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Ecological classification of Nigerian mangroves using soil nutrient gradient analysis

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Abstract

Direct gradient analysis was used to relate the structure of mangrove communities to soil nutrient gradients. The predominant cations in the alluvial soils were magnesium and calcium, the values ranging from 8.6 ± 0.9 to 24.6 ± 2.0 me per 100 g. Organic carbon was high in the soils, ranging from 3.5% to 10.4%. All soil nutrients varied seasonally, in response to wet and dry periods of the climate. Correlation of species with soil nutrients indicated the nutrient status of the soils to be best defined in terms of calcium for the A stratum (species > 3 m tall), calcium/postassium for the B stratum (species 1–3 m tall) and magnesium for the C stratum (species < 1 m tall). Ecological group classification shows that *Avicennia africana* and *Nypa fruticans* occurred almost exclusively at the highest calcium values of 20.8 and 17.6 me per 100 g, respectively. *Acrostichum aureum* and *Sesuvium portulacastrum* are insensitive to the magnesium gradient. The analysis revealed an overlapping range of occurrences for most of the species although with varying ecological optima along the gradient.

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).

Naidoo (1980) observed that cation concentration 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 and Egashira, 1976; Ukpong, 1995a).

In South Africa the occurrence of the mangrove species *Avicennia nitida* (Linn.) was related to a cation exchange capacity (CEC) range of 23.7–83.3 me per 100 g, while *Bruguiena spp* (Linn.) occurred within a CEC range of 41.0–67.6 me per 100 g (Naidoo, 1980). In Australia, Clarke and Hannon (1967) observed that CEC in mangrove soils ranges from 0.38 me per 100 g at the surface to 0.84 me per 100 g in the subsurface. In Nigeria, Ukpong (1992, 1995b) related the occurrence of mangroves to a CEC range of 21.0–56.8 me per 100 g, with organic carbon values ranging from 1.5% to 9.6% in the soils.

There exists a considerable overlap in values for soil nutrients from mangrove stands dominated by different species. Hence, the aim of this paper is to specify the location of individual mangrove 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 and Major, 1964). The basic approach is a direct gradient analysis (factor-gradient, 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 plant (see Appendix A).

