Changes in colour within the peat did not correspond to changes in texture, and therefore appear unrelated to the environment of deposition. The gradual change in colour from a reddish brown near the bottom of the core to a dark brown-black at the top appears to be associated with a gradual increase in redox potential from the bottom to the top of the peat (Cohen 1973). Furthermore, exposure of the core to air after extrusion from the corer itself resulted in rapid oxidative changes, particularly of the lower layers, to a uniform black colour.

4.1.2 Distribution of diatom taxa in Core 1

A total of thirteen diatom genera were identified positively and sixty-three species were recognised (Appendix A). The ecological data provided by Round (1957), Richardson (1968), Haworth (1969, 1976), Florin (1970) and Patrick (1977) enabled broad grouping of the taxa into various categories with respect to habitat preferences at a level which was satisfactory in terms of the broad ecological interpretations required. Changes in the diatom assemblages derived from the core were closely related to the changes in peat texture (Figs. 4.1 & 4.2), and for this reason diatom assemblages within each of the four texturally distinct zones of the core will be described.

Bottom peat zone (zone I)

The presence of epiphytic diatoms in the lowermost zone of the core (Figs. 4.1 & 4.2a) is indicative of the existence of aquatic macrophytes during early successional development. These macrophytes must have been in sufficiently low densities, however, to allow for the development of both planktonic and benthic diatom populations (Figs. 4.1 & 4.2a). This assemblage of diatoms, in conjunction with the presence of large, undecomposed, fibrous roots

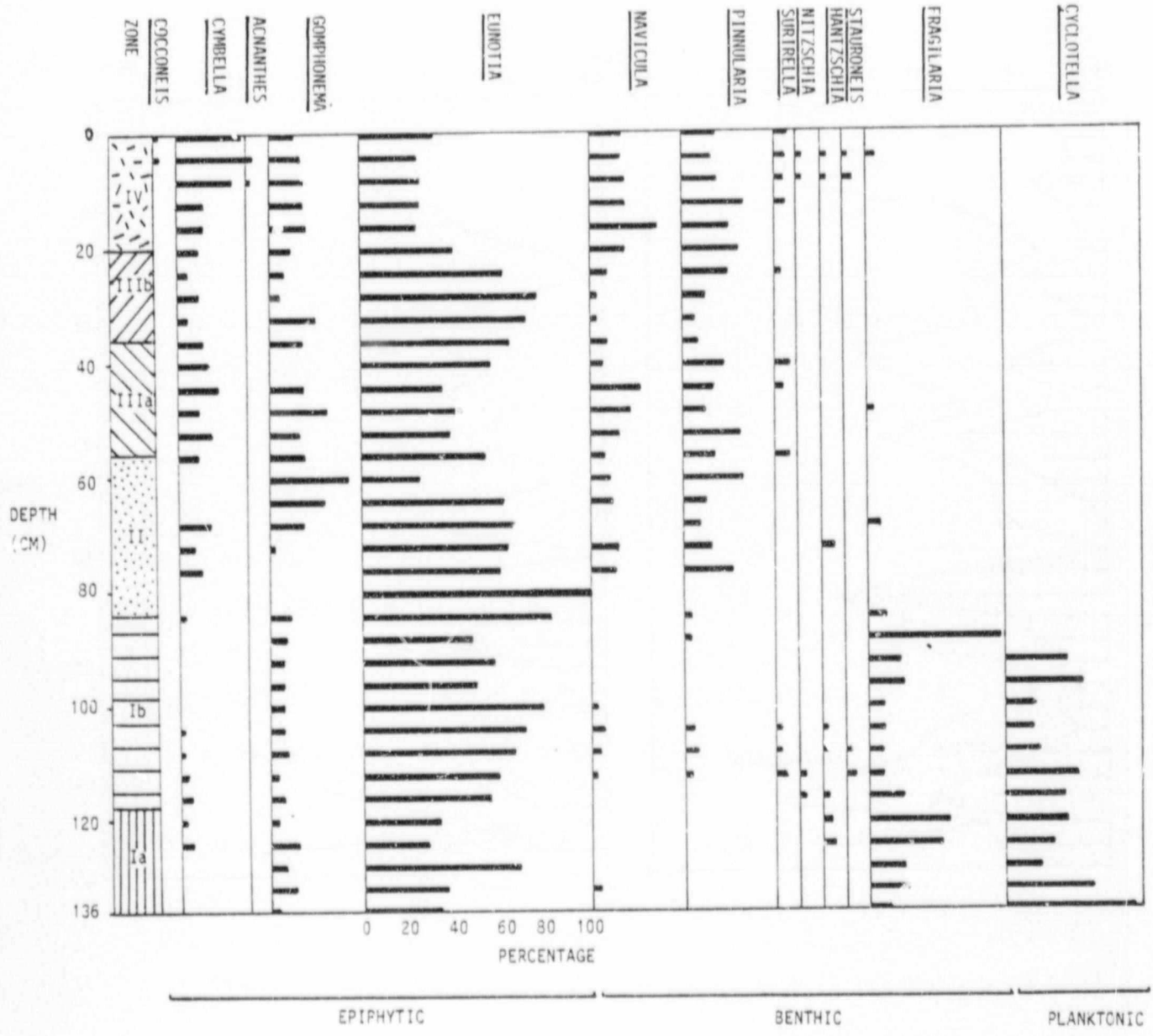


FIGURE 4.1 Percentages of the total of diatom taxa in a peat core (Core 1) taken from a well established peat bog.

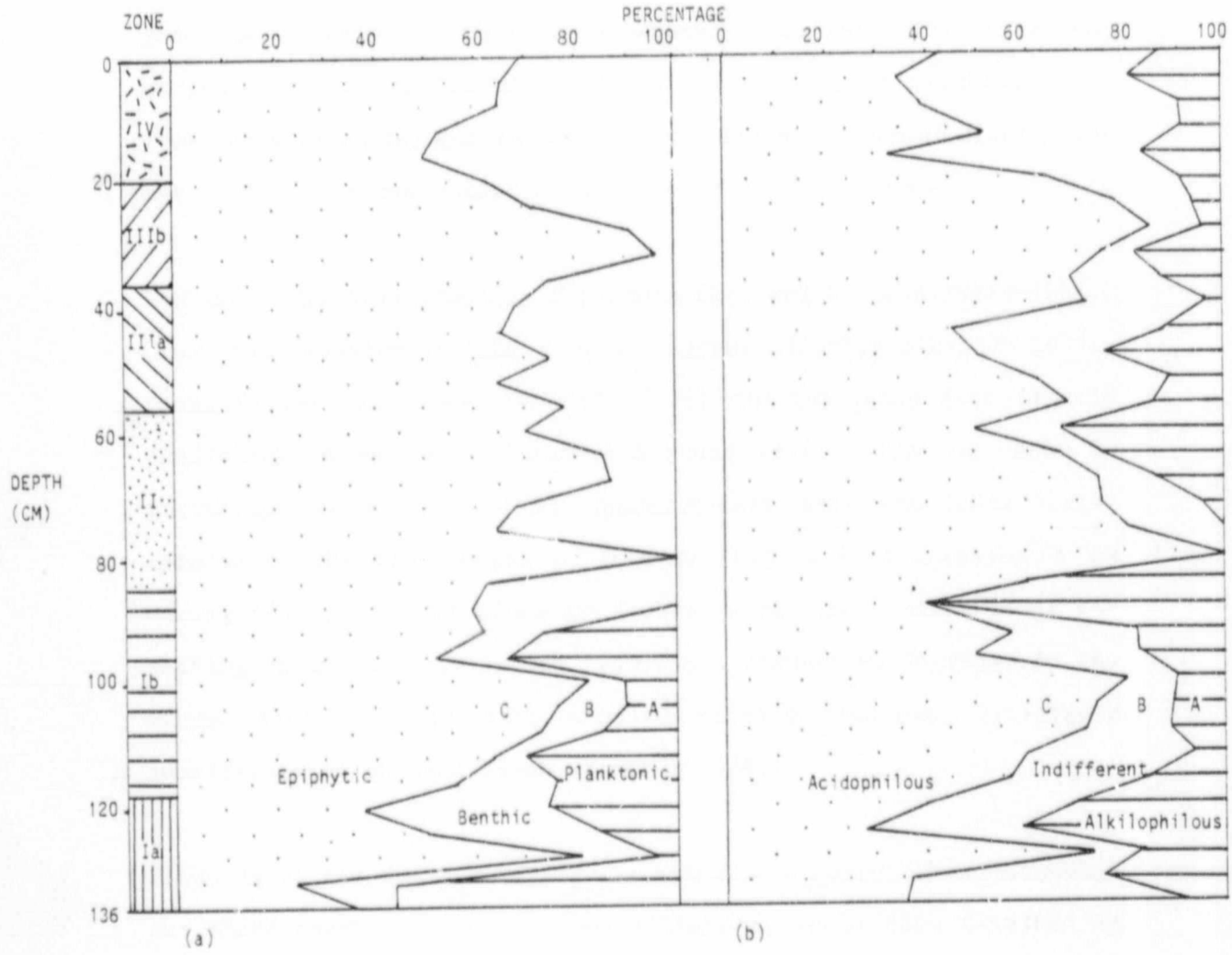


FIGURE 4.2 Ecological spectra: (a) proportion of taxa that are (A) planktonic, (B) benthic and (C) epiphytic; (b) proportion of taxa that are (A) alkilophilous, (B) indifferent and (C) acidophilous.

and rhizomes, suggests that tall, bottom-rooted, refractile emergent species such as *Typha capensis* would have been scattered at low densities within the water body which had a depth of between 0,88 and 1,36m. Prior to this there probably were less refractile submerged and floating-leaved plants as evidenced by a slightly finer lower zone (zone 1a) but almost complete decomposition of plant parts has left little recognisable evidence of their presence.

The two *Fragilaria* species, *F pinnata* Ehr. and *F. construens* (Ehr.) Grun. var. *construens* (Ehr.) Grun., favour slightly alkaline conditions (Round 1957, Haworth 1969, 1976) and the genus *Eunotia* acid conditions (Round 1957, Crabtree & Round 1967). The two peaks in percentage of *Fragilaria* at approximately 88cm and 120cm corresponded to the two troughs of *Eunotia* (Fig. 4.1) suggesting a pH during this period of close to neutral with minor shifts in pH resulting in an increase in one type and a respective decrease in the other. *Cyclotella*, the other dominant taxon in this zone, is largely indifferent to pH conditions (Haworth 1976).

Flooding of the Makuhira river system, as a result of the blockage and abandonment of river systems elsewhere, would have resulted in an influx of nutrients from the decomposing terrestrial vegetation (Moss 1980). This could account for the relatively high total numbers of diatoms in zone Ib which are indicative of high productivities during this period (Fig. 4.3). Since sedimentation rates were not determined however, any statement on productivity is of a rather speculative nature.

