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Synergistic effects of mangrove leaf litter and supplemental feed on water quality, growth and survival of shrimp (*Penaeus monodon*, Fabricius, 1798) post larvae

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A R T I C L E   I N F O

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A B S T R A C T

Shrimp based mangrove-aquaculture (silvo-aquaculture) is practiced in many countries of the world and leaf litter of different mangrove tree species is a potential nutrient source in these systems. The present study evaluated the effects of mangrove leaf litter from four mangrove species (*Sonneratia apetala*, *S. caseolaris*, *Avicennia officinalis* and *Heritiera fomes*) on the production of juvenile shrimp (*Penaeus monodon*) with and without supplemental feed. Fifteen-day-old post larvae (PL_{15}) with an average weight of 0.01 g were reared in 1100 L fibre-reinforced polyethylene tanks containing 1000 L of 10 ppt saline water and a water depth of 0.9 m. Leaf litter with or without supplemental feed was applied to the tanks according to a 4 × 2 factorial design. The PLs were stocked at a density of 100 per tank and the experiment was conducted for 4 weeks without any exchange of water. Both mangrove species and feed application affected shrimp performance and water quality parameters except dissolved oxygen (DO), chemical oxygen demand (COD) and zoo-plankton concentration. The average survival rate of juvenile shrimp ranged from 86 to 94% in the treatments with both leaf litter and feed, 75–82% in the treatments with only leaf litter and 88% in the treatment with only feed. However, 100% mortality was observed in the treatment without any leaf litter or supplemental feed. Combined, leaf litter and feed resulted in 21 to 33% higher weight gain of shrimp PL than based on the combined contributions of leaf litter only or feed only, indicating synergism. Among the different mangrove species, *S. apetala* (23.1%) contributed the highest to total weight gain followed by *A. officinalis* (21.6%), *S. caseolaris* (21.6%) and *H. fomes* (10%). The lower feed conversion ratio (FCR) (0.18–0.27) in the treatments combining leaf litter and supplemental feed as compared to the feed-only treatment (0.41) indicated that leaf litter (directly or by stimulating natural food production) contributed to supplemental feeding. The growth of phytoplankton also appeared to contribute in low FCR as evidenced by a positive correlation ($P < 0.001$, $r = 0.681^{**}$) between phytoplankton concentration and shrimp weight gain. The synergistic effect between leaf litter and supplemental feed can help the farmer to minimize the shrimp production cost by lowering the feed input and enhancing mangrove three coverage on pond dikes as an inexpensive source of natural food.

1. Introduction

Mangroves are highly productive ecosystems in terms of primary and secondary productivity in the coastal waterbodies of the tropics and subtropics. Mangrove roots and fallen leaf litter provide substrate for biofilm production, and provide nutrients to the water column which stimulate productivity (Gatune et al., 2014; Gatune et al., 2012; Reef et al., 2010; Verweij et al., 2008; Nordhaus et al., 2006). The leaves of

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mangrove trees enter the detritus pathway and substantially contribute to aquatic food webs supporting fisheries production (Hutchison et al., 2014). However, for leaves to contribute to productivity, the litter needs to go through various decomposition steps (Hutchison et al., 2014) that starts with the leaching of soluble compounds accompanied by microbial decomposition. The entire process is accelerated by shredders like crabs and other animals that feed directly on leaf litter, making it more accessible to adjacent fish communities (Kamruzzaman et al., 2019). Because mangroves support aquatic production, mangrove-based aquaculture systems, alternatively termed silvo-aquaculture have been developed in many Asian countries such as the Philippines (Aypa and Bagonguis, 2000), Indonesia (Sukardjo, 2000), Vietnam (Binh et al., 1997; Johnston et al., 2000), Thailand (Tanan and Tansutapanich, 2000), Myanmar (Win, 2000a, 2000b) and Malaysia (Sze and Ahmad, 2000). As aquaculture is considered as one of the main causes of the destruction of mangroves, silvo-aquaculture systems represent a more integrated approach to pond culture and may simultaneously help to conserve mangrove resources and enhance economic benefits to coastal communities where aquaculture is important (Fitzgerald, 2000). Different systems of silvo-aquaculture are practiced (Bosma et al., 2014; Primavera et al., 2007; Primavera, 2000). Most silvo-aquaculture systems are extensive, mainly relying on natural food produced from fallen mangrove leaves (Rejeki et al., 2020; Rejeki et al., 2019; Nga et al., 2006; Nga and Roijackers, 2002). In contrast, formulated feed is the most energy demanding and costly input used to enhance shrimp production. However, apart from being too costly for small-scale farmers, use of formulated feed has been associated with water pollution due to excess use of feed (Islam and Bhuiyan, 2016; De Schryver et al., 2008; Tacon, 2002). Some strategies have been evaluated worldwide to minimize the problem, one of which is the promotion and contribution of natural food (Porchas-Cornejo et al., 2010). Mangrove leaf litter is a natural food for shrimp (Gatune et al., 2014; Gatune et al., 2012; Nga et al., 2006; Hai and Yakupitiyage, 2005). In addition, litter can function as a shelter against predation (Nga et al., 2006; Hai and Yakupitiyage, 2005). Therefore, the combination of natural food and formulated feed should have a positive effect on all the production parameters of shrimp as observed by Porchas-Cornejo et al. (2012). The combined effect, or synergy can be identified by measuring the individual and combined effects of leaf litter and formulated feed. A positive synergistic effect, if any, would make shrimp aquaculture more productive in an environmentally friendly way. Such synergy could also help to align interests of farmers and mangrove restoration, and could be an effective way to minimize the conflicts between shrimp culture and mangrove loss (Ahmed et al., 2017; Bosma et al., 2014; Primavera, 2000). While there are potential benefits of mangrove leaf litter there are also potential detrimental effects, including the release of anti-nutrients from the leaves during decomposition, decreased oxygen levels and increased Biological oxygen demand (BOD), Chemical oxygen demand (COD), nitrite and total ammonium nitrogen (TAN) concentrations (Nga et al., 2006; Hai and Yakupitiyage, 2005; Nga and Roijackers, 2002). However, the positive and negative effects of mangrove leaf litter, as well as any synergistic effects, might differ depending on the species of mangrove.

