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Gap formation and regeneration of tropical mangrove forests in Ranong, Thailand

Nobuo Imai*, Masaaki Takyu, Yukito Nakamura and Takehisa Nakamura
*Laboratory of Forest Ecology, Department of Forest Science, Faculty of Regional Environmental Science, Tokyo University of Agriculture, Sakuragaoka 1-1-1, Setagaya-ku, Tokyo 156-8502, Japan; *Author for correspondence (e-mail: 96-nobuo@nodai.ac.jp; fax: +81-3-5477-2495)*

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Abstract

Tropical mangrove forests are characterized by clear zonation along a tidal gradient, and it has been supposed that the zonation is primarily controlled by soil factors. However, effects of disturbance on mangrove forests are still not well understood and may play an important role on the vegetation patterns and forest dynamics in some forest formations. In this study, the pattern of disturbance regime and its effects on regeneration of tropical mangrove forests along a tidal gradient were investigated in Ranong, Thailand. We established one or two 0.5 ha plots in four vegetation zones, i.e. *Sonneratia alba–Avicennia alba* zone, *Rhizophora apiculata* zone, Ra – *Bruguiera gymnorrhiza* zone, *Ceriops tagal–Xylocarpus* spp. zone. Gap size (percentage gap area to total study area and individual gap size) was the largest in Sa–Aa zone which is located on the most seaward fringe, and it declined from seaward to inland. Canopy trees of *S. alba* and *A. alba* had stunted trunks and showed low tree density. On the contrary, canopy dominants in the other three inland zones, e.g. *R. apiculata*, *B. gymnorrhiza*, and *Xylocarpus* spp., had slender trunks and showed high tree density. Accordingly, differences in disturbance regime among the four zones were resulted from the forest structural features of each zone. Disturbance regime matched with regeneration strategies of canopy dominants. Seedlings and saplings of *S. alba* and *A. alba*, which need sunny condition for their growth, were abundant in gaps than in understorey. By contrast, *R. apiculata*, *B. gymnorrhiza*, and *Xylocarpus* spp., which can tolerate less light than *S. alba* and *A. alba*, had greater seedling and sapling density under closed canopy than gaps. Many large gaps may enhance the abundance of *S. alba* and *A. alba* in Sa–Aa zone, and a few small gaps may prevent the light demanding species to establish and grow in the other inland zones. Correspondence of disturbance regime and regeneration strategies (e.g. light requirement) of canopy dominants may contribute to the maintenance of the present species composition in each of the vegetation zones.

Introduction

Tropical mangrove forests are characterized by a clear zonation along a tidal gradient. In southern Thailand, the mangrove forest change from *Sonneratia alba* and *Avicennia alba* mixed forest at the seaward fringe to *Rhizophora apiculata* dominant forest, then *R. apiculata* and *Bruguiera gymnorrhiza* mixed forest, and finally *Xylocarpus moluccensis* dominated forest at the point furthest inland (Miyawaki et al. 1985; Mochida et al. 1999). Zonation in mangrove forests is attributed to the response of individual species to variation in soil factors e.g. tidal inundation, salinity, soil sulfide concentrations, and soil redox potential, that vary across an intertidal range (Smith 1992; Ellison and Farnsworth 1993; McKee 1995; Chen and Twilley 1999; Sherman et al. 2003).

Mangrove forests are subjected to various natural disturbances such as hurricanes and cyclones, lightning, herbivory, disease, and flood at various spatial and temporal scales (Jiménez et al. 1985; Smith et al. 1994; Feller and McKee 1999; Sherman et al. 2000, 2001). Previous studies have suggested that disturbances might play the important roles for the establishment and growth of mangroves through changing in light, sediment, and biological condition (Rabinowitz 1978; Ball 1980; Putz and Chan 1986; Smith 1987, 1992; Osborne and Smith 1990; Smith et al. 1994). Sherman et al. (2000) observed that lightning, a common disturbance agent in Dominican Republic, created not only canopy gaps but also safe sites for the establishment of *R. mangle* by collapsing the peat mat. Pinzón et al. (2003) compared the regeneration conditions in natural and anthropogenic gaps in Micronesia, and they suggested that current harvesting practices did not seem to alter species richness, though *R. apiculata* might become less common as gaps were replaced gradually by *B. gymnorrhiza*. Although these studies described the importance of disturbance on mangrove vegetations, little is known about changes in disturbance regime along a tidal gradient. Differences in disturbance regimes among vegetation types may largely affect the distribution and regeneration of the major canopy dominants as well as soil factors do (Clarke and Allaway 1993; Chen and Twilley 1998; Ellison et al. 2000).

