Water Balance and Variations of Nutrients and Major Solutes along a River Transect Through the Okavango Delta, Botswana

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Abstract

Wetland goods and services provide a means of survival for many riparian rural communities in developing countries, particularly in the Sub-Saharan Africa. To sustain the provision of goods and services for human use, spatial and temporal variations in the quantity and quality of water in a given wetland should be adequately understood and managed. In this study we monitored the quantity and quality of surface water through the Okavango Delta for 2 years, from June 2008 to June 2010. Specifically we monitored precipitation over the Delta and surface inflow and outflow (via the Okavango and Thamalakane Rivers respectively) for water quantity, nutrients, cation and anion levels in the surface water along a river transect from Mohembo through the Delta to Lake Ngami. The study revealed that the water balance during the study period was similar to earlier reports. Most of the water inflow was via the Okavango River while surface outflow via the Boro River accounted for about 2% of total inflow. Calcium (Ca) and bicarbonate (HCO_3^-) were the most dominant cation and anion respectively across the river transect sampled except in Lake Ngami where sodium (Na) was the dominant cation. Total nitrogen (0.222 ± 0.018 to 0.698 ± 0.035 mg L^{-1}) and total phosphorus (0.042 ± 0.005 to 0.131 ± 0.024 mg L^{-1}) levels across the Delta were generally low. The N:P ratios suggest spatial and temporal P and N growth limitations in the Delta. N limitation seems to be ameliorated by biological nitrogen fixation. Since nutrient poor aquatic systems tend to be very sensitive to pollution, excessive P input into the Delta should be avoided to prevent eutrophication.

Keywords: Okavango Delta, tropical wetland, major ions, nutrient levels, nutrient limitation

Introduction

Wetlands have historically been regarded as waste lands. Consequently, many wetlands around the world have been extremely vulnerable to degradation or reclamation for agricultural and urban developments. The world has lost over 50% of its original wetlands over the past century (Barbier 1993). For instance, the United States of America and South Africa have respectively lost about 54% and 50% of their original wetlands during the last century. Wetlands perform many important functions which include water storage, water purification, modification of local climate, groundwater recharge, chemical attenuation and transformation and biological diversity (plants and animals) (Junk 2002). Due to high human population density and rampant poverty in many African countries, wetland goods and services provide a means of survival for many riparian rural communities (Schuyt 2005).

Hydrology is an integral component of wetland ecosystems. Water quantity and quality determine the capacity of wetlands to perform the various functions and services. While hydrological variations, such as in flood-pulsed systems, ensure wetland functioning, anthropogenically induced changes in these systems tend to be destructive of the wetland's functioning. For instance, high volume discharge of wastewater can increase wetland productivity which may affect other wetland functions such as main-

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tenance of biological diversity. It is therefore important to monitor water quantity and quality in natural wetland ecosystems vulnerable to human perturbations such as wastewater discharge.

In this study we monitored the quantity and quality of surface water through the Okavango Delta for two years from June 2008 to June 2010. Specifically we monitored precipitation over the Delta and surface inflow and outflow via the Okavango and Thamalakane Rivers respectively, for water quantity and nutrient, cation and anion levels in the surface water along a river transect from Mohembo through the Delta to Lake Ngami. Other physicochemical variables measured during the study have been reported in Gondwe and Masamba (2016). The objective of this study was to re-evaluate the water balance and water quality in the Okavango Delta in order to provide a baseline for a long term monitoring programme.

Materials and Methods

Study area

The freshwater Okavango Delta (19º 17' S, 22º 54' E) in northern Botswana is one of the world's largest inland deltas and is situated at the distal end of the Cubango-Okavango River Basin (CORB). The total catchment area of the CORB is 165,000 km², of which 82% is located in Angola drained by the Cubango and Cuito rivers which join near the Angola-Namibia border to form the Okavango River (Wilk *et al.* 2006). Much of the water that sustains the Delta comes through the Okavango River as runoff from the central Angolan highlands which experience about 1200 mm of rainfall per annum. Local precipitation over the Delta which falls between November and May is lower at approximately 490 mm/a (McCarthy *et al.* 2000). However, because of the large Delta area, the total volume of rainwater that annually falls over the Delta area is approximately 30-40% of the flood water brought in via the Okavango River (Snowy Mountains Engineering Corporation 1987, 1990). At the lower end of the Panhandle, the flood water spreads out into an alluvial fan (Delta) of swamps, channels and islands covering between 6,000 and 13,000 km² depending on prevailing floods and local precipitation (Gieske 1997). Currently the main distribution channel after the bifurcation of the Okavango River is the Jao-Boro channel which more or less bisects the Delta into western and eastern areas (Figure 1). The Jao-Boro channel passes through the urban village of Maun as the Thamalakane River and goes on to Lake Ngami. It has been estimated that the surface outflow in the Thamalakane River measured at Maun is only 2% of the total annual inflow via the Okavango River and precipitation over the Delta. This is because approximately 98% of the Delta's total inflow water is lost to the atmosphere through evapotranspiration estimated at 1500 mm y^{-1} (Wilson and Dincer 1976; Snowy Mountains Engineering Corporation 1987; Ramberg and Wolski 2008).

Study sites

Water quality parameters were monitored along the Okavango-Jao-Boro-Thamalakane River system at ten (10) sites which were: Mohembo, Drosky, Sepopa, Guma, Nxaraga, Boro, Maun, Tsanekona, Toteng and Lake Ngami (Figure 1). The justification for the selection of these sites was given in Gondwe and Masamba (2016), and was based on the belief that management and conservation of the Okavango Delta requires a clear understanding of the quantity and quality of the flood water as it flows the length of the Delta (from Mohembo to Lake Ngami). While water discharge into and out of the Delta is measured at Mohembo and Maun respectively, the quality of the water needs to be regularly monitored at several points across the Delta. Water quality as recorded at Mohembo portrays the baseline quality and reflects upstream activities and processes affecting the water before it enters the Delta. The Drosky and Sepopa study sites in the Panhandle area were chosen to capture changes in the water quality due

to human activities (e.g., livestock grazing) before the water spreads over the Okavango Delta proper which is represented by the Guma study site. Nxaraga study site in the seasonal swamp and Boro site at the southern edge of the Delta were chosen in order to determine the effect of the preceding wetland on the water quality. Wetlands are generally known to purify flow-through water. Further sites selected downstream included Maun, Tsanekona, Toteng and Lake Ngami were intended to capture any impacts of human activities in the river system.

Figure 1: Map of the Okavango Delta showing locations of water sampling sites (from Gondwe and Masamba, 2016).
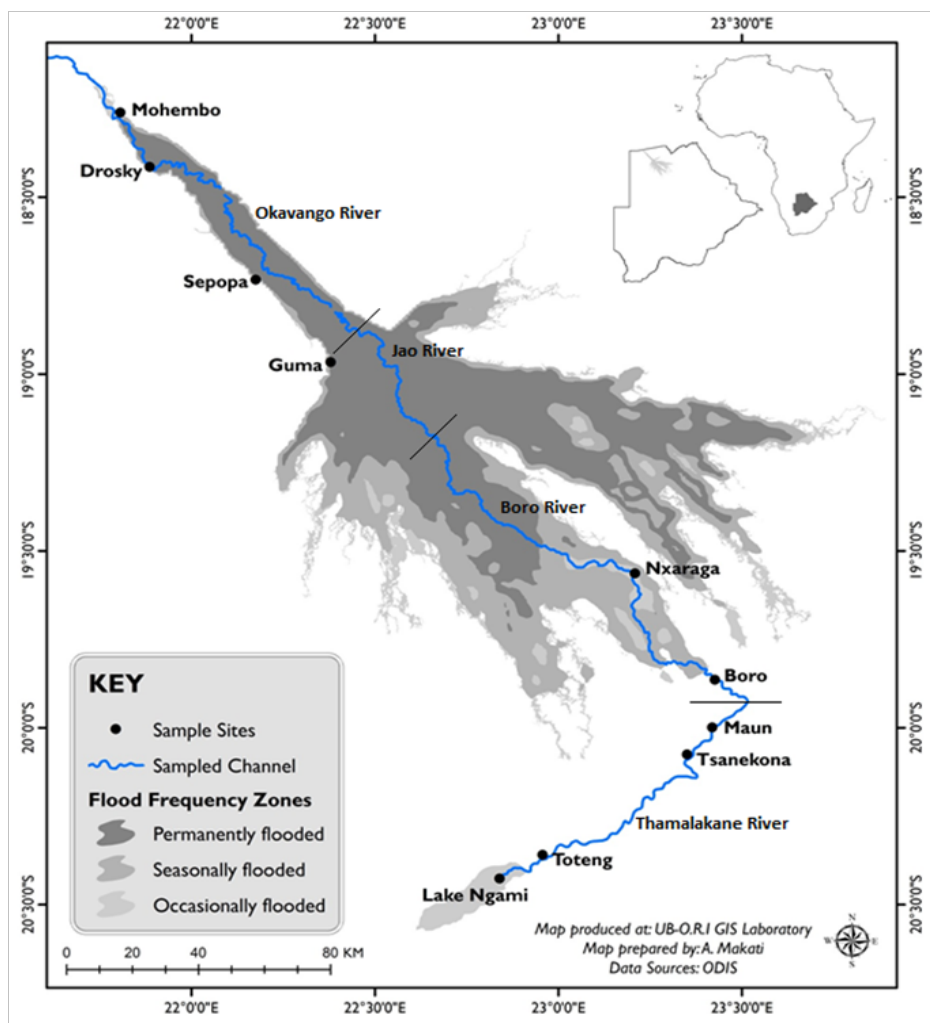
Sampling

Collection of water samples for this study was done collaboratively by field staff from the Okavango Research Institute (ORI), with Department of Water Affairs (DWA), Drosky's Cabins, Sepopa Water Works and Guma Lagoon Camp. All field workers attended a training workshop on data/sample collection and handling prior to the start of the sampling campaign in order to generate quality data. Field staff from the DWA, Drosky's Cabins, Sepopa Water Works and Guma Lagoon Camp collected samples from Mohembo, Drosky, Sepopa and Guma study sites respectively, while ORI field staff sampled Nxaraga, Boro, Maun, Tsanekona, Toteng and Lake Ngami.

