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The importance of the propagule–sediment–tide "power balance" for revegetation at the coastal frontier

Zhen-Ming Ge ,[1,2,4] Shi-Hua Li,[1] Li-Shan Tan,[1] Ya-Lei Li,[1] and Zhong-Jian Hu[3]

[1] *State Key Laboratory of Estuarine and Coastal Research, Institute of Eco-Chongming, East China Normal University, 200241 Shanghai, China*
[2] *Center for Global Change and Ecological Forecasting, East China Normal University, 200241 Shanghai, China*
[3] *Wenzhou Fisheries Technology Extension Service, 325000 Wenzhou, China*

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Abstract. Revegetation of pioneer plants is a critical phase in community establishment for mudflats in seriously degraded coastal wetlands. We tested a hypothesis of the importance of a "power balance" among propagule resilience and sedimentary and tidal disturbances for vegetation reestablishment. Our experiment used three types of propagules (seeds, seedlings, and corms) of native *Scirpus* species in the fringing flats with similar tidal flows and varying sedimentary intensities in the Yangtze Estuary. Regardless of the initial planting densities, the seed germination rate was extremely low in the field situation. Although the incubated seedlings were planted directly on the bare flat, the wave movement easily flushed the seedlings, even at the site with moderate sedimentary accretion. Failure of the revegetation practice using the seed and seedling materials indicated that the combined "growing and anchoring power" of young seedlings and "stabilizing power" of the sediment were insufficient to withstand the "dislodging power" of the tidal energy. In contrast, the planting approach with underground propagules (corms) proved to be feasible for vegetation establishment at the sites with moderate and low-level sedimentary intensities. The successful practice improved the tipping point of plant survival and tussock formation could be surpassed when the combined growing and anchoring power of seedlings that developed from corms with the stabilizing power of the sediment was greater than the dislodging power of the wave energy. However, at the site with high-level sedimentary intensity, the excessive sediment converted to the burying stress power as seedlings developed from the corms, revealing a burial threshold for seedling survival. The risk of seedling establishment was high when the burying stress power of the sediment far outweighed the combination of the growing power of the seedlings and the sediment removal power of the tidal current and surpassed the tipping point of vegetation die-off. Additionally, we checked the practice cost of the different approaches to ensure a highly cost-effective revegetation planning based on site suitability. This study highlights that understanding of the propagule–sediment–tide power balance offers a tool for improvement of the revegetation and management of site-specific sedimentary and hydrological environments for many degraded coastal ecosystems.

Key words: cost-effectiveness; decision making; hydrodynamics; intertidal flat; power balance; propagule; vegetation establishment.

Introduction

Coastal hardening, development, and reclamation have resulted in extensive losses of coastal wetlands worldwide (Murray et al. 2019). China's coastal region contributes more than 60% of the national gross domestic product (GDP). However, during recent decades, China's coastal wetlands have been enclosed by thousands of kilometers of seawalls, called the new "Great Wall," as land for economic development (Ma et al. 2014). As a result, many salt marshes and mangroves have been reclaimed, leaving only the bare intertidal flat (as shown in Fig. 1) with a significant reduction of ecological services, such as coastal protection, wildlife habitats, carbon sequestration, and pollutant filtering (Kirwan and Megonigal 2013). Based on the recent national development strategy for a sustainable economy, restoration of coastal ecosystems has been extensively taken into account for coastal management.

The absence of vegetation and propagule sources is the primary limitation for the colonization of the reclaimed bare mudflat with low elevation (Wolters et al. 2008, Friess et al. 2012). As the premier aim of revegetation of pioneer plant organization in dynamic coastal systems is a critical phase in community establishment and succession (Davy et al. 2011, Friess et al. 2012,

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[4] E-mail: zmge@sklec.ecnu.edu.cn

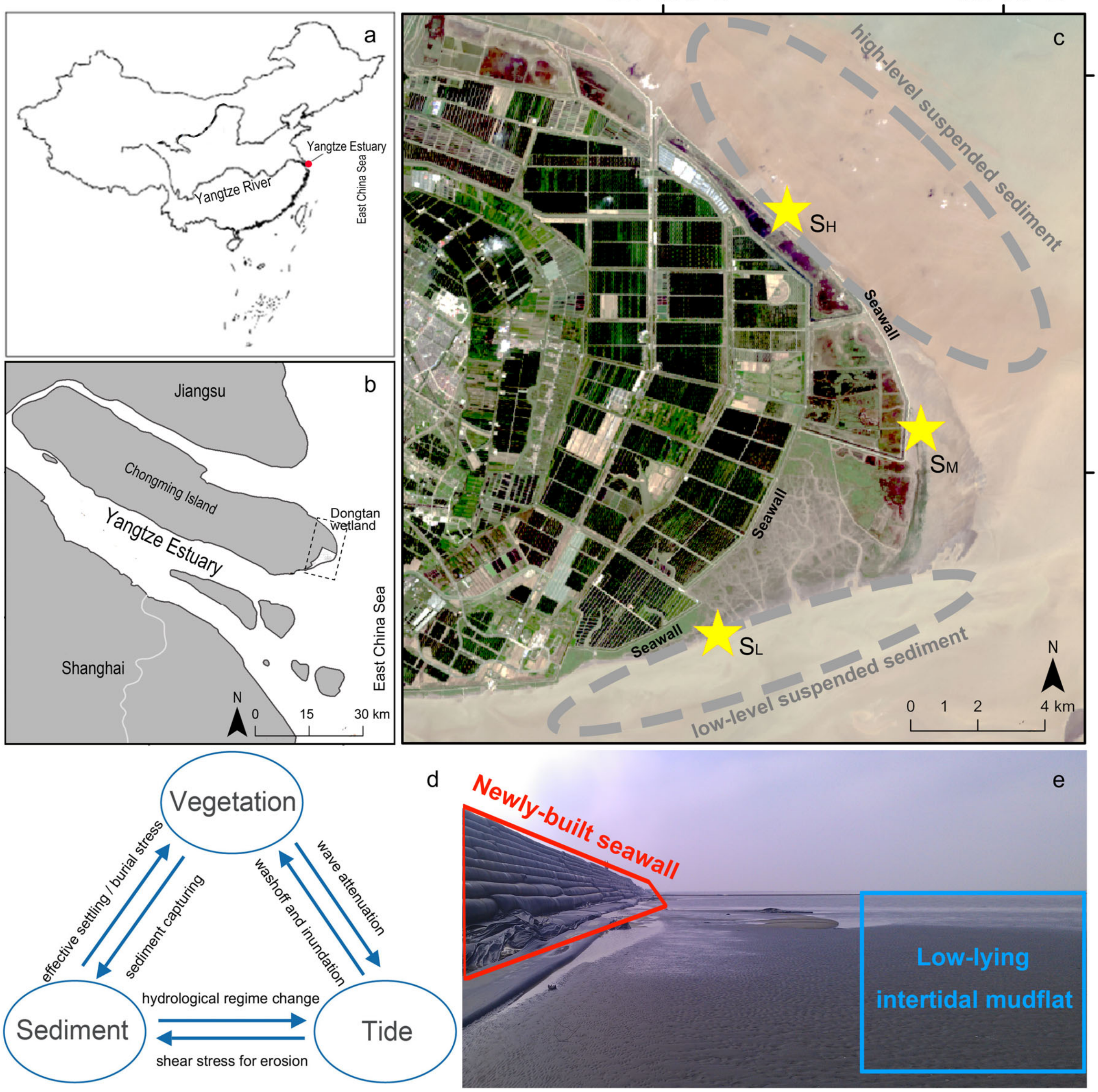

Fig. 1. Location of the Yangtze Estuary (a), Chongming Dongtan wetland (b) and the three sites (SH-site, SM-site and SL-site) selected for the revegetation practice (c). The panel (d) depicts the interaction between vegetation establishment and physical processes of sediment and tide, and the panel (e) shows the rest of low-lying intertidal flat after seawall construction.

