LITTER PRODUCTION AND DECOMPOSITION IN MANGROVES – A REVIEW

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Abstract: Litter production and decomposition are important in nutrient cycling and detritus based food chain. Litter production in mangrove varies widely with species, forest type, stand age, geographical location and environmental parameters (e.g. rainfall, temperature, wind). Higher rate of litter production is observed at the lower latitudes (tropical region) and it decreases linearly with increasing latitude (sub-tropical region). Decomposition of leaf litter is characterized by an initial leaching of soluble organic and inorganic compounds with subsequent colonization by micro-organisms, which initiates physical and biological fragmentation of plant material. Litter degradation rate varies with species, geographical location, degree and frequency of tidal inundation, climatic and edaphic factors and presence of litter consuming fauna in the mangrove forest. In mangroves, higher rate of microbial decomposition of litter is observed in litter with lower content of tannin and leaves with thin cuticle, wet season and lower tidal inundation classes.

INTRODUCTION

itter production is an indicator of primary ✓productivity and is important for nutrient cycling and export of nutrients and organic detritus to the estuarine ecosystem (Boto and Bunt, 1981; Gong et al. 1984; Gong and Ong, 1990; Lu and Lin, 1990; Steink et al., 1993ab; Lee, 1995; Ashton et al., 1999; Mfiling et al., 2005). In mangroves, litter production is about 30-60% of the total primary productivity (Bunt et al., 1979) and has significant effect on detritus based food webs in the coastal environment and coastal fisheries (Odum and Heald, 1975; Ong et al., 1984; Lee, 1995). The amount of organic matter exported to the aquatic ecosystem from the mangroves depends on the litter decomposition rates (Twilley et al., 1986; Robertson, 1988; Chale, 1993). In general, the dynamics of litter breakdown vary with species and geographical location (Ashton et al., 1999) and affected by chemical composition of litter such as nutrients and lignin content (Tam et al., 1998). Amount of litter production and amount of nutrients and organic matter released during the process of decomposition play an important role in nutrient cycling (Steink et al., 1993a; Lu and Lin, 1990), tree productivity and mangrove related food chain (Ashton et al., 1999). Present study aims at identifying the possible factors affecting litter

production and decomposition in mangroves from the available published literature.

Litter production

Litter production can be defined as the shedding of vegetative and reproductive plant parts caused by senescence, stress, mechanical factors (e.g. wind), a combination of these factors or by death and weathering of the whole plant in a given time period (Kozlowski, 1973). Mangrove litter production studies in different geographical locations are shown in Fig.1. The variation of litter production in mangroves may be related to species and geographical locations (Woodroffe *et al.*, 1988). Moreover, litter production and the percentage contribution of different litter components seem to vary with forest type, species, stand structural attributes and seasonal variation in climatic conditions.

Forèst Types

The rate of litter production varies with mangrove forest types (riverine, overwash, fringe, basin and scrub). Pool et al. (1975) reported that riverine forest produced higher amount of litter followed by overwash, fringe, basin and scrub

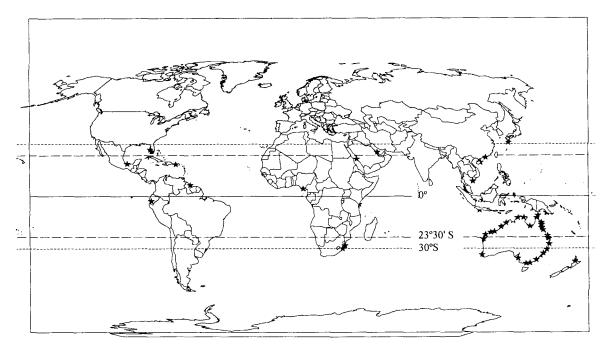


Fig. 1: World map showing the litter production studies in mangroves.

mangrove forests. Day et al., 1987 and 1996 documented that Rhizophora mangle produced higher amount of litter in riverine mangrove forest (12.06 t/ha/yr) followed by fringe (7.72-7.93 t/ha/yr) and basin mangrove forests (4.4 t/ha/yr). Similarly, R. mucronata in estuarine mangrove forest produced higher amount of litter (6.24 t/ha/yr) than in the fringing mangroves (4.41 t/ha/yr) in the North West coast of Sri Lanka (Amarasinghe and Balasubramaniam, 1992).

