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Dynamics of Litter Production and Decomposition: A Case Study from A Tropical Coastal Lagoon, Malaysia

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HIGHLIGHTS

- The total annual litter fall production was recorded ~1325 g/m², and leaves were the major contributor (59%) to litter production throughout the year.
- In litter decomposition, both the decay rate and the percentage of wet losses were high (50%) during the first ~30 days of the study.
- A significant difference (F = 14.19, $p < 0.001$) was found in the decay constant at different positions during the experimental period, and the pattern of loss was highest on the forest floor, followed by hanging and burial positions for both species.

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Dynamics of Litter Production and Decomposition: A Case Study from A Tropical Coastal Lagoon, Malaysia

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Abstract: Litter production and decomposition are key drivers of carbon dynamics and energy fluxes in mangrove ecosystems. Decomposition rates are influenced by both biotic and abiotic factors. However, limited information is available on litter production in tropical lagoon systems and the role of fauna in decomposition processes. This study therefore examined: i) the monthly rate of litter production, and ii) the decay pattern of leaf litter from two mangrove species, Bruguiera gymnorrhiza and Rhizophora mucronate, across three positions (forest floor, hanging and burial) using 0.50 mm mesh litter bags. Litter production was monitored over one year, while a 120-day research was carried out to examine the decay pattern of leaf litter in a tropical lagoon mangrove ecosystem. The total annual litter fall production was approximately 1,325 g/m2, with leaves contributing the largest portion (59%). Decomposition was characterised by both the decay rate and the percentage of wet losses, with approximately 50% loss occurring within the first 30 days of the study. Due to the different physicochemical characteristics of the leaf (i.e., toughness, lignin content, C: N ratio and other phenolic compounds) of two mangrove species, a significant change ($F = 4.55$, $p < 0.05$) were found in the decay pattern. There was also a significant difference ($F = 14.19$, $p < 0.001$) in the decay constant across positions during the experimental period, and the loss pattern was highest on the forest floor, followed by the hanging and burial positions for both species. These findings suggest that employing multiple positions in decomposition experiments can enhance understanding of ecological impacts on ecosystem functioning and dynamics in tropical mangrove ecosystems.

Keywords: Ecosystem Functions, Mangrove Forest, Litter Production, Decay Constant, Malaysia

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Abstrak: *Pengeluaran dan penguraian sampah adalah pendorong utama dinamik karbon dan aliran tenaga dalam ekosistem bakau. Kadar penguraian dipengaruhi oleh faktor biotik dan abiotik. Walau bagaimanapun, maklumat mengenai penghasilan sampah dalam sistem lagun tropika dan peranan fauna dalam proses penguraian masih terhad. Oleh itu, kajian ini meneliti: (i) kadar pengeluaran sampah bulanan, dan (ii) corak pereputan daun daripada dua spesies bakau, Bruguiera gymnorrhiza dan Rhizophora mucronata, di tiga lokasi (lantai hutan, tergantung dan tertanam) menggunakan beg sampel bahan lebat bersaiz 0.50 mm. Pengeluaran bahan lebat dipantau selama setahun, manakala kajian selama 120 hari dijalankan untuk meneliti corak pereputan daun dalam ekosistem bakau lagun tropika. Jumlah pengeluaran runtuhan tahunan adalah kira-kira 1,325 g/m², dengan daun menyumbang bahagian terbesar (59%). Penguraian dicirikan oleh kadar reput dan peratusan kehilangan lembapan, dengan kira-kira 50% kehilangan berlaku dalam 30 hari pertama kajian. Disebabkan oleh ciri fizikokimia daun yang berbeza (iaitu ketahanan, kandungan lignin, nisbah C: N dan sebatian fenolik lain) bagi dua spesies bakau, perubahan yang signifikan ($F = 4.55$, $p < 0.05$) ditemui dalam corak reput. Terdapat juga perbezaan yang signifikan ($F = 14.19$, $p < 0.001$) dalam pemalar reput merentasi posisi semasa tempoh eksperimen, dan corak kehilangan paling tinggi berlaku di lantai hutan, diikuti oleh posisi tergantung dan tertanam untuk kedua-dua spesies. Penemuan ini mencadangkan bahawa menggunakan pelbagai posisi dalam eksperimen penguraian boleh meningkatkan pemahaman tentang kesan ekologi terhadap fungsi dan dinamika ekosistem dalam ekosistem bakau tropika.*

Kata kunci: *Fungsi Ekosistem, Hutan Bakau, Penghasilan Sampah, Pemalar Pereputan, Malaysia*

