Management of Biological Invasions (2024) Volume 15, Issue 2: 251–273

Review

# Invasion mechanisms and management measures of *Sporobolus alterniflorus*

Guo Li[1], Qihui Li[1], Shoubin Wang[1], Weizhen Zhang[3], Yu Liu[2], Yumiao Zhang[3], Huanyu Wei[1] and Zheng Zheng[1]

[1]*Department of Environmental Science and Engineering, Fudan University, Shanghai 200433, China*
[2]*Fushengyuan Environment Technology (Jiangsu) Co., Ltd., Dongtai, 224237, China*
[3]*School of Ecological and Environment, Chengdu University of Technology, Chengdu, 610059, China*
*Corresponding author: Zheng Zheng (zzhenghj@fudan.edu.cn)*

**Citation:** Li G, Li Q, Wang S, Zhang W, Liu Y, Zhang Y, Wei H, Zheng Z (2024) Invasion mechanisms and management measures of *Sporobolus alterniflorus*. *Management of Biological Invasions* 15(2): 251–273, https://doi.org/10.3391/mbi.2024.15.2.06

**Received:** 3 May 2023
**Accepted:** 21 February 2024
**Published:** 20 May 2024

**Thematic editor:** Katherine Dafforn

**Copyright:** © Li et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

## Abstract

*Sporobolus alterniflorus* (*S. alterniflorus*) is a widespread invasive plant that poses significant threats to coastal wetland ecosystems and local economies worldwide. However, most existing management methods for *S. alterniflorus* are costly and provide only temporary relief due to reoccurrences and reinvasion. Additionally, limited attention has been paid to examining the application of invasion mechanisms in the design of management measures, hindering the development of effective strategies. In this paper, we reviewed the literature on the mechanisms and management of *S. alterniflorus* invasion. We identified the key factors enabling invasion mechanisms, analyzed how they are targeted in current control methods, and pointed out their implications for future research. We recommend that the invasion mechanisms of *S. alterniflorus* should be comprehensively considered during the design of management measures. Furthermore, future research on invasion mechanisms could focus on the joint effects and the relative roles of individual factors in successful invasion, the impact of *S. alterniflorus* invasion on the coupled human and natural systems, and the systematic review of studies at different scales.

**Key words:** biological invasion, ecological management, photosynthesis, reproduction, salt marsh

## Introduction

*Sporobolus alterniflorus*, a perennial halophyte native to the east coast of North America and the Gulf of Mexico, plays essential ecological roles in its native ecosystems. Due to its great capacity for siltation promotion, beach protection and dike preservation, *S. alterniflorus* has been intentionally introduced to salt marshes on the East Coast of the United States, China, New Zealand, the United Kingdom, and other regions around the world for ecological restoration (An et al. 2007; Daehler and Strong 1996; Xie et al. 2019). Given its strong reproductive ability and adaptability, *S. alterniflorus* has expanded rapidly, displacing native species in the introduced areas (Grosholz 2002; Sánchez et al. 1998). For example, the occupied area of *S. alterniflorus* in China exceeded 540 km$^2$ by 2015 (Liu et al. 2017a; Zhao et al. 2020c), posing significant threats to biodiversity and the local economy.

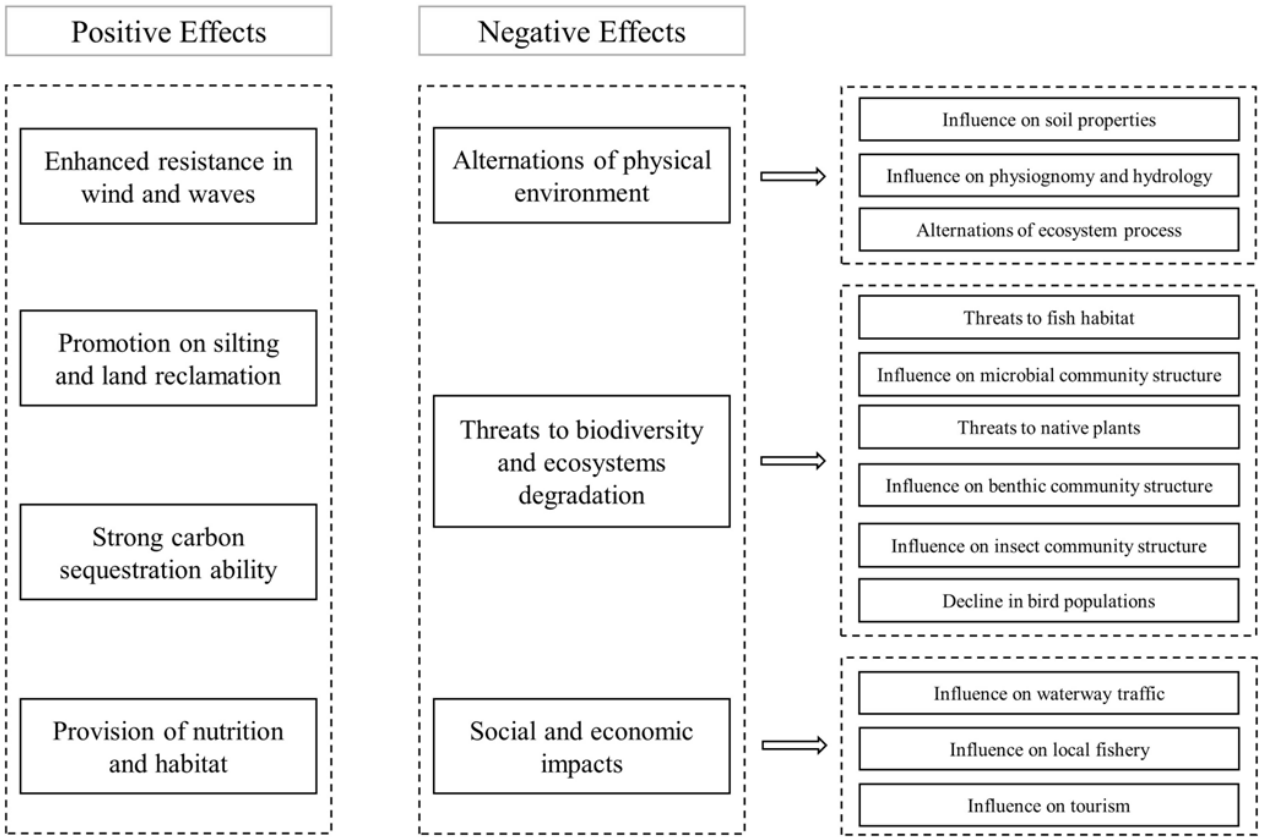



**Figure 1.** Positive and negative effects of *S. alterniflorus* invasions.

In addition, the well-developed root system of *S. alterniflorus* possesses the capacity to penetrate and disturb the soil, potentially disrupting soil structure. Moreover, the root system of *S. alterniflorus* can influence the distribution of soil moisture. The water absorption activities of its roots may lead to excessive drying in the vicinity of the root zone, rendering the soil more susceptible to weathering and erosion, thereby compromising soil stability (Figure 1). Due to its extensive environmental and social impacts, *S. alterniflorus* has been declared an invasive alien species in China, Japan and other countries (Xin et al. 2021; Kueffer 2017; Ormerod and Watkinson 2000).

However, effective control of *S. alterniflorus* is challenging, given its characteristics as a deep-rooted plant with high reproductivity, growth rate and resistance to abiotic stresses. The roots of *S. alterniflorus* are well-developed and often densely distributed in the soil layer up to 30 cm below the ground (Xiao et al. 2011). The stalks of *S. alterniflorus* are erect and tough, reaching heights of 1–3 m and diameters of 1 cm and above (Feng et al. 2018; Webb et al. 1984). This makes the mechanical removal of complete *S. alterniflorus* both costly and time-consuming. Its high reproductivity further exacerbated the situation. *Sporobolus alterniflorus* propagates via seed, rhizomes or vegetative fragments (Figure 2). Every square meter of *S. alterniflorus* can produce several million seeds, and a single *S. alterniflorus* clone can expand to approximately 200 plants over nine months (Daehler and Strong 1997). Moreover, *S. alterniflorus* has a high photosynthesis rate, contributing to its fast growth. Additionally, it possesses a well-developed

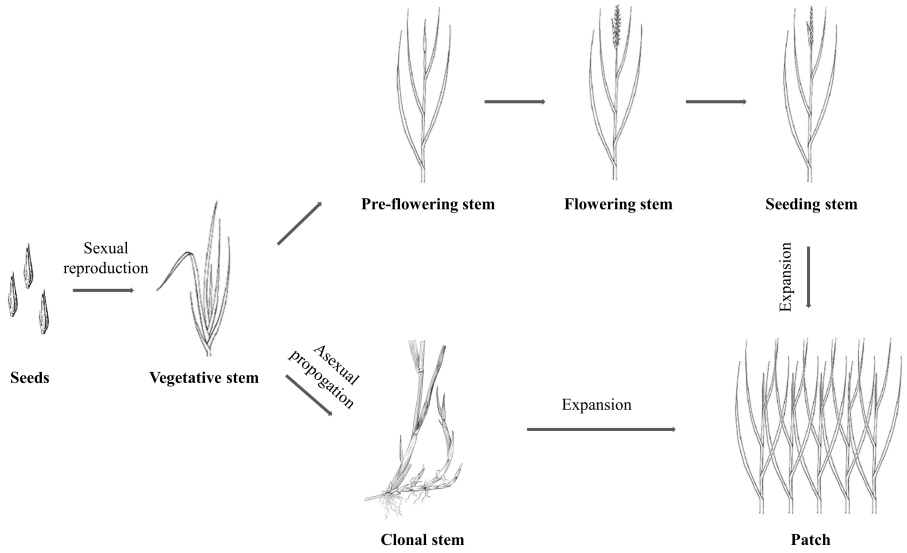



**Figure 2.** Sexual and asexual reproduction of *S. alterniflorus*.

aeration system and salt-secreting tissues in its stem, establishing strong tolerance to frequent flooding and high salinity (Pennings et al. 2003).

In recent years, as the negative impacts of *S. alterniflorus* have been increasingly pronounced, the literature on its management has been expanded rapidly. The management measures include physical control, chemical control, biological control, biological substitution control and integrated management (Wang et al. 2006; Wang et al. 2023; Xie et al. 2019). For example, in Chongming Dongtan, China, the optimal control efficacy of Gallant (Haloxyfop-R-methyl) herbicide application was 92% for continuous swards and 100% for small patches (Zhao et al. 2020a). However, in most cases, the control methods are costly and yield only short-term effects due to reoccurrences and reinvasion. Therefore, it remains an urgent task to improve and innovate existing control techniques, necessitating a deep understanding of the mechanisms that contribute to the successful invasion of *S. alterniflorus*. However, few studies have examined how the invasion mechanisms of *S. alterniflorus* guided the existing management measures and could inform future design of effective management measures.

