THUTO KE THEBE
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Population structure, species composition and distribution of riparian woody plant communities in the Okavango Delta, Botswana.

by

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Disclaimer

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Signature..

Dedication

This work is dedicated to my late mother Gabatsoswe Goitsemodimo who passed on when I was just about to finish my studies.

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Chapter 3: Tsheboeng, G., Murray-Hudson, M and Kashe, K., 2016. Classification of riparian plant communities along flooding frequency gradient in the Okavango Delta, Botswana. *IASTED, Environment and Water Resource Management* **Accepted.**

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Abstract

There is limited information on the species composition and distribution, population structure and dynamics and the underlying environmental controls of riparian woodland communities in the Okavango Delta. This study aimed to investigate these parameters, regeneration, and environmental controls of riparian woodland in the Okavango Delta. Tree species were identified in 101 (20 × 50m) plots. Sampling was done in 7 sites with different hydrological characteristics: Boro, Jao, Upper Panhandle, Seronga, Vumbura, Moremi and Santawani. Vegetation sampling was done from February 2012 to November 2013. The sampling plots were placed along a groundwater gradient from the main surface water body to the drier fringe of the riparian zone. Percentage canopy cover was estimated for each tree species from each plot using a Braun-Blanquet cover abundance scale. In each plot the circumference (>15cm) was measured from trees at 1.3m above ground level. The effect of land use on regeneration structure was studied by comparing the regeneration status of tree species between Moremi Game Reserve (Protected area) and Seronga (Communal, open-access area). Height of trees was estimated and individuals were assigned to 0-0.5m, 0.5-1m, 1-2m, 2-4m and >4m height classes. The influence of proximity to surface water was sought through subdividing each 20 × 50m plot into five 20m × 10m sub-plots, to give distance classes of 0-10m (closest to surface water), 10-20m, 20-30m, 30-40m and 40-50m (furthest from surface water). Tree height, basal area, species richness, cover and diversity were determined for each distance class. Vegetation communities were determined across sites with different flooding frequency regimes based on agglomerative hierarchical cluster analysis and indicator species analysis. Plant species and diversity were determined for each vegetation community. Multi-Response Permutation Procedures (MRPP) were used to evaluate the statistical validity of the separation between vegetation clusters. The Kruskal-Wallis test was used to compare species diversity and richness between vegetation communities. Independent sample Student's *t*-test was used to determine statistical difference in seedling density/ha and sapling density/ha between different sites. Indicator species analysis was used to determine the dominant species at each distance class and site. One-way ANOVA with Tukey test post hoc analysis were used to compare species diversity, richness, mean tree height, cover and basal area between distance classes and site. The four major vegetation communities identified were: *Croton megalobotrys-Hyphaene petersiana; Acacia erioloba-Diospyros lycioides*; *Syzygium cordatum-Phoenix reclinata;* and *Garcinia livingtonei-Acacia nigrescens.* Species richness was highest in the *Garcinia livingstonei-Senegalia nigrescens* community and lowest in the *Syzygium cordatum-Phoenix reclinata* community. MRPP showed that there was significant (p<0.05) difference between these vegetation communities. Species diversity and richness were significantly (p<0.05) higher in the *Garcinia livingstonei-Acacia nigrescens* community than in all others. Distance from surface water was positively correlated with all vegetation parameters except for mean species richness. Woodland community composition, density, cover and diversity varied significantly (p<0.05) between different sites. The population and regeneration structures of different riparian tree species varied with sites in the Delta. This study provided an inventory of riparian woodland plant communities which can be used as a baseline for future monitoring of vegetation change in the Okavango Delta. The results of this study imply that seed dispersal, germination and recruitment processes vary spatially. There is a potential to use woodland plant community composition and distribution and population structure to reconstruct the historical hydrological patterns of a given area where such information is not available.

Keywords: Flood, Indicator, Okavango, Vegetation and zonation

Thesis outline

Chapter 1 provides the general introduction of the study including the study area description and the problem statement. Chapters 2 to 7 are a series of manuscripts. Chapter 2 provides information on the classification of riparian plant communities while chapter 3 classifies riparian plant communities along flooding frequency gradient. Chapters 4 (within site) and 5 (inter-site) relate plant community composition and distribution to distance from river surface water. The population and regeneration structures of riparian plant communities are studied in chapters 6 and 7 respectively. Chapter 8 provides a synthesis of the key findings of the study.

Chapter 1: General Introduction

1.0 .0 Description of riparian ecosystems

Riparian plant communities occupy transition zones between terrestrial and aquatic systems which are characterized by gradients in environmental factors and ecological processes (Naiman et al., 1993). They are found in distinct zones along elevation (Nilsson and Svedmark, 2002), groundwater, flooding frequency and site-age gradients (Kalliola and Puhakka, 1988). In semi-arid environments, riparian plant communities are dynamic ecosystems showing high habitat heterogeneity and diverse ecological processes, and are often rich in biodiversity on the regional and continental scale (Naiman et al., 2005). Riparian zones play a significant role in riverine ecology through their direct and indirect effects on the hydrological cycle, water budget and soil moisture content (Simon et al., 2004). They also serve as natural bio-filters helping to prevent excessive sedimentation in aquatic environments thereby improving water quality (Reddy and Gale, 1994). Riparian zones help in temperature regulation through the provision of shade from vegetation (Daily, 1997). Vegetation in riparian zones through its root systems and stems disperses stream energy which helps in reducing soil erosion and flood damage (Carter, 1996). It also influences groundwater levels and flow rates through the process of evapotranspiration (Richardson et al., 2007). Riparian vegetation also serves as a diverse and productive habitat and food source to wildlife and domestic animals (Schulz and Leininger., 1990).

1.1.0 Distribution of riparian woody plant species in wetland ecosystems

On a global scale, wetland distribution is determined by climate, topography and geology (Cronk and Fennessy, 2000). There are different types of wetlands including salt marshes, tidal fresh water marshes, mangroves and peat lands covering approximately 6% surface area of the earth (Mitsch and Gosselink, 2000). Some of the major wetland systems along which riparian ecosystems are distributed include the Amazon, Pantanal in Brazil and the Everglades in Florida (Fraser and Keddy, 2005); the Okavango Delta in Botswana, Kafue flats in Zambia (Tumbare, 2004), Sudd on the Nile in Sudan, Inner Niger Delta in Mali and Mekong Delta in Vietnam (Mitsch and Gosselink, 2000). In these wetland systems the distribution of riparian woodland species may be influenced by flood pulse, depth to groundwater, the salinity of soil and water (Figure 1).

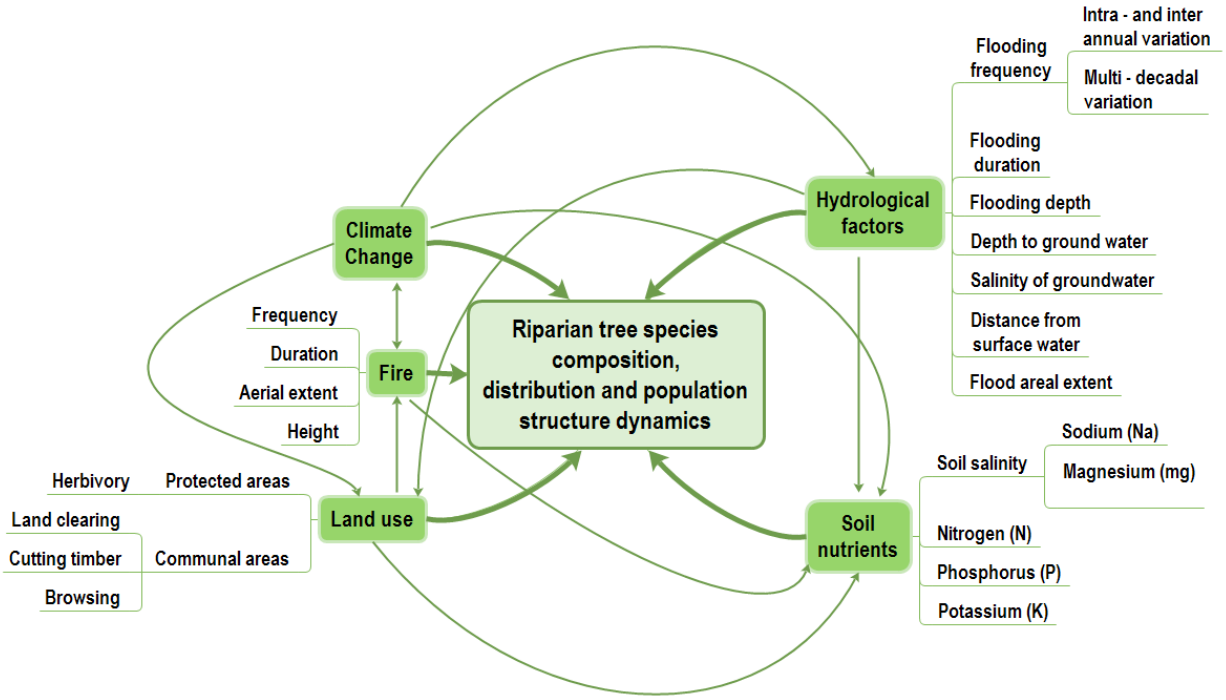

Figure 1: A conceptual framework of the factors that influence species composition and population structure of the riparian woodland communities. *This shows the interaction of the environmental variables in influencing the species composition, distribution and population structure of riparian trees. The direction of the arrow shows where the influence originates. The description of these factors is given in the preceding and following sections.*

1.1.1 Influence of flooding on the distribution and composition of riparian plant communities

The distribution of riparian woody species is influenced by environmental factors such as hydroperiod, which may be defined in terms of flood timing, frequency, depth and duration (Mitsch and Gosselink, 2000). Wetland plant species colonise sites with flooding depth, duration and frequency values to which they are adapted (Capon, 2005). Floods transport plant propagules and influence the soil moisture content in riparian woodland habitats (Friedman and Auble, 2000). Riparian plant diversity is highly variable due to variation in flooding regime (Gregory et al., 1991). Moist riparian zones in close proximity to the river channel are dominated by species tolerant of flooding while more elevated regions are inhabited by plant species less tolerant of flooding (Camporeale et al., 2005). Disturbance regimes from floods in riparian zones lead to higher species diversity than in adjacent upland terrestrial habitats (Gregory et al., 1991). During waterlogging which results from flooding, intolerant plant species die or do not germinate creating gaps for the establishment of flood tolerant ones (Denslow, 1980). This is in accordance with the Intermediate Disturbance Hypothesis (IDH), which states that biotic diversity and richness are expected to be high in habitats experiencing moderate (intermediate) disturbance levels (Connell, 1978). Disturbance regimes enable plant species with differing tolerances to co-exist resulting in an increase in diversity (Connell, 1978; Denslow, 1980).

In Central Amazonia it was found that plant species richness and diversity decreased with increasing flooding duration and depth (Ferreira and Stohlgren, 1999). This study supported the IDH in that there was higher species diversity in drier stream habitats than in riverine and lake habitats. In this case the drier stream and riverine habitats represent an intermediate level of disturbance. Out of a total of 54 species, the drier stream habitat had only six species that were unique to the drier conditions, while the riverine forest had 52 species with only three unique species (Ferreira and Stohlgren, 1999). This indicates that there was co-existence of species tolerant of dry and wet conditions in these habitats (Ferreira and Stohlgren, 1999) which supports the IDH as it predicts the co-existence of species tolerant of different conditions in response to intermediate levels of disturbance, resulting in high diversity (Connell, 1978). The lake habitat had a lower species richness of 33 with three unique to the lake conditions (Ferreira and Stohlgren, 1999). Even though the lake habitat had few unique species it appears that it may have experienced either high or low form of disturbance which excludes more species resulting in low species diversity. Lake habitats are usually light-limited, and there are also effects from permanent anoxic benthos and also the physiological stress of depth (Schindler and Scheurell, 2002). However, since these conditions are long-lived and not temporary (Schindler and Scheurell, 2002), they may not constitute a disturbance regime, or they may represent the low end of a disturbance regime. In another study conducted in the Waal and Ijssel rivers in the Netherlands, the abundance of woody plant species such as *Fraxinus excelsior* and *Quercus robur* decreased with increasing flooding duration (Vreugdenhil et al., 2006). This study also supported the IDH with an overall decrease in species richness with increasing flooding duration which progressively excluded flood intolerant species. These studies show that flooding is an important factor in influencing riparian tree species composition and distribution in wetland habitats. However, in the Okavango Delta the nature of the relationships between woody species and flood parameters has not been studied.

Generally plants are adapted to flooding through the development of aeranchyma tissue which facilitates oxygen transport under anaerobic conditions (Kozlowski, 1984; Ferreira and Stohlgren, 1999; Naiman et al., 2005). Other adaptations to flooding by woody plants include growth of adventitious roots and lenticels, reduction of photosynthesis, the capacity for anaerobic respiration and reduction in metabolism (Kozlowski, 1984). These adaptations enable woody plant species to inhabit wetland habitats and withstand the anoxic conditions associated with flooding. In the Pantanal *Inga vera* is the most abundant tree species adapted to grow in the riparian zones (Damasceno-Junior, 2005). Other common tree species in the Pantanal riparian regions include *Vochysia divergens*, *Cecropia pachystachya* and *Tabebuia heptaphylla* with *Albizia inundata* and *Triplaris gardneriana* dominant in the low regions (Damasceno-Junior, 2005). This indicates that riparian tree species are distributed along hydrological gradients to which they are adapted. This was also found in the Amazon wetlands where tree species richness was found to be negatively correlated with water level and flooding duration (Ferreira and Stohlgren, 1999). Tree species tolerant of flooding included *Macrolobium acaciaefolium*, *Burdachia primatocarpa* and *Eschweilera tenuifolia* (Ferreira and Stohlgren, 1999).

Other flood tolerant species in the Amazon wetlands that inhabit highly flooded areas include *Pseudobombax munguba*, *Laetia corymbulosa*, *Crataeva benthamii*, *Cecropia latiloba* and *Pterocarpus amazonum*. These species are adapted to a highly variable flooding depth which can reach 14m and a high flooding duration which may be up to 270 days annually (Junk, 1989). Generally, during the flooding phase their metabolic activity slows down, growth is reduced and complete dormancy is induced (Parolin and Wittmann, 2010). Examples of flood intolerant species in the Amazon include *Cecropia concolor*, *Vismia guinensis* and *V. japurensis* (dos Santos Junior et al., 2015). These species are not adapted to flooding as they experience a reduction in chlorophyll *a* in response to flooding which results in low photosynthesis (dos Santos Junior et al., 2015). In the Okavango Delta, riparian woodland species cannot tolerate extended periods of flooding; they generally access shallow groundwater from slightly elevated island and dryland margins (Ellery and Tacheba, 2003). Their tolerance of flooding has not been studied (Parolin and Wittmann, 2010). Common riparian tree species growing along the Tana River in Kenya include *Ficus sycomorus, Acacia elatior* and *Diospyros mespiliformis* (Hughes, 1990). *Ficus sycomorus* and *D. mespiliformis* also occur in the Okavango Delta (Ellery et al., 1993) which may imply that hydrological conditions in the Okavango Delta and the Tana River are similar. The Tana River floods between April and June which is the same period in which the

Delta is also flooded (McCarthy, 2006) but also has a shorter high flow between November and December (Hughes, 1990).

In the Congo River basin, riparian tree species are also distributed along flooding gradients to which they are adapted. Flood tolerant species in the Congo basin include *Alchornea cordifolia*, *Ficus asperifolia*, *Cleistopholis patens*, *Mimusops warneckei* and *Acio dewevrei* (Campbell, 2005). Occasionally flooded areas are colonised by flood intolerant species such as *Didelotia unifoliota*, *Guibourtia demeusei*, *Monopetalanthus pteridophyllum* and *Mitragyna stipulosa* (Campbell, 2005). In the Okavango Delta, the distribution of riparian tree species on the islands appears to be determined by soil and groundwater chemistry, distance from the water source, depth to groundwater and elevation (Ellery et al., 1993). Common riparian trees in the Delta include *Ficus natalensis*, *F. sycomorus*, *Diospyros mespiliformis*, *Phoenix reclinata* and *Garcinia livingstonei*, *Berchemia discolor*, *Senegalia nigrescens* and *Croton megalobotrys*, found on the fringes of the islands, with *Hyphaene petersiana* found on the island interiors (Ellery and McCarthy, 1994).

Flooding can also influence the productivity of riparian trees. It can lead to physical damage and uprooting of trees which may result in reduced growth and death (Richardson et al. 2007). Flooding can also lead to an overall reduction in plant photosynthesis (Pezeshki, 1994) which is a measure of productivity. This decline in photosynthesis results from reduced leaf water potential, low RuBisCo (Ribulose-1, 5-biphosphate carboxylase/oxygenase) activity (Pezeshki, 1994) and low leaf chlorophyll (McKevin et al., 1995). Leaf chlorophyll is critical for photosynthesis (Bowes, 1991). It absorbs sunlight which is used for the processes of photosynthesis while RuBisCO is a major enzyme involved in the production of glucose (Bowes, 1991). Due to low photosynthetic production, plant growth and accumulation of biomass are greatly reduced (Kozlowski, 2002). Low productivity could also result from reduced flow which leads to water supply below the plant's optimum requirements. That is, plants have different water requirements based on their tolerance to a given water availability range. If the water supply is above or below their optimum range, then physiological processes including productivity may be negatively affected or reduced (Kozlowski, 1984). Low water availability reduces plant regeneration which impedes vegetative and reproductive growth leading to low biomass accumulation and possibily eventual plant mortality (Kozlowski, 2002).

Flooding may also influence the resilience of riparian woodland communities (Stromberg and Richter, 1996). Resilience is defined as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity and feedbacks'' (Walker et al., 2004). The effect of flooding on the resilience of riparian plant communities is influenced by its role in the creation of suitable microsites for establishment of adapted riparian tree species (Stromberg and Richter, 1996). The floods create such microsites through alluvial deposition, nutrient deposition and scouring (Naiman et al., 2005). This creates new environments for colonization by new species (Nilsson and Svedmark, 2002). Floods are also significant in the initial stages of plant establishment through triggering germination and the provision of moisture to the germinated seedlings (de Oliviera et al., 2014). After germination, the seedlings require moist conditions from flooding for growth. If germination is followed by a dry spell then the seedlings may die (Grime, 1977). In addition to this, flooding also plays a critical role in hydrochory, the process through which water disperses seeds to suitable germination conditions (Nilsson and Svedmark, 2002).

Frequently flooded ecosystems are often resilient to frequent and intense flooding conditions as ther constituent species are adapted to constant flooding conditions (Naiman and Décamps, 1997). While in other wetland ecosystems such as the Amazon woodland species grow in areas that are perennially flooded for long durations (Junk, 1989), in the Okavango Delta riparian woodland vegetation does not grow in such areas (Smith, 1976). Instead riparian woodland grows in areas that are seldom flooded. Flood water reaches them through lateral groundwater flow (McCarthy, 2006) and during years of extremely high flooding. As a result the findings on the influence of flooding on riparian plant community composition, distribution and population structure from other wetland ecosystems may not be generalized to the Okavango Delta as their hydrological behaviour is different. In the Delta, flooding in the riparian zone during high floods may act as a disturbance which may offset the functioning of the woodland communities. This may change the woodland species composition and population structure dynamics. With little information on this in the Delta, the current study offers the opportunity for that to be understood.

1.1.2 The influence of river edge proximity on the species composition and distribution of riparian plant communities

The proximity of surface water influences riparian plant species composition and distribution through its influence on depth to groundwater. Depth to groundwater generally varies with the distance from the channel such that it is shallow in areas that are closer to the channel and deeper in those that are further away it (Lite et al., 2005). This was also found to be true in the Okavango Delta (McCarthy, 2006). In areas with relatively shallow groundwater (i.e. where plants are using it as a source of water), declining groundwater depth can lead to a reduction in plant species richness and total cover due to a decrease in the availability of a permanent water source to promote primary production (Stromberg and Richter, 1996). In habitats experiencing high evapotranspiration rates rainwater may leach salts that accumulate in the soil surface into the ground water table. If the groundwater table is shallow the root zone may then be exposed to a saline water layer leading to a reduction in plant growth (Naumburg et al., 2005) due to the harmful effects of salts and anoxic conditions.

Anoxic conditions in the root zone resulting from a shallow water table may also lead to a reduction in the plant primary production as a result of low oxygen content (Drew, 1997). Studies conducted in semi-arid regions of the United States of America riparian ecosystems (e.g. Shafroth et al., 2000; Lite et al., 2005) showed that woody plant species distribution and composition may be influenced by variation in groundwater depth with plants distributed along their preferred groundwater depths. This was shown in a study conducted in the Bill Williams River in Arizona where Shafroth et al (2000) found that *Populus fremontii* and *Salix gooddingii* saplings died as a result of a decline in groundwater (Figure 2). However, where the groundwater decline was smaller and water was still within reach of the roots of plants, there was lower mortality of the saplings of these species and their basal area increased (Shafroth et al., 2000).

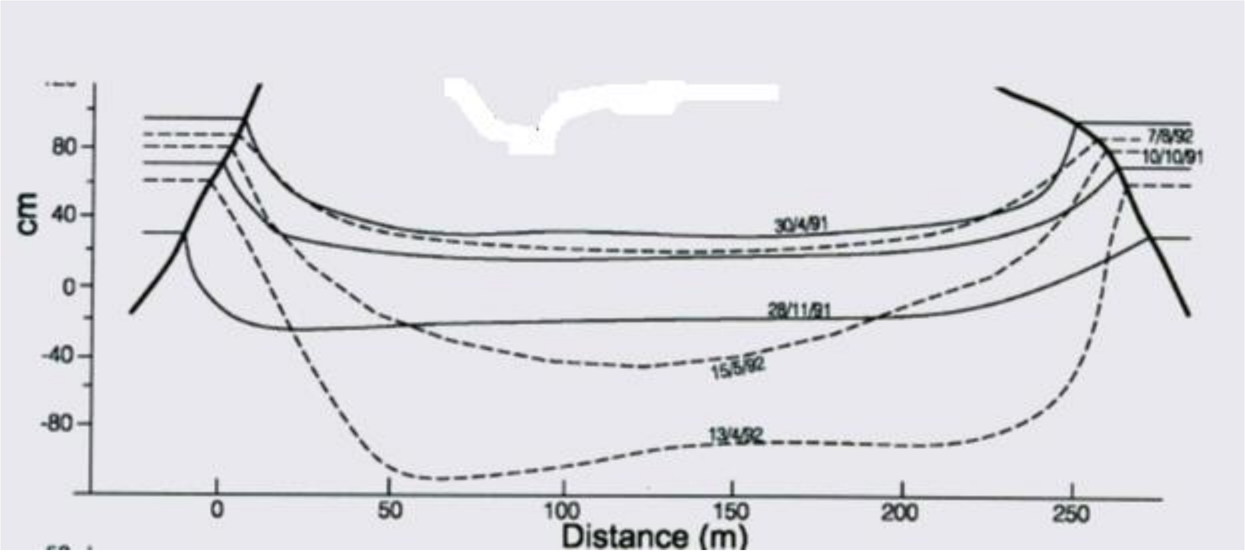

Figure 2: Groundwater decline may affect the survival of riparian plant species. *Note the decline of groundwater across different months in 1991 and 1992 in the Okavango Delta. Again note that generally groundwater takes a steep decline up to 50m from the river channel.*Adapted from McCarthy, (2006).

This suggests that as some of the saplings and seedlings died, they reduced competition for growth resources which resulted in an increase in the stem diameter of the surviving individuals. In the San Pedro River, Arizona, it was observed that the species richness was low in regions with deep groundwater indicating that it was limited by lack of water (Lite et al., 2005). In the Okavango Delta, Ellery et al (1993) observed a strong positive correlation between groundwater depth and woody plant species distribution. *Syzygium cordatum* and *Ficus verruculosa* tolerated a narrow range of annual groundwater depth fluctuations while species such as *Phoenix reclinata*, *F. sycomorus* and *Garcinia livingstonei* showed tolerance of a wider range of groundwater depth (Ellery et al., 1993; Figure 3).

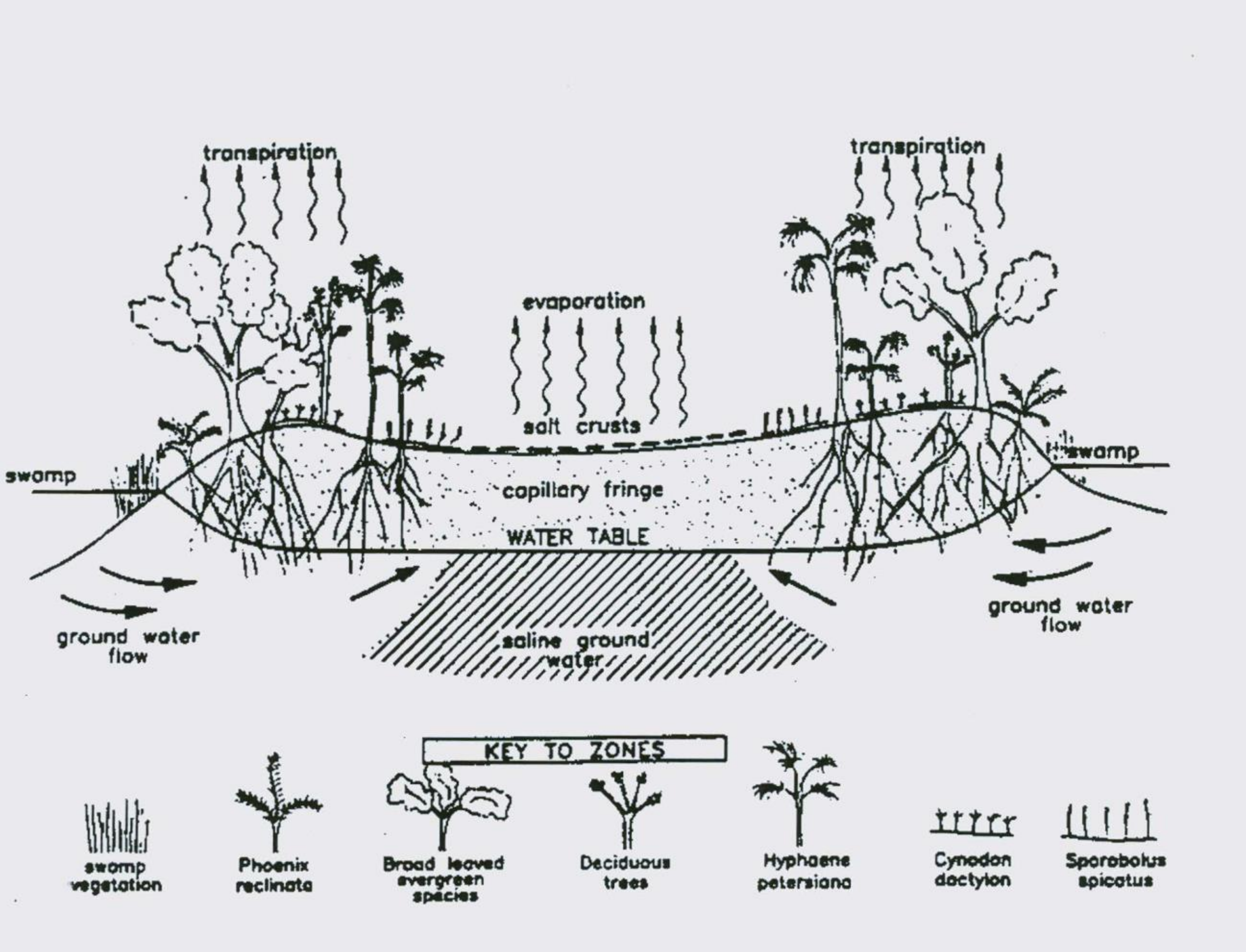

Figure 3: Riparian plant species are distributed along groundwater depth to which they are adapted (McCarthy et al., 1994).

1.1.3 Influence of soil salinity on the distribution and species composition of riparian plant communities

The distribution and community composition of riparian woody plant species may also be influenced by soil salinity. In a study conducted in the Lemon Catchment in Western Australia, it was found that woody plant species diversity decreased with increasing soil salinity (Doupe et al., 2006). Woody plant species such as *Melaleuca viminea* and *Hypocalyma augustifolium* were found in low soil salinity areas while *Xanthorrhoea pressii*, *Astartea fasciculata* and *Hakea* *lissocarpha* preferred high soil salinity areas (Doupe et al., 2006). Lymbery et al (2003) carried out an experimental study in the Collie River system, Western Australia, and confirmed that soil salinity influenced riparian woody plant species zonation in that system. They also found that plant species richness and diversity decreased with increasing soil salinity. In the Okavango Delta, Ellery et al (1993) found that soil salinity influenced the distribution of riparian woody plant species. Salinity levels in Delta soils are generally higher in areas further away from the channel than in those that are closer (McCarthy et al., 1994). Grass and sedge species such as *Sporobolus spicatus* and *Cyperus laevigatus* respectively were tolerant of high sodium content while woody plant species such as *Phoenix reclinata, D. mespiliformis, Garcinia livingstonei* and *Euclea divinorum* did not tolerate high sodium content (Ellery et al., 1993). Woody species that are tolerant of high salinity in the Okavango Delta include *Croton megalobotrys, Hyphaene petersiana* and *Acacia nigrescens* (Ellery et al., 1993).

1.1.4. The influence of fire on the distribution and species composition of riparian plant communities

Fire is one of the factors that may influence plant species composition and distribution in riparian plant communities (Mitsch and Gosselink, 2000). This has been found in other riparian ecosystems such as the Colorado River (Busch, 1995) and the Pantanal (de Oliviera et al., 2014). In Colorado River it was observed that *Tessaria sericea* was dominant after fire occurrence while *Populus fremontii* was completely excluded (Busch, 1995). In the Pantanal it was found that fire interacted with flooding to reduce plant density, regeneration and change plant species composition and distribution. Fire influences the species composition of riparian trees by eliminating the intolerant ones and creating gaps for colonization (de Oliviera et al., 2014).

Species that re-sprout easily are the ones that show resistance after burning (Dwire and Kauffman, 2003). Fire suppresses the establishment and recruitment of species that do not resprout easily (intolerant ones) after burning (Helm and Witkowski, 2012). Even though the influence of fire on riparian woodland species in the Okavango Delta has not been studied, it is likely that may be minimal since it seldom spreads in their zone due insufficient fuel (Heinl et al., 2007). Fire in the Delta originates in the seasonal floodplains and swamps because they are frequently flooded and have more fuel from grasses and sedges as compared to the riparian woodlands where growth of grass is limited by poor nutrient soils, high levels of herbivory and low water content (Heinl et al., 2007). In the riparian woodland communities it is expected that the effects of fire may be more pronounced in the seedlings and saplings because they are within its reach. This is because it may cause destruction to their meristem which is an important part in plant growth. As a result growth, recruitment and establishment of the affected species will be inhibited.

1.2.0 Regeneration and population structure of riparian woodland plant communities

Regeneration of riparian plant communities is an important component of development which is characterized by seed production, seed dispersal, seedling germination, survival and growth (Streng et al., 1989; Jones et al., 1994). The regeneration and population structure of a given vegetation community are influenced by prevailing environmental conditions at the time of seed release (Guilloy-Forget et. al., 2002). Seed dispersal ensures that the germinated seedling avoids competition from the parent plant. However, there are some instances in which seeds are dispersed into unfavourable habitats which prevent their germination and subsequent survival (Nathan and Muller-Landau, 2000). Environmental factors that generally influence regeneration and tree population structure in forests include fire, herbivory, flooding, pathogens, competition and light regime (Walker et al., 1986; Streng et al., 1989). When the intensity of these factors is beyond the tolerance levels of a given tree species its regeneration and population structure will be unstable (Helm and Witkowski, 2012; Traore et al., 2013). For instance, in the Escalante River, Utah there was an observed die-off in riparian tree species which was attributed to severe flooding (Irvine and West, 1979). Desiccation may also result in unstable population structure in riparian tree species as it prevents individuals from reaching later growth stages (Pettit and Froend, 2001). Anthropogenic factors may also affect the regeneration and the population structure of riparian tree species. These include activities such as land clearing for agriculture, timber harvesting and human settlements (Maitima et al., 2009). Other anthropogenic activities which may affect the regeneration of riparian tree species include dam construction in catchment areas, urbanization of catchment areas, changes to hydrology and climate (Parolin and Wittmann, 2010).

Recruitment is a term used in the description of the regeneration and population status of vegetation communities (Sop et al., 2011; Gurmessa et al., 2012; Helm and Witkowski, 2012). This refers to the transition of individuals from one growth stage to another (seedlings developing into saplings, and saplings growing into fully grown individuals capable of reproduction). Population and regeneration structures can be stable or unstable. A stable population structure is one in which there are more individuals in the smaller size diameter classes than in their large counterparts. This is usually termed the reverse J-shaped pattern (Sop et al., 2011). The reverse J-shaped recruitment pattern is regarded as stable because the individuals in the smaller size diameter classes replace the aging large ones, with initially very high mortality rate decreasing with increasing size (Helm and Witkowski, 2012). Conversely, the unstable population structure is characterized by more individuals in the larger diameter size classes than in the smaller ones (Helm and Witkowski, 2012). This is also called the J-shaped size class distribution pattern. It is referred to as unstable because once the individuals in the large diameter size class die they may not be adequately replaced by the few young ones (Sop et al., 2011). This type of population structure is usually associated with species that become (locally or otherwise) extinct (Gurmessa et al., 2012).

Other unstable population structures are characterized by bell-shaped, U-shaped and irregular recruitment patterns (Helm and Witkowski, 2012). The bell-shaped recruitment pattern has more individuals in the middle than in the lower and higher diameter size classes (Helm and Wikowski, 2012). This is usually an indication that there was large-scale recruitment of individuals from small diameter size classes into the middle ones from the previous years (Hamandawana, 2012). This could possibly represent an episodic recruitment event during favourable environmental conditions. The bell-shaped recruitment pattern may result from either temporary or long-term environmental bottlenecks which prevent germination of seedlings and their recruitment into the larger size classes. This could result from dry conditions which inhibit germination, fire, or extreme flooding which results in anoxic soil conditions, herbivory, or combinations of these (Jones et al., 1994). In the U-shaped recruitment pattern, there are more individuals in the lower and larger diameter size classes than in the middle ones. This could be an indication that in the past there was recruitment of individuals from the lower diameter size classes into the larger ones which recently stopped or slowed down (Helm and Witkowski, 2012). The U-shaped pattern could be due to episodic recruitment in which there is lack of development of juveniles into larger individuals. This can be due to unfavourable conditions in some years (Hamandawana, 2012). The U-shaped pattern can also result from selective removal of individuals in the middle diameter size classes either as a result of being preferred for human use or by herbivores (Gurmessa et al., 2012). In irregular population structures, there are usually some missing diameter size classes, and distributions do not follow any defined pattern (Helm and Witkowski, 2012). However, it is important to recognize that these distribution patterns may simply be a representation of a population structure at an instant in time.

1.2.1. The influence of land use on the regeneration and population structure of riparian plant communities

Globally land use is emerging as an important factor that threatens riparian woodland species (e.g. Pettit, 2002; Burton et al., 2005 and Sop et al., 2011). This is indicated by its often degrading and destructive effects on the riparian ecosystems (Burton et al., 2005). Examples of studies on the impact of land use on regeneration structure of populations of riparian trees include Ferreira et al. (2005) in the Tagus fluvial system in Portugal, Burton et al. (2005) in West Georgia, USA, who studied the impact of urbanization on woody riparian communities in the Middle Chattahoochee River Basin, Pettit, (2002) in Burdekin River catchment in Australia who studied the impact of livestock grazing on *Livistona lanuginosa* palm tree, and Salinas et al. (2007) in the Almanzora and Aguas river basins in Spain. All these studies concluded that land use activities such as urbanization and agriculture may have negative impacts on riparian woodland plant species (Pettit, 2002 and Burton et al., 2005). In Africa, many studies on tree population and regeneration structure have focused on land use in dry lands. These include

Shackleton (1993) in South Africa, Sop et al. (2011) in Burkina Faso, Helm and Witkowski (2012) in South Africa and Traore et al. (2013) in Burkina Faso. These studies have also indicated that land use activities such as human settlement, land clearing and agricultural activities may have a negative impact on woodland resources. In Botswana, studies on tree population structure have been carried out in the Chobe region (e.g. Ben-Shahar, 1996; Barnes, 2001 and Teren and Owen-Smith, 2010) while in the Okavango Delta there generally are few studies (Babitseng and Teketay, 2013; Neelo et al., 2013). The study by Neelo et al. (2013) was on the impact of flood recession farming on the population structure of selected species. It was confined to the villages of Tubu, Shorobe and Xobe, on the peripheries of the Delta. Babitseng and Teketay, (2013) investigated the impact of wine tapping in Shorobe village on *Hyphaene petersiana*. In the past riparian species in the Okavango Delta were also used for construction of canoes or ‘mekoro’. Common riparian trees that were historically used for this include *Philenoptera violacea*, *Acacia nigrescens*, *Diospyros mespiliformis* and *Garcinia livingstonei* (Ecosurv, 1988). The impact of this historical use on the regeneration and population structure of these riparian tree species may manifest itself now. In addition to this, the population and regeneration structures of riparian tree species may have been affected by historical clearing to reduce the spread of tsetsefly (Snowy Mountains Engineering Corporation, 1989). No integrated study of the distribution, species composition and population structure has been done to date.

1.3.0 Threats to riparian woody plant species including those of the Okavango Delta

Globally, riparian woody plant species are threatened by water abstraction, climate change and invasion by exotic plant species (Cronk and Fennessy, 2000). Other factors which threaten riparian woodland include agriculture (Poff et al., 1997) and human over-exploitation (Matiza and Chabwela, 1992). Changes in temperature and precipitation due to climate change can lead to hydrological alteration in wetlands which may ultimately affect the composition of riparian woodland communities (Van der Valk, 2006). Some plant species are likely to shift their geographical distributions in response to climate change consequently disturbing ecosystem functioning (Cowie, 2007). Plant species that do not tolerate new conditions caused by climate change may become extinct (Parish and Looi, 2007).

Riparian ecosystems are also threatened by the invasion of exotic plant species. This is because they may provide a favourable environment for the establishment of invasive species as river-floodplain systems act as conduits of seed dispersal (Naiman et al., 2005). Constantly changing water levels in the riparian zone also influence the establishment of invasive species (Davis et al., 2000). Seasonal increasing water levels in riparian zones create new niches ("gaps") for colonization by invasive species by killing those that are not tolerant of increased water levels (de Oliveira et al., 2014). This may also promote colonization by invasive species through enriching the riparian soils with nutrients (Davis et al., 2000). Declining water levels may also promote the establishment of invasive species by creating new niches as the species that are not tolerant of reduced water levels are excluded in the riparian zone (de Oliveira et al., 2014), exposing new area for colonisation, and/or providing favourable soil moisture conditions for germination. Once established, invasive species may displace native species from their area. In northern Australia mono-specific stands of the alien shrub *Mimosa pigra* (a Neotropical species) replaced sedge land and riparian plant species (Braithwaite et al., 1989) leading to biodiversity loss and local extinction of the native species. This species is also causing major problems in the Kafue flats in Zambia (Mumba and Thomposon, 2005).

Agriculture is also one of the threats to riparian woodland ecosystems (Porto and Clover, 2003). Riparian wetland ecosystems may offer land suitable for crop production which may result in deforestation due to clearing land for planting and cutting trees for fencing the fields (Reddy and Gale, 1994). Dam construction across wetlands to divert water for agricultural production reduces water flow to downstream areas and in the process may also prevent exchange of nutrients and sediments between upstream and downstream areas (Poff et al., 1997). These effects may result in die-offs of riparian plant species due to desiccation (Parolin and Wittmann, 2010). It is expected that the demand for agricultural land in riparian ecosystems will increase as the human population increases (Matiza and Chabwela, 1992).

In addition to the preceding threats, the Okavango Delta may also be threatened by a large and increasing elephant population (Natural Resources and People, 2007). Foraging on islands and the riparian strip could lead to over-exploitation of riparian woodland vegetation resources, with changes in reproductive potential and recruitment processes. This has been reported in other riparian forests where African elephants induced tree mortality and suppressed seedling recruitment resulting in transformation of woodland habitats into open grassland (O'Connor et al., 2007). Herbivory or damage by elephants on riparian trees is expected to vary seasonally in the Okavango Delta. It is likely to be more pronounced during the dry season as the elephants move to the Delta for water and browsing woodland species. Elephant damage to riparian trees includes felling (Hamandawana, 2012) and ring barking where the bark aroung the tree trunk is removed (Teren and Owen-Smith, 2010). This may result in the death of the damaged tree individual. While the Okavango ecosystem may cope with this at the right carrying capacity, increased elephant population above the carrying capacity of the ecosystem may put more pressure on the riparian woodland species due over-exploitation. This may result in a change in species composition with the preferred species failing to cope with over-exploitation. A change in species composition may reduce the role of riparian trees in removing toxic solutes which helps in maintaining the Delta as a freshwater ecosystem (Ellery and Tacheba, 2003; McCarthy et al., 1994). Skarpe et al (2004) found that due to the browsing pressure exerted by elephants in the Chobe area, vegetation species composition and distribution changed. *Acacia* and *Combretum* species were replaced by *Capparis tomentosa* and *Combretum mossambicense* (Skarpe et al., 2004).

