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Lateral Hydrological Connectivity Driven by Tidal Flooding Regulates Range-Expansion of Invasive *Spartina alterniflora* in Tidal Channel-Salt Marsh Systems

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ABSTRACT. Understanding how hydrological features affect habitat invasibility is crucial for predicting whether variations of such hydrological features may act as important inducement regulating range-expansion of invasive species in tidal channel-salt marsh systems. Although lateral hydrological connectivity (LC), or the hydrological connections between tidal channels and adjacent marsh flats, is an important hydrological feature, its effect on plant invasion has rarely been studied in depth. Here, we examined the effects of lateral hydrological connectivity on range-expansion of *Spartina alterniflora (S. alterniflora)* in tidal channel margins of a typical tidal channel-salt marsh system, in the Yellow River Delta, China. Field surveys and transplanting experiments showed that high LC greatly favors *S. alterniflora* to expand its invasion ranges along tidal channel margins by mediating such habitat physical forms of stress as soil salinity, soil moisture and soil hardness. In contrast, low LC, exacerbates those forms of stress, thereby significantly checking the lateral expansion of *S. alterniflora*. Moreover, human-made and naturally formed geomorphic structures in salt marshes (e.g., artificial ditches, pools, and hollow microtopography), particularly at high elevations, could potentially enhance LC over time, thereby making such sites prone to invasion by *S. alterniflora*. These results highlight the importance of lateral hydrological connectivity as an essential driver to regulate *S. alterniflora* lateral expansion along with the tidal channels. Our results imply that considering the relationships between hydrological processes and spread processes of exotic species should be incorporated into future management frameworks for risk assessment and ecological control of invasive plant species.

Keywords: biological invasion, hydrological connectivity, tidal channel margins; smooth cordgrass, invasive plant, management of salt marsh

1. Introduction

Coastal salt marshes are embedded in unique and complex geomorphological systems formed by the fluxes or dynamics of salt water and the sediments it contains that are driven by tidal hydrological processes (Person et al., 2020; Wang et al., 2021). Tidal channel systems are important geomorphic carriers for controlling tidal hydrological processes in salt marshes (Rinaldo et al., 2004; Fagherazzi et al., 2013). The systems may also serve as main conduits for the transfer of inert matter (e.g., sediment and nutrients), energy, or organisms — a transfer mediated by tidal waters — within or between different elements of a salt marsh landscape — a process referred to as hydrological connectivity (Pringle, 2001; Bracken et al., 2013). Because many studies have shown that hydrological connectivity is a major driving force behind the dynamics of water-mediated materials, biogenic elements, populations and communities (Racchetti et al., 2011; Keesstra et al., 2018; Liu and Wang, 2018), the feature has been widely applied to the assessment, restoration, and management of ecosystems, especially such riverine or catchment ecosystems as river-floodplain and hillslope-river systems (Lexartza-Artza and Wainwright, 2009). Although the concepts of hydrological connectivity and its applications originate from river systems, they can be conceptually and empirically employed to effectively regulate many important ecological processes in tidal channel-salt marsh systems given the structural and functional similarities between tidal channel systems and river systems (Liu et al., 2020; Wang et al., 2021).

Within the tidal channel-salt marsh systems, hydrological connections between tidal channels and adjacent marsh flats are established when tidal waters of channels spill over onto the adjacent marsh flats, and these connections are defined as lateral hydrological connectivity (referred to as LC; Larsen et al., 2017; Figure 1). Since many vital materials including sediments, biogenic elements, and propagules or organisms that are transported by the associated over-surface flows, LC plays a crucial role

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in regulating many ecological processes including biogeochemical cycles (e.g., carbon and nitrogen fluxes), habitat characteristics (e.g., physical stresses and nutrient levels), plant life history (e.g., seed dispersal and seedling establishment), and geomorphic processes (e.g., sediment transport and bio-sedimentation) (Fagherazzi et al., 2013; Cui et al., 2016; Wang et al., 2021). Previous studies have demonstrated that loss of LC was a major cause of the decline in fish functional diversity in river floodplain (Liu and Wang, 2018), and increased lateral hydrological connections with riverine wetlands could promote nitrogen removals from farmlands (Racchetti et al., 2010). Moreover, it has also been revealed that the restoration of LC notably facilitated the recovery of plants and macroinvertebrates (Paillex et al., 2009; Wang et al., 2021). Although many studies have related the above-mentioned ecological processes to the wide framework of LC (Cui et al., 2016), yet the ecological effects (e.g., habitat condition and ecological process alterations) induced by variations of LC in tidal channel-salt marsh systems are rarely explored.

