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Gradient analysis in mangrove swamp forests

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Abstract: Gradient analysis is used as a research method to investigate species occurrence relative to the complex environmental gradient characteristic of mangrove swamps. Physiographic mangrove habitats are sampled using quadrats located along transects established from the water channels inland. Ordination of species importance values along composite habitat transects reveals species modal gradations rather than marked zonation of the species as implied in Clementsian succession theories. Ordination of Pearson's correlation coefficients between composite quadrats of the habitat transect indicates mostly peaks and dips in the gradients, implying that the vegetation and environment are in a state of dynamic equilibrium with each other. There are constant species-environment adjustments and interactions along the gradient and hence an absence of stable conditions in the swamps. Mangroves are perpetuated along shorelines as long as their environmental tolerance limits are not exceeded and their growth is optimal relative to the habitat conditions in which they occur.

Resumen: Se usó el análisis de gradiente como un método de investigación de la ocurrencia relativa de las especies en el complejo gradiente ambiental característico de los bosques de manglar pantanosos. Los habitats fisiográficos del manglar fueron muestreados usando cuadros localizados a lo largo de transectos establecidos desde los canales de agua hacia tierra adentro. La ordenación de los valores de importancia revela gradaciones modales de las especies más que una zonación marcada de las especies, como esta implicado en las teorías sucesionales clemencianas. La ordenación de los coeficientes de correlación de Pearson entre los cuadros en los transectos indica principalmente picos y descensos en los gradients, lo que implica que la vegetación y el ambiente están en un estado de equilibrio dinámico uno con el otro. Existen ajustes constants entre las especies y el ambiente y sus interacciones a lo largo del gradiente, y por lo tanto en ausencia de condiciones estables en el pantano. Los manglares se mantienen a lo largo de la línea de la costa en tanto sus límites a las tolerancias ambientales no sean excedidos y su crecimiento sea óptimo en relación a las condiciones del habitat.

Resumo: A análise de gradientes foi utilizada como método para investigar a ocorrência de espécies em relação ao gradiente ambiental complexo característico das regiões pantanosas de mangal. Os habitats fisiográficos do mangal foram amostrados usando quadrados dispostos ao longo de transectos estabelecidos da margem dos canais para a terra firme. A ordenação dos valores de importância dos habitats complexos ao longo dos transectos revelou mais gradações nodais de espécies do que uma zonagem marcada, tal como implícito nas teorias sucessionais de Clements. A ordenação dos coeficientes de correlação de Pearson entre os quadrados compósitos dos habitats dos transectos indica, principalmente, a ocorrência de picos e depressões nos gradientes, implicando que a vegetação e o ambiente se encontram num estado de equilíbrio dinâmico entre si. Há, assim, um ajustamento e interacção constante espécies-ambiente ao longo do gradiente e, assim, a ausência de condições estáveis nas zonas pantanosas. Os mangais são perpetuados ao longo da linha de costa enquanto os seus limites de tolerância não forem excedidos e o seu crescimento for óptimo em relação às condições do habitat em que ocorrem.

Key words : Environment, ecological importance value, gradient analysis, habitat, mangrove, ordination, swamps.

Introduction

Mangrove swamps are complex ecosystems that occur along inter-tidal accretive shores in the tropics and sub-tropics (Walsh 1974). The swamps carry specialized estuarine trees in spatial zonation of species from the tidal channels inland and are interpreted as serial stages in a hydroseral succession (Chapman 1976). The belts of dominant mangrove species were described as separate plant communities (Kassas & Zahran 1967) which relate to salinity gradients (Ukpong 1991) and extent of tidal inundation (Tomlinson 1986). As the species appear to be zoned in only a general way, few studies have analysed the commonly encountered aberrant patterns or quirks in species distribution (Rabinowitz 1978; Ukpong 1995). Being influenced by the classical Clementsian zonation and succession concepts, earlier studies analysed and presented numerous tidy zonation and succession schemes for different mangrove swamps and regions as reviewed by Walsh (1974), Chapman (1976) and Tomlinson (1986).

