SANBI
Biodiversity for Life
South African National Biodiversity Institute

BOTHALIA – African Biodiversity & Conservation
ISSN: (Online) 2311-9284, (Print) 0006-8241

Environmental factors that influence species diversity of floodplain plant communities in different flooding phases in the Okavango Delta, Botswana

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Dates:

Published: 15 June 2020.

How to cite this article:

Tsheboeng, G., Bonyongo, M. & Murray-Hudson, M., 2020, 'Environmental factors that influence diversity of floodplain communities in different phases in the Okavango Delta, Botswana', *Bothalia* 50(1), a3. http://dx.doi.org/10.38201/btha.abc.v50.i1.3

Background and objectives: Species composition and distribution in seasonal floodplain plant communities are influenced by variation in flooding. However, the influence of intra-flooding variation phases on the diversity of seasonal floodplain plant communities has not been studied in the Okavango Delta. The objective of this study was to investigate environmental factors that influence species composition and distribution of seasonal floodplain communities before and after flooding. It was hypothesised that environmental factors that influence the species composition and distribution in seasonal floodplain communities will vary with intra-flooding seasons.

Methods: Flooding depth was measured in May (before flooding) and September (flood recession/after flooding) in forty 25 m^2 plots. Flooding duration was recorded as the number of weeks in which the plots were inundated. The soil was sampled before and after floods and analysed for pH, extractable P, K, Mg, Ca and Na. Plant identification and estimation of percentage cover were done in the 25 m^2 plots in which environmental variables were sampled. The relationship between environmental variables and seasonal floodplain plant community composition and distribution was sought using Non-metric Multi-dimensional Scaling. Paired *Student's t* test was used to compare the means of environmental variables before and after flooding.

Results: Factors that influenced the distribution of species before flooding were Na, K, water depth and flooding duration. After flooding, the factors that influenced species composition and distribution were K, Na, Mg, pH, water depth and flooding duration.

Conclusion: These results suggest that during flooding K and Mg are deposited in the floodplains due to lateral water flow. Our results also suggest that any water abstraction from the Okavango River Basin should take into consideration the importance of flooding duration and depth in sustaining species composition and distribution of seasonal floodplain plant communities so that such developments do not disturb the ecological functioning of the Delta.

Key words: Environmental factors, flooding, flood plain, Okavango Delta and vegetation.

Introduction

Seasonal floodplain plant communities are an important component of the ecology of the wetland ecosystems. They are dynamic and heterogeneous (Benstead et al. 1997; Toogood et al. 2008) with their species composition and distribution influenced by the variation in seasonal flooding, which is a function of topography (Merritt et al. 2009; Oliveria-Filho et al. 1994; Toogood, Joyce & Waite 2008). Lowly elevated floodplains usually have higher water levels and longer flooding duration than highly elevated ones (Growing, Spoor & Mountford 1998). This results in the lowly elevated floodplains being dominated by flood tolerant species such as *Hydrilla verticillata* (L.f.) Royle, which grows well when fully submerged and *Typha angustifolia* L. (Cronk & Fennessy 2000). Highly elevated floodplains are dominated by flood intolerant species such as *Chrysopogon nigritanus* (Benth.) Veldkamp, *Sporobolus spicatus* (Vahl) Kunth and *Imperata cylindrica* (L.) Raeusch. (Bonyongo, Bredenkamp & Veenendaal 2000).

The influence of flooding on plants is reflected in seasonal floodplain vegetation community composition and distribution (Oliveria-Filho et al. 1994). Each plant species is morphologically and physiologically adapted to a range of flooding depth and duration conditions (Cronk & Fennessy 2001; Edwards & Kollman 2002; Merritt et al. 2009). Morphological adaptation to flooding such as growth of hytrophied lenticels, aerenchyma tissue and adventitious roots enhance oxygen transport in plants, enabling them to survive flooding conditions (Kozlowski 1984). Physiological adaptations to flooding include germination inhibition, glycolysis and ethylene production (Naiman & Decamps 1997).

The influence of environmental factors that influence the plant species composition and distribution in seasonal floodplain communities has been studied in several wetland ecosystems such as the Pantanal (Pinder & Rosso 1998; Ponce & Da Cunha 1993), the Amazon (Junk 1997; Parolin et al. 2006), the Everglades (Davis & Ogden 1993), the Kafue (Rees 1978), including the Okavango Delta (Biggs 1976; Bonyongo et al. 2000; Ellery, Ellery & McCarthy 1993; Ellery & Tacheba 2003; Murray-Hudson 2009; Smith 1976; Tsheboeng, Bonyongo & Murray-Hudson 2014). In these wetlands flooding has been identified as the primary driver of the

