Acta Botanica Hungarica 42 (1–4), pp. 323–333, 1999/2000

DETERMINANTS OF STRUCTURE IN A NIGERIAN MANGROVE FOREST

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(Received: 25 August, 1999)

The aim of this study was to examine the variation in mangrove vegetation structure, in relation to measured environmental variables. To achieve this, a relatively undisturbed mangrove swamp was analysed. Vegetation variables included species frequency, density, coverage, tree height and basal area while environmental measurements were soil texture, bulk density, root content of soils, salinity, organic matter, carbonate and exchangeable cations of soils. Multiple regression analysis revealed the importance of salinity and soil texture as the determinants of mangrove structure. Nutrient cations of soils and field moisture were relatively less important. Canonical correlation analysis revealed that the vegetation structure was significantly related to the measured variables.

Key words: determinants, mangrove, Nigeria, structure

Introduction

Having studied vegetation and soils of mangrove swamps in western Australia, and West Malaysia, Clarke and Hannon (1967), and Dietmont and van Wijngaarden (1974) concluded that soils did not offer satisfactory explanation for the observed vegetation structure. This conclusion was obvious, considering the difficulty of obtaining sufficient vegetation and soil data in tidal mangroves. The mangrove swamp soils, being regularly flooded is often extremely soft, with high water table. The dense entanglement of *Rhizophora* props present difficulty of movement while sampling time is limited by the tidal cycles. Consequently, data, particularly in the vegetation subsystem, are usually not obtained in forms that could permit statistical correlations (Naidoo 1980). The soil data are often derived from laboratory analysis which may not give a true indication of field conditions (Ukpong 1992). Since mangroves are often discretely zoned along sea coast littorals, most studies have adopted the simplified approach of emphasising vegetation structure in relation to isolated soil variables obtained within the zonation e.g. soil salinity (Cintron et al. 1978, Ukpong 1991).

0236-6495/99/00/$ 5.00

In the present study a small, relatively undisturbed, densely vegetated mangrove forest was sampled for vegetation, soil and other environmental attributes. The aim was to examine the variation in vegetation structure in relation to the measured environmental variables.

Study site

The occurrence of mangroves (*Rhizophora mangle, R. racemosa, R. harrisonii, Avicennia africana*), commonly codominant species with *Nypa fruticans, Raphia hookeri, Raphia vinifera* and *Phoenix reclinata* in the brackish/saline estuarine forests of Nigeria reach their northernmost limits in the Creek Town Creek/Calabar River Swamp (Fig. 1). Located between latitudes 4°55′N and 5°00′N, about 20 km from the Atlantic Ocean coast, the climate is humid tropical with mean annual rainfall of 4021 mm. Although rainfall occurs throughout the year, there are peaks from May to August (1880

