Determinants of seed bank dynamics of two dominant helophytes in a tidal salt marsh

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Abstract

We investigated dynamics and spatial distribution of Scirpus mariqueter and Spartina alterniflora seed banks at Chongming Dongtan in the Yangtze River estuary, China. Five sites along an elevational gradient were chosen, one in each of the main zones (mudflat, Scirpus monoculture, Scirpus–Spartina mixture, Spartina monoculture and Spartina–Phragmites mixture). Three surveys were performed just after seed rain, before germination and after germination, respectively. During the period of November 2005 to May 2006, soil seed density of Scirpus mariqueter declined by 36%, and that of Spartina alterniflora by 58%. The spatial distributions of their seed banks were also different. Soil seed density of Scirpus mariqueter was not determined directly by seed production, but positively correlated with total aboveground biomass of the whole plant community. On the contrary, soil seed density of Spartina alterniflora just after seed rain (November) was significantly correlated with seed production, but had a poor relationship with the community's aboveground biomass. Our results indicated that other factors such as tidal movement might have had great influence on dispersal of Scirpus mariqueter, which would also affect its population dynamics. The understanding of this process can help us improve the conservation and restoration efforts.

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1. Introduction

Zonal patterns of the standing vegetation along the elevational gradient in salt marshes have been ascribed to the trade-off between competitive ability and stress tolerance to physical factors (Snow and Vince, 1984; Bertness, 1991; Bertness and Pennings, 2000). However, considering only the adults in plant communities may lead to biased conclusions about the determinants of community pattern (Underwood and Denley, 1984) because events in the early establishment stage also play critical roles in regulating plant distribution (Keddy, 1999; Davy, 2000). For instance, in a mangrove marsh where seedlings grow well in the whole area, it is the difference of dispersal ability of propagules that determines the zonal distribution of plants (Rabinowitz, 1978).

Soil seed banks contribute greatly to maintenance (Chang et al., 2001), regeneration (Martins and Engel, 2007) and recovery of vegetation (Huttl and Gerwin, 2007), especially after human or natural disturbances (Baldwin and Mendelsssohn, 1998). Compared with aboveground vegetation, seed banks are more tolerant of disturbances, diseases and herbivory. Under harsh environments, maintenance of species diversity and population recruitment depend greatly on seed banks. In fact, seed banks as source of genetic variation also play important roles in benign environments. Although there is not always high correlation between soil seed bank and aboveground veg-
ation (Brown, 1998; Egan and Ungar, 2000), seed banks are still efficient measures for vegetation recovery in conservation and restoration practices (McDonald et al., 1996), especially on sites with no remnant vegetation or with bare soil (Brown, 1998).

It is well accepted that seed availability and the post-dispersal environments are important determinants of the distribution and abundance pattern of marsh plants (Rand, 2000). Seed production is usually in accordance with above-ground vegetation, but seed dispersal through water, wind or animals can break this pattern (Koutstaal et al., 1987; Chambers and Macmahon, 1994). Therefore, seeds produced locally may contribute little to the emergence of juvenile plants even in an area with large seed banks if there are no suitable microenvironments for germination.

Tidal salt marshes are considered one of the most disturbed ecosystems, which experience natural disturbances such as fire and grazing and anthropogenic disturbances including eutrophication, pollution, over-fishing, sea level rise, reclamation, and biological invasion. On the other hand, salt marshes serve as important habitats for water fowl, marine fish and some other animals. It is urgent to conserve this type of sensitive ecosystem because of its huge ecosystem service values. However, relatively few studies (but see Baldwin et al., 1996; Baldwin and Mendelsson, 1998; Peterson and Baldwin, 2004) have been done to examine the effects of disturbances on seed banks in salt marshes, which may be the critical determinants of community dynamics.

We performed our study at Chongming Dongtan in the Yangtze River estuary, China, where the community composition is relatively simple with only three dominant vascular plants: native Scirpus mariqueter and Phragmites australis, and exotic Spartina alterniflora. Invasive plant Spartina alterniflora was intentionally introduced to China in 1979 for soil erosion control and coastal dike protection (Wang et al., 2006; Li et al., 2008), which expanded rapidly and has now become one of the most problematic exotic species in China (Chen et al., 2008; Ding et al., 2008). As a species endemic to the Yangtze River estuary that is important to many migratory birds, Scirpus mariqueter has attracted much attention over the last few years. It has experienced a remarkable decline and may become locally extinct since Spartina alterniflora dominated the seaward marsh while Phragmites australis thrived in high marsh near the dike.

