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Relationships between vegetation gradients and soil variables of mangrove swamps in southeastern Nigeria

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Summary

The vegetation and soils of mangrove swamps were studied in order to determinine the relationship between species variation and soil variables. The basic premise was that the vegetation and the soils are multivariate and could be viewed in terms of gradients. Principal components analysis, an eigenvector multivariate analytical technique, was used in the interpretation of the structure within the correlation matrix of the vegetation and soil data. The principal components analysis indicated the first four components of the soil system as: salinity (complex hydrochemical gradient); nutrient gradient; soil moisture gradient; and substrate texture gradient. The first four components of the vegetation system were indicated as: competition gradient; adaptation gradient; residual competition gradient; and site preference gradient. The soil salinity gradient was negatively correlated with vegetation competition and adaptation gradients ($r = -0{\cdot}38$; $r = -0{\cdot}35$), while the nutrient gradient was positively correlated with the residual competition gradient ($r = 0{\cdot}56$). It was observed that non-mangroves were more sensitive to soil nutrient levels than true mangrove species.

Key words: mangroves, principal components analysis, soil, vegetation

Résumé

On a étudié la végétation et les sols des marécages de mangroves pour déterminer la relation entre la variation des espèces et les variables des sols. Le principe de départ était que la végétation et les sols étaient multivariés et pouvaient être considérés en termes de gradients. Une analyse des principaux composants, une technique analytique multivariée de l'"eigenvector", fut utilisée pour l'interprétation de la structure dans la matrice de corrélation des données sur la végétation et les sols. L'analyse des principaux composants a montré que les quatre premiers composants du système sol étaient: la salinité (gradient du complexe hydrochimique); le gradient des nutriments; le gradient d'humidité du sol; et le gradient de texture du substrat. Les quatre premiers gradients du système végétation étaient donnés comme suit: gradient de compétition; gradient d'adaptation; gradient de compétition résiduelle; et gradient de préférence du site. Le gradient de salinité du sol était inversément lié à ceux de la compétition et de l'adaptation de la végétation ($r = -0{\cdot}38$; $r = 0{\cdot}35$), alors que le gradient des nutriments est

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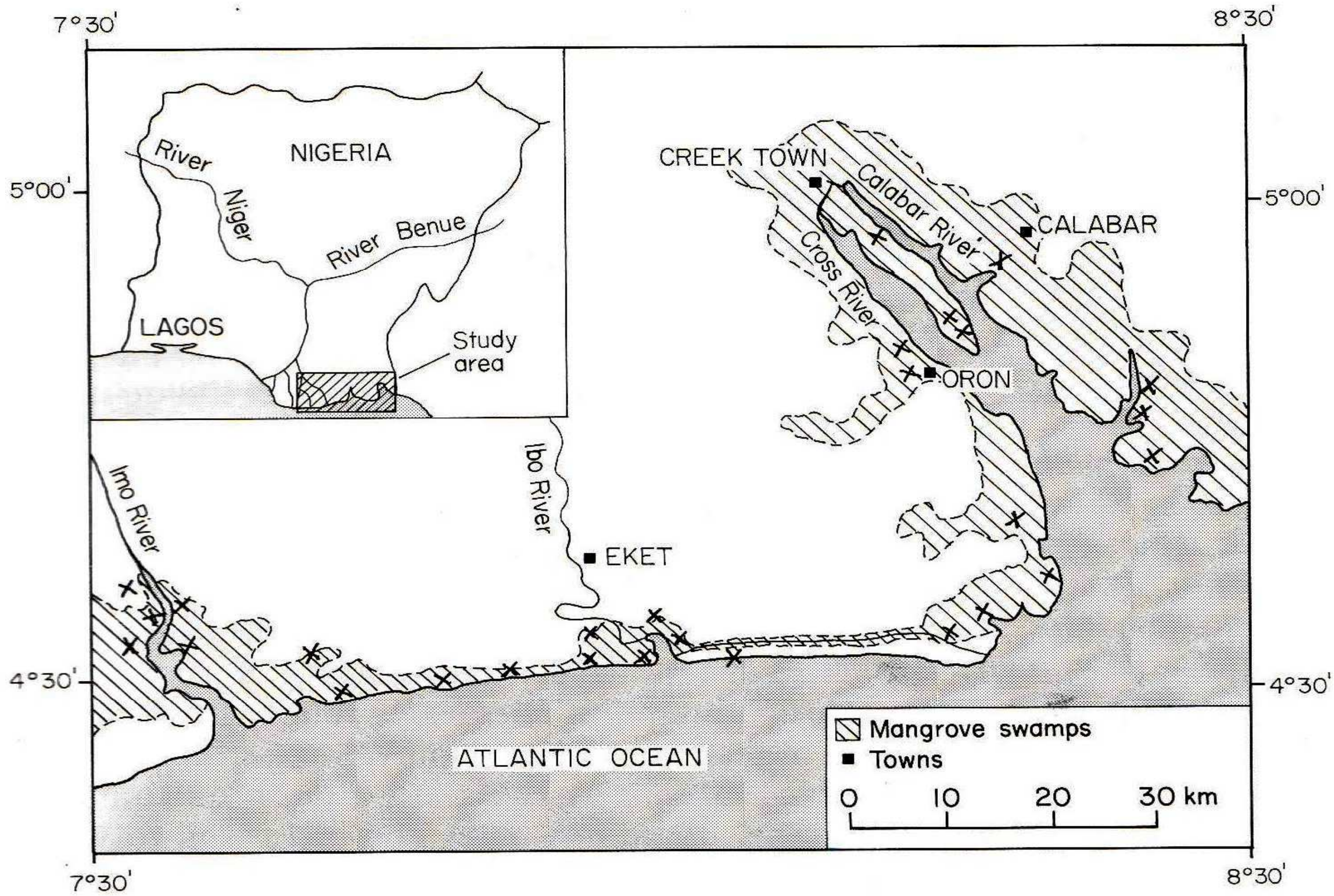