Considering the above, the present research investigated the effect of leaf litter from different mangrove species and formulated feed on shrimp production and water quality.

2. Methodology

2.1. Experimental design

The experiments were carried out at a farm located in Debhata, Satkhira, on the northern rim of the Sundarbans mangrove area in Bangladesh. They took place under ambient conditions, with rearing tanks covered with a transparent plastic roofing that allowed avoidance of large fluctuations in salinity due to heavy rain, while still maintaining the natural diurnal variation in light incidence. The experiment was set up according to a 4 × 2 factorial design with mangrove tree species (*Avecennia officinalis*, *Sonneratia apetala, S. caseolaris* and *Heritiera* fomes), as source of leaf litter serving as the first factor and food (with or without formulated feed) as the second factor (Table 1). In addition, there were two control treatments, one receiving only formulated feed and another receiving neither feed nor leaf litter. All treatments were executed in triplicates. The eight leaf litter treatments were analyzed as a factorial experiment. The two additional treatments, were used to explore synergy between formulated feed and leaf litter addition as well as to assess the effect of mangrove leaf litter on shrimp performance.

The shrimp were reared in 1100 L fibre-reinforced polyethylene tanks containing 1000 L of brackish water (salinity of 10 ppt) with a water depth of 0.9 m. Brackish water collected from a nearby canal was stocked in a pond and left to settle for one week. The top layer of water from this pond was transferred to the experimental tanks through a screen with 25 μm mesh size net to keep predators and their eggs and larvae out. Each tank was aerated using a single air stone (diameter 2 cm) connected to an air blower (RESUN, LP-100). Mangrove leaf litter was directly added in the culture tanks at a concentration of 1 g/L (wet weight). This loading rate was standardized following Hai and Yakupitiyage (2005). On the same day, 100 specific pathogens free (SPF) shrimp post larvae (PL) of 15 days old with an average weight of 0.01 g obtained from Desh Bangla Shrimp Hatchery, Batiaghata, Khulna, were stocked at a rate of 1 PL/10 L of water in each tank. The experiment assessing growth and survival was conducted over a four-week period and the water was not exchanged during the experiment. The survival and growth indices were calculated only at the end of the experiment.

2.2. Selection of mangrove species and collection of leaf litter

Selection of mangrove species was done following Rahman et al. (2020). Senescent leaves that fell down naturally, after changing color from greenish to yellowish, were collected from the selected mangrove species in the Sundarbans mangrove forest. The traps were 2 by 2 m, and installed beneath the selected mangrove species during winter (November 2018-January 2019). At regular intervals, the fallen leaves were recovered from the traps, separated by species and prepared for use in the experiment. The decomposition rates (% day^{-1}) of the selected mangrove species (*A. officinalis* = 1.6; *S. apetala* = 1.8; *S. caseolaris* = 1.4; *H. fomes* = 0.8) as identified by Alam et al. (2021), were expected to affect shrimp growth in fed and non-fed systems.

2.3. Feeding the shrimp PL and calculation of FCR

Shrimp growth was monitored weekly in the control treatment that received only feed at 5% body weight per day, and these data were used to adjust the feeding rate for all treatments. Feed "Titas Tiger" from Bismillah Feed Mills Limited, Mollahat, Bagerhat, with 12% of moisture,

Table 1
Design of experiment with treatment type.

Feeding type	Mangrove species			
	S. apetala	*S. caseolaris*	*A. officinalis*	*H. fomes*
Tanks with mangrove leaves				
Feed	Sa-F	Sc-F	Ao-F	Hf-F
No Feed	Sa-nF	Sc-nF	Ao-nF	Hf-nF
Tanks without mangrove leaves				
F				
nF				

Sa-F=*S. apetala* leaf litter and feed, Sc-F=*S. caseolaris* leaf litter and feed, Ao-F = *A. officinalis* leaf litter and feed, Hf-F = *H. fomes* leaf litter and feed, Sa-nF=*S. apetala* leaf litter and no feed, Sc-nF=*S. caseolaris* leaf litter and no feed, Ao-nF = *A. officinalis* leaf litter and no feed, Hf-nF = *H. fomes* leaf litter and no feed F = Feed only, nF = no feed.

36% of protein, 10% of lipid, 7% of fibre, 18% of ash, 1.9% of calcium and 1.7% of phosphorus, was fed once daily at 5% BW d^{-1}. After harvest, FCR was calculated as the total feed given divided by total shrimp biomass gain.

