

The spatial variation of the regeneration structure of riparian tree species in the Okavango Delta, Botswana.

Gaolatlhe Tsheboeng¹, Michael Murray-Hudson², Keotshepile Kashe² and Mmusi Mmusi²

Abstract

Riparian woodlands in the Okavango Delta play a significant role in the hydrological cycle, directly and indirectly. Despite their ecological importance, very little is known about their regeneration status in the Okavango Delta. The aim of this study was to investigate the spatial variation in the regeneration structure of different riparian tree species in the Okavango Delta. The sampling sites were Seronga, Boro, Moremi Game reserve, Santawani and Vumbura. These species were *Croton megalobotrys* Müll. Arg, *Philenoptera violacea* (Klotzsch) Schrire, *Senegalia nigrescens* Oliv and *Diospyros mespiliformis* Hochst. ex A. Dc. The height of individual trees was measured in randomly selected plots of 20m × 50m. Individuals were assigned to 0-0.5m, 0.6-1m, 1.1-2m, 2.1-4m and >4m regeneration classes. A total of 75 plots were sampled at intervals between February 2012 and April 2013. Linear regression was used to infer the regeneration status of each species. One way ANOVA followed by Tukey post hoc analysis were used to compare the seedling density/ha and sapling density/ha of different species across different sites. *Philenoptera violacea* showed a similar regeneration structure of reverse J shaped regeneration across all the sites. *D. mespiliformis* showed a reverse J shaped regeneration structure in Vumbura, Moremi and Boro while in Seronga it showed a U shaped regeneration structure. *Croton megalobotrys* showed U shaped regeneration structure in Santawani and Boro, a J shaped pattern in Vumbura and Moremi while in Seronga it exhibited an irregular structure. *S. nigrescens* showed a reverse J shaped regeneration structure in Vumbura and a J shaped structure in Moremi and Seronga. In Santawani it had a U shaped structure. Seedling and sapling density/ha for each species varied significantly ($p < 0.05$) among some sites. However, the sapling density of *D. mespiliformis* did not differ significantly among the sites. These results indicate that there is variation in the regeneration structure of different species in different sites. This calls for further research on the environmental factors that influence the regeneration of the woodland species in the Okavango Delta.

Key Words: Recruitment, Riparian woodland, vegetation dynamics and wetlands

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Introduction

Riparian plant species grow along the margins of wetland ecosystems. They are found in the transition zones between terrestrial and aquatic ecosystems (Naiman et al. 2005). The 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). Regeneration is defined as a process through which vegetation naturally renews itself (Borghetti and Giannini 2002) through natural seedling germination, re-sprouting or suckering (Pardos et al. 2005). Regeneration is usually assessed through the vertical analysis of the plant structure which involves the use of height classes (Gurmessa et al. 2012). These classes are seedlings, saplings, shrubs and adult individuals (Sop et al. 2011). A plot of the number of height classes against density of individuals gives an overview of the regeneration structure (Shackleton et al. 1993). The regeneration structure of different species in a given vegetation community is influenced by prevailing environmental conditions at the time of seed dispersal (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 influence the regeneration structure of plants 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 may be unstable (Helm and Witkowski, 2012; Traore et al. 2013). Unstable regeneration is one in which there is low or non-recruitment of individuals among the different regeneration classes. This implies that when there is low or non-recruitment, the aging individuals of a given species may not be replaced in the future when they die. If this persists, then the concerned species is threatened by local extinction (Shackleton et al. 1993). For instance, in the Escalante River, Utah, there was an observed die-off in riparian tree species which was attributed to severe flooding which led to an unstable regeneration (Irvine and West, 1979). Desiccation may also result in unstable regeneration structures of riparian tree species as it prevents individuals from reaching later growth stages (Pettit and Froend, 2001). Anthropogenic factors may also affect the regeneration 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).

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). Riparian vegetation serves as a natural bio-filter helping to prevent excessive sedimentation in aquatic ecosystems thereby improving water quality (Reddy and Gale, 1994). In the Okavango Delta, riparian woodlands play a critical role in the purification of surface water through the process of evapo-transpiration (McCarthy et al. 1994; Bauer, 2004; Wolski et al. 2006). The loss of water through evapo-transpiration helps to keep the water in the Delta less saline because salt accumulation is localized in the centre of islands (McCarthy et al. 1994). As a result of evapo-transpiration by riparian trees the groundwater table is lowered. This results in fresh groundwater and saline

groundwater not mixing 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 et al. 1994). The lowering of the water table by evapo-transpiration from riparian trees maintains a consistent recharge gradient towards the island centres, and away from the floodplain (McCarthy et al. 1994). As a result, floodplain water infiltrates the soils and moves laterally towards the island centre and continuous evapo-transpiration maintains this gradient permanently (McCarthy and Bloem, 1998; Bauer et al. 2002). Some of the riparian tree species that contribute significantly to evapo-transpiration are *Philenoptera violacea*, *Diospyros mespiliformis*, *Kigelia africana*, *Ekebergia capensis* and *Croton megalobotrys* (Lubinda, 2015). It has been found that trees with small trunks lose more water (Lubinda, 2015) while the relationship between tree height and water loss has not been studied. It is beyond the scope of the current study to investigate the relationship between tree height and water loss. The transpiring trees also selectively absorb toxic solutes resulting in fresh surface water (Ellery and Tacheba, 2003). This is significant since it prevents the salinization of surface water and makes it healthy for drinking by the local people (Bauer, 2004).