Fig. 1. Map of the study area showing location in Nigeria (insert). X=approximate transect location.

directement lié à celui de compétition résiduelle ($r=0{\cdot}56$). On a observé que les espèces non originaires des mangroves étaient plus sensibles au niveau des nutriments dans le sol que les vraies espèces de mangroves.

Introduction

Correlations between mangrove vegetation and soils have rarely been investigated beyond the presence/absence relationships of species to measured soil properties obtained from almost pure stands of the species (Clarke & Hannon, 1967; Naidoo, 1980). This approach is appropriate to stable sea coast littorals where the vegetation is monospecific and zonation apparent, but in river estuaries, where the mangrove habitat is dynamic and actively evolving due to channel deposition and abandonment, mixed mangrove stands are common. In southeastern Nigeria (Fig. 1), as in many parts of West Africa (Giglioli & Thornton, 1965; Ukpong, 1989), the occurrence of mixed stands of mangroves and the consequent overlap in values of soil properties between stands have indicated that a multivariate procedure to vegetation–soil relationships in the swamps is essential to a better understanding of the ecology of mangroves.

This paper aims to investige mangrove vegetation and soil in order to understand the interrelationships between these subsystems of the mangrove ecosystem. The basic premise is that the vegetation and the soil are multivariate systems. However, the soil may also be regarded as consisting of independently varying properties.

Methods

Selection of transects

Vegetation and soil sampling were performed in eighty 100 m^2 quadrats established at regular 20-m intervals along several transects from the water channels inland to the upland forest margins. The following criteria were observed in selection of the transects: (a) regular diurnal flooding by tides; (b) absence of recent disturbance through tree felling or empoldering of swamps; and (c) absence of interference with adjacent river channels through sand mining or dredging.

Vegetation and soil data

For the vegetation, rooted frequency and stem density measurements were made (Greig-Smith, 1975). Coverage values for the overstorey (>3 m) were determined by the crown-diameter method (Mueller-Dombois & Ellenberg, 1974); values for understorey (1–3 m) were estimated in 25 m^2 subquadrats while those for the groundlayer (<1 m) were estimated in 1 m^2 subdivisions. The relative frequency, relative coverage and relative density for each species were summed to obtain the ecological importance values of the species in the swamps (Stephenson, 1986).

