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# Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China

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## Summary

1. Phenotypic variation plays an important role in successful plant invasions. The spread of invasive species over large geographic ranges may be facilitated if plants can match their phenotype to local abiotic conditions. *Spartina alterniflora*, native to the United States, was introduced into China in 1979 and has spread over 19° of latitude along the eastern coast of China.

2. We studied patterns in vegetative growth and sexual reproduction of *S. alterniflora* at 22 sites at 11 geographic locations over a latitudinal gradient of ~2000 km from Tanggu (39.05°N, high latitude) to Leizhou (20.90°N, low latitude) in China. We further evaluated the basis of phenotypic differences by growing plants from across the range in a common garden for 2 growing seasons.

3. We found distinct latitudinal clines in plant height, shoot density and sexual reproduction across latitude. Some traits exhibited linear relationships with latitude; others exhibited hump-shaped relationships. We identified correlations between plant traits and abiotic conditions such as mean annual temperature, growing degree days, tidal range and soil nitrogen content. However, geographic variation in all but one trait disappeared in the common garden, indicating that variation largely due to phenotypic plasticity. Only a slight tendency for latitudinal variation in seed set persisted for 2 years in the common garden, suggesting that plants may be evolving genetic clines for this trait.

4. *Synthesis*. The rapid spread of *Spartina alterniflora* (*S. alterniflora*) in China has probably been facilitated by phenotypic plasticity in growth and reproductive traits. We found little evidence for the evolution of genetic clines in China, even though these exist for some traits in the native range. The considerable variation among clones, within provenances, that persisted in the common garden suggests a potential for the evolution of geographic clines in the future. Low fecundity of low-latitude *S. alterniflora* populations in China might result in a slower spread at low latitudes, but *S. alterniflora* is likely to continue to spread rapidly at high latitudes in China and into the Korean peninsula.

**Key-words:** biological invasions, common garden, invasion ecology, latitudinal gradient, phenotypic plasticity, *Spartina alterniflora*

## Introduction

A major obstacle to successful colonization by an introduced species is matching the introduced phenotype to the new biotic and abiotic environment. Many introductions fail because exotic species encounter unsuitable conditions in the introduced range (Davis, Grime & Thompson 2000; Sax & Brown

2000; Levine, Adler & Yelenik 2004). On the other hand, some introduced species rapidly spread to cover large geographic areas, suggesting that they are not limited by environmental variability (Kolar & Lodge 2001; Facon *et al.* 2006; Drenovsky *et al.* 2012). How is such rapid spread over a wide range of environmental conditions possible? In some cases, rapid evolutionary responses by the introduced species allow adaptive matching of genotype to environment (Mooney & Cleland 2001; Maron *et al.* 2004; Prentis *et al.*

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2008; Agrawal *et al.* 2015). In other cases, phenotypic plasticity of exotics may allow them to colonize a wide variety of habitats (Richards *et al.* 2006; Davidson, Jennions & Nicotra 2011; Castillo *et al.* 2014). A better understanding of these two processes would allow us to better understand why some introductions of exotic species fail, others succeed but remain confined to a small geographic area, and others spread to cover wide geographic areas (Richardson & Pyšek 2006; Colautti, Eckert & Barrett 2010; Moran & Alexander 2014).

The genus *Spartina* includes several species that are invasive outside their geographic range (Strong & Ayres 2013). Saltmarsh cordgrass, *Spartina alterniflora*, native to the Atlantic and Gulf Coasts of the United States, was introduced from native populations in North Carolina, Georgia and Florida into China in 1979 for agriculture and eco-engineering purposes. Seedlings and ramets were first transplanted in an experimental station located at the coast in Luoyuan, Fujian Province, in 1980 (Xu & Zhuo 1985). It rapidly spread through a combination of deliberate planting and natural dispersal, and now ranges over 19 degrees (20°N to 39°N) of latitude (An *et al.* 2007a; Zhang *et al.* 2012; Zuo *et al.* 2012) to represent the largest *Spartina* invasion in the world (Strong & Ayres 2013). Guo *et al.* (2015) examined the distribution and structure of genetic variation among three native populations at their source locations and five non-native populations in China. The study suggested that most of the non-native plants might be of Atlantic origin, while some individuals in the Hong Kong population could stem from genetic admixtures of Atlantic and Gulf origin, indicating at least some genetic variation within China.

*Spartina alterniflora* poses a double threat to Chinese saltmarsh native plants via direct competition with *Spartina* and pathogen infection (Li *et al.* 2014), and at low latitudes by invading and threatening mangroves (Zhang *et al.* 2012). *S. alterniflora* is now abundant throughout the middle intertidal of almost the entire coastline of China (An *et al.* 2007a; Zuo *et al.* 2012). Within this large geographic range, the phenotype of *S. alterniflora* varies considerably (Strong & Ayres 2013), indicating the potential for phenotypic plasticity.