In the present study, zonation of species in mangrove swamps is de-emphasized. The importance of physiographic change in mangrove habitats is considered as a primary factor in species distributional patterns. Rather than infer a seral change, the patterns in mangroves could be a response to an ever-changing series of habitats which result from geomorphic changes associated with the development of the estuarine or deltaic plain. Since the swamp landscape is essentially unstable, the mangroves have utilized their halophytic adaptations to achieve a dynamic balance with the environment such that the species are always perpetuated along shorelines (as long as their environmental tolerance limits are not exceeded) (Ukpong 1992). Under this dynamic equilibrium notion, zonation *per se* cannot be said to occur in mangroves since the dynamic conditions imply overlap both in species distribution and in the controlling factors of the environment. There may occur a continuous variation in the spatial distribution of species from the shorelines rather than marked changes between vegetation zones. An analytical framework is, therefore, desired which could expose the underlying dynamic patterns in mangrove species distribution in relationship to a constantly changing environment.

The aim of this study is to analyse the floristic and spatial characteristics of the mangrove vegetation and validate the issue of species zonation/succession along the complex environmental gradient which is assumed as given.

Methods

Habitat differentiation

To avoid a bias in sampling only the more accessible forest (which could probably obscure the varying gradients), the mangrove swamps in SE Nigeria (Fig. 1) were classified into physiographic habitats based on morphometry and topographic relations. The following habitats were recognized :

1. Distributary channel habitats are riverine mangrove wetlands in which the channels display evidence of abandonment and infilling of recent meander scars. The habitats assume the form of basin wetlands where depressions and slow water movement occur.
2. Point-bar habitats are found where there is intense sedimentation on the slip-off slopes of meanders. Minor channels within the point-bars do not show evidence of silting but terminate in permanent ponds or sandy/muddy surfaces in the landward sections of the swamps.
3. Braided-channel habitats are overwashed island habitats formed due to sedimentation within the river channels. They form "islands" or braids in the channels.
4. Interdistributary basin habitats are the low-lying (basin) areas between distributary channels characterised by seasonal freshwater flooding. Large quantities of sediments are supplied to the swamps seasonally by overland flow and wider tidal inundations.
5. Wooded levee habitats are natural levees of variable width that merge inshoreward into the low freshwater swamps.
6. Tributary creek habitats occurring along tributary creeks that join the river estuaries close to the beachridge sands.
7. Inter-riverine creek habitats occurring along interriverrine creeks that connect the river estuaries to each other through the beachridge sands. They are characterised by alternating erosion and deposition of sediments due to strong estuarine currents.

