



# Allometric growth and carbon storage in the mangrove *Sonneratia apetala*

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Received: 9 July 2020 / Accepted: 3 December 2020 / Published online: 19 January 2021  
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**Abstract** Allometric growth reflects different allocation patterns and relationships of different components or traits of a plant and is closely related to ecosystem carbon storage. As an introduced species, the growth and carbon storage of *Sonneratia apetala* are still unclear. To derive allometric relationships of the mangrove *S. apetala* and to estimate carbon storage in mangrove ecosystems, we harvested 12 individual *Sonneratia apetala* trees from four different diameter classes in the Futian National Nature Reserve, Guangdong, China. Allometric growth models were fitted. The results showed that diameter at

breast height (DBH) and wood density were better variables for predicting plant biomass (including above- and below-ground biomass) than plant height. There were significant power function relationships between biomass and DBH, with a mean allometric exponent of 2.22, and stem biomass accounted for 97% of the variation in *S. apetala* total biomass. Nearly isometric scaling relationships were developed between stem biomass and other biomass components. To better understand the carbon stocks of the *S. apetala* ecosystem, we categorized all trees into five age classes and quantified vegetation carbon storage. The *S. apetala* vegetation carbon storage ranged from 96.48 to 215.35 Mg C ha<sup>-1</sup>, and the carbon storage significantly increased with stand age. The allometric equations developed in this study are useful to estimate biomass and carbon storage of *S. apetala* ecosystems.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11273-020-09772-7>.

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**Keywords** Allometry · Biomass allocation · Carbon storage · Isometry · Stem biomass

## Introduction

Allometry is the study of the relative growth relationships of biological organs in terms of size and functional traits (Huxley 1932; Damuth 2001). Allometric growth is widely used to study the relationship

of the biomass and growth rate of two organs or traits and to investigate the effect of individual size on biological processes (Enquist and Niklas 2002; Niklas 2004; Enquist et al. 2007). An allometric model describes the proportionate relationship between the mass of two organs or components (Huxley 1932) and is often described as  $Y = bX^a$ , where  $Y$  and  $X$  are the sizes of the two organs or components, parameter  $a$  represents the allometric exponent, and parameter  $b$  reflects the allometric constant. Generally, when  $a = 1$ , there is an isometric relationship between traits in various parts of an organism, but when  $a \neq 1$ , there is an allometric relationship between them (Huxley 1932; Enquist and Niklas 2002). The allometric relationships between different components of plant biomass have been extensively investigated (e.g., Niklas 2004; Cheng and Niklas 2007). For example, Hui et al. (2014) found that below-ground biomass scales near isometrically with above-ground biomass, and the scaling exponent does not vary with tree age and density but increases with tree size, according to a large forest biomass database. In another biomass allocation study, Enquist and Niklas (2002) proposed that the universal allometric scaling factor of leaf biomass versus stem biomass and leaf biomass versus below-ground biomass for a mature tree is  $3/4$  and that of stem biomass versus below-ground biomass is 1. However, for non-woody plants and juvenile woody plants, allometric scaling between below- and above-ground biomass is an isometric relationship (Enquist and Niklas 2002).

The relationship between plant diameter at breast height (DBH) and tree height is important to explore plant growth. Three models are proposed to describe the relationship, including (1) the constant stress self-similarity model (Dean and Long 1986), which is considered the  $1/2$  power ( $H \propto \text{DBH}^{1/2}$ ) allometric growth relationship between DBH and tree height, (2) the elastic self-similarity model (McMahon 1973; Niklas and Enquist 2002a, b), which states that the power exponent is  $2/3$  ( $H \propto \text{DBH}^{2/3}$ ), and (3) the geometric self-similarity model (Norberg 1988), which indicates an isometric relationship ( $H \propto \text{DBH}$ ). There is no consensus on the value of the allometric exponent, as different studies produced different allometric exponents (West et al. 1999; Komiyama et al. 2008; Paul et al. 2016). Therefore, it is considered that the allometric exponent is not invariable but is influenced by individual size, life-type,

environmental factors, and species (Hayward et al. 2010; Hui et al. 2014; Enquist et al. 2017). Nevertheless, it remains unclear whether the allometric exponent of mangrove species is invariable, especially that of the introduced species *Sonneratia apetala*.

Mangrove forests are distributed mostly in tropical and subtropical areas along coastlines. The total mangrove area is 137,760 km<sup>2</sup> and covers 0.1% of Earth's surface area (Giri et al. 2011; Rivera-Monroy et al. 2017). Mangroves provide important ecological and economic services (Vo et al. 2012). Mangrove ecosystems produce and sequester a considerable amount of carbon compared to terrestrial and other wetland ecosystems and are referred to as an important source of "blue carbon" (Donato et al. 2011; McLeod et al. 2011; Migeot and Imbert 2012; Alongi 2014; Hamilton and Friess 2018). However, the total mangrove area is reduced at a rate between 0.16% and 0.39% per year worldwide due to deforestation, and Southeast Asia has the highest loss rate (Hamilton and Casey 2016). Reducing CO<sub>2</sub> emissions from deforestation and forest degradation (REDD +) is proposed as an effective approach for forest conservation through afforestation (UNFCCC 2008). Plantations are a common method for restoring mangrove forests in mainland China (Zan et al. 2003), and *S. apetala* is the main species for mangrove afforestation.

