FLORISTIC DIVERSITY IN THE OKAVANGO DELTA, BOTSWANA AS AN ENDOGENOUS PRODUCT OF BIOLOGICAL ACTIVITY

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Abstract

The floristic diversity of the Okavango Delta is described on the basis of herbarium material housed at the National Herbarium of South Africa in Pretoria, South Africa, and on the basis of existing unpublished lists. The flora is diverse with 134 families, 530 genera, and 1256 species represented. The most species rich families are the Poaceae, Cyperaceae, Asteraceae and Papilionoideae, each of which is represented by more than 50 taxa of species and lower rank. Few taxa at species level and lower appear to be particularly threatened.

An attempt is made in the present study to consider landscape level heterogeneity in the Okavango Delta by focussing on a number of important environmental gradients that contribute to floristic diversity. Channel bed vegetation appears to be determined by whether or not the channel receives water and sediments directly from the catchment (Okavango River, and its extension onto the Delta, the Nqoga River; i.e. primary channels), or whether the channel receives its water as over-spill via densely vegetated communities in areas flanking the primary source channel. In those channels which arise as overspill from the Okavango-Nqoga River system, the degree of channel confinement of flow by channel margin vegetation appears to be an important underlying environmental determinant. Channel margin vegetation immediately flanking the channel varies downstream with the clay content of the channel margin, and the duration of flooding. A floristic gradient exists away from the channel margin into backswamp areas, which is determined primarily by clay content and/or nutrient availability. The vegetation in backswamp communities themselves is determined by gradients in water depth, as well as by autogenic successional processes on floating rafts of organic matter. Heterogeneity in floodplain vegetation is determined by variation in soil chemistry and elevation associated with the mound building termite Macrotermes michaelseni. Once colonised, changes in soil and groundwater chemistry as well as the creation of topographic relief, caused by transpiration of large trees, leads to variation in vegetation distribution at the landscape scale. Similarly, vegetation on island fringes in the permanent swamps contributes to variation in groundwater and soil chemistry that is associated with variation in vegetation distribution at the landscape scale.

These landscape level gradients are largely the product of biological activity, and it is concluded that biological diversity within this ecosystem is generated primarily by the biota itself. The importance of recognising ecosystem engineers as well as the consequences of their activities for the ecosystem is considered vital for predictive purposes.

Introduction

The conservation of biological diversity has become one of the most important endeavours on the planet at the dawn of the twenty-first century. Many attempts are being made to quantify biodiversity globally as well as in different ecosystems, and to understand the reasons for observed patterns in community level heterogeneity. Many of the ecological explanations for diversity that exists within and between natural communities recognise the fact that most environments are characterised by gradients in the distribution of environmental conditions or resources, which is matched by heterogeneity in the distribution of species and communities. Alternatively, the distribution of environmental factors may be patchy, in which case distribution of species and communities is patchy. A third explanation centres around the fact that organisms themselves modify and diversify the environment, making it suitable for the existence of other organisms.

The diversity within natural communities may be due to all three types of heterogeneity, but ecology has traditionally focussed on the relationships between the distribution of natural communities and the underlying heterogeneity in the distribution of conditions and/or resources. Modification of the natural environment by biota is seldom considered an important source of environmental heterogeneity at the landscape scale. However, many organisms modify the environments in which they occur by altering physical conditions, resource availability, or by modifying the concentrations of toxins in the environment. The consequences of such modification are that the environment supports a different range of species and populations, with different dynamics, than if the original organism was not present. Jones et al. (1994) and Lawton (1994) have formalised the process by which an organism directly or indirectly modulates the availability of resources for other organisms, and called it *ecosystem engineering*.

Ecosystem engineering is spatially explicit, and it therefore contributes to heterogeneity at the local and landscape level. If communities and/or ecosystems are organised around the effects of engineers, the disappearance of engineers, for example due to disturbance, may be dramatic. Given this it is vital to understand the ways in which ecosystem engineers contribute to ecosystem structure and function, in order to adequately conserve local and regional levels of biodiversity.

This paper describes the floristic diversity of the Okavango Delta ecosystem as a means of establishing the value of this ecosystem as a storehouse of biological diversity. It then examines local and regional plant community diversity, and explains these in terms of the underlying environmental gradients responsible for ecological diversity. In many cases the underlying gradients are simply due to variation in abiotic conditions and resources, but in many cases they are the product of engineering by the biota. It is argued overall that an understanding of the origin of heterogeneity is vital for the adequate conservation of biodiversity of the Okavango Delta ecosystem.

The study area

The Okavango Delta is situated in the semi-arid Kalahari of northern Botswana, and forms part of an internal drainage system known as the Kalahari Basin.
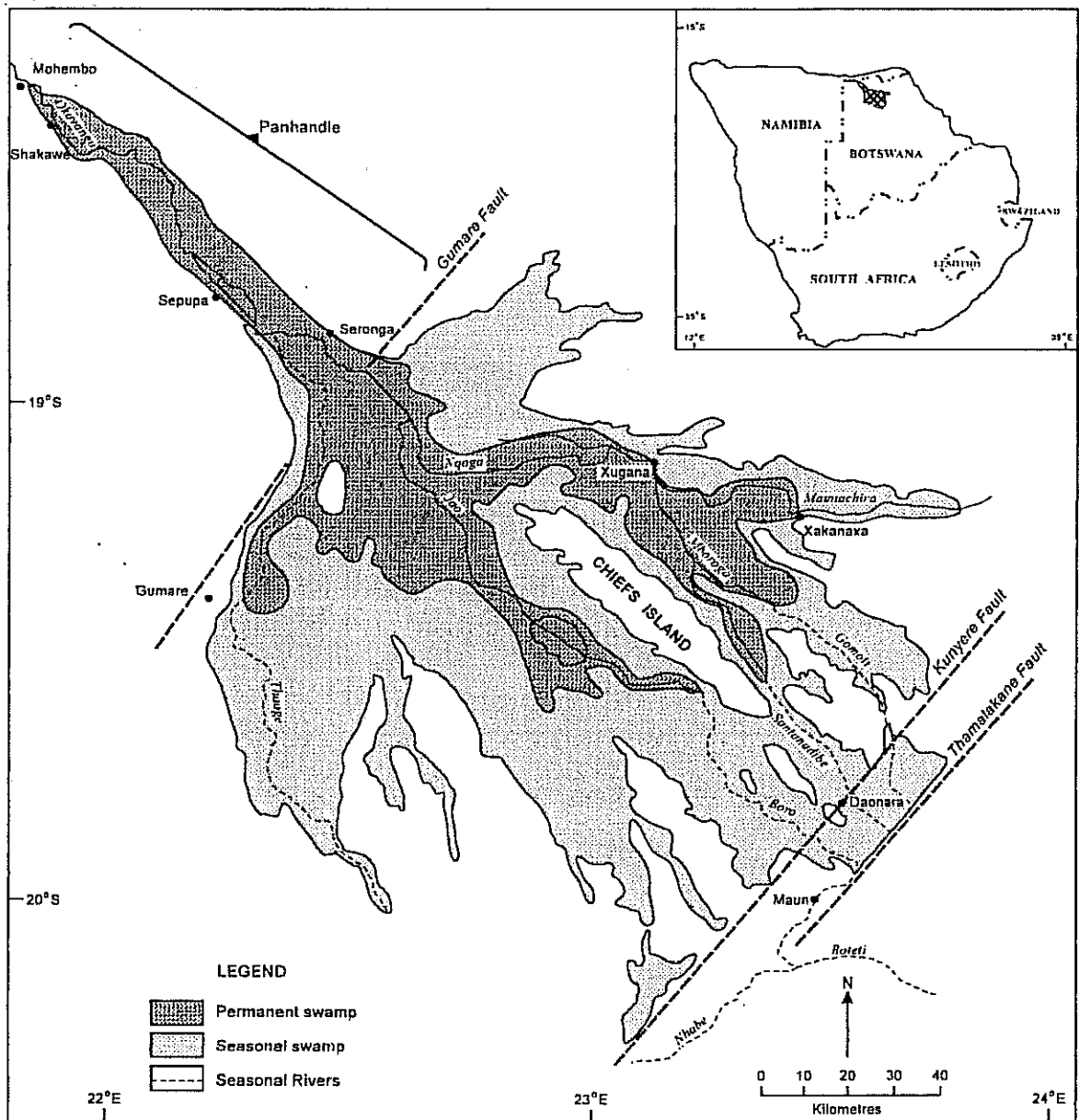
Fig. 1. Map of the Okavango Delta.

The Okavango River discharges into a graben structure, an extension of the East African Rift Valley system (Hutchins et al. 1976), and has produced a large alluvial fan of some 20 000 km² in extent (Fig. 1) with a shallow gradient of approximately 1:3 500 (McCarthy et al. 1997) and gently undulating local topography. The river catchment in the highlands of central and eastern Angola, where rainfall exceeds 1 000 mm.a^{-1}, supplies a total water inflow to the Delta of 11x10^9 m³.a^{-1} which is augmented by 5x10^9 m³.a^{-1} from the 650 mm of local summer rainfall. Peak discharge occurs at the head of the Delta in February or March.

Approximately 2% of the water entering the system each year (inflow plus rainfall) leaves as surface flow, less than 2% leaves as subsurface flow and the remainder is lost as evapotranspiration (Wilson and Dincer 1976, Dincer et al. 1981). In the

upper reaches of the Delta, the river is confined by a secondary subsiding graben (Hutchins et al. 1976; McCarthy et al. 1993a) in the region known as the Panhandle (Fig. 1), but downstream of the town of Seronga, water discharges onto the fan surface itself, giving rise to permanent swamps. The lower reaches of the Delta are flooded seasonally during the dry winter season, and peak discharge occurs in the Thamalakane river at Maun in August or September (Wilson and Dincer 1976).

Primary water distribution within the Okavango Delta occurs via channels, which serve as an arterial system supplying water to the permanent and seasonal swamps. The main distributary channel, the Nqoga River, is connected directly to the source channel, the Okavango River, but many channels are not so connected, and arise by leakage from the primary channels (Wilson and Dincer 1976). Secondary water distribution occurs mainly via overland flow through vegetated swamp. Around 170 000 Mg.a^{-1} of fine eolian sand are transported onto the Delta primarily as bed load, with a further 30 000 Mg.a^{-1} as suspended load consisting mainly of kaolinite (McCarthy et al. 1990). Dissolved solids average 30 Mg L^{-1} to give a total annual dissolved solid load of 450 000 Mg.a^{-1}, the bulk of which accumulates within the ecosystem (McCarthy and Metcalfe 1990).

Several habitats can be recognised in the Okavango (Smith 1976, Ellery and Ellery 1997), including permanent swamps, seasonal swamps and islands which vary in size from several metres to tens of kilometres across. Extending into the Okavango Delta from the surrounding Kalahari, are a number of extensive savanna habitats known as 'sandveld tongues'. These are dryland areas contained within the graben in which the Okavango is situated, and are particularly prominent in the south and east of the system.

The permanent swamps are permanently flooded, and are dominated by extensive stands of tall emergent species rooted in peat, including *Phragmites mauritianus* reedbeds, *Cyperus papyrus* swamp and *Miscanthus junceus* swamp, which generally occur close to the major distributary channels. Backswamps further away from channels are diverse, and dominated by short emergent communities such as *Pycreus nitidus* swamp or short emergent bog communities, or they may be more open and dominated by deep rooted sedges such as *Eleocharis* spp. and *Cyperus articulatus* and *Schoenoplectus corymbosus*. In the deepest habitats, submerged and floating leaved species dominate, including submerged beds of *Najas horridus*, *Rotala myriophylloides*, and *Ottelia* spp. and floating leaved *Brasenia schreberi*, *Nymphaea* spp. and *Nymphoides indica*.

The floodplains of the seasonal swamps are diverse, exhibiting zonation that is dependant on the depth and duration of flooding. Areas flooded for the longest duration may have submerged or floating leaved communities similar to those occurring in the permanent swamps. These give way to an emergent community dominated by *Cyperus articulatus*, *Schoenoplectus corymbosus* and the wild rice *Oryza longistaminata*. Areas flooded for the shortest periods are typically dominated by short grasslands of *Eragrostis inamoena*, *Panicum repens* and *Sorghastrum friesii*, followed by a zone dominated by *Imperata cylindrica* or *Cynodon dactylon*.

