Windows of opportunity for salt marsh establishment: the importance for salt marsh restoration in the Yangtze Estuary

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Abstract. Restoration has been promoted as an important strategy to reverse the decline of salt marsh ecosystems. Physical and biological processes limiting the colonization of bare tidal flats by pioneer salt marsh species are commonly recognized. Recently, the window of opportunity (WoO) concept has been proposed as a framework to provide an explanation for the initial establishment of biogeomorphic ecosystems on tidal flats under high physical stress. Understanding the thresholds for early seedling establishment and colonization is critical for the successful restoration and management of this threatened ecosystem. In this study, we investigated the WoOs for the establishment and colonization of a Scirpus maritimer salt marsh at a large-scale restoration site in the Yangtze Estuary. A set of field monitoring and measurements were conducted to identify the potential physical and biological thresholds that could provide a mechanistic insight on the establishment and colonization of this pioneer marsh. The results showed that the successful colonization and expansion of the Scirpus maritimer marsh on the tidal flat required passing both physical and biological thresholds to open WoOs for establishment and colonization. The concurrence of WoOs, that is, propagule availability in the early growing season at a suitable tidal flat elevation with a benign sedimentary regime together with the removal of competition from invasive species, is presumed to be essential for the success of Scirpus maritimer marsh establishment and colonization. In applying such ecological insights, the seed-sowing field experiment proved that by surpassing these thresholds, an Scirpus maritimer salt marsh can be successfully restored in a cost-effective manner. We suggest that these WoO-related establishment and colonization thresholds as well the cost-effectiveness of using these WoOs should be considered in future large-scale restorations of salt marshes.

Key words: establishment; restoration; salt marsh; Scirpus maritimer; windows of opportunity; Yangtze Estuary.

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INTRODUCTION

Salt marshes are among the most valuable ecosystems on earth in terms of the services they provide (Barbier et al. 2011, Gedan et al. 2011, Temmerman et al. 2013, Bouma et al. 2014). However, salt marshes are experiencing a global decline due to large-scale stochastic anthropogenic and climatological disturbances (Silliman et al. 2012, Kirwan and Megonigal 2013, Temmerman et al. 2013). To reverse this, restoration has been promoted as an important strategy in many coastal areas of the world (Temmerman et al. 2013, Silliman et al. 2015). Although considerable advances in the conservation and restoration of marsh habitats have been made, the limited degree of success indicates that there is still an urgent need to improve our understanding of the processes that control salt marsh establishment and persistence (Moreno-Mateos et al. 2012, Mariotti and Fagherazzi 2013, Bouma et al. 2014). By quantifying the occurrence of biogeomorphic ecosystems under high physical stress on tidal flats (Balke et al. 2011, 2014, Hu et al. 2015a, Cao et al. 2018). The WoO is a disturbance-free period of a defined minimum duration, which can be identified to hindcast and potentially predict the episodic events of pioneer vegetation establishment in coastal wetlands (Balke et al. 2014). By quantifying the occurrence of WoOs, it is possible to identify thresholds and describe the conditions required for the colonization of mudflats by pioneer plants; for example, Balke et al. (2011) documented the establishment of Avicennia mangrove that occurred whenever windows of opportunity opened and propagules were available. Studies on salt marshes have also demonstrated that the periodic colonization of pioneer seedlings at a suitable tidal flat elevation under relatively benign conditions was temporarily coincident with the early growing season (Zhu et al. 2012, Balke et al. 2013, 2014, Wang and Temmerman 2013). The WoO framework can be further used to predict the establishment patterns of the vegetation (e.g., see Hu et al. 2015a for a prediction of salt marsh vegetation establishment patterns in the Westerschelde Estuary, the Netherlands). However, within the context of coastal salt marsh restoration, there is still an urgent need to improve our understanding of the processes and thresholds that govern the establishment and persistence of certain plant species within salt marsh ecosystems (Silliman et al. 2015, Bouma et al. 2016, van Belzen et al. 2017, Cao et al. 2018).

