

Formation, colonization and fate of floating sudds in the Maunachira river system of the Okavango Delta, Botswana

K. Ellery*, W.N. Ellery, K.H. Rogers and B.H. Walker**

Botany Department, University of the Witwatersrand, P.O. Wits, 2050, Johannesburg (South Africa)

(Accepted for publication 26 April 1990)

ABSTRACT

Ellery, K., Ellery, W.N., Rogers, K.H. and Walker, B.H., 1990. Formation, colonization and fate of floating sudds in the Maunachira river system of the Okavango Delta, Botswana. *Aquat. Bot.*, 38: 315–329.

Two types of sudds, organic and plant sudds, form in the back-swamp communities of the Maunachira river system in the Okavango Delta. Floating organic sudds, which form as a result of gas production in the benthic detrital aggregate, provide an exposed surface for plant colonization. The sequence of establishment of plants is determined largely by the input of propagules from the surrounding communities after exposure. These sudds are extremely mobile and, as a result of wind action, bank up on the leeward side of water bodies. Rates of encroachment across open water are variable and relatively slow ($0.02\text{--}0.17\text{ m year}^{-1}$). A more rapid rate of encroachment (1.46 m year^{-1}) is achieved in plant sudd formation by the vegetative growth of the sudd-forming sedge *Pycnopus nitidus* (Lam.) J. Raynal. This species requires physical support for stolon extension which is provided by unconsolidated benthic detrital aggregations or the submerged plant *Websteria confervoides* (Poir.) Hooper which forms a base mat near the water surface. Both the organic and the plant sudds play an important role in determining community processes as they serve to provide a surface for establishment of short emergent species which would otherwise not become established.

INTRODUCTION

The term "sudd" is presently used to describe any floating vegetation mat in a wetland system (Denny, 1985; Thompson, 1985). Thompson (1985) divides sudd communities into two broad categories, organic sudds and plant sudds. Organic sudds are formed when floating islands or mats of organic substratum break away from the benthic detrital layer, float to the surface and become colonized by a variety of aquatic plant species (Fig. 1; Sita, 1970;

*To whom correspondence should be addressed.

**Present address: CSIRO Division of Wildlife and Rangeland Research, P.O. Box 84, Lyneham ACT 2602, Australia.

Smith, 1976). These sudds are usually small ($< 2 \text{ m}^2$), isolated, mobile units and the species which colonize them are known as sudd users (Thompson 1985). In some cases the submerged detrital aggregate does not become detached to form an isolated sudd, but instead it rises differentially to form a dome-shaped structure of which the most buoyant portion (ranging from 10 to 200 m^2 in area) becomes exposed (Fig. 1). Similar organic detrital sudds have been recorded in the Okefenokee swamps, GA, U.S.A., where mobile sudds are referred to as "batteries" and dome-shaped sudds as "bulges" (Cypert, 1961, 1972; Spackman et al., 1976).

The second category consists of plant sudds which are formed when species with a positive buoyancy grow out from channel and lake margins to form a floating mat (Thompson, 1985). These plants are referred to as sudd formers (Thompson, 1985) and include species such as *Pycneus* spp., *Leersia hexandra* Swartz and *Cyperus papyrus* L. In addition, many of the free-floating aquatic "weeds" such as *Eichhornia crassipes* (Mart.) Solms-Laub. and *Sagittaria molesta* D.S. Mitchell fall into this category (Mitchell, 1985). These sudds can be small and mobile, may line channel edges or can cover extensive areas and remain stationary. They are bound together by stems and rhizomes of the sudd-forming species (Sculthorpe, 1967) and provide an exposed surface upon which non-sudd formers, such as *Drosera* and *Xyris*, can establish (Thompson, 1985).

