Vol. 237: 111–120, 2002 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published July 18

Colonization success of common Thai mangrove species as a function of shelter from water movement

Udomluck Thampanya[1], Jan E. Vermaat[2,*], Carlos M. Duarte[3]

[1]Coastal Resources Institute, Prince of Songkla University, Hat Yai, Songkhla 90112, Thailand

[2]International Institute for Infrastructural, Hydraulic and Environmental Engineering, Delft, The Netherlands

[3]IMEDEA (CSIC-UIB), Instituto Mediterráneo de Estudios Avanzados, CSIC-Universidad, Illes Balears, C/Miguel Margués 21, 07190 Esporles, Mallorca, Spain

ABSTRACT: Seedling survival and growth of the 3 common SE Asian mangrove species *Avicennia alba*, *Rhizophora mucronata* and *Sonneratia caseolaris* were quantified experimentally along 2 spatial gradients of shelter: (1) between 2 stations, at the inner and outer end of the sheltered Pak Phanang Bay (SW Thailand); and (2) for each station, among plots across a gradient of vegetation density from the mangrove forest edge inwards. Exposure to water movement, quantified as gypsum clod card weight loss, was found to vary more than 5-fold between seasons, which contributed most of the variance accounted for (73%). Variation between plots was higher than that between the 2 stations: clod card loss ranged between 3.0 and 4.6 g d^{-1} in the plots, whereas the grand means of the 2 stations were 3.4 and 3.7 g d^{-1}, respectively. These differences between stations and plots were comparable to the patterns found for mangrove seedling survival. Survival was high (80 to 93%) in most treatments in *R. mucronata*, with the exception of the most exposed plot (30%). In the other 2 species, overall survival was significantly less but was highest in the outermost plots with the lowest tree density. This pattern confirms the successional status of these 3 mangrove species. Seedling growth, expressed as height increase, was significantly reduced with increasing neighboring tree density for *A. alba* and *S. caseolaris*, whereas *R. mucronata* showed an opposite pattern. Internode production of all 3 species was highest in the most exposed plots. Overall, relative growth rate, expressed as height increase, declined with the age of the seedlings.

KEY WORDS: Mangrove · Seedlings · Exposure · Water movement · Clod card · SE Asia

INTRODUCTION

Seedling establishment is a critical stage in the life cycle of most angiosperms (Silvertown 1982). The advanced developmental stage of viviparous mangrove seedlings, which develop while still attached to the mother tree in the Rhizophoreae genera, is generally interpreted to be adaptive (Tomlinson 1986) and to facilitate rapid establishment through rooting (Hutchings & Saenger 1987). After a period of positive buoyancy, dispersed propagules sink or become stranded, and successful rooting is the first step toward seedling establishment (Hutchings & Saenger 1987, Tomlinson 2000). However, establishment may be hindered by tidal current and wave buffeting (Clarke 1995) or lack of shelter from water movement (Clough 1982). Consequently, large proportions (as high as 90%) of already rooted seedlings may fail to become fully established (Delgado et al. 1999). Furthermore, post-establishment mortality during the first year is considerable: Hutchings & Saenger (1987) reported 22, 36 and 72% mortality in the first year for *Avicennia* sp., *Ceriops* sp., and *Rhizophora stylosa*, respectively. In this stage, possible

*Corresponding author. Present address: Institute for Environmental Studies, Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands.
E-mail: jan.vermaat@ivm.vu.nl

mortality sources include herbivory, drought or salinity stress, insufficient light, damage from drifting objects and strong water movement (Hutchings & Saenger 1987, Clarke 1995). Published relevant quantitative data on mangrove seedling survival and sources of mortality, however, are scarce (Hutchings & Saenger 1987, Clarke & Allaway 1993).

Our aim was to assess the effect of seasonal variation in exposure to water movement on the survival and growth of seedlings of 3 common SE Asian mangrove species at 2 spatial scales: (1) at a larger scale along a gradient from the river mouth to the sea in an enclosed bay (Pak Phanang Bay, Southern Thailand); and (2) at a smaller scale along a gradient of neighboring plant density from the edge of an expanding mangrove forest perpendicular into the forest. In addition to their interest in providing information on factors affecting the early success of mangrove seedlings, the goals set here are important to the design of successful large-scale mangrove rehabilitation schemes, such as those carried out at present in Thailand and neighboring countries (Field 1995, Havanond 1995).

MATERIALS AND METHODS

Study area. Pak Phanang Bay (8° 25.11′ N, 100° 09.18′ E) is a large, shallow bay, sheltered from the Gulf of Thailand by a long northwest-pointing sandbar (Fig. 1). The eastern side of the bay is largely occupied by mangrove forest with an area of approximately 90 km^2. The Pak Phanang River, 110 km long, discharges into the bay from the south. Tides are mixed diurnal and ranged between 0.1 and 0.7 m in August 1998, and between 0.7 and 1.3 m above the lowest low tide level in January 1999. Published average velocities are 0.6 m s^{-1} for ebb currents and 0.8 m s^{-1} for flood currents (JICA 1987). Annually, the area experiences 3 distinct seasons: hot-dry season (February to May), rainy season (June to September) and the highest rainfall period of monsoon season (October to January; Fig. 2), with an average annual rainfall of 2400 mm. The mean air temperature is 28°C and the water temperature ranges between 25 and 36°C. The experiment was conducted at the bay-side edge of the mangrove forest. Two stations with different exposure were selected: Stn 1, at the mouth of Pak Kwang Canal near the river mouth, and Stn 2, at the mouth of Ai Ho Canal 5 km away from Stn 1. At each station, 3 plots of 10 m × 30 m were set up at different densities of naturally occurring, neighboring plants: low, medium and high (Table 1). The 3 plots of Stn 1 were mostly occupied by *Sonneratia caseolaris* trees (2 to 5 m in height), saplings and seedlings with a few *Avicennia* spp. (*A. alba* and *A. officinalis*) saplings and seedlings, while all the plots of Stn 2 were occupied by *Avicennia* sp. trees, saplings and seedlings. The upper areas and hinterland are occupied by planted *Rhizophora apiculata* and *Rhizophora mucronata* (5 to 20 m in height). Soil textures of both stations are silty clay (53 % clay for Stn 1 and 56 % clay for Stn 2), and the substrate surface is relatively flat (+1 m elevation above mean sea level for both stations).

