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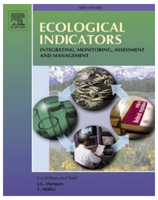

Life-history plasticity of intertidal salt marsh in response to sea level rise: Salinity and inundation modulate size-dependent flowering of *Spartina alterniflora*

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ABSTRACT

The life-history theory posits that the optimum threshold size for flowering determines the transition in resource allocation, resulting from trade-offs between reproduction, survival, and vegetative growth. The stresses such as drought and nutrient limit can induce flowering at smaller sizes in terrestrial ecosystems, but how the factors in coastal wetland influence the threshold size for flowering remains unclear. Here, we employed the widely distributed salt marsh plant, *Spartina alterniflora*, and established an in-situ mesocosm array along the estuarine gradient to manipulate sediment porewater salinity and inundation duration, the key factors jointly shaping species distribution of salt marsh community. We found that higher salinity reduced plant size and advanced flowering, whereas prolonged inundation increased plant size and delayed flowering. Consequently, the threshold size for flowering decreased with increasing salinity but increased with longer inundation duration. Furthermore, these abiotic factors affected the threshold size for flowering both directly and indirectly, with inundation duration emerging as the primary determinant. Given that salt marsh ecosystem productivity and functioning are threatened by the increasing salinity and inundation duration associated with sea-level rise, our findings suggest that shifts in plant life history strategies promote sexual reproduction for regeneration and may contribute to the ecosystem resilience under global change.

1. Introduction

Coastal ecosystems occupy the land-sea interface and show high primary production and carbon sequestration (Alongi, 2020). The abiotic environment of this ecosystem is characterized by high variability in salinity and tidal inundation, caused by tidal amplitude and freshwater discharge. Thus, salinity and inundation emerge as the two critical abiotic factors that limit plant growth and distribution (Perillo et al., 2018). Salt marshes, together with mangroves and seagrasses, are typical ecosystems in coastal wetland, and many common salt marsh plants usually form striking plant zonation pattern with high productivity (Davy, 2000; Liu and Pennings, 2021). Furthermore, salt marshes can generate a wide range of plastic responses in plant traits and fitness under strong abiotic variations (Bennett et al., 2009), becoming an ideal model system for studying how abiotic factors shape plant traits and life histories (Pennings and Bertness, 2001). Therefore, investigating phenotypic and life history variation in salt marsh plants could improve our understanding of individual fitness, population viability, primary productivity, and ecosystem functioning.

For plants in terrestrial ecosystems, flowering allows plants to shift

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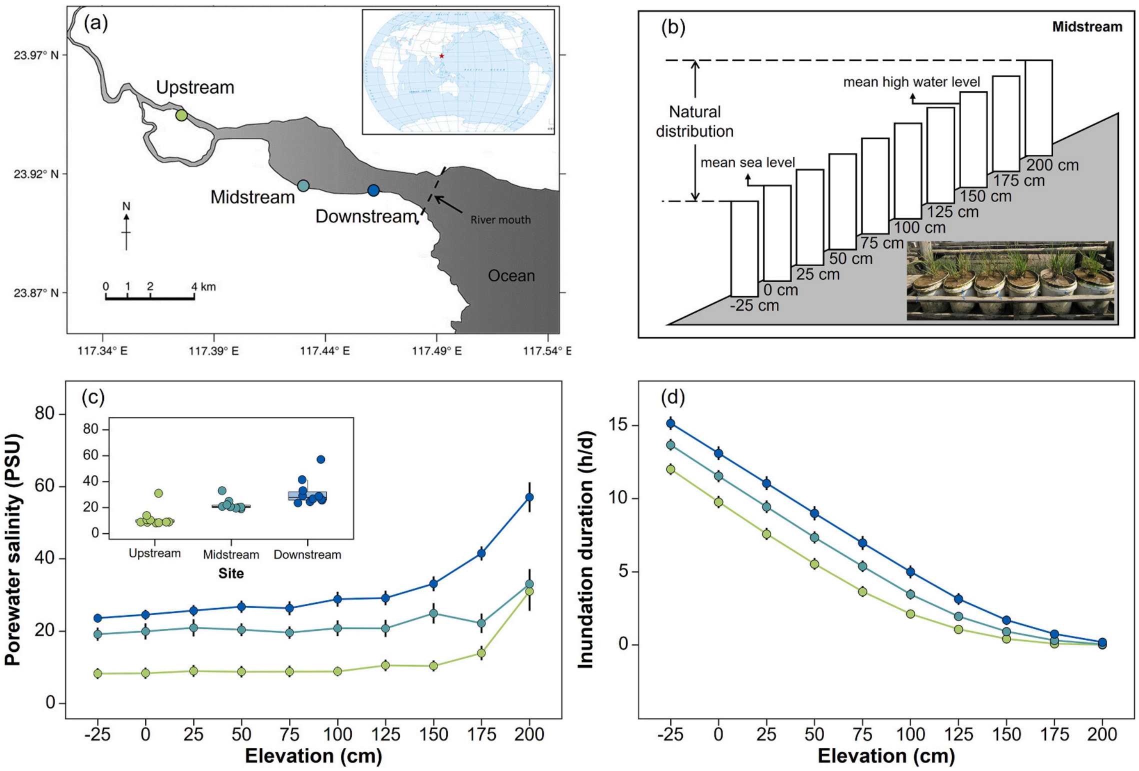