The extent of the Yangtze Estuary salt marsh that is characterized by the endemic Scirpus mariqueter, which has been identified as a favorable habitat for local biodiversity, has decreased due to the rapid expansion of the exotic Spartina alterniflora (Yuan et al. 2011). Based on ecological engineering aimed at controlling this invasive species, the newly formed tidal mudflats have made the restoration of the native S. mariqueter salt marsh possible (Hu et al. 2015b). The current restoration practice for salt marshes in this region typically involves the strategy of outplanting propagules (corms or plant patches), which is very cost- and labor-intensive (Hu et al. 2015b, Chen et al. 2019). The physical and biological processes that limit the colonization of bare tidal flats by pioneer salt marsh species have frequently been described but have not yet been quantified. An understanding of how to integrate and apply ecological knowledge to salt marsh restoration in the Yangtze Estuary is still lacking.

The objectives of our study are twofold. First, to investigate the potential WoOs for establishment on bare tidal flats in the restoration area, we conducted a series of field surveys and measurements to identify the potential physical and biological thresholds that could provide a mechanistic insight on the establishment and colonization of pioneer S. mariqueter in the marsh. Second, we aimed to include the WoO-based understanding in the design of a cost-effective technique for salt marsh restoration. We then conducted a seed-sowing experiment on the bare tidal flats to validate the effectiveness of the observed concurrence of WoOs for the establishment of S. mariqueter and to develop a new, innovative, cost-effective restoration technique. The results of this study highlight the value of the
WoO concept in creating a new cost-effective restoration strategy for coastal salt marshes and call for the integration of this concept into restoration practice.

METHODS

Study area

This study was conducted in the wetlands of the Chongming Dongtan Nature Reserve (31°26′–31°35′ N, 121°49′–122°02′ E) in the Yangtze Estuary of eastern China (Fig. 1a). The area has an eastern Asian monsoon climate with an average annual temperature of 15.5°C. The average winter temperature is 3°C, whereas the summer is hot and wet with an average temperature of 26°C. The average annual precipitation is ~1022 mm with 60% of the annual precipitation falling in the summer months; the average humidity is 82% (Yuan et al. 2011).

The tides in the Yangtze Estuary are irregularly semidiurnal. According to data collected over a 30-yr period at the nearby Waigaoqiao tidal gauge station, the local mean sea level is 2.17 m, the mean high water level is 3.5 m, and the mean low water level is 1.03 m relative to the local Wushong bathymetric benchmark. The mean tidal level was 2.5 m, and the mean tidal range was 2.47 m (Wang et al. 2014). The eastern fringe of wetlands in the Chongming Dongtan Nature Reserve is the major location for sedimentation of the considerable amount of silt that is deposited by the Yangtze River and has been growing rapidly (Yuan et al. 2014).

The extent of the endemic salt marsh that is characterized by S. mariqueter, which has been identified as a favorable habitat for local biodiversity, has decreased due to the rapid expansion of the exotic S. alterniflora (Yuan et al. 2011, 2014). S. alterniflora (smooth cordgrass) is a native of the Atlantic and Gulf coasts of North America and was introduced to the Chongming Dongtan Nature Reserve in the 1990s and has since rapidly expanded to over 18 km² during the past twenty years. Since late 2013, an ecological engineering project for the restoration of bird habitats spanning 24 km² (outlined in blue in Fig. 1b) has been conducted in the nature reserve (Chen et al. 2019). Simultaneously, control of the remnant S. alterniflora population and restoration of the native S. mariqueter salt marsh (Hu et al. 2015b) was undertaken on the intertidal flats outside the dike (outlined in red in Fig. 1b); that site was selected for this study.

