

Changes in properties of mangrove sediment due to foraging on *Kandelia obovata* leaves by crabs *Parasesarma plicatum* (Grapsidae: Sesarinae)

Guang C. Chen^{1,2}, Yong Ye^{1,*}

¹State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen 361005, Fujian, China

²Third Institute of Oceanography, State Oceanic Administration, Xiamen 361005, Fujian, China

ABSTRACT: Sesarmid crabs are important ecosystem engineers in mangroves because they remove a large proportion of mangrove leaf litter. However, the effects on mangrove sediments of sesarmid crab foraging on mangrove leaves has been poorly quantified. Through a laboratory experiment, the present study aimed to quantify changes in nutrient concentrations and enzyme activities in mangrove sediment due to foraging on *Kandelia obovata* leaves by *Parasesarma plicatum* crabs. Non-leaf foraging activity (i.e. the crabs were not fed with leaves) of *P. plicatum* had insignificant effects on the concentrations of sediment organic carbon (OC), total nitrogen (TN) and phosphate, but significantly increased sediment NO_3^- -N concentration. Sediment urease activity was inhibited while invertase activity was enhanced by crab activity. Compared with non-leaf foraging, crabs fed with *K. obovata* leaves showed different effects on sediment properties. Leaf foraging by crabs significantly increased sediment OC and TN concentrations, and activities of enzymes except for invertase and urease. Significant correlations were found among sediment nutrient concentrations and enzyme activities. Foraging on 1.00 g *K. obovata* leaves by *P. plicatum* resulted in accumulations of 154.94 mg OC and 10.26 mg TN in sediment. Removing crab faecal material from the sediment reduced these effects of leaf foraging by crabs on sediment properties, but there was still significant accumulation of OC and TN in the sediment compared with the control. The present study demonstrated that foraging on mangrove leaves by *P. plicatum* plays an important role on nutrient retention in mangrove sediment and that crab faecal material mediates this ecological function.

KEY WORDS: Leaf foraging · Mangrove · Sediment · *Kandelia obovata* · *Parasesarma plicatum*

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Mangrove sediment is a complex habitat, including physical, biological and chemical components (Chapman & Tolhurst 2007). Among the factors that control sedimentary processes, activities of fauna as well as flora in mangrove sediment have been considered as the main factors in determining the biogeochemical conditions of sediment (Marchand et al. 2004, Ferreira et al. 2007). Activities of large burrowing invertebrates have long been known to affect the physical and chemical components of mangrove sediment by altering sediment abiotic conditions and nutrient availability for biogeochemical processes (e.g. Botto & Iribarne 2000, Volkenborn et al. 2007). Many studies have dealt

with these roles of crabs in mangrove ecosystem functioning, and the ecological importance of crabs is well recognized (Kristensen 2008).

Sesarmid crabs are important macroinvertebrates in mangrove ecosystems, and they influence the structure and function of mangrove habitats through their burrowing (e.g. Botto & Iribarne 2000, Kristensen 2008) and leaf processing activities (e.g. Robertson & Daniel 1989, Micheli 1993, Lee 1997). In general, most sesarmid crabs actively dig and maintain burrows in mangrove sediments. The impacts of burrowing activities of crabs in field conditions were demonstrated by higher percentages of bacterial, vascular plant, and macroalgal fatty acid markers in sediments with crabs (Mchenga et al. 2007), higher organic matter and

*Corresponding author. E-mail: yeyong@xmu.edu.cn

water contents (Botto & Iribarne 2000), and more NH_4^+ -N release (Liu et al. 2005) in the burrow compartments than the adjacent areas without crabs. However, the effect of sesarmid crabs on mangrove sediments might be insignificant in the field, because it is usually difficult to separate the effect of these crabs from other processes such as the effect of plants.

Another reason that sesarmid crabs are important in mangrove ecosystems is because this crab group removes a large proportion of mangrove leaf litter from the mangrove floor through either direct consumption or burial of leaf litter in their burrows. The consumption and burial of litter within the mangrove forest by sesarmid crabs help to promote leaf decomposition processes, retain organic matter, and increase nutrient turnover within mangroves (Robertson 1986, Emmerson & McGwynne 1992, Werry & Lee 2005). The retention of nutrients is quite important for mangrove ecosystems as some mangroves are nutrient limited (mainly N and P) (Li 1997). Few studies have been conducted in the interest of quantifying this effect of leaf foraging by crabs on nutrient properties of mangrove sediment, though Nerot et al. (2009) found that the processing of senescent leaves of *Avicennia marina* by *Parasesarma erythroductyla* significantly accelerated the transfer of mangrove organic matter to the surface sediment, as shown by a higher C:N ratio.

Despite many studies on the ecological role of sesarmid crabs in mangrove ecosystems, information on this crab group is limited in China. In Jiulongjiang Estuary, *Kandelia obovata* (i.e. *K. candel* revised by Sheue et al. 2003) is the most dominant plant species, and *Parasesarma plicatum* (i.e. *Sesarma plicata* revised by Rahayu & Ng 2010) is a common crustacean peculiar to the mangrove forest (Chen et al. 2007). This sesarmid species has a particular feeding preference for leaves of *K. obovata* over other mangrove species (Chen & Ye 2008), and removes a large proportion of leaf litter from the mangrove sediment (Chen et al. 2008), implying a potential ecological role in retention of nutrients in mangrove ecosystems.