Balke et al. 2013, 2014). In the low-lying intertidal zone, plants cannot survive easily on the sediment bed due to strong tidal wave and higher frequency inundation (Bouma et al. 2009, Balke et al. 2011, Davy et al. 2011, Silliman et al. 2015), which further influences the further colonization of propagules and consequent vegetation expansion (Fagherazzi et al. 2004, Keddy 2011). Waves and tide often render revegetation unsuccessful, mainly due to seedling excavation and sediment erosion (Friess et al. 2012). Bottom shear stresses are much stronger in low-lying bare flats with an absence of marsh vegetation (removal or dieback) than in vegetated areas (Yang et al. 2008, Shi et al. 2012, Temmerman et al. 2012, Möller et al. 2014). Seedlings can only utilize short disturbance-free periods (called “windows of opportunity”) to settle and gain stability against the intensive hydrological disturbances, as has been shown for salt marsh and mangrove pioneers (Balke et al. 2011, Hu et al. 2015).

The establishment of plants in the coastal area also relies on favorable sedimentary regimes (Balke et al. 2012, Bouma et al. 2014). Sediment erosion with tidal flooding often results in the excavation of seedlings (Primavera and Esteban 2008, Balke et al. 2014). Generally, sediment accretion is identified as a benefit for initial seedling survival and anchorage (Balke et al. 2014, Schwarz et al. 2015). Thampanya et al. (2002) reported the seedling mortality of mangrove pioneer species due to burial stress with high rates of sedimentation. However, some studies have proposed an adaptive strategy for marsh plants against rapid sediment burial in tidal wetlands that involves forming adventitious roots (Sun et al. 2010).

Apart from the "physical disturbance power" of tidal scouring and sedimentary dynamics, the intrinsic "growing and anchoring power" of plant organization (propagules) under physical stress is crucial for successful revegetation in coastal areas. Most marsh vegetation is comprised of perennial species with a variety of sexual and asexual propagules, such as seeds, seedlings, rhizomes and corms, which can be used for revegetation (Gallego Fernández and García Novo 2007, Silliman et al. 2015, Silinski et al. 2016). Although the influences of various abiotic factors on plant establishment have been well studied based on flume and field experiments (Fagherazzi et al. 2004, Bouma et al. 2009, 2016, Balke et al. 2011, 2013), the effect of physical disturbances originating from hydrological and sedimentary dynamics on the colonization of different propagules is poorly understood (Fig. 1d).

Furthermore, the cost for coastal restoration projects depends on the ecosystem type, national economic strength, restoration project framework and engineering technique carried out (Blignaut et al. 2013, Bayraktarov et al. 2016). The review report by Bayraktarov et al. (2016) showed that the mean costs for marine coastal restoration were approximately eight times higher than the estimated costs for other aquatic and terrestrial areas. Tidal wetland restoration is challenging for revegetation projects, with high costs and high risks due to the relatively low survival rates of new plants under multiple stresses (Zedler et al. 2003, Zedler 2007). The low-lying bare flat is located far from existing vegetated marsh and diaspora source populations, and the revegetation practice may require high costs for propagule gathering, pretreatment/precultivation, transport and planting. Therefore, a cost-effective and technologically appropriate plan is needed.

China has one of the most turbid marine environments worldwide along its coasts and estuaries (Syvitski et al. 2005, Wang 2019). In China's coastal salt marshes, the pioneer halophytes *Scirpus* spp. (mainly including *S. mariqueter*, *S. triqueter*, and *S. planiculmis*) and *Suaeda* spp. (mainly including *S. salsa*, *S. microphylla* and *S. corniculata*) are the dominant native species colonizing the low tidal flats, with *Phragmites* and *Cyperus* species growing in high tidal land (Sun et al. 2010, Guan 2012, Ge et al. 2015). *Scirpus* species with strong adaptation to tidal inundation and high salinity have been identified as the crucial constructive species in the coastal frontier by establishment of self-sustaining ecogeomorphic ecosystems (Ge et al. 2008, Schibalski et al. 2018). The *Scirpus* mudflat is also well known as the most favorable habitat for shorebirds and waterbirds, because it provides sheltering places and food sources (Ma et al. 2004, Ge et al. 2009). However, during recent decades wetland reclamation has resulted in a great loss of the native *Scirpus* species (Li et al. 2009, Guan 2012, Ge et al. 2015).

In the 1970s and 1980s, the exotic *Spartina* species (from North America) were introduced into China for coastal ecological engineering due to their high survival rates and strong capacities to promote siltation. At present, the exotic species are no longer promoted, and reestablishment of native habitat-forming plant species is being increasingly taken into account. In this study, we conducted a revegetation experiment for the native saline-tolerant *Scirpus* species in coastal habitats at seaward margins in the Yangtze Estuary of eastern China. Three types of *S. mariqueter* propagules (seeds, seedlings, and corms) were used to verify the revegetation at mudflat sites with varying hydrological conditions. We hypothesized that the balance of the "physical disturbance power" of tidal scouring, the sedimentary intensity and the "growing and anchoring power" of different propagules would play decisive roles in the success of revegetation in the low-lying coastal mudflat. The practice costs of the different methods were also checked and compared at the same time to ensure development of a highly cost-effective approach for revegetation of the native species. Based on the framework of the propagule–sediment–tide "power balance," this study aimed to provide efficient measures for community-based revegetation projects in the seriously degraded coastal flats of China.

MATERIALS AND METHODS

Study area and site property

This study was conducted in the Chongming Dongtan wetland (31°25′–31°38′ N, 121°50′–122°05′ E) in the Yangtze Estuary of eastern China (Fig. 1). The Chongming Dongtan wetland is located on the eastern fringe of Chongming Island, facing the East China Sea. An eastern Asian monsoon climate is present with an average temperature of 15.5°C and annual precipitation of 1,022 mm/yr (Ge et al. 2008). The tides in the Yangtze Estuary are irregularly semidiurnal, and the range of two successive tides is unequal. At the Sheshan gauging station located 20 km east of the Chongming Dongtan wetland, the average tidal range is 2.5 m and has reached up to 3.5–4.0 m during normal spring tides (GSCI 1988, GSII 1996). The wind velocity over the Yangtze Estuary is highly variable, with multiyear averages of 3.5–4.5 m/s and a maximum recorded velocity of 36 m/s (GSII 1996). The peak current velocity during spring tides is ~2 m/s in the estuary channels and subtidal slopes, and the peak near-bed flow velocity is ~0.5 m/s at the front of the marsh edge (Yang et al. 2008, Shi et al. 2012).

Based on a pilot hydrodynamics survey in the Chongming Dongtan wetland in 2014, three sites of bare flats at elevations of ~2.8 m (based on the local Wusong bathymetric benchmark) with relatively similar wave exposure were selected for the revegetation experiment (Fig. 1c, e). The daily mean tidal inundation time was around 8 h, based on the tidal level records for the Chongming Dongtan wetland during 2014 and 2015. On the low-lying mudflat in the Chongming Dongtan wetland, the wave energy and bed shear stress were much stronger under combined current wave action than that of the marsh on the high flat (Yang et al. 2008, Shi et al. 2012), and the sedimentary intensity was site specific. Following the measuring approach of O'Brien et al. (2000), the sedimentary dynamics at the three study sites were monitored monthly or seasonally from 2014 to 2016, which covered the whole commencement period of revegetation and the consequent investigation of the plants. At each site, wooden poles (6–32 poles) with a length of 1.5 m were inserted into the soil at >5 m intervals, leaving approximately 40–50 cm of each pole exposed at the top above the soil surface. The initially exposed poles were considered a reference (zero point), and the accretion or erosion rates were determined as the relative positive or negative change from the initial length. The setup location of the poles was renewed every year. Based on measurement of the pole length, we calculated the continuous changes in relative elevation that indicated measurements relative to those made during the previous sampling period. Moreover, the absolute flat elevation was calculated as the accumulation of relative elevation over the investigation period. To check the validity, the absolute flat elevation of the observation sites was measured aperiodically using a Real Time Kinematic Global Position System (RTK-GPS, Ashtech by Trimble Inc., Sunnyvale, CA, USA) based on the local Wusong bathymetric benchmark.

