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Does energetic cost for leaf construction in *Sonneratia* change after introduce to another mangrove wetland and differ from native mangrove plants in South China?

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ABSTRACT

Exotic species invasions are serious ecological problems. Leaf construction cost (CC) and growth traits of two *Sonneratia* (*Sonneratia caseolaris* and *S. apetala*) and four native species (*Bruguiera gymnorrhiza*, *Kandelia obovata*, *Aegiceras corniculatum* and *Avicennia marina*) in Hainan and Shenzhen mangrove wetlands were compared to evaluate invasive potentials of *Sonneratia* after introduced to Shenzhen, their new habitat. There were no significant differences in CC and growth traits between two wetlands, suggesting *Sonneratia* did not lose any advantage in the new habitat and were competitive in both wetlands. CC per unit mass (CCM), CC per unit area (CCA) and caloric values of *Sonneratia* were significantly lower than those of native mangrove species while specific leaf area (SLA) was just the opposite. CCM of *S. caseolaris* and *S. apetala* were 6.1% and 11.9% lower than those of natives, respectively. These findings indicated the invasive potential of *Sonneratia* in Shenzhen after their introduction.

1. Introduction

Biotic invaders, brought about largely through human activities, are species that establish a new range in which they proliferate, spread, persist and damage natural environment (Mack et al., 2000). These invaders alter fundamental ecological properties and physical features of an ecosystem, leading to significant global economic losses (Barney et al., 2013; Simberloff et al., 2013; Marbuah et al., 2014; Doherty et al., 2015). Because of the damages caused by biotic invaders, many attempts have been made to construct lists of common traits shared by successful invaders (Parker et al., 2013; Simberloff et al., 2013). The exotic species having ruderal, early-successional life-history characteristics, such as high photosynthetic efficiency, rapid growth, early and high reproduction, short life spans and resistance to herbivore attack, are generally considered to have invasive potentials (Reichard and Hamilton, 1997). In the past two decades, some researchers showed that biological invasion was related to the unique energy-use strategies, especially the leaf construction cost (CC) of an invader (Nagel and Griffin, 2001; Martínez-Garza et al., 2013; Zhu et al., 2015). Construction cost, defined as a measure of the amount of glucose required to produce a unit leaf mass or leaf area (i.e. a glucose equivalent), is a quantitative measurement of the energy invested by a plant to construct a leaf (Williams et al., 1987). In general, low CC is associated with high relative growth rates (Poorter and Villar, 1997; Martínez-Garza et al., 2013; Zhu et al., 2015). However, most of the previous researches on CC focused on terrestrial ecosystems, especially among herbs (Feng et al., 2011; Tu et al., 2013; Wang et al., 2013; Zhu et al., 2015). Little is known about CC in coastal wetland plants. To our knowledge, only two research groups have investigated CC of mangrove species. Suárez (2003, 2005) reported the salinity effect on CC of three mangrove species, *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*, but not the importance of CC to invasive potentials. Our group compared the photosynthetic characteristics and CC of two *Sonneratia* species and their adaptation in Shenzhen Futian wetland (Li et al., 2011, 2016) but not the differences in CC of the same species in mangrove wetlands at different geographical locations.

Mangrove ecosystem, a unique intertidal wetland along tropical and subtropical coastlines, has high ecological values, particularly the ecosystem services it provides and the goods that can be extracted from the forest (Duke et al., 2007). However, mangrove forests have been rapidly disappeared in some regions, especially Asia and the Pacific region, where 70% of their original mangrove habitats have been lost

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(Polidoro et al. 2010). To mitigate the habitat loss, mangrove reforestation were initiated in many countries over the past few decades, and alien mangrove plants especially the fast-growing species were introduced to their new habitat (Ellison, 2000). As a consequence, these alien species not only create the risk of replacing the native mangrove species, they may also be invasive. It is important to know the risk of the alien species to local ones, and how the leaf CC affects their invasiveness.