Based on laboratory experiments, the present study aimed to investigate the ecological role of *Parasesarma plicatum* in modifying sediment properties, through studying the effects of leaf and non-leaf foraging activities of crabs on sediment nutrient concentrations and enzyme activities. The importance of crab faecal material on sediment properties was also investigated. The present study hypothesized that (1) leaf foraging by *P. plicatum* results in retention of nutrients and changes the enzyme activities in mangrove sediments; (2) leaf foraging has different effects on sediment characteristics from non-leaf foraging activities; and (3) crab faecal material mediate the effect of leaf

foraging on sediment properties. The present study might add useful information to the effort in understanding and quantifying the effect of crab activities on mangrove ecological processes.

MATERIALS AND METHODS

Experimental material sampling. Mangrove crab and leaf samplings were carried out in a mangrove forest (24° 24' N, 117° 55' E) at Jiulongjiang Estuary near Caoputou Village, Longhai County, Zhangzhou City, Fujian Province, China. The region is subtropical (mean annual temperature: 20.9°C), with most of the annual rainfall (1284 mm) derived from summer typhoons. The annual mean air temperature of this area is 21.0°C, averaging 20 yr data from the local meteorological station. The mean salinity of open water adjacent to the forest is 17 ppt, averaged over 2004 and 2005. Tides are semi-diurnal with an average range of 4 m (Chen et al. 2007).

This mangrove forest is dominated by *Kandelia obovata*, with *Aegiceras corniculatum*, *Bruguiera gymnorrhiza* and *Rhizophora stylosa* as minor species. Standing leaf litter stock on the mangrove floor is low in this forest due to a high removal rate by mangrove crabs and tidal flushing. Among the crustacean species reported, *Parasesarma plicatum* is the most common sesarmid crab (Chen et al. 2007).

Leaves and *Parasesarma plicatum* crabs for feeding experiments were collected during ebb tides in April 2007, when the crabs were active in the mangroves. Senescent leaves of *Kandelia obovata* were collected within the middle zone of this forest. These leaves were studied because they are the favorite mangrove species in the feeding preference study reported by Chen et al. (2008). Senescent leaves were collected via gently shaking the trees. Leaves with similar size and mass were then selected, cleaned and stored at 4°C until the experiment began. Leaf organic carbon (OC) content was analyzed using a rapid dichromate oxidation procedure, and total nitrogen (TN) content was analyzed using a Foss Kjeltex 2300 Analyzer Unit after Kjeldahl digestion. The OC and TN contents in leaf material were 537.70 ± 20.9 and 12.03 ± 0.63 mg g⁻¹ dry wt, respectively (n = 4).

Considering that sediment in the mangrove forest was intensively disturbed by mangrove roots and crabs, and a non-vegetated flat had much more uniform sediment than the mangrove forest, sediment for experiment was collected in the non-vegetated flat adjacent to the mangrove forest. Sediment therein has basic properties (pH 7.1, silt + clay > 95%) similar to the mangrove sediment (Chen et al. 2007). Before starting the experiment, visible macro-benthic fauna

Table 1. Background nutrient concentrations and enzyme activities per gram dry wt of sediment (n = 4); means \pm SD. OC: organic carbon, TN: total nitrogen

Nutrient	Concentration	Enzyme	Activity
OC (mg)	9.93 \pm 0.75	Invertase (U _g)	22.21 \pm 0.61
TN (mg)	0.97 \pm 0.00	Protease (U _d)	0.50 \pm 0.03
NH ₄ ⁺ -N (μ g)	9.93 \pm 1.74	Urease (U _N)	6.99 \pm 0.35
NO ₃ ⁻ -N (μ g)	67.73 \pm 31.23	Acid phosphatase (U _p)	0.45 \pm 0.04
PO ₄ ³⁻ -P (μ g)	12.45 \pm 0.58	Polyphenol oxidase (U _j)	0.11 \pm 0.01

were carefully removed to eliminate the disturbance from other benthic fauna, and 4 sediment subsamples were oven-dried to constant weight at 105°C to obtain water content (~50%) in sediments used in the experiment. The fresh sediment, after thorough mixing, was then filled into plastic containers (9 cm in diameter, 10 cm in depth). Each container was filled with 250 g dry wt of sediment and wetted with seawater of 17 ppt salinity (prepared by dissolving commercial natural sea salt in deionized water). The containers were conditioned for 2 d prior to treatment. Before treatment, 4 containers were randomly selected to determine the background values of sediment properties. Nutrient concentrations and enzyme activities of the sediment are given in Table 1.

Experimental design. A feeding experiment with *Parasesarma plicatum* was conducted from April to June 2007 to study the effects of leaf and non-leaf foraging activities as well as faecal material of crabs on sediment properties. During the experiment, laboratory temperature was kept at 25°C by an air conditioner. In order to estimate the effect of leaf foraging and crab faecal material on sediment properties, 4 treatments, i.e. CT, CR, KO and FR, were set up, with 4 replicates for each treatment. Treatment CT, without crabs, acted as the control. In treatment CR, crabs were kept in the containers to study the effect of non-leaf foraging activity of crabs on sediment properties, and these crabs were not supplied with mangrove leaves during the experiment.

Effects of leaf foraging by crabs were studied using mangrove leaves of *Kandelia obovata* (treatment KO). The crabs were allowed to colonize for 24 h after they were added to the containers and were then fed with about 1 g wet wt of *K. obovata* leaves every 2 d. The leaf was cut through the mid rib and weighed before being fed to the crab. One half of each leaf was put into the container, and the other was oven-dried to constant weight at 65°C to obtain dry wt and water content. After 48 h, remaining leaf material in the containers was collected, oven-dried to constant weights and weighed. Leaf material consumed was calculated by the dry wt fed to crabs minus the remaining material. Leaf decomposition by microorganisms was not con-

sidered because the decomposition is much lower than the removal by sesarimid crabs (Chen & Ye 2008).

