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Vegetation and its relation to soil nutrient and salinity in the Calabar mangrove swamp, Nigeria

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Abstract

The study examines vegetation – environment relationships. Vegetation measurements included species frequency, density, diameter and tree height, while environmental measurements were soil particle size distribution, acid properties (pH, Al, SO_4), nutrient cations (Ca, Na, Mg, K), organic carbon, nitrogen, phosphorus and chloride content. *Nypa fruticans* was the dominant species in the A stratum (> 3 m tall) while *Rhizophora mangle* was dominant in the B stratum (1–3 m tall). The C stratum (< 1 m tall) was dominated by mangrove, *Nypa* and *Raphia* saplings. Silt was dominant and the most variable particle size fraction. A principal components analysis of the soil data indicated the first three dominant components influencing the vegetation were salinity, nutrient and soil texture. Tree height and density correlated highly with the salinity and soil texture gradients ($P < 0.01$), while basal area correlated with salinity and nutrient gradients ($P < 0.01$). While *Avicannia africana* in the A stratum was influenced largely by the salinity and soil texture gradients. *Nypa fruticans* in the B stratum was influenced by salinity and nutrients.

Introduction

Although the mangrove swamps of the West African subformation have been described (Grewe, 1941; Jackson 1964; Giglioli and Thornton, 1965; Chapman, 1976), few studies have detailed the estuaries and inlets east of the River Niger delta. Keay (1953) maintained that in the inlets along the Nigerian-Cameroun coast, low wave energy regime and sediment accretion have allowed a structurally complex mangrove vegetation to develop. Consequent to an ever-wet humid tropical climate, low salinity gradient and increasing salt tolerance up-river and freshwater plant species have established effectively in the mangrove zone (Ukpong, 1991). The mangrove – *Rhizophora mangle* (May), *Rhizophora racemosa* (May), *Rhizophora harrisonii* (Keay) and *Avicennia africana* (Moldenke) commonly occur in mixed stands with the associes – *Nypa fruticans* (Thumb), *Phoenix reclinata* (Jacl.), *Acrostichum aureum* (Linn.), *Acutas afer* (Sw.), *Vossia cuspidata* (Sw.) and *Selaginella* ssp. (Linn.) (Ukpong, 1995). The accretive swamps, densely vegetated, represents "interface consocies", being transitional between littoral mangroves and up-river freshwater swamps.

This study represent an ecological investigation of mangrove communities occurring at the transitional zone where oceanic influences and freshwater inputs from upland streams are equally felt. The approach is quantitative, aimed at analysing the mangrove productivity measures with a view to establishing their relationships with the environment. Although the vegetation and environment are multivariate systems (Ukpong and Areola, 1995), the basic premise of this study is that the environment is multivariate, viewed in terms of gradients while the vegetation consists of independently varying communities and species.

Study area

The study area is the Creek Town Creek/Calabar River swamp (Figure 1). Located between latitudes 4 °55′N and 5 °00′N, about 20 km from the Atlantic coast in Nigeria, West Africa, the swamp experiences a humid

