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Volume 69 · Number 8 · August 2013

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ORIGINAL ARTICLE

Phosphorus biological cycle in the different *Suaeda salsa* marshes of the Yellow River estuary, China

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Abstract Much uncertainty exists in the phosphorus (P) cycle in the marshes of the intertidal zone. This study explored the P cycling 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 seasonal fluctuations and vertical distributions of P in different *S. salsa* marsh soils, and variations in P content in different parts of plants due to water and salinity status. The N/P ratios of the different *S. salsa* were 9.87 ± 1.23 and 15.73 ± 1.77, respectively, indicating that plant growth in MSM was limited by N, while that in LSM was limited by both N and P. The *S. salsa* litter in MSM released P to the environment throughout the year, while that in LSM immobilized P from the environment at all times. The P absorption coefficients of *S. salsa* in MSM and LSM were very low (0.0010 and 0.0001, respectively), while the biological cycle coefficients were high (0.739 and 0.812, respectively). The P turnovers among compartments of MSM and LSM showed that the uptake amounts of roots were 0.4275 and 0.0469 g m^{-2} year^{-1} and the values of aboveground parts were 1.1702 and 0.1833 g m^{-2} year^{-1}, the re-translocation quantities from aboveground parts to roots were 0.8544 and 0.1452 g m^{-2} year^{-1}, the translocation amounts from roots to soil were 0.0137 and 0.0012 g m^{-2} year^{-1}, the translocation quantities from aboveground living bodies to litter were 0.3157 and 0.0381 g m^{-2} year^{-1}, and the annual return quantities from litter to soil were less than 0.0626 and -0.0728 g m^{-2} year^{-1} (minus represented immobilization), respectively. P was an important limiting factor in *S. salsa* marshes, especially in LSM. *S. salsa* was seemingly well adapted to the low-nutrient condition and the vulnerable habitat, and the nutrient enrichment due to the import of N and P from the Yellow River estuary would be a potential threat to the *S. salsa* marshes.

Keywords Phosphorus · Biological cycle · *Suaeda salsa* marsh · Yellow River estuary

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Introduction

Phosphorus (P) has been regarded as a common limiting nutrient in ecosystems, which plays an important role in many biogeochemical processes (Hinsinger 2001; Zhang et al. 2005), such as participating in the composition of many P-containing compounds (nucleic acid, phospholipid, ribonucleotide and adenosine triphosphate), controlling the metabolism of carbohydrates in the photosynthesis process, and enhancing the stress-resistance and adaptation of plants (Lu 2003). P also has significant effects on other nutrient [carbon (C), nitrogen (N)] cycles (Newman and Lynch 2001; Tian et al. 2010), water body eutrophication and plant productivity (Compton et al. 2000; Hinsinger 2001).

The P cycle is one of the most complex cycles in wetland ecosystems, which is responsible for a series of important biogeochemical processes (Qin 2008). The productivity and trophic status of wetlands are usually dependent on the concentration of P in waters or soils. Wetlands have often been called the 'green filter' for their P retention capability and water purification capability (Coelho et al. 2004), and about 80–90 % of P is stored in soils due to the long turnover time of P in wetland ecosystems (Jiménez-Cárceles and Álvarez-Rogel 2008).

There has been intensely increasing interest in understanding the P cycle in wetland ecosystems because high input of nutrient (N, P) into wetlands, along with oxic surface and anoxic subsurface zones, potentially allow P to play a critical role in the biogeochemistry of wetlands (Walbridge 2000). Many studies have been conducted on the processes of the P cycle in different wetland ecosystems, such as salt marshes (Coelho et al. 2004; Bai et al. 2007), freshwater marshes (Hogan et al. 2004; Dunne et al. 2007; Zhang et al. 2011) and peatlands (Niedermeier and Robinson 2009). Tidal marshes are very important in coastal zones, which are sensitive to global climate change and human activities. In general, most of the P in tidal marshes is bound to clay and silt particles or is precipitated as mineral P, and changes in physical conditions, such as oxygen concentration, salinity or pH can alter this balance (Qin 2008). However, information on the processes of the P cycle in tidal marshes remains limited. In addition, current studies mostly focus on a certain process of the P cycle, while systemic and synthetic 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 (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 P 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, to some extent, influences water or salinity status and the succession of plants. 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* is the most prevalent plant in the tidal marsh

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). *Suaeda salsa* generally germinates in late April, blooms in July, matures in late September and completely dies in late November (Gu 1998). In the *S. salsa* distribution area, two phenotypes are generally formed due to the differences of water and salinity conditions in tidal marshes. In the middle marsh, the *S. salsa* is unfrequently and irregularly affected by the tide, so the salinity of sediment is low [electrical conductivity (0–5 cm), 5.58 ± 2.80 mS cm^{-1}] (Mou et al. 2010). The leaf and stem of *S. salsa* are green during the growth period and the plant is tall (Wang et al. 2006). In the low marsh, the *S. salsa* is frequently affected by the tide, so the salinity of sediment is very high [electrical conductivity (0–5 cm), 18.07 ± 0.43 mS cm^{-1}] (Mou et al. 2010). The leaf and stem of *S. salsa* are generally red–violet and the plant is very short (Wang et al. 2006). However, information on elemental biogeochemical processes of the tidal marshes in the Yellow River estuary is limited and the systemic and comparative studies on the P cycles of the two *S. salsa* marshes are still lacking.

In this paper, the P 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 P compartments, including aboveground living body, root, litter and soil. The purposes of this paper were: (i) to determine the distribution characteristics of P in the plant-soil system; (ii) to study the P turnovers among the compartments of *S. salsa* marsh; and (iii) to establish the P biological cycle compartment pattern of *S. salsa* marshes and evaluate the P cycle status.

Materials and methods

Study site

This study was conducted from April 2008 to November 2009 at two experimental plots in the *S. salsa* distribution area [middle *S. salsa* marsh (MSM), 37°45′57.0″N, 119°09′40.7″E; low *S. salsa* marsh (LSM), 37°46′38.9″N, 119°09′41.4″E] 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; summer is warm and rainy while winter is cold. The annual average temperature is 12.1 °C, the frost-free period is 196 days, and the effective accumulated temperature is about 4,300 °C. Annual evaporation is 1,962 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*, *Tamarix chinensis* and *Limoninum sinense*.

Study methods

Collection of soil samples

The seasonal dynamics of total phosphorus (TP) content in topsoil 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. The vertical distributions of TP 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 intervals, with 18 samples in total. The bulk density of each soil layer was determined simultaneously. The P stock (T_n, kg m^{-2}) in soil was calculated by Eq. (1):

$$T_n = \sum_{i=1}^{n} W_i \times P_i \times h/10 \tag{1}$$

where W_i (g cm^{-3}) is the soil bulk density of the i layer, P_i (%) is the TP content in the i layer and h is soil depth (10 cm).