Despite their importance, there is still lack of information on the regeneration structure of riparian tree species in the Okavango Delta. Several authors have characterized riparian tree species population structure elsewhere such as in South Carolina, U.S.A (Jones et al. 1994), Zimbabwe (Cumming et al. 1997), South Africa (O'Connor et al. 2007), Burkina Faso (Sop et al. 2011), Ethiopia (Gurmessa et al. 2012) while in the Okavango Delta there are few studies on riparian tree regeneration structure (Tsheboeng et al. 2016). Earlier studies on riparian vegetation (e.g., Ellery et al. 1993; Ringrose and Matheson, 2001) in the Okavango Delta did not address tree species regeneration structure. Ellery et al. (1993) studied plant distribution in the islands in relation to environmental variables. Ringrose and Matheson, (2001) spatially characterized riparian woodland in the distal regions of the Delta. Ellery et al. (1993) identified common tree species in the Okavango Delta such as *Diospyros mespiliformis*, *Garcinia livingstonei*, *Ficus thonningii* (Blume), *Ficus sycomorus*, *Hyphaene petersiana* and *Croton megalobotrys* distributed along soil salinity (primarily sodium and calcium concentration) and ground water chemistry (pH and conductivity) gradients. Other common woody plant species found in the Okavango Delta include *Vachellia tortilis* (Forssk.) Hyane, *Vachellia erioloba* E. Mey and *Colophospermum mopane* (J. Kirk ex Benth.) J. Kirk ex J. Léonard which are distributed along a flooding frequency gradient (Ringrose and Matheson, 2001). The recent study by Tsheboeng et al. (2017) on the regeneration structure of riparian tree species was limited to only two study sites of Seronga and Moremi. Due to differences in the hydrology across the different sites in the Okavango Delta (Gumbrecht et al. 2004) which has an impact on the growth of riparian tree species, the findings of Tsheboeng et al. (2017) cannot be generalized to the whole Okavango Delta. Other vegetation studies in the Okavango Delta (Bonyongo, 1999; Bonyongo, 2000; Ellery and Tacheba, 2003; Ellery et al. 2003; and Murray-Hudson, 2009) focused mainly on seasonal floodplain vegetation community composition and distribution. The aim of this study was therefore to investigate spatial variation in the regeneration structure of riparian tree species in the Okavango Delta. It was predicted that riparian tree species would show variation in regeneration structure across different sites in the Okavango Delta.

Materials and methods

The study area

The study was conducted in the Okavango Delta, Botswana. The selected study sites were 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) and Vumbura (Figure 1). These sites were distributed along a hydrological gradient that comprised frequently flooded sites (Seronga, Vumbura and Boro) and those that had low flooding frequency (Moremi and Santawani). Several study sites were chosen in order to have a representative geographical coverage in terms of hydrology in the Okavango Delta. Variation in hydrology across the different sites of the Delta is expected to result in variation in the regeneration structure of different riparian species. This is because the different riparian tree species have different preferences and tolerance to hydrology.

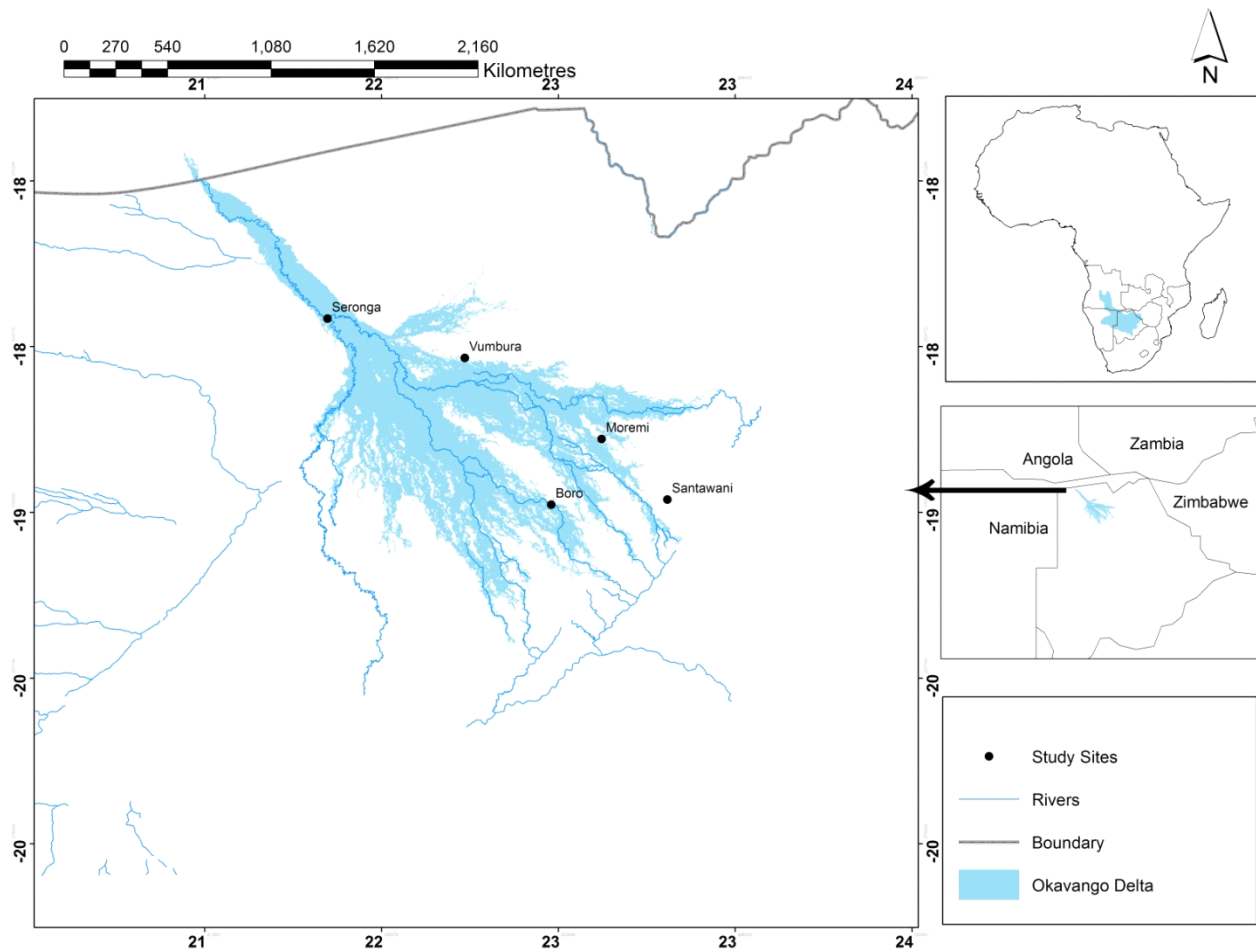


Figure 1: Map of the Okavango Delta showing the study sites

Source: (Tsheboeng and Murray-Hudson, 2013).