Within its native range (~27–45°N) in North America, *S. alterniflora* varies considerably in phenotype across latitude (Turner 1976; Kirwan, Guntenspergen & Morris 2009). Plants from high latitudes are smaller, and biomass correlates positively with mean annual temperature, growing degree days (Kirwan, Guntenspergen & Morris 2009) and tidal amplitude (Turner 1976). Different populations across the geographic range vary in stem height and diameter, leaf size, flowering time, palatability to herbivores and other traits, and many of these differences appear to be genetically based because they persist in common-garden experiments (Seneca 1974; Somers & Grant 1981; Seliskar *et al.* 2002; Salgado & Pennings 2005; Elsey-Quirk, Seliskar & Gallagher 2011). Genetic analyses show considerable genetic structure in *S. alterniflora* across the native range (Blum *et al.* 2007; Hughes 2014), consistent with local adaptation.

One limitation of biogeographic studies of *S. alterniflora* within the native range is a lack of knowledge of geographic

variation in reproductive biology. The ability of introduced plants to set seed, however, is a key factor affecting spread in the introduced range (Daehler & Strong 1994; Daehler 1998; Ayres *et al.* 2008). Moreover, the introduced range in China extends to lower latitudes (to ~20°N) than studied in the native range, including extensive areas where mangroves are common (Zhang *et al.* 2012), raising the possibility for more complicated latitudinal patterns than have been documented in the native range.

Here, we ask whether patterns of latitudinal phenotypic variation found in the native range of *S. alterniflora* have developed in China. If so, we ask whether that variation has a genetic basis or is driven by a direct response to differences in the environment. We distinguish between these possibilities using a common-garden experiment. If latitudinal trends found in nature are preserved in a common-garden environment, then they have a genetic basis, suggesting evolution of the phenotypes in the 35 years since introduction. If the latitudinal trends disappear in a common-garden environment, then those seen in nature are driven by plastic responses to differences in the environment. Based on the answers to these questions, we discuss the prognosis for further spread of invasive *S. alterniflora* in China.

## Materials and methods

### GEOGRAPHICAL SURVEY

We selected 11 geographical locations along the east coast of China, at ca. 2 latitudinal degree intervals, spanning the entire latitudinal gradient known to contain *S. alterniflora* (Fig. 1). These 11 locations ranged from Leizhou, Guangdong (20.90°N), in the south to Tanggu, Tianjin (39.05°N), in the north (Table 1). We conducted field surveys at the end of the 2012 and 2013 growing seasons. To standardize

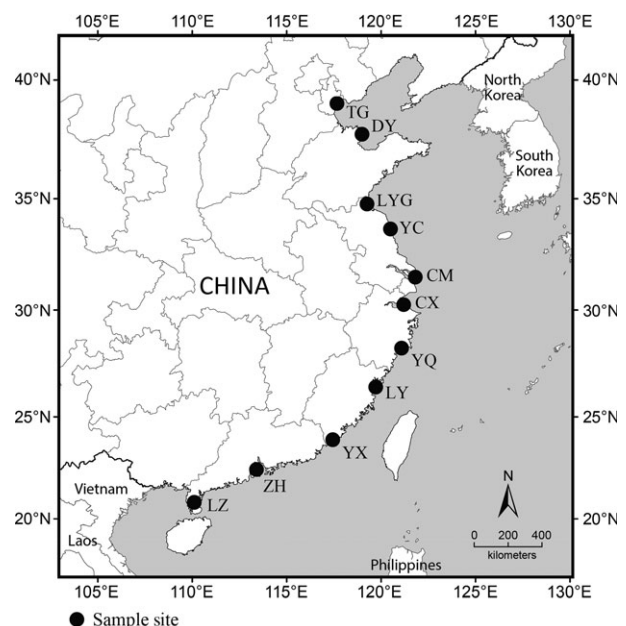


Fig. 1. Map of China showing the geographical survey sites.

phenology, we started at the southernmost location (Leizhou) when seed set began in late September and ended at the northernmost location (Tangu) when seeds were being set in late October (in China, *S. alterniflora* flowers earlier at low vs. high latitudes, Y. Zhang personal observation). The Cixi location was sampled only in 2012, and the Lianyungang location was sampled only in 2013.

At each location, we worked at two sites, 2–3 km apart (Table S1). At each site, we sampled five  $0.5 \times 0.5$  m quadrats that were located at  $> 30$ -m intervals. All quadrats were located within large ( $> 10$  m diameter) patches (Leizhou, Cixi and Dongying sites, only one quadrat per patch, placed in the middle of the patch) or in extensive continuous stands (all other sites) of *S. alterniflora*, depending on the distribution of *S. alterniflora* at the site. Because high marshes in China are intensively reclaimed for agriculture, aquaculture and industrial development (An *et al.* 2007b; Murray *et al.* 2014), all sampling locations represented lower marsh elevations.

In each quadrat, we counted the number of adult plants and flowering culms and measured the height of the three tallest *S. alterniflora* shoots (if present, flowering shoots were measured). We also collected 10 inflorescences, haphazardly selecting mature inflorescences with no herbivory and no shattering of the seeds within (or close to, if there were  $< 10$  suitable inflorescences within the quadrat) each of these quadrats. For each inflorescence, we counted the number of spikelets (seeds) and distinguished filled seeds from unfilled seeds. Filled seeds have an embryo, endosperm, and can potentially germinate and grow; unfilled seeds have neither of these tissues and cannot germinate or grow (Daehler & Strong 1994; Ayres *et al.* 2008). The filled seeds from each plot were collected and placed into separate zip-lock bags. Seeds were stored in 8 PSU seawater at 4 °C.

