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RESEARCH ARTICLE

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Critical tidal level for forestation with hypocotyl of *Rhizophora stylosa* Griff along the Guangxi coast of China

Abstract From August 2004 to August 2005, three replicate experimental platforms were constructed in a section of the tidal flats in Yingluo Bay, Guangxi Province to study the growth and physiological responses of *Rhizophora stylosa* Griff seedlings to tidal waterlogging stress in a diurnal tidal zone. A total of eight tidal flat elevation (TFE) treatments, i.e., 320, 330, 340, 350, 360, 370, 380 and 390 cm above Yellow Sea Datum (YSD), were created on each platform. The results showed that lower TFEs (320–330 cm YSD) slightly increased the seedling stem height of 1-year old seedlings, while higher TFEs (> 340 cm YSD) increased the seedling growth significantly. Moderate TFEs (350–370 cm YSD) favored the development of knots. Number of leaves, leaf conservation rate and leaf area per seedling all decreased dramatically with decreasing TFE. Lower TFEs caused large damage to Chl a, but Chl b was less affected. The Chl a/b ratio decreased with decreasing TFE. Prolonged waterlogging induced higher SOD activity in roots, while moderate TFE inhibited the SOD activity in leaves. The POD activity in roots and leaves increased with decreasing TFE. Waterlogging stress decreased the biomass of individual organs and entire seedlings. With increasing waterlogging, the biomass partitioning in 1-year old seedlings increased from leaf to stem. The survival rate decreased sharply from 88.9% to 40.0% as TFE decreased, while more than 80% of the seedlings were able to survive at the TFE level of 370 cm YSD and above. We propose that the local mean sea level should be adopted as the critical tidal level for forestation with hypocotyls of *R. stylosa* along the Guangxi coast.

Keywords *Rhizophora stylosa* Griff, diurnal tidal zone, tidal flat elevation, waterlogging stress, physiological response, critical tidal level for forestation

1 Introduction

Thriving on tropical and subtropical intertidal flats, mangrove trees have developed a series of particularly adaptive morphological, physiological and ecological mechanisms (Lin, 1999). Studies have revealed that mangrove trees express gradients of eco-physiological responses in organ construction, metabolism, biomass partition, related enzyme activities and hormone levels due to waterlogging stress (Naidoo, 1985; Skelton and Allaway, 1996; Chen et al., 2005). Owing to the expansion of cities and marine culture along coastal regions, China's mangrove forests quickly shrank from 659 to 237 km^2 in the period from 1980 and 2000, as a result of which the ecological value of mangrove wetlands decreased dramatically (Lan and Chen, 2006). It has therefore become an urgent issue to accelerate mangrove reforestation and restore the ecological functions of coastal wetlands in southeastern China. Adaptability studies in structure and physiology of mangrove plants in response to waterlogging stress would provide helpful information for the suitable selection of plantable flats and promote the level of mangrove afforestation in China.

The coastal zone along the Beibu Gulf supports the largest area of mangrove forests in China and has extensive areas of plantable flats. The tidal regime in the Beibu Gulf is diurnal, which is rarely found in other regions of the world. Diurnal and semi-diurnal tidal zones differ in hydrological, climatic and edaphic properties, and mangrove reforestation guidelines and techniques also differ between these zones. Research on the waterlogging-tolerance of mangrove plants in diurnal tidal habitats is, however, lacking in China.

Rhizophora stylosa Griff forests have a strong wind- and wave-reducing capacity owing to their dense tree crowns, high trunks and complicated propping roots; this species is therefore regarded as a perfect selection for mangrove reforestation and has been transplanted widely in China. We constructed three experimental platforms and created eight tidal flat elevation (TFE) treatments on each platform

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in Yingluo Bay in Guangxi Province, China and tested the waterlogging-tolerance of *R. stylosa* seedlings, focusing on their different responses in morphological construction, biomass partition and anti-active-oxygen enzymes to gradients of waterlogging stress. Our research is aimed at providing useful information for regional criteria on mangrove plantable flats in the Beibu Gulf.