Other herbivores may also affect the population structure and composition of riparian tree plant communities in the Okavango Delta. In the Khwai and Savuti area in northern Botswana, seedling and seed predation by giraffe, impala, beetles, monkeys and baboons was reported in *Acacia erioloba* (Barnes, 2001). Another study in the Chobe area, Northern Botswana found that damage to seedlings was caused by the trampling upon by zebra, buffalo and wildebeest and browsing by herbivores such as giraffe, impala and kudu (Ben-Shahar, 1996). Mathooko and Karuiki (2000) also cited wildlife herbivory as a disturbance to tree species recruitment.This suggests that elephants may not be the only herbivores that could have a significant effect on the distribution and relative abundance of riparian woodland species. Therefore, an increase in other herbivore species may also negatively the population structure and species composition of riparian plant communities in the Okavango Delta.

1.4.0 The problem statement

In the Okavango Delta, riparian woodland has been identified as a significant driver of the ecologically vital process of sequestration of dissolved salts through evapotranspiration (McCarthy et al., 1998). Evapo-transpiration from island fringe riparian woodland creates a permanent gradient of water flow from the floodplains and channels towards the islands (McCarthy et al., 1994). Evapo-concentration of the groundwater increases the density of groundwater under the islands, causing some solutes to precipitate (Ca and Mg carbonates) and leaving some in solution (e.g. Cl^- and Na^+) (McCarthy et al., 1998; Bauer et al., 2002). When the density of the sub-island groundwater reaches a certain threshold, it migrates as a relatively discrete mass downward through the matrix of less dense groundwater underlying the Delta generally to sink to the base of the sedimentary column. This removes the solutes from the biotic part of the Delta maintaining fresh surface water (McCarthy et al., 1994). Despite their positive contribution to the ecological functioning of the Okavango Delta, riparian woodlands are threatened by potential degradation due to climate change, overexploitation resulting from population increase of elephants, invasive species and agriculture (as discussed in section 1.3.0) which may lead to the loss of riparian plant communities. In order to conserve riparian vegetation resources in the face of these threats, we need to understand how flooding frequency affects these resources. However, in the Okavango Delta it is still not known how the woodland vegetation will respond to these threats and projected climate change. Currently there is lack of knowledge concerning riparian woodland species composition and distribution, population structure and dynamics and the underlying environmental controls.

Previous studies in the Delta (e.g. Biggs, 1976; Smith, 1976; Snowy Mountains Engineering Corporation, 1989; Ellery et al., 1991; Bonyongo, 1999; Bonyongo et al., 2000; Murray-Hudson, 2009) examined the relationship between plant community composition, distribution and hydrology and concluded that flooding duration, frequency and depth are the primary factors influencing vegetation zonation. However, these studies were mainly focused on herbaceous floodplain vegetation communities. Ellery et al. (1993) examined the relationship between woody and herbaceous plant species distribution and selected environmental variables. However, that study was limited in terms of its geographical location. It was conducted in the Maunachira-Ngoqa system, which is the extension of the main Okavango channel, and is characterised by perennial inundation, hence its findings may not be generalized to the whole Delta. Ringrose et al (2007) assessed the relationship between Delta drying and distal woody plant species and compositional changes. Their study was also limited in terms of geographical coverage in that it was conducted in the distal, short-duration seasonally inundated regions of the Delta.

This study aimed at investigating riparian woodland species composition, distribution, population structure and regeneration and their underlying environmental controls in the Okavango Delta. This will generate information on the baseline characteristics of riparian woodland communities to allow us to conserve and manage them sustainably.

1.5.0 Objectives

1.5.1 General objective

1. To investigate the population structure, species composition and distribution of riparian woodland plant communities in the Okavango Delta.

1.5.2 Specific objectives

1. To classify different riparian plant communities in the Okavango Delta.
2. To investigate the influence of flooding frequency on riparian plant community composition and distribution in the Okavango Delta.
3. To establish the influence of distance from surface water on the species composition and distribution riparian woody plant communities in the Okavango Delta.
4. To investigate the population structure of constituent species of riparian plant communities in the Okavango Delta.
5. To establish the regeneration structure of constituent species of riparian tree species in the Okavango Delta.

1.6.0 Study area

The study was conducted in the Okavango Delta in the Panhandle, Seronga, Jao, Vumbura, Moremi, Santawani, Boro and Tubu (Figure 4).

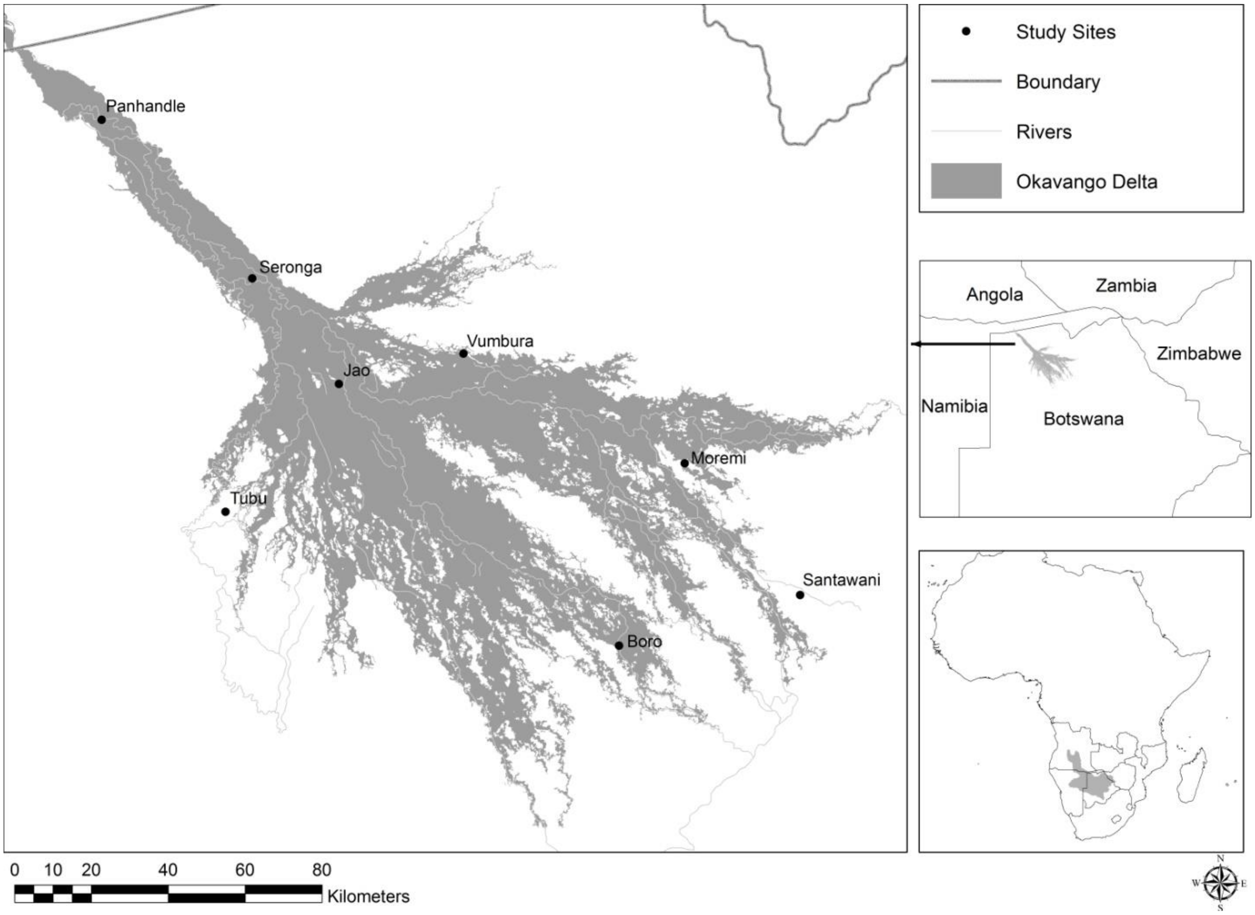

Figure 4: Location of the study sites in the Okavango Delta.

The Okavango Delta is located in the Northern part of Botswana and covers approximately 12 000 km^2 (McCarthy and Ellery, 1998). Both flooding and local rainfall determine the total area flooded in the Okavango Delta (Wolski et al., 2006). Local rainfall contributes about 6×10^9 m^3 per annum while annual floods from Angolan highlands between February and May contribute about 9×10^9 m^3 (Gumbricht et al., 2004). Flood propagation takes about 4 months to reach the Delta downstream areas due to the low topographic gradient, with the maximum extent of flooding occurring around July and August (McCarthy, 2006). The Okavango Delta experiences high potential evapo-transpiration (PET) of approximately 1800mm/annum (Snowy Mountains Engineering Corporation, 1987). About 96% of the total water inflow to the Okavango Delta is lost through evapo-transpiration, 2% is lost to deep groundwater while another 2% flows out of the Delta through the Thamalakane River (McCarthy and Ellery, 1998).

The Okavango Delta is characterized by three main hydrological systems, being permanent swamps, seasonally flooded floodplains and occasionally flooded floodplains (Gumbricht et al., 2004). Covering a total area of about 2 500 km^2, the permanent swamps are flooded all year round and their common plant species include *Phragmites australis*, *Cyperus papyrus*, *Phragmites mauritianus* (Snow Mountains Engineering Corporation, 1989). The seasonally flooded floodplains can be divided into primary and secondary floodplains (Biggs, 1976; Smith, 1976; Snow Mountains Engineering Corporation, 1989). The low-lying primary floodplains are those which are flooded annually for up to 4 to 8 months during average flooding conditions (Biggs, 1976). Common plant species found in primary floodplains include the large emergent sedges *Cyperus articulatus* and *Schoenoplectus corymbosus* (Bonyongo, 1999; Bonyongo et al., 2000). The secondary floodplains experience flooding duration of up to 5 months during years of average flooding (Gumbricht et al., 2004). Common plant species in the secondary floodplains include *Panicum repens*, *Setaria sphacelata* and *Eragrostis inamoena* (Bonyongo, 1999; Bonyongo et al., 2000). The tertiary floodplains are inundated only during high flooding conditions. Common plant species in the tertiary floodplains include *Sporobolus spicatus* and *Cynodon dactylon* (Bonyongo, 1999; Bonyongo et al., 2000).

Common woody plant species in the Okavango Delta include *Diospyros mespiliformis*, *Garcinia livingstonei*, *Ficus natalensis*, *F. sycomorus* and *Croton megalobotrys* (Table 1) distributed along soil salinity (Sodium and Chloride concentration) and ground water chemistry (pH and conductivity) and depth gradients (Ellery et al., 1993). *Diospyros mespiliformis*, *G. livingstonei* and *F. sycomorus* are found in regions characterized by shallow groundwater (Ellery et al., 1993) while *C. megalobotrys* and *Hyphaene petersiana* are tolerant of saline and deep groundwater conditions (Ringrose and Matheson, 2001). There are very few flood tolerant riparian woodland species in the Delta which include *Phoenix reclinata* and *Syzygium cordatum* (Ellery and Ellery, 1997). The riparian zones in the Delta are also characterized by dryland species. Examples of dryland communities occurring in the riparian zones of Okavango Delta are *Combretum* woodland, *Acacia* woodland and *Mopane* woodland (McCarthy et al., 2005).

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A baseline classification of riparian woodland plant communities in the Okavango Delta, Botswana.

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Abstract

In the Okavango Delta information on the riparian woodland vegetation community composition and distribution is generally lacking. Past studies in the Delta were mainly focused on the quantitative classification of seasonal floodplain herbaceous vegetation communities. The aim of this study was to determine riparian woodland vegetation communities in the Okavango Delta. Vegetation sampling was conducted from 20 × 50m randomly placed plots. The sampling plots were placed along a gradient from the main water body to the drier fringe of the riparian zone. Plant species present in each plot were recorded with their estimated percentage cover using the Braun-Blanquet cover abundance scale. Hierarchical cluster analysis was used to determine vegetation communities. Indicator species analysis was used to calculate indicator values for species groups defined from the cluster analysis. Plant species and diversity were determined for each vegetation cluster. Multi Response Permutation Procedures (MRPP) was used to compare vegetation clusters. The Kruskal-Wallis test was used to compare species diversity and richness between vegetation communities. Four vegetation communities identified were; *Croton megalobotrys-Hyphaene petersiana*, *Acacia erioloba-Diospyros lycioides*, *Syzygium cordatum-Phoenix reclinata* and *Garcinia livingtonei-Acacia nigrescens*. In this classification, *Syzygium cordatum-Phoenix reclinata* and *Garcinia livingstonei-Acacia nigrescens* plant communities are found in frequently flooded regions while. *Croton megalobotrys-Hyphaene petersiana* and *Acacia erioloba-Diospyros lycioides* are occasionally flooded regions. Total number of species was highest in *Garcinia livingstonei-Acacia nigrescens* and lowest in *Syzygium cordatum-Phoenix reclinata* vegetation community. Multi Response Permutation Procedures showed that there was significant (p<0.05) difference between vegetation communities. Species diversity and richness were significantly (p<0.05) high in *Garcinia livingstonei-Acacia nigrescens* vegetation community. This study provided an inventory of riparian woodland plant communities which can be used as a vital monitoring tool of vegetation change in the Okavango Delta.

Keywords: Flood, Indicator, Okavango, Vegetation and zonation.

Introduction

Riparian vegetation consists of plant species in a zone directly affected by the river water (Hancock et al. 1996). The distribution of tree species in riparian zones reflects their response and adaptation to prevailing environmental conditions including flooding frequency, soil, water quality and the rate of sedimentation (Gurnell 1997). Groundwater depth is another of the environmental factors influencing riparian tree species distribution with its decline causing a shift from mesic to xeric species (Castelli et al. 2000). Changes in species composition in riparian zones may be sharp or gradual depending on the rate of change of the prevailing environmental factor (Hancock et al. 1996). In the Okavango Delta common riparian woody species include *Diospyros mespiliformis*, *Croton megalobotrys* and *Garcinia livingstonei* distributed along soil salinity (Sodium and Calcium concentration) and ground water chemistry (pH and conductivity) gradients (Ellery et al. 1993). Other common woody tree species found in the Okavango Delta include *Acacia tortilis Acacia erioloba* and *Colophospermum mopane* distributed along a flooding frequency gradient (Ringrose and Matheson 2001).

Historically, the riparian states of Angola, Botswana and Namibia proposed the extraction of water from the Okavango (Lebotse 1999). Water abstraction from the Okavango Delta poses a threat as it may lead to a loss in biodiversity (Diederichs and Ellery 2001). Other threats to the Delta include climate change (Seavy et al. 2009) which can either result in excessive flooding or drying (or both). Deforestation resulting from agriculture has also been cited as one of the threats to the Okavango Delta (Reddy and Gale 1994) in addition to invasive tree species (Alonso and Nordin 2003). Human and elephant population growth and land use conflicts also threaten the Okavango Delta. The Okavango Delta floodplains are used for flood recession (*molapo*) farming.

With predicted human population increase, it is expected that the area of flood recession fields will increase leading to a potential land use conflict and degradation of riparian woodland vegetation. In order for these threats to be reduced there is need to understand the composition and distribution of riparian woodland vegetation communities in the Okavango Delta. Other studies elsewhere have studied species composition and distribution of riparian woodland species. Medina (1986) in Mexico, Roberts and Ludwig (1991) in Australia, Lyon and Sagers (2002) in Missouri and Fousseni et al. (2011) classified riparian vegetation communities. In the Okavango Delta information on the riparian woodland vegetation community composition and distribution is generally lacking. Previous studies (Murray-Hudson 2009, Ellery et al. 2003, Ellery and Tacheba 2003, Bonyongo 2000) in the Delta were mainly focused on the quantitative classification of seasonal floodplain vegetation communities. Information generated on the composition and distribution of riparian vegetation community composition and distribution will be useful in designing informed management policies that will be directly concerned with riparian vegetation conservation to promote the sustainable use of woodland resources. Information on vegetation classification can help to show changes in species composition as a result of environmental disturbances and hydrological changes. This could either be as a result of land use conflict or climate change. However, there has not been adequate information available on the ecology of riparian tree species in the Delta, in contrast with abundant literature in other wetland ecosystems on riparian tree species ecology.

The aim of this study was to determine riparian woodland vegetation community composition and distribution in the Okavango Delta. It was hypothesized that there will be different vegetation communities of riparian tree species as a result of different underlying environmental variables such as flooding, groundwater and herbivory that influence species composition and distribution.

Materials and Methods

The study was conducted in the Okavango Delta which is located in the Northern part of Botswana covering approximately 12 000 km^2 (McCarthy and Ellery 1998). Of the 12 000 km^2 the riparian woodland occupies approximately 840 km^2 (Wolski, 2007), or ~7%. The selected study sites were Boro, Moremi, Habu, Vumbura, Tubu, Upper Panhandle, Seronga and Jao (Figure 1). The total flooded area in the Okavango Delta is determined by flooding and local rainfall (McCarthy 2005) each contributing 9×10^9 m^3 and 6×10^9 m^3 of water per annum respectively (Gumbricht et al. 2004).

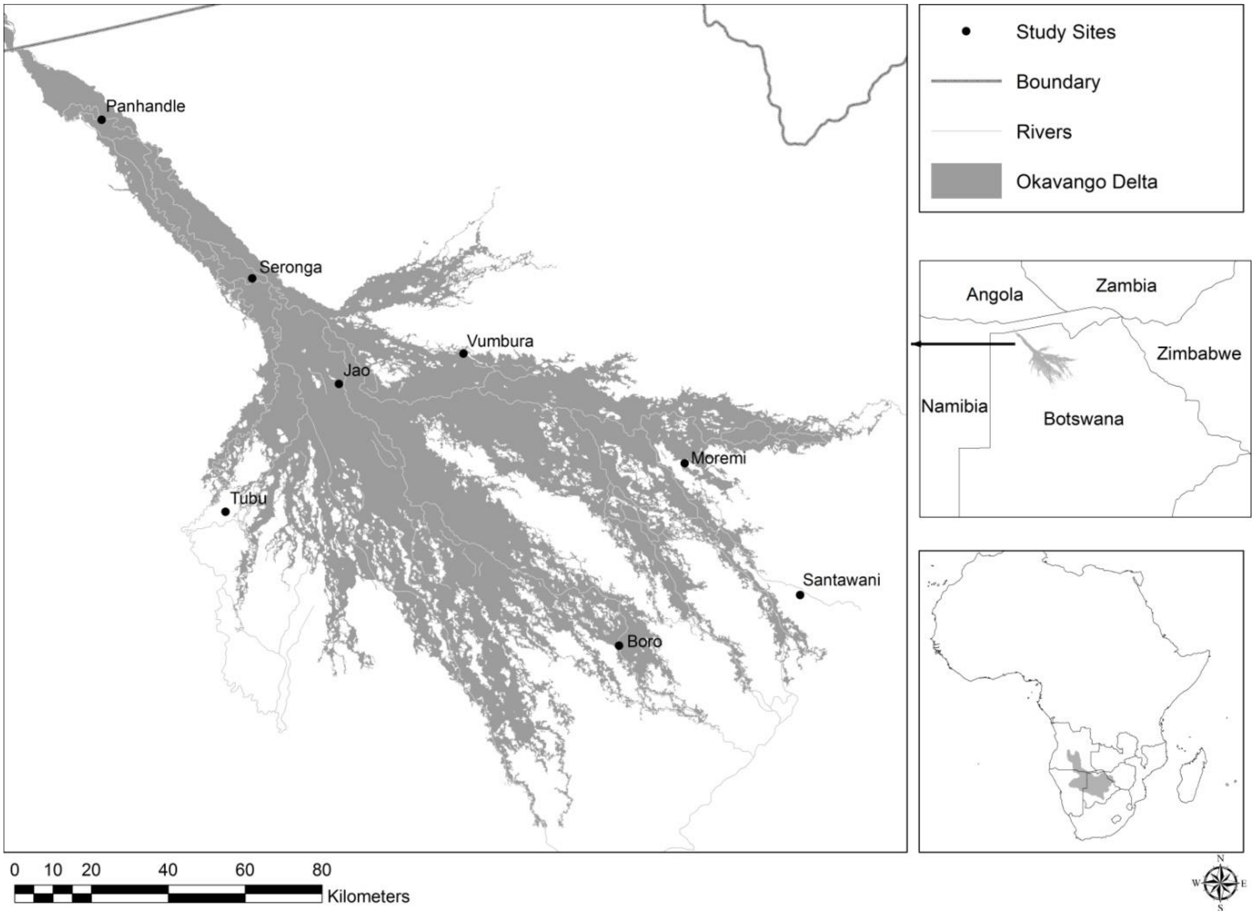

Figure 1: Map of the Okavango Delta showing the study sites.

Flood propagation takes about 4 months to reach the downstream areas of the Delta due to low topography with flood peak occurring around July and August (McCarthy 2005). The Okavango Delta experiences high evapo-transpiration which accounts for approximately 96% of the total water loss with 2% lost through soil infiltration while another 2% flows through the Thamalakane River (Ellery and McCarthy 1998). Vegetation in the Okavango Delta is made up of seasonal and riparian plant communities. Seasonal floodplains are classified into primary, secondary and tertiary plant communities (Biggs 1979). These floodplain classes are described in Biggs (1979) as follows: The primary floodplains are found on the low-lying areas and are flooded for a maximum of 8 months annually. The secondary floodplains are located on relatively highly elevated regions than the primary floodplains and are flooded for a maximum of 5 months annually. Tertiary floodplains are located on higher elevation than secondary floodplain and are flooded during years of high floods. The riparian zone characterized by woody species and low flooding frequency, is found on dry land after the tertiary floodplains. Plant community composition has been extensively described in Bonyongo et al (2000) as follows: Common plant species in the primary floodplains include *Cyperus articulatus*, *Schoenoplectus corymbosus* and *Miscanthus junceus*. In the secondary floodplains common species include *Panicum repens*, *Paspalidium obtusifolium* and *Setaria sphacelata*. Common plant species in the tertiary floodplains are *Imperata cylindrica*, *Vetiveria nigritana* and *Cynodon dactylon*. In the riparian zone common woodland species include *Acacia erioloba*, *Croton megalobotrys*, *Phoenix reclinata*, *Diospyros mespiliformis* and *Garcinia livingstonei* (Table 1). Riparian plant species found closer to the water or river bank include *Syzygium cordatum*, *Phoenix reclinata* and *D. mespiliformis*. Other species such as *Acacia nigrescens, A. erioloba* and *Combretum imberbe* are found further away from surface water.

Table 1: Characterization of different study sites in the Okavango Delta.

Study area	Coordinates	Location	Habitat type	Common woodland vegetation
Santawani	23˚37'8"E, 19˚32'11"S	Lower Delta	Dryland	*Acacia erioloba*, *Croton megalobotrys*
Moremi	23˚22'38"E	Lower Delta	Permanently flooded, Seasonally flooded and Dryland	*Hyphaene petersiana* Mart, *Kigelia africana* Lam Benth
Boro	23˚9'13"E, 19˚32'27"S	Lower Delta	Permanently flooded, seasonally flooded and dryland	*Combretum hereroense* Schinz, *A. erioloba*
Seronga	22˚17'8"E, 18˚48'42"S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Syzygium cordatum* Hochst. ex C Krauss, *Phoenix reclinata* Jacq
Jao	22˚33'40"E, -19˚1'57"S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*S. cordatum*, *P. reclinata*
Upper Panhandle	21° 52'13"E, -18° 21'53"S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Searsia quartiniana* A. Rich, *Elaeodendron transvaalense* (Burtt Davy) R.H. Archer
Vumbura	19˚17'9"S	Middle Delta	Permanently flooded, seasonally flooded and dry land	*Acacia nigrescens* Oliv, *Albizia harveyi* E. Fourn
Tubu	22˚19'5"E 19˚27'45"S	Middle Delta	Seasonally flooded and dryland	*C. megalobotrys*, *Ximenia americana* L

Vegetation sampling

The minimum sampling plot area from the reconnaissance studies in Boro and Seronga was determined to be $1000m^2$ with 20m × 50m dimensions. This plot is also widely used in plant studies (Sop et al. 2011) and it was suitable for the current study in order to enable its results to be compared with other studies elsewhere. Tree species were identified in randomly selected 20 × 50m plots. At each site there were 30 possible sampling plots selected in Google Earth Image out which a minimum of 10 were randomly selected. The plots were assigned numbers from 1 to 30 and randomization was done through random number selection in excel (Gentle 2006). The selected plots were then geo-located in the field using GPS. Vegetation sampling was done in the period between February 2012 and November 2013. This included the period (February to late April) when most of the plants were flowering and easy to identify (Heath and Heath 2009). Given that riparian woody species are distributed along soil salinity, ground water chemistry and flood frequency gradient (Ellery et al. 1993), the sampling plots were placed along a gradient from the main water body to the drier fringe of the riparian zone to include all the gradients. Specimens of unknown species were pressed and taken to the Peter Smith University of Botswana Herbarium (PSUB) at the Okavango Research Institute. Percentage cover was estimated for each tree species from each plot using Braun-Blanquet cover abundance scale. A total of 101 plots were sampled. This contributed to about 0.101 km^2 (or 0.01%) sampled area of the total riparian vegetation in the Okavango Delta. Despite this low percentage, the results are considered representative as they represent sites with different hydrological gradients (Table 1 and Chapter 3). This means that almost all the species that are present in the Delta were sampled.

Statistical analysis

Hierarchical cluster analysis (flexible β linkage, $\beta = -0.25$, Sorensen distance, data relativized by maximum) of species was performed in PC-ORD to determine vegetation communities. Indicator species analysis (ISA), (Dufrêne and Legendre 1997) was used to calculate indicator values for species in groups defined from the cluster analysis. It was also used to determine an ecologically meaningful number of vegetation communities, where mean *p* is minimized or the number of statistically significant indicator species maximized (McCune & Grace 2000). Monte Carlo testing was used to evaluate the statistical significance of indicator values for species. Multi-response Permutation Procedures (MRPP) (McCune and Grace 2000), a nonparametric method, was used to test for significant difference in plant species composition between different vegetation communities. It was conducted in PC-ORD using the Sorensen distance measure.

Multi Response Permutation Procedures were used because it does not require any assumptions underlying the distribution structure of vegetation communities (McCune & Grace 2000). The test statistic T was calculated as: $T = (\delta_{observed} - \delta_{expected})/s.dev\delta_{expected})$. This determines the separation between vegetation communities, with more negative values indicating stronger separation. Within group homogeneity is determined by within group agreement $A=1-(\delta observed/\delta_{expected})$. $A_{maximum} = 1$ when all items are identical within groups ($\delta=0$), $A=0$ when heterogeneity within groups equals expectation by chance, $A<0$ with more heterogeneity within groups than expected by chance. Nonmetric multi-dimensional scaling (NMS) (Kruskal 1964; Mather 1976) was used to infer site relationships. Sorensen distance, random starting configuration, 200 maximum iterations and 2-dimensions were selected with final stress of 20.

Species diversity, richness, Evennes and density were determined for each vegetation community. Shannon species diversity was calculated as,

$$H' = \sum_{i=1}^{S} pi \ln pi$$

where H' is Shannon diversity index, *S* is the total number of species in the community, *p* is the proportion of *S* made up of *i*th species (Shannon, 1948). Species richness was calculated as the sum of all species in a community. Simpson's species diversity index (1-D) (Simpson, 1949) was calculated as;

$$D = \frac{\sum \mathbf{n}(\mathbf{n}-\mathbf{1})}{\mathbf{N}(\mathbf{N}-\mathbf{1})}$$

where N is the total number of individuals of all the species and n represents the total number of individuals of a given species. This diversity index takes into account evenness and species richness. When species richness and evennes increase, diversity also increases. The values of Simpson's diversity index (1-D) range between 0 and 1 and the higher the value, the higher the species diversity.

Plant density/ha calculated as follows:

$$Density/ha = \frac{(Total\ number\ of\ individuals/0.1)}{Total\ number\ of\ plots\ sampled}$$

where 0.1 is a conversion of the area of the sampling plot (1 000m^2) to a hectare (10 000m^2).

Indicator value for each species was calculated as:

$$Indicator\ Value = Total\ \%\ species\ frequency\ + Total\ \%\ species\ abundance$$

following the method by Dufrêne and Legendre, (1997).

Relative percentage frequency for each species was calculated as;

$$\% \boldsymbol{Relative\ frequency} = \frac{\boldsymbol{Total\ number\ of\ plots\ in\ which\ the\ species\ occurs}}{\boldsymbol{Total\ number\ of\ plots\ sampled}} \times \mathbf{100}$$

Relative percentage abundance was calculated as;

$$\% \boldsymbol{Relative\ abundance} = \frac{\boldsymbol{Mean}\ \%\ \boldsymbol{canopy\ cover\ of\ a\ species\ in\ a\ group\ of\ plots}}{\boldsymbol{Mean}\ \%\ \boldsymbol{canopy\ cover\ of\ a\ species\ in\ all\ the\ plots\ in\ which\ it\ occurred}} \times \mathbf{100}$$

Species evenness was calculated as;

Evenness=$e^{H'}/S$ following Buzas and Gibson, (1969) where H' is Shannon diversity index and S is species richness. The Kruskal-Wallis test was used to test for statistical difference in mean species richness, species diversity and density between vegetation communities.

Results

Ecologically meaningful vegetation clusters (That is; the number of vegetation clusters or communities that are representative of the study area which may indicate the prevailing environmental variables in a given place) were determined at four clusters where the mean *p*-value was at a minimum (Figure 2). There was also a low mean *p* value and a high number of statistically significant indicator species at nine divisions which indicates a suitable level of division for the sub-classes.

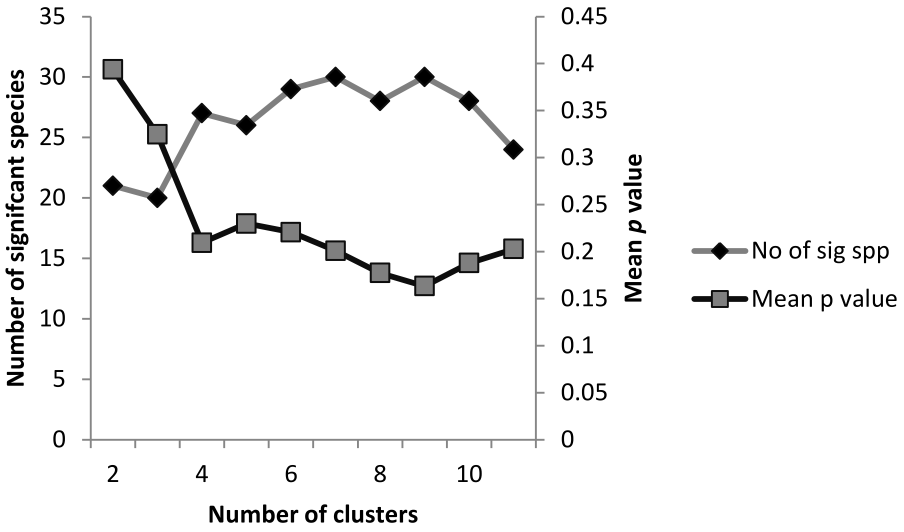

Figure 2: Variation in Number of Statistically Significant Indicator Species, and in Mean *p*-value of Indicator Species per cluster.

The major communities identified in the riparian woodland were as follows (named after their most dominant indicator species): *Croton megalobotrys-Hyphaene petersiana, Acacia erioloba-Diospyros lycioides, Garcinia livingstonei-Acacia nigrescens* and *Syzygium cordatum-Phoenix reclinata* (Figure 3).

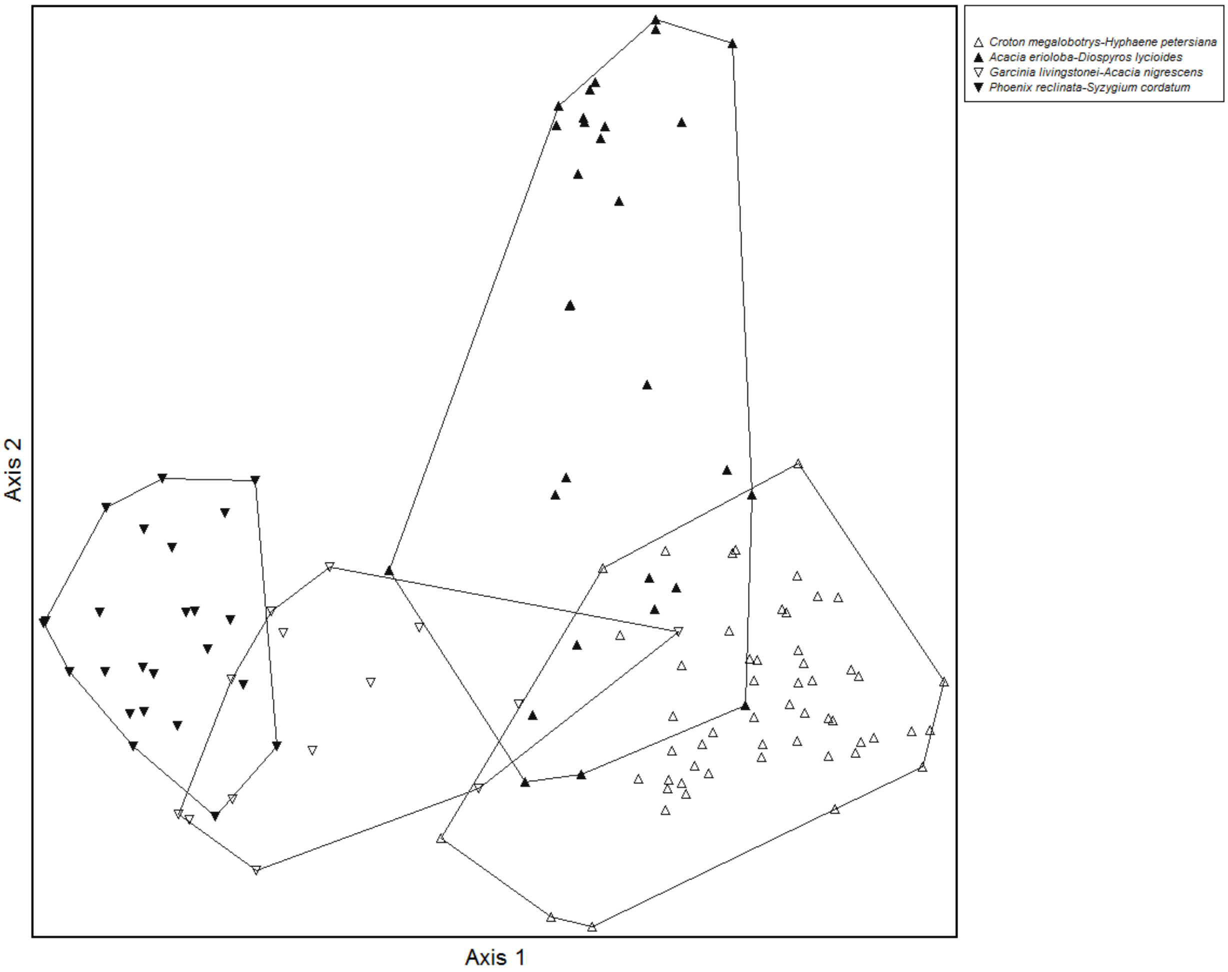

Figure 3: Non-metric multidimensional scaling distinction of riparian plant communities in the Okavango Delta. Axes 1 and 2 explained 33% and 63% of variance respectively.

Pairwise MRPP comparisons between vegetation communities all showed more negative T, A<1 and $p<0.05$ values indicating that there was significant difference between vegetation communities (Table 2).

Table 2: Multi-Response Permutation Procedures pairwise comparisons of vegetation clusters

Classes	**T**	**A**	***p***
CM-HP[1]vs AE-DL[2]	-33.86	0.168	<0.001
CM-HP vs GL-AN[3]	-30.10	0.165	<0.001
CM-HP vs SC-PR[4]	-46.76	0.292	<0.001
AE-DL vs GL-AN	-15.42	0.159	<0.001
AE-DL vs SC-PR	-27.08	0.253	<0.001
GL-AN vs SC-PR	-17.27	0.207	<0.001

[1]CM-HP (*Croton megalobotrys-Hyphaene petersiana*), [2]AE-DL (*Acacia erioloba-Diospyros lycioides*), [3]GL-AN (*Garcinia livingstonei-Acacia nigrescens*), and [4]SC-PR (*Syzygium cordatum-Phoenix reclinata*).

Description of different woodland vegetation communities

Croton megalobotrys-Hyphaene petersiana vegetation community

A total of 9 species were identified in the *Croton megalobotrys-Hyphaene petersiana* vegetation community. The dominant species in this community are *C. megalobotrys* and *H. petersiana*. This vegetation community is characterized by the presence of *P. violacea*, *C. mossambicense*, *Acacia tortilis* and *Kigelia africana*. Other woody species found in this community include *C. imberbe* and *Acacia hebeclada* (Table 3). This is a mixture of dryland and wetland tree and shrub species found in sites characterized by low flooding frequency and duration (Figure 3).

Table 3: Riparian plant community composition in the Okavango Delta.

Species	IV	P value	Growth form	Family
Croton megalobotrys-Hyphaene petersiana				
Croton megalobotrys	86.1	0.0002	Tree	Euphorbiaceae
Hyphaene petersiana	41.1	0.0056	Tree	Arecaceae
Philenoptera violacea	34.3	0.0358	Tree	Fabaceae
Searsia tenuinervis (Engl) Moffett	29.6	0.0010	Shrub	Anacardiaceae
Combretum mossambicense	28.4	0.0728	Shrub	Combretaceae
Acacia tortilis	28.2	0.0506	Tree	Fabaceae

Combretum imberbe	18.7	0.1634	Tree	Combretaceae
Kigelia africana	14.6	0.2424	Tree	Bignoniaceae
Acacia hebeclada	14.2	0.1286	Tree	Fabaceae
Acacia erioloba-Diospyros lycioides				
Acacia erioloba	69.3	0.0002	Tree	Fabaceae
Diospyros lycioides	52.4	0.0004	Shrub	Ebenaceae
Grewia flavescens	38.3	0.0016	Shrub	Tiliaceae
Terminalia sericea	23.7	0.0054	Tree	Combretaceae
Dichrostachys cinerea (L)	23.4	0.1738	Shrub	Fabaceae
Wight & Arn *Gymnosporia*	41.7	0.0192	Shrub	Celastraceae
senegalensis (Lam.) Loes	34.9	0.0266	Shrub	Ebenaceae
Ziziphus mucronata	23.2	0.0906	Shrub	Rhamnaceae
Phyllanthus reticulatus	21.9	0.4165	Shrub	Euphorbiaceae
Combretum hereroense	19.1	0.0752	Shrub	Combretaceae
Colophospermum mopane (J.Kirk ex Benth.) J.Kirk ex J.Léonard	14.5	0.0808	Tree	Fabaceae
Ximenia americana	13.1	0.2961	Shrub	Olacaceae
Grewia bicolour Juss	12.1	0.1308	Shrub	Tiliaceae
Garcinia livingstonei-Acacia nigrescens				
Garcinia livingstonei	86.6	0.0002	Tree	Guttiferae
Acacia nigrescens	66.8	0.0002	Tree	Fabaceae
Elaeodendron transvaalense	44.1	0.0060	Tree	Celastraceae
Gardinia volkensii	41.1	0.0002	Tree	Rubiaceae
Capparis tomentosa	39.4	0.0114	Tree	Capparaceae
Diospyros mespiliformis	36.7	0.0200	Tree	Ebenaceae

Berchemia discolor	34.6	0.0008	Tree	Rhamnaceae
Searsia quartiniana	29.6	0.0010	Shrub	Anacardiaceae
Ficus thonningii Blume	28.2	0.0004	Tree	Moraceae
Antidesma venosum E. Mey. ex Tul	22.0	0.0166	Tree	Euphorbiaceae
Friesodielsia obovata (Benth.) Verdc	21.0	0.0022	Shrub	Annonaceae
Ficus sycomorus L	20.4	0.0998	Tree	Moraceae
Burkea africana Hook	13.7	0.0244	Tree	Fabaceae
Dovyalis caffra (Hook.f. & Harv.) Hook.f.	12.9	0.2172	Shrub	Salicaceae
Acacia sieberiana DC	12.0	0.4187	Tree	Fabaceae
Syzygium cordatum-Phoenix reclinata				
Syzygium cordatum	74.5	0.0002	Tree	Myrtaceae
Phoenix reclinata	72.5	0.0002	Tree	Arecaceae
Acacia galpinii Burtt Davy	25.0	0.0010	Tree	Fabaceae

Mean species richness/plot in the *Croton megalobotrys-Hyphaene petersiana* community was 3.97 and evenness was 0.59. The Shannon and Simpson diversity indices in this community were 0.63 and 0.36 respectively (Table 4).

