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ENVIRONMENTAL DETERMINANTS OF MANGROVE VEGETATION STRUCTURE AS REVEALED BY REGRESSION ANALYSIS

ABSTRACT: The aim of the study was to analyze the mangrove vegetation in relation to environmental factors with a view to offering explanations for variations in the structural characteristics of the mangroves. Multiple regression analysis was used as the analytical tool to predict vegetation response to the environment. Salinity, soil magnesium and bulk density were the most important determinants of overstorey mangrove structure while tidal flood, exchangeable cations and topography were important in the understorey. The groundlayer stratum was determined by substrate texture, tidal flood and topography.

KEY WORDS: mangrove swamp, vegetation structure, multiple regression, soils

1. INTRODUCTION

Having studied vegetation and soils of mangrove swamps in West Australia, Clarke and Hannon (1967) and Dietmont and Van Wijngaarden (1974) concluded that soils alone did not offer satisfactory explanation for the observed vegetation structure. Therefore other parameters should be considered when seeking explanations for the occurrence of mangroves. The acquired information should also be of high quality and sufficient quantity to per, mit satisfactory statistical correlation (Naidoo 1980). Since mangroves are often discretely zoned along sea coast littorals, most studies have adopted the simplified approach of emphasizing vegetation structure in relation to isolated environmental variables e.g. soil salinity obtained from the zonation (Cintron *et al.* 1978, Ukpong 1991, 1992). In the present study, a small relatively undisturbed, densely vegetated mangrove forest was sampled for vegetation, soil and other environmental attributes. The aim was to analyze the structural characteristics of the vegetation in relation to the measured environmental attributes with a view to discerning the underlying relationships between the two sets of data (Kershaw 1984).

2. STUDY AREA

The occurrence of mangroves in the brackish/saline estuarine zone of Nigeria is prominent in the Creek Town/Calabar River Swamp (Fig. 1). Located between latitudes 4°55' E and 5° 00' E and longitudes 8° 15' E and 8° 20' E, about 20 km from the Atlantic coast, the Creek Town swamps experience a humid tropical climate which results in an annual rainfall of 4021 mm. There are two rain-