This review aims to improve the understanding of the invasion mechanisms and management measures of *S. alterniflorus*. We specifically address the following questions: (1) to identify the key factors contributing to the successful invasion of *S. alterniflorus* and explore their interlinkages; (2) to present the main management measures for *S. alterniflorus* and elucidate their connection with invasion mechanisms; and (3) to propose future research directions on invasion mechanisms and management measures of *S. alterniflorus*.

## Invasion mechanisms

The invasion mechanisms of *S. alterniflorus* are highly sophisticated (Figure 3). Propagule pressure, biological phenotype and genotype of *S. alterniflorus,*

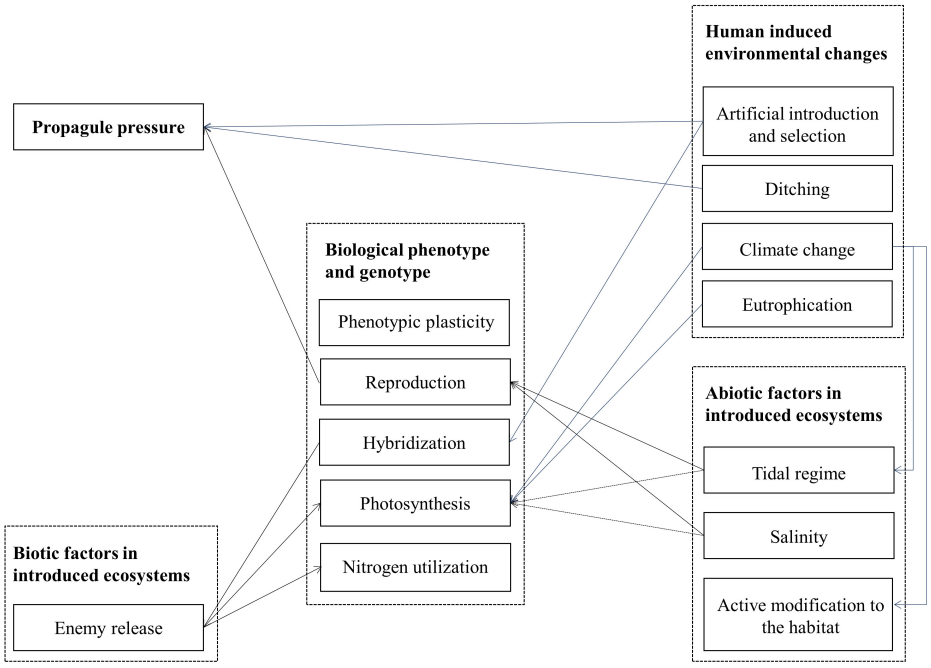



**Figure 3.** Invasion mechanisms of *S. alterniflorus*. Solid lines refer to well-established correlations, while dotted lines refer to correlations with little evidence.

and abiotic and biotic factors in introduced ecosystems are the three principal factors that determine the successful invasion of *S. alterniflorus*. These three factors, along with human-induced environmental changes, interact with each other during the invasion process.

### *Propagule pressure*

Propagule pressure is a major biotic factor for the successful establishment and spread of invasive species (Simberloff 2009; Li et al. 2014; Lockwood et al. 2005; Mason et al. 2008). In China, human-mediated long-distance dispersal is the key driver of the rapid spread of *S. alterniflorus* along coastal salt marshes (Xia et al. 2020). The high seed mobility of *S. alterniflorus* also contributes to its high propagule pressure in the introduced regions. Invasive *S. alterniflorus* produces 133 to 636 seeds per inflorescence, and its seeds disperse widely out of *S. alterniflorus* patches into other intertidal habitats (Deng et al. 2009; Xiao et al. 2009). Despite its capability to produce a large number of seeds, the seed viability varies under different environmental conditions. Deng et al. (2009) found a significant difference in the total seed production of *S. alterniflorus* in different habitats, possibly associated with its adaptability to specific environments. Therefore, we will further explore the growth potential of *S. alterniflorus* under different environmental conditions. In addition, anthropogenic disturbance may increase the propagule pressure of *S. alterniflorus*. Artificial levees, trenches, ditches, and pits in tidal salt marshes may trap more seeds of *S. alterniflorus* in high marshes and promote the emergence of its seedlings, resulting in higher propagule pressure (Ning et al. 2019; Xie et al. 2021).

*Biological phenotype and genotype*

Hybridization

Intraspecific and interspecific hybridization may facilitate the successful invasion of *S. alterniflorus* (Ellstrand et al. 2000). Intraspecific hybrid vigor plays an important role in the spread of invasive species (Glotzbecker et al. 2016; Roy et al. 2015), as demonstrated in the case of *S. alterniflorus*'s introduction to China. *Sporobolus alterniflorus,* initially introduced from North Carlolina, Georgia and Florida of the U.S. was cultivated together, and the most vigorous lineages were propagated (Qing et al. 2012; Shang et al. 2015). Hybrid vigor and artificial selection contributed to the differentiation of invasive *S. alterniflorus* in China from its American origins and facilitated the rapid adaptation and invasion of *S. alterniflorus* in the coastal area of China (Liu et al. 2020a; Qiao et al. 2019; Xia et al. 2020).

Interspecific hybridization between native species and invasive species has both genetic and ecological influences (Vilà et al. 2000). In terms of genetic effects, interspecific hybridization may dilute native species' gene pool and genetically assimilate the native population, leading to the loss of genetic diversity and adaptability of native populations (Abbott 1992; Ellstrand et al. 2000; Levin et al. 1996). Anttila et al. (1998) demonstrated that the invasion of *S. alterniflorus* in the salt marshes of San Francisco Bay led to genetic assimilation of a very large population of native *Spartina foliosa* due to the superior siting ability of *S. alterniflorus* pollen. Invasive *S. alterniflorus* pollen increased the seed set of native *S. foliosa* almost eightfold over that produced by native *S. foliosa* pollen, which failed to increase the seed set of invasive *S. alterniflorus*. Regarding ecological influence, hybrids may threaten native species by occupying resources or modifying abiotic and biotic factors in the introduced ranges (Ellstrand et al. 2000; Vilà et al. 2000). The hybrids of invasive *S. alterniflorus* have a higher recruitment rate and higher resistance to pathogens and herbivores than the parent species (Daehler and Strong 1997; Grosholz 2009).

*Sporobolus anglicus* (also named *Spartina anglica*) is derived from interspecific hybridization between the native *Spartina maritima* Fernald and invasive *S. alterniflorus* (Thompson 1991). This resulted in a sterile F1 hybrid named *Spartina* × *townsendii*, which later underwent chromosome doubling, resulting in the development of a newly fertile allopolyploid species identified as *Spartina anglica* (*S. anglica*). *S. anglica* exhibits robust vitality and strong reproductive capabilities, allowing it to rapidly spread and successfully invade (Muhammad and Ki 2022). This allopolyploid formation, marked by structural genome changes, renders *S. anglica* more dynamic than previously perceived (Huska et al. 2016). The successful invasion mechanism of *S. anglica* involves several key factors. Firstly, genomic recombination and enhanced adaptability are crucial for its successful adaptation to different environments. The combination of two parental

genomes through allopolyploidy, resulting in a new genomic composition, provides *S. anglica* with increased adaptability (Soltis and Soltis 1999), enabling it to thrive and reproduce more successfully in diverse environments. Secondly, the role of chromosome doubling further enhances the genetic diversity of *S. anglica*, providing richer genomic resources for better adaptation and colonization in the face of different habitats and ecosystems (Rieseberg and Willis 2007). Lastly, rapid dispersal is also a key factor in its successful invasion, likely associated with its rapid growth and reproductive strategies. Through seed propagation and the spread of underground rhizomes, *S. anglica* can quickly occupy new territories, further solidifying its invasion success (Daehler and Strong 1997). In summary, the invasive mechanism of *S. anglica* involves the synergistic effects of genome dynamics resulting from allopolyploid formation, thereby conferring adaptive advantages crucial for its successful colonization and ecological impact in diverse habitats.

Phenotypic plasticity

Phenotypic plasticity of invasive species allows them to adapt to various conditions in the introduced ranges, contributing to successful invasion (Castillo et al. 2014; Davidson et al. 2011; Zhu et al. 2007). *Sporobolus alterniflorus* exhibits high phenotypic plasticity, facilitating its rapid expansion (Crosby et al. 2017; Liu et al. 2022; Zhao et al. 2009). Numerous traits of invasive *S. alterniflorus*, including height and aboveground biomass, show considerable variation across latitudes and different abiotic conditions (Castillo et al. 2014; Proffitt et al. 2003; Zhang et al. 2008; Zhao et al. 2015a). He et al. (2012) also showed that *S. alterniflorus* develops more underground tillers in the mixed zone of *S. alterniflorus* and *Scirpus mariqueter* than in the monoculture of *S. alterniflorus* to acquire resources and occupy space, indicating *S. alterniflorus*'s plastic response to biotic conditions such as competitor pressure. Abundant evidence further proves that such variation is mainly attributed by phenotypic plasticity rather than genetic differences (Liu et al. 2017b; Liu et al. 2016, 2022). When planted in the common garden, *S. alterniflorus* lost its latitudinal variation in plant height, shoot density, aboveground biomass and flowering day (Chen et al. 2021; Liu et al. 2016, 2020b). Li et al. (2019) found only weak difference in the genetic structure and diversity among six populations of *S. alterniflorus* with different invasion histories in China.

Reproduction

Sexual reproduction through seedlings and asexual propagation by tillering and rhizomes are critical for the expansion of *S. alterniflorus* populations (Ma et al. 2019; Moffett et al. 2010; Xiao et al. 2010). Its transient seed bank duration is approximately 9 months, during which it can disperse and invade into new ranges (Xiao et al. 2009).

The extent to which sexual reproduction and asexual propagation of *S. alterniflorus* contribute to its range expansion is a topic of ongoing debate. Both field observations and laboratory experiments suggest that asexual reproduction is the primary factor driving the rapid spread of *S. alterniflorus* (Proffitt et al. 2003; Shang et al. 2015). Xu et al. (2014) also demonstrated that clonal ramets produced through asexual propagation exhibit larger biomass compared to sexual seedlings. Moreover, *S. alterniflorus* adults have demonstrated their ability to displace *S. mariqueter* through rhizoming and tillering, although the competitive advantage of *S. alterniflorus* seedlings may be weaker compared to adult *S. mariqueter* (Chen et al. 2004; Xiao et al. 2010). Nonetheless, the relative contribution of sexual and asexual reproduction may be influenced by various factors such as geographical location, habitat type, and biotic and abiotic factors (Honnay and Bossuyt 2005; Xu et al. 2014).

Geographical location is a crucial determinant that influences the reproductive dynamics of *S. alterniflorus* population. Different regions exhibit different environmental conditions, climatic variations and ecological stresses (Castillo et al. 2014; Dawson et al. 2012; Hayasaka et al. 2020; Xue et al. 2018; Zhao et al. 2015a), which influence the relative contribution of sexual and asexual reproduction. Sexual reproduction is more prevalent in areas where conditions are more stable and favourable, as it provides genetic diversity and promotes adaptation to changing environments.

