted species frequencies, with scaling to optimize species distances, and site scores derived from species.

Probabilistic distribution parameters along the duration gradient were then estimated for a reduced set of species which occurred at more than 4 sites, using GLMs based on Gaussian logistic regression (GLR) (Ter Braak and Looman 1986). This approach assumes a unimodal bell-shaped response curve, and allows the derivation of species optimum values (the value of the environmental variable at which the probability of occurrence is highest), tolerance (a measure of ecological amplitude, related to the breadth of the bell), and the maximum probability of occurrence. The probability of occurrence is related to the independent variable (in this case, average flood duration over the preceding three years) as follows:

$$\log\left(\frac{p(x)}{1-p(x)}\right) = b_0 + b_1x + b_2x^2 = a - \frac{(x-u)^2}{2t^2}, \text{ (Ter Braak and Prentice 1988), where } p(x) \text{ is the}$$

probability of occurrence of the given species at duration x , and b_0 , b_1 and b_2 are quadratic

coefficients which do not have an intrinsic ecological meaning, but can be transformed into u , t , and a , which can be interpreted as follows: u is the species' optimum (the value of x at the maximum probability of occurrence), t is its tolerance (a measure of ecological amplitude), and a is a coefficient related to the height of the peak (maximum probability of occurrence).

Distribution curves, statistics of model significance, and the quadratic coefficients were generated from CANOCO ordination software (Ter Braak and Smilauer 2006), assuming a Poisson error distribution and using a logarithmic link function.

The Hydrological And Spatial Species Distribution Models

The hydrological model is a hybrid reservoir-spatial model, which distributes annual Delta inflows in monthly time steps through a series of interconnected reservoirs, and distributes reservoir inflow spatially within each. Groundwater-surface water interactions are explicitly modeled, as are the effects of antecedent flood conditions. The development, structure and performance of this model are described in detail in Wolski et al (2006). The basic spatial unit is a 1 km by 1 km cell, and inundation duration in months is calculated for each cell for each year.

The species distribution sub-routine calls GLM coefficients from a specified array of species data, and generates maps of probability of occurrence for each species for each year of inflow record from the duration maps of the preceding 3 years. A second, rule-based, routine was developed which produces maps of the extent of 4 floodplain communities, defined based on the aggregated duration optima of species groups identified from cluster analysis (see Chapter 4), with two additional communities: savanna (areas not flooded within the historical record, SAV), and perennially flooded areas (PC). Monthly duration thresholds determined for the different communities are as follows: savanna <0 ; dry floodplain grassland 0 - 2; seasonally flooded grassland 2 - 6; seasonally flooded sedgeland 6 - 8; seasonal aquatic communities 8 - 11; perennially flooded areas >11 months.

Predictive accuracy of the species distribution model was tested by comparing the simulated species distributions, based on the observed inflow record (mean monthly duration for 2004, 2005 and 2006), of the 5 validation sites with the observed frequencies at those sites.

Scenarios Of Change

In this study, we use the results of hydrological and climate-change modeling described in Hughes et al (2006) and Andersson et al (2006) for their Okavango River Basin model. Future conditions are not simulated explicitly; instead the historical series of monthly rainfall and mean monthly temperature is modified to reflect the change simulated by the developments or global circulation models (GCMs) considered. The outputs of the Okavango River basin model are used as inputs to the Delta hydrological model. For simulation of development change and climate change effects on vegetation, the rule-based floodplain community model was used to produce output maps of community distribution, as these are easier to compare visually than single species maps.

Andersson's (2006) development scenarios were projected to the years 2015 and 2025, and consisted of a total of 16 different scenarios involving the development of irrigated agriculture, the abstraction of water to supply domestic riparian users, to supply water to a pipeline linking into the Namibian Eastern National Water Carrier, the development of dams in the upper catchment for hydro-power, and the effects of intensified land use (deforestation) in the upper catchment. For the purposes of testing the model in this study, 3 of the 16 scenarios were selected for simulation, involving: i) the development of all potential dams, ii) maximum potential irrigation, and iii) a combination of all these developments including extensive deforestation in the upper catchment, up to 2025.

GCMs used in this study include the HadCM3 (Hadley Centre, UK (Gordon et al. 2000)), the CCCmaCGCM2 (Canadian Centre for Climate Research (Flato and Boer 2001), and the

GFDL R30 (Geophysical and Fluid Dynamics Laboratory, USA (Knutson et al. 1999)). Again, a limited dataset was used, in which monthly inflow values are modified by a change factor obtained for each GCM under a single greenhouse gas scenario for the future period 2020-2050. No effects on rainfall intensities for time steps shorter than a month are considered.

Results

The overall correlation (Pearson r^2) between species space and 3-year average duration from the CCA ordination (axis 1) was 0.909. Monte Carlo testing showed that the relation between the species and axis 1 was significant (F-ratio 4.146, p-value 0.0020, 499 permutations under the full model). Note that only axis 1 is canonical, since there was only one environmental variable.

The GLM fit statistics for the 27 species set (Table 5-1) show that model significance for most species (18 of 27) was significant at $p < 0.05$. Some fits were very poor (p -value > 0.1); these species are either of intermediate duration optima (*Panicum repens*), or represented at few sites (*Cyperus longus*, *Paspalidium obtusifolium*). *Ludwigia stolonifera* and *Miscanthus junceus* have duration optima sufficiently close to the maximum of the recorded range that this may have affected the fit. The spread of frequencies among sites are simply too varied to allow a good fit for other species (e.g., *Potamogeton thunbergii*, *Setaria sphacelata*); this latter species clearly has a very broad tolerance range. Two species have modeled maximum probabilities of occurrence in excess of 1 (*Pechuel-Loeschia leubnitziaea*, *Chloris virgata*); these species both have strong preferences for dry habitats (optima < 1 month), and the modeled probability is not sufficiently constrained to stay below 1. The case of *Urochloa mosambicensis* is an extreme example of this, where a simple logistic curve could not be found to fit the data; the F-statistic and p-value are for a linear model. Ranges of estimated maximum probabilities (where these can be estimated well) lie between 0.89 and 0.083. Tolerance ranges vary widely from a maximum of

4.73 (*Setaria sphacelata*) to a minimum of 0.094 months; this latter is considered a misfit model, as *Pechuel-Loeschia leubnitziaea* has been observed to thrive in disturbed dryland situations.

