

## Article

# Decomposition and Variation in Carbon and Nitrogen of Leaf Litter Mixtures in a Subtropical Mangrove Forest

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**Abstract:** The decomposition of mangrove litter plays a crucial role in material circulation and energy flow within mangrove forests. Evaluating the decomposition-based variation in biogenic elements in litter is important for improving our understanding about their biogeochemical cycling in ecosystems. The main objective of this study was to examine the interaction effect during the decomposition process of mixed *Kandelia obovata* and *Avicennia marina* litter. Variations in C and N were also determined in the decomposing leaf litter mixtures. Our findings revealed that the decomposition rates were faster in summer than in winter, and increased with the proportion of *A. marina* litter. After 35 days of decomposition in summer, the remaining weights for different proportions of *K. obovata* (KO) and *A. marina* (AM) were 22.9% (KO:AM = 1:2), 27.2% (KO:AM = 1:1), and 31.2% (KO:AM = 2:1), respectively. Similarly, after 49 days of decomposition in winter, the remaining weights for the different KO:AM proportions were 27.7%, 35.4%, and 44.0%, respectively. Additionally, the decomposition of mixed *K. obovata* and *A. marina* litter had an influence on C content and N release dynamics. These results provide a scientific basis for understanding the decomposition of mixed mangrove litter and its implications for material circulation and energy flow within these ecosystems.

**Keywords:** mangrove forest; mixed effect; Olson model; litter bags; biogeochemical cycle



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## 1. Introduction

Mangroves are woody plant communities distributed in the intertidal zones of tropical and subtropical estuaries; they are primary producers in estuarine ecosystems and have many functions, such as purifying water, preventing and reducing disasters, and maintaining biodiversity [1,2]. Among the key processes that sustain mangrove ecosystems are the decomposition and nutrient cycling of mangrove leaf litter [3]. Litter is a product of the metabolism during forest growth and development, and it serves as a vital link in material circulation and energy flow, performing irreplaceable ecological functions [4]. Previous studies have indicated that the decomposition rates of mangrove leaf litter can vary significantly depending on the species composition and environmental conditions [5,6]. Benthic macrofauna organisms play a key factor in the initial phase of decomposition, influencing the decay rates of mangrove litters [6]. The nutrients returned by mangroves through litter are significant to the energy flow and material circulation of the wetland ecosystem. A mangrove leaf litter incubation experiment in controlled environmental conditions revealed the role of leaf litter leachates as a significant important food source to microbial communities in coastal waters and a potential carbon sequester through long-term burial in mangrove soil [7]. It is estimated that mangrove litter accounts for approximately 30%–60% of the total primary production in the mangrove ecosystem; deciduous leaves make up roughly 60%–79% of the entire litter [1,8]. After undergoing complex biological, physical, and chemical actions, decomposed litter yields a considerable amount of organic debris and is transported offshore, becoming a crucial food source for marine animals [2]. This

process is immensely significant to offshore fishery production and aquaculture, as well as the protection and sustainable management of mangrove ecosystems [9].

The accumulation and decomposition of litter have always been considered two of the main factors affecting ecosystem function. Among them, litter decomposition is a crucial ecological process in the ecosystem and an essential part of the ecosystem's biogeochemical cycle [10]. Litter decomposition determines the existing quantity and properties of the litter layer, and decomposition rates significantly impact the forest ecosystem's productivity [11,12]. Litter decomposition rates and their associated nutrient release rates determine the ecosystem's nutrient characteristics and the supply of available nutrients in the soil, which affects plants' nutrient absorption [13]. Therefore, litter decomposition has been considered significant by many researchers [14,15]. The decomposition of mangrove litter has been studied in numerous subtropical and tropical regions [16]. Some of these experiments have been conducted in a greenhouse [5] or controlled environment [17], but such studies have been rarely carried out in the field. In addition, research regarding mangrove litter has mostly focused on analyzing and comparing the leaf decomposition rates of different single tree species [18].

