

Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions

W. N. ELLERY¹, K. ELLERY¹ and T. S. McCARTHY²

Departments of ¹Botany and ²Geology, University of the Witwatersrand, PO Wits, Johannesburg 2050, South Africa

Summary

Vegetation on islands in the perennial swamps of the Okavango Delta exhibits a marked zonation pattern. Island fringes are generally characterized by a broad-leaf evergreen riparian community of *Syzigium cordatum*, *Ficus verruculosa*, *F. natalensis*, *F. sycamorus*, *Phoenix reclinata*, *Garcinia livingstonei* and *Diospyros mespiliformis*. This gives way towards island interiors to a community dominated by *Acacia nigrescens*, *Croton megalobotrys* and *Hyphaene ventricosa*. The central regions are characterized either by short, sparse grassland dominated by *Sporobolus spicatus* or are completely devoid of vegetation with sodium carbonate (trona)-encrusted soil surrounding a central pan of extremely high conductivity. An indirect gradient analysis indicated the important determinants of vegetation distribution as being not only elevation, depth to groundwater and distance from the water source, but also as groundwater chemistry (conductivity and pH) and soil chemistry (sodium concentration). These studies were supported by a direct gradient analysis approach with species tolerances to depth to groundwater, groundwater conductivity and soil-surface sodium concentrations having been established. Feedback interactions of vegetation and groundwater elevation and chemistry, as well as soil chemistry, are evident and appear to be responsible for the vegetation dynamics in the study area.

Key words: abiotic determinants, Okavango, riparian, vegetation dynamics

Résumé

La végétation des îles dans les marais permanents du delta de l'Okavango présente un schéma de zonation marqué. Le bord des îles se caractérise généralement par une communauté riveraine à larges feuilles toujours vertes de *Syzigium cordatum*, *Ficus verruculosa*, *F. natalensis*, *F. sycamorus*, *Phoenix reclinata*, *Garcinia livingstonei* et *Diospyros mespiliformis*. Celle-ci cède le pas vers l'intérieur à une communauté dominée par *Acacia nigrescens*, *Croton megalobotrys* et *Hyphaene ventricosa*. Les zones centrales, soit se caractérisent par une prairie courte et clairsemée où domine *Sporobolus spicatus*, soit sont complètement dénuées de toute végétation, avec un sol encroûté de carbonate de soude entourant un centre où la conductivité est très élevée. Une analyse indirecte du gradient indiquait que les facteurs déterminants pour la distribution de la végétation ne sont pas seulement la hauteur, la profondeur de la nappe aquifère ou la distance par rapport à une source, mais aussi la composition chimique de l'eau (sa conductivité et son pH)

et celle du sol (concentration en sodium). Ces recherches ont été confirmées par une approche directe de l'analyse du gradient, de la tolérance des espèces face à la profondeur de l'eau, sa conductivité et les concentrations en sodium de la surface du sol ayant été établies au préalable. Les interactions entre la végétation d'une part et le niveau et la composition chimique de la nappe aquifère d'autre part, ainsi que celle du sol sont évidentes et semblent être responsables de la dynamique de la végétation dans la zone étudiée.

Introduction

Riparian ecosystems are densely wooded zones located between an aquatic and an upland ecosystem, usually characterized by a high water table (Johnson & McCormick, 1979). Most quantitative studies on these ecosystems have been conducted in northern temperate, relatively moist areas, where the distinctive plant zonation pattern along an elevational gradient is determined by the hydroperiod which includes flood timing, frequency, intensity and duration (Mitch & Grosselink, 1986). Although the work in semi-arid and arid areas has been of a more limited nature, elevation and hence duration and extent of flooding have also been identified as the most important factors governing woody plant distribution (Simpson, 1975; Furness & Breen, 1978; Hughes, 1988, 1990), with soil texture and chemistry (Astle, 1969; Proctor & Craig, 1978; Hughes, 1988), human (Ramsey & Rose-Innes, 1963; Hughes, 1988) and geomorphological disturbance (Wyant & Ellis, 1980), all playing a secondary role.

The Okavango Delta, situated in a semi-arid region of northwestern Botswana, is an 18,000 km² alluvial fan which represents the terminal receiving basin of an internal drainage system that arises in the highlands of central Angola (Fig. 1). Scattered throughout the fan are islands of variable size and origin, many of which support a distinct riparian community of broad-leafed, evergreen trees and shrubs. The centre of the islands are usually either sparsely vegetated by grass species or are devoid of vegetation (Smith, 1976). The purpose of this study was to examine the determinants of vegetation zonation on islands in the Okavango Delta, and to elucidate any feedback interactions of vegetation on soil and groundwater chemistry as well as groundwater elevation.

Study area

The Okavango Delta fan is contained within a graben at the southern extremity of the East African Rift system (Hutchins, Hutton & Jones, 1976; Scholtz, 1975). It is made up of three physiographical regions, (1) the panhandle or entry corridor to the alluvial fan, (2) the permanent swamps on the upper reaches of the fan where overspill of the major distributary systems creates swamps of a permanent nature and (3) the seasonal swamps on the lower fan where overspill is of a seasonal nature (Fig. 1).

The climate is semi-arid and the local rainfall (490 mm y⁻¹) is greatly exceeded by evapotranspiration (1580 mm y⁻¹, Wilson & Dincer, 1976). Flood waters from the summer rains (December, January) in southern Angola reach the bottom end of the fan near Maun nearly four months later. Water levels vary seasonally by as much as 1.5 m in the panhandle, but in the central regions of the perennial swamps

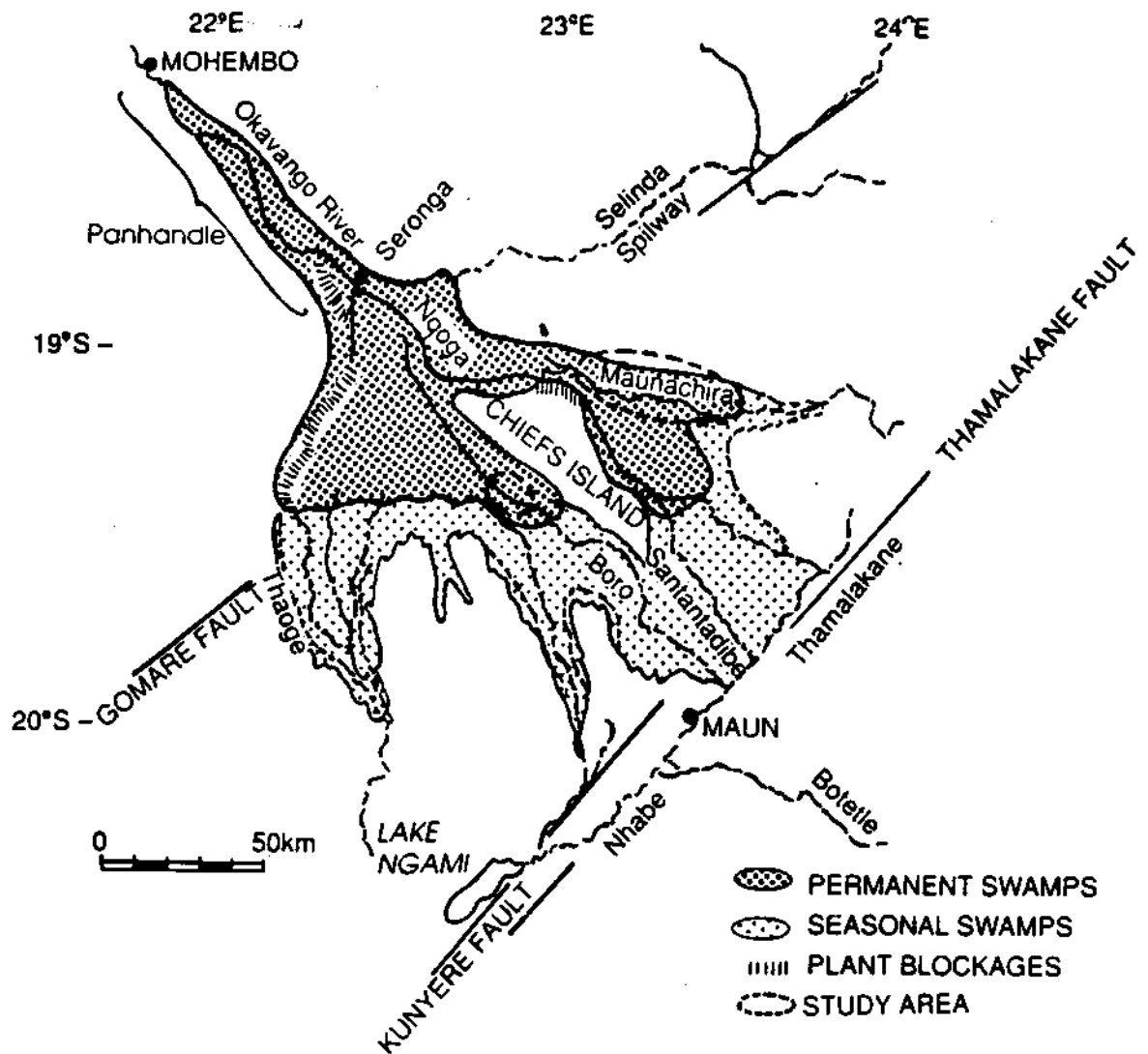


Fig. 1. A map of the Okavango Delta showing the location of the intensively studied areas.