Habitat type further complicates the reproductive scenario of *S. alterniflorus*. Different habitats present varying levels of competition, predation and resource availability, which can influence the adaptive advantage of sexual and asexual reproduction (He et al. 2012; Liu et al. 2016; Zhao et al. 2015b). In more competitive environments, asexual reproduction is at an advantage due to its ability to rapidly expand and monopolise resources. Meanwhile, in less competitive habitats, sexual reproduction is more favourable as it helps to introduce genetic diversity and enhance the evolutionary potential of populations.

Biotic and abiotic factors also play an important role in the regulation of reproductive strategies in *S. alterniflorus*. Interactions with herbivores, pathogens, or other plant species exert selective pressure on reproductive strategies (Avanesyan and Culley 2015; Daehler and Strong 1997; Grosholz 2009; Zhang et al. 2017). Similarly, abiotic factors such as soil composition, moisture levels and temperature variations influence seed germinationand the biomass of *S. alterniflorus* (O'Donnell and Schalles 2016; Zhu et al. 2019), influencing the balance between sexual and asexual reproduction.

### Photosynthesis

In addition to reproductive ability, photosynthesis is another key growth trait linked to the successful invasion of *S. alterniflorus*. *Sporobolus alterniflorus* is characterised by the $C_4$ photosynthetic pathway and has a higher net primary productivity than native plants (Zhang et al. 2010).

Compared to commonly observed native $C_3$ plants in the introduced ranges such as *S. mariqueter* and *Phragmites australis*, *S. alterniflorus* has a higher leaf area index and photosynthesis rate, leading to an increased growth rate and dry matter accumulation rate, as well as improved water, light, and nitrogen use efficiency (Zhao et al. 2005). At the beginning of the growing season, *S. alterniflorus* exhibits a significantly higher maximum net photosynthetic rate, stomatal conductance, and transpiration rate compared to *P. australis*, indicating its ability to quickly occupy land and resources (Jiang et al. 2009; Yuan et al. 2014).

Nitrogen

*Sporobolus alterniflorus* exhibits high nitrogen use efficiency. Various studies have demonstrated that invasive *S. alterniflorus* shows high interspecific competitiveness over native species under both nitrogen deficit and nitrogen-rich conditions (Liu et al. 2016; Zhao et al. 2015b; Zhao et al. 2009). Under nitrogen deficit conditions, the symbiotic relationship between *S. alterniflorus* and nitrogen-fixing bacteria facilitates the absorption of nitrogen, leading to improved physiological processes (Tyler et al. 2007). Nitrogen enrichment results in a rapid increase in the leaf area of *S. alterniflorus*, which impedes the growth of native species and contributes to the dominance of *S. alterniflorus* in interspecific competition (Zhao et al. 2008). Additionally, Xu et al. (2022) demonstrated that the high invasiveness of *S. alterniflorus* can be maintained under nitrogen-rich conditions, as its plasticity of light use reduces intraspecific competition and increases biomass production.

*Abiotic factors*

Habitat heterogeneity exerts a substantial influence on the invasion of *S. alterniflorus*, as abiotic factors play a pivotal role in mediating intraspecific competition. Many studies have shown that the performance and distribution of salt marsh plants are affected by various abiotic factors, including salinity (Silvestri et al. 2005), tidal regime (Pennings et al. 2005), nutrient availability (Levine et al. 1998), edaphic factors (Lu et al. 2020; Moffett et al. 2010; Xiao et al. 2017), meteorological factors (O'Donnell and Schalles 2016; Zhu et al. 2019), microtopography (Sanderson et al. 2001), and sometimes pollutants (Saiz-Salinas and Francés-Zubillaga 1997). Among these factors, tidal regime and salinity, which are closely associated with elevation, are considered to be the two most significant factors. Moreover, invasive *S. alterniflorus* has been shown to actively modify the habitat environment to facilitate successful invasion (Zheng et al. 2017). Following this, we will explore in more depth how these key factors affect the invasion ability of *S. alterniflorus*.

Tidal regime

The growth potential and interspecific competitiveness of *S. alterniflorus* are influenced by the tidal regime, which includes inundation depth, frequency, and duration. The relationship between inundation duration and the growth

potential of *S. alterniflorus* follows a parabolic trend, with optimal growing conditions observed at an inundation duration of 7 hours/day (Peng et al. 2018; Zhu et al. 2019). This species usually occupies tidal creeks, which offer a favorable inundation duration (Li et al. 2018; Allen 2000; Chen et al. 2020) and can tolerate submergence stress for up to six hours daily due to well-developed ventilation tissues (Luan et al. 2020; Xiao et al. 2005). However, persistent inundation effectively restrains the expansion of *S. alterniflorus*, leading to an over 80% reduction in biomass density and a significant decrease in plant height (Zhang et al. 2014). Moreover, tidal range has been proposed as a crucial factor influencing the distribution of *S. alterniflorus* (Li et al. 2018), with its range being proportional to the tidal range (Balke et al. 2016; McKee and Patrick 1988).

Controlled experiments were conducted to investigate the effects of inundation on the reproductive capacity and strategy of *S. alterniflorus*. The results showed that elevated inundation depths and frequencies significantly increased the number, height, and stem diameter of new clonal ramets during asexual propagation, while low and moderate inundation depths impeded asexual propagation (Zhang et al. 2014; Ma et al. 2019; Xue et al. 2018; Zhang et al. 2008; Zhang et al. 2020). However, elevated inundation frequencies did not significantly affect the seed setting rates of *S. alterniflorus* during sexual reproduction (Ma et al. 2019). Instead, elevated inundation depths reduced the seed setting rates, since the seeds prefer aerobic conditions for germination, and they can germinate with inundation duration below certain thresholds (Hayasaka et al. 2020; Xiao et al. 2011; Xue et al. 2018; Zhao et al. 2020c). These findings suggest that the two reproductive strategies of *S. alterniflorus* are complementary. In contrast, both asexual and sexual reproduction for *P. australis* and *S. mariqueter* were significantly inhibited by elevated inundation depths and frequencies (Xue et al. 2018). These results indicate that *S. alterniflorus* exhibits higher adaptability to inundation conditions than native *P. australis* and *S. mariqueter*. A field experiment suggested that *S. alterniflorus* produces the highest number of seeds with the highest germination rate in the middle intertidal zone, while it produces the lowest number of seeds with the lowest germination rate in the low intertidal zone (Zhu et al. 2011). The finding that elevated inundation disturbance negatively affects the sexual production of *S. alterniflorus* aligns with the outcomes of the earlier mentioned controlled experiments. However, considering interspecific competition in the field experiment, both the seed setting rate and germination rate are lower in the high intertidal zone than compared to the middle intertidal zone. This discrepancy might be attributed to competition with native species such as *P. australis* in the high intertidal zone (Xiao et al. 2009; Zhu et al. 2011).

Salinity

Salinity plays a crucial role in determining the distribution patterns of plant species in salt marshes (He et al. 2011; Moffett et al. 2010). Xiao et al.

(2005) found that the height and stem diameter of *S. alterniflorus* initially increased and then decreased with rising salinity levels. The optimum salinity range for the growth of *S. alterniflorus* is 10‰–20‰, and it can tolerate salinity levels as high as 43‰–60‰. Furthermore, transplant experiments have shown that both the asexual propagation and sexual reproduction capacity of *S. alterniflorus* decreased when salinity increased (Xue et al. 2018). Consistent findings were reported in a case study conducted in the Yellow River Delta, which employed satellite data analysis to detect and monitor the invasive process of *S. alterniflorus* at the patch scale (Chen et al. 2020). The study demonstrated that the expansion rate of *S. alterniflorus* slows down in areas with exceptionally high salinity.

Salt stress affects the competitive dynamics between native species and invasive *S. alterniflorus*. A field experiment conducted in Dongtan, China, revealed that native *P. australis* exhibited a higher growth rate than invasive *S. alterniflorus* at a low salinity of approximately 0.7%, while the growth rate of invasive *S. alterniflorus* increased, establishing competitive dominance as the salinity reached approximately 1.1% (Tang et al. 2016). Other field and laboratory studies have also supported the notion that *S. alterniflorus* possesses greater tolerance to high salinity compared to native species such as *P. australis* and *S. mariqueter* (He et al. 2011; Medeiros et al. 2013; Sutter et al. 2015; Wang et al. 2010; Xue et al. 2018).

Active modification to the habitat

*Sporobolus alterniflorus* actively modifies various soil environmental factors, including trace element content and microorganism community, to enhance its interspecific competitiveness and facilitate rapid invasion (Zheng et al. 2017). Several studies have documented significant alterations in soil bacterial communities following the invasion of *S. alterniflorus* (Liu et al. 2017a; Yang et al. 2016). The presence of *S. alterniflorus* led to a decrease in soil bacterial diversity but an increase in the indicator groups strongly associated with *S. alterniflorus*, including *Chloroflexia*, *Alphaproteobacteria*, and *Bacilli* (Gao et al. 2018). Additionally, Wang et al. (2019) demonstrated that *S. alterniflorus* contributed to increased wetland sulfur storage, as the areas occupied by *S. alterniflorus* exhibit higher concentrations of sulfur compared to areas occupied by native species *S. mariqueter* and unvegetated mudflats.

## Enemy release

The enemy release hypothesis is widely recognized as a potential mechanism explaining the impact of herbivores on the success of plant invasions (Keane and Crawley 2002). According to this hypothesis, invasive plants can escape specialist enemies, experiencing reduced pressure from native generalist herbivores in their introduced ranges (Blumenthal et al. 2009; Morriën et al. 2012). Consequently, invasive species often exhibit decreased

defense levels but increased competitive ability (Schaffner et al. 2011). There is substantial evidence supporting the enemy release hypothesis in the case of *S. alterniflorus* invasion. Zhang et al. (2017) demonstrated that plant-feeding nematodes exhibited reduced abundancy in the presence of invasive *S. alterniflorus* roots compared to native *P. australis* roots, indicating that invasive *S. alterniflorus* experiences lower pressure from plant-feeding nematodes than native species. Furthermore, several studies compared leaf functional traits between invasive *S. alterniflorus* and native *S. alterniflorus*, finding that invasive *S. alterniflorus* reallocated resources from enemy defense to growth, leading to higher photosynthetic capacity but weaker defense against herbivory (Qing et al. 2012; Liu et al. 2022). Qing et al. (2012) found that invasive *S. alterniflorus* allocated a higher proportion of leaf nitrogen to generate the photosynthetic protein Rubisco relative to cell walls compared to its native counterparts. Liu et al. (2022) also demonstrated that invasive *S. alterniflorus* exhibits larger leaf area and specific leaf area, reduced leaf thickness, and lower leaf toughness compared to native *S. alterniflorus*.