The hydrology of the Okavango Delta is characterized by annual flood pulses originating from the Angolan highlands which mainly occur between March and April in the Panhandle/Mohembo region reaching the distal region between May and October (McCarthy, 2006). On average the floods from Angola contribute about $6.0 \times 10^9 \text{ m}^3$ minimum and

approximately $16.4 \times 10^9 \text{ m}^3$ maximum inflow (Gumbrecht et al. 2004). As a result of the variation in total annual inflow, the total flooded area (flood extent) in the Okavango Delta varies between a minimum of 4 000 km² and 13 000 km² (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 changes in flooding magnitude in terms of duration and depth within a given year; that is, the year is characterized by high flooding levels at the beginning of floods and low flooding levels as the flood recedes.

Inter-annual flood variation is characterized by differences in flooding magnitude between two or more years. In this case inter-annual flood variation refers to the differences in the flooding magnitude over two consecutive years. The Okavango Delta floods also vary pluri-annually where there is a sequence of years showing low and high floods. For instance, there was a prolonged period of low flooding magnitude in the Okavango Delta from 1996-2008, followed by a period of high floods from 2009-2016 (Okavango Research Institute Monitoring Unit 2017). These flooding variations are a product of fluctuating rainfall levels in the catchment area in Angola. The flooding magnitude in the Delta is also influenced by local rainfall which is out of phase with the Angolan floods. Rainfall occurs during November and February with an annual mean of 500mm (Wilson and Dincer, 1976) while the floods arrive between March and April (MacCarthy, 2006). During summer the mean annual minimum temperatures in the Okavango Delta range between 14.8°C and 19.2°C while maximum temperatures range between 30.5°C and 40 °C (Ellery et al. 1991). In winter the annual mean average of minimum temperature ranges between 7.0°C and 10.0°C whereas summer yearly averages range between 25.3°C and 28.7°C (Ellery et al. 1991). However, with the general increase in temperatures in Botswana in recent years, the current temperatures should be higher than the estimates given here. The soils in the riparian zones of the Okavango Delta are generally sandy and saline (Ringrose et al. 2007).

Vegetation sampling

All the riparian woodland species in the 75 randomly selected plots were sampled. However, to compare the regeneration structure of the different plant species, data were collected on the species that were present in all the sites that were studied. The species that were common across the different sites were *Croton megalobotrys*, *Philenoptera violacea*, *Senegalia nigrescens*, and *Diospyros mespiliformis*. Sampling was done at intervals between February 2012 and April 2013. This included the period in which most plants were flowering and easy to identify. It was also a period when most plants germinated as it coincided with the rainy season. This was important as there was need to count the seedlings and saplings of the different species.

The height for the individual tree species was measured in fifteen plots of 20m × 50m which were selected randomly from each site and gave a total of 75 plots for all the sites. The seedlings and saplings height was measured using a demarcated 1m pole. The sampling plots were selected through random selection in excel. That is, prior to field sampling 30 potential plots at each sampling site were marked using Google Earth Imaging. Thereafter, the plots were assigned numbers from one to thirty which were subjected to random selection using the RANDBETWEEN function from which fifteen plots were selected for each site. The individuals from the different species were assigned to the following five regeneration classes ; 0-0.5m, 0.6-1m, 1.1-2m, 2.1-4m and >4m following a method by Gurmessa et al (2012). Individuals of each species were counted in each height class from each plot. The 0-0.5m high plants were classified as seedlings while 0.6-1m high plants were classified as saplings. The 1.1-2m and 2.1-4m high

plants were classified as shrubs and >4m plants were classified as fully grown adult individuals. The subdivision of adult individuals into these height classes helped us to gain an insight into the problems that occur at different growth stages (Sop et al. 2011).

Data analysis

The method for inferring the regeneration status of different tree species followed Shackleton et al (1993). Regression analysis was conducted between height classes and density of individuals/ha (N_i). The midpoints (m_i) of height classes were used as independent variables while log transformed N_i ($\ln N_i + 1$) was used as the dependent variable. In this analysis, negative coefficient of slope indicated ongoing recruitment of individuals between different regeneration classes while positive coefficient showed no recruitment. One way ANOVA followed by Tukey post hoc analysis were used to determine if there was any statistical difference in seedling and sapling densities of a given species between different sites. All statistical tests were conducted in Statistical Package for Social Sciences (SPSS version 22, Chicago, USA).

Results

One way ANOVA was used to compare the mean densities of the seedlings of each species across different sites. If ANOVA showed that there were differences in the densities of different species across different sites, Tukey test post hoc analysis was conducted to determine which sites contributed to the difference. The mean seedling density of *Croton megalobotrys* was significantly higher in Boro (df= 3, Mean square= 11.087, F= 2.68, $p= 0.023$) than in Seronga (Table 1). Other sites did not show any significant difference ($p>0.05$) (Table 1). *Senegalia nigrescens* had significantly (df= 3, Mean square= 399. 27, F=5.96) higher seedlings density in Seronga than in Vumbura ($p= 0.024$), Santawani ($p=0.003$) and Boro ($p=0.003$) (Table 1). The differences in Vumbura, Santawani and Boro were not statistically significant ($p>0.05$) (Table 1). Moremi was excluded from the analysis as it had no seedlings recorded for *S. nigrescens* (Table 1). The mean seedling density of *Diospyros mespiliformis* also showed significant difference across the study sites (df= 3, Mean square= 8 179.86, F=8.70, $p=0.0001$) (Table 1). The mean seedling density in Boro was significantly higher than in Vumbura ($p=0.048$), Seronga ($p=0.0001$) and Moremi ($p=0.0001$) (Table 1). There was no statistical difference in the mean seedling density across Vumbura, Moremi and Seronga ($p>0.05$) (Table 1). Santawani was excluded from the analysis as it had no seedlings of *D. mespiliformis* recorded (Table 1). For *Philenoptera violacea*, mean seedling density in Boro was significantly (df= 4, Mean square= 324.07, F=4.310) higher than in Seronga ($p=0.009$) and Moremi ($p=0.005$) but significantly lower than in Santawani ($p=0.009$). Seedling density in Vumbura, Moremi and Seronga did not differ significantly ($p>0.05$) (Table 1).

