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REGULAR ARTICLE

Appearance can be deceptive: shrubby native mangrove species contributes more to soil carbon sequestration than fast-growing exotic species

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Abstract
Background Increased recognition of mangrove high carbon storage potential has prompted carbon sequestration as one of the main goals in mangrove afforestation. In southern China, the introduced fast-growing *Sonneratia apetala* and native *Kandelia obovata* have been widely afforested since the mid-1980s. While *S. apetala* has spread extensively, the implications and ecosystem services are yet to be ascertained.
Methods Soil/root coring was conducted in two 12-year-old *S. apetala* and *K. obovata* plantations, respectively. Fine-root mass and soil physicochemical properties were obtained and compared.
Results Fine-root mass and soil organic carbon stock ranged between 129 and 394 g m^{-2} and 7.9 and 15.8 Mg C ha^{-1}, respectively. Soil organic carbon stock and fine-root mass were both significantly different between the forests. Organic carbon in soil is significantly correlated to fine-root mass and organic carbon in fine roots.
Conclusions The contribution to soil organic carbon by fine-root mass may be different between the two species. Growth and physiological traits not only may influence stand characteristics but also soil properties that drive overall carbon accumulation. Contrary to the original expectation driving the introduction, the shrubby native *K. obovata* may have higher potential as a carbon sink than the introduced *S. apetala*.

Keywords Mangrove afforestation · Carbon stocks · Fine-root biomass · Southern China · *Kandelia obovata* · *Sonneratia apetala*

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Introduction

Mangroves are highly productive and one of the most carbon-rich ecosystems in the world. Despite only occupying 0.5% of the global coastal area, mangrove forests account for 10–15% (24 Tg C y^{-1}) of the mean annual global coastal soil carbon storage (Collins et al. 2017; Duarte et al. 2013).

The majority of carbon in mangrove ecosystems is stored in the soil, as soil organic carbon decomposition is limited by generally anoxic conditions (Alongi 2009; Bouillon 2011; Chen et al. 2017a; Murdiyarso et al. 2015). Organic matter accumulation in mangrove ecosystems depends on autochthonous inputs from plant litter and roots in combination with allochthonous inputs from physical processes such as tidal transportation (Middleton and McKee 2001; Murdiyarso et al. 2015). On average, 58% of mangrove soil carbon is plant-derived, originating from litter and root production (Alongi 2014; Chen and Twilley 1999; Kristensen et al. 2008; Middleton and McKee 2001). As a major component of peat, roots have a more significant effect than litter on soil composition and vertical soil accretion (Alongi 2014; Chen and Twilley 1999; McKee 2011). Sustained favorable conditions for root production and organic matter accumulation therefore determine the long-term stability of carbon stock in mangrove ecosystems (Cahoon et al. 2003).

Coarse roots contribute more to total belowground biomass than fine roots (<2 mm in diameter) in terrestrial ecosystems (Eamus et al. 2002). However, fine roots may represent 66% of total roots biomass in mangrove ecosystems (Komiyama et al. 1987). Fine roots are important in water and essential nutrients acquisition and contribute significantly to biogeochemical cycling at the ecosystem level. All fine roots were assumed to contribute equally to soil carbon accumulation, and serve as the dominant pathways facilitating the transformation from aerial carbon to soil organic matter (Jackson et al. 1997).

Despite their crucial role in carbon sequestration (Jardine and Siikamäki 2014; Mcleod et al. 2011), mangrove forests have undergone an annual deforestation rate of 0.16%–0.39% since the 2000s (Alongi 2014; Hamilton and Casey 2016; Polidoro et al. 2010; Van Lavieren et al. 2012). To mitigate or reverse this trend, significant investments have been made in mangrove afforestation globally over the past several decades (Ellison 2000; Laffoley and Grimsditch 2009; Lunstrum and Chen 2014). Reforestation and afforestation have been found to significantly increase the soil carbon concentration and stock in mangrove ecosystem (Chen et al. 2017a; Feng et al. 2017; Ha et al. 2018; Lunstrum and Chen 2014).

Rapid coastal development in China has resulted in significant historical losses in mangrove coverage. The estimated mangrove area in 2015 was ~ 20,303 ha (Chen et al. 2017b), less than one-third of the historical extent (Li and Lee 1997; Ren et al. 2010). China has initiated many mangrove reforestation/afforestation projects since the 1980s (Li and Lee 1997). More than 2600 ha had been replanted by 2002 (Chen et al. 2009), and 2000 ha mangroves were planted annually during 2003–2007 (Ren et al. 2010). These large-scale efforts have resulted in a rebound of mangrove coverage, but the wider implications (e.g. for carbon sequestration and storage) of planting remain unclear. *Sonneratia apetala* Buch.-Ham. was introduced from Bangladesh to China in 1985, and has since become a popular species for mangrove afforestation programs due to its high adaptability and fast growth characteristics. Recent estimates suggest that *S. apetala* plantations cover 3800 ha in China, i.e. > 50% of total plantation area (Chen et al. 2009; Lu et al. 2014). Meanwhile, *Kandelia obovata* Sheue, H.Y. Liu & J. Yong, a native species mainly distributed along the coastline of southeastern China, has also been planted widely for mangrove afforestation. As *S. apetala* has recently invaded into many natural mangrove forests, the implications of its invasion for ecosystem function and services (e.g. competition with native species (Ren et al. 2009) and soil carbon stocks (Lunstrum and Chen 2014)) are of particular concern. Data on soil carbon storage by these two species would assist species selection in afforestation programs targeting the carbon sequestration function of mangrove ecosystems.