The aim of this study is to reveal the difference of disturbance regime among the vegetation zones and the effects of disturbance regime on regeneration of tropical mangrove forests in Ranong, Thailand. We established approximately 0.5 ha study plots in four vegetation zones along a tidal gradient and compared species composition, forest structure, gap characteristics, seedling and sapling density under gaps and closed canopy among the four zones.

Methods

Study site

This study was carried out in tropical mangrove forests located in the Ranong Biosphere Reserve, southwestern Thailand (9°50′ N and 98°35′ E). The study areas have been protected as the research area of Ranong Mangrove Forest Research Center (RMFRC) and primary forests are preserved well. In the RMFRC's reserved areas, four typical zonation patterns were identified as: (1) *Sonneratia alba*–*Avicennia alba* community, (2) *Rhizophora apiculata* community, (3) *R. apiculata*–*Bruguiera gymnorrhiza* community, (4) *Ceriops tagal*–*Xylocarpus* spp. community along an intertidal gradient from seaward fringe to inland (Mochida et al. 1999).

Ranong is the rainiest region in Thailand, and mean annual rainfall is 4200 mm with 190 rainy days per year in average. This area has a dry season from October to March. August is the wettest season (819.7 mm in monthly mean rainfall) and January is the driest (13.8 mm). Mean annual temperature is 26.7 °C, with the minimum in January (20.6 °C) and the maximum in March (34.5 °). The tidal regime at Ranong is predominantly semidiurnal with a mean range of 2.4 m and annual maximum of 4.4 m (Macintosh et al. 1991).

Field survey

To compare the species composition and forest structure among the four vegetation zones, we established six study plots in four vegetation zones from August 2003 to October 2004. Two study plots in the *S. alba*–*A. alba* forest (SA zone), SA-1 (6300 m^2) and SA-2 (4500 m^2), were established at the seaward fringe. In the *R. apiculata* forest (Ra zone) which was located about 200 m innerward from the seaward fringe, two study plots, Ra-1 (4800 m^2) and Ra-2 (3600 m^2) were established. One plot (6000 m^2) was set up in the *R. apiculata*–*B. gymnorrhiza* forest (RB zone) located about 100 m innerward from Ra-1. In the *Ceriops tagal*–*Xylocarpus* spp. forest (CX zone) which was located at the most inland zone, one plot (4800 m^2) was established.

In each plot, all trees taller than 2 m were tagged and stem diameter at breast height (DBH) was measured avoiding protrusions. Stem diameter of all *Rhizophora* species was measured above (ca. 30 cm) the highest prop root. All saplings (2 m tall and < 5 cm in DBH) and seedlings (0.5 m tall and < 2 m tall) were numbered and identified in each plot. Because seedlings of *X. granatum* and *X. moluccensis* could not be distinguished, they were counted as '*Xylocarpus* spp.' for both species. For the abundant tree species (*S. alba*, *A. alba*, *R. apiculata*, *B. gymnorrhiza*, *X. moluccensis*, *X. granatum*, *Excoecaria agallocha*, and *Heritiera littoralis*), we selected 8–216 trees taller than 0.5 m with no damage, and measured tree height and crown widths in two perpendicular directions. Tree height was measured using measuring tape for trees ≤ 2 m tall and a digital hypsometer for trees > 2 m tall (VertexIII, Haglöf, Sweden). Crown area was calculated as an ellipse from crown width in two perpendicular directions.

A canopy gap was defined as a hole with more than 10 m^2 in area in the forest canopy above 10 m in height. To estimate the projected gap area, we measured the maximum width between gap edges (length) and perpendicular width (width), and calculated gap area as ellipse form. Gap shape was described by eccentricity ratio (length/width), where 1 indicates a circular shape and a value > 1 indicates an elliptical shape. Total gap area, gap density and the percentage of gap area to total plot area were also calculated for each plot. Species name (if identified), DBH and the state (live or dead) of gapmakers (trees ≥20 cm DBH creating a gap) were recorded. Mortality factors i.e. standing dead, trunk broken, uprooted of gapmakers and others were also noted.