Fig. 1. Location of study sites in Zhangjiang Estuary (a) and schematic diagram of the elevation array set up in the midstream site, with 6 replicates in a block per elevation (b). The mean sea level is referred as Zhu et al. 2019 and the mean high water level is estimated using daily tidal rhythm data averaged from 2021 to 2022. The variations of sediment porewater salinity (c) and inundation duration (d) across elevations are shown for different sites.

from vegetative growth to reproduction, and represent a significant event in life-history transition (Galloway and Burgess, 2012). Previous studies found that the flowering response could be altered by photoperiodicity and temperature (Cleland et al., 2007; Takeno, 2012). In addition, environmental stress, such as drought and nutrient limit, is increasingly recognized as a critical factor that regulates flowering response (Kazan and Lyons, 2016). Plants often inhibit growth and accelerate flowering under environmental stress (Takeno, 2012), and such a flowering time acceleration promotes reproductive success (Anderson et al., 2012; Ehrlén and Valdés, 2020). Although the flowering decision adjustment optimizes plant fitness, it shortens the duration of resource accumulation for vegetative growth, resulting in smaller plant size (Colautti et al., 2010). The trade-off between vegetative growth and reproduction (Sugiyama and Bazzaz, 1998; Obeso, 2002; Hulshof et al., 2012) under environmental stress could be illustrated by the threshold size for flowering, representing the minimum size a plant to achieve before flowering (Wesselingh et al., 1997). It has been convinced that unfavorable growing conditions such as low nutrient levels (Jameson et al., 2022) and soil moisture (Méndez and Karlsson, 2004) were associated with a smaller threshold size for flowering. However, most studies on life history trade-offs mainly focused on terrestrial ecosystems, with less empirical attention to coastal salt marshes (but see Castillo and Figueroa, 2009; Gallego-Tévar et al., 2020). Therefore, it is urgent to examine whether the theory also applies to coastal ecosystems with high variability in multiple environmental factors.

Salt marshes are intertidal grasslands distributed across latitudes, and *Spartina alterniflora* is a representative dominant salt marsh plant widely distributed across temperate and subtropic coastal wetlands globally (Strong and Ayres, 2013). *S. alterniflora* displays substantial variations in plant phenotypic traits across different landscape locations (Richards et al., 2005), and previous common garden experiments have demonstrated that at the geographic scale, the variations in phenotypic traits derive from the genetic differentiation and the genetically based phenotypic plasticity differences (Liu et al., 2016, 2017, 2020; Chen et al., 2021). At the local scale, *S. alterniflora* also shows strong plasticity in response to salinity and tidal inundation. Previous transplanted experiments demonstrated a hump-shaped biomass change with tidal inundation in both its native and invasive ranges (Morris et al., 2013; Peng et al., 2018). Other studies found that the seed set decreased linearly with inundation duration (Xue et al., 2018) and the inflorescence biomass was significantly suppressed by the increasing salinity (Xiao et al., 2011). Due to the strong phenotypic plasticity and genetic variation to adapt to heterogeneous environments, *S. alterniflora* has become a model species for studying plant life history in salt marshes (Liu and Pennings, 2019; Jiang et al., 2025). However, previous research has primarily documented variations in single or multiple traits, yet rarely explored the life history trade-off in response to environmental stresses. Therefore, elucidating the life history trade-off can provide critical insight into the salt marsh response to global change factors including sea-level rise.

To address this question, we employed the salt marsh plant, *S. alterniflora*, and manipulated the sediment porewater salinity and tidal inundation duration by establishing an in-situ mesocosm array along the estuary. Specifically, we asked the following questions: (a) what are the patterns of plant size and flowering time across porewater salinity and inundation duration? (b) how does the threshold size for flowering in response to the two different environmental factors? (c) based on the above two questions, what is the prominent factor that modulates the variation of life history in salt marsh ecosystems? We hypothesize that the plants would exhibit strong plastic responses and different life-history strategies when facing salinity and inundation stresses to ensure plant survival and sexual reproduction, which is limited by the balance inherent to size-dependent growth.