S. apetala forests have been reported to demonstrate higher soil carbon accumulation rates as well as higher belowground root biomass than most native species (Ren et al. 2010, 2008). Chen and Twilley (1999) suggested that soil carbon is correlated with tree biomass, particularly root biomass. As fine-root biomass contributes significantly to soil carbon accumulation (Lai et al. 2016; Xiong et al. 2017), it is therefore reasonable to hypothesize that fine-root biomass accumulation and soil carbon storage will be higher in *S. apetala* forests than those of native mangroves, therefore promoting the further use of this species in mangrove afforestation.

This benefit, however, should only be considered if native species such as *K. obovata* offer inferior capacity for this ecosystem service. The objectives of this study were to 1) quantify the fine-root biomass and carbon accumulation profile of *S. apetala* and *K. obovata* plantations of identical histories; 2) estimate soil carbon stocks between these two mangrove forest types and unvegetated tidal flats; and 3) assess the suitability of *S. apetala* for afforestation with respect to the ecosystem function of carbon storage.

Materials and methods

Study sites

Hanjiang River Estuary (23.45°N, 116.43°E), located in Chenghai District, Shantou City, Guangdong Province, southern China (Fig. 1) has an annual mean temperature of 21.3 °C (13.7 °C in January and 28.3 °C in July), with an average annual precipitation of 1672 mm. Tides in the study area are irregularly semi-diurnal, with an average range of about 1.35 m. In 2005, *K. obovata* and *S. apetala* plantations were established on the tidal flats with a soil texture of sand 4.7%, silt 88.2% and clay 7.1%, with similar tidal levels ranged 1.45–1.55 m. The seedlings were planted about 3 m apart. Monitoring flooding duration by binding cameras on PVC tubes inserted in the ground at the edge of *K. obovata* and *S. apetala* forests, indicating that the flooding duration were 10.3 h for *K. obovata* and 10.6 h for *S. apetala,* respectively. Such tidal regimes are suitable for the growth of *K. obovata* and *S. apetala* (Chen et al. 2004; Cheng et al. 2015; Ye et al. 2003).

Field sampling

Field sampling was conducted in November 2016. For the survey of forest structure, three 10 m × 10 m plots were randomly set up in *K. obovata* and *S. apetala* plantations, while retaining a buffer of >10 m. In each plot, the stem diameter at breast height (DBH), tree height (m), and tree density were measured and the basal area of the plots calculated. Aboveground and belowground biomass were estimated by the species-specific allometric equations shown in Table 1. (Ren et al. 2010; Tam et al. 1995).

Root coring was conducted in *K. obovata* and *S. apetala* plantations. Three standard trees were randomly selected in each plot for root coring in the plantations of each mangrove species. For each root core sample, one soil core (1 m depth, 11 cm diameter) was