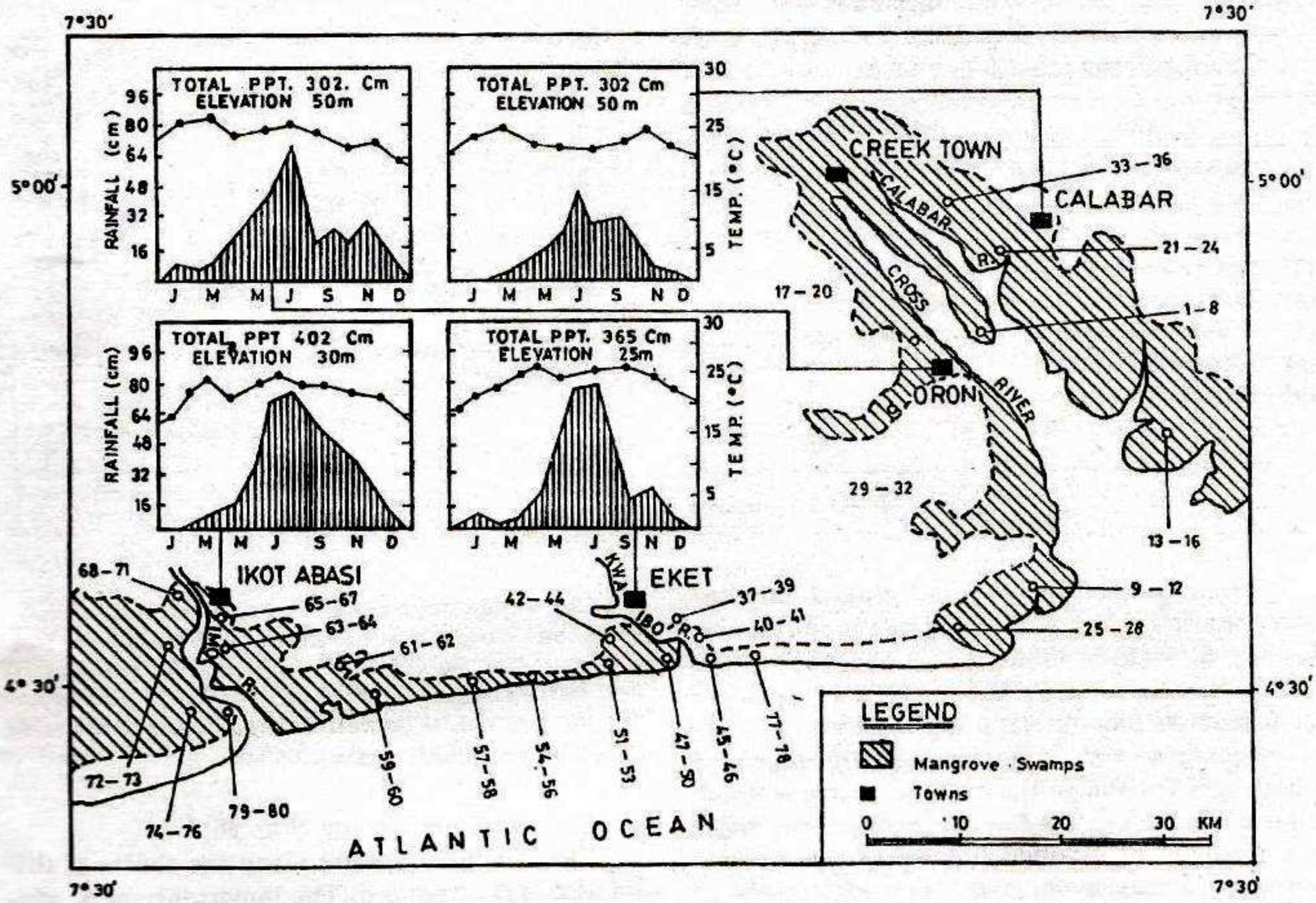

Fig. 1. Map of the study area in S.E. Nigeria, showing climatic regimes, extent of mangrove growth and location of transects. Quadrats on the transects are numbered (1-80).

8. Beachridge strand habitats are strand or dune habitats separated from each other by ebbflood rills/channels. Ocean waves cause the deposition of coarse sands on the shoreward slopes.

Vegetation sampling

Vegetation transects were established from the channels across the physiographic habitats. All species were sampled in at least two replicates of 10 x 10 m quadrats established at regular 20 m intervals along the transects to the landward limits of mangrove growth. Species >1 m tall were identified and enumerated in all quadrats. Frequency of occurrence and cover values of species were also recorded for each quadrat. The measures of relative frequency, relative density and relative coverage were summed to obtain the ecological importance value of each species in the habitats (Stephenson 1986). The distribution of quadrats among the habitats is presented in Table 1.

Synthesis of data

In order to observe the peaks and species modalities from the shores inland, the importance values of species were ordinated on one composite vegetation transect for each habitat, from which a direct (complex) environmental gradient relationship was inferred. The steepness of the gradient was further analysed by ordinating Pearson's r-values beneath the vegetation transect (Beschel & Webber 1962). The Pearson's correlation coefficients (r) were computed for all possible quadrat pairs sampled in the swamps. This was based on the number of species in each quadrat which usually exceeded five; although high correlations were encountered, these were exceptional rather than a general situation. The trends revealed by the mean r-values of composite quadrats for each habitat were ordinated as direct gradient plots with a transverse bar on each value indicating a probability of significance P = 0.05 from the t-test.

Table 1. Number of sampling quadrats in each of the physiographic habitats. Each quadrat was 10 m x 10 m.

	Habitat	Number of Quadrats
(a)	Distributary Channel	10
(b)	Interdistributary Basin	16
(c)	Tributary Creek	6
(d)	Inter-riverine Creek	9
(e)	Point-bar	8
(f)	Braided Channel	13
(g)	Wooded Levee	13
(h)	Beachridge strand	5
	Total	80

Results

It is necessary to give background into the interpretation of floristic gradations in vegetation. Beschel & Webber (1962) explained the significance of the ordinations and Pearson's correlation coefficients as follows : (i) A dip between two composite quadrats with a negative insignificant correlation signifies the presence of an ecotone which implies a change in species composition. (ii) Peaks and plateaus of significant positive correlations between composite quadrats are indications of high homogeneity in vegetation.