The conditions under which sudds form, their rate of development, s

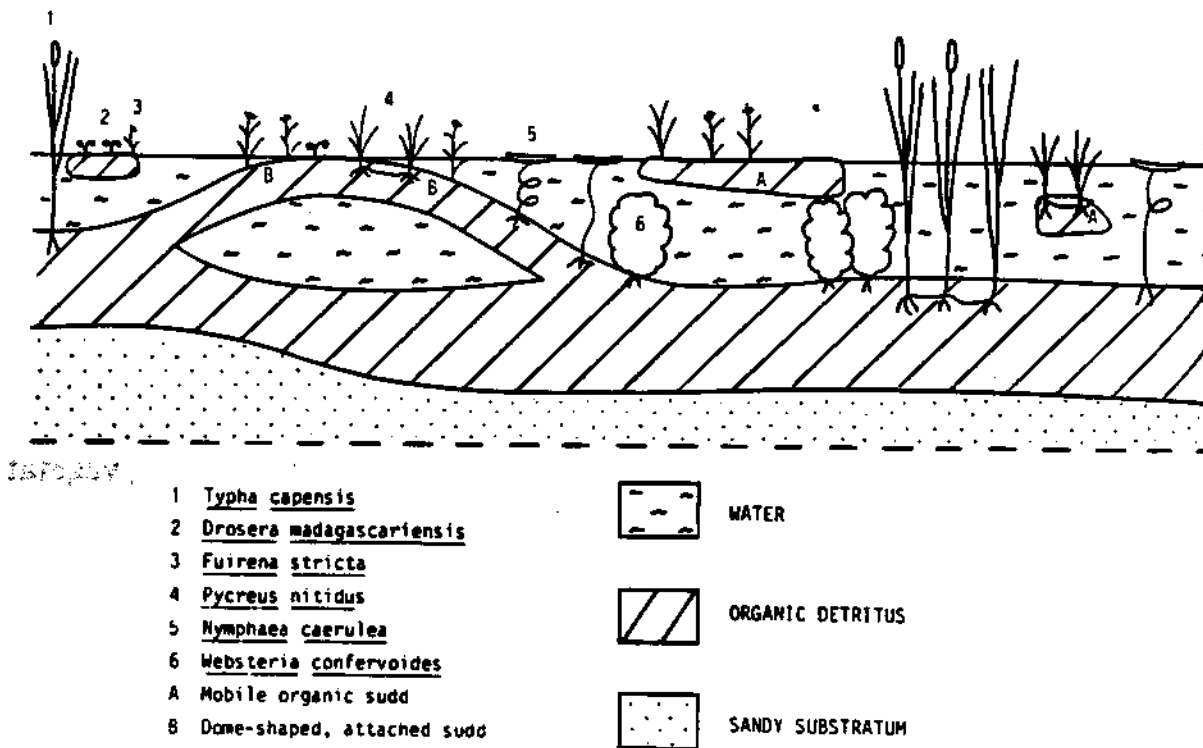


Fig. 1. Diagrammatic representation of a cross-section of a water body in the Maunachira river system of both mobile (A) and attached (B) organic sudds.

quence of colonization and their role in community processes are poorly understood. Organic sudds have been recognized to be extremely mobile both vertically and horizontally (McCabe, 1984; Mitchell, 1985). The longevity and fate of organic sudds, as well as the persistence of a viable seed bank (van der Valk, 1981, 1982), would appear important determinants of successional trends in wetland plant communities and do not appear to have been investigated in African wetlands to any extent.

In contrast, the formation and persistence of plant sudds appears contingent upon the ability of clonal plants to rapidly spread across the water surface (Junk, 1983). Most studies of floating plant sudd formation (Conway, 1949; Dansereau and Sedagas-Vianna, 1952; Swan and Gill, 1970; Junk, 1983; Lieffers, 1984) also suggest that an initial colonizing site or nucleus, such as an organic sudd or debris bank, is required before stolon growth can take place to expand the mat.

The aim of this study was to investigate the seasonal pattern of organic sudd formation, their permanence, plant species colonization and the effect of disturbance on sudd movement. The contribution of the persistent seed bank, as opposed to the input of propagules subsequent to exposure of organic sudds, to the establishment of plant species was also examined. This study further investigated the relative importance and character of different supporting substrata for the growth of *Pycnopus nitidus* (Lam.) J. Raynal, the main plant sudd-forming species in the north-eastern Okavango Delta (Ellery et al., 1990).

STUDY AREA

As detailed accounts of the Okavango Delta are provided elsewhere in the literature (McCarthy et al., 1986; Ellery et al., 1990) only a brief description is presented here. The Okavango Delta forms part of an internal drainage system situated in north-western Botswana between 19° and 20°S and 22° and 24°E (Fig. 2). Arising from the Okavango river, several main distributary systems spread out over the flat, Kalahari sands to cover an approximate area of 16 000 km², with permanent inundation occurring in the upper northern reaches and seasonal inundation in the southern reaches. The delta experiences summer rainfall (mean 415 mm year⁻¹, $n=11$) in the form of short thunderstorms, and relatively high temperatures throughout the year (mean summer and winter maxima are 32.2°C and 26.7°C respectively).

The Maunachira river system, situated in the north-eastern part of the delta, remains permanently flooded throughout the year with seasonal water level fluctuations of approximately 20 cm year⁻¹. It consists of a heterogeneous mosaic of islands, channels with submerged vegetation covering the channel bed, and back swamps dominated by submerged, floating-leaved, floating or