Data analysis

To understand the relationships between DBH (cm) and tree height (m), tree height was regressed onto DBH, using a hyperbolic allometric equation (Ogawa and Kira 1977; Aiba and Kohyama 1996):

$$1/H = 1/(a \times \text{DBH}) + 1/H_{\max}$$

where a is a constant and $H_{\max}$ (m) is the asymptotic maximum tree height. Departure from linearity of the relationship on ln–ln plots was examined by ANOVA using the sum of squares of residuals (RSS) when data were regressed linearly ($\text{df} = n-2$) and RSS when regressed by hyperbolic allometric equation ($\text{df} = n-3$) (Aiba and Kohyama 1997; Aiba and Kitayama 1999). Between-species differences in the relationship were tested by ANOVA using RSS when pooled data were regressed ($\text{df} = n1 + n2-3$) and RSS when data for two species were regressed separately ($\text{df} = n1 + n2-6$). A sequential Bonferroni test was applied for the multiple comparisons after ANOVA (Rice 1989).

Differences in the slopes and adjusted means of the regression lines between crown area and DBH as a covariate were tested among canopy dominants by analysis of covariance (ANCOVA). Differences in DBH of gapmakers and eccentricity ratio of gaps among plots were tested by one-way ANOVA. The Kolmogorov–Smirnov test was applied to test the differences in mean gap size among plots. We used chi-square test to examine the differences in the percentage of gap area, gap density and frequency distribution of mortality factors of gapmakers among six plots. Comparison of seedling and sapling densities between under gaps and closed canopy in each species were tested by chi-square test. All of the analyses above were performed with SPSS software (SPSS Inc., Chicago, IL, USA).

Results

Species composition and structure

In four zones, a total of 19 species were recorded. The number of species per plot increased from seaward to inland (Table 1). *Sonneratia alba*, *A. alba* and *Aegiceras corniculatum* were restricted to the SA zone and this zone had the smallest number of species. *Avicennia officinalis* showed bimodal distribution in SA zone and CX zone. Species composition in two rhizophoraceous zones (Ra and RB zone) was characterized by the presence of *Bruguiera* species (*B. gymnorrhiza*, *B. cylindrica*, and *B. parviflora*). *Rhizophora apiculata* and *B. gymnorrhiza* became dominant in two rhizophoraceous zones, although *B. gymnorrhiza* had greater abundance in RB zone. CX zone was the most species-rich among the four zones, because some landward species (e.g. *Cynometra iripa*, *Excoecaria agallocha*, and *Heritiera littoralis*) appeared only in this zone.

Table 1. Species composition for trees ≥5 cm in DBH in the six study plots.

	Seaward fringe SA zone				→ Ra zone				RB zone		Inland CX zone	
	SA-1		SA-2		Ra-1		Ra-2		RB		CX	
	Dens (ha^{-1})	RBA (%)	Dens (ha^{-1})	RBA (%)	Dens (ha^{-1})	RBA (%)	Dens (ha^{-1})	RBA (%)	Dens (ha^{-1})	RBA (%)	Dens (ha^{-1})	RBA (%)
Sonneratia alba	44.4	37.2	111.1	66.5								
Avicennia alba	46.0	52.5	31.1	21.6								
A. officinalis	6.3	6.1	11.1	6.8							27.1	8.2
Aegiceras corniculatum	38.1	1.0										
Rhizophora mucronata	52.4	3.1	11.1	0.8			5.6	0.2				
R. apiculata			26.7	4.4	1733.3	95.9	1883.3	93.4	1236.7	77.8	181.3	8.6
Bruguiera gymnorrhiza					10.4	0.3	19.4	3.0	73.3	16.0	116.7	2.8
B. cylindrica					18.8	3.7	113.9	2.1	180.0	4.1	6.3	0.1
B. parviflora							16.7	0.4	53.3	1.5		
Xylocarpus granatum					2.1	0.02	2.8	0.2	18.3	0.4	25.0	3.2
X. moluccensis									1.7	0.05	95.8	32.5
Excoecaria agallocha											227.1	21.9
Heritiera littoralis											310.4	16.0
Cynometra iripa											222.9	4.2
Others					2.1	0.1	30.6	0.7	8.3	0.1	79.2	2.7
Number of species	5		5		5		8		7		15	

Tree density (Dens) and relative basal area (RBA) of species ≥1% at least in one plot are shown in this table.

Table 2. Forest structural features of six study plots.