Although the direct competitive effects of Spartina alterniflora on Scirpus mariqueter have been studied (Chen et al., 2004), what remains unclear is the underlying mechanism of rapid decline of Scirpus mariqueter in this area.

Our aim was to investigate the spatial distribution of Scirpus mariqueter and Spartina alterniflora seed banks along an elevational gradient, and to examine the relationship between aboveground vegetation and soil seed banks. This may help us understand the decline of Scirpus mariqueter and facilitate our conservation and restoration efforts. More specifically, we asked three questions: (1) What are the seasonal dynamics and spatial distribution of the seed banks of Scirpus mariqueter and Spartina alterniflora along the elevational gradient? (2) What are the causes and consequences of this pattern of seed banks? (3) What management implications can be drawn from our results?

2. Materials and methods

2.1. Study area

Chongming Dongtan lies in the easternmost of Chongming Island in the Yangtze River estuary (31°25′–31°38′N, 121°50′–122°05′E), China, which is one of the most important stop over sites for migratory birds in the North Temperate Zone. The wetland continues to expand seaward at a rate of about 150 m year−1 (Ma et al., 2003). A dike built in 1998 enclosed all the supratidal zone so as to prevent the inner areas from tidal effects.

Tides in our study area are regular and semi-diurnal, with mean tidal range from 1.96 to 3.08 m (Sun et al., 2001), and maximum tidal range from 4.6 to 6 m above the Wusong Tidal Height datum (Yang et al., 2001). All parts of the wetland are submerged during the period of spring tide.

Dominant vascular plants in this area are Scirpus mariqueter, Phragmites australis, and Spartina alterniflora. They form several zones with different dominant plant communities (Table 1). Before the introduction of Spartina alterniflora, the two native species formed distinct plant zonation: Scirpus mariqueter dominated the seaward marsh while Phragmites australis thrived in high marsh near the dike. Spartina alterniflora first colonized Chongming Dongtan via propagules dispersed from Jiangsu province in mid-1990s and was later intentionally transplanted at several sites in the intertidal zone to promote sedimentation. It has rapidly expanded since then, and restricted Scirpus mariqueter to a narrow zone. It also competes with Phragmites australis. The former zonal pattern of plant communities has thus been broken, and the loss of native plant communities has become a big problem at Chongming Dongtan, where a national nature reserve was set aside.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Distance (m)</th>
<th>Plant community type</th>
<th>Elevation (m)</th>
<th>Flooding frequency</th>
</tr>
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<tbody>
<tr>
<td>S1</td>
<td>31°31.01′</td>
<td>121°57.69′</td>
<td>350</td>
<td>Mixed Sa-Pa</td>
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<td>3–4</td>
</tr>
<tr>
<td>S2</td>
<td>31°31.05′</td>
<td>121°58.04′</td>
<td>850</td>
<td>Sa monoculture</td>
<td>3.68</td>
<td>6–7</td>
</tr>
<tr>
<td>S3</td>
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<td>121°58.52′</td>
<td>1600</td>
<td>Mixed Sm-Sa</td>
<td>3.62</td>
<td>7–8</td>
</tr>
<tr>
<td>S4</td>
<td>31°31.05′</td>
<td>121°58.78′</td>
<td>2000</td>
<td>Sm monoculture</td>
<td>3.39</td>
<td>11–13</td>
</tr>
<tr>
<td>S5</td>
<td>31°31.01′</td>
<td>121°58.96′</td>
<td>2350</td>
<td>Mudflat</td>
<td>3.05</td>
<td>17–19</td>
</tr>
</tbody>
</table>

Sm: Scirpus mariqueter, Sa: Spartina alterniflora, Pa: Phragmites australis. Distance represents the distance of each site from the 1998 dike; elevation data were based on Wusong Tidal Height datum; and flooding frequency was expressed as flooding days per month (see details in Section 2).
for conserving the native biodiversity and maintaining the ecosystem integrity.

