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Article *in* Nordic Journal of Botany · January 2021

DOI: 10.1111/njb.02956

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NORDIC JOURNAL OF
BOTANY

Research

The sediment burial depth and salinity control the early developments of *Suaeda salsa* in the Yellow River Delta

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Nordic Journal of Botany
2021: e02956
doi: 10.1111/njb.02956

Subject Editor: Jean Yong
Editor-in-Chief: Sara Cousins
Accepted 9 November 2020
Published 16 January 2021

Sediment deposition is a common phenomenon in the estuary area. Pot control experiments were conducted to evaluate the interaction effects of sediment burial depth and salt stress on the seed germination and early seedling growth of *Suaeda salsa* (L.) Pall., an pioneer species of tidal wetland near the Yellow River Delta. The results showed that the percentage of seedling emergence, seedling emergence rate, seedling height, branch number, shoot biomass and root biomass were all significantly affected by salt stress and sediment burial depth. While the interaction of salt and burial depth significantly influenced the branch number, leaf biomass, shoot biomass and total plant biomass. Only 5 cm burial depth without salt stress should 6.25 ± 3.61% seedlings emergence. With the increasing of sediment burial depth and salt stress, percentage of seedling emergence, seedling emergence rate and plant height decreased significantly. However, under the salt treatment of 0 and 1%, the branch number increased dramatically with the increasing of sediment burial depth from 0 to 3 cm. The ratio of leaf to total biomass increased with increasing of burial depth, on the contrary, the ratio of root to total biomass decreased. 0–1 cm sediment burial depth was proved the suitable depths for seed germination of *S. salsa* in the coastal wetland of the Yellow River Delta. Our findings contribute to a better understanding of how to improve the seedling establishment of *S. salsa* under the dynamic changes of sediment deposition and salinity in the coastal wetland of the Yellow River Delta.

Keywords: biomass, salt stress, seed germination, sediment deposition, *Suaeda salsa*

Introduction

Coastal wetlands are regarded as the most vulnerable ecosystems to the interactive effects of seawater and land (Yang et al. 2007, Duarte et al. 2008). It is widely recognized that plant communities in salt marshes have a very low diversity (Adam 1990). Tidal wetlands are subject to numerous environmental factors that influence plant establishment, such as frequent tidal waves, high wind velocities, low levels of soil nutrients and sediment deposition (Maun 1998, Mou and Sun 2011, Yu et al. 2016).

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Plant establishment and population regeneration from seeds depend on successful germination, which occurs when and where environmental conditions are favorable for seedling survival and growth (Beas et al. 2013).

Among those environmental factors, sediment deposition is a major factor that not only affects the formation rate of tidal wetlands, but also directly influences seed germination and seedling emergence (Huang and Gutterman 1998, Benvenuti et al. 2001). This is especially evident in the Yellow River Delta of Shandong Province, China, where millions of tons of sediment are deposited every year (Cui et al. 2009). Before 2002, the low flows of the Yellow River led to a significant decrease in water supply to the delta, and caused serious wetland degradation. In order to restore the degraded wetlands, the government carried out a 'Water and Sand Regulation Project' in 2002 (Cui et al. 2009). During this project (from May to June each year), the Yellow River flooded the tidal wetlands near the estuary, resulting in a large amount of sediment being deposited in the tidal wetlands. The sedimentary rate in the estuary is generally 90–100 mm $year^{-1}$.

Previous studies have demonstrated that sediment/sand burial can affect seed emergence and survival (Zhang and Maun 1990, Benvenuti et al. 2001, Huang et al. 2004, Jarvis and Moore 2015); seedling morphological indices such as seedling height, branch number, shoot/root length, seedling biomass and biomass allocation (Li et al. 2006, Mou and Sun 2011, Mao et al. 2019, Vahabinia et al. 2019); and seedling physiological responses such as photosynthetic rate, chlorophyll content and soluble sugars (Perumal and Maun 2006, Mao et al. 2019). A suitable sediment burial depth can create favorable environmental conditions relating to temperature and water for seed germination, but excessive burial depth will cause oxygen deficiency or an increase in soil mechanical resistance, thus inhibiting seed germination and seedling emergence (Zhang and Maun 1990, Zhang et al. 2016). Species in different ecosystems have been shown to have differing suitable burial depths. For most species in inland sand dune ecosystems, the highest emergence percentage and plant biomass occur at shallow burial depths (1–2 cm), rather than at the surface (Maun and Riach 1981, Zhang and Maun 1990, Li et al. 2006). In freshwater wetlands or coastal wetlands, the sediment surface (0 cm) is the most suitable germination depth, providing sufficient humidity, temperature and nutrient conditions (Jurik et al. 1994, Mou and Sun 2011). However, plants in coastal wetlands are also exposed to high salinity owing to frequent tidal waves. Understanding the combined effects of salinity and sediment burial depth on the seed germination and seedling growth of wetland species is essential for the guidance of coastal wetland restoration.

