

Plasticity and selection drive hump-shaped latitudinal patterns of flowering phenology in an invasive intertidal plant

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Abstract. Patterns of flowering phenology can affect the success of plant invasions, especially when introduced species spread across a wide range of latitude into different climatic conditions. We combined a 4-yr field survey and a 3-yr common garden experiment with the invasive grass *Spartina alterniflora* that is now widespread along the coast of China to document the latitudinal pattern of flowering phenology, determine if phenology was related to climate or oceanographic variables, and determine whether phenology patterns were fixed versus plastic. In the field, first flowering day displayed a hump-shaped relationship with latitude, with low- and high-latitude plants flowering 100 d and 10 d earlier than plants at middle latitudes, respectively. Peak flowering day showed a similar hump-shaped relationship with latitude, with the interval between first and peak flowering day decreasing with increasing latitude. First flowering day had a hump-shaped relationship with annual growing degree days but a linear positive relationship with tidal range. In the common garden, first flowering day decreased linearly with increasing latitude of origin, as did peak flowering day, and the interval between first and peak flowering day increased with increasing latitude. First flowering day in the common garden had weak or no relationships with abiotic variables at the sites of origin. In both the field and common garden, first flowering day was later in site years for which plants were taller. These results indicate a high degree of plasticity in flowering phenology, with plants flowering later in the field at sites with intermediate temperatures and high tide ranges. Common garden results indicate some selection for earlier flowering at sites with low temperatures, consistent with a shorter growing season. Consistent with life-history theory, plants flowered later under conditions favoring vigorous growth. Earlier flowering and smaller size of plants at high and low latitudes suggests that *S. alterniflora* has already occupied much of the geographic range favorable for it on the East Coast of Asia.

Key words: adaptive evolution; biological invasion; common garden; flowering phenology; latitudinal gradient; *Spartina alterniflora*.

INTRODUCTION

The study of phenology—the timing of life cycle events (e.g., leaf emergence and senescence, flowering) has recently attracted renewed attention in part because of the possibility that it may help explain the process of biological invasions (Fridley 2012, Wolkovich and Cleland 2014). Some biological invasions are inconsequential, whereas others dramatically alter ecological systems (Vilà et al. 2011), and ecologists have repeatedly sought to evaluate the traits that determine the success of invasions (Davis 2009, van Kleunen et al. 2010). Phenology may affect invasion success because life history events

such as flowering and seed set need to be matched to the environment in the exotic range in order for an invasive species to flourish (Montague et al. 2008, Pau et al. 2011, Wolkovich and Cleland 2011).

Exotic species that spread across a wide latitudinal range need to match their phenology to the abiotic environment at many locations that differ in abiotic conditions. For example, at high latitudes, temporal niche space is compressed because of the shorter growing season, and exotic species have to avoid fitness costs associated with harsh cold events in the spring and fall (Pau et al. 2011). At lower latitudes, invasive plants might respond to higher temperatures with advanced flowering times (Menzel et al. 2006, Anderson et al. 2012). For example, invasive populations of *Capsella bursa-pastoris* in California flower at different times depending on local climate, with populations in hot desert climates flowering earlier than populations in snowy-forest and coastal

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redwood habitats (Neuffer and Hurka 1999, Simberloff 2009).

This matching of phenology to climate can occur through some combination of phenotypic plasticity and adaptive evolution (Davidson et al. 2011, Colautti and Barrett 2013, Hodgins et al. 2018). During a successful invasion, multiple introductions would likely result in a great deal of genetic variation (Dlugosch et al. 2015), and the genetic admixture, the interbreeding among different exotic sources, could facilitate invasion through hybrid vigor contributing to adaption (Rius and Darling 2014). Phenotypic plasticity itself is a functional trait that can evolve during an introduction (Ren et al. 2020). Therefore, these mechanisms are not mutually exclusive, with phenotypic plasticity most effective over short time scales (Davidson et al. 2011, Castillo et al. 2014) and evolution over longer time scales (Prentis et al. 2008, van Kleunen et al. 2018).

Because climate varies with latitude, plant phenology is also likely to vary with latitude. Latitude is a proxy of multiple abiotic variables including temperature, precipitation, and solar radiation that together influence the growth, reproduction, and phenology of plants (Li et al. 1998, Liu et al. 2016, Qiu et al. 2018). The complex interaction of these factors results in latitudinal clines in the field. Common garden experiments provide a classic experimental approach that provides insight into phenotypic plasticity and genetic differentiation of plant populations from multiple locations by growing them in a single environment (Colautti et al. 2009).

Most research on latitudinal variation in phenology has come from terrestrial plant systems in temperate environments (Munguía-Rosas et al. 2011, Pau et al. 2011, Wolkovich et al. 2014). Within temperate environments, plants often show linearly positive relationships between climate variables such as temperature and leaf or flower phenology (Hopkins 1924, Liang 2016, Richardson et al. 2019) because temperature has direct effects on physiological function (Tooke et al. 2005, Pau et al. 2011). Such linear relationships might not hold, however, if studies were extended across a broader range of climate, because additional variables such as precipitation might become important constraints on phenology at larger spatial scales (Bradley et al. 2011).

For plants that live in intertidal habitats, such as salt marshes and mangroves, phenological patterns such as flowering and seed set might be affected by oceanographic conditions such as tide range and inundation in addition to climate variables such as temperature and precipitation (Pastor-Guzman et al. 2018, Riddin and Adams 2019). For example, a recent study of the salt marsh grass *Spartina alterniflora*, which is native to the Atlantic and Gulf Coasts of the United States, found that soil temperature, which was driven by tidal inundation, was a key factor affecting phenology (O'Connell et al. 2019).

