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Monoculture or Mixed Culture? Relevance of Fine Root Dynamics to Carbon Sequestration Oriented Mangrove Afforestation and Restoration

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Fine root dynamics have the potential to contribute to ecosystem biogeochemical cycling, especially for carbon. This is particularly true in mangroves which are the most productive and carbon-rich ecosystems of the world. However, few studies comprehensively evaluated the contribution of mangrove fine root dynamics to soil organic carbon accumulation. In southern China, while the introduced fast-growing *Sonneratia apetala* and native shrubby *Kandelia obovata* have been widely used in mangrove reforestation/afforestation programs since the mid-1980s, their implications and ecosystem services are still unclear. Here we show distinct differences in fine root dynamic among 12-year-old *S. apetala*, *K. obovata* monocultures, and their mixed stand using root coring, ingrowth core, and intact-core methods. Soil organic carbon storage was examined by soil coring method. One-year observation showed significant differences among the three mangrove plantations in fine root biomass, necromass, turnover rate, and decomposition decay rate constant. Soil organic carbon stock was 15.8 ± 0.8, 7.8 ± 0.5, and 11.9 ± 1.6 Mg C ha^{-1} for *K. obovata*, *S. apetala* monocultures and their mixed stand, respectively. Live fine root biomass, fine root necromass, annual fine root production and fine root mass decay rate constant are significantly correlated to soil organic carbon content across plantations. We suggest that mangrove fine root dynamics were mainly affected by soil nutrient conditions and species composition. Mixed stands may not have higher soil organic carbon storage than monocultures. The functional trait of different mangrove species is responsible to determine the carbon storage function of mixed stands. Fine roots play an important role in carbon storage, and fine root dynamics have a significant effect on carbon sequestration in mangrove ecosystems. The shrubby native *K. obovata* had a higher potential for belowground carbon sequestration and storage than the tall introduced *S. apetala*.

Keywords: fine root dynamics, mangrove, monoculture, mixed plantation, organic carbon storage

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INTRODUCTION

Fine roots (<2 mm in diameter) are the most physiologically active component of the belowground plant biomass involved in resource acquisition, nutrient exchange and organic matter decomposition (Iversen et al., 2017). Fine roots account for 10–30% of total forest tree biomass and 30–50% of total net primary production in global terrestrial ecosystem (Castañeda-Moya et al., 2011; McCormack et al., 2015b). Consequently, fine root turnover represents a major pathway for carbon and nutrient fluxes from plants to soil (Dornbush et al., 2002). While inhabiting a relatively steady environment compared to their aboveground counterparts, fine roots dynamics are still influenced by internal and external moderators, e.g., the intensity of intraspecific competition (Wang D. et al., 2019), seasonal variation of temperature and precipitation (Ibrahim et al., 2020; Sun et al., 2020), nutrient availability (Wang W. J. et al., 2019), or species composition in the community (Caplan et al., 2019). These complex feedbacks pose significant challenges to understanding fine root dynamics and their implications for key ecosystem processes.

Mangrove ecosystems are among the most productive and ecologically important ecosystems of the world (Li et al., 2019). Mangroves are vital blue carbon resource, with their soil carbon comprising more than 50% of the total C stock within the system (Adame et al., 2017). Mangrove plants are capable of allocating higher proportions of their total biomass to belowground roots in response to nutrient limitation and anoxic condition (Castañeda-Moya et al., 2011). Recent studies suggested that mangrove fine roots have a higher contribution to soil C than that of litterfall, and the positive effect on soil C accretion is attributable mainly to fine root production (Poungparn et al., 2016; Liu et al., 2017; Xiong et al., 2017). Yet, few studies comprehensively evaluated the contribution of mangrove fine root dynamics to soil organic carbon accumulation.

In southern China, the introduced *Sonneratia apetala* Buch.-Ham. and native *Kandelia obovata* Sheue, H.Y. Liu & J. Yong have been widely used in many mangrove afforestation programs for almost three decades. *S. apetala* is a tall and fast-growing species, whereas *K. obovata* is a shrubby species that commonly forms forests with higher tree densities (He et al., 2018). More attention on the ecosystem services derivable from such afforestation programs, e.g., carbon sequestration, has been supposed for an improved approach to global mangrove restoration (Lee et al., 2019). *S. apetala* forests have been reported to demonstrate much higher soil carbon accumulation rates as well as higher belowground root biomass than those of the native species (Ren et al., 2009, 2010). However, studies of biomass and carbon allocation in tropical and subtropical mangrove ecosystems suggest that shrubby forests allocate relatively more biomass or carbon to roots than do tall mangroves under unfavorable environmental conditions (Lovelock, 2008; Castañeda-Moya et al., 2011, 2013). In addition, Chen et al. (2012) reported that mixed mangrove plantations had higher soil carbon accumulation than the monocultures. Therefore, how soil carbon storage may differ based on contrasting morphological and functional traits of these two species, as well as the community setting, e.g., monocultures versus mixed plantation, would have significant implications for species selection and habitat management in carbon-based mangrove afforestation programs. In this study, we investigated the fine root dynamics of *S. apetala* and *K. obovata* monocultures as well as mixed stands of both species. The linkage between their fine root dynamics and soil organic carbon sequestration was also explored to provide insights into the mechanism of fine root contribution to soil organic carbon accumulation. We hypothesized that fine root dynamics is dependent on plant trait and therefore affects soil C accumulation. To test these hypotheses, the present study examined (1) live fine root biomass and fine root necromass distribution, fine root productivity, turnover rate, and decomposition in *S. apetala* and *K. obovata* monocultures, and their mixed stands; (2) soil organic carbon stock profiles among these three mangrove plantations and unvegetated tidal flats; and (3) the effects of fine root dynamics on soil organic carbon accumulation.

MATERIALS AND METHODS

Study Sites

The study site was located in Hanjiang River Estuary of Chenghai District, Shantou City, Guangdong Province of China (23.45° N, 116.88° E) (**Figure 1**). The area is characterized by a subtropical monsoon climate, with 1,672 mm of annual precipitation, mostly between April and September. The seasonal mean air temperatures are: 21.0°C in spring (March–May), 28.3°C in summer (June–August), 23.7°C in autumn (September-November) and 15.2°C in winter (December–February), respectively. Tides are irregularly semi-diurnal with an range from 0.37 to 2.40 m. In 2005, two monospecific stands respectively dominated by *K. obovata* and *S. apetala* were established on the muddy tidal flats (4.7% sand, 88.2% silt, and 7.1% clay) at similar tidal elevation of 1.45–1.55 m. Every seedling was planted about 3 m apart. After 12 years, the of *K. obovata* (KO) and *S. apetala* (SA) monocultures experienced natural self-thinning process with different stem density, tree height and basal area per tree (He et al., 2020). Seedlings of *K. obovata* had also naturally colonized into stands of *S. apetala* and developed an understory shrub layer along the border of monospecific plantations, and finally became a mixed stand with both *S. apetala* and *K. obovata* (SK), with a density of 2,600 stems ha^{-1}. The average daily flooding period of these plantations is 10.3 h, which is suitable for the growth of both species (Ye et al., 2003; Chen et al., 2004; Cheng et al., 2015).

