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Elevated salinity and inundation will facilitate the spread of invasive *Spartina alterniflora* in the Yangtze River Estuary, China

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ABSTRACT

The exotic *Spartina alterniflora*, which is native to North America, has rapidly invaded the entire eastern coast of China in recent decades. It is not clear whether elevated salinity and inundation associated with accelerated sea-level rises and saltwater intrusion will further increase the already dramatic rates of plant invasions in the future. In this study, we conducted controlled experiments to quantify the independent impacts of flooding salinity, flooding depth, and flooding frequency on the invasive *S. alterniflora*, as well as on the native *Phragmites australis* and *Scirpus mariqueter* in the Yangtze River Estuary, China. The results showed that increasing flooding salinity significantly decreased the height, survival rates, number of new ramets, seed setting rates, and aboveground biomass for *P. australis* and *S. mariqueter*, whereas *S. alterniflora* was less severely affected than the two native species. Elevated flooding depths reduced the seed setting rates for *S. alterniflora*, but greatly increased the survival rates, number of new ramets, and aboveground biomass. Elevated flooding frequencies decreased the height of *S. alterniflora*, but promoted the generation of new ramets. In contrast, *P. australis* tended to have stronger negative responses to increased flooding depths and frequencies than *S. alterniflora*. The height and aboveground biomass of *S. mariqueter* also decreased significantly with the increase of flooding depths, whereas no significant decreases were observed for *S. mariqueter* among flooding frequency levels. Specifically, both asexual and sexual reproduction for *P. australis* were significantly inhibited by the foregoing experimental conditions, while *S. alterniflora* still had sustainable competitive advantages by either or both forms of reproduction. These findings suggest that *S. alterniflora* was more tolerant than native *P. australis* and *S. mariqueter*, which may facilitate the spread of invasive *S. alterniflora* in future scenarios of increased sea-level and saltwater intrusion, or even lead to the local extinction of the endangered *S. mariqueter* community.

1. Introduction

Estuarine and coastal wetlands, which comprise some of the most valuable and productive ecosystems on earth, play a critical role in sequestering carbon dioxide (CO_2), protecting coastal regions from storms, and providing suitable habitats for endangered species (Costanza et al., 2014; Kelleway et al., 2017). However, these vulnerable ecosystems continue to be lost or converted into other land use types for agriculture and aquaculture globally at a remarkable rate of 1–7% annually (Hopkinson et al., 2012; Mcleod et al., 2011). This is principally attributed to intense human impacts as well as global climate changes (Kirwan and Megonigal, 2013; Ma et al., 2014). Biological invasions are another common threat in estuarine and coastal wetlands that are likely causing an array of ecological, economic and health impacts on invaded areas (Bertness and Coverdale, 2013; Early et al., 2016).

Predicting the potential spread of invasive species under global climate change is essential because various invasive plants are well known to threaten native plants (Guo et al., 2013; Li et al., 2014a), decrease species diversity (Pyšek et al., 2012; Vilà et al., 2011), change ecosystem structure (Schirmel et al., 2016), increase ecosystem productivity (Ge et al., 2015), and alter biogeochemical cycling (Tamura et al., 2017) and geomorphological features (Schwarz et al., 2016), thus affecting ecosystem functions and services (Yuan et al., 2015). The synergistic feedbacks between global climate changes and invasive plants may be particularly harmful if these invasive plants have strong community and ecosystem impacts (Blumenthal et al., 2016; Vilà et al., 2011). However, it is not clear if global climatic changes will facilitate

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expansion of the distribution ranges of invasive plants.

As an ecotone zone, estuarine and coastal wetlands occur at the interface between land and the ocean; therefore, they are highly susceptible to global climate changes, especially sea-level rises (Kirwan et al., 2016, Morris et al., 2016). Regional and global evidence suggests that the accelerated sea-level rise will increase the risk of flood disasters and saltwater intrusion in estuarine and coastal wetlands (Cazenave and Cozannet, 2014; Zhou et al., 2017), thereby strengthening the current salinity and flooding stresses on both invasive and native marsh species. Transplant studies by Crain et al. (2004) confirmed that species in salt marshes were precluded from freshwater marshes by competition, whereas species in freshwater marshes were excluded from salt marshes by environmental stresses. In the early stages of community succession, the limitation of environmental factors would be especially preeminent (Davy et al., 2011). Accordingly, elevated salinity and inundation associated with sea-level rises and saltwater intrusion may influence the risk of invasion to native ecosystems.

Salinity is generally considered to limit plant growth and development via osmotic stress and ionic stress (Julkowska and Testerink, 2015; Munns and Tester, 2008). Tidal flooding and associated hypoxia or anoxia can lead to a low redox potential and the accumulation of toxic materials (e.g., ethylene and SO_4^{2-}), thereby affecting the ability of plants to carry out normal metabolic processes (Colmer et al., 2013; Colmer and Flowers, 2008). Halophytes have evolved structural and functional adaptations to cope with salinity and flooding stresses, including the selective accumulation of ions, synthesis of compatible solutes, compartmentalization, and induction of plant hormones to increase salt tolerances (Bui, 2013; Canalejo et al., 2014), as well as the formation of aerenchyma and development of adventitious root systems for effective internal aeration (Brownstein et al., 2013; Colmer and Flowers, 2008). Nevertheless, significant signs of stress beyond the range of tolerance may be evident in response to excessive salinity, including reduced growth, lowered photosynthesis, decreased stomatal conductance, and even die back (Achenbach et al., 2013).

Spartina alterniflora, an exotic C4 grass native to North America, was intentionally introduced to China in 1979 for erosion control and dike protection (Li et al., 2009). Since its initial appearance on the Chongming Dongtan wetland located on the eastern part of the Yangtze River Estuary, China (31°25′–31°38′ N, 121°50′–122°05′ E) during the 1990s, *S. alterniflora* has gradually colonized large areas of unvegetated mudflats and invaded the zone formerly inhabited by native *Phragmites australis* and *Scirpus mariqueter*, becoming one of the dominant plant species there (Li et al., 2009, 2014b). The area occupied by *S. alterniflora* was ~1500 ha in the Chongming Dongtan wetland, and > 6000 ha in the Yangtze River Estuary in 2012 (Ge et al., 2015). Some studies have demonstrated that the rapid expansion rate of *S. alterniflora* in China is largely ascribed to its higher photosynthesis efficiency, faster growth rate, greater primary productivity, stronger competitive ability and reproductive traits than native species (Ge et al., 2015; Liu et al., 2016).

There are two forms of reproduction for invasive *S. alterniflora*, and native *P. australis* and *S. mariqueter*: asexual and sexual. The former has high survival rates and growth rates, but its dispersal is usually restricted to short distances, while the latter allows gene shuffling and long-distance dispersal, which requires more energy investments, pollinators, and favorable conditions for seed germination (Albert et al., 2015; Barrett et al., 2008). The recently rapid spread of *S. alterniflora* in the Yangtze River Estuary, China seems to be attributed to efficient reproductive strategies that combine the advantages of sexual reproduction with those of vegetative propagation (He et al., 2012; Xiao et al., 2010). However, it has been well established that plants undergoing asexual and sexual propagation are likely to compete for limited resources, and their trade-offs, which vary widely among different species both in their phenotypic and genetic traits (Thompson and Eckert, 2004), may be manifested under stressful conditions or in competitive environments (Bonser, 2013). Therefore, studies evaluating how elevated salinity and inundation affect reproductive strategies are essential to prediction of the spread of invasive *S. alterniflora*.