Two soil samples to a depth of 40 cm were obtained in each quadrat and bulked for laboratory analysis. The procedures were: pH, in 1:2 soil to water suspension using glass electrode (Jackson, 1962); bulk density, in steel cores of volume 550 cm^3 (Buckman & Brady, 1969); field moisture content was determined by subtracting the weight of over-dry soil from the weight of field moist sample; particle size (sand, silt, clay), by the hydrometer method (Bougyoucos, 1962); organic carbon, by Walkley-Black wet oxidation (Jackson, 1962); chloride, by titration with $AgNO_3$ (USDA, 1969); available phosphorus, by Bray No. 1 method (Jackson, 1962); exchange acidity by extraction with barium acetate and titration with NaOH (Jackson, 1962); 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; extractable micronutrients (Mn, Fe, Cu, Zn) and aluminium were measured after extraction with 0·02 M EDTA using atomic absorption spectrophotometry (Isaac & Korber, 1971); acetate soluble sulphate, by turbidimetric determination (Tabatabai, 1974).

Synthesis of data

Since the vegetation and the soil were to be viewed in terms of gradients, and a correlation between the two subsystems was desired, an analytical technique capable of factoring the correlation (or variance–covariance) matrices of these subsystems into their characteristic roots and corresponding characteristic vectors was necessary. Principal components analysis (PCA) meets this requirement. It is a multivariate eigenvector analytical technique which has been found suitable for the interpretation of the structure within the correlation matrix of vegetation and environmental data (Austin, 1968; Barkham & Norris, 1970). With suitable standardization and adjustment of data, Swaine & Greig-Smith

(1980) and Ter Braak & Prentice (1988) have found PCA to be most appropriate in ecological research since its procedure requires a minimum of assumptions and is computationally unambiguous.

PCA was used in two main contexts: (a) to derive soil attribute loadings on the principal axes of variation; and (b) to derive species loadings on the principal axes of variation in which soil factor variables were included to help account for the influence of the soil on vegetation. For the former analysis, all soil variables being positively skewed in their distribution were transformed to $\log_{10}$. For the latter analysis, the frequency values of 20 most commonly encountered mangrove swamp species (treated as one item across all strata) were used in the vegetation ordination.

In the vegetation analysis which used unstandardized frequency data (Seal, 1964), soil measurements were processed and included with the aim of achieving a principal components solution in which the axes are extracted from the vegetation data, with the soil measurements contributing insignificant proportions to the total variance. In essence this transforms the principal axes into vegetation gradients, while soil loadings on the components reflect the correlation between the soil and vegetation gradients (Dagnelie, 1960; Austin, 1968). A computer program was designed to produce initially normalized and unrotated principal axes from which the patterns of variation in vegetation and soil systems were discovered. Then, to account for a better correlation between the factor variables and the principal axes, the factor variables were adjusted according to Walker & Wehrhahn (1971). The adjusted loadings are presented in this study.

Having established the main gradients of the soil system, the stand values of all soil variables were harmonized by converting them to a range of 0–100. Each value was then weighted by the corresponding factor variables as derived from the PCA of the soil data. The products were summed (over each of the components) and each value divided by 100. Hence, the final value for each stand represents the overall importance of the major gradient trends as interpreted from the PCA of soil data. These values were then included in a PCA of the mangrove species. Standardizations of this nature ensure that the soils do not influence the final analysis by contributing a large proportion of variance to the total extracted from the vegetation analysis (Walker & Wehrhahn, 1971). Varimax rotation was used to group maximally the factor variables into distinct clusters. However, the rotated solutions were not noticeably different from the PCA.

Results

Vegetation analysis

Sixty-eight species have a frequency greater than 5% in 80 quadrats. The highest number of species occurred close to the coastal beachridges as strand vegetation. True mangroves (with pneumatophores or aerial breathing roots) achieved tree status only in the middle and lower estuaries; along the beachridge zone, mangrove growth was stunted. The mangroves were *Avicennia africana* (Moldenke), *Rhizophora racemosa* (May), *Rhizophora mangle* (May) and *Rhizophota harrisonii* (Keay). Important associates included *Nypa fruticans* (Thumb), *Raphia*

Table 1. Mean frequency (%) of species in the mangrove swamps, including their importance values (I.V.) in 80 stands