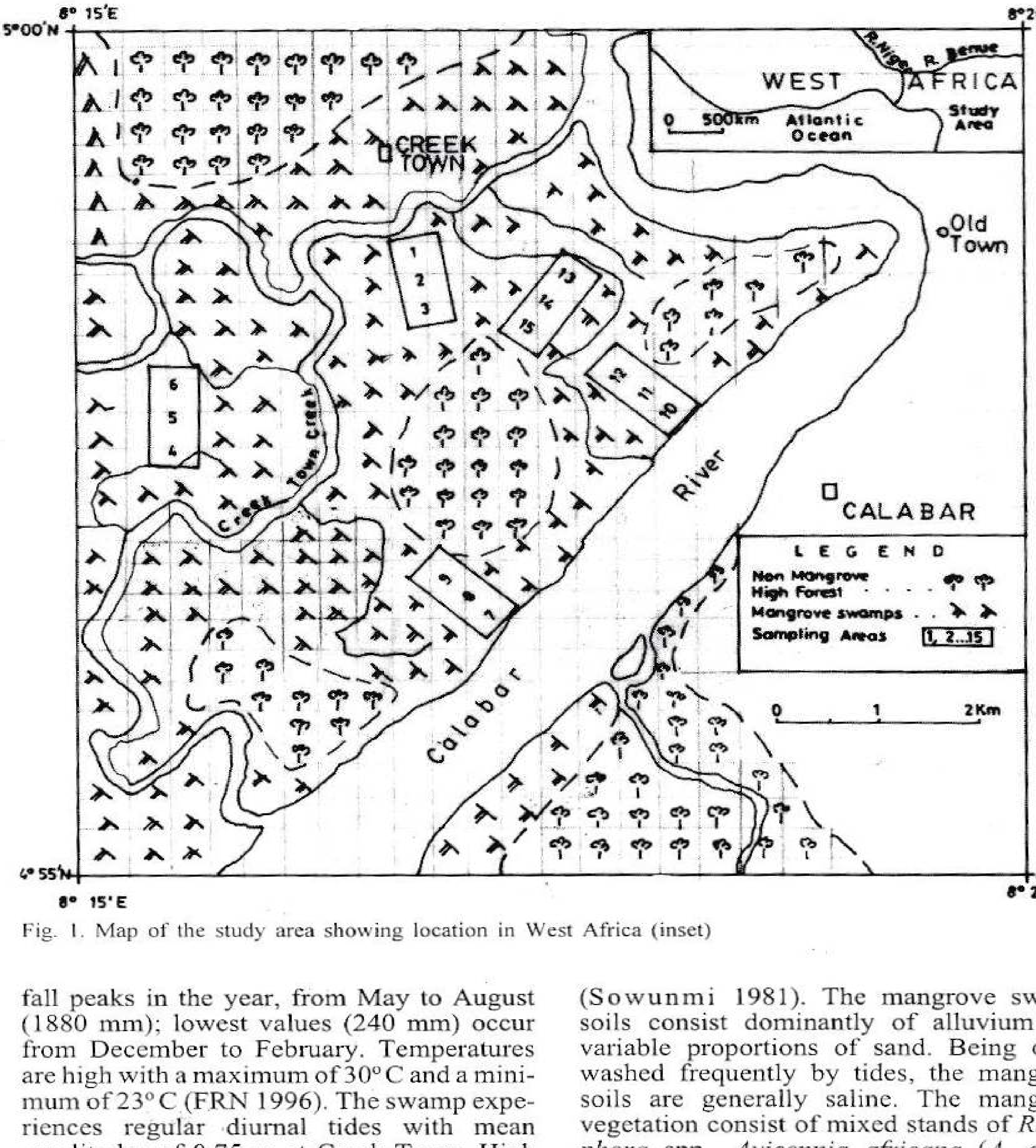

Fig. 1. Map of the study area showing location in West Africa (inset)

fall peaks in the year, from May to August (1880 mm); lowest values (240 mm) occur from December to February. Temperatures are high with a maximum of 30° C and a minimum of 23° C (FRN 1996). The swamp experiences regular diurnal tides with mean amplitudes of 0.75 m at Creek Town. High salinity (3.8 ± 0.4%) is limited to the dry season while lower salinity (0.5 ± 0.6%) occurs in the rainy season (Ukpong 1991).

Two surface formations are associated with the mangrove swamps namely; (i) alluvium of the Quaternary Period and (ii) Tertiary sands of the coastal plains. The alluvium and tertiary sands occur in alternating lateral sequences from the lower flood-plains towards the coastal beachridge zone and continental shelfs (Maron 1969).

The subsurface formation consists mainly of the Benin formation and the Afam Clay member and Agbada formation which are local intrusions in the Benin Formation (Sowunmi 1981). The mangrove swamp soils consist dominantly of alluvium and variable proportions of sand. Being overwashed frequently by tides, the mangrove soils are generally saline. The mangrove vegetation consist of mixed stands of *Rhizophora* spp., *Avicennia africana* (*A. geminans*), *Nypa fruticans* and several brackish water species such as *Triumfetta rhomboideae* and *Acrostichum aureum*.

3. METHODS

3.1. VEGETATION SAMPLING

The Greek Town Creek/Calabar River mangrove swamp was sampled in the relatively dry months between November and January. The criteria for stand selection were (i) mangroves (species with pneumatophores/viviparious fruits) occurred in the canopy layer and (ii) vegetation showed evidence of little disturbance in at least 0.5 hectare in size. Being generally shrubby the vegetation was arbitrarily stratified into A stratum (overstorey) (>3 m tall), B stratum (understorey) (1–3 m tall) and C stratum (groundlayer) (<1 m tall). Data were collected from fifteen 200 m^2 sample plots established from the water channels inland (see Fig. 1). The location of plots was determined by accessibility through the water channels.

Species frequency was obtained by recording the species as present or absent in each of the 15 plots and computed as:

$$\text{Freq (\%)} = \frac{\text{Number of occupied plots}}{\text{Total number of plots}} \ 100$$

Density of occurrence was regarded as the number of individual species (with defined stems) per unit area and was determined as simple count of species in the plots. Tree height was measured with a height measuring instrument called Hagar Altimeter. Tree circumference (excluding *Rhizophora* roots) was measured by a girthing tape then converted to basal area using the formula:

$$\text{Basal area} = \frac{C^2}{4\pi}$$

where C is the circumference of species at breast height and π is a constant 3.143 (Kershaw 1984). Crown cover was obtained in 25 m^2 sub-plots randomly establised within the sample plots using the crown-diameter method of Mueller-Dombois and Ellenberg (1974).

