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IS THERE VEGETATION CONTINUUM IN MANGROVE SWAMPS?*

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Mangrove vegetation in southeastern Nigeria was sampled in eighty 100 m^2 quadrats regularly spaced along transects established from the shores inland. Vegetation measurements included frequency, density and coverage from which the importance values of species were computed. Species were assigned anthropogenetic adaptation numbers based on their relative importance and the continuum indices for all species in the quadrats were computed. PEARSON's correlation coefficients were also computed for all possible pairs of quadrats along the transects. A direct gradient ordination of species importance values on one composite transect revealed the existence of floristic gradations rather than discrete zonation of species from the shores inland. An ordination of PEARSON's r-values between adjoining composite quadrats indicated the existence of unstable conditions which accounted for the occurrence of overlap in species population modes. An indirect gradient ordination, based on the continuum index verified the existence of vegetation continuum in several understorey dominant mangroves. The dynamic equilibrium concept was proposed as an appropriate concept for the analysis of mangrove ecosystems.

Keywords: continuum index, dynamic equilibrium, floristic gradation, gradient analysis, mangrove vegetation, ordination, zonation

Introduction

Mangrove swamp forests are complex ecosystems that occur along intertidal accretive shores in the tropics (WALSH 1974). The swamps are dominated by specialized estuarine trees which generally occur in zones of species from the shores inland, and are often interpreted as seral stages in a hydroseral succession (CLEMENTS 1936; RICHARDS 1964; CHAPMAN 1976). The distinct belts of dominant mangrove species have also been described as separate plant communities (KASSAS and ZAHRAN 1967), which are related to salinity

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*Being part of a thesis submitted by the author to the Department of Geography, Faculty gradients and extents of tidal inundations (WEST 1956). As the mangroves appear to be discretely zoned at a broadly generalized level, few studies have analysed the commonly encountered aberrant patterns or quirks in species distribution (with the notable exceptions of THOM 1967; THOM et al. 1975 and RABINOWITZ 1978). The previous studies, being influenced by the classical Clementsian zonation and succession concepts resulted in numerous tidy zonation and succession schemes for different mangrove swamps and regions as reviewed by CHAPMAN (1976).

In the present study, the zonation concept is de-emphasized, based on the observation by THOM (1967) that the importance of physiographic change in mangrove habitats has not been fully considered as an ecological factor. Rather than infer a seral change, the distributional patterns in mangroves could be primarily a response to an ever-changing series of habitats which result from geomorphic changes associated with the development of the estuarine or deltaic plain. The implication is that 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). Under this dynamic equilibrium notion, zonation per se cannot be said to occur in mangrove swamps since the dynamic conditions imply overlap both in vegetation and in the controlling factors of the environment. Consequently there may occur a continuous variation or vegetation continuum in the spatial distribution of species from the shorelines rather than sharp changes between vegetation zones.

Methods

To verify the existence or otherwise of a vegetation continuum in mangrove swamps, eighty 100 m^2 quadrats regularly spaced at 20-meter intervals along transects from the shorelines of three river estuaries in southeastern Nigeria were sampled, based on forest type differentiation. The forest types were modified after LUGO and SNEDAKER (1974) as (1) Distributary basin mangroves, (2) Point-bar mangroves, (3) Braided channel mangroves, (4) Interdistributary basin mangroves, (5) Wooded levee mangroves, (6) Tributary creek mangroves, (7) Interriverine creek mangroves and (8) Beachridge strand mangroves. Forest type differentiation eliminated a bias for establishing transects on more accessible and commonly encountered habitats.

Vegetation measures for the overstorey (> 3 m) included crown cover by the crown-diameter method (MUELLER-DOMBOIS and ELLENBERG 1974), species density and frequency. Measures for the understorey (< 3 m) were obtained in 25 m^2 sub-quadrats, while samplings were in 1 m^2 subplots. Due to the presence of extensive props on most mangrove species, basal area was not used as a measure of dominance. The relative measures of frequency, density and coverage were summed to obtain the importance values for species.