2.4. Water quality monitoring

Temperature, salinity, pH, and dissolved oxygen (DO) in each tank were measured daily using, respectively, a Hanna (Taiwan) digital thermometer, an Atago (Japan) hand refractometer, a (Eutech) pH meter (Singapore), and a Lutron (Taiwan) DO meter. Total Ammonia Nitrogen (TAN) and Nitrite-N (NO_2-N) were measured weekly by the colorimetric Nessler method, with color card and sliding comparator: HI 3826|TAN, HI 3873|Nitrite test; HANNA instruments.

Biological oxygen demand (BOD_5) was measured weekly. For this, two water samples were collected from each tank at a depth of 10–30 cm from the surface in 300 mL BOD bottles without collecting air bubbles. In one bottle, DO was fixed following the Winkler procedure to measure initial DO while other bottle was set to incubate for 5 days. Both sample types were analyzed at the Khulna University water quality laboratory. The BOD_5 was calculated by following the method outlined in APHA (1998).

Chemical oxygen demand (COD) was measured bi-weekly. Samples were collected from the middle of the tank at a depth of 10–30 cm from the water surface. The analysis was done following the Open Reflux (OR) method outlined in APHA (1998) at Khulna University.

2.5. Sampling and analysis of plankton

Phytoplankton and zooplankton samples were collected on day 1 and 28. Samples (15 L per sample) were collected at 9.00–11.00 h from 3 points in each tank and passed through a 45 μm mesh plankton net and combined. The concentrated samples were preserved in plastic bottles with 1 mL of Lugol's solution. The abundance estimations of plankton (individual. L^{-1}) were done using a 1 mL Sedgewick-Rafter (S-R) counting chamber. One mL of sample was poured into the S-R cell and left undisturbed for 15 min to allow the plankton to settle. The plankton in 10 randomly selected cells were then counted using a compound microscope (Lx 400; magnification-4×-100×, USA) and identified (where possible to genus level) using 5.1 M C-Mount CMOS Camera-Aptina MT9P001 CMOS (Color). Plankton were identified using keys by Prescott (1962), Edmondson (1982), Bellinger (1992) and Tomas (1997). Plankton abundance was calculated using the following formula:

$$N = (P \times C \times 100)/V.$$

where, N = the number of plankton organisms per liter, P = the number of plankton counted in 10 fields, C = the volume of concentrated sample (mL) and V = the volume (in L) of water in the sample.

2.6. Assessment of shrimp post larvae performances

Growth and survival indices were calculated at the end of the four-week period using the formula described by Busacker et al. (1990). After harvesting the shrimp juveniles were counted, placed on tissue paper to remove excess water and bulk weighed to calculate the average weight at harvest. Weight gain was calculated by deduction of initial weight from the final weight. Daily weight gain was calculated from final weight gain divided by the number of culture days. The formulae for calculation of feed conversion rate (FCR), survival rate (SR) and specific growth rate (SGR) were:

$$FCR\ (g\ g^{-1}) = \frac{Feed_{Tot}}{WG_{Tot}}$$

$$SR\ (\%) = \frac{Nf}{Ni} \times 100.$$

$$SGR\ (\%BW/day) = \frac{ln\ (BWf) - ln(BWi)}{D} \times 100$$

where $Feed_{Tot}$ (g) is the total amount of feed; WG_{Tot} (g) is the total weight gain between stocking and harvesting; N_f is the number of juvenile shrimp collected at final harvest; N_i is the number of PLs stocked; BW_f is the final average body weight (g); BW_i is the initial average body weight (g); and D is the duration of the experiment (day).

2.7. Calculation of synergy between feed and leaf litter

The calculation of individual and synergistic contributions of leaf litter and feed was done based on total weight gain in shrimp juveniles. The calculation was done as follows:

$$\text{Contribution of leaf litter}\ (\%) = \frac{\text{Total weight gain with leaf litter (g)}}{\text{Total weight gain with leaf litter and feed (g)}} \times 100$$

$$\text{Contribution of feed}\ (\%) = \frac{\text{Total weight gain with feed (g)}}{\text{Total weight gain with leaf litter and feed (g)}} \times 100$$

$$\text{Synergistic effect}\ (\%) = 100 - (\text{contribution of leaf litter} + \text{contribution of feed})$$

2.8. Statistical analysis

The data were analyzed using the IBM SPSS statistical software package version 26. One-way ANOVA was conducted to compare the synergistic effects of feed and mangrove leaf litter between the four mangrove species used. A factorial analysis was carried out, with the main factors feed and mangrove leaf litter species and the sampling date as a repeated measure factor using the general linear model (GLM). For the significant differences, a post-hoc Tukey HSD test was used to determine pair-wise differences ($P < 0.05$). Correlations among the different variables were assessed using Pearson's correlation coefficients. Principal component analysis (PCA) was performed using PRIMER 6, to help assess the relationships between environmental parameters based on a reduced number of composite variables. These composite variables are assumed to explain the covariation among the environmental parameters. The first principal component is a linear combination of the environmental parameters which explains as much as possible of the variation between samples. The second principal component, explains as much of the remaining variation, and so on. The different principal components are independent, unitless and normalized with a mean equal to 0 and a variance equal to 1. The meaning of each component was interpreted based on the relative size and sign of the coefficients of the regressions indicating the importance of each variable. The effect of the environmental parameters on PL performance (weight gain and survival) was analyzed with distance based linear models (DistLM) in the PRIMER 6 package.

