Vegetation ecology of the seasonal floodplains in the Okavango Delta, Botswana.

by

Mpaphi Casper Bonyongo.

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Department of Botany
University of Pretoria
PRETORIA

Supervisor: Prof. G. J. Bredenkamp

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1. Introduction

The Okavango River Delta is a large land locked alluvial fan located in the north western part of the semi-arid Kalahari basin of Northern Botswana. It covers an area of about 22 000 km^2 of which approximately 6 000 km^2 is permanent swamps, 10 000 - 12 000 km^2 is seasonal flooded grasslands and the rest is low lying dry savannah (McCarthy *et al.*, 1993). Water and sediments are distributed across the fan by meandering and isolated channels which are flanked by extensive swamps. The position of the channel and hence the distribution of water and sediments are constantly changing due to channel avulsion, leading to a fairly even distribution of sediments across the upper permanently flooded portions of the fan (McCarthy *et al.*, 1993). The Okavango Delta lies within the grabens at the southern extremity of the East African rift system (S.M.E.C., 1986; McCarthy, 1993a). It represents the terminal depository for the Okavango River system which drains from central Angola, as all the sediments transported by the River are deposited on the fan. The area is of international environmental importance as one of very few remaining relatively undisturbed inland Delta ecosystems in the world.

Seasonal flooding is the driving force behind the functioning of floodplain ecosystems in the Okavango Delta. When the water level rises in May - June, the trampled and grazed grasslands are flooded, nutrients are released and primary production of phytoplankton, attached algae and macrophytes explode, and aquatic herbivores of all kind from zooplankton to fish migrate in to feed and spawn (Merron, 1991; Project Memo., 1995). When the water level recedes from August - September, large terrestrial ungulates move in to feed on the grasses that established or resprouted in this zone, which is a reliable grazing resource during the dry season (Project Memo., 1995). It is thus likely that the seasonal floodplains are to a large extent an influential factor determining the amount of fish found in the perennial swamps and rivers and dependent predators such as crocodiles, fish eagles, herons, otters, and man. Similarly it is likely that the amount of wildlife found on the arid floodplains is regulated by the amount of high quality grazing produced on the seasonal floodplains after the water has receded.

The seasonal flood regime of the floodplains in the Delta is directly tied to the timing, duration and, magnitude of the Okavango River annual flood level, which in turn is determined by rainfall in its catchment area in Angola (Merron, 1991). In addition natural disturbances such as channel blockage by giant papyrus reeds (*Cyperus papyrus*) and sedimentation due to human activities, such as burning of the aquatic and floodplain vegetation, may result in constant changes in the distribution of water in the floodplains (McCarthy, 1993a; Biggs, 1979). Every year most of the vegetation of the Delta is burned. Hunters and safari operators deliberately cause nearly all the burning. These fires begin as early as the end of May and have a considerable effect on the local movement of animals. In seasonal burned floodplains, progress of rising flood is accelerated due to the removal of much of the vegetation, which act as a barrier (Paterson, 1976). Thus the spatial and temporal variation of the seasonal flooding is high. The annual alteration and interaction of the above parameters almost assure that no two flood seasons produce the same regularity, duration, or pattern of flooding over the Delta (Biggs, 1979). A massive alteration in water distribution down to the Delta will affect the distribution of aquatic vegetation types since these communities are dependent on water throughout the year. Some plant community types can however tolerate short periods of absence of surface water in dry seasons. The floodplain communities are known to be most sensitive to change in flooding regimes (S.M.E.C., 1989; Ellery *et al.*, 1993).

At least two types of flooding can be distinguished; regular floods and irregular floods. The latter occur predominantly along rivers and are caused by unpredictable changes in water levels of the river (Blom *et al.*, 1990). The sources of flooding have often been identified as heavy rainfall in catchment areas as it is the case with the Okavango Delta. The floodplains of the Okavango Delta experience regular seasonal flooding, but the lower parts of the floodplains experience irregular flooding since they only get flooded in years of exceptionally high floods.

Vegetation of the floodplains of the Okavango Delta exhibits a marked pattern of zonation in the seasonal floodplains along the moisture and elevational gradient (Ellery *et al.*, 1993). Clear vegetation zonation in floodplains was also reported in other systems like the Kafue Flats in Zambia (Ellenbroek & Werger, 1988), the Bengweula Basin in Zambia (Grimsdell & Bell, 1976), the Southern Sudd region of the Upper Nile in Sudan (Sutcliffe, 1976), the Nile River valley in Egypt, the Amazon Basin in Brazil, the floodplains along the Mississippi River in U.S.A, the Euphrates, Ganges, Bramahputra and Hwang Ho river in Asia (Brandy, 1990). Elevation directly influence the duration and extent of flooding and is likely to be the major factor governing vegetation zonation, resulting in an unique pattern of rainfed and seasonally flooded grassland types and their intermediates (Ellery *et al.*, 1993). Kozlowski (1984), Ellenboek & Werger, (1988), Ellery *et al.* (1993) and Blom *et al.* (1996) reported that species composition, and phytosociological position of vegetation of floodplains are influenced by factors such as flooding frequency, duration of flooding, depth of water, a variety of soil factors and flood tolerance of seedlings. Blom *et al.* (1996) pointed out that vegetation zones in the floodplains often reflect differences in flooding stress at the individual plant level. Transient floods particularly, induce vegetation zonation and small-scale spatial heterogeneity in terms of oxygen and nutrient availability (Biggs, 1979; Blom *et al.*, 1996).

While interaction between water, nutrients, grazing by large herbivores and fire have often been identified as driving forces behind the processes of vegetation dynamics in savanna ecosystem, the Okavango Delta seasonal floodplains are unique in the sense that vegetation processes are driven by these factors as well as by seasonal flooding.

Early and Middle Stone Age implements found at Chanoga, Toteng, Samedupe, Sehitwa and Kgwebe indicate that man has inhabited at least the southern periphery of the Delta for 100 000 years or more (Campbell, 1976). Apparently there are three factors which influenced human settlement in the Okavango Delta: the topography of the land which in the past influenced resource distribution, the spread of noxious insects, particularly tsetse fly (*Glossina morsitans*) and malaria mosquitoes (*Anopheles sp.*) and the historical mode of the people's subsistence themselves (Campbell, 1976). Habitation of wetlands by human beings, particularly floodplains is steadily increasing world wide, as the benefits of living in the floodplains outweigh the risks (Blom & Voesenek, 1996), especially in that seasonally flooded areas are among the most productive ecosystems in the world. The probability of flooding is increased by human activities such as removal of natural vegetation, improvement of drainage systems, overgrazing by livestock and wildlife and straightening of meanders to facilitate shipping (Blom & Voesenek, 1996). However such intensive human activities are minimal in the Okavango Delta, thus leaving it as one of the least disturbed wetland ecosystems in the world. Nevertheless, proposals and plans that could interfere and change this natural ecosystem have been tabled, with the most recent being the Boro dredging (S.M.E.C., 1989) and the Namibian pipeline (Bonyongo, *et al.*, 1996). The two proposals drew a lot of attention from environmental organisations, both locally and internationally.

Human utilisation of natural resources in the Okavango Delta is linked directly to the ecological integrity and productivity of the river and its floodplains and the woodlands, which provide opportunities for fishing, grazing for livestock and game, grasses for thatch, reeds and palms for building, fencing and basketry, clay for pottery, wild fruits and herbs for food and medicine, and wood for building boats and implements (Campbell, 1976; Afriyie, 1976). Tourism which is the third largest foreign exchange earner of foreign exchange for Botswana (I.U.C.N, 1993) is most active in the Okavango Delta. Tourism in Botswana is based upon wildlife in its natural habitat, and while there are many good wildlife areas in the country, there is no doubt that the Okavango Delta is the focus for a great diversity of species. It is in the Okavango Delta that semi-arid and wet lands integrate, and the Moremi Wildlife Reserve is the dry season visiting place for many species which spend the wet season in the drier areas surrounding the eastern part of the Delta (Campbell & von Richtner, 1976).

Utilisation of grazing resources by large herbivores on the floodplains has been observed to be spatially as well as temporally variable. As a result some vegetation zones are more heavily utilised by grazers than others. Differences in utilisation patterns of grass species are common in other ecosystems. McNaughton (1988) reported that mineral content of the foods is an important determinant of utilisation of forage resources within Serengeti National Park, Tanzania. He further reported that magnesium, sodium and phosphorus appear to be of particular importance in as far as forage utilisation is concerned. Seasonal patterns of flooding was found to determine the pattern of grazing in the Kafue Flats (Ellenbroek & Werger, 1988) and that is likely to be the case in the Okavango Delta floodplains. Digestibility, phenology and availability of grazing resources over time have also been associated with selectivity and utilisation of grazing resources (Valentine, 1990).

Water level fluctuations in the Okavango Delta floodplains are likely to influence not only accessibility, but also phenology of growth, availability and quality of the grazing resource. Furthermore species-specific differences in digestibility may occur. Prolonged flood deficits in floodplains have been observed to cause major changes in species composition of floodplain grasslands with areas previously dominated by perennials species giving way to annual species (Diarra, 1988). However little is known about the relative importance of water level fluctuation for plant community distribution and plant growth and utilisation patterns by herbivores of the Okavango Delta floodplains.

At present there is an increasing pressure to utilise water from the Okavango Delta. It is likely that substantial reduction of inflow will affect the seasonal floodplains. A broad understanding of the ecological function of the seasonal floodplains is of paramount importance, if the long term impact of flow changes on vegetation and wildlife populations are to be predicted with any certainty.

1.2. General objectives

This study will therefore focus on the following aspects:

i) vegetation zonation in relation to elevation gradient,

ii) variation in soil water regime and soil mineral nutrients along elevation gradients.

iii) phenology of growth, nutrient contents, digestibility and utilisation of grasses by herbivores in relation to flooding regimes.

These objectives in themselves lead to the formulation of hypotheses:

1.3. Hypothesis

H1 Vegetation zonation in the floodplains is due to variation in elevation, which influence the extent and duration of flooding.

H2 Vegetation zonation may be co-determined by soil water regime or variation in soil chemical and physical properties, or a combination of the above.

H3 Utilisation of grazing resources in the floodplains are temporally and spatially variable due to variation between vegetation zones in availability (quantity and time of biomass availability) and quality (nutrient content, digestibility and secondary compounds) in relation to flooding regimes.

CHAPTER 2

Study area

2.1. Location and General description

The Okavango Delta is located between 19^0 and 20^0 S and 22^0 and 24^0 W and has its main catchment in the Angolan Highlands (Ellery *et al.*, 1991). The main study site is by Nxaraga lagoon (19^0 35' S 23^0 10' W) on the Southwest side of Chief's Island in the Moremi Wildlife Reserve (D.S.L., 1987) (Fig.2.1). The Boro River, currently the main outflowing river from the Delta, seasonally floods the study site.

Two main river systems, the Cubango and the Cuito, drain into the Okavango River which spreads out into a deltaic shallow water body which covers approximately 22 000 km^2. The Okavango Delta swamps are divided into three physiographic regions; (i) the upper pan handle which is characterised by meandering channels flanked by permanent swamps which are confined between the shoulders of the Kalahari sand and laterally confined by what appears to be eroded fault scalps, and the permanent swamps which are largely unconfined around the apex of the fan itself, with perennial surface water up to 4 m. (ii) The low lying seasonally-indudated areas, the extent varies to a large degree depending on the magnitude of annual floods from Angola and the amount of local rainfall. (iii) The higher, dry land masses, of which there are three major examples: Moremi Wildlife reserve, Chief's Islands and Western sand-veld tangue (Paterson, 1976, McCarthy *et al.*, 1991, 1993). Within these three broad divisions is an interocking mosaic of habitat types which contributes most of the diversity of Delta's wildlife spectrum at all phylogenetic levels. Most of the conspicuous wildlife species utilise the last two zones to varying degrees, but the first provides suitable habitat for comparatively few large wild animals (Paterson, 1976).

The floodplains are divided into three areas: the primary floodplains which are the first to receive flood waters overflowing from the outlet channels in the seasonal swamps area, secondary floodplains which are higher-lying floodplains of grasslands elevated above primary floodplains by 1 m or less, and Island grassland which are short grassland dominated by *Sporobolus spicatus* and characterised by the presence of evaporates (Biggs, 1979). The primary floodplain community of the mid-Delta is dominated by sedges of *Scirpus inclinatus, Fimbristylis complanata* and other *Cyperus* species and the forbs *Alternanthera sessilis* and *Ludwigia stolonifera* (Biggs, 1979). This vegetation type is very dense and forms thick mats of mostly dead material when dry. The mean vegetation height is approximately 75 cm and these areas are flooded for a major part of each year, often to a depth of half a meter or more (Paterson, 1976). All secondary floodplain communities support open grasslands but herbaceous plant density and composition vary in accordance with flooding frequency, duration and utilisation by grazing animals. Secondary floodplains are characterised by tall grasses such as *Imperata cylindrica, Setaria sphacelata, Chloris gayana, Eragrostis lappula, Eragrostis inamoena, Paspalidium obtusifolium* and *Panicum repens*. The *Sporobolus spicatus* Island grassland community is not subject to flooding in average and poor flood years. During bigger floods, the flooding of Island grassland communities may vary between 0.01 and 0.03 m and the water table is low (Biggs, 1979). The main species from the upper catena positions are *Cynodon dactylon, Sporobolus acinifolius* and *Sporobolus spicatus*.

Another important component of the Okavango's physical environment is the large number of *termitaria* which occur through out the Delta. Widespread in the dry areas, they are of some importance to various animals as either vantagepoints or convenient browsing sites (Paterson, 1976). In the areas of permanent swamps, they provide sites for colonisation by woody species forming a category of very small islands and increasing the diversity of that zone (Paterson,1976). Here again they provide vantagepoints and lying-down places, for lechwe in particular. It is however the zone of seasonal flooding where they are most important. As well as performing the functions described above, they have been attributed with having a substantial effect on regulating the flow of flood waters and initiating the formation of new islands (Paterson, 1976). As many termite species are unable to establish mounds under conditions of annual flooding, most of the termitaria in the floodplains, may therefore have been formed under drier conditions than it is now.

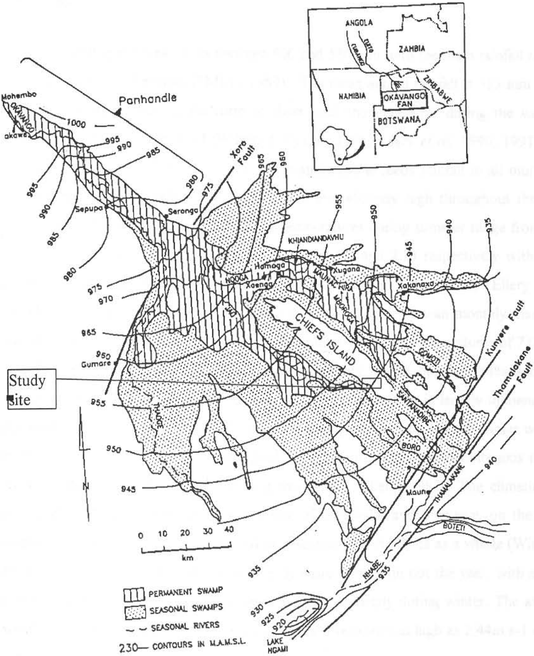


Fig. 2.1 Topography and vegetative zonation of the Okavango Fan (Stainstreet *et al*, 1993)

2.2. Climate

Annual rainfall in the area varies between 500 and 550 mm with the main rainfall months being November to February (SMEC, 1989). The mean annual rainfall is 515 mm $^{-1}$ (see fig. 2.7). Showers occur in the form of short local thunderstorms during the summer, November until March or April (Wilson & Dincer, 1976; Ellery *et al,* 1990; 1991). The annual evaporation is about 1800 mm, and evaporation exceeds rainfall in all months of the year (McCarthy, 1993b). The temperatures are relatively high throughout the year. The mean monthly maximum and minimum temperatures during summer range from 30.5 ^{0}C to 33.7 ^{0}C and 14.8 ^{0}C to 19.2 ^{0}C (see Fig. 2.2 and 2.3) respectively with mean relative humidity at 0800 hours between 50 and 78 % (Fig. 2.4 and 2.5) (Ellery *et al.*, 1991). The cooler, drier winter months (June - August) have a mean monthly maximum temperature of 25.3 ^{0}C to 28.7 ^{0}C and a mean monthly minimum temperatures of 7.0 ^{0}C to 10.0 ^{0}C (see Fig. 2.2 and 2.3), while relative humidity ranges between 43% and 63% (Ellery *et al.*, 1991). Frost seldom occurs. The summer weather is largely influenced by the southward movement of Inter - Tropical - Convergence - Zone and the winter weather by the northward movement of subtropical high pressure belt which has its axis not far south of the Tropic of Capricorn during this period (Ellery, 1987). The climatic data recorded in Maun, on the south eastern side of the Delta, and Shakawe, on the south western side of the Delta, are considered representative of the Delta as a whole (Wilson & Dincer, 1976; Ellery, 1987). Winds are mainly easterly through out the year, with a more north easterly wind blowing in the summer and south easterly during winter. The average wind speed for the year is 1.81 ms^{-1} which can reach velocities as high as 2.44m s-1 during early summer (Ellery, 1987).

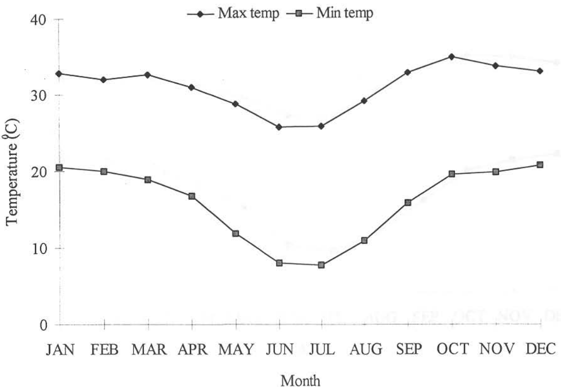


Fig. 2.2. Monthly average values for maximum and minimum temperature measured at Maun Station (Period of measurements 1986 to 1997; Source: Botswana Meteorological Services).

