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# Microcosm study on fate and dynamics of mangrove tannins during leaf litter leaching

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## Abstract

**Background** Mangrove tannins can participate in wetland biogeochemical cycling. However, their fate and dynamics during leaf litter leaching have yet to be elucidated in coastal aquatic environments.

**Methods** By using a simulated microcosm experiment, changes in leaf litter mass and tannin compounds, including total phenolics (TP), extractable condensed tannins (ECT), and bound condensed tannins (BCT), were examined in the litters and leachates of four common mangrove species: *Kandelia obovata* (Ko), *Aegiceras corniculatum* (Ac), *Sonneratia apetala* (Sa), and *Avicennia marina* (Am).

**Results** Leaching caused a notable decline in litter mass, TP, and ECT in the leaf litter of Ko, Ac, Sa, and Am, while BCT increased significantly in Ko and Ac. Loss in foliar TP was higher than in leaf litter mass, and loss in foliar ECT was higher than in TP of Ko and Ac, but Sa showed the opposite result. The temporal changes of TP and ECT concentrations in leachates followed a similar trend, with an initial increase followed by a decrease. ECT dynamics in Ko and Ac leachates correlated with their TP concentrations, while in Sa leachate, the peak ECT occurred 72 h later than its TP peak. The leachate ECT concentrations were highest in Ac, followed by Ko, and significantly lower in Sa. The peak TP and ECT proportions in leachates accounted for 9.2–23.9% and 7.7–9.4% of the total decreases in foliar TP and ECT, respectively.

**Conclusion** During the leaching process, tannins' fate was species-specific, while the dynamics were almost similar.

**Keywords** Mangrove tannins, Leaf litter decomposition, Leaching, Total phenolics, Condensed tannins

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## Introduction

Mangrove forests occupy approximately 170,600 km<sup>2</sup> along tropical and subtropical estuary wetlands and shallow coastlines worldwide, making up a unique vegetated ecosystem in intertidal regions (Bayen 2012; Lovelock et al. 2015). Mangroves are considered “green littoral guardians” since they possess potent ecological functions (Brander et al. 2012; Lovelock et al. 2015). Specifically, mangrove plants can serve as a vast carbon sink and offer detritus for food chains (Loneragan et al. 1997). The large, widely distributed, and stable root systems of mangrove plants not only act as a safe shelter for aquatic animals, including fish, shrimp, snails, and other aquatic organisms (Nagelkerken et al. 2008) but also spontaneously protect coastal buffer zones against natural disasters (Tamin et al. 2011).

Mangrove forests are highly productive ecosystems and are one of the richest carbon storages in the world (Donato et al. 2011). Although mangroves take up only 0.5% of the global coastal regions, they contribute 10–15% of the carbon storage from their living sediments (Alongi 2014). Mangrove forests also output tens of thousands of leaves functioning as the primary sources of organic matter through decomposition (Feller et al. 2010; Ndayambaje et al. 2022). Indeed, litter from estuarine mangroves comprises the largest proportion (30–60%) of total primary productivity in mangrove ecosystems (Bunt et al. 1979) and accounts for 40–95% of carbon storage (Wafar et al. 1997). Mangrove leaf litter is decomposed through various biotic or abiotic physicochemical procedures (Facelli and Pickett 1991), and litterfall is a primary pathway for the transfer of nutrients and energy to primary producers, consumers, and decomposers within a mangrove ecosystem (Robertson et al. 1992; Starr et al. 2005). Litter also plays a key role in the biogeochemical cycles of multiple essential elements in mangrove ecosystems, such as nitrogen, carbon, phosphorus, sulfur, iron, etc., and litterfall is an essential bridge linking mangrove plants and sediments (Attiwill and Adams 1993; Alongi 2014; Li et al. 2017).

Leaf and its litter contain a series of specific, crucial, and abundant secondary metabolites, especially vegetable tannins, the largest subgroup of natural macromolecular phenolic compounds (Salminen 2018). Tannins extracted from mangrove leaves can be classified into two types, hydrolysable tannins (HT) and condensed tannins (CT), and the latter type includes extractable condensed tannins (ECT) and bound condensed tannins (BCT). BCT can be further divided into protein-bound condensed tannins (PBCT) and fiber-bound condensed tannins (FBCT) (Hernes et al. 2001; Lin et al. 2006). A considerable number of studies have revealed that tannins, especially CT, are the key potential driving factors

for multifarious ecological processes in mangrove ecosystems, such as allelopathy (Lang et al. 2021), heavy metal chelation (Lang et al. 2023), carbon and nitrogen resorption (Kraus et al. 2004; Maie et al. 2008; Zhou et al. 2012), and microbial diversity alterations (Zhang et al. 2020). Lang et al. (2021) found that the purified CT (PCT) from *Kandelia obovata* and the leachate of *K. obovata* leaf litter acted as bioactive allelopathic compounds and exerted obvious inhibitory effects on the germination and growth of another mangrove species, *Aegiceras corniculatum*. Another recent study reported that tannins from *K. obovata* and *Avicennia marina* could chelate six kinds of widely distributed heavy metals (Cd, Zn, Cu, Pb, Cr, and Ni) in sediments of a subtropical mangrove swamp and spontaneously involved in the biogeochemical cycles of heavy metals within mangrove ecosystems (Lang et al. 2023). Plant tannins are also considered an important driver of immobilization and mineralization of nutrient elements, such as carbon and nitrogen (Kraus et al. 2004; Maie et al. 2008). Specifically, the additions of tannic acid extracted from 5 different tree species induced a similar decrease trend in carbon dynamics, namely carbon mineralization in forest soil for 30 days (Kraus et al. 2004).

Meanwhile, all these tannins could decrease N mineralization during 30 days of incubation (Kraus et al. 2004). In mangroves, tannins extracted and purified from senescent yellow leaves of a red mangrove species (*Rhizophora mangle*) could bind and precipitate dissolved organic nitrogen from aquatic environments and sediments (Maie et al. 2008). BCT, especially PBCT, in leaves of *K. obovata* was notably enhanced during leaf litter decomposition, and the increased CT contributed significantly to humification effects and prevented the loss of nitrogen nutrients in mangrove sediments by N immobilization (Zhou et al. 2012). Crude PCT extracted from senescent *R. mangle* leaves could induce the appearance of both prokaryotic and eukaryotic communities, potentially correlated with mineralizing nutrition elements, such as carbon, nitrogen, and phosphorus (Zhang et al. 2020).