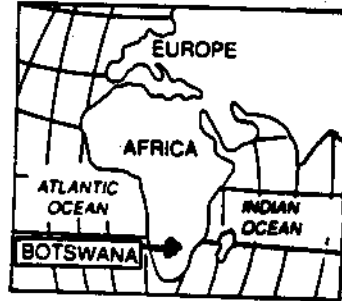
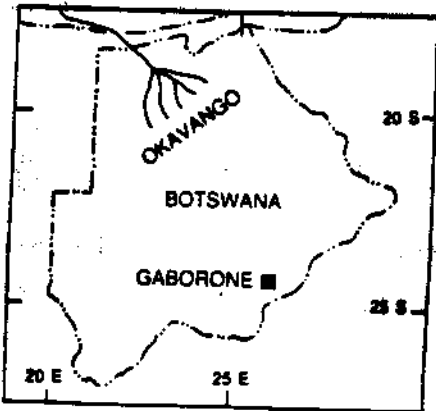
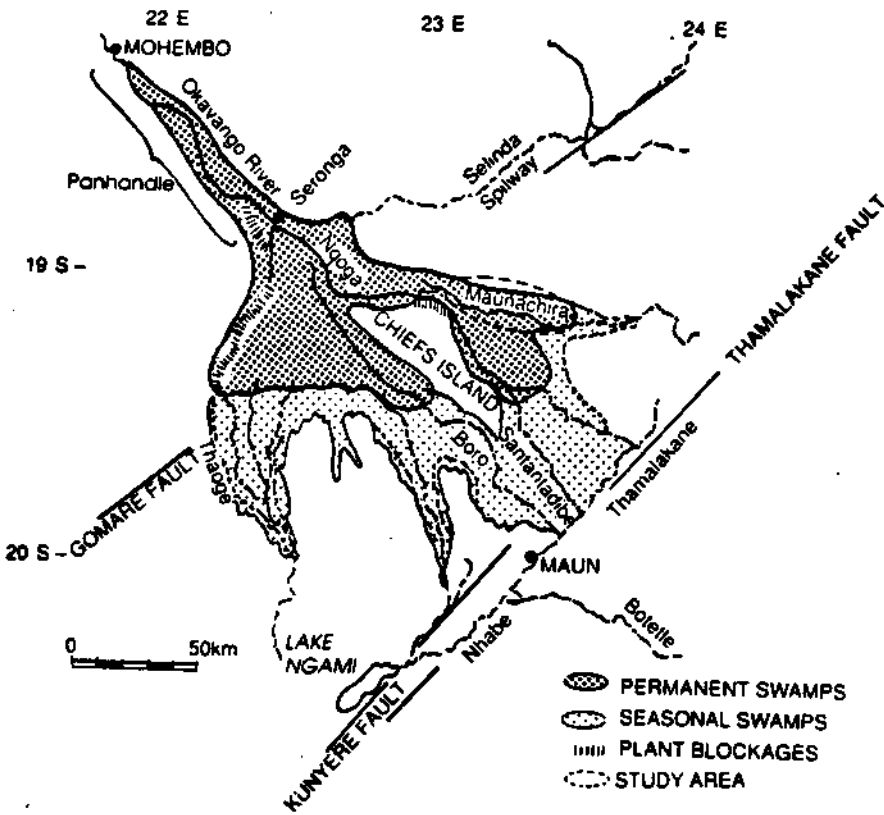


Fig. 2. Map showing the location of the Okavango Delta in north-western Botswana.

emergent species. The most commonly represented community in the back swamps is a plant sudd community dominated by the short, emergent species *P. nitidus* (Ellery et al., 1990). This is a small, robust, perennial sedge with leafy shoots which are connected by branching stolons (Haines and Lye, 1983). The leaves protrude above the surface of the water and vary in length from 15 to 60 cm depending on the water depth. *P. nitidus* spreads by rhizomatous growth at or close to the water surface, to form extensive floating sudds. Less common but still a prominent feature are the communities occupied by organic sudds which are most often found at the inflow to a lediba (Tswana

name for open water body, plural = madiba) where detrital accumulation is rapid and *Nymphaea caerulea* Sav. and *Typha capensis* (Rohrb.) N.E. Br. dominate. This study was carried out at sites where these three plant species were dominant.

METHODS

Season of formation, permanence and the effect of disturbance on organic sudd movement

A single site, in which water flow was negligible, was used for the study on organic sudd formation and movement. As the water body was relatively large (340 m × 75 m) with minimal tall, fringing vegetation, wind action was considered to be the most important disturbance factor operating over the entire water body for prolonged periods. A single path, utilized by hippopotamus (*Hippopotamus amphibius* L.) at least once a day and by small power boats on a less regular basis (approximately once a week during the winter months and only once a month during the summer), passed through the centre of the water body.

To determine the permanence, fate and species composition of the suds over a winter and summer period within the water body the following tasks were conducted on the suds encountered on each sampling occasion: (1) each new sudd was tagged; (2) its position was mapped; (3) the size of, and depth from the water surface to the sudd were measured (not all suds were floating at the water surface); (4) the frequency of occurrence of each plant species rooted and growing in the sudd was measured.

To determine the rate at which organic suds accumulating on the leeward edge of a lediba lead to a reduction in its area, comparisons of 1969 and 1983 aerial photographs at five different localities within the study area were made.

Plant species colonization of organic suds

To examine the seed bank composition of organic suds experiments were set up in which organic detrital samples were taken from the submerged rooting zone of plant communities where organic suds commonly arise (Treatment 1) as well as from existing suds which had been at the water surface for approximately 3 weeks (Treatment 2). For each of the above two treatments three (1 dm³) samples of organic matter were sorted to remove rhizomes, tubers and pieces of undecomposed litter (Pederson, 1981). The samples were placed into individual 20 × 30 × 5 cm plastic trays and staked in position ensuring that they floated permanently at the water surface, as in the case of natural suds. Small 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 (mesh size = 1 mm) stretched over a

frame allowing room for seedling growth. At 2-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.

Sudd formation as a result of P. nitidus growth

An oxbow-shaped water body, with extensive stands of *P. nitidus* at varying densities and in association with other species, was chosen for the growth studies of this species. To establish the extent to which *P. nitidus* stolon extension is influenced by support from an unconsolidated detrital layer or submerged plants (*Websteria confervoides* (Poir.) Hooper), the rate of extension growth of the sudd margin was measured under the following conditions: (1) with detrital support at <0.6 m depth and in the absence of *W. confervoides*; (2) with plant support (*W. confervoides* with 80–100% cover) at <0.6 m depth and in the absence of detritus; (3) with no support (detritus and *W. confervoides* both absent).