2. Materials and methods

2.1. Study area and species

Our study was carried out in the estuary of the Zhangjiang River (Fig. 1a), Fujian Province, southeast China (23° 53′–23° 57′ N, 117° 23′-117° 30′ E). Over the past five years (2018–2022), the annual average temperature was 22.9 ℃ and the annual average precipitation was 1219 mm. The estuary is 13.3 km long with a semidiurnal tide (maximum tidal height of 3 to nearly 8 m over several years, with an average annual range of 2.32 m; Lin, 2001). The influence of alternating flood and ebb tides, as well as freshwater discharge, results in a salinity gradient with fresher regions in the uppermost tidal reach of the river and salter regions near the river mouth (Zhang et al., 2012).

S. alterniflora is a globally invasive salt marsh species due to its strong adaptations and plasticity in heterogeneous intertidal habitats. It was introduced to China in 1979 (An et al., 2007) and has since spread across the entire coastline of China (Zhang et al., 2017). *S. alterniflora* arrived in the Zhangjiang Estuary in the late 1990s and is now widely spread across the estuary, with the most vigorous monospecific stands occurring in the mesohaline region (Zhang et al., 2012). The distribution and plant growth are thought to be affected by variations of tidal flooding (McKee and Patrick, 1988). In general, *S. alterniflora* exhibits a broad intertidal distribution (Fig. 1b), ranging from below the mean sea level to above the mean high water level with regularly flooded every day, spanning over an elevation of about 1.5 m (Peng et al., 2018; Zhu et al., 2019).

2.2. The experiment

2.2.1. Marsh organ design

To manipulate different salinity levels, we choose three sites along the Zhangjiang Estuary: upstream (23° 56′ 36.7″ N, 117° 22′ 42.5″ E; oligohaline, ~ 10 PSU), midstream (23° 54′ 59.5″ N, 117° 25′ 46.9″ E; mesohaline, ~ 20 PSU) and downstream (23° 54′ 46.5″ N, 117° 27′ 49.7″ E; polyhaline, ~ 30 PSU) site from the head of the estuary to the river mouth (Fig. 1c). To investigate the influence of inundation duration, we established in-situ mesocosm arrays, following the “marsh organ” design (Morris, 2007; Kirwan and Guntenspergen, 2012) at each site (Fig. 1d). The array was set at an interval of 25 cm elevation and a total of 10 elevations per site, spanning the intertidal distribution of *S. alterniflora*. Each elevation consisted of 6 replicate mesocosms in a block (n = 6; Fig. 1b), yielding 180 experimental units across all three sites.

The arrays were placed in the tidal creeks, with the second lower elevation along the array at the midstream site aligned to the mean sea level (elevation = 0 cm; the mean sea level was referred to Zhu et al. 2019, estimated using daily tidal rhythm data averaged over one year from Sep. 20th, 2016 to Sep. 20th, 2017, which was similar to the long-term tidal condition over the past two decades at nearby Dongshan tidal station). The alternative elevation at the midstream site was set at intervals of 25 cm, from −25 to 200 cm. The different elevation levels for the upstream and downstream sites were calibrated to be consistent with the midstream using the real-time kinematic GPS. Each mesocosm was constructed of a 28.5 cm diameter by 33 cm depth (18 L) plastic bucket with three 1 cm-diameter holes cut in the bottom to allow water exchange (Fig. 1b).

2.2.2. Environmental factors manipulation

For porewater salinity, we randomly selected 3 mesocosms per elevation at each site to collect sediment samples, and repeated the measurements every 2 months with 5 times in total over the experiment. Porewater salinity was detected by using the gravimetric saturation extract method, rehydrating the dried sediment samples in a known volume of fresh water, measuring the salinity of the supernatant after 24-hour equilibration, and back-calculating to the original porewater salinity (Pennings and Richards, 1998).

For inundation duration, we used paired pressure transducers (HOBO U20L-04) to record real-time data of tidal variation at 10-minute intervals for 8 months during the experiment at each site. One transducer positioned flush with the lowest-elevation mesocosm rim measured water pressure, while the other transducer mounted above the high tide level recorded barometric pressure. Water depth at the reference elevation was derived in real-time from pressure differentials, enabling calculation of daily submergence hours for each elevation treatment. Monthly means were computed as inundation duration.

2.2.3. Plant transplantation and traits collection

The plant materials were collected from ramets of a single clone in a thriving population near the midstream mesohaline site, and transplanted into each mesocosm. Thus, the *S. alterniflora* ramets were genetically uniform in this experiment, and the response to environmental gradients reflects phenotype plasticity. At the beginning of the growing season (February 25–27, 2022), we excavated a total of 180 plugs (15 cm diameter × 20 cm deep; 10.1 ± 0.3 ramets/plug) of *S. alterniflora*, and transplanted into the mesocosms containing sediment near the tidal creek from each site, with all visible plant and animal material removed. Transplant survival exceeded 98 %, with clonal ramets of only 3 mesocosms at lower elevations dying during the growing season.