Measurement on Fine Root Biomass and Necromass

Fine roots biomass and necromass were determined by the root coring method (He et al., 2018, 2020). Four plots of 10 m × 10 m (>10 m apart from each other) were randomly established at each plantation in each season over a year: October (autumn) of 2016, January (winter), April (spring) and July (summer) of 2017. The same sampling protocols were applied to all plots. At each sampling time, three standard trees were randomly selected in

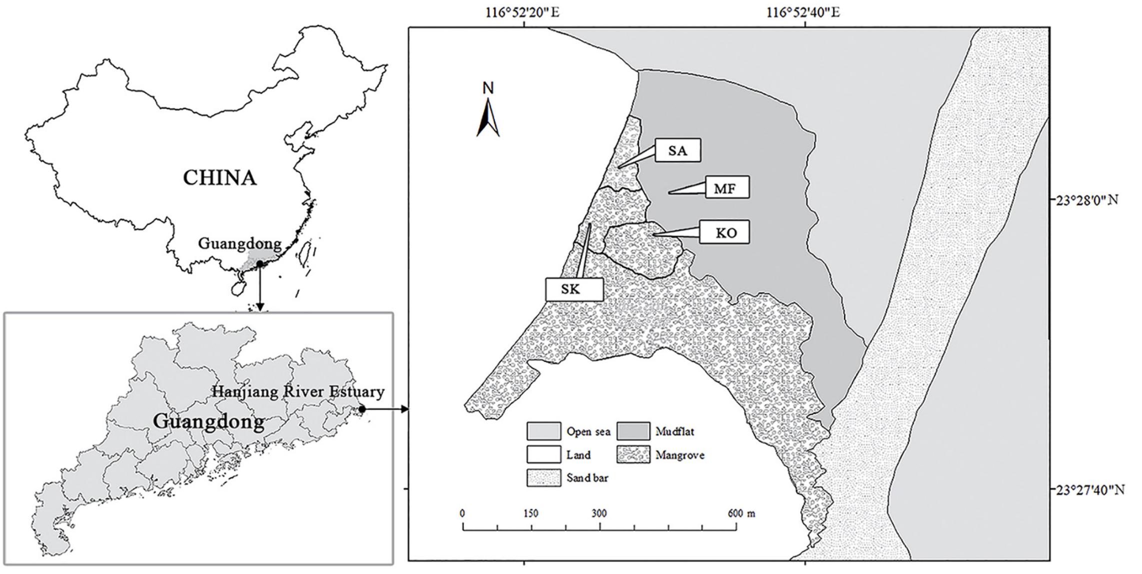

FIGURE 1 | Locality of the study mangrove forests at Hanjiang River Estuary, Guangdong Province, southern China.

each plot. One soil core (11 cm diameter × 1 m depth) was taken from the central position under the canopy of each standard tree selected. Then, each soil core was sectioned into five vertical segments (0–20, 20–40, 40–60, 60–80 and 80–100 cm depth). Three core segments of the same soil depth from each plot were pooled into a composite sample for subsequent root separation. In total, 45 samples were collected at each sampling time.

In the laboratory, the cores were washed over a 0.25 mm mesh sieve with tap water and roots over 2 mm in diameter were discarded. The remaining fine roots were then separated into live and dead fractions with 11 and 6% colloidal silica (Ludox TM, Sigma-Aldrich Inc., United States), following Robertson and Dixon (1993). Live fine roots would float on the top and dead fine roots sink to the bottom of the colloidal silica, as live fine roots have lower specific gravity than dead fine roots. The separated fine roots were then oven-dried at 65°C to a constant weight.

Measurement on Fine Root Production and Turnover Rate

Fine root production was estimated using the ingrowth core method (Poungparn et al., 2016). In early December 2016, a total of 36 ingrowths soil cores were vertically inserted into the forest substrate (3 replicates × 4 collection times × 4 plots per plantation) to 1 m depth until the top end of the core was level with the substrate surface. Each ingrowth cores composed of five sub-cores (11 cm diameter × 20 cm length) constructed by nylon mesh bags (1 cm pore size), and were completely filled with root-free soil collected from the adjacent unvegetated mudflat after sieving through a nylon mesh to ensure it was entirely root-free. Then every five cores were strung together onto a nylon rope to form a 1-m long ingrowth core. The ingrowth cores were retrieved after 90 (March 2017), 180 (June 2017), 270 (September 2017), and 360 (December 2017) days, respectively, and three cores were collected from each plot at each harvest time. The roots from the ingrowth cores were washed over a 0.25 mm sieve with tap water and were sorted into live and dead roots and oven-dried according to the methods mentioned previously.

Measurement on Fine Root Decomposition

Fine root decomposition was measured using an intact-core method that closely mimics in situ fine roots decay conditions (Dornbush et al., 2002). Since cores were sampled from field soil and maintained as intact units, the initial mass of fine roots within the cores was unknown. Hence, the mass loss estimated from the intact cores were estimated based on change in population means through time, but not change in individual samples. This approach required sufficient replicate cores to accurately quantify the mean fine roots mass at each sampling time. The number of cores required was determined prior to the experiment. For this purpose, initial sampling was conducted in the mangrove forest in early December 2016, with the coefficient of variation demonstrating no apparent decline after 11 samples. Therefore, this sample size was applied to the plantations in fine root decomposition experiment.

Based on the result of the pilot sample size experiment, eleven standard trees were randomly selected for root coring within each plantation in early March 2017. Four root cores (11 cm diameter × 1 m depth) were taken from the middle position under the canopy of each tree. Cores were vertically divided into five 20-cm segments: 0–20, 20–40, 40–60, 60–80, and 80–100 cm. For each core, segments were put in 0.1 mm pore size nylon mesh bag (11 cm diameter × 20 cm length), respectively. Then the five mesh bags were strung to form a 1-m intact soil core and placed into the ground holes, which had been excavated earlier from root core sampling to the corresponding depth interval. A total of 132 intact cores (11 replicates × 4 collection times × 3 plantations) were processed in all plantations. The intact cores were collected after 90 (June 2017), 180 (September 2017), and 270 (December 2017), and 360 (March 2018) days, respectively. Eleven intact cores were removed from each plantation at each collection time. Upon collection, fine roots (<2 mm) were washed over a 0.25 mm mesh sieve with tap water, then sorted and dried at 65°C until constant weight.

Soil Sampling

Soil cores were collected with PVC tubes (1 m depth × 11 cm diameter) in March 2017. Five soil cores were randomly collected from three mangrove plantations and the nearby mudflat (MF). The soil cores were sectioned into five layers (0–20, 20–40, 40–60, 60–80 and 80–100 cm). Soil samples were then air-dried for the following chemical analyses.

Fine Root and Soil Chemical Analyses

Organic carbon (OC), total nitrogen (TN) and total phosphorous (TP) content ($g \cdot kg^{-1}$) of fine roots from the decomposition experiment and the soil samples were measured in the laboratory. Fine roots from biomass determination in March 2017 were also measured, which provided the initial OC, TN, and TP contents of fine roots tissue. All mass values reported in this paper refer to ash-free dry mass. Dry fine roots and soil samples were ground to a fine powder. Soil samples were determined following the modified Walkley-Black method for measuring OC content in soil (Schumacher, 2002; Ha et al., 2017). The organic content of the fine roots samples were analyzed using loss-on-ignition method (Heiri et al., 2001; Ha et al., 2017). The TN concentration of fine roots and soil were measured with an elemental analyzer (Thermo-Finnigan EA1112, Milan, Italy). The TP content was determined using a $K_2S_2O_8$ digestion at high pressure followed by the ammonium molybdate spectrophotometry method (Xuluc-Tolosa et al., 2003; Song et al., 2015).

The soil bulk density was obtained by the ratio of the oven-dried mass of soil and the original wet sample taken by the volumetrically fixed PVC cores (He et al., 2018). The air-dried fine power of soil samples was also used for soil pH and salinity determination. Soil pH and salinity were measured with 1:2.5 (*w/v*) and 1:5 (*w/v*) ratio of soil to deionized water by pH meter and YSI-ProPlis multiprobe sensor (Incorporated, OH, United States), respectively (He et al., 2018).