The tannin components in leaf vary substantially among different mangrove species; specifically, *K. obovata* and *A. corniculatum* are rich in CT (Zhou et al. 2012; Wei et al. 2012; Feng et al. 2019), *A. marina* includes micromolecular HT (Zhou et al. 2010), and *Sonneratia apetala* contains approximately 86% HT and 14% CT (Zhou 2012). Our previous study compared TP and ECT concentrations and ECT profiles in seedlings and organs (root, stem, and leaf) of eight mangrove species in South China (Wang et al. 2014). However, the changes and dynamics of TP and ECT during leaf litter decomposition, particularly leaching that follows the entire decomposition process, have yet to be systematically studied in aquatic environments,

and variations among mangrove species are seldom known. The present study, based on a microcosm leaching experiment, aims to (1) examine the alterations in litter mass, TP, ECT, and BCT in leaf litter of four mangrove species, namely *K. obovata*, *A. corniculatum*, *S. apetala*, and *A. marina* after 216 h of the leaching process; (2) determine the dynamics of mangrove TP and ECT in leachates during 216 h of leaching of mangrove leaf litter; and (3) characterize the dynamics of litter leaching using a model to fit the time courses of the TP and ECT concentrations in leachates. The four species are typical dominant mangrove plants widely distributed in the tidal zones of southeastern China, with *K. obovata*, *A. corniculatum*, and *A. marina* being the native species, while *S. apetala* is an exotic species (Li et al. 2015; Feng et al. 2019). The present study will enhance our understanding of the fate and dynamics of TP and ECT during leaf litter leaching in natural mangrove forests. Not only that, but this microcosm study was conducted in the laboratory of the Guangdong Neilingding Futian Mangrove National Nature Reserve, China, and this well-protected wetland is listed as a site in the Ramsar Convention on Wetlands of International Importance. Hence, the research on mangrove tannin dynamics in the reserve is also crucial for further exploring its potential ecological processes, such as energy flow and biogeochemical cycles of nutrients (carbon stocks, nitrogen immobilization, etc.) and contaminants (organic pollutants and heavy metals).

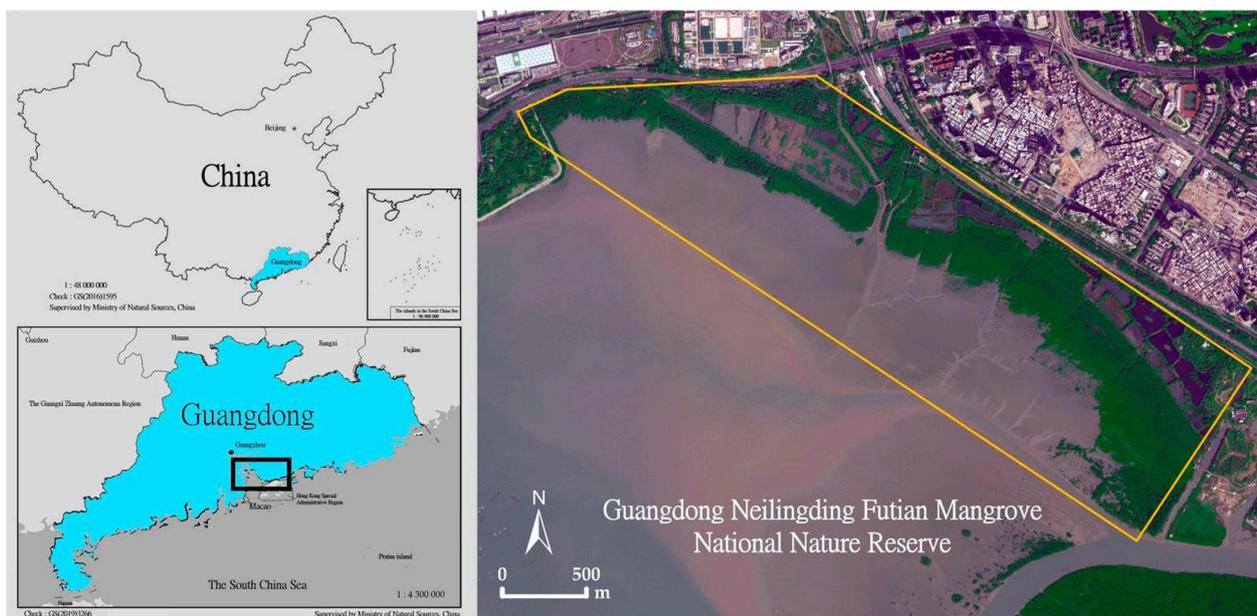
## Materials and methods

### Description of the sampling site

The sampling site was in the Guangdong Neilingding Futian Mangrove National Nature Reserve ( $22^{\circ} 32' 21'' - 22^{\circ} 32' 46''$  N,  $113^{\circ} 45' 18'' - 113^{\circ} 45' 49''$  E, Fig. 1, Lang et al. 2021), which is located on the northeastern coast of Shenzhen Bay, Shenzhen, China. The reserve covers approximately 367.64 ha of riverine mangrove forest. The mangrove plant community consists mostly of *K. obovata*, *A. corniculatum*, *A. marina*, and *S. apetala* that occupy almost 90% of the canopy layer in the mangrove forest. The region has a subtropical monsoon climate with some exceptions. The year-round weather of the reserve is warm, humid with a mean annual temperature of  $22^{\circ}\text{C}$  and a mean annual precipitation of 1927 mm. The average relative humidity is 79%. The reserve is subjected to semi-diurnal tides with a tidal amplitude range of  $-0.96$  to  $0.41$  m. In the reserve, various kinds of litter from different mangrove species with varying degrees of decomposition are found on the surfaces of the sediments, and the humus content in sediments reaches up to approximately 4%.

### Leaf litter collection

Yellowish senescent leaves from the four dominant species, namely *K. obovata*, *A. corniculatum*, *A. marina*, and *S. apetala*, were randomly collected from the sampling site (Fig. 1) during the growing season 2016. The leaves of each mangrove species were either freshly fallen or



**Fig. 1** A map of the Guangdong Neilingding Futian Mangrove National Nature Reserve, Shenzhen Bay, China (sampling location, Lang et al. 2021)

felled immediately after gently shaking the branch from an individual tree. For each species, 30 pieces of leaves were randomly sampled from 3–5 mangrove trees. The sampled leaves were stored in bilayer polyvinyl plastic bags and immediately brought back to the laboratory of the reserve. All leaves were gently cleaned using cotton swabs and then cleansed using deionized water three times. These leaves were then left to air-dry for 12 h until no visible water droplets were observed on their surfaces. The pre-treated samples were ready for use in the following microcosm experiment.

#### Microcosm experiment: setup and sampling

For each mangrove species, 10 g of pre-treated litter sample was soaked in 500 mL of artificial seawater (salinity of 10 parts per thousand, ppt) prepared by dissolving commercial sea salt in tap water in a conical flask (Lang et al. 2021). The flasks were shaken at a speed of 100 rpm using a shaking table and ASE 100 accelerated solvent extractor (Dionex, Waltham, MA, USA) to simulate the leaching of leaf litter during the decomposition process at room temperature (26 °C). The experiment lasted 216 h, and three replicates were prepared for each species. All the litter in each flask was retrieved at the beginning and the end of the leaching experiment. The litter was cleansed 3 times using deionized water, air-dried, and then freeze-dried by a freeze dryer (FD-1A-80, Shanghai, China). The litter was weighed and ground to powder before determining its TP, ECT, and BCT contents.

The leachates were also collected from each flask at 6, 12, 24, 48, 72, 96, 120, 144, 168, 192, and 216 h after the onset of leaching. The concentrations of TP and ECT in leachates and their temporal changes were determined.