Sonneratia mangrove species, including *Sonneratia caseolaris* (L.) Engl. (Sc) and *S. apetala* Buch.-Ham. (Sa), were purposefully introduced to the lower tidal mudflat areas of Futian Nature Reserve in Shenzhen from Dongzhai Harbor Mangrove Nature Reserve of Hainan Province, China for reforestation projects in the late 1990s (Wang et al., 2002). Sc was a native species in Hainan while Sa was introduced to Hainan from Bangladesh in 1985 but so adaptive to Hainan condition. Both species are known to have fast growth rates and high tolerance to various environmental stresses (Liao et al., 2004). They have also been planted in many other mangrove ecosystems in South China such as Guangdong, Guangxi and Fujian Provinces. The total area of *Sonneratia* (mainly Sa) planted in China reached 3800 ha, accounting for >50% of the replanted mangrove areas in China (Chen et al., 2009, 2015), and had proliferated in 22 counties in Guangdong Province since 2002 (Peng et al., 2016). Since their introduction in China, there have been subjects of debate and disagreements on whether *Sonneratia* should be planted or not, because of their invasive potentials and the possibility of replacing native mangrove species in the ecosystem (Liao et al., 2004). Our previous studies in Shenzhen found that *Sonneratia* had lower CC and higher photosynthetic rate than the native mangrove plants, indicating their invasive potential (Li et al., 2011, 2016). However, it is not clear whether growth and CC of *Sonneratia* after introduced to another mangrove wetland, a new habitat for them, are poorer or better than when they are in the original habitat.

The present study therefore aims to compare the leaf CC and growth traits of *Sonneratia* between Hainan Dongzhai Harbor Mangrove Nature Reserve (where they originally grown) and Shenzhen Futian Mangrove Nature Reserve (where they were introduced), as well as their differences with native mangrove species in both wetlands. The study also attempts to evaluate the invasive potential of the alien *Sonneratia* species after introduced to Shenzhen mangrove wetland. Two *Sonneratia* species (Sc and Sa) and four common and dominant native species, namely, *Bruguiera gymnorrhiza* (L.) Lamk (Bg), *Kandelia obovata* Sheue, Liu et Yong (Ko), *Aegiceras corniculatum* (L.) Blanco (Ac) and *Avicennia marina* (Forsk.) Vierh. (Am) in both mangrove wetlands were selected.

2. Materials and methods

2.1. Study sites

Two mangrove wetlands, namely Dongzhai Harbor Mangrove Nature Reserve (19°54′ N, 110°20′ E) in Haikou City of Hainan Province and Futian Mangrove Nature Reserve (22°31′ N, 114°05′ E) in Shenzhen city of Guangdong Province, were investigated. Both are designated National Nature Mangrove Reserves in China, representing typical natural mangrove ecosystems at two climate zones, tropical and subtropical climates, respectively (Chen et al., 2008). Dongzhai Harbor Mangrove Nature Reserve, in the northeast of Hainan Island, China, is the most well-preserved mangrove forest in China and is one of the most important international wetlands. It is characterized by a tropical monsoonal climate with an annual precipitation of 1685 mm, mean annual air temperature of 23.8 °C (with a low mean monthly temperature of 17.2 °C in January and a high mean monthly temperature of 28.4 °C in July), annual insolation length of day of 2240 h and the seawater salinity of 21.9 (Chen et al., 2008). Futian Mangrove Nature Reserve, located in an estuary of the Zhujiang River in Shenzhen, Guangdong Province, China, is characterized by a subtropical monsoonal climate with an annual precipitation of 1927 mm (Tam et al., 1998; Chen et al., 2008). The mean annual air temperature is 22 °C, with a low mean monthly temperature of 14 °C (in January) and a high mean monthly temperature of 28 °C (in July), and annual insolation length of day of 2209 h and the seawater salinity of <15.0.

2.2. Sample collection and treatment

In each Mangrove Nature Reserve, two *Sonneratia* species (Sc and Sa) and four dominant native mangrove species (Bg, Ko, Ac and Am) were sampled in summer days when plant growth was the highest, which were 25th August in Shenzhen and 5th September in Hainan, to reduce season influences. For each mangrove plant species, three mature healthy trees, each about 10–15 years old, in the centre of the mangrove wetland were randomly sampled. In each tree, 30 fully expanded mature un-shade leaves of similar sizes at different orientations in the canopies were collected and pooled together to form a composite sample. This means the three replicates of each species were made up of 90 leaves. Based on field observations and personal communication with the staff of the Nature Reserves, the three trees of the same species not only had similar ages and growth conditions, the environmental conditions of the sampling areas were also comparable. The leaves were washed with tap water and dried with absorbent paper. The leaf blade area was determined using a leaf area meter (Li-Cor 3100A, Li-Cor, USA) and specific leaf area (SLA) was calculated according to the formula: SLA = Leaf blade area/Leaf weight (Li et al., 2011). After SLA determination, leaves were dried at 70 °C for 72 h, weighed, ground and homogenized into fine powder, then stored in a desiccator to maintain dryness prior to subsequent analyses. The ash-free caloric values (△Hc), nitrogen concentration (N) and ash content (Ash) of the leaf samples were determined and calculated according to standard methods described by Li et al. (2011).