Spartina alterniflora was introduced to China in 1979 and has spread across a wide (~19°) range of latitude

(An et al. 2007). The deliberate introduction of *S. alterniflora* to China used plants and seeds sourced from relatively low latitudes in the United States: Morehead City, North Carolina (34.72 °N), Sapelo Island, Georgia (31.47 °N), and Tampa Bay, Florida (27.70 °N; Xu and Zhuo 1985). Interbreeding among these sources has generated genetic admixtures of *S. alterniflora* with greatly increased heritable variation that is likely accelerating the geographic invasion (Qiao et al. 2019). Cross-bred genotypes spread rapidly through the temperate region of China in the 1980s, and dispersed into lower-latitude subtropical and tropical regions in the following decades (An et al. 2007, Zhang et al. 2017). Within the introduced range, *S. alterniflora* plants vary greatly in vegetative traits and seed set, with geographic variation in vegetative traits largely caused by phenotypic plasticity, and geographic variation in seed set largely caused by rapid evolution in the new environment (Liu et al. 2016, 2017, Qiao et al. 2019, Liu et al. 2020a, b).

Both vegetative growth and seed set are closely related to flowering phenology (Berrigan and Koella 1994); therefore, known clinal patterns and adaptive mechanisms in these two traits are likely to inform our understanding of variation and adaptation in flowering phenology of *S. alterniflora* in China. In turn, adding information on flowering phenology to previous results on growth and seed set would make the understanding of evolution and adaptation in this plant invasion more comprehensive and integrative. In particular, variation in plant height is likely to influence phenology. Life-history theory assumes that plants trade off resources between growth and reproduction (Berrigan and Koella 1994, Fenner 1998). As a result, understanding the relationship between flowering phenology and plant height is important for understanding how plants respond to a changing environment (Weiner 2004, Agrawal 2020), particularly along a latitudinal gradient (Woods et al. 2012).

How plant phenology affects the spread of *S. alterniflora* in China is not understood. How phenology matches the new environment should determine invasion success (Wolkovich and Cleland 2014). *Spartina alterniflora* occupies lower latitudes in its introduced range in China than in the native range, but abiotic and biotic conditions in China are similar to those on the East Coast of North America where *S. alterniflora* evolved (Kirwan et al. 2009, Crosby et al. 2015). Given this, we might expect similar patterns in the two ranges. Understanding the pattern of flowering phenology across such a huge biogeographic scale in China, coupled with previous research on reproductive traits (Liu et al. 2016, 2017), should promote an understanding of evolution and invasion success of *S. alterniflora* in both the native and introduced ranges.

We have only a preliminary understanding of how and why flowering phenology of *S. alterniflora* varies across latitude in its native range, and almost no understanding of these issues in its introduced range in China. There

have been only a few studies of flowering phenology of *S. alterniflora* within its native range, with many of these studies limited to a narrow (6–9°) range of high-latitude populations (Somers and Grant 1981, Crosby et al. 2015). We know of only one study that examined flowering across almost the whole range (~17°) of this plant (Seneca 1974). These studies found a negative relationship between the flowering time of different *S. alterniflora* provenances and latitude of origin in a common garden, but failed to find a cline in flowering phenology in the field. Within the invasive range in China, one field study found that *S. alterniflora* plants at higher latitudes flowered later, and attributed this to cooler temperatures at high latitudes (Qiu et al. 2018). A common garden study found that flowering time was negatively related to latitude of origin in the field (i.e., high-latitude plants flowered earlier), suggesting that plant phenology had evolved in some populations since *S. alterniflora* was originally introduced (Zhang et al. 2008). These studies were not designed to determine the relative importance of phenotypic plasticity and genetic differences in driving latitudinal flowering patterns, and neither explored the possible contribution of oceanographic variables in shaping phenological patterns.

Here, we build on these previous studies by directly comparing new field and common garden results to document latitudinal variation in flowering phenology of introduced *S. alterniflora* in the field in China, identify whether latitudinal patterns are due to phenotypic plasticity or evolution, and link phenological variation to the dramatic invasion of success of this species. Specifically, we combined field surveys of *S. alterniflora* phenology and a common garden experiment to address three questions. (1) What is the pattern of flowering phenology of *S. alterniflora* across latitude in China? (2) Is the latitudinal pattern of flowering phenology of *S. alterniflora* in China related to climate or oceanographic variables? (3) To what extent are patterns of flowering phenology fixed versus plastic?

MATERIALS AND METHODS

Latitudinal variation in phenology in the field

To determine how flowering phenology of *S. alterniflora* varied across latitude in the field, we sampled six sites spanning most of the latitudinal distribution of *S. alterniflora* in China (Fig. 1). From 2014 to 2016, we sampled five sites, from Leizhou, Guangdong (20.90 °N) in the tropics to Dongying, Shandong (38.00 °N) in the temperate zone (Appendix S1: Table S1). Because the geographic range of *S. alterniflora* continued to expand during the course of the study, we added an additional low-latitude site, Danzhou, Hainan (19.74 °N), in 2017. *Spartina alterniflora* was present at this site as early as 2014, but not common enough to sample until 2017.

At each site, we ran a transect (~2 km long, ~50 m wide) along the coastline. All sampling was conducted at

lower marsh elevations or along creek banks in habitats experiencing daily tidal inundation, because high intertidal marshes in China are intensively reclaimed for economic development or occupied by mangroves and *Phragmites australis* (Murray et al. 2014, Liu et al. 2020b). In every case we sampled monospecific stands with vigorous *S. alterniflora* plants. In 2014, 2015, and 2016, we visited the sites weekly, starting in April–August depending on the site, but always before flowering began. We visited until we saw a plant flowering, and recorded the first date in each year on which we observed a plant flowering at each site. We defined flowering as shoots in which the panicle had emerged out of the uppermost leaf and bore visible pollen (modified from Qiu et al. 2018). In 2017, we deployed five permanent 0.5 × 0.5 m plots at each site in order to document not just the onset of flowering but also its peak. Plots were spaced >30 m apart from each other, and were all deployed on the edge of *S. alterniflora* stands, where flowering was more common than in the interior of continuous stands (authors' personal observation). Each week, we counted the number of flowering shoots in each quadrat until the end of the growing season, and at the end of the growing season we also measured the height of the three tallest shoots that flowered in each quadrat. The date of the first flowering day was averaged across the plots to yield a single data point for each site.

