UNIVERSITY OF BOTSWANA

Response of seasonal floodplain vegetation communities and soil nutrient status to flood variation in the Okavango Delta, Botswana

by

Gaolathe Tsheboeng

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Supervisors: Dr M.C. Bonyongo and Dr M.Murray-Hudson

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Thank you!

List of Tables

List of Figures

Abstract

Globally many seasonal floodplain ecosystems experience flooding regime variation leading to variation in vegetation community composition and distribution and soil nutrient status. The Okavango Delta natural flooding variation is ecologically important for biodiversity sustenance. In some years (and also sequences of years) the Okavango Delta receives low floods while it receives high floods in others. While this natural flood variability is significant for the ecological functioning of the Okavango Delta, its relationships with seasonal floodplain vegetation community composition and distribution have not been adequately investigated. It is not yet known how flooding variation associated with climate variability affects seasonal floodplain vegetation community composition and distribution, and soil nutrient status, in the Okavango Delta. The aim of this study was to determine the influence of flooding variation on seasonal floodplain vegetation communities and soil nutrient status.

Vegetation sampling was conducted between February and March 2010 following a modified Braun-Blanquet cover/abundance scale. Homogenous vegetation zones sampled by Bonyongo (1999) during a low flood were re-sampled. $25m^2$ minimum sampling plot area was used. Sampling was stratified and randomised between and within zones respectively. A total of 40 sites were sampled (5 sites per zone). In each site five plots were randomly selected and plant species cover and abundance estimated. Soil samples were collected in early February 2010 (middle of rainy season), mid May 2010 (flood propagation) and end of September 2010 (flood recession). Hierarchical cluster analysis was performed using Sorensen distance measure and Ward's linkage method. Multi-response Permutation Procedures (MRPP) testing was performed to test the hypothesis of no difference between vegetation community composition and distribution under low and high floods. Soil samples were analysed for pH, Na, Mg, K, Ca and P content. Vegetation communities showed a shift in spatial distribution and zones showed a change in vegetation community composition in response to a high flood. Plant species richness generally declined during a high flood. There was an increase ($p<0.05$) in plant species diversity in all vegetation zones except in zone 8. Mean percentage cover decreased ($p<0.05$) in flood intolerant and increased ($p<0.05$) in flood tolerant plant species in zones experiencing high flooding depth and prolonged flooding duration. Mg, Na, Ca and pH level did not differ significantly ($p>0.05$) between the flooding seasons of 2010 extended hydro-period. P and K differed ($p<0.05$) between flooding seasons. With the exception of P, all soil nutrients decreased ($p<0.05$) with increasing flooding depth and duration during an extended hydro-period of 2010. Flooding depth and duration, Na and pH influenced vegetation community composition and distribution during a high flood.

The results of this study corroborate earlier findings that flooding is the primary factor influencing seasonal floodplain vegetation community composition and distribution, and soil nutrient status, in the Okavango Delta. This suggests that changes in flooding regime variation (either from climate variation or other anthropogenic activities) will result in a shift in vegetation community composition and distribution and soil nutrient status in Okavango Delta seasonal floodplains. It is therefore recommended that stakeholders mandated with the Okavango Delta management take this into consideration when formulating policy on water resource use, and national climate change adaptation strategies.

Key words: High and low floods, Okavango Delta, Soil nutrients and Vegetation.

Table of contents

Disclaimer

The work contained in this thesis/dissertation was completed by the author at the University of Botswana between 08/06/2009 to 15/04/2011. It is original work except where due reference is made and neither has been nor will be submitted for the award of any other University.

Signature...

Dedication

This work is dedicated to my family, my late brother (Tsheboeng Tsheboeng) and late sister (Kelebonye Tsheboeng).

Thesis Outline

In chapter 1 the general introduction of the thesis is given including the problem statement, objectives, hypotheses and description of the study area. Chapter 2 investigates responses of seasonal floodplain vegetation communities to flood variation in the Okavango Delta. The influence of a high flood on soil nutrient content in the Okavango Delta seasonal floodplains is presented in chapter 3. Chapter 4 assesses the relationship between environmental variables (flooding depth, flooding duration, Na, K, Mg, Ca, P and pH) and plant species aiming to establish environmental variables influencing seasonal floodplain vegetation community composition and distribution. In chapter 5 syntheses of the findings of the whole study is provided.

CHAPTER 1

1.0 GENERAL INTRODUCTION

1.1 The importance of wetlands

Wetlands ecosystems play a critical role on earth such as providing many ecological, biological and hydrological functions, services and goods to humanity and to other life forms (Harting et al., 1997; Murkin, 1998; Greb and DiMichele, 2006). Ecosystem services can be broadly classified into supporting, provisioning, regulating and cultural services (Rodriguez et al., 2006). Examples of supporting services are primary production (Greb and DiMichele, 2006; van der Valk, 2006) and nutrient cycling (Brix and Schierup, 1989; Murkin, 1998). Provisioning services include food (Davies, 1987; Matiza and Chabwela, 1992; van der Valk, 2006) and freshwater (Thompson, 1996; Paris and Looi, 1999; Talkudar, 2003). Water purification (Reddy and Gale, 1994; Carter, 1996), flood regulation (Dugan et al., 1990; Daily, 1997) and climate regulation (Daily, 1997) are some of the regulatory services wetlands provide. Wetlands also provide cultural services to humanity. These include cultural heritage (Pereira et al., 2006), aesthetic information, spiritual information, recreation, science and education (de Groot et al., 2002).

1.2 Major wetlands of the world

About 6 % of the surface area of the Earth is covered by different types of wetlands including salt marshes, tidal freshwater marshes, mangroves, freshwater marshes, peatlands and freshwater swamps (Mitsch and Gosselink, 2000). In the Americas some of the major wetlands are the Amazon, Hudson Bay lowland, the Pantanal, Mississippi River basin and the Everglades (Fraser and Keddy, 2005). In Africa major wetlands include the Congo River basin, Lake Chad basin, River Nile basin (Fraser and Keddy, 2005), the Okavango Delta, the Kafue flats and the Zambezi River basin (Tumbare, 2004). Major Asian wetlands include the Central Russian Bi-Ob' River Valley and the Mekong and Brahmaputra Deltas (Mitsch and Gosselink, 2000). Australian wetlands include Gippsland Lakes, Coongie marshes and the Macquarie marshes (Environment Australia, 2001). Along lakes, rivers and delta margins there are often flat strips of land called seasonal floodplains (Junk et al., 1989; Hughes, 1988)**.**

1.3 Seasonal Floodplain ecosystems

Seasonal floodplains are areas flooded at regular or predictable intervals from rivers or lakes by lateral overflow or by rain, snow or groundwater with resulting changes to the physico-chemical environment (redoximorphic state (Eh), nutrient availability, soil salinity and pH) leading to morphological, anatomical, physiological and ethological responses from biota (Junk et al., 1989; Junk, 1997). They can be categorized based on flooding regimes defined in terms of flooding duration, frequency and depth (Junk, 1997; Finlayson et al., 2002; Gumbricht et al., 2004; Zambia Wildlife Authority, 2006). Phrases like semi-permanently flooded, occasionally flooded, intermittently flooded (Finlayson, 2002), primary floodplain, secondary floodplain and tertiary floodplain (Patterson, 1976; Bonyongo, 1999; Bonyongo et al., 2000) are often used to describe different classes of seasonal floodplains. These classes are a method of simplifying a continuum or step-wise sequence of hydro-period along an elevation gradient increasing away from supplying channel systems.

Located in areas of low elevation, semi-permanently flooded floodplains (also referred to as primary floodplains) may be flooded every year (Finlayson, 2002). In the Okavango Delta they are usually flooded for 4 to 8 months (Biggs, 1976; Meyer, 1999; Bonyongo and Mubyana, 2004). Their mean flooding depth is about 1m (Meyer, 1999). During high flood they may be submerged for 12 months (Biggs, 1976). Secondary floodplains (of intermediate elevation) are flooded for up to 5 months (Biggs, 1976; Meyer, 1999; Bonyongo and Mubyana, 2004). Occasionally flooded floodplains (also referred to as tertiary floodplains) are found in areas of higher elevation. In the Okavango Delta they are flooded at a regular period of approximately 10 year interval (Ramberg et al., 2006). Floodwaters reach them only during high flooding years (Patterson, 1976; Biggs, 1976). Their hydroperiod (flooding duration and depth) is highly variable. It is expected that during high floods the flooding depth will be higher and flooding duration prolonged in the primary, secondary and tertiary floodplains than during low flood.

1.3.1 The Flood pulse concept in seasonal floodplain ecosystems

The term flood pulse refers to alternating dry and wet conditions in floodplain ecosystems (Junk et al., 1989; Junk., 1997; Parolin et al., 2006). Alternating dry and wet conditions influence seasonal floodplain soil nutrient status (Junk et al., 1989; Junk, 1997; Bonyongo and Mubyana, 2004). Organic matter and soil nutrients accumulating during the dry phase are mobilized during the aquatic phase (Junk, 1997). Some nutrients may be carried in floodwater from the main river channel into the seasonal floodplains through lateral overflow. Others may be transported from the seasonal floodplains into the main river channel (Bayley, 1995; Junk, 1997). Seasonal floodplains may be nutrient rich habitats compared to upland habitats (Vallet et al., 2005). The flood pulse also governs vegetation community composition and distribution in seasonal floodplains (Junk et al., 1989). Plant species in seasonal floodplain ecosystems have developed adaptation strategies enabling them to survive during the dry and wet phases imposed by the flood pulse (Junk et al., 1989; Junk, 1997). They tend to be spatially distributed along hydrological gradients, often leading to a clear vegetation zonation (Bonyongo, 1999; Bonyongo et al., 2000; Van der Valk, 2006).

1.3.2 Vegetation zonation in seasonal floodplain ecosystems

Vegetation zonation is a common phenomenon in seasonal floodplains around the world. It is determined by hydro-period (Kozlowski, 1984; Bendix et al., 1999; Casanova and Brock, 2000; Cronk and Fennessy, 2001; van Eck et al., 2006; Li et al., 2010). Vegetation zonation has been observed in major wetlands such as the Pantanal (Ponce and Cunha, 1993; Pinder and Rosso, 1998), the Amazon (Junk et al., 1989; Parolin et al., 2006), the Everglades (Davis and Ogden, 1993), the Kafue (Rees, 1978; Zambia Wetland Authority, 2006) and the Okavango Delta (Ellery et al., 1991; Ellery et al., 1993; Bonyongo, 1999; Meyer, 1999; Ellery and Tacheba, 2003; Gumbricht et al., 2004; McCarthy et al., 2005). In the Pantanal seasonal floodplains dominant plant species are *Eleocharis elegans* (Kunth) Roem. & Schult, *Aeschynomene fluminensis* Vell, *Hydrolea spinosa* L, *Melochia simplex* A.St.-Hil and *Axonopus purpusii* (Mez) Chase (Pinder and Rosso, 1998). In the Kafue primary floodplains vegetation communities are dominated by *Vossia cupsidata* (Roxb.) Griff and *Oryza* spp while *Panicum repens* L, *Acroceras macrum* Stapf and *Leersia* spp dominate in secondary floodplains (Rees, 1978; Zambia Wetland Authority, 2006). In the Kafue tertiary floodplain vegetation communities are dominated by *Setaria sphacelata* and *Panicum maximum* (Rees, 1978; Zambia Wetland Authority, 2006).

The Okavango Delta primary floodplains are dominated by *Cyperus articulatus* L, *Schoenoplectus corymbosus* (Roth ex Roem. & Schult) J. Raynal, *Miscanthus junceus* (Stapf) Pilg, *Phragmites australis* (Cav.) Trin. (ex Steud) (Bonyongo, 1999; Bonyongo et al., 2000), *Ludwigia stolonifera* (Guill. &Perr.) P.H Raven, *Nymphaea nouchali* Burn.f. (Ramberg et al., 2010), *Panicum repens*, *Acroceras macrum*, *Vernonia glabra* (Steez) Vatke, *Ethulia conyzoides* L.f and *Potamogeton thunbergii* Cham. & Schltdl (Bonyongo, 1999; Meyer, 1999). In secondary floodplains dominant plant species are *Panicum repens* L, *Sorghastrum friessii* (Pilg.) Pilg, *Imperata cylindrica* (L) Raeusch (Gumbricht et al., 2004; McCarthy et al., 2005), *Paspalidium obtusifolium* (Delile) N.D. Simpson, *Vetiveria nigritana* (Benth.) Stapf, *Acroceras macrum* Stapf, *Chloris virgata* Sw and *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. ex M.B. Moss. Tertiary floodplains are dominated by *Sporobolus spicatus* (Vahl) Kunth, *Pechuel-loeschea leubnitziae* (Kuntze) O.Hoffm, and *Cynodon dactylon* (L.) Pers (Bonyongo, 1999; Meyer, 1999; Bonyongo et al., 2000; Gumbricht et al., 2004; McCarthy et al., 2005).

1.4 Threats to Okavango Delta seasonal floodplains

Globally it is estimated that almost 50% of wetlands and their associated seasonal floodplains have been lost and in some regions the wetlands losses approach 99% (van der Valk, 2006). Wetland and seasonal floodplain losses continue to occur despite the RAMSAR convention (Talukdar, 2003; Schuyt, 2007). The convention provides guidelines for both national and international cooperation for the conservation and sustainable use of wetlands (Wohlman, 2007).

The countries that signed the RAMSAR convention agreed to monitor and study wetland ecosystems to inform conservation and sustainable natural resources use policies (Wohlman 2007). In Botswana there are policies that directly affect the Okavango Delta management. These are: The Wildlife Conservation Policy of 1986, Tourism policy of 1990 and The National Conservation Strategy (Matiza and Chabwela, 1992). Other policies for the Okavango Delta Management include Botswana National Wetlands Policy and Strategy of 1999 which encourages the public to be active participants in wetland management through the utilization of local knowledge and institutions and Okavango Delta Management Plan which aims at promoting the sustainable utilization of the Okavango Delta (Jansen and Madzwamuse, 2003).

Many seasonal floodplain ecosystems around the world experience flooding variation leading to variation in vegetation community composition and distribution. Natural flooding variation has been observed in the Kafue flats (Rees, 1978), the Everglades (Gann et al., 2005), Pantanal (Alho, 2008) and the Amazon (Junk et al., 1989; Junk, 1997). It has also been observed in the Okavango Delta (Biggs, 1976; Smith, 1976; Høberg et al., 2002). Natural flooding variation in the Okavango Delta is ecologically important for biodiversity sustenance (McCarthy, 1992). At present the Okavango Delta is in a relatively pristine state supporting about 1,300 plant species (Ramberg et al., 2006). There is a potential loss of plant species diversity due to human induced changes to flooding variation caused by upstream water abstraction, resulting in a change in the Delta hydroperiod. In the past, the Namibian government has proposed to extract water from the Okavango Delta under the Namibian National Eastern water carrier project (Matiza and Chabwela, 1992). It has also jointly proposed with the Botswana and Angolan governments to extract water from the Okavango River basin for irrigation (Lebotse, 1999). Recently (July,

2011) the Namibian government advertised for the Feasibility Study for the Kavango link to the Eastern National Water Carrier and to the Cuvelai Water scheme. These proposals if implemented pose a threat to seasonal floodplain vegetation community composition and distribution in downstream areas as they might reduce the amount of water reaching them (Diederichs and Ellery, 2000).

Threats to the Okavango Delta seasonal floodplains could lead to loss of biodiversity. Loss of biodiversity can result from overgrazing in the Okavango Delta seasonal floodplains by livestock and wild animals (Matiza and Chabwela, 1992). The Okavango Delta is also faced with a potential threat of water pollution from chemicals, fertilizers, pesticides, solid and sanitary waste that could result from an increase in development (van der Heiden, 1992). Water pollution could lead to eutrophication (Mafabi, 1996; Sekomo et al., 2010). Invasive plant species are also a pontential threat to the Okavango Delta. Invasive plant species are species introduced in an ecosystem where they were not historically found displacing native species (van der Valk, 2006). Invasive plant species, *Salivinia molesta*, is reported in some habitats in the Okavango Delta (Alonso and Nordin, 2003). Potential upstream water abstraction poses a future threat to the Okavango Delta biodiversity (Matiza and Chabwela, 1992; Diederichs and Ellery, 2003).

1.5 Problem statement

Climate variation causes uncertainty on the magnitude of floods the Delta receives. In some years the Okavango Delta receives low floods while in others it receives high floods. It is documented that the 1972/1973 flooding season was low (Biggs, 1976). From 2005 to 2011 the

Delta has experienced an increase in flooding extent (Okavango Research Institute (ORI), 2011). It is only in recent years that such long-term seemingly cyclic behaviour has been identified in the hydrology of the Okavango (Wolski et al 2012). While this natural flood variability is significant for the ecological functioning of the Okavango Delta, its relationship with seasonal floodplain vegetation community composition and distribution have not been adequately investigated.

Previous studies (e.g. Ellery et al., 1993, Bonyongo, 1999, Bonyongo et al., 2000, Ellery et al., 2003, Ellery and Tacheba, 2003) during low flood conditions concluded that seasonal floodplain vegetation community composition and distribution are dependent on the seasonal floods. These studies showed that plant species are distributed along flooding duration and depth gradients to which they are adapted. Plant species that posses similar adaptation strategies are found in the same zone or floodplains (Bonyongo, 1999; Bonyongo et al., 2000; Ellery and Tacheba, 2003). There is lack of information regarding the influence of high flood on seasonal floodplain vegetation community composition and distribution in the Okavango Delta. Previous studies (Ellery et al., 1993, Bonyongo, 1999, Bonyongo et al., 2000, Ellery et al., 2003, Ellery and Tacheba, 2003) did not compare composition and distribution of plant communities between low and high flooding conditions. They were single-campaign studies conducted under low flooding conditions aimed at classifying seasonal floodplain vegetation communities.