Examples of modeled distribution curves for a few selected species are shown in Figure 5-1.

Simulated species distribution maps for the year 2007 (Figure 5-2) for four species from dry floodplain grasslands, seasonally flooded grassland, seasonally flooded sedgeland and seasonal aquatic communities show the different duration optima, and broad and narrow tolerance ranges clearly. *Eragrostis cylindriflora* is essentially a dryland species, which occurs in occasionally flooded areas; it has a broad distribution extending into seldom flooded areas around the periphery of the currently active floodplains in the Delta. *Cyperus sphaerospermus* is a sedge which occurs in floodplains which experience short floods regularly; it does not occur in the dry land savannas. *Panicum repens*, as has been noted, has a broad tolerance for flooding, and is found across floodplains of all types although it is most frequent in intermediate durations; in long duration floodplains it is restricted to peripheral zones and higher ground. *Leersia hexandra* is an aquatic grass which survives short periods of drawdown as rhizomes, and as seed; the general linear model gives it a low probability of occurrence throughout the perennially flooded zone (uniform grey shade in Figure 5-2 d). Accuracy of simulated species distributions was tested against 5 sites excluded from the model calibration data. The results are given in Table 5-2. The mean correctly predicted presence of species was 87%, while mean correct prediction of absence was 69%. In general, the model under-predicted frequencies of occurrence.

Output maps of simulations of the effects of human developments in the basin (Figure 5-3) do not show any striking changes in the overall distribution of floodplain communities. From Figure 5-4 it can be seen, however, that all scenarios simulated result in an overall increase in savanna (SAV), the area not prone to flooding. All scenarios presented also result in a net loss of

both intermediate duration communities, seasonally flooded grassland and sedgeland (SFG and SFS). SFG is simulated to decline by 36% under the combined full development scenario, with an 8% decline in SFS. The effects of constructing all potential dams in the catchment are to reduce the intermediate communities and increase the area of perennially flooded communities (PC). Abstraction of water to supply the full potential of irrigation in the basin reduces the area of flooding across all communities except DFG and SAC. The effects of deforestation in the catchment combined with damming to some extent balance the effects of abstraction for water supply and irrigation, although there is still a net loss of SFG and to a lesser extent SFS simulated.

Much more striking are the results of simulated changes in climate (Figures 5-5 and 5-6). There is a wide discrepancy in the inflow changes generated by the various GCMs; two of the three used here predict a general increase in river flows, while the third predicts a substantial decrease. The GFDL and CCCma GCM2 models result in simulated increases in overall flooded area, with large increases simulated by the CCCma GCM2 model. This scenario effectively transforms most of the present savanna into floodplains (a decline of 93% in SAV area), with a corresponding large increase in the extent of PC (an increase of 95%); the intermediate communities also increase. The HadCM3 simulation shows a pronounced reduction in flooded area, with a proportionately greater decline in the intermediate communities: SAV increases by 1941 km² while PC decreases by 564 km²; the bulk of the increase in SAV area thus comes from reductions in DFG, SFG and SAC.

Discussion

The comparison of predicted presence with observed presence shows that the model predicts species occurrence well. Prediction of absence was not as accurate, and this is attributable at least in part to the properties of the GLR curves. The tails of species distributions

approach zero asymptotically (Figure 5-1) and thus a species such as *Leersia hexandra*, for example, is modeled as occurring (albeit in very low probabilities) in conditions of very low flood duration. This effect may be remedied by using a minimum threshold probability as a filter, or by using a different shaped distribution model (Austin 2007). The difference between predicted and observed frequencies is to be expected since the curve estimation procedure is conservative, with the maximum probability always lower than the maximum observed frequency (Ter Braak and Prentice 1988). Modeled optima and tolerance ranges for species were in line with those suggested by the field survey.

Despite the overall performance of the model as expected, there are a number of potential sources of error. As the fit statistics for the GLMs indicated, some species are not well modeled. The derivation of the GLMs has been shown to be dependent on sampling intensity: Coudon and Gégot (2006) investigated the sensitivity of response curves to sampling characteristics with simulated and real data, and found that curve characteristics cannot be assessed reliably with logistic regression if species are too rare, or when their theoretical optimum lies near an extreme of the gradient. As Austin (2002) points out, the Gaussian logistic regression approach rests on two major assumptions: a) that distributions are unimodal along a gradient; b) that sampled communities are at equilibrium. While the first assumption is not an unreasonable one in this case, the second is unlikely to be true of these floodplain communities. The flood pulse in the Okavango is highly variable, both on an inter-annual scale and a long-term scale (decades) (Andersson et al. 2003), and hydroperiod conditions are never the same from year to year. It is thus likely that species composition is continually adjusting to the current conditions.

Other variables that were not included in the approach include species interactions (competition, allelopathy). Empirical determination of GLMs from a single environmental

variable ignores the effects of interactions and other environmental variables, but they are accounted for implicitly, because measured frequency reflects the realized niche, not the fundamental niche (Guisan and Thuiller 2005), and this measured frequency is the basis of the GLM. Further error may arise simply because the GLR curve is an inappropriate model (Austin 2007); we observed (Table 5-2) that in some cases the extremes of distribution were not zero, where it was evident that the species concerned could not survive the hydrological conditions of the site. Alternative curve fitting approaches such as those proposed by Huisman (1993), in which asymmetry can be accommodated by using different terms for the rising and falling limbs of the distribution, might improve performance. The aggregated community model, being based on the species habitat parameters estimated by the GLMs, is subject to the same sources of error, primarily in the calculation of optimum duration and tolerance ranges.

The current version of the hydrological model generates duration maps at a resolution of 1km². This represents a sixteen-fold generalization of the vegetation-duration dataset generated from MODIS imagery. This generalization, combined with potential geo-registration errors between model map output and site positions, represent further potential sources of error.

The selection of sampling period is considered to be an additional potential confounding factor. The end of the growing period (the rainy, warm summer) was selected to facilitate plant identification. However, as pointed out in the introduction, this resulted in many floodplains, especially those of low to intermediate duration (that is, that had been dry during the growing season) having many short-lived dry-land herbs. Sampling shortly after peak flood would give better representation to the effects of flooding.

