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The composition and distribution of species in relation to soil nutrient gradients in mangrove swamps in South Eastern Nigeria

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Abstract: Based on seasonal soil measurements, direct gradient analysis procedures were used to relate the structure of mangrove swamp communities and distribution of species to nutrient gradients. Magnesium and calcium were the predominant cations in alluvial soils, ranging from 8.6 ± 0.9 me 100 g^{-1} to 24.6 ± 2.0 me 100 g^{-1}, while potassium values were lower (0.11 ± 0.05 to 0.37 ± 0.1 me 100 g^{-1}). Organic carbon was high in the soils, ranging from 3.5% to 10.4%. All nutrients varied seasonally, reflecting the complex hydrology of estuaries. Simple correlations and stepwise multiple regression analysis of species with soil nutrients indicated the nutrient status of the soils to be best defined in terms of calcium for the A stratum, calcium/potassium for the B stratum and magnesium for the C stratum. Ecological group classification shows that *Avicennia africana* and *Nypa fruticans* occurred almost exclusively at the highest calcium values of 20.8 me 100 g^{-1} and 17.6 me 100 g^{-1}. *Acrostichum aureum* and *Sesuvium portulacastrum* are insensitive to the magnesium gradient due to their wide ecological amplitudes. Generally, the analysis revealed overlapping range of occurrences for most species although with varying ecological optima along the gradients.

Résumé: Des procédés analytiques ont été utilisés afin d'établir la structure et la distribution des espèces aux gradients nutritifs des communautés marécageuses de mangrove en se fondant sur les mesures saisonnières du sol et le gradient direct. Dans les sols alluviaux les cations dominants étaient le magnésium et le calcium variant de 8,6 ± 0, meq/100g à 24,6 ± 2,0 meq/100g alors que les valeurs en potassium étaient plus faibles (0,11 ± 0,05 à 0,37 ± 0,1 meq/100g. La teneur en carbone organique était élevée dans les sols, allant de 3,5% à 10,4%. Tous les éléments nutritifs variaient selon les saisons, reflétant l'hydrologie complexe des estuaires. Les corrélations simples et l'analyse de régression multiple pas à pas entre les espèces et les éléments nutritifs du sol ont infiqué que le statut nutritif des sols se définissait le mieux en termes de calcium pour la strate A, calcium/potassium pour la strate B et magnésium pour la strate C. La classification écologique en groupe montrent qu'*Avicennia africana* et *Nypa fruticans* apparaissaient presque exclusivement aux taux élévés de Calcium de 20,8 meq/100g et 17,6 meq/100g. *Acrostichum aureum* et *Sesuvium portulacastrum* sont insensibles au gradient de magnésium en raison de leur large plasticité écologique. En général, l'analyse a révélé des coïncidences dans les variations d'occurrence pour la plupart des espèces bien que l'optimum écologique fût varié tout le long des gradients.

Resumen: Basado en medidas estacionales del suelo, se utilizaron procedimientos de análisis de gradiente directo para relacionar la estructura de comunidades de manglar y la distribución de especies a gradientes de nutrientes. El magnesio y el calcio fueron los cationes predominantes en suelos aluviales, variando de 8.6 ± 0.9 me 100 g a 24.6 ± 2.0 me 100 g, mientras que los valores del potasio fueron más bajos (0.11 ± 0.05 a 0.37 ± 0.1 me 100 g). El carbono orgánico fue más alto en los suelos, variando de 3.5% a 10.4%. Todos los nutrientes variaron estacionalmente, reflejando la compleja hidrología de los estuarios. Análisis de correlación simple y de regresión múltiple de las especies con los nutrientes del suelo, indicaron que el estatus nutricional de los suelos está mejor definido en términos del calcio para el estrato A, calcio/potasio para el estrato B y magnesio para el estrato C. La clasificación ecológica mostró que *Avicennia* africana y *Nypa fruticans* se presentaron casi exclusivamente en los valores más altos de calcio de 20.8 me 100 g y 17.6 me 100 g. *Acrostichum aureum* y *Sesuvium portulacastrum* son insensibles al gradiente de magnesio debido a su amplitud ecológica. En general, los análisis mostraron un traslapamiento de la ocurrencia de la mayoría de las especies, aunque con óptimos ecológicos que variaron a lo largo de los gradientes.

Resumo: Com base em medidas sasonais usaram-se procedimentos directos de análise de gradientes no solo para relacionar a estrutura das comunidades de mangal e a distribuição das espécies com os gradientes em nutrientes. O magnésio e o cálcio forma os catiões predominantes nos solos aluviais, oscilando entre os 8,6 ± 0,9 me/100 g e os 24,6 ± 2,0 me/100 g, enquanto os valores do potássio se apresentaram mais baixos (0,11 ± 0,05 a 0,37 ± 0,1 me/100 g); o teor do carbono orgànico nos solos era alto situando-se no intervalo de 3,5% a 10,4%. Todos os nutrientes variaram etacionalmente, reflectindo a hidrologia complexa dos estuários. A análise de correlação simples e a correlação múltipla obtida pelo processo subtractivo entre as espécies e os nutrientes do solo indicaram que o estado nutricional do solo era mais bem definido pelo cálcio para o estrato A, cálcio/potássio para o estrato B e pelo magnésio para o estrato C. A classificação ecológica por grupos mostra que a *Avicennia africana* e a *Nypa fruticans* ocorrem quase exclusivamente nas situações de mais elevada concentração de cálcio, 20,8 me/100 g e 17,6 me/100 g. A *Acrostichum aureum* e a *Sesuvium portulacastrum*, devido à sua maior amplitude ecológica, revelaram-se insensíveis ao gradiente de magnésio. Geralmente, as análises revelaram intervalos de sobreposição para a ocorrência da maior parte das espécies se bem que com um óptimo ecológico variável ao longo dos gradientes.

Key words: Ecological groups, gradient analysis, mangroves, multiple regression, nutrient gradients, Nigeria, soil.

Introduction

Mangroves are trees that live in wet, loose soils of brackish-to- saline estuaries and shorelines in the tropics and subtropics. The mangrove soils are peaty, calcareous and sandy; salinity and nutrient levels fluctuate due to the complex hydrology of the littoral areas. Since the mangrove habitat is basically saline, several studies have attempted to correlate salinity to the standing crop of vegetation and productivity (Lugo 1980; Ukpong 1991). The importance of nutrient factors, however, has not received sufficient attention in mangrove ecology.

Naidoo (1980) observed that cation concentrations in mangrove soils show a correlation with extent of tidal inundation and seepage. Since true mangrove species (with viviparous fruits/pneumatophores) often exhibit zonation from the shore inland, the relationships between the mangroves and soil nutrients have been viewed in terms of differences in the values of soil nutrients between monospecific zones of species (Hynn-Cong- Tho & Egashira 1976; Moorman & Pons 1974; Ukpong 1995a).

In South Africa the occurrence of the mangrove species *Avicennia nitida* (Linn.) was related to a cation exchange capacity (CEC) range of 23.7 me 100 g^{-1} to 83.3 me 100 g^{-1}, while *Bruguiera* spp. (Linn.) occurred within a CEC range of 41 me 100 g^{-1} to 67 me 100 g^{-1} (Naidoo 1980). But Clarke & Hannon (1967), in Australia, observed that the CEC in mangrove soils ranges from 0.38 me 100 g^{-1} at the surface to 0.84 me 100 g^{-1} in the subsurface.