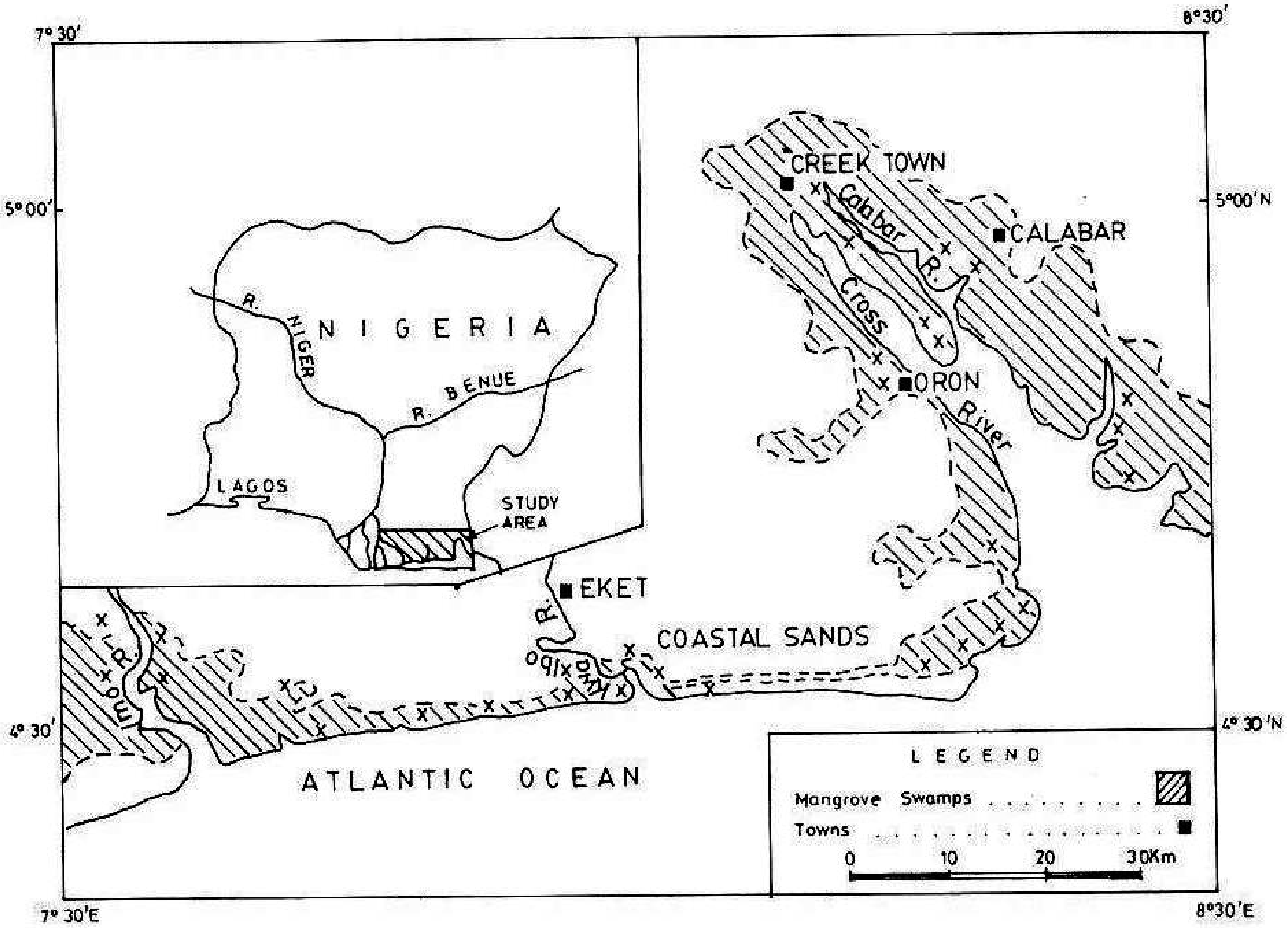

Figure 1. Map of the study area showing the mangrove swamps and location of transects X X X.

Study area

The study area, located in southeastern Nigeria, extends from longitude 7°30′E to 8°30′E and from latitude 4°35′N to 5°15′N and contains the estuaries of the Cross river (810 km^2), Kwa Ibo river (50 km^2) and Imo river (196 km^2) (Figure 1). The climate of the area is humid tropical, even-wet with an annual rainfall of 4021 mm (Nig. Met. Serv., 1996). Peak rainfall occurs in July–August while least rainfall occurs in December–February. In the estuaries, mean tidal amplitude is 2.01 m at spring tides and 1.07 m at neap tides. The most important mangrove trees in the swamps are *Avicennia africana* (Moldenke), *Rhizophora racemosa* (G.F. May), *Rhizophora mangle* (G.F. May) and *Rhizophora harrisonii (Jacq.)*, while the important associates are *Nypa fruticans* (Thumb), *Raphia vinifena* (L.), *Acrostichum aureum* (L.), *Sesuvium portulacastrum* (SW) and *Vossia cuspidata* (Ukpong, 1992).

Methods

Vegetation and soil sampling

Vegetation and soil measurements were obtained in eighty 10 × 10 m quadrats located at regular 20 m intervals along several transects established from the shore inland. The transects were established along various physiographic habitats after Lugo and Snedaker (1974) as:

1. wooded levees,
2. inter-distributary basin,
3. distributary basin,
4. interriverine creek,
5. point bar,
6. beach ridge sand,
7. braided channels.

Transect length was depended on the width of swamps, but each contained at least two quadrats, the first quadrat being located on the channel fringe.