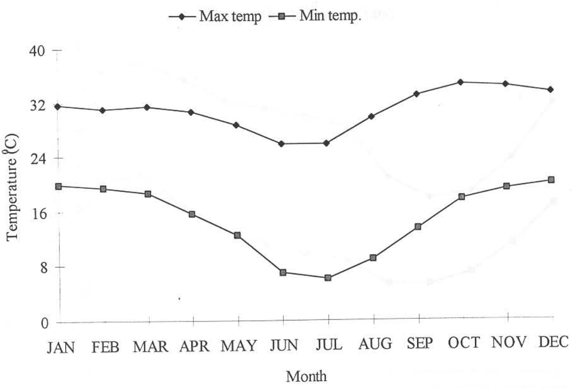


Fig. 2.3. Monthly average values for maximum and minimum temperature measured at Shakawe Station (Period of measurements 1986 to 1997; Source: Botswana Meteorological Services).

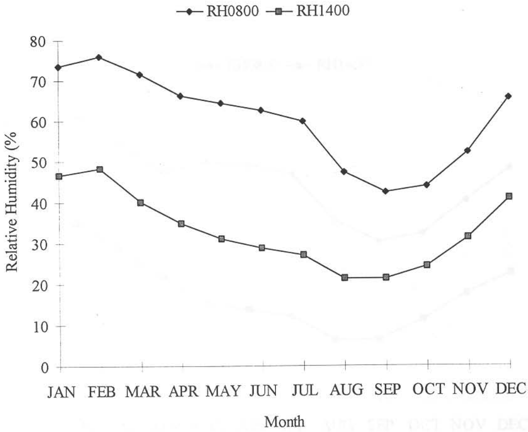


Fig. 2.4 Monthly average Relative Humidity in Maun (period of measurements: 1986 to 1997; source: Botswana Meteorological Services)

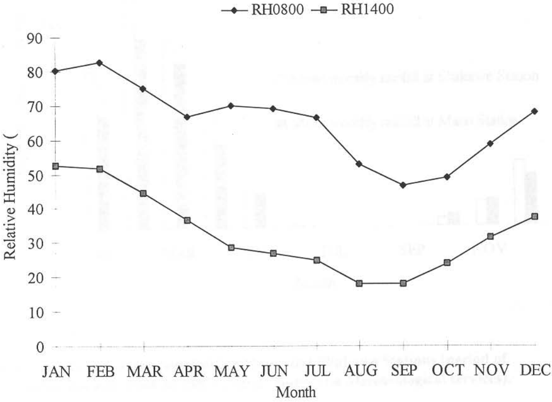


Fig. 2.5 Monthly average Relative Humidity in Shakawe (period of measurements: 1986 to 1997; source: Botswana Meteorological Services)

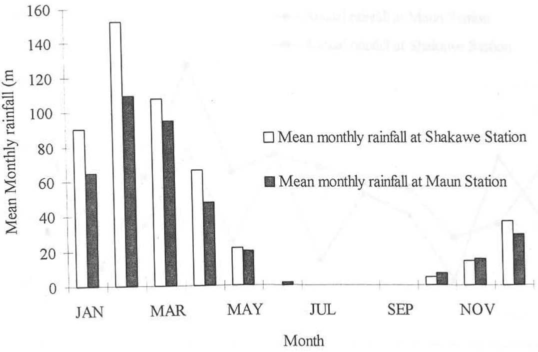


Fig. 2.6. Mean monthly rainfall for Maun and Shakawe Stations (period of measurement: 1986 to 1997; source: Botswana Meteorological services).

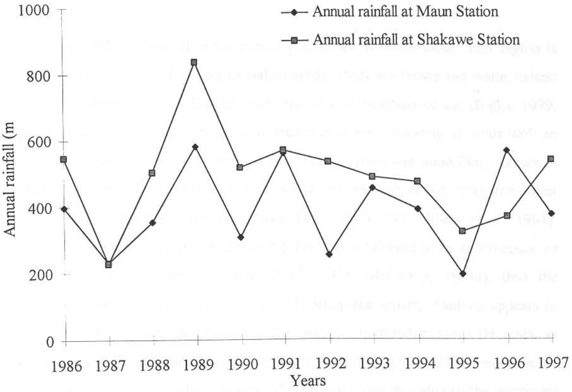


Fig 2.7. Annual rainfall for Maun and Shakawe Stations. (Period of measurement: 1986 to 1997; source: Botswana meteorological Services).

2.3. Geology and Soils

The Okavango Delta is located in the central part of the Kalahari basin. This region is covered with deep (up to 300 m thick) Kalahari sands. These are brown and white, deltaic and windborne, medium to fine grained sands and silts of the cenozoic age (Biggs, 1979; Ellery *et al.*, 1991). Soils in the main study area consist predominately of sands with an increase in the amount of peat and other organic matter in the lower floodplain. Lenses of calcrete and silcrete are interspersed in these sands and outcrops of old rocks, the oldest being the Archaen Basement Complex (Biggs, 1979; Ellery, 1987; Ellery *et al.*, 1991). The Okavango Delta lies in a seismically active area that is believed to be an extension of the East African Rift System (Hutchins *et al.*, 1976; McCarthy, 1993a), thus the Okavango Delta lies within an area of continued earthquake activity. Faulting appears to be important in determining the position of the Delta in the Kalahari sands (Hutchins *et al.*, 1976, Biggs, 1979; Ellery, 1987; McCarthy *et al.*, 1991). Two major faults (Thamalakane and Kunyere faults) striking NE-SW and down throwing to the northwest define the southern eastern limit of the Delta (Fig, 2.1). The parallel Gomare fault appears to trancect the Delta at the southern end of the Panhandle with down throwing to the southeast (Hutchins et al., 1976; McCarthy, 1993a). In the nine year period September 1965 to August 1964, a total of 38 events in the vicinity of the Delta were detected by the Rhodesian Meteorological Services (Hutchins *et al.*, 1976). A number of seismic events during 1952 (27 events ranging from 4.3 to 6,3 Richter Scale) has been postulated to have caused a major change in the drainage pattern in the Delta or more specifically in the north central part of the Delta and also increased the flow of the Boro River (S.M.E.C, 1989).

2.4. Topography

The topographic surveys show that the Delta has a suprisingly regular conical shape with a slope of about 1 in 3600. Relatively small irregularities provide the pattern of channels, islands and madiba (the local name for what are often incorrectly referred to as lagoons) (Wilson, 1976). The conical shape favours the spreading of flood waters, but the nature in this spreading is in some ways analogous to water spilled on a flat table top, the area of spill being nearly proportional to the amount spilled (Wilson, 1976). On the surface of the cone are three obvious ridges; Chief's Island, the Sandveld Tongue and Moremiland mass (Wilson, 1976). There are also some lesser ridges, and the one which runs from northwest from Beacon Island to beyond the upper Xudum is of particular interest. Its north western extremity is a narrow alluvial levee cut across by a few small but significant rivers and providing possibilities of engineering control works (Wilson, 1976).

2.5. Hydrology

The Okavango River, whose major tributaries are the Cubango River (catchment area 115 000 km^2) and Cuito River (catchment area 65 000 km^2) (McCarthy, 1993), enters Botswana at Muhembo. It has an average annual discharge of 11 500 x 106 m^3 with rainfall contributing approximately 5 000 x106 m^3 a^{-1} (Ellery *et al.*, 1991). The usual range of annual inflow is 7 x 109 m^3 to 15 x 109 m^3 (Ellery *et al.*, 1991). There is a regular seasonal rhythm to the inflow, which peaks between mid-March and early May, then recedes until November (S.M.E.C., 1989). The flood wave is slowed considerably during its passage across the Delta, and peaks discharge at the lower extremity occurs in July or August. The minimum discharge at Muhembo is in the range of 120 m^{3}s^{-1} to 200 m^{3}s^{-1} (S.M.E.C., 1989). The maximum discharge is more variable, ranging from around 400 m^{3}s^{-1} to 1000 m^{3}s^{-1} (S.M.E.C., 1989). Almost 97% of the inflows are lost to evapotranspiration and ground seepage (S.M.E.C., 1989, McCarthy, 1993a). Losses to ground water are considered minimal while a larger portion of the water is lost through evapotranspiration. Seasonal fluctuations in the water levels ranges from 0.9 m to > 3 m in both the panhandle and the lower reaches of the seasonal swamps while the central, permanent swamps have a considerably smaller annual rises and fall ranging from 0.15 m to 0.25 m (Ellery *et al.*, 1991).

In occasional years relatively small outflow volumes may reach the Mababe Depression or the Linyanti swamps via the Kwai or Magwegqana, but more generally all the outflows from the Delta is to the south from the Boro, Kunyere and Shashe Rivers (S.M.E.C., 1989). Of these, the Boro River predominates and it is the only one that flows every year as far as the Thamalakane fault at the distal end of the Delta (S.M.E.C., 1989). The Thaoge and Jao/Boro tributaries leave the Okavango River at the lower end of the Panhandle and carry water to the western and central region of the Delta respectively (McCarthy, 1993a). The Ngoga channel, which is a continuation of the Okavango, River carries water out towards the east. This channel formally linked to Mboroga River, but this linkage was broken as a result of channel blockage by vegetation and the failure of the lower Ngoga, a process which is still continuing today (McCarthy, 1993b). The Ngoga River supplies water to the Maunachira River, which takes water out towards the Kwai River and now also supplies the Mboroga-Santantadibe system (McCarthy, 1993b).

The hydrology of the Okavango Delta is never entirely stable. A complex interplay of vegetation, water, sediments deposition and other factors ensures that the Delta is forever changing (S.M.E.C., 1989). Small variations in relative volumes of flow in different channels occur every year, and on the decadal time scale of 5 - 15 years, significant inflow regimes occur in some distributaries (S.M.E.C., 1989). Vegetation, particularly, plays a remarkable role in controlling and regulating the physical environment (McCarthy & Ellery, 1993). Channel flanking by plants such as *Cyperus papyrus, Phragmites australis* and *Miscanthus junceus* forms permeable channel margins and facilitate a wide spread and distribution of water, at the same time regulates and localises the deposition of sediments. *Cyperus papyrus* also grows in failing, rapidly agradding channels, preventing avulsion and causing the formation of filter areas (S.M.E.C., 1989). This ensures that new channels which form, do so at some distance from the failing channel and, as a result, the swampy area ahead of the failing channel desiccates.

2.6 Vegetation

The deeper parts of the permanent swamps are dominated by the tall growing reed-sedge *Cyperus papyrus* and the fern *Thelypteris confluens* with *Vossia cuspidata* along the channel margins. In the swallow swamps, *Typha latifolia* and tall growing reed *Phragmites australis* are common (McCarthy, 1993b). Down stream *Cyperus papyrus* becomes stunted and gives way to a tall growing grass *Miscanthus junceus. Nymphaea* species are common in the swallow, slow flowing, open water together with a variety of emergent and submerged plants, notably *Eichhornia natans*, *Najas pectinata*, *Trapa natans* and *Typha capensis* (McCarthy, 1993b). On island margins large trees which include *Diospyros mespiliformis, Ficus sycomorus, Acacia nigrescens, Garcinia livinstonei, Combretum imberbe, Lonchocarpus capassa, Croton megalobotris, Kigelia africana* and palms such as *Phoenix reclinata* and *Hyphaene petersiana* are common. Grass species on the islands include *Cynodon dactylon*, with *Imperata cylindrica* on the moist margins and *Sporobolus spicatus* on the centre of the islands where the soils are drier and saline. Seasonal swamp areas are dominated by *Panicun repens, Cyperus articulatus, Oryza longistaminata, Scipus inclinatus, Paspalidium obtusiflium, Eragrostis inamoena, Setaria sphacelata, Schoenoplectus corymbosus.*

Biggs (1979) assessed the vegetation of the Okavango Delta and classified it into five vegetation groups namely aquatic vegetation, floodplain vegetation, riverine vegetation, marginal vegetation, and dryland vegetation. The aquatic vegetation type includes submerged, free floating, and rooted, water dependent plants. Floodplain vegetation types are intermediary between wetland and dryland types but are more associated with the wetland types. Riverine vegetation is represented by luxuriant, large tree species with overlapping crowns, forming a deep shade layer in which herbaceous sciophytes predominate. The marginal vegetation type occurs in soils slightly more elevated and slightly sandier than those supporting riverine woodland. Dryland vegetation is not normally subjected to surface inundation from floodwaters. Surface inundation may occur under certain circumstances and this may result in death of species which are not flood tolerant (Biggs, 1979).

CHAPTER 3

CLASSIFICATION AND DESCRIPTION OF FLOODPLAIN VEGETATION IN THE OKAVANGO DELTA.

3.1. Introduction

Vegetation description is the starting point of both small and large scale vegetation science research. Vegetation description aims to enable people, other than the observer, to build a mental picture of the area and its vegetation and to allow comparison and ultimate classification of different vegetation units (Kershaw, 1973). The description of vegetation, with or without concurrent recording of factors of the environment, has played a major part in the development of plant ecology and continues to be important (Greig-Smith, 1983). Vegetation description is therefore an essential and integral part of vegetation science as it provides a scientific inventory for conservation, monitoring and further research (Coetzee, 1993), and in general the preservation of biotic diversity.

Although a considerable proportion of ecological work has been directed towards the description of vegetation of various ecosystems in the world (Kershaw, 1973), not much has been done on the phytosociology of the Okavango Delta seasonal floodplain vegetation. Papers by Smith (1976), Biggs (1979), and Ellery *et al.* (1991), are some of a few publications on the vegetation of the Okavango Delta, but none of these paid special attention to a quantitative classification of seasonal floodplain vegetation. Biggs (1979) described vegetation types of the Okavango Delta using a visual physiognomic classification based on dominant species. Ellery *et al.* (1991) employed some quantitative objective methods of classification but concentrated on the vegetation of the back-swamps.

Methods employed to describe vegetation depend on a number of factors which include the purpose of the survey, scale of the study, the overall habitat type and resources available (Kershaw, 1973; Kent & Coker, 1992). Vegetation descriptions fall in two categories namely physiognomic or structural description, and floristic description

(Kershaw, 1973; Greig-Smith, 1983; Whittaker, 1980; Kent & Coker 1992). Physiognomic description is based on external morphology, life form, stratification and size of the species present while floristic description involves identification of the species present in the study area and their presence/absence is recorded (Kent & Coker, 1992). Physiognomic and structural methods have been used to describe vegetation at small scale (over large areas) such as world vegetation formations while floristic analyses have been used to describe vegetation at a large scale (small areas) particularly at the level of plant community (Kent & Coker, 1992).

Kent & Coker (1992) state that all methods for recognising and defining plant communities are methods of classification which aim at grouping together a set of individuals (sample plots) on the basis of their attributes (plant species). Therefore the end product of classification should be a set of groups derived from individuals where, ideally, every individual within a group is more similar to the other individuals in that group than to any individual in any other group (Kent & Coker, 1992). Phytosociological classification also seeks to investigate the interrelationships between species and their distribution patterns since species tend to occur in associations determined by their ecological tolerance of biotic factors, combined with intraspecific and interspecific interactions (Burgoyne, 1996). Methods of carrying out classification are many and varied. Kershaw (1973), Whittaker (1980) and Kent & Coker (1992) discussed these methods in detail of which the physiognomic or structural include Raunkaier's life-form classification, the structural-physiognomic classification schemes of Dansereau, Kuchler and Fosberg, and the floristic approach includes the Zurich-Montepellier (Braun-Blanquet) School, the Uppsala school, the Raunkaier (Danish) School and the Hybrid Schools.

The Braun-Blanquet approach to the study of vegetation is the most widely used throughout the world, and it has proven to be a reliable and efficient method for vegetation survey and classification in most countries (Werger, 1974). The analysis of vegetation has always been surrounded by disputes centred on the concept of plant community as viewed or presented by different authors (Werger, 1974). The concepts of plant community include the organismal concept which sees the community as a "superorganism", the concept of social structure, the individualistic concept which views the community as a changeable mixture of individualistically distributed plant species and the population structure which views the community as a system of interacting species and vegetation as a complex population pattern (Whittaker, 1980). Braun-Blanquet approach takes a practical, intermediate position that recognises the heterogeneity of species distributions but emphasises nonetheless the interaction between plants in the community, which has a certain individuality because of relative discontinuities between communities in the field. In this method an analysis of the vegetation as a rule is preceded by a preliminary survey of the area. This reconnaissance survey includes the study of general vegetation pattern and the establishment of the apparent relations of various vegetation types with geology topography and soil conditions (Whittaker, 1980).

The Braun-Blanquet method was virtually unknown in Africa south of the equator before 1969, except for work in Zaire, Rwanda and Burundi by Belgian phytosociologists (Werger, 1974). In 1969 a phytosociological survey of the Upper Orange River valley in which this method was applied, was initiated and since then a number of surveys were successfully carried out in Southern Africa (Werger, 1974). The method is based on several fundamental concepts and assumptions, e.g. the releve, which is a list of observations on species composition and habitat factors compiled in a sample plot or stand, equivalent in terms of vegetation description to a quadrat; minimal area which is the minimal size of an area in which the community is represented; homogeneity where the distribution of the plant species within a certain area is such that the probability of finding an individual of a plant species within that area of a given size is the same in all parts of the area; and the association which is a plant community of a specific constant species composition, having a definite specific structure and which is found under a particular set of environmental conditions (Westhoff & Van der Maarel 1978) found by grouping together various releves that have a number of species in common (Kent & Coker, 1992; Werger 1974; Whittaker 1980).

