

Water depth and biotic insulation: Major determinants of back-swamp plant community composition

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Abstract

Based on phytosociological data, a polythetic divisive classification technique resulted in the delineation of eight broad vegetation types in the back-swamp areas of the Maunachira River System of the Okavango Delta, Botswana. A detrended correspondence analysis indicated that water depth was the major environmental factor influencing the distribution of submerged, floating-leaved and tall, emergent species dominated communities. The remaining communities, with relatively distinct boundaries between each of them, were of short emergent species assemblages rooted in peat deposits with a water depth of less than 0.7 m. Their species composition was not related to water depth, conductivity, pH, redox potential, water temperature or total nitrogen or phosphorus concentrations in the water. The relationship between the present day wetland plant community composition and its environment may be masked by long term, biotic, 'insulating' processes such as the accumulation of resources during peat formation and clonal plant growth. This insulation process does not lead necessarily to long term community stability as has been previously suggested (Mitsch and Gosselink 1986).

Introduction

Both allogenic and autogenic processes are determinants of plant community distribution and change in all wetland ecosystems, and two complementary models have been proposed to explain the complex way these processes interact. Mitsch and Gosselink (1986) suggest that initially the major determinants are environmental, but as the ecosystem develops, there is a progressive accumulation of nutrient resources and peat which results in 'insulation' of the community from its environment. They propose that insulation results in a change from allogenic to

autogenic processes during ecosystem development, which in turn leads to increasingly stable communities. Breen *et al.* (1988) in their comparison of swamp and floodplain vegetation processes arrived at a similar model. They discuss the manner in which growth characteristics of clonal plants amplify spatial heterogeneity by differential accumulation of resources and modification of the physical and chemical environment. Breen *et al.* (1988) also emphasize the need to consider disruptive processes, such as floods, fire and herbivory, which oppose or break down isolation. These processes may return vegetation to an earlier successional state in

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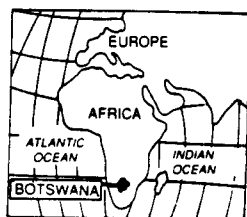
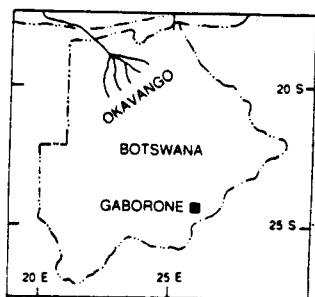
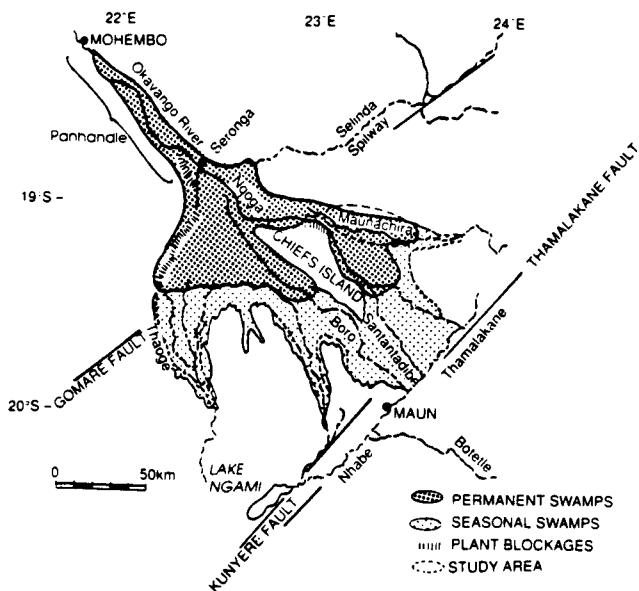


Fig. 1. Location of the Okavango Delta in northwestern Botswana.

which insulation (*sensu* Mitsch and Gosselink 1986) from the environment would be reduced.

The Okavango Delta, in the subtropical zone in semi-arid northwestern Botswana, is an endorheic alluvial fan comprising several distributary systems (Fig. 1). Channel activation and abandonment has been recognized as a dominant process influencing the structure and functioning of the system (Wilson 1973; Smith 1976; McCarthy *et al.* 1986). In the early nineteenth century, flow from the Okavango River was mainly down the Thoage River on the western side of the delta (Wilson 1973). During this time the Nqoga River System consisted of shallow swamps and pools with a few interconnecting channels formed by hippopotamus (*Hippopotamus amphibius*; Stigand 1923). During the later part of last century, the Thoage River became progressively

blocked with vegetation and the Nqoga River became the main offshoot of the Okavango River (Wilson 1973). During the 1920s, desiccation of the lower reaches of the Nqoga River has been accompanied by an increase in flow in the more northerly Maunachira River System (Fig. 1; Wilson 1973; Smith 1976). This long-term pattern of flooding, drying and reflooding has resulted in the development of a complex mosaic of wetland plant communities in the delta (Fig. 2).

The aim of this study was to describe the backswamp plant communities of the Maunachira River System and examine the influence of abiotic factors and environmental insulation as determinants of community distribution.

Study area

General description and topography of the Okavango Delta

The Okavango Delta, located between 19° and 20° S and 22° and 24° E (Fig. 1), has its catchment in the highlands of Angola. Two main river systems, the Cubango and the Cuito, drain into the Okavango River which spreads out into a deltaic shape over a shallow water body which covers approximately 16 000 km². Permanent swamps occupy a large area in the northwestern part of the delta (Fig. 1) and are characterized by deep, permanently flowing rivers and *madiba* (Tswana name for open-water bodies; singular = *lediba*). The southern part of the delta receives water only seasonally and consists of large islands and shallow grass and sedge covered floodplains.