Suaeda salsa, from the family of Amaranthaceae, is a typical annual succulent halophyte and one of the dominant species in the intertidal zone of coastal wetlands in northern China. In contrast with other dominant wetland species e.g. *Phragmites australis*, *S. salsa* only uses seeds for population expansion and restoration from disturbances. This species has important economic value because the seeds contain approximately 40% oil, and the young leaves and branches are a nutritious food source due to their high vitamin and amino acid contents (Zhao 1998). It is also known for a visually appealing 'red carpet' scene (Fig. 1), due to the high concentrations of betalain in its shoots, during the entire growing period in the intertidal zone (Wang et al. 2006). A previous study found that low levels of salt stress could stimulate the growth of *S. salsa* (Duan et al. 2007), and its seedlings could adapt to different levels of salt stress through regulating enzyme activities, ion balance, osmotic substances, chlorophyll content and some morphological indices such as branch number and biomass allocation (Guan et al. 2011). However,

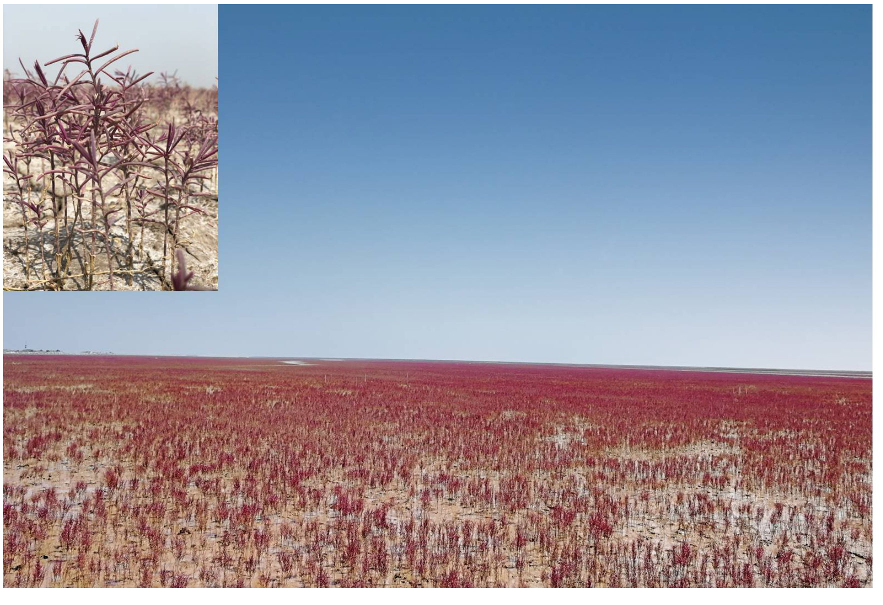

Figure 1. The *Suaeda salsa* plant and 'red carpet' scene in the coastal wetland of the Yellow River Delta.

how *S. salsa* responds to the interaction of sediment burial and salt stress in the intertidal zone is not clear.

In this study, we aimed to investigate how sediment burial depth and salinity influence the seedling emergence, plant growth and biomass allocation of *S. salsa*. We hypothesized that: 1) the two factors (sediment burial depth and salt stress) had an additive effects on seedling emergence and growth, 2) the largest seedling biomass occurs in a shallow sediment burial combined with low salt concentration condition, rather than in 0 cm burial depth and salt-free conditions and 3) the root biomass allocation increases with increasing sediment burial depth in order to absorb water and nutrients from the soil to support shoot and leaf growth.

Material and methods

Research region

The Yellow River Delta (37°35′–38°12′N, 118°33′–119°20′E) is located in Shandong Province in the middle of eastern China. It has a temperate semi-humid continental monsoon climate with distinctive seasons and a rainy summer. The annual average temperature is 12.2°C, and the frost-free period is 196 days. The annual average precipitation is 609.5 mm, 70% of which falls during the monsoon between June and August. The annual evaporation is 1962 mm (Song et al. 2016). The dominant soil types are classified as calcaric fluvisols, gleyic solonchaks and salic fluvisols (Food and Agriculture Organization), produced from the Loess Plateau and carried by the Yellow River. The dissolubility salt content in the upper soil layer (0–20 cm) is much higher (> 8 g kg^{-1}) (Yu et al. 2014).

As the pioneer plant of tidal wetlands, *Suaeda salsa* is often affected by sediment deposition due to tidal physical disturbance and Yellow River flooding during the 'Water and Sand Regulation Project' every year. The formation of a sediment layer approximately 5–6 cm thick (Guan et al. unpubl.) occurs in the *S. salsa* community during this project every year, which could have significant effects on the seedling emergence and growth of *S. salsa*.

Experimental design

Suaeda salsa seeds were collected in November, 2018 from the coastal wetlands of the Yellow River Delta. All seeds were stored in an ice-box under dark and dry conditions at 4°C before the experiment. The sediment used in this experiment was sampled from the Yellow River Delta Ecology Research Station of Coastal Wetland (37°45′50″N, 118°59′24″E). The sample depth was the surface 20 cm and the salt content of the sediment was 0.43%. This study was conducted in a research field at Yantai University in April 2019. Five sediment burial depths (0, 1, 3, 5 and 7 cm) and four salt levels (0, 1, 2 and 3% NaCl solutions) were investigated and a completely randomized block design was used. There were four replicates for each treatment and a total of 80 pots. Eight intact seeds were selected and planted in each plastic pot (20 cm in diameter, 20 cm in height) filled with sediment. After sowing, the pots were watered with different levels of NaCl solutions every two days until the end of the experiment, Purified water was used for the 0% salt treatment. The pots had drainage holes in the bottom. These holes were covered with nets to prevent sediment loss and allow drainage of excess water or salt solution.