In this study, the vegetation of the Okavango Delta floodplains was described at a community level, thus a floristic approached was employed. In phytosociological work done in the savanna (Bredenkamp, 1982, 1987; Brown *et al.*, 1996) and grassland (Fuls, 1993; Eckhardt, 1993; Coetzee, 1993; Coetzee *et al.*, 1995) biomes of South Africa agglomarative cluster analysis (Orloci, 1967) and divisive clustering (Bredenkamp *et al.*, 1991, 1995), were applied on the samples of total floristic composition to derive the first approximation of plant communitry types of the relevant area. After deriving the approximate main communities by applying the divisive clustering algorithim, TWINSPAN (Hill, 1979b) to the floristic data, further refinement is achieved by application of the Braun-Branquet procedures. A key concept of TWINSPAN is that with each division of a set of releves, a dichotomy can be made with a group of releves on one side characterised by one set of indicator species and a second group on the other side characterised by a second set of indicator species. The general principle of division is applied in a series of levels starting with a whole set of releves or species dividing them into two groups, those two into four, and those into eight and so on (Kent & Coker, 1992). The end product is a hierarchical classification, which can be presented in a diagram or in table form, and where plant communities are defined in terms of their total floristic composition, with emphasis on indicator or diagnostic species.

3.2. Objectives

The objectives of this study are to:

i) Classify the vegetation of seasonal floodplains of the Okavango Delta at Nxaraga Lagoon area using a floristic approach.

ii) Relate derived plant communities to certain environmental attributes, which probably determine their distribution within the area.

3.3. Methods

The total species composition and relative abundance of each species were recorded using the Braun-Branquet cover abundance scale, with the modification by Mueller-Dombois & Ellenberg (1974) and Ellenbroek (1987). The following modified Braun-Blanquet cover-abundance scale was used:

r	very rare with a negligible cover(usually a single individual);
+	present but not abundant and with a small cover value (less than 1 % of the sample plot area);
1	numerous but covering less than 1 % of the sample plot or not so abundant but covering 1 % to 5 % of the area;
2a	very numerous and covering less than 5 % of the plot area;
2b	covering between 6 to 12 % of the plot area independent of abundance;
2m	covering between 13 to 25 % of the plot area independent of abundance;
3	covering 26 to 50 % of the plot independent of abundance;
4	covering 51 to 75 % of the plot independent of abundance;
5	covering 76% to 100 % of the independent of abundance.

In a reconnaissance survey of the study area eight different zones were identified. Within each zone five plots of which one was permanently marked for monitoring purposes, were randomly selected. Floristic cover/abundance data were collected for each plot. A 5 m x 5 m plot size was selected after determining the minimum species area as described in Kershaw (1973), Mueller-Dombois & Ellenberg (1974), Werger (1974), Whittiker (1980), and Kent & Coker (1992). The sampling design was stratified in relation to zones but randomised within the zones. Overall 40 releves were selected from which data were collected. The cover-abundance data were then captured in TURBO(VEG), a software package for input, processing, and presentation of phytosociological data (Hennekens 1996a). Data were then subjected to a two-way indicator species analysis (TWINSPAN) (Hill, 1979b) in MEGATAB, a visual editor for phytosociological tables (Hennekens, 1996). Floristic data were collected when most of the species were in their flowering stage to allow easy identification.

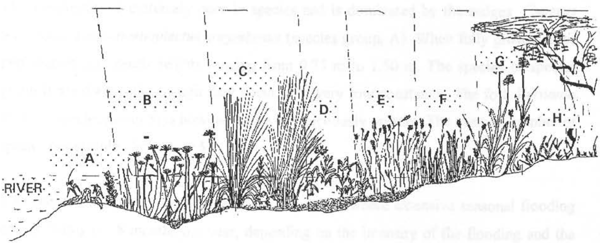
flowering stage to allow easy identification.

3.4. Results

3.4.1. Classification

The TWINSPAN classification followed by Braun-Blanquet procedures divided the floodplain vegetation into eight communities of which five were further divided into sub-communities. Ninety-nine species were recorded from which fifty-five were used in the phytosociological table (Table 3.1) and forty-four were classified as rare species are also included in the checklist (see Appendix 1) The eight communities and their sub-communities are the following:

1 *Cyperus articulatus-Schoenoplectus corymbosus* community
    1.1 *Typicum* sub-community
    1.2 *Cyperus articulatus-Alternanthera sessilis* sub-community
2. *Alternanthera sessilis-Ludwigia stolonifera* community
    2.1 *Alternanthera sessilis-Nymphaea nouchali* sub-community
    2.2 *Alternanthera sessilis-Pentodon pentandrus* sub-community
3. *Miscanthus junceus-Digitaria scalarum* community
    3.1 *Miscanthus junceus-Panicum repens* sub-community
    3.2 *Miscanthus junceus-Ethulia conyzoides* sub- community
4. *Paspalidium obtusifolium-Panicum repens* community
5. *Setaria sphacelata-Eragrostis inamoena* community
6. *Veteveria nigritiana-Setaria sphacelata* community
    6.1 Typicum sub-community
    6.2 *Veteveria nigritiana-Imperata cylindrica* sub-community
7. *Imperata cylindrica-Setaria sphacelata* community
8. *Sporobolus spicatus* community
    8.1 Typicum sub-community
    8.2 *Sporobolus spicatus-Cynodon dactylon* sub-community



A = *Alternanthera sessilis-Ludwigia stolonifera* community; B = *Cyperus articulatus-Schoenoplectus corymbosus* community; C = *Miscanthus junceus-Digitaria scalarum* community; D = *Paspalidium obtusifolium-Panicum repens* community; E = *Setaria sphacelata-Eragrostis inamoena* community; F = *Imperata cylindrica-Setaria sphacelata* community; G = *Veteveria nigritiana-Setaria sphacelata* community; H = *Sporobolus spicatus* community.

Fig. 3.1 Schematic cross-section showing the location of vegetation communities in relation to each other and the channel.

3.4.2. Description of the plant communities.

Vegetation of the seasonal floodplains of the Okavango Delta is mainly dominated by herbaceous species with seedlings of some woody species appearing rarely in secondary and tertiary floodplains. All species groups mentioned in the description of the communities refer to Table 3.1. Fig, 3.2 to 3.8 show pictures of the different vegetation communities.

1.*Cyperus articulatus-Schoenoplectus corymbosus* community

This community is extremely poor in species and is dominated by the sedges *Cyperus articulatus* and *Schoenoplectus corymbosus* (species group, A). When fully grown, these two species may reach heights ranging from 0.75 m to 1.50 m. The species of species group B are diagnostic, though they occur with very low constancy. The forb *Vernonia glabra,* (species group S) is however often conspicuously present. The average number of species per sample plot is only 5.

This community covers large areas of the floodplain where extensive seasonal flooding occurs during 6 - 8 months per year, depending on the intensity of the flooding and the annual rainfall in the catchment in the Angolan highlands and also in the Delta. This community is mainly located in the depressions of the floodplains (Fig.3.1) where the flooding depth ranges from 0.50 m to 1.0 m when floods are high during July-September and ranges between 0.20 m to 0.45 m during the rainy season in summer.

Grazing pressure is low in the centre of the zone where the water is deep, thus allowing the sedges to escape grazing. However, this community is heavily grazed on its edges where the water is shallower and ungulates have easy access. When the water recedes at the end of the flooding season, the vegetation is heavily utilised and trampled by ungulates, thus resulting in a thick layer of organic sedge peat.

Fig. 3.2 Vegetation of the *Cyperus articulatus-Schoenoplectus corymbosus* community

1.1. The Typicum sub-community

This sub-community is entire dominated by the sedges *Cyperus articulatus*, and *Schoenoplectus corymbosus* (species group A), and represents the typical sub-community of the *Cyperus articulatus-Schoenoplectus corymbosus* community. Characteristically the species of species group C are absent or poorly represented. Other species that may be found in this sub-community include *Paspalidium obtusifolium* (species group K) and *Vernonia glabra* (species group S). This sub-community is located towards the edges of the main community in shallower water, away from the main channel and is therefore also the most severely grazed of the two sub-communities. In most cases it borders on the *Paspalidium obtusiflolium-Panicum repens* community.

1.2. *Cyperus articulatus-Alternanthera sessilis* sub-community

This sub-community is also dominated by *Cyperus articulatus* (Species group A) though the presence of the forbs *Alternanthera sessilis, Ethulia conyzoides Potomagetum* *thumbergii* and *Nymphaea nouchali* (species group C), are diagnostic. This vegetation is located in deeper water in the centre of the depressions where inundation periods are longest, causing habitat for the aquatics *Potamogeton thunbergii* and *Nymphaea nouchalli*. Due to deep water this area is not grazed, as it is inaccessible for most ungulates.

2. *Alternanthera sessilis-Ludwigia stolonifera* community

This community is characterised by species group E which includes the hygrophylic forbs *Ludwigia stolonfera, Ludwigia leptocarpa*, and *Polygonum meismerianum* and also the hygrophylic grasses *Leersia hexandra* and *Oryza longistaminata*. Other species that may be considered as diagnostic are those of species group C, namely *Alternanthera sessilis, Ethulia conyzoides, Potamogeton thunburgii* and *Nymphea nouchalli*. *Vossia cuspidata*, and *Digitaria debilis* (species group D) and *Paspalidium obtusifolium* (species group K) are also prominently present. The average number of species per sample plot is 11.

The community is always situated adjacent to the channel (Fig.3.1) where depth of water may be deeper than 1 m when the river is in flood (June - July) and up to 0.50 m during the rainy season (during the summer months). This the wettest parts of the primary floodplain. Duration of inundation ranges between 6 to 8 months, including the rainy season. However, by the end of the dry season when the vegetation is not inundated, it may be so heavily utilised by grazers that most of the soil surface becomes bare.This community is divided into two sub-communities.

2.1. *Alternanthera sessilis-Nymphaea nouchali* sub-community

This sub-community occurs in the deepest water is characterised by the presence of species group F and also a high cover abundance of the water lily *Nymphaea nouchali* (species group C). Dominant species are *Alternanthera sessilis* and *Ludwigia stolonifera* (Species group E). Other common species include *Ethulia conyzoides* and *Potamogeton thunburgii* (species group C), *Vossia cuspidata* (species group D), *Leersia hexandra* (species group E), and *Cyperus articulatus* (species group A).

Fig. 3.3 . Vegetation of the *Alternanthera sessilis-Ludwigia stolonifera* community

2.2 *Alternanthera sessilis-Pentodon pentandrus* sub-community

This sub-community is located in somewhat shallower water more towards the edges of the *Alternanthera sessiles - Ludwigia stolonifera* community. In most cases it borders on the somewhat elevated *Cyperus articulatus-Schoenoplectus corymbosus* community. The species of group H are diagnostic and includes *Pentodon pentandrus, Pycnostychys coerolea, Brachiaria humidicola* and *Brachiaria arrecta*. *Alternenthra sessilis* (species group C), *Ludwigia stolonifera* (species group E) and *Pentodon pentandrus* (species group G) are dominant in this sub-community. Other common species that may be found include the hygrophilic grasses *Oryza longistaminata,* and *Leersia hexandra* (species group E).

3. *Miscanthus junceus-Digitaria scalarum* community

Miscanthus junceus, which is a tall-growing (3 m) aquatic perennial grass, *Digitaria scalarum* as well as *Nidorella residifolia, Cycmium tubulosom* and *Brachiaria dura* (species group I) are the diagnostic species in this community. Common species are *Digitaria debilis* (species group D), *Cyperus articulatus* (species group A), *Paspalidium* *obtusifolium* (species group K), *Panicum repens, Acroceres macrum, Eragrostis lappula* (species group L), and *Vernonia glabra* (species group S,). An average of 10 species was recorded per sample plot.

This community is located within the primary floodplain, often occurring as a narrow belt between the seasonally flooded *Paspalidium obtusifolium - Panicum repens* community, *Cyperus articulatus - Schoenopletus corymbosus* community and the *Alternanthera sesssils - Ludwigia stolonifera* community (Fig. 3.1). *Miscanthus junceus* is not utilised by herbivores except that elephants dig up the roots during the dry season when forage is scarce. In this community *Acroceres macrum* and *Panicum repens* (species group L*)* grow in the spaces between the *Miscanthus junceus* compact tussocks. These grasses are heavily utilised by lechwe and other herbivores during the rainy season and even during flooding. *Digitaria scalarum* grows within the *Miscanthus junceus* thickets thus earning valued protection from herbivores.

Fig. 3.4.Vegetation of the *Miscanthus junceus-Digitaria scalarum* community

3.1 *Miscanthus junceus-Panicum repens* sub-community

Miscanthus junceus (species group I,) is the dominant species, and *Cyperus dives* (species group J) is diagnostic, while *Eragrostis lappula* and *Panicum repens* (species group L) and *Eragrostis inamoena* (species group M) may be considered as differential species for this sub-community. *Acroceres macrum,* (species group L) *Digitaria debilis* (species group D), *Digitaria scalatrum* (species group I) and *Vernonia glabra* (species group S) are the dominant species of this sub-community.

It is located on the edges of the *Miscanthus junceus - Digtaria scalarum* community that is in the shallow waters of secondary floodplains.

3.2 *Miscanthus junceus-Ethulia conyzoides* sub-community

This sub-association is characterised by the absence of *Cyperus dives* (species group J) while the absence of *Eragrostis lappula* and *Panicum repens* (species group L) and *Eragrostis inamoena* (species group M) may be considered as of diagnostic value. Other species that differentiate this sub-community from the *Miscanthus junceus-Panicum repens* sub-community are *Ethulia conyzoides* and *Alternanthera sessilis* (species group C). Other common species include *Cyperus articulatus, Schoenoplectus corymbosus* (species group A), *Vossia cuspidata* (species group D), *Digitaria scalarum* (species (group I), *Acroceres macrum* (species group L), *Vernonia glabra* (species group S) and *Paspalidium obtusifolium* (species group K). This sub-community is located adjacent to the *Alernenthera sessilis - Ludwigia stolonifera* community, in shallower water on somewhat elevated terraces that are not inundated for long periods.

4. *Paspalidium obtusifolium-Panicum repens* community

Characteristic for this community is the high cover values of *Paspalidium obtusifilium* (species group K). *Panicum repens* is very prominent towards the edges of this community while *Paspalidium obtusifilium* dominates in the centre of the community. Other common species include *Cyperus articulatus, Schoenoplectus corymobosus* (species group A) *Panicum repens* and *Acroceres macrum* (species group L). The average number of species per sample plot is 8. This community is found in depressions in the secondary floodplains which are far from the main channel and which often do not receive river fed floods but get inundated during the rainy season. In dry years flooding may be restricted to the lower part of the zone or may not occur at all. When floods do occur the flooding depth ranges from 0.20 to 0.50 m in the centre of the depressions. This community occupies the shallower depressions bordering the *Cyperus articulatus-Schoenoplectus corymbosus* community and the *Setaria sphacelata-Eragrostis inamoena* community (Fig. 3.1). In some cases it borders the *Miscanthus junceus-Digitaria scalarum community*. There is a large transitional zone between this community and the seasonally wet *Cyperus articulatus-Schoenoplectus corymbosus* community. *Panicum repens* remains green during the dry season, thus attracting heavy utilisation from resident lechwe herds and other herbivores. This extensive grazing leaves much of the soil uncovered by the end of the dry season. When the rains or floods come, *Paspalidium obtusifolium* and *Panicum repens* start growing vigorously, thus attracting lechwe and other herbivores. Grazing occurs throughout the year. During flooding and early dry season, grazing is restricted to lechwe, but as the soils dry up and become harder, large animals such as buffalo, zebra, tsesebe, impala and wildebeest utilise the area.

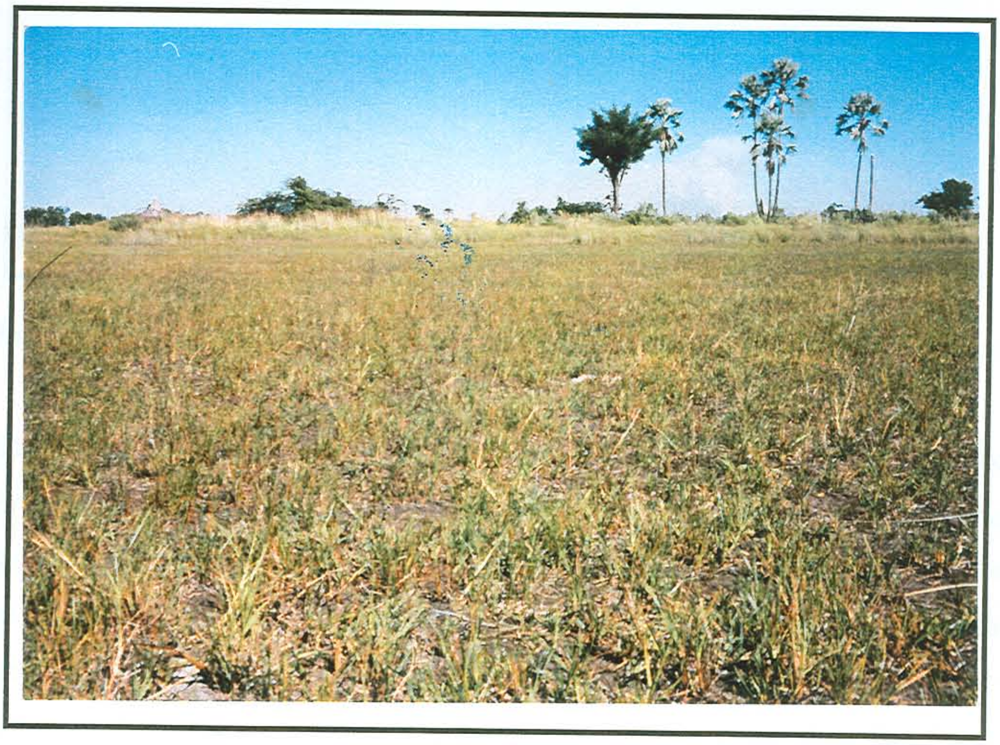


Fig 3.5 Vegetation of the *Paspalidium obtusifolium-Panicum repens* community

5. *Setaria sphacelata-Eragrostis inamoena* community

The high cover-abundance of *Setaria sphacelata* and *Eragrotis inamoena* (species group M) as well as the presence of species group N, are diagnostic for this community. Other species present in this community include *Panicum repens, Acroceres macrum Eragrostis lappula,* (species group L). The average number of species per sample plot is 9.

