

エジプト紅海沿岸のマングローブ林の林分構造

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Forest structure of gray mangrove (*Avicennia marina*) along Egyptian Red Sea coastKen Yoshikawa^{a)}, Masaki Inoue^{b)}, Ichidou Yoshimori^{b)}, Atsushi Nakashima^{c)},
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(Course of Environmental Ecology)

Established mangrove forests along the coastal area of the Arabian Peninsula and African side of the Red Sea are uniquely different from mangrove forests in other parts of the world because of their low biodiversity and harsh habitat of arid and highly saline conditions. Therefore mangrove forests in this area appear in patchy and scattered patterns at mouths of wadi or in sheltered lagoons with rare and irregular flooding. Most of them are pure forests of *Avicennia marina*, occasionally mixed with *Rhizophora mucronata* in the southern part of the Red Sea. In this study, we analyze the forest structure of *A. marina* and discuss the regeneration strategy and the forest dynamics of this unique mangrove species. Three experimental plots of 1000 to 2000 trees/ha were selected from north to south along the Red Sea coast. The highest tree size (6.8 m) suggested severe effects of the high salinity of the Red Sea (3.2 to 4.9‰) on tree growth. Dense mantle vegetation had developed at the forest edge facing the open sea to protect the forest interior against strong waves and wind. Tree growth was also prevented by severe drought on the landside edge of the forest. All the forests had a dense seedling bank throughout the forest floor, with a very high rate of turnover and regeneration, which seldom occurred in other forests.

Key words : Gray mangrove (*Avicennia marina*), the Red Sea, forest structure, seedling bank

1. Introduction

Mangroves are a group of trees which can grow under conditions of flooding with brackish water in tidal zones of tropical and subtropical regions³⁹⁾. More than 80 species are recorded as mangroves worldwide, with the highest species diversity in Southeast Asia followed by the Indian and African coastal areas³⁶⁾. Mangroves are used as many kinds of biomaterials, such as building materials, firewood, charcoal, fodder, medicine, etc.^{8, 28, 35)}, not only for local subsistence but also for a wide range of commercial demands. Mangrove forests can protect coastal areas from wave erosion²⁵⁾ and can defend against tsunamis⁹⁾, because of their dense structure above and below ground. They can also provide suitable habitat for many kinds of fish and birds^{12, 13, 14, 17, 29)}. Although mangrove forests are ecologically and sociologically invaluable, at least 35% of the area of mangrove forests has been lost in recent decades through human disturbance, losses that exceed those for tropical rain forests and coral reefs, two well-known threatened environments⁴⁰⁾, because of the good accessibility and convenience of these coastal areas for social development and their closeness to human milieu.

Established mangrove forests along the coastal area of the Arabian Peninsula and African side of the Red Sea are unique, differing from the world's other mangrove forests in their low biodiversity and harsh environmen-

tal conditions for tree growth. Different from Southeast Asia, with its big rivers and wide brackish water areas, suitable habitat for mangroves is seldom found along the Red Sea coast, because of the arid and semiarid climate of the hinterlands. Therefore mangrove forests in this area appear in patchy and scattered patterns at the mouths of wadi or in sheltered lagoons with rare and irregular flooding³⁾. Their distribution is limited by aridity and site topography. Regarding mangroves, as with other flora, only a small number of species can grow in such an arid and highly saline habitat. Therefore almost all mangrove forests in the Red Sea area, including the Gulf of Aqaba, are pure forests of *Avicennia marina*, occasionally mixed with *Rhizophora mucronata* in the southern part of the Red Sea²¹⁾.

Most of these mangrove forests nowadays are protected and managed by the government, at least in Saudi Arabia, Kuwait, Qatar, UAE, Oman and Egypt. However, a considerable number of mangrove forests

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are still continuously degraded under severe pressures²⁷⁾, such as firewood collection by local people, grazing by livestock (camels and sheep), and illegal cutting for development of residences or shrimp nurseries, just as with other mangrove forests around the world. Reforestation is the most effective countermeasure and it is producing considerably good results under sufficient support from JICA, *e.g.*, in Saudi Arabia^{23,24,33)}. However technical development and capacity building are still necessary in many countries.

As the reforestation trial in Egypt has just started, ecological research on *A. marina* forests is still limited^{1,15,16,18,22,32,35)}. In this study, we analyze the forest structure of *A. marina* established along the Red Sea coast and discuss a regeneration strategy and the forest dynamics of this unique mangrove species.

2. Climate conditions

The mean annual temperature at Hurghada is 24.5°C and the minimum monthly mean temperature is higher than 15°C (Fig. 1). Annual precipitation is only 5.3 mm and never exceeds 2mm in a month. The entire Egyptian Red Sea coastal area is considered "warm coastal desert" according to the categories of Meigs¹⁶⁾. Mangroves in the Red Sea grow only with sea water of high salinity at about 4‰ or more¹¹⁾ because of the scant supply of fresh water from river flows and rainfall. Incidentally, the sea water salinity in the tropical rain forest region of Southeast Asia is less than 3.5‰ due to dilution with river flows and heavy rain every day³⁷⁾.

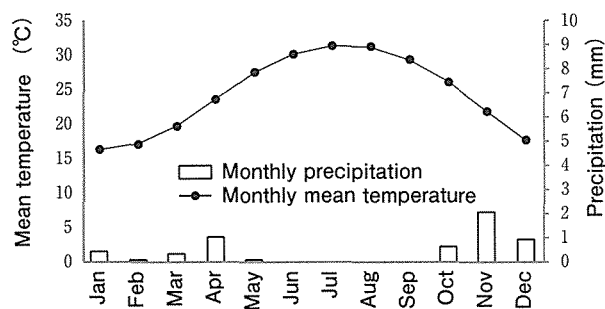


Fig. 1 Seasonal changes in air temperature and precipitation each month at Hurghada City.

3. Study sites and method

3-1. Study sites

Mangrove forest patches remaining in the Gulf of Aqaba and along the Red Sea coast number three and



Fig. 2 Locations of the three study sites (indicating National Park territory).

twenty-five, respectively, in Egypt as of 2010. Of these, twelve *A. marina* forests along the Red Sea coast were investigated in October 2009 and three relatively free from disturbance, such as livestock grazing and firewood collection, were selected as the study sites (Fig. 2).

Large stands (ca. 29 ha)³¹⁾ of *A. marina* within two lagoons occupy the center of Abu Monkar Island, an uninhabited island located 5 km off-shore from Hurghada City (Fig. 3 (a)). Both forests in the two lagoons have several channels within them. Beside one of these channels, one experimental plot (Plot Abu Monkar) 30 m in length and 15 m in width was established from the forest edge to the interior of forest where no human disturbance had occurred.

