



Research article

Re-invasion of *Spartina alterniflora* in restored saltmarshes: Seed arrival, retention, germination, and establishmentZhiyuan Zhao^a, Lin Yuan^{a,b,*}, Wei Li^a, Bo Tian^a, Liquan Zhang^a^a State Key Laboratory of Estuarine and Coastal Research, Institute of Estuarine and Coastal Research, Institute of Eco-Chongming, East China Normal University, 200241, Shanghai, China^b Yangtze Delta Estuarine Wetland Ecosystem Observation and Research Station (Ministry of Education & Shanghai Science and Technology Committee), 202162, Shanghai, China

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ABSTRACT

The invasive plant *Spartina alterniflora* presents a serious threat to the saltmarsh ecosystems in the Yangtze Estuary. Various measures have been implemented to control *S. alterniflora* and restore the natural saltmarshes in this area. However, many saltmarsh restoration activities often fail partly because of recursions of this invasive plant. In this study, we investigated the re-invasion of *S. alterniflora* in a restored saltmarsh in the Chongming Dongtan National Nature Reserve by analysing the aspects of seed arrival, retention, germination, and establishment, to better understand the potential factors that may influence the re-invasion of restored saltmarshes. The results showed that 1) tidal currents dispersed the seeds from the possible source area to the restored saltmarsh and adjacent mudflat. The spatio-temporal dynamics of arrived seeds were shown to vary greatly depending on the intertidal geomorphology, vegetation, and hydrodynamic processes. 2) Seed retention in the re-invaded area was shown to be greatly influenced by burial depth, and moderate sedimentation rates provided safe sites for the retention of arrived seeds. 3) Only when both the burial depth and inundation duration below certain thresholds, the retained seeds could germinate and establish in the recipient habitats successfully. The results from this study highlight that control efforts and the management of *S. alterniflora* should not only focus on the re-invaded areas of restored saltmarshes, but also on the possible source areas of re-invasive species.

1. Introduction

Biological invasions represent one of the most serious threats to natural ecosystems (Theoharides and Dukes, 2007). Various measures have been implemented to control invasive species and restore natural ecosystem functions (Yuan et al., 2011; Strong and Ayres, 2016). However, restored ecosystems often face immanent threats of re-invasion by the same or other unwanted exotic species (Galatowitsch et al., 2016; Pearson et al., 2016). In addition, re-invading species may take advantage of the newly available resources and habitats following restoration efforts (Kettenring and Adams, 2011; Cutting and Hough-Goldstein, 2013), and thus present significant challenges to the successful restoration of natural ecosystems. Despite re-invasions having potentially large influences on the outcomes as well as the costs of restoration efforts, the processes of re-invasion remain difficult to predict due to the lack of associated studies and available information (Gabler and Siemann, 2012; Pearson et al., 2016). Therefore, in-depth

investigations are needed to fully assess re-invasions and thus develop efficient measures to prevent re-invasions (Pearson et al., 2016; Banks et al., 2018).

Re-invasion, which refers to the re-establishment of non-indigenous species after the implementation of control measures, is not a simple repetition of the initial invasion process (Banks et al., 2018). After control measures, the entry of new species into a community may be facilitated by immigration processes via propagule influx and the windows of opportunity granted by the release of resources (Balke et al., 2011; Zhu et al., 2014; Tabak et al., 2018). For plants, this “classic” invasion pathway is similar between the initial invasion and re-invasion events, however, the legacy effects on habitat properties persist following suppression by the initial invader (Cuddington, 2011; Gabler and Siemann, 2012; Pearson et al., 2016). For example, the initial invader may alter the local soil organic carbon content (e.g. Yang et al., 2013) and settling flux of suspended sediment (e.g. Gao et al., 2014), which may favour the rapid adaptation and spread of re-invaders. In

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addition, changes in the re-invader (e.g. genotype or tolerance to control methods), environment (e.g. available open space), and species interactions (e.g. reduced native propagule sources or changes in macro and micro benthic communities) may also promote or hinder re-invasion (Gabler and Siemann, 2012; Pearson et al., 2016; Banks et al., 2018). Therefore, an in-depth understanding of the re-invasion processes may help managers to prevent re-invasions and guarantee restoration efforts (Gabler and Siemann, 2012; Pearson et al., 2016).

Spartina alterniflora (smooth cordgrass), a globally widespread and rapidly expanding invasive species of coastal areas, was introduced in Chongming Dongtan at the Yangtze Estuary in 1995. Since then, this alien species has gradually replaced the native *Scirpus mariqueter* and *Phragmites australis* saltmarshes, and has seriously degraded bird habitats (Yuan et al., 2011, 2014). From 2013 to 2016, large-scale ecological engineering of “*S. alterniflora* control and bird habitat optimization” (23.6 km²) was conducted in the Chongming Dongtan National Nature Reserve (CDNR) (blue area in Fig. 1b). Large swathes of *S. alterniflora*

were controlled by cutting and then drowning, and a variety of habitat types (pond, native saltmarsh, mudflat, and creek) were restored inside engineering area (i.e. the dark and light blue areas in Fig. 1b). Meanwhile, the *S. alterniflora* patches that remained on the natural tidal flats outside the dyke were eradicated with the use of herbicide (i.e. Gallant) in June 2014 and the native *S. mariqueter* saltmarsh was restored via the transplanting of this native species (i.e. the red-outlined area in Fig. 1b). However, re-invasion of *S. alterniflora* over the restored area was observed in 2016, which occurred as spotted small patches and increased to ca. 1.7×10^{-3} km². Because *S. alterniflora* only has a transient seed bank in which seeds persist for less than a year (Xiao et al., 2009), the re-invasion in the restored area can be attributed to the arrival of propagules (seeds or vegetative fragments) from other sources, i.e. the remaining *S. alterniflora* saltmarshes (the orange area in Fig. 1b).

