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WETLAND PLANT COMMUNITY COMPOSITION AND SUCCESSIONAL PROCESSES IN THE MAUNACHIRA RIVER SYSTEM OF THE OKAVANGO DELTA

Karen Ellery.

A dissertation Submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, for the Degree of Master of Science

Johannesburg 1987

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Master of Science in the University of the W[illegible]atersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

Karen Ellory

10th day of December, 1987.

ABSTRACT

The aim of this study was to examine the composition and major determinants of the wetland vegetation of the Maunachira river system and to investigate the successional trends which have followed the recent increase in inundation of this river system.

Six broad vegetation types were delineated from phytosociological data which were analysed using a polythetic divisive classification technique. A detrended correspondence analysis indicated that water depth was the major environmental factor influencing the distribution of submerged, floating-leaved and bottom-rooted emergent plant communities. The remaining communities were of short emergent species assemblages rooted in peat deposits and had water depths of less than 0,7m. Their species composition was not related to water depth, conductivity, pH, redox potentials, water temperature or total nitrogen or phosphorus concentrations, but appeared rather to be the result of plant successional processes which were not hydroseral in the classical sense.

Peat stratigraphical evidence in cores taken in each of the plant communities, as well as detailed studies of diatom succession in a single core taken in a community at an advanced successional stage, indicated that the development of many of the peatlands in the study area was initiated by the formation of floating sudds. These were largely independent of water depth and formed in one of two ways. In the first, small organic detrital sudds formed by the detachment of detrital material from the floor of water bodies dominated by *Nymphaea caerulea* Sav. or *Typha capensis* (Rohrb.) N.E. Br. or both. The fine detritus was supported in the root mass of these two species, whose corms and rhizomes acted as the nucleus of each sudd.

Gas production within these bottom detrital aggregates appeared to be the most important factor leading to their formation, and being related to temperature they formed largely during the summer months. They were extremely mobile and under the influence of wind action banked up on the leeward side of the water bodies. Mean rates of encroachment of these banks were estimated to be 0,05m a^{-1}, although this varied considerably within a single water body. Sudd formation also occurred by the vegetative growth of *Pycreus nitidus* (Lam.) J. Raynal into areas of open water from vegetation stabilised margins or from detrital floating sudds. Rates of encroachment by this species was shown to be as high as 1,25m a^{-1}, and was dependant on physical support for the semi-buoyant, extending stolons.

Both types of sudd provided an exposed surface for the colonisation and establishment of short emergent plant species. The initiation of peat bog development by these two processes is more rapid than by the more common hydoseral successional pathway. Results suggest that aggradation occurred both downwards in the form of detrital rain from the sudd and upwards as a result of surface accumulation of plant material. Further vertical accumulation appeared to be limited by the fluctuations in the present-day water level.

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CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION TO THE STUDY

Wetlands can be loosely defined as vegetated areas which are flooded either permanently or seasonally and are sometimes interspersed with areas of open water (Denny 1985a). The plant communities found within wetlands can be grouped into four broad categories based on different life forms, namely submerged, floating, floating-leaved and emergent. Operating at different spatial and temporal scales, climate, edaphic conditions, hydrology and biological factors all play a role in determining the distribution of such plant communities (Gosselink & Turner 1978). In hydrologically dynamic wetland systems such as alluvial fans and deltas however, which undergo a repetition of progressive erosional and depositional cycles on a much shorter time scale than can be affected by regional climatic factors (Klein & Dupre 1980, Galloway & Hobday 1983), the latter three factors become the most important determinants.

The Okavango Delta, situated in northwestern Botswana between 19° and 20° S and 22° and 24° E (Fig. 1.1), is at an altitude of 950m above sea level and is approximately 16 000km^2 in extent (Wilson & Dincer 1976). It is an internal drainage system that spreads out into a delta-shaped shallow alluvial fan which comprises several main distributary systems (Fig. 1.1). The permanent swamps cover a

