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# The effects of hydrological connectivity blocking on *Suaeda salsa* development in the Yellow River Delta, China

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Blocking of hydrological connectivity could greatly impact the sediment deposition process and change water and salinity conditions, which in turn affect plant germination, growth, and development in delta wetlands. A 2year experiment, which included the effects of soil burial, water, and salinity on germination, growth, and production, was conducted to examine the function of hydrological connectivity blocking on the development of Suaeda salsa, a halophyte species. The results demonstrated that soil burial, water, and salinity all had significant effects on seed germination, plant growth, and production (p < 0.05). Seed germination decreased as soil buried depth increased (< 4 cm), and seeds did not germinate successfully when the buried depth was > 4 cm. Seed germination was the highest at 0 cm burial. However, moderate burial was beneficial for seedling emergence; therefore, the survival rate was the lowest when seeds were distributed at the surface (0 cm). Water and salinity both significantly affected the germination, growth, and productivity of S. salsa. Moderate salinity (10-20 g/kg) and fluctuating water (0-10 cm water depth) were suitable for seed germination and plant growth. Low salinity (< 10 g/kg), High salinity (>20 g/kg), drought, and high water levels (long-term flooding with water depth > 10 cm) were not conducive to the growth of S. salsa, and biomass and seed yield were also reduced. As a halophyte, salinity that is too low or too high is unsuitable for S. salsa population. Water and salinity also significantly affected S. salsa population (p < 0.05). In particular, water can offset the hazards of high salt concentrations. Blocking of hydrological connectivity can influence seed germination, yield, and vitality. In this case, S. salsa may have died out from the coastal wetland due to the lack of hydrological connectivity restoration.

#### KEYWORDS

hydrological connectivity blocking, seed germination, seed yield and vitality, *Suaeda* salsa, the Yellow River Delta

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### Introduction

Hydrologic connectivity is a hydrologic process that supports the transfer of mass and energy between or among different water bodies and/or locations (soils, atmosphere, and vegetation) across a landscape (Lexartza-Artza and Wainwright, 2009; Bracken et al., 2013). Complete hydrological connectivity cannot only promote the cycle of energy and nutrients but also provide important habitats for animals and plants (Covino, 2017; Shao et al., 2019; Zheng et al., 2022). Wetland ecosystems with good hydrological connections can keep nutrients in the water body relatively stable in a mutable external environment and play a significant role in maintaining biodiversity (Noe et al., 2019; Norton et al., 2022). Hydrological connectivity is particularly important in delta wetlands, with intense interactions between saline and fresh water (Liu et al., 2020; Cui et al., 2022). In this context, delta wetlands are not only the habitat of many migratory waterfowl and are important for the protection base of biodiversity, but they also provide a buffer zone to maintain the dynamic balance of sea and land. They play a unique role in the material cycle, energy flow, and information transmission between rivers and oceans (Liu et al., 2021).

Suaeda salsa community is the main vegetation and the only pioneer plant in the salt marsh in the Yellow River Delta (YRD), China. It is mainly distributed in the transitional zone from land to beach, and provides an important habitat for birds and macrobenthos (Yu et al., 2012). Seed germination of S. salsa is highly susceptible to environmental factors such as water depth, salinity, and burial depth (Yu et al., 2012; Wang F. et al., 2015; Müller et al., 2019. Therefore, the distribution and growth of S. salsa may be vulnerable to changes in hydrological connectivity. In recent years, due to climate change and human activities such as roads and dams, the hydrological connectivity of the Yellow River has been seriously affected, the sediment transport process has been blocked, and the water-salt-sediment environment of coastal wetlands has also changed significantly (Wang S. et al., 2015; Saunders et al., 2016; Li et al., 2021). The amount of sediment entering the sea has decreased by 89% over the past 50 years, which has decreased the deposition rate of the YRD. Siltation and erosion in the estuary area have been altered, the amount of fresh water and salt water decreased dramatically, and soil salinity increased accordingly (Wang S. et al., 2015; Xue et al., 2022). Consequently, the salt marsh habitats of the YRD had deteriorated or many vegetation types had dried out (Liu, 2020). At the same time, the area of S. salsa shows a decreasing trend since 2006, and the dominance degree of S. salsa is decreasing continuously and the degree of fragmentation is severe (Zhang et al., 2022). Therefore, analyzing the ecological effects of dialectical hydrological connectivity on the development of S. salsa is of great significance.