Within a big lagoon (ca. 0.65 ha) along the shore 41 km south from Safaga City (Fig. 2), a dense man-

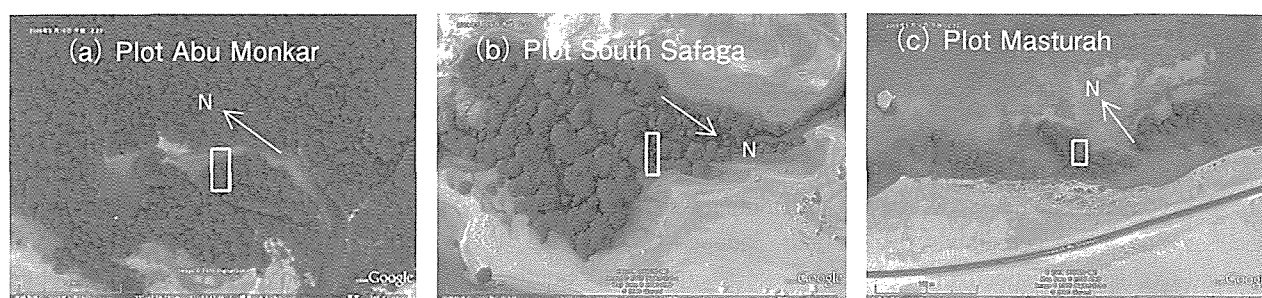


Fig. 3 Location of the experimental plot at each site. (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot Masturah.

grove forest had become established along a channel. Across the forest from the bank to the channel, one experimental plot (Plot South Safaga) (Fig. 3 (b)) 30 m in length and 5 m in width was established. As suggested by footprints and dung left around the forest, some of the trees had been slightly grazed by camels. However, the grazing pressure in this forest seemed less severe because of the long distance from the nearest Bedouin village.

In the Wadi El Gemal National Park (7,459 km²) (Fig. 2), which is located in the southernmost part of Egypt, more than six mangrove forests have become established at the mouths of wadis. Masturah is one of these mangrove forests, which developed at the mouth of Wadi Masturah. The inland part of the forest was grazed by camels coming from a small Bedouin village near Masturah. However, grazing activity was limited within the inland part of the forest with sandy ground conditions, because of the animals' avoidance of muddy and slippery ground conditions after the tide ebbed. Therefore, to avoid the effects of grazing, one experimental plot (Plot Masturah) 20 m in length and 10 m in width (Fig. 3 (c)) was established from the waterside forest edge to the interior.

3.2. Methods

A field survey was conducted in November 2009 for 17 days to measure the sizes of trees and examine environmental factors. Trees younger than three years old, estimated by changes in the inter-node length of the main stem, were considered seedlings and their heights and locations were measured. Stem diameters at 50 cm height from the ground were measured only for mature trees older than four years and bigger than 1 cm in diameter. Crown radii in four directions of mature trees were measured.

The salinity and pH of surface water and soil water

Table 1 Plot size and environmental conditions of each plot

Study Site	Plot Size (m ²)	Surface Water		Soil Water	
		pH	Salinity (%)	pH	Salinity (%)
Abu Monkar	450	7.4~8.1	3.2~3.4	7.1~7.9	3.7~4.1
South Safaga	150	7.6~8.1	3.7~3.8	6.9~7.4	4.3~4.9
Masturah	200	7.8	4.0~4.3	7.0~7.3	3.4~4.8

were measured using a salinity meter (Custom Coop., SA-02) and pH meter (Custom Coop., PH-01). Surface water was collected from 10 cm below the water surface at high tide and soil water was extracted using a ceramic porous cup at low tide from 30–40 cm depth below the forest floor where the main root system of *A. marina* was distributed (Table 1).

The ω index was calculated for different unit sizes to evaluate the overlapping of spatial distribution of mature trees and seedlings in a forest⁽²⁰⁾. At first, the γ and the γ (ind) indexes which were the overlap degree and the expected value of γ when species x and y were distributed completely independently were calculated as follows.

$$\gamma = \sqrt{\frac{m_{xy}^* m_{yx}^*}{(m_x^* + 1)(m_y^* + 1)}}$$

$$\gamma \text{ (ind)} = \sqrt{\frac{m_x}{(m_x^* + 1)} \cdot \frac{m_y}{(m_y^* + 1)}}$$

where m_x and m_y are the mean densities of species x and y , m_x^* and m_y^* are the mean crowding indexes of species x and y , m_{xy}^* is the mean crowding index of species x by species y .

$$m_x^* = \frac{\sum_{i=1}^Q X_i(X_i - 1)}{\sum_{i=1}^Q X_i} \quad \text{and} \quad m_{xy}^* = \frac{\sum_{i=1}^Q X_i Y_i}{\sum_{i=1}^Q X_i}$$

where X_i is number of individuals of species x in quadrat i and Q is the total number of quadrats.

When $\gamma \geq \gamma \text{ (ind)}$,

$$\omega(+) = \frac{\gamma - \gamma(\text{ind})}{1 - \gamma(\text{ind})}$$

and when $\gamma < \gamma(\text{ind})$,

$$\omega(-) = \frac{\gamma - \gamma(\text{ind})}{\gamma(\text{ind})}$$

then ω becomes 1, 0 and -1 where the distributions of species x and y are completely overlapping, independent and exclusive, respectively.

4. Results and discussion

4.1 Tree sizes and forest density

The mature tree density of the three experimental plots ranged from 1000 to 2000 trees/ha (Table 2). The mean and maximum heights of mature trees were 2 to 4 m and 3.5 to 6.5 m, respectively. The largest tree in Plot Masturah was 6.8 m in height and 32.8 cm in DBH, followed by 4.8 m, 21.5 cm in Plot Abu Monkar and 3.6 m, 9 cm in Plot South Safaga, showing the order of forest development stages.

Compared with an *A. marina* forest in Vietnam where the mean and maximum heights were 1.8 m and 5.1 m, respectively, and the tree density was more than 5000 trees/ha¹⁹⁾, the three experimental forests in this study were of small size and low density. An *A. marina* forest in Oman had almost the same size of trees as this study but the tree density (2000 to 8000 trees/ha)⁴¹⁾ was much higher than those of this study's sites.

The northwest part of the Gulf of Aqaba (28° latitude) is the northernmost extent of *A. marina* in the Red Sea^{21,30)}, and pure forests of *A. marina* can grow along the northern coast of the Red Sea, because of the mangroves, *A. marina* is the most tolerant of low temperatures and high salinity³⁹⁾.

Although *A. marina* can grow 20 to 30 m in height at Chennai (12° latitude, in India) with 1,376 mm in precipitation and 0.5 to 1.3‰ salinity of sea water³⁴⁾, the highest tree size estimated by D-H relations in this study (not present) was only 8.2 m in Plot Masturah. The salinity level of coastal areas of the Red Sea (3.2 to

4.9‰ as shown in Table 1) had a severe impact on their growth, as the optimal salinity for *A. marina* was reportedly 0.3 to 1.75‰^{7,10)}.