There is an urgent need to conduct a quantitative study on the comparison between seasonal floodplain vegetation community composition and distribution during low and high flood conditions. This will generate new information on how the Delta seasonal floodplain vegetation communities respond to flooding variation. Such information is essential to guide efforts at management planning and modeling assessments of the possible future for the Delta, in the context of climate change and basin development (Wolski et al 2008, Murray-Hudson et al 2006).

1.6 Research Questions

Below are the questions the study addresses:

1. How is the composition of vegetation communities affected by variation in flooding in seasonal floodplains in the Okavango Delta?
2. What is the influence of flooding variation on soil nutrient status in the Okavango Delta seasonal floodplains?
3. What are the environmental factors influencing the spatial distribution of vegetation communities during a high flood in the Okavango Delta?

1.7 Hypotheses

1. Plant species richness, diversity and mean percentage cover in seasonal floodplain vegetation communities will be lower during a high flood than during low flood.

2. Soil nutrient status (Ca, Na, K, Mg and P) will be lower during high flood conditions than during low flood conditions.

3. Flood duration and depth will be environmental factors influencing vegetation community distribution during a high flood event the Okavango Delta seasonal floodplains.

1.8 Objectives

1.8.1 General Objective

1. To determine the influence of flooding variation on seasonal floodplain vegetation community characteristics and soil nutrient status in the Okavango Delta.

1.8.2 Specific Objectives

1. To compare vegetation community composition and distribution between a high and low flood
2. To compare soil nutrient status during a high flood with soil nutrient content during a low flood and
3. To investigate the relationship between hydro-period, soil nutrients and vegetation community composition and distribution during a high flood.

1.9 Study area: The Okavango Delta

1.9.1 Topography and Geology

The Okavango Delta (Figure 1) has a low topographic gradient of 1:3300 (McCarthy et al., 2000; Gumbricht et al., 2004). Due to this low topographic gradient the annual flood wave takes about 4 to 5 months to reach the distal parts from Mohembo (McCarthy et al., 2000; Ramberg et al., 2006).

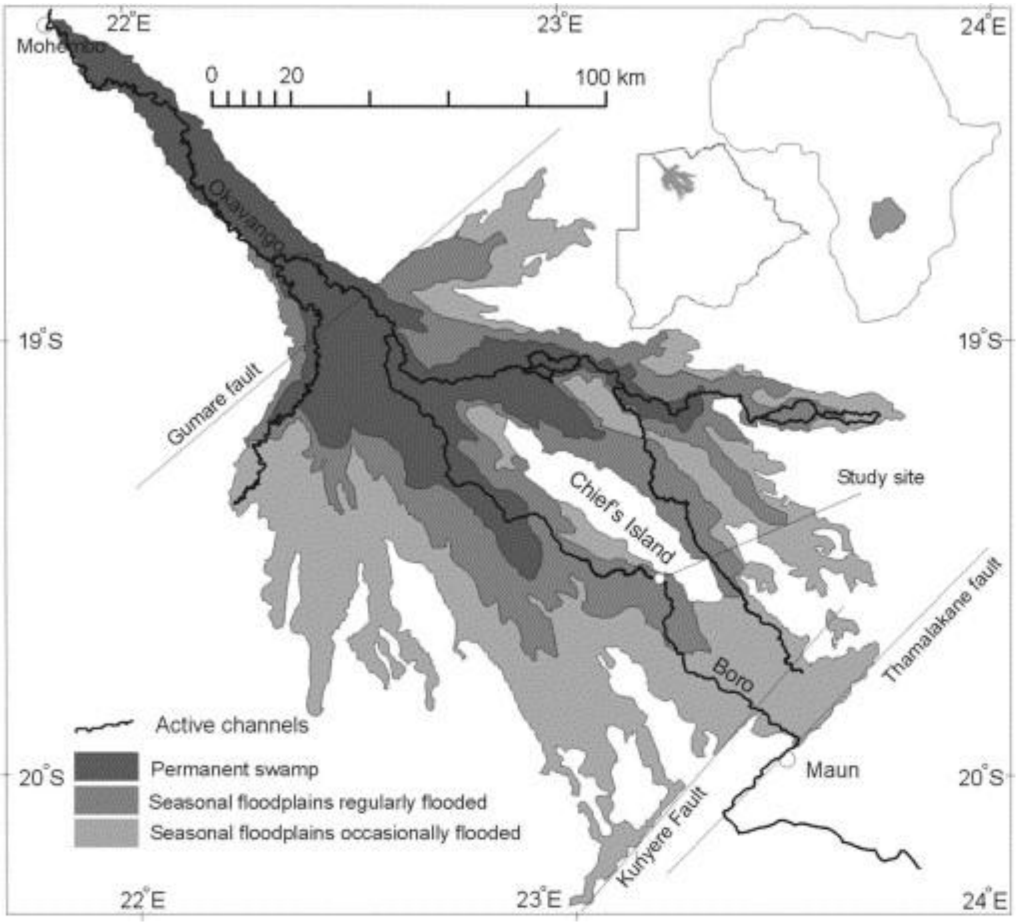

Figure 1: **The Okavango Delta and its seasonal floodplains (Wolski et al., 2006).**

1.9.2 Temperature

The Delta experiences mean monthly maximum and minimum summer temperatures ranging from 30.5°C to 40°C and 14.8°C to 19.2°Crespectively (Ellery et al., 1991; Bjorkvald and Boring 2002). During winter mean monthly maximum temperature ranges from 25.3°C to 28.7°C and minimum temperature ranges from 7.0°C to 10.0°C (Ellery et al., 1991).

1.9.3 Hydrology

The Okavango Delta is fed by local rainfall and seasonal floods from the Angolan highlands (Gumbricht et al., 2004). Local rainfall in the Delta is out of phase with the seasonal floods (Bjorkvald and Boring, 2002). Mean maximum rainfall in the Okavango Delta varies between 300 and 550mm/year (Wilson and Dincer, 1976; S.M.E.C., 1976; Wolski et al., 2005). The Delta experiences a high annual and inter-annual seasonal flood variation (McCarthy et al., 2003; Gumbricht et al., 2004). Total flooded area varies between 4 000 km^2 and 13 000 km^2 (McCarthy, 2006). Variation in the total flooded surface area magnitude is determined by inflow volume. The annual mean discharge varies between a low of 6.0×10^9 m^3 and a high of 16.4×10^9 m^3 (Gumbricht et al., 2004) of which approximately 96 % is lost through evapotranspiration while 2 % is lost through infiltration (Dincer et al., 1976). Another 2 % is lost as outflow through Thamalakane River (Dincer et al., 1976; McCarthy et al., 2005). The Okavango Delta receives the lowest inflow between September and November and receives the highest inflow between March and April. Low flooding regimes occur during low inflow years and high floods occur during high inflow years (Mendelsohn et al., 2010). The magnitude of flood in a given year is also influenced by the extent of flooding in the previous year. This is because floodwaters easily flow further on top of the existing water or saturated soil than unsaturated soil (Mendelsohn et al., 2010).

1.9.4 Hydrological regions and plant species distribution in the Okavango Delta

There are 3 hydrological regions in the Delta namely: permanent swamp, seasonally flooded floodplains and occasionally flooded floodplains (Gumbricht et al., 2004). Each hydrological region is characterized by a particular range of hydroperiod (Gumbricht et al., 2004; Wolski and

Savenije, 2006) and associated vegetation communities (Bonyongo, 1999; Bonyongo, 2000; Ellery and Tacheba, 2003; Wolski and Savenije, 2006; Ramberg et al., 2010) (Table 1).

Table 1: Hydrological regions in the Okavango Delta

Region	Area covered (Km^2)	Hydroperiod characteristics	Common plant species
Permanent swamp	2 500	Flooded all year round	*Phragmites australis*, *Cyperus papyrus* and *P. mauritianus*
Primary floodplain	690	Flooded every year for up to 4 to 8 months. May be flooded for 12 months during high flood	*Cyperus articulatus Schoenoplectus corymbosus* and *Miscanthus junceus*
Secondary floodplain	1 347	Flooded up to 5 months	*Panicum repens*, *Setaria sphacelata* and *Eragrostis inamoena*
Tertiary floodplain	7 100	Variable hydroperiod	*Sporobolus spicatus*, *S. acinifolius* and *Cynodon dactylon*

Adapted from Gumbricht et al., 2004

Chapter 2: Influence of flood variation on seasonal floodplain vegetation in the Okavango Delta.

2.0 Introduction

Ecological functioning and vegetation community composition and distribution of seasonal floodplains in many wetland ecosystems such as the Pantanal (Ponce and Cunha,1993; Junk, 1997; Pinder and Rosso, 1998; de Oliveira and Calheiros, 2000), the Amazon (Junk, 1989; Ayres, 1993; Rosules et al., 1999; Rosules, 2001; De Simone et al., 2003; Parolin et al., 2006), Mekong, Congo (Schöngart and Junk, 2007), Tana (Hughes, 1988), the Kafue (Rees, 1978) and the Okavango Delta (Wolski and Murray-Hudson, 2006; Mladenov et al., 2007) is driven by flood pulses. Flood pulses determine seasonal floodplain vegetation community composition and distribution (Oliveira-Filho et al., 1994). Flooding creates a gradient from highly flood tolerant species on the lower sites of the floodplains, to sensitive species on the more elevated parts of the floodplains (Kozlowski, 1984; Bonyongo, 1999; van Eck et al., 2006). It creates new habitats for colonization by flood tolerant plant species.

Flooding changes the initial physicochemical environment in seasonal floodplains. It deposits sediments and dissolved nutrients into seasonal floodplains which results in new habitats created (Junk et al., 1989). Flood waters transport seeds and nutrients to seasonal floodplains (Hupp, 1988; Poff et al., 1997). Floodplain vegetation community composition and distribution are controlled by among other things individual plant species' adaptation to a given flooding regime (Kozlowski, 1984; Sparks, 1995; Nilsson and Svedmark, 2002; Capon, 2005). Flooding may be a major factor influencing composition and distribution of plant species in seasonal floodplain ecosystems (Hupp, 1988; Blom and Voesenek, 1996; Friedman and Auble, 2000).

Flooding shows a high degree of variability in many wetlands (Alho, 2008). In some years, seasonal floodplains are exposed to low floods while in others they experience high floods (Junk, 1997). This hydro-period variability influences seasonal floodplain vegetation community composition and distribution (Hupp, 1988; Friedman and Auble, 2000). High floods cause a high disturbance which leads to plant responses different from those caused by low floods (Cronk and Fennessy, 2001). A long flood duration and high flooding depth lead to the removal of some plant species while at the same time the establishment of others is favoured (Casanova and Brock, 2000).

While the influence of hydro-period variability on seasonal floodplain vegetation communities has received significant attention elsewhere (Rees, 1978; Hughes, 1988; Oliveira-Filho et al., 1994; Parolin et al., 2006; Schöngart and Junk, 2007), the Okavango Delta has received relatively little attention. Several studies (Biggs, 1976; Smith, 1976; Bonyongo, 1999; Bonyongo, 2000; Ellery and Tacheba, 2003; Ellery et al., 2003; Murray-Hudson, 2009) have generally concluded that seasonal floodplain vegetation community composition and distribution in the Delta is flood driven. Therefore, different seasonal floodplains have different vegetation communities owing to their differences in hydro-period. With the exception of Murray-Hudson (2009), all these studies were conducted in years of relatively low floods. A localised study (Bonyongo, 1999) conducted in the Nxaraga Lagoon seasonal floodplains, during relatively low flood years, quantitatively identified 8 vegetation communities whose distribution and composition were dependent on seasonal flooding. Vegetation communities varied along an elevation gradient influenced by flooding depth and duration (Bonyongo, 1999). This study was conducted during low flood years (1996-1997) in which flooding depth and duration were relatively shallow and short respectively. However, from the year 2005, floods of the Okavango Delta increased annually, with the highest floods recorded in 2010 (Figure 2) (ORI, 2011). The 1996-1997 low flood season was preceded by 5 consecutive years of low flood while the 2010 high flood was preceded by 5 consecutive years of high floods (Mendelsohn et al., 2010). It is still not known how the seasonal floodplain vegetation community composition and distribution in the Okavango Delta will respond to an extended hydro-period.

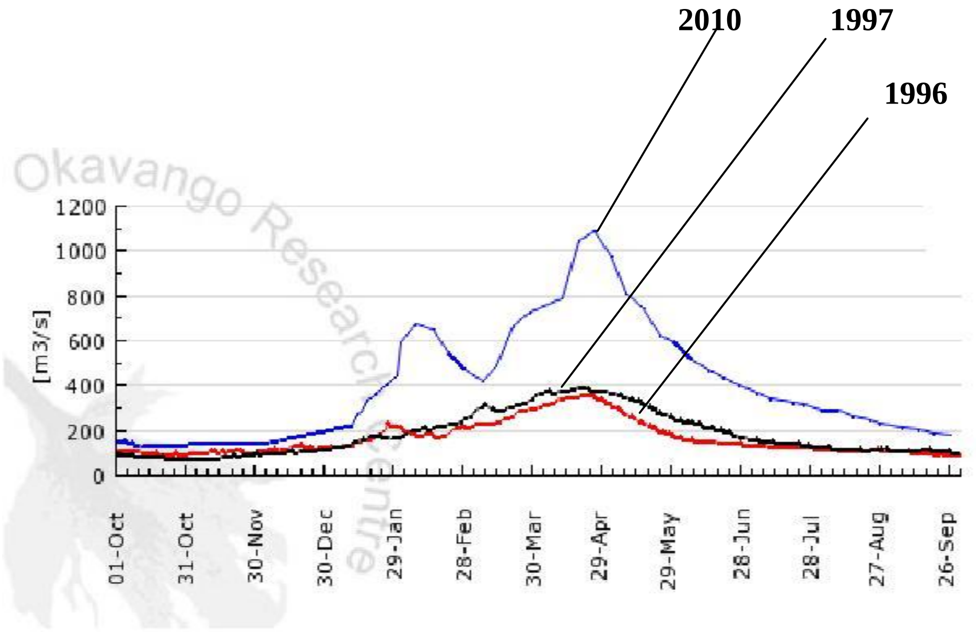

Figure 2: **Flood water discharge measured at Mohembo in the Okavango Delta, Botswana.**

Source :(ORI, 2011).

This study sought to establish how seasonal floodplain vegetation of the Okavango Delta responds to high flood with respect to species composition and distribution. The study compared the distribution and composition of seasonal floodplain vegetation communities identified during low flood (Bonyongo, 1999) to composition and distribution of vegetation communities identified during high flood.

2.1 Objectives

1. To compare seasonal floodplain vegetation community composition and distribution between low and high floods.

2.2 Materials and Methods

2.2.1 Study site

The study was conducted in the Nxaraga Lagoon (19º 35’ S 23º 10’ W) seasonal floodplains in the Okavango Delta (Figure 3).

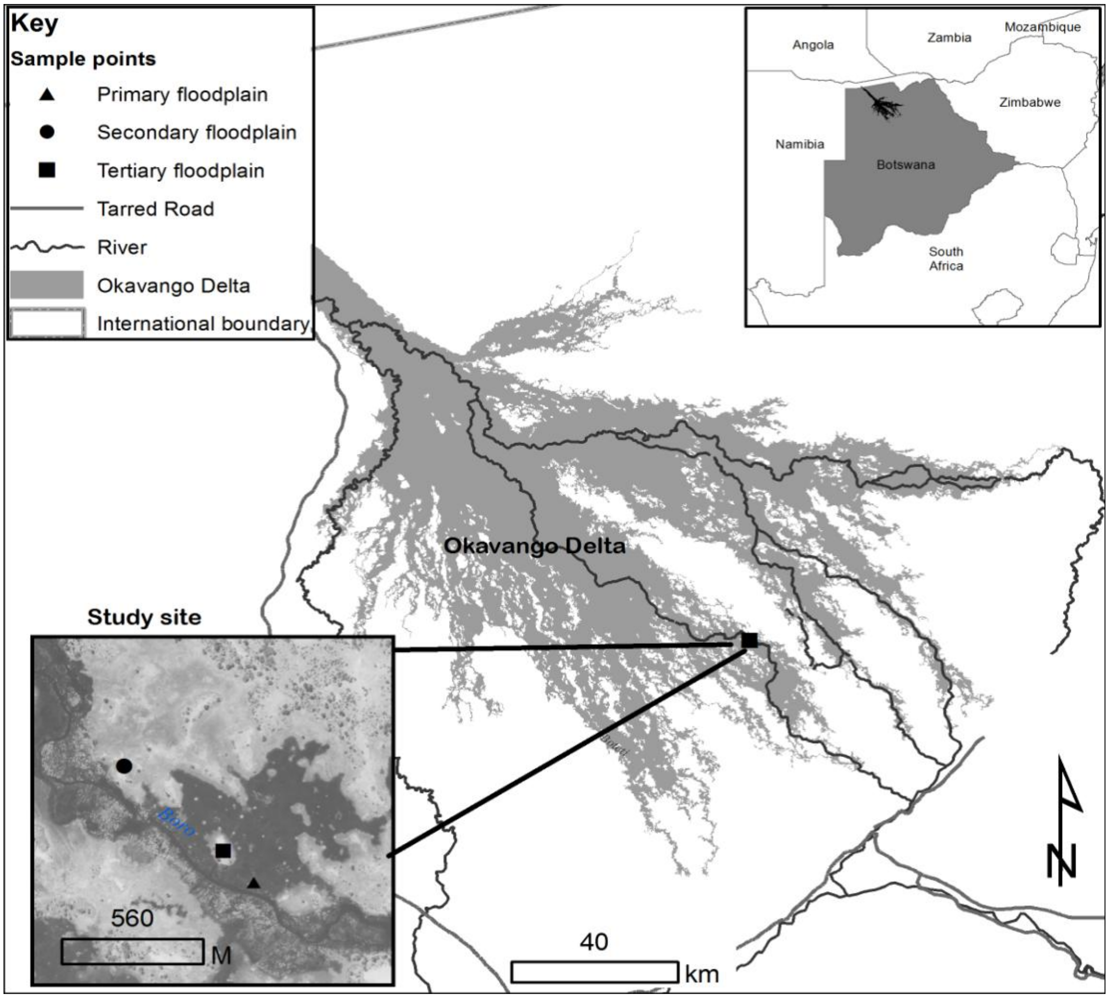

Figure 3: **Nxaraga Lagoon floodplains.** The insert on the top right corner shows the location of the Okavango Delta in Botswana. Note the insert on the bottom left corner which shows location of different floodplains in relation to the main river channel.

