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Geographical Variation and Influencing Factors of *Spartina alterniflora* Expansion Rate in Coastal China

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Abstract: Biological invasion poses a huge threat to ecological security. *Spartina alterniflora* was introduced into China in 1979, and its arrival corresponded with negative effects on native ecosystems. To explore geographical variation of its expansion rate in coastal China, we selected 43 *S. alterniflora* sites from Tianjin Coastal New Area to Beihai. The area expansion rate, expansion rate paralleling and vertical to the shoreline were analysed based on Landsat images and field survey in 2015. Simple Ocean Data Assimilation (SODA) and climate data were collected to statistically analyse the influential factors of expansion rate. Results showed that significant difference of *S. alterniflora* area expansion rate among different latitude zones ($P < 0.01$), increasing from 6.08% at southern (21°N–23°N) to 19.87% in Bohai Bay (37°N–39°N) along latitude gradient. There was a significant difference in expansion rate vertical to shoreline in different latitude zones ($P < 0.01$) with the largest occurring in Bohai Bay (256 m/yr, 37°N–39°N), and showed an decreasing tendency gradually from north to south. No significant difference and latitudinal clines in expansion rate paralleling to shoreline were observed. Expansion rate had significant negative correlation with mean seawater temperature, the lowest seawater temperature, current zonal velocity and meridional velocity and presented a reducing trend as these biotic factors increased; however, they were not significantly correlated with the highest seawater temperature and mean seawater salinity. We identified significant correlations between expansion rate and annual mean temperature, the lowest temperature in January and annual precipitation, but there was little correlation with annual diurnal difference in temperature and the highest temperature in July. The rapid expansion rate in high-latitude China demonstrated a higher risk of potential invasion in the north; dynamic monitoring and control management should be established as soon as possible.
Keywords: geographical variation; biological invasion; *Spartina alterniflora*; expansion rate; coastal wetlands; China

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1 Introduction

Biological invasion has adversely affected ecosystem functioning and biodiversity, posing a serious threat to human health (Elton, 1958), and has been recognized as a global environmental problem (Vitousek et al., 1996; Gurevitch and Padilla, 2004; Drenovsky et al., 2012; Strong and Ayres, 2016). *Spartina alterniflora* is a common dominant salt-marsh grass originally distributed along the Atlantic and Gulf coasts of North America. To date it has spread in many of the world's coastal areas by intentional introduction and natural dispersal, including the Pacific coast of the United States (Callaway and Josselyn, 1992; Feist and Simenstad, 2000), the European coast (Baumel et al., 2003; Campos et al., 2004), New Zealand (Pattridge, 1987), China (An et al.,

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2007) and South Africa (Adams, 2016). *S. alterniflora* was introduced in China in 1979 for ecological engineering (Chung, 2006). It has established well and spread extensively along China's coastal areas from Liaoning Province to Hainan Province, forming the largest *Spartina* distribution area in the world (Zhang et al., 2017). Its strong adaptive and reproductive ability allows *S. alterniflora* to expand rapidly (Levin et al., 2006; Li et al., 2009; Zhang et al., 2012), forming a tall, dense community and causing various negative influences on local coastal ecosystems (Daehler and Strong, 1996; Hedge et al., 2003; An et al., 2007), In England, wide expansion of *S. alterniflora* in open tideland has directly increased the emigration and mortality rate of *Calidris alpina* (Callaway and Josselyn, 1992). In Willapa Bay, Washington, USA, its invasion caused a 16%–20% reduction in habitat for breeding and stopover of aquatic birds in winter (Grevstad et al., 2003). In the Yangtze Estuary of China, the introduction and spread of *S. alterniflora* has resulted in a decrease in *Scirpus mariqueter* communities, a significant food resource for rare migrant birds (Chen et al., 2004). Some studies also suggested that *S. alterniflora* invasion has altered benthic community composition and diversity (Luiting et al., 1997; Neira et al., 2006) and impacted nutrient cycling processes (Enrefeld, 2003; Gao et al., 2018), endophytic bacterial community structures and diversity (Liao et al., 2018) and the soil ecosystem of coastal wetlands (Chen et al., 2007; Adams et al., 2012; Yang et al., 2016). Liu et al. (2019) revealed that seven national nature reserves in China had invaded by *S. alterniflora* at present. The rapid and extensive expansion of *S.alterniflora* and its negative effects has attracted public attention in China. Clarifying its geospatial expansion patterns is crucial for prediction of potential distribution and scientific management in the future.

The remote sensing technique is an effective tool to elucidate changing vegetation patterns associated with broad-scale inaccessible plant invasions (Zhang et al., 1997; Bancroft and Smith, 2001; Cohen and Goward, 2004; Bradley and Mustard, 2006; Murphy et al., 2013). Based on field observation and 2000 infrared photographs (1:6000 scale), Ayres et al. (2004) mapped community distribution and expansion of non-native *Spartina* and hybrids in San Francisco Bay, California, USA. The spread history of *S. alterniflora* in Willapa Bay, Washington, USA, over the last 100 years has been analysed using remotely sensed images and some historical materials (Civille et al., 2005). Numerous studies on *S. alterniflora* expansion were conducted with the help of 3S (GIS, GPS and RS) technologies in China (Zuo et al., 2012; Lu and Zhang, 2013). However, these previous studies mainly concentrated on a smaller scale, only representing a certain estuary or a coastal wetland type, such as the Chongming Dongtan National Nature Reserve, Shanghai (Huang et al., 2007), Jiuduansha Wetland, Shanghai (Lin et al., 2015) and Yueqing Bay, Wenzhou, Zhejiang Province (Wang et al., 2015). There still lacks research about the geographical variation in expansion rate of *S. alterniflora* and its influential factors across latitudinal gradients.

Environmental factors such as atmospheric temperature, salinity and hydrodynamic property were found to affect *S. alterniflora* expansion pattern (Idazkrin and Bortolus, 2011; Cao et al., 2014; Tang et al., 2014). The experiment in Atlantic coast of South America found that frost formation by cold temperature produced a negative effect on *S. alterniflora*, and this prevent it from expanding toward high-latitude salt marshes (Idazkrin and Bortolus, 2011). Liu et al. (2016) identified correlations between growth traits of *S. alterniflora* and abiotic conditions such as mean annual temperature, growing degree days, tidal range and soil nitrogen content, and all these may influence its expansion range and rate. Previous study has shown that elevated flooding frequencies promoted the generation of new *S. alterniflora* ramets, thus accelerated expansion rate (Xue et al., 2018). Meanwhile the study in Zhangjiang estuarine wetland showed the spatial and temporal heterogeneity of *S. alterniflora* was controlled by tidal inundation and meteorological regimes such as temperature and precipitation (Zhu et al., 2019). In addition, the reclamation also significantly reduced the expansion rate of *S. alterniflora* with changes in water and salt conditions (Liu et al., 2019). Although *S. alterniflora* expansion rate have been characterized by many empirical studies, most of these studies concentrated on expansion at regional scale. And the results from these plot-scale studies might not accurately reflect actual expansion variation of *S. alterniflora* at the large scale.