The transplanted plant plugs of *S. alterniflora* continued producing new individual ramets throughout the growing season. From early June 2022, we visited sites weekly until we saw the first plant flowering. We then visited every individual flowering clonal ramet at each mesocosm every ~ 3 to 7 days to record the date of flowering from June to October 2022. Flowering was confirmed upon panicle emergence from the uppermost leaf with bore visible pollen. We recorded the flowering day of an individual ramet as the sequential day number starting with day 1 on 1 January until the flower was observed (DOY, day of year), and calculated the average flowering day of all the flowering ramets for each mesocosm. At the end of the growing season, we examined whether each adult individual ramet with sclerenchymatous tissues was flowering (1) or not (0), measured the plant height, and calculated the average plant height of all the flowering ramets for each mesocosm. For the 180 mesocosms of the three sites, we measured a total of 7134 individual ramets of *S. alterniflora* (Appendix S2: Table S1).

2.3. Statistical analysis

To examine how the experimental setup including sites and manipulated elevations gives rise to intertidal environmental gradients, we applied linear mixed effect models to the measurements of sediment porewater salinity and tidal inundation duration. For both the porewater salinity and inundation duration, the fixed effects included site, elevation, and their interaction. The porewater salinity included block, time and mesocosm as the random effects, while inundation duration only included block and time (Appendix S1, Appendix S2: Table S2). We calculated the porewater salinity and inundation duration for each manipulated elevation to illustrate the intertidal environmental gradients at different sites.

To test the effects of salinity level and inundation duration on plant traits, we applied linear mixed effect models to analyze the flowering plant height and flowering day. In these models, salinity level, inundation duration and their interaction were included as fixed factors, while block and mesocosm were incorporated as the random effects. To determine the threshold size for flowering, we fitted logistic regression models for each mesocosm and elevation, regressing flowering probability against plant height. From the significant regression results, we estimated the plant height at which a ramet had a 50 % flowering probability as the threshold size for flowering (Wesselingh et al., 1997; Liu and Pennings, 2019). To assess the effects of salinity level and inundation duration on the threshold size for flowering, we also applied linear mixed effect models to the threshold size estimated for each

Table 1

Summary statistics of linear mixed effect models for plant height, flowering day, and threshold size for flowering. *F* is the statistics for the fixed effects and χ^2 is for the random effects. *P* value in bold indicates significant results ($P < 0.05$).

	(a) Plant height			(b) Flowering day			(c) Threshold size for flowering		
Factor effects	***df***	***F*/χ^2**	***P***	***df***	***F*/χ^2**	***P***	***df***	***F*/χ^2**	***P***
Fixed effect									
Salinity level (S)	2, 23	14.92	**<0.001**	2, 22	10.29	**<0.001**	2, 18	12.03	**<0.001**
Inundation duration (I)	1, 29	116.10	**<0.001**	1, 30	31.95	**<0.001**	1, 18	96.13	**<0.001**
S × I	2, 29	4.51	**0.02**	2, 31	6.98	**0.003**	2, 23	0.35	0.71
Random effect									
Block	1	88.92	**<0.001**	1	20.50	**<0.001**	1	67.78	**<0.001**
Mesocosm	1	32.67	**<0.001**	1	16.73	**<0.001**	–	–	–