(a) The Distributary Channel Habitat (Fig. 2a)

Analysis of the gradient for the distributary channel habitat reveals that *Rhizophora racemosa* occurs close to the channel, associated with *Nypa fruticans* and *Avicennia africana*. However *A. africana* has a wide amplitude, with diminishing importance value in the inner swamps. *R. mangle* and *Phoenix reclinata* show overlapping occurrence, resulting in a steep gradient in the third quadrat. The inner swamp is occupied by *Raphia* spp., *Triumfetta rhomboideae* and *P. reclinata*.

The r-values (Fig. 2a) show positive and significant correlations, an indication that there is no absolute break in the continuity of species modes. The last pair of quadrats correlate highly indicating that the vegetation falls short of a clear ecotone. The flood tolerance gradient in the distributary channel habitat is indicated as :

R. racemosa > *N. fruticans* > *A. africana* > *R. mangle* > *P. reclinata* > *Raphia* spp. > *T. rhomboideae* > *H. tilaceus*

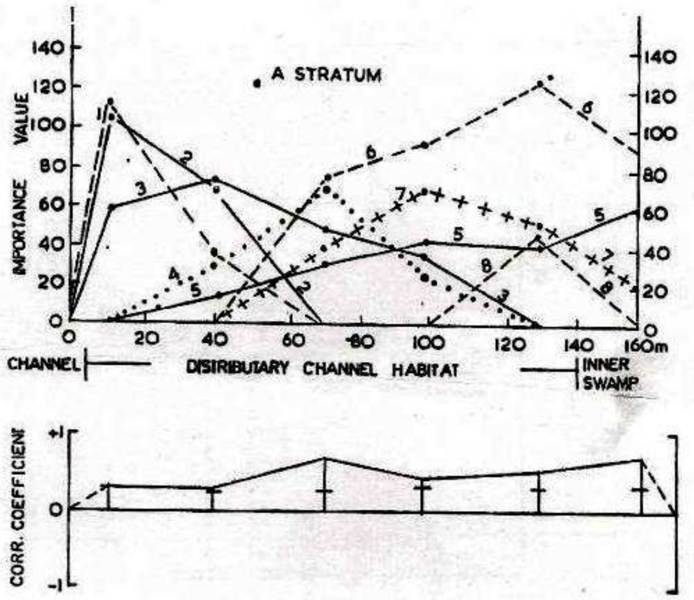

Fig. 2a. Composite transect through distributary channel habit. Code : 1=*R. racemosa*, 2=*N. fruiticans*, 3=*A. africana*, 4=*R. mangle*, 5=*P. reclinata*, 6=*Raphia vinifera*, 7=*T. rhomboideae*, 8=*H. tilaceus*; below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

(b) The Point-bar Habitat (Fig. 2b)

The dominant species along the shores of this habitat is *R. racemosa*. The importance of *A. africana* and *R. mangle* increases inshore. *Raphia* spp. has the widest amplitude in the habitat, where it is associated with *Pandanus candelabrum*.

The r-values between quadrats show significant positive correlations except the last pair (Fig. 2b). The dips and plateaux on the correlations indicate homogeneity among the vegetation components, particularly in the middle of the gradient with the highest r-values. The last pair of quadrats may be regarded as ecotonal. The flood tolerance gradient of species is indicated as :

R. racemosa > *A. africana* > *R. mangle* > *N. fruticans* > *R. harrisonii* > *Raphia* spp. > *P. candelabrum*.

(c) The Braided Channel Habitat (Fig. 2c)

On this gradient two species are dominant namely *N. fruticans* and *P. candelabrum*. On the shore *N. fruticans* is dominant. *P. candelabrum* is important in the middle of the gradient while in the inner swamp, *N. fruticans* again dominates. However, species of less importance, e.g., *Laguncularia racemosa*, have the widest amplitude.