Study plots	Basal area (m^{2}ha^{-1})	Tree density (ha^{-1})	Max height (m)	Max DBH (cm)	Sprouting stems (%)
SA-1	13.0	187.3	26.1	87.4	37.3
SA-2	11.3	191.1	23.3	65.2	5.9
Ra-1	25.6	1776.7	34.8	56.4	5.1
Ra-2	24.5	2072.2	35.9	56.3	1.1
RB	27.8	1571.7	38.6	62.4	2.4
CX	29.0	1291.7	25.7	121.4	42.4

Basal area increased from seaward to inland (Table 2). Tree density and maximum tree height increased from SA zone to RB zone, and decreased in CX zone. Maximum DBH showed a bimodal distribution, with one peak in the SA zone and the other higher peak in the CX zone.

The relationships between DBH and tree height were shown in Figure 1. The regressions of six tree species showed no significant departure from linearity on ln–ln plots (ANOVA, $p > 0.1$), while those for *R. apiculata* and *X. moluccensis* showed significant departure from linearity ($p < 0.05$). Because the hyperbolic allometric equation fitted to those two species and showed a higher determination coefficient than the linear regression on ln–ln plots in five of eight species, this hyperbolic allometric equation was adapted. *Rhizophora apiculata* and *B. gymnorrhiza* had greater tree height than dominant species in SA and CX zone did at a comparable DBH (Bonferroni test, $p < 0.05$). The regression curves in the CX zone were different only for *X. moluccensis* relative to *X. granatum*, *E. agallocha*, and *H. littoralis* ($p < 0.05$). Figure 2 shows the relationship between DBH and crown projection area for eight canopy dominants. The slopes of regression lines of canopy species in SA zone (*S. alba* and *A. alba*) were greater than those in the other three inland zones (*R. apiculata*, *B. gymnorrhiza*, and *X. moluccensis*) (ANCOVA, $p < 0.05$). Canopy trees of *S. alba* and *A. alba* reached more than 100 m^2 in crown area, on the contrary, most of the species growing in the other three zones had distinctively small crown.

