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Wetland plant community composition and successional processes in the Maunachira river system of the Okavango delta.

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Two types of sudd formation which have been described by Thompson (1985), namely organic detrital sudds and those that develop in association with floating plants, are common in this river system. Since only short term changes in the sudds could be directly observed during the period of this study, the conditions required for sudd initiation and establishment and subsequent species colonisation were examined.

2.2.2.1. The effect of disturbance on floating organic detrital sudds

Small organic sudds, ranging in size from $0,4m^2$ - $8,0m^2$ and formed by detachment of sections of the submerged detritus, floated at or near to the water surface (Plate 2.1). Since the sudds were noted to be extremely mobile, moving both horizontally across the water surface and vertically by further sinking or rising, it was postulated that the type and extent of disturbance would play an important role in influencing their future development. The final fate of the sudds a. the resultant species composition was considered important in determining later plant successional trends in bog development. The effect of disturbance on sudd movement and consequently on species composition was therefore determined. Wind action and the waves created by the movement of both hippopotamus and boats were noted to be sufficient to result in at least horizontal movement of the highly mobile sudds. The negligible water movement in sudd forming areas in the Maunachira river system suggest that this is unimportant in influencing sudd movement.

Two sites, both considered typical of water bodies of the area, were chosen:

(i) Disturbed site. Since the water body was large (340m x 75m) with little tall, fringing vegetation, wind action was considered to be a continual disturbance factor. A single path, utilised by

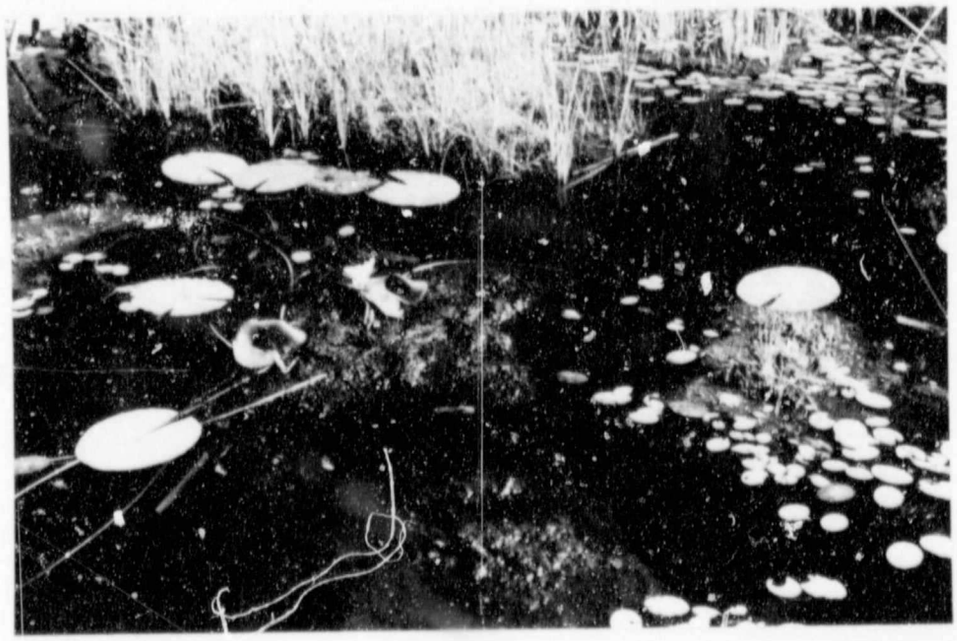

PLATE 2.1 Mobile, organic, detrital sudds floating at the water surface

hippopotami at least once during the night and by power boats on a less regular basis during the day (approximately twice a week during the winter tourist months and probably only once a month during the summer) passed through the centre of the water body. On the first sampling day fifty-nine sudds were recorded floating at or close to the water surface.

(ii) Undisturbed site. The small water body (75m x 12m) with tall fringe vegetation was considered sufficiently sheltered such that wind action would be minimal. Since there were no access pathways, boating and large animal activity was nil. Seventy-nine sudds were recorded on the first sampling day.

To examine the long term fate and species composition of the sudds the following tasks were done:

i) Each sudd was tagged,

ii) The position of each sudd was mapped,

iii) The size of, and depth from the water surface to the sudd was measured (not all sudds were floating at the water surface), and

iv) The percentage cover of each species on each sudd was estimated.

Most sudds ultimately banked on the leeward edge of the water body. To determine rates of fringe encroachment comparisons of 1969 and 1983 aerial photographs (1:50 000) were made from a fixed point (eg. a large tree) to the fringe edge on both the windward and the leeward side of the water body.

2.2.2.2 Colonisation of organic detrital sudds by plant species

The sequence of appearance of species which colonise newly uprisen sudds is dependent on (a) the seed bank already present in the sudd

and (b) an input of seeds from the surrounding vegetation. In the former case the timing of sudd emergence could be critical to the establishment of plant species whereas in the latter it would be less important (van der Valk & Davis 1978). To assess the importance of these two factors in determining the species composition of organic sudds, experiments were set up in which organic detrital samples from the rooting zone of plant communities in which detrital sudds commonly arise (treatment 1) as well as from existing sudds in the region of three weeks old (treatment 2), were taken.

For each of the above two treatments three samples of organic matter were sorted to remove rhizomes, tubers and pieces of undecomposed litter (Pederson 1981). They were placed into individual 20 x 30 x 3cm plastic trays and staked in position so that they were permanently floating on the water surface. Holes at the bottom of the tray ensured a constant water supply. To prevent an input of seeds from the surrounding areas, each tray was covered by fine mesh netting placed over a frame allowing room for seedling growth. At two month intervals the germinating seedlings were identified, counted and then removed as their presence would make successive counts increasingly inaccurate and may also have interfered with the germination and emergence of other seedlings. Differences between the two treatments would provide some indication of the importance of the seed bank as well as the input of seeds to the sequence of establishment of species on these sudds.

2.2.2.3 Growth of sudd forming plants

Pycreus nitidus, a stoloniferous sedge and frequent coloniser of the organic sudds, was observed growing vegetatively beyond the sudd margins to form a floating plant sudd. Swan & Gill (1970) have shown that the stages and rates of plant sudd development may be explored

by critical examination of the growth characteristics of key bog species. An oxbow shaped water body, with extensive *P. nitidus* growth at varying densities and in association with other species, was chosen for the growth studies of this species.

Rate of advance of Pycreus nitidus sudd margin

Since the *P. nitidus* sudd margins were not clearly distinguishable on the 1969 and 1983 aerial photographs, measurements of encroachment using the method described in Section 2.2.2.1 was not possible.

In areas dominated by *P. nitidus* both the accumulation of benthic organic detritus and the growth of a particular submerged plant species, *Websteria confervoides* (Poir.) Hooper, occurred close to the water surface. It was proposed that either the detritus or *W. confervoides* or both provided some support for the extension of *P. nitidus* stolons at or close to the water surface. The rate of the extension growth of the *P nitidus* sudd margin (Plate 2.2) advance was therefore measured under different conditions of *W. confervoides* density and depth to detritus:

- Detrital support;
  depth detritus < 0,6m, *W. confervoides* cover low (<5%)
- Plant support;
  depth detritus > 0,6m, *W. confervoides* cover high (80-100%)
- No support;
  depth detritus > 0,6m, *W. confervoides* cover low (<5%)

A permanent marker was placed at the margin of each *P. nitidus* sudd under the above conditions and the rate of sudd extension was determined by measuring the distance out of each shoot at 8 - 10 week intervals. Only a single replicate for each condition was estab-

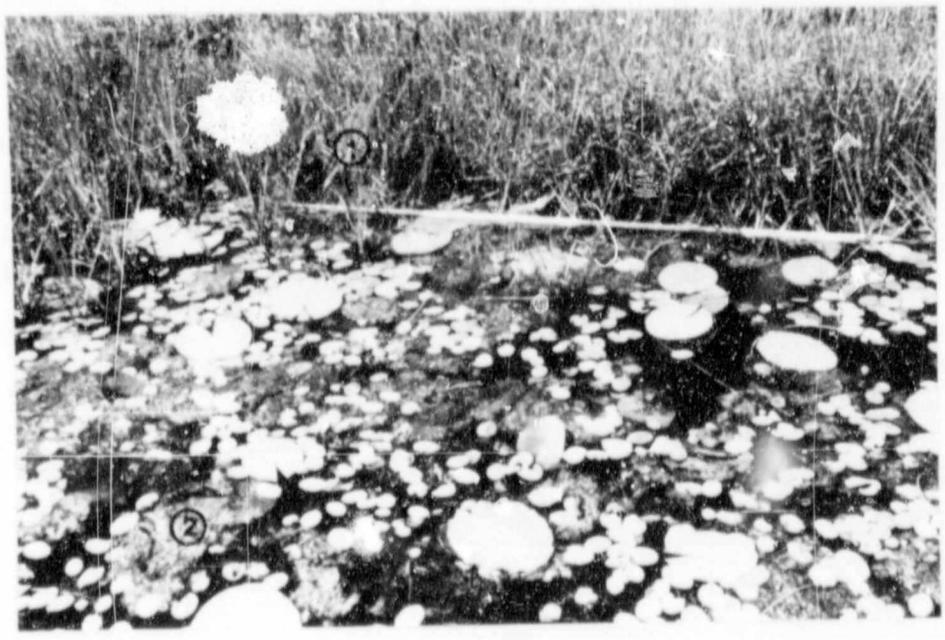

PLATE 2.2 Margin of a (1) P. nitidus sudd. In the foreground are (2) mats of blue green algae which are supported at the water surface by the submerged sedge W. confervoides

lished as the number of shoots within each treatment (n = 80) was sufficient to adequately describe the trends.