Nxaraga Lagoon seasonal floodplains receive floods between May and October (McCarthy, 2005). This area receives mean annual rainfall (between November and February) of approximately 550mm (Wilson and Dincer, 1976). Mean maximum summer temperature experienced in the Nxaraga Lagoon seasonal floodplains is 30.5 °C while minimum is 14.8 ºC. In winter mean maximum temperature ranges between 25.3 ºC and 28.7 ºC while minimum mean temperature ranges between 7.0 ºC and 10.0 ºC (Ellery et al., 1991). During summer mean relative humidity for the Nxaraga seasonal floodplains is from a minimum of 60% to a maximum of 70% while in winter it ranges between 43 % and 63 % (Ellery et al., 1991).

The study aimed to compare vegetation community composition and species distribution between 2010 and 1997 by re-sampling zones sampled by Bonyongo (1999). These zones were selected on the basis of homogenous vegetation cover, along an elevation gradient between channel (low) and dry land (high). The eight vegetation communities identified here by Bonyongo (1999) during a year of low flooding were, in terms of their dominant species, *Alternanthera sessilis-Ludwigia stolonifera* (Zone 1), *Cyperus articulatus-Schoenoplectus corymbosus* (Zone 2), *Miscanthus junceus-Digitaria scalarum* (Zone 3), *Paspalidium obtusifolium-Panicum repens* (Zone 4), *Setaria sphacelata-Eragrostis inamoena* (Zone 5),*Imperata cylindrica-Setaria sphacelata* (Zone 6), *Vetiveria nigritana-Setaria sphacelata* (Zone 7), and *Sporobolus spicatus-Cynodon dactylon* (Zone 8) (Bonyongo, 1999).

Zones found in the primary floodplains (low areas) were 1 and 2 while secondary floodplains zones (intermediate areas) were 3, 4, 5, 6 and 7. In tertiary floodplains (higher areas) there was only zone 8 (Figure 4). During the low flood of 1997 all the zones were flooded except for 6, 7 and 8 (Bonyongo, 1999).

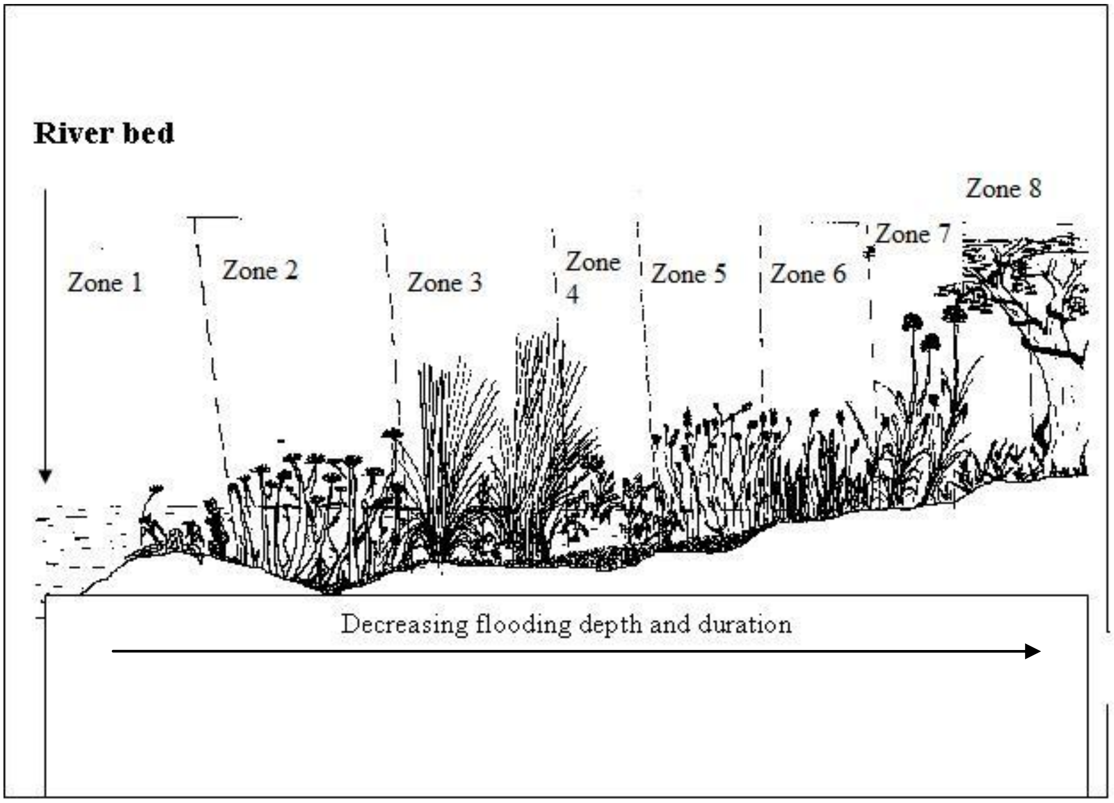

Figure 4: **Location of zones in relation to river bed.** ***Adapted from*** **Bonyongo (1999).**

2.2.2 Vegetation sampling

Vegetation composition and distribution were surveyed in late February and early March 2010. Minimum sampling plot area was 25m^2 (Bonyongo, 1999). Zones identified in the previous study during low floods by Bonyongo (1999) were re-sampled. Eight zones with homogenous vegetation cover were selected. A total of 40 sites were sampled, with five sites per zone. In each site five 5m x 5m plots were sampled (25 plots per zone) and plant species cover and abundance estimated following a modified Braun-Blanquet cover/abundance scale (Mueller-Dombois and Ellenberg, 1974) (Table 2). In total 200 plots were sampled.

Table 2: Modified Braun-Blanquet percentage cover/abundance scale.

Level	Description
5	75-100% plot cover
4	50-75% plot cover
3	25-50% plot cover
2B	15-25% plot cover
2A	5-15% plot cover
2M	1-5% plot cover, over 50 individuals
1	1-5% plot cover, 6-50 individuals
+	Less than 1% plot cover, 3-5 individuals
R	Less than 1% plot cover, 1-2 individuals

Plant species names were recorded in data sheet alongside their estimated cover. Nomenclature followed Germishuizen and Meyer (2007). Additional information on the plot physical state was also recorded. A total of 200 plots were sampled for vegetation in all the 8 vegetation zones. Mean plant species richness per zone was calculated as the total number of plant species divided by the total number of plots. The Shannon diversity index was determined for each zone.

2.3 Data analysis

The Kruskal-Wallis test was performed ($p = 0.05$) to test for statistical difference in mean species richness per zone between high and low flood conditions. It was also performed to test for statistically significant differences in mean percentage cover and species diversity between zones under high and low flooding years. Multi-response Permutation Procedures (MRPP) (McCune and Grace, 2002) testing was performed in PCOrd using Sorensen distance measure to test for the hypothesis of no difference between low and high flood vegetation communities. MRRP is a nonparametric method which tests for the hypothesis of no difference between two or more groups (McCune and Grace, 2000). Hierarchical cluster analysis (flexible β linkage, $\beta = -0.25$, Sorensen distance, data relativized by maximum) of sites was performed in PCORD. Species appearing in less than 3 sites were left out of the analysis. Indicator species analysis (ISA), (Dufrêne and Legendre, 1997) was used to calculate indicator values for species in groups defined from the cluster analysis. Monte Carlo testing was used to evaluate the statistical significance of indicator values for species. Random number of seeds used for Monte Carlo testing was 1 178.

2.4 Results

A total of 53 plant species were identified during the high flood of 2010, while 88 species were identified during the low flood of 1997. MRPP analysis of the 8 group division showed a chance-corrected within group agreement A= 0.549. The probability of a smaller or equal delta was $p <$ 0.05. The hypothesis of no difference between high and low flood vegetation communities was rejected. That is, there was a significant difference between high and low flood vegetation communities. Vegetation communities showed a shift in plant species composition and distribution (Table 3).

Table 3: A shift in seasonal floodplain vegetation communities' composition in response to a high flood.

Zone	**Low flood vegetation community**	**High flood vegetation community**
Zone 1	*Alternanthera sessilis-Ludwigia stolonifera*	*Oxycaryum cubense-Vossia cupsidata*
Zone 2	*Cyperus articulatus-Schoenoplectus corymbosus*	*Cyperus articulatus-Schoenoplectus corymbosus*
Zone 3	*Miscanthus Junceus-Digitaria scalarum*	*Miscanthus junceus-Pycreus flavescens*
Zone 4	*Paspalidium obtusifolium-Panicum repens*	*Eleocharis dulcis-Leersia hexandra*
Zone 5	*Setaria sphacelata-Eragrostis inamoena*	*Eragrostis inamoena-Panicum repens*
Zone 6	*Imperata cylindrica-Setaria sphacelata*	*Imperata cylindrica*
Zone 7	*Vetiveria nigritana-Setaria sphacelata*	*Vetiveria nigritana-Setaria sphacelata*
Zone 8	*Sporobolus spicatus-Cynodon dactylon*	*Sporobolus spicatus-Sporobolus acinifolius*

2.4.1 Description of zones during a high flood

Zone 1

Zone 1 was co-dominated by *Alternanthera sessilis* (L) R.Br and *Ludwigia stolonifera* during low flood. During high flood it was co-dominated by *Oxycaryum cubense* (Poepp & Kunth) Lye (Indicator species analysis value (ISV), 92.1%) and *Vossia cupsidata* (ISV, 71.9%) (Table 3). *Alternanthera sessilis* and *Ludwigia stolonifera* were absent during high flood. New plant species in order of decreasing cover were *Leersia hexandra* Sw, *Nymphoides indica* (L) Kuntze and *Persicaria senegalensis* (Meisn) Sojak and *Cyperus papyrus* L. Flood tolerant species include *Cyperus dives* Delile, *Sida cordifolia* L and *Nymphoides indica* (Appendix 1). Mean species per zone declined during high flood ($p < 0.05$) (Figure 5).

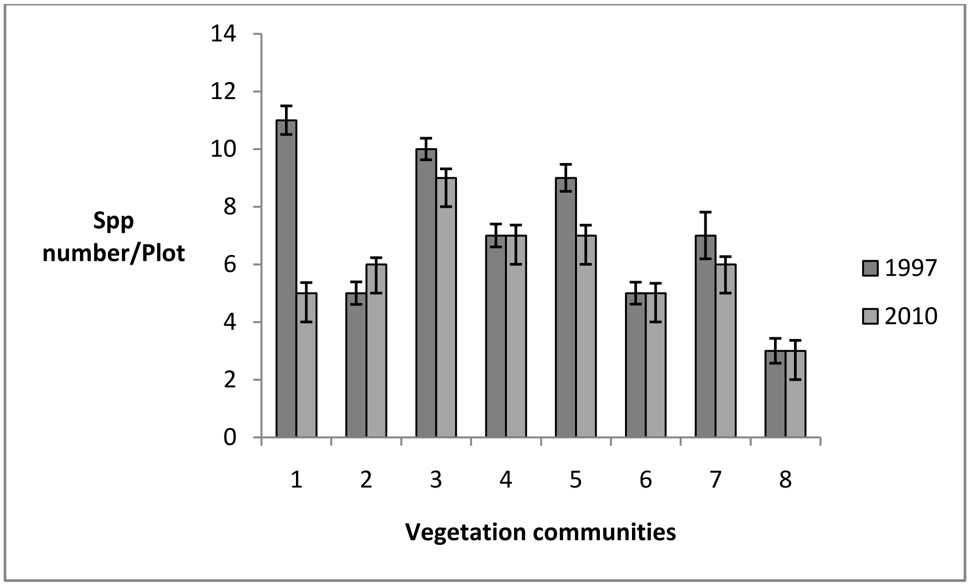

Figure 5: Mean species richness per plot in different vegetation zones under low and high floods.

The Shannon diversity index increased during high flood ($p < 0.05$) (Table 4).

Table 4: Shannon diversity index in seasonal floodplain vegetation zones during low and high flooding years.

Vegetation zone	1997	2010
Zone 1	0.50±0.08	1.29±0.10
Zone 2	0.37±0.06	1.54±0.05
Zone 3	0.68±0.09	1.56±0.04
Zone 4	0.60±0.05	1.60±0.06
Zone 5	0.79±0.04	1.43±0.06
Zone 6	0.02±0.02	0.94±0.03
Zone 7	0.47±0.09	1.40±0.06
Zone 8	0.13±0.03	0.42±0.11*

Zone 2

During low and high flood zone 2 was co-dominated by *Cyperus articulatus* (ISV, 56.7%) and *Schoenoplectus corymbosus* (ISV, 55.9%) (Table 3). *Schoenoplectus corymbosus* percentage cover increased during high flood ($p < 0.05$) (Table 5). Mean species per zone increased in response to high flood ($p < 0.05$) (Figure 5).

Table 5: 1997 dominant plant species percentage cover change in response to 2010 floods

Vegetation zone	Dominant species	1997 mean % cover	2010 mean % cover
Zone 1	*Alternanthera sessilis*	34.2±3.4	0*
	Ludwigia stolonifera	10.8±2.7	0*
Zone 2	*Cyperus articulatus*	35.8±3.4	32 ± 3.5
	Schoenoplectus corymbosus	4.2±1.4	30 ± 2.6*
Zone 3	*Miscanthus junceus*	62.5±3.2	82 ± 2.6*
	Digitaria scalarum	2.4±1.2	3 ± 1.2
Zone 4	*Paspalidium obtusifolium*	41.6±3.09	9 ± 1.5*
	Panicum repens	6.0±2.3	3 ± 1.2
Zone 5	*Setaria sphacelata*	15.0±3.4	3 ± 1.2*
	Eragrostis inamoena	20.7±2.2	20.5 ± 2.9
Zone 6	*Imperata cylindrica*	54.7±4.4	83 ± 2.9*
	Setaria sphacelata	1.8±0.08	3 ± 1.2
Zone 7	*Vetiveria nigritana*	65.5±4.2	43±4.0*
	Setaria sphacelata	3.6±1.3	15±3.6*
Zone 8	*Sporobolus spicatus*	35.4±3.7	65 ± 4.4*
	Cynodon dactylon	5.0±3.5	16 ± 5.0*

Significant difference at level $p = 0.05$

The Shannon species diversity index was higher under high flood conditions than under low flood ($p< 0.05$) (Table 4). New species found in this zone during high flood in order of decreasing cover were *Eleocharis dulcis* (Burm.f.), *Sacciolepis typhura* (Stapf) Stapf, *Nymphaea lotus* L and *Fuirena pubescens* (Poir) Kunth. Plant species present during both high and low floods included *Leersia hexandra* and *Oryza longistaminata* A.Chev & Roehr (Appendix 2).

Zone 3

During low flood *Miscanthus junceus* and *Digitaria scalarum* (Schweinf) Chiov were co-dominant in zone 3. *Miscanthus junceus* (ISV, 97.0%) and *Pycreus flavescens* (L) P.Beauv ex

Rchb (ISV, 12.5%) were dominant during a high flood (Table 3). *Miscanthus junceus* percentage cover significantly increased during a high flood ($p < 0.05$) (Table 5). Plant species found in both high and low floods in order of decreasing cover include *Cyperus articulatus* and *Leersia hexandra*. New species in order of decreasing cover included *Eleocharis dulcis*, *Fuirena pubescens*, *Oryza longistaminata* and *Sacciolepis typhura* (Appendix 3). Mean species richness per zone decreased during high flood ($p < 0.05$) (Figure 5). The Shannon diversity index was higher under high flood than under low flood ($p < 0.05$) (Table 4).

Zone 4

During low flood zone 4 was dominated by *Paspalidium obtusifolium* and *Panicum repens*. *Eleocharis dulcis* (ISV, 55.0%) and *Leersia hexandra* (ISV, 40.9%) were co-dominant in this zone during high flood (Table 3). *Paspalidium obtusifolium* and *Panicum repens* percentage cover was lower during high flood than it was during low flood ($p < 0.05$) (Table 5). Mean species richness per zone did not change in response to high flood ($p > 0.05$) (Figure 5). New species in zone 4 included *Sacciolepis typhura* and *Nymphoides indica*. Plant species absent from this zone during high flood include *Eragrostis inamoena* K.Schum, *Vetiveria nigritana* and *Setaria sphacelata*. Plant species found during both high and low floods include *Cyperus articulatus, Schoenoplectus corymbosus* and *Oryza longistaminata* (Appendix 4). The Shannon diversity index was significantly higher in this zone during high flood than during low flood ($p < 0.05$) (Table 4).

Zone 5

During low flood this vegetation zone was co-dominated by *Setaria sphacelata* and *Eragrostis inamoena*. It was co-dominated by *Eragrostis inamoena* (ISV, 91.7%) and *Panicum repens* (ISV, 66.4%) during high flood (Table 3). The percentage cover of *Setaria sphacelata* was significantly lower in 2010 than in 1997 (p<0.05) (Table 5). New species in this zone include *Oryza longistaminata*, *Leersia hexandra*, *Fuirena pubescens* (Poir) Kunth, *Eleocharis dulcis* and *Sacciolepis typhura*. Species absent during the 2010 high flood include *Brachiaria arrecta* (Hack ex T. Durand & Schinz) Stent, *Imperata cylindrica* and *Acroceras macrum*. Plant species present during both high and low floods include *Cyperus articulatus*, *Schoenoplectus corymbosus* and *Paspalidium obtusifolium* (Appendix 5). Mean plant species richness per zone decreased in response to high flood (p<0.05) (Figure 5). The Shannon diversity index significantly increased (Table 4).