Species and Geographical Location

Available data of litter production (Table -1) are plotted at different range of latitude with major mangrove species in Fig. 2 and describes that different mangroves show different rate of litter production in a particular place and litter production rate of a particular species varies with the geographical locations. Moreover, a significant negative correlation (r=-0.50, p<0.05) is observed when the available published values of total litter production in mangroves (Table -1) are plotted against the latitude (Fig. 3). This negative relationship explains that

highest litter production is observed at the lower latitudes (tropical region) and it decreases linearly with increasing latitudes (sub-tropical region).

The proportion of litter components also varies with species and geographical location. Rhizophora apiculata, R. mucronata, Sonneratia alba and Avicennia officinalis in Mandovi-Zuari estuaries, Central West Coast of India showed that the percentage contribution of litter components varied among species and the per cent contribution of leaves, flowers, fruits and misalliances varied from 43% to 68%, 3% to 8%, 10% to 19% and 10% to 39%, respectively (Wafar et al., 1997). Even the percentage contribution of litter component of a particular species varies with the geographical locations such as leaf litter of Bruguiera parviflora in Hinchinbrook Island, Australia (Duke et al., 1981) and Kuala Selangor, Malaysia (Mahmood et al., 2005) contributes about 40% and 71% of total litter production, respectively. Avicenia marina in Queensland, Australia (Mackey and Smail, 1995) and Al Khor, Qatar (Hegazy, 1998) contributes about 47% and 34% of leaf litter respectively.

Table-1: Rate of litter production by different mangrove species

Geographical location	Species	Dry weight (g/m²/day)	Source
I	2	3	4
Middle Horbour, Australia (33°55' S, 151°10' E)	A. marina	1.59	Goulter and Allaway (1979)
Hinchinbrook Island, Australia (18°15' S, 146°15' E)	Rhizophora spp. C. tagal B. gymnorrhiza B. parviflora Avicennia spp. Sonneratia alba	2.99 1.97 2.19 2.74 2.19 2.16	Duke <i>et al.</i> (1981)
Sungai Merbok, Malaysia (5°40' N, 100°25' E)	R. apiculata R. mucronata B. gymnorrhiza	2.76	Ong et al. (1980)
Western Port Bay, Australia (38°25' S, 145°12' E)	Avicennia spp.	0.55	Clough and Attiwill (1982)
Kuala Selangor, Malaysia (3°15' N and 101°18' E)	Avicennia spp. Sonneratia spp. Rhizophora spp.	4.22 3.84 4.32	Sasekumar and Loi (1983)
Matang Mangrove, Malaysia (4°50' N, 100° 36' E)	R. apiculata (Planted) R. apiculata R. mucronata Bruguiera spp.	1.91-3.12 2.09	Gong et al. (1984)
Tuvalu (7°28' S, 178°42' E)	R. stylosa	5.39	Woodroffe (1984)
Motupore Island, Papua New Guinea (9°31' S, 147°17' E)	R. stylosa	3.92	Leach and Burgin (1985)
Tabasco, Mexico (18°25' N, 93°10' W)	A. germinans	1.68	Lopez-Portillo and Ezcurra (1985)
Mgeni Estuary, South Africa (29°48' S, 31°03' E)	A. marina	1.91	Steinke and Charles (1986)
South-West Florida (26°02' N, 81°45' W; 25°02' N, 81°34' W)	Avicennia spp. Rhizophora spp.	1.22 2.22	Twilley et al. (1986)
Queensland and Port Clinton, Australia (18°05' S, 146°01' E; 22°35' S, 150°45' E)	S. alba S. caseolaris	2.48 2.56	Duke (1988)
St. Lucia and Richards Bay, South Africa (27°58' N, 32°24' E)	A. marina B. gymnorrhiza R. mucronata	2.78-2.89 2.00 2.66	Steinke and Ward (1988)
Darwin Harbour, Australia (12°26' S, 130°52' E)	C. tagal	1.88-2.04	Woodroffe et al. (1988)
Mai Po Marshes, Hong Kong (22°31' N, 114°05' E)	K. candel	2.18-3.44	Lee (1989)
Ohura Bay, Okinawa, Japan	Mixed mangrove	2.11-2.94	Hardiwinoto et al. (1989)
Ras Hatiba, Saudi Arabia (21°36' N, 39°9' E)	Avicennia spp.	2.16	Saifullah <i>et al.</i> (1989)
Hainan Island, China (19°51' N, 110°24' E)	B. sexangula	3.02-3.44	Lu and Lin (1990)

