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The performance and distribution of species along soil salinity gradients of mangrove swamps in southeastern Nigeria

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Abstract

Based on periodic soil salinity measurements direct gradient analysis procedures were used to relate the performance and distribution of mangrove swamp species to salinity gradients. Variations in soil salinity were due to distance from the coast, tidal incursions and freshwater inputs. All overstorey species showed statistically significant negative correlations with salinity while most groundlayer species were positively correlated with the same factor. Based on ecological group classification, no species was found to occur on the highest values of soil salinity. There were overlapping range of occurrences and ecological optima for most species along the gradients.

Introduction

One of the most important stress factors in mangrove ecosystems is salinity. Several studies have therefore attempted to correlate salinity to the standing crop of vegetation and productivity (Adams 1963; Good 1972; Lugo 1980). Walsh (1974) however maintained that the correlations often fail to identify directly the differences in primary production of mangroves due to overlapping responses of species to salinity, moreso as mangrove swamps vary in terms of tidaland freshwater inputs, duration of dry spells and concentrations of soluble salts in the water and soil (Chapman 1976; Cintron *et al.* 1978). Hence the aim of this paper is to investigate the pattern of species performance and distribution along a soil salinity gradient of mangrove swamps in an ever-wet environment. The basic approach is a direct gradient analysis (the factor-gradient of Whittaker 1978) in which species are assigned to ecological groups according to their modalities on a factor gradient (Waring & Major 1964; Whittaker 1967).

Study area

The study area for this investigation is the river estuaries located in the southeastern coastal zone of Nigeria. Mangrove vegetation occurs in the Creek Town Creek/Calabar River swamp, Cross River swamp, Kwa Ibo River swamp and Imo River swamp (Fig. 1). The area has a humid tropical climate. The annual rainfall is 4021 mm with a peak in July-August. Least rainfall occurs in December-February. Although the swamps experience regular tidal inundations, there are fluctuations in salinity between the rainy and relatively drier months. Tidal amplitude is low the mean being 2.01 m at spring tides and 1.07 m at neap

