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Research paper

Native *Phragmites* dieback reduced its dominance in the salt marshes invaded by exotic *Spartina* in the Yangtze River estuary, China

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ABSTRACT

Vegetation dieback occurs frequently in various ecosystems and causes tremendous consequences. We here examined the impact of native reed (*Phragmites australis*) dieback on the salt marsh communities invaded by exotic *Spartina alterniflora* through monitoring dynamics of component species of *Phragmites*-*Spartina* mixture, and comparing their performances in monoculture, dieback mixture and healthy mixture in Dongtan wetland of Yangtze River estuary, China. *Phragmites* showed poorer performance in dieback mixture compared with other communities. Survival rate (30 ± 4.08%), ramet density (37 ± 9.15 plants/m^2), plant height (130.71 ± 20.39 cm) and aboveground biomass (222.64 ± 5.66 g/m^2) of *Phragmites* in dieback mixture were all significantly lower than those in healthy mixture (68 ± 4.79%; 99 ± 17.24 plants/m^2; 185.06 ± 17.75 cm; 837.07 ± 205.13 g/m^2, respectively) (for all $P < 0.05$). By contrast, *Spartina* resprouted well with survival rate of 100% over the course of the experiment. Both ramet density and plant height of *Spartina* tended to be higher in dieback mixture than in healthy mixture, and its aboveground biomass (1042.19 ± 156.46 g/m^2) was significantly higher than that in healthy mixture (618.76 ± 129.50 g/m^2) ($P < 0.05$). Our results suggest that reduced dominance of native *Phragmites* due to its own dieback weakens its competition with exotic *Spartina*, which favors *Spartina* invasion in the salt marsh community.

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1. Introduction

Vegetation dieback occurs in various ecosystems such as forests (Mueller-Domobois, 1986; Anderegg et al., 2012) and wetlands (Goodman et al., 1959; Alber et al., 2008), and affects plant community structure (e.g., dominance shift of component species) and functions (e.g., carbon sequestration) (Breshears and Allen, 2002). Dieback, as a type of biotic disturbance, can be explained by individual and general causes (Ostendorp, 1989), such as extreme weather events (e.g., extreme drought) (Hoffmann et al., 2011; Anderegg et al., 2012), soil conditions (e.g., waterlogging) (Mendelssohn and McKee, 1988), biotic disturbance (e.g., attack by pathogens and herbivores) (Elmer and Marra, 2011; Gaeta and Kornis, 2011; Coverdale et al., 2012) and human activities (e.g., eutrophication and water table change) (Rea, 1996; Brix, 1999). Multiple processes such as the combination of physicochemical stresses (e.g., wet/dry oscillations) and trophic interactions (e.g., herbivory) also contribute to the dieback (Silliman et al., 2005).

Vegetation dieback in wetlands has led to huge ecological ramifications. Sudden dieback of *Spartina alterniflora* (*Spartina* used below) in coastal wetlands along the southeastern and gulf coasts of the United States affects more than 250,000 acres of the salt marshes and accelerates coastal erosion, leaving bare and barren sediments devoid of vegetation recovery (Silliman et al., 2005). The dieback of cosmopolitan *Phragmites australis* (*Phragmites* used below) in sizeable areas of Europe not only endangers its own growth (e.g., a relatively low productivity, low or clumped shoot density, delayed flowering and earlier senescence) (Brix, 1999), but also breaks the balance of processes between the progression and the retreat in reed-dominated ecosystems (den Hartog et al., 1989). Vegetation dieback also causes economic loss due to decline of ecosystem functioning and services (Ostendorp, 1989; Hübner et al., 2010).

