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Community structure, species diversity, and aboveground biomass of the Sundarbans mangrove swamps

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Abstract: Tropical mangrove ecosystems are highly productive and provide extensive ecosystem services. While there has been extensive research on mangroves both in tropical and sub-tropical regions of the world, there is limited available information on the community structure and biomass of mangroves in the Sundarbans, which is the world's largest block of mangrove vegetation. The community structure, species diversity, and aboveground biomass of mangroves in the Lothian Island of Sundarbans Biosphere Reserve were estimated and distinct community types were identified. Aboveground biomass was estimated as the product of tree volume and wood density. Twenty-one species including thirteen mangroves and eight mangrove associates were documented from forty sites distributed randomly over the island. Using cluster analysis, eight physically as well as compositionally homogeneous community types having different dominant species and structure, were identified from these forty sites. Four communities had *Avicennia marina* as dominant species but with different structure and habitat. In general the forest was dominated by small sized trees; only 2.7 % of the trees exceeded 10 cm dbh and 2.6 % exceeded 6 m height. Tree density ranged from 4,723 trees ha^{-1} to 23,751 trees ha^{-1}. Aboveground biomass was low and ranged from 8.9 t ha^{-1} to 50.9 t ha^{-1} in different communities, depending on the structural characteristics. Tidal inundation significantly affected the biomass. Soils were generally heavy, slightly alkaline (pH 7 to 7.98) with high salinity variation (0.5 to 25.5 ppt), and rich in organic matter and cations. Communities having low soil salinity and in close proximity to creeks had high complexity and diversity, while the highly saline stunted *Avicennia marina* communities were the least complex and diverse. The analysis revealed an expanding forest which will most likely ultimately develop into a mature mangrove forest.

Resumen: Los ecosistemas de manglar tropical son muy productivos y brindannumerosos servicios ecosistémicos. Si bien se ha llevado a cabo una amplia investigación sobre los manglares de las regiones tropicales y subtropicales del mundo, hay poca información disponible sobre la estructura de la comunidad y la biomasa de los manglares de los Sundarbans, que es el áreade vegetación de manglarmás grande en el mundo. Se estimaron la estructura de la comunidad, la diversidad de especies y la biomasa aérea de los manglares en la isla Lothian de la Reserva de la Biosfera de los Sundarbans y se identificaron los diferentes tipos de comunidad. La biomasa aérea fue calculadaa partir del producto del volumen del árbol por la densidad de la madera. Se registraron 21 especies, incluyendo 13 especies de mangle y ocho especies asociadas, en 40 sitios distribuidos al azar en la isla. Por medio de un Análisis de Clasificación, entre los 40 sitios se identificaron ocho tipos de comunidad que fueron homogéneos en términos físicos y de composición, los cuales difirieron en sus especies dominantes y su estructura. *Avicennia marina* fue la especie dominante en cuatro comunidades, pero éstas difirieron en estructura y hábitat. En general, el bosque estuvo dominado por árboles de tamañopequeño; sólo 2.7 % de los árboles superó 10 cm de DAP y 2.6 % tuvo más de 6 m de altura. La densidad de árboles varió de 4,723

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N ha^{-1} a 23,751 N ha^{-1}. La biomasa aérea fue baja y varió de 8.9 t ha^{-1} a 50.9 t ha^{-1}, dependiendo de las características estructurales de las diferentes comunidades. La inundación de las mareas afectó significativamente la biomasa. Los suelos fueronen general pesados, ligeramente alcalinos (pH 7 a 7.98), con salinidad muy variable (0.5 a 25.5 ppt) y ricos en materia orgánica y cationes. Las comunidades conuna baja salinidad en el suelo y ubicadas en la cercanía de los arroyos tuvieron una complejidad y una diversidad altas, mientras que las comunidades achaparradas de *Avicennia marina*, las cuales tienen una salinidad alta, fueron las menos complejas y diversas. El análisis reveló un bosque en expansión que muy probablementellegará en última instancia a convertirse en un manglar maduro.

Resumo: Os ecossistemas tropicais de mangal são altamente produtivas e prestam serviços ambientais extensos. Embora tenha havido uma extensa investigação sobre os mangais, tanto em regiões tropicais e como subtropicais do mundo, a informação disponível sobre a estrutura da comunidade e biomassa dos mangais nas Sundarbans, que é o maior bloco do mundo da vegetação de mangal, é limitada. A estrutura da comunidade, diversidade de espécies e biomassa aérea de mangais na Ilha Lothian, da Reserva da Biosfera da Sundarbans, foram estimadas e foram identificados tipos de comunidades distintas. A biomassa aérea foi estimada como o produto do volume da árvore e da densidade da madeira. Vinte e uma espécies, incluindo treze espécies de mangal e oito espécies associadas ao mangal, foram documentadas a partir de quarenta pontos distribuídos aleatoriamente ao longo da ilha. Utilizando a análise de cluster, foram identificados, numa base física e composicional, e a partir desses quarenta sítios, oito tipos de comunidades homogéneas com diferentes espécies dominantes e estrutura. Quatro comunidades tinham a *Avicennia marina* como espécie dominante, mas com estrutura e habitat diferente. Em geral, a floresta era dominada por árvores de pequenoporte; apenas 2,7 % das árvores tinham um DAP superior a10 cm e 2,6 % ultrapassou os 6 m de altura. A densidade das árvores variou de 4.723 N ha^{-1} a 23.751 N ha^{-1}. A biomassa aéreaera baixa e variou de 8,9 t ha^{-1} a 50,9 t ha^{-1}, dependendo das características estruturais das diferentes comunidades. A inundação provocada pelas marés afetou significativamente a biomassa. Os solos eram geralmente pesados, ligeiramente alcalinos (pH 7 a 7,98), com de alta variação de salinidade (0,5-25,5 ppt), e rico em matéria orgânica e catiões. As comunidades com baixa salinidade do solo e na proximidade de córregosapresentavam alta complexidade e diversidade, enquanto que as comunidades altamente salinas de *Avicennia marinaraquíticas* foram as menos complexas e diversificadas. A análise revelou uma floresta em expansão,o que provavelmente, irá finalmente tornar-se uma floresta madura de mangal.

Key words: Aboveground biomass, cluster analysis, community type, complexity index, mangroves, species diversity.

Introduction

The term "mangrove" refers to a group of taxonomically heterogeneous woody shrubs and trees growing in the intertidal zone of tropical and subtropical coasts. Worldwide there are 114 species of true mangroves belonging to 66 genera with species richness being greatest in the Indo-Pacific region (Tomlinson 1986). Recently their distribution has expanded to some temperate regions (Krauss *et al.* 2008). India is one of the 15 most mangrove-rich countries having 2.7 % of global total area of mangroves (Giri *et al.* 2011). Banerjee *et al.* (1989) and Naskar & Guhabakshi (1987) have reported 37 obligate mangroves and 32 mangrove associates from the Indian Sundarbans. The multi-species floristic pool in the Indo-Pacific (with around 60 species) has greater physical stability and ecological resilience than the Atlantic Coast mangroves (Blasco *et al.* 1996). The mangrove physical environment can be characterized by relatively high salinity and temperature, diurnal tidal inundation, occasional storms, and muddy anaerobic soil. High salinity in mangrove soils can be a limiting factor for many mainland species subsequently reducing the competition

(Kathiresan & Bingham 2001; Kathiresan 2005; Lacerda *et al.* 2002).

Mangrove communities are characterized by high productivity, high biomass and litter production (Alongi 2009; Boto & Bunt 1981; Mann 1982; Odum & Heald 1972). A recent study indicated that the Indian Sundarban mangrove ecosystem, on the whole, acts as a sink for CO_2 (Chanda *et al.* 2013). The structure and productivity of mangrove ecosystems are significantly affected by climatic conditions resulting in geographical variations in biomass and primary production. Productivity appears to decrease with latitude but is enhanced with increase in tidal amplitude (Woodroffe *et al.* 1988) and the greatest structural and floristic diversity is observed in the tropics (Bray & Graham 1964). Snedaker (1978) suggested that the value of mangroves is largely based on the production of organic matter as leaf litter that enters the estuarine system where it forms the basis for a complex food web. Mangroves provide a plethora of goods and services, ranging from coastal protection from storm and erosion to income for human society (Krauss *et al.* 2008). Mangrove ecosystem services play a crucial role in the maintenance of biodiversity, waste assimilation, cleansing, recycling, and renewal, as well as in protecting coastal areas from disturbance events (Alongi 2008; Dahdouh-Guebas *et al.* 2005; Hussain & Badola 2010; Vo *et al.* 2012). Globally, mangroves are generally undervalued, overexploited, and poorly managed (Ewel *et al.* 1998) as evidenced by destruction of 35 % of world mangrove forests by human activities over last two decades (Alongi 2002; Valiela *et al.* 2001).