The sea-level in the Yangtze River Estuary, China (Lusi Station) rose at a rate of 4.97 $mm \cdot yr^{-1}$ between 1961 and 2011 (NOAA, 2017), which is higher than the mean rate of global sea-level rise of 3.2 $mm \cdot yr^{-1}$ (1993–2010) (IPCC, 2013). The concurrent effects of increasing sea-levels and decreasing runoff inputs to the Yangtze River Estuary can further cause widespread saltwater intrusion (SOA, 2015). However, potential responses of exotic *S. alterniflora* to accelerated sea-level rises and aggravated saltwater intrusion relative to native species have been poorly understood to date, which may hinder our ability to facilitate pre-emptive and effective management of plant invasions.

In this study, we generalized the aforementioned salinity and flooding stresses into three aspects (flooding salinity, flooding depth, and flooding frequency), and conducted controlled experiments to quantify their independent impacts on invasive species *S. alterniflora*, as well as the two dominant native species, *P. australis* and *S. mariqueter*, in the Yangtze River Estuary, China. Our specific objectives were: (1) to compare the performance of invasive and native species in plant morphology, reproduction, and aboveground biomass; and (2) to investigate the trade-offs between asexual and sexual reproduction under salinity and flooding stresses. We hypothesized that invasive *S. alterniflora* was more tolerant than native *P. australis* and *S. mariqueter* to elevated salinity and flooding stresses because of the less severe impacts on the morphology, reproduction, and aboveground biomass for *S. alterniflora* than for *P. australis* and *S. mariqueter*, as well as the complementary phenomenon of two reproductive strategies under experimental conditions for *S. alterniflora*.

2. Materials and methods

2.1. Study area

The Chongming Dongtan wetland has an eastern Asian monsoon climate with an average annual temperature of 15.3 °C, an average humidity of 82%, and an average annual precipitation of 1022 mm. Tides in the wetland are irregular and semi-diurnal, with maximum and mean tide ranges of 4.62–5.95 and 1.96–3.08 m, respectively (Ge et al., 2016), while the salinity of soil pore water typically ranges from 4 to 18 ppt (Tang et al., 2014). Following the introduction of *S. alterniflora*, the marsh plant zonation paradigm changed from "*S. mariqueter–P. australis*" to "*S. mariqueter* (mean elevation ± SD: 3.25 ± 0.72 m, $n = 331$)–*S. alterniflora* (3.55 ± 0.73 m, $n = 404$)–*P. australis* (3.75 ± 0.57 m, $n = 1248$)" and "*S. alterniflora–P. australis*" (Ding et al., 2015; Tang et al., 2014). All three species are perennial grasses that propagate through asexual reproduction from rhizomes or vegetative fragments and sexual reproduction by seeds, while the relative contributions to their survival and expansion vary widely among sites (He et al., 2012; Packer et al., 2017).

2.2. Experiment setup

Three separate controlled experiments (flooding salinity, depth, and frequency) were conducted during the growing season (April–October) in 2014 in the open space near the Dongtan Wetland Park (31°31′ N, 121°56′ E) (see Fig. 1 for more details). In early April, we transplanted the seedlings of *S. alterniflora*, *P. australis*, and *S. mariqueter* and undisturbed soil (30 cm depth) from monodominant communities in the intertidal zone of the Chongming Dongtan wetland to plastic pots (height = 30 cm, $diameter_{top} = 32$ cm, $diameter_{bottom} = 26$ cm), then cut down seedlings of *S. alterniflora* and *P. australis* (about 20–30 cm) to the soil surface to prevent the death of individuals. The height of *S. mariqueter* was shorter than 5 cm and thus not trimmed. During the pretreatment phase (May–June), all pots were maintained under common garden conditions and watered every 2 days (~200 mL) with coarsely filtered canal water (2–5 ppt) to allow recovery and ensure the planned