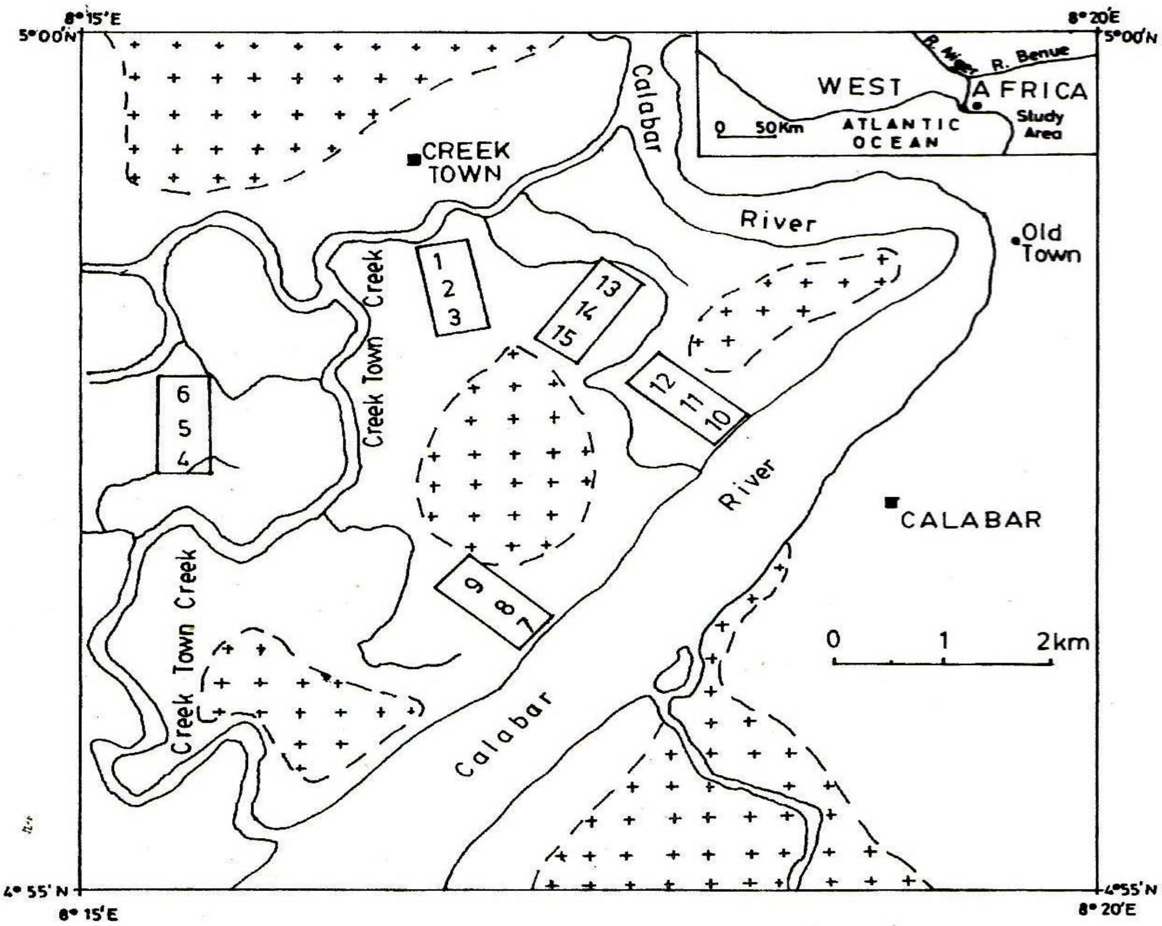

Fig. 1. Map of the study area showing approximate location of sample stands (1–15)

mm): lowest values (240 mm) occur from December to February. Temperatures are uniformly high with a maximum of 30 °C and minimum of 23 °C (FRN 1998). The swamps experience regular diurnal tides with mean amplitude of 0.75 m at Creek Town.

Methodology

Vegetation sampling

To obtain vegetation data, the Creek Town Creek/Calabar River mangrove swamp was sampled in the relatively dry months between November and January. The criteria for stand selection were (i) mangroves consisted members of the canopy layer and (ii) vegetation showed evidence of least disturbance within at least 0.5 hectare in size. The vegetation was stratified into A stratum (> 3 m tall), B stratum (1–3 m tall) and C stratum (< 1 m tall).

The mangroves were measured in fifteen 200 m^2 quadrats randomly located within the swamp. Quadrat location was determined by accessibility through tributary channels. Tree frequency, density, tree height, diameter at breast height and crown cover were obtained in 25 m^2 subquadrats established within the larger quadrats. Coverage for the C strata and seedling density were obtained in a further 1 m^2 subdivision.

Environmental sampling and laboratory methods

Using a semi-cylindrical corer, three soil samples to a depth of 60 cm were obtained from each quadrat and bulked for laboratory analysis: particle size distribution (% sand, silt, clay) was obtained by the hydrometer method (Bouyoucos 1962); bulk density in steel cores of volume 550 cm^3, and field moisture, from weight of oven-dry samples; organic matter by the Walkley–Black method (Walkley and Black 1934); chloride content by $AgNO_3$ titration method (USDA 1969). Exchangeable cations were extracted in 1 N ammonium acetate at pH 7 from which the concentrations of potassium, magnesium and calcium were determined by atomic absorption and sodium by flame photometry (Isaac and Korber 1971); cation exchange capacity was obtained as the summation of the exchangeable cations and exchange acidity. Exchangeable acidity was extracted with barium acetate and titration with NaOH (Jackson 1962). Carbonate was determined by the Bromo Thymol Blue indicator titration method. Root content was determined by passing known weight of soil through a 2 mm sieve, weighing the roots retained in the sieve and expressing the weight as percentage of soil (Ukpong 1995a). Total salinity was measured at the water table in the swamp using a portable refractometer calibrated against a Bisset Berman salinometer. At the same sites pH measurements were obtained using a portable pH meter with glass electrode.