4.2 Forest structure

Fig. 4 shows the spatial distribution of trees and the topography of plots. Hatched areas indicate a channel or open sea (the waterside). Both Plot Abu Monkar and Plot South Safaga were established from the forest edge to the interior and Plot Masturah had the forest edges on opposite sides which faced a channel and an inland bank (the landside), respectively.

Fig. 5 shows the changes in tree density from the waterside forest edge. Figs. 6, 7 and 8 show the relationships between the mature tree size parameters, including CPA, stem diameter and height, and the distance from waterside forest edge. In Plot Abu Monkar, the mature tree density (Fig. 5(a)) and tree sizes, especially heights (Fig. 6(c)), showed a gradual increase for about 10 m from the waterside forest edge toward the interior. However, both Plot South Safaga and Plot Masturah had higher tree densities (Fig. 5 and (c)) and bigger tree sizes (Fig. 7 and 8) at the waterside forest edge than at the interior.

Small trees were growing at the waterside forest edge of Plot Abu Monkar for about 5 m toward the interior of the forest where different-sized trees including the largest trees were growing densely. Such mantle vegetation in which big and small trees were coexisting at the forest edge was established in Plot Masturah the same as in Plot Abu Monkar, but the extent was less than 5 m from the forest edge. On the other hand, there were no small trees at the forest edge of Plot South Safaga. The dense mantle vegetation in Plot Masturah could protect the forest interior environment against strong waves and winds from the open sea. In Plot Abu Monkar and Plot South Safaga, however, the forest edge facing a channel provided no necessary advantage in the struggle against waves and winds. If there was a space between the forest edge and the channel, small trees could grow there to extend the

Table 2 Tree densities and sizes of mature trees in each plot

Study site	Number of Trees (N/ha)	Number of Seedling (N/ha)	Height(m)			Diameter (cm)			CPA		Basal Area (m ² /ha)
			Mean	Max	Min	Mean	Max	Min	Mean (m ² /N)	sum (ha/ha)	
Abu Monkar	1633	2600	2.34	4.79	0.65	7.2	21.5	1.5	8.9	1.5	12.2
South Safaga	1200	15133	1.95	3.59	1.02	3.5	9.0	0.5	5.3	0.6	1.3
Masturah	2200	2500	4.15	6.77	0.90	9.2	32.8	1.1	16.0	3.5	38.3

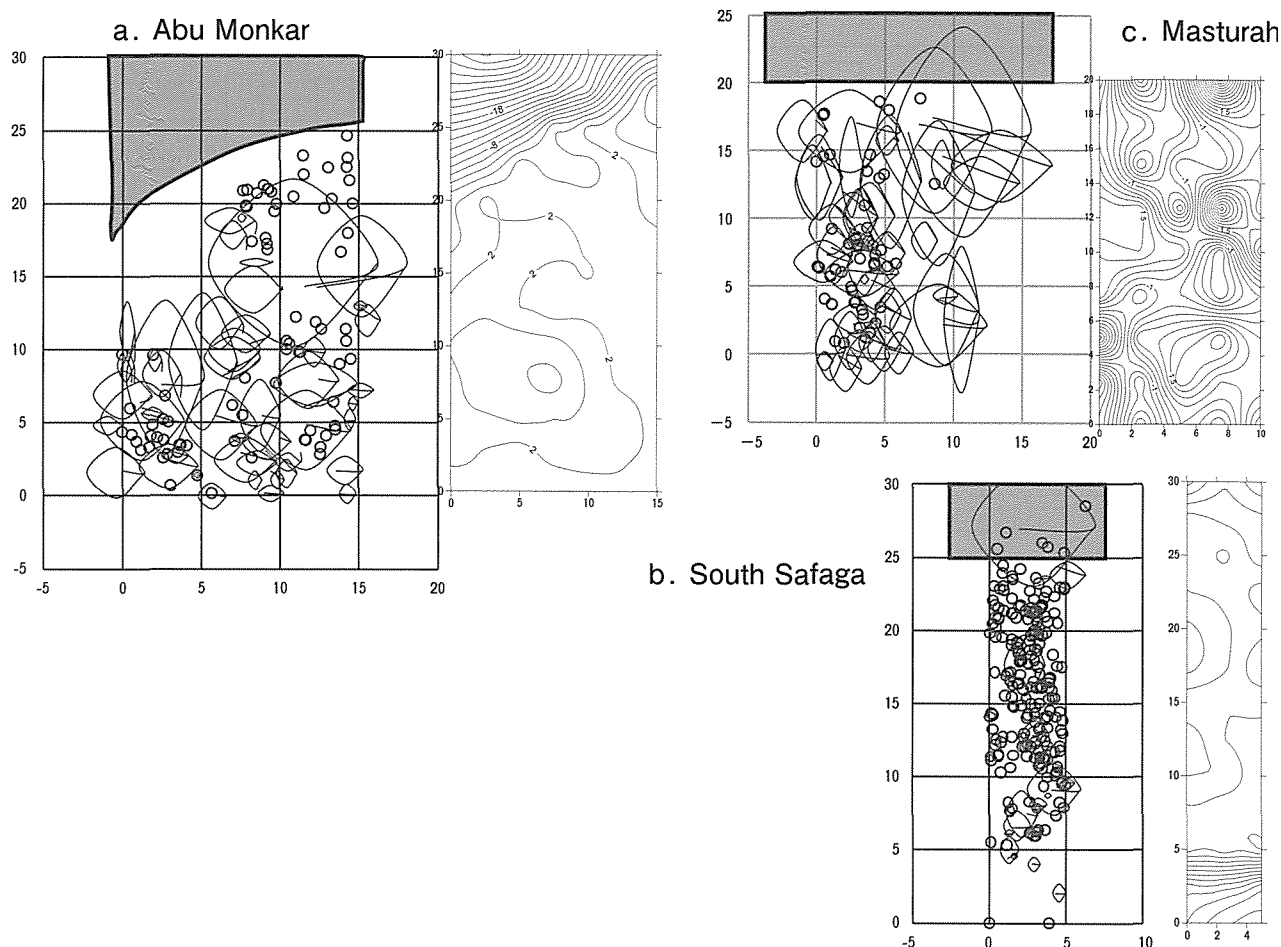


Fig. 4 Spatial distribution of trees and their crowns (left), and topography (right). (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot Masturah. Hatched areas are channels or open sea (the waterside).

forest area (Plot Abu Monkar), but the forest edge consisted only of large trees after the forest reached the edge of channel (Plot South Safaga and Plot Masturah). Therefore the forest edge structure was strongly determined by the external conditions.

Relatively small-sized trees were growing in the interior of all three forests, with constant tree density, namely 4 m, 2 to 3 m and 1 to 2.5 m in height and 20 to 30 trees, 20 trees and 5 to 10 trees/ha in Plot Masturah, Plot Abu Monkar and Plot South Safaga, respectively (Fig. 6(c), 7(c) and 8(c)).

