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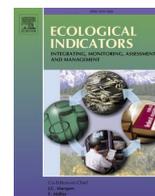
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## The role of mangrove fine root production and decomposition on soil organic carbon component ratios

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### ABSTRACT

Mangrove fine roots are an important contributor to soil organic matter (SOC), yet how their production and decomposition affect SOC accumulation across the sea-land gradient is still elusive. This study aimed to investigate the influencing path of biotic and abiotic factors of fine root production and decomposition dynamics on SOC component ratios involving particulate organic carbon (POC)/SOC, dissolved organic carbon (DOC)/SOC, and microbial biomass carbon(MBC)/SOC. Based upon sequential root coring and the litter bag method, the production, and decomposition of mangrove fine roots were investigated. The production and turnover rate of mangrove fine roots increased from 90.9 g·m<sup>-2</sup> to 510.9 g·m<sup>-2</sup> and 0.44 yr<sup>-1</sup> to 1.49 yr<sup>-1</sup> across the sea-land gradient respectively. After one year of decomposition, 69.5–80.8% and 58.3–69.2% of low-order and high-order fine roots remained, respectively. Decomposition rates of both low-order and high-order fine roots were significantly slower in the landward zone than in the seaward zones. Redundancy analysis (RDA) illustrated that vegetation biomass and soil salinity were respectively the main biotic and abiotic factors affecting the production and decomposition of mangrove fine roots and they explained 91.2% of mangrove fine root production and decomposition. Stepwise regression analysis indicated that the production of fine roots was mainly influenced by mangrove vegetation biomass while their decomposition was negatively affected by soil salinity. POC and SOC increased significantly from 20.13 t·ha<sup>-1</sup> to 58.71 t·ha<sup>-1</sup> and 78.42 t·ha<sup>-1</sup> to 139.01 t·ha<sup>-1</sup> respectively while DOC/SOC and MBC/SOC reduced from 0.33 to 0.24 and from 0.55 to 0.44 across the sea-land gradient. RDA results indicated that low-order fine root production was the major control of the ratio of SOC components among the production and decomposition of low-order and high-order fine roots, explaining 90.9% of SOC component ratio changes. Based upon structural equation modeling, the path coefficient of biotic and abiotic factors POC/SOC was 0.914 ( $P < 0.001$ ), indicating that mangrove fine root production affecting by vegetation biomass and soil salinity was the main drive of SOC accumulation. Nevertheless, mangrove fine root decomposition played a minor role in SOC component change. The information gained in this study will facilitate policy decisions concerning the restoration of mangrove forests in China.

### 1. Introduction

With an average carbon stock of 956 t·ha<sup>-1</sup>, mangrove forests are one of the richest tropical carbon storages (Alongi, 2012). Carbon stocks in mangrove ecosystems are in fact much higher than salt marshes, seagrasses and tropical rain forests (Alongi, 2014; Donato et al., 2011; Twilley et al., 1992). Soil plays a key role in mangrove C stock,

accounting for 49–98% of C in mangroves (Xiong et al., 2018). Although mangroves occupy only 0.5% of the global coastal area, they contribute 10–15% (24TgCyr<sup>-1</sup>) to coastal sediment carbon flux (Alongi, 2014). Soil carbon stocks of mangrove ecosystems are also five times higher than those of tropical terrestrial forests on a per unit area basis (Bouillon, 2011; Malhi et al., 2011). Therefore, the accumulation and dynamics of SOC in the mangrove ecosystem deserves more attention.

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The sequestration of fine root matter in soil, which is the balance between the production and decomposition of mangrove fine roots, is the major drive of SOC accumulation in mangrove forests (Chen et al., 2019; Garcia-Pausas et al., 2004; Krauss et al., 2014; Liu et al., 2017). The production and decomposition of mangrove fine roots are influenced by both abiotic (i.e. nutrient concentrations and availability, soil pH and salinity, tides...) and biotic factors (i.e. tree species and ages) which result from the local topography and hydrology. However, although soil available P concentration, salinity, temperature and tree species have been reported to have a great influence on mangrove fine root dynamics (Adame et al., 2017; Krauss et al., 2014), there is still uncertainty about the most significant factors affecting mangrove fine root production and decomposition. Due to differences in local topography and hydrology, mangrove forests distribute in strips across a sea-land gradient. It was reported that soil N and P concentrations and the age of mangrove forest increase across this sea-land gradient (Fromard et al., 2004; Hayes et al., 2017; Sherman et al., 2003). Mangrove community structure also changes across this gradient (Dung et al., 2016; Pongpam et al., 2016). Hence, mangrove fine root production and decomposition may change across the sea-land gradient. In addition, the branching order for fine roots could be another significant factor influencing the production and decomposition of mangrove fine roots (Lin and Zeng, 2017; McCormack et al., 2015). Based on the root position in the branching hierarchy of the root system, a root number is assigned. Generally, the distal roots are classified as the first-order whereas the root from which two first-order roots branched is classified as the second-order, etc (Pregitzer et al., 2002). Due to their different functions and composition, different branching order for mangrove fine roots might have different production and decomposition rates. Hence, it is necessary to investigate the variation of different orders for mangrove fine roots across the sea-land gradient in order to understand the influence of the branching order for mangrove fine roots on the production and decomposition of mangrove fine roots across the sea-land gradient.

The increase of mangrove fine root biomass and production favors the increment of SOC (Gleason and Ewel, 2002; He et al., 2018; Xiong et al., 2016), while the increase of mangrove fine root decomposition plays an opposite role (Ouyang et al., 2017; Robertson and Alongi, 2016). As mangrove fine root production and decomposition were affected by biotic and abiotic factors driven by topographic and hydrological conditions (e.g. the sea-land gradient), studying the influencing path of biotic and abiotic factors-mangrove fine root production and decomposition-SOC accumulation is vital to understand C sequestration in mangrove forests. Several SOC components, also known as soil labile C including microbial biomass C (MBC), dissolved organic C (DOC) and particulate organic C (POC) are sensitive indicators of SOC dynamics (Yang et al., 2009). The ratios of labile components to the total SOC (e.g. POC/SOC and DOC/SOC) are for instance used to measure the stability of SOC (Min et al., 2006). Though some studies of terrestrial forest have found that the turnover of fine roots increases soil POC and hence SOC accumulation (Angst et al., 2018; Hao et al., 2015; Lai et al., 2015), a thorough study on the path of biotic and abiotic factors- fine root production and decomposition-soil labile C component ratios are still needed. Path analysis based on structural equation modeling (SEM) is often used to describe the directed dependencies among a set of variables and it has been widely applied in biology and ecology (Oliveira et al., 2018). Reliable path analysis can be achieved using the SEM based upon partial least squares, with a relatively small number of samples (Xiao et al., 2020).

Mangrove community distributed in strips from landward to seaward in the natural mangrove forest of Yingluo Bay south China (Liang, 1996) and thus it is an ideal site for the investigation of fine root production and decomposition and their influence on SOC accumulation. The objectives of this study were to (1) investigate the change in production and decomposition of mangrove fine roots across the sea-land gradient along with their biotic and abiotic controlling factors; (2) clarify the influence path of biotic and abiotic factors-mangrove fine root

production and decomposition -SOC component ratios.