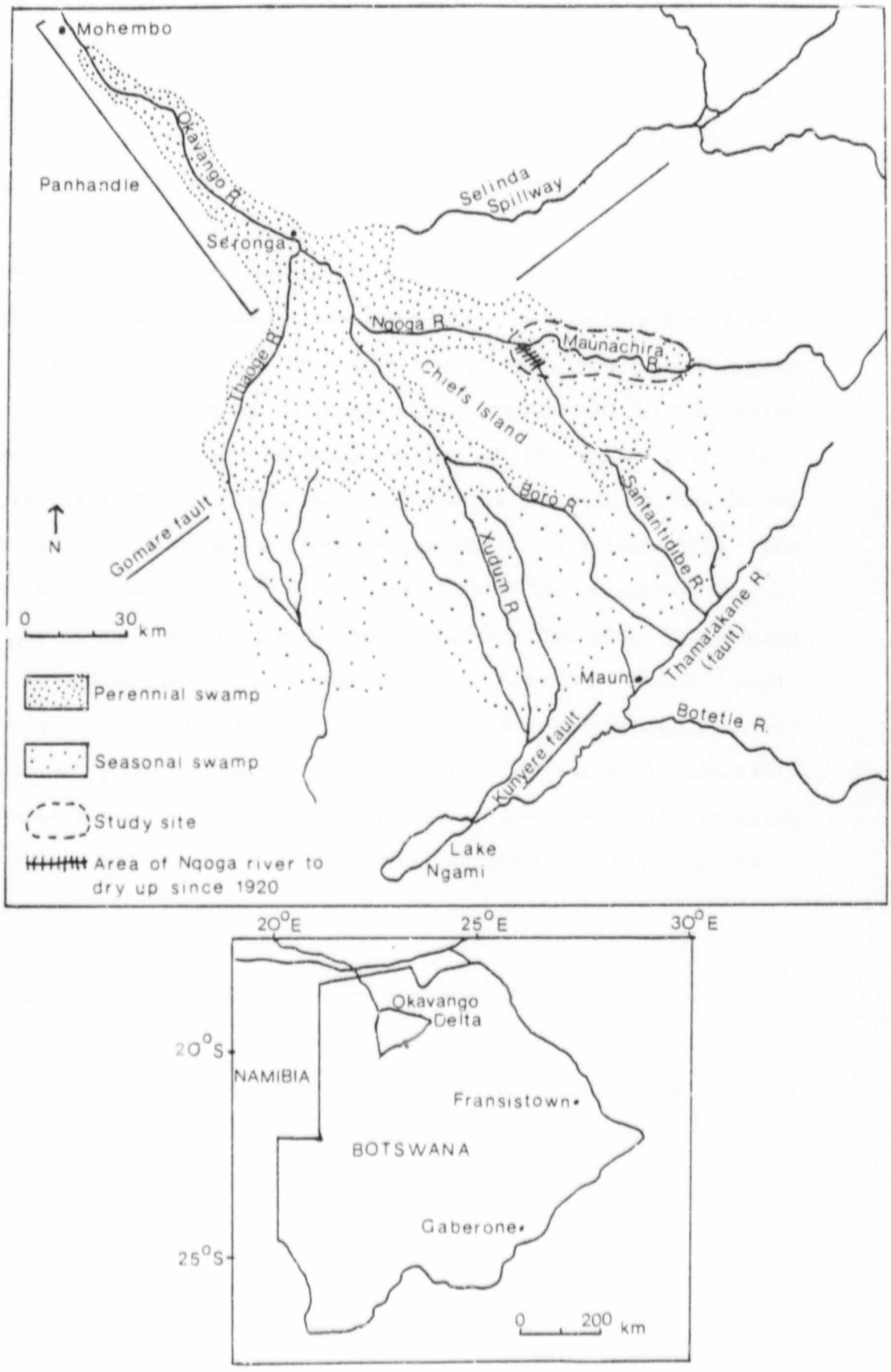


FIGURE 1.1 Map of the Okavango Delta, Botswana.

large area in the northwestern part of the delta (Fig. 1.1) and are characterised by deep, permanently flo ıg rivers and madiba (Tswana name for open water bodies, lediba = singular). The southern part of the delta receives water only seasonally and consists mainly of large islands and shallow grass and sedge covered floodplains.

Within the perennial swamps the river systems have been known to undergo periods of blockage and abandonment on a time-scale of 50 - 100 years (Wilson 1973). The most recent example of switching in flow is in the two most northeasterly river systems in the delta. A decrease in flow in the lower reaches of the Nqoga river since before the 1920's has been accompanied by an increase in flow in the more northerly Maunachira river system (Fig. 1.1; Wilson 1973). The increased inundation of this river system has resulted in many changes in the wetland plant communities and has been accompanied by the development of extensive peat deposits (Smith, pers. comm.[1]). This study aimed at examining the composition, determinants and plant succession of the relatively recently inundated Maunachira river system, and forms part of a larger study in which the causes and consequences of channel abandonment have been investigated.

The objectives of this study were therefore to:-

-provide a description of wetland plant communities in the Maunachira river system (excluding the channel and channel fringe communities),

---

[1] P.A. Smith, c/o Department of Water Affairs, Maun, Botswana.

-determine the influence of water depth, water chemistry and organic matter accumulation on community composition,

-investigate the mechanisms and stages of plant succession which result in the development of the peat bogs.

1.2 LITERATURE REVIEW

1.2.1 Wetland community distribution: Determinants and successional trends

In aquatic environments the continuum of vegetation from dry land to below water is termed a hydrosere (Clements 1916, Tansley 1939, Walker 1970, Birks & Birks 1980, Denny 1985a). In the classical form of the hydrosere distinct zones of vegetation occur at different elevations, each dominated by a different life form. On dry land terrestrial plants are present, and with an increase in the water depth there is a transition from emergent to floating-leaved to submerged plants, until it is too deep for plants to survive (Denny 1985a).

The standard concept of the vegetation zones in a hydrosere representing different successional stages as described by Tansley (1939), was based on Clement's (1916) concept of succession as an autogenic phenomenon; habitat modification (reaction) caused by species on a site allows new species to invade a site until a climax community is reached. Within wetlands the plant species in each particular community alter the conditions of the site mainly by autochthonous input of organic matter - altering the substratum in which the plants are rooting and resulting in a decrease in the water depth - until the establishment of different species is favoured (Tansley 1939, Sculthorpe 1967). A regular predictable sequence of hydroseral plant communities is considered to occur over time (Tansley 1939).

Tansley's (1939) examples are restricted to open water bodies controlled by autogenic factors (Walker 1970) and therefore do not cover a wide range of aquatic environments. Much work done since the

1950's (Penfound 1953, Swindale & Curtis 1957, Beschel & Webber 1962, Walker 1970, Raup 1975, van der Valk 1981, 1982, 1986) does not support this ontogenetic nature of succession, but instead has shown succession to be more irregular and variable and therefore less predictable.