Islands are typically surrounded by floodplain grassland or sedgeland, giving way to *Ficus verruculosa* (swamp fig) and *Syzygium cordatum* (water berry). In areas that are very infrequently (if ever) flooded, are tall broadleaved evergreen forests dominated by *Diospyros mespiliformis*, *Ficus sycomorus*, *F. thonningii*,

Garcinia livingstonei and *Phoenix reclinata*. This gives way laterally to deciduous woodlands dominated by species such as *Acacia nigrescens*, *Berchemia discolor*, *Combretum imberbe*, *Croton megalobotrys* and *Lonchocarpus capassa*. The palm *Hyphaene petersiana* occurs on the interior of these wooded island fringes, and stands of this species typically surround a short grassland dominated by *Sporobolus spicatus*, which grows in saline soils.

The mainland and sandveld areas are dominated by savanna woodlands, with the well known *Colophospermum mopane* being particularly dominant and widespread on heavy textured soils. Sandy soils tend to be dominated by the camel thorn *Acacia erioloba*.

Throughout the permanent and seasonal swamps is a network of channels in which the flow of water is sustained largely by the activities of hippopotamus. These are areas in which water flows rapidly, and are important from the point of view of water dispersion in the system.

Methods

Floristic analysis of the Okavango Delta

Species lists have been compiled from data supplied by the National Botanical Institute of South Africa, using data from the National Herbarium, Pretoria (PRE) computerised information system PRECIS. The quarter degree squares included in the analysis are illustrated in Figure 2. An additional full species list that was compiled by Mr PA Smith mainly from his own collection, and included in the Okavango Delta Ecological Zoning Report (SMEC 1989), has also been used. The floristic diversity of the entire system has been analysed by combining the two lists, and adjusting for nomenclatural differences using Arnold and de Wet (1993). The total number of species was estimated from these two lists based on the Peterson mark-recapture method of estimating population sizes in animal censuses as described by Sutherland (1996). The two censuses were the lists of SMEC (1989) and this study, and the "marked" individuals were those taxa at species and lower rank common to both studies.

An analysis of the life form spectrum of plants in the Delta was undertaken by assigning life form classes to genera based on the assumption that life form characters are conservative at genus level (Gibbs Russel 1987). The analysis of the life form spectrum was not straightforward as there were a large number of aquatic taxa that were present in the study area. As such, the selection of life forms was carried out by identifying all graminoid (grasses and sedges) taxa at species and lower rank. The remaining species and lower rank taxa were split into trees, shrubs, aquatic herbs (emergent, floating leaved, submerged and free-floating), non-aquatic herbs (creeping/climbing and non-creeping/climbing), and "other" taxa not included in the above (geophytes, parasites, and species with growth forms not clearly fitting any of the above). This is one of several ways of performing such an analysis as the removal of graminoid taxa first results in the removal of a large number of taxa that could be included in other life-form classes such as aquatic or herbaceous.
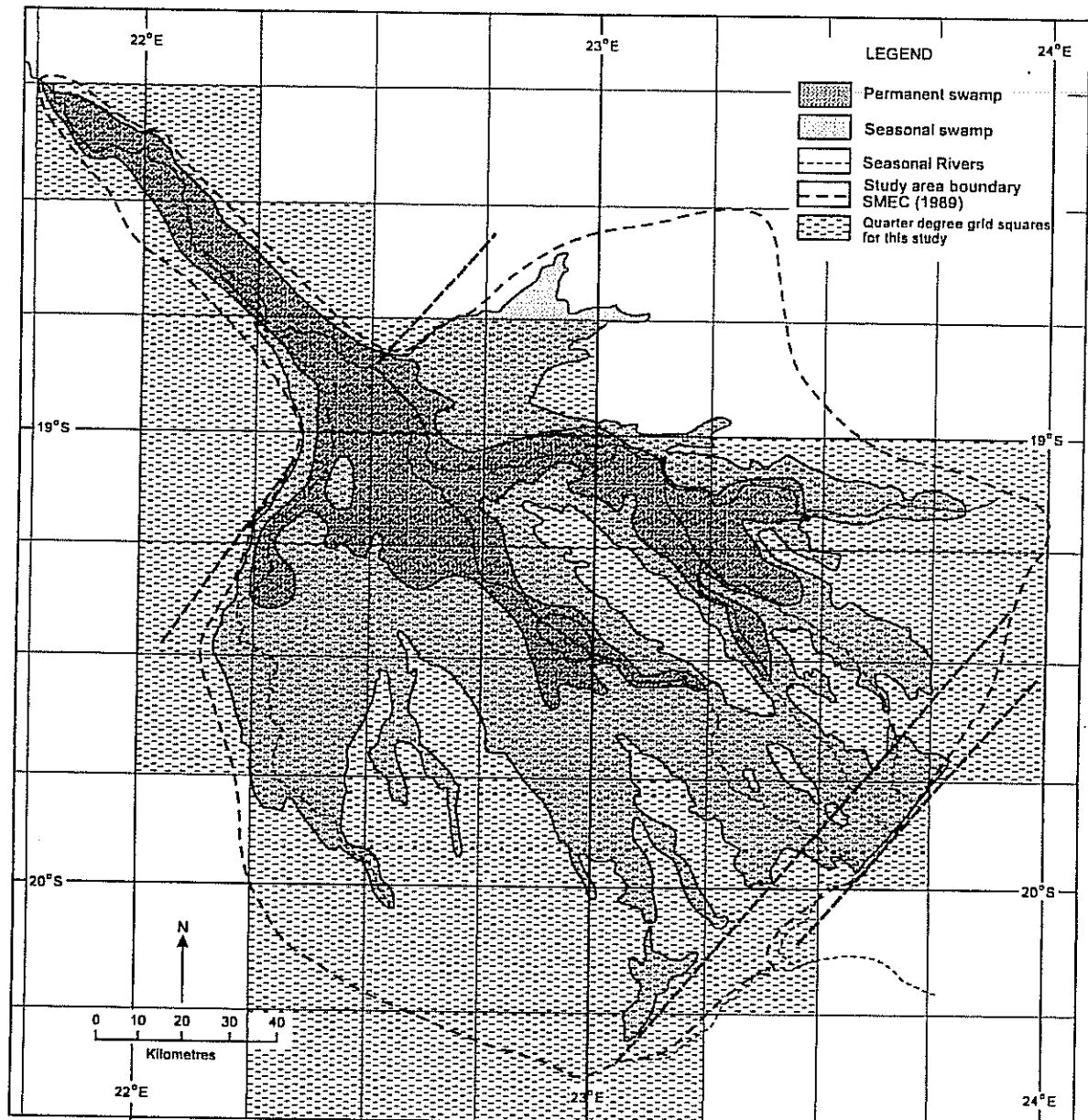
Fig. 2. Map showing the quarter degree grid squares selected for which data were supplied by the National Herbarium, Pretoria in the present analysis, and the area used in the floristic analysis by SMEC (1989).

Similarly, trees and shrubs could be aquatic. Nevertheless, this analysis performed does enable comparison with the life-form spectra of other biomes in the region.

Habitat preferences were identified primarily based on information provided in SMEC (1989) and Ellery and Ellery (1997).

Local and landscape level heterogeneity

Data from vegetation surveys carried out over the period of approximately 15 years by the authors and several additional co-workers, have been used as the basis for describing the most important patterns of community heterogeneity at the local and

landscape level, and for interpreting the underlying gradients responsible for this variation. For the purposes of this study, an attempt has been made to quantify heterogeneity along several of the most important environmental gradients in the study area, as indicated by the number of species turnovers. Species turnovers have been assumed to be reflected by the length of ordination axes (Jongman et al. 1995), with 4 standard deviation units representing approximately one species turnover. The sample scores along the first one or two ordination axes has thus been considered to provide an index of community level heterogeneity.

The most important gradients in several environments within the Okavango Delta have been identified, including channels and channel margins, backswamp communities in the permanent swamps, floodplain communities in the seasonal swamps, and island vegetation including the wetland – island vegetation interface. The underlying cause of the variation in species composition along these gradients has been the subject of many investigations involving a team of multidisciplinary researchers, details of which are provided in the original references cited here.

Nevertheless, in order to make results comparable, data analyses were redone, in many cases with additional data, using the Detrended Correspondence Analysis of ter Braak (1987). All of the default values were selected. However, in the case of environmental and species gradients perpendicular to the major distributary channel of the Okavango Delta, the Nqoga River system, new data is presented. Transects were carried out at right angles to the channel to a distance of approximately 100 m from the channel. Approximately 20 such transects were analysed over a channel distance of approximately 80 km. Due to downstream variation in vegetation distribution that corresponded to variation in vegetation distribution perpendicular to the channel, a single ordination of all of the data did not provide a clear picture of variation along transects perpendicular to the channel. As such the ordination of the full data set was used to determine the overall heterogeneity of the data set. Each transect was then analysed separately, and a linear regression performed of the axis one sample score against the distance from the channel bank. In all cases there was a significant correlation, but some were positive and others negative. Sample scores for all transects had median values of approximately 0, with scores spread on either side of this median in proportion to the variation in species composition. In order to make the entire data set internally consistent, all axis 1 sample scores of transects with a positive correlation between the ordination score and distance from the channel were multiplied by −1. All of the data from all of the transects was then combined and ordination scores were rescaled arithmetically to reflect the heterogeneity of the original ordination of all of the samples. Regression of axis 1 scores against distance from the channel provided an indication of heterogeneity in species composition perpendicular to the channel.

Results

Floristic analysis

The flora of the Okavango Delta is diverse, with 134 families, 530 genera, 1256 species and 1299 taxa of species and lower rank having been collected and

Table 1. The number of species and lower rank taxa in large genera (>10 species) in the flora of the Okavango Delta, Botswana.

Family	Genera	Species	Species and lower level
Poaceae	69	217	220
Cyperaceae	22	116	118
Asteraceae	42	79	80
Papilionoideae	24	67	74
Acanthaceae	18	46	47
Euphorbiaceae	18	39	39
Liliaceae	15	33	33
Malvaceae	7	30	30
Convolvulaceae	6	26	27
Amaranthaceae	15	23	27
Mimosoideae	7	22	26
Scrophulariaceae	15	24	24
Rubiaceae	9	22	24
Asclepiadaceae	15	21	21
Caesalpinoideae	12	21	21
Lamiaceae	12	19	19
Cucurbitaceae	11	17	17
Molluginaceae	5	15	16
Capparaceae	5	14	15
Commelinaceae	4	14	15
Combretaceae	2	14	14
Solanaceae	5	14	14
Orchidaceae	4	13	13
Sterculiaceae	4	13	13
Polygonaceae	3	11	12
Tiliaceae	3	11	12
Lythraceae	3	10	12
Lentibulariaceae	1	11	11
Onagraceae	2	10	11
Boraginceae	3	10	10

documented as part of this study. The number of taxa of species and lower rank in the PRECIS list provided by the NBI in South Africa is 951, while the list provided in SMEC (1989), was 1077. While there was considerable overlap between these two lists (729 taxa of species and lower rank), 222 species and lower rank taxa were on the PRECIS list but not on the SMEC (1989) list, while 348 species and lower rank taxa were on the SMEC (1989) list but not in the PRECIS list.

The most diverse families are the Poaceae, Cyperaceae, Asteraceae and Papilionoideae, each of which have greater than 20 genera and 50 taxa of species and lower rank, while an additional 26 families have 10 or more species and lower rank taxa represented (Table 1). Most genera (72%) are represented by one or two species, while a small number (6%) are represented by 10 or more taxa (Table 2).

The life-form spectrum of the Okavango Delta is dominated by herbaceous plants, which comprise a total of at least 72.5% of the flora if graminoid plants are combined with aquatic and non-aquatic herbs (Table 3). Woody plants make up 17.1% of the flora, split approximately evenly between shrubs and trees. The contribution of >10% of aquatic plants (excluding aquatic grasses, sedges, trees and

Table 2. Frequency of species by genus in the flora of the Okavango Delta.

Number of genera	Number of species
284	1
104	2
71	3
31	4
11	5
21	6-10
9	11-15
4	16-20
2	>20

shrubs) is noteworthy. Greater than 10% of the flora were life forms other than those mentioned above, including geophytes or taxa that could not be clearly assigned to one or other life-form class.

Of the total number of taxa present in the Okavango Delta, a high proportion (54%) occur in dryland settings on islands or on sandveld tongues (Table 4). However, many of these taxa are not present in the surrounding savanna habitats as they require a high water table. Therefore, despite the high proportion of the taxa being terrestrial, many of these species and lower level taxa are intimately associated with the wetland environments of the Okavango Delta. A large number of species and lower rank taxa occur in the permanent and seasonal swamps (219 taxa), and many in flooded grasslands (86 taxa) and a combination of flooded grassland and dryland settings (80 taxa). Relatively few species and lower rank taxa are associated with other habitats or habitat combinations. A small number of species and lower rank taxa are parasitic (18 taxa), or insectivorous (12 taxa).