Synthesis of data

A hypothesis was formulated that the structural development of mangrove vegetation was influenced by variation in environmental properties. To test the hypothesis, multiple regression analysis was used to investigate statistically the primary relationship between each structural property of the vegetation and a series of measured environmental variables. Multicollinearity among the variables was eliminated using Hauser's (1974) criteria. The multiple linear equation was of the form:

$$Y = a + b_1x_1 + b_2x_2 + \ldots + b_nx_n + SE,$$

where Y = dependent (vegetation) variable; a = Y intercept, b = partial regression coefficient, X = independent variable (environment), and SE = standard error of estimate.

To enable the more important environmental variables that accounted for mangrove structure to be discerned, the environmental variables selected by the regression analysis were linked with the vegetation data using canonical correlation analysis (COR). This analysis was aimed at exposing the joint structures of the two data sets (ter Braak and Prentice 1988). The environmental variables, being positively skewed in their distributions were transformed to log10 in order to meet the requirements of normality for parametric statistics (Gregory 1974).

Results

Vegetation analysis

The mangrove swamp is dominated by *Nypa fruticans* (Table 1). *Nypa fruticans* appears to thrive best, initially on soft tidal mud which is converted to firmer soil as the rootmat becomes complex. *Rhizophora mangle* is associated with *Nypa* in the inner swamp while *R. racemosa*, with extensive prop roots are adapted to channel margins. *Avicennia africana* could be found in pure stands along channel margins although it dominates in the inner somewhat less inundated swamps. *Rhizophora racemosa* apparently tolerates salt more than the other species and is regarded as the pioneer colonizers of mudflats (Keay 1953). Generally tree height decreased from the channel inlands, correlating with decreasing crown cover and basal area. Three species (*Avicennia africana, Rhizophora mangle, R. racemosa*) clearly show dominance in terms of basal area (Table 1).

Table 1

Mensuration data of vegetation in fifteen 200 m² quadrats

Species	Frequency (%)	Density (stems/ha)	Mean coverage (%)	Mean tree height (m)	Mean basal area (m²/ha)
A Stratum					
Nypa fruticans	60.0	153	29.0	4.8	–
Rhizophora mangle	66.7	100	16.3	4.9	4.3
Rhizophora vinifera	44.7	87	18.7	5.8	–
Rhizophora racemosa	44.7	87	16.7	7.7	2.8
Avicennia africana	60.0	80	7.3	5.2	3.5
B Stratum					
Rhizophora mangle	66.7	237	26.3	–	0.8
Nypa fruticans	66.7	213	20.3	–	–
Rhizophora racemosa	53.3	307	13.3	–	0.8
Avicennia africana	53.3	146	15.0	–	1.2
Conocarpus erectus	40.0	113	14.7	–	0.3
Phoenix reclinata	33.0	47	8.2	–	0.3
C Stratum					
Mangrove saplings	93.3	393	0.3	–	
Hypa fruticans	80.0	300	0.8	–	
Raphia spp.	53.3	200	0.6	–	
Conocarpus erectus	46.7	120	0.2	–	
Phoenix reclinata	46.7	120	0.2	–	
Vassia cuspidata	33.3	46	0.2	–	
Acrostichum aureum	26.7	144	0.5	–	

In the B stratum there was the expected increase in stem density, usually associated with understorey vegetation. *R. mangle* was dominant although *R. racemosa* had the highest density on account of fringing the creeks in almost pure stand. Inland, *Phoenix reclinata, Conocarpus erectus* and *Avicennia africana* were associated in mixed stands. The importance of mangrove and *Nypa* saplings in the C stratum was obvious: these species respond to dynamic tide transport due to buoyancy of their propagules. The occurrence of ferns, grasses and sedges (*Acrostichum aureum, Vossia cuspidata*, etc.) contrasts with the open ground layer often reported for littoral swamps (Giglioli and Thornton 1965).