Fig. 1. Location of the Chongming Dongtan Nature Reserve in the Yangtze Estuary, China, the ecological engineering area (outlined in yellow) and the study site (outlined in red) for salt marsh restoration.
**Monitoring salt marsh vegetation propagation**

To monitor the periodic colonization and propagation of salt marsh species in the study area, a series of multi-temporal remote sensing images from 2014 to 2018 (Table 1) were used. The multispectral satellite data were geometrically corrected by a series of nautical charts using ENVI 5.1 Imagine software (Harris Geospatial Solutions, Boulder, Colorado, USA) to generate suitable image bands based on spectral transformation, and the normalized difference vegetation index (NDVI) was used to initialize the data for efficient interpretation. An unmanned aerial vehicle (UAV, quadcopter Phantom 4 Pro: DJI, Shenzhen, China) was used to monitor the vegetation cover in July 2018. A low distortion wide-angle camera was mounted separately in the UAV, which acquired 20-megapixel images in red-green-blue (RGB) color. The images were acquired at a flight altitude of 80 m with a forward overlap of 80% and a lateral overlap of 60%. The mosaicking process was conducted with a Pix4D mapper (Pix4D: Prilly, Switzerland) by applying three consecutive phases of alignment to the overlapping images, reconstruction of the field geometry, and generation of the point cloud, the ortho-image and the DSM using the SfM technique. As a result, the habitat and vegetation classes of muddy flats, dike, and salt marsh of *S. mariqueter*, *S. alterniflora*, *Phragmites australis*, and *Carex scabrifolia* were identified and verified by the in situ field survey.

**Measurements of tidal flat morphology and sedimentary dynamics**

To identify the potential physical thresholds that may relate to the WoOs for the establishment and colonization of the pioneer plants, a set of measurements on tidal flat morphology and sedimentary dynamics were conducted. The tidal flat morphology of the study area was measured using a terrestrial laser scanning system (Rieg VZ-4000; Rieg Laser Measurement Systems GmbH, Horn, Austria) in April 2016 and March 2018. The absolute flat elevation, which was related to the minimum duration of inundation, was verified using a Real Time Kinematic Global Position System (RTK-GP; Ashtech, Alexandria, Virginia, USA).

To measure the sedimentary dynamics of our study area, two transects were laid out on the study site; each was ~400 m long and oriented perpendicular to the dike on the bare mudflat (Fig. 2a). The elevations along the transect were 2.2–3.4 m. Ten poles were inserted into the mudflats at approximately 30-m intervals along each transect, leaving the top 40 cm of each pole exposed. A record of the exposed height (above the mud surface) for each pole was made monthly from October 2017 to October 2018. The initial elevations of the mud surface were set to zero as a reference elevation, and the sedimentary dynamics were measured as the relative height change from the initial elevations (Zhu et al. 2012).

**Monitoring propagule availability**

To monitor the propagule availability of *S. mariqueter* in the study site during the physical WoOs on the bare tidal flats, a transect of ~400 m long was laid out oriented perpendicular to the margin of the *S. mariqueter* marsh. Along the elevational gradient of the transect, four sampling locations were established including the pioneer *S. mariqueter* marsh, the high tidal flat (2.8–3.4 m, HT), the middle tidal flat (2.4–2.8 m, MT), and the low tidal flat (2.2–2.4 m, LT; Fig. 2a). At each location (LT, MT, and HT), six sampling sites spaced 10 m apart were established and five soil cores were randomly extracted using a steel corer with an inner diameter of 10 cm and depth of 25 cm. At the sampling location in the pioneer *S. mariqueter* marsh, ten soil cores were randomly extracted using the same steel corer. The soil samples were collected monthly from September 2017 (seed set and the end of the growing season for *S. mariqueter*) to May 2018 (seedling colonization season). The soil samples were carefully sieved through a 1-mm mesh to count seeds or any propagules (corm and seedling) for each collection period.

| Data source | Image data | Spatial resolution (m) |
|-------------|------------|------------------------|
| Landsat-8   | 2014.7.31  | 30.0                   |
| Pleiades    | 2015.9.04  | 2.0                    |
| SPOT        | 2016.7.26  | 6.0                    |
| Pleiades    | 2017.7.24  | 2.0                    |
| UAV         | 2018.7.19  | 0.2                    |
Seed-sowing field experiment

