

Article

Interactive Effects of Intertidal Elevation and Light Level on Early Growth of Five Mangrove Species under *Sonneratia apetala* Buch. Hamplantation Canopy: Turning Monocultures to Mixed Forests

Zhongmao Jiang, Wei Guan, Yanmei Xiong, Mei Li, Yujun Chen and Baowen Liao *

Key Laboratory of State Forestry Administration on Tropical Forestry, Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou 510520, China; zhongmaojiang@163.com (Z.J.); guanwei1997@126.com (W.G.); xiongym@ritf.ac.cn (Y.X.); mangrovelime@163.com (M.L.); yujunchen@hotmail.com (Y.C.)

* Correspondence: baowenliao@caf.ac.cn; Tel.: +86-186-6466-1496

Received: 9 December 2018; Accepted: 20 January 2019; Published: 22 January 2019



Abstract: The introduced *Sonneratia apetala* Buch. Hamplantation plantations have occupied more than 3800 ha in China. The prevalence, fast growth rate, and high seed production of *S. apetala* have raised concerns about the risks to native mangrove habitats. Efforts are required to convert these introduced monocultures to mixed or native forests. In this study, we examined native mangrove colonization in the introduced *S. apetala* plantations at the Qi'ao Island, Zhuhai, China. A 12-month field study was conducted to evaluate the effects of intertidal elevation and light level on the survival and early growth of five native mangrove species, viz., *Bruguiera gymnorrhiza* (L.) Savigny, *Kandelia obovata* Sheue, Liu & Yong, *Aegiceras corniculatum* (L.) Blanco, *Avicennia marina* (Forssk.) Vierh., and *Rhizophora stylosa* Griff. Across intertidal elevations and light levels, the survival of *B. gymnorrhiza* was the highest. All the species had relatively higher survival rates under 30% canopy closure. Although the seedlings survived best at high intertidal elevation, the relative growth rate (RGR) was the highest at low intertidal elevation, and it was promoted by high light level. The stem height at low intertidal elevation was higher than that at high intertidal elevation, and it was the highest under 30% canopy closure. *B. gymnorrhiza* and *R. stylosa* at high intertidal elevation had relatively high leaf numbers, whereas *K. obovata* and *A. marina* showed a reverse tendency. The growth of stem diameter showed a decreasing trend initially and then increased with better performance at low intertidal elevations, and *B. gymnorrhiza* presented the best value under 30% canopy closure. *Bruguiera gymnorrhiza* showed the highest growth rate under similar conditions. Overall, intensive canopy thinning is an effective measure to promote native mangrove growth in *S. apetala* plantations. Additionally, increasing planting density especially at low intertidal elevations may improve native mangrove establishment and growth. Furthermore, *Bruguiera gymnorrhiza* is the best choice in the effort to plant native species in *S. apetala* plantations in the study area.

Keywords: intertidal elevation; light level; mangrove; restoration; survival

1. Introduction

Mangroves are the only forests bridging land and sea with a rich diversity of flora and fauna in the intertidal zones of tropical and subtropical coastlines [1,2]. Mangroves provide ecological services to humans, but they are also threatened by anthropogenic activities [3,4]. Mangrove habitats are becoming small or fragmented, which is attributable to anthropogenic activities, including aquaculture, agricultural reclamation, urbanization, and pollution explosion [5,6]. The mangrove forest area in

China was 250,000 ha, but it was reduced to 42,000 ha by 1956, and further shrunk to 21,000 ha by the end of the 1980s and to 15,000 ha by the end of 1990s, according to the National Investigation of Forest Resource [6]. In the early 1990s, China launched a 10-year mangrove reforestation program in degraded mangrove areas, through which the mangrove forest areas have recovered to 22,000 ha [6]. However, the exotic mangrove species *Sonneratia apetala* replaced the main native species (*Kandelia obovata* (Sheue, Liu & Yong) and *Bruguiera gymnorhiza* (L.) Savigny) in this program, owing to its higher survival rate and faster growth [7]. Since 1998, *S. apetala* has been widely planted as a pioneer species in Guangdong, Guangxi, Fujian, and Zhejiang Provinces. The planting area of *S. apetala* has exceeded 3800 ha in China [8]. For example, *Spartina alterniflora* Loisel. began to invade the Qi'ao Island in the early 1990s [9], and expanded its coverage to up to 227 ha by 1995. In 1999, *S. apetala* was introduced to control *S. alterniflora* invasion, eventually eradicating *S. alterniflora* in 2011 (only 0.63 ha remained for experimental purpose) [10,11]. However, *S. apetala* covered approximately 600 ha on Qi'ao Island by 2008 [7]. Such a large area of *S. apetala* plantation and its prevalence, fast growth rate, and high seed production has raised the concern whether the introduced species threaten the survival and development of native mangrove species [12].

Peng et al. [13] explored the dynamic changes in mixed stands under naturally spreading condition of native species in *S. apetala* plantations. The planting density of *S. apetala* directly affects the canopy gaps, which can affect the density of tree seedlings and saplings. For example, Ren et al. [14] reported that the native mangrove species, namely *K. obovata* and *Rhizophora stylosa* Griff., could invade 4-year-old *S. apetala* plantations, but disappeared after 10 years in Leizhou Bay, Guangdong. However, in the Sanjiang River of Qiongzhusan, Hainan, the native mangrove species such as *K. obovata*, *Aegiceras corniculatum* (L.) Blanco, and *Bruguiera sexangula* (Lour.) Poir. were naturally diffused in a 12-year-old *S. apetala* plantation. Furthermore, compared with those of a 5-year-old *S. apetala* plantation, the number of species remained basically unchanged, and the diversity index and uniformity index increased marginally [15]. The planting density of *S. apetala* in these two plantations was 2500 and 833 plants/ha, respectively. Similarly, shading has been reported to significantly limit *Xylocarpus granatum* Koenig seedling growth and might affect the establishment of *X. granatum* under forest canopies [16]. In contrast, *Rhizophora apiculata* Blume, *B. gymnorhiza*, and *Xylocarpus moluccensis* could have higher sapling and seedling densities under closed canopy than under open gaps [17].

Since 1999, *S. apetala* has been planted in approximately 600 ha in the Qi'ao Island, successfully controlling the further spread of *S. alterniflora* [7]. In addition to different canopy closures, this plantation also occupied high tide beaches and low tide beaches. Usually, *Avicennia marina* (Forssk.) Vierh., *B. gymnorhiza*, and *R. stylosa* survived or grew the best at high intertidal elevation. *Ceriops tagal* (Perr.) C.B. Rob. reached the maximum abundance at low intertidal elevation [18]. Therefore, the objective of the present study was to compare the growth and physiological responses of five native mangrove species seedlings at different light levels and intertidal elevations. We also attempted to examine the interactive effect of light level and intertidal elevation on the early development of five native mangrove species seedlings. The results will provide a theoretical basis for afforestation in *S. apetala* plantations using native species.

2. Materials and Methods

2.1. Study Sites

The study area is situated in the Qi'ao-Dangan Provincial Nature Reserve, located on the Qi'ao Island of Zhuhai in China. Its geographical location is 22°23'40"–22°27'38" N and 113°36'40"–113°39'15" E (Figure 1). The region has south subtropical marine climate with an average annual rainfall of 1964.4 mm, annual sunshine duration of 1907.4 h, and annual average temperature of 22.4 °C. The tide pattern is irregular and semidiurnal, and the average salinity of sea water is $18 \pm 2\text{‰}$. The average high tide level is 0.27 m, and the average low tide level is −0.24 m. The plantation of

S. apetala is fan-shaped in the tidal flat, and a small area of *K. candel* and *A. corniculatum* plantations was nearby.

