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Research Article

Analysis of vegetation structure of lake Chilwa floodplain, Zomba, Malawi

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ABSTRACT

The research aimed to explore plant species composition and distribution along the floodplain of lake Chilwa, which experiences heavy cyclic flooding and drying events—thereby understanding its impact on species composition and distribution, as well as the ecosystem's resilience. Six belt line transects (150 m × 6 m each) with 18 plots (30 m × 6 m each) were used for systematic sampling to identify plant species and estimate their abundance. Indicator species and classical clustering analyses identified plant communities within distinct hydroperiod zones. Shannon's diversity (H) and Simpson's diversity (1–D) indices measured the diversity of each community. The study found 129 species, predominantly herbs (50.4%), grass (31%), and sedge (12.4%), with Poaceae being the most diverse family. Three plant communities were identified, with community found in permanent waterlogged zone showing higher Shannon's diversity (H) and Simpson's diversity indices and its soil had balanced nutrients content. Compared to similar geographical floodplains, unique species composition was observed, notably the low abundance of *Cyperus papyrus* and *phragmites australis* species. These findings suggest that the cyclic flooding and drying of lake Chilwa change vegetation composition, leading to unique species assemblages and heterogeneous habitats, potentially enhancing long-term resilience and biodiversity of the ecosystem.

Key words: hydroperiod zone; plant communities; permanent waterlogged; seasonal inundation; water level fluctuation; seasonal waterlogged.

INTRODUCTION

Wetlands are susceptible and dynamic ecosystems due to fluctuations in water levels. Their shallow water undergoes significant changes throughout the year due to variations in temperature and precipitation during different seasons. This disrupts interactions between macrophytes and abiotic components, as well as biogeochemical processes, thereby altering substrate and nutrient availability, soil pH, and salinity (Casanova & Brock, 2000; Cronk & Fennessy, 2001; Maltby & Barker, 2009; van der Valk, 2012; Fynn *et al*., 2015; Ondiba *et al*., 2018). Depending on the ecosystem landscape and anthropogenic disturbances, these effects deviate beyond normal ranges when flooding and drying exceed the threshold, thus impacting community structure and productivity (Xie, Ren & Li, 2009). The level of mineral elements such as phosphorus and sulphur persistently remains high even after conditions return to norma (Muneepeerakul, Miralles-Wilhelm & Tamea, 2008). Furthermore, its mechanisms for shaping species composition and distribution are complex and unclear (Zhou & Zhang, 2008; Lan *et al*., 2021).

From the perspective of 'patch dynamics and habitat template concept,' different intensities of flooding frequency and duration are crucial in creating diverse ecological niches and microhabitats, allowing for the coexistence and adaptation of various species within the plant community (Trémolières, 2004). Niche assembly theory further suggests that the adaptability of individual species to ecological niches under coexistence conditions determines their presence and abundance (Zhou & Zhang, 2008). Nevertheless, species composition and community structure cannot solely depend on the distinctive adaptive features of each species but also species' extinction, immigration, and speciation, as asserted by neutral ecology theory (Volkov *et al*., 2003). These mechanisms seem to form premises for the 'intermediate disturbed hypothesis,' which predicts a selective process that eliminates less adaptable species and allows the survival of a limited number of highly resilient species to the pressure associated with more frequent flooding and drying events. Low flooding disturbances promote the invasion of more species, thus creating more competition among species, favouring resilient species. In contrast, habitats experiencing moderate flooding create a balance that neither strongly favours the most resilient species nor suppresses the establishment of less competitive ones, thereby facilitating the coexistence of various species, which leads to high species diversity (Connell, 1978, cited in Crandall, Hayes & Ackland, 2003).

Lake Chilwal's periodic flooding and drying cycles give distinctive patterns of high-water fluctuations compared to similar lakes in East Africa (Kafumbata, Jamu & Chiotha, 2014) because of its

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landscape features and climate change within the lake and its catchment area. Its basement is composed of hard, impermeable metamorphic and igneous rocks which do not conserve water. In addition, the high temperature experienced during the dry season causes water evaporation in open water and evapotranspiration in its floodplain (Chavula, 2000; Rivett *et al*., 2020). Furthermore, the lake's shallow depth and endorheic nature, coupled with reliance on seasonal precipitation as its primary water source, result in fluctuations in water levels. The irregular rainfall patterns in catchment areas cause water levels to rise when the inflow of water exceeds outflow, and conversely, when outflow surpasses water inflow, water levels fall. Thus, in the last century, the lake experienced complete desiccation nine times at intervals of 10 to 20 years. Most recently, partial drying occurred in the 2011–2012 and 2014–2015 seasons, followed by complete drying in 2018 and subsequent flooding in 2019 (Njaya *et al*., 2011; Kafumbata et., 2014; Rivett *et al*., 2020) and 2022–2023 rainy season.

Such ecological disturbance can result in two kinds of vegetation change: relative species abundance and changes in species composition (Leira & Cantonati, 2008). The dry conditions will likely promote the invasion of terrestrial and alien species into the wetland (Casanova & Brock, 2000). Moreover, species possess a unique ecological niche, finely tuned to their specific requirements along a hydrological gradient (Muneepeerakul *et al*., 2008). However, many studies in this area have focused on managing natural resources to ensure that the ecosystem continues supporting biodiversity. The Lake Chilwa ecosystem was destined as Ramsar site No: 869 under the Ramsar Wetland Convention in 1997 and the United Nations Educational, Scientific and Cultural Organization (UNESCO)'s Man and Biosphere (MAB) Reserve in 2006. It is home to diverse vertebrate species and contributes to the economy of Malawi mainly through fishing and rice farming (Dowsett-Lemaire *et al*., 2001; Mloza-Banda, 2004; EAD, 2010; Kafumbata *et al*., 2014). Understanding the effects of the lake's desiccation and flooding on floodplain vegetation also requires studying variables such as diversity and life forms. This can help assess changes in species composition and distribution, and the ecosystem's resilience (Nilsson & Grelsson, 1995, cited in Mloza-Banda, 2004).

OBJECTIVE

The research intended to explore the composition and distribution of plant species along the floodplain of Lake Chilwa.The hypothesis of the research suggested that plant species diversity was high in the middle zone of the floodplain because it experiences moderate pressure from flooding and drying events, creating a balance that neither strongly favours the most resilient species nor suppresses the establishment of less competitive ones, resulting in the coexistence of different species within the zone. The study's specific objectives were: -

1. To describe the floristic species composition of the floodplain.
2. To analyze the distribution of vegetation types across the floodplain.

MATERIALS AND METHODS

Study area

Lake Chilwa is the second largest lake in Malawi, located about 100 km away from Lake Malawi at latitude 15°30"S and longitude 35°30"E (see Figure 1a). Its basement consists of metamorphic and igneous rocks, including quartz, feldspar, and biotite gneisses, with Precambrian granitic rocks, forming its highlands landscape. These rocks resist erosion, resulting in little sedimentation in the bed layer- a distinctive feature not found in other lake basins in East Africa. Furthermore, its shores comprise lacustrine and alluvial deposits carried by highland rivers, with clay and silt soil predominant in the south and east and sandy soil deposited by floods in the north (Rivett *et al*., 2020). The tectonic depressed endorheic freshwater lake basin has a mean altitude of 627 m above sea level and is less than 5 m deep. A 25 m high sandbar, shaped by southeast winds from the Indian ocean 8000 years ago, encloses lake outlets in the north. The lake is also surrounded by Phalombe plain to the south, Mulanje mountain to the southeast, Zomba plateau to the west, and Mozambican mountains and hills to the east (Figure 1b).

The climate is influenced by the inter-tropical Convergence Zone (ITCZ) and tropical cyclone winds, resulting in a tropical savanna climate with three seasons: cool-dry season, hot-dry season, and rainy seasons (Chavula, 2000). The average annual temperature varies between 21°C and 24°C but increases gradually towards open water areas, where the maximum temperature can reach 39°C (Kambombe *et al*., 2021). The annual rainfall across the lake basin ranges from 1000 mm to 1600 mm and 2500 mm in its surrounding highland areas (Kambombe *et al*., 2021). Most of the open water in the lake originates from these highlands and is fed into the lake by six perennial rivers: Domasi, Likangala, Namadzi, Phalombe, Sombani, and Mnembo (Zegeren, 1998).

Study plots and sampling technique

Using a subjective sampling method, six sites, Swang'oma (S1), Kachulu (S2), Namasalima (S3), Mposa (S4), Chipakwe (S5), and Namanja (S6), were selected based on the presence of remnant vegetation in the habitats. At each site, three plots (50 m × 6 m each), representing different hydroperiod zones, were demarcated along a 150 m × 6 m belt line transect. Quadrats (4 m × 2 m each) were systematically laid out in all 18 plots to determine plant species composition, diversity, and zonation. The hydroperiod zones were delineated based on flooding duration, as described by (Semeniuk and Semeniuk,1995, cited in van der Valk, 2012), and historical records. Water depth measurements were taken twice during the study period to facilitate further comparison among the zones (refer to Table 1).

Soil samples from each plot were also collected and analysed at the Forestry Research Institute of Malawi (FRIM) Zomba office. The analysis included soil texture (sand, silt, and clay), organic matter, pH, and

Table 1. Shows a description of the three hydroperiod zones demarcated along the floodplain.

Hydroperiod zone	Initial water depth recorded	Final water depth recorded	Duration of flooding
Seasonal inundated	100 cm	84 cm	water present above the surface seasonally
Permanent waterlogged	46 cm	32 cm	water wetting the surface permanently
Seasonal waterlogged	14 cm	6 cm	seasonal surface water wetting

The measurements shown in **Table 1** of water depth were taken twice during the study period to facilitate further comparison among the zones. The delineation of the zones were based on flooding duration, as described by Semeniuk and Semeniuk (1995) in (van der Valk, 2012), and historical records.