2 Materials and methods

2.1 Descriptions of the research area

Our experiments were conducted in Yingluo Bay (21°28′N, 109°43′E), a core zone within the National Shankou Mangrove Reserve in Guangxi Province. Located in a subtropical monsoon region, Yingluo Bay has an average annual air temperature of 23.4°C. Average temperature in the coldest month, January, ranges between 14.2 and 14.5°C, with a minimum record of 2°C. Annual rainfall ranges between 1500 and 1700 mm and annual evaporation between 1000 and 1400 mm. The annual relative humidity reaches 80%. The tidal regime in Yingluo Bay is incomplete diurnal, and the diurnal tide appears in about 220 d of the year. The average tidal amplitude is 2.52 m, with the maximum recorded at 6.25 m. The local mean sea level (MSL) elevation is 359 cm Yellow Sea Datum (YSD). The average salinity of the seawater is 28.9 (Fan et al., 2005). Mangrove forests cover 80 hm^2 of Yingluo Bay. Among the nine true mangrove species recorded here, *R. stylosa* dominates most areas of the mangrove forests, with a height of 5 to 6 m and 90% coverage. Other familiar mangrove species include *Avicennia marina, Aegiceras corniculatum, Kandelia candel* and *Bruguiera gymnorrhiza* (Wen et al., 2002).

2.2 Methods

2.2.1 Treatment of tested seedlings

R. stylosa is a representative species at the intermediate-to-late succession stage in the Guangxi mangrove forests, and has developed a capacity for salt rejection and a viviparous reproduction strategy.

Three experimental platforms were established on the bare tidal flat, almost adjacent to the seaward mangrove forests of Yingluo Bay, with a distance of 1 m between neighboring platforms. Eight tidal flat elevation treatments were created on each platform in the form of eight steps. The construction of the platforms and steps were aimed at manipulating the tidal elevation and waterlogging stress; seedlings were exposed to similar environmental conditions of light, salinity, substrate properties and nutrient supply.

Mature hypocotyls of similar size were collected from *R. stylosa* parent trees in August 2004. The lengths of selected hypocotyls ranged between 29 and 31 cm, with fresh weights between 26 and 29 g. Plastic nursery bags, 15 cm in diameter and 20 cm high were packed with soil from the local intertidal flat and attached to the platforms before cultivation, making the upper planes of the substrate equal to the designated TFEs. One hypocotyl was planted in each nursery bag and fifty were allocated to one treatment on each platform. The eight treatments, i.e., elevations, were 320, 330, 340, 350, 360, 370, 380 and 390 cm YSD. These elevations were attained as follows: first, one section of the tidal flat at an elevation of about 300 cm YSD was proposed, based on forecasts from tidal tables issued by the State Oceanic Administration of China; next, the precise elevation of the flat was measured (mean error within ± 5 cm) by using a Total Station instrument (Topcon GTS721, Japan); then three experimental platforms were constructed on this flat and the eight steps at designed elevations on each platform were created using timbers, boards and bricks.

During our experiment, the seedlings were sprayed every 3 d with a 1/200 seawater solution of an original Malathion concentration (45%) in April, October and November.

2.2.2 Measurement of growth and physiological indices

In August 2005, the seedling survival rate in each treatment was established in situ. Twenty seedlings in each treatment were randomly harvested and the growth parameters, including stem height, number of knots, leaf scars, number of leaves and leaf area per seedling were measured. After that, the seedlings were separated into leaves, stems, roots, and the remaining hypocotyls and were oven-dried to constant weight at 80°C and then weighed.

The physiological indices included chlorophyll contents in leaf and anti-active-oxygen enzymes activities in leaves and roots. For measurement, the leaves were randomly selected from the second pair of mature leaves. Small circinal chips (0.5 cm in diameter) from the central area of leaves were sampled with a stiletto and twenty chips were assigned to the measurement of chlorophyll content. Fresh leaves, weighing 0.5 g, were assigned to enzyme activity measurements for leaves, and 1 g of fresh root radicles to enzyme activity in roots. Samples from every treatment in the same platform consisted of three replicates.