Detrital zone (zone II)

There was a sudden change in peat texture at the contact of zones I and II from a compact, fibrous lower peat layer (zone I) to a much

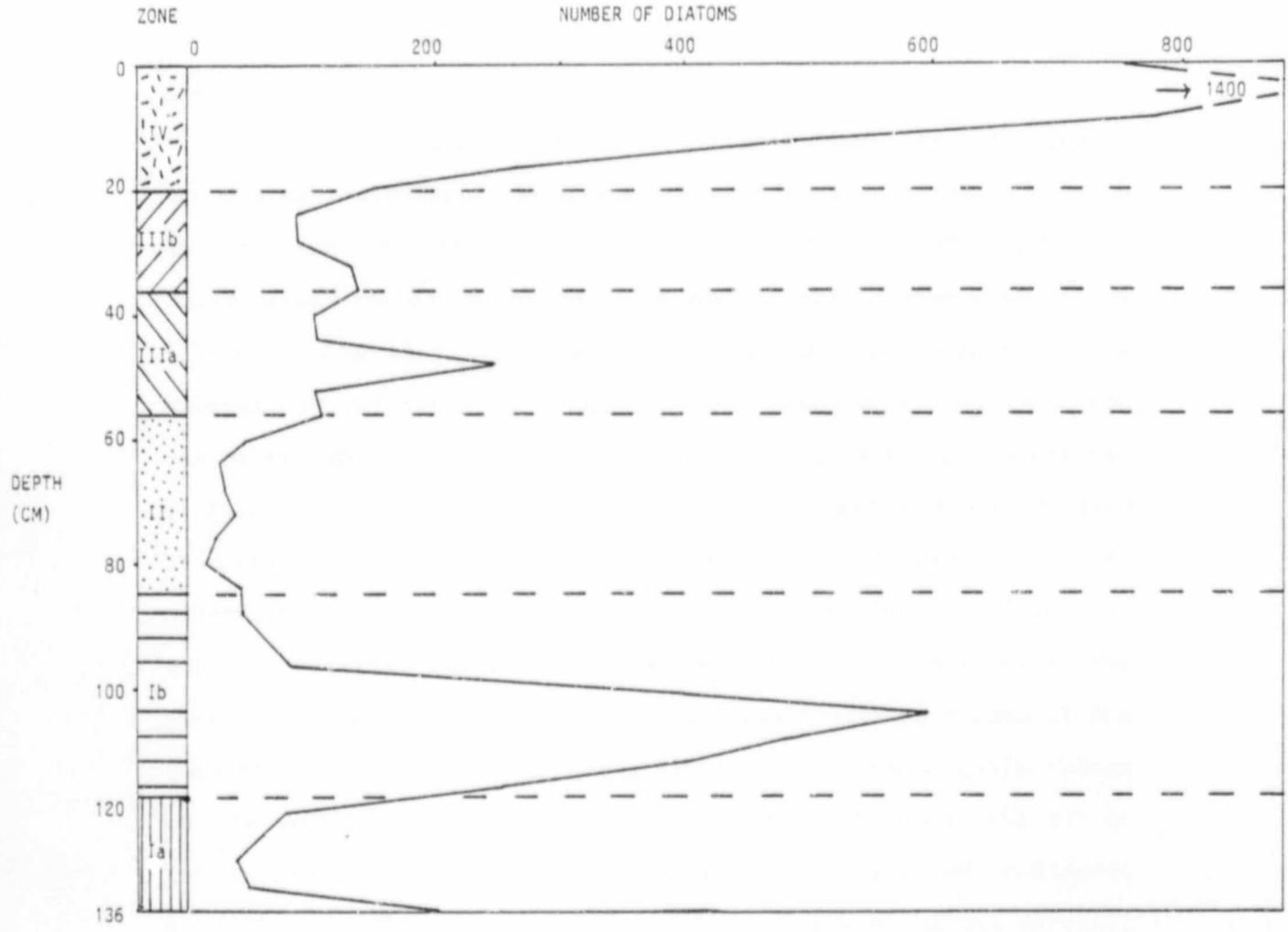


FIGURE 4.3 The distribution of the total numbers of diatoms in a core (Core I) taken from a well established peat bog.

finer detrital layer (zone II). This was accompanied by a change in the composition of the diatom assemblages from the lower one which exhibited a mixture of planktonic, benthic and epiphytic forms to the upper one in which epiphytic forms predominated and occured together with small numbers of benthic forms (Figs. 4.1 & 4.2a). No planktonic forms were found in the detrital zone. Such changes in the diatom assemblages could accompany hydroseral succession with an increase in emergent macrophytes creating light conditions unfavourable for all planktonic and most benthic diatom populations (Staub & Cohen 1979). The abrupt contact between these two zones however, as reflected in changes in peat texture as well as in the diatom assemblages, is not accounted for by gradual hydroseral infilling. It is therefore proposed that the formation of a sudd layer at a shallow depth resulted in the sudden switch in diatom taxa between zones I and II. During sudd formation a gradual "rain" of fine detrital material and diatoms from the bottom of the sudd would have occurred. The detrital zone (zone II) was therefore formed at the same time as the sudd layer (zone IIIa). Since the organic matter in the detrital zone originates from the sudd layer, the diatom assemblages would be expected to be similar, as is shown in Figures 4.1 and 4.2. The presence of lower diatom numbers in the detrital zone compared to the sudd forming zone (zone III) (Fig. 4.3) is most likely due to the fact that only a few diatoms would filter down past the dense sudd zone.

Sudd zone (zone III)

The sudd zone consisted mainly of fibrous rooting material which increased in its degree of compaction in the lower sections (zone IIIa). Since *P. nitidus* and *M junceum* plant parts predominate it is likely they played an important role in the early stages of sudd formation, during which time plant density would have been low and

colonisation by other species minimal. The peak in diatom numbers during this period (Fig. 4.3) was thus probably the result of low cover by emergent species which enabled development of the diatom flora. With the subsequent colonisation and establishment of later colonisers, total diatom numbers appear to have decreased.

Associated with this was an increase in epiphytic diatom forms relative to the other forms which was probably due to an increase in macrophyte diversity. The reason for the switch in dominance of the benthic algae from *Fragilaria* species to the diverse taxa *Navicula*, *Pinnularia*, and *Surirella* (Fig. 4.1) may have been due to a change in organic sediment type associated with *P. nitidus* and *M. junceum* to one associated with later sudd colonisers.

Surface peat Zone (zone IV)

The diverse macrophyte flora found in mature, well-established bogs (Section 3.1.3) supported the most diverse (Fig. 4.1) and abundant (Fig. 4.3) diatomaceous flora of all the zones. Between fifty and seventy percent of the diatom flora was epiphytic (Fig. 4.2a), and most species were generally indifferent to pH or else included genera which were usually found in slightly acid conditions (Fig. 4.2b).

The uppermost layer of this zone becomes exposed to the atmosphere during the periods when the water level is at its minimum. The action of seasonal alternate wetting and drying of the upper peat would lead to more complete and rapid decomposition than permanent inundation (Barlocher et. al. 1978, Valiela et. al. 1982). The large peak in diatom numbers in the surface peat zone (Fig. 4.3) is therefore probably due to continued diatom production and accumulation in the portion of the vertical sequence in which macrophyte organic matter decomposition rate is high and accretion is extremely

slow or even absent. The accumulation of diatom remains in this zone is therefore likely to continue until there is a change in the present-day water level fluctuations.

The second core taken from a different representative sample of the same community type exhibited the same patterns of peat texture and diatom stratigraphy as the first core, suggesting a similar pattern of development (Appendix B).

4.2 DISCUSSION

There is marked concordance in the changes in peat texture as well as in the diatom assemblages within each of the zones of the cores. In combination these features indicate that the vertical accumulation of peat bogs in the Maunachira river system is the result of two processes, namely organic hydroseral infilling from the sandy substratum upwards, and organic sudd formation at or close to the water surface. There is no evidence within the peat core of inorganic sedimentation, a process which is largely restricted to the main river courses in the delta (McCarthy et.al. 19186a).

The accumulation of humic acids during bog formation is generally common and contributes to decreased rates of decomposition and the accretion of organic matter (Thompson & Hamilton 1983). It is therefore not surprising that peat accumulation and development in the study area has taken place under slightly acid conditions, as indicated by the predominance of acidophilous diatom taxa throughout the vertical sequence. The presence of *Gomphonema*, *Eunotia* and

Pinnularia, species usually found in oligotrophic waters (Round 1957, Haworth 1976), during virtually all stages of bog development, also indicate little change in the nutrient-poor status of the water during this period.

Although the cores were taken from what was considered a "well developed" peat bog community, the presence of the middle detrital zone suggests that vertical peat accumulation is not yet at equilibrium with the present environmental conditions. In a 3-dimensional model of horizontal and vertical sudd development, Kratz and DeWitt (1986) have shown that the loose detrital zone decreases in size and becomes displaced by peat as the floating sudd layer gradually thickens. It is postulated that a similar sequence of development will take place in the peat bogs of the Maunachira river system. Most of the displacement by the thickening sudd mat will be in the detrital zone since vertical accumulation at the surface of the sudds is presently limited by the seasonal water level fluctuations.

The present study has indicated the potential for the use of cores in the interpretation of wetland succession, even in the absence of plant macrofossil or pollen remains due to fungal decomposition (Klein & Dupre 1980). The identification of diatom taxa to species level and the systematic dating of some of the zones within the core would provide a better indication of the sequence and the timespan of individual events in bog succession.

CHAPTER 5

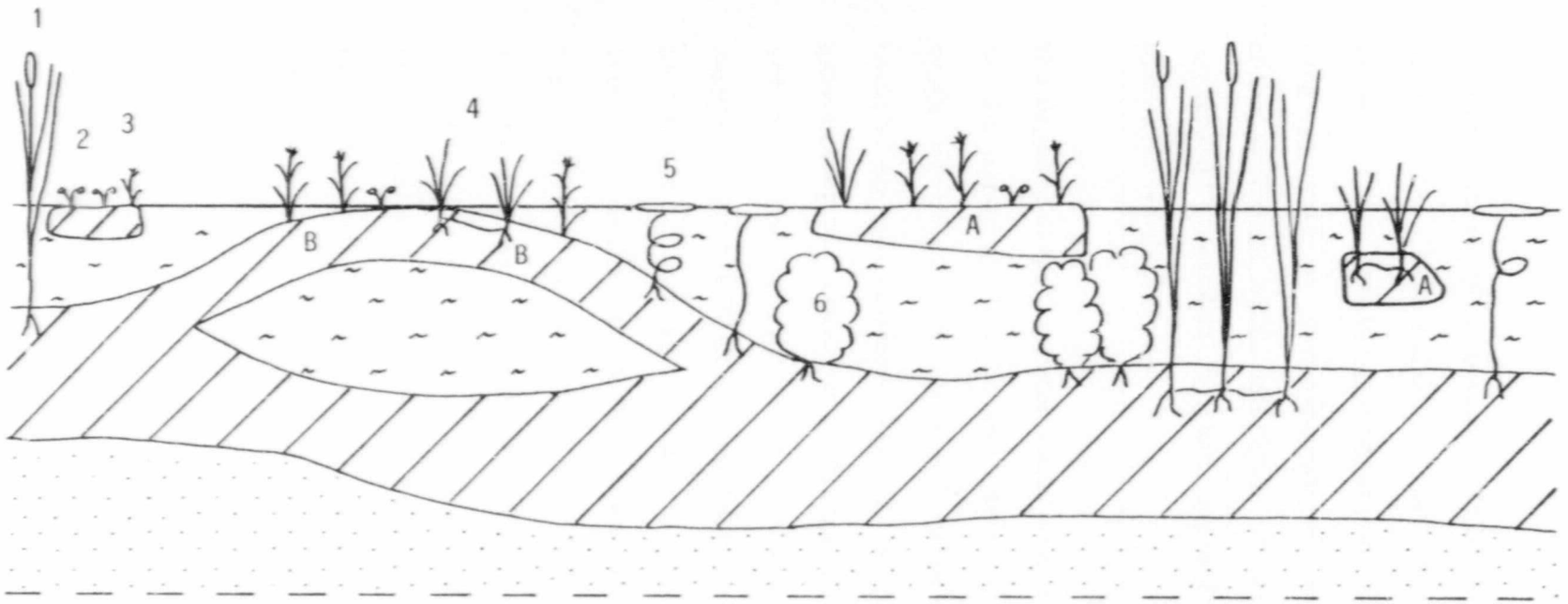
SUDD FORMATION AND DEVELOPMENT

The formation of sudds in the Maunachira river system was considered to be a crucial intermediate step in the transformation of a plant community dominated by submerged and floating-leaved species which rooted at depth, to one dominated by short emergent species which rooted at or close to the water surface. This component of the study was therefore aimed at determining the plant species associated with sudd development, environmental factors which affected their formation and aggregation, and the rates at which they encroached open water bodies previously colonised by bottom-rooted plant species.

