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An ordination study of mangrove swamp communities in West Africa

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Abstract

Mangrove vegetation and soil were analysed with a view to understanding the community structure and soil relationship in mangrove ecosystems. Coverage values of all plants, frequency, density and basal area for trees were obtained. Soil properties measured included pH, field moisture, bulk density, organic carbon, Al^{3+}, SO_4^{2-} and Cl^-. Principal components ordination of the vegetation data established six mixed mangrove community types. All soil properties varied significantly between the community types, but was most marked in the cases of CO_3^{2-} and SO_4^{2+}. Several tree species showed variation in dominance and density across the community types. Rank correlation of soil with vegetation ordination axes revealed greater correlation along Axis 1 than higher order axes. Soil Cl^- was observed to markedly correlate with hyperspace locations of *Nypa fruticans*, *Avicennia africana*, *Rhizophora mangle* and *Acrostichum aureum* communities. Soil classification showed that several soil properties could serve as indicators for community type differentiation. Additional environmental factors influencing mangrove distribution were inferred from the ordination patterns.

Introduction

Mangrove swamp forests occupy brakish and saline shorelines in the tropics and subtropics. In West Africa, particularly along the Nigerian – Cameroun coast, these swamps are characterised by daily tidal flooding, impaired draining in basin wetlands, a long rainy season and an organic substrate associated with high acid conditions. The development of large tracts of swamps in this area is aided by a low wave energy regime such that the river estuaries – where the most complex swamps occur – are depositional with sedimentation outstripping erosion (Ibe & Antia 1983).

Generally, mangrove species exhibit zonation in a spatial context from the shores inland (Chapman 1976; Snedaker 1982), which has been related to salinity gradients (Cintron et al. 1978; Ukpong 1991), tidal flushing (Giglioli & Thornton 1965) and soil type (Naidoo 1980). The fundamental observations, however, have been that: 1) There are numerous cases of aberrations and quirks in the distributional pattern of mangroves in which zonation cannot be readily recognized (Rabinowitz 1978; Ukpong 1992). 2) Mangrove forest types which relate to different sets of environmental conditions have been recognized in the field (Lugo & Snedaker 1974). 3) There is overlap in values for soil properties from mangrove stands dominated by different species (Clarke & Hannon 1967). According to Naidoo (1980), the least tested of these observations has been the relationship between mangrove vegetation and soil type. Due to the complex hydrology of estuaries e.g. tidal inflows, outflows and seapage, a direct gradient analysis is usually incapable of achieving a satisfactory correlation between vegetation distribution and soil type (See Clarke & Hannon 1976).

Indirect gradient analysis procedures appear to be a more fruitful approach in characterising vegetation and soil relationship in similar swamp forests (Bernard et al. 1983; Paratley & Fahey 1986; Ukpong 1992).

The purpose of this study is to examine mangrove vegetation and soil with a view to understanding the community structure and soil relationships in mangrove swamps. It is hypothesized that the distributional pattern in mangroves is influenced by soil characteristics. Hence the soils can be categorized using the mangrove species as indicators of the soil type.

Microrelief was also expected to influence variation in groundlayer vegetation, particularly through effects on tidal flooding; microtopographic mounds resulting from deposition of sediments, accumulation of wrack and entrapment of debris could facilitate establishment of less flood tolerant plants while depressions resulting from erosion or tree-fall could facilitate establishment of flood loving species.

Study area

The study area is the coastal zone between Nigeria and the Camerouns in West Africa, extending from longitude 7° 30′ E to 8° 30′ E and containing the estuaries of the Cross River, Kwa Ibo River and Imo River. The climate is humid tropical (Fig. 1). In the estuaries tidal amplitude is low averaging 2.01 m at spring tide and 1.07 m at neap tide. Mean salinity values range from 0.23% in the upper estuaries to 3.3% close to the ocean (Ramanathan 1981). The mangrove vegetation consists of mixed stands of *Rhizophora* spp., *Avicennia africana* (*A. germinans*), *Nypa fruticans* and several brackish water associes. *A. africana* (Moldenke) is associated with the West African mangrove subformation from the Senegal to Luanda and is synonymous with *A. germinans* which occur on the littorals of Mozambique, Mexico and Western Australia (Thom *et al.* 1975; Chapman 1976).

Methods

Using aerial photographs vegetation transects, oriented at right angles from the channels and creeks were established across mangrove forest types modified after Lugo and Snedaker 1974 as: (i) Distributary channel mangroves, (ii) Point-bar mangroves, (iii) Braided channel mangroves, (iv) interdistributary basin mangroves, (v) Wooded levee mangroves, (vi) Tributary creek mangroves, and (vii) Interriverine creek mangroves. Forest type differentiation eliminated a bias for locating transects only on the more accessible forests.

The vegetation, stratified into overstorey (>3 m tall), understorey (1–3 m tall) and groundlayer (<1 m tall) was sampled in at least two 10×10 m quadrats regularly spaced at 20 m intervals along each transect. A total of 80 quadrats were sampled. Vegetation measurements include tree height, tree basal area (excluding *Rhizophora* props), species density, frequency and crown coverage (Mueller-Dombois & Ellenberg 1974). Coverage values for the understorey and groundlayer were estimated visually in 5×5 m and 1×1 m subquadrats respectively. The 1×1 m subquadrats were further classified as mounds or depressions, based on the depth of water table below the surface at low times. While the water table occurred at the surface in depressions, it was much lower (<30 cm) in mound positions. The ecological importance value for each species was obtained as the sum of its relative density, relative frequency and relative coverage, excepts for groundlayer species which was the sum of two relative measures of frequency and coverage (Lindsay 1956).

Soil sampling was performed during low tides in the driest months of the year (November–April). Soil sample size were two replicates to a depth of 40 cm per 10×10 m quadrat for all parameters. pH was determined in 1:2 soil to water suspension using glass electrode; field moisture, from weight of oven-dry samples; bulk density, in steel cores of volume 550 cm^3; organic carbon, by Walkley-Black wet oxidation method (Jackson 1962); aluminium, by the aluminon method (Yuan & Fiskel 1959); acetate soluble sulphate (Bardsley & Lancaster 1965); carbonate, by the Bromo Thymol Blue titration method (Jackson 1962); and chloride by $AgNO_3$ titration (USDA 1969).