The method of extraction and measurement of chlorophyll content was developed by He et al. (1993). According to Zhao et al. (2002), superoxide dismutase (SOD) activity was measured as the amount of inhibition of photo-reduction of nitroblue tetrazolium (NBT). The peroxidase (POD) activity was measured by using a colorimetric method (Zhang et al., 2004).

2.3 Data analysis

Tests of significance of difference and correlation analysis were conducted using SPSS software.

3 Results

3.1 Growth of *R. stylosa* seedlings under gradients of waterlogging stress

3.1.1 Response of stems and knots to waterlogging stress

As can be seen in Fig. 1, at elevations below 340 cm YSD, the heavy waterlogging stress weakly promoted stem elongation of *R. stylosa* seedlings: heights of seedlings in the 320 and 330 cm YSD treatments were only 6.3% ($0.01 < p < 0.05$) and 2.3% ($p > 0.09$) greater than those of the 340 cm YSD treatment, respectively. Significantly stronger promotion was, however, found at the higher habitats ($>$ 340 cm YSD); differences in height between 390 and 340 cm YSD treatments reached 14.7 cm and the ratio of maximum to minimum height was 1.36.

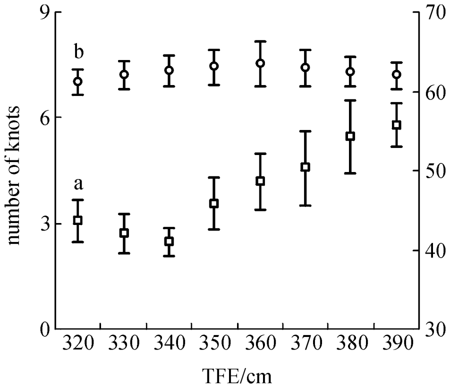

Fig. 1 Heights (a) and number of knots (b) of 1-year old *R. stylosa* seedlings with gradients of tidal flat elevations (TFE)

Moderate TFEs (350–370 cm YSD) favored the development of knots (Fig. 1), while fewer knots were counted in lower and higher treatments. However, the effect of waterlogging on knots was statistically not significant ($p > 0.05$), indicating that variation in height among the treatments was mainly induced by different growing speeds of intercalary sections.

3.1.2 Foliar development under gradients of TFE treatments

Foliar development of *R. stylosa* seedlings reacted dramatically to the gradient of waterlogging stress (Fig. 2). Ratios of maximum (390 cm YSD treatment) to minimum (320 cm YSD treatment) were 2.82 times in the number of leaves, 1.86 times in leaf area, and 2.74 times in the rate of leaf conservation. Intensive correlations prevailed among these three indices ($p < 0.001$). A low rate of leaf conservation, i.e., early defoliation, led to a reduction in the number of leaves which, in turn, brought about a more narrow leaf area, reducing the period of growth.

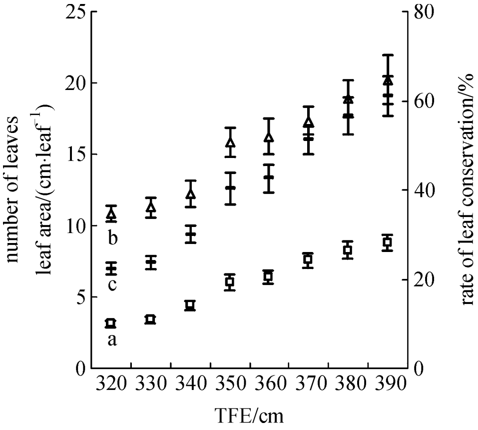

Fig. 2 Number of leaves (a), leaf areas (b) and rate of leaf conservation (c) of 1-year old *R. stylosa* seedlings with gradients of TFE

3.2 Changes of chlorophyll content and ratio of Chl a/b with gradients of waterlogging stress

The changing trend of Chl a content under gradients of waterlogging stress coincided with that of total chlorophyll content and the ratio of Chl a/b, which represents significant inhibition at the lower TFE habitats (Fig. 3). Chl b was, however, less affected and usually there were no significant differences between neighboring treatments. The maximum Chl b content, at 390 cm YSD, was only 12.5% higher than the minimum at 320 cm YSD, while the maximum Chl a, at 390 cm YSD, was 42.7% higher than the minimum at 320 cm YSD, indicating that Chl a was more damaged than Chl b.