1	2	3	4
Transkei estuaries, South Africa	Mixed mangrove	1.24	Steinke and Ward (1990)
Bonny Estuary, Nigeria (4°22' N, 7°12' E)	Rhizophora spp. Avicennia spp. Laguncularia spp.	2.32 1.76 2.24	Abbey Kalio (1992)
Dutch Bay, Kala Oya and Erumathivu, Sri Lanka (8°15' N, 79°50' E)	R. mucronata A. marina zone	1.71 1.02-1.51	Amarasinghe and Sri Lanka Balasubramaniam (1992)
Tritih, Java, Indonesia (7°58' S, 108°44' E)	R. mucronata (Planted)	2.26	Sukardjo and Yamada (1992)
Queensland, Australia (27°24' S, 153°8' E)	A. marina	2.40	Mackey and Smail (1995)
Onverwagt, Guyana (6°27' N, 57°38' W)	A. germinans	4.85	Chale (1996)
Gazi Bay, Kenya. (4°25' S, 39°30' E)	R. mucronata	1.15-2.51	Slim et al. (1996)
Churute Estuary, Ecuador (2°35' S, 79°40' W)	Rhizophora spp.	1.77-2.92	Twilley et al. (1997)
Mandovi-Zuari Estuaries, India	R. apiculata R. mucronata S. alba A. officinalis	3.21 3.23 4.66 2.79	Wafar et al. (1997)
Al Khor, Qatar (25°40' N, 51°35'E)	A. marina	4.65	Hegazy (1998)
Futian, China (22°31' N, 114°05' E)	A. corniculatum and K. candel	3.20	Tam et al. (1998)
Mekong Delta, Vietnam (8°47' N, 104°27' E)	R. apiculata (Planted)	2.58-4.76	Clough et al. (2000)
Okinawa, Japan (26° N, 128° E)	Mixed mangrove	3.55	Mfilinge et al. (2005)
Kuala Selangor, Malaysia (3°19' N, 101°14'E)	B. parviflora	2.89 (2.31-4.46)	Mahmood et al. (2005)

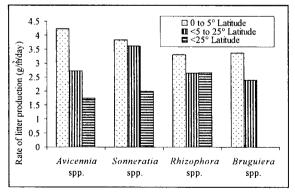


Fig. 2: Latitudinal variation in litter production by different mangrove species.

Stand Structural Attributes

Rate of litter production positively correlates with the stand structure (Aksornkoae and Khemnark, 1984;

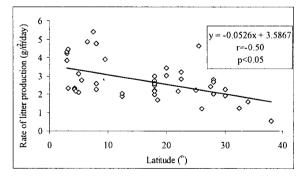


Fig. 3: Relationship between latitude and total litter production.

Lopez-Portillo and Ezcurra, 1985; Saberi, 1989). Mixed stands produce more litter compared to monospecific stand. Twilley *et al.* (1986) obtained higher amount of litter production (7.51-8.68 t/ha/yr) in mixed stand of *A. germinans*, *R. mangle* and *Lumnitzera racemosa*

in South-West Florida compared to pure stand of each of them (3.51-5.38 t/ha/yr). Stand density also influences the rate of litter production for example mangrove stand with density of 2180 stem/ha at Kuala Selangor, Malaysia (Mahmood and Saberi, 2005) produces almost twice amount of litter compared to the mangrove stand with density of 166 stem/ha at Siar Beach, Malaysia (Saberi, 1989).

Litter production rate seems to vary with stands age. Gong et al. (1984) estimated the rate of litter production in different aged (5 to 25 years old) stands of R. apiculata in Matang Mangrove Reserve, Peninsular Malaysia and obtained highest annual litter fall (11.40 t/ha/yr) in 25 years old stand followed by younger aged stands. Clough et al. (2000) reported that annual litter production and proportion of different litter components of 6 to 36 years old R. aviculata stands in Ca Mau Province, Southern Vietnam significantly varied with stands age. They obtained higher amount of litter production (18.79 t/ ha/yr) in 12 year old stand and lower (9.41 t/ha/yr) in 9 year old stand. Moreover, proportion of various litter components varied with the stands age. Leaves represented more than 75% of the total litter produced in 6 to 10 years old stands, while it was only 38% in 36 years old stands. Propagules represented less than 1% of the total litter fall in 6 to 12 old stands, but it was 26% and 38% in 21 and 36 years old stands, respectively. The contribution of flower to the total litter fall was much higher in older stands at 5.8% and 6.1%, in stands of 21 and 36 years old respectively. Rate of litter production usually increased with the increasing age of stands, but the rate almost remained constant after certain age.