5.1 RESULTS

5.1.1 Formation and colonisation of organic detrital sudds

Floating, mobile, organic sudds, ranging in size from $0,4m^2$ - $8,0m^2$, were formed by the detachment of sections of the submerged detrital deposits in areas dominated by the floating-leaved species *Nymphaea caerulea* and the emergent plant *Typha capensis* (Fig. 5.1). In some cases, however, the submerged detrital aggregate did not become detached to form mobile sudds, but instead rose differentially to form dome shaped structures of which the most buoyant portion (ranging from $1m^2$ - $200m^2$) became exposed at the



1 Typha capensis
2 Drosera madagascariensis
3 Fuirena stricta
4 Pycreus nitidus
5 Nymphaea caerulea
6 Websteria confervoides
A Mobile organic sudd
B Dome shaped attached sudd

WATER

DETRITUS

SAND

FIGURE 5.1 Diagrammatic representation of a cross-section of a water body illustrating the formation of both mobile and attached organic sudds.

water surface (Fig. 5.1). Similar organic detrital sudds have been recorded in the Okefenokee swamps, Georgia, USA; the mobile ones are referred to as batteries and the dome shaped ones bulges (Cypert 1961, 1972, Spackman et. al. 1976).

An examination of numerous mobile and attached organic detrital sudds in the field indicated that they were subject to similar patterns of plant species colonisation. The importance of both the seed bank as well as the addition of seeds subsequent to exposure in colonisation of sudds has been evaluated in experiments in which unexposed (treatment 1) and exposed (treatment 2) detritus were placed in seed trays.

The organic detrital sudds taken from a submerged position and placed at the water surface in seed trays contained viable *N. caerulea* seeds of which 183 seeds m^{-2} germinated within a month of being brought to the surface (Fig. 5.2a). The decreasing numbers of germinating *N. caerulea* seedlings at each subsequent sampling date and the lack of any other germinating species in this treatment suggest that the viable seed bank in the submerged detrital layer is limited to this species alone. In the second treatment where the organic detrital sudds had been exposed at the water surface for approximately three weeks prior to setting up the experiment, a greater species diversity was observed (Fig. 5.2b). A mean of 333 *Fuirena stricta* seeds m^{-2} germinated within a month of setting up the experiment and although further seeds germinated, numbers decreased steadily at each successive sampling date from May until December. In contrast, only sixteen *N. caerulea* seedlings m^{-2} were observed on the first sampling date. No further *N. caerulea* seedlings became established but during late winter/early spring (August) right through to mid-summer (December) both *Xyris capensis* and *Drosera madagascariensis* were present in low numbers (Fig.

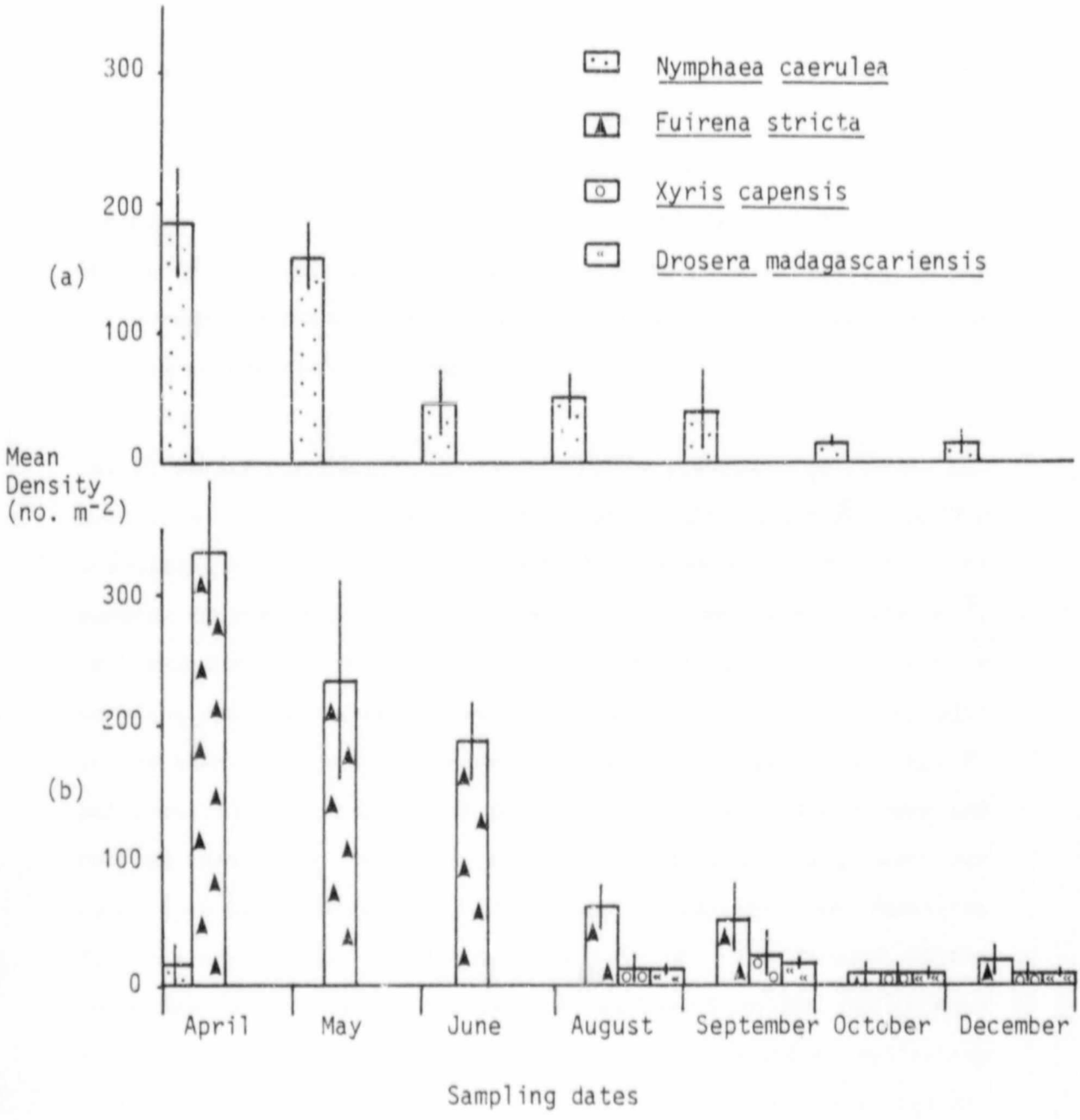


FIGURE 5.2 Mean densities of seedlings observed in the seedtrays with the organic detritus taken from (a) a submerged position (treatment 1, n=3) and (b) a floating position (treatment 2, n=3) on successive sampling days. Standard deviations are represented by the vertical bars.

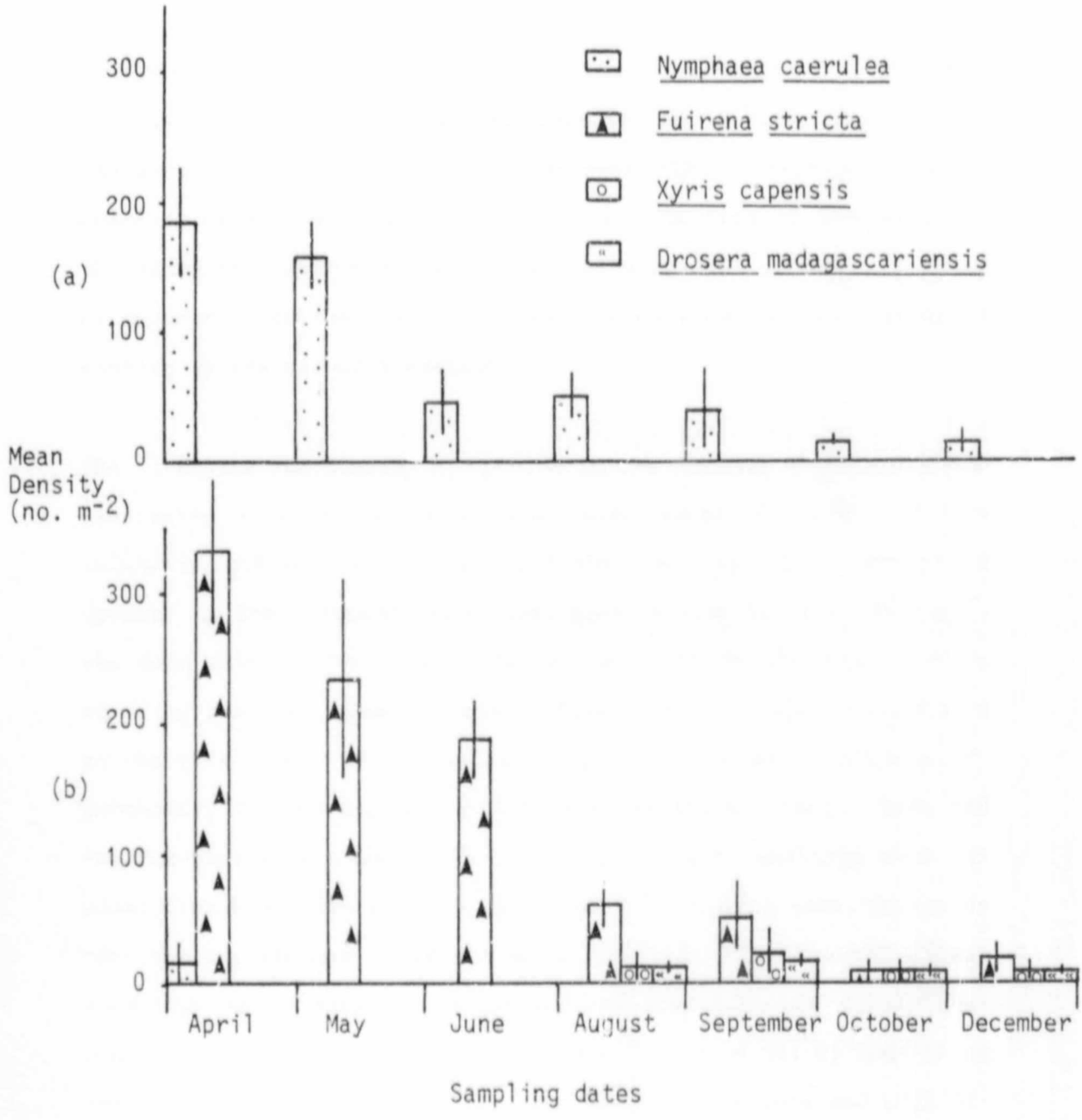


FIGURE 5.2 Mean densities of seedlings observed in the seedtrays with the organic detritus taken from (a) a submerged position (treatment 1, n=3) and (b) a floating position (treatment 2, n=3) on successive sampling days. Standard deviations are represented by the vertical bars.