2.3. Determination of leaf construction cost (CC)

The leaf CC per unit of mass (CCM, equivalent to grams glucose per gram dry mass, g(glucose) g^{-1}) was estimated according to the method described by Williams et al. (1987). Even though this method was originally used for calculating CCM of terrestrial plants, Suárez (2003, 2005) used the same method to investigate CCM of three mangrove species (*Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*) and demonstrated its feasibility on mangrove plants. The CCM was calculated as follows:

$$\mathrm{CCM} = {}^{[(0.06968\times\Delta\mathrm{H_c}-0.065)(1-\mathrm{Ash})+7.5(k\mathrm{N}/14.0067)]}\Big/_{\mathrm{EG}}$$

where k was the oxidation state of the N substrate (+5 for nitrate or −3 for ammonium). EG was the growth efficiency and was estimated to be 0.89 across species according to Penning de Vries et al. (1974). The leaf CC based on area (CCA, equivalent to grams glucose per square meter, g(glucose) m^{-2}) was calculated by the formula:

$$\mathrm{CCA} = {}^{\mathrm{CCM}}\big/_{\mathrm{SLA}}$$

2.4. Data analyses

CC, SLA and other growth traits (△Hc, N and Ash) among the six species in two mangrove wetlands were analyzed using a parametric two-way analysis of variance (ANOVA) with species and wetlands as the sources of variations. If the species effect was significant at $p \le 0.05$, a Student-Newman-Keuls (S-N-K) test for multiple comparisons was used to determine where the difference lies among six species. Differences in CC, SLA and other growth traits of each mangrove species between Hainan and Shenzhen mangrove wetlands were compared by independent sample t-test. All data fulfilled the assumptions of the parametric test, and no data transformation was needed. The statistical analyses were performed using SPSS 17.0 software (SPSS Inc., USA).

3. Results

3.1. Comparison of leaf CC between Hainan and Shenzhen and among species

No significant differences in leaf CCM and CCA of *Sonneratia* between Hainan and Shenzhen mangrove wetlands were found, but these indices differed significantly among six species according to two-way ANOVA (Fig. 1, Table 1). For CCM, the order in Hainan was Sa < Sc < Am < Ko < Bg < Ac and was Sa < Sc < Am < Bg < Ko < Ac in Shenzhen, while the orders for CCA in Hainan and Shenzhen were Sa < Sc < Am < Bg < Ko < Ac and Sc < Sa < Am < Bg < Ac < Ko, respectively (Fig. 1). Although the orders were different between two mangrove wetlands, the CCM and CCA of *Sonneratia* were always the lowest, Am was the second lowest, and the other three natives were higher, implying the location itself did not affect the CC trend among *Sonneratia*, pioneer and native mangrove species. The average decreases of CCMs in Sc and Sa (compared to native species) were 6.1% and 11.9%, respectively, and Sa had the lowest CCM while the native Ac had the highest value among six mangrove species. Among four native mangrove species, CCs of Am were the lowest, with 5.9% lower than the other three natives while its CCM was still 4.9% higher than *Sonneratia* (Fig. 1), i.e., even less energy cost was used for leaf construction in this exotic *Sonneratia* genus. Between two *Sonneratia* species, CCA of Sa and Sc were not significantly different (Fig. 1).

Table 1
F values of two-way ANOVA showing the effects of mangrove wetlands (Hainan and Shenzhen), mangrove species, and their interactions on the leaf CC and other growth traits.

Items	F-value		
	Wetlands (n = 2)	Species (n = 6)	Wetland × species
CCM	3.56^{NS}	28.12^{***}	3.74^{*}
CCA	2.18^{NS}	24.58^{***}	1.38^{NS}
SLA	2.48^{NS}	41.47^{***}	1.49^{NS}
$\triangle H_c$	3.02^{NS}	19.86^{***}	3.25^{*}
N	1.36^{NS}	116.47^{***}	5.40^{**}
Ash	2.15^{NS}	12.39^{***}	8.97^{***}

NS: not significant at $p \le 0.05$.
CCM: leaf construction cost (CC) per unit dry mass, CCA: leaf CC per unit area, $\triangle H_c$: ash-free caloric values, N: Nitrogen concentration, Ash: Ash content and SLA: specific leaf area.
* $p \le 0.05$.
** $p \le 0.01$.
*** $p \le 0.001$.