Table 4: Diversity indices (±SD), evenness (±SD) and density (±SD) in different vegetation communities

Vegetation community	**DIVERSITY INDICES** H′	**Simpson Diversity index (1-D)**	**Evenness**	**Total species richness**	**Mean species richness**	**Density (Number of individuals/ha)**
CM-HP	0.63±0.0.04	0.36±0.02	0.59±0.023	16	3.97±0.17	1 524±1.27
GL-SN	0.64±0.0.05	0.33±0.03	0.57±0.03	21	4.28±0.2	1 437±20.0
SC-PR	0.47±0.05	0.31±0.0.03	0.81±0.03	3	2.08±0.08	4 375±78.2
VE-DL	0.65±0.05	0.34±0.03	0.57±0.02	18	4.28±0.24	754±8.87

Acacia erioloba-Diospyros lycioides vegetation community

A total of 12 woody species were identified in the *Acacia erioloba-Diospyros lycioides* vegetation community. The dominant species in this vegetation community were *A. erioloba* and *D. lycioides*. Other species found in the *Acacia erioloba-Diospyros lycioides* vegetation community in order of decreasing IVs were *Grewia flavescens*, *Terminalia sericea*, *Ziziphus mucronata*, *Phyllanthus reticulatus* and *Combretum hereroense* (Table 3). The *Acacia erioloba-Diospyros lycioides* vegetation community was found in dryland areas further away from the river after the *Garcinia livingstonei-Acacia nigrescens* vegetation community. The Shannon and Simpson diversity indices in this vegetation community were 0.65 and 0.34 respectively. The mean species richness/plot and evenness were 4.28 and 0.57 respectively (Table 4).

Garcinia livingstonei-Acacia nigrescens vegetation community

A total of 15 species including the invasive *Mimosa pigra* L were found in this vegetation community in one plot in the Ngarange area. The *Garcinia livingstonei-Acacia nigrescens* vegetation community is co-dominated by *G. livingstonei* and *A. nigrescens* located after the *Croton megalobotrys-Hyphaene petersiana* vegetation community from the high water line. Other species found in this vegetation community in order of decreasing IVs include *Elaeodendron transvaalense, Gardinia volkensii, Capparis tomentosa, Diospyros mespiliformis* and *Berchemia discolor* (Table 3). Mean species richness/plot was 4.28. The Shannon and Simpson diversity indices in the *Garcinia livingstonei-Acacia nigrescens* were 0.64 and 0.33 respectively and evenness of 0.57 (Table 4).

Syzygium cordatum-Phoenix reclinata vegetation community

This species-poor (3) vegetation community was co-dominated by *S. cordatum* and *P. reclinata*. The other species that was found in this vegetation community was *Acacia galpinii* (Table 3). The *Syzygium cordatum-Phoenix reclinata* vegetation community was found in moist and usually waterlogged sites closer to the river surface water. The Shannon diversity and Simpson diversity indices in this vegetation community were 0.47 and 0.31 respectively. Mean species richness/plot and evenness were 2.08 and 0.81 respectively (Table 4). Density of individuals was high in *Syzygium cordatum-Phoenix reclinata* vegetation community (Table 4).

Discussion

Riparian woodland vegetation was classified into four communities: *Syzygium cordatum-Phoenix reclinata*, *Croton megalobotrys-Hyphaene petersiana*, *Garcinia livingstonei-Acacia nigrescens* and *Acacia erioloba-Diospyros lycioides*. In this classification, the *Syzygium cordatum-Phoenix reclinata* and *Garcinia livingstonei-Acacia nigrescens* communities were found in frequently flooded regions while the *Croton megalobotrys-Hyphaene petersiana* and *Acacia erioloba-Diospyros lycioides* communities were found in occasionally flooded regions. This zonation may be due to the adaptation (or tolerance) of different tree species to different hydrologic regimes to which they are exposed (Capon 2005, Kozlowski 1984, Sparks 1995). Other environmental variables that might have influenced the vegetation zonation include fire, herbivory and drought (Walker et al. 1986). Tree species with similar adaptation strategies to a given environmental variable were found in similar plant communities in the Ozark National river ways (Lyon and Sagers 2002) and the Murray River (Roberts and Ludwig 1991). These similarities may result from similar hydrologic patterns between the Delta and these rivers systems. The Murray River experiences mean annual rainfall of about 250mm and seasonal variability in inflow (Roberts and Ludwig 1991). The Ozark National Scenic River ways region is characterized by seasonal flooding and annual and inter-annual variation in inflows (Lyon and Sagers 2002). The hydrologic behaviour of these river systems is similar to that of the Okavango Delta and this could explain similar response of vegetation in terms of composition and distribution between these ecosystems. In both systems vegetation is distributed along the hydrologic conditions to which they are adapted.

Croton megalobotrys-Hyphaene petersiana consists of species that are tolerant to brackish groundwater, fresh groundwater and dryland conditions. *Philenoptera violacea*, *C. imberbe*, *C. megalobotrys* and *H. petersiana* are tolerant of brackish water and *K. africana* and *C. mossambicense* are tolerant of fresh ground water while *Acacia mellifera* and *S. tenuinervis* are tolerant of dryland (Hamandawana 2011, Ringrose et al. 2007). This vegetation community might have experienced variation in both groundwater type and level in the past. With *C. megalobotrys* and *H. petersiana* being dominant it shows that this vegetation community is found in saline habitats. These species are reported to prefer saline groundwater habitats (Ellery and Ellery 1997) even though it is not clear how are adapted to these conditions. However, the presence of both dryland and fresh ground water species indicates that this vegetation community was historically dry and its ground water was fresh. This can be explained by species adaptation to a given environmental regime. During dry conditions, drought and saline tolerant species would establish and upon flooding, the opportunistic species *C. megalobotrys* (Hamandawana 2012) also established itself in this community. It is expected that as flooding continues the drought tolerant species will be completely eliminated. Conversely, if flooding stops, dry conditions will set in and drought tolerant species will re-establish. This was observed during this study where dead stands of *Acacia erioloba* were found in regions that recently received flooding while seedlings and saplings of *S. cordatum* and *P. reclinata* were found in such areas.

The *Garcinia livingstonei-Acacia nigrescens* vegetation community is mostly dominated by fresh groundwater dependent species such as *D. mespiliformis*, *F. sycomorus*, *B. discolor*, *Acacia seiberiana*, *F. thonningii*, *Gardinia volkensii* and *Garcinia livingstonei* (Ellery and Ellery 1997).

This vegetation community is likely to be found on a substrate completely made up of fresh water because of its close proximity to the river surface water subjected to frequent flooding. *Acacia erioloba-Diospyros lycioides* was comprised of fresh groundwater, brackish ground water and dryland tolerant species. Fresh ground water tolerant species in this community were *A. erioloba* and *Z. mucronata* with *D. lycioides, G. bicolor, X. americana, C. mopane, G. flavescens* and *D. cinerea* the most common dryland species (Ringrose et al. 2007).

The occurrence of both fresh ground water and dryland tolerant species suggests that the *Garcinia livingstonei-Acacia nigrescens* community experiences dry conditions coupled with less saline ground water. This is true for the Okavango Delta which experiences flood pulsing characterized by alternating dry and wet conditions due to intra and multi decadal flood variations. These vegetation communities could be a product of flood variation in both long and short terms. Inter and intra annual flood variations can be influenced by channel blockage which causes flooding into the riparian zones (Ramberg et al. 2006). In the short term flooding variation in terms of extent and duration can affect seed dispersal and germination while in the long term it influences the establishment, composition and distribution of different vegetation communities.

Woody plant phenology has also been found to enable different species to survive dry and wet conditions. Evergreen and semi-evergreen woody species survive in areas where water remains available almost throughout the year for the process of primary production while the presence of deciduous trees is an indication of dry conditions (De Bie et al. 1998). In the Okavango Delta, the occurrence of evergreen *Diospyros mespiliformis*, *Ficus thonningii*, *G. livingstonei* in *Garcinia livingstonei-Acacia nigrescens*, *Syzygium cordatum*, *P. reclinata* in *Syzygium cordatum-Phoenix reclinata* vegetation community and the semi-evergreen *C. megalobotrys* and *P. violacea* in *Croton megalobotrys-Hyphaene petersiana* vegetation community is an indication that they experience water supply throughout the year. The water reaches these communities as it moves laterally underground from the permanent swamps into the islands raising the water table to enable the roots of individual trees to tap it (McCarthy 2006). It has been found that the evergreen and semi-evergreen minimize water loss through scleromorphic features and reduction in physiological activities (De Bie et al. 1998).

Deciduous tree species were common in the *Acacia erioloba-Diospyros lycioides* vegetation community. This is an indication that this vegetation community establishes in dry areas with low moisture content surviving on underground water. Tree species found in *Acacia erioloba-Diospyros lycioides* vegetation community are adapted to low flooding frequency conditions through the development of tap roots which help them to reach for very deep underground water (Roberts and Ludwig, 1991). Another form of adaptation to dry conditions in this community involves shedding of leaves which minimizes water loss through transpiration (De Bie et al. 1998).

Vegetation zonation similar to that found in the Okavango Delta has been documented elsewhere. Medina (1986) in Mexico, Roberts and Ludwig (1991) in Australia, Lyon and Sagers (2002) in Missouri, Fousseni et al. (2011) also observed zonation in riparian vegetation communities. These studies documented flooding to be one of the environmental factors influencing riparian vegetation community composition and distribution. Roberts and Ludwig (1991) cited the presence of high water table to be a significant variable in plant establishment. In Mexico, Medina (1986) discussed grazing disturbance and soil characteristics in addition to flooding to be environmental variables influencing riparian tree species composition and distribution. Other environmental variables influencing vegetation community distribution include elevation above the river, soil pH and soil particle size (Lyon and Sagers 2002). Fousseni et al. (2011) cited plant species distribution along moisture gradients in riparian vegetation communities in Togo.

Both species richness and Shannon diversity index were highest in *Acacia erioloba-Diospyros lycioides* and lowest in *Syzygium cordatum-Phoenix reclinata* vegetation community. This can be explained by the Intermediate disturbance hypothesis which states that diversity will be high in areas experiencing intermediate levels of disturbance and low in areas experiencing low and high disturbance levels (Connell 1978). This suggests that in the Okavango Delta *Acacia erioloba-Diospyros lycioides* experiences intermediate levels of disturbance while the *Syzygium cordatum-Phoenix reclinata*, because of its close proximity to the river, experiences high levels of disturbance from flooding. In some instances *Syzygium cordatum-Phoenix reclinata* community was found in highly water saturated soils which could have acted as high disturbance leading to low diversity. Intermediate levels of disturbance leads to the establishment of both flood and drought tolerant species leading to high diversity while in high flood disturbance only flood tolerant species survive leading to low diversity. *Syzygium cordatum* and *Phoenix reclinata* individuals were dense indicating tolerance to moist conditions.

Conclusion

This study provided baseline information on the different woodland vegetation communities in the Okavango Delta. The information can be used to identify zones of high species richness and diversity, key habitats and most importantly disturbed areas. The current vegetation classification also provides the first attempt in providing inventory of riparian woodland vegetation in the Okavango Delta. This can be used as a vital vegetation monitoring tool. Future changes in species composition would either indicate changes in hydrological regime or new form of disturbance. Vegetation classification can also help to detect occurrence of any exotic species. In the current study the invasive *Mimosa pigra* was detected. This will alert the ecosystem managers in the Okavango Delta to come up with strategies of preventing the spread of this invasive species. It is recommended that to ensure systematic vegetation monitoring, permanent plots should be established which can be visited from time to time to determine the status of the vegetation. Plot coordinates have been recorded during this study and can be readily provided to facilitate the establishment of the recommended monitoring plots. Future studies should determine the environmental variables influencing woodland vegetation zonation in the Okavango Delta. Information on woodland vegetation species composition changes with hydrology is also required. This will add to the current information and allow for comprehensive design of holistic management policies of riparian woodland vegetation in the Okavango Delta.

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Riparian plant community composition along a flooding frequency gradient in the Okavango Delta, Botswana.

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Abstract

In the Okavango Delta, information on the influence of flooding frequency on woody plant species in the riparian zone is generally lacking. The objective of this study was to determine the influence of flooding frequency on riparian woodland species composition and distribution in the Okavango Delta. Flood frequency follows a gradient from highest in the Panhandle to lowest in the distal distributaries such as Moremi. Vegetation sampling was done in 20m × 50m plots in the Panhandle, Seronga, Jao, Moremi and Boro between February 2012 and November 2013. Plant cover, seedling density, species richness and diversity were determined at each site. Plant percentage cover was estimated using a modified Braun-Blanquet cover/abundance scale. Twenty-five year flooding frequency was determined at each site from Landsat imagery. Indicator species analysis was used to determine characteristic species at each site. One-way ANOVA was used to compare vegetation parameters across sites. Riparian woodland vegetation community composition, density, cover and diversity varied significantly ($p<0.05$) along the flooding frequency gradient which characterizes the Delta. Variation in flooding frequency is clearly important for maintaining ecosystem heterogeneity in the Okavango Delta. This study has shown that there is a potential to use woodland vegetation composition and distribution in reconstructing historical hydrological gradients in areas where such information is not available. The study has also provided baseline information that can be used in establishing permanent plots for long term vegetation monitoring.

Key words: Braun-Blanquet, Hydrology, Okavango Delta, Vegetation dynamics

Introduction

Flooding frequency is one of the major environmental factors influencing riparian plant community distribution and species composition in wetland ecosystems (Kozlowski, 1984; Gregory et al. 1991; Ferreira and Stohlgren, 1999). It influences the soil moisture content which affects germination and growth in riparian woodland vegetation communities (Friedman and Auble, 2000). Due to variation in flooding frequency plant diversity in wetlands is highly variable (Gregory et al. 1991). Plant species establish in flooding frequency regimes to which they are adapted with those that are adapted to similar conditions forming a vegetation community (Gregory et al. 1991). Moist riparian zones closer to the river channel, with high flooding frequency are dominated by vascular plants tolerant of flooding while more elevated areas, with lower flooding frequency, are inhabited by plant species intolerant of flooding (Gregory et al., 1991; Camporeale et al. 2005). Such flood-intolerant species that are subjected to high flooding frequency may die, creating gaps for the establishment of their flood tolerant counterparts (Denslow, 1980). Conversely, in dry riparian zones (low flooding frequency) species that area strongly water-dependent may die and be replaced by those that are tolerant of dry conditions (de Oliveira et al. 2014).

Riparian plant communities are often characterized by high species diversity (Naiman et al. 2005). High species diversity in riparian zones can also be explained in part by the Intermediate Disturbance Hypothesis (Connell, 1978). The Intermediate Disturbance Hypothesis predicts that species diversity will be high in habitats experiencing intermediate levels of disturbance and lower in regions that are exposed to low or high disturbance regimes (Huston, 1979). In terms of flooding frequency, this means that we might expect riparian zones that experience intermediate flooding frequency levels to have higher species diversity than those that are subjected to low and high frequencies. This is because at intermediate disturbance levels, both pioneer species and dominant species co-exist (Connell, 1978). That is, plant species tolerant of intermediate flooding frequency and those that tolerate low and high frequency will co-exist resulting in high species diversity. In contrast, highly disturbed habitats (either due to low or high flooding frequency) and their associated severe stress prevent the recovery and re-establishment of vegetation (Grime, 1977). Stress in this case is defined as the external environmental constraints limiting primary production in vegetation which could include shortage and excessive supply of sunlight, water and mineral nutrients and production of growth inhibiting toxins (Grime, 1977). In terms of flooding, high frequency can result in anoxic conditions which may inhibit plant primary production and germination (Kozlowski, 1984). Low flooding frequency can also inhibit primary production and germination due to water stress. This is because plants grow better under optimum conditions for primary production and germination with high or low flooding causing physiological stress (Kozlowski, 1984).

In the Okavango Delta, the riparian woodland has been identified as a significant driver of the ecologically vital process of sequestration of dissolved salts through evapo-transpiration (McCarthy et al. 1998). As the water is lost to the atmosphere through evapo-transpiration, dissolved solutes accumulate around the island centres with toxic solutes accumulating in deep groundwater (McCarthy et al. 1998). This helps to maintain the surface floodplains, channels and lagoons as a freshwater system in the Okavango Delta (Bauer et al. 2002). Despite its positive contribution to the ecological functioning of the Delta, the riparian woodland is threatened by potential degradation due to climate change/variability (Murray-Hudson et al. 2006) which may lead to biodiversity loss. Other threats include potential large scale water abstraction and damming in the upstream regions of the Okavango basin which may reduce the amount of water reaching its downstream areas including the Delta in Botswana (Diederichs and Ellery, 2001). In the past there have been proposals from the three riparian states of Angola, Namibia and Botswana to abstract water from the Okavango basin (Lebotse, 1999). Even though these proposals have not yet been implemented, they may resurface in the future as a result of the continued acute water shortage and human population growth coupled with industrialization in these countries. Recently, it has been reported that the Angolan Government granted their Chinese counterparts 500 000ha of land along the Cubango area to be used for large scale production of rice (Capalandada, 2015) which may result in large volume of water abstraction. If this is implemented, it may also exacerbate the threat from climate change on the riparian plant communities. In order to conserve riparian vegetation resources from these threats, there is little that can be done without understanding how flooding frequency affects them. However, information on the influence of flooding frequency on riparian plant species is generally lacking in the Okavango Delta.

Past studies in the Delta (e.g. Biggs, 1976; Smith, 1976; Snowy Mountains Engineering Corporation, SMEC, 1989; Ellery, 1991; Bonyongo, 1999; Bonyongo et al. 2000; Murray-Hudson, 2009) were mainly focused on seasonal floodplain herbaceous plant communities. This is in contrast with abundant studies conducted elsewhere (e.g. Ferreira and Stohlgren, 1999; Natta, 2003; Damasceno-Junior et al. 2005; Wittman et al. 2006 and de Oliveira et al. 2014) that have investigated the influence of flooding frequency on riparian woodland plant community composition and distribution.

The current study was aimed at investigating the influence of flooding frequency on riparian plant community composition and distribution in the Okavango Delta. It was hypothesized that riparian woodland plant species composition, distribution, abundance, density and diversity will vary across different flooding frequency regimes. Information on the influence of flooding frequency on riparian woodland plant species composition and distribution may be used to reconstruct flooding histories of areas where little is known about their hydrology in the Okavango Delta. This may also be applicable in other tropical wetlands whose hydrologic behaviour is similar to that of the Okavango Delta.

Materials and methods

Study area

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

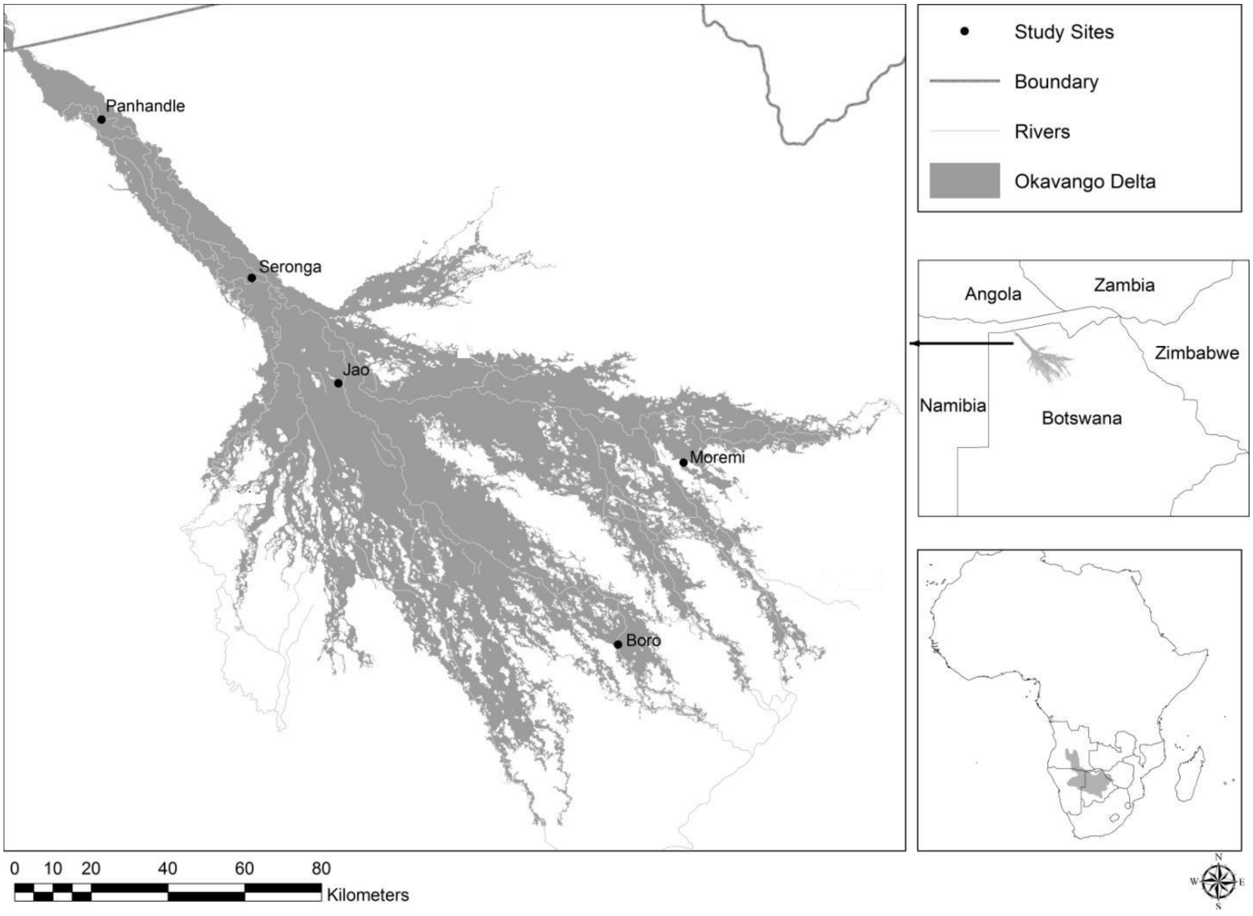

Figure 1: Map of the Okavango Delta showing the study sites.

The hydrology of the Okavango Delta is characterized by annual flood pulses originating from the Angolan highlands, the peak flows of which generally pass the Mohembo inlet region between March and April, reaching the distal region between May and October (McCarthy, 2006). The flood extent in the Delta shows intra and inter-annual variations (Wolski et al. 2006). Intra-annual flood variation refers to the quasi-regular changes in flooding magnitude in terms of duration and depth within a given year. Inter-annual flood variation is characterized by differences in flooding magnitude between two or more years. The Okavango Delta inflows also vary pluri-annually in which there are sequences of years with higher or lower inflows than average (Mazvimavi and Wolski, 2006). During the period of record (1933-present), inflows rose to reach a maximum between 1963 and 1969. Subsequently inflows declined to a minimum in 1995-1996 (Mazvimavi and Wolski, 2006), rising again to a maximum in 2010-2011. The Okavango Delta receives mean annual rainfall (between November and February) of approximately 550mm (Wilson and Dincer, 1976).

The selected study sites were the Panhandle, Seronga, Jao, Moremi and Boro characterized by contrasting hydrological conditions (Table 1). These sites were chosen because they represent different flooding frequencies from frequently flooded sites of Panhandle, Seronga and Jao to occasionally flooded sites of Moremi and Boro. Flooding frequency was determined from pre-classified Landsat images from 1989 to 2007 (Wolski, Unpublished data[1]).

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[1] P. Wolski is a Researcher at the University of Cape Town's Climate Systems Analysis Group

Table 1: Characterization of selected study areas: Adapted from Tsheboeng and Murray-Hudson, (2013). *Flooding frequency was calculated only for the plots that were sampled.*

Study area	**Habitat type(s)**	**Mean flooding frequency (years)**	**Number of plots sampled**
Moremi	Permanently flooded, seasonally flooded and Dryland	0.4	22
Boro	Permanently flooded, seasonally flooded and dryland	3	29
Seronga	Permanently flooded, seasonally flooded and dryland	9	15
Jao	Permanently flooded/Seasonally flooded/Dryland	9	11
Upper Panhandle	Permanently flooded/seasonally flooded/Dryland	9	16

Vegetation sampling

Woodland vegetation was sampled from 20m × 50m plots placed perpendicular to the river channel. The number of plots sampled differed at each site (Table 1) as a result of different vegetation types. Sites with dense vegetation had relatively few plots sampled as compared to sparsely vegetated ones. Furthermore in high flooding frequency sites of Seronga, Jao and Upper Panhandle there was comparatively few riparian vegetation plots to sample from because these area are perennially flooded, with proportionately few islands. Most of the area in these sites is covered by *Cyperus papyrus* species. In total 93 plots were sampled. In each plot, woody plant species present in each plot were recorded, their percentage cover estimated, circumference at breast height was measured using a measuring tape and height was estimated through visual inspection. Specimens of unknown plant species were collected and taken to the Peter Smith University of Botswana Herbarium (PSUB) for identification.

Data analysis

Agglomerative Hierarchical cluster analysis (flexible β linkage, $\beta = -0.25$, Sorensen distance, data relativized by maximum) was used to determine plant communities at each site. In Agglomerative cluster analysis, species with similar occurrences are grouped together to form a cluster in a step-wise manner (McCune and Grace, 2002). This step-wise process continues until all similar objects are joined into one cluster. In this study, the different clusters formed different vegetation communities. Flexible β linkage, which uses weighted mean distance between species to determine whether they belong to a one cluster or not (McCune and Grace, 2002) was used. This was relevant in our study as we classified species (based on percentage) that occurred in different number of plots. The use of $\beta = -0.25$ provided a perfect solution with low percentage chaining. Chaining describes the separation between clusters such that there is less separation when it is high and more separation when it is low (McCune and Grace, 2002). To further reduce percentage chaining and enhance perfect separation between clusters, the data were relativized by plot maximum (McCune and Grace, 2002). In this case, the percentage cover of each species was converted to a proportion of the highest cover in a given plot.

Indicator species analysis (ISA, Dufrêne and Legendre, 1997) was used to determine the indicator species from each site. Indicator species is determined through adding relative abundance and relative frequency of occurrence of a given species. The formula for the calculation of indicator values is given in detail in chapter 2. Nonmetric multi-dimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) was used to infer site relationships as influenced by flooding frequency. Sorensen distance, random starting configuration, 200 maximum iterations and 2-dimensions were selected with final stress of 20. Species diversity and richness were determined at each site (The methods are given in full in chapter 2). The vegetation data was subjected to normality and homogeneity of variance tests using Kolmogorov-Smirnov and Levene's test respectively. One-way ANOVA and Tukey post hoc were used to compare mean species diversity, richness, height and basal area across sites since the data met the normality and homogeinty of variance assumptions (df=4, p=0.088). The confidence level for all the analysis was set at 95% or p=0.05. Shannon species diversity and species richness were calculated as in chapter 2. Mean basal area, plant density (was calculated as in chapter 2) and height were also determined for each site. Basal area (BA) was calculated as; BA (m^2) = $\pi(dbh/2)^2$ (Hédl et al. 2009) where π = 3.14 and dbh is the diameter of the tree trunk at breast height. Basal area m^2/hectare at each distance class was calculated as; $Basal\ area = \frac{Sum\ of\ the\ basal\ area\ of\ each\ tree}{Area\ of\ the\ sample\ plot\ in\ hectares}$. In this case the sum of the basal area of each tree at each distance class was divided by 0.1 which is a conversion factor of (1 000m^2 / 10 000m^2). In this case, 1 000m^2 is the total area of the plot used in this study (20m × 50m) while 10 000m^2 is the total area of a hectare in m^2.

Results

In terms of flooding frequency, the Okavango Delta woodlands fell into 10 assemblages, with two assemblages occurring at each site. This indicates a wide spatial variation of tree species across the riparian woodland (Table 2).

Table 2: Indicator species in riparian plant communities at each site (flooding frequency).

Site	Species	Indicator value	*p*-value	Growth form	Family
Seronga					
	Elaeodendron transvaalense-Dovyalis caffra				
	Acacia nigrescens	79.5	0.02	Tree	Fabaceae
	Garcinia livingstonei	77.7	0.23	Tree	Guttiferae
	Phoenix reclinata	67.5	0.08	Tree	Arecaceae
	Acacia sieberiana	60.0	0.04	Shrub	Fabaceae
	Philenoptera violacea	57.1	0.33	Tree	Fabaceae
Syzygium cordatum-Searsia tenuinervis					
	Acacia luederitzii	57.1	0.13	Shrub	Fabaceae
	Diospyros mespiliformis	53.2	0.69	Tree	Ebenaceae
Jao					
	Garcinia livingstonei-Phoenix reclinata				
	Acacia nigrescens	50.0	0.44	Tree	Fabaceae
	Ficus sycomorus	71.0	0.36	Tree	Moraceae
	Berchemia discolor	50.0	0.47	Tree	Rhamnaceae
	Capparis tomentosa	52.4	0.80	Shrub	Capparaceae
	Elaeodendron transvaalense	50.0	0.45	Tree	Celastraceae
	Syzygium cordatum	58.8	0.45	Tree	Myrtaceae
	Grewia flavescens-Phyllanthus reticulatus				
	Searsia ternuinervis	87.7	0.044	Shrub	Anacardiaceae
	Gymnosporia	98.7	0.02	Shrub	Celastraceae

	senegalensis				
	Euclea divinorum	96.4	0.02	Shrub	Ebenaceae
	Diospyros lycioides	95.9	0.02	Shrub	Ebenaceae
	Diospyros mespiliformis	56.9	0.76	Shrub	Ebenaceae
	Ziziphus mucronata	98.1	0.02	Tree	Rhamnaceae
	Ximenia americana	94.6	0.07	Shrub	Olacaceae
	Acacia sieberiana	50.0	0.20	Shrub	Fabaceae
	Philenoptera nelsii	50.0	0.20	Tree	Fabaceae
Upper Panhandle					
	Phoenix reclinata-Syzygium cordatum				
	Ficus sycomorus	77.4	0.008	Tree	Moraceae
	Garcinia livingstonei-Searsia tenuinervis				
	Dichrostachys cinerea	62.4	0.03	Shrub	Fabaceae
	Euclea divinorum	73.4	0.02	Shrub	Ebenaceae
	Diospyros lycioides	50.0	0.08	Shrub	Ebenaceae
	Acacia nigrescens	69.7	0.08	Tree	Fabaceae
	Diospyros mespiliformis	81.7	0.008	Tree	Ebenaceae
	Berchemia discolor	50.0	0.08	Tree	Rhamnaceae
	Ximenia americana	50.0	0.09	Shrub	Olacaceae
	Grewia flavescens	50.0	0.09	Shrub	Tiliaceae
	Friesodielsia obovata	50.0	0.08	Shrub	Annonaceae
Boro					
	Hyphaene petersiana-Diospyros mespiliformis				
	Croton megalobotrys	62.2	0.02	Tree	Euphorbiaceae
	Kigelia africana	47.2	0.14	Tree	Bignoniaceae
	Acacia tortilis	34.8	0.23	Shrub	Fabaceae
	Acacia nigrescens	36.7	0.95	Tree	Fabaceae
	Garcinia	39.9	0.53	Tree	Guttiferae

	livingstonei				
	Philenoptera violacea-Gymnosporia senegalensis				
	Diospyros lycioides	62.0	0.26	Shrub	Ebenaceae
	Sclerocarya birrea	50.0	0.005	Tree	Anacardiaceae
	Combretum hereroense	42.8	0.04	Tree	Combretaceae
	Ximenia americana	30.7	0.07	Shrub	Olacaceae
Moremi					
	Croton megalobotrys-Hyphaene petersiana				
	Philenoptera violacea	57.8	0.07	Tree	Fabaceae
	Gymnosporia senegalensis	64.2	0.21	Shrub	Celastraceae
	Diospyros lycioides	51.7	0.24	Shrub	Ebenaceae
	Combretum mossambicense	52.5	0.15	Shrub	Combretaceae
	Acacia erioloba-Ziziphus mucronata				
	Searsia tenuinervis	24.7	0.47	Shrub	Anacardiaceae
	Colophospermum mopane	34.7	0.11	Tree	Fabaceae
	Sclerocarya birrea	20.0	0.20	Tree	Anacardiaceae
	Terminalia sericea	40.0	0.04	Tree	Combretaceae

There was spatial variation in mean cover, density, species diversity and richness in the Okavango Delta. The mean percentage cover was high in Boro and Panhandle but not significant (df=4, Mean square=2 128.40, F=0.570, *p*=0.72). Analysis of Variance showed that the density of trees was significantly higher (df=4, F=24.7, *p*=0.0001) in high flooding frequency sites (Seronga, Panhandle and Jao) than in the low flooding frequency sites (Moremi and Boro). Tukey post hoc analysis showed that in Seronga (df=4, Mean=711) mean seedling density was significantly higher than in Boro (Mean=380, *p*=0.0001) and Moremi (Mean=277, *p*=0.0001). In the Panhandle (df=4, Mean=960), seedling density was significantly higher than Boro

(Mean=380, *p*=0.0001). The mean seedling density ws also significantly higher in Jao (df=4, Mean=590) than in Moremi (Mean=277, *p*=0.007). Species richness was significantly higher in Seronga (df=4, Mean=13, *p*=0.028), Jao (Mean=16, *p*=0.002) and Panhandle (Mean=14, *p*=0.003) than in Moremi (Mean=9). Species diversity was significantly higher in Boro (df=4, Mean=1.40, p=0.0001), Jao (Mean=1.78, *p*=0.019), Panhandle (Mean=1.47, *p*=0.0001) and Seronga (Mean=1.44, *p*=0.023) than in Moremi (Mean=0.90) (Table 3).

Table 3: Variation in riparian woodland plant community in diversity, mean percentage cover and density across different sites in the Okavango Delta

Site	**Mean % cover**	**Woodland density (Number of individuals/ha)**	**Shannon H′ species diversity**	**Mean species richness**
Boro	34 ± 12^{a}	380 ± 31^{a}	1.40 ± 0.06^{a}	12 ± 0.59^{a}
Moremi	20 ± 9^{a}	277 ± 24^{a}	0.90 ± 0.13^{b}	9 ± 1.0^{b}
Jao	17 ± 5.2^{a}	590 ± 12^{b}	1.78 ± 0.10^{a}	16 ± 1.0^{a}
Panhandle	34 ± 12^{a}	960 ± 43^{b}	1.47 ± 0.11^{a}	14 ± 1.4^{a}
Seronga	24 ± 9.3^{a}	711 ± 46^{b}	1.44 ± 0.19^{a}	13 ± 1.8^{a}

*Similar letters in a column indicate no significant difference while different letters show that there is a significant difference.

Discussion

This study indicates that riparian woodland plant community composition varies along the flooding frequency gradient in the Okavango Delta. The riparian woody plant species inhabited flooding frequency gradients according to their specific water requirements with those that require more water colonizing sites of high flooding frequency while those that require less water occupying low flooding frequency sites. Species with similar adaptations co-exist along the flooding frequency gradient continuum (Parolin et al. 2004). In the Boro system which was characterized by low flooding frequency, the indicator species were *Hyphaene petersiana* and *Combretum hereroense*, which are tolerant of saline groundwater (Ellery et al. 1993) and deep groundwater table (Cole and Brown, 1976) respectively, *Sclerocarya birrea* and *Acacia tortilis* tolerant of dryland conditions (McCarthy and Ellery, 1994) while *Garcinia livingstonei* is tolerant of low groundwater salinity (Ellery et al. 1993). The co-occurrence of these species shows that there were microsites of both fresh and saline ground water along Boro. Saline groundwater is caused by evapo-transpirative concentration of solutes by the riparian vegetation (McCarthy, 2006). Woodland plant species fringing islands such as *Croton megalobotrys*, *Philenoptera violacea* and *H. petersiana* lose water through evapo-transpiration which depresses the groundwater table under the islands and increases salinity as a result of accumulation of solutes dominated by Ca, Mg and Na carbonate-bicarbonate (McCarthy and Ellery, 1994). As a result of the low groundwater table, water continuously moves laterally down-gradient from the swamp to underneath the islands (McCarthy and Ellery, 1994).

Depth to groundwater and salinity levels in the islands control plant species distribution with species zonation reflecting their tolerance envelopes for groundwater accessibility and salinity (Ellery et al. 1993). That is, fringes of the islands with relatively shallow groundwater depth and low salinity levels are colonized by tree species such as *Diospyros mespiliformis, G. livingstonei* and *F. sycomorus* while in the interior zones where groundwater levels were relatively low were colonized by deciduous trees such as *Acacia nigrescens* and *P. violacea* and the more interior regions were colonized by *H. petersiana* (Ellery et al. 1993). The distribution of tree species in the Delta may also be a product of flooding frequency variation. The presence of plant species tolerant of dryland conditions in Boro such as *Acacia tortilis*, *S. birrea* and *A. nigrescens* indicates that the Delta also experiences dry conditions. This occurs in both short term which is characterized by intra-annual flood pulsing and long term defined by inter-annual flood variation in which some years receive comparatively low flooding (Wolski et al. 2006) resulting in high groundwater table and the establishment of dryland species. In Lake Ngami, which is fed from the Okavango Delta through the Kunyere and Nhabe river outlfows, it was also found that dryland species established in elevated regions that were characterized by high groundwater table due to multi-decadal flood variation in which there were some dry years (Hamandawana, 2011).

In Moremi which also had low flooding frequency (Table 1), the characteristic species were *H. petersiana* which is tolerant of brackish groundwater (Ellery et al. 1993), *Gymnosporia senegalensis* and *Terminalia sericea* tolerant of dryland conditions (Cole and Brown, 1976) and *Z. mucronata* tolerant of fresh groundwater (Ringrose et al. 2007). The sites in Moremi are occasionally flooded which provide a window of opportunity for colonization by species tolerant of dryland conditions which are able to access deep groundwater resources. Indicator species in the Panhandle and Jao were a mixture of species that are tolerant of both shallow and deep groundwater table. Species that depend on access to a shallow groundwater table in the Panhandle and Jao include *Phoenix reclinata*, *Syzygium cordatum*, *Diospyros lycioides* and *Ficus sycomorus*. These species are also tolerant of low saline groundwater conditions (Ellery et al. 1993). Species that are tolerant to deep groundwater depth include *S. nigrescens*, *Ximenia americana* and *P. violacea*. In our study the presence of species tolerant of deeper groundwater in the frequently flooded sites (Panhandle and Jao) shows that there is within/intra site flooding variation. It may also be an indication of multi-decadal flooding variation which suggests that there were long periods of drying in the Panhandle and Jao in the past which promoted the colonization of dry land species.

Historical records show that there were channel blockages in the Panhandle and Jao regions (Snowy Mountains Engineering Corporation, 1989) which may have contributed to drying and establishment of dryland tolerant species in these sites. The results of this study also suggest that in the recent past with the increase in flooding frequency, deep groundwater tolerant species were replaced by flood tolerant ones. These species were limited to occasionally flooded regions within the water availability and flooding frequency continuum in both Jao and Panhandle. This is consistent with Ellery et al. (1993) who found that species tolerant of deep depth to groundwater occupy elevated regions which seldom receive floodwaters with those tolerant of shallow groundwater inhabiting frequently flooded sites closer to the river surface water in the Okavango Delta. This is also in agreement with Lite et al. (2005) in the San Pedro River in the U.S.A. who found that riparian plant species were distributed along flooding frequency and water availability requirements. They found that hydro-mesic species colonized sites closer to the river channel with high flooding frequency while xeric species occupied highly elevated regions with low flooding frequency (Lite et al. 2005).

Species diversity and richness were highest in Jao (high flooding frequency area) and lowest in Moremi (low flooding frequency area). The high diversity in Jao and Moremi could be an indication of the prevailing disturbance levels. Biotic diversity is expected to be high in habitats experiencing moderate (intermediate) disturbance levels (Connell, 1978). Disturbance regimes enable plant species to co-exist resulting in an increase in diversity (Connell, 1978; Denslow, 1980). In this study, high flooding frequency in Jao could act as an intermediate disturbance regime which enables high flood frequency tolerant species to co-exist with their flood intolerant counterparts. This is because new niches which favour both types of species are opened up. However, it is expected that with continuous flooding the new dominance order will eventually emerge, where species tolerant of high flooding frequency will dominate and some of the species tolerant to low flooding frequency will be eliminated, leading to an overall reduction in diversity and richness. This is supported by Lite et al. (2005) who found that xeric and pioneer hydro-mesic species were more abundant in low and high flooding frequency sites respectively. In Moremi, the lowest species diversity and richness could be an indication that low flooding frequency only favours the establishment of species tolerant of dry conditions.

Frequently flooded sites (Panhandle, Jao and Seronga) have high tree density while the low flooding frequency regions (Moremi and Boro) showed a low woodland density. The characteristic species at the frequently flooded sites was *Phoenix reclinata* which grows in clusters of individual stems contributing to high density. With these sites not limited by water, individuals in the woodland can afford to grow in high density due to low mortality from drying. Conversely, in the intermittently flooded and low flooding frequency regions water is a limiting factor which leads to relatively low woodland density. This is supported by the findings of Ferreira and Stohlgren, (1999) in the Amazon where they found high tree species density in habitats experiencing prolonged flooding duration.

Conclusion

This study has revealed spatial variation in riparian plant community composition and distribution along the major flooding frequency gradient from upstream to downstream in the Delta. The composition and distribution of riparian woodland species can be used as an indicator of the flooding frequency. This can be important especially in reconstructing flooding histories of areas where little is known about their past hydrology. Monitoring plots across different hydrologic sites can be designed and assessed for any changes that have occurred in terms of plant community composition, distribution, cover, diversity and density. Any changes in these may give insights on the hydrologic status of the Okavango Delta. In the past there have been efforts to use vegetation as bio-indicators of hydrologic status in the Okavango Delta. However, that has been limited to seasonal floodplain plant communities which only respond to short term changes in hydro-period. The woodland vegetation could be useful in monitoring hydrological changes in the long term. The study also suggested that any changes in the hydrological status of the Okavango Delta will disturb riparian plant community composition and distribution. Changes to the hydrological status of the Okavango Delta could result from climate change, upstream dam construction and large scale irrigation schemes. It is therefore recommended that there be no disturbance to the Okavango Delta hydrology as this may have a negative impact on riparian plant community composition and distribution. Therefore, it is important to keep the Okavango Delta in its hydrologic status which is characterized by flood pulsing in order to maintain its heterogeneous ecosystem.

