CHAPTER 4

FACTORS DETERMINING VEGETATION ZONATION IN THE SEASONAL FLOODPLAINS OF THE OKAVANGO DELTA.

4.1. Introduction.

Vegetation zonation is a common phenomenon in wetlands such as floodplains, salt-water marshes, inland and coastal swamps, lowland and upland mires, as well as agricultural wetlands such as rice paddies (Kozlowski, 1984; Singer & Munns, 1987; Armstrong *et al.*, 1994). The distribution of plant species and especially plant communities, is a result of all the present environmental factors, rather than a single or a few individual factors. Within any specific research problem, there are many environmental variables which could be measured, and it is often not easy to predict in advance which ones are going to be important (Kent & Coker, 1992). Many environmental factors that can be measured are not necessarily the most important factors that influence, or regulate the distribution of plant species (Bredenkamp, 1985). However, quantitative data on the individual environmental factors have often been used for ecological interpretation of the presence or absence of plant species in a given area (Bredenkamp & Theron, 1988). Bredenkamp (1985) pointed out that a good knowledge of the possible influence of some individual factors is valuable in interpreting the distribution of plant species and plant communities. One such factor is seasonal flooding.

Flooding is an important environmental factor that influence plant growth and plant species composition in different vegetation types in many parts of the world (Blom *et al.*, 1990). Flooding creates a gradient from highly flood resistant species on the lower sites of the wetlands, to intolerant species on the more elevated parts of then wetlands (Engelaar & Blom, 1995). Flooding regimes have also been identified as a primary agents determining nutrient status of soils in floodplains (Hughes, 1990; Blom *et al.*, 1990), hence determining and influencing plant biomass productivity. Plants occurring on frequently flooded sites have developed different morphological and physiological adaptations than those which occur in rarely flooded areas (Blom *et al.*, 1990). The most widely spread morphological adaptation to inundation are the formation of a root system of superficial roots and thick lateral roots containing aerenchyma, and rapid elongation of roots (Kozlowsky, 1984; Engelaar & Blom, 1995). In view of the enormous variety of flooding regimes that could occur, it would be most surprising if tolerance to flooding was based on a single adaptive feature strategy (Armstrong *et al.*, 1994). Broadly speaking, flooding resistance in plants is achieved by one or more features which improve gas exchange, as well as various metabolic features which help maintain a sufficient energy production to sustain cell integrity and avoid irreparable damage under oxygen stress (Armstrong *et al.*, 1994).

Literature, (Furness & Breen, 1980; Kozlowsky, 1984, Ellenbroek, 1987; Hughs *et al.*, 1990; Blom *et al.*, 1990, 1996; Roberts & Ludwig, 1991; Ellery *et al.*,1991; van de Rijt, *et al.*, 1996), indicates that vegetation zonation in seasonally flooded areas is caused by variation in hydrological characteristics of the rivers, variation of elevation of the flooded areas in relation to the water level of the feeding channel which results in variation in duration of flooding and extent of flooding. Other factors which are clearly important in determining vegetation zonation or species distribution include nutrient status, soil moisture retention capacity, grazing and browsing by wild and domestic herbivores, cultivation and other anthropogenic activities such as firewood collection and timber harvest (Hughes, 1990; Blom & Voesenek, 1996.). In most of the floodplains in the world, the rate of flow, seasonal flooding, frequency and or duration of flooding were found to be particularly important or critical (Sanchez *et al.*, 1996).

Flooding air dried soil sets in motion a series of physical, chemical and biological processes that profoundly influence the quality of soil as a medium of soil as a medium of plant growth. The nature, pattern and extent of the process depend on the physical and chemical properties of the soil and on the duration of submergence and chemical properties of the soil and on the duration of submergence (Ponnamperuma, 1984; Singer & Munns, 1987). The main chemical changes brought about by flooding or water logging air-dried soil are the disappearance of oxygen, accumulation of carbon dioxide, anaerobic decomposition of organic matter, transformation of nitrogen, and reduction of Fe(III), Mn(IV) and SO_4^{2-} (Ponnamperuma, 1984; Brandy, 1990). Draining and drying of flooded soils reverse most of these processes. The presence of a layer of standing water and differentiation of the soil profile into aerobic and anaerobic zones, have profound consequences on the ecology of flooded soils (Ponnamperuma, 1984). The surface of the water layer becomes the habitat of heterotrophic flora and fauna as well as algae and macrophytes.

Drastic restriction of gas exchange between flooded soils and atmosphere leads to accumulation in nitrogen, carbodioxide, methane and hydrogen gases, which build up pressure and escape as bubbles. Flooding air-dried soils causes indirect and direct electro-chemical exchange. One direct and almost instantaneous change is the dilution of soil solutions. This increases pH leading decrease in electrical conductance. When acid soils are kept flooded, its pH increases whereas the opposite occurs in alkaline soils (Ponnamperuma, 1984). The increase in pH of acid soils is mainly due to reduction of Fe(III) to Fe(II) (Ponnamperuma, 1984). The decrease in pH of sodic and calcarious soils are the results of accumulation of carbon dioxide (Ponnamperuma, 1984). .