#### Laboratory analyses

TP, including non-tannin phenolics, such as small molecular phenolic acids and tannin phenolics (CT and HT), in litter and leachate samples were determined by the Folin–Ciocalteu assay according to Makkar et al. (1993) and Salminen and Karonen (2011) with some modifications. Briefly, 100 mg of freeze-dried samples were weighed and extracted in an acetone/water solution with a volume ratio of 7:3 at 5 °C for 15 min by 3 times under ultrasonic conditions. After filtration for 30 min by a vacuum pump branded SHZ-DIIIABS (Lichen Technology Ltd., Shanghai, China), the supernatants were obtained and transferred into a conical flask (50 mL). This fraction was the tannin-containing extract (TP). Then 0.2 mL of extract was placed in a test tube and reacted with the Folin–Ciocalteu reagent in the presence of the sodium carbonate leachate in the dark for over 40 min before the absorbance was then read at 725 nm using a spectrophotometer (752 Pro, Lengguang Technology

Ltd., Shanghai, China) with background measurements of deionized water. The results of TP were expressed in mg tannic acid equivalents L<sup>-1</sup> solution. The ECT concentration was determined according to the butanol/HCl method (Terrill et al. 1992), revised by Zhou et al. (2012). In brief, 1 mL of TP extract from above was added to 6 mL of 95% butanol/HCl solution in a centrifuge tube with a maximum of 15 mL; after thoroughly mixing, the centrifuge tube was then kept in a constant-level (95 °C) boiling water bath for 75 min to allow color development. After boiling, the tube was cooled to room temperature, and the absorbance was read at 550 nm with background measurements using a butanol/HCl solution. Same as TP, the concentration of ECT was also expressed in mg tannic acid equivalents L<sup>-1</sup> solution.

The BCT content in the litter before and after leaching was determined by the same procedure for ECT assays, except that the 95% butanol/HCl solution volume was 10 mL (Zhou et al. 2012). Both air-dried and leached leaf litter was freeze-dried, weighed, and ground before determining their TP, ECT, and BCT contents.

#### Modeling

A simple model was used to fit the time courses of the TP and ECT concentrations in leachates to characterize the dynamics of litter leaching. Briefly, we considered that changes in the phenolic compound concentration in leachates were the net result of the rate of compound leaching ( $V_{\text{leach}}$ ) and that of phenolic compound consumption ( $V_{\text{con}}$ ):

$$d[C_{\text{sol}}]/dt = V_{\text{leach}} - V_{\text{con}}, \quad (1)$$

where  $[C_{\text{sol}}]$  is the concentration of the phenolic compound in the leachate.

We also assumed that both leaching and consumption processes were first-order reactions. Thus, the two rates could be computed as follows:

$$V_{\text{leach}} = k_{\text{leach}}[C_{\text{leaf}}], \quad (2)$$

$$V_{\text{con}} = k_{\text{con}}[C_{\text{sol}}], \quad (3)$$

where  $[C_{\text{leaf}}]$  is the litter mass of the phenolic compound in the leachates;  $k_{\text{leach}}$  and  $k_{\text{con}}$  are the rate constants for the leaching and consumption processes, respectively.

#### Statistical analysis

The normality of the data was tested using the Shapiro–Wilk test. Interspecies differences in the means of leaf tannins in litter and leachate at the same sampling time were examined using a parametric one-way analysis of variance (ANOVA), followed by a Bonferroni test for pairwise comparisons. The data fulfilled the assumptions

of the parametric ANOVA tests, and no data transformation was needed. Exponential functions corresponding to each leaf litter leaching process data point with coefficients ( $k$ ) were calculated using nonlinear regression.

## Results

### Alterations in litter mass, TP, ECT, and BCT in the leaf litter of four mangrove species after the leaching

After leaching in artificial seawater for 216 h, the leaves of all four mangrove species lost a large amount of both fresh and dry litter mass, ranging from 47.3–72.5% and 31.9–50.0% respectively due to the constant leaching of components in the leaf litter (Table 1). The greatest fresh and dry litter mass losses were in *S. apetala*. The order of fresh litter mass loss was *K. obovata* > *A. marina* > *A. corniculatum*, while the order was *A. corniculatum* > *K. obovata* > *A. corniculatum* in dry litter mass. In all four mangrove species, over 74.5% of the foliar TP was lost after leaching (Fig. 2). The percentage of the loss in foliar TP was higher than that in leaf litter mass in all four species, suggesting that phenolics might be preferentially leached in the leachates in comparison with nonphenolic compounds (Fig. 2; Table 1). For foliar ECT, its loss was also remarkable, ranging from 76.1 to 93.7% across various mangrove species (Fig. 2). Interestingly, the total amount of foliar BCT in *S. apetala*, *K. obovata*, and *A. corniculatum* increased after leaching (Fig. 2A–C). Moreover, the percentage loss in foliar ECT was higher than in TP from *K. obovata* and *A. corniculatum* (Fig. 2A, B). This result suggested that ECT was preferentially leached in both species among different types of TP. In contrast, in *S. apetala*, the percentage of the loss in ECT was lower than that in TP, suggesting that non-condensed tannins were preferentially leached (Fig. 2C). This phenomenon might be associated with phenolic composition in *S. apetala* as it contained a large quantity of non-CT phenolics, such as HT (Fig. 2C).

### Dynamics of observed and modeled TP and ECT concentrations in the leachates of leaf litter from the four mangrove species during the leaching process

In general, the dynamics of TP concentrations in the leachates of leaf litter from all four mangrove species gradually increased before reaching a peak. They then slowly decreased during the leaching process, all exhibiting exponential increases, indicating that the leaching process of TP had a higher speed at the early stage, but became slower and slower over time. However, the temporal patterns differed among the species (Fig. 3). Specifically, in terms of the early leaf litter decomposition stage (before reaching the peaks), the fastest increase in the leachate concentration of TP was found in *A. corniculatum*, followed by *S. apetala* (Fig. 3B, C). This result was consistent with their high  $k_{\text{leach}}$  and low  $k_{\text{con}}$  (Table 2). After reaching the peaks, TP concentrations decreased by 28% in *K. obovata* and *A. marina* leachates (Fig. 3A, D). This temporal trend differed from that in *A. corniculatum* and *S. apetala*, which slightly decreased after reaching the peaks (Fig. 3B, C). The fast decrease in TP concentrations in leachates from *K. obovata* and *A. marina* was associated with their low  $k_{\text{leach}}$  and high  $k_{\text{con}}$ , which were comparable (Fig. 3A, D; Table 2).