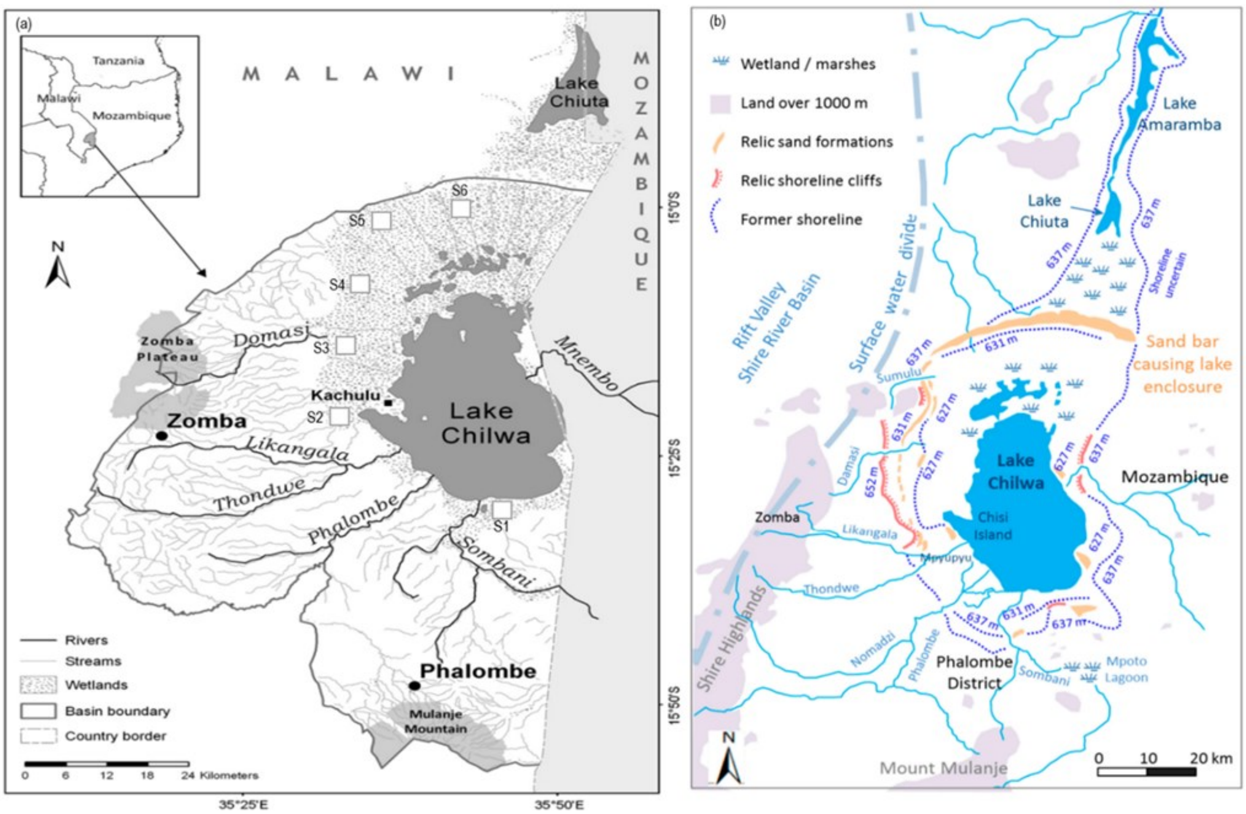

Figure 1. Map of lake Chilwa basin: (a) showing some physical features. Source: (Njaya *et al*., 2011), (b) showing altitude of different sites and former (relict) lake shorelines. Source: (Rivett *et al*., 2020).

mineral nutrients (calcium, magnesium, potassium, phosphorus, and nitrogen). Data were collected towards the end of the rainy season to maximize the identification of more species and facilitate the differentiation of hydroperiod zones.

Data analysis

Plant species were identified, estimated abundance, and categorized into families and life forms. Bar plots and pie charts were generated in R software version 4.14 (R Core Team, 2021) to illustrate dominant families, life forms and to compare soil properties across different zones. Indicator species analysis using Paleontological Statistics software (PAST) version 4.14 (Hammer *et al*., 2001), identified indicator species within each community. The species indicator value percentage (IndVal %) is calculated by multiplying specificity and fidelity and multiplying by 100 (Bakker, 2008). Hence, species with higher IndVal % showed a strong association (high specificity) with a particular hydroperiod zone and a higher probability of occurrence in that specific zone (Fidelity).

Shannon's diversity (H) and Simpson's diversity (1–D) indices using a vegan package of R software version 4.14 were used to measure the diversity of each community. Shannon diversity (H) index weighs more towards species richness, while Simpson's diversity (1–D) leans toward evenness (Van Der Maarel, 2005).

Classical clustering analysis performed using the paired group (UPGMA) based on Bray-Curtis in Past 4.14 software identified the association of plant communities. This analysis grouped plant species into larger clusters based on similarity indices, starting with the highest mutual resemblance, and decreasing as groups merge (Bisandu, Prasad & Liman, 2019).

Kruskal Wallis and ANOVA tests in Past 4.14 software checked whether significant differences among plant communities on species diversity existed.

RESULTS

Floristic composition

The study recorded 129 plant species from 75 genera and 23 families, comprising herbs 50.4% (65 species), grass 31% (40 species), and sedge 12.4% (16 species), as shown in Figure 2. The most dominant family, concerning the number of plant species, was Poaceae, with 39 species. Other families with a significant number of plant species included Cyperaceae with 16 species, Fabaceae with 14 species, and Asteraceae with 10 species, as illustrated in Figure 3. The most speciose genus was Cyperus, with 11 species out of 129 species. Although not among dominant families, certain species like *Typha domingensis* Pers, from Typhaceae family were among the most abundant species in deep flooded zone (seasonally inundated zone). It is the primary plant biomass of the wetland (Zegeren, 1998), thus exhibited a higher IndVal of 82.59% in community one (see Table 2).

Table 2. The indicator species of the three communities, with IndVal % above 70% in descending order and significant indicators below the critical p-value ($p < 0.05$) for each community. Each indicator species exhibited a highly significant value ($P < 0.001$), hence considered as genuine indicators of their respective communities.

Community Type	Family	Indicator Species	Life Form	Origin	IndVal %	p-value
Community one	Convolvulaceae	*Ipomoea aquatica* Forssk.	Herb	Native	100	0.0002
	Cyperaceae	*Cyperus mauritianus* P. Willemet	Sedge	Alien	100	0.0002
	Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	Herb	Alien	100	0.0002
	Salviniaceae	*Azolla filiculoides* Lam	Fern	Alien	100	0.0002
	Typhaceae	*Typha domingensis* Pers.	Grass	Native	82.59	0.0002
	Poaceae	*Vossia cuspidata* (Roxb.) Griff.	Grass	Native	81.64	0.0002
	Poaceae	*Phragmites mauritianus* Kunth	Reed	Native	79.7	0.0002
Community two	Acanthaceae	*Hygrophila schulli* M.R. Almeida & S. M. Almeida	Herb	Native	100	0.0001
	Poaceae	*Cynodon dactylon* (L.) Pers.	Grass	Native	100	0.0001
	Poaceae	*Pennisetum purpureum* Schumach.	Grass	Native	100	0.0001
	Polygonaceae	*Persicaria senegalensis* f. albotomentosa (R. A. Graham) K.L. Wilson	Herb	Native	100	0.0001
	Commelinaceae	*Commelina diffusa* Burm. f	Herb	Native	83.33	0.0006
	Poaceae	*Imperata cylindrica* (L.) Raeusch	Grass	Native	83.33	0.0008
	Poaceae	*Leersia hexandra* Sw.	Grass	Native	83.33	0.0008
Community three	Asteraceae	*Ageratum conyzoides.* L	Herb	Alien	100	0.0002
	Poaceae	*Hyperthelia dissoluta* (Steud.) Clayton	Grass	Native	83.33	0.0009
	Fabaceae	*Chamaecrista mimosoides* (L.) Greene	Herb	Native	83.33	0.0012

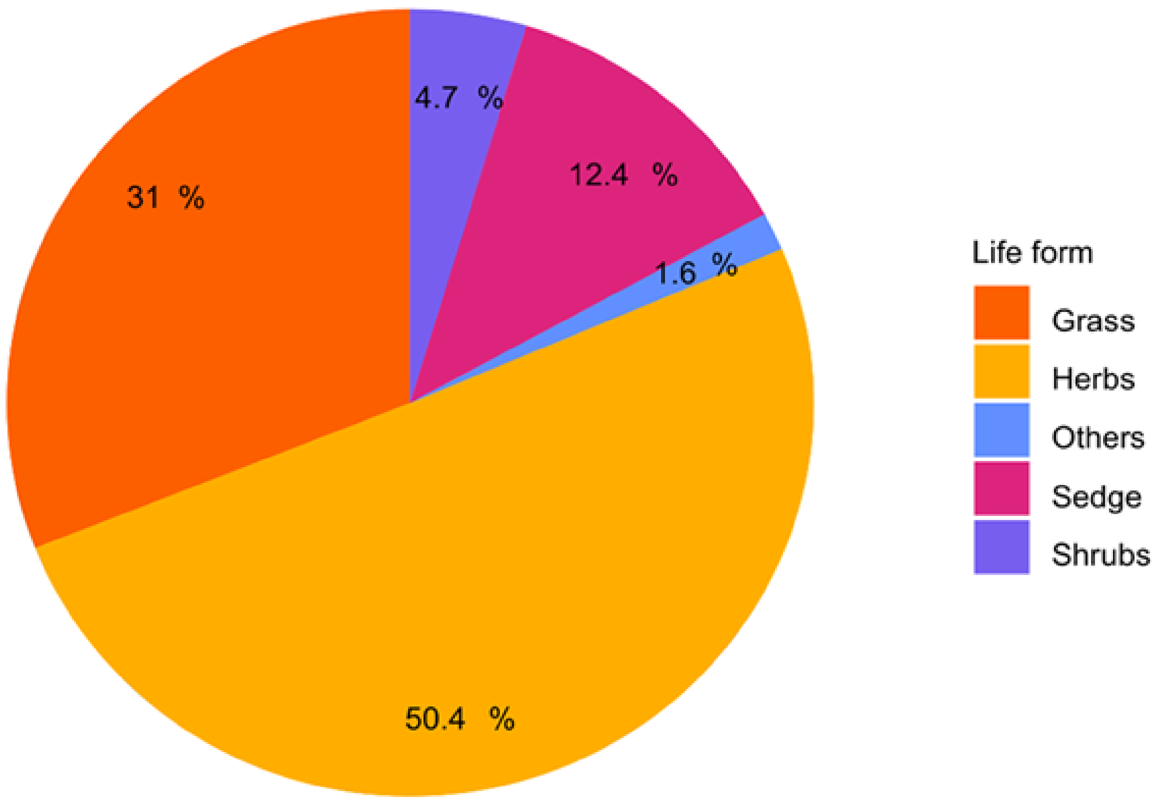

Figure 2. The plant species composition of Lake Chilwa floodplain shows the proportion of life forms. Grass and herbs were the most prevalent life forms recorded.

