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THE ROLE OF SESARMID CRABS IN THE MINERALIZATION OF LEAF LITTER OF *Rhizophora apiculata* IN A MANGROVE, SOUTHERN THAILAND

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ABSTRACT

Data of leaf fall within 28 weeks are reported from a mangrove forest at Ao Nambor, Phuket, Thailand. The analysis of foregut contents of five species of sesarmid crabs indicates that they are primarily herbivores. Consumption rate experiments and preference rate experiments in aquaria showed that brown and green leaves were preferred food sources for sesarmid crabs. Leaf removal by sesarmid crabs in mangrove forest indicated very large variations in feeding activity. Chemical composition of green, yellow and brown leaves of *Rhizophora apiculata* were analysed.

INTRODUCTION

Mangrove communities of the region have relatively high rates of primary production (Macnae, 1968; Christensen, 1978; Boto et al., 1984). Litter fall values were estimated from several mangrove forests to be within the range of 0.82-4.32 g dry wt $m^{-2}day^{-1}$ (Christensen, 1978; Ong et al., 1980; Duke et al., 1981; Aksornkoae and Khemnark, 1984; Chansang and Poovachiranon, 1990). Little of the foliage production is grazed by herbivores. Only 2.1 % of leaf production of the dominant mangrove forest entered the direct grazing pathway in an Australian study (Robertson and Duke, 1987). Percentage loss of leaf area to insect herbivory was estimated to be 2.75 % of the leaf area in the canopy of a Hong Kong mangrove (Lee, 1990).

Approximately 95 % of the foliage production enters the system as detritus (Robertson, 1986). The tide is an important factor controlling the export of floating detrital particles and most of the floating particles were exported during the ebb flow of spring tides. The leaf litter export, as floating particles, ranged from 2 to 7.7 % of daily leaf fall (Poovachiranon and Chansang, 1982; Woodroffe, 1985; Chansang and Poovachiranon, 1990). Most of the leaf litter is decomposed within the forest. Only a fraction is exported as suspended particles and dissolved organic matter.

Recent investigations indicate the role of certain macrofauna in utilizing mangrove litter (Malley, 1978; Nishihira, 1983; Leh and Sasekumar, 1985; Poovachiranon et al., 1986; Robertson, 1986). Leaf-eating crabs play an important role in the initial processing of litter in tropical mangroves of the Indo-West Pacific. The sesarmid crabs constitute a numerically dominant group of the mangrove fauna (MacNae, 1968). Leaf consumption rates by *Chiromantes onychophorum* and *C. eumolpe* in a mature *Rhizophora* forest amounted to 142 g dry wt $m^{-2}yr^{-1}$ or about 9.4 % of the litter production (Leh and Sasekumar, 1985), whereas *Sesarma messa* (Campbell) in northeastern Australia could remove at least 154 g dry wt $m^{-2}yr^{-1}$ or 28 % of the annual leaf fall of 556 g m^{-2} yr^{-1} (Robertson, 1986). Several species of sesarmid crabs which are similar to the species from other Indo-Pacific regions are also abundant in mangrove forests along the Andaman Sea coast of Thailand (Serene and Soh, 1970; Tantichodok, 1981; Nateewathana and Tantichodok, 1984).

In this paper we report quantitative measurements of the leaf fall from June 1986 to January 1987 (28 weeks). The study was also carried out to identify the natural diet of 5 species of sesarmid crabs. The preference rates of leaf removal (i.e. burial plus consumption) of *Rhizophora apiculata* leaves (decomposed leaves, senescent leaves, and green leaves) were

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measured from forest floors by mangrove-dwelling crabs. Feeding experiments with green leaves were conducted in laboratory as reported by Kofoed et al. (1985). They observed that few crabs stayed on the mud surface. Most of them moved to the trees by climbing on prop roots and branches to be at rest on the mangrove leaves at different levels above ground. During the dark period, when they were safe from predators, they would eat fresh leaves.

MATERIALS AND METHODS

Study Area

The Ao Nambor mangrove forest is situated on the southern coast of Phuket Island (98° 25' E, 7° 51' N), southern Thailand. *Rhizophora apiculata* is the most abundant species in the Ao Nambor mangrove. Detailed description of the mangrove forest structure has been reported by Chansang et al. (1982), The sampling sites are located between the high and mid-intertidal regions of the mangrove forest. Fifteen different locations were set up to observe leaf removal by crabs. Ten litter traps were placed in the vicinity of dominant stands of *R. apiculata*, especially along the banks of the channel from land to the edge of the mangrove forest (Fig. 1).