A permanent marker was placed at the margin of each *P. nitidus* sudd under the above conditions. The rate of sudd extension was determined by measuring the distance from the marker to each shoot ($n=80$) at 8–10 week intervals.

RESULTS

Seasonal patterns of organic sudd formation

Areas of organic sudd formation are dominated by the floating-leaved *N. caerulea* and tall emergent *T. capensis*. The fine detritus of each sudd is supported in the fibrous root system of individual plants of these two species, whose corms and rhizomes form the nucleus of each sudd. The size of the sudd, which ranges from <0.4 to >8.0 m², appears to depend upon the maturity and thus extent of the rooting system of these plants.

A total of 59 mobile suds were tagged in autumn (May; Fig. 3) and by late winter (August) 35 of these had sunk and no new suds had risen to the surface. During spring (August–October) there was little difference between the number of suds which sank and those which rose to the surface (14 and 12, respectively). In contrast, during the summer months (October–December) 44 suds rose to the water surface and only six of the original 59 suds sank. Of those that rose to the surface during spring and summer, 25% of them had previously been tagged; the rest were "new" suds which had formed since the first sampling occasion.

There thus appears to be a general trend of sudd formation and rising to the water surface in the summer months and sinking during the winter. Individual suds may rise and sink in successive seasons.

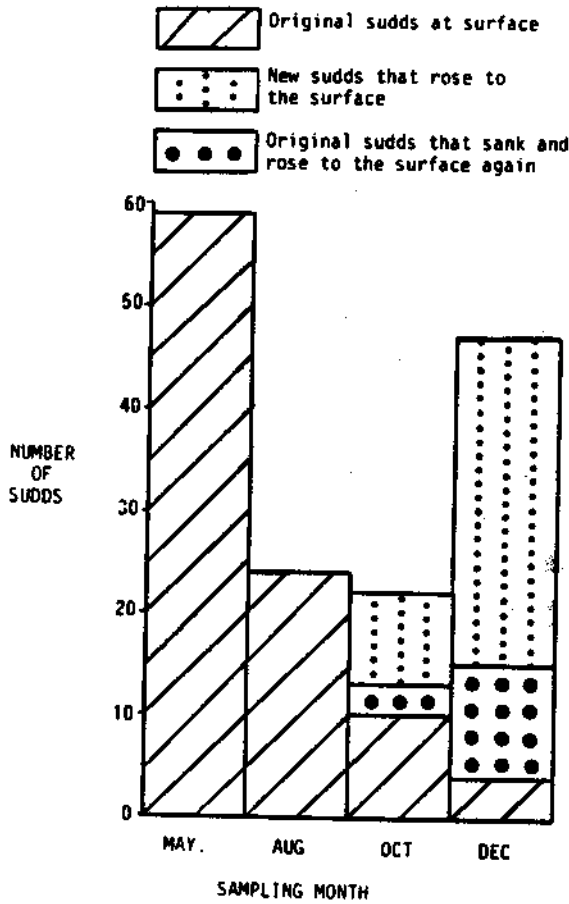


Fig. 3. Number of suds which remained at the water surface, sank, and rose to the surface during three time intervals (May–August, August–October, October–December).

Movement of suds in response to disturbance

With the exception of two large suds (>6 m²), all suds not already banked up against the edge of the lediba (water body) moved distances of 5 m or more from their original positions (Fig. 4). Had wave action caused by hippopotamus and boats passing along the central pathway been the major disturbance, the mobile suds could be expected to have moved both east and west away from the north–south-orientated path. All suds, 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 (Fig. 4a, b and c), suggesting that wind was the overriding environmental factor contributing to sudd movement. The suds eventually accumulated at different depths (i.e. not all were of the same buoyancy) on the leeward side of the lediba, leading to the formation of a heterogeneous fringe community.

While 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 m) during the 14-year period (0.05 m year⁻¹). Consid-