Soil acidity is common in all regions where precipitation is high enough to leach appreciable amounts of exchangeable bases. Alkalinity occurs where there is a large degree of base saturation. The presence of salts, especially calcium, magnesium and sodium carbonates also give rise to high amounts of hydroxyl ions over hydrogen ions. Other factors which cause change in pH include increase in hydrogen ions. Therefore any process which will encourage the maintenance of or build up of exchangeable bases will contribute towards the reduction in acidity and increase in alkalinity (Brandy, 1990).

Detailed descriptive studies on the structure and composition of a number of floodplain ecosystems in semi-arid and arid parts of Africa have been conducted (Hughes, 1990). However, there is still little understanding of flood related mechanisms critical to the growth and regeneration of vegetation in African floodplains. This is attributed to by the fact that accurate hydrological records are not available for many African rivers (Hughes, 1990). The Okavango River hydrological records are no exception.

With the advent of computers, a number of programs used for vegetation data analysis were introduced. Among those programs are those that are used for gradient analysis or ordination (Kershaw, 1973; Barbour *et al*, 1987; Kent & Coker, 1992). Gradient analysis has proved very useful in studying ecology of species (Miles, 1979), and together with classification they have furthered our understanding of vegetation relationships and variations.

In plant ecology, gradient analysis and ordination methods can help researchers to summarise plant community data, by providing an indication of the true nature of variation within the vegetation of the area under study, as well as enabling the distribution of individual species within different communities to be examined and compared (Kent & Coker, 1992). Gradient analyses also provide summaries of variation within sets of vegetation samples which can then be correlated with environmental controls to define environmental gradients (Kent & Coker, 1992). Gradient analysis and ordination techniques are a group of methods for data reduction and exploration leading to hypothesis generation. The methods are essentially descriptive and enable researchers to formulate ideas about the plant community structure as well as possible causal relationships between variation of vegetation and its environment (Kent & Coker, 1992).

Direct gradient analysis is used to display a variation in of vegetation in relation to environmental factors by using environmental data to order the vegetation samples. In this analysis environmental data are used directly to organise the information on vegetation (Kent & Coker, 1992). The method assumes that the underlying environmental gradients are known, and are quite distinct.

For direct gradient analysis, a computer program known as DECORANA (DEtrended CORrespondence ANAlysis) (Hill, 1979a.; Kent & Coker, 1992) is used. This program was designed primarily for ecologists who have collected data on the occurrence of a set of species in a set of samples. Its main purpose is to make ordination by the method of detrended correspondence analysis.

Indirect gradient analysis is a term applied to techniques which operate on a set of vegetation data by examining the variation within it. These ordinations are based on analysis of floristic data independently of any preconceived notions of controlling environmental factors or succession sequences (Kent & Coker, 1992). A second set of analysis is then performed once the major sources of variation in the vegetation data have been described and summarised (Kent & Coker, 1992). Only then are the environmental data compared and correlated with the summarised vegetation data in order to detect the possible environmental gradients, thus the environmental interpretation is indirect (Kent & Coker, 1992). This approach of using both species and environmental data in the actual ordination process is called canonical analysis (Kent & Coker, 1992). One of the methods commonly used for indirect correspondence analysis is a technique known as Canonical Correspondence analysis which is aided by a computer program known as CANOCO (ter Braak, 1986; Kent & Coker, 1992). Methods of indirect gradient analysis are much more widely used than those of direct gradient analysis. The main reason is that species data are usually very much easier to collect than environmental data. Ellery *et al.* (1993) used an indirect gradient analysis to elucidate relationships between distribution of plant species in the islands of the Okavango Delta and environmental variables using detrended correspondence analysis (DECORANA). The environmental variables which Ellery *et al.* (1993) included water depth, groundwater pH, and conductivity, soil sodium concentration (topsoil and subsoil) and soil calcium concentration (top soil and subsoil). Although distance from water source, depth of water are all correlated with plant distribution patterns of the Okavango Delta, Ellery *et al*. (1993) found that soil and groundwater also appear to be major determinants of woody species distribution. In contrast to woody species, the distribution of herbaceous species appears to be determined by the concentrations of sodium in the surface soils.

4.2. Objectives

The objectives of the study are:

i). To relate the derived plant communities to environmental attributes , which probably determine their distribution within an area.

ii). To examine variation in soil mineral nutrients (macro - elements) in relation to flooding.

4.3. Methods

4.3.1. Elevation

The elevation from the five permanently marked plots from each of the zones or community type were measured using a theodolite. A Benchmark of known elevation from sea level was located in the study area . That Benchmark was then used to measure elevation of the plots with reference to the sea level. The elevation of the riverbed at sea level was also measured. The difference in elevation of each of the plots with reference to the riverbed was calculated.

4.3.2. Duration and Depth of flooding

Duration of flooding was estimated by recording the number of weeks during which each zone was inundated during the flooding season. This was done for two flooding seasons (i.e 1996 and 1997). The depth of flooding was measured using a meter rule. In each zone, a number of measurements were taken from different parts of the zone, and an average reading was calculated. These readings were taken at the peak of the floods. The reading at which water the level no longer increased was recorded as the maximum flooding depth.