In Mexico, Thom (1967) related the occurrence of *Rhizophora* spp. (G.F. May; R. Keay) to soils with very high organic matter content (52.4%) while Giglioli & Thornton (1965) in Gambia, West Africa related the occurrence of some species to organic matter values ranging from 8.7% to 12.3%. In Nigeria, Ukpong (1992; 1995b) related the occurrence of mangroves to a CEC range of 21.0 me 100 g^{-1} to 56.8 me 100 g^{-1}, with organic carbon values ranging from 1.5% to 9.6% in the soils. The mangrove associes *Sesuvium portulacastrum* (Sw.) and *Paspalum vaginatum* (Sw.) occurred where 15% of the exchange complex was sodium (Giglioli & Thornton 1965).

There exists a considerable overlap in values for soil nutrients from mangrove stands dominated by different species. Sometimes the differences in values within stands are as great or greater than differences between stands. Hence, the aim of this paper is to specify the location of individual mangrove swamp species along gradients of soil nutrients. This follows the dictum that the actual distribution of plants in nature is determined by a complex of environmental factors although each plant has a certain tolerance for each factor (Waring & Major 1964). The basic approach is a direct gradients analysis (the factor - gradient of Whittaker 1978) in which species are assigned to ecological groups according to their modalities on the gradient of a factor determined as being of direct physiological importance to the plants.

Study area

The study area, located in Southeastern Nigeria, extends from longitude 7°30′E to 8°30′E and contains the estuaries of the Cross River (810 km^2), Kwa Ibo River (50 km^2) and Imo River (196 km^2). The vegetation and soils in the more marginal estuaries of Kwa Ibo River and Imo River were reported in an earlier study (Ukpong 1992). The three estuaries are linked together by a narrow coastal beachridge zone (Fig. 1). The most complex vegetation occurs in the Creek Town Creek/Calabar River swamp which is the northernmost limits of mangrove growth in the Cross River estuary (Ukpong 1995b). The climate of the area is humid tropical, ever - wet with an annual rainfall of 4021 mm (NMS 1980). Peak rainfall occurs in July August while least rainfall occurs in December - February. In the estuaries, tidal amplitude is low, the mean being 2.01 m at spring tides and 1.07 m at neap tides. The most important mangroves in the swamps are *Aviennia africana* (Moldenke), *Rhizophora racemosa* (G.F. May), *Rhizophora mangle* (G.F. May) and *Rhizophora harrisonii* (Jacq.), while the important associes are *Nypa fruticans* (Thumb), *Raphia vinifers* (L.), *Acrostichum aureum* (L.), *Sesuvium portulaeastrum* (SW) and *Vossia cuspidata* (L.) (Keay 1953; Savory 1953; Jackson 1964).

Methods

Vegetation and soils sampling

Vegetation and soil measurements were obtained in eighty 10m x 10m quadrats located at regular 20 m intervals along several transects established from the shore inland. The transects were established on various physiographic mangrove habitats modified after Lugo & Snedaker (1974) as : (i) wooded levees (ii) interdistributory basin (iii) distributary basin (iv) interriverine creek,

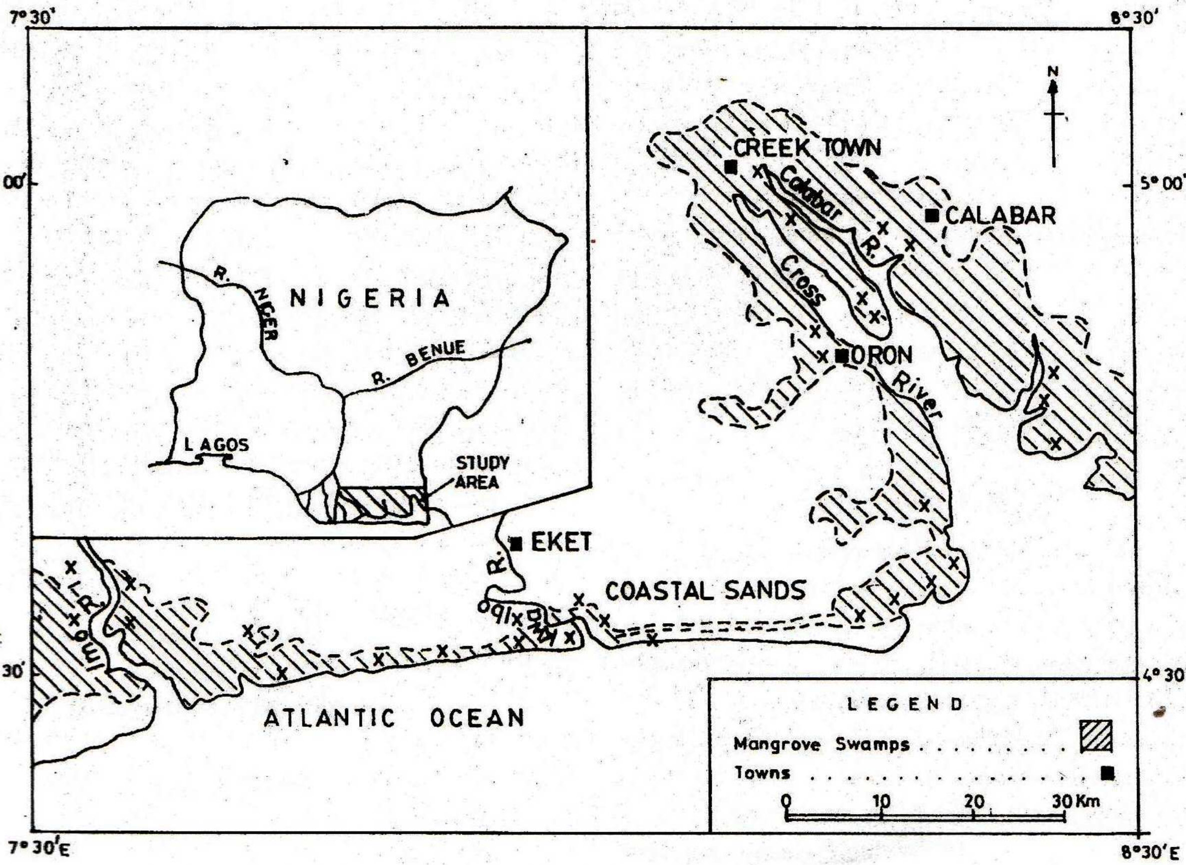

Fig. 1. Map of the study area showing location in Nigeria (inset) XXX = approximate transect locations.

(v) point bar (vi) beachridge sands and (vii) braided channels.

Habitat differentiation eliminated a bias for locating transects on similar more accessible forest types (Ukpong 1992). Transect length depended on the width of swamp, but each contained at least two quadrats, the first quadrat being located on the channel fringe. The distribution of quadrats among the swamps was as follows : Creek Town/Creek/Calabar River (15); Cross River (21); Kwa Ibo River (21); Imo River (20); Coastal beachridge (3).

Crown cover for trees (>3 m tall) in each quadrat was determined by the crown-diameter method (Mueller - Dombois & Ellenberg 1974). For the understorey species (1-3 m tall) coverage was estimated visually in 25 m^2 subquadrats while ground layer coverage (<1 m tall) was estimated in 1 m^2 subplots. Soils sampling was performed in the wet and dry seasons, at or close to the centre of each quadrat at low tides, using profile pits and a soil "corer" (Giglioli & Thornton 1965).