We took soil samples at each quadrat at the end of each growing season (September to November) and measured the soil water content (percentage of wet core mass made up of water) and porewater salinity (PSU) using the soil rehydration method (Pennings and Richards 1998). We identified the soil textural class using the field method of D.L. Lindbo (Vepraskas 2013). We measured the carbon and nitrogen content of a subsample of the soil samples ( $n = 3$  per location per year) with a Vario ELIII element analyzer after the soil subsample was air dried in the laboratory and pulverized using an oscillating mill.

We obtained climate and tide data for each location for the 10-year period of 2004–2013, which spanned much or all of the period during which *S. alterniflora* was present at each site. We summarized the data by calculating annual average daily temperature, the annual num-

ber of growing degree days ( $> 10$  °C), annual precipitation and annual mean tidal range. Growing degree days measure the number of degrees that daily temperatures exceed a threshold temperature necessary for significant plant growth and therefore reflect both the temperature and duration of the growing season (Kirwan, Guntenspergen & Morris 2009). Climate and tide data were obtained from the stations closest to each site (Table S1) in the Climate Information for the China meteorological data sharing service system (<http://cdc.nmic.cn/>) and in the tide tables published by the National Marine Data & Information Service (<http://www.nmdis.gov.cn>). Because the two sites at each location were close, each pair of sites shares common meteorological and tide data. Climate is known to be an important correlate of plant traits, with indices such as mean annual temperature explaining a substantial fraction of their total variation (Reich & Oleksyn 2004).

### COMMON-GARDEN EXPERIMENT

To determine the basis of phenotypic differences of *S. alterniflora* populations located at different latitudes, we conducted a common-garden experiment in the field. We set the common garden in a tidal mudflat of Yunxiao (23°55.079'N, 117°25.331'E). Plots were located within 10–20 m of existing *S. alterniflora* clones. Each plot ( $n = 10$ ) consisted of 10 PVC tubes (16 cm in diameter and 33 cm deep), which were organized into three rows and four columns. In April 2013, we placed ten seeds from a single source population into a single, haphazardly selected PVC pipe, such that each plot contained plants from each of the 10 latitudinal sites (Lianyungang location was sampled only in 2013 and so was not included in this experiment), but the location within the plot varied. One month later, after seeds had germinated, we thinned the seedlings to one per pipe. We surrounded each plot with a 1.5-m-high mesh and PVC fence barrier to reduce animal grazing. On 1 October 2013, we counted the number of shoots and the number of flowering culms and measured the height of the three tallest shoots in each pipe. We also collected all the mature inflorescences (i.e. no herbivory and no shattering of the seeds) from each pipe. For each inflorescence, we counted the number of spikelets (seeds), distinguishing filled from unfilled seeds. After one growing season, the PVC pipes were filled by roots and rhizomes. To provide room for the second year's below-ground growth, at the end of the first growing season, we separated a 15- to 20-cm rhizome (with one or two ramets growing from it) from the clone in

**Table 1.** Geographical survey. Location name, abbreviation (used in figures), latitude and longitude, annual average temperature (annual average of daily means  $\pm 1$  SE), annual number of growing degree days ( $> 10$  °C) ( $\pm 1$  SE), total annual precipitation ( $\pm 1$  SE) and mean tidal range of eleven survey locations on the coast of China. Locations are ordered from south to north. At each location, we sampled two sites (2–3 km apart). More precise geographical coordinates for each sampling site, weather station and tide gauge are provided in Table S1

Location	Abbreviation	Latitude (N)	Longitude (E)	Temperature (°C)	Growing degree days ( $> 10$ °C)	Precipitation (mm)	Mean tidal range (m)
Leizhou	LZ	20°54'	110°10'	23.1 $\pm$ 0.1	8362 $\pm$ 47	1646 $\pm$ 118	2.49 $\pm$ 0.01
Zhuhai	ZH	22°25'	113°37'	23.2 $\pm$ 0.1	8410 $\pm$ 40	1812 $\pm$ 149	1.87 $\pm$ 0.01
Yunxiao	YX	23°55'	117°28'	21.4 $\pm$ 0.1	7750 $\pm$ 48	1308 $\pm$ 111	2.76 $\pm$ 0.01
Luoyuan	LY	26°26'	119°45'	20.6 $\pm$ 0.1	7239 $\pm$ 63	1447 $\pm$ 104	5.24 $\pm$ 0.02
Yueqing	YQ	28°20'	121°12'	17.8 $\pm$ 0.1	6041 $\pm$ 72	1461 $\pm$ 108	5.28 $\pm$ 0.02
Cixi	CX	30°22'	121°13'	17.8 $\pm$ 0.1	5977 $\pm$ 53	1380 $\pm$ 74	5.23 $\pm$ 0.02
Chongming	CM	31°32'	121°58'	17.4 $\pm$ 0.1	5834 $\pm$ 50	1135 $\pm$ 30	2.81 $\pm$ 0.01
Yancheng	YC	33°42'	120°34'	15.0 $\pm$ 0.1	4967 $\pm$ 40	931 $\pm$ 69	2.10 $\pm$ 0.01
Lianyungang	LYG	34°46'	119°16'	14.1 $\pm$ 0.2	4754 $\pm$ 55	984 $\pm$ 60	3.97 $\pm$ 0.02
Dongying	DY	38°00'	118°57'	13.8 $\pm$ 0.1	4781 $\pm$ 28	587 $\pm$ 37	1.58 $\pm$ 0.01
Tangu	TG	39°03'	117°45'	13.4 $\pm$ 0.1	4679 $\pm$ 43	593 $\pm$ 43	2.71 $\pm$ 0.01