seasonal fluctuations are less than 20 cm. In the lower reaches of the fan, seasonal fluctuations are again large, typically in the region of 2 m.

Islands, made up predominantly of medium- to fine-grained sandy soils (McCarthy, McIver & Cairncross, 1986b), are an important component of the Okavango Delta and constitute between 10% and 20% of the area in the permanent swamps (McCarthy, Ellery & Ellery, in press). The extent of tree cover is variable with some islands having a complete tree cover and others only a narrow fringe close to the island edge with the centre of the island either colonized by herbaceous species or devoid of any vegetation. Islands in the permanent swamps which had a distinct riparian zone were examined in this study.

Methods

An investigation of overall relationships between vegetation distribution, elevation, depth to groundwater, distance to island edge, and soil and groundwater chemistry was conducted on six islands in the Maunachira–Nqoga river system (Fig. 1) during August 1990. These islands were variable in shape ranging from small and almost

symmetrical (100 m diameter) to long, thin and sinuous (approximately 4000 m long and 250 m wide). A single transect was located across the short axis of each island and at approximately 20 m intervals auger holes were dug to below the subsurface water level. Once the water level had equilibrated, the depth to water was measured and its conductivity was determined using a Hanna conductivity meter. Soil samples were taken from each auger hole at approximately 20 cm depth intervals. A measure of cover-abundance of the vegetation in 10 × 10 m stands was also made at each of these sites using cover scores of 1–8 which were represented by the intervals between 0, 1, 2, 5, 10, 25, 50, 75 and 100%, respectively.

Soil samples were milled to –200 mesh and were analysed for CaO, MgO and Na₂O by X-ray fluorescence spectrometry (XRF) on undiluted powder briquettes. Analytical precision was of the order of 15% (relative), which was considered adequate for the purposes of this study.

During April 1991 a similar study was conducted by locating a transect across an island on the Boro river system in the lower reaches of the permanent swamps (Fig. 1). In addition to measuring vegetation cover, elevation, depth to water, distance to island edge and groundwater conductivity, as had been done previously, the fluctuation of the groundwater level was determined over a 24 hour period.

An indirect gradient analysis approach was used to elucidate relationships between the distribution of species and environmental variables using the detrended correspondence analysis (DCA) option of the package of multivariate analyses of Ter Braak (1987). Environmental variables for each stand, included as a supplementary matrix, were depth to water, distance to water, groundwater pH and conductivity, soil sodium concentration (topsoil and subsoil) and soil calcium concentration (topsoil and subsoil). Since water depth and elevation, and CaO and MgO concentrations in the soil were so highly correlated, only the former in each case were used in the analysis.

Following the indirect gradient analysis, a direct gradient analysis was used to examine the tolerance ranges of 10 of the most common woody species to depth to water and groundwater conductivity. This was investigated during July 1991 by measuring depth to water and the conductivity of groundwater in auger holes located next to a total of 300 individuals.

Results

Cross-sectional island profiles: topography, groundwater distribution and soil/groundwater chemistry

Similar patterns of topography and soil/groundwater chemistry were seen on all of the six islands studied in the middle reaches of the permanent swamps, with only one of the islands represented here (Fig. 2). Details of island topography and soil and water chemistry of the other five islands have been described elsewhere (McCarthy *et al.*, in press).

Although the topography of Island A is variable, the gradients over the 220 m are shallow with a maximum elevation of only 0.80 m (Fig. 2). The islands seldom attain elevations greater than this, except for the marked topographic relief associated with termitaria, which may be in excess of 2 m above the surrounding soil surface.

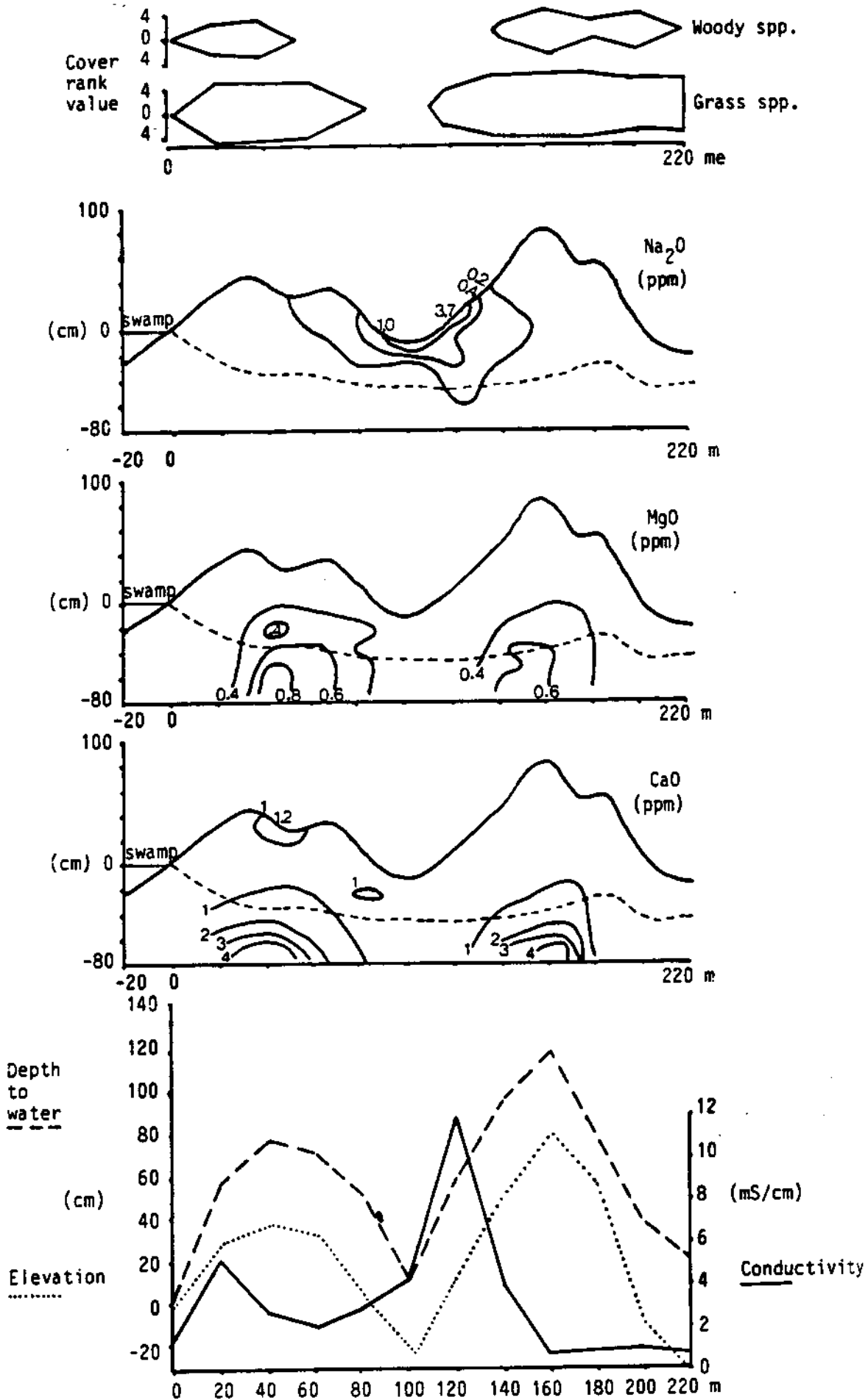


Fig. 2. Profiles across Island A showing vegetation cover, soil Na_2O , soil MgO, soil CaO, groundwater conductivity, depth to water, and elevation.