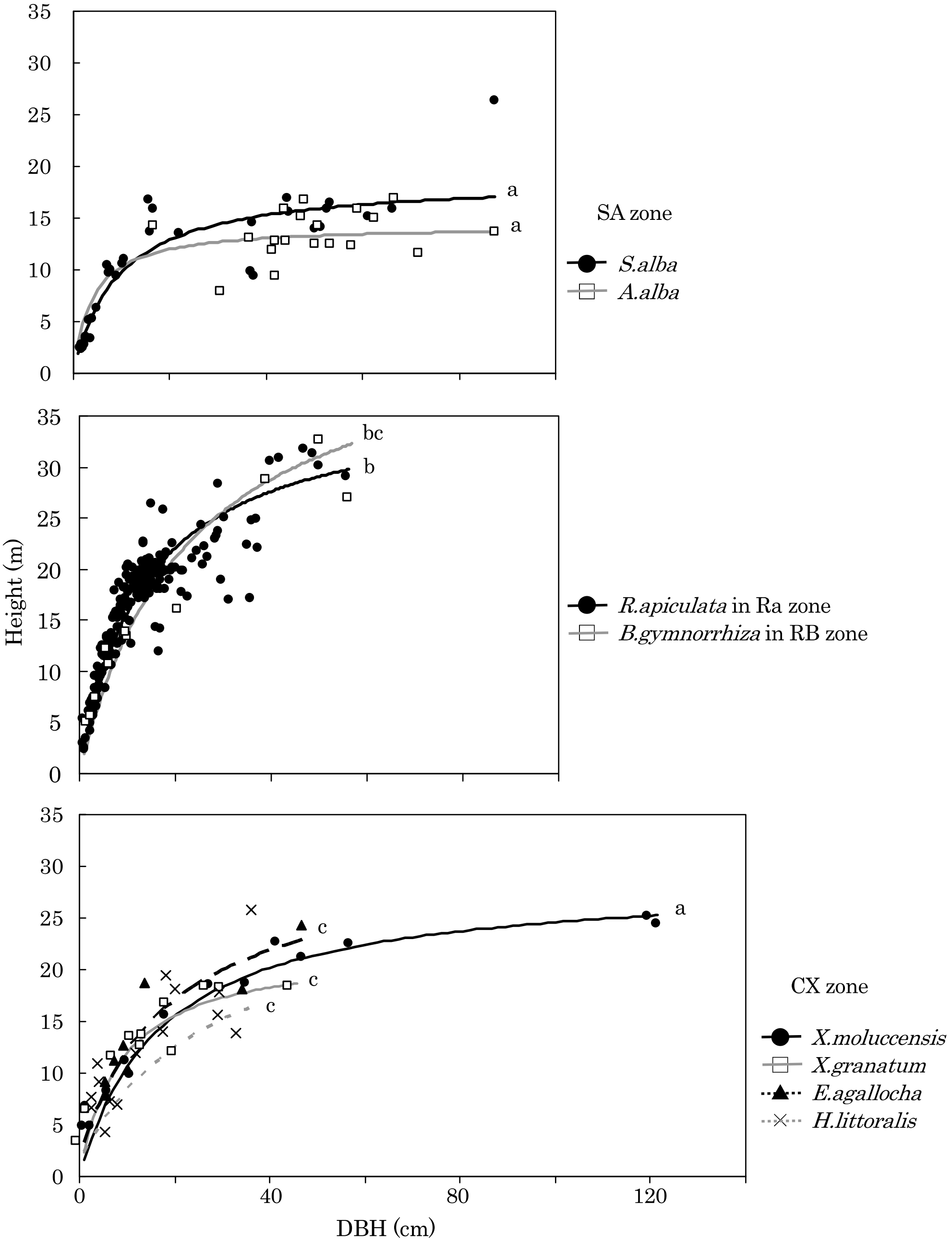

Figure 1. The relationship between trunk diameter at breast height (DBH) and tree height fitted to hyperbolic allometric equation, $1/\mathrm{H} = 1/(a \times \mathrm{DBH}) + 1/H_{\max}$, for each of the major canopy dominant species in the four vegetation zones. Species sharing the same letters did not differ significantly at $p < 0.05$.

Gap characteristics

Mean canopy gap size of the SA zone was significantly larger than those in the other three zones (Table 3, Kolmogorov–Smirnov test, $p < 0.05$). Many canopy gaps in SA zone were greater than 100 m^2 (Figure 3). By contrast, most canopy gaps in two rhizophoraceous zone and CX zone were < 50 m^2, and few were greater than 100 m^2. As a result, the percentage of gap area was greater in