In this study, re-invasion of *S. alterniflora* in a restored saltmarsh was investigated using a combination of field surveys and experiments in the CDNR. The study objectives were to better understand the processes

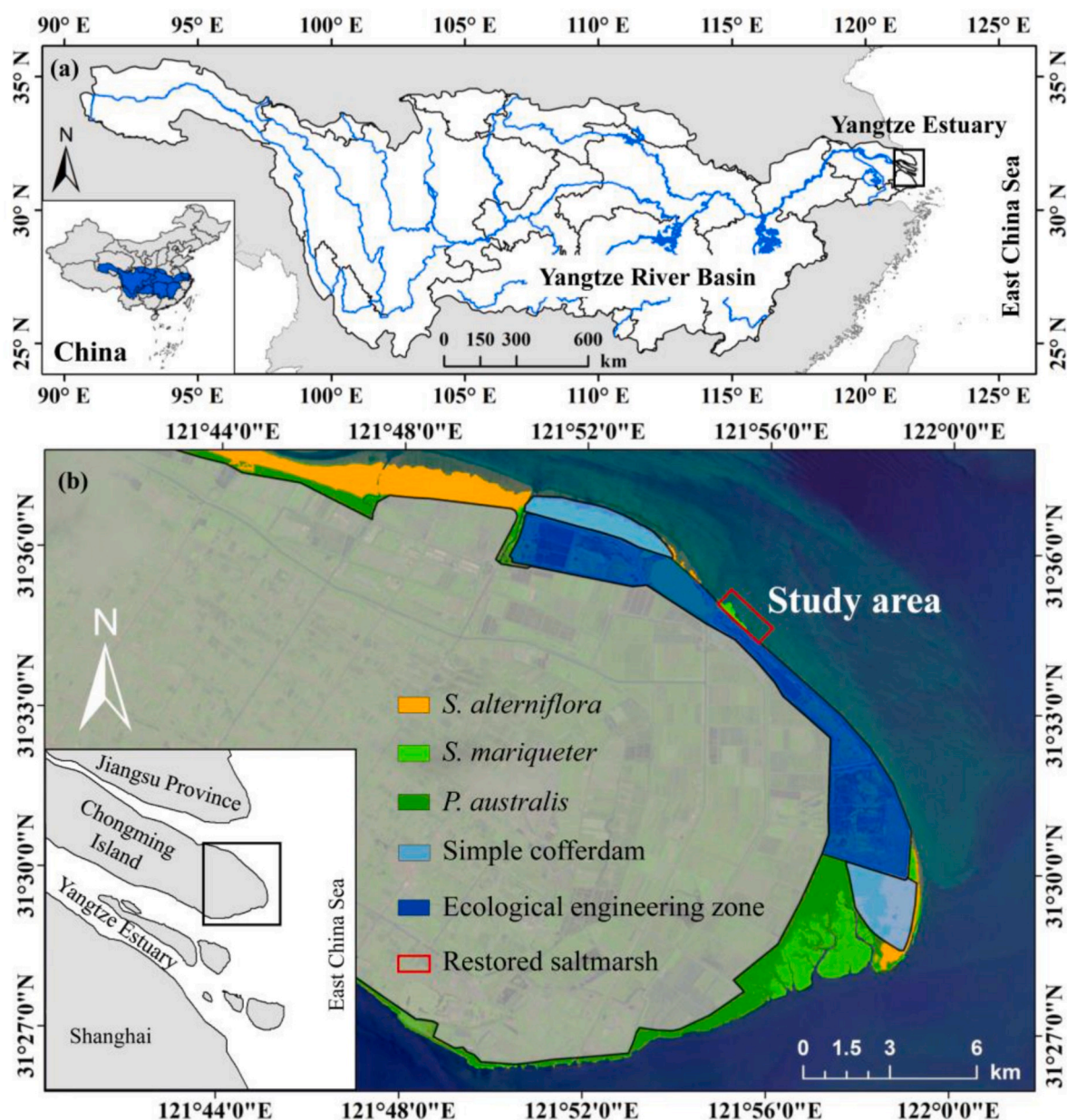


Fig. 1. Map of the study site. (a) The Yangtze River Basin and the Yangtze Estuary. (b) The location of study area in the Chongming Dongtan Nature Reserve. Native species: *Scirpus mariqueter* and *Phragmites australis*, invasive species: *Spartina alterniflora*.

underlying *S. alterniflora* re-invasion and to develop useful strategies for controlling its re-invasion and the restoration of natural saltmarsh. We specifically addressed the following questions: (1) are *S. alterniflora* seeds able to arrive at the restored saltmarsh through long-distance transport by tidal currents? (2) What is the fate of these arrived seeds in the restored area? (3) Do environmental factors influence the germination and establishment of the arrived seeds?

2. Materials and methods

2.1. Study area

The CDNR (31°25' - 31°38' N, 121°50' - 122°05' E) is located on the eastern fringe of Chongming Island at the mouth of the Yangtze River, China (Fig. 1a). The area has a northern, sub-tropical monsoon climate with an average annual temperature of 15.3 °C and an average annual precipitation of 1022 mm (Xiao et al., 2009). The CDNR is subjected to semi-diurnal tidal cycles with maximum and average tide heights of 4.62–5.95 m and 1.96–3.08 m, respectively (Hu et al., 2015a, 2015b).

The study site had undergone restoration for native *S. mariqueter* saltmarsh and was under threat of re-invasion by *S. alterniflora* from a source area at least 2 km away (Figs. 1b and 2b, c). In 2016, two transects were established along an elevation gradient. One transect was established in the restored *S. mariqueter* saltmarsh (RS) and the other transect was established on the adjacent mudflat (MD) (Fig. 2a). The initial elevation of the RS ranged from 1.8 to 3.1 m while that of the MD ranged from 1.8 to 2.6 m (local Wushong bathymetric benchmark), as determined by a terrestrial laser scanning system (Riegl VZ-4000, RIEGL Laser Measurement Systems GmbH, Austria).