In Dongtan wetland of Yangtze River estuary in China, portions of the salt marshes invaded by *Spartina* at high elevation have experienced *Phragmites* dieback since 2008, and the affected area is continuing to expand over years (personal observations). The dieback of native *Phragmites* occurs in its small pure stands surrounded by pure *Spartina* stands or in its mixture with *Spartina* (Fig. 1), resulting in premature senescence of *Phragmites*, which starts at the switch from vegetative to reproductive growth. Our

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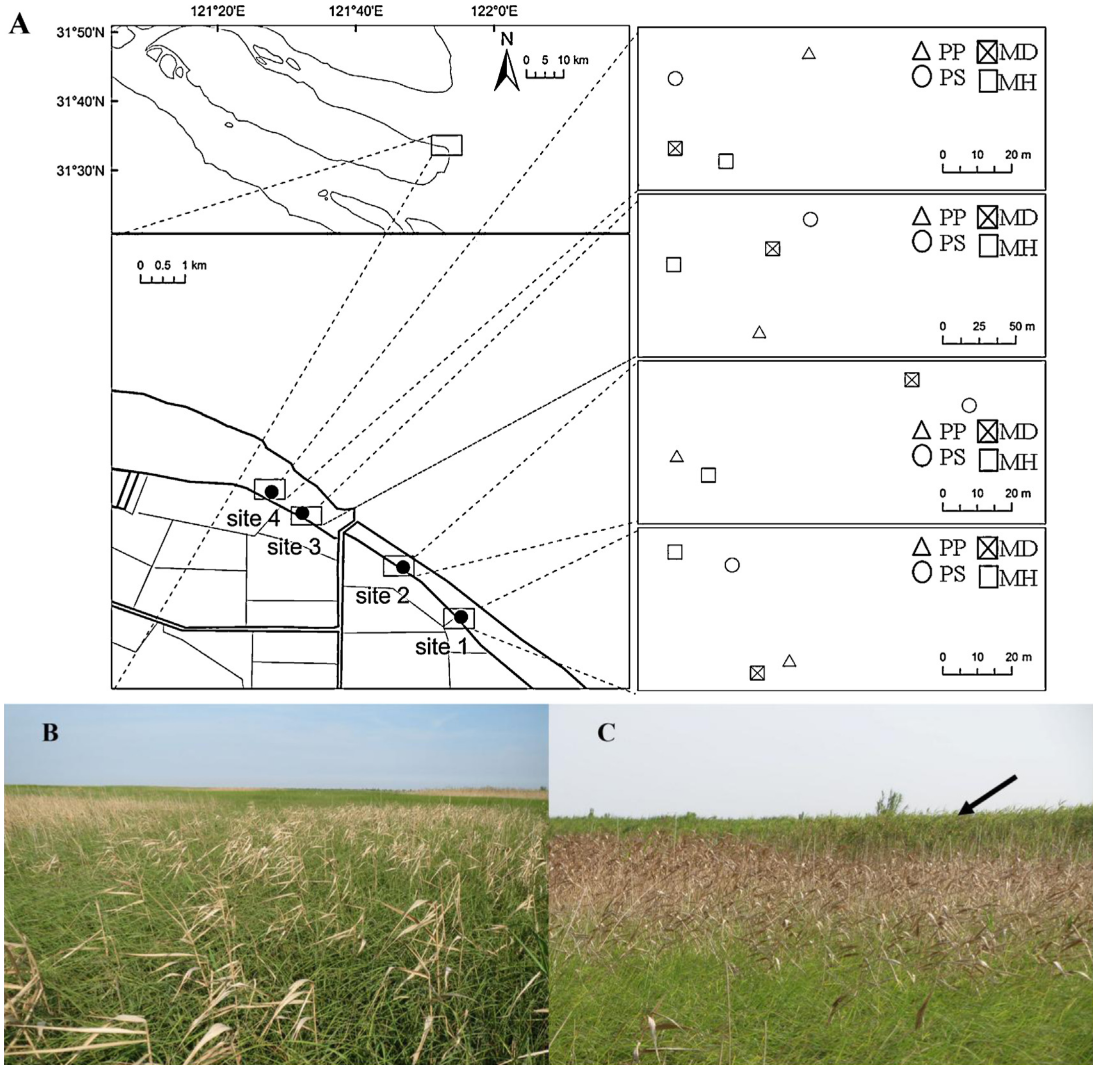