Data Analysis

The mean value of live and dead fine roots obtained in all four sampling times were used to analyze the distribution of fine root biomass and necromass. The dried fine root biomass and fine root necromass was used for calculating fine root production during each period of study using the Decision-Matrix method (Fairley and Alexander, 1985; Ostonen et al., 2005; Brunner et al., 2013; Xiong et al., 2017). Annual fine root production was calculated by summing up all production values between successive pairs of data throughout a full year (Brunner et al., 2013; Poungparn et al., 2016). The turnover rate of fine roots was calculated by dividing annual fine root production by mean biomass (Brunner et al., 2013). For calculating the fine root decay rate constant (k), data of decomposition experiment were fitted to the negative exponential decay model (Dornbush et al., 2002):

$$y = e^{-kt}$$

where y (%) is the percentage of initial mass remaining at time t (month), and k is the decay rate constant ($month^{-1}$).

The soil organic carbon stock was calculated by multiplying the soil bulk density and the soil organic carbon content. The organic carbon stock of the five soil layers was summed to estimate the soil organic carbon stock for each sampling site (He et al., 2020).

All statistical analysis were performed with R 3.5.0 (R Foundation for Statistical Computing, Vienna, Austria). Log - root transformations were applied to meet requirements for data normality and homogeneity of variances, if necessity. One-way ANOVA analyses were conducted to determine the differences of soil parameters among the three mangrove plantations and the adjacent mudflat at different depths, with plantation as a fixed factor. Live fine root biomass and fine root necromass within three plantations at different depths were also compared by one-way ANOVA. The difference in soil parameters, fine root mass (live and necromass), annual production, turnover and decomposition rate among sites and soil depths or seasons were compared by two-way ANOVAs, with soil depth or season, and species/sites as fixed factors. Linear regression was used to explore trends between soil nutrient content and fine root production. Relationships between fine root mass (live and dead) production and decay rate constants with organic carbon in soil were also determined by linear regression.

RESULTS

Spatial Variation of Soil Properties

The mean values of soil pH were highest in mudflat, and pH in the three mangroves soil tended to increase by soil depth (**Figure 2A**). Conversely, soil salinity was highest in KO, followed by SA and SK (there was no statistic variation between SA and SK), and lowest in mudflat soil (**Figure 2B**). Soil bulk density (SBD) in the four study sites increased with depth, with significant differences across soil depths and habitats ($p < 0.05$; **Figure 2C** and **Table 1**). The mean soil organic carbon (SOC) content (0–100 cm) was highest in KO (33.0 $g \cdot kg^{-1}$), nearly 1.6, 3.5, and 6.0 times higher than those of SK (21.0 $g \cdot kg^{-1}$), SA (9.6 $g \cdot kg^{-1}$), and MF (5.5 $g \cdot kg^{-1}$), respectively. The SOC content significantly decreased with soil depth in the two monocultures but no significant trend was found in SK and MF (**Figure 2D**). A significant difference was detected across habitats, with a significant difference also among soil depths ($p < 0.01$; **Table 1**). There were significant differences in soil total phosphorus content (STP) among soil depths and habitats ($p < 0.01$; **Figure 2E** and **Table 1**). Soil total nitrogen content (STN) showed a pattern similar to SOC content, that the STN content decreased significantly with depth in the monocultures ($p < 0.001$; **Figure 2F**). Significant difference among habitats was

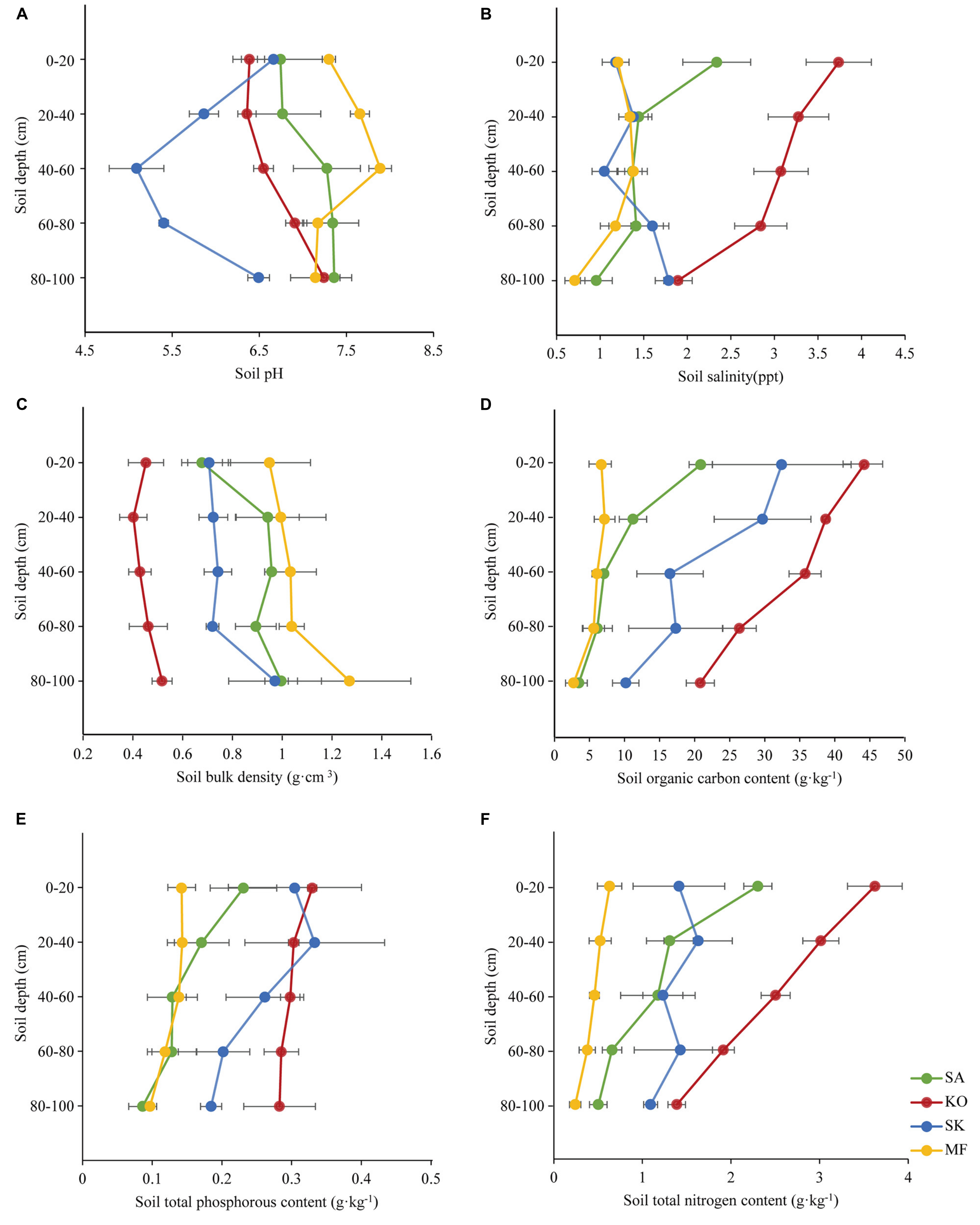

FIGURE 2 | Soil properties and their vertical distribution in *K. obovata* (KO), *S. apetala* (SA) monocultures, mixed plantation (SK), and mudflat (MF) at Hanjiang River Estuary, south China. **(A)** Soil pH. **(B)** Soil salinity. **(C)** Soil bulk density. **(D)** Soil organic carbon content. **(E)** Soil total phosphorous content. **(F)** Soil total nitrogen content. Error bars represent 1SE, and SE represents standard error ($n = 5$). Data of soil pH, salinity, bulk density, and soil organic carbon content in *K. obovata* and *S. apetala* monocultures and the mudflat are from He et al. (2018).

also detected ($p < 0.001$; **Table 1**). The mean soil organic carbon stock of KO was 15.8 ± 0.8 Mg OC ha^{-1}, almost 1.3, 2.0, and 3.4 times higher than those of SK, SA and MF, respectively.

