

Forest structure and species distribution along soil salinity and pH gradient in mangrove swamps of the Sundarbans

HEMA JOSHI* & M. GHOSE

Agricultural Science Unit, Indian Statistical Institute, 203 B.T. Road, Kolkata 700 108, India

Abstract: An analysis has been made in the Sundarbans mangroves to relate the community structure and distribution of species with soil salinity and pH gradients. Soil salinity (13.0 to 31.2 ppt) decreased with increasing distance from the tidal coast but no such trend was noticed in soil pH (7.0 to 7.9). Frequency of tidal inundation seemed to affect soil salinity. *Acanthus ilicifolius*, *Avicennia alba* and *A. marina* dominate the sites having regular diurnal tidal inundation. Maximum complexity index was noted on the least saline zone. Ecological group classification indicates that *Avicennia marina* and *A. officinalis* can tolerate wide range of soil salinity while *Aegiceras corniculatum*, *Ceriops decandra*, *Dalbergia spinosa*, *Derris trifoliata* and *Excoecaria agallocha* are restricted to low salinity areas. Most species had an optimum pH range except *Avicennia marina*, which occurred in varied pH conditions. *Acanthus ilicifolius* was relatively insensitive to pH and salinity gradient due to its wide ecological amplitudes.

Resumen: Se llevó a cabo un análisis en los manglares Sundarbans con el fin de relacionar la estructura de la comunidad y la distribución de especies con gradientes de salinidad del suelo y pH. La salinidad del suelo (13.0 a 31.2 ppt) decreció conforme aumentó la distancia desde la costa mareal, pero no se observó un tendencia similar para el pH del suelo (7.0 a 7.9). La frecuencia de inundaciones por mareas pareció afectar la salinidad del suelo. *Acanthus ilicifolius*, *Avicennia alba* y *A. marina* dominan los sitios inundados regularmente por la marea diurna. El índice de complejidad alcanzó su máximo en la zona menos salina. La clasificación de grupos ecológicos indica que *Avicennia marina* y *A. officinalis* pueden tolerar intervalos amplios de salinidad del suelo, mientras que *Aegiceras corniculatum*, *Ceriops decandra*, *Dalbergia spinosa*, *Derris trifoliata* y *Excoecaria agallocha* están restringidas a áreas de baja salinidad. La mayoría de las especies tuvieron un intervalo óptimo de pH excepto *Avicennia marina*, la cual se presenta en condiciones de pH muy variadas. *Acanthus ilicifolius* resultó ser relativamente insensible al pH y al gradiente de salinidad debido a su gran amplitud ecológica.

Resumo: Nos mangais de Sundarbans foi efectuada uma análise a fim de relacionar a estrutura da comunidade e a distribuição das espécies com os gradientes de salinidade e pH do solo. A salinidade do solo (13,0 a 31,2 ppt) decresceu com o aumento da distância da linha de marés se bem que esta tendência não tenha sido registrada no pH do solo (7.0 a 7.9). A frequência da inundaçao da maré parece afectar a salinidade do solo. A *Acanthus ilicifolius*, *Avicennia alba* e *A. marina* dominou as estações onde se verifica uma inundaçao diurna regular da maré. O valor máximo do índice de complexidade foi registrado na zona de menor salinidade. A classificação dos grupos ecológicos indica que a *Avicennia marina* e *A. officinalis* podem tolerar uma gama larga de salinidade do solo enquanto que a *Aegiceras corniculatum*, *Ceriops decandra*, *Dalbergia spinosa*, *Derris trifoliata* e *Excoecaria agallocha* estão restritas a áreas de baixa salinidade. A maior parte das espécies têm um intervalo óptimo de pH excepto a *Avicennia marina*, que ocorre em várias condições de pH. A *Acanthus ilicifolius* era relativamente insensível ao gradiente de pH e de salinidade devido à sua larga amplitude ecológica.

*Corresponding Author

Key words: Complexity index, gradient analysis, mangroves, soil pH, soil salinity.

Introduction

Mangroves are woody plants, which grow in loose wet soils of brackish-to-saline estuaries and shorelines in the tropics and subtropics. In India only 8% coastline is occupied by mangals (Saenger *et al.* 1983). Indian Sundarbans is covering an area of about 4266.6 sq. km (Banerjee 1964) and later the Directorate of Forest, Government of West Bengal in 1973 estimated the total area of mangroves in Indian Sundarbans at about 4263 sq. km. However, on the basis of satellite imagery the Forest Survey of India (1999) estimated the area of Indian Sundarbans as 2125 sq. km, excluding the anastomosing network of creeks and backwaters, which are part and parcel of mangrove ecosystem. Mangrove communities often exhibit distinct patterns of species distribution (Chapman 1976; Lugo & Snedaker 1974; Macnae 1968; Tomlinson 1986). Waring & Major (1964) reported that a complex of environmental factors determines the actual distribution of plants in nature, although each plant has a certain tolerance for each factor. Since the mangrove habitat is basically saline, several studies have attempted to correlate salinity with the standing crop of vegetation and productivity (Chen & Twilley 1998, 1999; Lugo 1980; Mall *et al.* 1987; Ukpong 1991). Local patterns of tidal inundation further influence soil characteristics that control species zonation of mangrove wetlands (Banerjee 1987; Naidoo 1980; Saha & Choudhury 1995; Walsh 1974; Watson 1928). Based on frequency of tidal inundation, mangrove forests have been classified into five types *viz.* overwash, fringe, riverine, basin and dwarf forests (Lugo & Snedaker 1974). Patches and zones of forest composition result from complex gradients of hydroperiod and soil conditions, such as nutrient limitation (Boto & Wellington 1984; Feller 1995; Ukpong 1998) and abiotic stressors as salinity and sulfide (Cintrón *et al.* 1978; Lugo 1978; Mckee 1993; Nickerson & Thibodeau 1985). The distribution of mangrove species, in many cases, can be explained primarily by salinity gradients (Ball 1998; Ukpong 1994).