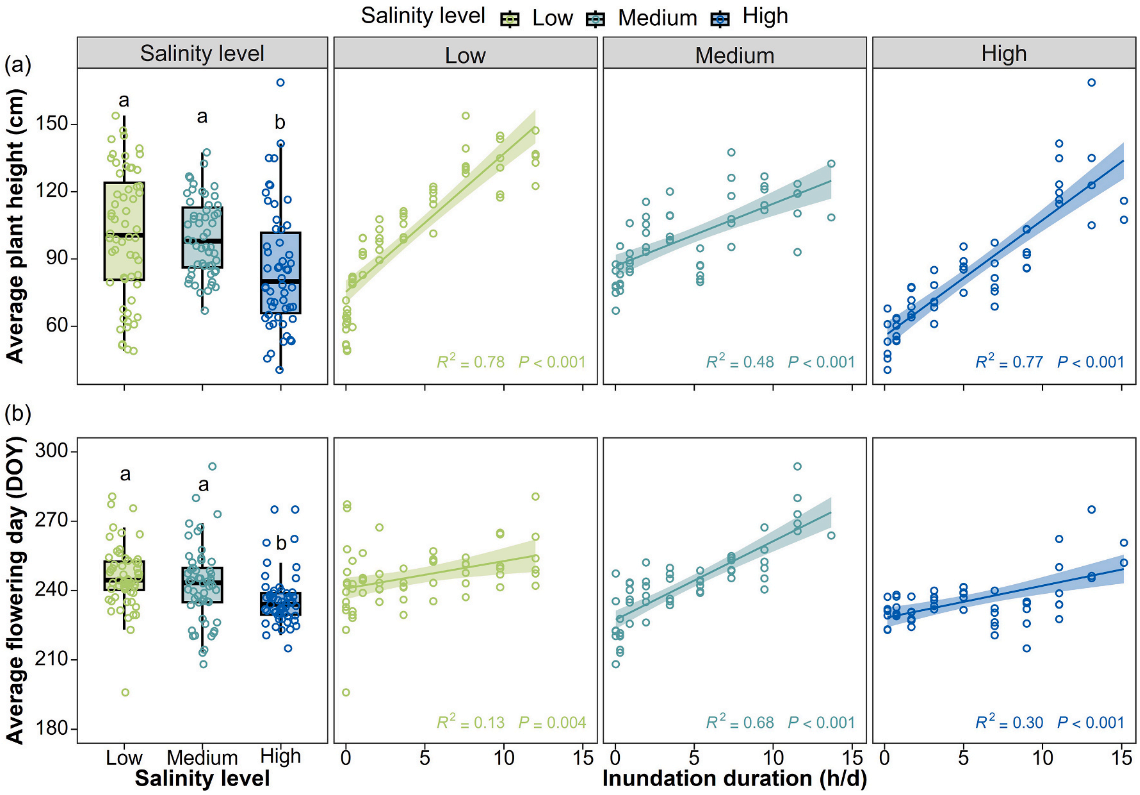

Fig. 2. The variation of the plant height (a) and flowering day (b) for different salinity levels, and alongside inundation duration for each salinity level. Dots represent the mesocosm means. The salinity levels correspond to different sites in the experiment (Fig. 1).

mesocosm, with salinity level, inundation duration and their interaction as fixed factors, and the block as the random effect. To visualize the impacts of salinity and inundation duration on plant traits, we conducted regression analyses of the average plant height, average flowering day and threshold size for flowering of different mesocosms against inundation duration and conducted multiple comparisons among salinity levels.

To determine whether environmental factors associated with our treatments affected the average plant height, average flowering day, and threshold size for flowering, we employed a structural equation model. The SEM allowed us to explicitly explore the direct effects of environmental factors (i.e., salinity level, inundation duration) on plant life history traits (i.e., plant height, flowering time), as well as to examine both the direct and indirect effects of these factors on the threshold size for flowering. We used the site values for salinity, elevation means for inundation duration and plant traits estimated for each mesocosm as input data. Indices including Chi-square, CFI (comparative fit index), TLI (Tucker-Lewis index), RMSEA (root mean square error of approximation), SRMR (standardized root mean squared residual) provided a comprehensive understanding of the model performance.

We performed all analyses using R v.4.1.2 statistical software (R Development Core Team, 2021), using *glm* function for logistic regressions, *lmer* function in the “lme4” package (Bates et al., 2015) for linear mixed effect models, *ghlt* function in the “muticomp” package (Hothorn et al., 2008) for multiple comparisons. Both *psem* function in the “piecewiseSEM” package (Lefcheck, 2016) and *sem* function in the “lavaan” package (Rosseel, 2012) were used for structural equation modelling.

3. Results

3.1. Life history traits in response to salinity level and inundation duration

Both the salinity level and inundation duration had a significant effect on plant height (Table 1a). The average plant height was 85.1 cm at the high salinity level, significantly lower than other levels (99.8 cm and 101.2 cm, Fig. 2a). For all salinity levels, the plant height increased linearly with inundation duration (Table 1a, Fig. 2a). The rate of increase varied, being faster at the low and high salinity levels, where the