To meet the requirements for parametric statistics, the vegetation and soil variables were tested for significant departures from normality. Where necessary, transformations were performed according to Gregory (1974).

Analysis

The following analytical steps were taken. 1) Principal components analysis (PCA) with matrix rotation was used as an indirect gradient analysis method to categorize the mangrove communities based upon vegetation composition. The coverage values of species, considered as an item across all strata of the vegetation (Wikum & Wali 1974) were used to obtain an ordination for the eighty quadrats; 2) An analysis of variance was used to separate species variation among the vegetation communities as determined by the PCA from variation within quadrats; 3) A Chi-square test (Conover 1980) was used to analyse frequency distribution of 15 common groundlayer species with respect to mounds and depressions among the community types. The total frequencies of mound and depression (1×1 m) subquadrats in each community type were

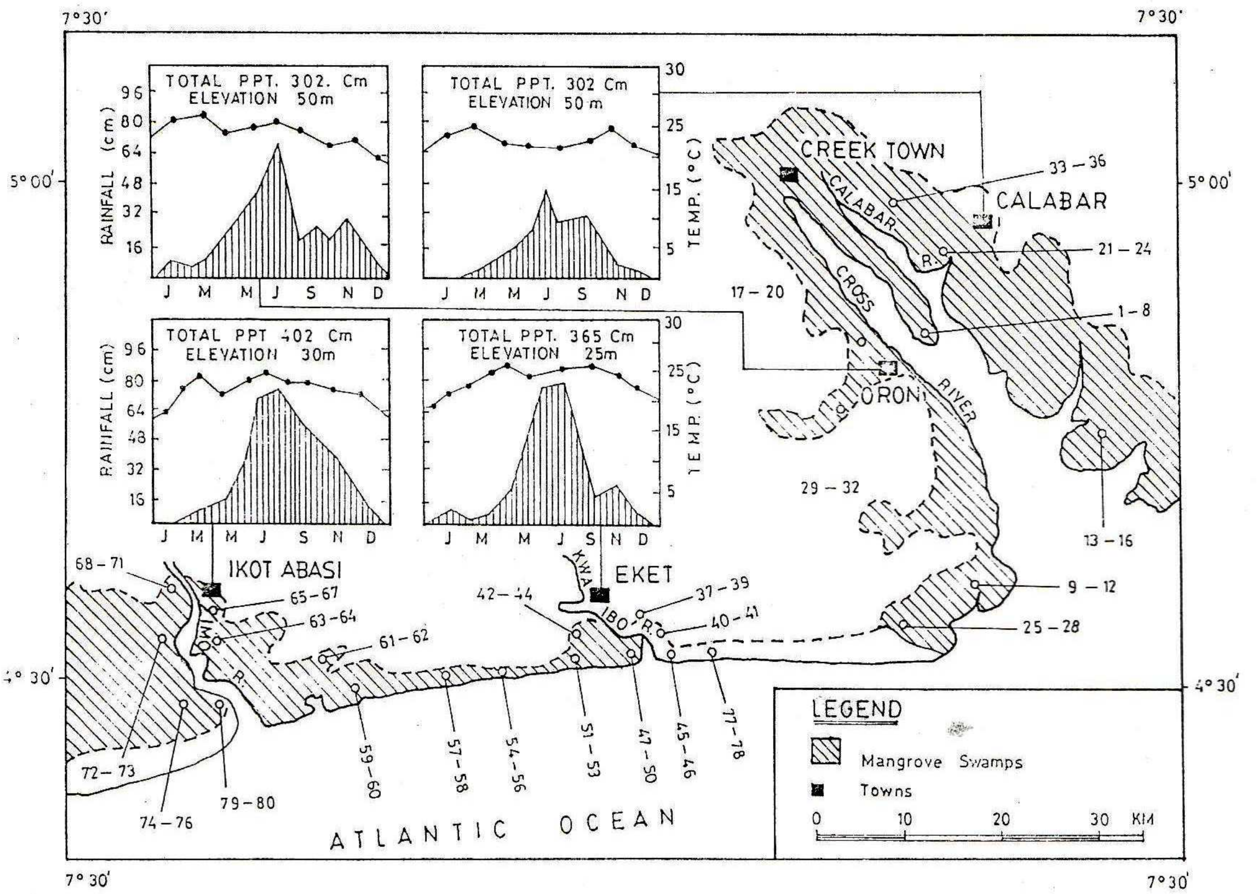

Fig. 1. Mangrove swamps of the Cross River, Kwa Ibo River and Imo River estuaries in West Africa showing transect locations and quadrat numbers. Included are the climatic data for four stations, indicating total annual rainfall (hatched graph) and temperature (line graph, above) conditions for swamp area.

used to determine the significance of frequency departures by groundlayer species in each community type which were then summed to obtain the final statistic (Paratley & Fahey 1986); 4) An analysis of variance was used to separate variation in soil properties among the vegetation communities; 5) Rank correlation coefficients were obtained for the soil variables with each PCA ordination axis of the mangrove vegetation.

Results

Vegetation ordination/community types

Six abstract mangrove community types were established by the first and second varimax rotated components of the PCA (Fig. 2). A transitional vegetation gradient was apparent from the positive end of the first ordination axis (community type 1), to the positive end of the second axis (community type 4), then to the negative end of the second axis (community type 6). Although the initial forest classification consisted of seven entities, none was distinctively segregated by the PCA ordination (see Table 1). However, certain forest types dominated in the PCA community types. The braided channel mangrove was largely represented in community type 1 while the interdistributary basin mangrove was represented in community type 2. To an extent the tributary creek mangrove and distributary channel mangrove coincided with community type 4 and 6 respectively. That there were no absolute coincidence of the initial physiographic forests with the PCA ordination could be attributed to the following: (i) the orientation of transects across all physiographic mangrove forest types were from river channels where the pioneer species are similar; and (ii) Boundaries between adjacent forests are subjective; the boundaries overlap and cannot be determined precisely where one forest type gives way to another. Where the habitat boundaries are clearly defined e.g. braided channel forests which occur exclusively on depositional bars,