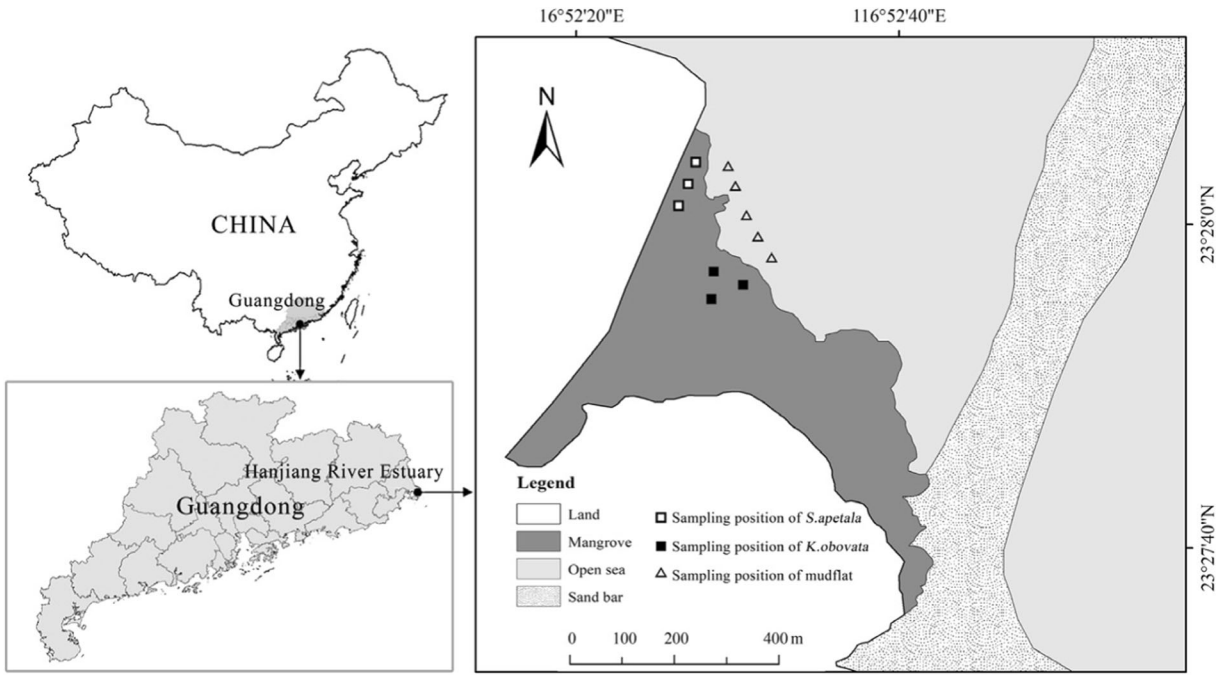

Fig. 1 Sketch showing the location of the sampling sites at Hanjiang River Estuary, Guangdong Province, southern China

Table 1 Allometric regression equations used to calculate the biomass of *Sonneratia apetala* and *Kandelia obovata*, respectively

Plantation	Biomass component	Allometric equation
S. apetala	Aboveground biomass	$Biomass = 0.280 \times (DBH^2 \times H)^{0.639}$
	Belowground biomass	$Biomass = 0.038 \times (DBH^2 \times H)^{0.759}$
K. obovata	Aboveground biomass	$Log(Biomass) = 2.814 + 1.053Log(DBH^2 \times H)$
	Belowground biomass	$Log(Biomass) = 2.433 + 0.990Log(DBH^2 \times H)$

taken from the middle position between trunk base and the vertical edge of canopy shade of each tree. Cores were divided into five vertical depth segments: 0–20, 20–40, 40–60, 60–80 and 80–100 cm. Three core segments of the same soil depth from each plot were pooled as a composite sample for subsequent root separation.

Soil sampling was carried out at the two mangrove plantations and the unvegetated mudflat nearby as comparison to compare the carbon sequestration effect of mangrove afforestation. For the repeated-measures data set, soil cores (1 m depth, 11 cm diameter) were randomly collected (five cores in *K. obovata* forest and mudflat, eight cores in *S. apetala* forest in accordance with their respective coverages) from each sampling site using PVC tubes. The cores were sectioned to 0–20, 20–40, 40–60, 60–80 and 80–100 cm layers.

Laboratory analysis

After root core sampling, the cores were washed over a 0.25 mm mesh sieve with tap water and fine roots (<2 mm in diameter) were sorted manually. Fine roots were then separated into live and dead fractions with 11 and 6% solutions of colloidal silica (Ludox® TM, Sigma-Aldrich Inc., USA) outlined by Robertson and Dixon (1993). The method relies on live fine root having lower specific gravity than dead fine roots that live roots float in the top and the dead roots material sinks to the bottom. After separation, fine roots were oven-dried at 65 °C to constant weight. Dry live fine-root samples were ground to fine powder and then analyzed by the loss on ignition method. In this method, organic matter was oxidized to carbon dioxide, water and ash at 550 °C during 4 h. Weight losses associated with water and carbon dioxide evolutions were quantified by recording sample weights before and after controlled heating (Ha et al. 2018; Heiri et al. 2001).

For soil analyses, each section of the soil samples was weighed and sliced vertically into two halves. One half of each section was oven-dried to constant weight at 65 °C to determine the water content and dry bulk density. The soil bulk density was obtained by the ratio of oven-dried mass per volume of wet sample taken by the volumetrically fixed PVC cores. The organic carbon mass was obtained by multiplying bulk density with the % soil organic carbon content (SOC). The other half of the soil sample was air-dried, some for soil texture measurement and the rest part of soil was ground to pass through a 250 μm sieve for pH, salinity and organic carbon content measurements. Soil texture (particle distribution among clay, silt and sand) was measured using a Malvern Mastersizer 3000 laser particle size analyzer (LPSA). Soil pH was measured with a 1:2.5 (*w*/*v*) ratio of soil to deionized water using a pH meter. Soil salinity was measured by YSI-ProPlus multiprobe sensor (YSI Incorporated, Ohio, USA) with a 1:5 (w/v) ration of soil to deionized water. Organic carbon content (measured in the % range) in soil was determined using modified Walkley - Black method (Ha et al. 2018; Schumacher 2002).

Data analysis

The data were analyzed by T-test, one-way, two-way ANOVAs and linear regression. For all tests, normality and homogeneity of variances were checked and data were transformed to meet the assumptions if necessary. Significance was determined at $\alpha = 0.05$ level. All statistical analyses were performed using SPSS 23.0 for Windows (SPSS Inc., USA).

T-test was used to compare the general structural features of the two mangrove forests and the total carbon stock in fine roots. A one-way ANOVA was used to compare the means of soil parameters among the two mangrove forests and the adjacent mudflat at different depths with habitat as a fixed factor. Live fine-root biomass and fine-root necromass within the two forests at different depths were also compared by two-way ANOVA. The difference of soil parameters and fine-root mass (live and necromass) among sites and soil

depths were compared by two-way ANOVAs, with soil depth and species/sites as fixed factors. Linear regression was used to explore mutual trends between soil bulk density, soil organic carbon density and fine-root biomass or necromass.

