The Population Structure of Riparian Tree Species in the Okavango Delta, Botswana: 50 Years of Independence and Conservation

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Abstract

Riparian woodlands in the Okavango Delta play a significant role of removing salts from surface water through transpiration. This function renders surface water healthy to drink by wildlife and the people. Despite their ecological importance, very little is known about the population structure distribution of these woodlands. We attempted to address this limitation by investigating the population structure of selected riparian tree species in the Okavango Delta. Riparian woodland plots were surveyed between February 2012 and April 2013 by recording plant species in 120 plots (20m × 50m) selected randomly at each study site. The most dominant tree species were selected for assessment. Circumference (>15cm) was measured for all individuals in a plot. Individuals of different plant species were categorized into diameter at breast height (dbh) classes of 0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70 and >70cm. Linear regression was used to infer recruitment status of each species. All the species showed stable population structures except for Combretum imberbe and Philenoptera violacea. Croton megalobotrys showed an inverted J-shaped population size class distribution pattern with more individuals in the lower dbh classes. Diospyros mespiliformis had a U-shaped size class distribution pattern with more individuals in the lower and higher dbh classes and few in the middle dbh classes. Syzygium cordatum showed a bell shaped dbh size class distribution pattern with more individuals in the middle classes. Kigelia africana, Philenoptera violacea, Garcinia livingstonei and Acacia nigrescens showed irregular population structures with some dbh classes missing. Combretum imberbe showed a J shaped population size class distribution pattern. The population structures in different tree species may result from the hydrological factors acting on the germination and subsequent growth stages. These results suggest that there is need to protect the seedlings of C. imberbe and P. violacea in exclosures to promote their recruitment into large size classes.

Keywords: Recruitment, riparian woodland, vegetation dynamics, wetlands

Introduction

Riparian plant communities are found in distinct zones along elevation (Nilsson & Svedmark 2002), groundwater and flooding frequency gradients (Kalliola & Puhakka 1988). They have high habitat heterogeneity and are rich in biodiversity (Naiman *et al.* 2005). This makes them important in the hydrological cycle, water budget, soil moisture content (Chihanga *et al.* 2004) and provision of human and wildlife habitats, food and cleansing of surface water (Schulz & Leininger 1990; Reddy & Gale 1994). Recent studies show that the soil in the riparian zone serves as a filter for groundwater as it removes pollutants in the form of acids, heavy metals and pesticides (Keestra *et al.* 2012). In the Okavango Delta riparian vegetation plays a significant role of removing salts from surface water through the process of transpiration (McCarthy *et al.* 1994). This riparian tree transpiration results in a net accumulation of solutes and salts in deep layers of groundwater where they do not mix with surface water (McCarthy

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et al. 1994). Consequently, this renders surface water suitable for consumption by both animals and humans (Bauer 2004). Despite their importance, riparian tree species are threatened by deforestation (Reddy & Gale 1994), climate change and invasive species (Cronk & Fennessy 2001). In order to avert the loss of vegetation there have been measures put in place by the Government of Botswana since independence from Britain 50 years ago. These include the international listing of the Okavango Delta as a Ramsar site in 1997 (http://www.ramsar.org/sites/default/files/documents/library/sitelist.pdf) and World Heritage site in June 2014 (http://whc.unesco.org/en/list/1432). The listings are broadly meant to protect the wetland ecosystems and promote their sustainable use (http://www.ramsar.org/about/theramsar-convention-and-its-mission; http://whc.unesco.org/ en/list/1432). Locally, there have also been efforts to protect the Delta. These include the Botswana National Wetlands Policy and Strategy of 1999 which promotes public involvement in wetland management through the utilization of local knowledge and institutions (Jansen & Madzwamuse 2003). The Government of Botswana in collaboration with the United States of America (U.S.A) has also established the Tropical Forest Conservation Fund Board (TFCFB) which promotes activities aimed at conserving, maintaining and restoring forests in Botswana including the Okavango Delta (http://www.forestconservation.co.bw/). There are other efforts to protect natural resources around the Delta through Community Based Natural Resources Management (Boggs 2004). In order for all these initiatives to enhance riparian vegetation conservation, it is vital that they are informed by empirical research results of the current status of the population structure of riparian plant species. Information about the status of population structure of riparian woodland is important in guiding policy on conservation and management, especially under the current socio-economic pressures within the Okavango-Cubango basin (National Conservation Strategy Agency 2008).