Fig 3.6 Vegetation of the *Eragrostis inamoena - Setaria sphacelata* community

This community is also situated within the secondary floodplains usually boarding the *Paspalidium obtusifolium-Panicum repens* community and *Veteveria nigritiana-Setaria sphacelata* community (Fig 3.1). The area occupied by this community can be described as temporarily flooded areas with shallow water, situated just above the flood line. In periods of low floods this area do not get inundated, and it seems that it does not depend much on flooding for maximum productivity. During larger river fed floods, this area floods only after most of the depressions are flooded and filled with water. The area is inundated during the rainy season but due of its elevation, rain water quickly drains off into the adjacent *Paspalidium obtusifolium-Panicum repens* community in the depressions, leaving only a thin layer of water ranging from 0.10 m to 0.25 m. The area is utilised by lechwe during the growing season. Utilisation seems to be moderate but may become heavy during the dry season, with the occasional visits by bulk grazers like buffalo, zebra and wildebeest and probably hippopotamus.

6. *Veteveria-nigritiana-Seteria sphacelata* community

The diagnostic species of this community are the tall (2 m) and dominant grass *Veteveria nigritiana* and *Setaria verticillata* (species group O). Other common species include annual grass *Setaria sphacelata* (species group M) and the forb *Vernonia glabra* (species group S). Species such as *Urochloa trichopus, Chloris virgata* (species group T) occur scattered. The average number of species per sample plot is 7.

This community forms a belt around the floodplain, just above the floodline, linking the floodplains with the woodlands. It boarders the *Imperata cylindrica-Setaria sphacelata* community and *Eragrostis inamoena-Setaria sphacelata* community (Fig, 2). Evidence of little utilisation of the dominating grass *Veteveria nigritiana* is sometimes noticeable when it starts developing new tillers at the beginning of the growing season. This community gets temporarily flooded during the rainy season but it may get flooded for a longer spell during years of extremely high floods. This community is subdivided into two sub-communities.

6.1 Typicum sub-community

Dominated by *Veteveria nigriatiana* (species group O) this vegetation represents the typical community. It is located towards the transition zone between the main community and *Eragrostis innamoena-Setaria sphacelata* community (Fig 3.1).

6.2 *Veteveria nigritina-Imperata cylindrica* sub community

Imperata cylindrica (species group P) is differential for this sub-community. It occurs towards the transition zone between the typical sub-community and the *Imperata cylidrica-Setaria sphacelata* community.

Fig. 3.7 Vegetation of the *Veteveria-nigritiana-Setaria sphacelata* community

7. *Imperata cylindrica-Setaria sphacelata* community.

The dominant and diagnostic species in this community is the perennial grass *Imperata cylindrica* (species group P). *Setaria sphacelata* and *Eragrostis inamoena* (species group M) are other common species found in this species-poor community. The average number of species per sample plot is only 5.

This community occupies the upper parts of the floodplains above the floodline and is not flooded annually (Fig. 3.1). It may, however, be temporarily flooded during the rainy season after heavy showers. No evidence of utilisation by large herbivores was noticed in this community but termite activity is high during the dry season. However, heavy utilisation was noticed after a fire.

Fig.3. 8 Vegetation of the *Imperata cylindrica-Setaria sphacelata* community.

8. *Sporobolus spicatus* community.

The only diagnostic species in this community is *Sporobolus spicatus* (species group Q), which occupies the highest parts of the floodplain above the floodline (Fig 3.1) and which forms extended monodominant stands. The average number of species per sample plot is only 3. In most cases it borders the *Eragrostis enamoena-Setaria sphacelata* community and the *Imperata cylindrica-Setaria sphacelata* community (Fig. 2). With such a high elevation, flooding is rare in this community. Evidence of grazing has been observed in the dry season. Utilisation of this species is mostly quite low, however evidence of heavy utilisation was noticed during extremely dry years.

This community is sub-divided into two sub-communities.

Fig. 3.9. Vegetation of the *spicatus* community.

8.1 Typicum sub-community

The only diagnostic in this sub-community is *Sporobolus spicatus,* thus representing the typical community. This sub-community is found on high ground close to the channel.

8.2 *Sporobolus spicatus-Cynodon dactylon* sub-community

In this sub-community, the diagnostic species are *Cynodon dactylon, Amaranthus thunbergii, Sporobolus acinifolius, Hermbstaedtia odorata* and *Gisekia species* (species group R). *Sporobolus spicatus* (species group P) is still the dominant. This sub-community occurs close to the woodlands, away from the flooded areas and is frequently visited by lechwe which graze weedy species such as *Amaranthus thunbergii.*

3.5. Discussion

Although the survey was done when most of the plant species were on their flowering stage, some of the species were difficult to identify because of differences in flowering time. For example, *Sorghum species* which was not recorded, later showed up to be strongly associated with the *Eragrostis innamoena-Setaria sephacelata* community and the *Veteveria nigritiana-Imperata cylindrica* community. There might be more such species. However this problem was also experienced by other researchers employing the floristic approach (Perkins 1997).

As stated before, the most important factor determining the species composition of the vegetation of the seasonal floodplains is the timing and duration of the seasonal flooding (Ellenbroek, 1987). Because of its dependence on an annually changing amount of rainfall in the catchment area in Angola, the flooding regime is also the driving force of the dynamics of the vegetation. This phenomenon sometimes interferes with classification and blurs the possibility for recognition of plant communities (Ellenbroek, 1987) as the communities may shift due to changes in habitat.

It must be emphasised however, that most of the plant communities in the Okavango Delta have existed for centuries, though they shift around in space and time to the areas suitable for them, depending on the prevailing environmental conditions. Channel blockage aggravating channel abandonment is still reported to be a common phenomenon in various parts of the Okavango Delta. The blockages therefore result in changes in water flow. As a result some floodplains fail to receive water or receive very little water, while others are deeply inundated. Consequently, vegetation of the seasonal floodplains changes once regular flooding ceases. Seasonal flooding seems to be the major determinant as well as the major driving force of the seasonal floodplain vegetation. It is therefore possible that the species composition at the time of survey was different from what it used to be in the past, and might be different in future, depending on the flooding regimes. This further proves as well as emphasises the importance of a

Table 3.1. Phytosociological table for floodplain vegetation in the Okavango Delta

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    Unique relevé nr.                     ¦         ¦               ¦          ¦               ¦          ¦
                                          ¦         ¦               ¦          ¦               ¦          ¦
                           111111111111111¦111111111¦111111111111111¦1111111111¦111111111111111¦1111111111¦111
                           566667777766667¦555555556¦334453334444444¦2233333422¦000000110112222¦0011111221¦788
                           267890123423455¦134567890¦458906781234567¦8901239067¦456789053670135¦1223489241¦906
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Species Group A
Cyperus articulatus    -hl 354444444443444¦344454555¦bbbbbabaaaabbb.¦.aaa..ab..¦......1.aab.a.1¦abbbbmb.bb¦aaa
Schoenoplect corymbosu -hl .mm3mmbbbmbbbbb¦mbbbbabm.¦..aaa...a.a.ab1¦..........¦.a......a.a....¦ba.abbaaa.¦a.b

Species Group B
Cyperus species        -hl b..b.b.........¦b........¦...............¦.a........¦...............¦..........¦...
Schizodium cornutum    -hl .m.........b..b¦........m¦...............¦..........¦...............¦..........¦.a.

Species Group C
Alternanthera sessilis -hl ..........+....¦baaam3m.m¦454444454444445¦bam44454mm¦..........b.1..¦..b.bb1.bb¦...
Ethulia conyzoides     -hl ..........aaaa.¦..aaabbbb¦aabbbaa.m..babb¦aaaaaa.a.a¦...............¦a.bba..1ab¦...
Potamogeton thunbergii -hl ...............¦..aa.b.bb¦.a.....ab.b..ba¦.bb..ab.a.¦...............¦..........¦...
Nymphaea nouchali      -hl a..............¦abaa.....¦.....aaaaaaaaaa¦.......a..¦...............¦..........¦...

Species Group D
Vossia cuspidata       -hl ........1a....1¦.........¦1a...bb.1aa.1.1¦m.11a1ba..¦.....a1a.......¦..abba....¦...
Digitaria debilis      -hl ...............¦.........¦a1...aab.a.ba..¦..b.aba.b.¦.....a.abb..bbb¦mmmabbb.m.¦.b.

Species Group E
Ludwigia stolonifera   -hl ...............¦.........¦b....m3b43bbbmm¦44b333b4bb¦...............¦...a......¦...
Polygonum meisnerianum -hl ...............¦.........¦.....a..a..1a..¦a.1a..aaaa¦.............1.¦....+....1¦...
Leersia hexandra       -hl .........+.....¦.........¦.b.....31abbabb¦a..aaa33.a¦............aa.¦..........¦.a
Oryza longistaminata   -hl ..........a....¦.........¦aa...a..b..1...¦aa11a.aa..¦...............¦..........¦ab.
Ludwigia leptocarpa    -hl ...............¦.........¦..aaa...a1aaa..¦.a.aa..1..¦...............¦..........¦...

Species Group F
Eleocharis dulcis      -hl ...............¦.........¦.1.....baaba...¦..........¦...............¦..........¦...

Species Group G
Persicaria limbata     -hl ......+........¦.........¦abaaa..........¦.....a....¦a1.............¦..........¦...

Species Group H
Pentodon pentandrus    -hl ...............¦.........¦......a.....a..¦bbmaba.abb¦...............¦a.bab..a..¦...
Pycnostachys coerulea  -hl ...............¦.........¦a.......a....1.¦aabaaa.a.1¦...............¦.........a¦...
Brachiaria arrecta     -hl ...............¦.........¦.a...bb........¦3m5..aa...¦...............¦..........¦...
Brachiaria humidicola  -hl ...............¦.........¦...............¦........55¦b....1.........¦.ba.......¦...

Species Group I
Miscanthus junceus     -hl ...............¦.........¦...............¦..+.......¦455555554545555¦5455545555¦...
Digitaria scalarum     -hl ...............¦.........¦...............¦..........¦.bm.mmbmbbbbbb.¦.b...bbbbb¦...
Nidorella resedifolia  -hl ...............¦.........¦............a..¦.......a..¦11......a.a.aaa¦a1....a.a1¦...
Cycnium tubulosum      -hl ...............¦.........¦...............¦..........¦..........+....¦......+...¦...
Brachiaria dura        -hl ...............¦.........¦...............¦..........¦....b.1........¦.b........¦...

Species Group J
Cyperus dives          -hl ...............¦.........¦........m......¦......aa..¦aba.aa.a.......¦..........¦...

Species Group K
Paspalidium obtusifoli -hl ............bbm¦.........¦aa1a1aa..a.ab.a¦.1.1ab....¦b.a...a.b.bb...¦ab.b.mb...¦544

Species Group L
Panicum repens         -hl ..........baaa.¦.........¦.............4.¦..........¦.b.bb.a.abbbbb.¦1.........¦mma
Eragrostis lappula     -hl ...............¦.........¦...............¦..........¦a..b.a+aa.a....¦..........¦...
Acroceras macrum       -hl ...............¦.........¦...............¦b........a¦3.bbmmbmbbma.bb¦.b.a.b.bb.¦mm.

Species Group M
Setaria sphacelata     -hl ...............¦.........¦1..............¦..........¦......1........¦..........¦...
Eragrostis inamoena    -hl ...............¦.........¦...............¦..........¦..abab.b.......¦..........¦...

Species Group N
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39241!906790123456234517 789018!6790235124581468807906937!234834567901245801235!1679!7904513501233624678912458!06789012345781 26789!345069
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ab.bb!aaaabaaa..baaaa.ma aaabib!.....+a.....++........11.!.....................!....!.........................!.............. .....!......
baaa.!a.b.ala.bbaaaa.abb .b.bi.!..11..1.....+............!..................+..!....!...al.....11.............!.............. .....!......

.....!.................. ......!+..b.....................!.....................!....!.........+...............!.............. .....!......
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b1.bb!.................. ......!.........................!.....................!....!.........................!.............. .....!......
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..a..!.................. ......!.........................!.....................!....!.........................!.............. .....!......
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.....!mma.bb.a.bab4343abbb bb+b3m!.bam1bab.b1b.....bbbbbbbb!................b.1ma!....!1.aa111..a..1............!.....+........ .....!......
.....!................1a baab..!..b333+...bm43.3a....a...!.....................!....!.........................!.............. .....!......
.b.bb.!mm.bambalba....1.bbb .b.a.b!a.1a.....b.a.....b.....bb!...................1a!...a!.........................!.............. .....!......

.....!.................. ......!34334334444.4353443m44444!aabbbbb.bbm.aabbmbm3m!.bb.!.1aaa113bbbbaaaaa.bb...ba!.............. .....!......
.....!.................. .abbbb!44433434433334bmm3333433m!.........b.......111.!....!.....11a1aab..a..........!.............. .....!......
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Eragrostis

Species Group N
Eragrostis cilianensis -hl ...............¦.........¦...............¦..........¦...............¦........

Species Group O
Digitaria eylesii      -hl ...............¦.........¦...............¦..........¦...............¦........
Aristida stipoides     -hl ...............¦.........¦...............¦..........¦...............¦........
Acacia tortilis        -jl ...............¦.........¦...............¦..........¦...............¦........

Species Group P
Vetiveria nigritana    -hl ...............¦.........¦...............¦..........¦...............¦........
Setaria verticillata   -hl ...............¦.........¦...............¦..........¦.........a.....¦........

Species Group Q
Imperata cylindrica    -hl .......1.......¦.........¦...............¦..........¦...............¦........

Species Group R
Sporobolus spicatus    -hl ...............¦.........¦...............¦..........¦...............¦........

Species Group S
Cynodon dactylon       -hl ...............¦.........¦...............¦..........¦...............¦........
Gisekia species        -hl ...............¦.........¦...............¦..........¦...............¦........
Amaranthus thunbergii  -hl ...............¦.........¦...............¦..........¦...............¦........
Hermbstaedtia odorata  -hl ...............¦.........¦...............¦..........¦...............¦........
Sporobolus acinifolius -hl ...............¦.........¦...............¦..........¦...............¦........

Species Group T
Vernonia glabra        -hl .......1.1.311.¦..aaaaabb¦........1.....1¦..+.....+.¦1.a.aa1a+aa+1.1¦1....11.

Species Group U
Urochloa trichopus     -hl ...............¦.........¦...............¦..........¦...............¦........
Chloris virgata        -hl ...............¦.........¦...............¦..........¦.........a.a...¦........
Sida cordifolia        -hl ...............¦.........¦...............¦..........¦...............¦........
Corchorus olitorius    -hl ..........+....¦.........¦...............¦..........¦..............1¦........
Pechuel-Loes leubnitzi -hl ...............¦.........¦...............¦..........¦.1.......+.....¦........
Hibiscus species       -hl ..........+...+¦.........¦...............¦..........¦...............¦........

Species Group V
Kohautia species       -hl ...............¦......+..¦...............¦..........¦.........aa....¦........
Gomphocarpus species   -hl ..........++...¦..aa.....¦...............¦.1........¦..a..+.++....1.¦........
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...|..........|...............11.... ......|.b..a...b.b3.33b..a......|a.aa..............a..|b...|11a.a........1...a.......|........+.. .....|.....a

...|..........|................... ......|......................aaab|...................|....|...........a..............|........... .....|......
...|..........|................... ......|.............+.a.ba......|...................|....|..........................|........... .....|.....a
...|..........|................... ......|.+..+1+.1................|...................|....|..........................|........... .....|.+....

...|..........|................... ......|......................1.....|4455555555545555545555|5554|...+..1......................|..............
...|..........|................... ......|.+..+.......................|...a...a...+.11..1a..11...|..........................|....+.........

...|..........|................... ......|..........................|b....3...............|maam|555555444555554444445555|.............. .....|...

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...|..........|................... ......|..........................|.a...................|...b|............b.a1.bab.....|.............. ..b..|abaa
...|..........|................... ......|a+......b....a..........|a..b...................|....|..........................|.............. .....|.1.1
...|..........|...............aa.... ....+.|....1...1...+.........+..|1+...................|....|..........................|............+.. ....+|a.++
...|..........|................... ......|.1.........................|+.1..................|....|..........................|4.............. .....|..1.
...|..........|................... ......|..........................|...................|....|..........................|.............. .....|.13a

.1|1....11.a1|........+..+..1..a..a .1a...|..+..........1..1a11........|.1....a.+aa+1..a+.+..|.....|....a..1...+........+1.aa1|................ ......|......