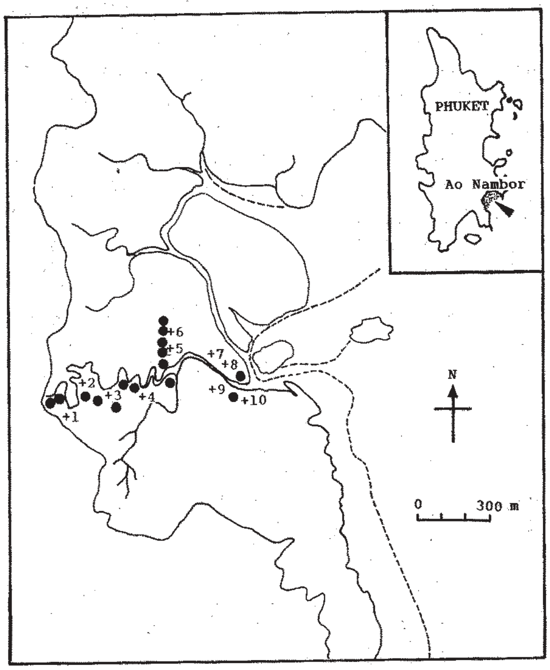

Fig. 1. The Ao Nambor mangrove forest, Phuket. Location of sites used in study of leaf fall (+) and leaf removal rate (●).

Crab collecting

Five species of sesarmid crabs were collected from Ao Nambor mangrove. Due to dense mangrove trees, a fishing method consisting of rod and line with bait was introduced to catch the sesarmid crabs from their burrows. Half of a dead fish with the tail tied to the line of a fishing rod was placed near the crab burrows. The smell would attract sesarmid crabs. The fishing rod was carefully moved when the crab seized the bait. Living specimens of five species of sesarmid crabs were kept in containers which were provided with wet sediment from the mangrove habitat. All specimens were separated for foregut contents studies and laboratory feeding experiments.

Gut contents analysis

Twenty five individuals of each species of sesarmid crabs were caught from all over the mangrove forest. They were preserved immediately in 10 % formalin solution and returned to the laboratory for analysis of stomach contents, measurements of carapace width, sex, and the approximate fullness of the proventriculus. Only full proventricula were used in the analysis. Stomach contents of the collected crabs were analysed in the following way: All material was removed from the stomach and stirred with distilled water in a square petri-dish (16 cm^2). The samples were smeared on a microscope slide, and five random fields were observed at 100x magnification for large material and at 400x magnification for microorganisms. The contribution of each food item to the total diet was expressed in terms of the percentage of the field occupied by the different categories recorded. The categories used in classifying the stomach contents were: vascular plant material, macroalgae, filamentous algae, crustacean debris, sand, silt, clay, fungal materials, diatoms, and unidentified debris.

Laboratory experiments

Leaf consumption rates of four species of sesarmid crabs were carried out in the laboratory at Phuket Marine Biological Center. Five living specimens of each sesarmid crab namely *Neoepisesarma versicolor*, *N. mederi*, *Chiromanthes brevicristatum* and *C. haswelli*) from Ao Nambor mangrove forest were measured to record wet weight and size (mixed sexes and sizes). Five crabs of each species were kept separate in cubic glass aquaria (0.046 m^3). Seventy five percent of the aquaria area was provided with 1-5 cm muddy sand forming a slope. The muddy sand was brought from the mangrove forest. The remaining area had about 2 cm depth of sea water (maximum and minimum temperatures were recorded daily during the experiments).

Food sources and leaf consumption rates

Mangrove leaves (*R. apiculata*) were divided into three categories. Green and yellow leaves were collected from the trees. Brown leaves were picked from the forest floor and classified according to different stages of decomposition. Leaves were collected daily. Three replications of each leaf category were conducted (9 aquaria tanks in total). Green, yellow and brown leaves of *R. apiculata* were cut into squares of 4 cm^2. Twenty pieces of each leaf sample were offered to the sesarmid crabs in the aquaria. The amount of consumed leaf was calculated as a percentage of dry weight by use of conversion factors of fresh weight into dry weight. The wet weight of leaf samples (4 cm^2) was multiplied with the average dry weight of oven dried (105 °C for 24 h) samples (n=100) of each category of leaf. The following relationship between dry weight (D) and fresh weight (F) was found (Regression analysis).

$D = 0.3801\ F$ for green leaf ($r^2 = 0.7465$, $n = 100$)

$D = 0.3880\ F$ for yellow leaf ($r^2 = 0.8573$, $n = 100$)

$D = 0.3624\ F$ for brown leaf ($r^2 = 0.3808$, $n = 100$)

Where r^2 = coefficient of determination and n = number of samples. The experiments were continuously conducted for 5 days, and the consumption rates expressed in mg dry wt g^{-1} crab day^{-1}. Leaves and seawater were changed daily.