While several authors have characterized riparian tree species population structures elsewhere (e.g., in South Carolina, U.S.A (Jones *et al.* 1994), Zimbabwe (Cumming *et al.* 1997), Kenya (Western & Maitum 2004), Burkina Faso (Sop *et al.* 2010), Ethiopia (Gurmessa *et al.* 2012); in the Okavango Delta, the status of riparian tree population structures has not been investigated. Earlier studies on riparian vegetation conducted in the Okavango Delta (e.g., Ellery *et al.* 1993; Ringrose & Matheson 2001) did not characterize the population structures of riparian tree species. The study by Tsheboeng & Murray-Hudson (2013) which characterized the spatial variation of the population size structure of selected riparian tree species was limited as it did not provide broad population structures of riparian tree species in the Delta. The aim of this study was to investigate broad population structures of riparian tree species in the Okavango Delta.

Materials and Methods

Study area

The study was conducted in the Okavango Delta, Botswana. The selected study sites were Upper Panhandle (21° 52′13″E, -18° 21′53″S), Jao (22°33′40″E,-19°1′′57″S), Seronga (22°17′8″E, 18°48′42″S), Boro (23°9′12″E, 19°32′27″S), Moremi Game Reserve (23°22′38″E, 19°17′9″S), Santawani (23°37′7″E, 19°32′11″S), Vumbura (22°53′41″E, 18°58′39″S) and Tubu (22°19′5″E, 19°27′45″S) (Figure 1). The selection of multiple sites was meant to have an adequate representation on population structures of selected species across the Delta. These sites are characterized by different flooding regimes. Upper Panhandle, Jao and Seronga are frequently flooded while Boro, Moremi, Tubu and Vumbura are seasonally flooded while Santawani is occasionally flooded (Tsheboeng 2016). The Okavango Delta is located in the northern part of Botswana and covers approximately 12 000 km² (McCarthy & 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 m³ per annum while annual floods from the Angolan highlands between February and May contribute about 9×10^9 m³ (Gumbricht *et al.* 2004). Flood propagation takes about 4 months to reach the Delta's downstream areas due to a low topographic gradient, with the maximum extent of flooding occurring around July and August (McCarthy 2006). The Okavango Delta experiences high evapo-transpiration ~1800mm/annum, (Snowy Mountains Engineering Corporation (here after SMEC) 1989). About 96% of the total water in the Okavango Delta is lost through evapo-transpiration, 2% is lost to deep groundwater while another 2% flows through the Thamalakane River (Ellery & McCarthy 1998).

Common woody plant species in the Okavango Delta include *Diospyros mespiliformis, Garcinia livingstonei, Ficus natalensis, Ficus 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 & Matheson 2001). There are very few flood tolerant riparian woodland species in the Delta which include *Phoenix reclinata* and *Syzygium cordatum* (Ellery & Ellery 1997). The riparian zones in the Delta are also characterized by dryland species. Examples of dryland species occurring in the riparian zones of Okavango Delta are *Combretum imberbe, Acacia tortilis* and *Colophospermum mopane* (McCarthy *et al.* 2005).

Vegetation sampling

The tree species that were selected are *C. megalobotrys, P. violacea, G. livingstonei, D. mespiliformis, K. africana, S. cordatum, A. nigrescens and C. imberbe.* These species were selected because they were common in the Okavango Delta and as such they would give representative information on the population structure of riparian plant communities. Vegetation was surveyed in the period between February 2012 and April 2013. However, this was not continuous. There were months in which we did not sample in this period. Circumference (>15cm) of the stems of selected species was measured at breast height using a measuring tape. All the individuals for each species with circumference >15cm were counted. In multi-stemmed individuals, circumference was measured for each stem (Sop *et al.* 2011). Plant species were recorded in the 20m × 50m plots which were selected randomly in all study sites. The plots were initially selected in Google Earth maps where they were numerically coded. The selected plots were then subjected to random number selection in Excel and plot coordinates from Google Earth maps used to locate them in the field. Fifteen plots were sampled from each site to give a total of 120 plots for all sites.

Data analysis

Diameter at breast height (dbh) was calculated from the circumference values. Data on dbh was then assigned 8 classes: 0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70 and >70cm. Density/ha of individuals was computed for each dbh class for the different species. The method for inferring the status of population structure of different tree species followed Sop *et al.* (2011). That is, to determine whether a given species population structure was stable or not. This was determined by analyzing the slope of a linear regression of dbh size classes. 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 good (strong) recruitment while positive slopes indicated poor (weak) recruitment (Shackleton *et al.* 1993). The slopes were interpreted following Shackleton *et al.*

(1993) as follows: A positive slope shows that there are more individuals in the large size classes than in the small ones. This implies that once the old and aging individuals are removed, they would not be adequately replaced hence the population structure is referred to as unstable. In the negative slope, there are many more individuals in the lower size classes than in the higher size classes. Therefore, as the old individuals die, they will be adequately replaced by younger ones hence it is referred to as a stable population structure.