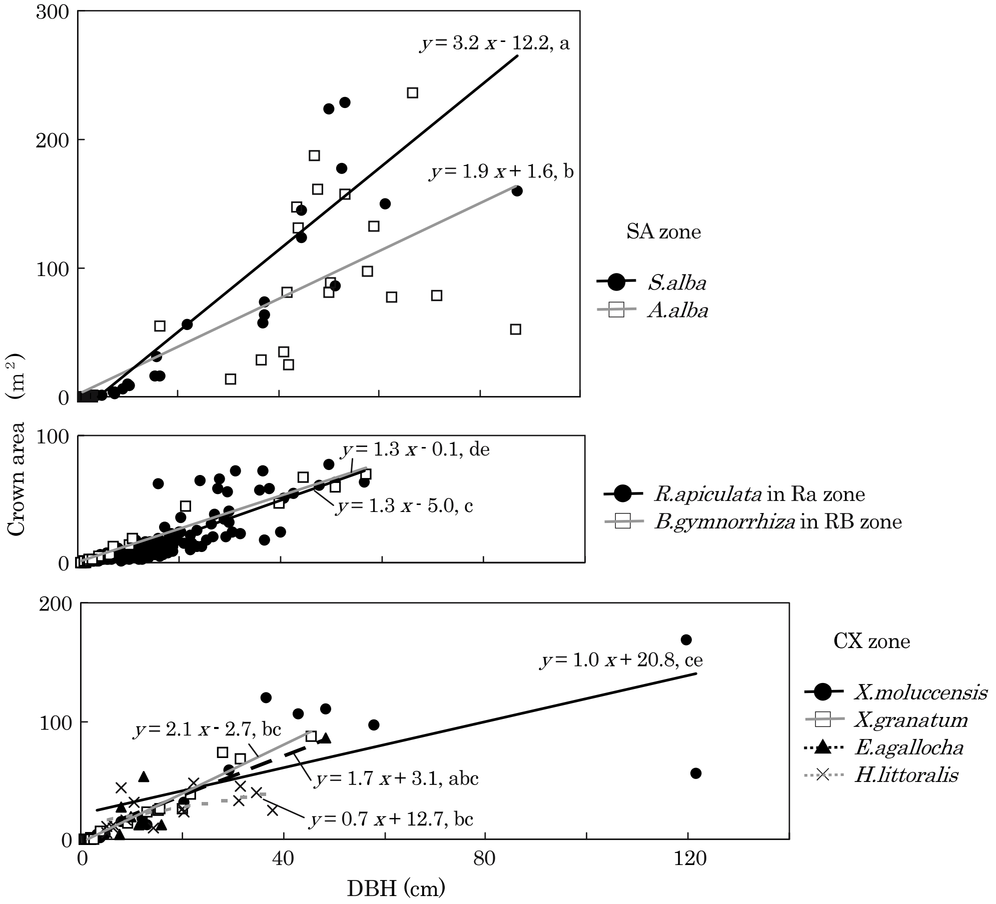

Figure 2. The relationship between DBH and crown projection area for each of the major canopy dominant species in the four vegetation zones. All of the regression lines were correlated significantly (Pearson's coefficient, $p < 0.05$). The differences in slopes and adjusted means of regression lines between crown area and DBH as covariate were tested among major canopy dominants by ANCOVA. Species sharing the same letters did not differ significantly at $p < 0.05$.

SA zone (27.5 and 23.1% in SA-1 and SA-2, respectively) than the other three zones (averaged 6.0%), though gap density did not differ significantly among the four zones (Table 3, chi-square test, $p > 0.1$).

Mortality factors of gapmakers were significantly different among the four zones (Table 3, chi-square test, $p < 0.001$). In SA zone, most canopy gaps were created by standing-dead of *S. alba* and/or trunk-broken of *A. alba*. Uprooting was a common cause of gap formation in the two rhizophoraceous and CX zones. Gap shape was significantly more elliptical in the two rhizophoraceous zones (eccentricity was ranged from 2.2 to 4.5) than the SA zone and the CX zone (1.3–1.4; ANOVA, $p < 0.05$), due to the high frequency of involvement of neighbor trees by gapmakers in the two rhizophoraceous zones (50.0–71.4%).

Regeneration patterns

Distribution pattern of sapling and seedling densities varied depending on species (Table 4). In SA zone, seedling and sapling densities of *S. alba* were higher under canopy gaps, compared to those under closed canopy. Saplings of *A. alba* emerged under canopy gaps but not under closed canopy. By contrast, in dominant species of the other three zones, seedlings and saplings were more abundant under closed canopy than gaps. Species composition of seedlings and saplings generally reflects the

Table 3. Gap characteristics and conditions of gapmakers of six study plots.

	SA zone		Ra zone		RB zone	CX zone	
	SA^{-1}	SA^{-2}	Ra^{-1}	Ra^{-2}	RB	CX	
Gap characteristics							
Total surveyed area (m^2)	6300	4500	4800	3600	6000	4800	
Total gap area (m^2)	1811.8	1039.5	237.3	259.6	467.1	204.7	
The percentage of gap area (%)	28.8	23.1	4.9	7.2	7.8	4.3	***
Density of gap (ha^{-1})	18.3	15.6	16.8	11.1	11.5	8.3	ns
Gap size (m^2)							
Mean	164.7	144.2	29.7	64.9	66.7	51.2	*
SD	56.7	36.9	6.1	26.0	20.9	27.1	
Maximum	698.2	401.9	70.1	137.3	185.1	127.7	
Eccentricity (length/width)	1.4	1.3	2.2	4.5	2.2	1.4	*
Gapmaker							
Number of gapmakers (ha^{-1})	27.0	17.7	16.0	11.1	13.3	8.3	*
DBH (cm)							
Mean	56.1	60.6	38.6	47.8	42.4	44.9	*
SD	5.8	9.0	3.3	6.0	4.9	9.6	
Maximum	101.9	83.3	50.7	62.4	61.4	70	
Percentage of gaps which involved the surrounding trees (%)	–	–	50	50	71.4	–	
Mortality factor of gapmakers (%)							
Standing dead	41.2	53.8	10	25	12.5	25	
Trunk-broken	52.9	30.8	30	–	12.5	25	***
Uprooted	–	–	40	75	75	50	
Unknown	5.9	15.4	20	–	–	–	

Difference in the percentage of gap area, gap density and mortality factors of gapmakers among plots were tested by chi-square test. Kolmogorov–Smirnov test was used to test the differences in gap size, and one-way ANOVA tested the differences in DBH of gapmakers and eccentricity among zones. *$p < 0.05$; ***$p < 0.001$; ns, not significant.

canopy species composition in each zone regardless of canopy conditions (gaps or closed canopy).