Vertical Profile and Seasonal Variation of Live Fine Root Biomass and Necromass

In three mangrove plantation types, live fine root biomass was significantly decreasing with soil depth ($p < 0.01$; **Figure 3A**). Similarly, fine root necromass in SA and KO was significantly negatively correlated with soil depth, while such pattern was reversed in SK ($p < 0.001$; **Figure 3B**).

The annual average live fine root biomass of the plantations was 35.2 ± 2.5 $g \cdot m^{-2}$ for SA, 88.0 ± 4.3 $g \cdot m^{-2}$ for KO, and 73.4 ± 6.7 $g \cdot m^{-2}$ for SK. Significant differences existed among plantation types and soil depths ($p < 0.001$; **Figure 3A** and **Table 1**). There was a significant interaction between plantation types and soil depth on live fine root biomass ($p < 0.05$; **Table 1**). In the two monocultures, KO exhibited higher live fine root biomass than SA in the upper soil layer (0–40 cm), where 72 and 66% of *K. obovata* and *S. apetala*'s live fine root biomass occurred, respectively. The overall fine root necromass peaked in KO, followed by SK and SA. Significant differences in fine root necromass existed among plantation types and soil depths ($p < 0.001$; **Figure 3B** and **Table 1**).

In terms of seasonal patterns, there were significant interactions between season and plantation on both live fine root biomass and fine root necromass ($p < 0.05$; **Figure 4** and **Table 1**). Among four seasons, the minimum live fine root biomass occurred in spring (**Figure 4**). However, the maximum live fine root biomass of SA and SK were detected in autumn, while that of KO was found in summer (**Figure 4**). Fine root necromass in all plantations were significantly higher than live fine root biomass, with significant differences among seasons and plantation types ($p < 0.05$; **Figure 4** and **Table 1**).

Fine Root Production and Turnover Rate

Annual fine root production of mangroves in the three plantations ranged between 143.4 and 166.6 $g \cdot m^{-2}$ yr^{-1}. The annual fine root production of KO and SK were 1.2 and 1.1 times higher than that of SA, respectively. Fine root production differed significantly among seasons, which had a significant interaction with plantation types ($p < 0.05$; **Tables 1, 2**). Annual fine root production was positively correlated to soil nutrient ($p < 0.001$; **Figure 5**).

Fine root turnover rate was fastest in SA (4.1 ± 0.5 yr^{-1}), followed by SK (2.2 ± 0.3 yr^{-1}), and slowest in KO (1.9 ± 0.3 yr^{-1}). KO and SK displayed similar fine root turnover patterns in the year, with maximum and minimum rates in spring and summer, respectively, while SA demonstrated an opposite seasonal pattern (**Figure 6**). A significant interaction effect between season and plantation was also detected ($p < 0.001$; **Table 1**).

Fine Root Decomposition

The fine root mass in the intact cores lost 85.5, 26.6, and 38.9% for SA, KO and SK, respectively, over a 12-month decomposition period. The average decomposition rate constant (k) of SA fine root was significantly higher than those for KO and SK ($p < 0.001$; **Figure 7A**). This suggests that SA fine roots were not as recalcitrant as those of KO and SK, with faster decomposition dynamics.

The initial chemical composition of fine root tissue differed significantly among plantation types ($p < 0.001$). SK fine roots were characterized by the highest organic carbon (OC) (549.8 ± 40.4 g kg^{-1}) and total nitrogen (TN) (11.0 ± 0.6 $g \cdot kg^{-1}$) contents, while the lowest fine root OC content was found in SA (328.2 ± 13.0 $g \cdot kg^{-1}$), and the lowest fine root TN content occurred in KO (7.1 ± 0.4 $g \cdot kg^{-1}$). Higher initial C/N ratio was associated with KO (65.3 ± 2.1) than in SA (35.5 ± 1.5) and SK (51.1 ± 2.9). After 12-month decomposition, the proportions of original fine root OC remaining in the intact cores were 12.3% for SA, 44.8% for SK, and 55.0% for KO. The proportion of original TN remaining had a similar pattern as that of OC, with SA, SK, KO at 21.6, 63.0, 76.4%, respectively. As with mass loss, there were significant differences in OC and TN loss among different plantation types ($p < 0.001$). The decomposition rate constant (k) indicated that fine root OC and TN loss rates were highest in SA, followed by SK and KO (**Figures 7B,C**). Fine root C/N ratio declined significantly through time within intact cores ($p < 0.001$; **Figure 7D**). The slopes indicate that the monthly decreases of fine root C/N ratio in KO and SK were significantly higher than that in SA ($p < 0.001$; **Figure 7D**).

Effect of Fine Root Dynamic on Soil Organic Carbon Accumulation

Soil organic carbon density in the three mangrove plantations was positively correlated to live fine root biomass and necromass ($p < 0.05$; **Figures 8A,B**). Similarly, significant positive correlation was detected between soil organic carbon density and annual fine root production ($p < 0.05$; **Figures 8C,D**). Soil organic carbon stock was highest in KO, followed by SK and SA, same as the profile exhibited by live fine root biomass, fine root necromass, and annual fine root production. The high fine root mass and productivity likely contributed to soil organic carbon storage in KO. Soil organic carbon was negatively correlated with the decay rate constant, indicating that slower fine root decomposition rate may be responsible for higher soil organic carbon stock. Overall, fine root dynamics seems to have a significant effect on mangrove soil organic carbon stock, and KO had higher potential for organic carbon accumulation than SA and SK through fine root production and turnover.

DISCUSSION

Key Drivers on Modifying the Fine Root Dynamics

Live Fine Root Biomass and Fine Root Necromass

The spatial pattern of live fine root biomass is in broad accordance with previous studies in mangrove forests, that live fine root biomass not only varied with mangrove species but

TABLE 1 | *F* values of two-way ANOVA testing the differences in fine root dynamics and soil variables among different mangrove species/ habitats and soil depth in Hanjiang River Estuary, south China.

Dependent variables	**Source of variance**				
	Plantation/Habitat	**Soil depth**	**Season**	**Plantation/ Habitat × Soil depth**	**Plantation/ Habitat × Season**
Soil pH	39.006**	NA	NA	4.213**	NA
Soil salinity (ppt)	64.778**	6.147**	NA	3.684**	NA
Soil bulk density (g·cm^{-3})	16.548**	2.746*	NA	0.936	NA
Soil organic carbon content (g·kg^{-1})	26.487**	4.749*	NA	1.326	NA
Soil total nitrogen content (g·kg^{-1})	40.198**	6.625**	NA	1.539	NA
Soil total phosphorous content (g·kg^{-1})	30.352**	4.696*	NA	0.634	NA
Live fine root biomass (g·m^{-2})	35.751**	18.636**	19.739**	3.593*	1.403
Fine root necromass (g·m^{-2})	27.064**	16.381**	5.63*	7.584**	2.003
Fine root production (g·m^{-2})	0.39	2.217	3.985*	1.808	11.401**
Fine root turnover rate (month^{-1})	30.416**	10.514	7.913**	3.7*	16.915**
Fine root mass decay rate constant (*k*)	3.559*	1.91	NA	1.328	NA

$^{*}p < 0.05$; $^{**}p < 0.001$.