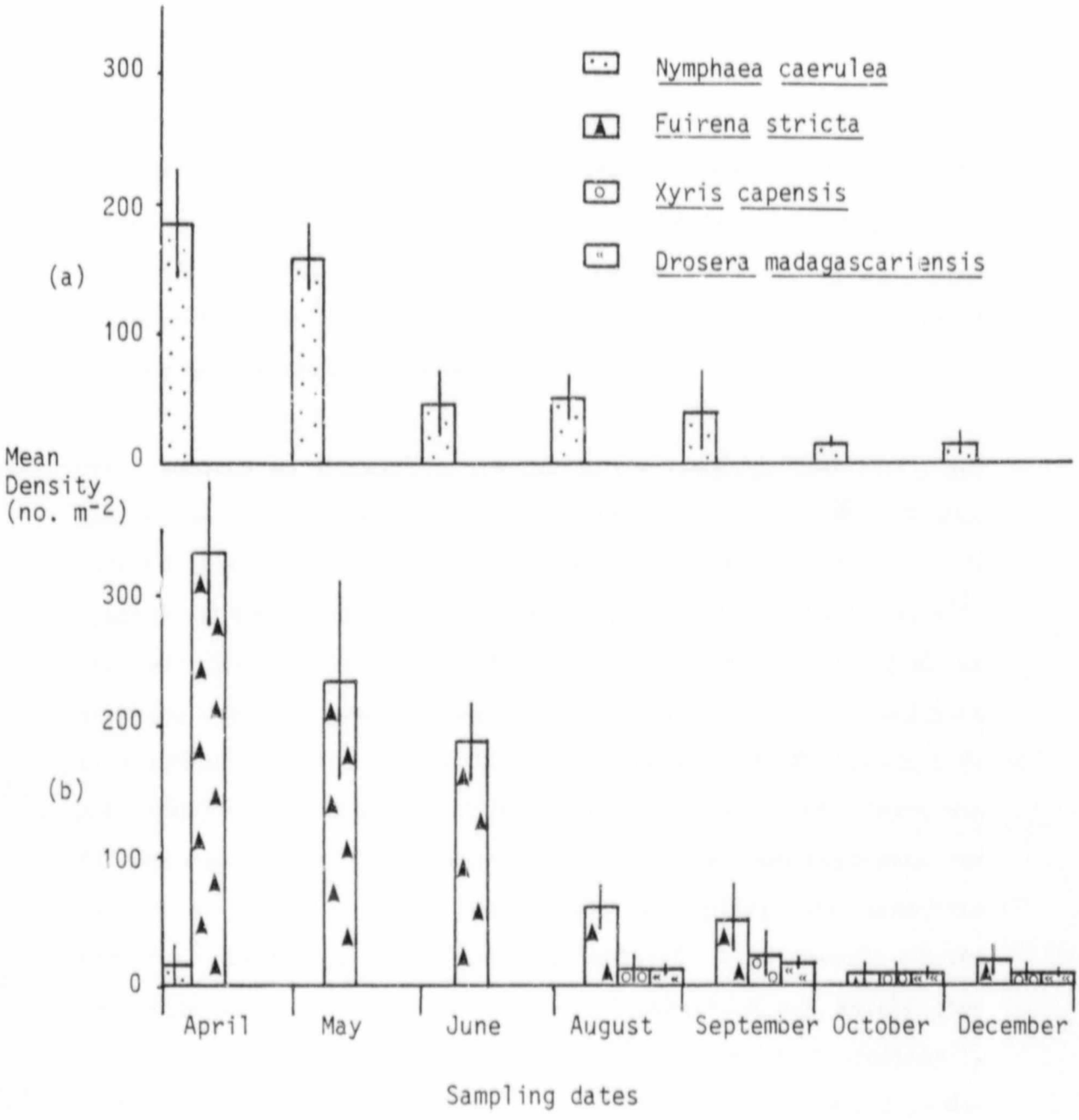


FIGURE 5.2 Mean densities of seedlings observed in the seedtrays with the organic detritus taken from (a) a submerged position (treatment 1, n=3) and (b) a floating position (treatment 2, n=3) on successive sampling days. Standard deviations are represented by the vertical bars.

5.2b). The lack of these species in the first treatment suggests that they were recruited during the time of exposure of these sudds at the water surface, and the germination of only a single *N. caerulea* seed in this treatment was probably due to the other *N. caerulea* seeds having germinated between the time of emergence of the sudds and their placement in the seed trays. In fact, a total of seven *N. caerulea* seedlings were removed from the sudds prior to setting up the second treatment.

The diversity and density of species in the seedbank experiments was contrasted with those on similar size sudds (0,20cm x 0,30cm colonising surface, n = 7) in the field. Whereas the diversity of species in the seedtrays was never greater than three species m^{-2}, the mean diversity on the sudds in the field during the year of sampling was much greater (mean = 6,88, S.D. = 2,64). In addition to the taxa found on the seedtrays species such as *P. nitidus*, *F. pubescens*, *C. pectinatus* and *Ludwigia leptocarpa* (Nutt.) Hara and *Panicum repens* were common in the field. Since seedlings were removed from the seedtrays at each successive sampling date, densities for the experiments could not be calculated. The density of the seedlings on the field sudds however remained high and fairly constant throughout the year (mean = $1250m^{-2}$, S.D. = 406,6) indicating continual seedling recruitment. The constant presence and high diversities of small seedlings on the sudds in the field, compared with the low diversity and a progressive decrease in seed germination in the seed bank experiments indicate the importance of a continual input of seeds from established plants in the surrounding areas. The detrital seedbank itself therefore plays only a minor role in the establishment of a short emergent vegetation on sudds exposed at the water surface.

5.1.2 The horizontal and vertical movement of organic detrital sudds

The role the highly mobile, floating, organic sudds play in the later successional trends is dependant upon their permanence and eventual fate. The patterns and rates of movements and the effects of disturbance on the sudds was therefore monitored over a winter and summer period.

5.1.2.1 Sudd movement in an undisturbed area

Vertical movement

A total of seventy-nine sudds were tagged on the first sampling day in May in a well protected, undisturbed water body (lediba). During the winter months (May - August) seventy-one percent of these sank and only a single new sudd rose to the surface (Fig. 5.3a). With the onset of spring (August - October) and summer (October - December) there was a decrease in the numbers of sudds which sank from twenty-four to zero percent of the total, respectively, and an increase in sudds which rose to the surface from twelve to twenty-six percent of the total, respectively (Fig. 5.3b & c). Of those that rose to the surface during both these time intervals, twenty-five percent of them had previously been tagged, the rest were "new" sudds which had formed since the first sampling occasion.

There thus appears to be a general trend of sudd sinking during the winter and rising in the summer. The reason for this trend was not established but probably was the result of changes in carbon dioxide or methane production due to increased rates of decomposition with higher summer temperatures (Wetzel 1983). The fine roots of *Nymphaea caerulea* and *Typha capensis* appear to prevent the gases from escaping, and serve as a matrix in which the fine detrital material is supported. The trapped gases result in the formation of buoyant floating sudds. In the winter months gas production from decompos-

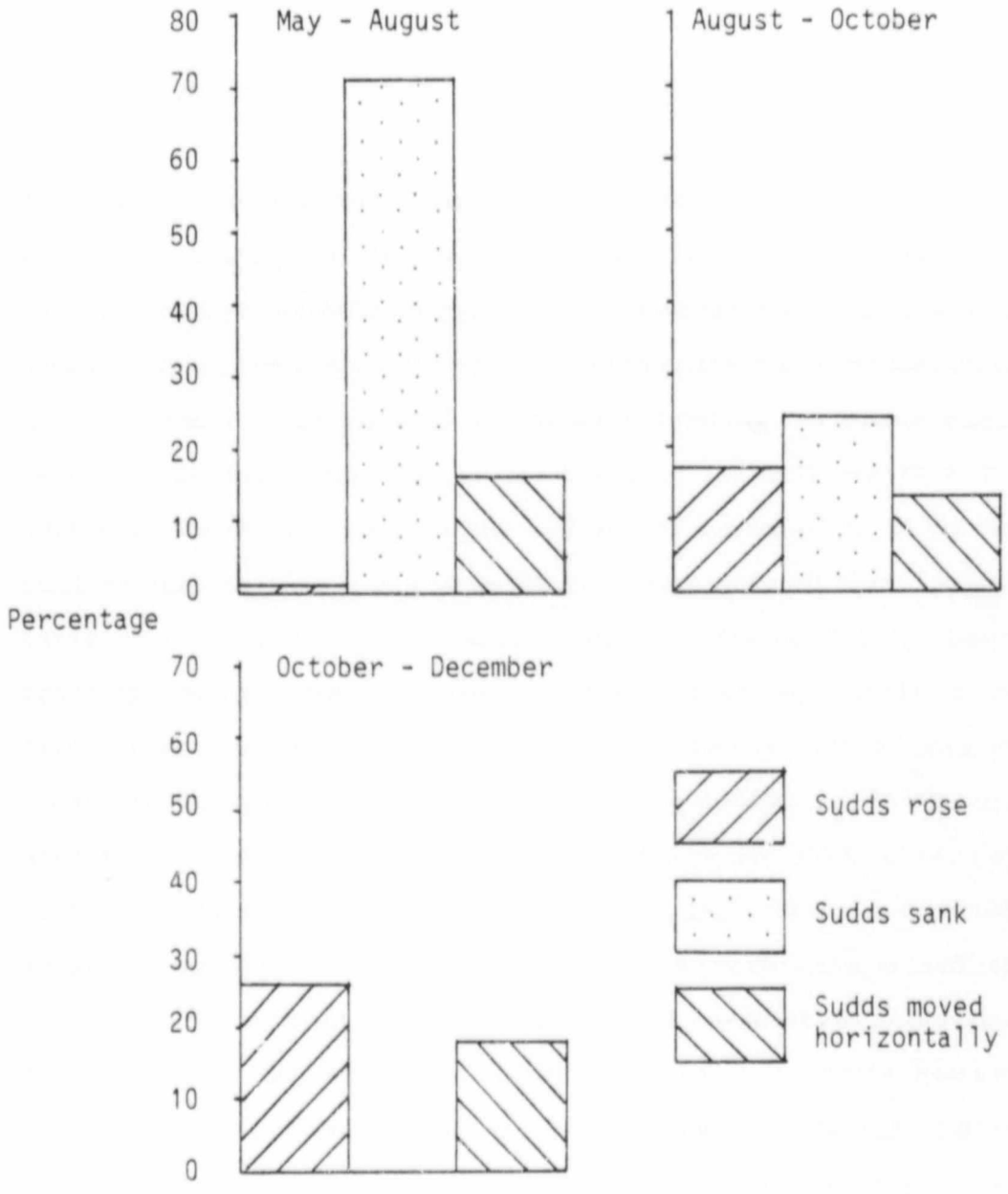


FIGURE 5.3 Percentage of sudds which rose, sank and moved horizontally in the undisturbed site during three time intervals (a) May - August, (b) August - October and (c) October - December.

ition decreases, few new sudds are formed, and many of the old sudds sink as gas is slowly lost to the atmosphere.