2.2. Measurement of seed arrival

To investigate the spatio-temporal dynamics of *S. alterniflora* seed arrival, three experimental sites, i.e. a high-elevation site (H), intermediate-elevation site (M), and low-elevation site (L), were selected along the elevation gradient of RS and MD (Fig. 2a). From August 2016 to April 2017, 15 sampling quadrats (3 rows and 5 columns, 1 × 1 m each) were constructed randomly at each site every month, and 4 soil samples (25 × 25 cm and at 10 cm in depth, for each)

were randomly taken in each quadrat. All soil samples were sieved for seeds using 1 mm mesh in the laboratory, and the density of arrived seeds was averaged per site (60 soil sample replicates) and expressed in no./m².

2.3. Experiment on retention of arrived seeds

To determine the retention of arrived seeds in the re-invaded areas, a manipulative experiment was conducted at the H, M, and L sites along both the RS and MD in April 2017 (the season for seed germination) (Fig. 2a). Prior to the experiment, layered soil cores were created in PVC pipes (5.6 cm in diameter, 25 cm in depth) with homogenized sediment. Ten colour-stained seeds (pre-inactivated through repeated freeze-thaw, Zhu et al., 2014) were placed at each of the following depths: 0 (soil surface), 1, 3, 5, 10, and 20 cm (Fig. 3a). Each soil layer was frozen at –20 °C before adding a new layer of sediment and the seeds to minimize mixing. After all layers were ready, all soil cores were removed from the PVC pipes and kept in a frozen state to enable easier deployment in the field (Zhu et al., 2014).

At the H, M, and L sites in both the RS and MD, five soil cores were deployed in a line according to the principle of surface consistency (Fig. 2a). After 1 month, all the soil cores were relocated and retrieved as completely as possible using PVC pipes with a larger diameter (11 cm in diameter, 35 cm in depth). After the *S. alterniflora* seeds were separated from the soil, the number of recovered seeds was recorded, and their original positions were identified according to seed colours. Seed retention (%) was then calculated as the number of recovered seeds divided by the total deployed seeds.

2.4. Measurement of hydrodynamic conditions

Hydrodynamic conditions (i.e. tidal currents, wave action, inundation depth, and duration) were considered to be key factors that affect *S. alterniflora* seed arrival and retention at the study site. Tidal current velocity and waves were measured using an Electromagnetic Current Meter (ALEC AEM-USB, JFE Shoji Trade Corporation, Japan) and Tide Wave Recorder (TGR-2050, RBR Ltd., Canada), respectively, during the spring tide from 25 April to 27 April 2017 at the H, M, and L sites in both the RS and MD (Fig. 2a). All instruments were mounted 5 cm above the

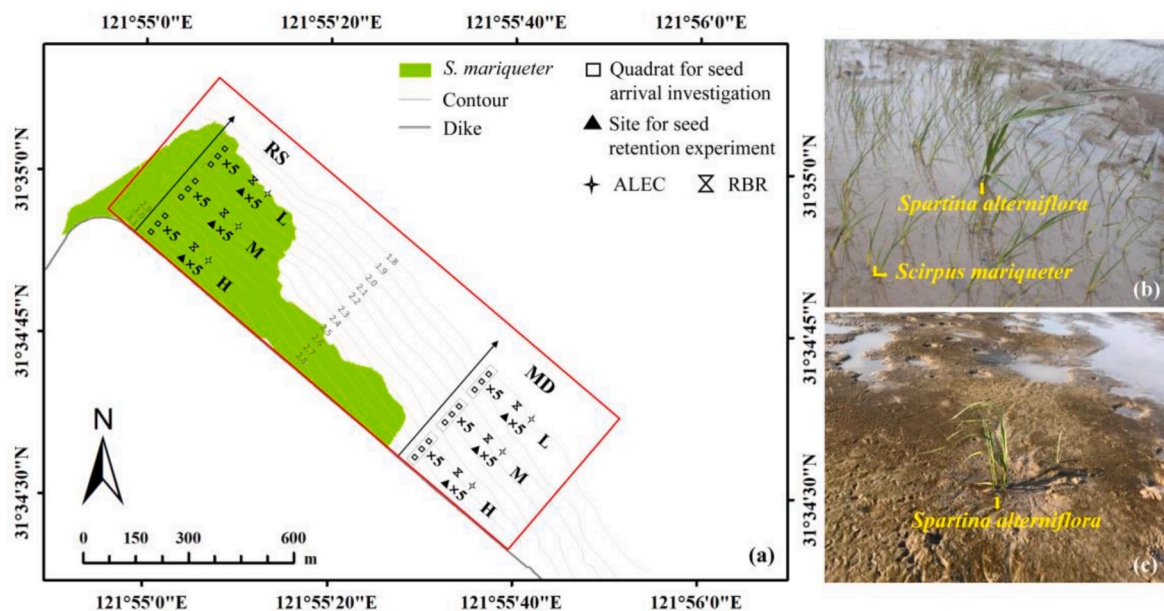


Fig. 2. (a) Schematic distribution of the transects and experimental sites in a restored saltmarsh (RS) and mudflat (MD). H: High-elevation site, M: Intermediate-elevation site, and L: Low-elevation site; RBR: Tide wave recorder; ALEC: Electromagnetic current meter. (b) *Spartina alterniflora* re-invading the RS populated with a native species: *Scirpus mariqueter*. (c) *S. alterniflora* re-invading the adjacent MD.

