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 m² 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 m² 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 (Bent stead 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.) Raesch. (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](http://abcjournal.org)

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).

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).
It was measured in 25 m² 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 m² 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>
<thead>
<tr>
<th>Environmental variables</th>
<th>Before flooding</th>
<th>After flooding</th>
<th>( p ) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Na</td>
<td>246.92 ± 218.91 mg/kg</td>
<td>177.73 ± 103.29 mg/kg</td>
<td>0.159</td>
</tr>
<tr>
<td>Mg</td>
<td>405.87 ± 389.24 mg/kg</td>
<td>297.59 ± 188.0 mg/kg</td>
<td>0.284</td>
</tr>
<tr>
<td>K</td>
<td>487.53 ± 367.68 mg/kg</td>
<td>322.05 ± 170.59 mg/kg</td>
<td>0.042*</td>
</tr>
<tr>
<td>Ca</td>
<td>1297.30 ± 1173.43 mg/kg</td>
<td>560.94 ± 378.33 mg/kg</td>
<td>0.028*</td>
</tr>
<tr>
<td>P</td>
<td>2380.45 ± 546.78 mg/kg</td>
<td>2565.64 ± 723.06 mg/kg</td>
<td>0.488</td>
</tr>
<tr>
<td>pH</td>
<td>6.87 ± 0.95</td>
<td>6.74 ± 0.77</td>
<td>0.565</td>
</tr>
<tr>
<td>Flooding duration (weeks)</td>
<td>68</td>
<td>54</td>
<td>0.0001*</td>
</tr>
<tr>
<td>Mean flooding depth</td>
<td>36.5 ± 15.01 cm</td>
<td>73.65 ± 22.64 cm</td>
<td>0.137</td>
</tr>
</tbody>
</table>

*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

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**Figure 2.** A biplot showing the interaction between Na, K, flooding depth (WD) and flooding duration (FD) and seasonal floodplain species before flooding.
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,
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 acini-folius 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 enhances 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 bulkiform 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;...
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 Vochysi a 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 Echinocloa 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

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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


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<th>Title</th>
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<th>DOI</th>
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## 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.

<table>
<thead>
<tr>
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<th>Full name</th>
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<tr>
<td>Aca eri</td>
<td><em>Acacia erioloba</em></td>
</tr>
<tr>
<td>Aca heb</td>
<td><em>Acacia hebeclada</em></td>
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<tr>
<td>Acr mac</td>
<td><em>Acroceras macrum</em></td>
</tr>
<tr>
<td>Ber ere</td>
<td><em>Berula erecta</em></td>
</tr>
<tr>
<td>Chl gay</td>
<td><em>Chloris gayana</em></td>
</tr>
<tr>
<td>Com imb</td>
<td><em>Combretum imberbe</em></td>
</tr>
<tr>
<td>Cyc tub</td>
<td><em>Cycnium tubulosum</em></td>
</tr>
<tr>
<td>Cym exc</td>
<td><em>Cymbopogon excavatus</em></td>
</tr>
<tr>
<td>Cyn dac</td>
<td><em>Cynodon dactylon</em></td>
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<tr>
<td>Cyp art</td>
<td><em>Cyperus articulatus</em></td>
</tr>
<tr>
<td>Cyp den</td>
<td><em>Cyperus denuudatus</em></td>
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<tr>
<td>Cyp div</td>
<td><em>Cyperus dives</em></td>
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<td>Cyp lon</td>
<td><em>Cyperus longus</em></td>
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<tr>
<td>Cyp pap</td>
<td><em>Cyperus papyrus</em></td>
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<td>Dig deb</td>
<td><em>Digitaria debilis</em></td>
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<tr>
<td>Dig sca</td>
<td><em>Digitaria scalarum</em></td>
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<tr>
<td>Ele dul</td>
<td><em>Eleocharis dulcis</em></td>
</tr>
<tr>
<td>Era ina</td>
<td><em>Eragrostis inamoena</em></td>
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<tr>
<td>Era lap</td>
<td><em>Eragrostis appula</em></td>
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<tr>
<td>Era rig</td>
<td><em>Eragrostis rigidior</em></td>
</tr>
<tr>
<td>Fim com</td>
<td><em>Fimbristylis complanata</em></td>
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<tr>
<td>Fui pub</td>
<td><em>Fuirena pubescens</em></td>
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<td><em>Gisekia africana</em></td>
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<td>Gom fru</td>
<td><em>Comphocarpus fruticosus</em></td>
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<td><em>Hyphaene persiana</em></td>
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<tr>
<td>Imp cyl</td>
<td><em>Imperata cylindrica</em></td>
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<tr>
<td>Lee hex</td>
<td><em>Leersia hexandra</em></td>
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<tr>
<td>Mis jun</td>
<td><em>Miscanthus junceus</em></td>
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<td>Nym lot</td>
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<td>Nymnou</td>
<td><em>Nymphoides nouchali</em></td>
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<td>Oxy cub</td>
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<td>Pan rep</td>
<td><em>Panicum repens</em></td>
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<td>Pas obt</td>
<td><em>Paspalidium obtusifolium</em></td>
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<td>Pec-loe</td>
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<td><em>Persicaria limbata</em></td>
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<td>Per sen</td>
<td><em>Persicaria senegalensis</em></td>
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<td>Pot thu</td>
<td><em>Potamogetum thunbergii</em></td>
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<td>Pyc fla</td>
<td><em>Pycreus flavescens</em></td>
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<td>Sac typ</td>
<td><em>Sacciolepis typhura</em></td>
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<tr>
<td>Sch cor</td>
<td><em>Schoenoplectus corymbosus</em></td>
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<td>Set sph</td>
<td><em>Setaria sphacelata</em></td>
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<td>Sid cord</td>
<td><em>Sida cordifolia</em></td>
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<td>Sor fri</td>
<td><em>Sorghastrum friesii</em></td>
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<td>Sph fri</td>
<td><em>Sphaeranthus friesii</em></td>
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<td><em>Sporobolus acinifolius</em></td>
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<td><em>Sporobolus spicatus</em></td>
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<td>Ziz muc</td>
<td><em>Ziziphus mucronata</em></td>
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*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.*