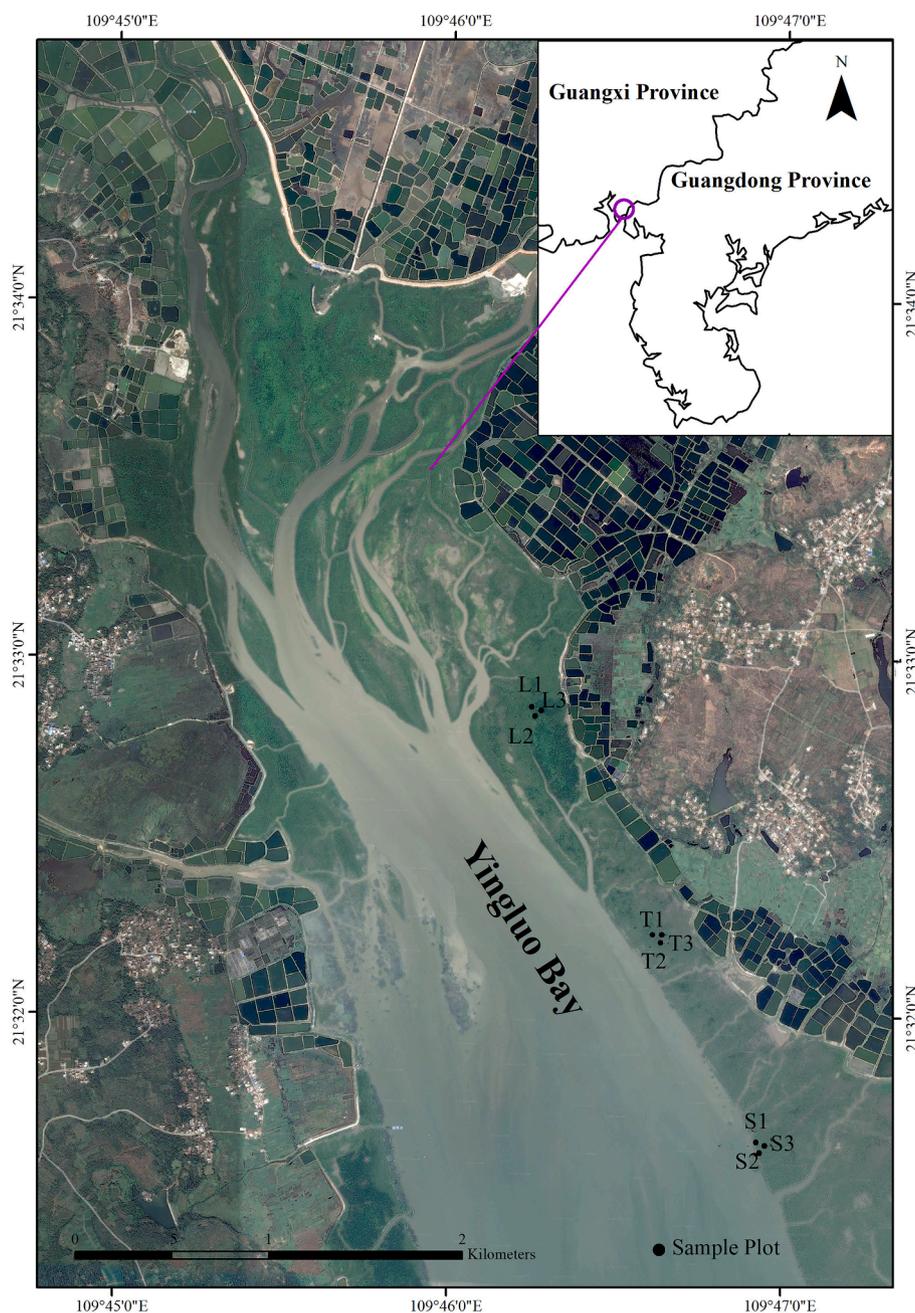
## 2. Materials and methods

### 2.1. Study area

The study area is located in the Zhanjiang Mangrove Nature Reserve (20°14'–21°35' N, 109°40'–110°35' E), in Yingluo Bay, south China (Fig. 1). *Avicennia marina*, *Aegiceras corniculatum*, *Kandelia obovate*, *Rhizophora stylosa*, and *Bruguiera gymnorhiza* are the dominant mangrove species. The annual minimum and maximum temperatures are 1.5 and 37.4 °C, respectively, with an average of 22.4 °C. Precipitation mainly occurs from April to September, with an average annual total value of 1816 mm. Tides are irregularly diurnal, with mean and maximum ranges of 2.5 m and 6.5 m, respectively. The spatial pattern on plant species across the sea-land gradient in Yingluo Bay has been established previously (Liang, 1996). Sampling sites were selected from land to sea and were categorized into three zones, namely seaward zone, transition zone, and landward zone. The seaward zone was near the sea and adjacent to the mudflat with an elevation of 1.6 m and was occupied by *Avicennia marina* as the dominant species. The landward zone located in the inland part with an elevation of 4.5 m was occupied by *Rhizophora stylosa* as the dominant species. The transition zone, with an elevation of 3.3 m, was in the middle of the seaward zone and landward zone and was dominated by *Aegiceras corniculatum* and *Kandelia obovate*. High-precision GPS (Garmin 629sc) was employed to record the elevation of soil or sediment surface in the mangroves, while Google earth was used to confirm the location of each observation. The mudflat adjacent to the seaward mangrove was selected as a baseline to compare its SOC density with that of mangrove forests. Figure 1

### 2.2. Survey of mangrove vegetation and collection of soil and fine root samples

In each zone, three quadrats (10 × 10 m) were randomly selected for the survey of the mangrove vegetation and the collection of soil and fine root samples. A >15 m buffering distance was retained between the quadrats. Within each quadrat, species of all the trees along with the number of each tree species were identified and recorded. Tree height (H) of *Kandelia obovate* and *Rhizophora stylosa* was measured by a laser rangefinder (ASDM150), while the H of other mangrove species was measured using a tape measure (Kauffman and Donato, 2012). Stem diameter (i.e. basal diameter (D<sub>0</sub>), tree diameter at 0.1 m height of *Kandelia obovate* (D<sub>0,1</sub>), tree diameter at 0.6 m height of *Bruguiera gymnorhiza* (D<sub>0,6</sub>) and diameter at breast height (DBH, stem diameter at 1.3 m height) were measured using a tape measure. In each intertidal zone, three quadrats (1 × 1 m) were selected for leaf litter collection. Above-ground biomass (AGB), below-ground biomass (BGB), and total forest biomass (TFB) were determined using species-specific allometric equations (He et al., 2017; Wang et al., 2014) (STable 1). Three standard trees were randomly selected in each quadrat and each season for root coring. The base area of each standard tree was divided into three parts at intervals of 120°. For each part, one soil core (60 cm depth, 10 cm diameter) was sampled from the middle position between the trunk base and the vertical edge of the canopy shade of each tree as a subsample (He et al., 2018). Subsamples around each standard tree were pooled into one sample for the estimation of fine root production. Three additional soil cores were also randomly sampled from each quadrat for the collection of fine roots for the decomposition experiment. Soil bulk density was estimated using a 5 cm diameter cutting ring at the soil layer at a depth of 0–20, 20–40, and 40–60 cm. Three subsamples of soil were also randomly sampled with soil coring in each quadrat. Each soil core was separated into segments by their depth (0–20, 20–40, 40–60 cm). Subsampled segments at the same depth taken from each quadrat were pooled as a composite sample for chemical analysis. All samples were stored separately at 4 °C before laboratory analyses.