Fig. 1. Sampling sites and patterns of *Phragmites* dieback in Dongtan wetland (Photos taken on August 19, 2012). (A) Sampling sites; (B) *Phragmites* dieback in the mixture of *Phragmites* and *Spartina*; (C) *Phragmites* dieback in the small patch surrounded by *Spartina* stands. PP, pure stands of *Phragmites*; PS, pure stands of *Spartina*; MD, dieback mixture of *Phragmites* and *Spartina*; MH, healthy mixture. Whitish plants are *Phragmites* and green ones are *Spartina*. Black arrowhead shows healthy *Phragmites* community. (For interpretation of the references to color in figure legend, the reader is referred to the web version of the article.)

preliminary study indicates that *Phragmites* dieback here is possibly attributed to the invasion by *Spartina* as the dieback distribution is always associated directly or indirectly with the invader (unpubl. data). Natural vegetation recovery in dieback areas in Europe has been rarely detected (Armstrong and Armstrong, 2001), while it has been observed in North America (Alber et al., 2008). In Dongtan wetland, we also found that both of *Phragmites* and *Spartina* in dieback patches could resprout successfully from the rhizomes through clonal growth.

Composition and interactions of organisms in communities strongly affect ecological processes (Chapin et al., 2011). Dongtan wetland with few dominant plant species including native and exotic species offers a natural laboratory and a unique opportunity to explore the ecological consequences (e.g., plant invasion and loss of biodiversity) caused by *Phragmites* dieback. More complete exploration of the consequences of native plant dieback is necessary to understand ecological regime shifts and ecosystem responses to disturbance in invaded habitats.

Whether *Phragmites* dieback will affect the community structure and even facilitate exotic *Spartina* invasion in Dongtan wetland is still unknown, given that the dieback is becoming more prevalent. To examine this issue, we monitored the dynamics of native *Phragmites* and exotic *Spartina* in field during the growing season, and compared their survival rates, ramet densities, plant heights and aboveground biomass in their respective monocultures, dieback and healthy mixtures.

2. Materials and methods

2.1. Study site

Field studies were carried out in Dongtan wetland on Chongming Island in the Yangtze River estuary, Shanghai, China (31°25′–31°38′ N, 121°50′–122°05′ E) (Fig. 1), which is recognized as the Wetland of International Importance and set aside as a National Nature Reserve for migratory birds. The island has a northern subtropical monsoon climate and the mean annual temperature is 15.3 °C. The average annual precipitation is 1022 mm with most of it occurring in the summer. The plum rain season (i.e., rainy season in South China) lasts from late June to mid July (Xu and Zhao, 2005). The wetland encompasses a total area of 32,600 ha, consisting of muddy flats and salt marshes. The salt marshes are

Table 1
Physicochemical properties of sediments in monitored field plots during the growing season. ORP, oxidation–reduction potential; Cond, electrical conductivity; SWC, soil water content. The values of all the parameters represent the average values ± standard errors ($n = 4$). The abbreviations are the same as in Fig. 1.

	ORP/mV	Cond/mS cm^{-1}	pH	SWC/%
PP	23.17 ± 24.98	9.44 ± 1.50	7.83 ± .0.06	47.01 ± 1.57
PS	87.99 ± 27.31	8.49 ± 1.01	7.79 ± 0.06	47.92 ± 2.70
MD	77.66 ± 34.11	9.19 ± 1.64	7.90 ± 0.08	45.78 ± 2.31
MH	86.77 ± 27.85	8.29 ± 1.76	7.85 ± 0.09	46.52 ± 1.63

dominated by native *Scirpus mariqueter* and *Phragmites*, and exotic *Spartina*, which was found first in Dongtan wetland in middle 1990s. Although *S. mariqueter* and exotic *Spartina* used to form the mosaics of their pure patches at lower elevation, *Spartina* drove *S. mariqueter* locally extinct there, and is now dominating lower marshes; native *Phragmites* and exotic *Spartina* form mosaics of their respective pure patches and/or their mixtures at higher elevation in the salt marshes, where *Phragmites* performs slight better than *Spartina* in healthy conditions.