Walker (1970) tested the theory of hydroseral development by examining stratigraphic information from British post-glacial hydroseres. Although he emphasised the importance of local topography and edaphic factors in controlling successional trends, change in water depth was found to be the key determinant of species replacement. The major finding of Walker's (1970) work, however, was that although there was an overall reduction of open water and subsequent formation and accumulation of peat, no single hydroseral successional pathway was found. The majority of sequences did however, involve a reedswamp stage (tall emergent species). In a similar analysis of the North American literature on wetland succession Tallis (1983) noted a similar variability with respect to successional trends but the common intermediate stage was a floating raft of vegetation. No real explanation is given for this variability by either of these authors, but Walker (1970) mentions that later stages in the successional sequence are most influenced by the nature of the dominant species first reaching the site. Although these findings were not elaborated on, it was a significant observation as it contributed to the shift from the holistic, community approach to plant succession (Clements 1916, Tansley 1939, Odum 1969, Walker 1970) to the reductionist approach where characteristics of the individual species were considered important. Gleason (1927), who stated "every species is a law unto itself and its distribution depends on migration, environmental and individual peculiarities", was the forerunner of the "individualistic" analysis of succession. This approach explicitly emphasises the importance of

the life history characteristics of individual species in determining patterns of succession (Connel 1972, Drury & Nisbet 1973, Connel & Slatyer 1977, Grime 1979, White 1979, Noble & Slatyer 1980, van der Valk 1981, 1982, 1986).

The studies in wetlands which have examined life history characteristics of plants have all concentrated on understanding germination and establishment requirements under conditions of drawdown and reflooding (Hall et. al. 1946, Meeks 1969, van der Valk & Davis 1976, 1978, 1979, Leck & Graveline 1979, Pederson 1981, van der Valk 1981, 1982). A model has been proposed by van der Valk (1981, 1982) in which successional changes (i.e. any quantitative change in vegetation) in wetlands can be predicted from information on three important life history characteristics of plants, namely potential life span, propagule longevity and propagule establishment requirements. In its present form this model is of limited value as only a single allogenic factor (drawdown) is taken into consideration. The process of sudd (floating vegetation mat) formation has the same effect as drawdown in that an exposed surface suitable for pioneer colonisation is provided. The size and lifespan of such sudds, therefore has important implications for the development of plant communities irrespective of water depth.

1.2.2. Sudd communities in Africa

"Sudd" or "Sadd" is the Arabic word for blockage and was first applied to the large rafts of floating *Cyperus papyrus* L. which blocked navigable rivers on the upper Nile (Migahid 1947, Rzoska 1974). The term "sudd" is presently used to describe any floating vegetation mat - whether the plants are rooted in a floating organic layer or have a positive buoyancy and actually form the sudd themselves (Denny 1985b, Thompson 1985).

Thompson (1985) divides the sudd communities into two broad categories according to their origin. Firstly, floating "islands" or "mats" of organic substratum which have broken away from the bottom organic layer, float to the surface and become colonised by plants such as *Cyperus*, *Pycreus* and *Ludwigia* species (Sita 1970, Smith 1976). These sudds are usually small, isolated and mobile and the species which colonise them are known as sudd users (Thompson 1985). Secondly, plants with a positive buoyancy such as *Pycreus*, *Leersia hexandra* Swartz and *C. papyrus* may, by growing across the water surface, actually form the sudd themselves and are known as sudd formers (Thompson 1985). Many of the aquatic "weeds" such as *Eichhornia crassipes* (Mart.) Solms-Laub. and *Salvinia molesta* D.S. Mitchell also fall into this category (Mitchell 1985). These sudds can be small and mobile, may line channel edges or can cover extensive areas of many hectares and remain stationary. They are bound together by stems and rhizomes of the sudd-forming species themselves (Sculthorpe 1967) and provide a surface upon which non-sudd formers such as *Drosera* and *Xyris* can establish (Thompson 1985).

Sculthorpe (1967) recognises a third type of sudd which is essentially the same as Thompson's (1985) organic sudd colonised by sudd users, although it does not arise from the bottom organic sludge. Instead it develops from the thickets of emergent vegetation, usually *C. papyrus*, which extend from the shoreline and are not anchored in the substratum. In windy weather, or more commonly in periods of large water level fluctuations, these plants may be torn off and float away from the area of origin (Sculthorpe 1967, Howard-William & Gaudet 1985). The sudd blockages in the Nile valley are formed from such islands which float downstream (Migahid 1947, Rzoska 1974).

All three types of sudds occur in the Okavango delta. The last type are formed in the main channel systems, are transported downstream and ultimately deposited in slow flowing open water bodies connected to the channels (McCarthy et. al. 1986a). The mobile organic sudds as well as those produced by sudd forming plants occur in water bodies of negligible flow velocity, not necessarily directly connected to the main channel systems. They appear to be important in the initiation of successional pathways which differ from the more classical hydroseral pathway of gradual infilling of autochthonous material from the bottom upwards (Section 1.2.1).

1.2.3 Sudd development and initiation of plant succession

Climate in the northern temperate zone has long been held responsible for the long-term expansion and retreat of floating sudds (Swan & Gill 1970, Griffin 1977, Tallis 1983). The longer summer growth period and shorter period of icing over in the winter in the more southerly regions of the United States temperate zone provide conditions more favourable for sudd growth than the colder, more northerly areas (Hanjy 1971, Sjörs 1980, Tallis 1983). The optimal conditions for plant growth in the tropics and subtropics may therefore explain the prevalence of sudd development in these regions (Sculthorpe 1967, Junk 1983, Howard-Williams & Gaudet 1985).

Although the literature on African swamps and peatlands is extensive (cf. Thompson, Howard-Williams & Mitchell 1985), it is mostly descriptive with little emphasis on changes in species composition over time, or the processes involved. Howard-Williams & Gaudet (1985) recognise two different types of perennial swamp communities in Africa with regard to their structure:-

(1) plants rooted in the substratum made up of sediments

or peat, i.e. reedswamp communities

(2) plants rooted in floating or almost floating mats, i.e. sudd communities.