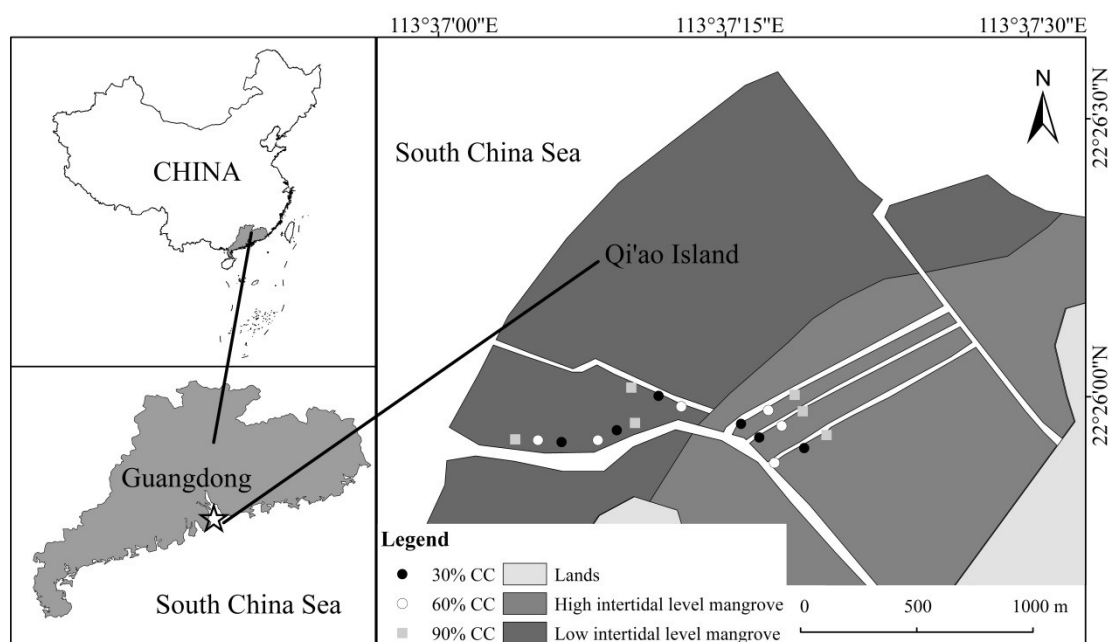


Figure 1. Sketch map of field trial sites in mangrove plantation at the Qi'ao Island. The abbreviations of sites refer to 30% canopy closure (30% CC), 60% canopy closure (60% CC) and 90% canopy closure (90% CC), respectively.

Five native species in Southern China (namely, *K. obovata*, *A. corniculatum*, *A. marina*, *B. gymnorrhiza*, and *R. stylosa*) were selected for the present study. The propagules of *K. obovata* and *A. corniculatum* were collected from Qi'ao Island. The propagules of *A. marina*, *B. gymnorrhiza*, and *R. stylosa* were collected from the Zhanjiang Mangrove National Nature Reserve (20°14'–21°35' N and 109°40'–110°35' E). The seeds of *A. corniculatum* and *A. marina*, and the hypocotyls of *K. obovata*, *B. gymnorrhiza*, and *R. stylosa* were collected from under the canopy. The length of propagules ($n = 50$) of *K. obovata*, *R. stylosa*, and *B. gymnorrhiza* was 19.32 ± 2.72 , 28.46 ± 3.48 , and 15.49 ± 1.32 , respectively, and their wet weight was 14.67 ± 3.75 , 19.44 ± 2.83 , and 22.37 ± 4.23 g, respectively. The mean wet weight of *A. corniculatum* and *A. marina* seeds was 0.008 ± 0.002 and 0.015 ± 0.004 g, respectively.

2.2. Experimental Design

We measured the canopy closure using fisheye lens camera (Nikon D750, Nikon Precision Shanghai Co., Ltd., Shanghai, China and SIGMA 8 mm F3.5 EX DG FISHEYE, Heshuo Optical Equipment Shanghai Co., Ltd., Shanghai, China) at the intersection of diagonals of the sample plot and selected the plots with 30%, 60%, and 90% canopy closure. The effects of wave action (tidal inundation time [18] and wave [19]) on young mangrove species across the intertidal zone were different, and the effects were relatively significant in the low intertidal zone. We measured the water level of the low tide zone and high tide zone using a water level logger (HOBO U20-001-0x, Onset computer corporation, Bourne, Massachusetts, America) at high tide; the average elevation difference of the tide zones was 0.87 ± 0.26 m. Quadrats of dimension 10 m $\times$ 10 m were created in the high tide beach and low tide beach with the canopy density of 30%, 60%, and 90%, respectively. Three repetitions per processing combination, a total of 18 sample plots, were performed.

In April 2017, the hypocotyls of *K. obovata* and *B. gymnorrhiza* were planted, and the seeds of *A. corniculatum* and *A. marina*, and the hypocotyls of *R. stylosa* were planted in June in each plot. Fifty propagules were planted in each sample plot to examine the frequency and period of germination under six processing combinations.

2.3. Measurement of Seedling Survival and Seedling Growth

From April 2017, a 12-month growth trial was set up, and seedling growth was measured once a month. The budding date of each propagule was recorded every 10 days, and the total number of propagules that survived was also counted in each sample plot. Other germination parameters, such as the stem height, stem basal diameter, and number of unfurled leaves, were measured at every 60 days after planting the propagules. The stem height and stem basal diameter of each seedling were determined directly using callipers. At the end of the trial, the seedlings were collected and separated into leaf, stem, and root components, and then dried at 65 °C to a constant mass to determine the biomass. The monthly relative growth rate (RGR) was determined, according to the method of Ye et al. [20].

2.4. Statistical Analyses

For one-parameter statistical tests, the analysis of variance (ANOVA) was performed using SPSS 21.0 for Windows (SPSS Inc., New York, NY, USA). The differences in growth and physiological responses of seedlings among the five species and six habitats were analyzed with the two-way ANOVA. Significant differences among multiple means were determined by the SNK test.

3. Result

3.1. Seedling Survival

During the 360-day trial, the number of seedlings that survived decreased gradually and differed significantly among the five species. There was a significant interactive effect of light level and intertidal elevation on the number of seedlings that survived among *A. corniculatum*, *B. gymnorrhiza*, *K. obovata*, and *R. stylosa*. There was no significant interactive effect of light level and intertidal elevation on *A. marina* (Table 1).

Table 1. F values of two-way ANOVA tests indicating the differences of five mangrove species surviving in varying light level and intertidal elevation.

Species	Sources of Variance		
	Light Level	Intertidal Elevation	Light Level × Intertidal Elevation
Ac	334 ***	9.21 ***	22.9 ***
Am	455 ***	31.6 ***	1.69 NS
Bg	31.7 ***	20.7 ***	12.3 ***
Ko	116 ***	55.7 ***	84.2 ***
Rs	85.2 ***	9.96 ***	14.2 ***

Note: NS means not significant at $p > 0.05$ ($n = 54$). *** Statistical significance at $p < 0.001$. Ac = *Aegiceras corniculatum*, Am = *Avicennia marina*, Bg = *Bruguiera gymnorrhiza*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*.

