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

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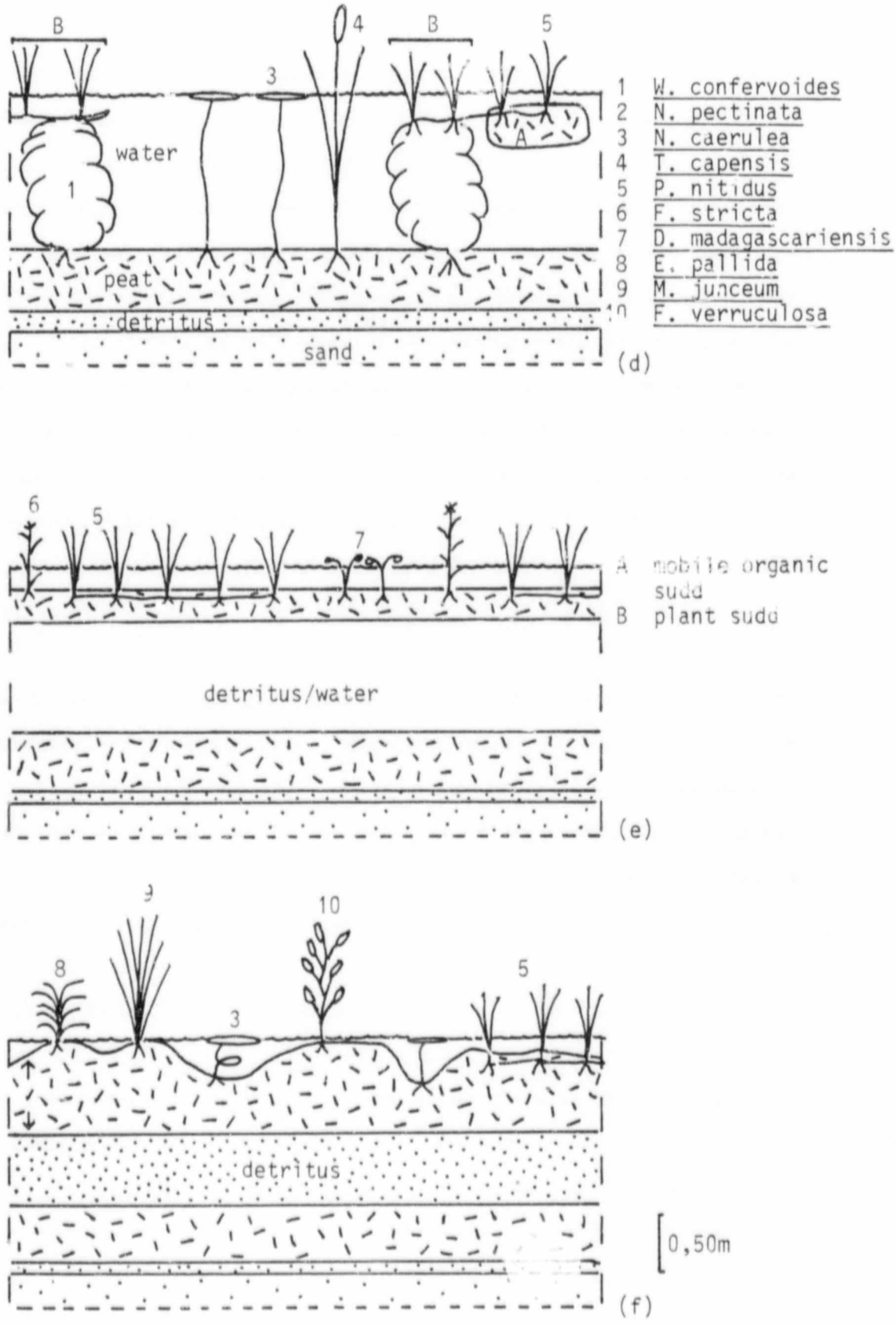

FIGURE 6.1 (Continued). (e), (f) and (g).

of inorganic sediment deposition, the gradual decrease in water depth is the result of organic carbon accretion. This provides a habitat suitable for the establishment firstly of floating-leaved species such as *Nymphaea caerulea* and *Brasenia schreberi* (Fig. 6.1b) and later of tall, bottom-rooted emergents such as *Typha capensis* and *Phragmites australis*, which usually occur in scattered clumps (Fig. 6.1c). This is an autogenic successional process in which the deposition of organic matter of early successional plants leads to a decrease in water depth and thereby facilitates the establishment of later colonisers. These mechanisms for change correspond to those proposed by Egler (1954) in a facilitation model of plant succession which was later corroborated by Connel & Slatyer (1977) and Noble & Slatyer (1980).