Due to structural differences, these two swamp types have different developmental processes and successional trends. The formation and accumulation of peat in reedswamp communities involves essentially a process of hydroseral vertical accumulation of undecomposed organic material until, and in the final stages, the water level limits further aggradation (Walker 1970, Sjors 1983). The rate of change in species composition therefore depends largely upon rates of infilling and thus the rate of change in water depth. In contrast to the reedswamp communities, the sudd swamps are not affected by water depth and, provided there is sufficient water present beneath the the floating sudds, are not limited to a particular zone in the hydrosere (Mitchell 1985). The successional changes of the sudd consist not only of thickening of the sudd layer but also of horizontal or lateral spread of the sudd (Kratz & DeWitt 1986). Despite differences in their structure, both swamp types result eventually in the development of peat bog communities.

1.3 THE STUDY AREA

1.3.1 General description of the Okavango Delta

The catchment of the Okavango Delta arises in the Angolan highlands and consists of two main river systems, the Cubango and the Cuito (Wilson & Dincer 1976). These drain into the Okavango river which flows through the Caprivi Strip in Namibia and enters Botswana near

the town of Mohembo (Fig. 1.1). Downstream of the town Seronga the Okavango river splits into several river systems, namely, the Magweggana or Selinda spillway, the Nqoga, Maunachira and Santantadibe rivers on the eastern side of Chiefs island and the Thaoge, Boro and Xudum rivers on the western side (Fig. 1.1).

The permanent swamps are dominated by extensive stands of *Cyperus papyrus* and *Phragmites* species. Other dominant plants are *Typha* spp., *Vossia cuspidata* (Roxb.) Griff., *Phoenix reclinata* Jacq. and *Ficus verruculosa* Warb. (Patterson 1976). In the seasonal swamps the more frequently flooded areas are dominated by *Cyperus denudatus* L. F. and *Fimbristylis complanata* (Retz.) Link, and the slightly drier areas *Imperata cylindrica* (L.) Raeuschel, *Setaria sphacelata* (Schumach.) Moss, *Chloris gayana* Kunth, *Eragrostis lappula* Nees and *Panicum repens* L. are common (Patterson 1976, Smith 1976).

1.3.2 Climate

The climatic data recorded in Maun, on the south eastern side of the delta (Fig 1.1), are considered representative of the delta as a whole (Wilson & Dincer 1976). The summer weather is largely influenced by the southward movement of the Inter-Tropical-Convergence-Zone and the winter weather by the northward movement of the subtropical high pressure belt which has its axis not far south of the Tropic of Capricorn during this period (Anderson 1976).

The mean annual rainfall for the delta is 415mm (Table 1.1) (1975 - 1985, range = 209 - 734mm), most of it occurring in the form of localised thunderstorms during the summer months from November until March or April (Anderson 1976). The mean monthly maximum temperature during this period ranges from 30,5^{o}C to 33,7^{o}C with a mean relative humidity at 8.00 hours between 60% and 78% (Table 1.1). The cooler,

TABLE 1.1 Mean climatic data measured at the Maun weather station from 1975-1985 (n = 11).

MONTH	MEAN MINIMUM TEMP. (°C)	MEAN MAXIMUM TEMP. (°C)	MEAN TEMP. (°C)	WIND VELOCITY (ms^{-1})	RELATIVE HUMIDITY (%) 8.00 hrs	14.00 hrs	RAINFALL (mm)
Jan.	19,2	32,4	25,8	1,77	58	46	85,1
Feb.	19,2	30,5	24,9	1,64	78	48	93,8
March	18,4	31,2	24,9	1,63	75	46	58,3
April	14,8	30,5	22,8	1,51	67	33	13,3
May	9,39	28,0	19,2	1,50	59	27	4,80
June	7,00	25,4	16,2	1,36	63	27	1,20
July	7,10	25,3	16,2	1,66	62	26	0,00
Aug.	10,0	28,7	19,4	1,80	50	21	0,10
Sept.	15,1	32,8	24,0	2,19	43	19	4,20
Oct.	18,6	33,2	24,1	2,44	46	25	22,0
Nov.	19,7	33,7	26,6	2,17	60	34	53,4
Dec.	19,1	33,0	26,1	1,89	69	44	7,88
							x=415,1

drier winter months (June - August) have a mean monthly maximum of 25,3°C to 28,7°C and the relative humidity ranges between 43% and 63% (Table 1.1). Frosts seldom occur in the delta itself (Tinley 1973).

Winds are mainly easterly throughout the year, with a more north easterly wind blowing in the summer and south easterly during the winter (Tinley 1973). The average wind speed for the year is 1,81m s^{-1} which can reach velocities as high as 2,44m s^{-1} during early summer (October, Table 1.1)

1.3.3 Geology

The Okavango delta is situated in what is termed the "middle Kalahari" basin (Cooke 1976). This region is covered with deep (up to 300m thick) Kalahari sands comprising brown and white, deltaic and windborne, medium- to fine-grained sands and silts of Cenozoic age (Hutchins et. al. 1976). Lenses of calcrete and silcrete are interspersed within these sands, and outcrops of older rocks, the oldest being the Archaen Basement complex, surface at intervals throughout the middle Kalahari (Hutchins et. al. 1976).

The area of the delta is seismically active and faulting appears to be important in determining the present position of the delta within the Kalahari basin (McCarthy et. al. 1986a). In the upper reaches of the delta the Okavango river is confined to a relatively narrow, fault-bound graben (Hutchins et. al. 1976) known as the "panhandle" (Fig. 1.1). Once the river leaves the confines of the panhandle it spreads across a flat area which is itself confined within a rifted graben. This graben is at right angles to that of the panhandle and is bound by the Thamalakane and Kunyere faults in the south east and

the Gomare fault in the north west (Hutchins et. al. 1976) (Fig. 1.1).