Results

Biomass and forest structure

Tree sizes of the two forests differed substantially, with an average height of 4.8 m for *K. obovata* and 8.5 m for *S. apetala*, respectively. The average DBH of *K. obovata* was 8.8 cm, which 60.7% of *S. apetala* (Table 2). Although the two forests were planted with the same initial density of 0.25 trees m^{-2}, the stem density of *K. obovata* forest was 7 times higher than that of *S. apetala* forest by 2016. Despite the *S. apetala* trees were much taller and larger, their aboveground and belowground biomass were both significantly lower than those of *K. obovata* ($p < 0.001$, Table 2).

Live fine-root biomass and fine-root necromass distributional patterns and organic carbon stock in fine-root

In the *S. apetala* forest, distribution of live fine-root biomass was concentrated in the upper 60 cm soil layer, which accounted for 63.4% of the total live fine-root biomass. And live fine-root biomass was significant different between soil depths ($p < 0.001$, Fig. 2a). Similarly, fine-root necromass in the *S. apetala* forest was significantly different among the different soil depths, overall decreasing with soil depth ($p < 0.001$, Fig. 2b). The distribution of live fine-root biomass in the *K. obovata* forest has a similar pattern – biomass was negatively correlated with soil depth ($p < 0.001$, Fig. 2a). The fine-root necromass of this species showed a similar distributional pattern in depth as that of fine-root biomass ($p < 0.01$, Fig. 2b).

The live fine-root biomass of *S. apetala* and *K. obovata* were 22.8 ± 8.9 and 84.89 ± 14.14 g m^{-2}, respectively. There are significant differences both between species and soil depths ($p < 0.001$; Fig. 2a and Table 3). Species and soil depth likewise had a significant interaction effect on the live fine-root biomass of *S. apetala* and *K. obovata* ($p < 0.001$; Fig. 2a and Table 3). 72% of live fine roots of *K. obovata* were found at the 0–40 cm depth interval, while the proportion of live fine roots of *S. apetala* at the same depth interval was 65%. There were significant differences between species and soil depths ($p < 0.001$; Fig. 2b, and Table 3). There was a significant interaction between species and soil depth on the overall fine-root necromass of both *S. apetala* (~ 82% of total fine-root biomass) and *K. obovata* (~ 78% of total fine-root biomass) was also detected ($p < 0.001$; Fig. 2b and Table 3). In the 0–40 cm depth layer, the fine-root necromass of *K. obovata* accounted for ~ 85% of total fine-root necromass while the proportion of fine roots of *S. apetala* at the same depth was 64%. The overall fine-root necromass of *K. obovata* was significant higher than that of *S. apetala* in all soil intervals ($p < 0.001$, Fig. 2b, Table 3). The live fine-root biomass and fine-root necromass per unit stem of *S. apetala* were both significant higher than those of *K. obovata* in the upper 80 cm soil layer (($p < 0.001$). Species and soil depth had significant interaction effects on fine-root necromass, while soil depth showed a significant effect on live fine-root biomass of these two species ($p < 0.001$; Fig. 2c, d and Table 3).

The mean fine-root organic carbon concentration of *S. apetala* and *K. obovata* were 32.8 and 50.48%, respectively. The organic carbon stock in fine roots of *K. obovata* up to 1 m depth was 198.8 ± 10.3 Mg C ha^{-1} and significant higher than that of *S. apetala* (42.4 ± 1.7 Mg C ha^{-1}).

Table 2 The general structural features of the two mangrove forests surveyed in Hanjiang River Estuary

Plantation	Density (trees ha^{-1})	DBH (cm)	Tree height (m)	Basal area (cm^2 $tree^{-1}$)	Aboveground biomass (t ha^{-1})	Belowground biomass (t ha^{-1})
S. apetala	1366.7 ± 145.3^a	14.5 ± 0.9^a	8.5 ± 0.3^a	190.0 ± 26.0^a	68.7 ± 10.7^a	15.3 ± 2.5^a
K. obovata	9533.3 ± 627^b	8.8 ± 0.3^b	4.8 ± 0.07^b	65.8 ± 4.7^b	187.2 ± 31.6^b	95.7 ± 15.6^b

Data are mean ± SE, $n = 3$. Different letters indicate significant differences between the two species. ($p < 0.05$). SE represents standard error