At the landside forest edge of Plot South Safaga (Fig. 5(c) and Fig. 7), the tree density became very high and the tree sizes remained small. Judging from the tide table in this region, the landside endmost part of Plot South Safaga was not submerged even at the highest tide in summer.

Although the sizes of trees and tree densities in the interior of the forests showed remarkable differences

among the three experimental plots in accordance with forest development, the interior structure seemed to be homogeneous within each forest. On the other hand, shrubby and dense mantle vegetation formed along the landside forest edge of Plot South Safaga, because tree growth there was prevented by severe drought stress and highly saline soil conditions due to the ground level being higher than high tide level in summer.

4.3 Regeneration

No regeneration was observed in the open sea at Plot Masturah (Fig. 5(b)) or in deep channels at either Plot Abu Monkar (Fig. 5(a)) or Plot South Safaga (Fig. 5(c)). The density of seedlings was about 30 seedlings/100 cm² at the outside and the interior of Plot Abu Monkar (Fig. 5(a)) and it decreased at the waterside forest edge. In Plot Abu Monkar and Plot Masturah, the highest regeneration occurred at 10 m internally from the forest edge, differing from the case of Plot South Safaga, where a high rate of regeneration

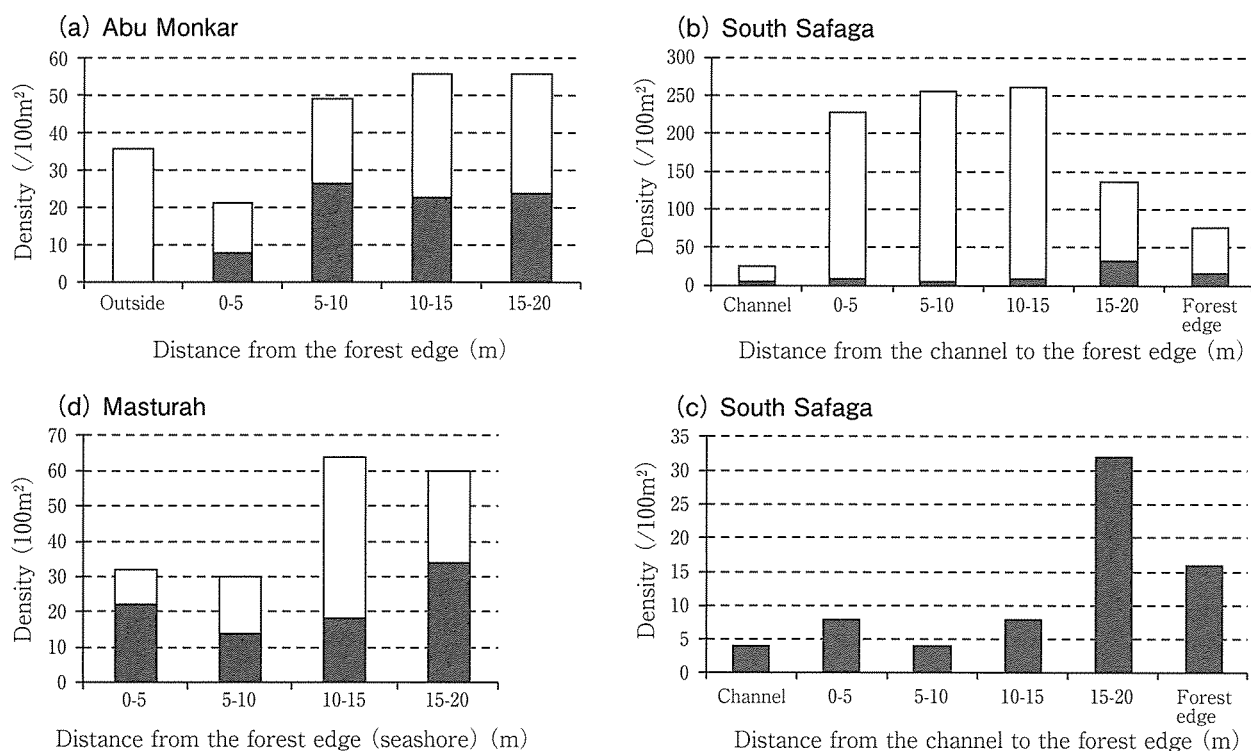


Fig. 5 Changes in tree density from the waterside forest edge of each plot. □Seedlings, ■mature trees. (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot South Safaga for mature trees only, (d) Plot Masturah.