The survival rate of the five mangrove species seedlings was different at different intertidal elevations. The survival rate of *B. gymnorrhiza* was the highest in each habitat, followed by *K. obovata* seedlings at low intertidal elevation. Conversely, the survival rate of *A. marina*, *A. corniculatum*, and *R. stylosa* was lower at the low intertidal elevation than at the high intertidal elevation. The number of *A. corniculatum*, *A. marina*, and *R. stylosa* seedlings that survived at the high intertidal elevation was higher than that at low intertidal elevation, whereas the number of *B. gymnorrhiza* and *K. obovata* seedlings that survived at low intertidal elevation was more than that at high intertidal elevation. The number of *A. corniculatum* and *A. marina* seedlings that survived decreased rapidly at low intertidal elevation, which may be dislodged by wave action. The number of *R. stylosa* seedlings that survived decreased rapidly in every habitat during 180 to 240 days (Figure 2). The number of species that survived showed a marginal decreasing trend with time at high intertidal elevation, whereas the survival rate was stable from 240 days. With an increase in canopy closure, the number of seedlings that

survived among the five mangrove species was also different. In the habitats of 60% and 90% canopy closure with lower light penetration, the average seedling survival rate of mangrove species decreased marginally (Figure 2). Intertidal elevation had a higher effect than light level on seedling survival.

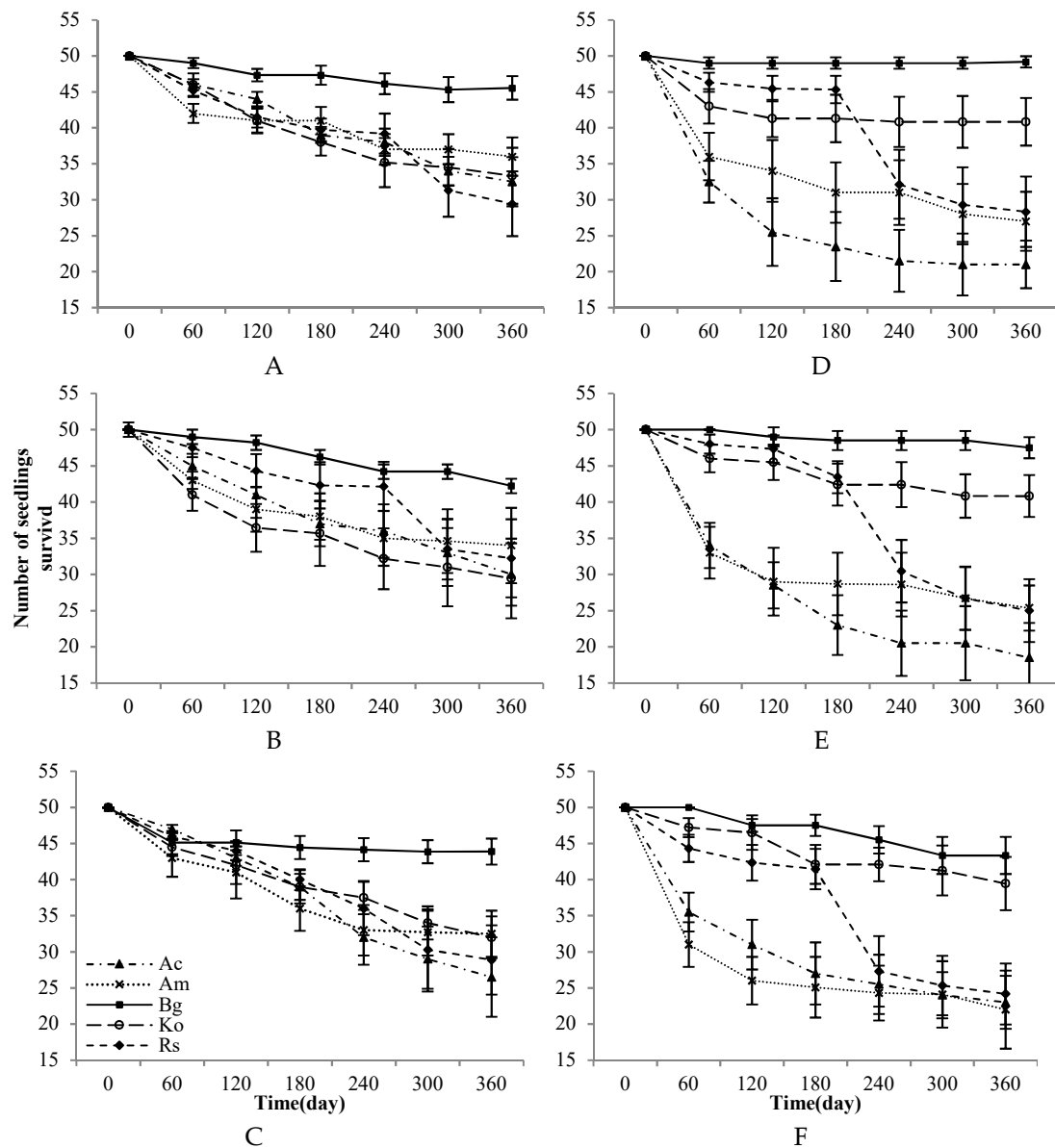


Figure 2. The number of seedlings of the five mangrove species surviving (Bg = *Bruguiera gymnorrhiza*, Ac = *Aegiceras corniculatum*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*, Am = *Avicennia marina*) (A) 30% canopy closure and high intertidal elevation, (B) 60% canopy closure and high intertidal elevation (C) 90% canopy closure and high intertidal elevation, (D) 30% canopy closure and low intertidal elevation, (E) 60% canopy closure and low intertidal elevation, (F) 90% canopy closure and low intertidal elevation.

3.2. Seedling Morphological Features and Growth Rates

Both intertidal elevation and light level had significant effects on the stem height, leaf number, and stem diameter (Table 2). The stem height differed significantly among intertidal elevations and light levels (Table 2). The annual cumulative increase in the stem height at low intertidal elevation was generally high at the same light level. The stem height in the understory of 30% canopy closure was the highest irrespective of intertidal elevation. We found that the stem height of *B. gymnorrhiza*, *A. corniculatum*, and *A. marina* under 30% canopy closure in high tide beach was lower than that under

60% canopy closure in low tide beach, respectively. Conversely, the stem height of *R. stylosa* under 30% canopy closure was higher than that under 60% canopy closure. The highest stem height of *B. gymnorrhiza*, *K. obovata*, *R. stylosa*, *A. corniculatum*, and *A. marina* under 30% canopy closure was 63.79, 56.32, 54.34, 42.13, and 41.67 cm, which was 36.22%, 85.31%, 30.21%, 53.62%, and 31.45% higher than that under 90% canopy closure at low intertidal elevation, respectively. The relative growth of *B. gymnorrhiza* decreased with time after 120 days, whereas the other species tended to grow steadily after 180 days (Figure 3).

The increase in leaf number among the species was significantly different at different light intensities, and *A. corniculatum* presented a significant difference in leaf number at different intertidal elevations (Table 2). *Bruguiera gymnorrhiza* and *R. stylosa* at high intertidal elevation generally presented relatively high leaf numbers, whereas *K. obovata* and *A. marina* showed a reverse tendency. The number of *A. corniculatum* differed marginally between 30% and 60% canopy closure but declined sharply under 90% canopy closure irrespective of intertidal elevation. The relative growth of *K. obovata* and *B. gymnorrhiza* decreased rapidly with time after 120 days, and the other species tended to grow steadily during the same period (Figure 4).