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, from which a direct environmental gradient relationship was inferred. The steepness of the gradient was further analysed by ordinating PEARSON's r-values beneath the vegetation transect (BESCHEL and WEBBER 1962). The PEARSON's correlation coefficients (r) were computed for all quadrat pairs in the swamps. This was based on the number of species in each quadrat which usually exceeded five (items); and although high correlations were encountered, these were exceptional rather than a general situation. The trends revealed by the mean r-values for composite quadrats 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.

The existence of vegetation continuum was also investigated without direct reference to the spatial position of species on the landscape. In effect, this was an indirect gradient analysis approach based on computations of a continuum index for each quadrat (CURTIS and McINTOSH 1951). A primary step in the analysis was the computation of the importance value for each species in a quadrat and the leading dominant species in the quadrat identified i.e. the species with the highest importance value. Quadrats with the same species as leading dominants were grouped together and the average importance value for the species determined. By a subjective evaluation the species were arranged in an order such that the leading dominant occurring in the least number of quadrats and the leading dominant occurring in the largest number of stands were allocated the least and highest anthropogenetic "adaptation" numbers. The adaptation numbers were arbitrary numbers used in ordering species on a phytosociological scale of importance (KERSHAW 1973). The leading dominants occurring between the two established indices were accordingly given their own numbers based on the number of quadrats in which they were dominants. Therefore species which frequently occur together and may have similar environmental requirements have the same or similar adaptation numbers.

Table 1

Species importance values for overstorey mangroves averaged for six composite quadrats from the shorelines (1) to the inner swamps (6)

Species	Quadrats						Mean transect value
	1	2	3	4	5	6	
Avicennia africana	92.6*	84.7**	69.7*	46.9	29.3	42.9**	61.0
Rhizophora mangle	17.6	38.6	72.1**	64.3**	17.3	28.3	39.7
Nypa fruticans	54.3	59.7*	29.0	7.1	32.6	32.7	35.9
Raphia vinifera	0.0	2.5	23.6	61.6*	74.3**	37.9*	33.3
Rhizophora racemosa	105.1**	26.4	0.0	0.0	0.0	0.0	21.9
Pandanus candelabrum	7.1	6.0	17.6	34.6	12.1	0.0	12.9
Rhizophora harrisonii	2.1	25.7	3.6	13.4	17.1	10.0	12.0
Triumfetta rhomboidea	0.0	0.0	16.4	15.4	36.8*	2.9	11.9
Phoenix reclinata	0.0	1.4	9.6	5.0	4.6	8.7	4.9
Drepanocarpus lunatus	0.0	1.4	0.0	5.0	0.0	0.0	1.1
Hibiscus tiliaceus	0.0	0.0	0.0	0.0	4.3	0.0	0.7
Conocarpus erectus	0.0	3.1	0.0	0.0	0.0	0.0	0.5
Mean quadrat value	23.2	20.8	20.1	21.1	19.0	13.6	

* Co-dominant species

** Dominant species for each composite quadrat

The quadrat continuum index was derived by multiplying the importance value of each species in the quadrat by the adaptation number of the species which were then summed to obtain the total index for the quadrat. For the ordination, the importance values of species formed the vertical axis of a graphical plot while the quadrat continuum indices formed the horizontal axis. The representation was a scatter of points for each species through which lines of best fir were inserted to portray the ecological amplitudes of the species.

Results

Table 1 summarizes the results of vegetation analysis for the overstorey on one composite transect. The importance values (I.V.) of species were averaged for composite quadrats and arranged in spatial positions corresponding to the maximum number of quadrats and transect length of the widest forest type. Four species were observed to show similar ecological amplitudes across the transect. In order of importance the species were (1) Avicennia africana, (2) Rhizophora mangle, (3) Nypa fruticans and (4) Rhizophora harrisonii. The most important species at the channel margins were Rhizophora racemosa (I.V. 105.1) and A. africana (I.V. 92.6). Given a successional interpretation both species could be regarded as pioneer colonizers of mudflats, although SAVORY (1953) and KEAY (1953) regarded only R. racemosa as pioneer species. In the second quadrat A. africana (I.V. 84.7) and N. fruticans (I.V. 59.7) were the dominant species. But since N. fruticans is an introduced species (MERCER and HAMILTON 1984), its importance along the transect reflects the extent of human interference in the ecology of the mangrove swamps.