Crown coverage for the C stratum and seedling density were obtained in 1 m^2 sub-plots. Ecological importance value (I.V.) for each species was obtained in each plot as the summation of the species relative frequency, density and cover (Stephenson 1986). The importance values permit species to be ranked and compared with each other based on the total relative quantitative values of species three most important structure attributes. The sum of the importance values for all species in the swamp would always add up to 300. Therefore the greater the importance value for a particular species, the higher would be the ecological importance of that species relative to other species in the swamp (Mueller-Dombois and Ellenberg 1974, Ukpong 1995).

3.2. SITE FACTORS AND THE ASSESSMENT OF INDEXES

In this study, attempting to quantify an index of stand location (SI) meant relating the stand to the nearest tidal channels. Tidal flow into the swamps result from over flooded channels and the extent, depth and duration of flood relate to the distance from such channels (Ukpong 1989). The distance from the channels to the upper edge of each plot was measured and expressed as a percentage of the distance from the channels to the landward limits the mangrove growth (Ukpong 1989). Hence, stand index was obtain as:

$$SI = \frac{\text{Distance of plot from channel (DPC)}}{\text{Distance of channel from ecotone (DCE)}} \ 100$$

where ecotone is defined as the transitional area between mangrove swamp and the adjoining lowland forest. To quantify a tidal flooding index (TFI), the fifteen sample plots were classified into three groups, depending on their location along the tide gradient from the channels to the landward ecotone. The lowest gradient, consisting of plots located nearest to the channels and flooded by initial tidal swell carried a score of 3. At the middle of the gradient, plots carried a score of 2 while the landward plots, being least inundated were scored 1. These scores (corresponding to verbal descriptions of tide conditions) were used to compute the mean tidal flooding index (TFI) for the sample plots.

Topographic variation is an important determinant of species zonation in mangroves (Tomlinson 1986). The establishment of groundlayer species was related to microtopographic mounds and depressions (Ukpong 1997).

It was therefore desirable to quantify a topographic index (TOI) which should express the relationship of species, particularly the groundlayer species, to mound and depression positions. The topographic index was computed as:

$$TOI = \frac{1 \ m^2 \ \text{mound subplots}}{1 \ m^2 \ \text{depression subplots}} \ 100$$

Since the plots were always flooded by diurnal tides, depression quadrats with water table at the surface during low tides were always dominant. The mound positions were subject to alternate flooding and exposure resulting in alternating reduction and oxidation processes.

Organic debris deposited (ODD) by tides on the swamp surface constitute an environmental factor because they help to trap floating propagules on mound positions which are favoured by less-salt tolerant groundlayer species. Debris deposit (ODD) was estimated in 1 m^2 subplots and computed as proportion of sample plot covered by debris.

Field pH was determined for soil water using a portable pH meter while soil water salinity measurements were obtained at the same sites using a portable refractometer calibrated against a Bisset Berman salinometer. Other parameters were analysed in the laboratory from soil cores obtained using a swamp corer (Giglioli and Thornton 1965), at the 0–30 cm layer.

Eight soil samples were collected from each plot and bulked for laboratory analysis. Particle size analysis was done following the method of Bouyoucos (1962); bulk density was estimated in cores of volume 550 cm^3; field moisture was assessed from weight of oven-dry samples; organic matter was determined by the Walkley-Black method and carbonate by the Brono-Thymol blue indicator titration method (Jackson 1962). Root content (RC) was determined by washing samples through a 2 mm sieve. The root materials retained after washing were air-dried and weighed and expressed as percentage of the weight of sample. Exchangeable cations were extracted in 1 N ammonium acetate at pH 7 from which the concentrations of potassium, magnesium and calcium were determined by atomic absorption and sodium by flame photometry; exchange acidity was determined by extraction with barium acetate and titration with NaOH; cation exchange capacity (CEC) was obtained as the summation of the exchangeable cations and exchange acidity.