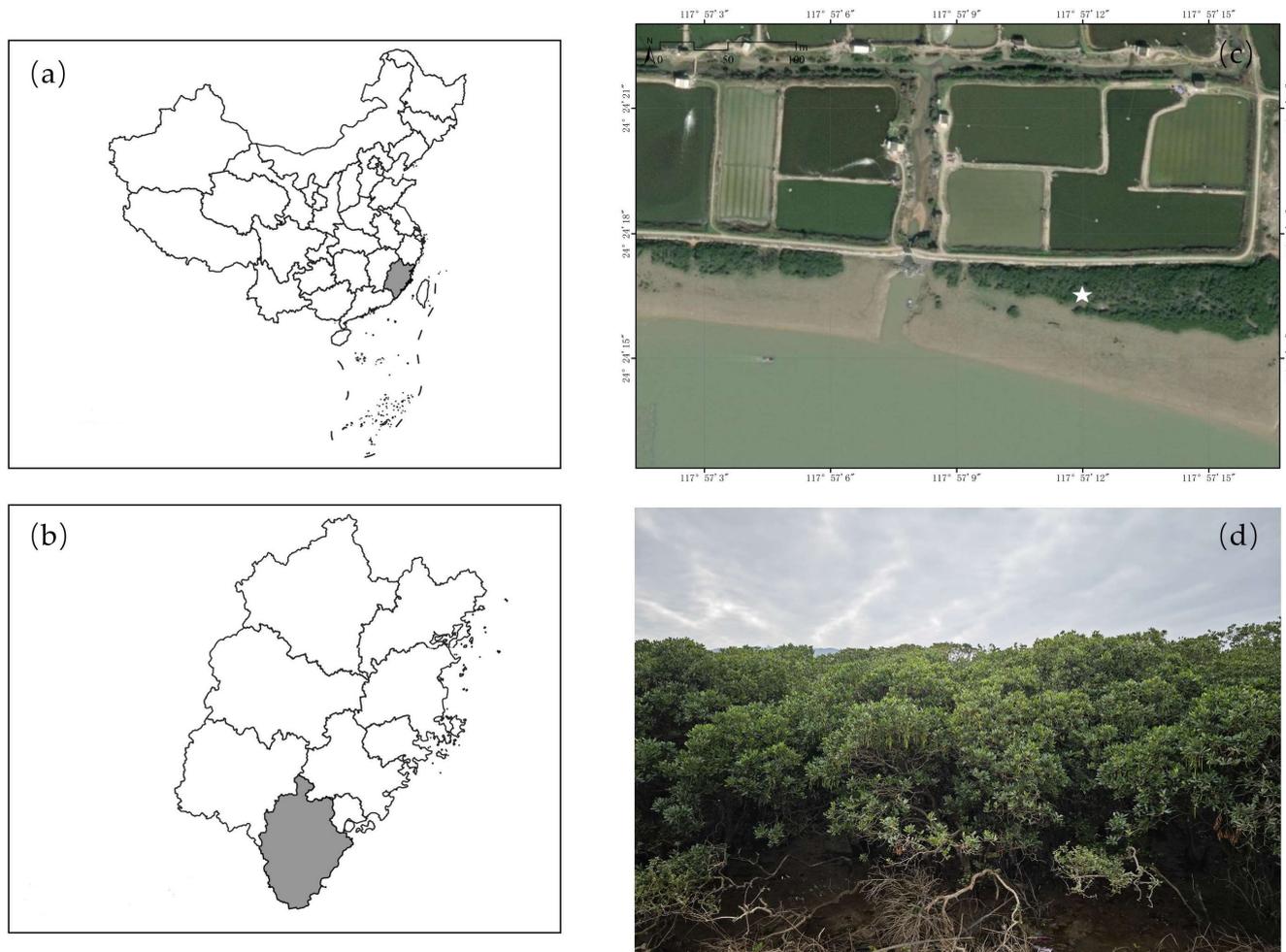
Species often do not exist singly; several or dozens of species live in communities in nature, so the litter that is produced is often not singular, but mixed. Although research results for a single tree species have important theoretical value, they do not reflect nature's real situation. Therefore, it is of great practical guiding significance to understand dynamic changes in the natural decomposition process and its material cycle and energy flow by studying the interaction effect of multiple types of mangrove litter. The Olson exponential decay model is a method used to analyze the decomposition of litter in ecosystems, especially the relationship between various factors and the decomposition rate [19]. The model is generally used in experimental studies of forest and soil ecosystem litter decomposition, but it is also applicable to the decomposition of litter in mangrove ecosystems [20]. In this study, the decomposition process of mixed *Kandelia obovata*, H.Y. Liu and J. Yong, and *Avicennia marina* (Forssk.) *Vierh* litter was investigated using the litterbag technique and the modified Olson exponential decay model, and these mixed mangrove litters' C and N levels were determined. This study aimed (i) to investigate the difference in the decomposition rates of the mixed mangrove litter, and (ii) to examine the dynamics of C and N in the mixed mangrove litter during decomposition.

## 2. Materials and Methods

### 2.1. Study Area

The study area was in the Mangrove Nature Reserve, Jiulong River Estuary, in Zhangzhou City, Fujian Province (Figure 1). This region has a subtropical oceanic climate with an annual average temperature of 21 °C and 1400 mm annual average precipitation. January is the coldest month, with an average temperature of 13 °C, and July is the warmest month, with an average temperature of 29 °C. Relative humidity can reach 80%, with about 2224 h annual sunshine. The local tides are semidiurnal, with an average range of 4 m. The mangrove wetland is dominated by *Kandelia obovata*. There are also some isolated populations of *Avicennia marina*, *Aegiceras corniculatum* (Linn.) Blanco, *Bruguiera gymnorrhiza* (Linnaeus) Savigny, and other species.

The water temperature ranges from 21.5 °C to 31.8 °C in summer, and ranges from 16.1 °C to 19.0 °C in winter, with salinity adjacent to the mangrove wetland, ranging from 12 to 26 [21,22]. The total phosphorus concentration is 0.09–0.12 mg/L, the total nitrogen concentration is 1.72–2.36 mg/L, and the chlorophyll a content ranges from 0.74 to 8.67 µg/L [22]. The high biomass values predominantly occur during the early spring season, with cryptophytes and dinoflagellates being the primary algae from September to December [22]. The primary sediment type is clayed silt, and the amount of soil C stored in the 100 cm soil profile was  $93.10 \pm 11.28 \text{ kg C m}^{-2}$  [23].



**Figure 1.** Study area's location in the Mangrove Nature Reserve, Jiulong River Estuary, Zhangzhou, Fujian. (a) The position of Fujian Province in China; (b) The position of Zhangzhou in Fujian Province; (c) Mangrove Nature Reserve of Jiulong River Estuary, Haimen Island, Fujian Province (white pentagram marks the location of the litter bags); (d) Photograph of mangrove landscape from the site by the authors.