Vegetation structure and zonation

The seasonally inundated zone was predominantly occupied by obligated wetland species such as *Vossia cuspidata* (Roxb.) Griff, *Pennisetum purpureum* Schumach, *Oryza longistaminata* A. Chev. & Roehr, and Aeschynomene, Cyperus, Persicaria and Typha species (refer Figure 8). In contrast, the permanent and seasonal waterlogged zones were inhabited by facultative wetland species, including *Cynodon dactylon* (L.) Pers, *Imperata cylindrica* (L.) Raeusch, *Leersia hexandra* Sw, *Panicum repens* L, and *Hygrophila schulli* M.R. Almeida & S.M. Almeida (see Figure 9).

In seasonally inundated zones, majority of prominent species recorded during wet conditions were also present during dry conditions such as *Typha domingensis* Pers., *Vossia cuspidata* (Roxb.) Griff., *Phragmites mauritianus* Kunth, Aeschynomene species and Cyperus species. In contrast, in the permanently waterlogged zones and seasonally waterlogged zones, few prominent species namely *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub, *Cynodon dactylon* (L.) Pers, *Imperata cylindrica* (L.) Raeusch, *Phragmites mauritianus* Kunth, *Chamaecrista mimosoides* (L.) Greene and *Hyperthelia dissoluta* (Steud.) Clayton and panicum species were also found dry conditions (see Table 3).

Three plant communities from different hydroperiod zones were identified. Species in plots demarcated in seasonally inundated zones belonged to community one. Its indicator species included *Ipomoea aquatica* Forssk, *Cyperus Mauritius* P. Willemet, and *Eichhornia crassipes* (Mart.) Solms, *Azolla filiculoides* Lam, *Typha domingensis* Pers, *Vossia cuspidata* (Roxb.) Griff, and *Phragmites mauritianus* Kunth. Community two comprises species in plots found in permanently waterlogged zones and indicator species were *Hygrophila schulli* M.R. Almeida & S.M. Almeida, *Cynodon dactylon* (L.) Pers, *Pennisetum purpureum* Schumach, *Persicaria senegalensis* f. albotomentosa (R. A. Graham) K. L. Wilson, *Commelina diffusa* Burm. F, *Imperata cylindrica* (L.) Raeusch, and *Leersia hexandra* Sw. In plant community three: *Ageratum conyzoides*. L, *Chamaecrista mimosoides* (L.) Greene, and *Hyperthelia dissoluta* (Steud.) Clayton were the indicator species, and these were found in plots demarcated in seasonally waterlogged zones. Community two was more diverse among these communities, as indicated by high Shannon's diversity (H) and Simpson's Diversity (1–D) indices shown in Table 4.

Plant zonation showed significant expansion of reeds communities, herbs, and water plants in coastal zones. In contrast, secondary grass and emergent herbs were predominantly featured in the upper zones of the floodplain (see Figure 4). *Phragmites mauritianus* Kunth, *Vossia cuspidata* (Roxb.) Griff, *Typha*

Table 3. List of prominent plant species found in the Lake Chilwa floodplain, comparing their presence during the wet and dry conditions.

Family	Species Name	Life form	Wet condition			Dry condition		
			SI	PW	SW	SI	PW	SW
Acanthaceae	*Hygrophila schulli* M.R. Almeida & S. M. Almeida	Herb		✓				
Asteraceae	*Ageratum conyzoides*. L	Herb			✓			
Commelinaceae	*Commelina diffusa* Burm. f	Herb		✓				
Convolvulaceae	*Ipomoea aquatica* Forssk.	Herb	✓			✓		
Cyperaceae	*Cyperus articulatus* L	Sedge	✓			✓		
Cyperaceae	*Cyperus esculentus* L	Sedge		✓				
Cyperaceae	*Cyperus mauritianus* P. Willemet	Sedge	✓			✓		
Cyperaceae	*Cyperus rotundus* L	Sedge	✓			✓		
Fabaceae	*Aeschynomene elaphroxylon* (Guill. & Perr.) Taub.	Herb	✓	✓		✓	✓	
Fabaceae	*Aeschynomene abyssinica* (A. Rich.) Vatke	Shrub	✓			✓		
Fabaceae	*Chamaecrista mimosoides* (L.) Greene	Herb			✓			✓
Poaceae	*Cynodon dactylon* (L.) Pers.	Grass		✓			✓	
Poaceae	*Hyperthelia dissoluta* (Steud.) Clayton	Grass			✓			✓
Poaceae	*Imperata cylindrica* (L.) Raeusch	Grass		✓			✓	
Poaceae	*Leersia hexandra* Sw.	Grass		✓				
Poaceae	*Oryza longistaminata* A. Chev. & Roehr.	Grass	✓	✓				
Poaceae	*Panicum dregeanum* Nees	Grass		✓				
Poaceae	*Panicum hygrocharis* Steud.	Grass		✓	✓		✓	
Poaceae	*Panicum maximum* Jacq.	Grass		✓	✓		✓	
Poaceae	*Panicum repens* L.	Grass		✓	✓		✓	
Poaceae	*Pennisetum purpureum* Schumach.	Grass		✓				
Poaceae	*Pennisetum unisetum* (Nees) Benth.	Grass			✓			
Poaceae	*Phragmites mauritianus* Kunth	Reed	✓	✓		✓	✓	
Poaceae	*Vossia cuspidata* (Roxb.) Griff.	Grass	✓	✓		✓		
Typhaceae	*Typha domingensis* Pers.	Grass	✓	✓		✓		

Table 3 shows comparative list of prominent plant species found in the Lake Chilwa floodplain across wet and dry conditions in hydroperiod zones.

Key: PW-Permanent waterlogged zone; **SW-**Seasonally waterlogged zone; **SI**-Seasonal inundated zone; **✓-**presence of species. In the table, some species are identified as indicator species within specific hydroperiod zones, with an IndVal exceeding 70% and a p-value below the critical threshold (p < 0. .(05Other species contribute to the dissimilarity, approximately 22.45% among the samples zones and sites. Unlike in seasonal inundation zone, very few prominent perennial species were recorded in permanent and seasonally flooded zones throughout all seasons.

domingensis Pers, *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub, *Oryza longistaminata* A. Chev. & Roehr, *Panicum repens* L, and *Panicum hygrocharis* Steud species overlapped between communities one and two. The spread of some species across community one and community two resulted in communities clustering into a single group (see Figure 5).Plant zonation showed significant expansion of reeds communities, herbs, and water plants in coastal zones. In contrast, secondary grass and emergent herbs were predominantly featured in the upper zones of the floodplain (see Figure 4). *Phragmites mauritianus* Kunth, *Vossia cuspidata* (Roxb.) Griff, *Typha domingensis* Pers, *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub, *Oryza longistaminata* A. Chev. & Roehr, *Panicum repens* L, and *Panicum hygrocharis* Steud species overlapped between communities one and two. The spread of some species across community one

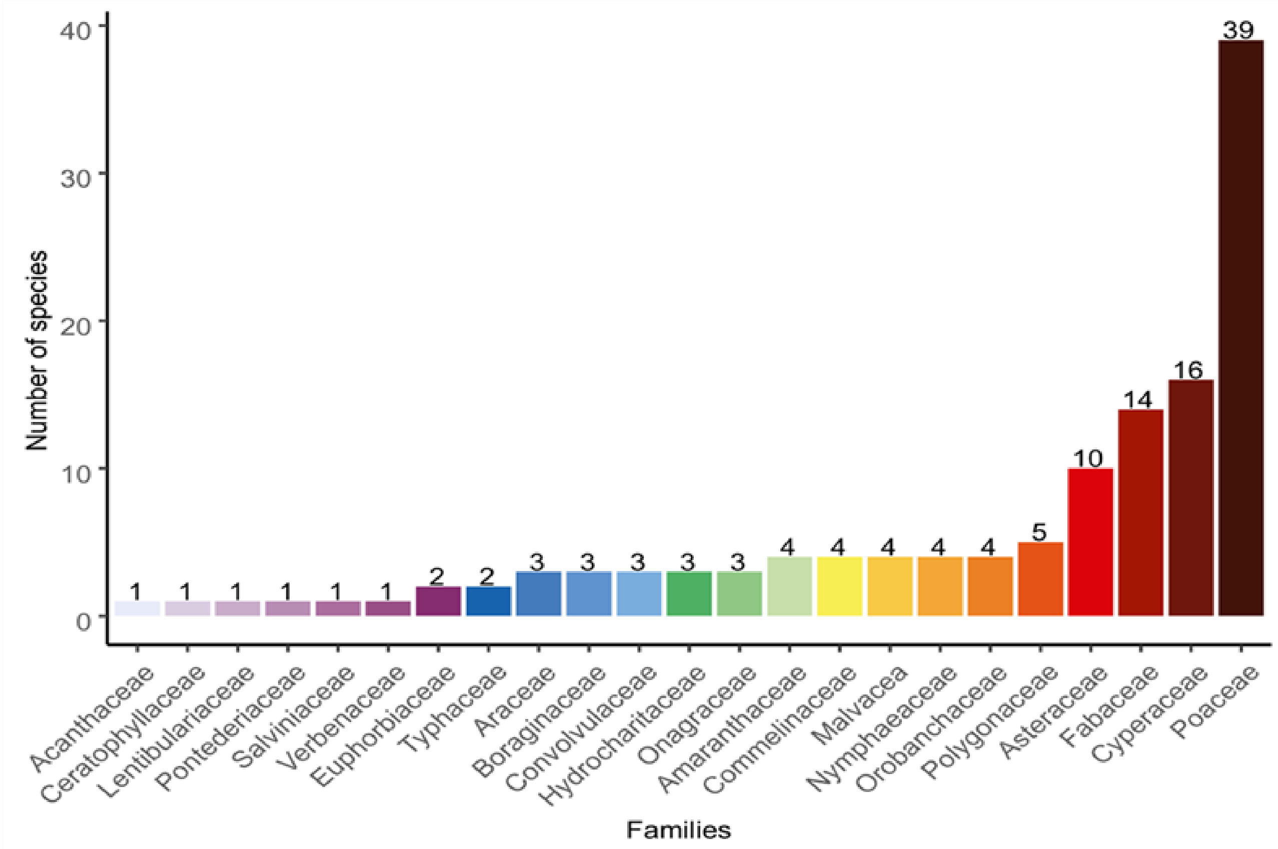

Figure 3. A bar plot depicts the number of plant species within families in the Lake Chilwa floodplain. The Poaceae family was the most dominant, with 39 out of 129 species recorded.