...|..........|..........1..a...... ......|....1........1.+...ababb.a|a.+.....1.a.1..bb....|1aam|..........................|......+............ .....|....
...|..........|.1.............a.1.... ....1+|...............a1..a1aaabb..|aa..b..........+...+|b...|..........................|.............. .....|....
...|..........|1..............1.1.... ......|.......+.+......11a........|1.+.1..........1.....|....|..........................|.............. .....|....
.1|...........|............+........... ......|....++.+.....a....1.+.1++..|....a.a.1.+...........|....|..........................|.............. .....|....
...|..........|................... ......|.........+......11.1.1.1...|...........1+...1....+..|....|..........................|.............. .....|....
...|..........|1a.....+.+.1.......1.. .....+|.............1.++1...+.......|1.....+1......1.....++.|....|..........................|.............. .....|....+.

...|..........b|.....a............... ......|...........................|11....................+|....|....+........+...........1a.|....a+..................|.....
1.|...........|................... ......|..........+.................|......................+|....|..........................+|...................|.....
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sound long-term vegetation monitoring programme to allow and facilitate comparison. Fossil evidence has shown that the present vegetation in Europe, for example, has no long history in the quartenary, but just temporary aggravation resulting from particular environmental and historical factors (Miles, 1979). Such might be the case with the vegetation of the Okavango Delta floodplains.

In view of the fact that vegetation is dynamic, with pronounced spatial and temporal variation (Miles, 1979), it is essential that classification studies of this nature be extended to a number of sites within the Delta to get a more comprehensive picture. However visits to different parts of the Delta revealed that a similar scenario exists in various parts of the Delta. Therefore one can argue that these results are representative, bearing in mind that flooding and factors such as utilisation of floodplain resources by wildlife as well as anthropogenic activities which influence vegetation in different ways, vary in space and time.

3.6. Conclusion and remarks

The application of the Braun-Blauquet approach in phytososiological research in various ecosystems in South Africa (Bredenkamp 1982; 1987, Coetzee 1993, Coetzee *et al.* 1995, Fuls 1993, Eckhardt 1993, Brown *et al.*, 1996 and Perkins 1997), was also successfully applied in the phytosociological study of the floodplain vegetation of the Okavango Delta in the Nxaraga lagoon area. However the application of this method in the floodplains of the Okavango is hampered by the fact that such kind of work has not been done extensively in the Okavango Delta, and other ecosystems in Botswana, thus leaving the researcher with no comparable reference on the Okavango Delta. It would be interesting to compile a formal syntaxonomy for the vegetation of the Okavango Delta, with the application of the Braun-Blanquet approach. For this, more work will have to be done.

Since not much work on classification of vegetation has been done in the floodplains of the Okavango Delta in the past, this leaves this study a very important one, particularly in view of the fact it provides baseline information on the vegetation of the Okavango Delta floodplains. The classification resulted in identification plant communities which can be related to environmental factors such as elevation, distance from the channel, flooding frequency and duration and soil physical and chemical properties.

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.

Community type	Soil chemical properties after flooding						
	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

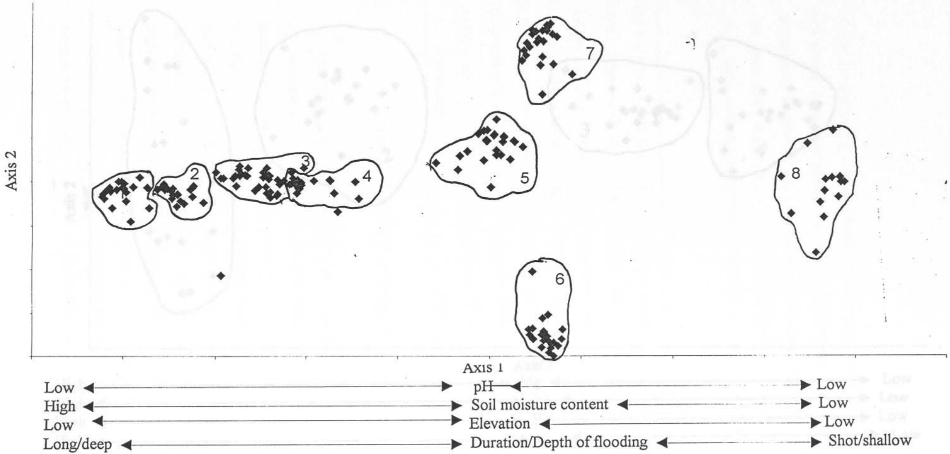
Table 4.4 Results of the chemical properties of soil middle of the rainy season.

	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.

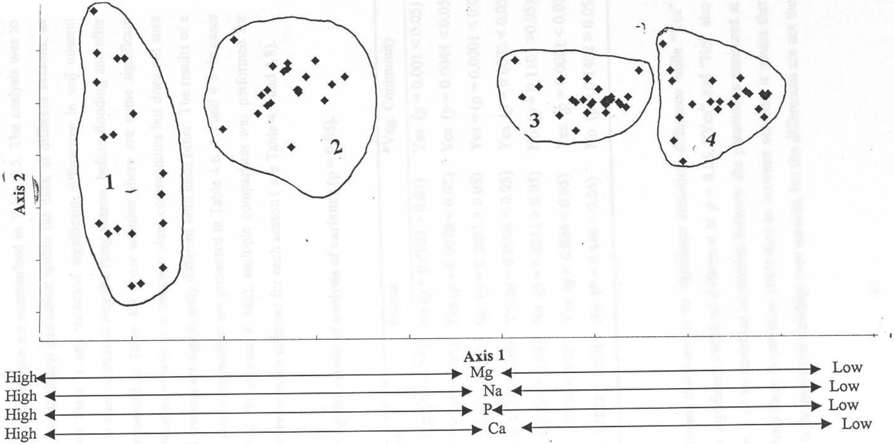
The first two axes in the stand ordination derived from DECORANA accounted for the large proportion of summed variation of axes 1 to 4. Eigen values of 0.956 and 0.826 for axes 1 and 2 were much greater than those for axes 3 and 4 (0.437 and 0.349), and hence only the first two axes are considered in 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 = *Alternanthera 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

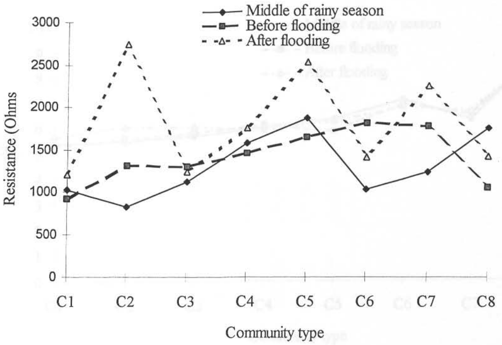
The results of the analysis of variance are summarised in Table 4.5. The analysis was to establish whether there was statistical interaction within the data, at different seasons, as well as establish whether there is any statistical significant differences in soil mineral contents in the vegetation 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

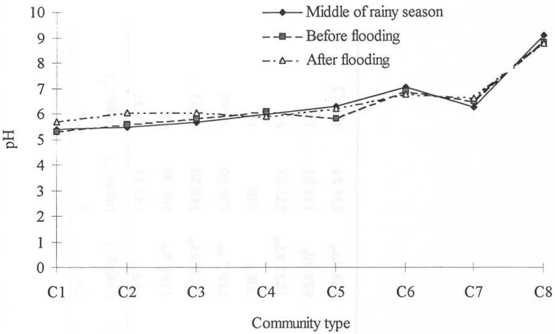
In Table 4.5, “No” means that there is no significant statistical difference while “Yes” means that there is a significant statistical difference at $p = 0.05$. “Yes” and “No” also indicate whether there is or no statistical interaction between the parameters measured at different seasons. Where there 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.

CHAPTER 5

QUALITY, QUANTITY AND UTILISATION OF FORAGE IN THE SEASONAL FLOODPLAINS OF THE OKAVANGO DELTA.

5.1. Introduction

Grasses, forbs and sedges cover the Okavango Delta floodplains. Among these herbaceous species, grasses are the most dominant. Grasses represent the most important plant family on earth, in numbers of individuals, biomass, area covered, diversity of habitats and value to man (Edwards, 1981; Gibbs-Russell *et al.*, 1991). Over 30 % of the land area of the earth is covered by grasses and savannah vegetation dominated by grasses (Gibbs-Russell *et al.*, 1991). Grazing and browsing by large domestic and wild herbivores are generally recognised as a major ecological factor in large parts of the world's uncultivated land, and have been suggested an important evolutionary forces (Miles, 1979; Cumming, 1982; McNaughton & Sabuni, 1988; Noy-Meir *et al.*, 1989; McNaughton, 1992). Evolution of the plant family Poaceae, and the animal family Bovidae, is extricably linked, with extraordinary adaptive radiation in both groups occurring contemporary from late Pliocene to late Pleistocene (McNaughton, 1979). Therefore grasslands are a prime example of vegetation controlled, or even created by grazing.

The grass sward structure can be due to the proximate effect of grazers on grass growth patterns, removing the upper canopy levels and stimulating basal tillering, but the developmental ability of grasses to respond in this fashion are evolutionary (McNaughton & Sabuni, 1988). It has been known for more than fifty years that a principal evolutionary response to herbivory is selection for prostrate genotypes. Thus the morphological evolution leading to meristem protection by physical isolation and physiological evolution leading to compensatory growth have been major features in grass evolution (McNaughton, 1979). The basal meristem of typical grasslands presumably evolved as an adaptation to grazing.

Discussions of co-evolution at the plant-herbivore interface have placed considerable emphasis on the evolution of novel anti-herbivore chemicals by plants and detoxification or avoidance mechanisms by animals (McNaughton, 1979; Cumming, 1982). Species response to herbivory vary, depending on genetics, intensity and frequency of defoliation, the tissues affected, developmental stage and time of attack and environmental factors (Brown & Ewel, 1988; McNaughton & Sabuni, 1988). High grazing pressure reduces vigour of potential dominants, thus maintaining a special diversity of swards (Miles, 1979; Noy-Meir *et al.*, 1989; Lutge *et al.*, 1996), increases mortality rate and reduced growth, alters resource partitioning and increased photosynthesis of residual tissues (Brown & Ewel, 1988).

Noy-Meir *et al.* (1989) listed the following set of inter-related hypotheses on grazing effects: i). The main effects of grazers on grasslands is the removal of living parts, which is selective and hence differential between plant species. ii). Grazing shifts the balance of relative species abundance, which is established in the ungrazed grassland mainly by competition for light, water and nutrients, towards a new stable balance which also depends on differential defoliation and regrowth. iii). Changes in species composition in response to changes in grazing intensity are consistent, reversible and continuous; hence grassland composition closely reflects grazing regime, once it has been established for some time. iv). The relative abundance of some plants in a community decreases consistently in response to increased grazing intensity (decreasers), while that of other species consistently increases (increasers); some species only appear at above certain grazing intensities (invaders). These hypotheses are commonly and readily recognised in literature. Though some of the above hypotheses are supported by much circumstantial evidence, there have been few direct tests (Noy-Meir *et al.*, 1989).

Grasslands offer grazing ungulates with a range of species which vary in their dietary qualities, morphology and structure (Reid, 1962b; Tothill & Peterson 1962; Cooper *et al.*, 1988; O'Connor, 1992). Seasonal floodplains of the Okavango Delta provide a valuable grazing resource to herbivores which include Lechwe (*Kobus leche*), buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), zebra (*Equus burchelli*) , tsesebe (*Damaliscus lunatus*), wildebeest (*Connochaetus taurinus*), warthog (*Phacochoerus aethiopicus*) and hippopotamus (*Hippopatamus amphibious*). Knowledge of the basis whereby herbivores select food is necessary for the understanding of their forage needs, and it is the underlying basis for understanding possible competitive interaction amongst them, as well as their impact on plant communities (Teague, 1989b; Vallentine, 1990; Omphile, 1997; Haschick & Kerley, 1997). King (1962) pointed out that a knowledge of the diet of grazing animals and browsing animals combined with a knowledge of composition of vegetation available to them, is of basic importance to the management of vegetation and development of efficient animal production system. Explanation of diet selection by browsing and grazing ruminants has always suggested that protein is often in limited supply, and may influence preference and selection (Downing, 1979; Diarra *et al.*,1993). Energy and mineral requirements particularly phosphorus, and the avoidance of secondary compounds and toxins have also been shown to influence selection and preference (van Soest, 1982; Woodward & Reed, 1989; Vallentine, 1990; van Duivenbooden, 1993; Omphile, 1997). Cell wall content is also generally regarded as one of the most significant factors affecting forage utilisation because it comprises of the major fraction of forage dry matter and it is correlated with forage dry matter and digestibility (van Soest, 1982; Paterson *et al.*, 1994).

Cooper *et al.*, (1988) divided chemical properties which influence plant selectivity, acceptability and forage quality into three categories: (a) nutrients, including proteins and various mineral elements: (b) fibre including cellulose, hemicelluloses and lignin, which influence physical toughness or tensile strength, as well as digestibility; (c) plant secondary metabolites, which may function as toxins or reduce the digestive availability of nutrients. Forage preference can also be influenced by plant structural characteristics such as spinescence, twiggy growth forms or life fibrousness and moribund material (Owen-Smith & Cooper, 1987; O'Connor, 1992; Haschick & Kerley, 1992; O'Reagain, 1990), species

composition (O'Reagain *et al.*, 1996), forage availability (Kennedy, 1962; Paterson *et al.*, 1994; Stuth *et al.*, 1995) and growth stage (Nelson & Moser, 1994).
Plant structure is defined in terms of the relative proportions of the different plant components present, the degree of leaf dispersion and the three dimensional distribution of leaf within the sward (O'Reagain, 1990). Plant environment also plays a major role in determining forage quality and influence selectivity. Plant environment includes those biotic and abiotic factors that influence growth and development of forages. Plants rarely grow in ideal environments; instead they experience environmental fluctuations and stress that modify morphology and rate of development, limit yield, and alter quality (Buxton & Fales, 1994). However, several grazing studies (Downing, 1979, Crawley, 1983; Cooper *et al.*, 1988; Gordon, 1989; O'Reagain & Mentis, 1979; O'Reagain, 1990) have failed to find a clear relationship between plant preferences and any single chemical or physical structural factor (Haschick & Kerley, 1997).

Forage quality can be defined as both a function of intake and digestibility. Traditional methods used to estimate forage quality have included the measurement of plant cell wall content and crude protein (CP) concentration, *in vitro* or *in vivo* estimates of digestibility and ultimately animal production (milk production or growth rate) (Reid, 1962a; Paterson, *et al.*, 1994; Mertens, 1994). Variation in forage quality which determines palatability and preference of plant species, results in selective grazing (Heady, 1964) with the palatable and thus preferred species subjected to higher grazing pressure than the unpalatable plant species. Heady (1964) and Diarra *et al.* (1995) pointed out that forage selectivity results from a highly complex interaction amongst three sets of variables operating over time; the plant being eaten, the animals doing the grazing, and the environment of both.

In the Okavango Delta seasonally flooded grasslands and in many other grassland ecosystems, it has been observed that adjacent areas of apparently homogeneous vegetation can be differently grazed, resulting in patch grazing. Patch grazing has been described as the frequent and intense grazing of localised areas within an apparently uniform sward (Vallentine, 1990; O'Connor, 1992; Lutge *et al.*, 1996). The resulting mosaic of uniform heavily grazed patches and leniently or ungrazed non patches may be desirable in that it promotes sward heterogeneity and also allows the animal to select a higher quality herbage than the sward average (Lutge *et al.*, 1996). Although patch grazing may have short-term advantages, in the long-term parch grazing is considered detrimental to the sward. Patch grazing is an inefficient utilisation of forage since a significant portion of the major forage plants are not grazed, or grazed only after they have been deteriorated by weathering, while others are damaged by repeated close grazing (Vallentine, 1990, Fuls, 1990).

Management of grasslands for conservation or for animal production requires thorough understanding of the effects of grazing regimes, and of protection from grazing, on grassland communities and populations. Grasslands grazed by livestock are particularly suitable for studying these effects, because animal density can be controlled and manipulated over a wide range (Noy-Meir *et al.*, 1989). Mainly domestic grazers graze most grassland ecosystems of the world. However, the same physiological and behavioural mechanisms involved, and the same mechanisms of plant responses to grazing, are likely to operate in domestic grazing systems as in systems grazed by large wild herbivores (Noy-Meir *et al.*, 1989). The additional complexity from the latter arises mainly from grazer population fluctuations and migrations, and from the greater opportunity that there may have been for evolution of mutual adaptations between certain herbivores and certain plants over a longer period of ecological interaction (Miles, 1979; Noy-Meir *et al.*, 1989).

Estimation of herbage yield or standing forage is important in grazing studies and management of grazing resources. Researchers generally agree that weight is one of the best quantitative measures of herbage yield (Reppert *et al.*, 1962). Other plant measures may be important in the way that they are related to or are indicative of herbage yield. Knowledge of herbage yield is seldom an end in itself, but it is usually important only as related to some grazing animal product or ecological response (Reppert *et al.*, 1962). Difficulties in measuring herbage yield are influenced by factors such as the type of vegetation, particular season of year, calibre of workers and resources available. Much depends on the ability of workers to define clearly and consistently the plant character to be measured (Reppert *et al.*, 1962).

Three general methods of measuring herbage yield are available: (a) direct measures (either harvested or visual estimates), (b) indirect measures of plant characters that are associated with actual weight, and (c) combination of direct and indirect measures (Reppert *et al.*, 1962). Direct measurements of yield, for most part involves plots of known area, although some work has been done with plotless methods. The methods of indirect estimation of herbage production are concerned with the relationship between selected plant factors and production (Reppert *et al*, 1962). Direct measurements include weights from clipped plots, weight estimates, actual plot weights and weight estimates combined in double sampling, actual total plot weight and species weight estimate combined, and actual weight of a single plant or plant shoot. Indirect methods of estimating herbage production include cover, height, height and cover combination, diameter and numbers, precipitation, dimension analysis, and capacitance meter. As for combination for direct and indirect methods, the desirable qualities of a weight method and the speed of an indirect measurement can be combined. For example, clipped weight and follier composition can be used together. Carter, (1962); Shepherd, (1962); Tothill & Peterson (1962); Branson (1962); Danckwerts & Trollope (1980); Reppert *et al.* (1962); Brown, (1954), Cook & Stubbendieck (1986); Barbour *et al.* (1987); Vallentine, (1990) and Hall *et al.*, (1993) defined, discussed, explained and elaborated on the above mentioned methods in detail.