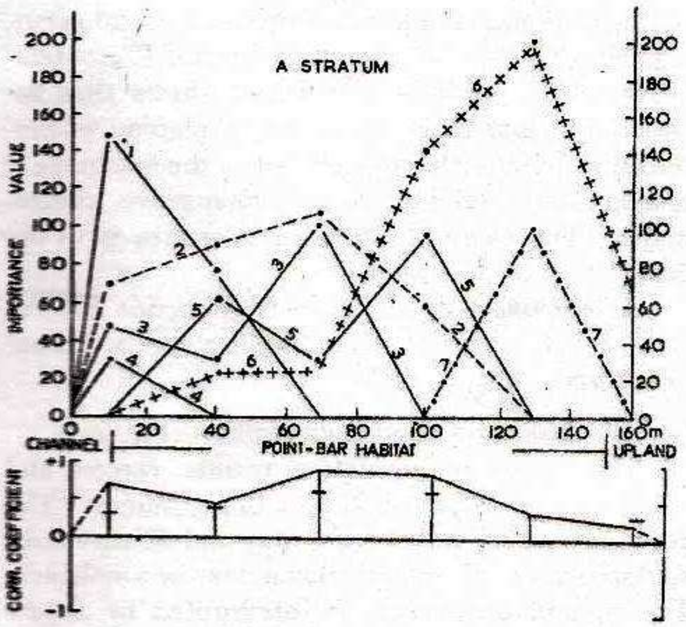

Fig. 2b. Composite transect through point-bar habitat. Code : 1=*R. racemosa*, 2=*A. africana*, 3=*R. mangle*, 4=*N. fruiticans*, 5=*R. harrisonii*, 6=*Raphia vinifera*, 7=*P. candelabrum*; below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

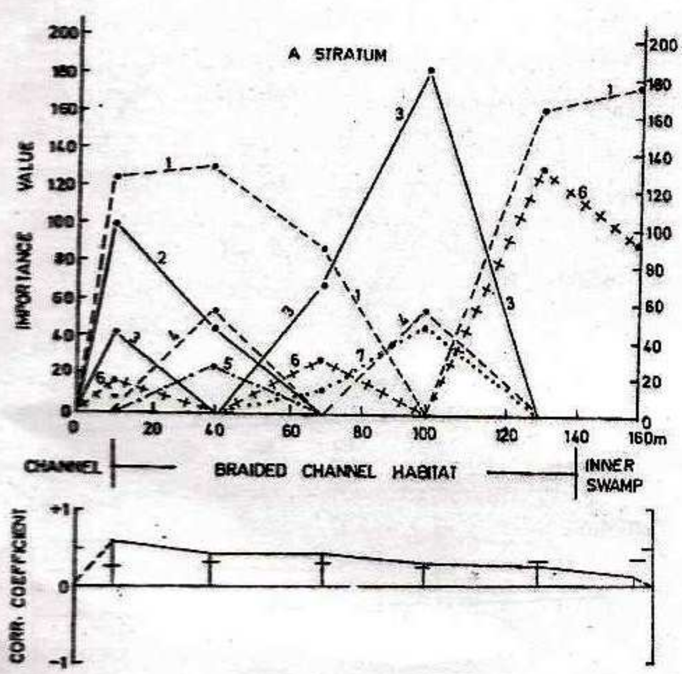

Fig. 2c. Composite transect through braided channel habitat (Overwashed Mangrove Island). Code : 1=*N. fruiticans*, 2=*R. racemosa*, 3=*P. candelabrum*; 4=*R. harrisonii*, 5= *C. erectus*, 6=*A. africana*, 7= *R. racemosa*, below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

The r-values between adjoining quadrats indicate that the vegetation gradients are not steep. There is a gradually sloping gradient towards the inner swamp with the last two pairs of quadrats being insignificantly correlated. Explanations of the insignificant correlations may be given in terms of : (i) The presence of distributary creeks in the inner swamps with a consequent change in species composition and (ii) The presence of silting ponds and permanently flooded areas that carry only ground layer species <1 m tall. The braided channel is the classic mangrove habitat where tidal inundation is most regular and complete. Hence species population reflect optimum adaptations to more or less uniform tidal conditions. The sequence of flood adaptation is :

N. fruticans > *R. racemosa* > *P. candelabrum* > *A. africana*.

(d) The Interdistributary Basin Habitat (Fig. 2d)

From the channel *R. racemosa* dominates in mixed stands with *A. africana*, *N. fruticans* and *R. mangle*. The species form overlapping modes and peaks inshoreward. *Drepanocarpus lunatus*, *Raphia* spp. and *P. reclinata* occur at the middle of the gradient. *Raphia* spp. achieve the widest amplitude among the lesser species.