each of the PVC pipes and transplanted each rhizome into a new set of plots (~5 m away from the former ones). On 20 September 2014, at the end of the second growing season, we conducted another set of measurements.

#### STATISTICAL ANALYSIS

For statistical analyses, we made the assumption that each quadrat in the field represented a different genetic individual and so treated each individual quadrat (in each year) as a true replicate. This assumption was based on the high clonal diversity observed in both the natural (Richards *et al.* 2004; Richards, Pennings & Donovan 2005; Travis & Hester 2005; Hughes 2014) and introduced (Deng *et al.* 2007; Wang *et al.* 2012) ranges of *S. alterniflora*.

To evaluate whether there were latitudinal trends in vegetative and sexual variables among populations, we analysed data from the geographical survey in 2012 and 2013, and the common-garden experiment in the first and second year, using regression, evaluating both linear and quadratic relationships. For the common-garden experiment, we used vegetative and sexual variables as response variables, with populations' location as predictor variables.

We used multivariate correlations to analyse the relationships between latitude and abiotic variables from the 11 field locations. In an effort to determine the relative influence of the different abiotic factors on vegetative growth and sexual reproduction, we used stepwise multiple regression to obtain the best regression models for variation in *S. alterniflora* phenotype (2012 and 2013 data pooled) in the field. The maximum number of variables in the final models was limited to three to avoid over-fitting the models. We performed data analysis with JMP 10.0 statistical software (SAS Institute 2012).

## Results

#### ABIOTIC CONDITIONS ACROSS LATITUDE

Abiotic conditions varied considerably among the survey locations. Annual average temperatures decreased from 23.2 °C (Zhuhai) at low latitudes to 13.4 °C (Tanggu) at high latitudes, and the annual number of growing degree days (> 10 °C) similarly decreased from 8410 degree days (Zhuhai)

at low latitudes to 4679 degree days (Tangdu) at high latitudes (Table 1). Annual precipitation also decreased from 1812 mm (Zhuhai) at low latitudes to 587 mm (Dongying) at high latitudes (Table 1). Tide range was greatest at intermediate latitudes (5.28 m at Yueqing) and varied threefold among sites (Table 1).

Porewater salinity in the fall varied fivefold among sites, ranging from 11.2 (Zhuhai) to 55.1 PSU (Liangyungang) (Table 2). High latitude sites tended to have saltier soil. Soil water content varied twofold, from 26.2 (Yangcheng) to 58.3% (Zhuhai), and soils tended to be driest at high latitudes and at sites with silty loam vs. clay soils (Table 2). Soil carbon and nitrogen varied threefold and fourfold among sites, respectively, but did not show latitudinal patterns (Table 2).

Several of the abiotic variables measured were correlated with latitude, and thus with each other (Table 3). In particular, annual average temperature, annual number of growing degree days, annual precipitation and soil water content were strongly correlated with each other, and soil nitrogen was strongly correlated with annual average temperature, annual number of growing degree days and soil water content.

#### PLANT PHENOTYPIC VARIABILITY ACROSS LATITUDE AND IN COMMON GARDEN

Plant height showed a hump-shaped relationship with latitude in the field, reaching its maximum at intermediate latitudes; however, height did not vary with latitude of origin in the common-garden experiment (Fig. 2a,b). The number of spikelets (seeds) per inflorescence increased from < 100 to > 400 with latitude in the field, but again showed no relationship with latitude of origin in the common garden (Fig. 2c,d). Seed set (proportion of seeds that are filled) increased sharply with latitude in the field, ranging from < 10 % at low latitudes to > 80% at high latitudes (Fig. 2e). Seed set increased with latitude of origin in the common garden, but the relationship was greatly diminished, with seed set ranging from 3 to 20% in the first growing season in 2013, and 3 to 25% in the

**Table 2.** Geographical survey. Soil physico-chemical properties of eleven survey locations on the coast of China at the end of growing season (September to November 2012, 2013). Data are means  $\pm$  1 SE, with samples averaged across quadrats within a site, sites within a location, and years, to give  $n = 20$  subsamples (salinity and water content) for each of 11 locations. Due to cost, carbon and nitrogen content were only measured in six subsamples (3 per year) per location