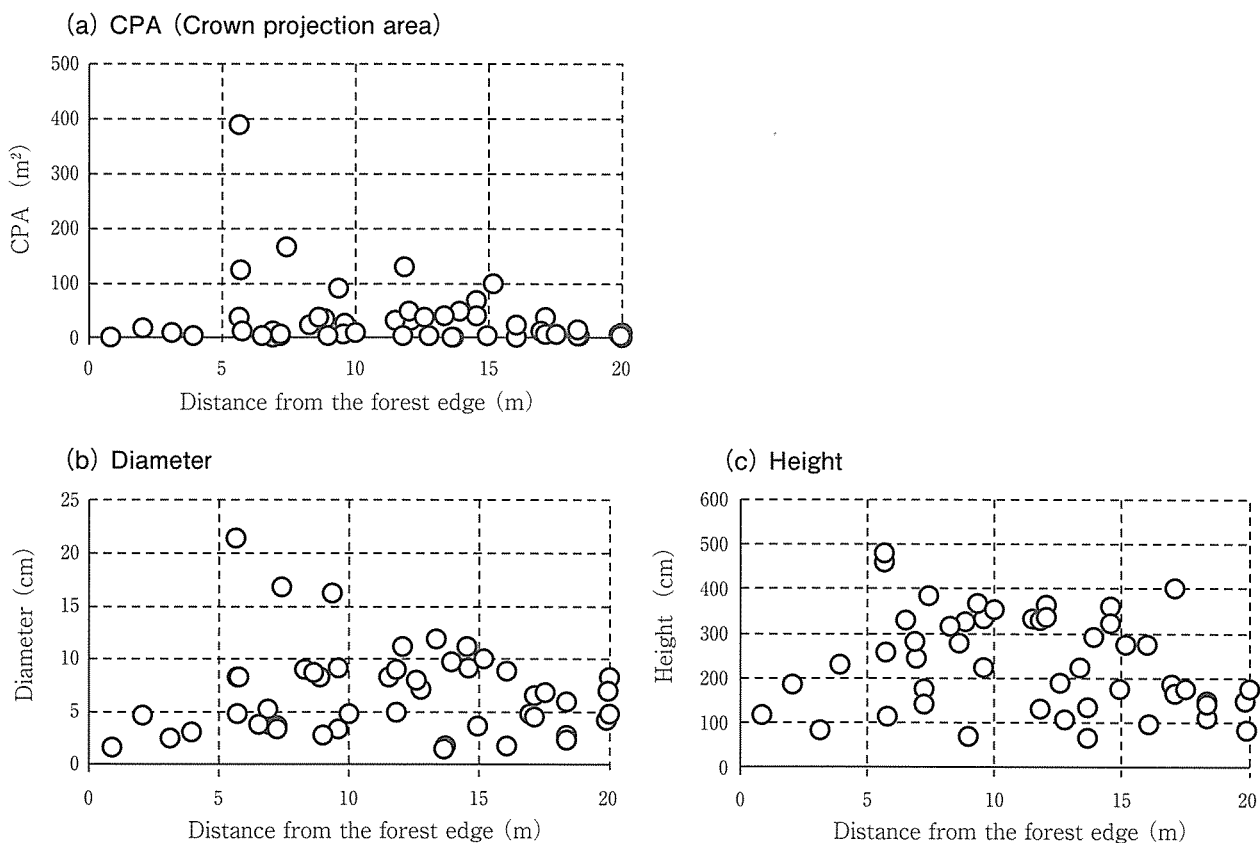


Fig. 6 Relationships between the mature tree size parameters ((a) CPA, (b) stem diameter and (c) height) and the distance from the waterside forest edge (Plot Abu Monkar).

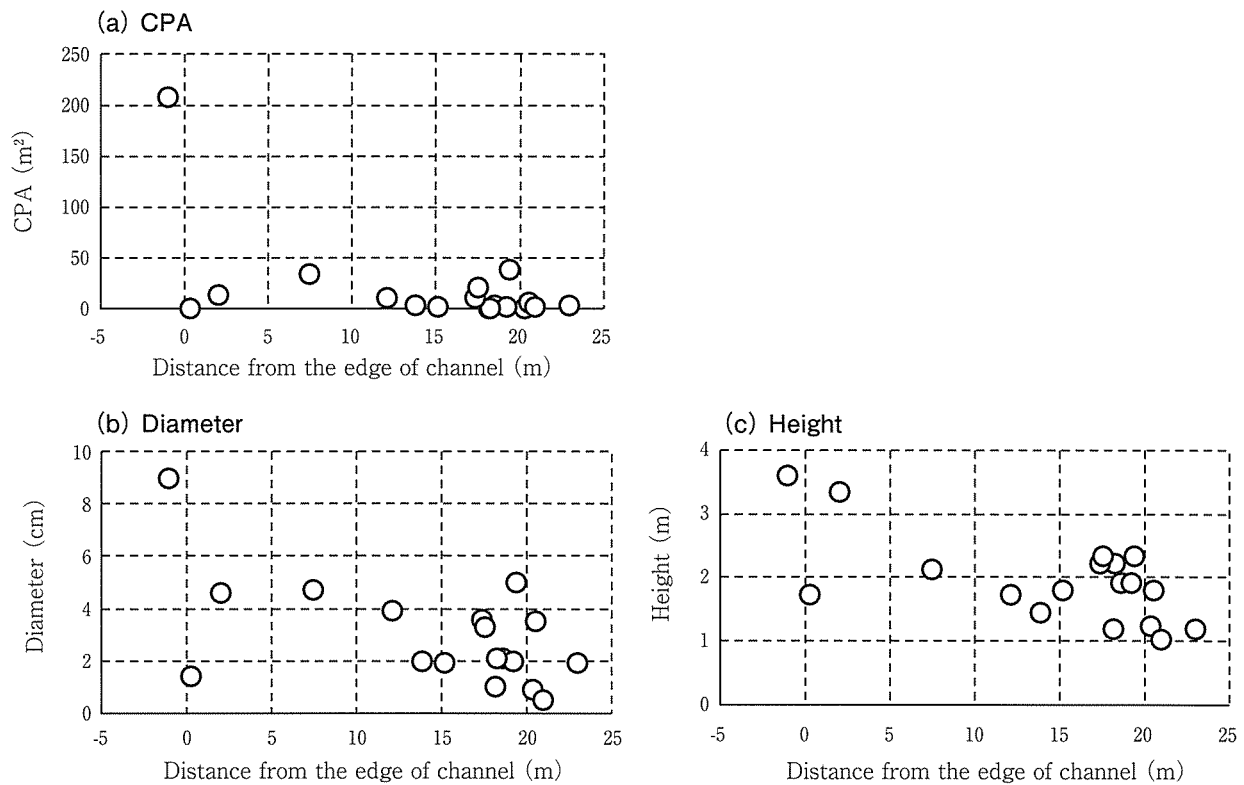


Fig. 7 Relationships between the mature tree size parameters ((a) CPA, (b) stem diameter and (c) height) and the distance from the waterside forest edge (Plot South Safaga).