Food source preference

In a short-term investigation to examine food preference, three categories of *R. apiculata* leaves were offered to each species of sesarmid crab at the same time. A preliminary experiment showed that eight pieces of each leaf type were enough for feeding crabs. Total consumption of crab was measured every 24 h by use of the method described above. Four species, *N. versicolor*, *N. mederi*, *C. brevicristatum* and *C. haswelli*, were used in experiments for 2 days with 9 replications. The food preference was measured by comparing consumption rates expressed in mg dry wt g^{-1} crab day^{-1}.

Leaf fall and leaf removal by crabs

Rates of leaf litter fall were monitored from June 1986 to January 1987. Ten 1 m^2 litter traps with a 1.2 cm nylon mesh were hung randomly beneath the tree canopy at about the highest water level. The locations were in high to low-intertidal forests along the mean channel of Ao Nambor mangrove forest (Fig.1). Every 2 weeks all litter was removed from the traps. Leaves were sorted out and oven-dried at 105 °C to constant weight.

Leaf removal experiments were setup to assess the influence of two factors, viz. time of inundation and abundance of crabs. Leaf removal rates were monitored using green , yellow, and brown leaves of *R. apiculata* collected in the mangrove forest and preweighed 3 h prior to use. A 1-m piece of nylon twine was tied to each petiole. Fifteen sites were distributed within the same vicinity as the litter fall experiment. Nine 1-m^2 plots were marked off with nylon string and 5 green leaves were tied randomly within one m^2 plot (3 replications). Leaves present in the plots were removed before the experiment started. Five yellow and brown leaves were also placed randomly in the plot. The number of unremoved leaves per m^2 represented the number of leaves likely to be excessive food for crabs which inhabited the plot of the forest floor (Robertson, 1986). The experiments in each area were measured every 24 h on 3 occasions. To avoid the influence of leaf litter fall during the experiments, a nylon net with a 1.2 cm^2 mesh size was hung over the experimental plots.

The mean size and area covered by crab burrows were measured, and exposure time during low tide at each site recorded within the plot. Data were compared with tide tables of the Hydrographic Department, Royal Thai Navy to estimate the mean exposure time per day during the year. The loss in weight was converted to dry weight using the above pre-established relationship between fresh and dry weight for *R. apiculata* leaves. Leaf preference with 3 types of leaves was analysed using standard one-way analysis of variance (Sokal and Rohlf, 1981). Means were compared using least significant differences at the $P < 0.05$ level of significance.

Chemical analyses

R. apiculata leaves of the three different categories were oven-dried at 105°C and ground for analyses of the nutritive value. Palatability of the food sources was assessed in terms of carbon, nitrogen and tannin content, determined for three replicate samples of each leaf type. Carbon and nitrogen analyses were made using a LECO Model 600 CHN elemental analyser. Tannin content was estimated according to the method of Allen et al. (1974).

RESULTS

Foregut contents (Food items)

The carapace widths of the studied crabs were 2.75 cm (±0.31 cm) for *N. versicolor*, 2.92 cm (±0.40 cm) for *N. mederi*, 2.31 cm (±0.29 cm) for *C. brevicristatum*, 1.91 cm (±0.33 cm) for *C. eumolpe* and 1.77 cm (±0.29 cm) for *C. haswelli*. The mean fresh weight was approximately 12.84 g (±5.32 g) for *N. versicolor*, 16.95 g (±7.82 g) for *N. mederi*, 5.36 g (±3.63 g) for *C. brevicristatum*, 3.87 g (±1.63 g) for *C. eumolpe* and 2.66 g (±1.22 g) for *C. haswelli*.

The five species of sesarmid crabs exhibited great variability in the amount of food in foreguts. The mean percentage of food items in relation to the total volume found in the proventriculus of five sesarmid crabs is given in Table 1.

The food which appeared to be picked up by the chelae and ingested by the crabs, was fragmented into different sizes depending on the type.