A total of 23 species and lower rank taxa are listed in the red data list of southern African plants (Hilton-Taylor 1996), of which 16 are considered not threatened due to an increase in population sizes or the discovery of more individuals or populations. Insufficient information is available for a further 3 taxa (*Crinum euchrophyllum*,

Table 3. Life form spectrum of the Okavango Delta based on the number of taxa at species level and lower.

Habitat	Life form	Number	Percentage
	Graminoid	324	24.9
	Trees	112	8.6
	Shrubs	111	8.5
Aquatic Herbs	Emergent	86	
	Floating leaved/stem	20	
	Submerged	28	11.6
	Free floating	17	
Non-aquatic Herbs	Creeper/climber	100	
	Non-creeping/climbing	367	36.0
	Other/unknown	134	10.3

Table 4. Distribution of species and lower level taxa in different habitat and habitat combinations of the Okavango Delta, Botswana.

	Drylands	Riverine Woodlands	Flooded Grasslands	Rainwater Pans	Seasonal Swamps	Permanent Swamps
Drylands	696					
Riverine Woodlands	2	43				
Flooded Grasslands	80		86			
Rainwater Pans	1		24	36		
Seasonal Swamps			25	1	8	
Permanent Swamps			16		219	4

Gossypium herbaceum subsp. *africanum*, and *Hyparrhenia nyassae*) to determine whether they deserve to be placed in a special conservation category. *Leersia denudata* and *Zeuxine africana* are not recognised in Botswana as warranting placement in a special category for conservation, but are suspected of warranting placement in a special category elsewhere in the southern African region. *Harpagophytum procumbens* subsp. *procumbens* is considered vulnerable, which means that it is likely to become endangered if steps are not taken in the near future to limit its decline.
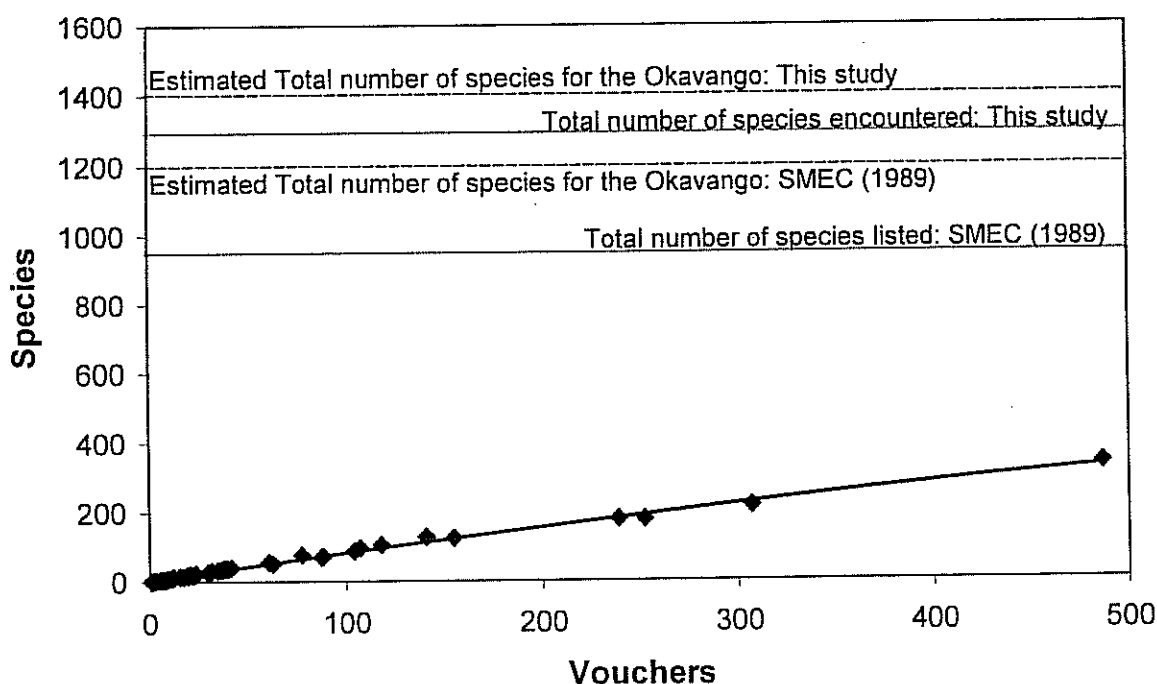

Fig. 3. Relationship between the number of species and vouchers (specimens) in each of the quarter degree grid squares for which data were provided by the National Herbarium, Pretoria. Actual and predicted numbers of species are also shown for SMEC (1989) and the present study.

Based on the current data it is possible to estimate the total species richness of the Okavango Delta (cf. Sutherland 1996). Based on the use of the mark-recapture method it is estimated that the total number of species and lower rank taxa in the Okavango Delta is 1405. It is also of interest to examine the relationship between the number of vouchers collected and the number of species and lower rank taxa represented by those vouchers in 49 quarter degree by quarter degree squares (Fig. 3). The relationship presented in Figure 3 appears to saturate as more and more vouchers are collected. Presumably, when collection starts, there is little duplication of species, but as the number of vouchers increases, there is increasing duplication of species and there is little new information added per voucher collected. It is assumed that the asymptote to this curve represents the number of species present in the ecosystem. The number of species listed in SMEC (1989), by PRECIS in this study, and estimates for the total number of species present in the system by SMEC (1989) and this study are also illustrated in Figure 3.

Landscape level heterogeneity

Channel bed vegetation

In a study of the vegetation distribution in one of the major distributary channels of the Okavango Delta, the Nqogha and Maunachira River system (Ellery et al. 1990), two environmental gradients (Eigenvalues of axes 1-4 were 1.00, 0.55, 0.25 and 0.18 respectively) were recognised as accounting for much of the variation in vegetation distribution. The most important environmental variable was the source of water: channel vegetation on the bed of channels that received water directly from
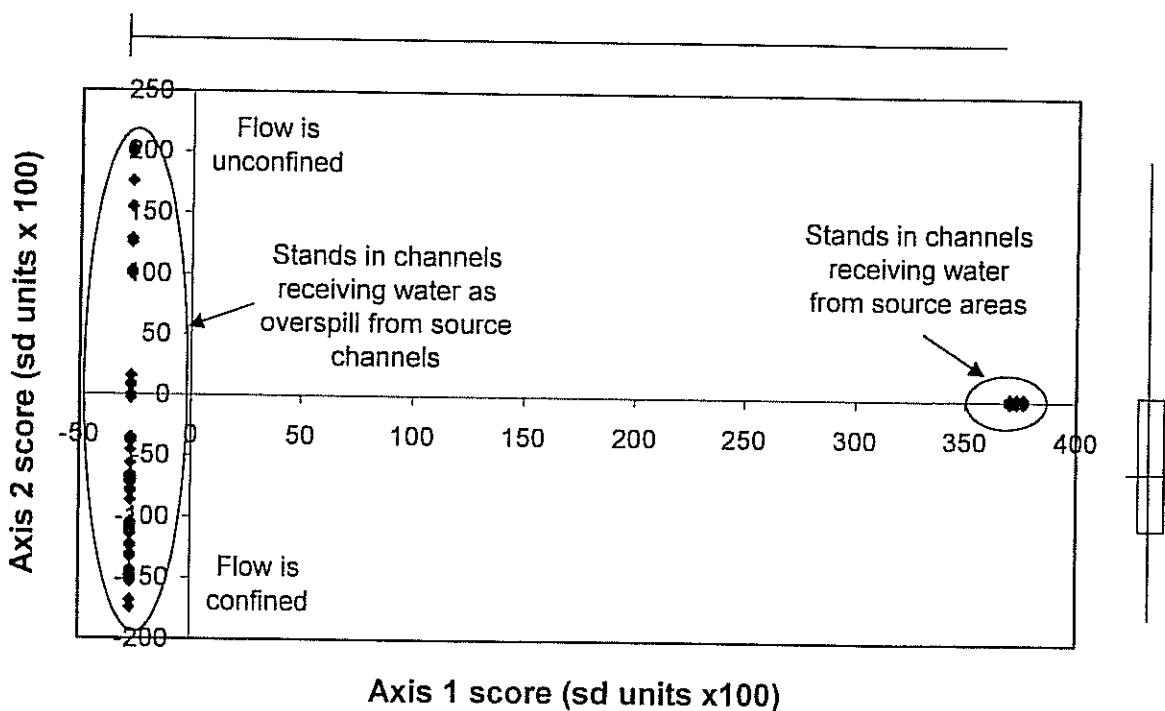

Fig. 4. Axis 1 and axis 2 scores from the sample ordination of channel vegetation from the Nqoga and Maunachira River system in the north-eastern region of the Okavango Delta.

source areas had a single species rooted in the channel bed, *Vossia cuspidata*, which occurred close to the edge of the channel only; channels that received their water supply as overspill from these source channels via filter areas, had a diverse flora that often occupied the entire width of the channel. When represented in ordination space, samples on channels which receive water directly from source areas were clustered together with a high positive value on the first axis of the ordination and a score of zero on the second axis of the ordination (Fig. 4). In contrast, those samples on channels with water derived as overspill from source channels, had a single low negative value on the first axis of the ordination, but had a wide range of values on the second axis of the ordination. Stands could therefore be divided clearly into two groups on the basis of water source, namely whether it was derived directly from the catchment and had not been processed materially by flow through the plant communities flanking the source channels, or whether it had been processed by communities flanking these source channels and therefore have suspended and bed-load sediment, and much of the plant nutrient supply removed.

The arrangement of stands that received their water supply as overspill from the source channels along the second axis of the ordination, reflected variation in environmental conditions downstream. The degree of confinement of flow within channels affects current velocity, and shows an overall decline downstream in the study area (Ellery et al. 1990). It is difficult to separate these effects. Current velocity is a physical variable that affects vegetation distribution, in that some species can tolerate high current velocities while others are unable to and occur in areas with low current velocities. However, in the case of channels in the Okavango, the degree of confinement of channels is controlled by vegetation processes in the channel margin, particularly by the giant sedge *Cyperus papyrus* (Ellery et al. 1995). Vegetation in the channel margin is rooted in peat deposits flanking the channel. It tends to encroach into channels from the channel margin such that the current velocity in the channel increases to accommodate flow. As such, channel hydraulics are controlled primarily by vegetation processes in the channel margin. However, this process appears to be governed to a large degree by nutrient supply, which declines downstream, and it is for this reason that channels become less confined, and experience lower current velocities, as one moves downstream.

Changes in species composition along this second gradient include decreased abundance of *Eichhornia natans* and *Vossia cuspidata*, and an associated increase in abundance of *Brasenia schreberi*, *Ceratophyllum demersum*, *Nesaea crassicaulis*, *Ottelia* spp. and *Rotala myriophylloides*.

It is possible to gauge the landscape level heterogeneity associated with these two gradients by examining the range of values covered by samples along each of the axes of the ordination. Stands on the first axis of the ordination cover a range of 4.0 standard deviation units, while the second axis of the ordination covers 3.8 standard deviation units (Table 5), as indicated by the box-and-whiskers plots above and to the right of the ordination diagram for axes 1 and 2 respectively (Fig. 4). This represents approximately one species turnover for each of these gradients. In this case the distance of channel covered in the analysis was in the region of 100km. Compared to other gradients in different environmental settings in the Okavango Delta, heterogeneity in the channel vegetation of the Okavango Delta is not particularly high (Table 5).

Table 5. Ranges of plot scores (standard deviation units) on the ordination axes of several data sets in which the vegetation distribution has been examined along selected environmental gradients in the Okavango Delta.