We calculated the first flowering day of *S. alterniflora* as the number of days from 1 January every year until the first flower was observed (at the site in 2014–2016, and in every individual quadrat in 2017; Schwartz 2013). We also calculated the peak flowering day (Denny et al. 2014) in 2017 as the date weighted by the proportion of quadrats in which *S. alterniflora* stems were flowering:

$$\text{Peak flowering day} = \frac{\sum_{t=1}^T n_t * d_t}{\sum_{t=1}^T n_t}$$

where T is the total number of observations (quadrats per site), n_t is the number of quadrats per site in which *S. alterniflora* was flowering at observation t , and d_t is the day of the year at observation t (Li et al. 2016).

To relate first flowering time to abiotic conditions, we obtained data on annual average temperature, the annual number of growing degree days (mean average temperature ≥10°C), annual precipitation and annual mean tidal range for each site for each year during the period 2014–2017 from the China Meteorological Data Service Center⁴ (CMDC) and from tide tables published by the National Marine Data & Information Service.⁵ We also calculated the annual range and mean diurnal range of temperature to quantify variability in

⁴<http://data.cma.cn>

⁵<http://www.nmdis.gov.cn>

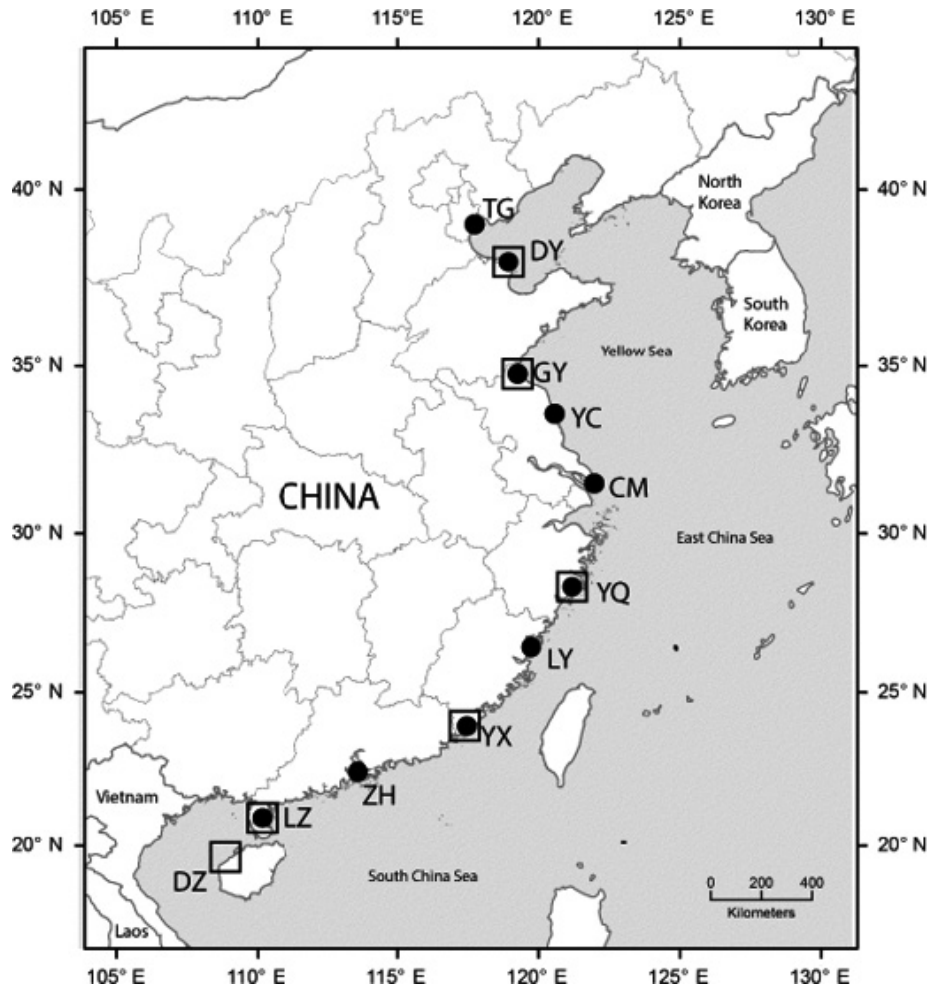


FIG. 1. Map of study sites. Filled circles indicate 10 sites where seeds were collected in 2014, and squares indicate 6 sites where phenology was monitored in 2014–2017. The full location names and their abbreviations can be found in Appendix S1: Table S1.

temperature that might affect plant phenology (Alexander et al. 2012). To determine how strongly the various abiotic variables were related to each other and to latitude, we performed all possible Pearson's correlations between these variables in each of 4 yr.