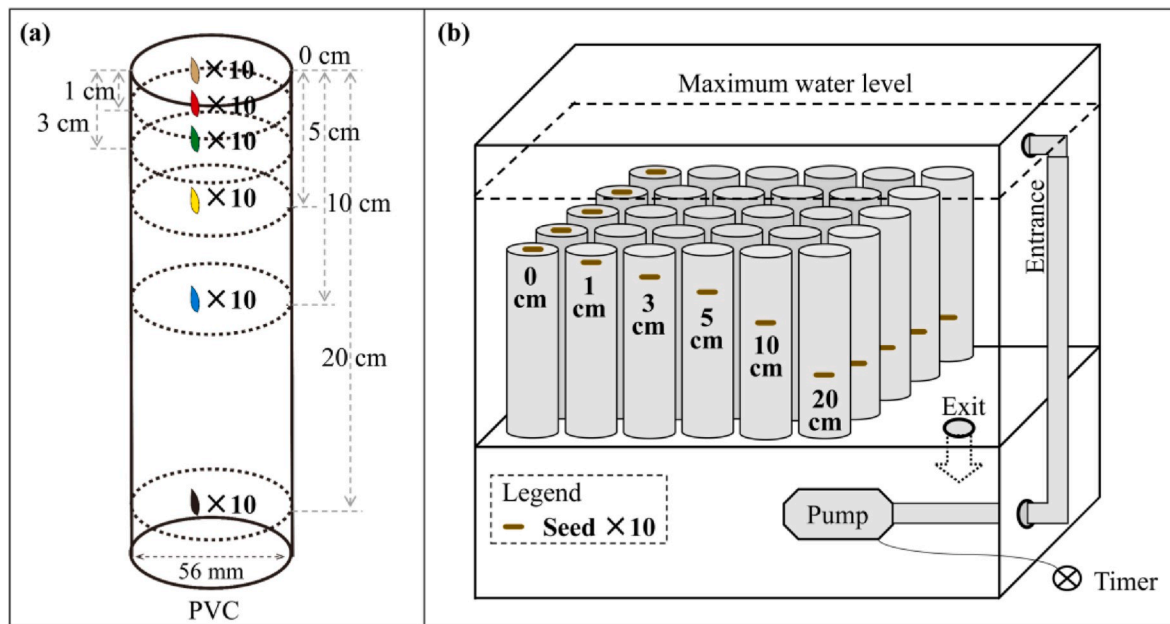


Fig. 3. (a) Layered soil cores with colour-stained seeds of *Spartina alterniflora*, and (b) design of mesocosm experiment on seed germination response to inundation and sediment burial. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mudflat surface and programmed to record measurements every 5 min (sample counter = 30, interval = 1 s).

2.5. Seed germination and establishment experiments

To estimate the influence of environmental factors on the germination and establishment of the arrived *S. alterniflora* seeds, a mesocosm experiment using a tidal simulation system was conducted in a greenhouse. The mesocosm system was composed of two layered tanks, an experimental tank (upper, 98 × 76 × 67 cm) and a reservoir (bottom), which were automatically filled with artificial seawater and drained by a pump with a timer (Fig. 3b). Pots used in the experiment were made of PVC pipes (11 cm diameter and 35 cm height) lined with sponges to create an even bottom surface and to facilitate water circulation at the bottom (Fig. 3b).

In March 2017, based on the mean daily tidal range and the daily inundation duration in CDNR (Cui et al., 2015), four tidal simulation systems were used to set four levels of inundation treatments: non-inundation (with only moist mud) and three semi-diurnal inundation duration treatments (5 cm inundation depth) of 2, 4, and 6 h each (i. e. 4, 8, and 12 h/day). The experimental tank of each tidal simulation system consisted of six treatment levels of sediment burial, i.e. 100 vernalized seeds (collected from the northern parts of CDNR in October 2016) were buried at depth of 0, 1, 3, 5, 10, and 20 cm below the surface of the PVC pipes using homogenized sediment. Each PVC pipe only set one burial depth treatment and each treatment was replicated five times in each tank (Fig. 3b).

After 40 days, the number of seedlings was recorded daily and the germination rates (R) for the different treatments were calculated as follows: $R (\%) = n/N \times 100\%$, where n is the number of seedlings, and N is the number of buried seeds.

2.6. Data analysis

For the field data, two-way ANOVA with a Tukey HSD post-hoc test was adopted to test for the effect of time and sites (with varied elevation) on seed arrival as well as the effect of burial depths and sites on seed retention. For RS transect and MD transect which leaning towards assessed each separately, a Pairwise Wilcoxon rank sum test was used to

test for differences in seed arrival and retention between them. The effects of inundation duration, burial depth, and their interactions on seed germination in the mesocosm experiment were tested using two-way ANOVAs, and a least significant difference (LSD) test was used to assess multiple comparisons. The level of statistical significance was set as $P < 0.05$.

To build the relationship between burial depth and seed status (i.e. retention and germination), the burial depth-based logistic function (Eq. (1)) was adapted. In general, the curve of the logistic probability law constitutes three meaningful phases: the start of change, steep change, and an irretrievable point (Vittinghoff et al., 2012). In this study, we calculated the EC_{20} of an up-regulated logistic curve (Eq. (2)) and the EC_{80} of a down-regulated logistic curve (Eq. (3)) to obtain the third point which reflects the burial-depth threshold for seed retention and seed germination, respectively. Data were $\log(x+1)$ transformed to satisfy the assumption of homogeneous of variance when quantifying the burial threshold for seed germination and establishment. All analyses were conducted using SPSS (IBM Corporation, version 22.0) and Origin (OriginLab Corporation, version 9.0).

$$f(D) = \frac{1}{1 + \exp\left[\frac{-(D-a)}{k}\right]} \quad (1)$$

$$EC_{20} = 10 \left[\log(X_0) + \frac{\log(0.25)}{P} \right] \quad (2)$$

$$EC_{80} = 10 \left[\log(X_0) + \frac{\log(4)}{P} \right] \quad (3)$$

where D represents the depth of burial; a , k , X_0 , and P represent the fitting parameters; X_0 represents the environmental factor value of the maximum slope point of the fitted curve; and P represents the absolute value of the maximum slope of the fitted curve.