Determination of litter and biomass

Litter production, aboveground biomass (AGB) and belowground biomass (BGB) were determined using 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 days. 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, because 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.

Determination of litter decomposition rates

Litter decomposition was studied with a litterbag technique at the two experimental plots from April 2008 to November 2009. 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. The experiment included nine sampling times (with different intervals), 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, sediment 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 mass loss (R, %) and decomposition rate (d^{-1}) were calculated by Eqs. (2)–(3) (Olson 1963; Liu et al. 2000).

$$R = [(W_t - W_0)/W_0] \times 100\% \tag{2}$$

$$W_t/W_0 = e^{-kt} \tag{3}$$

where 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. After 1 year decomposition, the annual P translocation amount from litter to soil was calculated by the change of P stock in litter.

Measurement of soil and plant samples

All soil and plant samples were ground (<0.25 mm) using a Wiely mill and analyzed for TC, TN contents by element analyzer (Elementar Vario Micro, German) and TP content by molybdate-ascorbic acid colorimetry (digested by H$_2$SO$_4$–H$_2$O$_2$) (The Committee of Agro-chemistry of the Chinese Society of Soil Science 1983).

Calculation of P stock and turnover

The P biological cycle characteristics of *S. salsa* marsh ecosystem can be expressed by absorption coefficient (A) and cycle coefficient (C), and their calculations were based on Eqs. (4)–(5) (Chen and Lindley 1983):

$$A = PAP/SP \tag{4}$$

$$C = PRP/PAP \tag{5}$$

where PAP (g m^{-2} year^{-1}) is the P absorption amount of plant, PRP (g m^{-2} year^{-1}) is the P return amount of plant and SP (g m^{-2}) is the P stock in soil (0–60 cm).

According to the calculation method of Li and Redmann (1992), the P stocks in plant compartments (P_n, g m^{-2}) and the P turnovers among plant compartments (F_a, g m^{-2} year^{-1}) were calculated by Eqs. (6)–(7):

$$P_n = C_n B_n \tag{6}$$

$$F_a = C_a B_a \tag{7}$$

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

Litter P stock (F_{da}, g m^{-2}) in aboveground dead plant, the P re-translocation quantities from aboveground parts to roots (F_{rt}, g m^{-2} year^{-1}), and the P uptake quantities of roots (F_r, g m^{-2} year^{-1}) were calculated by Eqs. (8)–(10):

$$F_{da} = C_d B_a \tag{8}$$

$$F_{rt} = F_a - F_{da} \tag{9}$$

$$F_r = F_a - F_{rt} + \Delta P_u \tag{10}$$

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

The P translocation amounts from litter to soil (F_s, g m^{-2} year^{-1}) and from roots to soil (F_T, g m^{-2} year^{-1}) were calculated by Eqs. (11)–(13):

$$F_s = F_l - F_y \tag{11}$$

$$F_T = T \times B_{Max} \times C_{Max} \tag{12}$$

$$T = P_m / B_{Max} \tag{13}$$

where F_l (g m^{-2}) is composed of F_{da} and F_p, F_p (g m^{-2}) is the P stock in un-decomposed litter previously accumulated in situ, F_y (g m^{-2}) is the P stock in un-decomposed litter after a period of time, T (%) is the turnover rate of root (Dahlman and Kucera 1965), P_m (g m^{-2}) is the deficit of maximum biomass and minimum biomass of root, B_{max} (g m^{-2}) is the maximum BGB and C_{max} (mg kg^{-1}) is the P content as root biomass reaches maximum.

Statistical analysis

The samples were presented as means of the replications, with standard error (SE). Statistical significance of differences at $p < 0.05$ between samples were analyzed using analysis of variance (ANOVA).

Results and discussion

P dynamics, distribution and stock in soils

Seasonal dynamics of P in topsoil

Although the TP contents in MSM and LSM topsoil had similar seasonal variations, neither of them was significant ($p > 0.05$, Fig. 1). Both of them increased from 25 April to 26 May (LSM) or 27 June (MSM) and significantly decreased until 25 August (LSM) or 25 September (MSM). After that, both increased again and then declined significantly. The maximum and minimum in MSM topsoil were observed on 27 June (823.38 ± 45.65 mg kg^{-1}) and 12 November (515.67 ± 130.19 mg kg^{-1}), while those in LSM topsoil
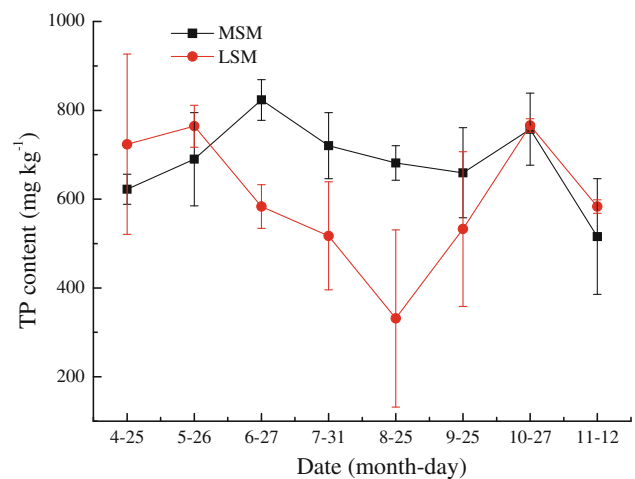

Fig. 1 Seasonal dynamics of TP content in topsoil (0–15 cm) of *Suaeda salsa* marshes. Values are means (±SE, $n = 10$); TP total phosphorus content, MSM middle *S. salsa* marsh, LSM low *S. salsa* marsh

occurred on 27 October (765.90 ± 15.22 mg kg^{-1}) and 25 August (331.38 ± 199.51 mg kg^{-1}), respectively. The seasonal variations of TP content in MSM and LSM topsoil were probably related to the distribution of soil organic matter (Bai et al. 2007; Qin et al. 2007), the mineralization of organic P (Qin et al. 2007; Xiao et al. 2011), plant absorption (Qin et al. 2006a), and the ebb and flow of the tide (Mou 2010) in different periods. The values in MSM topsoil in the summer were generally higher than those in LSM topsoil, while in the early spring and late autumn, the latter was much higher. The discrepancy of TP content in MSM and LSM topsoil was mainly related to the difference of water conditions. Compared with MSM, the LSM was more frequently affected by the tide (Mou 2010), which was favorable for the formation of anoxic conditions in topsoil. Under anoxic conditions, the iron oxide forms were directly correlated with the adsorption and desorption processes of P, which had significant influences on P dynamics and its availability in topsoil (Qin et al. 2006b). In addition, the organic matter in LSM topsoil (0.63 %) was generally lower than that in MSM topsoil (1.01 %) (Mou et al. 2010), which was not favorable for the conservation of P (Qin et al. 2007). Studies showed that the P stocks in topsoil (0–15 cm) of MSM and LSM during the growing season were 70.03–111.82 and 53.59–123.87 g m^{-2}, respectively.