The number of emerged seedlings was recorded every week and total seedling emergence was quantified as the cumulated percentage of emerged seedlings at the end of the experiment. The emergence rate was estimated using a modified Timson index of germination velocity: $\Sigma G/t$, where G is percentage of seedling emergence per day, and t is total germination period (Khan and Ungar 1984). The experiment was conducted for approximately eight weeks before flowering. The seedling height and branch number were measured and all of the plants were harvested when the experiment terminated. The leaf, shoot and root were separated, and all samples were dried at 60°C to a constant weight. The biomasses of the leaf, shoot and root were measured.

Statistical analysis

A generalized linear model (GLM) was used to detect the effects of burial depth and salt treatment on seedling emergence, seedling height, branch number, and the biomasses of leaf, shoot and root. A multiple comparison test was used to compare significant differences among treatment means ($p < 0.05$). Since no seedlings emerged from the 7 cm burial depth, this treatment was excluded from the analyses. All analyses were performed with SPSS ver. 20.0 (SPSS, IL, USA).

Results

Seedling emergence

GLM analysis showed that the seedling emergence percentage and rate were significantly affected by salt stress and burial depth ($p < 0.05$), but not by the interaction of the two factors (Table 1).

The percentage of seedling emergence decreased in response to increasing burial depth and salt stress (Fig. 2). The highest percentage of seedling emergence occurred at 0 cm burial depth under 0% and 1% NaCl concentrations. No seedlings emerged from 7 cm burial depth under any of the NaCl concentrations. Only 6.25% of seedlings emerged at 5 cm burial depth in the 0% NaCl treatment (Fig. 2A). As the NaCl concentration increased, no seedlings emerged from 5 cm burial depth (Fig. 2B–D).

Seedling emergence was also delayed by increasing burial depth of sediment and salt stress. At a 0 cm burial depth, seedlings emerged in the first week and reached the highest percentage in the second or third week (Fig. 2). At deeper depths however, the seedlings emerged from the second week at the earliest. Salt stress stretched the emergence percentage-time

Table 1. Generalized linear model analysis of seedling emergence and seedling growth indices of *S. salsa*. Values in bold mean significant at $p < 0.05$.

Index	Salt		Burial depth		Salt × burial depth	
	F-value	p-value	F-value	p-value	F-value	p-value
Percentage of emergence	6.311	**0.028**	42.212	**0.000**	1.371	0.251
Emergence rate	5.988	**0.031**	21.338	**0.001**	1.95	0.097
Seedling height	18.334	**0.000**	3.904	**0.031**	2.085	0.085
Branch number	6.487	**0.002**	7.199	**0.003**	2.715	**0.032**
Leaf biomass	24.328	**0.000**	0.909	0.415	5.823	**0.001**
Shoot biomass	20.206	**0.000**	5.165	**0.013**	2.730	**0.034**
Root biomass	27.357	**0.000**	7.037	**0.004**	1.471	0.227
Total biomass	7.522	**0.019**	0.864	0.468	3.713	**0.008**

curves in length, especially at 2% and 3% NaCl concentrations (Fig. 2C–D). Therefore, the highest seedling emergence rate occurred at 0 cm burial depth under both 0 and 1% NaCl concentrations (Fig. 3).

Seedling growth

Seedling height was significantly influenced by salt stress and burial depth ($p < 0.05$, Table 1), but not by an interaction of the two. As NaCl concentration increased, seedling height tended to decrease at all burial depths (Fig. 4A). In low NaCl concentrations (≤ 2%), the differences were not obvious. However, seedling height in the 3% NaCl concentration significantly decreased compared with that in the 0% NaCl treatment ($p < 0.05$). Similarly, there was no significant difference in seedling height among different burial depths in low NaCl concentrations. However, the burial treatment decreased the seedling height significantly when the NaCl