Despite these sources of uncertainty, the model produced species distributions that were credible and predicted species presences with an accuracy of 87%. The outputs from this model

are single species distribution maps for each year of the inflow record, a significant amount of data. For the purposes of detailed ecological assessment, this approach has merit: effects of change on particular species can be evaluated. For example, *Panicum repens* is an important dry season grazing resource for the Cape buffalo (*Syncerus caffer*) (Bonyongo et al. 2000). Changes in distribution of *P. repens* will clearly affect the distribution of this economically important mammal. Similarly, Rees (1978) notes that *Acroceras macrum* water meadows are important forage for the semi-aquatic Kafue lechwe (*Kobus leche kafuensis* Haltenorth); lechwe comprise a significant proportion of the wildlife biomass of the Okavango Delta (Snowy Mountains Engineering Corporation 1989).

For visualization and rapid comparison of distributional change, however, it is clearly better to use the plant community-based model, as the scenario maps show. The model shows shifts in community boundaries in response to changes in inflow, and the subtleties of these distribution changes have important implications for management. For example, the intermediate hydro-period floodplains show disproportionate sensitivity to changes in flow pattern, declining in extent under most simulated development and climate change scenarios. These floodplains are considered to play a large role in maintaining the high wildlife biomass and diversity of the Delta (Patterson 1976, Snowy Mountains Engineering Corporation 1989), and also provide critical nursery and forage grounds for fish (Merron and Bruton 1995). The ability to assess the potential effects of hydrological change on the extent of the SFG and SFS communities is clearly of great potential utility not only to land managers, but also to policy makers in the arena of developing international water accords.

Conclusions

Floodplain plant species distributions can be effectively modeled using empirically determined relationships with hydroperiod, and provide a useful tool for assessing the potential

effects of changing hydrological regime in flood-pulsed wetlands. Problems arise with deriving model parameters for species whose optima lie outside the sampled range, and also for those which are under-represented in the dataset. In the case of the Okavango floodplain species, increasing sample size by sampling sites at the extremes of duration appears to be a necessary step toward improving the spread and fit of species models. Model outputs were credible, and 87% accurate in predicting species presence, but there were discrepancies in predicted frequency. As the hydrological model is improved (an increase in resolution to 250m is planned for the next version), and more species distribution data become available, the predictive ability should improve.

Simulation runs with an aggregated community model using development and climate change scenarios indicate that floodplains characterized by intermediate ranges of flooding are susceptible to hydrological change of any kind. The simulated extents of seasonally flooded grassland and sedgeland declined under all development scenarios tested, and declined under a climate change scenario which reduced inflow. As climate change and development processes and rates become better known, improvements to the basic input parameters will be possible, and model performance further enhanced.

Table 5-1. Fitted model parameters and statistics for species GLMs.

Species	Optimum Duration	Tolerance	Maximum Probability Of Occurrence	F-stat	Model significance p-value
<i>Chloris virgata</i>	0.78	0.221	1	318.26	<1 E-06
<i>Cynodon dactylon</i>	1.37	2.42	0.32	6.5	0.006
<i>Cyperus denudatus</i>	7.86	3.55	0.38	2.63	0.0943*
<i>Cyperus longus</i>	4.49	2.03	0.08	1.13	0.341*
<i>Cyperus sphaerospermus</i>	5.52	0.919	0.48	10.56	0.0006
<i>Eleocharis dulcis</i>	7.88	0.872	0.14	11.71	0.0003
<i>Eleocharis variegata</i>	8.18	1.12	0.54	18.44	2 E-05
<i>Eragrostis cylindriflora</i>	<0	0.7	0.67	10.24	0.0007
<i>Eragrostis lappula</i>	4.6	1.69	0.22	3.24	0.058*
<i>Ipomoea coptica</i>	2.19	1.13	0.20	23.65	3 E-06
<i>Leersia hexandra</i>	11.22	2.75	0.89	19.44	1 E-05
<i>Ludwigia stolonifera</i>	9.1	2.05	0.30	2.4	0.114*
<i>Miscanthus junceus</i>	9.45	0.751	0.28	2.3	0.124*
<i>Nicolasia costata</i>	3.88	1.48	0.31	11.02	0.0005
<i>Nymphoides indica</i>	7.97	0.75	0.35	9.29	0.0012
<i>Nymphaea nouchali</i>	8.71	2.11	0.29	4.6	0.0214
<i>Oryza longistaminata</i>	11.91	4.22	0.58	6.06	0.008
<i>Panicum repens</i>	5.72	3.61	0.51	0.859	0.437*
<i>Paspalidium obtusifolium</i>	6.79	1.24	0.14	2.08	0.149*
<i>Pluchea leubnitziae</i>	0.81	0.094	1	566	<1 E-06
<i>Potamogeton thunbergii</i>	7.31	2.33	0.14	2.1	0.146*
<i>Rhynchospora holoschoenoides</i>	6.3	1.58	0.29	4.18	0.0288
<i>Sacciolepis typhura</i>	7.98	1.07	0.51	19.93	1.2 E-05
<i>Schoenoplectus corymbosus</i>	8.16	3.6	0.69	7.26	0.0038
<i>Setaria sphacelata</i>	4.61	4.73	0.20	0.179	0.1629*
<i>Trachypogon spicatus</i>	6.32	1.18	0.15	4.92	0.0171
<i>Urochloa mosambicensis</i>	<0	N/A	N/A	27.18	<1 E-05

*: Indicates those fits with significance p-value >0.05.

Table 5-2. Simulated and observed frequency of occurrence of species at validation sites.