During May 1986, vascular plant matter made up 54.84-81.57 % by volume of the foregut contents. Vascular tissue, mesophyll tissue, epidermal tissue and other plant particulates varied in length from 250 µm to 4 mm. *N. versicolor* and *N. mederi* had similar diets; they mainly consumed vascular plant matter (81.55-81.57 %). The small species of sesarmid crabs, *C. brevicristatum*, *C. eumolpe* and *C. haswelli*, consumed less plant material, viz. 64.73 %, 63.35 % and 54.84 %, respectively. The second most important category comprised sediment, i.e. sand, silt and clay particles (93±68 µm standard error). Sediment constituted from 14-42.74 % by volume of the foregut contents analysed. All crab species observed in the natural mangrove habitat displayed mud picking behaviour which may thus be the predominant mode of ingestion. The sediment was passed by the chelae to the mouthparts. *C. brevicristatum*, *C. eumolpe* and *C. haswelli* consumed surface sediment which amounted to 64.73 %, 63.35 % and 54.48 %, respectively, of the gut contents. In *N. versicolor* and *N. mederi*, the larger species, surface sediment only constituted 16.70 % and 14.00 % of the food consumed. Diatoms, found in most of the gut contents, constituted about 0.04-0.21 % of the food. Only one species, *C. eumolpe*, contained a small amount (0.10-0.20 %) of green (Chlorophyta) and brown (Phaeophyta) macroalgae. Filamentous algae

Table 1. Mean percentage composition of food items found in the proventriculus of sesarmid crabs.

Food Items	Species of crabs				
	N. versicolor	*N. mederi*	*C. brevicristatum*	*C. eumolpe*	*C. haswelli*
Vascular plant	81.55	81.57	64.73	63.35	54.84
Sand, silt, clay	16.70	14.00	33.67	36.20	42.74
Diatoms	0.21	0.11	0.11	0.04	0.18
Fungal material	0.05	0.24	0.06	0.08	0.16
Macroalgae	-	-	-	0.20	-
Filamentous algae	-	-	-	0.10	-
Crustacean debris	0.01	-	0.47	-	-
Unidentified debris	1.48	4.08	0.96	0.03	2.08
Carapace width (cm)	2.75±0.31	2.92±0.40	2.31±0.29	1.91±0.33	1.77±0.29
Wet weight (g)	12.84±5.32	16.95±7.82	5.36±3.63	3.87±1.63	2.66±1.22

occasionally occurred in the foregut. Leaf associated fungal hyphae and conidia were present in minute amounts (0.05-0.24 %). Unidentified debris ranged from 0.03-4.08 % of the food consumed by the sesarmid crabs.

Leaf consumption rates and preferences

Table 2 shows laboratory experiments on leaf consumption rates of *N. versicolor*, *N. mederi*, *C. brevicristatum* and *C. haswelli*. All the species picked up a small proportion of the leaf matter by the chelae. The mean consumption rates of yellow, green and brown leaves by *C. brevicristatum* were 28.50, 33.70 and 53.31 mg dry wt g^{-1} crab day^{-1}, respectively. This species showed the highest rate of leaf comsumption among sesarmid crabs. For *C. haswelli*, yellow, green and brown leaf mean consumption rates were 20.06, 22.60 and 37.40 mg dry wt g^{-1} crab day^{-1}, respectively. For both of these sesarmid species, the rates did not differ significantly ($P>0.01$) when offered yellow compared with green leaf categories.

The mean consumption rates of yellow, green and brown leaves were 18.5, 24.70 and 37.40 mg dry wt g^{-1} crab day^{-1}, respectively, for

Table 2. Leaf consumption rates (g dry wt g^{-1} crab day^{-1}) of four sesarmid crabs fed on three different categories of *R. apiculata* leaves in experimental aquaria.

Species	Green	Yellow	Brown	F-ratio
N. versicolor	0.0247	0.0185	0.0374	$F_{(2,6)}=21.67; P<0.001$
N. mederi	0.0126	0.0072	0.0257	$F_{(2,6)}=68.75; P<0.001$
C. brevicristatum	<u>0.0337</u>	<u>0.0285</u>	0.0531	$F_{(2,6)}=83.33; P<0.001$
C. haswelli	<u>0.0226</u>	<u>0.0206</u>	0.0374	$F_{(2,6)}=20.27; P<0.001$
	mean ratio	1.35:1:2.3		

Underlined means are not significantly different, LSD's test at $P<0.01$. The indicated categories of leaves were used for analysis of variance (F-ratio for one-way ANOVA).

Table 3. Leaf preference rates (g dry wt g^{-1} crab day^{-1}) by four sesarmid crabs fed on three different categories of *R. apiculata* leaves in experimental aquaria.