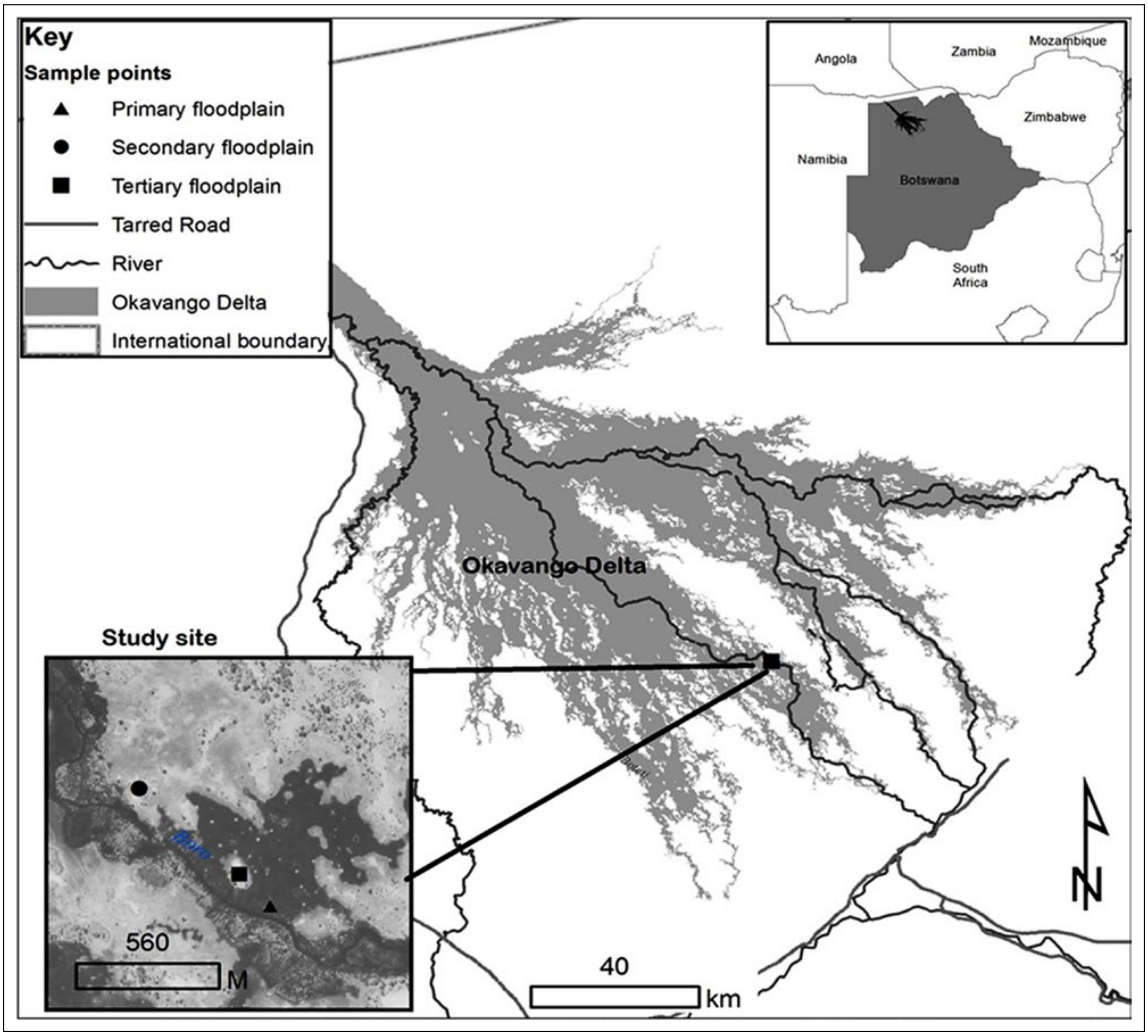

Figure 1. Map showing location of Nxaraga where the study was conducted. From Tsheboeng et al. (2014).

Table 1: Hydrological regions in the Okavango Delta

Region	Area covered (km²)	Hydroperiod characteristics	Common plant species
Permanent swamp	2 500	Flooded all year round	*Phragmites australis* (Cav.) Trin. ex Steud, *Cyperus papyrus* L and *P. mauritianus* Kunth
Primary floodplain	690	Flooded every year for 6 to 8 months. May be flooded for 12 months during high flood	*Cyperus articulatus* L, *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal and *Miscanthus junceus* (Stapf) Pilg.
Secondary floodplain	1 347	Flooded up to 5 months	*Panicum repens* L, *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex Moss and *Eragrostis inamoena* K.Schum.
Tertiary floodplain	7 100	Variable hydroperiod	*Sporobolus spicatus* (Vahl) Kunth and *Cynodon dactylon* (L) Pers.

Adapted from Gumbricht et al. (2004).

plant species composition and distribution in seasonal floodplain communities (Pinder & Rosso 1998; Ponce & Cunha 1993; De Oliveira et al. 2014).

In the Okavango Delta, previous studies have also attributed plant species composition and distribution in seasonal floodplain communities to flooding depth (Bonyongo et al. 2000; Murray-Hudson 2009). It has also been found that other environmental factors, including distance from the water source, ground water electrical conductivity, pH, soil chemistry (Ellery et al. 1993), timing of inundation, soil salinity, and nutrient and sediment supply (Ellery & Tacheba 2003) were responsible for controlling the species composition and distribution in seasonal floodplain plant communities. However, these conclusions were based on studies conducted during low flood. As a result they do not provide information on significant environmental factors determining seasonal floodplain vegetation community composition and distribution during a high flood.