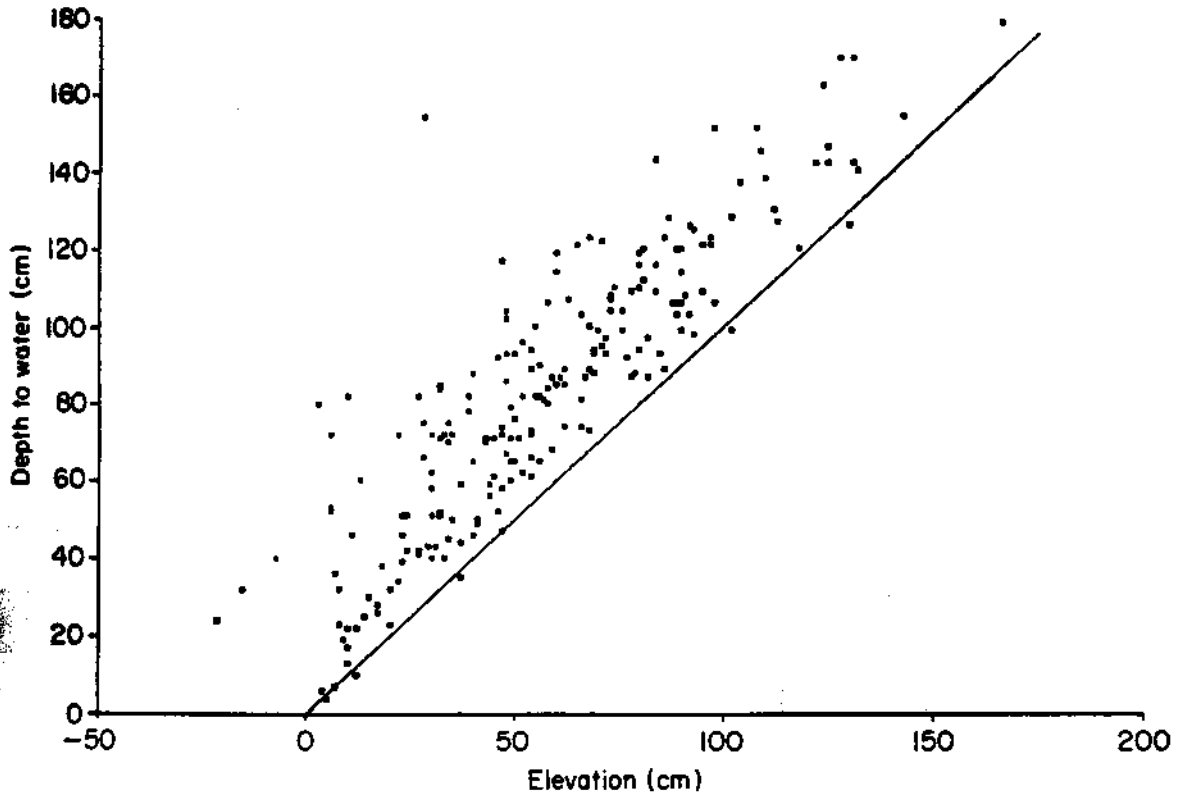


Fig. 3. Graph showing relationship between depth to water and elevation using data from all six islands.

The profile of soil chemistry across the island shows a close relationship with topography. Both CaO and MgO, which reflect the abundances of magnesium calcite in the soil profile, increase with depth, with concentration maxima corresponding to the topographic highs of the island (Fig. 2). The maxima of MgO are displaced slightly towards the centre of the island compared with those of CaO. In contrast to the MgO and CaO concentrations in island soils, Na₂O concentration reflects a pattern of increasing concentration towards the centre of the island, with maximum concentrations occurring at the soil surface (Fig. 2).

The conductivity of groundwater varies from being lower than 0.1 mS cm⁻¹ at the swamp edge to in excess of 10 mS cm⁻¹ in the central regions of the islands (Fig. 2). The highest peak of conductivity occurs immediately to the interior of the densely wooded fringe.

The water table beneath Island A is drawn down below that of the surrounding swamp water by as much as 0.50 m (Fig. 2). This relationship was evident on all islands as indicated by the plot of water depth and elevation (Fig. 3) where it can be seen that depth to water is always greater than elevation, indicating that the water table is always below that of the level of the surrounding swamp. The gradient of the water table is steepest at the island edges and flattens out towards the island centre (Fig. 2).

The island studied in the lower permanent swamps (Island X) shows a similar pattern to Island A in the middle reaches of the permanent swamps with regards to elevation, level of the water table and groundwater conductivity (Fig. 4). The maximum conductivity on Island X, however, is approximately three times higher than that of Island A. An additional feature of the work conducted on Island X was the accurate measurement of the level of the water table over a 24 h period. From

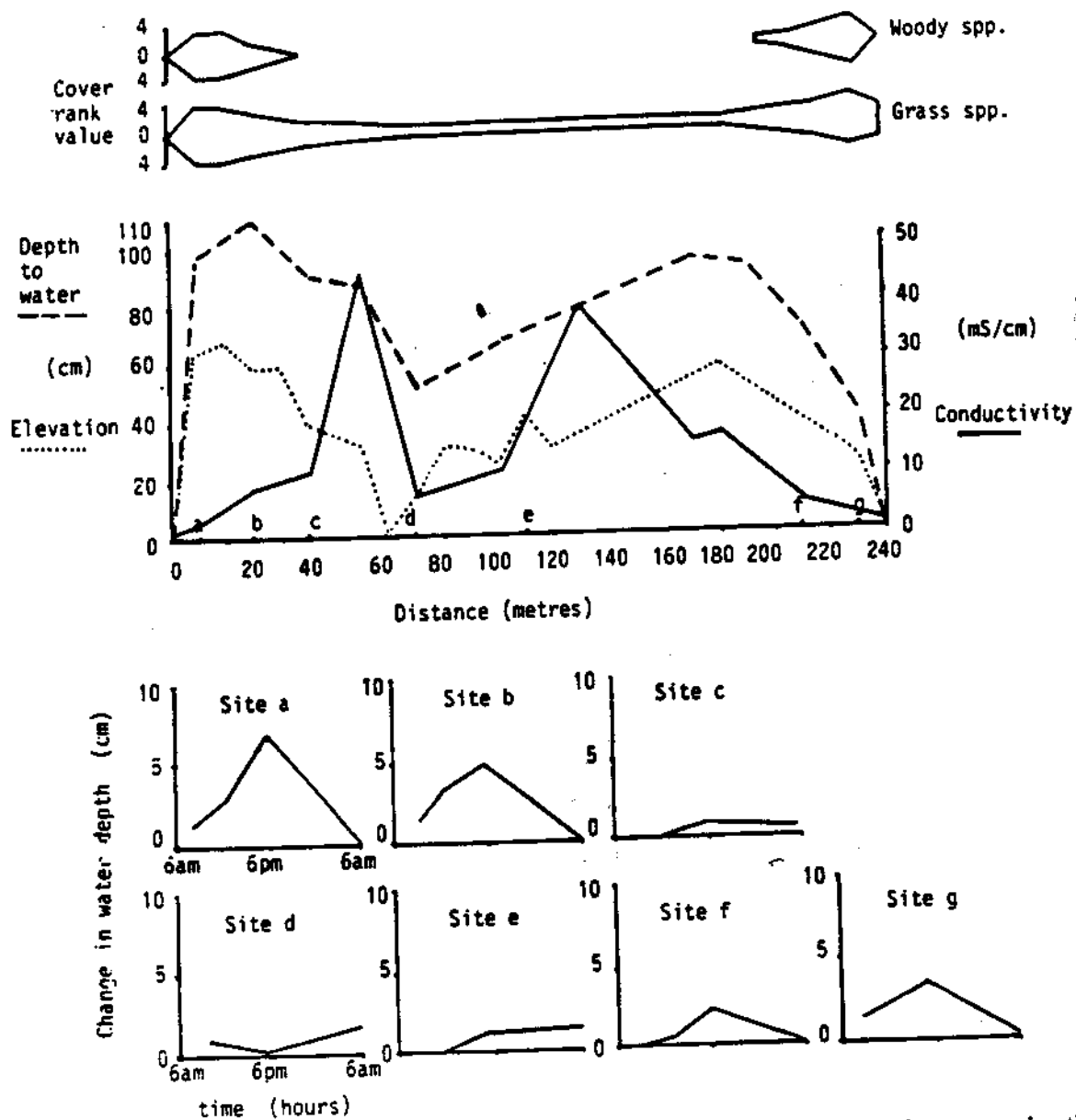


Fig. 4. Profile across Island X showing vegetation cover, groundwater conductivity, depth to water, elevation and change in water depth (relative to minimum water depth) at seven different sites (a-g) over a 24 hour period.