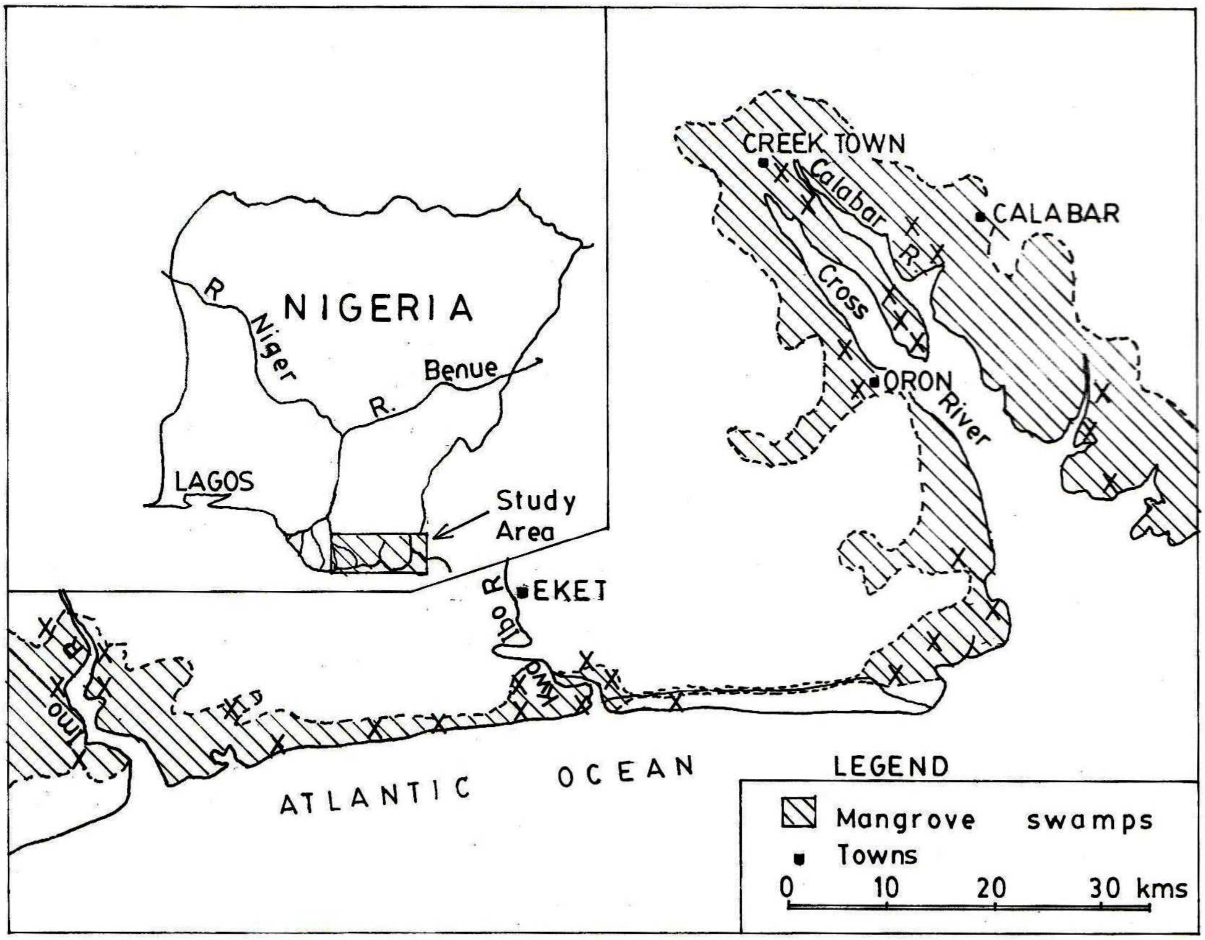

Fig. 1. Map of the study area showing location in Nigeria (insert). X, ...X indicate approximate position of transects.

tides. Species represented in the mangrove swamps include *Avicennia africana*, *Rhizophora racemosa*, *Rhizophora mangle*, *Rhizophora harrisonii* and *Laguncularia racemosa*. The non-mangrove associes include *Nypa fruticans*, *Raphia vinifera*, *Conocarpus erectus*, *Pandanus candelabrum*, *Phoenix reclinata*, *Acrostichum aureum* and *Vossia cuspidata* (Keay 1953; Savory 1953; Jackson 1964).

Methods

The vegetation and soils were sampled in eighty 10 × 10 m quadrats regularly spaced at 20 m intervals along transects established from the shores inland. From each quadrat, crown cover for trees taller that 3 m in height was determined by the crown-diameter method (Mueller-Dombois & Ellenberg 1974). Coverage values for understorey species (1–3 m tall) were by visual estimates in 25 m^2 subquadrats while those for the ground-layer (less than 1 m tall) were estimated in 1 × 1 m subplots. Also from each quadrat a swamp 'corer' (Giglioli & Thornton 1965) was used to obtain three soil samples at 20 cm intervals to a rooting depth of 60 cm. The soils were air-dried before laboratory analysis. Percentage salinity for each sample was determined from AgTu extracts and $AgNO_3$ (0.1 M) titration using potassium chromate as indicator, and calculated as total water soluble salts (chlorides + sulphates).

Results

Table 1 summarizes the results of soil analysis. The observed variations in soil salinity are due to the following factors:

1) Distance from the coast and tidal influence

Table 1. Ranges, means and SD for percentage soil salinity in four swamps (values are for a rooting depth of 0–60 cm).