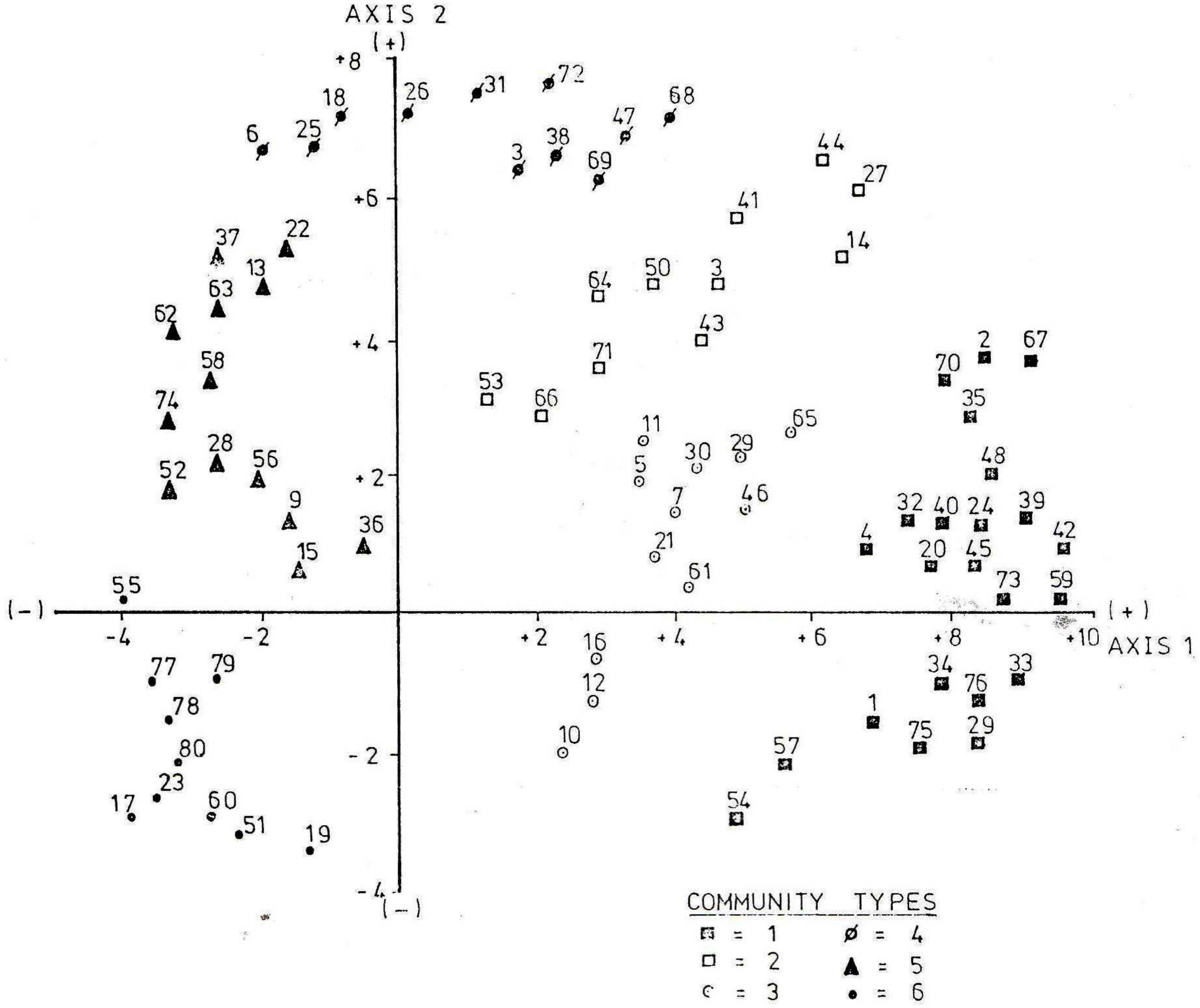

Fig. 2. Ordination of 80 mangrove quadrats on rotated components 1 (35.1%) and 2 (18.4%) of a principal components analysis. Community types are defined in the text

thirteen out of fifteen quadrats in the initial classification are retained in one PCA community (type 1).

The six PCA community types (Fig. 1) represented a transitional gradient from type 1 to type 6, which was not apparent in the physiographic forest type classification. Based on the highest importance values for each stratum, species variations along the transitional gradient are shown in Figure 3.

Community type 1

This is a *Nypa fruticana / Avicennia africana / Acrostichum aureum* community (Fig. 2 & 3). The quadrats representative of this mixed community type were primarily located on braided channel, wooded levee and point-bar forest types (Table 1). *A. africana* had the highest basal area while *R. racemosa* was next in dominance (Table 2). The highest stem densities in the understorey were also achieved by *A. africana* and *R. racemosa* (Table 3). The sapling layer was dominated by mangroves and *Nypa* (Table 4).

The frequency distribution of groundlayer species on microtopographic mounds and depressions within the community are shown in Figure 4. *Vossia cuspidata* ($p<0.025$) and *A. aureum* were largely restricted to depressions (Fig. 4a,e). *Triumfetta rhomboideae* and *Hibiscus tilaceus* occurred on mounds but were not statistically significant.

Table 1. Comparison of initial physiographic forest classification with PCA community types.