To study the effect of crab faecal material on sediment properties, another treatment, namely FR, in which crabs were fed the same as those in treatment KO, was set up. Faecal material in FR was removed daily from the sediment surface and oven-dried to constant weight. Because no obvious faecal

pellet was found on the sediment for treatment CR, treatment with faeces removed from unfed crabs was not set up.

In treatments CR, KO and FR, 1 crab was kept in each container. Crab sizes (carapace widths) and wet wts were sufficiently similar among these treatments ($p = 0.906$ for carapace widths and $p = 0.668$ for wet wts from one-way ANOVA analysis) to eliminate the influence of crab size: CR (17.18 \pm 0.75 mm, 2.49 \pm 0.46 g), KO (17.35 \pm 0.72 mm, 2.71 \pm 0.45 g), FR (17.42 \pm 0.82 mm, 2.46 \pm 0.40 g) (data: mean \pm SD). The container size was suitable for this crab experiment. A study carried out by Kwok & Lee (1995) also showed that *Parasesarma plicatum* crabs had good growth performance in a container with size similar to the present study and the survival period was up to 200 d. The experiment lasted for 2 mo during which deionized water was daily added to the containers to compensate for evaporation, and sediment moisture content in the containers was maintained at ~50%, similar to that in the field during the ebb tide period. Total amount of leaf material consumed by each crab in treatments KO and FR, and faecal material removed in treatment FR, were recorded.

Analyses of nutrient concentrations and enzyme activities in sediment. Crabs were removed from the containers at the end of the experiment. Sediment in each container was then fully mixed. Sediment OC concentration was analyzed using rapid dichromate oxidation procedure. TN concentration in sediment was analyzed using Foss Kjeltex 2300 Analyzer Unit after Kjeldahl digestion. The NH₄⁺-N content in the KCl (2 M) extracts was determined by Nessler's reagent colorimetric method. Sediment NO₃⁻-N was extracted with saturated CaSO₄ solution and NO₃⁻-N in the extracts was determined by the phenoldisulfonic acid colorimetry method. Sediment hydrochloric acid-ammonium fluoride-soluble (0.03 M NH₄F–0.025 M HCl) phosphorus concentration (PO₄³⁻-P) was determined by stannous chloride reduction method. All data were expressed in terms of 105°C oven-dried sediment weight.

Sediment enzyme activities were determined according to Guan (1986) and Zhang et al. (2005). Five

sediment enzymes (invertase, protease, urease, acid phosphatase, and polyphenol oxidase) were selected, as they are important in the transformation of different plant nutrients (e.g. N and P) and metabolism of OC in mangrove and coastal sediments (Zhang & Lin 1999, He et al. 2002). Enzyme activities were measured using air-dried sediment (moisture of about 6%), which had activities of these enzymes similar to fresh sediment (Zhang & Lin 1999).

For measuring invertase activity, 5 g of air-dried sediment was incubated for 24 h at 37°C with 15 ml 8% sucrose, 5 ml phosphate buffer at pH 5.5, and 0.1 ml toluene. The glucose released by invertase reacted with 3-5-dinitrosalicylic acid, and then was spectrophotometrically measured at 508 nm (UV 330, Unicam UV-vis). Invertase activities were expressed as units (U_g) per gram dry wt sediment ($1 U_g = 1 \text{ mg glucose released } d^{-1}$).

For measuring protease activity, 5 g of air dried sediment was incubated for 24 h at 30 °C with 20 ml 1% casein and 1 ml toluene. Then, 2 ml 0.05 mol l⁻¹ sulfuric acid and 12 ml 20% sodium sulfate were added. The amino nitrogen released by protease reacted with 1 ml 2% ninhydrin, and was then spectrophotometrically measured at 500 nm. Protease activities were expressed as units (U_a) g⁻¹ dry wt sediment ($1 U_a = 1 \text{ mg NH}_2\text{-N released } d^{-1}$).

To determine sediment urease activity (Askin & Kizilkaya 2005), 7.5 ml citrate buffer (pH 6.7) and 10 ml of 10% urea substrate solution were added to 10 g sediment, and subsequently incubated for 3 h at 37°C. The volume was made up to 100 ml with distilled water at 37°C. Then, 1 ml of filtrate was diluted to 10 ml with distilled water, and 4 ml of sodium phenolate and 3 ml of 0.9% sodium hypochloride were added. The released ammonium was spectrophotometrically determined at 578 nm. Urease activities were expressed as units (U_N) g⁻¹ dry wt sediment ($1 U_N = 1 \text{ mg NH}_4^+\text{-N released } d^{-1}$).

For measurement of acid phosphatase activity, 5 g of air-dried sediment was incubated for 2 h at 37°C with 20 ml disodium benzene phosphate dissolved in acetate buffer at pH 5 and 0.1 ml toluene. The phenol released by phosphatase reacted with 0.25 ml ammonium chloride-ammonium hydroxide buffer at pH 9.8, 0.5 ml 4-aminophenazon and 0.5 ml potassium ferricyanide, and was then spectrophotometrically measured at 510 nm (UV 330, Unicam UV-vis). Acid phosphatase activities were expressed as units (U_p) g⁻¹ dry wt sediment ($1 U_p = 1 \text{ mg phenol released } d^{-1}$).

For measuring polyphenol oxidase activity, 5 g of air dried sediment were incubated for 2 min in a 30°C water bath, with 10 ml distilled water, 6 ml 0.1% ascorbic acid and 10 ml 0.02 mol l⁻¹ catechol. Then, 3 ml

10% phosphoric acid were added and the filtrate was titrated with 0.005 mol l⁻¹ iodine. Polyphenol oxidase activities were expressed as units (U_I) g⁻¹ dry wt sediment ($1 U_I = 1 \text{ ml } 0.005 \text{ mol l}^{-1} I_2 \text{ consumed}$).