Three core samples were obtained at each point at 20 centimeter intervals to a rooting depth of 60 cm. The soils were air-dried before laboratory analysis. The following parameters were determined : pH, in 1:2 soil to water suspension using a glass electrode (Jackson 1962); organic carbon, by the Walkley - Black wet oxidation method (Jackson 1962); exchangeable cations (Ca^{++}, Mg^{++}, K^{+}, Na^{+}), by extraction with 1 N ammonium acetate at pH 7, then concentrations of calcium, magnesium and potassium determined by atomic absorption and sodium by flame photometry. Cation exchange capacity (CEC) was calculated as the summation of exchangeable cations and exchange acidity. Exchange acidity was determined by extraction with barium acetate and titration with NaOH.

Synthesis of data

To achieve meaningful relationships between soil nutrient variables and the vegetation, the variables were defined as independent, because the relative responses of two species to certain levels of nutrients would most likely determine which of the species is better adapted under the prevailing nutrient conditions. In addition, the mangrove swamp community consists of species with different tolerances (Connor 1969). Being that the nutrient status of mangrove soils is influenced by high water table and seepage (Clarke & Hannon 1967), an ecological approach was desired which would allow all the nutrient parameters to vary, yet allow the influence of one variable on the vegetation to be studied. One such approach adopted in the present study was to obtain seasonal soil nutrient measurements (in the relatively dry months of November to February, and the wetter months of April/May/August) and the mean values of the measurements used in a predictive multiple regression analysis. The regressions were run with raw and long transformation of all independent variables and those equations proving significant with the highest levels of explanation (coefficient of determination R^2) were selected for discussion.

Another approach was to use the mangrove swamp species as indicators of soil nutrient status. Since the nutrients are an important ecological factor (i.e., the nutrients could be limiting to the distribution and composition of species if present in excessive or insufficient quantities), a species distribution will be modified and narrowed by competition or interaction with other species to a zone within its physiological tolerance of soil conditions. Hence, the different species would show distinct distributions along gradients of the nutrient variables, since no two plant species completely coincide in their ecological response (Waring & Major 1964). Based on this observation, Ellenberg (1956) and Whittaker (1967) derived various "ecological groups" according to species responses to the most important nutrient (site) factors. Species were placed in one of five groups relating to the increasing intensity of a factor (see Appendix A). Diagrams of the distribution of species along the gradients of soil nutrients are expected to provide information on the ecological optimum and amplitude for each mangrove swamp species relative to the others and to nutrient resilience.

Nutrient variables for the establishment of gradients were those that were initially most highly inter-correlated with each other and with the species (Hauser 1974). Such variables, usually with positive coefficients, were most frequently retained in the regression equations. In the present study, calcium, potassium, magnesium and organic carbon were selected by the analyses as relating most clearly to plant occurrence.

Results and discussion

Soil analysis

Table 1 summarizes the results of the soil analysis. The mangrove soils have a high sink for cations, particularly in terms of exchangeable magnesium and calcium. The observed variations in soil nutrients, particularly the ex-

Table 1. Mean ± standard deviation (SD) for soil nutrients in five swamps (for a rooting depth of 0-60 cm).

Swamp	Ca (me 100 g^{-1})	Mg (me 100 g^{-1})	K (me 100 g^{-1})	CEC (me 100 g^{-1})	P (mg ml^{-1})	Org. C (%)	pH**
Creek Town Creek/ Calabar River (15)*							
November 1986	9.4 ± 1.9	13.3 ± 1.4	0.13 ± 0.04	38.8 ± 5.1	5.6 ± 0.4	5.5 ± 2.1	5.8 ± 0.1
January 1987	10.3 ± 0.8	15.2 ± 0.6	0.14 ± 0.02	36.7 ± 4.5	4.8 ± 0.6	5.5 ± 1.8	5.7 ± 0.1
August 1987	8.6 ± 0.9	10.5 ± 0.8	0.11 ± 0.05	29.6 ± 5.7	5.8 ± 0.2	5.8 ± 1.4	6.0 ± 0.2
Cross River Swamp (21)*							
December 1986	10.3 ± 7.5	17.6 ± 3.8	0.26 ± 0.02	40.3 ± 3.8	4.1 ± 0.3	9.8 ± 2.4	5.8 ± 0.2
February 1987	10.1 ± 2.5	17.6 ± 3.7	0.25 ± 0.01	35.9 ± 2.6	4.4 ± 0.5	10.4 ± 2.8	5.8 ± 0.2
May 1987	9.4 ± 1.5	15.5 ± 2.1	0.21 ± 0.02	37.3 ± 1.8	4.8 ± 0.2	10.4 ± 1.2	5.6 ± 0.3
Kwa Ibo River Swamp (21)*							
December 1985	14.6 ± 1.4	23.8 ± 1.5	0.25 ± 0.03	50.6 ± 7.4	2.5 ± 0.6	4.5 ± 1.6	6.4 ± 0.2
April 1986	12.2 ± 0.8	21.5 ± 1.3	0.24 ± 0.02	48.7 ± 6.5	2.8 ± 0.4	4.6 ± 1.2	6.6 ± 0.2
August 1987	12.5 ± 1.1	20.8 ± 2.4	0.18 ± 0.01	46.3 ± 2.7	3.1 ± 0.6	4.4 ± 0.8	6.2 ± 0.2
Imo River Swamp (20)*							
February 1986	15.5 ± 4.2	24.6 ± 2.0	0.21 ± 0.02	41.3 ± 3.3	2.8 ± 0.8	6.4 ± 2.2	6.2 ± 0.1
May 1987	24.0 ± 1.2	22.4 ± 1.7	0.18 ± 0.01	43.2 ± 1.5	3.6 ± 0.6	6.8 ± 2.4	6.0 ± 0.2
Coastal beachridge (3)*							
January 1986	2.6 ± 0.2	5.8 ± 0.1	0.37 ± 0.1	17.7 ± 1.7	2.2 ± 1.9	3.8 ± 0.1	6.5 ± 0.2
August 1987	1.8 ± 0.2	5.2 ± 0.1	0.35 ± 0.1	11.8 ± 1.5	2.0 ± 1.8	3.5 ± 0.4	6.2 ± 0.2

* Parentheses indicate number of samples for each swamp Org. C = organic carbon

** Not included in correlation/regression analysis.

changeable cations, are due to tidal influence and distance from the coast (Ukpong 1994).

Swamps inundated directly by Atlantic tides have higher cation concentrations in soils than the middle estuarine swamps. Hence, calcium and magnesium values are highest in the Imo River and Kwa Ibo River Swamps, located close to the Atlantic shoreline (Fig. 1). Much of Creek Town Creek/Calabar River Swamp and the Cross River Swamp are removed from the direct influence of Atlantic tides and consequently have lower calcium and magnesium concentrations in soils. The coastal beachridge, although constantly under the influence of salt spray,.is not regularly inundated by normal tides (except Atlantic storm waves). Therefore, calcium and magnesium values are much lower than in the estuaries although the beachridge is located along the coast. However, potassium concentrations were highest in the coastal beachridge soils and lowest in the upper estuarine Creek Town Creek/Calabar River Swamp soils. Cation exchange capacity (CEC) was highest in the Kwa Ibo River Swamp and Imo River Swamp (Table 1), probably due to the abundance of magnesium and calcium in sea water. The coastal beachridge, being irregularly inundated, has the lowest CEC values.