We treated each site year as an independent data point for analysis. Because we had relatively few sites (5 or 6) we could not rigorously test for site effects that were independent of latitude. Similarly, with only a few years, we could not test for carryover effects in which one year influenced the next. The year effects were tested in the first 3 yr (2014–2016) using ANCOVA with year as the main factor and latitude and latitude² as the covariates to determine whether the results would vary among different years. Because plots were only deployed in 2017, we used a mixed model (fixed effects: latitude + latitude²; random effect: plot) to test the effect of latitude on first flowering day. Because plant height is correlated with latitude and abiotic factors (Liu et al. 2016), we used a multiple regression for 2017 with plant height and latitude and latitude² as covariates to determine the

effect of plant height on first flowering time. Because sampling methods changed between 2014–2016 and 2017, we performed two analyses to evaluate whether first flowering time varied across latitude. According to the bioclimatic law, flowering time should be later with increasing latitude (Hopkins 1924), but we hypothesized that flowering time of *S. alterniflora* would instead display a hump-shaped relationship with latitude as was previously found for plant height (Liu et al. 2016), because flowering time is often positively correlated with size (Berrigan and Koella 1994). Therefore, at the very beginning, we conducted Akaike's information criteria (AIC) to select the best models (Vrieze 2012) in predicting relationships between the first and peak flowering day and the interval between them with latitude. First, we used quadratic regression to relate first flowering day to latitude for the period 2014–2016, with the data for the five sites in each of 3 yr combined into a single analysis ($n = 15$ site years). Second, we used quadratic regression to relate first and peak flowering days to latitude for 2017 ($n = 6$ sites). Finally, we used linear regression

to test if the interval between the first flowering day and the peak flowering day changed as a function of latitude in 2017. In each case, we evaluated latitude and latitude² as predictor variables, and selected the best model based on the smallest AIC score (Appendix S1: Table S2).

We next used multiple regression to evaluate whether first flowering date was related to abiotic variables. Given that the climate variables were strongly correlated with each other (see Results), we used growing degree days as a proxy for all three climate variables (growing degree days, annual average temperature, precipitation). We analyzed data for first flowering day from the six sites that were visited in any of the 4 yr, for a total of 21 site years. We tested for effects of growing degree days and tide range. The best model was selected based on AIC. To visualize these relationships, we also ran individual regressions for the 2014–2017 data to relate first flowering days to annual number of growing degree days ($\geq 10^\circ\text{C}$) and annual mean tidal range from the same year separately.

Common garden experiment

To evaluate the roles of genetic differences among populations and phenotypic plasticity in contributing to the latitudinal pattern of flowering phenology of *S. alterniflora*, we conducted a greenhouse common garden experiment at Xiamen University, Xiamen, Fujian (24.62°N , 118.31°E). The genetic differences were quantified as variation among provenances in the common garden, and phenotypic plasticity could be identified by comparing results from the common garden and the field. In particular, if the latitudinal trends found in nature disappeared or changed in the common garden, we attributed field patterns to plastic responses to different environments (Colautti et al. 2009, Liu et al. 2016). At the end of the growing season in 2014, we collected *S. alterniflora* seeds from 10 sites (Fig. 1; Appendix S1: Table S1) ranging from 20.9°N to 39.1°N . We did not collect seeds from the lowest-latitude site in Danzhou because *S. alterniflora* was still rare at this site. At each site, we haphazardly located 10 0.5×0.5 m quadrats, spaced at least 30 m apart. We haphazardly collected 10 mature, intact inflorescences from each quadrat, and then picked out the filled seeds (which can germinate) from every inflorescence (Ayres et al. 2008). The filled seeds from each quadrat were placed into separate, sealed plastic bags, and stored in 10 PSU (Practical Salinity Units) seawater at 4°C . In March 2015, we germinated seeds from each quadrat from each site and cultivated them in the laboratory under artificial light until seedlings were 7–8 cm tall. We transplanted one robust seedling from each quadrat into a 6-L (18 cm in diameter, 24 cm tall) plastic pot (10 sites $\times$ 10 quadrats = 100 seedlings), filled with a mixture of 50% Jiffy's peat substrate (Jiffy Products International BV, Moerdijk, Netherlands) and 50% vermiculite by volume. We placed the pots into 10 separate rectangular plastic pools in a

greenhouse, with each pool containing 10 seedlings, one from each of the 10 sites. The pools were filled with 10 PSU seawater mixed from sea salt so that the water level was about 2 cm above the soil level in the pots. The water was completely replaced once a month. Fresh water was added every other day as needed to maintain salinity. These soils and flooding regime did not precisely mimic the soil composition or the tidal regime experienced by plants in nature, which would have included periods of both lower and higher water levels, but did create a standard set of abiotic conditions in the common garden that allowed ready comparisons among plants from the different provenances. Moreover, the wet soil conditions in the pots were roughly comparable to the waterlogged soils found in creek-bank habitats in the field, which experience regular tidal flooding and never dry out for extended periods.

This common garden experiment ran over three growing seasons, from 2015 to 2017. In March of 2016 and 2017 we selected a single robust culm from each pot, repotted it in new media, and propagated it for another year using the same methods as above. Starting in late May of every year and continuing until the end of growing season in October, we recorded the date on which the first *S. alterniflora* shoot flowered in each pot. In 2017, we counted the number of flowering shoots in each pot monthly to calculate the peak flowering day and we also measured the height of the first two *S. alterniflora* shoots to flower in each pot. When fewer than two flowering shoots were present, we measured all the shoots.

Because the same clones were measured across the 3 yr, we analyzed the relationship between first flowering day and latitude of origin with the data for 10 provenances in the 3 yr (2015–2017) using repeated-measures ANCOVA to identify year effects. In the third year, 2017, we used a multiple regression with plant height and latitude and latitude² as covariates to determine the effect of plant size on first flowering day. We used linear regressions to relate first flowering day to latitude of origin in the 3 yr, and ran a separate analysis for peak flowering day in year 2017 because the peak flowering day could be calculated only in this year. Similarly, we also used linear regression to test the hypothesis that the interval between the first flowering day and the peak flowering day changed in the common garden as a function of latitude of origin in 2017.

To test the hypothesis that the climatic and tidal variables at the site of origin for each clone would explain the genetic differentiation in flowering phenology after the introduction of *S. alterniflora* into China, we used linear regression to analyze the relationships between first flowering day in the common garden of these 3 yr and annual number of growing degree days ($\geq 10^\circ\text{C}$), and annual mean tidal range of the origin sites from long-term averages. We chose to average the climate variables over the years 1981–2010 because this time period represents most of the years during which *S. alterniflora* was spreading along the coast of China after its

introduction in 1979. We calculated long-term averages for tide range only for the period 2008 to 2017 because tide data from earlier years are less available (Appendix S1: Table S1).