The presence of emergent species, which are more refractile than submerged and floating-leaved species (Wetzel 1983), results in the formation of an organic layer which is generally of a coarser texture than that formed in earlier stages (Fig. 6.1c). This upper organic layer, bound together by the roots of the bottom-rooted species, is associated with organic sudd initiation.

6.1.2 Sudd initiated plant succession

The formation of two types of sudds at or close to the water surface represents an opportunity for the development of short emergent plant communities which are largely independent of the depth to the benthic detrital aggregate, but are instead dependant on the depth of the floating organic layer. In the first type of sudd formation decomposition and gas production in the inorganic detrital layer in the rooting zone of *N. caerulea* and *T. capensis* leads to increased buoyancy of the submerged detrital mat. The corms and rhizomes of these species respectively, together with their roots and associated

detritus, rise to the surface either becoming separated from the remainder of the submerged detritus to form mobile sudds, generally less than 2,0m in diameter (Fig. 6.1d), or else they remain attached and form dome-shaped structures in which large areas of submerged detritus become exposed (up to 200m^2). In contrast with studies by van der Valk (1981, 1982) who suggests that a persistent seed bank is the important determinant of plant succession on exposed substrata in wetlands, it was shown in this study that an input of propagules from the surrounding vegetation result in the colonisation and establishment of a short emergent vegetation. The most common sudd colonisers in the Maunachira river system are *Fuirena stricta*, *Pycreus nitidus*, *Drosera madagascariensis* and *Xyris capensis*. A large proportion of the sudds remain afloat even during the winter months when gas production is low, and as a result of wind action they ultimately bank up on the leeward edge of the lediba, thereby resulting in a reduction in the size of the water body.

The mobile organic sudds and the vegetation stabilised banks form suitable substrata for colonisation by the sedge *P. nitidus*. The second type of sudd formation involves encroachment by this stoloniferous species, which requires some degree of physical support. This is provided mainly by submerged, unconsolidated detritus at a depth of less than 0,7m, or else by the submerged sedge *Websteria confervoides* (Fig. 6.1d). Initially a loose matrix of stolons is formed, but with the continual growth and death of plant parts, a more consolidated peat layer forms. Gas production from decomposition within the sudd maintains its buoyancy (Fig 6.1e).

It has been proposed in this study that both stochastic factors, such as the chance arrival and establishment of propagules at a favourable site, and the interactions between the species on the sudd layer itself - rather than environmental factors - determine the nature

and rate of species colonisation and replacement until a short emergent bog community with consolidated peat becomes established. Species such as *Eriochrysis pallida*, *Ficus verruculosa* and *Miscanthus junceum* eventually become dominant at advanced stages (Fig. 6.1f).

Vertical aggradation occurs both downwards in the form of detrital rain from the sudd, and upwards as a result of the surface accumulation of undecomposed plant material (Fig. 6.1f). The peat cores revealed a middle, loose detrital zone. It is postulated that peat accumulation in the Maunachira river system is not yet at equilibrium, but that in time the upper sudd peat and the bottom peat will eventually meet, resulting in a more continuous but stratified peat deposit than was observed within any of the cores within the study area. Peat accumulation at the surfaceat present appears to be limited by the seasonal water level fluctuations.

6.2 PEAT FORMATION IN THE MAUNACHIRA RIVER SYSTEM

Peat forms in areas where rates of plant production exceed rates of decomposition (Clymo 1983). Many interrelated factors, but primarily those which reduce rates of decomposition, have generally been considered to contribute to peat formation and include (i) a low energy hydrodynamic regime, (ii) low temperatures, (iii) a consistently high water table which results in (iv) anaerobic conditions, (v) acid conditions (pH < 5.5), and (vi) low nutrient availabilities, especially nitrogen and phosphorus (Moore & Bellamy 1974, Verry &

Boetler 1978, Stach et. al. 1982, Thompson & Hamilton 1983, Wetzel 1983, McCabe 1984, Malmer 1986).

Peat formation within the Maunachira river system has taken place in areas which have a consistently high water table and negligible flow rates. It does however appear to have taken place under relatively aerobic conditions. Evidence for this is provided by the abundance of fungal hyphae within the peat cores which appear to have facilitated the oxidative decomposition of the pollen grains as described by Klein & Dupre (1980). Temperatures in the waters of the delta also appear high; they were always in excess of 12°C at a depth of 1,0m, which is well above the temperatures which depress decomposition (Stach et. al 1982). The pH of peat waters was greater than 6,0 and the pH preferences of the diatom assemblages during peat deposition indicate a slightly acidic but close to neutral environment. These values are too close to neutral to sufficiently inhibit rates of decomposition (Thompson & Hamilton 1983).