Nevertheless, native herbivores, particularly generalists, can sometimes incorporate invasive plants into their food webs (Avanesyan and Culley 2015; Carroll and Fox 2007; Morrison and Hay 2011). *Laelia coenosa*, a major pest of the native salt marsh plant *P. australis*, was reported to successfully integrate *S. alterniflorus* into its diet (Ju et al. 2016). Zhang et al. (2019) demonstrated that *S. alterniflorus* monocultures can even sustain a higher population density of *L. coenosa* than *P. australis* monocultures due to the enemy-free space provided by the invasive *S. alterniflorus*. Moreover, invasive *S. alterniflorus* is able to evolve defense strategies against *L. coenosa* and developed increased resistance compared with native *S. alterniflorus* (Ju et al. 2016; Ma et al. 2015). Zhou et al. (2017) compared the plant-soil feedbacks of invasive *S. alterniflorus* and *P. australis* under *L. coenosa* attack and found that soils conditioned by *S. alterniflorus* exhibited higher inorganic nitrogen availability than those conditioned by *P. australis*, thereby generating a more pronounced increase in plant tissue nutrient concentration and photosynthesis rate for *S. alterniflorus*. This compensatory response mechanism may assist *S. alterniflorus* in adapting to foliar loss.

### *Human-induced environmental changes*

The resistance of native ecosystems to invasive *S. alterniflorus* is a crucial factor influencing its successful invasion. Disturbed ecosystems usually exhibit reduced resistance to *S. alterniflorus* invasions (Xie et al. 2021). *Sporobolus alterniflorus* is capable of efficiently colonizing disturbed areas, potentially outcompeting native species, owing to its broad ecological amplitude and high phenotypic plasticity (Catford et al. 2012; Davidson et al. 2011; Van Kleunen et al. 2010). Moreover, environmental disturbance can negatively impact the fitness, abundance, and diversity of native species,

thus generating vacant niches that can be exploited by *S. alterniflorus* (Bulleri et al. 2016; Shea and Chesson 2002).

Existing literature has predominantly focused on the influence of three human-induced environmental changes—climate change, eutrophication and ditching—on the invasion of *S. alterniflorus*. Climate change is predicted to facilitate the extensive range expansion of exotic species over the coming decades (Dawson et al. 2012). Rising sea levels lead to enhanced saltwater intrusion, resulting in increased inundation and elevated surface soil salinity. These alterations significantly contribute to the expansion of *S. alterniflorus* and the shrinkage of *S. mariqueter* in tidal marshes of the Yangtze River delta, as *S. alterniflorus* can better tolerate high salinity and inundation conditions than *S. mariqueter* (He et al. 2011). Jiang et al. (2022) found that *S. alterniflorus* exhibited elevated net photosynthetic rate, stomatal conductance, transpiration rate and water use efficiency with higher temperature, whereas *P. australis* showed reduced physiological functions.

The rapid intensification of agriculture and aquaculture leads to excessive loading of nitrogen and phosphorus in intertidal coastal ecosystems (Smith 2003). Eutrophication often promotes the invasion of exotic plants due to their high plasticity in nutrient acquisition (Davis et al. 2000; Dukes and Mooney 1999; Funk 2013; Zhao et al. 2009). Field observations and experiments conducted by Zhao et al. (2015b) demonstrated that nitrogen-enriched eutrophication significantly contributed to the successful invasion of *S. alterniflorus* in China. In addition, invasive *S. alterniflorus* can spread from low marshes to high marshes through anthropogenic ditches by long-distance seed dispersal. The ditches enhanced the propagule pressure of *S. alterniflorus* by trapping abundant seeds while mitigating the limitations imposed by natural abiotic resistance of the native ecosystem (Ning et al. 2019).

## Management measures

Major management measures for *S. alterniflorus* encompass physical control, chemical control, biological control, biological substitution and integrated management. When devising these measures, key factors such as reproduction, photosynthesis, submergence stress and enemy release are typically taken into account (Figure 4).

### *Physical control*

Physical control involves mechanical treatments, such as manual uprooting, mowing, plowing, shading, waterlogging and burning, to hinder the growth of *S. alterniflorus* and eventually lead to its death (Davis et al. 2004). The underlying mechanism of physical control is to reduce the biomass of *S. alterniflorus* by limiting photosynthesis, respiration, seeding, or rhizome reproduction (Xie et al. 2019). This approach yields effective weed control

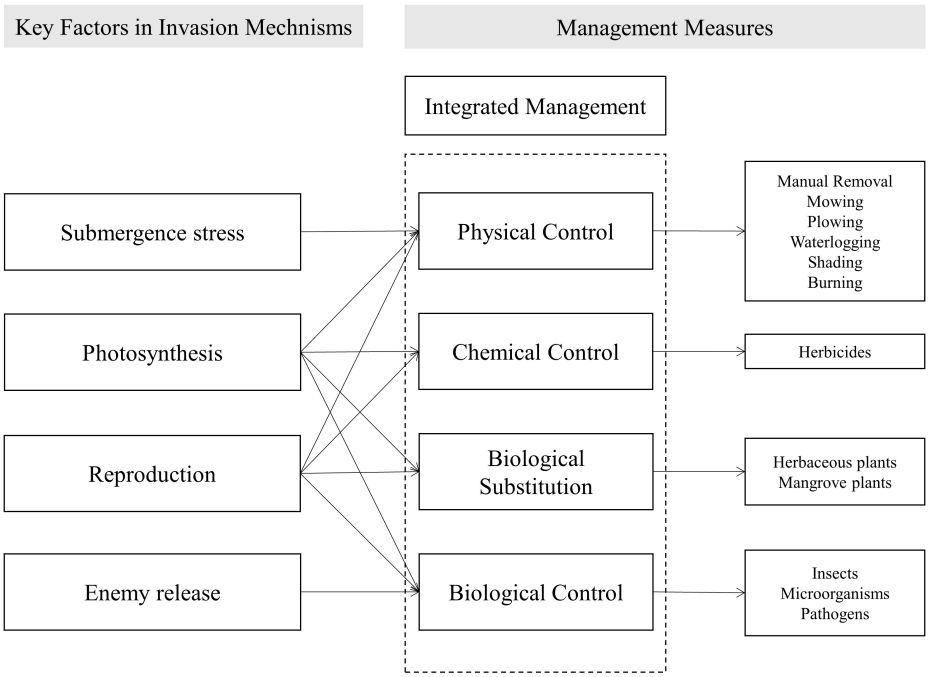



**Figure 4.** Key factors in invasion mechanisms and their associated management measure.

results within a short time while minimizing adverse environmental impacts but can be costly due to the need for multiple treatments. It is well-suited for regions with abundant human resources and a relatively short invasion history (Yuan et al. 2011).

The effective physical control for *S. alterniflorus* relies on appropriate timing, frequency and intervals of treatments (Tang et al. 2021). Actions such as uprooting, digging, or burial by pressure should be carried out prior to the flowering period of *S. alterniflorus* to prevent the dispersal of mature seeds, while the control of live seedlings is typically performed during the germination stage to achieve a high mortality rate (Li and Chen 2002). Meanwhile, mowing has been proved to be most effective during the flowering period (Yuan et al. 2011), when a significant portion of energy generated through photosynthesis is allocated to sexual reproduction (Tang et al. 2021). Therefore, mowing *S. alterniflorus* during the flowering period can effectively restrict the allocation of energy and resources to the rhizomes and roots, leading to inhibited growth thereafter (Li and Zhang 2008). Furthermore, Tang et al. (2021) proved that the highest removal efficacy was achieved when *S. alterniflorus* was first mowed at the start of the flowering period and given the second treatment when new shoots stopped growing. This approach resulted in substantial biomass removal in each treatment and a 70% decrease in growth in the following year (Tang et al. 2021).

The size of the infestation also affects the efficacy of physical control treatments. While physical control can effectively remove newly colonized seedlings or small patches of *S. alterniflorus*, a single method of treatment may not provide long-term control for large patches (Yuan et al. 2011).

Therefore, some studies have attempted to integrate multiple physical control measures. Zhao et al. (2014) and Zhao et al. (2017) found that while mowing effectively inhibited the growth of individual plants, it had limited impact on population density, spike rate and spike length. However, the combined approach of mowing and shading effectively suppressed sexual reproduction of *S. alterniflorus*, improving overall control effect compared to mowing alone. In addition, Tang et al. (2021) implemented a demonstration project using waterlogging and mowing for *S. alterniflorus* control. While waterlogging initially reduced the biomass and seed production of *S. alterniflorus*, the species quickly adapted to prolonged waterlogging stress. However, implementing waterlogging for approximately 3 months in combination with mowing achieved successful control and eradication of *S. alterniflorus*.

### *Chemical control*

Chemical control involves the application of herbicides to eradicate *Sporobolus alterniflorus*, requiring careful consideration of specificity, dosage, and application timing for precise targeting. The effectiveness of herbicides is also affected by factors such as wind, tidal cycle, and sediment coverage on stems and leaves (Wang et al. 2006). Commonly used herbicides in *Sporobolus alterniflorus* management include Glyphosate, ammonium glufosinate, imazamox (imidazolium nicotinate), and captan (flumioxazin) are. Herbicides act by disrupting cell division, chlorophyll synthesis and metabolic processes, ultimately leading to plant death (Taylor et al. 2004). In a cover-grass spraying trial conducted at Chongming Dongtan Nature Reserve, Shanghai, 92% of the sample plots were effectively eradicated within one month, with no residues observed in the sediment (Zhao et al. 2020b). However, the control effect of herbicides on underground roots is not significant. Additionally, the excessive or inappropriate use of herbicides poses potential risks to the ecosystem, and the impacts of herbicides for *S. alterniflorus* management on coastal salt marshes remains to be investigated (Liang et al. 2020).

### *Biological and biological substitution control*

Biological control involves the introduction of natural enemies, such as phytophagous and parasitic insects, microorganisms, and pathogens, to regulate the population of *S. alterniflorus* (Grevstad et al. 2003). This method has long-lasting effects and minimal negative impacts on the environment (Tang et al. 2007; Xu et al. 1989). Biological control agents of *S. alterniflorus* include *Littoraria irrorata* (Say), *Prokelisia marginata* (Van Duzee), *Clavieps purpurea* (Fr.) Tul., and *Fursarium* spp., etc. (Fisher et al. 2005; Grevstad et al. 2003). For instance, *Prokelisia marginata* (Van Duzee) in the eastern U.S. and San Francisco Bay region inhibited the seed production of *S. alterniflorus* by feeding on its bast, thereby imposing negative impacts on

the population dispersal of *S. alterniflorus* (Daehler and Strong 1997). However, since the natural enemies of *S. alterniflorus* are not native to the introduced regions, their introduction poses a potential threat to non-target plants and may even lead to new biological invasions.