Finally, to test the hypothesis that plants flowered later at sites favoring taller plants, we used linear regression to examine the relationship between the first flowering day and plant height, using data from both the field and common garden. This was done only in 2017, because height was only measured in this year.

We performed all data analyses using JMP 10.0 statistical software (SAS Institute 2012).

RESULTS

Over the first 3 yr of sampling in the field, first flowering day displayed a hump-shaped relationship with latitude (Fig. 2a, $R^2 = 0.87$, $P < 0.0001$). Analysis with ANCOVA indicated no effect of year but a strong effect of latitude and latitude² (Appendix S1: Table S3). In 2017, with the additional site, we again found a strong effect of latitude ($P < 0.0001$) and latitude² ($P < 0.0001$) and observed a hump-shaped relationship between first flowering day and latitude (Fig. 2c, $R^2 = 0.95$, $P = 0.011$). Plants at intermediate latitudes (YQ) flowered about 10 d later than those at high latitudes (DY), and about 100 d later than those at low latitudes (DZ). In 2017, peak flowering day also showed a hump-shaped relationship with latitude (Fig. 2c $R^2 = 0.93$, $P = 0.018$), and the interval between first and peak flowering decreased with increasing latitude, suggesting that the flowering period was shorter at higher latitudes ($R^2 = 0.94$, $P = 0.0015$).

Climate variables (temperature, growing degree days, precipitation) and tidal data from the field sites during the years of the study were typical of the long-term record (Appendix S1: Table S1). Climate variables were strongly correlated with each other and with latitude (Appendix S1: Table S4, Fig. S1). Tide range, however, was independent of latitude and unrelated to climate variables (Appendix S1: Table S4, Fig. S1). As a result, first flowering day showed a hump-shaped relationship when plotted against annual number of growing degree days ($\geq 10^\circ\text{C}$; Fig. 3a), but a linear relationship with tidal range, indicating that *S. alterniflora* flowered later in sites with a greater tidal range (Fig. 3c). The best multiple regression analysis for first flowering day included both growing degree days (linear and quadratic relationships) and tide range as predictor variables (Table 1).

In contrast to the hump-shaped pattern seen in the field, the first flowering day of *S. alterniflora* in the common garden decreased linearly with increasing latitude of origin in both 2015 and 2016, with individuals from higher latitudes flowering earlier (Fig. 2b, 2015: $R^2 = 0.13$, $P = 0.0011$; 2016: $R^2 = 0.07$, $P = 0.050$). In 2017, first flowering day was again negatively related to latitude of origin (Fig. 2d, $R^2 = 0.59$, $P = 0.0095$). The repeated-measures ANCOVA analysis indicated no

effect of year but a strong effect of latitude (Appendix S1: Table S5). Peak flowering day, measured only in 2017, was also negatively related to latitude of origin in the greenhouse (Fig. 2d, $R^2 = 0.47$, $P = 0.030$). In the common garden, the interval between first flowering day and peak flowering day in 2017 increased with increasing latitude, indicating that individuals from higher latitudes had a longer flowering period (Fig. 2d, $R^2 = 0.53$, $P = 0.017$).

First flowering day in the common garden was related to the annual number of growing degree days ($\geq 10^\circ\text{C}$), but the relationship was much weaker than that in the field, and linear rather than curved, with individuals from hotter sites flowering later (Fig. 3b). In contrast, the first flowering day in the common garden was not related to tide range at the site of origin (Fig. 3d). Using temperature and time data for the years 2015–2017 instead of the years 1981–2010 produced results that were almost identical (annual growing degree days, $R^2 = 0.26$, $P = 0.0040$; annual mean tidal range, $R^2 = 0.09$, $P = 0.11$).

In both the field and the common garden, first flowering day was correlated with plant height (Appendix S1: Table S6) such that flowering occurred later in site years for which plants were taller (Fig. 4). The relationship, however, was much stronger in the field (higher R^2 and steeper slope) than in the common garden (field: $R^2 = 0.47$, $P < 0.0001$, slope = 0.83; common garden: $R^2 = 0.045$, $P = 0.037$, slope = 0.38). Because both relationships were quite variable, there was only a marginally significant difference between the slope of the two linear regressions ($P = 0.073$).

DISCUSSION

The different latitudinal patterns in the field and common garden indicate a large degree of phenotypic plasticity in the timing of flowering, but also some selection since *S. alterniflora* was introduced to China for earlier flowering at high latitudes where the growing season is constrained. We observed a novel hump-shaped relationship between flowering phenology (first and peak flowering day) and latitude for *S. alterniflora* in China, and a novel relationship between first flowering day and tide range. Finally, the geographic pattern of phenology and earlier flowering time with smaller plant size suggests that future spread of *S. alterniflora* in East Asia may be slow. Our results suggest the adaptive mechanisms and major abiotic factors shaping the latitudinal flowering phenology of *S. alterniflora* in both the native and introduced ranges.