The pH of a soil significantly affects plant growth, primarily due to the change in availability of both essential elements such as phosphorus (P), as well as non-essential elements such as aluminium (Al) that can be toxic to plants at elevated concentrations (Black 1993; Slattery *et al.* 1999; Woodruff 1967). The importance of both soil salinity and pH for the growth of mangroves has been emphasized by Wakushima *et al.* (1994a, 1994b). Sundarbans shelters one of the most important mangrove communities of the world. A few published works deal with the community structure of this forest (Joshi & Ghose 2002; Matilal *et al.* 1986; Saha & Choudhury 1995). In this paper, we report on the structure and species distribution of mangroves in Lothian Island of the Sundarbans in relation to some physico-chemical parameters of the substratum. The aim of this paper is to specify the location of individual mangrove species along gradients of soil salinity and pH.

Study area

The present study was undertaken at Lothian Island of the western Sundarbans from November 1997 to February 2000. It is a small island of approximately 38 sq. km area, which extends from 88°18'10" E to 88°21'30" E longitude and 21°32'50" N to 21°42'30" N latitude. The island is regularly inundated by diurnal tide up to a certain distance from the northern coast. A North-South spinal road approaches from northern coast upto nearly middle of the island. Our study sites were selected on either sides of the spinal road.

Methods

Vegetation and soil sampling

Vegetation was studied and soil samples were collected from eight sites selected at a distance of 100 m away on either side of the spinal road. Site I to V were located at distances of 50 m, 500 m, 550 m, 750 m and 850 m from the northern coast. Site VI and VII were equidistant from the northern

coast, *i.e.*, at 1644 m and were selected on both the sides of the spinal road. Site VIII was situated at 2378 m from the northern coast of the island. These distances were selected at random using random number table. At sites I to III – quadrats of 16 m x 12 m, at sites IV and V – 4 m x 16 m and at sites VI to VIII – 8 m x 16 m were further demarcated into smaller quadrats of 4 m x 4 m. In order to determine the optimum quadrat size, varied sizes were studied and the optimum size for sampling purpose was determined as 4 m x 16 m (Joshi & Ghose, unpublished). In each 4 m x 4 m quadrat, all the individual plants were identified and their number, diameter (at 1.3 m for trees and at half height for herbs and plants below 1.5 m), and heights (using meter tape or Suunto height meter) were recorded. The frequency of tidal inundation was also recorded in each site.

Three soil samples were collected from each site from a rooting depth of 15 cm in polythene bags and brought to the laboratory. The soils were air-dried, crushed using a pestle and mortar and then passed through a 10-mesh (2 mm) screen before analysis. The soil analysis was completed within two months after collection. pH was determined in 1:2.5 soil to water suspension using a pH meter (Jackson 1978). Electrical conductivity was determined in supernatant of 1:5 soil-water mixture using a Systronics conductivity meter, and was converted into salinity (ppt) following the equation:

$$\text{Salinity (ppt)} = 0.064 \times \text{EC} \times \frac{\% \text{ water in soil}}{100} \times 10$$

where EC = Electrical conductivity (m mho cm⁻¹)

Analysis of data

Differences in soil salinity and pH among eight sites were analysed by one way ANOVA (SPSS 7.5.1 1996) using data from three random samples within each site. Direct gradient analysis (Whittaker 1978) was done to relate species distribution along gradients of soil salinity and pH. Based on the results of gradient analysis, mangrove species were placed in one of the following six groups as suggested by Whittaker (1967):

(1) Species which dominate and occur almost exclusively under the most nearly limiting conditions of the factor.

(2) Species of similar occurrence but with wider amplitude than those of group 1.

(3) Species which are especially frequent near the mid-point along the factor gradient.

(4) Species which dominate on the gradient where the factor being considered is in plentiful supply.

(5) Species which occur almost exclusively at the highest values of the factor being considered.

(0) Species which are indifferent to the factor and have a very wide amplitude.

Various structural indices, such as specific density (no. ha⁻¹) and importance value index (IVI) were calculated using the standard methodology (Cintron & Schaeffer Novelli 1984). Complexity index (I_c), established by Pool *et al.* (1977), was calculated as I_c = number of species x density x basal area x mean height x 10⁻⁵.