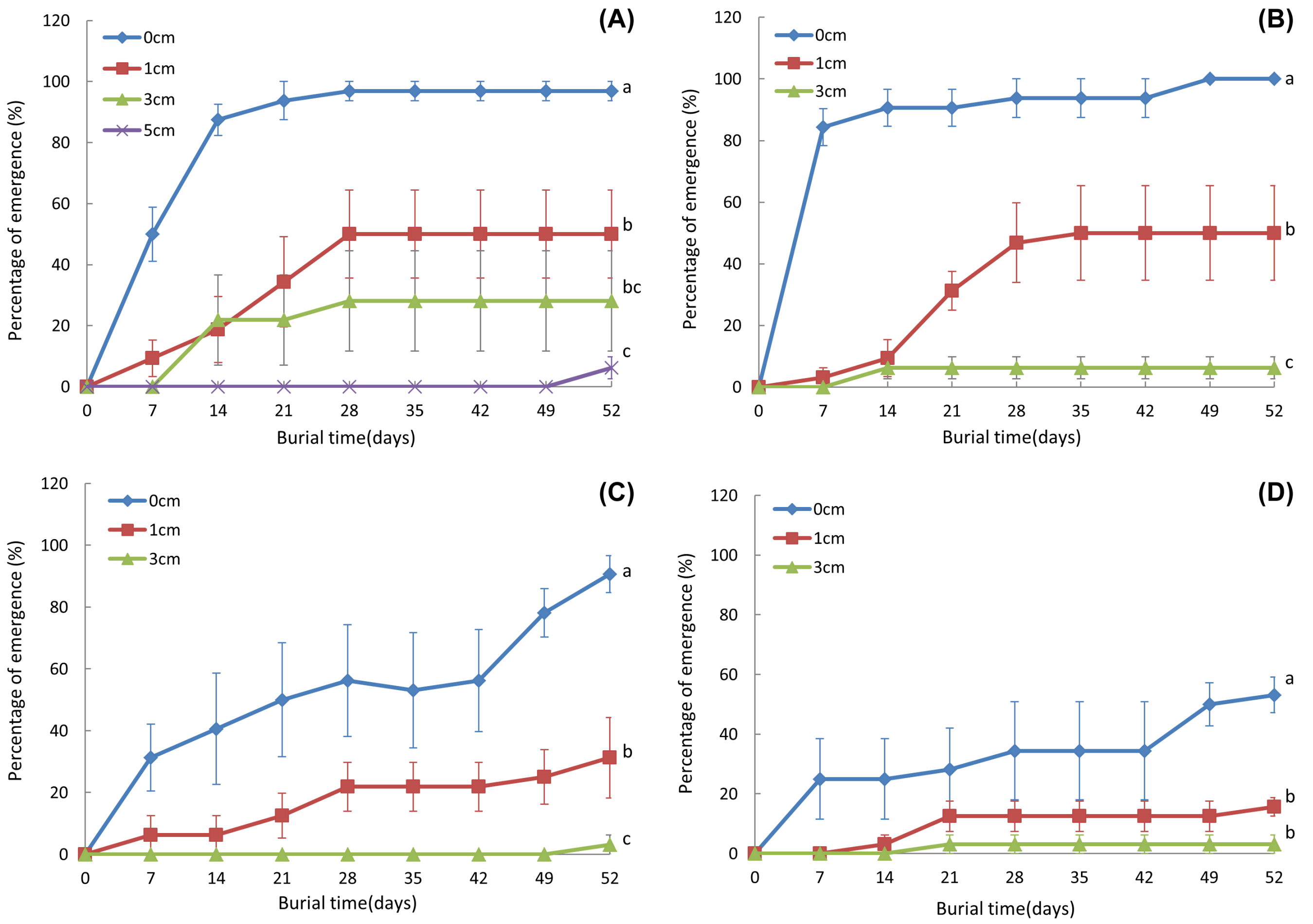

Figure 2. Emergence course of seedlings of *Suaeda salsa* under different sediment burial depth and salt stress. (A) Salt-free, (B) 1% NaCl solution, (C) 2% NaCl solution and (D) 3% NaCl solution. Values with the different letters are significantly different at $p < 0.05$. Vertical lines represent one standard error.

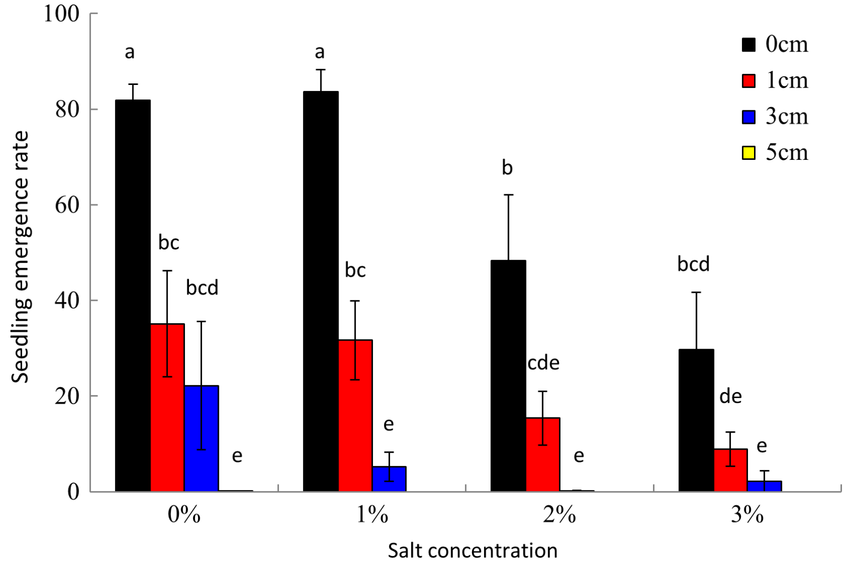

Figure 3. Seedling emergence rate of *Suaeda salsa* under the interactive effects of sediment burial depth and salt stress. Bars represent ± SE (n = 4). Different letters indicate significant differences from each other ($p < 0.05$).

concentration reached 3% ($p < 0.05$). The seedling height at 5 cm burial depth was not included because the data was insufficient for statistical analysis.

The branch number was significantly affected by salt stress, burial depth and an interaction of the two ($p < 0.05$, Table 1). The response of the branch number to burial depth and salt stress differed according to seedling height. With increasing burial depth, the branch number increased significantly in 0% and 1% NaCl treatments ($p < 0.05$, Fig. 4B). However, under the higher NaCl concentrations (2% and 3%), branch number did not significantly differ among different burial depths ($p < 0.05$). Furthermore, the branch numbers under low NaCl concentrations (0–2%) were not significantly different. However, under the 3% NaCl concentration, branch number significantly decreased at 1 cm and 3 cm burial depths. The highest branch numbers occurred at 1 cm burial depth in 0% NaCl solution and at 3 cm burial depth in 1% NaCl solution.

Biomass and biomass allocation

The leaf, shoot biomass and total biomass were significantly affected by salt stress and the salt stress-burial depth interaction, root biomass was affected by salt stress and burial depth, and shoot biomass was affected by salt stress-burial depth interaction ($p < 0.05$, Table 1). Generally, leaf, shoot, root and total biomass significantly decreased with increasing salt concentration, but there were insignificant differences between 1% and 2% NaCl concentrations. The effects of burial depth were inconsistent regardless of salt stress. The leaf, shoot, root and total biomass increased with increasing burial depth in the no-salt (0% NaCl) treatment (Fig. 5). However, the biomass of seedlings and different organs significantly decreased with burial depth under different NaCl concentrations ($p < 0.05$). Therefore, the highest biomass values occurred under 0% NaCl and 3 cm burial depth treatment.