The three study sites allocated to a high-level sedimentary rate (S_H), moderate sedimentary rate (S_M), and low-level sedimentary rate (S_L). The mean monthly and annual sedimentary rates at the S_H site were 1.2 cm and 14.6 cm, respectively, over the period from 2014 to 2015 (Fig. 2), with the highest rates (19.8–20.6 cm) observed during the Yangtze runoff flooding season (June–August). The mean monthly and annual sedimentary rates at the S_M site were 0.9 cm and 11.2 cm, respectively, over the period from 2014 to 2016. In comparison, the sedimentary intensity was lowest at the S_L site, with a mean monthly rate of 0.3 cm and annual rate of 3.6 cm over the period from 2014 to 2016 (Fig. 2). The physical and nutrient properties of the sediments at the three sites are listed in Table 1 (measured in November and December of 2014).

Propagule materials

Three types of *S. mariqueter* propagules (seeds, seedlings, and corms) were employed for the revegetation at the experimental sites. In autumn of 2013 and 2014, 100 kg of ripe *S. mariqueter* seeds were harvested from an existing *S. mariqueter* habitat. The seeds were mixed with fine sand at a volume ratio of approximately 1:2 (Fig. 3a), and the mixture was stored in 4°C incubators for vernalization. During the next spring season, the seed–sand mixtures were transported to the field for revegetation practice.

Some of the seeds after vernalization were cultivated for seedling germination. On average, 150 seeds were planted in a small sand bag (fiber material, 5 cm width and depth). The sand bags with seeds were grown in

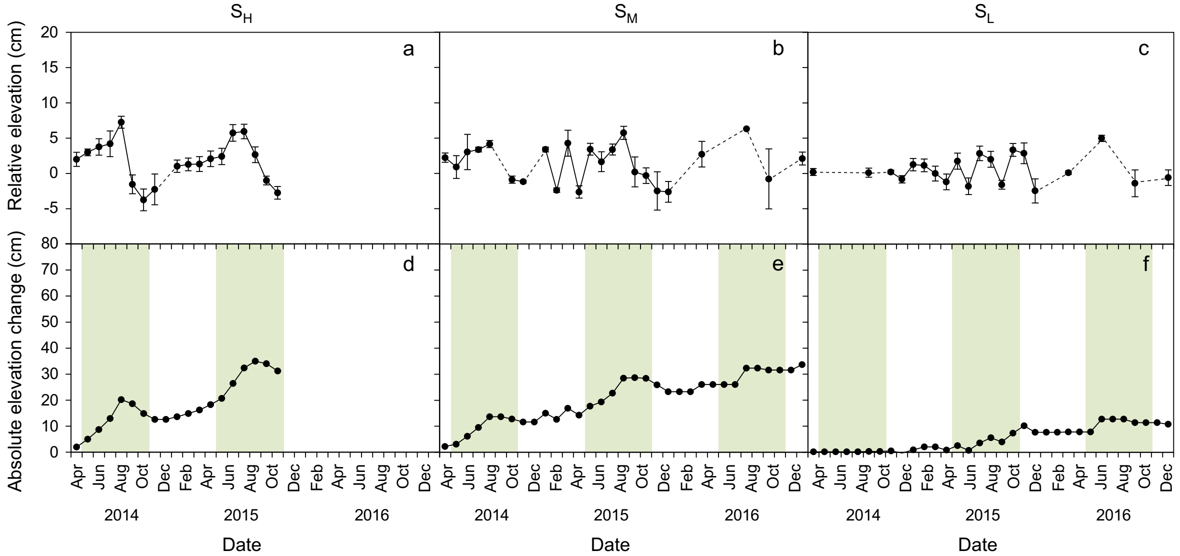

FIG. 2. Sedimentary dynamics in terms of the (a–c) relative elevation change and (d–f) absolute elevation change in the S_H site (a, d), S_M site (b, e), and S_L site (c, f) from 2014 to 2016. The gray belts indicate the growing seasons (April–October). Error bars show the ±SE.

TABLE 1. Summary of soil physical and nutrient properties at the S_H, S_M, and S_L sites in the study area.

Property	Site S_H	Site S_M	Site S_L
Grain size (μm)	16.99 ± 1.73	14.68 ± 1.35	34.31 ± 3.02
Bulk density (g/cm^3)	1.01 ± 0.04	0.96 ± 0.09	1.22 ± 0.14
pH	8.10 ± 0.04	8.15 ± 0.03	8.09 ± 0.03
SOC (%)	0.55 ± 0.18	0.72 ± 0.26	0.64 ± 0.13
TN (%)	0.06 ± 0.02	0.08 ± 0.03	0.06 ± 0.01
Available N (mg/kg)	14.72 ± 3.59	17.41 ± 3.22	15.64 ± 4.57

Notes: The values are presented as the mean ± SE at 15 cm soil depth. SOC, soluble organic carbon; TN, total nitrogen.

incubators at 25°C. When the seedling height reached 10–15 cm (Fig. 3b), the sand bags were transported to the field for revegetation practice.

In April and November of 2014, the soil bulks, which consisted of ripe *S. mariqueter* corms, were collected using stainless-steel tubes (7.5 cm diameter) from the same *S. mariqueter* habitat for seed harvesting. The depth of the sampled soil cores was ~10 cm (Fig. 3c), and on average approximately 10–15 corms were present in each soil core. The soil with corms were directly transported to the field for revegetation practice.

Planting practice

The outline of propagule planting at the different sites is listed in Table 2. To avoid potential effects of the seawall on sediment transport and wave reflection, the location of the experimental sites was >500 m from the seawall. Moreover, the revegetation experiment was carried out during a neap tide period (the highest tidal table was lower than 2.8 m at the local datum for 3–4 d), i.e., an inundation-free period with a critical minimum duration, to minimize the impacts of bed shear stress disturbance.

The seed–sand mixtures after vernalization treatment were planted at the S_H site and S_M site in April 2014 (in November at the S_L site). Three planting density levels were applied (i.e., low density [$\mathrm{LPD_{seed}}$], ~1,000 seeds/1 m^2; middle density [$\mathrm{MPD_{seed}}$], ~2,000 seeds/1 m^2; and high density [$\mathrm{HPD_{seed}}$], ~4,000 seeds/1 m^2). In a pilot study conducted in the laboratory, we tested the effect of the burial depth on the seed germination rate and showed that a burial depth of 5 cm induced the highest seed germination rate (66.8% ± 4.2%, Fig. 4); therefore, this depth was applied in the field planting. At the S_H site and S_M site, four planting strips (5 × 10 m) were set up for four replications and, at the S_L site, three planting strips (5 × 2 m) for three replications of each planting density.

The sand bags with seedlings were planted only at the S_M site in April 2014, with three planting density levels (low density [$\mathrm{LPD_{seedling}}$], ~200 seedlings/1 m^2; middle density [$\mathrm{MPD_{seedling}}$], ~400 seedlings/1 m^2; and high density [$\mathrm{HPD_{seedling}}$], ~800 seedlings/1 m^2). The burial depth of the sand bags was same as the bag height (~5 cm). Four planting strips (5 × 5 m) were set up for four replications of each planting density.