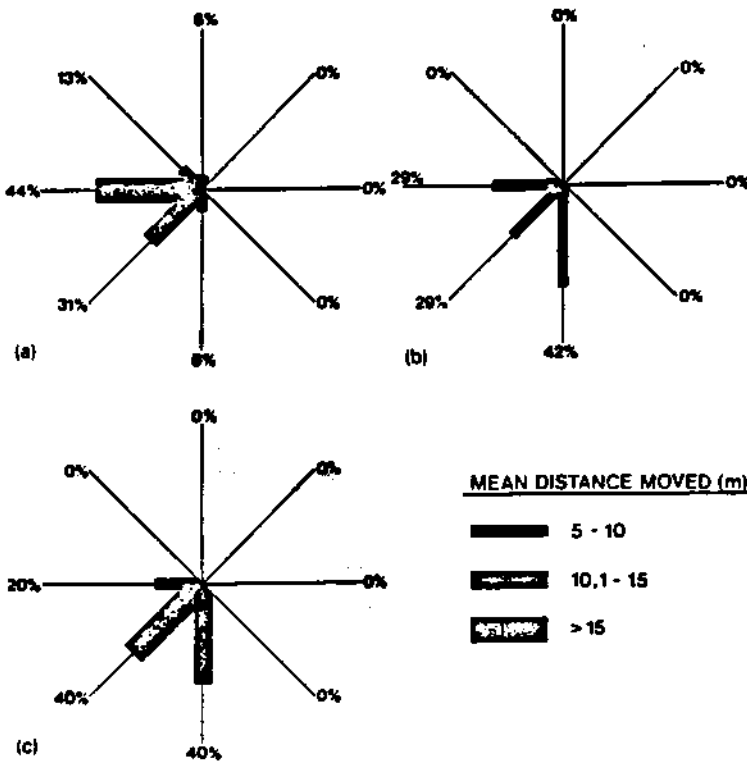


Fig. 4. Movement of sudds in the disturbed site during (a) winter, (b) spring and (c) summer. The length of bar indicates the percentage of sudds which moved in a particular direction, and width indicates the distance moved.

ering the size of some of the sudds, with diameters of >2.0 m, this rate of encroachment appears unexpectedly slow. It would appear that although a high percentage of the sudds bank up on the leeward edge, in terms of the entire length of the lediba (340 m) the overall contribution of the sudds to encroachment is relatively small. The presence of many sudds and extremely patchy nature of vegetation fringing most madiba however, indicate that with respect to the long-term successional development of the area as a whole, sudds may indeed be important.

Organic sudd colonization

The organic detritus taken from a submerged position and placed at the water surface in seed trays (Treatment 1) contained viable *N. caerulea* seeds of which a mean of 183 seeds m^{-2} germinated within a month of being brought to the surface (Fig. 5a). 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 floating-leaved species alone. In the second treatment, where the organic detrital sudds had been exposed at the water surface for approximately 3 weeks prior to setting up the experiment, a

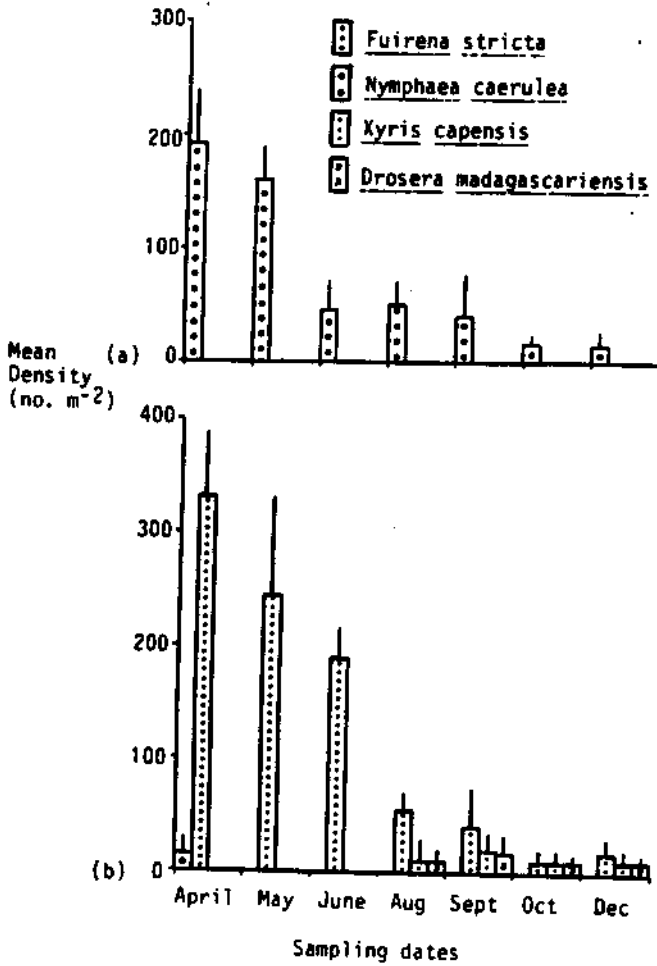


Fig. 5. Mean densities of seedlings observed in the seedtrays with the organic detritus taken from (a) a submerged position (Treatment 1, $n=3$) and (b) a floating position (Treatment 2, $n=3$) on successive sampling days. Standard deviations are represented by vertical bars.

greater species diversity was observed (Fig. 5b). A mean of 33 *Fuirena stricta* Steud. seeds m^{-2} germinated within a month of setting up the experiment and although further seeds of this species germinated, numbers decreased steadily at each successive sampling date from May until December. In contrast to the large number of *F. stricta* seeds, only 16 *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* Thunb. and *Drosera madagascariensis* DC were present in low numbers (Fig. 5b). The relatively high number of species in this treatment compared with that of the first suggest that these seeds were recruited during the 3 weeks' exposure at the water surface. Further, the germination of only a small number of *N. caerulea* in this treatment was probably due to the other *N. caerulea* seeds having germinated during the 3 weeks of exposure - when the samples were originally taken a number of *Nymphaea* seedlings were present.