2.2. Target species

Scirpus mariqueter (hereafter as Scirpus) is a perennial rhizomatous, corm-forming sedge mainly distributed in the salt marshes from the Yangtze River estuary to Hangzhou Bay. It is an endemic species to China which serves as food resources and creates habitats for migratory birds in this area. The aboveground shoot is usually composed of two leaves whose length ranges from 10 to 80 cm. It reproduces sexually (through seeds) and asexually (through corms) (Sun et al., 2001). At the end of the growing season (from May to October), all the aboveground shoots die while the belowground parts (i.e., corms and rhizomes) overwinter.

Spartina alterniflora (hereafter as Spartina) is a perennial rhizomatous grass native to the east coast of North America. It was introduced to China in 1979 for soil erosion control and coastal dike protection and has now become a problematic species invading the coast areas of China, from Liaoning to Guangxi province (Wang et al., 2006). The shoots can grow to 1–3 m in height with hard leaves 30–90 cm long. Spartina forms extensive rhizome systems in the 10–30 cm soil layer, which function as clonal reproductive organ. It also has great sexual reproductive capacity and can produce as many as 600 seeds per inflorescence (Wang et al., 2006). Some ramets can survive through the winter, but most die at the end of the growing season (from April to November) and form large amounts of standing dead litter with a low decomposition rate (Liao et al., 2008).

Phragmites australis (hereafter as Phragmites) is a perennial rhizomatous grass native to the east coast of North America. It cannot grow in hypersaline habitats, and thrives in brackish and freshwater wetlands. Phragmites is a long-lived clonal plant which mainly relies on vegetative growth rather than establishment of seedlings for recruitment (Mauchamp et al., 2001), though it can produce a large number of seeds. For this reason, we did not examine the soil seed bank of Phragmites, neither did we estimate its seed production.

2.3. Sites and transect

We placed a transect for vegetation and seed bank sampling near Buyugang from mudflat to the dike built in 1998 and chose five sites along the transect in different zones, which were 350–700 m apart from each other (Table 1, Fig. 1). The elevation of each site relative to the Wusong Tidal Height datum was determined in April 2005 using optical level gauge and a reference site with known elevation. Flooding frequency (expressed as flooding days per month) was estimated using tidal records of Wusong Station and the elevation data.

2.4. Vegetation sampling

Coverage of three dominant plants was estimated by eye to precision of 5% in six replicated 10 m × 10 m plots in August 2005. Growth and reproductive traits of Scirpus were investigated in August 2005, when it reached the maximum biomass of a year. At each site, six replicate quadrats of 0.5 m × 0.5 m were randomly selected, and all the aboveground shoots were clipped and carried to lab for further measurement. Ramet density and canopy height were determined and then the number of flowering shoots was counted (each flowering shoot of Scirpus contains one fruit). After that, all the materials were oven dried at 80°C to constant mass and weighed to obtain the total aboveground biomass. Ten fruits were randomly sampled from plants collected at each site to determine the average seed number per fruit. Seed production of Scirpus was estimated as fruit number (which equals the number of flowering shoots) × average seed number per
fruit, and the data were transformed to number of seeds per square meter.

Spartina and Phragmites were investigated in October 2005 after their sexual reproduction. Sampling was performed in the same way as used in Scirpus, and ramet density, canopy height, aboveground biomass and spike biomass were determined. The seed production of Spartina was estimated by dividing total spike biomass harvested in a quadrat by mean seed weight. The data were then transformed to number of seeds per square meter. Mean seed mass of Spartina was determined by weighing 1000 seeds after being oven-dried at 80 °C.

### 2.5. Seed bank sampling

In order to include the complete components of seed banks, we used a laborious method, i.e., physical separation of seeds from the soil, which could provide the total number of seeds present in soil seed banks (La Peyre et al., 2005) and allowed us to examine the direct effects of environmental factors on seed dispersal. This method is believed to identify the greatest number of species as compared to other methods though viable seeds may be overestimated (Gross, 1990). Three surveys of Scirpus and Spartina seed banks were performed after seed rain (November 2005), before germination (March 2006) and after germination (May 2006) at the same five sites as for the vegetation sampling. At each site, three 10 m × 10 m plots were randomly chosen, which were 30–50 m apart. Eight soil cores of 2.5 cm in diameter and 20 cm in depth were randomly taken in each plot with a steel sampler, and seeds on the ground were pooled together and made a sample of 3412 ± 985 seeds/m² in November, 2631 ± 908 seeds/m² in March and 2190 ± 1255 seeds/m² in May, respectively. In the last sampling at site S1 in May 2006, the seed density of Scirpus was 908 seeds/m² in