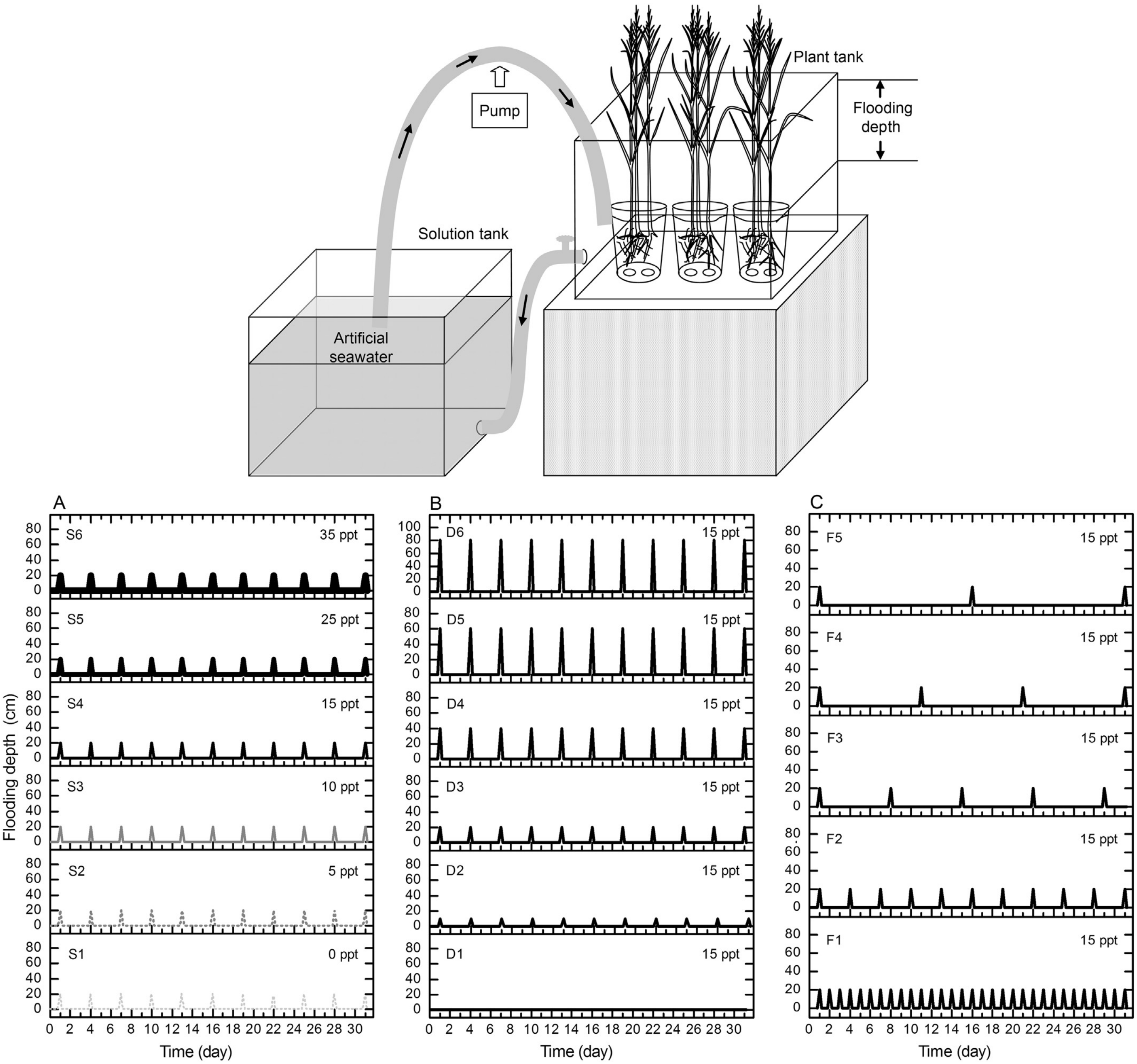

Fig. 1. Experimental design. The invasive (*Spartina alterniflora*) and native (*Phragmites australis* and *Scirpus mariqueter*) species were exposed to A. six flooding salinity levels (S1–S6: 0, 5, 10, 15, 25, and 35 ppt, at flooding depths of 20 cm and a flooding frequency of every 3 days); B. six flooding depth levels (D1–D6: 0, 10, 20, 40, 60, and 80 cm, with flooding salinity of 15 ppt and flooding frequency for every 3 days. The 0 cm level was flooded until reaching the maximum soil moisture content, ~200 mL per pot); and C. five flooding frequency levels (F1–F5: every day, and every 3, 7, 10, and 15 days, with flooding salinity of 15 ppt and flooding depth of 20 cm) for 3–4 months (the experimental treatments for *S. alterniflora* and *P. australis* were conducted from July to October, while those for *S. mariqueter* ran from July to September), respectively. Note: Each treatment was conducted twice a day (from 05:00 to 09:00 h, and from 17:00 to 21:00 h) to simulate two tide cycles in 1 day.

treatment effects on halophytes were not diluted by root damage during transplanting.

The experimental treatments for *S. alterniflora* and *P. australis* were conducted from July to October, while the treatments for *S. mariqueter* lasted from July to September because of the early senescence of this species. The flooding salinity treatments applied consisted of six levels (0, 5, 10, 15, 25, and 35 ppt) ranging from freshwater to seawater (Fig. 1A). Six flooding depth levels (0, 10, 20, 40, 60, and 80 cm) were deployed to mimic the realistic and expected flooding conditions (Fig. 1B), where the *P. australis*, *S. alterniflora*, and *S. mariqueter* zone in the intertidal marsh over an entire year were mainly inundated (with probabilities over 85%) at depths < 50, 60, and 72 cm (based on the tide tables in 2014 at Nanbao Station), respectively. Flooding frequencies also gradually decreased along elevation gradients from low to high marsh, where the low elevations were inundated everyday, high elevations were inundated once every 15 days during the spring tide, and the intermediate elevations captured the full range of tidal inundation from every day to every 15 days. Therefore, established five flooding frequency levels (every day, and every 3, 7, 10, and 15 days) to analyze their potential influences (Fig. 1C).

Importantly, levels of treatment factors (flooding salinity, depth, and frequency) were manipulated independently, and the two factors not of interest in a particular set of trials were maintained at the levels that most often appeared in the field across all levels of the manipulated factor (see Fig. 1 for more details). Interactions between treatment factors were not examined in this study. Variations in flooding duration from flood to ebb tide were not mentioned either because the relatively short period of controlled experiments (3–4 months) might not be sufficient to investigate the impacts of slight differences in time (< 1 h, based on the tide tables in 2014 at Nanbao Station) that the *P. australis* zone, *S. alterniflora* zone, and *S. mariqueter* zone experienced during a flood-ebb cycle (4–5 h). As a result, the irregular semi-diurnal tide cycle was simplified and conducted regularly twice a day in each treatment from 05:00 to 09:00 h and from 17:00 to 21:00 h.

There were 18 experimental units with 54 pots (3 species × 6 levels × 3 replicates) for the flooding salinity experiment, 18 experimental units for the flooding depth experiment, and 15 experimental units for the flooding frequency experiment. In each experimental unit, one transparent plastic tank (length = 97 cm, width = 76 cm, height = 70 cm) was filled with three pots of the same species as three replicates, and the other was filled with salt solution (Fig. 1). Both tanks were connected to each other through a tube and controlled by taps. For flooding depths of 40, 60, and 80 cm, tanks were replaced by larger buckets (height = 135 cm, diameter = 100 cm). The ebb and flow of tides were simulated using pumps (watt 750, flow velocity 60 L/min), while the time consumed in such processes was not included in the flooding duration (~4 h). Salt solution was made by mixing the commercially available sea salt (Shenzhen Jinchuangxing Industrial Co. Ltd., China) with pre-filtered canal water (2–5 ppt), while the freshwater was collected from the clean tap water and rainwater. Before implementing experimental treatments, salt concentrations in each tank were monitored using a hand-held refractometer (Master-S/Millα, Cat. No. 2491, ATAGO, Tokyo, Japan) and corrected to the initial conditions, either by adding water or sea salt.

2.3. Measurements

At the beginning of the controlled experiments, the number of seedlings per pot for *S. alterniflora*, *P. australis*, and *S. mariqueter* was about 12 ± 2 (mean ± SD, $n = 51$), 48 ± 9 ($n = 51$), and 306 ± 32 ($n = 51$), respectively. No significant differences were detected in height, stem diameter, and density within the same species. After 4 months of treatments, we counted *S. alterniflora* and *P. australis* individuals per pot and measured the height (cm) and stem diameter (mm) as morphological indicators in early November 2014, while those of *S. mariqueter* were measured in early October 2014. The survival rate (%) was determined as the ratio between the final and initial number of individuals per pot. When all individuals in a pot were dead at the end of controlled experiments, the survival rate was recorded as 0%. When there were newly generated individuals from rhizomes during the experiments or the number of newly generated individuals was more than the number of dead individuals in the pot, the survival rate was $>$ 100%.

The number of new ramets per pot, as a proxy for asexual reproduction, was obtained indirectly by subtracting the initial number of individuals from the final number of individuals. When there were no newly generated individuals or the number of newly generated individuals was less than the number of dead individuals in each pot, the number of new ramets was counted as 0. The seed setting rate (%) was measured to quantify the capacity for sexual reproduction, which could be calculated as the ratio between the number of individuals that contained mature seed and the final number of individuals per pot. For *S. alterniflora* and *P. australis*, individuals that contained mature seed were counted in each pot in early September 2014, while for *S. mariqueter*, they were measured in the middle of July because of the early maturity of this species. Consequently, the seed setting rate for *S. mariqueter* could not completely reflect the impacts of controlled treatments because of the short exposure period.

At harvest, the aboveground parts for all three species was clipped at the soil surface from each pot, then sealed in pre-labeled paper bags. After oven drying at 60 °C for 72 h, we measured the dry weight to the nearest 0.1 g and estimated the final aboveground biomass as $\text{g}\cdot\text{m}^{-2}$. The top soil samples (0–10 cm) were also collected monthly from each pot to analyze the variations in soil salinity ($\text{g}\cdot\text{kg}^{-1}$) and soil moisture content (%). There were no significant differences in soil salinity or soil moisture content within each species before implementing the controlled experiments. The soil electrical conductivity was measured using a digital conductivity meter (DDS-11A, Shanghai REX Instrument Factory, Shanghai, China), then converted into soil salinity content of dry soil. The loss-on-drying method was directly applied to measure the moisture content of soil samples.

2.4. Data analyses

All data analyses and figure plots were performed with SPSS (version 22.0; IBM Corporation, Armonk, NY, USA) and OriginPro (version 9.0; OriginLab Corporation, Northampton, MA, USA), respectively. Normality and homogeneity of variance were evaluated with the Kolmogorov–Smirnov test and Levene's test, respectively. When they failed, data transformation was conducted to meet the assumptions for statistical analyses. One-way analysis of variance was used to test the statistical significance. Subsequent multiple comparisons using the Least Significant Difference test were applied to separate mean values after detecting significant differences. Correlations were assessed with Pearson correlation coefficients, while stepwise regression analyses were implemented to evaluate the contributions of environmental gradients to the variations in invasive and native species.