Vertical distribution of P in soil

Similar vertical distributions of TP content were observed in the soil profile (0–60 cm) of MSM and LSM (Fig. 2a). For both, the TP content decreased at 0–30 cm depth and increased significantly at 30–60 cm depth, with the maximums (551.56 ± 0.94 mg kg^{-1} for MSM and

Fig. 2 Vertical distributions of TP content (**a**) and P stock (**b**) in the soil profile (0–60 cm) of *Suaeda salsa* marshes. Values are means (±SE, $n = 3$). MSM middle *S. salsa* marsh, LSM low *S. salsa* marsh
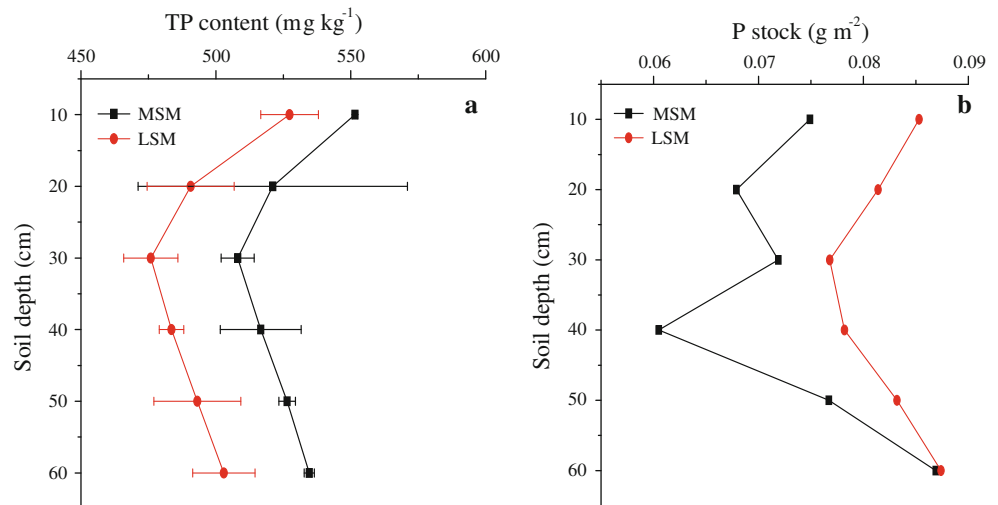
527.32 ± 10.67 mg kg^{-1} for LSM) and minimums (508.08 ± 6.13 mg kg^{-1} for MSM and 475.88 ± 10.03 mg kg^{-1} for LSM) being observed at 10 cm and 30 cm depths, respectively. Likewise, similar vertical distributions of P stock were observed in the soil profile (0–60 cm) of MSM and LSM except for the values at 30 cm depth (Fig. 2b), with the minimums (0.061 g m^{-2} for MSM and 0.077 g m^{-2} for LSM) being observed at 40 cm and 30 cm depths, respectively. The vertical variations of TP content and P stock were generally dependent on the spatial heterogeneity of soil organic matter (Bai et al. 2007) and the effects of changes in soil water conditions (Qin et al. 2006b; Xiao et al. 2012) resulting from the tide. Significantly higher TP content was observed in MSM compared to LSM (1.062 ± 0.003-fold, $p < 0.01$), whereas significantly lower P stock occurred in MSM compared to LSM (0.889 ± 0.032-fold, $p < 0.05$). The low TP content in LSM, as mentioned previously, was mainly dependent on the water conditions and organic matter in different soil layers, while high P stocks in LSM were mainly related to the high bulk density of different soil layers (Mou 2010). Studies indicated that, in August 2008, the total P stocks in MSM and LSM soils (0–60 cm) were 438.83 and 492.27 g m^{-2}, respectively.

P dynamics, stock and turnover in plants

Dynamics of plant biomass

Significant seasonal variations of AGB and BGB of *S. salsa* were observed in MSM and LSM (Fig. 3). In MSM, both increased with the improvement of hydrothermal conditions since 17 May, and reached the maximums on 31 August (902.08 ± 87.57 g m^{-2}) and 9 August (149.87 ± 4.84 g m^{-2}), respectively. After that, both decreased gradually with the coming of autumn, with the

minimums (63.00 ± 5.88 and 69.74 ± 15.78 g m^{-2}, respectively) occurring on 15 November. In LSM, both also increased since 17 May, but reached the maximums (253.28 ± 26.93 and 23.11 ± 1.23 g m^{-2}, respectively) on 31 August. Then, both decreased gradually and reached the minimums (136.45 ± 13.53 and 13.39 ± 1.37 g m^{-2}, respectively) on 15 November. Significantly higher AGB and BGB of *S. salsa* were observed in MSM compared to LSM (3.58 ± 0.52 and 5.46 ± 0.54-fold, respectively, $p < 0.05$). Moreover, significant seasonal variations of stem and leaf biomass of *S. salsa* were also observed in MSM and LSM (Fig. 3), with the maximums (661.22 ± 51.98 and 240.86 ± 38.57 g m^{-2} for MSM, and 111.37 ± 11.27 and 141.91 ± 17.43 g m^{-2} for LSM) being observed on 31 August. The stem and leaf biomass of *S. salsa* in MSM were also higher than those in LSM (4.90 ± 0.88 and 2.41 ± 0.33-fold, respectively), but only the difference of stem biomass between them was significant ($p < 0.05$).