Site Species	MOC		TSW		KIR		KOA		XHA	
	Obs	Pred	Obs	Pred	Obs	Pred	Obs	Pred	Obs	Pred
<i>Chloris virgata</i>	0	0	0	0	0	0	0.53	0.01	0	0.01
<i>Cynodon dactylon</i>	0	0	0	0.13	0.22	0.24	0.73	0.22	1	0.22
<i>Cyperus denudatus</i>	0.09	0.26	0.5	0.23	0.61	0.09	0	0.03	0	0.03
<i>Cyperus longus</i>	0	0	0.82	0.08	0.11	0.04	0	0	0.48	0.01
<i>Cyperus sphaerospermus</i>	0	0	0.5	0.17	0.28	0	0	0	0.04	0
<i>Eleocharis dulcis</i>	0.59	0.09	0	0	0	0	0	0	0	0
<i>Eleocharis variegata</i>	0	0.18	0.36	0.02	0	0	0	0	0	0
<i>Eragrostis cylindriflora</i>	0	0.01	0	0.11	0.17	0.33	1	0.49	0.13	0.49
<i>Fimbristylis complanata</i>	0.18	0.2	0.82	0.05	0.33	0.03	0	0.02	0.22	0.02
<i>Ipomoea coptica</i>	0	0	0	0.03	0	0.17	0.53	0.16	0.39	0.11
<i>Leersia hexandra</i>	0.73	0.43	0.09	0.04	0	0	0	0	0	0
<i>Ludwigia stolonifera</i>	0.82	0.06	0.05	0	0	0	0	0	0	0
<i>Miscanthus junceus</i>	0	0.22	0	0	0	0	0	0	0	0
<i>Nicolasia costata</i>	0	0	0.05	0.23	0	0.12	0	0	0	0
<i>Nymphoides indica</i>	0.5	0.03	0.14	0	0	0	0	0	0	0
<i>Nymphaea nouchali</i>	0.73	0.21	0.18	0.07	0	0	0	0	0	0
<i>Oryza longistaminata</i>	0.05	0.33	0	0.1	0.06	0.04	0	0	0	0
<i>Panicum repens</i>	0	0.27	0.95	0.32	0.94	0.23	0	0.13	0	0.13
<i>Paspalidium obtusifolium</i>	0.63	0.04	0	0.02	0	0	0	0	0	0
<i>Pechuel-Loeschia leubnitziae</i>	0	0	0	0	0	0	0.2	0	0	0
<i>Potamogeton thunbergii</i>	0.68	0.08	0.05	0.06	0	0	0	0	0	0
<i>Rhynchospora holoschoenoides</i>	0	0.03	0.77	0.12	0	0	0	0	0	0
<i>Sacciolepis typhura</i>	0.18	0.13	0.36	0.02	0	0	0	0	0	0
<i>Schoenoplectus corymbosus</i>	0.05	0.39	0.09	0.3	0	0.14	0	0.05	0	0.05
<i>Setaria sphacelata</i>	0	0.1	0.45	0.16	0.56	0.14	0	0.11	0	0.11
<i>Trachypogon spicatus</i>	0	0	0	0.03	0	0	0	0	0.04	0
<i>Urochloa mosambicensis</i>	0	0	0	0	0	0.13	0.27	0.53	0.3	0.53
Present	12	18	16	20	9	12	6	10	8	11
Correctly predicted presence	100%		88%		89%		83%		75%	
Correctly predicted absence	60%		54%		79%		77%		76%	
*Number of observed frequency > predicted	8		11		6		4		4	
*Number of observed frequency < predicted	4		3		2		1		2	

* These comparisons are between frequencies in cases where the species was both predicted and observed.

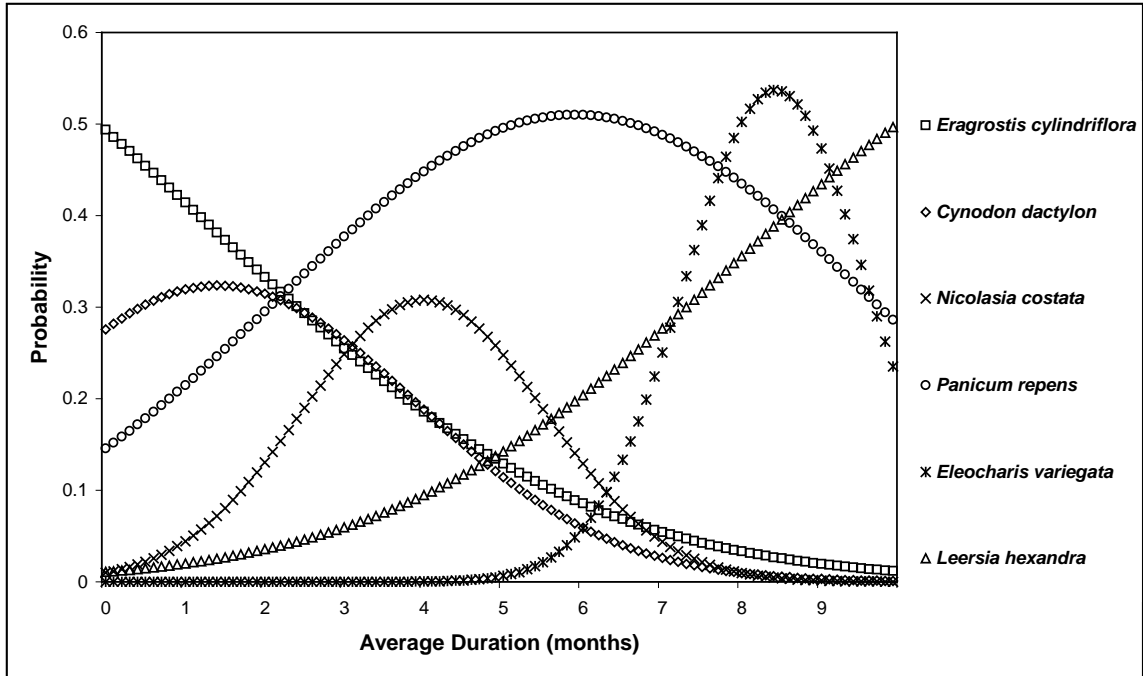


Figure 5-1. Modeled distribution curves for selected species representing low (*Eragrostis cylindriflora*, *Cynodon dactylon*), intermediate (*Nicolasia costata*, *Panicum repens*), and high (*Eleocharis variegata*, *Leersia hexandra*) flood duration communities.