2.2. Experimental design

Based on our field surveys on the distribution of *Phragmites* dieback in Dongtan wetland from 2009 to 2011, four types of plant communities were identified: healthy pure stands of *Phragmites* (PP), healthy pure stands of *Spartina* (PS) and their mixture either with dieback *Phragmites* (MD) or healthy *Phragmites* (MH). Because dieback mainly occurs at higher elevation, four similar sites (Fig. 1A) with all four types of plant communities at the similar elevation were randomly selected as spatial replicates. Environmental variables including oxidation–reduction potential, electric conductivity, pH and water content were repeatedly measured in each plot at low tide during the growing season. All the sites were affected by natural tides and the environmental differences were found to be not significantly different among the plant community types (see Table 1).

At each of the four sites, one 1.5 m × 1.5 m plot was established in each of four different plant communities in March of 2012. In each plot, four bamboo rods were inserted into the sediments to a depth of 0.5 m to mark the plots. Two centimeter-width red nylon ropes were used to enclose the plot at 1 meter above the surface of the sediment. In the 1.5 m × 1.5 m plots, the central 1 m × 1 m area was used to monitor ramet density and plant height, and the marginal 0.5 m belt was used as buffer area so as to avoid the potential edge effects. In addition, 0.5 m × 0.5 m iron square was laid in the center of 1 m × 1 m quadrat to measure aboveground biomass. Necessary maintenance in all plots (e.g., calibrating the sample square, reinforcing bamboo rods and maintaining the buffer zones) was regularly done to reduce the disturbance caused by wind and human activities.

2.3. Plant characteristics

Ramet densities of the previous year (2011) in all plots were recorded by counting the number of ramets at the beginning of the experiment. Both of the two plant species began to sprout in late March and ramet density in 1 m × 1 m core area was surveyed at the appointed dates (March 28, April 12, April 28, June 12, July 3 and September 11). Ten ramets of each plant species in 1 m × 1 m core area were randomly marked to monitor growth performance (e.g., plant height and survival rate).

Culms without any green leaf were considered as dead plants. Survival rates of *Phragmites* and *Spartina* in all plots were expressed as the percentage of living ramets in 10 marked ramets. In mid-September, aboveground plants in 0.5 m × 0.5 m sampling areas were harvested. All the plants were carefully cut at the ground level and aboveground parts were cleaned with tap water, oven-dried at 60 °C to constant weight. Total dry weight of each plant species in each plot was measured as aboveground biomass.

2.4. Statistical analysis

Experimental design was randomized block design with community type as fixed factor and site as blocking factor. Two-way analysis of variance (ANOVA), without consideration of interactive term, was used to examine the effects of community type and site on recovery variables (i.e., ramet density and plant height at the appointed date, living ramet density, survival rate and aboveground biomass). Recovery variables of *Phragmites* and *Spartina* were affected by community type, except for the aboveground biomass of *Spartina*, which was also affected by site. Repeated ANOVA was done to respectively analyze differences of ramet density and plant height of each plant with community type as between-factor variable and sampling time as within-factor variable. Tukey's HSD test was applied to examine the differences among four community types and among four sites, which was considered to be significant at the level of $P < 0.05$. All data were tested for normality and homogeneity prior to ANOVA. Square-root transformations were performed to make data (i.e., ramet density of *Phragmites* on April 28 and plant height of *Spartina* on April 28 and September 11) meet the assumptions for ANOVA. The Kruskal–Wallis test was used if data transformation failed to meet the assumptions of ANOVA. Statistical analysis was performed in *R* software (version 2.12.2, R Development Core Team, 2011).

3. Results

Previous year's (2011) ramet densities of *Phragmites* in its monoculture, dieback mixture and healthy mixture showed no significant difference (Fig. 2A; $F_{2,6} = 4.177$, $P > 0.05$), and so did *Spartina* (Fig. 2C; $F_{2,4} = 7.799$, $P > 0.05$). *Phragmites* and *Spartina* resprouted well in all plots at the beginning of the growing season in 2012 and typical dieback patches were visible as shown in Fig. 1B and C.