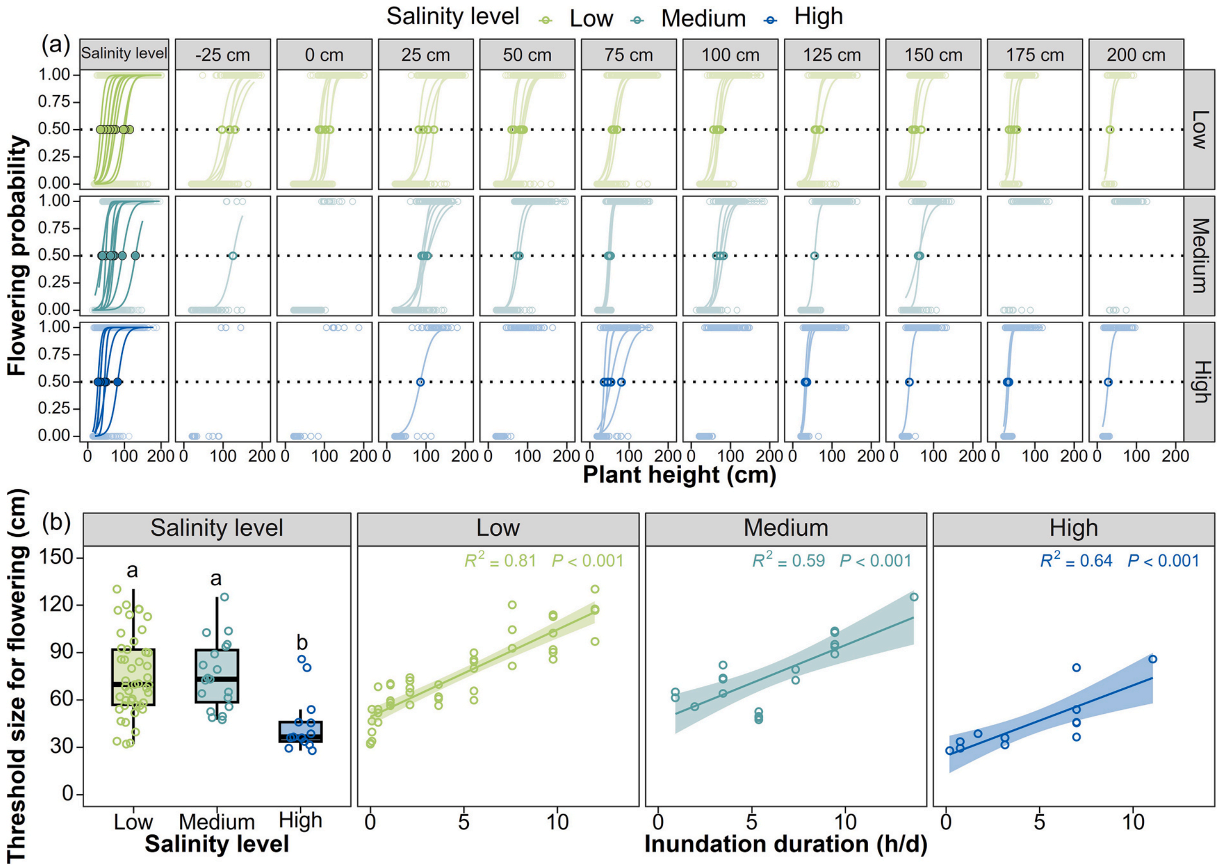

Fig. 3. Logistic regressions of the flowering probability against plant height, and threshold size for flowering is the height when 50% shoot flowering (a). For a given salinity level, the threshold size for flowering is estimated for each mesocosm (open circles) and elevation (closed circles). The variation of threshold size for flowering for different salinity levels, and alongside inundation duration for each salinity level (b).

plant height values nearly doubled as the inundation duration increased from 0 to 15.2 h/d (Table 1a, Fig. 2a).

S. alterniflora first flowered in June and continued flowering for the following five months. Both the salinity level and inundation duration significantly influenced the flowering day (Table 1b). The average flowering day was 236.1 days at the high salinity level, which was significantly earlier than the others (242.6 days and 245.9 days, Fig. 2b). For all salinity levels, the average flowering day increased linearly with inundation duration (Table 1b, Fig. 2b). The flowering day increased by nearly 60 days as the inundation duration increased at the medium salinity level, while the variation of the other two salinity levels was only half as much, representing a differential acceleration rate among salinity levels (Table 1b, Fig. 2b). Overall, these results showed salinity and inundation duration played critical roles in mediating the life history traits of salt marsh plants.

3.2. Flowering probability depends on the plant size and the environment

The flowering probability increased with plant height, and this relationship was estimated as the threshold size for flowering (Fig. 3a). This threshold was significantly affected by the salinity level and the inundation duration (Table 1c). The threshold size for flowering was 44.7 cm at the high salinity level, which was significantly lower than other levels (75.56 and 75.61 cm, Fig. 3b). At all salinity levels, we also discovered that the threshold size for flowering linearly increased with the inundation duration, and these values increased almost five times from 28.3 cm to 130.7 cm as the inundation duration increased (Fig. 3b). Thus, the flowering phase transition of *S. alterniflora* depends both on the plant growth and intertidal environmental factors.

3.3. Different factors modulate size-dependent flowering

To understand the direct effect of intertidal environmental factors on flowering phase transition and their indirect effect via plant life history traits, we conducted structural equation modeling (Appendix S2: Table S3, Fig. S1). The results (Fig. 4a) showed that the salinity level had no direct effect on the threshold size for flowering but could influence the threshold size indirectly by altering the plant height and flowering day. Inundation duration had a significantly direct effect on the threshold size for flowering and also exerted indirect effects by mediating the plant height and flowering day. The direct and indirect effects of inundation duration explained 0.80 of the standard effect size (Fig. 4b), demonstrating a larger total effect compared to the salinity level. Therefore, the inundation duration emerged as the primary determinant modulating the key life history switch that may affect the flowering decision and reproductive success of *S. alterniflora*.