Ordination of r-values reveals the existence of a steep gradient between the first and second

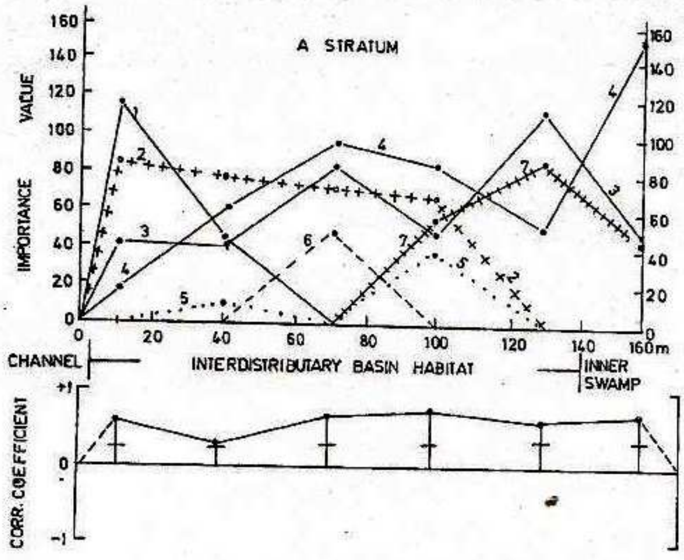

Fig. 2d. Composite transect through interdistributary basin habitat. Code : 1=*R. racemosa*, 2=*A. africana*, 3=*N. fruiticans*, 4=*R. mangle*, 5=*D. lunatus*; 6=*P. reclimata*, 7=*Raphia vinifera*, below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

quadrats (Fig. 2d). A plateau between the third and fourth quadrats indicates some homogeneity in this segment. Since all coefficients are significant, a continuum of species population is reflected in the habitat. The sequence of flood tolerance is of the order :

R. racemosa > *A. africana* > *N. fruticans* > *R. mangle* > *D. lunatus* > *P. reclinata* > *Raphia* spp.

(e) The Wooded Levee Habitat (Fig. 2e)

Mangrove species have the widest amplitudes on the wooded levees. *A. africana* dominates the channel margins. Inland, the importance of *R. racemosa* and *N. fruticans* decreases sharply as *A. africana* and *Rhizophora* spp. increases. The r-values between quadrats indicate that the gradients are steep. The gradients on the third and fifth quadrats indicate homogeneity in the vegetation. The flood tolerance gradient of species is indicated as :

A. africana > *R. recemosa* > *N. fruticans* > *R. mangle* > *R. harrisonii*.

(f) The Tributary Creek Habitat (Fig. 2f)

In this habitat, the most important species along the creek margins is *A. africana*. From the middle of the gradient, only non-true mangroves (without pneumatophores/viviparous roots) occur, e.g., *Raphia* spp., *T. rhomboideae* and *P. candelabrum*. The gradient of r-values shows that between the last three quadrats, a plateau is produced which may be interpreted as the existence of homogeneity among the non-mangrove components. The sequence of flood tolerance is of the order :

A. africana > *R. mangle* > *N. fruticans* > *R. racemosa* > *T. rhomboideae* > *Raphia* spp..> *P. candelabrum*.

(g) The Inter-riverine Creek Habitat (Fig. 2g)

The series of population trends, ranges and modalities are explicit across the gradient. The channel margin has *A. africana* and *R. racemosa* as dominants. *R. mangle* has a narrow amplitude. The upland continuum is interrupted by a pronounced ecotone dominated by *Raphia hookeri*. The r-values clearly depict the varying steepness of species modalities with an insignificant correlation between the last pair of quadrats. The sequence of flood tolerance is of the order :