*Sonneratia apetala* is a fast-growing, light-demanding, and highly adaptable species that originated in Bangladesh, India, and Sri Lanka (Jayatissa et al. 2002; Peng et al. 2016b). *S. apetala* was introduced to increase the mangrove area in China. It was first introduced to Dongzhai Port in China from Bangladesh in 1985 and from Dongzhai Port to the Futian National Nature Reserve, Shenzhen, in 1993 (Zan et al. 2003). In order to alleviate the degradation and destruction of mangroves, *Kandelia obovata*, *Sonneratia caseolaris*, and *S. apetala* are widely planted, and the afforestation area of *S. apetala* exceeds 50% of the total mangrove plantation area (Ren et al. 2009). The growth of *S. apetala* has attracted wide attention due to its shade intolerance, higher relative growth rate, and lower soil carbon sequestration capability than the same-age native species (Mittra et al. 2012; Peng et al. 2016b; He et al. 2018; Wu et al. 2020). Previous studies focused on the allometric growth of young *S. apetala* plantations, mostly those aged 10 years or younger (Ren et al. 2010; Lunstrum and Chen 2014), but the growth mechanisms of *S. apetala* remain

unclear. Accordingly, allometric growth equations and allometric exponents of *S. apetala* from different diameter classes need to be developed.

In this study, we developed allometric growth equations for *S. apetala* and quantified the carbon storage of *S. apetala* vegetation in different age classes. Based on different age classes of *S. apetala*, we hypothesized that its carbon storage increases with age. In this paper, we aimed to (1) develop allometric relationships between shoot biomass and other components of biomass, (2) construct an appropriate allometric equation of biomass with the DBH and wood density of *S. apetala*, (3) compare the difference in biomass allocation between *S. apetala* and other mangrove forests, and (4) assess the dynamic changes of carbon storage of *S. apetala* in different age classes.

## Materials and methods

### Study sites

The Futian National Nature Reserve (latitude 22°32'N and longitude 113°45'E) is located in the north of Shenzhen Bay, Shenzhen, Guangdong, China. The reserve is adjacent to the Mai Po Reserve in Hong Kong, which is the smallest mangrove reserve (368 ha) in China. The reserve has a typical subtropical monsoon climate with a mean annual temperature of 22.6 °C and a mean annual precipitation of 1794 mm (Lunstrum and Chen 2014; Yang et al. 2014). The tides in Shenzhen Bay are characterized as irregular semidiurnal tides and are often affected by typhoons from May to October. Species richness of the mangrove community is relatively low in Shenzhen Bay (Ren et al. 2011). The dominant species are *K. obovata*, *Avicennia marina*, and *Aegiceras corniculatum*. Exotic species mainly include *S. caseolaris* and *S. apetala*.

### Experimental design

In China, *S. apetala* has been planted for decades; the growth dynamics remain unclear, and the change in its carbon storage in different age classes is also not well understood. In order to better evaluate the growth of *S. apetala*, we set up the following two experiments in the Futian Natural Reserve.

### Experiment 1: Construction of allometric equations to determine the biomass of *S. apetala*

Tree harvesting was carried out from December 2017 to January 2018. Based on the field investigation, we selected 12 *S. apetala* individuals from four different diameter classes with similar diameter (mean diameter of 2.97 cm, 11.47 cm, 21.70 cm, and 37.39 cm) and height distribution in the Futian National Nature Reserve, that is, three trees per diameter class (Table S1). Based on the diameter class, trees of similar size were selected randomly. The age of the oldest tree exceeded 20 years. Measurements of DBH, tree height (H), and wood density ( $\rho$ ) were undertaken for each selected tree. The average wood density of 12 *S. apetala* in the Reserve is 0.478 g/cm<sup>3</sup>. The selected trees were harvested and divided into four components (stem, twigs, leaves, and roots). We excavated the sample trees, with a 1 m radius and up to 2 m in depth, and removed all roots for weighing. The roots included the coarse and fine roots, and their fresh weights were measured, respectively. The total fresh weight of the stems, twigs, leaves, and roots were also measured. A subsample from each component per harvested tree was transported to the laboratory for dry weight measurements following drying in an oven at 80 °C for 72 h until a constant weight was reached. We calculated the dry weight of each sample using the moisture content of the subsample.

The height and wood density of 12 harvested *S. apetala* trees were correlated with DBH (Fig. S1). The tree height was barely visual in the field survey, and it was difficult to accurately measure the height of the mangrove community; thus, DBH was used to construct allometric equations. Since wood density may be an important determinant of biomass (Chave et al. 2005; Komiyama et al. 2005), we chose DBH and wood density as independent variables for constructing allometric equations for tree biomass in this study. We compared several different DBH and wood density models and selected the best equation for the biomass estimation of *S. apetala*.