The covered seed trays gave some indication of the seed bank composition

and subsequent colonization of sudds during their early stage of development. To examine the extent to which an input of seeds or propagules from the surrounding communities determined species composition on the older sudds, the covered seed trays were compared with similar sized sudds (0.20 m × 0.30 m colonizing surface, $n=7$) in the field. Whereas the number of different species in the seedtrays was never greater than three, the mean number of species on the sudds in the field during the year of sampling was much greater (mean = 6.88, SD = 2.64). In addition to the taxa found on the seedtrays species such as *P. nitidus*, *Fuirena pubescens* (Poir.) Kunth, *Cyperus pectinatus* L., *Ludwigia leptocarpa* (Nutt.) Hara and *Panicum repens* L. were common in the field. As seedlings were removed from the seedtrays at each successive sampling date, densities over the time span of the experiments could not be calculated. The density of young seedlings on the field sudds, however, remained high throughout the year (mean = 1250 m⁻², SD = 406.6) indicating continual seedling recruitment.

The constant presence and high number of species on the sudds in the field compared with the low number of species and a progressive decrease in seed germination in the seed bank experiments indicates the importance of a continual input of propagules from established plants in the surrounding areas.

Pycnus nitidus extension growth and plant sudd development

In the absence of either detrital or submerged plant support, *P. nitidus* showed little extension growth (0.02 m year⁻¹, SD = 0.007; Table 1) over the 9-month study period. In contrast, the rates of extension growth in areas with organic detrital support were 1.10 m year⁻¹ (SD = 1.03) and 1.46 m year⁻¹ (SD = 1.27) in areas where *W. confervoides* was abundant (Table 1). The colonization of open-water bodies by *P. nitidus* therefore appears dependent on some sort of physical support for stolon extension and encroachment, and is much more rapid than organic sudd encroachment.

TABLE 1

Extension growth of *Pycnus nitidus* without support or with support either from submerged plants or from a submerged organic layer

	Extension growth (m year ⁻¹)	SD
No support	0.02	0.007
With organic support	1.10	1.03
With plant support	1.46	1.27

DISCUSSION

Organic sudds

Organic sudd deposits which develop from a submerged benthic detrital layer require the well-developed root systems of aquatic macrophytes to bind the detrital material (Ellery, 1987). Two species, *N. caerulea* and *T. capensis*, appear to be the only species in the study area which are capable of this. *Typha glauca* Godr. in eastern Canada (Hogg and Wein, 1988) and various species of *Nymphaea* in the Okefenokee swamps (Cypert, 1972; Spackman et al., 1976) have been shown to play similar roles. The development of organic sudds in the Okavango Delta is largely limited to deep water sites (> 1.5 m depth; Ellery, 1987) occupied by *N. caerulea* and *T. capensis*. The subsequent succession of species on the organic sudd is independent of water depth, but instead depends upon the fate of the sudds themselves.

The organic sudds of the Maunachira back swamps tend to form, or rise to the surface, during the summer and sink again during the winter months. This is probably the result of changes in the rate of microbial gas production during the different seasons (King, 1984; Hogg and Wein, 1988).

These organic sudds are extremely mobile and tend to move horizontally largely as a result of wind action. Since many of the sudds which remain at the water surface for long periods experience 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 of successional trends in species composition from seed bank studies in the study area would thus be limited. The succession of plant species on these sudds is instead dependent on the input of propagules from neighbouring plant communities. Prediction of plant successional trends would therefore require an understanding of the production and characteristics of propagules of species in the surrounding communities.

Most sudds ultimately bank up on the leeward edge of the water body and the sudd colonizers thus form part of the fringe vegetation. Since the rate of sudd deposition on the leeward edge of the water body is slow, reduction in the area of open water as a result of sudd formation appears relatively slow. However, evidence from analyses of peat cores taken in a number of plant communities in the Maunachira river system (Ellery, 1987), as well as the small-scale, patchy nature of the vegetation surrounding the madiba in general, indicate that organic sudd formation has in the past played an extremely important role in the successional development of the area as a whole.

In this study sudds have been shown to be locally important in providing a surface for the germination and establishment of species which would otherwise not become established. As reported by Lieffers (1984) in Alberta, the individual sudds at the waters edge become consolidated into a single unit by

the colonization, growth and spread of rhizomatous and stoloniferous species. Of particular interest in this study is the establishment of the sudd-forming plant *P. nitidus* which forms a dominant component of many plant communities in the Maunachira river system (Ellery et al., 1990).

Sudds initiated by the growth of P. nitidus

It appears that *P. nitidus* initially becomes established on floating organic sudds and it is from this position, either in the middle of the lediba or banked up on the leeward edge, that the species colonizes large areas of open water. It has been reported that in the initial stages of vegetative sudd formation the buoyant nature of sudd-forming plants enables them to encroach across and thereby colonize open water bodies (Junk, 1970; Swan and Gill, 1970; Liefers, 1984; Kratz and DeWitt, 1986). Strictly speaking *P. nitidus* is not a true sudd-forming plant as it is not sufficiently buoyant to colonize an area without some form of physical support. Benthic detrital infilling or submerged plant growth has to reduce the effective water depth to at least 0.60 m before *P. nitidus* encroachment can take place. In this situation *P. nitidus* performs the same function as other sudd-forming species in that a surface on which other species can become established is ultimately formed (Swan and Gill, 1970; Tallis, 1983; Liefers, 1984). It appears that the substratum which supports *P. nitidus* stolon extension is not sufficiently consolidated to provide a medium for establishment for other plant species on their own. Non-sudd-forming species were not observed rooting in the supportive, yet relatively unconsolidated, submerged layer.