The stem diameter of *B. gymnorrhiza*, *K. obovata*, and *A. corniculatum* differed significantly between light level, and high canopy closure decreased the increase in stem diameter at low and high elevations. The stem diameter of *R. stylosa* was generally higher at high intertidal elevations, approximately 1.34 times higher than that at the low intertidal elevations. Furthermore, *A. marina* was not significantly affected by intertidal elevation and light level (Table 2). The relative growth of *B. gymnorrhiza* was the highest under 30% canopy closure. The growth of all the species showed a decreasing trend initially and then increased with better performance at low intertidal elevations (Figure 5).

Table 2. F values of two-way ANOVA tests indicating the differences in morphological parameters in varying light levels and intertidal elevation among different mangrove species.

Species	Light Levels			Intertidal Elevation			Light Levels × Intertidal Elevation		
	Stem Height	Leaf Number	Stem Diameter	Stem Height	Leaf Number	Stem Diameter	Stem Height	Leaf Number	Stem Diameter
Ac	112 ***	12.7 ***	4.38 *	63.6 ***	23.0 ***	33.3 ***	41.6 ***	2.83 NS	0.35 NS
Am	39.2 ***	30.3 ***	3.92 *	22.2 ***	1.63 NS	2.22 NS	50.9 ***	1.46 NS	2.42 NS
Bg	85.2 ***	51.5 ***	3.13 NS	21.3 ***	0.24 NS	42.05 ***	30.6 ***	0.32 NS	1.45 NS
Ko	276 ***	43.1 ***	0.98 NS	36.5 ***	2.55 NS	27.3 ***	65.8 ***	0.19 NS	0.26 NS
Rs	26.7 ***	78.8 ***	13.0 ***	34.2 ***	5.32 NS	2.14 NS	21.1 ***	7.01 *	0.86 NS

Note: NS means not significant at $p > 0.05$ ($n = 54$). *** Statistical significance at $p < 0.001$, * Statistical significance at $p < 0.05$. Ac = *Aegiceras corniculatum*, Am = *Avicennia marina*, Bg = *Bruguiera gymnorrhiza*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*.

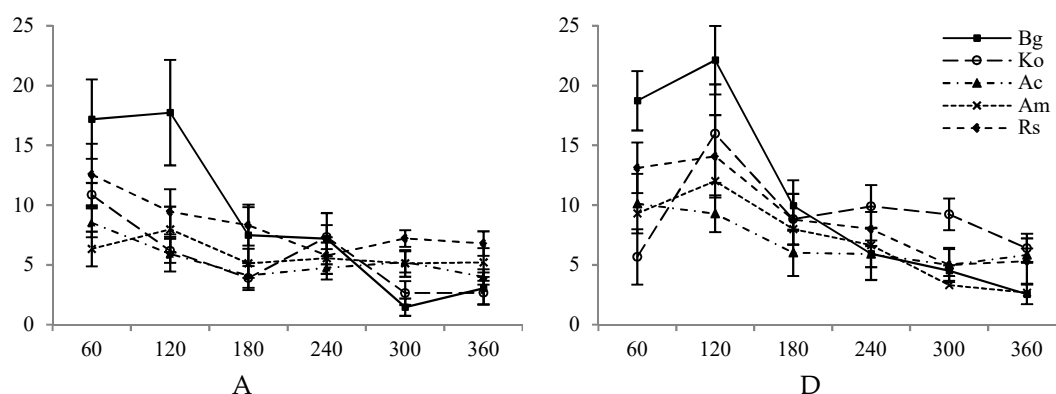


Figure 3. Cont.

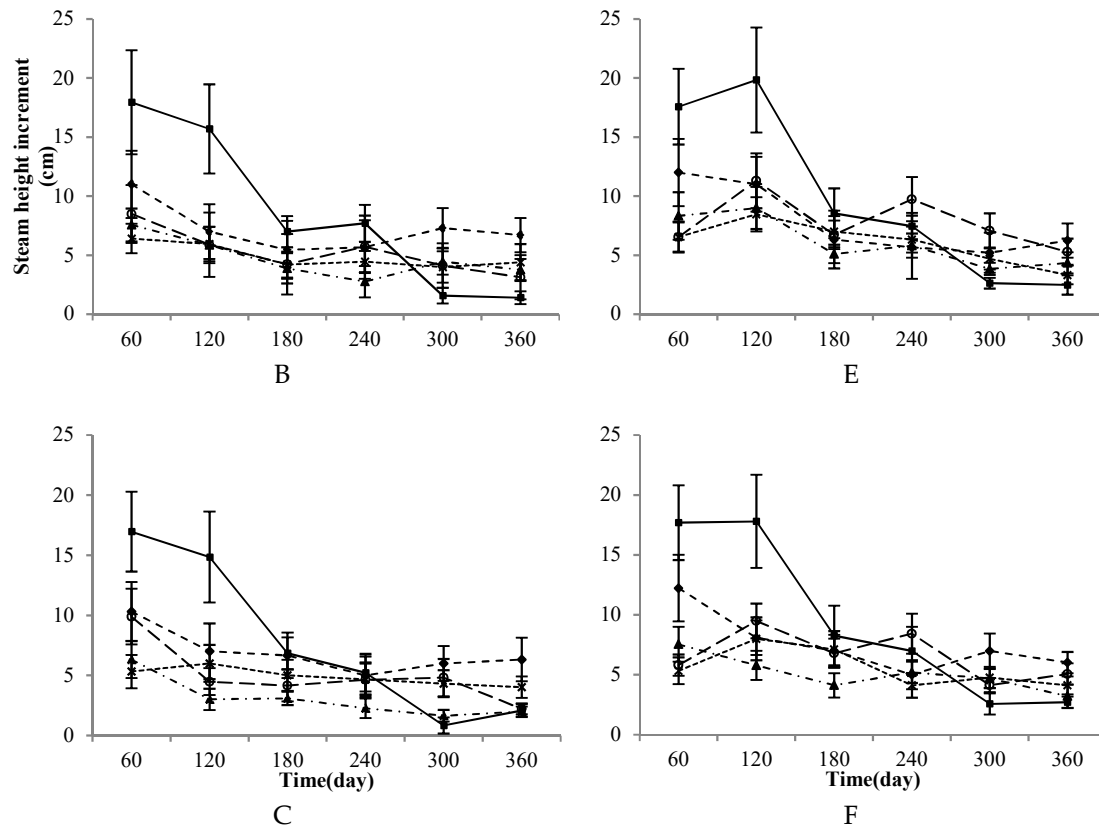


Figure 3. The steam height increment of seedlings of the five mangrove species (Bg = *Bruguiera gymnorrhiza*, Ac = *Aegiceras corniculatum*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*, Am = *Avicennia marina*) (A) 30% canopy closure and high intertidal elevation, (B) 60% canopy closure and high intertidal elevation (C) 90% canopy closure and high intertidal elevation, (D) 30% canopy closure and low intertidal elevation, (E) 60% canopy closure and low intertidal elevation, (F) 90% canopy closure and low intertidal elevation.

