



Seed dispersal capacity and post-dispersal fate of the invasive *Spartina alterniflora* in saltmarshes of the Yangtze Estuary



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ABSTRACT

Spartina alterniflora is one of the most serious invasive species in the coastal saltmarshes of China. Seeds are generally considered to be the main method for this species to colonise new habitat, but little is known quantitatively about the seed dispersal capacity and post-dispersal fate (i.e., germination and survival time). We measured the duration of seed flotation, seed persistence and seed germination of *S. alterniflora* in three intertidal zones [low intertidal zone (LIT), middle intertidal zone (MIT) and high intertidal zone (HIT)] in the Yangtze Estuary on the eastern coast of China. The results showed that (1) the flotation time of *S. alterniflora* seeds ranged from 3 to 13 days, and the values were higher in HIT and MIT than in LIT; (2) the period of seed germination was from February to June, mainly in March and April, and seed source affected seed germination as the values for seeds from HIT and MIT were much higher than those from LIT, while burial sites had no effect on germination percentages, and (3) the seed persistence was less than a year regardless of seed source, which was characterised by a transient seed bank, with values being higher in HIT and MIT than in LIT. Our results suggested that low marsh plants were far less able to produce successful seeds, or conversely, that the mid-marsh location had plants with the greatest seed production and seed mass, and the high- and mid-marsh plants had good seed flotation ability, germination and survival. Thus, plants in the mid- and high-marsh may contribute disproportionately to an invasion.

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1. Introduction

Species invasions are currently rated as one of the most important global-scale environmental problems, causing large losses in biodiversity as well as economic damage (Pimentel et al., 2005). Coastal wetlands are among the most vulnerable habitats to species invasion (Zedler and Kercher, 2004). One of the most notorious exotic species in wetlands is *Spartina* spp. (e.g. *Spartina alterniflora* & *Spartina anglica*), which have been deliberately or accidentally introduced to many coastal wetlands across the world (Wang et al., 2006a; Strong and Ayres, 2013; Sheehan and Ellison, 2014). The fast spread of *Spartina* spp. in the introduced areas caused several big invasion events, as seen in the marshes of western US, Europe and China where extensive seedling

recruitment has been reported as a primary mechanism for their explosive success (Gray et al., 1991; Ayres et al., 2008). Its seeds can be transported into a new habitat by the tide (Feist and Simenstad, 2000; Davis et al., 2004; Ayres et al., 2004), followed by seedling establishment and tussock expansion through vegetative growth (Sanchez et al., 2001; Davis et al., 2004; Xiao et al., 2010).

Spartina alterniflora was firstly introduced to China in 1979 to accelerate sedimentation and land formation via so-called 'ecological engineering' (Wang et al., 2006b; Li et al., 2009, 2014), and it is now widely distributed in coastal saltmarshes (Zuo et al., 2012; Ge et al., 2015). One example is in Chongming Dongtan Nature Reserve at the Yangtze Estuary, where *S. alterniflora* was introduced in the mid-1990s. The area of *S. alterniflora* growth amounts to approximately 25% of the total saltmarsh vegetation area at present (Ge et al., 2015). This invasion has changed the composition and distribution of plant communities and benthic communities and has threatened bird diversity and consequently

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bird population (Gan et al., 2009; Ma et al., 2009). Extensive seedling establishment in spring has been demonstrated as the crucial way for *S. alterniflora* to achieve a rapid range expansion in the Yangtze Estuary marshes (Xiao et al., 2010). A previous study also showed that *S. alterniflora* in these marshes had generally high seed yields that varied along elevation gradients and a transient seed bank (Xiao et al., 2009). Yet little is known quantitatively about the seed dispersal capacity and post-dispersal fate (i.e., germination and survival time).

In tidal saltmarshes, hydrochory is an adaptive trait for wetland plants to colonise new habitats (Xiao et al., 2009; Zhu et al., 2014). Most seeds can be dispersed locally or over long distances by tides, after arrival in a suitable habitat, soil and water conditions further affect the germination potential of both newly dispersed seeds and seeds already present in the soil seed bank (Elsey-Quirk et al., 2009). Consequently, seed floating capacity, spatial and seasonal pattern of seed survival are key factors in determining whether a wetland invader is able to colonize new habitats (van Leeuwen et al., 2014; Zhu et al., 2014).

In this study, we aim to understand the characteristics of seed dispersal capacity and post-dispersal fate of the invasive *S. alterniflora* in the salt marshes of Yangtze Estuary as well as the consequences for its invasion success. Specifically, we examine how 1) seed buoyancy duration, 2) germination performance and 3) seasonal seed survival vary with different seed sources and deposition sites along an elevation gradient. Such information could provide useful insights into the understanding of the invasion success and control & management of this invasive species.