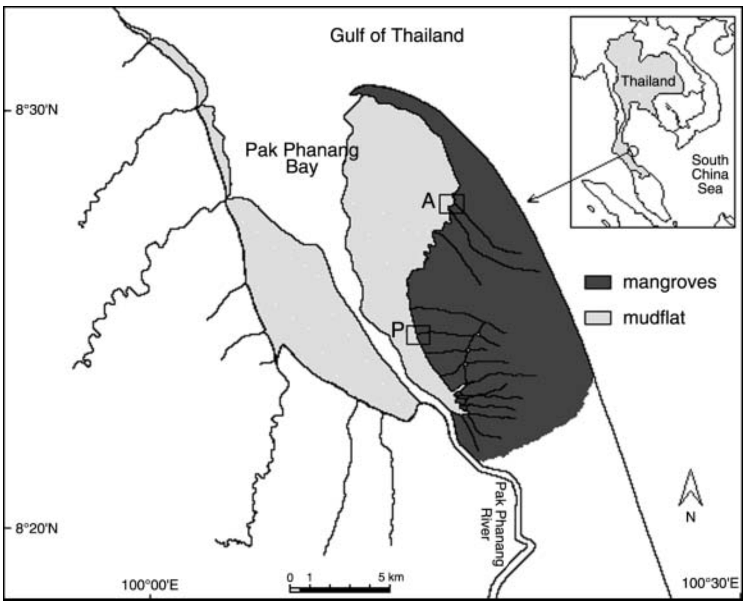

Fig. 1. Map of Pak Phanang Bay, southern Thailand, showing the 2 stations. A: Ai Ho; P: Pak Kwang

Measurement of water movement and other environmental parameters. The dimensionless water movement was quantified using the dissolution rate of clod cards (Doty 1971, Jokiel & Morrissey 1993). This inexpensive and practical method quantifies weight loss of a sparingly soluble substance such as plaster of Paris or gypsum. Reportedly, weight loss is directly related to water motion (Petticrew & Kalff 1991, Jokiel & Morrissey 1993, but see Porter et al. 2000 for a critical assessment). A large number of plaster of Paris clods of considerable size (30 to 40 g) were produced using ice-cube trays as templates and allowed to air-dry at room temperature (28 to 33°C) for 1 wk to reach constant weight. Thereafter, each clod was glued to a card of 5 cm × 7 cm rubber floor cover. After being oven-dried at 60°C for 24 h, the clod cards were pre-weighed before deployment. At the study site, each pair of clod cards was attached, using rubber elastic rings, to a piece (8 cm × 16 cm) of thin board with a hole punched in the middle. Fifteen pairs of clod cards were deployed randomly in each plot at both stations. The clod card set was fixed to the substrate with a stick. After being deployed for 24 h, the clod cards were collected and carefully carried back to the laboratory. Subsequently, they were allowed to air-dry for a week and were re-weighed after drying at 60°C for 24 h. Clod cards were deployed randomly in the diel and monthly (lunar) tidal cycle: low tide occurred at 15, 18, 8, 8, 23, 5 and 22 h, respectively, on subsequent days of deployment.

Data were analyzed using an ANOVA-general linear model (GLM) full factorial model comparing weight loss per day between seasons, stations and plots. Closed boxes (15 l) containing control clod cards were also deployed *in situ*, allowing the calculation of the diffusion factor (DF), sensu Jokiel & Morrissey (1993), as weight loss *in situ*/weight loss in still water. Salinity was measured *in situ* with a Wissenschaftlich Technische Werkstätte conductivity meter. Rainfall data were obtained from the meteorological stations surrounding the study area.

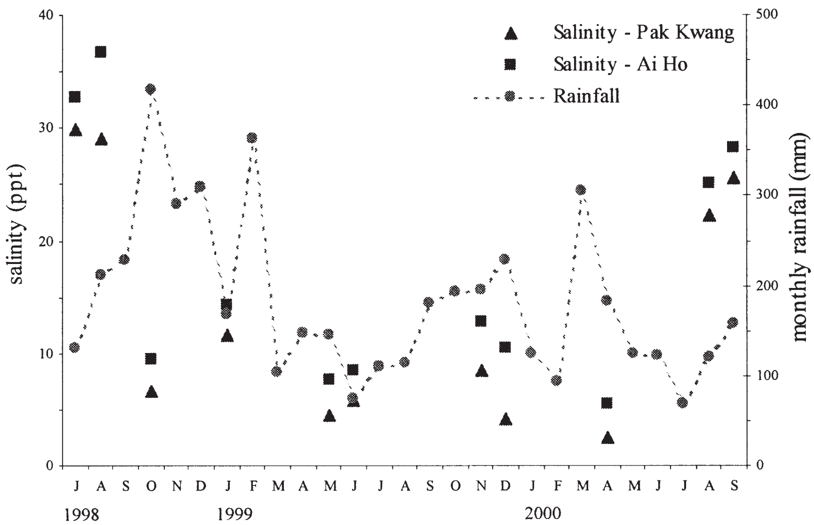

Fig. 2. Salinity (‰) measured at the 2 stations and mean monthly rainfall (mm) calculated from the meteorological stations adjacent to Pak Phanang Bay