This study, based on a combination of field investigation and multispectral remote sensing images from Landsat satellites, analysed: 1) the expansion rate of *S. alterniflora* at 43 sites over a latitudinal gradient of about 0.5° from Tianjin Coastal New Area (38°59′N) to Beihai (21°34′N); and 2) the main physical factors influencing the expansion rate of *S. alterniflora* in China, based on related marine and atmospheric environmental data. And we aimed to explore the geographical variation and influential factors of *S.alterniflora* expansion rate along China's coastal area. Our results could provide valuable information for predicting the further spread of *S. alterniflora* in China, and will assist decision making for local organizations concerned with effectively controlling and managing this invasive plant in the future.

2 Materials and Methods

2.1 Study area

The total distribution area of *S.alterniflora* in China reached 554 km^2 and ranged between the latitude 19°46′N and 40°47′N along coastal wetlands of China (Zhang et al., 2017) (Fig. 1). The area spans three climatic zones: warm temperature zone, tropical zone and subtropical zone. The meteorological conditions were obviously different in different *S. alterniflora* area. Annual mean temperature is between 7℃ and 25℃, with a mean temperature of the coldest and warmest months being –9℃–19℃ in January and 21℃–29℃ in July, respectively. Mean annual precipitation is 495–2174 mm. Annual mean seawater temperature is 12℃–26℃, Mean annual seawater salinity is 25‰–34‰. The concentration of total C, N and P were 0.064%–2.589%, 0.004%–0.186% and 108.76–817.22 mg/g, respectively. And pH in the habitat soil was 6.0–8.5, decreasing gradually with latitude. *S. alterniflora* always grow in coastal intertidal zone, especially in muddy coast, coastal estuary, delta region and silt coast. Lots of native plants, *Phragmites australis*, *S. mariqueter*, *Kandelia candel*, dominated the marshlands before *S.alterniflora* was introduced. At present, there are mainly single-dominant *S. alterniflora* communities accompanied by *P. australis* in the north of the Yangtze Estuary, *S. mariqueter*, *Suaeda salsa* and *Cyperus malaccensis* in the south.

2.2 Image data and processing

Landsat satellites have provided images of the world since the 1970s and have been widely used to study plant invasion (Huang and Zhang, 2007; Gavier-Pizarro et al., 2012; Roy et al., 2014; Wang et al., 2015). In this study, Landsat5 TM, ETM+ and Landsat8 Opertational Land Imager (OLI) imagery, covering the coastal area of China during 1980–2015, was used. Forty-three geographical locations were selected along coastal China at about 0.5 latitudinal degree intervals to analyse the expansion rate of *S. alterniflora* across latituninal gradients (Table 1). These locations ranged from Tianjin Coastal New Area, Tianjin (38°59′N) in the north to Beihai, Guangxi (21°34′N) in the south and represented the typical distribution area of *S. alteniflora* in China (Zhang et al., 2017, Liu et al., 2018), and their geography locations are described in detail in Table1. As the distribution area in Liaoning was small and has hardly changed in decades. Similarly, there were few left in Hainan after immediate removal and mangrove recovery as it was firstly discovered in 2015. In result, *S. alteniflora* sits in these provinces were not included in this study.

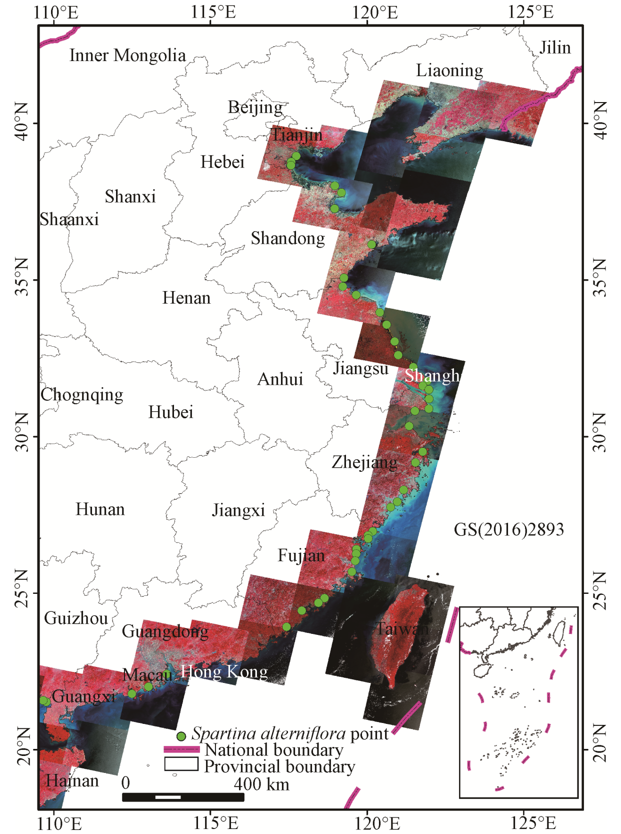

Fig. 1 Landsat8 Operational Land Imager images and distribution of *S.alterniflora* locations along coastal China

The Landsat data were downloaded freely from the United States Geological Survey (USGS) Global Visualization Viewer (http://glovis.usgs.gov/). To accurately distinguish *S.alterniflora* from mixed salt marsh vegetation communities, images acquired in spring and summer

Table 1 The geography information of *S. alterniflora* samples along coastal China