3.3. STATISTICAL ANALYSIS

The vegetational and environmental variables were transformed in order to meet the requirements for parametric statistics. Non-normality in the distribution was assessed in terms of skewness (Gregory 1974). The vegetational variables like crown cover values of the A and B strata and tree height were very slightly negatively skewed but more closely approximated to normal distribution after square-root transformations. Raw density values and seedling density showed normal distribution. Environmental variables were positively skewed but lognormal, except pH which very closely approximated normality untransformed. Hence a blanket transformation solution (excluding pH) to the log10 of the original values was applied to the environmental variables before inclusion in further analysis.

A linear model in the context of multiple regression which emphasized the estimation of the relationship between individual species and species attributes with the corresponding sets of environmental characteristics was used. The linear model is of the form:

$$Y = a + b_1 x_1 - - - b_n x_n \pm SE,$$

where Y – dependent variable (criterion-vegetation), a – Y intercept; b – partial regression coefficient; x – independent variable (predictor–environment); and SE – standard error of estimate.

In regression analysis, the extent of multicollinearity existing within the predictor variables may greatly influence the reliability of the models. Multicollinearity is encountered when there is a high level of intercorrelation between the predictors. For an assessment of relationships, an r-value of 0.80 and below may not pose serious multicollinear problems (Hauser 1974). However, with r greater than 0.80, the individual regression coefficients may not be distinctive and may result in high standard errors of estimates. In such a situation, only one of the highly correlated variables was included in the regression analysis. The analysis utilized stepwise elimination procedures to develop predictive models for vegetation response to the site properties. This is a search procedure which identifies those environmental variables having the strongest relationship with vegetation. The regressions were run such that the order of site variables was selected, using an analysis of variance with each step reducing the variance of the dependent vegetation variable in each iteration.

4. RESULTS AND DISCUSSION

4.1. FLORISTICS AND STRUCTURE OF THE VEGETATION

The mangrove A stratum (overstorey) is dominated by *Nypa fruticans* (Table 1) an introduced species (Mercer and Hamilton 1984). *Nypa* thrives best initially on soft tidal mud which is converted to firmer soil as the *Nypa* rootmat becomes complex. *Rhizophora mangle* is associated with *Nypa* in the inner swamps while *R. racemosa* associates with *Nypa* along the channel margins. *Avicennia africana* could be found in pure stands along channel margins although it dominates in the inner less inundated swamp. *Avicennia* appears to be more tolerant of salt than *Rhizophora,* hence it is found in the inner back swamps, behind the levees. *R. racemosa* is also highly tolerant of salt and is regarded as the pioneer colonizer of mudflats (Keay 1953). *Raphia vinifera,* basically an upland species, has become adapted to the mangrove zone due to the existence of a salinity gradient between the wet and dry season (Ukpong 1994).

The B stratum (understorey) showed the expected increase in stem density usually associated with understorey vegetation (Table 1). *R. mangle* was dominant although *R. racemosa* had the highest density on account of friging the creeks in pure stands. Inland, *Phoenix reclinata, Conocarpus erectus* and *A. africana* were associated in mixed stands. The importance of mangrove and *Nypa* saplings in the C stratum (groundlayer) was obvious: these species respond to dynamic tide transport due to buoyancy of their propagules. The occurrence of ferns, grasses and sedges (*Acrostictum aureum, Vossia cuspidata* etc) contrasts with the open mangrove groundlayer often reported for littoral swamps.

In the Gambia, similar swamps were described as "interface consocies" reflecting mangrove response to transitional environmental gradients (Giglioli and Thornton 1965).

Table 2 shows that a few *A. racemosa* trees were exceptionally tall (> 25 m, particularly along channel margins). Dominating on the ecotone, *Raphia* spp. achieve a mean height of 5.8 ± 2.5 m. Generally tree height decreased from the channels inland, correlating with decreasing crown cover and basal area. Three species (*A. africana, R. racemosa, R. mangle*) clearly show dominance in terms of basal area. The basal area mean for *Rhizophora* spp. range from 2.8 ± 0.9 to 4.3 ± 1.8 m^2/ha while the mean for *Avicennia* sp.