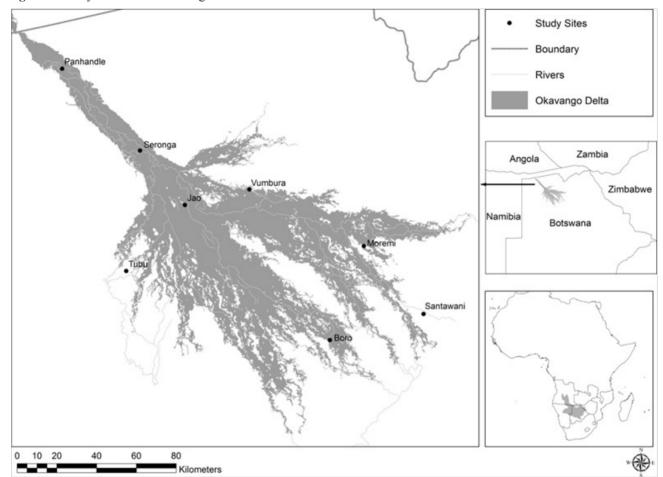


Figure 1: Study sites in the Okavango Delta.

Results

Croton megalobotrys showed a stable reverse J shaped recruitment pattern with more individuals in the 0-10cm size class and missing individuals in size classes 40-50, 50-60, 60-70 and >70cm (Figure 2A).

Philenoptera violacea showed unstable irregular recruitment pattern with more individuals in 0-10cm and 10-20m diameter size classes (Figure 2B). *Garcinia livingstonei* showed stable irregular recruitment pattern with few individuals in size classes 50-60cm and 60-70cm and the highest number of individuals in diameter size class 30-40cm (Figure 2C).

Diospyros mespiliformis showed a stable U shaped recruitment pattern with more individuals in the lower and higher diameter size classes (0-10, 10-20, 60-70 and >70cm) and lower individuals in the middle classes (Figure 2D).

Kigelia africana showed a stable irregular recruitment pattern. It was characterized by higher

number of young and old individuals, with relatively few middle sized trees recorded (Figure 3A).

Syzygium cordatum showed a stable bell shaped recruitment pattern with more individuals in 20-30cm dbh class and few in the lower and higher dbh classes (Figure 3B).

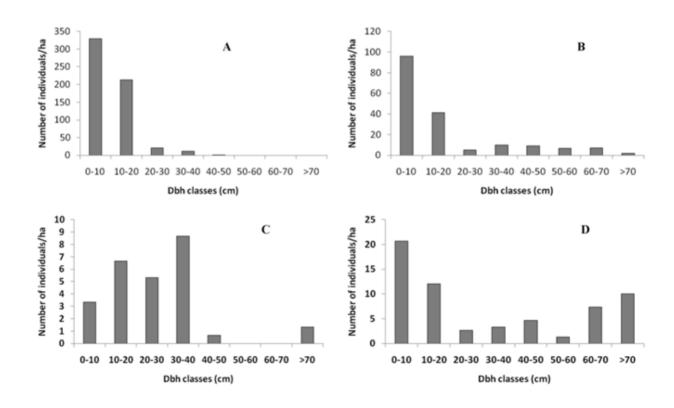
Acacia nigrescens showed a stable irregular recruitment with a high number of individuals in diameter size classes 0-10, 10-20 and 40-50cm (Figure 3C).

Combretum imberbe showed unstable J shaped recruitment pattern with more individuals in the higher size classes and missing individuals in size classes 10-20cm and 30-40cm (Figure 3D). Regression analysis showed that all species had on-going recruitment except for *P. violacea* and *C. imberbe* (Table 1).

Table 1: Regression analysis slope coefficients and mean quotient for different tree species.

Species	Slope coefficient	\mathbf{r}^2	
Croton megalobotrys	-0.985	0.63	
Garcinia livingstonei	-1.62	0.30	
Diospyros mespiliformis	-0.527	0.28	
Philenoptera violacea	0.259	0.99	
Acacia nigrescens	-0.89	0.45	
Kigelia africana	-0.597	0.041	
Combretum imberbe	1.06	0.17	
Syzygium cordatum	-1.20	0.30	

Figure 2: Population structures of C. megalobotrys (A), P. violacea (B), G. livingstonei (C) and D. mespiliformis (D).