3. Results

3.1. Effects of flooding salinity

Corresponding to the increasing flooding salinity, significant decreases in height ($F_{5,12} = 5.46$, $P = 0.008$) and aboveground biomass ($F_{5,12} = 12.07$, $P < 0.001$) were observed for invasive *S. alterniflora*, while no significant differences were detected in the stem diameter, survival rates, number of new ramets, and seed setting rates ($P > 0.05$) (Fig. 2). In contrast, except for stem diameter, there were significant decreases in height ($F_{5,12} = 122.59$, $P < 0.001$), survival rates ($F_{5,12} = 12.27$, $P < 0.001$), number of new ramets ($F_{5,12} = 4.53$, $P = 0.015$), seed setting rates ($F_{5,12} = 32.62$, $P < 0.001$) and aboveground biomass ($F_{5,12} = 12.27$, $P < 0.001$) for *P. australis* (Fig. 2). Relatively high flooding salinity levels (25 and 35 ppt) also exerted negative effects on the reproduction of *P. australis* through production of few or no ramets and seeds.

For *S. mariqueter*, death of all individuals could occur when the flooding salinity rose to 25 and 35 ppt for 2 months (Fig. 2), while the soil salinity was 5.7–6.9 $\text{g}\cdot\text{kg}^{-1}$. Additionally, we did not observe any significant changes in the seed setting rates for *S. mariqueter* ($P > 0.05$) because the seed setting period of this species was not fully covered in our controlled experiments. Native *P. australis* and *S. mariqueter* appeared to be more sensitive than invasive *S. alterniflora* to gradual increases in flooding salinity, resulting in greater decreases in aboveground biomass for *P. australis* (69.5%) and *S. mariqueter* (76.6%) than for *S. alterniflora* (48.3%) at high salt concentrations (35 ppt) when compared to the responses in freshwater (0 ppt).

3.2. Effects of flooding depth

As flooding depth increased, significant differences were detected in height for *P. australis* ($F_{5,12} = 11.26$, $P < 0.001$) and *S. mariqueter* ($F_{5,12} = 34.39$, $P < 0.001$), whereas no significant differences were observed in that for invasive *S. alterniflora* ($P > 0.05$) (Fig. 3A). Elevated flooding depths exerted insignificant effects on the stem diameter for all three species ($P > 0.05$) (Fig. 3B), as well as the survival rates for *P. australis* and *S. mariqueter* ($P > 0.05$), but significantly increased

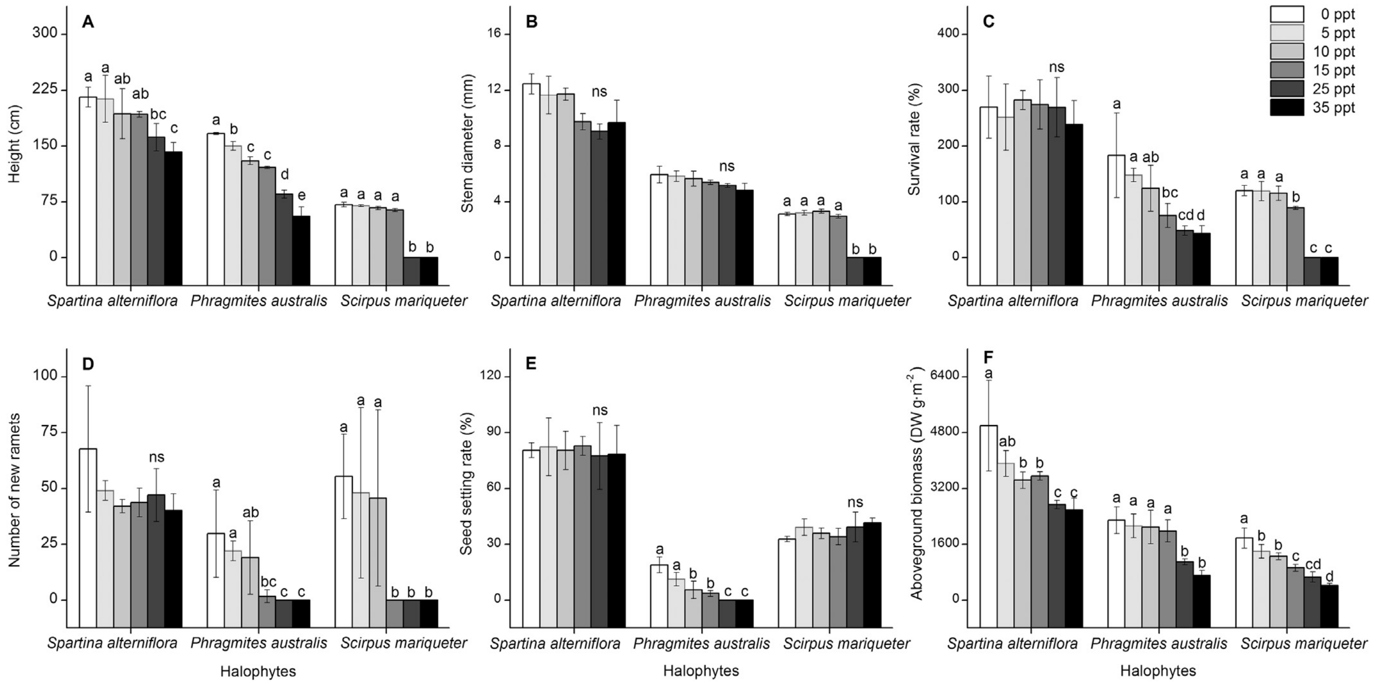

Fig. 2. Responses of invasive (*Spartina alterniflora*) and native (*Phragmites australis* and *Scirpus mariqueter*) species to six flooding salinity levels (0, 5, 10, 15, 25, and 35 ppt) at the end of the controlled experiments. Note: Mean ± SD, $n = 3$. Different lower case letters indicate significant differences ($P < 0.05$) among treatments of the same group according to the Least Significant Difference test; "ns" indicates no significant difference among treatments of the same group; "DW" indicates dry weight.

the survival rates for *S. alterniflora* ($F_{5,12} = 3.52$, $P = 0.034$) (Fig. 3C). The responses of invasive and native species based on the number of new ramets to varied flooding depths (10–80 cm) were not significant ($P > 0.05$) (Fig. 3D), while the seed setting rates for *S. alterniflora* ($F_{5,12} = 4.14$, $P = 0.020$) and *P. australis* ($F_{5,12} = 68.49$, $P < 0.001$) decreased significantly (Fig. 3E). There were significant decreases in aboveground biomass for *P. australis* ($F_{5,12} = 3.91$, $P = 0.025$) and *S. mariqueter* ($F_{5,12} = 15.50$, $P < 0.001$) (Fig. 3F), but *S. alterniflora* still had relatively high amounts of aboveground biomass at flooding depths of 10, 40, and 80 cm.