Data set	Axis 1		Axis 2	
	Minimum	**Maximum**	**Minimum**	**Maximum**
Channel bed vegetation	-0.27	3.73	-1.75	2.01
Channel margin vegetation	-1.89	1.63	-1.38	5.6
Channel margin – backswamp vegetation	-2.98	3.11		
Backswamp vegetation	-1.27	7.95	-1.18	3.70
Floodplain vegetation	-2.33	8.02	-2.22	5.31
Island vegetation	-2.57	6.35	-3.55	3.94

Channel margin vegetation

Vegetation in the channel margin of the Okavango, Nqoga and Maunachira River system has been described in several studies (McCarthy et al. 1988, Ellery et al. 1990, McCarthy and Ellery 1997), although this study represents the first attempt to include the entire data set of samples 5m from the channel from a variety of channel systems in a single analysis. The first axis of the ordination is considered to account for much of the variation in the data as a whole (Eigenvalues of axes 1-4 were 0.57, 0.27, 0.24 and 0.17 respectively), but the present analysis suggested that two environmental gradients were particularly important. The stands with high positive values on the first axis were in the Panhandle and upper Nqoga River in the proximal reaches of the system, while the stands with highly negative values on the first axis were in the middle to lower reaches of the permanent swamps (Fig. 5). There are several environmental gradients recognisable from the top to bottom of the channel system investigated, including a downstream decline in clay content and water nutrient status of the channel margin. Presumably these gradients underpin the observed changes in species composition. The arrangement of stands on the second axis was along a gradient of wetness, with stands with high positive values being susceptible to seasonal drying, while those with negative values were permanently flooded. Both of these gradients are physical gradients, although vegetation in the channel margin is responsible for the efficient trapping of clay-rich sediment and removal of dissolved nutrients in the channel margin, and therefore contributes to the character of the substratum. It is of interest that the upstream sites experience a wide range of flooding conditions, whereas those further downstream tend to be permanently flooded, reflecting a decrease in seasonal variation in the water level fluctuations downstream within the permanent swamps.

Downstream changes in species composition in the channel margin are distinct. *Phragmites mauritianus* dominates much of the panhandle, giving way to *Cyperus papyrus* which dominates much of the middle section of the system. This gives way to *Miscanthus junceus* which is the dominant species in the lower reaches of the permanent swamps, and which gives way downstream to the swamp fig *Ficus verruculosa* before grading into seasonal swamps.

The level of heterogeneity associated with these two gradients is similar to that for the channel bed vegetation, being 4.4 standard deviation units for the first axis,
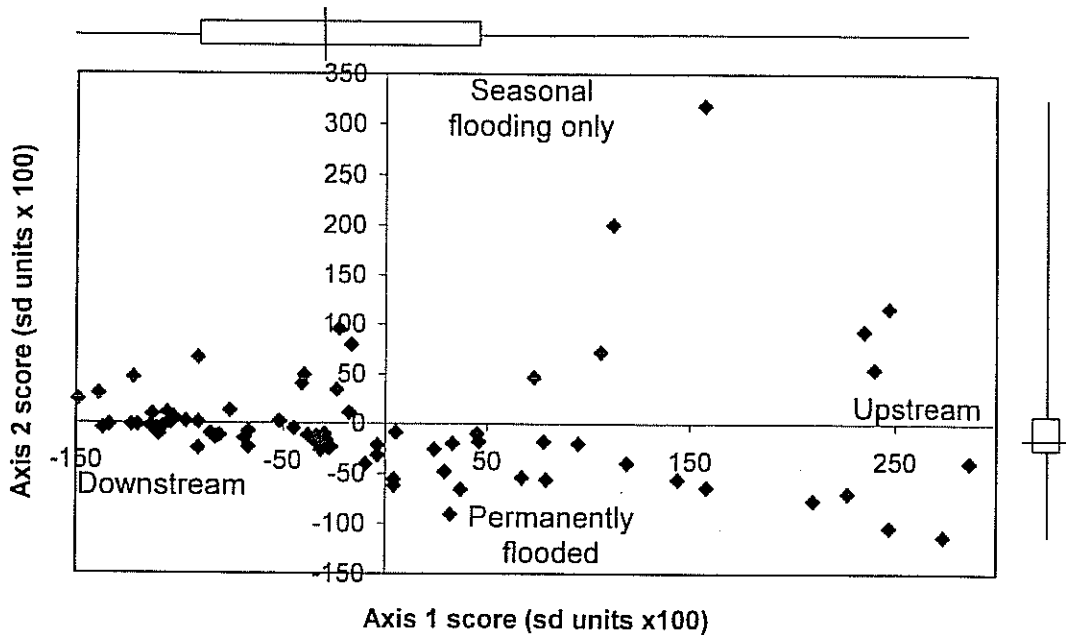
Fig. 5. Axis 1 and axis 2 scores from the sample ordination of channel margin vegetation (5 m from the channel bank) from the Okavango, Nqoga and Maunachira River system.

and 4.3 standard deviation units for the second axis of the ordination (Table 5), as indicated by the box-and-whiskers plots above and to the right of the ordination diagram for axes 1 and 2 respectively (Fig. 5). The length of channel represented in this study was in the region of 250km.

Channel margin – backswamp vegetation

The level of heterogeneity associated with vegetation change from the channel margin into the backswamp areas of the permanently flooded region of the upper region of the Delta (Nqoga River) is shown in Figure 6, which plots the rescaled sample score on axis 1 of individual transect ordinations against the distance of samples from the channel. There was a significant negative correlation (P<0.0001) between plot scores and distance from the channel, suggesting that species composition changes as one moves away from the main distributary channel (Fig. 7). It is unclear what underlies this gradient in species composition, but it is likely to be a combination of clay content, with stands close to the channel having a higher clay content than those further from the channel, as well as water nutrient status, with stands close to the channel receiving water of higher nutrient status than stands further from the channel. As water flows away from the upper distributary channel into the surrounding backswamp areas, in response to the hydraulic head in channels which are elevated relative to the surrounding backswamp areas (McCarthy et al. 1990), plant communities close to the channel remove nutrients from the water, thereby creating a gradient in nutrient supply at right angles to the channel axis (McCarthy et al. 1993b). This gradient is therefore one that is generated by the biota itself, creating a gradient in substratum characteristics and nutrient supply that is reflected by heterogeneity in community composition.
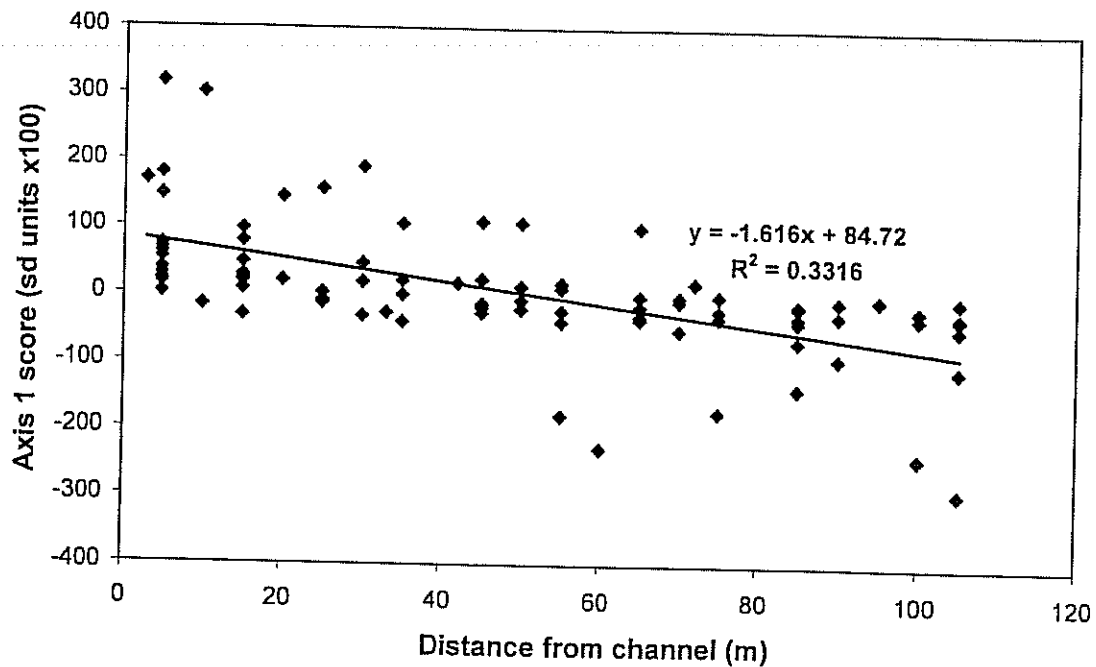
Fig. 6. Rescaled axis 1 scores from the sample ordination of vegetation perpendicular to the channel into the backswamp areas fringing the Nqoga River in relation to distance from the bank.
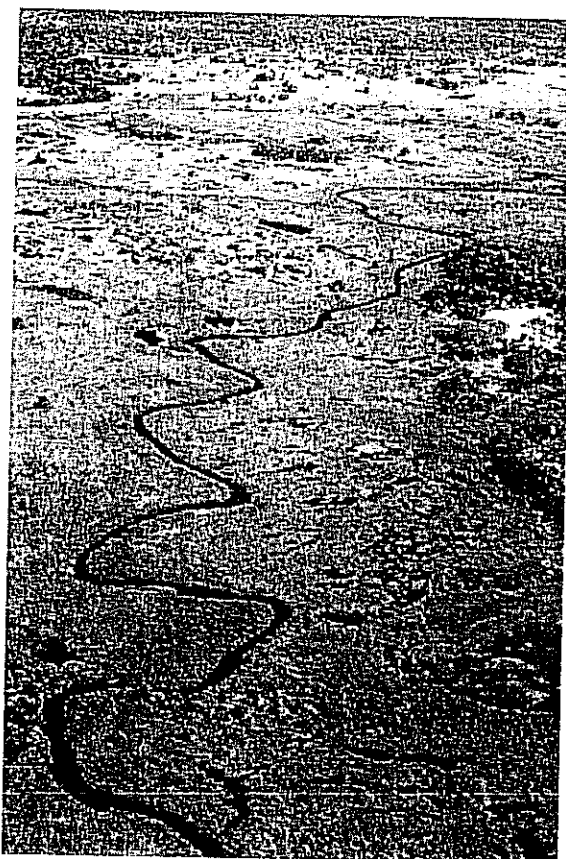

Fig. 7. Zonation of vegetation perpendicular to channels in the Okavango Delta as indicated by the more dense and luxuriant growth close to the channel, giving way to more open vegetation away from the channel.

This gradient is variable depending upon how far downstream in the system one starts a floristic analysis, but there is always a distinct zonation in species composition away from the channels. In the case of the transect shown in Figure 8, *Cyperus papyrus* is dominant close to the channel. It gives way laterally to *Imperata cylindrica* and *Miscanthus junceus*, with *Ficus verruculosa* being locally abundant 15m from the channel on the right bank.