During the past two decades there has been extensive research on the structure and function of tropical and subtropical mangrove ecosystems (Chen & Twilley 1999; Cole *et al.* 1999; Fromard *et al.* 1998; Mackey & Monsour 1995, Mandal & Naskar 2008; McGowan *et al.* 2010; Mckee & Faulkner 2000; Steinke *et al.* 1995; Tam *et al.* 1995; Upadhyay & Mishra 2008, 2010). Despite their importance in the conservation and ecology of estuarine ecosystems, very little information is available on the community structure and biomass of mangroves in the Sundarbans. Previous studies have described the vegetation structure (Matilal *et al.* 1986; Saha & Choudhury 1995) and biomass productivity and resource utilization (Chakrabarti 1987) of the Sundarbans mangroves. Roy Choudhuri (1991) determined the biomass of five and six-year-old mangrove plantations of Social Forestry Division in Sundarbans outside Reserved Forests. We previously estimated community structure, biomass and species distribution of natural mangroves in a small area of the Sundarbans (Joshi & Ghose 2002, 2003). This study aims to (i) determine the community structure and aboveground biomass of the Sundarbans mangrove forest; and (ii) to classify distinct community types based on species composition, structural parameters, aboveground biomass, edaphic, and tidal factors.

Study area

Sundarbans is situated in delta of the rivers, Ganges and Brahmaputra of the Indian subcontinent (Ghose 2001). Based on satellite imagery, the Forest Survey of India (1999) estimated the area of Indian Sundarbans as 2125 km^2, excluding the anastomosing network of creeks and backwaters, which are part and parcel of this ecosystem. In another estimate by Naskar (2004), the total area of Sundarbans in India including the reclaimed area is only 9,630 km^2; out of this, the mangrove forest area including rivers, creeks and canals is 4,267 km^2. Mangrove forests of the Sundarbans have not changed in the last 30 years (Giri *et al.* 2007). This study was undertaken at Lothian Island, situated in Saptamukhi estuary complex of the Sundarbans Biosphere Reserve from November 1999 to February 2003. It is a small island (~38 km^2), 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 becomes partly inundated during high tides. A North-South spinal road approaches from the northern coast to near the middle of the island.

Materials and methods

Community structure

Stratified random sampling was employed with data collection from 40 sites covering a total area of 3562 m^2 distributed over the island (Fig. 1). Random number table was used to generate the geographical coordinates (Lat-Long values) of these sites. A Global Positioning System (GPS - 12X, Garmin) was used to reach the exact sites. The island was visited during winter season every year and all the sites were visited once only. A quadrat of 4 m x 16 m size was used in the first eight sites (Joshi & Ghose 2002) for sampling trees including shrubs and climbers. The same size of the quadrat was used in the rest of the 32 sites. Herbs were

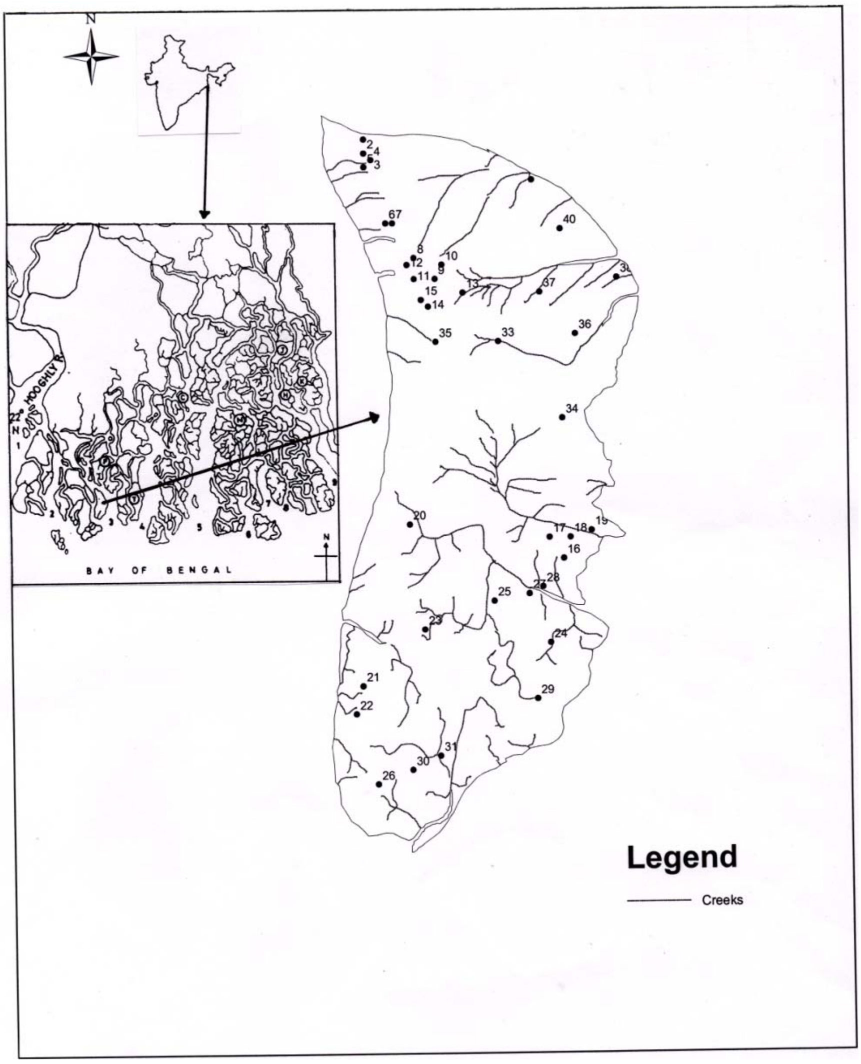

Fig. 1. Boundary map of Lothian Island showing the 40 study sites.

sampled by laying four 1 m x 1 m quadrats nested within the 4 m x 16 m quadrat. In each quadrat, all the trees (plants > 1 cm dbh) were identified and their number and diameter at breast height (dbh 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 category of tidal inundation (diurnal tides, spring tides, summer spring tides and no tides) was also recorded. Structural indices including density, basal area and importance value index (IVI) were calculated using standard methodology (Cintron & Schaeffer-Novelli 1984). The Complexity index (I_c), established by Pool *et al.* (1977), was calculated as I_c = number of tree species x density x basal area x mean height x 10^{-5}. Species diversity (Shannon-Wiener index, H′), dominance (Simpson's index, Cd), and evenness (Pielou's index, e) were determined for each site separately using all the species present (Pielou 1966; Shannon & Weaver 1963; Simpson 1949). Dominance-diversity curves were prepared by plotting the proportional abundance of each species against its rank of abundance.

Aboveground biomass

Aboveground biomass was estimated as the product of tree volume and wood density (Briggs 1977). Two formulae were employed for estimating tree volume, assuming that the trees are conical in shape irrespective of their branching pattern and leaf litter.

(i) Volume = [π $D^2/4$) x h (For herbs and smaller trees (height $\leq$ 3.9 m)]

(ii) Volume = [π $D^2/12$) x h^3/ $(h - b)^2$ (For large trees (height > 3.9 m)] where, b = 1.3 m, D = diameter (m) at 1.3 m, and h = height (m) of the plant.

For estimation of wood density, 10 to 25 wood samples from individual trees of each species (according to availability) that were approximately 30 cm long were cut and fresh weight taken. The diameter at two ends and middle was measured to obtain average diameter (cm). The exact length (cm) of the wood was also recorded to calculate the volume. For herbs, 50-60 plants were collected and their diameter, length, and fresh weight were recorded. All the samples were dried in oven at 105 °C, until they attained constant weight. Dry weight/volume was calculated to obtain the average wood density for every species. Total biomass of a site was the sum of biomass of all individuals of all species in that site. Variation in aboveground biomass in relation to tidal inundation was analysed by one way ANOVA (SPSS 7.5.1 1996).

Soil analysis

Three soil samples were collected from a rooting depth of 15 cm at each site. Samples were air-dried, crushed using a pestle and mortar and then passed through a 10-mesh (2 mm) screen before analysis. Standard methodology was followed for estimating soil salinity, pH, available potassium, and sodium (Jackson 1973). The International pipette method was employed for particle size analysis (Piper 1960). Organic carbon was estimated by the wet digestion method (Walkley & Black 1934). Available nitrogen was estimated following the potassium permanganate oxidation method (Subbiah & Asiza 1956). Olsen's bicarbonate extraction method (Olsen *et al.* 1954) was employed for estimation of available phos-phorus. Available calcium and magnesium were estimated using EDTA or Versenate titration method (Baruah & Barthakur 1997). To study the effect of various soil parameters on biomass production, a stepwise multiple regression was applied using the 2R module of the BMDP 7.01 software (BMDP 7.01 1993).

Community classification

Communities were classified using a multivariate approach. Data including species Importance values, soil parameters, above-ground biomass, and inundation categories of all the 40 sites were transformed to zero means variance one (z scores). A nearest-neighbor cluster analysis was performed on the transformed data taking absolute correlation as distance measure using the 2M module of the statistical package BMDP 7.01. The resulting community types were named according to the dominant species. The species composition, various structural parameters and diversity indices, aboveground biomass, and soil physico-chemical properties of a community type were estimated by computing the mean value of its constituent sites.