Sampling was conducted almost fortnightly for two years between June 2008 and June 2010.

On site measurements of surface water temperature (^{o}C), electrical conductivity (EC, μS cm^{-1}), dissolved oxygen (DO, mg L^{-1}), pH and turbidity (NTU) were conducted at all the ten study sites. These measurements were reported in Gondwe and Masamba (2016). For this study water samples were collected from below the water surface at each site into acid-washed polyethylene bottles. The water samples were transported within 24 hours of collection to the environmental laboratory at ORI for further sample processing and storage until analysis. Water samples for cation and anion analyses were filtered through 0.45μm GF/F filters within 24 hours of collection into clean polyethylene bottles which were immediately stored at 4 ^{o}C until analysis. Filtered water samples for major cation analysis were acidified before storage to pH 2 with nitric acid for preservation.

Analysis of water samples
All chemical analyses of water samples were done at the environmental laboratory at the Okavango Research Institute. Water samples were analyzed using standard methods for major cations which included calcium (Ca), magnesium (Mg), sodium (Na), potassium (K) and iron (Fe); anions including carbonates (CO_3^{2-}), bicarbonates (HCO_3^-), chlorides (Cl^-), and sulphates (SO_4^{2-}); dissolved silica and plant nutrients as total nitrogen (TN) and total phosphorus (TP). Total dissolved metals were determined using a SpectrAA 220 atomic absorption spectrophotometer (Varian Australia Pty Ltd,Victoria, Australia) equipped with a Varian GTA-110 furnace, either using acetylene/air for Na, K, Fe, Mn or acetylene/nitrous oxide for Ca and Mg. Chlorides (Cl^-) and sulphates (SO_4^{2-}) were determined using a Dionex ICS-3000 DC ion chromatography (Dionex Corp., USA). Total alkalinity as carbonate and bicarbonate were determined by direct titration of water samples with standardised HCl to pH 4.5 using a Mettler Toledo DL50 Autotitrator equipped with a Rondolino autosampler (Mettler-Toledo Inc., USA). Dissolved silica was measured using the reduced molybdosilicate spectrophotometric method. TN and TP were analysed using the continuous-flow AutoAnalyzer 3 (Bran+Luebbe, Germany). Total dissolved ions (TDI, mg L^{-1}), which is a measure of water salinity, was estimated from EC by multiplying by a conversion factor of 0.64 (i.e., TDI = 0.64*EC). Since dissolved silicic acid (H_4SiO_4) remains largely undissociated (i.e., unionized) in natural waters except at pH>9 and therefore does not significantly contribute to EC, the silica concentration (mg L^{-1}) was added to the TDI concentration to estimate total dissolved solids (TDS) concentration in surface waters along the study transect across the Delta.

Table 1: Characteristics of the meteorological stations which provided precipitation data used in this study.

Station	Latitude	Longitude	Elevation (m)
Shakawe Meteorology Station	18° 22'	21° 50'	1030
Seronga Police Station	18° 49'	22° 24'	985
Gumare Agriculture Station	19° 22'	22° 10'	962
Maun International Airport	19° 59'	23° 25'	945

Precipitation and river discharge data

Precipitation data used in this paper were collected by rain gauges at Shakawe meteorological station, Seronga police station, Gumare agriculture station and Maun airport (Table 1). The areal mean precipitation over the Delta was determined using the arithmetic-mean method (equation 1) by dividing the sum of rain depths (mm) recorded at Shakawe, Seronga, Gumare and Maun by the number of stations (4 stations) (Chow *et al.* 2003)

$$P = \frac{P_1 + P_2 + P_3 + \ldots\ldots\ldots + P_n}{n} = \frac{1}{n}\sum_{1}^{n} P_i \qquad\qquad (1)$$

where P is average precipitation over the catchment area for a given period, and P_1, P_2, P_3, ..., P_n are the precipitations in a given time period at stations 1,2, 3,….., n respectively within the catchment (n = 4 in our study). Discharge ($m^3 \, s^{-1}$) data for the study period for Mohembo and Maun were obtained from the DWA, Botswana. For both data sets (precipitation and discharge), an annual cumulative input was calculated from October to September of the following year.

Data analysis
Graphical plots presented in this paper were prepared using Sigmaplot 12.0 software (Systat Software Inc, USA). Linear relationships were tested for significance at alpha level of 0.05 in SigmaPlot 12.0 software.

Figure 2: (a) Monthly precipitation over the Okavango Delta and (b) water inflow (solid line) at Mohembo (Okavango River) and outflow (dashed line) at Maun (Thamalakane River) from 2007 to 2010.
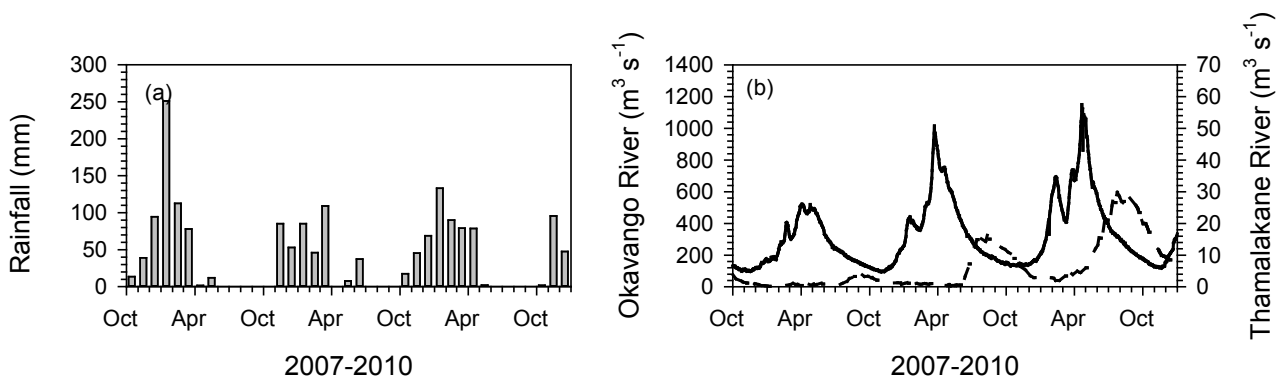
Results and Discussion

Precipitation and river discharge
Precipitation over the Delta area during the study period has been presented in Figure 2a. Precipitation over the Delta generally occurred between October and April/May while June-September was generally dry. Analysis of variance of means of annual precipitation totals for the 4 meteorological stations (Table 1) between 2006 and 2012 showed no significant differences (p=0.515). Consequently, annual totals were averaged to estimate average precipitation over the Delta (see above). The areal mean precipitation over the Delta generally shows high interannual variation, ranging from 400 to 720 mm y^{-1} for the period 2007-2010. The area of maximum inundation for the period 2007-2010 varied from 8,120-11,600 km^2 (http://www.okavangodata.ub.bw/ori/monitoring/flood_maps/), and a mean of 9,644 km^2. Assuming the mean area of maximum inundation of 9,644 km^2 represents the Delta swamp size, we estimated the annual precipitation over the Delta to have contributed approximately $5.8 \times 10^9 \, m^3$ over the 2007/08 rainy season, $4.1 \times 10^9 \, m^3$ over 2008/09 rainy season and $5.0 \times 10^9 \, m^3$ of water during the 2009/10 rainy season. These annual precipitation rates are consistent with estimates reported in previous studies (e.g., Gumbricht *et al.* 2004).