Environmental characteristics

Thirteen environmental variables were measured and their variability assessed using the coefficient of variation (Table 2). The mangrove substrate was loamy in texture with low variability of the particle size fractions, indicating uniform sedimentation from similar sources. Bulk density

Table 2

Summary of environmental data in fifteen 200 m^2 quadrates

Variable	Mean	Standard deviation	Coefficient of variation
Sand (%)	35.60	4.80	13.4
Silt (%)	43.20	9.20	21.2
Clay (%)	21.20	3.50	16.5
Bulk density (g cm^{-3})	0.75	0.16	21.3
Field moisture (%)	125.80	19.60	15.6
Organic matter (%)	6.22	0.90	14.5
Root content (%)	8.45	3.70	43.8
Salinity (soil water %)	2.91	1.60	54.9
Chloride content (soil %)	2.05	0.65	31.7
Carbonate (g/100 g)	7.20	2.50	34.7
Exchangeable acidity (me/100 g)	3.2	1.10	34.3
pH (field moist)	6.1	0.14	2.3
Cation exchange capacity (CEC) (me/100 g)	42.8	3.64	8.5

increased with sand content of soils while field moisture decreased with an increase in sand content. pH values indicated increasing alkalinity in *Avicennia* sp. stands than in *Rhizophora* spp. stands. The average field moist pH value stood at 6.1.

Laboratory determined chloride content of soils was lower than field soil water salinity. However, variability in salinity could be accounted for by freshwater inputs from upland streams, distance from ocean tides (Ukpong 1991) and subsurface seepage of freshwater across the mangrove high forest ecotone (Semeniuk 1983). The high values of organic matter showed a correlation with the fibrous root content of soils. Both values decreased with soil depth and were reflected in the peaty nature of the mangrove soils.

The soils had a large sink for cations as indicated in the high cation exchange capacity values.

Effect of environmental factors on vegetation structure

An attempt was made using multiple regression analysis to discern the environmental factors that account for variation in mangrove vegetation structure. The multiple regression utilised stepwise elimination procedures to develop predictive models for vegetation response to the environment. As a search procedure, the stepwise technique identifies those independent (environmental) variables having the strongest relationship with the dependent (vegetation) variables. The results are shown in Table 3. All the regressions presented have a multiple coefficient of determination (R^2) of 0.55 and higher. Since (R^2) is equal to the percentage of variation which the multiple regression is accountable for, i.e. the level of explanation, it follows that all the regression equations account for 55% or above of the

Table 3

Regression models for vegetation structure determinants in the mangrove swamps

Tree density	6.02 + 0.38 SAL – 0.34 BD + 2.51 OM ± 23.4% (R^2 = 58.8%)
Tree height	–12.44 + 0.78 SAN – 0.46 SAL + 0.37 BD ± 20.5% (R^2 = 66.3%)
Basal area	0.51 + 0.18 SAL – 0.11 CEC + 0.31 SAN + 0.07 OM ± 20.4% (R^2 = 84.3%)
Cover	90.20 – 0.62 FM – 0.24 SAL – 0.15 SI ± 26.4% (R^2 = 76.5%)
Seedling density	53.41 + 1.77 SI + 0.84 SAN – 0.21 SAL ± 12.6% (R^2 = 84.2%)

Where SAL = salinity, BD = bulk density, OM = organic matter, SAN = sand, CEC = cation exchange capacity, FM = Field moisture, SI = silt

Table 4

Percentage contribution of the independent (environmental) variables to the total variance of the regression equations

Vegetation properties	% Contribution of independent variables							Total vari-ance %
	SAL	SAN	BD	OM	CEC	FM	SI	
Tree density	41.2***		11.4*	6.2*	–	–	–	58.8
Tree height	20.5**	32.7**	1.7**	–	–	–	–	66.3
Basal area	54.3***	10.3*	–	5.5**	15.2**	–	–	84.3
Cover	18.2**	–	–	–	–	48.3*	10.0*	76.5
Seedl. density	10.0*	14.0**	–	–	–	–	60.2***	84.2

Where SAL = salinity, SAN = sand, BD = Bulk density, OM = organic matter, CEC = cation exchange capacity, FM = field moisture, SL = silt. *** = Significant at the 0.1% level; ** = Significant at the 1% level; * = Significant at the 5% level

variance. Table 4 shows the percentage contribution of each independent variable to the total variance of the regression equations.