There is an average slope of 1:3600 from the apex to the distal end of the delta (Wilson and Dincer 1976). In such a flat area, small topographic irregularities result in the mosaic of channels or rivers, *madiba*, swamps, floodplains and islands that exist in the delta (Wilson and Dincer 1976). Many of the smaller islands have their origins in ancient termite structures (Smith 1976). The *madiba* occur in slight depressions that appear to have been formed by river systems that were once much larger than today and large meanders (Fig. 2).

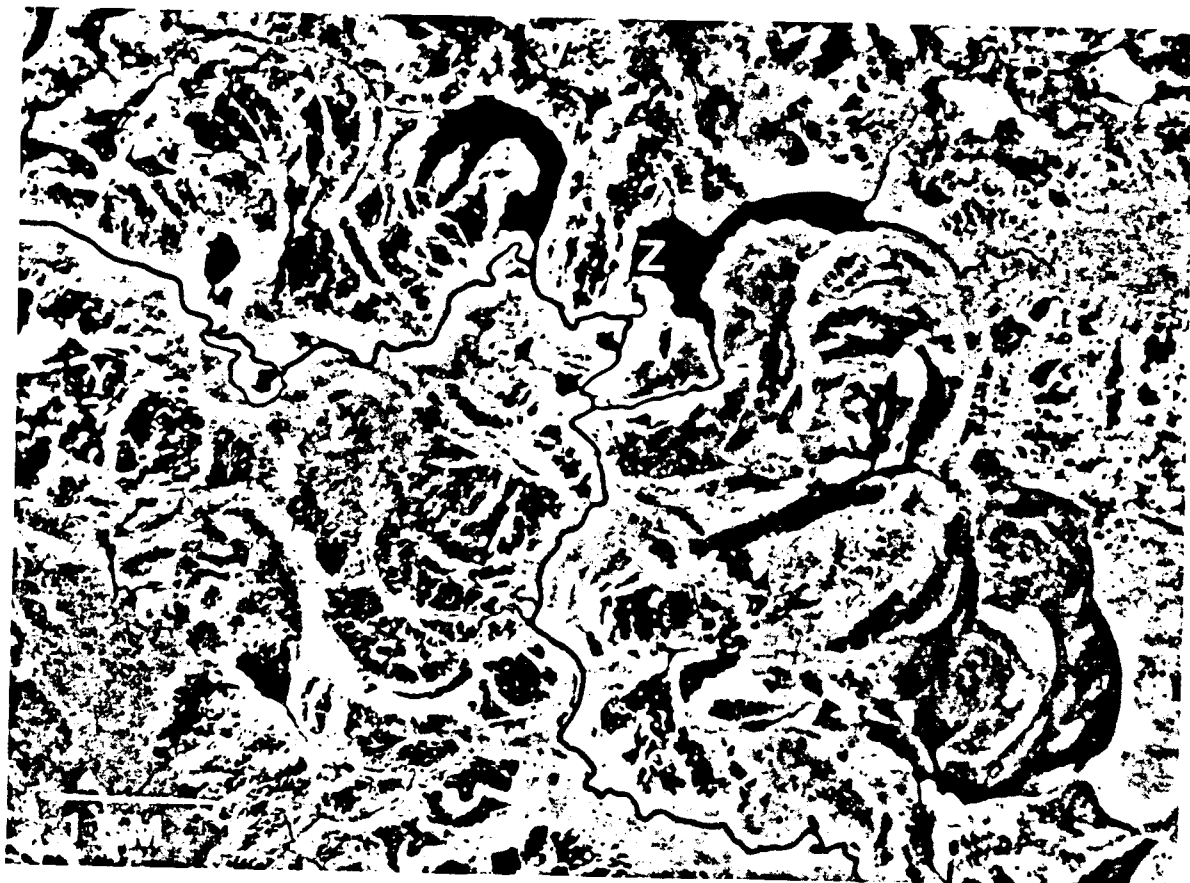


Fig. 2. Aerial photograph (1983) indicating the complex mosaic of communities in the Maunachira river system. V = island, W = river, X = emergent community, Y = floating-leaved community, Z = submerged (open water) community.

Climate

The mean annual rainfall for the delta is 415 mm (1975-1985, range = 209-734 mm), occurring mostly as localised thunderstorms during the summer months (November until March or April; Anderson 1976). The mean monthly maximum and minimum temperatures during the summer range from 30.5 °C to 33.7 °C and 14.8 °C to 19.2 °C, with a mean relative humidity at 0800 hours between 60 and 78%. The cooler, drier winter months (June-August) have a mean monthly maximum of 25.3 °C to 28.7 °C and minimum of 7.0 °C to 10.0 °C, and the relative humidity ranges between 43 and 63%. Frosts seldom occur (Tinley 1973).

Geology and hydrology

The Okavango Delta is located in the middle Kalahari basin (Cooke 1976). This region is covered

with deep (up to 300 m thick) Kalahari sands that are 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 in these sands and outcrops of older rocks, the oldest being the Archaen Basement complex, surface at intervals (Hutchins *et al.* 1976).