**Fig. 1.** The location of the mangrove study area in Yingluo Bay, Guangdong province of South China. S, T and L referred to the seaward zone, transition zone and landward zone, respectively.

### 2.3. Analysis of soil, fine root, and leaf litter samples

The subsampled soil (i.e. soils sampled at the same depth of layer and in the same quadrats) separated from fine roots were pooled into one single sample for chemical analysis. Each fresh soil sample was divided into two halves, one of which was air-dried at  $<20\text{ }^{\circ}\text{C}$  in an air-conditioned room for the determination of SOC and POC. Soil bulk density was calculated as the ratio of soil dry weight (a constant weight of soil dried by  $60\text{ }^{\circ}\text{C}$  oven) to soil sample volume. All plant residues in soil, including coarse roots, were removed through a  $0.15\text{ mm}$  mesh. The salinity of soils was determined by (soil:water = 1:5) using a salinity meter (YSI Incorporated, Ohio, USA). Soil pH was measured using a pH meter (soil:water = 1:2.5). SOC concentrations of the samples were determined by wet combustion with  $\text{K}_2\text{Cr}_2\text{O}_7$  (Jiang and Xu, 2006). Soil texture was measured using a Laser Particle Size Analyzer (Malvern

Instruments, Master Sizer 2000). According to the international classification standard of soil particle size, soil particle was classified into the clay ( $<2\text{ }\mu\text{m}$ ), silt ( $2\text{ } \sim 20\text{ }\mu\text{m}$ ), and sand ( $>20\text{ }\mu\text{m}$ ) (Wang et al., 2015). Soil total N (TN) of the surface soil layer was determined by a Kjeltec Analyzer Unit (Kjeltec 2300). Soil total P was determined by the vanadomolybdate yellow color method, after digestion of soil samples in a solution of  $\text{H}_2\text{SO}_4$  (98%)- $\text{HClO}_4$  (72%) (10:1; V: V) (Lu, 1999). For measuring POC, soil samples were dispersed using  $5\text{ g L}^{-1}$  sodium hexametaphosphate and placed on a reciprocating shaker ( $90\text{ rev min}^{-1}$ ) for 18 h (Cambardella and Elliott, 1992). The slurry was then poured over a  $53\text{ }\mu\text{m}$  sieve using deionized water. All of the material remaining on the sieve was further transferred into a dry vessel, oven-dried at  $60\text{ }^{\circ}\text{C}$  for 48 h and SOC was determined by the dichromate oxidation method. The other half of the fresh soil was used to measure Soil MBC and DOC. Soil MBC was determined by the fumigation-

extraction method, and 0.45 was used as an extraction efficiency coefficient to convert the difference between the fumigated and unfumigated soil (Wu et al., 1990). DOC was extracted from 10 g of fresh soil with 20 mL of distilled water (Wang et al., 2015). The extracted C concentration was determined by an automated TOC Analyzer (TOC-VCPH, SHIMADZU).

In the laboratory, after being washed using tap water and rinsed with purified water, the sampled leaf litter was oven-dried at 60°C to a constant weight. The dry mass of leaf litter was measured using an electronic balance. Coarse roots (>2 mm in diameter) were picked by hand, and fine roots (<2 mm) were collected over a 0.25 mm sieve. Fine roots were separated into live and dead (necromass) root fractions using 11% and 6% solutions of colloidal silica (Robertson and Dixon, 1993). The fine root fraction was further separated into low-order (the first two orders) and high-order roots (third-order or above). In the classification of fine roots, the distal roots were defined as first-order while second-order roots begin at the junctions of two first-order roots, and so forth (Pregitzer et al., 2002). Biomass of both the low- and high-order fine roots was obtained after drying at 60 °C to constant mass. Fine root samples were then ground to pass a 1 mm sieve and kept dry before chemical analysis. TOC concentrations of fine roots were measured by the method mentioned above.

#### 2.4. Fine-root production

Sequential root coring was used for studying fine root production. Soil cores were conducted in January, April, July, and October of 2017 with a coring device (10 cm diameter, 60 cm depth) in three quadrats (10 × 10 m) established in each intertidal zone. Within each quadrat, three soil cores were taken, hence 108 pairs of mixed samples were collected (three intertidal zones × three quadrats × three soil cores × four seasons). Mangrove fine root production was calculated by summing all production of fine roots between each pair of consecutive seasons according to the decision matrix (Fairley and Alexander, 1985). Production of fine roots between two consecutive seasons was calculated either by the differences in biomass and necromass or by only the differences in biomass. Since root sampling was not conducted in January 2018, the fine root production from October to January was estimated by the data that were collected in October of 2017 and January of 2017. The turnover rate of mangrove fine root was obtained by dividing annual fine root production by the mean biomass.

#### 2.5. Fine root decomposition

A fine root decomposition experiment was carried out using fine roots collected in November of 2016. After being separated from soil, the fine roots of each subsample were divided based on the root order. 9 subsamples (3 subsamples × 3 quadrates) from the same sampling zone were mixed by their root order together. Then, the mangrove fine roots were oven-dried at 60°C to constant weight. To prevent particles loss from nylon litter bags during the decomposition experiment, or during recovery of the bags and subsequent laboratory processing, 1 g (±0.01 g) of different order root samples were placed into 10 × 10 cm nylon litter bags with 0.1 mm pores to measure the decomposition rate of different order fine roots (Robertson and Alongi, 2016). Triplicates were applied for each root order. A total of 108 bags (3 intertidal zones × 3 quadrats × 2 root orders × 2 harvest times × 3 replicates) of samples were prepared. All bags were buried in a depth of 15 cm in the respective quadrants in January 2017. Three bags for each sample were retrieved in July 2017 and January 2018, respectively. The remaining mass in the litter bag was washed through a 0.15 mm sieve before being dried to constant weight at 60 °C and weighed.

$$\% \text{Mass remaining} (\% \text{yr}^{-1}) = \frac{\text{remaining fine root mass after one year}}{\text{initial fine root mass}} \times 100\%$$

$$\text{Decomposition mass fraction} (\% \text{yr}^{-1}) = 1 - \% \text{ Mass remaining} / \text{Mass remaining}$$

#### 2.6. The relative contribution of fine roots to soil

The relative contribution of low-order roots and high-order roots to the soil was calculated as follows

$$\text{Percent contribution} = \frac{\text{Annual remaining mass of low-order root} / \text{high-order root}}{\text{Total annual remaining mass of whole fine root}}$$

where:

$$\text{Annual remaining mass} = \text{Fine root production} \times \% \text{ Mass remaining}$$

$$\begin{aligned} \text{Total annual remaining mass of whole fine root} \\ = \text{Annual remaining mass of low-order root} \\ + \text{Annual remaining mass of high-order root} \end{aligned}$$