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Response of riparian plant community composition to distance from surface water in the Okavango Delta, Botswana.

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Abstract

The objective of this study was to determine the influence of distance from surface water on riparian plant communities in the Okavango Delta. Vegetation sampling was conducted in 7 sites within the Okavango Delta in 20 × 10m belted plots placed perpendicular to the river bank. The plots were placed at 0-10m, 10-20m, 20-30m, 30-40m and 40-50m distance classes increasing further away from the river bank. Tree height, basal area, species richness, plant canopy cover and diversity were determined for each distance class. Indicator species analysis was used to determine the characteristic species at each distance class. Single factor ANOVA and Tukey post hoc analysis were used to compare species diversity, mean tree height, cover and basal area between distance classes. Correlation between distance from surface water and vegetation parameters was sought using Spearman regression analysis. All parameters except for species richness varied significantly ($p<0.05$) along distance from surface water. Distance from surface water positively correlated to all vegetation parameters except for mean species richness/plot. These results show that distance from surface water influences riparian plant community composition and distribution in the Okavango Delta. This implies that riparian plant species can be indicators of hydrologic conditions in the Delta.

Key words: Riverine, Okavango, Tree and Woodland

Introduction

Distance from surface water may control the distribution of riparian plant communities through its influence on the depth to ground water. Along the lateral gradient of the riparian corridor, depth to ground water increases with increasing distance from surface water (Lite *et al.,* 2005). As a result riparian plant species colonise sites with depth to groundwater to which they are adapted along the distance from surface water continuum (Capon, 2005). Moist riparian zones in close proximity to surface water with shallow depth to groundwater are characterized by species tolerant of flooding while more elevated areas found in far reaches from surface water, with relatively deeper depth to groundwater are inhabited by plant species intolerant of flooding (Camporeale *et al*., 2005). The effect of distance from surface water and depth to groundwater on riparian plant communities have been extensively studied in semi-arid regions such as the San Pedro and Hassayampa rivers where a decline in water table resulted in death of some plants, reduction in primary production and abundance (Stromberg *et al*., 2007), Bill Williams River in Arizona where it was found that *Populus fremontii* S. Watson and *Salix gooddingii* C.R. Ball saplings died in response to a decline in groundwater depth (Shafroth, Stromberg & Patten, 2000) and in the Potomac river (Everson & Boucher, 1998).

In the Okavango Delta, studies on the riparian plant communities are few (e.g.Tsheboeng & Murray-Hudson, 2013; Tsheboeng, Murray-Hudson, Kashe, 2016) and have not investigated the influence of environmental drivers such as distance from surface water on riparian plant community composition and distribution. The present study provides new insights and ecological analysis on the effect of distance from surface water on riparian plant species composition and distribution. It investigates the influence of distance from surface water in 20m × 10m belted plots that were placed at 10m intervals perpendicular to the river bank along a 50m transect. A minimum of ten transects were placed at each site. Tree height, mean plant canopy cover, basal area, species richness, diversity and indicator species were determined at each plot. We predicted that these parameters will decrease with increasing distance from surface water. Indicator woodland species were also predicted to differ along distance from surface water gradient.

The Okavango Delta provides an excellent opportunity to study the effect of distance from surface water on woody riparian plant communities in riparian regions as currently there are no major abstraction and impoundment of its inflow. Therefore, it offers a natural and relatively undisturbed environment for such study. Furthermore, the Delta has well defined zones of riparian plant communities. However, in the future the inflow of water in the Okavango Delta may decrease as a result of major water abstractions (Andersson *et al.*, 2006) and climate change (Murray-Hudson, Wolski & Ringrose, 2006). Low water flow into the Delta either as a result of excessive abstraction or climate change may promote the encroachment of dryland species at the expense of the riparian counterparts. Understanding effects of surface water on the species composition and distribution of riparian plant communities can help us to understand how they will change in response to climate change and anthropogenic pressures on the water resources of the Delta. Such information may also be significant in understanding and maintaining wetland ecosystem functions (Naiman & Decamps, 1997).

Material and Methods

Study area

The study was conducted in the Okavango Delta. The selected study sites were Boro, Jao, Upper Panhandle, Seronga, Vumbura, Moremi and Santawani (Figure 1).

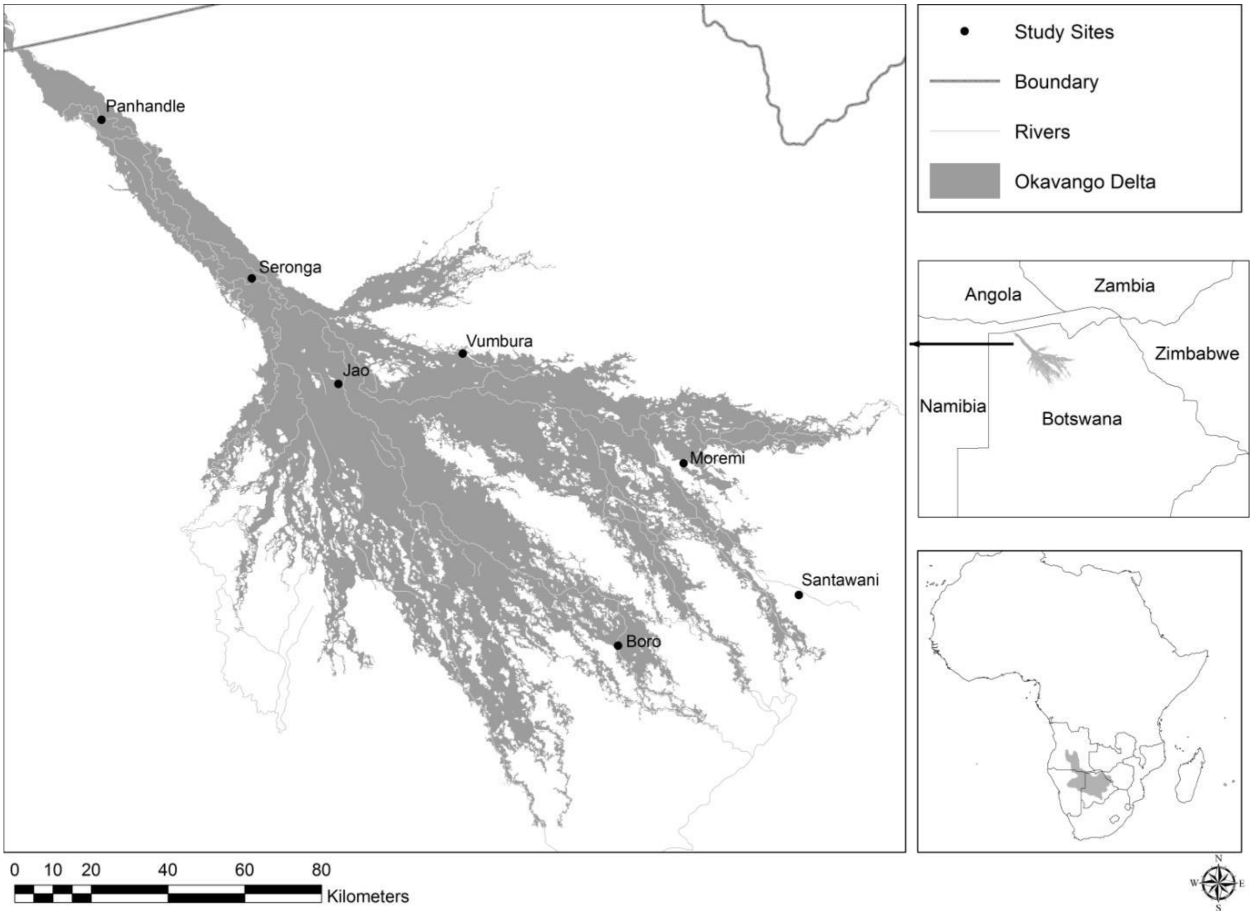

Figure 1: Map of the Okavango Delta showing the study sites.

The Okavango Delta experiences both intra and inter-annual flood variation with some months within a year and between years experiencing different flooding magnitudes (Ramberg *et al.*, 2006). In years of low flooding the maximum flooded area is 3 000km^2 while during high floods it is about 13 000km^2 (McCarthy, 2006). The Okavango Delta, characterized by extremely high evapo-transpiration rate which contributes to 98% water loss of the total inflow is fed by local rainfall (300-500mm/year) and floods from Angolan highlands (Gumbricht, McCarthy & McCarthy, 2004). Flooding occurs in late April or early May at the Panhandle which is the upper region of the Delta (McCarthy, 2006) and reaches the distal regions in August (McCarthy *et al.*, 2004). The Okavango Delta flood water recedes between September and November (Wilson & Dincer, 1976). Common woodland species include *Acacia erioloba* E. Meyer, *Croton megalobotrys* Müll. Arg, *Phoenix reclinata* Jacq, *Diospyros mespiliformis* Hochst. ex A. DC and *Garcinia livingstonei* T. Anderson (Table 1). The soil in the riparian zone is sandy and saline (Ringrose *et al.*, 2007). The soil salinity in the Okavango Delta is influenced by flooding. During flood peak the salinity reduces and increases at low flooding phase. Flooding frequency also influences soil salinity in the Okavango Delta. Salinity is high in low flooding frequency floodplains and low in high flooding frequency regions (Bonyongo & Mubyana, 2004).

Table 1: Characterization of different study sites in the Okavango Delta. From: Tsheboeng, Murray-Hudson & Kashe, 2016.

Study area	Coordinates	Location	Habitat type	Common woodland vegetation
Santawani	23˚37'8"E, 19˚32'11"S	Lower Delta	Dryland	*Acacia erioloba* E. Meyer, *Croton megalobotrys* Müll. Arg
Moremi	23˚22'38"E	Lower Delta	Permanently flooded, Seasonally flooded and Dryland	*Hyphaene petersiana* Mart, *Kigelia africana* Lam Benth
Boro	23˚9'13"E, 19˚32'27"S	Lower Delta	Permanently flooded,	*Combretum hereroense* Schinz,

			seasonally flooded and dryland	*A. erioloba*
Seronga	22˚17'8"E, 18˚48'42"S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Syzygium cordatum* Hochst. ex C Krauss, *Phoenix reclinata* Jacq
Jao	22˚33'40"E, -19˚1'57"S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*S. cordatum, P. reclinata*
Upper Panhandle	21° 52'13"E, -18° 21'53"S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Sersia quartiniana* A. Rich, *Elaeodendron transvaalense* (Burtt Davy) R.H. Archer
Vumbura	22° 53′ 41″ E 18° 58′ 39″ S,	Middle Delta	Permanently flooded, seasonally flooded and dry land	*Acacia nigrescens* Oliv, *Albizia harveyi* E. Fourn

Vegetation Sampling

Riparian woody vegetation was sampled between February 2012 and November 2013. Sampling during these times was meant to maximize identification since most the species were in a flowering stage. Riparian woody vegetation was sampled in randomly selected 20m × 50m plots subdivided into 20m × 10m belted plots placed perpendicular to surface water at 0-10m, 10-20m, 20-30m, 30-40m and 40-50m intervals. The distance was measured from high water point. There was no defined distance between the 20m × 50m plots as they were placed in discreet islands found in the Okavango Delta (Gumbricht *et al*., 2004). In earlier studies on the riparian vegetation in the Okavango Delta (Tsheboeng & Murray-Hudson, 2013; Tsheboeng *et al*., 2016) it was observed that at 50m there were few or no woodland species present. In some instances this was as a result of flooding from the adjacent floodplain which led to the exclusion of the woodland species. The absence of woodland vegetation at 50m from the channel could have also resulted from an increase in groundwater salinity towards the island center (Ellery, Ellery & McCarthy, 1993). It is against this background that transects were 50m long during this study as beyond this distance there was almost no woody vegetation. The 20m × 10m plots were used to maximize the inclusion of seedlings in the sampled area. Seedlings in the Okavango Delta are sparsely distributed and using a plot size that is smaller than 20m × 10m may result in some of them being missed during the counting. From each plot plant species were identified, tree height and stem size measured. Stem circumference was measured using a measuring tape at breast height (1.3m) while tree height was visually estimated. Seedlings of all the species in a plot were counted. The seedling was defined as an individual of height >0-0.5m. Fifteen plots were sampled for each distance class leading to a total of 75 per site.

Statistical analysis

Indicator species analysis was used to determine characteristic species at each distance class. It is as described by McCune & Grace, (2002) conducted in *a priori* determined groups. The indicator species is the characteristic species that is exclusive to a particular group. Two groups were determined at each distance class using Agglomerative Hierarchical cluster analysis. The Agglomerative Hierarchical cluster analysis groups species based on their co-occurrence in the sampling plots (McCune & Grace, 2002). That is; species that were found together in most of the plots are put in one community or vegetation cluster. Monte Carlo test was used to determine if the observed indicator value for each species was significant (Dufrêne & Legendre, 1997).

Circumference at breast height was converted to diameter at breast height (dbh) using the formula; Diameter (d) = Circumference (C)/π, where π = 3.14. Basal area/ha, mean tree height, Shannon & Weiner diversity index and mean species richness/plot were calculated for each distance class. The formula for calculating Shannon & Weiner diversity index is given in chapter 2. Basal area was calculated as in chapter 3.

Kolmogorov-Smirnov was used to test for normality and the Levene's test was used to test for homogeneity of variance in the vegetation data. The data met all the assumptions and as a result single factor ANOVA and Tukey post hoc analysis were used to determine if there were any statistically significant differences between these vegetation parameters among distance classes (0-10m, 10-20m, 20-30m, 30-40m and 40-50m). Correlation was sought between basal, mean tree height, diversity and richness and distance from surface water using Spearman regression analysis.

Results

Mean basal area (m^2/ha) was significantly lower at 0-10m (df=4, Mean=2.9, *p*=0.0001) than at 20-30m (df=4, Mean=4.6) while at 10-20m (df=4, Mean=2.4) it was significantly lower than at 20-30m (df=4, Mean=4.6, *p*=0.0001) and 40-50m (df=4, Mean=4.0, *p*=0.015) distance classes (Fig 2A). Mean tree height was significantly higher at 20-30m (df=4, Mean=11) than at 0-10m (df=4, Mean=6 *p*=0.0001), 10-20m (df=4, Mean=6.5 *p*=0.011), 30-40m (df=4, Mean=9 *p*=0.011) and 40-50m (df=4, Mean=8 *p*= 0.022) distance classes. Distance classes 30-40 and 40-50m had the same tree height and were both significantly (*p*=0.0001) higher than 0-10 and 10-20m

(Figure 2B). There was no significant (df=4, Mean square=4.29, F=0.303, *p*=0.875) difference in mean species richness between distance classes (Figure 2C). Plant species diversity at 20-30m (df=4, Mean=1.18) class was higher than at all the distance classes. However, the significant difference was at 30-40m (df=4, Mean=0.81, *p*=0.025) (Figure 2D).

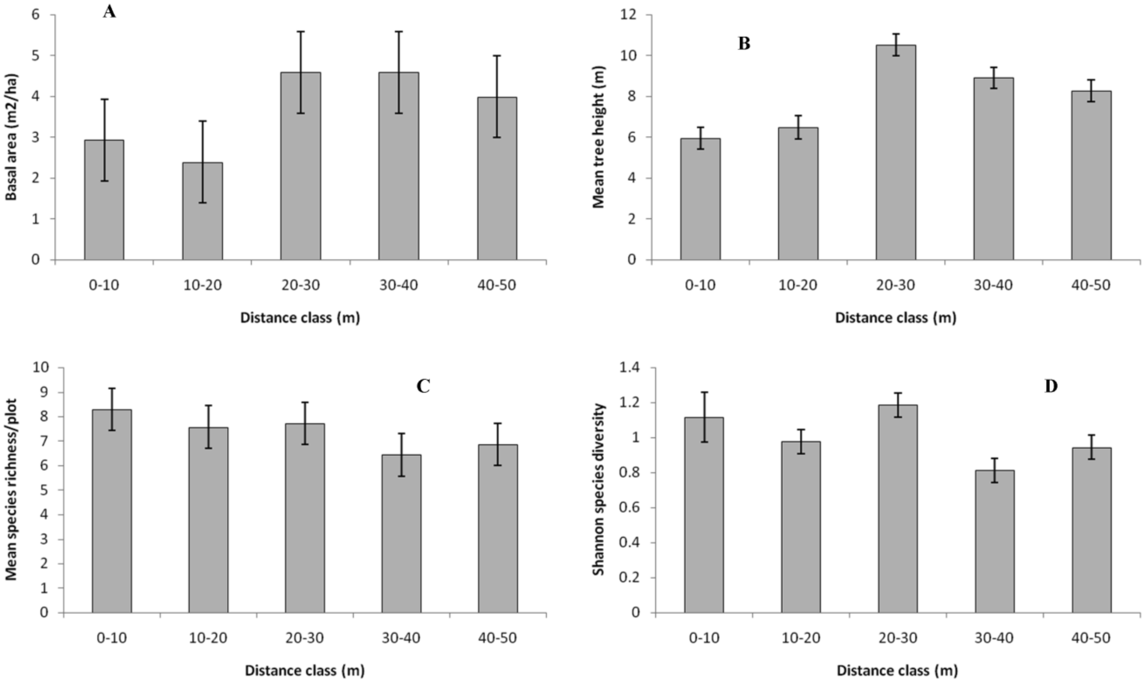

Figure 2: Variation of mean (±SD) basal area (A), tree height (B), species richness/plot (C) and diversity (D) in the Okavango Delta.

Riparian woodland tree species dominance varied with increasing distance from surface water. *Croton megalobotrys* Müll. Arg had significantly (Indicator value= 90.1, *p*=0.0002) high indicator value at the 40-50m distance class while *Phoenix reclinata* Jacq (Indicator value=24.8, *p*=0.0002) and *Syzygium cordatum* Hochst. ex C. Krauss (Indicator value=18.3, *p*=0.0002) had significantly high indicator values at all distance classes except at 40-50m (Table 2).

Table 2: Variation in indicator values of common woodland species at each distance class.

Species	0-10	10-20	20-30	30-40	40-50
Syzygium cordatum	94.8*	77.7*	59.8*	65.7*	18.3
Phoenix reclinata	93.7*	98.1*	85.2*	87.1*	24.8
Croton megalobotrys	56.6*	57.4*	54.3*	61.2*	90.1*
Diospyros lycioides Desf	46.7*	30.5*	27.9*	21.4*	19.8
Philenoptera violcea (Klotzsch) Schrire	38.7*	39.6	40.3*	33.7	42.9
Hyphaene petersiana	36.4*	35.3*	37.8*	38.7*	26.3
Garcinia livingstonei	30.7	25.6	67.7*	73.5*	27.9
Euclea divinorum Heirn	29.9*	21.6	22.0	16.6	19.3
Diospyros mespiliformis	27.8	30.1	25.2	28.8	35.3
Acacia erioloba	21.2*	22.8*	29.5*	22.4	22.0

*****Significant maximum indicator value at *p*<0.05.

Mean woodland canopy cover was significantly higher at 0-10m (df=4, Mean=58) than in all distance classes (10-20m (df=4, Mean=45 *p*=0.047) 20-30m (df=4, Mean=43, *p*=0.017), 30-40m (df=4, Mean=40 *p*=0.008) and 40-50m (df=4, Mean=40, *p*=0.014))))). Mean seedling density was significantly (*p*<0.05) higher at 0-10m than at 40-50m (Table 3).

Table 3: Woodland vegetation communities, mean percentage cover and seedling density at each distance class

Distance class (m)	**Vegetation community**	**Mean percentage cover**	**Mean seedling density (Individuals/ha)**
0-10	*Croton megalobotrys-Gymnosporia senegalensis*, *Syzygium cordatum-Phoenix reclinata*	58±1.02*	5 745±177*
10-20	*Croton megalobotrys-Hyphaene petersiana, Phoenix reclinata-Syzygium cordatum*	45±1.63	3 130±779
20-30	*Croton megalobotrys-Philenoptera violacea, Phoenix reclinata-Syzygium cordatum*	43±1.69	3 767±158
30-40	*Croton megalobotrys-Hyphaene petersiana, Phoenix reclinata-Syzygium cordatum*	40±1.39	3 121±992
40-50	*Croton megalobotrys-Phoenix reclinata, Phoenix reclinata-Syzygium cordatum*	40±1.38	2 818±158

*Significantly different at *p*<0.05.

There was a weak negative relationship (*p*>0.01) between species richness, diversity and distance from surface water. Height, basal area and distance from surface water showed a weak positive relationship (Table 4). Tree height showed significant (p<0.01) correlation with distance from surface water.

Table 4: Spearman correlation between vegetation parameters and distance from surface water.

Vegetation characteristic	**Correlation Coefficient**	**R^2**	***p*-value**
Basal area	0.079	0.0062	0.010*
Height	0.070	0.0049	0.0070*
Species richness	-0.082	0.0067	0.32
Species diversity	-0.185	0.0342	0.30

*Correlation significant at p<0.01

Discussion

This study has shown that there was a significant change in riparian plant community composition, distribution, species diversity, tree height, mean plant cover, mean seedling density and mean basal area with variation in distance from surface water. Only species richness showed statistically insignificant change with variation in distance from surface water. The differences in riparian woodland species composition were attributed to individual species tolerance to ground water level along the lateral gradient from surface water. In our study, species tolerant to wet conditions including *S. cordatum* Hochst.ex C.Krauss and *P. reclinata* Jacq were found closer to surface water while those that preferred dry conditions such as *Hyphaene petersiana* Mart and *Philenoptera violacea* (Klotzsch) Schrire occupied areas further away from the river surface water. *Croton megalobotrys* Müll. Arg was found throughout the distance classes suggesting that it is able to adapt to moisture and ground water level changes across the different distance classes. However, its significantly high indicator value at 40-50m class could probably be an indication that it prefers relatively low water table.

Changes in riparian species composition and distribution along distance from surface water gradient in the Okavango Delta is in agreement with findings from Stromberg & Richter (1996), Shafroth *et al*. (2000) and Baird, Stromberg & Maddock (2005) who observed that woodland plant species tolerant of wet conditions and high ground water levels were dominant at sites closer to the river bank while those that prefer dry conditions and adapted to low ground water level dominate sites far from the river bank. In a riparian forest of Rio Paraguai, Pantanal, Brazil, Damasceno-Junior *et al*. (2005) also found that flood intolerant species occupied highly elevated and occasionally flooded regions while flood tolerant species inhabited regularly flooded regions.

The similarities of these results with those of other studies conducted elsewhere (Stromberg & Richter, 1996; Shafroth *et al.,* 2000; Baird *et al.,* 2005; Damasceno-Junior *et al.,* 2005) in terms of changing species composition with surface water availability suggest that vegetation distribution follows similar patterns across different riparian ecosystems as result of their ecological function, adaptation and evolution. Plant species with similar adaptation strategies may occupy similar microsites along the distance from surface water and ground water gradient. Riparian plant species have morphological adaptations which enable them to survive and grow in low ground water table (Shafroth *et al.*, 2000). In the Okavango Delta species adapted to long dry conditions have tap roots which help them to reach for deep ground water (Ellery *et al.*, 1993). These species include; *Acacia erioloba* E. Mey, *Acacia tortilis* (Forssk) Hayne, *Acacia mellifera* (Vahl) Benth, *Colophospermum mopane* (J. Kirk ex Benth) J. Kirk ex J. Léonard (Ringrose *et al.,* 2007). In this study these species were found in areas further away from surface water which agreed with the results of a study conducted by Ellery *et al.* (1993) in the Okavango Delta. This was coupled with a decrease in plant cover with increasing distance from surface water. This observation may also be influenced by ground water level which decreases with increasing distance from surface water in the Delta (McCarthy & Ellery, 1994). A similar observation was made in San Pedro River, Arizona, by Stromberg & Richter (1996) who found a decrease in plant canopy vigour with a reduction in ground water level.

There was no significant change in species richness with variation in distance from surface water. This is in agreement with Lite *et al*. (2005) who observed no overall variation in species richness in the San Pedro River with distance above the channel. Lack of significant difference in species richness across different distance classes could probably be an indication that distance from surface water does not have an influence on the number of species that establish in the riparian zone. Distance from surface water could only be influencing species composition and distribution instead of species richness. In this case, this is true because this study revealed that species richness and distance from surface water had a weak negative correlation. The negative relationship between distance from surface water and species richness could also be an indication that these two factors are related in the long term instead of short term.

Because it is an indirect driver (mediated by surface water-groundwater relationships) the effects of distance from surface water may only manifest themselves over the long term. In this study its relationship with species richness was recorded at one point in time while the current vegetation community is likely to be a product of its (and those of other drivers) cumulative influence over a long period of time. The Okavango Delta experiences flooding multi-decadal flooding variation which is characterized by wet and dry conditions (Mazvimavi & Wolski, 2006). The Delta experienced an increase in annual inflow between 1963 and 1969 and low inflows in 1995 and 1996 (Mazimavi & Wolski, 2006). In recent years the inflows into the Delta was at a maximum during the 2010-2011 flooding season. This quasi-cyclicity between multi-decadal wet and dry periods (Wolski *et al.*, 2012) may pose an episodic disturbance which may prevent the establishment of stable states in riparian tree species. As a result the relationship between distance from surface water and species composition may show if it is sought on the long term instead of a snapshot study as is the case with ours.

The negative relationship between distance from surface water and species richness also suggests that there could be other environmental factors influencing the riparian woodland species richness (Lite *et al.,* 2005). One of these factors is likely to be the groundwater salinity regime (Ringrose *et al.,* 2007). McCarthy, (2006) observed that as the distance from surface water increases, groundwater salinity levels also increase in the Okavango Delta. This may lead to woodland species tolerant to salinity and dry conditions colonizing areas further away from the surface water towards the island centre. In this study, salt-tolerant *H. petersiana* (Ellery & Ellery, 1997) was found in areas further away from the river bank towards the saline island centres. Ellery *et al.* (1993) also observed vegetation zonation along salinity gradient in the Okavango Delta in which the fringes of the islands were occupied by riparian woodland species of *Syzygium cordatum* Hochst.ex C. Krauss, *Ficus sycomorus* L, *Phoenix reclinata* Jacq, *Garcinia livingstonei* T. Anderson and *Diospyros mespiliformis* Hochst. ex A. DC. The islands interiors were characterized by *Croton megalobotrys* Müll. Arg, *Acacia nigrescens* (Oliv.) P.J.H. Hurter and *Hyphaene petersiana* Mart with the centre of the islands dominated by the grass *Sporobolus spicatus* (Vahl) Kunth.

The basal area was significantly greater in the 20-30m, 30-40m and 40-50m distance classes while tree height was only significantly higher in the latter two. This could be an indication that large woody plants are not tolerant of shallow groundwater and occasional anaerobic soil conditions induced by flooding associated with the river bank. Shrubs such as *Diospyros lycioides* Desf and *Euclea divinorum* Hiern that contribute to short height and small basal area/ha were dominant closer to the surface water. These species are adapted to moist conditions associated with high water table more than the large woody trees. Large tree species such as *Combretum imberbe* Wawra adapted to salinity and dry conditions (Ellery *et al.*, 1993) were found further away from surface water as salinity increases. Other large tree species such as *G. livingstonei* T. Anderson, *D. mespiliformis* Hochst. ex A. DC, *P. violacea* (Klotzsch) Schrire and *S. nigrescens* (Oliv.) P.J.H. Hurter were mostly common in the 20-30m distance class resulting in a larger basal area. Therefore, if surface water reaches the riparian zone, large trees would be eventually excluded from the Okavango Delta. Conversely, if the riparian zone was to completely dry then the Delta would be dominated by large trees tolerant to dry conditions.

Plant species diversity also varied with variation in distance from surface water. It was higher at 20-30m than at 10-20, 30-40m and 40-50m distance classes. This could probably be attributed to differences in water table depth between these distance classes. The 20-30m distance class has a relatively higher water table than the 30-40m distance class. Low water table at 30-40m distance class excludes dry conditions intolerant plant species. Conversely, conditions at 20-30m distance class are more moderate due to a relatively high water table leading to habitat colonization by both competitive and opportunistic plant species and subsequently high species diversity. This is consistent with the intermediate disturbance hypothesis which predicts that at intermediate disturbance levels species diversity increases due to the co-existence of both competitive and opportunistic species (Huston, 1979). At 0-10m distance class the water table is high and excludes species that are not tolerant of high moisture content. Conversely, conditions at 40-50m class are relatively dry and exclude species tolerant to high moisture content hence reducing species diversity.

Conclusion

This study provided new information on the influence of distance surface water on riparian plant species composition and distribution in the Okavango Delta. It has shown that riparian plant species composition, species diversity, tree height and basal area change significantly along the distance from surface water gradient. The results of this study can be useful in formulating riparian woodland management strategies. The results suggest that in order to conserve the riparian woodland vegetation, the natural inflow in the Okavango Delta has to be maintained. Changes in the inflow of the Okavango Delta from developments such as construction of upstream dams may reduce the inflow into the Delta and possibly change species composition in the riparian zone towards the dry land species.

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Spatial variation of the influence of distance from surface water on riparian plant communities in the Okavango Delta, Botswana.

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Abstract

Background and objectives: Understanding the environmental factors that influence riparian vegetation community composition and distribution is significant in understanding and maintaining wetland ecosystem functions. This can help in designing and improving policy aimed at conserving wetlands such as the Okavango Delta. However, in the Okavango Delta, information on the influence of distance from surface water is limited. The objective of this study was to determine the relationship between distance from surface water and riparian plant communities across different sites in the Okavango Delta.

Methods: Vegetation sampling was conducted in 20m × 10m belted plots placed perpendicular to the river bank at 0-10, 10-20, 20-30, 30-40 and 40-50m distance classes. Basal area, species richness, cover and diversity were determined for each distance class. One way-Analysis of Variance and Tukey post hoc analysis were used to compare species diversity, richness, cover and basal area between distance classes.

Results: Basal area, cover, diversity and richness differed significantly (p<0.05) between distance classes in all the sites. Plant species composition also varied with distance from surface water. These results show that variation of distance from surface water influences riparian vegetation community composition and distribution in the Okavango Delta.

Conclusion: In order to maintain the riparian vegetation communities, maximum efforts should be made to maintain the current natural flooding regime.

Key words: Cover, Distance, Okavango, Tree and Woodland

Introduction

Riparian plant communities, found along river banks, are transition zones between terrestrial and aquatic systems (Naiman & Decamps 1997). In semi-arid environments, riparian plant communities are dynamic environments showing high habitat heterogeneity, diverse ecological processes and are often rich in biodiversity on a regional and continental scale (Naiman *et al.* 2005). Their distribution is controlled by soil redox conditions, flooding, soil chemistry and light intensity (Everson & Boucher 1998). Surface water availability and fluvial disturbance are also environmental factors that influence plant species composition and distribution along lateral gradients in riparian habitats (Malanson 1993). Along the lateral gradient of the riparian corridor, flooding disturbance decreases with increasing distance from surface water due to an increase to depth to groundwater (Lite *et al*. 2005). Depth to groundwater influences plant species distribution, abundance and age structure in riparian zones because it decreases the availability of a permanent water source (Stromberg & Richter 1996). Decline in groundwater may result in a reduction in plant species abundance, cover, productivity and death (Stromberg *et al*. 2007) while a shallow groundwater table can support high plant species density (Naumburg *et al*. 2005). However, excess water may lead to anoxic conditions in the root zone resulting in stress to tree species due to reduced respiration (Drew 1997).

Studies in other riparian wetland ecosystems (e.g. Stromberg & Richter 1996; Shafroth *et al*. 2000; Lite *et al*. 2005; Stromberg *et al*. 2007) have shown that depth to ground water as influenced by distance from surface water is an important environmental variable that influences the distribution and composition of riparian plant communities. Riparian plant species tolerant of wet conditions and low depth to ground water were dominant at sites closer to surface water while those that prefer dry conditions and adapted to high depth to ground water were dominant in highly elevated sites which were relatively far from surface water (Stromberg & Richter 1996). A decline in depth to ground water with increasing distance from surface water may change riparian plant community composition leading to a reduction in abundance of species that depend on it for survival (Shafroth *et al.* 2000; Baird *et al.* 2005). However, some riparian plant species have developed morphological adaptations to cope with dry conditions imposed by high depth to ground water table (Shafroth *et al.* 2000). These adaptations include tap roots which help them to reach for deep ground water (Ellery *et al.* 1993). Due to different tolerance levels, riparian plant species are found in different microsites in the riparian zone. Plant species that are tolerant of shallow depth to ground water inhabit regularly flooded sites while those that prefer deep depth to ground water occupy occasionally flooded sites (Damasceno-Junior *et al*. 2005). Depth to ground water has also been found to significantly influence riparian vegetation community composition in San Pedro River, Arizona in which an increase to depth of ground water resulted in loss of canopy vigour (Stromberg & Richter 1996).

In the Okavango Delta, information on the influence of surface water and depth to ground water on riparian plant communities is generally limited. The study by Ellery *et al.* (1993) found a strong correlation between depth to groundwater and woody plant species distribution in the Okavango Delta. Changes in plants structure was positively correlated to depth to groundwater and elevation. It was generally found that *Diospyros mespiliformis* Hochst. EX A.D.C, *Garcinia livingstonei* T. Anderson, *Croton megalobotrys* Müll. Arg and *Acacia nigrescens* Oliv preferred relatively shallow depth to ground water as compared to *Acacia erioloba, Acacia tortilis* (Forssk) Hayne, *Acacia mellifera* (Vahl) Benth and *Colophospermum mopane* (J. Kirk ex Benth) J. Kirk ex J. Léonard. However, the study was limited in terms of geographical coverage as it only covered a single island. That study has also not investigated the effect of distance from surface water on riparian plant species composition and distribution.

Understanding the influence of distance from surface water on riparian woodland community composition and distribution may help in understanding and maintaining wetland ecosystem functions (Naiman & Decamps 1997). This is because in order to design management strategies for riparian plant communities, it is important to understand their composition and distribution patterns as influenced by the underlying environmental factors (Snyder *et al*. 2002). With increasing demands for water in riparian states of Angola, Botswana and Namibia, the Okavango Delta faces a potential threat of overexploitation of its surface water resources. This may have negative impact on the riparian plant community composition and distribution. Low water flow into the Delta may promote the encroachment of dry land species at the expense of riparian species. This could negatively affect the overall functioning of the Delta system which may negatively affect the livelihoods of communities that are economically dependent on riparian woodland species.

The recent study by Tsheboeng *et al.* (2016; in press), investigated the influence of distance from surface water on riparian plant species composition and distribution in the Okavango Delta. However, that study was limited as it did not address the inter-site spatial response of plant species to distance from surface water. The aim of the current study was to determine the effect of inter-site spatial response of riparian plant communities to distance from surface water. It was hypothesized that species richness, diversity, tree height, basal stem area and cover will decrease with increasing distance from surface water in all the sites. Woodland species composition was also predicted to differ along distance from surface water in all the sites.

Materials and Methods

Study area

The study was conducted in the Okavango Delta. The selected study sites were Boro, Jao, Upper Panhandle (UPH) and Seronga (Figure 1; Table 1).

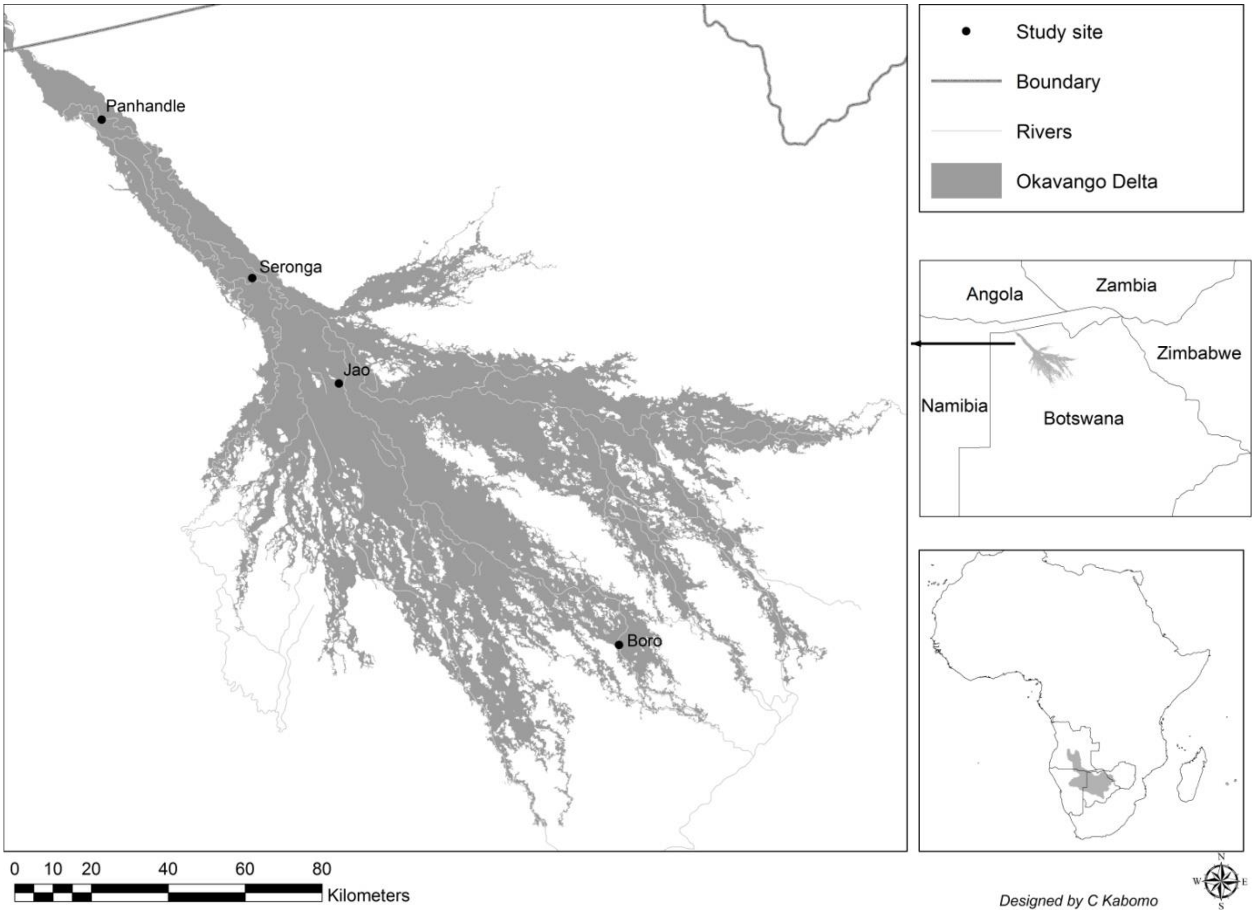

Figure 1: Sampling sites in the Okavango Delta.

The hydrology of the Okavango Delta is characterized by annual flood pulses originating from the Angolan highlands, the peak flows of which generally pass the

Mohembo inlet region between March and April, reaching the distal region between May and October (McCarthy 2006). The flood extent in the Delta shows intra and inter-annual variations (Wolski *et al.* 2006). Intra-annual flood variation refers to the quasi-regular changes in flooding magnitude in terms of duration and depth within a given year. Inter-annual flood variation is characterized by differences in flooding magnitude between two or more years. The Okavango Delta inflows also vary pluri-annually in which there are sequences of years with higher or lower inflows than average (Mazvimavi & Wolski 2006). During the period of record (1933-present), inflows rose to reach a maximum between 1963 and 1969. Subsequently inflows declined to a minimum in 1995-1996 (Mazvimavi & Wolski 2006), rising again to a maximum in 2010-2011. The Okavango Delta receives mean annual rainfall (between November and February) of approximately 550mm (Wilson & Dincer 1976). In the Okavango Delta groundwater depth varies with distance from surface water such that it is higher and lower in sites closer to and further away from the permanent swamps respectively (McCarthy 2006).

Common woodland species include *Acacia erioloba* E. Meyer, *Acacia nigrescens*, *Croton megalobotrys*, *Phoenix reclinata* Jacq, *Diospyros mespiliformis* and *Garcinia livingstonei*. The soil in the riparian zone is fine sand (Ringrose *et al*. 2007) resulting in high permeability. The soil salinity in the Okavango Delta is influenced by flooding and transpiration by riparian vegetation (McCarthy & Ellery 1994). During flood peak the salinity reduces and increases at low flooding phase. This is because the flood waters dilute the salts. Salinity is also high in low flooding frequency floodplains and low in high flooding frequency regions (Bonyongo & Mubyana 2004).

Table 1: Characterization of different sampling sites in the Okavango Delta.