The variations in soil salinity both before and after six flooding depth treatments are shown in Table S1. No significant differences

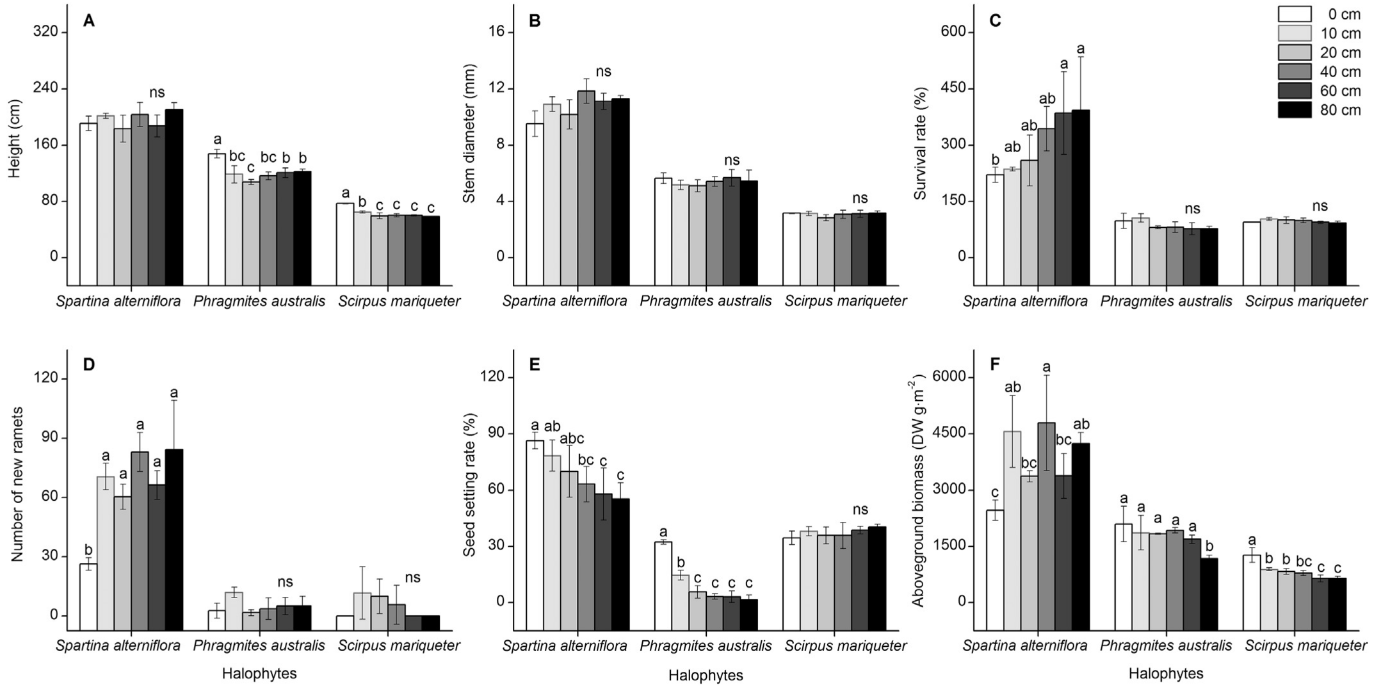

Fig. 3. Responses of invasive (*Spartina alterniflora*) and native (*Phragmites australis* and *Scirpus mariqueter*) species to six flooding depth levels (0, 10, 20, 40, 60, and 80 cm) at the end of the controlled experiments. Note: Mean ± SD, $n = 3$. Different lower case letters indicate significant differences ($P < 0.05$) among treatments of the same group according to the Least Significant Difference test; "ns" indicates no significant difference among treatments of the same group; "DW" indicates dry weight.

($P > 0.05$) were observed in soil salinity from 10 to 80 cm levels within each species, while the 0 cm level had relatively few negative effects on the accumulation of soil salinity due to the limited input of salt solution. These findings suggest that the performance of invasive and native species at flooding depths of 10–80 cm were mainly dependent on the variations in flooding depths and not soil salinity.

The maximum height and aboveground biomass for *P. australis* ($r = -0.634$, $P = 0.005$; $r = -0.495$, $P = 0.037$) and *S. mariqueter* ($r = -0.593$, $P = 0.009$; $r = -0.532$, $P = 0.023$) occurred at 0 cm, which was ascribed to low stress from soil salinity. For *S. alterniflora*, the low soil salinity at 0 cm was likely to facilitate the generation of new ramets, whereas the number of new ramets at 0 cm was significantly lower than that at the rest of the flooding depths (10–80 cm) ($F_{5,12} = 16.48$, $P < 0.001$) (Fig. 3D), indicating that the low soil moisture content (36.9 ± 1.5%, mean ± SD, $n = 3$) at 0 cm might be partly responsible for fewer newly generated ramets ($r = 0.487$, $P = 0.040$). The relatively high amount of aboveground biomass at flooding depths of 10, 40, and 80 cm for *S. alterniflora* were partly attributed to the large number of newly generated ramets ($r = 0.480$, $P = 0.043$).

3.3. Effects of flooding frequency

According to the monthly variations in soil salinity in the flooding frequency experiments (Table S1), the soil salt contents for the frequency of "every day" were significantly higher than those for other frequencies ($P < 0.05$). However, these differences gradually diminished as the experimental periods increased for all three species. Consequently, it was evident that the performance of invasive and native species in the flooding frequency experiments could be influenced by soil salinity. For instance, there were significant negative correlations between soil salinity and height ($r = -0.674$, $P = 0.006$), survival rates ($r = -0.873$, $P < 0.001$), number of new ramets ($r = -0.845$, $P < 0.001$), and seed setting rates ($r = -0.884$, $P < 0.001$) for *P. australis*. Although the correlations between soil salinity and variables for *S. alterniflora* and *S. mariqueter* were not significant, there were significant differences in soil salinity among the flooding frequency levels for these species.

Height ($F_{4,10} = 5.11$, $P = 0.017$), survival rates ($F_{4,10} = 18.07$, $P < 0.001$), number of new ramets ($F_{4,10} = 7.13$, $P = 0.006$), and seed setting rates ($F_{4,10} = 9.47$, $P = 0.002$) for *P. australis* were significantly decreased in response to elevated flooding frequencies from every 15 days to every day (Fig. 4), which were consistent with the results of the flooding salinity experiments and highlighted the adverse impacts of soil salinity. However, no significant differences were observed for *S. mariqueter* among flooding frequency levels ($P > 0.05$) (Fig. 4). Although there was a significant decrease in height ($F_{4,10} = 8.99$, $P = 0.002$) for *S. alterniflora*, the stem diameter, survival rates, seed setting rates and aboveground biomass were all not affected by various flooding frequencies ($P > 0.05$) (Fig. 4). The flooding frequency of every day was conducive to generate ramets ($F_{4,10} = 8.09$, $P = 0.004$) for *S. alterniflora*, and the soil moisture content seemed to play an important role in regulating its ramets ($r = 0.630$, $P = 0.012$).

3.4. Variations across environmental gradients

In flooding salinity experiments, regression analyses were conducted to quantitatively describe the contributions of soil salinity to the variations of invasive and native species in plant morphology, reproduction and aboveground biomass at the end of the controlled experiments. Some 62.9% of the decrease in height for invasive *S. alterniflora* resulted from the gradual increase of soil salinity (Fig. 5A), while no significant relationship was detected between soil salinity and survival rates for *S. alterniflora* (Fig. 5B). Although the number of new ramets for *S. alterniflora* was not significantly affected by flooding salinity treatments (Fig. 2D), the increased soil salinity caused by elevated flooding salinity levels could explain 23.1% of the variation in its number of new ramets (Fig. 5C). There was no significant relationship between soil salinity and seed setting rates for *S. alterniflora* (Fig. 5D). About 65.0% of the variations in aboveground biomass for invasive *S. alterniflora* were attributed to the increase of soil salinity (Fig. 5E).