Results

Floristic composition of community types

A total of 21 species (12 trees, 3 shrubs, 3 herbs, and 3 climbers), including 13 true mangroves and 8 mangrove associates were documented from the 40 sites (Table 1). Eight distinct community types (CT) were identified from the cluster analysis (Fig. 2). The first three groups separated three distinct sites (CT1, CT2, and CT3) from the rest. The fourth division separated a small group of coastal sites dominated by *Avicennia alba* (CT4). The next two divisions separated two communities (CT5, CT6) dominated by herb *Suaeda maritima* and *Sesuvium portulacastrum*, respectively. The seventh division distinguished a smaller *Avicennia marina* dominated community (CT7), and a dense mixed vegetation community (CT8). Further divisions were truncated because beyond this level the divisions were not ecologically meaningful. The species composition and Importance values of the constituent species of these community types are shown in Table 2 and described below:

CT1 (Sandy *Excoecaria* community) – Community type 1 was observed at a single site located on the southern landward portion of the island with no tidal inundation. The community was dominated by a single tree species *Excoecaria agallocha* (IVI = 137.5) along with dense spiny climbers *Caesalpinia bonduc*, Caesalpinia crista and *Derris-trifoliata.*

CT2 (Coastal *Avicennia marina* community) - Community type 2 was observed at a single site located near eastern coast of the island that experiences diurnal inundation. The eastern coastline of the island was eroding and a sand shoal was progressing towards the island. This community had an almost single species population of *A. marina* (IVI = 278) with a few individuals of *E. agallocha.*

CT3 (*Aegiceras* community) - Community type 3 was observed at a single site situated about 2.5 km from northern coast and inundated during spring tides only. A tidal creek was running near

Table 1. Species encountered and their percentage distribution within 40 sites of Lothian Island.

Species	Abbreviation	Family	% of sites
Trees			
Aegiceras corniculatum (L.) Blanco	AC	Myrsinaceae	50.0
Avicennia alba Blume	AA	Avicenniaceae	20.0
Avicennia marina (frosk.) Vierh.	AM	Avicenniaceae	75.0
Avicennia officinalis L.	AO	Avicenniaceae	32.5
**Brownlowiatersa* (Linn.) Kostern	BT	Tiliaceae	2.5
Bruguiera gymnorrhiza (L.) Lamak.	BG	Rhizophoraceae	2.5
Ceriops decandra (Griff.) Ding Hou	CD	Rhizophoraceae	57.5
Ceriops tagal (Pierre.) Robins	CT	Rhizophoraceae	2.5
Excoecaria agallocha L.	EA	Euphorbiaceae	42.5
Heritiera fomes Buch. Ham.	HF	Sterculiaceae	10.0
Lumnitzera racemosa Willd.	LR	Combretaceae	2.5
Xylocarpus mekongensis Pierre	XM	Meliaceae	5.0
Shrubs			
Aegialitis rotundifolia Roxb.	AR	Plumbaginaceae	52.5
#Phoenix paludosa Roxb.	PP	Arecaceae	27.5
**Dalbergia spinosa* Roxb.	DS	Papilionaceae	10.0
Herbs			
**Acanthus ilicifolius* L.	AI	Acanthaceae	57.5
**Suaeda maritima* Dumort.	SM	Chenopodiaceae	12.5
**Sesuvium portulacastrum* L.	SP	Aizoaceae	17.5
Climbers			
**Caesalpinia bonduc* (L.) Roxb.	CB	Caesalpiniaceae	7.5
**Caesalpinia crista* L.	CC	Caesalpiniaceae	5.0
**Derris trifoliata* Lour.	DT	Papilionaceae	32.5

*mangrove associates/ back mangrove (Naskar 2004), # monocot species.

the site. Climber *D. trifoliata* (IVI = 152) dominated the community. Among trees, *Aegiceras corniculatum* (IVI = 63.8) was the dominant species. Shrubs and herbs were present.

CT4 (Coastal *Avicennia alba* community) – Community type 4 was observed at 3 sites in the diurnally in undated northern tip of the island. *Avicennia alba* (IVI = 187.4) among others was the dominant species; herb *Acanthus ilicifolius* provided the ground cover.

CT5 (Stunted *Avicennia marina* community with *Suaeda maritima* ground cover) - Community type 5 was observed at 3 sites situated in middle of the island with no tidal inundation. Soil remained dry except during rains and storms. Herb *S. maritima* (IVI = 184.4) was the dominant species. *A. marina* (IVI = 96.7) was the dominant tree species, which was bushy showing branching from the base with stunted height. Shrub *Aegialitis rotundifolia* along with few other trees were present in small densities.

CT6 (Stunted *Avicennia marina* community with *Sesuvium portulacastrum* ground cover) – Community type 6 was observed at 5 sites that occupied different pockets in the interior of the island, with three inundated diurnally and two during spring tides only. Herb *S. portulacastrum* (IVI = 148.4) was the dominant species; *A. ilicifolius* and *S. maritima* were less in number. Stunted bushy A. marina (IVI = 69.9) was the dominant tree species, followed by *Ceriops-decandra*.

CT7 (Tidal *Avicennia marina* community) - Community type 7 was observed at 10 sites in the northern portion of the island and all but two were inundated diurnally. *Avicennia marina* (IVI = 188) was the dominant tree species. This community was distinctly different from CT2, for *A. marina* trees were larger in size with more height and diameter, along with a good density of herb *A. ilicifolius*.

CT8 (Dense mixed vegetation community) - Community type 8 was observed at 16 sites in the middle and southern elevated portion of the island

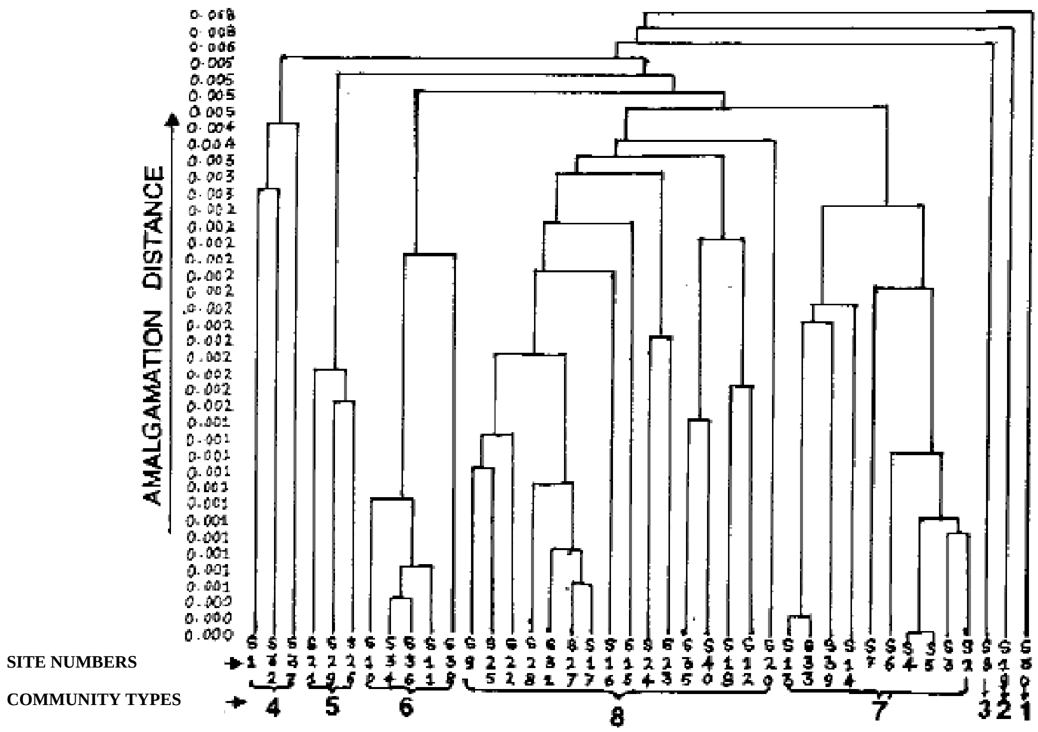

Fig. 2. Dendrogram showing the classification of eight communities from forty sites.

that is intersected by various creeks and inundated during spring tides only. The community had dense mixed vegetation with eighteen species including trees, shrubs, herbs, and climbers. *Ceriops decandra* (IVI = 73.5) was the dominant species followed by *E. agallocha*, and shrubs *A. rotundifolia* and *Phoenix paludosa.* Climber *D. trifoliata* was abundant while *C. bonduc* and *C. crista* occurred at one or two sites. Some rare tree species were recorded in this community –*Heritiera fomes* at four locations, and *Brownlowia tersa*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, and *Lumnitzera racemosa* at a single location.