Table 1: Mean seedling density (individuals/ha) of different riparian tree species in the Okavango Delta.

Species	Sites				
	Vumbura	Santawani	Moremi	Boro	Seronga
<i>Croton megalobotrys</i>	65±2.3 ^{ab}	60±7.4 ^{ab}	38±5.08 ^{ab}	168±9.08 ^a	38±2.08 ^b

<i>Senegalia nigrescens</i>	150±10 ^a	74±5.0 ^a	No value	50±1.7 ^a	915±76.0 ^b
<i>Diospyros mespiliformis</i>	798±13.9 ^a	No value	63±4.2 ^a	1306±103 ^b	127±10 ^a
<i>Philenoptera violacea</i>	390±8.7 ^a	361±24 ^a	298±19.8 ^a	331±11.0 ^b	306±5.9 ^a

*Similar letters show no significant difference ($p>0.05$) while different letters show significant difference ($p<0.05$) across the row/sites.

One way ANOVA and Tukey test were also used to compare the mean sapling densities of different species across different sites. The mean seedling density of *Croton megalobotrys* was significantly ($df= 3$, Mean square= 5. 419, $F=7.521$) higher in Moremi ($p=0.033$) and Boro ($p=0.014$) than in Santawani (Table 2). Vumbura, Moremi and Boro did not differ significantly from each other ($p>0.05$) (Table 2). Seronga was excluded from the analysis as there were no saplings of *C. megalobotrys* recorded there (Table 2). For *Senegalia nigrescens*, the mean sapling density was significantly higher ($df=3$, Mean square= 4.921 , $F=3.778$) in Seronga than in Vumbura ($p=0.020$) and Santawani ($p=0.029$) (Table 2). Vumbura, Santawani and Boro did not differ significantly between each other ($p>0.05$) the same way as Boro and Seronga did not differ ($p>0.05$). We did not include Moremi in the analysis since there were no saplings of *S. nigrescens* recorded there (Table 2). The sapling density of *Diospyros mespiliformis* did not differ significantly between the different sites ($df=3$, Mean square= 1.176 , $F=1.611$, $p=0.188$). However, Santawani was excluded from the analysis as we did not record any saplings of *D. mespiliformis* there (Table 2). The mean sapling density of *Philenoptera violacea* was significantly ($df=4$, Mean square= 8.660 , $F=14.725$) higher in Boro than in Vumbura ($p=0.0001$), Seronga ($p=0.0001$), Moremi ($p=0.0001$) and Santawani ($p=0.0001$) (Table 2). Vumbura, Seronga, Moremi and Santawani did not differ significantly in terms of their sapling density ($p>0.05$) (Table 2).

Table 2: Mean sapling density (individuals/ha) of different riparian tree species in the Okavango Delta.

Species	Sites				
	Vumbura	Santawani	Moremi	Boro	Seronga
<i>Croton megalobotrys</i>	47±1.3 ^a	29±1.9 ^{ab}	37±2.5 ^{ac}	31±1.07 ^{ac}	No value
<i>Senegalia nigrescens</i>	4±0.3 ^a	7±0.5 ^a	No value	23±1.0 ^{ac}	92±2.3 ^c
<i>Diospyros mespiliformis</i>	23±1.5 ^a	No value	13±0.8 ^a	16±0.6 ^a	31±3.0 ^a
<i>Philenoptera violacea</i>	10±0.9 ^a	41±2.7 ^a	28±2.0 ^a	44±1.5 ^b	13±1.04 ^a

To estimate the level of disturbance experienced by each species, we used tree/shrub ratio. Our analysis indicated that *Croton megalobotrys* and *Senegalia nigrescens* tree/shrub ratios were high in Moremi. *Diospyros mespiliformis* tree/shrub ratios were high in both Boro and Seronga while that of *Philenoptera violacea* was high in Seronga (Table 3).

Table 3: Tree/shrub ratios of different riparian tree species in the Okavango Delta.

Species	Sites				
	Vumbura	Santawani	Moremi	Boro	Seronga
<i>Croton megalobotrys</i>	1.01	1.6	4.1	2.1	0.3
<i>Senegalia nigrescens</i>	No value	1.4	2.5	0.76	0.9
<i>Diospyros mespiliformis</i>	0.76	No value	No value	1.3	1.3
<i>Philenoptera violacea</i>	0.24	0.76	0.73	0.42	4

We used regression analysis to infer the regeneration status of different tree species. *Croton megalobotrys* had poor regeneration in all the sites except in Seronga while *Senegalia nigrescens* showed ongoing regeneration in all the sites except in Moremi. *Diospyros mespiliformis* and *Philenoptera violacea* showed ongoing recruitment in all the sites (Table 4).

Table 4: Assessing the regeneration status of different tree species using regression analysis slope coefficients in the Okavango Delta.

Species	Sites				
	Vumbura	Santawani	Moremi	Boro	Seronga
<i>Croton megalobotrys</i>	0.193*	0.154	0.399*	0.150*	-0.252
<i>Senegalia nigrescens</i>	-0.163	-0.149	0.862	-0.129	-0.347*
<i>Diospyros mespiliformis</i>	-0.378*	No value	-0.469*	-0.211*	-0.215
<i>Philenoptera violacea</i>	-0.290*	-0.158	-0.290*	-0.335*	-0.381*

*Significant at $p < 0.05$

For the regeneration structure analysis, we plotted the number of individuals/ha against height classes. *Croton megalobotrys* showed a U shaped regeneration structure in Vumbura (Figure 2A), Santawani (Figure 2B) and J shaped pattern in Moremi (Figure 2C). In Boro *C. megalobotrys* showed a U shaped regeneration structure (Figure 2D) while in Seronga it did not show U, reverse J or J shape pattern (Figure 3).