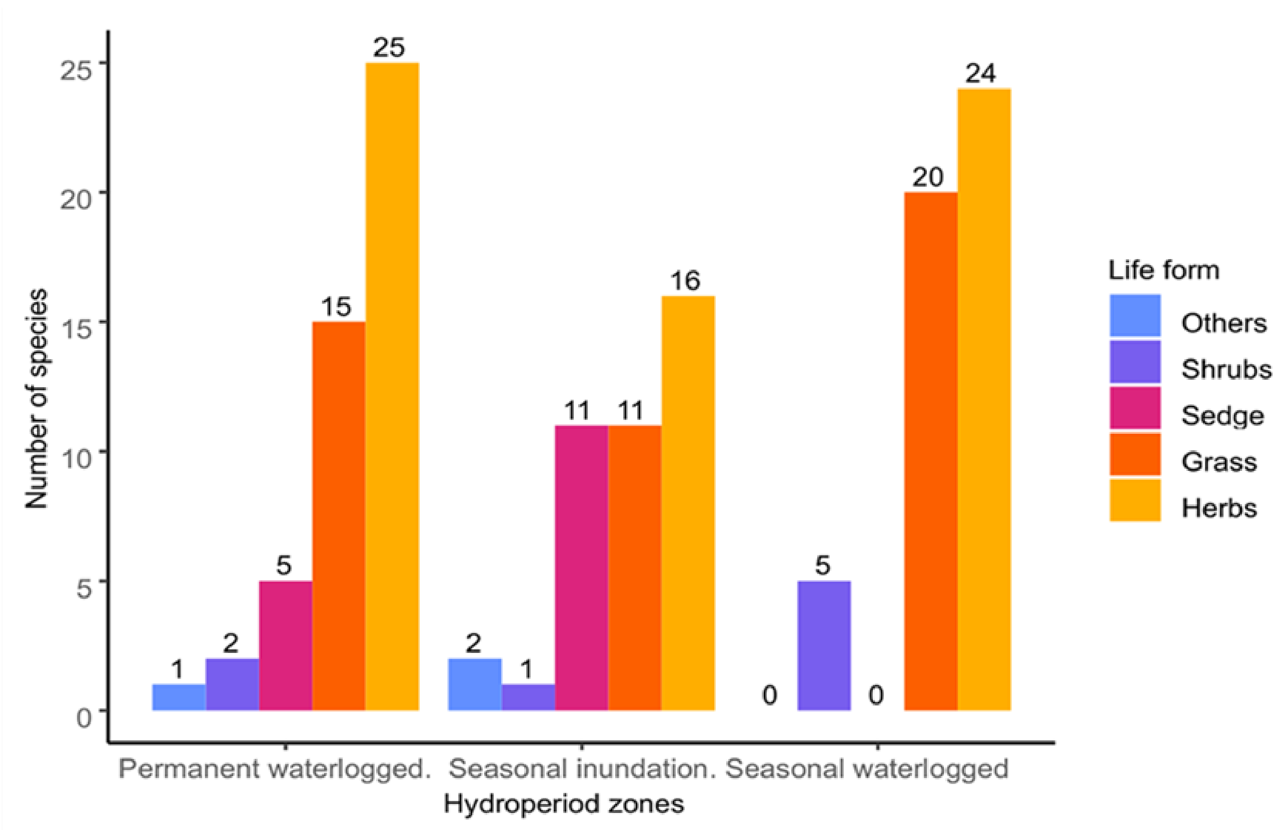

Figure 4. A comparison of plant life forms in various hydroperiod zones along the Lake Chilwa floodplain. The pattern showed that grass and herb species were prominent across all zones, while sedge were prominent in seasonally inundated zones.

Table 4. Simpson and Shannon Weiner diversity indices of plant communities of the floodplain.

Diversity Index	Community one	Community two	Community three
Simpson Diversity (1–D)	0.9484	0.9517	0.9511
Shannon Weiner (H)	2.9928	3.0799	3.0438

The comparison of the diversity indices in **table 4** show community two was more diverse, as indicated by higher Simpson diversity and Shannon Weiner indices values.

Table 5. Shows soil properties across different zones of Lake Chilwa floodplain.

Zones	Soil properties							
	Texture (%)	pH (-log [H+])	TCa (%)	TMg (%)	TOC (%)	TN (%)	TP (meq %)	TK (meq %)
Permanent waterlogged S1	sandy	4.74	3.4	2.6	5.228	0.089	7.95	0.07
Permanent waterlogged S2	sandy	5.57	2	1.8	1.788	0.007	2.8	0.07
Permanent waterlogged S3	sandy	4.51	4.4	1.4	1.169	0.058	4.9	0.09
Permanent waterlogged S4	sandy	4.49	2.4	1.6	0.138	0.285	3.15	0.08
Permanent waterlogged S5	sandy	7.25	5.6	1.2	5.709	0.261	2.45	0.12
Permanent waterlogged S6	sandy	9.2	2.6	0.8	4.334	0.217	7.8	0.08
mean value		5.96	3.4	1.567	3.061	0.153	4.842	0.085
Seasonal inundated S1	sandy	4.68	2.6	2.4	3.041	0.196	8.8	0.06
Seasonal inundated S2	sandy	5.02	2.8	2.2	3.921	0.21	3.15	0.08
Seasonal inundated S3	sandy	5.12	1.8	2.4	3.852	0.193	3.15	0.06
Seasonal inundated S4	sandy	5.67	3	2.2	4.196	0.189	3.15	0.08
Seasonal inundated S5	sandy	5.98	6.2	2.2	3.783	0.169	2.45	0.07
Seasonal inundated S6	sandy	6.5	3	2.4	4.058	0.203	9.8	0.1
mean value		5.495	3.233	2.3	3.809	0.193	5.083	0.075
Seasonal waterlogged S1	sandy	5.23	2.8	2.4	0.138	0.021	9.2	0.07
Seasonal waterlogged S2	sandy	5.6	0.6	2.6	0.413	0.086	3.04	0.08
Seasonal waterlogged S3	sandy	5.01	4.2	1.8	2.156	0.076	3.85	0.08
Seasonal waterlogged S4	sandy	5.49	4.2	2.8	1.72	0.186	3.15	0.07
Seasonal waterlogged S5	sandy	5.2	8.2	1.6	3.715	0.052	2.02	0.09
Seasonal waterlogged S6	sandy	7.34	5	1.6	4.132	0.196	8.15	0.14
mean value		5.645	4.167	2.133	2.046	0.103	4.902	0.088

Table 5 shows the highest pH mean value and the lowest mean total magnesium content in permanent waterlogged zones, while total organic carbon was highest in seasonal inundated zones. Seasonal waterlogged zones had the highest total calcium content and the lowest total organic carbon content.

Key: TCa stands for total calcium, TMg for total magnesium, TOC for total organic carbon, TN for total nitrogen, TP for total phosphorus, and TK for total potassium.

and community two resulted in communities clustering into a single group (see Figure 5).

Physicochemical properties of soil across floodplain zones

As shown in Table 5 and Figure 6, the total organic carbon content was significantly different across all the zones, with the seasonally inundated zones having the highest content (3.809%) and the seasonally waterlogged zones having the lowest content (2.046%) Soil pH and total magnesium also varied significantly, with permanently waterlogged zones exhibiting a higher soil pH value (5.960) and lowest level of total magnesium (1.567%) compared to the other two zones .Total calcium content differed significantly between the seasonally waterlogged zones and the other zones, with

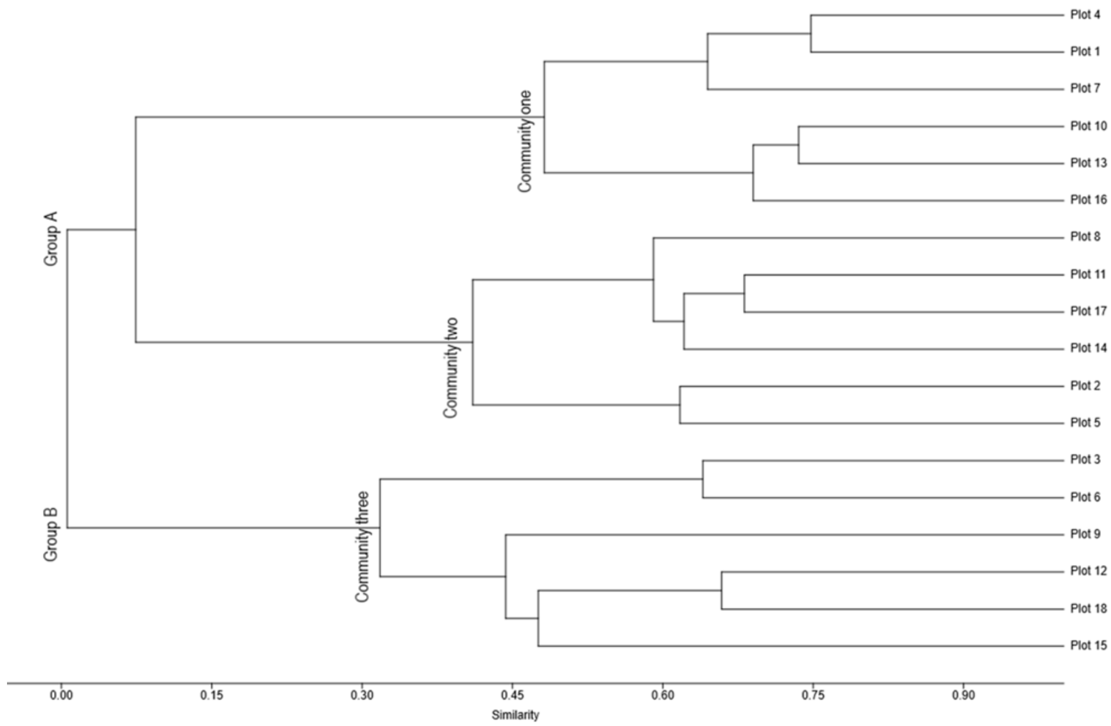

Figure 5. The cluster analysis dendrogram (scale indicates the similarity percentage among the communities) revealed two distinct groups: Group A consisted of plant communities one and two, found in plots demarcated in seasonal inundation and permanent waterlogged zones. Group B comprised plant community three in plots demarcated in the seasonal waterlogged zone.