Species	Frequency	I.V.	Species	Frequency	I.V.
Nypa fruticans	40·1	43·2	*Drepanocarpus* spp.	8·8	5·4
Avicennia africana	58·8	80·5	*Hibiscus tilaceus*	8·9	17·4
Rhizophora racemosa	47·9	56·4	*Cyperus articulans*	6·3	38·9
Rhizophora mangle	47·5	50·9	*Acrostichum aureum*	20·2	38·8
Pandanus spp.	19·2	12·3	*Paspalum vaginatum*	7·0	13·1
Rhizophora harrisonii	22·8	13·9	*Ipomoeae carica*	8·0	15·2
Raphia hookeri	15·9	13·8	*Selaginella* spp.	6·5	8·9
Conocarpus erectus	9·7	7·1	*Ipomoeae cylindrica*	8·8	11·5
Phoenix rechinata	11·2	7·9	*Acutas afer*	7·9	13·5
Sesuvium spp.	9·4	8·6	*Triumfetta* spp.	6·7	5·2

Table 2. Summary of soil analysis (mean ± SD) for the surface soil layer (0–40 cm) of the mangrove swamps

Soil variables	$\bar{X} \pm$ SD	Soil variables	$\bar{X} \pm$ SD
pH (air dry)	4·9 ± 0·1	Sodium (me/100 g)	10·1 ± 1·3
Bulk density (gcm^{-3})	0·79 ± 0·1	Potassium (m,e/100 g)	0·20 ± 0·04
Field moisture (%)	129·2 ± 13·0	CEC (me/100 g)	46·1 ± 10·7
Sand (%)	32·5 ± 4·6	Exch- acidity (me/100 g)	4·3 ± 2·1
Clay (%)	18·1 ± 7·6	Carbonate (me/100 g)	5·2 ± 1·2
Silt (%)	49·4 ± 8·0	Manganese (ppm)	334·2 ± 63·1
Organic carbon (%)	5·8 ± 1·3	Iron (ppm)	1554·9 ± 471·1
Chloride (%)	4·1 ± 0·2	Copper (ppm)	3·0 ± 0·8
Phosphorus (ppm)	3·2 ± 1·1	Zinc (ppm)	48·6 ± 24·4
Calcium (me/100 g)	11·9 ± 3·6	Sulphate (me/100 g)	0·09 ± 0·01
Magnesium (me/100 g)	19·2 ± 4·8	Aluminium (me/100 g)	0·10 ± 0·01

hookeri (Thumb), *Pandanus candelabrum* (Gaertn.) and *Phoenix reclinata* (Jacl.) (Table 1). due to large inputs of freshwater from upland streams, high forest species, e.g. *Acutas afer* (Sw.) and *Selaginella* spp. (Sw.) have encroached into the mangrove zone. Overstorey vegetation occurred in 76 quadrats, in which *A. africana* and *N. fruticans* were the most important mangrove and associate respectively. As expected, there was an increase in stem density of the understorey dominants, particularly *A. africana, N. fruticans* and *R. mangle*.

The importance of groundlayer species, e.g. *Acrostichum aureum* (Linn.), *Hibiscus tilaceus* (Linn.), *Cyperus articulans* (Linn.) and *Paspalum vaginatum* (Sw.) were enhanced by xerophytic adaptations which enable them to occur in both alluvial and strand zones.

Soil analysis

The summary of soil analysis is presented in Table 2. Silt (49·4 ± 8·0%) was the most variable soil textural property while sand (32·5 ± 4·6%) was the least varied. The ratio of exchangeable magnesium (19·2 ± 4·8 me/100 g) to extractable

Table 3. Variable loadings from the principal components analysis of soil data for the first four components. (Only variables accounting for the major gradient trends are included)

Variable	SC_1*	SC_2	SC_3	SC_4
pH	0·71	0·36	0·21	0·09
Bulk density	0·44	0·28	−0·68	0·02
Field moisture	0·41	0·24	−0·65	0·11
Sand	−0·52	−0·39	0·13	−0·61
Clay	0·49	0·36	0·01	−0·68
Silt	0·41	0·26	−0·05	0·71
Organic carbon	−0·53	0·15	0·61	0·00
Chloride	0·80	0·13	−0·28	0·14
Phosphorus	−0·57	0·68	0·22	0·06
Calcium	0·39	0·71	0·29	0·21
Magnesium	0·35	0·59	0·17	−0·10
Sodium	0·78	0·38	0·18	0·10
Potassium	0·46	0·69	0·09	−0·12
CEC	0·58	0·74	0·18	0·05
Exchange acidity	−0·48	−0·03	0·67	−0·18
Soluble sulphate	0·86	0·03	0·33	0·08
Proportion of total variance	40·5	18·2	11·6	5·5