In general the harvesting and weighing of herbage on plots of known area have been accepted as a standard approach for many years though with time non-destructive and less labour intensive methods were favoured, but validated by the harvesting method. Herbage yield of a pasture can be measured in terms of animal performance. The yield of pasture herbage in terms of animal performance has been expressed as animal days per acre, gain per acre, milk production per acre, or energy production per acre (Woofolk, 1962, Reid, 1962a, Lucas, 1962). However, the above mentioned parameters are more applicable in tame pastures. In natural systems such as the Okavango Delta, which supports a huge number of various wild herbivores, it is always difficult and costly to monitor such parameters.

Considerable research efforts have been devoted in recent years to the development of quicker and more efficient methods for estimating dry mater yield amongst which the disc pasture meter which is a more practical technique has evolved (Bransby & Tainton, 1977). Calibration of the disc meter involves establishing a regression relationship between disc settling height and yield of herbage below the disc (Bransby & Tainton, 1977; Danckwerts & Trollope, 1980). Reasonably accurate estimates of dry matter yield of standing crop can be made with a disc pasture meter. The disc meter dry matter relationship, however, is influenced by many factors such as moisture content of the herbage, growth face of the pasture and the degree to which the pasture has been trampled when measurements are taken during grazing (Austin *et al.*, 1981). If any of these factors change it is necessary to recalibrate the instrument and it is this part of the procedure which requires more time (Bransby & Tainton, 1977; Austin *et al.*, 1981). With the advent of computers and computer modelling, powerful and robust quantitative technique (Whittaker, 1987) such as models which estimate biomass production as well standing crop of various grassland ecosystems (Penning de Vries *et al.*, 1982; Powell & Pulles 1996) have been introduced. However such methods have not been fully exploited mainly because many researchers and have limited understanding of computer modelling and its application to natural resource management.

Estimation of herbage yield is deemed difficult, quantification of forage utilisation has proved even more difficult. Forage utilisation is defined as the degree to which animals have removed current growth of herbage within reach of the grazing animals. The concept can be applied to a single plant, a group of plants or to the range or pasture forage as a whole. Many researchers consider correct quantification of herbage yield and utilisation, and correct as well as efficient utilisation of forage as the most important items in range and pasture management. Numerous methods for measuring or determining forage utilisation have been developed. Some are more rapid or may be more detailed and accurate than others (Cook & Stubbendieck, 1986). The methods adopted by a given researcher will be those that best fit the purpose of his study, manpower available, and kind of vegetation (Cook & Stubbendieck, 1986). Some of the methods commonly used to assess forage utilisation include ocular estimate-by- plot, ocular estimate-by-average of plant, actual weight differences, weight before and after grazing, reduction in height, stubble-height-class, height weight ratio, stem count, short-cut, percent of plant ungrazed or grazed, twig tagging and estimate of twig utilisation. The above mentioned methods are defined, explained and discussed in detail in Brown (1954) and Cook & Stubbendieck (1986).

5.2 Objectives

The objectives of this study are:

5.2.1. To investigate the difference in chemical composition and digestibility of the most dominant grasses and sedges in the study site floodplain.

5.2.2. To correlate plant chemical composition, fibre content and digestibility with grazing pressure.

5.2.3. To estimate and compare standing biomass from the different vegetation zones in the floodplains, using a disc pasture meter

5.2.4. To compare and estimate grazing intensity amongst vegetation zones.

5.3. Methods

5.3.1. Forage quality through chemical analysis

Plant samples of eight dominant grasses, two dominant forbs and two dominant sedges were collected at maturity. Samples were dried at 60 ^{0}C for forty-eight hours and ground to uniformity using a grinder. Samples were analysed for crude protein (CP) using the standard micro-Kjeldahl method (Jones *et al.*, 1991) where CP = nitrogen concentration x 6.25. The cell components were analysed sequentially by determining the Neutral Detergent Fibre (NDF), Acid Detergent Fibre (ADF), and Acid Detergent Lignin (ADL) by the methods of Goering & van Soest (1982) using the Fibertec System M. Cellulose was estimated from the difference between ADF and ADL, and lignin from the difference between ADL and ash (Cooper *et al.*, 1988). *In vitro* dry matter digestibility was determined using the method of Tilley & Terry (1963) and Minson & McLeod (1972). Sodium and Potassium were determined using the Flame Photometer while calcium, magnesium, manganese, iron, zinc and copper were determined by an Atomic absorption spectroscopy (Dean, 1995). Phosphorous was measured colourimetrically following the conversion of phosphomolybdates which on reduction to with hydrazine sulphate give a blue colour.

5.3.2. Forage yield and utilisation

Forage yield or standing biomass was estimated at maturity, using the disc pasture meter as described in Bransby & Taiton (1977) and Danckwerts & Trollope (1980). Utilisation of forage was estimated using the percent of grazed method using the following ranking scale:

5	75 - 100% grazed - very high grazing intensity.
4	51 - 75% grazed - high grazing intensity
3	26 - 50 % grazed - moderate grazing intensity
2	16 - 25% grazed - light grazing intensity
1	0 - 15 % grazed - very light or no grazing at all.

Ungrazed swards were located and used as standards or references for the subjective ranking. The grazing intensity assessment was done at the beginning of the growing season (November), middle of the rainy season (February through March) which was at peak biomass, beginning of the dry season (before floods-May through June) and after floods (September through October).

5.4 Results:

5.4.1. Chemical analysis to determine forage quality

The results of the chemical analysis are presented in Table 5.1. Based on literature that has pointed out that digestibility, crude protein content, phosphorus and fibres are more influential as far as forage quality is concerned, emphasis will be placed on those attributes in interpreting the results. The forb *Ludwigia stolonifera* was found to contain the highest amount of crude protein (9.96 %), followed by the grass *Paspalidium obtusifolium* with 6.40 % then the forb *Alternanthera sessilis* with 6.41%. The grass *Setaria sphacelata* was found to contain the lowest amount of crude protein with 3.48 %. The forb of *Alternanthera sessilis* has the highest *in vitro* dry matter digestibility with 70.90 % while *Veteveria nigritiana* has the lowest *in vitro* dry matter digestibility with 24.32 %.

The plant mineral contents and critical values used to interpret and discuss the results are from Jones *et al*. (1991). P consists of 0.15% to 1 % of the dry weight of most plants with sufficient values ranging from 0.20 % to 0.40%. Critical values of P are normally less than 0.20 % when deficient and greater than 1.00 % when they are in excess. Results in Table 5.1 show that P values range from 0.038 % (*Setaria sphacelata)* to 0.138 % (*Ludwigia stolonifera*). The results show that all the samples are lower than the minimum value of the range, thus implying that P is deficient in all the plants sampled.

K consists of 1.00% to 5.00% of dry weight of leaf tissues with sufficient values ranging from 1.50 % to 5.00 % in recently matured leaf tissues for many plants. K content are considered deficient when it is less than 1.50 % and excess when they it is more than 3.00%. Table 5.1 shows that K content ranges from 0.90 % (*Setaria sphacelata*) to 2.35 % (*Alternanthera sessilis*). The K contents of *Eragrostis inamoena* (1.20 %), *Cyperus articulatus* (1.02 %), *Imperata cylindrica* (1.26 %), *Setaria sphacelata* (0.90 %),and *Veteveria nigritiana* (1.20 %) are lower than the critical level. The other plant species from Table 5.1 are within the sufficiency range but no one is in the excess range.

Mg plant content ranges between 0.15 % to 1.00 % of dry weight in leaf tissue, with sufficiency values being about 0.25 %. Results presented on Table 5.1 range from 0.085 % (*Setaria sphacelata*) to 0.226 % (*Acroceres macrum*). All the plant species are below the sufficiency level of 0.25 %. *Acroceres macrum, Alternanthera sessilis, Ludwigia stolonifera*, and *Paspalidium obtusifolium* are the only four species whose Mg contents are within range.

Ca content in plants ranges between 0.20 % and 3.00 % of the dry weight in leaf tissue, with sufficiency values ranging from 0.30 % to 1.00 %. The results from Table 5.1 range from 0.149 % (*Paspalidium obtusifolium*) to 0.800 % (*Ludwigia stolonifera*). *Panicum repens*, *Setaria sphacelata* and *Paspalidium obtusifolium* are out of the sufficiency range, while the rest are within the range but no one is in excess.

Leaf sufficiency content of Mn ranges from 10 to 50 ppm in the dry matter in mature leaves. Levels my reach 200 ppm or more before severe toxicity symptoms develop. Table 5.1 shows a range from 29 ppm (*Setaria sphacelata*) to 143 ppm (*Ludwigia stolonifera*). *Panicum repens, Imperata cylindrica, Miscanthus junceus, Sporobolus spicatus, Veteveria nigriana* and *Paspalidium obtusifolium* are within the sufficiency range while the rest are above sufficiency range but below the toxicity level.

The leaf sufficiency content of Zn ranges from 15 to 50 ppm in dry matter in mature leaves, while with some species, deficiency will not occur until Zn is as low as 12 ppm. A small amount of Zn, as little as 1 to 2 ppm, may be sufficient to distinguish between deficiency and sufficiency. Some plants can accumulate considerable quantities of Zn without harm to the plant. Values of Zn from Table 5.1 range from 12 ppm (*Cyperus articulatus*) to 54 ppm (*Alternanthera sessilis)*. Only *Cyperus articulatus* is below the sufficiency value with a reading of 12 ppm.

The Cu sufficiency range in leaves ranges between 3 to 7 ppm of dry matter, while toxicity range begins at 20 to 30 ppm . Values of Cu from Table 5.1 ranges from 2.0 ppm (*Sporobolus spicatus*) to 7.5 % (*Ludwigia stolonifera*). Only *Sporobolus spicatus* is lower than the sufficiency range.

The leaf content of Fe ranges from 10 to 1000 ppm in the dry matter with sufficiency ranging from 50 to 75 ppm, although total iron my not relate to sufficiency. Values from Table 5.1 shows a range from 27 ppm (*Setaria sphacelata* and *Panicum repens*), 285 ppm (*Ludwigia stolonifera*). *Ludwigia stolonifera* and *Alternanthera sessiles* have values exceeding the critical sufficiency level of 75 ppm, while the rest of the plant species from Table 5.1 have Fe values less than the lower critical value of 50 ppm, but still fall within the general leaf content range.

Table 5.1. Table showing results of plant chemical analysis.

	PLANT CHEMICAL PROPERTIES OR CHARACTERISTICS															
							%	%	%	%	%	%				
SPECIES	%IVDMD	%ODM	%NDF	%ADF	%ADL	%ASH	CP	Na	P	K	Mg	Ca	Mn	Zn	Cu	Fe
ACMA	44.92	46.14	69.90	40.00	5.40	9.40	5.50	0.09	0.0476	2.23	0.226	0.346	99	19	4.0	42
ERIN	43.6o	43.50	76.00	42.80	5.50	5.85	4.21	0.045	0.050	1.20	0.105	0.258	57	27	4.0	39
CYAR	35.95	38.18	72.10	36.50	3.80	5.35	4.76	0.21	0.058	1.02	0.110	0.298	106	12	3.0	29
SESP	37.33	38.23	77.70	48.20	6.90	6.05	3.48	0.11	0.038	1.98	0.085	0.193	29	16	3.0	27
PARE	37.61	37.61	74.70	41.30	5.10	6.05	4.21	0.14	0.058	1.80	0.102	0.199	31	23	3.5	27
ALSE	70.90	71.08	32.50	18.40	2.90	7.20	6.41	0.12	0.073	2.35	0.175	0.400	153	54	3.5	11
IMCY	28.11	29.09	75.60	41.20	5.10	5.55	4.72	0.22	0.067	1.26	0.114	0.267	40	20	3.5	40
MIJU	30.98	31.72	79.10	49.20	7.00	5.75	4.21	0.26	0.064	1.05	0.094	0.252	48	39	3.0	31
SPSP	38.69	38.09	76.20	42.10	4.30	8.70	4.81	0.27	0.097	0.90	0.136	0.302	60	44	2.0	33
VENI	26.03	26.69	76.20	40.80	5.70	4.80	5.41	0.32	0.098	1.20	0.113	0.243	40	22	4.0	39
LUST	53.76	54.53	51.20	31.10	5.10	12.45	9.96	0.19	0.138	2.35	0.205	0.800	143	31	7.5	28
PAOB	49.41	48.84	73.40	37.20	2.40	6.60	6.60	0.30	0.088	2.23	0.179	0.149	45	28	3.0	33

Legend:

ACMA - *Acroceres macrum*, ERIN - *Eragrostis inamoena*, CYAR - *Cyperus articulatus*, SESP - *Setaria sphacelata*, PARE - *Panicum repens*, ALSE - *Alternanthra sessilis*, IMCY - *Imperata cylindrica*, MIJU - *Miscanthus junceus*, SPSP - *Sporobolus spicatus*, VENI - *Veteveria nigritina*, LUST - *Ludwigia stolonifera*, PAOB - *Paspalidium obtusifolium*.

5.4. 2. Forage yield using Disc pasture meter.

The results of forage yield estimations are presented in Tables 5.2, 5.3 5.4 and 5.5. Figures 5.1 to 5.16 show the calibration curves for the four communities assessed. For the estimation carried out at maturity (mid April), *Imperata cylindrica - Setaria sphacelata* community had the highest yield with 4 209 Kg/ha while *Sporobolus spicatus - Cynodon dactylon* community had the lowest yield with 2 250 Kg/ha (Table 5.2). For the estimation carried shortly before flooding (mid June), *Imperata cylindrica - Setaria sphacelata* community had the highest yield with 4 046 Kg/ha while *Paspalidium obtusifolium - Panicum repens* community had the least yield with 1 653 Kg/ha (Table 5.3). From maturity (mid April) to shortly before floods, 64 % herbage from *Paspalidium obtusifolium - Panicum repens* community was left, while for *Sporobolus spicatus - Cynodon dactylon* community, the herbage had increased by 16% (Fig 5.13). For *Eragrostis inamoena - Setaria sphacelata* community 97 % of the herbage was left while for *Imperata cylindrica - Panicum repens* community 96 % of the herbage was left (Fig 5.13). After flooding (early November) 14 % of herbage estimated at maturity was left in *Paspalidium obtusifolium - Panicum repens* community, while 25% was left in *Sporobolus spicatus - Cynodon dactylon* community, 66% was left in the *Eragrostis inamoena - Setaria sphacelata* community and 75 % was left in the *Imperata cylindrica - Setaria sphacelata* community.

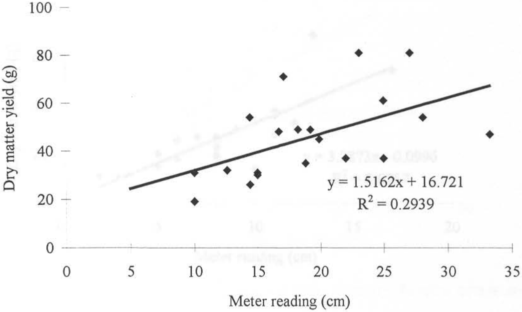


Fig 5.1 Calibration curve for *Eragrostis inamoena - Setaria sphacelata* community at maturity

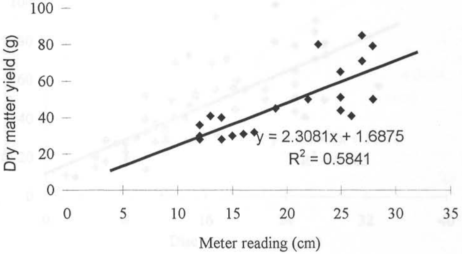


Fig 5.2. Calibration curve for *Eragrostis inamoena- Setaria sphacelata* community shortly before flooding.

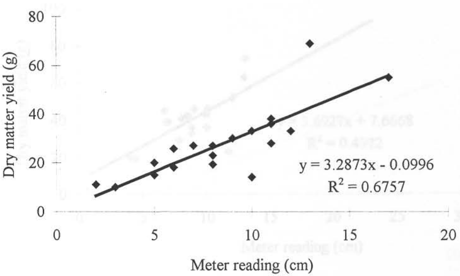


Fig 5.3 **Calibration curve for** ***Eragrostis inamoena*** **-** ***Setaria sphacelata*** **community after flooding**

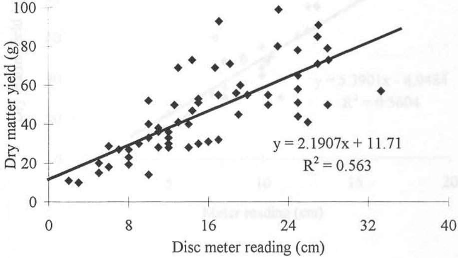


Fig 5. 4 **Calibration curve for the** ***Eragrostis inamoena*** **-** ***Setaria sphacelata*** **community for combined data collected at maturity, before flooding and after flooding**

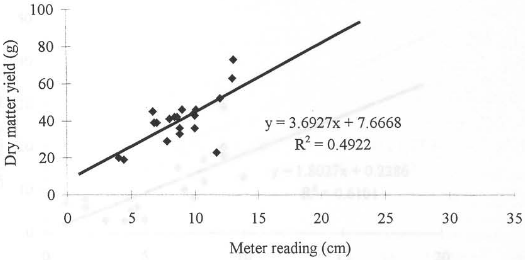


Fig 5.5 **Calibration curve for *Sporobolus spicatus* - *Cynodon dactylon* community at maturity**.