Furthermore, the previous studies on the species composition and distribution of seasonal floodplain communities did not consider the intra-flooding variation phases of middle of rainfall season, before flooding and after flooding. To address this, the current study aimed to investigate environmental factors determining seasonal floodplain vegetation community composition and distribution before flooding and after flooding during a high flood year in the Okavango Delta. It was hypothesised that environmental factors that influence the species composition and distribution in seasonal floodplain communities in the Okavango Delta will vary with flooding phases.

Materials and methods

Study site

This study was conducted in the Okavango Delta in the Nxaraga lagoon area (Figure 1).

The Okavango Delta is fed by local rainfall and seasonal floods from the Angolan highlands (Gumbricht, McCarthy & McCarthy 2004), which are asynchronous (McCarthy & Ellery 1998). The total flooded area in the Okavango Delta ranges between 4 000 km^2 and 13 000 km^2 (McCarthy 2006). This variation is influenced by the seasonal variation in the local rainfall and flood discharge (Gumbricht et al. 2004). The Delta receives the lowest inflow between September and November and receives the highest inflow between March and April (McCarthy & Ellery 1998). Mean maximum rainfall in the Okavango Delta ranges between 300 and 550 mm/year (Wilson & Dincer 1976). The annual mean flood discharge ranges between 6.0×10^9 m^3 and 16.4×10^9 m^3 (Gumbricht et al. 2004) of which approximately 96% is lost through evapotranspiration while 2% is lost through infiltration (Wilson & Dincer 1976). Another 2% is lost as outflow through Thamalakane River (Wilson & Dincer 1976).

There are three hydrological regions in the Delta namely: permanent swamp, seasonally flooded floodplains (primary and secondary floodplains) and occasionally flooded floodplains (tertiary floodplains) (Gumbricht et al. 2004). Each hydrological region is characterised by a particular range of hydroperiod (Wolski et al. 2006) and associated vegetation communities (Bonyongo et al. 2000) (Table 1).

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°C respectively (Ellery 1991). 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 1991).

Hydrology and vegetation sampling

Flooding depth (in centimetres) was measured using a calibrated 2 m PVC pipe in mid-May 2010 (flood propagation) and end of September 2010 (flood recession).

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

It was measured in 25 m^2 permanent plots in each of the hydrological regions (Table 1) per flooding season (before flooding and flood recession) where vegetation and soil were also sampled. A total of 40 plots were sampled. The soils were collected from the centre of each permanent plot using a soil auger at a maximum depth of 30 m. Flooding duration was recorded as the number of weeks in which the permanent plots remained inundated.

Vegetation was sampled from randomly selected plots during the same period when flooding parameters were sampled. The plots were placed in different floodplains of primary (10 plots), secondary (15 plots) and tertiary (15 plots) (Bonyongo et al. 2000; Gumbricht et al. 2004; Table 1). The dimension for the vegetation plots were 5 × 5 m. This is the minimal sampling plot area that was determined by Bonyongo et al. (2000) for sampling the seasonal floodplain vegetation in this study area. In each plot, plant percentage cover was estimated following the modified method by Braun-Blanquet (Mueller-Dombois & Ellenberg 1974). The Braun-Blanquet method was used to estimate plant species percentage cover using an ordinal scale (Table 2). Percentage cover was estimated for the emergent plant species only.

Measured environmental variables

The soil was sampled before and 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 at a depth of 30 cm from the same 25 m^2 plots where plant species were sampled. A detailed analysis of soil samples is given in Tsheboeng et al. (2014).

Statistical data analysis

The relationship between environmental variables and seasonal floodplain vegetation community composition and distribution was sought using Non-metric Multidimensional Scaling (NMS) (Kruskal 1964; Mather 1976) in PC-ORD version 6. 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. The total 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 & Grace 2000), hence it was suitable for analysing the relationship between seasonal floodplain vegetation communities and environmental variables in the Okavango Delta. The paired *Student's t* test was used to compare means of environmental variables before and after flooding.

Results

Flooding depth was significantly ($p < 0.05$) higher in all hydrological zones after flooding than before flooding (Table 3). The content of K, Ca and flooding duration were significantly higher ($p < 0.05$) before than after floods (Table 3).

Table 3: Mean (± standard error) soil nutrient content before flooding and after flood recession in seasonal floodplain zones (N = 40)

Environmental variables	Before flooding	After flooding	*p* value
Na	246.92 ± 218.91 mg/kg	177.73 ± 103.29 mg/kg	0.159
Mg	405.87 ± 389.24 mg/kg	297.59 ± 188.0 mg/kg	0.284
K	487.53 ± 367.68 mg/kg	322.05 ± 170.59 mg/kg	0.042*
Ca	1297.30 ± 1173.43 mg/kg	560.94 ± 378.53 mg/kg	0.028*
P	2380.45 ± 546.78 mg/kg	2565.64 ± 723.06 mg/kg	0.488
pH	6.87 ± 0.95	6.74 ± 0.77	0.565
Flooding duration (weeks)	68	54	0.0001*
Mean flooding depth	36.5 ± 15.01 cm	73.65 ± 22.64 cm	0.137

*Significant difference at $p < 0.05$.