3. Results

The experimental results showed the significance of leaf litter of mangrove species as source of natural food for the shrimp PL. A positive effect of both mangrove species ($P < 0.05$) and feed ($P < 0.001$) was observed for survival rate but there was no interaction effect ($P > 0.05$) between the two factors. The survival rate ranged from 76 to 94% where the highest survival rate was observed for Sa-F and the lowest was for Sc-nF (Fig. 1a). Though there was a higher survival rate (85–94%) for leaf

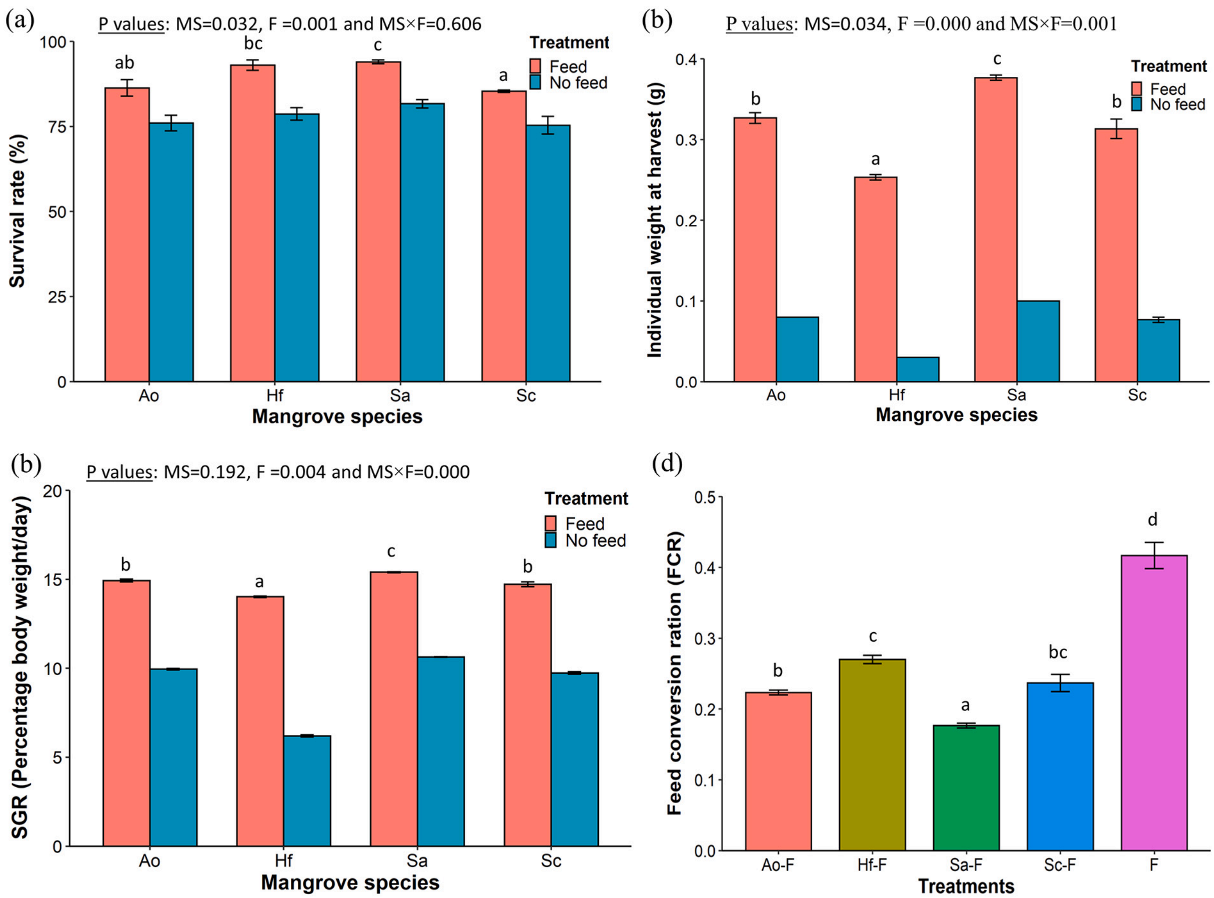

Fig. 1. (a-d): The performances of shrimp PL in different treatments with four types of mangrove leaf litter with and without supplemental feed: (a) Survival (%), (b) Individual weight at harvest (g), (c) Specific growth rate (SGR; %BW d^{-1}) and (d) Feed conversion ratio (FCR) in fed treatments. Letters above bars in graphs indicate statistical differences between leaf litter types (main factor) ($P < 0.05$). The abbreviation to express P values used are MS for mangrove species, F for feed and MSxF as interaction term.

litter and supplemental feed combined, there were also good survival rates (75–81%) in the treatments with only leaf litter (Fig. 1a). In the treatment with feed only, the survival rate was 88% but in the treatment without leaf litter or feed all the shrimp died before day 8. For individual weight gain and SGR, there was a significant interaction between mangrove species and feed ($P < 0.001$). Among the treatments, the highest (0.37 g) average individual body weight gain was recorded in treatment Sa-F and the lowest (0.03 g) in treatment Hf-nF (Fig. 1b). The same was observed for SGR (Fig. 1c). The average individual weight gain in the treatment with feed only was 0.17 g. When looking at FCR, Sa-F showed the best performances of all treatments (Fig. 1d). The highest FCR (0.41) was found for the treatment with formulated feed only whereas the lowest (0.18) was found for treatment Sa-F.