INTRODUCTION

Mangrove forests are the world's most productive wetland ecosystems in intertidal coastal zones of tropical and subtropical countries (Kathiresan 2002; Roy & Krishnan 2005, Proffitt *et al.* 2006; Hoque *et al.* 2015a; 2015b; Islam *et al.* 2024) and are dispersed over 123 countries (Billah *et al.* 2022). Mangrove ecosystems are unique and provide numerous ecosystem functions and services such as biodiversity provisions and blue carbon sinks (Islam *et al.* 2024). Mangrove litter production is an important ecosystem function and makes significant contributions to the nutrient budget of the surrounding ecosystems. The quantification of litter production is important to assess the net productivity of a mangrove ecosystem (Lee 1999; Imgraben & Dittmann 2008). A large portion of the mangrove's above-ground primary productivity comes from leaf litter, which is also reported to be the main source of mangrove litter (Hoque *et al.* 2015b). Furthermore, litter breakdown is related to three primary components: (i) leaching of soluble inorganic compounds; (ii) physical fragmentation and biological decomposition; and (iii) microbial degradation of refractory organics such as cellulose and lignin (Valiela *et al.* 1985; de Oliveira *et al.* 2013; Zimmer 2019). Studies have revealed that litter leaching accelerates litter decomposition by generating ideal positions for microbes and by enhancing the litter's palatability to detritus feeders (Zimmer 2019).

Nutrient cycling (Lu & Lin 1990; Steinke *et al.* 1993) and productivity (Ashton *et al.* 1999) of mangrove depend on the rate of nutrient and organic matter release during the decomposition process (Islam *et al.* 2024). This is also determined by both the physicochemical characteristics of litters, such as the toughness of lignin and other phenolics (Kristensen *et al.* 2008; Zimmer 2019; Kamal *et al.* 2020), and the surrounding environment, such as temperature and moisture (Smith & Bradford 2003; Zimmer 2019), as well as the decay rate of litters (Triadiati *et al.* 2011).

Decomposition depends on the degree and frequency of tidal inundation, climatic factors such as temperature, humidity and rainfall, substrate positions and the presence of leaf detritus-consuming fauna (Twilley *et al.*1986; Tam *et al.* 1990; Mackey & Smail 1996; Alongi 2009; Galeano *et al.* 2010; Islam *et al.* 2024). Studies by Fourqurean and Schrlau (2003) demonstrated that litterfall in burial creates anoxic positions, which may slow down the decomposition process. To understand the differences within different environmental setups and positions, i.e., forest floor, hanging, and burial positions, studies on litterfall decomposition are important to examine.

Litter production and decomposition are important indicators of ecosystem functioning and are directly linked to nutrient dynamics and energy transfers in mangrove habitats (Kristensen *et al.* 2008; Zimmer 2019). Leaf litter is the major contributor (30%–70 %) to annual detritus production (Kamal *et al.* 2020) and nutrient release (Kristensen *et al.* 2008; Ainley & Bishop 2015; Zimmer 2019). Litter production of different species has been studied for decomposition analysis (Lima & Colpo 2014; Nordhaus *et al.* 2017), and the effect of environmental conditions (Ainley & Bishop 2015), and pollution (Hayes *et al.* 2017) on leaf litter decomposition is relatively well understood. However, decay and decomposition of leaf litter have rarely been studied in Malaysia (Hoque 2015; Kamal *et al.* 2020; Hossain & Othman 2005; Ashton *et al.* 1999; Japar Sidik 1989; Ong *et al.* 1980; Islam *et al.* 2024). Previous studies on litter decomposition rates for different positions in mangrove ecosystems in a tropical mangrove are somewhat limited. In this respect, the present study was carried out to determine the annual litter production along with the decomposition rates in different positions of the two dominant mangroves, i.e., *Rhizophora mucronata* and *Bruguiera gymn*orrhiza.

The following corresponding hypotheses were tested to broaden the understanding of the mangrove ecosystem functioning and dynamics:

1. Based on stand structure, litter production would be different in different seasons (Kamruzzaman *et al.* 2019) and is influenced by climatic factors such as rainfall, air temperature and wind speed.

2. Different positions of leaf litter may change the decomposition rate in the mangrove ecosystem (Bradford *et al.* 2002; Kamruzzaman *et al.* 2019).

MATERIALS AND METHODS

Litter production and decomposition experiments were carried out in the tropical Seitu lagoon, Terengganu, Malaysia (Fig. 1). The species composition of mangroves in this lagoon has already been described in our previous investigations (Islam *et al.* 2022). High aquaculture and fisheries significance are associated with this wetland. It covers an area of 1,025 km^2 with an approximate length of 14 km (Salim *et al.* 2015), and the depth ranges from 0.3 to 3.2 m. Tidal ranges are less than 2 m (Phillips 1985). Due to the shallow structure of this lagoon, aquaculture activities, especially cage culture, are increasing considerably (Zainol *et al.* 2021). The tropical humid climate is characteristic of the region, and average rainfall was recorded at 208 mm month^{-1} (Nordhaus *et al.* 2017). This lagoon system hosts characteristics of mangrove habitats (Islam *et al.* 2022).