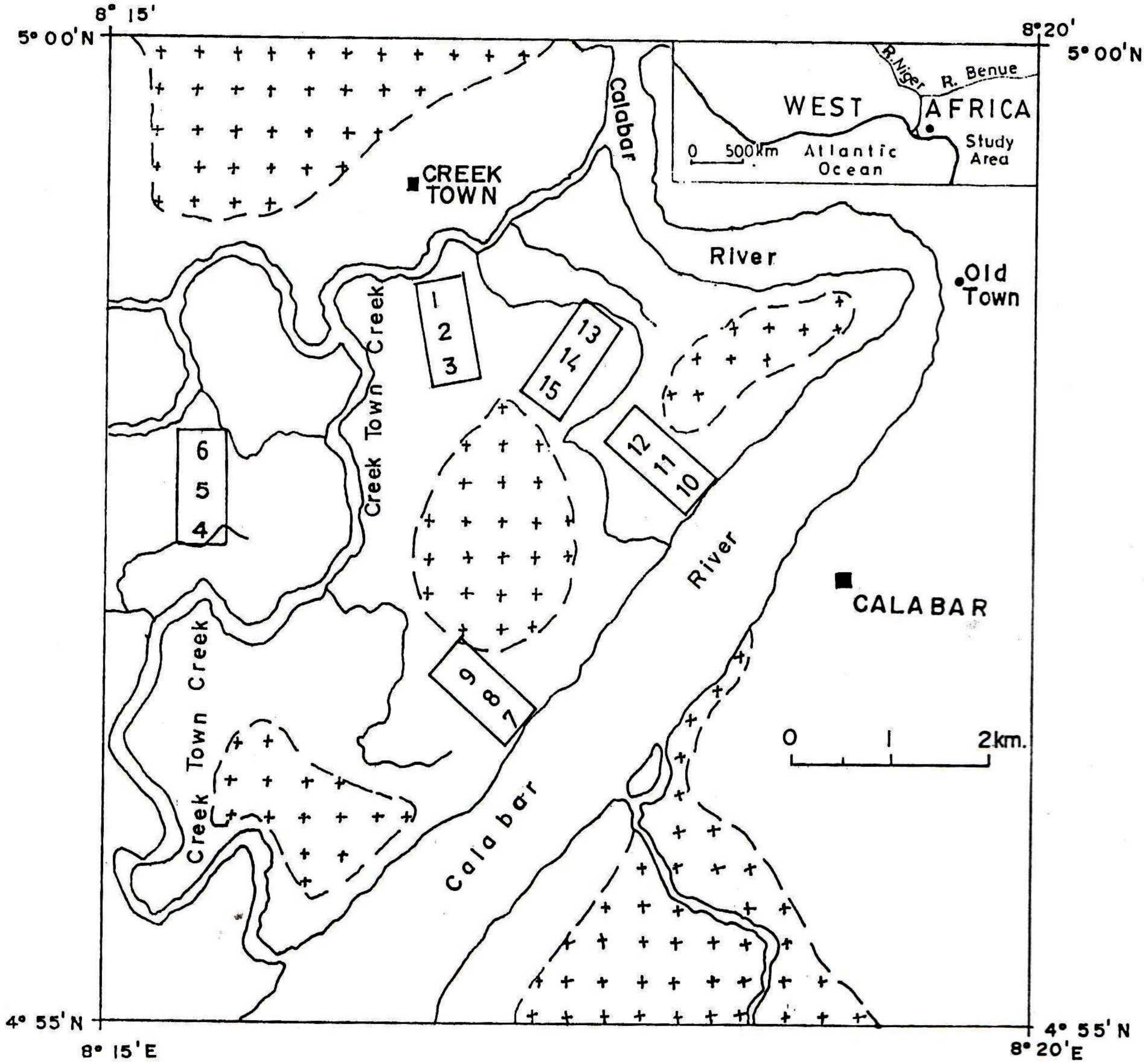

Figure 1. Map of the study area showing location in West Africa (inset) and approximate positions of sample plots (1–15); +++ = non-mangrove upland forest species on elevated segments.

tropical climate. Annual rainfall averages 4021 mm, distributed with a peak in July/August (1800 mm). Least rainfall occurs in December/February (240 mm). Maximum temperature averages 30°C while minimum is 25°C. Relative humidity is constantly high, averaging 80% (Nig. Met. Serv., 1983). In the Calabar river, tidal amplitude is low, being 2.01 m at spring tide and 1.07 m at neap tide. Mean salinity values range from 0.23% in the upper estuary to 3.3% close to the ocean (Ramanathan, 1981).

Methods

Vegetation and soil data

The Creek Town Creek/Calabar River mangrove swamp was sampled in fifteen 400-m^2 quadrats. The quadrats, regularly spaced at 20-m intervals, were located on environmental transects established at right angles from the creeks across the mangrove forests (see Figure 1). The quadrat size of 20 × 20 was considered adequate in the A stratum because it incorporated the microtopographic variations representative of the swamp landscape.

The vegetation was stratified into A stratum (> 3 m tall), B stratum (1–3 m tall) and C stratum (< 1 m tall). Species frequency and density were obtained among the quadrats. Tree height was measured with a Hagar Altimeter. Diameter at breast height (excluding *Rhizophora* props) was measured with a girthing tape. Crown cover for the A stratum was obtained by the crown-diameter method (Mueller-Dombois and Ellenberg, 1974). The B and C strata vegetation were sampled in 25 m^2 and 1 m^2 subquadrats respectively.