Crown cover for trees (>3 m tall) in each quadrat was determined by the crown-diameter method (Mueller-Dombois and 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. Soil sampling was performed in the wet and dry seasons within each quadrat at low tides, using profile pits and a soil 'corer'. Three core samples were obtained at each point to a rooting depth of 60 cm and the soils were air-dried before laboratory analysis: pH was determined 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 pH7, then concentrations of calcium, magnesium and potassium determined by atomic absorption and sodium by flame photometry. 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 (Cannor, 1969). Being that the nutrient status of mangrove soils is influenced by high water table and seepage (Clarke and Hannon, 1967), an ecological approach was desired which would allow all the nutrient parameters to vary, yet allow the influence of one variable to be studied. To achieve this, seasonal soil nutrient measurements (in the relatively dry months of November/February, and the wetter months of April/August) were used in a predictive multiple regression analysis. The equations that proved significant with the highest level of explanation (coefficient of determination R^2) were interpreted and discussed (see Appendix B).

The mangrove swamp species were also used 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 condition. 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 and 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 intercorrelated 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 or organic carbon were selected by the analysis as relating most clearly to plant occurrence.

Results and discussion

Soil analysis

Table 1 summarizes the results of the soil analysis. The mangrove soils are noted to have a potentially high sink for cations (Naidoo, 1980). The observed variations in soil nutrients, particularly the exchangeable cations, may be due to tidal influence and distance from the coast (Ukpong, 1994). Swamps inundated directly by Atlantic tides appear to have higher cation concentrations in soils than the middle estuarine swamps (Ukpong, 1998). This may be the explanation for the higher calcium and magnesium values in the Imo river and Kwa Ibo river swamps, located close to the Atlantic shoreline than in the Creek Town Creek/Calabar river swamp and the Cross river swamp which are removed from the direct influence of Atlantic tides. The coastal beachridge is not regularly inundated by normal tides (except Atlantic storm waves), which probably explain why calcium and magnesium values are much lower than in the estuaries although the beach ridge is located along the coast. CEC was highest in the Kwa Ibo river swamp and Imo river swamp probably due to the abundance of magnesium and calcium in sea water.

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

Swamp	Ca (me per 100 g)	Mg (me per 100 g)	K (me per 100 g)	CEC (me per 100 g)	P ($\mu g\,ml^{-1}$)	Org.C (%)	pH**
Creek Town Creek/ Calabar Town (15)*							
Nov. 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
Jan. 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
Aug. 1987	8.6 ± 0.9	10.5 ± 0.8	0.11 ± 0.05	29.6 ± 5.7	5.8 ± 0.2	5.8 ± 0.4	6.0 ± 0.2
Cross river swamp (21)*							
Dec. 1986	10.3 ± 7.5	17.6 ± 3.8	0.26 ± 0.02	40.03 ± 3.8	4.1 ± 0.3	9.8 ± 2.4	5.8 ± 0.2
Feb. 1987	10.1 ± 2.5	17.2 ± 4.7	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)*							
Dec. 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
Apr. 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
Aug. 1986	12.5 ± 1.1	20.8 ± 2.4	0.18 ± 0.01	46.3 ± 2.7	3.1 ± 2.6	4.4 ± 0.8	6.2 ± 0.2
Imo river swamp (20)*							
Feb. 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	14.0 ± 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)*							
Jan. 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
Aug. 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 sample for each swamp, Org.C = Organic Carbon.
**Not included in correlation/regression analysis.

Available phosphorus levels were highest in the Creek Town/Calabar river and Cross river swamp soils (Table 1). There was a relationship between the phosphorus levels and pH values – high phosphorus correlated partially with increasing acidity 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 those of the Cross river and Creek Town Creek/Calabar river with species of *Rhizophora* as dominant.

Seasonal values of cation concentration (Ca^{++}, Mg^{+}, K^{+}) in the soils showed tidal imports to be the main source. Replenishment of cations occurs through flooding and subsurface seepage of tidal waters across the mangrove habitats. Freshwater inputs, for example rainfall and runoff 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 (Table 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, for example *Triumfetta rhornboideae, Sesuvium portulacastrum, Drepanocarpus lunatus* and *Acrostichum aureum*, occur abundantly on the sandy substrates.

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, for example *Raphia vinifera, Vossia cuspidata* and *Selaginella* spp.