Accumulating evidence shows that changes in habitat characteristics and ecological processes can increase the invasibility of native ecosystems, thereby greatly promoting biological invasions (Salomidi et al., 2013; Ning et al., 2019). One exotic species that seriously threatens global coastal ecosystems is *Spartina alterniflora* (hereafter *S. alterniflora*), which was introduced, intentionally and accidentally, into many salt marshes on the western coast of the USA and in western Europe, Australia, New Zealand, South Africa, and East Asia and has since spread widely (Strong and Ayres, 2009). In recent decades, the invasive species has successfully invaded almost all mudflats and stretches of salt marshes at low elevations in China's coastlines (Liu et al., 2018), and now continues to expand its range rapidly landwards to salt marshes at higher elevations along the margins of tidal channels (Ning et al., 2020; Sun et al., 2020), leading to a series of adverse biogeomorphological and ecological consequences, such as changes in the density of marsh drainage and configuration of landscapes (Schwarz et al., 2016, 2018). Suitable physical features of the environments (e.g., low salinity, high inundation and ample stocks of nutrients) have been shown to make a habitat significantly more invasible by creating convenient niche windows for *S. alterniflora* to spread over new territories (Tang et al., 2014; Ning et al., 2021). However, remarkably little is known about the extent to which LC between tidal channels and adjacent marsh flats may affect habitat invasibility, and in turn, regulating the expansion process of *S. alterniflora* into tidal channel-salt marsh systems.

The present study sought to predict how far invasive *S. alterniflora* will spread laterally along the tidal channels by exploring the relationship between LC and the lateral expansion of *S. alterniflora* into marshlands at different elevations — low, middle, and high — that form a typical tidal channel-salt marsh system (see Figure 1). We hypothesized that LC between the tidal channels and adjacent marsh flats could regulate the range-expansion of *S. alterniflora* by influencing different forms of the associated physical stresses. Firstly, we developed a robust method of measuring such LC in tidal channel-salt marsh systems, based on the high temporal resolution observations of tidal flooding in the field. Secondly, we conducted field surveys and transplanting experiments to test the potential effects of LC on the expansion of *S. alterniflora* and associated changes in the physical forms of stress seen in the chosen habitat. Finally, based on the results, we discussed the implications of regulating the hydrological connectivity in salt marshes, and would obtain useful insights into curtailing the landward invasion of *S. alterniflora*.

2. Materials and Methods

2.1. Study Area and Targeted Species

The study was conducted at a typical tidal channel-salt marsh system, which has been invaded by the invasive *S. alterniflora* (37°49′ ~ 37°50′ N, 119°03′ ~ 119°05′ E), located in the Yellow River Delta, northern China (Figure 2a). The study region has a warm temperate continental monsoon climate; the average annual temperature is 12.8 ℃ and the average annual precipitation is 559.1 mm (Xie et al., 2019). The tides are irregular and semidiurnal: the average range of the neap tide is 0.46 ~ 0.78 m and that of the spring tide is 1.06 ~ 1.78 m (Wang et al., 2021). Vegetation within the region shows clear zones along the elevation gradient (Cui et al., 2011). The native annual plant, *Suaeda salsa* dominates most of intertidal and uptidal marshes, whereas other plants such as *Tamarix chinensis*, *Limonium sinense*, *Phragmites australis* and *Salicomia europaea* are distributed mainly in the high marshes (He et al., 2012a). Importantly, the exotic *S. alterniflora*, a worldwide invasive species, has occupied most of marshes at low and middle elevations and is rapidly expanding its invasion range landward along the tidal channel margins (see Figure 1; Ning et al., 2021).

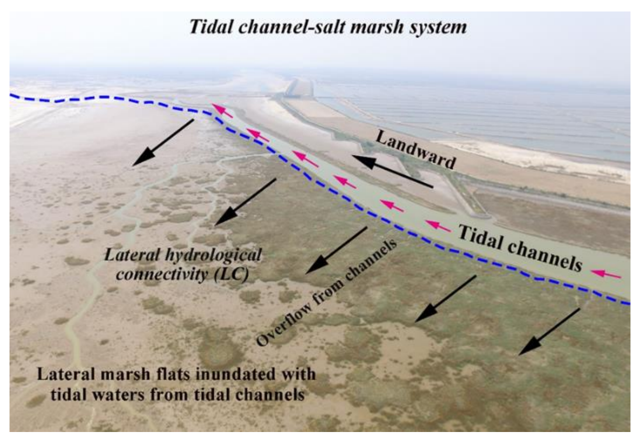

Figure 1. Conceptual diagram of the lateral hydrological connectivity between tidal channels and adjacent marsh flats in a tidal channel-salt marsh system. The orange arrows point to lateral overflows from tidal channels into marsh flats. The vegetation (green parts of the photo) represents the invasive *S. alterniflora*. Photo credit: Z. Ning.