Discussion

Disturbance regime, such as gap size and mortality factor of gapmakers, changed drastically along a tidal gradient in tropical mangrove forest in Ranong, Thailand. In the SA zone, most canopy gaps were significantly large and created by standing-dead and/or broken-trunks. Because highly tapering trees (low height: DBH ratio) were more liable to stem breakage than uprooting, and vice versa (Peltola et al. 2000), uprooting was a less common mortality factor for *S. alba* and *A. alba* which had large crowns and stunted trunks. Tree density was significantly low due to the low density of shrub in SA zone. These forest structural features (large canopy trees and lack of the vertical overlap of trees) may facilitate creating the large gaps in this forest. By contrast, in the other three inland zones, canopy trees of *R. apiculata*, *B. gymnorrhiza*, and *Xylocarpus* spp. had slender trunks and small crowns. They created small canopy gaps that were caused by uprooting. These results imply that the crowns of the emergent trees are exposed above the canopy layer to strong winds and eventually induce uprooting in these forests. The uprooted gapmaker, especially *R. apiculata*, usually involved the surrounding canopy and understorey trees, and action may lead the forests to increase the proportion of multiple and elliptical gaps in the two rhizophoraceous zones. Although most canopy gaps in the CX zone were created by uprooted *X. moluccensis*, these were single and circular gaps, probably due to the relatively low tree density in this forest. Accordingly, differences in the disturbance regime among the four zones resulted in different forest structure and architectural features of canopy dominants. Pinzón et al. (2003) also found that species-specific disturbance agents are inherent in mangrove forests in Kosrae, Micronesia. However, their results differed from the present study in that snapping off (trunk-broken in this study) was a common cause of natural gap formation and there were no standing dead trees of *S.alba* and a few uprooted trees of *R. apiculata* and *B. gymnorrhiza*.

Disturbance regime matched with regeneration strategies of canopy dominant species in each zone. Because *S. alba* and *A. alba* need high light conditions for their growth (Lee et al. 1996; Panapitukkul et al. 1998; Kitao et al. 2003), their seedling and sapling densities were greater in gaps than in the understorey. Formation of many large gaps may facilitate establishment and growth for *S. alba* and *A. alba* in SA zone. On the contrary, the other canopy dominants (*R. apiculata*, *B. gymnorrhiza*, and *Xylocarpus* spp.) can tolerate less light than *S. alba* and *A. alba* (Putz and Chan 1986; Tamai and Iampa 1988; Robertson et al. 1990; Clarke et al. 2001; Allen et al. 2003; Kitao et al. 2003; Krauss and Allen 2003) and they showed greater seedling and sapling densities under closed canopy than gaps in each forest. These species may not need large gaps for their establishment and growth (Clarke 2004). A low number of large gaps may prevent the light demanding species from establishing and growing in inland zones. Accordingly, the correspondence of disturbance regime and regeneration strategies (e.g. light requirement) of canopy dominants may contribute to the maintenance of the present species composition in each vegetation zone.

Clarke and Kerrigan (2000) proposed that gap-phase regeneration of mangroves appears to follow a simple 'direct replacement' model in which a species population is replaced by members of the same species in forest gaps. This contrasts with tropical rain forests in which micro-succession, i.e. replacement of pioneer species by late successional species, can be seen after gap formation (Swaine and Whitmore 1988; Whitmore 1989). The direct replacement model was explained by the low species diversity (absence of the gap specialists) due to the severe intertidal environments (Clarke and Kerrigan 2000). But, the correspondence of disturbance regime and regeneration strategies of canopy dominants may also support this hypothesis.