Data analysis. The difference in each nutrient parameter and enzyme activity among the treatments was tested by using one-way analysis of variance (ANOVA). Pearson correlation coefficients were calculated to determine the relationships between sediment properties and enzyme activities by using the SPSS procedure CORRELATION. All statistical analyses were performed using SPSS 13.0 for Windows.

RESULTS

Amount of eaten leaf and faecal material

During the 2 mo experiment, all crabs behaved normally and were observed scraping materials from the sediment surface and burrowing. A total of 4.04 ± 0.14 and 4.30 ± 0.32 g dry wt *Kandelia obovata* leaf material were consumed by *Parasesarma plicatum* in treatments KO and FR, respectively. Leaf materials consumed in these 2 treatments were similar in weight ($p = 0.218$). In treatment FR, 3.93 ± 1.08 g faecal material were removed from sediment surface.

Sediment nutrient concentrations

Sediment nutrient concentrations significantly varied among the 4 treatments (see Figs. 1 & 2). There was no significant difference in sediment OC concentration between treatments CT and CR (Fig. 1). Treatments KO and FR with *Kandelia obovata* leaf consumed had significant higher OC concentrations than CT and CR treatments. Sediment OC concentration was highest in treatment KO, followed by treatment FR.

Similar to sediment OC concentration, both CT and CR treatments had significant lower sediment TN concentrations than those in treatments KO and FR. Sediment TN concentration in KO was the highest among the 4 treatments. Sediment C:N ratio also changed with the treatments, and was highest in treatment KO and lowest in treatment CT.

Sediment NH₄⁺-N concentration in treatment CT was significantly higher than those in the other 3 treatments (Fig. 2). Treatment CR also had a high sediment NH₄⁺-N concentration. The other 2 treatments (KO and FR) with *Kandelia obovata* leaf consumed had comparable sediment NH₄⁺-N concentrations.

The concentration of sediment NO₃⁻-N was highest in treatment CR, followed by a concentration of $131.44 \mu\text{g g}^{-1}$ in the control (CT). Sediment NO₃⁻-N

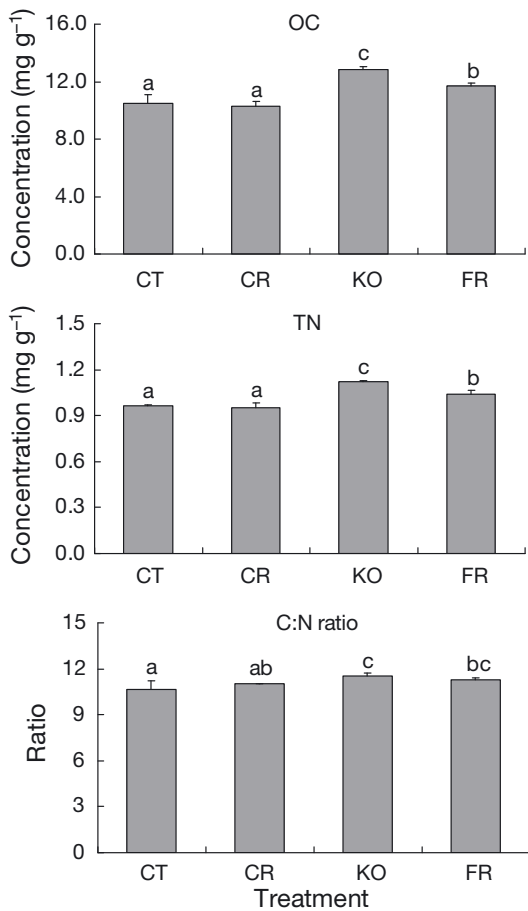


Fig. 1. Concentrations of sediment organic carbon (OC) and total nitrogen (TN), and C:N ratios in the 4 treatments; means \pm SD. Letters above columns: significant differences at 0.05 level. Treatments: CT: control without crabs; CR: crabs not fed with mangrove leaves during the experiment; KO: leaf foraging treatment in which crabs were fed *K. obovata* leaves; FR: leaf foraging treatment in which crabs were fed *K. obovata* leaves, and faecal materials were removed daily

concentrations in treatments KO and FR were significantly lower than those in treatments CR and CT.

Contrary to sediment OC and TN concentrations, sediment phosphate concentration in treatment KO was the lowest, following treatment FR. Concentrations in CT and CR were similar, with values of $\sim 12.5 \mu\text{g g}^{-1}$.

Sediment enzyme activities

Sediment enzyme activities were significantly affected by leaf foraging behaviors of *Parasesarma plicatum* (Fig. 3). For invertase, the highest activity was found in treatment CR, much higher than those in the 2 leaf foraging treatments (KO and FR). Sediment protease activity in KO was significantly higher than in the other 3 treatments, while the mean value in treatment