Water and salinity conditions are the most typical environmental factors in the intertidal zone of the Yellow River estuary, which might influence plant biomass directly. Current studies have shown that soil moisture was an important factor to influence the biomass accumulation of plants. Wang et al. (2008) indicated that proper water stress was favorable for 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) also found that salinity stress had significant effects on the growth, biomass accumulation and allocation of *Salsola nitraria* and *Halogeton glomeratus*. Similar conclusions 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. The *S. salsa* in
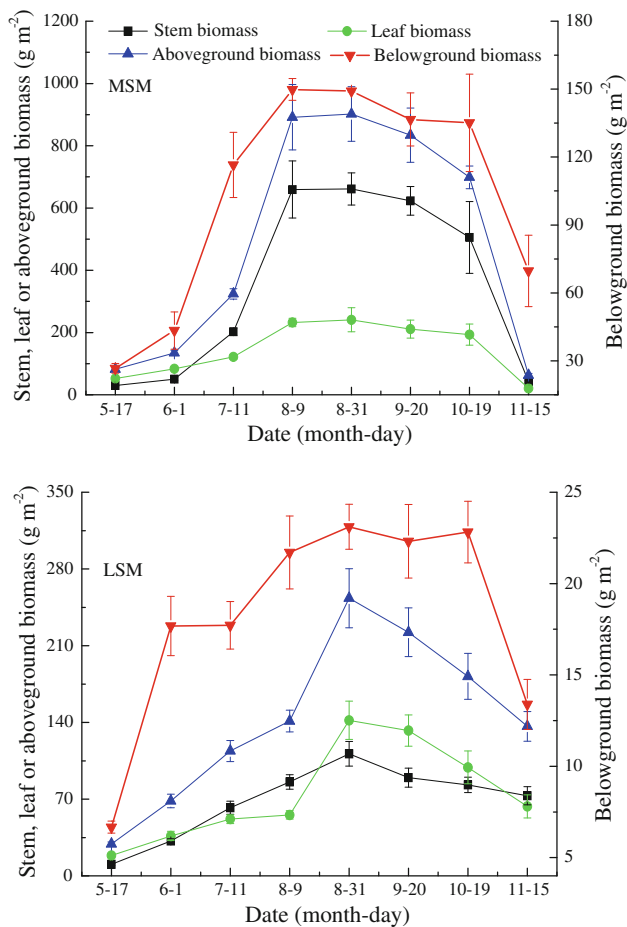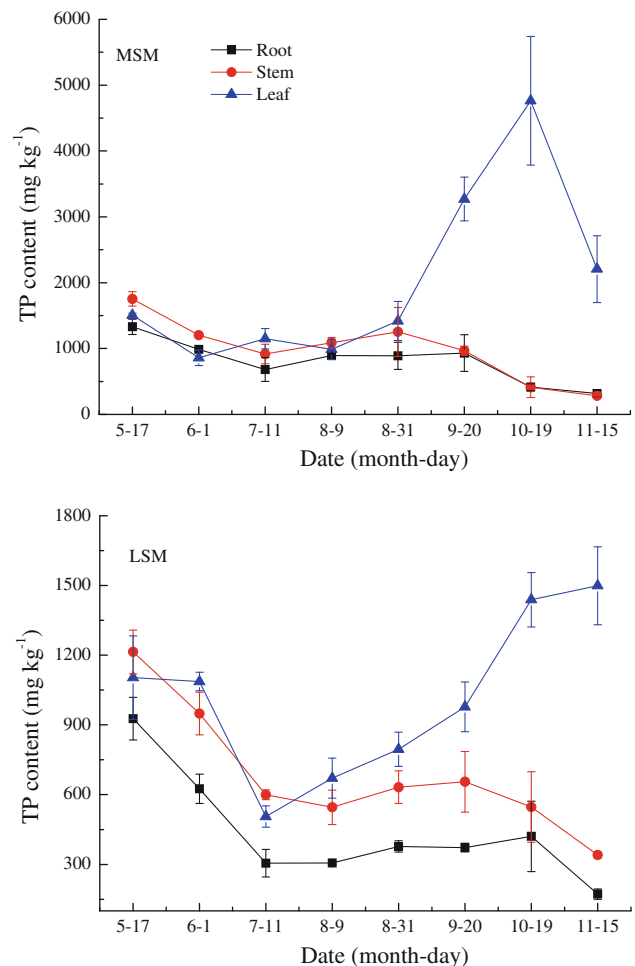
Fig. 3 Seasonal dynamics of *Suaeda salsa* biomass in MSM and LSM. Values are means (±SE, *n* = 5). MSM middle *S. salsa* marsh, LSM low *S. salsa* marsh

LSM was more frequently affected by ocean currents and tides compared to MSM (Ruan et al. 2008), and it generally confronted both severe salinity stress and seawater inundation stress, which caused its low biomass.

Dynamics of P content in plants

There were similar variations of TP content in the root and stem of *S. salsa* in MSM and LSM (Fig. 4). Both were high at the initial stage, after which the values generally decreased and reached the minimums (317.11 ± 49.36 and 282.38 ± 17.73 mg kg^{-1} for MSM, and 172.15 ± 22.29 and 340.77 ± 13.28 mg kg^{-1} for LSM) on 15 November. Fluctuations of TP content were observed in the leaves of *S. salsa* in MSM and LSM (Fig. 4). In MSM, the values in the leaves had no significant change before 31 August, after which the values increased significantly and reached the maximums ($4{,}763.87 \pm 977.67$ mg kg^{-1}) on 19 October. By comparison, the values in the leaves in LSM decreased significantly before 11 July and increased from 11 July to

Fig. 4 Seasonal dynamics of TP content in different parts of *Suaeda salsa*. Values are means (±SE, *n* = 3). MSM middle *S. salsa* marsh, LSM low *S. salsa* marsh

15 November, with the minimum (505.63 ± 45.76 mg kg^{-1}) and maximum ($1{,}498.73 \pm 167.55$ mg kg^{-1}) being observed on 11 July and 15 November, respectively. The fluctuation of TP content in the leaves before 31 August was mainly related to the 'dilution effect' caused by biomass increase (Sun et al. 2007), and then, the increase of TP content was correlated with the P transfer mechanism from root or stem to leaf and seed during seed growth in autumn. The TP content in different parts of *S. salsa* in MSM and LSM differed significantly ($p < 0.05$), in the order of leaf > stem > root, indicating that the P was mainly accumulated in the leaves. Although the TP content in the root, stem and leaf of *S. salsa* in MSM were higher than those in LSM (2.12 ± 0.20, 1.62 ± 0.12, and 2.15 ± 0.33-fold, respectively); only the values in root between them had significant difference ($p < 0.05$).

As the most typical environmental factors in the Yellow River estuary, water and salinity conditions also might influence the accumulation of P in plants directly. Braekke

(1990) showed that the changes in water condition (drainage) occurring in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) wetlands had important effects on nutrient (N, P, and K) accumulation in AGB. Qin (2008) indicated that water condition was the key factor to induce the significant differences of P 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 affected the seasonal dynamics of N and P in the shoots of *Spartina alterniflora*. The growth rhythm and ecological characteristics of plants might also affect P accumulation (Bragato et al. 2006). In this study, the *S. salsa* in the Yellow River estuary formed two phenotypes resulting from the differences of water and salinity conditions. As mentioned previously, the growth rhythms of the two phenotypes were different, which, to some extent, influenced the seasonal dynamics of P in *S. salsa*. In addition, many studies have shown that the succulence degree (Liu et al. 2006), peroxidase content (Wang et al. 2006), pigment accumulation and photosynthesis (Ruan et al. 2008) of the two phenotypes' leaves were significantly different, which might affect the absorption and allocation of P greatly.