## 2.2. Experimental Setup

Newly fallen *Kandelia obovata* and *Avicennia marina* leaves were collected from the mangrove wetland in Jiulong River Estuary on 10 July (summer) and 10 December (winter), respectively. Collected leaf litter samples were air-dried for 48 h for later use. The leaf litter decomposition study was conducted using the litter bag technique; 36 g of dried leaf litter samples were placed in 200 × 200 mm nylon litter bags with 1 mm size 2 mesh, which can prevent small organisms from invading, allowing for water and dissolved substances to pass through, and maintain the integrity of litter samples. Table 1 shows that five sample types were treated in the litter decomposition experiment, including two single-species treatments (36 g *K. obovata* and 36 g *A. marina*), and three different mixed-proportions treatments (18 g *K. obovata* and 18 g *A. marina*; 24 g *K. obovata* and 12 g *A. marina*; and 12 g *K. obovata* and 24 g *A. marina*).

**Table 1.** Two single-species and three mixed-species treatments in the litter decomposition experiment.

	Treatment Group	Abbreviation	Weight of Samples (g)	
Single-species treatments	<i>Kandelia obovata</i>	KO	KO = 36	
	<i>Avicennia marina</i>	AM	AM = 36	
Mixed-species treatments	<i>Kandelia obovata:Avicennia marina</i> =1:2	KO:AM = 1:2	KO = 12	AM = 24
	<i>Kandelia obovata:Avicennia marina</i> =1:1	KO:AM = 1:1	KO = 18	AM = 18
	<i>Kandelia obovata:Avicennia marina</i> =2:1	KO:AM = 2:1	KO = 24	AM = 12

Litter bags were arranged on the sediment inside the mangrove forest (24°24′16″ N, 117°57′12″ E) within a 20 m × 20 m range. Bags were tied to tree trunks with nylon ropes. Three litter bags for each treatment type were collected randomly from study sites on days 7, 14, 21, 28, and 35 in summer, and days 7, 14, 21, 35, 49, and 77 in winter, after deployment, and brought back to the laboratory. Leaf litter samples were gently rinsed under freshwater to remove sediments and particles, and then oven-dried at 80 °C to a constant weight. After being weighed, dried leaf litter samples were analyzed for total N and C content. Total N content was determined via the Kjeldahl acid-digestion method using an H<sub>2</sub>SO<sub>4</sub> mixed catalyst. C content was determined via dichromate and concentrated sulfuric acid oxidation colorimetry using an ultraviolet spectrophotometer [24].

### 2.3. Physiological and Biochemical Features of *Kandelia obovata* and *Avicennia marina* Leaves

*K. obovata* leaves range from elliptical to obovate, with the presence of tannins and other secondary metabolites, such as alkaloids and glycosides, that confer resistance to environmental stressors. The species exhibits a unique salt-secretion mechanism, with specialized salt glands in the leaves that excrete excess sodium ions, maintaining osmotic balance [25,26]. *A. marina* leaves are leathery and elliptical, and the epidermis is composed of a layer of cells with a thick cuticle, which helps to reduce the evaporation of water and serves as a protective layer against saltwater inundation. *A. marina* is a halophyte with a high tolerance to salinity, exhibiting both salt-exclusion and salt-secretion strategies allowing for it to cope with high-salt environments [27,28].

### 2.4. Parameters' Calculation

Leaf litter decay constants were calculated using a mathematical model described by Olson (1963) [29]. When the Olson model was used to fit the temporal dynamics of litter decomposition, we further estimated the half-life of litter decomposition (the time required for 50% decomposition), T<sub>50</sub>, and the time required for 95% decomposition, T<sub>95</sub>.

$$\frac{X_t}{X_0} = e^{-kt}, \quad (1)$$

where  $X_0$  is the initial weight,  $X_t$  is the remaining weight at time  $t$ , and  $k$  is the decay rate coefficient. The C and N residues were calculated from the ratios of the initial and remaining amounts, expressed as a percentage.

The calculated remaining weight value of the mixed litter is as follows:

$$\text{Calculated value (\%)} = \frac{M_1 \times MR_1 + M_2 \times MR_2}{M_1 + M_2} \times 100, \quad (2)$$

where 1 and 2 represent two species of mixed litter; M represents the weight of different species in the mixed litter; MR represents the remaining weight (%) of different species in the mixed litter.