River inflow and outflow at Mohembo and Maun respectively for the study period, 2008 to 2010, are presented in Figure 2b. There were high intra- and inter-annual variations for both inflow and

outflow measurements. The mean inflow at Mohembo and outflow at Maun between October 2007 and September 2010 were 330 and 6 $m^3 s^{-1}$, respectively. Although the annual discharge at Mohembo varied considerably, the mean was slightly higher than previously reported by McCarthy *et al.* (1998) at 292 $m^3 s^{-1}$ and Bauer (2004) at 300 $m^3 s^{-1}$. Due to the Delta's low topographic gradient of about 1:3500, peak inflows observed at Mohembo in April reached the southern distal area of Maun in September (Figure 2b), which is again consistent with earlier studies (Wolski *et al.* 2006). For instance, McCarthy and Ellery (1998) and Gumbricht *et al.* (2004) have previously reported that the flood water takes about 3-5 months to traverse the 250 km distance from Mohembo to the distal areas of the Delta. During the study period, total inflow at Mohembo increased by over 60% from 7.9 x 10^9 m^3 in the 2007/08 flood season to 12.8 x 10^9 m^3 in the 2009/10 flood season. Precipitation contributed 42%, 28% and 28% to the total water inflow into the Delta in 2007/08, 2008/09 and 2009/10 flood seasons, respectively. An inflow of ~9 x 10^9 m^3 per annum has been reported by Gumbricht *et al.* (2004). Total outflow from the Delta through the Thamalakane River at Maun concomitantly increased from 0.04 x 10^9 m^3 in 2007/08 to 0.36 x 10^9 m^3 in 2009/10. During the whole study period annual outflow recorded at Maun on the Thamalakane River was ≤3% of the total annual inflow at Mohembo.

Major ions

Anions

Mean concentrations for HCO_3^-, Cl^- and SO_4^{2-} anions have been presented in Figure 3a-c. At the prevailing neutral to slightly acidic pH levels in the river system (Gondwe and Masamba 2016), HCO_3^- was the most dominant anion in the river system accounting for 97.2±0.6% of the total anionic concentration in the water, while CO_3^{2-} was consistently below detection except on a few occasions at Lake Ngami when pH was higher than 8.4 (Figure 3d). Mackay *et al.* (2011) have reported HCO_3^- dominance of over 90% throughout the Delta. HCO_3^- concentration and its anionic dominance generally increased from Mohembo to Lake Ngami (Figure 3a), while Cl^- concentrations at anionic dominance of 1.9±0.3% (Figure 3c) remained stable at 0.80±0.06 mg L^{-1} between Mohembo and Tsanekona but more than doubled thereafter to 1.88±0.46 mg L^{-1} at Lake Ngami. Sulphate (SO_4^{2-}) concentrations, which had a mean anionic dominance of 0.8±0.3%, declined from around 1.08±0.34 mg L^{-1} at Mohembo to 0.13±0.03 mg L^{-1} between Guma and Tsanekona but slightly increased thereafter to Lake Ngami (Figure 3b). While Cl^- is considered a conservative element in the Delta and therefore tended to remain stable across the sampled river system, the decline in SO_4^{2-} concentration (Fig 5b) between Mohembo and Nxaraga could be partly due to the dissimilatory sulphate reduction by obligate anaerobes such as *Desulfovibrio*, which use SO_4^{2-} as a terminal electron acceptor during catabolism of organic compounds such as ethanol and carbohydrates in reducing ecotones in the permanently flooded swamps. Sulphate reducing bacteria can be found in almost all anaerobic organically rich environments including marine, estuarine and freshwater sediments (Brown 1982). In aquatic systems where SO_4^{2-} concentrations are high, dissimilatory SO_4^{2-} reduction may account for a significant proportion of the total carbon mineralized there (Jørgensen 1977). In the current study SO_4^{2-} concentration increased between Nxaraga and Lake Ngami probably because water turbulence facilitated aeration of the river water which led to the re-oxidation of reduced sulphides (S^{2-}) to SO_4^{2-}. Sulphate concentrations along the river transect were generally higher during the wet than dry season. Generally the hot but rainy season in the flood-pulsed Okavango Delta is characterised by lower flood water levels, compared to the dry season when flooding occurs, which allows aeration of the water column and subsequent oxidation of the reduced sulphides to SO_4^{2-}.

Figure 3: Concentrations of (a) bicarbonate (HCO$_3^-$), (b) sulphate (SO$_4^{2-}$), (c) chloride (Cl$^-$) anions and (d) their respective dominance along the study transect across the Delta.
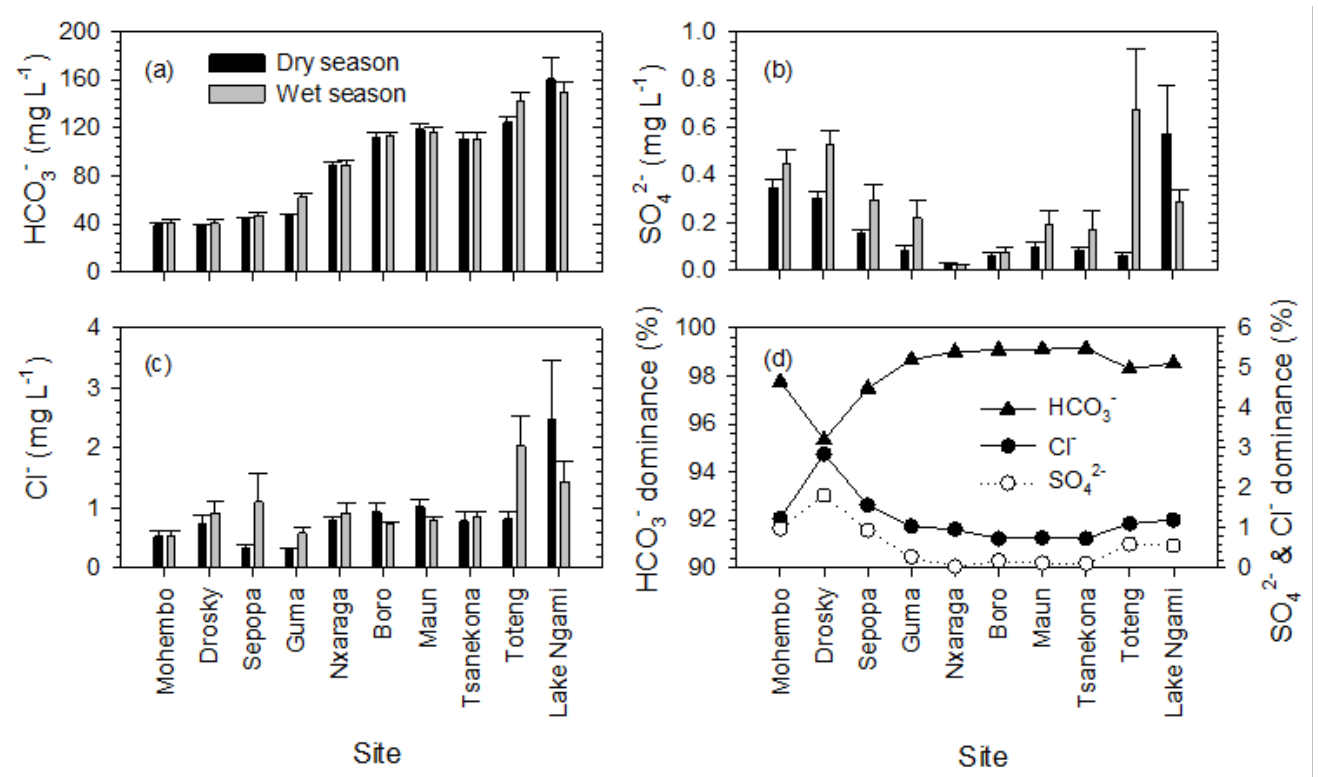
Cations

Concentrations of Na, K, Mg, Ca and Fe have been presented in Figure 4a-e. Similar to earlier studies (e.g., MacKay *et al.* 2012), Ca was the most abundant cation at all the study sites (i.e., Ca>Na>Mg>K>Fe) except in Lake Ngami where Na was the most dominant (i.e., Na>Ca>Mg>K>Fe) (Figure 4f). Concentrations of all five cations in the inflowing water at Mohembo were generally low at < 4 mg L^{-1} as also reported by McCarthy and Ellery (1994) and MacKay *et al.* (2011). Although the concentrations of the cations were low, they increased from Mohembo to Lake Ngami (Figure 4) partly due to the high evapotranspirative water loss which exceeds annual precipitation over the Delta area by a factor of three (Wilson and Dincer 1976; Dincer *et al.* 1978). A much higher increase of approximately 3-4 fold in the cation concentrations was observed between the upper Panhandle (Mohembo and Drosky) and the distal (Boro and Maun) areas of the Delta. The evapotranspiration varies spatially in the Delta in that it is generally higher in seasonal and occasional floodplains than in permanent swamps due to higher water temperatures and shallower water levels (Mackay *et al.* 2011; Akoko *et al.* 2013; Gondwe and Masamba 2016).