Vegetation–soil relationships

Table 2 shows that calcium, magnesium, potassium, phosphorus and organic carbon were highly correlated with the species. CEC had a high intercorrelation with

Table 2. Mean (± 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 coefficient (r)*				
	Mean ± SD	Ca	Mg	K	P ·	Org.C
Avicennia africanna	(A) 22.9 ± 9.4	0.44	−0.51	NS	−0.39	0.62
Rhizophora mangle	(A) 12.6 ± 10.3	0.62	−0.48	NS	−0.42	0.56
Rhizophora racemosa	(A) 12.1 ± 9.6	0.63	NS	NS	−0.32	0.61
Nypa fruticans	(A) 15.9 ± 10.8	0.53	0.41	0.36	−0.32	0.61
Raphia vinifera	(A) 4.3 ± 3.6	0.61	0.34	NS	NS	−0.53
Rhizophora harrisonni	(A) 3.8 ± 4.2	0.46	−0.42	NS	NS	−0.42
Laguncularia racemosa	(A)[a] 0.7 ± 0.3	0.54	NS	0.38	NS	0.41
Conocarpus erectus	(B) 1.2 ± 0.8	−0.44	NS	0.37	0.39	NS
Pandanus candelabrum	(B) 1.4 ± 1.2	0.33	−0.36	0.42	NS	NS
Phoenix reclinata	(B) 0.9 ± 0.6	−0.48	−0.45	0.38	−0.40	NS
Triumfetta rhomboideae	(C) 0.9 ± 1.5	NS	0.47	NS	NS	−0.34
Acrostichum aureum	(C) 6.6 ± 4.8	NS	0.64	NS	NS	NS
Sesuvium portulacastrum	(C) 8.4 ± 2.2	−0.35	0.49	NS	0.41	0.58
Vossia cuspidata	(C) 3.2 ± 2.4	−0.40	0.61	NS	0.40	0.39
Selaginella spp	(C) 0.6 ± 0.9	NS	0.38	0.34	NS	0.52

*$r > 0.36$, $P < 0.05$; $r > 0.48$, $P < 0.01$; NS = not significant; A = A stratum; B = B stratum; C = C stratum; a = low frequency of occurrence 3.8%.

the other nutrients, but as the sum of exchangeable cations could not be given the status of a factor gradient. Likewise, pH alone could 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 to *Rhizophora mangle, R. racemosa* and *Raphia vinifera.* Potassium was positively correlated with B stratum species while magnesium was correlated mostly with the C stratum components of the vegetation being particularly relevant to *Acrostichum aureum* and *Vossia cuspidata.* Available phosphorus showed mostly significant negative correlations with the species and on this account, as reported by Wikum and 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 negatives 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.

Multiple regression analysis showed that the composition of species in the swamps was explained by all soil variables although some variables were more important than others. For example, 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%:

$$\begin{aligned} A.\ africana\ Y &= -82.31 + 0.0424(\text{Mg}) + 0.076\,(\text{Ca}) \\ &\quad + 0.068(\text{Org.C}) - 0.063\,(\text{CEC}) \\ &\quad + 0.049\,(\text{P}) \pm 16.5\,(R^2 = 62.1\%). \end{aligned}$$

The occurrence of *R. mangle* and *R. racemosa* was similarly explained by calcium (34.7%, 38.6%) from the total variance of 77.5% and 78.3%, respectively. *Nypa fruticaus* 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%.

In the B stratum, the performance of *Conocarpus erectus* was mainly explained by available phosphorus (31.3%) and calcium (18.8%) from a total variance of 56.7%:

$$\begin{aligned} C.\ erectus\ Y &= -11.56 + 0.252\,(\text{P}) + 0.183\,(\text{Ca}) \\ &\quad - 0.069\,(\text{K}) \pm 15.3\,(R^2 = 56.7\%). \end{aligned}$$

Other species, for example, *Pandamus 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%).