The middle of the transect was dominated by R. mangle (I.Vs. 72.1 and 64.3) in the third and fourth quadrats, respectively. R. mangle occurred in association with A. africana (I.V. 69.7) in the third quadrat and Raphia vinifera (I.V. 61.6) in the fourth quadrat. The inner swamps (quadrats 5 and 6) were dominated by R. vinifera (I.V. 74.3) and A. africana (I.V. 42.9) in association with Triumfetta rhomboidea (I.V. 36.8) and R. vinifera (I.V. 37.9), respectively. The species R. vinifera, T. rhomboidea and A. africana were the last landward major vegetation components of the vegetation transect. The highest mean importance value of 23.2 occurred at the shoreline and decreased to 13.6 in the last quadrat. Since these values showed a decrease inshorewards, a gradual floristic gradation was inferred during which the dominants replaced each other in importance along the transect. Clearly, there was no absolute discontinuity for the major species although certain minor associes e.g. Drepanocarpus lunatus, Hibiscus tiliaceus and Conocarpus erectus were restricted to narrow sections of the transect.

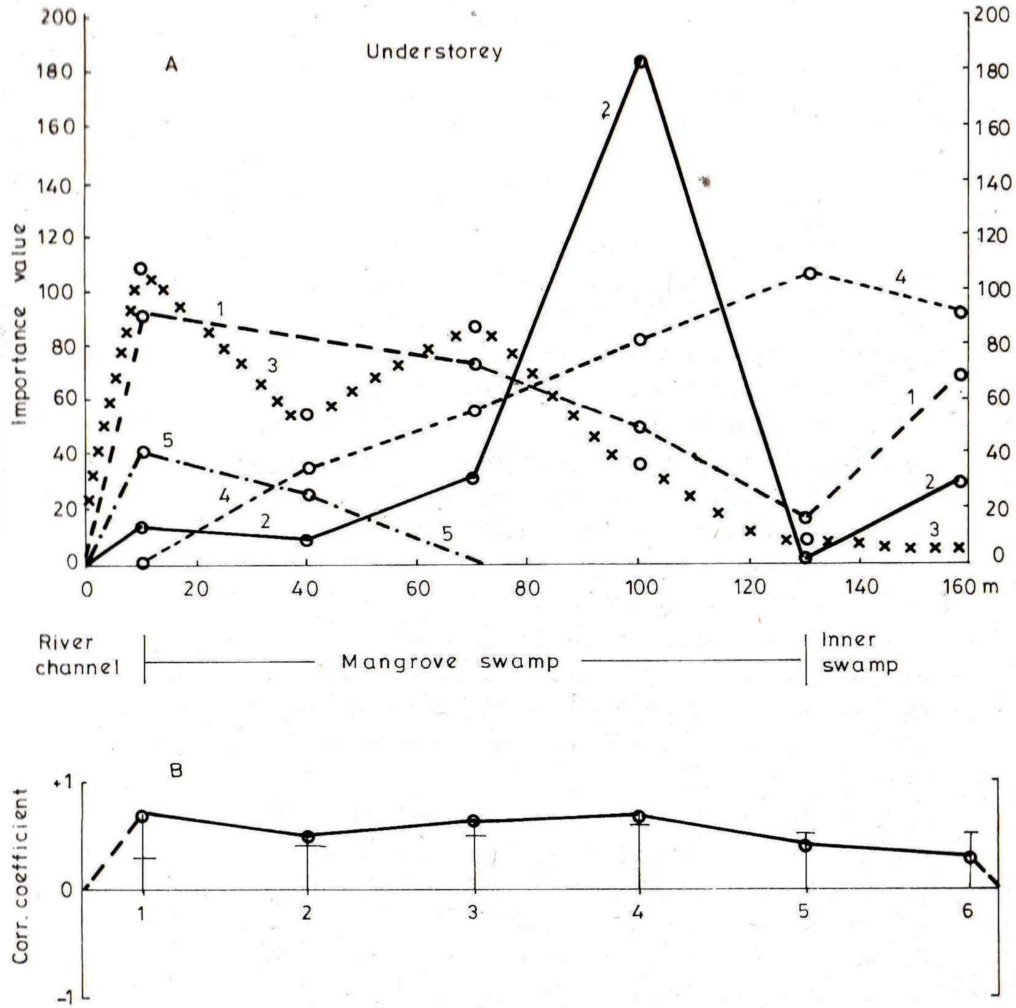

Fig. 1. Composite transect of mangrove swamp

A: Importance values for understorey mangroves across six composite quadrats, (1) Avicennia africana, (2) Rhizophora mangle, (3) Nypa fruticans, (4) Raphia vinifera, (5) Rhizophora racemosa. B: correlation coefficients of the vegetation between adjoining quadrats. Probability at P = 0.05 level is indicated by -.

The ordination of species importance values and PEARSON's r-values for the understorey vegetation is shown in Fig. 1. The trend of species modalities and peaks from the channels (upper diagram) showed that A. africana,

R. mangle, N. fruticans and R. vinifera had the widest ecological amplitudes. This was similar to the overstorey species modes in Table 1. Particularly, R. mangle appeared to depict a very steep gradient about the middle of the transect. However, the PEARSON's r-values (lower diagram) indicated that the species gradients were not steep; although the first four correlations were significant. There was a gradually sloping gradient from the first to the second quadrat, and a gently rising gradient to the highest positive correlation on the fourth quadrat. Then the gradient dipped into insignificant positive correlations on the fifth and sixth quadrats. Were the transect to be