Physiographic	Vegetation	Corresponding PCA community types	Vegetation components
Braided channel mangroves (15)	*Nypa fruticans*	Type 1 (13)*	*Nypa fruticans*
	Rhizophora racemosa		*Avicennia africana*
	Raphia vinifera		*Rhizophora racemosa*
			Vossia cuspidata
			Raphia vinifera
Interdistributary basin mangroves (6)	*Acrostichum aureum*	Type 2 (4)*	*Acrostichum aureum*
	Hibiscus tilaceus		*Avicennia africana*
	Vossia cuspidata		*Nypa fruticans*
Wooded levee Mangroves (15)	*Avicennia africana*	Type 1 (5)*	*Avicennia africana*
	Drepanocarpus lunatus	Type 2 (5)*	*Acrostichum aureum*
		Type 3 (3)*	*Triumfetta* spp.
			Drepanocarpus spp.
Point-bar mangroves (9)	*Avicennia africana*	Type 1 (5)*	*Avicennia africana*
	Rhizophora racemosa		*Rhizophora racemosa*
	Hibiscus tilaceus	Type 3 (2)*	*Hibiscus tilaceus*
			Avicennia africana
Tributary creek mangroves (16)	*Rhizophora mangle*	Type 4 (9)*	*Acrostichum aureum*
	Acrostichum aureum		*Rhizophora mangle*
	Sesuvium spp.	Type 3 (5)*	*Sesuvium* spp.
			Conocarpus erectus
			Acrostichum aureum
Interriverine creek mangroves (9)	*Hibiscus tilaceus*	Type 5 (5)*	*Hibiscus tilaceus*
	Rhizophora mangle		*Pasapalum vaginatum*
	Pandanus spp.		*Raphia hookeri*
	Phoenix reclinata		*Phoenix reclinata*
	Languncularia racemosa	Type 6 (2)*	*Pandanus* spp.
			Ipomoea cairica
			Rhizophora racemosa
Distributary Channel mangroves (10)	*Conocarpus* spp.	Type 6 (6)*	*Conocarpus* spp.
	Rhizophora racemosa		*Sesuvium* spp.
	Cyperus articulans		*Cyperus articulans*
	Selaginella spp.		*Selaginella* spp.
			Acutas afer
		Type 5 (2)*	*Hibiscus tilaceus*

( ) Parentheses indicate number of quadrats in the initial classification.
( )* Asteriks indicate number of initial quadrats retained within the corresponding PCA community type (quadrats lacking clear species representation are excluded).

Community type 2

This is an *Avicennia africana/Acrostichum aureum* community (Figs 2 & 3), represented by 11 quadrats primarily located on wooded levee, interdistributary basin and ditributary channel forests (Table 1). The most mature stands of *N. fruticans* with heights exceeding 11.5 m and mean coverage (24.6%) occurred in this community type. However, in terms of basal area, *A. africana* was dominant (Table 2). In the understorey *A. africana* and *Rhizophora* spp. were the most numerous (Table 3). The sapling layer was dominated by mangroves, *Nypa* and *Pandanus candelabrum*. Figure 4a shows that *Acrostichum aureum* was restricted to topographic mounds ($p<0.05$) within the community type.

Table 2. Dominance of some overstorey tree species (Basal area in m²/ha, excluding *Rhizophora* props), and significance of ANOVA test for variation among six community types. (n): not significant, $p<0.10$; (*): $p<0.05$; (**): $p<0.025$. Unmarked species had low frequencies (<5%) and were not tested.

	Community types						
	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	
Number of quadrats	(23)	(11)	(12)	(11)	(13)	(10)	r^2
Basal area (m²/ha)							
Avicennia africana (*)	10.2	8.4	4.5	7.8	0.9	0.3	0.24
Rhizophora racemosa (*)	6.5	0.8	7.2	0.2	3.3	1.6	0.21
Rhizophora mangle (**)	0.4	1.5	0.6	9.4	4.2	2.3	0.29
Rhizophora harrisonii (*)	0.2	0.7	0.5	2.6	0.4	2.0	0.20
Conocarpus erectus (n)	0.2	0.0	0.0	0.0	0.6	3.6	0.13
Phoenix reclinata (n)	1.1	0.4	0.2	1.0	0.2	0.8	0.09
Pandanus candelabrum (*)	0.1	0.2	0.0	0.3	1.1	0.6	0.20
Other species	6.8	0.9	0.5	2.1	1.2	0.6	
Total basal area (*)	25.5	12.0	13.5	23.4	11.9	11.8	

Table 3. Density of understorey species between 1–3 m tall (stems/hectare), and significance of ANOVA test for variation among six community types. $p<0.10$; (*): $p<0.05$; (**): $p<0.025$. Unmarked species had low frequencies (<5%) and were not tested.

	Community types						
	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	
Number of quadrats	(23)	(11)	(12)	(11)	(13)	(10)	r^2
Density (stems/ha)							
Avicennia africana (*)	374	436	167	335	31	150	0.20
Rhizophora racemosa (*)	278	182	250	45	162	380	0.25
Nypa fruticans (*)	74	57	75	133	23	10	0.22
Rhizophora mangle (**)	39	155	83	200	462	120	0.30
Rhizophora harrisonii (n)	9	36	33	0	31	10	0.14
Pandanus candelabrum (*)	0	18	17	45	77	60	0.24
Raphia hookeri (*)	0	9	93	0	123	0	0.26
Drepanocapus lunatus (n)	17	55	0	0	31	0	0.13
Other stems	17	82	141	81	62	16	
Total (n)	808	1030	859	839	1002	746	

Community type 3

The 12 representative quadrats of this community type were primarily located on wooded levee, point-bar and tributary creek forest types. It is an *Avicennia africana/Rhizophora recemosa/Acrostichum aureum* community type. *R. racemosa* was dominant in terms of basal area, when compared to *A. africana* (Table 2). This pattern was reflected in understorey stem density (Table 3). Several groundlayer species showed strong affinity for microtopographic mounds (Fig. 4a,e,f), but the pattern was most marked in the distribution of *A. aureum* ($p<0.01$) and *T. rhomboideae* ($p<0.05$).

Community type 4

Eleven quadrats, primarily located on tributary creek and interriverine creek forests were representative of community Type 4 (Table 1). It is an *Avicennia africana/Rhizophora mangle/Acrostichum aureum* community type (Figs 2 & 3). The highest mean basal area was achieved by *R. mangle* and *A. africana* (Table 2). In the understorey, *N. fruticans* and *R. man-*

Table 4. Density of saplings less than 1 m tall (saplings/hectare), and significance of ANOVA test for variation among six community types. $p<0.10$; (*): $p<0.05$; (**): $p<0.025$. Unmarked species had low frequencies (<5%) and were not tested.