2. Materials and methods

2.1. Study area

We conducted this study in the northern part of Chongming Dongtan Nature Reserve in the Yangtze Estuary (31°25′–31°38′N and 121°50′–122°05′E) (Fig. 1). This natural reserve has a sub-tropical monsoon climate. The mean annual temperature is 15.2 °C, and the lowest temperature is 2.8 °C in January. The average precipitation is 1025 mm and is concentrated in the summer months. The total area of the Reserve is approximately 24600 ha, where 10,000 ha are above sea level, characterised by tidal flats.

The Reserve is one of the largest sanctuaries for migratory birds in East Asia and an overwintering area for some waterbirds endangered in China, such as *Cygnus columbianus*, *Grus monacha* and *Platalea minor* (Ma et al., 2004). It was listed in Chinese Protected Wetlands in 1992 and was designated as internationally important under the Ramsar Wetlands Convention (2002). The Reserve was dominated by *Scripus mariqueter* and *Phragmites australis* before 1995, with *Scripus mariqueter* dominating tidal flats from 2.0 to 2.9 m and *Phragmites australis* covering tidal flats above 2.9 m. *S. alterniflora* was first introduced to the Nature Reserve in the mid-1990s. Since then, this species has gradually invaded large areas formerly inhabited by *Phragmites australis* and *Scripus mariqueter*. A mono-dominant community in the northern part of the Nature Reserve has been observed since 2003 (Huang et al., 2007).

Three intertidal zones with distinct elevations: low intertidal zone (2.4 m–2.9 m, LIT), middle intertidal zone (2.9 m–3.5 m, MIT) and high intertidal zone (3.5 m–3.9 m, HIT) were first identified according to a report by Xiao et al. (2009) (Fig. 1). Tides in Chongming Dongtan are regular and semidiurnal, and the influence of tides on intertidal zones varies with elevation and season. In winter, MIT and HIT are drained, whereas the LIT is submerged daily; however, all three intertidal zones are submerged during the period of the spring tide (Yang et al., 2001).

2.2. Seed collection

At the beginning of November 2008, three transects were established 100 m apart along the intertidal gradient from the inland dyke to the sea water (Fig. 1). In each intertidal zone, along each transect, one sample plot (2 × 2 m) was randomly selected. The number of fruiting culms and the total culms in the plots were recorded; thereafter, 10 typical plants were sampled for measurements of their height, mean spike length, and the number of seeds per flowering culm was counted for estimation of seed production (seeds·m⁻²) (Equation (1)). After seeds were taken back to the laboratory for further tests and air-dried for 7 days, the seed mass (g·1000 seeds⁻¹) was measured (Table 1).

Equation (1) below is used to determine seed production:

$$\text{Seed production/m}^2 = \text{total culms/m}^2 \times \text{proportion of culms that flower} \times \text{average number of seeds/flowering culm} \quad (1)$$

2.3. Seed flotation capacity, germination and survival tests

2.3.1. Seed flotation capacity

In November 2008, a group of 200 *Spartina alterniflora* seeds collected from each sample plot were put into 1000 mL glass cups with standing water collected from the neighbouring creek to examine the seed flotation time. Water levels and salinities were maintained by adding fresh water. The number of floating seeds was recorded daily at 12:00, and the water in the cups was stirred for 1 min with a glass rod. The tests were terminated when no floating seeds were observed in the glass cups.

2.3.2. Seed germination

In spring, the three intertidal zones (HIT, MIT and LIT) are generally submerged during the period of spring tide (Yang et al., 2001), and this provides a chance for *Spartina alterniflora* seeds to disperse long-distance over the trans-intertidal zone. In December 2008, 600 *S. alterniflora* seeds collected from each sample plot (HIT, MIT or LIT) were divided into three double-layered nylon mesh bags (200 seeds for each bag), and these three bags were buried in LIT, MIT and HIT along each transect at a depth of 5 cm. There were 9 bags for each transect and 27 bags in total for the three transects. By exhuming and re-burying seed bags, germinated seeds were counted and removed monthly from January 2009 until no germination was observed. The monthly and total germination were expressed as mean percentage of germinable seeds.

2.3.3. Seed survival

Spartina alterniflora seeds collected from each sample plot were stored in a growth chamber (4 °C, 12 h of daytime and 12 h of night time, 75% humidity) beginning in December 2008. The test for seed survival began in March 2009, when 200 seeds from each sample plot were put on filter paper moistened with distilled water and then placed in glass Petri dishes with a diameter of 9 cm. The temperature was set at 25 °C for 12 daytime hours and 20 °C for 12 night time hours, and air humidity was set at 75%. Then, germinated seeds were counted and removed daily until no germinated seeds were recorded for a week. The results were expressed as mean percentage of germinable seeds.

2.4. Data analysis

Differences among the seed sources (LIT, MIT and HIT) in seed flotation time, total germination, and survival were tested by one-way ANOVA. When necessary, the data collected from laboratory

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