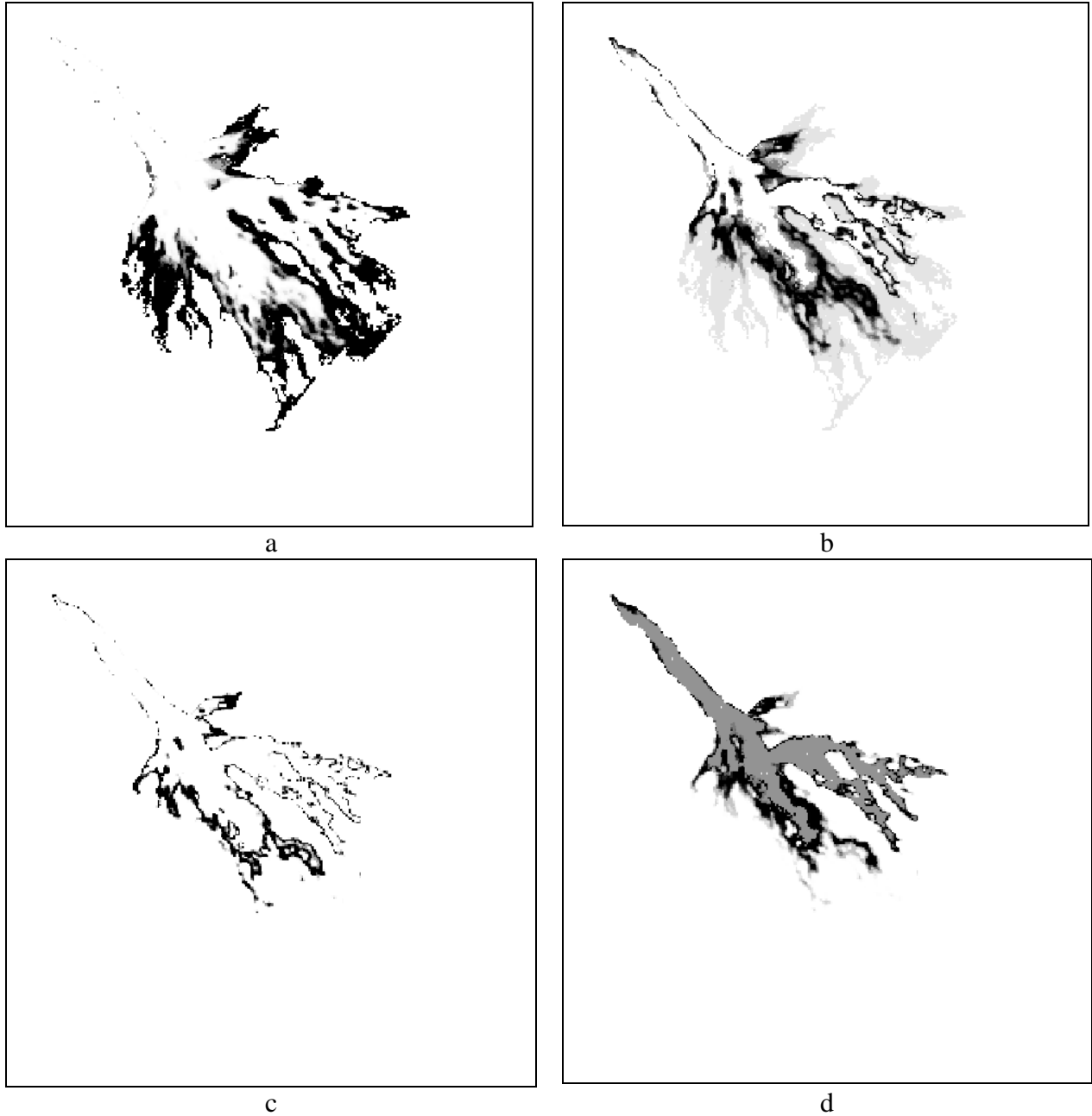


Figure 5-2. Simulated 2007 distributions of a) *Eragrostis cylindriflora*; b) *Cyperus sphaerospermus*; c) *Eleocharis variegata*; d) *Leersia hexandra*: species typical of DFG, SFG, SFS and SAC respectively. Darker shades indicate higher probability of occurrence.