The soil bulks with corms were planted at the S_H site and S_M site in April 2014 (in November at the S_L site). Three planting density levels were applied (i.e., low density [$\mathrm{LPD_{corm}}$], 1 bulk/1 m^2; middle density [$\mathrm{MPD_{corm}}$], 2 bulks/1 m^2 (not done at S_L site); and high density [$\mathrm{HPD_{corm}}$], 4 bulks/1 m^2). The burial depth of the soil bulks was same as the bulk height (~10 cm). At the S_H site and S_M site, four planting strips (5 × 20 m) were set up for four replications and, at the S_L site, three planting strips (5 × 3 m) for three replications of each planting density.

At the same site, the distances between the different approaches (propagule types) and between the different planting densities was more than 10 m and 5 m, respectively.

Vegetation monitoring

After planting practice, monthly censuses were conducted during the growing season (April–October) in each year. In each planting strip for each revegetation approach (propagule type) and planting density, 4–10 quadrats (1 × 1 m) were randomly selected for consecutive measurements of the seed germination rate in the place of seed planting, seedling survival rate in the place

FIG. 3. (a) Seed–sand mixture, (b) sand bags with seedlings, and (c) corm bulks of *S. mariqueter* used for the revegetation experiment.

TABLE 2. Layout of the revegetation experiment in the mudflat frontier with the seeds, seedlings and corms of *Scirpus mariqueter*.

Site, propagules, and planting density	Planting depth	Planting area	Density
S_H			
Seeds	5 cm	200 m^2	
Low			~1,000 seeds/m^2
High			~4,000 seeds/m^2
Corms	0–10 cm	400 m^2	
Low			1 bulk with ~ 15 corms/m^2
Middle			2 bulks with ~ 30 corms/m^2
High			4 bulks with ~ 60 corms/m^2
S_M			
Seeds	5 cm	200 m^2	
Low			~1,000 seeds/m^2
Middle			~2,000 seeds/m^2
High			~4,000 seeds/m^2
Seedlings	5 cm	100 m^2	
Low			~200 seedlings/m^2
Middle			~400 seedlings/m^2
High			~800 seedlings/m^2
Corms	0–10 cm	400 m^2	
Low			1 bulk with ~ 15 corms/m^2
Middle			2 bulks with ~ 30 corms/m^2
High			4 bulks with ~ 60 corms/m^2
S_L			
Seeds	5 cm	30 m^2	
Low			~1,000 seeds/m^2
High			~4,000 seeds/m^2
Corms	0–10 cm	45 m^2	
Low			1 bulk with ~ 15 corms/m^2
High			4 bulks with ~ 60 corms/m^2

of seedling and corm planting, and plant density. The seed germination rate was calculated as the occurrence rate of sprouts from the location of the buried seeds. The seedling survival rate was calculated as the remaining seedlings from the initial planting amount. For all three planting approaches, the plant density was calculated as the number of shoots per unit area in each monitoring quadrate.

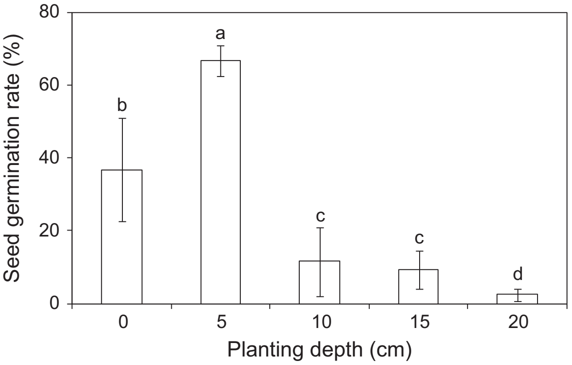

FIG. 4. Germination rates of *S. mariqueter* seeds grown in incubators under different burial depth treatment conditions. Different letters above the bars indicate significant differences between the treatments ($P < 0.05$). Error bars show the ±SE.

Cost accounting

The cost input is high for the revegetation practice in coastal bare flats due to recruitment of propagules, pretreatment (seed vernalization), precultivation (seedling incubation), transport, and planting. We itemized the actual labor cost for every subcategory expense for each planting approach employed in this study. The Chinese currency was converted into U.S. dollars with a constant exchange rate of 675:100 for the present study.

Data analysis

The measured variables from vegetation monitoring were expressed as the mean ± SE for each sampling plot in the three experimental sites, respectively. The main effects of propagule type, site, and initial planting density on the plant growth (seasonal peak shoot density in the later growing season of the first year), as well as their interactive effects were tested through the analysis of variance (ANOVA). The data set met the assumption of homogeneity of variance. The statistical analyses were performed by the SPSS version 23.0 software (SPSS, Chicago, Illinois, USA). The significance level was set at $P < 0.05$.

RESULTS

Performance of the seeds

The germination rate (emergence of sprouts/seedlings) of seeds planted at the S_M site was much lower than the values obtained through the pilot study conducted in the laboratory. In June (around 1.5 months after planting) of the first year, the mean germination rates of seeds of *S. mariqueter* were only 0.025% and 0.019% for the $\mathrm{HPD}_{\mathrm{seed}}$ and $\mathrm{MPD}_{\mathrm{seed}}$, respectively (Fig. 5), and no sprouts were present in the area under the $\mathrm{LPD}_{\mathrm{seed}}$. Up to August, the mean germination rates of the seeds were 0.11%, 0.11%, and 0.063% under the $\mathrm{HPD}_{\mathrm{seed}}$, $\mathrm{MPD}_{\mathrm{seed}}$, and $\mathrm{LPD}_{\mathrm{seed}}$, respectively. Low emergence rates of the sprouts led directly to a low number of new seedlings. At the end of August, the densities of standing *S. mariqueter* were only on average 4.5 shoots/m^2, 2.1 shoots/m^2, and 0.63 shoots/m^2 under the $\mathrm{HPD}_{\mathrm{seed}}$, $\mathrm{MPD}_{\mathrm{seed}}$, and $\mathrm{LPD}_{\mathrm{seed}}$, respectively, which were the seasonal peak values. After August, the number of seedlings declined

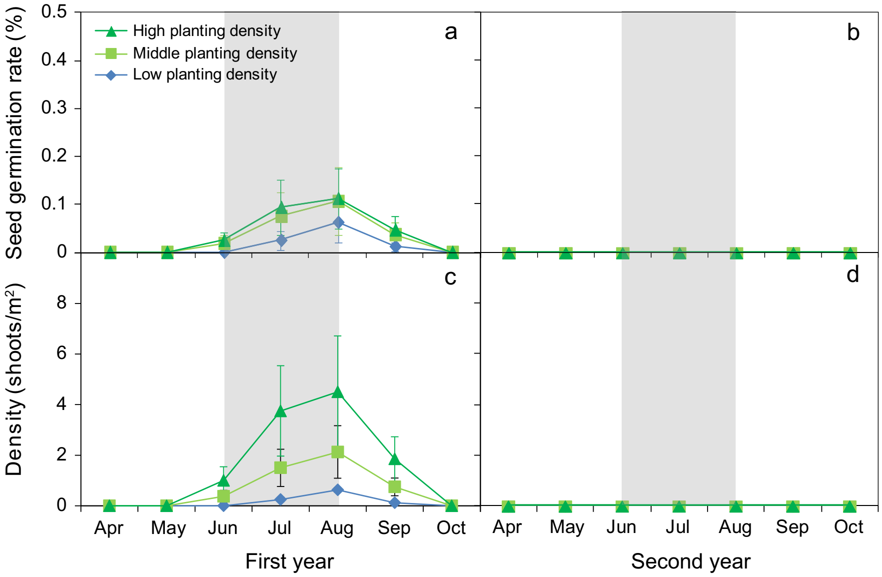

FIG. 5. (a, b) Seed germination rate and (c, d) shoot density (emergence) during the first and second years after the revegetation experiment using a seed planting approach. The gray belt indicates the highest seasonal sedimentary rate. Error bars show the ±SE.

rapidly, and the number of new *S. mariqueter* was reduced to zero in October regardless of the initial planting densities. Uprooted *S. mariqueter* seedlings could be found in the mudflat (Fig. 6a). Over the second year, no *S. mariqueter* was found at any of the planting locations at the S_M site.