The ratio of leaf to total biomass increased with increasing burial depth and NaCl concentrations until 2%. In contrast, the ratio of root to total biomass decreased and the shoot biomass ratio remained relatively constant among all treatments (Fig. 6).

Discussion

As one of the dominant species in the intertidal zone of coastal wetlands in the Yellow River Delta, *Suaeda salsa* is influenced by numerous environmental factors, especially high sediment deposition and salt stress. In this study, successful seedling emergence occurred at sediment depths down to 5 cm without added salt solution. Only treatments shallower than a 3 cm burial depth showed seedling emergence with increasing salt stress. Contrary to our first hypothesis, the interactive effects of salt stress and burial depth did not significantly influence seedling emergence (Table 1), in fact the seedling emergence rate decreased significantly under the same burial depth with increasing salt stress. The highest percentage of seedling emergence occurred on the soil surface (0 cm burial depth), as similarly reported by a previous study, which found that highest percentage of seedling emergence occurred when seeds were placed near or on the soil surface (Boyd and Van Acker 2003). However, seeds in different ecosystems perform different strategies to adapt to burial depth, for instance, the highest percent emergence of *Calamovilfa longifolia* seedlings occurred at 1–2 cm depths (Maun and Riach 1981), and that of *Nitraria sphaerocarpa* at 2 cm depth (Li et al. 2006). These species all live in sand dune ecosystems; shallow burial maintains a moist environment around their seeds to prevent them from drying out (Baskin and Baskin 1998). In tidal wetlands, the sediment surface (0 cm) could provide adequate humidity, temperature and nutrient

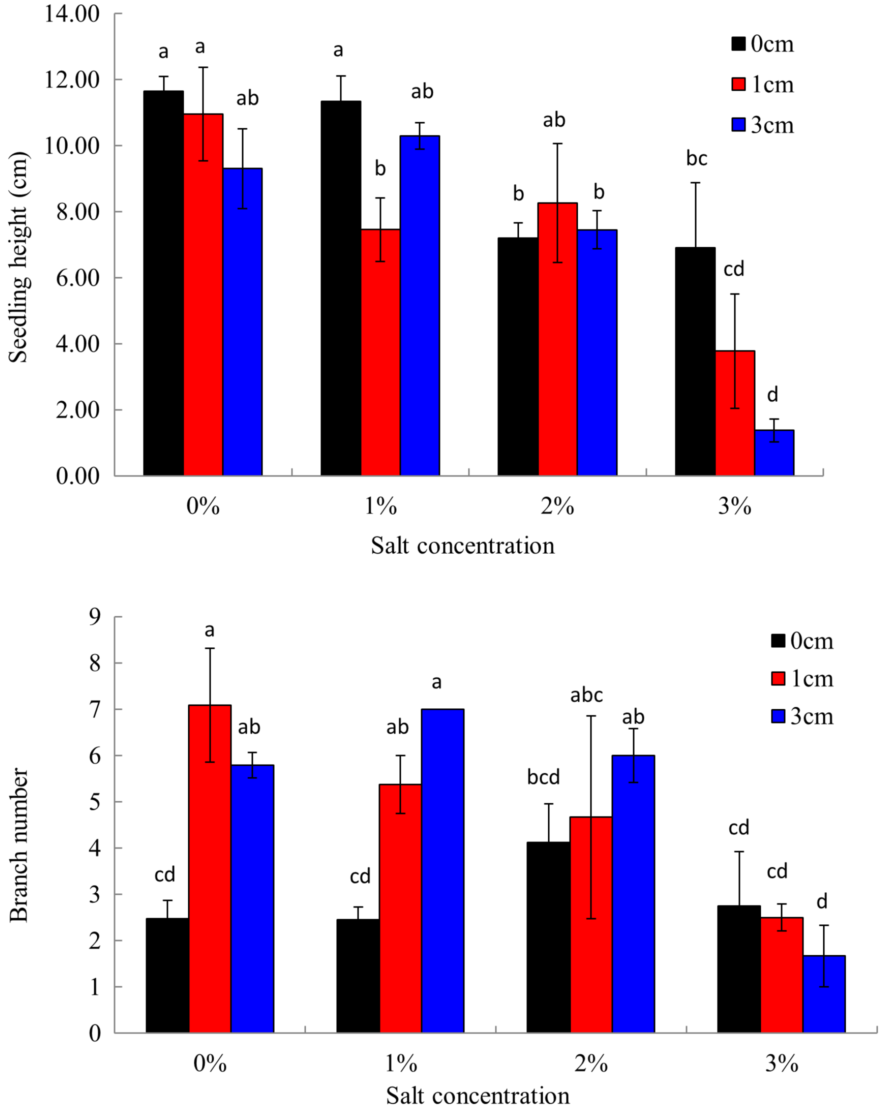

Figure 4. Means (± SE) seedling height and branch number of *Suaeda salsa* under the interactive effects of sediment burial depth and salt stress. Different letters indicate significant differences from each other ($p < 0.05$).

conditions propitious to the rapid germination of *S. salsa* seeds (Gleason et al. 2003, Guan et al. 2019). Based on the present results, the low seedling emergence percentage caused by the salt stress and burial depth could be one of the reasons that the density of *S. salsa* is lower in the tidal wetlands than in the upland wetlands of the Yellow River Delta.