Seedling survival and growth. Seedlings of *Avicennia alba*, *Sonneratia caseolaris* and *Rhizophora mucronata* were transplanted in May 1999, at the end of the hot-dry period. In each plot of both stations, 30 seedlings of each species were transplanted with 2 m × 2 m spacing. These transplanted seedlings were in the post-cotyledonary phase, during which their survival appears to be largely resource dependent, i.e. independent of nutritional support from the parent (Clarke 1995). The seedlings of *A. alba* and *S. caseolaris* were obtained by carefully shoveling up newly established natural seedlings in an adjacent area, while the seedlings of *R. mucronata* were collected under mature trees upstream. The transplanted seedlings were tagged after planting and recovered after a month. We then measured the height and number of internodes on the main stem and repeated these measurements at approximately 3 mo intervals until the plants were more than 1 yr old (September 2000). However, due to the very high monsoon water levels in December 1999 to February 2000 the still submerged *Rhizophora* and *Avicennia* spp. seedlings could not be monitored. Only *S. caseolaris* seedlings, which had grown fast enough to reach the water surface, were monitored during that time. Since there were slight differences in initial seedling sizes (with a mean height of 36, 37 and 16 cm for *Avicennia*, *Rhizophora* and *Sonneratia* spp., respectively), data on seedling height were transformed into relative growth rates (RGR_H) (Hunt 1982) prior to analyses. At each visit we also recorded the number of surviving seedlings and analyzed seedling survival using a factorial GLM. Since growth was measured on the same experimental units (i.e. the seedlings) a repeated-measures design was used to properly separate effects of time from treatment in ANOVA (Potvin et al. 1990).

Table 1. Densities (ind. per 100 m^2) of neighboring plants existing in the low-, medium- and high-density plots in 2 stations in Pak Phanang Bay. Mangrove plants were classified as seedlings (<1.5 m), saplings (between 1.5 and 2.5 m) or trees (>2.5 m)

Station	Plot	Seedling	Sapling	Tree
Pak Kwang	Low	97	5	2
	Medium	253	24	13
	High	389	76	18
Ai Ho	Low	68	3	1
	Medium	282	26	11
	High	338	41	24

RESULTS

Water movement

There was a significant difference in clod card dissolution between the 2 stations ($p < 0.001$; Table 2). Average clod card weight loss per day at Ai Ho Canal (3.78 ± 0.08 g d^{-1}) was somewhat higher than at Pak

Table 2. Three-way ANOVA examining the effects of stations, neighboring plant densities (plots) and seasons (months) on clod card weight loss (g d^{-1}). Presented are df, SS, the percentage of variance explained (factor SS/total SS × 100) and the level of significance (p)

Factors	df	SS	% variance	p
Station	1	31	1	0.000
Plot	2	324	8	0.000
Month	6	2905	73	0.000
Station × plot	2	34	1	0.000
Station × month	6	39	1	0.000
Plot × month	12	104	2	0.000
Station × plot × month	12	35	1	0.000
Residual	1147	513	13	
Total	1188	4002	100	

Kwang Canal (3.46 ± 0.07 g d^{-1}). Clod card dissolution rates were also significantly different between plots of different neighboring plant densities and between seasons ($p < 0.001$; Table 2). The plots with the lowest density had the highest clod card dissolution rates (4.38 ± 0.10 g d^{-1}), while those with the highest density had the lowest (3.16 ± 0.09 g d^{-1}). In general, most of the variation (73%) was accounted for by the seasonality term (Table 2), with the lowest clod card weight loss in July 1998 and the highest in October 1998 (Fig. 3), a pattern coupled with the monsoon period (cf. Fig. 2). Also, the lower maximum clod card dissolution rates in November 1999, compared to those of October 1998 (cf. Fig. 3), coincided with lower rainfall in that period. The larger-scale exposure effect (stations) accounted for only 1% of total variance, while the smaller-scale exposure effect (neighboring plant density) contributed 8%.

The DF was subsequently calculated but only from January 1999 onward, due to loss of control clod card boxes for the first 3 measurements. Average DF was highest at the most exposed plot of Ai Ho Canal in April 2000 (9.24 ± 0.10) and lowest at the densest plot of Ai Ho Canal in May 1999 (2.20 ± 0.03).

Seedling survival

Significant differences in seedling survival were detected between species and at the smaller-scale exposure (plot) level but not at the larger-scale exposure (station) level (Table 3). Most of the variation (47%) was explained by the difference in species, while the difference in neighboring plant density and the interaction between species and neighboring plant density explained 11 and 13% of the total variation, respectively.

Survival curves of *Avicennia* and *Sonneratia* spp. were comparatively similar but very different from those of *Rhizophora* sp. (Fig. 4). The numbers of surviving seedlings of the first 2 species declined throughout the experimental period, whereas those of *R. mucronata* remained fairly constant until after the monsoon season, when mortality was particularly apparent in the low-density plot at Ai Ho. In *A. alba*, mortality was spread evenly over the whole period, while *S. caseolaris* experienced 2 periods of high mortality (June to September 1999 and November 1999 to February 2000; Fig. 4). Also, *Avicennia* and *Sonneratia* spp. seedlings had higher survival rates in the plots with low plant density, i.e. at high exposure. In contrast, *R. mucronata* seedlings survived much better in the less exposed,