Explanations for the performance of C stratum species were largely in terms of magnesium which

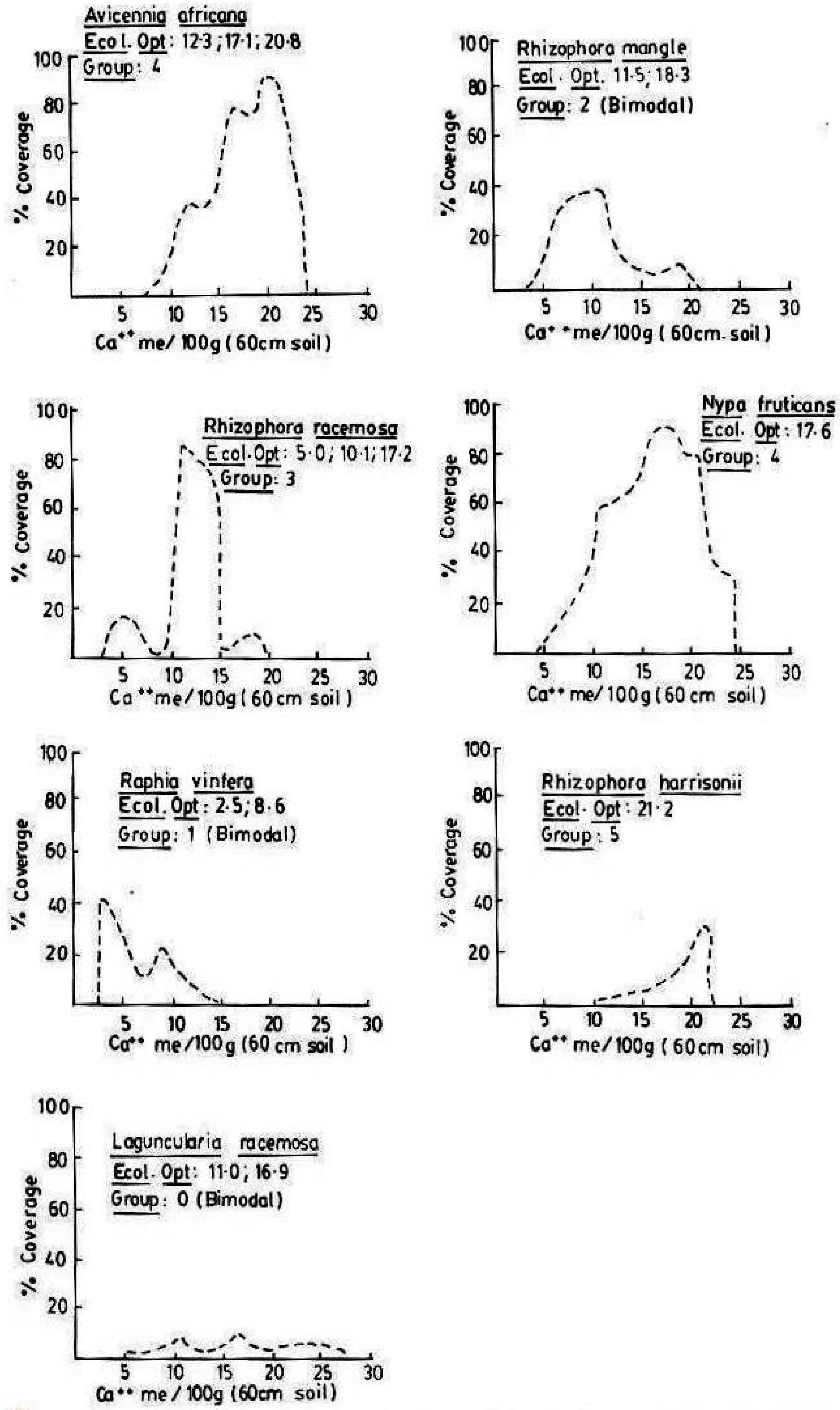

Figure 2. Classification of overstorey/A stratum species along calcium (nutrient) gradients of the mangrove swamps.