Tessier and Raynal (2003) indicated that the N/P ratio was an effective indicator to estimate nutrient limitation and N saturation. Koerselman and Meuleman (1996) found that the growth of marsh plants was limited by N if the N/P ratio was less than 14. If the N/P ratio was between 14 and 16, the growth was limited by both N and P. If the N/P ratio was more than 16, the growth was limited by P. The relationship was applied to discussing the nutrient limitations of *S. salsa* in MSM and LSM. Results showed that the N/P ratios in *S. salsa* of MSM were mostly less than 14 in the growing season (average N/P ratio: 9.87 ± 1.23), indicating that plant growth was limited by N (Table 1). Differently, the N/P ratios in *S. salsa* of LSM in late spring were less than 16, which implied that plant growth was limited by both N and P. In summer, the N/P ratios were more than 16, suggesting that plant growth was limited by P. From late summer to early winter, the N/P ratios were less than 14, indicating that plant growth was limited by N (Table 1). The average N/P ratio (15.73 ± 1.77) in the growing season was less than 16 (Table 1), indicating that *S. salsa* in LSM was generally limited by both N and P, but the limitation of P was more significant. Moreover, the N/P ratios in different parts of the plant changed significantly during the growing season, which was mainly dependent on the nutrient absorption status of the plants and the nutrient supply status of soil in different periods. Studies showed that the P stocks in root, stem and leaf of *S. salsa* in MSM and LSM were 0.0221–0.1339, 0.0120–0.8283, 0.0451–0.9204 and 0.0023–0.0111, 0.0128–0.0704, 0.0204–0.1424 g m^{-2}, respectively. The P

uptake amounts of aboveground parts were 1.1702 and 0.1833 g m^{-2} year^{-1}, the P uptake quantities of roots were 0.4275 and 0.0469 g m^{-2} year^{-1}, the P re-translocation amounts from aboveground parts to roots were 0.8544 and 0.1452 g m^{-2} year^{-1}, and the P translocation quantities from roots to soil were 0.0137 and 0.0012 g m^{-2} year^{-1}, respectively.

Dynamics of litter production and P content in litter

Similar changes of *S. salsa* litter production were observed in MSM and LSM (Fig. 5). Both of them were low at the initial stage, after which the values generally increased and reached maximums (579.90 ± 98.91 and 46.25 ± 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. In fact, 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 in the growing season was mainly correlated with 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 ($p > 0.05$). Different seasonal dynamics of TP content were observed in *S. salsa* litter in MSM and LSM (Fig. 5). Both of them decreased significantly from 17 May to 11 July, and then, the variations were opposite, with the maximums ($1,507.92 \pm 15.99$ mg kg^{-1} for MSM and $1,103.80 \pm 103.68$ mg kg^{-1} for LSM) and minimums (533.88 ± 102.32 mg kg^{-1} for MSM and 342.68 ± 25.50 mg kg^{-1} for LSM) being observed on 17 May and 11 July, respectively. Although the TP content in *S. salsa* litter in MSM was generally higher than that in LSM (1.62 ± 0.16-fold); they had no significant difference ($p > 0.05$). The variations of TP content in *S. salsa* litter were mainly related to the different P translocation mechanisms when aboveground parts withered (Mou et al. 2010). Studies showed that the P stocks in *S. salsa* litter in MSM and LSM were 0.0005–0.3157 and 0.0002–0.0381 g m^{-2}, respectively, and the P translocation quantities from aboveground living bodies to litter were 0.3157 and 0.0381 g m^{-2} year^{-1}, respectively.
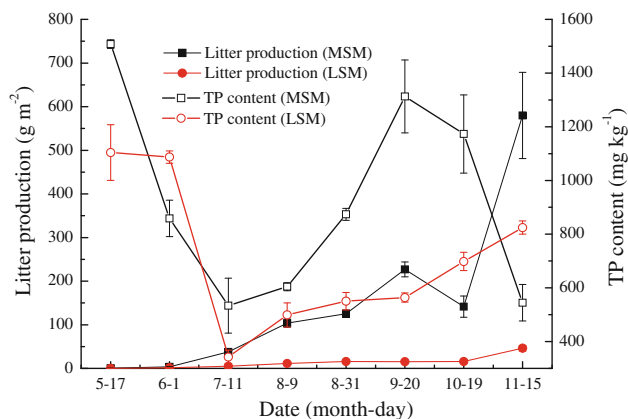
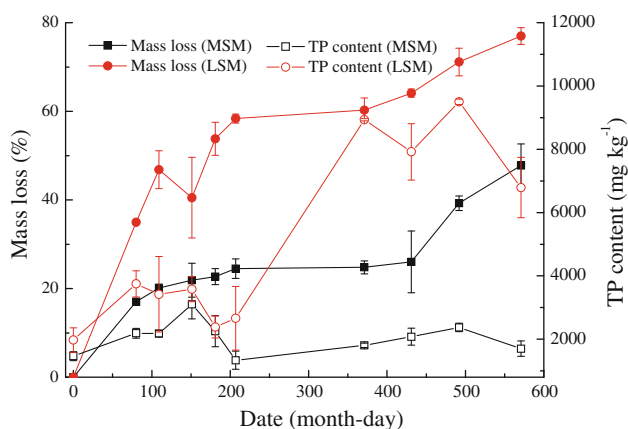### Dynamics of litter decomposition and P content in litter

The mass loss of *S. salsa* litter in MSM and LSM generally increased during decomposition, and the local decrease was related to the determinate error (Fig. 6). Both litter masses decreased rapidly from April to November in 2008 (0–207 days), accounting for 51.29 and 75.81 % of the total loss in the experiment, respectively, which was