Figure 4: (a) Sodium (Na), (b) Potassium (K), (c) Calcium (Ca), (d) Iron (Fe), (e) Magnesium (Mg) as concentrations and (f) their dominance along the study transect across the Delta. The legend for (f) is Ca=●, Na=O, K=▼ and Mg=Δ.
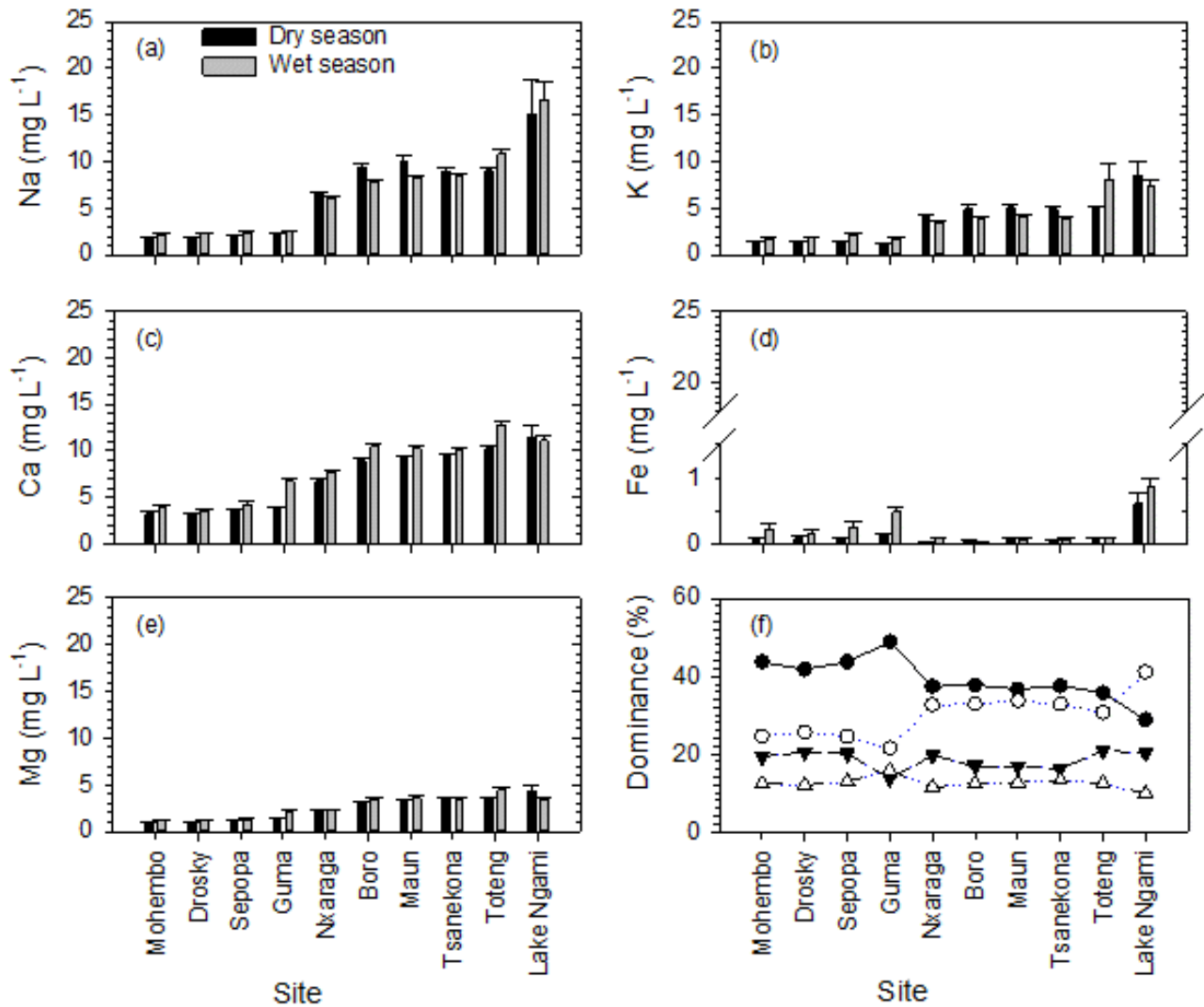

Total dissolved ions (TDI)

The TDI concentrations, as estimated from Electrical Conductivity (EC), were lower, but slightly increased with distance down the river from Mohembo to Guma, downstream of Guma TDI steeply increased to Lake Ngami during both dry and wet seasons (Figure 5a). Since TDI concentration represents the sum concentration of dissolved major cations and anions (i.e., $\sum K^+ + Na^+ + Mg^{2+} + Ca^{2+} + CO_3^{2-} + HCO_3^- + SO_4^{2-} + Cl^-$) in a water sample, we tested the relationship between the two variables in the surface waters along the study transect. TDI was positively correlated to the sum of the major ions (i.e., $\sum$[cations + anions]) in the surface water (Figure 5c; Table 2). Separate strong positive correlations were also observed between TDI and the sum of cations ($\sum[K^+ + Na^+ + Mg^{2+} + Ca^{2+}]$) (Figure 5d; Table 2) and anions ($\sum[CO_3^{2-} + HCO_3^- + SO_4^{2-} + Cl^-]$) (Figure 5d; Table 2) which show that both cations and anions evapoconcentrate as water flows down the study transect from Mohembo to Lake Ngami (see Atekwana *et al.* 2016 and references therein). As discussed above, CO_3^{2-} concentrations were only sporadically detected at Toteng and Lake Ngami where much higher pH values were observed. Data in Figure 5d and Table 2 show that cations contribute much less to TDI than anions. The gradients of the

plots also indicate that both cations and anions contribute more to TDI during the rainy season than dry season. This can be attributed to evapoconcentration and higher wet- than dry-atmospheric deposition of cations and/or anions in the Delta.

Silica, which is also a dissolved solute, varied from a mean concentration of 7.37 ± 0.18 mg L^{-1} in the upper Delta (Mohembo to Guma) to 24.06 ± 0.49 mg L^{-1} between Boro and Lake Ngami (Figure 5b). Dissolved silica exists as unionised SiO_2 or $Si(OH)_2$ forms at pH<9 and as a result it was not included in EC measurements because of poor, or lack of, correlation with EC at all sites sampled except at Sepopa ($r^2 = 0.7456$) which is probably also explained by evapoconcentration.

Figure 5: TDI (mg L^{-1}) along the river transect (a) and relationship between TDI and the sum of major ions (b), the sum of cations (c) and the sum of anions (d). See Table 2 for linear equations and correlation coefficients.
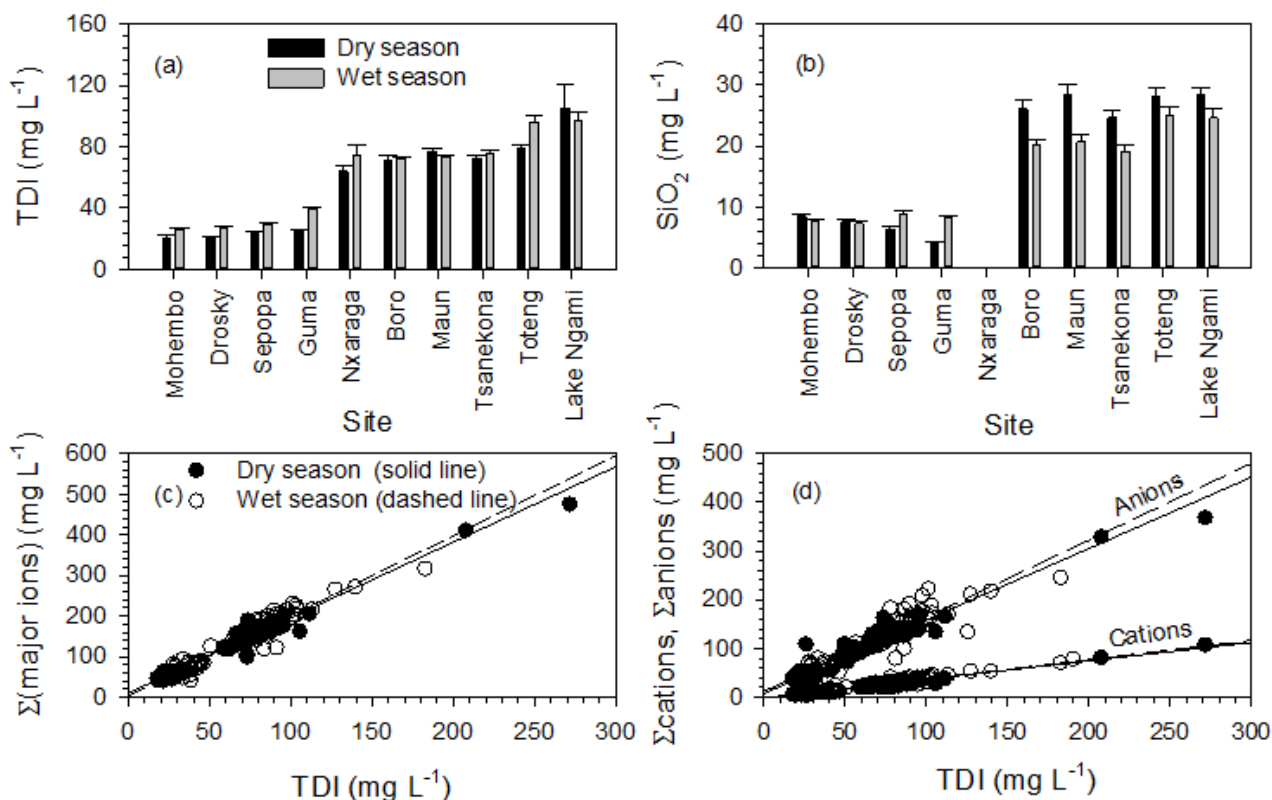
Using the daily discharge rates as measured at Mohembo and Maun between 2008 and 2010, TDS (i.e., TDS=TDI (mg L^{-1}) + SiO_2 (mg L^{-1})) input into the Delta via the Okavango River was estimated at 256,197-415,104 t y^{-1}. Previous studies have reported TDS input at 400,000 t y^{-1} (McCarthy and Metcalfe 1990; Gumbricht *et al.* 2004; Zimmermann *et al.* 2006). Loss of solutes through surface outflow in the Thamalakane River measured at Maun varied between 3,994-45,926 t y^{-1}, which is approximately 2-11% of the total solutes brought in by the Okavango River. McCarthy and Metcalfe (1990), Gumbricht *et al.* (2004) and Zimmermann *et al.* (2006) estimated the average solute loss via surface outflow at 7% of total input measured at Mohembo. In view of the large amounts of solutes deposited in the Delta each year, it is surprising that the Delta has remained a freshwater ecosystem instead of a saline water body or saltpan like the downstream Makgadikgadi Pans. The Delta's freshwater status is attributable to a simple but important characteristic feature of the Okavango Delta (McCarthy *et al* 1986, 1991), which is the permanent sequestration of most solutes under the numerous