	Community types						
	Type 1 (23)	Type 2 (11)	Type 3 (12)	Type 4 (11)	Type 5 (13)	Type 6 (10)	r^2
Density (saplings/ha)							
Mangroves (**)	2448	665	608	682	321	170	0.20
Nypa (n)	230	182	225	245	95	330	0.14
Raphia (*)	9	46	50	18	177	0	0.22
Drepanocarpus (n)	43	9	17	0	8	0	0.08
Pandanus (*)	30	64	33	81	38	80	0.21
Other saplings	86	149	109	97	82	61	
Total (*)	2846	1105	1042	1123	718	641	

Table 5. Means and standard deviation of soil properties (at 0–40 cm depth) in six mangrove community types. Sample size was 2 replicates per 10×10 m quadrat. The significance of F-test for variation among community types is indicated by (n) not significant; (*): $p<0.05$; (**): $p<0.01$; (***): $p<0.001$.

Community	Sample size	pH	Field moisture % (g cm^{-3})	Bulk density (%)	Organic carbon (me/100 g)	Aluminium (me/100 g)	Soluble sulphate (me/100 g)	Carbonate %	Chloride
1 (23)[a]	46	5.6±0.8	144.2±8.2	0.74±0.12	5.8±2.2	0.17±0.02	0.05±0.02	5.3±2.2	2.8±0
2 (11)	22	5.6±0.9	136.1±5.1	0.82±0.18	8.9±3.5	0.32±0.06	0.06±0.08	9.4±3.6	3.5±0
3 (12)	24	4.7±0.5	151.3±2.5	0.67±0.07	7.2±0.9	0.27±0.05	0.09±0.02	12.5±5.7	3.8±0
4 (11)	22	5.8±0.8	142.6±6.3	0.83±0.15	5.9±2.7	0.19±0.09	0.10±0.05	9.2±2.8	3.6±0
5 (10)	26	4.8±0.7	125.7±9.4	0.95±0.06	3.6±2.9	0.35±0.11	0.14±0.03	14.8±3.1	3.1±0
6 (10)	20	4.6±0.7	149.8±3.5	0.90±0.08	9.2±0.8	0.22±0.07	0.07±0.04	10.9±4.8	2.9±0
Significance		(*)	(*)	(*)	(*)	(*)	(**)	(***)	(*)

[a] Number in parentheses indicate number of 10×10 m quadrats in each community.

gle were the most important species. Figure 4 shows that the groundlayer was relatively open. *H. tilaceus* and *S. portulacastrum* showed affinity for mounds while *V. cupidata* and *A. aureum* showed affinity for depressions but were not statistically significant.

Community type 5

This community type (*Rhizophora racemosa/Rhizophora mangle/Hibiscus tilaceus*) was represented by 13 quadrats primarily located on tributary creek, wooded levee, distributary channel and interriverine forest types. In terms of basal area, *R. mangle, R. racemosa* and *P. candelabrum* were dominants (Table 2). The sapling layer included *Raphia* spp. (177 s/ha)(Table 4). Three groundlayer species showed affinity for microtopographic depressions but was most marked in the case of *C. articulans* ($p<0.05$). *H. tilaceus* was largely restricted to mounds ($p<0.025$) (Fig. 4-g,h).

Community type 6

The 10 quadrats representative of this community type occurred primarily on interriverine creek, point-bar and distributary channel forest types (Table 1). It is a *Conocarpus erectus/Rhizophora racemosa/Cyperus articulans* community. *Laguncularia racemosa* (I.V.23.4) is a rare species which did not occur elsewhere in the swamps (Fig. 3). The understorey dominants were *R. racemosa, R. mangle* and *A. africana*. *Nypa*, mangroves and *Pandanus* were important in the sapling layer (Table 4). Two groundlayer

Table 6. Spearman's rank correlation coefficient of soil properties along four principal component ordination axes for mangrove vegetation in West Africa. Significance levels are shown as (*): $p<0.05$; (**): $p<0.01$; (***): $p<0.001$. Correlations without notes are not significant.

	Mangrove swamp forest ordination			
	Axis 1	Axis 2	Axis 3	Axis 4
Soil properties				
pH	−0.18	0.04	0.25	0.36(*)
Field moisture	−0.45(**)	0.15	−0.35(*)	0.08
Bulk density	−0.09	0.23	0.38(*)	0.13
Organic carbon	0.52(**)	−0.12	0.11	−0.20
Aluminium	−0.08	0.17	−0.06	−0.35(*)
Soluble sulphate	−0.37(*)	0.21	0.15	−0.02
Carbonate	0.24	0.48(**)	−0.02	0.09
Chloride	0.46(**)	−0.62(***)	0.12	0.05

species (*T. rhomboideae* and *Hibiscus tilaceus*) were restricted to mound positions ($p<0.01$) (Fig. 4-f,g).

The same pattern was observed for *I. cairica* and *P. vaginatum* (Fig. 4-b,d), but with lower statistical significance. *S. portulacastrum* and *C. articulans* (Fig. 4-c,-h) showed affinity for depressions ($p<0.025$; $p<0.05$).

Analysis of variance tests among the community types revealed significant variation in species dominance (Table 2). *R. mangle* achieved the highest significance ($p<0.025$) with basal area ranging from 0.2 m^2/ha in Type 1 to 9.4 m^2/ha in Type 4. Total species basal area also varied significantly ($p<0.05$).

Variation in understorey stem density are reported in Table 3. *A. africana* had the highest density in Type 2 but was least represented in Type 5 while *R. racemosa* was most numerous in Type 6 but least represented in Type 4. *R. mangle* varied significantly ($p<0.025$) with the highest representation in Type 5 and lowest in Type 1. Mangrove saplings varied significantly across the communities ($p<0.025$)(Table 4). *Pandanus; Raphia* and total saplings also varied significantly ($p<0.05$).

Soil – Vegetation relationships

The community types contrasted with each other by having varied soil properties (Table 5). The soils were moderately acidic with pH values ranging from 4.6±0.7 to 5.8±0.8. Soils associated with *A. africana* were less acidic than *Rhizophora* soils. Field moisture content of soils represented mean conditions at low tides between November and April which are relatively dry months in the study area.