Once hydrological connectivity blocking occurs in a delta, its effects on *S. salsa* community are unpredictable; hence,

a greenhouse experiment was conducted to test it. In this experiment, seed germination and growth of *S. salsa* were subjected to different conditions that represent the situation of hydrological connectivity blocking. The purpose of the study was to solve those questions: (1) Do the hydrological connectivity blocking have negative or positive effect on *S. salsa* development? (2) What is the way that hydrological connectivity blocking affects *S. salsa* development? The results can provide valuable implications for the management of hydrological system and the restoration of degraded wetlands in the YRD.

### Materials and methods

#### Site description

The study area is located in the YRD (118°3381811°2081, 37°353781°12378118y Dongying City, Shandong Province, China. The study area has a warm temperate continental monsoon climate, with distinctive seasons and rainy summers. The average annual temperature is 12.1°C. The frost-free period lasts 196 d per year in this region. The annual average rainfall in the study area is 551.6 mm, whereas the annual average evaporation is 1,962 mm. Approximately 70% of the precipitation occurs from June to August. Surface water in this area is mainly affected by precipitation and upriver water, particularly by the water-sediment regulation of the Yellow River at the end of June since 2002. The main soil types are tidal and salt soil. *S. salsa* and *Phragmites australis* are dominant species in the YRD (Guan et al., 2020).

### Experiment design

#### Seed preparation

Fully developed seeds of *S. salsa* local genotypes were collected in October 2019 from the YRD National Natural Reserve. All seeds were kept under dark and dry conditions at 4°C until the start of the germination experiments. Soil for the experiment was collected from a depth of 20 cm near the YRD in 2019. All experiments were conducted in a greenhouse located at Ludong University, China. At the beginning of the experiment, seeds were surface-sterilized in an aqueous solution of 0.1% KMnO<sub>4</sub> for 10 min to avoid fungal attack, and subsequently rinsed with distilled water before being used in seed germination experiments.

# Experiment 1: Effects of soil burial depth on seed germination in 2019

Germination experiments at different buried depths were conducted in a barrel (radius: 5 cm and height: 15 cm). Seeds were germinated at 0 cm (M0), 1 cm (M1), 2 cm (M2), 4 cm (M4), and 6 cm (M6) buried depths, respectively. The soil was collected from the YRD. The salinity, water content, bulk density, electrical conductivity and pH of the initial experimental soils were 1.12 g/kg, 27.18%, 1.09 g/cm<sup>3</sup>, 478  $\mu$ m/cm, and 8.92, respectively. For each treatment, there were three replicates of 50 seeds each. During seed germination in buried soil, seeds were irrigated with distilled water to maintain saturation. All seeds were subjected to an alternating diurnal regime of 12 h of light at 25°C and 12 h of darkness at 15°C for 21 days. Seeds were considered germinated when the radicle protruded 1 mm from seed coat. Germination was recorded daily for 14 days, and seedling survival was recorded at the end of the experiment. The entire experiment lasted 4 weeks.

## Experiment 2: Effects of water and salt on germination and growth of *Suaeda salsa* in 2019

After the burial experiment, S. salsa seeds were planted in a barrel (radius: 15 cm and height: 35 cm) at a depth of 1 cm (according to the result of the soil burial experiment) to investigate the effects of the water-salt gradient on their germination and growth. The experiment began with three water treatments [long-term flooding (5-15 cm, F), periodic flooding (0-10 cm, S), and long-term drought (drought to saturated, D)], and four salinity treatments (i.e., 0, 10, 20, and 30 g/kg) in an orthogonal design. Salinity was controlled by adding a sea salt solution (obtained from seawater), in which Na<sup>+</sup> and Cl<sup>-</sup> were the most important ions (Table 1). Treatment D was carried out every 7 d. Treatment S was injected twice daily, and water was emptied after 2 h of water injection. Water control of the F treatment was performed every 2 d. Percent germination was recorded every day. A seed was considered germinated when the coleoptiles were elongated to 1 mm. The entire experiment lasted 16 weeks, and height, density, biomass, content of Na<sup>+</sup> and Cl<sup>-</sup> in each part were recorded and examined at the end.