Regarding the native *P. australis*, soil salinity could explain 77.5%, 57.6%, 43.1%, 81.8%, and 46.7% of the variations in height, survival rates, number of new ramets, seed setting rates, and aboveground biomass, respectively (Fig. 5F–J). For native *S. mariqueter*, the contributions of soil salinity to the variations in height, survival rates, and number of new ramets were 58.5%, 60.4%, and 54.7%, respectively (Fig. 5K–M). There was no significant relationship between soil salinity and seed setting rates for *S. mariqueter* (Fig. 5N). The aboveground biomass of *S. mariqueter* decreased significantly along the increased soil salinity gradients, and soil salinity could explain 72.4% of the variations in aboveground biomass (Fig. 5O).

In flooding depth experiments, there were non-linear responses of survival rates, seed setting rates, and aboveground biomass with increasing flooding depths. The contribution of flooding depth levels (10–80 cm) to the variations in survival rates and seed setting rates for invasive *S. alterniflora* was 41.5% and 44.4%, respectively (Fig. 6A–B). There was no clear tendency in aboveground biomass of *S. alterniflora* among flooding depth levels (10–80 cm) (Fig. 6C). Elevated flooding depths (10–80 cm) could explain 51.4%, 77.7%, and 68.5% of the variations in survival rates, seed setting rates, and aboveground biomass for *P. australis* (Fig. 6D–F), as well as 39.4% of the variations in survival rates for *S. mariqueter* (Fig. 6G). No significant relationship was detected between flooding depths (10–80 cm) and seed setting rates for *S. mariqueter* (Fig. 6H). Some 69.8% of the decrease in aboveground biomass for *S. mariqueter* resulted from the gradual increase of flooding depth (Fig. 6I). In flooding frequency experiments, the performance of all three species was influenced by salinity and flooding; therefore, we could not establish the empirical equations to quantify the regression relationships between flooding frequencies and variables.

4. Discussion

4.1. Relative tolerance to salinity and inundation

For most plants, elevated salinity would bring hyperosmotic and hyperionic stresses. However, plants differed greatly in their tolerance to salinity, as reflected in their various growth responses (Munns and Tester, 2008). For instance, when compared with previous studies (Tang et al., 2014; Wang et al., 2006, 2010), our controlled experiments showed that invasive *S. alterniflora* was less severely affected than native *P. australis* and *S. mariqueter* in plant morphology, reproduction, and aboveground biomass to flooding salinity of 25 and 35 ppt, which further increased the upper limit of salinity ranges to predict the potential impacts of accelerated sea-level rises and saltwater intrusion on these species. Linear regression analyses were subsequently conducted to evaluate the variations of invasive and native species across soil salinity gradients as an important supplement to the formerly used analysis of variance (Tang et al., 2014; Wang et al., 2006).

Some studies have provided evidence that the higher tolerance of invasive *S. alterniflora* relative to the native species might be at least partially attributable to the secretory glands, which allow salt excretion and ensure the survival of *S. alterniflora* individuals in hypersaline conditions (Medeiros et al., 2013; Wang et al., 2006). The sulfate availability that occurs in response to the addition of salt solutions under high flooding salinity levels could satisfy the requirement of *S. alterniflora* for sulfate, promoting it to thrive (Medeiros et al., 2013; Sutter et al., 2015), while concurrently threatening the growth and reproduction of native *P. australis* and *S. mariqueter*. Nevertheless, the significant negative effects of elevated salinity stress associated with sea-level rises and saltwater intrusion on both invasive and native

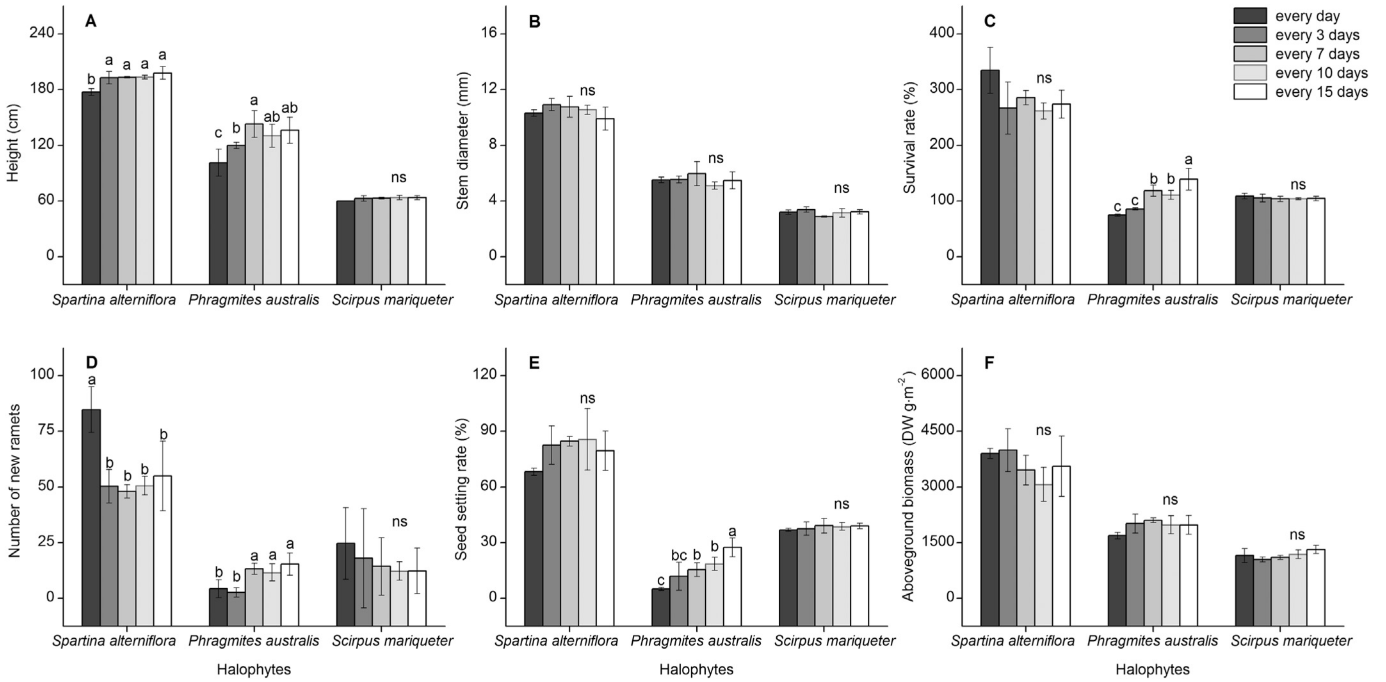

Fig. 4. Responses of invasive (*Spartina alterniflora*) and native (*Phragmites australis* and *Scirpus mariqueter*) species to five flooding frequency levels (every day and every 3, 7, 10 and 15 days) at the end of the controlled experiments. Note: Mean ± SD, $n = 3$. Different lower case letters indicate significant differences ($P < 0.05$) among treatments of the same group according to the Least Significant Difference test; "ns" indicates no significant difference among treatments of the same group; "DW" indicates dry weight.

species should not be ignored. Indeed, these could lead to dwarf plants, reduced survival rates, decreased primary productivity, and even barrenness and death.