Study area	Coordinates	Location	Habitat type	Common

				woodland vegetation
Boro	23°9'13''E, 19°32'27''S	Lower Delta	Permanently flooded, seasonally flooded and dryland	*Combretum hereroense* Schinz, *Acacia erioloba* E. Meyer
Seronga	22°17'8''E, 18°48'42''S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Syzygium cordatum* Hochst. ex C Krauss, *Phoenix reclinata* Jacq
Jao	22°33'40''E, -19°1'57''S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Syzygium cordatum, P. reclinata*
Upper Panhandle	21° 52'13''E, -18° 21'53''S	Upper Delta	Permanently flooded, seasonally flooded and dryland	*Sersia quartiniana* A. Rich, *Elaeodendron transvaalense* (Burtt Davy) R.H. Archer

Vegetation Sampling

Riparian woody vegetation was sampled between February 2012 and November 2013. Sampling during these times (between February and April) and (November to April) was meant to maximize identification of species since most of the plants were in a flowering stage (Heath & Heath 2009). Riparian woody vegetation was sampled in five 10m × 20m belted plots placed perpendicular to the surface water-dry land boundary covering a 50m distance at 0-10m, 10-20m, 20-30m, 30-40m and 40-50m intervals. The distance was measured from the current high water line. From each plot, all plant species were identified; estimates of cover made, and tree height and stem size measured. Stem circumference was measured using a measuring tape at breast height (1.3m) while tree height was visually estimated. Plant species diversity, richness, basal area and density were calculated for each distance class. At each site 75 plots were sampled.

Statistical analysis

Change in woodland species composition was determined at each distance class based on cover/abundance across the different sites. Dominant species were determined from mean percentage cover at each distance class. The species with the highest percentage cover was regarded as dominant. Mean percentage cover variation was also determined for five common species at each site. Mean species diversity, richness, basal area and canopy cover were calculated for each distance class at each site. Formulas for calculating species diversity and richness are given in chapter 2 while for Basal area the formula is given in chapter 3. Data was tested for normality using Kolmogorov-Smirnov while homogeneity of variance was tested using the Levene test. After all the assumptions of normality and homogeneity of variance were met ($p>0.05$) One-way ANOVA was used to test for statistical significant differences between these vegetation parameters among distance classes (0-10m, 10-20m, 20-30m, 30-40m and 40-50m). Where there was statistical significant difference, Tukey test was used to determine the distance class that contributed to it.

Results

One-way ANOVA showed that mean basal was not significantly higher in 0-10 and 40-50m in Boro (df=4, Mean square=0.225, F=1.039, *p*=0.386) and Seronga (df=4, Mean square=0.053, F=0.454, *p*=0.769). In Jao, Tukey post hoc analysis showed that mean basal area was significantly higher at 0-10m than at 10-20m (Mean=0.28, *p*=0.0001), 20-30m (Mean=0.062, *p*=0.001), 30-40m (Mean=0.059, *p*=0.0001) and 40-50m (Mean=0.074, *p*=0.0001). In UPH it was higher (df=4, Mean square=0.102, F=1.55, *p*=0.189) at 10-20m (Figure 2).

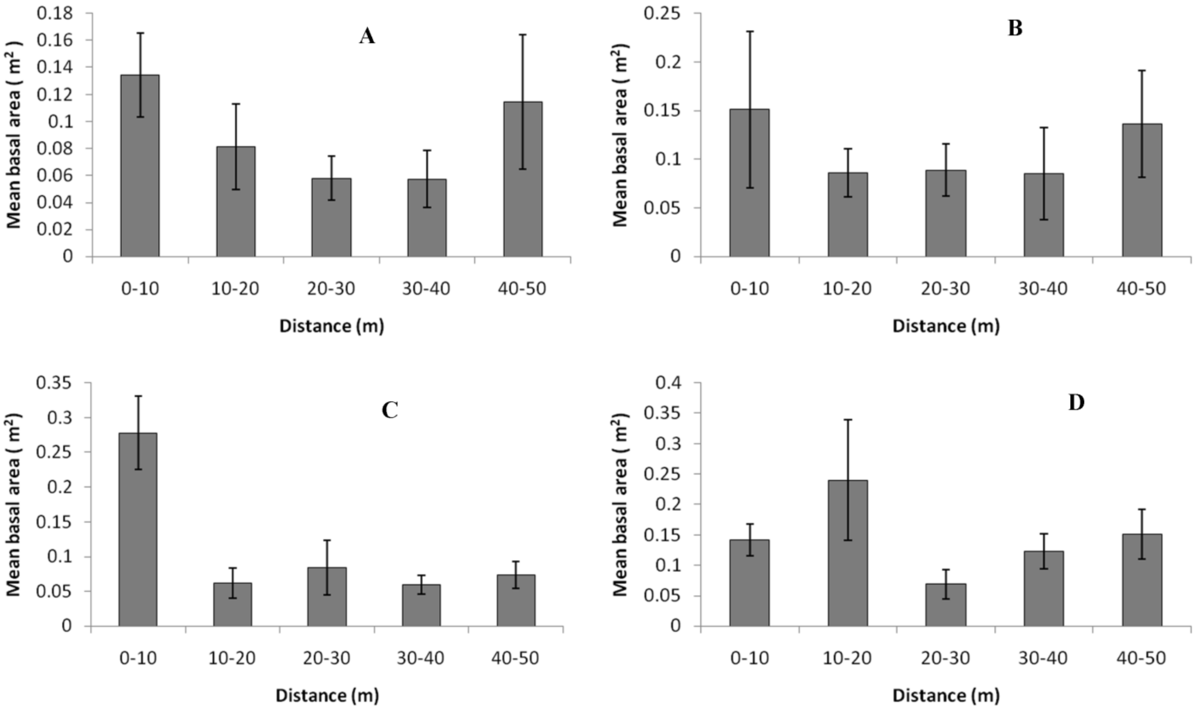

Figure 2: Mean basal area variation with distance from surface water in Boro (A), Seronga (B), Jao (C) and UPH (D).

Mean percentage cover differed between the distance classes across all sites. It was significantly higher in 0-10 (df=4, Mean=9.12, *p*=0.023) and 20-30m (df=4, Mean=4.30) in

Boro while in Jao it was marginally significantly higher in 0-10m (df=4, Mean=12.50, *p*=0.055) than at 30-40m (df=4, Mean=6.59) (Figure 3).

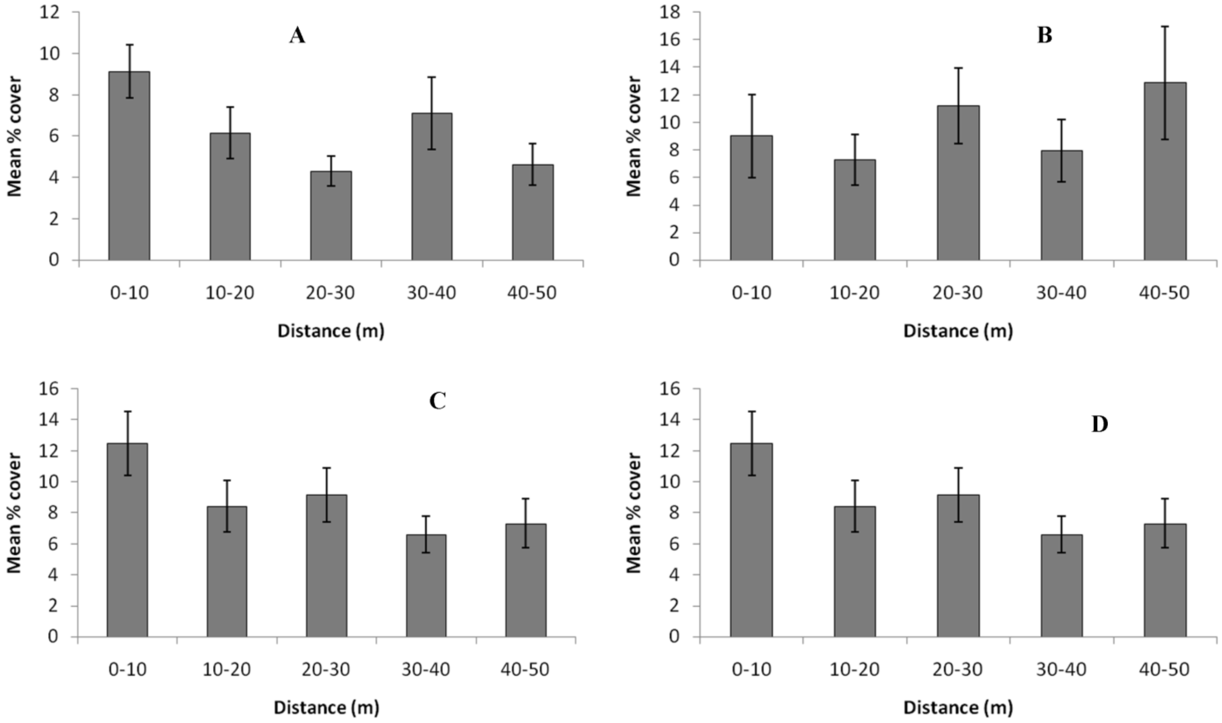

Figure 3: Mean percentage cover variation with distance from surface water in Boro (A), Seronga (B), Jao (C) and UPH (D).

In Boro all the species showed low mean percentage cover at 40-50m (Figure 4). The same result was also observed in Jao except for *G. livinstonei* which had high mean percentage cover at 0-10m and 40-50m. In UPH all the species showed high percentage cover in all the species at 0-10m except for *A. nigrescens*. At 40-50m *S. cordatum* is the only species that showed a decrease in mean percentage cover (Figure 4).

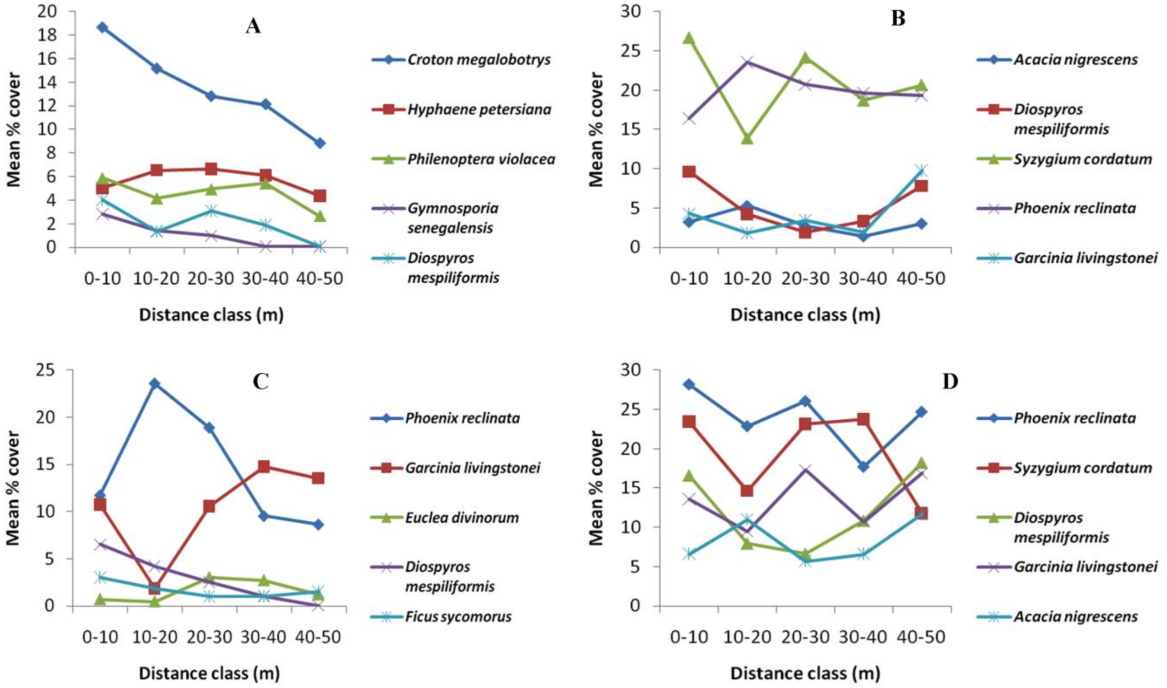

Figure 4: Mean individual species cover variation with distance from surface water in Boro (A), Seronga (B), Jao (C) and UPH (D).

Mean species richness also showed variation between distance classes in different sites. However, that variation was only significant in Boro where it was significantly higher at 0-10m (df=4, Mean=7) than at 20-30m (df=4, Mean=6, *p*=0.056), 30-40m (df=4, Mean=5, *p*=0.0001) and 40-50m (df=4, Mean=5, *p*=0.006). Mean species richness in Boro was also significantly higher in 10-20m (df=4, Mean=6) than at 30-40m (df=4, Mean=5, *p*=0.014) (Figure 5).

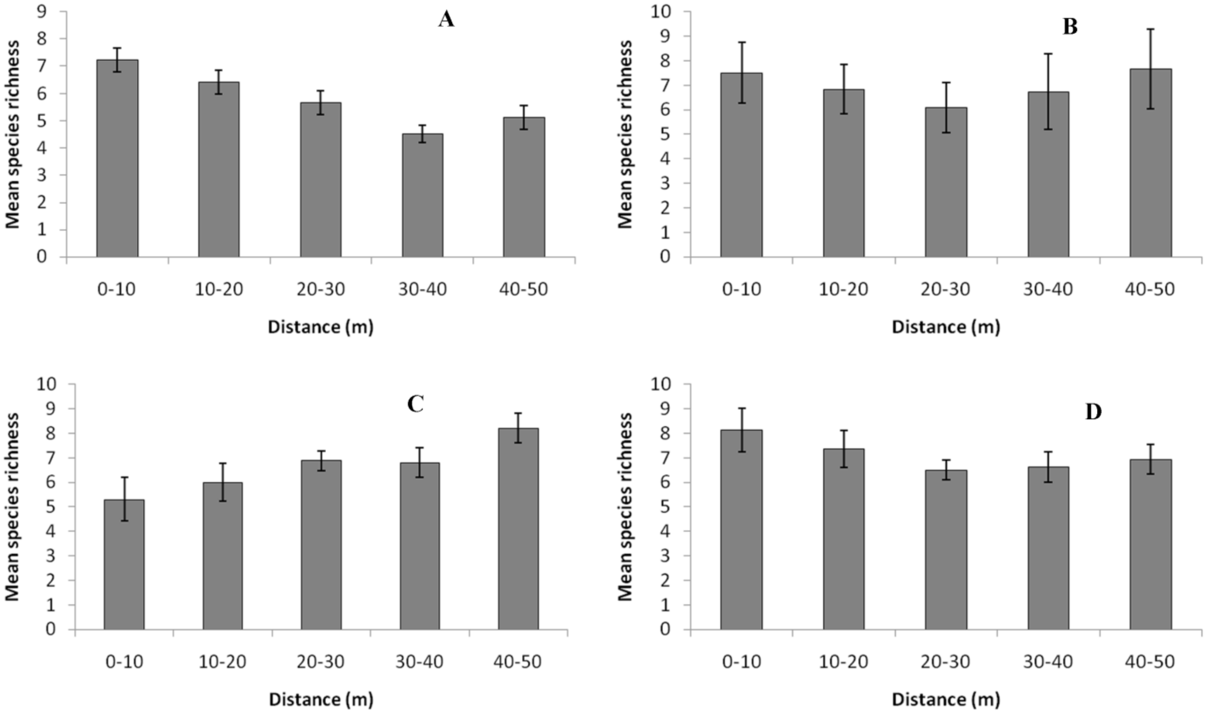

Figure 5: Mean species richness variation with distance from surface water in Boro (A), Seronga (B), Jao (C) and UPH (D).

Mean species diversity was significantly higher at 0-10m (df=4, F=5.17, Mean=1.08, *p*=0.0001) and 10-20m (df=4, Mean=0.97, *p*=0.016) than at 30-40m (df=4, Mean=0.64) in Boro (*p*<0.05). There was no significant difference (*p*>0.05) in species diversity between distances classes in Seronga (df=4, Mean square=0.105, F=0.300, *p*=0.876), Jao (df=4, Mean square=0.119, F=0.664, *p*=0.620) and UPH (df=4, Mean square=0.075, F=0.617, *p*=0.652) (Figure 6).

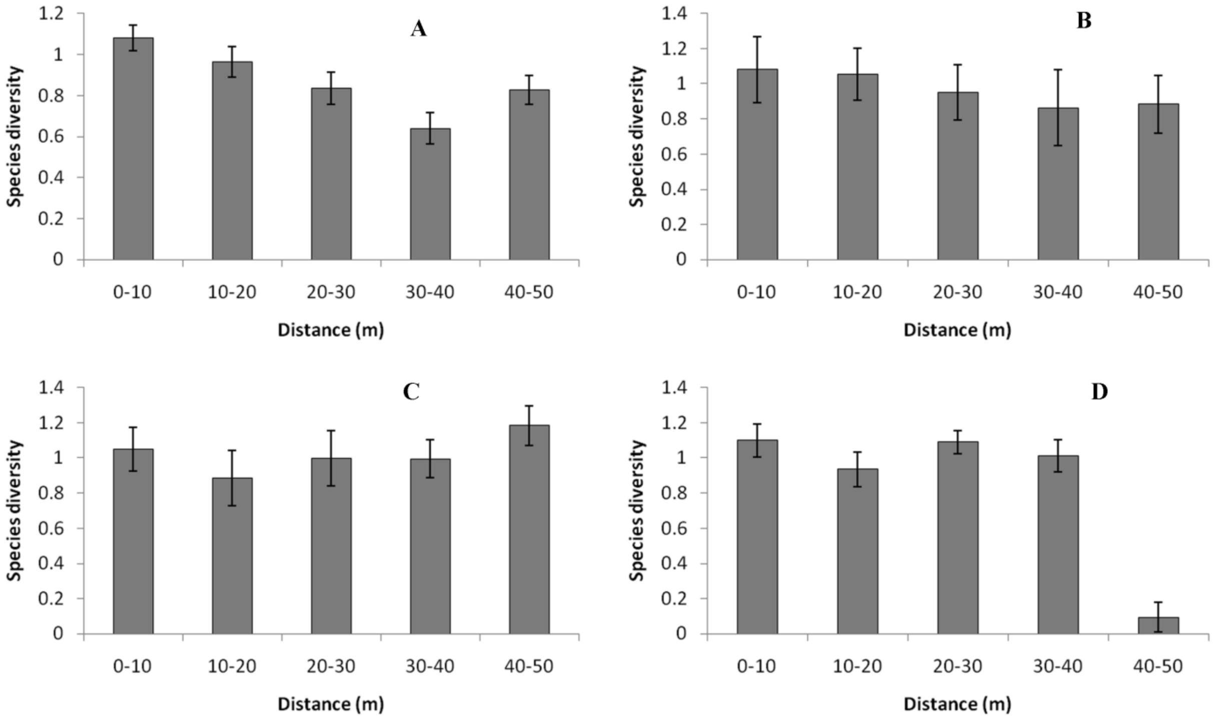

Figure 6: Mean species diversity variation with distance from surface water in Boro (A), Seronga (B), Jao (C) and UPH (D).

Riparian woodland tree species composition and dominant species changed along distance from surface water gradient (Table 2).

Table 2: Variation in composition of riparian woodland species at each distance class. *Species are listed in descending order of mean percentage cover.*

	Distance class (m)				
Site	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**
Boro	*Croton megalobotrys* *Diospyros lycioides* *Philenoptera violacea* *Hyphaene petersiana*	*Croton megalobotrys* *Hyphaene petersiana* *Philenoptera violacea* *Acacia nigrescens*	*Croton megalobotrys* *Hyphaene petersiana* *Philenoptera violacea* *Dichrostachys mespiliformis*	*Croton megalobotrys* *Hyphaene petersiana* *Philenoptera violacea* *Combretum imberbe*	*Croton megalobotrys* *Hyphaene petersiana* *Philenoptera violacea* *Acacia nigrescens*

Kigelia africana	*Combretum mossambicense*	*Acacia nigrescens*	*Diospyros mespiliformis*	*Combretum imberbe*
Diospyros mespiliformis	*Gymnosporia senegalensis*	*Combretum mossambicense*	*Kigelia africana*	*Ficus sycomorus*
Gymnosporia senegalensis	*Diospyros mespiliformis*	*Gymnosporia senegalensis*	*Acacia hebeclada*	*Combretum mossambicense*
Combretum imberbe	*Kigelia africana*	*Kigelia africana*	*Combretum mossambicense*	*Acacia hebeclada*
Ficus sycomoros	*Euclea divinorum*	*Diospyros lycioides*	*Diospyros lycioides*	*Diospyros lycioides*
Acacia nigrescens	*Diospyros lycioides*	*Ficus sycomorus*	*Acacia nigrescens*	*Euclea divinorum*
Combretum mossambicense	*Sclerocarya birrea*	*Euclea divinorum*	*Euclea divinorum*	*Kigelia africana*
Euclea divinorum	*Combretum imberbe*	*Combretum hereroense*	*Garcinia livingstonei*	*Diospyros mespiliformis*
Garcinia livingstonei	*Combretum hereroense*	*Acacia erioloba*	*Gymnosporia senegalensis*	*Gymnosporia senegalensis*
Sclerocarya birrea	*Garcinia livingstonei*	*Garcinia livingstonei*	*Ximenia americana*	*Albizia harveyi*
Ziziphus mucronata	*Searsia tenuinervis*	*Searsia tenuinervis*	*Acacia erioloba*	*Acacia erioloba*
Acacia hebeclada	*Acacia erioloba*	*Dichrostachys cinerea*	*Acacia tortilis*	*Searsia tenuinervis*
Phyllanthus reticulatus	*Phyllanthus reticulatus*	*Acacia tortilis*	*Grewia bicolor*	*Acacia tortilis*
Elaeodendron transvaalense	*Acacia tortilis*	*Albizia harveyi*	*Dichrostachys cinerea*	*Dichrostachys cinerea*
Acacia erioloba	*Ficus sycomorus*	*Ximenia americana*	*Albizia harveyi*	*Phyllanthus reticulatus*
Berchemia discolor	*Grewia retinervis*	*Berchemia discolor*	*Phyllanthus reticulatus*	*Combretum hereroense*
Combretum hereroense	*Albizia harveyi*	*Grewia bicolor*	*Berchemia discolor*	*Garcinia livingstonei*
Dichrostachys cinerea	*Dichrostachys cinerea*	*Combretum imberbe*	*Grewia retinervis*	*Colophospermum mopane*
Grewia flavescens	*Ziziphus mucronata*	*Ziziphus mucronata*	*Boscia albitrunca*	*Elaeodendron transvaalense*
Acacia tortilis	*Acacia sieberiana*	*Acacia sieberiana*	*Capparis tomentosa*	*Grewia flavescens*
Albizia harveyi	*Berchemia discolor*	*Grewia flavescens*		*Grewia retinervis*
Colophospermum		*Acacia*		*Boscia*

	mopane		*hebeclada*		*albutrinca* *Capparis tomentosa* *Acacia sieberiana*
Seronga	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**
	Syzygium cordatum	*Phoenix reclinata*	*Syzygium cordatum*	*Phoenix reclinata*	*Syzygium cordatum*
	Phoenix reclinata	*Syzygium cordatum*	*Phoenix reclinata*	*Syzygium cordatum*	*Phoenix reclinata*
	Diospyros mespiliformis	*Acacia nigrescens*	*Garcinia livingstonei*	*Ficus sycomorus*	*Garcinia livingstonei*
	Garcinia livingstonei	*Diospyros mespiliformis*	*Acacia nigrescens*	*Philenoptera violacea*	*Diospyros mespiliformis*
	Acacia sieberiana	*Burkea africana*	*Elaeodendron transvaalense*	*Diospyros mespiliformis*	*Burkea africana*
	Acacia nigrescens	*Capparis tomentosa*	*Ficus thonnigii*	*Garcinia livingstonei*	*Albizia harveyi*
	Searsia quartiniana	*Phoenix violacea*	*Searsia quartiniana*	*Elaeodendron transvaalense*	*Acacia nigrescens*
	Elaeodendron transvaalense	*Garcinia livingstonei*	*Diospyros mespiliformis*	*Searsia quartiniana*	*Elaeodendron transvaalense*
	Antidesma venosum	*Ficus sycomorus*	*Gymnosporia senegalensis*	*Acacia nigrescens*	*Dovyalis caffra*
	Ekebergia capensis	*Ficus thonnigii*	*Euclea divinorum*	*Albizia harveyi*	*Philenoptera violacea*
	Dovyalis caffra	*Elaeodendron transvaalense*	*Capparis tomentosa*	*Gymnosporia senegalensis*	*Ficus sycomorus*
	Kigelia africana	*Antidesma venosum*	*Acacia sieberiana*	*Burkea africana*	*Capparis tomentosa*
	Euclea divinorum	*Euclea divinorum*	*Philenoptera violacea*	*Dovyalis caffra*	*Euclea divinorum*
	Diospyros lycioides	*Ximenia americana*	*Ficus sycomorus*	*Antidesma venosum*	*Searsia quartiniana*
	Burkea africana	*Acacia sieberiana*	*Antidesma venosum*	*Capparis tomentosa*	*Gymnosporia senegalensis*
	Gardinia volkensii	*Ekebergia capensis*	*Combretum mossambicense*	*Combretum mossambicense*	*Combretum mossambicense*
	Capparis tomentosa	*Combretum imberbe*	*Dichrostachys cinerea*	*Euclea divinorum*	*Antidesma venosum*
	Ficus sycomorus	*Dovyalis caffra*	*Diospyros lycioides*	*Searsia tenuinervis*	*Ximenia americana*

	Philenoptera violacea *Gymnosporia senegalensis* *Croton megalobotrys* *Hyphaene petersiana* *Searsia tenuinervis* *Dichrostachys cinerea* *Phyllanthus reticulatus* *Grewia retinervis*	*Searsia quartiniana* *Albizia harveyi* *Phyllanthus reticulatus* *Croton megalobotrys* *Dichrostachys cinerea*	*Ximenia americana* *Phyllanthus reticulatus*	*Gardinia volkensii* *Ekebergia capensis* *Croton megalobotrys* *Ximenia americana* *Sclerocarya birrea* *Phyllanthus reticulatus* *Diospyros lycioides*	*Searsia tenuinervis* *Croton megalobotrys* *Dichrostachys cinerea* *Phyllanthus reticulatus*
Jao	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**
	Syzygium cordatum *Phoenix reclinata* *Garcinia livingstonei* *Diospyros mespiliformis* *Ficus sycomorus* *Acacia nigrescens* *Philenoptera nelsii* *Diospyros lycioides* *Berchemia discolor* *Ficus thonnigii* *Euclea divinorum* *Elaeodendron transvaalense* *Kigelia africana*	*Phoenix reclinata* *Syzygium cordatum* *Acacia nigrescens* *Diospyros mespiliformis* *Burkea africana* *Capparis tomentosa* *Philenoptera violacea* *Garcinia livingstonei* *Ficus sycomorus* *Ficus thonnigii* *Elaeodendron tranvaalense* *Antidesma venosum* *Euclea*	*Phoenix reclinata* *Garcinia livingstonei* *Acacia nigrescens* *Euclea divinorum* *Diospyros mespiliformis* *Ficus thonnigii* *Diospyros lycioides* *Berchemia discolor* *Ficus sycomorus* *Capparis tomentosa* *Gymnosporia senegalensis* *Ximenia americana* *Hyphaene*	*Garcinia livingstonei* *Phoenix reclinata* *Acacia nigrescens* *Euclea divinorum* *Hyphaene petersiana* *Capparis tomentosa* *Ficus thonnigii* *Diospyros lycioides* *Berchemia discolor* *Philenoptera violacea* *Diospyros mespiliformis* *Gymnosporia senegalensis* *Acacia karoo*	*Garcinia livingstonei* *Phyllanthus reclinata* *Acacia nigrescens* *Kigelia africana* *Acacia galpinii* *Capparis tomentosa* *Hyphaene petersiana* *Phyllanthus reticulatus* *Elaeodendron transvaalense* *Ficus sycomorus* *Ficus thonnigii* *Euclea divinorum* *Philenoptera*

	Capparis tomentosa *Gymnosporia senegalensis* *Ziziphus mucronata* *Searsia tenuinervis* *Phoenix reticulatus* *Hyphaene petersiana*	*divinorum* *Ximenia americana* *Acacia sieberiana* *Ekebergia capensis* *Combretum imberbe* *Dovyalis caffra* *Searsia quartiniana* *Albizia veriscolor* *Phyllanthus reticulatus* *Croton megalobotrys* *Dichrostachys cinerea*	*petersiana* *Philenoptera violacea* *Syzygium cordatum* *Grewia flavescens* *Acacia karoo* *Searsia tenuinervis* *Combretum mossambicense* *Croton megalobotrys* *Phyllanthus reticulatus* *Kigelia africana* *Sclerocarya birrea* *Eleodendron transvaalense*	*Ficus sycomorus* *Croton megalobotrys* *Ximenia americana* *Elaeodendron transvaalense* *Searsia tenuinervis* *Combretum mossambicense* *Phyllanthus reticulatus* *Grewia bicolor* *Combretum hereroense* *Acacia sieberiana* *Dovyalis caffra*	*violacea* *Acacia karoo* *Grewia bicolor* *Grewia flavescens* *Combretum mossambicense* *Ximenia americana* *Searsia tenuinervis* *Berchemia discolor* *Combretum hereroense* *Diospyros mespiliformis* *Dichrostachys cinerea* *Gymnosporia senegalensis* *Croton megalobotrys* *Diospyros lycioides* *Ziziphus mucronata* *Syzygium cordatum* *Phoenix nelsii*
UPH	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**
	Phoenix reclinata *Syzygium cordatum* *Diospyros mespiliformis* *Garcinia livingstonei* *Acacia*	*Phoenix reclinata* *Syzygium cordatum* *Acacia nigrescens* *Garcinia livingstonei* *Diospyros*	*Phoenix reclinata* *Syzygium cordatum* *Garcinia livingstonei* *Diospyros mespiliformis* *Acacia*	*Syzygium cordatum* *Phoenix reclinata* *Diospyros mespiliformis* *Garcinia livingstonei* *Acacia*	*Phyllanthus reclinata* *Diospyros mespiliformis* *Garcinia livingstonei* *Syzygium cordatum* *Acacia*

nigrescens	*mespiliformis*	*nigrescens*	*nigrescens*	*nigrescens*
Albizia veriscolor	*Philenoptera violacea*	*Philenoptera violacea*	*Philenoptera violacea*	*Acacia tortilis*
Phoenix violacea	*Combretum imberbe*	*Croton megalobotrys*	*Kigelia africana*	*Philenoptera violacea*
Ficus sycomorus	*Croton megalobotrys*	*Berchemia discolor*	*Croton megalobotrys*	*Diospyros lycioides*
Combretum imberbe	*Berchemia discolor*	*Ficus sycomorus*	*Acacia tortilis*	*Searsia quartiniana*
Diospyros lycioides	*Ficus sycomorus*	*Searsia quartiniana*	*Acacia erioloba*	*Gardinia volkensii*
Searsia quartiniana	*Kigelia africana*	*Gardinia volkensii*	*Acacia sieberiana*	*Albizia veriscolor*
Euclea divinorum	*Gymnosporia senegalensis*	*Diospyros lycioides*	*Gymnosporia senegalensis*	*Terminalia sericea*
Antidesma venosum	*Friesodielsia obovata*	*Acacia erioloba*	*Dichrostachys cinerea*	*Baphia massaiensis*
Friesodielsia obovata	*Searsia quartiniana*	*Capparis tomentosa*	*Ximenia americana*	*Dichrostachys cinerea*
Croton megalobotrys	*Antidesma venosum*	*Antidesma venosum*	*Searsia quartiniana*	*Friesodielsia obovata*
Searsia tenuinervis	*Euclea divinorum*	*Gymnosporia senegalensis*	*Diospyros lycioides*	*Gymnosporia senegalensis*
Gymnosporia senegalensis	*Grewia flavescens*	*Grewia flavescens*	*Albizia versicolor*	*Commiphora africana*
Gardinia volkensii	*Combretum hereroense*	*Friesodielsia obovata*	*Friesodielsia obovata*	*Euclea divinorum*
Dichrostachys cinerea	*Dovyalis caffra*	*Dichrostachys cinerea*	*Antidesma venosum*	*Croton megalobotrys*
Vachellia sieberiana	*Gardinia volkensii*	*Ximenia americana*	*Capparis tomentosa*	*Antidesma venosum*
Ximenia americana	*Diospyros lycioides*	*Combretum hereroense*	*Gardinia volkensii*	*Capparis tomentosa*
Berchemia discolor	*Ximenia americana*		*Grewia flavescens*	*Elaeodendron transvaalense*
Combretum mossambicense	*Phyllanthus reticulatus*		*Boscia albutrinca*	*Grewia flavescens*
Capparis tomentosa	*Elaeodendron transvaalense*		*Euclea divinorum*	*Boscia albutrinca*
Dovyalis caffra			*Combretum mossambicense*	*Ficus sycomorus*
Ekebergia capensis			*Elaeodendron transvaalense*	*Searsia tenuinervis*

Searsia tenuinervis	*Ximenia americana*
Hyphaene petersiana	*Acacia seiberiana*
Ficus sycomorus	*Dovyalis caffra*
Phyllanthus reticulatus	*Hyphaene petersiana*
Combretum hereroense	*Acacia erioloba*
Dovyalis caffra	*Berchemia discolor*
Terminalia sericea	*Combretum mossambiecense*
	Combretum hereroense

Discussion

There was variation in species composition along distance from surface water gradient across different sites. Species tolerant of shallow and deep groundwater table were found at 0-10m and 40-50m distance from surface water respectively across all the sites while those tolerant of deep groundwater table such as *Acacia tortilis, Philenoptera nelsii* and *Combretum imberbe* (Ringrose *et al.* 2007) colonized dry areas found further away from surface water at 40-50m distance class. This is supported by the findings of Stromberg & Richter, (1996), Shafroth *et al.* (2000) and Baird *et al.* (2005) who found that woodland plant species tolerant to wet conditions and high groundwater levels are dominant at sites closer to the river bank while those that prefer dry conditions and adapted to low groundwater level dominate sites far from the river bank. The results of this study were also supported by Damasceno-Junior *et al.* (2005) in the Pantanal, Brazil who found that flood intolerant species occupied low flooding frequency microsites while flood tolerant species inhabited regularly flooded regions.

In the Okavango Delta riparian plant species composition may also be influenced by the intra-and multi-decadal flood variation. The hydrology of the Okavango Delta is characterized by flooding variation which occurs within and between years (Wolski *et al.* 2006). Due to this variation some years or series of years receive low floods while others experience high flooding (Wolski *et al.* 2006). During high and low floods the groundwater depth becomes shallow and deep, respectively (McCarthy 2006). This may have consequences for riparian plant species composition and distribution. The shallow groundwater brings the toxic salts that were initially deposited in the deep layers of the ground within reach of plant roots (McCarthy *et al*. 1998). Therefore, shallow groundwater may pose danger to plant survival through salt toxicity and roots submersion which leads to anoxia. This may lead to elimination or exclusion of plants that are not adapted to these new conditions imposed by rising groundwater level. Dead individuals of *Croton megalobotrys*, *Acacia nigrescens*, *Diospyros mespiliformis* and *Philenoptera violacea* were observed in this study and their death could be an indication of their inability to withstand flooding and salinity. Conversely, during low flooding, the ground water may be too deep to be reached by plants roots resulting in water stress. Only plants that are tolerant of dry conditions through development of deep tap roots to reach deep groundwater layers and shedding of their leaves to minimize water loss may survive while those that are intolerant of dry conditions may be eliminated. This may explain the variation in riparian species composition along distance from surface water found in the Okavango Delta.

Plant cover also varied along distance from surface water gradient in the different study sites. In Boro, *C. megalobotrys*, *Hyphaene petersiana*, *P. violacea*, *Gymnosporia senegalensis* and *D. mespiliformis* showed a decrease in mean percentage cover from high in 0-10m to low in 40-50m. This could be due to an increase in groundwater level with increasing distance from surface water coupled with increasing salinity levels (McCarthy 2006). At 0-10m groundwater level was likely to be optimum for plant primary production which was shown by high percentage cover. An increase in the distance from surface water may lead to a reduction in percentage cover as a result of deep groundwater and increased salinity. *Diospyros mespiliformis* and *P. violacea* are tolerant to fresh and shallow groundwater (Ellery *et al.* 1993) which explains a decrease in their percentage cover at regions further away from surface water which were characterized by deep groundwater depth. Conversely, *H. petersiana* and *C. megalobotrys* tolerate deep groundwater table and saline water (Ellery *et al.* 1993) and as a result their percentage cover was expected to increase with increasing distance from surface water. However, that was not the case which could be an indication that salinity and groundwater levels at 40-50m distance class have exceeded their tolerance levels. The same trend was observed in Jao in which mean percentage cover of *Phoenix reclinata*, *Garcinia livingstonei*, *Euclea divinorum*, *D. mespiliformis* and *Ficus sycomorus* decreased with increasing distance from surface water. This could also be due to water stress that results from increasing groundwater table as the distance from surface water increases. This could be that these species prefer shallow groundwater table (Ellery *et al.* 1993). A similar observation, though with different species, was made in San Pedro River, Arizona, by Stromberg & Richter, (1996) who found a decrease in plant canopy cover with an increase in groundwater level.

Species richness varied with distance from surface water in all the sites. This is in agreement with Lite *et al.* (2005) who also observed variation in species richness in the San Pedro River with increasing distance from surface water. It implies that different species establish along the groundwater depth gradients to which they are adapted along distance from surface water gradient in both the Okavango Delta and San Pedro River. Salinity tolerance may also determine species richness along the distance from surface water gradient. McCarthy, (2006) found that as the distance from surface water increases, salinity levels also increase in the Okavango Delta. This leads to woodland species tolerant of salinity and deep groundwater table colonizing areas further away from the surface water. In this study distribution of species seemed to be influenced by salinity gradients. For instance, in Boro, species that are tolerant to saline conditions such as *H. petersiana* and *C. imberbe* were found in the 40-50m distance class which could be associated with high salt levels. This is consistent with Ellery *et al.* (1993) who observed plant zonation along salinity gradient in the Okavango Delta where the fringes of the islands with low salinity levels were colonized by riparian woodland species of *Syzygium cordatum*, *Ficus sycomorus*, *Phoenix reclinata*, *Garcinia livingstonei* and *Diospyros mespiliformis*. The island interiors with relatively high salinity levels than the fringes were colonized by *Croton megalobotrys*, *S. nigrescens* and *Hyphaene petersiana* with the centre of the islands with overall high salt levels were dominated by non woody species of *Sporobolus spicatus* (Vahl) Kunth. This zonation suggests that each distance class from surface water different woody species have different levels of salinity which they can tolerate and beyond which they may be completely excluded.

The current study has also indicated that mean basal area also varied with distance from surface water across different sites. It was high at 0-10m and 40-50m in Boro and Seronga and significantly high at 0-10 and 10-20m in Jao and UPH respectively. High mean basal in Boro at sites closer to the permanent swamp and those that were at 40-50m could be an indication that depth to groundwater in these sites was suitable for the establishment of large woody species. Examples of these species found at 0-10m in the Boro system include *Diospyros mespiliformis, Ficus sycomorus, P. violacea* and *Garcinia livingstonei* which have contributed to large basal area. In Seronga species which contributed to the larger basal area at 0-10m were *Syzygium cordatum, D. mespiliformis* and *G. livingstonei.* These species are tolerant of shallow groundwater conditions (Ellery *et al.* 1993) which may explain their establishment at 0-10m as this distance class was associated with shallow groundwater depth.

Plant species diversity was significantly high at 0-10m than 10-20m in Boro, in Seronga it was significantly high at 0-10m and 40-50m while in Jao and UPH it was high at 0-10m. High species diversity at this distance classes may imply that there was intermediate level of disturbance (Huston 1979) caused variation in depth to ground water depth as a result of variation in flooding magnitude during both short and long periods. During high floods species that do not prefer permanent flooding and those that are tolerant to it may co-exist. The co-existence of these two sets of species may lead to an increase in species diversity as predicted by the intermediate disturbance hypothesis. The hypothesis predicts that at intermediate disturbance levels species diversity increases due to the co-existence of both competitive and opportunistic species (Huston 1979). However, diversity may eventually decrease if flooding in the riparian zone occurs for a prolonged duration enough to kill the species that are intolerant of flooding. Conversely, if there is long term drying and high depth to groundwater in the riparian zone, species that prefer wet conditions will die resulting in a decrease in species diversity.

In the Boro and Seronga systems, the 0-10m distance class was colonised by species such as *P. violacea*, *D. mespiliformis*, *G. livingstonei* and *F. sycomorus* which prefer shallow groundwater, *Ziziphus mucronata*, *Acacia hebeclada*, *A. nigrescens*; *Dichrostachys cinerea* which are tolerant of deep depth to groundwater; *Combretum imberbe* and *Hyphaene petersiana* adapted to saline groundwater conditions (Ringrose *et al.* 2007). Therefore, the co-existence of these species with different preferences of groundwater chemistry and depth may have led to an increase in diversity at 0-10m in Boro and Seronga. Jao had significantly high species diversity at 40-50m while in UPH diversity was significantly lower at this distance class. This was because of species at 40-50m which tolerated dry conditions and resulted in high species diversity. Some of these species were *Acacia galpinii*, *A. nigrescens*, *Grewia bicolor*, *D. cinerea* and *Philenoptera nelsii* which were not observed in other distance classes probably due to unfavourable flooding and groundwater conditions. Conversely, in UPH, species diversity was significantly lower at 40-50m distance class. This is because it was dominated by species that are mostly tolerant of deep groundwater table while those that prefer shallow groundwater were excluded. Conversely, other distance classes in UPH had species that were tolerant of both high and low groundwater tables co-existing which resulted in high diversity suggesting that they may have experienced intermediate disturbance levels from flooding. This is in agreement with Pollock *et al.* (1998) who also found that there was an increase in species diversity at sites that experienced intermediate levels of flooding disturbance. Generally, the consistency of the results of this study with those of other wetlands elsewhere suggests that functionally these ecosystems are similar in terms of the influence of hydrology on vegetation communities.