this preliminary study it is evident that greater water loss takes place closer to the island edge, which corresponds to the zone of dense woody vegetation, and that maximum water loss occurs during the late afternoon at five of the seven sites with recharge taking place overnight (Fig. 4; sites a, b, c, f and g). Water loss from islands therefore appears to be by transpiration in the densely wooded fringe.

There is a negative correlation between the maximum amount of water transpired and conductivity (Fig. 5), suggesting that conductivity itself may play an important role in regulating the distribution of plant species.

The distribution of vegetation elements

Overall patterns of distribution

The marked zonation of vegetation on islands is clearly visible in aerial photographs (Fig. 6), and is particularly striking when one visits the area. The fringe is

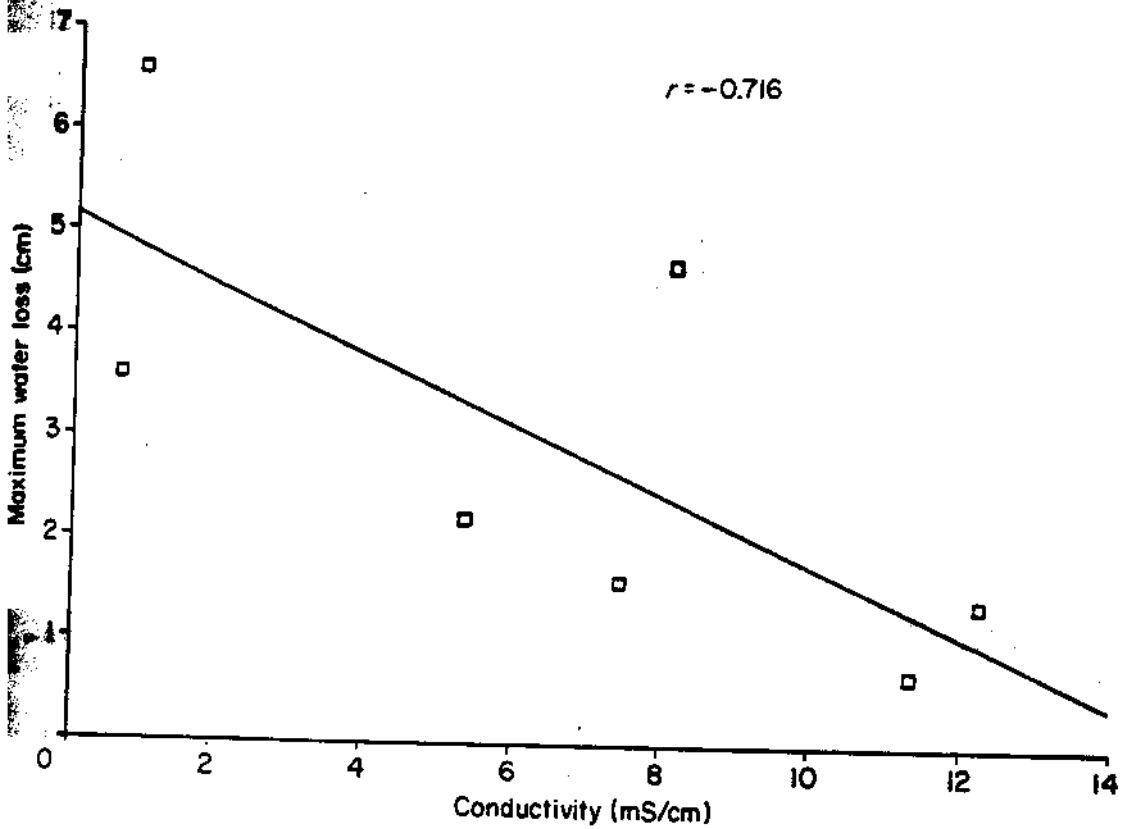


Fig. 5. Graph showing relationship of maximum water loss over a 24 hour period and conductivity.

characterized by tall, dense stands of broadleaf, mainly evergreen trees, with woody plant species such as *Diospyros mespiliformis* Hochst. ex A. DC., *Garcinia livingstonei* T. Anders., *Ficus natalensis* Hochst., *F. sycamorus* L., *Hyphaene ventricosa* Kirk and *Croton megalobotrys* Muell. Arg. Herbaceous species such as *Panicum maximum* Jacq. and *Setaria verticillata* (L.) Beauv. occur in this outer zone beneath the woody species. In contrast, many of the island centres are virtually barren, with sparse cover of the grass *Sporobolus spicatus* (Vahl) Kunth growing on trona (sodium carbonate)-encrusted soil (Fig. 6C). Many of the islands have a depressed region near the centre where no plant species are found; this frequently associated with the margins of a saline pan, and in the case of Island A, with a high conductivity.

This zonation of vegetation is illustrated in the two island profiles presented in this study (Figs 2 and 4). The decline in the cover of both woody and herbaceous species with distance from the island edge, suggests that some feature related to distance is probably determining the distribution of these species. From the plotted environmental variables in Fig. 2 it appears that neither MgO nor CaO soil concentration is affecting plant distribution, nor does depth to water (or the highly correlated elevation), because for any given depth, woody and herbaceous species are in some cases present and in others absent (Fig. 2). In contrast, both surface sodium concentration and groundwater conductivity are related to distance from the island edge, and either or a combination of these could be responsible for the zonation of vegetation characteristic of islands. Both island profiles (Figs 2 & 4) indicate that tree distribution may be restricted by a groundwater conductivity of greater than 10 mS cm^{-1} .

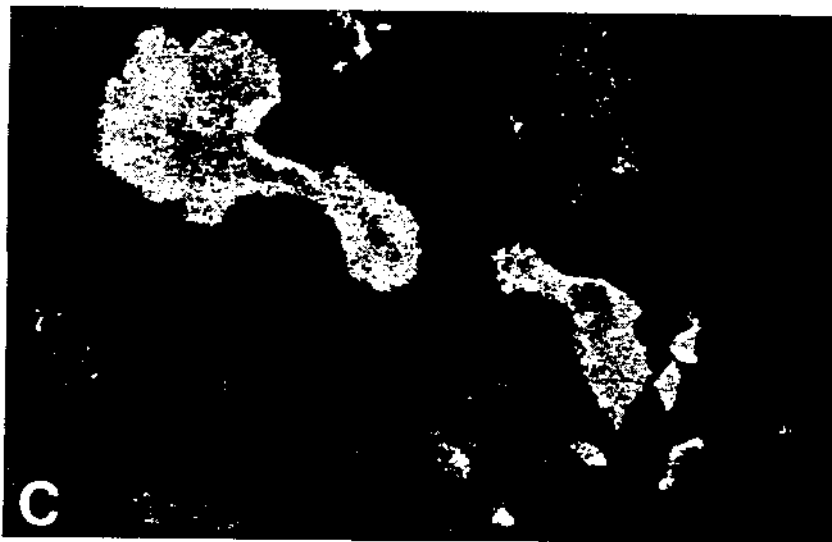
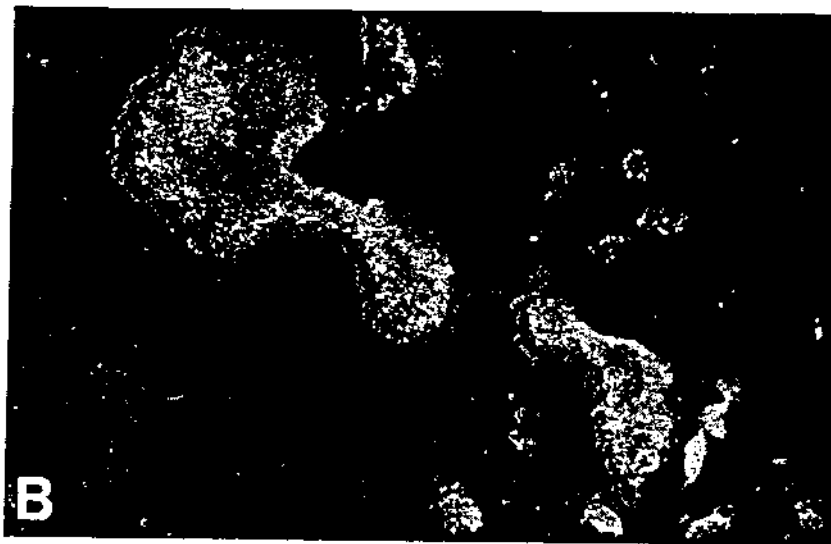