To verify the observed concurrence of WoOs for the establishment of *S. mariqueter* and to test a new cost-effective restoration technique, a seed-sowing experiment was conducted on the bare tidal flats in the restoration area (Fig. 2a). The seeds used were collected in November 2017 from a mature *S. mariqueter* marsh near our study site. Before being transported to the field for sowing, the seeds were mixed with fine sand at a volume ratio of ~1:2 and were stored in 4°C incubators for vernalization. After treatment, the germination rate of the vernalized seeds was up to ~80% based on a preliminary experiment. In the middle of April 2018 (based on the observation of the earliest occurrence of seedling colonization on the bare mudflat), the sowing of the vernalized seeds of *S. mariqueter* was conducted at three sites within the elevational gradient (HT 2.8 m, MT 2.5 m, and LT 2.2 m). At each site, *S. mariqueter* seeds were sown on three replicate experimental plots (each 1 × 1 m) and covered with 3–5 cm of sediment. To compare the effects of seedling density on the establishment outcome, two seed-sowing densities (high density, 5000 seeds/m² and low density, 500 seeds/m²) were applied to the three replications at each experimental site (Fig. 2b). The seedling emergence and the shoot density on the experimental plots were monitored biweekly from April to October 2018. The number of emerged seedlings and the shoot density were monitored by a photograph taken 1 m above each plot on each monitoring date; counts from the images were conducted in the laboratory.
Data analysis

The measured variables from the sedimentary measurements and propagule (seeds) observations were expressed as the mean ± SD for each sampling site along the elevational gradient. The primary effects of initial seed-sowing density and site on the parameters (seedling emergence, shoot density, height, and reproduction) of plant growth at the three experimental sites were tested with a one-way analysis of variance (ANOVA) using the SPSS 23.0 statistical software package (SPSS, Chicago, Illinois, USA), depending upon the results of the test for homogeneity of variances. The level of statistical significance was set at $P < 0.05$. The data were plotted using the OriginLab 8.0 package.

RESULTS

Salt marsh vegetation propagation and dynamics

The results for salt marsh vegetation propagation and cover changes in the study area from 2014 to 2018 using sequential aerial images are presented in Figs 3, 4. In 2014, the tidal flat in the southern part of the study area (outside the newly built dike of the ecological engineering project) was covered with a large area of *S. alterniflora* (33.1 ha) and small patches of *S. mariqueter* (3.3 ha), which included a 0.12-ha site (indicated by a red square in Fig. 4a) that was restored by outplanting corms of *S. mariqueter* in April 2014 (Hu et al. 2015b). In 2015, after controlling *S. alterniflora* by applying the herbicide Gallant (haloxyfop-r-methyl) and by cutting, the area covered by *S. alterniflora* decreased rapidly to 3.0 ha, leaving a large area of bare mudflat. The area covered by *S. mariqueter* increased slowly to 6.8 ha in 2015 (Fig. 4b). Thereafter, the *S. mariqueter* marsh expanded rapidly seaward and northward to the bare mudflats by natural propagation, and the area covered by *S. mariqueter* reached 19.4 ha in 2016, 39.2 ha in 2017 and 64.8 ha in 2018 (Fig. 4c–e). With continuous control of the remnant patches of *S. alterniflora* by applying Gallant annually, its cover had decreased to 0.4 ha by 2018. The results indicate that after controlling *S. alterniflora*, the *S. mariqueter* marsh was able recover rapidly by natural propagation into potential suitable habitat in the study area.

Tidal flat morphology and sedimentary dynamics on the study site

The results of the tidal flat morphology of the study area in April 2016 and March 2018 showed that the elevation of the tidal flats in the study area ranged from 1.8 to 3.8 m (relative to the local Wushong bathymetric benchmark; Fig. 5). As the Chongming Dongtan Nature Reserve is the major site for sedimentation of the substantial amount of silt deposited by the Yangtze River, the 2.2 m and 3.2 m isobaths in the study area in 2016 moved ~75 m and 115 m seaward, respectively, in 2018. This elevational change due to sedimentation surpassed the establishment threshold for *S. mariqueter* in the Yangtze Estuary (Cui et al. 2020). In addition, the accretion of new habitat opened wide WoOs for salt marsh vegetation establishment and propagation.