### 2.6. Data analysis

As there were no significant differences in seed number of both Scirpus (ANOVA, F_{2,315} = 2.06, p = 0.13) and Spartina (ANOVA, F_{2,315} = 0.23, p = 0.79) among the three plots, eight samples in each plot were pooled, which gave three replicates per site. Seed numbers of Scirpus and Spartina were then analyzed using two-way ANOVA in which time and site were treated as two fixed effects. To estimate the total seed bank size across all the sites at different times, data at all sites during each sampling were pooled together and made a sample size of n = 15. The data on Scirpus seed bank were log transformed to improve the homogeneity of variance.

Relationships between soil seed density and seed production and between seed density (or corm density) of soil seed banks and aboveground biomass of the whole plant community were analyzed using linear regression. Total aboveground biomass of the whole plant community in November 2005 was estimated as the sum of the maximum biomass of three dominant plants (sampling time for Scirpus was in August 2005 and that for both Spartina and Phragmites in October 2005), as their biomass decreases slowly between the growth peak and senescence at the end of the growing season. Scirpus dies in early November and will be washed out or buried within a short period of time, so there are almost no aboveground parts remaining in winter. In May, just after germination, its aboveground biomass is still very small and can be neglected. Spartina and Phragmites also die in winter, but they leave a large proportion of standing dead litter with low decomposition rate (Liao et al., 2008). Thus, residual aboveground biomass of the whole plant community in March 2006 and May 2006 was estimated as the sum of Spartina and Phragmites biomass obtained in October sampling, although it might be overestimated.

### 3. Results

#### 3.1. Aboveground vegetation

Common plant communities at Chongming Dongtan showed distinct zonation: Scirpus occupied the seaward area where Spartina dominated the middle marsh and formed mixture with Phragmites in high marsh (Fig. 2a). Aboveground biomass of these three dominant plants and seed production of Scirpus and Spartina showed site-related variation (Fig. 2b and c).

#### 3.2. Spatial and temporal variation of soil seed banks

The number of Scirpus seeds showed significant spatial and temporal variation as well as significant interaction (Table 2). In general, seed number per square meter was higher in high marsh than in low marsh. Spatial distributions of Scirpus seed banks at all sampling times were not consistent with its aboveground vegetation (all R² < 0.2, all p > 0.5) and seed production (all R² < 0.2, all p > 0.5), but seed production was positively correlated with aboveground biomass (R² = 0.91, p < 0.05). In high marsh (sites S1 and S2), Scirpus died out several years ago, but its seed bank remained and the highest seed density was found at site S1 (Fig. 2d). The peak of seed bank size in middle and low marshes (sites S2–S5) after seed rain (November 2005) occurred at site S4 where Scirpus had the highest seed production, but more seeds were found at site S3 in the later two samplings (Fig. 2d).

The seasonal changes of Scirpus seed bank were not consistent. Some sites had the highest number in winter (sites S3 and S4) while others (sites S2 and S5) had the highest number in early spring (Fig. 2d). On the whole, seed bank size continuously declined after seed rain with an average (all n = 15) of 3412 ± 985 seeds/m² in November, 2631 ± 908 seeds/m² in March and 2190 ± 1255 seeds/m² in May, respectively. In the last sampling at site S1 in May 2006, the seed density of Scir-