The total weight gain based on feed only was 15.3 g and the total weight gain based on leaf litter ranged from 2.4 to 8.2 g ($P < 0.05$; Table 2). The contribution of leaf litter to total weight gain ranged between 10 and 23%. The contribution of feed ranged between 43 and 64%. Combined, leaf litter and feed resulted in 21 to 33% higher weight gain than based on the combined contribution of leaf litter alone or feed alone. Among the different mangrove species, Sa contributed most to total weight gain, Hf the least while Sc and Ao at intermediate level (Table 2).

Significant main effects were observed for all the water quality parameters except DO, COD and zooplankton concentration (Table 3). A significant interaction ($P < 0.05$) between mangrove species and feed was found for BOD_5, while all water quality parameters, except DO, changed over time ($P < 0.05$). The average pH in different treatments ranged from 7.87–7.93 and differed significantly ($P < 0.01$) between mangrove species. The lowest pH was observed in the feed only treatment (Table 3). The pH in different treatments was affected ($P < 0.01$) by mangrove species but not by feeding ($P > 0.05$). The pH decreased over time in all treatments ($P < 0.001$) (Table 3).

For BOD_5, there were effects of mangrove species and feed ($P < 0.05$) as well as their interaction ($P < 0.001$). Among mangrove species, the

Table 2
Contribution of leaf and feed in individual weight gain during nursery from PL_{15} to juvenile shrimp for 04-week.

Considered factors	Mangrove species				P-value
	Sa	Sc	Ao	Hf	
Total weight gain with leaf and feed (g)	35.4 ± 0.89^{c}	26.7 ± 1.91^{ab}	28.2 ± 0.96^{b}	23.6 ± 0.98^{a}	***
Total weight gain with leaf litter only (g)	8.2 ± 0.21^{c}	5.8 ± 0.58^{b}	6.1 ± 0.32^{b}	2.4 ± 0.10^{a}	***
Total weight gain with feed only (g)	15.3 ± 1.28				n.a.
Contribution of leaf litter (%) to weight gain	23.1 ± 0.56^{b}	21.6 ± 1.78^{b}	21.6 ± 1.88^{b}	10 ± 0.75^{a}	***
Contribution of feed (%) to weight gain	43.1 ± 3.33^{a}	57.1 ± 2.92^{bc}	54.1 ± 3.16^{b}	64.8 ± 5.36^{c}	**
Synergistic effect (%)	33.8 ± 3.81^{b}	21.3 ± 1.34^{a}	24.2 ± 2.61^{ab}	25.1 ± 5.84^{ab}	*

Presented values are the mean ± SD. Small letter on the superscript indicate significant differences, according to Tukey HSD test ($P < 0.05$). P value is expressed as a symbol ($P < 0.001$: ***; $P < 0.01$: **; $P < 0.05$: *).

Table 3
ANOVA table (repeated measure) for water quality parameters observed in shrimp nursery tanks during a 4-week incubation period, with different combinations of feed and leaf litter mangrove species.

Parameter	Leaf litter mangrove species (MS)				Feed (F)		*P*-values						
	Sa	Sc	Ao	Hf	Yes	No	MS	F	MSXF	Time (T)	MSXT	FXT	MSXFXT
pH	7.93 ± 0.02[b]	7.91 ± 0.01[ab]	7.89 ± 0.02[a]	7.87 ± 0.03[a]	7.87 ± 0.06	7.90 ± 0.03	**	ns	ns	***	ns	ns	ns
DO(mg/L)	5.37 ± 0.03	5.34 ± 0.03	5.35 ± 0.04	5.34 ± 0.03	5.35 ± 0.02	5.35 ± 0.04	ns	ns	ns	ns	ns	ns	ns
BOD_5 (mg/L)	2.54 ± 0.14[c]	2.14 ± 0.03[b]	2.36 ± 0.06[bc]	1.92 ± 0.08[a]	2.28 ± 0.33[b]	2.20 ± 0.19[a]	***	*	***	***	***	ns	*
COD (mg/L)	49.5 ± 3.27	45.0 ± 8.88	48.4 ± 6.58	41.1 ± 5.02	43.5 ± 9.47	45.3 ± 5.94	ns	ns	ns	***	ns	ns	ns
TAN (mg/L)	0.15 ± 0.12	0.11 ± 0.09	0.15 ± 0.09	0.19 ± 0.15	0.24 ± 0.11[b]	0.08 ± 0.07[a]	ns	**	ns	***	ns	**	ns
NO_2-N(mg/L)	0.27 ± 0.09[c]	0.19 ± 0.10[b]	0.25 ± 0.08[c]	0.17 ± 0.08[a]	0.22 ± 0.12[b]	0.20 ± 0.08[a]	*	**	ns	***	ns	**	ns
Phytoplankton (inds/mL)	23.3 ± 6.64[c]	13.8 ± 6.66[ab]	18.0 ± 7.81[bc]	9.2 ± 2.58[a]	17.2 ± 9.81[b]	11.7 ± 4.92[a]	***	***	ns	***	***	***	ns
Zooplankton (inds/mL)	4.59 ± 1.88	2.92 ± 1.02	4.17 ± 2.04	2.50 ± 0.00	3.00 ± 1.04	3.96 ± 1.98	ns	ns	ns	***	ns	ns	ns

Presented values are the mean ± SD. Small letter used as superscript to indicate significant differences for main effect mangrove species (MS) and feed (F) according to Tukey HSD test ($P < 0.05$). *P* value is expressed as a symbol ($P < 0.001$: ***; $P < 0.01$: **; $P < 0.05$: *; ns: not significant, $P > 0.05$).

highest BOD_5 (2.54 mg/L) was observed for Sa and the lowest (1.92 mg/L) for Hf (Table 3). Overall, the BOD_5 increased with time ($P < 0.001$), and different mangrove species affected the BOD_5 differently (MS x T, $P < 0.001$), while this was not the case with feeding (F x T, $P > 0.05$).