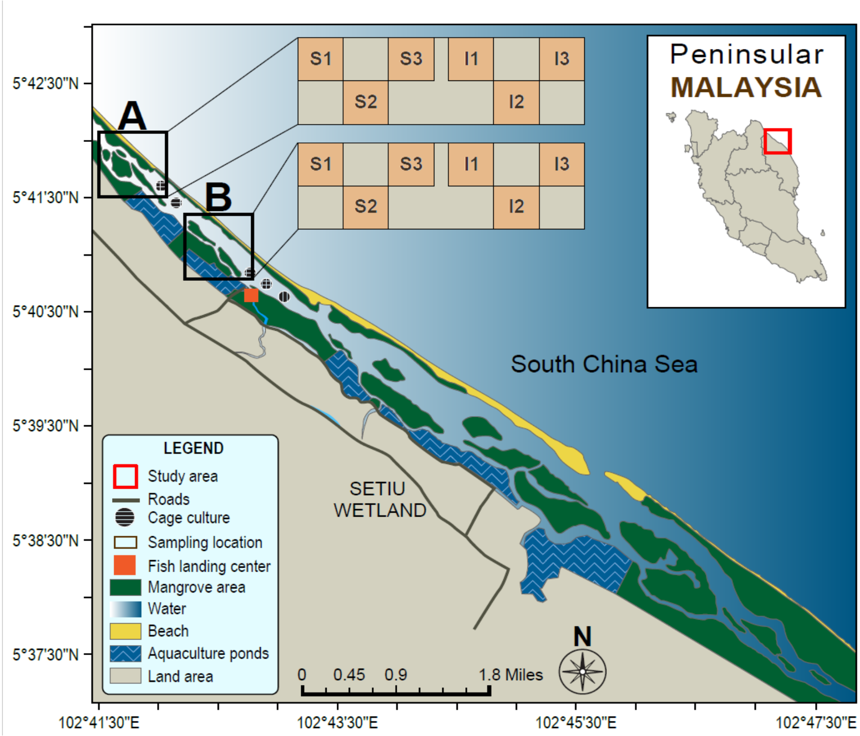

FIGURE 1: Study area map of Setiu lagoon showing sampling location, Terengganu, Malaysia.

Litterfall Study

A total of 12 litter traps were prepared using a plastic polyvinyl chloride (PVC) pipe and installed across two sampling sites (Site A: 5°41'43.8"N, 102°41'37.9"E; Site B: 5°40'58.9"N, 102°42'30.6"E; Fig. 1). Each trap measured 1 m × 1 m and was fitted with a conical nylon bag (mesh size: 1 mm × 1 mm). At each site, three traps were placed at the shore site (S) and three at the island site (I), randomly distributed within every 10 m × 10 m subplots above the tide level under the forest canopy, following the method of Brown (1982). The trapped litterfalls were collected monthly from September 2021 to August 2022, placed in labelled plastic bags, and brought back to the laboratory for further processing. Samples from each trap were sorted into leaves, twigs, stipules, flowers, propagules, and branches and then air-dried for 24 h. Subsequently, the samples were oven-dried at 60°C until a constant weight was achieved. The dried samples were then cooled in a desiccator to room temperature before being weighed to determine monthly litterfall production.

The Decomposition Study

In the present investigation, a field experiment was carried out at one forest plot (Site A: 5°41'43.8"N 102°41'37.9"E; Fig. 1) in the intertidal area of Setiu lagoon. This mangrove habitat is characterised by sandy sediment (Table 1). Tree species richness in this mangrove system is high, including 20 true mangrove species dominated by *R. mucronata*, *B. gymnorrhiza*, *Avicennia alba*, *Ceriops tagal*, *Sonneratia alba* and the palm *Nypa fruticans*. The mean stem density ranged between 1,533 and 3,800 individuals/ha (Islam *et al.* 2022). The riverbank is dominated by *N. fruticans,* especially in freshwater feeder canals or rivers, and vegetation in the middle zone is mainly composed of *R. mucronata* and *B. gymnorrhiza* (Islam *et al.* 2022; Rahman *et al.* 2023).

TABLE 1. Abiotic parameters measured in the Setiu wetland during the study period.

Environmental matrices	Temp. (°C)	pH	Salinity (PSU)	Dissolved oxygen (mg/L)	Soil texture		
					Sand (%)	Silt (%)	Clay (%)
Surface water	28.33 ± 0.58	7.18 ± 0.02	12.42 ± 1.14	5.46 ± 2.19	-	-	-
Pore water	27.67 ± 0.58	6.93 ± 0.04	6.67 ± 0.83	-	-	-	-
Sediment	29.00 ± 2.00	5.90 ± 0.36	-	-	79.00 ± 4.00	7.33 ± 0.58	13.67 ± 3.51

Note. mean (± SD); n = 5

The study reported that *R. mucronata* (relative density, 23.66%) is the most dominant species in the Setiu lagoon, followed by *B. gymnorrhiza* (15.53%) (Islam *et al.* 2022). Thus, in the present investigation, we considered leaf litter from these two major mangrove species for the decomposition experiment and tested our hypotheses.