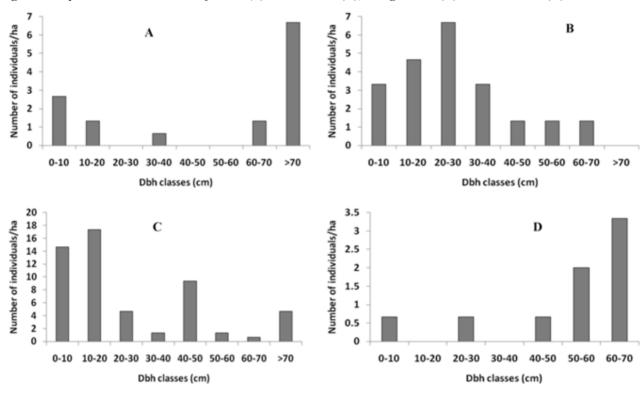


Figure 3: Population structures of K. africana (A), S. cordatum (B), A. nigrescens (C) and C. imberbe (D).

Discussion

Generally the riparian tree species of this study, in the Okavango Delta, showed five population size class distribution patterns namely: reverse J shaped, bell shaped, J shaped, U shaped and irregular. *Croton megalobotrys* showed a reverse J shaped population structure in which there were more individuals in the lower size classes than in the higher size classes. This stable population structure suggests that this species is not threatened by local extinction because individuals in the lower size classes will be recruited into the larger size classes to replace the die offs (Helm & Witkowski 2012). These results also suggest that the prevailing conditions in the Delta are favorable for this species' growth. High number of individuals in the lower size classes of *C. megalobotrys* is an indication of a high rate of germination (Gurmessa *et al.* 2012), while few individuals in the larger size classes may indicate herbivore selective browsing of large trees. Even though it was not quantified, evidence of destruction by elephant on *C. megalobotrys* was observed during this study. Other studies have documented elephant damage to woodland vegetation (e.g. Cumming *et al.* 1997; Western & Maitum 2004; Hamandawana 2012).

G. livingstonei, K. africana, P. violacea and A. nigrescens were characterized by irregular population structure pattern with some missing size classes (except for P. violacea and A. nigrescens). The absence of size classes at 50-60 and 60-70cm (G. livingstonei), 20-30, 40-50 and 50-60cm (K. africana) may have also resulted from past fires, grazing, browsing and moisture stress. Browsing and grazing may result in the loss of individuals in a given size class because they are preferred by herbivores (Gurmessa et al. 2012). In this case the results suggest that the missing size classes in G. livingstonei and K. africana are those that were selectively removed by herbivores specifically elephants. The Okavango Delta is a habitat which is home to a high density of elephants. This results in the elephants' overexploitation of preferred tree species (Skarpe et al. 2004). During this study elephant damage on G. livingstonei was observed in all the studied sites. Elephant damage through bark stripping was also

observed in the stands of A. nigrescens while P. violacea were destroyed in the canopy.

Another explanation of the missing size classes is prolonged soaking in water (which characterized sites such as Seronga, Jao and the Panhandle) during this study which may have led to the death of individuals intolerant to waterlogged soils. Waterlogging results in anoxic conditions which starve plants of oxygen necessary for respiration (Kozlowski, 1984). Shallow groundwater tables as a result of the high floods of 2010-2011 and 2013-2014 (http://www.okavangodata.ub.bw/ori/monitoring/ flood maps/) may have also contributed to die offs of individuals of G. livingstonei and K. africana as a result of the cumulative effects of soaking of their roots and resultant anoxic conditions (Kozlowski, 1984) due to shallow groundwater depths. Groundwater depths in the Delta become shallow as a result of recharge from flooding (McCarthy et al. 1994). It can be noted that the recent high flooding of 2009-2014 led to extreme elevations of groundwater levels which soaked the roots of trees and increased mortalities by starving them of oxygen. Shallow groundwater tables may also have brought salts into contact with the roots of these plants. During low flooding conditions, salts such as sodium accumulate in the center of the islands and deeper groundwater layers where they do not come into contact with tree roots (McCarthy et al. 2006). However, during high flooding conditions as groundwater tables become shallow they bring the salts closer to the soil surface in contact with the roots of plants (McCarthy et al. 1994). The missing size classes for Garcinia livingstonei and K. africana can be explained by their intolerance of saline conditions (Ellery et al. 1993). Moribund stands of G. livingstonei and K. africana that may have resulted from elevated salinities due to shallow groundwater that were observed in February 2015 at Vumbura.