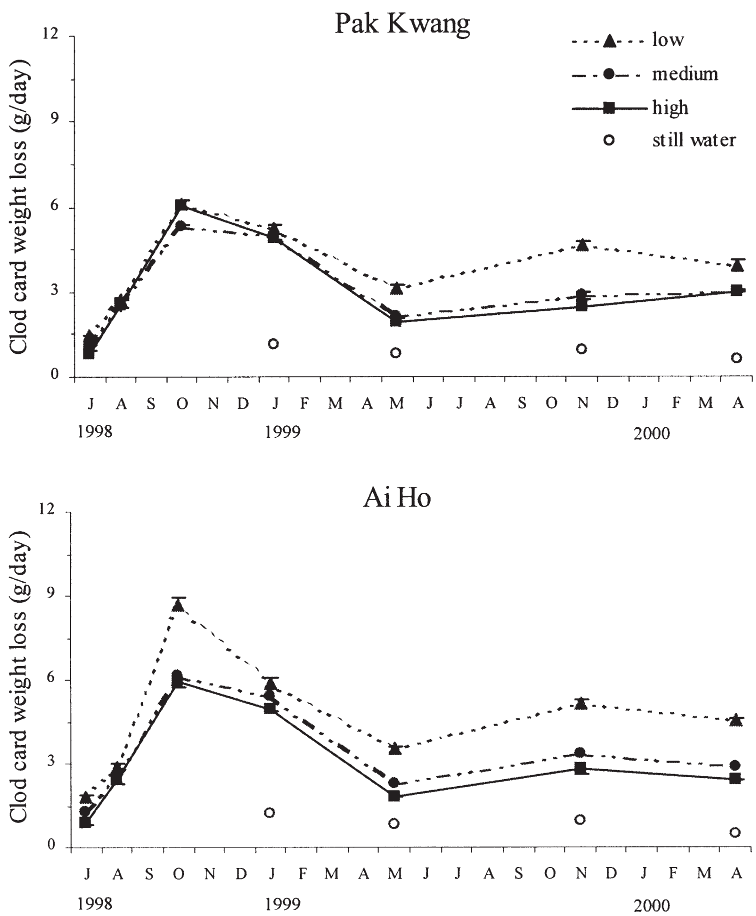

Fig. 3. Seasonal pattern of clod card dissolution (g d^{-1}) at 3 plots of different neighboring tree density (low, medium and high) and in still water of the 2 stations. Presented are means ± standard error (SE)

denser plots (Fig. 4). After a 1 yr cycle, between 8 and 40% of the *S. caseolaris* had survived, with survival being highest in the outermost low-density plots (Table 4). Likewise, *A. alba* had the highest survival at the lowest density of neighboring trees, with the mortality rate ranging between 30 and 85%. In *R. mucronata*, mortality rates after 1 yr were relatively low in the medium and high plant-density plots (13 and 15%), but comparatively high in the low plant-density plots (43%, Table 4).

Table 3. Three-way ANOVA examining the effects of species, stations and neighboring plant densities (plots) on seedling survival

Factors	df	SS	% variance	p
Station	1	32	1	0.394
Plot	2	518	11	0.006
Species	2	2186	47	0.000
Station × plot	2	6	<1	0.948
Station × species	2	7	<1	0.919
Plot × species	4	599	13	0.019
Station × plot × species	4	35	1	0.934
Residual	30	1291	28	
Total	47	4613	100	