Swamp	Range	Mean ± SD
Creek Town Creek/ Calabar River (15)*		
November 1986	3.2–3.8	3.4 ± 0.2
January 1987	3.6–4.2	3.8 ± 0.4
August 1987	0.2–1.5	0.5 ± 0.6
Cross River Swamp (21)*		
December 1986	4.9–6.8	6.1 ± 0.4
February 1987	3.6–4.5	4.0 ± 0.3
May 1987	0.8–2.4	1.2 ± 0.6
Kwa Ibo River swamp (21)*		
December 1985	5.6–6.2	5.9 ± 0.5
April 1986	3.1–4.5	3.9 ± 0.8
August 1987	0.6–2.6	1.8 ± 0.6
Imo River swamp (20)*		
February 1986	5.6–6.8	5.8 ± 1.3
May 1987	2.2–4.5	3.8 ± 0.9
Coastal beachridge (3)*		
January 1986	6.4–6.7	6.6 ± 0.2
August 1987	0.8–3.1	2.7 ± 0.5

* Parentheses indicate number of samples for each swamp.

– swamps located near the coast are inundated by ocean tides (Fig. 1). Hence salinity is high for the coastal beachridge soils, ranging from 0.8% to 6.7%. High salinities also characterise the lower Cross River swamp (0.8% to 6.8%), the Imo River swamp (2.2% to 6.8%) and the Kwa Ibo River swamp (0.6% to 6.2%). The lowest values (0.2% to 4.2%) occur in the Creek Town Creek/ Calabar River swamp which is located about 20 km from the coast.

2) Freshwater inputs – periodic salinity values indicate the influence of freshwater inputs e.g. rainfall and runoff from upland areas. In all swamps, mean soil salinities are lowest in August, which is the peak of the rainy period. The values range from 0.5 ± 0.6% in the Creek Town Creek/ Calabar River swamp to 2.7 ± 0.5% in the coastal beachridge. Highest salinities occur in the relatively drier months between November and February, ranging from 3.4 ± 0.2% for November in the Creek Town Creek/Calabar River swamp to 6.6 ± 0.2% for January in the coastal beachridge. Salt pans were characteristic of the beachridge soils between the 40–60 cm depth in January.

The coastal beachridge does not support extensive mangrove growth since it is erosional and affected by Atlantic storm waves. Strand forest species e.g. *Ipomoea cairica*, *Sesuvium portulacastrum*, *Triumfetta rhomboideae*, *Drepanocarpus lunatus* and *Acrostichum aureum* occur abundantly on sandy substrates together with shrubby *Rhizophora racemosa* and *Avicennia africana* which never achieve tree status. The species *D. lunatus*, *T. rhomboideae*, and *A. aureum* also occur up-river in fresh/brackish water zones but are more abundant near the coastal sands where there is little competition from such versatile species as *Nypa fruticans* and *Raphia vinifera*. The estuarine swamps, being sheltered from direct ocean waves by spits and bars across the estuaries are accreative. Hence the swamps achieve a higher structural complexity than the coastal beachridge, and contain, in addition to the mangroves, several highforest invaders of the tidal zone e.g. *Raphia vinifera*, *Vossia cuspidata*, *Acutas afer* and *Selaginella* spp. consequent to the low wave energy regime, high annual rainfall (about 4021 mm) and high freshwater inputs. Therefore apart from salinity which shows marked spatial and seasonal variations, the structural complexity of estuarine swamps relate to intensity of wave action and rainfall.

The correlations between species and soil salinity are shown in Table 2. Only species with frequency of occurrence of 4% and above in the sampled quadrats are included. The understorey (B stratum) mangroves which were represented in the A stratum had closely similar correlation coefficients to the A stratum dominants and so were excluded from the table, on account of having similar distributional patterns. All mangrove species e.g. *Avicennia africana*, *Rhizophora racemosa* and *Rhizophora harrisonii* are negatively correlated with soil salinity at statistically significant levels. These indicate that mangroves are facultative or salt tolerant on the basis of morphological and physiological adaptations. The level of adaptation varies between species. Species which are highly correlated with salinity e.g. *Avicennia africana* ($r = -0.67$) and *Rhizophora racemosa* ($r = -0.69$) are most frequently found along shore

Table 2. Ranges, means and SD for coverage values of selected species (frequency ⩾4.0%) and the product-moment correlations between these values and soil salinity.