In the field, we observed a hump-shaped relationship between flowering time (both first flowering day and peak flowering day) and latitude. To the best of our knowledge, this is a novel pattern of flowering phenology. Many other studies have reported linear relationships between flowering time and latitude, and the different results that we obtained may reflect the broad

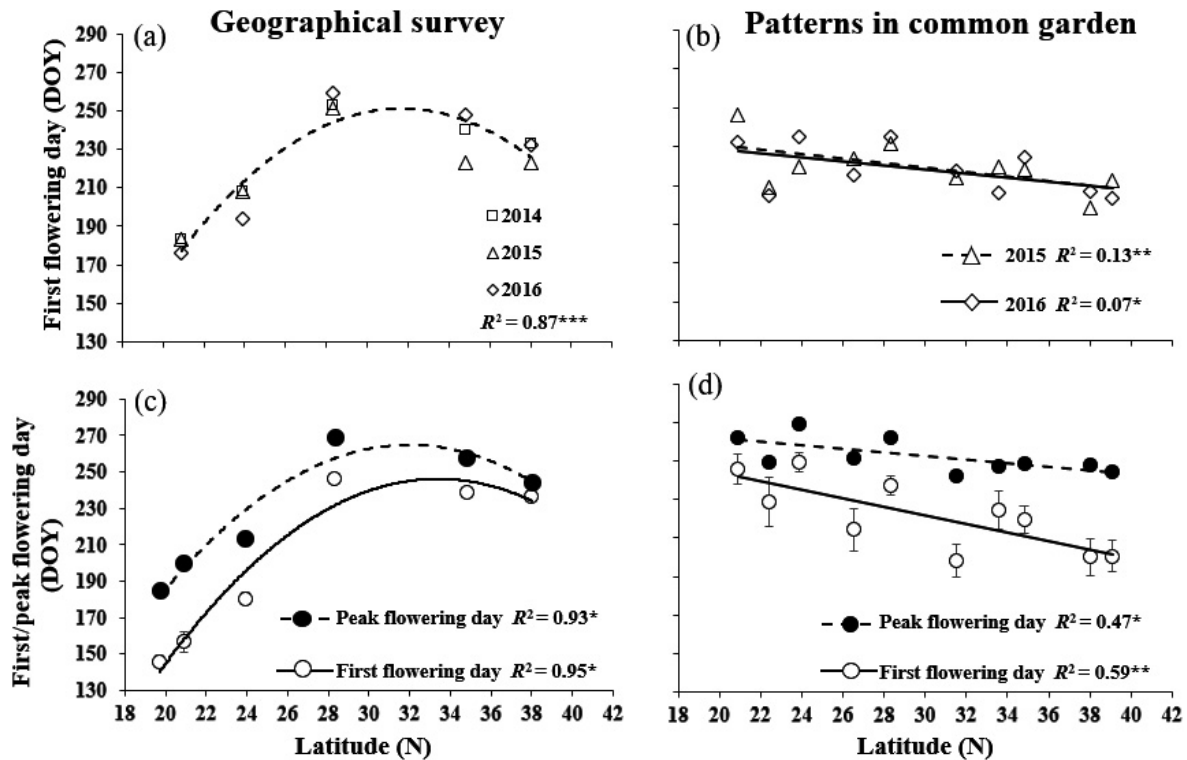


FIG. 2. The relationship between *Spartina alterniflora* flowering phenology variables and latitude in the geographical survey (a), (c) and the common garden (b), (d). (a) First flowering day in 2014–2016 at five field sites; (b) first flowering day in 2015 and 2016 in the common garden; (c) first flowering day and peak flowering day in 2017 at six field sites, values are means and SE, error bars are not shown if smaller than symbols; (d) first flowering day and peak flowering day in 2017 in the common garden, values are means and SE, error bars are not shown if smaller than symbols. DOY: day of year. Significance levels, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. See Appendix S1: Table S3 and S5 for full statistical analysis.

latitudinal range (19.7 °N to 38 °N) of our study compared to the narrower latitudinal range of many previous ones (Montague et al. 2008, Liang 2016). Many past studies have found that flowering phenology advances at low latitudes because warmer climates increase physiological activity (Menzel et al. 2006, Anderson et al. 2012, O'Connell et al. 2019), and this is a reasonable explanation for the significantly earlier flowering time of *S. alterniflora* at low latitudes in China. Light availability such as photoperiod and radiation intensity may be another factor in driving plant phenology along latitude (Craufurd and Wheeler 2009), but here we follow most other studies in considering temperature as the most important meteorological factor shaping plant phenology, especially under current global climate change (Wilczek et al. 2010, Pau et al. 2011, Schwartz 2013). The earlier flowering time at high latitudes is likely related to the shorter growing season at high latitudes, which limits the time available to complete the life cycle (Munguia-Rosas et al. 2011, Schwartz 2013). We also found that first flowering time was positively correlated with tide range. To our knowledge, this is the first report of this phenomenon, and it is likely driven by tide range affecting plant growth and thereby advancing flowering

phenology, as we discuss below. The gap between first and peak flowering dates was shorter at high latitudes, consistent with previous reports of a compressed flowering season at high latitudes (Qiu et al. 2018). All else being equal, a compressed flowering season should lead to more effective pollination (Fagan et al. 2010), and this may partially explain the higher seed set observed for *S. alterniflora* at high latitudes in China (Liu et al. 2016, Qiu et al. 2018). Thus, by combining an understanding of phenology with previous work on reproductive traits, we gain a more comprehensive and integrated understanding of evolution and adaptation in plant invasion across latitude.

In the common garden, flowering time (both first flowering day and peak flowering day) was negatively related to latitude of origin. This result was consistent with previous reports of rapid evolution in traits related to sexual reproduction of *S. alterniflora* in China (Liu et al. 2016, 2017). It suggests an adaptive response at high latitudes (earlier flowering in regions where the growing season is more compressed). Whether the cline observed in the common garden is also adaptive at low latitudes remains to be determined. A companion study of flowering phenology across the entire latitudinal