Horizontal movement

Although the lediba was considered "undisturbed", all the sudds moved horizontally in similar directions, with the actual direction shifting between seasons, suggesting a disturbance common to all the sudds. During the winter and spring period sudds moved predominately in a south and south westerly direction and during the summer months mainly north and south (Fig. 5.4a, b & c). The only possible disturbance factor resulting in the horizontal movement of sudds was wind because neither large animals nor boats entered this isolated water body. Since the wind directions reported by Tinley (north easterly during summer and south easterly in winter, 1973) do not directly account for the patterns of sudd movement during these periods, it is suggested that the fringing vegetation and lediba orientation played an important role in influencing wind directions within the lediba itself. The tall *Miscanthus junceum* and shrubby *Ficus verruculosa* fringing the lediba must have interrupted the easterly wind movement sufficiently to cause movement of sudds along the length of the lediba which had a northerly to south easterly orientation (Fig. 5.4d). The most rapid changes in the lediba shape as a result of sudds banking up against the lediba edge, were therefore at the northern and south and south-eastern ends. Whereas short emergent species became established at these encroaching areas, *N. caerulea* and *T. capensis* continued to dominate in the rest of the deep water lediba.

5.1.2.2 Sudd movement in an area subject to disturbance

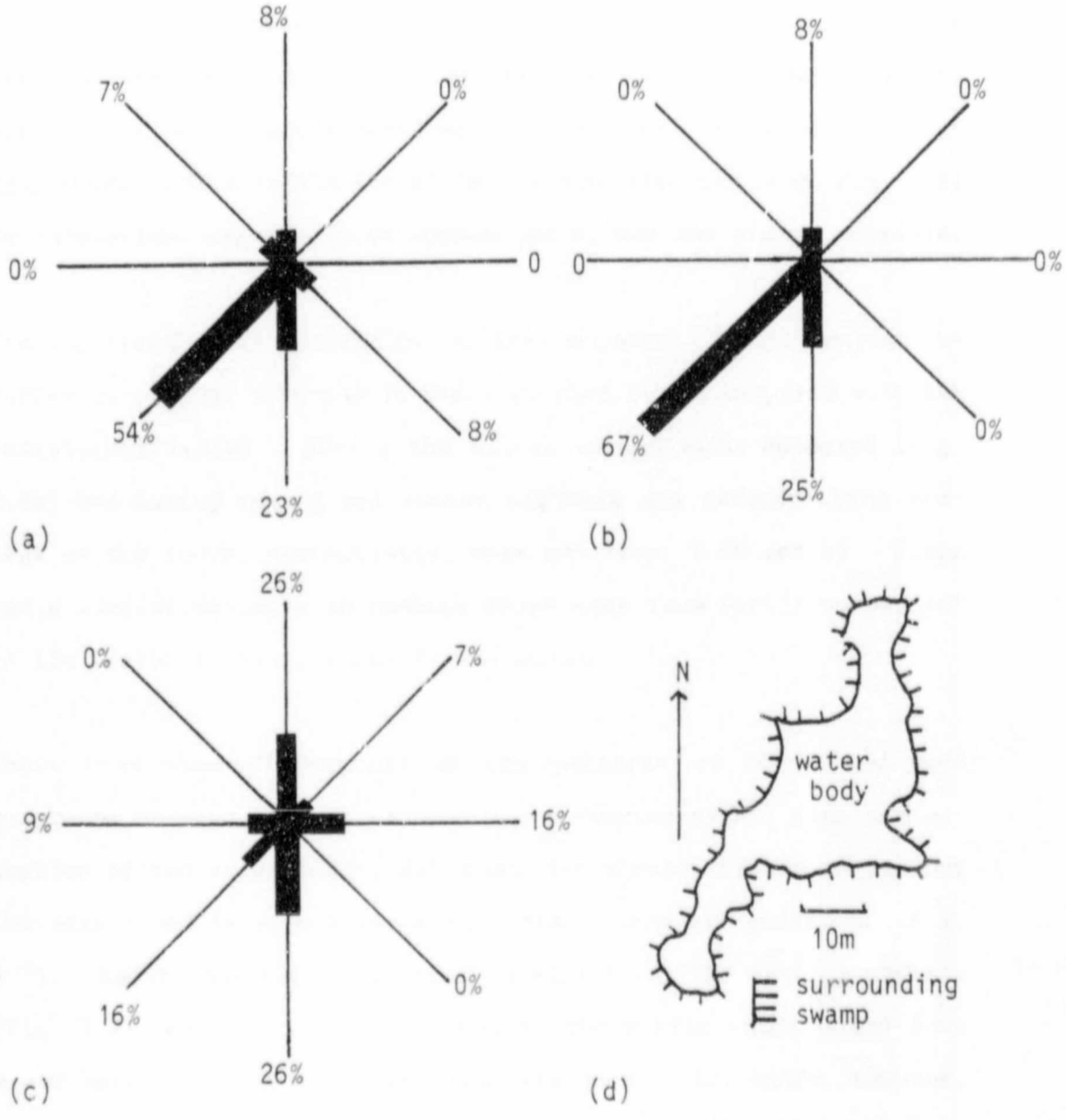


FIGURE 5.4 Movement of sudds in the undisturbed site during (a) winter, (b) spring and (c) summer. The length of bar indicates percentage of sudds which moved in a particular direction, and width indicates the distance moved. (d) indicates the orientation of the water body.

Most of the lediba which constituted the disturbed site consisted of open water colonised by the submerged plant *Najas pectinata*. At the northern end however, dominated by the floating-leaved *N. caerulea*, floating sudds occurred. There were limitations to tagging sudds in this lediba (total length approximately 340m, Fig. 5.5) as relocation, especially of sunken sudds, was not always possible.

Similar trends with respect to vertical movement of sudds during the different seasons occurred in the disturbed lediba compared with the undisturbed lediba. During the winter no new sudds appeared (Fig. 5.6a) but during spring and summer eighteen and seventy-three percent of the sudds, respectively, were new (Fig. 5.6b and c). There was a similar decrease in numbers which sank from forty-two percent in the winter to ten percent in the summer.

There were some differences in the patterns of horizontal sudd movements between the undisturbed and disturbed site. With the exception of two large sudds, all sudds not already banked up against the edge moved large distances from their original positions (Fig. 5.7). Had hippopotami and boats passing along the central pathway (Fig. 5.5) been the major disturbance, the mobile sudds would have moved both east and west away from the path. All sudds, however, moved onto the western side of the path. Their movement was mainly in a westerly direction during the winter months and a south-westerly direction in the spring and summer, suggesting that wind was again the overriding driving force of movement. The sudds eventually accumulated at different depths (i.e. not all are floating at the surface) on the leeward side of the lediba, leading to the formation of a heterogeneous fringe community (Plate 5.1).

5.1.2.3 Rate of organic sudd encroachment

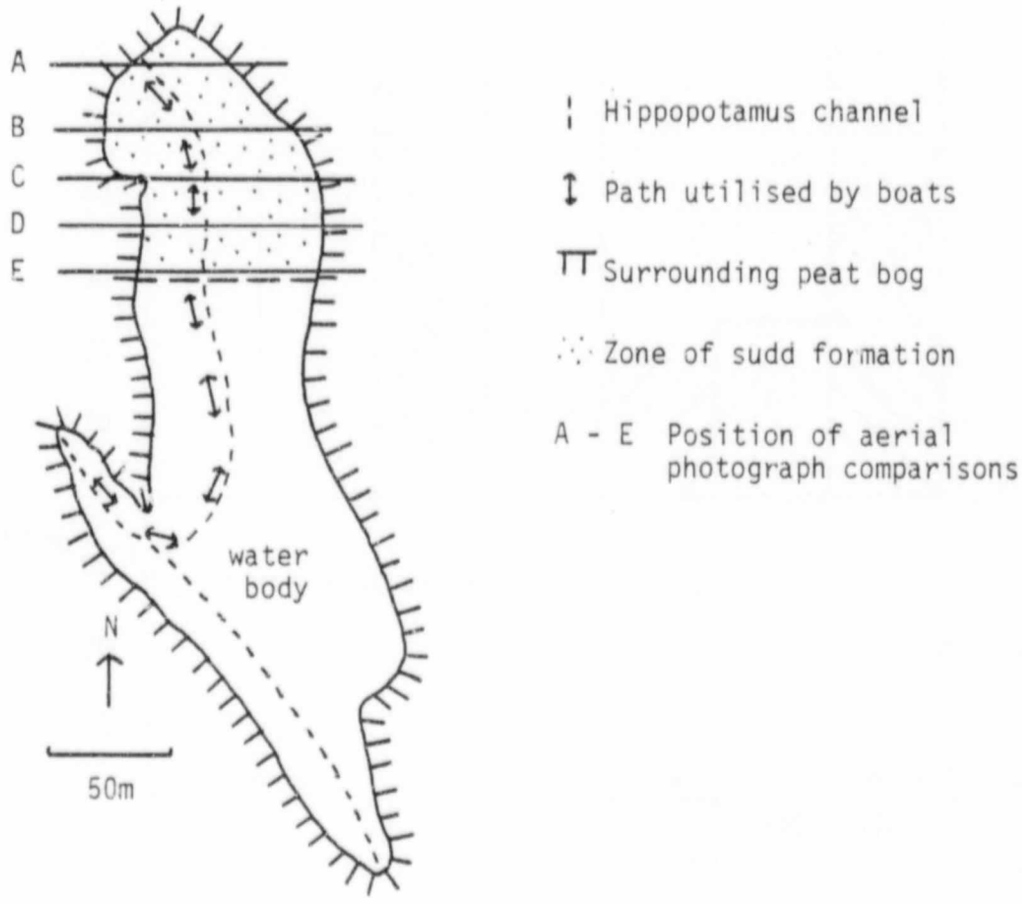


FIGURE 5.5 Diagrammatic representation of the disturbed site indicating the zone of sudd formation and the positions at which sudd encroachment was measured.