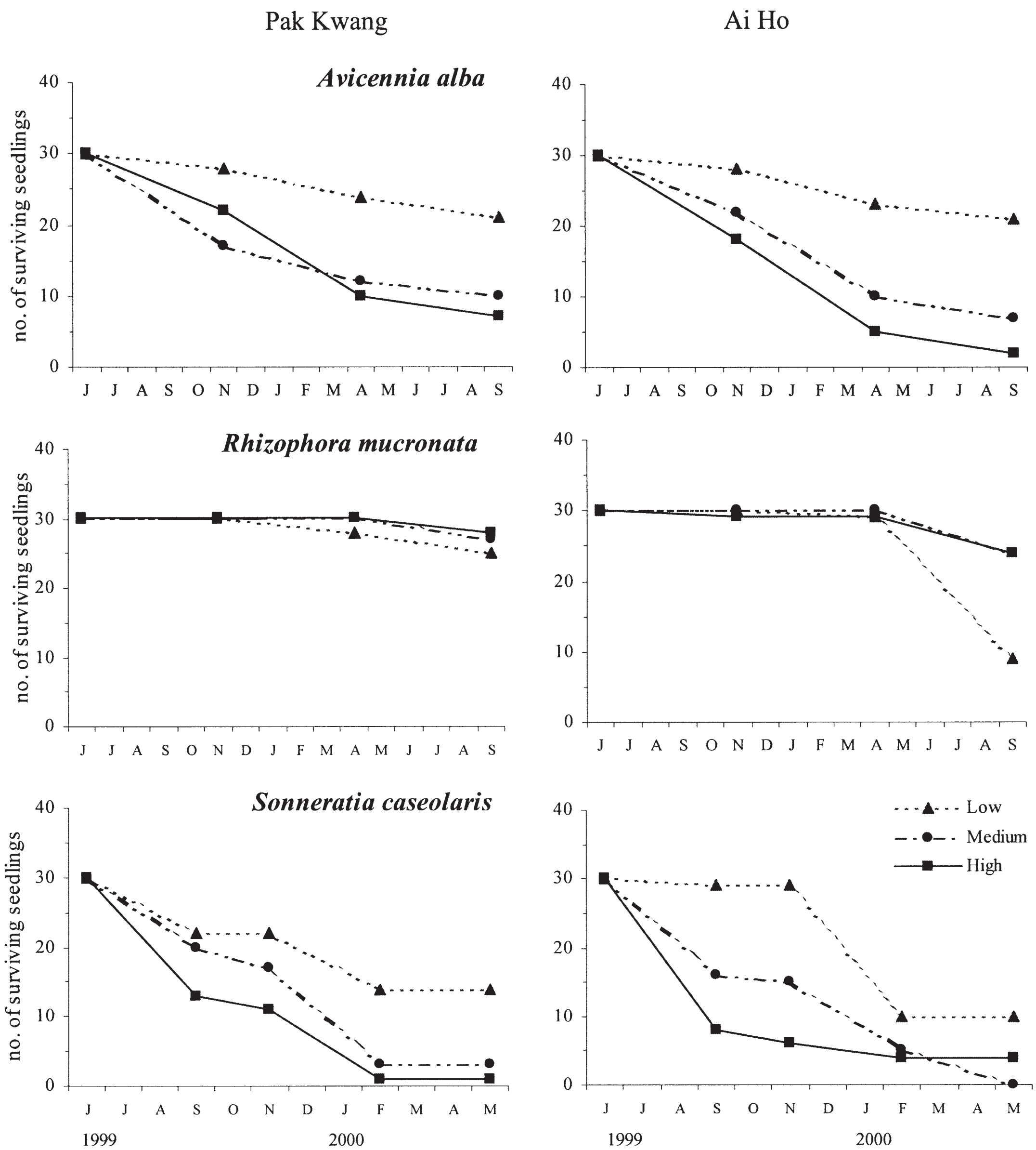

Fig. 4. Survival curves of *Avicennia alba*, *Rhizophora mucronata* and *Sonneratia caseolaris* seedlings at 3 plots of different neighboring tree density at Pak Kwang and Ai Ho canals

Table 4. Mortality rate (%) after 1 yr of the 3 mangrove species in the plots of increasing neighboring plant density. Presented are means ± standard error (SE) calculated from both stations

Species	Neighboring plant density		
	Low	Medium	High
Avicennia alba	30.0 ± 0.0	71.7 ± 5.0	85.0 ± 8.3
Rhizophora mucronata	43.3 ± 26.7	15.0 ± 5.0	13.3 ± 6.7
Sonneratia caseolaris	60.0 ± 6.7	95.0 ± 5.0	91.7 ± 5.0

Seedling height

First, the data of all 3 species were combined and analyzed using repeated-measures GLM to examine the effect on seedling growth of the factors time, species, stations and plots of different neighboring plant density. We found that the repeated-measures factor (time) and its interaction with stations, and its interaction with species and plots were all significant ($p < 0.05$). We also found highly significant differences in RGR_H between species and between the 2 stations ($p < 0.001$; Table 5), and slight significant differences between plots of contrasting density ($p < 0.05$; Table 5). The *Sonneratia caseolaris* seedlings had the highest RGR_H, while those of *Avicennia alba* had the lowest (Table 6). Overall, RGR_H declined with increasing age of the seedlings (Fig. 5).

Subsequently, the data of each species were analyzed separately in order to examine the effect of the larger (station) and smaller (plot) scales of exposure on each species individually. The significant difference in RGR_H was detected between the 2 stations for all species ($p < 0.05$; Table 5). The factor plots were not significant for *Avicennia alba* and barely significant for *Sonneratia caseolaris* ($p = 0.052$; Table 4) but highly significant for *Rhizophora mucronata* ($p < 0.001$; Table 5). RGR_H of *Avicennia* and *Sonneratia* spp. seedlings at Ai Ho Canal were substantially higher than at Pak Kwang Canal (Table 6). Similar to seedling survival, *R. mucronata* seedlings exhibited a significantly higher RGR_H in the high-density plot (0.753 ± 0.058 mm cm^{-1} mo^{-1}) than in the low-density plot (0.715 ± 0.058 mm cm^{-1} mo^{-1}).

Number of internodes produced

Monthly internode production was analyzed in the same way as RGR_H. We found that the effect of time (repeated measures) and its interaction with stations were not significant, while its interaction with species and with plots was significant ($p < 0.05$). The number of internodes produced per month was significantly different between species, between plots and between the 2 stations ($p < 0.001$; Table 7). The interaction between stations and species, as well as stations and plots, was highly significant ($p < 0.001$; Table 7) while the interaction between plots and species was just significant ($p < 0.05$; Table 7). As with RGR_H, a significant difference in monthly internode production between the 2 stations was detected for *Avicennia* and *Sonneratia* spp. ($p < 0.05$; Table 7) but not for *Rhizophora mucronata*. In addition, the factor plots were highly significant for *R. mucronata* ($p < 0.001$; Table 7) but were just significant for *Sonneratia* and *Avicennia* spp. ($p < 0.05$; Table 7). The interaction between stations and plots was significant for all 3 species ($p < 0.05$). In accordance with height increment, the *S. caseolaris* seedlings had the highest monthly internode production, while *R. mucronata* had the lowest, and the internode production of *Avicennia* and *Sonneratia* spp. seedlings at Ai Ho Canal were substantially higher than at Pak Kwang Canal (Table 6, Fig. 6). *R. mucronata* seedlings had a higher internode production in the lower neighboring plant-density plot (0.658 ± 0.017, 0.539 ± 0.014 and 0.532 ± 0.015 internode mo^{-1} at the plots of low, medium and high density, respectively).