### 2.5. Statistical Analysis

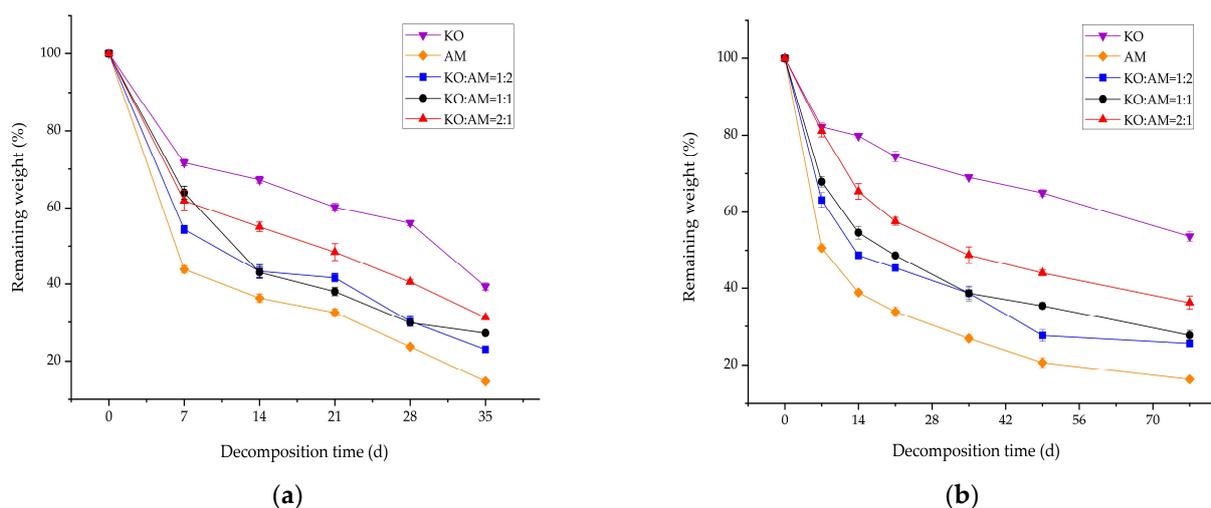
This study data were analyzed using Origin 2023b (OriginLab Corporation., Northampton, MA, USA) [30] and SPSS 24.0 (IBM Corporation, Armonk, NY, USA) [31]. Data were tested for normality using the Kolmogorov–Smirnov test ( $p = 0.064 > 0.05$ ); dif-

ferences between data groups were detected using Pearson correlation analysis and *t*-test. If the difference between the observed value and the calculated value was not significant ( $p > 0.05$ ), the mixing effect was not obvious; if the observed value was significantly greater than the calculated value ( $p < 0.05$ ), there was a positive mixing effect; and if the observed value was significantly less than the calculated value ( $p < 0.05$ ), there was a negative combination effect. If the difference between summer and winter was not significant ( $p > 0.05$ ), the seasonal change has no obvious effect on the remaining weight of the mixed litter; if the difference between summer and winter is significant ( $p < 0.05$ ), the remaining weight of the mixed litter obviously changes between summer and winter.

### 3. Results

#### 3.1. Remaining Weight of Mixed Litter Decomposition

Figure 2 shows a gradual decrease in the leaf litter's remaining weight for each treatment group as decomposition time increases. For instance, during the winter decomposition process from day 0 to day 77, the remaining weight of *A. marina*'s leaf litter decreased from 100% to 16.2%. The decomposition rates were higher in summer than they were in winter. For example, after 21 days of summer decomposition, KO's remaining weight was 60.2%, and the remaining weight of KO:AM = 1:1 was 38%; conversely, in winter, KO's remaining weight was 74.5% ( $p < 0.01$ ), while that of KO:AM = 1:1 was 48.6% ( $p < 0.01$ ). These results show that seasonal changes have an obvious effect on the remaining weight of mixed litter.



**Figure 2.** Remaining weight of *K. obovata* and *A. marina* leaf litter mixture (%) in (a) summer and (b) winter during decomposition.

Of the two mangrove species, leaf litter decomposition rates were higher in *A. marina* than in *K. obovata*. After 14 days' summer decomposition, the rate of *K. obovata*, according to weight, was 67.2%, while that of *A. marina* was 36.3%. Correspondingly, the negative slope of *K. obovata* and *A. marina* are  $-0.634$  and  $-1.078$ , respectively. This indicated that *A. marina* decomposed more easily than *K. obovate*.

Mixed litter decomposition rates, from highest to lowest, were as follows: treatment group KO:AM = 1:2 > KO:AM = 1:1 > KO:AM = 2:1. After decomposing for 35 days in the summer, the remaining rates of KO:AM = 1:2, KO:AM = 1:1, and KO:AM = 2:1, according to weight, were 22.9%, 27.2%, and 31.2%, respectively. After decomposing for 49 days in winter, the remaining rates of KO:AM = 1:2, KO:AM = 1:1, and KO:AM = 2:1, according to weight were 27.7%, 35.4%, and 44.0%, respectively. These results show that decomposition rates increased in the mixed-treatment groups as the amount of *A. marina* leaf litter increased.

### 3.2. Mathematical Model Fitting

In this study, the modified Olson exponential decay model was used to obtain the regression equation and the correlation coefficient, R, between the natural logarithm of R in Table 2 and the decomposition time, t, of various litter types. The correlation coefficient R of all treatment groups reached significant levels, and the mixed decomposition digital model's fitting effect was good.

**Table 2.** Olson natural logarithm model's decomposition coefficients, R, for *Kandelia obovata* and *Avicennia marina* leaf litter during mixed decomposition.