#### 2.7. Statistical analyses

One-way ANOVA, Duncan multi-comparisons, and principal component analysis (PCA) were applied to analyze the differences in samples taken from the seaward, transition and landward zones. Differences between high and low-order roots were analyzed using t-tests (SPSS 20.0). Redundancy analysis (RDA) and multiple stepwise regression analysis were employed to identify the main controls (i.e. soil properties and vegetation biomass) on the production and decomposition rate of mangrove fine roots using CANOCO 5.0 and SPSS. Mangrove fine root production and decomposition rate of low-order roots and high-order roots were selected as the response variables, while vegetation biomass of mangroves, soil total N, total P, pH, bulk density and salinity were set as explanatory variables in RDA. In addition, RDA was applied to analyze the influence of mangrove fine root production and decomposition on the ratio of SOC components. The production and decomposition rate of low-order and high-order fine roots are set as explanatory variables, while POC/SOC, MBC/SOC as well as DOC/SOC were set as response variables. Before RDA, the original data was  $\log(x + 1)$  transformed and standardized to avoid the influence of different data dimensions. The Monte Carlo test (999 times) was applied to forward select the significant explanatory variables at 0.05 significant level during the RDA process. The latent variable "Biotic & abiotic factors", "Production", "Decomposition", "POC/SOC" and "DOC/SOC & MBC/SOC" were set based on the measured variables that were selected by RDA and stepwise regression and the SEM was built using partial least squares in smartPLS 3.0. Path analysis and bootstrapping were conducted. The path coefficients were acquired, meanwhile, the reliability and validity of the model were verified. All results are represented as mean ± standard deviation and statistical significance was reported at  $\alpha = 0.05$  unless otherwise stated.

### 3. Results

#### 3.1. Vegetation biomass and soil properties in different intertidal zones

Average N, P concentrations clay content and silt content and salinity of topsoil in mangrove forests were significantly higher than those of mudflat ( $P < 0.05$ ) and they also significantly increased from the seaward to the landward (1.3 g·kg<sup>-1</sup>–1.9 g·kg<sup>-1</sup>, 149.7 mg·kg<sup>-1</sup>–346.7 mg·kg<sup>-1</sup>, 3.3 ppt–7.3 ppt, respectively for N, P and salinity) ( $P < 0.05$  Table 1). The pH and bulk density of mangrove soil however showed a significant decline trend across the sea-land gradient (5.7–5.2 and 0.74–0.55 g·cm<sup>-3</sup> for pH and soil bulk density) ( $P < 0.05$ ) and they were significantly lower than those in the bare flat. Soil clay and silt contents

**Table 1**  
Physico-chemical characteristics of the 0–20-cm soil layer and the vegetation biomass of mangrove forests in relation to different zones (mean ± SD).

	Location			
	Bare flat	Seaward zone	Transition zone	Landward zone
<b>Physico-chemical characteristics</b>				
Soil salinity (%)	1.1 ± 0.1A	3.3 ± 0.1B	4.7 ± 0.2C	7.3 ± 0.2D
Soil total N (g·kg <sup>-1</sup> )	0.6 ± 0.1A	1.3 ± 0.1B	1.6 ± 0.2C	1.9 ± 0.1D
Soil total P (mg·kg <sup>-1</sup> )	63.3 ± 5.8A	149.7 ± 19.8B	263.3 ± 25.2C	346.7 ± 50.3D
Bulk density(g·cm <sup>-3</sup> )	1.34 ± 0.05A	0.74 ± 0.05B	0.63 ± 0.03C	0.55 ± 0.03D
pH	6.1 ± 0.1A	5.7 ± 0.3B	5.6 ± 0.3B	5.2 ± 0.1C
Clay(%)	3.04 ± 0.3A	6.4 ± 0.68B	7.7 ± 1.63BC	9.3 ± 1.5C
Silt(%)	17.32 ± 1.2A	42.1 ± 1.6B	45.9 ± 4.3BC	50.5 ± 4.6C
Sand(%)	79.64 ± 1.2A	51.5 ± 0.9B	46.4 ± 6.3BC	40.2 ± 5.2C
<b>Mangrove vegetation</b>				
Above-ground biomass(t·ha <sup>-1</sup> )	–	39.93 ± 2.12 A	95.05 ± 14.73A	269.01 ± 55.59B
Below-ground biomass(t·ha <sup>-1</sup> )	–	26.91 ± 2.83A	36.47 ± 2.79A	94.84 ± 11.06B
Leaf litter biomass (g·m <sup>-2</sup> )	–	4.4 ± 1A	8.1 ± 1.8A	93.6 ± 9.9B

Different capital letters indicate significant differences among zones (P < 0.05).

significantly increased across the sea-land gradient, while sand content showed an obvious decreasing trend (P < 0.05). The comprehensive variation of soil properties (i.e. soil pH, total N concentration, total P concentration, clay content, silt content, sand content, bulk density as well as soil salinity) across the sea-land gradient is given in [Supplementary material \(STable 2 & SFig. 1\)](#). It can be observed that mangrove vegetation biomass also showed a significant increase from the seaward to the landward (P < 0.05, [Table 1](#)) with AGB and BGB of 39.93–269.01

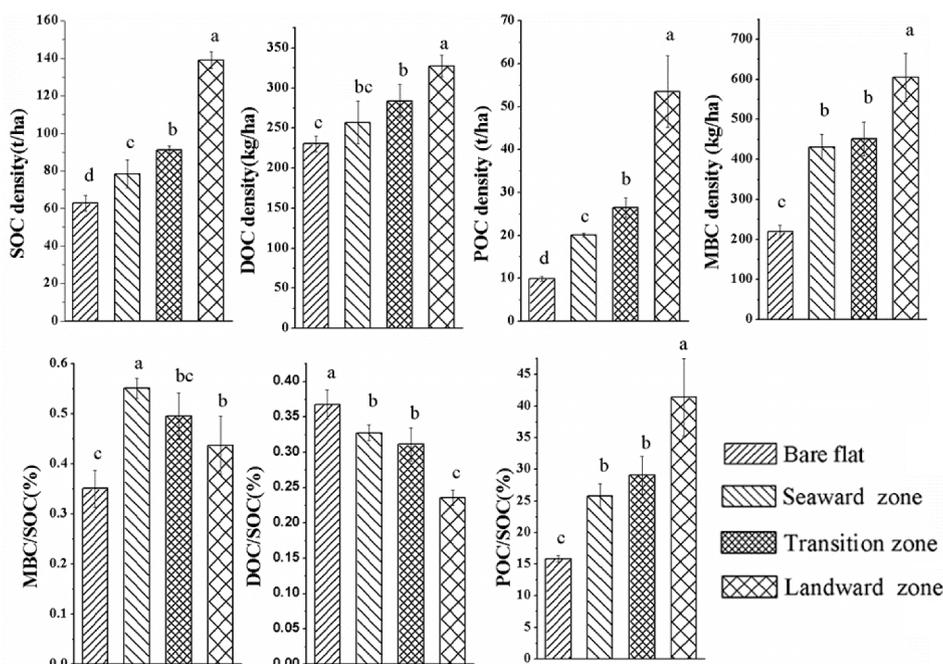
t·ha<sup>-1</sup> and 26.91–94.84 t·ha<sup>-1</sup>, respectively. The average leaf litter biomass in seaward zones was also significantly higher than that of in seaward and transition zones.