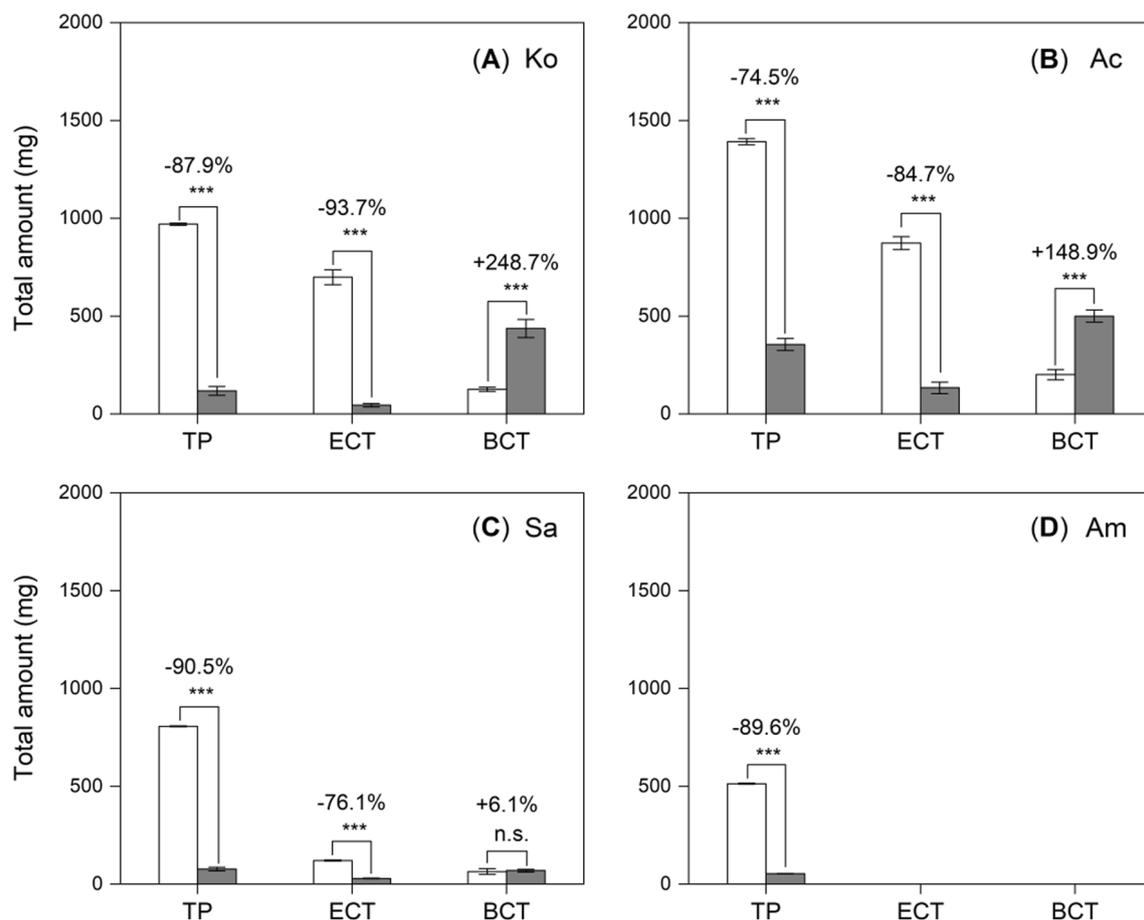
Similar to TP dynamics, the ECT concentration in the leachates of leaf litter from the three mangrove species displayed an initial increase and a subsequent decrease during the leaching process, suggesting that ECT was a vital component in TP (Fig. 4). However, some apparent differences existed in the dynamics of ECT concentrations in the leachates across species (Fig. 4). First, the trends of ECT concentrations in leachates from *K. obovata* and *A. corniculatum* were synchronized with those of their TP concentrations, while the peak time of ECT concentration in *S. apetala* leachate was approximately 72 h later than that of its TP (Figs. 3, 4). In addition, the increase in the ECT concentration in *K. obovata* leachate was slow (Fig. 4A). After reaching the peaks, the decrease in the ECT concentration in *K. obovata* leachate was swift (85%) (Fig. 4A). In comparison with *K. obovata*, the

**Table 1** Fresh and dry mass in leaf litter of four mangrove species before and after the leaching process

Species	Fresh litter mass			Dry litter mass		
	Before (g)	After (g)	Loss (%)	Before (g)	After (g)	Loss (%)
Ko	10.0±0.0 a	2.9±0.1 a	71.0 a	2.9±0.1 a	1.9±0.1 ab	34.5 a
Ac	10.1±0.0 a	5.3±0.1 b	47.3 b	4.7±0.1 b	3.2±0.1 c	31.9 a
Sa	10.1±0.0 a	2.8±0.1 a	72.5 a	3.2±0.1 a	1.6±0.1 a	50.0 b
Am	10.0±0.0 a	3.9±0.1 c	60.7 c	3.8±0.1 c	2.2±0.1 b	42.1 b

Data shown are means ± standard errors (±SE) of three replicates for each species. Different letters denote significant differences among mangrove species in fresh or dry litter mass at  $p < 0.05$  according to one-way ANOVA followed by the Bonferroni test