Results and discussion

Soil pH and salinity

The average soil pH was slightly alkaline (7.53) ranging from 7.05 at site III to 7.89 at site V (Fig. 1). Similar results were also reported by Sah *et al.* (1985) and Pal *et al.* (1996) while working with some other mangrove soils of the Sundarbans. Soil pH had no uniform rise or fall with increasing distance from the tidal coast. Salinity ranged from 13.01 ppt at site VIII to 31.25 ppt at site II. There were significant differences among sites in soil salinity (F = 20.655, P ≤ 0.001) and pH

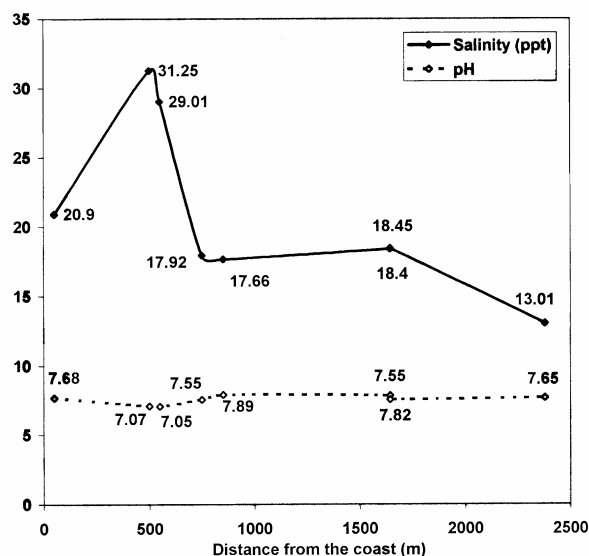


Fig. 1. Soil pH and salinity at different distances from the tidal coast during dry winter season.

($F = 76.139$, $P \leq 0.001$). Soil salinity decreased with increasing distance from the tidal coast. Naidoo & Raiman (1982) reported soil salinity to be related with extent of tidal inundation and seepage in the mangrove soils of Sipingo and Mgeni, South Africa. In the present study, sites I to VI were regularly inundated by diurnal tides and sites VII and VIII were inundated during spring tides. The duration of inundation was more in sites situated closer to the coast. The lower salinity value at site VIII is probably due to less frequency of tidal inundation.

Structure of mangrove forest

A total of ten species (8 obligate mangroves and 2 mangrove associates) were found in eight sites (Table 1). However, Banerjee *et al.* (1989) and Naskar & Guha Bakshi (1987) reported 37 obligate mangroves and 32 mangrove associates in the whole of Indian Sundarbans. With the exception of *Acanthus ilicifolius* (herb), *Aegialitis rotundifolia* (shrub) and *Derris trifoliata* (twiner), all are trees. *Avicennia alba* is more concentrated near the coast (4583 plants ha⁻¹) whereas *A. officinalis* at landward site (1016 plants ha⁻¹). Considerable density of *A. marina* occurs in almost all the sites, irrespective of increasing distance from the coast. Many new species exist at 2378 m away from the coast with varying densities (e.g. *Aegiceras corniculatum*, *Ceriops decandra*, *Dalbergia spinosa* and *Derris trifoliata*). *Acanthus ilicifolius* occurs, though in varied numbers, in all the sites. Specific density of *A. ilicifolius* was maximum in site III (133,229 plants ha⁻¹). Among tree species, the

maximum density occurs in *Aegiceras corniculatum* (15,938 plants ha⁻¹) in site VIII. The affinity between distance from the tidal coast and distribution of a particular species was reported by Joshi & Ghose (2002). Mangrove species respond differently to different tidal regimes. Saha & Choudhury (1995) reported that mangrove forest experiencing total diurnal inundation is dominated by *Avicennia alba* and *A. marina* while *Acanthus ilicifolius*, *Ceriops decandra* and *Excoecaria agallocha* dominate sites that are not completely inundated. Pal *et al.* (1996) reported that *Acanthus ilicifolius*, *Avicennia alba* and *A. officinalis* occur dominantly in soils with high salinity, and frequent and long duration tidal inundation in various islands of the Sundarbans. The present study also shows that *Acanthus ilicifolius*, *Avicennia alba* and *A. marina* dominate the site having regular diurnal tidal inundation.

Table 2 indicates that the forest is largely composed of small sized trees. *Avicennia marina* occupied the maximum basal area (1.62 m²). *Acanthus ilicifolius* had the highest importance value (118.0). Among tree species *Avicennia marina* got the highest importance value (85.4) followed by *A. alba* (28.4). The forest is largely dominated by *Avicennia marina* which pointing to its wide adaptability in different environments.

Complexity index (I_c) gives quantitative picture of the structural complexity of vegetation (Pool *et al.* 1977). The I_c values decreased upto site IV, and then increased gradually as the distance from the tidal coast increased (Table 3). The

Table 1. Specific density (no. ha⁻¹) of mangroves at eight sites in Lothian Island.

Species	SITES (Distance from the coast, m)							
	I (50)	II (500)	III (550)	IV (750)	V (850)	VI† (1644)	VII† (1644)	VIII (2378)
<i>Acanthus ilicifolius</i> L.	18021	36875	133229	16445	11719	3672	625	78
<i>Aegialitis rotundifolia</i> Roxb.	–	–	–	–	–	–	5000	625
<i>Aegiceras corniculatum</i> (L.) Blanco	–	–	–	–	–	–	–	15938
<i>Avicennia alba</i> Blume	4583	156	52	195	195	–	–	–
<i>Avicennia marina</i> (Forsk.) Vierh.	1146	4740	1771	3164	2734	7031	4453	–
<i>Avicennia officinalis</i> L.	–	104	–	–	–	–	–	1016
<i>Ceriops decandra</i> (Griff.) Ding Hou	–	–	–	–	–	–	–	6719
* <i>Dalbergia spinosa</i> Roxb.	–	–	–	–	–	–	–	78
* <i>Derris trifoliata</i> Lour.	–	–	–	–	–	–	–	33516
<i>Excoecaria agallocha</i> L.	–	–	–	–	–	–	–	78

* = Mangrove associate, † = Sites VI & VII are equidistant and were selected on both sides of spinal road.