Relationship of P. nitidus density to depth

Since the results from the previous section indicated a relationship between *P. nitidus* growth and detrital depth, the data from the original vegetation survey with respect to these two factors were examined further. To cover the variability in this relationship a transect one metre wide was also set up across the oxbow shaped water body where extensive growth of *P. nitidus* occurred. A total of one hundred and sixty 1,0m x 1,0m quadrats were examined to determine:-

- depth to supporting layer (either organic detritus or the submerged plant *W. confervoides*)
- percentage cover of *P. nitidus* shoots.

The relationships between the depths and the cover of *P. nitidus* were thus determined.

CHAPTER 3

WETLAND PLANT COMMUNITIES OF THE MAUNACHIRA RIVER SYSTEM

3.1 RESULTS

3.1.1 Wetland communities: TWINSPAN cluster analysis

The two-way phytosociological table which represents the output from the TWINSPAN cluster analysis (Table 3.1) serves to highlight the indicator species upon which the divisions in the hierarchical arrangement of stands (Fig. 3.1) 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.3.1, A-H). In order 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. The classification has therefore been accepted and the floristic basis for the division of stands, as presented in Figure 3.1, is described below.

Two species, *Cyperus papyrus* and *Trapa natans* L., were found exclusively as dominants in stands 45 and 49 respectively. These two

TABLE 3.1 The percentage cover abundance, on the TWINSPAN scale of 1 - 5, of each of the species in each of the stands.

SPECIES	2 5	2 4	1 3	1 2	1 6
Cyperus papyrus					
Trapa natans					
Websteria confervoides				1	1
Brasenia schreberi	2	2			
Nymphaea caerulea			1	1	2
Utricularia reflexa var. reflex.					1
Utricularia stellaris					1
Cyperus articulatus	1	1			
Eliocharis dulcis	1				2
Utricularia benjaminiana		1	1	2	1
Typha capensis				2	2
Najas pectinata	5	5	4	5	5 5
Lagarosiphon verticillifolius			1	1	2
Vallisneria aethiopica		1		1	
Ottelia ulvifolia					2
Sacciolepis africana					
Ottelia muricata					
Fuirena stricta					
Nymphoides thunbergiana					
Blue-green algae					
Potamogeton thunbergii					
Xyris capensis					
Drosera madagascariensis					
Miscanthus junceum					
Cyperus pectinatus					
Pycreus nitidus					
Cyperus mwinilungensis					
Ludwigia leptocarpa					
Phragmites australis					
Eliocharis acutangula					
Alisma plantago-aquatica					
Schoenoplectus corymbosus					
Panicum repens					
Scirpus cubensis					
Utricularia gibba subsp. exoleta					
Pycreus mundtii					
Thelypteris confluens					
Fuirena pubescens					
Torenia thouarsii					
Floscopa glomerata					
Oldenlandia lancifolia					
Mikania sagittifera					
Panicum parvifolium					
Ficus verruculosa					
Crassocephalum picridifolium					
Azolla pinnata var. africana					
Fuirena umbellata					
Nesaea crassicaulis					
Hypnum and Philonotis (Mosses)					
Imperata cylindrica					
Neohyptis paniculata					
Habenaria schimperiana					
Scleria woodii					
Xyris sp.					
Vossia cuspidata					
Criochrysis pallida					
Group	A				
Average no. species	5,3				

TABLE 3.1 The percentage cover abundance, on the TWINSPAN scale of 1 - 5, of each of the species in each of the stands.

| SPECIES | STAND NUMBER | | |

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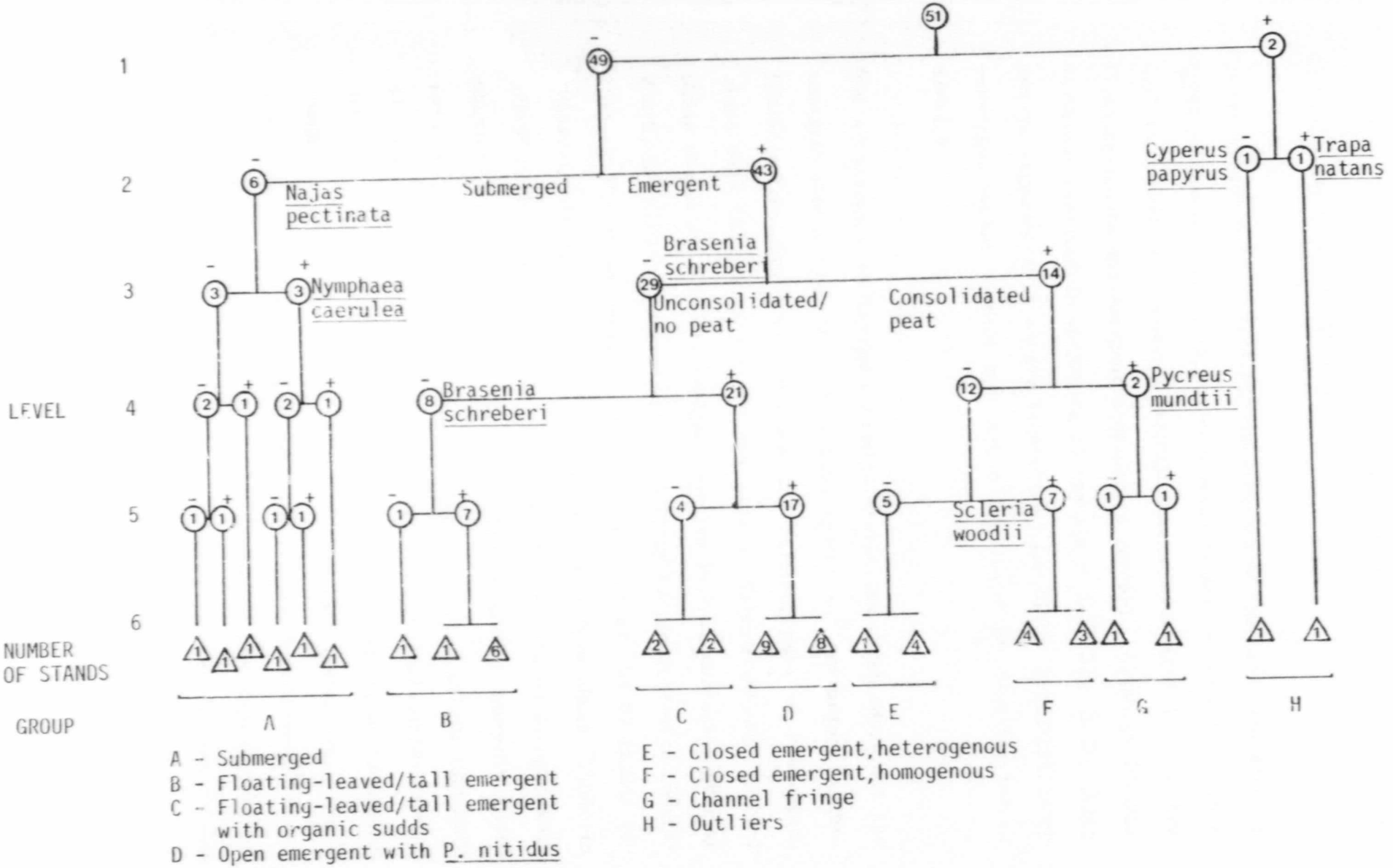


FIGURE 3.1 Hierarchical classification of stands derived from a Two Way Indicator Species Analysis (TWINSPAN). Enclosed values represent the number of stands in the parent (◯) and final (△) groups.

stands were therefore separated from the rest of the stands (n=49-) at the first dichotomy (Fig. 3.1) which floristically had nothing in common with any of the other stands.