The highest value was associated with *A. africana/R. racemosa* which dominate along shorelines while the lowest value occurred inland, associated with *R. racemosa/R. mangle* stands. A correlation was observed between bulk density and field moisture; the former tends to increase with a decrease in the latter.

High organic carbon content of soils were associated with *A. africana* and *C. erectus*. Aluminium values tend to increase with decrease in soluble sulphate. Carbonate content varied significantly with the highest values associated with *R. racemosa* communities. Chloride concentrations were higher in soils associated with *A. africana* communities while lower values occurred in dominantly *Rhizophora* spp. soils. Similar observations were made along the Lagos lagoon (Jackson 1964) and in the Gambia, West Africa (Giglioli & Thornton 1965).

Rank correlation of soil with the first four PCA ordination axes revealed greater correlation along Axis 1 than higher order axes (Table 6). Axis 1 emphasized the importance of chlorides, soluble sulphate, organic carbon and field moisture. Along Axis 2, carbonate and chlorides were important. Bulk density and field moisture correlated significantly along Axis 3. Along Axis 4, acid conditions were emphasized in terms of pH and aluminium.

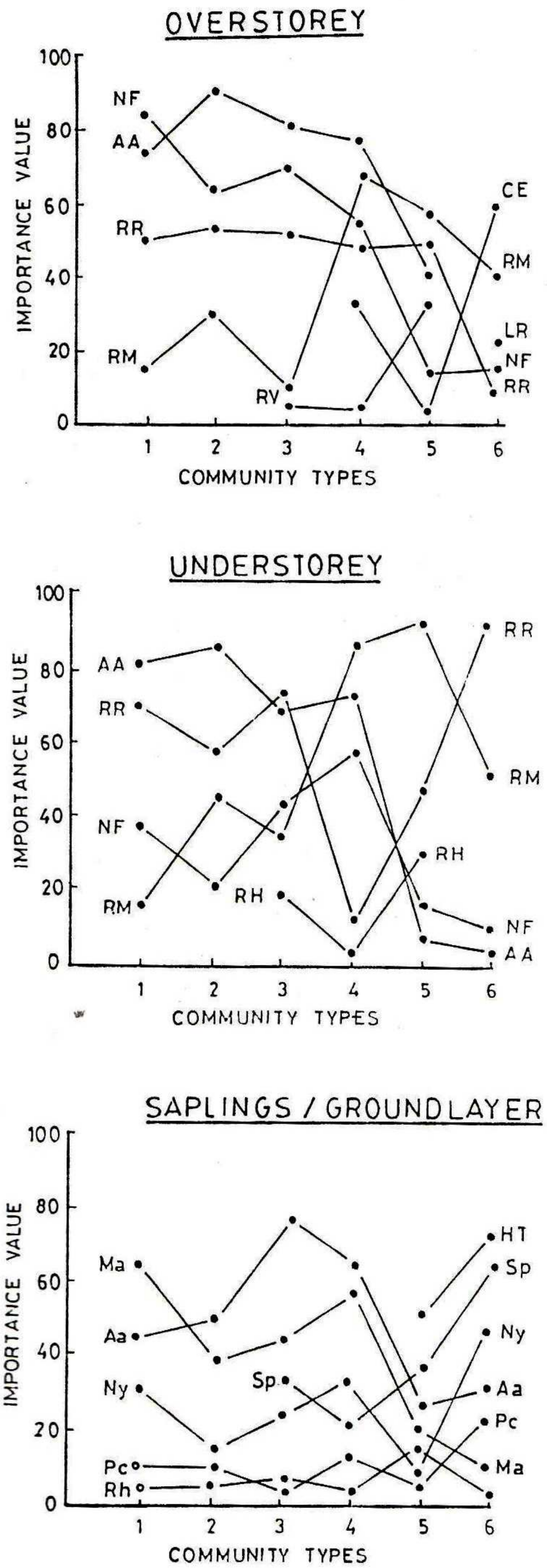

Fig. 3. Graphic representation of the importance values of species along the transitional gradient from community type 1 (freshwater/brackish) to community type 6 (brackish/saline): NF = *Nypa fruticans*, AA = *Avicennia africana*, RR = *Rhizophora racemosa*, RM = *Rhizophora mangle*, Rh = *Raphia hookeri*, MA = mangrove samplings, Aa = *Acrostichum aureum*, Sp = *Sesuvium portulacastrum*, Ht = *Hibiscus tilaceus*, CE = *Conocarpus erectus*, LR = *Laguncularia racemosa*, Ny = *Nypa* saplings, Pc = *Pandanus candelabrum*.

Discussion

Zonation

The mangroves are in most instances organized into zones, particularly along the channel margins. *A. africana* and *N. fruticans* often fringe certain segments in almost pure stands. However, each zone could be occupied by one of the community types that are units of the mangrove vegetation, or a zone may contain a mosaic of more than one communities depending on local topography or soil conditions. This results in quirks in the distributional pattern of species along the transects. Physiographic forest type classification indicates that species zonation also relates to tidal inundation and morphological characteristics of the species. While *R. racemosa* with extensive prop roots can withstand wave buffetting along the main tidal channels, *A. africana* fringe the less dynamic tributary levees. With progressive stabilization of substrates and decrease in the length of inundation, *R. mangle, R. harrisonii, P. reclinata, T. rhomboidea* and *Drepanocarpus* form monodominant zones in the inner swamps. This implies that zonation is also a function of habitat change which may be induced by geomorphic processes of swamp landscape evolution.