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
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<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
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<td>2</td>
<td>0.31</td>
<td>4.91</td>
<td>0.014</td>
</tr>
<tr>
<td>Site</td>
<td>9.45</td>
<td>4</td>
<td>2.34</td>
<td>37.10</td>
<td>0.000</td>
</tr>
<tr>
<td>Time × site</td>
<td>1.41</td>
<td>8</td>
<td>0.18</td>
<td>2.76</td>
<td>0.021</td>
</tr>
</tbody>
</table>
Fig. 2 – Aboveground vegetation and soil seed bank at five sites (sites S1 to S5) along the transect. (a) Coverages of the three dominant plants (*Scirpus mariqueter*, *Spartina alterniflora*, and *Phragmites australis*) in August 2005; (b) aboveground biomass of the three dominant plants; (c) seed production of *Scirpus mariqueter* and *Spartina alterniflora*; (d) soil seed density of *Scirpus mariqueter* and (e) soil seed density of *Spartina alterniflora* at three sampling times (November 2005; March 2006; and May 2006); and (f) corm density of *Scirpus mariqueter* in May 2006. Data are expressed as mean ± standard error (n = 6 for vegetation, and n = 3 for seed and corm samples). Sm: *Scirpus mariqueter*, Sa: *Spartina alterniflora*, Pa: *Phragmites australis*. Different upper cases indicate significant differences among sites, and different lower cases indicate significant differences among sampling times at each site at the significant level of 0.05 (post hoc Duncan’s test).
pus in 10–20 cm layer was 6791 ± 4446 m−2 (n = 3), about fivefold as that in 0–10 cm layer (1358 ± 861 m−2, n = 3).

Aboveground biomass of the whole plant community also affected the seed bank size of Scirpus. A positive correlation (marginally significant, $R^2 = 0.68$, $p = 0.09$) was found between Scirpus seed number just after seed rain (in November) and total aboveground biomass (Fig. 3a), whereas later in March and May, Scirpus seed number was significantly ($R^2 = 0.79$, $p < 0.05$; $R^2 = 0.78$, $p < 0.05$) correlated with residual aboveground biomass in winter (Fig. 3b and c).

Our sampling in May showed that the number of corms decreased with increasing elevation in Scirpus meadow (sites

Fig. 3 – Relationship between seed (or corm) density in soil and aboveground biomass (or seed production). (a) Scirpus seed density in November 2005 vs. total biomass; (b) Scirpus seed density in March 2006 vs. residual biomass; (c) Scirpus seed density in May 2006 vs. residual biomass; (d) Scirpus corm density in May 2006 vs. Scirpus biomass; and (e) Spartina seed density in November 2005 vs. Spartina seed production. See details in Section 2 for estimation of total aboveground biomass and residual aboveground biomass of the community. Sm: Scirpus mariqueter; and Sa: Spartina alterniflora.
S2–S4), but corms were not found near the mudflat (S5) occupied by sparse patches of Scirpus (Fig. 2f). There was a significant relationship between corm number of Scirpus in May and its maximum aboveground biomass ($R^2 = 0.95$, $p = 0.005$, Fig. 3d).

As for Spartina, time, site and their interaction all had significant effects on the size of its seed banks (Table 3). Similarly, the seed bank size of Scirpus in middle and high marshes (sites S1–S3) was greater than that in low marsh (sites S4 and S5). A significant relationship was found between soil seed density and seed production just after seed rain in November 2005 (Fig. 3e, $R^2 = 0.88$, $p = 0.02$). At that time, most seeds were found at site S2 where seed production was the highest (Fig. 2c and e).

Seed number of Spartina declined rapidly after November at most sites except for site S1 where most seeds were found in March (Fig. 2e). Spartina seed bank reached its peak size in November ($2818 \pm 810$ seeds/m$^2$), and then decreased to $1392 \pm 581$ seeds/m$^2$ in March and $815 \pm 290$ seeds/m$^2$ in May. In the last sampling at site S1 in May 2006, the seed density of Spartina in 10–20 cm layer was $424 \pm 306$ m$^{-2}$ ($n = 3$), about fivefold as that in 0–10 cm layer ($85 \pm 85$ m$^{-2}$, $n = 3$).

The relationship between seed bank size of Spartina and aboveground biomass of the whole plant community was poor for all three samplings (data not shown, all $p > 0.1$).

### 4. Discussion

#### 4.1. Seed bank dynamics

Seed banks are dynamic and influenced by seed production, dispersal, persistence and turnover (Leck and Simpson, 1994). At our study site, a typical Chinese tidal salt marsh, dispersal appeared to be an important factor determining spatial distribution of seed banks while persistence and turnover might also have a great influence on it. Therefore, the initial seed production might have contributed little to the final distribution pattern of soil seed banks.