Fig. 6. Aerial photographs of a group of islands showing the dense riparian plant community characteristic of islands in the permanent swamps of the Okavango Delta. Photographs were taken in (A) 1937 (oblique photograph), (B) 1969 and (C) 1983 to show the decline in woody species during the period. The dumbbell shaped island is 1 km long.

Indirect gradient analysis

Based on the Eigen values, axes 1 and 2 contribute most to the distribution of species in the ordination (Eigen values of 0.93 and 0.89 respectively, Table 1). Depth to water appears to contribute most to the distribution of species along the first axis with groundwater pH, sodium concentration in the subsoil and distance to water, and

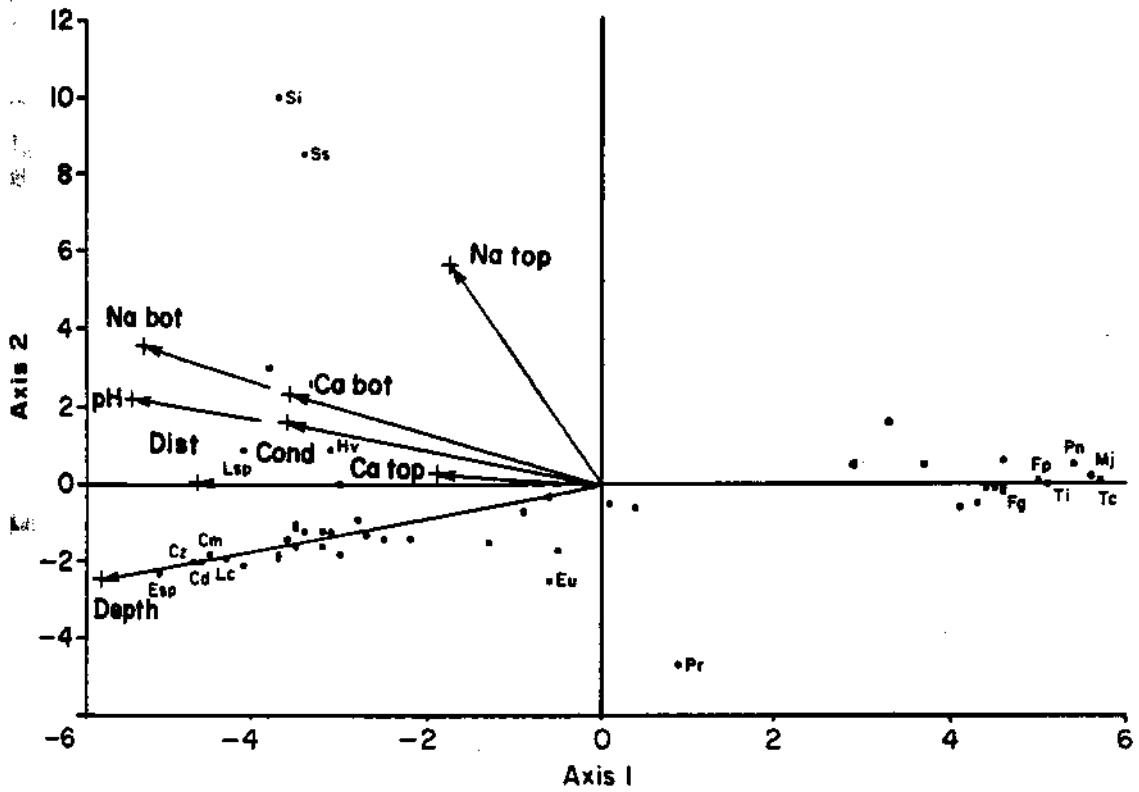


Fig. 7. Axes 1 and 2 of the DECORANA derived species/environmental factors biplot. Cz—*Combretum zeyheri*, Cm—*Croton megalobotrys*, Cd—*Cynodon dactylon*, Esp—*Eragrostis* sp., Eu—*Euclea undulata*, Fg—*Floscopa glomerata*, Fp—*Fuirena pubescens*, Hv—*Hyphaena ventricosa*, Lsp—*Ledebouria* sp., Lc—*Lonchocarpus capassa*, Mj—*Miscanthus junceus*, Pr—*Phoenix reclinata*, Pn—*Pycreus nitidus*, Si—*Cyperus laevigatus*, Ss—*Sporobolus spicatus*, Tc—*Thelypteris interrupta*, Tc *Typha capensis*.

a lesser extent groundwater conductivity and calcium concentration in the subsoil all contributing to species distribution. A number of these variables are however quite strongly correlated with one another (weighted correlation coefficients: depth and distance to water = 0.68, pH and subsoil Na = 0.68, conductivity and subsoil Na = 0.66, conductivity and pH = 0.63, Table 1).

The distribution of species along axis 1 certainly reflects their distribution with respect to their tolerance to flooding, and hence water depth, with species on the right of the first axis (*Typha capensis* (Rohrb.) N.E. BR., *Pycreus nitidus* (Lam.) J. Raynal, *Miscanthus junceus* (Stapf) Pilg., *Thelypteris interrupta* (Willd.) K. Iwats. and *Fuirena pubescens* (Poir.) Kunth; Fig. 7) all occurring in permanently flooded conditions. The species at the other end of the first axis (*Combretum zeyheri* Sond., *Cynodon dactylon* (L.) Pers., *Croton megalobotrys*, *Lonchocarpus capassa* Rolfe and *Ledebouria* sp.; Fig. 7) are characteristic of a fully terrestrial habitat.

The sodium concentration of the soil surface is most highly correlated to the distribution of species along the second axis of variation (Table 1). Whereas herbaceous species such as *Cyperus laevigatus* L. and *Sporobolus spicatus* at the top end of the axis are able to tolerate a high sodium concentration in the surface soils, species such as *Phoenix reclinata* Jacq. and *Euclea undulata* Thunb. at the bottom end of the axis cannot tolerate a high sodium concentration despite their occurrence in fully terrestrial conditions (Fig. 7).

Table 1. DECORANA derived Eigen values (EIG), weighted correlation coefficients (wcc) between environmental factors (top = topsoil, bot = soil below 20 cm) and the axes, and wcc between different environmental factors

	AX1	AX2	AX3	AX4	DEP.	COND.	Ph	Ca top	Ca bot	Na top	Na bot
EIG	0.93	0.89	0.73	0.63							
DEP.	-0.78	-0.26	0.03	-0.16	1						
COND.	-0.48	0.17	-0.17	0.13	0.28	1					
pH	-0.73	0.24	0.08	0.13	0.50	0.63	1				
Ca top	-0.25	0.03	0.21	-0.16	0.33	0.05	0.21	1			
Ca bot	-0.48	0.25	0.03	-0.20	0.36	0.10	0.40	0.62	1		
Na top	-0.23	0.60	-0.03	0.02	0.07	0.24	0.38	0.39	0.43	1	
Na bot	-0.71	0.38	0.00	-0.07	0.48	0.66	0.68	0.31	0.38	0.62	1
DIST	-0.62	0.01	0.01	0.06	0.69	0.43	0.47	0.03	0.14	0.11	0.01

Direct gradient analysis

Auger holes placed next to a number of representatives of 10 of the most common woody species provided further insight into the distribution of woody species. Since conductivity represents an integrated measure of groundwater and soil chemistry (McCarthy *et al.* in press) and is a simple field measurement, groundwater conductivity was considered in the direct gradient analysis.