### 3.2. SOC, POC, and DOC of the different intertidal zones

SOC density of mangrove forests significantly increased across the sea-land gradient with a range of 78.42–139.01 t·ha<sup>-1</sup> and is significantly higher than that of mudflat (62.88 t·ha<sup>-1</sup>) (P < 0.05). POC density, MBC density, and DOC density showed a similar trend with SOC density. The value locating in landward (58.71 t·ha<sup>-1</sup>, 605.9 kg·ha<sup>-1</sup>, 327.6 kg·ha<sup>-1</sup>) was also significantly higher than those in seaward zones (20.13 t·ha<sup>-1</sup>, 431.6 kg·ha<sup>-1</sup>, 256.9 kg·ha<sup>-1</sup>) and transition zone (27.12 t·ha<sup>-1</sup>, 452.0 kg·ha<sup>-1</sup>, 283.9 kg·ha<sup>-1</sup>) ([Fig. 2](#)). The ratio of POC to SOC (POC/SOC) in mangrove forests ranged from 25.8 to 41.4% and it was significantly higher than that in the mudflat (15.87%) (P < 0.05). Moreover, the increase of POC from mudflat to the seaward zone accounted for 65.11% of SOC increment. Moreover, from the seaward zone to the transition zone, the increase of POC accounted for 54.5% of SOC increment. From the transition zone to the landward zone, the increase of POC accounted for 66.1% of the total SOC increment. These results suggested that the increase of SOC was attributed largely to the increment of POC. MBC/SOC and DOC/SOC only accounted for 0.44–0.55 and 0.24–0.33% respectively and showed a decreasing trend from the seaward zone to the landward zone (P < 0.05) ([Fig. 2](#)).

### 3.3. Fine root biomass, necromass, production and turnover rate across the sea-land gradient

Annual mean fine root biomass (<2 mm) increased from seaward (207.3 g·m<sup>-2</sup>) to landward zone (343.4 g·m<sup>-2</sup>). Low-order fine roots accounted for 65.6%–79.3% of fine root biomass (<2mm). The biomass of low-order fine roots varied significantly among seasons in the same zone ([STable 3](#)). However, the biomass of higher-order fine roots remained relatively stable. Moreover, fine root necromass also increased significantly from seaward to landward gradient across four seasons (P < 0.05). Low-order fine roots accounted for 86.2–88.4% of the fine root necromass. Similar to fine root biomass, low-order root necromass also



**Fig. 2.** Density of soil organic carbon fraction and the percentage of organic carbon fraction in different zones (mean ± S.D.). Different lowercase letters indicate significant differences among zones (P < 0.05).

varied significantly among seasons.

The production of mangrove fine roots was significantly higher ( $P < 0.05$ ) in the landward ( $510.9 \text{ g}\cdot\text{m}^{-2}$ ) than that in the seaward ( $90.9 \text{ g}\cdot\text{m}^{-2}$ ) and transition ( $191.8 \text{ g}\cdot\text{m}^{-2}$ ) zones (Table 2). Low-order roots accounted for the most (83.04%–88.6%) of the overall fine root production in the three zones. The turnover rate of mangrove fine roots ranged from  $0.44 \text{ yr}^{-1}$  to  $1.49 \text{ yr}^{-1}$  and the highest and lowest values were found in the landward and seaward zone, respectively (Table 2). The turnover rates of mangrove low-order fine roots were 0.47, 0.78, and  $1.64 \text{ yr}^{-1}$  for the seaward, transition, and landward zone, respectively. The turnover rates of high-order fine roots were 0.33, 0.23, and  $0.85 \text{ yr}^{-1}$ , in the seaward, transition, and landward zone, respectively. The turnover rate of low-order mangrove roots was significantly higher than that of the high-order fine roots ( $P < 0.05$ ).

### 3.4. Decomposition of mangrove fine roots and chemistry of root tissues

After one year of decomposition, 58.3–80.8% of fine root mass remained in the soil (Fig. 3). The remaining mass fractions of fine roots in both branching-order groups increased across the sea-land gradient. In other words, the highest values occurred in the landward zone, while the lowest occurred in the seaward zone. The remaining mass fraction of low-order mangrove fine roots was significantly higher than that of high-order roots in the same sampling zone ( $P < 0.05$  Fig. 3). According to the remaining mass fraction, the decomposition mass fraction was 19.2%–30.5% and 30.8%–41.7% for low-order and high-order roots, respectively. The decomposition mass fraction of both high-order and low-order fine roots decreased across the sea-land gradient. Combined with fine root production, the relative contributions of low-order mangrove fine roots to soil organic matter accumulation were 85.4–90.2%.

### 3.5. Multivariate statistical analysis

The relationship of soil properties and vegetation biomass of mangroves to the production and decomposition of fine roots was analyzed by setting soil physical and chemical properties (i.e. soil salinity, total P concentration, total N concentration, bulk density, clay content, silt content, sand content, and pH) and vegetation biomass as explanatory variables along with the production and decomposition of fine roots as response variables. After the Monte Carlo test (999 iterations,  $P < 0.05$ ), vegetation biomass and soil salinity remained in the RDA model, explaining 91.2% of the mangrove fine root production and decomposition rate variation (Fig. 4). Details of the Monte Carlo test are given in the Supplementary material (Table 4). The first axis, which was positively correlated with mangrove vegetation biomass and salinity, explained 90.9% of the change in the response variable. Hence, the first axis reflected the influence of mangrove biomass and salinity on the production and decomposition rate of mangrove fine roots. In addition, based on the sample score, the samples are distributed across the sea-land gradient. These results suggested that the vegetation biomass of

mangroves and soil salinity are the dominant controls of mangrove fine root production and decomposition. Stepwise regression equations regarding the significant controls of mangrove fine root production and decomposition are summarized in Table 3. Production of low-order fine roots was significantly associated with vegetation biomass and soil salinity ( $P < 0.01$ ), while the production of high-order fine roots was significantly related to vegetation biomass ( $P < 0.01$ ). The decomposition of both low-order and high-order fine roots was also significantly affected by soil salinity ( $P < 0.01$ ).

In order to clarify the relationship of the production and decomposition of fine roots to the ratio of SOC components, RDA was conducted by setting POC/SOC, MBC/SOC as well as DOC/SOC as response variables and the production and decomposition of low-order and high-order fine roots as explanatory variables (Fig. 5). After a forward selection using the Monte Carlo test, only the production of low-order fine roots remained the significant variable affecting the ratio of SOC component ratios, and it reflected 90.9% of eigenvalues. Details of the Monte Carlo test are summarized in the Supplementary material (Table 5). The first axis could explain 90.9% of the changes in the ratio of SOC components and it was positively correlated with the production of low-order fine roots. Hence, the first axis reflected the influence of low-order fine root on the ratio of SOC components. In addition, the distribution of samples along the first axis confirmed that the change in the production of low-order fine roots along the sea-land gradient was the dominant control of the ratio of SOC components. It should be noticed that the production of low-order fine roots was positively associated with POC/SOC, but negatively correlated with MBC/SOC and DOC/SOC.