Feeding did influence the TAN concentration ($P < 0.01$), whereas mangrove species did not ($P > 0.05$). The TAN concentration increased over time ($P < 0.001$), and the increase was more with feed than without feed (FxT, $P < 0.05$) (Table 3).

NO_2-N concentrations ($P < 0.05$) increased faster with feeding than without feeding (FxT, $P < 0.05$). In our experiments the concentrations never rose above 1 mg/L, never reaching toxic levels. Among the mangrove species, Sa and Ao as source of leaf litter resulted in higher NO_2-N concentrations than Sc and Hf ($P > 0.05$) (Table 3).

The three most abundant phytoplankton species were *Cladophora nitellopsis, Closterium tumidium and Pediastrum tetras*. The variation in zooplankton were less and the most abundant species was *Acartia tonsa*. The factors of mangrove leaf litter and feeding both affected the phytoplankton concentration ($P < 0.05$). The highest phytoplankton concentrations were observed with Sa leaf litter (23.3 inds/mL) and the lowest with Hf leaf litter (9.2 inds/mL). Phytoplankton concentrations increased over time, with both leaf litter and feeding causing a faster increase in phytoplankton concentration at the end of the experiment (MS x T and F x T; $P < 0.001$).

Pearson correlation analysis among different parameters showed that the majority of variables were correlated (Table 4), the nature of which was further analyzed with principal component analysis.

Principal component analysis showed that environmental parameters (Fig. 2, Table 5) were influenced by both the factors 'feeding' and 'mangrove leaf litter species'. Leaf litter from different mangrove species and feed both provided nutrients which led to a higher density of phytoplankton, and higher BOD_5 in the water column (PC1, Table2). The latter correlated with plankton density causing turbidity and reduced sunlight incidence and hence also reduced water temperature. Differences between mangrove species were responsible for 77% of the variation among treatments for PC1, with Sa and Ao leaf litter resulting in higher phytoplankton concentrations. Feeding and leaf litter input reduced the dissolved oxygen concentration while they increased the TAN concentration in the water column (PC2, Fig. 2, Table 5), although the average concentration stayed below 0.25 mg TAN/L (Table 3). The results also show that the effect of feed addition was intermediate between leaf litter addition and leaf litter combined with feed.

Environmental parameters individually accounting for more than 40% of the variation in shrimp performance were phytoplankton abundance, TAN and NO_2 concentrations and temperature (DistLM). Combined, environmental parameters explained 89% of the total variation seen in shrimp performance in terms of average weight gain and survival.

Table 4
Pearson's correlations among different important variables. The following parameters from 9 treatments, with 3 replicates each ($n = 27$), were included in the analysis: pH, DO, BOD_5, COD, TAN, NO_2-N, phytoplankton, zooplankton, weight gain and survival rate. The parameters DO, zooplankton and survival rate are not shown because they did not show any significant correlations.

		pH	BOD_5	COD	NO_2-N	Weight gain
BOD_5	Pearson Correlation	0.646**				0.335
	Sig. (2-tailed)	0.000				0.088
COD	Pearson Correlation	0.576**	0.650**			0.212
	Sig. (2-tailed)	0.002	0.000			0.289
TAN	Pearson Correlation	−0.473*	−0.258	−0.301	0.024	0.484*
	Sig. (2-tailed)	0.013	0.194	0.127	0.904	0.010
NO_2-N	Pearson Correlation	0.425*	0.641**	0.238		0.616**
	Sig. (2-tailed)	0.027	0.000	0.233		0.001
Phyto plankton	Pearson Correlation	0.475*	0.795**	0.503**	0.729**	0.681**
	Sig. (2-tailed)	0.012	0.000	0.007	0.000	0.000

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

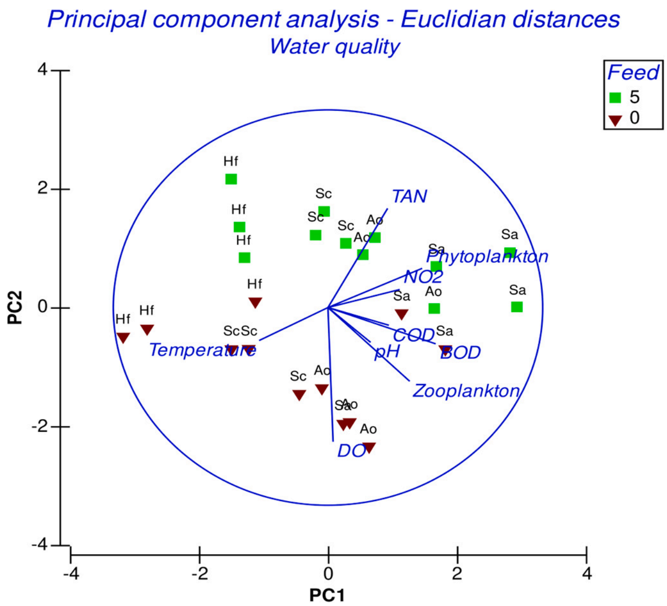

Fig. 2. Principal components analysis (PCA) of environmental parameters based on Euclidian distances. PC1 and PC2 = principal component axis 1 and 2, showing effects of Feed (5% bw d^{-1} feed; no feed) and Mangrove Species leaf litter (Sa, *Sonneratia apetala*; Ao, *Avicennia officinalis*; Sc, *Sonneratia casiolaris*; Hf, *Heritiera fomes*).