### Experiment 3: Germination of seeds produced in experiment 2 in 2020

Germination experiments were conducted in a dish (radius: 5 cm). Seeds were germinated under saturated conditions at 10 g/kg salinity (the ideal germination condition). In this experiment, all seeds produced in experiment 2 were used in this experiment without replicates. During seed germination, the seeds were irrigated with distilled water to maintain moisture. The experiment lasted for 21 days. Percent germination was recorded daily. Seeds were considered germinated when the coleoptiles were elongated to 1 mm.

TABLE 1 Concentrations of main salt ions in the Yellow River Delta (Unit: mg/kg).

Na <sup>+</sup>	$Mg^{2+}$	К+	Ca <sup>2+</sup>	Cl-	HCO <sup>3-</sup>	SO4 <sup>2-</sup>	CO <sub>3</sub> <sup>2-</sup>
387,210	510	66.5	1232.5	433,100	175,680	4115.5	0

#### Data analysis

Statistical analyses were performed using SPSS 20 and Origin 9.2. One-way analysis of variance (ANOVA) was used to determine the effects of burial depth, water regime, and salinity on the germination and growth of *S. salsa*. To meet the assumptions of homoscedasticity, some growth and photosynthetic parameters were log-transformed or square-root transformed. Before the analyses, graphs with residuals were applied to examine the rationality of the model assumptions and the reliability of the data. Multiple comparisons of means were performed using Duncan's test; different letters in **Figures 1**, **2** indicate significant differences at a significance level of 0.05. Values represent the mean  $\pm$  SE of three replicates.

### Results

# Effects of soil burial on the germination and survival of *Suaeda salsa*

Analysis of differences indicated that soil burial depth had significant negative effects on germination percent (p < 0.01). As the burial depth increased, the seed germination percent decreased gradually (**Figure 1A**). Seed germination percent was the highest at M0. When the burial depth was  $\geq 4$  cm, there was no seed germination. However, the seedling survival percent changed significantly (**Figure 1B**). The survival percent at M1 was the highest, followed by the germination rates at M2 and M0 treatments. The survival percent were not significantly different between burial depths of M1 and M2.

# Effects of water depth and salinity on the germination and survival of *Suaeda* salsa

Although *S. salsa* is a halophyte, salinity and water both showed significant effects on its germination and growth (p < 0.01). The germination percent of *S. salsa* decreased as soil salinity increased, and high salinity was detrimental for seed germination. After 4-week growth, the seedling survival percent was slightly lower than the seed germination percent in all treatments (**Figures 2A,B**). Water significantly affected germination of *S. salsa* (p < 0.01). At the period of seed germination, the germination percent was higher in F and S, especially in S. In treatment D, the seed germination percent was the lowest, even at 0 g/kg salinity. In treatment S, except for the 30 g/kg salinity, the seed germination percent at 10 g/kg salinity was the highest, even at 30 g/kg salinity, and the germination percent was up to 30%. Subjected to treatments S and D, the



0 cm (M0), 1 cm (M1), 2 cm (M2), 4 cm (M4), and 6 cm (M6) buried depths. Different letters indicate significant differences in different buried depth. The data was 0 at M4 and M6.

seedling survival percent did not decrease much more than the germination percent. The S treatment was the most ideal one for *S. salsa* under medium and low salinity conditions (salinity was  $\leq$  20 g/kg). The F treatment ( $\leq$  15 cm) was suitable for *S. salsa* growth at lower salinity.

# Effects of water and salt on the growth of *Suaeda salsa*

Water and salinity had significant complex effects on the growth of S. salsa. Medium to low salinity ( $\leq 20$  g/kg) and moderate water (periodic flooding at 0–10 cm) were beneficial to the growth of S. salsa (**Table 2**). Drought and high salinity (salinity was > 30 g/kg) were detrimental to the growth of *S. salsa*. In the F and D treatment, the height was the highest at 0 g/kg, and the density and total biomass were the highest at 10 g/kg. While in the S treatment, the height and total biomass were the highest at 10 g/kg. In all treatment, biomass at 10 g/kg salinity was the highest, and biomass was mainly distributed in stems and leaves. In the D treatment, by contrast, root biomass accounted for most of the total biomass. Results of water content

were interesting. Salt tolerance gradually increased as water conditions improved. In D treatment, water content was the most at 10 g/kg salinity. In F and S treatment, water content was the most at 20 or 30 g/kg salinity. Multi-way variance analysis indicated that the effects of water are the first priority in salt habitats, and the combined effect of salt and water is also important in regulating *S. salsa* growth.