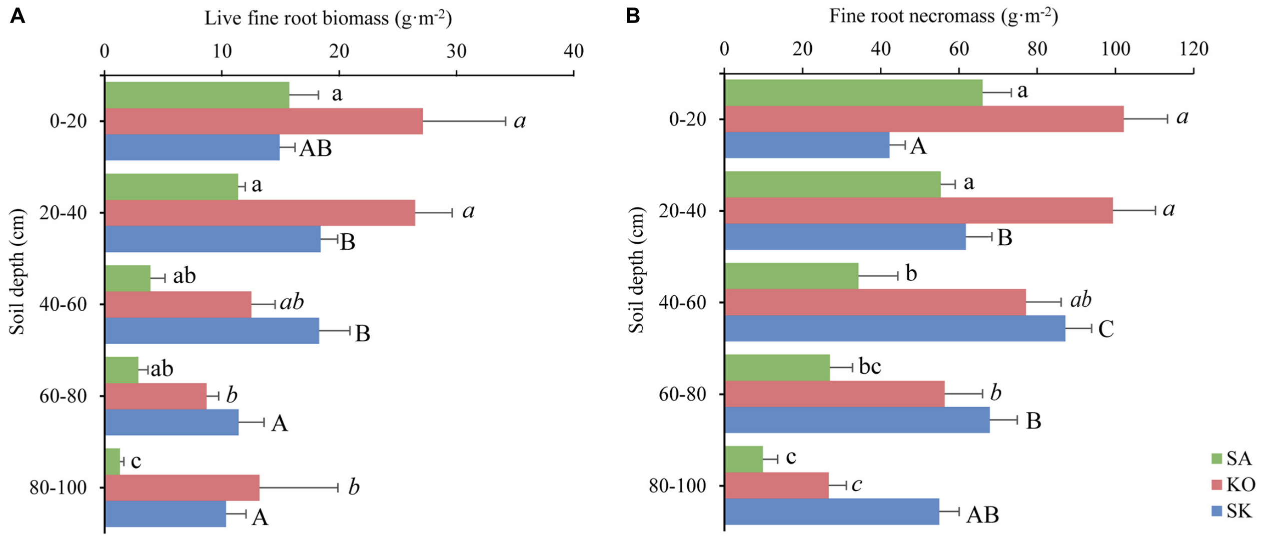

FIGURE 3 | Spatial distribution of live fine root biomass **(A)** and necromass **(B)** (mean ± 1SE) in *K. obovata* (KO), *S. apetala* (SA) monocultures and mixed plantation (KS) at Hanjiang River Estuary, south China. Different letters indicate significant differences among different soil depths within the same plantation type ($p < 0.05$).

also with soil depth (**Figure 3**; Ha et al., 2017; He et al., 2018, 2020). Usually, live fine roots mainly occurred in shallow soil layers (Adame et al., 2017; Ha et al., 2017; Xiong et al., 2017). The observed high amounts of fine roots in surface soil layers were attributed to the availability of nutrients and less anoxic conditions (Yuan and Chen, 2010; Srikanth et al., 2016; He et al., 2018). In the current study, the profile of live fine root biomass differed between the two monospecific plantations (**Table 1**). Live fine root biomass was concentrated at different soil layers between monocultures of *K. obovata* (0–40 cm) and *S. apetala* (0–60 cm) (**Figure 3**), which is closely related to their morphological traits. More superficial fine roots were required in *K. obovata* to ensure gas exchange and nutrient uptake due to the absence of typical pneumatophores (Okello et al., 2019; Al-Khayat and Alatalo, 2021). In contrast, pneumatophores in *S. apetala* helps reduce stress from anoxic conditions, allowing supportive and absorptive roots to penetrate into deeper soil layers (He et al., 2018, 2020).

Usually, large amounts of dead fine roots accumulate in mangrove substrate (Chalermchatwilai et al., 2011). Consistent with studies on *Rhizophora* and *Avicennia* species, dead fine roots accounted for >80% of the total fine root mass in both KO and SA plantations (**Figure 3**) (Alongi and Dixon, 2000; Alongi et al., 2000, 2003). Other studies support that this fine root necromass component is refractory and may be able to provide long-term carbon storage (Tamooh et al., 2008). Fine root necromass in KO significantly higher than that of SA may reflect *K. obovata* has higher capacity in long-term carbon storage than *S. apetala*. Besides, SK had significantly higher fine root mass than SA. This profile may be attributed to the complementary vertical niches in both above and belowground space utilization

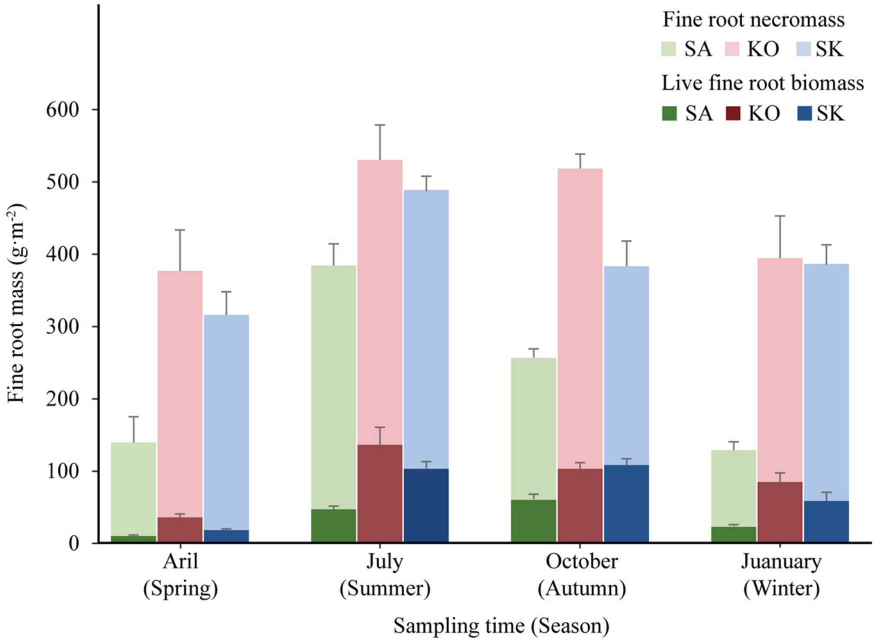

FIGURE 4 | Seasonal variation of live fine root biomass and fine root necromass (mean ± 1SE) in SA, KO, and SK plantation at Hanjiang River Estuary, south China.

TABLE 2 | Fine root production (mean ± SE, $n = 4$ plots) in the three plantations in Hanjiang River Estuary, south China.

Duration	**Production (g·m^{-2})**		
	SA	**KO**	**SK**
March–May (Spring)	63.1 ± 17.3	11.6 ± 1.5	15.6 ± 5.0
June–August (Summer)	22.8 ± 8.6	65.1 ± 16.1	44.8 ± 17.6
September–November (Autumn)	52.1 ± 3.4	15.7 ± 1.7	22.2 ± 8.3
December–February (Winter)	5.5 ± 1.2	74.3 ± 8.9	79.5 ± 5.4
Annual	143.4 ± 17.8^{a}	166.6 ± 26.6^{b}	162.1 ± 24.7^{b}

Data labeled with different letters are significantly different ($p < 0.05$).

in this mixed-species zone. The seasonal pattern of live fine root biomass and necromass may be species specific (**Figure 4**), dependent on fine root growth and mortality in accordance with the soil environment, e.g., temperature, moisture content, redox condition, and nutrient availability (Xiong et al., 2017).

Fine Root Production and Turnover

Characterized by the intolerance to canopy shade and fast growth rate of *S. apetala*, SA was featured with significantly lower stem density, resulting in its lower fine root production than KO. In SK, the colonizing *K. obovata* increased the overall tree density in the original *S. apetala* plantation. Complementary root traits in the same assemblage drove the two mangrove species to make more sufficient utilization of belowground space (Brassard et al., 2011; Rolo and Moreno, 2012; Lai et al., 2017). Root systems can continuously adjust to changes in soil conditions and floral composition to maximize plant return (Ward et al., 2013). These responses resulted in significantly higher fine root production of SK than SA (**Table 2**). However, the growth of the colonizing *K. obovata* was hampered due to shading from *S. apetala*'s canopy (Peng et al., 2016; Jiang et al., 2019). In general, significantly lower overall stem density and fine root production was evident in the mixed SK than KO monoculture (**Table 2**). Therefore, the presence of complementary rooting traits was a key determinant on fine root productivity in the mixed stand, also affecting the density of trees (Brassard et al., 2011).