Table 5. Result of repeated-measures general linear model (GLM) examining the effects species, stations and neighboring plant densities (plots) on seedling height increase (RGR_H) for all 3 species and each species separately. The repeated-measures factor (time) was significant in all cases ($p < 0.05$)

Factors	All species			*Avicennia alba*		
	df	SS	p	df	SS	p
Species	2	54.907	0.000			
Station	1	16.129	0.000	1	1.702	0.000
Plot	2	2.985	0.001	2	0.020	0.828
Station × plot	2	6.661	0.000	2	0.774	0.002
Station × species	2	17.866	0.000			
Plot × species	4	8.278	0.000			
Station × plot × species	4	8.273	0.000			
Within + residual	222	42.245	0.000	64	3.459	

Factors	*Rhizophora mucronata*			*Sonneratia caseolaris*		
	df	SS	p	df	SS	p
Station	1	0.162	0.027	1	14.102	0.001
Plot	2	0.853	0.000	2	6.047	0.052
Station × plot	2	0.081	0.288	2	9.609	
Within + residual	131	4.220		27	24.704	0.003

Table 6. Overall RGR_H and number of internodes produced of the 3 mangrove species at Pak Kwang and Ai Ho Canals. Presented are means ± SE

Species	RGR_H ($mm\ cm^{-1}\ mo^{-1}$)		Internode ($internode\ mo^{-1}$)	
	Pak Kwang	Ai Ho	Pak Kwang	Ai Ho
Avicennia alba	0.436 ± 0.017	0.777 ± 0.033	0.649 ± 0.028	1.011 ± 0.041
Rhizophora mucronata	0.720 ± 0.036	0.743 ± 0.035	0.568 ± 0.013	0.579 ± 0.013
Sonneratia caseolaris	1.395 ± 0.108	2.158 ± 0.139	1.855 ± 0.096	2.918 ± 0.138

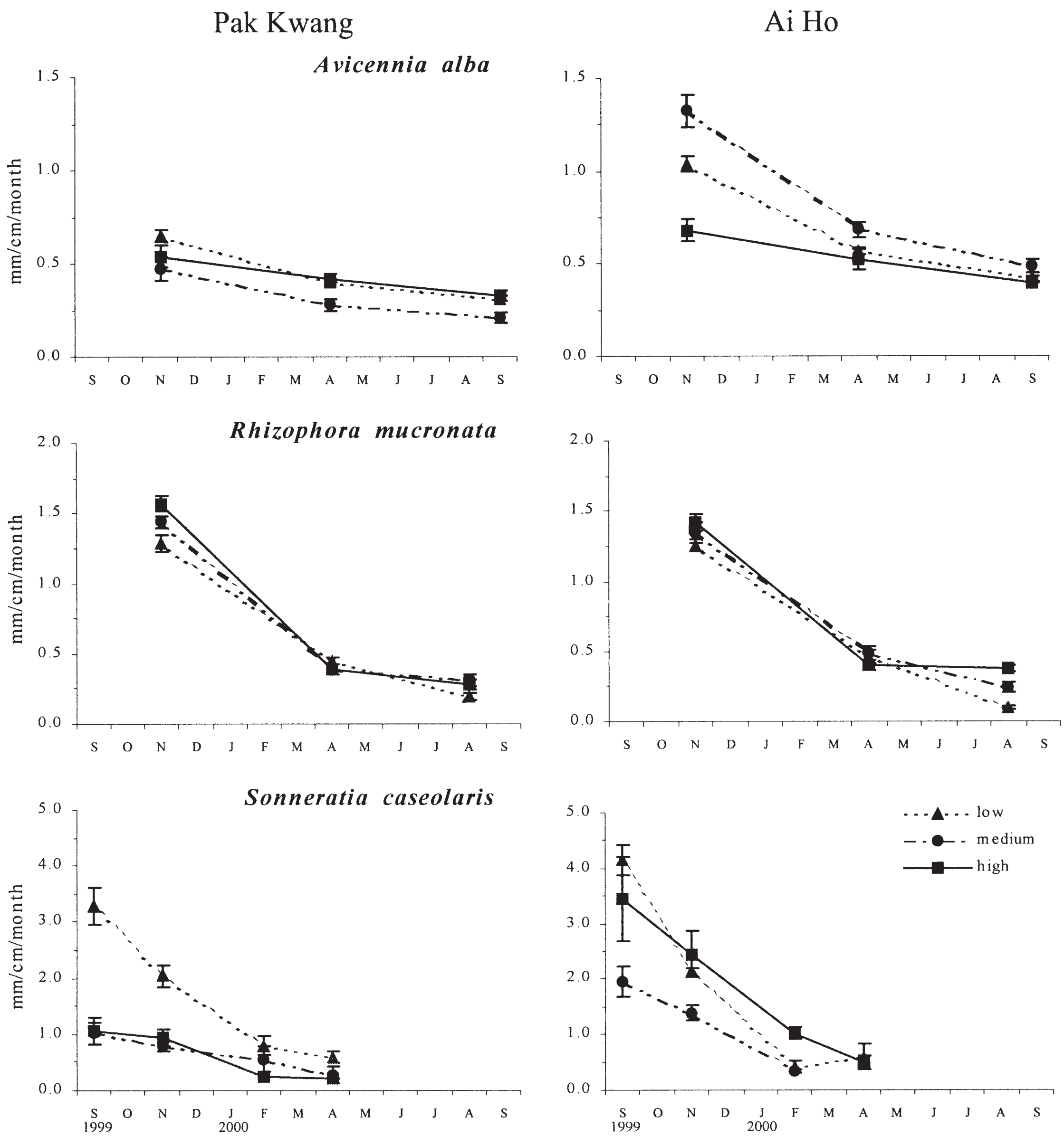

Fig. 5. Relative growth rate expressed in height ($mm\ cm^{-1}\ mo^{-1}$) of *Avicennia alba*, *Rhizophora mucronata* and *Sonneratia caseolaris* seedlings at 3 plots of different neighboring tree density at Pak Kwang and Ai Ho Canals. Presented are means ± SE. The graphs of each species have a different scale on the *y*-axis