 $Na^+$  and  $Cl^-$  were similarly distributed in each treatment, with the leaf content being the highest, followed by that in the stems and roots (**Figures 3A**-**F**). In the 0 salinity treatment,  $Na^+$ and  $Cl^-$  were more evenly distributed in the root-stem-leaf. In the same salinity value, content of  $Na^+$  was the highest in the S treatment, followed by that in the stems and roots in F and D treatments, respectively. The difference in  $Cl^-$  concentration in each treatment was not significant. In the same water regime, contents of  $Na^+$  and  $Cl^-$  increased as salinity increased.

# Effects of water-salt treatments on the seed yield and vitality

Seeds are the foundation of the establishment and development of plant communities; therefore, seed yield



and vitality are deemed as the preconditions of vegetation establishment and development. There was no seed production in the 0 g/kg and highsalt treatments (except for S30, **Table 3**). Seeds were produced at F10, S10, D10, F20, and S20 treatment. In the following year, the germination rates of seeds produced in the S10, F10, S20, and F20 treatments were higher than that in the D treatment. Although seeds were produced in the S30 treatment, their germination rate was 0%.

### Discussion

Germination and seedling emergence are critical stages in the life cycle of plants, particularly for annual halophytes, since they determine whether they can be established in variable environments (salt marshes or deserts) (Merino-Martín et al., 2017; Duan et al., 2018; Müller et al., 2019). In delta wetlands, the mutable deposition process, water regime (timing, duration, and depth), and soil salinity are outstanding environmental problems resulting from lack of hydrological connectivity (Dou et al., 2016). Therefore, adequate hydrological connectivity often determines the growth and distribution of plants. Once hydrological connectivity is blocked, the water cycle process changes, affecting the sediment deposition process and soil salinity, and finally affecting seed germination and plant growth (Wang S. et al., 2015).

Because of the interaction of fresh and saltwater, the sediment thickness in the YRD is variable. Seed germination is regulated by burial depth during the process of deposition (Mou and Sun, 2011). However, the effects were two-sided. Moderate buried depths could generally stimulate more germination and seeding than surface deposition of seed, because burial provides a moist environment around seeds and prevents them from desiccation (Sun et al., 2010). Excessive sediment may prevent seedling sprouting and affect survival because the emergence cannot reach the sediment surface or the seeds are unable to germinate due to lack of oxygen, light, and temperature fluctuation (Sun et al., 2010; Wu et al., 2013). In our study, the initial germination rate decreased and was negatively correlated with burial depth. A large percentage of seedlings emerged at shallow burial depths ( $\leq$  2 cm), but deep burials (> 2 cm) significantly reduced seedling



emergence. Similar relationships have also been recorded in other studies. The survival of seedlings is important for plant development. Many studies have indicated that germination rate determines colonization rate. However, many seedling emergences could not successfully colonize the site because of the effects of environmental factors (Duan et al., 2018). In our experiment, although initial germination was the highest at a burial depth of 0 cm, the final survival rate was the lowest. The final survival rate was the highest at 1 cm burial depth, with lower mortality of initial emergences. Mortality was lowest at a buried depth of 2 cm, but the initial germination rate was also low. This result is similar to those of Mou's findings (Mou and Sun, 2011). The most probable factors that could influence the germination and survival of S. salsa may be the micro-environmental factors surrounding the seeds, such as temperature, humidity, oxygen, and light (Müller et al., 2019). Different burial depths would substantially change these micro-environmental factors and significantly affect seed germination (Limón and Peco, 2016). Under surface conditions, poor water and temperature retention can result in

high seedling emergence mortality. Instead, a moderate buried depth could maintain a high seedling emergence survival with suitable influences of micro-environment factors (Soares et al., 2021).

Due to the interaction of fresh water and saline water, water logging and salt content are considered the two key environmental factors for plant establishment, succession, and productivity in the delta wetlands (Hou et al., 2020; Chen et al., 2022; Hussain et al., 2022). Waterlogging stress decreases the availability of carbon dioxide for salt marsh plants while also rendering oxygen levels deficient in the soils. Simultaneously, water influences plant growth through nutrient uptake via restricted transpiration rates and membrane permeability (Wang and Jiang, 2007). Furthermore, excess salinity from seawater affects plant growth via both osmotic stress and ionic toxicity (Wang F. et al., 2015; Louati et al., 2018). In our study, low water and low salinity showed significant positive effects on seed germination, seedling growth, and productivity. High water and salinity negatively affect seed germination and plant growth, and the effects of drought are