Zone 6

Imperata cylindrica and *Setaria sphacelata* co-dominated zone 6 in the 1997 low flood. During high flood zone 6 was co-dominated by *Imperata cylindrica* (ISV, 91.2%) (Table 3). The mean percentage cover for *Imperata cylindrica* was significantly greater under high flood conditions (p<0.05). Mean species richness per zone did not change (Figure 5). The Shannon diversity index was significantly greater under high flood conditions (p<0.05) (Table 4). New species in this zone include *Acacia erioloba* E. Mey, *Cyperus longus* L. Var. Longus and *Fuirena pubescens*. Plant species present in both high flood and low flood include *Imperata cylindrica*, *Setaria sphacelata* and *Vernonia glabra* (Steez) Vatke (Appendix 6).

Zone 7

Vetiveria nigritana (ISV, 77.4%) and *Setaria sphacelata* (ISV, 77.4%) co-dominated in zone 7 under both low and high flood conditions (Table 3). The mean percentage cover of *Vetiveria nigritana* was significantly ($p<0.05$) lower under high flood conditions, whereas that of *Setaria sphacelata* was significantly higher ($p<0.05$) (Table 5). Mean species richness per zone decreased under high flood ($p>0.05$) (Figure 5). The Shannon diversity index was higher under high flood conditions than under low flood conditions ($p<0.05$) (Table 4). New species introduced in zone 7 include *Cyperus longus*, *Fuirena pubescens* and *Oryza longistaminata*. Plant species present in both high and low floods include *Vetiveria nigritana*, *Panicum repens* and *Schoenoplectus corymbosus*. Plant species absent from zone 7 during high flood include *Digitaria debilis* (Desf) Wild, *Chloris virgata* and *Setaria verticillata* (L) P.Beauv (Appendix 7).

Zone 8

This zone was co-dominated by *Sporobolus spicatus* and *Cynodon dactylon* during low flood. During high flood *Sporobolus spicatus* (ISV, 87.5%) and *Sporobolus acinifolius* Stapf (ISV, 29.2) were co-dominant (Table 3). Both *Sporobolus spicatus* and *Cynodon dactylon* percentage cover significantly increased during high flood ($p<0.05$) (Table 5). Mean species richness per zone did not change in response to high flood (Figure 5). The Shannon diversity index increased in response to high flood ($p>0.05$) (Table 4). New species include *Nidorella resedifolia, Cyperus longus* and *Eragrostis rigida* A. Camus. Species found in both low and high floods include *Sporobolus spicatus*, *Sporobolus acinifolius* Stapf and *Cynodon dactylon*. Species absent during high flood include *Cyperus dives*, *Eragrostis cilianensis* All Vign ex Janchen and *Acacia tortilis* (Forssk) Hayne (Appendix 8).

2.5 Discussion

Previous studies done elsewhere (Rees, 1978; Hughes, 1990; Kingsford, 2000; Lite et al., 2005; Capon, 2005) show that vegetation community composition and distribution changes in response to high flooding conditions. During flooding soil oxygen is eliminated which can lead to low nutrient absorption (Kozlowski, 1984; Kozlowski, 1997; Ellery and Tacheba, 2003). Plant species which are tolerant of anoxia and the accompanying redoximorphic changes replace flood intolerant species under extended hydro-period conditions (Kozlowski, 1997). Plant species which have the ability to develop aerenchyma tissue for oxygen transport are tolerant of flooding (Kozlowski, 1984; Naiman and Decamps, 1997).

In the Okavango Delta, vegetation communities' composition changed from seasonal floodplain grass species to aquatic grass and sedge species in response to a high flood. *Vossia cupsidata* and *Oxycaryum cubense* replaced *Alternanthera sessilis* and *Ludwigia stolonifera* as co-dominants from zone 1. *Eleocharis dulcis* and *Leersia hexandra* replaced *Paspalidium obtusifolium* and *Panicum repens* from zone 4. *Panicum repens* and *Paspalidium obtusifolium* are likely to be intolerant of prolonged flooding duration and high flooding depth which could be the reason they were replaced by *Eleocharis dulcis* and *Leersia hexandra* as co-dominants from zone 4. *Panicum repens* replaced *Setaria sphacelata* in zone 5. During the high flood of 2010, zone 5 experienced flooding duration and flooding depth (when compared to low flood of 1997) which were probably favourable to *Panicum repens* growth. This could also suggest that the flooding conditions in zone 5 were unfavourable to *Setaria sphacelata* (Lubke et al., 1984) since it tolerates shallow flooding depth and short flooding duration (Bonyongo, 1999). *Pycreus* *flavescens* replaced *Digitaria scalarum* (Schweinf) Chiov as the co-dominant species in zone 3. It tolerates a variety of habitats including swamp edges (Eastern Arc Mountains and Coastal forests CEPF plant assessment project participants, 2006) suggesting that conditions during a high flood in zone 3 (found on the edge of the main channel) were favourable to its growth. This is generally consistent with the findings by Rees, (1978) in which during a high flood *Echinochloa stagnina* (Retz) P. Beauv replaced *Oryza barthii* A.Chev and *Brachiaria rugulosa* Stapf from those zones experiencing prolonged flooding duration and high flooding depth. Conversely, Bonyongo, (1999) concluded that *Alternanthera sessilis* and *Ludwigia stolonifera* are tolerant of prolonged flooding duration and deep flooding depth. Their elimination from zone 1 could be an indication that the high flood of 2010 had exceeded their optimum flooding duration and depth tolerance.

Another potential factor which could have led to the absence of *Alternanthera sessilis* and *Ludwigia stolonifera* from zone 1 during high flooding conditions is flow velocity. It is expected that during high flooding conditions zone 1 lying closer to the river channel will experience higher flow velocity which might favour *Vossia cuspidata* since it prefers relatively high flows (Ellery and Ellery, 1997). Though *Alternanthera sessilis* and *Ludwigia stolonifera* are associated with permanent water (Ellery and Ellery, 1997), they do not withstand high flow velocity and as a result they were eliminated from zone 1 during a high flood of 2010.

Soil water content could also be another factor influencing seasonal floodplain vegetation community composition and distribution in the Okavango Delta. During low flood of 1997, zones 1, 2 and 3 alternated between wet and dry phases (Bonyongo, 1999). Alternating dry and wet periods might have led to *Alternanthera sessilis* and *Ludwigia stolonifera* seeds remaining dormant during the dry season and germinating during the wet season to colonise flooded areas. *Alternanthera sessilis* and *Ludwigia stolonifera* are adapted to colonising flooded areas through spongy floating stems (Ellery and Ellery, 1997). Since *Vossia cuspidata* and *Oxycaryum cubense* are not adapted to drying, they were completely excluded from zone 1 during low flood of 1997. However, during high flood, zone 1 was permanently flooded and this might have favoured the establishment of clonal *Vossia cuspidata* and *Oxycaryum cubense* which are adapted to permanent water through their floating stems (Ellery and Ellery, 1997) at the expense of the less competitive *Ludwigia stolonifera* and *Alternanthera sessilis*. This is because clonal plant species tend to be dominant in wetland systems (Ellery and Ellery, 1997).

Differences in mean species percentage cover are an indication of variation in plant species' tolerance of high flooding. The observed increase in percentage cover of *Schoenoplectus corymbosus* and *Miscanthus junceus* suggests that they are tolerant of prolonged flooding duration and high depth of flooding. *Schoenoplectus corymbosus* and *Miscanthus junceus* are adapted to permanent flooding through their erect stems which range between 1 and 2m tall (Ellery and Ellery, 1997). The tall erect stems allow *Schoenoplectus corymbosus* and *Miscanthus junceus* to remain emergent and absorb insolation together with carbon dioxide for use in the process of photosynthesis and oxygen for respiration. *Vetiveria nigritana* percentage cover decrease after high flood inundation suggests that it is intolerant to prolonged flooding duration and high depth of flooding. The decrease in *Paspalidium obtusifolium* percentage cover could be due to competition from the more competitive species establishing during a high flood of 2010.

Paspalidium obtusifolium could also be shaded by tall *Schoenoplectus corymbosus* and *Miscanthus junceus*. Shading will probably reduce the amount of sunlight energy absorbed by *Paspalidium obtusifolium* for the process of photosynthesis hence the reduction in mean percentage cover. Light availability is a limiting resource for understorey species primary production (Lite et al., 2010). Kotowski et al (2010) in their experimental study on waterlogging and canopy interactions as controls to floodplain plant species recruitment found that canopy presence prevented the establishment of understorey plant species probably due to high sunlight attenuation. To survive shading, shade tolerant plant species had high biomass in leaves combined with a small size and relatively low growth rate (Kotowski et al., 2010). Plant species in drier zones (*Sporobolus spicatus*, *Cynodon dactylon* and *Imperata cylindrica*) showed an increase in percentage cover probably indicating their tolerance to prolonged dry conditions. *Setaria sphacelata* is an example of plant species tolerance to flooding and drier conditions. In zones experiencing prolonged flooding duration and high depth of flooding it showed a decline in percentage cover while it showed an increase in mean percentage cover in dry zones. This is consistent with findings from previous studies (Trebino et al., 1996; Insausti et al., 1999; Capon, 2005).

The reduction in species richness in zones 1, 2, 3, 4 and 7 with extended hydro-period observed in the Okavango Delta seasonal floodplains is consistent with the findings from the San Pedro River floodplains (Lite et al., 2005), where they found a decrease in plant species richness with increasing flooding duration and depth. It was also consistent to the findings from studies in Amazonia seasonal floodplains in which species richness decreased with increasing flooding duration and depth (Ferreira, 1997; Ferreira and Prance, 1998). A decline in species richness during a high flood could be due to selective pressure of adaptation to prolonged flooding duration and high flooding depth (Ferreira, 1997). It could also be due to low soil nutrient content and plant species intolerance to prolonged flooding duration (Ellery and Tacheba, 2003). Literature (e.g. Kozlowski, 1984; Kozlowski, 1997) indicate that in flood intolerant plant species mineral nutrient absorption is low due to root decay. Villar et al., (1996) observed a decrease in phosphorous and nitrogen content in plant tissue after flooding in their study in Lower Paraná River seasonal floodplains. Prolonged flooding duration can also lead to production of toxins in the form of reduced S, Fe, ethanol and Mn harmful to plant species (Cronk and Fennessy, 2001; Ellery and Tacheba, 2003). These toxins destroy plant cell membrane through dissolving lipids in flood intolerant plants (Kozlowski, 1984).

There was a pronounced reduction of species richness during a high flood of 2010 in zone 1. This could explain the significant decrease of total plant species from 88 during low flood (1997) to 53 during high flood (2010). A possible explanation for this could be that fluctuations between dry and wet phases during low flood of 1997 hold the zone in a transitional/early succession stage. At early/transitional succession stage both opportunistic and competitive species co-exist leading to an increase in plant species diversity (Huston, 1979). However, in 2010 following successive years of prolonged inundation, competitive, clonal *Vossia cuspidata* and *Oxycaryum cubense* have established and consequently removing other less competitive species such as *L stolonifera* and *Alternanthera sessilis*. As a result this might have led to a reduction in plant species richness in zone 1 observed in 2010.

There was a general increase in plant species diversity in all the zones except in zone 8. High floods represent a strong perturbation (Cronk and Fennessy, 2001) leading to the removal of some plant species while the establishment of others is favoured (Hupp, 1988; Poff et al., 1997; Casanova and Brock, 2000). This could suggest that zones 1 up to 7 experienced flooding disturbances (Huston, 1979) leading to new species colonising empty spaces created by the elimination of species such as *Alternanthera sessilis* and *Ludwigia stolonifera* increasing species diversity. It is expected that zones 1 and 2 which are located closer to the channel experienced higher flood disturbance levels than other zones located far from the channel. This could suggest that zones 3 and 4 with higher species diversity than others might have experienced intermediate flooding disturbance (Huston, 1979). Zone 8 is rarely flooded and during the vegetation sampling period it was not flooded. Plant species composition and distribution in zone 8 could be determined by tolerance to high Na content (Ellery and Tacheba, 2003). High Na content is toxic to many plant species in the Okavango Delta seasonal floodplains. The distribution of some plant species such as *Phoenix reclinata* Jacq and *Euclea undulata* Thunb in the Okavango Delta seasonal floodplains is restricted by high soil Na concentration (Ellery et al., 1993). The presence of *Sporobolus spicatus* is usually an indication that the floodplain area is saline (McCarthy et al., 1998; Ellery and Tacheba, 2003), in this case zone 8. *Sporobolus spicatus* tolerates high Na content (Ellery et al., 1993) through the development of Na excreting salt glands (Ramadan, 2001).

An increase in plant species diversity during high flooding conditions could be attributed to succession. Deposition of sediments acts as a disturbance leading to the re-initiation of succession processes on these floodplains (Diederichs and Ellery, 2000). During high flooding conditions increasing flooding depth and duration could also act as a sufficient disturbance in combination with sediment deposition to re-set the community to an early succession stage (Capon, 2005). At early succession stage opportunistic and competitive species can co-exist leading to an increase in species diversity (Huston, 1979). *Alternanthera sessilis* and *Ludwigia stolonifera* are examples of opportunistic species. Competitive species are represented by *Vossia cuspidata* and *Oxycaryum cubense* (Ellery and Ellery, 1997). This implies that the observed high species diversity is because most vegetation communities are in transitional stage. At peak floods and flood recession it is expected that diversity would decrease due to elimination of some plant species owing to their poor adaptation (Connell, 1978).

Summary

In the seasonal floodplains at Nxaraga in the Okavango Delta, as a result of extended hydroperiod:

- Vegetation communities showed a shift in spatial distribution and zones showed a change in plant species composition.
- There was a general decline in plant species richness.
- Plant species diversity increased in all vegetation zones except for zone 8 found on the elevated drier floodplains.
- Plant species cover declined in flood intolerant species in zones experiencing high flooding depth and prolonged flooding duration. It increased in plant species tolerant to prolonged flooding duration and high flooding depth.
- Mean percentage cover increased in dry zones and decreased in zones experiencing high flooding depth and prolonged duration of flooding.

In chapter 3, the influence of a high flood regime on soil nutrient status in the Okavango Delta seasonal floodplains will be explored.

Chapter 3: Influence of flood variation on soil nutrient status in the Okavango Delta seasonal floodplains.

3.0 Introduction

Soil nutrient dynamics in seasonal floodplain ecosystems are highly complex (Dezzeo et al., 2000) due to flood pulses and changing redoximorphic state (Mitsch and Gosselink, 2000; Gallardo, 2003). Flood pulses facilitate soil nutrient exchange between rivers and their associated seasonal floodplains (Valett et al., 2005). During floods, soil nutrients dissolve in floodwaters and may be transported from seasonal floodplain surfaces into adjacent rivers (Lowes et al., 2008). Soil nutrients may also be transported from the river main channel into seasonal floodplains through lateral flow (Junk et al., 1989). During flooding the soil becomes highly reduced in redoximorphic state (Eh) resulting in a pH shift increasing the mobilization of soil nutrients (P, N, Mg, Ca, Na and K) (Mitsch and Gosselink, 2000). These nutrients include those that were left from the previous flood and those released from organic matter decomposition accumulated during dry periods (Gabe, 2009). Soil flooding also causes hypoxia leading to a reduction in the soil nutrient content available to plants (Chen et al., 2005). Due to hypoxia, organic matter decomposition rate is reduced (Gallardo, 2003) leading to low soil nutrient content release (Teyler and Olsson, 2001).

The relationship between flood pulsing (hydroperiod) and soil nutrients has been extensively studied elsewhere (Terrill et al., 1991; Yavitt et al., 1993; Dezzeo et al., 2000; Antheunisse and

Verhoeven, 2008; Humphries, 2008) while in the Okavango Delta it has received little attention. Bonyongo, (1999) and Bonyongo and Mubyana, (2004) concluded that soil nutrient status in the Okavango Delta seasonal floodplains is influenced by hydro-period (flooding duration and depth). Due to soil moisture content gradient, seasonal floodplains experience unequal distribution of soil nutrients. Generally soil nutrient content is higher in primary floodplains, followed by secondary floodplains with tertiary floodplains having low soil nutrient content (Bonyongo, 1999; Bonyongo and Mubyana, 2004). These studies were conducted during a low flood (Figure 2) in which flooding duration and depth were short and shallow respectively.

Recently the Okavango Delta has experienced an increase in seasonal flooding with the highest inflow since 1969 recorded in 2010 (ORI, 2011). During a high flood, flooding duration is prolonged and flooding depth increases. The surface area inundated (flood extent) also increases and as a result some tertiary floodplains which are usually not flooded during low floods become inundated. However, it is still not known how the soil nutrient content in the Okavango Delta seasonal floodplains is influenced by a high flood. The aim of this study was to investigate the influence of a high flood regime on soil nutrient content in the Okavango Delta seasonal floodplains. We hypothesized that soil nutrient content in floodplains would be lower under extended hydroperiod than under short duration shallow flooding. The Okavango Delta seasonal floodplains are important for the local people as they use them for crop production (*molapo* farming or flood recession farming). Since flooding may be an important process in nutrient cycling in the Delta there is need to establish how flooding variation affects its soil nutrient dynamics. Soil nutrient availability is significant as it supports primary production in seasonal floodplain vegetation communities (Bonyongo, 1999).

3.1 Objectives

1. To determine floodplain soil nutrient content during a high flood and
2. To compare floodplain soil nutrient content during a high flood to that found under a low flood in an Okavango Delta seasonal floodplain.