Table 7. Result of repeated-measures GLM examining the effects of species, stations and neighboring plant densities (plots) on number of internodes produced per month for all 3 species and each species separately. The repeated-measures factor (time) was not significant ($p = 0.121$), nor was its interaction with stations ($p = 0.288$), while its interaction with species and its interaction with density were significant ($p < 0.05$)

Factors	All species			*Avicennia alba*		
	df	SS	p	df	SS	p
Species	2	84.406	0.000			
Station	1	25.557	0.000	1	4.242	0.000
Plot	2	16.958	0.000	2	0.796	0.016
Station × plot	2	12.248	0.000	2	0.598	0.043
Station × species	2	22.241	0.000			
Plot × species	4	13.667	0.014			
Station × plot × species	4	18.259	0.000			
Within + residual	222	62.010		64	5.769	
Factors	***Rhizophora mucronata***			***Sonneratia caseolaris***		
	df	SS	p	df	SS	p
Station	1	0.005	0.604	1	21.420	0.003
Plot	2	0.625	0.000	2	15.591	0.033
Station × plot	2	0.361	0.000	2	22.971	0.002
Within + residual	131	2.518		27	54.503	

DISCUSSION

As confirmed by our results, water movement varied between the 2 stations and between plots of different existing tree density, with most of the variation being seasonal. Water movement was higher in the monsoon season of October to January than in the other months of the year. The variation of shelter at the smaller (plot) scale was considerably higher than at the larger (station) scale. Shelter increased gradually from the mangrove forest edge to the interior, similar to patterns found by others (Leonard & Luther 1995). We found that water movement at the bottom of this mangrove-fringed bay was relatively low as <5% of the initial weight of the deployed clod cards dissolved per day. The DF values calculated from our data ranged between 2 and 9, which is considerably less than the ranges reported for tropical intertidal seagrass beds (10 to 15, Erftemeijer & Herman 1994) and a coral reef flat and lagoon (5 to 25, Jokiel & Morrissey 1993). This is not unexpected, given the fine texture of sediment of Pak Phanang Bay (Kamp-Nielsen et al. 2002), indicative of low sediment erosion rates and low velocities reported for mangrove systems elsewhere (Wolanski 1992).

Apparently, the initial size of the seedlings was large enough to prevent them being attacked by crabs. Therefore, none of them were damaged by this sort of predator. In addition, only a few crabs were observed in the area. Seedling survival differed significantly between the 3 species and with increasing tree density between plots Seedling mortality was spread equally over the year in *Avicennia alba*, which was not the case in the other 2 species. In *Sonneratia caseolaris*, 2 periods of increased mortality were observed, which coincided with heavy rainfall, to which its smaller seedlings may be more sensitive than those of the other species. After 1 yr, the mortality rate in the low plant-density plots was highest in *Rhizophora mucronata* but lowest in *Avicennia* and *Sonneratia* spp. (Table 4). The observed maximum survival in the most exposed and open plots of both *Avicennia* and *Sonneratia* spp. is in agreement with their role as pioneer species (Clough 1982, Tomlinson 1986, Panapitukkul et al. 1998). Our observation suggested that the main cause of high mortality of *R. mucronata* in the most exposed plots was uprooting by waves or drifting objects colliding against the lengthy, rigid seedlings. The higher mortality in the exposed, mangrove front area may be a factor explaining the later appearance along the successional series of this species (Tomlinson 1986).

Seedling growth varied strongly between species. Growth of *Avicennia* and *Sonneratia* spp. differed significantly between the inner and outer sites of the bay. *A. alba* had a higher seedling growth at the exposed site of Ai Ho, near natural stands, than at the inner site of Pak Kwang (Figs. 5 & 6, Table 6). Growth of *S. caseolaris* followed the same pattern but its survival was higher at Pak Kwang, near natural stands, than at Ai Ho. Growth of *Rhizophora mucronata* was not significantly different between the 2 bay sites but RGR_H increased with increasing neighboring vegetation densities. The seedlings of *S. caseolaris* had the highest growth in terms of both height increase and production of internodes along the main stem. We found the annual number of internodes produced for *Sonneratia, Avicennia* and *Rhizophora* spp. to be 30.3 ± 1.7, 13.2 ± 0.3 and 6.5 ± 0.2, respectively, which did not differ substantially from those of naturally established seedlings (28.8 ± 2.1 and 17.6 ± 0.8 for *S. caseolaris* and *A. alba*, Panapitukkul et al. 1998, Duarte et al. 1999; 6.1 ± 0.3 for *R. mucronata*, Duarte et al. 1999, Thampanya et al. unpubl.). The observed decline in relative seedling growth with age is a common phenomenon in terrestrial plants ('ontogenetic drift', Van Andel & Jager 1981).