Biological substitution is an ecological control technique that utilizes economically or ecologically valuable native plants to replace invasive plants, following the principles of plant community succession (Zhou et al. 2015). This approach is environmentally friendly and cost-effective, making it particularly suitable for areas with favorable soil conditions and competitive native plants. The commonly used plants for the biological substitution of *S. alterniflorus* include native herbaceous plants such as *P. australis* and *S. mariqueter*, as well as mangrove plants such as *Kandelia candel*, *Sonneratia caseolaris* (L.) Engl. and *Sonneratia apetala* Buch-Ham (Li 2021; Tang et al. 2007). These plants contribute to reducing the dominance of *S. alterniflorus* and preventing its further spread. Native *P. australis*, for instance, has shown significant suppressive effects on the growth of *S. alterniflorus*, and the restoration of the local ecological environment can be achieved through the removal of *S. alterniflorus* and the transplantation of *P. australis* (Chen et al. 2012). However, Chen et al. (2012) found that in the third growing season after transplanting, the density and spike rate of *P. australis* decreased significantly, with a survival rate of only 25%, allowing for the potential re-invasion of *S. alterniflorus*. Therefore, biological substitution techniques necessitate regular monitoring and management. In addition, these methods impose certain environmental requirements, limiting their scope of application.

### *Integrated management*

Physical, chemical, and biological control methods each possess distinct strengths and weaknesses, and employing a single management measure is usually insufficient to achieve rapid and long-lasting effects. Therefore, integrated management approaches that leverage various control techniques are recommended to create efficient management systems, tailored to specific local conditions. Gu (2019) reported a successful integrated management system in Chongming Dongtan, China, incorporating mowing, waterlogging, herbicide application and a unique technique called crushing and fermenting. The crushing and fermenting method was creatively proposed, involving the cutting, crushing, and mixing of the aboveground part of *S. alterniflorus* with enzyme bacteria, followed by spraying to accelerate the decomposition of the underground part of *S. alterniflorus* and increase the soil nutrients. This approach not only improved treatment efficiency and reduced the negative impacts on the ecosystem, but also yielded long-lasting results. However, the implementation of integrated management approaches remains challenging due to their site-specific nature, requiring comprehensive planning that considers local economy, climate and other factors.

## Recommendation for future research

Although recent research on the invasion mechanism of *S. alterniflorus* has made significant progress, there are still substantial knowledge gaps that need addressing for effective management design. While the contribution of individual factors to the successful *S. alterniflorus* invasion has been widely studied, only understanding the independent impacts of each factor is inadequate to achieve effective and precise management. The joint effects of different factors and their relative importance in successful invasion remain unclear. For instance, further investigation is required to understand the combined effects of salinity and tidal regime on sexual production, the relative roles of asexual and sexual propagation in expansion, and the contributions of phenotypic plasticity and hybridization to trait changes.

Moreover, although some studies have demonstrated the effects of human-induced environmental changes on *S. alterniflorus* invasion, as discussed above, the response of *S. alterniflorus* invasion to the coupled human and natural systems still remains poorly understood. Integrating this evidence into management strategies would be highly valuable for regulating human interventions and coping with uncertainties associated with climate change. While most existing studies have applied controlled experiments and field experiments to reveal the invasion mechanisms of *S. alterniflorus* at the individual level and small scale, an increasing number of studies have applied geographic information system and modeling to examine the ecological dynamics of *S. alterniflorus* at the community level and large scale. Investigating the invasion mechanisms of *S. alterniflorus* at different spatiotemporal scales will be important for comprehensively understanding and interpreting the invasion mechanisms, providing valuable guidance for the effective control of invasive *S. alterniflorus*.

Most of the existing management measures for *S. alterniflorus* aim to hinder its growth and reproduction, targeting various factors in the invasion mechanism, including reproduction, photosynthesis, submergence stress and enemy release. Specifically, the timing, interval and frequency of successive treatments in physical and chemical control are typically based on *S. alterniflorus*'s reproductive and photosynthetic patterns. Biological control methods introduce natural enemies of *S. alterniflorus*, which disrupt the enemy-free space for invasive *S. alterniflorus* in the introduced areas. However, certain factors in the invasion mechanisms, such as phenotypic plasticity, hybridization and abiotic factors, have received little consideration in the design of management measures, despite their potential significance in achieving effective control. The reinvasion of *S. alterniflorus*, which often occurs after the implementation of biological substitution methods, is an example. The competitiveness of the plant used as a substitute for *S. alterniflorus* tends to decline after three or more growing seasons, which may be attributed to *S. alterniflorus*'s plastic response to competitor pressure and

genetic assimilation of a significant portion of the introduced plant through interspecific hybridization. Therefore, supplementary measures may be necessary to prevent reinvasion, such as modifying abiotic factors that influence interspecific competition to enhance the competitiveness of the transplanted plant, preventing interspecific hybridization and integrating physical and chemical control methods. In conclusion, a full consideration of the invasion mechanism is recommended in the design of management measures for *S. alterniflorus*.

## Authors' contribution

Guo Li: literature collection, literature analysis, and writing – original draft preparation. Qihui Li: literature compilation, literature analysis and writing – review and editing. Weizhen Zhang and Yu Liu: curation and writing – review and editing. Yumiao Zhang: conceptualization and methodology. Huanyu Wei: investigation and resources. Zheng Zheng and Shoubin Wang: supervision, writing – review and editing, and funding acquisition. All authors contributed to the article and approved the submitted version.

## Acknowledgments

This research is supported by Donation from ABA Chemicals and Government Project of Dongtai-Fudan Joint Innovation Center for Coastal Wetland Conservation. We are grateful to the reviewers for their insightful comments. Their expertise and attention to detail have undoubtedly enhanced the clarity and coherence of the manuscript.

## References

Abbott RJ (1992) Plant Invasions, Interspecific Hybridization and the Evolution of New Plant Taxa. *Trends in Ecology& Evolution* 7: 401–405, https://doi.org/10.1016/0169-5347(92)90020-C

Allen JR (2000) Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quaternary Science Reviews* 19: 1155–1231, https://doi.org/10.1016/S0277-3791(99)00034-7

An SQ, Gu BH, Zhou CF, Wang ZS, Liu YH (2007) *Spartina* Invasion in China: Implications for Invasive Species Management and Future Research. *Weed Research* 47: 183–191, https://doi.org/10.1111/j.1365-3180.2007.00559.x

Anttila CK, Daehler CC, Rank NE, Strong DR (1998) Greater Male Fitness of a Rare Invader (*Spartina alterniflora*, Poaceae) Threatens a Common Native (*Spartina foliosa*) with Hybridization. *American Journal of Botany* 85: 1597–1601, https://doi.org/10.2307/2446487

Avanesyan A, Culley TM (2015) Herbivory of native and exotic North-American prairie grasses by nymph *Melanoplus* grasshoppers. *Plant Ecology* 216: 451–464, https://doi.org/10.1007/s11258-015-0449-9

Balke T, Stock M, Jensen K, Bouma TJ, Kleyer M (2016) A global analysis of the seaward salt marsh extent: The importance of tidal range. *Water Resources Research* 52: 3775–3786, https://doi.org/10.1002/2015WR018318

Blumenthal D, Mitchell CE, Pysek P, Jarosik V (2009) Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences* 106: 7899–7904, https://doi.org/10.1073/pnas.0812607106

Bulleri F, Badalamenti F, Iveša L, Mikac B, Benedetti-Cecchi L (2016) The effects of an invasive seaweed on native communities vary along a gradient of land-based human impacts. *PeerJ* 4, https://doi.org/10.7717/peerj.1795

Carroll SP, Fox CW (2007) Dissecting the evolutionary impacts of plant invasions: bugs and beetles as native guides. *Global Change Biology* 13: 1644–1657, https://doi.org/10.1111/j.1365-2486.2007.01403.x

Castillo JM, Grewell BJ, Pickart A, Bortolus A, Peña C, Figueroa E, Sytsma M (2014) Phenotypic plasticity of invasive *Spartina densiflora* (Poaceae) along a broad latitudinal gradient on the Pacific Coast of North America. *American Journal of Botany* 101: 448–458, https://doi.org/10.3732/ajb.1400014

Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA, Rejmánek M, Bellingham PJ, Pergl J, Horvitz CC (2012) The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology Evolution & Systematics* 14: 231–241, https://doi.org/10.1016/j.ppees.2011.12.002

Chen MM, Ke YH, Bai JH, Li P, Lyu MY, Gong ZN, Zhou DM (2020) Monitoring early stage invasion of exotic *Spartina alterniflora* using deep-learning super-resolution techniques based on multisource high-resolution satellite imagery: A case study in the Yellow River Delta, China. *International Journal of Applied Earth Observation and Geoinformation* 92: 102180, https://doi.org/10.1016/j.jag.2020.102180

Chen XC, Liu WW, Pennings SC, Zhang YH (2021) Plasticity and selection drive hump‐shaped latitudinal patterns of flowering phenology in an invasive intertidal plant. *Ecology* 102: e03311, https://doi.org/10.1002/ecy.3311

Chen ZY, Li B, Zhong Y, Chen JK (2004) Local competitive effects of introduced *Spartina alterniflora* on *Scirpus mariqueter* at Dongtan of Chongming Island, the Yangtze River estuary and their potential ecological consequences. *Hydrobiologia* 528: 99–106, https://doi.org/10.1007/s10750-004-1888-9

Chen ZY, Wang GX, Liu JE, Xu WW, Wang G (2012) Competitive Ability of Two Propagules of *Spartina alterniflora* With Native Species in the Coastal Wetlands of North Jiangsu. *Advances in Marine Science* 30: 380–389, https://doi.org/10.3969/j.issn.1671-6647.2012.03.008

Crosby SC, Angermeyer A, Adle, JM, Bertness MD, Deegan LA, Sibinga N, Leslie HM (2017) *Spartina alterniflora* Biomass Allocation and Temperature: Implications for Salt Marsh Persistence with Sea-Level Rise. *Estuaries and Coasts* 40: 213–223, https://doi.org/10.1007/s12237-016-0142-9

Daehler CC, Strong DR (1996) Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. *Biological Conservation* 78: 51–58, https://doi.org/10.1016/0006-3207(96)00017-1

Daehler CC, Strong DR (1997) Hybridization between introduced smooth cordgrass (*Spartina alterniflora*; Poaceae) and native California cordgrass (*S. foliosa*) in San Francisco Bay, California, USA. *American Journal of Botany* 84: 607, https://doi.org/10.2307/2445896

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* 14: 419–431, https://doi.org/10.1111/j.1461-0248.2011.01596.x

Davis MA, Grime JP, Thompson (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–536, https://doi.org/.10.1046/j.1365-2745.2000.00473.x

Davis HG, Taylor CM, Civille JC, Strong DR (2004) An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *Journal of Ecology* 92: 321–327, https://doi.org/10.1111/j.0022-0477.2004.00873.x

Dawson W, Rohr RP, Kleunen MV, Fischer M (2012) Alien plant species with a wider global distribution are better able to capitalize on increased resource availability. *New Phytologist* 194: 859–867, https://doi.org/10.1111/j.1469-8137.2012.04104.x