*SC_1 . . ., SC_4=soil principal components

cations was high, probably due to the high concentration of magnesium in seawater. The high CEC (46·1 ± 10·7 me/100 g) of the soils suggests that mangrove swamps have a potentially high sink for cations, particularly magnesium, calcium and sodium. From the range of values observed, it is obvious that soils closer to the ocean equilibrate with higher concentrations of magnesium, calcium and sodium than soils of the upper estuaries.

Variation in available phosphorus indicated the influence of geogenetic parameters, e.g. the spatial location of swamps relative to upland freshwater sources. Lower values occurred where marine influences were stronger than terrestrial influences. Considering the pH values of the soils, phosphorus could have been fixed by iron and aluminium.

Chloride content was lowest in the Creek Town/Calabar River swamp indicating the influence of dilution of tidal waters by freshwater sources (Fig. 1). The more littoral swamps had higher values due to tidal imports. The mean value for all swamps stood at 4·1 ± 0·2%. Although soil salinity is usually much higher than surface water salinity in mangrove swamps, it is less variable due to the effects of subsurface seepage from the terrestrial zones (Ukpong, 1989).

Principal components analysis of soil data

The adjusted loadings on the first four components of the analysis are presented in Table 3. The four components account for 75·8% of the variation in the data.

The first component (SC_1) is a salinity gradient in view of the high loadings for chloride, sodium and soluble sulphate. However, considering the instability of the swamps landscape other secondary gradients may be recognized: CEC, phosphorus and organic carbon achieve significant loadings, depicting a residual nutrient factor. Acid conditions associated with organic litter decomposition produce sulphides, indicated by the positive loading for soluble sulphate. The loading for pH, however, shows increasing alkalinity on this first axis. Generally SC_1 is a complex hydrochemical/salinity gradient in which factor interaction is influenced by tidal regime and subsurface water seepage.

The second soil component (SC_2) is a nutrient supply gradient considering the loadings for CEC, calcium, potassium, magnesium and phosphorus.

Tentatively, the third soil component (SC_3) is interpreted as a soil moisture regime gradient. Field moisture, bulk density and exchange acidity achieve significant loadings. Field moisture relates to exchange acidity in terms of the reduction of acid conditions by seepage and tidal flooding through elimination of stagnancy in depressions and pools.

The fourth component (SC_4) is a gradient of substrate texture; silt (positive) correlates with negative loadings for clay and sand. The component defines favourable sites for the establishment of mangroves.

Vegetation-soil relationships

The results presented in Table 4 show that the principal components (VC_1 . . ., VC_4) were indeed species gradients because the soil factor variables on SC_1 . . ., SC_4 having been standardized, contributed insignificant proportions to the total variance.

The first principal component of the vegetation (VC_1) is a competition gradient, in view of the high positive and negative loadings for *A. africana, R. mangle, R. racemosa, R. harrisonii* and *N. fruticans*. The positively loaded species are macrophytes that occur frequently along the shores while those with negative loadings are frequently found in the inner swamps. In comparing plant species there is a tendency to exclude competition from the range of environmental factors to which each species is most adapted. The sedges (*H. tilaceus, C. articulans*) achieve high negative loadings and show spatial segregation with *A. africana, R. racemosa* and *N. fruticans* (positives). Furthermore, the sedges correlate with sand (negative) to confirm VC_1 as a competition gradient since they generally occur on sandy substrates not dominant along alluvial shorelines. The positively loaded species, being the most frequently encountered (Table 4), correlate with a positive loading for organic carbon, which indicate the influence of crown cover and rootmat to the organic matter status of the soils. Considering the loadings for calcium, magnesium, pH and organic carbon, a soil nutrient factor is emphasized. The competition gradient is therefore determined by species relations to soil nutrients.