Table 2. Structural characteristics of the species recorded from eight sites at Lothian; values are means \pm SD for DBH (cm) and height (m), and total basal area is the sum of individual basal areas (m²).

Species	Number of individuals	Mean DBH (cm)	Mean height (m)	Total basal area (m ²)	Importance value index (IVI)
<i>Acanthus ilicifolius</i>	4389	0.8 \pm 0.3	1.0 \pm 0.43	0.31	118.0
<i>Aegialitis rotundifolia</i>	72	1.3 \pm 0.6	0.8 \pm 0.55	0.01	8.5
<i>Aegiceras corniculatum</i>	204	2.9 \pm 0.8	4.2 \pm 0.69	0.15	12.0
<i>Avicennia alba</i>	102	7.2 \pm 4.3	6.2 \pm 2.31	0.57	28.4
<i>Avicennia marina</i>	445	4.8 \pm 3.9	4.1 \pm 2.37	1.62	85.4
<i>Avicennia officinalis</i>	15	8.7 \pm 4.7	5.7 \pm 2.5	0.11	7.7
<i>Ceriops decandra</i>	86	1.5 \pm 0.4	2.4 \pm 0.67	0.02	6.2
<i>Dalbergia spinosa</i>	1	2.5	7.8	0.001	0.6
<i>Derris trifoliata</i>	429	0.6 \pm 0.3	–	0.72	28.3
<i>Excoecaria agallocha</i>	1	16.0	7.4	0.02	4.8

Table 3. Complexity index of mangrove trees at different sites of Lothian Island. Values are means \pm SD for total density (number of individuals per hectare), total basal area (sum of individual basal areas calculated per hectare) and stand height. I_c = no. of species \times stand density \times stand basal areas \times stand height $\times 10^{-5}$.

Site (Plot area)	Number of species	Total density (no. ha ⁻¹)	Total basal area (m ²)	Stand height (m)	Complexity index (I_c)
I (192 m ²)	2	2865 \pm 2430	9.8 \pm 12.8	4.4 \pm 2.3	2.5
II (192 m ²)	3	1667 \pm 2662	4.2 \pm 3.7	8.0 \pm 5.3	1.7
III (192 m ²)	2	912 \pm 1216	7.6 \pm 8.1	8.8 \pm 3.4	1.2
IV (256 m ²)	2	1680 \pm 2099	6.6 \pm 7.1	4.9 \pm 0.2	1.1
V (256 m ²)	2	1465 \pm 1795	7.1 \pm 5.2	7.0 \pm 2.3	1.5
VI (128 m ²)	1	7031	10.1	3.1	2.2
VII (128 m ²)	2	4727 \pm 387	19.2 \pm 25.9	2.2 \pm 2.1	4.0
VIII (128 m ²)	6	4076 \pm 6339	5.7 \pm 6.6	4.8 \pm 2.5	6.8

maximum I_c value (6.8) at site VIII indicates the high density and high number of species in the that coincides with the lowest soil salinity (Fig. 1). On the contrary, the I_c values are lower at sites having high soil salinity. Generally mangrove vegetation is more luxuriant in soils with lower salinities (Kathiresan *et al.* 1996).

Species distribution and “ecological group” classification

The modalities of species on the soil salinity and pH gradient are presented in Figs. 2 & 3. They provide information on the ecological optimum and amplitude for each mangrove species relative to the others.

Fig. 2 shows that *Aegiceras corniculatum*, *Ceriops decandra*, *Dalbergia spinosa*, *Derris trifoliata* and *Excoecaria agallocha* belong to Ecological Group 1 occurring almost exclusively under the most limiting conditions (*i.e.*, lowest values) of salinity in the mangrove soils. All these species have ecological optima at salinity 13.01 ppt. *Aegialitis rotundifolia* belongs to Group 3 since it dominates at midpoint of the gradient and has ecological optima at 18.45 ppt. *Avicennia alba* also belongs to Group 3 and is bimodal with ecological optima at salinity values of 17.7 and 20.9 ppt. *Avicennia marina* and *A. officinalis* dominate where the salinity values are more (Group 4) but are not totally excluded from the sites where salinity is less pointing to their wide ecological amplitudes. *Avicennia marina* has ecological optima at salinity 18.4 and

20.9 ppt. *Avicennia officinalis* is also bimodal having ecological optima at salinity 13.01 and 31.25 ppt. *Acanthus ilicifolius* has the widest amplitude (17.66 to 29.01 ppt) and is relatively insensitive to the salinity gradient (Group 0).