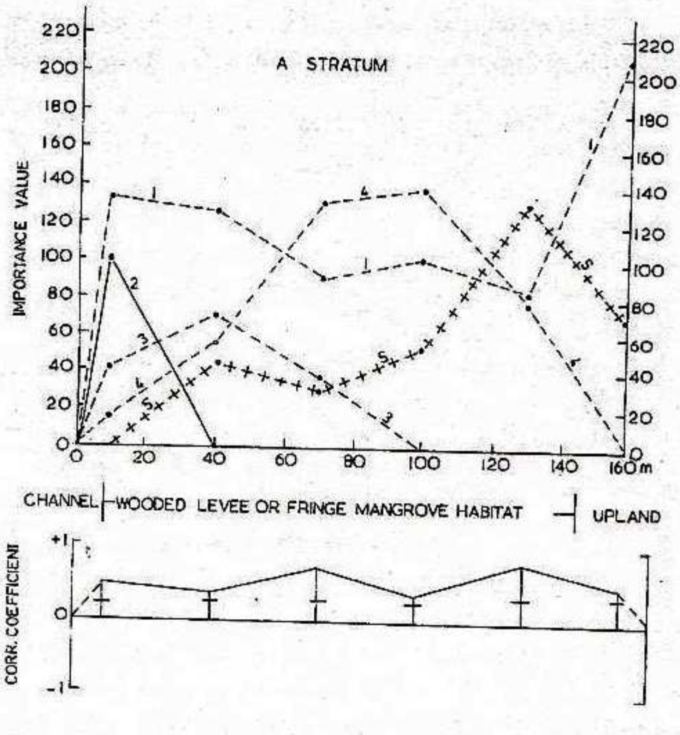

Fig. 2e. Composite transect through wooded levee habitat. Code : 1=*A. africana*, 2=*R. racemosa*, 3=*N. fruiticans*, 4=*R. mangle*, 5=*R. harrisonii*; below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

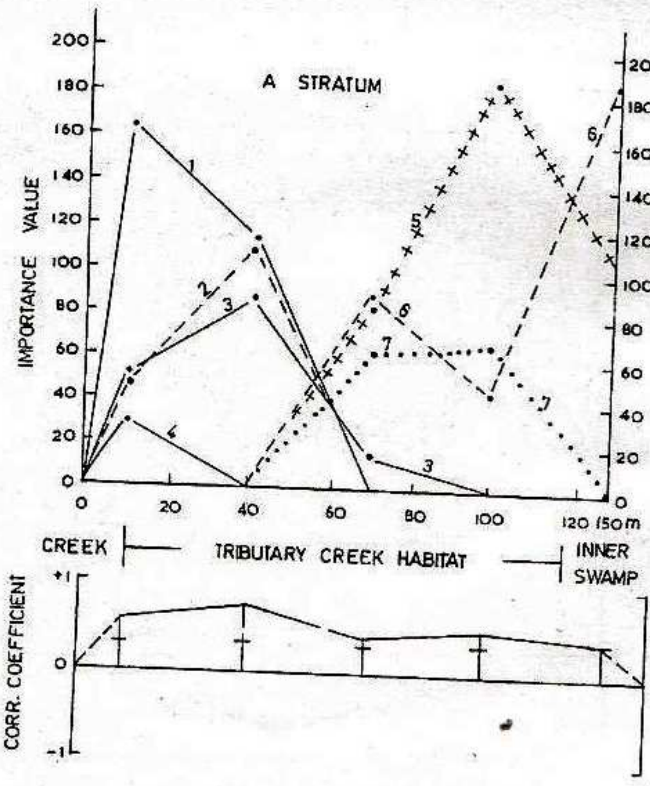

Fig. 2f. Composite transect through tributary creek. Code : 1=*A. africana*, 2=*N. fruiticans*, 3=*R. mangle*, 4=*R. racemosa*, 5=*Raphia vinifera*, 6=*T. rhomboideae*, 7=*P. candelabrum*; below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

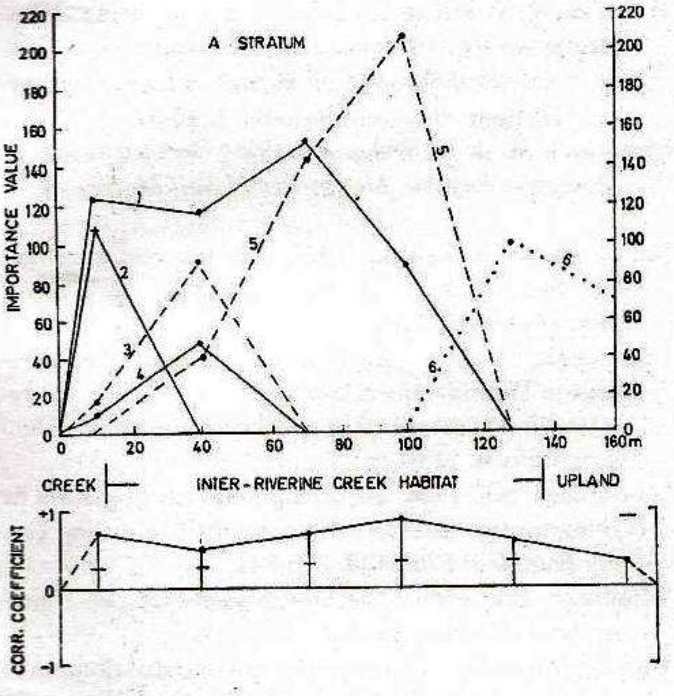

Fig. 2g. Composite transect through inter-riverine creek habitat. Code : 1=*A. africana*, 2=*R. racemosa*, 3=*R. harrisonii*, 4=*P. candelabrum*, 5=*R. mangle*, 6=*Raphia hookeri*; below are the correlation coefficients between adjoining composite stands; - indicate probability at P = 0.05 level.