4. Discussion

Flowering phenology is crucial to optimizing sexual reproduction for individuals and populations, but we still know little about their contribution to the life history strategies of salt marsh plants in coastal wetlands. In this study, we employed an in-situ experimental mesocosm setup in the coastal salt marsh, evaluating the variation of size-dependent flowering under two different environmental stresses along the estuary. In general, increasing salinity and prolonged inundation duration reflect the intensification of the environmental stresses, yet the responses of *S. alterniflora* appear to be the opposite. The increasing salinity reduces plant height, accelerates flowering time, and results in a smaller threshold size for flowering. In contrast, the prolonged

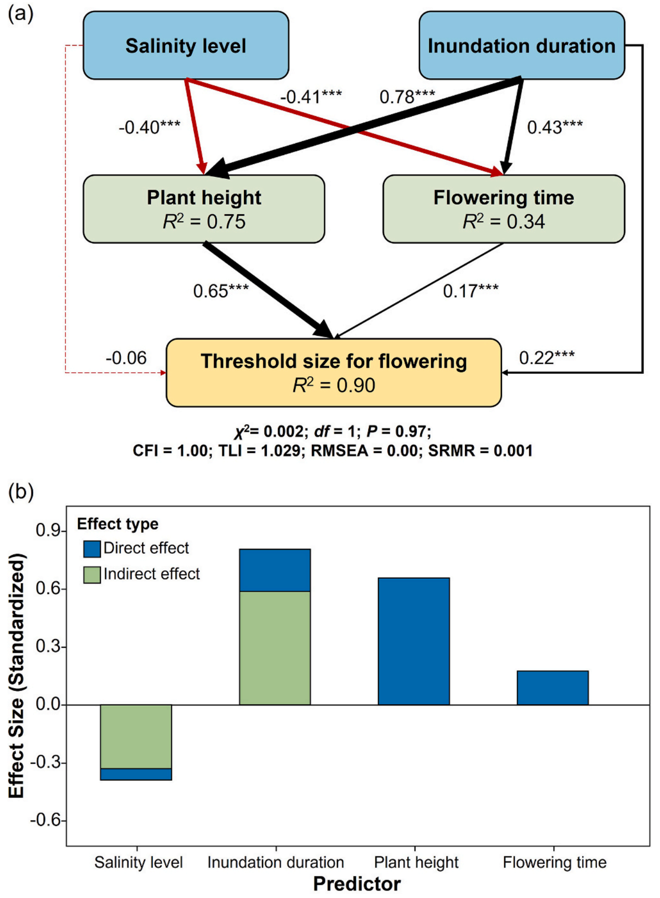

Fig. 4. The results of the structural equation model show the direct effects of salinity levels and inundation duration on threshold size for flowering, and their indirect effects mediated by plant height and flowering time (a). Black and red arrows denote positive and negative effects, and solid and dashed lines indicate the effects' significance or nonsignificance (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). The amount of variance explained by the model (R^2) is shown for each predictor in the model. The standardized effect sizes of driving factors of threshold size for flowering (b).

inundation duration promotes a taller height of the plant, delays flowering time, and increases the threshold for flowering. These variations may impact individual fitness in response to the two key environmental factors linked to sea-level rise and driven by global climate change. Therefore, this study offers new insights into flowering strategies under various environmental stresses, enhancing our understanding of salt marsh ecosystem resilience under climate change.

The vegetations in coastal wetlands face salt stress from the seawater and the saline sediments, and this condition may become a lethal threat when exceeding the plant tolerance. *S. alterniflora* responds by reducing plant size and accelerating flowering, like other *Spartina* species (Castillo and Figueroa, 2009), thereby ensuring early seed production before potential death. In contrast, the inundation stress that emerges from tidal cycles is countered by increasing plant height and delaying flowering, allowing access to sufficient oxygen and light for resource accumulation (Castillo et al., 2005; Crosby et al., 2015; Liu and Pennings, 2019). This "escape syndrome" helps *S. alterniflora* avoid submergence until conditions favor sexual reproduction, resulting in a trade-off between vegetative growth and early sexual reproduction. The species shows distinct flowering strategies: accelerated under salt stress and delayed under inundation stress, driven by size-dependent resource availability and flowering costs (Kawamura and Takeda, 2006). These flexible strategies, reflecting strong phenotypic plasticity, enhance individual fitness and population viability in dynamic salt marsh environments.