Species		Coverage (%)		Correlation Coefficient (r)
		Range	Mean ± SD	
Avicennia africana	(A)	5.5–98.5	22.9 ± 19.4	– 0.67**
Rhizophora mangle	(A)	5.0–80.4	12.6 ± 10.2	– 0.41*
Rhizophora racemosa	(A)	4.5–82.5	12.1 ± 9.6	– 0.69**
Nypa fruticans	(A)	4.0–96.5	15.9 ± 10.8	– 0.59**
Raphia vinifera	(A)	1.5–77.2	4.3 ± 3.6	– 0.61**
Rhizophora harrisonii	(A)	2.5–33.4	3.8 ± 4.2	– 0.48*
Laguncularia racemosa	(A)[a]	0.4– 1.6	0.7 ± 0.3	– 0.39*
Conocarpus erectus	(B)	0.8– 2.6	1.2 ± 0.8	– 0.32
Pandanus candelabrum	(B)	0.6– 3.8	1.4 ± 1.2	0.28
Phoenix reclinata	(B)	0.5– 1.8	0.9 ± 0.6	0.26
Triumfetta rhomboideae	(C)	0.5– 2.7	0.9 ± 1.5	0.42*
Acrostichum aureum	(C)	4.0–14.3	6.6 ± 4.8	0.65**
Sesuvium portulacastrum	(C)	3.5–12.0	8.4 ± 2.2	0.57**
Vossia cuspidata	(C)	2.5– 6.4	3.2 ± 2.4	– 0.43*
Selaginella spp.	(C)	0.5– 2.2	0.6 ± 0.9	– 0.24

** significant at the 1% level
* significant at the 5% level
A = A stratum; B = B stratum; C = C stratum,
a = Low frequency of occurrence 3.8%

margins while species with lower levels of correlation e.g. *Rhizophora mangle* (r = – 0.41) and *Laguncularia racemosa* (r = – 0.39) occur most frequently in the inner somewhat less inundated swamps. It is inferred that *Avicennia africana* and *Rhizophora racemosa* are more adapted to saline conditions associated with regular tidal inundations than *Rhizophora mangle* and *Laguncularia racemosa* which occur in saline but irregularly flooded areas.

Among the non-mangroves that occur most frequently in the tidal swamps, *Nypa fruticans*, *Raphia vinifera*, *Conocarpus erectus* and *Vossia cuspidata* are negatively correlated with salinity and display facultative tendencies similar to the true mangrove species. These indicate a high level of adaptation particularly with respect to *Raphia vinifera* and *Vossia cuspidata* which also occur in upland freshwater areas. However, certain non-mangroves e.g. *Acrostichum aureum*, *Phoenix reclinata*, *Sesuvium portulacastrum*, *Triumfetta rhomboideae* and *Pandanus candelabrum* are positively correlated with salinity. Since it is unlikely that species performance will increase with increasing salinities, the positive correlations indicate the intensitivity of the species to the salinity range within which they occur.

From the correlations obtained, three groups of species relationships to salinity were apparent; (a) negative relationships of true mangroves to salinity; (b) negative relationships of non-mangroves to salinity and (c) positive relationships of non-mangrove beachridge strand species to salinity. The last group occur on the most consistently saline substrates of the beachridge sands, affected by direct ocean tides while the former two groups are associated with estuarine tides. Since some species of the coastal beachridge also occur up-river within the estuaries, the last group represents species of very wide ecological amplitudes.

The modalities of species on soil salinity gradients are presented in Fig. 2 and Fig. 3. The mangroves and associes obviously share a niche attribute of tolerance for changing salinities. However each species also has special niche relations to a particular range of the factor.