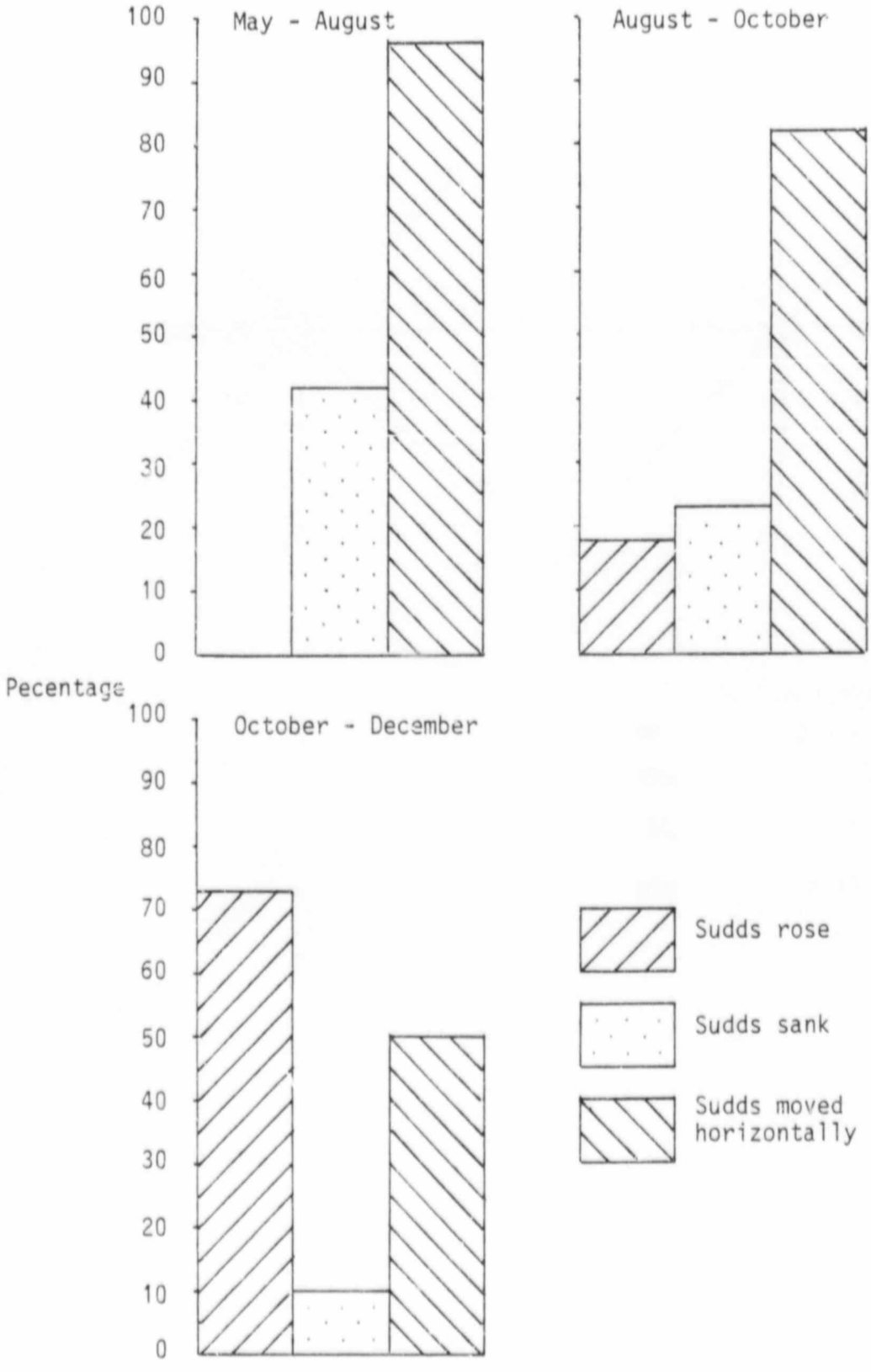


FIGURE 5.6 Percentage of sudds which rose, sank and moved horizontally in the disturbed site during three time intervals (a) May - August, (b) August - October and (c) October - December.

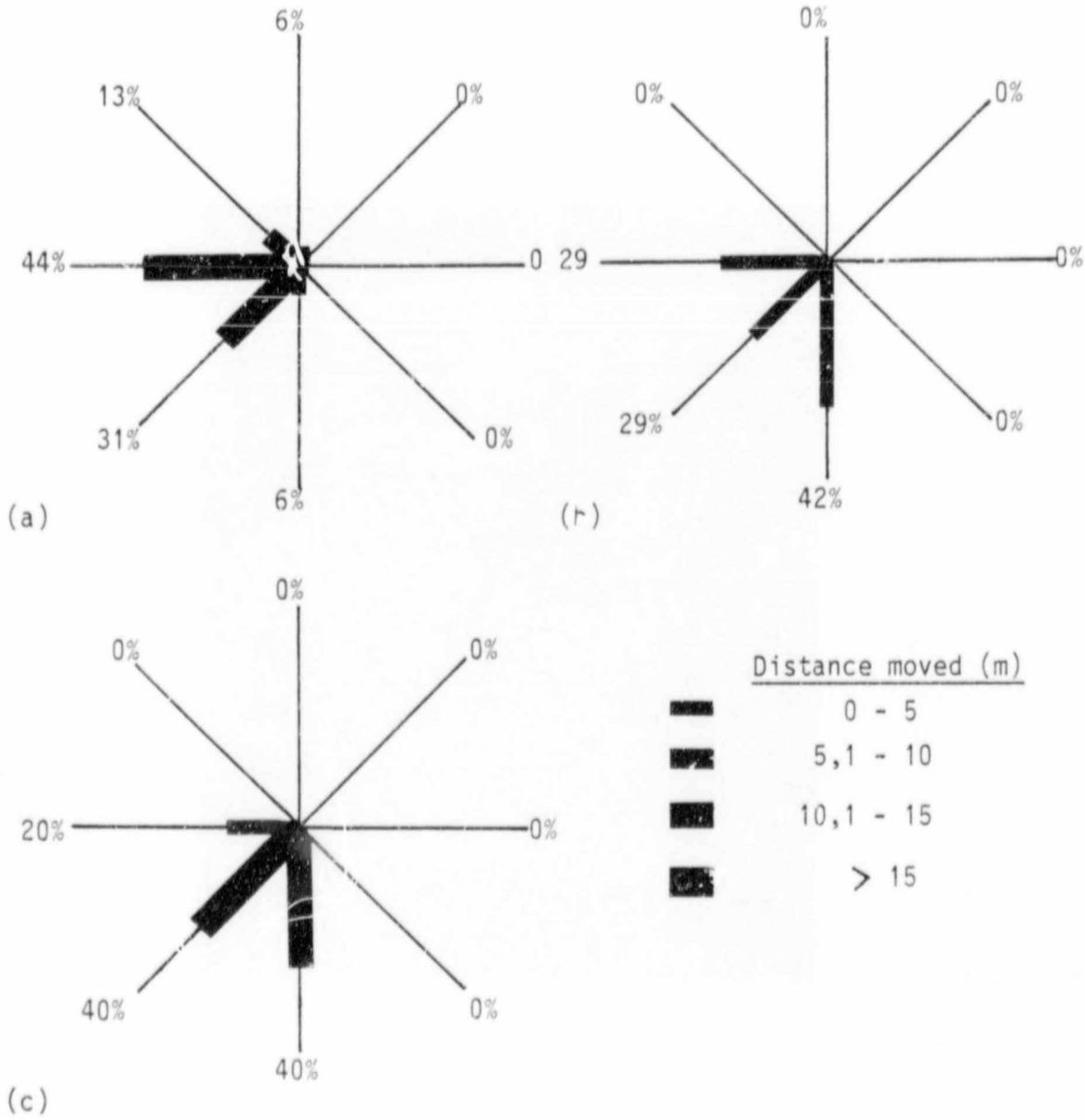


FIGURE 5.7 Movement of sudds in the disturbed site during (a) winter, (b) spring and (c) summer. The length of bar indicates the percentage of sudds which moved in a particular direction, and the width indicates the distance moved.

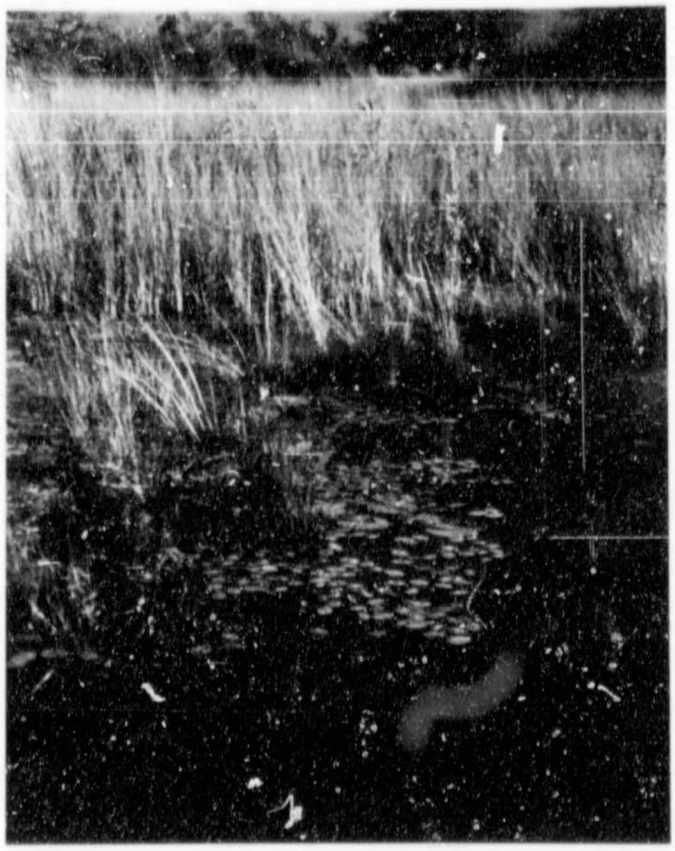


PLATE 5.1 A heterogeneous fringe community formed as a result of banking up of sudds on the leeward edge of the water body

PLATE 5.1 A heterogeneous fringe community formed as a result of banking up of sudds on the leeward edge of the water body

In order to determine the rate at which the fringe was encroaching across the lediba as a result of sudds banking up against the lediba edge, comparisons of 1969 and 1983 aerial photographs at five different localities were made (Fig. 5.5). Whilst no measurable change had occurred on the windward edge of the lediba the leeward edge had encroached an average distance of 0,71 m (range = 0,23 - 2,47) during the fourteen year period (0,05m a^{-1}). This wide range in measured rates of encroachment at different sites in a single water body illustrates the role the sudds play in altering the shape of the water body. Although no rates of mobile organic sudd encroachment were found in the literature, an average rate of 0,05m a^{-1} is slow compared with some of the rates of encroachment of a water body by the vegetative growth of sudd forming plants as shown in the following section.

5.1.3 *Pycreus nitidus* floating sudds

Pycreus nitidus is an important sudd forming species within the study area. It is present within stable fringe communities and on floating organic detrital sudds from which it colonises open water areas by stoloniferous growth (Fig. 5.8). It is a small, robust, perennial sedge with unbranched roots and leafy shoots which are connected by branching stolons (Haines & Lye 1983; Plate 5.2). The leaves protrude above the surface of the water and vary in length from 15cm - 60cm depending on the water depth. Colonisation of open waters by *P. nitidus* was examined in this study with respect to those conditions relating to depth which enable its expansion by stoloniferous growth. Field observations indicated that although the stolons of *P. nitidus* have positive buoyancy, they tend to sink when the leafy shoots and inflorescences become large. The extent to which the stolons and their emergent shoots are supported therefore appears to influence the rates at which the species colonises