Implications for management of riparian plant species in the Okavango Delta

The results of this study can be useful in guiding riparian woodland management strategies. It has been shown that distance from river surface water influences riparian vegetation community distribution and composition in the studied sites. Therefore, in order to conserve the riparian woodland vegetation, there is need not to change the flood extent in the Okavango Delta. Construction of upstream dams may reduce the amount of water that reaches the Delta. This may result in a change in species composition such that riparian plants species are replaced by dry land ones. The change in species composition may impact negatively on the livelihoods of the inhabitants of the villages around the Okavango Delta. The people in the Delta rely on riparian vegetation for fruits which serve as food. The riparian vegetation also helps in the provision of fresh water through the process of evapo-transpiration. The loss of water through evapo-transpiration helps to keep surface water fresh in the Delta because salt accumulation is localised in the centre of islands (McCarthy & Ellery 1994). The transpiring trees also selectively absorb toxic solutes resulting in good quality surface water (McCarthy & Ellery 1994). This is significant since it prevents surface salinisation and makes the water healthy for drinking by the local people. The results of this study also suggest that we can use riparian plant species as indicators of long term change in the hydrology of the Okavango Delta. Furthermore, the results on species composition may be used as a baseline data to monitor future changes in riparian communities caused by climate change, upstream water abstraction or human destruction. At the moment monitoring in Botswana is biased towards animals while there are minimal efforts to monitor vegetation change over time. The results of our study may also inform future research which will improve our understanding of the ecological functioning of the riparian plant communities in the Okavango Delta. Future research has to study the influence of flooding frequency and duration on riparian plant community composition and distribution.

Conclusion

This study showed that riparian woodland characteristics differed significantly with distance from surface water within and between in all the sites. This variation was attributed to changing depth to ground water with changing distance from surface water. As the distance from surface water increases, it is expected that depth to ground water also increases. As result different species establish in microsites to which they are adapted along the gradient of distance from surface water. These results suggest that plant species composition, basal area and species richness may be used as indicators of the hydrologic status of a given site in the Okavango Delta. This will be useful in areas where the information on that is not available.

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Spatial variation of population size structure of selected riparian tree species in the Okavango Delta, Botswana.

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Abstract

Transpiration by riparian trees in the Okavango Delta (Botswana) creates a salinity gradient which facilitates continuous water movement from the swamps to the islands. This leads to salt accumulations underneath islands which minimizes surface water salinity. The aim of this study was to investigate spatial variation in population size structure of riparian tree species in the Delta. It was hypothesized that riparian tree population structure will vary spatially due to different hydrological conditions. Riparian vegetation was surveyed in Boro, Santawani, Moremi, Vumbura and Seronga from a total of 75 plots measuring 20m × 50m. Species chosen for this study in terms of their dominance were *Croton megalobotrys* Müll. Arg, *Philenoptera violacea* (Klotzsch) Schrire, *Diospyros mespiliformis* Hochst. Ex A.DC and *Acacia nigrescens* Oliv. Diameter at breast height (dbh) was measured for tree individuals with stem diameter >2.5cm. Linear regression analysis was used to infer population size class distribution of each species. *Croton megalobotrys* Müll. Arg showed a reverse J size class distribution (SCD) pattern in Boro, Santawani and Vumbura while it showed a bell shaped pattern in Moremi. *Philenoptera violacea* (Klotzsch) Schrire showed an irregular size class distribution pattern with some missing size classes in Boro and Santawani while it showed a reversed J shaped size class distribution pattern with more individuals in the lower size classes in Vumbura. *Diospyros mespiliformis* Hochst. Ex A.DC showed a U shaped SCD pattern in Boro and irregular pattern in Seronga and Vumbura. *Acacia nigrescens* Oliv showed irregular SCD pattern with some missing size classes in Boro and Santawani and reverse J shaped SCD pattern with more individuals in the lower size classes in Seronga.

Key words: Diameter at breast height (dbh), Okavango, Recruitment, Size class distribution (SCD) and Species.

Introduction

Riparian vegetation communities are transition zones between terrestrial and aquatic systems (Naiman et al. 1993). They play a significant role due to their provision of ecosystem services and products to both human and animal populations. Ecosystem services performed by riparian tree species include primary production which produces food, nutrient cycling (Murkin 1998) and water purification through the process of evapotranspiration (McCarthy et al. 1994). Riparian tree species hold the soil together through their roots which helps to reduce erosion due to floods (Carter 1996). Riparian habitats serve as corridors and connecting elements which help to maintain regional diversity (Naiman et al. 1993). In the Okavango Delta though, riparian tree habitats are frequently fragmented by floodplains and channels (McCarthy et al. 1994, Gumbricht et al. 2004). Although they do not form continuous corridors, they are also significant in maintaining local diversity. They provide habitat to primates (monkeys and baboons), birds, bats, insects and snakes and provide forage to both grazing and browsing animals (Skarpe et al. 2004). Trees provide timber which is used for building human shelter (van der Valk 2006). In the Okavango Delta tree species such as *Diospyros mespiliformis* Hochst. Ex A.DC are also used for the construction of traditional canoes which are used as a mode of transport by the local riparian communities (Heath & Heath 2009).

The Okavango Delta is characterized by riparian tree-covered islands which play a significant role in the sequestration of potentially toxic solutes (McCarthy et al. 2012). The islands serve as a sink for dissolved solutes. Evapotranspiration by riparian trees lowers the water table under the islands relative to the water surface of the surrounding swamps. This creates a gradient which facilitates continuous movement of water from the swamps to the islands. As the trees transpire they leave dissolved solutes behind resulting in salinity increase in the groundwater. As a result of this, salt accumulations occur underneath islands and minimize surface water salinity (McCarthy et al. 1994). Similar processes are beginning to be identified in other sub-tropical major wetlands, such as the Everglades (e.g. Wetzel et al. 2005, Sullivan et al. 2010). In the context of the Okavango Delta, this is a critical ecological process for the long-term sustainability of the system (McCarthy et al. 1993).

Globally, riparian tree species are threatened by loss due to deforestation for agriculture (Reddy & Gale 1994), climate change (Seavy et al. 2009) and invasive species (Cronk & Fennessy 2001). In Botswana there is a policy framework designed to conserve and protect the Okavango Delta. These include the National Conservation Strategy (Matiza & Chabwela 1992), the Botswana National Wetlands Policy and Strategy of 1999 and the Okavango Delta Management Plan which attempt to engage the public as active participants in wetland management through the utilization of their indigenous knowledge and local institutions (Jansen & Madzwamuse 2003). The Okavango Delta is also a declared Ramsar site, a wetland of international importance. Despite these efforts to conserve the Delta's biodiversity and ecology, the threats of deforestation, climate change and invasion by alien species persist, and as human populations around the periphery of the Delta grow, these damaging activities increase. An additional threat is increasingly posed by a large and rapidly growing population of African elephant, *Loxodontus africanus* (Natural Resources and People 2007). Given the critical ecological function of the riparian woodlands, little can be done to ensure the sustainability of the Delta and its ecosystem processes and services without better knowledge of the current status and trends of tree populations. The information could also be used in modelling the possible future of the Okavango Delta in the context of vegetation resources utilization, climate change and basin development. In order for the tree species to be sustainably used their ecology has to be understood together with the ecological consequences of that use (Naiman et al. 1993).While several authors (e.g. Walker et al. 1986, Jones et al. 1994, Sop et al. 2011, Gurnman et al. 2012) characterized the spatial variation of riparian tree species population structure elsewhere, in the Okavango Delta this has not been done. Previous studies in the Okavango Delta only classified riparian tree species in relation to local environmental gradients in specific locations (Ellery et al. 1993, Ringrose & Matheson 2001).

The aim of this study was to investigate the spatial variation of population structure of selected riparian tree species in the Okavango Delta. Variation of riparian tree species population structure was studied in sites selected along hydrological (flooding) gradients. Flooding has been found to be the overriding factor influencing the vegetation ecology of the Okavango Delta (Ellery et al. 1993). The effects of other influences, for example those of elephants and fire were inferred based on field observations.

Materials and Methods

Study area

The study was conducted in Seronga (22˚17'8"E, 18˚48'42"S representing the Upper panhandle), Boro (23˚9'13"E, 19˚32'27"S representing the lower Delta), Santawani (23˚37'8"E, 19˚32'11"S, representing the lower Delta), Vumbura (19˚17'9"S, representing the northern-Delta) and

Moremi game reserve (23˚22'38"E, also representing the lower Delta) (Figure 1 & Table 1). Selection of the study sites in the upper, middle and lower parts of the Delta was designed to allow comparison of the population structure of riparian trees from regions exposed to different hydrological regimes.

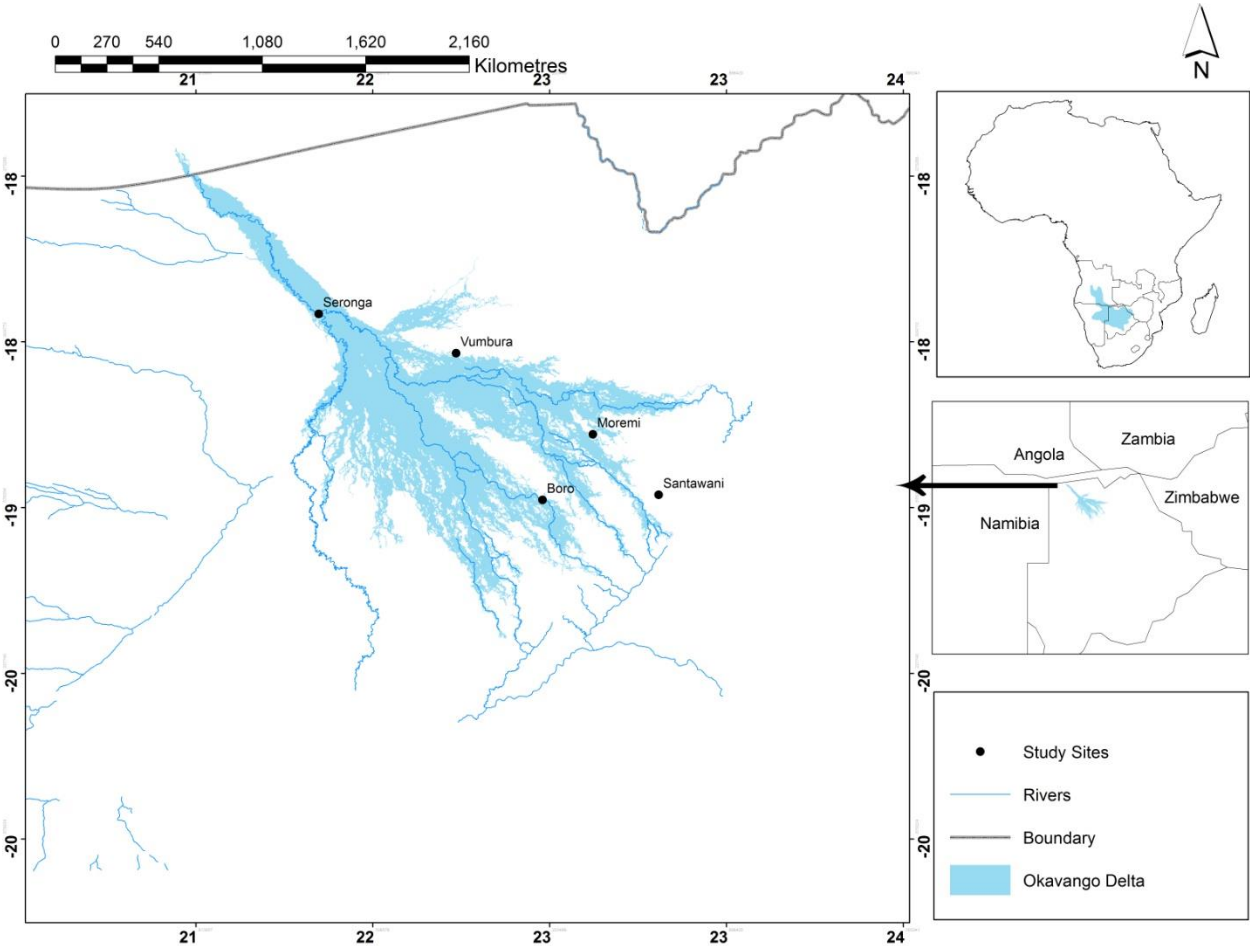

Figure 1: The map of the Okavango Delta showing study sites.

Table 1: Characterization of selected study areas based on field observations.

Study area	Habitat type	Land use activity	Examples of herbivores present
Santawani	Dry land	Agriculture, Tourism, wildlife habitat and human settlement	Giraffe, Elephant, Buffalo and Impala
Moremi	Dry land	Tourism, wildlife habitat	Buffalo, Elephant and Impala
Boro	Permanently flooded, seasonally flooded and dry land	Tourism, agriculture, human settlement and wildlife habitat	Cattle, Elephant, Impala and Buffalo
Vumbura	Permanently flooded, seasonally flooded and dry land	Tourism and wildlife habitat	Buffalo, Elephant, Kudu and Impala
Seronga	Permanently flooded, seasonally flooded and dry land	Agriculture, Tourism, agriculture and wildlife habitat	Cattle, Elephant, Impala, Donkeys and Goats

The Okavango Delta flood pulse originates from the Angolan highlands arrives in the Upper Panhandle region between March and April (Björkvald & Boring 2002) and reaches the distal regions between May and October (McCarthy et al. 2005). The Delta experiences both intra and inter-annual flood variation (Wolski et al. 2006). Inter-annual flood variation refers to the differences in flooding magnitude between two or more years (Björkvald & Boring 2002). Mean annual rainfall in the Okavango Delta ranges between a high of 550mm in Shakawe (Wilson & Dincer 1976) to a low of 450mm in Maun (Bonyongo & Mubyana 2004).

Common riparian tree species found in the Okavango Delta include *Diospyros mespiliformis*, *Garcinia livingstonei* T. Anderson, *Ficus natalensis* Hochst, *F. sycomorus* L, *Hyphaene petersiana* Mart and *Croton megalobotrys* Müll. Arg (Ellery e tal. 1993). Other common woody tree species found in the Okavango Delta include *Acacia tortilis* (Forsk) Hayne, *Acacia erioloba* E. Meyer and *Colophospermum mopane* (J. Kirk ex Benth) J. Kirk ex J. Léonard (Ringrose &

Matheson 2001), but these are restricted to dry land areas or relict floodplains which do not receive water under the prevailing hydro-climatic conditions. Tree species common to all sites were selected for the study. These were *C. megalobotrys*, *Acacia nigrescens*, *D. mespiliformis* and *Philenoptera violacea* (Table 2). This enabled comparison of their population structure between different sites.

Table 2: Characteristics of riparian tree species selected for study in the Okavango Delta, Botswana (after Ellery et al. 1993, Heath & Heath 2009).

Tree species	**Family**	**Deciduous/Evergreen**	**Distribution**	**Mode of reproduction**	**Height***	**Uses**
Diospyros mespiliformis	Ebenaceae	Evergreen	Sandy soils close to water	Seed	20m	Fruits eaten, Canoe and furniture construction
Acacia nigrescens	Leguminosae	Deciduous	Dry woodland and island edges	Seed	18m	Fire wood, Fence posts and Furniture
Philenoptera violacea	Leguminosae	Deciduous	Dry woodland and island edges	Seed	10m	Canoe construction
Croton megalobotrys	Euphorbiaceae	Evergreen	Floodplain margins and on fringes of islands	Seed	15m	Fruits mixed with bark to treat malaria, Fruits mixed with vegetable to treat wounds

*Average height of fully grown tree.

Vegetation sampling

Riparian vegetation sampling was conducted between February 2012 and April 2013 from randomly selected plots measuring 20m × 50m. In each plot the circumference (>15cm) was measured from tree individuals (Sop et al. 2011) at 1.3m above ground. For multi-stemmed trees, circumferences of the stems were summed up (Sop et al. 2011).

Data analysis

The diameter for individual trees was computed from the circumference. A total of 75 plots were sampled. Tree species from each study site were categorized into 8 dbh classes namely 0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70 and >70cm. The method for inferring recruitment status of different plant species followed Shackleton et al (1993). Recruitment status of each species was determined by analyzing the slope of a linear regression of dbh size classes calculated from circumference values. Circumference at breast height was converted to dbh using the formula; Diameter (d) = Circumference (C)/π, where π = 3.14. Dbh midpoint (mi) was used as the independent variable while the density of individuals (N_i) in each dbh class was used as the dependent variable. N_i was transformed by $\ln(N_i + 1)$ since some classes had zero individuals. The regression was then done using $\ln(N_i + 1)$ and ln(mi). Negative slopes indicated on-going recruitment with more individuals in smaller size classes than in larger size classes while positive slopes indicated little recruitment or possibly episodic recruitment (Helm & Witkowski 2012).

Results

Table 3: Regression analysis slope coefficients for different tree species populations in the study sites.

Tree species	Site	Slope coefficient	R^2
Croton megalobotrys	Boro	-3.78	0.84
	Santawani	-2.95	0.80
	Vumbura	-3.60	0.80
	Moremi	-3.30	0.70
Diospyros mespiliformis	Boro	-1.20	0.21
	Seronga	-1.97	0.49
	Vumbura	-0.43	0.25
Philenoptera violacea	Boro	-1.43	0.20
	Santawani	-0.84	0.096
	Vumbura	-2.08	0.50
Acacia nigrescens	Boro	-1.74	0.30
	Santawani	-0.064	0.00
	Seronga	-2.19	0.65

Croton megalobotrys showed a reverse J size class distribution with more individuals in the lower size classes indicating stable populations in Boro (Figure 2A) with a slope coefficient of -3.78 and R^2 of 0.84 indicating strong recruitment (Table 3), Santawani (Figure 2B) and Vumbura (Figure 2C) also with a strong recruitment indicated by high negative slope coefficient and R^2 (Table 3) while a bell shaped pattern for populations in Moremi indicated an unstable population (Figure 2D) but apparently also with strong recruitment as indicated by both high negative coefficient and R^2 (Table 3).

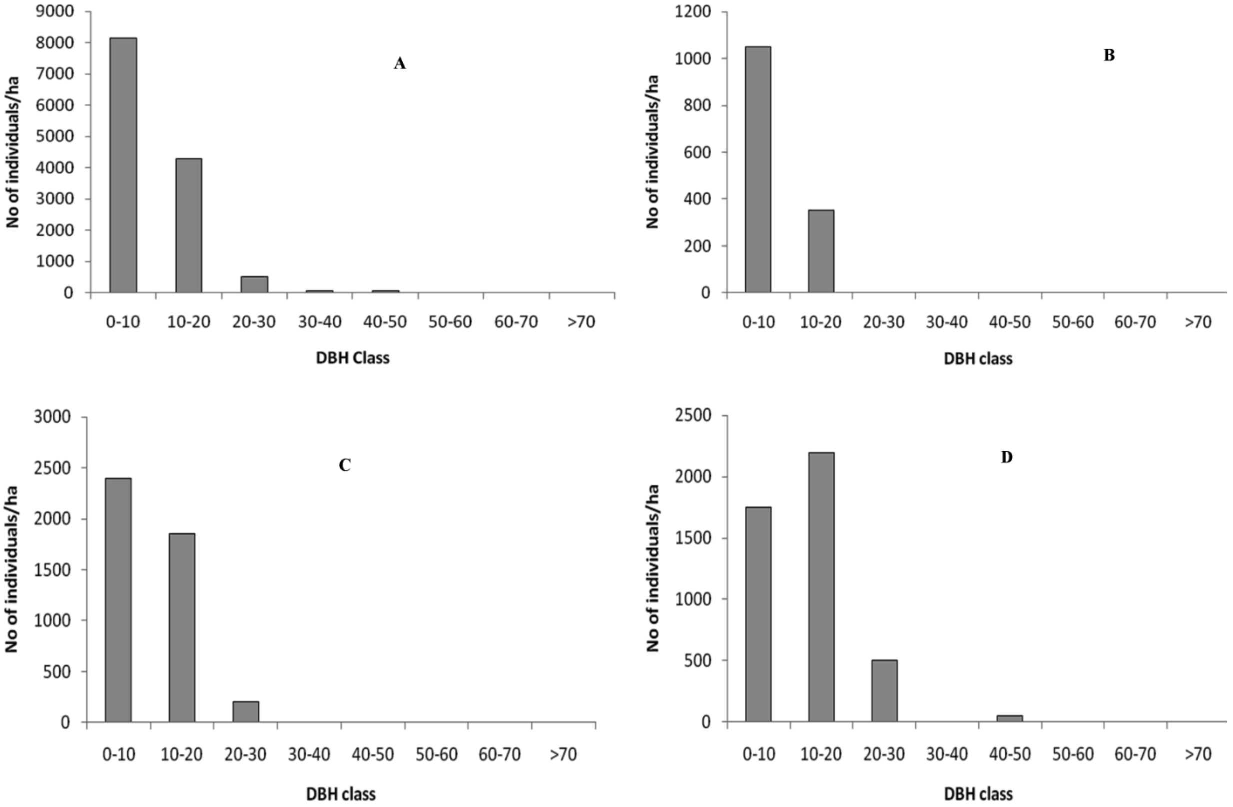

Figure 2: Population size structure distribution of *Croton megalobotrys* in Boro (A), Santawani (B), Vumbura (C) and Moremi Game Reserve (D).

Philenoptera violacea (Klotzsch) Schrire showed an irregular size class distribution with some missing size classes indicating an unstable population in Boro (Figure 3A) and Santawani (Figure 3B) while in Vumbura it showed a reverse J shaped size class distribution in which there were more individuals in the lower size than larger size classes (Figure 3C). It showed a low negative slope coefficient value and R^2 in Santawani indicating weak recruitment while in Boro it showed a relatively high negative slope coefficient but with low R^2. Only in Vumbura were both the negative slope coefficient and R^2 high indicating strong recruitment (Table 3).

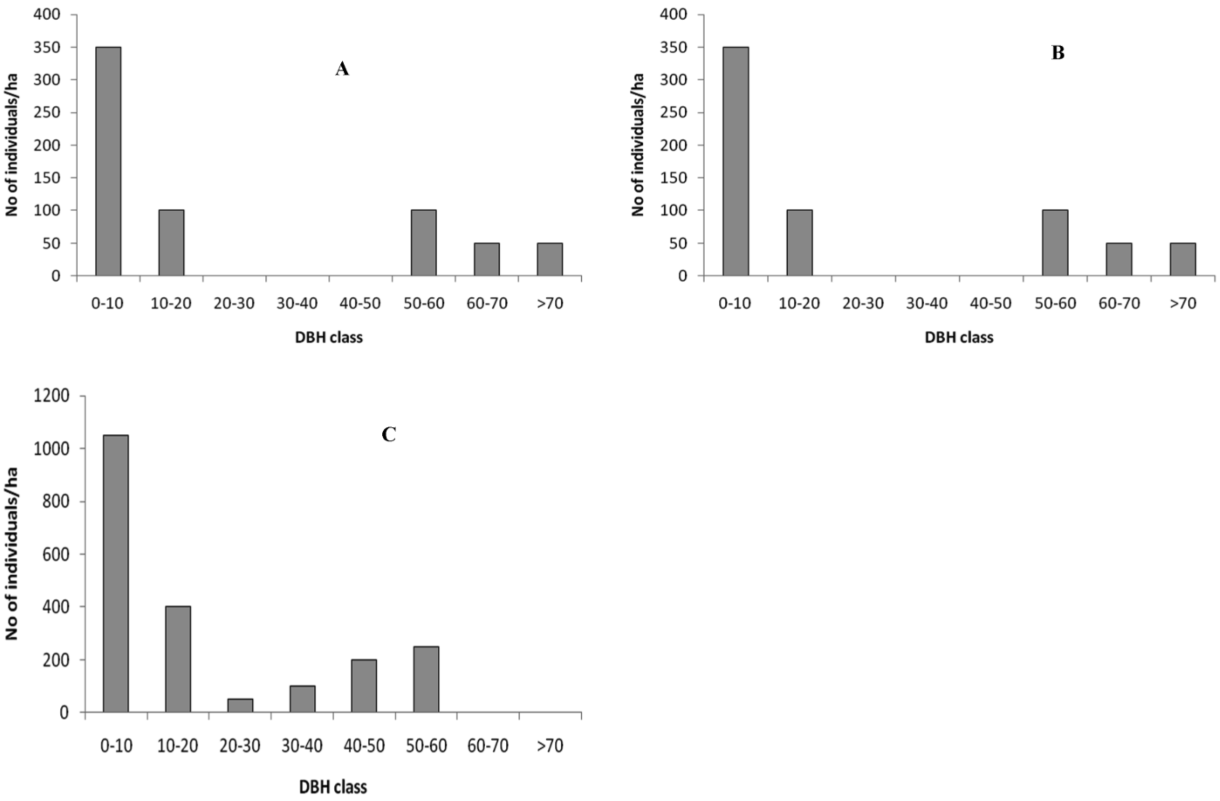

Figure 3: Population size structure distribution of *Philenoptera violacea* in Boro (A), Santawani (B) and Vumbura (C).

Diospyros mespiliformis showed a U shaped size class distribution with more individuals in the lower and higher size classes than in the middle size classes in Boro (Figure 4A) and irregular size class distribution with some missing size classes in Seronga (Figure 4B) and Vumbura (Figure 4C). This indicates that *D. mespiliformis* populations in these two areas are unstable. They showed the lowest negative slope coefficient and R^2, indicating weak recruitment in Vumbura while in Boro and Seronga it showed high negative slope coefficients indicating strong recruitment, although the R^2 was low in both sites (Table 3).

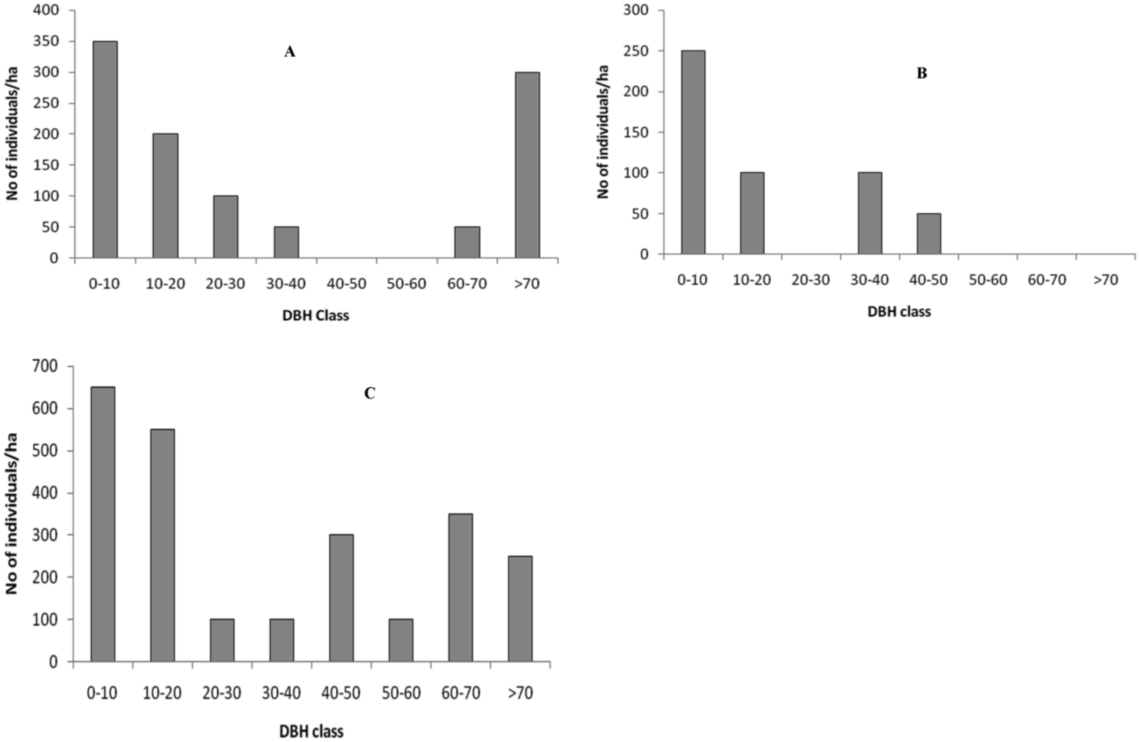

Figure 4: Population size structure distribution of *Diospyros mespiliformis* in Boro (A), Seronga (B) and Vumbura (C).

Acacia nigrescens Oliv showed irregular size class distribution with some missing size classes indicating an unstable population in Boro (Figure 5A) and Santawani (Figure 5B). It showed a reverse J shaped size class distribution with more individuals in the lower size classes indicating a stable population in Seronga (Figure 5C). *Acacia nigrescens* showed high recruitment in Boro and Seronga although for Boro the R^2 was low. It showed a very low recruitment in Santawani with R^2 of 0.00 indicating no correlation between diameter size class and the density of individuals (Table 3).

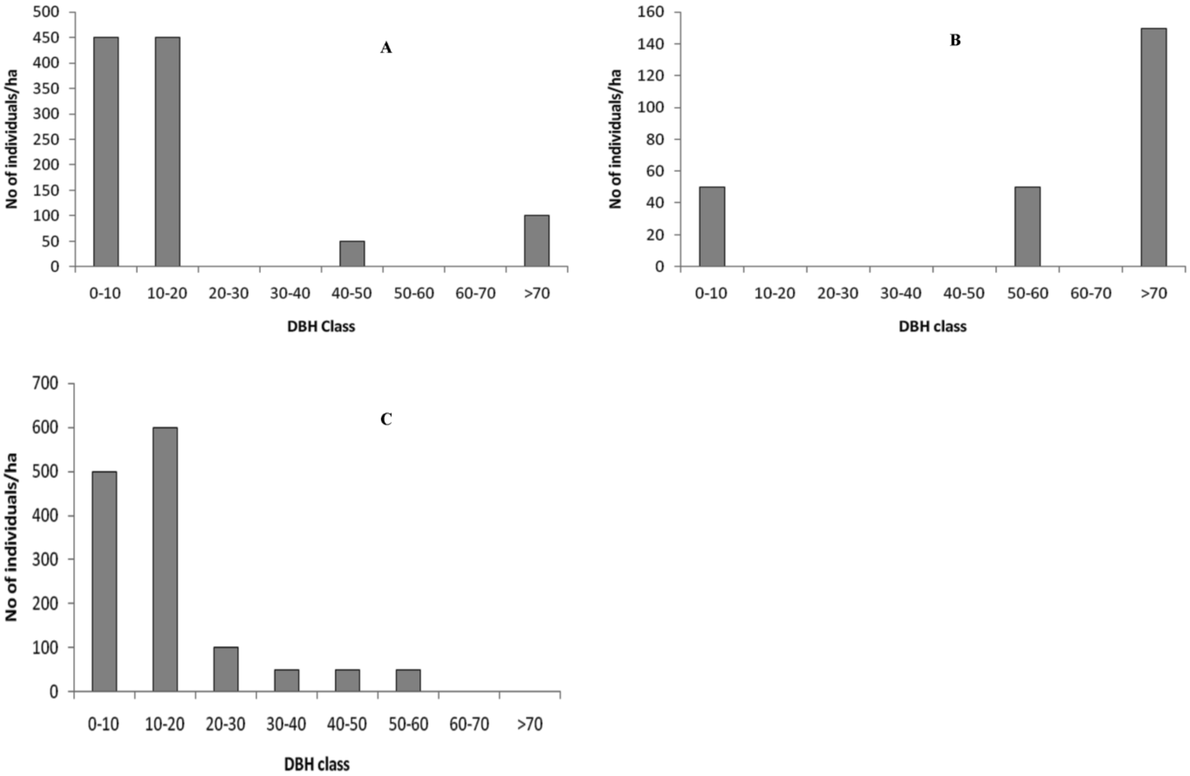

Figure 5: Population size structure distribution of *Acacia nigrescens* in Boro (A), Santawani (B) and Seronga (C).

Discussion

The majority of sampled population had structures indicating on-going recruitment. There was no significant difference between sites in terms of recruitment. Tree species showed spatial variation in their population size structure between different study sites. This variation could be due to differences in species reproductive strategy, competition, hydrology and disturbance from fire and elephant damage. *Croton megalobotrys* showed a reverse J shaped size class distribution indicating a stable population in Boro, Santawani and Vumbura with most individuals in the lower dbh class and few individuals in the higher classes. This could suggest that it has a high rate of germination but low recruitment. *C. megalobotrys* is an opportunistic species which colonizes floodplain margins and produces a large number seeds to enhance its survival through massive germination of seedlings. It also produces toxins in both leaves and seeds which renders it unpalatable to browsers to enhance its survival and recruitment of seedlings into large size classes (Hamandawana 2012). However, not all of the germinated seedlings are recruited into the larger size classes as some die due to browsing by larvae of some butterflies (Ellery & Ellery 1997). In Boro *C. megalobotrys* individuals were observed stripped bare of leaves by caterpillars, stems bored by insects and seeds consumed by squirrels which apparently are resistant to the toxins.

Seed dispersal is an important component in tree population structure distribution (Hampe 2004). It allows seeds to reach suitable microsites for germination and establishment (Nathan & Muller-Landau 2000). However, in some instances seeds could be dispersed in unsuitable habitats which could prevent their germination and establishment. Recruitment, establishment and survival of riparian tree species including *C. megalobotrys* are cited in literature to be influenced by the hydrological regime (Irvine & West 1979). As a typical R strategist (Hamandawana 2012), *C. megalobotrys* produces a large number of fruits which fall and germinate around the parent trees in large numbers. The species invests energy in a large food store, toxic shell and oils to maximize numbers of individuals in areas in which conditions may be suitable in the short term. Once established riparian tree species can also be threatened by excessive flooding which results in fatal anoxic conditions (Kozlowski 1984). Dead stands of *C. megalobotrys* probably due to waterlogging that resulted from the extensive flooding of 2011 were observed in Boro. These factors present survival and recruitment bottlenecks into larger size classes. This is consistent with Irvine and West (1979) who in the Escalante River, Utah, observed die-offs in riparian tree species due to periodic water fluctuation with severe flooding cited as the probable cause of tree mortality.

In Moremi Game Reserve the *C. megalobotrys* population size class distribution was bell shaped with fewer individuals in the lower and higher dbh classes than in the middle classes. This indicates an unstable population (Helm & Witkowski 2012). High numbers of individuals in the middle classes could be due to an episodic recruitment event that could have occurred when the conditions were favourable (Hamandawana 2012). Generally the sites in Moremi Game Reserve were dry during the field survey which might have prevented *C. megalobotrys* seed germination. Water from flooding or directly from rainfall is a germination requirement for activating metabolic processes required for a seed to germinate (Kozlowski 2002).

Philenoptera violacea and *Acacia nigrescens* showed irregular size class distribution in Boro and Santawani while *Diospyros mespiliformis* was characterized by irregular size class distribution in Seronga and Vumbura. In both study sites *P. violacea* and *A. nigrescens* had some missing size classes while *D. mespiliformis* only showed missing size classes in Seronga. The missing size classes in *P. violacea, A. nigrescens* and *D. mespiliformis* could result from variable growth and unequal mortality rates in subsequent classes probably resulting from fire and elephant suppression (Hamandawana 2012). The current high elephant population density in the Okavango Delta is likely to result in the over-exploitation of preferred species in a given size class (Skarpe et al. 2004).

Elephant-induced mortality of trees, suppressing recruitment of preferred tree species, has been reported elsewhere (e.g., Cumming et al. 1997, O'Connor et al. 2007). Along the Linyanti River in northern Botswana, 16% of dead *A. nigrescens* were killed by elephants with the remaining percentage probably due to other confounding factors such as wind and fire (Teren & Owen-Smith 2010). The dbh size classes for the 16% mortality were not given. Giraffe browsing has also been cited as another factor leading to missing size classes in *A. nigrescens* (Teren & Owen-Smith 2010). *Acacia nigrescens* also had more mature individuals than juveniles in Boro which suggests that it may be threatened by local extinction. Few individuals in the lower size classes of *A. nigrescens* are probably due to the inability of its seeds to reach suitable sites for germination and establishment. *Acacia nigrescens* produces seeds in pods which rely on water and wind for dispersal. If the flood water does not reach these seeds they cannot be dispersed to suitable germination sites and as a result they will remain dormant hence leading to few individuals in the lower size classes. If they germinate they will have to compete with the parent plant for survival. The same survival challenge could be faced by *P. violacea* which also produces its seeds in pods.

Diospyros mespiliformis showed a U shaped size class distribution in Boro characterized by more individuals in the lower and higher dbh classes. High individuals in the larger and lower size classes could be due to episodic recruitment events that could have occurred when the conditions were favourable (Hamandawana 2012) and slowed down during the onset of unfavourable conditions for its establishment. Tree establishment may take place at intervals of many decades or centuries in response to prevailing moisture conditions (Young & Lindsay 1988). In the Okavango Delta flooding dynamics could have an influence on riparian tree population size structure distribution. The quasi-cyclicity between multi-decadal wet and dry periods (Wolski et al. 2012) poses an episodic disturbance which may prevent the establishment of stable states in *D. mespiliformis* at Boro, instead inducing periods of high or low recruitment. This suggests that its population size structure distribution is driven by physical (allogenic) rather than autogenic processes (Baker & Walford 1995).

Extremely low flooding conditions are capable of preventing the establishment of *D. mespiliformis* individuals in the middle size classes. In the years of relatively high floods when the water reaches the riparian zone, large stands of individuals in the lower size classes establish but do not reach maturity before dying in response to drying and elephant destruction. This may prevent individuals in the lower size classes from reaching later growth stages (Pettit & Froend 2001). The larger size classes individuals of *D. mespiliformis* especially those with a dbh >70cm may have been recruited during the 1970s period of more extensive, longer and deeper flooding and recruitment might have slowed down in the 1990s when the floods were low.

High numbers of individuals in the higher dbh classes could also be due to their resistance to elephant damage owing to their big size (Teren & Owen-Smith 2010) while high numbers of individuals in the lower size classes could be attributed to its high germination rate (Zida 2009). *D. mespiliformis* grows in close proximity to surface water which exposes its seedlings to favourable soil and moisture conditions (Traore et al. 2013). *D. mespiliformis* also seems to attempt to maximize its germination and eventually establishment through production of edible fruits which are eaten by fish, birds and bats. The seeds of *D. mespiliformis* have been also observed in jackal dung (Heath & Heath 2009). Thus this suggests that *D. mespiliformis* unlike *C. megalobotrys* invests reproductive effort in trying to establish new individuals in areas far from the parent to reduce competition for vital resources such as moisture, space and sunlight insolation. Pettit & Froend (2001) discuss that there is need for seed fall to correspond with favourable site conditions in order to maximize their germination and establishment. In the Okavango Delta the seed fall in *D. mespiliformis* seems to be timed to correspond with optimum hydrological conditions which promote massive seedling germination. However, it also appears that most of them are removed before they could reach the maturity stage.

Few individuals in the middle size classes of *D. mespiliformis* could result from constant browsing and grazing pressures (Gurmesa et al. 2012). This suggests that browsers and grazers particularly elephant prefer *D. mespiliformis* individuals belonging to the middle dbh classes which are likely to be more nutritious and easy to have access to than mature ones. Preference of mid-size class individuals of *D. mespiliformis* by elephant suggests that they are probably within their feeding height. Elephant damage was observed in Boro in which *D. mespiliformis* individuals in the middle dbh classes were heavily impacted. Continued foraging pressure on *D. mespiliformis* populations may prevent any individuals from reaching fruiting age. This species is already included in the Botswana red data and protected tree species list (Setshogo & Venter 2003). The local loss of *D. mespiliformis* will also remove an important component of elephants and other herbivores' diet.

While elephant damage is a possible cause of variation of tree species population structure in the Okavango Delta it should be noted that there could be other confounding factors such as fire. Evidence of fire occurrence was observed during this study even though its actual year could not be established. Heinl et al. (2007) found that the fire return interval in drier areas which encompass the riparian zone ranged between 7 and 8 years. Individuals found in the lower size classes could be within the fire trap which suppresses their recruitment into the larger size classes (Jacobs & Biggs 2002). Lack of recruitment of individuals into the larger size classes will reduce the sexual reproduction of *P. violacea*, *D. mespiliformis* and *A. nigrescens* through a reduction in seed production. When the current individuals existing in the larger size classes eventually die, lack of seed input will result in their local extinction (Helm & Witkowski 2012). Influence of fire on riparian tree species population structure was also observed in the Colorado River floodplain in which *Tessaria sericea* (Nutt.) Shinners was dominant after fire occurrence with *Populus fremontii* S. Watson completely excluded (Busch 1995). However, without further study it is not possible to attribute size-class distributional anomalies to the effects of fire in the Delta.

Conclusions

This is the first study of the population demographics of riparian trees in the Okavango Delta. The differences observed in recruitment patterns between sites are probably the result of a combination of hydrological factors with other environmental factors such as herbivory acting on both the germination and subsequent growth stages. Reproductive and successional strategies such as competition must be important drivers for the differences observed between species population structure within sites. This study clearly raises many new questions, including the primary one: what are the principal drivers of recruitment in riparian woodlands in the Delta? Questions related to this are: Do different reproductive and dispersal strategies explain the variation we observe, or are major allogenic episodic events the main cause? How important is the role of the different scales of hydrological variation in stimulating or facilitating regenerative events?