Ko: *K. obovata*, Ac: *A. corniculatum*, Sa: *S. apetala*, and Am: *A. marina*

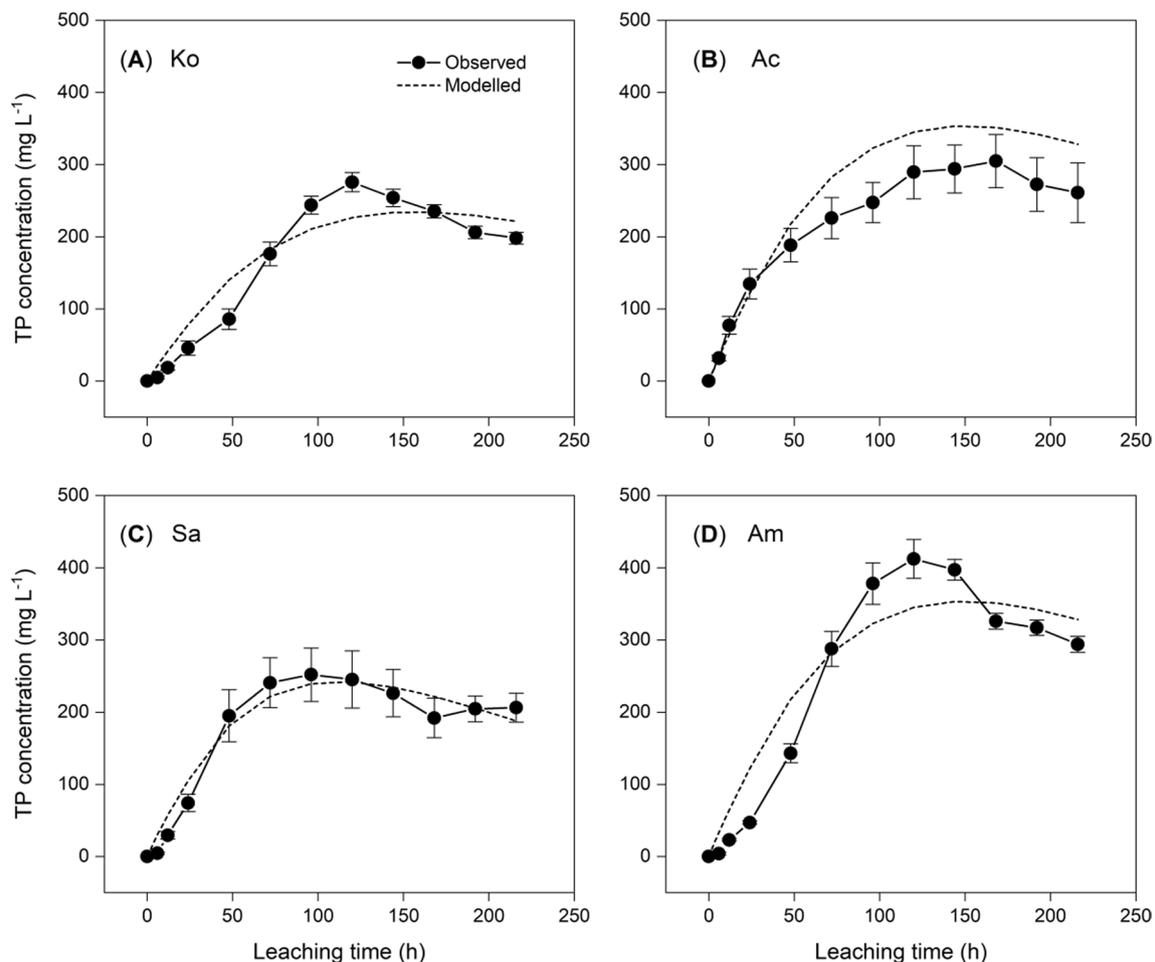


**Fig. 2** Alterations in total phenolics (TP), extractable condensed tannins (ECT), and bound condensed tannins (BCT) in the leaf litter of the four mangrove species after 216 h of the leaching process. **A** Ko: *K. obovata*, **B** Ac: *A. corniculatum*, **C** Sa: *S. apetala*, and **D** Am: *A. marina*. The blank and filled bars are the total amounts measured before and after 216 h of the leaching process, respectively. Numbers indicate the percentage change in the total amount of the compound after leaching. The black line segment centered on the blank and filled bar in A–D indicates the standard errors ( $\pm$  SE), calculated based on the mean of three individual replicates for each phenolic compound in each species. \*\*\* $P < 0.001$ , n.s.: not significant when compared between concentrations before and after leaching using the Bonferroni test

temporal changes of ECT concentration in *A. corniculatum* leachates had two increasing phases, with a fast initial increase reaching  $40 \text{ mg L}^{-1}$  within 12 h, followed by a relatively slow rise (Fig. 4B). The ECT concentration continuously, although slowly, increased in a quasilinear fashion in the leachates from *S. apetala*. This was consistent with its high  $k_{\text{leach}}$  and low  $k_{\text{con}}$  (Table 3). Finally, the ECT concentrations in their leachates followed the declining order of *A. corniculatum* > *K. obovata* > *S. apetala* (Fig. 4C).

We modeled the time courses of both TP and ECT concentrations in the leachates using exponential functions. Then we compared them against observations to probe the subtle changes in the TP and ECT concentrations (Figs. 3 and 4). The fitted time courses consisted of an increasing and a decreasing phase and generally matched well with the observed ones. The

increase in TP concentration in the leachate from *A. corniculatum* could be well described using exponential functions (Fig. 3). However, for the other three species, transient TP concentrations were overestimated during the increase phase (Fig. 3). This may be ascribed to an initial time lag at the very beginning. The observed decrease in TP concentrations in *K. obovata* and *A. marina* leachates was slow compared to that modeled (Fig. 3A, D). However, the decrease in leachate TP concentrations from the other two species (*A. corniculatum* and *S. apetala*) could be approximated using exponential functions (Fig. 3B, C). Small differences existed between the observed and modeled time courses of ECT concentrations in *S. apetala* leachate. Still, such difference in *K. obovata* and *A. corniculatum* was large (Fig. 4). In *K. obovata* leachate, the exponential functions not only underestimated transient ECT



**Fig. 3** Dynamics of the observed (solid line) and modeled (dotted line) concentrations of total phenolics (TP) in leachates of leaf litter from the four mangrove species during 216 h of the leaching process. **A** Ko: *K. obovata*, **B** Ac: *A. corniculatum*, **C** Sa: *S. apetala*, and **D** Am: *A. marina*. The black line segment centered on the bold blank dot in **A–D** indicates the standard errors ( $\pm$ SE), calculated based on the mean of three individual replicates of each phenolic compound in each species

**Table 2** The best-fit model for the time course of total phenolic (TP) concentrations in leachates of leaf litter from the four mangrove species under 216 h of the leaching process

Species	Fitted equation	R <sup>2</sup>
Ko	$d[C_{soil}]/dt = 0.0059 [C_{leaf}] - 0.0060 [C_{soil}]$	0.92
Ac	$d[C_{soil}]/dt = 0.0129 [C_{leaf}] - 0.0028 [C_{soil}]$	0.98
Sa	$d[C_{soil}]/dt = 0.0110 [C_{leaf}] - 0.0059 [C_{soil}]$	0.96
Am	$d[C_{soil}]/dt = 0.0062 [C_{leaf}] - 0.0062 [C_{soil}]$	0.94

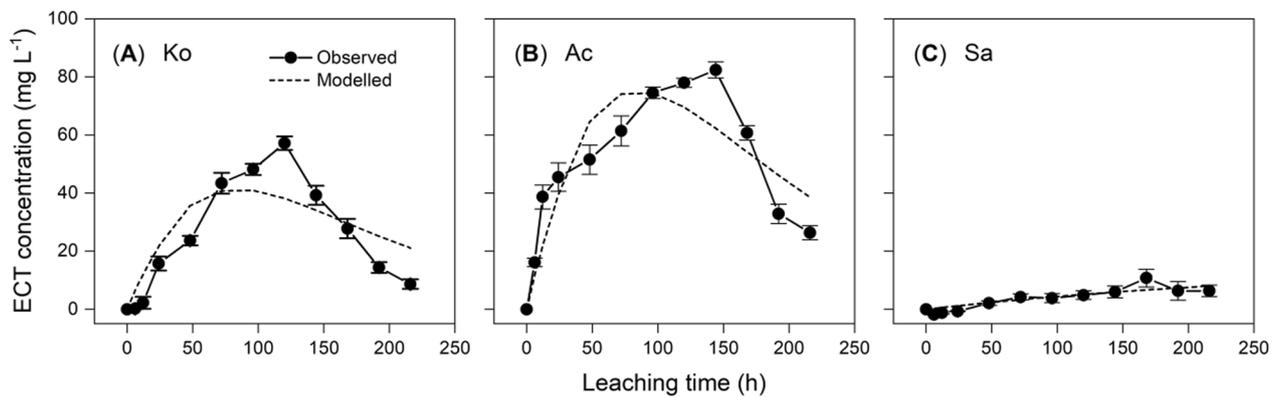
R<sup>2</sup>: regression coefficients; C<sub>soil</sub> is the concentration of the phenolic compound in the leachate; C<sub>leaf</sub> is the weight of the phenolic compound in the leaf; Ko: *K. obovata*, Ac: *A. corniculatum*, Sa: *S. apetala*, and Am: *A. marina*

concentrations but also yielded a peak that reached earlier than the observation (Fig. 4A). For *A. corniculatum*, the initial fast increase in ECT concentrations

was approximated using exponential functions; however, our model overestimated transient ECT concentrations during the second increasing phase, when the actual rate of increase was slow (Fig. 4B). The observed decrease in leachate ECT concentrations in both *K. obovata* and *A. corniculatum* was faster than the modeled value (Fig. 4A, B). All these differences between observed and modeled values suggest that leaf litter leaching was not a simple first-order reaction that assumed the reaction rate was proportional to the substrate concentration (Figs. 3 and 4).