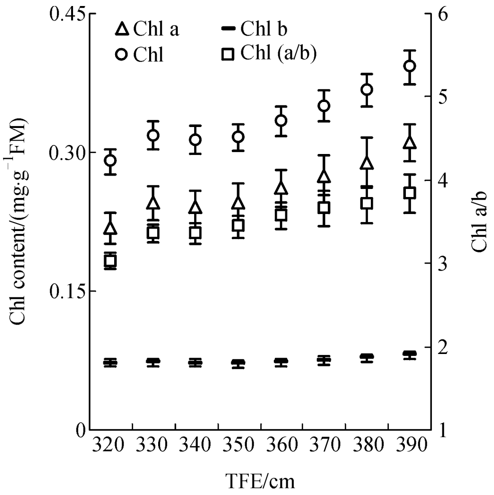

Fig. 3 Chlorophyll content and Chl (a/b) ratios in mature leaves of 1-year old *R. stylosa* seedlings with gradients of TFE

3.3 Anti-active-oxygen enzymes response to gradients of waterlogging stress

As indicated in Fig. 4, SOD activities in roots of *R. stylosa* seedlings in the 350 cm and lower YSD treatments were significantly ($p < 0.05$) higher than those in the 360 cm and above YSD treatments; the maximum was 19.5% higher than the minimum, showing a certain degree of promotion at lower TFE habitats.

The response of SOD in leaves differed with that in roots to waterlogging stress. At the TFE lower than 340 cm YSD, longer waterlogging promoted SOD activity significantly ($p < 0.01$); however, at TFE levels higher than 340 cm YSD, the trend was reversed ($p < 0.01$).

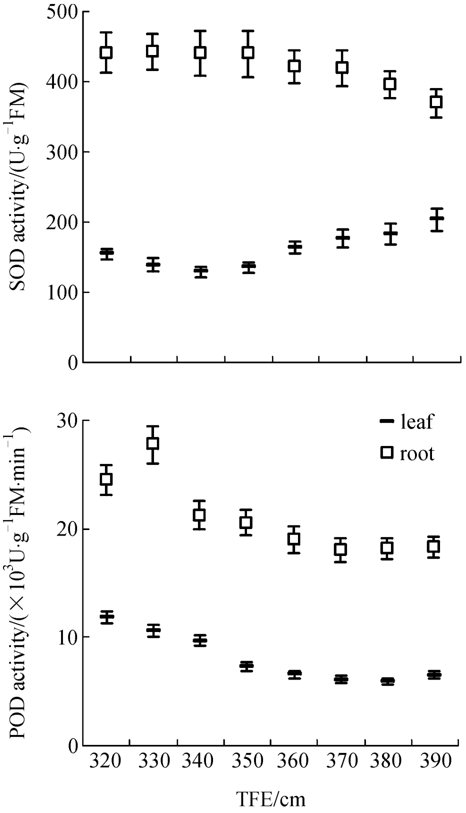

Fig. 4 SOD and POD activities in mature leaves and roots of 1-year old *R. stylosa* seedlings with gradients of TFE

The waterlogging response of POD in leaves agreed with that in roots, where the lower TFE habitats promoted POD activity significantly ($p < 0.01$).

In the same TFE treatment, SOD and POD activities in roots were significantly higher than those in leaves, at 0.82–2.39 and 1.06–2.08 times, respectively.