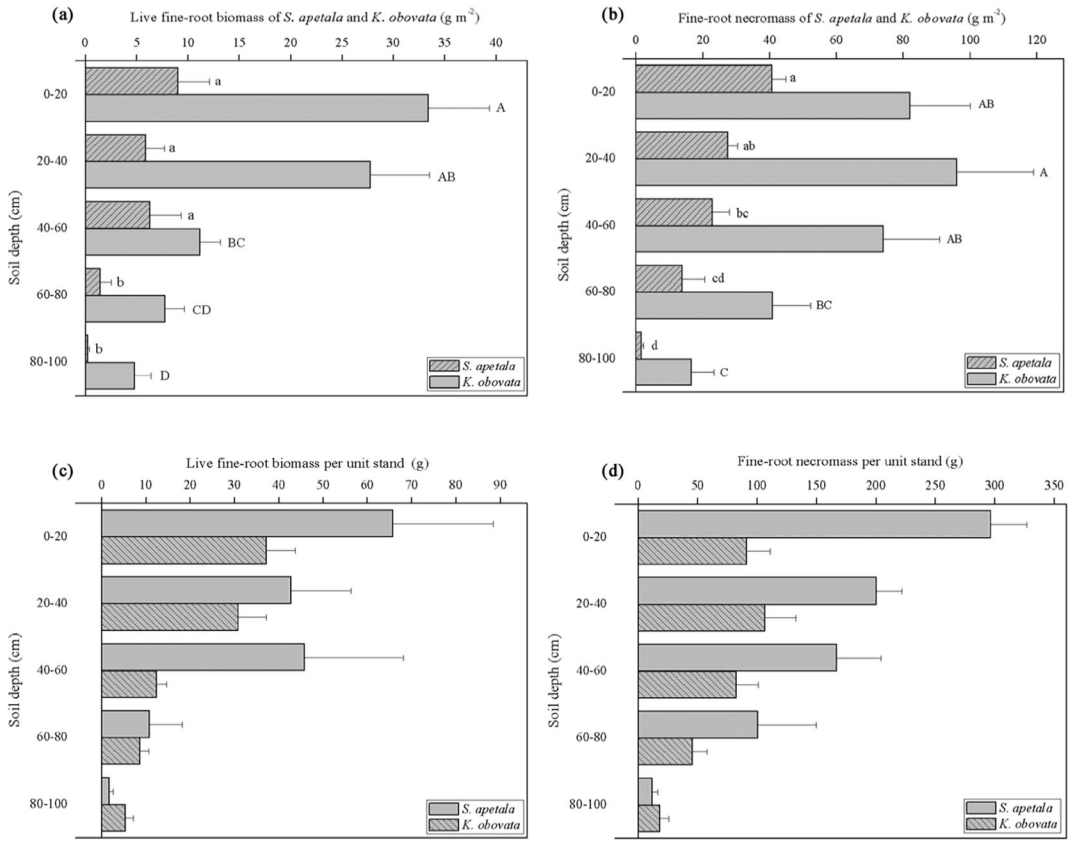

Fig. 2 Vertical distributional patterns of live fine-root biomass **(a)**, fine-root necromass **(b)**, live fine-root biomass **(c)** and fine-root necromass **(d)** per unit stand (mean ± 1SE) in *S. apetala*and and *K. obovata* forests at Hanjiang River Estuary, south China. Different letters indicate significant differences among the different soil depths. ($p < 0.05$)

Table 3 *F* values of two-way ANOVA testing the differences in live fine-root biomass, fine-root necromass and soil variables among different mangrove species/ sites and soil depth in Hanjiang River Estuary, south China

Dependent variables	Sources of variance		
	Species/Sites	Soil depth	Species/Sites × Soil depth
Live fine-root biomass (g m^{-2})	40.147**	16.345**	1.828**
Fine-root necromass (g m^{-2})	14.328**	12.402**	0.738**
Live fine-root biomass per unit stand (g)	0.019	16.345**	1.828
Fine-root necromass per unit stand (g)	32.395**	16.953**	5.179**
Soil pH	9.975**	1.883	1.764
Soil salinity (ppt)	68.574**	12.266**	0.893
Soil clay content (%)	4.623*	1.672	0.847
Soil bulk density (g cm^3)	24.07**	2.055	1.273
Soil organic carbon concentration (%)	74.379**	11.744**	1.538
Soil organic carbon stock (Mg C ha^{-1})	86.923**	19.669**	1.961
Soil organic carbon stock per unit stand (Mg C)	66.456**	9.924**	7.795**

* significance at $p < 0.05$ ($n = 75$ to 85)

** significance at $p < 0.001$ ($n = 75$ to 85)

Soil physicochemical properties and their vertical distribution patterns

K. obovata and *S. apetala* forest had higher clay content than that of mudflat (Fig. S1). Soil salinity was highest in *K. obovata* forest, followed by *S. apetala* forest, and lowest in mudflat soils (Fig. 3a). Conversely, the mean value of soil pH was highest in mudflat, and pH in *S. apetala*, *K. obovata* forest soil tended to increase by soil depth (Fig. 3b).