Poungparn et al. (2016) suggested that the variability of fine root production across seasons was underpinned by soil temperature. As mangroves are commonly occur in oligotrophic environments (Xiong et al., 2017), most mangrove species are highly responsive to variations in nutrient availability (Adame et al., 2017). The positive correlation between annual fine root production and soil nutrients suggests that mangrove fine root production may be nutrient dependent at our study sites (**Figure 5**).

The turnover rates calculated in the present study were within the range of 0.15–9.60 yr^{-1}, used in 17 ecosystem models parameterized for terrestrial forests (McCormack et al., 2015a). Our results support that slower fine root turnover rates resulted in greater standing fine root biomass (McCormack et al., 2015b).

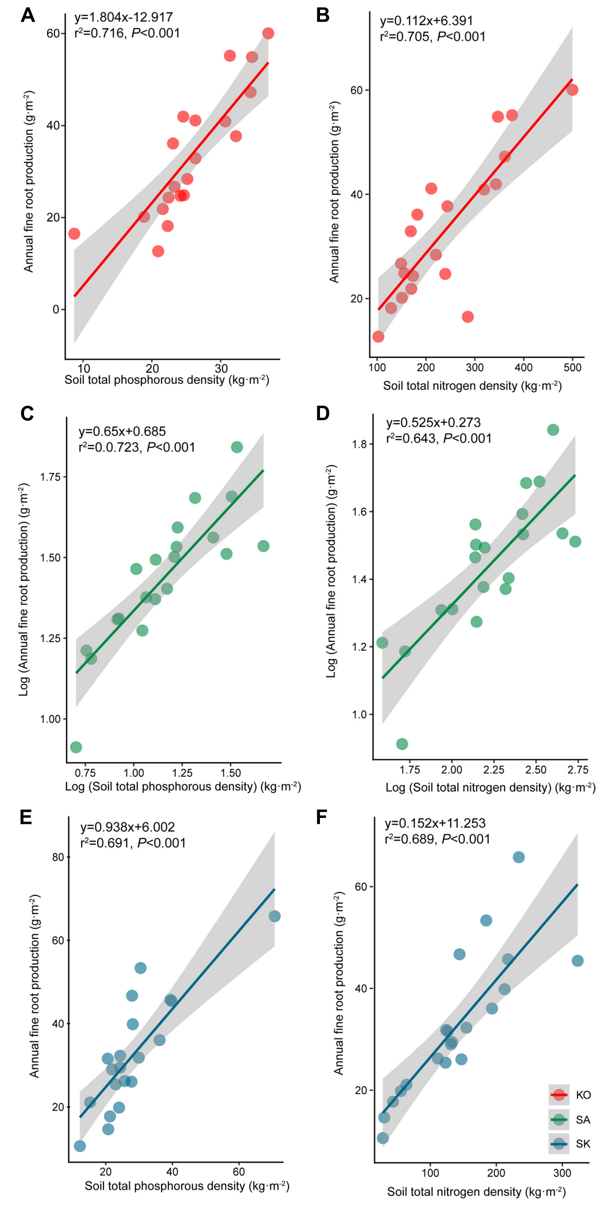

FIGURE 5 | Regression analysis between soil total phosphorous **(A–C)** and nitrogen content **(D–F)** and annual fine root production for *S. apetala* (SA), *K. obovata* (KO) monocultures and the mixed (SK) plantations at Hanjiang River Estuary, south China.

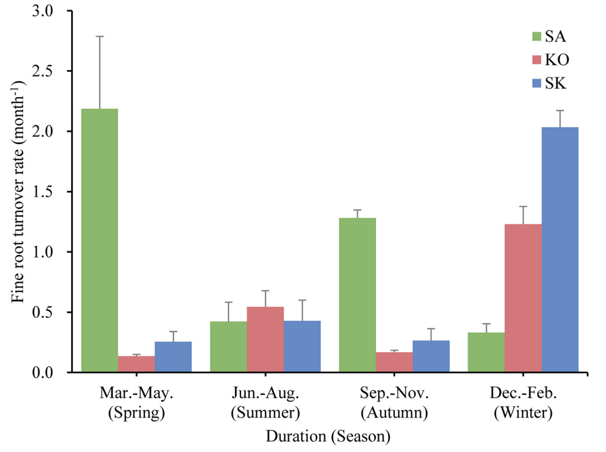

FIGURE 6 | Fine root turnover rate (month^{-1}) for *S. apetala* (SA), *K. obovata* (KO) monocultures and the mixed (SK) plantations in different seasons over a year at Hanjiang River Estuary, south China.

Lower fine root turnover rate coupled with higher nutrient content suggested that fine roots may be maintained as long as the nutrients obtained outweigh the cost of keeping them alive. This agrees with the results of root lifespan analysis by Eissenstat and Yanai (1997) that roots in nutrient-rich environments should live longer than in nutrient-limited conditions. Previous studies have demonstrated that soil temperature at least partly control the timing and duration of fine root growth (Yuan and Chen, 2010; Xiong et al., 2017; Muhammad-Nor et al., 2019; Poungparn et al., 2020). Since coarse roots generally do not show seasonal dynamics (Xiong et al., 2017), the pronounced seasonal variation of fine root turnover rate suggests that fine roots represent the most dynamic component in mangrove root systems and are the major contributor to root turnover (**Figure 6**).

Fine Root Decomposition

Our results in fine root decomposition were consistent with previous studies in showing generally lower decomposition rates in mangrove fine roots compared with those of terrestrial ecosystems (Silver and Miya, 2001; Huxham et al., 2010). Species identity is the main driver of fine root decomposition which may be attributed to the difference in physiology and biochemistry (Ouyang et al., 2017). In the current study, highest soil pH in SA may attribute to the faster organic matter and fine root debris decomposition rate of *S. apetala* than that of *K. obovate* (He et al., 2018). *S. apetala* aerates the sediment through their pneumatophores (**Figure 7A**), increases oxygenation of the sediment and general permeability of their root system, resulting in faster fine root decay, compared with fine root of *K. obovata* that limited oxygen transport from above-ground parts (Ouyang et al., 2017). Apart from oxygen transport, different relative nutrient concentrations in fine roots represented as initial C/N ratio between these species may be responsible for such difference (Solly et al., 2014; Sariyildiz, 2015; Ouyang et al., 2017). *S. apetala* had higher initial TN and lower OC contents compared with *K. obovata*, resulting in a lower initial C/N ratio in its fine roots. In SK, the higher fine roots initial TN and OC contents may be attributed to the colonization of *K. obovata* at the understory, contributing to their slower decomposition than in SA (Huxham et al., 2010). The composition of plant community may also affect fine root decomposition through species specific rhizospheric microbial activities (Prieto et al., 2017).