Available phosphorus levels were highest in the Creek Town/Calabar River and Cross River Swamp soils (Table 1). Closer to the coast, the Kwa Ibo River, Imo River and beachridge soils had lower values. There was a relationship between phosphorus levels and pH values; high phosphorus levels correlated with increasing acid conditions while lower phosphorus levels correlated with increasing alkalinity. The coastal swamps, being narrowed to levees of higher elevation than the swamps of the middle estuaries, are relatively better drained. Consequently, soils of the Imo River and Kwa Ibo River Swamps, with *Avicennia africana* as dominant species, are less acidic than the Cross River and Creek Town Creek/Calabar River soils which have species of *Rhizophora* as dominant elements.

Organic carbon content of soils varied greatly among stands, among the major swamps and with distance inland from the shore. The beach ridge soils with strand and shrubby vegetation had low organic carbon content (3.5 ± 0.4% to 3.8 ± 0.1%) while the more complex swamps had values ranging from 4.4 ± 0.8% in the Kwa Ibo River Swamp to 10.4 ± 2.8% in the Cross River Swamp.

Seasonal values of cation concentration (Ca^{++}, Mg^{++}, K^{+}) in the soils showed tidal imports to be the main source of cations. The values were highest during the relatively dry months (November - February) and lowest in the wet months (May-August). Replenishment of cations occurs through flooding and subsurface seepage of tidal waters across the mangrove habitats. Freshwater inputs, e.g. rainfall and run off from upland areas, intensified during the rainy period (May- August), tend to flush out and deplete the nutrient cations. However, levels of available phosphorus were higher in the rainy months than in the dry months, except in the coastal beachridge soils where phosphorus content was generally low with a January value of 2.2 ± 1.9 $\mu g\ ml^{-1}$ and an August value of 2.0 ± 1.8 $\mu g\ ml^{-1}$.

The coastal beachridge had the lowest nutrient levels when compared to the tidal swamps, partly because it is not regularly flooded by tides. The beachridge is erosional and consequently strand species, e.g. *Triumfetta rhomboideae, Sesuvium portulacastrum, Drepanocarpus lunatus* and *Acrostichum aureum,* occur abundantly on the sandy substrates, together with stunted *Avicennia africana* and *Rhizophora* spp. Although *T. rhomboideae, D. lunatus* and *A. aureum* also occur up-river in fresh/brackish water zones, the species are more abundant near the coastal sands where there is little competition from such versatile species as *Nypa fruticans* and *Raphia* spp.

The estuarine swamps have the highest nutrient levels since they are accretive, being sheltered from storm waves by depositional spits and bars across the estuaries. Hence, these swamps achieve a higher structural complexity than the coastal beachridge and contain, in addition to the mangrove swamp species, several high forest invaders of the tidal zone, e.g. *Raphia vinifera, Vossia curpidata* and *Selaginella* spp.

Vegetation-soil relationships

From the correlation matrix used to derive the multiple regression equations that related species occurrence to nutrient levels, calcium, magnesium, potassium, phosphorus and organic carbon were found to be highly correlated with species (Table 2). The understorey (B stratum) mangrove swamp species which were represented in the overstorey (A stratum) had similar correlation coefficients to the A stratum dominants and so were excluded from the table on account of having similar distributional patterns. Sodium, being a minor element essential to plant growth (Waring & Major 1964), was excluded from the table. CEC had a high intercorrelation with the other nutrients, but as the sum of exchangeable cations, could not be given the status of a factor gradient. Likewise, pH alone could

Table 2. Means (± SD) for coverage values of selected species (frequency > 4.0% and the product-moment correlations between these values and the logarithm of soil nutrient variables).

Species	Coverage (%)	Correlation Coefficients				
		Ca	Mg	K	P	Org. C
A stratum						
Avicennia africana	22.9 – 9.4	0.44	-0.51	N.S.	-0.39	0.62
Rhizophora mangle	12.6 – 10.2	0.62	-0.48	N.S.	-0.42	0.56
Rhizophora racemosa	12.1 – 9.6	0.63	N.S.	N.S.	-0.32	0.61
Nypa fruticans	15.0 – 10.8	0.53	0.41	0.36	-0.41	0.63
Raphia vinifera	4.3 – 3.6	0.61	0.34	N.S.	N.S.	-0.53
Rhizophora harrisonii	3.8 – 4.2	0.46	-0.42	N.S.	N.S.	-0.42
Laguncularia racemosa	0.7 – 0.3	0.54	N.S.	0.38	N.S.	0.41
B stratum						
Conocarpus erectus	1.2 – 0.8	-0.44	N.S.	0.37	0.39	N.S.
Pandanus candelabrum	1.4 – 1.2	0.33	-0.36	0.42	N.S.	N.S.
Phoenix reclinata	0.9 – 0.6	-0.48	-0.45	0.38	-0.40	N.S.
Triumfetta rhomboideae	0.9 – 1.5	N.S.	0.47	N.S.	N.S.	-0.34
Acrostichum aureum	6.6 – 4.8	N.S.	0.64	N.S.	N.S.	N.S.
C stratum						
Sesuvium portulacastrum	8.4 – 2.2	-0.35	0.49	N.S.	0.41	0.58
Vossia cuspidata	3.2 – 2.4	-0.40	0.61	N.S.	0.40	0.39
Selaginella spp	0.6 – 0.9	N.S.	0.38	0.34	N.S.	0.52

If $r > 0.36$, $p < 0.05$; $r > 0.48$, $p < 0.01$; N.S. = Not significant not be considered as a nutrient status indicator since, in mangrove swamps, pH relates to the level of sulphides in the soils (Hesse 1961).

Calcium showed significant positive correlation with the A stratum species but was particularly relevant with respect to *Rhizophora mangle, R. racemosa* and *Raphia vinifera.* Potassium was positively correlated with the B stratum species at a low level of statistical significance while magnesium was positively correlated mostly with the C stratum components of the vegetation, being particularly relevant with respect to *Acrastichum aureum* and *Vossia cuspidata.* Organic carbon was positively correlated with A stratum species, particularly with *Nypa fruticans, Avicennia africana, R. racemosa* and with the C stratum species, particularly *S. portulacastrum* and *Selaginella* spp. Available phosphorus showed mostly significant negative correlations with the species and on this account, according to Wikum & Wali (1974), is of doubtful value for establishing nutrient gradient relationships. The positive correlations are indications that the structural development of the species are enhanced at the levels of nutrients occurring in the swamp soils, while negative correlations are a reverse of this relationship. On this account the nutrient status of the soils may be defined in terms of saturation of the exchange complex by calcium, magnesium and to a lesser extent potassium. Organic carbon, within which the nutrient cations are initially held before being released for uptake by plants (Knapp 1974), may be regarded as a primary nutrient source.