Regardless of the initial planting densities, no sprouts (or seedlings) of *S. mariqueter* were found in the planting area of the S_H site and S_L site over the 2-yr observation period.

Performance of the seedlings

The seedling planting approach was carried out at the S_M site. Within one month after planting, the survival rate of the planted *S. mariqueter* seedlings remained at approximately 100% under all initial planting densities. Thereafter, the mean survival rates declined rapidly to 15%, 27%, and 21% in August under the $HPD_{seedling}$, $MPD_{seedling}$, and $LPD_{seedling}$, respectively (Fig. 7). After approximately two months, erosion gullies were observed on the sides of the *S. mariqueter* patches (Fig. 6b), and the young seedlings were easily swept away with the sand bags by the tidal current. By September and October, the number of *S. mariqueter* seedlings decreased to zero (i.e., all planted seedlings disappeared from all of the planting locations). Over the second year, no *S. mariqueter* seedlings were observed in any of the planting locations.

Performance of the corms

S. mariqueter sprouts grew from the corms underground quickly after planting at all three sites (Fig. 6c). In May (around 1 month after planting) of the first year, the shoot density (reflecting the survival rate) of *S. mariqueter* was higher at the S_H site than at the other two sites, regardless of the initial planting density. However, the shoot densities decreased sharply thereafter

FIG. 6. (a) Seedlings dislodged (uprooted) by wave movement in the site used for the seed planting approach, (b) erosion gullies around the seedling patches in the site used for the seedling planting approach, and (c) newly developed sprouts in the site used for the corm planting approach.

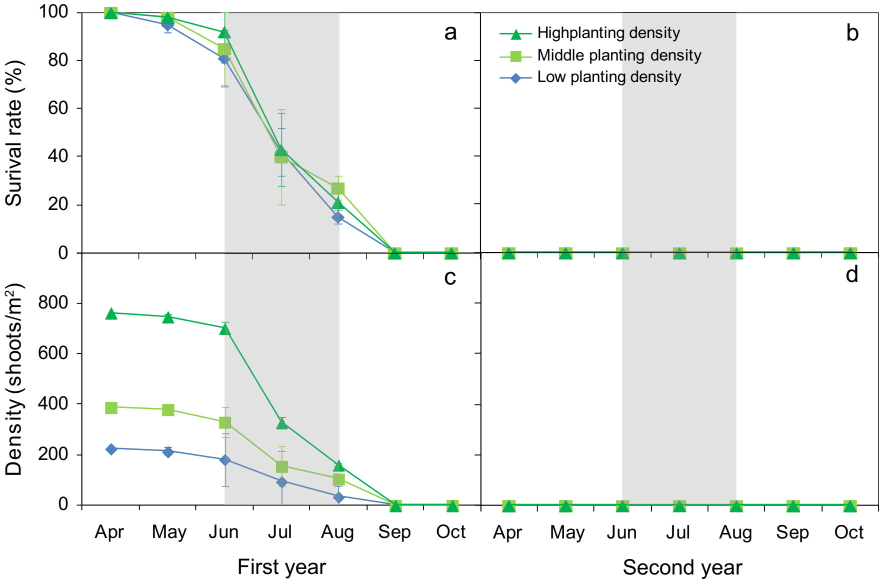

FIG. 7. (a, b) Survival rates of the seedlings and (c, d) the shoot densities (emergence) during the first and second years after the revegetation experiment using the seedling planting approach. The gray belt indicates the highest seasonal sedimentary rate. Error bars show the ±SE.

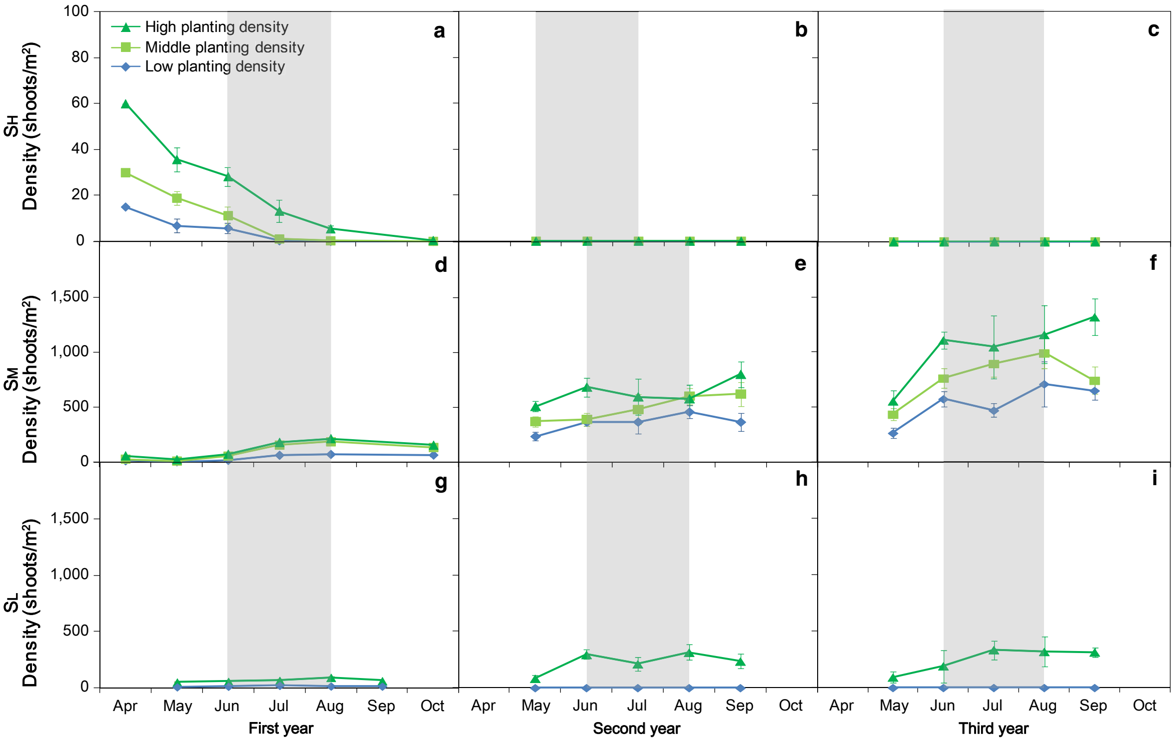

FIG. 8. Shoot density (emergence) at the (a–c) S_H site, (d–f) S_M site, and (g–i) S_L site from the first to third years after the revegetation experiment using the corm planting approach. The gray belt indicates the highest seasonal sedimentary rate. Error bars show the ±SE.

(Fig. 8a). As observed, most of the newly grown seedlings were deeply buried by the sediments. The shoot densities were on average 0.4 shoots/m^2, 0.05 shoots/m^2, and 0 shoots/m^2 under the HPD_{corm}, MPD_{corm}, and LPD_{corm}, respectively, at the end of October. Over the second and third monitoring years, no *S. mariqueter* seedling was found in the planting area of the S_H site regardless of the planting density (Fig. 8b, c).