Species	Green	Yellow	Brown	Total	F-ratio
N. versicolor	0.0171	0.0022	0.0061	0.0254	$F_{(2,18)}$=133.33; P<0.001
N. mederi	0.0053	0.0012	0.0148	0.0213	$F_{(2,18)}$=76.92; P<0.001
C. brevicristatum	0.0186	0.0032	0.0219	0.0437	$F_{(2,18)}$=60
C. haswelli	0.0230	0.0086	0.0158	0.0474	$F_{(2,18)}$=33.33; P<0.001
		mean ratio		5.2:1:5.9	

Underlined means are not significantly different, LSD's test at P<0.01. The indicated categories of leaves were used for analysis of variance (F-ratio for one-way ANOVA).

N. versicolor, while *N. mederi* consumed less, viz. 7.20, 12.6 and 25.70 mg dry wt g^{-1} crab day^{-1} of yellow, green and brown leaf, respectively.

It was observed that a relatively small quantity of yellow leaf material was eaten by sesarmid crabs. The results of laboratory studies (Table 3) indicate that large *Neoepisesarma* spp. crabs probably consumed less food than the smaller species of *Chiromanthes* spp., in comparison based on crab weight. There were highly significant (P<0.01) differences between the mean consumption rates of yellow, green and brown leaves in the preference experiment among *N. versicolor* and *C. haswelli*. They preferred to graze more on the green leaves. Yellow, brown and green leaf mean consumption rates were 2.00, 6.10 and 17.1 mg dry wt g^{-1} crab day^{-1}, respectively, for *N. versicolor*. The total leaf consumption was 25.40 mg dry wt g^{-1} crab day^{-1}. *C. haswelli* ingested 47.40 mg dry wt g^{-1} crab day^{-1} (8.60, 15.80 and 23.0 mg dry wt g^{-1} crab day^{-1} of yellow, brown and green, respectively).

The large species *N. mederi* preferred brown leaves. Mean consumption rates were 1.20, 5.30 and 14.8 mg dry wt g^{-1} crab day^{-1} for yellow, green and brown leaves, respectively. However, the total consumption rate of 21.30 mg dry wt g^{-1} crab day^{-1} was less than the amounts consumed by the small species *C. brevicristatum* and *C. haswelli*. *C. brevicristatum* which inhabits water logged environments had a total consumption rate of 43.70 mg dry wt g^{-1} crab day^{-1}. However, the mean rates did not differ significantly (P>0.01) in comparison between green and brown but were significantly different between green with yellow and brown with yellow (P<0.01). The mean rates of yellow, green and brown were 3.2, 18.6 and 21.9 mg dry wt g^{-1} crab day^{-1}, respectively.

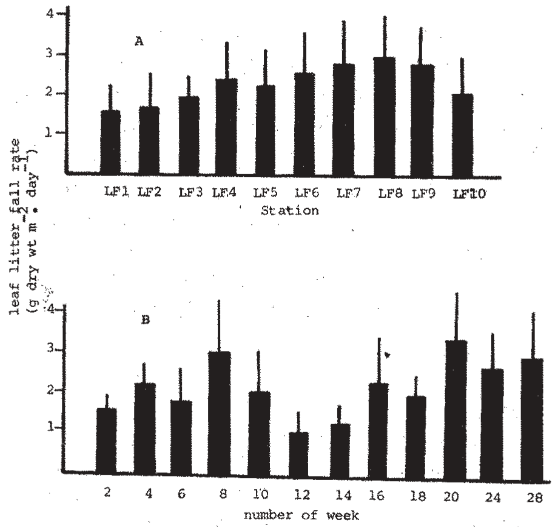

Fig. 2. Mean (±SD) rate of leaf litter fall (A) at stations LF1 - LF10 in high to low-intertidal forest, and (B) during 28 weeks from June 1986 to January 1987, in the *Rhizophora* zone at Ao Nambor mangrove forest.

Leaf litter fall

Fig. 2 shows mean daily value for total leaf litter of *R. apiculata* production obtained at sites in Ao Nambor. The Figure also illustrates the fluctuation of mean daily values (2 weeks production) during June 1986-January 1987. Total leaf litter fall ranged from 1.0354 to 3.4148 g dry wt m^{-2} day^{-1} with an average of 2.1924±1.1818 g dry wt m^{-2} day^{-1}. *R. apiculata* leaves dominated in this mangrove forest. The mean rate of leaf litter fall during week numbers 20, 24 and 28 (December to January) were remarkably increased. The values averaged 3.4148, 2.7031 and 2.9871 g dry wt m^{-2} day^{-1}, respectively.

Table 4. Mean (±SD) potential of removal rates (g dry wt m^{-2} day^{-1}) by sesarmid crabs, fed on three categories of *R. apiculata* leaves at station 1-15 in the Ao Nambor mangrove forest.