At the second level of division the presence of the indicator species *Najas pectinata* (Parl.) Magnus at a cover of greater than 25% (Table 3.1) separated the submerged aquatic communities (n=6-) from the floating-leaved and emergent communities (n=43+). Although further divisions resulted in splitting of the six stands (Fig. 3.1), these can be regarded as a single vegetation type (Group A) dominated by submerged aquatic plants and with a low cover of floating-leaved species.

The 43 stands with emergent vegetation which represent the emergent communities (Fig. 3.1) split into two major groups. *Brasenia schreberi* J.F. Gmel. and the floating mats of blue-green algae were indicators for the one side of this dichotomy (n=29-) while the short (<1,0m), emergent species *Fuirena pubescens* (Poir.) Kunth, *Eriochrysis pallida* Munro and *Ficus verruculosa* were indicators of the other (n=14+). Further division of the 29 stands resulted in the splitting off of Group B (n=8-) from those stands in Groups C & D (n=21+). The stands which constituted Group B were characterised by floating-leaved and bottom rooted emergent plant species. The floating-leaved *B. schreberi* was a strong indicator of this community while emergents *Eliocharis acutangula* (Roxb.) Schult., *E. dulcis* (Burm. F.) Hensch. and *Schoenoplectus corymbosus* (Roth. ex Roem. & Schult.) J. Raynal were weak indicators. The 21 stands which were separated from those in Group B were characterised by the presence of sudds which were either of the organic detrital type (Group C) or included the sudd forming species *Pycreus nitidus* (Group D). The stands in Group C however had similar emergent vegetation to those in Group B (Fig. 3.1), but the colonisation of the

organic sudds in the stands in the former group by *Fuirena pubescens*, *F. stricta* Steud. and *Cyperus pectinatus* L. led to their inclusion in the dichotomy with Group D instead. Subsequent observations showed that the sudds in the Group C division were mobile, and in many cases therefore only ephemerally associated with the submerged and bottom rooted emergent species of the communities themselves. For this reason stands in Group C may better have been classified in combination with Group B stands.

The remaining stands (n=14+) were dominated by short emergent vegetation rooted in peat at or close to the water surface. Stands 1 and 41 represented channel fringe communities (Group G) and were separated from the rest of the stands (n=12-) based on the presence of *Pycreus mundtii* Nees in the former two stands and its absence in the latter. Further division of the 12 stands was due to the presence of *Scleria woodii* C.B. CL. in homogeneous closed emergent stands which constituted Group F (Fig. 3.1) while the stands in Group E were not associated with any indicator species. The emergents *Miscanthus junceum*, *C. pectinatus* and *P. nitidus* were however dominant throughout this group. Although all the stands in Group F had similar species composition (Table 3.1) the origin of the communities in the two subgroups (F1 and F2, Fig. 3.1) within this group were completely different. The stands in the first subgroup had the moss species (*Philonotis falcata* (Hook.) Mitt. and *Hypnum* spp.) as strong indicators and the fern *Thelypteris confluens* (Thunb.) Morton and the sedge *F. pubescens* as weak indicators, with all species rooting in a consolidated peat deposit. In contrast the second subgroup of stands had no strong indicator species, and the plants were instead rooted in shallow sandy deposits and therefore represented shallow floodplain communities.

Considered as a whole the analysis was successful in distinguishing groups of stands with distinct floristic characteristics. It is suggested that the stands in the Groups G and H should not be separated but instead be included in one of the other six major groups. This is discussed in more detail in a general description of each of the vegetation types derived from the cluster analysis incorporating measured environmental factors (Section 3.1.3).

3.1.2 Species distributions in relation to environmental variables: DECORANA ordination analysis

The first two axes in the stand ordination derived from detrended correspondence analysis accounted for a large proportion of the summed variation of axes 1 to 4. Eigen-values of 0,49 and 0,35 respectively for axes 1 and 2 were much greater than for axes 3 and 4 which were 0,09 and 0,07 respectively. For this reason only the former two axes have been presented.

The groups of vegetation types derived from the cluster analysis superimposed on the ordination diagram (Fig. 3.2a) showed good agreement with the classification. Along the horizontal axis the groups consisted of submerged macrophytes (Group A), floating-leaved and bottom rooted species (Group B) and tall, bottom rooted emergent species with organic detrital sudds (Group C). The groups of stands extending along the vertical axis (Groups D - G; Fig. 3.2a) were largely dominated by short emergent plants. This similarity in grouping for the two multivariate methods is, in part, to be expected as the first step in both the TWINSPAN classification and the DECORANA ordination is to perform an ordination by reciprocal averaging. In the former analysis this assists in the formation of each of the dichotomies, and in the latter it results in the formation of the first axis. However, since the groupings along the second

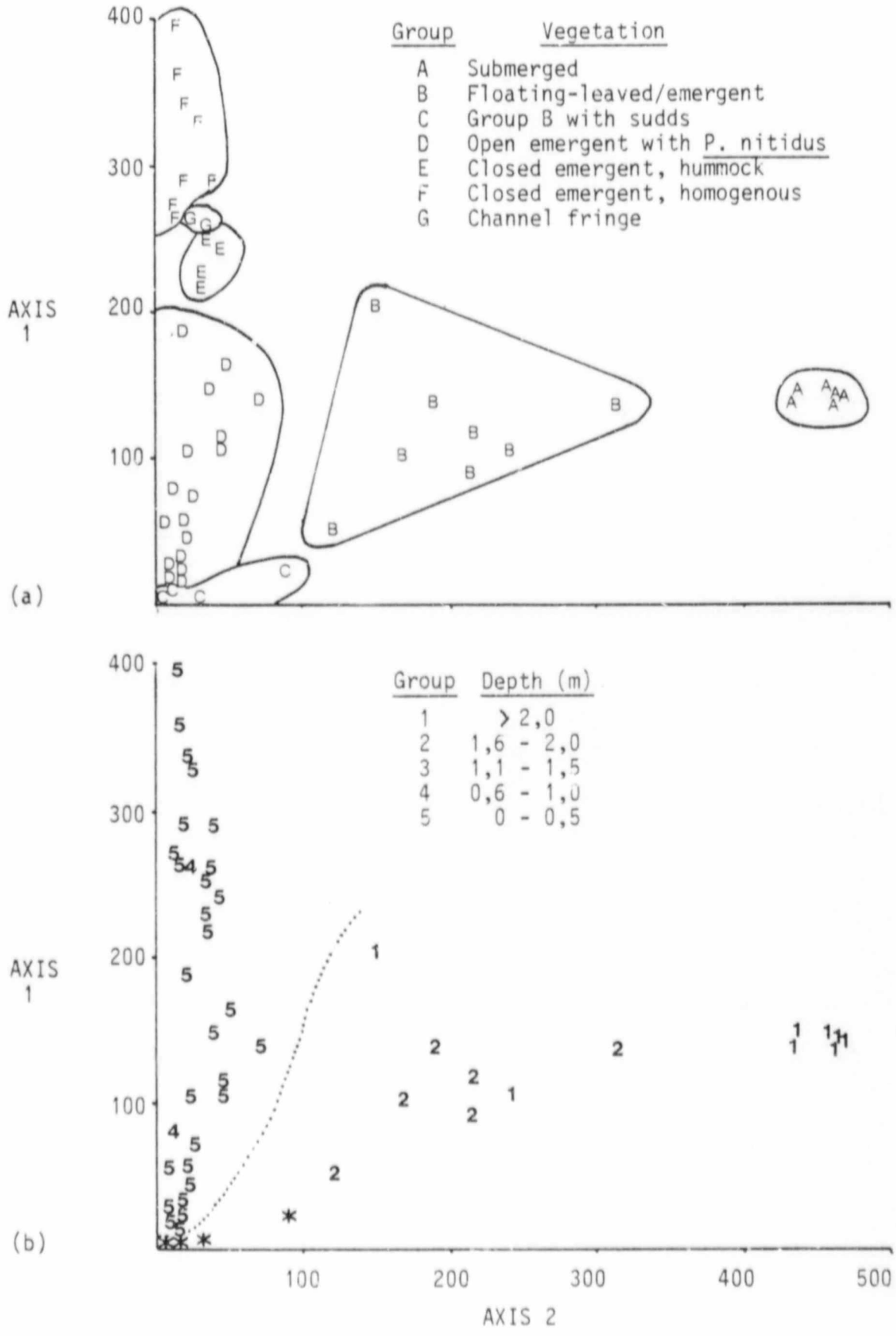


FIGURE 3.2 Two-dimensional ordination of the 51 stands sampled. Superimposed are (a) the vegetation groups derived from the classification and (b) the measurements of water depth, (c) pH, (d) Eh, (e) oxygen concentration, (f) conductivity, (g) total phosphorus and (h) total nitrogen of the water.