The most frequently occurring environmental parameter in the equations is salinity. Vegetation response to salinity is well marked particularly with respect to tree density and basal area where salinity accounts for 41.2% and 54.3% of the total variances for both equations as shown in Table 4. Substrate texture as represented by silt is important for the rooting and establishment of mangrove propagules. Silt contributes 60.2% to the total variance of 84.2% extracted for the seedling density equation. Besides salinity, sand texture was next in importance, retained in three equations but being particularly marked for the tree height equation where it accounted for 32.7% of the total variance of 66.3%. Field moisture was an important determinant of plant cover, contributing 48.3% to the total variance of 76.5%. Bulk density, organic matter and exchangeable cations were relatively less significant determinants of the mangrove structural characteristics (Table 4). Other environmental properties measured but not reflected in the regression equations were eliminated from the analysis on the basis of multicollinearity (Hauser 1974).

As a further step towards determining the effects of the measured environment on the vegetation, canonical correlation analysis (COR) was performed directly on the data. The matrix of environment and vegetation data was now described in terms of vectors with eigenvalues greater than 0.42 (which together explained 82.4% of the variance in the initial environment/vegetation data matrix). Primarily, this eigenvalue technique pre-

Table 5

Canonical factor structure of environment-vegetation relations (only weights > 0.03 on two correlations are reported)

Environmental weights		Vegetation weights	
r_1			
Sand	–435	Basal area (A)	+582
Salinity	–572	Seedling density	+433
Carbonate	–398	Tree density	+387
pH	–427	Coverage (B)	+425
Organic matter	+388	–	–350
r_2			
Root content	+422	Coverage (A)	+523
Field moisture	+625	Seedling density	+423
Bulk density	+342	Coverage (C)	+308
Silt	+511	Tree height	+411
CEC	–336	Density (C)	+394

(A) = A stratum; (B) = B stratum; (C) = C stratum

sented the canonical weights in terms of vectors. However, since the relationship of vectors to the initial data is known, the canonical weights have been expressed in terms of the environmental and vegetation properties as shown in Table 5. The first correlation (r_1 = 88.5%) and second correlation (r_2 = 76.2%) are significant with p less than 0.01. This implies that the environment and vegetation are related in two significant ways. Table 5 reports the canonical weights (+0.3) on the two significant correlations.

On the first correlation, environmental properties with large weights are salinity, sand and pH. The vegetation properties with large weights are basal area, seedling density and coverage. The positively weighted vegetation properties reflect high performance in relation to negatively weighted and diminishing importance of the environmental properties. The positive weights on the vegetation properties also indicate adaptation or tolerance, such that vegetation increases are not affected by hostile environmental conditions dominated by salinity, coarse substrates and increasing acidity.

On the second correlation, both environmental properties and vegetation properties are positively weighted showing that vegetation increases occur as the environmental properties are enhanced, particularly field moisture, silt content of substrates and root content. Most responsive to these environmental properties are seedling density, tree height and density of C stratum species. These are highly significant joint structures which explain structural variations in the mangrove vegetation.

Conclusion

Multiple regression analysis and canonical correlation analysis have been used to investigate possible environmental determinants of vegetation structure in mangrove forests. A previous applications of multiple regression was in the prediction of species distribution in relation to soil nutrients (Ukpong 1995b). Likewise, canonical correlation (COR) was applied to soil-species studies in estuarine mangroves (Ukpong 1994). However, inferences in these studies were not related to vegetation biomass characteristics. The present study has shown that soil water salinity, substrate textural characteristics, field moisture and bulk density of soils are important determinants of variations in tree basal area, tree coverage, tree height, seedling density and other structural characteristics of the mangrove forest. Primarily, the study is a possible input into mangrove ecosystem management and conservation procedure.

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