The monthly measurements at the low tidal flat (2.2–2.4 m, LT), middle tidal flat (2.4–2.8 m, MT), and high tidal flat (2.8–3.4 m, HT) sites were combined to evaluate the sedimentary dynamics of the study area (Fig. 6). The tidal flats in the study area showed a gradual steady accretion from October 2017 to October 2018. By October 2018, the relative accretions at HT, MT, and LT had reached 15.1 ± 1.0 cm, 22.7 ± 1.9 cm, and 14.5 ± 2.6 cm, respectively. A relatively high level of sedimentary accretion was observed during the period from July to October 2018, whereas the tidal flat was relatively stable with a mean accretion rate of 1.4 cm per month from October 2017 to June 2018.
Propagule availability of *S. mariqueter* on bare tidal flats

The spatial–temporal dynamics of *S. mariqueter* propagules (seeds or seedlings) along a transect from the *S. mariqueter* marsh to the bare tidal flats on the study area are presented in Fig. 7. The results showed that the seed density on the soils of the existing *S. mariqueter* marsh reached $220.5 \pm 96.3/m^2$ and $176.4 \pm 53.6/m^2$ after seed setting in October 2017 and March 2018, respectively, and thereafter, the number of seeds decreased sharply to $6.3 \pm 2.1/m^2$ by May 2018. Almost no seeds or any other propagules (corms or seedlings) were observed on the bare tidal flat.

Fig. 4. Salt marsh vegetation propagation and cover changes on the study area from 2014 to 2018. Notes (a) The large area of *Spartina alterniflora* and small patches of *Scirpus mariqueter* in July 2014; (b) after applying herbicide and cutting in August 2015, *S. alterniflora* was effectively controlled; (c–e) successful propagation of *S. mariqueter* in the marsh from July 2016 to 2018. The restored area (red square) was created by outplanting corms of *S. mariqueter* in April 2014.
from October 2017 to early April 2018. Only a few seeds (7.5 ± 7.0/m²) were sporadically found on the bare tidal flats at the HT and MT sites in January and March and at the LT site in December, March, and April. In early May 2018, a sudden recruitment of *S. mariqueter* seedlings (just germinated, see Fig. 2c) occurred on all the sites (HT, MT, and LT) with densities of 75.5 ± 29.0/m², 72.3 ± 27.5/m², and 30.2 ± 15.7/m², respectively (Fig. 5). The differences in seedling density between the LT and HT sites were significant (*P* < 0.05). During April and early May, which is the period that coincided with a flush of seed germination on the existing *S. mariqueter* marsh, the average daily temperature exceeded 15°C and the buoyant seedlings could potentially be dispersed to the bare tidal flats by tidal water and become established. The spatial–temporal dynamics of the *S. mariqueter* propagules (seeds, seedlings, or corms, if any) indicated that the colonization of mudflats by *S. mariqueter* occurred whenever WoOs opened (e.g., when tidal flat elevation was higher than 2.2 m) and propagules were available (i.e., during natural recruitment of *S. mariqueter*).