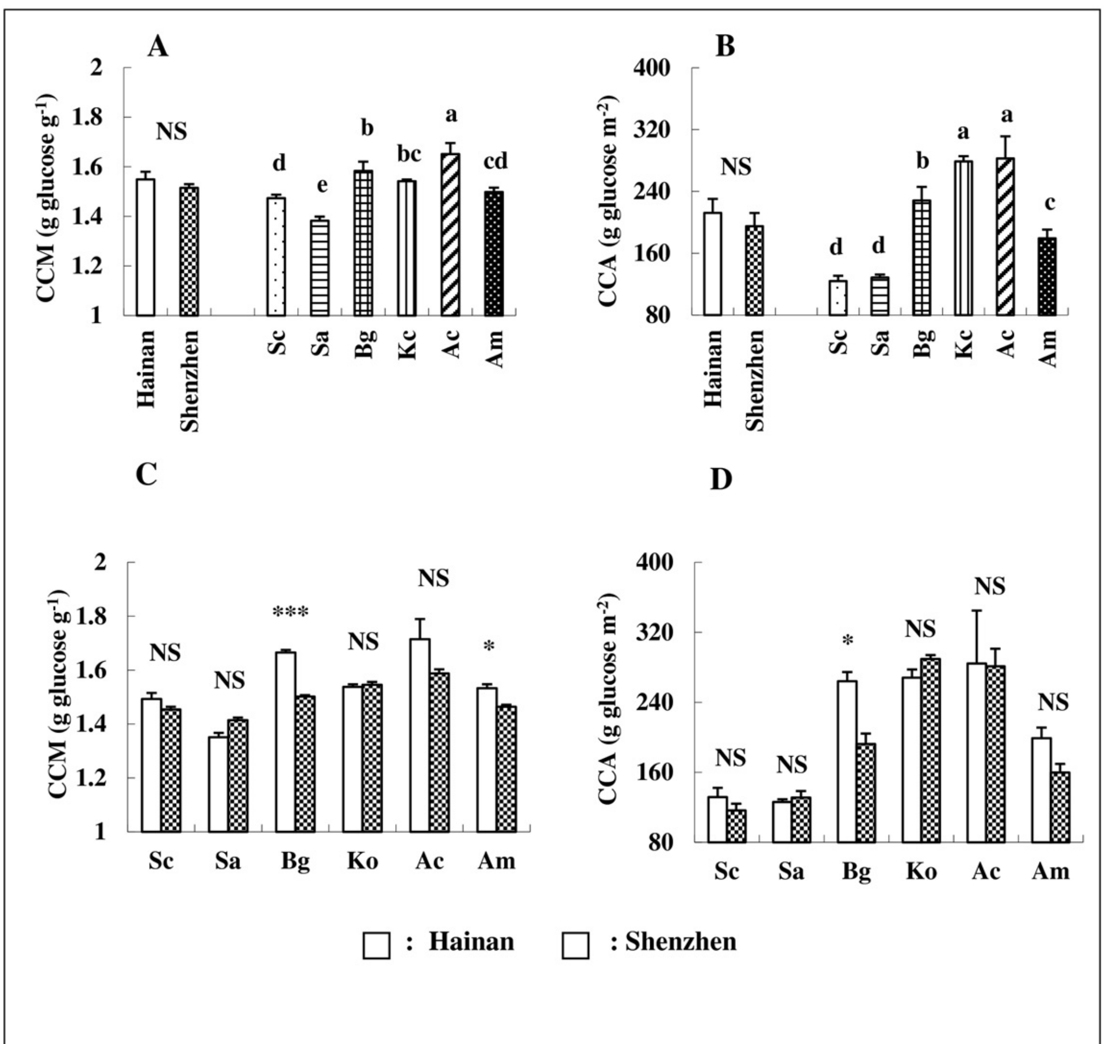

Fig. 1. Comparisons of construction cost (CC) of six mangrove plant species in two mangrove wetlands: Shenzhen where *Sonneratia* were introduced and Hainan where *Sonneratia* were originally colonized. CCM: CC per unit mass, CCA: CC per unit area. Error bars = 1 SE. NS indicates no significant difference while * and *** indicate significant difference between Hainan and Shenzhen mangrove wetlands at $p \le 0.05$ and at $p \le 0.001$, respectively; different letters indicate significant difference among six mangrove species according to ANOVA test at $p \le 0.05$.