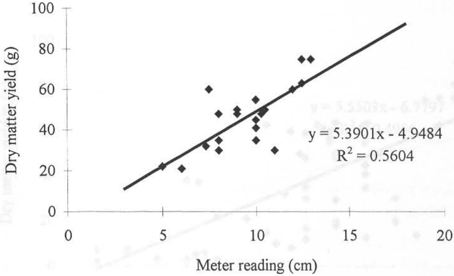


Fig 5.6. Calibration curve for *Sporobolus spicatus* - *Cynodon dactylon* community before flooding.

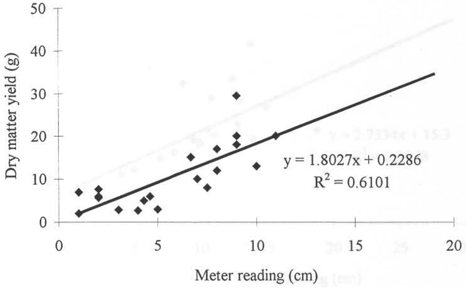


Fig 5.7 Calibration curve for *Sporobolus spicatus* - *Cynodon dactylon* community after floods.

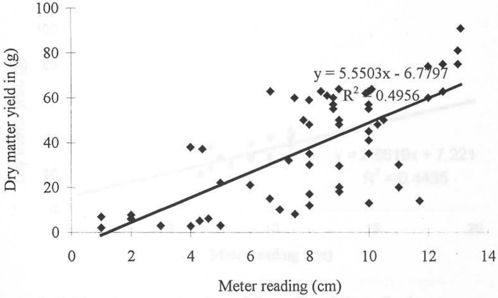


Fig. 5.8. Calibration curve for *Sporobolus spicatus* community for combined data collected at maturity, before flooding and after flooding

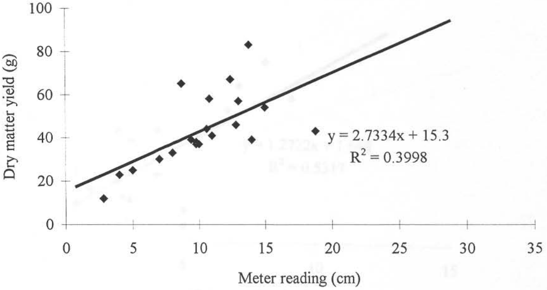


Fig 5.9 Calibration curve for *Paspalidium obtusifolium - Panicum repens* community at maturity.

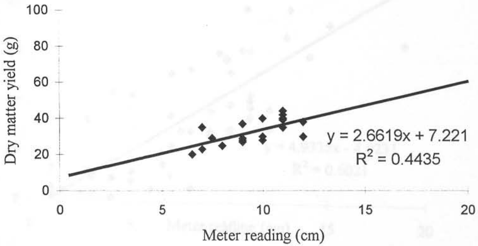


Fig 5.10. Calibration curve for *Paspalidium obtusifolium- Panicum repens* community shortly before flooding before flooding

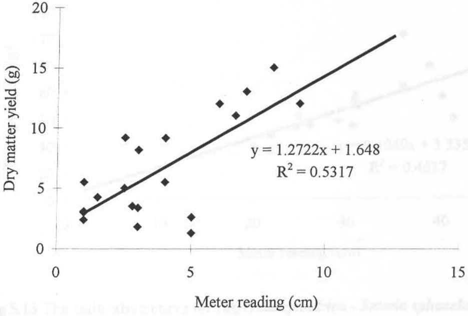


Fig 5.11 Calibration curve for *Paspalidium obtusifolium - Panicum repens* community after flooding

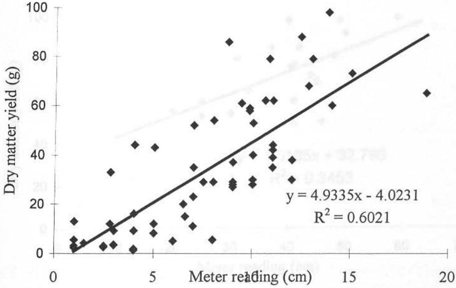


Fig.5.12 Calibration for the *Paspalidium obtusifolium - Panicum repens* community for combined data collected at maturity, before flooding and after flooding

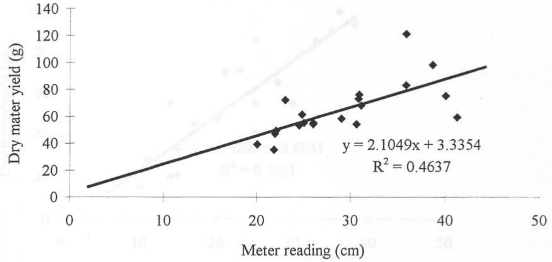


Fig 5.13 The calibration curve for *Imperata cylindrica - Setaria sphacelata* community at maturity

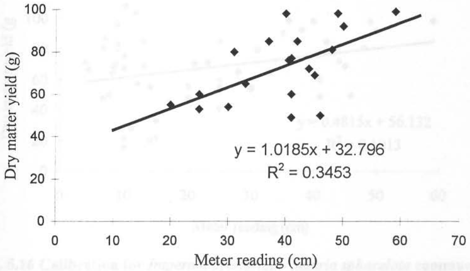


Fig 5.14 Calibration curve for *Imperata cylindrica - Setaria sphacelata* community shortly before flooding.

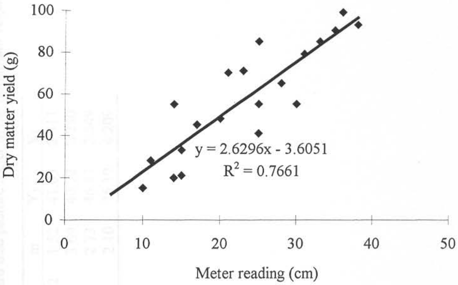


Fig. 15. Calibration curve for *Imperata cylindrica-Setaria sphacelata* community after flooding.

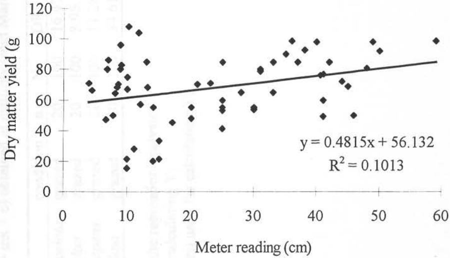


Fig. 5.16 Calibration for *Imperata cylindrica - Setaria sphacelata* community for combined data collected at maturity, before flooding and after flooding

Table 5.2. Regression analysis: (Y_1 = mx + c) obtained at maturity (mid March) with a standard disc pasture meter in the floodplain vegetation

Community type	condition	n	N	DR	r	c	m	Y_1	Y_2
Eragrostis inamoena - Setariga sphacelata	grazed	20	100	16.42	0.54	16.72	1.52	41.83	2 311
Sporobolus spicatus - Cynodon dactylon	grazed	20	100	8.95	0.70	7.67	3.69	40.72	2 250
Paspalidium obtusifolium-Panicum repens	grazed	20	100	11.28	0.63	15.3	2.73	46.13	2 549
Imperata cylindrica - Setaria sphacelata	grazed	20	100	34.61	0.68	3.34	2.10	76.19	4 209

n = number of samples used in the regression analysis
N = number of samples used in calculating Y_1
DR = Mean disc meter reading (cm) used for calculating Y_1
Y_1 = yield in g/disc meter
Y_2 = yield in kg/ha
r = correlation coefficient

Table 5.3. Regression analysis: ($Y_1 = mx + c$) obtained shortly before flooding (mid June) with a standard disc pasture meter in the floodplain vegetation

Community type	condition	n	N	DR	r	C	m	Y_1	Y_2
Eragrostis inamoena - Setaria sphacelata	grazed	20	100	16.85	0.76	1.67	2.31	40.73	2 250
Sporobolus spicatus - Cynodon dactylon	grazed	20	100	9.75	0.74	4.95	5.39	47.61	2 630
Paspalidium obtusifolium-Panicum repens	grazed	20	100	8.53	0.66	7.22	2.66	29.92	1 653
Imperata cylindrica - Setaria sphacelata	grazed	20	100	39.71	0.59	32.80	1.02	73.24	4 046

n = number of samples used in the regression analysis
N = number of samples used in calculating Y_1
DR = Mean disc meter reading (cm) used for calculating Y_1
Y_1 = yield in g/disc meter
Y_2 = yield in kg/ha
r = correlation coefficient

Table 5.4. Regression analysis: ($Y_1 = mx + c$) obtained after flooding (mid November) with a standard disc pasture meter in the floodplain vegetation

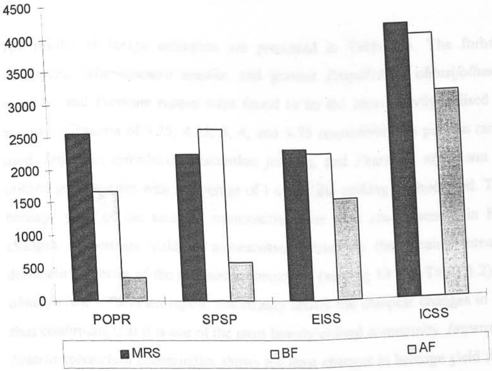
Community type	condition	N	N	DR	r	c	m	Y_1	Y_2
Eragrostis inamoena - Setaria sphacelata	grazed	20	100	8.35	0.76	0.10	3.29	27.83	1 538
Sporobolus spicatus - Cynodon dactylon	grazed	20	100	5.70	0.78	0.23	5.39	10.48	579
Paspalidium obtusifolium-Panicum repens	grazed	20	100	3.84	0.73	1.65	1.27	6.52	360
Imperata cylindrica - Setaria sphacelata	grazed	20	100	23.15	0.87	3.61	2.63	57.27	3 164

n = number of samples used in the regression analysis
N = number of samples used in calculating Y_1
DR = Mean disc meter reading (cm) used for calculating Y_1
Y_1 = yield in g/disc meter
Y_2 = yield in kg/ha
r = correlation coefficient

Table 5.5. Combined regression analysis: ($Y_1 = mx + c$) obtained before flooding, after flooding and middle of the raining season with a standard disc pasture meter in the floodplain vegetation

Community type	condition	n	N	DR	r	c	m	Y_1	Y_2
Eragrostis inamoena - Setaria sphacelata	grazed	60	300	13.87	0.74	11.71	2.19	42.08	2536
Sporobolus spicatus - Cynodon dactylon	grazed	60	300	8.13	0.70	6.78	5.55	51.90	2826
Paspalidium obtusifolium-Panicum repens	grazed	60	300	7.88	0.77	4.02	4.93	34.60	1884
Imperata cylindrica - Setaria sphacelata	grazed	60	300	32.49	0.32	56.13	0.48	71.73	3393

n = number of samples used in the regression analysis
N = number of samples used in calculating Y_1
DR = Mean disc meter reading (cm) used for calculating Y_1
Y_1 = yield in g/disc meter
Y_2 = yield in kg/ha
r = correlation



POPR = *Paspalidium obtusifolium-Panicum repens* community, SPSP = *Sporobolus spicatus* community, EISS = *Eragrostis inamoena-Setaria sphacelata* community, ICSS = *Imperata cylindrica - Setaria sphacelata* community, MRS = Middle of the Raining Season, BF = Before Floods, AF = After Floods.

Fig. 5.17 Bar chart showing the variations in herbage yield (Kg/ha) of the four communities from which yield was estimated.

5.4.3. Forage utilisation individual species.

The results of forage utilisation are presented in Table 5.6. The forbs *Ludwigia stolonifera*, *Alternenthera sessilis*, and grasses *Paspalidium obtusifolium*, *Acroceres macrum*, and *Panicum repens* were found to be the most heavily utilised species with average utilisation of 3.75, 4.25, 4, 4, and 3.75 respectively, as per the ranking method used. *Imperata cylindrica*, *Miscanthus junceus*, and *Veteveria nigritiana* are the least utilised grass species with an average of 1 as per the ranking method used. The changes in herbage yield of the assessed communities over time are presented in Fig 5.13. The changes in herbage yield in communities relates to the grazing intensities on the dominating species of the assessed communities (see Fig 13 and Table 5.2). *Paspalidium obtusifolium* - *Panicum repens* community shows the sharpest changes in herbage yield, thus confirming that it is one of the most heavily utilised community. *Imperata cylindrica* - *Setaria sphacelata* communities shows the least changes in herbage yield thus confirming that it is one of the least utilised communities.

Table 5.6. Table showing utilisation of individual plant species using the percentage grazed and ranking system.

	Period of grazing intensity assessment				
Species	BGS	MGS	MDS	AF	AVERAGE
Acroceres macrum	3	3	5	5	4.25
Eragrostis inamoena	2	2	4	5	3.25
Cyperus articulatus	3	2	2	3	2.50
Setaria sphacelata	2	2	4	4	3
Panicum repens	3	3	4	5	3.75
Alternenthera sessilis	3	4	5	5	4.25
Imperata cylindrica	1	1	1	1	1
Miscanthus junceus	1	1	1	1	1
Sporobolus spicatus	1	2	3	5	2.75
Paspalidium obtusifolium	3	4	4	5	4
Veteveria nigritina	1	1	1	1	1
Ludwigia stolonifera	3	3	5	4	3.75

Legend:

BGS: Beginning of the Growing Season, :**MGS:** Middle of the Growing Season, **MDS**: Middle of the Growing Season, **AF**: After floods.

5.4.4 Correlation of forage utilisation with forage quality (single factor analysis).

The results of correlation between grazing intensity and individual forage quality parameters are presented in figures 5.14 to 5.19. A significant positive correlation between digestibility and grazing intensity or degree of utilisation was obtained, with a high value of r = 0.80 (Fig.5.14). NDF, ADF and ADL are negatively correlated with grazing intensity, with a values of r = -0.51 (both NDF and ADF) and r = -48 (ADL). Ash is positively correlated with grazing intensity with a value of r= 0.53. CP is also positively correlated with grazing intensity with a low value of r = 0.38. The results of correlation between grazing intensity and mineral contents are not reported because the correlation coefficients are low.

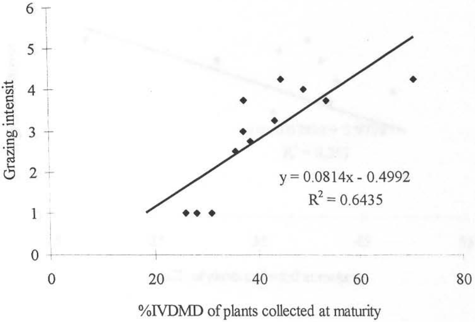


Fig 5.18 Regression curve of correlation between % IVDMD and mean grazing intensity

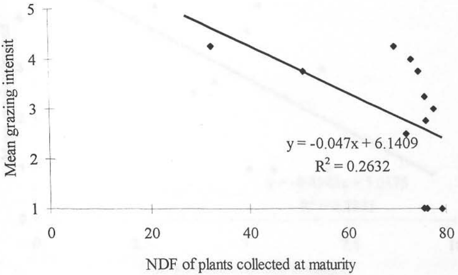


Fig 5.19 Regression curve of correlation between NDF and mean grazing intensity

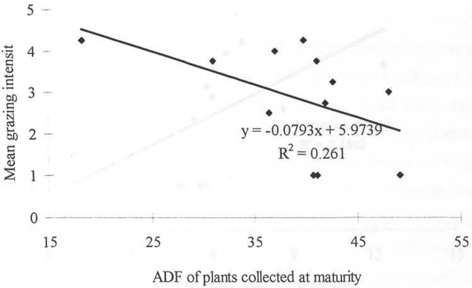


Fig 5.20 Regression curve of correlation between ADF and mean grazing intensity.

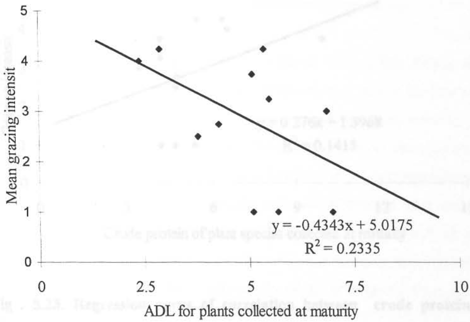


Fig 5.21 Regression curve for correlation between ADL and grazing intensity

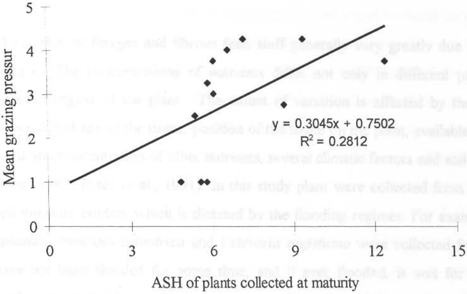


Fig 5.22 Regression curve of correlation between ASH and mean grazing intensity

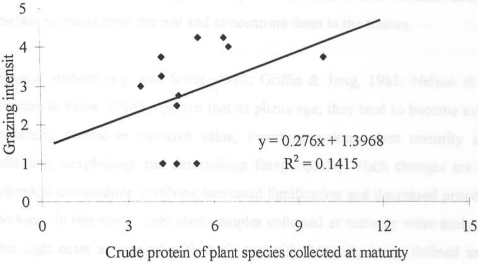


Fig . 5.23. Regression curve of correlation between crude protein and grazing intensity.