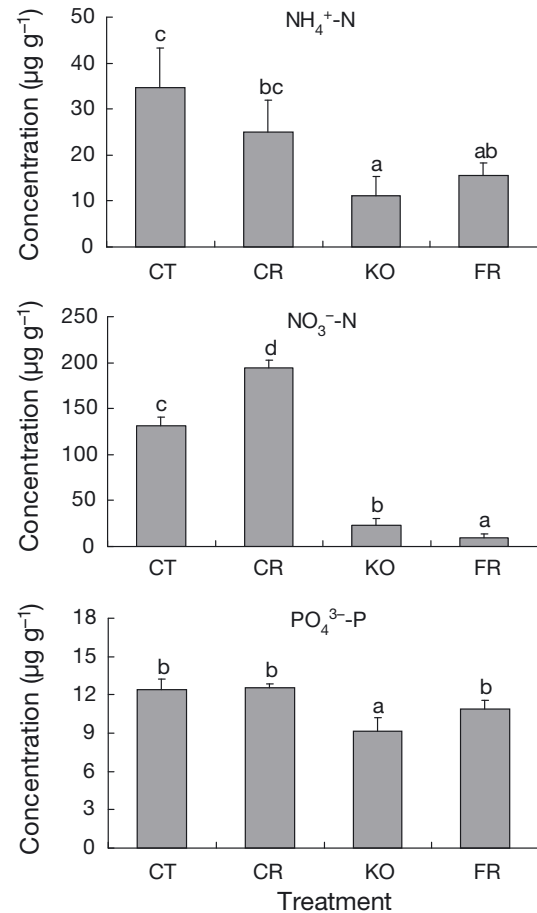


Fig. 2. Concentrations of sediment NH₄⁺-N, NO₃⁻-N and PO₄³⁻-P in the 4 treatments; means \pm SD. Letters above columns: significant differences at 0.05 level. See Fig. 1 for abbreviations

CR was the lowest. Urease activities in CR, KO and FR were significantly lower than that in treatment CT without crab individuals, indicating that sediment urease activity was inhibited by crabs. Acid phosphatase activities were high in FR and similarly much lower in treatments CT and CR. Sediment polyphenol oxidase activity was high in KO sediment and similar in the other 3 treatments.

Significant correlations were found among these nutrient parameters and enzyme activities (Table 2). Sediment OC concentration was significantly and positively correlated with TN concentration and C:N ratio. Both sediment OC and TN concentrations had positive correlation with activities of protease, phosphatase and polyphenol oxidase, and were negatively correlated with NH₄⁺-N, NO₃⁻-N, phosphate concentrations, as well as invertase activity. Sediment invertase and protease activities were significantly correlated with all sediment nutrient properties except sediment C:N ratio. Sediment invertase activity was significantly correlated with only sediment C:N ratio.

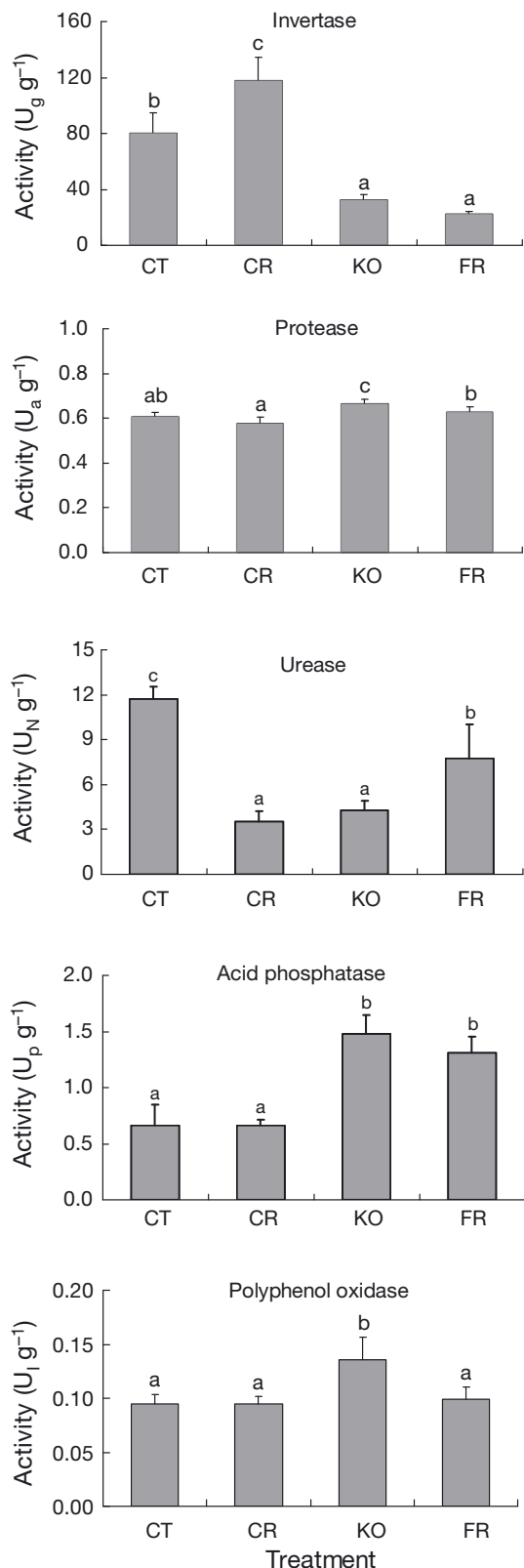


Fig. 3. Activities of 5 sediment enzymes in the 4 treatments; means \pm SD. Letters above columns: significant differences at 0.05 level. See Fig. 1 for abbreviations