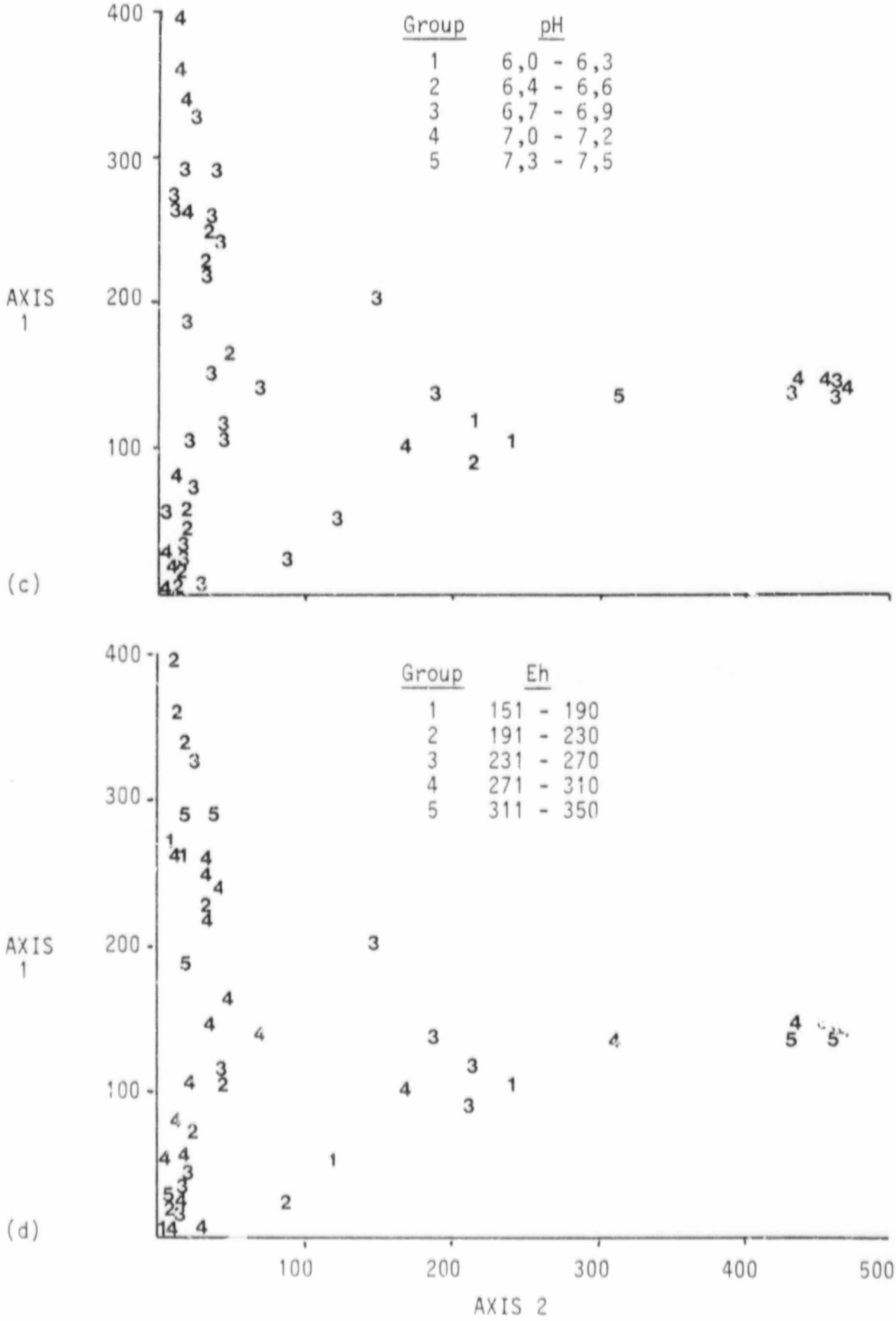
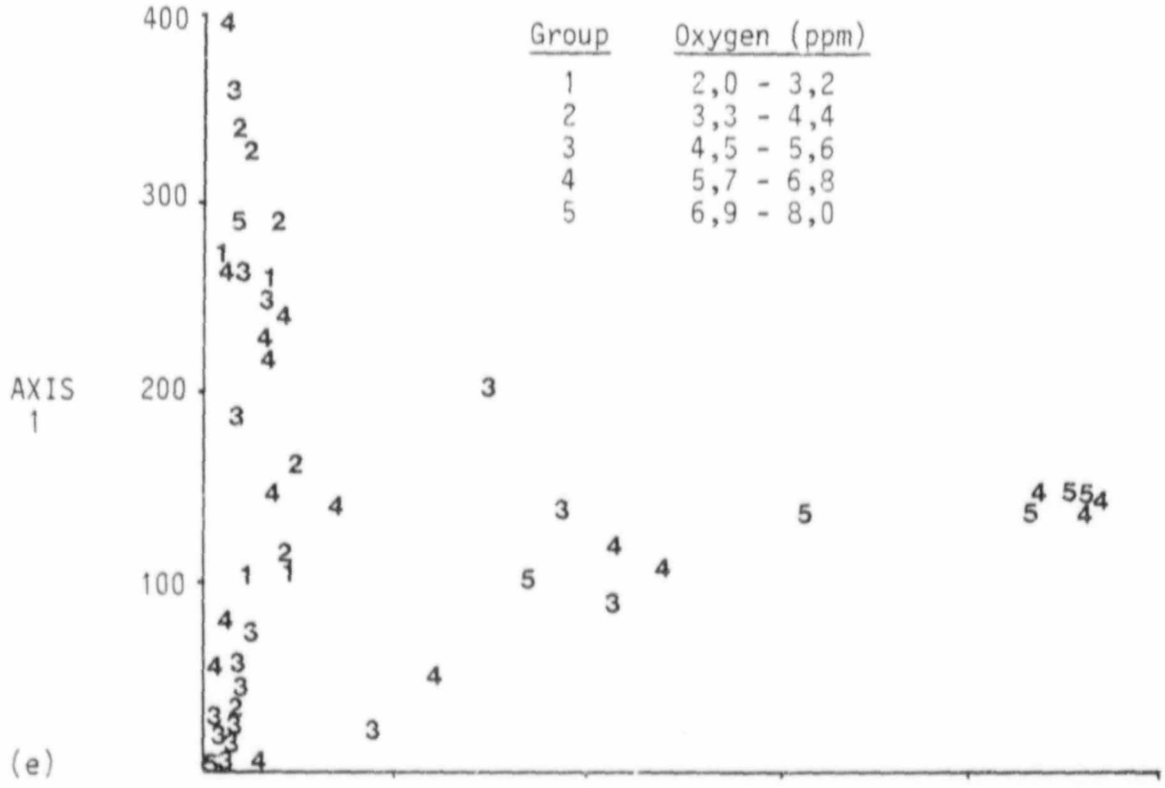


FIGURE 3.2 (Continued). (c) & (d).