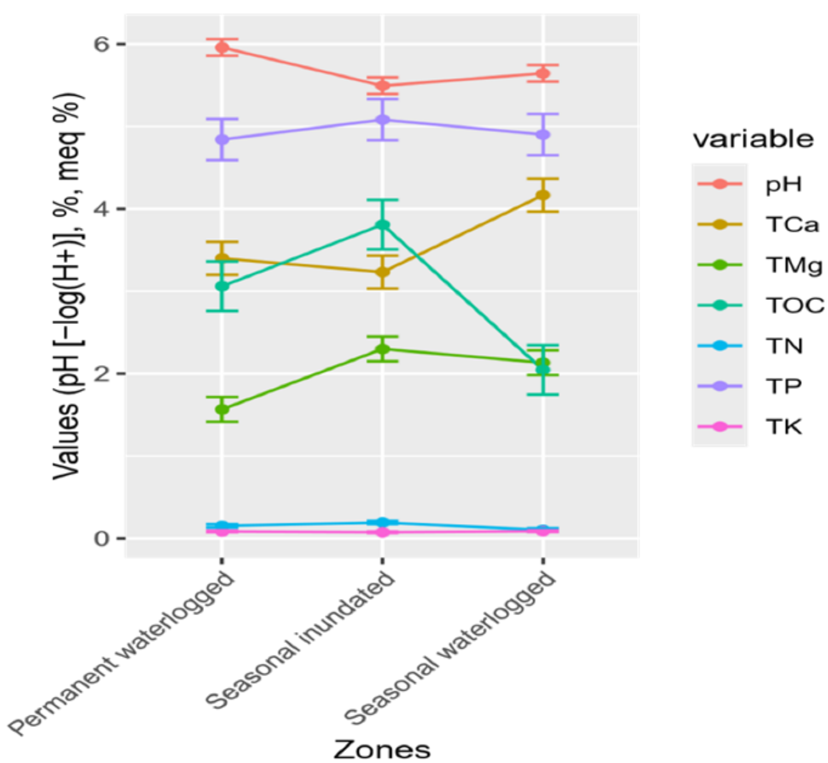

Figure 6.The line plots with error bars, comparing soil variables across different hydroperiod zones. The seasonally inundated zone had highest total organic carbon content. The permanently waterlogged zone had intermediate nutrient levels for most parameters, slightly less acidic, and lowest total magnesium content compared to the other zones. Although the seasonally waterlogged zone had highest total calcium content, it had the lowest overall nutrients levels. Inconclusively, the levels of total nitrogen, total phosphorus and total potassium were relatively similar across all the three zones.

Key: TCa stands for total calcium, TMg for total magnesium, TOC for total organic carbon, TN for total nitrogen, TP for total phosphorus, and TK for total potassium.

the seasonally waterlogged zones a having a higher total calcium content (4.167.(%The minimal variation in total potassium, total phosphorus, and total nitrogen across all zones is shown by the overlap of their error bars in Figure 6 .Additionally, the soil texture was similar across all zones, consisting of over 90 %sand particles and less than 5 %each of clay and silt. This indicates that the soil was predominantly sandy, based on the classification using soil triangle chart.

DISCUSSION

Species composition

The vegetation composition shows the Poaceae family as the most abundant, constituting 30.2% of the herbaceous species, which make up 95.3% of all recorded species. Unstable conditions due to heavy floods and anthropogenic activities may have hindered the growth of woody plants accustomed to stable environments. The tropical and savanna climate of lake Chilwa grassland makes it ideal for the growth of scattered stunted trees or shrub species such as *Brachystegia boehmii* Taub and *Terminalia sericea* Burch. ex-DC (Dowsett-Lemaire, *et al*. 2001; Kindt *et al*., 2014; Kindt *et al*., 2011). However, waterlogged, and saturated soil conditions persisting in the plain may have promoted the growth of Poaceae species while hindering growth of woody species due lack of adaptive features by their root system. On the contrary, *Aeschynomene elaphroxylon* (Guill. & Perr.) (22), as illustrated in Figures 7a and *Aeschynomene abyssinica* (A. Rich.) Vatke (21) species, as referred to in Figures 7b, might have required conditions in the permanent waterlogged zone for the germination and establishment of their propagules, as well as development and maturity niches in the seasonal inundation conditions.

Aeschynomene species, Poaceae, and other reed communities exist as annual plants, potentially enabling them to exploit favourable environmental conditions persistent within a season for growth and development. These species and certain floating and submerged herb species can utilise increased soil nutrients influenced by floods to overgrow and propagate invasively within habitats. Additional adaptive features include extensive roots, rhizomes, and stolons, facilitating rapid growth, vegetative reproduction, and high seed production for quick colonisation (Trémolières, 2004). Furthermore, using C3 and C4 photosynthetic pathways (Peterson, 2013) may enable reed communities to maximize energy utilisation in dynamic habitats.

This explains why some perennial wetland grass, reeds, herbs, shrubs and sedges species can also thrive in various waterlogged conditions despite significant lowering of water levels and loss of soil moisture during the dry seasons. These prominent species include *Cyperus species*, *Aeschynomene species*, *Phragmites mauritianus* Kunth, *Vossia cuspidata* (Roxb.)Griff, and *Typha domingensis* Pers, in seasonally inundated zones. *Phragmites mauritianus* Kunth, *Oryza longistaminata* A. Chev.& Roehr, *Cynodon dactylon* (L.) Per, *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub, and Panicum species in permanently flooded zones, and *Chamaecrista mimosoides* (L.) Greene, *Hyperthelia dissoluta* (Steud.) Clayton in seasonally flooded zones as shown in Table 3.

The recovery of woody and herbaceous plants in the plain might also have been hindered by intense fire and the cutting down of trees for fish drying and curing (Mloza-Banda, 2004; Mloza-Banda, 2005). Fire can volatilise significant elements such as nitrogen and sulphur, alter soil pH, salinity, and moisture, destroy vegetation seedlings, and inhibit coppice regrowth of trees.

Vegetation structure and zonation

The higher Shannon Weiner and Simpson diversity indices in community Two, compared to communities One and community Three (see Table 4), may be attributed to the effects of flooding regime and upland disturbances on plant communities' size and structure. Increased competition within the niches of community One and community Three might reduce species' evenness and richness, while creating a complex mosaic of habitats within the community Two, thus leading to high diversity (Arias *et al*., 2018).

Seasonal fluctuations between dry and wet conditions in waterlogged zones may promote the invasion of native facultative species and secondary grasses. Additionally, agricultural nutrient runoff may encourage the invasion of alien species, such as *Ageratum conyzoides* L., as indicated in Table 2. Similarly, inundation conditions promote interspecific competition among community One species, favouring flood-tolerant species like sedges, bulrush grasses, and reeds. These species can fully utilise destabilised substrates and niches, occupying mosaic patches. Moreover, floods enrich soil nutrients, potentially leading to eutrophication, which may facilitate the invasion of alien species such as *Eichhornia crassipes* (Mart.) Solms and *Azolla filiculoides* Lam (refer Table 2). These invasive species may limit the growth of other submerged and emergent vegetation within the habitat.Moderate flooding conditions in the permanent waterlogged habitat of community Two may sustain favourable niches and substrates, moderate soil moisture, balanced soil nutrient content, and available seed banks. These conditions might create heterogeneous microhabitats, reducing species competition and allowing for species coexistence, thereby balancing species richness and evenness. The habitat of community Two might have also served as an ecological buffer zone to plant community One, as illustrated in Figure 5, where certain species with broad niches from community One, such as *Phragmites mauritianus* Kunth, *Vossia cuspidata* (Roxb.) Griff, and *Typha domingensis*, *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub, *Oryza longistaminata* A. Chev. & Roehr, *Panicum repens* L, and *Panicum hygrocharis* Steud, Pers, (see Figures 7a–7c), might inhabit community Two to exploit niches for growth, germination of their propagules, and completion of their life cycles. Futhermore, the zone might also have been offering protection from high nutrient influx (Maltby & Barker, 2009), and substrate for morphological plastic plants (Leira & Cantonati, 2008).

The distinct hydrological and stable conditions in their respective habitats might also cause significant differences in the herbaceous stratum layers in all three hydroperiod zones. As shown in Figures 7a–7c, seasonal inundation and seasonal waterlogged zones showed less foliage cover of the understorey plants than permanently waterlogged zones, possibly due to high competition that eliminated some ferns, small grasses, and herbs. In contrast, the coexistence of different species in permanently waterlogged zones might have resulted in a denser understorey herbaceous stratum layer. As shown in Figure 1a, sites S5 and S6 have a large floodplain area, followed by sites S4, S3, and S2, then site S1. Due to the absence of drainage channels, the accumulated water within the lake flooded more in the low-lying northern and western areas, 627 above sea level, where the two former sites are located, compared to the latter sites, which is slightly higher in elevation, 631 above sea level, (see Figure 1b). Specifically, seasonally inundated, and permanent waterlogged zones show a significant expansion of reeds, grass, sedges, rushes, herbs, and water plants community compared to seasonal waterlogged zones (refer Figure 4).