Four soil samples to a depth of 40cm were obtained from each quadrat and bulked for laboratory analysis. The procedures were: Bulk density, in steel cores of volume 550 cm^3 (Blake, 1965); field moisture content, by subtracting the weight of oven-dry soil from the weight of field-moist samples; particle size (% sand, silt, clay) by the hydrometer method (Bouyoucos, 1962); pH in 1:2 soil to water suspension using glass electrode (Jackson, 1962); exchange acidity by extraction with barium acetate and titration with NaOH (Jackson, 1962); aluminium, extracted with 0.02M EDTA and determined by atomic absorption spectrophotometry (Isaac and Korber, 1971); acetate soluble sulphate, by turbidimetric determination (Tabatabai, 1974); organic carbon, by Walkley-Black method; total nitrogen by the Kjedahl method and available phosphorus by the Bray method (Jackson 1962). Carbonate was determined by the Bromo Thymol Blue method; chloride by $AgNO_3$ titration (USDA 1969); exchangeable cations (K, Mg, Ca, Na) by extraction in 1 N ammonium acetate and determination by atomic absorption (Ca, Mg) and flame spectrometry (K, Na); cation exchange capacity (CEC) was obtained as the summation of exchangeable cations and exchange acidity.

Synthesis of data

To meet the requirements for normality in parametric statistics, transformations were performed on the vegetation and soil variables following Gregory (1974). Since the environment was to be viewed in terms of gradients, an analytical technique of factoring the correlation matrix of the soil data into its characteristic roots and corresponding characteristics vectors was necessary. Desired, therefore, was an environmental ordination technique capable of generating ecological spaces in which the relationships among the entities in the data set are clearly depicted (Gauch, 1982; Adesina, 1994). Principal components analysis (PCA) meets this requirement (Barkham and Norris, 1970; Terr Braak and Prentice, 1988; Ukpong and Areola, 1995).

To link the vegetation with the environment, the principal components of the environmental subsystem were correlated pairwise with the vegetation variables.

Stepwise multiple regression procedures were used to identify the order of environmental gradients (rotated PCA scores) having the strongest relationship with each vegetation variable. The regressions were run such that the order of environmental gradients was selected using an analysis of variance with each step reducing the variance of the vegetation in each iteration. The model "linear" equation is of the form:

$$Y = a + b_1x_1 + b_ix_i + b_nx_n \pm \text{SE},$$

where:

Y = dependent variable (vegetation-criterion);
a = Y intercept, b = partial regression coefficient,
x = independent variable (environmental gradient-predictor), and
SE = Standard Error.

Result and discussion

Vegetation analysis

The summary of vegetation analysis of the A stratum is presented in Table 1. *Nypa fruticans* has the highest density and cover, although with a lower frequency of occurrence than *Rhizophora mangle*. *Nypa* palm is not a native but was introduced into West Africa in 1906 (Mercer and Hamilton, 1984). The mature palms thrive on firm soils progressively stabilized by extensive root-mat. Consequently *Nypa* occurs in mixed stands with *R mangle* and *Aricannia africana* in the inner swamp and with *Rhizophora racemosa* along the channel banks. The mangroves (*R. mangle*, *R. racemosa*, *A. africana*) show dominance in terms of basal area, ranging from 2.8 m^2/ha to 4.3 m^2/ha. While the crown spread is dominated by *Nypa*, the mangrove canopy layer remains relatively uniform in height except for *R. racemosa* which, supported by props, exceeds 7.7 m along the channels (Table 1). Species density and frequency indicate a mixed forest where niche relations overlap.

Stem density is higher in B stratum than in A stratum (Table 2). In density, coverage and basal area,

Table 1. Summary of vegetation analysis of the A stratum in fifteen 400 m^2 quadrats

Species	Frequency (%)	Density (stems/ha)	Mean Coverage (%)	Mean tree height (m)	Mean basal area (m^2/ha)
Nypa fruticans	60.0	153	29.0	4.8	–(23)*
Rhizophora mangle	66.7	100	16.3	4.9	4.3 (15)
Raphia vinifera	44.7	87	18.7	5.8	–(13)
Rhizophora racemosa	44.7	87	16.7	7.7	2.8 (13)
Avicennia africana	60.0	80	7.3	5.2	3.5 (12)
Phoenix reclinata	26.7	27	3.3	4.0	0.3 (4)
Conocarpus erectus	13.3	13	1.3	5.0	0.4 (4)
Pandanus candelabra	13.3	13	0.7	3.3	0.5 (4)

*Parentheses indicate actual number of trees measured.
– Basal areas of these palms could not be measured due to extensive fronds.