Abiotic Factors Influencing the Litter Production

Higher rate of litter production in mangroves is usually observed during the dry season (Aksornkoae and Khemnark, 1984; Bunt, 1995). Lugo and Snedakar (1975) observed that dry season associated with increased soil and water salinity and higher rate of evapotranspiration, facilitates the plants to shed their leaves in energetically cheaper way. Lopez-Portillo and Ezcurra (1985) reported that 74% variability in

the seasonal litter production of A. germinans in the Laguna de Mecoacan, Tabasco, Mexico was associated with the seasonal temperature fluctuation and mean soil salinity.

Wind velocity, temperature, evaporation and rainfall may have significant influence on litter production in mangroves. Sasekumar and Loi (1983) reported that wind, temperature, evaporation and rainfall were responsible for less than 50% of the variation in litter fall of Avicennia, Sonneratia and Rhizophora stands in South Banjar Mangrove Forest, Malaysia. In a similar study, Mfiling et al. (2005) observed a significant positive correlation between total rate of litter production and wind speed and temperature, while, total litter production did not correlate significantly with rainfall.

Litter production of *R. mangle* and *A. germinans* in South-Eastern Mexican mangrove forest increased with increasing air temperature and rainfall (Day et al., 1996). Avicennia germinans in Guyana, South Africa showed highest leaf fall during the months of higher temperature (30°C) and rainfall (Chale, 1996). Similarly, *A. germinans*, Aegiceras corniculatum and Kandelia candel in Futian National Nature Reserve, China showed higher litter fall during the rainy summer season and lower in the drier winter. High temperature, longer duration of light, higher-evapotranspiration rate and more freshwater flushing during the rainy summer months are probably the factors responsible for the highest litter fall during the summer rainy season (Tam et al., 1998).

The variability of litter production in mangroves may also depend on tidal inundation (Wafar et al., 1997). Litter production of A. marina in low, mid and high tidal range at Brisbane River Estuary, South-East Queensland, Australia varied from 8.31 to 9.22 t/ha and higher rate of litter production was observed in the mid tidal level compared to low and high tidal level (Mackey and Smail, 1995).

Litter Decomposition

The physical forces and grazing action of macro and micro-fauna fragment the mangrove litter (Sasekumar, 1974; Valiela et al. 1985) and

decomposition continues through the microbial decay of detritus (Fell et al., 1975; Cundell et al., 1979; Bremer, 1995). Mangrove litter decomposition process, role of macro and micro-organisms and the factors affecting the decomposition process were documented by a number of researchers. Decomposition of organic matter occurs in three phases such as leaching of soluble components, microbial oxidation of refractory components such as cellulose and lignin, and physical and biological fragmentation (Valiela et al., 1985).

Leaching

Rapid loss of dry weight of litter at the initial stage of decomposition is due to the leaching process. Leaching fraction contains readily soluble organic compounds and nutrients, which is accelerated by the physical disturbances (Camilleri and Ribi, 1986; Tam et al., 1990). Leaf litter of Aegiceras corniculatum, Avicennia marina, A. officinalis, K. candel, R. apiculata, R. mangle, R. mucronata and S. alba showed different rates of dry weight loss during the leaching phase (Van der Valk and Attiwill, 1984; Tam et al., 1990, 1998; Wafar et al., 1997; Davis et al., 2003), which may be due to the differences in initial content of soluble organic and inorganic compound in litter (Japar Siddik, 1989).

Microbial Decomposition

Microbial colonization on degraded litter is usually observed after the leaching of soluble carbohydrate and tannin (Cundell et al., 1979). Rate of microbial decomposition of mangrove leaf litter varied with species, geographical location and stand structure (Table-2). It has been reported that significantly higher weight loss (87%) due to the microbial decomposition was observed with K. candel followed by A. marina (67.4%) and A. corniculatum (39.8%) at the end of 12 weeks in Sai Keng mangrove forest, Hong Kong (Tam et al., 1990). Tam et al. (1998) reported 88% loss of dry weight for K. candel leaf litter after 42 days and 68% loss for A. corniculatum after 70 days in Futian National Nature Reserve, China. Comparatively higher rate of litter decomposition was observed with S. alba followed by Rhizophora spp. and B. parviflora (Bremer, 1995; Ashton et al., 1999). Leaching of tannin, waxy cuticle and thick epidermis delay the colonization of the micro-organisms. Therefore, litter with different tannin content and thickness of cuticle may be responsible for different rate of microbial decomposition in different species (Cundell et al., 1979).