	Water regime	Salinity (g/kg)				
		0	10	20	30	
Height (cm)	F	$54.8 \pm 3.31a$	$45\pm7.35b$	$48.4\pm3.50 ab$	$22.4\pm4.50c$	
	S	$47.2\pm4.92b$	$57.6\pm3.77a$	$32.4 \pm 1.85 \text{c}$	$29.8\pm2.79c$	
	D	$29\pm2.00a$	$25.6\pm3.26b$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Density (plant/pot)	F	$51.00\pm4.50a$	$56.00\pm1.00a$	$20.00\pm4.00b$	$6.00\pm0.00c$	
	S	$50.50\pm0.50a$	$41.50\pm3.50b$	$48.50\pm3.50a$	$11.00\pm1.00c$	
	D	$7.50\pm1.50b$	$14.50\pm0.50a$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Total dry biomass (g/pot)	F	$49.12\pm 6.55c$	$128.68 \pm 1.68a$	$106.74\pm5.84b$	$41.76\pm1.00c$	
	S	$56.64\pm2.76b$	$121.12\pm25.74a$	$49.60\pm20.93b$	$49.80\pm3.77b$	
	D	$5.69\pm0.48b$	$38.10 \pm \mathbf{0.40a}$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Dry biomass of root (g/pot)	F	$2.84\pm0.13b$	$5.18\pm0.10a$	$2.73\pm0.17b$	$1.94\pm0.01c$	
	S	$3.68\pm0.16\text{b}$	$13.22\pm0.49a$	$2.06\pm0.22 bc$	$1.60\pm0.14c$	
	D	$1.39\pm0.40\text{b}$	$4.52\pm0.33$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Dry biomass of stem (g/pot)	F	$17.92\pm2.67c$	$45.06\pm1.48a$	$26.24\pm3.64b$	$13.22\pm0.46c$	
	S	$19.72\pm1.37b$	$41.01\pm12.19a$	$18.42\pm2.94b$	$12.29\pm1.01\text{b}$	
	D	$1.67\pm0.26b$	$6.30\pm0.17a$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Dry biomass of leaf (g/pot)	F	$28.36\pm3.76b$	$78.45\pm0.87a$	$77.78 \pm 4.85a$	$26.60\pm0.56b$	
	S	$33.25\pm1.66b$	$66.89 \pm 15.20a$	$29.12\pm17.89b$	$35.91\pm3.50b$	
	D	$2.63\pm0.16\text{b}$	$27.28\pm0.42a$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Total water content (%)	F	$53.83\pm0.17c$	$64.22\pm0.74b$	$72.65\pm2.52a$	$70.78\pm0.50a$	
	S	$60.14\pm0.76c$	$63.77\pm0.93c$	$70.27\pm3.69$	$77.95 \pm 1.43a$	
	D	$22.27\pm0.66b$	$40.83\pm0.42a$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Water content of root (%)	F	$8.61\pm0.85c$	$41.73\pm2.37a$	$15.31\pm0.47b$	$14.58\pm1.73b$	
	S	$7.81\pm0.76c$	$35.37\pm1.09a$	$11.41\pm0.29b$	$12.89\pm1.72b$	
	D	$28.27\pm5.29a$	$26.48 \pm 1.54a$	$0.00\pm0.00\text{b}$	$0.00\pm0.00\text{b}$	
Water content of stem (%)	F	$45.33\pm1.93\text{d}$	$50.54\pm1.13c$	$57.29\pm0.78b$	$62.61\pm0.86a$	
	S	$47.81\pm2.66c$	$56.43 \pm 1.94 \text{b}$	$60.52\pm1.50\text{b}$	$70.58 \pm 1.64a$	
	D	$18.38\pm0.66\text{b}$	$27.15\pm0.99a$	$0.00\pm0.00c$	$0.00\pm0.00c$	
Water content of leaf (%)	F	$63.79\pm0.69c$	$73.55\pm0.52b$	$79.72\pm2.45a$	$78.94\pm0.20a$	
	S	$73.19\pm0.79b$	$74.17\pm1.19\text{b}$	$82.29\pm2.45a$	$83.35\pm1.83a$	
	D	$22.12\pm1.06b$	$46.35\pm0.27$	$0.00\pm0.00c$	$0.00\pm0.00c$	

TABLE 2 Growth characteristics of *S. salsa* subjected to water [long-term flooding (5–15 cm, F), periodic flooding (0–10 cm, S), and long-term drought (drought to saturated, D)] and salt treatments.