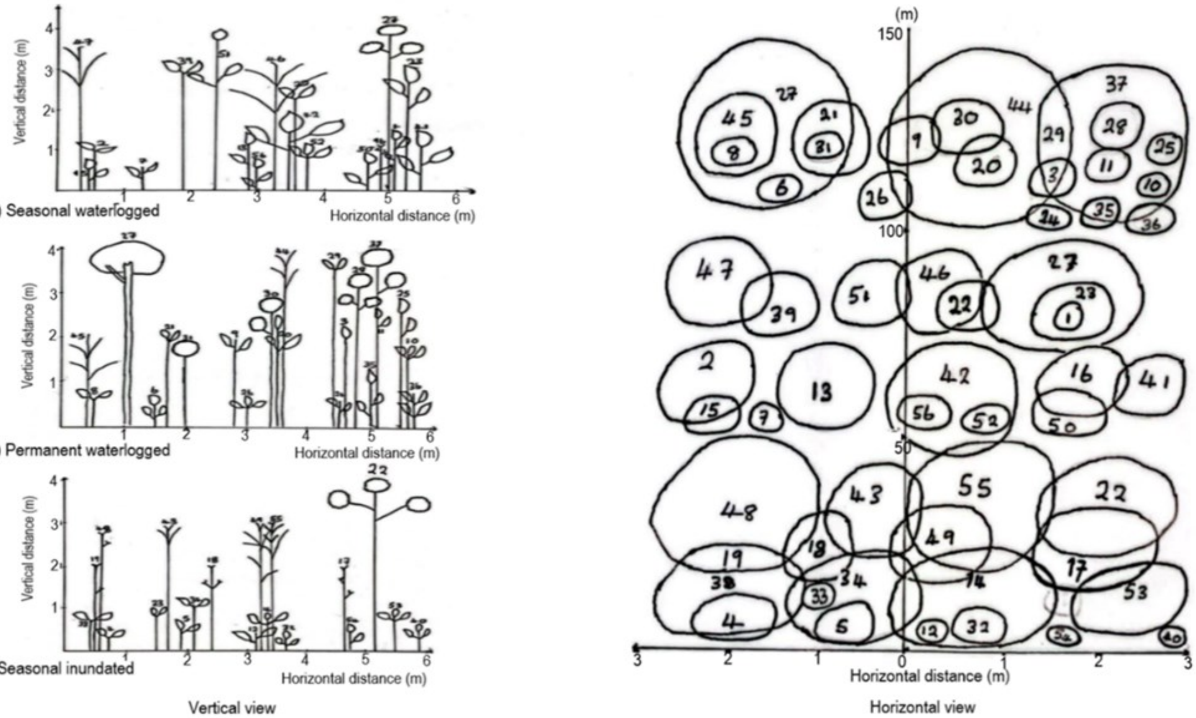

Figure 7a. Vegetation profile for Swang'oma site (S1). **I**. Vertical view of the profile; **II**. Horizontal view of profile.

1-*Hygrophila schulli*; **2-***Alternanthera sessilis* (L.) DC; **3** -*Amaranthus spinosus* L.

4-*Lemna aequinoctialis* Welw; **5-***Pistia stratiotes*. L; **6-** *Zantedeschia albomaculata* (Hook.) Baill.

7-*Adenostemma caffrum*. DC; **8-***Ageratum conyzoides*. L; **9-***Bidens pilosa*.

10-*Pseudognaphalium luteoalbum* (L.) Hilliard & B.L. Burt.

11-*Trichodesma zeylanicum* (Burm. F.) R. Br.; **12-** *Ceratophyllum demersum* L.

13-*Commelina diffusa* Burm. F;**14-***Ipomoea aquatica* Forssk.; **15-***Ipomoea purpurea* (L.) Roth.

16-*Cyperus articulatus* L; **17-***Cyperus esculentus* L;**18-** *Cyperus mauritianus* P. Willemet.

19-*Cyperus rotundus* L; **20-***Euphorbia indica* Lam; **21-** *Euphorbia hirta* L.

22-*Aeschynomene elaphroxylon* (Guill. & Perr.) Taub; **23** -*Aeschynomene pfundii* Taub.

24-*Chamaecrista absus* (L.) H. S. Irwin & Barneb; **25-** *Chamaecrista mimosoides* (L.) Greene.

26-*Indigofera antunesiana* Harms; **27-***Neltuma glandulosa* (Torr.) Britton & Rose.

28-*Rhynchosia hirta* (Andrews) Meikle & Verdc; **29-** *Senna petersiana* (Bolle) Lock.**30-***Sesbania sesban* (L.) Merr.; **31-***Tephrosia purpurea* (L.) Pers; **32-***Ottelia exserta* (Ridl.) Dandy.**33-***Stratiotes aloides* L; **34-***Utricularia reflexa* Oliv; **35-***Sida acuta* Burm. f; **36-***Sida alba* L.

37-*Thespesia garckeana* F. Hoffm; **38-***Nymphaea nouchali* Burm. F.

39-*Ludwigia abyssinica* A. Rich; **40-***Ludwigia adscendens* (L.) H. Hara.

41-*Rhamphicarpa fistulosa* (Hochst.) Benth; **42-***Cynodon dactylon* (L.) Pers.

43-*Echinochloa pyramidalis* (Lam.) Hitchc. & Chase; **44-***Hyperthelia dissoluta* (Steud.) Clayton.

45-*Loudetia simplex* (Nees) C. E. Hubb.; **46-***Panicum dregeanum* Nees.

47-*Pennisetum purpureum* Schumach.

48-*Phragmites mauritianus* Kunth.; **49-***Vossia cuspidata* (Roxb.) Griff.

50-*Persicaria capitata* (Buch. -Ham. ex D. Don) H. Gross.

51-*Persicaria senegalensis* f. albotomentosa (R. A. Graham) K. L. Wilson.

52-*Persicaria strigosa* (R. Br.) H. Gross.

53-*Eichhornia crassipes* (Mart.) Solms; **54-***Azolla filiculoides* Lam; **55-***Typha domingensis* Pers.

56-*Phyla nodiflora* (L.) Greene. Bottom of Form

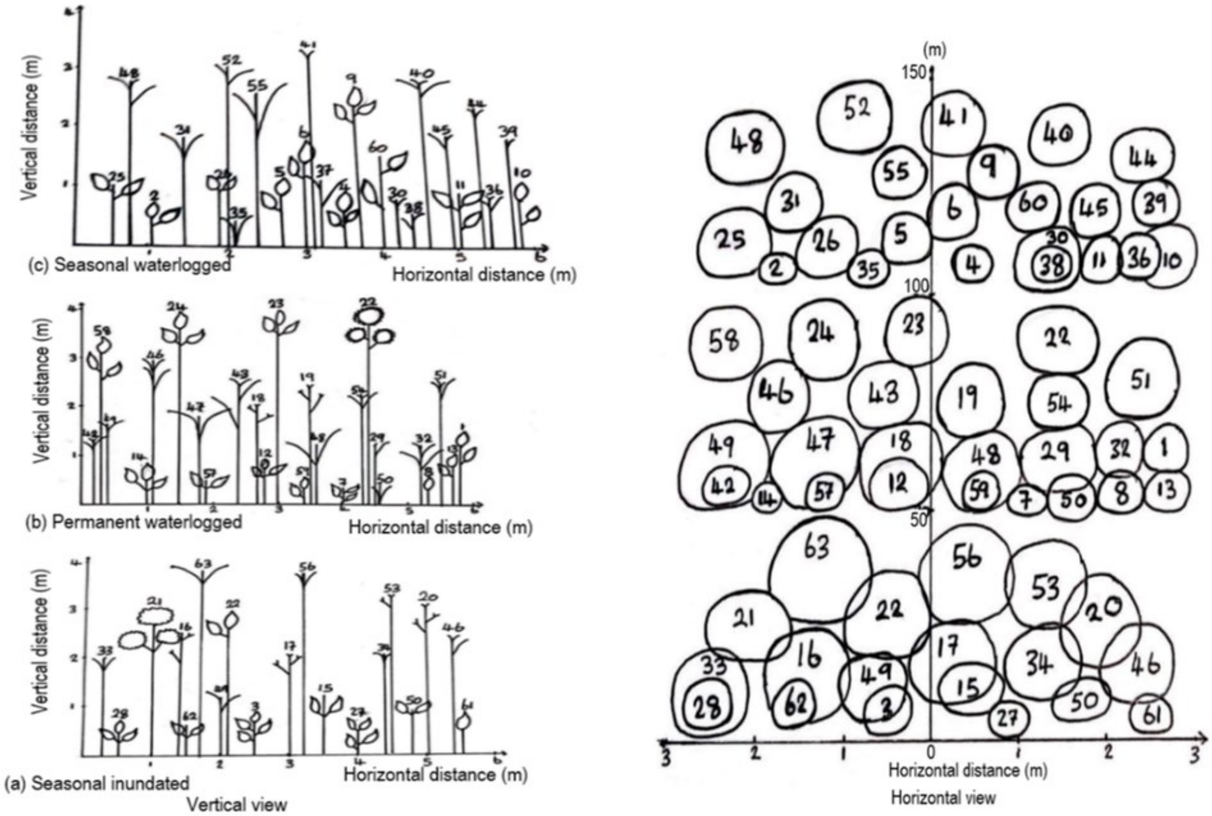

Figure 7b. Vegetation profile for Mposa site (S4). **I**. Vertical view of the profile; **II**. Horizontal view of profile.

1-*Hygrophila schulli* M. R. Almeida & S. M. Almeida; **2-***Amaranthus thunbergii* Moq.

3-*Lemna aequinoctialis* Welw; **4-***Ageratum conyzoides*. L; **5-***Bidens setigera*. (Sch.BIP.) Sheriff.

6-*Bidens stepped*. (Steetz) Sherff var. Steppia; **7-***Grangea maderaspatana* (L.) Poir.

8-*Sphaeranthus randii* S. Moore; **9-***Heliotropium indicum* L.

10-*Trichodesma physaloides* (Fenzl); **11-***Commelina benghalensis* L.

12-*Commelina diffusa* Burm. F.; **13-***Commelina grossa* C.B. Clarke.

14-*Commelina nyasensis* C.B. Clarke; **15-***Ipomoea aquatica* Forssk.

16-*Cyperus articulatus* L; **17-***Cyperus digitatus* Roxb.; **18-***Cyperus distans* L.f.

19-*Cyperus esculentus* L.

20-*Cyperus mauritianus* P. Willemet; **21-***Aeschynomene abyssinica* (A. Rich.) Vatke.

22-*Aeschynomene elaphroxylon* (Guill. & Perr.) Taub; **23-***Aeschynomene uniflora* E. Mey.

24-*Hibiscus cannabinus* L; **25-***Sida acuta* Burm.f; **26-***Sida alba* L.; **27-***Nymphaea lotus* L.

28-*Nymphaea nouchali* var. caerulea (Savigny); **29-***Sopubia lanata* Engl.**30-***Acrachne racemosa* (B. Heyne ex Roem. & Schult.) Ohwi; **31-***Aristida junciformis* Trin. & Rupr.

32- *Cynodon dactylon* (L.) Pers.; **33-***Diplachne fusca* (L.) P. Beauv. ex Roem. & Schult.

