



Sulfur biological cycle of the different *Suaeda salsa* marshes in the intertidal zone of the Yellow River estuary, China

Zhigao Sun^{a,*}, Xiaojie Mou^{a,b}, Hongli Song^{a,b}, Huanhuan Jiang^{a,b}

^a Key Laboratory of Coastal Zone Environmental Processes, Yantai Institute of Coastal Zone Research (YIC), Chinese Academy of Sciences (CAS); Shandong Provincial Key Laboratory of Coastal Zone Environmental Processes, YICCAS, Yantai, Shandong 264003, PR China

^b University of Chinese Academy of Sciences, Beijing 100049, PR China

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ABSTRACT

To evaluate the sulfur (S) biological cycle status in the marshes of the intertidal zone, this study explored the S biogeochemical processes in the two *Suaeda salsa* marshes [middle *S. salsa* marsh (MSM) and low *S. salsa* marsh (LSM)] of the Yellow River estuary during April 2008 to November 2009. Results showed that soil S fluctuated seasonally and varied with depth in both MSM and LSM. The variations in S content in different parts of plant were significantly influenced by water and salinity. The *S. salsa* litter in MSM and LSM released S to the decomposition environment throughout the year. The S absorption coefficients of *S. salsa* in MSM and LSM were very low (0.0031 and 0.0004, respectively), while the S biological cycle coefficients were high (0.9014 and 0.8625, respectively). The S turnovers among compartments of MSM and LSM indicated that the uptake amounts of roots were 1.237 and 0.160 g m⁻² yr⁻¹ and the values of aboveground parts were 3.885 and 1.276 g m⁻² yr⁻¹, the re-translocation quantities from aboveground parts to roots were 2.770 and 1.138 g m⁻² yr⁻¹, the translocation amounts from roots to soil were 0.154 and 0.018 g m⁻² yr⁻¹, the translocation quantities from aboveground living bodies to litter were 1.115 and 0.138 g m⁻² yr⁻¹, and the annual return quantities from litter to soil were less than 1.096 and 0.188 g m⁻² yr⁻¹, respectively. Although S was not a limiting nutrient in *S. salsa* marshes, its high biological cycle rate might significantly inhibit the production and emission of methane (CH₄), which had important significances to reduce CH₄ emission from the Yellow River estuary. The S quantitative relationships determined in the compartment model might provide some scientific basis for us to reveal the special inhibition mechanism in future studies.

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1. Introduction

Sulfur (S) is the fourth important nutrient [after nitrogen (N), phosphorus (P) and potassium (K)], which plays an important role in many biogeochemical processes, such as participating in the composition of protein, aminophenol and chlorophyll, controlling the metabolism of carbohydrates in the photosynthesis process, and influencing the respiration and the stress-resistance of plants (Lu, 2003; Li et al., 2007a). The S cycle is one of the most complex cycles in wetland ecosystems, which is responsible for a series of important biogeochemical processes, such as carbon mineralization, water acidification and pyrite formation (Nedwell and

Watson, 1995; Mandernack et al., 2000). There has been increasing interest in understanding the S cycle in wetland ecosystems because high inputs of organic matter into wetland soils, along with oxic surface and anoxic subsurface zones, potentially allow S to play a critical role in the biogeochemistry of wetlands (Giblin and Wieder, 1992).

Many studies have been conducted on the processes of the S cycle in different wetland ecosystems, such as salt marshes (Thamdrup et al., 1994; Madureira et al., 1997; Zhou et al., 2007), freshwater marshes (Spratt and Morgan, 1990; Küsel et al., 2001; Liu and Li, 2008), peatlands (Wieder and Land, 1988; Mandernack et al., 2000) and mangrove swamps (Zhang, 1996; Lallier-verges et al., 1998; Ferreira et al., 2007). Some studies adopted S isotope (³⁴S) techniques to identify the sources of organic matter (Peterson et al., 1985; Moncreiff and Sullivan, 2001) or to reconstruct the historical patterns of S cycle in wetlands (Bottrell and Coulson, 2003). Tidal marshes are very important in coastal zones, which are sensitive to global climate change and human activities. The sulfate (SO₄²⁻) content in tidal marshes is very high, and the dynamic equilibrium of SO₄²⁻ and its reduction products constitute the special S

* Corresponding author at: Key Laboratory of Coastal Zone Environmental Processes, Yantai Institute of Coastal Zone Research (YIC), Chinese Academy of Sciences (CAS); Shandong Provincial Key Laboratory of Coastal Zone Environmental Processes, YICCAS, Yantai, Shandong 264003, PR China. Tel.: +86 0535 2109121; fax: +86 0535 2109000.

E-mail address: zgsun@yic.ac.cn (Z. Sun).

cycle system of tidal marshes (Xing et al., 2007). However, information on the processes of the S cycle in tidal marshes remains limited. In addition, current studies mostly focus on a certain process of the S cycle, while systematic and experimental studies are lacking. The compartment model has been widely and successfully applied in previous research and is a common approach to study the element cycles of ecosystems (Reuss and Innis, 1977; Wallance et al., 1978). Most compartment model studies have, however, focused on grassland ecosystems (Reuss and Innis, 1977; Li and Redmann, 1992; Li et al., 2003), forest ecosystems (Liu and Yu, 2005; Wu et al., 2006) and freshwater marsh ecosystems (Sun and Liu, 2007; Liu and Li, 2008), and information on the S cycle of tidal marshes remains scarce.

The Yellow River is well known as a sediment-laden river. Every year, approximately 1.05×10^7 tons of sediment is carried to the estuary (Cui et al., 2009) and deposited in the slow flowing landform, resulting in vast floodplain and special marsh landscape (Xu et al., 2002). Sediment deposition is an important process for the formation and development of tidal marshes in the Yellow River Delta. The deposition rate of sediment in the Yellow River not only affects the formation rate of tidal marshes, but also influences the water or salinity gradient and the succession of plants from the land to the sea. Tidal marsh is the main marsh type, with an area of 964.8 km², accounting for 63.06% of the total area of the Yellow River Delta (Cui et al., 2009). *Suaeda salsa*, an annual C₃ plant, is one of the most prevalent halophytes in the tidal marshes of the Yellow River estuary. As a pioneer plant, it has strong adaptations to environmental stresses, such as high salinity, flooding and sediment burial (Han et al., 2005). In the *S. salsa* distribution area, two phenotypes are generally formed in the middle marsh and low marsh, respectively, due to the differences of water and salinity status. However, information on elemental biogeochemical processes of the tidal marshes in the Yellow River estuary is limited and the systematic and comparative studies on the S cycle of the two *S. salsa* marshes are still lacking.

In this paper, the S biological cycle of the two *S. salsa* marshes in the intertidal zone of the Yellow River estuary was systemically and comparatively studied. The *S. salsa* marsh was divided into four S compartments, including aboveground living body, root, litter and soil. The objectives of this paper were (i) to examine the distribution characteristics of S in the two plant-soil systems, (ii) to determine the S turnovers among the compartments of *S. salsa* marshes, and (iii) to establish the S biological cycle compartment model of *S. salsa* marshes and evaluate the S cycle status.

2. Materials and methods

2.1. Study site

This study was conducted from April 2008 to November 2009 at two experimental plots (each 400 m × 400 m) in the *S. salsa* distribution area [middle *S. salsa* marsh (MSM) and low *S. salsa* marsh (LSM)] in the intertidal zone of the Yellow River estuary, located in the Nature Reserve of Yellow River Delta (37°35'N–38°12'N, 118°33'E–119°20'E) in Dongying City, Shandong Province, China. The nature reserve is of typical continental monsoon climate with distinctive seasons, and the average temperature in spring, summer, autumn and winter are 10.7 °C, 27.3 °C, 13.1 °C and –5.2 °C, respectively. The annual average temperature is 12.1 °C, the frost-free period is 196 d and the effective accumulated temperature is about 4300 °C. Annual evaporation is 1962 mm and annual precipitation is 551.6 mm, with about 70% of precipitation occurring between June and August. The soils in the study area are dominated by intrazonal tide soil and salt soil (Tian et al., 2005), and the

main vegetations include *Phragmites australis*, *S. salsa*, *Triarrhena sacchariflora*, *Myriophyllum spicatum* and *Tamarix chinensis*.