contributed between 21.4% and 32.2% of the total variances for each of the species. Magnesium contributed 28.5% and 26.7% to the total variances that explained the performance of *Acrostichum aureum* and *Sesuvium portulacastrum*, respectively:

$$A.\ aureum\ Y = 46.4 + 0.682\,(\text{Mg}) - 0.471(\text{Org.C}) - 0.258\,(\text{P}) - 0.156\,(\text{K}) - 0.11\,(\text{Ca}) \pm 15.7(R^2 = 52.3\%),$$

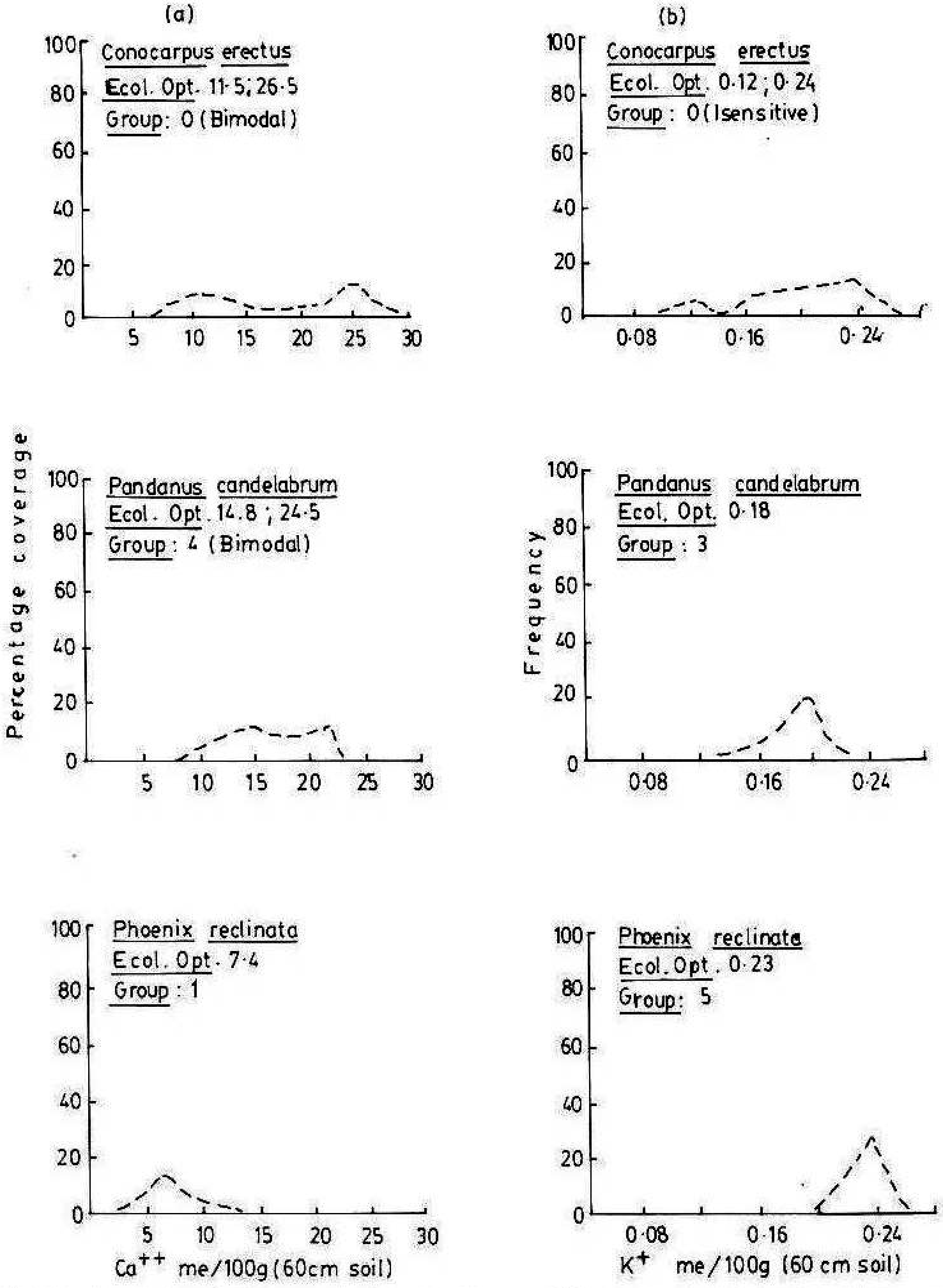

Figure 3. Classification of understorey/B stratum species along (a) calcium and (b) potassium (nutrient) gradients of the mangrove swamps.