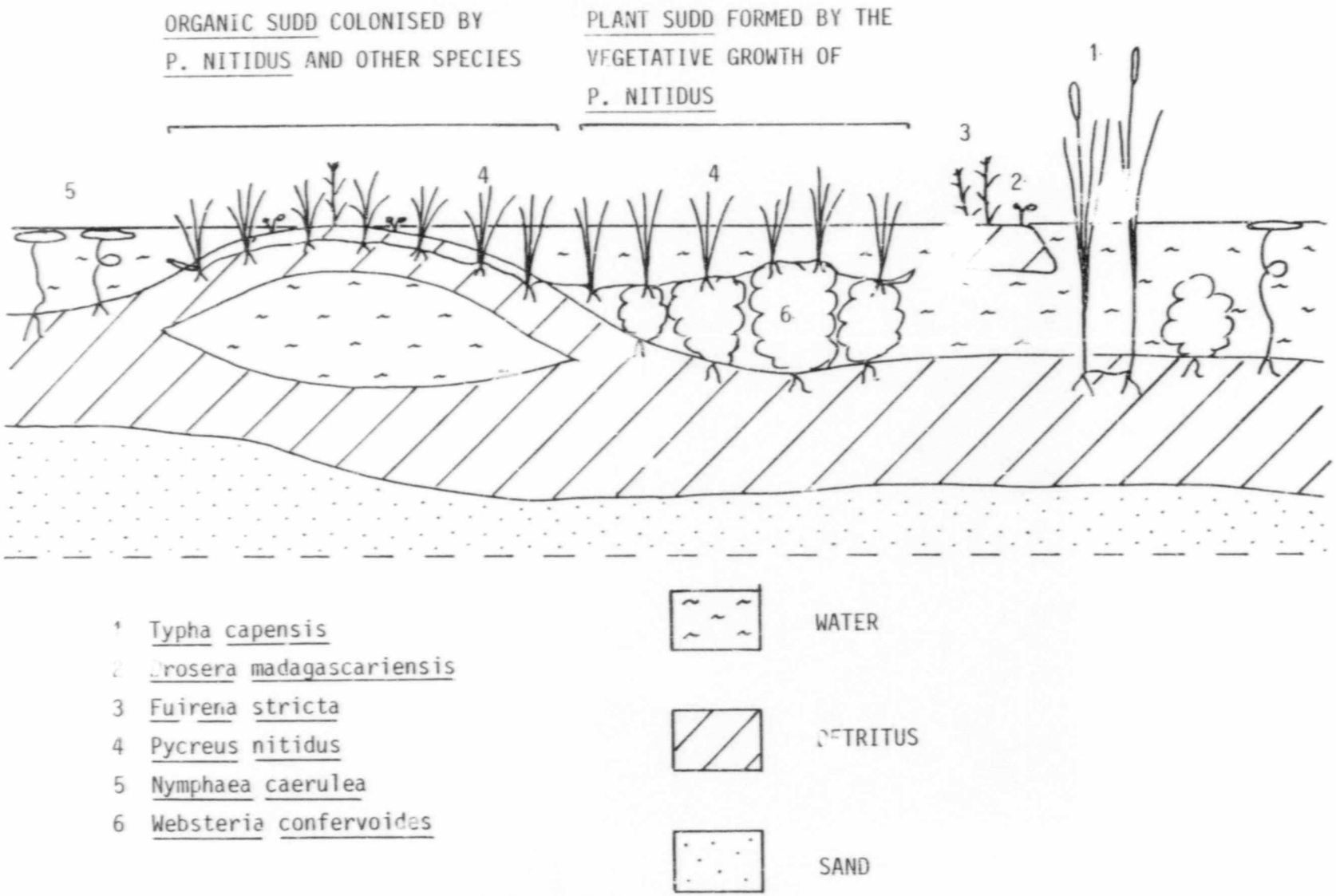


FIGURE 5.8 Diagrammatic representation of a cross-section of a water body illustrating the vegetative spread of P. nitidus which initiates the formation of a sudd layer beyond the influence of an organic detrital sudd.

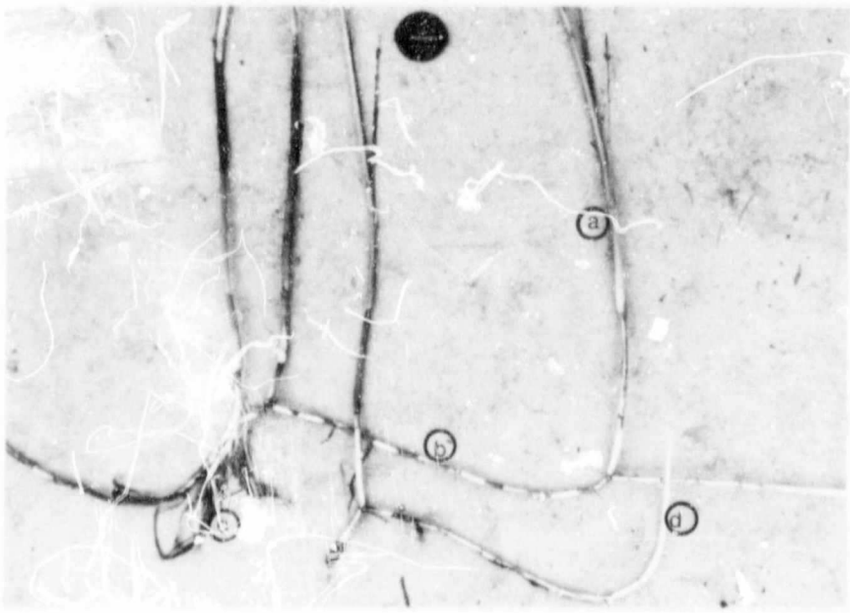


PLATE 5.2 Pycreus nitidus plant: (a) shoot with leaves, (b) extending stolon, (c) roots and (d) young shoot forming.

open water bodies. It was proposed that support is offered by either (i) the presence of an organic detrital layer or (ii) the growth of extensive beds of the submerged species *Websteria confervoides* at or close to the water surface, or by both.

To investigate each of these relationships in turn, rates of extension of *P. nitidus* were measured in areas where the submerged sedge *Websteria confervoides* was absent and the benthic detrital aggregate was at a depth of greater than one metre (i.e. no support); areas with no submerged plant cover but with the detrital aggregate at a depth of less than 0,6m; and areas with a high density of *W. confervoides* which was also at a depth of less than 0,6m.

In the absence of any support, *P. nitidus* showed only a slight extension growth of 0,02 m a^{-1} (S.D. = 0.007; Table 5.1). In contrast, the rates of colonisation in areas with organic detrital support were 1,10 m a^{-1} (S.D. = 1.03) and 1,46 m a^{-1} (S.D. = 1,27) in areas where *W. confervoides* was also abundant (Table 5.1). The detrital aggregate, although often only loosely consolidated, supported *P. nitidus* stolons sufficiently to enable their extension - as did the submerged sedge *W. confervoides*. These results therefore suggest that the colonisation of open water bodies by *P. nitidus* is dependant on the physical support of its stolons by submerged plant species or detritus at a shallow depth and is much more rapid than organic sudd encroachment.

The relationship between depth and *P. nitidus* growth was examined further by combining the percentage cover data of *P. nitidus* from a transect set up across an established, heterogeneous virtually monospecific, vegetative sudd with the data from the original vegetation survey (n=32) where *P. nitidus* occurred in association with many other species (Fig. 5.9). There was a peak in percentage cover

TABLE 5.1 Mean rates of P. nitidus stolon extension with (1) plant support, (2) detrital support and (3) no support. The number of replicate shoots for each treatment is 80.

TREATMENT	STOLON EXTENSION RATE (M ANNUM^{-1})	STANDARD DEVIATION
HIGH W. CONFERVOIDES COVER (>90% cover, < 0,60m deep)	1,46	1,27
SHALLOW DETRITAL LAYER (<0,60m deep)	1,10	1,03
NO DETRITAL OR PLANT SUPPORT	0,02	0,007

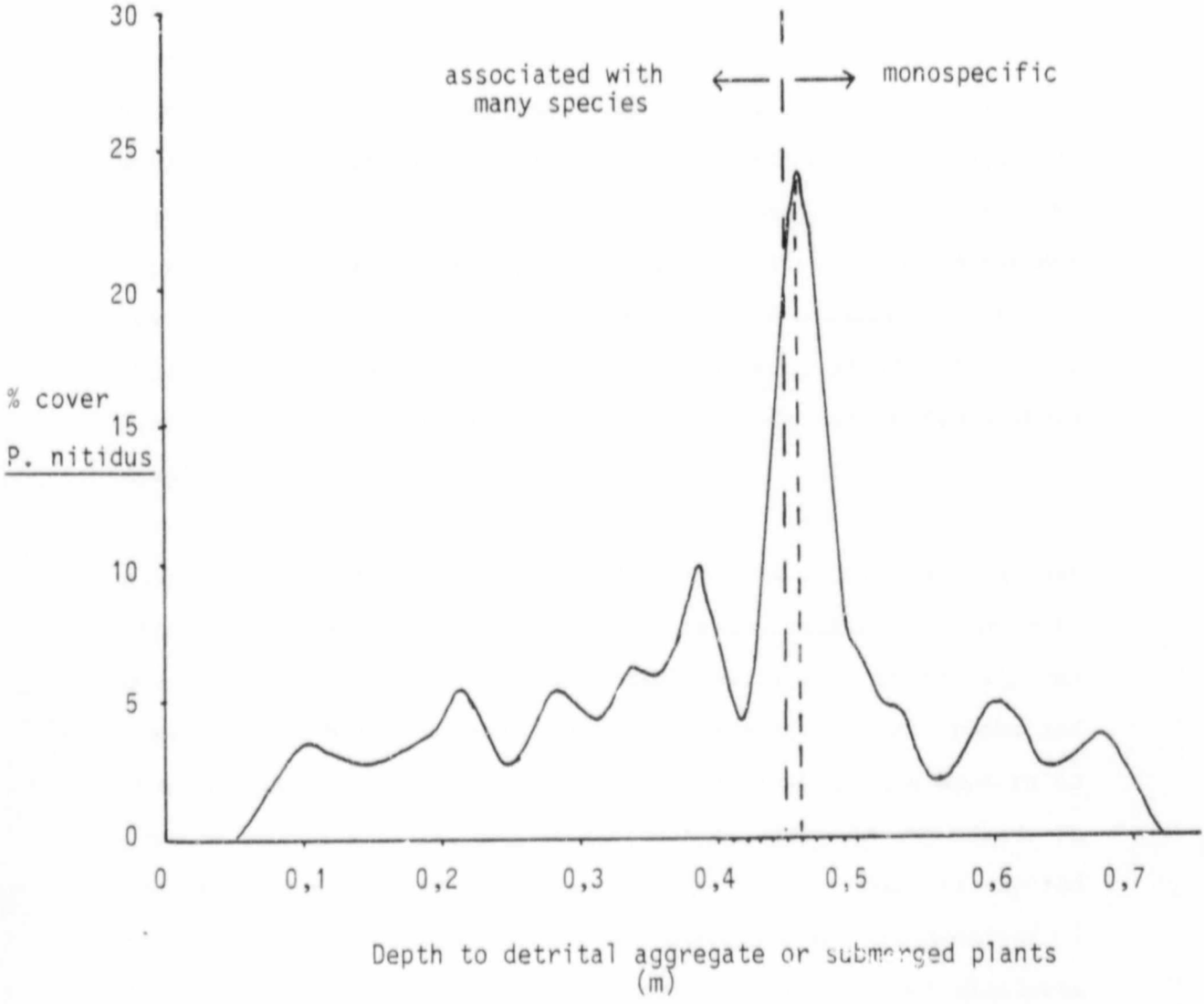


FIGURE 5.9 Relationship between percentage cover of P. nitidus and depth to the supporting layer consisting of either detrital aggregate or submerged plant growth.

at 0,46m (twenty-four percent) and percentage cover decreased as depth became both shallower and deeper (zero percent at 0,05m and 0,72m). Maximum percentage cover corresponds closely to the division between the monospecific stands of *P. nitidus* and those in which it occurs with other species (Fig. 5.9). Since *P. nitidus* occurs in monospecific stands between depths of 0,70 and 0,45m. it is suggested that the formation of *P. nitidus* sudds occurs in areas where the depth to the detrital aggregate is shallower than 0,70m and maximum cover is achieved where the water depth is approximately 0,45m. At shallower water depths, colonisation by other species appears to lead to reduced cover by *P. nitidus*, possibly due to competitive displacement.

A prerequisite to colonisation by those species which occur together with *P. nitidus* at depths shallower than approximately 0,45m however, is the development of a suitable surface in which they can germinate and become rooted. The mat formed by stolons, roots and dead undecomposed aerial plant parts of this species appears to provide such a surface, the development of which is dependant on stolon abundance, shoot densities and the turnover times of exposed plant parts. The stolon and shoot densities, and the turnover of aerial portions appears to be sufficiently high at depths shallower than 0,45m and therefore represents a critical depth below which mat development is inadequate to allow colonisation by other species.

The distribution of the secondary colonisers (mainly *C. pectinatus*, *M. junceum*, *F. stricta*, *F. pubescens*, *Drosera madagascariensis*, *P. repens* and *Ficus verruculosa*) on the sudds was extremely patchy as a result of opportunistic colonisation or limited seed dispersal. A gradual settling of the floating sudd was observed as secondary colonisers, usually less buoyant than the sudd formers themselves (Lieffers 1984), became established and peat

formed and accumulated at the surface. Complete sinking did not occur however, probably due to the trapping of gases within the upper sudd layer (Sculthorpe 1967, Lieffers 1984).