In previous studies, there were more allometric equations for above-ground biomass and fewer equations for below-ground biomass because of the difficulty associated with below-ground sample collection and measurements. In our study, we constructed above- and below-ground biomass allometric

**Table 1** Allometric equations describe total biomass (kg) of *Sonneratia apetala*. The standard error of the estimate (SE), allometric equation parameter ( $a$ ,  $b$ ,  $c$ ), coefficient of determination ( $R^2$ ), Akaike information criterion (AIC), bias and root

mean square error (RMSE), model bias (% error) and  $\Delta W$  ( $\Delta W = W_{\text{predicted}} - W_{\text{measured}}$ ) are presented. Equations 1–5 are described in the text

Equation	$a$	$b$	$c$	$R^2$	AIC	RMSE	% error	$\Delta W$
Equation (1)	0.155	2.365		0.988	126.242	36.276	8.8	10.5
SE	0.097	0.175						
Equation (2)		2.031		0.991	120.405	30.916	44.1	8.9
SE	0.006							
Equation (3)	0.442	2.259		0.994	118.467	26.237	12.5	7.6
SE	0.200	0.128						
Equation (4)	2.005	2.218		0.996	111.560	19.676	9.1	5.7
SE	0.279	0.052						
Equation (5)	2.378	2.595	2.086	0.997	111.183	17.820	20.0	5.1
SE	1.477	0.499	0.106					

equations and compared our results with the allometric equations reported in previous studies.

The below- to above-ground biomass ratios for each *S. apetala* was calculated and the confidence interval of mean was examined. Then we compared this ratio with the below- to above-ground biomass ratios of other five mangrove species (*A. corniculatum*, *A. marina*, *Bruguiera gymnorrhiza*, *K. obovata*, and *S. caseolaris*) published in the literature.

#### Experiment 2: Assessing the carbon storage in different age classes of *S. apetala*

According to planting record of the year for *S. apetala* in the Futian National Nature Reserve, plots of five age classes (13 year, 14 year, 19 year, 21 year, and 26 year) were set up in July 2017 (Fig. S2). Each plot was 10 m  $\times$  10 m. There were six plots for the 13-year age class, five plots for the 14-year age class, four plots for the 19-year age class, six plots for the 21-year age class, and four plots for the 26-year age class, that is, a total of 25 plots. At plantation establishment, the stand density of *S. apetala* was 2000 plants/hm<sup>2</sup> in all of the plots. Considering the variation in stand density as plants grow, we first measured the DBH of all mangrove plants in each plot in 2017. In July 2018 and 2019, the DBH of all mangrove plants were re-measured. In order to analyze the growth situation of different age classes of *S. apetala*, the relative growth rate (RGR) was calculated using the DBH data (Lambers and Poorter

1992). Allometric equations developed above were used to estimate the mangrove biomass. Carbon stocks of the mangrove vegetation were quantified as the vegetation biomass multiplied by the average carbon concentration of all species, that is, 40.5% (Peng et al. 2016a), in 2017, 2018 and 2019.

#### Data analysis

All of the data were log-transformed to meet the normal distribution requirement before analysis. We calculated the average DBH, average height, and standard deviation (SD) of the 12 harvested trees and tested the significant differences among the four diameter classes using one-way ANOVA followed by least significant difference (LSD) multiple comparisons. Standard major axis (SMA) regressions were used to estimate the allometric constant ( $a$ ) and exponent ( $b$ ) using the package “smatr” in R 3.5.0 (Warton et al. 2012).

For the 12 harvested trees of *S. apetala* in the Futian National Nature Reserve, we constructed allometric equations for the above- and below-ground biomass using DBH and wood density. Before fitting the allometric equations, we examined the relationships between DBH and three biomass components and wood density. Because the data showed heteroscedasticity, natural logarithmic transformations of the data were applied to construct equations. We built additive allometric equations for *S. apetala* biomass. The allometric equations were developed as follows:

$$\log_{10}(M) = a + b \times \log_{10}(\text{DBH}) \quad (1)$$

$$\log_{10}(M) = \log_{10}(p) + b \times \log_{10}(\text{DBH}), \quad (2)$$

$$\log_{10}(M) = a + \log_{10}(p) + b \times \log_{10}(\text{DBH}), \quad (3)$$

$$\log_{10}(M) = a \times \log_{10}(p) + b \times \log_{10}(\text{DBH}), \quad (4)$$

$$\log_{10}(M) = a + b \times \log_{10}(p) + c \times \log_{10}(\text{DBH}), \quad (5)$$

where  $M$  represents the biomass of each component, and  $p$  is the wood density of each harvested tree. The allometric equation was assessed using the adjusted coefficient of determination ( $R^2$ ), Akaike information criterion (AIC) (Akaike 1974), bias, and root mean square error (RMSE). Adjusted  $R^2$  and AIC were used to evaluate model fitness using independent variables. The bias reflected a relative error in the regression function, % error =  $100 \times (W_{\text{predicted}} - W_{\text{measured}}) / W_{\text{measured}}$  (Chave et al. 2005).  $\Delta W$  ( $\Delta W = W_{\text{predicted}} - W_{\text{measured}}$ ) was calculated for assessing difference between values of predicted and measured biomass. In view of  $R^2$  and model bias, we

selected the best model for estimation of biomass of *S. apetala*.