3.4 Biomass partition among sections in gradients of TFE habitats

Lower TFE habitats clearly inhibited biomass accumulation of *R. stylosa* seedlings (Table 1). Generally, the biomass of seedlings at the upper layers were significantly higher than those of the under layers ($p < 0.01$). Among the three neonatal sections, the most violent response to gradients of waterlogging stress occurred in leaves, less so in roots and the least in stems. Ratios of maximum to minimum biomass were 8.58 in leaves, 2.73 in roots and 1.32 in stems. Correlation coefficients were 0.996 between total and leaf biomass, 0.993 between total and root biomass and 0.985 between total and stem biomass, indicating high correlation in waterlogging response among the neonatal sections of *R. stylosa* seedlings.

The remaining hypocotyl biomass ranged from 9.22 to 12.18 g, while the average biomass of the original hypocotyls was 15.01 g. A transfer of nutrient material from hypocotyls to neonatal sections occurred in all treatments; more was transferred at the lower TFE levels and less at higher levels; longer waterlogging led to more loss in hypocotyl biomass.

All absolute values of sectional biomass increased with increasing TFE habitats; however, the partition ratios among sections changed greatly (see Table 1). Root partition ratios showed little response and only fluctuated between 20.9% and 25.4% and little or no significant differences occurred between most pairs of neighboring treatments. Stem partition ratios decreased significantly from 69.6% to 39.8% with an increase in TFE, while at the same time, the leaf partition ratios increased rapidly from 9.5% to 35.4%. Higher TFE habitats favored leaf growth more than stem growth; in other words, the effect of

Table 1 Biomass partition in 1-year old *R. stylosa* seedlings with gradients of TFE (mean ± *SE*)

treatment/ cm YSD	biomass/g					proportion in neonatal biomass/%		
	stem	leaf	root	remaining hypocotyl	total	stem	leaf	root
320	2.92 ± 0.19	0.40 ± 0.03	0.88 ± 0.04	9.22 ± 0.53	13.43 ± 0.85	69.6 ± 4.5	9.5 ± 0.6	20.9 ± 1.0
330	3.06 ± 0.19	0.45 ± 0.03	1.01 ± 0.06	9.41 ± 0.56	13.92 ± 0.92	67.8 ± 4.3	10.0 ± 0.7	22.2 ± 1.3
340	3.21 ± 0.19	0.59 ± 0.04	1.29 ± 0.07	9.92 ± 0.62	15.00 ± 1.20	63.1 ± 3.8	11.5 ± 0.8	25.4 ± 1.4
350	3.42 ± 0.21	1.30 ± 0.07	1.49 ± 0.08	10.45 ± 0.73	16.66 ± 0.97	55.1 ± 3.4	20.9 ± 1.1	24.0 ± 1.3
360	3.55 ± 0.18	1.77 ± 0.09	1.63 ± 0.12	11.06 ± 0.66	18.01 ± 1.33	51.1 ± 2.6	25.5 ± 1.3	23.5 ± 1.7
370	3.64 ± 0.32	2.33 ± 0.16	1.85 ± 0.13	11.56 ± 0.82	19.38 ± 1.74	46.5 ± 4.1	29.8 ± 2.1	23.7 ± 1.6
380	3.71 ± 0.22	2.85 ± 0.17	2.14 ± 0.13	12.02 ± 0.93	20.72 ± 1.97	42.6 ± 2.5	32.8 ± 1.9	24.6 ± 1.5
390	3.85 ± 0.22	3.42 ± 0.18	2.40 ± 0.13	12.18 ± 0.98	21.85 ± 1.82	39.8 ± 2.3	35.4 ± 1.8	24.8 ± 1.4

waterlogging stress on *R. stylosa* seedlings is largely concentrated on the leaves. Lower TFE habitats, i.e., longer waterlogging stress, led to early defoliation, smaller number of leaves and narrower leaf areas, which reduced the photosynthetic output, and brought about a reduction of material transportation to stem and root and less accumulation of biomass.

3.5 Survival status of 1-year old *R. stylosa* seedlings under gradients of waterlogging stress

As the TFE decreased, the survival rate of *R. stylosa* seedlings declined from 88.9% to 40.0% (Fig. 5). A rapid change of seedling mortality occurred between the 350 and 330 cm YSD levels; however, the survival rate changed evenly in the 350 cm and above YSD treatments; it was higher than 80% in the 370, 380 and 390 cm YSD treatments.