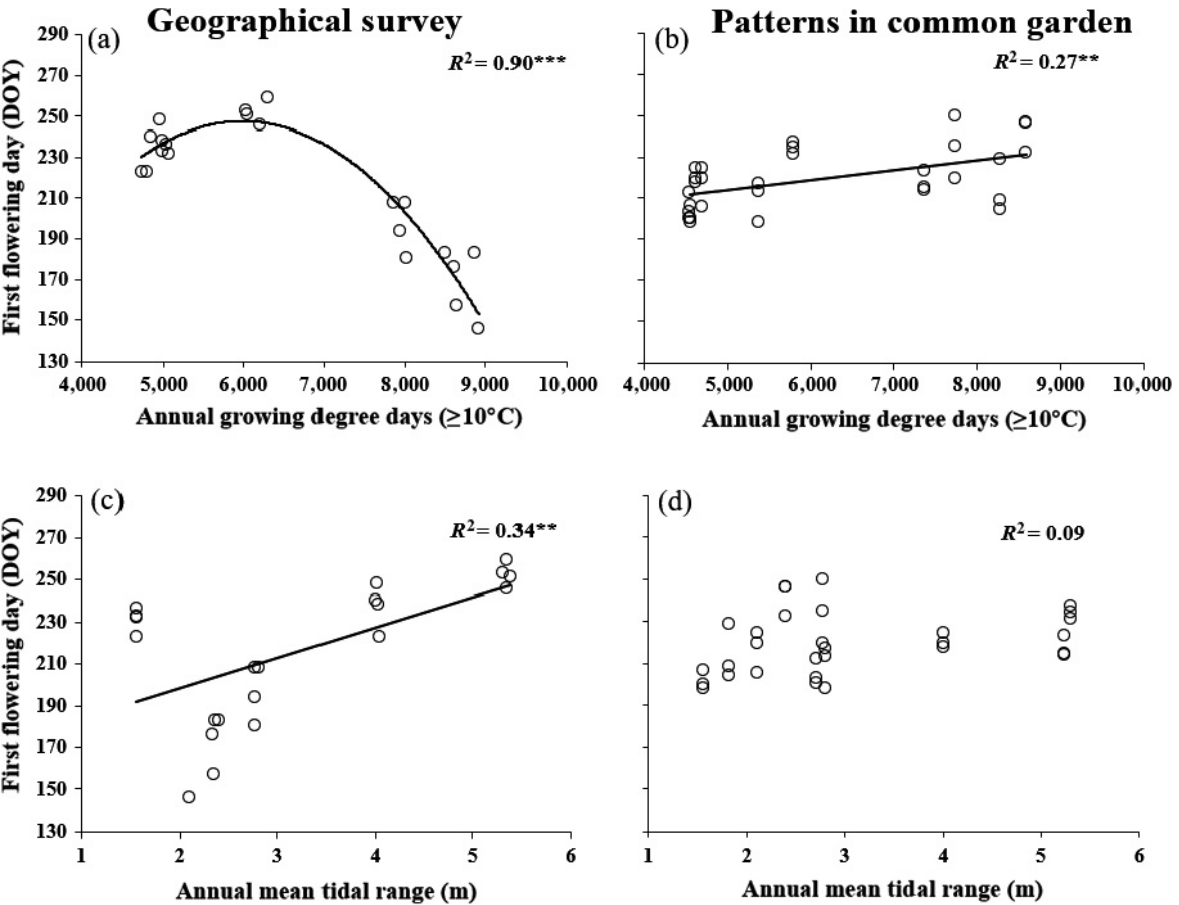


FIG. 3. The relationship between the first flowering day of *Spartina alterniflora* and abiotic variables in the geographical survey (a), (c) and the common garden (b), (d). (a) First flowering day in 2014–2017 in field versus the annual growing degree days ($\geq 10^{\circ}\text{C}$) in 2014–2017, (b) first flowering day in 2015–2017 in the common garden versus the annual growing degree days ($\geq 10^{\circ}\text{C}$) (long-term average) at sites of origin, (c) first flowering day in 2014–2017 in field versus annual mean tidal range in 2014–2017, (d) first flowering day in 2015–2017 in the common garden versus the annual mean tidal range (long-term average) at sites of origin, DOY: day of year. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 1. Best regression model for variation in *Spartina alterniflora* first flowering day in the field. Data are 2014, 2015, 2016, and 2017 combined from *Spartina alterniflora* growing at six field sites, $n = 21$.

Variable	Model	R^2	P
First flowering day	$-56.28 + 0.10 \text{ Growing degree days}^* + 4.34 \text{ Tidal range} - 8.45e^{-6} \text{ Growing degree days}^{2**}$	0.92	<0.0001

* $P < 0.01$,
** $P < 0.001$.

range in the native range would be helpful in interpreting this new cline in the introduced range. The dramatic difference between the pattern of flowering in the common garden and in the field indicates that the field pattern was partly driven by phenotypic plasticity as plants responded to local abiotic conditions. Moreover, although the first flowering day in the field was related

to tide range, this relationship disappeared in the common garden, again suggesting that the field patterns were largely driven by phenotypic plasticity. The observed negative relationship between flowering date and latitude in the greenhouse, although weaker than the field pattern, is consistent with results from many other invasive plants in common garden experiments (Pau et al. 2011, Novy et al. 2013, Li et al. 2015). Given that all the *S. alterniflora* plants on the coast of China had a common origin four decades ago, this indicates rapid and perhaps ongoing selection for earlier flowering at sites with a shorter growing season as occurs in the native range (Seneca 1974, Somers and Grant 1981, Crosby et al. 2015).