S. salsa generally germinates in late April, blooms in July, matures in late September and completely dies in late November (Gu, 1998). The tide in the intertidal zone of the Yellow River estuary is irregular semidiurnal tide and the mean tidal range is 0.73–1.77 m (Li et al., 1991). The *S. salsa* in the low marsh generally distributed in the range 0.5–2 km (Li et al., 1991), at a very low elevation of –1.0 to 0.9 m (Song et al., 2010). Thus, the *S. salsa* in LSM is frequently and greatly inundated by the tide, which caused the moisture and salinity of topsoil is high (Table 1). Also, the *S. salsa* in LSM is very short (average height during growth peak, 33.64 ± 7.96 cm) and its leaf and stem are red-violet during the growth season. Comparatively, the *S. salsa* in the middle marsh generally distributed in the range 1–4 km (Li et al., 1991), at a higher elevation of 1.0–2.5 m (Song et al., 2010). Thus, the *S. salsa* is infrequently and irregularly flooded by the tide, which caused the moisture and salinity of topsoil is low (Table 1). Differently, the *S. salsa* in MSM is tall (average height during growth peak, 52.51 ± 9.91 cm) and its leaf and stem are green. The comparison of physical and chemical properties of topsoil (0–20 cm) in MSM and LSM are shown in Table 1.

2.2. Study methods

2.2.1. Collection of soil samples

Since the substantial root of *S. salsa* was most in upper 15 cm and most of the S transfers between soil and plant occurred in the upper zone (Mou, 2010), the seasonal dynamics of total sulfur (TS) content in topsoil (0–15 cm) was studied at the two experimental plots from April to November in 2009. Ten soil samples were collected per month at a sampling depth of 0–15 cm and soil bulk densities were determined at the same time. The vertical distributions of TS content in the soil profile were studied in August 2008. Three soil profiles (depth: 60 cm) were sampled at each experimental plot at 10 cm interval, with 18 samples in total. The bulk density of each soil layer was determined simultaneously. The S stock (T_n , kg m⁻²) in soil was calculated by Eq. (1):

$$T_n = \sum_{i=1}^n W_i \times S_i \times \frac{h}{10} \quad (1)$$

where W_i (g cm⁻³) is the soil bulk density of the i layer, S_i (%) is the TS content in the i layer and h is soil depth (10 cm).

2.2.2. Determination of litter and biomass

Litter production, aboveground biomass (AGB) and belowground biomass (BGB) were determined using a quadrat method (50 cm × 50 cm, five replications) at the two experimental plots from May to November in 2008, with a sampling frequency of 20 d. On the sampling dates, the aboveground part of plant was clipped near the ground, and the stem, leaf and standing dead litter were separated immediately in the laboratory. The new litter distributed in the quadrat was also collected. Roots in the quadrat were dug out and washed carefully. All samples were weighed after being dried at 80 °C for 48 h. In the growing season, since little parts of the plant or the litter could be carried away or redistributed in tidal marshes during the ebb and flow, the AGB and litter production were standing crops.

2.2.3. Determination of litter decomposition rates

Litter decomposition was studied with a litterbag technique at the two experimental plots from April 2008 to November 2009. In order to weaken the fragmentation impact of snowfalls and strong winds in winter, the standing litter (collected on April 5, 2008)

Table 1
Comparison of physical and chemical properties of topsoil (0–20 cm) in MSM and LSM.

Types	Soil depth (cm)	Bulk density ^a (g cm ⁻³)	Grain composition ^a (%)	Soil moisture ^b (cm ⁻³ cm ⁻³)			pH ^a	Electrical conductivity (EC) ^b (mS cm ⁻¹)	Soil organic matter (SOM) ^a (%)	Total nitrogen (TN) ^a (mg kg ⁻¹)	Total phosphorus (TP) ^a (mg kg ⁻¹)	Ammonium nitrogen (NH ₄ ⁺ -N) ^a (mg kg ⁻¹)	Nitrate nitrogen (NO ₃ ⁻ -N) ^a (mg kg ⁻¹)
				Clay	Silt	Sand							
MSM	0–10	1.33 ± 0.03	8.67 ± 0.66	49.67 ± 0.53	41.66 ± 0.14	0.289 ± 0.013	8.55 ± 0.06	5.58 ± 2.80	1.07 ± 0.06	455.90 ± 162.07	521.09 ± 49.91	2.82 ± 0.95	1.36 ± 0.47
	10–20	1.29 ± 0.12	12.17 ± 0.03	64.67 ± 0.03	23.15 ± 0.06	0.375 ± 0.005	9.03 ± 0.42	11.52 ± 2.29	0.56 ± 0.08	474.25 ± 102.45	551.56 ± 0.94	2.58 ± 0.89	1.29 ± 0.11
LSM	0–10	1.64 ± 0.03	10.14 ± 0.04	57.13 ± 0.14	32.74 ± 0.18	0.346 ± 0.031	8.86 ± 0.04	18.07 ± 0.43	0.93 ± 0.04	505.45 ± 70.22	527.32 ± 10.69	2.01 ± 0.67	0.76 ± 0.07
	10–20	1.61 ± 0.01	9.77 ± 0.01	65.98 ± 0.07	24.24 ± 0.08	0.382 ± 0.006	8.97 ± 0.08	7.85 ± 0.75	0.89 ± 0.02	492.25 ± 41.95	490.67 ± 16.14	1.36 ± 0.27	0.87 ± 0.01

^a Values were means (±S.E.) of samples ($n = 3$ for bulk density, grain composition and pH; $n = 5$ for SOM, TN, TP, NH₄⁺-N and NO₃⁻-N) collected from middle *Suaeda*, *salsola* marsh (MSM) and low *S. salsa* marsh (LSM) in May 2009.

^b Values were means (±S.E.) of the observation/measurement results (soil moisture and EC) from April to November in 2009 ($n = 8$).

was selected for use in this study. The two types of *S. salsa* litter were washed in distilled water, cut into 10 cm segments and oven-dried at 80 °C for 48 h. Each 20 cm × 20 cm litterbag was made of nylon netting (0.5 mm mesh) and filled with 15 g litter (Oven-dried weight). On 21 April 2008, the litterbags were randomly placed on each experimental plot of *S. salsa* community. In order to prevent the litterbag from being carried away by the tide, the litterbags were attached to a pipe embedded approximately 1.0 m into the soil. The experiment included nine sampling times (I, 11 July 2008; II, 9 August 2008; III, 20 September 2008; IV, 20 October 2008; V, 15 November 2008; VI, 26 April 2009; VII, 25 June 2009; VIII, 25 August 2009; IX, 12 November 2009), and on each sampling date, three or four litterbags were retrieved from each plot. After retrieval, these litterbags were immediately taken back to the laboratory, and the plant roots, lichen, soil and macro-invertebrates were removed from the remaining litter. All litterbags were further cleaned gently in deionized water and weighed after being dried at 80 °C for 48 h. Litter standing crop (X_{st} , g m⁻²), mass loss (R , %) and decomposition rate (d^{-1}) were calculated by Eqs. (2)–(4) (Olson, 1963; Liu et al., 2000).

$$X_{st} = \frac{x}{(1 - \beta)} \quad (2)$$

$$R = \left[\frac{W_t - W_0}{W_0} \right] \times 100\% \quad (3)$$

$$\frac{W_t}{W_0} = e^{-kt} \quad (4)$$

where β (%) is the residual rate of litter, x (g m⁻² yr⁻¹) is the annual average production of litter, W_0 (g) is the original dry mass, W_t (g) is the dry mass at time “ t ”, k is the decay constant and t (d) is decomposition time in days.