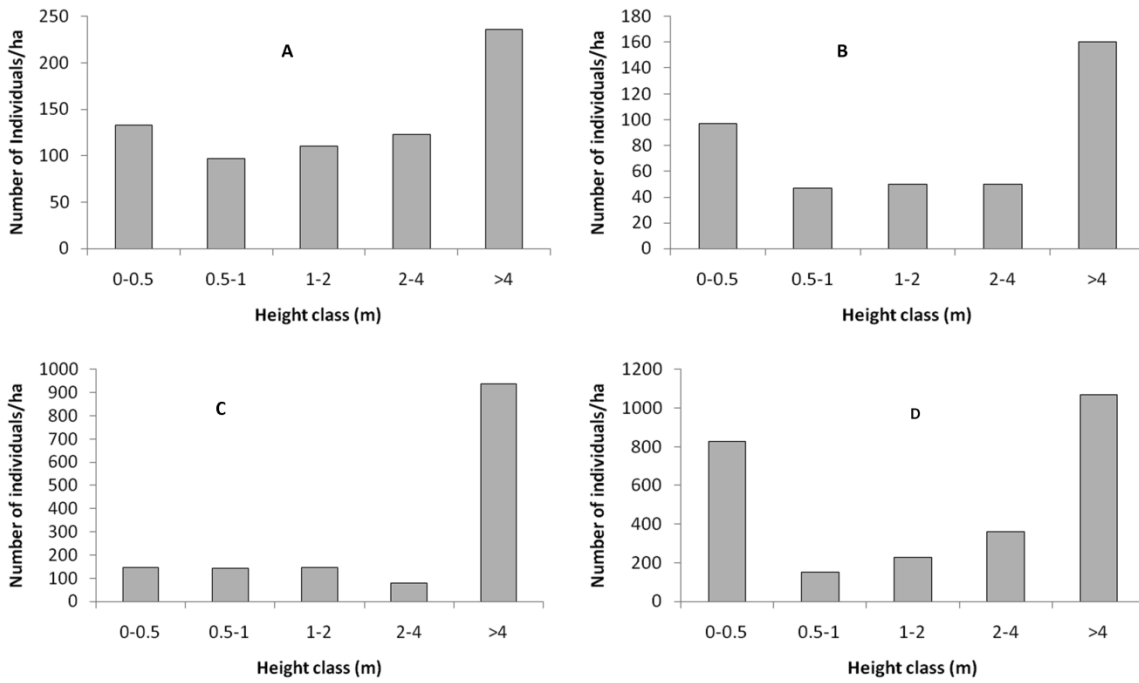


Figure 2: Regeneration structure of *Croton megalobotrys* in Vumbura (A), Santawani (B), Moremi (C) and Boro (D).

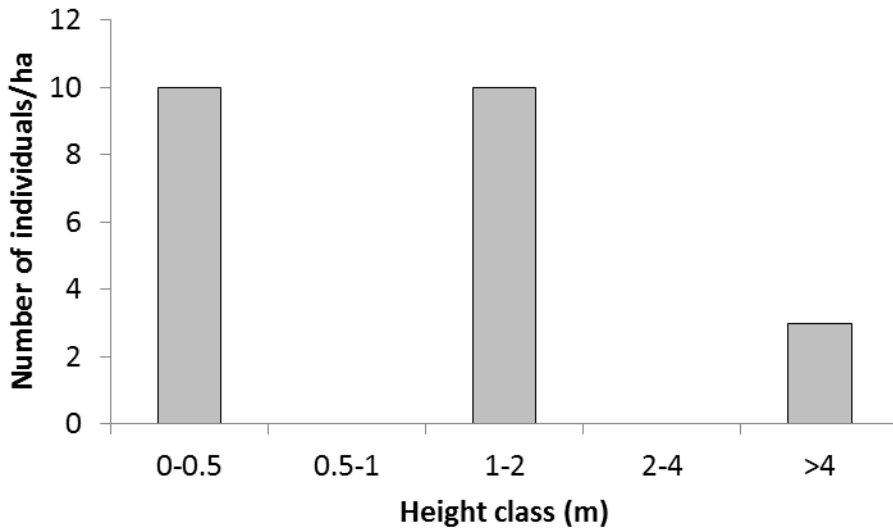


Figure 3: Regeneration structure of *Croton megalobotrys* in Seronga.

Philenoptera violacea showed a reverse J shaped regeneration structure across all the sites (Figure 4A-4D and Figure 5).