A possible caveat to our results is that we had only one common garden, which was located at low latitudes in a subtropical region (24.62°N). Our results would have been stronger if we had reciprocal transplant experiments or multiple common gardens at different

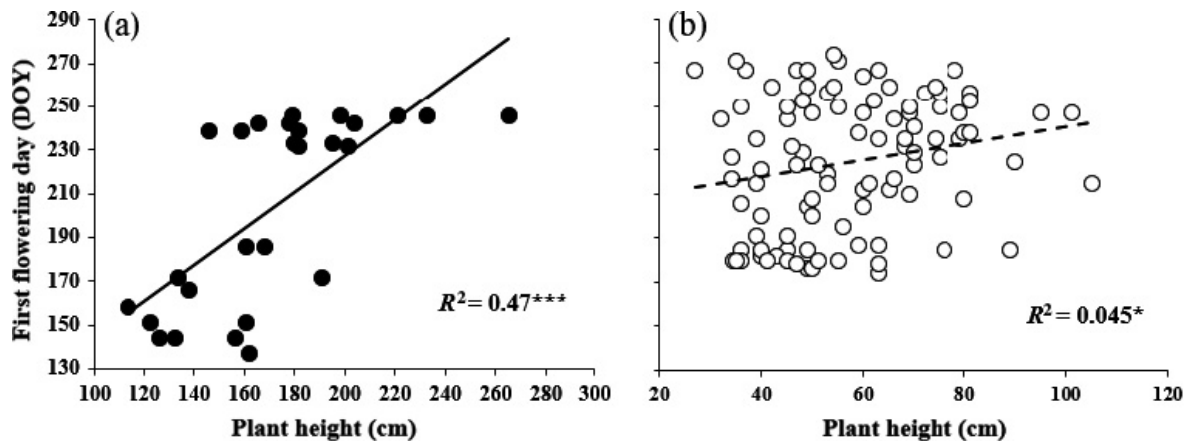


FIG. 4. The relationship between the first flowering day and plant height in the year 2017 for *Spartina alterniflora* (a) in the field, and (b) growing in the common garden. DOY: day of year. Significance levels: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. See Appendix S1: Table S6 for full statistical analysis.

latitudes. However, a previous study with *S. alterniflora* in China conducted with a common garden at higher (31.30 °N) latitudes also found a negative relationship between first flowering day and latitude of origin (Zhang et al. 2008), suggesting that our results are at least partially robust to the latitude at which the common garden was established. Nevertheless, it would be informative to also have data from a common garden close to the high-latitude range limit of *S. alterniflora*.

In a proximate sense, the timing of flowering was likely driven in part by plant size. Life-history theory suggests that the optimum size for reproduction will differ among populations or dates due to trade-offs between survival and size-specific fecundity (Berrigan and Koella 1994). In general, conditions allowing rapid growth favor delayed reproduction because larger individuals have higher fecundity (Hesse et al. 2008). Previous work in the native range of *S. alterniflora* found that flowering occurred at a greater size in microhabitats, sites or years where plants attained larger size (Liu and Pennings 2019). The same pattern was found in our study in China: Plants flowered later (e.g., delayed flowering to allow more growth) at sites where plants grew larger (Fig. 4). Previous work suggested that plants grow larger at intermediate latitudes in China because high-latitude sites rarely reach the thermal optimum for photosynthesis of around 30°C (Giurgovich and Dunn 1979, Więski and Pennings 2014), whereas low-latitude sites commonly exceed it (Liu et al. 2016). Moreover, the large tidal range found at intermediate-latitude sites likely improves the drainage of toxins and infiltration of oxygen in soils (Mendelssohn and Morris 2002), further enhancing the growth (and favoring a delay in flowering time) of *S. alterniflora* plants at intermediate latitudes in China. To our knowledge, this is the first study implicating tide range as a factor mediating flowering phenology, probably because tide range is a factor that would only

apply to intertidal ecosystems, which have received less attention in terms of plant phenology. A few prior studies have suggested the effect of tidal elevation or frequent submergence on flowering phenology of *S. alterniflora* at a local scale, with higher elevation and less inundation correlated with earlier flowering, although in these studies growing degree days still was the main driver of flowering time (Crosby et al. 2015, O'Connell et al. 2019). The combination of these findings suggests that the effect of tide range, intertidal elevation, and inundation time on plant phenology deserves more attention in intertidal ecosystems. It is likely that the general bioclimatic law of phenology (Hopkins 1924) will need to be expanded for intertidal plants to include hydrological variables as additional explanatory factors. However, mesocosm studies will be required to confirm this apparent link between tide range and first flowering time experimentally.

The earlier flowering time at low and especially high latitudes in China, coupled with the smaller size of plants at these latitudes (Liu et al. 2016, 2017), suggests that *S. alterniflora* already occupies much of the geographic range favorable for it on the east coast of Asia. As *S. alterniflora* continues to spread north into North Korea (Kim 2016) and possibly beyond, it may reach a latitude at which flowering is no longer possible, as has been found at 48 °N for introduced populations on the West Coast of North America (Riggs 1992). At this point, further expansion will be possible only through clonal growth and the transport of rhizome fragments following disturbances. As *S. alterniflora* continues to spread south into Vietnam, it will be increasingly less vigorous due to warm temperatures (Liu et al. 2016, Liu and Pennings 2019), and will face increasing competition from tropical mangroves (Zhang et al. 2012, Peng et al. 2018). Thus, the era of rapid geographic spread of exotic *S. alterniflora* on the Asian coastline (Strong and Ayres 2013) may be coming to an end.

By combining field surveys across a wide latitudinal range with a common garden experiment, our study expanded our inference range beyond that of some other studies that have focused on northern sites with a narrower latitudinal range (Montague et al. 2008, Liang 2016). We encourage future phenological studies to cover the whole distribution of the species under consideration, and to interrogate field results with common garden experiments. We found that invasive plants could respond to natural selection in their new range using a combination of phenotypic plasticity and evolution. At geographic scales, these mechanisms might contribute to novel phenological patterns, such as the hump-shaped pattern of flowering phenology that we observed. Global warming is likely to favor advanced flowering time in many plant species (Munguía-Rosas et al. 2011). In the case of *S. alterniflora*, however, warm temperatures are not just associated with earlier flowering, but also with lower seed set (Liu et al. 2016, Qiu et al. 2018) and smaller size (Fig. 4), indicating important temperature constraints on plant success and the spread of exotic species.

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