3.2 Materials and Methods

3.2.1 Soil sampling

The study was conducted in the Nxaraga Lagoon seasonal floodplains in the Okavango Delta (See chapter 2 for a detailed description of the study area). Forty sampling sites from an earlier study (Bonyongo, 1999) were re-sampled between February and September 2010.Soil samples were collected from five sites in each of 8 pre-defined zones. One 5m x 5m permanent plot was established in each site. From each permanent plot soil samples were collected at a depth of between 0 and 30 cm using a soil auger. A total number of 5 soil samples were collected from each vegetation zone and an overall total number of 40 samples for all the vegetation zones per sampling season (middle of rainy season, before floods and after floods). A total of 120 soil samples were collected at the end of three flooding seasons. The soil samples were oven-dried at 80 °C for 24 hours, then ground using pestle and mortar before being sieved through a 2 mm mesh. They were then analysed for pH, extractable Na, P, Ca, Mg and K using standard Laboratory methods (Environmental Protection Agency, 1996) at the Okavango Research Institute. pH was determined from a 1:1 soil-water suspension using a pH electrode model 330i. K and Na content were determined using Sherwood Flame Photometer 410 while Mg and Ca content was determined using Varian atomic absorption spectrophotometer AA 220 (Kalisz and Łachacz, 2009). P analysis was done using Bran + Luebbe Auto analyser 3.

3.3 Statistical Data analysis

Differences in soil nutrient content between flooding seasons (middle of rainy season, before floods and after floods) during the extended hydroperiod of 2010 were tested for significance using single factor ANOVA. The Tukey test was performed post hoc to establish which flooding season and vegetation zone was responsible for differences in soil nutrient content and pH level between flooding seasons and vegetation zones respectively. The Tukey test was also used to compare means of soil nutrient content between low and high floods within floodplain vegetation zones. Correlations between flooding depth, duration of flooding and soil nutrient status were sought using Spearman's Rank correlation. All analyses were carried out using SPPS version 19, 2010.

3.4 Results

Soil nutrient status in 2010

There was no significant difference in Mg, Ca, Na content and pH level between flooding seasons of 2010 extended hydro-period. P and K content significantly differed between flooding seasons. P content was higher in zone 1 in the middle of the rainy season than before the onset of flooding ($p<0.05$). It was lower in zones 2, 3, 4,5, 6, 7 and 8 in the middle of rainy season than before the onset of flooding ($p<0.05$). P content was lower in the middle of the rainy season than after flooding ($p<0.05$). K content was lower in the middle of the rainy season than before the onset of flooding (*p*<0.05). All the soil nutrient contents (except P) and pH levels were higher in the tertiary floodplains than in the primary and secondary floodplains (*p*<0.05).

*3.4.1 Soil nutrient status in different vegetation zones during a high flooding year***.**

Na, Ca, K and Mg content was highest (*p*<0.05) in zone 8 in the middle of the rainy season. P content was highest in zone 1 (*p*<0.05) (Table 6).

Table 6: **Mean (±standard error) soil nutrient content in the middle of rainy season in seasonal floodplain zones.**

Vegetation zones	pH	Na (mg/Kg)	Ca (mg/Kg)	K (mg/Kg)	Mg (mg/Kg)	P (mg/Kg)
Zone 1	5.4±0.1	76.3±18.1	284.4±82.3	68.7±12.2	110.5±31.0	29.33±4.63
Zone 2	5.5±0.02	55.22±5.4	410.2±54.8	66.8±8.3	111.5±22.6	26.45±4.35
Zone 3	5.4±0.1	54.7±3.3	651.0±214.8	78.9±20.6	167.7±44.5	18.94±0.01
Zone 4	5.5±0.1	45.64±8.4	718.25±211.9	63.2±12.1	253.3±91.6	18.83±3.68
Zone 5	5.7±0.2	51.4±3.3	258.0±58.1	53.8±3.0	55.5±11.3	33.42±2.12*
Zone 6	8.1±0.3	207.86±77.0	1877.3±785.1*	221.3±87.8	1367.3±793.8*	11.34±2.75
Zone 7	5.8±0.1	62.93±24.7	835.0±277.0	44.42±0.0	288.5±131.5	22.13±3.55
Zone 8	9.7±0.1	873.21±25.4*	3672.8±197.2*	641.7±135.5*	1328.1±548.5*	31.94±1.18

*Significantly higher at *p*<0.05 level

Na, Mg, Ca, K content and pH were highest (*p*<0.05) in vegetation zone 8 prior to inundation. P was highest (*p*<0.05) in zone 5 (Table 7).

Table 7: **Mean (±standard error) soil nutrient content prior to flooding in seasonal floodplain zones.**

Vegetation zone	**pH**	**Na (mg/Kg)**	**Ca (mg/Kg)**	**K (mg/Kg)**	**Mg (mg/Kg)**	**P (mg/Kg)**
Zone 1	5.6±0.1	121.2±31.0	2190.0±1661.2	473.2±130.3	594.7±172.0	51.67±8.57
Zone 2	5.5±0.1	86.7±1.0	1300.3±98.3	270.1±65.2	331.1±16.5	62.54±12.57*
Zone 3	5.9±0.2	118.6±11.2	777.0±665.4	320.3±90.1	332.8±43.1	34.72±4.74
Zone 4	5.8±0.1	109.4±8.9	772.5±570.0	258.4±49.9	233.0±46.8	51.27±14.62
Zone 5	6.1±0.1	82.3±23.6	267.8±1.1	134.7±40.1	116.0±12.0	57.26±15.72
Zone 6	7.2±1.0	369.4±293.9	2037.9±251.2	1020.7±690.4	419.1±153.1	21.53±4.73
Zone 7	6.9±0.3	245.9±47.4	1872.5±32.3	1195.39±325.1	1107.6±308.6	31.61±14.10
Zone 8	9.2±0.3*	1021.1±455.5*	3918.4±185.7*	1986.93±65.2*	2147.2±591.1*	35.95±12.71

*Significantly higher at *p*<0.05 level

After a high flood Na, K content and pH were highest (p<0.05) in vegetation zone 8. Ca and Mg content was significantly (*p*<0.05) highest in zone 7. P content was highest (p<0.05) in vegetation zone 1 (Table 8).

Table 8: Mean (±standard error) soil nutrient content after flood recession in seasonal floodplain zones.

Vegetation zone	**pH**	**Na (mg/Kg)**	**Ca (mg/Kg)**	**K (mg/Kg)**	**Mg (mg/Kg)**	**P (mg/Kg)**
Zone 1	5.6±0.8	67.2±6.7	191.5±99.1	107.1±33.3	51.03±23.0	98.83±73.75
Zone 2	5.3±0.5	80.5±10.0	824.0±339.1	130.4±60.7	128.3±48.0	102.64±17.69*
Zone 3	6.0±0.6	113.8±18.5	257.8±83.5	90.5±28.8	108.7±47.0	20.65±5.06
Zone 4	5.6±0.2	87.1±8.8	348.7±25.9	223.51±69.5	79.0±11.0	26.25±9.9
Zone 5	7.7±0.7	73.8±6.7	145.6±25.8	110.4±25.1	65.0±9.9	7.54±0.79
Zone 6	8.1±0.3	153.66±3.3	954.5±118.8	336.6±14.5	600.3±243.0	11.56±3.99
Zone 7	6.9±0.6	276.7±93.7	3227.0±260.0*	379.87±230.2	1100.5±637.0*	37.94±16.50
Zone 8	8.5±0.2*	752.5±71.1*	1386.5±380.3	586.1±131.9*	411.7±114.7	25.43±8.3

*Significantly higher at *p*<0.05 level

3.4.2 Comparison of soil nutrient status between vegetation zones under high and low flooding conditions.

Ca content was lower ($p<0.05$) in zones 1, 2, 3, 4 and 5 and higher in zone 7 ($p<0.05$) under high flood conditions than under low flood conditions (Figure 6). Other differences (zone 6) were not found to be significant at the $p<0.05$ level.

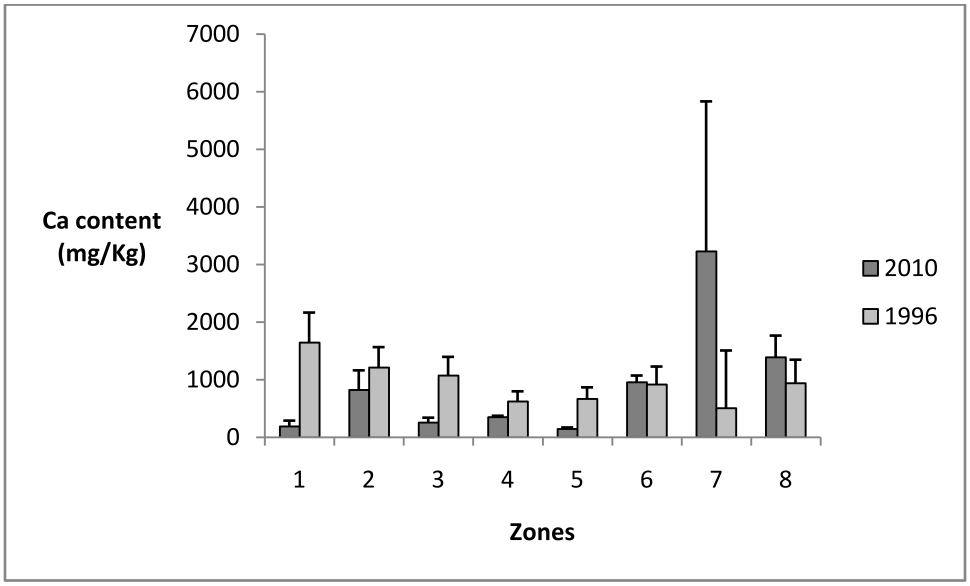

Figure 6: Mean Ca content after low and high floods. Notice the pronounced difference in Ca soil content in zone 7 between high and low flood conditions

Na content decreased ($p<0.05$) in vegetation zones 2 and 8 and increased ($p<0.05$) in zones 4, 5 and 6 (Figure 7).

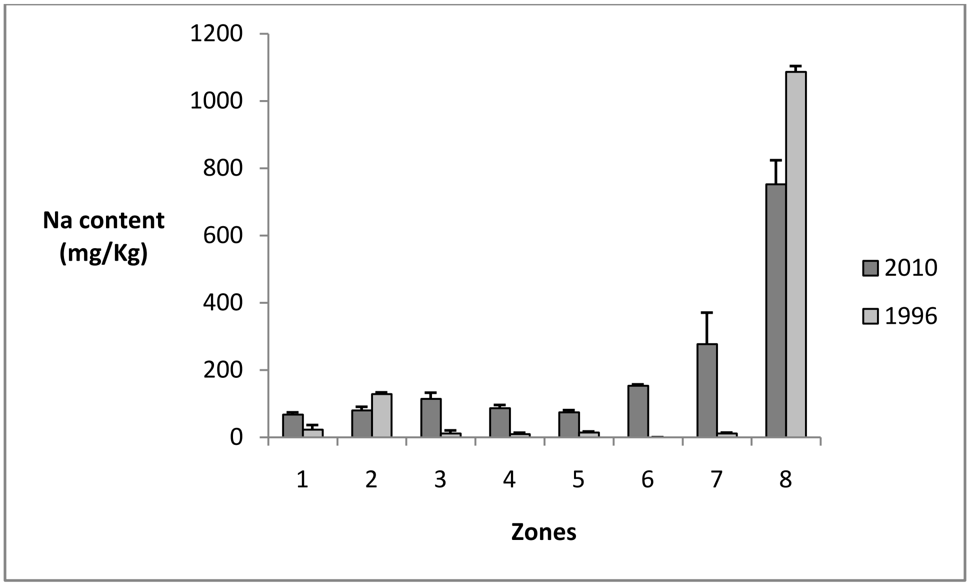

Figure 7: Mean Na content after low and high floods.

Mg content decreased (*p*<0.05) vegetation zones 1 and 5 and increased (*p*<0.05) in zones 6, 7, 8 (Figure 8).

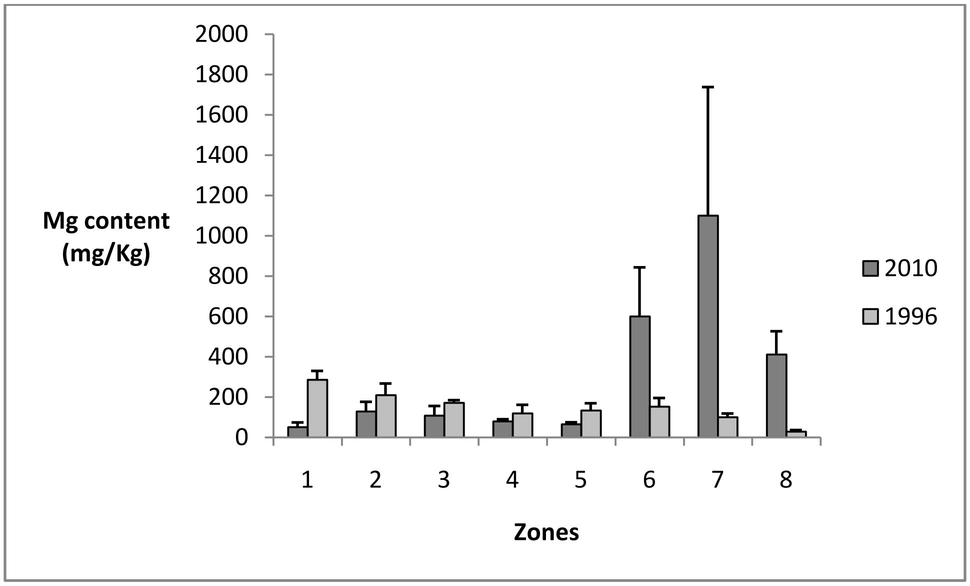

Figure 8: Mean Mg content after low and high floods. Notice the pronounced difference in Mg soil content in zones 6, 7 and 8 between low and high flood conditions

K content decreased in vegetation zones 1 and 3 and increased in zone 6, 7 and 8 (*p*<0.05) (Figure 9).

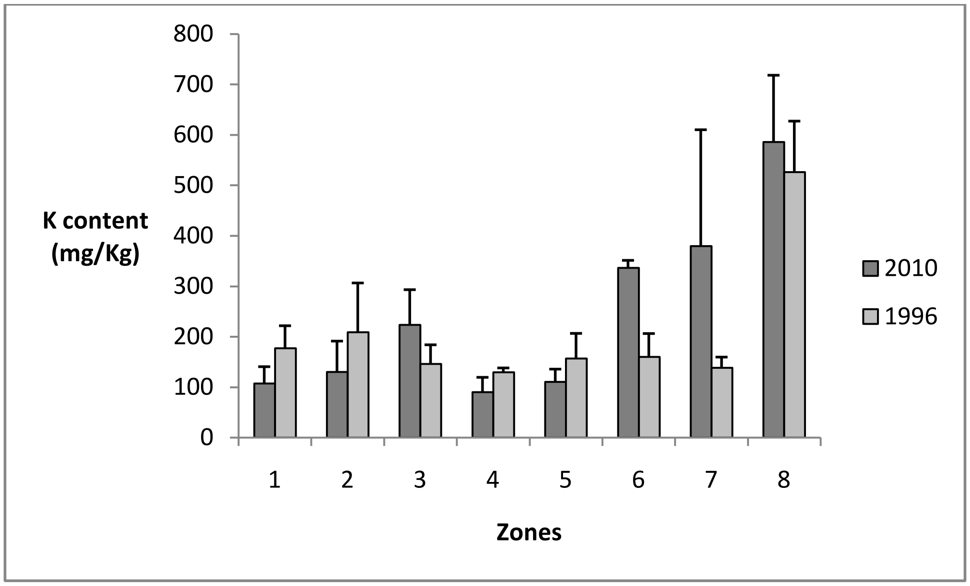

Figure 9: Mean K content after low and high floods. Notice pronounced difference in K content in zones 6 and 7 between low and high flood conditions

pH significantly decreased after a high flood in zone 1 increased in zone 6 (Figure 10).

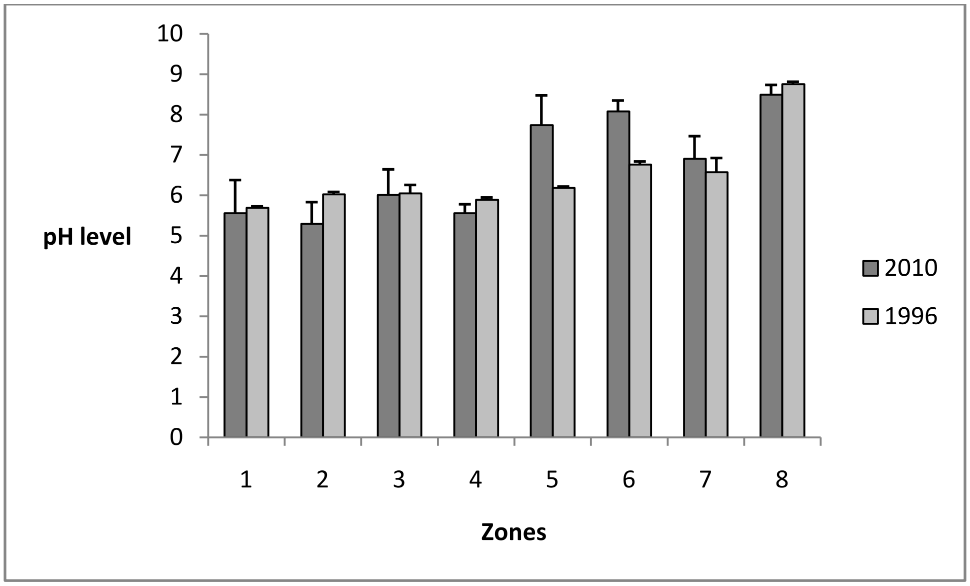

Figure 10: Mean pH after low and high floods.

P content was significantly ($p<0.05$) higher in all zones after high flood than after low flood (Figure 11).