S. portulacastrum $Y = 58.2 + 0.431\,(\mathrm{Mg}) + 0.226(P) - 0.182\,(\mathrm{Ca}) + 0.09\,(\mathrm{Org.C}) \pm 13.7$ $(R^2 = 49.8\%)$.

The multiple regression equations clearly emphasized the importance of calcium, magnesium and organic carbon to the composition of species in 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 define more appropriately the nutrient status of the soils on account of having overlapping values between stands in addition to being positively correlated with most species.

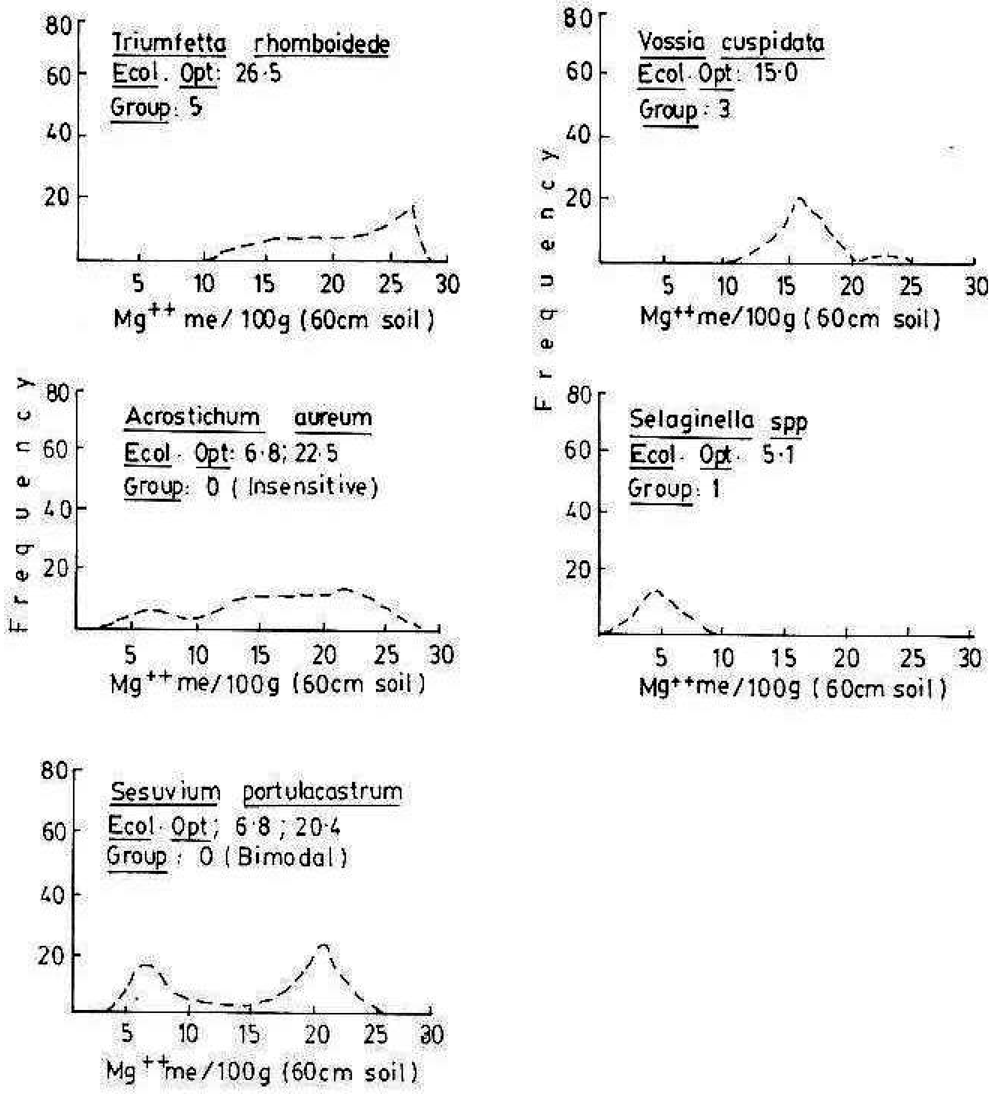

Figure 4. Classification of groundlayer/C stratum species along magnesium (nutrient) gradients of the mangrove swamps.