3. Results

3.1. Spatio-temporal dynamics of seed arrival

Seed arrival assessments revealed that only a few seeds were found after October 2016 in the MD and after March 2017 in the RS, and the density of arrived seeds was higher in the MD than in the RS ($P < 0.05$, Fig. 4). The highest density of arrived seeds in the MD (21.3 ± 5.3 per m^2) was recorded in October 2016, which is also the period of seed rain (i.e. seeds falling from the mother plant) at the source site. In the RS, the highest recorded density of 8.0 ± 3.7 per m^2 was recorded the following spring in April 2017 (Fig. 4). There was no obvious difference in the density of arrived seeds among the H, M, and L sites ($P > 0.05$). Overall, the density of arrived *S. alterniflora* seeds was highest in the M site in MD, and in the H site in RS (Fig. 4).

3.2. Retention of the arrived seed

The retention rates of seeds increased with greater burial depth at all sites both in the RS and MD ($P < 0.001$, Fig. 5a and b). However, there were no differences in seeds retention among the H, M, and L sites within or between the RS and MD ($P > 0.05$, Fig. 5a and b). Overall, the retention rates of buried seeds (at depths of 1, 3, 5, 10, and 20 cm) were all higher than those of the surface seeds (i.e. depth: 0 cm) ($P < 0.001$). Only the H site in the RS managed to retain seeds at the surface, while

the surface seeds in all other sites were lost (Fig. 5a and b). Once buried, seed retention increased remarkably. When the *S. alterniflora* seeds were buried deeper than the thresholds of 0.8 cm in RS and 1.3 cm in MD, seeds were well retained and avoided being washed away by the tide (Fig. 5c).

3.3. Hydrodynamic properties of the study site

Water levels in the study area showed typical tidal ranges for a meso-tidal estuarine system (Fig. 6). Similar trends were found in the maximum inundation depth, inundation duration, average current velocities, and the maximum current velocities both in RS and MD, i.e. site L > site M > site H. However, the experimental sites in the MD showed relatively deeper inundation depths, longer inundation durations, and higher current velocities than the corresponding sites in the RS, which can be attributed to the relatively lower elevation of MD (Fig. 2a). The average magnitude of wave energy increased from the dyke towards the sea in the RS, however, wave energy density was relative lower in the MD compared with that in the RS (Fig. 6).

3.4. Seed germination and establishment

The effects of inundation, sediment burial, and their interactions on seed germination and establishment were highly significant ($P < 0.001$, Fig. 7a). Overall, inundation (with durations of 4, 8, and 12 h/d)