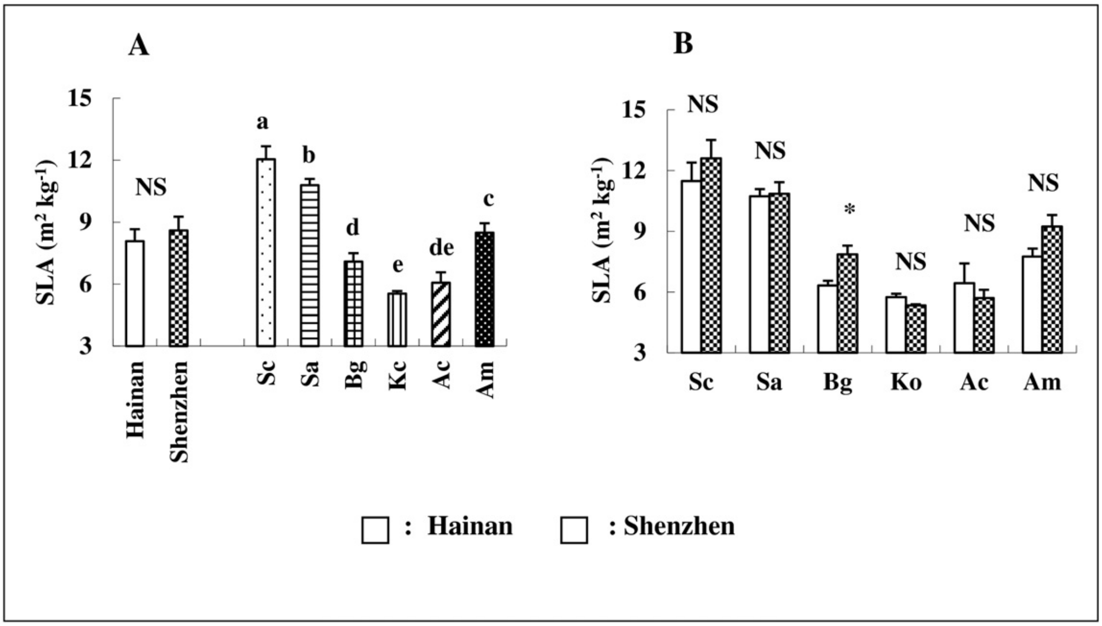

Fig. 2. Comparisons of specific leaf area (SLA) of six mangrove plant species in two mangrove wetlands: Shenzhen where *Sonneratia* were introduced and Hainan where *Sonneratia* were originally colonized. Error bars = 1 SE. NS indicates no significant difference while * indicate significant difference between Hainan and Shenzhen mangrove wetlands at $p \leq 0.05$; different letters indicate significant difference among six mangrove species according to ANOVA test at $p \leq 0.05$.

3.2. Comparison of SLA between Hainan and Shenzhen and among species

Like CCM and CCA, SLA of *Sonneratia* in two mangrove wetlands was comparable but significantly differed from that of the four native species (Fig. 2, Table 1). Contrary to CC, SLA of *Sonneratia* species was significantly higher than that of native mangroves in Shenzhen and Hainan (Fig. 2). The increases of SLA of Sc and Sa in Hainan mangrove wetland, when compared to the mean values of four native species, were 75.0% and 63.5%, respectively, while the respective increases in Shenzhen were 79.2% and 54.3%. These results suggested a large assimilatory surface was produced by *Sonneratia* to enhance their light interception. Among the four native mangrove species, SLA of Am was the highest but was still lower than that of *Sonneratia* (Fig. 2). The SLA value sequences of six mangroves in the two wetlands followed the same trend of *Sonneratia* > Am > other native mangrove plants (Fig. 2), almost the opposite to the trend of CC.

3.3. Comparison of other growth traits of Sonneratia between Hainan and Shenzhen and among species

Same as CC and SLA, the two mangrove wetlands in different geographical locations did not cause any significant differences in other growth traits, including ash-free caloric values (△Hc), nitrogen concentration (N) and ash content (Ash), while significant differences were