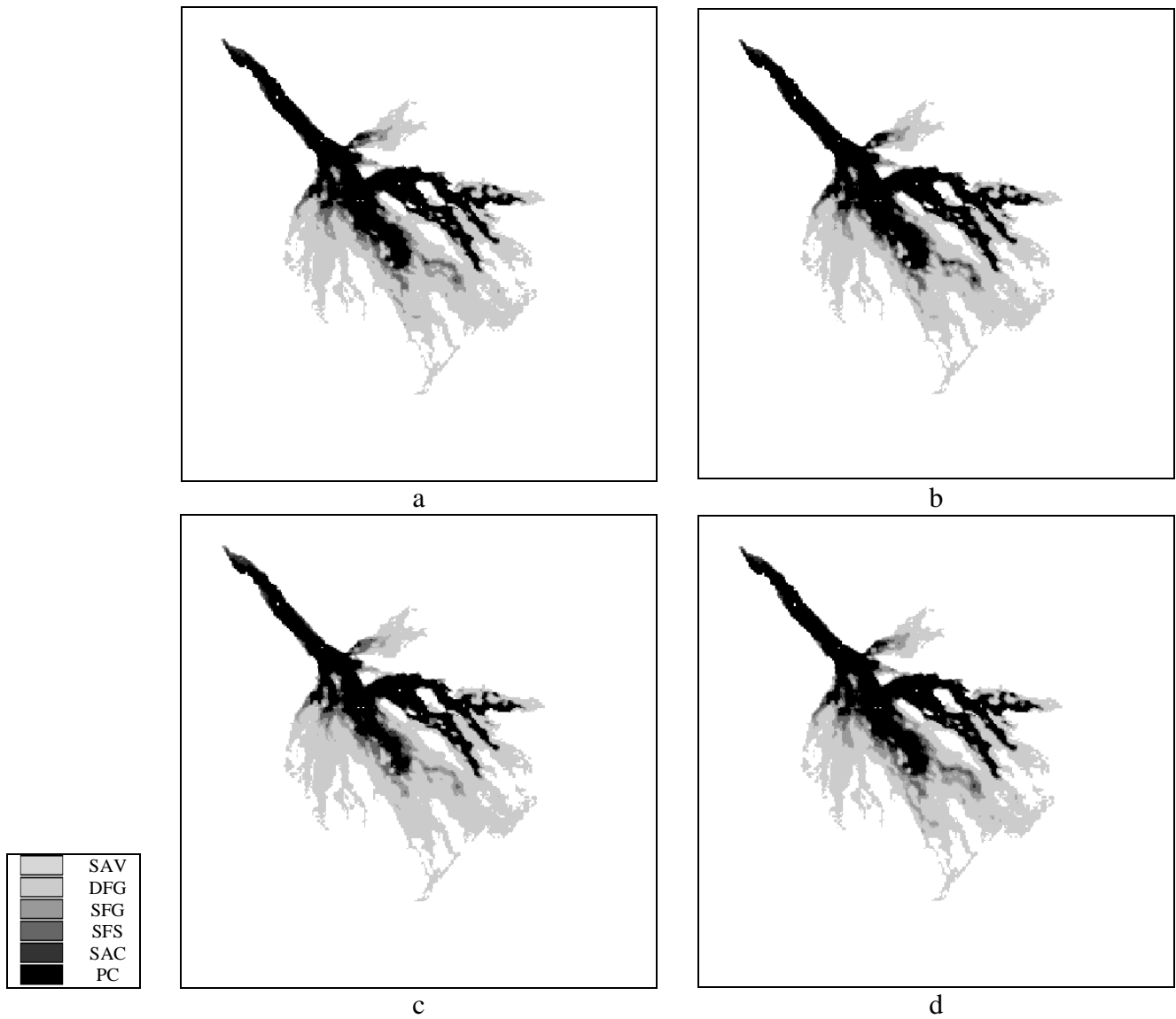


Figure 5-3. Simulated distributions of floodplain communities for the year 2025 under development scenarios: a) reference situation; b) all potential dams constructed; c) maximum development of potential irrigation; d) combination of all dams, maximum irrigation and other withdrawals including supply to Windhoek in Namibia, and deforestation in the catchment. SAV = Savanna, DFG = Dry Floodplain Grassland, SFG = Seasonally Flooded Grassland, SFS = Seasonally Flooded Sedgeland, SAC = Seasonal Aquatic Communities, PC = Perennially flooded Communities.

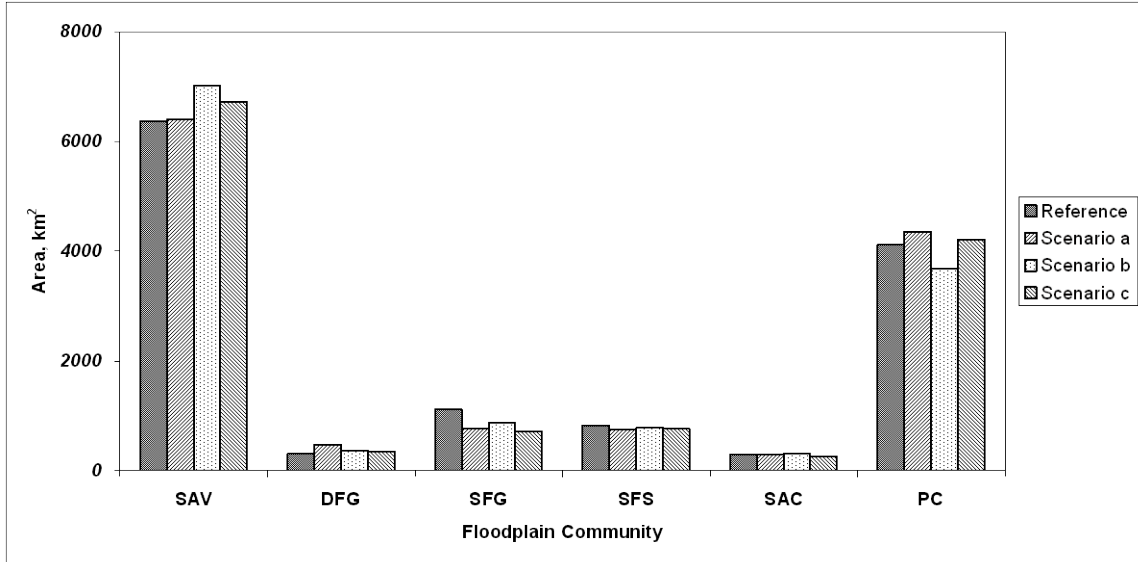


Figure 5-4. Changes in extent of floodplain communities resulting from simulations of different 2025 development scenarios in the Okavango basin. Scenario a – all potential dams constructed in catchment; Scenario b – full development of potential upstream irrigation; Scenario c – a combination of all dams, full irrigation and water abstraction, but including a 2km deforestation buffer around all catchment streams. Floodplain classes as for Figure 5-3.