At the S_M site, the shoot density of *S. mariqueter* decreased during the earlier first growing season and thereafter increased rapidly (Fig. 8d). In August, the shoot densities achieved the seasonal maximum of 216.0 shoots/m^2, 187.3 shoots/m^2, and 72.8 shoots/m^2 on average under the $\mathrm{HPD}_{\mathrm{corm}}$, $\mathrm{MPD}_{\mathrm{corm}}$, and $\mathrm{LPD}_{\mathrm{corm}}$, respectively. After October, the number of *S. mariqueter* plants declined due to senescence and loss of aboveground organs from tidal overwash, regardless of the planting density. In the second year, *S. mariqueter* grew out again, with seasonal peaks of 460.5 shoots/m^2, 624.2 shoots/m^2, and 802.4 shoots/m^2 on average under the $\mathrm{HPD}_{\mathrm{corm}}$, $\mathrm{MPD}_{\mathrm{corm}}$, and $\mathrm{LPD}_{\mathrm{corm}}$, respectively, in the later growing season. In the third year, the shoot densities further increased, reaching a seasonal maximum of 652.8 shoots/m^2, 744.0 shoots/m^2, and 1,320.5 shoots/m^2 on average under the $\mathrm{HPD}_{\mathrm{corm}}$, $\mathrm{MPD}_{\mathrm{corm}}$, and $\mathrm{LPD}_{\mathrm{corm}}$, respectively, in August or September (Fig. 8f).

At the S_L site, the number of newly grown *S. mariqueter* was lower by an average of approximately twofold than that at the S_H site in the first year regardless of the initial planting density (Fig. 8g). During the later growing season of the first year, the seasonal maximum of *S. mariqueter* shoots was on average 94.5 shoots/m^2 and 8.0 shoots/m^2 under the $\mathrm{HPD}_{\mathrm{corm}}$ and $\mathrm{LPD}_{\mathrm{corm}}$, respectively ($\mathrm{MPD}_{\mathrm{corm}}$ was not conducted). In the second and third monitoring years, *S. mariqueter* grew out again, with a seasonal maximum of 314.4 shoots/m^2 and 335.2 shoots/m^2 under the $\mathrm{HPD}_{\mathrm{corm}}$, respectively. However, no *S. mariqueter* seedlings were found under the $\mathrm{LPD}_{\mathrm{corm}}$ over the second and third years (Fig. 8h, i).

Importance analysis

An ANOVA test indicated the significant main effects of propagule type and selected site on the plant growth in terms of vegetation establishment, and the interactive effect of propagule × site was also significant (Table 3). The effect of initial planting density was not notable, and no strong interactive effect of site × planting density and propagule × planting density was observed for the plant growth.

As shown in Fig. 9, the number of newly grown *S. mariqueter* from the planted corms was low under the slight sedimentary rate (at the S_L site). With the increase in the sedimentary rate, the survival rate of the plants increased (at the S_M site), whereas a further higher sedimentary intensity resulted in reversion to a low survival rate or even vegetation die-off (at the S_H site).

TABLE 3. Main and interactive effects of propagule type, selected site, and initial planting density on the plant growth.

Factors	df	*F*	*P*
Propagule	2, 19	16.226	0.025*
Site	2, 19	9.898	0.048*
Planting density	2, 19	0.256	0.790
Propagule × Site	2, 19	9.898	0.048*
Site × Planting density	4, 19	0.750	0.619
Propagule × Planting density	4, 19	1.707	0.344

*Significance at $P < 0.05$.

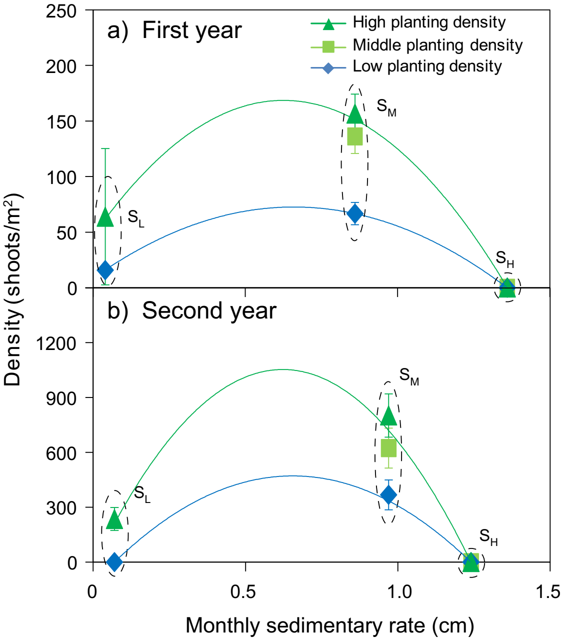

FIG. 9. Shoot density (seasonal peak values measured in the later growing season) curves (quadratic equation) under site-specific monthly sedimentary rates in the (a) first and (b) second years after the corm planting practice. Error bars show the ±SE.

Costs of the different approaches

We checked the item-by-item cost inputs of the revegetation practice including only the value of labor (average salary per day), because the cheap costs for equipment were negligible. On average, for all working procedures, the costs (unit price per m^2) of the seed planting approach were lowest (US\$0.96–2.38 per m^2), whereas the cost of seed gathering was highest (Table 4). The expenses for the seedling planting approach were highest (US\$2.00–4.30 per m^2) due to the highest input for seedling incubation. The costs of the corm planting approach were slightly higher (US\$1.13–2.50 per m^2) than those of the seed planting approach (Table 4). Regardless of the planting approach, the costs of the revegetation practice increased with the increasing planting density.

DISCUSSION

Previous studies revealed that the plant–wave–sediment interaction played a key role in initial seedling establishment (Bouma et al. 2009, Balke et al. 2013, Schwarz et al. 2015, Silinski et al. 2016), vegetation patches (Balke et al. 2012, Bouma et al. 2013, Wang and

TABLE 4. Cost input (labor cost) for different revegetation approaches.

Propagules, pretreatment, and planting density	Cost input (US$)				Working hours (person hours)	Average unit price (US$/m^2)
	Gathering	Pretreatment	Transport	Planting		
Seeds, moderate availability, pretreated (sieving, vernalization)						
LDP	300	15	20	50	130	0.96
MDP	500	20	20	80	205	1.55
HDP	800	30	20	100	315	2.38
Seedlings, hard availability, pretreated (seed collection, incubation)						
LDP	100	45	30	25	65	2.00
MDP	150	60	30	40	95	2.80
HDP	250	100	30	50	145	4.30
Corm bulks, easy availability, not pretreated						
LDP	300		50	100	150	1.13
MDP	450		50	150	215	1.63
HDP	750		50	200	335	2.50

Note: LDP, low-density planting; MDP, middle-density planting; HDP, high-density planting.

Temmerman 2013, Bouma et al. 2016), and landscape spatial structure (Temmerman et al. 2012, Schwarz et al. 2018) in salt marshes or mangroves. However, a down-to-earth understanding based on the mechanistic processes underlying the multi-status thresholds from the bare flat to early establishment of pioneer marsh species is still needed to improve. Our practice not only indicated the importance of tidal disturbances and sedimentary intensity on controlling the fate of newly planted *S. mariqueter* on a bare flat but also highlighted the role of the propagule types (e.g., seeds, seedlings, and corms) as a crucial driver determining pioneer plant establishment under unfavorable hydrological stresses. Accordingly, we suggest the importance of the propagule–sediment–tide "power balance" for revegetation in a low-lying bare flat (Fig. 10).