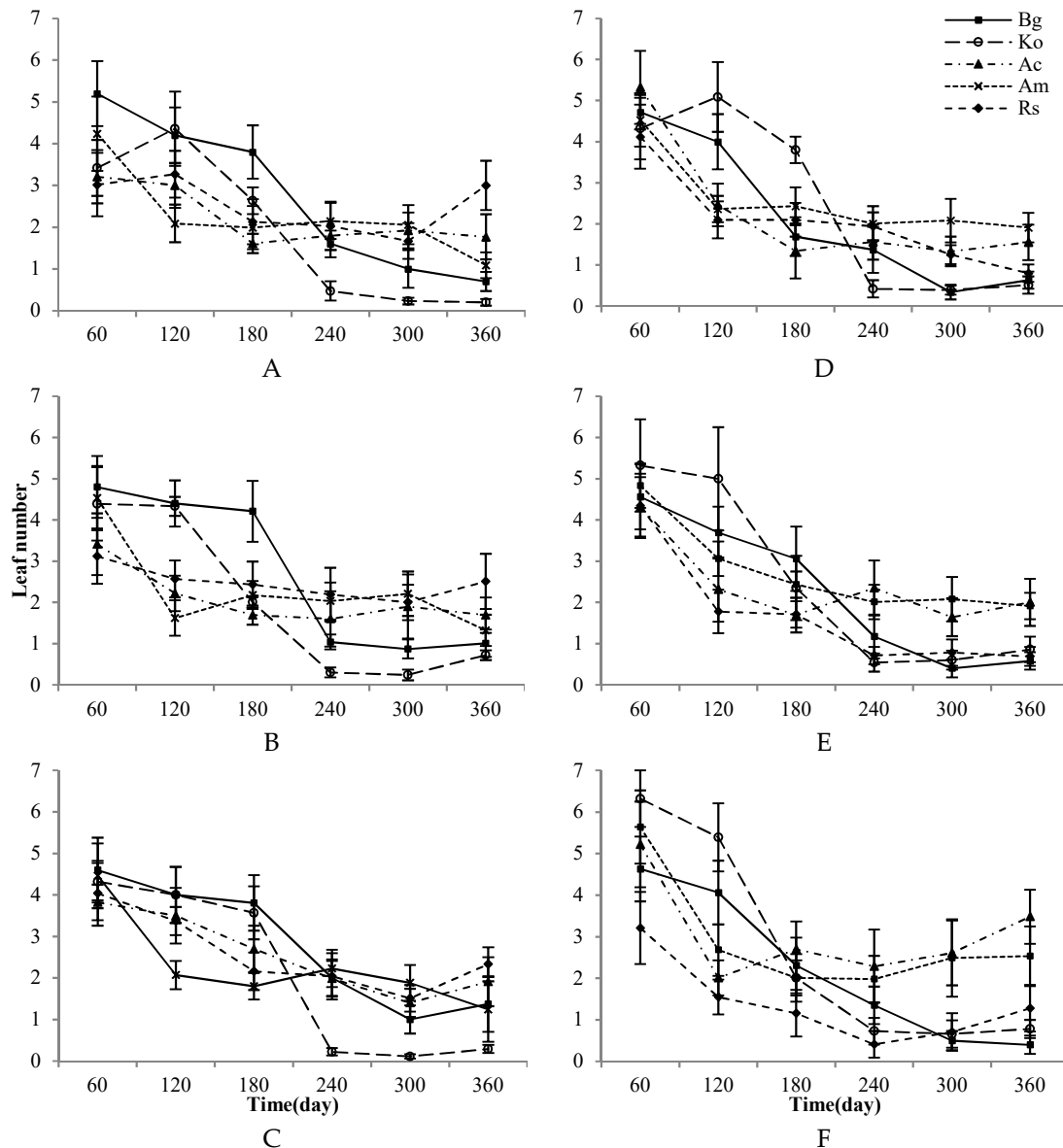


Figure 4. The leaf number of seedlings of the five mangrove species (Bg = *Bruguiera gymnorrhiza*, Ac = *Aegiceras corniculatum*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*, Am = *Avicennia marina*) (A) 30% canopy closure and high intertidal elevation, (B) 60% canopy closure and high intertidal elevation (C) 90% canopy closure and high intertidal elevation, (D) 30% canopy closure and low intertidal elevation, (E) 60% canopy closure and low intertidal elevation, (F) 90% canopy closure and low intertidal elevation.

A significant interactive effect of intertidal elevation and light intensity on the RGR was observed. The RGR of all the species significantly decreased with the decrease in light intensity. *Bruguiera gymnorrhiza*, *K. obovata*, and *R. stylosa* at high intertidal elevation presented higher RGR, whereas *A. corniculatum* and *A. marina* showed better performance at low intertidal elevation under 30% and 60% canopy closure. The RGR of *K. obovata*, *A. corniculatum*, and *A. marina* was significantly affected under 90% canopy closure at high and low intertidal elevations (Table 3).