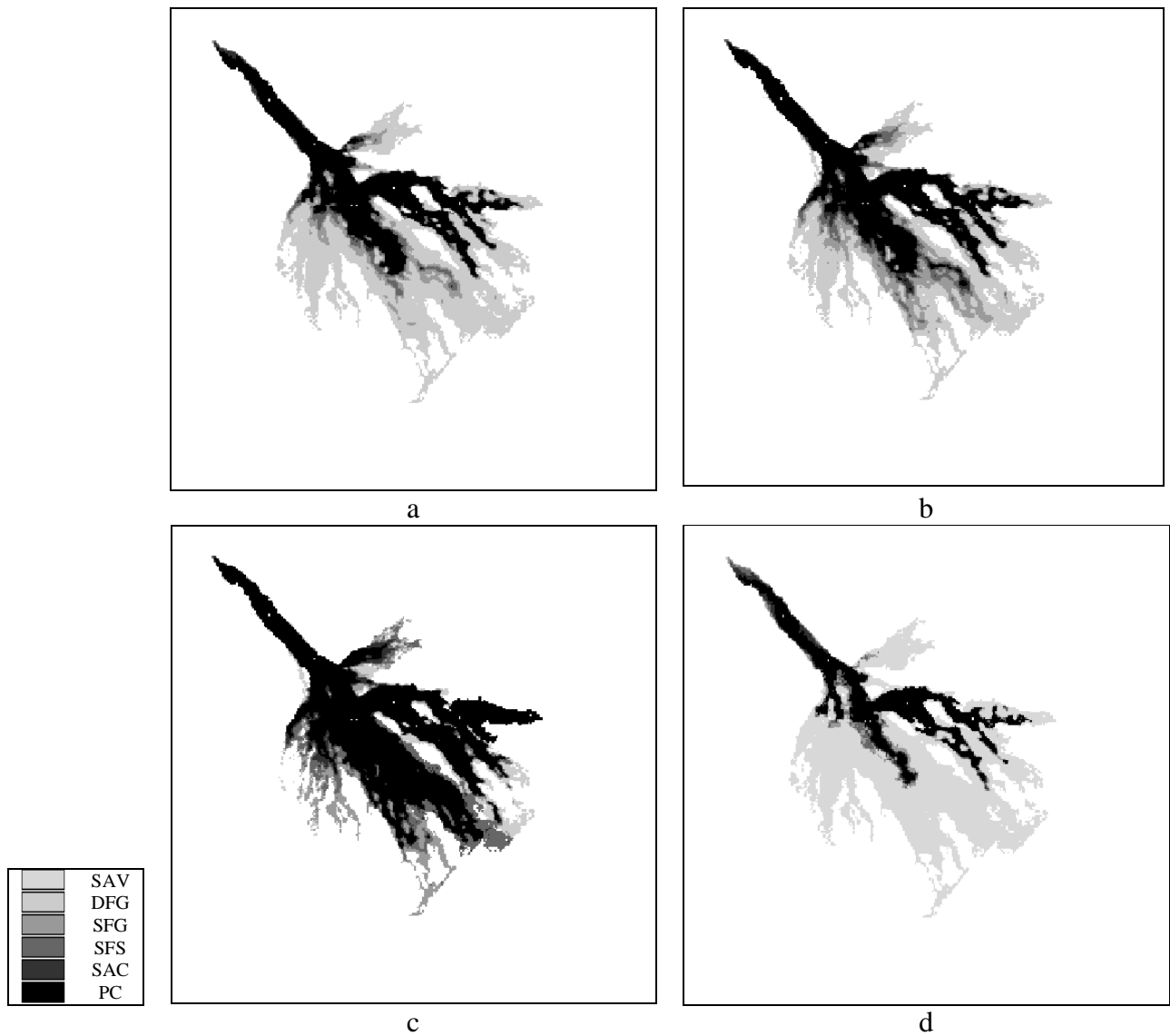


Figure 5-5. Simulated distributions of floodplain communities for climate change scenarios for the period 2020-2050: a) reference situation; b) GFDL; c) CCCma GCM2; d) HadCM3. Floodplain classes as for Figure 5-3.

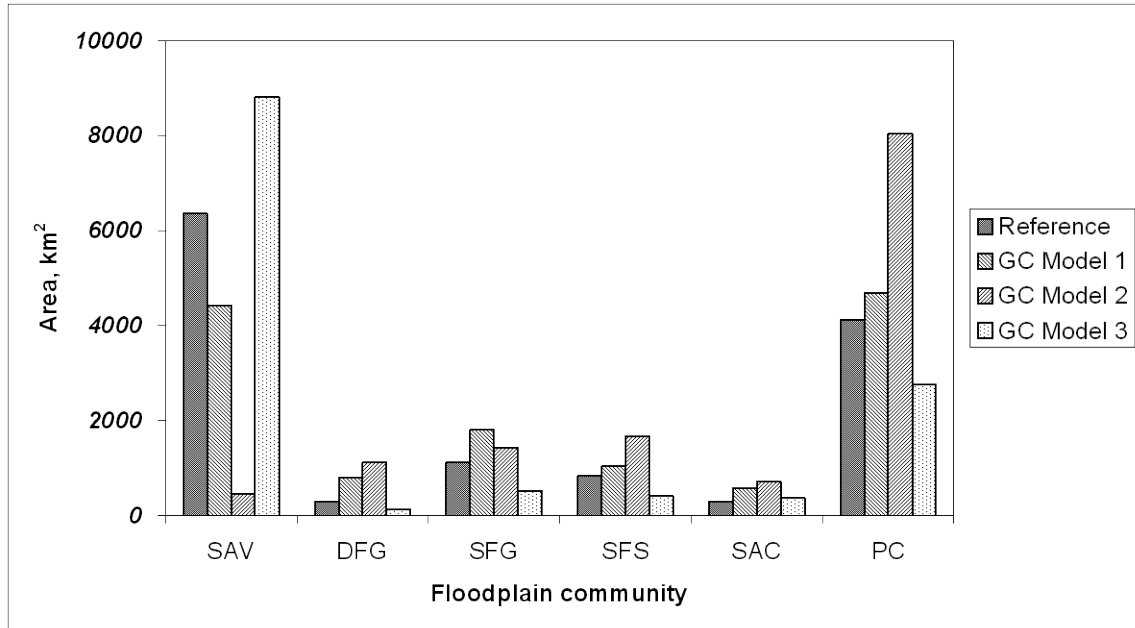


Figure 5-6. Changes in extent of floodplain communities resulting from simulations of different climate change scenarios for 2020-2050 affecting the Okavango basin. GC Model 1 – GFDL, GC Model 2 – CCCma GCM2; GC Model 3 – HadCM3. Floodplain classes as for Figure 5-3.

CHAPTER 6 CONCLUSION

The strong relationships between floodplain species composition and flood frequency and duration identified in this study demonstrate clearly the dependence of the ecology of the system on hydrology. In this regard, this study has produced three potential tools for supporting policy development and management: a scheme for monitoring floodplain vegetation, a low-cost, simple method for monitoring flood extent from satellite imagery, and a spatial model for testing hypotheses about vegetation-hydrology relationships.

The dichotomous key presented in Chapter 2 will allow practitioners to monitor the status of floodplains within their jurisdiction. The capacity limitations of regulatory agencies make the undertaking of large scale monitoring impossible, but leaseholders of the controlled hunting areas (which make up the bulk of the Delta's area) are required under the terms of their leases to monitor the state of their areas. The use of this approach will ensure that floodplain monitoring data are consistent to allow subsequent analysis.

The use of MODIS imagery for interpreting the spread of the flood pulse across the Delta (Chapter 3) appears to have great potential. The use of a simple threshold approach in the 250m resolution band 1 was shown to produce results consistent with much more detailed interpretations from higher resolution Landsat TM, and to return approximately 90% accuracy against a set of 30 sample sites. The acquisition and interpretation of MODIS imagery for this purpose is well within the capacity of the University of Botswana's Harry Oppenheimer Okavango Research Centre geographic information systems laboratory.