Acanthus ilicifolius and *Avicennia* spp. have been reported to dominate in the soils with high salinity while *Aegiceras* sp. and *Excoecaria agallocha* in soils with low salinity (Matilal *et al.* 1986; Pal *et al.* 1996). Cintron *et al.* (1978) reported that salt-tolerant species like *Avicennia* could adjust to

about 90 ppt salinity (*i.e.*, about 2.5 times the concentration of seawater). Mangrove seedlings require low salinity (Hwang & Chen 2001; Smith *et al.* 1996) but their salt tolerance increases as they grow (Bhosale 1994; Kathiresan & Bingham 2001). The interspecific differences in salt tolerance reflect a physiological continuum ranging from moderately salt tolerant glycophytes to highly salt tolerant and apparently obligate halophytes (Ball 1996).

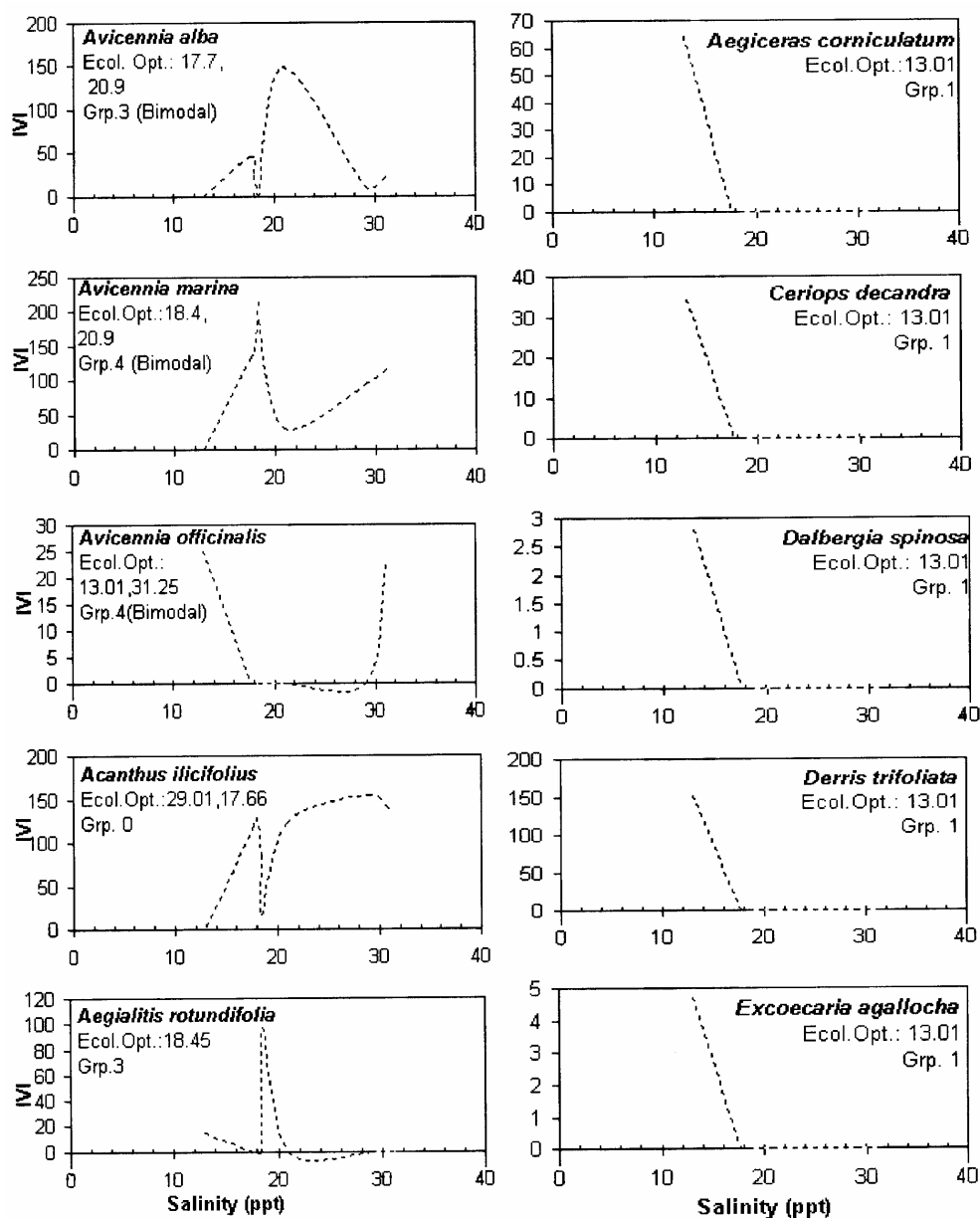


Fig. 2. Performance of different mangrove species along soil salinity gradient.

Fig. 3. shows the species performance on pH gradient. *A. officinalis* belongs to Ecological Group 2 with pH optima at 7.07 and 7.65 (Bimodal). *Aegialitis rotundifolia*, *Aegiceras corniculatum*, *Ceriops decandra*, *Excoecaria agallocha*, *Derris trifoliata* and *Dalbergia spinosa* belong to Group 3 since they dominate at about the midpoint of the gradient. These species are unimodal with optima

at pH 7.55 or 7.65. *Avicennia alba* also dominates at midpoint of the gradient (Group 3) and has two ecological optima although dominating particularly at pH 7.68. *Avicennia marina* belongs to Group 4 with peaks at pH 7.82 and 7.55. *Acanthus ilicifolius* (Group 0) is relatively insensitive to pH since it has the widest ecological amplitude with slight optima at pH 7.05, 7.68 and 7.89.