4.3.3. Soil pH. extractable Na, P, K, Ca, Mg

The above soil characteristics were determined by the Soil Science Laboratory at the University of Pretoria as described in N.A.S.A.W.C. 1991. Soil samples were collected during the rainy season, as well as before and after flooding to. The soils samples were collected from the same 40 plots described in Chapter 3. The collection, sampling equipment, transport, storage and drying, grinding and sieving were done as described in Chapman (1976), Landon (1984) and Anderson & Ingrim (1989). Analysis of variance was performed using a split-plot design and SAS System. A multiple comparison was used to determine the statistical significance between communities.

4.3.4. Ordination.

The floristic data were ordinated using the computer program DECORANA (Hill, 1979a). The following environmental factors were used: elevation, duration of flooding, depth of flooding, soil pH, extractable Na, P, K, Ca, Mg.

4.4 Results:

4.4.1 Elevation, duration of flooding and depth of flooding

The elevation of the eight zones or communities described in chapter 3 were found to lie between 946-948 m above sea level. The results of elevation measurements are presented in Table 4.1. The riverbed in the study area is 945 m above sea level on average. The *Sporobolus spicatus* communities occupy the highest points of the floodplain with an average of 2.36 m (n = 5) above the riverbed, followed by *Imperata cylindrica-Setaria sphacelata* and *Veteveria nigritiana-Setaria sphacelata* communities with an average of 2.20 m (n = 5) and 2.01 m (n = 5) respectively (Table 4.1). The *Cyperus articulatus-Schoenoplectus corymbosus* community occupies the lowest position with an average elevation above the riverbed of 1.19 m (n = 5) followed by the *Alternanthera sessils-Ludwigia stolonifera* community with an average elevation above the riverbed of 1.27 m (n = 5)

Table 4.1..Table showing mean elevation above sealevel **(EASL, n** = 5), mean elevation above riverbed **(EARB, n** = 5), mean duration of flooding **(DF, n = 5),** mean maximum depth of flooding (**MDpF n** = **20)** for flooding seasons 1996 and 1997 in each zone or community type.

Community /Zone	X EASL (m)	X EARB (m)	X DF (wks)1996	X DF (wks) 1997)	X MDpF (m)1996	X MDp (m)1997
Alternanthera sessils-Ludwigia stolonifera	946.63	1.27	20	23	0.39	0.50
Cyperusarticulatus-Schoenopletus corymbosus	946.57	1.19	13	16	0.51	0.78
Miscanthus junceus-Digitaria scalarum	947.15	1.77	9	12	0.33	0.48
Paspalidium obtusifolium-Panicum repens	947.03	1.61	5	9	0.17	0.35
Setaria sphacelata-Eragrostis inamoena	947.20	1.83	0	5	0	0.15
Veteveria nigritiana-Setaria sphacelata	947.38	2.01	0	0	0	0
Imperata cylindrica-Setaria Sphacelata	947.50	2.20	0	0	0	0
Sporobolus spicatus-Cynodon dactylon	947.67	2.36	0	0	0	0

The mean duration of flooding and mean flooding depth were low in 1996 compared to 1997 (see Table 4.1). Hydrological records revealed that the floods in 1996 were lowest since 1940 (Water Affairs, 1996). Mean depth of flooding was highest in the *Cyperus articulatus-Schoenoplectus corymbosus community* in both years (Table 4.1). The duration of flooding was longest in the *Alternanthera sessilis-Ludwigia stolonifera* community followed by the *Cyperus articulatus-Schoenoplectus corymbosus* community.

4.4.2. Soil pH, Na, P, K, Ca, Mg.

The results of the soil analysis are presented in Tables 4.2, 4.3 and 4.5.

Table 4.2. Table showing mean chemical properties of soils after flooding.

	Soil chemical properties after flooding						
Community type	PH	Resist (Ohms)	P (mgkg^{-1})	Ca (mgkg^{-1})	K (mgkg^{-1})	Mg (mgkg^{-})	Na (mgkg^{-1})
Alternanthera sessilis-Ludwigia stolonifera	5.69	1200	21.12	1646.60	177.00	286.40	23.20
Cyperus articulatus–Schoenoplectus corymbosus	6.02	2740	3.44	1210.50	208.60	210.00	128.60
Miscunthus junceus - Digitaria scalarum	6.05	1240	12.34	1074.00	146.20	171.60	11.40
Paspalidium obtusifolium-Panicum repens	5.89	1740	5.99	620.80	129.80	119.20	9.80
Eragrostis inamoena-Setaria sphacelata	6.18	2520	4.37	666.80	156.60	134.00	14.20
Imperata cylindrica-Setaria sphacelata	6.76	1400	4.52	918.80	159.80	152.00	0.00
Veteveria nigritiana-Setaria sphacelata	6.57	2240	6.42	507.60	138.20	99.60	11.80
Sporobolus spicatus-Cynodon dactylon	8.75	1407	2.53	941.60	526.20	29.20	1087.00