**Seed-sowing experiments for *S. mariqueter***

The results of the seed-sowing experiment at the HT (2.8 m), MT (2.5 m), and LT (2.2 m) sites on the bare tidal flat along an elevational gradient showed that the seedlings of *S. mariqueter* emerged from all sites within one month after seed-sowing. From early May to August, the shoot number under high-density seed-sowing was significantly higher than that under low-density seed-sowing for all sites (Fig. 8, *P* < 0.05), whereas there was no significant difference in shoot number under low-density seed-sowing and high-density seed-sowing late in the growing season (Fig. 8, *P* < 0.05). The seasonal peaks in shoot number occurred in late September and reached 611.1 ± 176.4/m² and 588.9 ± 105.4/m² under high-density seed-sowing and low-density seed-sowing, respectively, on the HT sites (the upper graph in Fig. 8); 533.3 ± 212.1/m² and 499.9 ± 173.2/m² under high-density and low-density seed-sowing, respectively, on the MT sites (the middle graph in Fig. 8); and 488.9 ± 153.7/m² and 477.8 ± 109.3/m² under high density and low-density seed-sowing, respectively, on the LT sites (the lower graph in Fig. 8). The peaks in shoot numbers on the LT sites were lower than those on the HT sites and the MT sites, although the differences among the sites were not significant (*P* > 0.05).

**DISCUSSION**

Reversing the global decline of salt marshes through restoration requires an in-depth understanding of how various environmental constraints affect tidal marsh establishment and colonization thresholds (Bouma et al. 2014, Stillman et al. 2015, Cao et al. 2018). WoO concept provides a framework to understand the occurrence and absence of such colonization and establishment events under physical and biological forcing (Balke et al. 2011, 2014, Hu et al. 2015a, van Belzen et al. 2017, Cao et al. 2018). The present study is the first to emphasize the importance of WoO-related thresholds in the
colonization and establishment of the pioneer salt marshes in the Yangtze Estuary. The surpassing of both physical and biological thresholds is needed to open WoOs for the initial colonization and establishment of pioneer *S. mariqueter*, and this concept could be successfully applied to a new restoration practice of seed-sowing with low cost and high efficiency.

**WoO-related thresholds for the establishment of *S. mariqueter***

A temporary absence of physical and biological disturbance during a WoO is understood to allow plants to gain stability against normal forces and to settle on and expand into tidal flats (Balke et al. 2011, 2014, Hu et al. 2015a, Cao et al. 2018). Identifying these thresholds is important.
for the successful establishment and colonization of plants in physically stressful coastal wetlands, as a temporary change in threshold will presumably open WoOs for the initial establishment to occur (Balke et al. 2011, 2014, Wang and Temmerman 2013).

In the present study, salt marsh vegetation propagation and field measurements showed that the physical and biological thresholds must be passed before the pioneer *S. mariqueter* can successfully establish and propagate. (1) To allow seedling establishment, tidal flat elevation needs to pass a tipping point that reflects the tolerance threshold (irreversible growth) of plants to the duration of inundation (Cui et al. 2020); that threshold was determined to be 2.2 m in elevation for *S. mariqueter* in the Yangtze Estuary. (2) To avoid smothering or erosion, the stranded seedlings require a relatively benign period of sedimentation dynamics (less than ±1 cm in

Fig. 8. The shoot density of *Scirpus mariqueter* under the high density (HD) and low density (LD) seed-sowing on the HT (high tidal flat), MT (middle tidal flat), and LT (low tidal flat) sites (the descriptions of the sites are the same as in Fig. 6) from April to late September 2018. The pictures were taken in late August 2018.
erosion/accretion during the months of April and May) for successful establishment on the bare tidal flat (Cao et al. 2018). (3) A flush of buoyant seedlings germinated from seeds and dispersed by tidal water from the existing S. mariqueter marsh during April and early May is needed to colonize the bare tidal flats of suitable elevation, which presumably occurs whenever WoOs open and propagules are available (Balke et al. 2011, 2014). (4) The cover of S. alterniflora should be controlled to <10% of salt marsh vegetation total cover, as this invasive species occupies an overlapping niche with and could outcompete the native S. mariqueter (Huang et al. 2008). However, the study area still faces a threat of re-invasion by S. alterniflora from the remaining sources (Zhao et al. 2020a, 2020b); therefore, annual control of the re-invasion of this invasive plant is critical for the successful restoration of the native S. mariqueter marsh.