Community structure

The forest was dominated by a large number of small trees showing a typical diameter density distribution that followed a reverse J-shaped curve with only 2.7 % of the trees exceeding 10 cm dbh, and 2.6 % exceeding 6 m height (Fig. 3). Stunted *A. marina* community (CT5) had the smallest stand diameter (2 cm) and height (1.1 m). The greatest stand diameter (6 cm) and height (4.3 m) occurred in the coastal *A. alba* community (CT 4) (Table 3). The dense mixed vegetation community (CT8) had a low stand height of 2.1 m. Total tree density was highest in the *Aegiceras* (CT3, 23,751 N ha^{-1}) and the dense mixed vegetation (CT8, 21,270 N ha^{-1}) communities; and lowest in the coastal *A. alba* (CT4, 4,723N ha^{-1}) and the tidal *A. marina* (CT7, 8,200 N ha^{-1}) communities. However, the highest density of trees with dbh ≥ 10 cm occurred in CT4 (556 N ha^{-1}) and CT7 (498 N ha^{-1}). The largest total basal area (76.3 m^2 ha^{-1}) occurred in the *Aegiceras* community (CT3) and smallest (8.15 m^2 ha^{-1}) in the coastal *A. marina* community (CT2). The largest total basal area (20.3 m^2 ha^{-1}) of trees also occurred in CT3 and the smallest (4.9 m^2 ha^{-1}) occurred in the stunted *A. marina* community (CT5). However, the herbs occupied very large basal areas (4.2 - 6.6 m^2 ha^{-1}) in both of the stunted *A. marina* communities (CT5 and CT6) (Table 3).

The complexity index (I_c) ranged from 4.1 to 73.3. The highest complexity occurred in the *Aegiceras* (CT3, 73.3) and the dense mixed (CT8, 62.1) communities, mainly due to high density and basal area, and high density and number of species, respectively. The lowest complexity occurred in the stunted *A. marina* (CT5, 4.1) and the coastal *A. marina* (CT2, 7.5) communities mainly because of their low basal area. The coastal *A. alba* community (CT4) having highest stand height had low complexity due to sparsely populated trees.

The lowest and the highest values of species richness and the Simpson's index occurred in the

Table 2. Mean values of relative density (RD), relative frequency (RF), relative dominance (R Do), and importance value index (IVI) of mangroves in the eight communities. Full species names provided on Table 1.

C T	Species	RD (%)	RF (%)	RDo (%)	IVI
1	*Excoecaria agallocha*	37	22.2	78.3	137.5
	Ceasalpinia crista	32.4	16.7	4.37	53.4
	Derris trifoliata	18.5	22.2	1.61	42.3
	Others (AC, AO, CB)	12	39	15.7	66.8
2	*Avicennia marina*	98.2	80	99.6	277.8
	Excoecaria agallocha	1.8	20	0.4	22.2
3	*Derris trifoliata*	57.7	21.1	73.3	152.1
	Aegiceras corniculatum	27.5	21.1	15.3	63.84
	Ceriops decandra	11.6	21.1	1.68	34.31
	Avicennia officinalis	1.75	15.8	7.51	25.05
	Others (AR, EA, AI)	1.5	21	2.2	24.7
4	*Avicennia alba*	48.2	46.5	92.6	187.4
	Acanthus ilicifolius	37.8	21.2	1.74	60.73
	Avicennia marina	11.6	27.5	5.51	44.62
	Others (AC)	2.38	4.76	0.06	7.2
5	*Suaeda maritima*	92.3	46.7	45.5	184.4
	Avicennia marina	5.97	46.7	43.7	96.7
	Others (CD, XM, AC, AO, AR)	1.8	6.7	10.7	19.2
6	*Sesuvium portulacastrum*	90.5	23.8	42.6	148.4
	Avicennia marina	1.7	24.5	43.7	69.86
	Ceriops decandra	1.48	14.4	5.84	21.67
	Others (AC, SM, AR, AI, EA, AO, DT, DS)	6.3	37	16.4	60.1
7	*Avicennia marina*	48.8	52.7	86.9	188.4
	Acanthus ilicifolius	39	23.7	6.59	69.32
	Others(AA, AR, SM, SP, AO, CD)	12	24	9.4	45.2
8	*Ceriops decandra*	40.2	17.9	15.4	73.5
	Excoecaria agallocha	10.5	14.2	28.6	53.3
	Phoenix paludosa	19.3	10.9	22.4	52.6
	Aegialitis rotundifolia	17.1	14.2	20.4	51.6
	Others (AC, DT, AM, AI, AO, HF, SP, BT, CC, DS, CB, BG, LR, CT)	13	43	13.6	69.2

coastal *A. marina* community (CT2) and the dense mixed community (CT8), respectively (Fig. 4). The highest heterogeneity was reported in the *Excoecaria* (CT1, 2.06) and dense mixed (CT8, 1.88) communities; and lowest in the coastal *A. marina* (CT2, 0.13) and stunted *A. marina* (CT5, 0.43) communities. The low and high evenness caused low and high heterogeneity in CT6 and CT4, respectively. Community types 1, 3, and 8 had most equitable "broken stick" dominance diversity curves with resource shared by all species (Fig. 5). The "geometric series" distribution indicating a low diversity and dominance by one or few species was seen in community types 2 and 5.

Aboveground biomass

Among trees, wood density was the highest for *C. decandra* (705.2 kg m^{-3}) and *H. fomes* (647.1 kg m^{-3}), and the lowest for *A. rotundifolia* (458 kg m^{-3}) (Table 4). The herb *S. portulacastrum* had extremely low density (3.1 kg m^{-3}) because of large moisture content.

The total aboveground biomass ranged from 8.9 t ha^{-1} (CT5) to 50.9 t ha^{-1} (CT7) (Fig. 6). The most productive tree species were *A. alba* (34.5 t ha^{-1} in CT4) and *A. marina* (26.5 t ha^{-1} in CT7), and the least productive was *C. decandra* (0.03 to 3.9 t ha^{-1}, CT8). The biomass production of herbs ranged from 0.03 to 1.4 t ha^{-1} and that of pneumatophores from 0.2 to 12.9 t ha^{-1}.

The mean aboveground biomass was highest in the *Aegiceras* (CT3, 35.2 t ha^{-1}) and coastal *A. alba* (CT4, 32.7 t ha^{-1}) communities, and lowest in the stunted *A. marina* community (CT5, 6.5 t ha^{-1}) (Table 5).

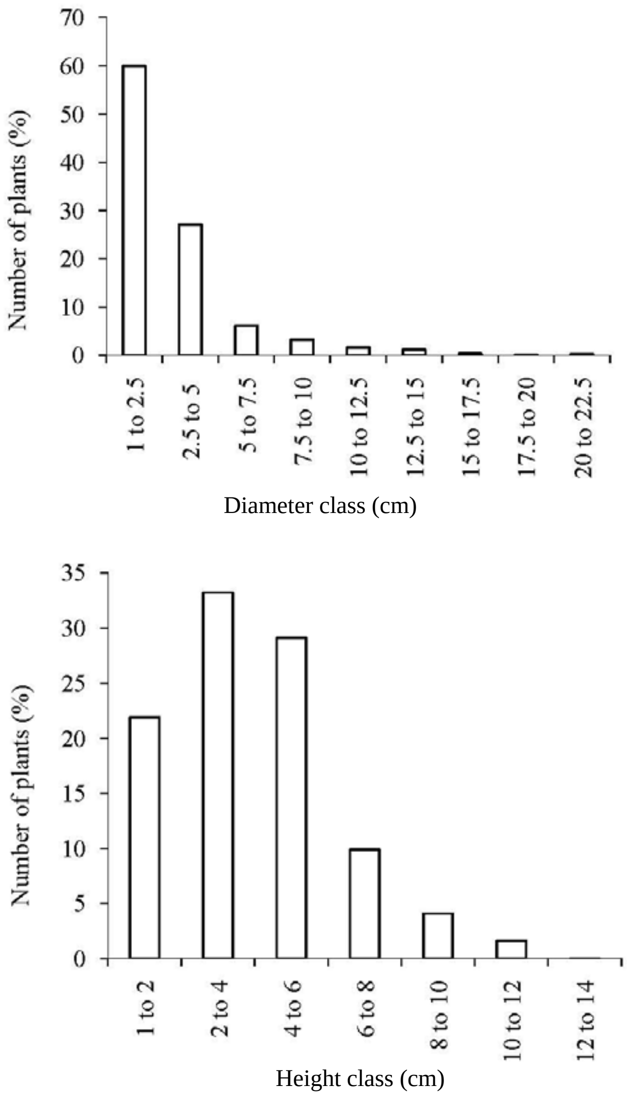

Fig. 3. Diameter and height distribution of mangrove trees in the Lothian island, Sundarbans.

Correlation analysis between structural parameters and aboveground biomass depicted the arrangement of communities according to the degree of maturity (Fig. 7). Communities with high biomass (CT3, CT4, and CT7) had a low total density but a high density of plants with dbh > 10 cm.