Site	Porewater salinity (PSU)	Water content (%)	Carbon (%)	Nitrogen (%)	C/N Ratio	Soil texture
LZ	21.9 $\pm$ 0.4	48.2 $\pm$ 2.1	0.55 $\pm$ 0.05	0.04 $\pm$ 0.00	13.78 $\pm$ 0.53	Silty loam
ZH	11.2 $\pm$ 0.5	58.3 $\pm$ 0.9	1.61 $\pm$ 0.10	0.14 $\pm$ 0.01	11.94 $\pm$ 0.17	Silty loam
YX	28.9 $\pm$ 1.1	47.4 $\pm$ 2.6	1.79 $\pm$ 0.10	0.11 $\pm$ 0.01	16.51 $\pm$ 0.29	Clay
LY	31.4 $\pm$ 0.4	43.2 $\pm$ 2.0	0.86 $\pm$ 0.02	0.07 $\pm$ 0.00	12.97 $\pm$ 0.92	Clay
YQ	25.5 $\pm$ 1.0	47.8 $\pm$ 0.6	1.19 $\pm$ 0.01	0.06 $\pm$ 0.00	19.82 $\pm$ 0.22	Clay
CX	11.4 $\pm$ 0.2	43.6 $\pm$ 1.1	1.29 $\pm$ 0.02	0.06 $\pm$ 0.00	20.80 $\pm$ 0.94	Clay
CM	15.6 $\pm$ 0.5	38.0 $\pm$ 1.4	1.70 $\pm$ 0.06	0.07 $\pm$ 0.01	24.73 $\pm$ 1.91	Silty loam
YC	25.5 $\pm$ 2.2	26.2 $\pm$ 2.7	1.68 $\pm$ 0.24	0.06 $\pm$ 0.02	38.31 $\pm$ 6.81	Silty loam
LYG	55.1 $\pm$ 6.7	40.0 $\pm$ 4.3	0.94 $\pm$ 0.09	0.05 $\pm$ 0.00	18.27 $\pm$ 0.55	Clay
DY	32.7 $\pm$ 0.8	31.0 $\pm$ 2.0	1.25 $\pm$ 0.05	0.03 $\pm$ 0.00	44.98 $\pm$ 4.30	Silty loam
TG	33.6 $\pm$ 1.9	38.4 $\pm$ 3.2	1.72 $\pm$ 0.38	0.04 $\pm$ 0.01	41.00 $\pm$ 5.26	Clay

**Table 3.** Geographical survey. Pearson's correlation coefficients showing relationships between latitude and abiotic variables. Locations were treated as replicates ( $n = 11$ ). Significant correlations ( $P < 0.05$ ) are in bold

	Latitude	Temperature	Growing degree days	Precipitation	Mean tidal range	Soil porewater salinity	Soil water content	Soil nitrogen
Latitude	1.00							
Temperature	<b>-0.98</b>	1.00						
Growing degree days	<b>-0.97</b>	<b>0.99</b>	1.00					
Precipitation	<b>-0.94</b>	<b>0.91</b>	<b>0.88</b>	1.00				
Mean tidal range	-0.10	0.04	-0.02	0.30	1.00			
Soil porewater salinity	0.46	-0.53	-0.48	-0.53	0.08	1.00		
Soil water content	<b>-0.78</b>	<b>0.80</b>	<b>0.80</b>	<b>0.83</b>	0.21	-0.35	1.00	
Soil nitrogen	<b>-0.60</b>	<b>0.63</b>	<b>0.63</b>	<b>0.60</b>	-0.09	-0.42	<b>0.65</b>	1.00

second growing season in 2014. Variation in seed set was the only trait that continued to show a latitudinal pattern for two growing seasons in the common garden.

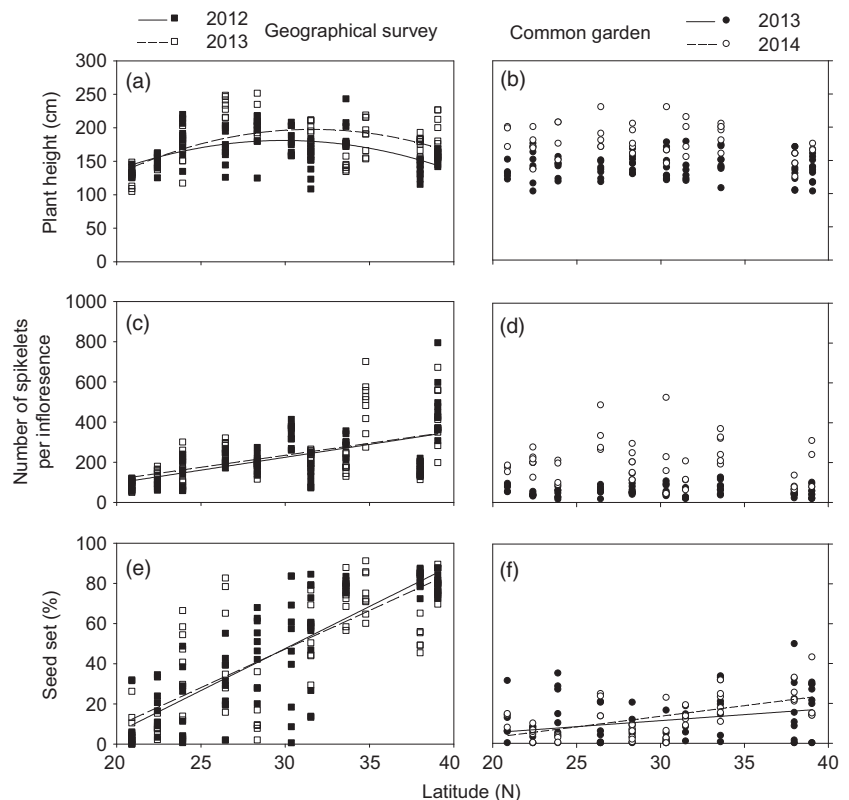
Shoot density decreased ca. 40% with increasing latitude in the field, but showed no relationship with latitude of origin in the common garden (Fig. 3a,b). The percentage of culms flowering peaked at mid-latitudes in the field, and this relationship was also apparent but weaker in the common garden in the first year, then disappeared in the second year (Fig. 3c, d). Seed production, measured as the number of spikelets/m<sup>2</sup>, increased from low latitudes to an asymptote at high latitudes; no pattern was seen in the common garden (Fig. 3e,f).