In the present study, sediment burial treatment did not dramatically affect the seedling height when the salt stress was lower than 2% NaCl concentration, while the branch number increased significantly with increasing burial depth in 0% and 1% treatments. The positive effects of sediment burial on seedling growth would be beneficial for maintaining the population of *S. salsa* and encouraging further growth in salt marshes. Previous studies have also shown that seedlings successfully emerging in deeper locations had a higher seedling height, aboveground biomass or a longer root system (Li et al. 2006, Liu et al. 2016). However, with increasing salt stress, the stimulating effects disappeared and the inhibiting effects were significantly enhanced. This could be explained by the salt tolerant characteristics of *S. salsa*, which is able to grow well under a moderate saline environment (Guan et al. 2011), while in strong saline conditions, its growth is inhibited, especially with the interaction of sediment burial.

Consistent with our second hypothesis, the biomass showed increasing trends with increasing sediment burial depth under no salt stress, especially the leaf biomass and total biomass. After seedling emergence, the aboveground parts, such as the leaf, will accumulate more biomass through photosynthesis, and the stimulation of suitable burial depths on root growth could help seedlings absorb more nutrients from the soil to support shoot and leaf growth (Perumal and Maun 2006). However, for seeds placed in a saline environment, part of the energy required for seedling emergence was found to be determined not only by burial depth but also by

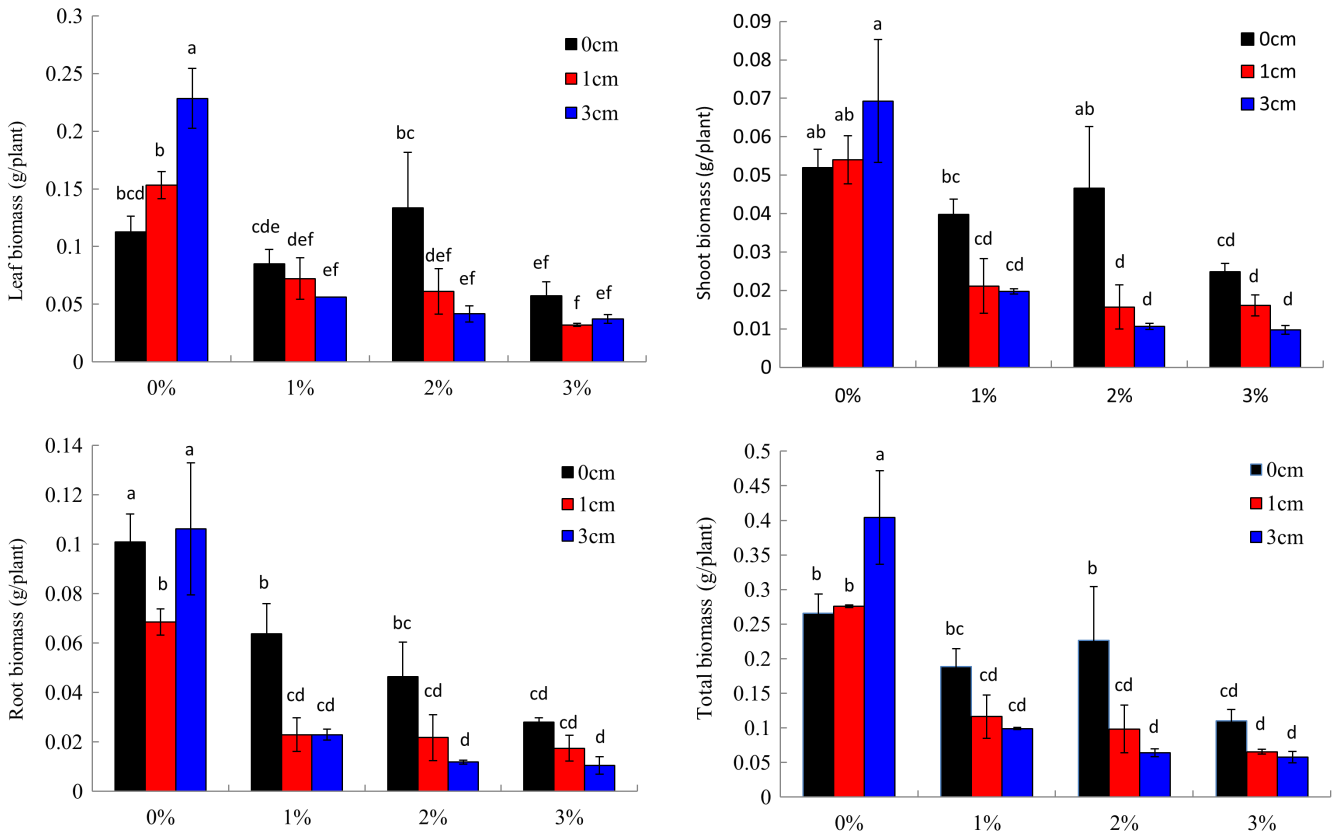

Figure 5. Means (± SE) leaf biomass, shoot biomass, root biomass and total biomass of seedlings of *Suaeda salsa* and allocated proportion of biomass under the interactive effects of sediment burial depth and salt stress. Different letters indicate significant differences from each other ($p < 0.05$).