The calculation of X_{st} is based on the following presumptions (Liu et al., 2000): (i) ecosystem is very stable and decomposition is the only means of litter loss; (ii) litter standing crop changes dynamically and the value is the net sum of accumulation and decomposition amounts; (iii) although litter decomposition rate has significant seasonal change, the annual decomposition rate is generally steady. In the context, the annual decomposition rate can be regarded as a constant (α) and the residual rate (β) is calculated by $1 - \alpha$. However, *S. salsa* marsh is an open ecosystem, although litter produced during the growing season decomposes *in situ*, a portion may be exported or redistributed by the tide. In this study, the litter standing crop calculated by Eq. (2) was a theoretical maximum and it was higher than the actual value. Moreover, since the definite litter amount carried away by the tide was not quantified, the S standing crop estimated by litter standing crop and average S content was also a theoretical maximum, and ‘<<’ was used to show that the actual value was far less than the theoretical one. After 1 year, the annual S translocation amount from litter to soil was calculated by the variation of S stock in litter.

2.2.4. Measurement of soil and plant samples

Soil and plant samples were ground (<0.25 mm) using a Wiley mill and analyzed for Total carbon (TC), TS contents by element analyzer (Elementar Vario Micro, German). Soil organic matter (SOM) was measured by K₂Cr₂O₇ oxidation method (The Committee of Agro-chemistry of the Chinese Society of Soil Science, 1983).

2.2.5. Calculation of S stock and turnover

The S biological cycle characteristics of *S. salsa* marsh ecosystems can be expressed by absorption coefficient (A) and cycle

coefficient (C), and their calculations were based on Eqs. (5) and (6) (Chen and Lindley, 1983):

$$A = \frac{PAS}{SS} \quad (5)$$

$$C = \frac{PRS}{PAS} \quad (6)$$

where PAS ($\text{g m}^{-2} \text{yr}^{-1}$) is the S absorption amount of plant, PRS ($\text{g m}^{-2} \text{yr}^{-1}$) is the S return amount of plant and SS (g m^{-2}) is the S stock in soil (0–60 cm).

According to the calculation method of Li and Redmann (1992), the S stocks in plant compartments (S_n , g m^{-2}) and the S turnovers among plant compartments (F_a , $\text{g m}^{-2} \text{yr}^{-1}$) were calculated by Eqs. (7) and (8):

$$S_n = C_n \times B_n \quad (7)$$

$$F_a = C_a \times B_a \quad (8)$$

where C_n (mg kg^{-1}) is the S content of compartment, B_n (g m^{-2}) is the biomass in the compartment, C_a (mg kg^{-1}) is the S content as AGB reaches maximum and B_a (g m^{-2}) is the maximum AGB.

Litter S stock (F_{da} , g m^{-2}) in aboveground dead plant, the S re-translocation quantities from aboveground parts to roots (F_{rt} , $\text{g m}^{-2} \text{yr}^{-1}$) and the S uptake quantities of roots (F_r , $\text{g m}^{-2} \text{yr}^{-1}$) were calculated by Eqs. (9)–(11):

$$F_{da} = C_d \times B_a \quad (9)$$

$$F_{rt} = F_a - F_{da} \quad (10)$$

$$F_r = F_a - F_{rt} + \Delta S_u \quad (11)$$

where C_d (mg kg^{-1}) is the S content of aboveground dead plant, B_a (g m^{-2}) is the quantity of aboveground dead plant and ΔS_u (g m^{-2}) is the net S increment of root in the growing season.

The S translocation amounts from litter to soil (F_s , $\text{g m}^{-2} \text{yr}^{-1}$) and from roots to soil (F_T , $\text{g m}^{-2} \text{yr}^{-1}$) were calculated by Eqs. (12)–(14):

$$F_s = F_l - F_y \quad (12)$$

$$F_T = T \cdot B_{\max} \cdot C_{\max} \quad (13)$$

$$T = \frac{P_m}{B_{\max}} \quad (14)$$

where F_l (g m^{-2}) is composed of F_{da} and F_p , F_p (g m^{-2}) is the S stock in un-decomposed litter previously accumulated *in situ*, F_y (g m^{-2}) is the S stock in un-decomposed litter after a period of time, T (%) is the turnover rate of roots, P_m (g m^{-2}) is the deficit of maximum BGB and minimum BGB, B_{\max} (g m^{-2}) is the maximum BGB and C_{\max} (mg kg^{-1}) is the S content as BGB reaches maximum.

2.3. Statistical analysis

The samples were presented as means of the replications, with standard error (S.E.). The analysis of variance (ANOVA) tests (SPSS for windows 11.0) was employed to determine if samples differed significantly ($p < 0.05$).

3. Results and discussion

3.1. S dynamics, distribution and stock in soils

3.1.1. Seasonal dynamics of S in topsoil

Similar seasonal variations of TS content were observed in MSM and LSM topsoil, but only the former was significantly different during the growing season ($p < 0.05$) (Fig. 1A). TS content generally decreased before 26 May and increased from 26 May to 31 July.

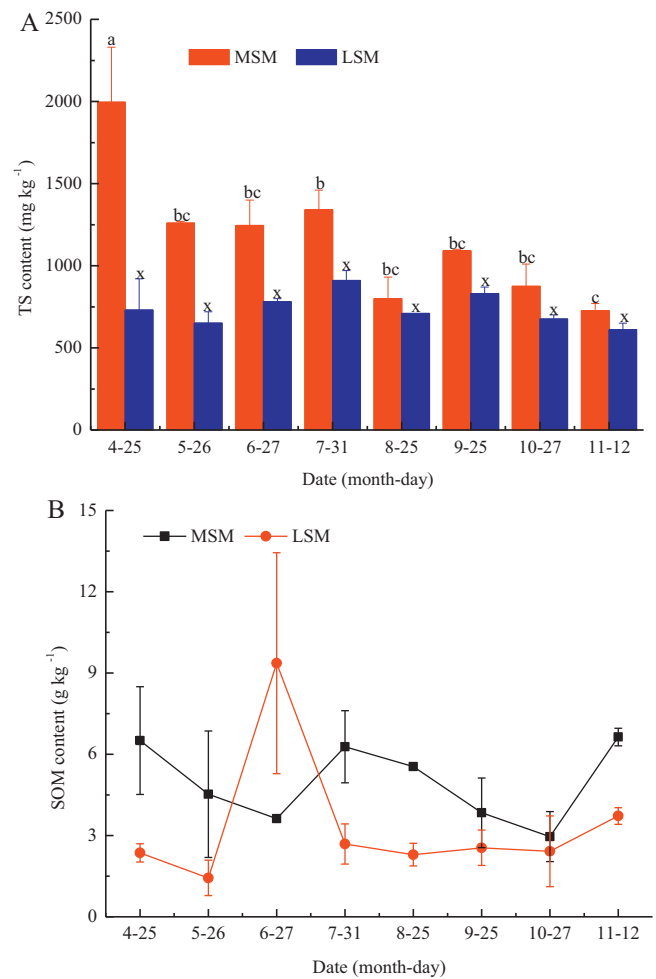


Fig. 1. Seasonal dynamics of TS (A) and SOM (B) content in topsoil (0–15 cm) of *Suaeda salsa* marshes. Values were means (\pm S.E., $n = 10$). TS, total sulfur; SOM, soil organic matter; MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh. Bars with different letters (a, b for MSM) were significantly different at the level of $p < 0.05$. Bars with same letter (x for LSM) were not significantly different at the level of $p < 0.05$.