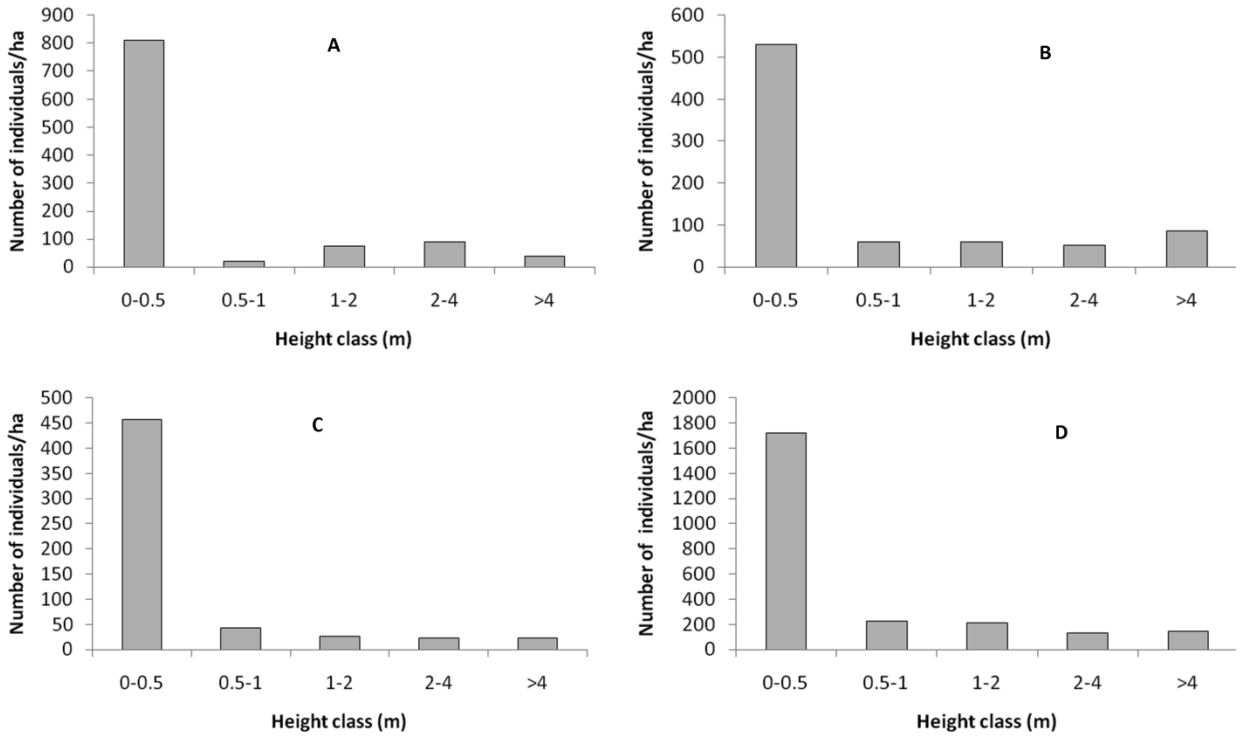


Figure 4: Regeneration structure of *Philenoptera violacea* in Vumbura (A), Santawani (B), Moremi (C) and Boro (D).

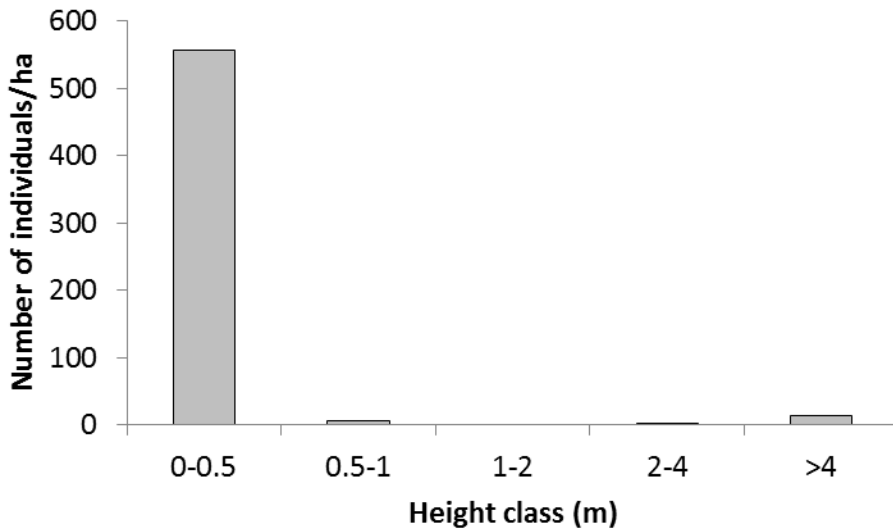


Figure 5: Regeneration structure of *P. violacea* in Seronga.

Senegalia nigrescens showed a reverse J shaped regeneration structure in Vumbura (Figure 6A) and have a J shaped regeneration structure in Moremi (Figure 6C) and Seronga (Figure 7). It showed a U shaped structure in Santawani (Figure 6B) and Boro (Figure 6D).

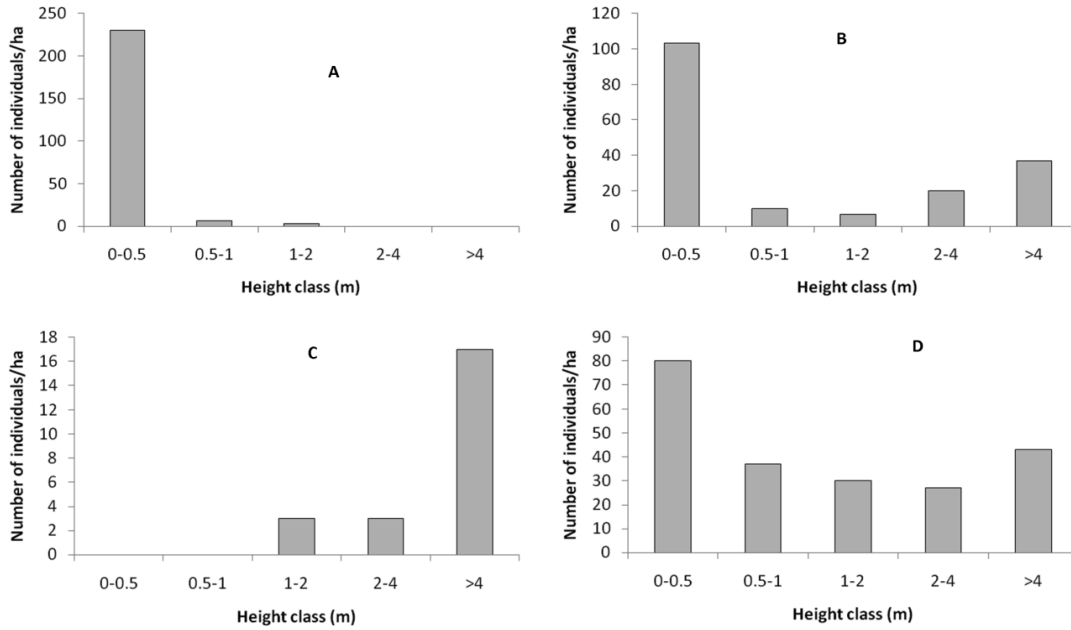


Figure 6: Regeneration structure of *Senegalia nigrescens* in Vumbura (A), Santawani (B), Moremi (C) and Boro (D).