R. mangle dominates the B stratum. Mixed occurrences of species are most pronounced in the B stratum, which represent the survivors of recently established species vigorously competing for openings in the canopy. Since canopy gaps are infrquent, few of these species ever appear to evolve into "trees." *R. racemosa* has the highest density. *Raphia vinifera*, an up-river freshwater species achieve a density of 173 s/ha, about twice in the A stratum. Apart from the fern *Acrostichum*, sp., the sedges *Triumfettta rhomboideae*, *Cyperus articulans*, *Ipomoea cairica*) dominated on the ecotones where the substrates are less silty and somewhat better drained.

The C stratum (Table 3) is dominated by mangroves, *Nypa* and *Raphia* saplings. These seedlings or propagules are highly bouyant and readily transported by tidal current. Hence they are seasonally dispersed along tributary creeks. *Acutas afer*, *Vossia cuspidata* and *Selaginella* spp. are up-river plants that have low salinity stress. They occur on sandy mounds and wrack deposits, i.e. the delivery of large amounts of plant debris. *Acrostichum aureum*, *Sesuvium* spp. and *Paspalum vaginatum* are true tidal swamp species found on the levees particularly among mature mangrove.

In general, two classes of plants make up the mangrove vegetation of the area: (a) genera and higher taxa usually found in brackish/saline mangrove habitats e.g. *N. fruticans* and *Rhizophora* spp. which may be succeeded (on littorals) by *A. africana*, *Acrostichum* spp. and *P. vaginatum*, and (b) species of genera that have become adapted to life in freshwater/brackish mangrove interface, e.g. *Raphia vinifera*, *V. cuspidata*, *Acutas afer* and *Selaginella* spp. Apart from the channel margins where *R. racemosa* may occur in pure stands as pioneer species (Keay, 1953), species zonation is not distinct, even in the canopy layer (Ukpong, 1992a).

Table 2. Summary of vegetation analysis of the B stratum

Species	Frequency (%)	Density (stems/ha)	Mean coverage (%)	Mean basal area (m^2/ha)
Rhizophora mangle	66.7	237	26.3	3.5 (36)*
Nypa fruticans	66.7	213	20.3	–(28)
Rhizophora racemosa	53.3	307	13.3	2.8 (26)
Avicennia africana	53.3	146	15.0	2.2 (24)
Raphia vinifera	46.7	173	14.3	–(18)
Conocarpus erectus	40.0	113	14.7	1.7 (18)
Phoenix reclinata	33.3	47	8.2	1.4 (12)
Drepanocarous lunatus	33.3	53	6.2	0.6 (12)
Pandanus candelbabra	33.3	33	4.7	0.4 (8)
Triumfetta rhomboideae	26.6	27	2.1	0.1 (8)
Raphia hookerii	26.6	16	1.0	–(8)
Cyperus articulans	20.0	16	1.5	0.2 (4)
Ipomoea cairica	13.3	13	1.5	0.2 (4)
Cyperus papyrus	13.3	13	0.3	0.1 (4)

*Parentheses indicate actual number of trees measured.

Soil analysis

The mangrove soils may be described according to the soil map of Africa (D'Hoore, 1963) as "juvenile soils on marine alluvium", or "weakly developed soils." Silt was the most common (44% ± 10) but also the most variable soil particle followed by sand (35% ± 5) or clay (21% ± 5, Table 4). Low bulk density (0.73 +

Table 3. Summary of vegetation analysis of the sapling layer C stratum

Species	Freq-uency (%)	Densi-ty (stems /ha)	Mean cover-age (%)
Mangrove saplings	93.3	393	0.3
Nypa fruticans	80.0	300	0.8
Raphia spp.	53.3	200	0.6
Conocarpus erectus	46.7	120	0.2
Phoenix reclinata	46.7	120	0.2
Drepanocarous lunatus	40.0	120	0.1
Pandanus candelbabra	33.3	107	0.2
Acutas afer	33.3	98	ins.*
Vossia cuspidata	53.3	46	0.2
Selaginella spp.	26.7	–	0.4
Acrostichum aureum	46.7	144	0.5
Sesuvium spp.	46.7	–	0.3
Paspalum vaginatum	13.3	26	0.1

* = insignificant.