1.3.4 Topography and the hydrological regime

The Okavango river entering Botswana at Mohembo (Fig. 1.1) has an average annual discharge of 11500 x $10^6 m^3$ (Wilson & Dincer 1976). The outflow of the Okavango delta, measured at the Botetle river, amounts to only 2% of the total input (inflow and precipitation). This is largely due to losses by evapotranspiration; losses to groundwater are considered to be minimal (Wilson & Dincer 1976).

The delta is a broad cone with an average slope of 1:3600 from the apex to the distal end (Wilson & Dincer 1976). In such a flat area only relatively small irregularities on the surface result in the mosaic of channels or rivers, madiba (water bodies), swamps, floodplains and islands which exist in the delta (Wilson & Dincer 1976). Many of the smaller islands have their origin in ancient termitaria (Smith 1976). The madiba occur in slight depressions which appear to have been formed by once much larger flowing river systems than are present today.

The present-day rivers within the delta have a history of blockage and abandonment (Wilson 1973). In the early part of last century flow from the Okavango river was mainly down the Thaoge river on the western side of the delta (Wilson 1973). During this time the Nqoga river was a shallow swamp area with few interconnecting hippopotamus (*Hippopotamus amphibius* L.) channels (Stigand 1923). During the last century the Thaoge river became progressively blocked with vegetation and subsequently has become largely moribund. Accompanying this the Nqoga river became the main offtake of the Okavango river (Wilson 1973). Even more recently (during the 1920's)

desiccation of the lower reaches of the Nqoga river has occurred, accompanied by an increase in flow in the more northerly Maunachira river system (Smith 1976) in which this study is based.

1.3.5 The Maunachira River system

The permanently inundated Maunachira river system is situated on the north eastern edge of the delta (Fig. 1.1). The study was conducted in this river system in order to examine and document the plant successional changes taking place and the processes involved in an area of recently increased inundation. The study sites were situated between Xugana and Xakanika madiba along the length of the river system (Fig. 1.2).

The Maunachira river system derives its water mainly from filter flow and from a single narrow crosscut channel linking with the main Nqoga river (Fig. 1.2). Unlike many other parts of the delta, variations in water level during the year are minimal, seldom exceeding 20cm even in times of very high floods (Wilson & Dincer 1976). Navigation is therefore possible at all times of the year along the length of the river (average depth of 2,0m) from Xakanika lediba to the crosscut channel. Oxbow shaped madiba occur at irregular intervals down its length (Fig 1.2) and the flow rates within the river itself are approximately $0,3ms^{-1}$ (Ellery W.N., in prep.), while the madiba and filter communities away from the river have negligible flow.

The channel upstream of Dxerega lediba (Fig. 1.2) is lined largely by the giant sedge *C. papyrus* but proceeding downstream it decreases in stature and dominance until only small, isolated patches occur just upstream of Xakanika lediba. *Miscanthus junceum* (Stapf) Stapf a tall spiky grass, and *Ficus verruculosa* a shrubby bush, become the major channel liners within this area.

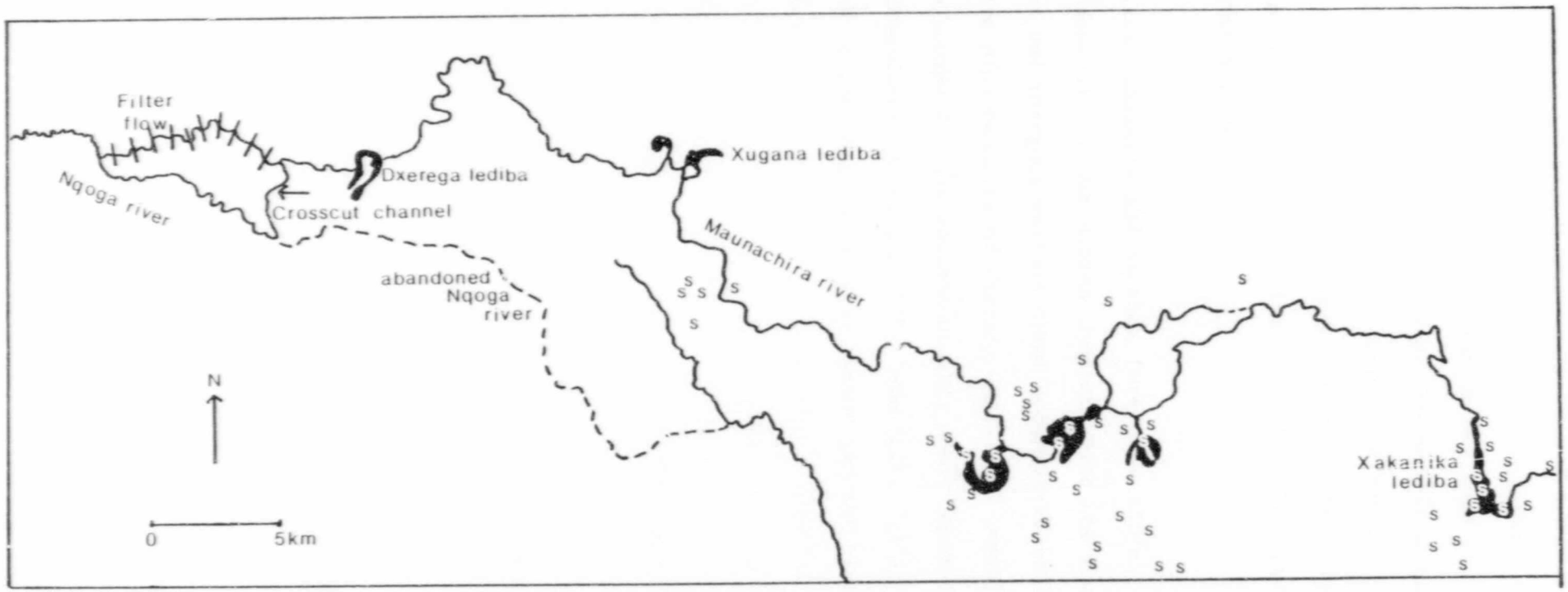


FIGURE 1.2 The Maunachira river system: the position of stands (s) in the study site.