The simple correlation and multiple regression analysis 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.

Since unstandardized values of the variables are used in establishing the gradients, the minimum and maximum levels of each gradient corresponded to the minimum and maximum values of the variables in the stands.

Ecological group classification

Species modes on the nutrient gradients are presented in Figures 2–4. The mangroves obviously share a niche attribute for different cation concentrations in soils. Figure 2 shows that in the A stratum *Raphia vinifera* belongs to ecological group I (see Appendix A), occuring almost exclusively under the most limiting conditions (i.e. lowest values) of calcium in the mangrove soils. The lower optimum corresponds to calcium values obtained in up-water swamp soils since *R. virifera* is basically a fresh water species. The second optimum indicates adaptation and ability of *Raphia* spp. to compete with true mangrove species in tidal swamps. Occurrence of *R. mangle* is similar to *R. vinifera* although the former has a wider amplitude than the latter.

Rhizophora recemosa belongs to ecological group 3 and occurs within a soil calcium range of 2.8–19.0 me per 100 g. In amplitude, *R. racemosa* is similar to *R. mangle* on the calcium gradient.

Avicennia africanna and *Nypa fruticans* belong to ecological group 4 since they dominate where calcium is in plentiful supply. Both species occur within a closely similar calcium range (4.9–21.4 me per 100 g) and are often found in mixed stands along shorelines.

Rhizophora harrisonii is restricted to the highest values of calcium (21.2 me per 100 g) and therefore belongs to ecological group 5. *Laguncularia racemosa* (ecological group O) is relatively insensitive to the calcium gradient since it occurs behind the coastal beachridges where calcium values are low and on the estuarine levees where calcium values are relatively high.

Figure 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, 1995b), 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. 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.

The distribution of C stratum species along soil magnesium gradients (Figure 4) shows the *Selaginella* spp. belongs to ecological group 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, sand therefore belongs to ecological group 3. *Triumfetta rhomboideae* belongs to ecological group 5. Other ground layer species (*Acrostichum aureum, Sesuvium portulacastrum*) have very wide ecological amplitudes reflecting insensitivity to the magnesium gradient.

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.

Hence, the gradients enable autecological information concerning the ecological optimum and amplitude for each species, relative to a nutrient factor, to be obtained and analyzed.

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 and Hannon (1967), in Australia, reported a CEC range from 0.38 ± 0.08 to 0.84 ± 0.59 me per 100 g in the subsurface. In South Africa, Naidoo (1980) reported a CEC range from 23.7 to 83.3 me per 100 g. But in the present study CEC values range from 11.8 ± 1.5 to 50.6 ± 7.4 me per 100 g. In Mexico, Thom (1967) related the occurrence of mangroves to soils with very high organic matter content (52.4%) while Giglioli and Thornton (1965) related mangroves to organic matter values ranging from 8.7% to 12.3%. In the present study, organic carbon values in the mangrove soils range from $3.5 \pm 0.4\%$ to $10.4 \pm 2.8\%$. Tidal imports, distance from the coast, freshwater runoff and seepage influence the level of cation concentration in the soil. Organic carbon contents of soils 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 (ground layer) species. Organic carbon is significant for both A and C strata but its values vary markedly 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 recognizable patterns along the gradients can reasonably 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.

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.

Appendix B

The linear regression equations were of the order:

$$Y = a + b_1X_1 + b_2X_2 + \cdots + b_nX_n \pm \text{SE},$$

Where Y = dependent (species) variables; a = Y intercept; b = partial regression coefficient; X = independent (nutrient) variable; SE = standard error of estimate.

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