Deng ZF, Deng ZW, An SQ, Wang ZS, Liu YH, Ouyang Y, Zhou CF, Zhi YB, Li HL (2009) Habitat choice and seed-seedling conflict of *Spartina alterniflora* on the coast of China. *Hydrobiologia* 630: 287–297, https://doi.org/10.1007/s10750-009-9822-9

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends in Ecology& Evolution* 14: 135–139, https://doi.org/10.1016/S0169-5347(98)01554-7

Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the United States of America* 97: 7043–7050, https://doi.org/10.1073/pnas.97.13.7043

Feng JX, Huang Q, Chen H, Shen QQ, Huang JR, Li ZF (2018) Effects of *Spartina alterniflora* invasion on benthic faunal community in saltmarsh and mangrove wetland. *Chinese Journal of Ecology* 37: 943, https://doi.org/10.13292/j.1000-4890.201803.012

Fisher AJ, DiTomaso JM, Gordon TR (2005) Intraspecific groups of *Claviceps purpurea* associated with grass species in Willapa Bay, Washington, and the prospects for biological control of invasive *Spartina alterniflora*. *Biological Control* 34: 170–179, https://doi.org/10.1016/j.biocontrol.2005.04.014

Funk JL (2013) The Physiology of Invasive Plants in Low-Resource Environments. *Conservation Physiology* 1: 1–17, https://doi.org/10.1093/conphys/cot026

Gao GF, Li PF, Zhong JX, Shen ZJ, Chen J, Li YT, Isabwe A, Zhu XY, Ding QS, Zhang S (2018) *Spartina alterniflora* invasion alters soil bacterial communities and enhances soil $N_2O$ emissions by stimulating soil denitrification in mangrove wetland. *Science of The Total Environment* 653: 231–240, https://doi.org/10.1016/j.scitotenv.2018.10.277

Glotzbecker GJ, Walters DM, Blum MJ (2016) Rapid movement and instability of an invasive hybrid swarm. *Evolutionary Applications* 9: 741–755, https://doi.org/10.1111/eva.12371

Grevstad FS, Strong DR, Garcia-Rossi D, Switzer RW, Wecker MS (2003) Biological control of *Spartina alterniflora* in Willapa Bay, Washington using the planthopper *Prokelisia marginata*: agent specificity and early results. *Biological Control* 27: 32–42, https://doi.org/10.1016/S1049-9644(02)00181-0

Grosholz E (2002) Ecological and Evolutionary Consequences of Coastal Invasions. *Trends in Ecology& Evolution* 17: 22–27, https://doi.org/10.1016/S0169-5347(01)02358-8

Grosholz E (2009) Avoidance by grazers facilitates spread of an invasive hybrid plant. *Ecology Letters* 13: 145–153, https://doi.org/10.1111/j.1461-0248.2009.01409.x

Gu YF (2019) Technologies and Their Effects on Ecological Control of *Spartina alterniflora* in Chongming Dongtan. *Journal of Shanghai Jiaotong University (Agricultural Science)* 37: 83–88, https://doi.org/10.3969/J.ISSN.1671-9964.2019.05.014

Hayasaka D, Nakagawa M, Maebara Y, Kurazono T, Hashimoto K (2020) Seed germination characteristics of invasive *Spartina alterniflora Loisel* in Japan: implications for its effective management. *Scientific Reports* 10: 2116, https://doi.org/10.1038/s41598-020-58879-7

He YL, Li XZ, Craft C, Ma ZG, Sun YG (2011) Relationships between vegetation zonation and environmental factors in newly formed tidal marshes of the Yangtze River estuary. *Wetlands Ecology and Management* 19: 341–349, https://doi.org/10.1007/s11273-011-9220-8

He YL, Li XZ, Guo WY, Ma ZG (2012) Division of labor in rhizomatous species: Comparative performance of native and invasive species in the tidal marshes of the Yangtze River estuary, China. *Journal of Experimental Marine Biology & Ecology* 422: 122–128, https://doi.org/10.1016/j.jembe.2012.04.010

Honnay O, Bossuyt B (2005) Prolonged clonal growth: escape route or route to extinction? *Oikos* 108: 427–432, https://doi.org/10.1111/j.0030-1299.2005.13569.x

Huska D, Leitch IJ, de Carvalho JF, Leitch AR, Salmon A, Ainouche M, Kovarik A (2016) Persistence, dispersal and genetic evolution of recently formed *Spartina homoploid* hybrids and allopolyploids in Southern England. *Biological Invasions* 18: 2137–2151, https://doi.org/10.1007/s10530-015-0956-6

Jiang LF, Luo YQ, Chen JK, Li B (2009) Ecophysiological Characteristics of Invasive *Spartina alterniflora* and Native Species in Salt Marshes of Yangtze River Estuary, China. *Estuarine, Coastal and Shelf Science* 81: 74–82, https://doi.org/10.1016/j.ecss.2008.09.018

Jiang XH, Xie LJ, Ye SY, Zhou P, Pei LX, Chen H, Zhao LH (2022) Responses of photosynthetic characteristics of *Phragmites australis* and *Spartina alterniflora*. *Acta Ecologica Sinica* 42: 7760–7772, https://doi.org/10.5846/stxb202106011444

Ju RT, Chen YY, Gao L, Li B (2016) The extended phenology of *Spartina* invasion alters a native herbivorous insect's abundance and diet in a Chinese salt marsh. *Biological Invasions* 18: 2229–2236, https://doi.org/10.1007/s10530-015-0981-5

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology& Evolution* 17: 164–170, https://doi.org/10.1016/S0169-5347(02)02499-0

Kueffer C (2017) Plant invasions in the Anthropocene. *Science* 358: 724–725, https://doi.org/10.1126/science.aao6371

Levin DA, Francisco-Ortega J, Jansen RK (1996) Hybridization and the Extinction of Rare Plant Species. *Conservation Biology* 10: 10–16, https://doi.org/10.1046/j.1523-1739.1996.10010010.x

Levine JM, Brewer JS, Bertness MD (1998) Nutrients, competition and plant zonation in a New England salt marsh. *Journal of Ecology* 86: 285–292, https://doi.org/10.1046/j.1365-2745.1998.00253.x

Li B, Chen JK (2002) Ecology of biological invasions: achievements and challenges. *World Sci-Tech Research and Development* 24: 26–36, https://doi.org/10.16507/j.issn.1006-6055.2002.02.005

Li FF, Gong L, Li JS, Liu XY, Zhao CY (2019) Low genetic differentiation yet high phenotypic variation in the invasive populations of *Spartina alterniflora* in Guangxi, China. *PLoS ONE* 14: e222646, https://doi.org/10.1371/journal.pone.0222646

Li HP, Zhang LQ (2008) An experimental study on physical controls of an exotic plant *Spartina alterniflora* in Shanghai, China. *Ecological Engineering* 32: 11–21, https://doi.org/10.1016/j.ecoleng.2007.08.005

Li J, Liu YJ, Liu MY (2021) Research on Information Extraction of *Spartina alterniflora* Based on Sentinel-2A Image. *Journal of North China University of Science and Technology (Natural Science)* 43: 14–19, https://doi.org/10.3969/j.issn.2095-2716.2021.03.003

Li RX, Yu Q, Wang YW, Wang Z B, Gao S, Flemming B (2018) The relationship between inundation duration and *Spartina alterniflora* growth along the Jiangsu coast, China. *Estuarine, Coastal and Shelf Science* 213: 305–313, https://doi.org/10.1016/j.ecss.2018.08.027

Li ZJ, Wang WQ, Zhang YH (2014) Recruitment and herbivory affect spread of invasive *Spartina alterniflora* in China. *Ecology* 95: 1972–1980, https://doi.org/10.1890/13-2283.1

Liang QY, Yan ZZ, Li XZ (2020) Influence of the herbicide haloxyfop-R-methyl on bacterial diversity in rhizosphere soil of *Spartina alterniflora*. *Ecotoxicology and Environmental Safety* 194: 110366, https://doi.org/10.1016/j.ecoenv.2020.110366

Liu M, Yu Z, Yu X Q, Xue Y Y, Huang B Q, Yang J (2017a) Invasion by Cordgrass Increases Microbial Diversity and Alters Community Composition in a Mangrove Nature Reserve. *Frontiers in Microbiology* 8: 2503, https://doi.org/10.3389/fmicb.2017.02503

Liu WW, Strong DR, Pennings SC, Zhang YH (2017b) Provenance-by-environment interaction of reproductive traits in the invasion of *Spartina alterniflora* in China. *Ecology* 98: 1591–1599, https://doi.org/10.1002/ecy.1815

Liu WW, Maung-Douglass K, Strong DR, Pennings SC, Zhang YH (2016) Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. *Journal of Ecology* 104: 173–181, https://doi.org/10.1111/1365-2745.12487

Liu WW, Chen XC, Strong DR, Pennings SC, Kirwan ML, Chen XL, Zhang YH (2020a) Climate and geographic adaptation drive latitudinal clines in biomass of a widespread saltmarsh plant in its native and introduced ranges. *Limnology and Oceanography* 65: 1399–1409, https://doi.org/10.1002/lno.11395

Liu WW, Zhang YH, Chen XC, Maung-Douglass K, Strong DR, Pennings SC (2020b) Contrasting plant adaptation strategies to latitude in the native and invasive range of *Spartina alterniflora*. *New Phytologist* 226: 623–634, https://doi.org/10.1111/nph.16371

Liu WW, Wang WW, Zhang YH (2022) Differences in leaf traits of *Spartina alterniflora* between native and invaded habitats: Implication for evolution of alien species competitive ability increase. *Ecological Indicators* 138: 108799, https://doi.org/10.1016/j.ecolind.2022.108799

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology& Evolution* 20: 223–228, https://doi.org/10.1016/j.tree.2005.02.004

Lu LY, Shao XX, Yang H, Wu M, Lou KX, Hua KD (2020) Response of *Spartina alterniflora* Growth to Soil Chemical Properties in Coastal Wetland of Zhejiang. *Forest Research* 33: 177–183, https://doi.org/10.13275/j.cnki.lykxyj.2020.05.022

Luan ZQ, Yan DD, Xue YY, Shi D, Xu DD, Liu B, Wang LB, An YT (2020) Research progress on the ecohydrological mechanisms of *Spartina alterniflora* invasion in coastal wetlands. *Journal of Agricultural Resources and Environment* 37: 469–476, https://doi.org/10.13254/j.jare.2019.0124

Ma D, Ju RT, Li B (2015) Preference of *Laelia coenosa* for native and introduced populations of invasive *Spartina alterniflora*. *Biodiversity Science* 23: 101–108, https://doi.org/10.17520/biods.2014156

Ma X, Yan JG, Wang FF, Qiu DD, Jiang XP, Liu ZZ, Sui HC, Bai JH, Cui BS (2019) Trait and density responses of *Spartina alterniflora* to inundation in the Yellow River Delta, China. *Marine Pollution Bulletin* 146: 857–864, https://doi.org/10.1016/j.marpolbul.2019.07.022