ID	Location	Latitude (N)	Longitude (E)	Province/Municipality	Location
1	Beitangkou	38°57′36″	117°44′19″	Tianjin	Binhai New Area
2	Beidagang	38°46′10″	117°34′45″	Tianjin	Binhai New Area
3	Mapengkou	38°39′45″	117°34′10″	Tianjin	Binhai New Area
4	Wuhaozhuang	38°00′33″	118°58′16″	Shandong	Binzhou
5	Yellow River Delta	37°47′17″	119°10′53″	Shandong	Dongying
6	Shouguang	37°16′44″	118°57′54″	Shandong	Weifang
7	Jiaozhou Bay	36°08′00″	120°08′47″	Shandong	Qingdao
8	Ganyu	35°04′11″	119°15′45″	Jiangsu	Lianyungang
9	Linhong River Estuary	34°47′29″	119°13′28″	Jiangsu	Lianyungang
10	Guyuan	34°31′20″	119°39′07″	Jiangsu	Lianyungang
11	Binhai	33°57′55″	120°24′31″	Jiangsu	Yancheng
12	Sheyang River Estuary	33°34′24″	120°37′29″	Jiangsu	Yancheng
13	Dafeng	33°02′8″	120°52′52″	Jiangsu	Yancheng
14	Yangkou Town	32°36′07″	120°59′32″	Jiangsu	Nantong
15	Bingfang Town	32°12′57″	121°28′24″	Jiangsu	Nantong
16	Qidong	31°46′24″	121°55′07″	Jiangsu	Nantong
17	North Beach of Chongming	31°37′16″	121°46′24″	Shanghai	Chongming
18	East Beach of Chongming	31°29′58″	121°58′30″	Shanghai	Chongming
19	Jiuduansha	31°12′13″	121°58′35″	Shanghai	Pudong New Area
20	Nanhui Wetland	30°53′15″	121°58′16″	Shanghai	Pudong New Area
21	JinhuiPort	30°49′14″	121°31′42″	Shanghai	Fengxian
22	Hangzhou Bay	30°20′00″	121°20′35″	Zhejiang	Ningbo
23	Xinagshan Port	29°31′02″	121°46′24″	Zhejiang	Ningbo
24	Sanmen Bay	29°10′14″	121°32′27″	Zhejiang	Ningbo
25	Yueqing Bay	28°17′54″	121°10′03″	Zhejiang	Wenzhou
26	Oujiang Estuary	27°55′09″	120°57′42″	Zhejiang	Wenzhou
27	Feiyunjiang Estuary	27°44′44″	120°45′09″	Zhejiang	Wenzhou
28	Lisan Bay	26°58′34″	120°10′53″	Fujian	Ningde
29	Funing Bay	26°50′40″	120°01′50″	Fujian	Ningde
30	Sandu Bay	26°44′33″	120°02′11″	Fujian	Ningde
31	Luoyuan Bay	26°24′09″	119°39′39″	Fujian	Fuzhou
32	Aojiang Estuary	26°15′33″	119°39′03″	Fujian	Fuzhou
33	Minjiang Estuary	26°02′02″	119°37′17″	Fujian	Fuzhou
34	Fuqing Bay	25°41′01″	119°30′56″	Fujian	Fuzhou
35	Quanzhou Bay	24°50′21″	118°38′34″	Fujian	Quanzhou
36	Anping	24°41′20″	118°26′41″	Fujian	Quanzhou
37	Jiulong River Estuary	24°26′32″	117°54′59″	Fujian	Zhangzhou
38	Zhangjiang Estuary	23°55′25″	117°25′57″	Fujian	Zhangzhou
39	Qiao Island	22°24′57″	113°36′33″	Guangdong	Zhuhai
40	Tanjiang Estuary	22°00′38″	113°01′20″	Guangdong	Jiangmen
41	Zhenhai Bay	21°47′14″	112°29′42″	Guangdong	Jiangmen
42	Shankou Mangrove Reserve	21°31′36″	109°45′38″	Guangxi	Beihai
43	Dandou Sea	21°34′34″	109°39′37″	Guangxi	Beihai

in northern coastal areas and those in autumn and winter in the south were normally used. We also tried to select scenes at lower tide levels and with less than 10% cloud cover.

A maximum likelihood supervised classification method was employed using standard false-colour composites of Landsat8 images to obtain the current distribution and initial distribution at the time of earliest emergence of *S. alterniflora* at each location.

To assist with remote sensed imagery interpretation and verification, we performed a field inventory at the 43 selected geographical locations in June and July 2015. At each location, five to 10 sites were randomly selected. Some were located in single, dense community patches; others were located at the junctions of different communities. The GPS coordinate locations and plant compositions were recorded.

As *S. alterniflora* always grows in intertidal zones (Wang et al., 2006), we built a mask that covered intertidal mudflats to facilitate image interpretation. According to its habitat traits, the mask was defined as external area of varied embankment boundary. Four interpretation classes were defined in the supervised classification method: *S. alterniflora*, mudflat, open water and other coastal vegetation. Half of the field sites were used as training samples and the remainder were used to assess the accuracy of the *S. alterniflora* distribution maps. The classification results based on a maximum likelihood supervised classification method with ENVI5.1 software (Exelis Visual Information Solutions Institute 2013) were then visually revised and analysed statistically. Spatial analysis of the *S. alterniflora* map was performed in ArcGIS10.2.1 (ESRI 2013).

2.3 Expansion rate analysis

Three expansion traits of *S. alterniflora* were analysed: annual average area growth rate, expansion rate paralleling to the shoreline and it vertical to the shoreline. Eq. (1) was used to calculate the annual average area growth rate (P):

$$P = \sqrt[n]{\frac{A_n}{A_0}} - 1 \tag{1}$$

where A_n represents the distribution area of *S. alterniflora* in year n at each location, A_0 is the initial area at the time of the earliest emergence of *S. alterniflora* there.

S. alterniflora usually exhibits a lateral expansion pattern vertical to the shoreline, and long-distance expansion paralleling to the shoreline. The neighbour measurement method proposed by Andow et al. (1993) was used to calculate the linear expansion rate of *S. alterniflora* at each location. Ideally, the invasive plants would expand out radially from the initial establishment population when they enter into a new region, and then form a circular distribution range (Hengeveld, 1989). However, the expansion would be disturbed by geographical barriers and human activity and usually formed an irregular distribution. This must be taken into account in the linear expansion rate measuring method (Shigesada and Kawasaki, 1997). In the study, the expansion distance in the neighbour measurement method was obtained by calculating the average distance increment of geographical boundaries in adjacent asymmetrical regions (Δr) following the formula in Eq. (2) (Shigesada and Kawasaki, 1997):

$$\Delta r = \sqrt[2]{\left(\Delta r_{\min}{}^2 + \Delta r_{\max}{}^2\right)/2} \tag{2}$$

where $\Delta r_{\min}$ and $\Delta r_{\max}$ represent the nearest and farthest distances from the original geographical boundary to the current boundary of *S. alterniflora* distribution, respectively. Based on the neighbour measurement method, the linear expansion rate (V) is described using Eq. (3) (Shigesada and Kawasaki, 1997):

$$\begin{aligned} V_x &= \sqrt[2]{\left(D_{x\min}{}^2 + D_{x\max}{}^2\right)/2}\Big/t \\ V_y &= \sqrt[2]{\left(D_{y\min}{}^2 + D_{y\max}{}^2\right)/2}\Big/t \end{aligned} \tag{3}$$

where V_x and V_y represent the expansion rate vertical and parallel to the shoreline, respectively; $D_{x\min}$ and $D_{x\max}$ represent the shortest and farthest expansion distance of *S. alterniflora* patches vertical to the shoreline since they established in the location; $D_{y\min}$ and $D_{y\max}$ represent the shortest and farthest expansion distance parallel to the shoreline; and t is the number of years during which *S. alterniflora* has invaded the location.