Factors that influence floodplain plant community composition and distribution

Before floods factors

NMS ordination showed that before flooding, important factors that influence the distribution of seasonal floodplain communities were Na, K, flooding depth and flooding duration (Figure 2).

Before flooding Na, Mg, K, Ca and pH were negatively correlated with species along Axis 1, but positively correlated to those along Axis 2. Flooding duration and P were negatively correlated with species oriented along Axis 2 while flooding depth was positively correlated to both axes (Table 4 and Figure 2).

After flooding

After flooding the significant factors that influenced the species composition in seasonal floodplain communities

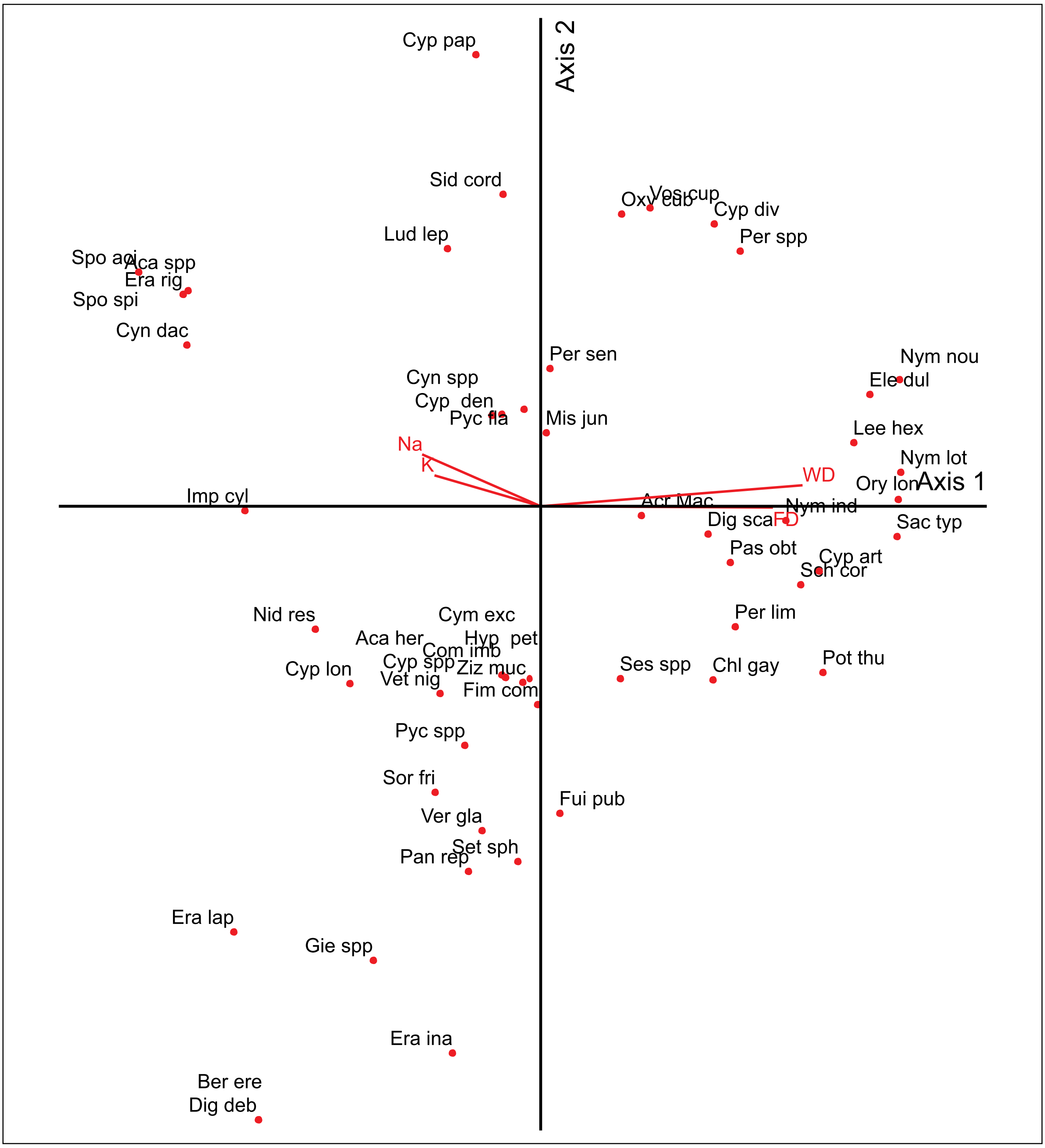

Figure 2. A biplot showing the interaction between Na, K, flooding depth (WD) and flooding duration (FD) and seasonal floodplain species before flooding.

were K, Na, Mg, pH, flooding depth and flooding duration (Figure 3).

After flooding Na, Mg, K and Ca were negatively correlated with species distributed along axes 1 and 2. Flooding duration and pH were negatively correlated to axes 1 and 2 respectively. Flooding depth was positively correlated to both axes, while P was negatively correlated to species along axis 2 (Table 5 and Figure 3).