#### RELATIONSHIP BETWEEN *S. ALTERNIFLORA* PHENOTYPE AND ENVIRONMENTAL FACTORS

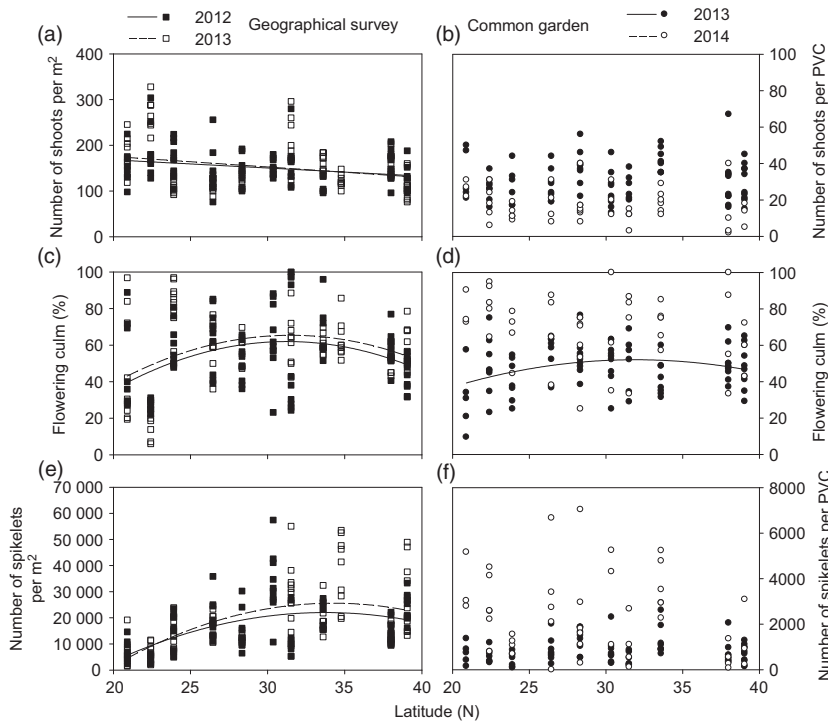
Because temperature, growing degree days, precipitation, soil water content and soil nitrogen all correlated with latitude, all of these variables individually predicted variation in *S. alterniflora* traits in the field (Figs S1–S6). The best multiple regression models for *S. alterniflora* traits identified temperature, growing degree days, precipitation, soil nitrogen and mean tidal range as the most important predictors of variation in *S. alterniflora* traits in the field (Table 4, Figs S1–S6).

#### Discussion

We found that all the traits of *S. alterniflora* that we measured in the field varied across latitude. This variability is



**Fig. 2.** End of growing season individual plant traits in relation to latitude for *Spartina alterniflora* populations growing in different field sites along a latitudinal gradient and a common garden in the Yunxiao field site. Trendlines are given only for significant relationships. In different sites: (a) plant height ( $R^2 = 0.25$ ,  $P < 0.0001$  for 2012, and  $R^2 = 0.28$ ,  $P < 0.0001$  for 2013), (c) number of spikelets/inflorescence ( $R^2 = 0.35$ ,  $P < 0.0001$  for 2012, and  $R^2 = 0.29$ ,  $P < 0.0001$  for 2013) and (e) seed set ( $R^2 = 0.68$ ,  $P < 0.0001$  for 2012, and  $R^2 = 0.64$ ,  $P < 0.0001$  for 2013); in common garden: (b) plant height, (d) number of spikelets/inflorescence and (f) seed set ( $R^2 = 0.09$ ,  $P = 0.005$  for the first growing season in 2013, and  $R^2 = 0.38$ ,  $P < 0.0001$  for the second growing season in 2014).