Ramet density of *Phragmites* was lower in dieback mixture (MD) than those in pure *Phragmites* stand (PP) and healthy mixture (MH) during whole growing season (Fig. 2B; $F_{2,9} = 4.766$, $P > 0.05$). At the end of the experiment, ramet density of *Phragmites* in dieback mixture (37 ± 9.15 plants/m^2, mean ± SE) was significantly lower than that in healthy mixture (99 ± 17.24 plants/m^2) (Fig. 2B; $F_{2,6} = 6.775$, $P < 0.05$). Moreover, living ramet density of *Phragmites* was significantly lower than those of other two community types (Fig. 3A; $F_{2,6} = 9.923$, $P < 0.05$) and its survival rate decreased significantly in dieback mixture (30 ± 4.08%) compared with its monoculture (80 ± 4.08%) and healthy mixture (68 ± 4.79%) (Fig. 3B; $F_{2,6} = 36.111$, $P < 0.05$). There were significant differences of plant height of *Phragmites* in the three communities throughout the growing season (Fig. 4A; $F_{2,51} = 28.435$, $P < 0.05$). Furthermore, aboveground biomass of *Phragmites* in dieback mixture (222.64 ± 5.66 g/m^2) was the lowest compared with those in its monoculture (800.97 ± 160.17 g/m^2) and in healthy mixture (837.07 ± 205.13 g/m^2) (Fig. 4B; $F_{2,6} = 4.875$, $P < 0.05$).

Spartina grew well over the course of the experiment and its survival rates in the three communities (i.e., PS, MD and MH) were all 100%. *Spartina* in dieback mixture experienced greater increase in ramet density (from 68 ± 16.81 to 195 ± 35.57 plants/m^2) than in healthy mixture (from 56 ± 16.05 to 146 ± 18.22 plants/m^2) despite no significant difference between them (Fig. 2D; $F_{2,9} = 9.150$, $P > 0.05$). The height of *Spartina* in dieback mixture