Most species have a fairly wide tolerance to depth to water with the exception of *Syzygium cordatum* Hochst. and *Ficus verruculosa* Warb.—both swamp fringe trees (Fig. 8a). These two species were also associated with low conductivity water with a conductivity tolerance of less than 1 mS cm^{-1} (Fig. 8b). *Ficus sycamorus*, with one single tree rooted in water with a conductivity greater than 1 mS cm^{-1} , showed a similar pattern to the above two species. Tree species which exhibited a great tolerance of groundwater of high conductivity were *Phoenix reclinata* (max. 4 mS cm^{-1}), *Garcinia livingstonei* (max. 5 mS cm^{-1} kill Sup.), *Ficus natalensis* (max. 7 mS cm^{-1}) and *Diospyros mespiliformis* (max. 8 mS cm^{-1} ; Fig. 8b). *Acacia nigrescens* Oliv. and *Croton megalobotrys* showed a similar tolerance pattern to *mespiliformis* although in both cases a single tree was found in the vicinity of groundwater with a conductivity between 12 and 13 mS cm^{-1} . *Hyphaene ventricosa* exhibited an extremely wide range of tolerance of groundwater conductivity, being found rooting in water with a conductivity of less than 1 mS cm^{-1} as well as up to 17 mS cm^{-1} (Fig. 8b). In water with a conductivity greater than 4 mS cm^{-1} this was by far the most frequently encountered species. Possibly the distribution of these species at lower groundwater conductivities is limited by competitive exclusion, those species only able to tolerate lower conductivities. It can be assumed that 17 mS cm^{-1} is close to the upper limit of tolerance of this species as higher groundwater conductivities were recorded (up to 44 mS cm^{-1}) but woody species were absent at these sites.

The direct gradient analysis of woody species distribution in relation to water depth and groundwater conductivity has shown that despite the fact that species such as *P. reclinata*, *F. sycamorus* and *G. livingstonei*, and to a lesser extent *mespiliformis* and *F. natalensis*, can be found over a wide range of depths to water

(Fig. 8a), their distribution appears to be limited by groundwater conductivity (Fig. 8b).

The occurrence of the four most common grass species found on the islands in relation to sodium concentration in the topsoil is illustrated in Fig. 9. *Miscanthus junceus* is an aquatic species confined to island fringes and is tolerant of low sodium concentration. *Cynodon dactylon* and *Imperata cylindrica* (L.) Raeuschel are found further away from the fringe, still in soils of reasonably low sodium concentration, and *Sporobolus spicatus* is able to tolerate a wide range of sodium concentration. At extremely high concentrations, *S. spicatus* disappears altogether, leaving barren, iron-encrusted soil.

Discussion

Determinants of plant zonation patterns

The zonation pattern of plant species consisting of a tall, dense woodland of mixed composition closest to the water source, which decreases in both stature and species numbers away from the water source until either herbaceous species dominate or bare ground occurs, is common on the islands in the permanently flooded areas of the Okavango Delta. This pattern of riparian zonation in semi-arid areas is most commonly attributed to elevation and water depth which both increase with increasing distance from the water source (Simpson, 1975; Ferness & Breen, 1978; Hughes, 1988, 1990; Dunham, 1989). In a general description of the island vegetation in the Okavango Delta, Smith (1976) also ascribed island tree distribution to water supply preferences.

This study has shown a more complex pattern of factors determining species distribution. Although distance from water source, depth to water and elevation are all correlated with plant distribution patterns in the Okavango Delta, soil (sodium and calcium concentration) and groundwater (pH and conductivity) chemistries also appear to be major determinants of the woody species distribution. Consideration of the most common woody species on the islands indicates a relationship between their distribution and groundwater conductivity. Species tolerant of low conductivities such as *Ficus verruculosa*, *Syzigium cordatum*, *Diospyros mespiliformis*, *Phoenix reclinata*, *Ficus natalensis*, *F. sycamorus* and *Garcinia livingstonei* occur at the island edges, but as conductivity increases towards the island centres species tolerant of higher conductivity such as *Croton megalobotrys*, *Acacia nigrescens* and *Hyphaene ventricosa* dominate until at greater than 17 mS cm^{-1} no woody species are found. In regions at the island centre where groundwater conductivity is less than 17 mS cm^{-1} , it is likely that the high sodium concentrations in the soil surface limit the establishment of any woody species.

Further evidence for the role conductivity plays in regulating the distribution of plant species is the significant negative correlation between groundwater conductivity and maximum amount of water transpired. This limitation to water loss is most likely due to the high osmotic potential of soil moisture associated with high conductivity, with greater amounts of energy required to move water into the symplast as conductivity increases. It is probable that those species occurring in areas of high conductivity have adaptive mechanisms that enable survival in these conditions.