Table 4.3. Results of the chemical properties of soils before flooding

	Soil chemical properties before flooding						
Community type	PH	Resist (Ohms)	P (mgkg^{-})	Ca (mgkg^{-1})	K (mgkg^{-1})	Mg (mgkg^{-1})	Na (mgkg^{-1})
Alternanthera sessilis- Ludwigia stolonifera	5.28	918	18.54	1548.8	111.2	185.8	54.2
Cyperus articulatus – Schoenoplectus corymbosus	5.56	1300	8.56	1045.6	101.8	127.2	16.6
Miscunthus junceus - Digitaria scalarum	5.82	1290	12.73	1052.4	136.6	147.8	23.6
Paspalidium obtusifolium-Panicum repens	6.07	1450	4.96	693.2	79.8	79.6	23
Eragrostis inamoena-Setaria sphacelata	5.82	1640	5.02	650.4	80.2	84.6	3.8
Imperata cylindrica-Setaria sphacelata	6.85	1180	5.05	1214.8	380.6	90.6	5.0
Veteveria nigritiana-Setaria sphacelata	6.46	1760	3.39	378.8	76.2	65.8	4.6
Sporobolus spicatus-Cynodon dactylon	8.78	1048	2.98	897.6	319.4	26.6	280.8

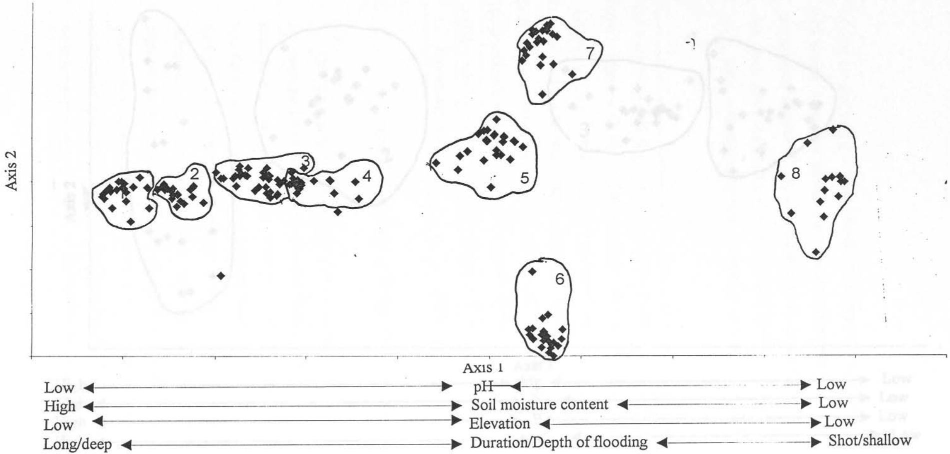
Table 4.4 Results of the chemical properties of soil middle of the rainy season.

	Soil chemical properties in middle of the rainy season flooding						
Community type	PH	Resist (Ohms)	P ($mgkg^{-1}$)	Ca ($mgkg^{-1}$)	K ($mgkg^{-1}$)	Mg ($mgkg^{-1}$)	Na ($mgkg^{-1}$)
Alternanthera sessilis- Ludwigia stolonifera	5.39	1020	21.82	2071.6	147	315	71
Cyperus articulatus – Schoenoplectus corymbosus	5.47	820	9.64	1910.4	187.8	287.4	50.6
Miscunthus junceus- Digitaria scalarum	5.63	1120	9.5	1258.4	161.8	182.6	33.8
Paspalidium obtusifolium-Panicum repens	5.98	1560	5.6	1494.8	170.2	217	24.4
Eragrostis inamoena-Setaria sphacelata	6.29	1860	6.82	806.8	124.6	133.8	26.8
Imperata cylindrica-Setaria sphacelata	7.03	1020	5.96	1568	142.2	187	11.4
Veteveria nigritiana-Setaria sphacelata	6.25	1220	7.62	988	203	180.6	20.2
Sporobolus spicatus-Cynodon dactylon	9.04	1740	4.86	870	213	30.4	30