Experimental design

For the decomposition study, the experiment was conducted over four months (120 days) from October 2021 to January 2022, taking into account the high decomposition rate of litter in the mangrove ecosystem (Oliveira *et al.* 2013; Loria-Naranjo *et al.* 2018; Kamal *et al.* 2020).

The "confined loss" litter bag technique is an established and accepted method of investigating the decomposition rate of leaf litter (Mosom 1980; Fell *et al.* 1984; Middleton & Mckee 2001). Senescent leaves were collected from the forest floor at study sites (Lecerf & Chauvet 2008). In the laboratory, the leaves were then air-dried at room temperature for 48 h to remove moisture from the leaves (Imgraben & Dittmann 2008). A litter bag (20 cm × 15 cm; 0.5 mm mesh) was filled with 10 g of dried leaf material and set up on the study site (Fig. 2).

FIGURE 2: On-field pictures of litter bags at different positions.

A total of 72 bags (2 species × 3 treatments × 3 replicates × 4 times) were tied at hanging positions, forest floor positions and burial positions. During the study, randomly selected litter bags were collected from the study sites on 15, 30, 60 and 120 days. In the laboratory, the leaves from the collected bags were gently rubbed and washed under tap water on a sieve (220 μm mesh size) to remove the sediment. Then, the litter was dried at 60°C for 96 h to obtain a constant mass (Silva *et al.* 2007).

To assess differences in degradation rates, we calculated the percentage loss day^{-1}. This approach was used instead of fitting the data to exponential models because we were more interested in the refractory material contributing to organic matter accumulation than the pattern of loss over time. Total percentage remaining (X) for leaves were calculated from the weight at the end of the study (X_t) and the initial biomass (X_o) as: X = 100 (X_t/X_o). Total percentage loss (L = 100 – X) was then divided by the number of days in the study (Middleton & Mckee 2001).

Data analysis

Decay constant (*k*), half-life ($T_{0.5}$) and 95% lifespan ($T_{0.95}$). The negative single exponential decay model was followed to describe the decomposition process (Olson, 2007). The equation is as follows:

$$W_t = W_0 \, e^{-kt}$$

Where W_0 (g) is the initial dry mass, W_t (g) is the dry mass at time "t", *k* is the decay constant, and t (day) is the decomposition time in days.

Half-life ($T_{0.5}$) and 95% lifespan ($T_{0.95}$) were estimated from *k* values using Equation (1) (Bockheim *et al.* 1991) and Equation (2) (Chandrashekara 1997):

$$t_{(0.5)} = \frac{\ln(0.5)}{(-k)} = \frac{-0.695}{(-k)} \qquad (1)$$

$$t_{(0.95)} = \frac{\ln(0.05)}{(-k)} = \frac{-2.996}{(-k)} \qquad (2)$$

Statistical Analysis

One-way and Two-way Analysis of Variance (ANOVA) were used to test whether the studied variable (i.e., weight remaining, decay constant) was different among sampling time (5 levels; 0, 15, 30, 60 and 120 days) or treatments (three levels; forest floor, hanging position and burial position) or species (two levels) by using arcsine square root transformed data (SAS JMP 1998). Further, post-hoc pairwise comparisons were also performed in cases of significant differences (Sokal & Rohlf 1981). Single degree of freedom contrasts of interest was conducted to distinguish among three or more levels of factors where ANOVA indicated a significant difference (SAS JMP 1998). All statistical analyses were performed in Past (ver. 4.03) and R Studio.

RESULTS

Litterfall Biomass Production and Seasonal Change

A relatively high leaf litter production (58.98 g/m^2) was recorded in March, followed by December (58.22 g/m^2), May (56.61 g/m^2), and January (56.26 g/m^2), as shown in Fig. 3. Peak flower and propagule litterfalls were 18.04 g/m^2 and 4.52 g/m^2, respectively, recorded in September, with the highest fruit litterfall recorded in November (39.54 g/m^2) (Fig. 3). Branch litterfall was almost similar all over the year, with small fluctuations in the study area. With some exceptions, the total monthly litterfall production of the forest did not fluctuate throughout the year (Fig. 3).

The total litterfall production at site A was higher in the North-west monsoon (752.25 g/m^2) compared to the south-west monsoon (538.31 g/m^2) (Table 2). In site B, the litterfall production in the dry and North-west monsoons was 609.05 g/m^2 and 755.51 g/m^2, respectively (Table 2). In a year, a total of 1,290.57 g/m^2 litterfall production was recorded in site A and 1,364.55 g/m^2 in site B (Table 2).