Season	Treatment Group	Olson Model (Coefficient, Day <sup>-1</sup> )	Correlation Coefficient (R)	R <sup>2</sup>	Observed Rates (k)	Calculated Rates (k')	T <sub>50</sub> (Day)	T <sub>95</sub> (Day)
Summer	KO	ln R = -0.0645-0.0225t	0.9593	0.9202 **	0.0225 d	-	27.9	130.3
	AM	ln R = -0.2287-0.0471t	0.9604	0.9223 **	0.0471 a	-	9.9	58.8
	KO:AM = 1:2	ln R = -0.1773-0.0374t	0.9655	0.9322 **	0.0374 b	0.0353	13.8	75.4
	KO:AM = 1:1	ln R = -0.1574-0.0364t	0.9680	0.9370 **	0.0364 b	0.0321	14.7	78.0
	KO:AM = 2:1	ln R = -0.1293-0.0295t	0.9718	0.9444 **	0.0295 c	0.0289	20.1	104.8
Winter	KO	ln R = -0.1015-0.0070t	0.9643	0.9299 **	0.0070 d	-	84.5	413.5
	AM	ln R = -0.4684-0.0204t	0.9104	0.8288 **	0.0204 a	-	11.0	123.9
	KO:AM = 1:2	ln R = -0.3320-0.0160t	0.9122	0.8322 **	0.0160 b	0.0159	22.6	166.5
	KO:AM = 1:1	ln R = -0.2813-0.0149t	0.9292	0.8635 **	0.0149 bc	0.0137	27.6	182.2
	KO:AM = 2:1	ln R = -0.1741-0.0124t	0.9460	0.8950 **	0.0124 c	0.0115	41.9	227.6

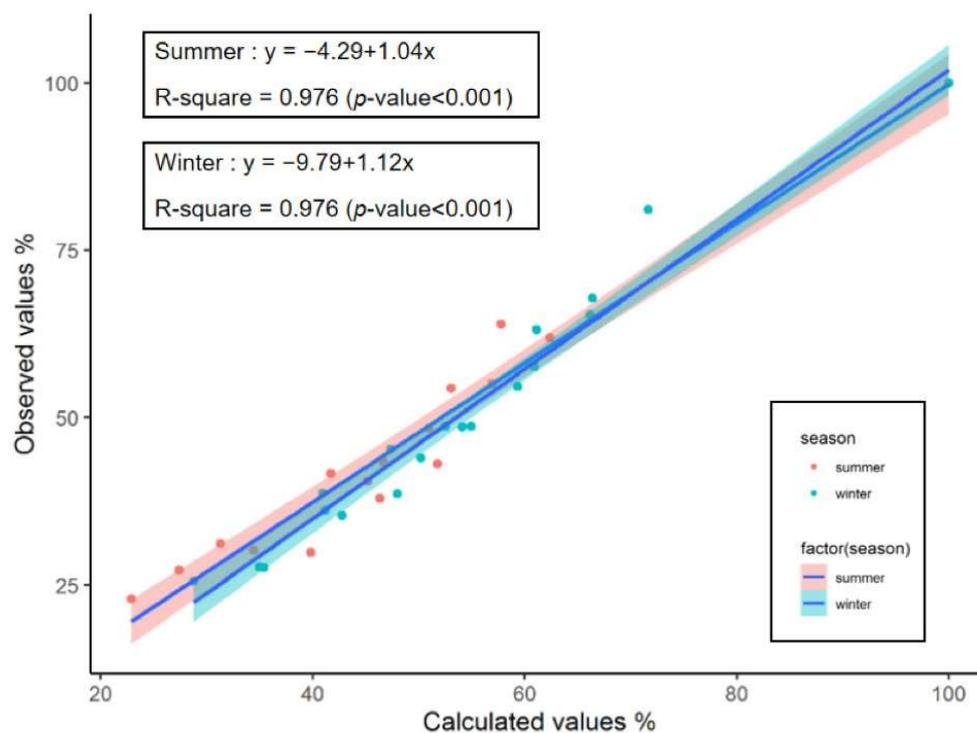
Note: significance: \*\*:  $p < 0.01$ . Different lowercase letters indicate a significant difference among the treatment groups with different litter contents within the same variable ( $p < 0.05$ ).

Table 2 shows that the k value of each equation was used to estimate the decomposition dynamics of various litter types at the time of 50% decomposition (T<sub>50</sub>) and the time of 95% decomposition (T<sub>95</sub>). Regression analysis showed that the correlation coefficients of the five treatment groups all reached a significant level in summer and winter. The decomposition coefficients of the five treatment groups were AM > KO:AM = 1:2 > KO:AM = 1:1 > KO:AM = 2:1 > KO. In summer, T<sub>50</sub> of the five treatment groups ranged from 9.9 to 27.9 d, and T<sub>95</sub> ranged from 58.8 to 130.3 d. In winter, T<sub>50</sub> of the five treatment groups ranged from 11.0 to 84.5 d, and T<sub>95</sub> ranged from 123.9 to 413.5 d. There were some differences between the T<sub>50</sub> and T<sub>95</sub> of the different leaf litter treatment groups. The decomposition coefficient k of *A. marina* was the largest, and the decomposition rate was the fastest. The decomposition rate of *K. obovata* was the slowest, at 27.9 d for 50% and 130.3 d for 95% (in summer), and at 84.5 d for 50% and 413.5 d for 95% (in winter). When the leaves of two mangrove plants decomposed separately, the decomposition rates k of *A. marina* were greater than those of *K. obovata*. For example, in summer, the decomposition rate k of *A. marina* was 0.0417 d<sup>-1</sup>, and that of *K. obovata* was 0.0225 d<sup>-1</sup>, indicating that *A. marina* decomposed faster than *K. obovata*.