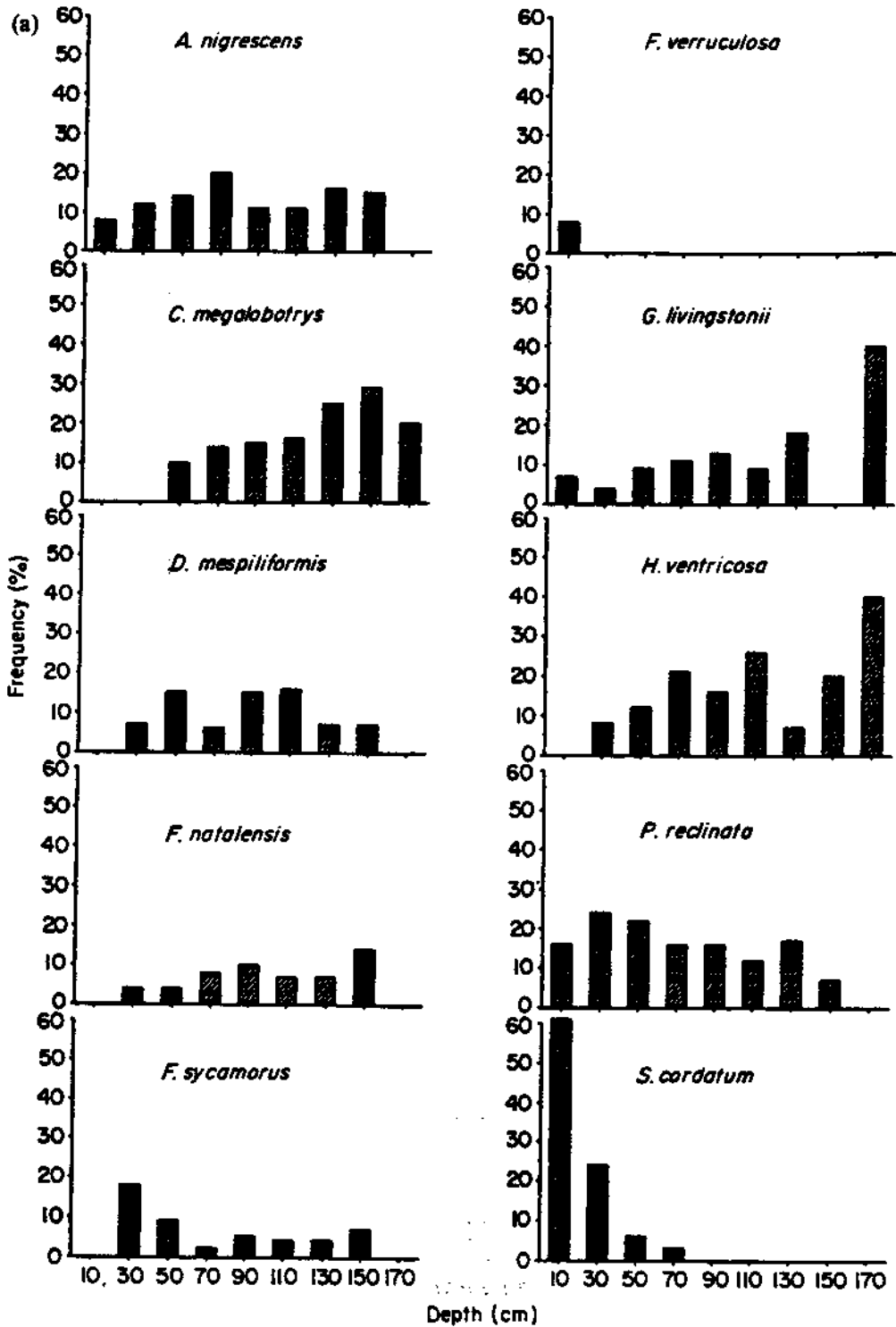
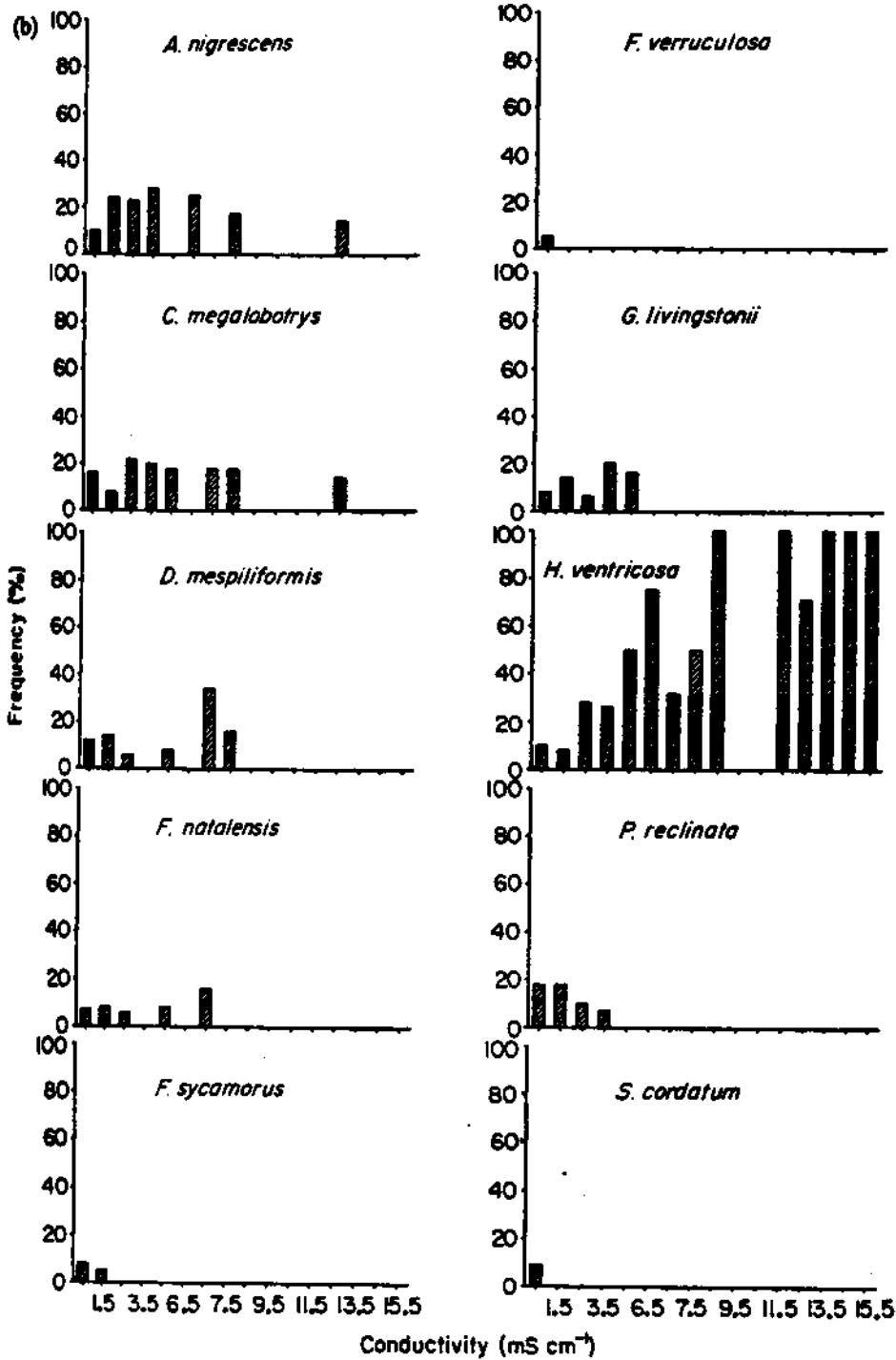


Fig. 8. Frequency distribution (%) of 10 of the most common woody species in relation to (a) depth to water and (b) (opposite) conductivity of the groundwater.

In contrast to the woody species, the distribution of herbaceous species appears to be determined by the concentrations of sodium in the surface soils. Again, close to the island edge sodium concentrations are usually low and species such as *Panicum maximum* and *Setaria verticillata* are found, but with increasing sodium concentrations away from the edge, the hardy grass *Sporobolus spicatus* and the sedge *Cyperus laevigatus* are common. At high sodium concentrations (>1%) herbaceous species are absent altogether.



It is proposed that the influence of soil and groundwater chemistry on the distribution of woody and herbaceous species is more common than previously thought—particularly in semi-arid systems where recharge of the surrounding groundwater from a river or swamp system is likely to occur. This is in contrast to moist temperate areas where the ratio of evaporative loss to rainfall is not high, and where it seems likely that groundwater recharges the river system rather than the other way round. In this case it is unlikely that there would be a concentrating effect of minerals through evaporative losses but, rather, there would be a flushing of salts into the river or swamp, which would transport material downstream.

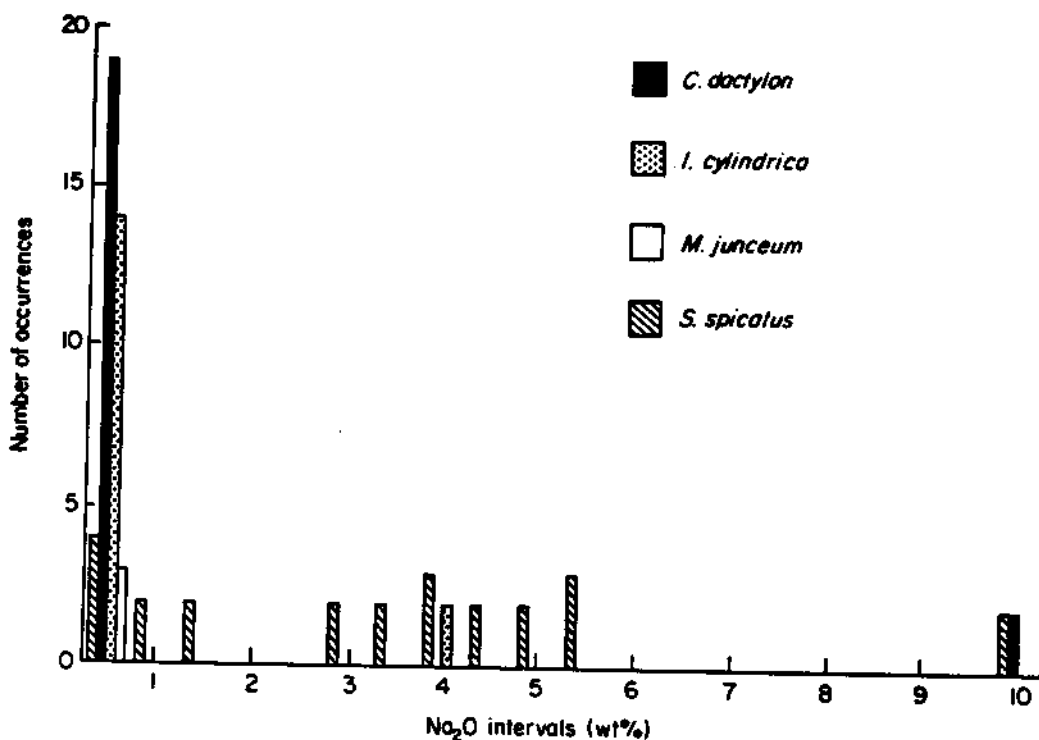


Fig. 9. Distribution of four of the most common grass species in relation to surface soil sodium concentrations.