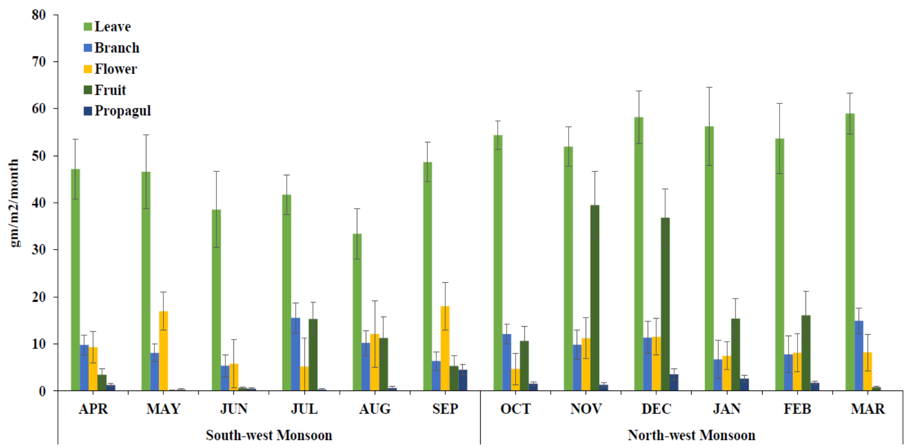

FIGURE 3: Seasonal changes of litter production at Setiu mangrove forest.

TABLE 2. Seasonal (gm/m^2/season ± SD) and annual litter production (gm/m^2/yr ± SD) of various components of two different stations in Setiu mangroves during the study period.

		Litterfall components					
Study sites	Season	Leaf	Branch	Flower	Fruit	Propagule	Total
Site A	South-west Monsoon	321.08 ± 18.70^b	77.97 ± 10.94^a	63.10 ± 5.27^a	70.43 ± 18.93^b	5.73 ± 1.11^b	538.31 ± 45.07^b
	North-west Monsoon	402.69 ± 18.90^a	80.28 ± 3.69^a	69.33 ± 11.85^a	169.23 ± 27.34^a	30.72 ± 2.81^a	752.25 ± 52.53^a
	Total	723.77 ± 57.70	158.25 ± 1.63	132.43 ± 4.40	239.66 ± 69.86	36.45 ± 17.66	1290.57 ± 151.26
Site B	South-west Monsoon	411.70 ± 10.88^a	18.09 ± 2.31^b	145.93 ± 16.21^a	30.33 ± 4.70^b	6.57 ± 2.08^b	609.05 ± 21.01^b
	North-west Monsoon	349.53 ± 8.46^b	34.75 ± 4.98^a	85.37 ± 7.20^b	262.28 ± 26.72^a	23.57 ± 1.85^a	755.51 ± 20.40^a
	Total	761.23 ± 43.95	52.84 ± 11.78	231.29 ± 42.82	292.62 ± 164.01	30.14 ± 12.02	1364.55 ± 103.55
	Yearly mean	742.50	105.54	181.86	266.14	33.29	1327.56

Notes: The means within a column for each station with different alphabets are significantly different (n = 12, Tukey test, p < 0.05)

The total litterfall production showed a significant correlation with the monthly climate variables, i.e., mean rainfall and wind speed (Fig. 4). The correlation of litterfall production with wind speed was significantly high (r^2 = 0.73, p < 0.05). However, the Pearson correlation value was not so significant with rainfall (r^2 = 0.33, p < 0.05) throughout the year.