The ebb and flow of tide in estuarine and coastal wetlands could largely determine the physiological activities and biological processes of halophytes through influences on the availability of oxygen and light (Brownstein et al., 2013; Colmer et al., 2013). Although Wang et al. (2006) demonstrated that the ramet number and biomass of *S. alterniflora* were significantly improved when water availability increased from non-immersion (at 10 cm below the soil surface) to full-immersion (at 10 cm above the soil surface), our controlled experiments further confirmed that fluctuations in the water level (10–80 cm) could not significantly affect the number of new ramets, and the few ramets at the 0 cm level might be partly attributed to the lower soil moisture content relative to other flooding depth levels. Additionally, the establishment of regression equations might advance the previous results and help quantify the contributions of elevated flooding depths (10–80 cm) to the variations of three species in growth and reproduction performance.

Contrary to the significant linear decreases of biomass in response to elevated flooding salinity from 0 to 35 ppt, we found that the aboveground biomass of *P. australis* followed a bell-shaped pattern with a distinct optimum flooding depth of 40 cm above the soil surface. This response was consistent with the results of Kirwan & Guntenspergen (2012), who found that biomass followed parabolic relationships with elevation. Shelford's law of tolerance states that each plant has a certain minimum, maximum, and optimum environmental factor. Thus, when flooding salinity and depths are above the optimum level, a decrease in biomass accumulation will tend to be accompanied by a decrease in organic accretion that affects tidal wetland stability. *S. alterniflora* and *S. mariqueter* coped well with various flooding depths and even submergences in our controlled treatments, which could explain their natural distribution at the forefront of the Chongming Dongtan wetland.

The impacts of flooding frequency on both invasive *S. alterniflora* and native *P. australis* and *S. mariqueter* were not as obvious in previous studies, while they were well documented in our controlled experiments. Specifically, we found no significant differences in the number of new ramets and seed setting rates for *S. alterniflora* with increasing flooding frequencies from every 15 days to every 3 days; however, significant decreases in these two variables were observed for *P. australis*. These findings were consistent with the results of field measurements collected from a high marsh to low marsh in the Chongming Dongtan Wetland by Yuan (2014), indicating that invasive *S. alterniflora* was more tolerant to frequent tidal inundation than native species. When compared with the relatively large amount of aboveground biomass for *P. australis* in the middle and high elevations of the Chongming Dongtan Wetland (Yuan, 2014), variations in response to the flooding frequency levels in the present study were not significant, which might be ascribed to the short period of experimental treatments (3–4 months).

4.2. Trade-offs between asexual and sexual reproduction

Both asexual and sexual reproduction were considered to be the key determinants of success in establishing populations and colonizing new areas (Barrett et al., 2008). Our results showed that, at the flooding depth of 0 cm, invasive *S. alterniflora* produced fewer ramets and higher seed setting rates than those at other flooding depths, while the performances at 80 cm were the opposite, with more ramets and lower seed setting rates than at the rest of the flooding depths. Similarly, as flooding frequencies increased, significant increases were observed in the number of new ramets for *S. alterniflora*, whereas slight and insignificant decreases in the seed setting rates were shown, indicating a complementary phenomenon of two reproductive strategies for *S. alterniflora*.

With the increase of abiotic stresses in these controlled experiments, the reproduction capacity for native *P. australis* in both vegetative propagation (number of new ramets) and sexual reproduction (seed setting rate) was significantly decreased, whereas invasive *S. alterniflora* tended to enhance its competitive advantages by either or both forms of reproduction (asexual and sexual) simultaneously. Sexual reproduction by native *S. mariqueter* was not significantly affected by elevated

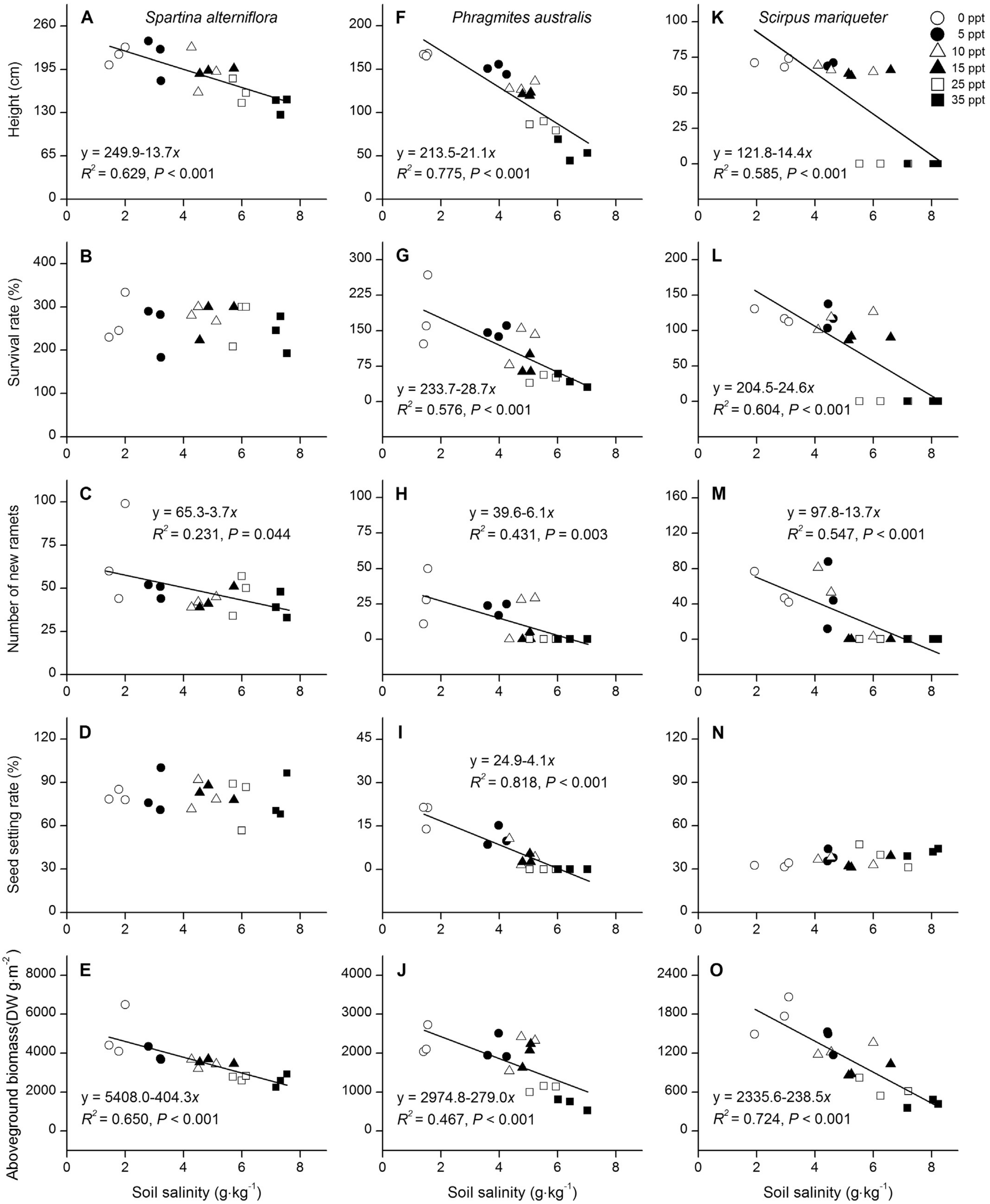

Fig. 5. Regression relationships between soil salinity of the last months measurements and height, survival rates, number of new ramets, seed setting rates, and aboveground biomass for invasive (A–E. *Spartina alterniflora*) and native (F–J. *Phragmites australis* and K–O. *Scirpus mariqueter*) species in flooding salinity experiments. Note: "DW" indicates dry weight.