DISCUSSION

Among the macrobenthos, the dominating mangrove crabs have a considerable impact on mangrove ecosystem functioning (Smith et al. 1991, Kristensen 2008). Both crab activity and leaf foraging produce measurable changes in the sediment properties (Posey 1987, Botto & Iribarne 2000) and can affect sediment biological process (Olafsson & Ndaro 1997) in intertidal ecosystems. Through leaf foraging, *Sesarma plicatum* crabs caused the accumulation of sediment OC, as well as TN. Sediment C:N ratio was also increased, similar to the result reported by Nerot et al. (2009). Sediment OC and TN concentrations in mangroves in Jiulongjiang Estuary were lower than those in some other mangroves in China, such as Futian mangrove and Mai Po mangrove (Li 1997, Tam & Wong 2000, Alongi et al. 2005, Chen et al. 2007). Thus, the retention of nutrients in mangrove sediments seems to be very important in Jiulongjiang Estuary. From the differences between the final concentrations in the KO and CR treatments, a crab foraging 1.00 g *Kandelia obovata* senescent leaves (containing 537.70 mg OC and 12.03 mg TN), caused the accumulation of 154.94 mg OC and 10.26 mg TN in sediment during the 2 mo experiment, indicating that the return efficiency of TN was high while the assimilation efficiency of TN was low by crabs. It has been reported that some sesarmid crabs are capable of utilizing carbon but not nitrogen from senescent mangrove leaves (Thongtham & Kristensen 2005). The relationship between crab growth performance and N utilization from mangrove leaves is also species specific (Kwok & Lee 1995). *Chironanthes bidens* and *Parasesarma plicatum*, 2 sesarmid species, had good growth performance on mangrove leaves alone, while crabs fed on yellow *K. obovata* leaves had lower survivorship than those fed on brown *K. obovata* leaves, yellow *Avicennia marina* or brown *A. marina* leaves, because the yellow *K. obovata* leaves had a much higher C:N ratio (Kwok & Lee 1995). Their results indicated that the survival and the growth depend on the leaf C:N ratio or N availability. When fed with senescent leaves with low available nitrogen, the crabs must thus obtain supplementary N sources such as sediments. Therefore, *P. plicatum* in the present study had low assimilation efficiency of TN from senescent *K. obovata* leaves, resulting in high amounts of TN accumulated due to leaf foraging.

The present study used senescent leaves in leaf foraging treatments, and the faeces production (dry wt) accounted for 91% of the leaf material ingested, i.e. *Parasesarma plicatum* had low assimilation efficiency on senescent *Kandelia obovata* leaves (~9%) by leaf weight. Kwok & Lee (1995) also reported such low efficiency of 9.2% on the same leaf material by sesarmid

Table 2. Correlation coefficients (Pearson's r) among sediment parameters. *p < 0.05, **p < 0.01, ***p < 0.001. -: insignificant linear correlation. OC: organic carbon, TN: total nitrogen

Parameter	OC	TN	C:N ratio	NH ₄ ⁺ -N	NO ₃ ⁻ -N	PO ₄ ³⁻ -P
TN	0.932***	-	-	-	-	-
C:N	0.752**	0.598	-	-	-	-
NH ₄ ⁺ -N	-0.648*	-0.744**	-0.666*	-	-	-
NO ₃ ⁻ -N	-0.804**	-0.859***	-0.549	0.737**	-	-
PO ₄ ³⁻ -P	-0.898***	-0.954***	-0.556	0.690*	0.734*	-
Invertase activity	-0.793**	-0.802**	-0.500	0.626*	0.976***	0.690*
Protease activity	0.778**	0.866**	-0.393	-0.679*	-0.751**	-0.912***
Urease activity	-0.251	-0.128	-0.680*	0.480	0.141	0.335
Acid phosphatase activity	0.902***	0.868***	0.750**	-0.730**	-0.873***	-0.742**
Polyphenol oxidase activity	0.811**	0.721**	0.667*	-0.499	-0.432	-0.530

crabs and suggested that yellow *K. obovata* leaves were the poorest food for crabs. The crabs in the present study were provided access to sediment as well as leaves, and they were observed to feed on sediment. The crabs therefore might be partly satiated with sediment detritus and have less dependence on the leaf material. Thongtham & Kristensen (2005) also found that crabs with access to sediment had a much lower leaf consumption rate of mangrove leaves than those fed singly on leaf material.

Through leaf foraging and assimilation, sesamid crabs reduced mangrove leaf litter to faecal fragments (Werry & Lee 2005) and increased decomposition rate of mangrove leaf litter, resulting in the retention and recycling of nutrient matter within the mangrove system (Lee 1997). When crab faecal material was removed from sediment surface, sediment OC and TN concentrations significantly decreased compared with the concentrations in the leaf foraging treatment, while a higher PO₄³⁻-P concentration was measured, indicating a different pattern for foraging *Kandelia obovata* leaves. This demonstrated that crab faecal material mediated the retention and recycling of nutrient matter within the mangrove system. Effects of crab faecal material on sediment properties were expressed as differences in sediment properties between treatments KO and FR, calculated by sediment nutrient concentrations in KO minus those mean values in FR. The accumulated OC and TN in sediments were 91.35 and 5.76 mg, respectively, after crabs discharged 1 g of faecal material into the sediment.

The present study recorded no significant effect of crab non-leaf foraging activity on sediment OC, TN and PO₄³⁻-P concentrations, though the crabs not fed with mangrove leaf material were observed to utilize sediment materials. However, non-leaf foraging increased sediment NO₃⁻-N concentration. This was because the non-leaf foraging treatment increased crab burrowing activities, which increased dissolved

oxygen and nitrification levels in the sediment (Mchenga et al. 2007).

Contrary to crab non-leaf foraging activity, leaf foraging by *Parasesarma plicatum* crabs intensively decreased sediment NO₃⁻-N concentration, probably due to enhanced denitrification activity in the sediment. Organic matter in the mangrove sediment accumulated by crab leaf foraging provided a carbon source for denitrification, and increased microbial respiration rates, but decreased nitrification rates in a hydric ecosystem (Strauss & Lamberti 2000). The enhancement of denitrification in the sediment was also recorded in the presence of high density of *Corophium volutator* (Pelegri et al. 1994). These contrary effects of crab leaf foraging and non-leaf foraging activities co-exist in the field and might result in a counteract effect on sediment characteristics. In a mangrove in Queensland, sediment NO₃⁻-N concentration at a plot from which the crabs were removed was similar to that at a control plot, though the NH₄⁺-N concentration was higher at the control plot (Smith et al. 1991).