RDA and stepwise regression showed that soil salinity and vegetation biomass are the most important factors influencing the production and decomposition of fine roots which played a significant role in SOC component ratios. Therefore, an SEM was built to analyze how soil salinity and vegetation biomass affect SOC component ratios. In the SEM, the latent variable “Biotic & abiotic factors” referred to vegetation biomass and soil salinity, “Production” the production of the low-order and high-order fine roots, “Decomposition” the decomposition of the low-order and high-order fine roots. Outer loading of this SEM ranged from 0.944 to 1.000, showing that these latent variables could well reflect the change of measured variables. The  $R^2$  of variables were all higher than 0.861. Reliability and validity indexes of the SEM are shown in Table 4. As shown in Fig. 6, the path coefficient of Biotic & abiotic factors-Production, Biotic & abiotic factors-Decomposition as well as Production-POC/SOC were significant ( $P < 0.001$ ), nevertheless, the path coefficients of Production-DOC/SOC & MBC/SOC and Decomposition- DOC/SOC & MBC/SOC were not significant ( $P > 0.05$ ). In addition, the path coefficient of Biotic & abiotic factors-Production-POC/SOC was 0.914 ( $P < 0.001$ ), indicating that fine root production affected by vegetation biomass and soil salinity played an important role in POC/SOC change.

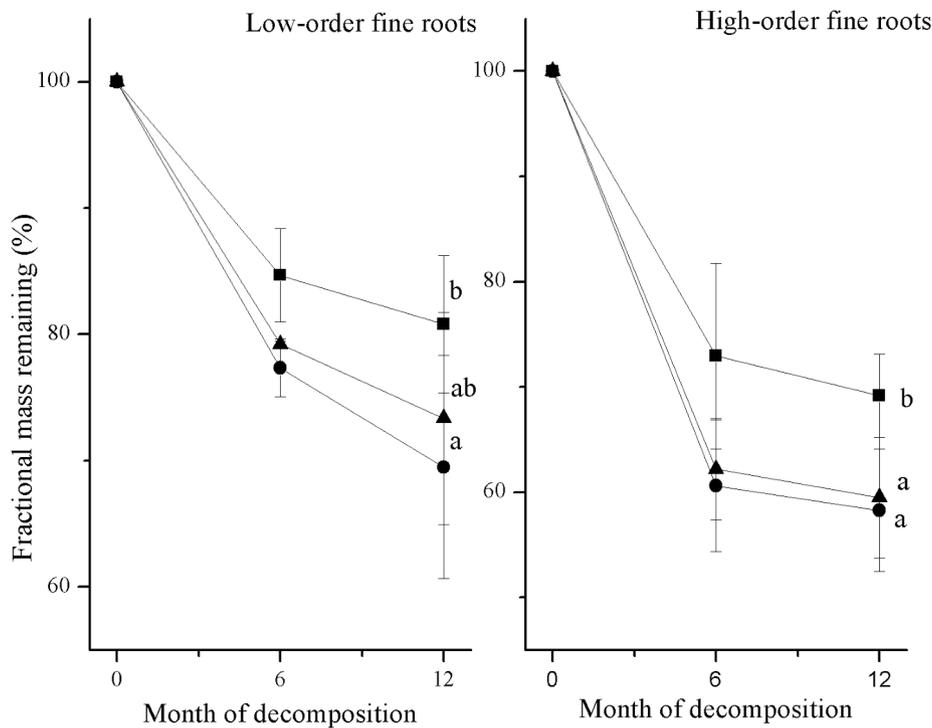
## 4. Discussion

### 4.1. Significant biotic and abiotic factors influencing mangrove fine root production and decomposition

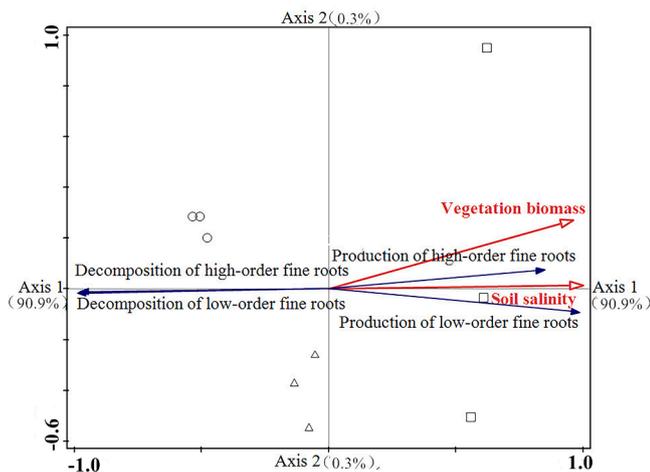
RDA and stepwise regression indicated that vegetation biomass was the key biotic factor influencing the production of mangrove low-order and high-order fine roots. In particular, the production of mangrove fine roots increased with the increase of vegetation biomass. The increase of vegetation biomass indicates an increase in primary productivity, which further leads to an increase in fine root production (Pregitzer and Euskirchen, 2004; Wen, 1999; Yuan and Chen, 2010). It could be also observed that the production of fine roots and vegetation biomass showed an increasing trend across the sea-land gradient. In most cases, the forest age of mangroves increases across the sea-land gradient (Fromard et al., 2004; Hayes et al., 2017; Marchand, 2017). The

**Table 2**  
Production, turnover rate of mangrove fine roots (mean  $\pm$  SD).

Location	Production ( $\text{g m}^{-2}\text{yr}^{-1}$ )		Total	Turnover rate ( $\text{yr}^{-1}$ )		Total
	Low order	High order		Low order	High order	
Seaward zone	75.5 $\pm$ 6.0Aa	15.4 $\pm$ 4.1Ab	90.9 $\pm$ 9.9A	0.47 $\pm$ 0.04Aa	0.33 $\pm$ 0.09 Ab	0.44 $\pm$ 0.02 A
Transition zone	166.9 $\pm$ 19.6Ba	25 $\pm$ 7.2Ab	191.8 $\pm$ 21.3B	0.78 $\pm$ 0.12Ba	0.23 $\pm$ 0.07Ab	0.59 $\pm$ 0.09B
Landward zone	452.9 $\pm$ 34.4Ca	58.1 $\pm$ 4.1Bb	510.9 $\pm$ 38.6C	1.64 $\pm$ 0.06Ca	0.85 $\pm$ 0.02Bb	1.49 $\pm$ 0.05C



**Fig. 3.** Fractional mass remaining during litter decomposition of fine roots in different zones and root branching orders (mean  $\pm$  S.D.). Different lowercase letters indicate significant differences in the branching order of different zones ( $P < 0.05$ ). Circles, triangles, and squares referred to the samples taken from seaward, transition, and landward zone, respectively.