	Mean potential of removal rates		
Station	Green	Yellow	Brown
1	8.2835 (2.3905)	7.1649 (0.3261)	6.7037 (1.6437)
2	2.0905 (1.8998)	1.2632 (0.5675)	1.3409 (1.1929)
3	6.1830 (0.2444)	4.7465 (1.1261)	5.6333 (2.3684)
4	4.1051 (1.3828)	1.5046 (1.2004)	2.3683 (1.0970)
5	1.6175 (0.9580)	1.1511 (0.7458)	2.3516 (0.8037)
6	4.6626 (0.4334)	3.8338 (0.0860)	3.6643 (1.3903)
7	2.1708 (0.5956)	1.4691 (0.7669)	1.3892 (1.7333)
8	3.8348 (0.4137)	2.8712 (1.7761)	2.7147 (0.9765)
9	0.8320 (0.7369)	0.3880 (0.5742)	1.3570 (1.7649)
10	3.6870 (1.4951)	4.0833 (0.3723)	4.3851 (1.0850)
11	6.0225 (1.9205)	4.2577 (0.7348)	3.5004 (1.8936)
12	7.6822 (0.4217)	5.7096 (0.1075)	4.3279 (1.7566)
13	6.4870 (0.3331)	5.3027 (0.2423)	5.1219 (1.2541)
14	6.5799 (1.8076)	3.7006 (1.3054)	5.4803 (1.4753)
15	6.9262 (0.8720)	3.4618 (0.3309)	4.4414 (0.2399)
mean	4.7443 (2.5174)	3.3939 (2.0161)	3.6767 (2.0272)

Underlined means are not significantly different, LSD's test at P<0.001. The indicated categories of leaves were used for analysis of variance (one-way ANOVA $F_{(2,30)}$=14.644; P<0.001).

Leaf removal rates by sesarmid crabs in Ao Nambor mangrove forest indicate very large variations in feeding activity. Often leaves were drawn into burrows, but only some amount of leaf material was immediately eaten. A most interesting observation is that the crabs obviously prefer green leaves, a fact that was also confirmed in the feeding experiments in laboratory and directly observed in the field. Table 4 demonstrates that mean leaf removal rates ranged from 0.3880 to 7.1649 g dry wt m^{-2} day^{-1} for yellow leaves. Brown leaf removal rates ranged from 1.3409 to 6.7037 g dry wt m^{-2} day^{-1} Green leaf removal rates ranged from 0.8320 to 8.2835 g dry wt m^{-2} day^{-1}. There were highly significant (P <0.001) differences between the mean removal rates of green leaves compared with yellow and brown leaves. However, the rates did not differ significantly (one-way ANOVA, $F_{(2,30)}$= 14.644, P>0.001) between yellow and brown leaf categories. There were significant positive correlations between mean removal rates and area of crab burrows (r = 0.6972; P<0.001) and tidal exposure periods (r= 0.6156; P<0.001), as shown in Table 5.

Table 5. Correlation coefficients of linear regression between the potential of leaf removal rates (R) and area covered by crab burrows (A) and between the potential of leaf removal rates (R) and exposure period (T):Results derived from Table 6.

Correlation	r	r^2	F-ratio
R and A	0.6972 P<0.001	0.4862 P<0.01	$F_{(1,15)}$=40.6917 P<0.01
R and T	0.6156 P<0.001	0.3789 P<0.05	$F_{(1,15)}$=26.1985 P<0.01

F=ratio for one-way ANOVA.
r is the correlation coefficient and r^2 is the critical coefficient.

Table 6. Mean total potential of removed rates (g dry wt 9 m^{-2} day^{-1} ±SD) at crab burrows (cm^2 9 m^{-2}), and mean exposure period (min day^{-1} ±SD). Stations 1-15 in the Ao Nambor mangrove forest.

Station	Total potential of removal rate	Area covered by burrows (mean size of burrow)	Exposure time
1	66.4561 (10.8841)	683.58 (8.3)	1341 (99)
2	14.0838 (10.9152)	363.22 (5.7)	1206 (121)
3	49.6883 (10.9506)	605.36 (7.7)	1202 (124)
4	23.9321 (10.9802)	471.32 (5.7)	1067 (70)
5	15.3604 (4.1953)	291.70 (3.9)	1008 (48)
6	36.4818 (3.2353)	580.10 (6.2)	1204 (138)
7	16.1986 (9.1995)	395.83 (2.7)	1298 (146)
8	28.2599 (7.0549)	201.29 (2.5)	1168 (167)
9	7.7309 (8.7981)	203.90 (3.1)	786 (32)
10	36.4640 (6.9301)	269.24 (3.7)	1001 (119)
11	41.3417 (13.6370)	642.59 (4.4)	1386 (93)
12	53.1590 (5.9559)	669.99 (7.0)	1386 (93)
13	50.7348 (2.3860)	506.24 (4.9)	1386 (93)
14	47.2826 (12.6481)	543.12 (4.5)	1386 (93)
15	44.4885 (2.2079)	402.13 (3.9)	1386 (93)