tree islands in the Delta facilitated by evapotranspiration of the woodland trees on the islands fringes. The evapotranspiration of the trees lowers the groundwater table under the islands which creates groundwater gradients driving large lateral flows of groundwater towards the centre of the islands from the surrounding floodplains. The water loss to the centre of islands is probably higher in the seasonal floodplains than in the permanent swamps primarily because of the absence of a significant peat layer in the seasonal floodplains that could potentially reduce infiltration. For instance an infiltration study in the Delta in Phelo's seasonal floodplain near Nxaraga observed rapid recession of the groundwater table in the floodplain after the cessation of the floods which was primarily attributed to transpirative loss of the water by floodplain vegetation and woodland trees (Ramberg *et al.* 2006). Due to the lateral flow of the groundwater, several studies have shown high concentrations of solutes in the order of 25,000 mg L^{-1} (Gieske 1996) under these islands in the seasonal swamps. As fresh swamp water flows under the islands, the dense saline water flows deeper into the centre of the islands stabilizing the whole system. Generally older and larger forested islands are common in the seasonal and occasional swamps of the Delta while smaller and younger grassland islands dominate the permanent swamps (Gumbricht *et al.* 2004). As a result most of the chemical sedimentation beneath islands due to transpiration by deep rooted trees primarily occurs in the seasonal and occasional swamps of the Delta.

This study observed a continued increase of approximately 38±12% in Na, K, Mg and Ca concentrations with distance along the river from Boro to Lake Ngami which is probably due to the continued evaporative loss of surface river water and to a lesser extent anthropogenic pollution of the water, such as Cl^-, SO_4^{2-} and TSS brought in with effluent water.

Table 2: Equations and correlation coefficients between total dissolved ions (TDI) and the sum of ions in surface water along the river transect through the Okavango Delta.

Y-axis	Season	Equation	r^2	n
Σ(cations+anions)	Dry	y = 1.8595*TDI + 10.0739	0.9734	139
	Wet	y = 1.9704*TDI + 4.1926	0.9474	167
Σ(cations)	Dry	y = 0.3791*TDI - 1.0358	0.9731	140
	Wet	y = 0.3978*TDI - 2.1568	0.9463	169
Σ(anions)	Dry	y = 1.4631*TDI + 12.8741	0.9588	147
	Wet	y = 1.5770*TDI + 7.3227	0.9051	169

Plant nutrients

Nutrient concentrations in the water column

Nitrogen (N) and phosphorus (P) are two of the most important macronutrients for primary production in both terrestrial and aquatic ecosystems (Conley *et al.* 2009). Most limnologists measure N and P as total nitrogen (TN) and total phosphorus (TP) respectively because these represent N and P values already in biomass and/or dissolved and available for assimilation into active biomass (Dodds 2003). Both TN and TP have been shown to be better predictors, than dissolved inorganic N and P, of nutrient status in a wide variety of aquatic systems (Dodds 2003). In fact TP is strongly correlated with phytoplankton biomass in a variety of aquatic systems (Dillon and Rigler 1974) such that current management strategies of inland water bodies of reducing P loading to control eutrophication are based on this relationship (Smith and Shapiro 1981). This is because concentrations of inorganic N tend to be typically lower in most aquatic systems including wetlands due to their high loss to denitrification processes and high assimilation rates (Cronberg *et al.* 1995).

TP and TN in the flood water at Mohembo were low at 0.042±0.005 and 0.222± 0.018 mg L^{-1}, respectively (Figure 6a & c). These nutrient concentrations are consistent with concentrations reported by Cronberg *et al.* (1995), Garstang *et al.* (1998), Krah *et al.* (2006), Ramberg *et al.* (2010) and MacKay *et al.* (2011). Ramberg *et al.* (2010) reported an average of 0.023 mg L^{-1} TP and 0.36 mg L^{-1} TN in inflow water at Mohembo. As flood water flows downstream, TP declined slightly to 0.035±0.004 mg L^{-1} at Tsanekona but increased thereafter by more than 3-fold to 0.131±0.024 mg L^{-1} at Lake Ngami. The low TP concentrations across the Delta are again consistent with values reported by Krah *et al.* (2006) and MacKay *et al.* (2011). The observed decline in TP across the Delta may be partly explained by high uptake of the phosphorus by dense stands of *Cyperus papyrus* and *Phragmites australis* which flank the primary channels in the Panhandle and permanent swamp regions (Garstang *et al.* 1998; MacKay *et al.* 2011; Mosimane 2015). These nutrients are necessary to sustain the high productivity rates of the papyrus stands in this environment where nutrients are generally low throughout the year. The absorbed nutrients are then efficiently utilized and conserved through reallocation within the plant. The nutrient abstraction by these macrophytes, combined with other factors including high sedimentation of suspended material facilitated by high water retention time and immobilization of both P and N in peat as indicated by lower C:P and C:N ratios of peat material than in living vegetation (Garstang *et al.* 1998), results in nutrient deficiency in the rest of the Delta (McCarthy and Ellery 1998). In fact, a general reduction in biological productivity with distance from channels into the backwaters and from the Panhandle to distal areas near Maun has been reported from satellite imagery (McCarthy *et al.* 1993). Garstang *et al.* (1998) estimated a *C. papyrus* biomass of about 3.5 x 10^4 kg ha^{-1} on channel fringes which decreases significantly with distance to 3.5 x 10^3 kg ha^{-1} in the backwaters and distal areas of the Delta.

The slight decline in the TP concentration from 0.042±0.005 to 0.035±0.004 mg L^{-1} across the Delta has previously been reported as well (see MacKay *et al.* 2011), and may be attributed to an observation (McCarthy *et al.* 1989) that over 70% of tissue P (compared to <50% N) is internally recycled by vegetation in the Delta, particularly by the *C. papyrus* in the permanent swamp, through translocation from senescing aerial shoots to younger tissues or to perennial belowground rhizome system. According to Johnston (1991) nutrient translocation, also known as internal recycling, helps perennial wetland vegetation to conserve already assimilated nutrients, which consequently reduces their net nutrient uptake from the soils and/or water.

Unlike TP, TN increased by approximately 3-fold from 0.222±0.018 mg L^{-1} at Mohembo to 0.698±0.035 mg L^{-1} at Maun, despite potential loss of N to denitrification in the anaerobic environments. The observed increase in TN could partly be attributed to an influx of fixed N from N$_2$- fixing autotrophic cyanobacteria and diazotrophs such as sulphate reducing bacteria common in anaerobic wetland environments (Śantrůčková *et al.* 2010). Although a wide occurrence of cyanobacteria mats has been reported in the Delta (Garstang *et al.* 1998; Marazzi 2014), diazotrophs have not been adequately studied but their nitrogenase activity is likely to be higher in the permanent swamps dominated by highly productive *C. papyrus*. This is because diazotrophs are generally associated with plant rhizosphere and sediments characterised by high availability of labile C sources (Śantrůčková *et al.* 2010). The potential of N$_2$-fixation to increase N concentrations in aquatic ecosystems varies from 5-70% of fixed N depending on physico-chemical conditions such as temperature, pH and water content in the system (e.g., Belnap 2001). However, the increase in N concentration can be significant as has been observed in Lake Victoria, East Africa (Hecky 1993; Lehman and Branstrator 1994) and in Lake 226 at the Experimental Lakes Area (ELA), northwestern Ontario, Canada, which was artificially made N-deficient by addition of NO$_3^-$ and PO$_4^{3-}$ at N:P weight ratio of 5 (Schindler 1977). In Lake 226, N-deficiency created a bloom of N$_2$-fixing cyanobacteria which was later succeeded by a high abundance of

non N_2-fixing algal species (*e.g., Limnothrix redekei*) which gained some competitive advantage over N_2-fixing species when some of the fixed N was recycled back into the environment (Schindler *et al.* 2008).