4.4.3. Ordination.

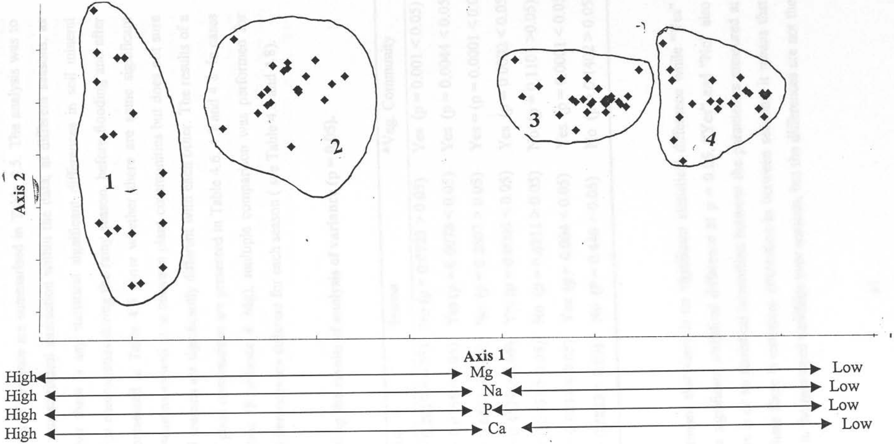
The first two axes in the stand ordination derived from DECORANA accounted for the large proportion of summed variation of axes 1 to 4. Eigen values of 0.956 and 0.826 for axes 1 and 2 were much greater than those for axes 3 and 4 (0.437 and 0.349), and hence only the first two axes are considered in the analysis. The distribution of the releves along the first and the second axes is presented in Fig. 4.1. The third and fourth axes contributed very little to environmental interpretation of the communities and they are therefore not reported here. In a scatter diagram (Fig. 4.1) distinct discontinuities in the distribution of the releves are observed. The plant communities are restricted to specific spatial areas in the diagram along the first axis. Plant communities of wetter parts of the floodplains are restricted to the left part of the diagram while plant communities of the drier parts of the floodplains are restricted to the right part of the diagram. The discontinuities are more distinct in the communities lying in the secondary floodplains (i.e. *Imperata cylindrica - Setaria sphacelata* community, *Eragrostis inamoena - Setaria Spahecelata* community, *Veteveria nigritiana - Setaria sphacelata* community), *Sporobolus spicatus* community). In communities lying in the wetter primary floodplains (*Alternanthera sessilis- Ludwigia stolonifera* community, *Cyperus articulatus-Schoenoplectus corymbosus* community, *Miscanthus junceous-Digitaria scalarum* community and *Paspalidium obtusifololium-Panicum repens* community) discontinuities are noticeable but are not very distinct. The vegetation gradient of the first axis is primarily associated with the elevation and soil moisture regime (duration and extent of flooding), and soil pH. From left to right the inundation increases both in duration and depth, while pH changes from acidity to alkalinity. The second axis does not show association with any environmental gradient. It is possible though that it might illustrate soil gradients such as soil texture, soil depth and drainage and these factors were not investigated in this study.

Since the discontinuities in the wetter areas were not very clear, releves from those areas were ordinated separately to determine the possible environmental gradients associated with these communities. The releves from the drier areas were also ordinated separately even though clear discontinuities were observed from the combined ordination. The subsequent distribution of the releves along the first and the second axes from the separate ordinations are presented in Fig. 4.2 . In addition to the main gradients observed from the combined ordination, more gradients were revealed from the second ordination. From the separate ordinations, the vegetation gradient of the first axis is primarily associated with the depth flooding, P, Mg, Na and Ca. The second axis did not show any environmental gradient once again. For the drier areas (secondary floodplains) no interpretable gradients were noticed along the second axis, hence the separate ordination graph is not presented



1 = *Alternanthéra sessilis* - *Ludwigia stolonifera* community; 2 = *Cyperus articulatus* - *Schoenoplectus corymbosus* community; 3 = *Miscunthus junceus* - *Digitaria scalarum* community; 4= *Paspalidium obtusifolium* - *Panicum repens* community; *Eragrostis inamoena* - *Setaria sphacelata* community; 6 = *Imperata cylindrica* - *Setaria sphacelata* community; 7 = *Veteveria nigritiana* - *Setaria sphacelata* community; 8 = *Sporobolus spicatus* community

Fig 4.1 **The relative position of the syntaxa along the first two axes of the ordination of floristic data**



1 = *Alternanthera sessilis* - *Ludwigia stolonifera* community; 2 = *Cyperus articulatus* - *Schoenoplectus corymbosus* community; 3 = *Paspalidium obtusifolium* - *Panicum repens* community; 4 = *Miscanthus junceus* - *Digitaria scalarum* community.

Fig 4.2 The DECORANA ordination of the releves of the wet areas (primary floodplain).

4.4.4 Statistical analysis

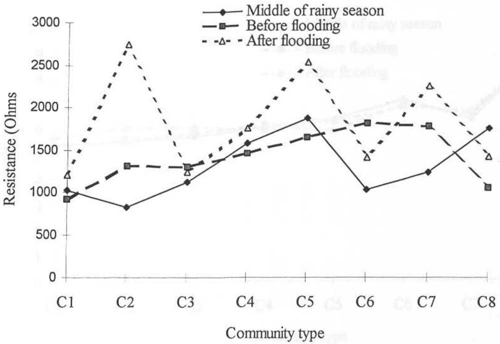
The results of the analysis of variance are summarised in Table 4.5. The analysis was to establish whether there was statistical interaction within the data, at different seasons, as well as establish whether there is any statistical significant differences in soil mineral contents in the vegetation communities during the rainy season, before flooding and after flooding. The results presented in Table 4.6 show whether there are some significant differences in between seasons as well as in between plant communities but does not sure which communities and seasons are significantly different with each other. The results of a multiple comparison of plant communities are presented in Table 4.6, 4.7 and 4.8. In cases where there is interaction (Resistance & Mg), multiple comparison was performed for each season since the differences are different for each season (see Table 4.7 and 4.8).