2.4 Environmental data collecting and processing

In order to learn the relationship between the expansion rate of *S. alterniflora* and environmental factors, we obtained ocean and atmospheric environmental data for each location. The Simple Ocean Data Assimilation reanalysis dataset (SODA) (version 2.1.6) provided by

Carton et al. (2005) was used to analyse seawater features in the *S. alterniflora* habitat. The SODA dataset includes six global ocean variables in 40 vertical depths from the ocean surface with a horizontal resolution of 0.5° × 0.5°, and has monthly statistics data from January 1957 to December 2008. In this study, we focused on SODA's oceanic temperature, oceanic salinity, zonal velocity and meridional velocity on the ocean surface. For our study we selected the SODA dataset for 1 January 1979 to 31 December 2008 (360 mon), latitude 17.25°N–41.25°N and longitude 107.25°E–124.25°E (Fig. 2). The data were obtained freely from the International Research Institute for Climate and Society (IRI). We summarized the monthly statistics data by calculating annual average seawater temperature, annual highest seawater temperature, annual lowest seawater temperature, annual average seawater salinity, annual average seawater zonal velocity and annual average seawater meridional velocity. The seawater data at the 43 locations were retrieved from the nearest SODA data points to each location.

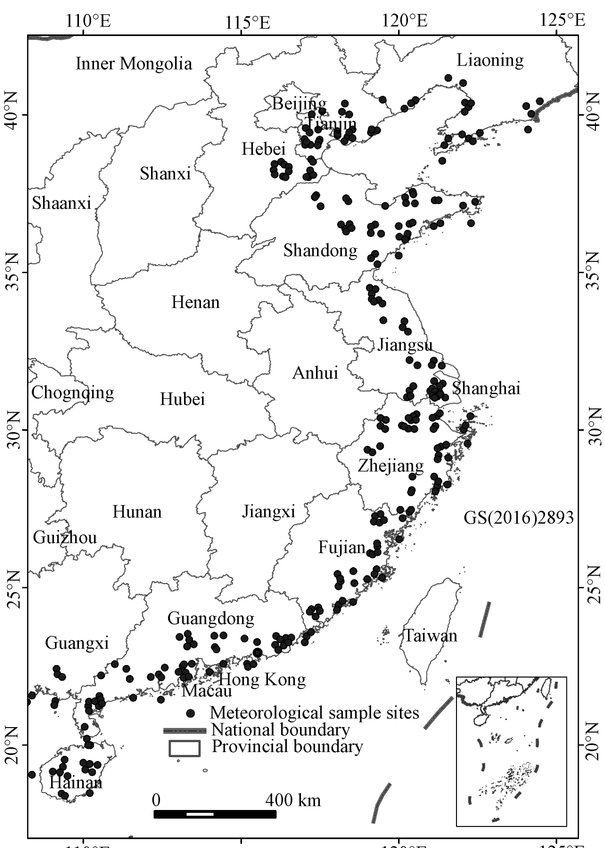

Fig. 2 Distribution map of sampling sites from SODA datasets along coastal China

Multi-year meteorological statistical data sets (1981–2010) from 285 weather observational stations along coastal China were used as our atmospheric environmental data source to analyse the influences of climate on the expansion rate of *S. alterniflora* (Fig. 3). Five climate variables were selected: annual mean temperature, annual precipitation, annual diurnal difference in temperature, the lowest temperature in January and the highest temperature in July. All the climate data were obtained from the China Meteorological Data Sharing Service System (http://data.cma.cn/) and the climate data at the selected 43 locations were retrieved from the nearest weather observational stations to each location selected.

3 Results

3.1 Geographical variation in the expansion rate along latitude

One-way ANOVA demonstrated a significant difference in the annual average area growth rate of *S. alterniflora*

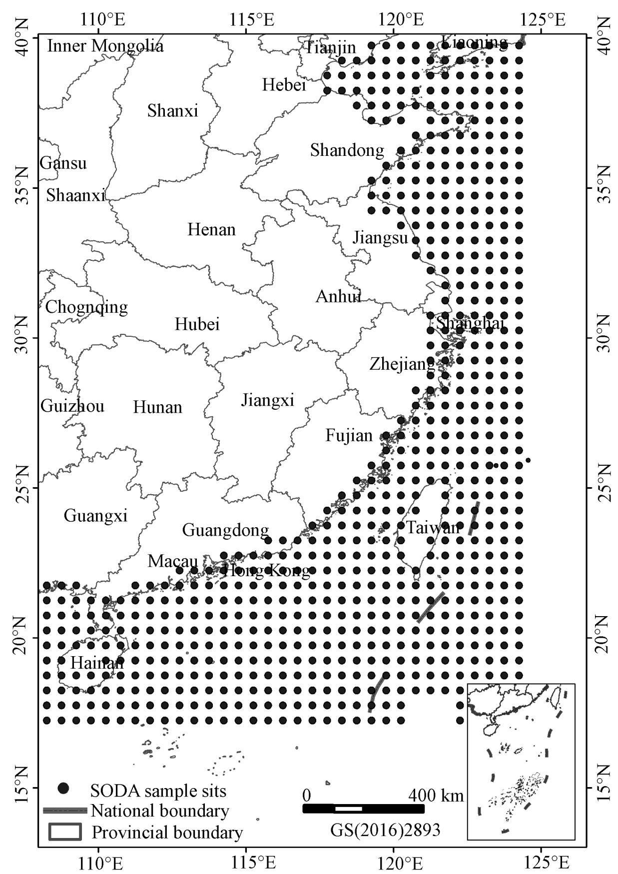

Fig. 3 Distribution map of sampling sites from China meteorological data sharing service system along coastal China

among different latitude zones ($F_{8,34}$ = 3.815, P = 0.003), increasing from 7.66% at southern coastal areas (21°N–23°N) to 19.87% at coastal areas in Bohai Bay (37°N–39°N) (Fig. 4). According to the regression analysis results, the expansion rate had a significant positive correlation with latitude and showed a gradually increasing tendency from south to north in China (Fig. 5). *S. alterniflora* expanded most rapidly at the New Coastal Area of Tianjin (38°46′10″N, 117°34′45″E) with an annual mean expansion rate of 31.6%.