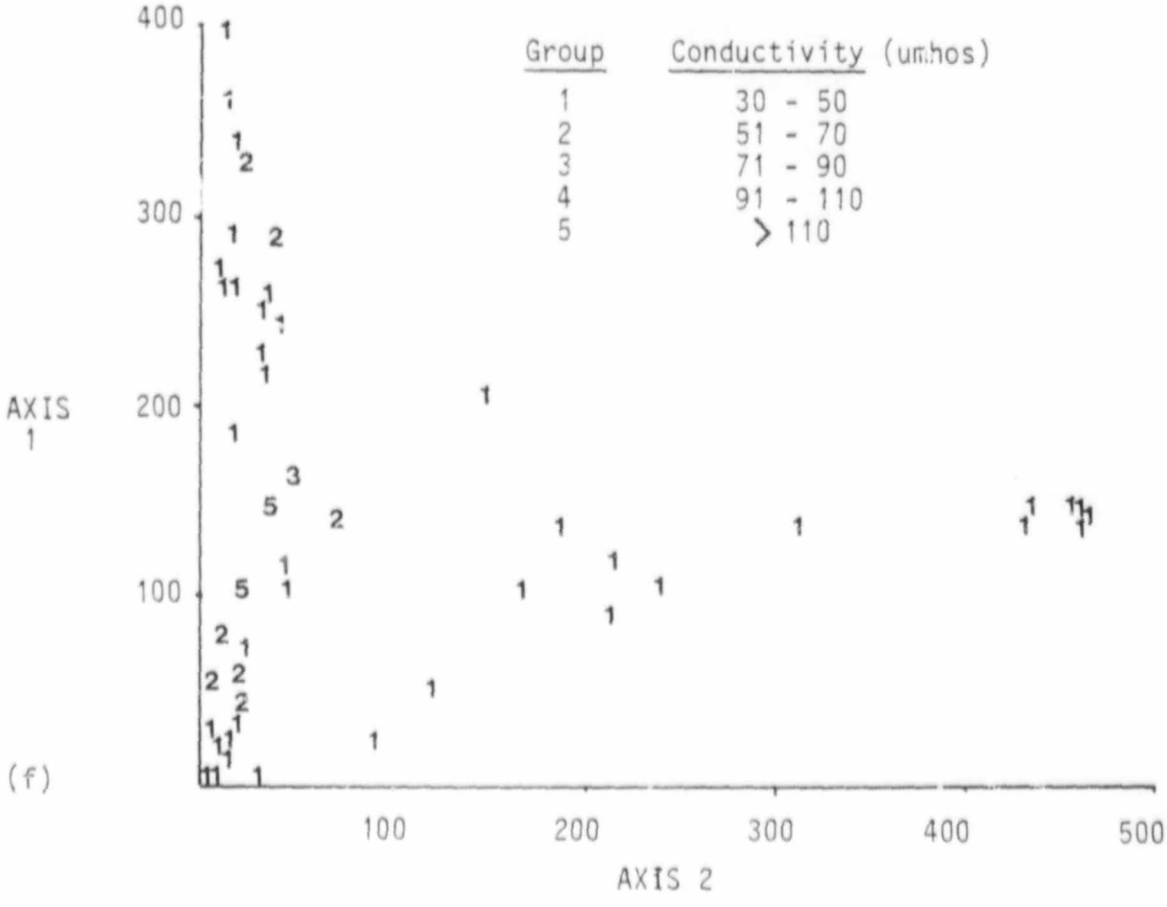
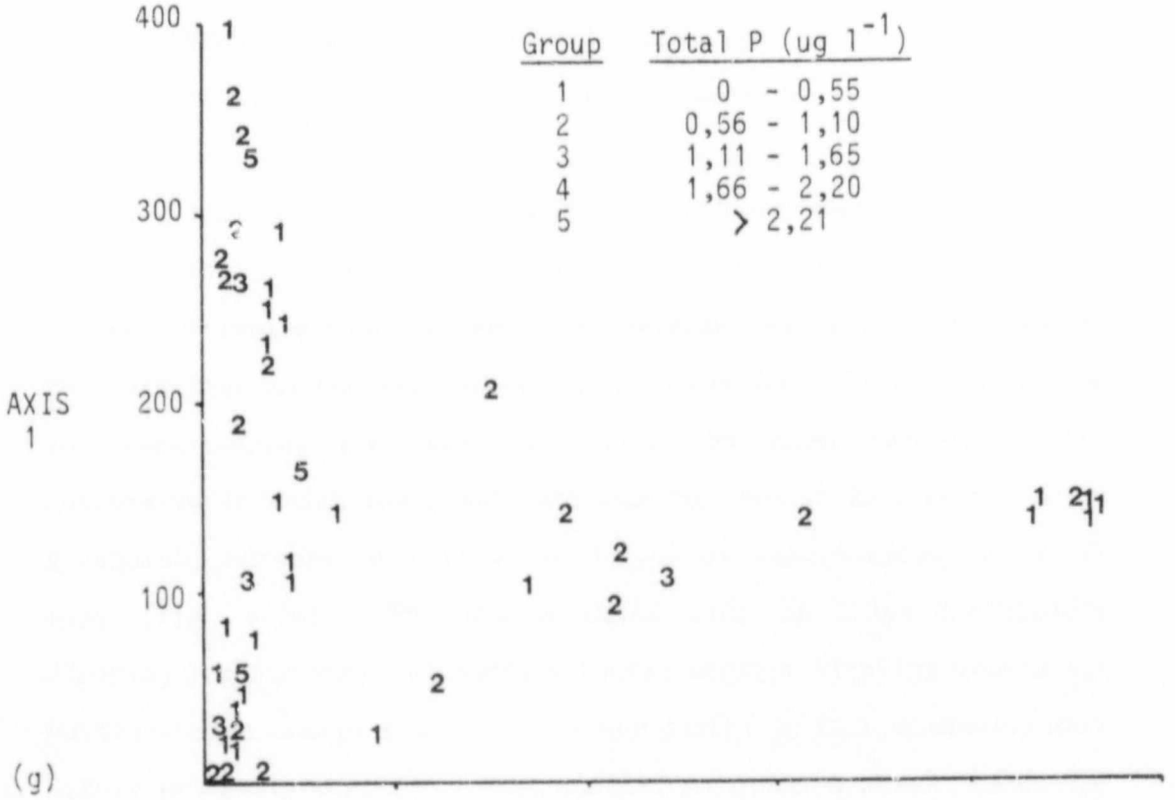


FIGURE 3.2 (Continued). (e) & (f).



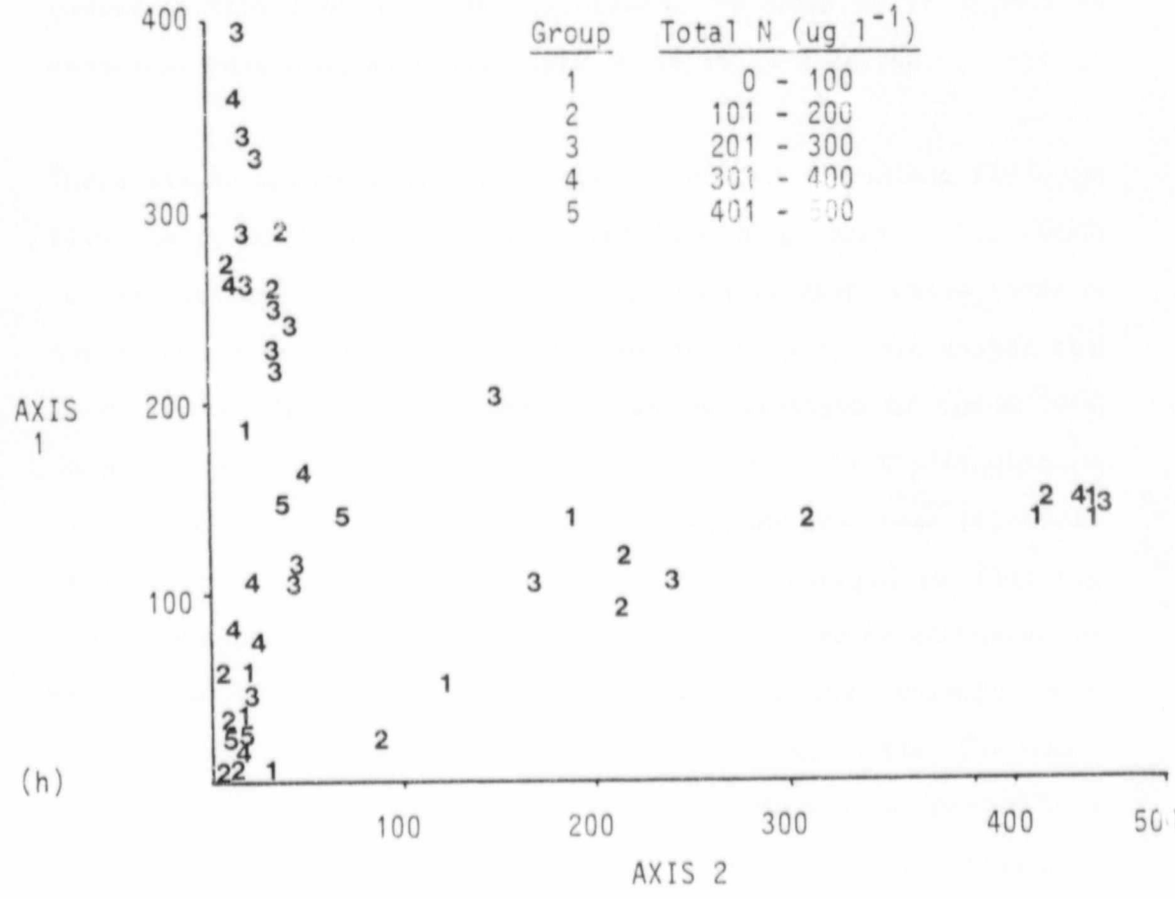


FIGURE 3.2 (Continued). (g) & (h).

axis in DECORANA also corresponded to the groupings in TWINSPAN, comparisons between the two analyses can be made.