The biomass production in Lothian island was low (8.9 to 50.9 t ha^{-1}) as compared to other mangrove areas (Table 6). There were significant differences in aboveground biomass among the four inundation categories ($F_{3,36} = 5.203$, $P < 0.01$). Very low biomass occurred in the stunted *A. marina* communities (CT5, CT6) with no tidal inundation, while the highest biomass occurred in the tidal *A. marina* (CT7) and the coastal *A. alba* (CT4) communities, with long duration diurnal inundation.

Soil characteristics

In general, soils were heavy, slightly alkaline (pH 7 to 7.98) with high salinity, rich in organic matter and cations (Table 7). The surface soil (0-15 cm depth) in CT1 was an exception and composed of nearly pure sand (98.6 %) with extremely low values of organic carbon (0.12 %) and salinity (0.5 ppt) due to low sodium and potassium content. CT2 also had high sand (39 %) due to its coastal location, and low salinity (8.9) accompanied with low values of potassium, sodium, calcium and magnesium but with high phosphorus content. Soils in the *Aegiceras* (CT3) and dense mixed (CT8) communities also had low salinity. High salinity was observed in the stunted *A. marina* (CT5, 25.5 ppt), coastal *A. alba* (CT4, 24.7ppt), and tidal *A. marina* (CT7, 24.1 ppt) communities along with high sodium and NPK values. *Aegiceras* (CT3) and tidal *A. marina* (CT7) communities had high organic carbon.

Soil parameters explained only 29 % variation of aboveground biomass in the stepwise regression analysis. Out of total 29 % variation, magnesium explained 13.7 % and phosphorus 8 %, both influencing biomass negatively. Among non nutrient parameters, salinity negatively influenced biomass, explaining 0.2 % variation.

Discussion

This study revealed new findings in regard to mangrove community structure and aboveground biomass of the Indian Sundarbans. Such a study is ecologically significant and useful in forest management. Multivariate analysis enabled clear-cut grouping of eight distinct communities. The results placed the Sundarbans mangroves among those with low biomass although higher values have been reported for Asia. The study identified water availability as the most important environmental factor controlling the variations in mangrove forest structure and biomass.

Distinctness of community types

Curtis (1933) was the first to study and describe the Gangetic delta in detail, emphasizing ecological, physiognomy, and floristic components. Other classifications emphasized species composition (Blasco 1975; Champion & Seth 1968; Naskar 1983), or included tidal influence and topo-

Table 3. Structural characteristics of mangroves in the eight communities. Values are means ± SD for total density, total basal area, and stand height.

CT	Taxa	No. of species	Total density (trees ha^{-1})	Density (trees ha^{-1}) dbh> 10cm	Total basal area (m^2 ha^{-1})	Mean dbh (cm) dbh< 10cm	Mean dbh dbh>10cm (cm) (n)	Mean stand diameter (cm)	Stand height (m)	Complexity index (I_c)
1	Trees	3	11719		12.6	3.3		3.7	3.6±0.9	16
	Climbers	3	15313		1.8	1				
2	Trees	2	17032		8.15	2.3		2.5	2.7±1.0	7.5
3	Trees	4	23751	391	20.3	2.6	12.5(5)	3.3	3.8±1.2	73.3
	Shrubs	1	703		0.1	1.4				
	Herbs	1	78		0.002	0.6				
	Climbers	1	33516		55.9	0.6				
4	Trees	3	4723 ± 2211	556	13.5±9.14	3.7	11.7(22)	6.0	4.3±2.8	8.23
	Herbs	1	7257 ± 9508		0.4±0.5	0.8				
5	Trees	5	15105 ± 2731		4.9±0.54	1.9		2.0	1.1±0.5	4.07
	Shrubs	1	208 ± 361		0.1±0.2	2.3				
	Herbs	1	207500 ± 71458		4.2±0.9	0.5				
6	Trees	5	17282 ± 6551	208	9.0±2.5	2.1	13.5(4)	2.6	1.7±1.0	13.2
	Shrubs	2	1969 ± 3389		0.6±0.8	1.9				
	Herbs	3	634750±400091		6.6±4.5	0.5				
	Climbers	1	469 ± 1048		0.01±0.03	0.6				
7	Trees	4	8200 ± 8835	498	15.8±8.28	3.8	12.9(60)	5.0	3.7±2.3	19.2
	Shrubs	1	500 ± 1581		0.1±0.3	1.3				
	Herbs	3	22788 ± 40429		1.6±3.7	0.7				
8	Trees	10	21270 ± 96051	391	13.9±9.1	2.1	13.7(25)	2.9	2.1±1.1	62.1
	Shrubs	3	17236 ± 22125		13.0±12.2	3.0				
	Herbs	2	889 ± 913		0.05±0.1	0.8				
	Climbers	3	1748 ± 3624		0.86±2.5	0.6				

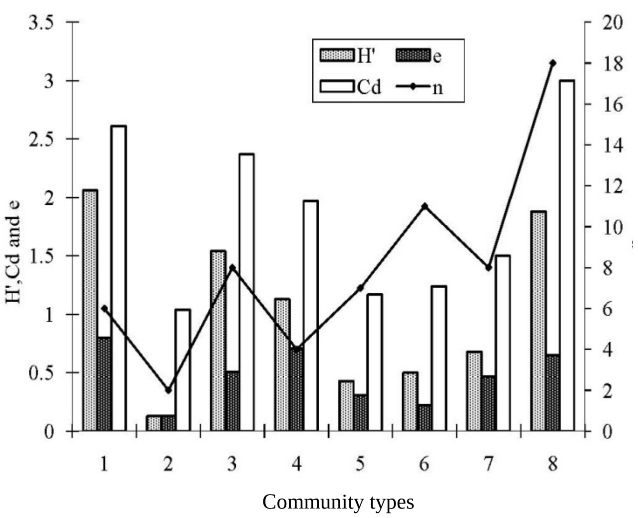

Fig. 4. Diversity indices of mangroves in the eight communities. n refers to the number of species.

graphy along with indicator plants to classify the Gangetic Sundarbans (Chakraborty 1984; Rao & Shastry 1972, 1974). Lugo & Snedaker (1974) were the first to combine physiographic and structural attributes of mangrove wetlands of Florida with local conditions of topography and hydrology to formulate the classic ecological classification system. Complex cluster analysis techniques were used by Bunt & Williams (1981) to define 'association-groups' in northeastern Australia and Ross *et al.* (1992) to subdivide Florida Keys into physically and compositionally homogeneous 'ecological site units'. In this study, a multivariate clustering technique was used for the first time to classify the Sundarbans mangroves into eight communities that differed from each other in species composition, structural parameters, biomass, tidal inundation, and physical and chemical soil properties. The coastal *A. marina* (CT2) and the stunted *A. marina* (CT5, CT6) communities were structurally different from the tidal *A. marina* community (CT7) having large trees with greater height