The expansion rate paralleling to the shoreline was larger than it vertical to the shoreline, at 294 and 131 m/yr, respectively (Fig. 6). And the later showed significant difference in different latitude zones ($F_{8,34}$ = 2.381, P = 0.003) with the largest occurring in Bohai Bay (256 m/yr, 37°N–39°N) (Fig. 6). Regression results indicated that the expansion rate vertical to the shoreline

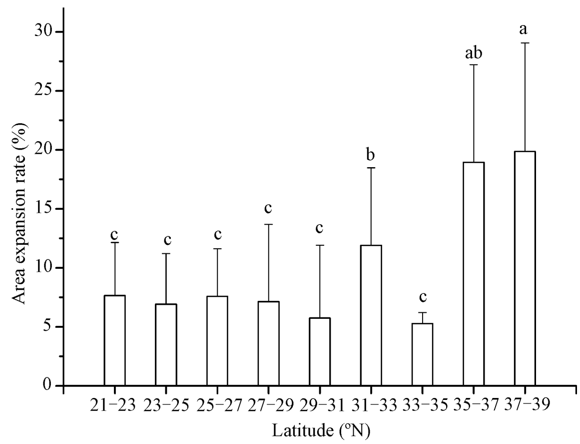

Fig. 4 Comparison of *Spartina alterniflora* areal annual expansion rate in different latitudinal gradients between 1990 and 2014. The different letters represent significant difference at the 0.05 level

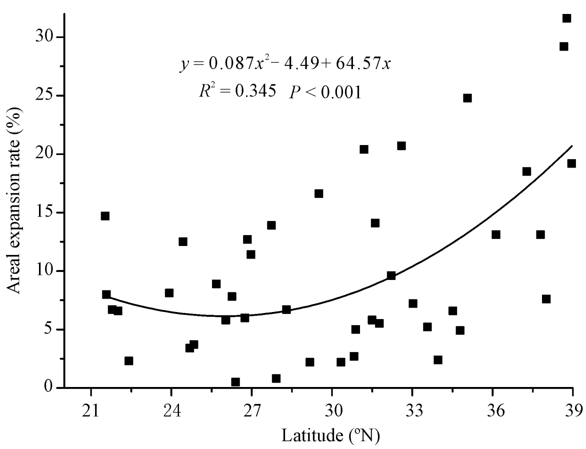

Fig. 5 Regression analysis of *Spartina alterniflora* areal annual expansion rate with latitude

also increased gradually from south to north, but no significant difference was observed in expansion rate paralleling to the shoreline (Fig. 7).

3.2 Relationship between expansion rate and environmental factors

The mean seawater temperature was between 10.42℃ and 28.16℃ along coastal China. The regression results indicated that area growth rate and expansion rate paralleling and vertical to the shoreline and vertical to the shoreline, had significant negative correlation with mean seawater temperature and the lowest seawater temperature (Fig. 8). However, they were not significant correlated with the highest seawater temperature. Similarly, there were no significant correlations between them and mean seawater salinity, which ranged from 29.6‰ to 34.8‰ along coastal China. There was only a small difference in current velocity among coastal areas in China, slightly higher in Guangdong and Taiwan.

The area expansion rate of *S. alterniflora* was influenced negatively by zonal velocity and meridional velocity (Fig. 9). The population area tended to increase faster in the north, where the current velocity was relatively slower. According to the regressive results being presented, the annual area growth rate was significantly related to annual mean temperature, the lowest temperature in January and annual precipitation, but it had little correlation with annual diurnal difference in temperature and the highest temperature in July (Fig. 10).

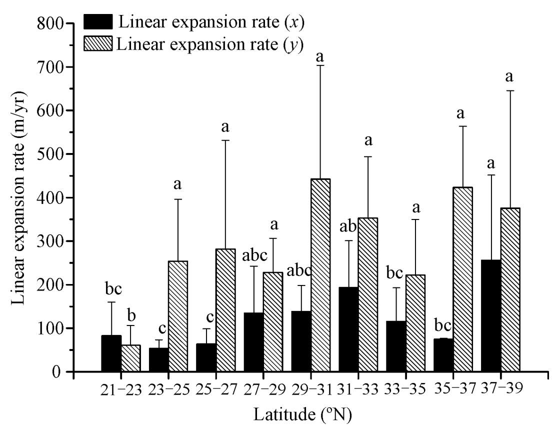

Fig. 6 Comparison of *Spartina alterniflora* linear expansion rate in different latitudinal gradients. The different letters represent significant difference at the 0.05 level linear expansion rate(x) and linear expansion rate (y) represents *Spartina alterniflora* linear expansion rate vertical to shoreline and paralleling to shoreline, respectively

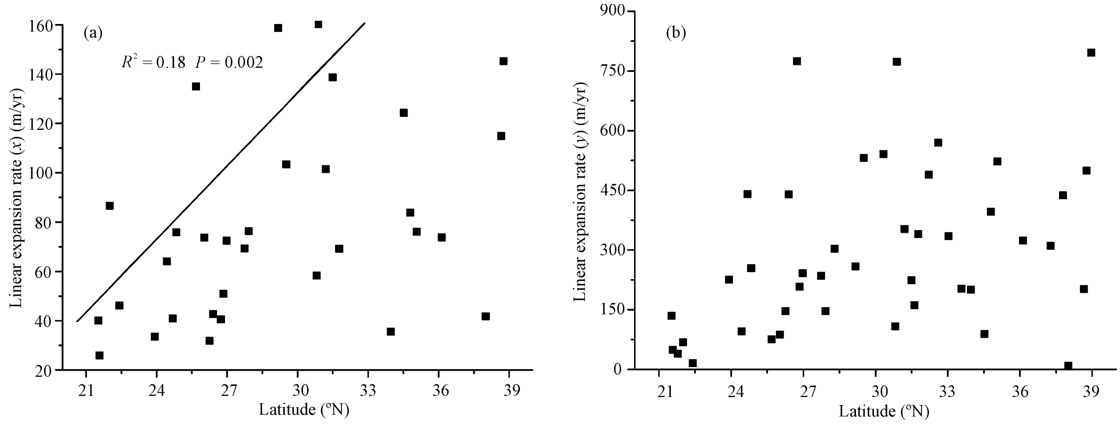

Fig. 7 Regression analysis of *Spartina alterniflora* linear expansion rate with latitude: (a) linear expansion rate vertical to shoreline; (b) linear expansion rate paralleling to shoreline