This area is seismically active and faulting appears to be important in determining the position of the delta in the Kalahari basin (McCarthy *et al.* 1986). 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). Once the river leaves the confines of the panhandle, it spreads across a flat area confined in 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 southeast and the Gomare Fault in the northwest (Fig. 1; Hutchins *et al.* 1976).

The Okavango River, entering Botswana at Mohembo (Fig. 1), has an average annual discharge of $11\,500 \times 10^6 \text{ m}^3$. Rainfall has been estimated to contribute approximately $5000 \times 10^6 \text{ m}^3 \text{ a}^{-1}$ (Wilson and Dincer 1976). The outflow of the Okavango Delta, measured at the Botetle River, amounts to only 2% of the total input. Losses to groundwater are considered to be minimal; the bulk of the water loss is due to evapotranspiration (Wilson and Dincer 1976). Seasonal fluctuations in water level are large (0.9 – >3.0 m) in both the panhandle and the lower reaches of the seasonal swamps while the central, permanent swamps have a considerably smaller annual rise and fall (0.15–0.25 m; Wilson and Dincer 1976).

The Maunachira River System

The permanently inundated Maunachira River System is located on the northeastern edge of the delta (Fig. 1). The Maunachira River System derives its water mainly from filter flow through upstream papyrus (*Cyperus papyrus*) communities and from a single narrow crosscut channel linking it with the main Nqoga River. Variations in water level during the year are minimal, seldom exceeding 20 cm even during peak floods (Wilson and Dincer 1976). Navigation is possible at all times of the year along the length of the river (average depth of 2.0 m). Oxbow-shaped *madiba* occur at irregular intervals. Flow rates within the river itself are approximately 0.3 m s^{-1} (Ellery 1988), but in the *madiba* and back-swamp communities away from the river, which form the basis for this study, flow rate is less than 0.03 m s^{-1} .

The islands are scattered throughout and form a relatively small portion of the Maunachira River System compared with the mosaic of submerged, floating-leaved and emergent back-swamp plant communities. The back-swamp communities are characterized by extensive peat deposits of varying degrees of consolidation. Apart from the preliminary, qualitative and descriptive work of Gibbs-Russel and Biegel (1973) and Smith (1976), the distribution and major determinants of the wetland vegetation of the Maunachira River System have not been examined in detail.

Methods

Multivariate techniques of classification and ordination were used to describe the wetland plant communities of the Maunachira River System to examine the influence of major abiotic factors. The stratigraphy of peat cores taken in representatives of each of the major vegetation types derived from the classification analysis, was also examined. These cores provided insight into processes such as peat formation and resource accumulation, which had taken place during community development.

The vegetation stand positions were determined from 1983 aerial photographs (scale 1:5000). Fifty-one stands were selected in homogeneous patches of vegetation, to include the range of variation of back-swamp plant communities in the Maunachira River System.

Species – area curves (Mueller-Dombois and Ellenberg 1974) were constructed for 15 plant communities, and a minimum stand size ($3.5 \text{ m} \times 3.5 \text{ m}$) was determined. Cover of each species, expressed as a percentage of the area of the stand, was estimated in each stand.

A polythetic divisive form of classification based on ordination using reciprocal averaging was performed using the TWINSPLAN (Two Indicator SPecies ANALYSIS) program devised by Hill (1979a). The program was run with only a single alteration to the normal program (cf. Hill 1979a) – the minimum number of stands required for each division was reduced to one.

The DECORANA (DEtrended CORrespondence ANALYSIS) program, an eigenvector ordination technique based on reciprocal averaging (Hill 1979b), was used to ordinate stands. The vegetation data were entered into the DECORANA program in the same form as for the TWINSPLAN program using the detrended correspondence analysis ordination. Two stands (45 and 49), dominated by species that did not occur in other stands, were omitted from the analysis. Their inclusion caused distortion of the first axis because they were placed at extreme positions of 2.3 and 10.0 respectively, with all other stands being placed at 0.0.

Abiotic parameters thought to be important in determining vegetation distribution in wetlands