Mason RB, Cooke JC, Moles AT, Leishman MR (2008) Reproductive output of invasive versus native plants. *Global Ecology and Biogeography* 17: 633–640, https://doi.org/10.1111/j.1466-8238.2008.00402.x

McKee KL, Patrick WH (1988) The relationship of smooth cordgrass (*Spartina alterniflora*) to tidal datums: a review. *Estuaries* 11: 143–151, https://doi.org/10.2307/1351966

Medeiros DL, White DS, Howes BL (2013) Replacement of *Phragmites australis* by *Spartina alterniflora*: the role of competition and salinity. *Wetlands* 33: 421–430, https://doi.org/10.1007/s13157-013-0400-6

Moffett KB, Robinson DA, Gorelick SM (2010) Relationship of Salt Marsh Vegetation Zonation to Spatial Patterns in Soil Moisture, Salinity, and Topography. *Ecosystems* 13: 1287–1302, https://doi.org/10.1007/s10021-010-9385-7

Morriën E, Duyts H, Van Der, Putten WH (2012) Effects of native and exotic range-expanding plant species on taxonomic and functional composition of nematodes in the soil food web. *Oikos* 121: 181–190, https://doi.org/10.1111/j.1600-0706.2011.19773.x

Morrison WE, Hay ME (2011) Herbivore Preference for Native vs. Exotic Plants: Generalist Herbivores from Multiple Continents Prefer Exotic Plants That Are Evolutionarily Naive. *PLoS ONE* 6: e17227, https://doi.org/10.1371/journal.pone.0017227

Muhammad BL, Ki JS (2022) Hybrid origin of the invasive *Spartina anglica* inferred from chloroplast and nuclear ITS phylogenies[J]. *Aquatic Botany*, 178: 103484, https://doi.org/10.1016/j.aquabot.2021.103484

Ning ZH, Xie T, Liu ZZ, Bai JH, Cui BS (2019) Native herbivores enhance the resistance of an anthropogenically disturbed salt marsh to *Spartina alterniflora* invasion. *Ecosphere* 10: e02565, https://doi.org/10.1002/ecs2.2565

O'Donnell JPR, Schalles JF (2016) Examination of Abiotic Drivers and Their Influence on *Spartina alterniflora* Biomass over a Twenty-Eight Year Period Using Landsat 5 TM Satellite Imagery of the Central Georgia Coast. *Remote Sensing* 8: 477, https://doi.org/10.3390/rs8060477

Ormerod SJ, Watkinson AR (2000) Large-scale ecology and hydrology: an introductory perspective from the editors of the Journal of Applied Ecology. *Journal of Applied Ecology* 37: 1–5, https://doi.org/10.1046/j.1365-2664.2000.00560.x

Peng D, Chen LZ, Pennings SC, Zhang YH (2018) Using a marsh organ to predict future plant communities in a Chinese estuary invaded by an exotic grass and mangrove. *Limnology and Oceanography* 63: 2595–2605, https://doi.org/10.1002/lno.10962

Pennings SC, Selig ER, Houser LT, Bertness MD (2003) Geographic variation positive and negative interactions among salt marsh plants. *Ecology* 84: 1527–1538, https://doi.org/10.1890/0012-9658(2003)084[1527:GVIPAN]2.0.CO;2

Pennings SC, Grant M, Bertness MD (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *Journal of Ecology* 93: 159–167, https://doi.org/10.1111/j.1365-2745.2004.00959.x

Proffitt CE, Travis SE, Edwards KR (2003) Genotype and elevation influence *Spartina alterniflora* colonization and growth in a created salt marsh. *Ecological Applications* 13: 180–192, https://doi.org/10.1890/1051-0761(2003)013[0180:GAEISA]2.0.CO;2

Qiao HM, Liu WW, Zhang YH, Zhang YY, Li QS (2019) Genetic admixture accelerates invasion via provisioning rapid adaptive evolution. *Molecular Ecology* 28: 4012–4027, https://doi.org/10.1111/mec.15192

Qing H, Cai Y, Xiao Y, Yao YH, An SQ (2012) Leaf nitrogen partition between photosynthesis and structural defense in invasive and native tall form *Spartina alterniflora* populations: effects of nitrogen treatments. *Biological Invasions* 14: 2039–2048, https://doi.org/10.1007/s10530-012-0210-4

Rieseberg LH, Willis JH (2007) Plant speciation. *Science* 317: 910–914, https://doi.org/10.1126/science.1137729

Roy D, Lucek K, Walter RP, Seehausen O (2015) Hybrid 'superswarm' leads to rapid divergence and establishment of populations during a biological invasion. *Molecular Ecology* 24: 5394–5411, https://doi.org/10.1111/mec.13405

Saiz-Salinas JI, Francés-Zubillaga G, 1997. Tidal zonation on mud flats in a polluted estuary caused by oxygen-depleted water. *Journal of Experimental Marine Biology and Ecology* 209: 157–170, https://doi.org/10.1016/S0022-0981(96)02685-8

Sánchez JM, Otero XL, Izco J (1998) Relationships between vegetation and environmental characteristics in a salt-marsh system on the coast of Northwest Spain. *Plant Ecology* 136: 1–8, https://doi.org/10.1023/A:1009712629733

Sanderson EW, Foin TC, Ustin SL (2001) A simple empirical model of salt marsh plant spatial distributions with respect to a tidal channel network. *Ecological Modelling* 139: 293–307, https://doi.org/10.1016/S0304-3800(01)00253-8

Schaffner U, Ridenour WM, Wolf VC, Bassett T, Müller C, Müller-Schärer H, Sutherland S, Lortie CJ, Callaway RM (2011) Plant invasions, generalist herbivores, and novel defense weapons. *Ecology* 92: 829–835, https://doi.org/10.1890/10-1230.1

Shang L, Qiu SY, Huang JX, Li B (2015) Invasion of *Spartina alterniflora* in China is greatly facilitated by increased growth and clonality: a comparative study of native and introduced populations. *Biological Invasions* 17: 1327–1339, https://doi.org/10.1007/s10530-014-0796-9

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology& Evolution* 17: 170–176, https://doi.org/10.1016/S0169-5347(02)02495-3

Silvestri S, Defina A, Marani M (2005) Tidal regime, salinity and salt marsh plant zonation. *Estuarine Coastal & Shelf Science* 62: 119–130, https://doi.org/10.1016/j.ecss.2004.08.010

Simberloff D (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution and Systematics* 40: 81–102, https://doi.org/10.1146/annurev.ecolsys.110308.120304

Smith VH (2003) Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science & Pollution Research* 10: 126–139, https://doi.org/10.1065/espr2002.12.142

Soltis DE, Soltis PS (1999) Polyploidy: recurrent formation and genome evolution. *Trends in Ecology& Evolution* 14: 348–352, https://doi.org/10.1016/S0169-5347(99)01638-9

Sutter LA, Chambers RM, Perry III JE (2015) Seawater intrusion mediates species transition in low salinity, tidal marsh. *Aquatic Botany* 122: 32–39, https://doi.org/10.1016/j.aquabot.2015.01.002

Tang GL, Shen LH, Weng WH, Zhang JE, Liao BW, Liu JL, Teng XS (2007) Effects of using *Sonneratia apetala* to control the growth of *Spartina alterniflora Loisel*. *Journal of South China Agricultural University* 28: 10–13, https://doi.org/10.7671/j.issn.1001-411X.2007.01.003

Tang L, Gao Y, Li B, Wang Q, Wang CH, Zhao B (2016) *Spartina alterniflora* with high tolerance to salt stress changes vegetation pattern by outcompeting native species. *Ecosphere* 5: 1–18, https://doi.org/10.1890/ES14-00166.1

Tang L, Zhou QS, Guo W, Li P, Gao Y (2021) Importance of high severity in a physical removal treatment for controlling invasive *Spartina alterniflora*. *Ecological Engineering* 171: 106375, https://doi.org/10.1016/j.ecoleng.2021.106375

Taylor CM, Davis HG, Civille JC, Grevstad FS, Hastings A (2004) Consequences of an Allee Effect in the Invasion of a Pacific Estuary by *Spartina alterniflora*. *Ecology* 85: 3254–3266, https://doi.org/10.1890/03-0640

Thompson JD (1991) The biology of an invasive plant. *Bioscience* 41: 393–401, https://doi.org/10.2307/1311746

Tyler AC, Lambrinos JG, Grosholz ED (2007) Nitrogen Inputs Promote the Spread of an Invasive Marsh Grass. *Ecological Applications* 17: 1886–1898, https://doi.org/10.1890/06-0822.1

Van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245, https://doi.org/10.1111/j.1461-0248.2009.01418.x

Vilà M, Weber E, Antonio CM (2000) Conservation Implications of Invasion by Plant Hybridization. *Biological Invasions* 2: 207–217, https://doi.org/10.1023/A:1010003603310

Wang CH, Lu M, Yang B, Yang Q, Zhang XD, Hara T, Li B (2010) Effects of environmental gradients on the performances of four dominant plants in a Chinese saltmarsh: implications for plant zonation. *Ecological Research* 25: 347–358, https://doi.org/10.1007/s11284-009-0662-x

Wang Q, An SQ, Ma ZJ, Zhao B, Chen JK, Li B (2006) Invasive *Spartina alterniflora*: Biology, Ecology and Management. *Acta Phytotaxonomica Sinica* 44: 559–588, https://doi.org/10.1360/aps06044

Wang YT, He YL, Qiao PY, Mei BL, Wang XJ, Han GX, Xie BH (2023) Control Effects Of Different Herbicides on *Spartina alterniflora*. *Ecological Indicators* 154: 110824, https://doi.org/10.1016/j.ecolind.2023.110824

Wang ZY, Zhang HY, He CQ, Liu C, Liang X, Chen XP (2019) Spatiotemporal variability in soil sulfur storage is changed by exotic *Spartina alterniflora* in the Jiuduansha Wetland, China. *Ecological Engineering* 133: 160–166, https://doi.org/10.1016/j.ecoleng.2019.04.014

Webb JW, Dodd JD, Koerth BH, Weichert AT (1984) Seedling Establishment of *Spartina alterniflora* and *Spartina patens* on Dredged Materials in Texas. *Gulf and Caribbean Research* 7: 325–329, https://doi.org/10.18785/grr.0704.03

Xia L, Geng QF, An SQ (2020) Rapid Genetic Divergence of an Invasive Species, *Spartina alterniflora*, in China. *Frontiers in Genetics* 11, https://doi.org/10.3389/fgene.2020.00284

Xiao DR, Zhang LQ, Zhu ZC (2009) A study on seed characteristics and seed bank of *Spartina alterniflora* at saltmarshes in the Yangtze Estuary, China. *Estuarine, Coastal and Shelf Science* 83: 105–110, https://doi.org/10.1016/j.ecss.2009.03.024

Xiao DR, Zhang LQ, Zhu ZC (2010) The range expansion patterns of *Spartina alterniflora* on salt marshes in the Yangtze Estuary, China. *Estuarine, Coastal and Shelf Science* 88: 99–104, https://doi.org/10.1016/j.ecss.2010.03.015