Table 3 shows the multiple regression equations predicting species structure along the nutrient parameters. All regressions had a multiple coefficient of determination (R^2) of 0.42 and higher. Since R^2 is equal to the percentage variation which the multiple regression is accountable for, i.e., the level of explanation, it follows that all the regression equations account for 42% or above of the variance. The composition of species was observed to be explained by all soil variables although some variables were more important than others. In the A stratum, the occurrence of *Avicennia africana* was highly explained by magnesium (36.5%) and calcium (16.5%), out of a total variance of 62.1%. The occurrence of *R. mangle* and *R. racemosa* was highly explained by calcium (34.7%; 38.6%) from the total variance of 77.5% and 78.3%, respectively. *Nypa fruticans* related highly to organic carbon (28.6%) and CEC (14.3%). *R. harrisonii* was explained by CEC (39.2%) and calcium (12.3%), out of a total variance of 68.1%. The occurrence of *Laguncularia racemosa,* a rare species, was mostly explained by potassium (42.5%) from a total variance of 69.3%. Magnesium and calcium were retained in all the A stratum regression equations while potassium was the least represented.

In the B stratum (Table 3), the performance of *Conocarpus erectus* was mainly explained by available phosphorus (31.3%) and calcium (18.8%), from a total variance

Table 3. Multiple regression equations based on the performance of species along soil nutrient parameters. The linear regression equations were of the order : $Y = a_1 + b_1 X_1 + b_2 X_2 + ... b_n X_n \pm SE$; where Y = dependent (species) variable, a = Y intercept, b = partial regression coefficient, X = independent (nutrient) variable, SE = standard error of estimate.

A Stratum (overstorey)	
Avicennia africana	Y = -82.31 + 0.0424 (Mg) + 0.076 (Ca) + 0.068 (Org.C) - 20.063 (CEC) + 0.049 (P) ± 16.5 (R^2 = 62.1%)
Rhizophora mangle	Y = 78.74 + 0.824 (Ca) + 0.382 (Mg) + 0.374 (Org.C) - 0.368 (P) - 0.185 (CEC) - 15.3 (R^2 = 77.5%)
Rhizophora racemosa	Y = 52.63 + 0.724 (Ca) + 0.661 (Org.C) + 0.531 (Mg) - 0.365 (P) - 0.242 (K) - 15.1 (R^2 = 78.3%)
Nypa fruticans	Y = 71.35 + 0.489 (Org.C) - 0.371 (CEC) + 0.343 (Mg) + 0.196 (Ca) - 0.082 (P) ± 13.9 (R^2 = 76.5%)
Rhizophora harrisonii	Y = 47.42 - 0.324 (CEC) + 0.311 (Ca) - 0.201 (Org.C) + 0.094 (Mg) + 0.011 (P) ± 13.2 (R^2 = 68.1%)
Laguncularia racemosa	Y = 21.33 - 0.442 (K) + 0.410 (CEC) - 0.328 (Ca) + 0.142 (Mg) ± 12.8 (R^2 = 69.3%)
B stratum (understorey)	
Canacarpus erectus	Y = -11.56 + 252 (P) + 0.183 (Ca) - 0.069 (K) + 15.3 (R^2 = 56.7%)
Pandanus candelabrum	Y = 16.24 - 0.366 (Ca) + 0.261 (CEC) 0.225 (Mg) - 0.158 (Org.C) ± 117.3 (R^2 - 61.3%)
Phoenix reclinata	Y = 9.2 = 0.261 (Mg) + 0.165 (P) - 0.120 (Ca) ± 16.5 (R^2 = 56.5%)
C Stratum (groundlayer)	
Triumfetta rhomboideae	Y = -10.7 + 0.892 (Mg) + 0.321 (Org.C) - 0.088 (P) - 0.027 (CEC) ± 18.3 (R = 49.2%)
Acrostichum aureaum	Y = 46.4 + 0.682 (Mg) - 0471 (Org.C) - 0.258 (P) - 0.156 (K) -0.11 (Ca) ± 15.7 (R = 52.3%)
Sesuvium portulacastrum	Y = 58.2 + 0.431 (Mg) + 0.226 (P) - 0.182 (Ca) + 0.09 (Org.C) ± 13.7 (R^2 = 49.8%)
Vossia cuspidata	Y = -17.3 + 0.284 (Mg) - 0.151 (Ca) - 0.084 (Org.C) + 0.062 (CEC) + 0.041 (P) ± 18.2 (R = 44.5%)
Selaginella spp	Y = -9.2 + 0.341 (Mg) + 0.265 (Org.C) + 0.092 (Ca) ± 12.5 (R = 42.6%)

of 56.7%. *Pandanus candelabrum* was related to calcium (35.7%) and CEC (17.3%) while *Phoenix reclinata* was mainly explained by magnesium (36.2%) and phosphorus (16.4%). Calcium was retained in all equations for the B stratum species.

Explanations for the performance of C stratum species were largely in terms of magnesium which contributed between 21.4% and 32.2% of the total variance for each of the species. Magnesium contributed 28.5% and 26.7% to the total variance that explained the performance of *Acrostichum aureum* and *Sesuvium portulacastrum*, respectively. Organic carbon was also retained in all the equations, although with lower level of explanations than magnesium.

The multiple regression equations clearly emphasized the importance of calcium, magnesium and organic carbon to the composition of species in the mangrove swamps. However, variation in organic carbon was observed to be related to density and coverage of the different species in the stands and could not be specified as a nutrient factor. Calcium and magnesium appeared to more appropriately define the nutrient status of the soils on account of having overlapping values between stands in addition to being positively correlated with most species.

The simple correlation and multiple regression analyses have selected three nutrient variables for the establishment of nutrient gradients. These are : calcium for the A stratum species; potassium/calcium for the B stratum species; and magnesium for the C stratum species. Unstandardized values of the variables are used in establishing the gradients. Consequently, the minimum and maximum levels of each gradient also corresponded to the minimum and maximum values of the variables in the stands.

Ecological group classification

The modalities of species on the nutrient gradients are presented in Figs. 2-4. The mangrove obviously share a niche attribute for different cation concentrations in soils. Fig. 2 shows that in the A stratum *Raphia vinifera* belongs to Ecological Group I (see Appendix A), occurring almost exclusively under the most limiting conditions (i.e., lowest values) of calcium in the mangrove soils. The species is bimodal with ecological optima at calcium values of 2.5 me 100^{-1} and 8.6 me 100 g^{-1}. The lower optimum corresponds to calcium values obtained in up-river swamp soils since *R. virifera* is basically a fresh water species. The second optimum indicates adaptation and ability of *Raphia* sp. to compete with true mangrove species in tidal swamps.

Rhizophora mangle belongs to Ecological Group 2, occurring within a calcium range of 3.1 to 20.8 me 100 g^{-1}. The species is bimodal, with optima at calcium values of 11.5 me 100 g^{-1} and 18.3 me 100 g^{-1}. Occurrence of *R. mangle* is similar to *R. vinifera* although the former has a wider amplitude than the latter.

Rhizophora racemosa belongs to Ecological Group 3 and occurs within a soil calcium range of 2.8 me 100 g^{-1} to 19.0 me 100 g^{-1}. The species dominates at about the midpoint of the gradient and has three ecological optima although dominating particularly at the 10.1 me 100 g^{-1} value. In amplitude, *R. racemosa* is similar to *R. mangle* on the calcium gradient.

Avicennia africana and *Nypa fruticans* belong to Ecological Group 4 since they dominate where calcium is in plentiful supply.

A. africana has optima at calcium values of 12.3, 17.1 and 20.8 me 100 g^{-1}, while *N. fruticans* has an optimum at a value of 17.6 me 100 g^{-1}. Both species occur within a closely similar calcium range (4.9 to 21.4 me 100 g^{-1}) and are often found in mixed stands along shorelines.