Landscape-scale and long-term geomorphological processes (e.g. peat accumulation, erosion, and sea level change) are known to principally control the water and soil conditions in mangroves. Vegetation and soil conditions might have interactively changed along tidal gradients and the interaction may be influenced by the geomorphic

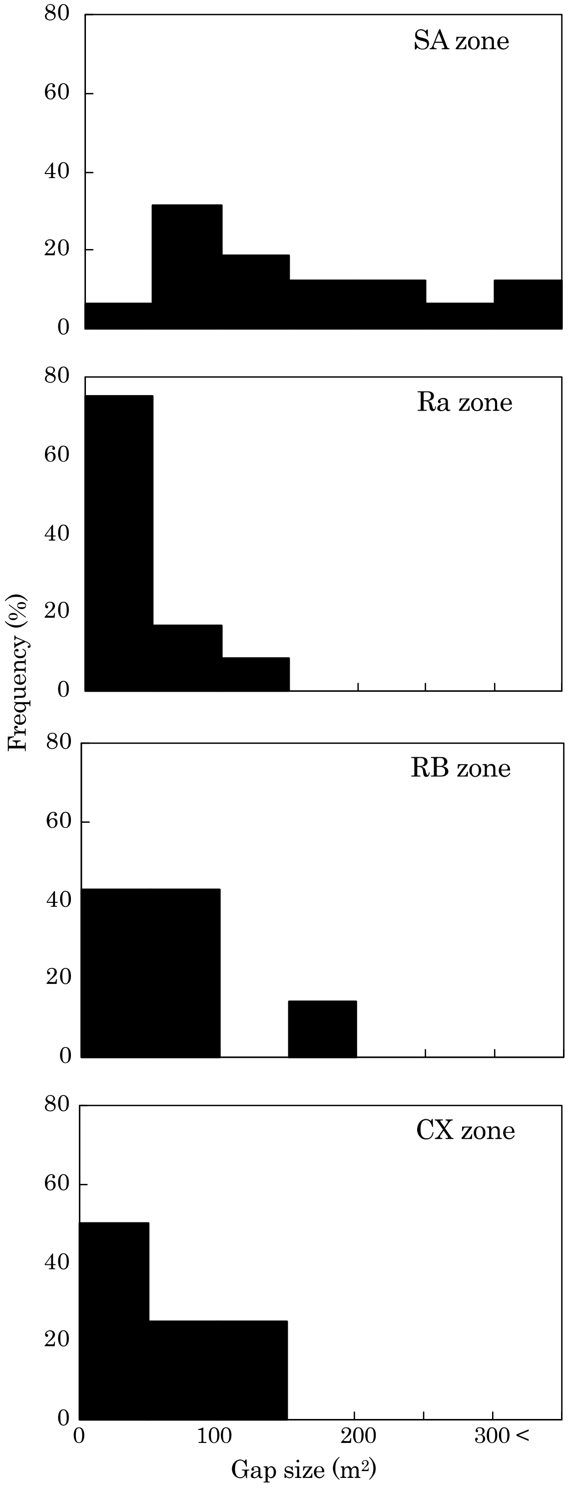

Figure 3. Frequency distribution of gap sizes in the four vegetation zones.

Table 4. Comparison of seedling (0.5 m tall and < 2 m tall) and sapling (2 m tall and < 5 cm in DBH) densities (ha^{-1}) under closed canopy and canopy gaps among the four zones.

	Seedling		Sapling	
	Closed	Gap	Closed	Gap
SA zone				
S. alba	18.4	218.2***	27.6	48.5*
A. alba	–	–	–	38.5
Ra zone				
R. apiculata	238.6	851.1***	430.8	492.7*
RB zone				
B. gymnorrhiza	3.5	–	10.6	–
B. cylindrica	127.3	85.1**	247.5	85.1***
R. apiculata	122.0	63.9***	286.4	149.0***
CX zone				
X. moluccensis	280.8	145.3***	26.1	96.9***
X. granatum			8.7	–

Differences in seedling and sapling densities between canopy conditions were tested by chi-square test. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

characteristics. Water and soil factors primarily regulate the spatial pattern of species composition and forest structure of mangrove forests (Thom 1967; Thom et al. 1975; Wolanski et al. 1992; Woodroffe 1992). For example, Fujimoto and Miyagi (1993) supposed that environmental changes i.e. the ground level rising, might enhance the forest succession from *S. alba* forest to *R. apiculata* forest, because some large trees of *S. alba* were observed with no saplings in *R. apiculata* forests on Pohnpei Island. Furthermore, our study demonstrated that species composition and forest structure might control the disturbance regime in each vegetation zone. Then, in short-term forest dynamics at least a few generations without a large geomorphological change, species composition and forest structure may change little in each forest zone because of the disturbance regime and regeneration strategies of dominant species in each zone. Accordingly, the clear zonation of mangrove forest is, in the short-term, maintained stably by the intrinsic factors of each zone, i.e. difference in disturbance regime among the four zones, though it develops as a result of long-term succession along geomorphological process.

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