Plotting all of the measured environmental variables of the stands on the first two axes of the scatter diagram (Fig. 3.2b - h) leads to the conclusion that the dominant environmental factor influencing the variation in the vegetation types in the Maunachira river system is water depth, i.e. the depth from the water surface to the substratum in which the plants are rooting (Fig. 3.2b), as there was a general increase in mean water depths of stands along the first axis (Fig. 3.2b). The stands which made up Group C comprised floating organic detrital sudds situated amongst floating-leaved and bottom-rooted emergent species. Water depths in this community were either extremely shallow or else similar to those at which the bottom rooted-species rooted. For this reason the mean water depths of stands in this community are represented by an asterisk.

There was an apparent discontinuity in the depth gradient along the first axis, delineated by the dotted line (Fig. 3.2b). The stands to the left of the line were less than a metre deep, while those on the right, with the exception of those in Group C, were deeper than 1,6m. An analysis of the physical characteristics of cores taken through the organic detritus and peat deposits in representatives of each of the vegetation types within the study area best illustrate this depth discontinuity. The change from submerged to floating-leaved and bottom-rooted emergent communities can be accounted for by changes in the water depth associated with the accumulation of benthic organic detritus (Groups A, B and C; Fig. 3.3). The sudden decrease in depth to organic detritus along the x axis (dotted line, Fig. 3.2b) however, is the result of the formation of floating sudds (Groups C & D; Fig. 3.3). These sudds have a column of water beneath them and float at or close to the water surface, thus enabling

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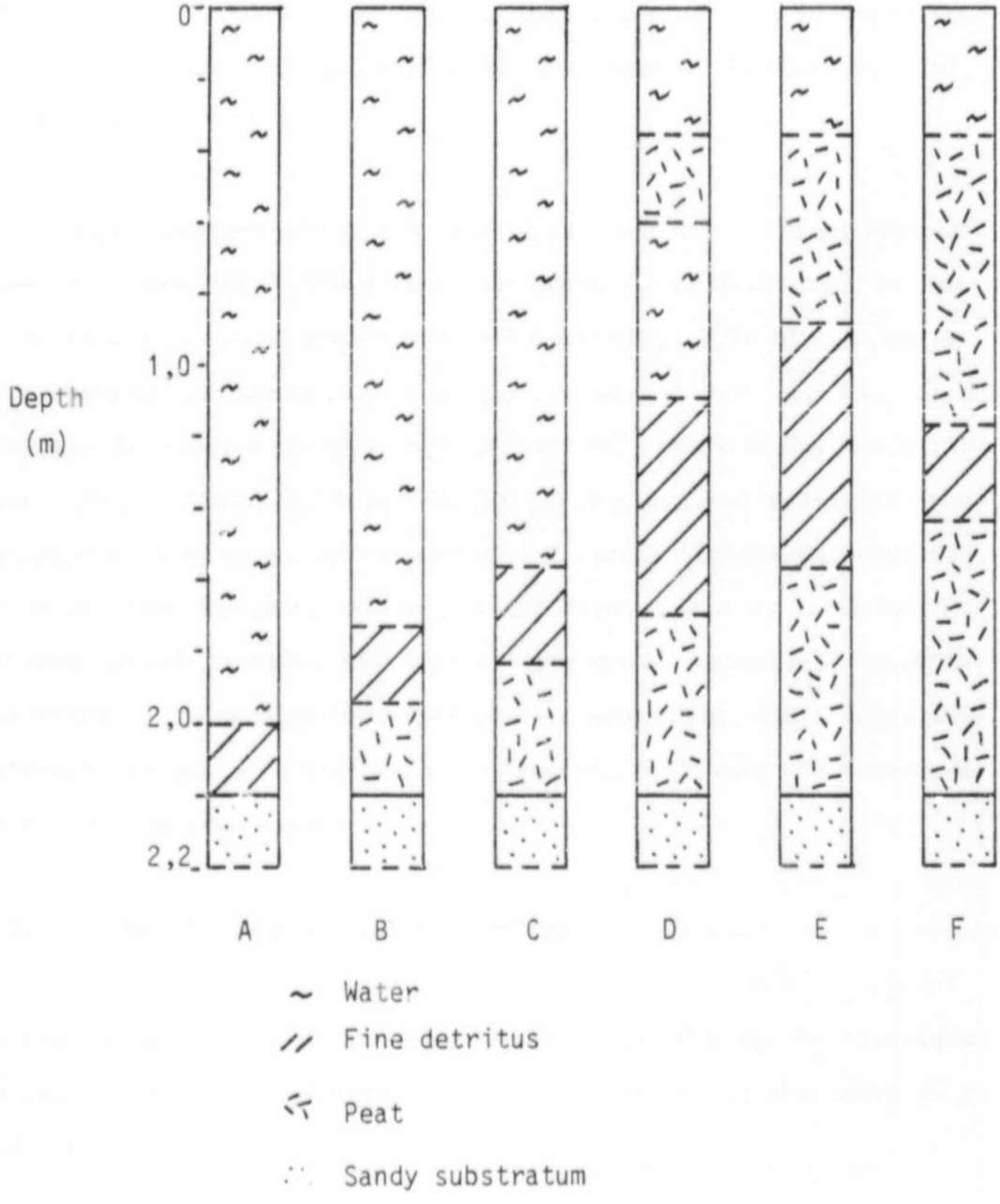

FIGURE 3.3 Cores showing vertical distribution of peat, detritus and water in each of the vegetation types derived from the Two Way Indicator Species Analysis (TWINSPAN). A = submerged, B = floating-leaved/emergent, C = floating-leaved/emergent with occasional sudd, D = open emergent with P. nitidus floating sudd, E = closed emergent hummock and F = closed emergent homogeneous community.

colonisation by shallow-rooted emergent species. The increase in thickness of the sudd layer in each respective vegetation type (Groups D, E, F and G; Fig. 3.3) is indicative of peat accumulation which accompanies successional sudd development (Sculthorpe 1967, Kratz & DeWitt 1986).

The stands arranged along the second axis of the stand ordination were therefore not related to water depth (Fig. 3.2b) nor to any other single measured environmental factor (Fig. 3.2c-h). 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 (namely Groups A, B and C) the program was run again with the omission of the latter three groups. Although a different distribution for the remaining stands was achieved, again no correlations between stand distribution and environmental variables could be elucidated. It is suggested that these communities simply represent different stages of a successional sequence following the formation of a floating sudd layer.

3.1.3 Community and habitat description

On the basis of the information acquired from the two multivariate techniques a general description of communities for the Maunachira river system is provided.

Submerged communities (Group A)

The submerged communities occur in water bodies which range in size from a few square metres to the large oxbow shaped madiba (>100m^2) which characterise the Maunachira river system. These communities are generally low in diversity (5,3 species/stand, Table 3.1) with the submerged species *Najas pectinata*, which is the only species

common to all the stands, having up to 90% cover. The average depth to the sand where the plants are rooting is 2,5m, the thickness of the detrital sludge being 0,5m, and the mean water depth being 2,0m. Other submerged plants such as *Lagarosiphon verticillifolius* Oberm. and *Websteria confervoides* occur in 50% or less of the stands, as do floating-leaved plants *Nymphaea caerulea* and *Brasenia schreberi*. Emergent plants (*Typha capensis* and *Eliocharis dulcis*) sometimes occur in which case they have low cover abundances of 10% or less (Table 3.1).

Floating-leaved/tall, bottom-rooted emergent communities (Group B)

The floating-leaved/tall bottom-rooted emergent communities, which occur close to the edge of open water bodies (Fig. 3.3, Group B), are not as deep as the submerged communities having an average water depth of 1,7m and a detrital layer of approximately 1,0m thick. These communities seem to be protected to a certain degree from the wind as the floating-leaved plants, which are susceptible to vigorous wind action, are more common than the stands in the open water bodies (Table 3.1). Although the floating-leaved *N. caerulea* and *B. schreberi* plants dominate there is an "understory" of submerged *W. confervoides* and an emergent component of *Eliocharis acutangula*. Two of the stands have the tall emergent *Typha capensis* while four stands have *Phragmites australis* (Cav.) Steud. (Table 3.1).

Floating-leaved/tall bottom-rooted emergent communities with sudds (Group C)

The species composition of these plant communities and the water depth is similar to that in Group B. The distinguishing feature is the presence of organic detrital sudds and floating mats of a close association of blue-green algae and various *Utricularia* species.

The occurrence of the algal mats in this group is due to the presence of the submerged plant *Websteria confervoides* which grows up to the water surface where it provides a "platform" upon which the semi-buoyant algal mats can become established. High cover (6 - 25%) of the emergent sedge *E. acutangula* and the presence of *S. corymbosus* (Table 3.1) prevents movement of the algal mats which would result in their breaking up and sinking. *Cyperus pectinatus* and *Drosera madagascariensis* DC. seedlings have been observed colonising these algal mats.