Water dispersal is an important mechanism that determines the spatial distribution of seed banks in wetlands (Welling et al., 1988). However, in coastal marshes, tide is an intense and frequent ‘disturbance’ that is quite different from that of rivers and lakes. It plays critical roles in seed dispersal and deposition in some marshes (Hopkins and Parker, 1984; Huiskes et al., 1995). Compared with small herbivores, tidal water can disperse much more seeds though it is not a very selective agent (Chang et al., 2005). According to a previous study (Chen et al., 1992), Scirpus seeds can float on water surface for several days, which facilitates its long-distance dispersal. It can be inferred that the distribution of Scirpus seeds may be heavily influenced by tidal regime besides the location of mother plants.

Aboveground vegetation has been demonstrated to act as a barrier that traps moving seeds in mountain slopes (Isselini-Nondedeu and Bedecarrats, 2007) and wetlands (Smith and Kadlec, 1985). In the high marshes where populations of Spartina and Phragmites were quite dense, velocity of tide was greatly reduced (Neira et al., 2006); and many seeds carried by tide would sink to the bottom. This might be the reason why we observed positive relationship between seed number of Scirpus and total aboveground biomass of the plant community because higher aboveground biomass was more effective in reducing water velocity. Previous data (Wang, unpublished data) of Scirpus seed bank before the massive invasion of Spartina did not show high density of seeds in the high marsh, which provided us with evidence for the effects of standing biomass. Driftline material has been found to promote the dispersal of seeds or fruits (Koutstaal et al., 1987), and concentrate seeds of many species higher up the marsh (Wolters and Bakker, 2002). However, this might have played minor roles in our study area because wracks were not common during the sampling periods; and if any, they piled up more frequently in middle to low marshes. On the contrary, belowground corms would not be affected by tide, so the corm number was solely determined by the vegetative growth of Scirpus plants.

The Spartina seed bank seemed to be more affected by its own seed production, but tidal effects also played important roles. We found significant relationship between its soil seed density and seed production just after seed rain (in November), but the pattern disappeared the next March and May probably because of tidal transportation of seeds during this period.

Scirpus and Spartina seed banks all exhibited gradual decrease trend during our study period. This decline might be caused by tidal transportation of seeds to sea (Hutchings and Russell, 1989; Huiskes et al., 1995), foraging birds (Yu et al., 1992; Espinar et al., 2004) and other factors such as germination and decomposition. Therefore, the seaward sites (site S4 for Scirpus and sites S2 and S3 for Spartina) which were suitable habitats for waterfowl and frequently flushed by tide showed the highest decrease of seed number from November to next March. From March to May, seed bank density of Scirpus decreased at most sites except in high marsh near the dike (site S1), where soil desiccation and shading could inhibit seed germination (Chen et al., 2005). For Spartina, however, soil seed density decreased remarkably only at site S1 near the dike. What remains unknown is whether or not it was caused by high germination rate.

Scirpus has a persistent seed bank which can last for at least 2 years (Ou et al., 1992a; Bekker et al., 1998b); thus it becomes the “memory” of previous aboveground vegetation. Annual seed production of Scirpus was much less than the size of its soil seed bank, whose contribution to its soil seed bank was less than 42% even in best performed Scirpus meadow (site S4). Therefore, a large portion of the seed bank must have accumulated over the previous years. On the contrary, Spartina has a transient seed bank (Sayce and Mumford, 1990), which ‘reflects the seed bank output of the current vegetation rather than that of the vegetation growing at some time in the past’ (Hutchings and Russell, 1989). Surprisingly, the estimated seed production of Spartina was also much less than its soil seed bank, which contributed less than 22% to the soil seed bank at all sites in November. Seeds produced in previous years
might not be the source of extra seeds because Spartina has a transient seed bank with short longevity. Many fewer seeds of Spartina were found in deeper layer (10–20 cm) than those in surface layer (0–10 cm) in the final sampling, indicating that few seeds produced 2 or more years ago were preserved.