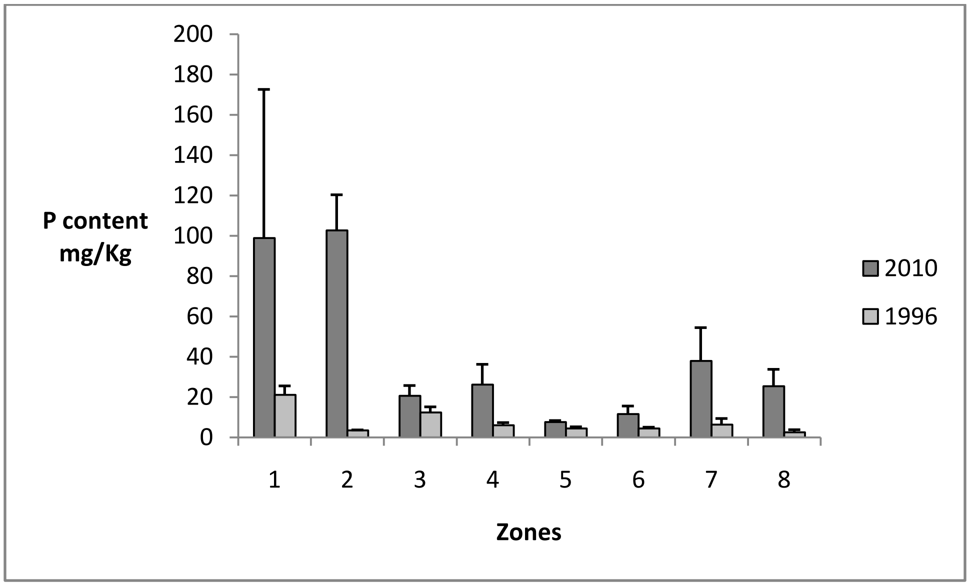

Figure 11: Mean P content after low and high floods. Note high P content in zones 1 and 2.

3.4.4. Correlation between flooding depth, duration of flooding and soil nutrient content (Na, Ca, K, Mg, and P) and pH level

In 2010, Na, Ca, K, Mg content and pH level were negatively correlated with flooding depth and duration. P content was positively correlated to flooding depth and duration (Table 9).

Table 9: Correlation between flooding depth, duration of flooding and soil nutrient content and pH level.

Soil nutrient	Flooding depth	Flooding duration
Na	-0.43*	-0.49*
Ca	-0.47*	-0.54*
K	-0.40*	-0.40*
Mg	-0.59*	-0.70*
P	0.60*	0.52*
pH	-0.50*	-0.48*

Correlation is significant at $p = 0.01$ level

3.5 Discussion

Soil nutrient content varied between high and low flood. With the exception of Phosphorous (P) soil nutrient content generally increased with decreasing flooding depth and duration during both low and high flooding conditions. Potassium (K), Calcium (Ca), Magnesium (Mg) and Sodium (Na) content was lower in zones 1, 2 and 3 and increased in zones 6, 7 and 8 in response to a high flood. These results are consistent with previous studies findings. High potassium (K) content in zones experiencing low flooding depth and short flooding duration was also observed in the seasonal floodplains of the Orinoco river (Dezzeo et al., 2000) and in the Rhine and Narow rivers seasonal floodplains (Antheunisse and Verhoeven, 2008). In a study conducted in the Careiro Islands in the central Amazon Na content was higher in dry zones than in flooded zones (Alfaia and Falcao, 1993). The findings of this study also agree with the results from a study conducted in a Mongolian lake in which Ca content decreased with an increase in moisture content (Strauss and Schickhoff, 2007). Humphries (2008) also observed that Ca content increased with decreasing moisture content in a study conducted on the Lower Mkuze seasonal floodplain in South Africa.

Low Ca, Mg, K and Na content in vegetation zones 1, 2, 3, 4 and 5 after a high flooding could be due to leaching and dilution (De Datta, 1981; Day, Jr, 1982; Yavitt et al., 1993; Mengel et al., 2001, Jobbagy et al., 2000; Conklin, 2005; Brady and Weil, 2008). Flooding increases the solubility of mineral nutrients (Ca, Mg and K) and Na (Kozlowski, 1997) and their mobilization (Mitsch and Gosselink, 2000) due to attendant changes in redoximorphic status. It could be expected that during a high flood more soil nutrients dissolve in water and lost through leaching as water infiltrates the soil. Zones 1, 2, 3, 4 and 5 experienced high flooding depth and long flooding duration which would suggest that they had more soil nutrients dissolving in the water and lost through leaching. Another factor that could lead to reduced soil nutrients during high flood is the rate of decomposition of organic matter. During flooding water displaces oxygen from the soil (Lobo and Joly, 1998; Hefting et al., 2004) leading to anaerobic conditions (Kozlowski, 1984; Moorhead and McAuthur, 1996; Kozlowski, 1997). Under anaerobic conditions the rate of decomposition of organic matter declines resulting in low soil nutrient content (Gallardo, 2003). In this study it is likely that zones 1, 2, 3, 4 and 5 experienced anaerobic conditions due to their relatively high flooding depth and long flooding duration, resulting in low organic matter decomposition rate, and hence low soil nutrient content. In contrast K, Mg, Na and pH increased in vegetation zones 6, 7 and 8 under high flood conditions.

The observed increase in K, Mg, Na and pH after high floods in zones 6, 7 and 8 could be attributed to increased organic matter decomposition rates, evapotranspiration and lateral flow deposition. Sediment deposition in floodplains leads to an increase in soil nutrients (Moorhead and McArthur, 1996). Water and sediments from the main river channel are a source of dissolved nutrients to the floodplains (Junk et al., 1989; Junk, 1997). During high flood vegetation zones 1, 2, 3 and 4 were almost converted into permanent swamps and as a result the soil nutrients could be transported away from them into the peripheral zones 6, 7 and 8 through lateral flow (Junk, 1997). Increased soil nutrients in zones 6, 7 and 8 could also be attributed to organic matter accumulation and decomposition. During low floods they were not inundated (Bonyongo, 1999; Bonyongo and Mubyana, 2004) and as a result organic matter may be accumulated (Junk, 1997). When they received the water during high floods organic matter decomposition may be triggered and nutrients released (Gabe, 2009). Furthermore, when it dries organic matter mineralises into soil nutrients such as Ca increasing the soil content of these cations (Kalisz and Łachacz, 2009). P content was higher after high flood than after low flood in all vegetation zones. P has a strong affinity to fine clay particles and it could be expected that during high floods more sediment is deposited and consequently leading to high P content (Mitsch and Gosselink, 2000; Gallardo, 2003; Harry et al., 2006). High flood is expected to lead to anoxic conditions due to increased water depth and prolonged waterlogging leading to mobilization of P resulting in its increase (Mitsch and Gosselink, 2000; Gallardo, 2003). Under aerobic conditions P binds to iron oxides. Due to prolonged anaerobic conditions imposed by flooding iron (Fe) bound to P is reduced from Fe (III) to Fe (II), releasing P from iron-phosphate complex (Mitsch and Gosselink, 2000; Gallardo, 2003; Brady and Weil, 2008).

Anaerobic conditions were likely to be more pronounced in zones experiencing relatively high flooding depth and prolonged flooding duration (Zones 1 up to 5) during a high flood hence the observed higher P content in these zones than zones 6, 7 and 8. In both flooding regimes the soil samples were collected during the rainy season, during floods and after floods. During low floods zones 6, 7, 8 were not flooded and it is expected that their soil was dry during all the sampling duration while during high floods they (zones 6, 7 and 8) were submerged under water for the whole sampling duration. It is expected that during low flooding conditions P reacts with Ca, Al, Fe oxyhydroxides due to aerobic conditions consequently reducing its content in the soil. During low flooding conditions there was dense vegetation population in all zones (Bonyongo, 1999) and as a result they might have utilized high P content (Mubyana et al., 2003). Conversely, there was low species richness during high flood which might have contributed to low P content utilization by plants and hence its high concentration in the soil.

Summary

- Mg, Ca, Na and pH level did not differ significantly between flooding seasons.
- P and K content significantly differed between flooding seasons.
- There was significant difference in soil nutrient status between primary and tertiary floodplains and between secondary and tertiary floodplains.
- Soil nutrient content decreased with increasing flooding depth and duration except P during a high flood. P content was high in zones experiencing high flooding depth and prolonged flooding duration.

The next chapter will establish a key environmental variable determining seasonal floodplain vegetation community composition and distribution in the Okavango Delta.

Chapter 4: Factors influencing seasonal floodplain vegetation community composition and distribution during a high flood in the Okavango Delta.

4.0 Introduction

Seasonal floodplain vegetation communities are dynamic and heterogeneous (Benstead et al., 1997; Toogood et al., 2007). Significant environmental variable determining vegetation community composition and distribution is seasonal flooding variation influenced by topography (Oliveria-Filho et al., 1993, Toogood et al., 2008; Merritt et al., 2009). For instance, floodplains found on lowly elevated areas usually have higher water levels and long flooding duration than floodplains found on highly elevated areas (Growing et al., 1998). Consequently floodplains found on lowly elevated areas are often dominated by flood tolerant species such as *Hydrilla verticillata* (L.F) Royle which grows well when fully submerged and *Typha angustifolia* L which grows in water depths exceeding 1m (Cronk and Fennessy, 2000). Highly-elevated floodplains are dominated by flood intolerant species such as *Vetiveria nigritana*, *Sporobolus spicatus* and *Imperata cylindrica* (Bonyongo, 1999; Bonyongo et al., 2000).

The influence of flooding on plants is reflected in seasonal floodplain vegetation community composition and distribution (Oliveria-Filho, 1993). Each plant species is morphologically and physiologically adapted to a more or less specific range of flooding depth and duration conditions (Cronk and Fennessy, 2000; Edwards and Kollman, 2002; Merritt et al., 2009). Morphological adaptations to flooding such as growth of hypertrophied lenticels, aerenchyma tissue and adventitious roots enhance oxygen transport in plants, enabling them to survive flooding conditions (Kozlowski, 1984; Kozlowski, 1997). Physiological adaptations to flooding include germination inhibition, glycolysis and ethylene production (Naiman and Decamps, 1997).

Seasonal floodplain vegetation community composition and distribution along environmental gradients has been observed in several seasonal floodplain systems, including some in the Okavango Delta (Biggs, 1976; Smith, 1976; Ellery et al., 1993; Bonyongo, 1999; Ellery and Tacheba, 2003). In the Okavango Delta previous studies attributed vegetation zonation in seasonal floodplains to differences in flooding depth and duration (Bonyongo, 1999), distance from the water source, ground water electrical conductivity, pH, soil chemistry (Ellery et al., 1993), timing of inundation, soil salinity, nutrient and sediment supply (Ellery and Tacheba, 2003). These studies were all conducted during low flood. However, since 2005 there has been an annual increase in the Okavango Delta’s inflow (ORI, 2011). As a result the studies conducted during low flood do not provide information on significant environmental factors determining seasonal floodplain vegetation community composition and distribution during a high flood. Therefore, environmental factors influencing seasonal floodplain vegetation communities’ distribution during a high flood in the Okavango Delta are still unknown. This study aimed to investigate environmental factors determining seasonal floodplain vegetation community composition and distribution during a high flood in the Okavango Delta. We hypothesized that flooding duration and depth are significant in determining seasonal floodplain vegetation community composition and distribution in the Okavango Delta during a high flood.

4.1 Objective

1. To determine key environmental variables influencing seasonal floodplain vegetation community composition and distribution

4.2 Materials and methods

4.2.1 Study site

The study was conducted in the Nxaraga Lagoon seasonal floodplains (See chapter 2 for a detailed description).

4.2.2 Hydroperiod & Vegetation sampling

Flooding depth was measured using a calibrated 2m PVC pipe in early February 2010 (middle of rainy season), mid May 2010 (flood propagation) and end of September 2010 (flood recession).It was measured in forty 25m^2 permanent plots per flooding season (middle of rainy season, flood propagation and flood recession) where vegetation and soil were sampled. Flooding duration was recorded as the number of weeks in which the permanent plots remained inundated. See a detailed description of vegetation communities sampling in chapter 2.

4.2.3 Soil pH, extractable P, K, Mg, Ca, and Na

The soil was sampled in the middle of the rainy season, before floods, after floods and analysed for pH, extractable P, K, Mg, Ca and Na at the University of Botswana-Okavango Research

Institute Laboratory. They were collected from the same 25m^2 plots where plant species were sampled. Soil sampling and analysis procedure is outlined in chapter 3.

4.3. Data analysis

The relationship between environmental variables and seasonal floodplain vegetation community composition and distribution was sought using Non-metric multi-dimensional scaling (NMS) (Kruskal, 1964 and Mather, 1976) in PC-ORD version 5.10 (McCune and Mefford, 2006). NMS was used to relate soil nutrients, flooding depth and duration to vegetation community composition and distribution. The following parameters were used in the NMS: Sorensen distance measure, random starting configuration, 50 runs with real data, 3 dimensions and 100 iterations. Monte Carlo test was performed with 20 runs. Number of iterations was 70 in the final solution. NMS does not require assumptions about the underlying distribution of vegetation communities. It does not assume linear relationships between environmental variables (McCune and Grace, 2000) hence it was suitable for analysing the relationship between seasonal floodplain vegetation communities and environmental variables in the Okavango Delta. The Kruskal-Wallis test was used to compare means of flooding duration and depth between a low and high flood.

4.4 Results

Flooding depth was significantly (*p*<0.05) higher in all vegetation zones during high flood than during low flood (Table 10).

Table 10: Flooding depth (FDp) during low (1997) and high (2010) flood.

Zone	FDp (m) (1997)	FDp (m) (2010)
1	0.5	1.62*
2	0.78	1.18*
3	0.48	0.72*
4	0.35	0.83*
5	0.15	0.6*
6	0	0.5*
7	0	0.32*
8	0	0.12*

**Significant difference at* $p<0.05$

Flooding duration was significantly (*p*<0.05) higher during high flood in all vegetation zones than during low flood (Table 11).

Table 11: Flooding duration (FD) during low (1997) and high (2010) flood.

Zone	FD (weeks) (1997)	FD (weeks) (2010)
1	23	P*
2	16	P*
3	12	P*
4	9	P*
5	5	P*
6	0	12*
7	0	6*
8	0	3*

P denotes permanently flooded. **Significant difference at* $p<0.05$

4.4.1 Factors determining floodplain vegetation composition and distribution

NMS ordination showed that flooding duration, Na content, flooding depth and pH were environmental variables influencing vegetation community composition and distribution in the Okavango Delta (Figure 12). Four environmental variables (flooding duration, depth of flooding, Na and pH) explained most of the variance in vegetation communities during high flood. There is strong correlation between the environmental variables and vegetation community composition and distribution. Dimensions (axes) 1 and 2 contributed a large proportion of variation in the seasonal floodplain vegetation communities. There was a strong positive correlation between axis 1 and plant species distribution in Nxaraga lagoon seasonal floodplains. Axis 2 showed a weaker positive correlation with plant species distribution in Nxaraga lagoon seasonal floodplains. Axes 1 and 2 correlation with plant species was 0.203 and 0.069

respectively.

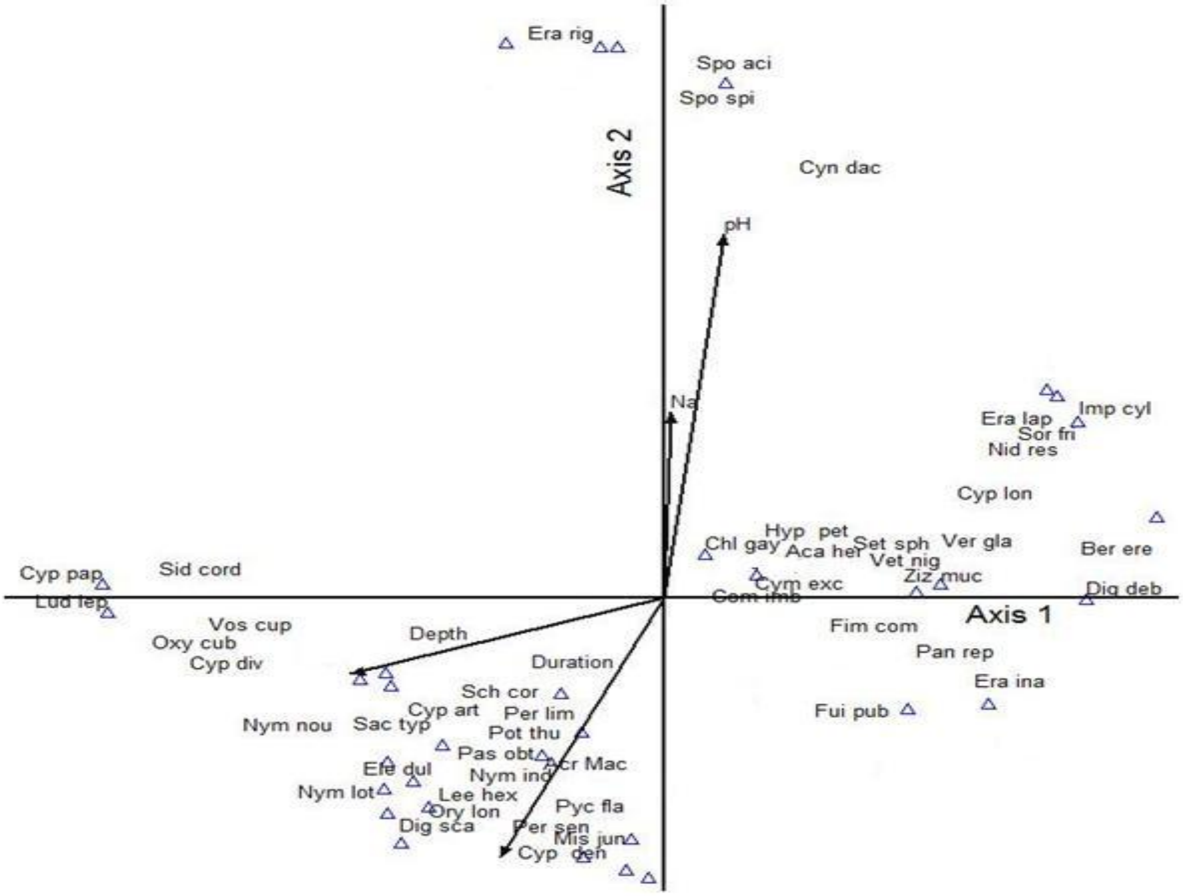

Figure 12: NMS biplot of plant species in seasonal floodplains at Nxaraga. *Plant species names are given in full in Appendix 14. Environmental variables are indicated by arrows, with the length representing the relative strength of the relationship. The longer the arrow, the stronger the relationship and vice-versa. Notice the longer arrows of flooding duration and pH.*

Na and pH are closely oriented with axis 2. Other environmental variables included in the ordination were K, P, Mg and Ca. However, these variables explained less variation in vegetation communities' composition and distribution during high flooding conditions. During a high flood of 2010, plant species such as *Eleocharis dulcis*, *Vossia cupsidata*, *Oryza longistaminata*, *Cyperus articulatus*, *Miscanthus junceus*, *Ludwigia leptocarpa* (Nutt) H. Hara and *Oxycaryum cubense* preferred long flooding duration and high flooding depth while *Panicum repens*, *Cynodon dactylon*, *Digitaria debilis* (Desf) Willd and *Sida cordifolia* L preferred areas which were flooded for a short period and had low flooding duration. Areas with high Na content and pH were preferred by *Sporobolus spicatus*, *Sporobolus acinifolius*, *Eragrostis rigida* A. Camus, *Cynodon dactylon* and *Eragrostis lappula* Nees, while *Imperata cylindrica*, *Vetiveria nigritana*, *Setaria sphacelata* and *Vernonia glabra* (Steez) Vatke preferred areas with relatively low Na content and pH level (Figure 12).