It has been stated that mangroves are naturally stressed ecosystems (Kennealy 1982). An ecological factor, which may be present in excessive or insufficient quantities, could be limiting to the distribution and composition of species. The species distribution may further be narrowed by competition or interaction with other species to a zone within its physiological tolerance of the factor

(Waring & Major 1964). Wakushima *et al.* (1994a, 1994b) suggested that soil pH and salinity in dry season are the important factors governing the zonal distribution of Japan and Thai mangroves. From the present observations, it is revealed that most of the species occupy a zone to which it is best adapted, however, there are overlapping occurrences of different species although with varying

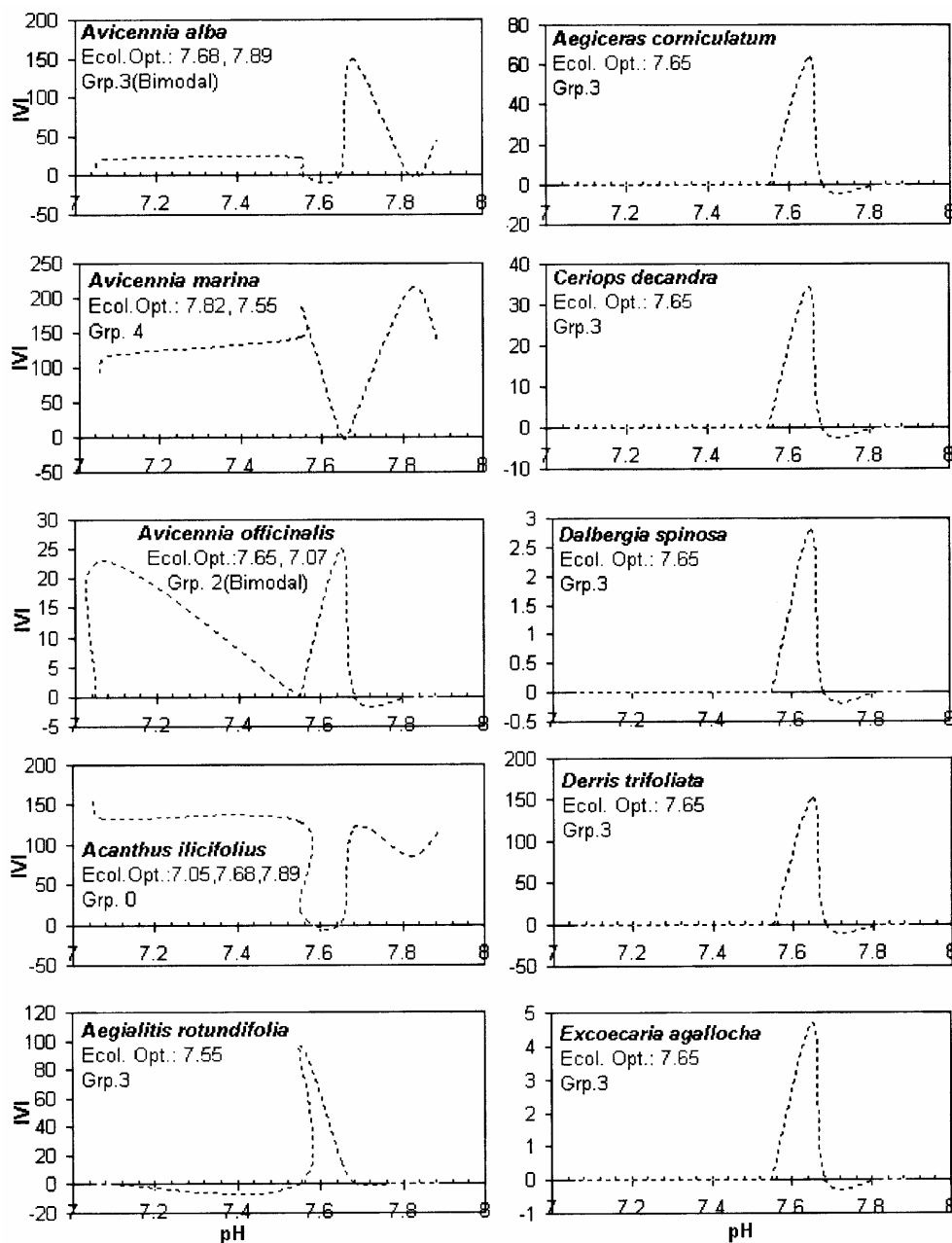


Fig. 3. Performance of different mangrove species along soil pH gradient.

ecological optima along salinity and pH gradients. The mangroves obviously share a niche attribute for these two factors in soil.