At an average rate of sudd spread of 1.28 m year^{-1} , originating from the banks and many different organic sudd loci, an area rapidly becomes colonized by *P. nitidus*. Unfortunately processes involved in vertical sudd build-up, which would lead to maturation of the wetland, could not be determined within the timespan of the study. However, similar to observations made by Swan and Gill (1970), Henjý (1971) and Liefers (1984), the establishment of secondary colonizers seems dependent upon the initial establishment of a loose organic matrix derived mainly from dead shoots which become trapped by the underlying stolons.

The distribution of the secondary colonizers (mainly *C. pectinatus*, *Miscanthus junceum* (Stapf) Stapf, *F. stricta*, *F. pubescens*, *D. madagascariensis*, *Panicum repens* and *Ficus verruculosa* Warb.) on the sudds formed by the stoloniferous growth of *P. nitidus* was noted to be extremely patchy, which suggests that opportunistic colonization or limited seed dispersal determine the distribution of these species. A gradual settling of the floating sudd was observed as secondary colonizers, usually less buoyant than the sudd formers

themselves (Lieffers, 1984), became established and peat formed and accumulated at the surface. Complete sinking, however, did not occur.

Implications of sudd formation for community development

Although the literature on African swamps and peatlands is extensive (cf. Thompson et al., 1985), it is mostly descriptive with little emphasis on changes in species composition over time, or the processes involved. Howard-Williams and Gaudet (1985) recognize two different types of perennial swamp communities in Africa with regard to structure: (a) reedswamp communities, i.e. plants rooted in the substratum made up of sediments of peat; (b) sudd communities, i.e. plants rooted in floating or almost floating mats. Due to structural differences, these two swamp types have different developmental processes and successional trends.

The formation and accumulation of peat in reedswamp communities essentially involves a process of hydrosere vertical accumulation of undecomposed organic material until the water level limits further aggradation (Walker, 1970; Sjörs, 1980). The rate of change in species composition in these communities depends largely upon relatively slow rates of autochthonous infilling (decades to centuries), although deposition of silt at lake inflows has been shown in northern temperate regions to produce rapid (decades) changes in species composition (Tallis, 1983). In contrast to the reedswamp communities, the sudd-initiated communities are not affected by water depth and, provided there is sufficient water present beneath the floating sudds, are not limited to a particular zone in the hydrosere (Mitchell, 1985). This study and other studies in tropical and subtropical regions (Sculthorpe, 1967; Junk, 1970, 1983) have indicated that plant sudds can encroach open-water bodies over very short timespans of months to a few years. By enabling the rapid transformation of submerged, floating-leaved and bottom-rooted tall emergent dominated plant communities to one dominated by plant species tolerant of a shallow water depth, sudd initiation and development represents a "jump" in the rate at which shallow-rooted species are able to establish. As subsequent organic matter accumulation is from the top down, the effective water depth remains relatively constant throughout community development even in systems with large water level fluctuations (Hogg and Wein, 1988).

As sudds are a prevalent feature of tropical and subtropical wetlands (Sculthorpe, 1967; Howard-Williams and Gaudet, 1985), the conditions under which sudds form, the determinants of their development and their effects on wetland ecosystem dynamics all need further investigation if sudd-initiated plant community development is to have a place in general models of wetland development.

ACKNOWLEDGEMENTS

We gratefully acknowledge the Office of the President and the Department of Water Affairs, Botswana, for their co-operation and permission to conduct the study in Botswana. Special thanks to Mr. P. Smith for valuable advice and information. The Claude Harris Leon Foundation Trust, the CSIR and the University of the Witwatersrand provided financial support for the study.