Table 4. Summary of soil conditions for 0.4 m depth

Soil properties	Mean value	Standard error	C.V.* (%)
Bulk density (g cm^{-3})	0.73	0.14	19.2
Field moisture (%)	124.70	18.50	14.8
Sand (%)	34.66	4.70	13.6
Silt (%)	44.20	10.20	23.3
Clay (%)	21.14	4.60	21.8
pH (field moist)	6.05	0.12	1.9
pH (air dry)	4.80	1.20	25.0
Exchange acidity (me/100g)	4.66	0.56	12.1
Aluminium (me/100g)	0.23	0.05	21.7
Soluble sulphate (me/100g)	0.07	0.03	42.8
Organic Carbon (%)	6.43	0.80	12.4
Total nitrogren (%)	0.09	0.03	33.3
Phosphorus (Ug ml^{-1})	1.22	0.35	28.7
Calcium (me/100g)	12.80	1.82	14.2
Magnesium (me/100g)	16.73	3.64	21.8
Potassium (me/100g)	0.08	0.03	37.5
Sodium (me/100g)	0.48	0.12	25.0
CEC (me/100g)	34.75	4.65	13.4
Carbonate (me/100g)	7.85	3.22	41.0
Chloride (%)	2.70	1.58	58.5

*Coefficient of variation: 0–15% (least variation), 15–35% (moderate); > 35% (most varied).

0.14 g cm^3) and high field moisture (124% ± 18) values reflect the saturation of soils by tides. Field moist and air-dry pH values are low (respectively 6.05 ± 0.1 and 4.8 ± 1.2) whereas exchangeable acidity (4.7 ± 0.6 me/100 g) is large, indicating acidic conditions of mangrove soils (Boto and Wellington 1984). The large organic carbon values (6.4 ± 0.8%) reflect the peaty nature of soils and the preponderance of roots and pneumatophores. The soils have a high capacity to absorb cations particularly magnesium and calcium which may be due to the abundance of these cations in tidal water.

Exchangeable potassium and sodium values (respectively 0.08 ± 0.03 me/100 g and 0.48 ± 0.12 me/100 g) are relatively small. Because the soils are appreciably acidic, phosphorous is probably fixed by iron and aluminium. The soils contain large amounts of carbonate (7.8 ± 3.2%) probably due to inflow of marine sediment by estuarine processes. Values of soluble sulphate (0.07 ± 0.03 me/100 g) and aluminium (0.23 ± 0.05 me/100 g) are large and may be the main contributors to exchange acidity.

Total nitrogen values (0.09 ± 0.03%) were low. Chloride content was highly variable; despite tidal import of saline water, the soil could be almost fresh at the peak of the rains.

The Creek Town/Calabar River mangrove soils differ from those reported elsewhere in Nigeria (Ukpong, 1992b), where CEC was higher (45.0 me/100 g) and clay the most variable textural property (CV = 23.8%). In South Africa, Naidoo (1980) reported predominantly clayey soils with large concentrations of sodium (11.7–45.2 me/100 g). The differences are probably due to local geogenetic parameters and habitat variables e.g. mineralogy of adjacent coastlands, frequency of tidal flooding and salt spray (Ukpong, 1994).

Variable loadings from the principal components analysis of the soil data are presented in Table 5. Three components accounted for 62.9% of the variation.

Component 1: This soil component is a salinity gradient in view of the high loading for chloride, sodium, soluble sulphate and aluminium. Soil acidity is emphasized in view of the high loading for pH and exchange acidity. The component indicates environmental stress in mangroves.

Component 2: This soil component is a nutrient gradient, emphasized by organic carbon, total nitrogen, phosphorus and CEC. pH and exchange acidity also load-highly, as nutrient status determinants.

Component 3: This soil component is a soil texture gradient where silt correlates with negative loadings

Table 5. Selected loadings from the principal component analysis of soil data

Soil properties	Component 1	Component 2	Component 3
Bulk density	+0.220	+0.182	–0.540*
Sand	–0.086	+0.211	–0.501*
Silt	+0.250	+0.070	+0.576*
Clay	+0.274	+0.082	–0.664*
pH (field moist)	+0.513*	–0.357	+0.207
Exchange acidity	+0.576*	–0.382	+0.084
Aluminium	+0.611*	+0.094	+0.125
Soluble sulphate	+0.750*	+0.136	+0.281
Organic Carbon	–0.298	+0.542*	+0.256
Total nitrogren	–0.262	+0.601*	+0.113
Phosphorus	–0.188	+0.617*	–0.294
Sodium	+0.699*	+0.483	+0.076
CEC	+0.243	+0.790*	+0.140
Chloride	+0.932*	+0.088	–0.168
Proportional of total variance	35.4%	15.6%	11.9%

*Gradient determinant attributes.

for clay and sand, indicating favourable sites for the establishment of mangroves.