In the A stratum (Fig. 2), *Rhizophora racemosa*

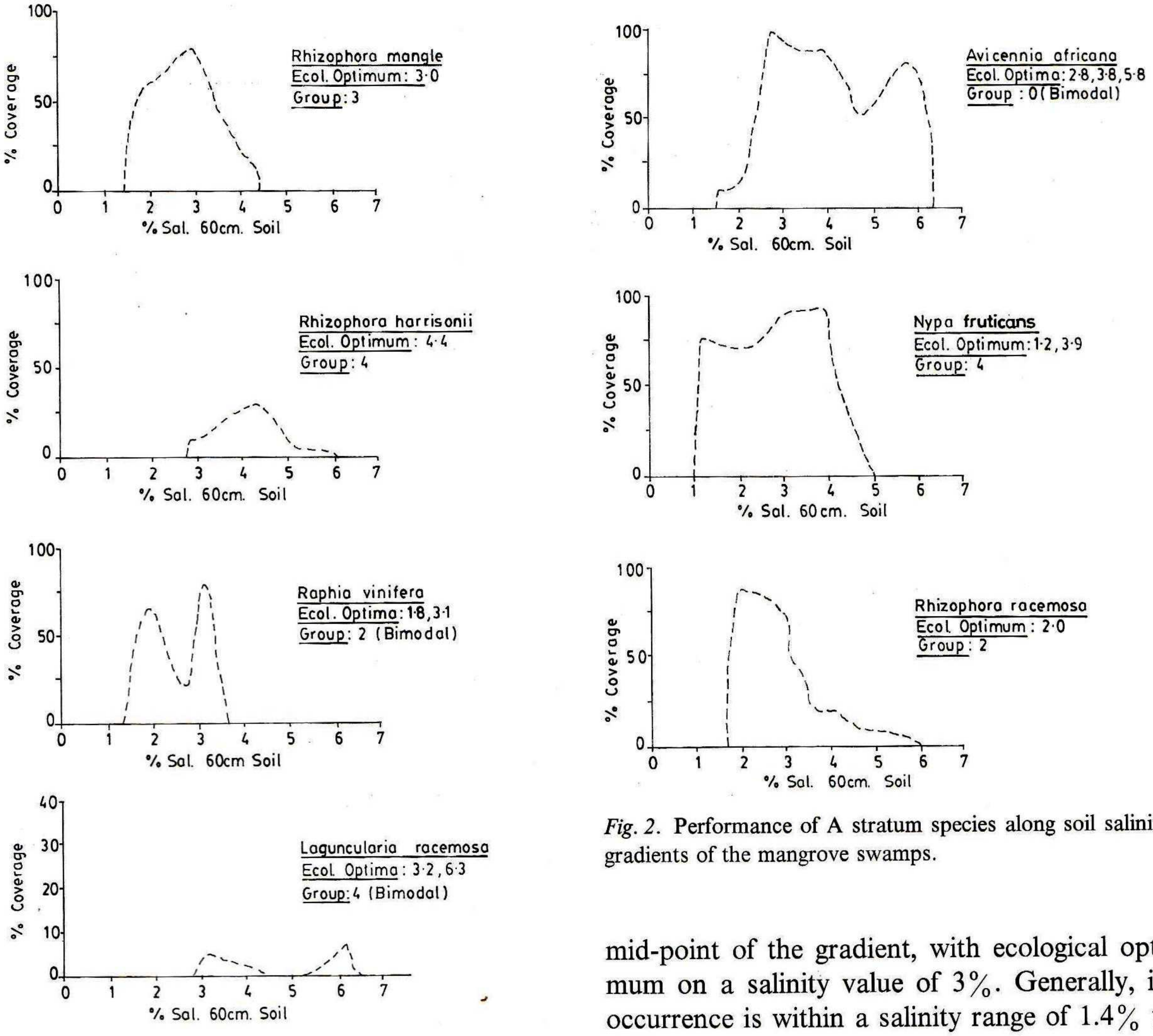

Fig. 2. Performance of A stratum species along soil salinity gradients of the mangrove swamps.

and *Raphia vinifera* belong to Ecological Group 2 (see Appendix). Both species have similar occurrences under the most nearly limiting conditions of salinity. Although *Raphia* is bimodal, the first ecological optimum on a salinity value of 1.8% is closely similar to the 2% observed for *Rhizophora racemosa*. The second ecological optimum for *Raphia* (3.1%) indicate the level of adaptation achieved by this species in the mangrove swamps. *Rhizophora racemosa* however has a wider ecological amplitude within a salinity range of 1.7% to 5.9% while *Raphia*, being a freshwater invader of the swamps occurs within a narrower range of 1.3% to 3.6%.