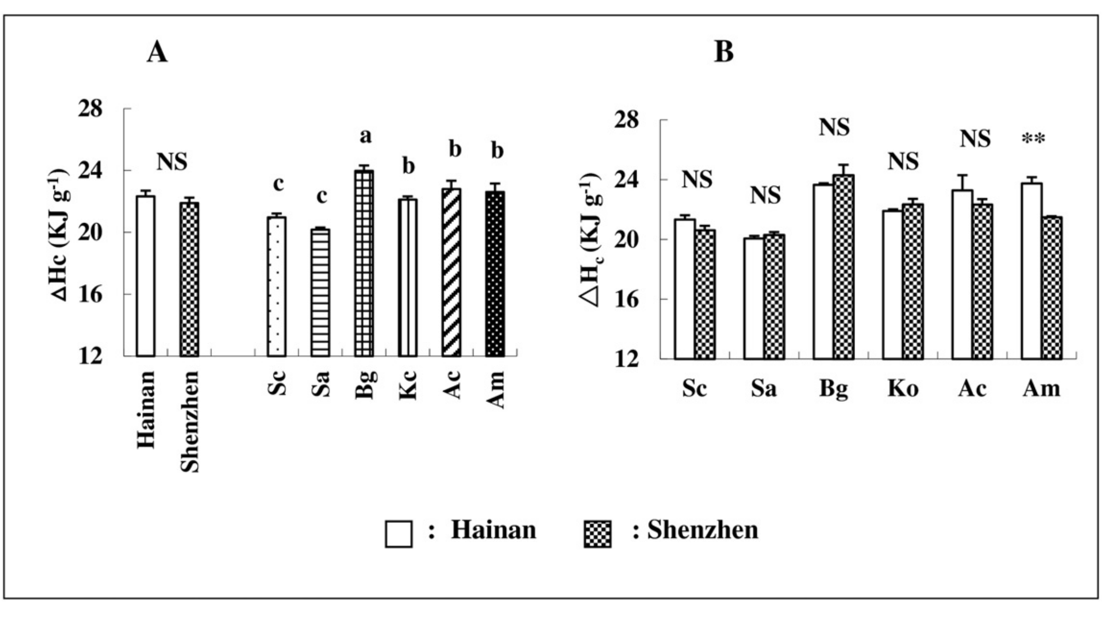

Fig. 3. Comparisons of ash-free caloric values (△Hc) of six mangrove plant species in two mangrove wetlands: Shenzhen where *Sonneratia* were introduced and Hainan where *Sonneratia* were originally colonized. Error bars = 1 SE. NS indicates no significant difference while ** indicate significant difference between Hainan and Shenzhen mangrove wetlands at $p \leq 0.01$; different letters indicate significant difference among six mangrove species according to ANOVA test at $p \leq 0.05$.

found among six species (Figs. 3 and 4, Table 1). Species variations on △Hc were similar to CC, with *Sonneratia* haing the lowest value (Fig. 3). Nitrogen concentration of Am was the highest, followed by that of Sc, and Ac had the lowest value. Ashes of Am and Bg were the highest. *Avicennia marina* in Shenzhen mangrove wetland had significantly higher N than that in Hainan (Fig. 4).

4. Discussion

Low CC was associated with high relative growth rate (Poorter and Villar, 1997; Zhu et al., 2015). Invasive species with low CC could utilize carbon resources more efficiently and invested less energy per unit of leaf produced, allowing the saved energy for the investment of other competitive strategies, such as seed production, biomass productivity and faster growth rate (Nagel and Griffin, 2001; Martínez-Garza et al., 2013; Zhu et al., 2015). However, *Sonneratia* species in Futian Nature Reserve in Shenzhen, considered as their new habitat, had comparable CC as in Hainan, their original habitat, suggesting that the exotic species introduced or transplanted to a new habitat did not need to invest additional energy for their adaptation and growth. The lower CC of *Sonneratia* than the natives also indicated that less energy and resource were needed to construct the biomass of *Sonneratia*, giving advantages to this exotic genus. Not only CC, SLA and other growth traits of *Sonneratia* in the two mangrove wetlands were also similar. SLA was a plant trait extremely important in the regulation and control of plant functions, such as carbon assimilation and carbon allocation (Lambers and Poorter, 1992), and high SLA was associated with high relative growth rates and higher invasive potentials (Hamilton et al., 2005; Feng et al., 2011). Like CC, low leaf caloric value was characterized by a high-growth strategy since high one was associated with high resource requirement for leaf production and low grow rate (Poorter and Villar, 1997). Ash content was negatively correlated with caloric value and affected plant growth rate (Cassida et al., 2005) while N was related to photosynthetic ability (Feng et al., 2009). The comparable values in SLA and growth traits of *Sonneratia* between their original and introduced habitats in Hainan and Shenzhen, respectively, indicated that this genus did not lose any advantage when introduced or transplanted to a new habitat even though the climate is different, with subtropical weather in Shenzhen and tropical weather in Hainan.