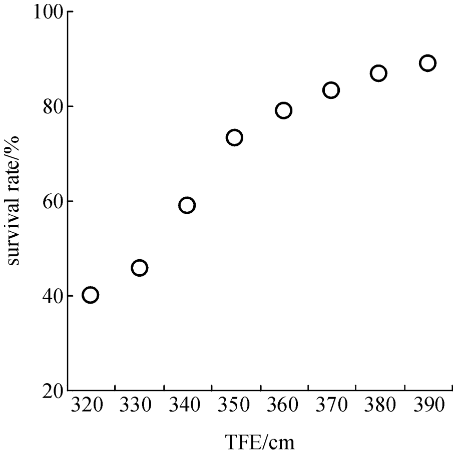

Fig. 5 Survival rate (%) of 1-year old *R. stylosa* seedlings with gradients of TFE

4 Discussion

4.1 Growth and physiological response of mangrove seedlings to waterlogging stress

Given the circumstance of periodic tidal inundation, rapid stem elongation of mangrove trees led to a reduction of the time when the trees were waterlogged; a greater oxygen transfer through the above-water stem and leaves was helpful in lessening anoxia damage in roots; meanwhile, once the stems grew more quickly, leaves would be exposed for longer periods of sunlight for photosynthesis to occur (Ye et al., 2004). However, the response of different mangrove species may vary with the waterlogging habitat. Ellison and Farnsworth (1997) treated *R. mangle* seedlings with different water levels in simulated tanks and found that longer waterlogging promoted stem elongation. Transplanted in the field, *R. mangle* seedlings at the lowest tidal flat attained the largest stem elongation (Farnsworth and Ellison, 1996). Ye et al. (2004) planted *K. candel* seedlings on two intertidal flats with different waterlogging levels and found higher stem increments during the first four months in the lower intertidal zone compared to those in the upper zone. In contrast, Kitaya et al. (2002) found that stem growth of *R. apiculata* seedlings decreased with increasing elevation. According to our experiment, lower TFEs with prolonged waterlogging had limited effect on the promotion of stem growth of *R. stylosa* seedlings. In general, higher TFEs favored stem elongation of *R. stylosa* seedlings.

Leaves play a vital role in producing organic material to maintain survival and growth. Their performance under waterlogging stress effectively seals the fate of the seedlings. Pezeshki et al. (1989) recorded that leaf growth of *A. germinans*, *Laguncularia racemosa* and *R. mangle* seedlings was significantly inhibited under waterlogging stress and total leaf areas decreased. In a green house experiment simulating semidiurnal tides in Xiamen, China, (Chen et al. 2005a), *K. candel* seedlings grown under a treatment of 2 h submergence per tidal cycle (a short period of waterlogging in their experiment) attained the largest mature leaf area and biomass. Field results from intertidal flats of Xiamen, China (Chen et al., 2006) showed that at 162 cm YSD (moderate waterlogging habitat), *K. candel* seedlings had the largest leaf area per seeding and leaf biomass. However, *B. gymnorrhiza* may be an exception. Misra et al. (1984) reported that the greater area and thickness of full-grown leaves of *B. gymnorrhiza* seedlings, responding to longer submergence, may help in overcoming the limitations imposed on photosynthesis. In our experiment, three foliar indices reacted dramatically to gradients of waterlogging stress, i.e., the number of leaves declined, with narrower leaf areas and a smaller rate of leaf conservation occurring at lower TFE habitats.

Photosynthetic rates and Chl a/b ratios in leaves of some mangrove species and associated species were found to be correlated (Das et al., 2002). In our experiment, longer waterlogging mainly injured Chl a, leading to a decrease in the Chl a/b ratio as the TFE declined. It is reasonable to deduce that the photosynthetic rate of *R. stylosa* seedlings in our experiment decreased as the TFE declined, consistent with biomass accumulation. As waterlogging stress increased, damage and loss of photosynthetic tissues increased; a shortage of organic material supply would inevitably lead to slower growth and even to death. Simulating semidiurnal tides in a green house, Hovenden et al. (1995) found that *A. marina* seedlings in the longest inundation treatment (8.5 h per tide) had the lowest root and total biomass.