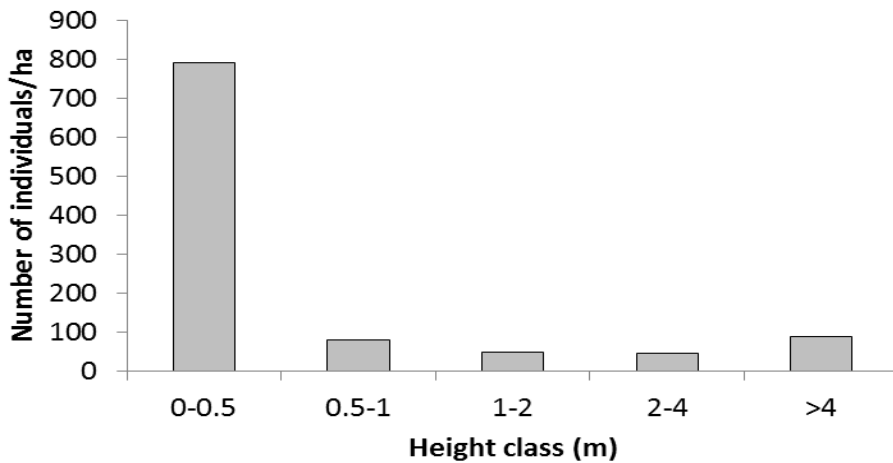


Figure 7: Regeneration structure of *Senegalia nigrescens* in Seronga.

Diospyros mespiliformis showed a reverse J shaped regeneration structure in Vumbura (Figure 8A), Moremi (8B), and Boro (Figure 8C). It showed a U shaped regeneration pattern in Seronga (Figure 8D).

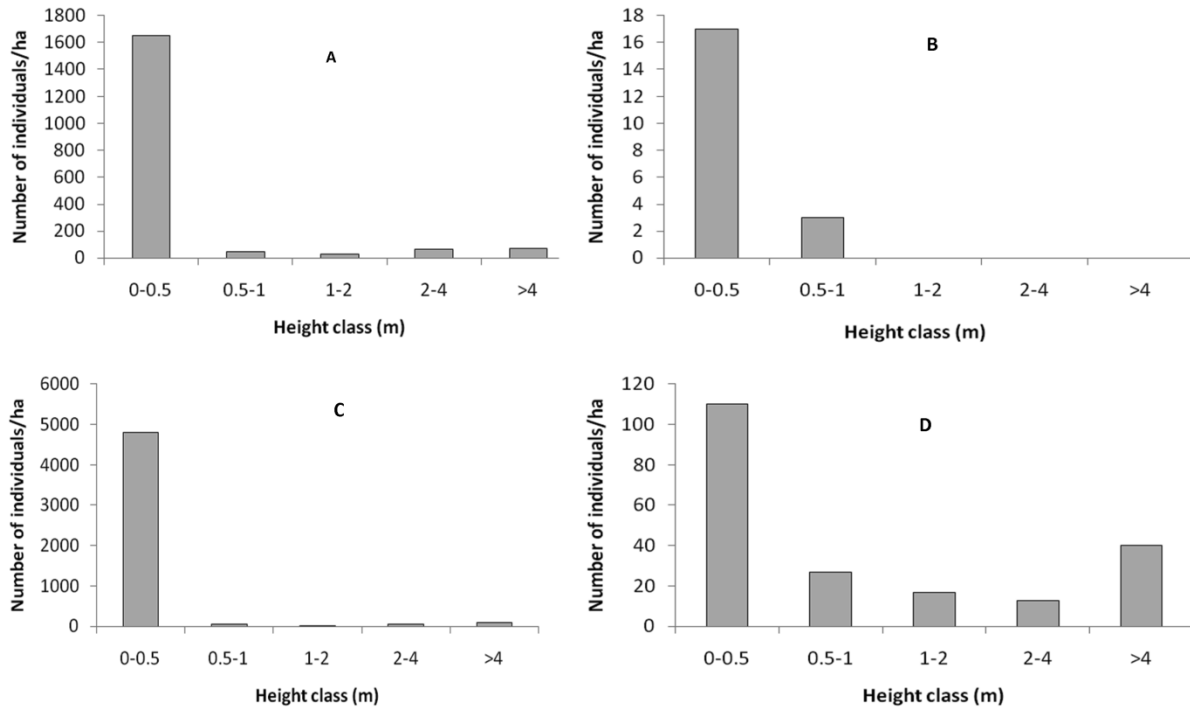


Figure 8: Regeneration of *Diospyros mespiliformis* in Vumbura (A), Moremi (B), Boro (C) and Seronga (D).

Discussion

Tree species in the Okavango Delta showed different regeneration structures and mean seedling and sapling densities across different sites. *Philenoptera violacea* showed a reverse J shaped regeneration pattern in all the sites, *Diospyros mespiliformis* showed a reverse J shaped regeneration pattern in all sites except in Seronga where it was characterized by a U shaped pattern. *Senegalia nigrescens* showed a reverse J shaped regeneration pattern only in Vumbura and U shaped pattern in Boro and Santawani. Generally tree species with a reverse J shaped regeneration structure are considered to be stable since seedlings replace the dead individuals (Sop et al. 2011). Higher individuals in the lower regeneration classes could be an indication of a high rate of germination but low recruitment caused by competition from surrounding trees (Gurmessa et al. 2012). In our study this may be indicated by higher seedling densities than sapling densities for all the species which suggests that not all the germinated seedlings are recruited into the sapling stage. This could be a result of the canopies of large trees blocking sunlight needed for food production from reaching the seedlings. This may also suggest that

individuals in the larger regeneration classes are an indication of herbivore selective pressure on large trees (Mathooko and Karuiki, 2000). There was evidence of herbivory which involved felling of tree individuals in different sites.