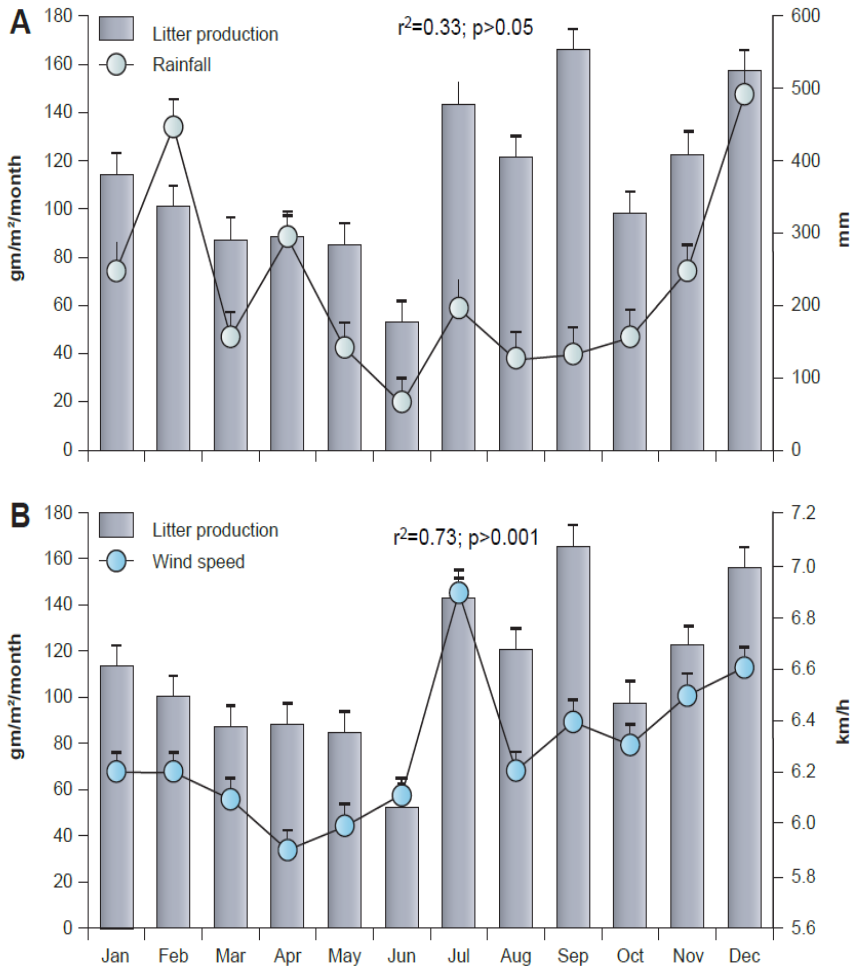

FIGURE 4: Relation between monthly total litter production and (A) Rainfall and (B) Wind speed in Setiu mangrove forest.

Dry Mass and Decay Constant

The most rapid mass loss was found within the first 15 days for both mangrove species, with the remaining dry mass of 63%, 80%, 82% for *R. mucronata* and 59%, 64%, 77% for *B. gymnorrhiza* on the forest floor, hanging position, and burial position, respectively (Figs. 5a and 5b). The remaining dry mass was found to be 26% for the forest floor, 35% for the hanging position, and 43% for the burial position at the end of the experiment for *R. mucronata* (Fig. 5a). Considering the whole decomposition period, the mean dry mass showed the following pattern: burial position

> hanging position > forest floor for *R. mucronata* (Fig. 5a) and hanging position > burial position > forest floor for *B. gymnorrhiza* (Fig. 5b).

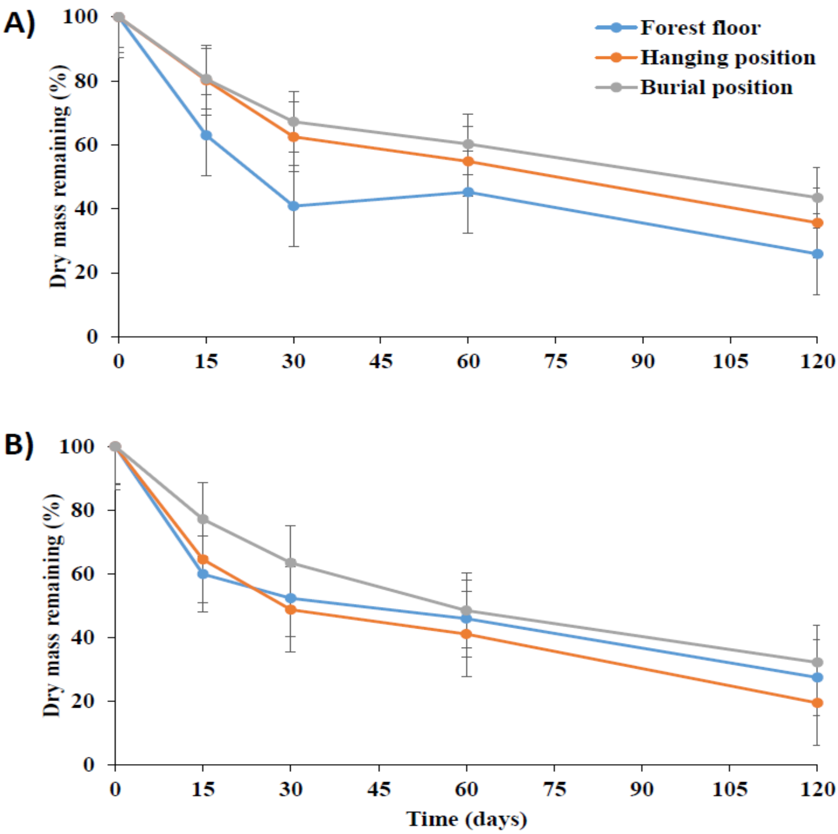

FIGURE 5: Dry mass remaining of (A) *R. mucronata* and (B) *B. gymnorrhiza* at different positions in Setiu mangrove forest.