34-*Echinochloa stagnina* (Retz.) P. Beauv.; **35-***Eragrostis aethiopica* Chiov.

36-*Eragrostis aspera* (Jacq.) Nees; **37-***Eragrostis gangetica* Steud.

38-*Eragrostis pilosa* (L.) P. Beauv; **39-***Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.

40-*Hyparrhenia rufa* (Nees) Stapf; **41-***Hyperthelia dissoluta* (Steud.) Clayton.

42-*Imperata cylindrica* (L.) Raeusch.; **43-***Leersia hexandra* Sw.

44-*Leptocarydion vulpiastrum* (De Not.) Stapf; **45-***Loudetia simplex* (Nees) C.E. Hubb.

46-*Oryza longistaminata* A. Chev. & Roehr.; **47-***Panicum dregeanum* Nees.

48-*Panicum maximum* Jacq.; **49-***Panicum repens* L.; **50-***Panicum hygrocharis* Steud.

51-*Pennisetum purpureum* Schumach.; **52-***Pennisetum unisetum* (Nees) Benth.

53-*Phragmites mauritianus* Kunth (reeds); **54-***Setaria sphacelata* (Schumach.) Mos.

55-*Sporobolus pyramidalis* P. Beauv.; **56-***Vossia cuspidata* (Roxb.) Griff.

57-*Persicaria limbata* (Meisn.) H. Hara.

58-*Persicaria senegalensis* f. albotomentosa (R. A. Graham) K. L. Wilson.

59-*Persicaria strigosa* (R. Br.) H. Gross; **60-***Polygonum plebeium* R. Br.

61-*Eichhornia crassipes* (Mart.) Solms.

62-*Azolla filiculoides* Lam; **63-***Typha domingensis* Pers

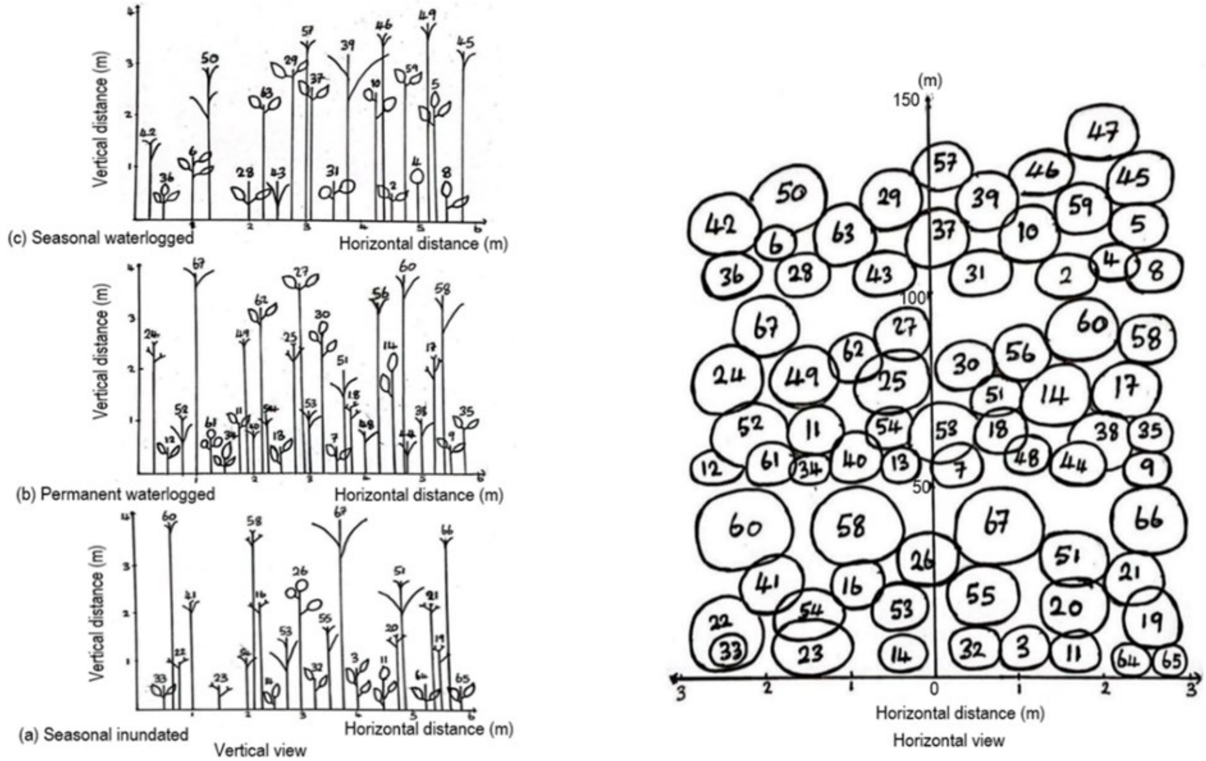

Figure 7c. Vegetation profile for Namanja site (S6). **I**. Vertical view of the profile; **II**. Horizontal view of the profile.

1-*Hygrophila schulli* M.R. Almeida & S.M. Almeida; **2-***Amaranthus thunbergii* Moq.

3-*Lemna aequinoctialis* Welw; **4-***Ageratum conyzoides*. L; **5-***Bidens setigera*. (Sch.BIP.) Sheriff.

6-*Bidens stepped*. (Steetz) Sherff var. Steppia. 7-*Emilia basifolia* L. Burt.

8-*Pseudognaphalium luteoalbum* (L.) Hilliard & B.L. Burt. 9- *Sphaeranthus randii* S. Moore.

10-*Trichodesma physaloides* (Fenzl); 11-*Ceratophyllum demersum* L.

12-*Commelina diffusa* Burm. F;**13-***Commelina nyasensis* C.B. Clarke; **14-***Ipomoea aquatica* Forssk.

15-*Bolboschoenus maritimus* (L.) Palla; **16-***Cyperus alterniflorus* R. Br; **17-***Cyperus distans* L.f.

18-*Cyperus esculentus* L; **19-***Cyperus laevigatus* L; **20-***Cyperus mauritianus* P. Willemet.

21-*Cyperus rotundus* L; 22-*Schoenoplectiella articulata* (L.) Ley.

23-*Schoenoplectus litoralis* (Schrad.) Palla; **24-***Scleria melanomphala* Kunth.

25-*Scleria nyasensis* C.B. Clarke; **26-***Aeschynomene abyssinica* (A. Rich.) Vatke.

27-*Aeschynomene nilotica* Taub; **28-** *Chamaecrista absus* (L.) H.S. Irwin & Barneb.

29-*Chamaecrista mimosoides* (L.) Greene; **30-***Hibiscus cannabinus* L; **31-***Sida alba* L.

32-*Nymphaea mexicana* A. Gray; **33-***Nymphaea nouchali* var. caerulea (Savigny).

34-*Rhamphicarpa fistulosa* (Hochst.) Benth; 35-*Sopubia lanata* Engl.**36-***Striga asiatica* (L.) Kuntze.**37-***Acrachne racemosa* (B. Heyne ex Roem. & Schult.) Ohwi; **38-***Acroceras macrum* Stap.

39-*Aristida junciformis* Trin. & Rupr; **40-***Cynodon dactylon* (L.) Pers.

41-*Diplachne fusca* (L.) P. Beauv. ex Roem. & Schult; **42-***Eragrostis aspera* (Jacq.) Nees.

43-*Eragrostis gangetica* Steud; **44-***Eriochloa meyeriana* (Nees) Pilg.

45-*Hyparrhenia filipendula* (Hochst.) Stapf.

46-*Hyparrhenia nyassae* (Rendle) Stapf; **47-***Hyperthelia dissoluta* (Steud.) Clayton.

48- *Imperata cylindrica* (L.) Raeusch; **49-***Leersia hexandra* Sw.

50-*Leptocarydion vulpiastrum* (De Not.) Stapf. 51-*Oryza longistaminata* A. Chev. & Roehr.

52-*Panicum dregeanum* Nees; **53-***Panicum repens* L; **54 -***Panicum hygrocharis* Steud.

55-*Setaria geminata* (Forssk.) Veldkamp; **56-***Pennisetum purpureum* Schumach.

57-*Pennisetum unisetum* (Nees) Benth.; 58-*Phragmites mauritianus* Kunth.

59-*Sporobolus pyramidalis* P. Beauv; 60-*Vossia cuspidata* (Roxb.) Griff.

61-*Persicaria limbata* (Meisn.) H. Hara.

62-*Persicaria senegalensis* f. albotomentosa (R.A. Graham) K.L. Wilson.

63-*Polygonum plebeium* R. Br; **64-***Eichhornia crassipes* (Mart.) Solms.

65-*Azolla filiculoides* Lam; **66-***Typha capensis* (Rohrb.) N.E. Br.; **67-** *Typha domingensis* Pers.