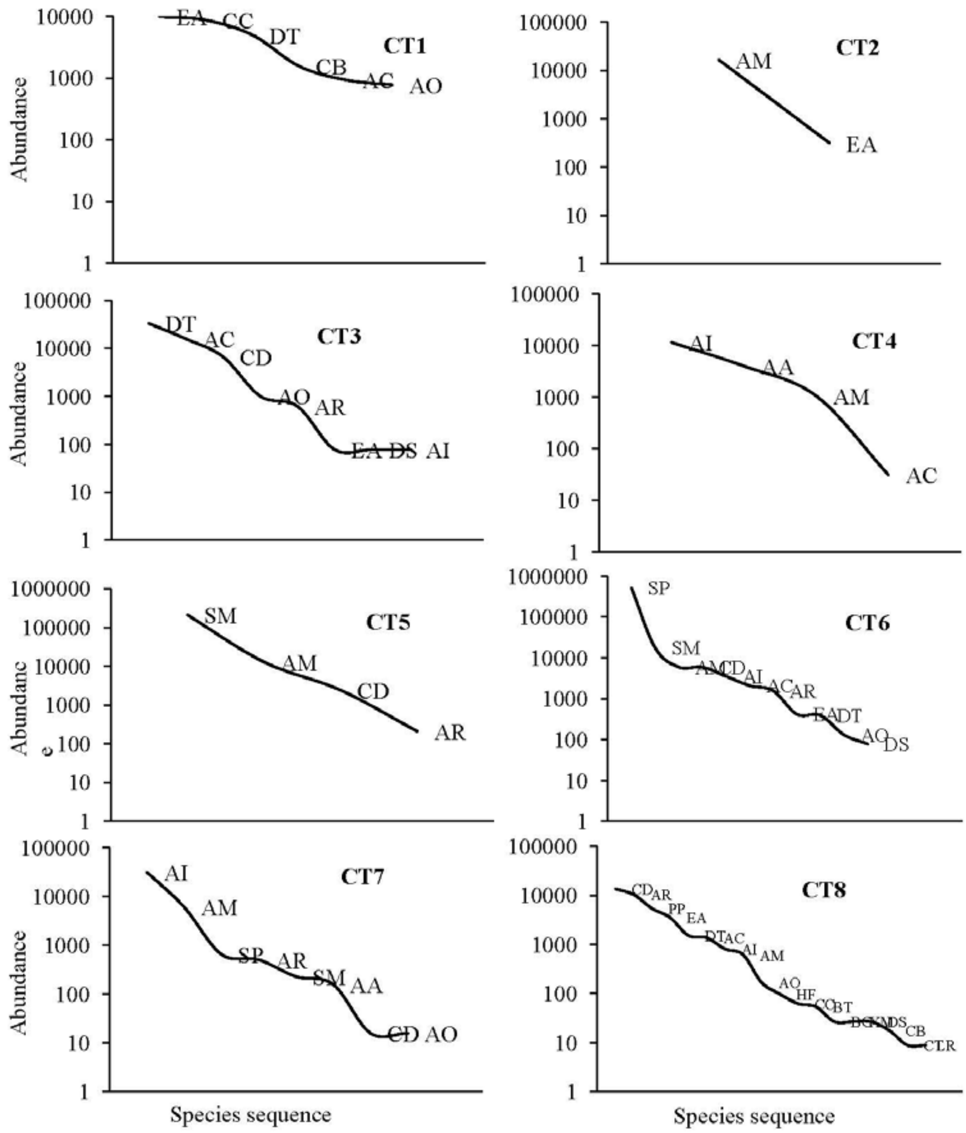

Fig. 5. Dominance diversity curves for the mangroves in the eight communities. See Table 1 for species abbreviations.

and diameter. This is similar to the observation reported by Middelburg *et al.* (1996) in an east African mangrove forest where the creek and river fringing *A. marina* stands were much taller (12-19 m) than those on elevated areas (about 2-3 m; scrub type).

Structural parameters of community types

This study documented 13 obligate mangroves and 8 mangrove associates in Lothian Islandas opposed to 37 obligate mangroves and 32 mangrove associates reported for the entire Indian Sundarbans (Banerjee *et al.* 1989; Naskar & Guhabakshi 1987). Other researchers reported fewer number of species in Indian mangroves, *i.e.*, 12 in Andamans and Nicobar islands (Thothathri 1981), 19 in the west coast of India (Tomlinson 1986), 20 in Bombay and Salsette islands (Navalkar 1956), 7 to 9 in Kerala (Nameer *et al.* 1992; Ramachandran *et al.* 1985) and 8 in Gujarat (Singh 1999). In contrast, mangroves of the Atlantic coast were generally dominated by only two species (*Rhizophora mangle* L. and *Avicennia-germinans* L.) that together constitute more than 80 % of the mangroves (Blasco *et al.* 1996).

The forest structure was simple and largely composed of small-sized trees in all the forty sites. The distribution of diameter densities for all the trees exhibited a reverse J-shaped pattern indi-

Table 4. Wood density of mangroves and mangrove associates. (C.V. % = SD/ mean x 100).

Species	Sample size	Density (dry wt. kg m^{-3})	C.V.%
Acanthus ilicifolius	58	330.8	29.8
Aegialitis rotundifolia	10	458.0	34.1
Aegiceras corniculatum	10	546.8	4.7
Avicennia alba	25	591.2	12.7
Avicennia marina	25	612.5	11
Avicennia officinalis	25	587.5	8.1
Brownlowia tersa	6	609.4	10.0
Ceriops decandra	10	705.2	6.5
Excoecaria agallocha	10	498.1	10.7
Heritiera fomes	10	647.1	6.2
Phoenix paludosa	10	343.0	16.5
Sesuvium portulacastrum	39	3.1	35.3
Suaeda maritima	16	635.1	20.8
Avicennia pneumatophores	40	454.2	13.5
Heritiera pneumatophores	6	295.4	13.9

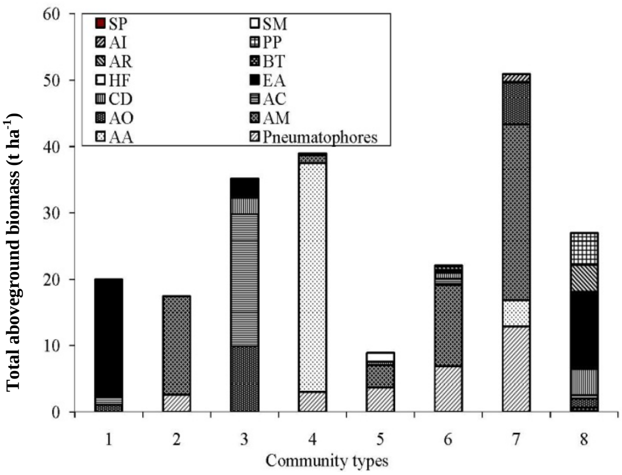

Fig. 6. Total aboveground biomass produced by different species in the eight communities. See Table 1 for species abbreviations.

cating an expanding or evolving population. There was little stratification at some locations with shrub and herb layers along with seedlings. *Avicennia marina* and *C. decandra* were generally dominant. Roy Choudhury (1991) recorded average height and diameter of *Avicennia* species from Indian Sundarbans as 3.8-6.0 m and 12.5-17.0 cm, respectively, which is much larger than the values obtained in this study (2.9 m and 3.5 cm, respectively). However, he worked on 5-year-old mangrove plantations raised by Social Forestry Division instead of natural forest. The high density of *A. corniculatum* (15938 N ha^{-1}) in Lothian Island was comparable to Harinbhanga Island (16400 N ha^{-1}) in the eastern Sundarbans (Matilal *et al.* 1986) and may be attributed to relatively low soil salinity. Fromard *et al.* (1998) observed that density was the most discriminating factor for early development stage of mangroves – a young stand matures by decreasing the number of individuals. They reported higher density (17,333 N ha^{-1}) for *Avicennia* spp. in the pioneer stage than mature stage (558 N ha^{-1}) in French Guiana. Cole *et al.* (1999) noticed shorter canopies and more density in Pohnpei Island, which experienced large-scale disturbances in the past than on Kosrae Island in Micronesia. Mackey & Monsour (1995) also found taller *A. marina* individuals to be far apart and arrived at the similar conclusion - the mature community had trees with low density and high dbh and height. These observations are similar to our study, where communities with short trees with small diameters and low basal areas had very high density; while the density of large sized trees in some other communities was low. This variability may be due to different growth rates of the tree species or different ages of the communities.

Table 5. Mean aboveground biomass in the eight communities.

CT	Mean biomass (t ha^{-1})	Range
1	19.96	-
2	17.40	-
3	35.2	-
4	32.73	10.26 - 45.73
5	6.46	3.91 - 11.48
6	19.40	12.71 - 25.37
7	27.69	14.10 - 45.1
8	29.39	7.31 - 55.43

Pool *et al.* (1977) documented structural complexity (I_c) as low as 0.9 for scrub mangroves and as high as 97.5 for the fringe mangroves in Puerto Rico, which are comparable to our findings. They included small individuals (dbh 2.5 - 10 cm) for computation of complexity index because it affects the total basal area very little, but greatly increases the number of stems measured empha-