S. cordatum showed a bell shaped population structure with more individuals in the middle 20-30cm diameter size class than in the lower and higher diameter size classes. This may be an indication of episodic recruitment in which in some years the individuals from the lower size classes were not recruited to the higher classes (Gurmessa et al. 2012). This recruitment pattern may result from the temporary environmental bottlenecks which prevent germination of seedlings and their recruitment into the larger size classes. The environmental bottlenecks that may impede germination and recruitment of tree individuals in the larger size classes include dry conditions which inhibit germination or extreme flooding which results in anoxic conditions (Jones et al. 1994). In the Okavango Delta this may result from pluri-annual flood variations which have dry and extreme flooding phases. Flooding in the Okavango Delta varies intra- and inter-annually depending on inflow and precipitation (Wolski et al. 2006). This may have an influence on the establishment of species such as S. cordatum that prefer regular flooding (Ellery & Ellery 1997). During years of low flooding the water table will drop (McCarthy & Ellery 1994) and as a result the roots of S. cordatum may not reach it. This may lead to the death of some of its individuals and reduced recruitment into the next growth stage. Conversely, when the floods are optimally high, they will favor the germination and establishment of S. cordatum and encourage the recruitment of its individuals from the lower classes into the larger size classes. Syzygium cordatum is known in the literature as a species well adapted to flooding (Coates Palgrave 1983). Information on how this particular species has adapted to flooding is scanty. However, generally species adapt to prolonged flooding through hypertrophy (increase in volume/size) of lenticels, development of aerenchyma and adventitious roots (Kozlowski 1984). The bell-shaped population structure in S. cordatum may be an indication of the interaction between dry and wet phases in the flood cycle of the Delta. That is, the middle size class individuals may have been recruited during the period of more extensive, prolonged and deeper flooding which may have been optimal for the growth of S. cordatum. The bell-shaped pattern also implies that this period was followed by drying conditions which minimized or completely stopped recruitment in S. cordatum due to die offs of its individuals before they could reach the larger size classes. The effects of flooding on the population structure of *S. cordatum* may be compounded by rainfall. Rainfall over the Delta may play an important role in promoting germination of riparian plants because it is out phase with flooding (Gumbricht *et al.* 2004)

D. mespiliformis showed a U shaped recruitment pattern in which there were more individuals in the lower and higher size classes than in the middle dbh classes. In contrast, Traoré et al. (2013) observed a reverse J shaped recruitment pattern in this species in Burkina Faso's woodland zone. This contradistinction could be due to episodic recruitment in which there are some years with no recruitment to the middle size classes in the Delta (Gurmessa et al. 2012). Episodic recruitment in D. mespiliformis may result from flooding variations as observed for S. cordatum in which sequences of low flooding years have resulted in low recruitment of individuals into the middle size classes. Conversely the high numbers of individuals in the lower and higher size classes suggest that they were recruited during the years of extensively high floods. These variations may affect the population structure of D. mespiliformis as follows: the intra-annual flood variation may trigger seedlings germination if the water reaches the riparian zone. In order for the seedlings of D. mespiliformis to grow into the next growth stage and eventually establish as fully grown trees they require adequate moisture supply (Traoré et al. 2008). Therefore, if the germination of seedlings is followed by several years of high flooding to supply adequate moisture to the seedlings of D. mespiliformis then they will be able to grow into the next regeneration stage. However, if germination is followed by years of relatively low floods or extremely high flooding then the seedlings will die before they are recruited into the next growth stages. Dry conditions and extreme flooding result in low moisture and anoxic conditions respectively which impede germination of woody species (Jones et al. 1994). The U shaped structure of D. mespiliformis in the Delta suggests that there was a sequence of optimally wet years with favourable growth conditions in which it experienced massive recruitment and dry years during which recruitment was low. Historically the inflows in the Delta were high between 1963 and 1969 and declined to a minimum in 1995-1996 (Mazvimavi & Wolski 2006), rising again to a maximum in 2010-2011 which presented a cycle of favourable-unfavourable-favourable conditions for the recruitment of *D. mespiliformis*.