of greater length, it is possible that the correlations could have become negative, indicating the existence of a prominent ecotone at the mangrove/high forest margins. However, explanations for the insignificant correlations could be given in terms of (i) the presence of terrestrial deposits in the inner swamps with a consequent change in species composition, and (ii) the presence of silting ponds or permanently flooded areas that carry only groundlayer mangroves and samplings. Since the swamps experience diurnal flooding, the population modes reflect optimum adaptations to the environment. The sequence of dominance from the channels reflects largely the competitive abilities of the component species, e.g. species that dominate channel margins do so on the basis of suitably adapted rooting system, which is also a requirement for a wide amplitude across the unstable swamp landscape. Since the gradient (Fig. 1, lower diagram) dips gently towards the inner swamp, it is related to short-term changes in the swamp landscape (BESCHEL and WEBBER 1862), e.g. erosional and depositional tendencies that create zones of vigorous competition between species, such that the less vigorous species are replaced to relatively more stable (plateaux) areas along the gradient. As there is no positively correlated pair of composite quadrats (with similar r-values) that depict a uniformly stable (plateaux) condition, it implies that stable environmental condition which allows for the existence of sharp discontinuities in vegetation did not occur in the swamps.

Finally, a continuum index ordination was attempted for the understorey mangroves. This was because in each 100 m^2 quadrat, the importance values of understorey species could be obtained by summing the relative measures of frequency, density and coverage in four 25 m^2 subquadrats. The anthropogenetic "adaptation" numbers used for calculating the continuum indices are given in Table 2, while the average importance values for species used in the ordination are given in Table 3. The leading dominant occurring in the least number of quadrats was Laguncularia racemosa while the leading dominant occurring in the largest number of quadrats was Avicennia africana. Both species represented the two extremes of an environmental gradient between which an interrelationship of environmental factors determined the importance of the other species.