Table 4.5. Table showing the results of analysis of variance ($p = 0.05$).

Variable	Interaction	Season	*Veg. Community
pH	No ($p = 0.2819 > 0.05$)	No ($p = 0.0723 > 0.05$)	Yes ($p = 0.001 < 0.05$)
Resistance	Yes ($p = 0.0158 < 0.05$)	Yes ($p = 0.0078 < 0.05$)	Yes ($p = 0.0044 < 0.05$)
P	No ($p = 0.6582 > 0.05$)	No ($p = 0.2607 > 0.05$)	Yes = ($p = 0.0001 < 0.05$)
Ca	No ($p = 0.4679 > 0.05$)	Yes ($p = 0.0005 < 0.05$)	Yes ($p = 0.0002 < 0.05$)
K	No ($p = 0.3767 > 0.05$)	No ($p = 0.6211 > 0.05$)	No ($p = 0.1101 > 0.05$)
Mg	Yes ($p = 0.0033 < 0.05$)	Yes ($p = 0.004 < 0.05$)	Yes ($p = 0.0001 < 0.05$)
Na	No ($p = 0.6883 > 0.05$)	No ($P = 0.446 > 0.05$)	No ($p = 0.1402 > 0.05$)

* vegetation

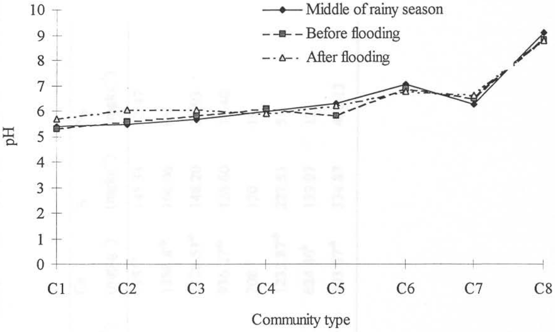
In Table 4.5, "No" means that there is no significant statistical difference while "Yes" means that there is a significant statistical difference at $p = 0.05$. "Yes" and "No" also indicate whether there is or no statistical interaction between the parameters measured at different seasons. Where there is statistical interaction in between seasons, it means that there are differences in the measured variables over seasons, but the differences are not the same. Taking resistance for example, the plant community that has the highest resistance in the middle of the rainy season will not always have the highest resistance before floods and after floods. In this case the differences do not follow the same pattern. Where there is no interaction, it means that the differences are always the same if there are any. Taking pH for an example, the *Alternathera sessilis – Ludwigia stolonifera* community will always have the lowest pH while the *Sporobolus spicatus* community will always have the highest pH at all seasons. In this case there is no interaction. Fig. 4.3 illustrates a situation where there is statistical interaction while Fig. 4.4 is an example of a case where there is no interaction. The graphical display (Fig. 4.3), shows that there are differences in resistance between the soil types and also between the different seasons. The significant interaction is observed in the graph's tendency not to show any consistent pattern, and this means that although there are differences in resistance between community types, these differences are not the same for the different seasons.



Legend

C1 = *Alternanthera sessilis- Ludwigia stolonifera* community, C2 = *Cyperus articulatus - schoenoplectus corymbosus* community, C3 = *Miscunthus junceus- Digitaria scalarum* community C4 = *Paspalidium obtusifolium-Panicum repens* community, C5 = *Eragrostis inamoena-Setaria sphacelata* community, C6 = *Imperata cylindrica-Setaria sphacelata* community, C7 = *Veteveria nigrtiana-Setaria sphacelata* community C8 = *Sporobolus spicatus-Cynodon dactylon* community

Fig.4.3. Figure illustrating statistical interaction of resistance in different communities in different seasons.



Legend

C1 = *Alternanthera sessilis- Ludwigia stolonifera* community, C2 = *Cyperus articulatus - schoenoplectus corymbosus* community C3 = *Miscunthus junceus- Digitaria scalarum* community C4 = *Paspalidium obtusifolium-Panicum repens* community C5 = *Eragrostis inamoena-Setaria sphacelata* community C6 = *Imperata cylindrica-Setaria sphacelata* community C7 = *Veteveria nigrtiana-Setaria sphacelata* C8 = *Sporobolus spicatus-Cynodon dactylon* community

Fig 4.4 Figure illustrating no statistical interaction on pH in different seasons

Table 4.6 Table showing the results of multiple comparison to determine statistical significance for variables with no interactions. Figures with the same superscripts are not significantly different