**Fig. 3.** End of growing season population plant traits in relation to latitude for *Spartina alterniflora* populations growing in different field sites along a latitudinal gradient and a common garden in the Yunxiao field site. Trendlines are given only for significant relationships. In different sites: (a) number of shoot/m<sup>2</sup> ( $R^2 = 0.07$ ,  $P = 0.014$  for 2012, and  $R^2 = 0.07$ ,  $P = 0.010$  for 2013), (c) percentage of culms flowering ( $R^2 = 0.13$ ,  $P = 0.002$  for 2012 and  $R^2 = 0.12$ ,  $P = 0.004$  for 2013) and (e) number of spikelets/m<sup>2</sup> ( $R^2 = 0.26$ ,  $P < 0.0001$  for 2012, and  $R^2 = 0.33$ ,  $P < 0.0001$  for 2013); in common garden: (b) number of shoot/PVC, (d) percentage of culms flowering ( $R^2 = 0.08$ ,  $P = 0.045$  for the first growing season in 2013) and number of spikelets/PVC.

**Table 4.** Best regression models for variation in *Spartina alterniflora* phenotype (data from 2012 and 2013 pooled) in the field. Quadrats treated as replicates ( $n = 183$ )

Variable	Model (* = $P < 0.05$ , ** = $P < 0.01$ , *** = $P < 0.001$ )	$R^2$	$P$
Height	143.93*** - 0.04 Precipitation*** + 15.85 Mean tidal range*** + 388.12 Soil nitrogen***	0.36	< 0.0001
Shoot density	186.04*** + 0.03 Precipitation** - 12.46 Mean tidal range*** - 1.27 Soil porewater salinity***	0.29	< 0.0001
Spikelets/inflorescence	683.14*** - 112.41 Temperature*** + 0.23 Growing degree days*** + 47.45 Mean tidal range***	0.47	< 0.0001
Seed set	180.81*** - 6.16 Temperature*** - 0.76 Soil water content** + 136.10 Soil nitrogen*	0.68	< 0.0001
Percentage of culms flowering	-21.57 + 32.19 Temperature*** - 0.08 Growing degree days*** - 0.06 Precipitation***	0.19	< 0.0001
Seed production	37110.06*** - 4.97 Growing degree days*** + 2665.60 Mean tidal range*** + 58225.72 Soil nitrogen*	0.35	< 0.0001

consistent with previous studies of *S. alterniflora* in its native range that have found high variability in productivity and phenology across latitude (Turner 1976; Kirwan, Guntenspergen & Morris 2009). Our study, however, is the first to our knowledge to look at latitudinal variation in reproductive parameters in either the native or introduced range of this plant, which is a key factor affecting *S. alterniflora* spread, and we found that seed set increases linearly with latitude in China. High trait variation across the geographic range that largely disappeared in the common garden suggests great phenotypic plasticity.

The variation that we observed in field populations of *S. alterniflora* in China was correlated with a number of environmental variables. Many of these variables were correlated with each other across latitude. For this reason, unambiguously identifying any one as the key abiotic driver is difficult, which means that individual predictors must be interpreted with caution. In addition, some of our sites lacked closely co-located climatological and tide stations, introducing uncer-

tainty into the analysis. Nevertheless, the pattern of phenotypic variation observed was consistent in some cases with what is known about the biology of *S. alterniflora* in its native range. Previous studies have shown that *S. alterniflora* height and biomass increase with temperature throughout most of the native range (Turner 1976; Kirwan, Guntenspergen & Morris 2009; Idaszkin & Bortolus 2011), although sites in Florida which represent the Atlantic Coast low-latitude range limit of *S. alterniflora* have been under-represented in these studies. Other work shows that periods with extreme high temperatures reduce *S. alterniflora* productivity because the thermal optimum for photosynthesis in *S. alterniflora* is approximately 30 °C (Giurgevich & Dunn 1979; Dunn *et al.* 1987; Więski & Pennings 2014). Whether this thermal optimum explains the hump-shaped relationships we found in China for plant height, per cent of culms flowering and seed production vs. average annual temperature (Fig. S1) is unclear, because although low-latitude sites have the highest average temperatures, they do not necessarily experience the

most severe heat waves (Table S2). Another possibility is that, at extremely low latitudes in the introduced range, the phenology of *S. alterniflora* is not yet adapted to local conditions, such that it reproduces before achieving high peak biomass (Y. Zhang, personal observation).

Within the native range, *S. alterniflora* production also increases with tidal range (Turner 1976), consistent with our observations of greater height and reproduction with increasing tide range in the introduced range (Table 4). The physiological mechanism underlying this pattern has not been studied, but it is likely that a large tidal range improves drainage of toxins and infiltration of oxygen in marsh soils (Mendelssohn & Morris 2000).

In the native range, eutrophication usually increases performance of *S. alterniflora* (Gallagher 1975; Chalmers 1979; Bertness & Pennings 2000; Bertness *et al.* 2008), and we found positive relationships between soil nitrogen content and several aspects of *S. alterniflora* performance (Table 4). Similarly, it is consistent with results from the native range that shoot density would increase with greater precipitation and decrease with greater soil salinity (Table 4). Precipitation partially mediates soil salinity, and high salinity is stressful, even to halophytic plants (Więski & Pennings 2014).