**Mass balances of TP and ECT in the leaf litter of four mangrove species and their dynamic changes in leachates during the leaching process**

The decreased values of dry mass in TP and ECT in leaf litter of the four mangrove species after 216 h of



**Fig. 4** Dynamics of observed and modeled extractable condensed tannin (ECT) concentrations in the leachates of leaf litter from the three mangrove species during 216 h of the leaching process. **A** Ko: *K. obovata*, **B** Ac: *A. corniculatum*, and **C** Sa: *S. apetala*. The black line segment centered on the bold blank dot in **A–C** indicates the standard errors ( $\pm$  SE), calculated based on the mean of three individual replicates of each phenolic compound in each species

**Table 3** The best-fit model for the time course of extractable condensed tannins (ECT) concentrations in leachates from the three mangrove species during 216 h of the leaching process

Species	Fitted equation	R <sup>2</sup>
Ko	$d[C_{soil}]/dt = 0.0108 [C_{leaf}] - 0.0108 [C_{soil}]$	0.83
Ac	$d[C_{soil}]/dt = 0.0108 [C_{leaf}] - 0.0107 [C_{soil}]$	0.71
Sa	$d[C_{soil}]/dt = 0.0017 [C_{leaf}] - 0.0016 [C_{soil}]$	0.83

R<sup>2</sup>: regression coefficients; C<sub>soil</sub> is the concentration of ECT in the leachate; C<sub>leaf</sub> is the weight of ECT in the leaf; Ko: *K. obovata*, Ac: *A. corniculatum*, and Sa: *S. apetala*

the leaching process and their dry mass dynamics in leachates were calculated (Tables 4 and 5). Specifically, the maximums of TP and ECT in leachates were generally found in the 96–144 h and 120–168 h of the periods, respectively. This was because the main leaching processes of foliar TP and ECT were concentrated mainly in the early stage. After the leaching process, the

proportions of TP and ECT peaks accounted for 9.2–23.9% and 7.7–9.4% of the total decreases of foliar TP and ECT from the four mangrove species, respectively (Tables 4 and 5), indicating that internal/external factors, such as light, temperature, and microorganisms in the aquatic environment, might affect the phenolics/tannins dynamics during the leaching process. In addition, these proportions in TP were 1.1–1.5 times larger than those in ECT (Table 4). Compared to their BCT increase values, the proportions of theoretically calculated ECT values in leachates from *K. obovata* and *A. corniculatum* leaf litter were both more than 50% after leaching; however, the proportion of theoretically calculated ECT values in the leachates from *S. apetala* leaf litter accounted for 95.7% (Table 5).

**Table 4** Mass balances of total phenolics (TP) in the leaf litter of four mangrove species before and after 216 h leaching and their dynamic changes in leachates during the leaching experiment

Species	Decrease of TP <sup>a</sup> (mg)	Weight dynamics of TP in leachates (mg)											P (%) <sup>b</sup>
		6 h	12 h	24 h	48 h	72 h	96 h	120 h	144 h	168 h	192 h	216 h	
Ko	852.1 ± 25.6 (87.9%)	1.6	6.5	12.7	24.1	46.6	63.6	<b>70.9</b>	64.8	61.4	52.8	50.8	9.3
Ac	1036.3 ± 33.1 (74.5%)	15.9	45.2	77.7	93.7	103.9	122.5	132.4	<b>147.2</b>	142.0	123.3	114.9	14.2
Sa	729.5 ± 10.9 (90.5%)	1.4	7.3	18.5	44.8	57.6	<b>66.9</b>	61.4	52.7	49.4	46.0	42.5	9.2
Am	459.3 ± 15.7 (89.6%)	1.0	5.7	11.7	39.7	77.2	101.1	<b>109.6</b>	102.0	84.2	80.6	74.8	23.9

<sup>a</sup> Decrease of TP = weight of TP in leaf litter before leaching – after leaching, and percentage (value in bracket) = decrease of TP/total TP before leaching

<sup>b</sup> P means the proportion = peak value of TP in leachate/calculated value of TP in leachate after leaching; the bold figure in each line indicates the peak weight of TP in leachate

Ko: *K. obovata*, Ac: *A. corniculatum*, Sa: *S. apetala*, and Am: *A. marina*

**Table 5** Mass balances of condensed tannins (ECT and BCT: extractable and bound forms, respectively) in leaf litter of three mangrove species before and after 216 h leaching and their dynamic changes in leachates during the leaching experiment

Species	Dynamics of ECT and BCT in leaf litter (mg)		Theoretical calculation value of ECT in leachates (mg) <sup>c</sup>	Dynamics of ECT in leachates from different leaching processes (mg)												P (%) <sup>d</sup>
	Decreases of ECT <sup>a</sup>	Increases of BCT <sup>b</sup>		6 h	12 h	24 h	48 h	72 h	96 h	120 h	144 h	168 h	192 h	216 h		
Ko	654.8 ± 10.5 (93.7%)	311.6 ± 10.1 (47.6%)	343.2 ± 10.3 (52.4%)	0.1	1.1	7.9	11.8	21.7	24.1	<b>28.6</b>	19.6	13.9	7.2	4.3	8.3	
Ac	739.2 ± 22.9 (84.7%)	299.0 ± 11.7 (40.4%)	440.2 ± 15.5 (59.6%)	8.0	19.3	22.7	25.8	30.7	37.3	39.0	<b>41.2</b>	30.4	16.4	13.2	9.4	
Sa	92.0 ± 5.3 (76.0%)	4.0 ± 0.5 (4.3%)	88.0 ± 4.7 (95.7%)	0.0	0.0	0.0	1.2	2.6	2.7	3.2	4.0	<b>6.8</b>	4.8	4.1	7.7	

<sup>a</sup> Decrease of ECT = weight of ECT in leaf litter before leaching – after leaching, and percentage (value in bracket) = decrease of ECT/Total ECT before leaching

<sup>b</sup> Increases of BCT = weight of BCT in leaf litter after leaching – before leaching, and percentage (value in bracket) = increase of BCT/decrease of ECT

<sup>c</sup> Calculated value of ECT in leachates = decrease of ECT – increase of ECT – increase of BCT, and percentages (value in bracket) = ECT in leachate / decrease of ECT

<sup>d</sup> P means the proportion = peak value of ECT in leachate/theoretically calculated value of ECT in leachate after leaching