The lower case letters indicate significant differences at p < 0.05.

similar. Our results are agreed with formers' result, in which no matter single effect or integrated effects of salinity and waterlogging could restricted plant growth, and could reduce plant height and leaf area (Merino-Martín et al., 2017; Lu et al., 2022). As a halophyte, *S. salsa* thrives in the presence of NaCl. At lower salinity levels, *S. salsa* can absorb Na<sup>+</sup> and Cl<sup>-</sup> and store them in the vacuoles to lower the plant water potential, thereby improving its ability to absorb water from the soil (Song et al., 2011). In addition, salinity could enhance ATPase and PPase activities, which endows *S. salsa* with more energy to transfer Na<sup>+</sup> and Cl<sup>-</sup> to vacuoles (Zhang et al., 2010). However, at higher salinity levels, increasing osmotic stress and ionic toxicity would retard the absorption of water and nutrients, and subsequently weaken the photosynthesis and metabolic activity (Li et al., 2022). In this study, Na<sup>+</sup> was mainly distributed in the leaves and stems. The Cl<sup>-</sup> species were mainly distributed in the leaves, and in the 0-salt treatment, Cl<sup>-</sup> was more evenly distributed in the root-stem-leaf. This is in agreement with Zhang's study, which indicated that waterlogging can increase Na<sup>+</sup> and Cl<sup>-</sup> concentrations in the leaves.

Studies have shown that salt and waterlogging significantly affect seed yield and quality (Wang F. et al., 2015; Li et al., 2020; Meng et al., 2022). Greater water depth and longer flooding time had a higher impact on the yield, and the yield reduction rate was significantly positively correlated with flooding depth and time (Duan et al., 2018). No significant correlations were found between the seed quality and waterlogging. Salt greatly reduces the seed yield of non-halophytes, particularly of some important cash crops (Yadav et al., 2011) and non-halophytes

TABLE 3 Seed production of *S. salsa* subjected to water [long-term flooding (5–15 cm, F), periodic flooding (0–10 cm, S), and long-term drought (drought to saturated, D)] and salt treatment (0, 10, 20, and 30 g/kg).

	Seed produced (Yes/No)	Seed quantity	Seed germination rate in the next year (%)
F0	No	0	0
S0	No	0	0
D0	No	0	0
F10	Yes	516	93
S10	Yes	621	99
D10	Yes	98	28
F20	Yes	246	62
S20	Yes	407	71
D20	No	0	0
F30	No	0	0
S30	Ye	23	0
D30	No	0	0

show significant yield reductions in soils with increasing salinity (Galvan-Ampudia and Testerink, 2011). However, moderate salinity significantly promotes the reproductive growth of halophytes (*S. salsa*) and increases their number of flowers, number of seeds, and quality (Guo et al., 2018). The seed vitality of halophytes was significantly higher than that under non-saline conditions. In this study, seed yield and vitality at salinities of 10 and 20% were better than those at a salinity that was too low or high. Seed yield and vitality in the S and F treatments were better than those in the D treatment.

### Conclusion

In delta wetlands, hydrological connectivity blocking could result in the modification of sediment processes, water regimes, and salinity values, which would further alter the germination, seedling, and growth of S. salsa. In this study, we found that blocked ephemeral hydrological connectivity may favor S. salsa germination and growth owing to changes in water and salinity. Blocking shortterm hydrological connectivity is suitable for S. salsa growth and development. However, blocking long-term hydrological connectivity (inundation, drought, or excess salinity) is harmful for S. salsa growth. The effects of long-term blocking of hydrological connectivity on the S. salsa population were reflected in the seed yield and quality; long-term blocking sharply reduced the seed yield and vitality. Overall, the findings of this study provide a scientific basis for the protection and restoration of hydrological connectivity and S. salsa habitats in delta wetlands.

### Data availability statement

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

### **Ethics statement**

Authors state that the research was conducted according to ethical standards.

### Author contributions

XW, JSY, and JBY contributed to the conception of the study. YZ and TZ performed the experiment and helped to perform the data analyses. XW and BG contributed significantly to analysis, manuscript preparation, performed the data analyses, and wrote the manuscript. JSY and JBY helped to perform the analysis with constructive discussions. All authors contributed to the article and approved the submitted version.

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### Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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