Foraging *Kandelia obovata* leaves by *Parasesarma plicatum* increased activities of sediment enzymes including protease, acid phosphatase and polyphenol oxidase with the increases in sediment OC and TN concentrations, indicating enhanced biochemical processes in mangrove sediment. Differences in enzyme activities depend on sediment organic matter content, the composition and activity of living organisms inhabiting the sediment, and the intensity of biological processes (Kuprevich & Shcherbakova 1971). Burrowing and leaf foraging by mangrove crabs can modify substances available to microbials (Kristensen 2008). During the leaf foraging process, organic components as sources of energy for sediment microbes and substrates of sediment enzymes are returned to the mangrove ecosystem and then accumulate; thus, the growth and activity of microorganisms are enhanced, resulting in increasing enzyme activities.

Mangrove leaves are rich in tannins (Benner et al. 1990, Lee et al. 1990, Marchand et al. 2005). Though processed by crab gut passage, tannins originating from leaves might still be an important compound in faecal material. Accumulation of tannins might restrain some microorganisms in sediment, and consequently, might inhibit activities of some enzymes in the sediment. Invertase activity in the sediment was significantly lower in the 2 leaf foraging treatments than in the crab and control treatments (CR and CT), indicating that crab leaf foraging activity inhibited sediment invertase activity. This effect on sediment invertase showed a contrary trend to other sediment enzymes such as protease, phosphatase and polyphenol oxidase. It is supposed that the inhibition of sediment invertase activity may be due to the tannin content in the sediment.

The microbial population both mineralizes and immobilizes phosphorus in a sediment system (Halstead & Mckercher 1975). Phosphatase is adaptive, and the intensity of its excretion by microorganisms is determined by their need for phosphorus, indicating that phosphatase activity in sediment is closely associated with the presence of available forms of phosphorus and the activity of sediment organisms (Kuprevich & Shcherbakova 1971). Increased microbial biomass in sediment with the increases in organic matters as a result of crab leaf foraging activity might hence lead to a greater demand and absorption for available inorganic phosphorus ($\text{PO}_4^{3-}\text{-P}$). On the other hand, the returned phosphorus in mangrove sediment after crab gut passage was insignificant as *Kandelia obovata* leaves are poor in phosphorus (Li 1997). Thus, sediment-originating phosphorus may act as an important source for the sediment organisms. This absorption of $\text{PO}_4^{3-}\text{-P}$ may account for the decrease in sediment $\text{PO}_4^{3-}\text{-P}$ concentration due to crab leaf foraging.

Overall, the present study concluded (1) foraging *Kandelia obovata* leaves by *Parasesarma plicatum* crabs resulted in the retention of nutrients and changed the enzyme activities in a mangrove sediment; (2) for *P. plicatum* crabs, leaf foraging activity had stronger enhancement on most sediment characteristics than non-leaf foraging activity; and (3) crab faecal material played an important role in mediating the effect of crab leaf foraging on mangrove ecological processes. The present study further demonstrated the importance of sesarimid crab in mangrove ecological processes.

Acknowledgements. This work was supported by Programs for National Natural Science Foundation of China (40476040, 41076049) and New Century Excellent Talents in University (NCET). We thank X. L. Mao and S. R. Yang for their dedicated work in the field and/or laboratory.

LITERATURE CITED

- Alongi DM, Pfitzner J, Trott LA, Tirendi F, Dixon P, Klumpp DW (2005) Rapid sediment accumulation and microbial mineralization in forests of the mangrove *Kandelia candel* in the Jiulongjiang Estuary, China. *Estuar Coast Shelf Sci* 63:605–618
- Askin T, Kizilkaya R (2005) The spatial variability of urease activity of surface agricultural soils within an urban area. *J Cent Eur Agric* 6:161–166
- Benner R, Hatcher PG, Hedges JI (1990) Early diagenesis of mangrove leaves in a tropical estuary: bulk chemical characterization using solid-state ^{13}C NMR and elemental analysis. *Geochim Cosmochim Acta* 54:2003–2013
- Botto F, Iribarne O (2000) Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuar Coast Shelf Sci* 51:141–151
- Chapman MG, Tolhurst TJ (2007) Relationships between benthic macrofauna and biogeochemical properties of sediments at different spatial scales and among different habitats in mangrove forests. *J Exp Mar Biol Ecol* 343: 96–109
- Chen GC, Ye Y (2008) Leaf consumption by *Sesarma plicata* in a mangrove forest at Jiulongjiang Estuary, China. *Mar Biol* 154:997–1007
- Chen GC, Ye Y, Lu CY (2007) Changes of macro-benthic faunal community with stand age of rehabilitated *Kandelia candel* mangrove in Jiulongjiang Estuary, China. *Ecol Eng* 31:215–224
- Chen GC, Ye Y, Lu CY (2008) Seasonal variability of leaf litter removal by crabs in a *Kandelia candel* mangrove forest in Jiulongjiang Estuary, China. *Estuar Coast Shelf Sci* 79: 701–706
- Emmerson WD, McGwynne LE (1992) Feeding and assimilation of mangrove leaves by the crab *Sesarma meineri* de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. *J Exp Mar Biol Ecol* 157:41–53
- Ferreira TO, Otero XL, Vidal-Torrado P, Macías F (2007) Effects of bioturbation by root and crab activity on iron and sulfur biogeochemistry in mangrove substrate. *Geoderma* 142:36–46
- Guan SY (1986) Soil enzymes and its methodology. Agricultural Press, Beijing, p 274–340
- Halstead RL, Mckercher RB (1975) Biochemistry and cycling phosphorus. In: McLaren AD, Paul EA (eds) *Soil biochemistry*, Vol 4. Marcel Dekker, New York, NY, p 31–63
- He B, Wen GY, Yuan X, Liang H, Liu S (2002) Studies on soil physical and chemical properties and enzyme activities of different mangrove communities in Yingluo Bay of Guangxi. *Sci Silvae Sin* 38:21–26 (in Chinese)
- Kristensen E (2008) Mangrove crabs as ecosystem engineers, with emphasis on sediment processes. *J Sea Res* 59:30–43
- Kuprevich VF, Shcherbakova TA (1971) Comparative enzymatic activity in diverse types of soil. In: McLaren AD, Skujins J (eds) *Soil biochemistry* Vol 2. Marcel Dekker, New York, NY, p 167–201
- Kwok PW, Lee SY (1995) The growth performances of two mangrove crabs, *Chiromanthes bidens* and *Parasesarma plicata* under different leaf litter diets. *Hydrobiologia* 295: 141–148
- Lee SY (1997) Potential trophic importance of the faecal material of the mangrove sesarimid crab *Sesarma messa*. *Mar Ecol Prog Ser* 159:275–284
- Lee KH, Moran MA, Benner R, Hodson RE (1990) Influence of soluble components of red mangrove (*Rhizophora man-*