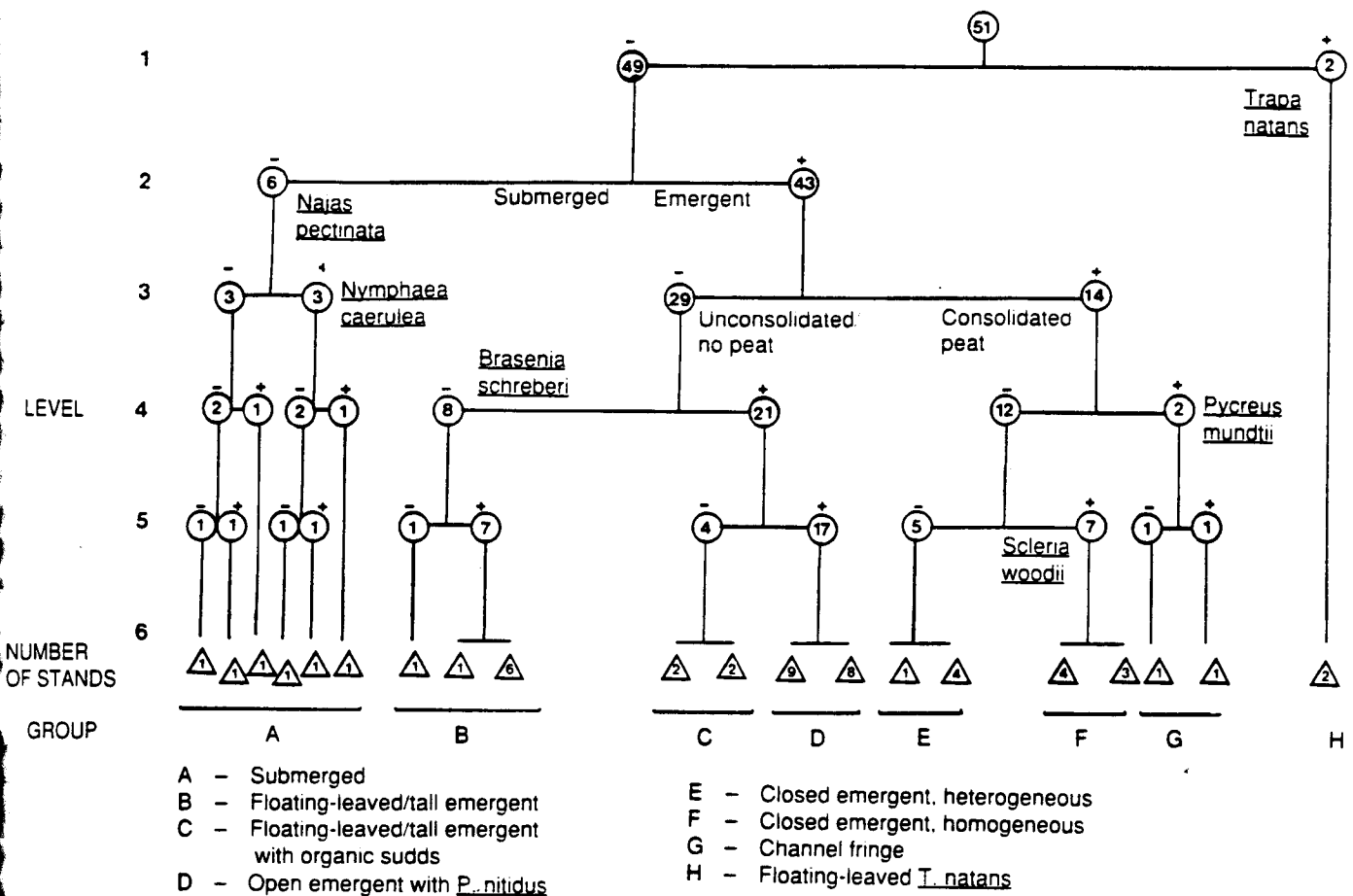


Fig. 3. Hierarchical classification of stands derived from TWINSpan. Enclosed values represent the number of stands in the parent (circular) and final (triangular) groups.

were measured. Two measures of depth, water depth (the depth from the water surface to the peat or organic detrital layer in which plants were rooted) and depth to sandy substratum (the depth from the water surface, through the organic layer, to the sandy substratum in which the initial colonizers must have been rooted), were taken. Redox potential and pH of the water were measured at a depth of 15 cm with a Schotte Gerate model CG819 meter using platinum and combined electrodes, respectively. Electrical conductivity, used as an estimate of total dissolved solids concentration, and temperature were measured with a YSI model 33 meter, and dissolved oxygen concentration was measured with a YSI model 51B oxygen meter equipped with thermocouple.

Two one-liter water samples were collected for total nitrogen and phosphorus analyses in each plant stand. Samples were taken in acid washed bottles (10% HCl) and preserved with 0.1 ml for-

malin. Since no facilities for storing samples at a low temperature were available and two weeks elapsed before analysis, only total concentrations were measured. The pairs of water samples from each sampling point were mixed prior to analysis. Triplicate sub-samples were digested by persulphate (Wetzel and Likens 1979). Nitrogen was determined by the salicylate method (Cataldo *et al.* 1975) with absorbance read at 410 nm on a DMS 100 visible spectrophotometer. Phosphorus concentration was determined by the molybdenum blue method (Wetzel and Likens 1979). Absorbance was read at 882 nm.

To provide a historical perspective, a single peat core, to the depth of the sandy substratum, was collected at each site. These were obtained using a 65 mm diameter piston corer, modified from Wright *et al.* (1984), that had been sharpened to facilitate penetration. A piston held at the peat surface prevented compaction during sampling. Gross features

of the peat stratigraphy including color, texture and recognizable plant parts were recorded.

Results

The two-way phytosociological table (see Appendix), representing the output from the TWINSpan cluster analysis, highlights the indicator species upon which the divisions in the hierarchical arrangement of stands (Fig. 3) were made. This grouping of stands, derived from six levels of division, resulted in the delimitation of eight major plant communities or vegetation types (Fig. 3, A-H). These ranged from deep-water communities dominated by submerged plants (Group A) to communities dominated by floating-leaved (Group B and H) and tall, bottom-rooted species (Group C) to emergent communities in shallow water (Groups D-G). To test the robustness of the data set, the program was run a second time excluding a random sample of 25% of the stands (Gauch 1982). The resultant grouping was similar to the one derived from the full data set. This classification, in combination with the environmental data, forms the basis for community and habitat descriptions.

The first two axes in the stand ordination derived from DECORANA accounted for a large proportion of the summed variation of axes 1 to 4. Eigenvalues of 0.49 and 0.35 for axes 1 and 2 were much greater than for axes 3 and 4 (0.09 and 0.07) and hence only the first two axes are considered in the analysis.