Given the critical ecological function that the riparian woodland performs in the Delta, and the emerging understanding that riparian trees in other major tropical and sub-tropical wetland systems may fill similar roles, we consider further investigation of these questions a priority for land use and management authorities. In the short term interests of conserving tree diversity in the Delta, perhaps consideration should be given to the establishment of a number of strategically situated enclosures to remove the threat of elephant damage and provide nuclei for seed production and dispersal. We are currently involved in research aimed at designing a model of environmental controls of riparian tree species in the Okavango Delta. Future research should also focus on germination studies of the soil seed bank of these species to determine their regeneration potential.

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Regeneration status of riparian tree species in two different land use types in the Okavango Delta, Botswana.

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Abstract

Human communities from the Okavango Delta benefit from the services and goods provided by the wetland ecosystem through its riparian vegetation. These include food and timber products used for the construction of shelter and canoes. Despite their importance, the regeneration structure of riparian tree species in the Delta is currently unknown. Therefore, in order to manage riparian trees sustainably information on the current regeneration status of the trees under different land uses is needed. Moremi game reserve (Protected area) and Seronga (Communal area) were selected for the study. The riparian tree species present in the study areas were *Croton megalobotrys* Müll. Arg, *Philenoptera violacea* (Klotzsch) Schrire, *Acacia nigrescens* Oliv and *Diospyros mespiliformis* Hochst. ex A. Dc. The height of each individual tree was estimated in 20m × 50m randomly selected plots. Individuals were assigned to 0-0.5m, 0.5-1m, 1-2m, 2-4m and >4m regeneration classes. A total of 30 (15 from each site) plots were sampled. Linear regression was used to infer regeneration status of each species. The independent sample Student's *t*-test was used to determine the significance of differences in seedling density/ha and sapling density/ha between different sites at p<0.05. *Diospyros mespiliformis* populations showed an unstable regeneration structure in both sites while *Philenoptera violacea* regeneration was stable regardless of land use type. *Croton megalobotrys* and *S. nigrescens* showed an unstable regeneration pattern in Seronga while in Moremi it was stable. This study has shown that the regeneration structure of *Croton megalobotrys* and *A. nigrescens* is affected by land use. This implies that there is need for an intervention to conserve the two species in Seronga where the current land use appears to be incompatible with regeneration; *Diospyros mespiliformis* also needs to be conserved in both Moremi and Seronga.

Key words: Conservation, Regeneration, Riparian, Okavango and Wetlands.

Introduction

The riparian plant communities of wetland ecosystems perform ecological, biological and hydrological functions which provide goods and services to humanity (Harting et al. 1997). Services performed by wetlands include nutrient cycling and transport which benefits crop production (Murkin 1998; Brevik et al. 2015), food production (Van der Valk 2006), provision of freshwater (Talkudar 2003) for both human beings and animals, and flood and climate regulation (Daily 1997). Vegetation in riparian zones through its root systems and stems disperses hydraulic energy which helps in reducing soil erosion and flood damage (Carter 1996). It helps to keep the soil in the riparian zone intact and serves as a filter for groundwater by removing pollutants such as acids, heavy metals and pesticides (Keesstra et al. 2012).

Human communities in the Okavango Delta, a large flood-pulsed wetland in northern Botswana (Mazvimavi and Wolski 2006) benefit from the services and goods provided by riparian vegetation. These services include timber products used for building shelters (Heath and Heath 2009) and for the construction of canoes, locally known as "mekoro" which are used as a means of transport in economic activities such as fishing and tourism (Ecosurv 1988). Historically, common riparian trees that were used for constructing mekoro include *Philenoptera violacea*, *Acacia nigrescens*, *Diospyros mespiliformis* and *Garcinia livingstonei* (Ecosurv 1988). One of the riparian palm tree species, *Hyphaene petersiana*, is used for the production of traditional beer, "muchema", for subsistence and economic use (Babitseng and Teketay 2013). Riparian woodland species in the Okavango Delta are also used for the direct service of provision of food. These include species such as *Berchemia discolor*, *D. mespiliformis*, *G. livingstonei*, *Sclerocarya* *birrea*, *Grewia spp* and *Ximenia spp* (*X. caffra* and *X. americana*) (Heath and Heath 2009; Neelo et al. 2015). Seasonal floodplains in the Okavango Delta are used for flood recession farming (molapo farming) which relies on the soil moisture and nutrients from the receding flood that give crops an early start and extend the growing season. Molapo farming fields are fenced using tree species such as *Acacia erioloba*, *Acacia tortilis*, *Acacia mellifera* and *Acacia hebeclada* (Neelo et al. 2013).

There are several threats to riparian plant communities at a global scale which include loss due to deforestation for agriculture (Reddy and Gale 1994), climate change (Seavy et al. 2009) and out competition by invasive species (Cronk and Fennessy 2001). In the Okavango Delta these threats have the potential to reduce the role of riparian woodland in evapo-transpiration. Evapo-transpiration by riparian trees lowers the groundwater table which results in the fresh surface water-shallow groundwater sub-systems in the Okavango Delta (McCarthy and Ellery 1994). Fresh groundwater and saline groundwater do not mix because of density differences. Saline water is much more dense than fresh, and consequently, the fresh groundwater lies in a layer on top of the saline groundwater (McCarthy and Ellery 1994). Riparian tree species that contribute to evapo-transpiration are *Philenoptera violacea*, *Diospyros mespiliformis*, *Kigelia africana*, *Ekebergia capensis* and *Croton megalobotrys* (Lubinda 2015).

Analysis of the size-class structure of tree species populations gives information on the regenerative capacity of a population (Guilloy-Forget et al. 2002). Knowledge of the impact of land use on the regeneration structure of the riparian woodland will be helpful in formulating recommendations on sustainable management of woody resources in the Delta. The information on regeneration of a given species can also be used to make predictions about its response to utilization and climate change and can be used to design appropriate land management strategies. This information can also be used to enhance efforts to restore species threatened by local extinction due to overexploitation (Guilloy-Forget et al. 2002). Despite this, few studies (Babitseng and Teketay 2013; Neelo 2013) have focused on the influence of land use on the population dynamics of riparian plant communities in the Okavango Delta where land use has been identified as one of the potential factors threatening this sub-region's wetland ecosystems (Hermy and Verheyen 2007). Some of the common land use types that may pose threats to wetland ecosystems in this environment include deforestation and devegetation from arable farming, grazing and human settlements (Hermy and Verheyen 2007).

Previous studies on the influence of land use on regeneration potentials of woodland species include Ferreira et al. (2005) in the Tagus fluvial system in Portugal, Burton et al. (2005) in West Georgia, USA, Pettit (2002) in Australia and Salinas et al. (2007) in the Almanzora and Aguas river basins in Spain, Shackleton (1993) in South Africa, Sop et al. (2011) in Burkina Faso; Helm and Witkowski (2012) in South Africa and Traore et al. (2013) in Burkina Faso. These studies concluded that communal land use may have a negative impact on the woodland resources. In Botswana most studies on the structure of woodland species were focussed in the Chobe region (Ben-Shahar 1996; Barnes 2001; Teren and Owen-Smith 2010). These studies focused on the influence of herbivory by elephants on the population structure of woodland species and their results cannot be generalized to the Okavango due the limitation of the species studied. Therefore impacts on the upland woodland might be very different, since in Chobe

Baikaiaea woodlands are the mostly affected while in the Delta it tends to be *Colophospermum mopane* and *A. erioloba*.

In the Okavango Delta, studies on the effect of land use on regeneration of riparian tree species are few and were generally localized or focused on one species. Neelo et al. (2013) investigated the impact of flood recession farming on the population structure of selected species. It was confined to the *molapo* (floodplain) fields of the villages of Tubu, Shorobe and Xobe, all three of which fall in the category of communal land use. Babitseng and Teketay (2013) investigated the impact of wine tapping in Shorobe village on *Hyphaene petersiana*. Their study did not investigate the influence of land use on riparian tree species. They found that wine tapping negatively affected the regeneration of *H. petersiana*. The aim of this study was therefore to bridge this gap by investigating the effect of land use on the regeneration of common tree species in the Okavango Delta by hypothesizing that the regeneration status of different riparian tree species differs across different land use types.

Materials and methods

Study area

The study was conducted in the Okavango Delta, Botswana. The study sites were Moremi Game Reserve (MGR) and Seronga (Figure 1). These sites were selected because they are gazetted for different types of land use (MGR is a protected area, while Seronga is zoned for communal agriculture and livestock rearing), and exposed to different land use activities. This allowed us to better understand how contrasting land use types affect the regeneration of riparian tree species.

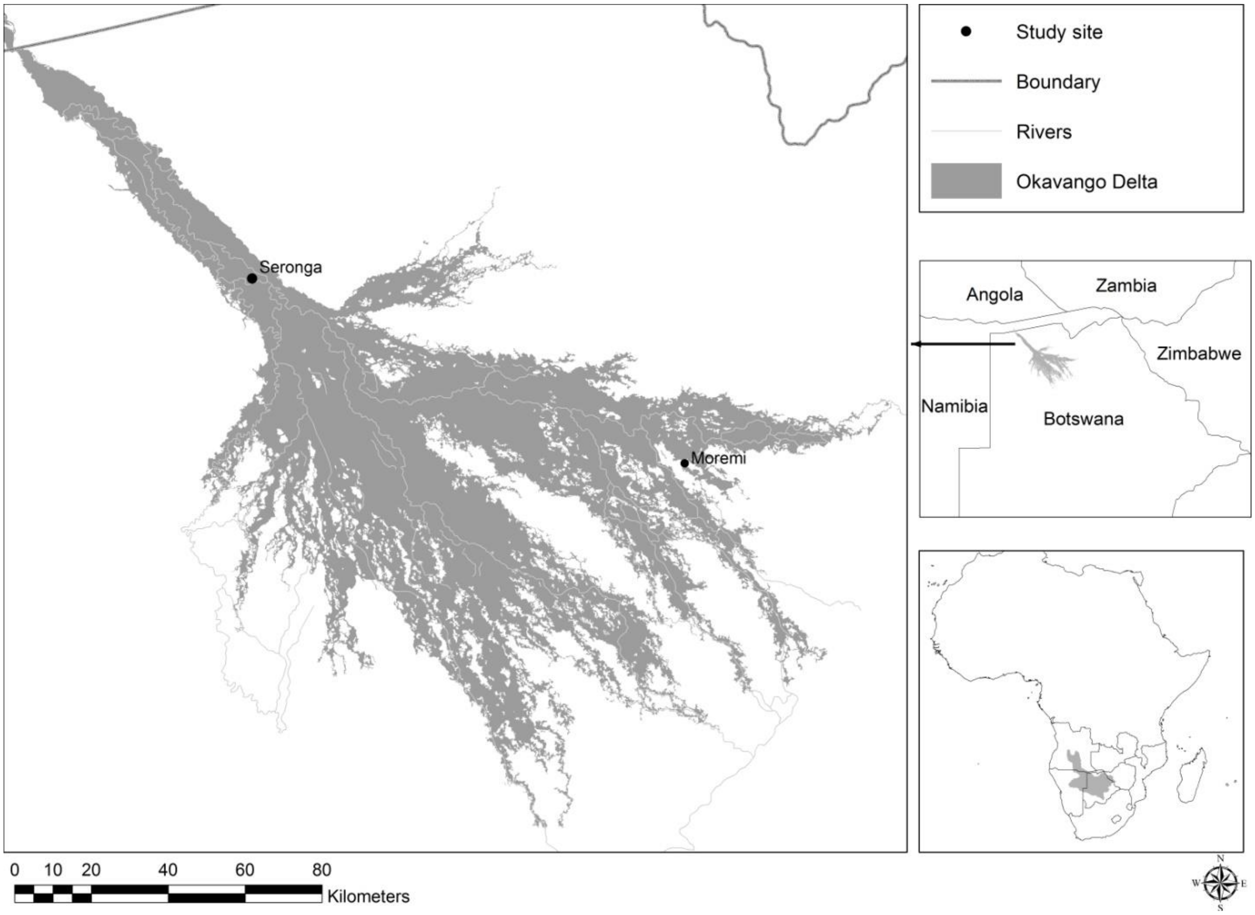

Figure 1: The Okavango Delta, showing the study sites.

Seronga (22˚17'8"E, 18˚48'42"S) is a communal area which is mainly used for human settlement, livestock grazing and arable agriculture. By 2011, the human population in Seronga was 2,674 (Central Statistics office Botswana 2011). The main economic activities in Seronga are farming at a subsistence scale with common crops planted being maize, groundnut, millet and watermelon (Jackson et al. 2008). These crops are supported by rainfall (mean ca. 500mm/annum) which mostly falls during the summer from November to April (Department of Meteorological Services Botswana 2004). The livestock in Seronga include cattle, goats and donkeys. Another livelihood activity in Seronga is tourism which involves game viewing and sight-seeing from dugout canoes (*mekoro*) (Mbaiwa et al. 2008). The dugout canoes are made from large riparian trees such as *D. mespiliformis*, *P. violacea*, *A. nigrescens* and *G. livingstonei* (Ecosurv 1988), or *Pterocarpus angolensis* from the sandveld hinterland, or, more recently, fibre-glass. The individual trees suitable for the construction of the canoe are either burnt or chopped down (Mbaiwa et al. 2008). With the exception of *P. angolensis*, these are some of the common riparian trees in Seronga (Tsheboeng and Murray-Hudson 2013) and their distribution is influenced by flooding frequency, salinity and groundwater level (Ellery et al. 1993).

Moremi Game Reserve (23˚22'38"E, 19˚17'9"S) is primarily used for the conservation of fauna and flora and wildlife-based tourism. It was established in 1963 for the conservation of wildlife and covers ca. 4 610 km^2 (Mbaiwa 2005). Before the establishment of Moremi Game Reserve part of the area was inhabited by human beings for a period of over 10 000 years mainly by the Basarwa who used its veld products including woodland and wildlife resources (Tlou 1985). Since 1963, Moremi Game Reserve has been largely free from human utilization of its woodland resources (Mbaiwa 2005).

The Reserve's woody species include dry land and riparian tree species. Common riparian tree species in Moremi are *C. megalobotrys*, *H. petersiana*, *P. violacea* and *D. mespiliformis*. The composition of tree species in Moremi Game Reserve may be influenced by flooding frequency, herbivory and fire (Tsheboeng and Murray-Hudson 2013). Common herbivores in Moremi Game

Reserve are mainly elephant, buffalos, giraffe, zebra, kudu and impala, which have transformed the woodland structure from trees to shrubs (Ben-Shahar 1996).

Vegetation sampling

Sampling was done between February 2012 and April 2013 for easier identification plant species since most of them had flowers and leaves during this period (February-April of each year) (Heath and Heath 2009). Woody species height was estimated in 20m × 50m plots that were selected randomly from the study sites. The randomization process for selecting quadrats involved selecting potential study quadrats in Google Earth images. The selected quadrats were assigned numbers and were chosen based on a randomly generated list (“RAND” function in MS Excel ver. 7). The plots were geo-located using a Garmin GPS and the coordinates stored in a spreadsheet. A total of 15 quadrats were sampled from each site.

Woody species were assigned to the following four height (regeneration) classes; 0-0.5 (seedlings), 0.5-1 (saplings), 1-2 and 2-4 (shrubs) and >4m (trees). The subdivision of individual trees into these height classes helps to gain insight into the processes that might occur in different growth stages (Sop et al. 2011). The numbers of woody specimens in each height class in each quadrat were counted by species type. A range pole was used to estimate the height of different woody species in 20m × 50m quadrats selected randomly from the study sites.

Data analysis

Interpretation of regeneration status of different tree species was carried out with procedures suggested by Shackleton (1993). Status was determined by analyzing the slope of a linear regression of height classes. Height class midpoint (mi) was used as the independent variable while the mean number of individuals (N_i) in each height class was used as the dependent variable. N_i was converted to ln (N_i+ 1) since some classes had zero individuals. The log conversion is to get the curve to approximate a straight line, whose slope is linear, not a power function. The regression was then done between ln (N_i + 1) and ln (mi). Negative slopes indicate on-going regeneration while positive slopes indicate poor (weak) regeneration (Shackleton 1993). A positive slope is a result of the population having more individuals in the larger size classes than in the lower size classes. Negative slopes indicate on-going recruitment in which there are more individuals in the lower size classes than in the upper ones. The graphs were put on a similar scale in order to allow for the comparison of regeneration structure between land use types. This was done by converting the density of individuals to a percentage of the maximum for each species at each site. The independent sample Student's *t*-test was used to determine if there was any statistical difference in seedling and sapling density/ha of a given species between different sites. All statistical tests were conducted in IBM SPSS Statistics for Windows, Version 22.0 (IBM Corporation 2013).

The tree/shrub ratio was calculated for each species by dividing the total number of trees by the total number of shrubs. Tree/shrub ratio is used to detect if a given plant population is disturbed or not. A high tree/shrub ratio may be interpreted as an indication of disturbance of the population in question (Gurmessa et al. 2012). In this study, individuals with a height ranging between 2-4m were classed as shrubs, while trees were regarded as individuals with heights >4m (Setshogo and Venter 2003).

Results

There was no significant difference in mean seedling densities of *D. mespiliformis* (df=1, T statistic=-0.74, *p*=0.50) and *C. megalobotrys* (df=1, T statistic=0.01, *p*=0.204) between Moremi and Seronga, while *P. violacea* seedling densities were significantly higher (df=1, T statistic=-2.3, *p*=0.030) in Seronga than in Moremi. There were no seedlings of *A. nigrescens* in Moremi (Table 2).

Table 2: Mean (±SD) seedling density (individuals/ha) of common riparian tree species in Moremi and Seronga.

	Sites	
Species	**Moremi**	**Seronga**
Croton megalobotrys	38 ± 5.08^{a}	38 ± 2.08^{a}
Acacia nigrescens	0^{a}	915 ± 76.0^{b}
Diospyros mespiliformis	62 ± 4.2^{a}	125 ± 10^{a}
Philenoptera violacea	298 ± 19.8^{a}	306 ± 5.9^{b}

**Similar superscript letters across the row indicate that there was no significant difference (p>0.05) while different letters show that there was significant difference (p<0.05).*

There was no significant difference in mean sapling densities of *D. mespiliformis* between Moremi and Seronga (df=1, T statistic=-0.622, *p*=0.54). The mean sapling density of *A. nigrescens* was significantly higher in Seronga than in Moremi (df=1, T statistic=-24.05, *p*=0.001) while that of *P. violacea* was insignificantly higher in Moremi (df=1, T statistic=2.13, *p*=0.07) (Table 3).

Table 3: Mean (±SD) sapling density (individuals/ha) of common riparian tree species in Moremi and Seronga.

	Sites	
Species	**Moremi**	**Seronga**
Croton megalobotrys	37±2.5^{a}	0^{b}
Acacia nigrescens	0^{a}	92±2.3^{b}
Diospyros mespiliformis	13±0.8^{a}	31±3.0^{a}
Philenoptera violacea	28±2.0^{a}	13±1.04^{b}

**Similar superscript letters across the row indicate that there was no significant difference (p>0.05) while different letters show that there was significant difference (p<0.05).*

Tree/shrub ratio was used as a measure of the level of disturbance experienced by each species. Our analysis showed that the tree/shrub ratio of *Croton megalobotrys* and *A. nigrescens* was higher in Moremi than in Seronga, while that of *Diospyros mespiliformis* and *P. violacea* was higher in Seronga than in Moremi (Table 4). This implies that *C. megalobotrys* and *A. nigrescens* were highly disturbed in Seronga than in Moremi while *D. mespiliformis* and *P. violacea* were highly disturbed in Moremi than in Seronga.

Table 4: Tree/shrub ratio of common riparian species in Moremi and Seronga.

Sites		
Species	**Moremi**	**Seronga**
Croton megalobotrys	4.1	0.3
Acacia nigrescens	2.5	0.9
Diospyros mespiliformis	0	1.3
Philenoptera violacea	0.73	4.0

The regression slope showed no on-going regeneration of *Croton megalobotrys* and *A. nigrescens* in Moremi and a weak on-going regeneration in Seronga. *Diospyros mespiliformis* and *P*. *violacea* showed weak regeneration in all the sites (Table 5).

Table 5: Regression analysis slope coefficients for different tree species in Moremi and Seronga.

	Sites	
Species	**Moremi**	**Seronga**
Croton megalobotrys	0.399*	-0.252
Acacia nigrescens	0.862	-0.347*
Diospyros mespiliformis	-0.469*	-0.215
Philenoptera violacea	-0.290*	-0.381

*Significant at $p<0.05$

Comparison of the regeneration structure between the two land use types indicates that *Croton megalobotrys* populations had a J shaped regeneration structure in Moremi (Figure 2A) and an irregular structure in Seronga (Figure 2B). *Philenoptera violacea* showed a reverse J shaped structure in both sites (Figure 2C and 2D). However, in Seronga (Figure 2D) the population had a missing height class at 1-2m.

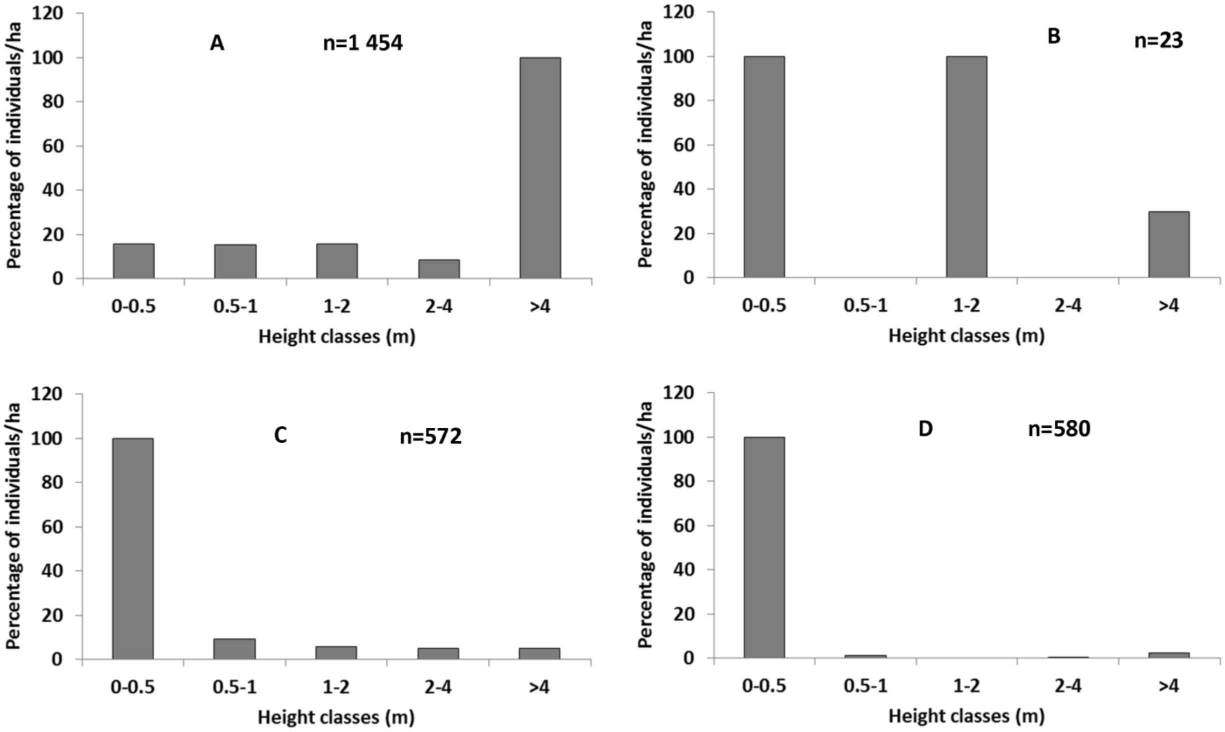

Figure 2: Regeneration structure of *Croton megalobotrys* (A: Moremi, B: Seronga) and *Philenoptera violacea* (C: Moremi, D: Seronga) in Moremi and Seronga.

Acacia nigrescens populations had a J shaped regeneration structure in Moremi (Figure 3A) and reverse J shaped pattern in Seronga (Figure 3B). *Diospyros mespiliformis* populations were characterised by an unstable regeneration structure in both sites. In Moremi they had only two size classes at 0-0.5m and 0.5-1m and were missing individuals in the 1-2m, 2-4m and >4m size classes (Figure 3C), while in Seronga there was a U shaped size class distribution pattern (Figure 3D).

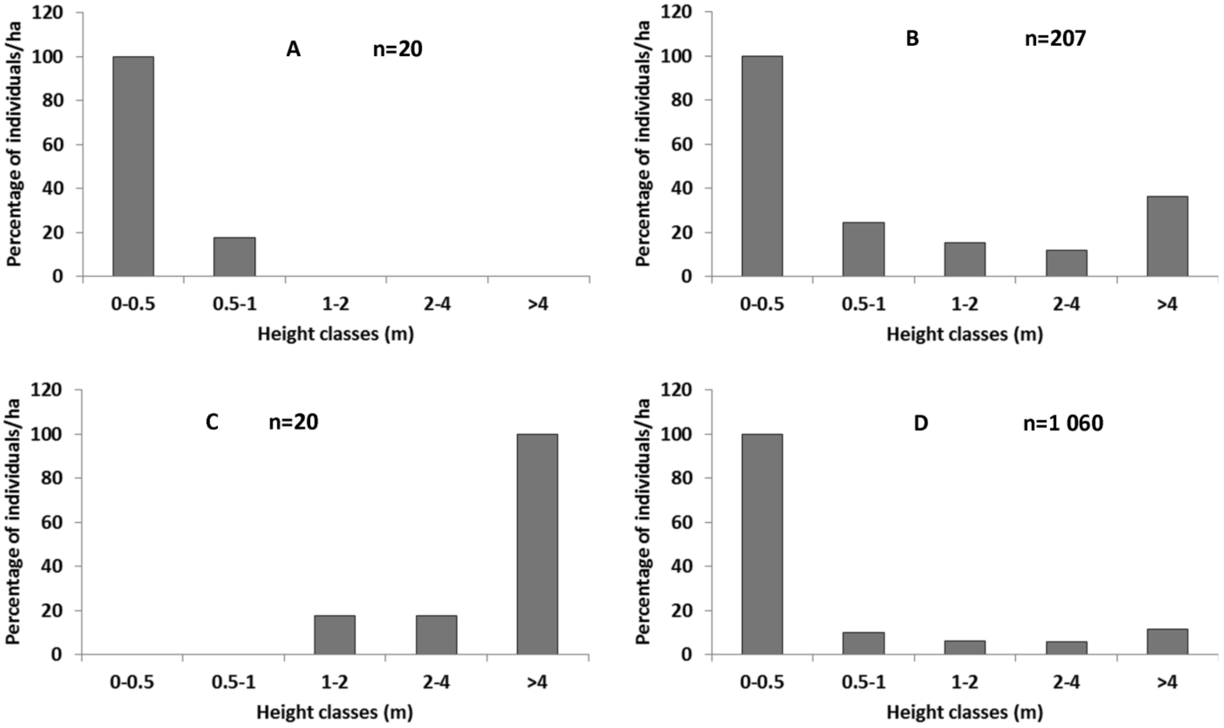

Figure 3: Regeneration structure of *Diospyros mespiliformis* (A: Moremi and B: Seronga) and *Acacia nigrescens* (C: Moremi, D: Seronga) in Moremi and Seronga.

Discussion

From the present study it was evident that riparian tree species in study areas with different land uses showed a wide variation in regeneration dynamics. This was further corroborated by the observed different densities of seedlings and saplings and tree/shrub ratios of the riparian tree species between the different land use types. The overall regeneration structures of the riparian tree species studied were also different between the two land use types. Specifically, land use type had an influence on the regeneration of *D. mespiliformis* and *P. violacea* as shown by their higher tree/shrub ratios in Seronga than in Moremi. These observations indicate low disturbance due to the predominance of tree-sized individuals of these species in Seronga compared to Moremi. Contrary to the metrics exhibited by *D. mespiliformis* and *P. violacea* populations, the tree/shrub ratios of *C. megalobotrys* and *A. nigrescens* were higher in Moremi than in Seronga. This implies that *C. megalobotrys* and *A. nigrescens* populations were less disturbed in Moremi Game Reserve than in Seronga. High tree/shrub ratios indicate low disturbance by showing that there were more individuals of tree size than of shrubs (Gurmessa et al. 2012).

The seedling densities of *D. mespiliformis* and *C. megalobotrys* were not influenced by land use, as they did not differ significantly between Moremi and Seronga. This implies similarities in the seed dispersal efficiency and germination rates for these species across the two land use types. Conversely, the seedling densities of *P. violacea* and *A. nigrescens* appear to be influenced by land use as they were significantly more seedlings in Seronga than in Moremi. This could suggest that the environmental bottlenecks that impede the germination and survival of seeds of these two species were more pronounced in Moremi than in Seronga. This is particularly true for

A. nigrescens which had no seedlings in Moremi. Factors associated with land use which may result in the removal of seedlings of *A. nigrescens* and *P. violacea* seedlings in Moremi include herbivory by browsers such as impala and kudu (Barnes 2001). This observation is consistent with a previous study conducted in the Chobe area, northern Botswana which found that trampling by zebra, buffalo and wildebeest, and browsing by giraffe, impala and Kudu caused damage to seedlings of tree species (Ben-Shahar 1996). This is also true for *P. violacea* in Moremi because there was evidence of trampling on seedlings by herbivores. The absence of seedlings of *A. nigrescens* may suggest that they were either completely killed by grazing and trampling by herbivores or there was no germination at the time of this study probably due to lack of seeds.

In terms of regeneration structure, *D. mespiliformis* showed a U-shaped regeneration pattern in Seronga, characterized by more individuals in the lower size classes than in the mid-tree-sized classes. The U-shaped regeneration pattern may be an indication of episodic recruitment which might be caused by a severe prolonged drought that causes mortality of an entire cohort of plants of this species (Helm and Witkowski 2012; Traore´ et al. 2012). In episodic recruitment there is variation in terms of growth of individuals across different size classes between the years (Helm and Witkowski 2012). This could be an indication that in the past there was recruitment of individuals from the lower size classes (Helm and Witkowski 2012). This may result from the selective removal of individuals in the middle size classes before they are recruited into the next growth stage (Gurmessa et al. 2012). The removal of individuals in these classes in Seronga may result from herbivory and cutting of trees for poles to use in the construction of kraals and homes. Herbivory by elephants has been shown to cause deaths of individuals as a result of ring barking of individual trees (Ben-Shahar 2001) as observed in Seronga during this study. Another form of herbivory may be by livestock feeding and trampling on seedlings and saplings. The current U-shaped regeneration structure of *D. mespiliformis* may also depict the historical use of the species. In the past it was one of the riparian tree species used for the construction of canoes (Ecosurv 1988). In Moremi, the regeneration of this species was characterized by two classes of 0-0.5m to 0.5-1m. There were no individuals observed in 1-2m, 2-4m and >4m classes. The missing size classes indicate low recruitment of seedlings of *D. mespiliformis* into the large height classes (Traore´ et al. 2012). This phenomenon was supported by the species weak negative regression slope in Moremi. Generally, the negative regression slope of height classes indicates that there is on-going recruitment (Shackleton 1993). However, a weak slope shows that the recruitment is very low as indicated for *D. mespiliformis*.

Croton megalobotrys had an irregular regeneration structure with missing individuals in 0.5-1m and 2-4m height classes in Seronga while it exhibited a reverse J-shaped pattern in Moremi. Land use also had an influence on the regeneration structure of *A. nigrescens* which was characterized by a J-shaped pattern in Moremi. These population structures reflect a poor reproduction and recruitment (Gurmessa et al. 2012) which may be caused by herbivory from wildlife and agricultural and human settlement. The poor recruitment of these species in Moremi is also shown by positive regression slopes of regeneration which indicate poor (weak) regeneration (Shackleton 1993). The missing individuals of *A. nigrescens* in 0-0.5m and 0.5-1m height classes in Moremi may have resulted from trampling by wildlife herbivores. Damage on *A. nigrescens* was mainly from ring barking by elephants. The J-shaped regeneration structure may be an indication that it might experience local extinction in the future as the old, dying trees will not be replaced. This result is in agreement with Helm and Witkowski (2012) who reported that the J-shaped regeneration pattern indicate that there are few individuals in the lower size classes to replace older trees when they die.

Philenoptera violacea showed a healthy reverse J-shaped pattern in all the sites. The reverse J-shaped regeneration is regarded as healthy because individuals in the lower size classes grow and replace those that die in the larger size classes (Mwavu and Witkowski 2009). This regeneration pattern also shows that individuals are selectively removed in the subsequent height classes (Senbeta and Teketay 2003; Gurmessa et al. 2012). This is particularly true for *P. violacea* in Seronga which did not have individuals in the 1-2m size class while the 0.5-1, 2-4 and >4 classes had very few individuals. The death of individuals may have negatively affected its regeneration structure as shown by a weak negative regression coefficient. In Seronga the cutting of mature individuals of *P. violacea* is probably for the production of poles used for the construction of kraals and huts. Furthermore, in the past this species was used for the construction of mekoro (Ecosurv 1988). The extent of mekoro carving in Seronga at the moment is not known. However, it is expected to reduce with the use of modern fibre glass and aluminium boats for which reason the current regeneration structure of *P. violacea* in Seronga may be a reflection of the disturbance it experienced in the past.

The removal of seedlings of *P. violacea* could be due to herbivory by goats and cattle while the bigger trees were probably destroyed by elephants and other factors. *Philenoptera violacea* had significantly lower seedling densities in Moremi than in Seronga which suggests that they could be browsed and trampled by wild herbivores such as Kudus, Buffaloes and Elephants. These results are supported by Hamandawana (2012) who found that elephants initiate spatial expansion of bush by selective destruction of mature trees. Mathooko and Karuiki (2000) also found that herbivory disturbed the regeneration of tree species in Njoro, Kenya. The impact of elephant damage was also observed in the Miombo forest in the Zambezi valley in Zimbabwe where the regeneration of trees was negatively affected (Cumming et al. 1997). In this area woodland species in the >3m regeneration class were lower in areas heavily affected by elephant damage (Cumming et al. 1997). The results of this study are also consistent with those from the Kruger National Park where it was suggested that high elephant herbivory led to an unstable population structure of *Sclerocarya birrea* (Helm and Witkowski 2012).

The causes of the unhealthy regeneration structure of *C. megalobotrys* in Seronga were more likely to be caused by environmental instead of anthropogenic factors. The species was expected to have a stable structure because it is not commonly used for construction because it is not strong (Heath and Heath 2009). *Croton megalobotrys* is also not preferred by browsers as it produces toxins that repel herbivores (Hamandawana 2012). Herbivores can only influence its regeneration structure through trampling on the seedlings. Unidentified caterpillars observed feeding on *C. megalobotrys* which may have a negative influence on its regeneration structure by killing the seedlings through defoliation. The missing individuals at 0.5-1m could be due to death as a result of unfavourable environmental conditions such as prolonged drying as they require moisture for their survival at this growth stage when their roots are not yet developed enough to reach for deep seated underground (Pettit and Froend 2001).

Croton megalobotrys also showed an unstable J shaped regeneration structure in Moremi characterized by few individuals in the lower height classes. This observation is in agreement with the fact that its regeneration structure may not be influenced by anthropogenic disturbances. The J shaped structure suggests the species experiences intermittent recruitment of individuals from the lower height classes into the larger height classes in Moremi Game Reserve (Gurmessa et al. 2012). This episodic recruitment may be driven by processes such as flooding. This suggests that seedlings of *C. megalobotrys* germinated during years with favourable moist conditions and were recruited into the mature stands. However, during dry periods, the recruitment of seedlings into the mature trees was probably minimized hence the current J shaped regeneration pattern. This may also be influenced by the intra and inter-annual flooding variations (Wolski et al. 2006) experienced by the Okavango Delta. That is, if the germination of seedlings is followed by dry periods then their recruitment into the next stage will be minimal (Pettit and Froend 2001).

In addition to land use, flooding in Seronga and Moremi may be the confounding factor that influences the regeneration of riparian tree species in the Okavango Delta. The Delta is characterized by both intra- and inter-annual variation of flood magnitude (Wolski et al. 2006). Historically, inflows in the Delta were high between 1963 and 1969 and declined to a minimum in 1995-1996 (Mazvimavi and Wolski 2006), rising again to a maximum in 2010-2011. These variations may affect the regeneration of riparian tree species as dry conditions and extreme flooding have been observed to result in low moisture and anoxic conditions respectively which impede the germination of woodland species (Jones et al. 1994). The effect of extreme flooding on regeneration was by Irvine and West (1979) in the Escalante River of Utah where death of the individuals of riparian tree species were attributed to anoxic conditions. In a comparative study conducted in the temperate Blackwood River and the subtropical Ord River, Pettit and Froend (2001) found that drying resulted in unstable population structures in riparian tree species as it prevents individuals from reaching later growth stages. The influence of flooding on the regeneration of riparian tree species was also observed in the Murray River floodplain in South Australia where the recruitment in *Eucalyptus camaldulensis* and *E. largiflorens* was episodic in response to flooding with the former being tolerant of prolonged flooding conditions while the latter preferred short flooding conditions (George et al. 2005). Our results suggest that the regeneration structure of riparian tree species in both Seronga and Moremi may also be influenced by flooding variations in the Okavango Delta while the U shaped regeneration pattern in *D. mespiliforms* in Moremi may be an indication of historical sequences of multi decadal flood variations.

Conclusion

This study has shown that land use has an influence on the regeneration structure of *D. mespiliformis*, *A. nigrescens* and *C. megalobotrys*. *Croton megalobotrys* exhibited an unstable regeneration pattern in both sites while *A. nigrescens* showed an unhealthy regeneration pattern in Seronga. *Diospyros mespiliformis* had unstable regeneration patterns in both Moremi and Seronga. These variations indicate that land use has an influence on riparian tree regeneration patterns, implying that seed dispersal, germination and recruitment processes are spatially variable. It is therefore recommended that species with unstable irregular and J-shaped regeneration patterns should be protected in enclosures to promote seed production and dispersal by reducing damage by cattle. The Seronga community and other communities around the Okavango Delta should be educated on sustainable methods of conserving riparian woodland. Future research should strive to enhance conservation by establishing the extent of use of riparian tree species in the Delta by the local human communities and quantify the influence of herbivory and short and long term flood variations on riparian tree species.

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The population structure and species composition of riparian plant communities in the Okavango Delta, Botswana: A Synthesis.

8.0.0 Introduction

Globally, riparian plant communities are important for provision of food (Schulz and Leininger, 1990), water and shade which regulates temperature (Daily, 1997). Riparian plant communities are also important in reducing soil erosion and flood damage in riverine and wetland habitats (Carter, 1996) and serve as bio-filters which improve water quality in aquatic environments (Reddy and Gale, 1994). In the Okavango Delta, riparian woodland species play the additional critical role of maintaining the fresh water surface ecosystem through evapo-transpirative sequestration of solutes (McCarthy et al. 1998). Despite their importance, riparian plant communities are globally and locally threatened by climate change (Malmqvist and Rundle, 2002), land clearing for agriculture (Porto and Clover, 2003) and over exploitation/harvesting of the veld products (Matiza and Chabwela, 1992). In order to conserve riparian plant communities, there is need to understand their ecological functioning, community composition and establish the status of their population and regeneration structures. The information generated will be used to guide policy on the conservation of these communities.

In the Okavango Delta there is still a complete lack of information on the species distribution and community composition of riparian trees, and status of their population structure and regeneration processes. The current study aimed at filling this knowledge gap. Its general aim was to assess the population size structure, species composition and distribution of riparian woodland communities in the Delta. The specific objectives were to record and analyse:

- Riparian plant community species composition and distribution
- The spatial variation of species population size structure
- The influence of land use on regeneration structure
- The influence of surface water proximity on community composition, distribution and structure
- The influence of flooding frequency on composition and distribution in the Delta.

This chapter provides a synthesis of the information generated in this study. It is intended to bring the ideas together and give an integrated summary of the ecology of the riparian woodland vegetation in the Okavango Delta.

8.1.0 Classification of riparian plant communities in the Okavango Delta

Four major riparian woodland communities identified in the Okavango Delta were: *Croton megalobotrys-Hyphaene petersiana, Acacia erioloba-Diospyros lycioides*, *Garcinia livingstonei-Acacia nigrescens* and *Syzygium cordatum-Phoenix reclinata* (Chapter 2). These different plant assemblages were related to the adaptation of the different tree species to varying hydrologic and other environmental regimes, in a similar manner as has been documented elsewhere (e.g., Kozlowski, 1984; Sparks, 1995; Capon, 2005). This was supported by the results of chapter 3 in which plant community composition was shown to vary along a large-scale gradient of flooding frequency. Riparian plant communities identified in the Delta along the flooding frequency gradient were (Figure 1): *Hyphaene petersiana-Diospyros mespiliformis* and *Philenoptera violacea-Gymnosporia senegalensis* in Boro (Low flooding frequency), *Croton megalobotrys-Hyphaene petersiana* and *Acacia erioloba-Ziziphus mucronata* in Moremi (Low flooding frequency), *Phoenix reclinata-Syzygium cordatum* and *Garcinia livingstonei-Searsia tenuinervis* in the Upper Panhandle (High flooding frequency), *Garcinia livingstonei-Phoenix reclinata* and *Grewia flavescens-Phyllanthus reticulatus* in Jao (Intermediate flooding frequency). In Seronga (High flooding frequency) woodland communities were *Elaeodendron transvaalense-Dovyalis caffra* and *Syzygium cordatum-Searsia tenuinervis*.