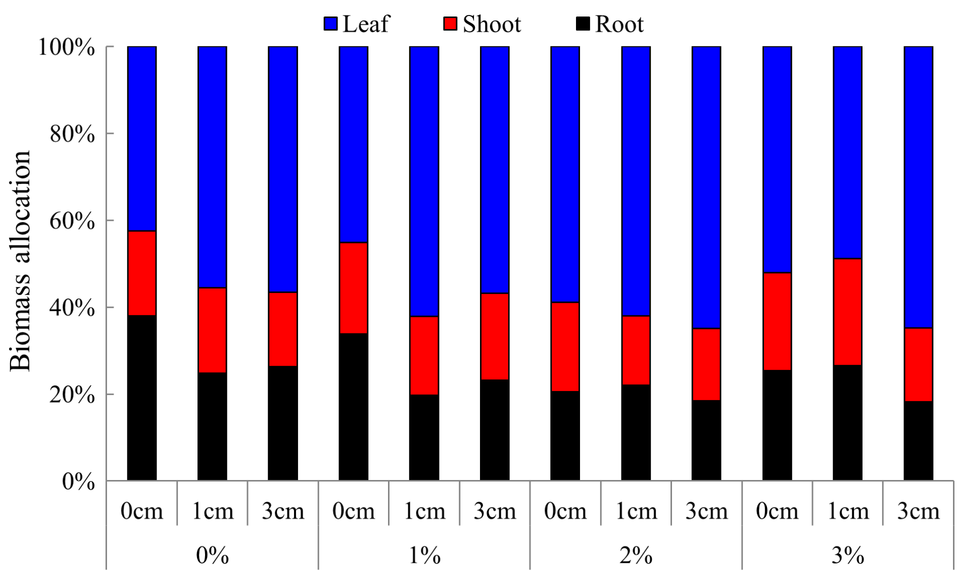

Figure 6. Allocated proportion of leaf, shoot and root biomass of *S. salsa* seedlings under the interactive effects of sediment burial depth and salt stress.

soil salt stress (Cabaço et al. 2008, Zhang et al. 2018). Greater burial depth or higher salt stress would cost greater reserves of carbohydrates and other nutrients in the seeds (Jarvis and Moore 2015). The present study also showed that biomass decreased significantly with increasing burial depth under all salt treatments, the GLM results also indicated that the interaction of burial depth and salt stress significantly influenced the leaf, shoot and total biomass of *S. salsa* (Table 1).

The pattern of biomass allocation is also one of the major adaptation mechanisms of plants (Maun and Riach 1981, Guan et al. 2011). In this study, the leaf biomass ratio tended to increase with increasing burial depth and salt stress, while the root biomass ratio decreased, which is contrary to our third hypothesis. Zhao et al. (2007) found that when the seeds of *Nitraria sphaerocarpa* were subject to increasing burial depth, there was a tendency for both biomass allocation to the roots and biomass allocation to belowground stems to increase. While for the seeds of *Castanea crenata*, the root/mass ratio decreased significantly and the ratio of belowground stems increased (Seiwa et al. 2002). Based on the specific environment inhabited by *S. salsa*, it is necessary for the species to use more energy for the growth of aboveground parts, more leaves should be produced for photosynthesis, which is favorable for emerging from the burial deposit. This also reflects the important adaptive strategies of *S. salsa* to cope with the rapid sediment burial of tidal wetlands in the Yellow River Delta.

In conclusion, although sediment burial significantly decreased the seedling emergence percentage and rate of *S. salsa*, the branch number was stimulated under moderate salinity. This may be partially explained the superior adaptability of *S. salsa* to rapid sediment burial in tidal wetlands; it allocates a greater amount of resources and energy to the leaves, which perform photosynthetic activity rapidly. A sediment burial depth greater than 3 cm exceeded the germination depth for *S. salsa* seeds under a high saline environment. A 0–1 cm sediment burial depth was found to be the most suitable for seedling emergence of *S. salsa* in the tidal wetlands of the Yellow River Delta. These findings will help to guide restoration projects of degraded tidal wetlands.

Acknowledgements – We thank the Yellow River Delta Ecology Research Station of Coastal Wetland, Chinese Academy of Sciences, for the help with field work.
Funding – This work was financially supported by the National Natural Science Foundation of China (U1806218 and 41871091).
Conflicts of interests – The authors have no competing interests.

Author contributions

Bo Guan: CRediT contribution not specified. **Lin Zhang**: Data curation (equal); Investigation (lead). **Mei Li**: Data curation (equal); Investigation (lead). **Hongxiang Zhang**: CRediT contribution not specified. **Xiaolong Zhang**: CRediT contribution not specified. **Guangxuan Han**: CRediT contribution not specified. **Junbao Yu**: Funding acquisition (equal).

References

Adam, P. 1990. Saltmarsh ecology. – Cambridge Univ. Press.

Baskin, C. C. and Baskin, J. M. 1998. Seeds, ecology, biogeography and evolution of dormancy and germination. – Academic Press.

Beas, B. J. et al. 2013. Seed bank responses to wetland restoration: do restored wetlands resemble reference conditions following sediment removal? – Aquat. Bot. 108: 7–15.

Benvenuti, S. et al. 2001. Light, temperature and burial depth effects on *Rumex obtussifolius* seed germination and emergence. – Weed Res. 41: 177–186.

Boyd, N. S. and Van Acker, R. C. 2003. The effects of depth and fluctuating soil moisture on the emergence of eight annual and six perennial plant species. – Weed Sci. 51: 725–730.