The groups of vegetation types derived from the cluster analysis superimposed on the ordination diagram (Fig. 4a) showed good agreement with the classification. Along the horizontal axis both Group A (submerged macrophytes) and Group B (floating-leaved and bottom-rooted, emergent species) were separated from each other and the rest of the groups. The remainder of the groups (Groups C-G) were in a similar position on the first axis but were separated by the second. Group C communities were dominated by tall, bottom-rooted emergent species associated with an occasional organic detrital sudd and the communities in Groups D-G were largely dominated by short e-

mergent plants.

Analyses of water samples indicated that slightly acid to neutral (pH 6.0-7.3) waters of Maunachira River System were well oxygenated (oxygen saturation 24-105%) with extremely low concentrations of dissolved solids (conductivity 110 $\mu\text{S cm}^{-1}$). Total phosphorus and nitrogen were within the ranges of undetectable to 2.0 and undetectable to 500 $\mu\text{g l}^{-1}$, respectively. Plotting of the measured environmental variables of stands on the first two axes of the scatter diagram, however, indicated that there was no relation between the stand arrangement of the ordination and any of the environmental factors except water depth. Only this environmental factor has been superimposed on the stand ordination (Fig. 4b).

The general increase in the rooting depth of plants in the stands along the first DECORANA axis (Fig. 4b) suggests that the dominant environmental factor influencing the variation in vegetation in the Maunachira River System is water depth. There is, however, an apparent discontinuity in the depth gradient along the first axis, delineated by a dotted line in Figure 4b. An analysis of the physical characteristics of cores taken through the organic detritus and peat deposits illustrates this discontinuity. The differences in water depth between submerged, floating-leaved and bottom-rooted emergent communities can be accounted for by differences in depth to the organic substratum, which is in turn dependent upon the extent of accumulation of benthic organic detritus on the lower substratum as well as local topography (Groups A and B; Fig. 5). These communities may represent different stages in a hydrosere succession in which accumulations of organic matter result in a gradual decrease in water depth. The difference in water depth between these communities (Groups A and B) and the rest of the communities (Groups C-G, along the second axis), however, is the result of the formation of extensive peat sudds (Fig. 5). These sudds initially have their roots beneath them and float at or close to the water surface, thus enabling colonization by shallow-rooted emergent species. The increase in thickness of the sudd layer (Groups C-G; Fig. 5) appears to be a pattern of peat accumulation similar to that

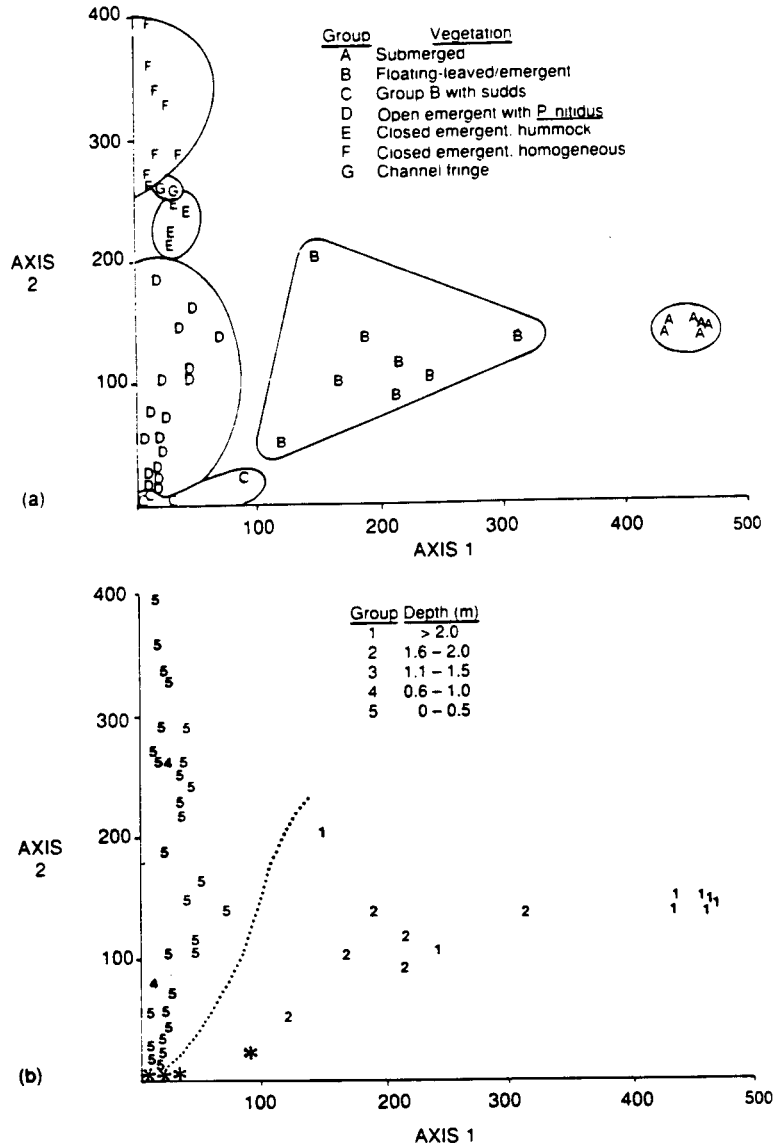


Fig. 4a/b. Two-dimensional ordination (DECORANA) of the 51 stands sampled. Superimposed are (a) the vegetation groups derived from the classification and (b) measurements of water depth. Water depths of Group C are represented by an asterisk as they are deep water communities (> 1.6 m) with occasional organic sudds floating at the surface. The dotted line represents a depth discontinuity along axis 1.

described by Sculthorpe (1967) and Kratz and DeWitt (1986). Vertical aggradation results from surface accumulation of undecomposed plant material and from detrital rain from the lower surface of the sudd.