It has been reported that CC and caloric values of a species increased, while SLA, N and Ash decreased significantly with latitude (Villar and Merino, 2001) and altitude (Zhang et al., 2012). In theory, CC and caloric values of *Sonneratia* in Shenzhen should be higher than that in Hainan while SLA, N and Ash should be the opposite, as Shenzhen's latitude is 2°38′ higher and the average annual temperature is 1.8 °C lower than Hainan. However, CC and caloric values of *Sonneratia* were comparable in the two mangrove wetlands, suggesting that it was not necessary for this genus to allocate more energy to encounter the difficulties of

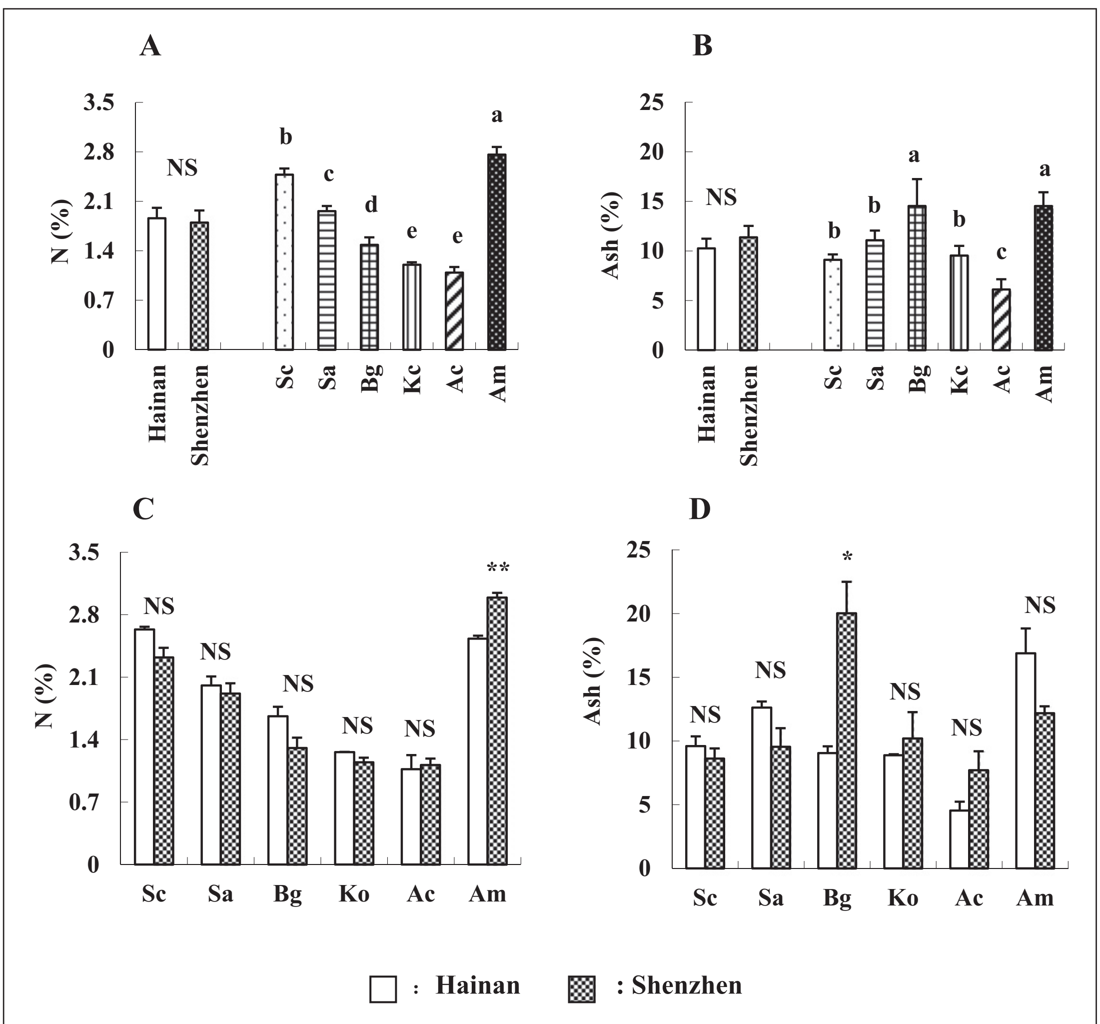

Fig. 4. Comparisons of nitrogen concentration (N) and ash content (Ash) of six mangrove plant species in two mangrove wetlands: Shenzhen where *Sonneratia* were introduced and Hainan where *Sonneratia* were originally colonized. Error bars = 1 SE. NS indicates no significant difference while * and ** indicate significant difference between Hainan and Shenzhen mangrove wetlands at $p \leq 0.05$ and at $p \leq 0.01$, respectively; different letters indicate significant difference among six mangrove species according to ANOVA test at $p \leq 0.05$.