Table 5
ANOVA of principal components 1 and 2 for factors feed and mangrove species and multi comparisons (Tukey test).

Principal component	PC1		PC2	
Temperature	*−0.321*		0.167	
pH	0.198		0.176	
Dissolved oxygen	0.024		**0.679**	
BOD_5	**0.501**		0.184	
COD	0.284		0.089	
Total ammonia N (TAN)	0.277		**−0.502**	
Nitrite (NO_2)	*0.334*		−0.091	
Phytoplankton	**0.438**		−0.199	
Zooplankton	*0.381*		0.373	
Interpretation	Higher plankton biomass contributing to turbidity and biological oxygen demand		Increased oxygen consumption and TAN release due to nutrient inputs	
ANOVA model significance	***		***	
r^2	0.89		0.85	
Variance source	Sign.	%SS	Sign.	%SS
Mangrove species	**	77.0	***	22.2
Feed	***	11.2	*	68.4
Mean multi-comparisons by Feeding				
Feed	a		b	
No feed	b		a	
Mean multi-comparisons by Mangrove Species				
Sonneratia apetala (Sa)	a		ab	
Avicennia officinalis (Ao)	b		a	
Sonneratia caseolaris (Sc)	c		ab	
Heritiera fomes (Hf)	d		b	

The main parameters explaining principal components 1 and 2 and indicated 'bold'.

4. Discussions

4.1. Synergistic effect of mangrove leaf litter and supplemental feed on shrimp performance

In all treatment combinations of our experiments, survival was above 75%, with on average a 10% higher survival observed in fed treatments (Fig. 1a). Using the same concentration (1 g/L) of mangrove *(Rhizophora apiculata* and *Avicennia officinalis*) leaf litter and 10%BWd^{-1} supplemental feed, Hai and Yakupitiyage (2005) observed 80% survival. The high survival (75–81%) of PL with only leaf litter in our experiments demonstrates that litter directly or indirectly via the food web contributes to the nutrition of the shrimp during their nursery period. Decomposing mangrove leaf litter releases nutrients supporting natural food production (Nga et al., 2006) and microbial biofilm development which in turn is of nutritive value to penaeid shrimp post larvae (Gatune et al., 2012, 2014). We observed 10–23% contributions by only leaf litter to weight gain, whereby the effect of various mangrove species differed ($P < 0.001$) (Table 2). The differences in decomposition rate of organic matter among the species might be the cause of differences in the contributions of leaf litter to weight gain. Mangrove leaf litter with a higher decomposition rate results in more decomposing organic matter or detritus in the system (Alam et al., 2021). In turn, from this detritus more nutrients are released for algae production (Fazi and Rossi, 2000) which serves as a direct or indirect source of food to heterotrophs (Verweij et al., 2008; Nordhaus et al., 2006; Roijackers and Nga, 2002). Alam et al. (2021) identified that *S. apetala* (Sa) leaf litter had the highest decomposition rate from among the mangrove species and contributed to the highest weight gain of shrimp juvenile, as was also found in this experiment. As a consequence, Sa leaf litter in combination with supplemental feed led to more phytoplankton and more synergy. Zooplankton, phytoplankton and bacteria are natural foods for shrimp PL and juveniles (Porchas-Cornejo et al., 2012) that contribute up to 50–70% of the nutritional requirements of shrimp (Martinez-Cordova and Enriquez-Ocana, 2007; Enríquez, 2003; Tacon, 2002). Phytoplankton has been found to be nourishing and even vital to shrimp nutrition during the post larvae stages (Thong, 2017). Not surprisingly, in our experiment, there was a significant positive correlation between phytoplankton concentration and shrimp production (Table 4). The provision of 1 g/L leaf litter combined with 5%BWd^{-1} supplemental feed in this experiment led to better shrimp growth than in an experiment with *R. apiculata, A. officinalis* and *Excoecaria agallocha* leaf litter and 10% BWd^{-1} supplemental feed conducted by Hai and Yakupitiyage (2005). It should be mentioned, however, that an empirical comparison in this regard is difficult as environmental conditions in both experiments were different.

Commercially-formulated feed was clearly a more complete nutrient source for the PL than mangrove leaf litter and a higher growth was realized based on feed than based on leaf litter (Table 2). However, when combined, mangrove leaf litter and supplemental feed resulted in a higher growth rate than expected presumably because of the cumulative effects of leaf litter and feed (Table 2). This resulted in a lower FCR in the treatment with leaf litter and feed than the treatment with only feed. Martinez-Cordova et al. (2011) similarly identified that utilization of natural food contributes to the lowering of FCR in shrimp culture. We also found that, in the treatments with leaf litter, lower FCRs were observed in those treatments where more plankton was present.