Discussion

This study showed that there was variation in environmental factors that influence species composition and distribution of seasonal floodplain plant communities in the Okavango Delta. Factors that significantly influenced plant species composition before flooding are Na, K, water depth and flooding duration. However,

Figure 3: A biplot showing the interaction between Na, K, Mg, pH, flooding depth (WD) and flooding duration (FD) and seasonal floodplain species after flooding.

Table 4: The relationship between environmental variables and species distribution along ordination axes before flooding (N = 40)

Environmental factor	1	2
	r	r
Na	-0.474	0.314
Mg	-0.306	0.148
K	-0.448	0.239
Ca	-0.288	0.067
P	0.137	-0.154
pH	-0.357	0.210
Flooding duration (weeks)	0.660	-0.035
Flooding depth	0.701	0.039

after flooding there were additional factors of K, Mg and pH. This suggests that during flooding these cations are deposited on floodplains due to lateral water flow resulting in their increased concentration in these habitats. Another explanation of this could be evapo-concentration of K and Mg as the flood recedes, which results in increased concentrations of these elements. As a result their influence on the composition and distribution of seasonal floodplains becomes significant.

Species whose distribution was influenced by Na, Mg, K and pH include *Sporobolus spicatus*, *Sporobolus acinifolius* Stapf, *Cynodon dactylon* and *Imperata cylindrica*. These species are generally adapted to saline conditions that are associated with these chemicals. *Sporobolus* species are adapted to salinity through increased area of the root; stem, leaf blade and leaf sheath (Hameed, Ashraf & Naz 2011). Enlargement of these organs enhance the excretion of saline ions such as Na^+ and Cl^- in large quantities (Flowers & Colmer 2008). To further enhance the excretion of saline ions, *Sporobolus* species have increased vesicular hair density and developed aerenchyma tissue (Hameed, Ashraf & Naz 2011). *Cynodon dactylon* survives saline conditions through exclusion of toxic ions through leaves enhanced by increased density of vesicular hairs on both adaxial and abaxial leaf surfaces (Marcum 1999). *Imperata cylindrica* has also been found to survive saline conditions in wetland ecosystems (McDonald 2004). This plant copes with salinity through anatomical adaptations such as increased succulence of the midrib and cortical parenchyma, which may help in the sequestration of ions (Hameed, Ashraf & Naz 2009). In addition to this, Hameed, Ashraf & Naz (2009) found that *Imperata cylindrica* develops enlarged bulliform cells, which help in folding the leaves to minimise water loss during salt stress. Other anatomical adaptation strategies in *Imperata cylindrica* include reduced root area, which helps it to absorb Na^+ and Cl^- in lower quantities and development of aerenchyma tissue to enhance ion excretion (Hameed, Ashraf & Naz 2011).

Flooding duration and depth influenced species composition and distribution before flooding and after flooding. This may have implications for their survival during drought conditions caused by climate change. It is predicted that hydrological changes resulting from climate change will affect species composition and distribution such that only species that are tolerant of drought conditions survive during low water levels (Middleton 2009). The influence of flooding duration and depth is important from a management point of view in the Okavango Delta. Flooding can be manipulated from upstream impoundments of the Okavango River Basin, which will reduce the inflow into the distal regions such as the Okavango Delta in Botswana, which in turn may result in changes in floodplain species community composition and distribution. This suggests that any water abstraction from the Okavango River Basin should take into consideration the fact that flooding duration and depth are important in sustaining the species composition and distribution of seasonal floodplain plant communities such that those developments do not disturb this. However, experimental studies are still needed to give accurate predictions of seasonal floodplain plant communities to flooding duration and depth. In this study, species that were influenced by water depth include *Oryza longistaminata* A.Chev. & Roehr, *Nymphaea lotus* L., *Leersia hexandra* Sw., *Eleocharis dulcis* (Burm.f.) Trin. ex Hensch and *Nymphaea nouchali* Burm.f. These species are tolerant of prolonged flooding duration and high depth. They survive flooding conditions through development of fleshy, hollow stems and adventitious roots that grow from the submerged nodes (Ellenbroek 2012). These adaptations help in the absorption of oxygen and carbon dioxide for the processes of respiration and photosynthesis respectively. For the absorption of light they have developed large leaves to increase the surface area (Ellenbroek 2012).