Rhizophora harrisonii is restricted to the highest values of calcium (21.2 me 100 g^{-1}) and therefore belongs to Ecological Group 5. Its range of distribution lies between calcium values of 10.0 me 100 g^{-1} and 21.3 me 100 g^{-1}.

Languncularia racemosa (Ecological Group 0) is relatively insensitive to the calcium gradient since it occurs behind the coastal beachridges where calcium values are low and on the estuarine levees calcium values are relatively high. *L. racemosa* has the widest ecological amplitude in the A stratum with slight optima at calcium values of 10.2 me 100 g^{-1} and 16.9 me 100 g^{-1}.

Fig. 3 shows the structure and distribution of B stratum species on (a) calcium and (b) potassium gradients. Since decreasing values of calcium correlate with increasing potassium concentrations in mangrove soils (Ukpong 1995), coverage and frequency of species show different modal positions on the width of the respective gradients. Hence, while *Phoenix reclinata* belongs to Ecological Group 1 on the calcium gradient, the same species belongs to Group 5 on the potassium gradient. *Pandanus candelabrum* belongs to Ecological Group 4 on the calcium gradient and is bimodal while its frequency distribution on the potassium gradient is unimodal in Ecological Group 3.

The nutrient-insensitive species (*Conocarpus erectus*) belongs to the same ecological group (Group 0) on both the calcium and potassium gradients because it has a wide ecological amplitude in the mangrove swamps.

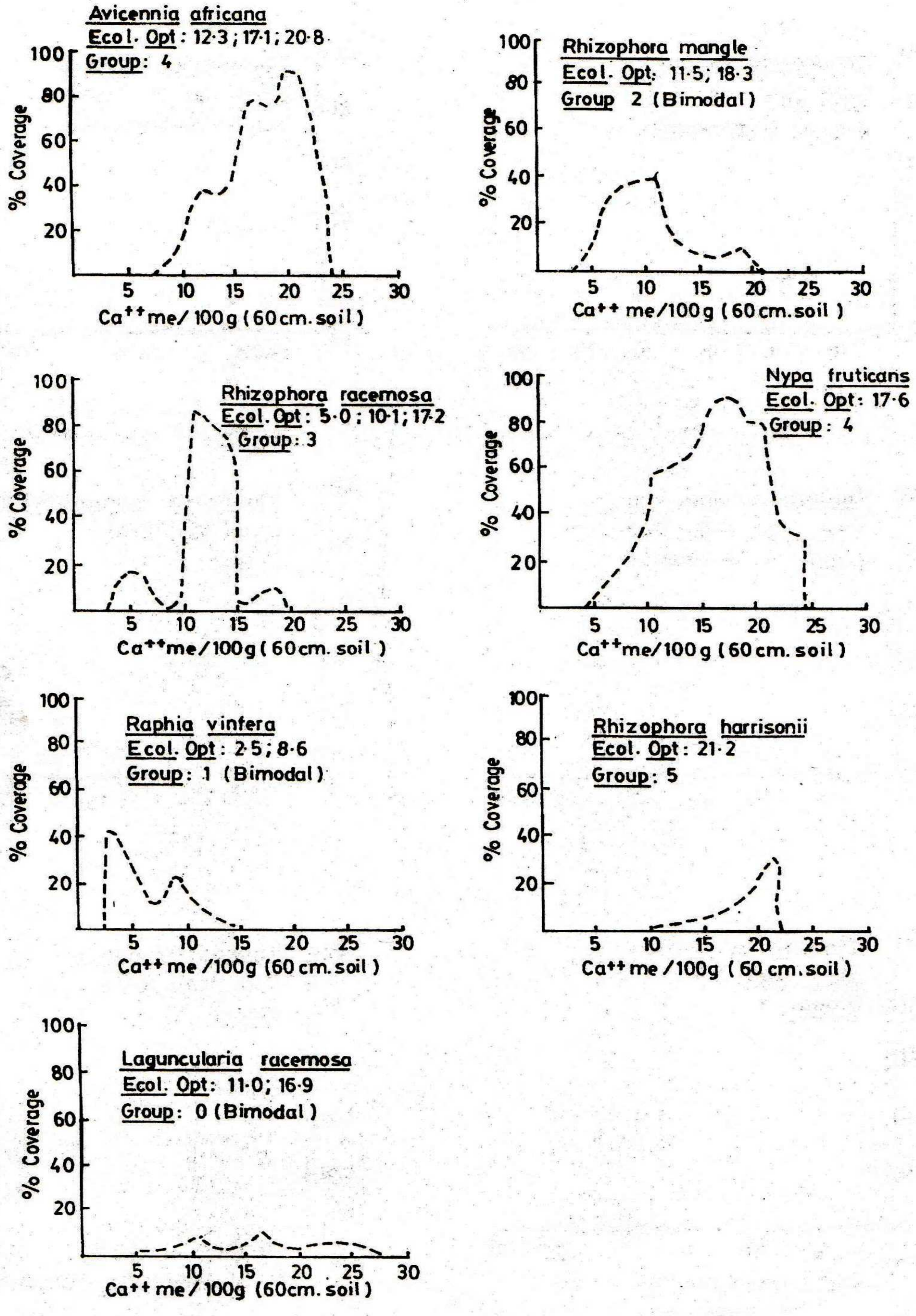

Fig. 2. Performance of A stratum species along calcium (nutrient) gradients of the mangrove swamps.