Conclusions

Soil salinity decreased with increasing distance from the tidal coast, although an initial increase was seen. Less frequency and duration of tidal inundation can be cited as the probable reason for low soil salinity at the landward sites. Sites having regular diurnal inundation are dominated by *Acanthus ilicifolius*, *Avicennia alba* and *A. marina*. There is no uniform rise or fall in pH with increasing distance from the tidal coast. Results of direct gradient analysis show that different mangrove species have different distributions along the soil salinity and pH gradient. Species like *Avicennia marina* and *A. officinalis* are found in wide ranges of soil salinity. *Aegiceras corniculatum*, *Ceriops decandra*, *Excoecaria agallocha* are restricted to the soil having low salinity. It seems that most mangrove species have an optimum pH range like terrestrial plants, but they can tolerate higher salinity. *Avicennia marina* occurred in varied pH conditions. *Acanthus ilicifolius* seems insensitive to these gradients because of wide ecological amplitudes. The complexity of vegetation increased with decrease in soil salinity.

Acknowledgements

We thank Professors S. Bandopadhyay and A. Choudhuri of Indian Statistical Institute, Kolkata for their help in sampling and statistical assistance. We are also thankful to the Conservator and Joint Director, Sundarbans Biosphere Reserve, and DFO, South 24 Parganas, West Bengal for the necessary permission and help they provided for the fieldwork. We thank the two anonymous reviewers for comments on earlier version of our manuscript. Last, but not the least, we thank the field assistants for their sincere help during the fieldwork.

References

- Ball, M.C. 1996. Comparative ecophysiology of mangrove forest and tropical lowland moist forest. pp. 461-469. In: S.S. Mulkey, R.L. Chazdon & A.O. Smith (eds.) *Tropical Forest Plant Ecophysiology*. Chapman and Hall, New York.
- Ball, M.C. 1998. Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River floodplain, northern Australia. *Global Ecology and Biogeography Letters* **7**: 73-82.
- Banerjee, A.K. 1964. *Forests of Sundarbans, Centenary Commemoration Volume*. Writer's Building, Kolkata, India.
- Banerjee, L.K. 1987. Ecological studies on the mangals in the Mahanadi estuarine-delta Orissa: India. *Tropical Ecology* **28**: 117-125.
- Banerjee, L.K., A.R.K. Sastry & M.P. Nayar. 1989. *Mangroves in India, Identification Manual*. Botanical Survey of India, Kolkata.
- Bhosale, L.J. 1994. Propagation techniques for regeneration of mangrove forests – A new asset. *Journal of Non-timber Forest Products* **1**: 119-122.
- Black, C.A. 1993. *Soil Fertility Evaluation and Control*. Lewis Publishers, Boca Raton, FL.
- Boto, K.G. & J.T. Wellington. 1984. Soil characteristics and nutrient status in a northern Australian mangrove forest. *Estuaries* **7**: 61-69.
- Chen, R. & R.R. Twilley. 1998. A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. *Journal of Ecology* **86**: 37-52.
- Chen, R. & R.R. Twilley. 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River estuary, Florida. *Estuaries* **22**: 955-970.
- Chapman, V.J. 1976. *Mangrove Vegetation*. J. Cramer, Vaduz, Germany.
- Cintron, G., A.E. Lugo, D.J. Pool & G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* **10**: 110-121.
- Cintron, G. & Y. Schaeffer-Novelli. 1984. Methods of studying mangrove structure. pp. 91-113. In: S.C. Snedaker & J.G. Snedaker (eds.) *The Mangrove Ecosystem: Research Methods*. UNESCO, Paris.
- Feller, I.C. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs* **54**: 477-505.
- Forest Survey of India. 1999. *The State of Forest Report*. Forest Survey of India, Ministry of Environment and Forests, Dehra Dun.
- Hwang, Y.H. & S.C. Chen. 2001. Effects of ammonium, phosphate and salinity on growth, gas exchange characteristics, and ionic contents of seedlings of mangrove *Kandelia candel* (L.) Druce. *Botanical Bulletin of Academia Sinica* **42**: 131-139.