A temporary absence of physical disturbance during a "window of opportunity" period is well accepted to allow plant organizations to gain stability against average forces and to settle down and expand on tidal flats (Balke et al. 2011, 2014, Hu et al. 2015). The window of opportunity for vegetation establishment in coastal regions is also generalized as seasonal low flooding or spring neap tidal cycles (Balke et al. 2014, Silinski et al. 2016). We followed the principle and conducted revegetation experiment during a hydrodynamically and geomorphologically calm period. However, the seed planting approach could not establish vegetation patches regardless of the planting density. The seed germination rate of *S. mariqueter* was satisfactory in the incubators (pilot study), while the number of sprouts in the field was extremely low. Intensive inundation and predation by benthos may significantly reduce the effective germination rate in the field. On the other hand, generally the soil bulk density is high and aeration is poor due to persistent sediment tamping, whereas in the laboratory, we use a sandy substrate with high aeration. Therefore, no sprouts emerged at the S_H site, which was consistent with the pilot study results showing a significantly lower germination rate under a burial depth of >15 cm. Although the seeds at the S_M site outgrew from the soil, the young seedlings were easily flushed away by the tidal current. As observed in both the laboratory and the field experiments, the young *S. mariqueter* seedlings had much larger aboveground organs than the size of the root materials (Fig. 6a); therefore, the drag force by waves should be much higher than the anchorage force of the roots, resulting in uprooting. Balke et al. (2011) declared that a crucial threshold (tipping point) during seedling establishment was that root growth had to reach a minimum size to anchor inside the soil. Our results indicated that the growing and anchoring power of *S. mariqueter* seedling that developed from seeds might be insufficient to withstand the dislodging power of the tidal currents (Fig. 10a). Nevertheless, our observation covering 2–3 yr cannot absolutely affirm the failure of the seed planting approach. The seed shell of *S. mariqueter* is relatively rigid and should be enough to form a long-term seed bank. Further tracking is necessary to assess the cross-temporal germination potential.

The time lag of seed germination may also miss the window of opportunity. Therefore, we also directly planted the *S. mariqueter* seedlings together with the substrate during a neap tide period. At the S_M site, the initial survival rate of the seedlings was high due to favorable sedimentary rate benefiting the seedling settling. However, after around 2 months the survival rate of *S. mariqueter* decreased rapidly due to serious excavation around the seedlings until they were uprooted (Fig. 6b). Self-scouring is a common phenomenon for the seedling clusters that were suddenly planted in mudflat pioneer zones, which result in failure of vegetation

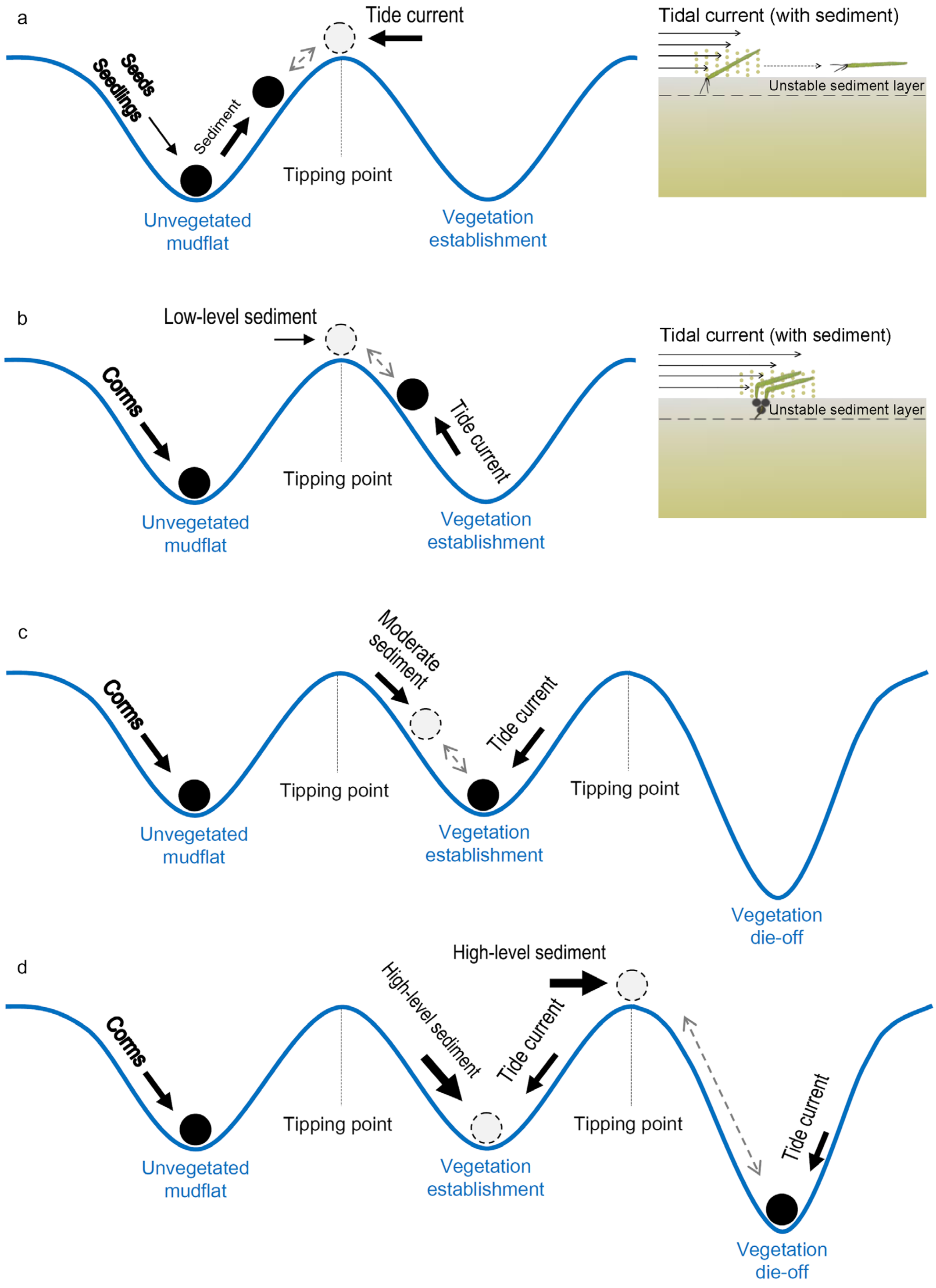

FIG. 10. Conceptual diagrams corresponding to the propagule–sediment–tide “power balance” for revegetation in the coastal marsh frontier. A dashed circle and solid circle separated by a double-headed arrow indicates the uncertainty between two statuses. The thickness of arrows indicates the relative power strength (P). (a) $P_{\text{sediment}} + P_{\text{seed/seedling}} < P_{\text{tide}}$, hard to leap over the tipping point for vegetation establishment due to tidal flush. (b) $P_{\text{sediment}} + P_{\text{corm}} \approx P_{\text{tide}}$, grudgingly feasible method to leap over the tipping point for vegetation establishment due to low-level sedimentary environment. (c) $P_{\text{sediment}} + P_{\text{corm}} > P_{\text{tide}}$, fully feasible to leap over the tipping point for vegetation establishment under moderate sedimentary environment, with slight risk of reaching a tipping point of burial stress. (d) $P_{\text{sediment}} + P_{\text{corm}} \gg P_{\text{tide}}$, high risk of leaping over the tipping point for vegetation die-off due to deep sediment burying.

establishment (Bouma et al. 2009). Based on the previous transplanting and flume experiments (van Wesenbeeck et al. 2008, Zhao et al. 2019), seedling clusters diverted stresses imposed by water currents, leading to erosion and restricted growth of plants. Van Wesenbeeck et al. (2008) also found that higher density of tussocks had deeper erosion gullies around the patches, which indicated a scale-dependent (also density-dependent) feedback showing the beyond-tussock negative effect in relation to size or density of the tussock. Additionally, *S. maritimus* has been identified as a relatively poor sediment trapper (Silinski et al. 2016); thus, a small patch size might not obtain sufficient sedimentation against the self-scoured erosion for survival. This could be the reason the seedling planting approach from low to high densities did not fulfill the revegetation aim. Accordingly, the combined growing and anchoring power of newly planted seedlings with the stabilizing power of sediment were revealed to be less than the dislodging power resulting from hydrodynamic force, leading to failure to surpass the survival threshold (Fig. 10a).