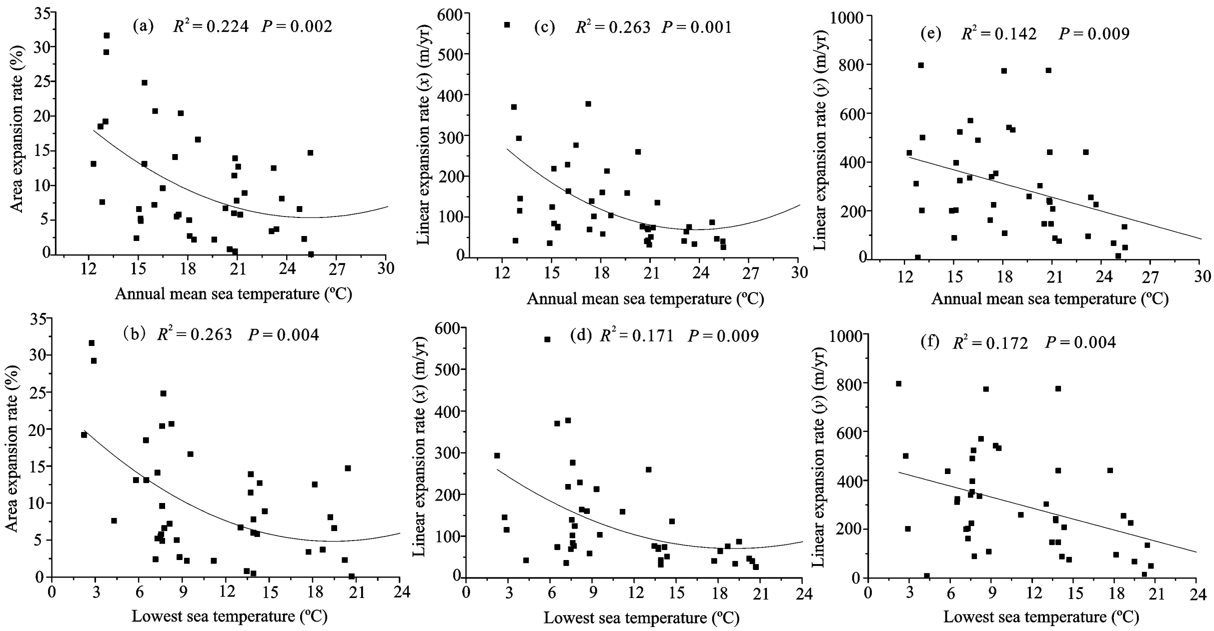

Fig. 8 Regression analysis of *Spartina alterniflora* area expansion rate with seawater temperature: (a) area expansion rate with annual mean seawater temperature; (b) area expansion rate with the lowest seawater temperature; (c) linear expansion rate vertical to shoreline with annual mean seawater temperature; (d) linear expansion rate vertical to shoreline with the lowest seawater temperature; (e) linear expansion rate paralleling to shoreline with annual mean seawater temperature; (f) linear expansion rate paralleling to shoreline with the lowest seawater temperature

4 Discussion

4.1 Variation in the expansion rate along latitudinal gradient

We found that the expansion rate of *S. alterniflora* varied along a latitude gradient, and was relatively higher in the north than in the south. The annual average area growth rate was about 30% in the Tianjin Coastal area (37°N–39°N) (Fig. 11a), and it also reached 20% in the Ganyu tidal flat (35°N–37°N) (Fig. 11b) and Jiuduansha wetland (31°N–33°N) (Fig. 11c). The area increased only by 5% in the Dandou Sea (21°N–23°N) (Fig. 11d). Similarly, the expansion rate vertical to the shoreline was 256 m/yr in Tianjin (37°N–39°N), but was only 30 m/yr in the Zhangjiang Estuary (23°N–25°N) and 25 m/yr in the Dandou Sea (21°N–23°N). *S. alterniflora* distributions had a large latitude span, resulting in significant differences in environmental characteristics. So it is possible that environmental changes over a large scale, rather than genetic differentiation, affect population demographical characteristics (Bernik et al., 2016).

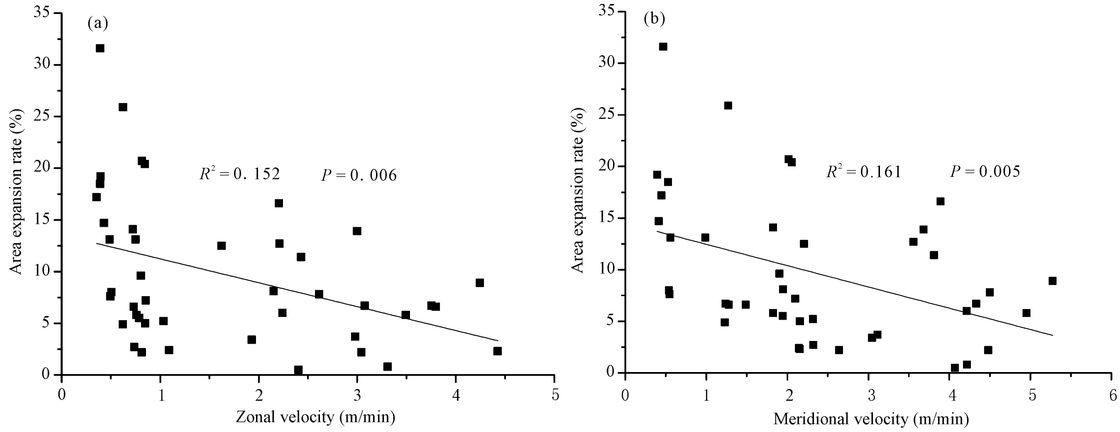

Fig. 9 Regression analysis of *Spartina alterniflora* expansion rate with current velocity: (a) area expansion rate with current zonal velocity; (b) area expansion rate with current meridional velocity

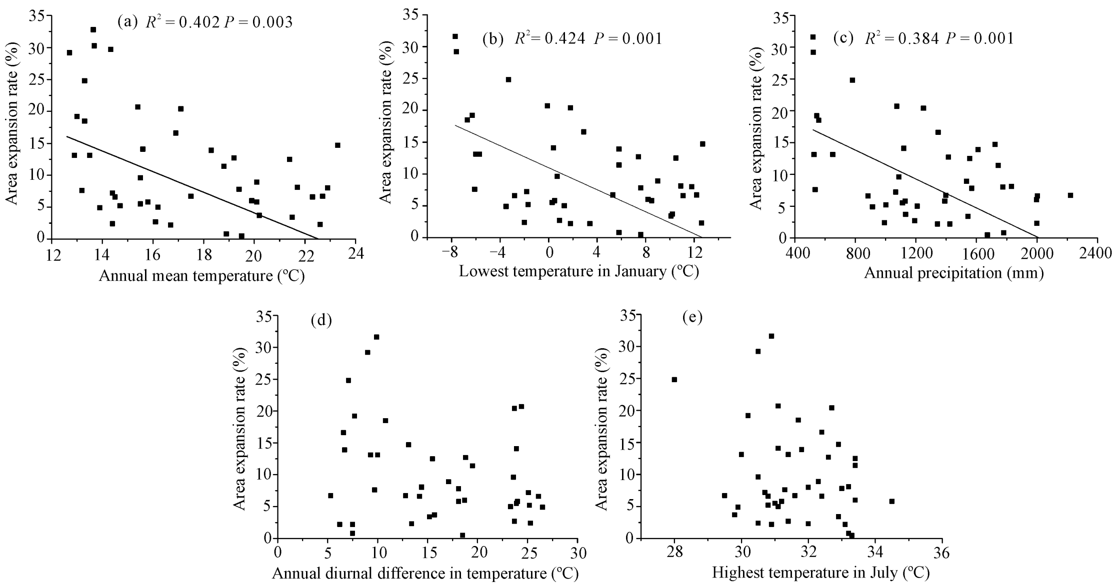

Fig. 10 Regression analysis of *Spartina alterniflora* area expansion rate with climate characteristics: (a) area expansion rate with annual mean temperature; (b) area expansion rate with the lowest temperature in January; (c) area expansion rate with the annual precipitation; (d) area expansion rate with the annual diurnal difference in temperature; (e) area expansion rate with the highest temperature in July

Similarly, recent studies also revealed rapid invasion rate of *S. alterniflora* in Coastal China (Mao et al., 2019), but its conclusion that Jiangsu Province had the largest expansion with an invasive rate of 715 ha/yr, followed by Zhejiang during the period of 1990–2015 is inconsistent with our findings. The difference of two calculating methods on annual expansion rate might mainly contribute to variable results. Lacking of data on geographical variation of expansion rate in its native and other invasive ranges means that comparisons can not be made between different geographical ranges.