4.2. Invasion history

Generally, seeds buried deeper are older; and thus vertical distribution of seeds is usually a good indicator of seed longevity (Bekker et al., 1998a) except in severely disturbed soils, e.g., cultivated land (Grundy et al., 1999). Regular sedimentation of the marsh provides better protection of seeds and makes it easier to determine their ages. In high marsh of Chongming Dongtan, sedimentation rate is less than 5 cm year$^{-1}$ (personal observation), so the Scirpus seeds in 10–20 cm layer were produced more than 2 years ago and were not able to remain viable (Ou et al., 1992a). In contrast to the common pattern that soil seed density declines with soil depth (Espinar et al., 2005), the seed density of Scirpus in 10–20 cm layer was four times higher than that in 0–10 cm layer in high marsh (site S1). This indicates that the seed input was greater in early years and then declined, which was consistent with the fact that this area was previously dominated by Scirpus, but now has been replaced by Spartina and Phragmites (Wang et al., 2007).

Spartina was transplanted in the Dongtan wetland 5–7 years ago, and has expanded rapidly since then. It invaded the Scirpus zone and accelerated the successional processes in the salt marsh through promoting sedimentation, which led to competitive exclusion of the pioneer native species (Wang et al., 2007). The invasion processes can be directly reflected by vegetation change, but are also recorded in soil seed banks with a time lag. Seed bank dynamics of Scirpus in the upper layer is mainly regulated by seed dispersal, germination, and tidal effects, whereas the lower layer which is less affected by recent events acts as the record of population history as affected by former dispersal events. On the other hand, corms can also record the population history with a shorter time lag because the life span is only 1 or 2 years (Ou et al., 1992b). For example, the corms sampled in May 2006 actually reflected the Scirpus distribution in 2004 and 2005, when it had neither died out at site S2 nor occupied the seaward site S5. Therefore, studying seed banks and vegetative propagules can not only help us predict the future of plant populations, but also improve our understanding of its invasion history.

4.3. Implications for management

After the introduction of Spartina to Chongming Dongtan, Scirpus populations declined rapidly because of direct competition with Spartina (Chen et al., 2004) and sedimentation effects of this invasive plant which functioned as an ecosystem engineer, and greatly modified the microenvironments. Expansion rate of Spartina front into Scirpus community has been much higher than that of Scirpus into mudflats these years, so the width of pure Scirpus zone decreased from 1.5–1.9 km to less than 500 m (Wang, unpublished data). The area of Scirpus community at Dongtan dropped more than 50% in recent years; and in some northern areas, the population has gone locally extinct (Wang et al., 2007).

Our study showed that tidal water most likely transported a considerable proportion of Scirpus seeds from low marsh to high marsh which was not suitable for its germination and survival because of shading and desiccation. Furthermore, reproductive allocation shifted from vegetative structures in mudflats to sexual ones in Scirpus meadows at higher elevation (Sun et al., 2001), where Scirpus was closer to the Spartina zone and would suffer more from Spartina competition. The consequent decline of sexual reproduction (due to competitive effects, see Chen et al., 2004) and reduced allocation to vegetative propagules (due to the altered life history strategy along the elevational gradient) would limit its recruitment. Colonization rate in mudflats might then be reduced because of decrease in seed supply. Sea level rise and reduced sediment supply carried by the Yangtze River might also affect the seaward expansion of Scirpus. These can all contribute to the decline of Scirpus and may even cause its local extinction.

To protect the endemic Scirpus as well as the habitats created by it, it is urgent to control Spartina, not only because of its direct competitive effects, but also due to the trap of Scirpus seeds in places that are unfit for their germination. Using the stratified dispersal model, Grevstad (2005) concluded that effective control strategies were those that first eradicate the plants in frontier patches where potential vegetative growth is the greatest. In low marshes, frequent tidal submergence can also improve the control efficiency of mowing (Gao et al., 2009).

On the other hand, Spartina patches in low marsh have more direct negative effects on adjacent Scirpus populations. Thus, the control measures are better taken for the seaward patches of Spartina first. In the meantime, it also seems necessary to seed Scirpus so as to restore its populations. Previous study has shown that sowing pre-germinated seeds under 0.5 cm soil layer can markedly improve the establishment of Scirpus maritimus in mudflats (Clevering, 1995), which may also be useful for Scirpus mariqueter. In reclaimed Spartina areas, the driftline and remaining belowground rhizome system may help prevent Scirpus seeds from being washed out, but it also needs more efforts to avoid the reinvasion or recolonization of Spartina.

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REFERENCES