This study proved that the corm planting approach is feasible for establishment of *S. mariqueter* at the S_M site and S_L site (but not the S_H site). The underground rhizomes are some of the most important organs for reproduction and expansion on tidal flats (Mitsch 2005). Compared to that of mature seeds, generally the budding speed of *S. mariqueter* corms is faster so that the outgrown seedlings may utilize the window of opportunity efficiently. Especially, the corms of *S. mariqueter* have a plump ellipsoid shape (see Fig. 6c), which has a greater specific surface area than that of newly germinated roots from the seeds. As a result, the anchoring force of the corms for seedling residence may resist the dislodging force of the tidal current (Fig. 10b). Balke et al. (2011, 2013) demonstrated that a sufficient size or biomass of the underground propagule (such as mangrove roots) is needed to exceed the critical bed shear stress and drag forces from wave energy for vegetation colonization.

The in situ sedimentary processes on tidal flats should affect the seedlings from the top side (e.g., the immobilization function or burial stress). Fortunately, we employed study sites with a natural gradient of sedimentary intensities. In the first year, the survival rate of the seedlings that developed from corms at the S_L site with the lowest sedimentary rate and irregular seasonal erosion was much lower, even with a high planting density, than that at the S_M site. Generally, the hydrodynamic energy is higher at the erosive marsh edge, and thus the coarse sediment at the S_L site may be the result of high tidal turbulence wiping away fine sediment. The soil, which is mainly composed of coarse silts with a high bulk density, will inhibit root growth and rhizome development underground (e.g., Hossler and Bouchard 2010). Nevertheless, the shoot number of *S. mariqueter* continued to increase annually with the initial high planting density. This result is consistent with the conclusion of Silliman et al. (2015), who declared that clumped planting positively affected propagule survival and tussock expansion in coastal wetlands. At the S_M site with a moderate sedimentary rate, the first-year survival rate of seedlings was highest, and the standing seedlings formed a dense shoot community of ~700–1,300 shoots/m^2 in relation to the initial planting density within 3 yr, reaching approximately 40–70% of a common natural *Scirpus* community. Based on the positive feedback between vegetation establishment and sedimentary processes (van De Koppel et al. 2001, Mudd et al. 2010, Kirwan et al. 2011, Fagherazzi et al. 2012, Bouma et al. 2016), the newly formed dense tussocks could promote mudflat accretion and reduce hydrodynamic energy by sediment trapping and wave attenuation; thus, the intensity of tidal disturbance would further decrease with the increasing canopy density and marsh elevation, thereby improving the tipping point of plant survival and tussock formation. Thus, the tipping point may be surpassed because the combined growing and anchoring power of seedlings developed from corms with the stabilizing power of sediment is greater than the dislodging power of wave energy (Fig. 10c).

The S_H site located in an area with a high level of suspended sediment, with a rate of 19.8–20.6 cm deposition during the growing seasons. A negative feedback between flat elevation and sediment deposition demonstrates that low-lying mudflats are inundated frequently by sediment-rich floods, probably leading to high sedimentation rates (Temmerman et al. 2003, Wang and Temmerman 2013). However, the high sedimentary intensity killed almost all the seedlings starting in early June (~2 months after planting). Heavy soil burial would suffocate the seedlings, and root growth and plant photosynthesis would be limited due to low oxygen conditions and soil phytotoxins (Terrados et al. 1997, Maun 1998, Thampanya et al. 2002). Some marsh species possess an adaptive strategy that enables them to survive under rapid sediment burial by increasing their aboveground biomass and stem height (Sun et al. 2010, Balke et al. 2013). However, the adaptive mechanisms of plants may be disrupted under excessive burial stress. The case at the S_H site indicated that sediment was a double-edged sword (i.e., excessive sediment was identified as a burying stress power for plants). Comparing the sedimentary intensities between the S_H site and the S_M site indicated a short-term (growing season) burial threshold of >15 cm for the survival of *S. mariqueter* corms in the field situation. In contrast, tidal wave energy may be identified as an advantageous factor that removes sediment and mitigates burying stress. We suggest a high risk of seedling establishment when the burying stress power of the sediment far outweighs the combination of the tolerance of the seedlings and the sediment removal power of the tidal current, thereby surpassing the tipping point of vegetation die-off (Fig. 10d).

In addition, we assessed cost and effectiveness of the techniques and performed a risk estimation for coastal revegetation practices. The investment of the seed planting approach was lowest due to the accessibility of seeds, which can easily be planted in fields. The seedling plant approach was the most expensive method due to the high cost of seedling cultivation before the field installation. However, the risks of the seed and seedling planting approaches were relatively high for *Scirpus* revegetation in low-lying mudflats. Although the expense for corm bulk gathering and the labor cost for planting were the highest, no other expense was required because the sampled bulks could be planted directly without pretreatment. More importantly, the corm planting approach successfully implemented *Scirpus* revegetation at two sites and achieved a high survival rate of the plants and continuing expansion of tussocks. Although the revegetation practices with middle and high planting densities were associated with high costs, an initial high planting intensity led to the highest survival rate, whereas the low planting density failed to reestablish the pioneer vegetation at the S_L site. A site selection strategy based on the environmental suitability may avoid revegetation project failure in the coastal area (Wolters et al. 2008). We found that the tidal flat with a moderate sedimentary rate (e.g., ~10 cm during growing season) is favorable for *Scirpus* revegetation by the corm planting approach, and a low planting intensity can be cost effective. At the tidal flat with a poor sediment regime, a high planting density is an effective measure if the underground colonization system is established quickly. However, the tidal flat with a high sedimentary intensity (e.g., >15 cm during growing season) is not recommended for revegetation practices at present.

CONCLUSIONS

The present study carried out in China was the first revegetation practice for native *Scirpus* species in the low-lying bare flats. We highlighted the importance of the power balance of propagule and sedimentary and tidal disturbance for vegetation reestablishment in the coastal mudflat frontier and found that the initial establishment phase was the crucial starting point for successful revegetation. The use of underground propagules (e.g., *S. mariqueter* corms) can maximize seedling survival and formation of tussock structures due to rapid seedling development and adaptive morphology, which can anchor the plants inside the sediment layer against strong tidal wave energy on low-lying bare flats. The seed and seedling planting approaches are not recommended for large-scale revegetation planning. The germination rate of seeds in the field situation was extremely low, and the newly grown seedlings from seeds with thin root tissues and self-scouring around the seedlings resulted in insufficient anchoring power to withstand the dislodging power of wave movement.

The successful practice indicated that the tipping point of plant survival and tussock formation could be surpassed when the combined growing and anchoring power of seedlings developed from corms with the stabilizing power of the sediment were greater than the dislodging power of the wave energy. Additionally, a low planting-density approach was cost-effective at the site with a moderate sediment intensity, and a high planting density at the site with poor sediment conditions. However, a high-level sediment intensity over the burial threshold led to burying stress power, resulting in vegetation die-off.

Moreover, changes in hydrological characteristics due to a sea level rise may be speculated to enhance the water depth (or tidal range) and alter sedimentary processes. The increased stresses may create a higher risk for initial plant establishment and expansion on low-lying coastal mudflats. Understanding the propagule–sediment–tide power balance presented herein offers a tool to predict revegetation in site-specific sedimentary and hydrological environments. Additionally, our findings provide fundamental insights that can be used to improve revegetation and management for many coastal ecosystems and mitigate the adverse impacts of sea level rises, especially for the large number of seriously degraded wetlands in front of the new “Great Wall” along China’s coastline.

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