The stands arranged along the second DECORANA axis were not related to water depth (Fig. 4b) or to any other single measured environmental factor. Since the distribution of these stands along the second axis may have been strongly influenced by the position of the stands along the first axis

(especially Groups A and B), the program was run again with the omission of these two groups. Although a different distribution for the remaining stands was obtained, again no correlations between stand distribution and environmental variables were evident. Although it is possible an environmental variable not measured in this study was responsible for this observed pattern, it is suggested that the second-axis stands (Groups C-G) may have become insulated from abiotic environmental influences over time and that the autogenic processes

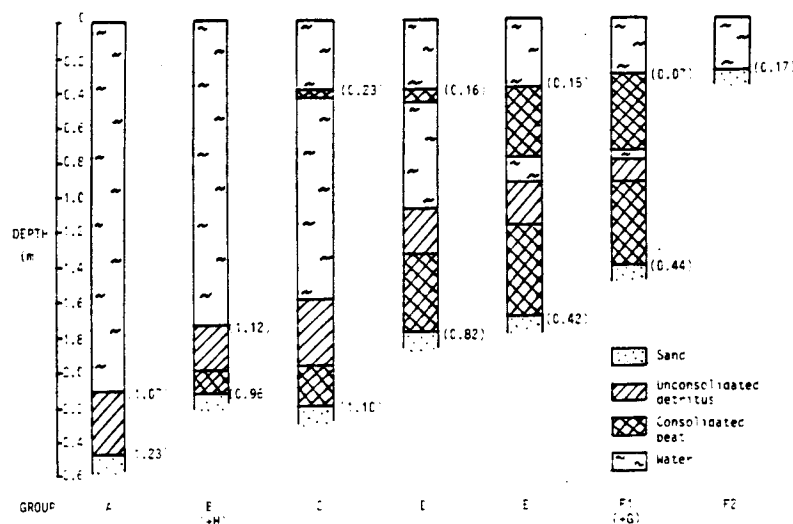


Fig. 5. Cores showing vertical distribution of peat, detritus and water in each of the vegetation types derived from the classification. A = submerged; B, H = floating-leaved/emergent; C = floating-leaved/emergent with organic sudd; D = open emergent with *P. nitidus* and floating sudd; E = closed emergent hummock and F, G = dense, closed emergent homogeneous community. The figures in parentheses represent standard deviations (m).

of floating sudd and peat development are primarily responsible for the differences in species composition of the communities.

Community descriptions

Submerged communities (Group A). The communities dominated by submerged species occurred in water bodies which ranged in size from a few square meters to the large, oxbow-shaped *madiba* (> 1000 m²), and had an average water depth of 2.1 m (Fig. 5). These communities had few species (mean = 5.3 species/stand, Appendix). *Najas pectinata*, common to all the stands, had up to 90% cover. Other submerged species such as *Lagarosiphon verticillifolius* and *Websteria confervoides* occurred in fewer than 50% of the stands, as did the floating-leaved species *Nymphaea caerulea* and *Brasenia schreberi*. The emergent species *Typha capensis* and *Eleocharis dulcis*, when present, had a cover of 10% or less (Appendix).

Floating-leaved and tall, emergent communities (Group B). The communities dominated by floating-leaved and tall, emergent species occurred close to the edge of open-water bodies with an average water depth of 1.7 m and a detrital layer ap-

proximately 0.5 m thick (Fig. 5). Although buoyant floating-leaved species *N. caerulea* and *B. schreberi* were dominant, there was an understory of the submerged species *W. confervoides* and an emergent subcomponent of *Eleocharis acutangula*. The tall, emergent species *T. capensis* and *Phragmites australis* occurred in some of the stands (Areas of organic sudd < 1%) of

Floating-leaved and tall, emergent communities with organic sudds (Group C). The floristic distinguishing feature of these plant communities, and compared with those in Group B, was related to the occurrence of both floating organic detrital sudds and floating blue-green algal mats. The organic sudds, which ranged in size from 0.4-8.0 m², formed by detachment of buoyant sections of submerged detritus that floated to the water surface. These sudds were colonized mainly by Group D emergent species such as *Fuirena stricta*, *Panicum nitidus*, *Cyperus pectinatus* and *Drosera madagascariensis*. Also floating on the water surface were small (0.001-0.5 m²) mats consisting of blue-green algae in close association with various *Utricularia* species. Since these mats were susceptible to erosion and frequently broke up and re-floated again, they did not form a stable colonizing sudd thus the. However, occasionally both *C. pectinatus* and Group E

madagascariensis mats.

Open, emergent (Group D) short, emergent detrital accumulation represented the Maunalandy subcommunity out the water 0.47-0.30 m. *trata* existed dominated

tratum (Group E) floating-leaved and floating ion species

madagascariensis were found established on these mats.