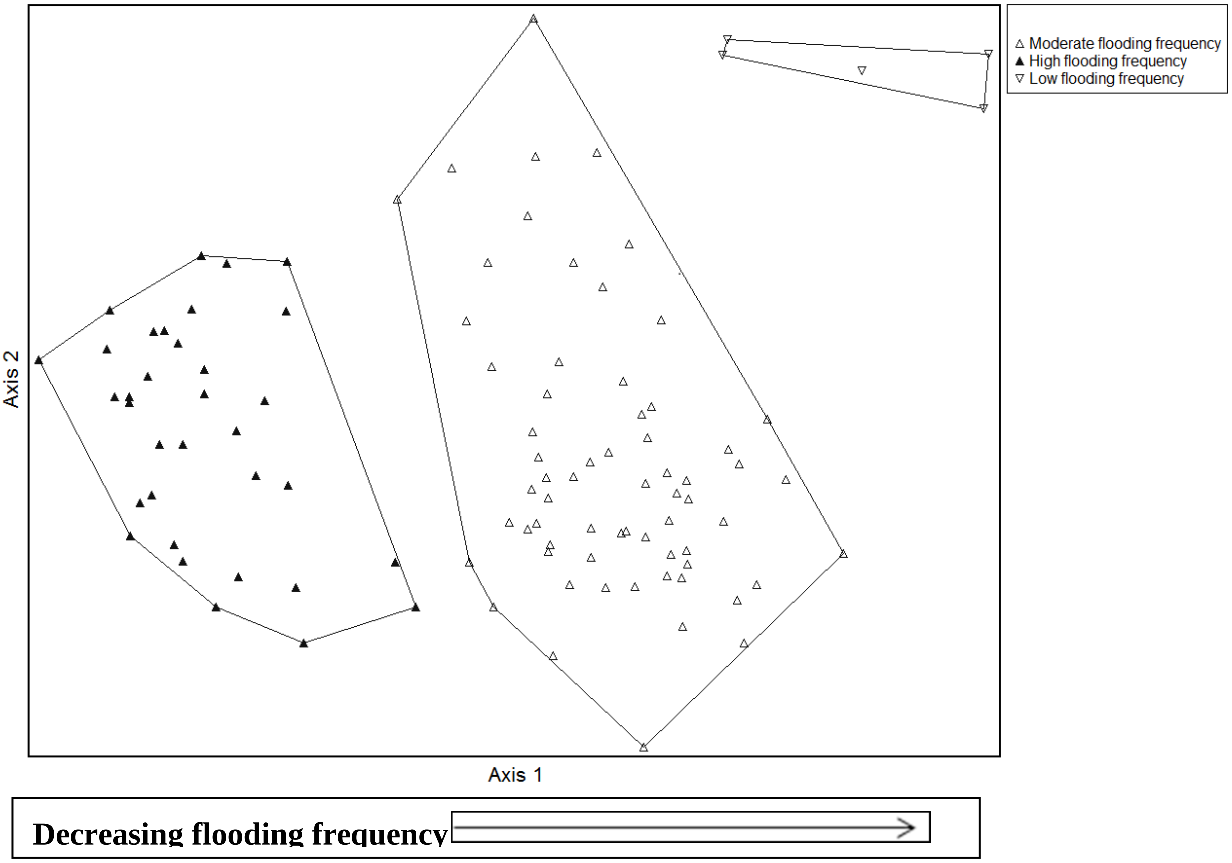

Figure 1: Different plant community assemblages along flooding frequency gradient in the Okavango Delta Botswana

The different plant community assemblages therefore show that flooding variation in the Okavango Delta is important in maintaining a heterogeneous ecosystem and as a result it should not be modified by any anthropogenic activities for the sustenance of woodland resources. The results of chapters 2 and 3 were further supported by the findings of chapters 4 (within-site variation) and 5 (inter-site variation) in which spatial variation was found in community composition, distribution, species diversity, species richness, tree height, mean percentage cover and mean basal area with distance from surface water across different sites. This variation is attributed to the varying tolerance (or conversely, ability to access and utilise) of individual species of groundwater depth or soil moisture availability along the lateral gradient away from surface water. In the Okavango Delta groundwater depth increases with distance from surface water due both to the high evapo-transpiration losses caused by the water dependent riparian trees (McCarthy, 2006) and the permeability characteristics of the substrates.

The influence of flooding on plant community composition and distribution functionally similar to those in the Delta has been documented in other semi-arid riparian ecosystems elsewhere. Medina, (1986) in Mexico, Roberts and Ludwig, (1991) in River Murray in Australia, Lyon and Sagers (2002) in the Ozark National Scenic river ways in Missouri and Fousseni et al., (2011) in the Galangashi-Barkolsii region also found different plant species assemblages along flooding frequency and duration gradients in riparian regions. These rivers have similar hydrologic behaviour as the Okavango Delta. They experience variation in their inflow over short and long periods of time. The river Murray experiences mean annual rainfall of about 250mm and seasonal variability in inflow (Roberts and Ludwig, 1991). The Ozark National Scenic River is characterized by seasonal flooding and annual and inter-annual variation in inflows (Lyon and Sagers, 2002). This could explain the similarity in response of vegetation in terms of composition and distribution as found in the Okavango Delta. In both systems vegetation is distributed along the hydrologic conditions to which they are adapted.

In terms of the influence of flooding frequency on riparian plant species composition and distribution (Chapters 3-5) this study is consistent with Stromberg, (1993) and Pollock et al. (1998) who also found that there was an increase in species diversity at sites that experienced intermediate levels of flooding disturbance. In a riparian forest of the Rio Paraguai in the Pantanal of Brazil, Damasceno-Junior et al. (2005) also found that flood intolerant species occupied highly elevated and occasionally flooded regions (remained non-flooded for 23 years) while flood tolerant species inhabited regularly flooded regions as in the Okavango Delta. Vegetation zonation along hydrological gradients in the Delta was similar to that found by Stromberg et al. (1996) in the San Pedro river in Arizona, U.S.A, Shafroth et al. (2000) in the Bill Willams River in North America and Baird et al. (2005) in the South Fork Kern and San Pedro Rivers who found that woodland plant species tolerant of wet conditions and high ground water levels were dominant at sites closer to the river bank while those that prefer dry conditions and adapted to low groundwater level dominate sites far from the river bank. These similarities suggest that riparian plant species respond similarly in response to flooding across the different riparian ecosystems. This could be due to the similarities in terms of hydrologic conditions that prevail in these sites and the Okavango Delta. Generally the depth to groundwater increases with increasing distance from surface water in the Pantanal (Damasceno-Junior et al. 2005) and the San Pedro River (Stromberg et al. 1996) as it happens in the Okavango Delta (McCarthy et al. 1994).

Other environmental variables that may influence riparian plant community composition and distribution in the Delta include fire, herbivory and drought (Walker et al. 1986). However, these may be overridden by flooding. Though not quantified, the influence of these variables on Delta riparian woodland communities was observed during this study. Both recent and old fire signs were observed. For instance in Jao, the *Garcinia livingstonei-Phoenix reclinata* community was heavily burnt during the time of this study (Figure 2).

Figure 2: Fire could be one of the factors influencing riparian plant species composition and distribution in the Okavango Delta. *Stands of Phoenix reclinata-Syzygium cordatum were burnt in Jao in 2014.*

Herbivory and physical damage through felling of trees and ring barking by the elephants was also observed during this study (Figure 3). Species that were mostly affected by herbivory and damage were *Dovyalis caffra*, *Diospyros mespiliformis*, *Acacia nigrescens*, *Phoenix reclinata*, *Garcinia livingstonei* and *Philenoptera violacea*. The damage caused by elephants may influence plant species composition by selecting against some species and excluding it locally. Alternatively, the removal of some species by elephants may open up new colonization spaces and opportunities for new ones especially if the removed species suppressed the growth of others.

Figure 3: Elephant damage to riparian plant species in Seronga in the Okavango Delta. *Note the destruction of elephants on Phoenix reclinata and Philenoptera violacea.* Picture by Mr Mmusi Mmusi.

8.1.1 Up-scaling of the response of riparian plant community to distance from surface water to the whole of Okavango Delta.

Overall all plant characteristics except for species richness differed significantly between different distance classes (Figure 4 and Table 1).

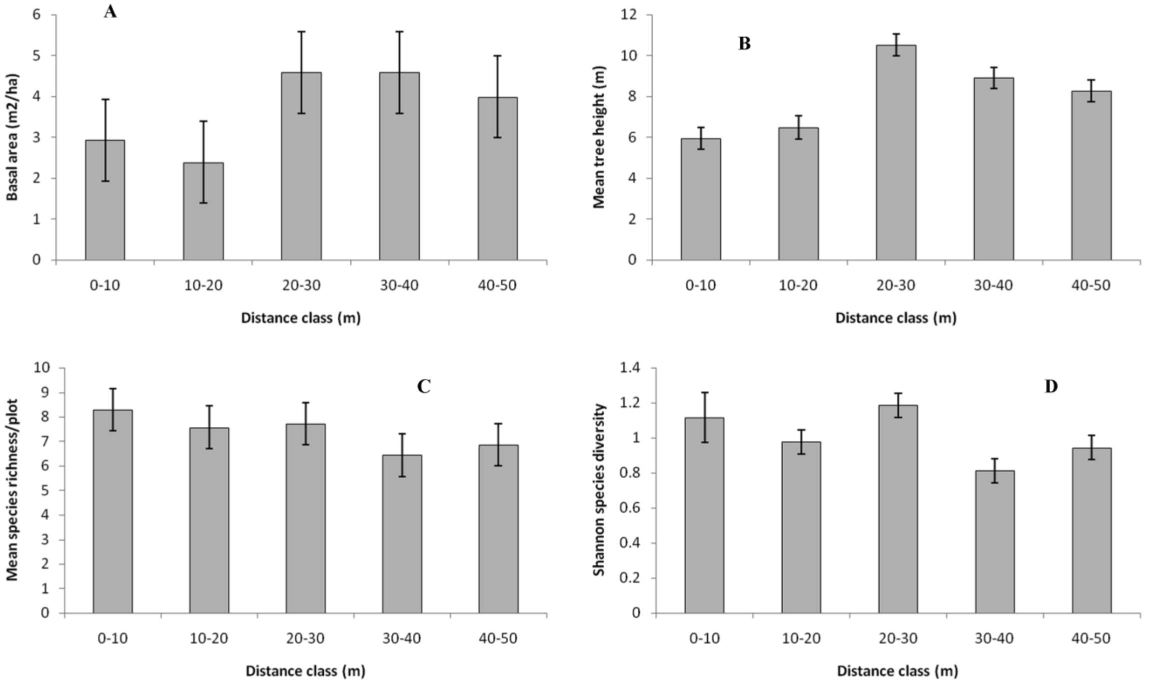

Figure 4: Variation of mean (±SD) basal area (A), tree height (B), species richness/plot (C) and diversity (D) with distance from surface water in the Okavango Delta.

These differences were attributed to individual plant species tolerance of depth to groundwater along the lateral gradient from surface water as already discussed in the previous section. This emphasizes the influence of hydrology on species composition and distribution of riparian plant communities. It implies that inflows to the Delta should not be changed, in their range of variation, the rate of variation and the distribution of that variation within and between years and between decades.

Table 1: Woodland vegetation communities, mean percentage cover (±SD) and seedling density (±SD) at each distance class.

Distance class (m)	**Riparian plant community**	**Mean percentage cover**	**Mean seedling density (Individuals/ha)**
0-10	*Croton megalobotrys-Gymnosporia senegalensis*, *Syzygium cordatum-Phoenix reclinata*	58±1.02*	5 745±177*
10-20	*Croton megalobotrys-Hyphaene petersiana*, *Phoenix reclinata-Syzygium cordatum*	45±1.63	3 130±779
20-30	*Croton megalobotrys-Philenoptera violacea*, *Phoenix reclinata-Syzygium cordatum*	43±1.69	3 767±158
30-40	*Croton megalobotrys-Hyphaene petersiana*, *Phoenix reclinata-Syzygium cordatum*	40±1.39	3 121±992
40-50	*Croton megalobotrys-Phoenix reclinata*, *Phoenix reclinata-Syzygium cordatum*	40±1.38	2 818±158

*Significantly different at $p<0.05$.

8.2.0 Population structures and regeneration status of riparian plant communities

Riparian tree species showed spatial variation in their population size structure. The population structure of the various species was different at different sites along the flooding frequency gradient. The population structure also varied between species within a given site (Chapter 6). The spatial variation in population structure of riparian tree species may be due to differences in their reproductive strategies, competition, hydrology and disturbance from fire and elephant damage at a given site.

In terms of regeneration, riparian tree species in the Okavango Delta showed different patterns across two different land use types: 1) Moremi Game Reserve (a protected area, characterised by wildlife); and 2) Seronga (a communal resource area, characterised by open access intense livestock grazing and resource gathering) (Chapter 7). The regeneration structure of tree species in Seronga and Moremi may be a reflection of their historical use. In the past, the riparian woodland resources in villages around the Delta were disturbed by their harvesting for firewood, cutting poles for fencing, bridge making, house building, cutting for road construction and clearing for horticultural activities (Snowy Mountains Engineering Corporation, hereafter referred to as SMEC, 1989). Moremi Game Reserve is no longer a human settlement and it used to be inhabited by the San people prior to the 1960s that were dependent on riparian woodland vegetation for their livelihood (Tlou, 1985). Since trees are long-lived, the current populations that we find in Moremi Game Reserve cannot be considered as having developed entirely free of the influence of humans. Seronga is still inhabited by humans and as a result the current population structure observed there might be a product of both the historical and current use.

In addition to the potential human impact on riparian tree species in Seronga, livestock and wild animal’s impact may also be vital in both Seronga and Moremi, respectively. Livestock and game herbivory and trampling on seedlings and saplings of the riparian tree species may prevent them from growing into trees. This may also be a product of historical influence. In the past there was a widespread of rinderpest pandemic from 1896 to the early 1940s around the Okavango Delta (SMEC, 1989). During the tsetse fly pandemic cattle and wildlife were almost wiped out in the Delta (Tlou, 1985). During this period woodland populations established (SMEC, 1989) and due to the reduced numbers of livestock and wildlife as a result of the Tsetse fly pandemic, they may have attained a healthy regeneration and population structures. Furthermore, since the tsetse fly preferred the floodplain and woodland areas, human settlements were established long distances from the Delta region (Tlou, 1985). This may also have greatly reduced the impact of human beings on the riparian tree species resulting in their successful establishment and attainment a healthy population structure. However, with the end of the tsetse fly epidemic in the 1940s (SMEC, 1989) the impact of humans, livestock and wildlife on woodland species was restored to date hence the assertion that the current population structure in the Okavango Delta could be a product of both historical and current land use. Some of the riparian plant species may have established in the period between 1896 and 1940 when there was low disturbance from livestock, wildlife and people. During this period it is predicted that the plant species attained a stable J shaped population structure. The period after the 1940s characterized by the absence of Tetsefly and increase in wildlife, human population and livestock probably marked the increased disturbance in riparian tree species resulting in unstable population structures such as J shaped, U shaped, irregular and bell shaped.

The results of this study also suggest that seed dispersal, germination and recruitment processes that influence the population and regeneration structure of riparian tree species vary spatially. This implies that a heterogeneous landscape and hydrological regime must be maintained for tree species to have healthy population dynamics. In the Delta both short and long term flooding and rainfall variation may have an influence on the population structure of riparian tree species. Historically inflows in the Delta were high between 1963 and 1969 and declined to a minimum in 1995-1996 (Mazvimavi and Wolski 2006), rising again to a maximum in 2010-2011 (Figure 5).

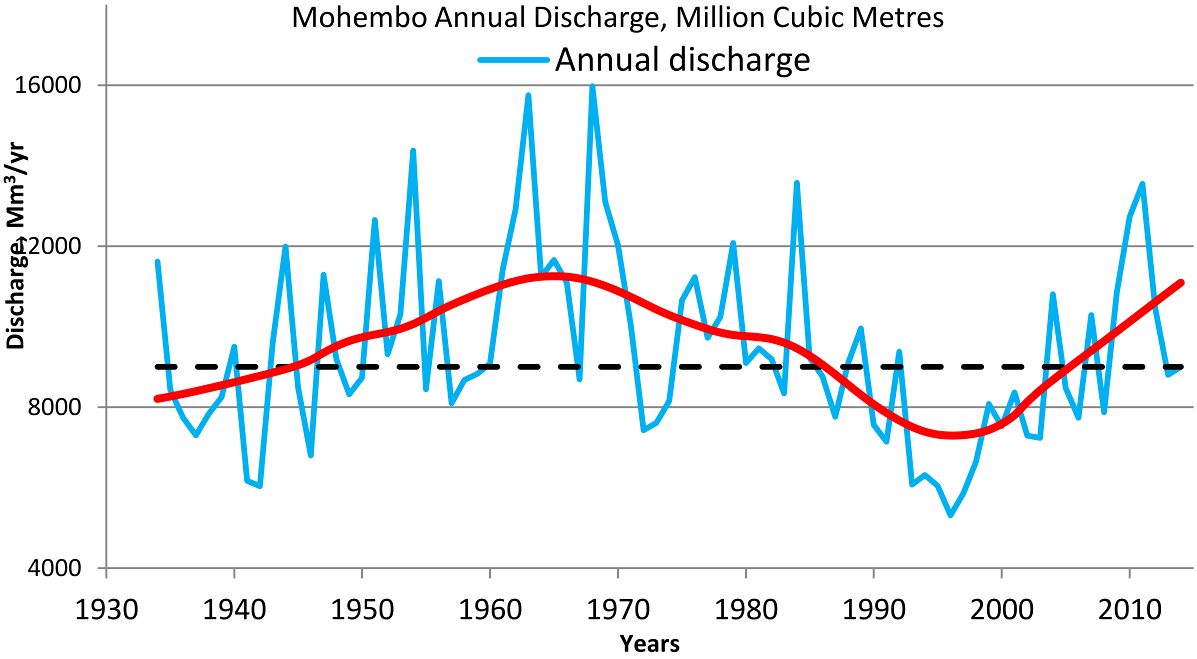

Figure 5: The quasi-cyclicity between multi-decadal wet and dry periods in the Okavango Delta, Botswana. *Inflow data measured at Mohembo*. Data was provided by Department of Water Affairs, Maun, Botswana.

The quasi-cyclicity between multi-decadal wet and dry periods (Wolski et al., 2012) could pose an episodic disturbance which may prevent the establishment of stable states in riparian tree species instead inducing periods of high or low recruitment. The flooding variation and rainfall may affect the population structure of riparian tree species as follows: the intra-annual flood variation and seasonal rainfall may trigger seed germination if the water reaches the riparian zone. In order for their seedlings to grow into the next stage and eventually establish as fully grown trees they require adequate moisture supply (Traoré et al. 2008). Therefore, if germination is followed by several years of high flooding and rainfall to supply adequate moisture to the seedlings of these species, they may then be recruited into the next growth stage. However, if germination is followed by years with relatively low floods (and low rainfall) or extremely high flooding then the seedlings may die before they are recruited into the next growth stages. This is because both dry and extreme flooding conditions result in low moisture and anoxic conditions, respectively which may impede germination of woodland species (Jones et al. 1994).

The Okavango Delta experienced high floods between the 1960s and 1970s which may have promoted massive recruitment in riparian plant species as a result of favourable hydrologic conditions. However, this recruitment may have stopped in response to dry conditions that occurred in the period between 1980s and 1990s. The period between 2008 and 2010 was also characterized by the return of high floods which might have once again triggered massive recruitment in riparian plant species. In the current study, it is possible that individuals in the larger size classes of *Philenoptera violacea*, *Garcinia livingstonei*, *Diospyros mespiliformis*, *Kigelia africana*, *Acacia nigrescens* and *Combretum imberbe* (c.f. Section 8.2.1, Figure 8) were recruited during the wet periods of the 1960s, 1970s and 1980s. The large dbh classes of 50-60cm, 60-70cm and >70cm represent big individuals with stem circumferences ranging from 157cm to over 220cm. To amass this size trees must have taken a lot of time dating back from the 1960s or even before that. Individuals in the middle size classes of these species are likely to have been recruited during the wet period of the 1990s while individuals in the smaller dbh classes may have been recruited around the 2000s. However, these are only assumptions. Only future studies on the estimation of ages of the stands of the riparian woodland vegetation may give us good estimations on the historical recruitment period of the tree species in the Okavango

Delta. The influence of flooding on regeneration was also observed in the Escalante River, Utah by Irvine and West (1979) who recorded dead individuals in riparian tree species which was attributed to anoxic conditions. Pettit and Froend (2001) in a comparative study conducted in the temperate Blackwood River and the subtropical Ord River in Australia found that drying resulted in unstable population structure in riparian tree species as it prevented individuals of *Eucalyptus camaldulensis* from reaching later growth stages. Episodic recruitment influenced by hydrological conditions was also reported in the River Murray floodplain in South Australia where recruitment in *E. camaldulensis* and *E. largiflorens* was episodic in response to flooding. *Eucalyptus camaldulensis* and *E. largiflorens* preferred prolonged flooding conditions and short flooding conditions respectively (George et al. 2005).

The population structure of riparian tree species in the Delta may also be an indicator of the return periods of multi-decadal events/shocks, such as main channel blockage. Channel blockage may influence the population structure of riparian tree species in the Delta through its influence on hydrology. This occurs as a result of bedload deposition which results in vertical aggradation of the sediment load (McCarthy et al. 1992) and vegetation blockage (McCarthy et al. 1997, c.f. Figure 6). Reduced water flow results in vegetation blockage as a result of the reduced ability of the channel to transport bedload, to maintain its cross-section and to move floating material

(McCarthy et al. 1997).

Figure 6: Channels may be blocked by plant debris in the Okavango Delta. *At the initial stage water continues to flow below the plant debris but over time as more plant matter is trapped the channel water flow reduces and in some cases stops completely*. Picture supplied by Mr Mmusi Mmusi.

Historical examples of blocked channels in the Delta include Nqoga and Gomoti (Snowy Mountains Engineering Corporation, 1989; c.f. Figure 7). The Nqoga channel is the primary distributary of flow to other major channels in the Okavango Delta (SMEC, 1989) and its blockage may negatively impact on the vegetation communities along it and in the downstream areas.

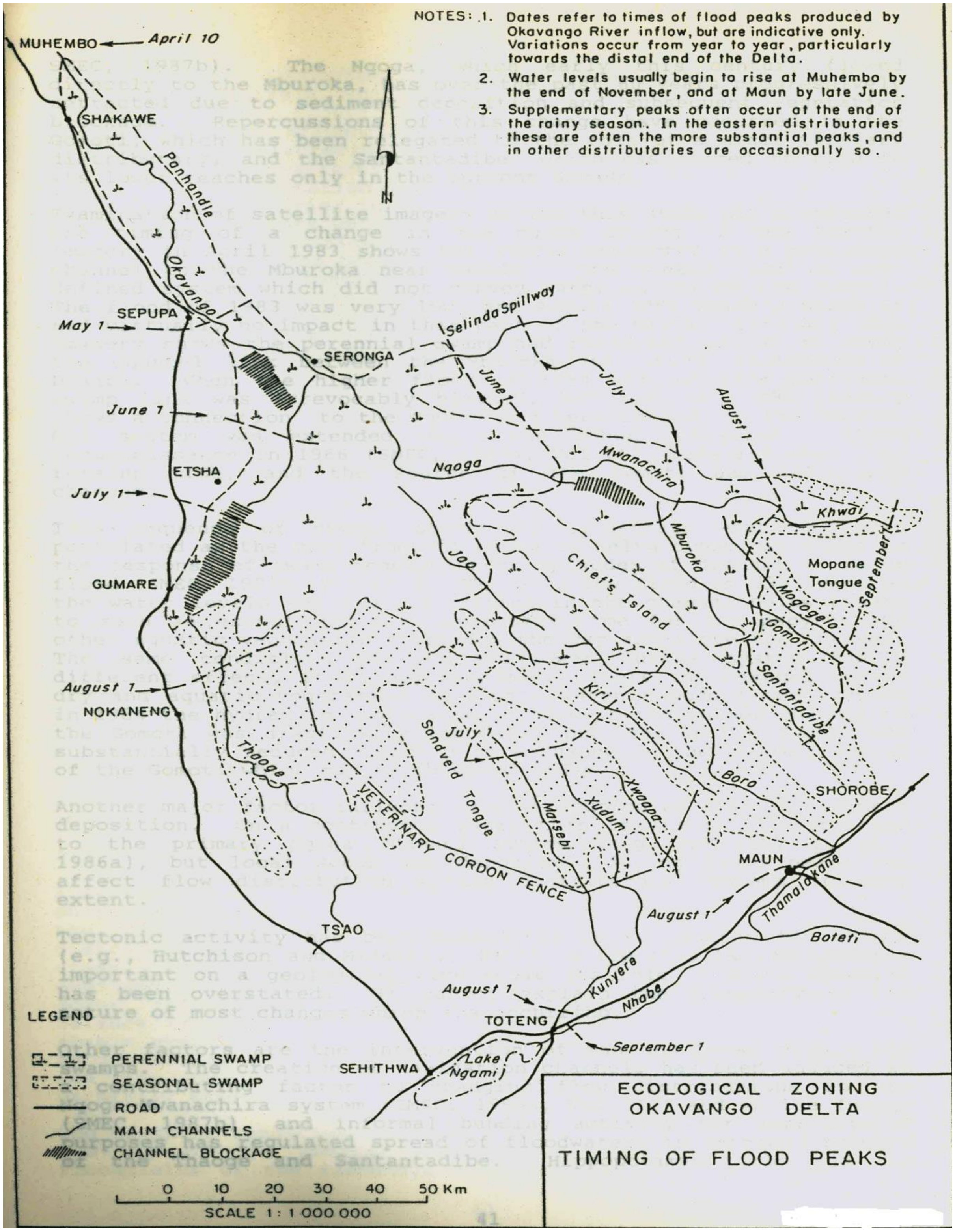

Figure 7: Historical major channel blockages and dates for flood peaks in the Okavango Delta (Snowy Mountains Engineering Corporation, 1989). *Note the blockage of the Nqoga channel. The Thaoge channel was also blocked around the Gumare area.*

Channel blockage may have an influence on the population structure of riparian woodland plant species. The effect of the progressive rise in water levels in failing sections of the channel is to lift the saline groundwater in close proximity to the soil surface, where soils on the small islands in the permanent swamps rapidly become completely toxic to all plant life, with last species being grasses like *Sporobolus spicatus* and Imperata *cylindrica* (McCarthy et al. 1997). In this study flooding frequency (Chapter 3) and distance from surface water (which influences groundwater depth) (Chapters 4 and 5) have been shown to be important factors that influence species composition and population structure of riparian plant species (Chapters 6 and 7). When the channel is active, riparian plant species establish in the hydrologic microsites characterized by different flooding frequency (Chapter 3) and depth to groundwater which they are adapted along the lateral gradient from surface water (Chapters 4 and 5). This is also expected to have an influence on the population structure of riparian plant species. During the period when the channel is active, it is expected that the riparian plant species will have a reverse J-shaped population structure with individuals skewed towards the juveniles indicating on-going recruitment (Chapter 6 and 7). However, when the channel gets blocked and its flooding ceases, the riparian plant species may show population structures such as U shaped, bell-shaped and J-shaped which are indicative of unequal recruitment between the size classes. However, this may be applicable to the species that prefer frequent flooding such as *Diospyros mespiliformis*, *Garcinia livingstonei*, *Syzygium cordatum* and *Phoenix reclinata* (Chapters 3, 4 and 5).

The U shaped structure characterized by more individuals in the smaller and larger size classes may indicate that the individuals in the larger size classes were recruited before the channel was blocked when the hydrologic conditions were favourable. However, few individuals in the middle size classes may be an indication that the recently flowing channel was blocked and the recruitment of the individuals into the middle classes stopped. An example of this was *Diospyros mespiliformis* Hochst. Ex A.DC which showed a U shaped size class distribution pattern in Boro. Another example of episodic recruitment was evident in *Croton megalobotrys* in Moremi Game Reserve where it showed a bell shaped population structure with fewer individuals in the lower and higher dbh classes than in the middle classes. High numbers of individuals in the middle classes in *C. megalobotrys* could also be due to an episodic recruitment event that probably occurred when the conditions were favourable (Hamandawana 2012). Generally the sites in Moremi Game Reserve were dry during the field survey which might have prevented the germination of *C. megalobotrys* seeds. Water from flooding or rainfall is a requirement for activating metabolic processes required for a seed to germinate (Kozlowski 2002).

Species that prefer dry and occasionally flooding conditions such as *Acacia erioloba*, *Acacia nigrescens* and *Combretum imberbe* may show J shaped population structures as the non-existence of floods may favour them because they would be able to reach the deep groundwater layers. For instance, *A. nigrescens* showed irregular size class distribution in Boro and Santawani. The irregular size class distribution could result from variable growth and unequal mortality rates in subsequent classes probably resulting from fire and elephant damage (Hamandawana 2012). This may also be a product of historical channel blockage in the Okavango Delta. While this could be the case, it should be noted that the effects of channel blockage on both set of species will be influenced by rainfall. For both sets of species, rainfall is important in promoting germination and sustains the seedlings and saplings to a point where they would be able to develop deep roots to reach for the ground water sources. Rainfall is also vital to recharge groundwater in areas that are permanently isolated from flooding due to permanent channel blockage. Furthermore, it should be noted that the effects of channel blockage will take several decades as trees take a very long periods of time to grow and respond to changes in their environment.

8.2.1 Overall trends of the population structure of riparian tree species in the Okavango Delta

Generally riparian tree species showed different population structures in the Okavango Delta. *Croton megalobotrys, Diospyros mespiliformis, Garcinia livingstonei*, *Kigelia africana, A. nigrescens* and *Syzygium cordatum* showed stable population structures while *Philenoptera violacea* and *Combretum imberbe* had unstable recruitment patterns (Figures 8 and 9).

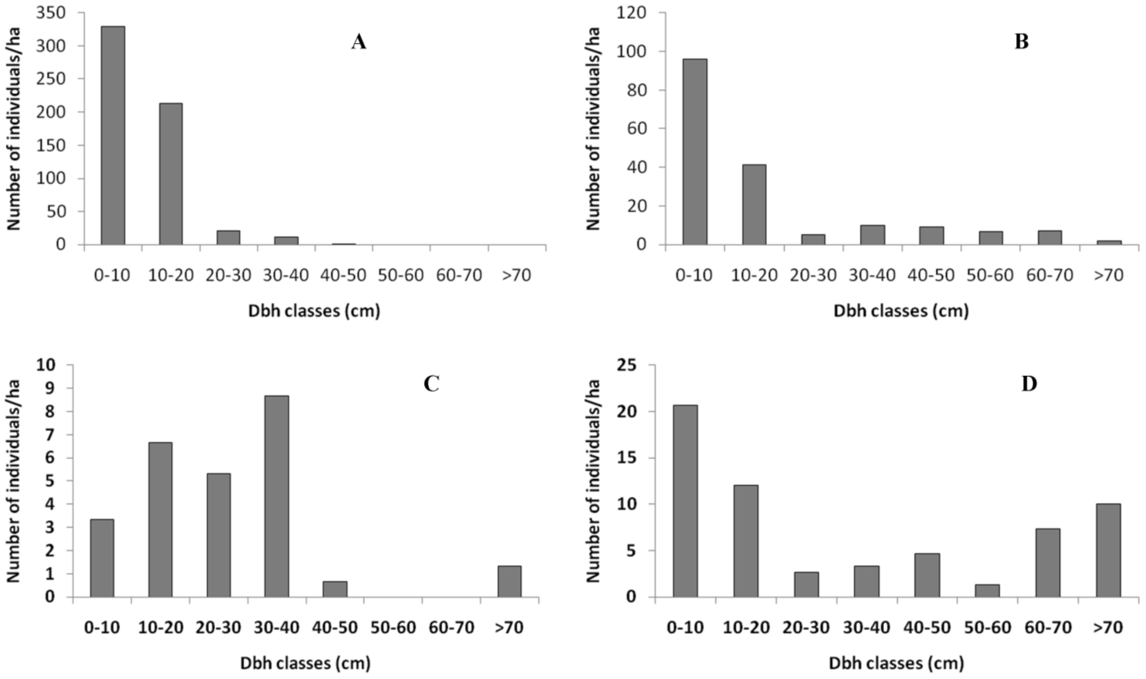

Figure 8: Population structures of *Croton megalobotrys* (A), *Philenoptera violacea* (B), *Garcinia livingstonei* (C) and *Diospyros mespiliformis* (D) in the Okavango Delta.

This reflects variation in the response of riparian tree species to different environmental conditions in the Delta. The results also show that dispersal mechanisms, germination and growth rates differ between the studied species. Environmental factors that may influence the population structure of riparian tree species are discussed in detail in chapters 6 and 7.

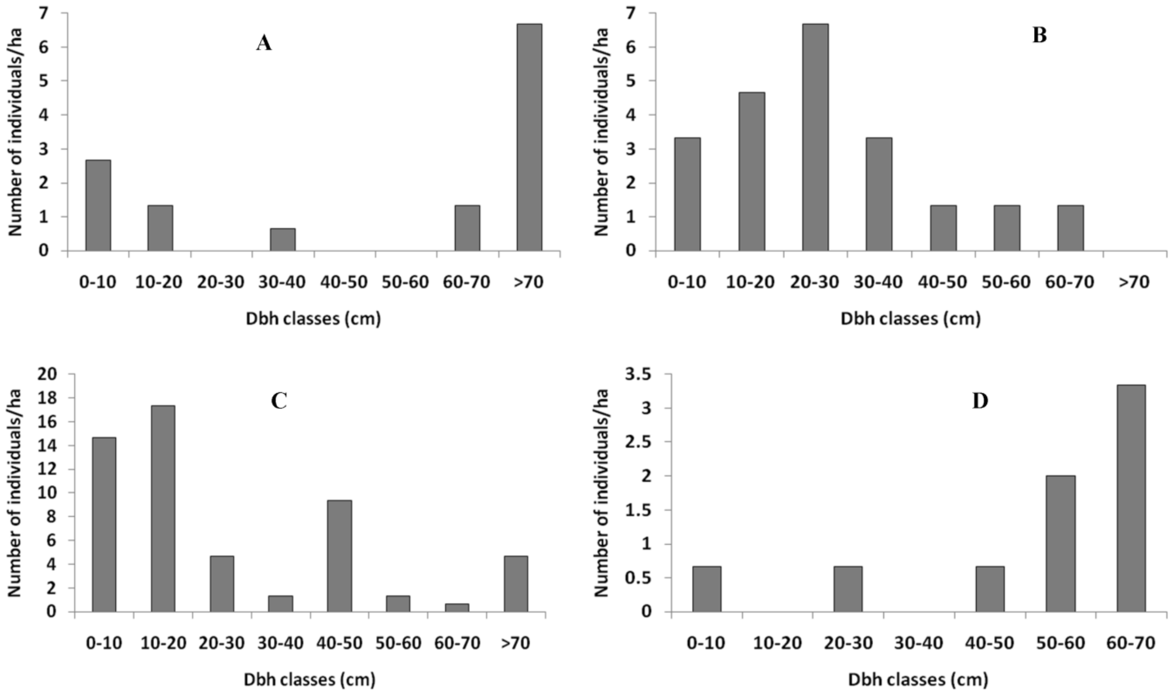

Figure 9: Size class population structures of *Kigelia africana* (A), *Syzygium cordatum* (B), *Acacia nigrescens* (C) and *Combretum imberbe* (D) in the Okavango Delta.

Summary

- Four riparian plant communities characterised by dominance of *Croton megalobotrys-Hyphaene petersiana, Acacia erioloba-Diospyros lycioides, Garcinia livingstonei-Acacia nigrescens* and *Syzygium cordatum-Phoenix reclinata* respectively were identified in the Delta (Chapter 2).

- The composition and distribution of the riparian communities in the Delta was related to flooding frequency (Chapter 3) and distance from surface water (chapters 4 and 5).
- Intra-, inter-annual and multi-decadal flood variation may also influence these riparian plant assemblages in the Delta (Chapters 2, 3, 4 and 5).
- In order to maintain a heterogeneous ecosystem in the Delta there is need for the pulsing and variable nature of flooding to prevail.
- The spatial variation in the population structures of riparian tree species suggest that their dispersal mechanisms, germination and growth rates also vary spatially.
- The population structure is likely to be the product of short and long-term flood and local rainfall fluctuations.
- Flooding and rainfall may influence seed germination and seedling establishment and future recruitment into the next growth stage.

8.3.0 Implications for management and recommendations

In order for the riparian vegetation to be sustainably used, their ecology has to be understood together with the ecological consequences of that use (Naiman et al. 1993). In the short term interests of conserving tree diversity in the Delta, consideration should be given to the establishment of a number of strategically situated enclosures to avert the threat of elephant damage and provide nuclei for seed production and dispersal.

This study has provided a baseline method for classifying riparian woodland vegetation in the Okavango Delta. In chapters 3, 4 and 5, it was shown that riparian plant species were distributed along flooding frequencies they preferred. This implies that if we know the flooding frequency of a given area we may be able to predict its species composition. The information from vegetation classification can be used to identify zones of high species richness and diversity, key habitats and disturbed areas. The current vegetation classification also provides the first attempt in providing inventory of riparian woodland plant communities in the Okavango Delta. This can be used as a vital vegetation monitoring tool. Future changes in plant species composition would either indicate changes in hydrological regime or new form of disturbance. Vegetation classification can also help to detect occurrence of any exotic species. In the current study the potentially invasive alien species *Mimosa pigra* (Mumba and Thompson, 2005) was detected in one of the plots in the Ngarange area. Even though this species has not started to behave invasively in the Delta, it may require monitoring to ensure that it does not do so in the future. It is recommended that to ensure systematic vegetation monitoring, permanent plots should be established which can be visited on a regular schedule to determine the status of the vegetation. Plot coordinates have been recorded during this study and can be readily provided to facilitate the establishment of the recommended monitoring plots.

The current study has shown that a reduction in the inflow which is likely to reduce flooding frequency in some areas of the Delta may result in encroachment of dry land woodland species. These species will be mostly *Acacia spp* such as *Acacia tortilis*, *Acacia hebeclada* and *Acacia nilotica.* Encroachment of the *Acacia* and other dry land species in the Delta will reduce its habitat quality as they are not preferred sources of forage by most of the herbivores. This may ultimately negatively affect the tourism sector which heavily depends on wildlife through game viewing for its income. Encroachment of dry land species will also negatively impact on the livelihoods of the human communities who live around the Delta and depend on fruit trees such *Diospyros mespiliformis*, *Garcinia livingstonei* and *Hyphaene petersiana* for food. This implies that the natural flow in the Delta has to be maintained.

In this study it was shown that the populations of some species in Seronga have a size class structure strongly skewed towards small individuals while others are skewed towards large individuals and others had few individuals in the middle size classes which might have resulted from overharvesting in the past. If this overharvesting continues into the future, the concerned species may locally become extinct. Local extinction will negatively affect the communities around the Delta who depend on riparian woodland species for construction poles and food. This may lead them into using alternative woody resources which they will also overharvest and eventually become locally extinct. Therefore, in order to avoid this, there is need to establish the extent of woody resources harvesting in communities around the Delta and its influence on the population structure of riparian tree species. If indeed overharvesting will be found to have a negative effect on the population structure of riparian tree species then the communities would have to be taught about the importance of sustainable use of the woody and other natural resources at their disposal.

8.4.0 Limitations of the study

- The study did not investigate the influence of other factors such as fire, soil nutrients and herbivory on the population structure and species composition of riparian palnt communities.

- The study did not assess the germination status of the soil seed bank.
- The study could not disentangle the influence of elephants on the population structure from that of hydrology.
- The study does not provide information on the long term changes in the population structure and species composition of riparian plant communities.

8.5.0 Future work

Given the critical ecological function that the riparian woodland performs in the Okavango Delta, there is need for further investigation on;

- The principal factors influencing recruitment in riparian woodlands.
- The role of dispersal and reproductive strategies that influence spatial variation on the population structure of riparian tree species in the Okavango Delta.
- The influence of hydrological variation in stimulating regenerative events of riparian plant species.
- The long term changes of the population dynamics of riparian tree species in the Delta.
- Design a study that will disentangle the influence of elephants on population dynamics from hydrological impacts.

8.6.0 Conclusion

This is the first study of population demographics of riparian trees in the Okavango Delta and the first classification of their communities. Generally, the results of this study show that flooding is an important component that influences population structure and riparian plant community composition and distribution in the Delta. This influence seems to be in both short and long term through intra and multi-decadal (including year to year) variation as shown by the response of the population structure of different species. The results suggest that a heterogeneous landscape and hydrological regime must be maintained for tree species to have healthy population dynamics. Therefore, in order to sustain the riparian vegetation communities, the seasonal flood pulse into the Okavango Delta should be maintained. The study has also shown that the riparian tree population structure varies between sites, implying that seed dispersal, germination and recruitment processes vary spatially. This variation implies that environmental variables that drive population structure in the Delta vary spatially in terms of their effect. Apart from hydrology, herbivory from elephants may also influence riparian population dynamics in the Delta. Though not quantified, destruction of elephants on trees through felling and debarking was observed during the current study. Therefore, it was difficult to disentangle the effects of elephants and flooding on the population dynamics of riparian plant communities. Future studies should consider separating the effects of these two important variables on population structure of riparian communities.

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