The model calculation results indicated that the T<sub>50</sub> of the mixed treatment group was the fastest, followed by that of KO:AM = 1:1 and KO:AM = 2:1, all of which were shorter than that of *K. obovata*. For example, in summer, KO:AM = 1:2's T<sub>50</sub> was 13.8 d, KO:AM = 1:1's was 14.7 d, and KO:AM = 2:1's was 20.1 d; all these were shorter than *K. obovata*'s 27.9 d. In the decomposition process of mixed fallen leaves from two mangrove plants, the observed values of decomposition rates, k, for each mixed-treatment group were higher than the calculated values. For example, in summer, KO:AM = 1:1 had a decomposition rate k of 0.0364 d<sup>-1</sup> (95%CI: 0.0231-0.0460), and its calculated value was 0.0321 d<sup>-1</sup> (95%CI: 0.0242-0.0400), indicating that the mixture of *K. obovata* and *A. marina* litter had an obvious promotional effect on decomposition.

Figure 3 compares the observed values and the calculated values for *K. obovata* and *A. marina* mixed litter based on simple additive effects. Comparing the observed remaining weight of each mixed litter treatment group in summer and winter with the calculated remaining weight, we found that the observed remaining weight appeared to be significantly

lower than the calculated values in the mixed-litter decomposition process, indicating that the overall mixing effect was non-additive antagonistic ( $p < 0.01$ ).

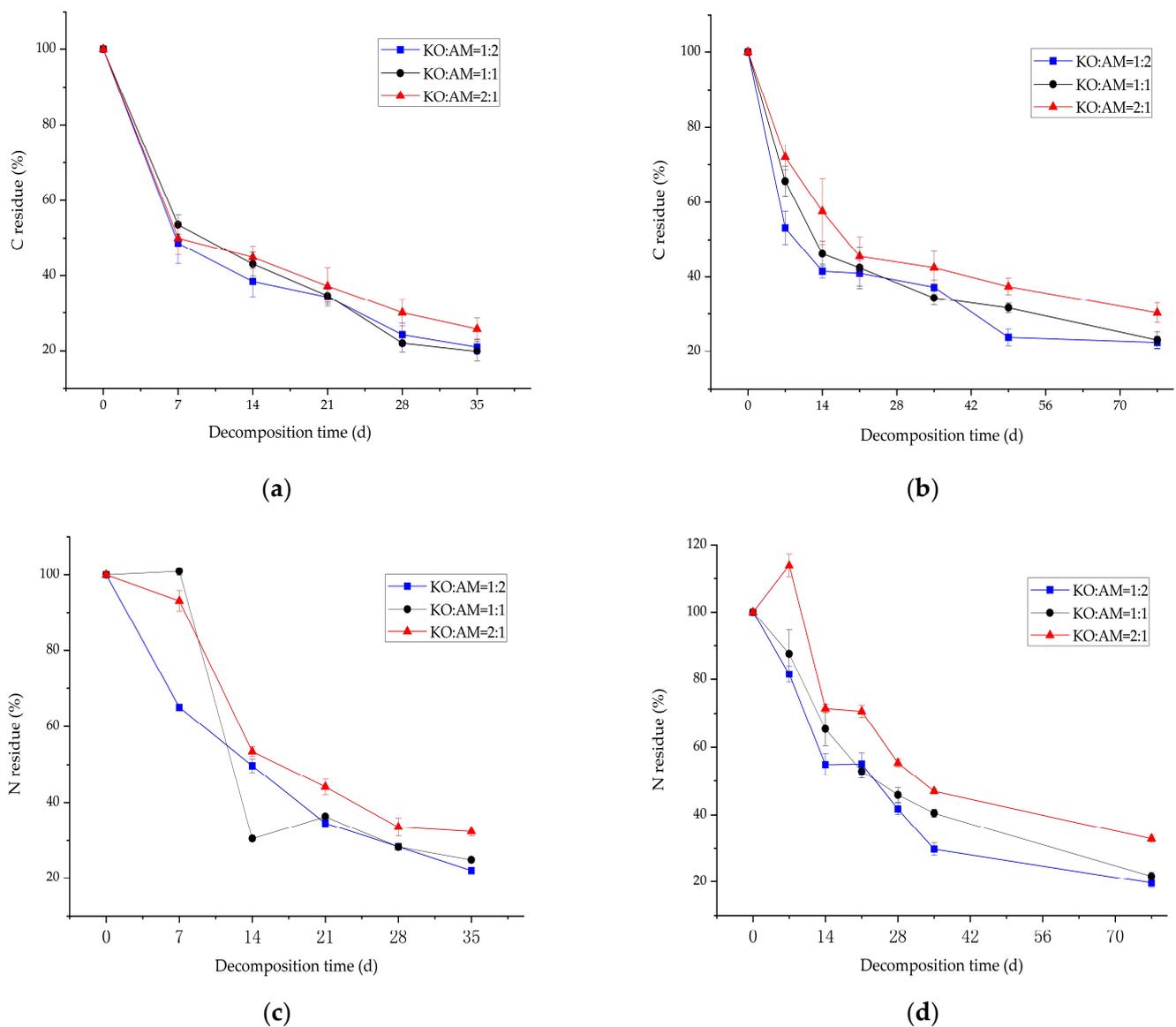


**Figure 3.** The correlation between the calculated and observed remaining weight values of *K. obovata* and *A. marina* leaf litter mixture. (The shaded part indicates 95% confidence interval).