Open, emergent communities with *Pycnus nitidus* (Group D). These communities were dominated by short, emergent species rooted in extensive floating detrital accumulations and were the most commonly represented communities in the back-swamps of the Maunachira River System. The depth to the sandy substratum varied greatly from 2.5 to 1.2 m but the water depth was more consistent (range 0.47-0.30 m, mean 0.4 m, Fig. 5). Three vegetation strata existed: an upper stratum (0.80-1.20 m tall) dominated by *Miscanthus junceum*, a middle stratum (0.10-0.30 m) dominated mainly by *P. nitidus* and *C. pectinatus* and a lower stratum with floating-leaved species *N. caerulea* and *B. schreberi* and floating blue-green algal mats. The most common species in the middle stratum, *P. nitidus*, was a buoyant 'sudd-forming' plant (Thompson 1985). It has been shown (K. Ellery, pers. comm.) that *P. nitidus* initially became established on floating inorganic sudds such as were found in Group C. (From this position, it grew across the water surface, without organic detrital support, to colonize large areas of open water. By this means the original organic sudd nucleus formed only a small proportion (<1%) of the total area covered by the floating *P. nitidus* sudd. Over time an extensive, loose, floating detrital layer developed beneath the *P. nitidus* sudd, and with sufficient consolidation, the floating organic layer became colonized by species such as *Panicum repens*, *Fuirena pubescens* and *D. madagascariensis*.

Dense, emergent communities with hummocks and hollows (Group E). In contrast to the communities in Group D, the plants in these communities were rooted in consolidated peat of a much coarser nature consisting of large, partially decomposed, recognizable plant parts. An examination of the vertical profile of the peat of Groups D and E (Fig. 5) suggests that peat accumulation on the floating layer in communities in Group D had led to the formation of a thicker, more consolidated sudd layer and thus the establishment of species characteristic of Group E. The species in Group E communities

ranged from tall emergents such as *M. junceum*, to short emergent species such as *Eriochrysis pallida*, *Ficus verruculosa*, *Crassocephalum picridifolium* and *Thelypteris confluens*, to the floating-leaved species *B. schreberi*, *N. caerulea* and *Potamogeton thunbergii* (Appendix). The large number of different species in this group (mean 17.6 species/stand, Appendix) was due to the heterogeneous nature of the communities on a small scale in the form of hummocks and hollows. The raised hummock areas, usually 1-1.5 m in diameter with the center of the hummock at or near the water surface, supported short emergent species. The tall emergent and floating-leaved species were found in hollows of similar size which were usually 0.5-0.7 m deep.

Dense, emergent communities with a homogeneous substratum (Group F). The communities in Group F were characterized by the absence of hummocks and hollows and had a shallow (<0.35 m, Fig. 5), homogeneous substratum. Floating-leaved species, usually found in slightly deeper water, were not present. The four major co-dominants, *M. junceum*, *P. nitidus*, *E. pallida* and *Scleria woodii*, formed a mixed emergent stratum. Other species not encountered in previous groups but common here, were the orchid *Habenaria schimperiana*, *Xyris capensis* and various mosses such as *Hypnum* spp. and *Philonotis falcata*. Mosses were absent in Group F2 (Appendix) which comprised three floodplain communities in which peat deposits were absent and the plants were rooted in sand. These communities, dominated by *E. pallida* and *S. woodii*, occurred on the periphery of the Maunachira River System. They never dried out, but the water level dropped close to the level of the sand during the dry, late summer months. The species in Group F1 grew at the same water depth as Group F2 species but were rooted in a thick consolidated layer of peat with the depth to the sandy substratum being an average 1.42 m.

Channel-fringe (Group G) and *Trapa natans* communities (Group H). Areas dominated by *Trapa natans* (stands 45 & 49) were uncommon in the study area and were found almost exclusively where

rivers discharged into *madiba*. The deposition of allochthonous detrital matter was high and may have included fine inorganic sediments. These plant communities were floristically distinguished in the analysis because the dominant species were not common elsewhere. However, based on environmental (water depth approximately 1.7 m) and life-form (dominance by bottom-rooted species with a floating-leaved habit) characteristics, it is suggested that these stands should not form a separate group in the classification but should be placed instead with those in Group B. It is also suggested that stands 1 and 41 (Group G), channel-fringe communities with mixtures of both tall and short, emergent vegetation, shallow water and consolidated peat deposits, should be placed in the category of dense, emergent communities with a homogeneous substrata (Group F1). The floristically distinguishing feature of the two stands in Group G was the almost complete dominance by the tall grass *M. junceum* which had a higher cover than in areas away from the channel margin where the allochthonous nutrient supply was lower. The low cover of short, emergent species such as *P. nitidus*, *Pycneis mundtii* and *F. pubescens* may be attributed to low light availability beneath the dense *M. junceum* canopy.

Discussion

It is generally accepted that vegetation composition changes gradually in both space and time unless a discontinuity in the physical and chemical environment occurs (Whittaker 1970; Mitsch and Gosselink 1986; Breen *et al.* 1988). The aggregation of plant species into discrete communities implicates discontinuities as major determinants of community boundaries. However, it has been pointed out (Breen *et al.* 1988) that such discontinuities can arise or be amplified as a consequence of the growth and metabolism of aquatic plants, especially clonal species which tend to dominate wetland habitats. At any time the spatial heterogeneity of communities therefore reflects both the initial conditions of the environment and the extent to which they have been modified by the component species (Connell

and Slatyer 1977). Over time, the influence of movement processes increases as the accumulation of peat thus, nutrient resources, also a consequence of formed growth, dampens the influence of external water and insulates the communities from fluctuations in the abiotic environment (Mitsch and Gosselink 1986). These concepts of autogenic control of community composition appear relevant to examples of wetland types across a wide range of latitudes (Mitsch and Gosselink 1986; Breen *et al.* 1988).