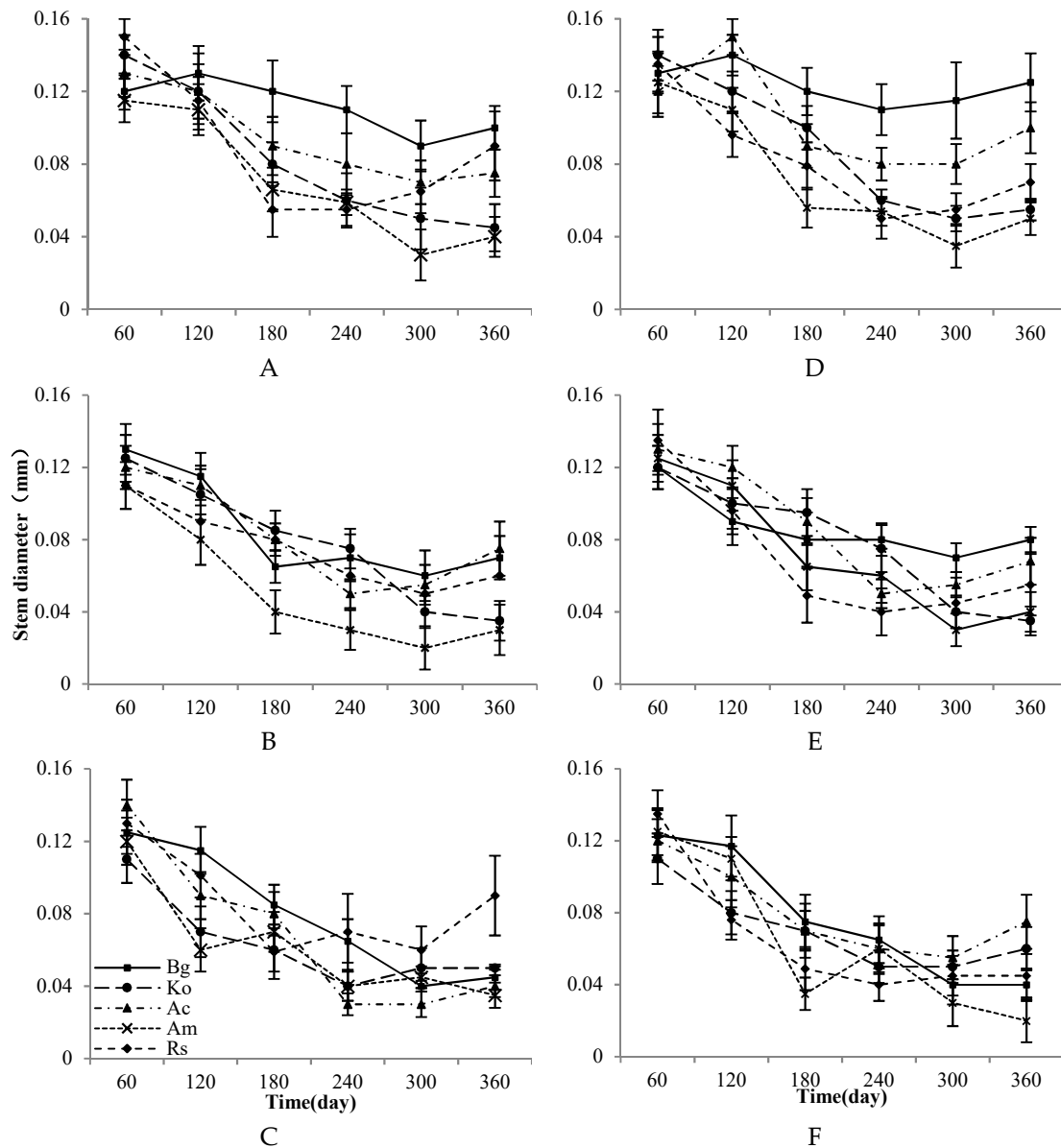


Figure 5. The stem diameter of seedlings of the five mangrove species (Bg = *Bruguiera gymnorrhiza*, Ac = *Aegiceras corniculatum*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*, Am = *Avicennia marina*) (A) 30% canopy closure and high intertidal elevation, (B) 60% canopy closure and high intertidal elevation (C) 90% canopy closure and high intertidal elevation, (D) 30% canopy closure and low intertidal elevation, (E) 60% canopy closure and low intertidal elevation, (F) 90% canopy closure and low intertidal elevation.

Table 3. The relative growth rate (RGR, mean $\pm$ SE) ($\text{mg g}^{-1} \text{ day}^{-1}$) of five mangrove species planted in varying light level and intertidal elevation.

Species	HL and 30% CC	HL and 60% CC	HL and 90% CC	LL and 30% CC	LL and 60% CC	LL and 90% CC
Bg	223.2 $\pm$ 43.5a	184.6 $\pm$ 32.4b	144.3 $\pm$ 25.3c	207.6 $\pm$ 35.4a	190.3 $\pm$ 26.3b	152.4 $\pm$ 24.3c
Ko	172.3 $\pm$ 23.6a	98.3 $\pm$ 18.5b	54.7 $\pm$ 9.7c	166.4 $\pm$ 21.3a	102.3 $\pm$ 24.5b	62.5 $\pm$ 12.6c
Ac	122.3 $\pm$ 31.2b	101.3 $\pm$ 26.4c	64.4 $\pm$ 15.4d	142.3 $\pm$ 21.7a	120.4 $\pm$ 21.2b	87.3 $\pm$ 13.4d
Rs	167.4 $\pm$ 32.4a	143.4 $\pm$ 17.6b	103.4 $\pm$ 20.3c	151.3 $\pm$ 25.3b	139.5 $\pm$ 19.4b	87.3 $\pm$ 16.3d
Am	87.32 $\pm$ 17.3b	52.4 $\pm$ 12.6c	40.5 $\pm$ 8.3c	136.4 $\pm$ 13.2a	125.4 $\pm$ 26.3a	90.3 $\pm$ 22.1b

Note: Values with different letters mean statistical significant differences at 0.05 level among treatments. HL = High intertidal level, LL = Low intertidal level, 30% CC = 30% canopy closure, 60% CC = 60% canopy closure, 90% CC = 90% canopy closure, respectively. Ac = *Aegiceras corniculatum*, Am = *Avicennia marina*, Bg = *Bruguiera gymnorrhiza*, Ko = *Kandelia obovata*, Rs = *Rhizophora stylosa*.

4. Discussion

4.1. Seedling Survival in the Understory

The survival rate of mangrove species seedlings in a mangrove forest is primarily driven by the habitat structure [21]. Mangroves have an interspecific difference in tolerance limits to shading and intertidal position at the early stage [22,23]. The survival rate of four mangrove species, namely, *A. marina*, *B. gymnorrhiza*, *C. tagal*, and *R. stylosa*, was higher at high intertidal elevation than at low intertidal elevation, irrespective of the light level, and the seedlings survived better in light gaps than under the canopy in the high intertidal position [18]. In the present study, *A. corniculatum*, *A. marina*, and *R. stylosa* were relatively more sensitive at low intertidal elevation, whereas *K. obovata* exhibited better performance at low intertidal elevation. *Rhizophora stylosa*, *B. gymnorrhiza*, and *K. obovata* survived better than the other two species during the first two months, which may be related to their bigger hypocotyls [24].

Bruguiera gymnorrhiza and *K. obovata* presented higher survival rate under low light irradiance condition than *A. corniculatum* in *S. apetala* plantations [25]. We also found that *B. gymnorrhiza* and *K. obovata* had higher survival rates than the other species under 90% canopy closure. Overall *B. gymnorrhiza* performed best in low intertidal position and under low light irradiance condition throughout the study.

4.2. Early Growth Response of Seedlings to Light Level

A 12-month study showed that *B. gymnorrhiza* was the most stable and exhibited an adaptive response to low light condition, followed by *K. obovata* and *A. corniculatum* in the understory of *S. apetala* plantations in China [25]. The height of *R. apiculata* and *Bruguiera cylindrica* (L.)Bl. in the gaps was more than 2 and 5 times higher than that in the canopy, respectively [26]. The seedlings of *B. gymnorrhiza* and *K. obovata* under the canopy had lower leaf number and stem basal diameter than those in the gaps [27,28]. Similarly, Chen et al. reported that the leaf number and stem basal diameter of *A. marina* were higher in the gaps than in the canopy, indicating that *A. marina* seedlings might be shade-intolerant [29]. The results of the present study conducted in *S. apetala* plantations grown at different light levels under field conditions confirm these previous findings.

It has been reported that the RGR of *R. apiculata* and *B. gymnorrhiza* decreased with decrease in irradiance from full sunlight to canopy shade environment [30]. In the present study, the RGR of *K. obovata*, *A. corniculatum*, and *A. marina* was significantly affected by the low light level regardless of the intertidal elevation, indicating light level is the main limiting factor affecting early biomass accumulation in seedlings.

4.3. Responses to Intertidal Elevation

High tidal inundations stimulated the early growth of seven mangrove species, especially the stem height [31]. It has been reported that the stem height of *Laguncularia racemosa* (L.) Gaertn. f. seedlings was considerably higher under tidal flooding than under no flooding condition [32]. Similarly, recent studies on growth and physiology have shown that *A. marina* seedlings are tolerant to low intertidal elevation, but not to canopy shade [29]. A growth trial with five native mangrove species also supported such a pattern. The leaf number of *K. obovata* [20] and *A. marina* [29] seedlings increased significantly with water level, which is consistent with the observations of the present study, mainly in *K. obovata* and *A. marina* seedlings. We also found the seedlings of *K. obovata* and *A. marina* at the low intertidal elevation improved their ability to capture light energy by increasing the stem height to adapt to flooding stimulation and increased leaf number to increase the ability to capture light energy.

In a present study, all species presented higher stem height at the low intertidal position, and the stem height growth exhibited no particular trend with waterlogging from seedlings to 300-day-old

plants. This is similar to the findings of Hovenden et al. [33], who reported that the stem height of *A. marina* did not change significantly with flooding after the seedlings were 12-month old.