adaption and/or low temperature when introduced to the new habitat in Shenzhen. The occurrence of extreme conditions, such as extremely low temperature and frosts, affects the success of a tropical species extends into the subtropical region. The temperature of Shenzhen in winter was lower than that of Hainan. Not only air temperature, water temperature in Shenzhen Bay where Futian Nature Reserve locates is lower than that in Haikou in Hainan. Sc were all dead in the next cold winter after its introduction into Futian Nature Reserve in Shenzhen, but the other *Sonneratia* species, Sa, survived through the entire cold winter in 1993. Sc was re-introduced in 1994 and became successful in the following years (Chen, 2007). The two *Sonneratia* species survived even in the "snow disaster" of China in 2008 (Lu et al., 2011). More than 20 years of field observations showed that these two *Sonneratia* species gradually adapted to the cold winter and successfully colonized the subtropical mangrove wetland in Futian Nature Reserve in Shenzhen. Like air temperature, water temperature did not affect the CC and other growth traits of *Sonneratia* species in Shenzhen.

Feng et al. (2011) reported that leaf CC of an invader *Ageratina adenophora* did not change after introduced to new habitats in China and India from its original habitat in Mexico and this species had higher photosynthetic ability, N, SLA and photosynthetic energy-use efficiency (PEUE) in the new habitat, thus allowed it to grow faster and be a very noxious invader after introduction. Li et al. (2014, 2016) found that the net photosynthetic rates (P_n) of *Sonneratia* in Shenzhen (13.7 μmol m^{-2} s^{-1} for Sa and 13.2 μmol m^{-2} s^{-1} for Sc) were higher than in Hainan (12.2 and 12.0 μmol m^{-2} s^{-1} in Sa and Sc, respectively). Therefore, like *A. adenophora*, although no significant different CC was found between *Sonneratia* grown in the original and introduced habitats, higher photosynthetic ability and PEUE would make *Sonneratia* more competitive and invasive in the new habitat.

Avicenna marina, a pioneer mangrove species, may be the only plant species competed with *Sonneratia* in mangrove wetlands as they occupy the same foreshore tidal zone. In the present study, the growth traits of Am were the best among the four native plant species in both Shenzhen and Hainan mangrove wetlands. However, faster growth and wider dispersion of *Sonneratia* than Am were observed during our field surveys (data not shown), which might be attributed by their lower CC and caloric value but higher SLA, P_n and PEUE than Am. Li et al. (2016) reported that *Sonneratia* in Futian, Shenzhen had 32% higher assimilation rate, coupling with 7.7% lower CC, leading to 72% higher PEUE and 51% higher relative growth rate in biomass than those of the native mangrove species, and concluded that *Sonneratia* were competitive and invasive. The present study together with our previous work revealed that *Sonneratia* could persist and proliferate in new ranges, especially introduced to a habitat without virulent or at least debilitating associates. The invasive potential of this introduced genus should not be ignored. Between the two *Sonneratia* species, Sa appeared to be more invasive as its CCM was significantly lower than that of Sc. Additionally to leaf CC, other variables such as leaf longevity, susceptibility to herbivore attack and photosynthetic efficiency, also affect the leaf production and the invasiveness of an exotic species. More in-depth research should be devoted to the invasiveness of *Sonneratia* and the cost-benefit analysis of their leaf production, particularly *S. apetala*.

5. Conclusion

The construction cost (CC), specific leaf area (SLA) and other growth traits of *Sonneratia* in Futian mangrove wetland in Shenzhen did not differ significantly from that in Dongzhai Harbor mangrove wetland in Hainan, suggesting that this genus did not lose any advantage after introduced to Shenzhen from Hainan. Among six tested mangrove species, leaf CC declined in the trend of *Sonneratia* < Am < other natives, while the trend for SLA was the opposite in both mangrove wetlands. *Sonneratia* also had significantly lower caloric values but higher SLA, N and Ash than the four native species. These results indicated that *Sonneratia* could out-compete native mangrove species and their invasive potentials in Shenzhen should not be ignored. The study also showed that the above indices could be regarded as inherent traits of a species and used to evaluate the invasiveness of an alien species. Between two *Sonneratia* species, the invasiveness of *S. apetala* was higher than that of *S. caseolaris* as the former species had lower CC, and deserved more attention.

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