The findings of this study also agree with results from studies conducted elsewhere (e.g. Gregory et al. 1991;

Table 5: The relationship between environmental variables and species distribution along ordination axes after flooding (N = 40)

Axis	1	2
	r	r
Na	-0.521	-0.139
Mg	-0.540	-0.027
K	-0.565	-0.217
Ca	-0.353	-0.237
P	0.142	-0.148
pH	-0.774	0.091
Flooding duration (weeks)	0.660	-0.314
Flooding depth	0.660	0.035

Junk 1997; Rees 1978; Zeilhofer & Schessl 1999). However, it should be noted that these studies did not investigate the intra-annual variation of environmental factors that influence the species composition and distribution in seasonal floodplain communities. In a study in the Pantanal seasonal floodplains, Zeilhofer and Schessl (1999) found that seasonal floodplain vegetation community composition and distribution were influenced by flooding depth and duration gradient. A short grassland vegetation community dominated by flood tolerant *Vochysia divergens* Pohl was found in longer-duration, deeply flooded sites, whereas a medium tall grassland vegetation community occurred in areas experiencing short flooding duration and shallow flooding depth. The influence of flooding depth and duration on seasonal floodplain plant communities was also observed in the Amazon seasonal floodplains (Gregory et al. 1991; Junk 1997; De Simone et al. 2003). The findings of Rees (1978) from a study conducted in the Kafue seasonal floodplains also agree with the observation made in this study. In that study, floodplain plant communities were distributed according to their tolerance to flooding duration and depth gradient. Regions that were frequently flooded with high flooding duration and depth were dominated by *Vossia cuspidata* (Roxb.) Griff and *Echinochloa stagnina* (Retz.) P.Beauv. In the Okavango Delta past studies also found that flooding duration and depth influence vegetation community composition and distribution (e.g. Biggs 1976; Bonyongo et al. 2000; Ellery & Tacheba 2003; Ellery et al. 1993; Murray-Hudson 2009; Smith 1976; Tsheboeng et al. 2014).

Conclusion and implications for management of floodplain plant communities in the Okavango Delta

This study has shown that there are seasonal variations in the environmental factors that influence the species composition and distribution of seasonal floodplain plant communities in the Okavango Delta. Factors that influenced plant species composition and distribution before flooding were Na, K, water depth and flooding duration. After flooding there were additional factors of K, Mg, pH. From a management perspective, this study suggests that the influence of these environmental factors should be considered before any major developments such as impoundments are implemented so that the species composition and distribution are not disturbed. To make accurate quantitative projections on the changes of species composition and distribution that may result from changes in hydrological regime, future experimental studies are needed. Those studies should quantify the quantity of water needed to sustain the seasonal floodplain plant communities in the Okavango Delta. Future studies should also investigate the changes in soil nutrient content and toxic substances associated with extended flooding duration. Such studies should also investigate the influence of flooding on primary production of seasonal plant communities.

Acknowledgements

The authors would like to thank the Carnegie-RISE Corporation of New York for sponsoring this study. We would also like to thank Mr K. Makati and Mr I. Mosie who helped with field data collection. The Environmental Laboratory at the Okavango Research Institute (ORI) is thanked for helping with soil sample analysis. We would like to thank the staff at Pete Smith University of Botswana Herbarium at the Okavango Research Institute for helping with identification of plant specimen.

Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Author's contributions

GT, MB & MM-H designed the study. GT & MB collected data. GT analysed data and wrote the manuscript. MM-H and MB commented on the initial drafts of the manuscript.

References

Benstead, P., Drake, M., Jose, P., Mountford, O., Newbold, C. & Treweek, J., 1997, 'The grassland guide. Managing flooding and coastal wet grasslands for wildlife', RSBP. Royal Society for the Protection of Birds, Sandy, UK.

Biggs, R.C., 1976, 'The ecology of chief's island and adjacent floodplains of the Okavango Delta', Proceedings of the symposium on the Okavango Delta and its future utilization held in Gaborone, Botswana. Gaborone, Botswana.

Bonyongo, M.C., Bredenkamp, G.J. & Veenendaal, E., 2000, 'Floodplain vegetation in the Nxaraga Lagoon area, Okavango Delta, Botswana', *South African Journal of Botany* 66, 15–21, DOI: 10.1016/S0254-6299(15)31046-2.

Cronk, J.K. & Fennessy, M.S., 2001, 'Wetland plants: biology and ecology', CRC Lewis Publishers, New York.

Davis, S.M. & Ogden, J.C., 1993, 'Everglades: The ecosystem and its restoration', St. Lucie Press, Delray Beach, Florida

De Oliveira, M.T., Damasceno-Junior, G.A., Pott, A., Filho, A.C., Suarez, Y.R. & Parolin, P., 2014, 'Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence,' *Forest Ecology and Management* 331, 256–263, DOI: 10.1016/j.foreco.2014.08.011.

De Simone, O., Junk, W.J. & Schmidt, W., 2003, 'Central Amazon Floodplain Forest: root adaptations to flooding', *Russian Journal of Plant Physiology* 50, 848–855, https://doi.org/10.1023/B:RUPP.0000003285.70058.4c.

Edwards, P.J. & Kollman, J., 2002, 'Life history of evolution in Lodoicea maldivica (Arecaceae),' *Nordic Journal of Botany* 22, 227–238, https://doi.org/10.1111/j.1756-1051.2002.tb01371.x.

Ellenbroek, G.A., 2012, 'Ecology and productivity of an African wetland system: the Kafue Flats, Zambia', Dr W. Junk Publishers, Dordrecht.

Ellery, K., Ellery, W.N., Rogers, K.H. et al., 1991, 'Water depth and biotic insulation: Major determinants of backswamp plant community composition', *Wetlands Ecology and Management* 1, 149–162, https://doi.org/10.1007/BF00177289.