However, considering the mixing effect over the two seasons (summer and winter) of decomposition separately, it was found that, during the summer decomposition process, there was no significant difference between the slope (1.04) and 1 ( $p < 0.01$ ), but the intercept ( $-4.29$ ) was significantly lower than 0 ( $p < 0.01$ ), indicating that there was a positive mixing effect on the decomposition process of *K. obovata* and *A. marina* mixed litter in summer, where the actual decomposition rates were faster than the calculated rates. During the winter decomposition process, the slope (1.12) was not significantly different from 1 ( $p < 0.01$ ), and the intercept ( $-9.79$ ) was significantly lower than 0 ( $p < 0.01$ ), which indicated that, during winter, the decomposition speed was slightly slower than calculated for litter with a faster mixed decomposition, but did not deviate from the expectations for litter with a slower mixed decomposition. Through linear fitting, we found that the additive effect explained 97.6% of the variability reported for mixed-litter decomposition in the summer and winter, and the decomposition of mixed mangrove litter was faster in summer than in winter.

### 3.3. Dynamic Changes in C and N from Mixed-Litter Decomposition

When *K. obovata* and *A. marina* leaves were mixed and decomposed in different proportions, changes in the C residue in each mixed-treatment group were consistent during summer and winter; generally, they first decreased quickly, and then decreased slowly with time (Figure 4a,b).



**Figure 4.** Variations in C and N residue (%) in mixed decomposition of *K. obovata* and *A. marina* leaf litter in summer (a,c) and winter (b,d).

C residue showed an obvious downward trend during the summer decomposition of mixed *K. obovata* and *A. marina* leaves. After 0–7 d of decomposition, the residue of C rapidly decreased, and then slowly and steadily decreased. After 14 days of decomposition, the residues of C in treatment group KO:AM = 2:1 were always slightly higher than those in treatment groups KO:AM = 1:2 and KO:AM = 1:1. At 21 days, the residues of C differences among the three treatment groups were the smallest. During the 21–35 d decomposition period, C residues were as follows: KO:AM = 2:1 > KO:AM = 1:2 > KO:AM = 1:1, 25.7%, 20.9%, 19.8%, respectively. C residues also showed an obvious downward trend during the winter decomposition process of mixed *K. obovata* and *A. marina* leaves. After 0–21 d of decomposition, residue rates of C in the three treatment groups rapidly decreased to about 40%. Treatment group KO:AM = 1:2's residue obviously decreased after 14 days of decomposition; treatment group KO:AM = 1:1's residue decreased more slowly over time. C residues in different litter types differed in different sampling periods, but showed a consistent trend; residue obviously decreased in the initial stage, fluctuated in the middle stage, and tended to stabilize in the later stage. However, treatment group KO:AM = 2:1's C residues were always higher than those of the other two treatment groups during the

entire winter decomposition period, and after 77 days of decomposition, the values were as follows: KO:AM = 2:1 > KO:AM = 1:1 > KO:AM = 1:2, 30.3%, 23.1%, 22.4%.

The change trend of N residue in the summer mixed-treatment group was different from that of the winter mixed-treatment group (Figure 4c,d); however, with an extended decomposition time, the N residue generally first increased and then decreased.

In summer, the KO:AM = 1:2 treatment group's N residue decreased rapidly, from 100% to 49.70%, from day 0 to 14 days after decomposition; when decomposition ended, this treatment group's residue was only 22.0%, a 78.0% decrease. The KO:AM = 1:1 treatment group showed an obvious fluctuation and decline during the 0 ~ 21 d decomposition period. N residue in the KO:AM = 1:1 treatment group was higher than the initial N residue at decomposition day 7; N residue significantly declined, in a linear trend, during decomposition days 7 ~ 14. Treatment group KO:AM = 2:1's N residue gradually decreased, and then tended to flatten with increased decomposition time; its N residue was higher than those of the other two treatment groups. After 35 days of litter decomposition, the N residues in three different mixed-proportions treatment groups were as follows: KO:AM = 2:1 > KO:AM = 1:2 > KO:AM = 1:1, 32.4%, 24.9%, 22.0%, respectively. In winter, at decomposition day 14, the residue of N in treatment group KO:AM = 2:1 was higher than those in treatment groups KO:AM = 1:2 and KO:AM = 1:1; the residues for these groups were as follows: KO:AM = 2:1 > KO:AM = 1:1 > KO:AM = 1:2, 71.5%, 65.3%, 54.9%, respectively. In fact, during the whole litter decomposition process from 0 to 77 days in winter, treatment group KO:AM = 2:1's N residues were always higher than those of the other two treatment groups. At the end of decomposition, the N residues in the three different mixed-proportions treatment groups were as follows: KO:AM = 2:1 > KO:AM = 1:2 > KO:AM = 1:1, 32.9%, 21.6%, 19.6%, respectively.