Community type	PH	P (mgkg^{-1})	Ca (mgkg^{-1})	K (mgkg^{-1})	Na (mgkg^{-1})
Alternanthera sessilis- Ludwigia stolonifera	5.45^{a}	20.52^{a}	1755^{b}	145.33	52.47
Cyperus articulatus – Schoenoplectus corymbosus	5.68^{a}	7.21^{a}	1388.8^{ab}	166.06	65
Miscunthus junceus - Digitaria scalarum	5.84^{a}	11.52^{a}	1128.53^{ab}	148.20	22.93
Paspalidium obtusifolium-Panicum repens	5.98^{a}	5.51^{a}	936.27^{ab}	126.60	18.40
Eragrostis inamoena-Setaria sphacelata	6.10^{a}	5.40^{a}	708.^{a}	120	16
Imperata cylindrica-Setaria sphacelata	6.88^{b}	4.53^{a}	1233.87^{ab}	227.53	5.4
Veteveria nigritiana-Setaria sphacelata	6.49^{b}	5.78^{a}	624.80^{b}	139.07	12
Sporobolus spicatus-Cynodon dactylon	8.88^{c}	3.46^{b}	903.07^{ab}	334.87	466.13

Table 4.7 Table showing the multiple comparison for resistance. Figures with the same superscripts are not significantly different

Community type	Resistance (ohms) Mid raining season	Resistance (ohms) Before floods	Resistance (ohms) After floods
Alternanthera sessilis- Ludwigia stolonifera	1020^{a}	918^{a}	1200^{a}
Cyperus articulatus – Schoenoplectus corymbosus	820^{a}	1300^{a}	2740^{b}
Miscunthus junceus - Digitaria scalarum	1120^{a}	1290^{ab}	1240^{a}
Paspalidium obtusifolium-Panicum repens	1560^{bc}	1450^{ab}	1740^{ab}
Eragrostis inamoena-Setaria sphacelata	1860^{c}	1640^{ab}	2520^{b}
Imperata cylindrica-Setaria sphacelata	1020^{a}	1180^{ab}	1400^{a}
Veteveria nigritiana-Setaria sphacelata	1220^{ab}	1760^{b}	2240^{b}
Sporobolus spicatus-Cynodon dactylon	1740^{c}	1048^{ab}	1407^{a}

Table 4.8 Table showing the multiple comparison for magnesium. Figures with the same superscripts are not significantly different

Community type	Mg (mgkg^{-1}) Mid raining season	Mg (mgkg^{-1}) Before floods	Mg (mgkg^{-1}) After floods
Alternanthera sessilis- Ludwigia stolonifera	315^{d}	111.2^{a}	286.4^{d}
Cyperus articulatus – Schoenoplectus corymbosus	287.4^{cd}	101.8^{a}	210^{cd}
Miscunthus junceus - Digitaria scalarum	182.6^{b}	136.6^{a}	171.6^{c}
Paspalidium obtusifolium-Panicum repens	$217b^{c}$	79.8^{a}	119.2^{b}
Eragrostis inamoena-Setaria sphacelata	133.8^{b}	80.2^{a}	134^{bc}
Imperata cylindrica-Setaria sphacelata	187^{b}	380.6^{b}	152^{bc}
Veteveria nigritiana-Setaria sphacelata	180.6^{b}	76.2^{a}	99.6^{ab}
Sporobolus spicatus-Cynodon dactylon	30.4^{a}	319.4^{b}	29.20^{a}

4.5. Discussion

Distribution of vegetation of the Okavango Delta floodplains was found to be influenced by elevation gradient which in turn determines the extent, depth and duration of flooding as it is the case with most similar systems (Furness & Breen, 1980; Kozlowsky, 1984, Ellenbroek, 1987; Hughes *et al.*, 1990; Blom *et al.*, 1990, 1996; Roberts & Ludwig, 1991; Ellery *et al.*, 1991; van de Rijt *et al.*, 1996). However, tolerance of flooding seems to be the major factor influencing and determining vegetation distribution or zonation in wetland systems. For example species of the *Alternanthera sessilis-Ludwigia stolonifera, Cyperus articulatus–Schoenoplectus corymbosus*, *Paspalidium obtusifolium-Panicum repens* and the *Miscanthus junceus-Digitaria scalarum* communities are all tolerant to flooding, hence they are located in areas which are subjected to prolonged deep flooding (primary floodplains). Species of the of the *Eragrostis inamoena-Setaria sphacelata, Imperata cylindrica-Setaria sphacelata, Veteveria nigritiana-Setaria sphacelata* and *Sporobolus spicatus* communities cannot tolerate prolonged flooding (secondary floodplains), but may handle short periods of flooding, thus they are located in elevated areas which low flooding intensity (see Table 4.1). Snaydon (1987) concluded that response of plant populations to environmental variation depends on the pattern and magnitude of environmental variation and the biological attributes. He further argued that environmental variation in space and time should be considered separately. Variation in time can be categories on the basis of form (e.g. random vs cyclic), frequency and amplitude. while variation in space can be categories on the basis of dimension (horizontal v vertical), scale and amplitude (Snaydon, 1987).

Although the above mentioned factors were identified as the most important factors governing vegetation zonation, there might be other important factors which are not easily noticeable. Factors such as past natural disasters and historical landuse practices may conspire against environmental differences (Grieg-Smith, 1983; Haore, 1997). Haore (1997) pointed out that it must be emphasised that correlation between environmental variables and vegetation distribution is no proof of causal relationship, and additional experimental information and ecological knowledge are required to support such a supposition. Numerous detailed studies have been carried out on the flooding tolerance of individual species and their adaptation to flooding, but not much is known about the critical minimum and maximum flood levels needed for germination, resprouting and establishment of seedlings (Furnes & Breen, 1980). Hughes (1990) argued that floodplain vegetation growth could only be sustained above a critical elevation receiving floods of critical maximum frequency and duration. It therefore follows that any alteration of the flooding regime, especially reducing the intensity and duration of flooding may result in adverse effects on the overall productivity of the floodplain ecosystem or change is species composition.