The organic sudds were colonised mainly by short emergent plants such as *F. stricta*, *P. nitidus*, *C. pectinatus* and *D. madagascariensis*. The origin, permanence and fate of these sudds is examined in detail in Chapter 5.

Open emergent communities with Pycreus nitidus (Group D)

These communities are dominated by short emergent plants rooted in unconsolidated peat deposits and are the most commonly represented communities in the Maunachira river system. The average water depth is only 0,40m deep although the depth to the sandy substratum varies greatly from 2,5 to 1,2m. This community has three main vegetation layers: an upper layer (0,80 - 1,20m) dominated by *Miscanthus junceum*, a middle layer (0,10 - 0,30m) dominated mainly by *P. nitidus* and *C. pectinatus* and a lower layer with floating-leaved species *N. caerulea* and *B. schreberi* and blue-green algal mats. The most common plant in the middle layer, *P. nitidus*, usually occurs as a floating sudd growing across the water surface. With sufficient consolidation of the peat in the sudd layer, plants such as *Panicum repens*, *F. pubescens* and *D. madagascariensis* become established.

Closed emergent hummock communities (Group E)

The plants in these communities range from the tall emergent species such as *M. junceum* to short emergent plants such as *Eriochrysis pallida*, *Ficus verruculosa*, *Crassocephalum picridifolium* (DC.) S. Moore and *Thelypteris confluens* to the floating-leaved plants *B. schreberi*, *N. caerulea* and *Potamogeton thunbergii* Cham. & Schlechtd.. This mixture of plants of different life forms is a result of the heterogeneous nature of the stands on a small scale in the form of hummocks and hollows. The raised hummock areas, usually 1 - 1,5m in diameter with the centre of the hummock at or near the water surface, supports short emergent plants. The tall emergent and floating-leaved plants are found in similar sized hollows which are usually approximately 0,5 - 0,7m deep. This results in the high diversity of plants found in this group (mean of 17,6 species/stand, Table 3.1). The peat is of a coarser texture than is found in the previous groups and consists mainly of large, undecomposed, recognisable plant parts.

Closed emergent homogeneous communities (Group F)

The communities in Group F differ from those in Group E by having a shallow water depth and a homogeneous substratum. No floating-leaved plants are thus present. The four major co-dominants - *M. junceum*, *P. nitidus*, *E. pallida* and *Scleria woodii* form a mixed emergent layer. Other species not encountered in previous groups but common here are the orchid *Habenaria schimperiana* Hochst. ex. A. Rich., *Xyris capensis* Thunb. and various moss species such as *Hypnum* spp. and *Philonotis falcata*. The mosses are absent in Group F2 (Fig. 3.1) which comprise three floodplain communities in which peat deposits are absent and the plants are rooted in sand. These communities, on the periphery of the Maunachira river system, dominated by *E. pallida* and *S. woodii*, do not dry out a[illegible]ge but the water level drops close to the level of the s[illegible] drier

late summer months. The plants in Group F1 grow at the same water depth as Group F2 but are rooted in a thick consolidated layer of peat, the depth to the sandy substratum being a total of 1,5m.

It is suggested that stands 1 and 41, both fringe communities with (a) an admixture of both tall and short emergent vegetation, (b) a shallow water depth and (c) a consolidated peat deposit, should be placed in the category of closed, emergent, homogeneous communities (Group F1). The distinguishing feature of these two stands is the complete dominance by the tall grass *M. junceum*. The dense rank growth of plants in these stands compared with the more diffuse growth in areas away from the channel margin was probably the result of increased nutrient availabilities due to their proximity to the channels. The short emergent species such as *P. nitidus*, *P. mundtii* and *F. pubescens* occur at extremely low densities, probably due to low light availabilities at or close to the water surface.

Anomalous communities (Group H)

Cyperus papyrus frequently occurs as a channel lining species in the upper parts of the study area. Since this region was examined in detail in another study (Ellery, W.N., in prep.) only one site (stand 45) was included in the present study. *C. papyrus* rooted in peat close to the water surface is the dominant plant growing 2,0 - 3,0m tall, with an undercanopy of the fern *Thelypteris interrupta* and a twining scrambler *Mikania sagittifera* B.L. Robinson, both of which occur at low densities.

Areas dominated by *Trapa natans* (stand 49) are uncommon in the study area and found almost exclusively where rivers discharge into madiba. The deposition of allochthonous detrital matter is high and may include fine inorganic sediments. This plant community is dis-

tinguished in the analysis by the dominant plant not being common elsewhere. On the basis of a water depth of approximately 1,8m and a dominance by bottom rooted plants with a floating-leaved habit, this stand should have been placed with those in Group B.

3.2 DISCUSSION

A complex mosaic of habitats exists in the Maunachira river system today. The varied history in flow patterns in the Maunachira river system, as demonstrated by a considerable variety of fossil channels, meander bends and oxbow shaped configurations on the 1983 aerial photographs (Plate 3.1), indicate many past perturbations under different flow regimes. This heterogeneity may represent different stages of temporal succession (Watt 1947, Pickett 1976) or spatial expression of environmental heterogeneity (Whittaker 1967, Levin 1976), although the two factors are not necessarily mutually exclusive. A series of cores taken in each of the vegetation types of the study area indicate both hydroseral and sudd initiated plant successional processes contributing to each of these communities. The mosaic of communities therefore seem to represent post-disturbance patches (Whittaker & Levin 1977) at different stages in a successional sequence which, if not disturbed by a change in flow patterns, would culminate in short emergent bog communities with consolidated peat. It is suggested that those communities which have little peat accumulation and plants rooted largely in the sandy substratum, occur in areas which have been subjected to the most recent perturbation caused by an increase in flooding. The formation and vertical accumulation of peat in the other communities indicate

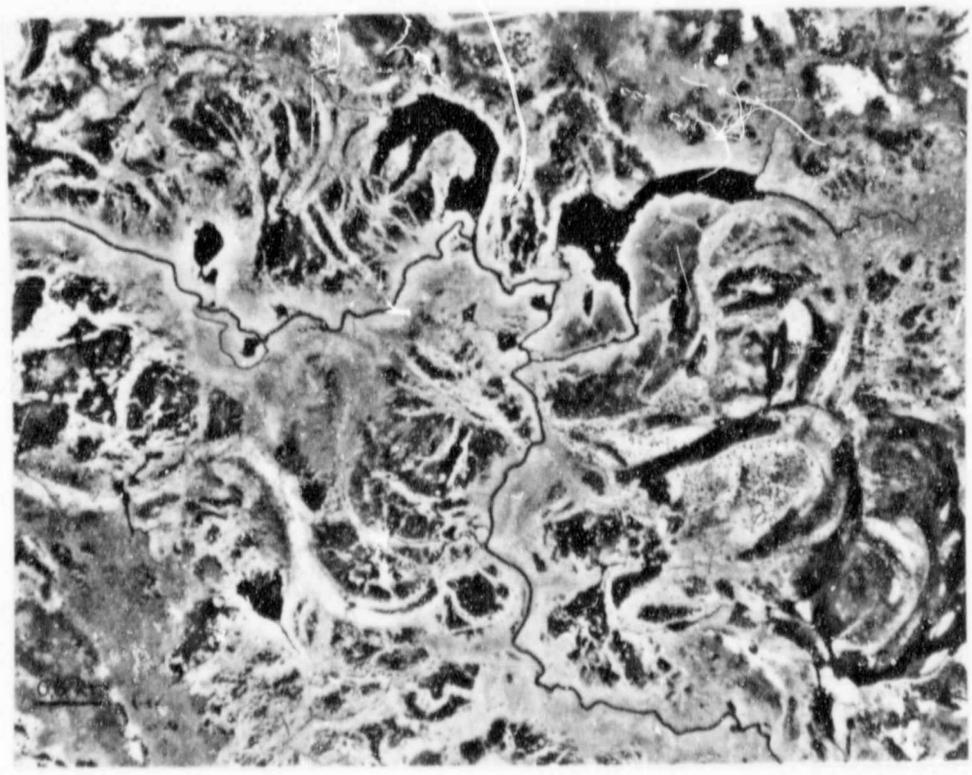

PLATE 3.1 Aerial photograph (1983) indicating a mosaic of habitats in the Maunachira river system

less recent disturbances; the communities with a well developed peat bog (Groups E, F & G; Fig. 3.1) having been established for the longest period. The mechanisms for such a sequence, based on evidence from the phytosociological data and peat cores, are proposed below.