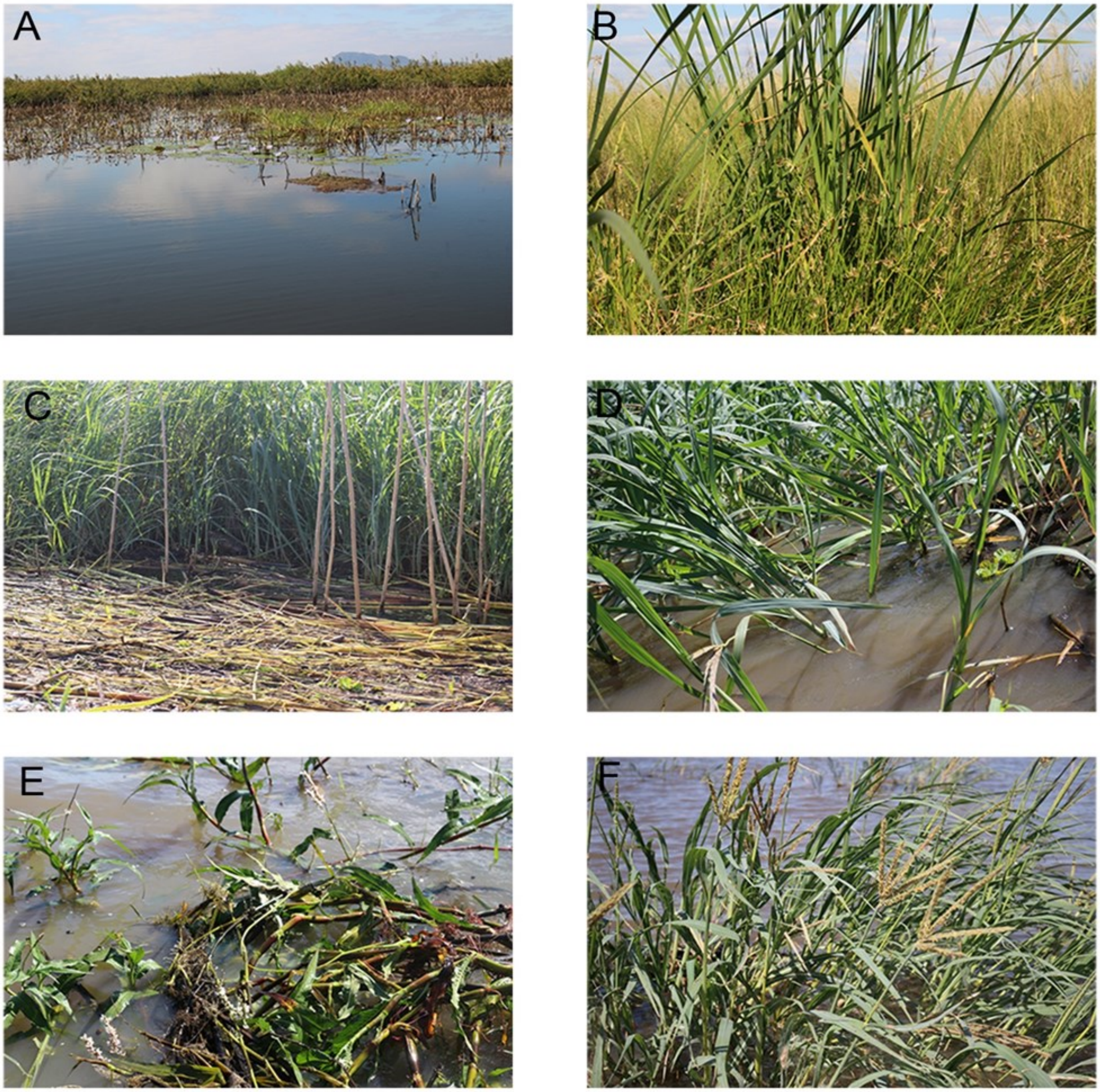

Figure 8. Vegetation view of seasonally inundated zones of lake Chilwa floodplain.

A-Aeschynomene species; **B**-Typha & Cyperus species; **C**-*Pennisetum purpureum* Schumach.

Physicochemical properties of soil across floodplain zones.

Agricultural activities and geological features, such as the igneous and mica pyroxenites rocks forming the basement of Lake Chilwa, as well as waste deposits and waterlogged conditions caused by floods, may influence the stability of soil nutrients like total phosphorus, total potassium and total nitrogen across different waterlogging zones in the floodplain.

Additionally, the frequency and duration of waterlogging appear to be crucial for the levels of soil organic matter, magnesium, calcium and soil pH. Moderate flooding and waterlogged conditions in permanently waterlogged zones can enrich the soil nutrients by promoting the decomposition of more organic materials. This process increases levels of total organic carbon, potassium, and total nitrogen as the organic matter decays, while also minimizing nutrients leaching. Futher more, these conditions may promote the coexistence of different species and enhance microbial activity, resulting in balanced and less depleted nutrients levels.

Typha domingensis Pers. and *Phragmites mauritianus* Kunth are prominent species in seasonally inundated zones. Being heavy feeders, they can deplete nutrients in these zones, thereby lowering the levels of some nutrients. Additionally, prolonged and frequent flooding in these areas can trigger nutrient leaching and anaerobic decomposition of organic matter. This leads to a loss of some nutrients from the soil into the atmosphere, thus affecting the dynamics of soil nutrients.

The intermittent wet and dry cycles determine soil mineralization, which may favour calcium solubility and mobility within the seasonally waterlogged soil. On the other hand, anthropogenic activities and invasive species might deplete some nutrients in the area.

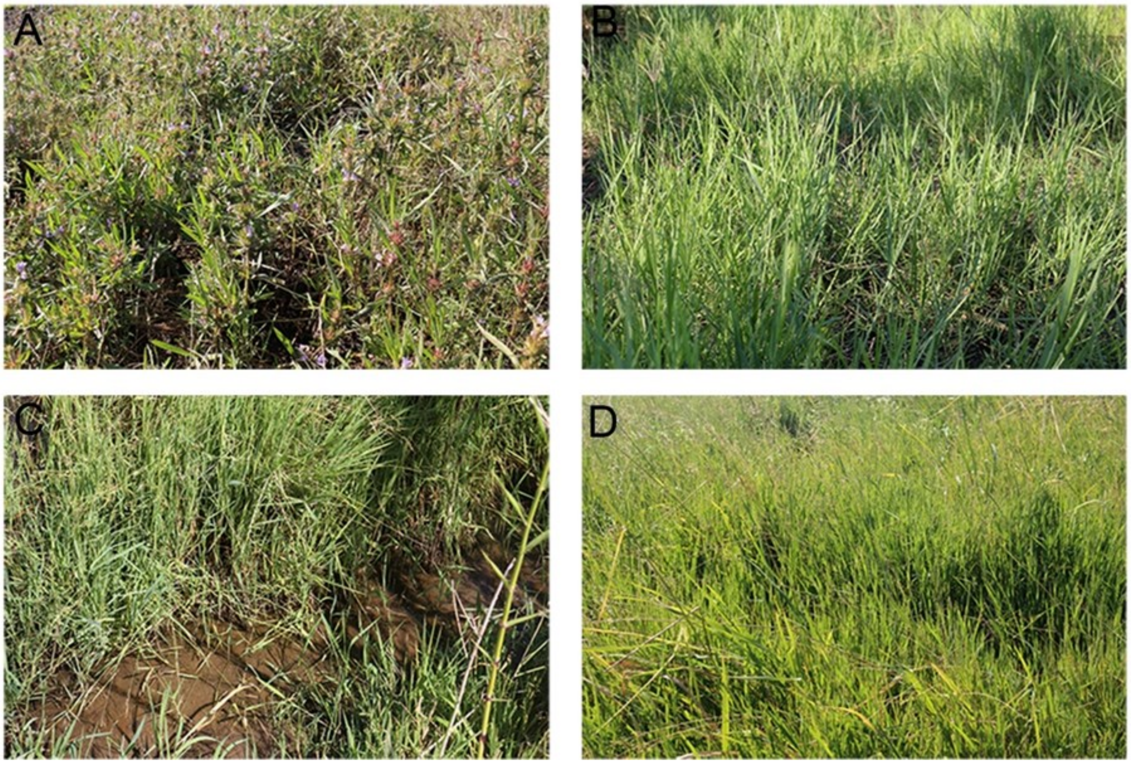

Figure 9. Vegetation view of permanently and seasonally waterlogged zones of lake Chilwa floodplain. **A**-*Hygrophila schulli* M.R. Almeida & S.M. Almeida; **B**-*Panicum repens* L; **C-***Leersia hexandra* Sw; **D**-*Imperata cylindrica* (L.) Raeusch.

CONCLUSION

Consistent with the study hypothesis and comparative previous research studies by (Gaudet, 1992; Musila, Kinyamario & Jungerius, 2001; Martinez & Psuty, 2003; Maltby & Barker, 2009; Raulings et al. ;2010 , Rongoei et al. ;2014 ,Fynn et al. ,(2015 ,the study results reveal that flooding regimes shape the biodiversity and ecological characteristics of the floodplain. The regular flooding and drying cycles significantly influence patterns and unique differences in species composition, vegetation structure, and soil nutrient dynamics. These natural processes regulate the ecosystem, allowing it to recover and maintain balance. This regulation affects soil physicochemical properties, promotes unique species compositions such as the dominance of Typha domingensis Pers, and results in the absence of prominent wetland species like Cyperus papyrus. It also leads to the evolution of less viable plants like Aeschynomene species and the shift of some species, typically found in swamps and marshes, into floodplain grasslands.

The high species diversity, dense understorey foliage cover, and balanced soil nutrient levels in moderately flooded zones create a buffer zone that supports the ecosystem. The survival of prominent perennial species throughout all seasons is also crucial for maintaining ecological balance, functioning, and resilience. The small-scale sampling may have influenced the negative correlation between species richness and evenness, thereby affecting significant differences in Shannon Weiner and Simpson diversity indices among the communities, as shown by the Kruskal-Wallis's test ($P= 0.5647$) and ANOVA tests ($P= 0.9996$) exceeding the critical P-value ($P > 0.05$), thus large-scale research was needed to capture more reliable data on species diversity.

The failure of floods to reach the floodplain could negatively affect plant species composition and distribution, impacting the floodplain ecosystem's ecological functions. These functions include providing food and habitats for wildlife and plant communities, recharging and discharging groundwater, recycling nutrients, and filtering pollutants (Cronk & Fennessy, 2001; Maltby & Barker, 2009). Additionally, continued flooding and drying have the potential to alter vegetation composition, resulting in a unique species composition. This process can also create microhabitat heterogeneity that promotes species coexistence and allows macrophytes to adapt differently, leading to high diversity and enhancing the resilience of the ecosystem.

Conservation efforts should focus on preserving natural hydrological regimes and water flow in these areas to maintain the diverse ecological niches and balance within the floodplain ecosystem. Minimizing land disturbances can also sustain diverse plant species and their ecological functions. The introduction of the invasive *Neltuma glandulosa*)Torr.) Britton & Rose, in the southern floodplain of Lake Chilwa threatens natural vegetation mosaics, potentially leading to the extinction of local species. Additionally, constructing dams and water channels for irrigation in these zones may have permanent detrimental effects on the ecosystem's vegetation dynamics and soil properties.

Monitoring and studying all environmental factors influencing wetland vegetation is essential to fully understand vegetation dynamics, species composition changes, and trends in vegetation structure. Wetland ecosystems are particularly sensitive to climate change, thus for further research study, it crucial to assess its potential impacts on flooding patterns and their subsequent effects on floodplain vegetation. This research is vital for developing adaptive management strategies in the face of global environmental changes.

Other research studies can also focus on the specific mechanisms of soil nutrient dynamics under varying flooding conditions and can provide insights into how nutrient availability and soil properties change, affecting plant growth and competition.

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