Stand structural characteristics influence the microbial decomposition of mangrove litter. A microbial decomposition study in basin mangrove forests in South-West Florida showed that about 89% and 79% of initial dry wet loss for A. germinans, while 54% and 35% for R. mangle in mixed mangroves and monospecies stand, respectively after 148 days (Twilley et al., 1986). Ashton et al. (1999) studied the leaf litter decomposition of R. apiculata, R. mucronata, B. parviflora and S. alba in Matang mangrove forest in Peninsular Malaysia and recorded significantly higher rate of decomposition in virgin jungle as compared to clear-felled. Irrespectively, Bosire et al. (2005) observed comparatively higher decomposition rate of S. alba and R. mucronata leaf litter in natural mangrove forest followed by reforested and bare areas

Association of micro-organisms and their abundance play an important role in mangrove litter decomposition, their abundance is also influenced by the stand structure (Bosire et al., 2005). Different saprophytic micro-flora are involved in the decomposition process, but fungi are the primary decomposers of mangrove litter because of their ability to degrade cellulose and lignin, which together form the major component of cell wall (Hutchings and Saenger, 1987). Fell et al. (1975) conducted a detailed study on associated micro-organisms at various stages of leaf litter decomposition of R. mangle in Miami, Florida, Bahamas, Caribbean, India and Indo-Pacific regions. They observed that within the first 24 hours of submergence, the leaves were attacked by Phycomycetes of the genus Phytophthora, a variety of other saprophytes such as, Fusarium and Penicillium. In the second and third weeks, the cellulolytic fungi (Zalerion, Lulworthia) had appeared and by the end of the third week majority of the phycomycetes had disappeared.

Table-2: Comparison of leaf litter degradation rate with different mangrove species in different places

Geographical location, method	Species	Leaves lit	ter loss	Sources
of experiment, stand conditions and season		Litter loss (%)	Days	
Matang Mangrove forest, Malaysia Litter on string	Rhizophora spp. Bruguiera spp.	75-90 80	20 20	Ong et al. (1980)
Queensland, Australia Litter bags (Summer)	R. stylosa A. marina C. tagal	50 50 50	39 10 27	Robertson (1988)
Matang Mangrove forest, Malaysia Litter on strings Litter bags	R. apiculata	94-98 80	180 180	Japar Sidik (1989)
Arabian Gulf region Litter bags (December)	A. marina	46	150	Hegazy, (1998)
Shenzhen, China Litter bags (Summer)	A. corniculatum K. candel	68 88	70 42	Tam et al. (1998)
Matang Mangrove forest, Malaysia Litter bags (Wet months) Cleared areas Virgin Jungle Reserve	B. parviflora R. mucronata S. alba	35 53 33 68 85 93	56 56 56 56 56 56	Ashton <i>et al.</i> (1999)
Tomago, Newcastel, Australia Litter bags (Summer) Landward Shoreward	A. marina	53 95	360 360	Dick and Osunkoya (2000)
Merbok Estuary, Kedah, Malaysia Litter on strings	A. officinalis B. gymnorrhiza B. parviflora R apiculata	79 79	1	Ashton (2002)
Gazi Bay, Kenya (Dry and wet season) Natural forest Reforested areas	S. alba	98-99 92-94 56-68	28	Bosire et al., (2005)
Bare areas (Dry and wet season) Natural forest Reforested areas Bare areas	R. mucronata	56-84 52-60 12-25	28	unin Turk Turk
Kuala Selangor, Malaysia (Dry months) Litter bags Litter on strings (Wet months) Litter bags Litter on strings	B. parviflora	63 100 86 100	150 60 150 20	Mahmood and Saberi (2005)

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Bremer (1995) reported that green and senescent leaves of S. alba and R. apiculata in Morib mangrove forest, Malaysia contained terrestrial mycoflora (Pestalotia, Trichoderma, Aspergillus, Penicillium and Alternaria) and a number of yeast species. He isolated Labyrinthula and thraustochytrids after 24 hours of decay from both the species and found them associated at all stages of leaf litter decomposition. It was observed that fungi diversity varied from site to site, such as 100 species were identified in Brunei (Hyde, 1988), 60 species in Hong Kong (Vrijmoed et al., 1994), 60 species in Australia (Kohlmeyer and Volkmann-Kohlmeyer, 1991) and 100 in Malaysia (Alias et al., 1995).