These environmental factors therefore appear to play little or no part in promoting organic matter accretion and thus peat formation within the Maunachira river system. It seems likely however that low nutrient concentrations in the system play a crucial role. Several important processes contribute to the poor nutrient status of the waters of the river system. Firstly, the catchment of the Okavango delta is nutrient poor being essentially of Kalahari sands and crystalline rock (Smith 1976), and water entering the delta via the Okavango river may be classified as oligotrophic. Secondly, the Maunachira river system receives the bulk of its flow from "filter" communities (Wilson 1973) which serve to trap any suspended material and effectively remove plant nutrients (Smith 1976, Gaudet 1977).

Once the already nutrient poor waters enter the Maunachira river, further depletion of available nutrients takes place by the formation of peats which are recognised to be nutrient sinks (Moore & Bellamy 1974). It is therefore not surprising that the measures of both total nitrogen and total phosphorus obtained in this study were both within the range of "ultra-oligotrophy" (Wetzel 1983) and are likely to severely limit the decomposer component in the system (Chamie & Richardson 1978).

A further very important constraint on decomposition is the refractile nature of the plant material. Although no work has been done in the Okavango Delta on the nutrient content of plant material, studies elsewhere have indicated a high cell wall fraction (up to 83% for the tropical sedge *Scirpus cubensis* Poeppig & Kunth ex Kunth, Howard-Williams & Junk 1977) and a correspondingly low protein content (less than 5%, Howard-Williams & Gaudet 1985). These are also considered to limit the rate and extent of decomposition, since the plant material itself forms the main nutrient source for the organisms of decay (Clymo 1983).

It is therefore suggested that both nutrient limitations and the refractile nature of organic matter produced within this system may provide severe limitations to the decomposer component, and may thus be primary determinants of peat formation and accumulation. Since peat formation in a subtropical, low altitude environment such as the Okavango Delta is an unusual feature (Thompson & Hamilton 1983) and yet is such a dominant process in the Maunachira river system, rates and determinants of peat accumulation are regarded as important aspects of the delta's structure and functioning, and should be investigated in detail in further studies.

6.3 CONCLUSIONS

The Okavango Delta experiences periodic but major shifts in the distribution of water flow, with an increase in inundation in one area usually being accompanied by a decrease elsewhere (Wilson 1973). This study has examined part of a single river system in which past changes in flow patterns, namely an increase in flow during this century, have resulted in the formation of a mosaic of habitats at different stages of development. Since the results indicate that water depth is the major determinant of the distribution of the aquatic macrophytes, the depth and extent to which an area becomes inundated are the most important factors influencing the establishment of the initial colonising communities. The mechanisms for change once these communities become established are, firstly, the gradual decrease in water depth by autochthonous hydroseral infilling and, secondly, the formation of a floating sudd layer at or close to the water surface. A better understanding of each of the stages of change can be gained by further autecological studies of key species (such as *P. nitidus*), in which various aspects of vegetative growth, plant competition, propagule dispersal and germination requirements are examined.

Although there is obviously at present a general trend in reduction of open water due to peat formation in the Maunachira river system, the histories flow in other river systems indicate a feedback loop in which both peat accumulation and inorganic sedimentation further upstream will result in dramatic changes in the hydrological regime within this river system with flow being diverted elsewhere in the delta (McCarthy et. al. 1986a). To gain a better understanding of these processes at the broad ecosystem level, further work is re-

quired to elucidate the major determinants and rates of peat formation and accumulation.

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APPENDIX A

List of diatom taxa present in peat cores taken from the Maunachira river system

Acnanthes buccula Choln.

Acnanthes sp1 and 2

Cocconeis placentula Ehr.

Cocconeis sp1 and 2

Cyclotella sp1, 2, 3, and 4

Cymbella cryptocephala Hustedt

C. perpusilla A. Cleve

Cymbella sp1

Eunotia asterionelloides Hustedt

E. exigua (Breb.) Rabh.

E. mesiana Choln.

E. pectinalis (Kutz.) Rabh. var.1, 2 and 3

E. rhomboidea Hustedt

E. tenella (Grun.) Hustedt

E. valida Hustedt var.1 and 2

Eunotia sp1, 2, 3, 4 and 5

Fragilaria pinnata Ehr.

F. constreuns(Ehr.) Grun. var. *venter* (Ehr.) Grun.

Gomphonema angustata (Kutz.) Rabh.