Table 1. Vegetation composition and distribution analysis in 15 sample plots of mangrove vegetation (average values)

Species	Importance Value (I.V.)[1]	Frequency %	Density (stems/ha)	Mean Cover (%)
		A. Stratum (overstorey)		
Nypa fruticans	76	60	15	29
Rhizophora mangle	55	66	90	16
Raphia vinufera	49	44	87	18
Rhizophora racemosa	46	44	78	16
Avicennia africana	40	60	90	7
		B. Stratum (Understorey)		
Rhizophora mangle	50	66	237	26
Nypa fruticans	44	66	213	20
Rhizophora racemosa	42	53	307	13
Avicennia africana	32	53	146	15
Conocarpus erectus	27	40	113	14
Phoenix reclinata	16	33	47	8
		C. Stratum(Groundlayer)		
Mangrove saplings	48	93	393	0
Nypa fruticans	52	80	300	0
Raphia spp.	36	53	200	0
Conocarpus erectus	20	46	120	0
Phoenix reclinata	20	46	120	0
Vossia cuspidata	13	33	46	0
Achrostichum aureum	26	26	144	0

[1]Ecological Importance Value is the summation of the species relative frequency, density and cover (for details see the text).

Table 2. Morphometric data of trees (A Stratum – overstorey) in 15 sample plots of mangrove vegetation

Species	Tree height (m)		Basal area (m^2/ha)	
	Range	Mean ± SD	Range	Mean ± SD
Nypa frutican	3–7	4 ± 1(25)*	–	–
Rhizophora mangle	3–8	4 ± 1(15)	3–9	4 ± 1(10)
Raphia vinifera	3–10	5 ± 2(13)	–	–
Rhizophora racemosa	3–26	7 ± 7(13)	1–5	2 ± 1(8)
Avicennia africana	3–10	5 ± 2(12)	2–6	3 ± 1(12)
Phoenix reclinata	3–4	4 ± 1(4)	–	– (4)
Conocarpus erectus	3–6	5 ± 2(4)	–	– (4)
Dreponacarpus spp.	3–4	3 ± 1(4)	–	– (4)

*Parenthesis indicate actual number of trees measured.
"–" Species without basal area data had <0.5 m^2/ha, except for *Nypa fruticans* which could not be girthed.

stood at 3.5 ± 1.4 m^2/ha. The mean tree basal area of the plots is 13.6 ± 2.8 m^2/ha. *A. africana*, *R. racemosa* and *R. mangle* constitute 84.5% of the total basal area.

4.2. SITE PROPERTIES OF THE PLOTS

Environmental variables measured for the analysis are presented in Table 3. The mangrove soils had a loamy texture with low variability of the particle-size fractions, indicating uniform sedimentation from similar sources. Sample variation showed decrease in sand content from the channels inland. Stirring of water along the channels and flocculation leads to the coarse sediments settling out of suspension while silts and clays are transported by tides into the inner swamps.

Furthermore, pneumatophores, roots and organic debris act as coarse sediment traps thus producing a substrate texture gradient across the swamp from the margins inland. Bulk density increased with sand content of samples while field moisture showed a decrease. Field moisture was related to the saturation of clay fractions which made the substrates almost fluid mass.

Although the mangrove mud was moderately acidic (pH: 6.08 ± 0.13) field observations indicated increasing alkalinity in *Avicennia* dominated stands than in *Rhizophora* stands. Root content (8.45 ± 3.7%) was also observed to be high in all plots and showed a correlation with organic matter content, which decreased with substrate depth. Generally the soil was observed to be peaty, containing a high proportion of organic material apparently derived from the overlying wrack deposits and roots which undergo very slow decomposition due to anaerobic conditions associated with regular flooding. Variability in salinity (2.9 ± 1.6%) could be explained in terms of freshwater inputs from upland streams, distance from ocean tides (Ukpong 1991), and subsurface seepage of freshwater across the mangrove/high forest ecotone (Semeniuk 1983).

Carbonate content has been noted to be high in mangrove soils, perhaps due to the large molluscan population usually associated with saline or brackish swamps (Kassas and Zahran 1967) and to the precipitation of calcium carbonate along the fresh/salt water mixing zone. It is probable that the high salinity of soil water in the dry season generates a net flow of sea water to upstream, thus bringing oceanic calcium carbonate to the mangroves. The mangrove soils have potentially large sink for cations, especially in terms of exchangeable magnesium and calcium. CEC was therefore high (35.36 ± 3.70 me/100 g). The environmental significance of topography index (TOI) tidal flooding index (TFI) and stand index (SI) relate to alternate flooding of soils and their exposure resulting in alternating reduction and oxidation processes.