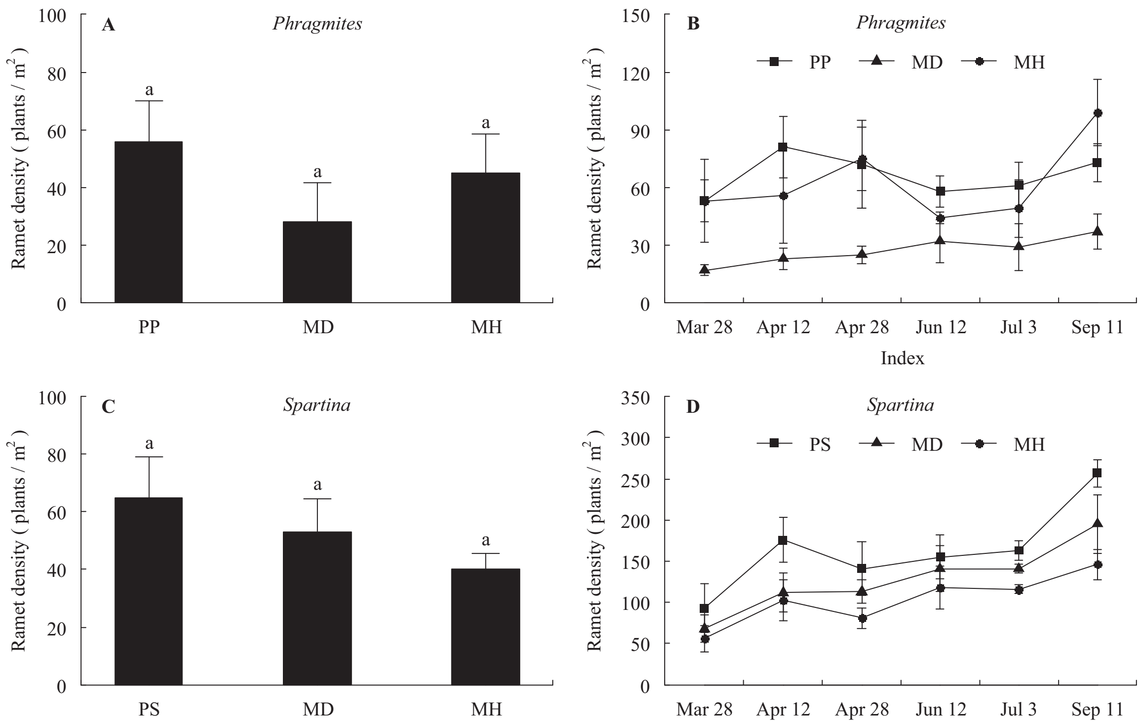

Fig. 2. Ramet density of component species. (A) and (C) ramet density of *Phragmites* and *Spartina* in 2011 (i.e., before the experiment), respectively; (B) and (D), ramet density of *Phragmites* and *Spartina* over the growing season of 2012, respectively. Error bars represent the standard errors ($n = 4$). The different letters indicate significant differences ($P < 0.05$). The abbreviations are the same as in Fig. 1.

was the highest with the average value of 132.25 ± 20.56 cm but no significant difference of this trait was found between dieback mixture and healthy mixture where the height of *Spartina* (127.83 ± 17.25 cm) was the lowest (Fig. 4C; $F_{2,56} = 0.347$, $P > 0.05$). However, aboveground biomass of *Spartina* was significantly higher in dieback mixture (1042.19 ± 156.46 g/m^2) than in healthy mixture (618.76 ± 129.50 g/m^2) (Fig. 4D; $F_{2,6} = 39.683$, $P < 0.05$).

4. Discussion

Vegetation dieback has become a serious threat to coastal and inland wetlands worldwide in face of environmental change. The dieback has been documented to have considerable consequences to the dieback species themselves (Brix, 1999), and associated communities and ecosystems (den Hartog et al., 1989), and may eventually lead to the degradation of coastal wetlands (Silliman et al., 2005; Hübner et al., 2010). We here focused on the *Phragmites* dieback in salt marsh wetlands in the Yangtze River estuary, which provide important ecosystem services (Li et al., 2009). Our study examined the impact of dieback on the invaded salt marsh communities and revealed that recovery of native *Phragmites* is strongly disturbed by its own dieback compared with those in healthy communities (Figs. 2–4), while the growth of invasive *Spartina* is indirectly improved owing to weaker competition from the natives and more available resources (e.g., space, light and nutrients) under dieback conditions. The different responses of the two dominant species, *Phragmites* and *Spartina*, to dieback showed the shifts in their relative dominance and alteration of competitive relationships, which may change community structure and functions. Peñuelas et al. (2000) have reported that *Phillyrea latifolia*

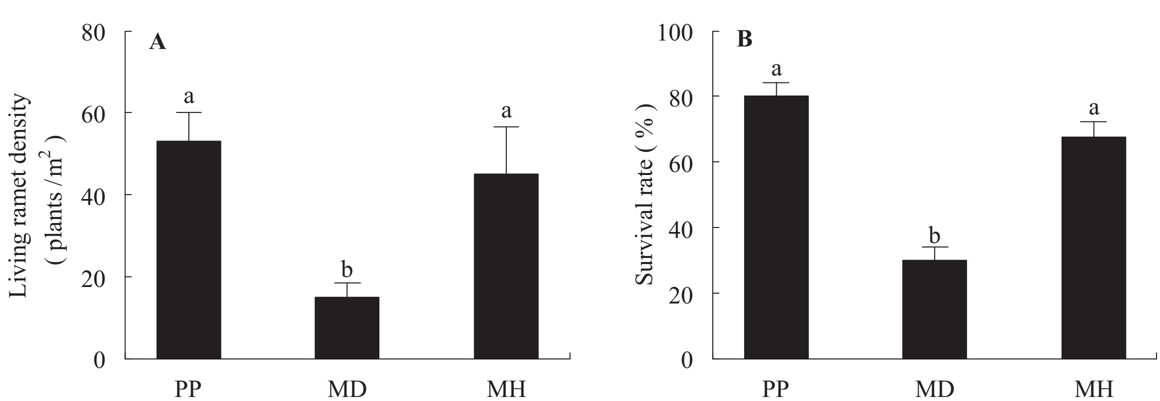

Fig. 3. Living ramet density and survival rate of *Phragmites* in 2012. (A) living ramet density; (B) survival rate. Error bars represent the standard errors ($n = 4$). The different letters indicate significant differences ($P < 0.05$). The abbreviations are the same as in Fig. 1.