The heterogeneity that is associated with this gradient is considerable, being almost 6.1 standard deviation units along the first axis of ordination (Table 5), corresponding to approximately 1.5 species turnovers. This gradient operates over distances of 100m, suggesting that the heterogeneity away from the main distributary channel of the Okavango Delta is considerably steeper, since it contributes to greater than one species turnover over a distance of approximately 100m, than the most important gradients downstream along the entire length of the main distributary channel system described above, which has lower heterogeneity over tens to hundreds of kilometres.
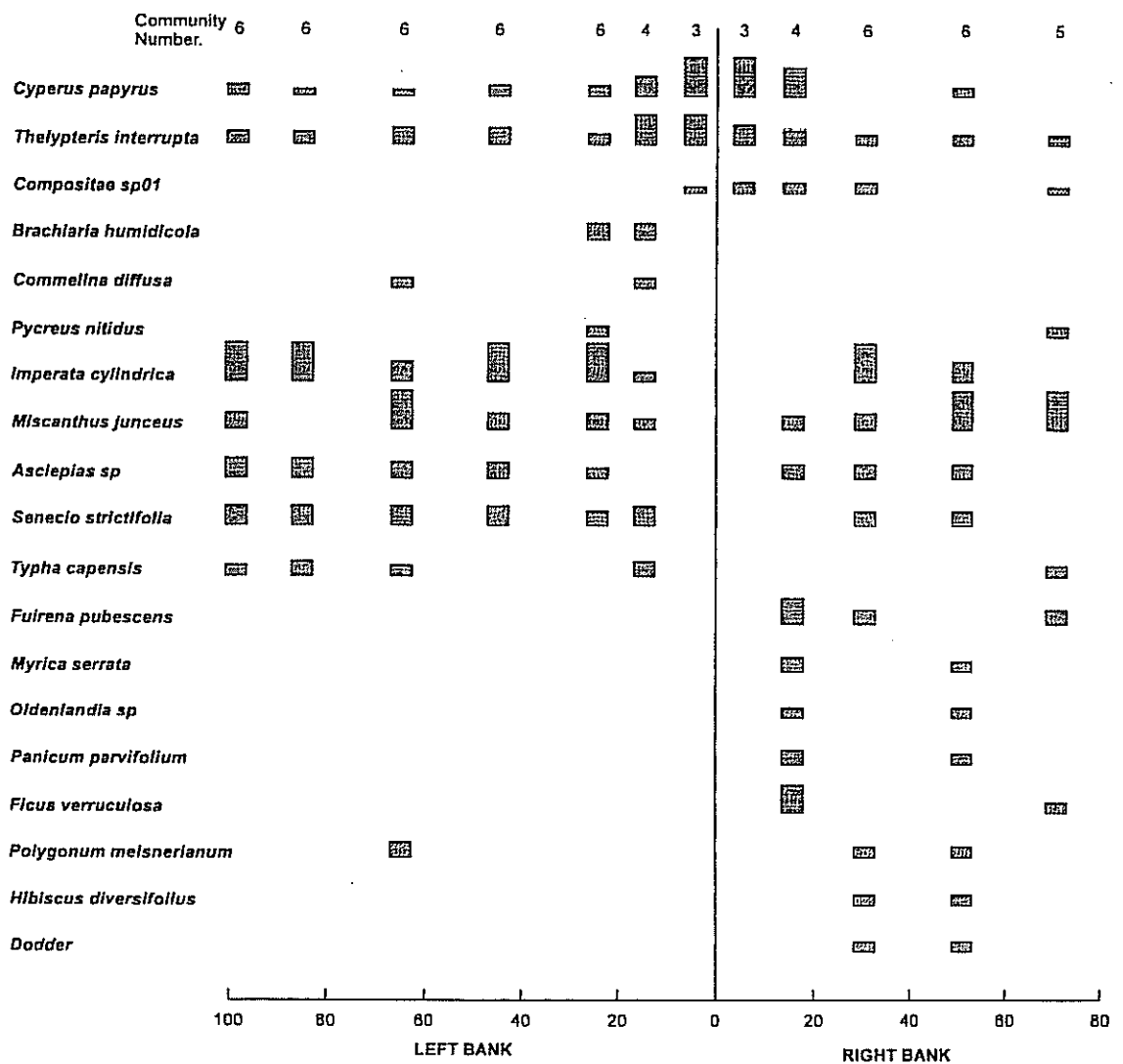
Community Number.	6	6	6	6	6	4	3	3	4	6	6	5
Cyperus papyrus	▪	▪	▪	▪	▪	▪	▪	▪	▪		▪	
Thelypteris interrupta	▪	▪	▪	▪	▪	▪	▪	▪	▪	▪	▪	▪
Compositae sp01							▪	▪	▪	▪		▪
Brachiaria humidicola					▪	▪						
Commelina diffusa			▪			▪						
Pycreus nitidus					▪							▪
Imperata cylindrica	▪	▪	▪	▪	▪	▪				▪	▪	
Miscanthus junceus	▪		▪	▪	▪	▪		▪	▪	▪	▪	
Asclepias sp	▪	▪	▪	▪	▪			▪	▪	▪		
Senecio strictifolia	▪	▪	▪	▪	▪	▪			▪	▪		
Typha capensis	▪	▪	▪		▪						▪	
Fuirena pubescens								▪	▪		▪	
Myrica serrata								▪		▪		
Oldenlandia sp								▪		▪		
Panicum parvifolium								▪		▪		
Ficus verruculosa								▪			▪	
Polygonum meisnerianum			▪						▪	▪		
Hibiscus diversifolius									▪	▪		
Dodder								▪	▪			

```
 100    80    60    40    20     0    20    40    60    80
        LEFT BANK                      RIGHT BANK
```

Fig. 8. Typical zonation of species perpendicular to the channel axis at a site on the upper Nqoga River in the upper reaches of the permanent swamps. Bar heights are proportional to percentage cover.

Backswamp vegetation

The distinction between channel margin vegetation and backswamp vegetation is not clear, but the gradient between the two has been highlighted in the above section. In a separate study of the landscape level heterogeneity of backswamp communities of the Maunachira River system, Ellery et al. (1991) identified water depth as the environmental gradient most strongly associated variation on the first ordination axis, while variation on the second axis was associated with autogenic successional processes on floating rafts of organic matter (Ellery et al. 1990), to give rise to a diverse array of plant communities (Fig. 9). Once again this highlights the importance of both physical (water depth) and biological processes (plant succession on floating rafts of organic matter) in contributing to landscape level heterogeneity.

Species that occupy deep water habitats include *Najas horridus* and *Websteria confervoides*, giving way with a decrease in water depth to floating leaved species such as *Brasenia schreberi*, *Nymphaea caerulua* and *Nymphoides indica*, which often occur together with *Typha capensis*. Once water depth decreases sufficiently as a consequence of successional processes associated with the accumulation of organic matter, floating rafts of peat rise up from the bottom of these open water communities, to be colonised by short emergent species such as *Cyperus pectinatus*, *Ludwigia macrocarpa*, *Pycreus nitidus* and *Xyris capensis*. Once stabilised by these species, particularly by *Pycreus nitidus*, these areas are colonised by the tall grass *Miscanthus junceus*, following which plant succession leads to the creation of a short emergent bog community which is diverse, and is not dominated by any particular species. Common species here include *Crassocephalum picridifolium*, *Fuirena pubescens*, *Ficus verruculosa*, *Imperata cylindrica* and *Thelypteris confluens*, and the presence of *Eriochrysis pallida* indicates a particularly advanced seral stage.

The heterogeneity that is associated with these two gradients respectively is 9.2 standard deviation units for the first axis of the ordination, and 4.9 standard deviation units for the second axis (Fig. 9), suggesting relatively high levels of heterogeneity associated with these gradients (Table 5). These gradients operate over tens to hundreds of metres, suggesting exceptionally high levels of heterogeneity at the landscape scale.

Floodplain vegetation

A number of studies of floodplain vegetation have been carried out in the Okavango Delta (Dangerfield et al. 1998, Ellery and McCarthy 1998, Ellery et al. 1998, McCarthy et al. 1998), and generally reveal variation in species composition in relation to the depth and duration of flooding as illustrated in Figure 10. However, a single study in the vicinity of Mombo at the northern end of Chiefs Island will be reported here as it highlights the most important vegetation and environmental gradients present (McCarthy et al. 1998). Additional data from a clay-rich floodplain in the same area has been analysed jointly with the data reported in McCarthy et al. (1998). Floodplains in the vicinity of Mombo are either clay rich, comprising the burned remains of peat deposits that existed in the area at a time when water was
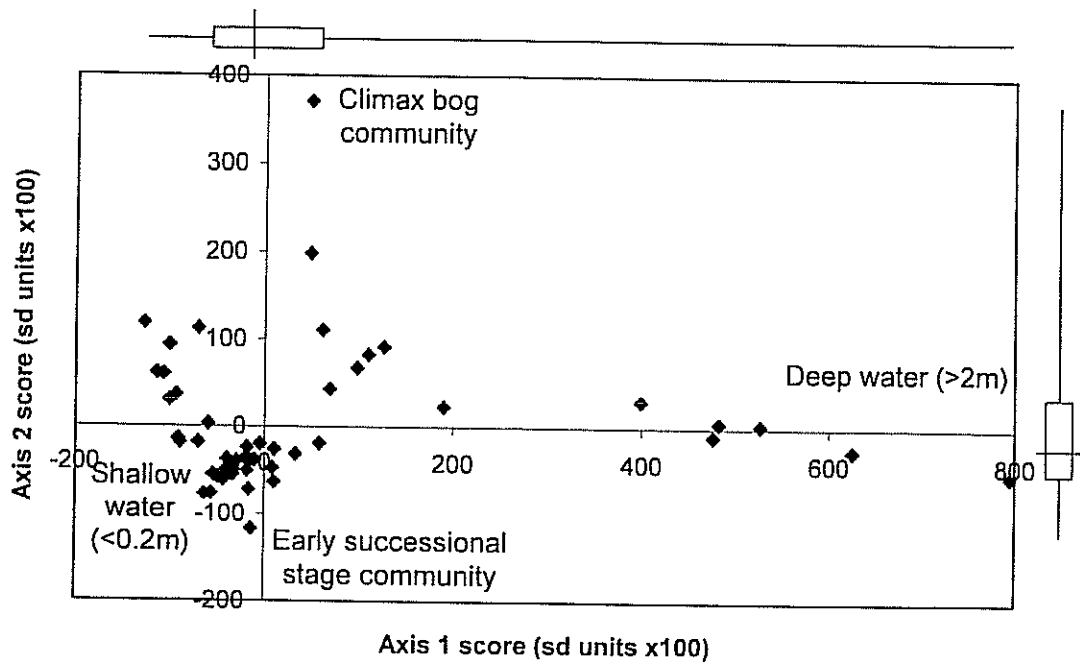
Fig. 9. Axis 1 and axis 2 scores from the sample ordination of backswamp vegetation from the Maunachira River system.

Fig. 10. Typical zonation of species in response to variation in water depth in the seasonal swamps of the Okavango Delta from floating leaved communities in deeper areas, giving way to emergent communities with a decrease in the depth and duration of flooding. Woodland communities dominate areas free of flooding.

more abundant in this area than it is at present (cf. Ellery et al. 1989), or else are sandy, being reworked fluvial or eolian sediments typical of the upper reaches of the Okavango Delta. This difference in substratum is highlighted on the first axis of the ordination, in which stands on these two substrates were separated from each other (Fig. 11). Species typical of the floodplains with the clay rich substrate included *Leersia hexandra*, *Ludwigia stolonifera*, *Paspaludium obtusifolium*, *Phragmites mauritianus*, *Polygonum meisnerianum* and *Sesbania* sp., while those typical of the floodplains with the sandy substrate included *Eragrostis inamoena*, *Panicum repens*, *Schoenoplectus corymbosus* and *Vernonia* sp..

The arrangement of stands on the second axis of this ordination (Fig. 11) was associated with variation in elevation and soil chemistry associated with termite mounds (Fig. 12) and vegetated islands which originated as small termite mounds (McCarthy et al. 1998; Ellery et al. 1998). This gradient is generated purely by the biota on these floodplains, by a combination of processes. Termites create mounds in sandy floodplain habitats by local enrichment of fine material in the soil. Kaolinite is used as the mortar to bind sand grains in the construction of mounds (McCarthy et al. 1998). The creation of topographic relief in this way provides habitat suitable for the establishment of trees which are unable to tolerate flooding in the root zone for lengthy periods (Ellery et al. 1998). Once colonised by trees, transpiration by trees lowers the groundwater table, and because trees are selective in their uptake of plant nutrients, there is accumulation of these dissolved solutes in the soil, particularly calcium, which precipitates out of solution as calcium carbonate, and leads to the creation of topographic relief (McCarthy et al. 1993, Ellery et al. 1998). These nutrient rich hotspots also become favoured sites for ungulate grazers and browsers, which spend a disproportionate share of their time locally in these areas (McCarthy et al. 1998), further changing soil chemistry by importing nutrients into these areas. These nutrients accumulate in the soil at or close to the surface. This combination of processes causes island growth, and ultimately large islands, a hundred metres or more in diameter, are created over considerable time periods (McCarthy et al. 1998, Ellery et al. 1998).

Changes in species composition associated with this gradient are from those species typical of the floodplains on a sandy substrate described above, through *Cynodon dactylon* and *Imperata cylindrica* grasslands, to *Phoenix reclinata* dominated forests in situations where elevation is sufficient to prevent flooding. The zone of *P. reclinata* gives way to broadleaved evergreen forest with *Diospyros mespiliformis*, *Ficus sycomorus* and *F. thoningii*, which gives way to deciduous woodland with *Acacia nigrescens*, *A. sieberana*, *Lonchocarpus capassa* and *Ziziphus mucronata*. The palm *Hyphaene petersiana* occurs towards the centre of islands, and the grass *Sporobolus spicatus* dominates island interiors where soils are saline.