- Jackson, M.L. 1978. *Soil Chemical Analysis*. Prentice Hall of India Pvt. Ltd., New Delhi.
- Joshi, H. & M. Ghose. 2002. Structural variability and biomass production of mangroves in Lothian Island of Sundarbans, India. pp. 146-158. In: S. Javed & A.G. de Soyza (eds.) *Research and Management Options for Mangrove and Saltmarsh Ecosystems*. ERWDA, Abu Dhabi, UAE.
- Kathiresan, K. & B.L. Bingham. 2001. Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* **40**: 81-251.
- Kathiresan, K., N. Rajendran & G. Thangadurai. 1996. Growth of mangrove seedlings in intertidal area of Vellar estuary southeast coast of India. *Indian Journal of Marine Sciences* **25**: 240-243.
- Kenneally, K.F. 1982. Mangroves of Western Australia. pp. 95-110. In: B.F. Clough (ed.) *Mangrove Ecosystem in Australia: Structure, Function and Management*. Australian Institute of Marine Sciences, Australia.
- Lugo, A.E. 1978. Stress and ecosystems. pp. 62-101. In: J.H. Thorp & J.W. Gibbons (eds.) *Energy and Environmental Stress*. DOE 771114. Department of Energy, Washington, D.C.
- Lugo, A.E. 1980. Mangrove ecosystems: sucessional or steady state? Tropical succession. *Biotropica* supplement **12**: 65-72.
- Lugo, A.E. & S.C. Snedaker. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* **5**: 39-64.
- Macnae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific Region. *Advances in Marine Biology* **6**: 72-270.
- Mall, L.P., V.P. Singh, A. Garge & S.M. Pathak. 1987. Ecological studies on mangrove forests of Ritchie's Archipelago in relation to substrata. *Tropical Ecology* **28**: 182-197.
- Matilal, S., B.B. Mukherjee, N. Chatterjee & M.D. Gupta. 1986. Studies on soil & vegetation of mangrove forests of Sundarbans. *Indian Journal of Marine Sciences* **15**: 181-184.
- Mckee, K.L. 1993. Soil physicochemical properties and mangrove species distribution – reciprocal effects? *Journal of Ecology* **81**: 477-487.
- Naidoo, G. 1980. Mangrove soils of the Beachwood area, Durban. *Journal of South African Botany* **46**: 293-304.
- Naidoo, G. & F. Raiman. 1982. Some physical and chemical properties of mangrove soils at Sipingo and Mgeni, Natal. *Journal of South African Botany* **48**: 85-90.
- Naskar, K.R. & D.N. Guha-Bakshi. 1987. *Mangrove Swamps of the Sundarbans: An Ecological Perspective*. Naya Prokash, Kolkata, India.
- Nickerson, N.H. & F.R. Thibodeau. 1985. Association between pore water sulfide concentrations and the distribution of mangroves. *Biogeochemistry* **1**: 183-192.
- Pal, D., A.K. Das, S.K. Gupta & A.K. Sahoo. 1996. Vegetation pattern and soil characteristics of some mangrove forest zones of the Sundarbans, West Bengal. *Indian Agriculturist* **40**: 71-78.
- Pool, D.J., S.C. Snedaker & A.E. Lugo. 1977. Structure of mangrove forests in Florida, Puerto Rico, Mexico and Costa Rica. *Biotropica* **9**: 195-212.
- Saenger, P., E.J. Hageral & J.D.S. Davie (eds.) 1983. *Global Status of Mangrove Ecosystems*. IUCN, Ave du Mont Blanco, 1196, Gland, Switzerland.
- Sah, K.D., A.K. Sahoo & S.K. Gupta. 1985. Electrochemical properties of some mangrove muds of the Sundarbans. pp. 372-374. In: L.J. Bhosale (ed.) *Proceedings of the National Symposium on Biology, Utilization and Conservation of Mangroves*. Shivaji University, Kolhapur, India.
- Saha, S. & A. Choudhury. 1995. Vegetation analysis of restored and natural mangrove forests in Sagar Island, Sundarbans, East coast of India. *Indian Journal of Marine Sciences* **24**: 133-136.
- Slattery, W.J., M.K. Conyers & R.L. Aitken. 1999. Soil pH, aluminium, manganese, and lime requirement. pp. 103-128. In: K.I. Peverill, L.A. Sparrow & D.J. Reuter (eds.) *Soil Analysis: An Interpretation Manual*. CSIRO Publishing, Collingwood, Australia.
- Smith, S.M., Y.Y. Yang, Y. Kamiya & S.C. Snedaker. 1996. Effect of environment and gibberellins on the early growth and development of the red mangrove. *Rhizophora mangle* L. *Plant Growth Regulation* **20**: 215-223.
- SPSS 7.5.1. 1996. *SPSS for Windows*. SPSS Inc., Chicago, Illinois 60606.
- Tomlinson, P.B. 1986. *Botany of Mangroves*. Cambridge University Press, Cambridge.
- Ukpong, I.E. 1991. The performance and distribution of species along soil salinity gradients of mangrove swamps in southeastern Nigeria. *Vegetatio* **95**: 63-70.
- Ukpong, I.E. 1994. Soil-vegetation interrelationships of mangrove swamps as revealed by multivariate analyses. *Geoderma* **64**: 167-181.
- Ukpong, I.E. 1998. The composition and distribution of species in relation to soil nutrient gradients in mangrove swamps in South Eastern Nigeria. *Tropical Ecology* **39**: 55-67.
- Wakushima, S., S. Kuraishi & N. Sakurai. 1994a. Soil salinity and pH in Japanese mangrove forests and

- growth of cultivated mangrove plants in different soil conditions. *Journal of Plant Research* **107**: 39-46.
- Wakushima, S., S. Kuraishi, N. Sakurai, K. Supappibul & S. Siripatanadilok. 1994b. Stable soil pH of Thai mangroves in dry and rainy seasons and its relation to zonal distribution of mangroves. *Journal of Plant Research* **107**: 47-52.
- Woodruff, C.M. 1967. Crop response to lime in midwestern U.S. pp. 207-227. *In*: R.W. Pearson & F. Adams (eds.) *Soil Acidity and Liming*. American Society of Agronomy, Madison, WI.
- Walsh, G.E. 1974. Mangroves: A review. pp. 51-174. *In*: R. Reimold & W. Queen (eds.) *Ecology of Halophytes*. Academic Press, New York.
- Waring, R.H. & J. Major. 1964. Some vegetation of the California redwood region in relation to gradients of moisture, nutrients, light and temperature. *Ecological Monographs* **34**: 167-215.
- Watson, J. 1928. *Mangrove Forests of the Malay Peninsula*. Malayan Forest Records 6. Fraser & Neave, Ltd., Singapore.
- Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biological Review* **49**: 207-264.
- Whittaker, R.H. 1978. Direct gradient analysis. *In*: R.H. Whittaker (ed.) *Ordination of Plant Communities*.