Seed production is very important for population expansion of *S. alterniflora* (Daehler and Strong, 1994; Ayres et al., 2008; Xiao et al., 2010), the experiment of its vegetative growth and sexual reproduction along coastal China found that the seed set of *S. alterniflora* ranged from close to zero at low latitudes to over 80% at high latitudes along coastal China (Liu et al, 2016). And geographical variation in expansion speed of *S. alterniflora* along a latitude gradient may be attributed to abundant seed supply supporting new populations at high latitudes and the low at low latitudes.

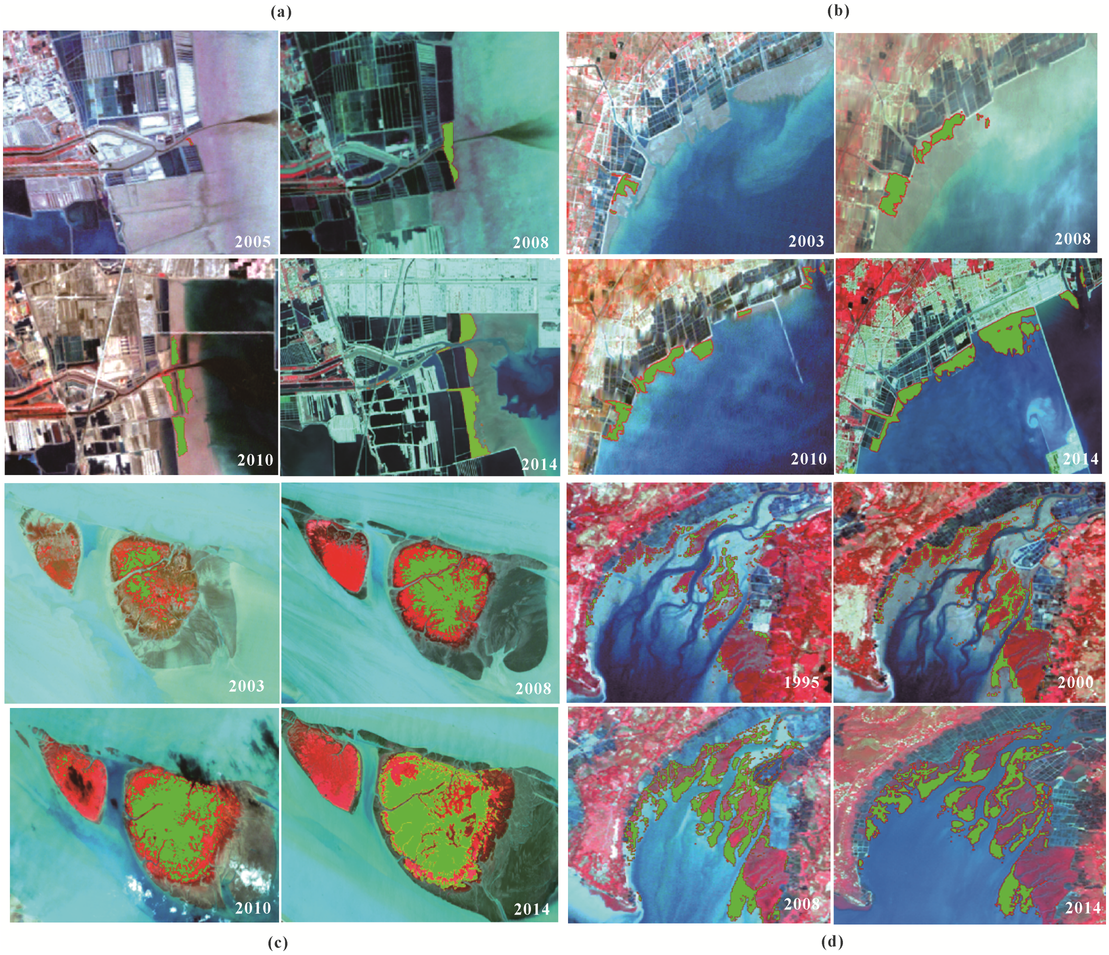

Fig. 11 Expansion process of *S. alterniflora* in Beidagang of Tianjin (a), Ganyu of Jiangsu Province (b), Jiuduansha of Shanghai (c) and Dandouhai of Guangxi (d)

An alternative explanation of the geographical variation may lie in seed viability. The seeds of *S. alterniflora* are generally dormant until the second spring, and they can reach maximum germinability after being soaked in seawater at 2℃–4℃ for 3 mon (Deng et al., 2006). Zhu et al. (2011) indicated that the germination percentage of *S. alterniflora* seeds under changed temperature was higher than under constant temperature. Both of these suggestions may explain the higher expansion rate of *S. alterniflora* in the north of China. Our results were consistent with the previous speculation that the high seed germinability and high cold tolerance were the main reasons for the rapid expansion of *S. alterniflora* in the New Coastal Area of Tianjin (Yuan et al., 2008). However, the lower seed bank reserves and the narrower tidal flat resulting from reclamation may both influence the expansion of *S. alterniflora* in the south of China (Liu et al., 2016). Additionally, in Guangxi province *S. alterniflora* always grows at the outer edge of mangrove forest, and the competition with taller mangrove trees also limits its expansion to the higher salt marsh.

Vegetative reproduction can effectively ensure the maintenance and regeneration of *S. alterniflora* populations (Pattridge, 1987; Davis et al., 2004; Adams et al., 2012). The mechanism by which it expands rapidly through the strong tiller ability of rhizome fragments, after setting down numerous seeds by sexual propagation, provide a possible explanation of its wide invasion in China. Study of vegetative propagation of *S. alterniflora* showed that rhizome length and vegetative propagation ability were all influenced by the soil organic matter in the habitat (Padgett and Brown, 1999). Liu et al. (2016) also found that the quantity of seed produced was positively correlated with soil nitrogen content. Our field survey showed that the soil organic matter was 1.72% in Tianjin, which is significantly higher than in other coastal regions in China, and this may contribute to the higher expansion rate vertical to shoreline in the New Coastal Area of Tianjin. However, we failed to find an obvious difference in expansion rate paralleling to the shoreline across latitudinal gradients. This may have been because of the uncertainty of the influencing factors, such as sea current and wind speed. Additionally, *S. alterniflora* in northern China was at an early stage of invasion, and the abundant wetland resource and suitable tidal flat elevation also provided favourable conditions for its rapid expansion (Davis et al., 2000; Zhang et al., 2004). So far, *S. alterniflora* population distribution is not extensive in northern China, but there is a high potential risk of invasion. Dynamic monitoring and management of this invasive plant, therefore, should be enhanced in the future.