Physical factors (wind, temperature, moisture, rainfall, salinity, tidal height, frequency of tidal inundation, current action and pH) play a significant role in litter decomposition by accelerating the degradation process. Most of the physical factors are responsible for mechanical breakdown of litter into smaller size and also affect the role of macro and micro-organisms in the decomposition process (Tam et al., 1990; Dick and Osunkoya, 2000; Moore et al., 1999; Prause et al., 2002, Prescott, 2005).

Moisture content accelerates the litter decomposition process by creating favourable environmental condition for the decomposers (Swift et al., 1979; Prescott, 2005). Hesse (1961) reported that optimum decomposition occurred at 50% moisture and alternate wetting and drying accelerate the rate of decomposition. The leaf litter of R. apiculata and B. parviflora degraded faster during the wetter months in Malaysian mangroves (Japar Sidik, 1989; Mahmood and Saberi, 2005), similarly leaf litter of S. alba and R. mucronata showed higher rate of decomposition during the wet season in Kenyan mangroves (Bosire et al., 2005). Mackey and Smail (1996) studied the leaf litter decomposition of A. marina during the winter and summer seasons at two different tidal conditions in Brisbane River Estuary, Queensland, Australia. They observed significantly higher rate of leaf litter decomposition during the summer season and at low tidal level. They also mentioned that the summer months are wetter and more humid, which enhanced the activity of microbial decomposers. Moreover, leaf litter decomposition rate

depends on air and water temperature by affecting the population size of microbial decomposers and invertebrate. Apart from moisture content and tidal level, salinity has great influence on the rate of litter decomposition and comparatively higher rate is usually observed in saline water than in fresh water (Heald, 1971; Odum and Heald, 1975).

Feeding and Mechanical Breakdown by Micro and Macro-Organisms

Sesarmid crabs (Robertson and Daniel, 1989; Micheli, 1993; Steinke et al., 1993b), Gastropod snails (Slim et al., 1996), Nematodes, Copepods (Aksornkoae and Khemnark, 1984) and Amphipod (Poovachiranon et al., 1986; Robertson and Duke, 1987; Bosire et al., 2005) are responsible for the mechanical breakdown and consumption of a portion of litter. Sesarmid Crabs consume a significant amount of mangrove detritus (Leh and Sasekumar, 1985) and act as an important group in the ecological functioning of the mangrove ecosystem (Robertson and Daniel, 1989; Lee, 1998).

Crabs usually graze comparatively fresh leaves (Mahmood and Saberi, 2005) and the consumption of litter by crabs depends on their presence or absence and presence of them in mangroves (Leh and Sasekumar, 1985). The grazing rate also varies with the species and geographical locations. About 79% of leaf litter of A. officinalis, B. gymnorrhiza, B. parviflora and R. apiculata was consumed by sesarmid crab within 24 hours at Merbok mangrove, Malaysia (Ashton, 2002), while, 53% to 69% of B. parviflora leaf litter in Kuala Selangor Mangrove, Malaysia was grazed by Crabs (Sesarma versicolor) within 30 days (Mahmood and Saberi, 2005).

Robertson (1986) studied the removal of R. stylosa leaf litter by Crabs (S. messa) from the mangrove forest at North-Eastern, Australia. He reported that the range of daily leaf litter removal by Crabs was 0.24 to 0.66 g/m^2 , which was 22.2% to 42% of the total daily litter production. He also observed that higher amount of leaf litter was removed during the day time. Seasonal variation in the removal of leaf litter by Crabs was also observed by Mia et al., 2001. Mahmood and Saberi (2005) reported that B.

parviflora leaf litter loss due to feeding plus mechanical breakdown was comparatively higher during the wet season. Moreover, leaf litter loss due to feeding and mechanical breakdown by Crabs was also affected by the tidal inundation class (Japar Sidik, 1989).

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