Rhizophora mangle belongs to Ecological Group 3 since its dominance is restricted to the mid-point of the gradient, with ecological optimum on a salinity value of 3%. Generally, its occurrence is within a salinity range of 1.4% to 4.4%.

Nypa fruticans and *Rhizophora harrisonii* belong to Ecological Group 4 since they dominate where salt concentrations appear to be in plentiful supply. *Nypa fruticans* occurs within a salinity range of 1.0% to 5.1% and achieves ecological optima on values of 1.2% and 3.9%. *Rhizophora harrisonii* occurs within a salinity range of 2.7% to 6.2% with an optimum on 4.4%. *Nypa fruticans* is bimodal with optima in the brackish and saline zones while *Rhizophora harrisonii* is basically a saline water species.

Avicennia africana dominates within a salinity range of 1.5% to 6.3%. The three ecological optima on values of 2.8%, 3.8% and 5.8% indicate that the species has a very wide amplitude and is indifferent to the salinity factor (Ecological

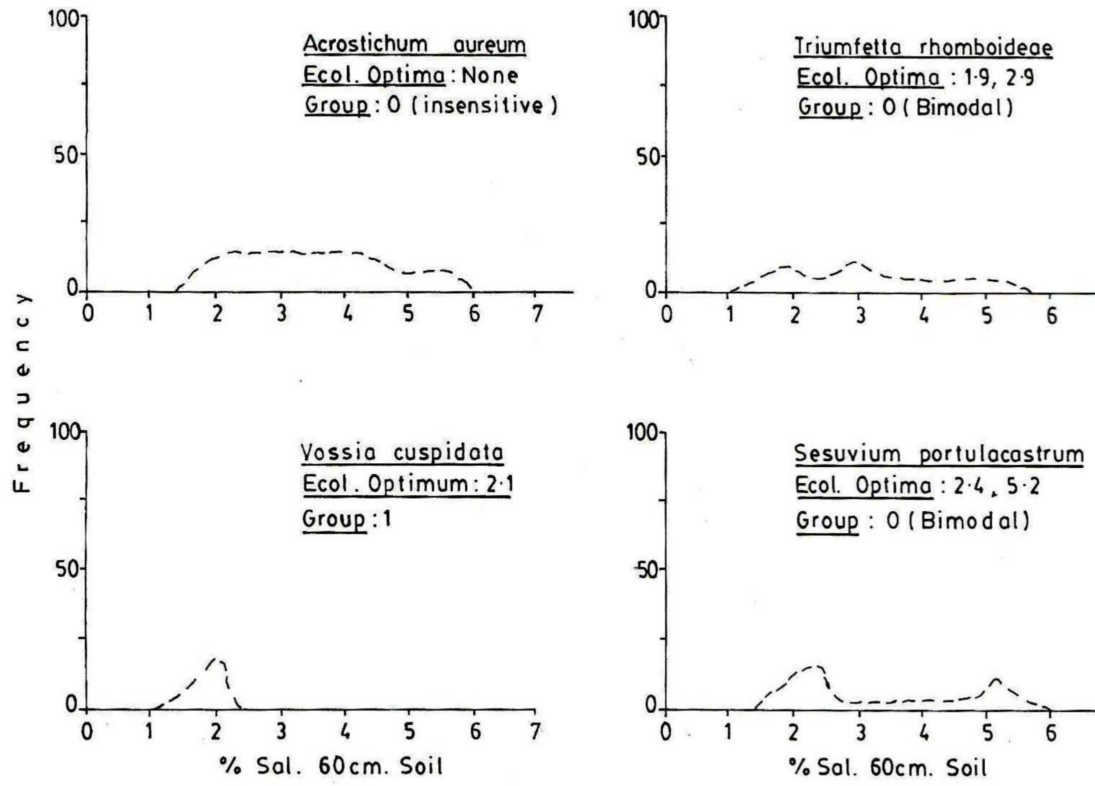

Fig. 3. Distribution of groundlayer species along soil salinity gradients of the mangrove swamps.