Anti-active-oxygen enzymes play effective roles in lessening the injury from active oxygen accumulation under waterlogging stress (Monk et al., 1987). Ye et al. (2001, 2003) reported that SOD and POD activities in leaves of *K. candel* seedlings increased dramatically with prolonged waterlogging. Chen et al. (2005a) found that SOD and POD activities increased in order to resist further injury when the submergence time was more than 8 h per tidal cycle. Our research revealed that SOD activity in roots and POD activity in roots and leaves were promoted by lower TFEs; at the same level, the SOD and POD activities in roots were significantly higher than those in leaves, indicating that waterlogging stressed roots more than leaves. Although anti-active-oxygen enzymes were capable of lessening the injury from active oxygen accumulation, additional material and energy were used, occupying the energy that was supposed to partition for growth. As the TFE declined, fewer organic products were available, while more material and energy were used elsewhere; thus, biomass accumulation would certainly decrease and the original balanced growth disturbed.

4.2 Critical tidal level for *R. stylosa* reforestation on the Guangxi coast

A critical tidal level (CTL) for reforestation was regarded as one of the most important indices in the guideline for selecting plantable intertidal flats. Zhang et al. (2001) maintained that the local MSL determines the lowest elevation of the natural distribution of mangrove forests and therefore it could be regarded as the critical tidal level for mangrove reforestation. In contrast, Mo (2002) reported that the seaward fringe of mangrove forests overlapped approximately with the local MSL, but it could be higher or lower in particular areas. Fan (2000) found that mangrove forests developed into big forest patches even when it occupied flats below the local MSLs along some well-shaded coasts of bays and lagoons. Wen et al. (2002) concluded that the *R. stylosa* population not only dominates the high tidal flats with higher nutrition and high salinity, but also adapts well to low flats with low nutrition and low salinity. According to our surveys, about 50% of the mangrove forests in Yingluo Bay are located below the local MSL, most of which are *R. stylosa* forests. In our waterlogging experiment, the seedling survival rate at 350 cm YSD treatment (elevation below the local MSL) was 73.3%, which partially explains our observations that mangrove forests can be located below the local MSL.

The critical tidal level for reforestation of a species may differ between localities. For *K. candel*, Liao et al. (1996) suggested that the CTL should not be more than 22 cm lower than the local MSL in Shenzhen (22°32′N, 114°03′E) and not more than 30 cm lower in Dongzhaigang (19°56′N, 110°34′E). Chen et al. (2006) proposed that the CTL for *K. candel* should be higher than 455 cm YSD (127 cm above the local MSL) in Xiamen (19°56′N, 110°34′E). The wide variation in these proposed CTLs for *K. candel* reminds us of the necessity to conduct more studies on waterlogging physiology to form regional criteria on plantable flats for mangrove plants.

The treatments in our experiment leaned to the middle and lower TFEs, since it aimed at determining the lowest limit of the CTL. Chen et al. (2006) suggested that the definition of the CTL for *K. candel* in Xiamen should be where the seedlings attain a survival rate of above 65% and heights of above 35 cm within 6 to 12 months from colonization. We believe that the defined duration of 6 to 12 months is not long enough to assess the real effect of waterlogging stress, and 24 months may be more practical. We suppose furthermore, that the survival of two-year old seedlings might be 60%. Provided the survival rate in the second year is the same as that in the first year, the survival rate in the first year should be 78% or higher. Based on our experimental results, *R. stylosa* seedlings at the 360 cm YSD treatment attained a survival rate of 78.9% and ratios of height, number of leaves, leaf area and seedling biomass to their maxima in the eight treatments were 87.2%, 72.7%, 80.3% and 82.4%, respectively. In this case, we propose that the local MSL should be adopted as the CTL for reforestation with *R. stylosa* hypocotyls along the Guangxi coast.

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