One of the relationships we found was inconsistent with what is known about the physiology of *S. alterniflora*. Shoot height decreased with increasing precipitation (Table 4), a result that is inconsistent with findings from the native range (Więski & Pennings 2014) and difficult to explain physiologically. We speculate that this relationship is driven primarily by the low height of plants at low-latitude sites (which happen to receive more precipitation), as discussed above, rather than by precipitation per se.

An extraordinary result that we found was that seed set ranged from close to zero at low latitudes to over 80% at high latitudes, a relationship that was preserved to some degree in the common garden. The fact that seed set varies with latitude suggests that the mechanisms promoting the *S. alterniflora* invasion, and consequently the speed of this invasion, might also vary with latitude. In particular, seed supply supporting the founding of new populations may be abundant at high latitudes and low at low latitudes. Consistent with this speculation, we observed much higher densities of seedlings, in the field, at high vs. low latitudes (Y. Zhang, personal observation). At the moment, we do not know the mechanism underlying this geographic variation in seed set. To the best of our knowledge, data on geographic variation in seed set in the native range are lacking, but clearly, this is an interesting topic that has been overlooked in the native range.

Whatever the mechanisms, the low sexual reproductive activity as shown by minimal seed set and very low numbers of flowering culms of *S. alterniflora* at low latitudes in China indicates that the spread of *S. alterniflora* might be slower in southern China than it has been in the north. Although the spread of *S. alterniflora* at low latitudes continues and threatens native mangroves (Zhang *et al.* 2012; Li, Wang & Zhang 2014), a slower rate of spread might allow more time for control of *S. alterniflora* and create conditions conducive to

greater success of control. In contrast, the prolific seed set at high latitudes suggests that the spread of *S. alterniflora* in northern China and into the Korean peninsula is likely to be inexorable.

The variation that we observed among sites in nature largely disappeared in the common garden, indicating that it was primarily due to plastic responses to the environment. The latitudinal pattern of the percentage of culms flowering, however, persisted for 1 year in the common garden, and the latitudinal pattern of seed set persisted for 2 years. Persistent maternal influences are a possible explanation for the slight tendency of interpopulation persistence of seed set differences in the common garden. In some cases, such transgenerational phenomena are viewed as epigenetic, and these have been found in invasive plants (Richards *et al.* 2006). Our common-garden plants were started from seed, reducing the potential for persistent maternal effects. It is notable that the between-site differences in the common garden were less than those among locations within sites. A caveat to the latter result is that *Spartina* species are wind-pollinated and clones from different geographic locations would have been able to cross-fertilize in the common garden. Thus, the pattern of seed set needs to be confirmed with a common-garden experiment in which plants from each location are reproductively isolated from plants from other locations. Within its native range, *S. alterniflora* is known to have a high level of phenotypic variation across abiotic gradients within a single site (Valiela, Teal & Deuser 1978; Richards, Pennings & Donovan 2005) and across geographic distances (Gallagher 1975; Turner 1976; Seliskar *et al.* 2002; Kirwan, Guntenspergen & Morris 2009). Much of this variation, especially within a site, is plastic, and single genotypes can display a wide variety of phenotypes if abiotic conditions are manipulated (Valiela, Teal & Deuser 1978; Chalmers 1979; Bertness & Pennings 2000). Some of the variation, however, both within sites (Gallagher *et al.* 1988; Wang *et al.* 2012) and across latitude (Seliskar *et al.* 2002; Salgado & Pennings 2005), has a genetic component and persists in a common garden. We currently are unable to connect our findings to the only published work on genetic differentiation of *S. alterniflora* in China (Guo *et al.* 2015).

While phenotypic differences among locations largely disappeared in our common-garden experiment, we did find a high level of phenotypic variation among clones from all sites that persisted in the common garden (Figs 2 and 3). Our observations indicate that phenotypic variation of *S. alterniflora* at any site in the field in China is much greater than in the native range in the United States (Y. Zhang, D. Strong & S. Pennings, personal observations). The ecological and genetic mechanisms explaining this variation among clones within a site are currently unknown, but deserve increased attention. Regardless of the mechanisms producing this variation, the remarkable range of phenotypic variation that exists indicates that there is ample potential for natural selection to produce or strengthen genetically based geographic clines. We predict that the geographic clines that we observe now,



which are largely due to phenotypic plasticity, will develop a strong genetic component in the future.

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## Data accessibility

All data for this publication are deposited in the Georgia Coastal Ecosystems Long-Term Ecological Research repository at <http://gce-lter.marsci.uga.edu/public/data/data.htm> (Pennings 2015).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Geographical coordinates for each sampling site, weather station and tide gauge.

**Table S2.** Monthly mean temperature of eleven survey locations.

**Figure S1.** *Spartina alterniflora* growth in relation to mean annual temperature.

**Figure S2.** *Spartina alterniflora* growth in relation to mean annual growing degree days.

**Figure S3.** *Spartina alterniflora* growth in relation to total annual precipitation.

**Figure S4.** *Spartina alterniflora* growth in relation to soil water content.

**Figure S5.** *Spartina alterniflora* growth in relation to soil nitrogen.

**Figure S6.** *Spartina alterniflora* growth in relation to mean tidal range.