The bold figure in each line indicates the peak value of ECT weight in leachate

Ko: *K. obovata*, Ac: *A. corniculatum*, and Sa: *S. apetala*

## Discussion

### Alterations in litter mass and phenolics of mangrove leaf litter during the leaching process

Leaf litter decomposition is a critical ecological process of natural mangrove ecosystems, as it serves as a key step contributing to biogeochemical cycles in mangrove forests and is involved in many essential ecological functions, such as material circulation and energy flow (Robertson et al. 1992; Starr et al. 2005). Leaching follows the entire process of leaf litter decomposition, and the rapid leaching phase is the fundamental process at the preliminary stage of decomposition (Hernes et al. 2001; Zhou 2012). In the present study, fresh and dry litter mass of the four mangrove species declined remarkably after 216 h of leaching. Indeed, under the mechanical action of the tide, the constituents of the leaf litter constantly seep out, resulting in a substantial loss of litter mass at the initial stage of its decomposition (Ibrahima et al. 1995). Interestingly, the loss rates of these mangrove leaf litter masses in our study, even without any tidal action, were 47–73%, which were higher than those of other similar field studies on mangrove litterfall after 1–3 weeks with values ranging from 14 to 40% (Camilleri and Ribí 1986; Davis et al. 2003; Davis and Childers 2007; Lin et al. 2007). This difference might be due to the usage of the table concentrator in our microcosm study, which accelerated the leaching process. Changes in the external environment, such as rainfall, tide variation, and bioturbation, contributed greatly to decomposing the leaf litter in mangrove forests (Woitchik et al. 1997; Proffitt and Devlin 2005). Besides, the loss rates in leaf litter mass varied among the four mangrove species due to their differences in leaf textures. Leaves of *K. obovata* possess a thicker stratum corneum with a wax layer than those of *S. apetala* (Li 2006). Deng et al. (2015) also reported that the litter of evergreen shrubs, *Rhododendron*, did not decompose easily due to its thick stratum corneum.

The leaching process of mangrove leaf litter caused a massive loss of phenolics, such as CT and HT (Zhou et al. 2010, 2012). Hernes et al. (2001) reported that more than 30% loss of tannins from decomposing leaves was easily obtained during a leaching test. In the present study, the decreases of leaf litter TP (87.9% in *K. obovata*, 74.5% in *A. corniculatum*, 90.5% in *S. apetala*, and 89.6% in *A. marina*) and ECT (93.7% in *K. obovata*, 84.7% in *A. corniculatum*, and 76.1% in *S. apetala*) were notably apparent during leaching over 9 days (Fig. 2). This result was similar to the findings of Lin et al. (2006) that declines were visibly found in TP contents of *K. obovata* (84.3%) and *Bruguiera gymnorrhiza* (95.7%) leaves with changes in colors, such as yellow, orange, brown, and black, in the Jiulong River Estuary, Fujian, China. In addition, in South Florida, USA, total phenolic contents of *R. mangle*

and *Avicennia germinans* leaf litter decreased by 88% of the initial concentration after 24 d incubation (Pelegri and Twilley 1998). Lin et al. (2006), Pelegri and Twilley (1998), and our present study indicated that the tissues and cells of mangrove leaves burst and then continuously released the water-soluble tannins from leaves into leachates during the leaching process. BCT from the leaf litter of *K. obovata* and *A. corniculatum* was also enhanced prominently, but the increase in *S. apetala* was minimal after 216 h of the leaching process (Fig. 2; Table 5). This phenomenon might be because free ECT in *K. obovata* and *A. corniculatum* leachates was liable to combine with bio-macromolecules released from the ruptured cells and tissues such as proteins, polysaccharides, etc., then formed BCT and promoted the spontaneous increase (Zhou et al. 2012; Zhou 2012). However, Zhou (2012) found that the proportion of HT in TP from *S. apetala* leaf litter accounted for 86%. The HT belongs to esters composed of phenolic carboxylic acids (ellagic acid, etc.) and polyols (primarily the composition of glucose), which have unstable chemical structures (Khanbabaee and van Ree 2001). Therefore, they were easily hydrolyzed compared to the linked CT by C–C bonds. The hydrolysis of HT produced gallic acid and other small phenolic acids as well as large amounts of phenolics that acted as energy materials and provided sufficient carbon sources for microbes to enhance their activity and diversity (Bhat et al. 1998; Kraus et al. 2004). The products from degraded HT then triggered the microorganisms in *S. apetala* leachate to become more vigorous and richer, and most of the free ECT might be largely degraded, leading to a tiny increase in BCT from *S. apetala* leaf litter.

### Key revelations of the variations of TP and ECT during the leaching process of mangrove leaf litter

The concentrations of TP and ECT in leachates of leaf litter from all four mangrove species except *S. apetala* exhibited exponential growth at the early stage during leaf litter decomposition (Figs. 3 and 4), and the litter mass also showed significant decreases after 216 h leaching (Table 1). Similarly, Davis et al. (2007) reported that the loss rate of *R. mangle* leaf litter mass was the fastest in the first 1–2 days under leaching treatment. Chale (1997) soaked *A. marina* leaf litter with filtered river water and found that 19% of its leaf litter mass was lost after 24 h when subjected to leaching. In the present study, the temporal variations of ECT concentrations in leachates of *K. obovata* and *A. corniculatum* synchronized with those of the respective TP concentrations, while the peak of ECT concentration in *S. apetala* leachate occurred approximately 72 h later than that of its TP (Figs. 3 and 4). This was mainly because the TP component of *S.*