Figure 6: (a) Total nitrogen (TN), (b) total phosphorus (TP), (c) TN and TP relationship and (d) TN:TP ratio along the study transect across the Delta.
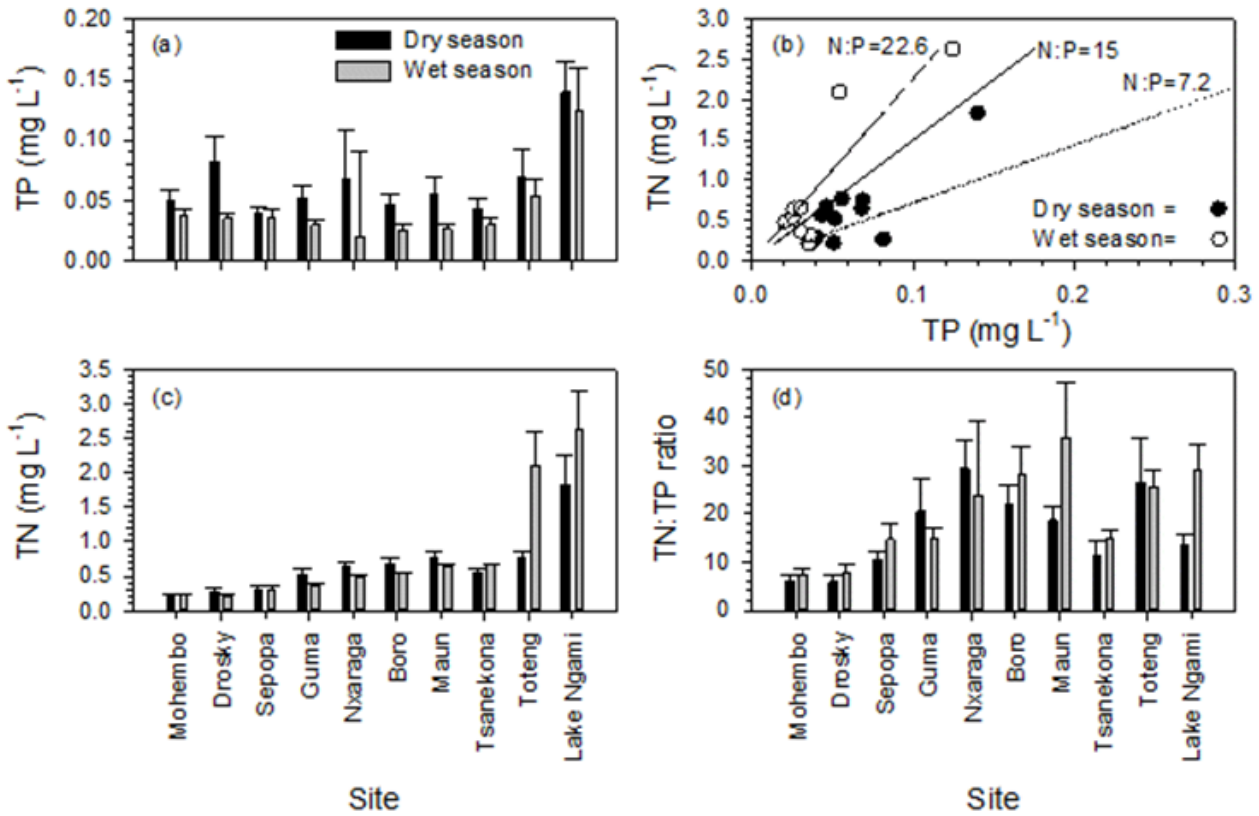
Limiting nutrient

In terrestrial and aquatic systems the relative availability of N and P does not only control plant biomass, but also species composition of the plant communities (Koerselman and Meuleman 1996). This is probably because different plant species have differential requirements for N and P. The N:P ratio is commonly used to determine the nutrient, between N and P, that limits primary production in a given ecosystem. The N:P ratio is generally determined using TN and TP because dissolved nutrients, especially P, diminish rapidly when available due to uptake by algae and other aquatic plants (Håkanson *et al.* 2007; Schindler *et al.* 2008). Generally, ecosystems with TN:TP weight ratios lower than 7:1 are said to be N limited and their algal communities tend to be dominated by N_2-fixing species. In contrast, ecosystems with TN:TP mass ratios higher than 7:1 are P limited and tend to be dominated by non-N_2-fixing species. For instance, experimental eutrophication of Lake 227 at the Experimental Lakes Area, Canada with N and P fertilizers (N:P mass ratio of 12:1) led to a dominance by chrolophytes (Schindler *et al.* 1973; 2008). In contrast, N_2-fixing heterocystic *Anabaena spiroides* Klebs dominated in Lake 226 which was supplied with N-deficient fertilizer at N:P ratio of 5:1. When the N:P loading ratio of Lake 227 was lowered from 12:1 (1969-1974) to 5:1 in 1975, N_2-fixing heterocystic algae (*Aphanizomenon gracile*) became dominant in the water column (Schindler *et al.* 1977; Findlay *et al.* 1994). Thus the N:P ratio acts as an important determinant of species composition in natural phytoplankton com-

munities (Smith 1983). The boundary between N limitation and P limitation is however not very clear as indicated by conflicting conclusions from different studies around the world. For instance, Abell *et al.* (2010) reviewed data for 121 New Zealand lakes for nutrient limitation and classified majority of them as P limited (TN:TP >15:1) and few N limited systems (TN:TP<7.1). Guildford and Hecky (2000) associated TN:TP mass ratios >22.6 (>50 by mol) with P limitation and TN:TP ratios < 9.1 indicated N limitation. On the other hand Smith (1983) compiled data from 17 lakes worldwide and concluded that N_2-fixing cyanobacteria were abundant in systems with TN:TP mass ratios <29, but rare at TN:TP ratios >29.

The TN:TP mass ratios in the Okavango Delta varied from 6.73±0.87 at Mohembo to 23.39±3.69 at Boro (Figure 6d). Similar increasing TN:TP ratios from the Panhandle region to the distal regions along the Boro River have been reported by Marazzi (2014). Although both TP and TN further increased by about 3- and 10-fold respectively from Boro to Lake Ngami, the water remained at TN:TP ratio of around 21.28±2.19 (Maun to Lake Ngami) which may be associated with evaporative concentration in the river system (Figure 6d). There are several conclusions which could be drawn from these TN:TP mass ratios in terms of nutrient limitation and phytoplankton species composition. The N:P thresholds derived by Abell *et al.* (2010) suggest that algal growth in the Panhandle region of the Delta potentially experienced N limitation during both dry and wet seasons (TN:TP=5.97±0.81), and should favour proliferation of N_2-fixing cyanobacteria which are generally better N competitors than other algal species in N limited environments (Smith 1983; Levine and Schindler 1999). The rest of the study transect probably experienced co-limitation by N and P during the dry season (TN:TP=12.17±0.73) and P limited during the wet season (TN:TP =23.35±3.00). Mackay *et al.* (2011) have previously suggested potential P limitation along the Boro River where they also reported mass TN:TP ratios of around 20.4. The algal assemblage in this part of the Delta would be co-dominated by diatoms, green algae and cyanobacteria especially during the dry season when N and P were co-limiting algal growth. Despite the varying TN:TP ratios, Marazzi (2014) observed widespread occurrence of N_2-fixing cyanobacteria across the Delta which suggests a widespread N deficiency across the whole studied river system. The abundance of N_2-fixing cyanobacteria were found to be higher in the permanent and seasonal swamps where TN:TP ratios suggested N and P co-limitation or P-limitation than in the Panhandle region where TN:TP ratios favoured cyanobacteria dominance (Marazzi 2014). It is possible that N_2-fixation by cyanobacteria and other microbes might have shifted nutrient limitation from N- to P-limitation by raising N availability relative to P in the permanent and seasonal swamps as has been observed in other ecosystems around the world (Schindler 1977; Schindler *et al.* 2008). N_2-fixation is likely to have been enhanced by higher water temperatures in the rest of the Delta than in the Panhandle region (see Marazzi 2014).

According to Koerselman and Meuleman (1996) and Bedford *et al.* (1999), the relationship between nutrient concentrations and N:P ratios can also be examined by plotting N concentrations against P concentrations (Figure 6c). Data in Figure 6c show that P-limitation (N:P ratio ≥22.6) seems to prevail during the wet season while N limitation (N:P ratio ≤9.1) prevails during the dry season when available N is probably higher than P. P limitation during the wet season could be attributed to input of fixed N from N_2-fixation which is expected to be higher during the wet season when water temperatures in the Delta are much higher than during the dry season (see Gondwe and Masamba 2016). Similar results have been observed in tropical wetlands in Belize (Rejmánková *et al.* 2004) and Yucatan Peninsula, Mexico (Vargas and Novelo 2007) where N_2-fixation rates were higher during warmer wet seasons than during the winter months. Warmer temperatures may also result in increased rates of other biological processes such as methanogenesis in the Okavango Delta during the warmer wet period as

compared to the cooler dry season (Gondwe and Masamba 2014; Masamba *et al.* 2015). This study's results from the Okavango Delta contradict an earlier study by Mackay *et al* (2011) which found TN in the Delta to be much higher during the flooding period which occurs during the dry season. Mackay *et al* (2011) results suggest P-limitation, not N-limitation, during the dry season and probably the opposite during the wet season.