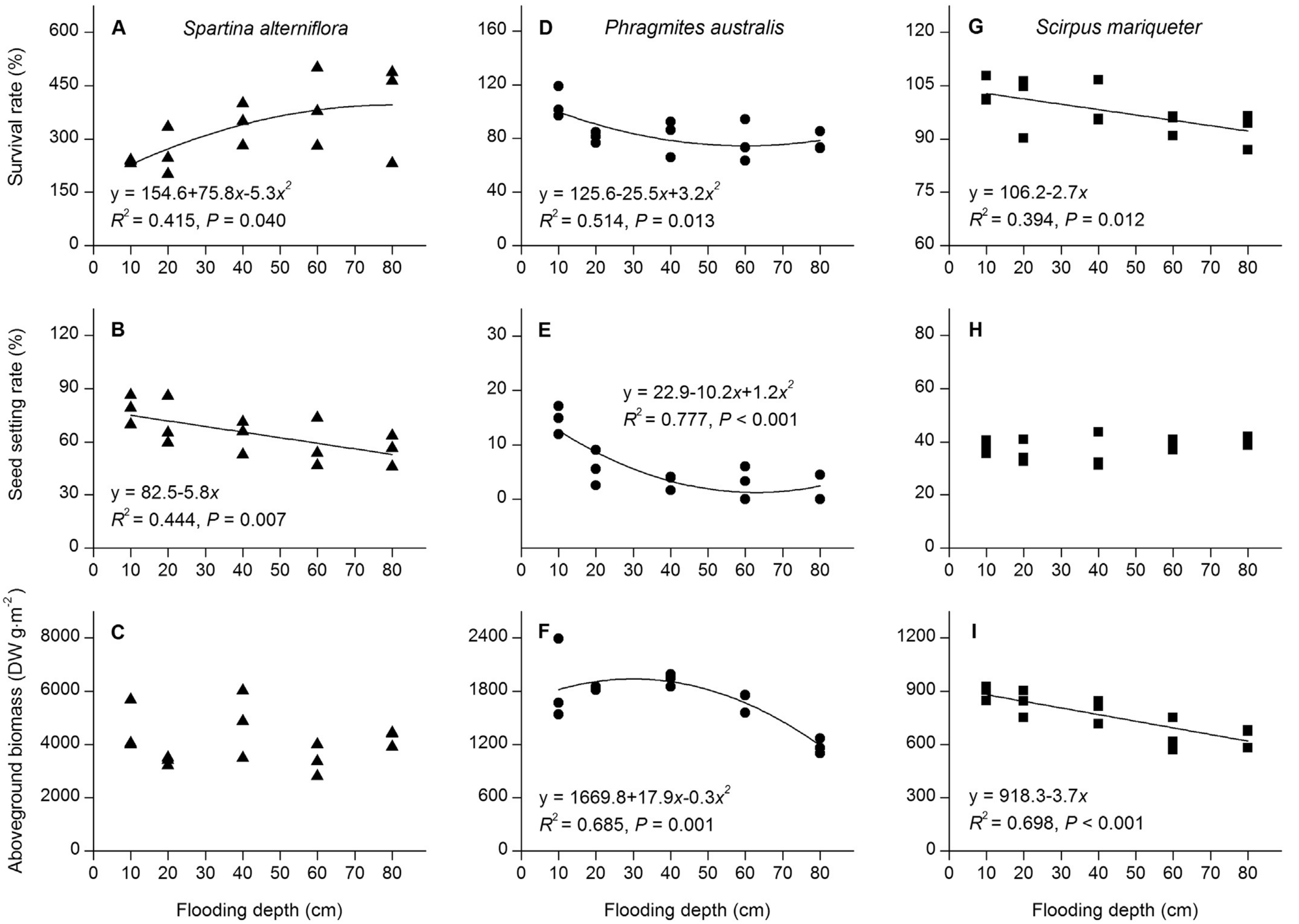

Fig. 6. Regression relationships between flooding depth (10–80 cm) and survival rates, seed setting rates, and aboveground biomass for invasive (A–C. *Spartina alterniflora*) and native (D–F. *Phragmites australis* and G–I. *Scirpus mariqueter*) species in flooding depth experiments. Note: "DW" indicates dry weight.

salinity and inundation in this study because its seed setting period was not fully covered in the controlled experiments; however, the asexual reproduction of *S. mariqueter* was obviously inhibited. Overall, the establishment and dispersal of native *P. australis* and *S. mariqueter* would be more influenced by elevated salinity and inundation than those of invasive *S. alterniflora* under the anticipated sea-level rise and aggravated saltwater intrusion.

Nevertheless, in this study, we mainly focused on the elevated environmental stresses while minimizing the interspecific relationships by allowing only one species to grow in each treatment pot. This was done because recent evidence already demonstrated that invasive *S. alterniflora* had great competitive effects on native species and could potentially exclude the natives locally (Li et al., 2009; Tang et al., 2014). We also observed that invasive *S. alterniflora* was more resistant to elevated salinity and inundation than the two native species in our controlled experiments. As a result, exotic *S. alterniflora* might become aggressive and gradually replace the native species in future scenarios of accelerated sea-level rise and saltwater intrusion. The distribution ranges for the *S. mariqueter* community have decreased greatly in recent decades (Ding et al., 2015; Li et al., 2014b), and elevated salinity and inundation would further decrease the abundance of threatened *S. mariqueter* communities, possibly leading to the local extinction of this species.

Since the variations in salinity and inundation associated with sea-level rises and saltwater intrusion are most likely to occur simultaneously under field conditions, this study attempted to pinpoint the independent impacts of flooding salinity, flooding depth, and flooding frequency on the performance of invasive and native species to provide an initial assessment to better explain their complex combined effects on plant invasions. Additionally, sea-level rise and saltwater intrusion were not the only two aspects of risk for plant invasions because the increased atmospheric CO_2 concentration and temperature were also reported to alleviate the effects of salinity on *P. australis*, then facilitate its growth in more saline habitats (Eller et al., 2014). Thus, there is an urgent need to accurately evaluate the full consequences of global climate changes, as well as the anthropogenic factors on the potential to invade native ecosystems.

5. Conclusions

In this study, we found that invasive *S. alterniflora* was more tolerant to increased salinity and flooding stresses than the two native species, *P. australis* and *S. mariqueter*. *S. alterniflora* also had sustainable competitive advantages by either or both forms of reproduction (asexual and sexual) under experimental conditions, which might further facilitate the expansion of *S. alterniflora* in the Yangtze River Estuary, China, in future scenarios of increased sea-level and saltwater intrusion. However, relying on the independent impacts of salinity and inundation on marsh species to predict future changes in species distribution and community composition may be inadequate. More work is needed to determine the relative importance of biotic and abiotic processes regulating the impacts of plant invasions on native ecosystems. Additionally, measures protecting the native *P. australis* and *S. mariqueter* communities should be strengthened, and the roles that invasive

S. alterniflora play in native ecosystems should be evaluated from more balanced and objective perspectives.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2018.06.008.

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