Table 1 Dynamics of N/P ratio in different parts of *Suaeda salsa*

Type	Item	Date								Mean value (±SE)
		5–17	6–1	7–11	8–9	8–31	9–20	10–19	11–15	
MSM	Root	9.13	7.31	8.74	5.71	5.66	5.28	8.86	15.05	8.22 ± 1.12
	Stem	11.07	7.89	11.78	5.03	4.68	4.96	11.68	16.54	9.20 ± 1.51
	Leaf	16.93	17.19	20.58	22.31	12.54	7.05	4.97	11.53	14.14 ± 2.19
	Plant	13.53	10.97	14.02	8.64	6.82	5.93	5.91	13.12	9.87 ± 1.23
LSM	Root	10.58	15.57	26.50	15.99	12.27	12.89	9.87	21.35	15.63 ± 2.02
	Stem	13.05	12.94	23.05	18.67	13.71	14.15	12.96	16.93	15.68 ± 1.29
	Leaf	18.36	15.24	32.59	20.82	14.21	10.87	11.15	11.93	16.90 ± 2.56
	Plant	15.31	14.56	26.50	19.30	13.89	11.72	11.39	13.17	15.73 ± 1.77

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

Fig. 5 Seasonal dynamics of *Suaeda salsa* litter production and TP content in litter. Values are means (±SE, $n = 3$). MSM middle *S. salsa* marsh, LSM low *S. salsa* marsh

Fig. 6 Dynamics of mass loss and TP content during *Suaeda salsa* litter decomposition. Values are means (±SE, $n = 3$). MSM middle *S. salsa* marsh, LSM low *S. salsa* marsh

mainly dependent on the hydrothermal condition during the growing season. From November 2008 to April 2009 (207–371 days), 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 days), both of the mass losses rapidly increased, and mass losses reached 47.78 ± 4.86 and 77.00 ± 1.88 % after 571 days, respectively. In general, significantly higher *S. salsa* litter mass losses were observed in LSM compared to MSM during decomposition (2.14 ± 0.11-fold, $p < 0.01$). The TP content in *S. salsa* litter in MSM increased significantly from 0 to 151 days and then decreased rapidly until 207 days. After that, the values gradually increased from 207 to 492 days and decreased until 571 days (Fig. 6). By contrast, the variations of TP content in *S. salsa* litter in LSM were more complex, with the high values being observed from 371 to 571 days (Fig. 6). The variations of C/P ratios in *S. salsa* litter in MSM and LSM were opposite to those of the corresponding TP contents (Fig. 6; Table 2) and significant negative correlations ($r = -0.898$, $p < 0.01$; $r = -0.939$, $p < 0.01$, respectively) occurred between them, indicating that C/P ratios might have significant influence on the P dynamics of *S. salsa* litter during decomposition. This result was similar to the conclusion reported by Qin (2008). In addition, the TP content in *S. salsa* litter in MSM and LSM during decomposition was 91.23–211.55 and 120.75–481.16 % of the initial value, respectively, which implied that P might accumulate in the litter most of the time (Fig. 6). Similar results were also reported by Davis (1991) who found that the N and P accumulated in *Cladium jamaicense* and *Typha domingensis* litter during the decomposition experiment. Nielsen and Andersen (2003) indicated that the remaining P in the mangrove leaf litter increased with time of decomposition to 174 and 220 % of the initial amount in the litter in sand flat and mangrove sediment, respectively, although about 50 % of the dry weight had been lost. The incorporation of P into the litter was probably associated with humic acids and metal bridging, especially caused by iron (Fe), which also accumulated in considerable amounts in the litter (Nielsen and Andersen 2003). In addition, the increase

Table 2 Dynamics of C/P ratio in *Suaeda salsa* litter in MSM and LSM during decomposition

Sampling date (yyyy-mm-dd)	Decomposition time (day)	C/P (mean ± SE, n = 3)		Sampling date (yyyy-mm-dd)	Decomposition time (day)	C/P (mean ± SE, n = 3)	
		MSM	LSM			MSM	LSM
2008-04-21	0	281.58 ± 25.98	195.80 ± 34.41	2008-11-15	207	332.05 ± 78.11	177.05 ± 65.55
2008-07-11	80	194.49 ± 15.30	110.17 ± 9.58	2009-04-26	371	216.31 ± 14.24	46.24 ± 0.63
2008-08-09	109	190.50 ± 11.15	136.64 ± 46.54	2009-06-25	431	172.53 ± 18.58	52.92 ± 5.55
2008-09-20	151	139.25 ± 19.16	104.69 ± 12.06	2009-08-25	492	177.07 ± 9.04	42.78 ± 1.35
2008-10-20	181	191.51 ± 44.05	165.60 ± 23.41	2009-11-12	571	232.80 ± 34.21	66.97 ± 8.79

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

of P in *S. salsa* litter might also be ascribed to the P immobilization by microbes from the P sources (such as tidewater and topsoil) in the decomposition environment if the marsh was limited by P (Yang et al. 2006). As mentioned previously, since the LSM was more limited by P, the P immobilization amounts in *S. salsa* litter in LSM were generally higher than those in MSM.

Studies showed that the decomposition rates of *S. salsa* litter in MSM and LSM were 0.3780 year^{-1} and 1.1880 year^{-1}, respectively. Because the *S. salsa* litter in LSM could be decomposed completely within 1 year, the P standing crop of litter approximated 0 g m^{-2}. The annual P release amount from litter to soil was about 0.0626 g m^{-2} year^{-1}, indicating that the litter generally released P to the decomposition environment. By comparison, the *S. salsa* litter in MSM decomposed slowly and the annual P return amount from litter to soil approximated −0.0728 g m^{-2} year^{-1} (minus represented immobilization), indicating that the litter immobilized P from the decomposition environment throughout the year. Because the actual input amounts 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 P release/immobilization amount should also be slightly more than 0.0626 and −0.0728 g m^{-2} year^{-1}, respectively. However, since some litter was removed gradually by the tide and only part could be decomposed in situ, the actual P release/immobilization amount might be less than 0.0626 and −0.0728 g m^{-2} year^{-1}. In LSM, because the P immobilized in the litter could be easily or gradually carried away by the tide, the *S. salsa* marsh might be lacking in P, indicating that P might be an important limiting nutrient. This result was consistent with the conclusion mentioned above.

P allocation and cycle in plant-soil systems

P allocation in plant-soil systems

Studying the allocation of P in the plant-soil systems of MSM and LSM showed that the aboveground living body was the main P stock of the plant subsystem with the mean values of 0.648 and 0.116 g m^{-2}, accounting for 76.35 and 87.44 % of the total P stock of the plant subsystems,

respectively (Table 3). In the two plant-soil systems, the P stocks of the plant subsystem were very low, accounting for only 0.19 and 0.03 % of the total P stock, respectively. Soil P was the main P stock of the two plant-soil systems, accounting for 99.81 and 99.97 %, respectively. The high proportion of soil P indicated that it was the circulation hinge in the process of P cycling, which could prevent the P from being lost easily. In addition, higher P stock of the plant subsystem and lower soil P and total P stock were generally observed in MSM compared to LSM (Table 3).