- gle) leaves on microbial decomposition of structural (lignocellulosic) leaf components in seawater. *Bull Mar Sci* 46: 374–386
- Li MS (1997) Nutrient dynamics of a Futian mangrove forest in Shenzhen, South China. *Estuar Coast Shelf Sci* 45: 463–472
- Liu M, Hou LJ, Xu SY, Yu J, Ou DN, Liu QM (2005) Experimental simulation of the effects of macrobenthos on the microcycling of nitrogen in the Yangtze estuarine and tidal flat ecosystem. *Acta Ecol Sin* 25:1132–1137
- Marchand C, Baltzer F, Lallier-Vergès E, Albéric P (2004) Pore-water chemistry in mangrove sediments: relationship with species composition and developmental stages (French Guiana). *Mar Geol* 208:361–381
- Marchand C, Disnar JR, Lallier-Vergès E, Lottier N (2005) Early diagenesis of carbohydrates and lignin in mangrove sediments subject to variable redox conditions (French Guiana). *Geochim Cosmochim Acta* 69:131–142
- Mchenga ISS, Mfilinge PL, Tsuchiya M (2007) Bioturbation activity by the grapsid crab *Helice formosensis* and its effects on mangrove sedimentary organic matter. *Estuar Coast Shelf Sci* 73:316–324
- Micheli F (1993) Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. *J Exp Mar Biol Ecol* 171:165–186
- Nerot C, Meziane T, Provost-Govrich A, Rybarczyk H, Lee SY (2009) Role of grapsid crabs, *Parasesarma erythroductyla*, in entry of mangrove leaves into an estuarine food web: a mesocosm study. *Mar Biol* 156:2343–2352
- Olafsson E, Ndaro SGM (1997) Impact of the mangrove crab *Uca annulipes* and *Dotilla fenestrata* on meiobenthos. *Mar Ecol Prog Ser* 158:225–231
- Pelegri AP, Nielsen LP, Blackburn TH (1994) Denitrification in estuarine sediment stimulated by irrigation activity of the amphipod *Corophium volutator*. *Mar Ecol Prog Ser* 105: 285–290
- Posey MH (1987) Influence of relative mobilities on the composition of benthic communities. *Mar Ecol Prog Ser* 39: 99–104
- Rahayu D, Ng PKL (2010) Revision of the *Parasesarma plicatum* (Latreille, 1803) species-group (Crustacea: Decapoda: Brachyura: Sesarmidae). *Zootaxa* 2327:1–22
- Robertson AI (1986) Leaf-burying crabs: their influence on energy flow and export mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *J Exp Mar Biol Ecol* 102:237–248
- Robertson AI, Daniel PA (1989) The influence of crabs on litter processing in high intertidal mangrove forest in tropical Australia. *Oecologia* 78:191–198
- Sheue CR, Liu HY, Yong JWH (2003) *Kandelia obovata* (Rhizophoraceae), a new mangrove species from Eastern Asia. *Taxon* 52:287–294
- Smith TJ, Boto KG, Frusher SD, Giddins RL (1991) Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuar Coast Shelf Sci* 33:419–432
- Strauss EA, Lamberti GA (2000) Regulation of nitrification in aquatic sediments by organic carbon. *Limnol Oceanogr* 45:1854–1859
- Tam NFY, Wong YS (2000) Spatial variation of heavy metals in surface sediments of Hong Kong mangrove swamps. *Environ Pollut* 110:195–205
- Thongtham N, Kristensen E (2005) Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neopisesarma versicolor*) offered different food sources. *Estuar Coast Shelf Sci* 65:213–222
- Volkenborn N, Hedtkamp SIC, van Beusekom JEE, Reise K (2007) Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuar Coast Shelf Sci* 74:331–343
- Werry J, Lee SY (2005) Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. *Mar Ecol Prog Ser* 293:165–176
- Zhang Y, Lin P (1999) The seasonal and spatial dynamics of soil enzyme activities under *Kandelia candel* mangrove forest. *J Xiamen Univ* 38:129–136
- Zhang YM, Wu N, Zhou GY, Bao WK (2005) Changes in enzyme activities of spruce (*Picea balfouriana*) forest soil as related to burning in the Eastern Qinghai-Tibetan Plateau. *Appl Soil Ecol* 30:215–225

Editorial responsibility: Pei-Yuan Qian,
Kowloon, Hong Kong SAR

Submitted: March 13, 2010; Accepted: October 4, 2010
Proofs received from author(s): November 25, 2010