Islands occur scattered throughout and may range in size from a few square metres in the form of termitaria to several square kilometres. Large trees are usually scattered across them with a dense riparian woodland close to the waters edge. Frequently an open evaporite area with high concentrations of sodium bicarbonate (McCarthy et. al. 1986b) exists on the islands and supports only the very hardy *Sporobolus spicatus* (Vahl) Kunth and *Juncellus laevigatus* (L.) C.B. CL. (Smith 1976).

The river channels and islands form a relatively small portion of the Maunachira river system compared with the submerged, floating-leaved and emergent wetland plant communities which dominate. Extensive peat deposits of varying degrees of consolidation and water depth occupy a major portion of this area. Apart from the work done by Gibbs-Russel & Biegel (1973) and Smith (1976) the wetland vegetation of the Maunachira river system has not been described in any detail.

CHAPTER 2

MATERIALS AND METHODS

2.1 PLANT COMMUNITY DESCRIPTION

In order to describe the wetland plant communities of the Maunachira river system and to examine the influence of major environmental determinants, two approaches of multivariate analysis, namely, classification and ordination, were used. Classification techniques involve grouping similar entities together in clusters (Gauch 1982), the properties common to a group being abstracted to serve as a description of that group (Mueller-Dombois & Ellenberg 1974). This method implies discontinuities in composition between units in the field (Mueller-Dombois & Ellenberg 1974). The ordination technique aims at portraying the sample and species relationships as faithfully as possible in low-dimensional space, the end product usually being a 2-dimensional graph in which similar samples are near one another and dissimilar samples far apart (Orloci 1978, Noy-Meir 1979, Gauch 1982). This frequently enables an environmental interpretation for sample distribution.

2.1.1 Field measurements

2.1.1.1 Stand selection

The sampling of stands for community descriptions was conducted between June and August 1984. The position of stands was located from 1983 aerial photographs (scale 1:50 000) after an initial two month reconnaissance of the area. Fifty-one stands (Fig. 1.2) were selected, in homogenous patches of vegetation, so as to cover the variation in the range of wetland plant communities in the Maunachira river system. The vegetation of channel and channel fringes has been the subject of a separate study (Ellery W.N., in prep.), and for this reason was excluded from the present study.

2.1.1.2 Determination of minimum stand size

To adequately represent the species composition of each community, a minimum stand size was determined by constructing species - area curves using the technique described by Mueller-Dombois & Ellenberg (1974) for a variety (n=15) of plant communities in the study area. Within each of the communities in which this was carried out all species were recorded within several quadrats with an area of $0,25m^2$. The quadrat size was doubled ($0,5m^2$) and the species recorded, and then doubled again ($1,0m^2$) and so on until no new species were recorded. The species numbers were then plotted against stand size for each community resulting in a number of species - area curves. The largest of the minimum stand sizes determined from these analyses was used for all communities (Fig. 2.1). The point on the graph where an increase in 10% of the total sample size yielded only 5% more species was plotted. A line was drawn from the origin through this point. A further line was drawn, parallel to this line, touching the species - area curve tangentially. This intersection point, protracted to the x-axis, resulted in a minimum stand size of $9,4m^2$. Quadrats with an area of $9,4m^2$ would have sides each measuring approximately 3,1m x 3,1m. As a conservative measure 3,5m x 3,5m stands were used.