Thereafter, the value increased slightly and decreased significantly after 25 September. The maximums of TS content in MSM and LSM topsoil were observed on 25 April and 31 July, respectively, while the minimums occurred on 12 November. The seasonal variations of TS content in MSM and LSM topsoil were probably related to the distribution of SOM, the mineralization of organic S, plant absorption, and the ebb and flow of the tide in different periods (Hao et al., 2003; Li and Liu, 2007; Li et al., 2009; Mou et al., 2010). Significantly higher TS contents were observed in MSM topsoil during the growing season compared to LSM topsoil ($p < 0.05$) (Fig. 1A), which was mainly dependent on the effects of tidal inundation. Compared with MSM, the LSM was more frequently affected by the tide, which was favorable for the formation of anoxic conditions in topsoil (Mou, 2010). Under anoxic conditions, the SO_4^{2-} in topsoil could be easily deoxidized, which might induce significant S loss although a portion sulfide could be retained in the topsoil by organics or metals (Li et al., 2009). The differences of TS content between the two marshes were also related to SOM (Wang et al., 2003). Although there were no significant correlations between TS and SOM in MSM and LSM topsoil ($p > 0.05$), the SOM contents in LSM were lower than those in MSM during the growing season except on 27 June (Fig. 1B), implying that the topsoil in LSM was generally unfavorable for the conservation of S (Wang et al., 2003; Li et al.,

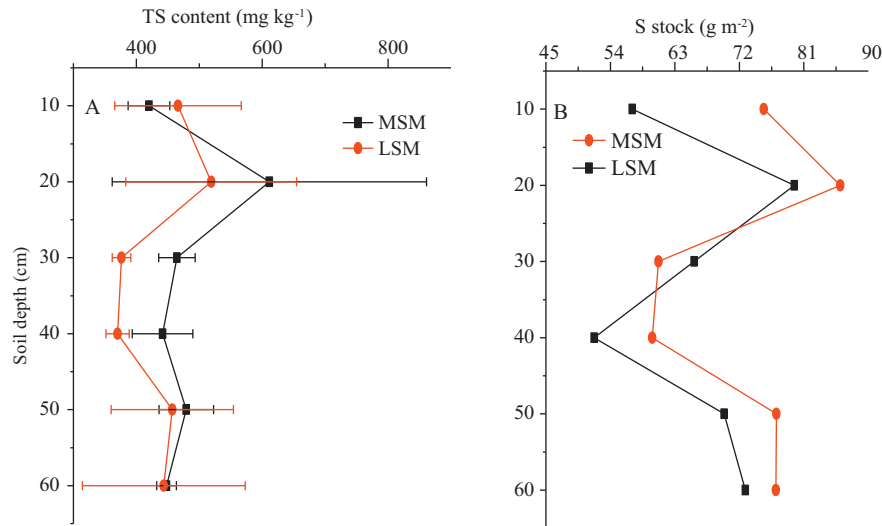


Fig. 2. Vertical distributions of TS content (A) and S stock (B) in the soil profile (0–60 cm) of *Suaeda salsa* marshes. Values were means (\pm S.E., $n=3$). MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

2009). Studies showed that the S stocks in MSM and LSM topsoils (0–15 cm) during the growing season were 98.456–270.924 and 98.653–147.171 g m^{-2} , respectively.

3.1.2. Vertical distribution of S in soil

Similar vertical distributions of TS content were observed in the soil profile (0–60 cm) of MSM and LSM (Fig. 2A). For both, the TS content increased at 0–20 cm depth and decreased significantly at 20–40 cm depth, with the maximums and minimums being observed at 20 cm and 40 cm depths, respectively. Then, TS in both soils increased at 40–50 cm depth and decreased slightly at 50–60 cm depth. Similar vertical distributions of S stock were observed in the soil profile of MSM and LSM (Fig. 2B), with the maximums and minimums occurring at 20 cm and 40 cm depths, respectively. The vertical distributions of TS content and S stock were mainly dependent on the spatial heterogeneity of SOM (Wang et al., 2003; Li et al., 2009). Higher TS contents and lower S stocks were generally observed in MSM compared to LSM (Fig. 2). The low TS contents in LSM, as mentioned before, was mainly dependent on the active SO_4^{2-} reduction reaction under anoxic conditions, while high S stock in LSM might be related to the high bulk density of different soil layers (Table 1). Calculations indicated that, in August 2008, the total S stocks in MSM and LSM soils (0–60 cm) were 396.864 and 436.291 g m^{-2} , respectively.

3.2. S dynamics, stocks and turnovers in plants

3.2.1. Dynamics of plant biomass

Significant seasonal variations of AGB and BGB of *S. salsa* were observed in MSM and LSM ($p < 0.05$) (Fig. 3A and B). MSM biomass increased with the improvement of hydrothermal conditions since 17 May and reached the maximums on 31 August (AGB) and 9 August (BGB). Thereafter, AGB and BGB decreased gradually with the coming of autumn, with the minimums being observed on 15 November. The AGB and BGB in LSM also increased since 17 May, attaining the maximums on 31 August. Then, both decreased gradually and reached the minimums on 15 November. Significantly higher AGB and BGB of *S. salsa* were observed in MSM compared to LSM ($p < 0.05$). Significantly seasonal variations of stem and leaf biomasses of *S. salsa* were also observed in MSM and LSM (Fig. 3C and D), with the maximums occurring on 31 August. The stem and

leaf biomasses of *S. salsa* in MSM were also higher than those in LSM, but only the stem biomass was significantly different ($p < 0.05$).

Water and salinity gradients are the most typical environmental factors in the intertidal zone of the Yellow River estuary, which might influence plant biomass directly. Soil moisture influences the biomass accumulation of plants in both positive and negative ways. Wang et al. (2008a) indicated that proper water stress favored the biomass accumulation of *Calamagrostis angustifolia* in the Sanjiang Plain, while severe water stress had significant restraint on that of *Zoysia* (Wang et al., 2009). He and Li (2008) found that salinity stress had significant effects on the growth, biomass accumulation and allocation of *Salsola nitraria* and *Halogeton glomeratus*. Similar results were drawn by Rawat and Banerjee (1998) who showed that low salt concentrations generally stimulated the growth and biomass production of *Dalbergia sissoo*, while high salt concentrations were significantly inhibiting. Song (2012) also indicated that the growth of *S. salsa* was significantly stunted as it was watered with high concentration saline water. In this study, the growth of *S. salsa* was mainly influenced by water and salinity stresses. The *S. salsa* in LSM was more frequently affected by the ocean currents and tides compared to MSM (Ruan et al., 2008), and it generally confronted both severe salinity stress and sea-water inundation stress, which caused its low biomass.

3.2.2. Dynamics of S content in plant

There were similar changes of TS content in the stem and leaf of *S. salsa* in MSM and LSM (Fig. 4). TS in both aboveground parts were low at the initial stage, after which the values increased and reached the maximums on 1 June. Thereafter, TS in both aboveground parts generally decreased, with the minimums occurring on 15 November. By comparison, TS in both roots were high at the initial stage and decreased gradually during the growing season. The variations of TS content in the roots and aboveground parts before 1 June were probably related to the S translocation mechanism from roots to aboveground parts at the initial stage (Li, 2007). TS content in different *S. salsa* parts in MSM and LSM differed significantly ($p < 0.01$), in the order of leaf > stem > root, indicating that the S was mainly accumulated in the leaves.

As the most typical environmental factors in the Yellow River estuary, water and salinity gradients might also influence the S accumulation in plants directly. Braekke (1990) showed that the changes in water condition (drainage) occurring in Scots pine (*Pinus*