Community types

Indirect gradient analysis of mangrove vegetation resulted in six mixed community types out of the initial seven physiographic forest classification (Table 1). This suggests that other factors, apart from the ones measured affect plant distribution in the mangrove swamps. Several species e.g. *A. africana*, *Rhizophora* spp. and *P. reclinata* show overlapping occurrences across the community types, which imply overlap in environmental requirements or tolerance of environmental stress. Species dominance in the community types, however, define ecological optima where the species achieve the highest level of competition and adaptation. Certain species associations are limited e.g. an association of the upland forest invaders such as *Vossia cuspidata, Selaginella* spp. with true tidal swamp species such as *Conocarpus erectus* and *Phoenix reclinata.* This is more appropriately an 'Interface consocies' where the species achieve relative mix due to changing environmental conditions such as topography. Since the community types are identifiable with physiography, the ordination indicates that in estuarine

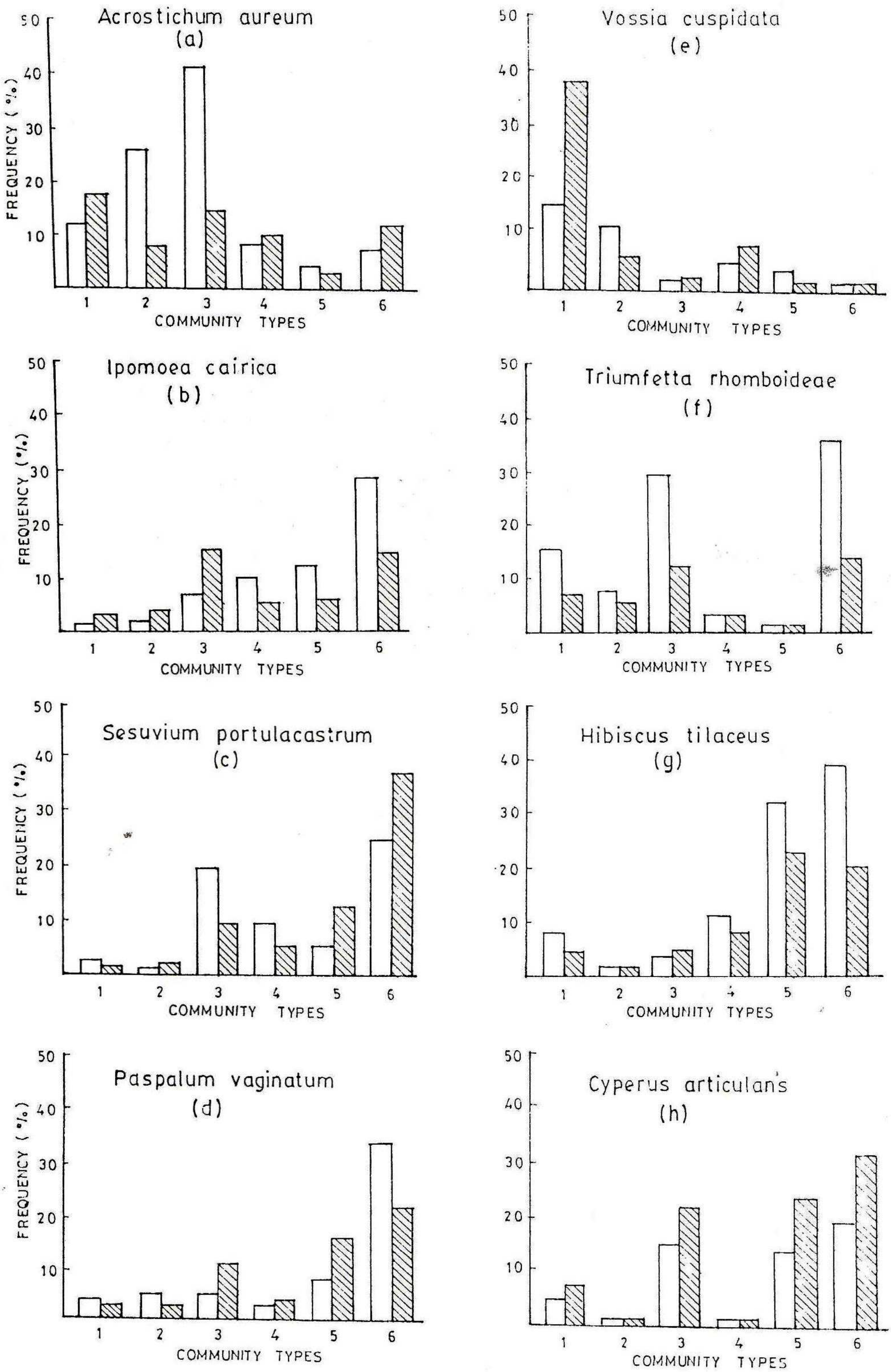

Fig. 4. Frequency distribution of (a) *Acrostichum aureum*, (b) *Impmoea cairica*, (c) *Sesuvium portulacastrum*, (d) *Paspalum vaginatum*, (e) *Vossia cuspidata*, (f) *Triumfetta rhomboideae*, (g) *Hibiscus tilaceus* and (h) *Cyperus articulans* on mounds (white) and depressions (stripe) among six mangrove community types in West Africa.

environments, the typographic control over mangrove distribution is a most important ecological factor.

Human factor is reflected in Community Type 1 where *Nypa fruticans* is dominant. *Nypa*, according to Mercer and Hamilton (1984) was introduced into West Africa in 1906. Its dominance is initially due to the relatively low taxonomic diversity of mangrove swamps and the species ability to deal with high amptitude unpredictable stresses e.g. continually changing salinities. *Nypa* seedlings achieve easy mobility due to the bouyancy of water and the rapid hydrodynamic transport associated with tides. Upon colonization of mudflats, its extensive rootmat converts the soft mud into firmer substrates and displace the initial communities (*R. racemosa/A. africana*) inland where they become associated with *R. mangle* and *P. reclinata*.

In the groundlayer, *A. aureum, I. cairica, Sesuvium* spp. and *V. cuspidata* each show the highest frequency of occurrence in different community types and were either restricted to microtopographic mounds or depressions in the communities. This dynamic relations between microtopography and plants are influenced by strong periodic physical forces e.g. sediment accumulation from the upland forest zone during the wet season, tidal sorting of sediments and variable accumulation of wrack by tides. Salinity fluctuations due to freshwater inputs also determine which species establish on mound or depression positions. The intensity of these forces vary between the community types. Although most species are capable of adapting to the rigorous conditions, microtopographic differences constitute an important ecological factor in the distribution of groundlayer species.