Group 0). This confirms observations by Jackson (1964) that *Avicennia africana* is often associated with higher salinities than most mangrove species along the Nigerian shoreline.

Laguncularia racemosa belongs to Ecological Group 4, since it dominates where salt concentrations are pleniful. The species is bimodal, with ecological optima on salinity values of 3.2‰ and 6.3‰. Occurrences were observed within a salinity range of 2.8‰ to 6.6‰, mostly along interriverine creeks behind the coastal beachridges. Being shrubby, it had very low crown cover and barely achieved tree status.

Most groundlayer species belong to Ecological Group 0. These are insensitive species with wide ecological amplitudes on the salinity gradient (Fig. 3). *Acrostichum aureum* occurs within a salinity range of 1.4‰ to 6.0‰ with no clearly defined ecological optimum. *Triumfetta rhomboideae* occurs within a range of 1.0‰ to 5.6‰ and is bimodal with optima on 1.9‰ and 2.9‰. *Sesuvium portulacastrum* is bimodal with ecological optima on salinity values of 2.4‰ and 5.2‰ found within a range of 1.4‰ to 6.0‰.

Vossia cuspidata belongs to Ecological Group 1, since it occurs exclusively under the most nearly limiting conditions of salinity in the swamps. Its occurrence is within the salinity range of 1.0‰ to 2.3‰, with an optimum on 2.1‰. This reflects the fact that *Vossia cuspidata* is basically a freshwater species that has acquired greater competitive ability due to large freshwater inputs and the consequent seasonal variations in salinity.

There are overlapping tolerances of mangrove swamps species to salinity. Also, species distribution modes appear to reflect a temporal transition along gradients from freshwater/brackish zones to the saline zone. This observation is supported by field observations in other estuarine and mangrove swamp forests. For instance, the vegetation communities described by Fagbami *et al.* (1988) for the Niger delta (immediately to the west of the present study area) consisted of species within three overlapping communities, namely (a) freshwater community in which *Raphia* spp. and *Acrostichum aureum* were represented; (b) saline/freshwater community in which *Avicennia africana* of *Acrostichum aureum* were represented and; (c) salt tolerant plants consisting of mangrove forest, coastal marsh and fern colony. Species populations within these communities reflect their level of adaptation to salinity along a gradient from the freshwater/brackish up-river areas, through brackish/saline estuarine swamps to saline coastal areas.

Conclusion

Of the eleven species commonly encountered in the mangrove swamps in southeastern Nigeria, none was found to dominate almost exclusively at the highest values of salinity along the gradients. *Laguncularia racemosa* occurs at very high salinities in depressions behind the coastal beachridges but this is not an exclusive situation; at lower salinities, its occurrence overlapped with other mangrove species, *Avicennia africana* has the widest ecological and sociological amplitude in the A stratum. In the groundlayer *Acrostichum aureum*, *Triumfetta rhomboideae* and *Sesuvium portulacastrum* have wide amplitudes, similar to *Avicennia africana*. Although some species may be confined to certain salinity ranges, there are also overlapping ecological optima along the gradient. However, considering that salinity is a stress factor, each ecological optimum indicates a salinity value on which a species achieves the highest level of competition and adaptation such that other species are (theoretically) excluded from that niche.

Acknowledgements

Mangrove species in the swamps were identified by Keay (1953) and Savory (1953).

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Appendix

Characteristics of ecological species groups.

Group	General characteristics
1.	Dominant species occurring almost exclusively under the most nearly limiting conditions of the environment or factor.
2.	Species of similar occurrence but with wider amplitude than those of Group 1.

3. Species found at the mid-point of the factor gradient.
4. Species which dominate where the factor in consideration is in plentiful supply.
5. Species occurring almost exclusively at the highest values of the factor along the grandient.
0. Indifferent species with a very wide amplitude.