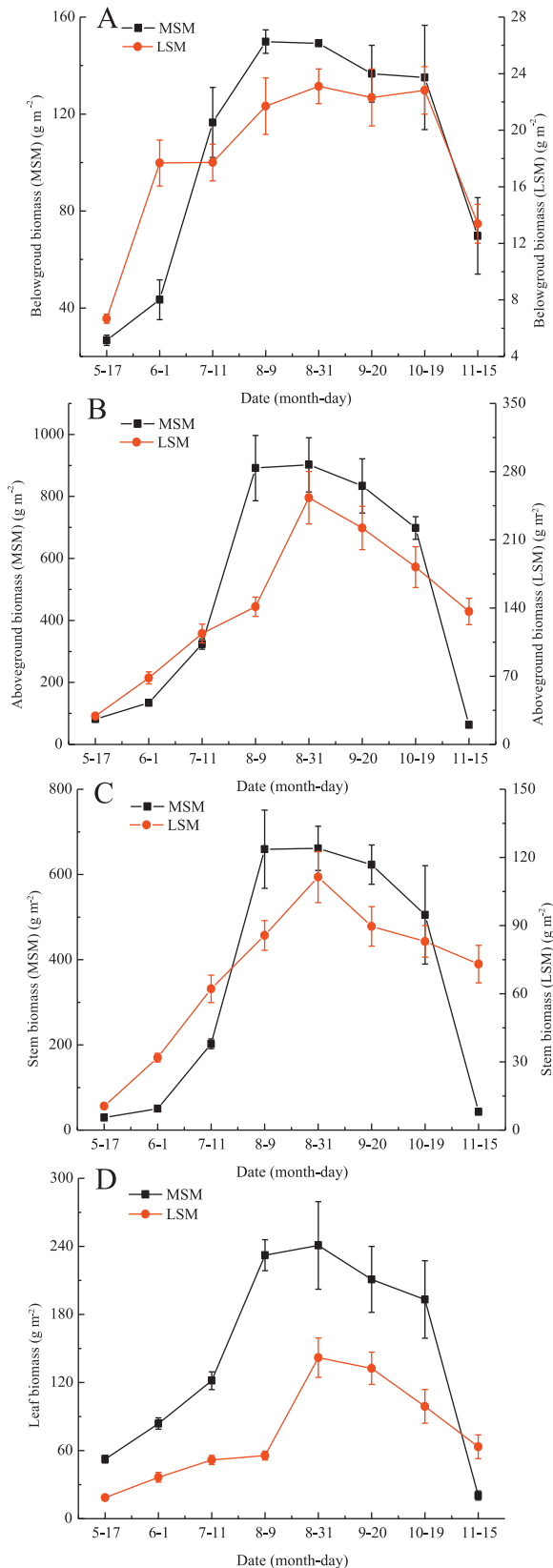


Fig. 3. Seasonal dynamics of *Suaeda salsa* biomass (A, belowground biomass; B, aboveground biomass; C, stem biomass; D, leaf biomass) in MSM and LSM. Values were means (\pm S.E., $n = 5$). MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

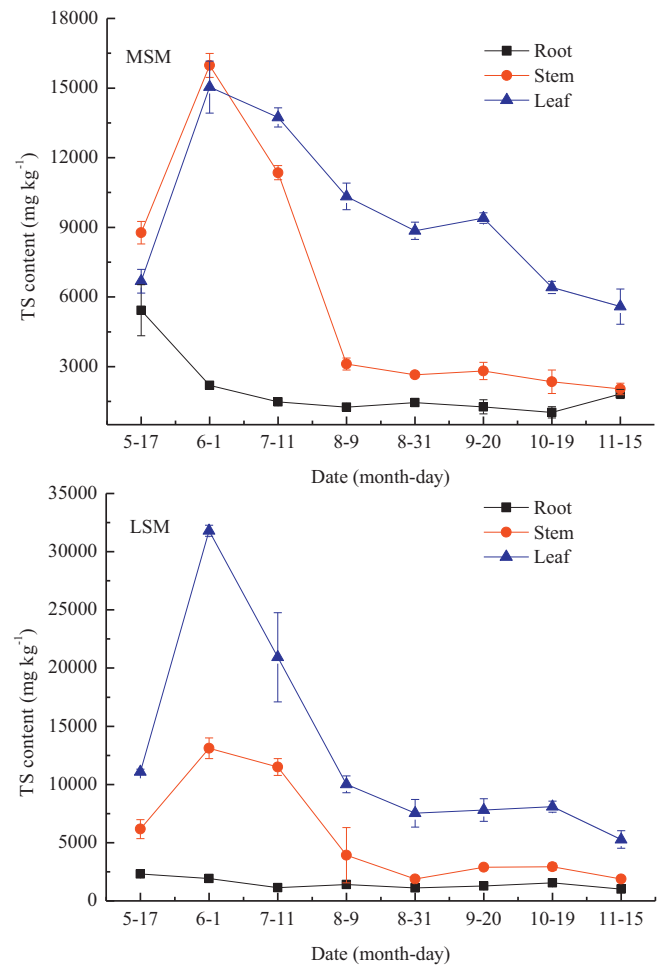


Fig. 4. Seasonal dynamics of TS content in different parts of *Suaeda salsa*. Values were means (\pm S.E., $n = 3$). MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

sylvestris) and Norway spruce (*Picea abies*) wetlands had significant influences on nutrient (N, P, K and S) accumulation. Li (2007) indicated that water condition was the key factor to induce the significant differences of S absorption and allocation between typical meadow *C. angustifolia* and marsh meadow *C. angustifolia*. Stribling and Cornwell (2001) also found that the salinity gradient in the Chesapeake Bay significantly influenced the seasonal dynamics of N, P and S in the shoots of *Spartina alterniflora*. The growth rhythm and ecological characteristics of plants might also affect S accumulation (Pevery et al., 1995). In this study, the *S. salsa* in the Yellow River estuary formed two phenotypes resulting from the differences of water and salinity gradients. The growth rhythms of the two phenotypes were different as mentioned before, which, to some extent, affected the seasonal dynamics of S in *S. salsa*. Moreover, many studies have showed that the succulence degree, peroxidase content, pigment accumulation and photosynthesis of the two phenotypes' leaves were significantly different (Liu et al., 2006; Wang et al., 2008b; Ruan et al., 2008), which might influence the absorption and allocation of S greatly. Although significantly lower TS contents were observed in LSM topsoil compared to MSM topsoil (Fig. 1A), the leaves of *S. salsa* in LSM appeared to accumulate higher S at the early summer (Fig. 4). Because the S nutrient has important influences on plant stress-resistance (Lu, 2003; Wu et al., 2007), one possible explanation is that, in order to adapt the severe environmental stresses in LSM in seedling establishment stage, the *S. salsa* may have a special strategy which can enhance

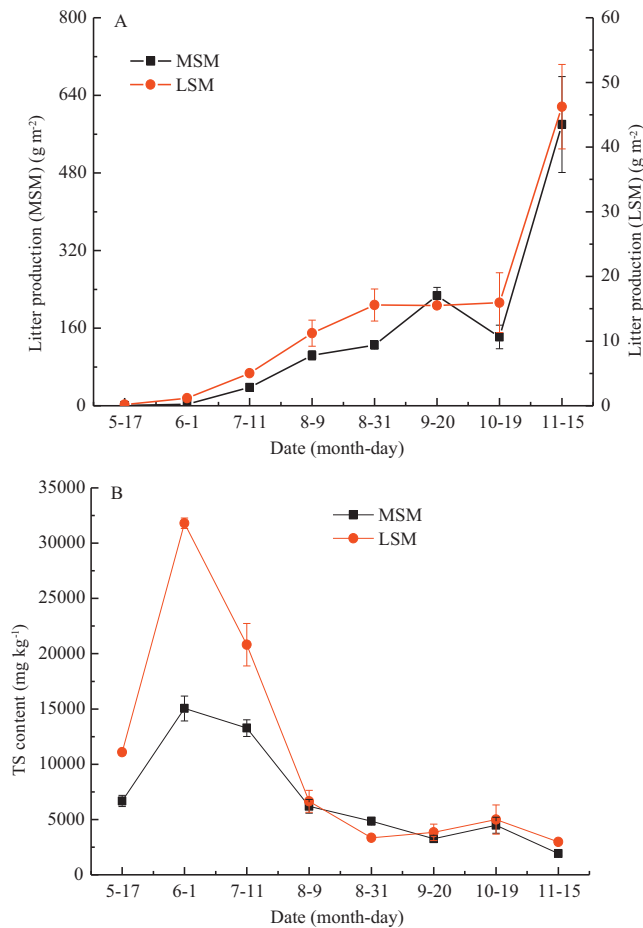


Fig. 5. Seasonal dynamics of *Suaeda salsa* litter production (A) and TS content (B). Values were means (\pm S.E., $n=3$). MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

stress-resistance and promote physiological processes (such as photosynthesis and respiration) by accumulating more S nutrient in aboveground parts (especially in the leaves) (Rausch and Wachter, 2005; Li et al., 2007a). But this presumption requires to be verified.

Studies showed that the S stocks in root, stem and leaf of *S. salsa* in MSM and LSM were 0.095–0.217, 0.087–2.297, 0.114–2.400 g m⁻² and 0.014–0.035, 0.065–0.714, 0.205–1.158 g m⁻², respectively. The S uptake amounts of aboveground parts were 3.885 and 1.276 g m⁻² yr⁻¹, the S uptake quantities of roots were 1.237 and 0.160 g m⁻² yr⁻¹, the S retranslocation amounts from aboveground parts to roots were 2.770 and 1.138 g m⁻² yr⁻¹, and the S translocation quantities from roots to soil were 0.154 and 0.018 g m⁻² yr⁻¹, respectively.