Croton megalobotrys (Santawani and Boro) *D. mespiliformis* (Seronga) and *S. nigrescens* (Santawani and Boro) showed a U shaped regeneration structure characterized by more seedlings and mature individuals. This suggests that there is variable growth between height classes in *C. megalobotrys*, *D. mespiliformis* and *S. nigrescens* across the different sites resulting in episodic recruitment. In episodic recruitment, there are some years in which the individuals from the lower size classes are not recruited into the higher classes (Gurmessa et al. 2012). This may be a result of flooding variation in which a sequence of low flooding years resulted in the low recruitment of individuals into the middle size classes. Generally the Okavango Delta is characterized by multi-decadal flooding variation depending on its inflow magnitude (Mazvimavi and Wolski, 2006). High flooding conditions may result in waterlogging which could also have an influence on the recruitment of individuals across the regeneration classes. During this study water-logging, which may have impeded recruitment, was observed in Seronga. This is supported by the findings of Dixon (2003) who found that high water in the Wisconsin River (U.S.A) flow may impede germination and establishment of tree species by covering suitable recruitment habitats during seed dispersal. This is because waterlogging may impose anoxic conditions which may induce mortality in the individuals of different species and negatively impact on their regeneration (Friedman and Auble, 2000; Kozlowski, 1984). Furthermore, episodic recruitment may result from competition among species. In the Okavango Delta, high density of *Phoenix reclinata* in Seronga may have shaded the juveniles of other riparian tree species resulting in their mortality and episodic recruitment.

Episodic recruitment may be a result of a series of disturbances such as herbivory which target middle size class individuals (Helm and Witkowski, 2012). This is especially true because of the high elephant population in the Okavango Delta which may over-exploit woodland species resulting in the death of those individuals due to their debarking (Skarpe et al. 2004). Debarking leads to the death of trees barks act as a protective layer against water loss in plants. The most inner tissue of the bark, the phloem, transports carbohydrates in the plant (Ewers et al. 1991). When the bark is removed its role in plant survival is reduced or eliminated. The impact of elephants on the regeneration of tree species could also be indicated by the tree/shrub ratio which is a measure of disturbance (Gurmessa et al. 2012). The higher tree/shrub ratio indicates low disturbance and the lower tree/shrub ratio indicates high disturbance. That is, the high tree/shrub ratio shows that there are more tree individuals while the low ratio indicates that there are more shrub individuals of a given species (Gurmessa et al. 2012). In our study, the tree/shrub ratios suggest that *C. megalobotrys* is mostly disturbed in Seronga, *S. nigrescens* in Vumbura, *D. mespiliformis* in Moremi and Santawani and *P. violacea* in Vumbura. The spatial variation in the disturbance levels of these species suggests that the environmental factors such as herbivory which influence their regeneration also vary spatially.

The current regeneration status of the species under study may also be influenced by seed dispersal. The spatial variation in the regeneration structures of the tree species in the Delta suggests that their dispersal mechanisms may also vary spatially. Regeneration could be high or non-existent depending on prevailing environmental conditions at the time of seed release. Gradual seed dispersal may lead to regular regeneration patterns due to broader conditions

evolving at the time of seed release, thus increasing the probability of seeds finding suitable conditions for germination (Guilloy-Forget et al. 2002). For seeds to germinate they require moisture, oxygen and sunlight. However, excessive moisture due to water-logging can prevent seeds from germinating as excessive water may starve them of oxygen (Kozlowski, 1984). Drying also impedes seed germination. In Santawani, a dry habitat, there were no seeds or individuals of *D. mespiliformis* as this species requires moist conditions for site colonization.

Even though the influence of fire on riparian woodland species in the Okavango Delta has not been studied, it could be one of the factors that influence spatial variation in the regeneration of riparian tree species. However, its influence is likely to be minimal due to 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 compared to the riparian woodlands where the growth of grass is limited by poor soils, high levels of herbivory and low water content (Heinl et al. 2007). In our study the effects of fire may be more pronounced in the seedlings and saplings because they are within its reach. Fire 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 could be inhibited.

The influence of fire has been found in other riparian ecosystems such as the Colorado River (Busch, 1995) and the Pantanal (de Oliveira et al. 2014). In the Colorado River it was observed that *Tessaria sericea* became dominant after the occurrence of fire while *Populus fremontii* was completely excluded (Busch, 1995). In the Pantanal it was found that fire interacted with flooding to influence the regeneration of riparian plant species. Fire influences the regeneration of riparian trees by eliminating the intolerant ones and creating gaps for colonization (de Oliveira et al. 2014). Species that re-sprout easily are the ones that show resistance after burning and regenerate (Dwire and Kauffman, 2003) while the regeneration of those that are intolerant is suppressed (Helm and Witkowski, 2012).

In addition to the current ecological factors influencing the population structure of the riparian tree species, historical harvesting of riparian trees for traditional dug-out canoe (*mokoro*) carving might be manifesting itself now. The study by Ecosurv (1988) showed that riparian trees such as *D. mespiliformis*, *S. nigrescens* and *P. violacea* were used for *mokoro* construction. The preferred diameter for *mokoro* construction was about 65cm (Ecosurv, 1988) which could correspond to individuals in the higher height classes. It is also documented that *D. mespiliformis*, *C. megalobotrys*, *P. violacea*, *G. livingstonei*, *C. imberbe* and *S. nigrescens* were among the mostly preferred species for fuelwood in the Okavango Delta with 92.4% of the households using them (Mmopelwa et al. 2009). This might also be the reason for the irregular, U shaped and J shaped regeneration patterns shown by these riparian tree species. The missing size classes especially in the lower size classes might be the ones that are targeted by fuel wood harvesters.

Conclusion

This study has shown that there is variation in regeneration structure of *Diospyros mespiliformis*, *Senegalia nigrescens* and *Croton megalobotrys* across different sites. *Philenoptera violacea* showed J shaped regeneration structure across all the sites. Our study has implications for management. Due to the significant role played by the riparian woodland in the health of the Okavango Delta, it is important for further investigation on the factors that influence the

regeneration structure of riparian woodland vegetation across different sites. Riparian woodland species with poor regeneration should be protected through enclosures which will help to reduce elephant damage to promote seed production and dispersal. Efforts should also be made to restore the species with unhealthy regeneration structure through enrichment plantations that will serve as seedlings nurseries.

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