Figure 2 shows the series of curves derived for five understorey mangrove species and associes, based on continuum index plots. The curves

Table 2

Anthropogenetic "adaptation" numbers for understorey mangroves and associes

Species	Adaptation numbers
Laguncularia racemosa	1
Pandanus candelabrum	1
Triumfetta rhomboidea	2
Drepanocarpus lunatus	2
Raphia vinifera	2
Rhizophora harrisonii	3
Rh. mangle	4
Rh. racemosa	4
Avicennia africana	5

Table 3

Average importance values for understorey mangroves and associes in 80 stands

Number of stands	Leading dominants	A. africana	N. fruticans	R. racemosa	R. mangle	D. lunatus	R. vinifera	P. candelabrum	T. rhomboidea	L. racemosa	R. harrisonii
29	Avicennia africana	200	17	53	25	7	-	2	-	-	11
4	Nypa fruticans	28	117	16	61	-	-	8	-	-	-
20	Rhizophora racemosa	35	34	214	6	-	2	8	-	-	4
14	Rh. mangle	23	22	-	179	5	11	24	7	-	4
1	Drepanocarpus lunatus	-	-	-	-	191	-	-	48	-	-
3	Raphia vinifera	-	-	-	-	-	161	17	15	-	-
5	Pandanus candelabrum	31	-	73	11	-	-	176	-	-	-
1	Triumfetta rhomboidea	-	-	-	29	-	-	131	143	-	-
1	Laguncularia racemosa	67	-	-	-	-	-	109	-	123	-
2	Rhizophora harrisonii	77	-	-	47	-	18	-	-	-	159

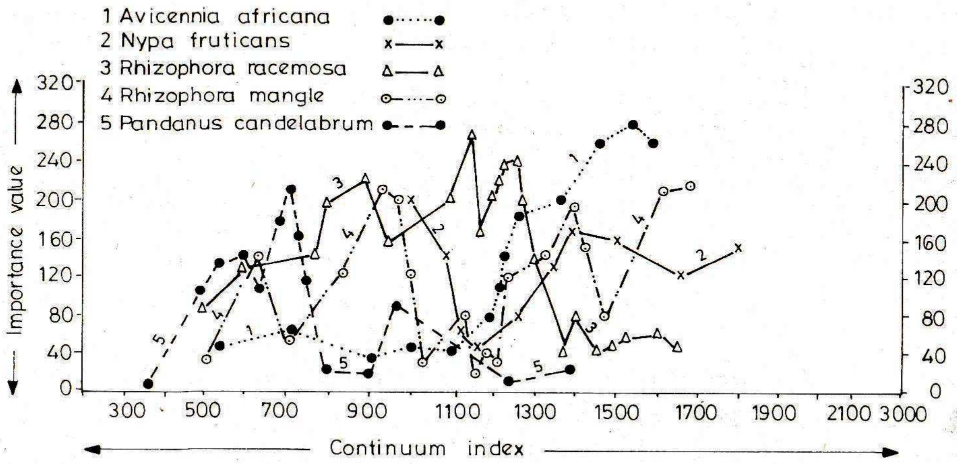

Fig. 2. Continuum index ordination for five understorey dominants of the mangrove swamps

were drawn through scatter points of best fit. As pointed out by KERSHAW (1973), the fact that no groups of curves occur in zones of the continuum index imply that there is no discrete and recognizable associations within the vegetation community. In addition, a continuous overlap of many adjacent dominants (Fig. 2) was clearly demonstrated over a considerable range of the index in this study.

Conclusion

There is no doubt that, in detail, there exists a measure of vegetation continuum in mangrove swamps from the shores inland. This implies that environmental factors also display continuous gradation in consonance with the floristic pattern. Although vegetation zonation may be discerned at a broadly generalized level of investigation, it is apparent that the mangrove swamp being highly unstable does not allow for occurrences of the "tidy" species zones often discussed in the literature on mangroves. It appears that the dynamic equilibrium concept in which the vegetation is viewed as constantly adjusting to the unstable swamp landscape would be a more appropriate concept for the analysis of spatial patterns in mangrove vegetation.

This however is not a capitulation from the CLEMENTSian zonation viewpoint. Essentially, it is a proposal.

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