It is noteworthy that the concurrence of WoOs, that is, a suitable tidal flat elevation, a benign sedimentary regime, the absence of competition from the invasive species, and propagule availability, which are presumed to be essential for the successful establishment and colonization of S. mariqueter, is similar to the requirements identified in a study on seedling establishment of the mangrove species Avicennia alba (Balke et al. 2011). As one of the most important pioneer colonizers of salt marshes in the Yangtze Estuary, S. mariqueter appears to be well adapted to establish and colonize the dynamic bare mudflats. Our field measurements showed that the seed production of a mature S. mariqueter marsh could reach 1724.4 ± 101.3 seeds/m². After seed set, most seeds were held on the existing marsh as the mature seeds of S. mariqueter, which are relatively heavy. When the temperature rose in spring (from April to May), the seeds germinated rapidly into buoyant seedlings. A flush of buoyant seedlings could then be easily dispersed by tidal water to suitable habitat (pass the threshold of propagule availability). The present study is the first to identify the importance of the availability of buoyant seedlings for the successful colonization of S. mariqueter when other WoOs open, but further studies are needed on the physical thresholds of seed buoyancy and their dispersal on the dynamic tidal flats.

Integrating the WoO concept into practice for salt marsh restoration

To verify the observed concurrence of WoOs for the colonization and establishment of S. mariqueter on the bare tidal flats and to develop a new cost-effective restoration technique, a seed-sowing experiment was conducted on the study site. The principle of the design was to attempt to surpass the multiple thresholds and create a concurrence of WoOs for the successful establishment of S. mariqueter. Hence, a bare tidal flat with an elevation gradient of 2.2–2.8 m and a stable erosion/accretion rate of less than ±1 cm during the months of April and May were selected for the experiment. The vernalized seeds were sown in spring (daily average temperature above 15°C), which would not only surpass the threshold of propagule availability and promote rapid germination and establishment on the bare tidal flat, but also avoid potential physical disturbances at the site. In addition, there was no significant difference in plant density at the end of the growing season between the initial seed-sowing at high density (5000 seeds/m²) and at low density (500 seeds/m²), which indicates that the cost could be further reduced. Compared with our previous restoration practice on the study area in 2014 by outplanting corms (Hu et al. 2015b), the plant density at the end of the growing season by the seed-sowing technique could reach 478–4811 ind/m², which was much higher than the 73–216 ind/m² achieved by corm outplanting (Hu et al. 2015b: Table 1).

Restoration has been promoted as an important strategy to reverse the global decline of salt marshes (Temmerman et al. 2013, Silliman et al. 2015). To increase the efficacy of restoration with no added cost or reduced cost has also become an important concern for the restoration efforts in physically stressful coastal wetlands (Bouma et al. 2014, Silliman et al. 2015). The current restoration practice for native S. mariqueter in the Yangtze Estuary typically adopts the strategies of outplanting corms or plant patches, which is very costly and labor-intensive. The cost inputs of corm bulks or plant patches for outplanting were estimated at $75–100 per 100 m² (Hu et al. 2015b, Chen et al. 2019). The cost of the seed-sowing practice in this study could be reduced to $15–20 per 100 m², as seed-sowing on the bare tidal flat was much easier and required much less labor and transportation. As S. mariqueter is
an endemic species which well adapts to colonize on accreting mudflats in the Yangtze Estuary, there may be some limitations of applying this technique to the situations elsewhere (such as dredge spoil or other degraded salt marshes). While the findings of this study, most importantly, highlight the value for the use of the WoO concept in a new cost-effective restoration strategy for the coastal salt marshes and calling for the integration of this concept into practice (Silliman et al. 2015).

In conclusion, our study on the establishment and colonization of pioneer S. maritimus highlights the importance of identifying both the physical and biological thresholds in the physically stressful coastal wetlands to ensure the restoration success of these valuable ecosystems. The surpassing of both physical and biological thresholds is needed to open WoOs for the initial colonization and establishment of pioneer S. maritimus. We suggest that restoration practices on degraded salt marshes should include these WoO-related colonization and establishment thresholds in the management plan to successfully restore large-scale salt marsh ecosystems in a cost-effective way.

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