4.5 Discussion

Flooding duration, flooding depth, Na content and pH level were environmental factors influencing vegetation community composition and distribution during a high flood in the Okavango Delta seasonal floodplains. Seasonal floodplain vegetation community composition and distribution is determined by individual plant species' relative tolerance of flooding duration and depth (Kozlowski, 1984; Bonyongo, 1999; Bonyongo et al., 2000; Ellery and Tacheba, 2003). Plant species found in zones 1, 2, 3, 4 and 5 such as *Vossia cupsidata*, *Leersia hexandra* and *Cyperus articulatus* are tolerant of prolonged flooding duration and high flooding depth. *Imperata cylindrica*, *Vetiveria nigritana* and *Sporobolus spicatus* found in zones 6, 7 and 8 respectively are intolerant to prolonged flooding duration and high flooding depth during high flood. This is consistent with Bonyongo (1999), who found that flood tolerant species occurred in zones experiencing prolonged flooding duration and high flooding depth whereas flood intolerant species inhabited zones experiencing short flooding duration and shallow flooding depth.

Other studies in the Okavango Delta also concluded that flooding duration and depth significantly influence vegetation community composition and distribution (e.g. Biggs, 1976; Smith, 1976; Ellery et al., 1993; Bonyongo et al., 2000; Ellery and Tacheba, 2003; Murray-Hudson, 2009). However, it should be noted that depth and duration of inundation are less closely oriented with axis 1, particularly duration of inundation which is far from axis 1. Seasonal floodplain vegetation communities' composition and distribution are influenced by hydrological conditions occurring across much longer time scales than the observed period in this study. As a result seasonal floodplain vegetation communities' composition and distribution patterns do not come out clearly when described in terms of hydrological conditions observed within a short period of time.

The findings of this study also agree with results from studies conducted elsewhere (e.g. Rees, 1978; Gregory et al., 1991; Junk, 1997; Zeilhofer and Schessl, 1999). In a study in the Pantanal seasonal floodplains Zeilhofer and Schessl (1999) found that seasonal floodplain vegetation community composition and distribution was governed by flooding depth and duration gradient. A short grassland vegetation community dominated by flood tolerant *Vochysia divergens* Pohl was found in longer and deep flooded sites whereas a medium tall grassland vegetation community occurred in areas experiencing short flooding duration and shallow flooding depth. This agrees with observations made in this study in which flood tolerant *Oryza longistaminata*, *Sacciolepis typhura* and *Leersia hexandra* inhabited areas experiencing prolonged flooding duration and deep flooding depth. Vegetation zonation along flooding depth and duration gradients was also observed in the Amazon seasonal floodplains (Gregory et al., 1991; Junk, 1997; De Simone et al., 2003). The findings of Rees (1978) in the Kafue seasonal floodplains also agree with the observation made in this study. Vegetation communities were spatially distributed according to their tolerance to a given flooding duration and depth gradient (Rees, 1978). In the primary floodplains the vegetation community was dominated by *Vossia cupsidata* and *Echinochloa stagnina* (Retz.) P. Beauv.

Ordination results also showed that Na and pH levels in the soil influenced the seasonal floodplain vegetation community composition and distribution in the Okavango Delta. Na content is influenced by the flood. *Sporobolus spicatus*, *Cynodon dactylon*, *Sporobolus acinifolius* and *Eragrostis lappula* Nees were found in areas having high Na and pH levels. These species are salt tolerant and confined to saline habitats because they cannot compete with other plant species in less saline habitats (Cronk and Fennessy, 2000). They are able to withstand saline habitats through morphological adaptations such as the development of bicellular glands in *Sporobolus spicatus* excreting Na and Cl ions (Ramadan, 2001).

While ordination results showed that flooding duration, Na content, flooding depth and pH are environmental factors which are strongly correlated with seasonal floodplain vegetation community composition and distribution; it is important to note that there could be some confounding factors. Bonyongo (1999) found that *Ludwigia stolonifera*, *Alternanthera sessilis*, *Paspalidium obtusifolium*, *Acroceras macrum* and *Panicum repens* were amongst the most heavily grazed plant species in the Nxaraga Lagoon seasonal floodplains. Seasonal veldt fires have also been cited as one of the factors influencing floodplain vegetation community composition and distribution in the Delta (Ellery et al., 2003).

Summary

- Flooding depth and duration, Na and pH influenced vegetation community composition and distribution in the Okavango Delta.

- Axes 1 and 2 explained most of the variation in seasonal floodplain vegetation communities.
- Plant species distribution was probably influenced by their tolerance to flooding duration, depth and Na.

The synthesis of the whole study is provided in chapter 5.

Chapter 5:

5.0 Synthesis

The aim of this study was to determine the influence of flooding variation on seasonal floodplain vegetation communities in the Okavango Delta. The study generated vital information on the following:

- The influence of flood variation on seasonal floodplain vegetation community composition and distribution
- The influence of flood variation on seasonal floodplain soil nutrient status
- The environmental variables influencing seasonal floodplain vegetation community composition and distribution during a high flood.

In Chapter 1, background information on the relationship between vegetation zonation and flood pulse in different wetland ecosystems was presented and discussed. It was hypothesized that seasonal floodplain vegetation community composition and distribution will change in response to variation in flooding. This hypothesis was supported by the results in Chapter 2 which indicated that flooding variation influences seasonal floodplain vegetation community characteristics in the Okavango Delta. Seasonal floodplain vegetation communities showed a spatial shift in their distribution while zones showed a change in plant species composition in response to a high flood. For instance, *Vossia cuspidata* and *Oxycaryum cubense* replaced *Alternanthera sessilis* and *Ludwigia stolonifera* as co-dominant plant species in zone 1. In zone 3 the co-dominant species changed from *Miscanthus junceus* and *Digitaria scalarum* to *Miscanthus junceus* and *Pycreus flavescens*. *Eleocharis dulcis* and *Leersia hexandra* replaced

Paspalidium obtusifolium and *Panicum repens* as co-dominant species in zone 4. In zone 5, co-dominant species during a high flood changed from *Setaria sphacelata* and *Eragrostis inamoena* to *Eragrostis inamoena* and *Panicum repens*. Plant species composition of vegetation communities in zones 1, 2, 3, 4, 5 and 6 were dominated by seasonal floodplain grasses such as *Paspalidium obtusifolium, Panicum repens* to aquatic sedges such as *Oryza longistaminata*, *Eleocharis dulcis*, *Cyperus articulatus* and *Schoenoplectus corymbosus*. Vegetation community composition and distribution changes were dependent on individual plant species adaptation to flooding conditions. Plant species tolerate flooding through development of aeranchyma tissues, hypertrophied lenticels and adventitious roots which facilitate oxygen transportation (Kozlowski, 1984; Naiman and Decamps, 1997). Flood tolerant plant species such as *Cyperus articulatus* and *Schoenoplectus corymbosus* occupied lowly-elevated zones experiencing high flooding depth and prolonged flooding duration.

There was a general decline in plant species richness in the zones. Low plant species richness could be due to low soil nutrient content and plant species intolerance to prolonged flooding duration and high flooding depth (Ellery and Tacheba, 2003). It was observed that there was a general decline in soil nutrient content in zones experiencing prolonged flooding duration and high flooding depth (Chapter 3). In flood intolerant plant species soil nutrient absorption is low due to root decay (Kozlowski, 1984). A study by Villar et al., (1996) in the Lower Paraná River seasonal floodplains showed that P and N content decreased in plant tissue due to flooding. Prolonged flooding duration could lead to production of toxins in the form of reduced S, Fe, ethanol and Mn which are harmful to plant species (Cronk and Fennessy, 2001). Toxins released under flooding conditions destruct plant cell membrane through lipid dissolution in flood intolerant plants (Kozlowski, 1984) which could be the reason for a decline in plant species richness in the Okavango Delta seasonal floodplains.

Plant species diversity increased in all vegetation zones except for zone 8 found in the elevated and drier floodplains. An increase in plant species diversity could be attributed to disturbance. Disturbance can be defined as an occurrence that disrupts ecological communities by changing resources availability or the physical environment (White and Pickett, 1985). Prolonged flooding duration and high flooding depth could act as a disturbance to flood intolerant plant species. The flood intolerant plant species will be eliminated from the seasonal floodplains they inhabited prior to high floods. As a result there will be space created for colonization by new species at an early succession stage (Capon, 2005). At an early succession stage, opportunistic and competitive species can co-exist due to niche partitioning leading to an increase in species diversity (Huston, 1979). Vegetation communities are probably at a transitional stage during the early succession stage and it is expected that species diversity would decrease at flood peak and recession. This is because some plant species would not be adapted to flooding conditions at flood peak and recession and consequently will be eliminated.

Mean plant species percentage cover changes are likely to have been an indication of differences in different plant species tolerance to flooding. During a high flood of 2010, mean plant species percentage cover declined in flood intolerant plant species whereas it increased in flood tolerant plant species in zones experiencing high flooding depth and prolonged flooding duration. Mean plant species percentage cover also increased in some plant species such as *Setaria sphacelata*, *Sporobolus spicatus* and *Imperata cylindrica,* which increased in the tertiary floodplains experiencing shallow flooding depth and short flooding duration. Increase in mean percentage cover in tertiary floodplains could be an indication of plant species adaptation to short flooding duration and shallow flooding depth. The findings in Chapter 2 are consistent with the results from studies elsewhere (e.g. Rees, 1978; Hughes, 1990; Ferreira, 1997; Ferreira, 1998; Kingsford, 2000; Lite et al., 2005; Capon, 2005) in which vegetation community composition and distribution changed in response to flooding variation. It is therefore possible to make predictions on vegetation community composition and distribution under a given flooding regime in the Okavango Delta. Flood tolerant species, mostly sedges and aquatic grasses, will be restricted to sites experiencing prolonged flooding duration and high flooding depth. Flood intolerant species will be found in rarely flooded floodplains.

Chapter 3 supported the hypothesis that seasonal floodplain soil nutrient content will decrease during a high flood. Soil nutrient (Ca, Mg and K and Na) content decreased except P which increased during a high flood. A decrease in soil nutrient content could be attributed to leaching, dilution, plant absorption and decrease in organic matter decomposition rate (Yavitt et al., 1993; Mengel et al., 2001 and Conklin, 2005). A decrease in organic matter decomposition rate is due to anoxic conditions resulting from prolonged flooding conditions (Day, Jr, 1982). Increase in P content could be attributed to anoxic conditions imposed by high flooding conditions which could lead to its release from P-Fe, P-Ca and P-Al compounds (Brady and Weil, 2008). Similar observations were reported by several authors (Terrill et al., 1991; Alfaia and Falcao, 1993; Strauss and Schickhoff, 2007; Antheunisse and Verhoeven, 2008; Humphries, 2008). Mitsch and Gosselink, (2000), Gallardo, (2003) and Harry et al., (2006) showed that P increases with increasing moisture content. Bonyongo and Mubyana, (2004) also found that P content increased with increase in soil moisture content in the Okavango Delta seasonal floodplains. The results from Chapter 3 suggest that high floods in the Okavango Delta might lead to low soil Ca, Mg, K, Na and pH levels while soil P content increases. This shows that it is vital for the Okavango Delta seasonal floodplain to experience alternating dry and wet conditions to balance the availability of soil nutrients essential for plant growth since this is not the case during a high flood.

Chapter 4 demonstrated that flooding duration, flooding depth, Na and pH are key environmental factors influencing seasonal floodplain vegetation community composition and distribution in the Okavango Delta. This compliments the findings in Chapter 2 in which vegetation communities showed a significant change in composition and distribution in response to prolonged flooding hydroperiod. Previous studies (Biggs, 1976; Smith, 1976; Gregory et al., 1991; Ellery et al., 1993; Junk, 1997; Bonyongo, 1999; Zeilhofer and Schessl, 1999; Ellery and Tacheba, 2003; Murray-Hudson, 2009) also reported that flooding duration and depth are the primary determinants of seasonal floodplain vegetation community composition and distribution. Plant species were distributed along flooding duration and depth gradient probably based on their tolerance. Flood tolerant species occupied lowly elevated zones experiencing prolonged flooding duration and high flooding depth. Vegetation community composition and distribution was also influenced by individual plant species tolerance to soil Na content. Plant species probably tolerant to high Na content were found in saline habitats.

5.1 Management implications and recommendations

5.1.1 Water abstraction and vegetation dynamics

This study demonstrated that flooding variation influences seasonal floodplain vegetation community composition and distribution in the Okavango Delta. There is currently minimal water abstraction from the Okavango Delta. However, with projected increase in human population in the Okavango Basin states (Angola, Namibia and Botswana); water abstraction could be inevitable in the future. Even though proposals for water abstraction from the Okavango Delta by Namibia (Diederichs and Ellery, 2000), Angola (Talukdar, 2003) and Botswana (Lebotse, 1999) governments have been abandoned, there is potential that they may be implemented in the future. This is so because there is still acute water shortage in Botswana, Namibia and Angola. Recently (July, 2011) the government of Namibia advertised the expression of interest for the Kavango link to the Eastern National Water Carrier project which intends to abstract water from the Okavango basin.

Depending on the amount abstracted, water abstraction particularly by Angola and Namibia will reduce the amount of water reaching the Okavango Delta downstream areas in Botswana (Diederichs and Ellery, 2000). Consequently the flood extent in terms of floodplain area covered will be reduced, flooding duration will be short and depth of flooding will be shallow. Wolski and Murray-Hudson, (2005), present two groups of scenarios resulting from the Okavango Delta water abstraction: Scenarios showing small effect on the seasonal floodplains inundated area and scenarios showing a reduction in seasonal floodplains and permanent swamps flooded area. An increase in dry land area resulting from a reduction in seasonal floodplain and permanent swamp area will result in the less productive woody vegetation encroachment (Murray-Hudson et al., 2006). Bush encroachment might alter the quality of habitat and grazing pastures provided to wildlife by floodplain vegetation. It is therefore, recommended that high volume water abstraction such as for agriculture and mining from the Okavango Delta which has the potential to upset its ecological functioning be prohibited.

5.2. Limitations of the study

Vegetation was sampled in the middle of the rainy season. As a result it does not provide information on vegetation community composition and distribution during and after the floods. Some plant species that were present during the sampling period of this study may be absent during and after the flood. Those that were absent during this study sampling period may be present during and after the floods. The soil samples were collected during the middle of the rainy season, before and after floods. This does not provide information on the soil nutrient status at the flood peak. The study findings may not be generalized to the whole Delta because it was localised to Nxaraga Lagoon seasonal floodplains. The study has not established how different seasonal floodplain plant species are adapted to colonizing and occupying areas which have suitable hydrological conditions. There was also inadequate consideration given to other potentially significant environmental variables influencing seasonal floodplain vegetation community composition and distribution in the Okavango Delta. The study only focused on flooding duration, depth of flooding and soil nutrients excluding other important hydrological factors such as soil moisture content and current flow velocity.

5.3. Future work

There are still numerous questions which this study did not address. The following questions should be addressed in future studies:

- What are the eco-physiological adaptations enabling plant species to survive high flood conditions in the Okavango Delta seasonal floodplains?
- What is the optimum flooding depth for dominant plant species in the Okavango Delta seasonal floodplains?
- How does flooding variation influence organic matter decomposition in the Okavango Delta seasonal floodplains?
- How does organic matter decomposition influence soil nutrient content in seasonal floodplains?
- What is the plant tissue nutrient content of dominant species during a high flood in the Okavango Delta seasonal floodplain vegetation communities?
- How does flow velocity influence seasonal floodplain vegetation community composition and distribution in the Okavango Delta?
- How do shorter periods of drawdown influence seed germination in the Okavango Delta?
- How do grazing and silt deposition influence seasonal floodplain vegetation community composition and distribution in the Okavango Delta?

Answers to the above questions will add to the current information generated in this study. This will improve the applicability of the current study findings on the Okavango Delta conservation and management practices.