A. africana > *R. racemosa* > *P. candelabrum* > *R. mangle* > *R. hookeri*

(h) The Beachridge Strand Habitat (Fig. 2h)

The coastal beachridges do not carry true mangroves except along ebbflood rills. Mangrove growth is scrubby ? *A. africana* and *R. racemosa*. The species are more or less sharply zoned and a generalized sequence is shown in Fig. 2h. *S. portulacastrum*, *Ipomoea cairica*, *Remeira maritina* and *Sporobolus viginicus* may be regarded as the pioneer strand species. On the landward slopes, *Hibiscus tilaceus* and *Selaginella* spp. grade into the adjoining lowland forests.

Conclusion

It may be concluded that species which have wide ecological amplitudes along the gradients are capable of bearing great fluctuations in environmental conditions whereas species with narrow amplitudes are restricted to areas where the environment is relatively stable. Species dynamics, therefore, relates to the morphology of the habitats. On the dynamics of mangrove habitats, inferences may be based on : (i) The short-term changes, e.g. changes in the velocity of tidal currents and sedimentation rate (Furukawa & Wolanski 1996); (ii) The long-term change, e.g. sedimentation in habitats over a long period of time (Fujimoto *et al.* 1996). Thus the occurrence of mangroves often cited in the literature relates to two geomorphologically contrasting situations : (i) The accreting shoreline habitat; (ii) The stable shoreline habitat (Ukpong 1992; Cahoon & Lynch 1997).

Most studies that cite certain species of mangroves as pioneers relate to the stable shoreline habitats. On accreting shorelines, the vegetation is not stable. The mangroves tend to fluctuate in populations and adjust to the center of active accretion (Wright *et al.* 1997). Hence on accretive shores, which generally occur in estuarine systems, mangrove tend to be in a state of dynamic

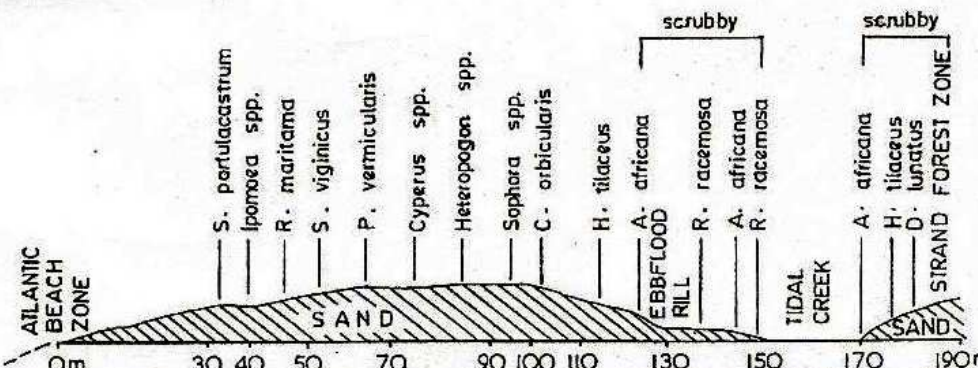

Fig. 2h. Diagramatic representation of vegetation zonation across the coastal beachridge sands near Mkpanak, Kwa Iboe River estuary.

equilibrium relative to their position along environmental gradients. The complex gradient (Figs. 2a-g) may be related to the dynamics of the mangrove habitats thus : (a) each vegetation peak relates to a change in habitat conditions involving a complex of environmental processes that tends to achieve relative stability; (b) a dip in the gradient following a peak relates to short-term changes of less complex nature, e.g., erosional and depositional tendencies, that have created a zone of vigorous interaction and competition between species; (c) a plateau in the gradient relates to the most stable conditions that can be obtained in the swamps.

The rarity of plateaus in the gradients examined indicate that stable environmental conditions are few in the mangrove swamps. What is obtained, generally, is a complex of dynamic equilibrium situations along the gradients. Since the coastal strand beachridge is apparently stable, being affected only by occasional Atlantic storm waves, species zonation is sharp, compared with the estuarine habitats where vegetation continnua or gradations are observed along the gradients.

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