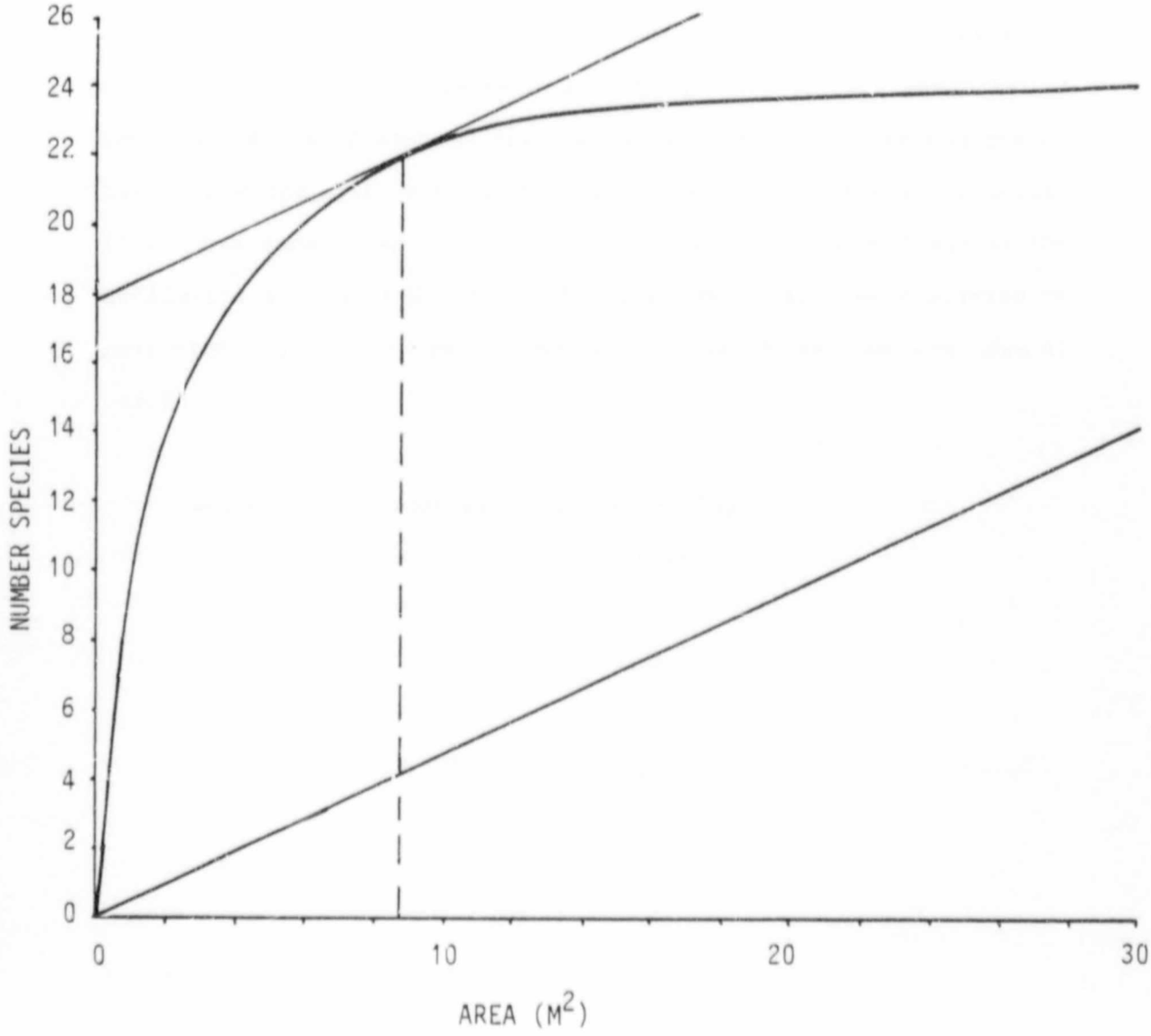


FIGURE 2.1 Species-area curve derived from a diverse emergent bog community.

2.1.1.3 Measurement of species cover

Since many wetland plants in the study area spread by vegetative growth the delimitation of a single individual in density counts presents many problems. A relatively crude estimate of species quantities, however, is satisfactory for most purposes of vegetation description (Mueller-Dombois & Ellenberg 1974). An estimate of cover abundance of each of the species expressed as a percentage of the area of the stand similar to the system devised by Braun-Blanquet (1965) was made. For the purposes of data entry and analysis in the ordination and classification the cover abundance was converted to corresponding percentage values as indicated by van der Maarel (1979).

Scale	Percentage cover	Corresponding % cover
1	<1	0,1
2	1 - 5	2,5
3	6 - 10	7,5
4	11 - 25	17,5
5	26 - 50	37,5
6	51 - 100	75,0

2.1.1.4 Environmental variables

Water depth and depth to inorganic substratum

In a comprehensive review on the zonation of plants in wetlands, Spence (1982) pinpoints water depth, and its associated factors such as light attenuation, temperature and degree of oxygenation, as the major determinants of species distribution in wetlands. Two measures of depth were taken in this study:

i) Depth to the sandy substratum - representing the depth at which the initial colonisers of the area became established,

ii) Depth to organic or peat layer - representing the depth at which the plants were rooting at the time of the survey (i.e. water depth).

The average of ten measures of each depth in each stand were taken.

Water chemistry

Various aspects of water chemistry are important determinants of species distribution in wetlands (van der Valk & Bliss 1971, Glaser 1983, Lieffers 1984, Malmer 1986). Redox potential and pH were measured with a Schotte Gerate model CG819 meter using a combined electrode. Electrical conductivity, used as an estimate of total dissolved solids, and temperature were measured with a YSI model 33 meter, and dissolved oxygen concentrations using a YSI model 51B oxygen meter equipped with a thermocouple.

Two one litre samples were collected for nutrient analyses at each stand in acid washed bottles (10% HCl) and preserved with 0,1ml formalin. Since no facilities for storing samples at a low temperature were available and two weeks elapsed between sample collection and the time of analysis, only total concentrations were measured.

The pairs of samples from each sampling point were mixed prior to the analyses. Triplicate samples were digested by persulphate digestion (Wetzel & Likens 1979). Total nitrogen was determined by the salicylate method (Cataldo et. al. 1975) with absorbance read at 410nm on a DMS 100 visible spectrophotometer. Total phosphorus concentrations were determined by the molybdenum blue method (Wetzel

& Likens 1979). The same spectrophotometer was used, and absorbance read at a wavelength of 882nm.

2.1.2 Data entry and analysis

2.1.2.1 Classification

A polythetic divisive form of classification, based on ordination using reciprocal averaging, was performed using the TWINSPAN (Two Way INdicator SPecies ANalysis) program devised by Hill (1979a). TWINSPAN is an improved version of the Indicator Species Analysis (Hill et. al. 1975) and classifies by dichotomies first the stands then the species (Hill 1979a). The term polythetic refers to divisions based upon the presence or cover of more than one species. The monothetic approach whereby a division is made on a single species is much simpler but is more prone to misclassifications (Orloci 1978, Gauch 1982). The divisive method uses the whole set of sampling units at the outset and repeatedly divides it into smaller groups of increasing similarity (Gauch 1982, Pielou 1984). This is preferable to agglomerative techniques in which the method proceeds from single entities being grouped at successive steps (Gauch 1982, Pielou 1984), as it can be used on large data sets and new data can easily be included (Hill et. al. 1975).