5.5. Discussion.

The quality of forages and fibrous feed stuff generally vary greatly due to a number of factors. The concentrations of nutrients differ not only in different parts but also in different organs of the plant. The extent of variation is affected by the type of plant, physiological age of the tissue, position of the tissue on the plant, available nutrients in the substrate, concentration of other nutrients, several climatic factors and soil conditions (van Soest, 1982; Jones *et al.*, 1991). In this study plant were collected from soils of varying soil moisture content which is dictated by the flooding regimes. For example *Sporobolus spicatus, Imperata cylindrica* and *Veteveria nigritiana* were collected from areas which have not been flooded for some time, and if ever flooded, it was for a short period. *Ludwigia stolonifera, Alternanthera sessilis, Paspalidium obtusifolium, Cyperus articulatus* and *Miscanthus junceus* were collected from areas which are flooded almost every year for a period exceeding four months. It therefore follows that the soils physical and chemical characteristics are differ with variation in flooding regimes. Chemical composition of some plant species may differ because of their inherent ability to withdraw certain nutrients from the soil and concentrate them in the tissues.

Several authors (e.g. van Soest, 1982; Griffin & Jung, 1983; Nelson & Moser, 1994; Buxton & Fales, 1994) reported that as plants age, they tend to become more mature and generally decline in nutritive value, therefore making plant maturity a major factor affecting morphology and determining forage quality. Such changes are due to altered chemical composition involving increased lignification and decreased proportion of leaves to stem. In this study, only plant samples collected at maturity were analysed (because of the high costs associated with such analysis). Maturity being defined as the period at which most of the plants had completed seeding and probably stopped growing. Therefore the results do not reflect nutritional quality of the investigated plant species at different growth stages.

van Soest (1982) pointed out that in making generalisation about the variation in forage quality, it must be noted that there are exceptions. For example, not all leaves are higher in digestibility than stems. There are some notable plants such as maize for example, which do not decline in nutritive value with age and maturity. Parts of certain plants may not change in quality with age. For example, leaves of alfalfa, which have little structural function (van Soest 1982). Generally the concentration of N, P, K, S, Cu, and Zn in perennial leaves or tops of annuals decrease with age of the tissue, whereas the concentrations of Ca, Mg, Al, B, Fe, and Mn tend to increase with age (Jones *et al.*, 1991). In grasses, the structural function of the leaves or function of the stem as a storage organ cause stems to be of higher nutritive value then the leaves. Factors influencing quality of stems include diameter, and whether they are filled with pith or hollow. If stems are larger, lignified tissues may be thinly distributed. Consequently in this case the stems are more digestible. It must also be noted that this generalisation is not always true. The results in Table 5.1 show that *Miscanthus junceus, Cyperus articulatus* and *Veteveria nigritiana* are the among the least digestible plant species yet field observation showed that they have the largest stem sizes at maturity. Pith is usually much less lignified than cortex, therefore hollow stems tend to be less digestible, with exceptions though. For example, *Panicum repens* and *Paspalidium obtusifolium* are hollow stemmed. *Paspalidium obtusifolium* has an *in vitro* dry matter digestibility of 49.41 % which is high, while *Panicicum repens* has an *in vitro* dry matter digestibility of 37.61 % which is quite low (see Table 5.1).

It is documented that concentration of nutrients and fibres vary with plant parts, but plants samples in this study were polled, i.e. leaf tissues and stem tissues were not separated. These could possibly lower results of plant chemical analysis. Recently, the developed mature leaf has been the organ of choice for most routine total analysis, but some situation require other choices. These situations are usually related to the manner in which different elements accumulate in or move to different tissues as their concentration varies with the substrate (Jones *et al.*, 1991). Costs and time associated with a high number of samples were once again, the main reason for not sampling at different growth stages, as well as the reason for selecting the entire plant for total analysis. This is indeed a short coming in this study. Jones *et al.* (1991) pointed out that in early investigations selecting the entire plant, or the tops in annual plants negatively impacted the relationship found between plant analysis and available nutrients. This study had no intention to establish the relationship between plant analysis and available nutrients, but to compare the relative amount of nutrients between different species at a given point in time. The usefulness of determining nutritive values of plants depends upon how broad appraisal of nutritive content is to be made. Chemical analysis are useful for measuring differences between plant species, effects of stage of growth, and effects of site quality on the chemical constituents (Jones *et al.*, 1991). A chemical analysis for a plant constituent merely indicates that the plant is comparatively high or low in that particular constituent. There are no two chemical constituents that are directly associated in all plant material. For instance, browse plants are comparatively high in lignin whereas grasses are comparatively low, yet from the stand point of nutritional value, grasses are high in some respects, and shrubs are better in others (Cooper *et al.*, 1988).

The results from Table 5.1 show that the P contents in all the plant are all below the critical values as described by Jones *et al.* (1991). This is not surprising because phosphorus is generally the most deficient major element in the soils and plants of Botswana (APRU, 1980) and Southern Africa in general. Grasses in Botswana rarely contain more than 0.1 % P in the grass dry matter (APRU, 1980).

The study identified variation in utilisation of different plant species (Table 5.2), but it could not establish the preferences of individual species by individual animals. In general forbs are more heavily utilised than grasses which implies that forbs are better than grasses in terms of nutritional value (see table 5.1) Estimation of forage yield using the disc pasture meter was successfully. However, there were limitation in using the disc pasture in the study area. The disc pasture meter was applicable only in four communities namely *Sporobolus spicatus* community, *Eragrostis inamoena-Setaria sphacelata* community, *Imperata cylindrica-Setaria sphacelata* community and the *Paspalidium obtusifolium-Panicum repens* community because the average height of the plants in those community at maturity when crude protein is low explains the low correlation. Owen-Smith (1982) reported that crude protein content of most tropical grasses falls below 5% at maturity, which is regarded as the critical level necessary for maintenance of most herbivores during dry season. Except for *Ludwigia stolonifera* which had crude protein content of 9.69 % almost all the species from Table 5.1 are within the range of 5 +-1% from the critical level reported by Owen-Smith (1982), thus implying that protein is limiting .

A high negative coefficient of determinants (R^2 =-0.75) between NDF and %IVDMD was obtained thus showing that the two factors are inversely related. It therefore follows that digestibility and fibre content are the most crucial elements influencing forage utilisation with 75 % of the variation in digestibility explained by fibre conent. For example *Veteveria nigritiana, Miscanthus junceus* and *Imperata cylindrica* are the least digestable while they have the highest fibre content (see Table 5.1) and the lowest grazing intensity at all seasons (see Table 5.2). Table 5.5 shows that grazing intensity varies with season on the different species. During the raining (growing) season utilisation was low to moderate for all because during that period the growth rate out weighs the off-take rate. Forbs of *Alternanthera sessilis* and *Ludwigia stolonifera* heavily utilised all year because they grow in the primary floodplains which maintain a high level of soil moisture all year round, thus allowing for growth of green forbs all year round. Forbs in the floodplains are very critical grazing resource. *Sporobolus spicatus, Eragrostis inamoena,* and *Setaria sphacelata* are heavily utilised during floods because they grow in areas which get flooded for a short period or not flooded at all. When floods start receding, herbivores utilise the primary floodplains, thus putting more pressure on the forbs. This variation in grazing pressure over season shows that there is a pattern of grazing in the floodplain regulated by seasonal flooding.

5.6. CONCLUSION

Variation in forage quality results in variation in utilisation by herbivores. Forage quality and availability also determine the seasonal pattern of utilisation. In the seasonal floodplains, there is a self sustaining rotational grazing system controlled and regulated by seasonal flooding. Therefore flooding plays an important role in regulating forage availability and number herbivores utilising forage in the seasonal floodplains of the Okavango Delta. No single combination of forage quality determinants was found to influence forage utilisation. However a strong correlation between forage digestibility and utilisation was obtained thus implying that this study identified digestibility as one of the most important determinants of forage utilisation. Forbs in the floodplains are a crucial resource because of their high forage value and prolonged availability.

CHAPTER 6

General discussion and conclusion

The study successfully addressed the general objectives and the hypothesis listed in section 1.2 and 1.3 of chapter 1 respectively. Hypothesis 1 which stipulated that vegetation zonation in the seasonal floodplains is due to variation in elevation which influence extent and duration of flooding was found to be true. Hypothesis 2 which stipulated that vegetation zonation may be co-determined by soil water regimes and variation in soil chemical and physical properties, or a combination of both was also found to be true. This was supported by a successful ordination of floristic data using DECORANA (Hill, 1979b) which showed clear gradients illustrating variation in elevation, soil moiture, and soil chemical characteristics. The results of ordinations indicate a floristic relationship amongst the vegetation communities and emphasise the relation between environmental gradients and vegetation units.

However, the interaction of environmental factors and vegetation distribution may not be that obvious. The most obvious environmental gradient like elevation and soil moisture may not necessarily be the most important. It must be noted that environmental factors are manifested at different levels land (Haore, 1997). For example an environmental factor such as elevation and rainfall can govern vegetation at subcontinental scale as well as at local scale. However, at local scale aspect and slope, terrain, soil moisture and chemical biotic and abiotic factors play a major role, while overall precipitation and elevation play a lesser role (Haore, 1997). In local cases like the Okavango Delta seasonal floodplains elevation may be as important as it is at subcontinental.

The vegetation of the study area is relatively heterogeneous. Classification obtained by TWINSPAN (Hill, 1979a) and refined by Braun-Blanquet procedures resulted in vegetation units which are easily distinguishable in the study area. Knowing the differences and similarities of vegetation communities is important for designing management plans for systems such as the Okavango Delta. Therefore a detailed description of the floodplain vegetation communities given in chapter 3 is essential in understanding how different communities are likely to respond to disturbance such as fire, drought and overgrazing. Due to the corresponding results obtained from TWINSPAN (Hill, 1979a) and the Braun-Blanquet analyses of total floristic data sets, TWINSPAN may be useful as well as an extremely good first approximation to create a basic classification which may be refined by the application of the Braun-Branquet procedures (Bredenkamp *et al.*, 1991).

Analysis of soil chemical properties indicated that in most cases there are significant differences in soil mineral contents amongst different communities. Soil mineral content also vary with season. Knowledge and understanding of the relationship between soil and vegetation provides basic foundations in conservation and management of vegetation, particularly in that they are interdependent in so far that destruction of one leads to the destruction of the other. Seasonal flooding seemed to have an influence on the contents of mineral nutrients in the soil, thus further substantiating the fact that seasonal flooding is the driving force of ecosystem functioning in the floodplains of the Okavango Delta and other similar ecosystems.

Hypothesis 3 which stipulated that utilisation of grazing resources in the floodplains are temporality and spatially variable due to variation between vegetation zones in availability and quality was also found to be positive. Plant species vary widely in their nutritional value as well as their utilisation by herbivores. However, no single combination of chemical composition or nutritional value of the plant species was found to be responsible for determining selection of plant species by herbivores. Its common practice when assessing veld condition to assign species to palatable and unpalatable categories. Palatability assessments are usually based on subjective judgement by experienced observers. It can therefore be concluded that species which are heavily utilised are more palatable than those which are not heavily utilised. The manner in which herbivores select their forage is fairly complex. Although factors such as digestibility and crude proteins are known to be of critical importance in determining selectivity, their influence is not always very clear.

Grazing pressure on individual species was determined. Such information is very important because gives it a good picture of the relative importance of local species to the local wildlife population. Grazing pressure on individual species varies over time. Some species are heavily grazed only during dry periods when wet area species are limited. This shows that selectivity at times is a function of availability rather than quality. For example, *Sporobolus spicatus* is among the least digestible species, but heavily grazed during dry periods, when most of the palatable species are not available.

With the ever growing pressure to utilise water from the Okavango river and the Okavango Delta, as well as the apparent decline in inflow, the future of the Okavango Delta, and the flora and fauna it supports is bleak. It is therefore critical that intensive scientific research programmes be embarked upon to generate information useful to policy makers, landuse planners, natural resource managers and researchers, particularly when drawing management plans and environmental impact assessments.

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Summary

This study forms a baseline for the long-term study of the ecological functioning of the seasonal floodplains of the Okavango Delta. As an introduction, the Okavango Delta physiography is described. The climate, soils and geology, topography, hydrology and vegetation are briefly described. Phytosociology and patterns of vegetation of the seasonal floodplains of the Okavango Delta were studied. Grasslands in the floodplains exhibit a marked zonation pattern along various environmental gradients. Application of the Braun-Blanquet methods of vegetation survey followed by a polythetic divisive classification technique (TWINSPAN) resulted in delineation of eight vegetation communities of which five were further divided into sub-communities. The eight communities are *Cyperus articulatus-Schoenoplectus corymbosus* community, *Alternanthera sessilis-Ludwigia stolonifera* community, *Miscanthus junceus-Digitaria scalarum* community, *Imperata cylindrica-Setaria sphacelata* community, *Paspalidium obtusifoloium-Panicum repens* community, *Setaria sphacelata-Eragrostis inamoena* community and *Sporobolus spicatus* community.

Ordination of floristic data was performed using DECORANA. The environmental factors include soil pH, elevation, depth and duration of flooding, Na, P, K, Ca and Mg. Ordination of floristic data successfully identified discontinuities which agreed well with field observation. Elevation, which influences duration and extent of flooding (moisture gradient), was identified as the main determinant of variation in spatial distribution of vegetation communities. Other environmental factors such as soil physical and chemical properties also contribute to spatial arrangement of vegetation but their implication in terms of zonation is not always clear.

The study investigated the variations in soil mineral nutrients content in relation to seasons and flooding regimes. Soils samples were collected during the raining season, before flooding and after flooding, and analysed for pH, Na, P, K, Ca, and Mg. An analysis of variance was performed using the using the Turkey's test to establish whether there is any

significant statistical difference and statistical interaction in soil mineral contents of different vegetation communities at different seasons at p= 0.05. The results showed that in some cases are signifcant differences while in some cases there is non. The forage quality of most dominant species in the study area was investigated and correlated with gazing pressure. Digestibilty was found to the highest correlation with grazing intentity.

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Appendix 1 : Alphabetical species list

Acacia tortilis (Forssk.) Hayne
Acroceres macrum Stapf.
Alternanthera sessilis (L.) DC.
Amaranthus thunbergii Moq
Andropogon gayanus Kunth
Aristida species
Aristida stipoides Lam.
Blainvillea gayana
Brachiaria arrecta (T. Durand & Schinz) Stent
Brachiaria dura
Brachiaria humidicola (Rendle) Schweickerdt
Cenchrus cilliaris L.
Chloris virgata Sw.
Colophospermum mopane
Combretum embebe Wawra
Commelina diffusa
Conyza species
Corchorus olitorius L.
Corchorus species
Cycnium tubulosum (L.F.) Engl.
Cymbopogon excavatus (Hotchst.) Stapfex
Cynodon dactylon (L.) Pers.
Cynodon dactylon (L.) Pers.
Cyperus articulatus L.
Cyperus dives Del.
Cyperus longus L.
Cyperus species
Dactylocteni aegytium (L.) Wild.
Dactylocteni giganteum
Dicoma schinzii
Digitaria debilis (Desf.) Wild.
Digitaria eylesii C.E. Hubb.
Digitaria scalarum (Schweinf.) Chiov.
Echinochloa colona
Echinochloa staginina (Retz.) Beauv.
Eleocharis dulcis (Burn.f.) Hensch.
Eragostis cilianensis (All.) F.T. Hubb.
Eragrostis inamoena K. Schum.
Eragrostis lappula Nees
Eragrostis lehmanniana
Eragrostis species
Ethulia conyzoides L.f
Fimbristylis complanata (Retz.) Link
Fimbristylis species

Eragrostis lehmanniana
Eragrostis species
Ethulia conyzoides L.f
Fimbristylis complanata (Retz.) Link
Fimbristylis species
Gisekia africana
Gisekia species
Gomphocarpus species
Hermbstaedtia odorata
Hermbstaedtia species
Hibiscus calyphyllus
Hibiscus cannabinus L.
Hibiscus species
Hyphaene petersiana
Imperata cylindrica (L.) Raeusch.
Indigofera flavicans
Justicia matammensis
Kohautia species
Kyllinga alba Nees
Leersia hexandra Sw.
Lessertia benguellensi
Ludwigia leptocarpa (Nutt.) Hara
Ludwigia stolonifera (Guill. & Perr.) P.H. Raven
Miscunthus junceos (Stapf) Pilg.
Nesia quadrangula
Nidorella resedifolia
Nymphaea nouchali
Nymphoides indica
Oldenlandia species
Oryza longistaminata A. Chev. & Roehr
Panicum dregeanum Nees
Panicum repens L.
Panicum subalbidum Kunth
Paspalidium obtusifolium (Delile) N.D. Simpson
Pentodon pentandrus
Perchuel-Loes leubnitzi (Kuntze) O.Hoffm.
Persicaria limbata (Meisn.) H. Hara
Phoenix reclinata
Phragmites australis (Cav.) Steud.
Pogonarthria squarrosa (Roem. & Schult.) Pilg.
Potamogeton thunberii Cham.& Schltdl
Pycnostachys coerulea Hook.
Pycreus nitidus
Schizodium cornutum (L.) Schltr.
Schoenoplectus corymbosus (Roth ex Roem. & Schult.) J.Raynal
Sclerocarya birrea (A.Rich.) Hochst. Spp. caffra.

Sesbenia microphylla Harms
Setaria sphacelata
Setaria verticillata (L.) P. Beauv.
Sida cordifolia L.
Solanum nigrum L.
Sorghum vertisicor Anderss
Sporobolus acinifolius Stapf.
Sporobolus Africanus (Poir.) Robyns & Tournay
Sporobolus spicatus (Vahl) Kunth
Tephrosia capensis
Tephrosia purpurea
Urochloa trichopus (Hochst.) Stapf
Vernonia glabra (Steetz)
Veteveria nigritiana (Benth.) Stapf
Vossia cuspidata (Roxb.) Griff.