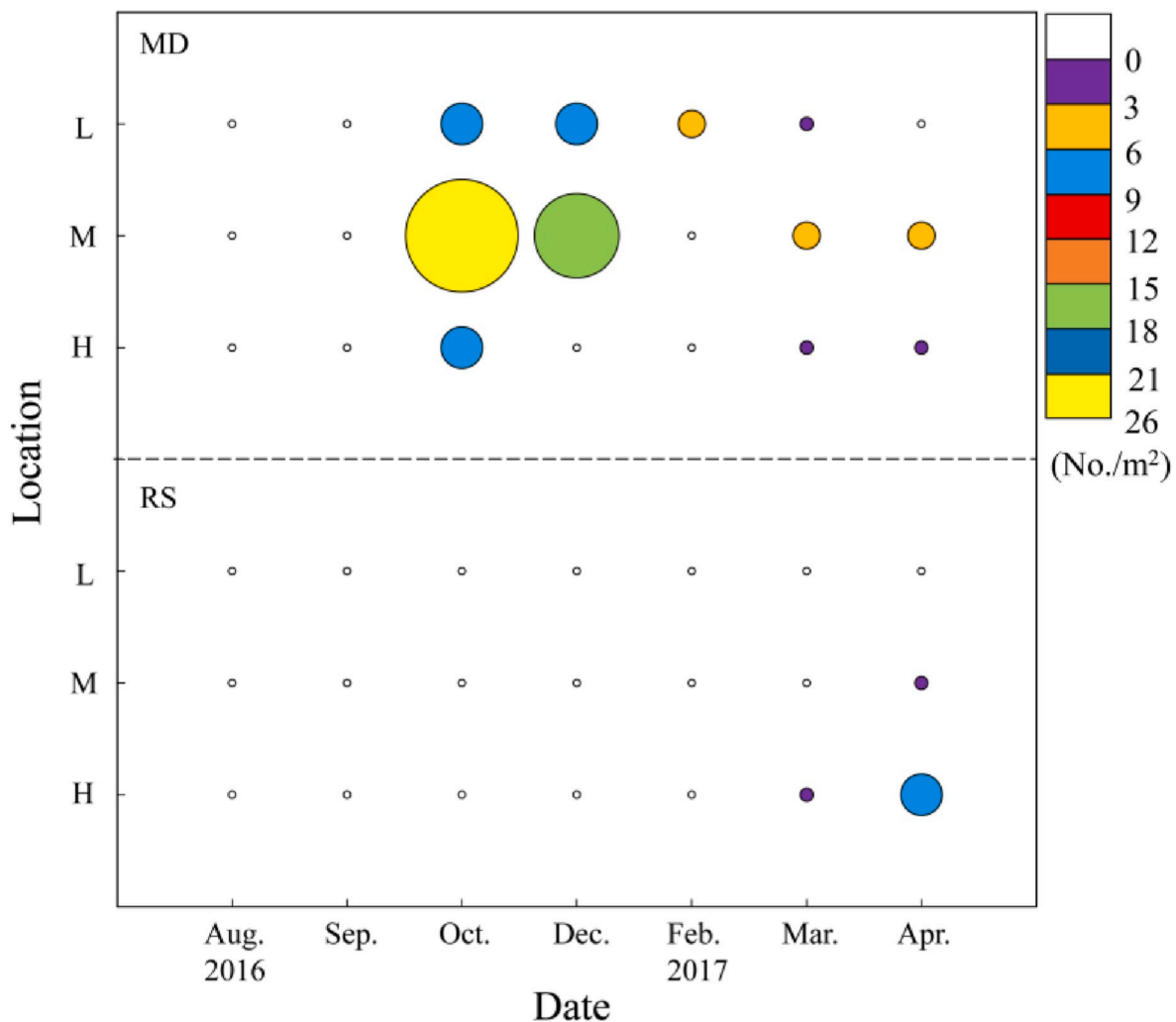


Fig. 4. Spatio-temporal dynamics of *Spartina alterniflora* seed arrival at the high-elevation (H), intermediate-elevation (M), and low-elevation (L) sites in a restored saltmarsh (RS) and mudflat (MD).

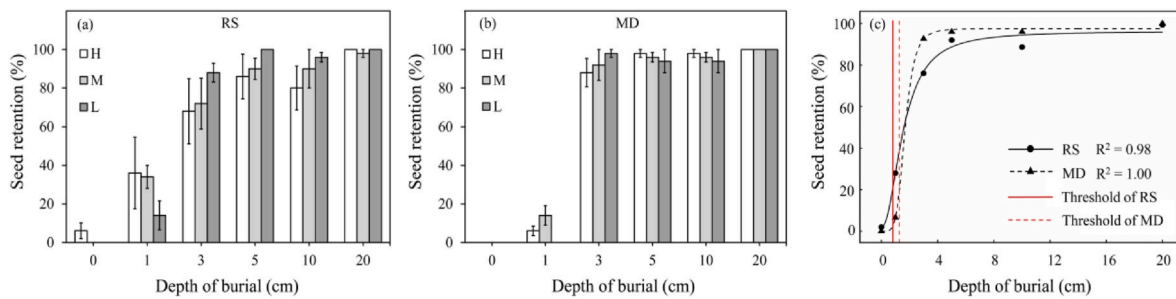


Fig. 5. (a and b) Seed retention rates of *Spartina alterniflora* under different burial depths at the high-elevation (H), intermediate-elevation (M), and low-elevation (L) sites in a restored saltmarsh (RS) and mudflat (MD). (c) Fitted curves of *S. alterniflora* seed retentions to burial depth, showing the thresholds.

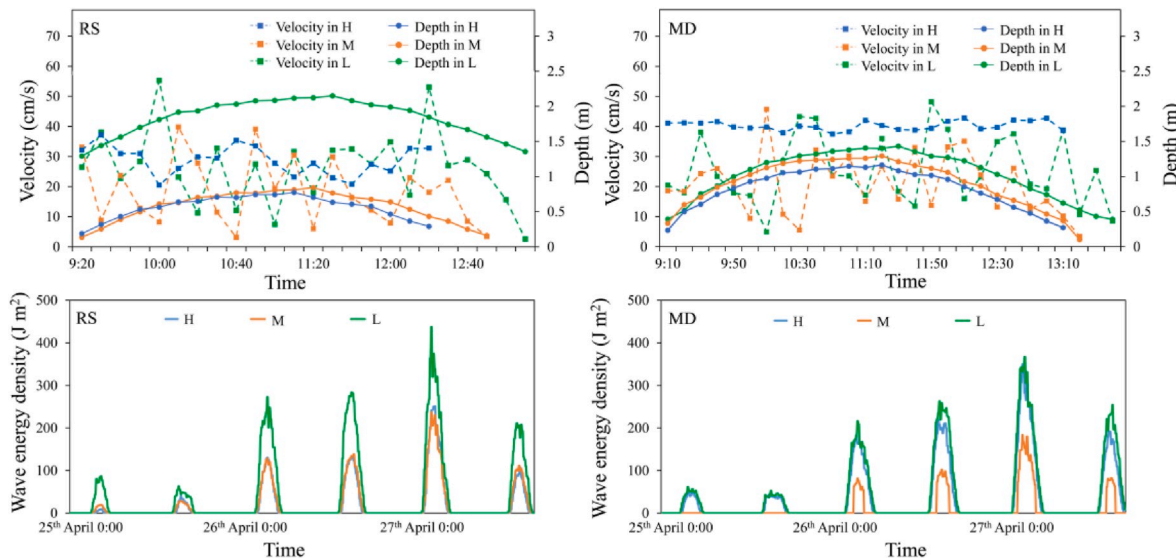


Fig. 6. Inundation depth and current velocity measurements at high tide (top panels), and tidal wave energy during spring tide (bottom panels) at the high-elevation (H), intermediate-elevation (M), and low-elevation (L) sites in a restored saltmarsh (RS) and mudflat (MD).

resulted in higher germination and establishment rates than non-inundation (with duration of 0 h/d; $P < 0.05$), while no significant differences were detected among treatments of different inundation durations ($P > 0.05$, Fig. 7a). In addition, there were no significant differences among the mean germination and establishment rates of seeds buried at shallower depths (i.e. at depths of 0, 1, and 3 cm; $P > 0.05$, Fig. 7a), which were all significantly higher than those for seeds buried at the depth of 5 cm ($P < 0.05$, Fig. 7a). When buried at shallower depths than 7.8, 5.3, 5.4, and 5.5 cm, seeds of *S. alterniflora* could germinate and establish successfully under inundation durations of 0, 4, 8, and 12 h/d, respectively (Fig. 7b).