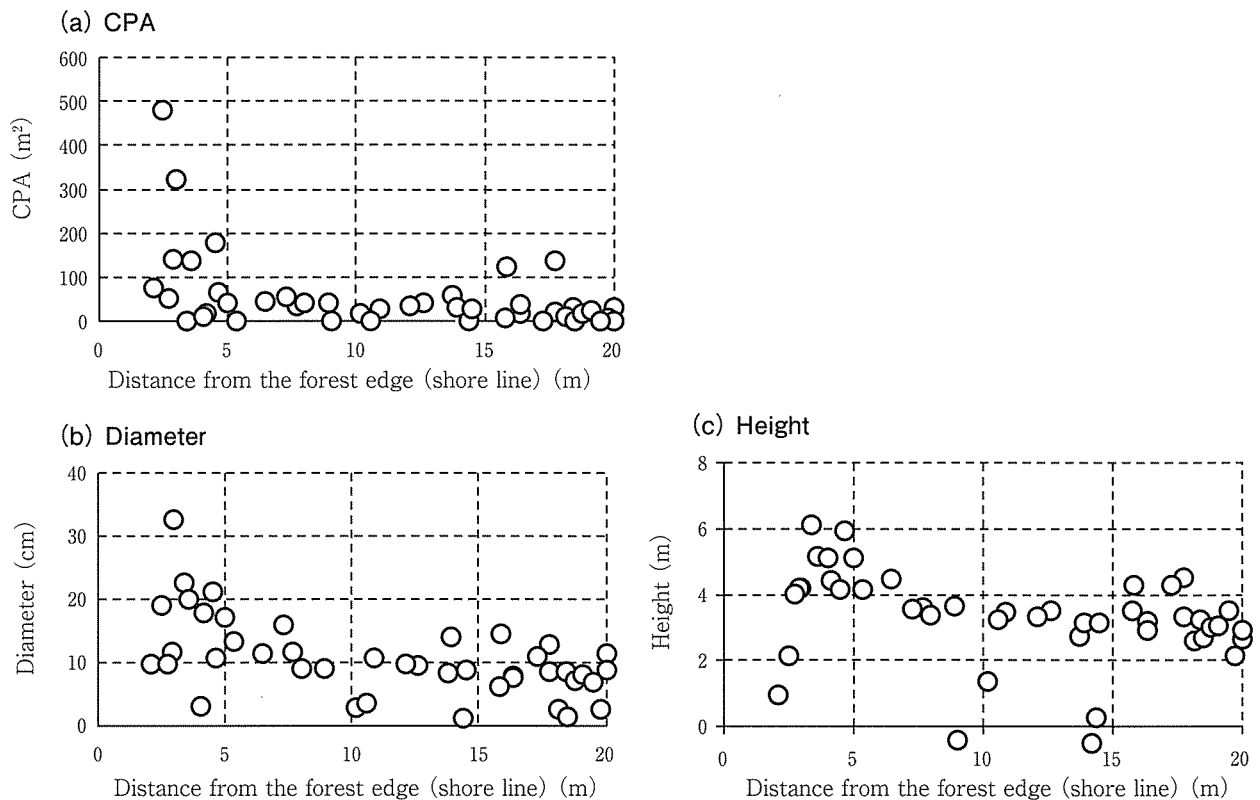


Fig. 8 Relationships between the mature tree size parameters ((a) CPA, (b) stem diameter and (c) height) and the distance from the waterside forest edge (Plot Masturah).

occurred from the waterside edge and continued at the same level for all parts of the interior (Fig. 5(c)). The regeneration density also decreased under the landside shrubby mantle vegetation at Plot South Safaga, because of the effect of high soil salinity on the growth of the seedlings⁴²⁾. Fig. 9 shows the changes in the cumulated CPA (total canopy coverage per 1 m² of forest floor) as the distance from the waterside edge of forest increases. There were remarkable differences in canopy structure of the forest interior between Plot South Safaga and the other two plots, indicating light conditions at the forest floor at Plot South Safaga and dark conditions under dense canopy at the other two plots. Fig. 10 shows the relationships between regeneration density and cumulated CPA. All plots showed a negative relationship suggesting a strong inverse effect of canopy coverage on regeneration activity. However, at Plot Abu Monkar and Plot Masturah, suppression of regeneration could be detected at the forest interior where the cumulated CPA exceeded about 1–1.5 m²/m².

It is necessary for some leaves of the seedlings of *A. marina* to stay above water for a sufficient period of time each day to ensure aerial gas exchange for metab-

olism and growth³⁸⁾. Therefore, matured seeds dispersed by waves can settle and germinate only at the seashore between the high tide and low tide lines, where natural mangrove forests have been established. Although a strong negative effect of canopy coverage on regeneration density was detected, the light conditions of the forest interior at Plot Abu Monkar and Plot Masturah were still sufficient to allow germination and survival of seedlings even under the dense canopies. As a result, regeneration seldom occurs outside forests which have already expanded to the edge of deep channels or the open sea and the forest interior is the main site for regeneration because of sufficient light conditions and suitable tide levels for germination and growth of seeds.

The heights of seedlings under the forest canopy at Plot Abu Monkar were 20 to 30 cm with several exceptions which could grow larger and some seedlings growing outside the forest exceeded 30 cm in height (Fig. 11 (a)). At Plot Masturah (Fig. 11(c)), small seedlings 20 to 30 cm in height grew all over the forest floor and large seedlings over 40 cm in height appeared at the interior beyond 5 m from the forest edge. Very large seedlings higher than 1 m in height grew at the edge of

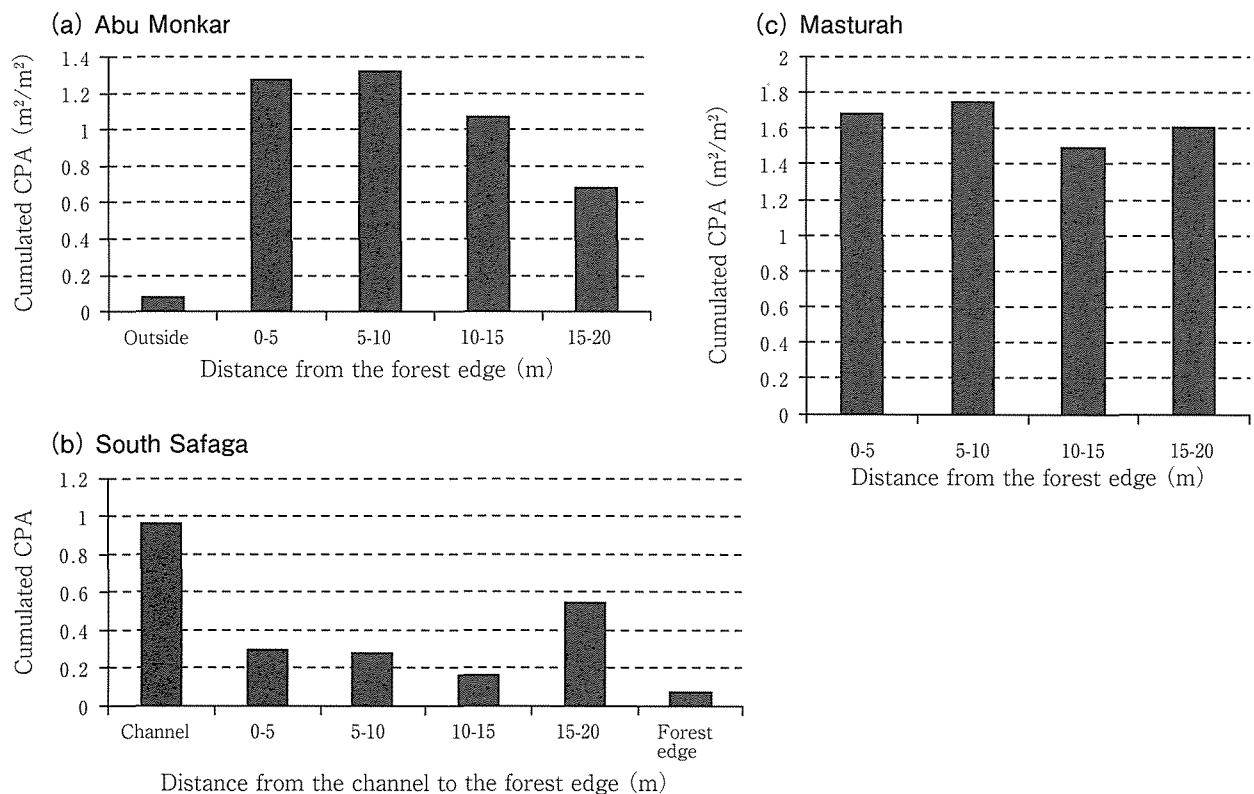


Fig. 9 Changes in cumulated CPA from the waterside edge of forest at each plot. (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot Masturah.