The amount of variance extracted by the principal components analysis reflects the importance of soil properties as significant components of the environment.

Vegetation – environment relationships

The linear correlations between vegetation and environmental gradients (Table 6) show that the salinity gradient is correlated with tree height ($r = 0.77$; $p < 0.001$), seedling density is positively correlated to the salinity gradient ($r = 0.54$; $p < 0.05$), and species dominance is determined by salinity variations in view of the negative correlation ($r = –0.71$; $p < 0.001$) of the salinity gradient with the basal area.

The nutrient gradient, correlated positively with basal area ($R = 0.65$; $p < 0.01$) and B stratum coverage ($R = 0.68$; $p < 0.01$) shows that wood volume and B stratum productivity in mangroves vary with nutrient availability. With a negative but probably not significant correlation ($R = –0.42$), tree density apparently decreases or is insensitive to nutrient variations.

The soil texture gradient is an important determinant of tree height ($r = 0.67$; $p < 0.01$) and density ($r = 0.56$; $p < 0.05$), indicating that mangrove wood

Table 6. Product-moment correlation between vegetation characteristics and environmental gradients

Vegetation characterics	Salinity gradient	Nutrient gradient	Soil texture gradient
Tree height	0.77***	–0.19	0.67**
Tree density	–0.31	–0.42*	0.56*
Basal area	–0.71***	0.65**	–0.34
Coverage (B stratum)	0.26	0.68**	0.21
Seedling density	0.54*	–0.13	0.62**

Significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table 7. Predictive multiple regression equations based on the performance of vegetation along environmental gradients (SAL = salinity; NUT = nutrient; TEX = soil texture)

(A stratum)		
Tree coverage	$Y =$	2.95 – 0.82 SAL + 0.66 NUT +0.14 TEX ± 17.5% (R^2=74.1%)
Basal area	$Y =$	27.24 – 4.33 SAL + 2.68 TEX +1.95 NUT ± 21.6% (R^2 = 72.6%)
Tree height	$Y =$	1.64 – 0.62 SAL + 0.54 TEX –0.08 NUT ± 24.8% (R^2 = 66.1%)
Rhizophora racemosa	$Y =$	–26.4 + 0.91 NUT + 0.65 SAL –0.21 TEX ± 23.9% (R^2 = 62.3%)
Avicennia africana	$Y =$	16.9 + 2.62 SAL + 1.88 TEX +0.61 NUT ± 15.8% (R^2 = 71.2%)
Nypa fruticans	$Y =$	0.97 + 1.88 TEX + 0.66 NUT +0.42 SAL ± 18.6% (R^2 = 73.7%)
(B stratum)		
Raphia vinifera	$Y =$	0.34 + 0.06 TEX + 0.04 NUT –0.03 SAL ± 26.8% (R^2 = 59.4%)
Rhizophora racemosa	$Y =$	27.60 + 0.84 TEX – 0.41 SAL –0.11 NUT ± 31.4% (R^2 = 49.3%)
Nypa fruticans	$Y =$	1.45 + 0.65 SAL – 0.40 NUT +0.22 TEX + 14.5% (R^2 = 85.1%)
Avicennia africana	$Y =$	6.84 + 2.01 NUT + 0.08 TEX –0.02 SAL ± 17.2% (R^2 = 64.9%)
(C stratum)		
Acrostichum aureum	$Y =$	–0.17 + 0.24 NUT + 0.19 TEX +0.08 SAL ± 18.9% (R^2 = 66.5%)
Sesuvium spp	$Y =$	–0.26 + 0.18 NUT – 0.40 TEX +0.02 SAL ± 28.9% (R^2 = 51.7%)
Vossia cuspidata	$Y =$	–2.95 + 0.17 SAL + 0.06 NUT –0.04 TEX ± 21.5% (R^2 = 60.7%)