Xiao K, Li HL, Wilson AM, Xia YQ, Wan L, Zheng CM, Ma Q, Wang CY, Wang XS, Jiang XW (2017) Tidal groundwater flow and its ecological effects in a brackish marsh at the mouth of a large sub-tropical river. *Journal of Hydrology* 555: 198–212, https://doi.org/10.1016/j.jhydrol.2017.10.025

Xiao Q, Zheng HL, Ye WJ, Chen Y, Zhu Z (2005) Effects of waterlogging on growth and physiology of *Spartina alterniflora*. *Chinese Journal of Ecology* 24: 1025–1028, https://doi.org/CNKI:SUN:STXZ.0.2005-09-009

Xiao Y, Tang JB, Qing H, Zhou CF, Kong WJ, An SQ (2011) Trade-offs among growth, clonal, and sexual reproduction in an invasive plant *Spartina alterniflora* responding to inundation and clonal integration. *Hydrobiologia* 658: 353–363, https://doi.org/10.1007/s10750-010-0505-3

Xie BH, Han GX, Qiao PY, Mei BL, Wang Q, Zhou YF, Zhang AF, Song WM, Guan B (2019) Effects of mechanical and chemical control on invasive *Spartina alterniflora* in the Yellow River Delta, China. *PeerJ* 7: e7655, https://doi.org/10.7717/peerj.7655

Xie T, Wang Q, Ning ZH, Chen C, Cui BS, Bai JH, Shi W, Pang B (2021) Artificial modification on lateral hydrological connectivity promotes range expansion of invasive *Spartina alterniflora* in salt marshes of the Yellow River delta, China. *Science of The Total Environment* 769: 144476, https://doi.org/10.1016/j.scitotenv.2020.144476

Xin Y, Zhou CY, Wang L, Liu JE, Li XZ (2021) The Evaluation of an Ecological Engineering System for the Utilization of *Spartina alterniflora* in Chongming Dongtan. *Journal of Ecology and Rural Environment* 37: 1394–1403, https://doi.org/10.19741/j.issn.1673-4831.2020.0751

Xu, GW, Zhuo, RZ, Cao, H, Li, XG (1989) Annual Changes of Biomass of *Spartina alterniflora* and the Relationships Between Biomass and Tidal Land Habits. *Chinese Journal of Plant Ecology* 13: 230–235

Xu WW, Wang GX, Liu JE, Chen ZY, Hang ZQ, Wang H (2014) Two reproductive mode of *Spartina alterniflora* on coastal wetland of North Jiangsu. *Acta Ecologica Sinica* 34: 3839–3847, https://doi.org/10.5846/stxb201212041739

Xu X, Zhou CH, He Q, Qiu SY, Zhang Y, Yang J, Li B, Nie M (2022) Phenotypic plasticity of light use favors a plant invader in nitrogen-enriched ecosystems. *Ecology* 103: e3665, https://doi.org/10.1002/ecy.3665

Xue L, Li XZ, Zhang Q, Yan ZZ, Ding WH, Huang X, Ge ZM, Tian B, Yin QX (2018) Elevated salinity and inundation will facilitate the spread of invasive *Spartina alterniflora* in the Yangtze River Estuary, China. *Journal of Experimental Marine Biology and Ecology* 506: 144–154, https://doi.org/10.1016/j.jembe.2018.06.008

Yang W, Jeelani N, Leng X, Cheng XL, An SQ (2016) *Spartina alterniflora* invasion alters soil microbial community composition and microbial respiration following invasion chronosequence in a coastal wetland of China. *Scientific Reports* 6: 26880, https://doi.org/10.1038/srep26880

Yuan L, Zhang LQ, Xiao DR, Huang HM (2011) The application of cutting plus waterlogging to control *Spartina alterniflora* on saltmarshes in the Yangtze Estuary, China. *Estuarine, Coastal and Shelf Science* 92:103–110, https://doi.org/10.1016/j.ecss.2010.12.019

Yuan Y, Li DZ, Wang KY (2014) Research Progress in Mutual Invasion of *Phragmites australis* and *Spartina alterniflora* Communities. *Wetland Science* 12: 533–538, https://doi.org/10.13248/j.cnki.wetlandsci.2014.04.018

Zhang BH, Han S, Wang J, Liu YQ, Yu YP (2020). Landscape Simulation of Coastal Wetlands to Support Ecological Restoration: A Case Study of the Jiangsu Yancheng Wetland Rare Birds National Nature Reserve. *Journal of Hydroecology* 41: 41–47, https://doi.org/10.15928/j.1674-3075.2020.04.006

Zhang J, Ju RT, Pan H, Pan SF, Wu J (2019) Enemy-free space is important in driving the host expansion of a generalist herbivore to an inferior exotic plant in a wetland of Yangtze Estuary. *Biological Invasions* 21: 547–559, https://doi.org/10.1007/s10530-018-1845-6

Zhang P, Neher DA, Li B, Wu JH (2017) The Impacts of Above- and Belowground Plant Input on Soil Microbiota: Invasive *Spartina alterniflora* Versus Native *Phragmites australis*. *Ecosystems* 21: 469–481, https://doi.org/10.1007/s10021-017-0162-8

Zhang XM, Tang YP, Song WY (2014) Study of Growth Characteristics of *Spartina alterniflora* Loisel to Different Water Level Gradient in Constructed Wetland. *Haihe Water Resources* 19: 54–56, https://doi.org/10.3969/j.issn.1004-7328.2014.03.019

Zhang YM, Wang Q, Lu M, Jia X, Geng YP, Li B (2008) Variation and phenotypic plasticity in life history traits of *Spartina alterniflora* along the east coast of China. *Biodiversity Science* 16: 462, https://doi.org/10.3724/SP.J.1003.2008.08108

Zhang YH, Ding WX, Luo JF, Donnison A (2010) Changes in soil organic carbon dynamics in an Eastern Chinese coastal wetland following invasion by a $C_4$ plant *Spartina alterniflora*. *Soil Biology and Biochemistry* 42, 1712–1720, https://doi.org/10.1016/j.soilbio.2010.06.006

Zhao CJ, Deng ZF, Zhou CF, Guan BH, An SQ, Chen L, Lu XM (2008) Effects of nitrogen availability and competition on leaf characteristics of *Spartina alterniflora* and *Phragmites australis*. *Chinese Journal of Plant Ecology* 32: 392–401, https://doi.org/10.3773/j.issn.1005-264x.2008.02.017

Zhao GQ, Zhang LQ, Liang X (2005) A comparison of photosynthetic characteristics between an invasive plant *Spartina alterniflora* and an indigenous plant *Phragmites australis*. *Acta Ecologica Sinica* 25: 1604–1611, https://doi.org/10.3321/j.issn:1000-0933.2005.07.011

Zhao H, Yang W, Xia L, Qiao YJ, Xiao Y, Cheng XL, An SQ (2015b) Nitrogen-Enriched Eutrophication Promotes the Invasion of *Spartina alterniflora* in Coastal China. *CLEAN - Soil Air Water* 43: 244–250, https://doi.org/10.1002/clen.201300844

Zhao JH, Zhang XB, Shen MY, Wang YD, An SQ (2020a) Prediction of Potential Areas of Surviving Smooth Cordgrass (*Spartina alterniflora*) in China. *Wetland Science and Management* 16: 42–46, https://doi.org/10.3969/j.issn.1673-3290.2020.03.11

Zhao XJ, Liu XY, Gong L, Deng ZZ, Bai JD, Li JS, Zhao CY (2014) Control of *Spartina alterniflora* by integrated technique of mowing plus shading. *Chinese Journal of Ecology* 33: 2714–2719, https://doi.org/10.13292/j.1000-4890.2014.0235

Zhao XJ, Zhao CY, Liu XY, Gong D, Deng ZZ, Li JS (2015a) Growth characteristics and adaptability of *Spartina alterniflora* in different latitude area along China coast. *Ecological Science* 34: 119–128, https://doi.org/10.14108/j.cnki.1008-8873.2015.01.018

Zhao XJ, Li JS, Liu XY, Gong L, Zhao CY (2017) Combined effects of mowing and shading on growth and survival of *Spartina alterniflora*. *Guihaia* 37: 303–307, https://doi.org/10.11931/guihaia.gxzw201604005

Zhao YJ, Qing H, Zhao CJ, Zhou CF, Zhang WG, Xiao Y, An SQ (2009) Phenotypic Plasticity of *Spartina alterniflora* and *Phragmites australis* in Response to Nitrogen Addition and Intraspecific Competition. *Hydrobiologia* 637: 143–155, https://doi.org/10.1007/s10750-009-9992-5

Zhao ZY, Xu Y, Yuan L, Li W, Zhu XJ, Zhang LQ (2020b) Emergency control of *Spartina alterniflora* re-invasion with a chemical method in Chongming Dongtan,China. *Water Science and Engineering* 13: 24–33, https://doi.org/10.1016/j.wse.2020.03.001

Zhao ZY, Yuan L, Li W, Tian B, Zhang LQ (2020c) Re-invasion of *Spartina alterniflora* in restored saltmarshes: Seed arrival, retention, germination, and establishment. *Journal of Environmental Management* 266: 110631, https://doi.org/10.1016/j.jenvman.2020.110631

Zheng J, Liu JF, Wu ZY, Hong W, He ZS, Lan YS, Liu SD (2017) Soil microbial community of mangrove forests and its responses to the invasion of *Spartina alterniflora* in the Minjiang River Estuary. *Acta Ecologica Sinica* 37: 7293–7303, https://doi.org/10.5846/stxb201608141667

Zhou JH, Ju RT, Li B, Wu JH (2017) Responses of soil biota and nitrogen availability to an invasive plant under aboveground herbivory. *Plant and Soil* 415: 479–491, https://doi.org/10.1007/s11104-017-3179-z

Zhou T, Liu SC, Feng ZL, Liu G, Gan Q, Peng SL (2015) Use of exotic plants to control *Spartina alterniflora* invasion and promote mangrove restoration. *Scientific Reports* 5: 1–13, https://doi.org/10.1038/srep12980

Zhu XD, Meng LX, Zhang YH, Weng QH, Morris J (2019) Tidal and meteorological influences on the growth of invasive *Spartina alterniflora*: evidence from UAV remote sensing. *Remote Sensing* 11: 1208, https://doi.org/10.3390/rs11101208

Zhu ZH, Liu JX, Wang XA (2007) Review of phenotypic plasticity and hierarchical selection in clonal plants. *Chinese Journal of Plant Ecology* 31: 588–598, https://doi.org/10.17521/cjpe.2007.0075

Zhu ZC, Zhang LQ, Xiao DR (2011) Seed production of *Spartina alterniflora* and its response of germination to temperature at Chongming Dongtan, Shanghai. *Acta Ecologica Sinica* 31: 1574–1581, https://doi.org/10.3724/SP.J.1077.2011.00311