Table 4 shows that the vegetation competition gradient (VC_1) is negatively correlated at a statistically significant level ($r = -0{\cdot}38$, $P < 0{\cdot}01$) with the soil salinity/complex hydrochemical gradient (SC_1). The negative correlation indicates that the species (*A. africana, R. mangle, R. racemosa, R. harrisonii, N. fruticans, H. tilaceus* and *A. aureum*) that determine the competition gradient are not obligate halophyates or salt loving plants, but are facultative on the basis of salt tolerance. An increase in soil salinity levels may lead to a decrease in the importance of species along the competition gradient.

Jackson (1964) and Giglioli & Thornton (1965) had observed the occurrence of luxuriant stands of *A. africana* and *R. mangle* in areas where salinities averaged 2·5%. However, the species (including *R. harrisonii* and *N. fruticans*) become shrubby and stunted where salinities exceed 3·8% (Ukpong, 1991). VC_1

Table 4. Variable loadings from the principal components analysis of species data for the first four components. Included are SC$_1$ . . ., SC$_4$ derived from previous analysis of soil data (only variables accounting for the gradients are included)

Variable	VC$_1$	VC$_2$	VC$_3$	VC$_4$
Avicennia africana	0·73	0·25	−0·22	0·26
Rhizophora mangle	−0·57	0·32	0·34	0·05
Rhizophora racemosa	0·54	−0·15	0·46	0·34
Rhizophora harrisonii	−0·59	0·18	0·33	0·22
Nypa fruticans	0·76	0·10	0·17	−0·18
Hibiscus tilaceus	−0·46	−0·02	0·43	0·17
Ipomoeae cairica	−0·08	0·43	−0·65	0·14
Drepanocarpus lunatus	0·26	−0·19	0·01	0·50
Phoenix reclinata	−0·45	0·16	0·25	0·48
Acrostichum aureum	0·67	−0·48	0·24	0·16
Cyperus articulans	−0·51	−0·16	−0·10	0·44
Raphia hookeri	−0·34	0·01	−0·61	−0·25
Ipomoeae cylindrica	−0·03	0·45	−0·35	0·11
Paspalum vaginatum	0·20	0·51	0·08	0·38
Selaginella spp.	0·08	0·46	−0·18	−0·29
Mangrove Seedlings	−0·36	0·05	0·22	−0·33
pH	0·50	0·21	0·18	−0·02
Field moisture	0·36	0·04	−0·25	−0·42
Sand	−0·43	−0·24	0·20	0·30
Silt	−0·32	0·30	0·21	−0·38
Organic carbon	0·58	0·12	−0·43	0·09
Chloride	0·28	0·44	0·40	−0·24
Calcium	0·47	−0·07	−0·56	−0·32
Magnesium	0·40	−0·06	−0·61	0·13
Sodium	−0·32	0·41	0·56	−0·14
Potassium	0·33	0·19	0·51	0·11
Sulphate	−0·09	−0·23	−0·47	−0·31
SC$_1$	−0·38**	−0·35**	0·09	0·11
SC$_2$	−0·24*	0·31*	0·56**	−0·21
SC$_3$	0·16	0·02	−0·27*	−0·27*
SC$_4$	−0·26*	−0·19	0·12	0·28*
Proportion of total variance	0·33	0·17	0·14	0·12

VC$_1$ . . ., VC$_4$=Vegetation principal components.
**Significant at 1% level; * . . . at 5% level.

is also negatively correlated with the soil nutrient supply gradient (SC$_2$) and the gradient of substrate texture (SC$_4$) at $P<0\cdot05$. Clearly, species relationships to soil salinity levels, cation concentrations and physical site quality (field moisture, sand, silt) are emphasized along the competition gradient. The mangrove swamp soils are generally not favourable to species performance.