4.2 Correlations between expansion rate and environmental factors

The correlation analysis indicated that the expansion rate of *S. alterniflora* was related to seawater temperature and current velocity, but not to seawater salinity. It was possible that seed germination rate was influenced by seawater temperature, leading to higher seed amounts and rapid rate of expansion in the north (Deng et al., 2006). The previous study found that intermediate current disturbance in the middle tidal zone was favourable to seed germination and nutrient supplement, promoting plant growth and seed production. In contrast, powerful and frequent tides in the low tidal zone inhibited seed germination, resulting in a decrease in seed production (Zhu et al., 2011).

Additionally, ocean currents can influence seed production and seedling growth, so affecting the expansion rate of *S. alterniflora*. Rapid expansion generally occurs in coastal areas with lower current velocity. Previous research has shown that sandy sediments and eroding beaches, coupled with strong tidal currents, are not good environments for seedlings to take root and then develop into bigger patches; however, silt sediment produced by slow tide currents favours the root formation of seedlings (Civille et al., 2005). The ocean current velocity map along coastal China showed that velocity was relatively slower in the north than in the south. This could explain the relatively slow expansion rate of *S. alterniflora* in the northern Yancheng mudflat and the Guangxi mudflat, where strong tidal currents exist, and the rapid spread in estuaries such as Sheyang Estuary, Yellow River Estuary and Yangtze River Estuary, where the intertidal zones experience slow tidal currents.

S. alterniflora has a high salt tolerance ranging between 10‰ and 60‰ (Pennings et al., 2003). The value of seawater salinity in our study was between 29‰ and 34‰, an optimum salinity range. This may explain why there was no significant correlation of the expansion rate of *S. alterniflora* with seawater salinity.

We found that the expansion rate of *S. alterniflora* was correlated negatively to lowest temperature in January, indicating that population expansion may not be limited by lower temperature, but could be affected by higher temperature in winter. It was also speculated that it could expand northward along coastal China. Additionally, Liu et al. (2016) found that there was hump-shaped correlation of plant height, stem diameter and aboveground biomass with abiotic conditions in China. Previous studies have also shown that *S. alterniflora* plant height and biomass increase with temperature along most of the native coastal area (Kirwan et al., 2009; Idaszkin and Bortolus, 2011). Whatever the mechanisms are, these findings demonstrated that there may be different geographical variation patterns between plant phenotypic characteristics and the expansion rate of *S. alterniflora*.

It has been proved that other factors can also have impacts on the expansion rate of *S. alterniflora*, such as human disturbances and geological conditions (Feist and Simenstad, 2000; Liu et al., 2014). Our results indicated that its distribution in Jiuduansha, Shanghai, expanded up to the current 2646 ha at an annual average areal increase rate of 20.4% since being planted in 1995. This was because of the southern training jetty project in the Yangtze River Estuary from 1997 to 2000, which clearly promoted sediment retention and silt deposition. On Qi'ao Island, Guangdong Province, large numbers of *Sonneratia apetala* were introduced into the mudflat initially covered by *Spartina alterniflora* in 2000; this resulted in a 75% decline in *S. alterniflora* in 2003 (Tang et al., 2007). Geological conditions also can influence its expansion rate. For example, decrease in freshwater input from the upper Yangtze River led to an increase in salinity, promoting competition between *S. alterniflora* and *P. australis* in northern Chongming Island (Li et al., 2009), and this brought rapid expansion of *S. alterniflora* the 2000s (Zhang et al., 2017). In contrast, *S. alterniflora* expanded slowly seaward in Wuhaozhuang Island (Shandong Province), showing approximately a 7% annual increase in cover, owing to restriction created by a shell beach. Shell accumulation also changed the soil properties for *S. alterniflora* in a saltmarsh of Wuhaozhuang Island, causing extensive damage to the species; a storm surge and hurricane accelerated the eventual death of the plants (Zhang et al., 2006).

4.3 Prediction and management implications

We found that *S. alterniflora* showed a tendency to invade the Gulf of Bohai northward, and that *P. australis* and *Suaeda heteroptera*—currently dominating the Liaohe River Delta—may be eradicated by *S. alterniflora* in future. Previous studies found that the optimum salinity of *S. heteroptera* ranged between 3 mg/g and 5 mg/g. When the salinity content reaches 15.4 mg/g, seedling growth is inhabited and seedlings may even die (Song and Liang, 2010). However, *S.alterniflora* has high salt tolerance ranging between 10 and 60 mg/g. This demonstrates that *S. alterniflora* has wider salt amplitude than *S. heteroptera* which may be outcompeted and displaced. Similarly, rapid expansion of *S. alterniflora* in the Yangtze River Estuary would bring about a large decrease in *S. mariqueter* (Chen et al., 2004). The extensive reduction in native plants would negatively affect habitats of rare wetland birds such as *Grus japonensis* and *Larus saundersi*, and the shorebird *Charadrius* sp.

The slower expansion of S.*alterniflora* in southern China was also speculated to be related to the lower adaptability of some ecotypes in high temperatures (Liu et al., 2016). However, its invasion into mangrove communities cannot be neglected, and dynamic monitoring should be conducted on the south coast (Zhang et al., 2012).

In addition to the environmental influences we observed, soil properties and topographic factors may also affect the expansion rate of *S. alterniflora*. In future studies, simulation based on ecological niche models involving numerous environmental variables are likely to predict its potential global invasion distribution. Human controls should also be conducted to avoid its wider expansion, and physical control measures could be implemented (Hedge et al., 2003; Major et al., 2003; Adams et al., 2016; Strong DR and Ayres, 2016).

5 Conclusions

In this study, 43 *S. alterniflora* sites were selected to analyse three expansion traits of *S. alterniflora*: annual average area growth rate, expansion rate paralleling to the shoreline and it vertical to the shoreline. And the aim is to explore the geographical variation of *S.alterniflora* expansion rate and the influencing factors. The climate and seawater dataset were considered. The analysis results demonstrated that there was geographical variation in expansion rate of *S. alterniflora* along Coastal China, and it exhibited an increasing expansion tendency from south to north. The areal annual expansion rate increased from 7.66% to 19.81%, and it was significantly correlated with annual mean seawater temperature, the lowest seawater temperature, annual mean temperature and the lowest temperature in January. The expansion rate vertical to shoreline showed significant difference in different latitude zones with the largest occurring in Bohai Bay (256 m/yr), but no significant difference was observed in expansion rate paralleling to the shoreline. These findings will provide a significant support for its invasion prediction in the future. Additionally, the potential effects of terrain characteristics, mudflat types and scales, population competition and artificial disturbance on expansion rate of *S. alterniflora* should be considered in future research.

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