Water depth is a major environmental determinant of species distribution in wetlands (Wilby 1970; Van der Valk and Bliss 1971; Hiron 1974; Williams and Walker 1974; Van der Valk and Hiron 1976; Birks and Birks 1980; Slack *et al.* 1982; Spence 1982; Glaser 1983; Sanville *et al.* 1984). Within the back-swamps of the Mauricie River (shaded in the DECORANA axis (Fig. 4b) can be related to water depth. These differences in depth appear to be the result of a build-up of organic matter. A geomorphic successional sequence from submerged floating-leaved plants, to tall emergent communities on consolidated peat can be inferred. However, the distribution of the extensive, undisturbed communities, usually structurally distinct and separated in the ordination analysis by the second axis, is unrelated to measured environmental factors. How the vertical boundaries which separate these communities in the field arise, in the apparent absence of discontinuities in the major environmental variables, is uncertain. We propose a hypothesis to address this question and to integrate the separate developed concepts of community isolation (Breen *et al.* 1988) and insulation (Mitsch and Gosselink 1986).

Abrupt transitions between early successional, submerged, floating-leaved, and tall emergent communities illustrate the manner in which different plant life forms may cause discontinuities in the environment along a water depth gradient. In the absence of plants, a gradient in light climate would exist along the depth gradient. Floating-leaved and emergent plants, which are themselves restricted to water specific depths, create distinct barriers to effects

ence of biomass movement at the water surface and plant canopy. Thus, distinct and isolated communities are formed. However, since they are still subject to water level fluctuations, the degree of insulation from the abiotic environment is low.

The development of floating sudds is an extreme example of how insulation might develop (Mitsch and Gosselink 1986; Hogg and Wein 1988) when the stress of water level fluctuations is overcome and replaced by a stable regime in which the peat is always saturated. With a reduction in external environmental stress and disturbances, the autogenic processes of plant growth, metabolism and decay become the main agents of heterogeneity within and between communities. The low growing, guerdunachira (*Rhynchospora*) (shoots widely spaced from each other; Lovett-Doust 1981) growth form of *P. nitidus*, for example, makes it a good sudd-forming species which traps resources in a different way (Breen *et al.* 1988). A tall, phalanx (shoots in contact with one another; Lovett-Doust 1981) growth form of *M. junceum*, through its dense tufts, provides a relatively open and exposed sudd surface for the colonization by other species (K. Ellery, pers. comm.). The dense tufts of *M. junceum* appear primarily responsible for the hummock formation that creates much diversity within the mature communities on consolidated peat.

The degree to which these late successional, sudd-derived communities are insulated from the external environment needs closer examination. In the Maunachira River System the exposed peat surface and dense growth of emergent plants such as *M. junceum* are very susceptible to fire (Smith 1976). Thus, the very process implicated in insulation can increase the potential influence of other environmental factors and does not necessarily lead to a stable, entirely autogenically controlled community. In this context, Breen *et al.* (1988) discussed the interplay between autogenically derived barriers to resource movement in isolating wetland communities and disruptive mechanisms which might operate at many different intensities and time scales to retard or arrest community change. Since no natural ecosystem can be entirely insulated from the effects of the external environment, the percep-

tion that wetland ecosystems move towards an insulated, stable state is clearly an oversimplification. Rather, systems should be viewed in the context of opposing insulating and disruptive mechanisms.

Breen *et al.* (1988) emphasized the role of high energy events such as floods, fire, and other disturbances as disruptive mechanisms. Studies in the Okavango Delta suggest that feedback from the very process of resource accumulation which promotes insulation can also be important. McCarthy *et al.* (1986) propose that the process of channel abandonment and activation which results in a periodic wetting and drying of areas of the Okavango Delta results from an interplay between peat forming processes and sedimentation. Plant growth and peat accumulation, particularly at the fringe of channels, confines water flow and bed load sediment to within channels, causing channels to become progressively raised above the surrounding back-swamps where further peat accumulation also excludes much of the potential water flow. Water shed laterally from the raised channel then creates a new channel, usually by eroding and enlarging a small hippopotamus trail. While the bulk of the flow is diverted, the old channel system, including the back-swamp areas, becomes increasingly dry and susceptible to burning. Slow burning peat fires result in the collapse of the peat deposits, thus lowering the land surface and initiating reflooding (Ellery *et al.* 1989) and the plant succession described above. Resource accumulation in the Okavango Delta does not necessarily lead to long-term stability but instead sets off a diffuse set of interactions which later feed back to disrupt the insulation.

This study suggests that the relationship between the present wetland plant community distribution and its environment may be masked by long-term, biotic, insulating processes such as the resource accumulation properties in peat formation and clonal plant growth. The processes leading to the disruption of this insulation and resetting of community processes in the study area are poorly understood. Fires that differ in intensity and timing during the drying phase would reset community processes to different degrees. As a result, successional stages may be skipped or repeated, thereby contributing

to the overall heterogeneity observed in the back-swamp vegetation. This study serves to integrate the concepts of community isolation, insulation and disruption and illustrates their usefulness as components of a model of community processes in wetland systems.

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