3.2.3. Dynamics of litter production and S content in litter

Similar changes of *S. salsa* litter production were observed in MSM and LSM (Fig. 5A). Both were low at the initial stage, after which the values generally increased and reached the maximums (579.90 \pm 98.91 and 46.25 \pm 5.52 g m⁻², respectively) at the final stage. Because the *S. salsa* in MSM and LSM did not completely die on 15 November, the actual litter productions were slightly more than the above values. Actually, the *S. salsa* in MSM produced significant amounts of litter at the end of the growing season, and the low litter production determined on 19 October might be related to the low litter standing crop resulting from the strong scouring action of the tide. The low litter production of *S. salsa* in LSM was

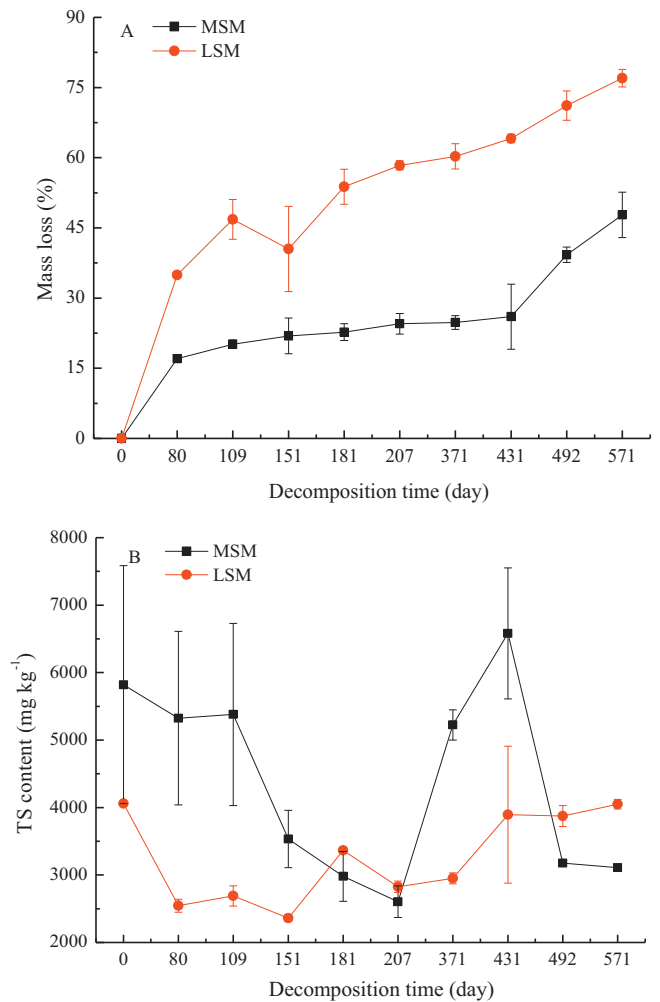


Fig. 6. Dynamics of mass loss (A) and TS content (B) during *Suaeda salsa* litter decomposition. Values were means (\pm S.E., $n=3$). MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

mainly related to its low biomass and the strong scouring action of the tide. Although the litter production of *S. salsa* in LSM was much lower than that in MSM, they had no significant difference ($p > 0.05$). Similar dynamics of TS content in *S. salsa* litter were also observed in MSM and LSM (Fig. 5B). TS in both *S. salsa* litters were low at the initial stage, after which the values generally increased and reached the maximums on 1 June. Thereafter, TS in both *S. salsa* litters generally decreased, with the minimums being observed on 15 November. Comparatively, the TS contents in LSM litter were generally higher than those in MSM litter, but they had no significant difference ($p > 0.05$). The variations of TS content in MSM and LSM litters were mainly dependent on the different S translocation mechanisms as aboveground parts withered (Mou et al., 2010). In addition, significantly higher TS contents in LSM litter were observed at the initial stage compared to MSM litter (Fig. 5B), which might be related to the high S content in the leaves of *S. salsa* in LSM as mentioned before. As the leaves withered, although some S nutrient in the litter was transferred to the other parts, a portion still could be retained. Studies indicated that the S stocks in MSM and LSM litters were 0.002–1.115 and 0.002–0.138 g m⁻², respectively, and the S translocation quantities from aboveground living bodies to litter were 1.115 and 0.138 g m⁻² yr⁻¹, respectively.

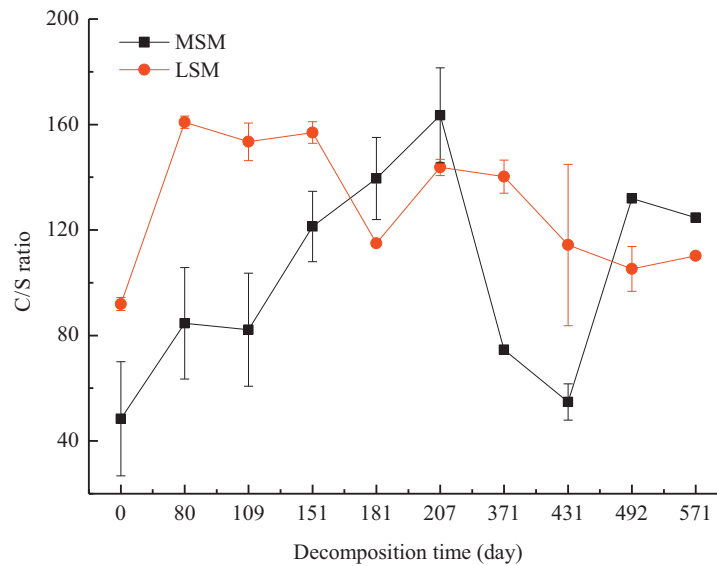


Fig. 7. Dynamics of C/S ratio in *Suaeda salsa* litter in MSM and LSM during decomposition. Values were means (\pm S.E., $n=3$). MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

3.2.4. Dynamics of litter decomposition and S content in litter

The mass loss of *S. salsa* litter in MSM and LSM generally increased during decomposition (Fig. 6A). Both litter masses lost rapidly from April to November in 2008 (0–207 d), accounting for 51.29% and 75.81% of the total loss in the experiment, respectively, which was mainly dependent on the proper hydrothermal condition during the growing season. From November 2008 to April 2009 (207–371 d), both the masses decreased slowly due to the low temperature and the mass loss only increased by 0.28% and 1.92%, respectively. After April 2009 (371 d), both the mass losses rapidly increased, and the values reached $47.78 \pm 4.86\%$ and $77.00 \pm 1.88\%$ after 571 d, respectively. Significantly higher *S. salsa* litter mass losses were observed in LSM compared to MSM during decomposition ($p < 0.01$).

The TS contents in MSM litter decreased gradually from 0 to 207 d and increased rapidly until 431 d. Then, the values rapidly decreased (Fig. 6B). By contrast, the variations of TS content in LSM litter were not significant, with the high values being observed from 431 to 571 d (Fig. 6B). During decomposition, the coefficients of variation (CV) of C/S ratio in MSM and LSM litters were 37.78% and 19.03%, respectively, indicating that the values in MSM litter had greater fluctuation than those in LSM litter (Fig. 7). Because the fluctuations of TC content in MSM and LSM litters were approximate (the CVs were 5.47% and 5.52%, respectively) but those of TS content were greatly different (the CVs were 32.70% and 20.41%, respectively), the great fluctuations of C/S ratio in MSM litter, to a great extent, were dependent on the changes of TS content. Moreover, the variations of C/S ratio in MSM and LSM litters were generally opposite to those of the corresponding TS content (Figs. 6B and 7) and significant negative correlations occurred

between them ($r = -0.969$, $p < 0.01$; $r = -0.962$, $p < 0.01$, respectively), which further indicated that the S dynamics in *S. salsa* litter had significant influence on the variations of C/S ratio. This result was similar to the conclusion reported by Li et al. (2006, 2007a). The TS contents in *S. salsa* litter in MSM and LSM during decomposition were 24.61–62.16% and 58.13–99.75% of the initial value, respectively, indicating that S might be released from the litter at all times. The increase of S in *S. salsa* litter in some periods was ascribed to the S immobilization by microbes from the S sources (such as tidewater and topsoil) in the decomposition environment (Blair, 1988). Similar result was also reported by Li et al. (2007b) who found that the increase of S in *C. angustifolia* litter was mainly related to the external biological immobilization from marsh water.