REFERENCES

- Conway, V.M., 1949. The bogs of Central Minnesota. *Ecol. Monogr.*, 19: 173-206.
- Cypert, E., 1961. The effects of fire in the Okefenokee Swamp in 1954 and 1955. *Am. Midl. Nat.*, 66: 483-503.
- Cypert, E., 1972. The origin of houses in the Okefenokee prairies. *Am. Midl. Nat.*, 87: 448-458.
- Dansereau, P. and Sedagas-Vianna, F., 1952. Ecological study of the peat bogs of eastern North America. I. Structure and evolution of vegetation. *Can. J. Bot.*, 30: 490-520.
- Denny, P., 1985. Wetland vegetation and associated life forms. In: P. Denny (Editor), *The Ecology and Management of African Wetland Vegetation*. Junk, Dordrecht, pp. 1-18.
- Ellery, K., 1987. Wetland plant community composition and successional processes in the Maunachira river system of the Okavango Delta. MSc Thesis, Wits University, Johannesburg, 125 pp (unpublished).
- Ellery, K., Ellery, W.N., Rogers, K.H. and Walker, B.H., 1990. Water depth and biotic insulation: Major determinants of back-swamp plant community composition. *Wetlands Ecol. Manage.* 1(2): in press.
- Haines, R.W. and Lye, K.A., 1983. *The Sedges and Rushes of East Africa*. East Afr. Nat. Hist. Soc., Nairobi.
- Henjý, S., 1971. The dynamic characteristics of littoral vegetation with respect to changes in water level. *Hidrobiologia (Bucuresii)*, 12: 71-86.
- Hogg, E.H. and Wein, R.W., 1988. The contribution of *Typha* components to floating mat buoyancy. *Ecology*, 69: 1025-1031.
- Howard-Williams, C. and Gaudet, J.J., 1985. The structure and functioning of African swamps. In: P. Denny (Editor), *The Ecology and Management of African Wetland Vegetation*. Junk, Dordrecht, pp. 153-176.
- Junk, W.J., 1970. Investigations on the ecology and production-biology of the "floating meadows" (*Paspalo-Echinochloetum*) on the middle Amazon. I. The floating vegetation and its ecology. *Amazonia*, 2: 449-495.
- Junk, W.J., 1983. Ecology of swamps on the middle Amazon. In: A.J.P. Gore (Editor), *Ecosystems of the World, Vol. 4B. Mires: Swamp, Bog, Fen and Moor. Regional Studies*. Elsevier, Amsterdam, pp. 269-294.
- King, G.M., 1984. Methane production of Okefenokee peats. In: A.D. Cohen, D.J. Casagrande, M.J. Andreijko and R.J. Best (Editors), *The Okefenokee Swamp: its Natural History, Geology and Geochemistry. Wetland Surveys*, Los Alamos, New Mexico, pp. 371-379.
- Kratz, T.K. and DeWitt, C.B., 1986. Internal factors controlling peatland-lake ecosystem development. *Ecology*, 67: 100-107.
- Lieffers, V.J., 1984. Emergent plant communities of oxbow lakes in northeastern Alberta: Salinity, water-level fluctuation and succession. *Can. J. Bot.*, 62: 310-316.
- McCabe, P.J., 1984. Depositional environments of coal and coal-bearing strata. In: R.A. Rha-

- mani and R.M. Flores (Editors), *Sedimentology of Coal and Coal-bearing Sequences*. Spec. Publ. Int. Assoc. Sedimentologists, Vol. 7. Blackwell, London, pp. 13-42.
- McCarthy, T.S., Ellery, W.N., Rogers, K.H., Cairncross, B. and Ellery, K., 1986. The roles of sedimentation and plant growth in changing flow patterns in the Okavango Delta, Botswana, *S. Afr. J. Sci.*, 82: 588-591.
- Mitchell, D.S., 1985. Surface floating aquatic macrophytes. In: P. Denny (Editor), *The Ecology and Management of African Wetland Vegetation*. Dr. W. Junk, Dordrecht, pp. 109-124.
- Pederson, R.L., 1981. Seed bank characteristics of the Delta marsh, Manitoba: Applications for wetland management. In: B. Richardson (Editor), *Selected Proceedings of the Midwest Conference on Wetland Values and Management*. St. Paul, Minnesota, pp. 61-69.
- Sculthorpe, C.D., 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold, London, 610 pp.
- Sita, P., 1970. Etude de la vegetation de l'île M'bamou (Stanley-pool). Office de la Recherche Scientifique et Technique Outre-Mer, Congo-Brazzaville.
- Sjörs, H., 1980. An arrangement of changes along gradients, with examples of successions in boreal peatlands. *Vegetatio*, 43: 1-4.
- Smith, P.A., 1976. An outline of the vegetation of the Okavango drainage system. In: Symposium on the Okavango Delta. Botswana Soc., Gaborone, pp. 93-112.
- Spackman, W., Cohen, A.D., Given, P.H. and Casagrande, D.J., 1976. Comparative study of the Okefenokee Swamp and the Everglade-Mangrove complex of southern Florida. Coal Res. Section, Pennsylvania State University.
- Swan, J.M.A. and Gill, A.M., 1970. The origins, spread and consolidation of a floating bog in Harvard Pond, Petersham, Massachusetts. *Ecology*, 51: 829-840.
- Tallis, J.H., 1983. Changes in wetland communities. In: A.J.P. Gore (Editor), *Wetland Ecosystems of the World*. Vol. 4A. Mires: Swamp, Bog, Fen and Moor. General Studies. Elsevier, Amsterdam, pp. 311-347.
- Thompson, K., 1985. Emergent plants of permanent and seasonally flooded wetlands. In: P. Denny (Editor), *The Ecology and Management of African Wetland Vegetation*. Junk, Dordrecht, pp. 43-108.
- Thompson, K., Howard-Williams, C. and Mitchell, D.S., 1985. Cross-indexed bibliography of African wetland plants and vegetation. In: P. Denny (Editor), *The Ecology and Management of African Wetland Vegetation*. Junk, Dordrecht, pp. 237-316.
- Van der Valk, A.G., 1981. Succession in wetlands: A Gleasonian approach. *Ecology*, 63: 688-696.
- Van der Valk, A.G., 1982. Succession in north temperate wetlands. In: B. Gopal., R.E. Turner, R.G. Wetzel and D.F. Whigham (Editors), *Wetlands. Ecology and Management*. Nat. Inst. Ecol. Int. Sci., Publ., pp. 169-179.
- Walker, D., 1970. Direction and rate in some British Post-Glacial hydroseres. In: D. Walker and R.G. West (Editors), *Studies in the Vegetation History of the British Isles*. Cambridge University Press, London, pp. 117-139.