Soil bulk density (SBD) tended to increase by depth (Fig. 3c). The mean SBD for the entire 1 m soil column were 0.45 ± 0.03, 0.89 ± 0.04 and 0.94 ± 0.08 g·cm^{-3} in the *K. obovata* forest, *S. apetala* forest and mudflat, respectively, with a significant difference in SBD among the sites ($p < 0.001$; Table 3). The mean soil organic carbon (SOC) concentration (0–100 cm) of *S. apetala* (0.96%) and *K. obovata* (3.30%) forests were, respectively, about 1.8 and 6 times higher than that of the mudflat (0.55%). The SOC concentration significantly decreased with depth for *K. obovata* and *S. apetala* forest but no significant trend is evident for the mudflat (Fig. 3d). SOC concentration was, however, significant different across the sites ($p < 0.001$; Table 3). The mean organic carbon stock in soil of the *K. obovata* forest was15.81 ± 0.77 Mg C ha^{-1}, about 2.01 and 3.35 times higher than those of *S. apetala* and mudflat, respectively. There is also a significant difference in soil organic carbon density among the sites ($p < 0.001$; Table 3), with a significant effect between soil depth ($p < 0.001$; Table 3). Significant difference in soil organic carbon density per unit stem between species and soil depth, respectively, with a significant interaction effect between species and soil depth were detected ($p < 0.001$; Table 3).

Fine-root mass and organic carbon in fine-root in relation to soil organic carbon accumulation

Soil organic carbon density in both the *K. obovata* and *S. apetala* forests was positively correlated to live fine-root biomass and fine-root necromass ($p < 0.001$; Fig. S2). Similarly, in both the *K. obovata* and *S. apetala* forests, a significant positive correlation was found between organic carbon in fine roots and in soil (Fig. 4). Generally, organic carbon in *K. obovata* forest soil was significantly higher than that of *S. apetala* forest as the same profile exhibited by live fine-root biomass and fine-root necromass, suggesting a higher fine-root biomass contribution to soil organic carbon enrichment in *K. obovata* ($p < 0.001$).

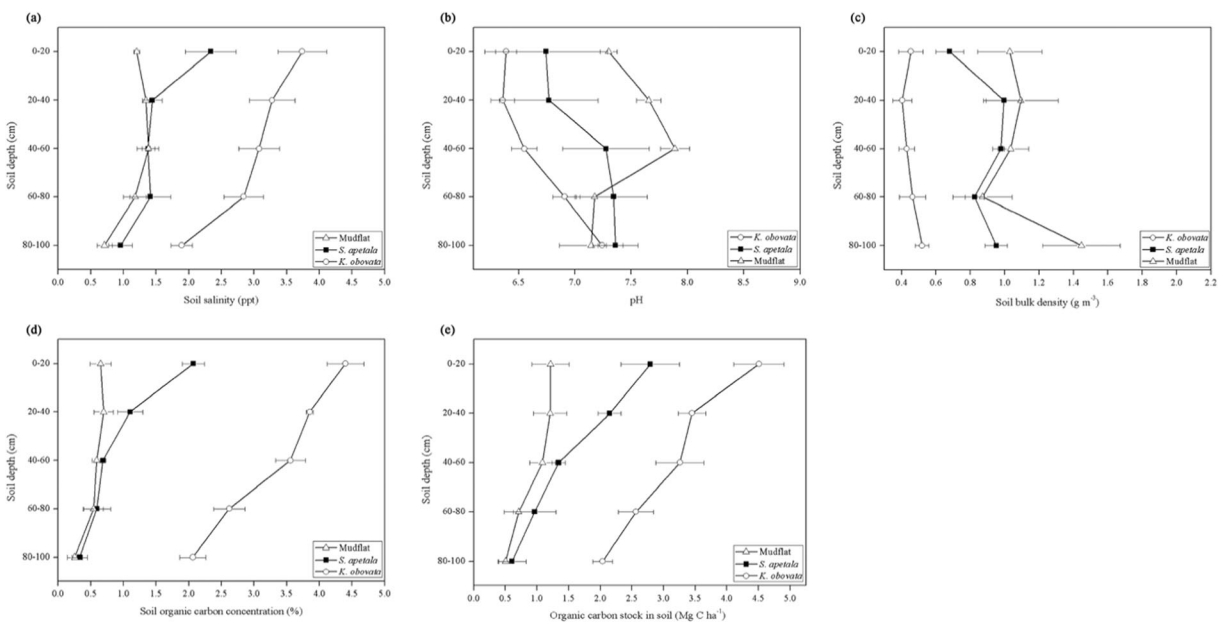

Fig. 3 The soil physicochemical properties and their vertical distribution for the three sites at Hanjiang River Estuary, south China. Error bars represent 1SE ($n = 5$ to 8)