Decay constants differed significantly within species, among treatments, and over investigation time (ANOVA; $p < 0.05$; Table 3). The average decay constant (k), considering the whole decomposition period, showed the following pattern: forest floor > hanging position > burial position for *R. mucronata* and *B. gymnorrhiza* (Table 3). Overall, for *R. mucronata,* the mean decay constant was found to be 0.018 g/g/day ($r^2 = 0.93$; $p < 0.05$) at hanging position, 0.021 g/g/day ($r^2 = 0.82$; $p < 0.05$) at the forest floor and 0.013 g/g/day ($r^2 = 0.95$; $p < 0.05$) at burial treatment. For *B. gymnorrhiza,* it was found to be 0.017 g/g/day ($r^2 = 0.91$; $p < 0.05$) at hanging, 0.020 g/g/day ($r^2 = 0.81$; $p < 0.05$) at the forest floor, and 0.012 g/g/day ($r^2 = 0.94$; $p < 0.05$) at burial position (Table 3). The lowest half-life ($T_{50\%}$) was found at 33 days on the forest floor for *R. mucronata*, while *B. gymnorrhiza* reached half-life at 34 days (Table 3).

TABLE 3. Decomposition constant (*k*), half-life ($t_{0.50}$) and 95% lifespan ($t_{0.95}$) of *R. mucronata and B. gymnorrhiza* in different positions obtained from negative single exponential equations.

Treatment	Species	r^2	k(g/g/day)	Equation	$T_{50\%}$(days)	$T_{95\%}$(days)
Hanging position	*R. mucronata*	0.93	0.018	$W_t = 90.397e^{-0.008x}$	57	166
	B. gymnorrhiza	0.91	0.017	$W_t = 84.057e^{-0.013x}$	34	176
Forest floor	*R. mucronata*	0.82	0.021	$W_t = 79.585e^{-0.009x}$	33	142
	B. gymnorrhiza	0.81	0.020	$W_t = 79.585e^{-0.009x}$	34	149
Burial position	*R. mucronata*	0.95	0.013	$W_t = 89.758e^{-0.009x}$	53	230
	B. gymnorrhiza	0.94	0.012	$W_t = 89.758e^{-0.009x}$	58	249

The mean rate of remaining dry mass and decay constant was greater on the forest floor in the hanging and burial positions (Table 4). Dry weight loss of leaf litter varied significantly with decomposition time (F = 308.55; $p < 0.001$), among positions (F = 24.20; $p < 0.001$), and between species (F = 15.91; $p < 0.001$) (Table 4). On the other hand, for the decay constant rate, the significant value was F = 4.55 ($p < 0.05$) with decomposition time, F = 14.19 ($p < 0.001$) among positions, and F = 65.83 ($p < 0.001$) between species (Table 4).

TABLE 4. Summary of ANOVA for weight remaining, decay constant (*k*) in leaf litter after 120 days of decomposition, comparing differences between species (*R. mucronata*, and *B. gymnorrhiza*) and litter bag positions (forest floor, hanging position, and burial position).

Source of variation	df	Weight remaining			Decay constant (k)		
		MS	F	p	MS	F	p
Species	1	627	15.91	***	0.0001	4.55	*
Position	2	954	24.20	***	0.0003	14.19	***
Treatment	4	12.157	308.55	***	0.0015	65.83	***
Residuals	82	39			0.0002		

Notes: *** $p < 0.001$, ** $p< 0.01$, * $p < 0.05$, ns: not significant)

DISCUSSION

Litter Production

The mangroves at Setiu Lagoon are dominated by *R. mucronata* and *B. gymnorrhiza* (Islam *et al.* 2022), where they play a significant role in litter production and nutrient inputs into the adjacent ecosystems via decomposition processes. Litterfall production in mangroves depends on tree density, species, forest types and geographical location (Day *et al.* 1996; Hossain & Hoque 2008). The total litterfall in the mangrove forest of Setiu Lagoon was found to be 1,327.56 g/m^2/yr (Table 2), which was like several other *R. mucronata*-dominated mangroves in the tropical region. Litterfall production at the Kuala Sibuti mangroves was higher (1,640.82 g/m^2/yr) compared to the Setiu mangrove forest (Hoque *et al.* 2015a). Clough *et al.* (2000) also reported higher litterfall production in *R. apiculata-dominated* mangrove forests in Ca Mau province, Vietnam.

The percentage (56%) of leaf components and non-leaf components (44%) was remarkable compared to the other findings elsewhere. In a subtropical mangrove forest on Okinawa Island, leaf litterfall ranged from 52.8 to 67.9% in five subsequent study periods (Sharma *et al.* 2012). This study also revealed that total litter production was higher in the north-west monsoon than in the south-west monsoon. Angsupanich and Aksornkoae (1994) also reported significant seasonal changes regarding litterfall production in Phangnga Bay, Thailand. The highest leaf litterfall was also recorded from January to February (the north-west monsoon) (Duke *et al.* 1981). The flowering time of *R. mucronata* and *B. gymnorrhiza* was found in the south-west monsoon, especially from June to August, and following the sequence of flowering, fruiting was observed in the North-west monsoon, especially in the months of November and December. Similar trends in flowering and fruiting of *R. mucronata* were also reported in north-eastern Australia (Williams *et al.* 1981) and Papua New Guinea (Leach & Burgin 1985). Generally, rainfall throughout the year and constant temperature in the tropical region may govern the phenology of mangroves.