Table 8. Percentage contribution of the soil gradients to the total variance of multiple regression analyses

Vegetation/species characteristics		% Contribution Salinity	Nutrient	Soil texture	Total
Tree Coverage	(A)	58.5**	12.4*	3.2	74.1
Basal area	(A)	44.8**	13.2*	14.6*	72.6
Tree height	(A)	35.9**	8.5*	21.8*	66.1
Rhizophora racemosa	(A)	17.1*	31.9**	13.3*	62.3
Avicennia africana	(A)	38.4**	4.2	28.6*	71.2
Nypa fruticans	(A)	17.2*	21.7*	35.8**	73.7
Raphia vinifera	(B)	7.3*	24.2*	27.9*	59.4
Rhizophora racemosa	(B)	62.5**	16.2*	6.4*	85.1
Nypa fruticans	(B)	6.8*	4.2	38.3**	49.3
Avicennia africana	(B)	2.6	52.6**	9.7*	64.9
Acrostichum aureum	(C)	0.9	45.2**	20.4*	66.5
Sesuvium spp	(C)	1.5	41.6**	8.6*	51.7
Vossia cuspidata	(C)	41.6**	17.3*	1.8	60.7

Significance: ** = 1% level; * = 5% level
(A) = A stratum; (B) = B stratum; (C) sapling layer

productivity increases with textural variations tending to silt-loam. The soil texture gradient correlates with seedling density ($r = 0.62$; $p < 0.01$) indicating clay being a favourable substrate for rooting of mangrove propagules.

The model linear equations based on regressing the vegetation on environmental gradients are shown in Table 7. The gradients in the regression models portray the order of their importance in each case. The percentage contribution of the gradients to the total variance of each model is shown in Table 8.

In the A stratum, the salinity gradient occurring with negative coefficients in the biomass models indicate environmental stress in mangroves (Table 7). The salinity gradient alone explained more than 50% of the total variation in tree cover, basal area and tree height. The soil texture gradient was marginally significant in explaining basal area variation (14.6%) and tree height (21.8%). *A. africana* was largely influenced by salinity and soil texture, *R. racemosa* by nutrient and salinity, and *N. fruticans* by soil texture with salinity and nutrients contributing lower but significant levels. This shows that although the species may share niche relations to changing salinities yet other environmental demands vary significantly.

Environmental determinants observed for species in the B stratum differ from those observed for similar species in the A stratum. Soil texture gradient was more important in the B stratum for *R. racemosa* and *Raphia* sp., accounting for more than 50% of the total variation. *Nypa* was mostly influenced by the salinity gradient (62.5%) from a total explained variance of 85.1%. *A. africana* was more significantly influenced by the nutrient gradient (52.6%) than in the A stratum. The positive coefficients in Table 7 emphasize soil texture and nutrients as determinants of B stratum performance.

In the C stratum, *A aureum* and *Sesuvium portulacastrum* (Linn.) which are tidal swamp species are insensitive to the salinity gradient (Ukpong 1991), while *V. cuspidata* being an upland invader of the tidal zone reflects negative relationships with salinity.

Conclusion

The mangrove swamp, whether along a consistently saline littoral or a freshwater/brackish interface is a stressed ecosystem. Vegetation performance is influenced by three main gradients viz: salinity, nutrient and soil texture. Salinity is a gradient of environmental stress in that the vegetation shows adaptation or tolerance but is not salt loving. Positive relationships of species to the nutrient and soil texture gradients are indicative of the importance of soil texture and nutrient relationships to mangrove ecosystem productivity.

Mangrove swamp species, e.g. *Nypa*, *Rhizophora* spp., and *A. africana*, dominate at the fresh/brackish water interface because the salinity gradient, modulated by tidal flooding, restricts vigorous competition from versatile upland species, e.g. *Raphia* spp. and *Selaginella* spp., to the less inundated ecotones. As the dynamic processes of accretion and sedimentation are vigorous in mangroves, the soil texture gradient is particularly large and is coupled to a build-up of nutrients available to the upland invaders of the ecosystem. This observation is synonymous with the habitat evolution sequence emphasized by Thom (1967) in Mexico, except that in Nigeria mangroves are usually replaced by non-mangrove upland invaders of the ecosystem, e.g. *Raphia* spp, *Acutas afer* and *Selaginella* spp (Table 3), due to their increasing adaptation to tidal conditions.

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