Establishment of P biological cycle pattern and assessment of P cycle status

Based on the above-mentioned studies, the compartment pattern on the allocation and circulation of P in *S. salsa* marsh was established, and the quantitative relationships among compartments were determined (Fig. 7). According to the compartment pattern, this paper calculated the P absorption and cycle coefficients of *S. salsa* in MSM (0.0010, 0.739) and LSM (0.0001, 0.812), and compared them with the values of different plants in other marsh ecosystems in China (Table 4). Results showed that the P absorption coefficients were very low while the cycle coefficients were very high, indicating that the P absorbed by *S. salsa* was much lower compared with the P stock in soil. In addition, the limited P in *S. salsa* ecosystems had strong mobility and high biological cycle rates. As mentioned previously, because water and salinity are the most important environmental factors in the Yellow River estuary, the low P absorption capacities of *S. salsa* might be significantly affected by the intense inundation and high salinity conditions in tidal marshes.

The P absorption and cycle coefficients of the plants along the latitudinal gradient also had different variations (Table 4). The P absorption coefficients of different plants (*Kandelia candel*, *Bruguiera sexangula*, *Rhizophora stylosa*, *Phragmites australis*, *S. alterniflora* and *Scirpus mariqueter*) in the low or mid-low latitude regions (19°51′–31°14′N) were very low (0.0011–0.0117), while the cycle coefficients were generally high (0.50–0.71). In the mid-high latitude region

**Table 3** Phosphorus allocation among compartments of *Suaeda salsa* marsh ecosystem

| Type | Item | Root* | Aboveground living body* | | Litter* | Plant subsystem | Soil (0–60 cm)** | Plant-soil system |
			Stem	Leaf				
MSM	P stock (g m^{-2})	0.079 ± 0.016	0.333 ± 0.116	0.315 ± 0.114	0.122 ± 0.045	0.849	438.83	439.68
	Percent (%)	9.27[a]	39.28[a]	37.07[a]	14.37[a]	0.19[b]	99.81[b]	100[b]
LSM	P stock (g m^{-2})	0.007 ± 0.001	0.041 ± 0.007	0.075 ± 0.018	0.009 ± 0.004	0.133	492.27	492.40
	Percent (%)	5.48[a]	30.70[a]	56.74[a]	7.08[a]	0.03[b]	99.97[b]	100[b]

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

* Values are means (±SE, $n = 8$)

** Values are determined in August 2008

[a] Percent of plant subsystem

[b] Percent of plant-soil system

Fig. 7 Phosphorus biological cycle compartment pattern of the *Suaeda salsa* marsh ecosystems. Numerals in panes were the P stocks of compartments (g m^{-2}), numerals above arrowhead were the P turnovers among compartments (g m^{-2} year^{-1}), *less than the value. [M]MSM middle *S. salsa* marsh, [L]LSM low *S. salsa* marsh, the *minus* represented P immobilization
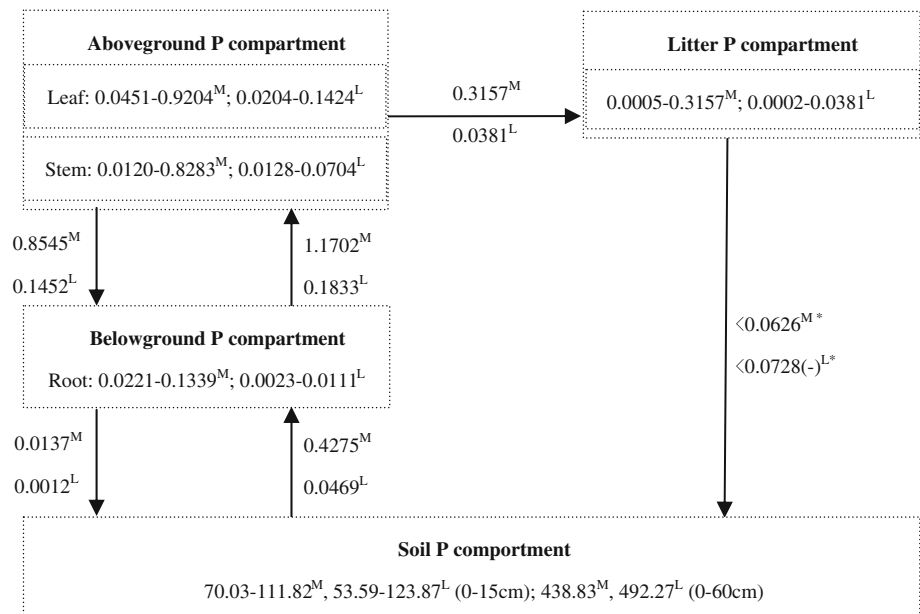
(47°35′N), the absorption and cycle coefficients of different plants (*C. angustifolia* and *Carex lasiocarpa*) ranged from 0.352 to 0.634 and 0.091 to 0.352, respectively. In this paper, the study site in the Yellow River estuary is located in the mid-low latitude region (37°45′–37°46′N), and the P absorption and cycle coefficients of *S. salsa* were generally in accordance with above-mentioned variations. The variations of cycle coefficients were mainly related to the regular changes of heat status, water conditions and precipitation along the latitudinal gradient, which had great influences on litter decomposition and nutrient recycling. Although temperature, water and precipitation might have some effects on plant growth, the P absorption capacities, to a great extent, depended on plant species, growth rhythm, eco-physiology characteristics, and the nutrient supply status in habitat (Qin 2008).

The evaluation of P biological cycle status indicated that P was an important limiting factor in *S. salsa* marshes, especially in LSM. *S. salsa* might exhibit a special adaptive strategy against the low-nutrient conditions and the vulnerable habitat. There were several probable reasons.