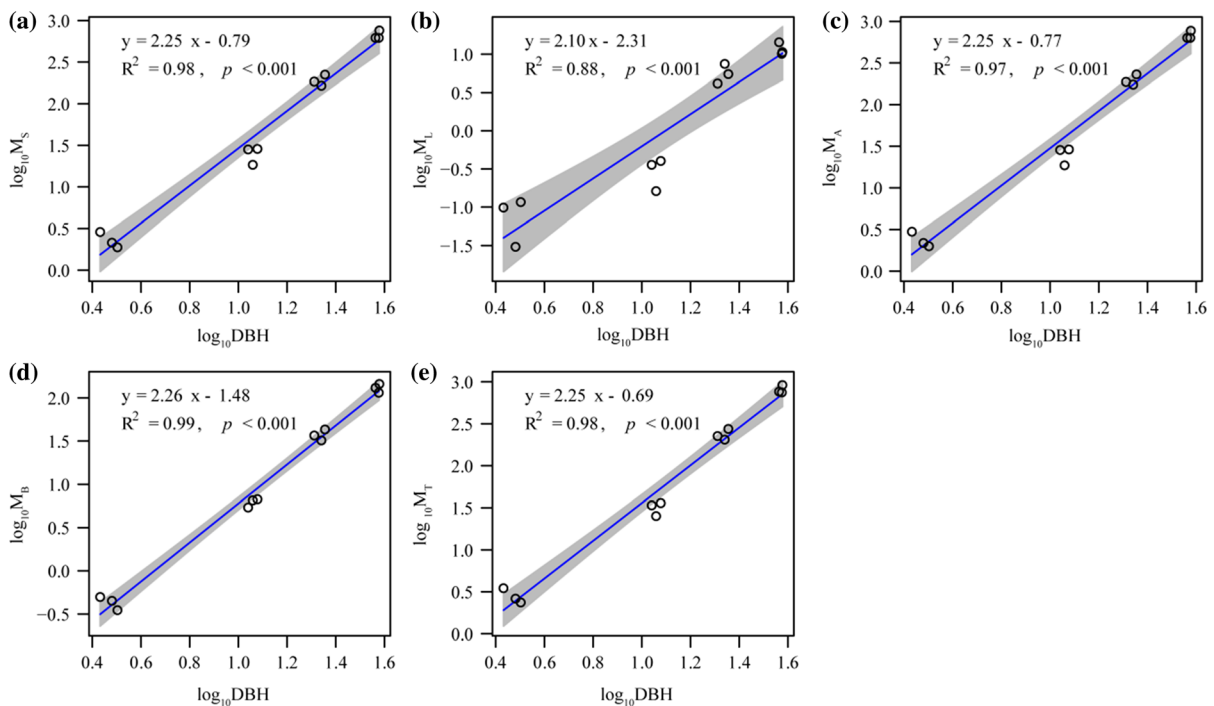
The ratios of the below- to above-ground biomass of six mangrove plants were analyzed using one-way ANOVA. As the RGR data of different age classes of *S. apetala* followed a non-normal distribution, the Kruskal–Wallis test was used for comparative analysis. Linear regression analysis was applied to develop relationships between the carbon stocks and five age classes of *S. apetala*.

Statistical analysis of all data was performed using R 3.5.0 (The R Project for Statistical Computing, [www.r-project.org](http://www.r-project.org)).

## Results

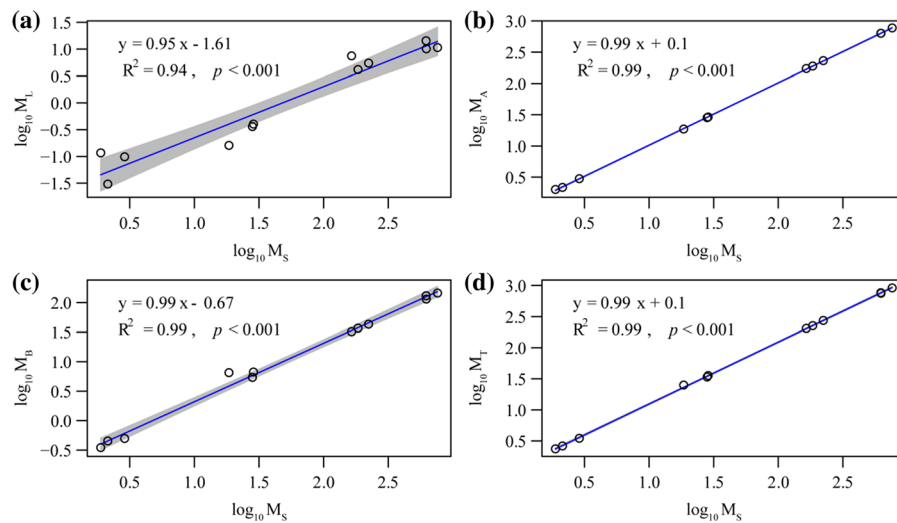
### Allometric relationships of *S. apetala* biomass

In *S. apetala* plantations, the DBH of *S. apetala* had a strong allometric relationship with its biomass (Fig. 1). The allometric exponent was 2.10 between the DBH and leaf biomass ( $M_L$ ), and the maximum



**Fig. 1** Relationship between different components of biomass and DBH of *Sonneratia apetala*. (a) stem biomass ( $M_S$ ), (b) leaf biomass ( $M_L$ ), (c) above-ground biomass ( $M_A$ ), (d) below-

ground biomass ( $M_B$ ), (e) total biomass ( $M_T$ ). The shaded areas represent the 95% confidence interval