Ordination of floristic data successfully identified discontinuities that agreed well with the field observations. The elevation and moisture gradient were obvious from the field while chemical gradients were not noticeable until an ordination was performed. The chemical gradients were more pronounced in the separate ordination of the data, especially releves from the wet areas (primary floodplains). Generally P, Ca, Mg, and Na decrease with the increase in elevation and decrease in moisture within the primary floodplain (see Fig.4.2). This shows that flooding regimes are primary agents determining the nutrient status of the soils in the seasonal floodplains.

Analysis of variance of soil chemical characteristics over seasons revealed that there are no significant differences in pH, P, K and Na at $p = 0.05$ (Table 4.5). Ca and Mg showed some statistical significance over seasons. It is not surprising that there is no significant difference in P over seasons because P is not a mobile element. Its surprising however that the results in Table 4.5 show that there is no significant statistical difference in Na and K contents between vegetation communities as well as between seasons. Taking *Sporobolus spicatus* community for example, the average Na content in the middle of the raining season is 30 $mgkg^{-1}$ (see Table 4.4), while the average Na content after flooding is 1087 $mgkg^{-1}$ (see Table 4.2). This appears to be a significant difference in Na content between seasons, as well as between vegetation communities but statistical analysis showed no significant difference. With Na salts highly soluble one would expect Na contents to vary over seasons, with low values during the raining season and high values during the dry season (after floods). Na would be lost to deeper parts of the soil due to leaching during the rainy seasons, but would be expected to rise to the surface as the ground water table rises with flooding. K salts are also highly soluble, thus one would expect significant variations over seasons.

Ca salts are sparingly soluble, depending on the form. For example, carbonates are less soluble while sulphates are more soluble. However, during the flooding microbial activity results in the production of carbonic acid which reacts with Ca salts, thus releasing Ca into the soil (Totolo, 1999. Pers. com.). This explains why there is an increase in Ca after the flooding. Mg salts are also not highly soluble and one would expect it not to differ over seasons as the statistical analysis shows that there are no significant differences. Resistance showed significant differences over season as well as among communities. This is highly possible because resistance depends on the amount of ions in the soil. Concentration of ions varies with changes in soil moisture regimes, thus resulting in significantly different resistance over seasons. Soil pH, resistance, P, Ca, and Mg showed significant statistical significance between communities while Na and K showed no significant statistical difference (see table 4.5).

The soil mineral contents in different communities vary because of the differences in soil organic matter and soil moisture which influence soil biological and chemical activities. For example, when decomposition slows or above ground litter fall increases, the accumulating surface mass of decomposing organic matter increases cation exchange capacity. In the absence of an increased base supply, this decreases the base saturation and hence the pH of the soil (Miles,1987). In the floodplains accumulation of organic matter depends on the type of species in vegetation communities and relative utilisation by herbivores. For example there is more litter accumulation in communities lying in the primary floodplains because species in those areas are heavily utilised by herbivores, resulting in trampling of plant material to the ground, hence an increase in litter. The decomposition rate in these area is higher than in the drier areas thus the soil in those areas are acidic while the soils in drier areas like *Sporobolus spicatus* community are alkaline because the decomposition rate is low. Plants vary in such attributes as nutrients demands and uptake, nutrients return and chemical composition (Miles, 1987). This results in variation in soils mineral contents as shown by the results in table 4.5. Plants therefore affect the soil both directly and indirectly resulting and hence affect soil productivity.

On average, there is an increase in the amount of elements after flooding in cases which showed significant differences, as well as in cases which did not show significant differences. This could be due to the fact that as floodwater comes, it comes along with dissolved salts which are then deposited in the floodplains. As flood recedes, a substantial amount of soil water evaporates, thus leaving a high concentration of salts on the surface of the soil. Flooding also results in the raising of the ground water table. As a result salts which were leached probably during the rainy season move to the surface of the soil through capillary movement, and that contributes to the increase of salts concentration.

4.6. Conclusion

Elevation and duration of flooding are the major factors which influence vegetation zonation in the seasonal floodplains. This was revealed by successful ordination of floristic data using DECORANA which showed clear gradients illustrating variance in moisture and elevation. Ordination also revealed other gradients such as pH and soil mineral content gradients are probably depended on the moisture gradient because soil moisture influences the soil biological and chemical characteristics. However it must be noted that ordination techniques are not capable of identifying all factors which determine vegetation zonation because of its complexity. The soils of the seasonal floodplains of the Okavango have existed for a long period of time. Therefore seasonal flooding does not bring about massive change in soil mineral contents. Mineral contents possibly deviate from an equilibrium long-term average with season.