The present study showed that the RGR of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* was significantly enhanced by high inundation elevation, especially at high light level, whereas *A. corniculatum* and *A. marina* showed better performance at low intertidal elevation under 30% and 60% canopy closure. In another study, the seedlings of *A. marina* presented higher RGR at lower intertidal elevation, and *B. gymnorrhiza* and *R. stylosa* seedlings showed negligible disparity between eight different tidal flat elevations [32]. A previous study in Hong Kong showed that *K. obovata* had stronger resilience to high intertidal elevation than *B. gymnorrhiza* [34].

4.4. Interactive Effects of Intertidal Elevation and Light Level

Grime reported that morphological plasticity of plants is closely related to the individual's ability to exploit habitats [35]. The relative growth of *R. stylosa*, *A. marina*, and *C. tagal* was higher at the high intertidal elevation than at the low intertidal elevation. Moreover, it was higher in gaps than in the canopy. The growth of *B. gymnorrhiza* was the highest under all conditions [18]. The specific leaf area of *B. gymnorrhiza* ($71.0 \pm 2.8 \text{ cm}^2 \text{ g}^{-1}$) were significantly different from that of *R. stylosa* ($45.4 \pm 1.0 \text{ cm}^2 \text{ g}^{-1}$) and *K. obovata* ($48.6 \pm 0.8 \text{ cm}^2 \text{ g}^{-1}$), which may be related to the fact that *B. gymnorrhiza* can tolerate shaded conditions better than the other species [36]. The results showed that the survival of all five species studied and the growth of three species (*A. corniculatum*, *A. marina*, and *R. stylosa*) were high under adverse conditions. Moreover, *B. gymnorrhiza* showed the best performance in the six interactive treatments.

4.5. Turning Monocultures to Mixed Forests

Species diversity and structural complexity are important factors that enhance both ecosystem productivity and stability [37]. A previous study showed successful recruitment of natural mangrove species into artificial mangrove monocultures in Kenya. Bosire et al. confirmed that mixed stands of plantations with natural mangrove species are achievable [38]. Furthermore, Ren et al. [14] reported that the native species *A. marina*, *A. corniculatum*, *K. obovata*, and *R. stylosa* can occupy the understory of 4 to 10-year old *S. apetala* plantations in Leizhou Peninsula of Southern China. These studies proved the possibility of establishing mixed forests using native species under introduced species. Our study results also demonstrated the adaptability of different mangrove species to intertidal elevation and light intensity. Light gaps in mangrove forests are often created by episodic events such as violent wind storms [39], lightning strikes [40], and single tree falls [41]. Two ways to achieve stable mixed forests are as follows: (1) planting propagules of *A. corniculatum*, *A. marina*, and *R. stylosa* two times at low intertidal position, and (2) choosing natural gaps or thinning the canopy of *S. apetala* plantations with tree pruners at high intertidal position.

5. Conclusions

The adaptability to light levels and intertidal elevations of five native mangrove species in China was explored in a 12-month field experiment. Although the seedlings of all five native species survived better at high intertidal elevation, the stem height of all species at low intertidal elevation was higher than that at high intertidal elevation, and it was the highest under 30% canopy closure. The RGR was the highest at low intertidal elevation, and it was promoted by high light level. The survival rate and growth rate of *B. gymnorrhiza* were the highest across intertidal elevations and light levels. *Bruguiera gymnorrhiza* was the best acclimated native species in *S. apetala* plantations in the study area. Simultaneously, periodical thinning of canopy artificially in the dense canopies of *S. apetala* plantations is an effective measure. In addition, increasing the planting density of seedlings would promote the establishment and growth of native species especially at low intertidal elevations.

Author Contributions: B.L. conceived the idea and Y.X. designed the experiment; Z.J., W.G., M.L. and Y.C. carried out field and laboratory analyses; Z.J. wrote the manuscript and Y.X. helped with the revision.

Acknowledgments: This work was supported by the National Natural Science Foundation of China (grant numbers 41676080, 41876094); the National Key Research and Development Program of China (2017YFC0506103). We are grateful to Shuping Ding for establishment of the experimental plots and for data collection in Qi’ao Island.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Luo, Z.; Sun, O.J.; Xu, H. A comparison of species composition and stand structure between planted and natural mangrove forests in Shenzhen Bay, South China. *J. Plant Ecol.* **2010**, *3*, 165–174. [[CrossRef](#)]
2. Satyanarayana, B.; Mohamad, K.A.; Idris, I.F.; Husain, M.-L.; Dahdouh-Guebas, F. Assessment of mangrove vegetation based on remote sensing and ground-truth measurements at Tumpat, Kelantan Delta, east coast of Peninsular Malaysia. *Int. J. Remote Sens.* **2011**, *32*, 1635–1650. [[CrossRef](#)]
3. Palacios, M.L.; Cantera, J.R. Mangrove timber use as an ecosystem service in the Colombian Pacific. *Hydrobiologia* **2017**, *803*, 345–358. [[CrossRef](#)]
4. Duke, N.C.; Meynecke, J.-O.; Dittmann, S.; Ellison, A.M.; Anger, K.; Berger, U.; Cannicci, S.; Diele, K.; Ewel, K.C.; Field, C.D.; et al. A world without mangroves? *Science* **2007**, *317*, 41–43. [[CrossRef](#)] [[PubMed](#)]
5. Rama Chandra Prasad, P.; Mamtha Lakshmi, P.; Rajan, K.S.; Bhole, V.; Dutt, C.B.S. Tsunami and tropical island ecosystems: A meta-analysis of studies in Andaman and Nicobar Islands. *Biodivers. Conserv.* **2012**, *21*, 309–322. [[CrossRef](#)]
6. Zan, Q.; Wang, B.; Wang, Y.; Li, M. Ecological assessment on the introduced *Sonneratia caseolaris* and *S. apetala* at the mangrove forest of Shenzhen Bay, China. *Acta Bot. Sin.* **2003**, *45*, 544–551.
7. Liao, B.; Guan, W.; Zhang, J.; Tang, G.; Lei, Z.; Yang, X. Studies on dynamic development of mangrove communities on Qi’ao Island, Zhuhai. *J. South China Agric. Univ.* **2008**, *29*, 59–64.
8. Li, M.; Liao, B. Introduction and ecological impact of *Sonneratia apetala*. *Prot. For. Sci. Technol.* **2008**, *3*, 100–102.
9. An, S.; Gu, B.; Zhou, C.; Wang, Z.; Deng, Z.; Zhi, Y.; Li, H.; Chen, L.; Yu, D.; Liu, Y. *Spartina* invasion in China: Implications for invasive species management and future research. *Weed Res.* **2007**, *47*, 183–191. [[CrossRef](#)]
10. Chen, H.; Liao, B.; Liu, B.; Peng, C.; Zhang, Y.; Guan, W.; Zhu, Q.; Yang, G. Eradicating invasive *Spartina alterniflora* with alien *Sonneratia apetala* and its implications for invasion controls. *Ecol. Eng.* **2014**, *73*, 367–372. [[CrossRef](#)]
11. Zhou, T.; Liu, S.; Feng, Z.; Liu, G.; Gan, Q.; Peng, S. Use of exotic plants to control *Spartina alterniflora* invasion and promote mangrove restoration. *Sci. Rep.* **2015**, *5*, 1–13. [[CrossRef](#)] [[PubMed](#)]
12. Ren, H.; Lu, H.; Shen, W.; Huang, C.; Guo, Q.; Li, Z.; Jian, S. *Sonneratia apetala* Buch.Ham in the mangrove ecosystems of China: An invasive species or restoration species? *Ecol. Eng.* **2009**, *35*, 1243–1248. [[CrossRef](#)]
13. Peng, Y.; Zhou, Y.; Chen, G. The restoration of mangrove wetland: A review. *Acta Ecol. Sin.* **2008**, *28*, 786–797.
14. Ren, H.; Jian, S.; Lu, H.; Zhang, Q.; Shen, W.; Han, W.; Yin, Z.; Guo, Q. Restoration of mangrove plantations and colonisation by native species in Leizhou bay, South China. *Ecol. Res.* **2008**, *23*, 401–407. [[CrossRef](#)]
15. Chen, Y.; Liao, B.; Zheng, S.; Li, M.; Song, X. Dynamics and species-diversities of artificial *Sonneratia apetala*, *Sonneratia caseolaris* and *Kandelia candel* communities. *Chin. J. Appl. Ecol.* **2004**, *15*, 924–928.
16. Allen, J.A.; Krauss, K.W.; Hauff, R.D. Factors limiting the intertidal distribution of the mangrove species *Xylocarpus granatum*. *Community Ecol.* **2003**, *135*, 110–121. [[CrossRef](#)]
17. Imai, N.; Takyu, M.; Nakamura, Y.; Nakamura, T. Gap formation and regeneration of tropical mangrove forests in Ranong, Thailand. *Plant Ecol.* **2006**, *186*, 37–46. [[CrossRef](#)]
18. Smith, T.J., III. Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. *J. Exp. Mar. Biol. Ecol.* **1987**, *2*, 133–146. [[CrossRef](#)]
19. Chen, Y.; Chen, W.; Zheng, S.; Zheng, D.; Liao, B.; Song, X. Researches on the mangrove plantation in Panyu, Guangdong. *Ecol. Sci.* **2001**, *20*, 25–31.
20. Ye, Y.; Tam, N.F.Y.; Wong, Y.S.; Lu, C.Y. Does sea level rise influence propagule establishment, early growth and physiology of *Kandelia candel* and *Bruguiera gymnorrhiza*? *J. Exp. Mar. Biol. Ecol.* **2004**, *306*, 197–215. [[CrossRef](#)]