The vegetation data were entered into the TWINSPAN classification program on the converted percentage scale (Section 2.1.1.3). The program was run with only a single alteration to the normal program (cf. Hill 1979a) - the minimum number of stands in each division being reduced to a single stand. The stands and species hierarchical classifications were used to produce an arranged data matrix, like the Braun-Blanquet table, in which the relationship between the two were exhibited as clearly as possible. The resultant hierarchy was

displayed as a dendrogram showing relations both within and between sample groups (Hill 1979a).

2.1.2.2 Ordination

The DECORANA (DEtrended CORrespondence ANAlysis) program, an eigenvector ordination technique based on reciprocal averaging (R.A.) and developed by Hill (1979b), was used. The eigen-value for each gradient or axis and the position of a sample along each gradient was determined. The first axis was calculated by R.A. but subsequent axes were calculated using detrended sample and species scores (Hill 1979b).

In numerous studies detrended correspondence analysis has been found to give easily interpretable ordinations in comparisons with other ordination methods (Lahti & Vaisanen 1987) and was originally used as a solution to the problem of curvilinear distortion in linear ordinations (Hill 1979a, Hill & Gauch 1980, Gauch 1982). Unfortunately it eliminates the "arch effect" from the ordination, whether this arch is real or not (Williamson 1983, Beals 1984, Minchin 1987, Wartenberg et. al. 1987). However, since the most important use of the ordination is the ecological interpretation of the resulting axes, DCA was considered suitable for the purposes of this study.

The vegetation data were entered into the DECORANA ordination program in the same form as for the TWINSPAN program, using the detrended correspondence analysis option. Two stands (45 and 49), both dominated by species which did not occur in any of the other stands, were omitted from the analysis as their inclusion caused distortion of the first axis by placing them at relative positions of 2,3 and 10,0 respectively, with all other stands being placed at 0,0.

The four axes produced by the program were plotted to display 2-dimensional arrangements of stands based on their similarities. The environmental data for each of the stands were superimposed on the graphs to provide a framework in which to interpret their distribution and to identify possible successional trends.

2.2. DETERMINATION OF PEAT BOG SUCCESSION

"Bog" is the term used to describe peat covered areas which have short vegetation, a high water table, low pH, low nutrients and low oxygen saturation (Zoltai & Pollet 1983, Hofstettner 1983). There are many methods which can be used to study the successional trends of peat bog development. They fall into two categories:

(i) Studies on the same area, either by examination of cores to determine past events or long-term studies in which species changes in permanent plots are measured,

(ii) Comparisons of spatially separate communities which are considered to represent different stages of succession.

In the latter case all ecological factors except the time of disturbance or start of the successional sequence must be held as constant as possible (Mueller-Dombois & Ellenberg 1974). Since this is not usually possible such studies should be done in conjunction with those concentrating on a single area to determine the successional trends. When successional changes are rapid, direct observations are extremely valuable, but most successional sequences require long study periods (Birks & Birks 1980). Evidence from the past in the form of a photographic record or from information in sediments or peat deposits, in the form of both inorganic and organic materials, can be utilised (Birks & Birks 1980).

2.2.1 Long term changes: Vertical aggradation as a component of bog succession

Long-term changes, particularly those associated with vertical infilling of peat deposits, could not be observed within the time frame of this study. Evidence of past events was therefore examined by analysis of stratigraphy and of diatom assemblages from cores. Since pollen preservation in the peats was poor, as a result of fungal attack on the exine, pollen analyses were not possible.

2.2.1.1 Coring and peat stratigraphy

Six sites, representing each of the major vegetation types derived from the classification analysis, were selected for the collection of peat cores. Each core was obtained using a 65mm diameter piston corer, modified from Wright et. al. (1984), that had been sharpened at the end to facilitate penetration. A one-way valve on the piston prevented compaction of the peat. The peat cores were extruded horizontally in the field into perspex gutters and the gross features of the peat stratigraphy including colour, texture and where possible recognisable plant parts, were described. Further analyses were carried out only on two cores taken from a mature peat bog. Two centimetre sections were collected from them, stored in acid washed bottles, preserved with 0,1% formalin and analysed later in the laboratory for diatoms.

2.2.1.2 Diatom analyses

Subsamples of approximately $0,5cm^3$, taken from alternate two centimetre sections of the cores, were treated with a 1:1 mixture of sulphuric and nitric acid to remove organic matter (Round 1957). The residue, consisting mainly of diatoms, was washed to remove the

acids by centrifuging with distilled water numerous times (Round 1957). The diatoms were then suspended in 10ml of distilled water. Triplicate samples of 0,2ml of the suspension were mounted in Naphrax diatom mountant (Refractive Index = 1,74). Diatom identifications were made, using the reference works of Husdedt (1930 - 1966), Cleve-Euler (1951 - 1955), and Cholnoky (1966), at 1000x magnification under oil immersion using a Zeiss microscope with phase contrast. All taxa were identified to the level of genus, and although each of the different species were recognised, positive identification was not always possible using a light microscope. Identification to genus level did however enable the distinction of broad ecological trends within each of the cores and was therefore considered satisfactory for the present study.

Since the middle sections of the cores had so few diatoms, the usual method of counting a minimum number of diatom valves per sample (Haworth 1969, 1976; Javakul et. al. 1983, Engstrom et. al. 1985) was not possible. Instead, the diatom taxa were recorded and counted in four transects across the width of the coverslip (22mm) at 100x magnification. The mean of the triplicate slides for each sample was used for the analysis. Diatom numbers were thus recorded both as absolute counts, which gives an indication of productivity and sedimentation rates (Round 1957, Haworth 1976), and as percentages of the total sum which provides an indication of the nature of the environment at the time of deposition.

2.2.2 Short term changes: Horizontal extension as a component of bog succession

Results from the ordination analysis and an examination of peat stratigraphy indicated that sudd formation was an important component of the successional sequence in the Maunachira river system.

Author Ellery Karen
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