Ellery, W.N. & Tacheba, B., 2003, 'Floristic Diversity of the Okavango Delta, Botswana', In: Alonso, L.E. & Nordin, L.A (eds), 'A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: High water survey', RAP-Bulletin of Biological Assessment 25, 69–96.

Ellery, W.N., Ellery, K. & McCarthy, T.S., 1993, 'Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions', *African Journal of Ecology* 31, 118–134, https://doi.org/10.1111/j.1365-2028.1993.tb00526.x.

Flowers T.J. & Colmer, T.D., 2008, 'Salinity tolerance in halophytes', *New Phytologist* 179, 945–963, https://doi.org/10.1111/j.1469-8137.2008.02531.x.

Gregory, S.V., Swanson, F.J., Mckee, W.A. & Cummins, K.W., 1991, 'Ecosystem perspective of riparian zones', *Bioscience* 41, 540–551, DOI: 10.2307/1311607.

Growing, D.J.G., Spoor, G. & Mountford, O. 1998, 'The influence of minor variations in hydrological regime on grassland plant communities: implications for water management', In: 'Joyce, C.B & Wade, P.M (eds), European wet grasslands: biodiversity, management and restoration', Wiley, Chichester, 217–227.

Gumbricht, T., McCarthy, J. & McCarthy, T.S., 2004, 'Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes', *Earth Surf. Process Landforms* 29, 15–29, DOI: 10.1002/esp.1008.

Hameed, M., Ashraf, M. & Naz, N. 2009, 'Anatomical adaptations to salinity in cogon grass (Imperata cylindrical (L.) Raeuschel) from the Salt Range, Pakistan', *Plant and Soil* 322: 229–238, DOI: 10.1007/s11104-009-9911-6.

Hameed, M., Ashraf, M. & Naz, N., 2011, 'Anatomical and physiological characteristics relating to ionic relations in some salt tolerant grasses from the Salt Range, Pakistan', *Acta Physiologiae Plantarum*', 33, 1399–1409, DOI: 10.1007/s11738-010-0674-8.

Junk, W.J., 1997, 'General aspects of floodplain ecology with special reference to Amazonian floodplains', In Junk, W.J (ed), 'The central Amazon floodplain: Ecology of a pulsing system – Ecological Studies', 126, 3–20.

Kozlowski, T.T., 1984, 'Plant responses to flooding of soil', *Bioscience* 34,162–167.

Kruskal, J.B., 1964, 'Nonmetric multidimensional scaling: a numerical method', *Psychometrika* 29, 115–129, https://doi.org/10.1007/BF02289694.

MacDonald, G.E., 2004, 'Cogongrass (Imperata cylindrica) – biology, ecology, and management', *Critical Reviews in Plant Sciences* 23, 367–380, https://doi.org/10.1080/07352680490505114.

Marcum, K.B., 1999, 'Salinity tolerance mechanisms of grasses in the subfamily Chloridoideae', *Crop Science* 39, 1153–1160, https://doi.org/10.2135/cropsci1999.0011183X003900040034x.

Mather, P.M., 1976, 'Computational methods of multivariate analysis in physical geography', John Wiley and Sons, London.

McCarthy, T.S. & Ellery, W.N., 1998, 'The Okavango Delta', *Transactions of the Royal Society of South Africa* 53, 157–182, https://doi.org/10.1080/00359199809520384.

McCarthy, T.S., 2006, 'Groundwater in the wetlands of the Okavango Delta, Botswana, and its contribution to the structure and function of the ecosystem', *Journal of Hydrology*, 320, 264–282, https://doi.org/10.1016/j.jhydrol.2005.07.045.

McCune, B. & Grace, J.B., 2000, 'Analysis of ecological communities', MjM software, Gleneden Beach, Oregon, U.S.A.

Merritt, D.M., Scott, M.L., Poff, N.L., Auble, G.T. & Lytle, D.A., 2009, 'Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds', *Freshwater Biology*, 55, 206–225, doi:10.1111/j.1365-2427.2009.02206.x.

Middleton, B.A., 2009, 'Vegetation status of the Keoladeo National Park, Bharatpur, Rajasthan, India', US Geological Survey, Report 2009-5193.

Mueller-Dombois, D. & Ellenberg, H., 1974, 'Aims and methods of vegetation ecology', John Wiley & Sons, New York.

Murray-Hudson, M. 2009, 'Floodplain vegetation responses to flood regime in the seasonal Okavango Delta, Botswana', PhD thesis, University of Florida, Florida.

Naiman, R.J. & Decamps, H., 1997, 'The ecology of interfaces: Riparian zones', *Annual Review of Ecology and Systematics* 28, 621–658, https://doi.org/10.1146/annurev.ecolsys.28.1.621.

Oliveira-Filho, A.T., Vilela, E.A., Gavilanes, M.L. & Carvalho, D.A., 1994, 'Effects of flooding regime on understorey bamboos on the physiognomy and tree species composition of a tropical semi-deciduous forest in southern Brazil', *Vegetation* 113, 99–124, https://doi.org/10.1007/BF00044229.