21. Clarke, P.J. Effects of experimental canopy gaps on mangrove recruitment: Lack of habitat partitioning may explain stand dominance. *J. Ecol.* **2004**, *92*, 203–213. [\[CrossRef\]](#)
22. Minchinton, T.E. Canopy and substratum heterogeneity influence recruitment of the mangrove *Avicennia marina*. *J. Ecol.* **2001**, *89*, 888–902. [\[CrossRef\]](#)
23. Berger, U.; Adams, M.; Grimm, V.; Hildenbrandt, H. Modelling secondary succession of neotropical mangroves: Causes and consequences of growth reduction in pioneer species. *Perspect. Plant Ecol.* **2006**, *7*, 243–252. [\[CrossRef\]](#)
24. Kamruzzaman, M.; Osawa, A.; Mouctar, K.; Sharma, S. Comparative reproductive phenology of subtropical mangrove communities at Manko Wetland, Okinawa Island, Japan. *J. For. Res.* **2017**, *22*, 118–125. [\[CrossRef\]](#)
25. Peng, Y.; Diao, J.; Zheng, M.; Guan, D.; Zhang, R.; Chen, G.; Lee, S.Y. Early growth adaptability of four mangrove species under the canopy of an introduced mangrove plantation: Implications for restoration. *For. Ecol. Manag.* **2016**, *373*, 179–188. [\[CrossRef\]](#)
26. Tamai, S.; Iampa, P. Establishment and growth of mangrove seedling in mangrove forests of southern Thailand. *Ecol. Res.* **1988**, *3*, 227–238. [\[CrossRef\]](#)
27. Ye, Y.; Wong, Y.S.; Tam, N.F.Y. Acclimation of a dominant mangrove plant (*Kandelia candel*) to soil texture and its response to canopy shade. *Hydrobiologia* **2005**, *539*, 109–119. [\[CrossRef\]](#)
28. Krauss, K.W.; Allen, J.A. Factors influencing the regeneration of the mangrove *Bruguiera gymnorrhiza* (L.) Lamk. on a tropical Pacific Island. *For. Ecol. Manag.* **2003**, *176*, 49–60. [\[CrossRef\]](#)
29. Chen, Y.; Ye, Y. Early responses of *Avicennia marina* (Forsk.) Vierh. to intertidal elevation and light level. *Aquat. Bot.* **2014**, *112*, 33–40. [\[CrossRef\]](#)
30. Ball, M.C. Interactive effects of salinity and irradiance on growth: Implications for mangrove forest structure along salinity gradients. *Trees* **2002**, *16*, 126–139. [\[CrossRef\]](#)
31. Delgado, P.; Hensel, P.F.; Jiménez, J.A.; Day, J.W. The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary. *Aquat. Bot.* **2001**, *71*, 157–178. [\[CrossRef\]](#)
32. He, B.; Lai, T.; Fan, H.; Wang, W.; Zheng, H. Comparison of flooding-tolerance in four mangrove species in a diurnal tidal zone in the Beibu Gulf. *Estuar. Coast. Shelf Sci.* **2007**, *74*, 254–262. [\[CrossRef\]](#)
33. Hovenden, M.J.; Curran, M.; Cole, M.A.; Goulter, P.F.E.; Skelton, N.J.; Allaway, W.G. Ventilation and respiration in roots of one-year-old seedlings of grey mangrove *Avicennia marina* (Forsk.) Vierh. *Hydrobiologia* **1995**, *295*, 23–29. [\[CrossRef\]](#)
34. Ye, Y.; Tam, N.F.Y.; Wong, Y.S.; Lu, C.Y. Growth and physiological responses of two mangrove species (*Bruguiera gymnorrhiza* and *Kandelia candel*) to waterlogging. *Environ. Exp. Bot.* **2003**, *49*, 209–221. [\[CrossRef\]](#)
35. Grime, J.P. Plant strategies and vegetation processes. *J. Ecol.* **1980**, *68*, 704–706.
36. Sharma, S.; Kamruzzaman, M.; Rafiqul Hoque, A.T.M.; Hagihara, A. Leaf phenological traits and leaf longevity of three mangrove species (Rhizophoraceae) on Okinawa Island, Japan. *J. Oceanogr.* **2012**, *68*, 831–840. [\[CrossRef\]](#)
37. Wardle, D.A.; Zackrisson, O. Effects of species and functional group loss on island ecosystem properties. *Nature* **2005**, *435*, 806–810. [\[CrossRef\]](#)
38. Bosire, J.O.; Dahdouh-Guebas, F.; Kairo, J.G.; Wartel, S.; Kazungu, J.; Koedam, N. Success rates of recruited tree species and their contribution to the structural development of reforested mangrove stands. *Mar. Ecol. Prog. Ser.* **2006**, *325*, 85–91. [\[CrossRef\]](#)
39. SmithIm, T.J.; Robblee, M.B.; Wanless, H.R.; Doyle, T.W. Mangroves, hurricanes, and lightning strikes. *BioScience* **1994**, *44*, 256–262. [\[CrossRef\]](#)
40. Pajmans, K.; Rollet, B. The mangroves of galley reach, Papua New Guinea. *For. Ecol. Manag.* **1977**, *1*, 119–140. [\[CrossRef\]](#)
41. Ewel, K.C.; Zheng, S.; Pinzon, Z.S.; Bourgeois, J.A. Environmental effects of canopy gap formation in high-rainfall mangrove forests. *Biotropica* **1998**, *30*, 510–518. [\[CrossRef\]](#)