The second vegetation component (VC$_2$) depicts vegetation adaptation gradient since species with the highest loadings (*P. vaginatum, Ipomoeae* spp. (Linn.) and *Selaginella* spp.) are not true mangroves. These species also occur up-river in freshwater zones and their importance in tidal swamps reflect adaptation to saline/brackish habitat. *Acrostichum aureum* shares niche relations with these species on account of its wide ecological amplitude in mangrove swamps (Chapman, 1976). Considering the loadings for chloride and sodium, a soil salinity factor is emphasized, to which species show varying adaptations. The soil factor relates to stress because the soil salinity/complex hydrochemical gradient (SC_1) correlates negatively with VC_2 at a significant level ($r = -0{\cdot}35$, $P < 0{\cdot}01$). This negative relationship between the species (*P. vaginatum, Ipomoeae* spp.) and soil salinity indicates sensitivity of the non-mangrove associates to the soil salinity gradient. Clearly, the performances of these species are expected to increase with a decrease in salinity. The nutrient supply gradient (SC_2) however correlates positively with VC_2 ($r = -0{\cdot}32$, $P < 0{\cdot}05$), an indication that non-mangroves which load highly on VC_2 make higher nutrient demands on the soils than true mangroves. The true mangroves (*R. mangle, A. africana*) that load highly on VC_2 are often associated in mixed stands with *A. aureum* and *Ipomoeae* spp. and therefore share site relations in terms of nutrient availability.

The third vegetation component (VC_3) is a residual competition gradient between the mangroves (*R. racemosa, R. mangle, R. harrisonii*) and strand associates (*Ipomoeae* spp., *H. tilaceus, Raphia hookeri*). The loadings for mangroves (positives) indicate spatial segregation with the associates (negatives). The soil factor emphasizes nutrient supply considering the loading for calcium, magnesium, potassium and organic carbon. A gradient of salt spray along the strand beachridge zone is represented by chloride, while soluble sulphate relates to acid conditions associated with organic litter decomposition in saline ponds and ebbflood rills of the beachridges. The residual competition gradient (VC_3) is positively correlated ($r = 0{\cdot}56$, $P < 0{\cdot}01$) with the nutrient supply gradient (SC_2), similar to the correlation of vegetation adaptation gradient (VC_2) with SC_2. The highly loaded species on both vegetation components are mainly mangrove associates which confirms the previous interpretations that non-mangroves are more sensitive to soil nutrient levels than true mangroves. Considering the significant correlation ($r = -0{\cdot}27$, $P < 0{\cdot}05$) of VC_3 with the soil moisture regime gradient (SC_3), tidal flushing of the soil is an important determinant of species composition along the residual competition gradient. The true mangroves (*Rhizophora* spp.) are spatially segregated from the strand species (*Ipomoeae* spp., *Raphia*) on the basis of flood tolerance.

The fourth vegetation component (VC_4) is a 'site preference' gradient. Non-mangroves and strand species (*D. lunatus, P. reclinata, C. articulans, P. vaginatum*) correlate significantly with high negative loadings for bulk density, field moisture and silt. There is clearly an inverse preference by the species for soil moisture and textural characteristics. Soil moisture regime, related to tidal influence emphasizes a dispersal gradient considering the high loading for mangrove seedlings.

Conclusion

A correlation of PCA loadings for mangrove species with soil measurements has provided information for developing explanations for the distribution of mangroves in terms of their relationship to the soil factors. However, the percentage of total variation in the vegetation and soil data could be more exact if: (i) the importance attributed to each species and each soil property in a quadrat were the absolute ecological significance of the species and soil property; and (ii) there were no errors in the measurements of species and soil properties. These problems arise mainly due to the hostile swamp environment (e.g. unstable and malodorous mud, extensive prop roots and inaccessibility) and limitations on sampling time imposed by tidal cycles.

Salinity and nutrients are the most variable soil properties in the mangrove swamps. Their values relate to the spatial location of swamps relative to ocean and freshwater sources, and correspond to a transitional gradient in the vegetation. The highest salinity levels are associated with true mangroves such as *A. africana* and *Rhizophora* spp. which dominate the lower estuaries. High, intermediate and low values overlap considerably among the beachridge strand species (e.g. *Ipomoeae* spp., *C. articulans*). The relationship of nutrient cations to species variation was closely similar to that obtained for salinity levels.

What is apparent, therefore, is a transitional environmental gradient in the mangrove swamps. To quantify appropriately the transitional factors in terms of soil measurements would require the inclusion of freshwater seepage estimates, tidal frequencies, extent and duration of inundations and perhaps a correlation of these with spatial location of stands from the ocean. However, these were parameters not measured in this study.

As a precursor to more detailed studies designed for management and conservation of mangrove ecosystems, this study has identified several soil variables as influencing the spatial distribution and composition of species in the swamps. Other environmental factors (not measured) which influence soil composition and therefore species distribution have been noted.

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