Table 6 shows that the mean total leaf removal rates of three leaf categories within an area of 9 m^2 increased markedly with increasing exposure time and increasing number of crab burrows. The size of sesarmid crabs inhabiting the experimental plots also influenced leaf removal rates positively. The mean exposure time was more than 1300 minutes day^{-1}, which influenced the mean total leaf removal rates. They ranged from 41.3417 to 66.4561 g dry wt 9m^{-2} day^{-1} (see data from station 1, 11, 12, 13, 14 and 15 in Table 6).

Small sesarmid crabs made burrows with average areas of 2.7 cm^2 and 2.5 cm^2. Small crabs were probably not able to drag leaves down into their burrows, as indicated by the low values of 16.1986 and 28.2599 g dry wt 9 m^{-2} day^{-1} at stations 7 and 8.

Table 7 shows chemical composition of the different categories of *R. apiculata* leaves. The nitrogen content revealed great difference. The highest level of nitrogen (1.16 %) was found in green leaves. Brown leaves contained 0.72 % N while yellow leaves contained only

Table 7. The chemical composition of different categories of *R. apiculata* leaves: mean concentrations of C, N and tannins as % of dry weight (±SD); each mean is the result of three replicate analysis.

	Green	Yellow	Brown
Carbon	46.44 (0.05)	45.79 (0.06)	47.84 (0.08)
Nitrogen	1.16 (0.02)	0.48 (0.02)	0.72 (0.03)
Tannins	9.00 (0.23)	9.95 (0.25)	7.55 (0.16)
C/N	40.03	95.40	66.44

0.48 % N. Carbon contents did not vary much. Values ranged from 45.79 to 47.84 %. The highest level of tannins, 9.95 %, was found in yellow leaves. However, high tannin levels were also measured in brown and green leaves, viz. 7.55 % and 9.00 %, respectively.

DISCUSSION

The analyses of foregut contents of *N. versicolor*, *N. mederi*, *C. brevicristatum*, *C. eumolpe* and *C. haswelli* indicate that these crabs are primarily herbivores. Their diets consisted of 55-82 % mangrove plant matter. Leh and Sasekumar (1985) found that sesarmid crabs occasionally consumed brachyuran crabs and their moults, gastropods, juvenile bivalves, oligochaetes, nematodes, ants, mosquito larvae and spiders. However, these food items were not found in the present foregut contents analysis. Yet, the sesarmid crabs are believed to be omnivorous based on observations in the mangrove forest, where they would ingest moulted crabs and fish bait (pers. obs). Leaf materials may probably provide carbon and nitrogen for their normal growth metabolism. Partially decomposed leaves contained much higher nitrogen contents than senescent leaves, but nitrogen required by crabs may also come from bacteria and other microorganisms such as benthic diatoms living on the mud surface.

Kofoed et al. (1985) estimated C and N assimilation efficiencies of sesarmid crab (*N. versicolor* and *C. dussumieri*) by gravimetric analysis and ^{14}C-experiments. The animals nearly always assimilated C and N in the same proportions as found in the food (C:N = 30:1). This ratio must be insufficient to satisfy the nitrogen demand of crabs as the C:N ration of animal tissue is in the range of 7-9.

Robertson (1986) found that consumption of only senescent leaf material by crabs (*S. messa*) would not supply sufficient nitrogen provided a C/N ratio of 17 in the diet. This statement is in accordance with Rusell-Hunter (1970).

The results in Table 7 clearly point at importance of the C/N ratio, and suggest that crabs preferentially eat fresh green and decomposed brown leaves rather than yellow leaves with a high C/N ratio. Table 3 confirms the figures of preferred food by sesarmid crabs and shows that consumption of fresh green and brown leaf types was 5 to 6 times higher than consumption of leaves of the senescent yellow type.

Robertson (1986) suggested that senescent leaves may satisfy the crab's carbon requirements (leaf consumption in terms of carbon is 62 g C m^{-2} yr^{-1}), but the nitrogen required by crabs is likely to come from bacteria and other microbes which they remove from the mud surface layer by picking of flocculent detrital material. If so, *S. messa* would thus consume 62/17 = 3.6 gN $m^{-2}yr^{-1}$, which would represent 12 % of the estimated production of bacteria.