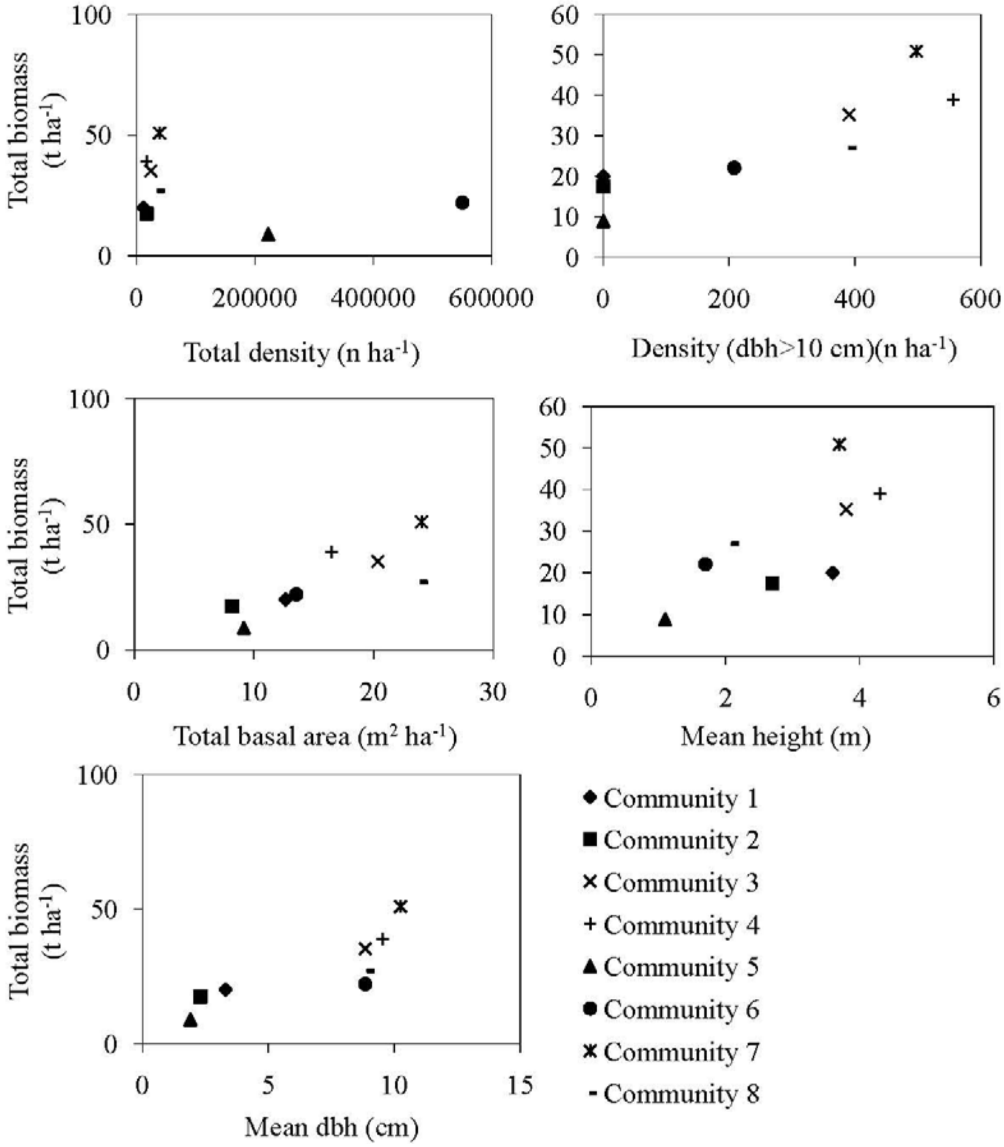

Fig. 7. Correlation between aboveground biomass and the structural characteristics of mangroves in the eight communities.

sizing the importance of a large number of stems. Fromard *et al.* (1998) also reported similar I_c values ranging from 18 to 71 for the mangroves of French Guiana. In Lothian, many communities had a major portion of trees with dbh < 2.5 cm, and hence trees with dbh > 1 cm were included in the computation of structural indices. I_c values of 6.9 to 14.1 for disturbed and 87.1 to 260 for undisturbed mangroves of Andaman islands of India have been reported (Singh *et al.* 1990; Singh & Odaki 2004). Mall *et al.* (1991) observed huge differences in complexity of monogeneric and mixed mangrove forest in Andaman Islands of India, *i.e.*, 166 and 722, respectively. Such high values in Andaman Islands may be because of its location in more equatorial latitude and greater maturity of the forest than in Lothian.

The overall values of heterogeneity and evenness for the mangroves of Lothian Island were 2.26 and 0.52, respectively. Slightly higher heterogeneity and evenness (2.74 and 0.82) were reported by Nazrul-Islam (1995) for the mangroves of Bangladesh Sundarbans. Saha & Choudhury (1995) estimated heterogeneity of 2.8 for tree species in Sagar Island of Indian Sundarbans, close to Lothian Island. Our dominance diversity

Table 6. Aboveground biomass in various mangrove forests of the world.

Latitude (°)	Height (m)	Major species	Locality	Total above ground biomass (t ha^{-1})	Reference
1.2	15.5 - 26.4	*So, Rh.a., Br*	Indonesia	178.2 - 436.4	Komiyama *et al.* (1988)
4.5		*Rh. a.*	Malay	460	Putz & Chan (1986)
8	11	*Rh. a.*	Thailand	159.1	Christensen & Delmondo (1978)
4.2	3.9- 10.3	*Rh*	Sri Lanka	71 - 240	Amarasinghe & Balasubramanium (1992)
12	12.5 - 22.5	*Rh.mu & a., Br.g. & .t.*	Andaman Isl., India	124 - 214	Mall *et al.* (1991)
21	5.2 - 5.4	*Av. spp.*	Sundarbans, India	101.9 - 118.7	Roy Choudhuri (1991)
21	1.1 - 3.8	*Av. spp., E.a., Ag.c., Ag.r., C.d., P.p.*	Sundarbans, India	8.9 - 50.9	This study
24	5.5	*Rh. mu*	Japan	108.1	Suzuki & Tagawa (1983)
27.2	16.4	*Av.m.*	Australia	341	Mackey (1993)
33.5	7	*Av.m.*	Australia	220.8	Briggs (1977)
37	2.7	*Av.m.*	Australia	104.1	Woodroffe (1985)
5	3.5 - 22.7	*La.r., Av.g.*	Fr. Guiana	31.5 - 315	Fromard *et al.* (1998)
8.5	38	*Rh. b.*	Panama	279.2	Golley *et al.* (1975)
14	10.6	*Rh. r.*	Senegal	60.0	Doyen (1986)
16	13	*Rh.m , Av.g.*	Guadeloupe	52.8 - 152.3	Imbert & Rollet (1989)
18	7.5	*Rh.m.*	Puerto Rico	62.9	Golley *et al.* (1962)
26	1 - 6.3	*Rh.m, La.r.*	Florida	7.9 - 124.6	Lugo & Snedakar (1974)

Species abbreviations: *Ag.c. Aegiceras corniculatum, Ag. r. Aegialitis rotundifolia, Av.g. Avicennia germinans, Av.m. Avicennia marina, Br.g. Bruguiera gymnorrhiza, C.d. Ceriops decandra, C.t. C. tagal, E.a. Excoecaria agallocha, La.r. Laguncularia racemosa, P.p. Phoenix paludosa, Rh.a. Rhizophora apiculata, Rh.b. R. brevistyla, Rh.m. R. mangle, Rh.mu. R. mucronata, Rh.r. R. racemosa, So. Sonneratia* spp.

curves are comparable with those by Saha & Choudhury (1995). Their curves approached *geometric series* in both restored and natural mangrove forests. We obtained such curves in degrading coastal *A. marina* (CT2) and the stunted *A. marina* (CT5) communities, both having very low diversity. This type of distribution occurs in communities of relatively few species wherein a single environmental factor predominates so that only one species is best fit to survive and becomes numerically dominant (Whittaker 1975).

Variations in aboveground biomass

This is the first report of biomass value of natural mangroves in the Indian Sundarbans. Because the felling of trees in the reserve forest is strictly prohibited, we could not prepare regression equations based on tree height or dbh, nor could we apply the regression models developed by other researchers. Woodroffe (1985) stated that the regression models and the importance of tree height or diameter as the independent variable to estimate biomass value vary between mangrove stands. Even for the same mangrove stand, the regression models would be different for areas of different tree height and density (Steinke *et al.* 1995; Tam *et al.* 1995). The biomass production in Lothian Island was low as compared to other mangrove areas of the world. Highest values for biomass occurred in mature stands of *Brugueira gymnorrhiza* (406.6 t ha^{-1}; Komiyama *et al.* 1988) and *Rhizophora apiculata* (436 - 460 t ha^{-1}; Putz & Chan 1986). The lowest values were for shrubby *Rhizophora mangle* (7.9 t ha^{-1}; Lugo & Snedaker 1974) and *A. marina* (6.8 t ha^{-1}; Woodroffe 1985) stands, young plantation of *B. gymnorrhiza* (5.8 t ha^{-1}; Roy Choudhuri 1991) and pioneer *Laguncularia racemosa* stands (31.5 t ha^{-1}; Fromard *et al.* 1998). The only comparable data on biomass production of *Avicennia* spp. from India was reported

Table 7. Mean values of soil physico-chemical parameters in the eight communities. Sediment and organic carbon are percentages. Nitrogen (N), Potassium (K), Phosphorus (P), Sodium (Na), Calcium (Ca), and Magnesium (Mg) are in parts per million (ppm).

CT	pH	Salinity	Sand	Silt	Clay	Organic C	N	K	P	Na	Ca	Mg
1	7.9	0.5	98.6	0.6	0.7	0.1	62.5	24.7	11.3	204.2	1593.2	510.7
2	7.0	8.9	39.0	27.5	33.4	0.7	83.1	85.5	14.8	516.7	2585.2	778.3
3	7.6	13.0	10.1	48.8	41.0	0.9	69.5	71.3	7.9	739.0	3086.2	1641.6
4	7.8	24.7	37.1	33.4	29.4	0.6	79.0	110.3	14.7	733.7	6532.7	3331.8
5	7.5	25.4	7.8	47.1	45.0	0.6	93.0	146.0	14.0	934.7	3567.2	1495.7
6	7.7	20.0	11.8	42.4	45.7	0.4	72.6	130.0	14.6	814.8	4108.2	3721.0
7	7.4	24.1	9.3	42.6	48.0	0.9	98.4	116.4	13.5	1068.6	4408.8	2055.0
8	7.5	14.9	23.2	43.0	33.7	0.6	79.0	103.2	11.0	695.5	3947.9	1459.2

by Roy Choudhuri (1991), where he estimated 101.9 and 118.7 t ha^{-1} biomass, much higher than biomass estimates in this study. This may be because he studied 5 and 6 years old artificial mangrove plantations raised by Social Forestry Division having larger trees, and sun dried the harvested samples only for 48 hours instead of oven drying to constant weight while estimating biomass. Moreover we have estimated biomass from mean tree volume and wood density instead of harvesting the whole tree.