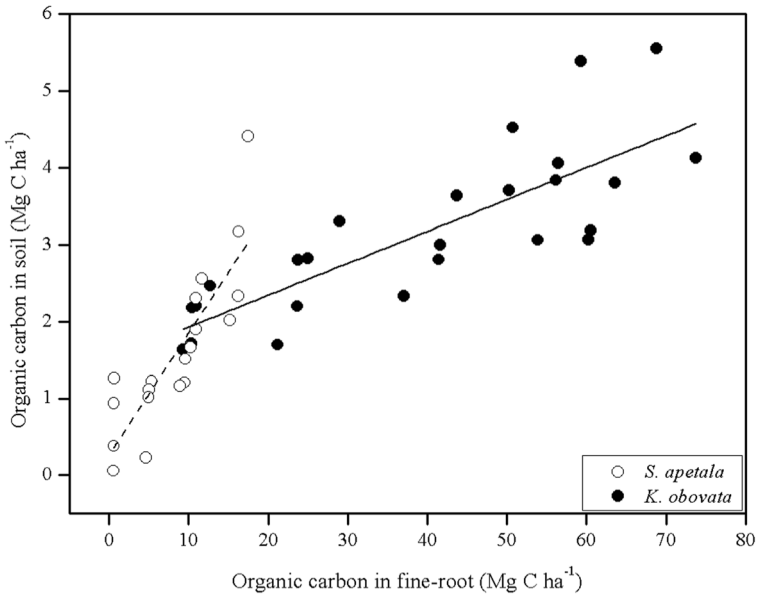

Fig. 4 Regression analysis between organic carbon in soil and in fine roots for *S. apetala* and *K. obovata* forests in Hanjiang River Estuary, south China. Linear best fits for: *S. apetala* (dashed line, $y = 0.158\times + 0.267$, $r^2 = 0.721$, $p < 0.001$); *K. obovata* (solid line, $y = 15.953\times$-10.716, $r^2 = 0.647$, $p < 0.001$)

Discussion

Vertical distribution of live fine-root biomass and fine-root necromass

Data obtained in the present study are in accordance with earlier reports that higher live fine-root biomass is found in the upper layers of soil in mangrove forests (Claus and George 2005; Ha et al. 2018; Komiyama et al. 2000; Tamooh et al. 2008; Xiong et al. 2017). In mangroves, concentrated development of live fine-root biomass in the upper soil layer may be a physiological adaption to promote uptake of water and nutrients effectively in the periodically inundated hypoxic environment. This soil layer is characterized by high organic matter accumulation and relatively higher nutrient availability, as in terrestrial forests (Claus and George 2005; Tamooh et al. 2008). Notwithstanding, the profile of live fine-root biomass per tree varied between the two mangrove species may be attributed to their morphological differentiation. The native and shrubby *K. obovata* mostly only reach half of the height of the introduced *S. apetala* in height on average, and the mean value of basal area per tree of *K. obovata* was significant lower than that of *S. apetala*. Therefore, the live fine roots of *K. obovata* being concentrated at more superficial soil layers compared with *S. apetala* is consistent with its smaller aboveground growth, which requires less investment in anchorage in the unstable substrate. In addition, the lack of pneumatophores may require *K. obovata* to develop more superficial fine roots to enhance gas exchange and nutrient uptake in the anoxic soils. Flooded conditions have been reported to impede the fine-root growth of *K. obovata* (Chen et al. 2004). In contrast, pneumatophore development in *S. apetala* helps reduce stress from anoxia, potentially allowing supportive as well as absorptive roots to penetrate deeper soil layers. Mangrove species that develop pneumatophores (e.g. *Avicennia* spp.) are long known to improve soil aeration compared to those without (e.g. *Rhizophora* spp.), resulting in significant differences in the degree of anoxia (e.g. reflected by sulphide concentrations, Hesse 1961). This difference in anoxia may translate to differences in organic matter decomposition and C accumulation capacity, which corroborates with results detected in the present study. The generality of this pattern, however, needs to be substantiated with more comparisons between the two groups of species.

The notion that most of the fine-root biomass accumulated in mangrove soils are dead was based on data on *Rhizophora* and *Avicennia* species (Alongi et al. 2000; Alongi and Dixon 2000; Alongi et al. 2003). This pattern also applies to *S. apetala* and *K. obovata* in the current study, with dead fine roots representing 78%–82% of the total fine-root biomass in both species. The high proportion of fine roots being necromass, which is generally refractory, suggests that this component of mangrove production may act as long-term storages of

carbon. However, to what extent is contribution is species-specific requires data from a wider range of species and growth conditions.

Fine-root contribution to carbon accumulation in soil

Higher soil pH in the *S. apetala* forest may reflect its faster decomposition of organic matter and fine root debris compared with *K. obovata* (unpublished data). Fine roots likewise mediate an array of ecosystem processes including cycling and storage of water (Iversen et al. 2017). When fine roots take up water from the saturated soil, 90%–99% of salt is excluded by roots and diffuse the salt back to the soil (Passioura et al. 1992; Moon et al. 1986). Soil salinity differed between *S. apetala* and *K. obovata* may reflect their physiological preferences for the way in which water-use efficiency related to growth.