Kofoed et al. (1985) found that crab grazing only constituted 2-3 % of the total leaf production if eaten as fresh leaf material on the tree. The remaining primary production is eaten by crabs as it falls to the ground as litter, thus crab grazing on the tree canopy at nighttime does not seem to be a question of energy supply. Therefore, their conclusion is that crabs probably move to the tree by night to get a needed supply of nitrogen to their diet. Table 7 shows that fresh green leaf is richer in nitrogen than aged litter material so this would be a simple way to improve the nitrogen balance for sesarmid crabs. Another nitrogen source may come from mangrove propagules. Robertson et al. (1990) reported that 2.7-25.9 % of dispersed mangrove propagules of *Rhizophora* species were attacked by crabs in tropical Australia.

Several interesting aspects remain, however, to be addressed. Robertson (1986) mentions details of the interaction between crabs and leaves at both the organism and population levels. For instance, what are the proportions of various chemical constituents of *Rhizophora* leaves assimilated by sesarmid crabs? The ^{14}C assimilation by two species of *N. versicolor* and *C. dussumieri* studied by Kofoed et al. (1985) showed mean assimilations of 43±9 % and 69±11 %, respectively, from barley hay. These values together with the short gut passage time

(8 hours for *N. versicolor* and 19 hours for *C. dussumeiri*) suggest that the animals are efficient herbivores. The results suggest that the bulk of carbohydrates (= structural components) which in the food material constitutes more than 70 % by weight, is hydrolyzed and absorbed through passage of the gut. The higher assimilation efficiency found in *C. dussumeiri* is in accordance with the slower gut passage time.

The chemical composition of different categories of decomposed *R. stylosa* leaves were shown by Poovachiranon et al. (1986). The least decomposed leaves contained some starch (0.36 % dry weight). This component may be hydrolyzed and easily absorbed through passage of the crab guts.

Another question is how the crab deals with the high concentration of soluble tannins in the senescent leaf material. Table 7 shows high concentrations of soluble tannins, viz. 9.00 %, 9.95 % and 7.55 % for green, yellow and brown leaves, respectively. There are no indications of an effect of tannins on consumption and preference rates by different sesarmid crab species (Tables 2 and 3). The crabs may have special physiological mechanisms which prevent poisonous tannins from interfering with digestion. In contrast, individuals of the amphipod *Parhyale hawaiensis* (Dana), are much affected by amounts of soluble tannins which do not affect sesarmid crabs in feeding rate experiments (Poovachiranon et al., 1986).

At the population level an important question concerns seasonal and spatial (between estuaries) variation in removal rates of leaves. How is removal rate influenced by crab densities and other factors? The present study shows that the initial leaf litter degradation is positively correlated with tidal exposure time as well as crab density. In the high intertidal *Rhizophora* forest (longer exposure time), sesarmid crabs are more abundant than in the low intertidal habitat (Nateewathana and Tantichodok, 1984). The importance of litter processing by crabs increases with height of the intertidal zone in tropical Australia, whereas in new world mangrove forests the reverse is found (Robertson and Daniel, 1989).

The results of the potential leaf removal rates by sesarmid crabs probably represent overestimates of the true rates in the Ao Nambor mangrove. The present figure of 3.3933 g dry wt $m^{-2}day^{-1}$ for leaf removal is higher than leaf litter fall rate of 2.1924 g dry wt $m^{-2}day^{-1}$. Presumably, leaf litter on the mangrove forest floor should be cleaned up by the leaf-burying crabs. However, this was not observed. There are a number of probable explanations for this discrepancy. Firstly, each leaf fell on the mangrove floor at different times in nature, influencing the probability of leaf burial by crabs. In comparison, the total amount of leaf litter was placed on the forest floor at the beginning of the experiment. Secondly, most of the leaf litter which fell during ebbing high tide would be excluded from consumption by sesarmid crabs. Only a small amount of this leaf litter would accumulate on the forest floor at low tide. Thirdly, the 15 plots used for leaf removal experiments may represent activities of sesarmid crabs where these were most abundant.

Nevertheless, the present studies on potential rates of leaf removal and leaf preferences show that leaf-eating crabs are important in the first step of degradation of leaf litter, both in terms of green, aged yellow, and decomposed brown leaves. Our results suggest that in the Ao Nambor mangrove forest where leaf-burying crabs are abundant, the crabs, especially *Neoepisesarma* sp., play a key role as a major link between primary and secondary production with human beings at the end of the food chain. Sesarmid crabs are collected by local people and sold as human food at the market. These crabs have been named "Pu Kaem (salted crabs)" or "Pu Samair ".

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