The species diversity, tree height, density, and biomass increase with decreases in latitude (Tam *et al.* 1995). However, biomass is also related to species composition, community structure, growth forms, and age of the plant community (Knox 1986; Lugo & Snedaker 1974; Mall *et al.* 1991; Woodroffe 1985). This study revealed that the density of trees with dbh > 10 cm and the basal area were the most influential factors for biomass production. Fromard *et al.* (1998) observed large biomass differences (180 to 315 t ha^{-1}) for *Avicennia germinans* populations with similar height but with different basal area. Komiyama *et al.* (1988) obtained biomass values of 178.2 and 436.4 t ha^{-1} for two stands of Indonesian *Rhizophora apiculata* of the same height; Ong *et al.* (1981) reported biomass values of 147 and 314 t ha^{-1} for two Malaysian populations of *R. apiculata* (height = 15 m). Similarly in this study, communities with similar height (CT1, CT3, and CT7) and different basal area produced different biomass. Hence it is necessary to know all the structural characteristics of a stand to be able to compare the values of their corresponding biomasses.

Soil characteristics

The particle size analysis of Lothian soil indicated that soils were generally heavy and silt was the dominant particle. Silt has been reported as the dominant particle in most of the islands of Sundarbans (Chattopadhyay *et al.* 1986; Pal *et al.* 1996; Sarkar *et al.* 1991). Sand content was high in coastal communities. According to Naskar & Guhabakshi (1987), sand occurs only along the sea-face where the strength of the tides and the roughness of water are greater, preventing the fine particles from settling. Matilal *et al.* (1986) reported the western islands of the Indian Sundarbans to be more sandy (6-7 %) than eastern islands (1-2 %). In this study, soil reaction was slightly alkaline as reported in previous studies (Pal *et al.* 1996; Sah *et al.* 1985). Sodium along with salinity was especially high in the tidal *A. marina* community (CT7) in the northern diurnally inundated region, and the stunted *A. marina* communities (CT5, CT6) in the middle dry elevated portions of the island. Naskar & Guhabakshi (1987) reported that the salt contents of Sundarbans soil were mostly chlorides and sulphates of sodium and magnesium. Ellison *et al.* (2000) observed comparatively lower soil salinity (5-15 ppt) in the Sundarbans of Bangladesh (Eastern Sunderbans). This is because following a tectonic activity in the Bengal basin, the drainage pattern shifted eastwards, resulting in substantial reduction in freshwater flow into the western side of the Sundarbans, and a natural west-to-east salinity gradient across the delta (Deb 1956).

Vegetation-environment interactions

The structure of a mangrove forest at any time is a function of its successional stage, species composition, zonation, propagule dispersal, growth, and survival; all influenced by a number of biotic as well as abiotic factors such as propagules predation, herbivory, human interference, storm damage, tidal influence, freshwater input, sedimentation rate, nutrient availability and light

(Krauss *et al.* 2008; McGowan *et al.* 2010). In this study, sites having diurnal inundation were dominated by *A. alba*, *A. marina*, and *A. ilicifolius*. Similar observations were made by Saha & Choudhury (1995) and Pal *et al.* (1996) where they observed that *A. ilicifolius*, *A. alba*, and *A. marina* occur dominantly in soils with high salinity, and frequent and long duration tidal inundation in various islands of the Sundarbans. Tree height and diameter were also related to the type of inundation and had higher values in the diurnal inundated coastal *A. alba* (CT4) and tidal *A. marina* (CT7) communities. The dense mixed vegetation community (CT8) which is inundated only during spring tides, had low tree height and diameter. The freshwater turnover is a crucial factor for structural development - riverine and basin mangroves show taller canopies than the scrub, fringe, and overwash type (Pool *et al.* 1977). Tall forest formation also occurs along creeks (Durrington 1973) or on the most seaward margin of mangrove stands which are inundated by all high tides (Dowling 1986). However, a tidal storm is the most important climatic factor causing enormous damage to mangrove forests, particularly in the Caribbean and the Bay of Bengal (Kathiresan & Bingham 2001). Frequent violent cyclones (four to eight per year) occur from August to November in the Sundarbans resulting in forests characterized by short canopies and higher densities of smaller trees (Fosberg 1971). Forests that were not affected by hurricanes had taller canopies, less dense stands, but greater diameters in south Florida and Puerto Rico (Pool *et al.* 1977).

There were significant differences in biomass values in relation to tidal inundation. Communities having long duration diurnal inundation had high biomass values. Environments flushed adequately and frequently by seawater and exposed to high nutrient concentrations are more favourable for mangrove ecosystem development and exhibit high rates of net primary productivity (Lugo & Snedaker 1974). Chen & Twilley (1999) noticed 50 % decline in biomass production bet-- ween 5 and 10 km distance from the estuary mouth along the Shark River estuary, Florida. In an earlier study, we also reported a decrease in aboveground biomass with increase in distance from the coast (Joshi & Ghose 2002).

Generally mangrove vegetation is more luxuriant in soils with lower salinity (Kathiresan *et al.* 1996). Hyper salinity stunts tree growth in *A. marina* stands (Selvam *et al.* 1991; Selvam & Ravichandran 1998). In Senegal, hyper salinity (from a decade of low rainfall and high evaporation) has caused complete destruction of mangrove vegetation (Diop *et al.* 1997). With increasing salinity, the values of a number of structural and functional parameters of mangrove forests decrease (Cardona & Botero 1998; Cintron *et al.* 1978; Naidoo 1990). The stunted mangroves in the hyper saline soils have much lower canopies, more main stems and smaller leaves (Pool *et al.* 1977). In this study, high complexity and diversity in *Aegiceras* (CT3) and mixed vegetation (CT8) communities may be attributed to lower salinity and close proximity of creeks. The *geometric series* distribution in community type 2 and 5 was due to a stressful environment. Community type 2 had very low salinity; however, it was experiencing soil erosion along with progression of a sand shoal towards it. Community type 5 had hyper saline soil coupled with a lack of tidal flushing. Odum (1983) points out that the stress, either natural (e.g., change in salinity, physiologically dry soil, over siltation, lowering of land by erosion, cyclones and tidal surges) or anthropogenic (e.g., cultivation, cutting for timber, firewood) tend to steepen the dominance diversity curves.

Higher soil salinity was observed in communities with diurnal inundation (CT4, CT7) due to regular ingress of sea water, and in dry uninundated communities (CT5, CT6) due to accumulation of salts form high surface evaporation. It appears that lack of water was the primary stress rather than salinity in the stunted *A. marina* communities (CT5, CT6). It is interesting to note that the sites with structurally developed *A. alba* (CT4) and tidal *A. marina* (CT7) communities, both having diurnal inundation, also had high salinity. According to Naskar & Guhabakshi (1982), the underground water table is shallow and enriched with high salt contents in the Sundarbans. During dry seasons, the salt molecules move along with water to the surface soil by capillary action (Yadav *et al.* 1981) and accumulate in toxic amount for plant growth (Chattopadhyay *et al.* 1983). On the other hand, the communities adjacent to creeks - dense mixed (CT7) and *Aegiceras* (CT3) communities- had lower soil salinity than those with diurnal inundation (CT4, CT7), due to regular lateral seepage of ground water. Close proximity of a creek increases the movement of water table, and the larger and deeper the creek, the greater the water pressure and lateral movement of water table (Bandopadhya 1986).

Among soil nutrients, nitrogen and phosphorus have been implicated as the nutrients most likely limiting primary productivity of mangrove ecosystems (Boto & Wellington 1984). Nitrogen was found to limit growth of *A. marina* in South Africa (Naidoo 2009) and New Zealand (Lovelock *et al*. 2007b). In more tropical latitudes, phosphorus limited growth in high intertidal scrub forests (Boto & Wellington 1983; Lovelock *et al*. 2007a). However, in this study, regression of biomass with soil parameters explained only 29 % variation. This may be because nutrient availability in the mangrove soils varies between and within mangrove stands (Feller *et al*. 2003). The availability of nutrients to mangrove plant production is further controlled by a variety of biotic and abiotic factors such as tidal inundation, elevation in tidal frame, soil type, redox status, microbial activities of soil, and plant species (Reef *et al*. 2010).

Conclusions

We provide new and useful information on the forest structure and aboveground biomass of mangroves, particularly in view of the paucity of a detailed analysis in the Indian Sundarbans. This study has found that a variety of forest types and structures, with different dominant species exist within the island. The species composition and prevailing conditions of vegetation structure and biomass indicates an evolving or expanding forest that seem conducive to sustain a mature forest ultimately. The mangrove forests are under immense pressure from clear cutting, land-use change, hydrological alterations, chemical spill, and climate change (Blasco *et al*. 2001). The information generated from this study will serve as a baseline and offers an interesting array of attributes for further research.

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