Cabaço, S. et al. 2008. The impact of sediment burial and erosion on seagrasses: a review. – Estuar. Coast Shelf Sci. 79: 354–366.

Cui, B. et al. 2009. Evaluating the ecological performance of wetland restoration in the Yellow River Delta, China. – Ecol. Eng. 35: 1090–1103.

Duan, D. et al. 2007. Seed germination and seedling growth of *Suaeda salsa* under salt stress. – Ann. Bot. Fenn. 44: 161–169.

Duarte, C. M. et al. 2008. The charisma of coastal ecosystems: addressing the imbalance. – Estuar. Coasts 31: 233–238.

Gleason, R. A. et al. 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. – Wetlands 23: 26–34.

Guan, B. et al. 2011. Physiological responses of halophyte *Suaeda salsa* to water table and salt stresses in coastal wetland of Yellow River Delta. – Clean Soil Air Water 39: 1029–1035.

Guan, B. et al. 2019. Soil seed bank and vegetation differences following channel diversion in the Yellow River Delta. – Sci. Total Environ. 693: 133600.

Huang, Z. and Gutterman, Y. 1998. *Artemisia monosperma* achene germination in sand: effects of sand depth, sand/moisture content, cyanobacterial sand crust and temperature. – J. Arid Environ. 38: 27–43.

Huang, Z. et al. 2004. Factors influencing seed dormancy and germination in sand, and seedling survival under desiccation, of *Psammochloa villosa* (Poaceae), inhabiting the moving sand dunes of Ordos, China. – Plant Soil 259: 231–241.

Jarvis, J. C. and Moore, K. A. 2015. Effects of seed source, sediment type and burial depth on mixed-annual and perennial *Zostera marina* L. seed germination and seedling establishment. – Estuar. Coast. 38: 964–78.

Jurik, T. W. et al. 1994. Effects of sediment load on seedling emergence from wetland seed banks. – Wetlands 14: 159–165.

Khan, M. A. and Ungar, I. A. 1984. The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* willd. – Am. J. Bot. 71: 481–489.

Li, Q. et al. 2006. Effects of sand burial depth and seed mass on seedling emergence and growth of *Nitraria sphaerocarpa*. – Plant Ecol. 185: 191–198.

Liu, B. et al. 2016. Effects of burial depth and water depth on seedling emergence and early growth of *Scirpus planiculmis* Fr. Schmidt. – Ecol. Eng. 87: 30–33.

Mao, P. et al. 2019. Effects of seed size and sand burial on germination and early growth of seedlings for coastal *Pinus thunbergii* Parl. in the northern Shandong peninsula, China. – Forests 10: 281.

Maun, M. A. 1998. Adaptations of plants to burial in coastal sand dunes. – Can. J. Bot. 76: 713–738.

Maun, M. A. and Riach, S. 1981. Morphology of caryopses, seedlings and seedling emergence of the grass *Calamovilfa longifolia* from various depths in sand. – Oecologia 49: 142–167.

Mou, X. and Sun, Z. 2011. Effects of sediment burial disturbance on seedling emergence and growth of *Suaeda salsa* in the tidal wetlands of the Yellow River estuary. – J. Exp. Mar. Biol. Ecol. 409: 99–106.

Perumal, V. J. and Maun, M. A. 2006. Ecophysiological responses of dune species to experimental burial under field and controlled conditions. – Plant Ecol. 184: 89–104.

Seiwa, K. et al. 2002. Effects of burying depth and seed size on seedling establishment of Japanese chestnuts, *Castanea crenata*. – For. Ecol. Manage. 164: 149–156.

Song, D. et al. 2016. Change characteristics of average annual temperature and annual precipitation in coastal wetland region of the Yellow River Delta from 1961 to 2010. – Wetland Sci. 14: 248–253, in Chinese with English abstract.

Vahabinia, F. et al. 2019. Environmental factors' effect on seed germination and seedling growth of chicory (*Cichorium intybus* L.) as an important medicinal plant. – Acta Physiol. Plant. 41: 27.

Wang, C. et al. 2006. Identification of betacyanin and effects of environmental factors on its accumulation in halophyte *Suaeda salsa*. – J. Plant Physiol. Mol. Biol. 32: 195–201, in Chinese with English abstract.

Yang, J. et al. 2007. Water fluxes at a fluctuating water table and groundwater contributions to wheat water use in the lower Yellow River flood plain, China. – Hydrol. Process. 21: 717–724.

Yu, J. et al. 2014. The spatial distribution characteristics of soil salinity in coastal zone of the Yellow River Delta. – Environ. Earth Sci. 72: 589–599.

Yu, J. et al. 2016. Distribution of carbon, nitrogen and phosphorus in coastal wetland soil related land use in the modern Yellow River Delta. – Sci. Rep. 6: 37940.

Zhang, H. et al. 2018. The best salt solution parameter to describe seed/seedling responses to saline and sodic salts. – Plant Soil 426: 313–325.

Zhang, J. and Maun, M. A. 1990. Sand burial effects on seed germination, seedling emergence and establishement of *Panicum virgatum*. – Holarct. Ecol. 13: 56–61.

Zhang, J. et al. 2016. Effect of shifting sand burial on soil evaporation and moisture-salt distribution in a hyper-arid desert. – Environ. Earth Sci. 75: 1417.

Zhao, K. 1998. The halophytes in China. – Science Press, Beijing, in Chinese.

Zhao, W. et al. 2007. Effects of sand burial disturbance on seedling growth of *Nitraria sphaerocarpa*. – Plant Soil 295: 95–102.