Levels of heterogeneity associated with differences in substratum type in the region of Mombo are high at over 10 standard deviation units on the first axis of the ordination, while those associated with floodplain elevation, the presence of termite mounds or densely vegetated islands that originated as termite mounds are similar, at approximately 7.0 standard deviation units (Table 5). These gradients operate over tens of metres, suggesting high levels of heterogeneity at the landscape scale on these floodplain environments, which are considerably more diverse than they would be in the absence of termites and trees.
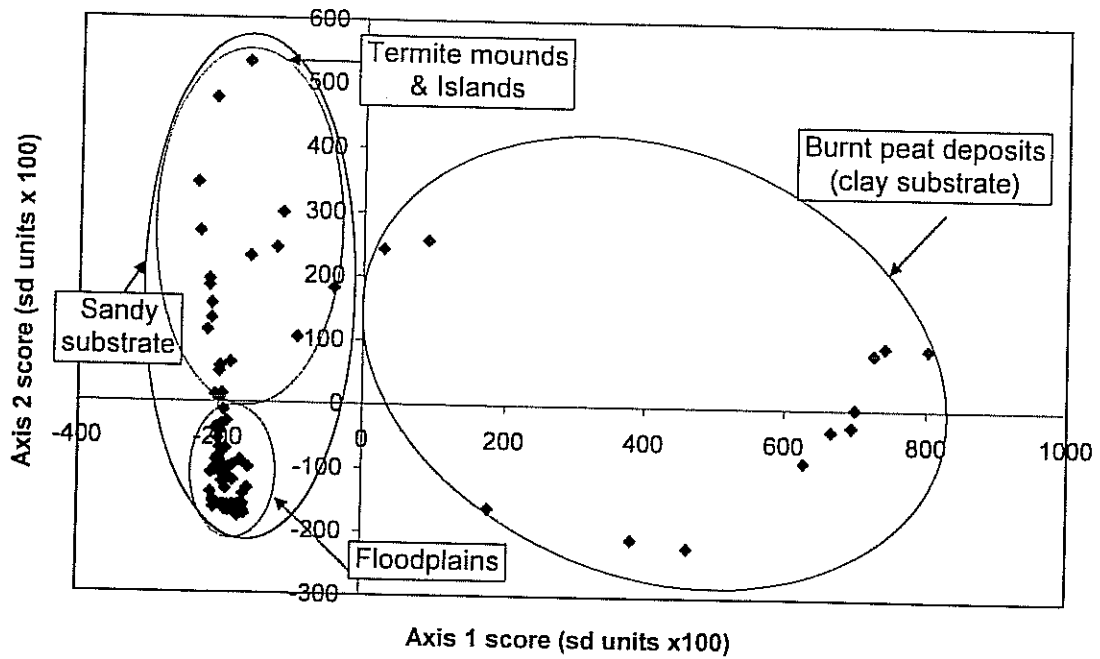
Fig. 11. Axis 1 and axis 2 scores from the sample ordination of floodplain vegetation in the nortwestern part of Chief's Island.

Fig. 12. An elevated termite mound free of seasonal flooding that is colonised by a woody plant in the floodplains of the Okavango Delta.

Island vegetation in the permanent swamps

Heterogeneity on islands in the permanent swamps (Fig. 13) is generated primarily by a single gradient, namely, changes in the total dissolves solid concentration of groundwater associated with selective uptake of dissolved solids in the root zone by plants, and by salinisation of surface soils as a consequence of evaporation from the soil surface in the centres of islands (McCarthy et al. 1993c, Ellery et al. 1993). This gradient is reflected in the ordination of stands from islands throughout the permanent swamps, where the arrangement of stands on the first axis is related to groundwater conductivity and soil salinity (Fig. 14). Stands with high positive values occur at low elevation and where groundwater is fresh with conductivities of less than 0.5mS.cm^{-1}, while those with negative values occur either where soils are saline, or where groundwater conductivities are exceptionally high at greater than 5mS.cm^{-1}. Associated with this gradient in conductivity is the height of the land surface above the water table. The depth to the water table is partly related to elevation of the land surface (topographic relief), which is mainly created by the precipitation of calcium carbonate in the root zone of trees in the island fringe, as described in the previous section, and partly related to the elevation of the water table itself, which is drawn down beneath islands by transpiration in the densely wooded island margins (Fig. 15a). The difference between water demand by this plant community and water supply from the surrounding swamp results in a steep hydraulic gradient from swamp to island fringe, which is maintained beneath the islands themselves, which are typically characterised by a central depression.
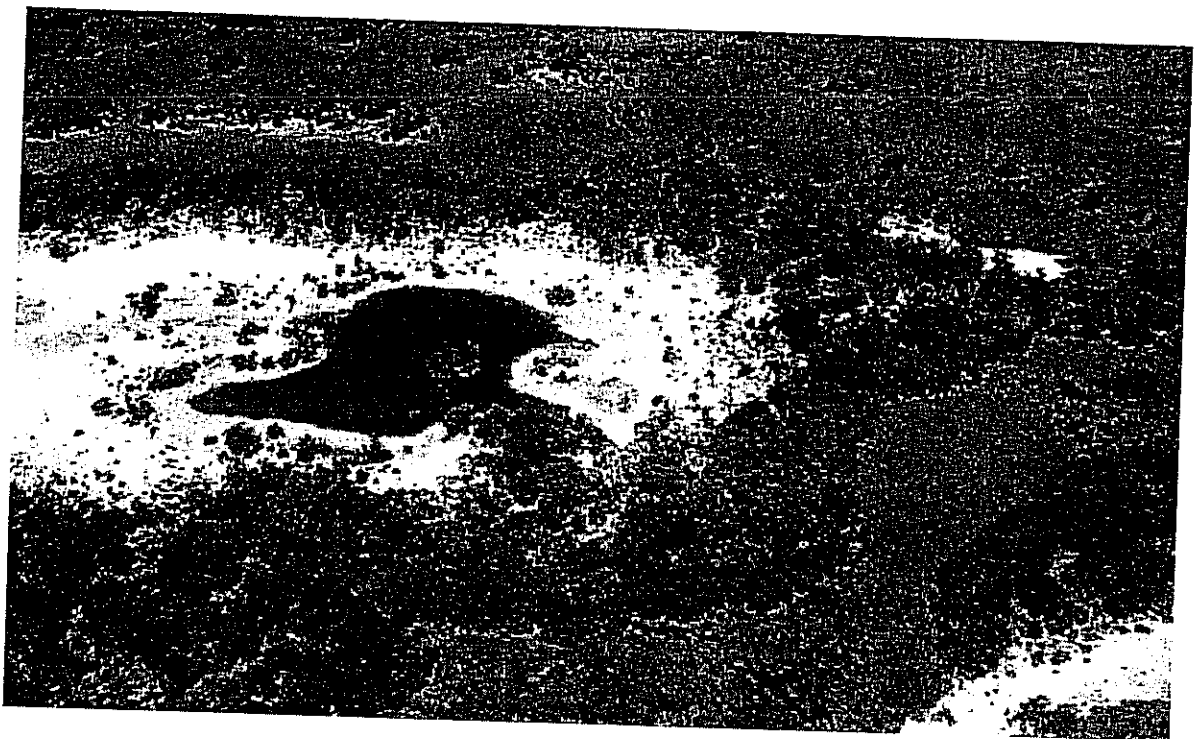

Fig. 13. Zonation of vegetation on a typical island of the Okavango Delta from flooded grass and sedge dominated floodplains through a broadleaved evergreen forest to deciduous woodland, and into a short, sparse grassland surrounding a central depression filled with saline water ("pan").
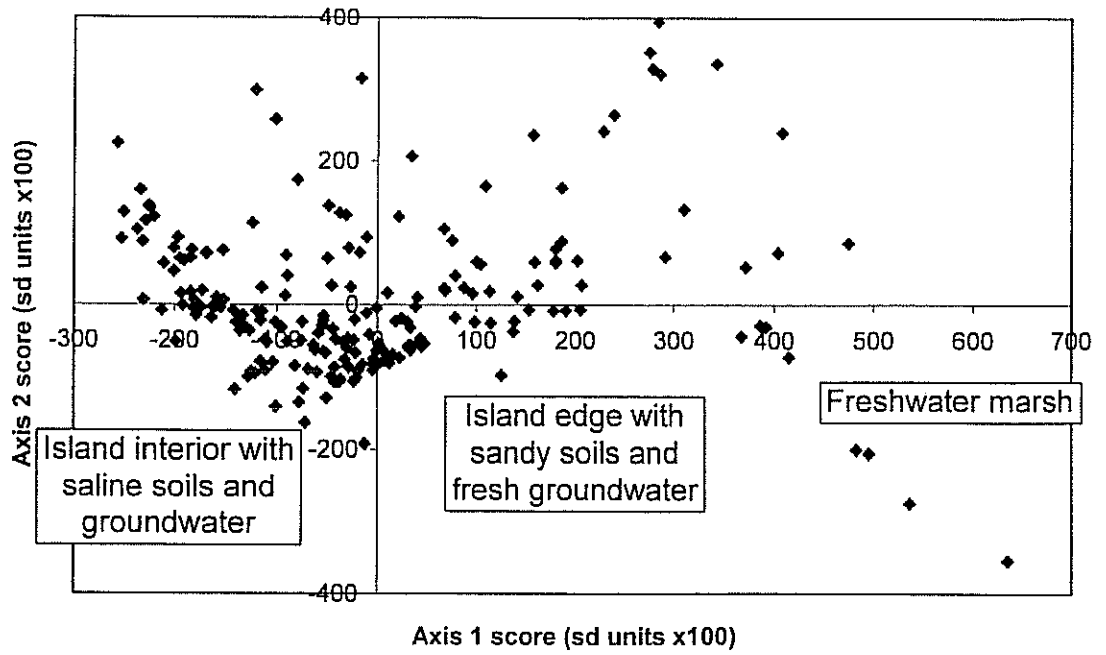
Fig. 14. Axis 1 and axis 2 scores from the sample ordination of island vegetation throughout the permanent swamps.
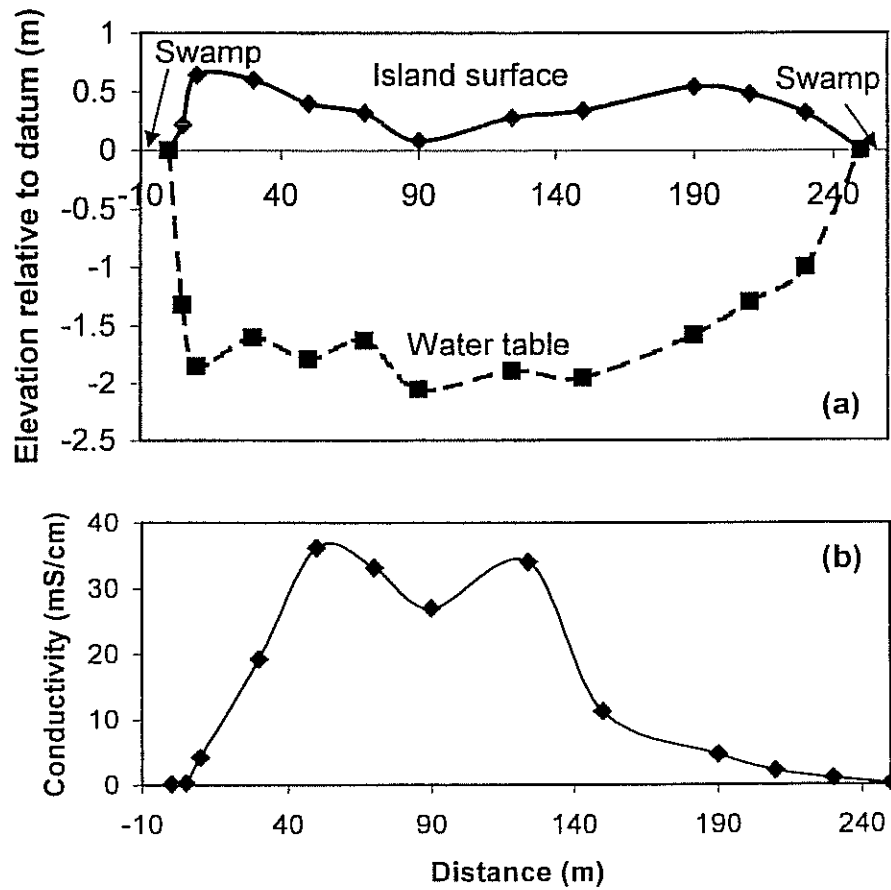

Fig. 15. Topography and groundwater elevation (a) and groundwater conductivity (b) of an island on the upper Boro River (after McCarthy and Ellery 1994).
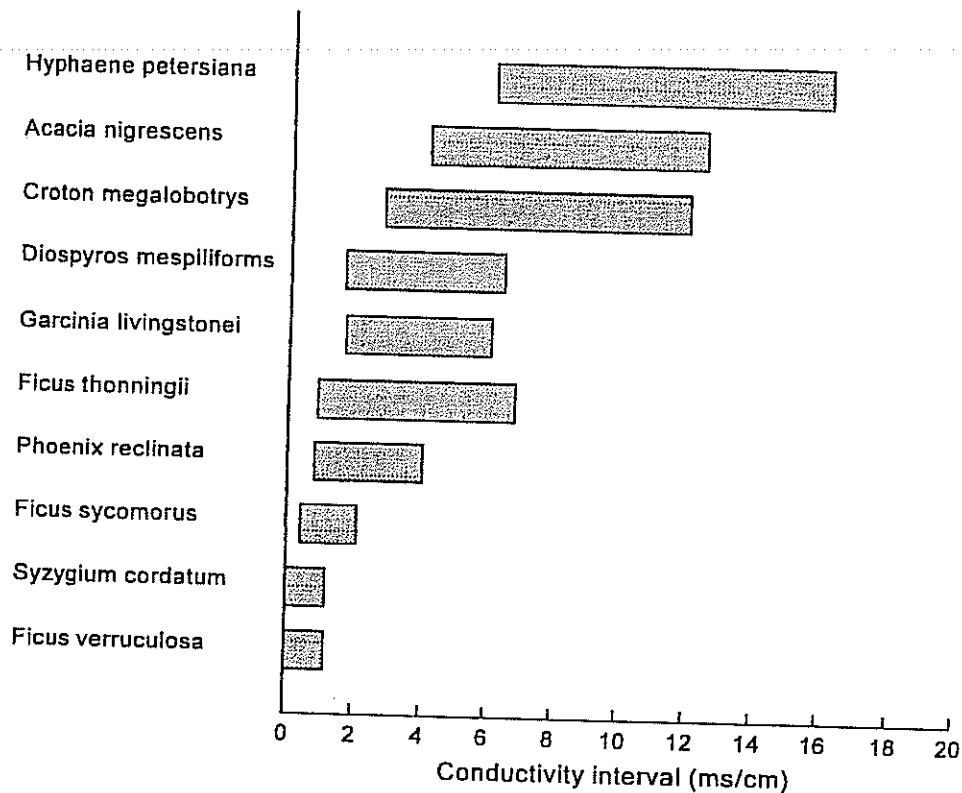
Fig. 16. The range of tolerance of plant species to the concentration of dissolved solutes, as indicated by groundwater electrical conductivity.