Feedback interactions of woody species on soil and groundwater chemistry and groundwater elevation

From this study it is evident that riparian vegetation plays an important role in regulating groundwater levels beneath islands. The level of the groundwater drops off rapidly at the island edge, where cover by woody elements is greatest. Within this area evaporation from the soil surface would be minimal due to dense shading by the woody fringe, suggesting that transpiration accounts in large measure for the lowering of the water table in this zone. In addition, studies of daily cycles of water loss in the soil profile indicate greatest water loss from the densely wooded fringe zone. Furthermore the pattern of water loss, with minimum water levels in the soil profile occurring in the late afternoon rather than at midday, also suggests that transpiration rather than evaporation leads to water loss beneath islands.

The peaks of groundwater conductivity observed on the two islands just inside of the dense riparian vegetation appears to be the result of interactions between transpirational losses and local recharge. Plants actively regulate the uptake of dissolved solutes (Peel, 1974), and the removal of water and relatively small amounts of dissolved substances results in marked changes in groundwater chemistry that are observed beneath islands. The removal of groundwater by the dense fringe zone therefore results in an increase in the conductivity of the groundwater. Due to lateral movement of water from the swamp to replace transpired water, there appears to be some degree of flushing, with highest conductivity measured just to the interior of the densely wooded fringe. It is of interest that the conductivity of water in the island centre is lower than it is adjacent to the fringe. The central topographic depression may result in flushing by rainwater, or perhaps it is the result of the virtual absence of transpirational water loss from the island

interiors, which results in lower salt concentrations in the groundwater compared with immediately adjacent to the wooded fringe. In the island centres there must be evaporative water loss from the soil surface to result in the precipitation of sodium at the soil surface (McCarthy & Metcalfe, 1990).

In a study by McCarthy & Metcalfe (1990) it was shown that over longer timespans (thousands of years) the removal of water by trees in the island fringes results in the precipitation of calcium and magnesium carbonates, resulting in soil volume expansion and contributing to increased topographic relief near the island edges. The displacement of MgO maxima towards the centre of the island compared to those of CaO is due to the fact that groundwater recharge is by lateral movement from the island edge, and that magnesium precipitation occurs at higher conductivity than calcium during the formation of magnesium calcite (McCarthy *et al.* in press).

Implications for vegetation dynamics

This study demonstrates the importance of the wooded fringe of islands in the Okavango Delta as a major determinant of groundwater elevation beneath islands, of groundwater as well as soil chemistry and of island topography.

On the other hand, groundwater conductivity and soil chemistry (particularly sodium concentration in the soil surface) appear to strongly influence the distribution of vegetation. This effect is illustrated in a sequence of aerial photographs of islands in the middle reaches of the permanent swamps of the Maunachira-Nqoga river system, where the distribution of woody elements has changed over the period from 1937 to 1989 (Fig. 6). The photograph taken in 1937 was taken obliquely, with a fairly well-developed, wide fringe, but with trees still present on the interior of the islands (Fig. 6A). The second, taken vertically in 1969 illustrates fringes of reduced width, and interiors still relatively well wooded (Fig. 6B). In 1983 woody species were virtually absent from the island interiors, and the fringes were reduced to being very narrow (Fig. 6C). During a visit to the island during 1990 it was noted that a trona (sodium carbonate) encrusted area free of vegetation exists near the centre of the island. These rapid changes in the distribution of woody species on several islands in the study area suggest that it must be environmental changes which take place over short time-spans that determine woody species dynamics on islands. These are most likely to be the result of increases in groundwater conductivity or soil surface and subsurface sodium concentration.

Conclusion

Conventionally it has been accepted that elevation and water depth are the major determinants of riparian vegetation zonation. This study has shown that while water depth and elevation contribute to the distribution of woody species on islands in the Okavango Delta, groundwater salinity is also a major determinant. In contrast, the distribution of grass species appears to be determined by surface sodium carbonate (trona) accumulations. It is suggested that the influence of both high groundwater salinity and surface salt accumulations on species distributions may be more important in semi-arid area than in moist areas due to evapotranspirational losses greatly exceeding rainfall in semi-arid areas. Further,

it has been shown that vegetational processes contribute to groundwater salinization and that this process accounts for short-term (decades) vegetation dynamics on the islands in the Okavango Delta.

Acknowledgments

The authors would like to thank: Mr Dave Hartley and the staff of Okavango Explorations, as well as Mr Paul Rawson of Gametrackers for providing logistical support for this study, and Mr Tim House for willing assistance in the field. An anonymous referee contributed to the contents. Research funding was provided by the University of the Witwatersrand.

References

- ASTLE, W.I. (1969) The vegetation and soils of Chishinga Ranch, Luapula Province, Zambia. *Kirkia* 7, 73–102.
- DUNHAM, K.M. (1989) Vegetation-environment relations of a Middle Zambesi floodplain. *Vegetatio* 83, 13–24.
- FURNESS, H.D. & BREEN, C.M. (1980) The vegetation of seasonally flooded areas of the Pongola floodplain. *Bothalia* 13, 217–230.
- HUGHES, F.M.R. (1988) The ecology of African floodplain forests in semi-arid zones: a review. *J. Biogeography* 15, 127–140.
- HUGHES, F.M.R. (1990) The influence of flooding regimes on forest distribution and composition in the Tanzi River floodplain, Kenya. *J. appl. Ecol.* 27, 475–491.
- HUTCHINS, D.G., HUTTON, S.M. & JONES, C.R. (1976) The Geology of the Okavango Delta. In: *Symposium on the Okavango Delta*. Botswana Soc., Gaborone, Botswana.
- JOHNSON, R.R. & MCCORMICK, J.F. (1979) Strategies for the protection and management of floodplain wetlands and other riparian ecosystems. *Proceedings of the Symposium Callway Gardens, Georgia*. U.S. Forest Service General Technical Report WO-12, Washington, D.C.
- MCCARTHY, T.S., MCIVER, J.R. & CAIRNCROSS, B. (1986b) Carbonate accumulation on islands in the Okavango Delta. *S. Afr. J. Sci.* 82, 588–591.
- MCCARTHY, T.S. & METCALFE, J. (1990) Chemical sedimentation in the semi-arid environment of the Okavango Delta, Botswana. *Chem. Geol.* 89, 157–178.
- MCCARTHY, T.S., ELLERY, W.N. & ELLERY, K. (in press) Vegetation induced, subsurface precipitation of carbonate as an aggradational process in the permanent swamps of the Okavango (Delta) Floodplain, Botswana. *Sedimentology*.
- MITSCH, W.J. & GOSSELINK, J.G. (1986) *Wetlands*. Van Nostrand Reinhold, N.Y.
- PEEL, A.J. (1974) *Transport of Nutrients in Plants*. Butterworth, London.
- PROCTOR, J. & CRAIG, G.C. (1978) The occurrence of woodland and riverine forest on the serpentine of the Great Dyke. *Kirkia* 11, 129–132.
- RAMSEY, J.M. & ROSE-INNES, R. (1963) Some quantitative observations on the effects of fire on the Guinea savanna vegetation of Northern Ghana over a period of eleven years. *African Soils* 18, 41–84.
- SCHOLTZ, C.H.J. (1975) *Seismicity, Tectonic and Seismic Hazard of the Okavango Delta*. U.N. Development Programme/FAO, BOT/71/506. Project Report, Gaborone.
- SIMPSON, C.D. (1975) A detailed vegetation study on the Chobe River in N.E. Botswana. *Kirkia* 10, 185–227.
- SMITH, P.A. (1976) An outline of the vegetation of the Okavango drainage system. In: *Symposium on the Okavango Delta*. Botswana Soc., Gaborone, Botswana.
- TER BRAAK, C.J.F. (1987) *CANOCO—a FORTRAN Program for Canonical Community Ordination (Partial) (Detrended) (Canonical) Correspondence Analysis and Redundancy Analysis (version 2.1)*. ITI-TNO, Wageningen.
- WILSON, B.H. & DINCER, T. (1976) An introduction to the hydrology and hydrography of the Okavango Delta. In: *Symposium on the Okavango Delta*. Botswana Soc., Gaborone, Botswana.
- WYANT, J.G. & ELLIS, J.E. (1990) Compositional patterns of riparian woodlands in the Rift Valley, northern Kenya. *Vegetatio* 89, 23–37.

(Manuscript accepted 8 June 1992)