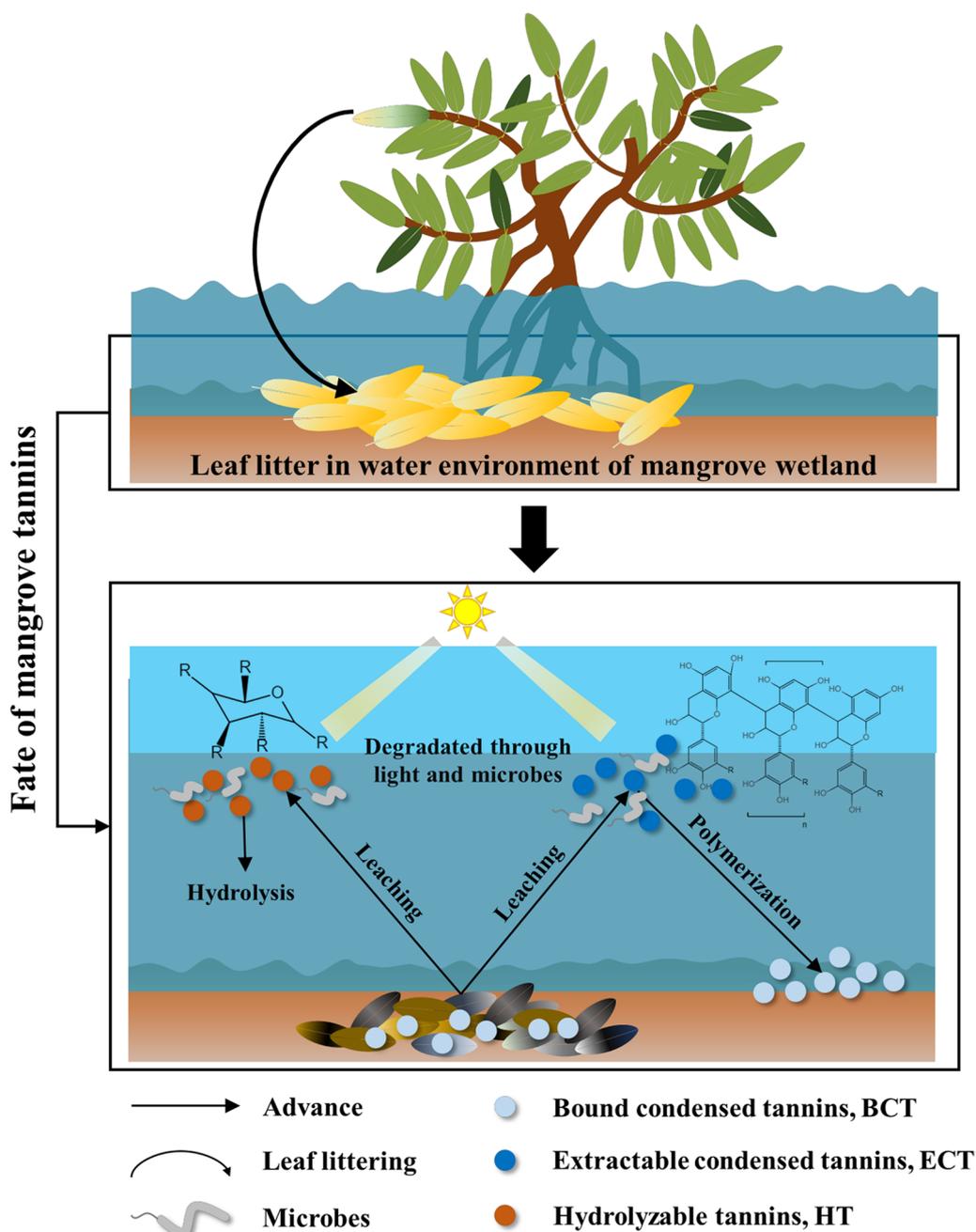
*apetala* contained a bulk of HT, and such chemical properties were more active, causing them to be more prone to degradation (Zhou et al. 2010). When comparing the four mangrove species, the ECT contents in leaves before leaching and ECT loss after leaching followed the same declining order of *K. obovata* > *A. corniculatum* >> *S. apetala*. At the same time, the ECT concentration in *K. obovata* leachate contained less ECT than that in *A. corniculatum* (Fig. 4). The CT in *K. obovata* litter (mainly composed of procyanidin) with an oligomer structure possessed a smaller molecular mass and was easier to decompose by microorganisms than the CT in *A. corniculatum* litter which was mainly composed of prodelphinidin with a higher molecular mass and thus tended to bind with extracellular proteins inhibiting microbial activities (Zhang et al. 2010; Zhou 2012). The ECT concentrations in leachates of three mangrove species (*K. obovata*, *A. corniculatum*, and *S. apetala*) followed the same temporal trend, with increases at the early stage and then decreases with time (Fig. 4). This finding was mainly because the leaching process resulted in the loss of the CT in oligomeric forms at the early stage of leaf litter decomposition, which caused an increase in the degree of CT polymerization. However, the greater the degree of CT polymerization, the more stable the CT structures were, resulting in lower solubility and increased difficulty in eventual decomposition (Zhou et al. 2012; Zhou 2012).

The concentrations of TP and ECT in the leachate from mangrove leaf litter were fitted by regression equations, and the mass balances and dynamics of TP and ECT concentrations in leachates during the leaching process were calculated (Figs. 3 and 4; Tables 2, 3, 4, 5). These simulated effects of the fitted equations for TP and ECT dynamics were reasonable. Nevertheless, they did not achieve the optimum efficiency (Figs. 3 and 4; Tables 2 and 3). Moreover, the maximum values of TP and ECT in leachates accounted for only a small part of the decrease in foliar TP and ECT after leaching (Tables 4 and 5). These results indicated that phenolics/tannins could be affected by other internal/external factors during the leaching process. At the start of leaf litter decomposition dominated by the leaching process, the fate of mangrove ECT could be divided into two parts: (1) a portion of ECT would rebuild a new part of BCT, causing an increase in BCT content in litter (Fig. 2; Table 5); and (2) another portion of ECT would appear in leachates (Fig. 4; Table 5), precipitate via self-polymerization, and be degraded by sunlight and microbes. Maie et al. (2008) reported that mangrove tannins' potential conversion pathways in natural intertidal zones included self-polymerization, sediments' adsorption, binding to soluble organic materials, and degradation. However, due to their unstable chemical properties, HT in mangrove litter was

hydrolyzed rapidly into polyols, gallic acid, ellagic acid, and other small phenolic acids when the litter decomposed (Zhou 2012). Based on the present findings, a schematic model showing the fate of mangrove tannins during leaf litter decomposition was proposed (Fig. 5).

## Conclusion

The present microcosm study shows that the litter mass, TP, and ECT in the leaf litter of *K. obovata*, *A. corniculatum*, *S. apetala*, and *A. marina* (except ECT) declined remarkably after 216 h of leaching, demonstrating rapid decomposition processes of these mangrove leaves with fast leaching of some phenolic compounds to surrounding environments. Furthermore, BCT in *K. obovata* and *A. corniculatum* leaf litter was significantly enhanced, but the increase in *S. apetala* leaf litter was minimal. The loss proportion in foliar TP was higher than that in leaf litter mass in all four mangrove species, and the loss proportion in foliar ECT was higher than that in TP in *K. obovata* and *A. corniculatum*. In contrast, the opposite result was found in *S. apetala*. The variations of TP and ECT concentrations in the leachates of all mangrove species followed the same temporal trend, with an increase at the early stage and then a decrease as decomposition proceeded. The temporal variations of ECT concentrations in *K. obovata* and *A. corniculatum* leachates synchronized with their respective TP concentrations, while the peak time of ECT concentration in *S. apetala* leachate was later than that of its TP. In addition, the ECT concentrations in their leachates followed the declining order of *A. corniculatum* > *K. obovata* >> *S. apetala*. After the leaching process, the proportions of peak TP and ECT concentrations in leachates from the leaf litter of all four mangrove species accounted for 9.2–23.9% and 7.7–9.4% of the total decreases of foliar TP and ECT, respectively. Due to the differences in leaf characteristics of mangrove species probably, the fate of tannins during the decomposition process was species-specific. However, the dynamics of tannins in leaves of the four species were almost similar, suggesting that although mangrove species differ in various tannins, such as content and category, those tannins own a similar variation trend in aquatic environments. The present study provides useful information on the fate and dynamics of TP and ECT from litterfall, helping further explore potential ecological processes, such as energy flow and biogeochemical cycles of nutrients (carbon stocks, nitrogen immobilization, etc.) and contaminants (organic pollutants and heavy metals) in natural mangrove forests, thereby benefiting the management and conservation of mangrove ecosystems.



**Fig. 5** A schematic working model elaborating the fate of mangrove tannins during leaf litter leaching

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**Author contributions**

LT, ZHC, and TFY conceived the ideas and designed the experiments; ZHC, KHX, WJ, GCJ, HM, FYJ, LMD, and LFL collected the data; XJL, LWF, JMG, WYB, and CXX analyzed the data. ZHC, TFY, and LT wrote the first draft of the manuscript. All authors read and approved the final manuscript.

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**Availability of data and materials**

The datasets used during the study are temporarily confidential.

**Declarations****Ethics approval and consent to participate**

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**Consent for publication**

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**Competing interests**

The authors declare no competing interest.

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