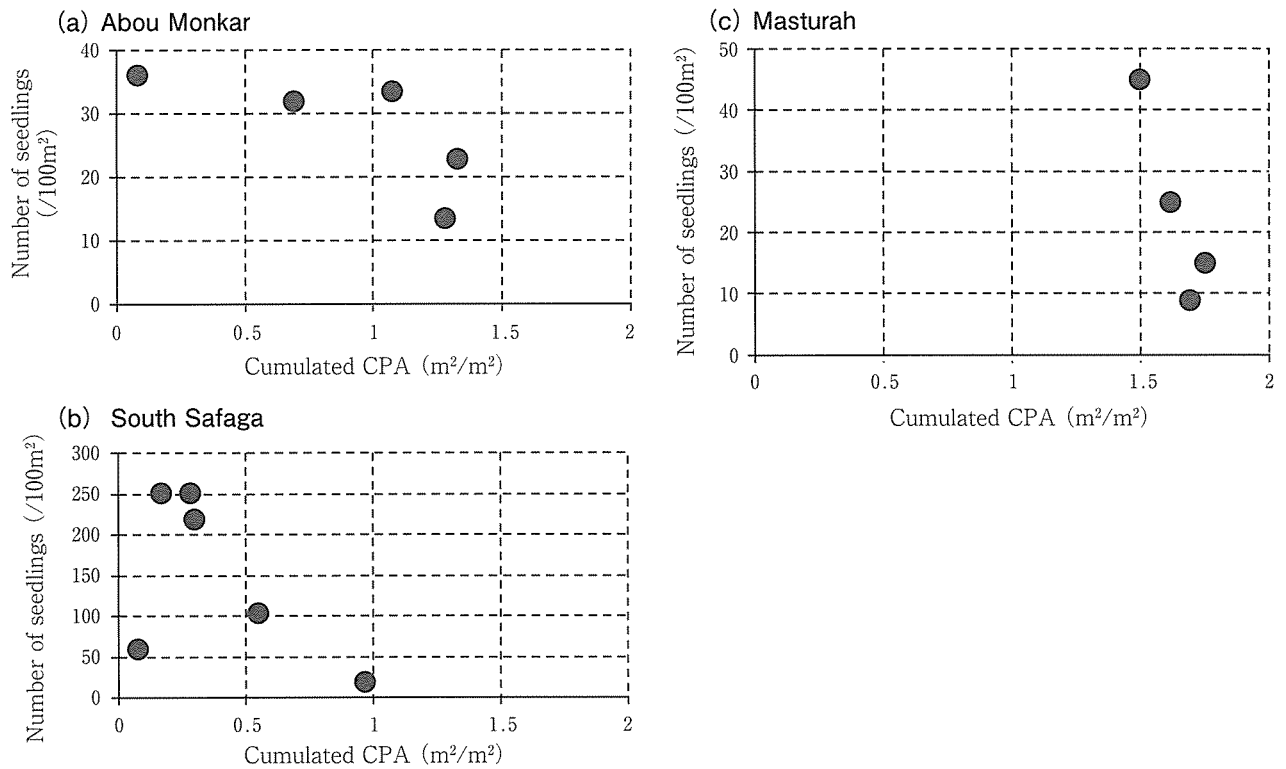


Fig. 10 Relationship between regeneration density and cumulated CPA. (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot Masturah.

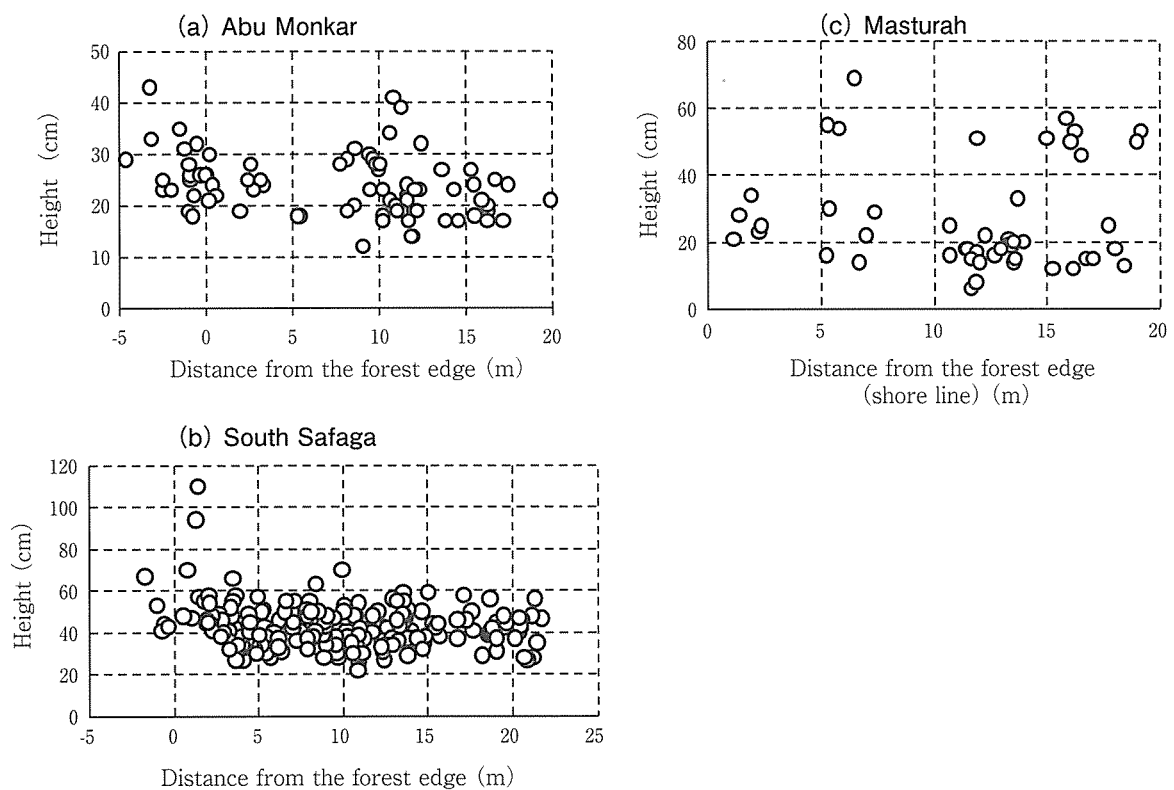


Fig. 11 Relationship between heights of seedlings and the distance from the waterside forest edge. (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot Masturah.

the channel at Plot South Safaga (Fig. 11(b)) and relatively large seedlings 30 to 60 cm in height produced dense vegetation throughout the forest floor including the landside forest edge.

All the seedlings at Plot Abu Monkar and 78% at Plot Masturah were yearlings (Table 3). Two-year seedlings comprised the largest cohort at Plot South Safaga. However, only 3.3% of the seedlings were older than three years. The average height of the yearlings showed slight differences among the experimental plots ranging from 20.4 to 38.1 cm. The average height increased as age progressed, but the relationship between age and height showed a slight difference between Plot South Safaga and Plot Masturah, reflecting differences in site conditions.