There are steep gradients in groundwater conductivity beneath islands (Fig. 15b) as a result of transpiration by plants in the island fringe and selective uptake of dissolved solutes by plants. Heterogeneity of island vegetation is similar to that described in the previous section for the floodplains on sandy substrates, and the tolerance of different species to differences in groundwater conductivity contributes to marked zonation of vegetation (Fig. 16). This heterogeneity is induced primarily by biological processes, particularly by transpiration of trees in dense closed forests in the island fringes. Levels of heterogeneity as indicated by the range of scores on the first axis of the ordination are high, at almost 9.0 standard deviation units (Table 5). This heterogeneity is observed over distances of tens to hundreds of metres, suggesting that these are exceptionally steep environmental gradients.

Regional environmental gradients within the Okavango Delta wetland ecosystem

There are a number of regional gradients that have been described for the Okavango Delta that must be associated with heterogeneity of the biota in the ecosystem. The most notable of these is associated with differences in the hydrological regime. Within the Panhandle, seasonal water level fluctuations are high at more than 1 metre, mainly reflecting dramatic differences in inflow over the annual cycle – all of which is confined in a relatively narrow depression less than 15 km wide on average. In the permanent swamps however, seasonal water level fluctuations are small at less

than 30 cm, primarily because variation in supply along the main channel system which supplies water to the permanent swamps is relatively constant as much of the inflow in the Panhandle has been lost to backswamp areas. Seasonal water level fluctuations in the seasonal swamps are greater than in the permanent swamps due to large differences between demand and supply. Clearly these differences are likely to contribute to regional heterogeneity within the system, as reflected in the marked differences in the vegetation of the permanent and seasonal swamps described by Smith (1976).

A second important regional environmental gradient is the total dissolved solid load in both surface and groundwater. The conductivity of surface water varies by only a factor of two from the top of the Panhandle to the toe of the Delta, despite 96-98% of the surface water being lost to the atmosphere by evapotranspiration (Wilson and Dincer 1976). This is a consequence of transpiration being the predominant means of water loss from the system, and many of the dissolved solids are therefore likely to be accumulating in the soil and groundwater. There is therefore a strong likelihood that regional variation in groundwater conductivity is much more marked than variation in surface water conductivity, and this too must be reflected in biotic heterogeneity, as the roots of many woody plants extend into the groundwater. The regional variation in groundwater conductivity is reflected in the distribution of the two species of palm that occur in the Okavango Delta, *H. petersiana* and *P. reclinata*. The latter species is only tolerant of fresh water with a low conductivity (1-5mS.cm⁻¹; Ellery et al. 1993), and its distribution is restricted to the Panhandle and upper fan region (SMEC 1989). In contrast, *H. petersiana* is tolerant of a much wider range of conductivities (5-16ms.cm⁻¹; Ellery et al. 1993), and its distribution is widespread in the Delta, but it is common on the lower reaches of the Delta where it often is the dominant species – a situation not observed in the upper reaches of the system. The distribution of other species is likely to be influenced by this or other similar regional gradients.

Discussion

The Okavango Delta as a biome

The concept of a terrestrial biome is based on three main criteria: that it is mappable at a continental or subcontinental scale of no larger than 1:10 million; that it is defined primarily on the basis of dominant and co-dominant life forms of plants; and that it is determined secondarily on the basis of climatic features that affect the biota (Rutherford and Westfall 1986). Furthermore, the concept refers to the climax vegetation and is therefore not an unnatural or anthropogenic system.

The Okavango Delta in its own right fulfils three of these criteria, and we believe that it should therefore be mapped at the biome level. The Okavango Delta is mappable at a subcontinental scale. Plants are mainly hemicryptophytes, with their perennating organs at or close to ground level. The wetland environments in the Okavango Delta support few trees, and are dominated by grasses and sedges. The islands are small relative to the extent of wetland, and these support concentric zones of broadleaved evergreen riparian forest at the island edges, a mixture of trees

and grasses towards the island interior, and grassland in the central regions of the islands. Larger islands such as Chiefs Island, as well as the sandveld tongues, support a mixture of grasses and trees (savanna). At an appropriate mapping scale then, the wetland habitats predominate, and they are made up primarily of grasslands and sedgelands.

It is difficult to directly compare differences in the life form spectrum of the Okavango Delta with other biomes in southern Africa, due to differences in the ways in which dominance and co-dominance are quantified (cf. Gibbs Russel 1987, Rutherford and Westfall 1986). Nevertheless, if one uses percentage canopy cover of different life forms, as used by Rutherford and Westfall (1986), there are appreciable differences between the Okavango Delta and the surrounding savanna habitats of the Kalahari. The permanent and seasonal swamps of the Okavango Delta are dominated by grasses, sedges and herbs (hemicryptophytes), while the sandveld tongues and surrounding savanna habitats are co-dominated by trees (phanerophytes) and grasses (hemicryptophytes). Based on dominant and co-dominant life forms alone, the wetland habitats of the Okavango Delta are clearly distinguishable from the surrounding savanna habitats. These occupy an area of approximately 10 000 km^2; (Wilson and Dincer 1976), which is more than an order of magnitude larger than the smallest mappable unit area required for mapping biomes (314 km^2 Rutherford and Westfall 1986). Based on these criteria (dominant and co-dominant life forms and mapping scale), as well as the fact that it is one of southern Africa's most pristine wetland ecosystems, and is not of anthropogenic origin, the Okavango Delta is considered to represent a southern African biome.

The extent to which climate determines the life form spectrum of the biota of the Okavango Delta is open to question. From the perspective of water supply, which is recognised in terrestrial ecosystems to be derived primarily from rainfall, the Okavango Delta receives two-thirds of its water supply from water other than direct rainfall. Furthermore, water supply is most abundant during the dry season, when the Okavango experiences its maximum extent of inundation (Wilson and Dincer 1976). Given this, the duration of the growth season experienced by plants based on water supply alone (cf. Ellery et al. 1991), would be considerably extended relative to the duration sustained by rainfall alone. As such the notion of climate alone determining the distribution of extensive wetland systems such as the Okavango Delta needs to be revisited.

Rutherford (1998) has presented a revised and refined distribution map of southern African biomes, with the inclusion of both Etosha and Makgadikgadi Pans as "nama-karoo", a biome dominated by grasses and shrubs. The Okavango Delta is certainly mappable at the same scale as these two areas. Furthermore, neither the Etosha nor the Makgadikgadi can be considered as terrestrial for the same reasons as the Okavango is not terrestrial, and on this basis a revised biome distribution incorporating the Okavango Delta is proposed (Fig. 17). It is furthermore suggested that the Etosha, Makgadikgadi and Okavango be mapped as wetlands or endorheic basins rather than nama-karoo, on the basis of vegetation structure, mapping scale, the fact that they are not of anthropogenic origin. The normal climatic features that determine biome-level distributions are overridden by the addition of large quantities of water by drainage from elsewhere in the region in the case of these three systems.
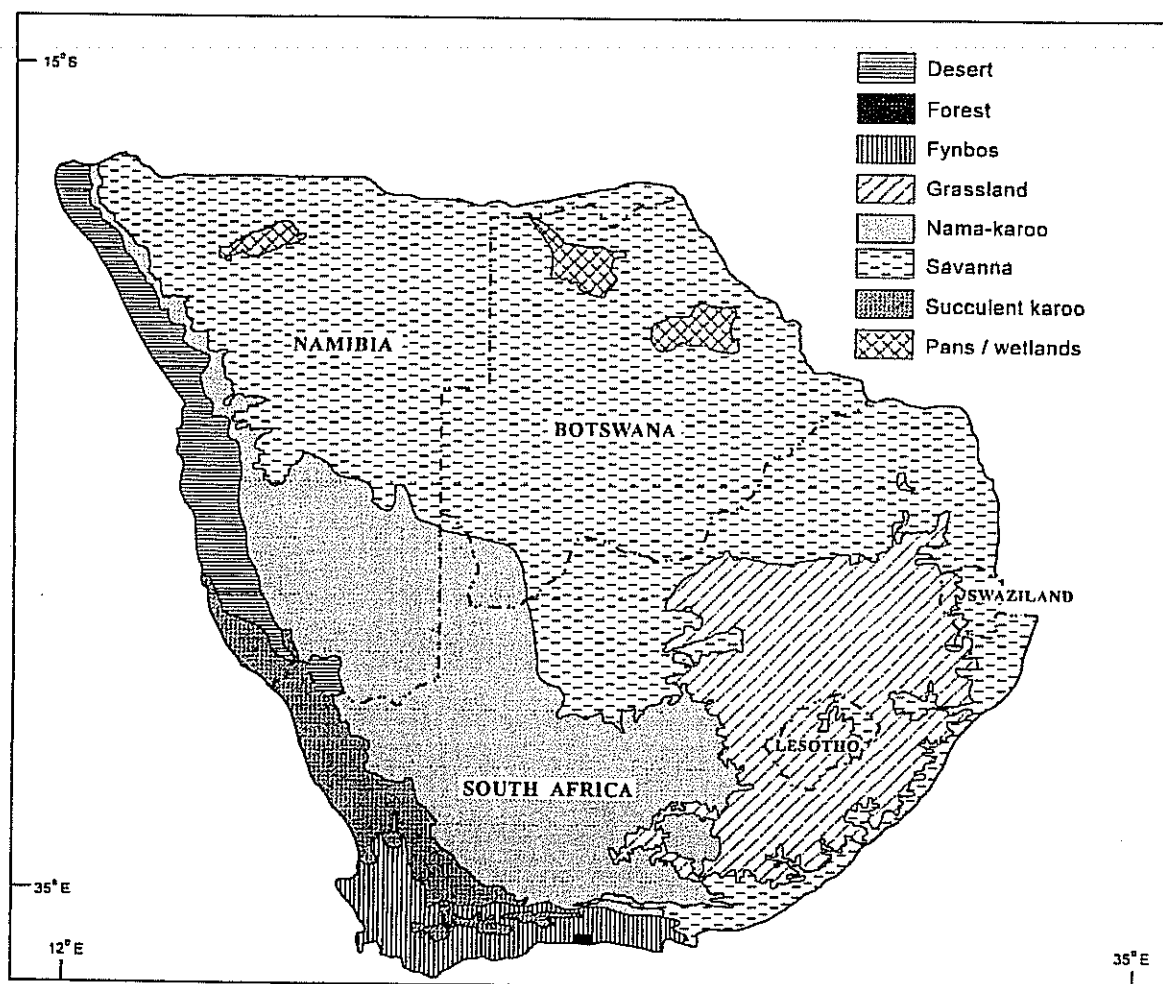
Fig. 17. The proposed distribution of biomes in southern Africa including the Okavango Delta (modified after Westfall 1998).

Floristic analysis

Collection of plant material in the Okavango Delta has been ongoing for many decades, having been carried out largely by a single individual, Mr PA Smith. The collection on which the SMEC (1989) report is based lists 1077 species and lower rank taxa, and estimates a total of 1200 species to potentially occur in the Okavango Delta. Information used in this study was based on additional data provided by PRECIS, which lists 951 species and lower rank taxa. The present study attempts to combine the two lists, incorporating name changes, and it includes 1299 species and lower rank taxa. It must be noted that there are large differences between the PRECIS list and the SMEC (1989) list (Table 6). The SMEC (1989) list includes 348 species and lower rank taxa that are not in the PRECIS list, while the PRECIS list includes 222 species and lower rank taxa that are not on the SMEC (1989) list, with 729 species and lower rank taxa common to both lists. Some of these differences may simply be due to material not being present in one or other of the collections, or they may be partly due to differences in the boundaries of the two studies.