Under the two specific environmental stresses across the intertidal zone, our study found that *S. alterniflora* represents a wider range of morphological and phenological variation across salinity and inundation, leading to a highly altered pattern of plant height and flowering time (Fig. 2). Previous studies focused on both large geographic scales and fine microhabitat scales. At a geographic scale, it has been proved that *S. alterniflora* flowers earlier at smaller sizes during the growing season, associated with the stressed high temperatures at lower latitudes under global climate change in East Asia (Chen et al., 2021; Liu et al., 2022). At a fine spatial scale, a long-term field survey in the U.S. showed that microhabitat-driven variation mediates plant phenology of *S. alterniflora*, resulting in varying soil temperatures, and causing delayed phenology for marsh channel edge plants with colder temperatures in winter (O'Connell et al., 2020). However, there is still a lack of research focused on the local scale. Notably, although stress-induced threshold size for flowering has been documented (Liu and Pennings, 2019) at a local scale across different locations, the key abiotic drivers and the intrinsic linkage of flowering time remain unresolved. Our experimental manipulation of environmental factors at local-scale resolutions bridges this knowledge gap, complementing the existing results from fine scales to large scales. Together, this knowledge may improve our understanding of multi-scale trait variations in *S. alterniflora*, offering valuable insights for predicting marsh resilience, productivity, or other ecosystem services.

Flowering phenology exhibits strong plasticity across environmental gradients, with plant height serving as a dominant factor of flowering onset in herbaceous species (Sun and Frelich, 2011; Anderson et al., 2012). Terrestrial plants tend to flower earlier under heat stress, drought stress and nutrient stress, as well as delay flowering under cold stress and salt stress (Takeno, 2012; Kazan and Lyons, 2016). Crucially, terrestrial plants in stressful conditions consistently have a smaller threshold size for flowering, reflecting the balance inherent to size-dependent growth to ensure plant survival and sexual reproduction (Skarpaas et al., 2016; Jameson et al., 2022). These patterns have been proved not only in herbaceous monocarpic plants (Wesselingh et al., 1997) but also in herbaceous perennial plants of terrestrial ecosystems (Méndez and Karlsson, 2004). However, the threshold size for flowering of *S. alterniflora* increases with inundation duration but decreases with salinity in coastal salt marsh in our study (Fig. 3). We suggest these shifts in strategies emerge due to the great habitat heterogeneity across the estuarine and elevational gradients at the local scale in coastal ecosystems, whereas terrestrial ecosystems may require large-scale habitats to achieve.

Using the globally distributed salt marsh plant, *S. alterniflora*, we demonstrate its size-dependent flowering plasticity across environmental gradients, highlighting the strong morphological and phenological responses to contrasting environmental stresses. Previous studies have also shown that species in the genus *Spartina* exhibit high phenotypic plasticity, with enhanced stress tolerance and competitive ability (Castillo et al. 2014; Grewell et al. 2016). Under global change, species typically respond to the intensifying environmental stresses through three strategies: range shift, adaptive evolution and phenotypic plasticity (Donelson et al., 2019). Sea-level rise and salt intrusion are increasingly submerging low intertidal habitats, threatening plant survival and salt marsh resilience (Kirwan and Guntenspergen, 2012). At the local scale, as the squeeze from both the seaward and landward is caused by rising sea level and seawall constructions, the potential intertidal distributions of salt marshes are restricted. While adaptive evolution may require several generations to enhance plant survival and sexual reproduction (Anderson et al., 2012), phenotypic plasticity enables rapid adjustments in traits like plant height and flowering time to ensure sexual reproductive success (Sultan, 2000). We emphasize that size-dependent flowering plasticity is highly modulated by inundation duration, and this phenotypic plasticity provides an effective solution for salt marsh maintenance in response to sea-level rise. Furthermore, our study may be useful to predict the contribution of plant life history strategies to ecosystem resilience under global change.

CRediT authorship contribution statement

Jiayu Wang: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Xincong Chen:** Writing – review & editing, Formal analysis, Data curation. **Yueyue Wang:** Writing – review & editing, Investigation, Data curation. **Yasong Chen:** Writing – review & editing, Investigation, Data curation. **Hao Wu:** Writing – review & editing, Investigation. **Serina S. Wittyngham:** Writing – review & editing. **Matthew L. Kirwan:** Writing – review & editing, Supervision. **Yuanye Zhang:** Writing – review & editing, Formal analysis. **Wenwen Liu:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Conceptualization. **Yihui Zhang:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Statement on inclusion

Our study brings together authors from two different countries, including scientists based in China where the study was carried out. Collaboration between Chinese and international researchers was forged before the study designed in 2022, ensuring the diverse sets of perspectives they represent was considered from the onset.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113790.

Data availability

The data that support the findings of this study are openly available in the Figshare Data Repository (https://doi.org/10.6084/m9.figshare.29370194).

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