**Fig. 4.** Redundancy analysis (RDA) of the production and decomposition of mangrove fine roots, vegetation biomass along with soil properties. Circles, triangles and squares referred to the samples taken from seaward, transition and landward zone, respectively.

mangrove margins expanded outward during the development of mangrove in Yingluo Bay. Consequently, the age of mangrove forests in the landward zone is much older than that in the seaward zone (Zhu et al., 2011, 2013). As the vegetation biomass increases with the age of mangrove forest, thus the production of mangrove fine roots increased constantly across the sea-land gradient. Adame et al. (2014) and Xiong et al. (2016) found that the biomass of fine roots was positively associated with their production, which was in line with our study. Results of stepwise regression (Table 3) demonstrated that the increase of soil salinity was beneficial for the increment of mangrove low-order fine root production. Low-order fine roots of mangroves are critical to water and nutrients uptake (McCormack et al., 2015). The increase of soil salinity is

**Table 3**

Stepwise regression of production and decomposition of fine roots with soil properties and vegetation biomass.

	Regression Equation	R <sup>2</sup>	R <sub>adj</sub> <sup>2</sup>	P value
PL	PL = 0.65Vegetation biomass + 47.07salinity-130.74	0.995	0.993	<0.01
PH	PH = 0.139Vegetation biomass + 6.84	0.943	0.934	<0.01
DL	DL = -2.87Soil salinity + 40.11	0.867	0.848	<0.01
DH	DH = -2.81Soil salinity + 52.05	0.773	0.741	<0.01

PL, PH, DL, DH are abbreviation of production of low-order fine roots, production of high-order fine roots, decomposition of low-order fine roots, decomposition of high-order fine roots respectively.

adverse to water uptake by mangrove fine roots and hence the increase of mangrove fine root production should be an adaption of mangroves to the increment of soil salinity (Adame et al., 2014; Ball, 1988). Consequently, soil salinity was positively correlated with the production of mangrove low-order fine roots.

Based on RDA and stepwise regression, soil salinity was found as the most significant abiotic factor affecting the decomposition of mangrove fine roots (Fig. 4 and Table 3). It suggests that the increase of soil salinity is adverse to the decomposition of mangrove fine roots. The increase of soil salinity is often seen as adverse to physical or chemical leaching of DOC from dead roots and hence reduces its decomposition by microorganisms at the early stage of fine root decomposition (Olsen et al., 1996). Also the increase of salinity inhibits soil microorganisms and thus reduces the decomposition of acid-nonhydrolyzable organic matter (lignin, e.g.) at the intermediate stage of fine root decomposition (Cotrufo et al., 2015; Luo et al., 2017; Wang et al., 2016). Also, the variation of soil salinity was coupled with soil redox potential change across the sea-land gradient, and they could affect microbial community structures comprehensively and hence impact fine root decomposition (Marchand, 2017; Stagg et al., 2017; Yan et al., 2015). The very similar trend of DOC/SOC, MBC/SOC as well as soil salinity likely indicated that soil salinity might affect the leaching of DOC from mangrove fine roots

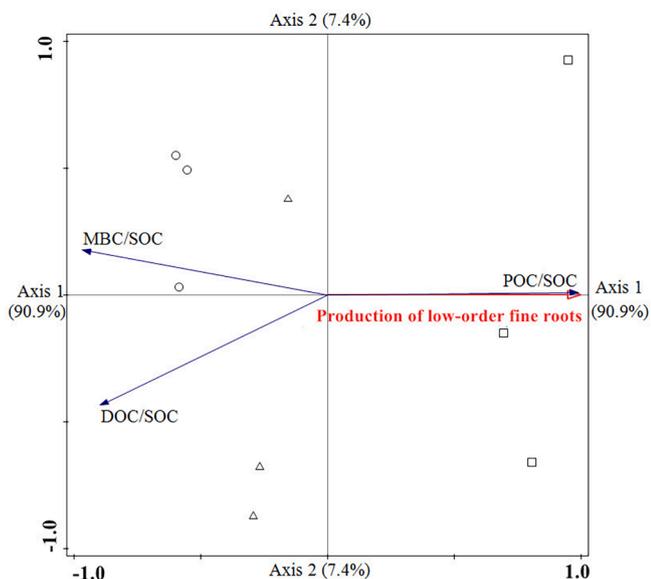


Fig. 5. Redundancy analysis (RDA) of the production and decomposition of mangrove fine roots and the ratios of SOC components. Circles, triangles and squares referred to the samples taken from seaward, transition and landward zone, respectively.

and hence inhibit soil microbes and consequently reduced the decomposition of mangrove fine roots. The increase of soil salinity has been found to be adverse to soil microorganisms in previous studies (Shah and Shah, 2011; Yan et al., 2015). With the increase of soil salinity, MBC/SOC decreased significantly, indicating that the increase of soil salinity inhibits microbial activities and hence the decomposition of mangrove fine roots.

4.2. Influencing path of soil biotic & abiotic factors-mangrove fine roots-SOC components

SOC density varied across the sea-land gradient, similar to the tendency of vegetation biomass of mangroves and mangrove fine root production, but opposite to the variation of soil salinity and mangrove fine root decomposition, indicating that biotic and abiotic factors resulted from the sea-land topographic and hydrologic gradient, as well as the production and decomposition of mangrove fine roots were likely to be important factors affecting SOC accumulation. Though leaf litter was considered as an important source of soil C pool (Kristensen et al., 2008), in mangrove forest it only accounted for 17.4%, 11.2%, and 9.6% of the corresponding average dead fine root biomass in the seaward, transition, and landward zones, respectively. Due to the export of aboveground mangrove litter by tides, mangrove root systems contributed more to SOC accumulation (Chen and Twilley, 1999; Ono et al., 2015). RDA results showed that the production of low-order fine roots played an important role in SOC components (Fig. 5), suggesting that mangrove fine roots were a significant contributor to SOC accumulation in the mangrove forest ecosystem.

As discussed above, vegetation biomass and soil salinity were respectively the most important biotic and abiotic factors affecting the

production and decomposition of mangrove fine roots. The production and decomposition of mangrove fine roots nevertheless were important to SOC accumulation. SEM, moreover, showed that biotic and abiotic factors (i.e. vegetation biomass and soil salinity) could affect POC/SOC by influencing mangrove fine root production (Fig. 6). In our study, the production of mangrove fine roots in the landward zone was 5.62 times that in the seaward zone, while POC/SOC in the landward zone was 1.6 times higher than that of in the seaward zone. The path coefficient of “Production-POC/SOC” was 0.928 (P < 0.001). These results indicated that fine root production was an important source of POC in the mangrove forests. The increase of production and turnover rate of mangrove fine roots may indicate more root debris entered the soil carbon cycle (Matamala et al., 2003; Tamooch et al., 2008; Yang et al., 2004), which promotes the accumulation of soil POC and SOC. POC accounted for a large part of SOC increment (54.5%–66.1%), therefore, the increase of SOC could be largely attributed to the increase of fine root production. As a consequence, POC accumulation due to the production of mangrove fine roots should be the main cause of SOC accumulation in the mangrove ecosystem. Although previous researches have reported that fine root production also promoted the increment of MBC and DOC due to the root secretion during the growth of roots (Luglia et al., 2014; Sun et al., 2017), our study showed that the path coefficients of “Production-DOC/SOC & MBC/SOC” was not significant (P > 0.05), indicating that the influence of mangrove fine root production on DOC/SOC and MBC/SOC was relatively small. DOC and MBC were affected by the decomposition process of plant residues (Cotrufo et al., 2015). Due to the frequent tidal scour, soil DOC and MBC originating from root production could be easily washed away (Alongi, 2014; Wang et al., 2015). It should be noticed that the variations in the production of