When feed is applied in excess, it can be detrimental to shrimp production performance by deteriorating water quality (Chainark and Boyd, 2010; Pandit and Nakamura, 2010). However, in our study, in all treatments the water quality stayed within the safe limits though both leaf litter and feeding affected water quality during the four-week period of our experiments and the effects became most pronounced towards the end of the experiment.

4.2. Effect on water quality and PL performance

A dissolved oxygen level lower than 2 mg/L reduces the growth rates of *P. vannamei* (Seidman and Lawrence, 1985). Allan and Maguire (1991) estimated the lethal level (96 h LC_{50}) of DO for juvenile *P. monodon* is 0.9 mg/L. The DO level in our study was similar between treatments for survival and growth. With a similar concentration of mangrove leaf litter Hai and Yakupitiyage (2005) observed that DO levels ranged from 4.9–5.0 mg/L with an aeration regime whereas Nga et al. (2006) observed DO levels to decrease (4.0–0 mg/L) and mangrove leaf litter leachate concentrations (0-10 g/L) to increase over time. In our study, all the tanks were aerated, so the outcome of this experiment is relevant to well-managed pond settings with sufficient oxygen.

Leaf litter application affects pH and is in turn affected by mangrove species (Marschner and Noble, 2000; Deano and Robinson, 1985). In our study, the pH differences between treatments were small but significant ($P < 0.05$). The positive correlation between pH and BOD_5 and the slightly higher pH observed in treatments with leaf litter suggest that differences in decomposition rates of the different species of leaf litter caused the observed differences in pH as found previously by Alam et al. (2021). The pH values observed in our study were within the optimum range (7.5–9.0) for shrimp production (FAO, 1986) and, therefore had little influence on PL performances.

Decomposition of mangrove leaf litter or feed led to significantly differing levels of BOD in the tanks. Decomposition of organic matter not only enhances the microbial loads (Little et al., 2008) but facilitates biofilm development on the decomposing leaf litter (Gatune et al., 2012, 2014). In our study, the BOD_5 was higher in the treatments with leaf litter than in those with supplemental feed only. We found a positive correlation ($r = 0.795^{**}$; $P > 0.05$) between the BOD_5 and phytoplankton abundance which in turn also positively correlated ($r = 0.681^{**}$; $P > 0.01$) with shrimp performance (Table 5). The mangrove species Sa with the higher BOD_5 concurred with the highest observed shrimp growth while Hf had the lowest BOD_5 and resulted in the lowest growth performance. The differences in decomposition rates of different mangrove species caused the differences in BOD_5 among the treatments (Alam et al., 2021). Previously, Alam et al. (2021) found that the BOD_5 and decomposition rate of leaf litter were positively correlated while another work shows that this depends on how refractive the leaves are to biological breakdown (Rojas-Tirado et al., 2017). The higher the BOD, the more rapidly oxygen will be depleted (Banrie, 2012) which might cause stress in non-aerated system (Boyd, 2018). The BOD_5 levels observed in our study were below 25 mg/L, as recommended by Kasnir et al. (2014).

Both leaf litter and feed are a source of nitrite (NO_2-N) and total ammonium nitrogen (TAN) (Dutra and Ballester, 2017). The amount of fed nitrogen (N) that is not retained in animal weight gain increases the TAN and NO_2-N concentrations in the water column (Hari et al., 2004). The latter is an intermediate product resulting from microbial nitrification and denitrification (Wickins, 1976a, 1976b). In our study, the positive correlation between pH and BOD_5 suggests that more biodegradable organic matter (OM i.e., BOD) in the water column concurred at a (slightly) higher pH. More TAN correlated with a lower pH and more biodegradable OM (BOD) in the water column as well as with lower nitrite concentrations (Table 4). We interpret this as being indicative of better conditions for nitrification and denitrification. Chen and Lei (1990) identified the safe value of TAN and NO_2-N for *P. monodon* juvenile to be 3.7 mg/L and 3.8 mg/L, respectively, whereas Banrie (2012) advised to maintain concentrations of nitrite and ammonia below 1 mg/L and 0.5 mg/L, respectively, as was the case in our study.

5. Conclusions and recommendations

The present study showed that, when feed and leaf litter are combined, extra growth and survival can be realized by the synergistic effect between leaf litter and feed. Of the four mangrove species tested, *S. apetala* appeared to be the best, followed by *A. officinalis* and *S. caseolaris.* The least effective mangrove species was *H. fomes.* Our results also show how the use of a mangrove species may help increase shrimp pond productivity by providing valuable food input into the pond. Thus, we think that planting mangroves along the margins of shrimp ponds can not only serve as an inexpensive source of food but that their presence will provide a higher pond productivity and lower FCR than in fed ponds with no mangrove trees in or adjacent to the pond. However, additional research questions need to be addressed to justify changes in customary practice of coastal shrimp farming in favour of silvo-aquaculture including: (i) what maximum leaf litter concentrations are possible before a high oxygen demand will negatively impact shrimp yields? (ii) What are the long-term impacts of leaf litter on water quality and shrimp performance both under mesocosm conditions and in large culture ponds? Answering these questions will provide practical guidelines for mangrove based silvo-aquaculture to farmers.

Declaration of Competing Interest

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

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