The low TN:TP ratios in the flood water at Mohembo (Figure 6d), which are slightly below the Redfield ratio of 7:1 by mass, are rather unexpected for the Okavango River system which is dominated by runoff from relatively undisturbed catchments in the Central Angolan Highlands. Runoff water from undisturbed catchments tend to have high TN:TP ratios because P concentrations in the soils generally tend to be very low (see Downing and McCauley 1992). It is not clear if the low TN:TP ratios can be associated with high P leaching and runoff from relatively small irrigated agricultural schemes operating along the Okavango River in the Zambezi province (formerly known as the Caprivi strip) Namibia. Further research is therefore needed to directly assess the impact of these irrigation schemes and other upstream development activities on the quality of the water of the Okavango River at Mohembo and as it flows into the Panhandle swamp.

It is also important to assess nutrient availability to wetland plants for conservation purposes. Besides the laborious traditional field fertilization experiments (Chapin *et al.* 1986), assessment of plant species and communities for nutrient availability is commonly done by analysing plant tissues for N:P ratios (Koerselman and Meuleman 1996). Several studies in European wetlands (see Koerselman and Meuleman 1996; and references therein) have confirmed that N:P ratios of plant tissues correlate with N:P supply ratios. Generally, those studies highlight the same finding that an N:P ratio of <14 in plant tissue indicates N limitation while an N:P ratio >16 indicates P limitation. These critical N:P ratios have been used to classify emergent macrophyte species in the Everglades as either N or P limited (Daoust and Childers 1999). Although the current study did not assess the nutrient status of vegetation in the Delta, N and P concentrations in vegetation reported by two previous studies (Bonyongo 1999; Mosimane 2015) suggest that vegetation in the Delta could be limited by N. Nitrogen and P concentrations in plant tissues from the seasonal floodplain reported by Bonyongo (1999) indicated a mean N:P ratio of 12.29±0.80 while Mosimane (2015) reported a mean N:P ratio of 11.87±0.59 (by mass). Since the research objectives of the above two studies were not primarily focused on nutrients levels in plant tissues, only a few plant samples were collected in an ad hoc manner. We therefore suggest that future studies should rigorously reassess the nutrient status of the vegetation in the Delta for purposes of informing management strategies with regard to nutrient pollution in the Delta.

Conclusion

Wetlands act as natural water purifiers and have been deliberately constructed and used to improve the quality of various effluents in many parts of the world. In the Okavango Delta the role of evapotranspiration in increasing concentrations, particularly of cations, anions and silica, was evident as also shown by earlier studies. High evapotranspiration in the Delta is consistent with the disparity between huge inflow and little outflow in the Delta. Analysis of nutrient data showed spatial and temporal N and P limitation in the Delta. N limitation is probably ameliorated by biological nitrogen fixation indicated by widespread abundance of nitrogen fixing cyanobacterial species in the Delta.

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References

Abell, JM, Özkundakci, D and Hamilton, DP 2010. 'Nitrogen and phosphorus limitation of phyto plankton growth in New Zealand lakes: implications for eutrophication control', *Ecosystems, vol.13, 7, pp.966-977.*

Akoko, E, Atekwana, EA, Cruse, AM, Molwalefhe, L and Masamba, WR 2013. 'River-wetland interac tion and carbon cycling in a semi-arid riverine system: The Okavango Delta, Botswana', *Bio geochemistry, vol.114, 1-3, pp.359-380.*

Atekwana, EA, Molwalefhe, L, Kgaodi, O and Cruse, AM 2016. 'Effect of evapotranspiration on dis solved inorganic carbon and stable carbon isotopic evolution in rivers in semi-arid climates: The Okavango Delta in North West Botswana', *Journal of Hydrology: Regional Studies, vol.7, pp.1-13.*

Barbier, EB 1993. 'Sustainable use of wetlands valuing tropical wetland benefits: economic methodol ogies and applications', *Geographical Journal, vol.159, pp.22-32.*

Bauer, P 2004. 'Flooding and salt transport in the Okavango Delta, Botswana: Key issues for sustain able wetland management', *PhD Thesis, ETH Zurich, Zurich, 175 pp.*

Bauer, P, Gumbricht, T and Kinzelbach, W 2006. 'A regional coupled surface water/ground water model of the Okavango Delta, Botswana', *Water Resources Research, vol.42, 4, W04403, DOI:10.1029/2005WR004234*

Belnap, J 2001. 'Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In Biological soil crusts: Structure, function, and management', , *Springer Berlin Heidelberg, pp. 241-261.*

Bedford, BL, Walbridge, MR and Aldous, A 1999. 'Patterns in nutrient availability and plant diversity of temperate North American wetlands', *Ecology, vol.80, 7, pp.2151-2169.*

Bonyongo, MC 1999. 'Vegetation ecology of the seasonal floodplains in the Okavango Delta, Botswa na', *MSc Thesis, University of Pretoria, Pretoria, South Africa.*

Brown, KA 1982. 'Sulfur in the environment: A review', *Environmental Pollution (Series B), vol.3, 1, pp.47-80.*

Chapin III, FS, Vitousek, PM and Van Cleve, K 1986. 'The nature of nutrient limitation in plant com munities', *American Naturalist, vol.127, pp.48-58.*

Conley, DJ, Paerl, HW, Howarth, RW, Boesch, DF, Seitzinger, SP, Karl, E, Karl, E, Lancelot, C, Gene, E and Gene, E 2009. 'Controlling eutrophication: nitrogen and phosphorus', *Science, vol.123, pp.1014-1015.*

Cronberg, G, Gieske, A, Martins, E, Nengu, JP and Stenström, IM 1995. 'Hydrobiological studies of the Okavango Delta and Kwando/Linyanti/Chobe River, Botswana: I Surface water quality analysis', *Botswana Notes and Records, vol.27. pp.151-226.*

Daoust, RJ and Childers, DL 1999. 'Controls on emergent macrophyte composition, abundance, and productivity in freshwater Everglades wetland communities', *Wetlands, vol.19, 1, pp.262-275.*

Dillon, PJ and Rigler, FH 1974. 'The phosphorus-chlorophyll relationship in lakes', *Limnology and Oceanography, vol.19, 5, pp.767-773.*

Dincer, T, Hutton, LG. and Kupee, BBJ 1979. 'Study using stable isotopes, of flow distribution, sur face/groundwater relations and evapotranspiration in the Okarango Swamp, Botswana', *Iso*

tope Hydrology 1978, IAEA, Vienna, vol.1, pp.3-26.

Dodds, WK 2003. 'Misuse of inorganic N and soluble reactive P concentrations to indicate nutrient status of surface waters', *Journal of the North American Benthological Society*, vol.22, 2, pp.171-181.

Downing, JA and McCauley, E 1992. 'The nitrogen: phosphorus relationship in lakes', *Limnology and Oceanography*, vol.37, 5, pp.936-945.

Findlay, DL, Hecky, RE, Hendzel, LL, Stainton, MP and Regehr, GW 1994. 'Relationship between N2-fixation and heterocyst abundance and its relevance to the nitrogen budget of Lake 227', *Canadian Journal of Fisheries and Aquatic Sciences*, vol.51, 10, pp.2254-2266.

Garstang, M, Ellery, WN, McCarthy, TS, Scholes, MC, Scholes, RJ, Swap, RJ and Tyson, PD 1998. 'The contribution of aerosol- and water-borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana', *South African Journal of Science*, vol.94, pp.223-229.

Gieske, A 1996. 'Vegetation driven ground water recharge below the Okavango Delta (Botswana) as a solute sink mechanism–an indicative model', *Botswana Journal of Earth Sciences*, vol.3, pp.33-37.

Gieske, A 1997. 'Modelling outflow from the Jao/Boro river system in the Okavango Delta, Botswana', *Journal of Hydrology*, vol.193, 1, pp.214-239.

Gondwe, MJ and Masamba, WR 2014. 'Spatial and temporal dynamics of diffusive methane emissions in the Okavango Delta, northern Botswana, Africa', *Wetlands Ecology and Management*, vol.22, 1, pp.63-78.

Gondwe, MJ and Masamba, WRL 2016. 'Variation of physico-chemical parameters along a river transect through the Okavango Delta, Botswana', *African Journal of Aquatic Science*, vol.41, 2, pp.205-215.

Guildford, SJ and Hecky, RE 2000. 'Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship?', *Limnology and Oceanography*, vol.45, 6, pp.1213-1223.

Gumbricht, T, McCarthy, J and McCarthy, TS 2004. 'Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes', *Earth Surface Processes and Landforms*, vol.29, 1, pp.15-29.