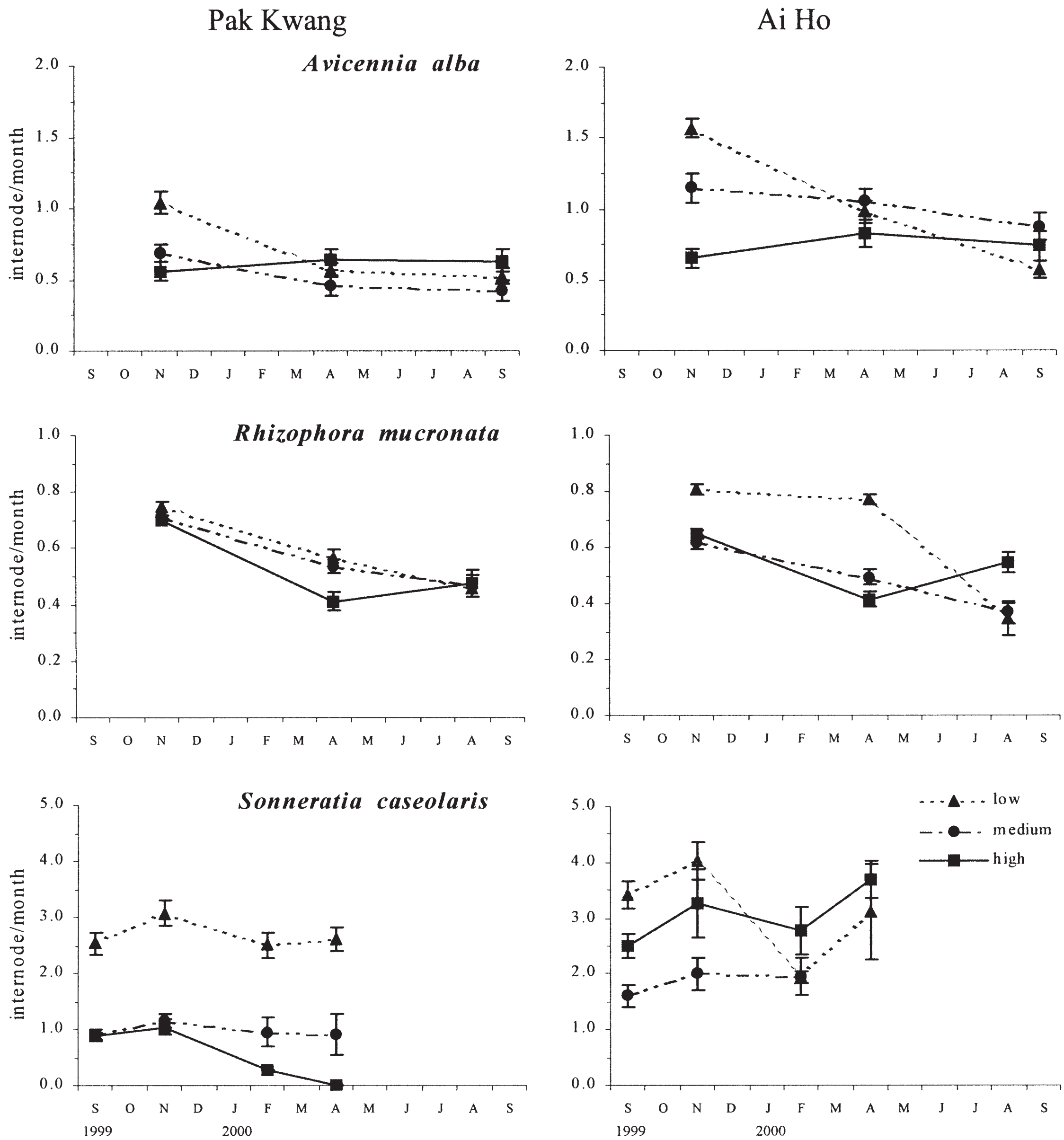

Fig. 6. Number of internodes produced (internode mo^{-1}) of *Avicennia alba*, *Rhizophora mucronata* and *Sonneratia caseolaris* seedlings at 3 plots of different neighboring tree density at Pak Kwang and Ai Ho Canals. Presented are means ± SE. The graphs of each species have a different scale on the *y*-axis

Our results confirm the higher survival of *Avicennia alba* and *Sonneratia caseolaris* at the outer, colonizing front of the mangrove forest and provide an explanation for their role as pioneer species in the Pak Phanang Bay mangrove area (Panapitukkul et al. 1998). These species appear to be affected negatively by density of adult plants. These effects may be derived from the shading associated with increasing tree density. *Rhizophora mucronata* shows an opposite pattern, with the best seedling performance associated with denser stands, in agreement with their successional role, as climax species in natural SE Asian mangrove forests. The first 2 species are also capable of establishing themselves on the open mudflat, so that mangrove rehabilitation is probably not needed if natural colonization by these species is not prevented. In addition, the cost for replanting mangrove with *Rhizophora* sp. is relatively high: in Thailand, this was estimated at \$US500 ha^{-1} (Plathong 1998). However, intensive human exploitation activities (such as fishing by push net and trawler) and traffic across the mudflat by local fishing boats are major sources of disturbance, dislodging numerous mangrove seedlings. The creation of temporary reserved areas excluding these activities may be sufficient to enable natural colonization. If the replanting of economical species such as *Rhizophora* is required, areas with some existing plants are suggested as the most suitable for planting.

In summary, our results demonstrate contrasting effects of exposure and neighboring plant density on the performance of the seedlings of the 3 most important species in the mangrove forest studied. These effects are consistent with the role of the species in the successional series, suggesting that exposure and density are important determinants of mangrove species succession. The results obtained may, in addition, provide a basis for the selection of suitable target species for afforestation programs in different mangrove areas.

Acknowledgements. The authors are grateful to the Coastal Resources Institute and the Faculty of Natural Resources of the Prince of Songkla University, in general, and to Dr. Somsak Boromthanarat, in particular, for giving useful suggestions and providing all research facilities. We thank Nawee Noon-anand, Chamnan Worachina, Phollawat Saijung and the fishermen at Pak Phanang West village for their friendly assistance in field data collection. We are also grateful to Prof. Patrick Denny for critically reading the manuscript. This study is funded by the Netherlands Foundation for the Advancement of Tropical Research, WOTRO project WB 84-412.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: June 1, 2001; Accepted: March 19, 2002
Proofs received from author(s): June 21, 2002