4.3. THE CORRELATION BETWEEN SITE FACTORS AND VEGETATION

The multiple regression analysis involved eight vegetation characteristics and seventeen individual species regressed on environmental variables. One out of the eight vegetation char-

Table 3. Site properties in 15 sample plots of mangrove vegetation

Variable	Mean	Standard Deviation	Coefficient of Variation (%)
Sand (%)	35.6	4.8	13
Silt + clay (%)	64.4	6.3	9
Bulk density (g cm^{-3})	0.7	0.2	21
Field moisture (%)	125.8	19.6	15
pH (field moist)	6.1	0.1	2
Organic matter (%)	6.2	0.9	14
Root content (%)	8.2	3.7	44
Debris deposit (%)	4.5	3.5	77
Salinity(%) (soil water)	2.9	1.6	54
Carbonate (g/100g)	7.2	2.5	34
Exchangable Magnesium (me/100 g)	17.8	3.6	20
Exchangable Calcium (me/100 g)	13.6	1.7	12
Exchangable Sodium (me/100 g)	0.5	0.1	28
Exchanageble Potassium (me/100 g)	0.1	0.0	30
CEC (me/100 g)	35.4	3.7	10
• TOI (%)[1]	25.0	8.5	34
• TFI[2]	2.0	1.8	94
• SI[3]	40.0	25.0	62

[1]Topographic index, [2]Tidal flooding index, [3]Stand index (see the text for details).

acteristics and eleven out of the seventeen species did not yield independent variables with statistically significant t-values. For all regressions a multiple coefficient of determination (R^2) of 45% and higher were included in the models. Forty-five percent appeared to be the dividing value between the higher and lower coefficients. Since R^2 is equal to the percentage of variation which the multiple regression is accountable for, i.e. the level of explanation, it follows that the regression equations presented in this study account for 45% or above of the variance. The order or sequence of the environmental variables in the equations indicate their relative importance to each other in predicting the dependent vegetation attribute.

All environmental variables were retained in the equations as shown in Table 4. However, some variables occurred more frequently than others. The most frequently occurring parameter in the A stratum (overstorey) regressions are salinity (five times) and magnesium (four times). Other variables e.g. stand index (SI) and bulk density occur three times each while silt + clay, organic matter and sand content of the substrates are retained in two equations each. The most important determinants of mangrove structure in the A stratum relate to a salinity/magnesium nutrient complex (Table 5). While salinity is s stress factor, magnesium indicate nutrient availability (Naidoo 1980, Ukpong 1998, 2000). Salinity is overwhelmingly important in determining tree basal area, contributing 55% to the total variance of 77%. Salinity also contributed 26% and 21% to the total variances of 55% and 66% extracted for the tree density and tree height equations respectively. Since tree basal area, density and height are indicators of productivity, it means that salinity, as a stress factor determines the level of mangrove productivity. The ecological importance of *R. reacemosa* and *A. africana* are also significantly influenced by salt concentrations. Magnesium (nutrient cation) is a determinant of tree coverage, contributing 19% to the total variance of 75%. The importance of nutrients in species importance is indicated by the significant contribution of magnesium to the *R. racemosa* and *A. african* equations. Stand index (SI) is significant in the basal area and tree density equatons, contributing 12 and 10% to the total variances of 54 and 77% respectively. The location of stand relative to marine and terrestrial influence therefore affects the structural characteristics of the mangrove vegetation. Bulk density significantly influences tree density, tree height and the importance of *R. racemosa*, presumably on account of affecting root penetration. Sand

Table 4. Regression models predicting vegetation structure along environment parameters

A. Stratum – Overstorey

Tree density (stems/ha) = 6.02 ± 0.38 (SAL) – 0.34 BD + 0.28 (SI) +2.51 (OM) ± 23.4% (R = 54%)

Tree height (meters) = –12.4 + 0.78) (SAN) – 0.46 (SAL) + 0.37 (BD) + 0.11 (SI) ± 20.5% (R^2 = 66%)