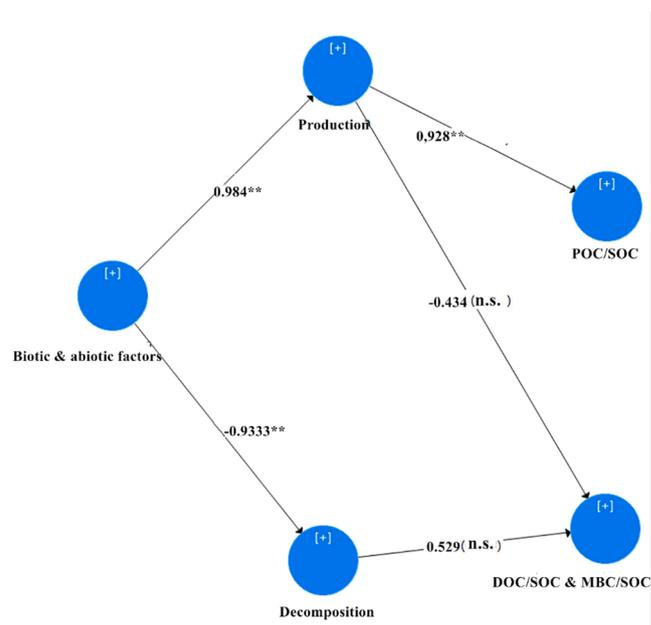


Fig. 6. The structural equation modeling (SEM) for pathway analysis of fine roots attributes to SOC accumulation in mangrove. \*\* referred to P < 0.01; \* referred to P < 0.05, n.s. indicates no significance.

Table 4 Reliability and validity of structural equation model.

	Cronbach's Alpha	CR	AVE	DOC/SOC and MBC/SOC	POC/SOC	Decomposition	Production	Biotic & abiotic factors
DOC/SOC and MBC/SOC	0.889	0.947	0.900	0.949				
POC/SOC	1.000	1.000	1.000	-0.796	1.000			
Decomposition	0.937	0.970	0.941	0.947	-0.818	0.970		
Production	0.989	0.995	0.989	-0.943	0.928	-0.963	0.995	
Biotic & abiotic factors	0.979	0.990	0.980	-0.915	0.939	-0.933	0.984	0.990

low-order fine roots along the sea-land gradient were the dominant control of the ratios of SOC components (Fig. 5). The relative contributions of low-order mangrove fine roots to soil organic matter accumulation were 85.4–90.2%. Compared to high-order fine roots, low-order fine roots showed obvious seasonal variations, therefore, low-order roots accounted for most of fine root production (83.0%–88.6%) (Table 2). The turnover rate of low order root was 0.47, 0.78, and 1.64  $\text{yr}^{-1}$ , which was higher than that of the high-order fine root (0.33, 0.23 and 0.85  $\text{yr}^{-1}$ ). Hence, lower-order roots are the fast-cycling units in mangrove fine root systems compared to high-order fine roots. In addition, low-order fine roots accounted for a large amount of underground biomass compared with high-order fine roots. As a comparison, Xiong et al. (2016) reported that low-order roots of mangroves were estimated to contribute 43–82% of their total fine root biomass which was similar to our results (65.6%–79.3%). The contribution of low-order fine roots of the terrestrial forest was much lower than in our study. According to Lin and Zeng (2017), the biomass of low-order fine roots (including the first and second orders) in a terrestrial forest accounted only for 24% of total fine roots biomass. McCormack et al. (2015) also found the biomass of low-order (including the first three orders) accounted for 11–58% of the total biomass of fine roots in woody forest ecosystems. For all these reasons low-order fine roots through their production are of great importance for SOC accumulation in mangrove forests.

SEM illustrated that the decomposition of mangrove fine roots have a relatively small impact on DOC/SOC and MBC/SOC ( $P > 0.05$ ), although previous studies found a positive relationship among DOC/SOC, MBC/SOC, and so soil organic matter decomposition (Chen et al., 2016; Deng et al., 2016; Yan et al., 2019). Soil DOC/SOC and MBC/SOC in terrestrial forest ecosystem ranged from 0.8–1.26% and 1–4% respectively, however, which are much higher than those in the mangrove of Yingluo Bay (Jiang and Xu, 2006; Sparling, 1992; Zhang et al., 2009). Higher soil salinity and anoxic conditions of mangrove habitat also weaken the correlation of fine root decomposition with soil DOC and MBC (Ouyang et al., 2017). In addition, tidal flooding might also take away a large part of DOC originating from mangrove decomposition (Alongi, 2014; Wang et al., 2015). Therefore, the decomposition of mangrove fine roots has a minor influence on MBC and DOC. Though previous studies reported that the small-organic molecules resulting from decomposition by microorganism might reform into mineral combined organic C and be stabilized in soil and be a pathway of SOC accumulation in the terrestrial forest ecosystem (Cotrufo et al., 2015), the slow decomposition rate of fine roots due to the special environment of mangrove habitat indicated that the amount of small organic molecules in soil due to the decomposition of mangrove fine roots is likely very low. Besides, the highest decomposition rate of mangrove fine roots occurred in the seaward zone, which was about 1.35–1.59 times of those in the landward zone, while the production of mangrove fine roots in the landward zone was 5.62 times of that in the seaward zone. It was also suggested that the decomposition of mangrove fine roots have a minor effect on SOC accumulation, compared to the production of mangrove fine roots. Even though the decomposition of mangrove fine roots has a smaller effect on SOC accumulation, it should be noticed that opposite to the change of mangrove fine root production, the decomposition of mangrove fine roots decreased across the sea-land gradient, which may exacerbate the increment of SOC accumulation across the sea-land gradient.

## 5. Conclusions

The production of mangrove fine roots increased while their decomposition decreased across the sea-land gradient in the mangrove forest ecosystem of Yingluo Bay. The production of mangrove fine roots was enhanced by the increase of mangrove vegetation biomass. Nevertheless, soil salinity was the main inhibitor of mangrove fine root decomposition. SOC along with its components such as POC, DOC, and MBC increased across the sea-land gradient. The production of low-

order fine roots was the major control of the ratios of SOC components, which accounted for 90.9% of SOC component ratio changes. SEM showed the influence path of biotic and abiotic factors-fine root production and decomposition -SOC component ratios. The increment of fine root production due to the increase of vegetation biomass and soil salinity is the main drive of POC/SOC increase. Nevertheless, mangrove fine root decomposition played a minor role in SOC component changes. Collectively our results indicated that although the accumulation of SOC in mangrove ecosystems was a comprehensive result of the production and decomposition of mangrove fine roots, the production of low-order fine roots plays a vital role in the accumulation of SOC.

## CRedit authorship contribution statement

**Yasong Zhang:** Investigation, Writing - original draft, Writing - review & editing. **Ling Xiao:** Writing - original draft, Writing - review & editing. **Dongsheng Guan:** Investigation, Writing - original draft, Writing - review & editing. **Yujuan Chen:** Investigation. **Mikael Motelica-Heino:** Writing - review & editing. **Yisheng Peng:** Investigation. **Shing Yip Lee:** Writing - original draft.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107525>.

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