Combretum imberbe showed a J shaped recruitment pattern characterized by more individuals in the larger dbh size classes. According to Traoré et al (2013) this recruitment pattern is mostly found in aging populations that are threatened by extinction. Therefore, the J shaped population structure of C. imberbe observed in this study implies that it is threatened by local extinction in the Okavango Delta. The unfavorable J shaped recruitment pattern of C. imberbe may result from wind and bird dispersal of seeds to unsuitable sites for germination causing seeds to remain dormant for prolonged periods. The recruitment pattern may also result from debarking by elephants in the middle size classes which prevents the juveniles from reaching canopy height (Teren & Owen-Smith 2010). Findings by Teren and Owen-Smith (2010) in their study in the Linyanti region suggest that mature C. imberbe's resistance to bark stripping and its size, which is too large to be felled by elephants, explain its J shaped recruitment pattern. This suggests that the immature individuals in the lower size classes will be targeted by elephants rather than the mature trees.

The current population structures of different riparian tree species in the Okavango Delta may also be the result of historical environmental stresses such as Tsetse fly outbreak and channel blockages. The Okavango Delta experienced the outbreak of Tsetse fly from the late 1890s to the early 1940s (SMEC 1989). During this period woodland populations may have attained a healthy population structures due to the reduced grazing/browsing pressure as numbers of livestock and wildlife fell because of the Tsetse fly pandemic (SMEC 1989). Furthermore, since the tsetse fly preferred the floodplain and woodland areas, human settlements were established far away from the Delta region (Tlou 1985).

This may have also have facilitated the successful establishment of riparian tree species by reducing human impact. 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 result of historical environmental stress. The period after the 1940s was characterized by the absence of Tsetse fly and increase in wildlife and human and livestock populations which may have increased disturbance in riparian tree species resulting in unstable J shaped, U shaped, irregular and bell shaped population structures.

The current population structure of riparian tree species in the Okavango Delta may also be a product of historical channel blockages. Channel blockages may influence the population structures of riparian tree species in the Delta through its influence on hydrology. This occurs as a result of bed load deposition which results in vertical aggradation of the sediments (McCarthy et al. 1993) and vegetation blockages (McCarthy et al. 1997). As a result of the channel blockages, water ceases to flow. Historical examples of blocked channels in the Delta include Ngoga and Gomoti (SMEC 1989). The Ngoga channel is the primary distributary of water to other major channels in the Okavango Delta (SMEC 1989) and its blockage may have negatively impacted on vegetation communities along it and in the downstream areas. When the channel is active, riparian plant species establish in the hydrologic microsites characterized by different flooding frequencies and groundwater depths which they are adapted to along the lateral gradient from surface water. All these factors are also expected to have an influence on the population structures of riparian tree 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. However, when the channel gets blocked and its flooding ceases, the riparian plant species may show U shaped, bell-shaped and J-shaped population structures which are indicative of unequal recruitment of different size classes. This may be particularly so for species tolerant of frequent flooding such as D. mespiliformis, G. livingstonei and S. cordatum (Ellery & Ellery 1997). Species that prefer dry and occasional flooding conditions such as A. nigrescens and C. imberbe (Ringrose et al. 2007) may show reverse J shaped population structures as the dry conditions may favour them because they would be able to tap deep groundwater. For instance, A. nigrescens showed irregular size class distribution in Boro and Santawani that are occasionally flooded and dry habitats respectively. The irregular size class distribution could result from variable growth and unequal mortality rates in subsequent classes probably resulting from fire and elephant suppression in addition to hydrological conditions (Hamandawana 2012).

Conclusions and implications for management

Overall riparian tree species showed contrasting population structures in the Okavango Delta. *C. megalobotrys, D. mespiliformis, G. livingstonei, K. africana, A. nigrescens* and *S. cordatum* showed stable population structures while *P. violacea* and *C. imberbe* are showing unstable recruitment patterns. The population structures of the different tree species may result from the hydrological factors acting on the germination and subsequent growth stages. As we celebrate 50 years of Independence this year, we have to think of strategies to conserve riparian tree species with unstable population structures. Conservation activities may include the protection of seedlings of *C. imberbe* and *P. violacea* in exclosures to promote their recruitment into large size classes in order to ensure that they attain a stable population structure and remain a significant part of the Okavango Delta ecosystem. Communities around the Okavango Delta should also be taught about sustainable uses of riparian tree species. We conclude by recommending that the insights from this study be used when design-

ing a monitoring system. The information garnered from monitoring the health of our riparian trees can be used to guide the formulation of policies and resource-use strategies. All these actions would enhance the conservation of the Okavango Delta's riparian tree species.

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