The soil bulk density (SBD) in the two mangrove forests was lower than that of the adjacent mudflat, while clay content in soil in these two mangrove forests was higher than mudflat. This may be due to the development of mangrove roots and soil organic matter enrichment that led to more porous and less compact substrate (Grellier et al. 2017; Ha et al. 2018). Organic matter in mangrove forests including fine roots also enhance particle aggregation and soil cohesion (Grellier et al. 2017). There is a significant positive correlation between the distributional patterns of live fine-root biomass, fine-root necromass and organic carbon in soil among the different soil layers. Fine roots contributed 37 to 81% of total belowground root biomass in the study sites, which is much higher than the 0.2 to 17.9% reported from terrestrial forests (Komiyama et al. 2000, 1987). This reaffirms that fine roots are a primary contributor to total belowground root biomass in mangroves (Tamooh et al. 2008), and a significant source of soil C in mangrove ecosystems (Ouyang et al. 2017). The much higher live fine-root biomass in mangroves may be due to a combination of high live fine-root productivity, low mortality rate, and high turnover (Huxham et al. 2010; Tamooh et al. 2008), which may help the trees survive in an environment characterized by high energy demand but low nutrient availability. The higher fine-root productivity may also be the consequence of a higher belowground carbon allocation. For belowground carbon accumulation, the rate of root production must exceed that of carbon loss (Middleton and McKee 2001). Root decomposition rate is a key determinant (Gleason and Ewel 2002; Tamooh et al. 2008), which is primarily driven by soil salinity, rainfall, latitude and mangrove forest types (e.g. riverine vs other mangroves) (Ouyang et al. 2017). The decomposition rate of fine roots in mangrove forests was much lower than the average for terrestrial forests at similar latitudes (Albright 1976; McKee et al. 2007; McKee and Faulkner 2000; Middleton and McKee 2001; Silver and Miya 2001; Van der Valk and Attiwill 1984). Hence, the large amount of undecomposed fine-root necromass may reflect the low decomposition rate that contribute to the high organic matter accumulation. The vertical distribution of the dead fine roots reflect also the recalcitrant nature of fine roots, making them significant long-term C storages (Tamooh et al. 2008). Organic carbon in fine roots of *S. apetala* and *K. obovata* were not only varied with depth but also with mangrove species. Significant correlation between organic carbon in fine roots and in soil was also detected, suggesting that fine roots have a high contribution to soil organic carbon accumulation.

Implication for carbon-based mangrove afforestation

There were significant differences in live fine-root biomass and fine-root necromass found between these two forests as well as a significant difference was detected for organic carbon in soil. Without the effect of stand density of these two forests, fine-root mass per tree of *S. apetala* was significant higher than those of *K. obovata*, and a similar result was detected in soil organic carbon stock per tree. However, due to its intolerance to canopy shade and fast growth characteristics, the *S. apetala* forest was featured with lower tree density, and might not have a high live fine-root biomass, fine-root necromass and soil carbon stock per unit as *K. obovata* forest does. The difference in stem density of forests of the same age suggest there is a difference in the self-thinning pattern of *S. apetala* and *K. obovata*, with the former species demonstrating much more significant self-thinning due to its intolerance to shade. Under the effect of stem density in the forest, *K. obovata* may have higher fine-root productivity compared to that of *S. apetala*. The balance between productivity and decomposition of fine roots in the anoxic soil environment strongly determines the carbon sequestration and storage potential of mangrove ecosystems. The data obtained in the present study suggest *K. obovata* has a higher potential than *S. apetala* for

belowground carbon sequestration and storage, which is opposite to the pattern of vegetation carbon stocks estimated based on only above-ground and coarse root biomass using allometric equations (Wang et al. 2013, 2017).

The absence of a shrub layer in mangrove forests has been attributed to the combined stresses of light limitation under dense canopies and the saline environment (Janzen 1985). Multi-canopy mangrove vegetation may, however, be established naturally or artificially with shade-tolerant species (Hogarth 2015). In the subtropics, tall introduced *S. apetala* can coexist with some shrubby native species (e.g. *K. obovata*, *Aegiceras corniculatum* (L.) Blanco and *Bruguiera gymnhoriza* (L.) Poir.) in mixed stands by partitioning vertical niches in the aboveground space (Peng et al. 2016). Similar niche differentiation in the belowground space may also exist between root systems of different species, such as the two species in this study. Contrary to simple above-ground, individual-based appearances and assessments, the native *K. obovata* is preferred to the fast growing introduced *S. apetala* as a species for afforestation for its higher fine-root biomass and larger contribution to soil carbon density at the forest scale, especially for restoration programmes with carbon sequestration as the primary objective.

Conclusion

The live fine-root biomass, fine-root necromass, organic carbon in fine roots and soil carbon stock of 12-year mangrove plantations respectively dominated by the introduced *S. apetala* and native *K. obovata* suggest different potential for belowground carbon sequestration and storage. Contrary to expectation based on individual tree growth, the shrubby native *K. obovata* forest supported higher live fine-root biomass and fine-root necromass than the fast-growing introduced *S. apetala* forest. For the two mangrove species, most of the fine roots concentrated in the upper 60 cm of sediment, with detailed vertical distribution reflecting their morphological and physiological traits (e.g. presence/absence of pneumatophores, and the consequence for soil oxygen availability). A significant linear relationship exists between soil organic carbon and live, dead fine-root biomass as well as organic carbon in fine roots, suggesting that fine roots play an important role in carbon sequestration and storage in mangroves. The overall soil organic carbon stock in the *K. obovata* forest was significantly higher than that of *S. apetala*. Thus, *K. obovata* is preferred to *S. apetala* for soil carbon sequestration and storage in mangrove restoration programmes. As *S. apetala* can coexist with some shrubby native species, introduce shrubby native species (e.g. *K. obovata*) to *S. apetala* plantations establish mixed communities should be recommendable for improving organic carbon stock in the existing *S. apetala* plantations.

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