G. apicatum Ehr.

G. gracile Ehr.

Gomphonema sp1, 2, 3, 4 and 5

Hantzschia amphioxys (Ehr.) Grun.

Hantzschia sp1

Navicula mutica Kutz.

Navicula sp1, 2, 3, 4 and 6.

Nitzschia subacicularis Hustedt

Nitzschia sp1, 2 and 3

Pinnularia borealis Ehr.

P. brevicostata A. Cleve

P. gibba Ehr.

P. sublinearis (Grun.) A. Cleve

Pinnularia sp1, 2, 3, 4 and 5

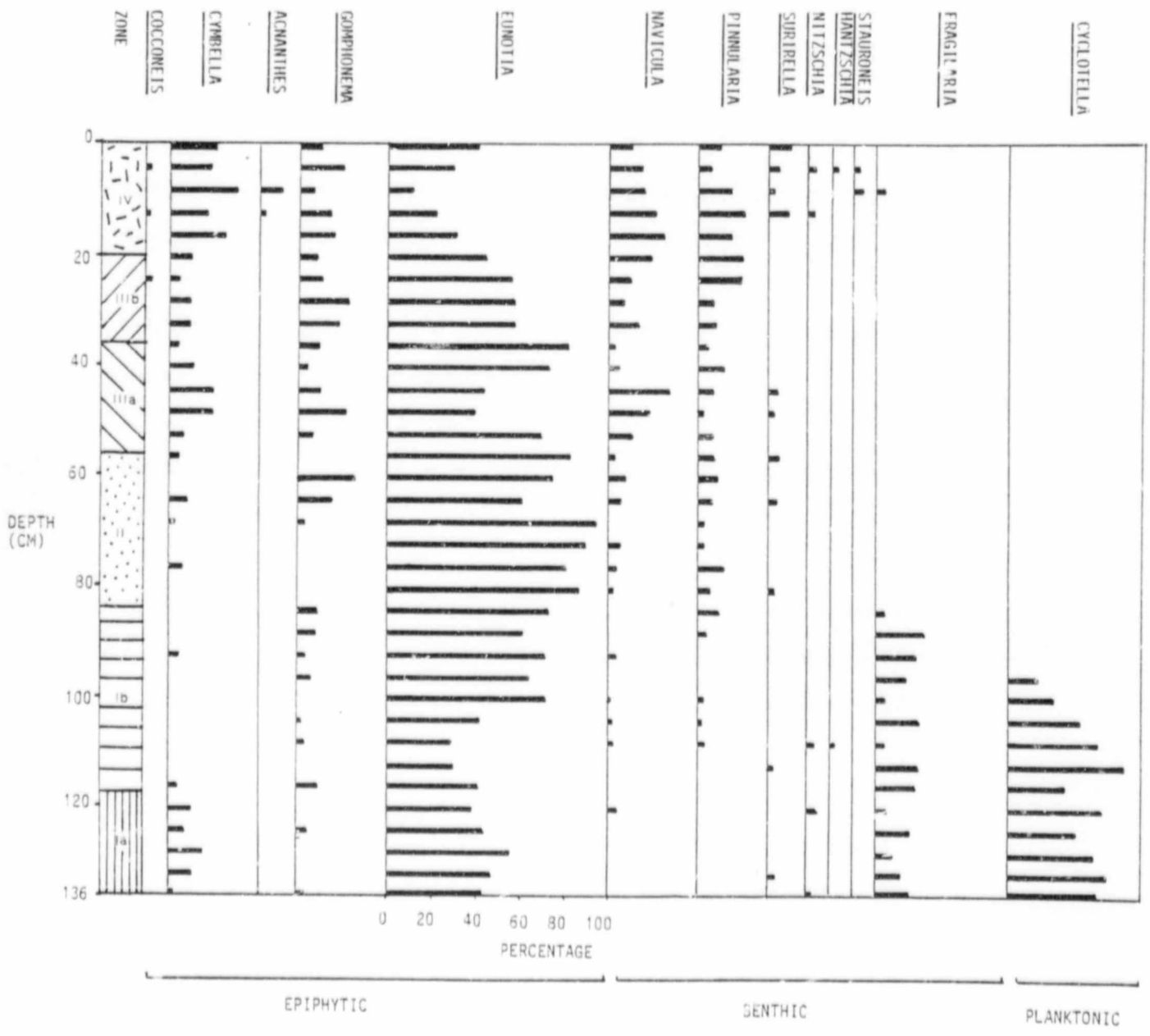
Surirella sp1

Stauroneis claaseniae Choln.

Stauroneis sp2 and 3

APPENDIX B

Percentages of the total of diatom taxa in a peat core (Core II) taken from a well established peat bog



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