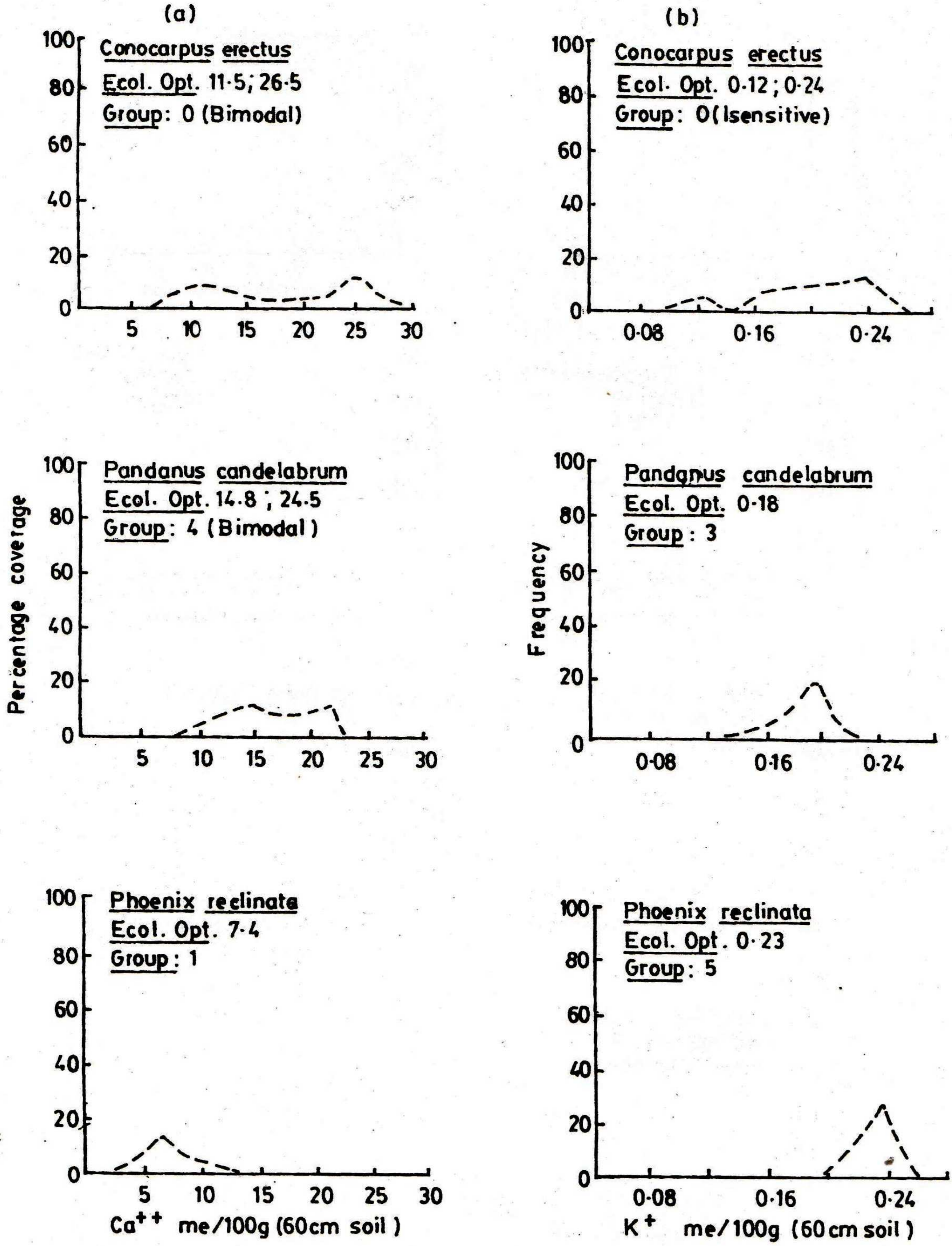

Fig. 3. Performance and distribution of B stratum species along (a) calcium, and (b) potassium gradients of the mangrove swamps.

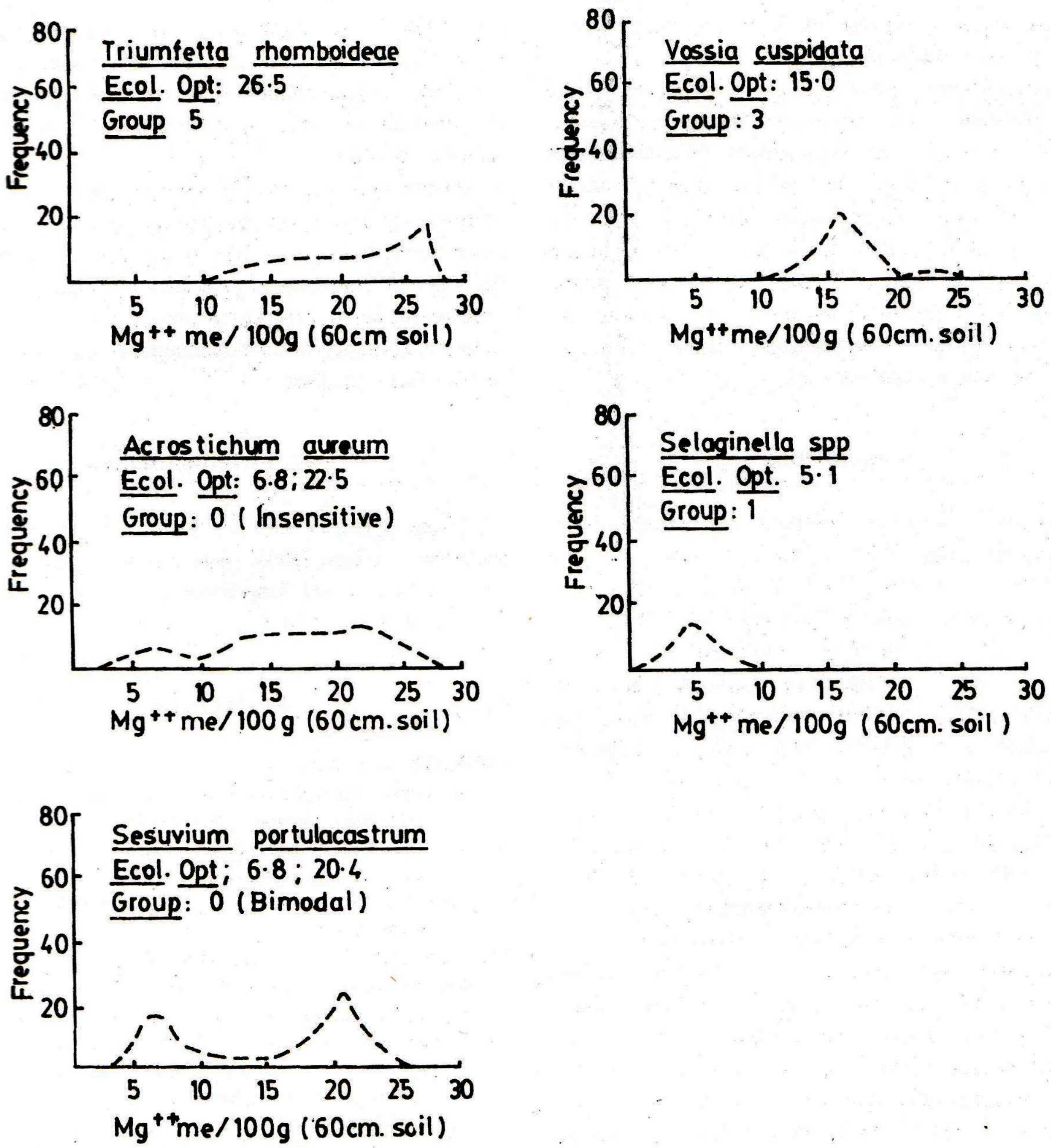

Fig. 4. Distribution of groundlayer species along magnesium (nutrient) gradients of the mangrove swamps.

The distribution of C stratum species along soil magnesium gradiants (Fig. 4) shows that *Selaginella* spp. belongs to Ecological Group 1, with optimum at a magnesium value of 5.1 me 100 g^{-1}. Occurrence is within the values of 1.9 me 100 g^{-1} to 8.6 me 100 g^{-1}. *Selaginella* spp. dominate as strand species on the beachridge, under the most limiting conditions of magnesium.

Vossia cuspidata occurs at about the mid-point of the magnesium gradient, between values of 10.1 me 100 g^{-1} and 24.5 me 100 g^{-1}, and therefore belongs to Ecological Group 3, with an optimum at a value of 15.1 me 100 g^{-1}. *Triumfetta rhomboideae* belongs to Ecological Group 5, dominating almost exclusively at the highest value of magnesium (26.5 me 100 g^{-1}) along the gradient. Other groundlayer species (*Acrostichum aureum, Sesuvium portulacastrum*) have very wide ecological amplitudes. *A. aureum* shows insensitivity put with slight optima on magnesium value of 6.8 me 100 g^{-1} and 22.5 me 100 g^{-1}. The lower value corresponds with the first optimum for *S. portulacastrum* (6.9 me 100 g^{-1}) while the second value is also closely similar to the second optimum obtained for *S. portulacastrum* (20.4 me 100 g^{-1}).