Table 6. Collecting intensity and species richness of southern African biomes (Gibbs-Russell 1987) and the Okavango Delta (this study) based on data from PRECIS. Area refers to the area searched for data based on the number of quarter degree grids searched (cf. Gibbs Russell 1987).

Biome	No. specimens	No. taxa	Area (km²)	Specimens /km²	Taxa/ km²	Specimens /taxon
Desert	1334	497	41292	0.03	0.01	2.7
Fynbos	52650	7316	36628	1.36	0.19	7.2
Grassland	27685	3788	111888	0.25	0.03	7.3
Nama-karoo	7685	2147	198468	0.04	0.01	3.6
Succulent karoo	6484	2125	50516	0.13	0.04	3.1
Savanna	50460	5788	632034	0.08	0.01	8.7
Okavango	2865	961	32634	0.09	0.03	3.0

However, there may be differences in nomenclature which were not detected in the present analysis.

The attempt made in this study to independently estimate the total number of species in the Okavango Delta is based on data from PRECIS and the SMEC (1989) list. It is of interest to compare the relationships between the numbers of specimens, taxa, and area sampled for the Okavango Delta, with other biomes in southern Africa (Table 6). The size of the area sampled for the Okavango Delta to compile species lists in this study is similar to some of the areas sampled by Gibbs Russell (1987) for a similar floristic analysis of biomes in southern Africa, as is the number of specimens and taxa. The density of species in the Okavango Delta (0.029 taxa. km^{-2}) is greater than for the savanna, nama-karoo and desert biomes, and is similar to the grassland and succulent karoo biomes. The number of specimens per taxon for the Okavango Delta on the PRECIS database is lower than for most biomes, suggesting that the area is in need of collection, and that with more intensive collection new taxa are likely to be discovered. However, based purely on this floristic analysis, the Okavango Delta is considered to deserve special attention from a conservation perspective.

The Okavango Delta: an ecosystem engineered by plants

While the role of organisms as modifiers of flows and the spatial distribution of resources has been recognised for some time, studies in the Okavango Delta in northern Botswana suggest that resource flows within it are determined by the activities of a small number of key plant and animal species that initiate and amplify both physical and chemical gradients, such as current velocity, topography, nutrient supply and the concentration of toxins in the groundwater and soil, thereby increasing spatial heterogeneity and consequently biotic diversity on both a local and a landscape scale. It is argued that heterogeneity within the ecosystem as a whole is primarily the product of biotic processes as plants and animals greatly modify the flow of resources within the system, and that this is true at various scales of resolution. In the discussion that follows, we describe the impact of plants and animals on ecosystem dynamics, to further demonstrate the extent to which the ecosystem is a product of biological activity.

Regulation of water flow in channels by biota

Plant species on channel margins are rooted in peat and receive their water supply from the channels as the peaty margins are permeable to water flow (McCarthy et al. 1988), and the channel water surface can be elevated by as much as 50 cm relative to the surrounding backswamp (McCarthy et al. 1990). The giant sedge *Cyperus papyrus* is common in the fringes of upper channels and forms an entangled mat of roots and rhizomes which floats and rises with the flood (Ellery et al. 1995). Papyrus grows from the channel margins into the channel, confining flow and increasing flow rate. The associated changes in hydraulic head result in water loss from the channel and a decline in discharge downstream. This reduces the ability of the flow to transport bedload, and the peat margins prevent bedload escaping from the channels, which instead is deposited on the channel bed, causing aggradation (McCarthy et al. 1992). The prolific growth of the papyrus mat enables aggradation of the channel margins at a rate that is concomitant with deposition of sediment along the channel bed to produce vegetation levees, resulting in an increase in the hydraulic gradient away from the channel (McCarthy et al. 1986). The combination of these processes eventually results in constriction which ultimately leads to complete failure of the channel.

As water is lost from these channels, papyrus takes up nutrients from the water, creating very steep gradients in nutrient availability away from primary channels that are reflected in plant biomass (McCarthy et al. 1993b) and species composition over tens of metres marginal to the channel as described in this study. A dense fringe of papyrus in the channel margin gives way rapidly to more open backswamp vegetation communities dominated by a relatively diverse flora including *Ficus verruculosa, Leersia hexandra, Miscanthus junceus, Pycreus nitidus, Senecio strictifolia, Thelypteris interrupta* and *Typha capensis*.

Increased discharge away from an aggrading primary channel, in the absence of sediment loss, means that erosion is a common feature in backswamp areas. New channel systems are initiated along the network of hippopotamus (*Hippopotamus amphibius*) trails in backswamp areas, especially those parallel to the steepest hydraulic gradient, as these provide loci of increased hydraulic transmissivity (McCarthy et al. 1998). Erosion widens these hippo trails. The location, sinuosity and ultimate planform geometry of channels within the delta is therefore inherited from the original network of hippo trails.

A consequence of erosion in backswamp areas, and simultaneous aggradation in primary channels of up to 6 cm a^{-1} is that channels migrate by a process of avulsion where flow from an aggrading primary channel is diverted to a new channel system (McCarthy et al. 1986, 1992). Avulsion may be local, associated with migration of channels over tens of kilometres, or may be radical, and result in diversion of water from one region to another, such as the major avulsion of the Thaoge into the Nqoga River late in the last century (Wilson and Dincer 1976). Several such avulsion events have been recorded in historic time, and are followed by the occurrence of subsurface peat fires, which release nutrients previously tied up in peat deposits to create local sites of high productivity and forage quality compared with the surrounding swamp or floodplain environments (Ellery et al. 1989).

Clearly, fluvial processes would occur irrespective of whether plant or animal life was present. However, bedload dominated rivers with high seasonal fluctuations in discharge are braided whilst the Okavango Delta channels are sinuous, and show no evidence of braiding (Stanistreet et al. 1993). Biota therefore affect the entire physical structure of the river system. Papyrus and hippopotami impact on local scale current velocity, discharge and nutrient gradients, but because they regulate hydrology, they influence the water distribution over the entire surface of the Okavango, and therefore have an impact at the widest scale of the entire ecosystem.

The role of biota in affecting floodplain morphology

Large mounds constructed at densities of up to 6 ha^{-1} by the termite *Macrotermes michaelseni* in the floodplain environments of the delta are enriched in clays and nutrients, promoting the growth of grasses with high forage quality such as *Cynodon dactylon*, which attract grazers and mixed feeders such as impala (*Aepyceros melampus*; McCarthy et al. 1998). Due to their elevation these mounds are colonised by woody plants which are unable to survive prolonged flooding of the root zone, and a vegetation zonation around these small islands results from differences in the depth and duration of flooding.

The growth of trees increases transpirational water loss from these islands, a depression of the water table follows and a hydraulic head between the edge of the island and the centre is created, so that swamp water replaces transpiration losses (McCarthy et al. 1993). Because plants remove solutes selectively, and in small quantities relative to the amounts of water, transpiration generates a salinity gradient in the groundwater, and silica and carbonate saturate and precipitate in the soil (McCarthy and Ellery 1993, McCarthy et al. 1993). This causes both lateral and vertical island growth. It is remarkable that transpiration by large trees in the island fringe leads to the creation of topographic relief. In the Okavango Delta which receives exceptionally small quantities of clastic sediments, precipitation of dissolved solutes in the soil in this way is an important aggradational process, particularly in the lower reaches of the system.

Plant distribution is affected by tolerance to groundwater salinity, with the palm *Phoenix reclinata* and broadleaved evergreen trees dominant on island fringes where water is fresh, through deciduous trees and the palm *Hyphaene petersiana* which dominate where groundwater salinity is intermediate, to the saline interior which supports only the grass *Sporobolus spicatus* (Ellery et al. 1993).

Despite evapotranspiration being the most important means of water loss from the system, the concentration of dissolved chemicals in surface water increases by only a factor of 2 down the length of the Delta (Wilson and Dincer 1976). Transpiration by trees confines salinisation exclusively to the groundwater beneath islands, while surface water remains remarkably fresh. The focussing of toxic salts locally, particularly on islands within the Okavango Delta ecosystem, is the reason that surface water of the Okavango remains fresh in a setting in which a shallow saline lake would be expected since evaporation exceeds rainfall during every month of the year (Fig. 18).
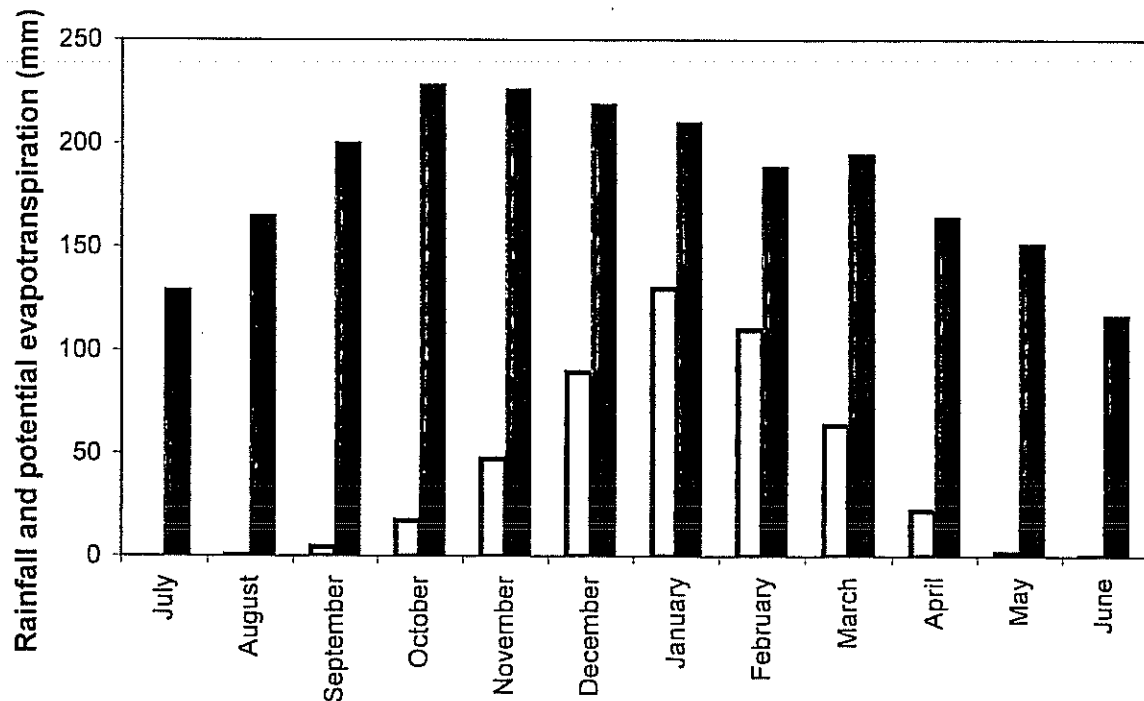
Fig. 18. Monthly rainfall (open bars) and potential evapotranspiration (solid bars) for the Okavango Delta.

Conclusion

Organisms create and amplify environmental heterogeneity at local and regional scales. Conventional approaches that describe the species richness, *beta* diversity and resource flows, or the role of individual organisms in community level processes, would miss the landscape level importance of critical organisms. We propose that our view extends the concept of "ecosystem engineering" to the level of an ecosystem, and highlights the importance of not only identifying the engineers, but also considering the consequences of their activities for the ecosystem. The initiation of subtle, or extremely localised gradients may have large impacts, and it is often these large impacts that are important.

We also propose that the processes described here for the Okavango Delta are not unique, but that they are more evident in this ecosystem as a consequence of its setting. It is an aggradational environment with an unusual sediment load and a semi-arid climate, and animal and vegetation processes control patterns of both clastic, but more particularly of chemical sedimentation on the surface of the fan. Consequently the spatial heterogeneity on the surface of the fan is demonstrably generated primarily by the ecosystem itself. Such a view allows predictions of various impacts at a level that would be impossible using more traditional approaches. For example, one might anticipate widespread salinisation if island vegetation, particularly broadleaved evergreen trees, was cleared extensively for any reason. This prediction is unlikely if the role of trees in changing groundwater chemistry beneath islands was not recognised. An understanding of the nature and extent of ecosystem engineering, and the impact of this on environmental processes at the broadest scale, is thus essential for the conservation of biological diversity.

Acknowledgements

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