5.1.4 Rate of successional change in the Maunachira river system

The dating of peat cores, not done in this study due to lack of time and funds, would have provided an indication of the rates of change in plant communities during bog development. Comparisons of aerial photographs taken in 1939, 1969 and 1983 indicate little or no change in vegetation in areas dominated by submerged, floating-leaved and emergent plants (i.e. mainly open water areas) has occurred during the 44 year period. In contrast it has been shown in this chapter that it is possible to measure rates of encroachment of organic sudds over a fourteen year period (between 1969 and 1983), and even shorter term changes during early sudd formation can be observed within a single year (Section 5.1.3). The hydroseral phase of succession is therefore relatively slow in comparison with the sudd initiated phase.

The short life span of some of the river systems in the delta, however, indicates that these successional changes can take place within a comparatively short space of time. Since the Nqoga river consisted of shallow pools and floodplain areas during the early part of last century (Stigand 1923), many of the successional developments, in particular the vertical accumualtion of peat, have taken place within a timespan of less than 200 years. This is comparable to rates of change in tropical and subtropical wetlands where floating sudd formation is common and primary productivity is high (Junk 1983), and is considerably quicker than most successional changes taking place in northern temperate regions where primary

production is generally lower, and vertical peat accumulation therefore more gradual (Tallis 1983).

5.2 DISCUSSION

5.2.1 Organic detrital sudds

Organic sudd formation, especially that of the smaller sudds (<2,0 m^2) has been shown to be a dynamic process. The sudds rise and sink seasonally, and move horizontally eventually banking up on the leeward edge of the water body. Seed bank studies are frequently used as a predictive tool for short term successional trends in wetlands on exposed organic substrata, such as is provided by the sudds (van der Valk & Davis 1978, Pederson 1981, van der Valk 1982). Successional changes in an area where most propagules are dispersed to the site however, are generally stochastic and not amenable to predictive models (van der Valk 1982). Since many of the sudds in the Maunachira river system remain at the water surface for long periods and there is a continual input of propagules from the surrounding vegetation, neither the timing of sudd rising nor a large seed bank appear to be crucial for the establishment of a new community. Prediction on successional trends from seedbank studies in the study area would thus be limited.

Similar to observations made by McCabe (1984) and Mitchell (1985), most sudds ultimately bank up on the leeward edge of the water body, the sudd colonisers thus forming part of the fringe vegetation. As reported by Lieffers (1984), the individual sudds at the edge become consolidated into a single unit by the colonisation, growth and

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spread of rhizomatous and stoloniferous species. Since the rate of sudd encroachment across the water body is slow (0,05 m a^{-1}) and the organic sudd forming areas occupy only a small proportion (<1%) of the total Maunachira river system, it would seem that the sudds play a minor role in the successional sequences of the area as a whole. They are however locally important in providing a surface for the germination and establishment of species which would otherwise not become established. Of particular interest is the establishment of the sudd forming plant *P. nitidus* which is dominant in many plant communities in the Maunachira river system.

5.2.2 Sudds initiated by the growth of *Pycreus nitidus*

As in many documented sequences of floating plant sudd formation (Conway 1949, Dansereau & Sedagas-Vianna 1952, Swan & Gill 1970, Junk 1983, Lieffers 1984) field observations indicated that *P. nitidus* requires an initial colonising site, in the form of stationary or mobile organic sudds, prior to stolon extension. In the initial stages of vegetative sudd formation, it has been reported that the buoyant nature of sudd forming plants enables them to encroach across and thereby colonise open water bodies (Junk 1970, Swan & Gill 1970, Lieffers 1984, Kratz & DeWitt 1986). Strictly speaking *P. nitidus* is not a true sudd forming plant since it is insufficiently buoyant to colonise an area without some form of physical support; benthic detrital infilling and submerged plant growth has to reach a depth of at least 0,70m prior to the initiation of *P. nitidus* stolon extension. The detrital layer below the water surface supporting *P. nitidus* vegetative propagation is insufficiently consolidated to provide a rooting medium for the growth and establishment of non-sudd forming, short emergent species. In this situation *P. nitidus* performs the same function as other sudd forming species in that it

ultimately provides a surface on which other species can become established (Swan & Gill 1970, Tallis 1983, Lieffers 1984).

At an average rate of sudd spread of 1,25m a^{-1}, originating from the banks and many different organic sudd loci, an area rapidly becomes colonised by *P. nitidus*. Unfortunately rates of sudd build-up or maturation could not be determined within the timespan of the study. However, similar to observations made by Swan & Gill (1970), Henjy (1971) and Lieffers (1984), the establishment of secondary colonisers seems dependant upon the initial establishment of a loose organic matrix derived mainly from dead shoots which become trapped by the underlying stolons.

5.2.3 Implications of sudd formation in the successional sequence

Organic sudd deposits which develop from a submerged benthic layer can form regardless of the water depth, provided the roots of the aquatic macrophytes provide sufficient binding of the detrital material. Two species, *T. capensis* and *N. caerulea*, appear to be amongst the only species in the study area which perform this function. In the northern temperate regions several species of *Nymphaea* have been shown to play a similar role (Cypert 1972, Spackman et. al. 1976). In contrast to mobile organic sudds, the sudds formed by the vegetative growth of *P. nitidus* in the Maunachira river system require some form of support at a depth of less than 0,70m for initial invasion of open water areas.

Although the two different types of sudds examined in this study have different origins, both have a similar functional role in the successional sequence. First, they provide a colonising surface, in areas occupied by deep-rooted plants, on which short emergent species can become established, thereby increasing the diversity of

the system. Second, they result in a reduction in areas of open water. Third, the short emergent secondary colonisers are more refractile than the deep water vegetation, which results in increased rates of vertical accumulation (Cypert 1972). Finally, sudd formation results in the bottom sediment acting as nutrient sinks since there is a space separation of the root zone from the bottom deposits and nutrients are removed from vegetative cycling (Howard-Williams & Gaudet 1985).

By enabling the rapid transformation of submerged, floating-leaved and bottom rooted, tall emergent communities to ones dominated by short, shallow emergent communities, sudd development represents a "jump" in the classical hydroseral successional sequence. The accumulation of reedswamp detritus or sediment up to the mean water level characteristic of hydroseral pathways (Walker 1970) is therefore circumvented in the case of communities which originate as sudds.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

6.1 A HYPOTHESIS FOR BOG DEVELOPMENT IN THE MAUNACHIRA RIVER SYSTEM

The present day sandy substratum which occurs beneath all the plant communities of the Maunachira river system has been assumed in the present study to be the initial colonising surface on which aquatic macrophytes became established upon inundation of the area. Based on the evidence from phytosociological studies and studies on peat stratigraphy, bog development has been divided into two distinct phases: (i) A period of gradual hydroseral infilling in which species compositions are determined by water depths alone, (ii) A phase in which sudd formation occurs by one or a combination of processes in which the benthic detrital aggregate floats to the water surface, or sudd formation is initiated by growth of the stoloniferous species *Pycreus nitidus*.

6.1.1 Succession as a result of hydroseral infilling

The submerged species *Najas pectinata* and *Websteria confervoides* typically occur in the deepest areas of water bodies within the study area, and therefore represent the plant communities which become colonised in the initial stages of the hydroseral successional pathway (Fig. 6.1a). Since there is no evidence in the peat cores

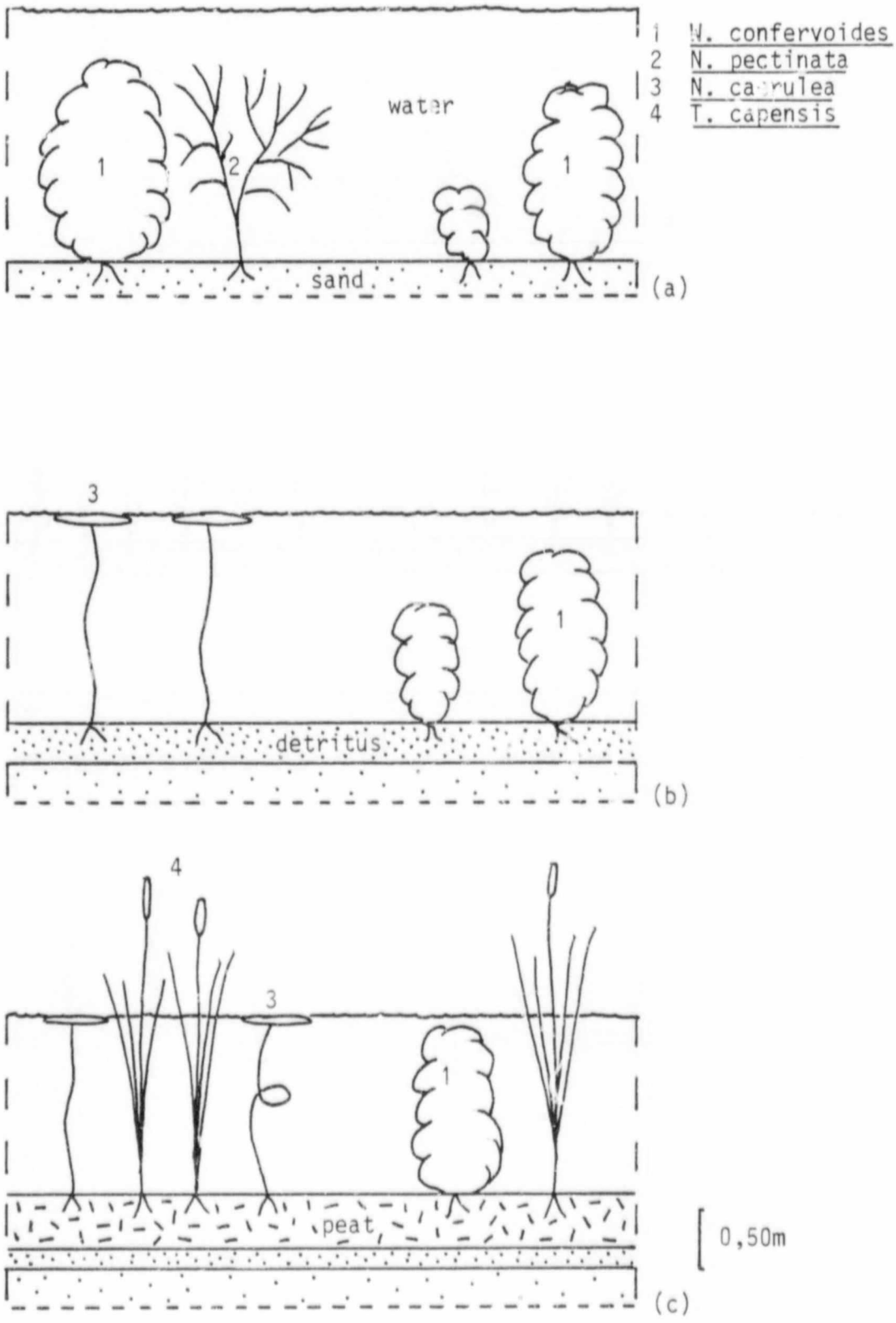

FIGURE 6.1 Summary of the hypothesis for wetland plant succession in the Maunachira river system: (a) deep water, submerged community, (b) floating-leaved community, (c) floating-leaved and emergent community, (d) organic and plant sudd formation, (e) consolidation of sudd layers and (f) diverse, short emergent community exhibiting vertical peat accumulation.