Soil relations

The mangroves are not restricted to specific soil conditions although each community tends to show niche relations to certain soil attributes (Table 5). Hence several soil properties could serve as indicators for community type differentiation. For example, higher acidity prevails in soils associated with *Rhizophora* communities than in *Avicennia* communities. *Rhizophora* spp. have extensive fibrous root system which form thick fibrous peat-like mud. Hart (1962) maintains that root decomposition in *Rhizophora* fibrous muds leads to accumulation of sulphides which lowers the pH of *Rhizophora* soils. *Avicennia* does not produce fibrous mud. Consequently *Avicennia* soils are less acidic. High organic carbon values occur in communities dominated at the tree layer by *A. africana* and the groundlayer by *Sesuvium* spp., *Acrostichum* and *Cyperus*. Entrapment of organic residues by the sedges and ferns could significantly increase the organic content of the soils. High organic matter in tidal swamps is also associated with a slow rate of silting (Moorman & Pons 1974).

Chloride content of soils is highest in *A. africana/R. racemosa* communities and lowest in soils associated with *N. fruticans/C. erectus*. Chloride values, however, correlate with the spatial location of stands from oceanic tides. While *A. africana* and *R. racemosa* dominate close to the mouth of estuaries and along major tidal channels, *N. fruticans* is dominant in the middle estuaries in the brackish water zone.

The most apparent plant reaction in the communities appear to be the addition of organic material to the soil which tend to modify some physical and chemical properties of the soils.

Relationships between the vegetation communities in theoretical hyperspace (Fig. 2) indicate that proximity to oceanic tides and freshwater inputs are additional environmental factors that determine community type variation. A transitional gradient is apparent from the freshwater/brackish environment to brackish/saline environment (see Fig. 3). Due to the complex hydrology of estuaries, subsurface inflow of both fresh and saline water probably regulate the influence of each other along the length of the gradient. Salinities in the swamp therefore remain intermediate between those of fresh and seawater. However, interannual variability in salinity could be wide being related to normal climatic shifts from wet to dry periods. Thus the spatial extent of the mangrove communities, defined in terms of salinity fluctuations, undergo periods of expansion and contraction due to environmental stress.

Correlation of soil variables with PCA ordination axes emphasize the importance of some variables in community type variation. The results (Table 6) are interpretable in terms of gradients since the vegetation is regarded as multivariate.

Axis 1, dominated by *N. fruticans* and *A. africana* communities, represents a nutrient and salinity gradient in view of the correlations with organic carbon and chloride ($p<0.01$) and soluble sulphate ($p<0.05$). The gradient indicates tidal flooding (field moisture?) as influencing the organic content and salinity of soils. Due to tidal transport, the mangrove swamps are characterised by a high degree of organic debris mobility. The debris trapped within the mangrove communities probably contribute to the importance of organic carbon on this axis.

Axis 2 represents a major salinity gradient (chloride: $p<0.001$) when compared to the first axis. Occupied by *A. africana/R. mangle* and *Acrostichum aureum* communities, this gradient relates to the spatial location of the communities relative to tidal channels and freshwater inputs from upland areas. Apart from *A. africana* which may fringe the channels, *R. mangle* and *A. aureum* favour more inland locations. The significance for carbonate ($p<0.01$) is indicative of a *Rhizophora* spp. community. There is preponderance of oysters on *Rhizophora* props which contribute to the carbonate content of the soils. Axis 3 represents a gradient of substrate structure, in view of the correlations with bulk density and field moisture ($p<0.05$). High bulk density correlates with low field moisture (see Table 5) and this could adversely affect the development of mangrove roots, particularly in the less inundated inner swamps.

Axis 4 represents a gradient of soil acidity, considering the correlations with aluminium and pH ($p<0.05$). Quadrats that load highly on this axis consist of *T. rhomboideae/I. cairica* and *Acrostichum* communities in the groundlayer and *Rhizophora* spp. in the overstorey. These species have been related to increasing soil acidity, presumably on account of the decomposition of their roots and formation of sulphides (Hart 1962, Giglioli Thornton 1965). In addition, microenvironmental stress is created when microtopographic mounds undergo repeated wetting and exposure following the tides while the depressions remain constantly flooded. Hence species on mounds occur on sediments that are alternately reduced and oxidized while the depressions are in a permanently reduced condition.

Conclusion

Unlike the physiographic forest type classification where habitat boundaries overlap, the PCA ordination produces separate community types based on variation in species characteristics. Variations in species dominance and density show that the mangrove community structure is defined by a few species e.g. *Rhizophora mangle, R. racemosa, A. africana, R. harrisonii, P. candelabrum* and *Nypa fruticans*. Variations in carbonate content and soluble sulphate levels of soils, being highly significant, appear to be the most important determinant of species composition in the community types. However, while carbonate content has been related to the occurrence of *Rhizophora* spp., soluble sulphate indirectly relates to the vegetation as a component of soil salinity. Microtopographic control over species distribution is related to sediment profiles that are alternately reduced and oxidized due to variable tide levels.

An additional advantage of the indirect ordination method is that some habitat forces which could not be measured directly may be inferred from the vegetation patterns. For example, since mangrove soils are waterlogged and regulargly flooded, oxygen deficiency could contribute to environmental stress. Therefore, apart from certain species e.g. *A. africana* that posses pneumatophores which facilitate oxygen intake by roots from the free atmosphere, most species experience oxygen deficiencies. This could be accountable for the wide ecological amplitude of *A. africana* and the relatively restricted occurrences of other species.

Soil acidity factor, which is important in waterlogged soils, could further be understood if organic matter decomposition, indexed by hydrogen sulphide levels, are used to account for variation in hydrogen ions among the mangrove community types. Other factors such as topographic relation of stands which determines seepage and freshwater passing through the swamps are also important but difficult to quantify (Semeniuk 1983).

This study has shown that there is a high variability of the forces that influence mangrove distribution and community structure. The mangrove swamps experience varying conditions of salinity concentrations, nutrient levels, substrate structure and acidity mediated by tidal movement over relatively short time scales. These indicate a high degree of ecosystem resilience. Due to frequent tidal flooding, soil salinity (significant along two PCA-rank correlation axes) is a superior determinant of the extent and nature of vegetation cover. However, the influence of other environmental parameters need to be analysed before community asemblages in mangroves can be properly understood.

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