#### 4. Discussion

The decomposition rate of *Rhizophora mangle* and *Avicennia schaueriana* litter in two Brazilian subtropical mangroves was higher in summer than in winter [32], which was consistent with the results of this study; both underscore the influence of seasons on litter decomposition rates. The faster decomposition rates observed during summer compared to winter suggest that microbial activity and enzymatic processes are often more pronounced in warmer temperatures [33]. Mechanical fragmentation resulting from the activities of the macrofauna allows for the release of soluble molecules and greatly increases the surface area of the leaves available for colonization by microorganisms, which accelerates their decomposition [6]. Litter leachates were identified as a significant food source for microbial communities in coastal waters [7]. Furthermore, there were differential decomposition rates between *A. marina* and *K. obovata* leaves, highlighting the species-specific variations in litter decomposition within mangrove ecosystems [33]. *A. marina*'s faster decomposition could be attributed to its biochemical composition and inherent traits, because, compared with *K. obovata*, *A. marina* has less condensed tannins, making it more difficult for it to form insoluble complexes with protein and other biopolymers during the decomposition of litter. This is beneficial for the further decomposition of organic matter [5]. The litter's decomposition rate increased with an increase in the mass of *A. marina* leaves in the mixed-treatment group, ranked as follows: AM > KO:AM = 1:2 > KO:AM = 1:1 > KO:AM = 2:1 > KO. Due to its high content of condensed tannins, *K. obovata* decomposes at a significantly slower rate compared to *A. marina* and the mixture of *A. marina* and *K. obovata*. When the overall effect of the mixed decomposition of litter is equal to the sum of the simple addition of various factors, it is called an additive effect. When the overall effect exceeds the sum of the simple addition of various factors, a positive, non-additive effect will be generated; when the opposite occurs, a negative non-additive effect is generated [5,34]. The effect of mixing *K. obovata* and *A. marina* in different proportions has a significant positive or negative non-additive effect on litter decomposition, KO:AM = 1:2 (positive non-additive effect) and KO:AM = 2:1 (negative non-additive effect). Compared to the treatment of KO:AM = 2:1, the treatment

of KO:AM = 1:2, which had fewer condensed tannins, was more prone to decomposition in the mixed-mangrove litter. A high nitrogen content and low lignin and tannin concentrations in leaves were considered favorable for rapid decomposition [18]. This result emphasizes the importance of species composition and the proportion of species that influences litter decomposition dynamics within mangrove environments.

The essence of ecosystem operation is material circulation and capacity flow. The nutrient dynamic law of litter can directly describe the quantity and efficiency of material circulation, and, to some extent, indirectly indicate the efficiency of nutrient circulation and capacity flow in the mangrove ecosystem, which has important ecological significance. In *K. obovata* mangrove forest, C releases are very similar to dry weight loss [35]. We found a similar pattern in the process of the mixed decomposition of *K. obovata* and *A. marina* litter in our study, where C residue showed a downward trend, which was fast at first and then slow during the mixed decomposition of litter, and the C residue in the treatment group KO:AM = 2:1 was always higher than that in the treatment groups KO:AM = 1:1 and KO:AM = 1:2, indicating that the C loss in treatment group KO:AM = 2:1 was slower. This may also be related to the different biochemical compositions and inherent traits of the litter of *K. obovata* and *A. marina* [36]. During the initial decomposition process, the initial C content showed obvious differences between *K. obovata* and *A. marina*, which might have affected the amount of C released at each subsequent time point [37]. In addition, *K. obovata* has high amounts of condensed tannin, a low N content, and high C/N value; this means that it is not easy to decompose, and promotes the retention of C in the decomposition process of treatment group KO:AM = 2:1 of mixed mangrove litter [38,39]. However, the influencing factors regarding the mixing effect on nutrient dynamics may vary, including the microorganism, environmental temperature, moisture content, and oxygen levels, which are all crucial conditions that affect C dynamics during the litter decomposition process [40–43]. When the temperature and moisture content were too high or too low (together with a lack of oxygen), the number of microorganisms and their activity were limited, thus affecting the C release rates [44,45].

In the three mixed-treatment groups we investigated, it was found that N enrichment occurred at the early stage of the mixed decomposition of litter. Loría-Naranjo et al., who reported similar patterns in N dynamics for *Rhizophora racemose* leaves, suggested that, in *Rhizophora racemose* mangrove forests, the N residual in the leaf litter increased during the first week, irrespective of the season [16]. In the early stage of decomposition, under the influence of leaching, N was released in the form of N-containing salt, and external nutrient input or decomposer fixation led to N accumulation in litter. In addition, during the mixed decomposition of *K. obovata* and *A. marina* litter, the N residue was also affected by the proportion of *K. obovata* in the mixed litter. At the later stage of decomposition, the N residue basically showed KO:AM = 2:1 > KO:AM = 1:1 > KO:AM = 1:2, and the N residue in the treatment group KO:AM = 2:1 was significantly higher than that in the other two groups, which may be because the mixed decomposition of the treatment group KO:AM = 2:1 has a negative, non-additive effect, which reduces organic matter content, meaning that N is retained or N input into the organic matter [46]. However, its mechanism was more complicated, and microbial communities also play a crucial role in N dynamics during mangrove litter decomposition [47].

## 5. Conclusions

This study provides new insights into the decomposition dynamics of leaf litter mixtures associated with variations in C and N in a subtropical mangrove forest. The results have demonstrated the following: (i) *A. marina* decomposed faster than *K. obovata*, and the summer decomposition was faster than winter decomposition; (ii) the decomposition rates increased with an increase in the proportion of *A. marina* leaves in the mixture; (iii) the mixing litter had a significant promoting effect on the decomposition of single-species litter; (iv) the decomposition of the leaf litter mixture had an influence on C and N release dynamics, which is mainly related to the proportions of *K. obovata* and *A. marina* in

mixed litter. However, its influence was more complicated. The reason for this might be related to the litter's physical and chemical composition, the number of microorganisms, the environmental temperature, the moisture content, the oxygen content, and other factors. Understanding the C and N dynamics during mixed-litter decomposition is essential for comprehending nutrient cycling in mangrove ecosystems. Further research is needed to unravel the specific microbial processes and interspecific interactions that drive the observed patterns in C and N release, with potential implications for nutrient availability and ecosystem functioning in mangrove wetlands.

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