The quality of fine root litter carbon can also affect the carbon-use efficiency of decomposers, leading to differences in the fine root decomposition process (Manzoni et al., 2010). The investment in enzyme production increases with the complexity

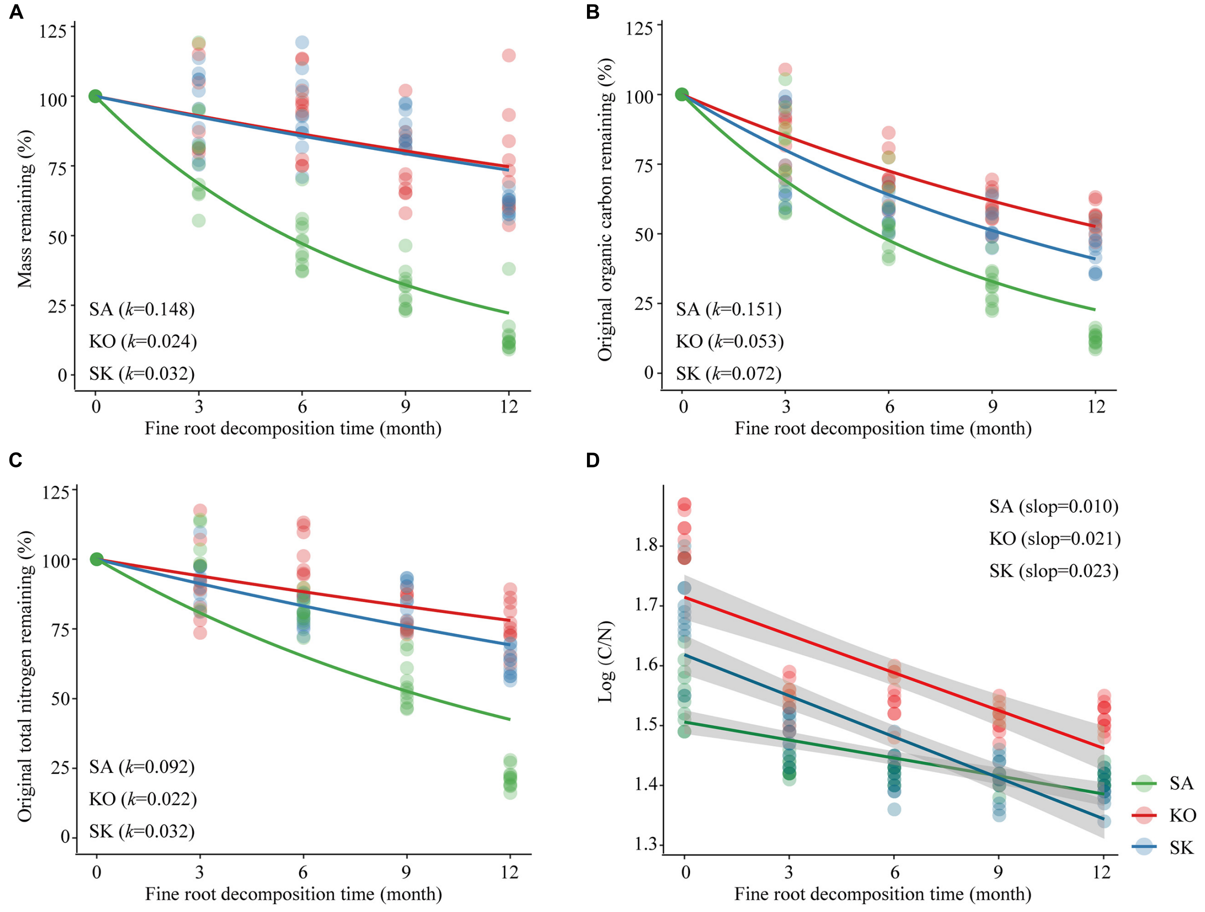

FIGURE 7 | Loss of mass **(A)**, organic carbon **(B)**, total nitrogen **(C)** and changes in C/N **(D)** for fine root of *S. apetala* (SA), *K. obovata* (KO) monocultures and the mixed (SK) plantations upon decomposition at Hanjiang River Estuary, south China. k values were estimated based on the negative exponential decay model. Data were normalized such that 100% equals the $t = 0$ intercept of the exponential decay regression. Linear best fits for (d): SA ($y = -0.01x + 1.506$, $r^2 = 0.513$); KO ($y = -0.021x + 1.714$, $r^2 = 0.562$); SK ($y = -0.023x + 1.619$, $r^2 = 0.668$). All regressions are significant ($p < 0.001$).

and content of substrates such as cellulose, tannins, and lignin (Prieto et al., 2017; Song et al., 2017; Pradisty et al., 2021). The organic carbon loss during fine roots decomposition is mainly attributed to the degradation of these components (Melillo et al., 1989). Fine root decay is an important source of minerals in mangrove soil (Silver and Miya, 2001). A meta-analysis of decomposition studies in mangrove also identified a strong relationship between soil nitrogen content and fine root decomposition rate (Poret et al., 2007). The accumulation or release of nutrients derived from decomposing fine root primarily depends on the quality of fine root substrate and the stoichiometric requirements of the microbial decomposers (Song et al., 2017). Net N loss occurs generally when the initial N content is between 6 and 28 $g \cdot kg^{-1}$ or the C/N ratio is lower than the critical threshold of 5–15. In the present study, the initial fine root N content (7.2–11.0 $g \cdot kg^{-1}$) was in the lower range of the threshold, resulting in N loss in all three mangrove plantations. Consistent with studies on mangrove leaves and branch, the C/N ratio decreased during fine root decomposition as N immobilization occurred via microbial activities. Accumulation of refractory fine root material with enhanced nitrogen levels represents a nutrient storage mechanism within mangrove ecosystems (Cebrián and Williams, 1998). However, in our study, the fine root C/N ratios were > 15 over the decomposition period, but net N loss still took place (**Figures 7C,D**). This unexpected trend may be attributed to the adaptation of microbial decomposer communities to nutrient-limited substrates in mangroves, shifting their stoichiometric requirements. Additionally, decomposers may decrease their C use efficiency to adapt to the low N concentration substrates, thus increasing the critical C/N ratios of fine root litter for net N mineralization in mangrove ecosystems.

Effect of Fine Root Dynamics on Soil Organic Carbon Accumulation

Mangrove plants strongly influence C sequestration in soil through detritus input (He et al., 2020). In this study, soil C increased over time after mangrove plantations had been established on mudflats, as has been reported before (Liu et al., 2014; Kelleway et al., 2016). A high proportion of mangrove soil C is derived from fine roots (Strand et al., 2008; He et al., 2018). This underpins the significantly positive correlation