Tree cover (%) = –14.82 + 0.48 (TFI) + 0. 29 (Mg) + 0.2 (OM) – 0.07 (Sitcl) ± 24.5% (R^2 = 75%)

Basal area (m^2/ha) = 0.51 + 0.18 (SAL) – 0.11(SI) + 0.06 (SAN) + 0.03 (Mg) ± 20.4% (R^2 = 77%)

R. racemosa (% cover) = 71.85 – 0.83(Mg) – 0.62 (SAL) + 0.2 (BD) ± 18.4% (R^2 = 45%)

A. africana (% cover) = –85.26 + 0.47 (Mg) + 0.28 (Sitcl) – 0.04 (SAL) ± 16.4% (R^2 = 50%)

B. Stratum – Understorey

Density (stems/ha) = 14.71 – 1.76 (FM) – 1.71 (SI) + 0.42 (TOI) – 0.22 (TFI) ± 38.6 (R^2 = 65%)

Cover (%) = 90.20 – 0.62 (CEC) – 0.24 (TFI) – 0.15(SI) + 0.06 (SAL) ± 26.4 (R^2 = 73%)

R. mangle (stems/ha) = –54.30 – 1.72 (SAN) – 0.45 (TOI) + 0.34(Mg) + 0.25 (CEC) =0.11 (TFI) ± 21.7% (R^2 = 51%)

C. Stratum – Groundlayer

Seed Density(stems/ha) = 53.41 + 2.16(TOI) + 1.84 (Sitcl) + 1.41 (ODD) – 0.81 (SAL) ± 12.6% (R^2 = 84%)

A. aureum (stems/ha) = –0.14 + 0.56 (TFI) + 0.25 (RC) – 0.05 (CO_3) – 0.03 (Sitcl) – 0.01(SAL)

V. cuspidata (% freq.) = 0.34 + 0.44 (TOI) + 0.29 (TFI) + 0.18 (Sitcl) – 0.08 (CEC) ± 24.6% (R^2 = 70%)

SAL – salinity(%), TFI – tidal flooding index, SI – stand index, Sitcl – silt + clay (%), OM – organic matter (%), BD – bulk density (g cm^{-3}), SAN – sand (%), Mg – magnesium (me/100 g), CEC – cation exchange capacity (me/100 g), TOI – topographic index, FM – field moisture (%), CO_3 – carbonate (g/100 g), RC – root content (%), ODD – organic debris deposit %).

Table 5. Percentage contribution of each site variable to the total variance of the regression equations. For explanations see Table 4

Vegetation/Species	Contribution of explanatory variable (%)								Total variance (%)
	SAL	Mg	TFI	SI	Sitcl	OM	BD	SAN	
(Overstorey)									
Tree density (stems/ha)	26	–	–	10	–	6	12	–	54
Tree height(m)	21	–	–	3	–	–	9	32	65
Tree cover (%)	–	18	43	–	4	10	–	–	75
Basal area (m^2/ha)	54	4	–	14	–	–	–	4	76
R. racemosa (% cover)	18	19	–	–	–	–	7	–	44
A. africana (% cover)	6	38	–	–	6	–	–	–	50
(Understorey)									
Density (stems/ha)	–	–	6	–	12	25	–		65
Cover (%)	3	–	9	56	–	–	–	22	74
R. mangle (stems/ha)	–	6	4	5	9	–	29	6	53
R. vinifera (stems/ha)	18	8	3	7	15	–	–		51
(Groundlayer)									
Seed Density (stems/ha)	3	–	58	–	14	–	8	–	83
A. aureum (stems/ha)	3	30	–	6	5	27	–	–	71
V. cuspidata (% freq.)	–	16	46	–	5	–	–	4	71

appears to be the most important soil textural property in the A stratum (overstorey) which accounts for 23% out of the total variance of 66% extracted for tree height analysis. Organic matter influences tree density and coverage while % silt + clay influence tree coverage and *Avicennia* spp.