Håkanson, L, Bryhn, AC and Hytteborn, JK 2007. 'On the issue of limiting nutrient and predictions of cyanobacteria in aquatic systems', *Science of the Total Environment*, vol.379, 1, pp.89-108. Hecky, RE 1993. 'The eutrophication of Lake Victoria', *Proceedings-International Association of Theoretical and Applied Limnology*, 25, pp.39-39.

Johnston, CA 1991. 'Sediment and nutrient retention by freshwater wetlands: effects on surface water quality', *Critical Reviews in Environmental Science and Technology*, vol.21, 5-6, pp.491-565.

Jørgensen, BB 1977. 'The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark)', *Limnology and Oceanography*, vol.22, 5, pp.814-832.

Junk, WJ 2002. 'Long-term environmental trends and the future of tropical wetlands', *Environmental Conservation*, vol.29, 04, pp.414-435.

Koerselman, W and Meuleman, AF 1996. 'The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation', *Journal of Applied Ecology*, vol.33, 6, pp.1441-1450.

Krah, M, McCarthy, TS, Huntsman-Mapila, P, Wolski, P, Annegarn, H and Sethebe, K 2006. 'Nutrient budget in the seasonal wetland of the Okavango Delta, Botswana', *Wetlands Ecology and Management*, vol.14, 3, pp.253-267.

Lehman, JT and Branstrator, DK 1994. 'Nutrient dynamics and turnover rates of phosphate and sulfate in Lake Victoria, East Africa', *Limnology and Oceanography*, vol.39, 2, pp.227-233.

Levine, SN and Schindler, DW 1999. 'Influence of nitrogen to phosphorus supply ratios and physico chemical conditions on cyanobacteria and phytoplankton species composition in the Experi mental Lakes Area, Canada', *Canadian Journal of Fisheries and Aquatic Sciences*, vol.56, 3, pp.451-466.

Marazzi, L 2014. 'Biodiversity and biomass of algae in the Okavango Delta (Botswana), a subtropical flood-pulsed wetland', PhD Thesis, Department of Geography, University College London, pp. 426

Mackay, AW, Davidson, T, Wolski, P, Mazebedi, R, Masamba, WR, Huntsman-Mapila, P and Todd, M 2011. 'Spatial and seasonal variability in surface water chemistry in the Okavango Delta, Bo tswana: a multivariate approach', *Wetlands*, vol.31, 5, pp.815-829.

Mackay, AW, Davidson, T, Wolski, P, Woodward, S, Mazebedi, R, Masamba, WR and Todd, M 2012. 'Diatom sensitivity to hydrological and nutrient variability in a subtropical, flood-pulse wet land', *Ecohydrology*, vol.5, 4, pp.491-502.

Masamba, WR, Gondwe, MJ and Murray-Hudson, M 2015. 'Physicochemical controls of diffusive methane fluxes in the Okavango Delta, Botswana', *Wetlands Ecology and Management*, vol.23,4, pp.617-635.

McCarthy, TS, McIver, JR and Cairncross, B 1986. 'Carbonate accumulation on islands in the Oka vango Delta, Botswana', *South African Journal of Science*, vol.82, pp.588-591.

McCarthy, TS, McIver, JR, Cairncross, B, Ellery, WN and Ellery, K 1989. 'The inorganic chemistry of peat from the Maunachira channel-swamp system, Okavango Delta, Botswana', *Geochimi ca et Cosmochimica Acta*, vol.53, 5, pp.1077-1089.

McCarthy, TS and Metcalfe, J 1990. 'Chemical sedimentation in the semi-arid environment of the Okavango Delta, Botswana', *Chemical Geology*, vol.89, 1-2, pp.157-178.

McCarthy, TS, McIver, JR and Verhagen, BT 1991. 'Groundwater evolution, chemical sedimentation and carbonate brine formation on an island in the Okavango Delta swamp, Botswana', *Ap plied Geochemistry*, vol.6, 6, pp.577-595.

McCarthy, TS, Franey, NJ, Ellery, WN and Ellery, K 1993. 'The use of SPOT imagery in the study of environmental processes of the Okavango Delta, Botswana', *South African Journal of Sci ence*, vol.89, 9, pp.432-436.

McCarthy, TS and Ellery, WN 1994. 'The effect of vegetation on soil and ground water chemistry and hydrology of islands in the seasonal swamps of the Okavango Fan, Botswana', *Journal of Hy drology*, vol.154, 1, pp.169-193.

McCarthy, TS and Ellery, WN 1998. 'The Okavango Delta', *Transactions of the Royal Society of South Africa*, vol.53, 2, pp.157-182.

McCarthy, TS, Cooper, GRJ, Tyson, PD and Ellery, WN 2000. 'Seasonal flooding in the Okavango Delta, Botswana-recent history and future prospects', *South African Journal of Science*, vol.96, 1, pp.25-33.

Mosimane, K 2015. 'A first quantification of biogenic silica pools in an evaporation-dominated wet land system: The Okavango Delta, Botswana', MPhil Thesis, University of Botswana, Botswa na.

Ramberg, L and Wolski, P 2008. 'Growing islands and sinking solutes: processes maintaining the en dorheic Okavango Delta as a freshwater system', *Plant Ecology*, vol.196, 2, pp.215-231.

Ramberg, L, Hancock, P, Lindholm, M, Meyer, T, Ringrose, S, Sliva, J, Van As, J and Vander Post, C 2006. 'Species diversity of the Okavango delta, Botswana', *Aquatic Sciences*, vol.68, 3, pp.310-337.

Ramberg, L, Lindholm, M, Hessen, DO, Murray-Hudson, M, Bonyongo, C, Heinl, M, Masamba, W, VanderPost, C and Wolski, P 2010. 'Aquatic ecosystem responses to fire and flood size in the Okavango Delta: observations from the seasonal floodplains', Wetlands Ecology and Management, vol.18, 5, pp.587-595.

Rejmánková, E, Komárková, J and Rejmánek, M 2004. 'δ15N as an indicator of N2-fixation by cyano bacterial mats in tropical marshes', Biogeochemistry, 67(3), pp.353-368.

Šantrůčková, H, Rejmánková, E, Pivničková, B and Snyder, JM 2010. 'Nutrient enrichment in tropi cal wetlands: shifts from autotrophic to heterotrophic nitrogen fixation', Biogeochemistry, vol.101, 1-3, pp.295-310.

Schindler, DW, Kling, H, Schmidt, RV, Prokopowich, J, Frost, VE, Reid, RA and Capel, M 1973. 'Eu trophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972', Journal of the Fisheries Board of Canada, vol.30,10, pp.1415-1440.

Schindler, DW 1977. 'Evolution of phosphorus limitation in lakes', Science, vol.195, 4275, pp.260-262.

Schindler, DW, Hecky, RE, Findlay, DL, Stainton, MP, Parker, BR, Paterson, MJ, Beaty, KG, Lyng, M and Kasian, SEM 2008. 'Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment', Proceedings of the National Acade my of Sciences, vol.105, 32, pp.11254-11258.

Schuyt, KD 2005. 'Economic consequences of wetland degradation for local populations in Africa', Ecological Economics, vol.53, 2, pp.177-190.

Smith, VH 1983. 'Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton', Science, vol.221, 4611, pp.669-671.

Smith, VH and Shapiro, J 1981. 'Chlorophyll-phosphorus relations in individual lakes. Their impor tance to lake restoration strategies', Environmental Science and Technology, vol.15, 4, pp.444-451.

Snowy Mountains Engineering Corporation 1987. 'Study of open water evaporation in Botswana', Ministry of Mineral Resources and Water Affairs, Department of Water Affairs, Gaborone, Bo tswana.

Snowy Mountains Engineering Corporation 1990. 'Southern Okavango Integrated Water Develop ment Project', Department of Water Affairs, Gaborone, Botswana.

Vargas, R and Novelo, E 2007. 'Seasonal changes in periphyton nitrogen fixation in a protected tropi cal wetland', Biology and Fertility of Soils, vol.43, 3, pp.367-372.

Wilk, J, Kniveton, D, Andersson, L, Layberry, R, Todd, MC, Hughes, D, Ringrose, S and Vanderpost, C 2006. 'Estimating rainfall and water balance over the Okavango River Basin for hydrologi cal applications', Journal of Hydrology, vol.331, 1, pp.18-29.

Wolski, P, Savenije, HHG, Murray-Hudson, M and Gumbricht, T 2006. 'Modelling of the flooding in the Okavango Delta, Botswana, using a hybrid reservoir-GIS model', Journal of Hydrology, vol.331, 1, pp.58-72.

Wilson, BH and Dincer, T 1976. 'An introduction to the hydrology and hydrography of the Okavango Delta', in: Symposium on the Okavango Delta (pp. 33-48), Botswana Soc Gaborone, Botswa na.

Zimmermann, S, Bauer, P, Held, R, Kinzelbach, W and Walther, JH 2006. 'Salt transport on islands in the Okavango Delta: numerical investigations', Advances in Water Resources, vol.29, 1, pp.11-29.