4. Discussion

4.1. Spatio-temporal dynamics of seed arrival

Among the possible dispersal strategies for *S. alterniflora*, colonization by seed plays a critical role in the natural (re)establishment and range expansion of this species (Xiao et al., 2010). The results from this study further demonstrated this general invasion pathway and emphasized the important role of seed dispersal and colonization in successful re-invasion. Because *S. alterniflora* is characterized by a transient seed bank, in which seeds persist for less than 1 year (Xiao et al., 2009), arrival of the yearly-formed fresh seeds from outside source areas should be the only source contributing to re-invasion in the study area. Before September, there was no detectable seed bank at the study site. However, new *S. alterniflora* seeds appeared across the study area from

September to April the following year, which coincided with the period of *S. alterniflora* seed rain in the source area. This study further demonstrated that the seeds that arrived in the restored site were probably dispersed from the source area via tidal currents, despite the nearest source area of *S. alterniflora* being at least 2 km away from the restored site.

The dispersal of *S. alterniflora* seeds from source areas to recipient areas by tidal currents is not a linear process; rather, it is highly variable over space and time, and depends on the interactions among the local geomorphology, vegetation, and hydrodynamic forcing (Friess et al., 2012; Zhu et al., 2014). In CDNR, the total remaining area of *S. alterniflora* outside the ecological engineering area was ~85.3 ha in 2015. These mature *S. alterniflora* populations are capable of producing up to 84,000 seeds/m² every year, with a seed viability as high as 60% (Xiao et al., 2010). However, the number of seeds arriving at the restored site was very low, with the highest observed density being 26 seeds/m². The large discrepancy between seed density at the source area and recipient habitat can be attributed to the great losses incurred during dispersal by tidal currents (Chang et al., 2008; Zhu et al., 2014). In addition, the highest densities of arrived seeds were recorded at different sites in the MD and RS, which can be attributed to the weaker wave energy found at these sites. To fully assess the potential of re-invasion of the restored saltmarsh by *S. alterniflora* seeds from source areas, future research should focus on the effects of hydrodynamic forcing over space (site geomorphology, sediment accretion or erosion, and vegetation coverage) and time (period of seed dispersal, germination, and establishment).

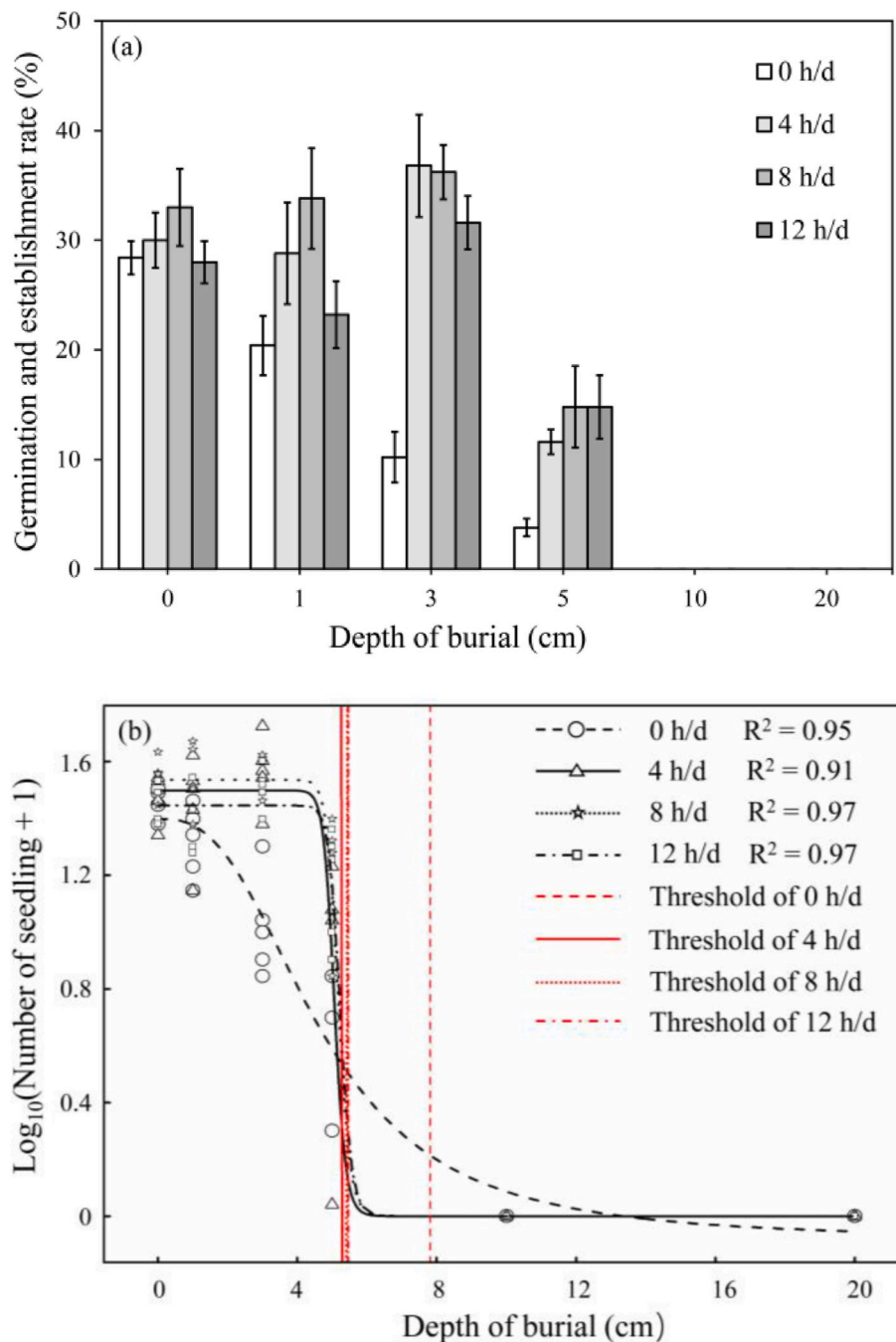


Fig. 7. (a) Germination and establishment rates of *Spartina alterniflora* seeds under different inundation duration and burial-depth treatments. (b) Fitted curves of seed germination and establishment in relation to burial depths, showing the thresholds.