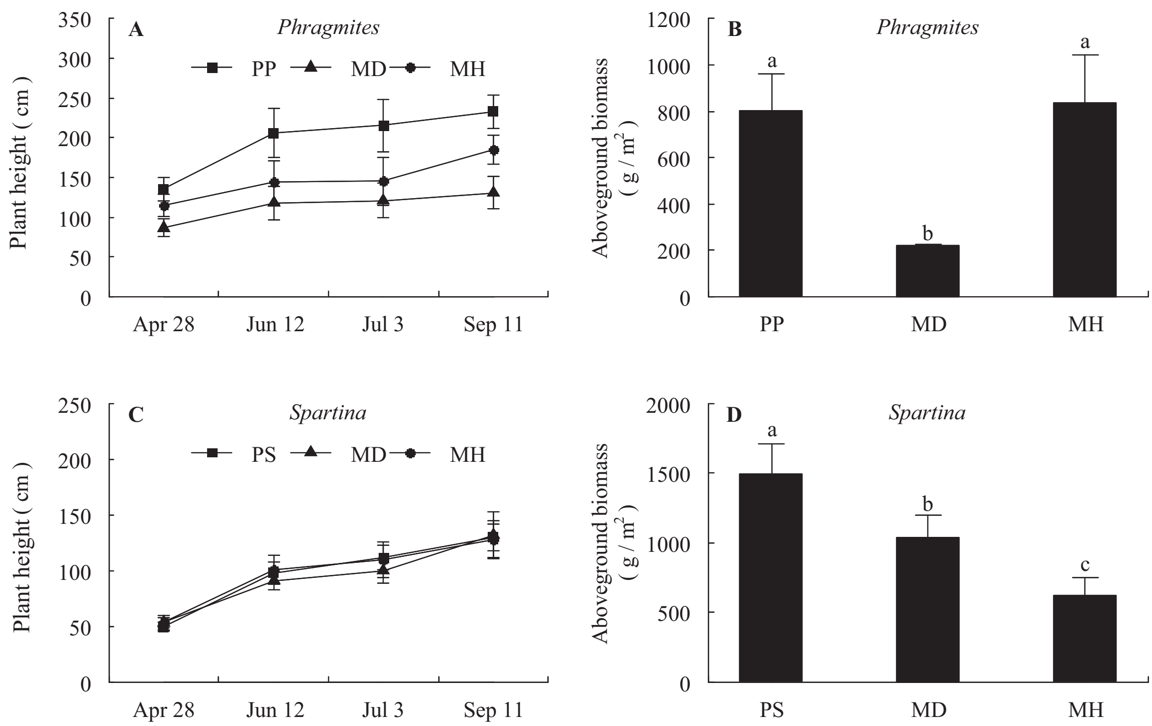

Fig. 4. Plant height and aboveground biomass of *Phragmites* and *Spartina* in 2012. (A) and (C), plant height of *Phragmites* and *Spartina*, respectively; (B) and (D) aboveground biomass of *Phragmites* and *Spartina*, respectively. Error bars represent the standard error ($n = 4$). The different letters indicate significant differences ($P < 0.05$). The abbreviations are the same as in Fig. 1.

was expected to replace *Quercus ilex* due to the latter's dieback. The current case also indicates that *Spartina* invasion appeared to be facilitated as a consequence of *Phragmites* dieback.