Floodplain plant species vary widely in their habitat preferences, and species composition is strongly correlated with long-term frequency and duration of inundation. Cluster analysis of species produced a hierarchical set of communities: 4 major, with 8 sub-communities. The use of

Gaussian logistic regression to model distributions along a flood duration gradient has helped to determine duration optima and tolerances for the more common species. The results of this exercise in Chapter 4 indicate that sampling of more floodplains in the duration range 8-12 months will improve model fits for species in these habitats. Generalized linear model coefficients from the GLRs were used (Chapter 5) to parameterize a spatial hydrology model to produce species and community distribution maps at a scale of 1km², with a mean accuracy of prediction of presence of 87%.

As illustrated in Chapter 5, the spatial vegetation model can be used to simulate changes in species or community distribution resulting from alterations in hydrology, such as upstream water abstraction, deforestation, or climate change. The ability to model single species offers great potential for investigating habitat change and upward trophic effects on, for example, selective grazers, such as Cape buffalo (*Syncerus caffer*) or red lechwe (*Kobus leche*).

The simulated effects of climate change are generally much greater than those of development; different global climate models, however, also predict change in different directions (drier or wetter). The high degree of uncertainty involved in predicting climate change and consequently its possible effects on system functioning suggest that instead of focusing on managing to avoid such disturbances, efforts should be directed at developing a resource use and management system that can accommodate ecosystem change: the human component is the most receptive to management (although possibly the least flexible). Exploration of alternative systems of resource use, and different structures for management (Hahn et al. 2006) before change occurs would appear a prudent course of action. Such exploration can only be based on the behavior of conceptual models of system function to stimulate thought and debate on possible future states of the system. Such models help to unify perspectives among stakeholders

and provide a common basis of understanding. In this regard, the hydro-ecological models described in Chapter 5 are an important early step towards articulating our concept of Delta ecology. Temporal testing of the models, to improve confidence in their ability to predict species distribution change, and extension of the classification system to include assemblages of perennially inundated floodplains are needed. The models will be reviewed, refined and improved as more data become available.

APPENDIX 1
VEGETATION SURVEY SITE DATA

Site Code	Coordinates: UTM Zone 34 S; Datum WGS 84		Date completed	Locality Name	Frequency Stratum	Number of Transects	Total Number of Quadrats	Number of Core Quadrats	Flood state at time of survey
	Easting	Southing							
BOB	724069	7825022	17-Apr-07	Bobo	2	3	40	27	dry
BOK	732931	7821944	16-May-07	Bokoro	4	2	35	25	wet
CHA	703725	7851938	13-Jul-07	Chao	5	1	35	31	wet
HBK	672444	7841718	12-Apr-07	Horseback	3	1	33	28	wet
IV2	725917	7825856	14-Mar-07	Ivory 2	1	3	38	26	dry
KIR	708023	7829330	28-Mar-07	Kiri	3	5	38	18	dry
KOA	728756	7821640	18-Apr-07	Kolobahatse A	1	5	34	15	dry
KOB	726729	7820543	19-Apr-07	Kolobahatse B	1	4	38	22	dry
KUA	736725	7808128	20-Apr-07	Kunoga	3	4	37	21	dry
MAM	684705	7822605	24-Apr-07	Mamoxinxha	2	3	35	23	wet
MAX	736266	7811652	03-May-07	Maxhanasesunda	1	3	38	26	dry
MIL	727828	7837924	25-May-07	Nxaraga	3	3	30	28	wet
MOC	689481	7863255	23-Mar-07	Mombo central	5	3	33	22	wet
MOM	688267	7871024	21-Mar-07	Mombo	5	2	37	28	wet
MOS	689680	7870351	22-Mar-07	Mombo south	4	2	32	25	wet
MPO	732434	7829186	17-May-07	Moporota	5	3	35	23	wet
NTS	724322	7838584	24-May-07	Ntswi	4	3	39	27	wet
NX1	689164	7841330	03-Apr-07	Nxabega 1	5	3	36	24	wet
NX2	688060	7839986	04-Apr-07	Nxabega 2	5	3	36	24	wet

APPENDIX 1 continued.

Site Code	Coordinates: UTM Zone 34 S; Datum WGS 84		Date completed	Locality Name	Frequency Stratum	Number of Transects	Total Number of Quadrats	Number of Core Quadrats	Flood state at time of survey
	Easting	Southing							
NXA	727489	7836509	18-May-07	Nxaraga	4	3	40	28	wet
SEL	678014	7835038	11-Apr-07	Selby	2	5	34	14	dry
TSU	737079	7802066	04-May-07	Tsutsubega	1	2	30	22	dry
TSW	693444	7815862	25-Apr-07	Tshwaramasepa	4	3	34	22	wet
XAA	731970	7830521	23-May-07	Xaa	4	5	37	18	wet
XAN	708319	7840463	16-Mar-07	Xaxaba north	2	2	39	31	dry
XAS	708120	7837970	27-Mar-07	Xaxaba south	2	2	37	29	dry
XHA	697992	7802480	26-Apr-07	Khanyani	1	3	35	23	dry
XUS	716610	7796727	10-May-07	Xudum south	3	2	34	26	wet
XWN	718409	7805718	08-May-07	Xwaapa north	3	3	38	26	wet
XWS	722345	7801062	09-May-07	Xwaapa south	2	3	35	23	dry

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BIOGRAPHICAL SKETCH

Michael Murray-Hudson grew up in Botswana, in southern Africa. His undergraduate degree was a double major in Geology and Zoology, an early indication of a schizoid approach to life. He started out working as a consulting hydro-geologist, but after 2 years he changed tack, and wrote the text for a photographic natural history of the Okavango Delta. In 1986, he set up an environmental consulting company with a friend, and worked on a wide variety of impact assessments and water-related assignments all over southern Africa. Frustration with the ability to effect change in policy drove him back to school in 2000 to do an MS in systems ecology, following which he took up a research fellowship in wetland ecology at the University of Botswana's Okavango Research Centre. He returned to the University of Florida to complete this PhD in 2005. He has resumed his post at the Okavango Research Centre to continue working on the effects of hydrological change on Delta ecosystems.