Studies showed that the decomposition rates of *S. salsa* litter in MSM and LSM were 0.3780 yr^{-1} and 1.1880 yr^{-1} , respectively (Table 2). Because the *S. salsa* litter in LSM could be decomposed completely within 1 year, the S standing crop approximated 0 g m^{-2} and the annual S return amount was about $0.188 \text{ g m}^{-2} \text{ yr}^{-1}$. By comparison, the *S. salsa* litter in MSM decomposed slowly and the annual S return amount approximated $1.096 \text{ g m}^{-2} \text{ yr}^{-1}$ (Table 2). These results indicated that the *S. salsa* litter in MSM and LSM released S throughout the year. Because the actual input amount of *S. salsa* litter in MSM and LSM were slightly more than 579.90 and 46.25 g m^{-2} as mentioned before, the theoretical S release amount should also be slightly more than 1.096 and $0.188 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively. However, since some litter was removed gradually by the tide and only part could be decomposed *in situ*, the actual S release amount might be less than 1.096 and $0.188 \text{ g m}^{-2} \text{ yr}^{-1}$ (Table 2).

Table 2
Sulfur standing crop and returning amount of *Suaeda salsa* litter in MSM and LSM.

Types	Annual input amount ($\text{g m}^{-2} \text{ yr}^{-1}$)	Annual decomposition rate (yr^{-1})	Litter standing crop (g m^{-2})	Average S content (mg kg^{-1})	S standing crop (g m^{-2})	S return amount ($\text{g m}^{-2} \text{ yr}^{-1}$)
MSM	$>579.90^a$	0.3780	$\ll 1534.13^b$	4850.0	$\ll 7.441^b$	$<1.096^c$
LSM	$>46.25^a$	1.1880	0	3261.5	0	$<0.188^c$

MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

^a Slightly more than the value.

^b Far less than the value.

^c Less than the value

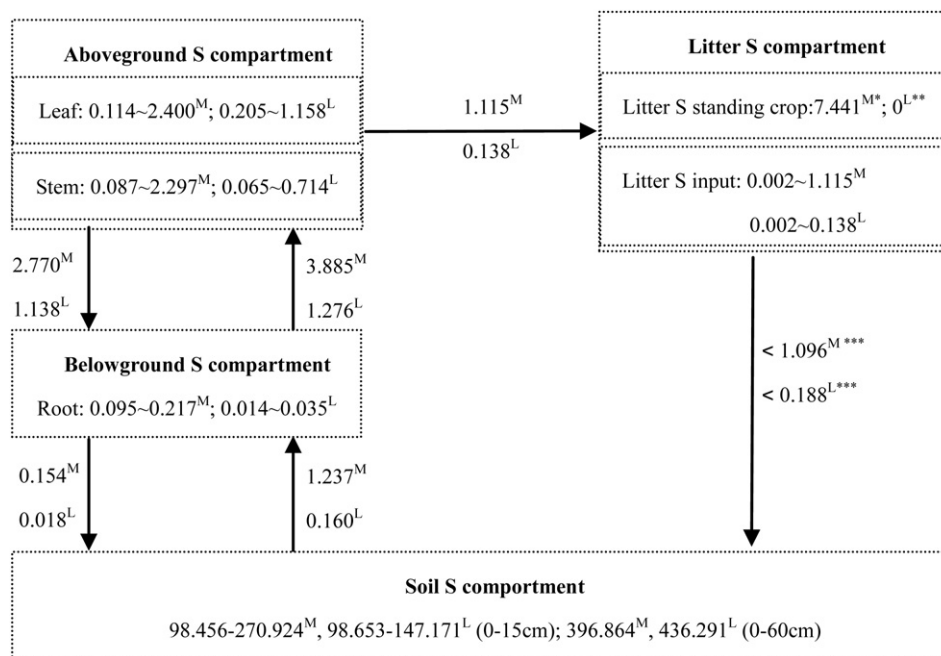


Fig. 8. Sulfur biological cycle compartment model of the *Suaeda salsa* marsh ecosystems. Numerals in panes were the S stocks of compartments (g m^{-2}); numerals above arrowhead were the S turnover among compartments ($\text{g m}^{-2} \text{ yr}^{-1}$); *Far less than the value; **approximate the value as mentioned previously; ***less than the value. ^MMSM, middle *S. salsa* marsh; ^LLSM, low *S. salsa* marsh.

3.3. S allocation and cycle in plant–soil systems

3.3.1. S allocation in plant–soil systems

The study of S allocation in the plant–soil systems of MSM and LSM showed that the aboveground living body was the main S stock of the plant subsystem, with the mean values of 2.668 and 1.078 g m^{-2} , accounting for 79.35% and 92.06% of the total S stock of the plant subsystems, respectively (Table 3). In the two plant–soil systems, the S stocks of plant subsystem were very low, accounting for only 0.84% and 0.27% of the total S stock, respectively. Soil S was the main S stock of the two plant–soil systems, accounting for 99.16% and 99.73%, respectively. The high percent of soil S indicated that it was the circulation hinge in the process of S cycle, which could prevent the S from being lost easily.

3.3.2. Establishment of S biological cycle model and assessment of S cycle status

Based on the above-mentioned studies, the compartment model on the allocation and circulation of S in *S. salsa* marshes was established, and the quantitative relationships among compartments were determined (Fig. 8). According to the compartment model, the S absorption and cycle coefficients of *S. salsa* in MSM and LSM were calculated and the values were 0.0031, 0.9014 and 0.0004,

0.8625, respectively. This indicated that although the S absorbed by *S. salsa* was very low, the limited S in the *S. salsa* ecosystems had strong mobility and high biological cycle rate. Because water and salinity are the most typical environmental factors in the Yellow River estuary, the low S absorption capacities of *S. salsa* in tidal marshes might be significantly affected by the intense inundation and high salinity.

The assessment of S biological cycle status indicated that although S was not a limiting nutrient in *S. salsa* marshes, its high cycle rate might have significant influences on the production and emission of methane (CH_4). First, the S stocks in MSM and LSM soils (0–15 cm) (98.5–270.9 and 98.7–147.2 g m^{-2} , respectively) were generally higher than those in freshwater marsh and alpine tundra soils (Table 4). Although the S in soil absorbed by *S. salsa* was very low, the high S stock can provide large amount of substrates for the mineralization of organic S and the dissimilatory reduction of SO_4^{2-} . Second, because the SO_4^{2-} reducing bacteria (SRB) could compete for H_2/CO_2 and ethylic acid (CH_3COOH) with methanogens (MA) and the former had more strong affinity to the reaction substrates, the coexistence of SRB and SO_4^{2-} would inhibit the production and emission of CH_4 (van der Gon et al., 2001). In this study, the SO_4^{2-} concentration in *S. salsa* marshes in the Yellow River estuary was very high (0.62–1.50%), and the

Table 3
Sulfur allocation among compartments of *Suaeda salsa* marsh ecosystems.

Types	Items	Root ^a	Aboveground living bodies ^a		Litter ^a	Plant subsystem	Soil (0–60 cm) ^{**}	Plant–soil system
			Stem	Leaf				
MSM	S stock (g m^{-2})	0.157 ± 0.038	1.274 ± 0.292	1.394 ± 0.291	0.537 ± 0.129	3.362	396.864	400.226
	Percent (%)	4.67 ^a	37.89 ^a	41.46 ^a	15.97 ^a	0.84 ^b	99.16 ^b	100 ^b
LSM	S stock (g m^{-2})	0.025 ± 0.003	0.298 ± 0.071	0.780 ± 0.131	0.068 ± 0.015	1.171	436.291	437.462
	Percent (%)	2.13 ^a	25.45 ^a	66.61 ^a	5.81 ^a	0.27 ^b	99.73 ^b	100 ^b

^a Percent of plant subsystem.