**Fig. 2** Bivariate plots between stem biomass and other biomasses of *Sonneratia apetala*. (a) the allometric relationship between stem biomass ( $M_s$ ) and leaf biomass ( $M_L$ ), (b) the allometric relationship between stem biomass ( $M_s$ ) and above-ground biomass ( $M_A$ ), (c) the allometric relationship between

stem biomass ( $M_s$ ) and below-ground biomass ( $M_B$ ), (d) the allometric relationship between stem biomass ( $M_s$ ) and total biomass ( $M_T$ ). The shaded areas represent the 95% confidence interval

**Table 2** Allometric equations describe below-ground biomass (kg) of *Sonneratia apetala*

Equation	<i>a</i>	<i>b</i>	<i>c</i>	$R^2$	AIC	RMSE	% error
Equation (1)	0.028	2.336		0.983	85.982	6.778	4.7
SE	0.020	0.201					
Equation (2)		1.514		0.956	95.414	10.913	42.5
SE	0.014						
Equation (3)	0.079	2.230		0.991	78.342	4.930	8.9
SE	0.041	0.146					
Equation (4)	3.380	1.963		0.998	60.482	2.164	21.8
SE	0.183	0.034					
Equation (5)	0.878	3.288	1.982	0.998	58.586	2.155	19.9
SE	0.414	0.382	0.007				

allometric exponent was 2.26 between the DBH and below-ground biomass ( $M_B$ ). The allometric exponent was 2.25 among the DBH and stem biomass ( $M_s$ ),  $M_B$ , and total biomass ( $M_T$ ). Although the scaling exponents were different, the average was about 2.22 ( $R^2 > 0.88$ ). The allometric exponent was about 2.25 between the DBH and above-ground biomass ( $M_A$ ),  $M_B$ , and  $M_T$ , and the coefficient of determination of the equation was greater than 0.97.

Stem biomass was the main biomass component part of *S. apetala* and accounted for about 97.56% and 81.05% of the variations in the above-ground biomass

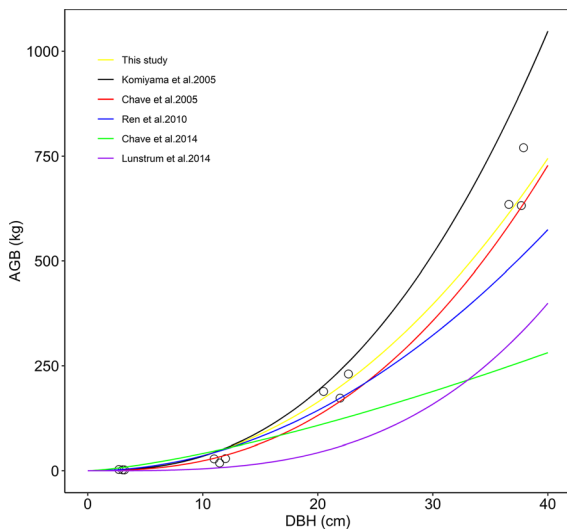
and total biomass, respectively. Although the allometric exponent of stem biomass and leaf biomass had the smallest value (0.95), the allometric exponent was close to 1 for  $M_s$  and  $M_L$ ,  $M_A$ ,  $M_B$ , and  $M_T$  (Fig. 2). In particular, the allometric exponent was higher than 0.99, which was similar to the isometric growth between  $M_L$  and  $M_A$ ,  $M_B$ , and  $M_T$ .

#### Allometric equations for *S. apetala* biomass

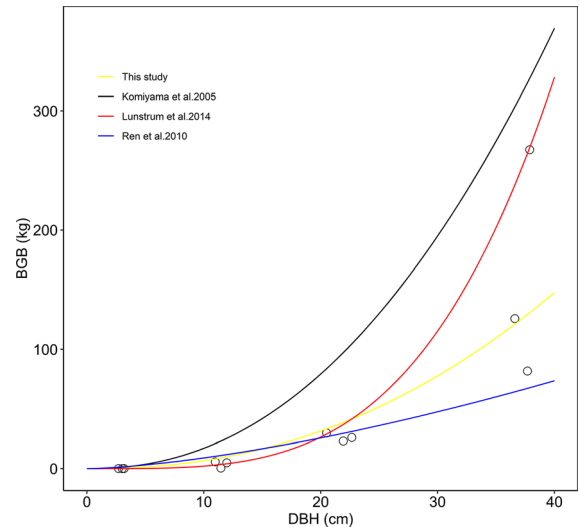
In this study, we used DBH and wood density to construct allometric equations for the above- and

**Table 3** Allometric equations describe aboveground biomass (kg) of *Sonneratia apetala*

Equation	<i>a</i>	<i>b</i>	<i>c</i>	R <sup>2</sup>	AIC	RMSE	% error
Equation (1)	0.127	2.370		0.988	121.890	30.259	10.0
SE	0.080	0.175					
Equation (2)		1.982		0.989	118.259	28.271	56.1
SE	0.007						
Equation (3)	0.364	2.265		0.993	114.677	22.405	14.6
SE	0.180	0.129					
Equation (4)	2.098	2.187		0.996	108.540	17.350	14.5
SE	0.290	0.054					
Equation (5)	1.699	2.462	2.107	0.996	109.784	16.811	21.3
SE	1.185	0.559	0.119				

