



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 (CO₂), 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 Megoñigal, 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 $4.97 \text{ mm}\cdot\text{yr}^{-1}$ between 1961 and 2011 (NOAA, 2017), which is higher than the mean rate of global sea-level rise of $3.2 \text{ mm}\cdot\text{yr}^{-1}$ (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 \pm SD: $3.25 \pm 0.72 \text{ m}$, $n = 331$)–*S. alterniflora* ($3.55 \pm 0.73 \text{ m}$, $n = 404$)–*P. australis* ($3.75 \pm 0.57 \text{ m}$, $n = 1248$)” 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 pre-treatment 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

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