5.4. Conclusion

Flooding duration and depth are key hydroperiod variables influencing seasonal floodplain vegetation community composition and distribution in the Okavango Delta. Plant species were distributed along a hydroperiod gradient to which they are adapted. Some plant species are tolerant to shorter hydroperiod. Conversely, other plant species are tolerant to longer hydroperiod. Plant species tolerant to prolonged flooding duration and high flooding depth were found in primary and secondary floodplains. Plant species tolerant to shallow flooding depth and short flooding duration were found in tertiary floodplains. Tolerance to flooding by plant species is achieved through morphological and physiological strategies. Mean percentage cover could be an indication of plant species tolerance to flooding. An increase in mean plant species percentage cover could be an indication that the plant tolerates flooding. A decrease in plant species mean percentage cover probably indicates intolerance to flooding. Declining species richness could also indicate that some plant species are intolerant to flooding. Probably flooding acts as a disturbance eliminating flood intolerant plant species hence a decrease in mean plant species richness.

Tolerance to salinity also influences seasonal floodplain vegetation community composition and distribution. Salt tolerant plant species were found in zones with high Na content and pH level. Salt tolerant species possess morphological and physiological adaptations which enable them to survive high Na content. Plant species that do not possess the necessary adaptation strategies are excluded from zones with high Na content. There could be confounding factors such as grazing and fire, influencing vegetation community composition and distribution in the Okavango Delta seasonal floodplains. Heinl et al (2007) found that there was a strong positive correlation between flooding frequency and fire frequency. Floodplains with higher flooding frequency (flooded about every second year) showed the highest fire frequency with a mean fire return interval of approximately 5 years. In wetter and drier areas the mean fire return interval ranged between 7 and 8 years. Bonyongo (1999) found that *Ludwigia stolonifera*, *Alternanthera sessilis*, *Paspalidium obtusifolium*, *Acroceras macrum* and *Panicum repens* were amongst the most heavily grazed plant species in the Nxaraga Lagoon seasonal floodplains. However, fire and grazing were not considered because they were not within the scope of the current study.

Flooding influences seasonal floodplain soil nutrient status. A decrease in soil nutrient status during flooding could be an indication that organic matter decomposition rate has reduced. Organic matter decomposition releases nutrients from plant tissues leading to their increase in the soil. Flooding could also influence soil nutrient status through leaching and dilution. It is therefore likely that soil nutrients were lost through leaching or were still locked in undecomposed organic matter hence a decline in their content in response to flooding. Plant absorption was probably one of the factors that could have led to low soil nutrient status. This suggests that some plant species are adapted to soil nutrient absorption during high flood. It can be argued that increase in mean percentage cover in some plant species was an indication of increased primary production. As a result more soil nutrients were probably absorbed to boost primary production.

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Appendices

Appendix 1: Plant species composition changes in zone 1

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Alternanthera sessilis (L.) R.Br. *Potamogeton thunbergii* Cham. & Schltdl. *Digitaria debilis* (Desf.) Willd. *Ludwigia stolonifera* (Guill. & Perr.) P.H.Raven *Polygonum meisnerianum* Cham. & Schltdl *Eleocharis dulcis* (Burm.f.) Trin. ex Hensch *Persicaria limbata* (Meisn.) H.Hara *Pentodon pentandrus* (K.Schum.) Vatke *Pycnostachys coerulea* Hook. *Brachiaria arrecta* (Hack. Ex T. Durand and Schinz) Stent *Brachiaria humidicola* (Rendle) Schweick. *Miscanthus junceus* (Stapf) Pilg. *Nidorella residifolia* DC. *Panicum repens* L. *Acroceras macrum* Stapf. *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss *Vernonia glabra* (Steez) Vatke *Gomphocarpus spp* R.Br.	*Oxycaryum cubense* (Poepp. & Kunth) Lye *Sida cordifolia* L. *Cyperus papyrus* L. *Persicaria spp* (L.) Mill. *Nymphoides indica* (L.) Kuntze *Persicaria senegalensis* (Meisn.) Sojak	*Cyperus dives* Delile *Vossia cupsidata* (Roxb.) Griff *Nymphaea nouchali* Burn.f. *Paspalidium obtusifolium* (Delile) N.D. Simpson *Eleocharis dulcis* (Burm.f.) Trin. Ex Hensch *Cyperus articulatus* L. *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal *Leersia hexandra* Sw *Ludwigia leptocarpa* (Nutt.) H. Hara

Appendix 2: Plant species composition changes in Zone 2

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Schizodium cornutum (L.) Schltr. *Alternanthera sessilis* (L.) R. Br. ex DC. *Ethulia conyzoides* L.f. *Persicaria limbata* (Meisn.) H.Hara *Paspalidium obtusifolium* (Delile) N.D. Simpson *Panicum repens* L. *Corchorus olitorius* L. *Hibiscus spp* L. *Imperata cylindrica* (L.) Raeusch. *Vernonia glabra* (Steez) Vatke *Kohautia spp* Cham.& Schltdl *Gomphocarpus spp* R.Br.	*Eleocharis dulcis* (Burm.f.) Trin. ex Hensch *Sacciolepis typhura* (Stapf) Stapf *Nymphaea lotus* L. *Fuirena pubescens* (Poir.) Kunth	*Cyperus articulatus* L. *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal *Leersia hexandra* Sw *Nymphaea nouchali* Burn.f. *Oryza longistaminata* A.Chev. & Roehr *Vossia cupsidata* (Roxb.) Griff. *Potamogetum thunbergii* Cham. & Schltdl. *Vossia cupsidata* (Roxb.) Griff

Appendix 3: Plant species composition changes in zone 3

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Alternanthera sessilis (L.) R.Br. *Ethulia conyzoides* L.f. *Digitaria debilis* (Desf.) Willd *Ludwigia stolonifera* (Guill. & Perr.) P.H.Raven *Polygonum meisnerianum* Cham. & Schltdl *Persicaria limbata* (Meisn.) H.Hara *Pentodon pentandrus* (K.Schum.) Vatke *Pycnostachys coerulea* Hook. *Brachiaria humidicola*(Rendle) Schweick *Nidorella residifolia* DC. *Brachiaria dura* Stapf *Cyperus dives* Delile *Eragrostis lappula* Nees *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. ex M.B. Moss *Eragrostis inamoena* K.Schum. *Chloris virgata* Sw. *Corchorus olitorius* L. *Pechuel-loeschea leubnitziae*(Kuntze) O.Hoffman *Setaria verticillata* (L.) Beauv *Kohautia spp* Cham. & Schltdl *Gomphocarpus spp* R.Br.	*Eleocharis dulcis* (Burm.f.) Trin. ex Hensch *Fuirena pubescens* (Poir.) Kunth *Cyperus denudatus* L.f. *Oryza longistaminata* A.Chev. & Roehr *Pycreus flavescens* (L.) P.Beauv. ex Rchb. *Oxycaryum cubense* (Poepp. & Kunth) Lye *Nymphoides indica* (L.) Kuntze *Potamogetum thunbergii* Cham. & Schltdl *Sacciolepis typhura*(Stapf) Stapf *Gomphocarpus fruticosus* (L.) Aiton f. *Cynodon spp* Rich. *Imperata cylindrica* (L.) Raeusch *Persicaria senegalensis* (Meisn.) Sojak	*Miscanthus junceus* (Stapf) Pilg. *Cyperus articulatus* L. *Acroceras macrum* Stapf *Leersia hexandra* Sw. *Vossia cupsidata* (Roxb.) Griff. *Cycnium tubulosum* (L.F.) Engl. *Panicum repens* L. *Paspalidium obtusifolium* (Delile) N.D. Simpson *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J. Raynal *Digitaria scalarum* (Schweinf.) Chiov. *Vernonia glabra* (Steez) Vatke

Appendix 4: Plant species composition changes in zone 4

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Schizodium cornutum (L.) Schltr *Digitaria debilis* (Desf.) Willd. *Brachiaria arrecta* (Hack. ex T. Durand & Schinz) Stent *Miscanthus junceus* (Stapf) Pilg. *Cycnium tubulosum* (L.f.) Engl. *Brachiaria dura* Stapf var. *Cyperus dives* Delile *Panicum repens* L. *Eragrostis lappula* Nees *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. ex M.B.Moss *Eragrostis cilianensis* (All.) Vignolo ex Janch *Eragrostis inamoena* K.Schum. *Urochloa trichopus* (Hochst.) Stapf *Chloris virgata* Sw. *Sida cordifolia* L. *Corchorus olitorius* L. Var *Pechuel-loeschea leubnitziae* (Kuntze) O.Hoffm. *Hibiscus spp* L. *Digitaria eylesii* C.E.Hubb. *Aristida stipoides* Lam *Acacia tortilis* (Forssk.) Hayne *Vetiveria nigritana* (Benth.) Stapf *Setaria verticillata* (L.) P.Beauv *Vernonia glabra* (Steetz) Vatke *Gomphocarpus spp* R.Br. *Gisekia spp* L. *Amaranthus thunbergii* Moq *Hermbstaedtia odorata* (Burch.) T.Cooke var.	*Eleocharis dulcis* (Burm.f.) Trin. ex Hensch *Sacciolepis typhura* (Stapf) Stapf *Nymphoides indica* (L.) Kuntze *Potamogetum thunbergii* Cham. & Schltdl *Persicaria limbata* (Meisn.) H.Hara *Eleocharis dulcis* (Burm.f.) Trin. ex Hensch	*Leersia hexandra* Sw *Cyperus articulatus* L. *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal *Oryza longistaminata* A.Chev. & Roehr. *Paspalidium obtusifolium* (Delile) N.D. Simpson *Nymphaea nouchali* Burm.f. *Acroceras macrum* Stapf

Appendix 5: Plant species composition changes in zone 5

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Brachiaria arrecta (Hack. Ex T. Durand & Schinz) Stent *Miscanthus junceus* (Stapf) Pilg. *Brachiaria dura* Stapf *Cyperus dives* Delile *Acroceras macrum* Stapf *Eragrostis lappula* Nees *Eragrostis cilianensis* (All.) Vign. ex Janchen *Urochloa tricopus* (Hochst.) Stapf *Chloris virgata* Sw. *Sida cordifolia* L. *Corchorus olitorius* L. Var *Pechuel-loeschea leubnitziae* (Kuntze) O.Hoffm. *Hibiscus spp* L. *Vetiveria nigritana* (Benth.) Stapf *Setaria verticillata* (L.) P.Beauv. *Imperata cylindrica* (L.) Raeusch. *Kohautia spp* Cham. & Schldtl. *Gomphocarpus spp* R.Br. *Gisekia spp* L. *Amaranthus thunbergii* Moq. *Hermabstaedita odorata* (Burch.) T.Cooke	*Oryza longistaminata* A.Chev. & Roehr. *Leersia hexandra* Sw *Nymphoides indica* (L.) Kuntze *Fuirena pubescens* (Poir.) Kunth *Eleocharis dulcis* (Burm.f.) Hensch. *Sacciolepis typhura*(Stapf) Stapf *Potamogetum thunbergii* Cham. & Schltdl *Fimbristylis complanata* (Retz.) Link *Cyperus longus* L. Var. longus *Digitaria debilis* (Desf.) Wild. *Niderolla resedifolia* DC. *Persicaria limbata* (Meisn.) H.Hara *Berula erecta* (Huds.) Coville	*Cyperus articulatus* L. *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal *Paspalidium obtusifolium* (Delile) N.D. Simpson *Panicum repens* L. *Eragrostis inamoena* K. Schum. *Vernonia glabra* (Steez) Vatke *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. ex M.B.Moss *Eragrostis lappula* Nees *Cycnium tubolusum* (L.f.) Engl.

Appendix 6: Plant species composition in zone 6

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Schoenoplectus corymbosus *Digitaria debilis* (Desf.) Wild *Leersia hexandra* SW *Brachiaria arrecta* (Hack. ex. T. Durand & Schinz) Stent *Miscanthus junceus* (Stapf) Pilg. *Cyperus dives* Delile *Panicum repens* L. *Eragrostis cilianensis* (All.) Vignolo ex Janch *Eragrostis inamoena* K.Schum. *Digitaria eylesii* C.E. Hubb *Vetiveria nigritana* (Benth.) Stapf *Kohautia spp* Cham. & Schldtl *Gomphocarpus spp* R.Br.	*Acacia erioloba* E. Mey. *Ziziphus mucronata* Willd *Cyperus longus* L. Var. longus *Sphaeranthus incisus* Robyns *Sorghastrum friessii* (Pilg.) Pilg *Fuirena pubescens* (Poir.) Kunth *Cycnium tubulosum* (L.f.) Engl. *Nidorella resedifolia* DC. *Acroceras macrum* Stapf *Eragrostis lappula* Nees *Combretum imberbe* Wawra	*Imperata cylindrica* (L) Raeusch *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. Ex M.B. Moss *Vernonia glabra* (Steez) Vatke *Cynodon dactylon* (L.) Pers.

Appendix 7: Plant species composition changes in zone 7

Species present under low flood conditions only (Eliminated spp)	**Species present under high flood conditions only (new spp)**	**Species present in both low and high flood conditions (Resistant spp)**
Digitaria debilis (Desf.) Wild. *Persicaria limbata* (Meisn.) H.Habara *Acroceras macrum* Stapf *Eragrostis cilianensis* (All.) Vignolo ex Janch. *Eragrostis inamoena* K.Schum. *Urochloa trichopus* (Hochst.) Stapf *Chloris virgata* Sw. *Pechuel- loeschea leubnitziae* (Kuntze) O.Hoffm. *Hibiscus spp* L. *Setaria verticillata* (L.) P.Beauv *Kohautia spp* Cham. & Schldtl. *Gomphocarpus spp* R.Br. *Cynodon dactylon* (L.) Pers. *Amaranthus thunbergii* Moq *Hermbstaedita odorata* (Burch.)	*Cyperus longus* L. Var. longus *Niderolla resedifolia* DC. *Fuirena pubescens* (Poir.) Kunth *Ziziphus mucronata* Willd *Cyperus articulatus* L. *Fimbristylis complanata* (Retz.) Link *Chloris gayana* Kunth *Combretum imberbe* Wawra *Acacia herbaclada* DC. *Hyphaene petersiana* Klotzsch ex Mart *Cymbopogon excavatus* (Hochst.) Stapf ex Burtt Davy *Oryza longistaminata* A.Chev. & Roehr. *Nymphoides indica* (L.) Kuntze	*Vetiveria nigritana* (Benth.) Stapf *Panicum repens* L. *Vernonia glabra*(Steetz) Vatke *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss *Sida cordifolia* L. *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal *Imperata cylindrica* (L.) Raeusch. *Leersia hexandra* Sw.

Appendix 8: Plant species composition changes in zone 8

Species present under low flood conditions only (Eliminated spp)	Species present under high flood conditions only (new spp)	Species present in both low and high flood conditions (Resistant spp)
Cyperus dives Delile	*Niderolla resedifolia* DC.	*Sporobolus spicatus* (Vahl) Kunth
Eragrostis cilianensis All. Vign. Ex Janchen	*Pechuel-loeschea leubnitziae* (Kuntze) O.Hoffman	*Cynodon dactylon* (L.) Pers.
Hibiscus spp L.	*Gisekia Africana* (Lour.) Kuntze	*Sporobolus acinifolius* Stapf
Aristida stipoides Lam	*Cyperus longus* L. Var. longus	
Acacia tortilis (Forssk.) Hayne	*Eragrostis lappula* Nees	
Gisekia spp L.	*Hyphaene petersiana* Klotzsch ex Mart.	
Amaranthus thunbergii Moq	*Eragrostis rigida* A. Camus	
Hermbstaedtia odorata (Burch.) T.Cooke var		

Appendix 9: Full plant species names for Figure 11

Abbreviation	Full name
Vet nig	*Vetiveria nigritana*
Pan rep	*Panicum repens*
Cyp lon	*Cyperus longus*
Ver gla	*Vernonia glabra*
Set sph	*Setaria sphacelata*
Sid cord	*Sida cordifolia*
Nid res	*Niderolla resedifolia*
Fui pub	*Fuirena pubescens*
Sch cor	*Schoenoplectus corymbosus*
Imp cyl	*Imperata cylindrica*
Ziz muc	*Ziziphus mucronata*
Cyp art	*Cyperus articulatus*
Fim com	*Fimbristylis complanata*
Cyn dac	*Cynodon dactylon*
Chl gay	*Chloris gayana*
Com imb	*Combretum imberbe*
Aca her	*Acacia hebeclada*
Hyp pet	*Hyphaene petersiana*
Cym exc	*Cymbopogon excavatus*
Ory lon	*Oryza longistaminata*
Lee hex	*Leersia hexandra*
Nym ind	*Nymphoides indica*
Oxy cub	*Oxycaryum cubense*
Cyp div	*Cyperus dives*
Vos cup	*Vossia cupsidata*
Nym nou	*Nymphaea nouchali*
Pas obt	*Paspalidium obtusifolium*
Cyp pap	*Cyperus papyrus*
Ele dul	*Eleocharis dulcis*

Per sen	*Persicaria senegalensis*
Lud lep	*Ludwigia stolonifera*
Aca eri	*Acacia erioloba*
Era rig	*Eragrostis rigida*
Sph inc	*Sphaeranthus friesii*
Sor fri	*Sorghastrum friesii*
Cyc tub	*Cycnium tubulosum*
Acr Mac	*Acroceras macrum*
Era lap	*Eragrostis lappula*
Sac typ	*Sacciolepis typhura*
Pot thu	*Potamogetum thunbergii*
Nym lot	*Nymphaea lotus*
Mis jun	*Miscanthus junceus*
Cyp den	*Cyperus denudatus*
Era ina	*Eragrostis inamoena*
Pyc fla	*Pycreus flavescens*
Dig sca	*Digitaria scalarum*
Gom fru	*Gomphocarpus fruticosus*
Dig deb	*Digitaria debilis*
Per lim	*Persicaria limbata*
Ber ere	*Berula erecta*
Spo spi	*Sporobolus spicatus*
Pec-loe	*Pechuel-loeschea leubnitziae*
Spo aci	*Sporobolus acinifolius*
Gis afr	*Gisekia africana*