There are overlapping occurrences of mangrove swamp species along the nutrient gradients. The species distribution modes indicate where the nutrients in consideration are of predictive value. The precise range of nutrient values within which a species occurs is predicted along the gradient, including points of maximum species population and coverage structure. Hence, the gradients enable autecological information concerning the ecological optimum and amplitude for each species, relative to a nutrient factor, to be obtained and analysed.

Conclusions

Mangrove swamps vary geographically in terms of soil nutrient levels. The values for nutrients obtained in this study differ from those obtained elsewhere in other mangrove swamps. Clarke & Hannon (1967), in Australia, reported a CEC range from 0.38 ± 0.08 me 100 g^{-1} in the subsurface to 0.84 ± 0.59 me 100 g^{-1} in the subsurface. In South Africa, Naidoo (1980) reported a CEC range from 23.7 me 100 g^{-1} to 83.3 me 100 g^{-1}. But in the present study CEC values range from 11.8 ± 1.5 me 100^{-1} to 50.6 ± 7.4 me 100 g^{-1}. In Mexico, Thom (1967) related the occurrence of mangrove to soils with very high organic matter content (52.4%) while Giglioli & Thornton (1965) related mangrove to organic matter values ranging from 8.7% to 12.3%. In the present study, organic carbon values in the mangrove soils range from 3.5 ± 0.4% to 10.4 ± 2.8%. Tidal imports, distance from the coast, freshwater runoff and seepage influence the level of cation concentrations in the soil. Organic carbon contents of soil are related to species coverage, tree height and distance from the shore.

Swamps dominated by *Avicennia africana* have less acidic soils than swamps dominated by *Rhizophora* spp. The estuarine swamps, being accretive, have higher nutrient levels and consequently a more complex vegetation than the erosional coastal beachridge. Calcium is an important mineral nutrient, explaining the structure of A stratum (overstorey) mangroves, while calcium and potassium explain B stratum structure/distribution. Magnesium is significant for the distribution of C stratum (groundlayer) species. Organic carbon is significant for both A and C strata but values vary markedly between stands and between swamps.

Results of direct gradient analysis show that different plant species of mangrove swamps have different distributions along the soil nutrient gradients. Hence, the locations of individual species along nutrient gradients can be specified. The distribution of recognizeable patterns along the gradients can therefore be accounted for in terms of nutrient variation.

Overlapping occurrences of species and the ecological optima or points at which maximum population densities occur can be attributed to functional relationships between the nutrients and vegetation measures. Hence, mangrove swamp species that belong to the same ecological group reflect a similarity in their functional relationships to the nutrient factor gradients.

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References

Clarke, D.L. & N.J. Hannon. 1967. The mangrove swamps and salt marsh communities of the Sydney district. I. Vegetation, soils and climate. *Journal of Ecology* **55:** 752-771.

Connor, D.J. 1969. Growth of grey mangrove (*Avicennia marina*) in nutrient culture. *Biotropica* **1:** 36-40.

Ellenberg, H. 1956. Cited in Whittaker R.H. 1967. *Biological Review* **49:** 207-264.

Giglioli, M.E.C. & T. Thornton. 1965. The mangrove swamps of Keneba, lower Gambia river basin. I. Descriptive notes on climate, the mangrove swamps and the physical composition of their soils. *Journal of Applied Ecology* **2:** 81-104.

Hauser, D. 1974. Some problems in the use of stepwise regression techniques in geographical research. *Canadian Geographer* **XVIII:** 148-158.

Hesse, P. 1961. Some differences between the soils of *Rhizophora* and *Avicennia* mangrove swamps in Sierra Leone. *Plant and Soil* **14:** 335-346.

Hynn-Cong-Tho & K. Egashira. 1976. Some chemical, physical and mineralogical properties of acid sulphate soils from the Mekong Delta in Vietnam. *Journal of the Faculty of Agriculture*, Kyushu University. **20:** 151-164.

Jackson, M.L. 1962. *Soil Chemical Analysis*. Englewood Cliffs, N.J. Prentice-Hall Inc.

Jackson, M.L. 1964. Notes on the West African vegetation. I. Mangrove vegetation at Ikorodu, Western Nigeria. *West African Science Association Journal* **9:** 98-111.

Keay, R.W. 1953. *Rhizophora* in West Africa. *Kew Bulletin* **1:** 121-127.

Knapp, B. 1974. *Soil Processes*. George Allen & Unwin, London.

Lugo, A.E. 1980. Mangrove ecosystems : successional or steady state ? In : Tropical succession. *Biotropica* Suppl. 65-72.

Lugo, A.E. & S. Snedaker. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* **5:** 39-64.

Moorman, F.R. & L.J. Pons. 1974. Characteristics of mangrove soils in relation to their agricultural land use and potential. *Proceedings of the International Symposium on Biological Management of Mangroves* Honollulu, Hawaii. **2:** 548-560.

Mueller-Dombois, D. & H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology.* J. Willey, London.

Naidoo, G. 1980. Mangrove soils of the Beachwood area, Durban. *Journal of South African Botany* **46:** 293-304.

Nigerian Metcrological Services (NMS). 1980. *Climatic Data for Calabar Airport*, Lagos.

Savory, H.J. 1953. A note on the ecology of *Rhizophora* in Nigeria. *Kew Bulletin* **1:** 127-128.

Thom, B.G. 1967. Mangrove ecology and deltaic geomorphology Tobasco, Mexico. *Journal of Ecology* **55:** 301-342.

Ukpong, I.E. 1991. The performance and distribution of species along soil salinity gradients of mangrove swamps in southeastern Nigeria. *Vegetatio* **95:** 63-70.

Ukpong, I.E. 1992. The structure and soil relations of *Avicennia* mangrove swamps in southeastern Nigeria. *Tropical Ecology* **33:** 1-16.

Ukpong, I.E. 1994. Soil-vegetation interrelationships of mangrove swamps as revealed by multivariate analyses. *Geoderma* **64:** 167-181.

Ukpong, I.E. 1995a. Classification - analytic models for vegetation and nutrient relations of mangrove swamps in West Africa. *Acta Botanica Hungarica* **39:** 17-29.

Ukpong, I.E. 1995b. Mangrove soils of the Creek Town Creek/Calabar River Swamp, Southeastern Nigeria. *Tropical Ecology* **36:** 103-115.

Waring, R.H. & J. Major. 1964. Some vegetation of the California redwood region in relation to gradients of moisture, nutrients, light and temperature. *Ecological Monographs* **34:** 167-215.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biological Review **49:** 207-264.

Whittaker, R.H. 1978. Direct gradient analysis. *In*: R.H. Whittaker (ed.) *Ordination of Plant Communities. Handbook of Vegetation Science 5.* Dr. W. Junk, The Hague.

Wikum, D.A. & M.K. Wali. 1974. Analysis of North Dakota gallery forest: Vegetation in relation to topographic and soil gradients. *Ecological Monographs* **44:** 441-464.

Appendix A

Characteristics of ecological species groups

Group	General characteristics
1	Species which dominate and occur almost exclusively under the most nearly limiting conditions of the factor
2	Species of similar occurrence but with wider amplitude than those of Group 1.
3	Species which are especially frequent near the mid-point along the factor gradient.
4	Species which dominate on the gradient where the factor being considered is in plentiful supply.
5	Species which occur almost exclusively at the highest values of the factor being considered.
0	Species which are indifferent to the factor and have a very wide amplitude.