4.2. Potential *S. alterniflora* re-invasion by seeds

After seeds arrive in a recipient habitat, the retention of the seeds before their successful germination and establishment in spring could be a bottleneck, imposed by the high instability of the intertidal environment (Marion and Orth, 2012; Zhu et al., 2014). Physical disturbances (e.g. hydrodynamic forces and sedimentation regimes) can greatly influence the dislodgment of initially deposited seeds (Chang et al., 2008; Koch et al., 2010). In the present study, the field experiment regarding the retention of *S. alterniflora* seeds revealed a nonlinear, positive correlation between seed retention and burial depth. Seed retention was enhanced after reaching a burial threshold of 0.8–1.3 cm, which is the boundary depth below which newly deposited seeds of *S. alterniflora* can

avoid being washed away by tidal currents and waves. Huge amounts of silt brought in by the Yangtze River are deposited the boundaries of the CDNR (Hu et al., 2015a, 2015b). The accretion rates of the restored saltmarsh in this study was 0–1 cm per month during October 2016 to March 2017 and 1–5 cm per month during April to September in 2017 (Chen et al., 2019). These moderate sedimentation rates found during the main periods of dispersal and germination at the restored saltmarsh can provide safe sites for the newly deposited re-invader seeds and a window of opportunity for their germination and successful establishment in spring at the study site (Hu et al., 2015a, 2015b; Cao et al., 2018).

However, the retention of arrived seeds at the recipient habitat does not guarantee successful (re)establishment for most saltmarsh plants,

because the physical disturbances in intertidal flats (e.g. sedimentation dynamics and hydrodynamic forces) can greatly influence seed germination and establishment (Balke et al., 2011; Cao et al., 2018; Tabak et al., 2018). In the present study, the results of the mesocosm experiments with treatments of different burial depths and inundation durations indicated the critical importance of sediment burial depth on the potential establishment (re-invasion) of *S. alterniflora* seeds. Seeds of *S. alterniflora* were able to germinate and establish successfully at burial depths that were shallower than the threshold. However, these responses were also shown to be influenced by inundation duration. Our previous field mesocosm experiment in the CDNR assessed the influence of intertidal elevation on the establishment and survival of *S. alterniflora* and indicated a threshold elevation of 2.5 m, which corresponds to a mean daily inundation duration of 10 h/d (Cui et al., 2015). The discrepancy of inundation duration thresholds between these two mesocosms experiments may be explained by the stronger hydrodynamic forcing (current velocity and wave energy) at the lower elevation sites. Therefore, future studies should examine the effects of interactions between hydrodynamic forcing and sedimentation dynamics on seed germination and establishment of *S. alterniflora* during re-invasion.

4.3. Implications for control of *S. alterniflora* re-invasion

The successful prevention and control of *S. alterniflora* re-invasion in restored saltmarshes and adjacent mudflats require an in-depth knowledge on the probability of propagule dispersal from source areas and the processes controlling seed germination and establishment at the recipient habitats. The present study is the first to quantify seed arrival at a recipient habitat and the effects of hydrodynamic forcing and sedimentation conditions on the re-establishment of the globally invasive species *S. alterniflora* on saltmarshes in the Yangtze Estuary. Our results indicated that: (1) *S. alterniflora* seeds were transported to the restored area via tidal currents, and the spatio-temporal dynamics of arrived seeds varied greatly depending on the intertidal geomorphology, vegetation, and hydrodynamic processes; (2) arrived seeds benefited from moderate sediment burial, which provided the re-invaders with favourable “safe” conditions and an opportunity to germinate and persist at the recipient habitat; and (3) sedimentation conditions regulated the germination and establishment of the retained seeds, resulting in a higher probability of successful re-invasion only when re-invaders were buried shallower than a threshold burial depth. In addition, the interaction between hydrodynamic forcing and sedimentation dynamics may also play an important role in *S. alterniflora* seedling establishment in the restored saltmarsh and adjacent mudflats.

The results of this study highlight the need to expand the current management strategy for the prevention and control of *S. alterniflora* re-invasion in the restored saltmarsh and adjacent mudflats of the CDNR. Control efforts should not only focus on the re-invaded areas of the restored saltmarsh and adjacent mudflats, but also on possible source areas of *S. alterniflora*. Furthermore, the use of barrier zones to effectively stop invader seed dispersal would be almost impossible to implement in these dynamic intertidal environments, thus control measures should be adopted at the source areas. For example, the following measures may be applied: mowing of the above-ground parts of adult plants before flowering to remove all flowering heads prior to seed ripening (Yuan et al., 2011), and the use of herbicides to control adult plants and prevent seed production (Patten et al., 2017). Secondly, the re-invader *S. alterniflora* and the native species *S. maritima* share almost overlapping niches in the re-invaded restored saltmarsh and adjacent mudflats (Huang et al., 2008); therefore, the species-specific Gallant herbicide can be used to selectively kill *S. alterniflora* (Zhao et al., 2020). Thirdly, the establishment of the re-invader *S. alterniflora* in the restored saltmarsh usually shows a random “satellite” pattern, in which uncontrolled expansion can result in the invader outcompeting the native *S. maritima*. Thus, intervention at an early stage can prevent a much larger control effort at later stages. Currently, there are

established guidelines for management and control of re-invasion by *S. alterniflora* in the restored saltmarsh in the CDNR. These guidelines are based on the control strategies drawn from this study, and such control efforts are currently being implemented.

Declaration of competing interest

None declared.

Author contributions

ZZ and WL performed field and mesocosm experiments; ZZ, LY and BT developed the analyses; ZZ, LY and LZ wrote and edited the manuscript. All authors gave the final approval for the publication of the manuscript.

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