Several environmental variables were indicated as determining B stratum vegetation structure (Table 5). Tidal flooding index (TFI) occurred in all four equations but with low levels of statistical significance (P<0 .5) CEC and topographic index (TOI) occurred in each of the three equations while salinity, magnesium and stand index (SI) were retained in two equations. A high percentage of contribution (56%) by CEC in the understorey coverage equation indicate the importance of nutrient availability in the structural composition of this stratum. The coefficient of CEC in the understorey coverage regression, being negative implies that the higher the CEC the lower is the percentage cover of the mangroves. Field moisture and stand index relate highly (24%; 22%) to mangrove density, out of a total variance of 65%. The negative significant impact of field moisture on species density means that the drier is the site (farther from the river flooding), the higher is the density. Since non-mangroves generally dominate at the landward drier portions of swamps, a structural variation in species composition is reflected from the shores inland. Sand, representing substrate texture was significant in determining the importance of *R. mangle*. Since sand content of substrates decreased with distance inland, where *R. mangle* is the dominant mangrove, it implies that fresh mud texture is favourable to establishment and growth of the species. Salinity and topographic index (TOI) were important in the *R. vinifera* equation. TOI was also significant in the *R. mangle* and understorey density equations (Table 5). These selections were obvious: as topographic variations increased, mangrove density decreased while non-mangrove density increased as the ecotone is approached. *R. vinifera* is basically a freshwater species and the importance of salinity (18%) in that equation could be negative; that is, negative correlation. On the other hand the equation could indicate increasing tolerance of non-mangroves to salt concentrations at the mangrove/high forest ecotone. Generally, salinity is of less importance in determining B stratum mangrove structure.

Tidal flooding, topography and silt/clay substrates are the most significant determinants of C stratum (groundlayer) in mangrove structure (Table 5). Topographic index (TOI) contribute 58 and 45% out of the 84 and 70% total variances extracted for the seedling density and *V. cuspidata* equations respectively. Tidal flooding and root content of substrates significantly determine the importance of *A. aureum*, a circu-mestuarine fern.

Silty and clayey substrates (14%) facilitate the establishment of mangrove seedlings out of a total variance of 84%. *A. aureum* dominate on topographic mounds where soil is formed on wrack deposits. When established, the species develops a dense fibrous rootmat around its clusters and raise the substrate associated with it to mound positions. This probably explains the root content in the *Acrostichum* equation although a larger part of the roots may have been *Nypa* roots. *Vossia cuspidata* is ecotonal and the importance of TOI (45%) out of a total variance of 70% relates to topographic mound positions. Carbonate, CEC and organic debris deposits (ODD), retained in one equation each and at lower levels of statistical significance ($P<0.05$) are regarded as relatively less important in the C stratum analysis.

5. CONCLUSION

The role of environmental variables in determining mangrove vegetation structure have been assessed. Salt concentrations significantly influenced the ecological importance of *R. racemosa* and *A. africana*. The importance of nutrients was indicated by the significant contribution of soil magnesium to the *R. racemosa* and *A. africana* regression equations. In the overstorey, stand index is significant in determining basal area and tree density while the location of stands relative to marine and terrestrial influences generally affects the structural characteristics of the mangrove vegetation. Organic matter relates to silt as the favourable soil textural attribute where nutrient cations are retained in mangrove swamps. A high percentage of contribution (56%) by CEC (cation exchange capacity) in the understorey coverage equation indicates the importance of nutrient in determining species composition of the B stratum. Salinity and topographic index were important in the *R. vinifera* equation indicating that lesser inundation and salinity were the determinants of *Raphia* spp. occurrence in the mangrove zone. In the C stratum, silty and clayey substrates were significant in the establishment of mangrove propagules. The results of this study show clearly that mangrove structure relate significantly to several environmental variables.

6. SUMMARY

Results of species analysis (Table 1), structural data (Table 2) and summary of environmental variab-

les (Table 3) are presented for the Creek Town mangroves. West African (Fig. 1). *Nypa fruticans* was dominant in the A stratum while *Rhizohora mangle* was dominant in the B stratum. The C stratum was dominated by mangrove saplings. *Rhizophora mangle* had the largest basal area (Table 2). The most variable soil properties in the mangrove swamps were debris deposit, tidal flooding index and stand index (Table 3). Multiple regression analysis showed that several environmental variables significantly influenced the mangrove vegetation (Table 4). The contribution of the variables to the total variance of the regression models are shown in Table 5. The result shows that several variables like salinity, sand content, bulk density, topographic index, tidal flooding index and % silt + clay are highly correlated with the mangrove vegetation structure.

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