3.2.1 Hydroseral changes in water depth as a major determinant of succession

In many studies on environmental control of species distribution in wetlands, water depth has been shown to be the major determinant (Walker 1970, van der Valk & Bliss 1971, Howard-Williams & Walker 1974, van der Valk & Davis 1976, Slack et. al. 1980, Birks & Birks 1980, Spence 1982, Glaser 1983, Sanville et. al. 1986). This applies, in part, in the Maunachira river system where the distribution of the submerged, floating-leaved and tall emergent species is determined largely by water depth, since, with the exception of a few deep (>3,0m) oxbow madiba and the shallow floodplain communities (Group F2, Fig. 3.1), the depth to the sandy substratum is fairly constant with an average depth of 2,1m (S.E. = 0,17). It appears therefore that the extent of accumulation of a benthic detrital layer from autochthonous hydroseral infilling determines the water depth and thus the species composition of the area.

3.2.2 Sudd formation: Properties of species determining successional changes

In contrast to the submerged, floating-leaved and tall, bottom-rooted emergent communities, the distribution of short emergent species in the stands sampled in this study is unrelated to water depth. Field observations and an examination of peat cores indicated that the formation of a sudd layer or an exposed peat surface pro-

vides a surface upon which short, emergent species tolerant of shallow water can become established. Birks & Birks (1980) stated that the main controlling factor of the distribution of wetland species is the height of the water table, but, with the onset of peat formation, other factors such as nutrient concentrations and pH became the important determinants. Since none of the other measured factors in this study, including pH, total nitrogen and total phosphorus, conductivity and temperature could alone account for the distribution of stands along the second axis in the ordination (Groups D - F; Fig. 3.1), the following three factors are suggested as being important.

(1) Factor interaction may be obscuring the influence of any single determinant.

(2) A factor other than the ones measured may be a major environmental determinant. Although studies in which various parameters have been measured using surface water samples have shown clear correlations between chemical characteristics and species distribution (Walker 1970, Walker & Coupland 1970, van der Valk & Bliss 1971, Glaser 1983), correlations are more likely to be detected by measurements of chemical factors of the interstitial water or of the peat itself, instead of surface water samples (Summerfield 1974, Stanek 1975, Giller & Wheeler 1986). However, chemical analyses of interstitial water and water-logged peats are difficult to carry out and poorly understood, because samples are usually exposed to air prior to analyses, thereby altering conditions considerably (Richardson et. al. 1978).

An indication of nutrient concentrations in the system are frequently obtained by chemical analysis of the plants themselves (Boyd 1978). Wetland plants are typically perennial and rhizomatous or

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An indication of nutrient concentrations in the system are frequently obtained by chemical analysis of the plants themselves (Boyd 1978). Wetland plants are typically perennial and rhizomatous or

stoloniferous, which possibly allows for a strategy of strong nutrient conservation (Prentki et. al. 1978). When nutrient elements are in short supply in the system, as is the case in the Maunachira river system (total P <2,2ug l^{-1} and total N <500ug l^{-1}, Fig. 3.2g & h, both in the range of ultra-oligotrophy as defined by Wetzel 1983), recycling of nutrients within clonal plants has been shown to prevail (Bayly & O'Neill 1972, Howard-William & Lenton 1975, Mason & ryant 1975, Howard-William & Gaudet 1985). However, it has been documented that luxury uptake of nutrients is common in emergent swamp plants (Bayly & O'Neill 1972, Ulehlova et. al. 1973). Nutrient concentration measures within the plant pool would thus reflect the ability of a particular species, or of species combinations, to retain nutrients rather than provide evidence for their availability to plants in general. This type of nutrient measure would therefore give little indication of the effect of nutrients on species distributions and would thus be of limited value.

(3) The distribution of the short emergent plant communities may not be determined by an environmental factor as such but may instead be controlled by interactions among the plant species (such as interference, exploitative competition and allelopathy), predators and parasites or merely by stochastic factors such as the chance arrival of a propagule at a site and chance germination (Hutchinson 1953, van der Valk 1986). Howard-Williams & Walker (1974) found that environmental factors alone could not explain the present distribution of *Typha domingensis* Pers. the dominant swamp plant at Lake Chilwa, Malawi. It had a vigorous vegetative reproductive growth and often occurred in pure stands, thereby influencing the local environmental conditions and thus "controlling" the remaining species composition. Any variation was due to a change in *T. domingensis* itself or due to chance factors favouring the introduction of a new species.

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Many species in the short emergent communities of the Maunachira river system exhibit vegetative growth, of which the stoloniferous sedge *P. nitidus* is the most common. It spreads to form a major component of the floating, dense sudds which cover extensive areas and is also a common component in all the other short emergent communities (Table 3.1). It is proposed that during the initial stages of sudd formation *P. nitidus* responds positively to space availability and effectively outcompetes other species for space and available nutrients. Either a change in *P. nitidus* itself, such as a change in height or density of the plant or stochastic factors allow for the germination and establishment of other species during peat or bog development.

The suggestion that peat bogs arise by a combination of hydroseral infilling and floating sudd formation has been evaluated in a detailed examination of two cores taken from a mature bog community (Chapter 4). The initial stages of bog formation, i.e. the formation and horizontal spread of sudd communities, were studied in the field over a period of twelve months (Chapter 5).

CHAPTER 4

PEAT STRATIGRAPHY: FROM OPEN WATERS TO PEAT BOGS

An examination of the peat stratigraphy of the two cores taken from a closed, emergent bog community (Group F1; Fig. 3.1) based mainly on peat texture, together with comparisons of textural attributes of cores taken from each of the major plant communities within the study area (Fig. 3.3) has in part contributed to the interpretation of the peat stratigraphical sequence. The presence of diatom assemblages within the peat deposits themselves has also contributed to the interpretation of environmental conditions present at the time of deposition, and in combination, it has been possible to evaluate the significance of hydroseral, as well as sudd initiated, plant succession in the development of peat bogs.

4.1 RESULTS

4.1.1 Description of Core 1

The core could be divided into four main zones based upon a visual impression of colour and texture of the peat, with two subdivisions distinguishable in each of the first and third zones (Table 4.1). Whereas the transitions between zone II (detrital zone) and the zones above and below it were abrupt, those between the other zones and

TABLE 4.1 Peat stratigraphical zones in a core (Core I) taken from a well established peat bog.

DEPTH (m)	ZONE		MACROSCOPIC DESCRIPTION		
			COLOUR	DEGREE COMPACTION	TEXTURE
0	IV	Surface peat	dark brown-black	diffuse	Very fibrous. Mainly large, living and dead rooting matter of present community. A little fine granular organic material.
20	IIIb	Sudd	dark brown-black	compact	Fibrous. Dead and living rooting material. Dead P. nitidus and M. junceum rhizomes and roots. Fine granular organic material.
40	IIIa		dark brown	very compact	Ditto Zone IIIb.
60	II	Detrital	red brown	very diffuse	Very fine granular organic material. No recognisable plant parts. High water content.
80					
100	Ib	Bottom peat	red brown	compact	Fibrous, partially decomposed roots and rhizomes. Some fine granular organic material.
120	Ia		red brown grading to light grey	very compact	Coarse, granular organic detritus grading to grey sand. Few large undecomposed roots and rhizomes.
136					

subzones were gradual. The lowest zone (zone I, bottom peat) consisted of a fibrous peat layer with no recognisable plant parts grading from a compact, fibrous, mainly organic upper section (zone Ib) to a more compact but finer textured lower layer containing some inorganic grey sands (zone Ia). This zone of the core is similar to the organic layer found in modern bottom-rooted emergent communities; the lower, slightly finer layer derived from less refractile submerged plants and the upper layer from more refractile, bottom-rooted emergent species.

A very fine, loose, detrital zone with a high water content and no recognisable plant parts constituted the second zone (zone II, detrital zone). A similar peat stratigraphy of a loose detrital zone between two compact peat zones was obtained in the Okefenokee swamps (Cohen et. al. 1984). This pattern was attributed by these authors to the development of a horizontal floating sudd layer which preceded vertical peat accumulation. The evidence from the series of peat cores from different vegetation types (Fig. 3.3) indicate that a similar sequence of events in the Maunachira river system is likely to have taken place. Zone II therefore consists of detritus which would have rained down from the floating sudd layer during sudd development to rest on the more compact organic layer of the previous emergent plant communities (zone Ib). The third and fourth zones, as with the bottom peat zone, consisted of a fibrous peat layer, but in contrast they had recognisable living as well as dead plant parts. Zone III appears to represent a sudd forming zone which is distinguishable from the uppermost zone (zone IV, surface peat) by the presence of a compact layer of *Pycreus nitidus* and *Miscanthus junceum* rhizomes and roots which would have formed a major component of the developing sudd. It is thus likely that the surface peat (zone IV) has formed as a result of surface accumulations of many different secondary colonisers of the sudd layer (zone III).

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