As the initial growth of *A. marina* seedlings is supported by reserved nutrients within the seeds for five to seven months^{5,38)}, seedlings from seeds of the same size

can reach the same minimum height²⁾, namely 20 to 30 cm in this region. Judged by the height of the yearlings, Plot South Safaga seemed to be the best site among the three forests for survival and growth of seedlings just after germination. The dense vegetation of seedlings established on the forest floor is a seedling bank⁶⁾ preparing for immediate replenishment of canopy trees with seedlings after gap formation, but the age distribution of the seedlings in each plot indicated a short-term turnover, within one or two years after germination.

4.4 Spatial relationship between mature trees and seedlings

The ω index of Plot Abu Monkar (Fig. 12(a)) and Plot South Safaga (Fig. 12(b)) remained almost zero for all unit sizes, which indicated an independent spatial distribution of mature trees and seedlings. On the other hand, the ω of Plot Masturah (Fig. 12(c)) approached

Table 3 Density (/100cm²) and average height (cm) of seedlings in each plot

Age (yrs)	1		2		3		4<	
Location	n	Mean*	n	Mean*	n	Mean*	n	Mean*
Abu Monkar	31	25±6						
South Safaga	45	38±8	91	43±8	4	54±19	1	70
Masturah	20	20±10	1	24	2	46±9	3	55±7

* : Mean ± SD

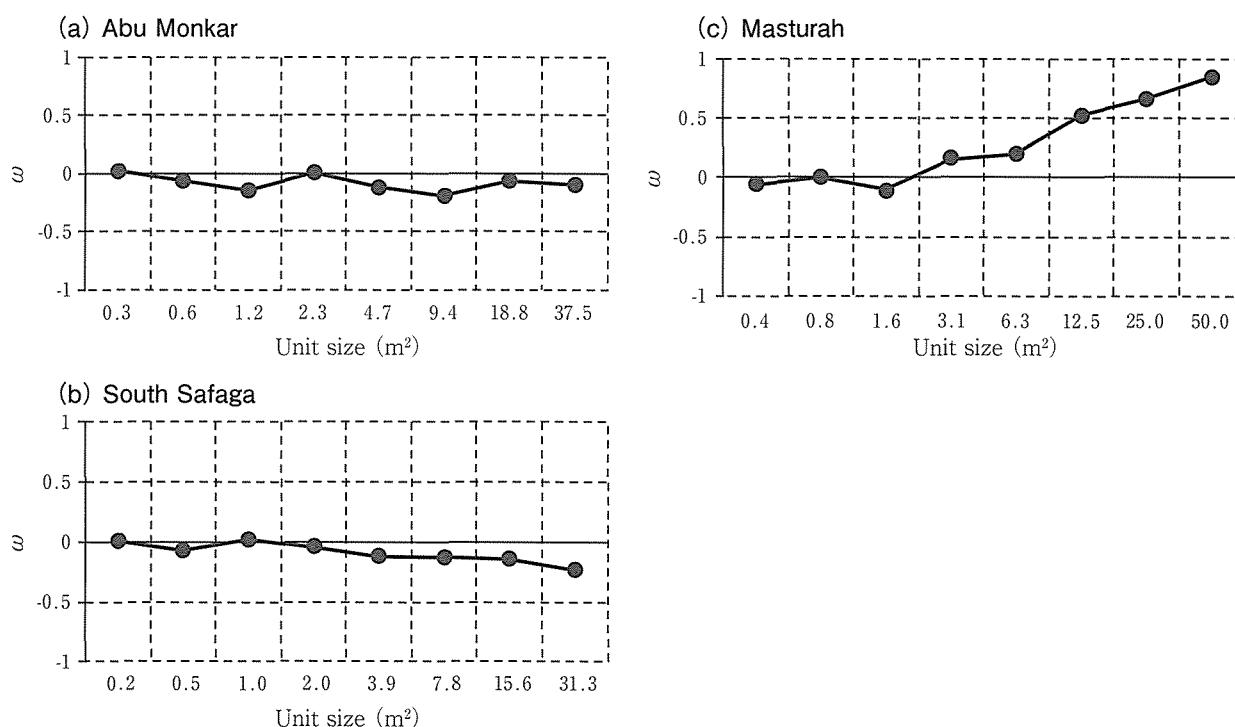


Fig. 12 Changes in the ω index with unit size. (a) Plot Abu Monkar, (b) Plot South Safaga, (c) Plot Masturah.

unity as the unit size increased, which indicated an overlapping distribution of mature trees and seedlings with each other.

Judging from Fig. 4, the overlapping distribution at Plot Masturah seemed to have been caused by the aggregation of seedlings under small mature trees.

Distribution of seedlings independently from mature trees at Plot Abu Monkar and Plot South Safaga suggests extensive regeneration or maintenance of the seedling bank throughout the forest canopy. There is no settlement of seedlings for more than one year in Plot Abu Monkar because of severe environmental conditions on the forest floor caused by the closed forest canopy. No seedlings older than two years outside of the forest, where the yearlings can grow higher than those growing within the forest interior suggests effects of some other factor controlling the settlement and growth of seedlings in this area. Under spaces and open canopy at Plot South Safaga, a great number of seedlings can grow at least for two years and some of them show active recruitment of upper layer members to close canopy gaps.

Seedlings of *A. marina* can germinate and establish dense seedling banks under a wide range of environmental conditions, for example from open land to dark forest floor under dense canopy, because of their high degree of shade tolerance⁴⁾ and the complete dependence of their initial growth upon reserved nutrients within the seeds⁵⁾. The size and structure (age) of a seedling bank should be affected by the productivity of the seed source, the energy allocation strategy of the mother plant and the site conditions above and below the ground²⁶⁾. Therefore, seed productivity and the factor(s) affecting seedling survival will be the main targets of future study.

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エジプト紅海沿岸のマングローブ林の林分構造

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アラビア半島沿岸と紅海のアフリカ側沿岸に成立しているマングローブ林は、種組成の単純さと生育環境の厳しさによって、世界の他の地域のマングローブ林と大きく異なるものである。ここのマングローブ林は不規則で滅多に起こらない洪水に依存して、ワジの入り口やラグーンの内側に、パッチ状に小さな林分を形成している。ほとんどの林分はヒルギダマシ (*Avicennia marina*) の純林で、紅海の南部では一部でヤエヤマヒルギ (*Rhizophora mucronata*) が混生する。本研究ではそのヒルギダマシ林の林分構造を解析し、本種の再生産戦略や林分動態について検討した。林分密度が1,000から2,000本/ha の林分を3つ選んだ。最大樹高は6.8 mしかなく、紅海の高い塩分濃度が本種の成長を強く抑制していることが示唆された。林分の縁が海に開いている林分では、林内への波や風の影響を抑制するために、高密度のマント群落が発達していた。林分の陸側でも乾燥によって成長が抑制されていた。どの林分でも林床には高密度な稚樹バンクを持っていたが、林外での更新は限られていた。

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