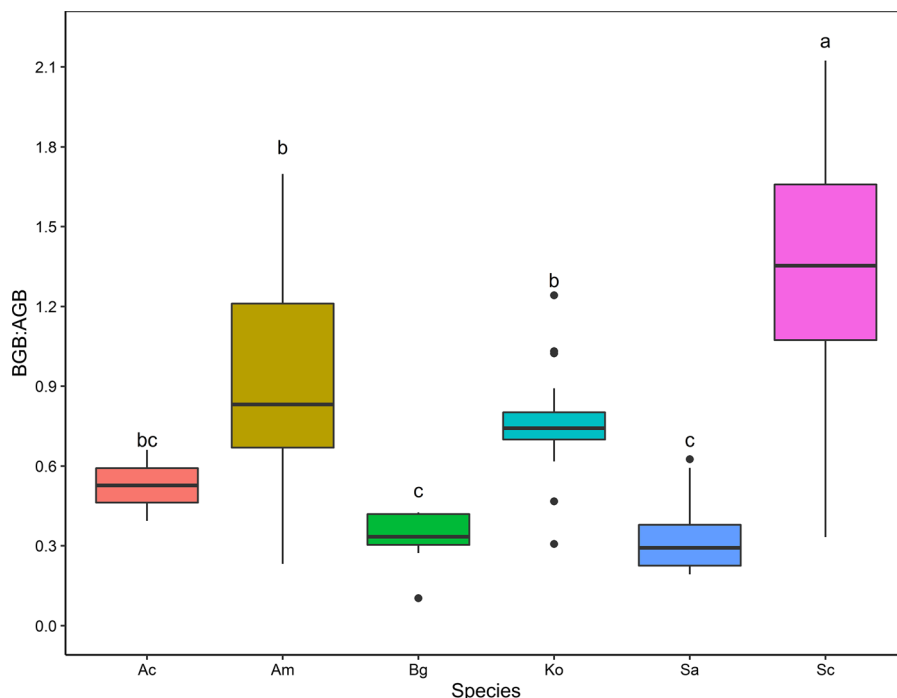
**Fig. 3** Comparison with previous studies for the estimation above-ground biomass (AGB) of *Sonneratia apetala*

below-ground biomass of *S. apetala* in the Futian National Nature Reserve (Tables 1, 2, 3). We found that Eqs. (4) and (5) were better models for above- and below-ground biomass of *S. apetala*, respectively. Meanwhile, the use of DBH overestimated the total biomass of *S. apetala* compared to the use of wood density and DBH. Compared to previous allometric equations, we found that DBH and wood density were good predictors for the above- and below-ground biomass of *S. apetala* in this study (Figs. 3, 4).

**Fig. 4** Comparison with previous studies for the estimation below-ground biomass (BGB) of *Sonneratia apetala*

The below- to above-ground biomass ratios of *S. apetala* and other mangrove species

Different mangrove forests had different ratios of below- and above-ground biomass (Fig. 5) (Tam et al. 1995; Khan et al. 2009; Hoque et al. 2011; Pham et al. 2016). The one-way ANOVA results showed that there were significant differences in the ratios between *S. apetala* and *A. marina*, *K. obovata*, and *S. caseolaris*, but no significant difference between *S. apetala* and *A. corniculatum* and *B. gymnorrhiza*. The average



**Fig. 5** Ratios of below-ground biomass (BGB) to above-ground biomass (AGB) of the mangrove forests. Ac, *Aegiceras corniculatum*; Am, *Avicennia marina*; Bg, *Bruguiera gymnorhiza*; Ko, *Kandelia obovata*; Sa, *Sonneratia apetala*; Sc, *Sonneratia caseolaris*

ratio of *S. apetala* was lower than that of the native species except for *B. gymnorhiza*. *S. apetala* allocated more carbon to above-ground biomass, The ratio of the six mangrove forests ranged from 0.10 to 2.12, with an average of 0.83.

The changes in carbon storage of *S. apetala* in different age classes

The differences in the RGR of *S. apetala* between 13 and 14 year, 14 year and 19 year, 19 year and 21 year, and 21 year and 26 year were significant (Fig. 6). *S. apetala* showed a stable growth overall in the Reserve. We estimated carbon storage using the allometric equations of biomass and RGR. Carbon storage of *S. apetala* significantly increased with stand age and increased from 2017 to 2019 for each age class (Fig. 7). It is worth mentioning that carbon storage of *S. apetala* increased rapidly in the 19 year and 21 year age classes from 2017 to 2019. The carbon storage of *S. apetala* vegetation ranged from 96.48 to 215.35 Mg C ha<sup>-1</sup> in the reserve, with an average of 145.59 Mg C ha<sup>-1</sup>. The stand age effect on the above- and below-ground carbon storage was significant. The mean

carbon storage of *S. apetala* vegetation was 21.61 Mg C ha<sup>-1</sup> year<sup>-1</sup> across the five age classes.