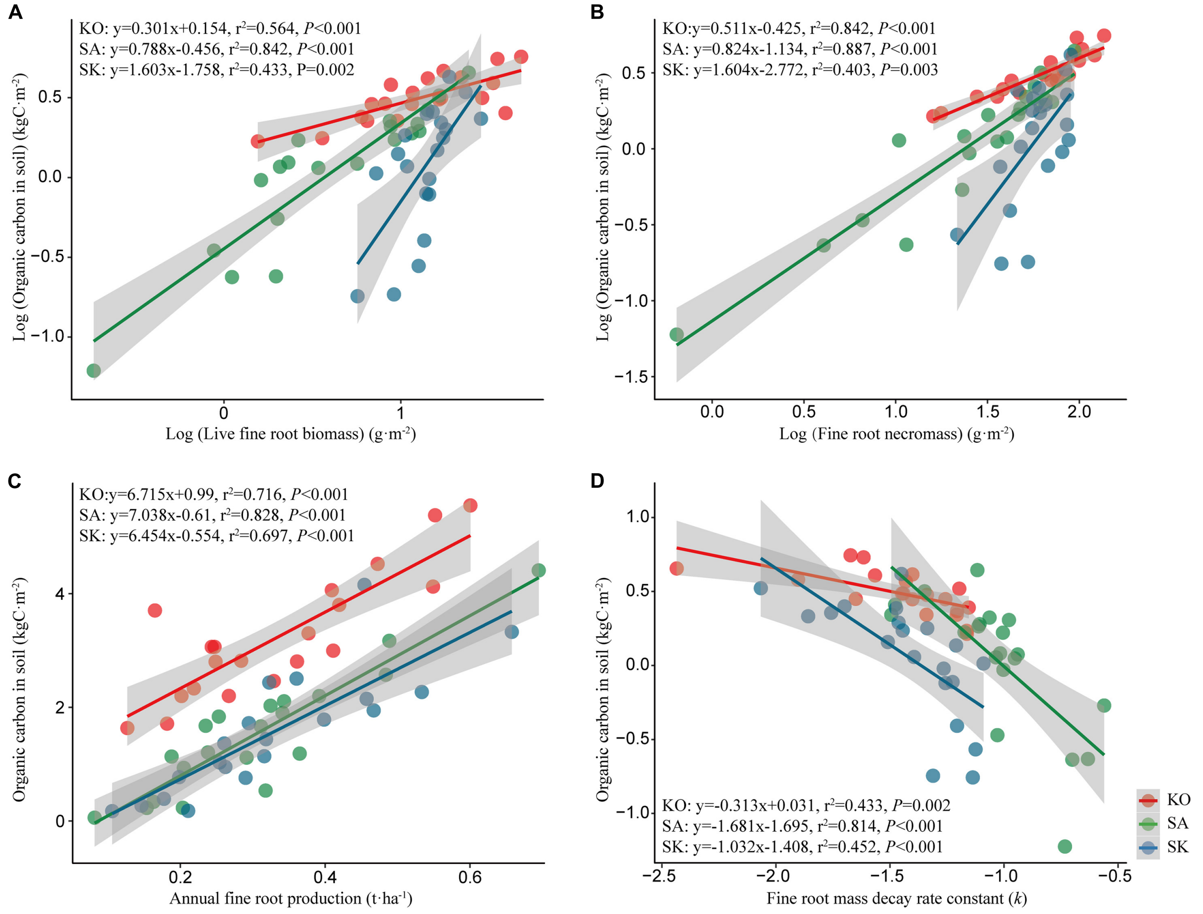

FIGURE 8 | Regression analysis between organic carbon in soil and live fine root biomass **(A)**, fine root necromass **(B)**, annual fine root production **(C)**, and fine root mass decay rate constant **(D)** for *S. apetala* (SA), *K. obovata* (KO) monocultures and the mixed (SK) plantations at Hanjiang River Estuary, south China.

between the spatial distributional patterns of live fine root biomass, necromass, and soil organic carbon across different soil layers, reiterating the contribution of fine roots dynamics to soil vertical accretion and formation (Castañeda-Moya et al., 2011). Simulation models of organic matter content and bulk density also predict that variations in fine root turnover (continuous production, mortality and decomposition) have a strong effect on soil organic carbon accumulation, as has been confirmed by the current study and other empirical studies (Castañeda-Moya et al., 2011; Liu et al., 2017). Therefore, the increased fine root productivity, coupled with reduced fine root decomposition in the anoxic soil environment enhance carbon storage by mangroves. The higher fine root productivity may represent higher belowground carbon allocation and leads to more C inputs to soil, contributing to the high proportion of ecosystem carbon stored underground in mangroves (Donato et al., 2011). For belowground carbon accumulation, root production rate must exceed carbon loss rate from soil (Middleton and McKee, 2001). This may be supported by a large amount of undecomposed fine root necromass may contribute to the high organic matter accumulation. Therefore, a significant correlation between organic carbon in soil and fine root metrics (biomass, necromass, production and decomposition rates) reflects the importance of fine root contribution to soil organic carbon, and the significant effect of fine root dynamics have on soil organic carbon accumulation (**Figure 8**). The much greater contribution of *K. obovata* fine roots to soil organic carbon accumulation than *S. apetala* was due to the significantly slower turnover rates of fine roots of *K. obovata* relative to those of *S. apetala*.

Implications of Species Traits for Carbon-Based Mangrove Afforestation

Our study revealed significant differences associated with species traits with respect to the fine root dynamics (live fine root biomass, fine root necromass, productivity, turnover rate and decomposition rate) as well as soil organic carbon content. In this study, SA had lower fine root mass and productivity due to the intensive demand for light and fast-growing characteristics of *S. apetala* (Chen et al., 2012; Zhu et al., 2020), with significantly stronger self-thinning effect compared with the *K. obovata* plantation. Combining with its higher fine root turnover and decomposition rates, fine roots of *S. apetala* may have a lower contribution to soil organic carbon accumulation than those of *K. obovata*, as the balance between productivity and decomposition of fine roots in the anoxic environment crucially determines the belowground carbon storage in mangrove soils.

Competition for light under a dense canopy in an osmotically-stressed environment is the major hurdle for the establishment of an understory shrub layer in mangrove vegetation (Janzen, 1985; Hogarth, 2015). Chen et al. (2012) suggested that mixed species stands had higher soil carbon storage than monocultures in mangrove plantations. Peng et al. (2016) also reported that mixed mangrove communities might play a more important role in carbon accumulation than monocultures. In the current study, the mixed SK had higher fine root mass and productivity, and lower fine root turnover rate and decomposition rate than SA, attributable to the positive effect of colonization by *K. obovata*. However, our data also indicated that KO had higher potential than SK for belowground carbon storage. The growth and development of *K. obovata* in the mixed stand were limited by light availability under the dense canopy of *S. apetala*, resulting in its lower stem density than in KO. Impacted by the reduced stem density, the mixed SK may not have higher fine root mass and productivity than KO. Despite the presence of *K. obovata* fine roots has changed the overall fine root litter substrate quality in SK, the mixed fine root litter may still have faster decomposition rates than their counterparts in KO. Combining with our previous study which indicating the sediment carbon pool of *S. apetala* plantation reached a stable state after 12 years of growth, while that of *K. obovata* plantation gradually stabilized upon long-term growth (Wu et al., 2020). Therefore, the native *K. obovata* is preferred to the fast-growing *S. apetala* for mangrove afforestation for its fine root dynamics and contribution to soil carbon storage at the forest scale, especially for long-term carbon-based mangrove restoration programs. Where the tall *S. apetala* has been introduced, it can coexist with some shrubby native species (e.g., *Kandelia obovata*, *Aegiceras corniculatum*) by partitioning vertical spatial niches both above- and belowground. In locations where *S. apetala* has already established (e.g., Southern China), eradication is not an effective option but native species can still be introduced to the *S. apetala* plantations to establish mixed stands to improve the capacity of mangrove plantations for carbon sequestration. This approach of conducting mangrove restoration or reforestation using multiple species with complementary functional traits and niches would prove to bring significantly more ecosystem benefits than the monospecific approach (Lee et al., 2019).

CONCLUSION

Our analyses show that mangrove fine root dynamics (fine root mass, production, turnover rate, and decomposition rate) were mainly affected by soil nutrient condition and species composition. In addition, season (temperature) also contributed to the dynamics of fine root mass, production, and turnover. The fine root dynamics and soil organic carbon stock of 12-year mangrove plantations respectively dominated by the introduced S. apetala and native *K. obovata* suggested the latter species had a higher potential for belowground carbon sequestration and storage than *S. apetala*. Apart from the previous studies, the differences in fine root dynamics and soil organic carbon storage between the colonized *S. apetala* plantation and the *K. obovata* monoculture indicated that mixed communities may not have higher soil organic carbon storage than monocultures. Functional trait of different mangrove species is a key factor to determine the carbon storage function of mixed stands. A significant linear correlation exists between soil organic carbon and live, dead fine root biomass, productivity as well as decomposition rate, suggesting that fine roots play an important role in carbon storage, and fine root dynamics have a significant effect on carbon sequestration in mangrove ecosystems. The overall soil organic carbon stock in the *K. obovata* monoculture was significantly higher than that of *S. apetala*. Therefore, *K. obovata* is recommended in soil carbon sequestration and storage oriented mangrove restoration programs rather than *S. apetala*. These two mangrove species have contrasting but complementary functional traits. For enhanced carbon accumulation, the native *K. obovata* can be introduced to existing *S. apetala* plantations to establish mixed communities.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

ZYH, YP, and ZH originally planned and designed the research. ZYH, YP, HS, and ZY performed the field work. ZYH, HS, ZY, LZ, and MW contributed to the laboratory analysis. XY produced all the figures. ZYH wrote the first draft of the manuscript. YP, ZH, and SL further improved the manuscript. All the authors commented and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.763922/full#supplementary-material

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