In the field, weaker growth of *Phragmites* in dieback patches was possibly caused by previous-year dieback as many smaller roots of decaying rhizomes and shorter and intensely lignified adventitious roots with broken tips were found (personal observations). Clevering (1999) reported that a lower total dry weight of *Phragmites* at dieback sites was related to thin rhizomes. The dieback *Phragmites* is usually of smaller size with blockages in vascular tissues and dead rhizome apices (Armstrong et al., 1996), which hampers the uptake of oxygen and nutrients (Morris, 1980; Morris and Dacey, 1984; Čížková-Končalová et al., 1992). At dieback sites, narrower rhizomes with shorter life span normally accumulate much less soluble sugar and starch during the period of vegetative growth, which might have an important impact on shoot growth next year (Dinka and Szeglet, 2001). Thus, poorer growth of *Phragmites* in dieback mixture might be attributed to the partial loss of re-growing capacity and weakened rhizomes.

After a previous drought-dieback, plants tended to die or produce poor performance, for example, regeneration (Lloret et al., 2004). If ramet density of *Phragmites* declines due to its previous-year dieback, the growth of remaining *Phragmites* plants in small pure stands surrounded by *Spartina* stands (Fig. 1B) should be improved because they can gain more space, light and nutrients at an individual level, meaning that native *Phragmites* dieback benefits itself and then continues to effectively resist *Spartina* invasion. In contrast, if the case happens in the patches as shown in Fig. 1C, the impact will be different depending on competitive outcomes of the remaining *Phragmites* and *Spartina*. However, if resprouting and regeneration of *Phragmites* are suppressed under dieback conditions, more available resources can be released and become available to other species (exotic *Spartina* in the current case), meaning that *Spartina* may outcompete the natives and its invasion in the salt marshes probably will accelerate. *Phragmites* in dieback mixture in Dongtan wetland resprouted vigorously at the beginning of the growing season, but its ramet density was significantly lower than that in healthy patches (Fig. 2; $P < 0.05$), which was opposite to the results reported by Dinka and Szeglet (2001) who found that the shoot number was much higher in die-back stands than in vigorous reed stands. The performance of *Phragmites* measured as survival rate, plant height and aboveground biomass, were significantly poorer than those in its monoculture and healthy mixture (Figs. 3 and 4; for all, $P < 0.05$), manifesting that the growth of native *Phragmites* was obviously restricted by its own dieback, which substantially increased resource availability for other co-existing species (e.g., *Spartina*) in the mutual ecosystems.

On the contrary, the performances (e.g., survival rate, ramet density, plant height) of *Spartina* in dieback mixture evidently were enhanced over time (Figs. 2–4). The aboveground biomass of *Spartina* was significantly higher in dieback mixture than that in healthy mixture (Fig. 4B; $P < 0.05$), demonstrating that *Spartina* benefited from *Phragmites* dieback. In the field-scale transplantation experiments, *Spartina* managed to recolonize the dieback areas and even replaced the other dominant native species *Juncus roemerianus* in salt marshes (Ogburn and Alber, 2006). Remarkably, *Spartina* in China is a very aggressive invader with many superior traits such as fast growth, great leaf area index, a well-developed belowground system and capability of exploiting exogenous nutrient resource (Wang et al., 2006; Peng et al., 2010). Therefore, any appropriate chance (e.g., *Phragmites* dieback) may very likely contribute to the growth of the exotic, which will change ecosystem processes, accelerating its invasion and altering nutrient cycling (Liao et al., 2008). Accordingly, *Spartina* seemed to be favored by *Phragmites* dieback and its invasion is consequently facilitated under dieback conditions.

Dieback has been reported to be an episode without a gradual pattern in many ecosystems (Lloret et al., 2004), and long-term surveys of vegetation response to dieback have not been documented well (Lloret et al., 2011). In Dongtan wetland, we used the permanent-plot method (Ostendorp, 1989) to investigate impacts of dieback. Although the current study is based on short-term investigation, the consequences of *Phragmites* dieback are multiple: reducing recovery and dominance of native plant, altering competitive relationships of dominant species, both of which may change community structure and functions, consequently accelerating *Spartina* invasion which has been validated to lead to a series of ramifications (Li et al., 2009). Dieback needs more attention from ecologists and managers for its frequent recurrence, which may break ecological threshold of current dynamic equilibrium (Hartmann, 2011) to induce dramatic shifts in ecosystem functioning.

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