The rate of litterfall production is influenced by climatic and environmental variables, particularly wind speed, rainfall, temperature and evaporation (Hossain & Hoque 2008; Ye *et al.* 2013). Sasekumar and Loi (1983) also stated that climatic and environmental factors play a driving force for less than 50% variability of litter production in *Sonneratia*, *Avicennia* and *Rhizophora*-dominated mangroves in Malaysia. In subtropical mangroves in Japan and China, total litterfall production was found to be related to temperature and wind speed (Mfiling *et al.* 2005; Sharma *et al.* 2012;

Ye *et al.* 2013). Likewise, the present findings indicated that wind speed also had a profound influence on litterfall production in the semi-arid mangrove forests of Karachi, Pakistan (Farooqui *et al.* 2012).

Leaf Litter Decomposition in Different Positions

To our knowledge, this study is the first to investigate the leaf litter decomposition in different environmental conditions in a tropical lagoon ecosystem in Malaysia. Although there was a variation in the litter decomposition rate at the forest floor, hanging, and burial positions, it is likely a common phenomenon found in other studies (Steinke & Ward 1987; Mall *et al.* 1991; Tam *et al.* 1998). However, the trend of the overall decomposition pattern under different positions suggested that litter decomposition under different positions differed significantly during the study period (Fig. 5).

Results showed that the decay rate was higher for both species in the first 15 days of the decomposition process (Fig. 5), as reported in several decomposition studies (Robertson *et al.* 1992; Dick & Osunkoya 2000; Aké-Castillo *et al.* 2006; Barroso-Matos *et al.* 2012). This rapid weight loss results from the high leaching of soluble compounds such as sugars, organic acids, proteins and phenols (Mfilinge *et al.* 2002; Davis *et al.* 2003; Kristensen *et al.* 2008). During the decomposition experiment, the litterfall lost was 20% of its original mass in the first 60 days, and this loss continued to 50% of its original weight by the end of the experiment (196 days) (Kamruzzaman *et al.* 2019). The litter on the forest floor lost 50% of its original dry mass after 33 and 34 days for *R. mucronata* and *B. gymnorrhiza*, respectively (Table 3; Fig. 5). This decomposition rate was almost the same (32 days) compared to the decomposition study of the mass loss of leaves of *Rhizophora mangal* in the experiment (Silva *et al.*, 2007). These differences can be explained by the fact that the forest floor is exposed to higher biotic and abiotic agents, such as soil fauna, light, physical abrasion, temperature and water (Austin & Vivanoco 2006; Bokhorst & Wardle 2013) compared with burial and hanging positions.

Previous studies reported that the higher decomposition rate observed on the forest floor positions compared to burial positions was expected, as the forest floor litter materials are exposed to a wide range of biotic (sediment macrofauna, microfauna, and microbes) (Ashton *et al.* 1999) and abiotic positions (hydroperiods) (Liu *et al.* 2012; Chambers *et al.* 2016). In the case of burial leaf litter, they are exposed to anoxic positions and therefore litter materials are subjected to anaerobic microbial degradation (de Angelis *et al.* 2010; Loría-Naranjo *et al.* 2019; Fiard *et al.* 2022). Bokhorst and Wardle (2013) also mentioned that decomposition is primarily related to substrates (litter) and soil type. However, Kamruzzaman *et al.* (2019)

reported that there was no significant difference in mass loss at different positions (forest floor and burial position) or sites during the experiment period.

CONCLUSION

The results of this study support Robertson and Daniel's (1989) hypothesis that physical factors may be more significant in governing the litter production in tropical mangroves. It is known that the major portion of the litterfall is flushed by the tidal water and transported to nearby ecosystems (Heald & Odum 1970). Fast decay rates highlight the importance of mangrove litter to liberate limited nutrients for the ecosystem, contributing to carbon and nitrogen budgets. Overall, these findings suggest that the decomposition rate depends on different positions associated with the ecological parameters of the surrounding environment and is the main basis for nutrient availability and storage in a mangrove ecosystem.

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AUTHORS' CONTRIBUTIONS

Mohammad Ahsanul Islam: Conceptualisation, field investigation and laboratory treatments, original draft preparation, reviewing and editing.

Abu Hena Mustafa Kamal: Conceptualisation, funding acquisition, supervision, project investigation, reviewing and editing.

Md Khurshid Alam Bhuiyan and Md Masum Billah: Visualisation, reviewing and editing.

AFM Arifur Rahman: Field investigation and laboratory treatments.

Mohd Hanafi Idris: Conceptualisation, field investigation, funding acquisition, reviewing and editing.

DATA AVAILABILITY

All data generated or analysed during this study are included in this published article. More detailed data can be provided upon request to the corresponding author.

DECLARATIONS ETHICAL APPROVAL

Not applicable.

COMPETING INTERESTS

The authors declare no competing interests.

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