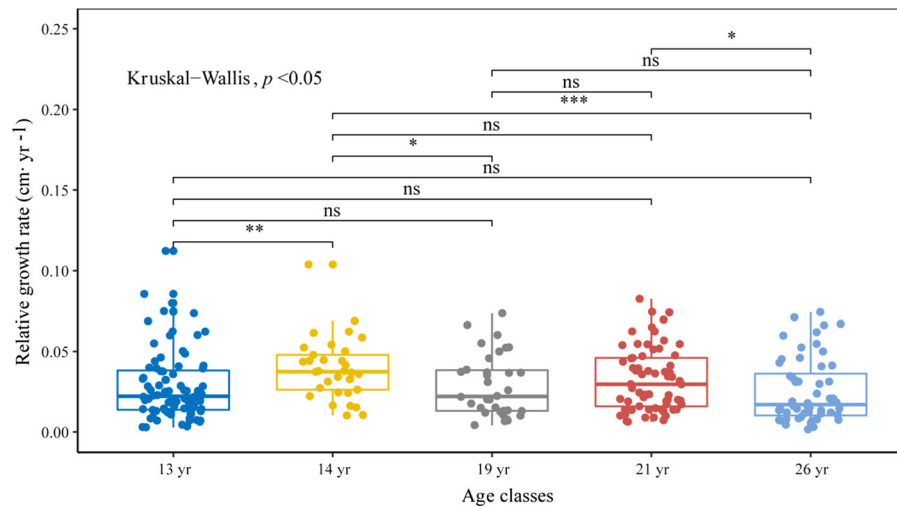
## Discussion

This study systematically analyzed the allometric growth and carbon storage of *S. apetala*, elucidated the underlying growth mechanism, and provided useful information pertaining to *S. apetala* plantations.

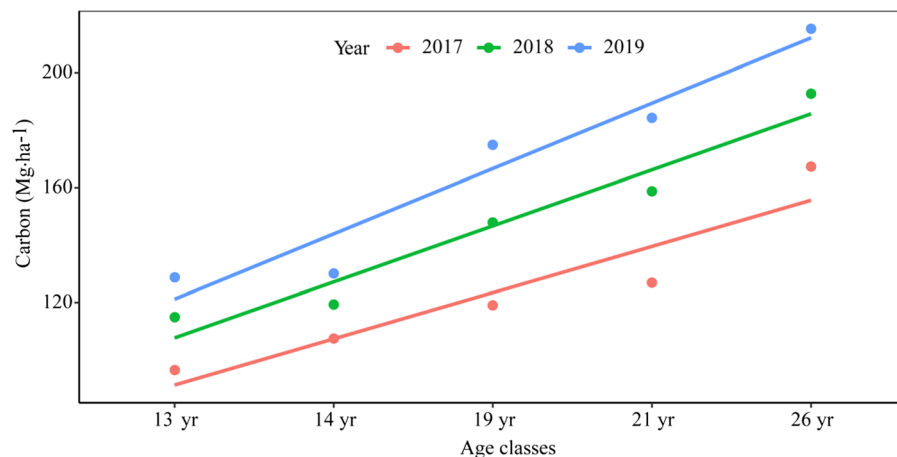
### Allometric growth of *S. apetala*

The allometric exponent (0.58) between the DBH and height of *S. apetala* supported the constant stress self-similarity model (Dean and Long 1986) and the elastic self-similarity model (McMahon 1973; Niklas and Enquist 2002a, b), explaining that *S. apetala* effectively transmitted the wind pressure downward in order to reduce mechanical damage. The taller the *S. apetala* trees, the larger their diameter, which conformed to the elastic self-similarity model (McMahon 1973). *S. apetala* can grow up to more than 19 m in the study area, which is similar to the height in the native





**Fig. 6** The relative growth rate on diameter at breast height of *Sonneratia apetala* in different age classes



**Fig. 7** Carbon storage of *Sonneratia apetala* vegetation in different age classes from 2017 to 2019. The lines represent significant regressions ( $p < 0.05$ )

area. This study showed that the pioneer species *S. apetala* has a strong adaptability to colonize new environments (Jayatissa et al. 2002; Ren et al. 2009). The average wood density of *S. apetala* is  $0.478 \text{ g/cm}^3$  in Shenzhen in China, which is slightly lower than  $0.52 \text{ g/cm}^3$  in India and  $0.537 \text{ g/cm}^3$  in South-East Asia (Chave et al. 2009; Zanne et al. 2009). Thus, a change in the wood density of *S. apetala* may have a limited influence on its biomass.

There were similar allometric exponents between the DBH and the biomass of the different components of *S. apetala*. The results indicated that the growth of *S. apetala* conformed to certain models. Stem biomass was the main biomass component of *S. apetala*, and

the proportion of stem to total biomass was higher than 97%. Interestingly, stem biomass was proportional to above-ground biomass, below-ground biomass, and total biomass and showed isometric relationships (Niklas 2004). A  $3/4$  power function was found between stem biomass and leaf biomass (Enquist and Niklas 2002; Niklas and Enquist 2002a, b), but the relationship between stem biomass and root biomass was isometric, which is consistent with our study.

We constructed allometric equations for *S. apetala* biomass using DBH and wood density. Wood density is an important trait indicative of mechanical and physiological properties (Swenson and Enquist 2007). Previous studies developed allometric equations with

DBH and wood density to determine the growth of mangroves (Chave et al. 2005; Komiyama et al. 2005). In this study, we found that Eq. (4) for the total biomass and above-ground biomass with DBH and wood density had a higher  $R^2$  and lower bias compared to other functions, indicating that Eq. (4) was the most suitable estimate of the total biomass and above-ground across different sizes of *S. apetala*. For the below-ground biomass of *S. apetala*, Eq. (5) was a better model for the estimation.