Parolin, P., Ambrüster, N. & Junk, W.J., 2006, 'Two Amazonia trees react differently to periodical flooding', *Tropical Ecology* 47, 243–250.

Pinder, L. & Rosso, S., 1998, 'Classification and ordination of plant formations in the Pantanal of Brazil', *Plant Ecology* 136, 151–165, https://doi.org/10.1023/A:1009796616824.

Ponce, V.M. & Da Cunha, C.N., 1993, 'Vegetated earth mounds in tropical savannas of central Brazil: A synthesis', *Journal of Biogeography*, 20, 219–225.

Rees, W.A., 1978, 'The Ecology of Kafue Lechwe: soils, water levels and vegetation', *Journal of Applied Ecology* 15, 163–176, DOI: 10.2307/2402928.

Smith, P., 1976, 'An outline of the vegetation of the Okavango Drainage system', Proceedings of the symposium on the Okavango Delta and its future utilization, National museum, Gaborone, Botswana.

Toogood, S.E., Joyce, S. & Waite, S., 2008, 'Response of floodplain grassland communities to altered water regimes', *Plant Ecology* 197, 285–298, DOI: 10.1007/s11258-007-9378-6.

Tsheboeng, G., Bonyongo, M. & Murray-Hudson, M., 2014, 'Flood variation and soil nutrient content in floodplain vegetation communities in the Okavango Delta', *South African Journal of Science* 110, 1–5.

Wilson, B.H. & Dincer, T., 1976, 'An introduction to the hydrology and hydrography of the Okavango Delta', Proceedings of the Symposium on the Okavango Delta and its future utilization, National Museum, Gaborone, Botswana.

Wolski, P., Savenije, H.H.G., Murray-Hudson, M. & Gumbricht, M., 2006, 'Modelling of the flooding in the Okavango Delta, Botswana, using a GIS model', *Journal of Hydrology* 331, 58–72, DOI: 10.1016/j.jhydrol.2006.04.040.

Zeilhofer, P. & Schessl, M., 2000, 'Relationship between vegetation and environmental conditions in the Northern Pantanal of Mato Grosso, Brazil', *Journal of Biogeography* 27, 159–168, https://doi.org/10.1046/j.1365-2699.2000.00357.x.

Supplementary Information

Supplementary Table 1: Full plant species names for Figures 2 and 3. *Please note that some of these names are no longer considered to be current (e.g. *Acacia erioloba*), however, since these are the names that were entered into the software used for the analyses, they are provided here for reference purposes.

Abbreviation	Full name
Aca eri	*Acacia erioloba*
Aca heb	*Acacia hebeclada*
Acr mac	*Acroceras macrum*
Ber ere	*Berula erecta*
Chl gay	*Chloris gayana*
Com imb	*Combretum imberbe*
Cyc tub	*Cycnium tubulosum*
Cym exc	*Cymbopogon excavatus*
Cyn dac	*Cynodon dactylon*
Cyp art	*Cyperus articulatus*
Cyp den	*Cyperus denudatus*
Cyp div	*Cyperus dives*
Cyp lon	*Cyperus longus*
Cyp pap	*Cyperus papyrus*
Dig deb	*Digitaria debilis*
Dig sca	*Digitaria scalarum*
Ele dul	*Eleocharis dulcis*
Era ina	*Eragrostis inamoena*
Era lap	*Eragrostisl appula*
Era rig	*Eragrostis rigidior*
Fim com	*Fimbristylis complanata*
Fui pub	*Fuirena pubescens*
Gis afr	*Gisekia africana*
Gom fru	*Gomphocarpus fruticosus*
Hyp pef	*Hyphaene petersiana*
Imp cyl	*Imperata cylindrica*
Lee hex	*Leersia hexandra*

Abbreviation	Full name
Lud lep	*Ludwigia stolonifera*
Mis jun	*Miscanthus junceus*
Nid res	*Niderolla resedifolia*
Nym ind	*Nymphoides indica*
Nym lot	*Nymphoides lotus*
Nymnou	*Nymphoides nouchali*
Ory lon	*Oryza longistaminata*
Oxy cub	*Oxycaryum cubense*
Pan rep	*Panicum repens*
Pas obt	*Paspalidium obtusifolium*
Pec-loe	*Pechuel-loeschea leubnitziae*
Per lim	*Persicaria limbata*
Per sen	*Persicaria senegalensis*
Pot thu	*Potamogetum thunbergii*
Pyc fla	*Pycreus flavescens*
Sac typ	*Sacciolepis typhura*
Sch cor	*Schoenoplectus corymbosus*
Set sph	*Setaria sphacelata*
Sid cord	*Sida cordifolia*
Sor fri	*Sorghastrum friesii*
Sph fri	*Sphaeranthus friesii*
Spo aci	*Sporobolus acinifolius*
Spo spi	*Sporobolus spicatus*
Ver gla	*Vernonia glabra*
Vet nig	*Vetiveria nigritana*
Vos cusp	*Vossia cuspidata*
Ziz muc	*Ziziphus mucronata*