First, although the P stocks in MSM and LSM soils (0–60 cm) (438.83 and 492.27 g m^{-2}, respectively) were generally higher than those of freshwater marsh and alpine tundra soils (Table 5), the P in tidal marshes was generally adsorbed or bound by clay, organic matter, Fe^{2+} and the hydroxide/oxide of aluminum (Wang and Liu 2002; Qu et al. 2010), which caused the supply of available P in marsh soils to be limited. Moreover, since the *S. salsa* marsh was an open ecosystem frequently affected by the tide, the low available P in soil could be easily removed during the ebb and flow of the tide, which also might be an

Table 4 Comparison of P absorption and cycle coefficients of the plants in different marsh ecosystems in China

Location	Geographical location	Site	Plant	Absorption coefficient	Cycle coefficient	References
Sanjiang Plain	47°35′17″N, 133°31′35″E	Honghe	*Carex lasiocarpa*	0.352	0.108	He and Zhao (2001)
			Typical meadow *Calamagrostis angustifolia*	0.634	0.352	Qin (2008)
			Marsh meadow *C. angustifolia*	0.591	0.091	
Yellow River estuary	37°45′57.0″N, 119°09′40.7″E	Dawenliu	*Suaeda salsa*			This study
	37°46′38.9″N, 119°09′41.4″E		A*	0.0010	0.739	
			B**	0.0001	0.812	
Yangtze River estuary	31°06′20″ –31°14′00″N, 121°53′06″–122°04′33″E	Shangsha	*Phragmites australis*	0.0081	0.51	Liu and Yang (2008)
			Spartina alterniflora	0.0056	0.72	Yang et al. (2009a)
			Scirpus mariqueter	0.0067	0.59	Yang et al. (2009b)
		Zhongsha	*P. australis*	0.0091	0.53	Liu and Yang (2008)
			S. alterniflora	0.0117	0.71	Yang et al. (2009a)
			S. mariqueter	0.0042	0.65	Yang et al. (2009b)
		Xiasha	*P. australis*	0.0031	0.36	Liu and Yang (2008)
			S. alterniflora	0.0053	0.62	Yang et al. (2009a)
			S. mariqueter	0.0011	0.11	Yang et al. (2009b)
Jiulong River estuary	24°26′10″–24°27′38″N, 117°54′12″–117°55′31″E	Longhai	*Kandelia candel*	–	0.500***	Lin (2001)
Shatian Peninsula	21°28′22″–21°37′00″N, 109°37′00″-109°47′00″E	Shatian	*Bruguiera sexangula*	–	0.583***	
Hainan Island	19°51′-20°01′N, 110°32′–110°37′E	Dongzhaigang	*Rhizophora stylosa*	–	0.462***	

* *Suaeda salsa* in middle marsh

** *S. salsa* in low marsh

*** Coefficients were calculated according to the data in reference

important cause of the low P absorption coefficient of *S. salsa.*

Second, litter decomposition was generally regarded as an effective way for nutrient return; however, this study drew different conclusions. In MSM, the *S. salsa* litter released P to the environment throughout the year, with an annual P return amount of 0.0626 g m^{-2}. Since *S. salsa* litter was gradually removed by the tide and the release of P from litter to soil was also influenced by the tide, the actual P return amount was far lower than 0.0626 g m^{-2}. By contrast, the *S. salsa* litter in LSM immobilized P from the environment at all times during decomposition (with an annual P immobilization amount of 0.0728 g m^{-2}), and the litter could also be easily or gradually carried away by the tide, indicating that the litter in LSM acted as an important source of P loss. This also might be an important reason to conclude that the *S. salsa* in LSM was especially limited by P.

Third, the P absorption capacities of *S. salsa* in MSM and LSM were very low and intense inundation or high salinity might inhibit the capacity as mentioned above, indicating that the *S. salsa* in tidal marshes (especially in LSM) was very limited by P. This result was consistent with the conclusion drawn by the study of N/P ratios in *S. salsa.*

Based on the above analysis, the available P was very limited in *S. salsa* marshes, indicating that the ecosystems were lacking in P. Moreover, the P in *S. salsa* marshes had high biological cycle rates, which indicated that the lack of P might be very severe.

Mistch and Gosselin (2000) indicated that N and P are often the most limiting nutrients in marshes, and the cycle status of N or P not only affects the structure and function of marshes, but also, to some extent, influences the stabilization and health of ecosystems. In this sense, the current *S. salsa* marsh was unstable and vulnerable. However, the *S. salsa*

Table 5 Comparison of P stocks in freshwater marsh, tidal marsh and alpine tundra soils

Type	Site	Plant	P stock (g m^{-2})	Soil depth (cm)	References
Freshwater marsh ecosystem	Sanjiang Plain	Typical meadow *C. angustifolia*	443.18	0–60	Qin (2008)
		Marsh meadow *C. angustifolia*	371.98		
Tidal marsh ecosystem	Yellow River estuary	*Suaeda salsa*			This study
		A*	70.03–111.82	0–15	
		B**	53.59–123.87		
		A*	438.83	0–60	
		B**	492.27		
Alpine tundra ecosystem	Changbai Mountain	Felsenmeer alpine tundra vegetation	59	0–10	Wei et al. (2005)
			46	10–20	
		Lithic alpine tundra vegetation	25	0–10	
			24	10–20	
		Typical alpine tundra vegetation	62	0–10	
			64	10–20	
		Meadow alpine tundra vegetation	76	0–10	
			90	10–20	
		Swamp alpine tundra vegetation	62	0–10	
			78	10–20	

* *Suaeda salsa* in middle marsh

** *S. salsa* in low marsh

was seemingly well adapted to the low-nutrient condition and the vulnerable habitat. At present, the import of N and P from the Yellow River estuary is increasing due to human activities (Bulletin of Shandong Oceanic Environmental Quality 2009). Loading of excessive N and P to the estuary ecosystem may cause changes in ecological function, and often has undesirable environmental and economic consequences (Sun and Liu 2008). As *S. salsa* is probably well adapted to the low-nutrient environment, the nutrient enrichment is a potential threat to the *S. salsa* marshes. Excessive nutrient loading from the Yellow River estuary may lead to the invasion of nutrient-rich species (such as *Phragmites australis*, *Triarrhena sacchariflora* and *Tamarix chinensis*) and cause severe degradation of the ecosystem in the long-term if measures are not taken.

Conclusions

This paper established the P biological cycle compartment pattern of the two *S. salsa* marshes (MSM and LSM) in the intertidal zone of the Yellow River estuary, and evaluated the P cycle status of ecosystems. Results have demonstrated that: (i) the P uptake amounts of roots were 0.4275 and 0.0469 g m^{-2} year^{-1} and the values of aboveground parts were 1.1702 and 0.1833 g m^{-2} year^{-1}, the re-translocation quantities from aboveground parts to roots were

0.8544 and 0.1452 g m^{-2} year^{-1}, the translocation quantities from roots to soil were 0.0137 and 0.0012 g m^{-2} year^{-1}, the translocation amounts from aboveground living bodies to litter were 0.3157 and 0.0381 g m^{-2} year^{-1}, and the annual return quantities from litter to soil were less than 0.0626 and −0.0728 g m^{-2} year^{-1} (minus represented immobilization), respectively; (ii) the P in *S. salsa* marshes (especially in LSM) was an important limiting factor. The *S. salsa* was seemingly well adapted to the low-nutrient condition and the vulnerable habitat, and the nutrient enrichment due to the import of N and P from the Yellow River estuary would be a potential threat to the *S. salsa* marshes.

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