Several equations have been developed to estimate biomass for *S. apetala*. For example, Komiyama et al. (2005)'s model overestimated above-ground biomass and below-ground biomass, and Lunstrum and Chen (2014) reported an underestimate of above-ground biomass in this study, which was influenced by 6-year-old *S. apetala* forests. For the diameter class larger than 10 cm, the published equations (Chave et al. 2005, 2014; Ren et al. 2010; Lunstrum and Chen 2014) underestimated the above-ground biomass in this study. Based on a comparison of common equations of below-ground biomass, the estimation of Ren et al. (2010) produced the lowest below-ground biomass estimates, which might have been caused by regional environmental differences. The other equations basically overestimated the below-ground biomass (Komiyama et al. 2005; Lunstrum and Chen 2014). The different allometric equations with different estimates of biomass were affected by region, environmental conditions, and age.

#### Allocation of *S. apetala* biomass

The ratio of below-ground to above-ground biomass reflects the plant carbon allocation strategy (Wilson 1988). The ratio varied among different mangrove forests (Fig. 4). The average ratio of the mangrove forests was higher than that of upland forests (Cairns et al. 1997), indicating greater carbon allocation to below-ground biomass in the mangrove forests. The ratio of *S. apetala* was lower than that of other mangrove forests but still higher than that of the upland forests. The greater allocation to above-ground biomass by *S. apetala* was related to its biological characteristics of the greater height and DBH and strong colonization ability (Jayatissa et al. 2002; Ren et al. 2009; Peng et al. 2016b).

#### Carbon storage of *S. apetala*

In the Reserve, *S. apetala* still grow, further showed that it has strong adaptability. Mangrove ecosystems have a high carbon sequestration potential (Alongi 2012, 2014) and can be effective in mitigating climate change (Murdiyarso et al. 2015). In our study, we found that the average carbon storage of *S. apetala* plantations was 145.59 Mg C ha<sup>-1</sup>, which is equivalent to the average total carbon storage in a subtropical forest (Liu et al. 2018) and is consistent with a previous study (Li et al. 2019). Based on three years of field measurements, carbon storage of *S. apetala* vegetation significantly increased with stand age class. The carbon storage of *S. apetala* vegetation in Futian is comparable to that in other locations (Liu et al. 2014; Schile et al. 2017) but is higher than that of terrestrial forest ecosystems (Pregitzer and Euskirchen 2004; Donato et al. 2011; Alongi 2014) and other wetland ecosystems (McLeod et al. 2011; Migeot and Imbert 2012), and is lower than that reported for Micronesia and the Atlantic coast (Kauffman et al. 2011; Kauffman and Bhomia 2017). Previous studies reported that carbon stocks of live mangrove biomass ranged from 75.8 to 150.3 Mg ha<sup>-1</sup>, which was lower than our estimate of the *S. apetala* (Simard et al. 2019; Ouyang and Lee 2020). Mangrove ecosystem carbon storage had large variations. The reasons for the difference in carbon storage of mangrove forests include stand age, tree species, geographical environment, tree richness, and species diversity (Pregitzer and Euskirchen 2004; Kauffman et al. 2011; Kauffman and Bhomia 2017; Schile et al. 2017; Liu et al. 2018). Meanwhile, some studies found that external environment factors (e.g., upstream rivers and adjacent waters) contributed more to mangrove carbon storage than the production of the mangrove trees (Li et al. 2018). Carbon sink of *S. apetala* may be affected by the external environment. Overall, *S. apetala* is an ideal species that can improve mangrove restoration and carbon storage. For carbon sinks study of *S. apetala*, we also need to consider sediment organic carbon and dead biomass component due to their potential carbon storages (Ouyang and Lee 2020).

## Conclusions

In this study, we developed allometric relationships among DBH and height, wood density, and the biomass of the different components of *S. apetala*. Our results showed DBH and wood density were better predictors of *S. apetala* biomass. The average allometric exponent was 2.20 between DBH and biomass. Near-isometric scaling relationships were found among different components of biomass, which is supported by the growth-hydraulic model (Niklas 2004). Stem biomass accounted for more than 97% of the variation in total *S. apetala* biomass. The ratio of below- to above-ground biomass of *S. apetala* was lower than that of other mangroves and higher than that of upland forests. Mangrove forest ecosystems appear to store more carbon than terrestrial ecosystems and other wetland ecosystems, and the carbon storage of *S. apetala* vegetation increased with stand age. In this study, the allometric equations of *S. apetala* were developed for the Futian National Nature Reserve and applications to other regions need to be verified. The sample capacity of *S. apetala* was relatively small in this study. But nevertheless, our results showed that the restoration of mangrove forests will alleviate land degradation, mitigate climate change, and increase carbon storage over time.

**Acknowledgements** We thank Stuart Hamilton for his constructive revision that greatly improved the paper, and the Shenzhen Mangrove Wetlands Conservation Foundation (MCF) for help in the field works.

**Author contributions** DZ, SY designed the experiment; DZ, MW, QY, ZL, ZH, HY performed the field experiments; DZ analyzed data; DZ, SY, DH wrote and edited the manuscript.

**Funding** This study was financially supported by the National Natural Science Foundation of China (Grant 31770513), Shenzhen Science and Technology Innovation Committee (Project no. JCYJ20180504170040910), Urban Administration and Law Enforcement Bureau of Shenzhen Municipality (201802), and the Zhang-Hongda Science Foundation at Sun Yat-sen University.

**Data availability** The datasets generated during and/or analysed during the current study is available in the Appendix A.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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