^b Percent of plant–soil system; MSM, middle *S. salsa* marsh; LSM, low *S. salsa* marsh.

^{*} Values were means (\pm S.E., $n = 8$).

^{**} Values were determined in August 2008.

Table 4
Comparison of S stock in freshwater marsh, tidal marsh and alpine tundra soils.

Types	Sites	Vegetations	S content (g m ⁻²)	Soil depth (cm)	References
Freshwater marsh ecosystem	Sanjiang Plain	Typical meadow <i>Calamagrostis angustifolia</i>	238.22–288.01	0–20	Liu and Li (2008) Li (2007)
		Marsh meadow <i>C. angustifolia</i>	260.75	0–60	
Tidal marsh ecosystem	Yellow River estuary	<i>Suaeda salsa</i>	271.06	0–60	This study
		<i>S. salsa</i> in the middle marsh	98.46–270.92	0–15	
		<i>S. salsa</i> in the low marsh	396.86	0–60	
		<i>S. salsa</i> in the middle marsh	98.65–147.17	0–15	
Alpine tundra ecosystem	Changbai Mountain	<i>S. salsa</i> in the low marsh	436.29	0–60	Wei et al. (2005)
		Felsenmeer alpine tundra vegetation	118	0–10	
		Lithic alpine tundra vegetation	74	10–20	
		Typical alpine tundra vegetation	90	0–10	
		Meadow alpine tundra vegetation	97	10–20	
		Swamp alpine tundra vegetation	86	0–10	
			78	10–20	
	129	0–10			
	225	10–20			
	68	0–10			
	34	10–20			

Table 5
Comparison of CH₄ fluxes from freshwater marsh, tidal marsh, mangrove swamp, bog and fen ecosystems.

Types	Sites	Vegetations	CH ₄ fluxes ^a (mg m ⁻² h ⁻¹)	Observation periods	References
Freshwater marsh	Sanjiang plain, China	<i>Carex lasiocarpa</i>	12.8	2002.6–2003.4	Song et al. (2003) Yang et al. (2006) Ding et al. (2003)
			10.8	2003.6–2003.9	
			(21.6–66.5)	2001.8	
		<i>Deyeuxia angustifolia</i>	8.56	2002.6–2003.4	
	Zoige Plateau, China		1.59	2003.6–2003.9	Song et al. (2003) Yang et al. (2006) Ding et al. (2003) Yang et al. (2006) Ding et al. (2003) Wang et al. (2002)
		<i>Carex pseudocuraica</i>	11.4	2003.6–2003.9	
		<i>Carex meyeriana</i>	(17.2–45.0)	2001.8	
		<i>Carex muliejsis</i>	2.87 (0.51–8.20)	2001.5–2001.9	
Tidal marsh	Yellow River estuary, China	Bare flat	0.079	2009.8	Wang et al. (2011)
		<i>Suaeda salsa</i>	–0.038		
	Yangtze River estuary, China	Bare flat	0.04	2004.5–2005.4	
		<i>Scirpus mariqueter</i>	2.06		
	Minjiang River estuary, China	<i>Cyperus malaccensis</i>	0.60	2007.5–2008.4	
Mangrove swamp	Macrotidal Salt Marsh Bay, Canada	<i>Spartina alterniflora</i> , <i>Plantago maritima</i> , <i>Spartina patens</i> .	0.067 (0.008–0.458)	1993.7–1993.9	Magenheimer et al. (1996)
	Changning River estuary, China	<i>Bruguiera gymnorrhiza</i> , <i>Bruguiera sexangula</i>	(0.0249–0.0482)	1996.5	Ye et al. (2000)
Bog or fen	Brisbane River, Queensland, Australia	<i>Avicennia marina</i> ,	(0.003–17.4)	2004.4, 2005.2, 2005.7	Allen et al. (2007)
	Puerto Rico	<i>Aegiceras corniculatum</i> , <i>Avicennia germinans</i> ,	0.17	1991.4–1991.7,	
		<i>Laguncularia racemosa</i>		1991.9–1992.1	
		<i>Rhizophora mangle</i>	1.75		
		<i>R. mangle</i> , <i>A. germinans</i>	3.42		
Bog or fen	Sikaneva fen, Ruovest, Finland	<i>Sphagnum balticum</i> , <i>Carex rostrata</i> , <i>Scheuchzeria palustris</i>	<1 (wintertime)	2005.3–2006.2	Rinne et al. (2007)
	Lowland blanket bog, Glencar, Co Kerry, Ireland		3.5 (summertime)		
		<i>Racomitrium lanuginosum</i> , <i>Calluna vulgaris</i>	0.49	2003.8–2005.9	
		<i>Schoenus nigricans</i> , <i>Molinia caerulea</i>	0.80		
		<i>Rhynchospora alba</i>	0.87		
		<i>Sphagnum cuspidatum</i> , <i>Sphagnum auriculatum</i>	(0.48–2.10)		

^a Means in different observation periods. Values in bracket were the range of CH₄ fluxes.

high S biological cycle rate and the anoxic conditions resulting from high moisture might enhance the dissimilatory reduction of SO_4^{2-} , which, to a great extent, would reduce the CH_4 emission from *S. salsa* marshes. Similar results were also reported by some related studies. *Dise and Verry (2001)* found that the addition of SO_4^{2-} [$(\text{NH}_4)_2\text{SO}_4$] significantly reduced the CH_4 emission from peatland in northern Minnesota, and the total CH_4 flux from $(\text{NH}_4)_2\text{SO}_4$ treatment plots was one third lower than from control plots. *Nedwell and Watson (1995)* showed that the addition of 5 mM SO_4^{2-} significantly inhibited the formation of CH_4 by 49% relative to the controls, while addition of $\text{SO}_4^{2-} \geq 500 \mu\text{M}$ significantly decreased the rate of CH_4 production by the peat in New Galloway. Another study indeed indicated that the CH_4 fluxes from *S. salsa* marsh and bare flat in the Yellow River estuary were very low (0.079 and $-0.038 \text{ mg m}^{-2} \text{ h}^{-1}$, respectively) (*Wang et al., 2011*), approximating the values in most tidal marshes and some mangrove swamps (Table 5). Moreover, the values were slightly less than those in most mangrove swamps, bogs and fens, and far less than those in freshwater marshes (Table 5). The low CH_4 emissions implied that the significant inhibition mechanism as mentioned above might be widely existed in most tidal marshes and some mangrove swamps. Perhaps, the inhibition mechanism in *S. salsa* marshes was more significant than that in other marshes due to the high S cycle rate, which had important significances to reduce carbon emission (CH_4) from the Yellow River estuary. The S quantitative relationships determined in the compartment model might provide some scientific basis for us to reveal the special inhibition mechanism in future studies.

4. Conclusions

This paper established the S biological cycle compartment model of the two *S. salsa* marshes (MSM and LSM) in the intertidal zone of the Yellow River estuary, and assessed the S cycle status of ecosystems. Results have demonstrated that: (i) the S uptake amounts of roots were 1.237 and $0.160 \text{ g m}^{-2} \text{ yr}^{-1}$ and the values of aboveground parts were 3.885 and $1.276 \text{ g m}^{-2} \text{ yr}^{-1}$, the re-translocation quantities from aboveground parts to roots were 2.770 and $1.138 \text{ g m}^{-2} \text{ yr}^{-1}$, the translocation amounts from roots to soil were 0.154 and $0.018 \text{ g m}^{-2} \text{ yr}^{-1}$, the translocation quantities from aboveground living bodies to litter were 1.115 and $0.138 \text{ g m}^{-2} \text{ yr}^{-1}$, and the annual return quantities from litter to soil were less than 1.096 and $0.188 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively; (ii) Although S was not a limiting nutrient in *S. salsa* marshes, its high biological cycle rate might significantly inhibit the production and emission of CH_4 , which had important significances to reduce CH_4 emission from the Yellow River estuary.

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