2.2. Lateral Hydrological Connectivity: Measurement and Calculation

In tidal channel-salt marsh systems, tidal channels are the main carriers for transporting tidal waters to salt marshes. If tidal water within the tidal channels keeps accumulating until it spills onto the adjacent marsh surface (see Figure 1), a hydrological connection is established between tidal channels and the marsh flats adjacent to the channels — referred to as LC (Larsen et al., 2017; Wang et al., 2021); in quantitative terms, LC is defined as the duration over which tidal water exists at a specific site, or the hydroperiod of that site (Jencso et al., 2009; Xie et al., 2021). Therefore, the LC of a specific site in the tidal channel-salt marsh system is calculated as follows:

$$LC = T_i / 365(days) \times 24(hours) \times 60(min) \quad (1)$$

where T_i is the annual cumulative inundation duration of a specific site on the adjacent marsh flats (usually calculated to the nearest 10 min). The longer the tidal waters are retained, the higher the LC is. If a site is always inundated with tidal waters (i.e., continuously presents tidal water levels), the LC is 1.

To better obtain the accurate tidal flooding dynamics of the study area, we set the water level logger (Odyssey Z412, Dataflow Systems, Christchurch, New Zealand) at the margins of the tidal channel to auto-record the depth of tidal water relative to the datum plane on the soil surface at a high temporal resolution (every 10 min) from September 2017 to October 2018. Then, the tidal level dynamics in a whole year at the record site were obtained by adding its absolute elevation and time-series water depths together, and the cumulative duration of inundation at any site in this area can be calculated by the inundation analysis using Fortran 90 (ANSI standard, Washington DC, USA), which is based on the relationships of tidal levels and elevations (Wang et al., 2021; Xie et al., 2021). We measured the absolute elevations (ellipsoid height, elevation relative to the Reference Ellipsoidal Surface) of our experimental sites and those of the water level logger record site (see Figure 2a) with a GPS device (4600-LS, Trimble GPS, Sunnyvale, California, USA) to obtain the dynamics of the duration for which each experimental site was inundated and its corresponding LC.

2.3. Field Transect Surveys and Seedling Transplant Experiments

The field surveys and experiments were conducted on adjacent marsh flats at three elevational marsh zones of the tidal channel-salt marsh system (i.e., low marsh, middle marsh and high marsh, Figure 2(a)). We determined these elevational marsh zones based on the tidal ranges and the vegetation types reported earlier (Wang et al., 2018b; Xie et al., 2019). The low marsh lays between the lowest average tide and the mean high-water neap (MHWN); the high marsh lays between the mean high-water spring tide (MHWS) and the highest average tide; and the middle marsh lays between the MHWN and MHWS (Adam 1993; Ning et al., 2021). In each elevational marsh zone, five parallel transects were marked, progressively farther away from the tidal channels, 0, 50, 100, 200, and 350 m away from the border of *S. alterniflora* belt (Figure 2(a)).

To quantify the lateral expansion ranges of *S. alterniflora* at the adjacent marsh flats of the three elevational marsh zones (i.e., low, middle and high marsh) in tidal channel-salt marsh system, ten width of the invasive plant expansion belts were randomly measured with a tapeline at each elevational marsh zone in August 2017, and the average values of the 10 lateral expansion distances were then calculated. To further examine the effect of lateral hydrological connectivity between the tidal channels and adjacent marsh flats on the lateral expansion of *S. alterniflora*, a field manipulation experiment was conducted in May 2018, which involved transplanting *S. alterniflora* seedlings along the five parallel transects (Figure 2(a)). Each transect consisted of eight quadrats, each measuring 1 m × 1 m with a gap of at least 5 m between adjacent transects. Substrate blocks (20 cm in diameter and 15 cm in depth), each containing 10 to 20 emerging sexual seedlings of *S. alterniflora*, were dug up from the nearby tidal channel margins using a transplanter and immediately placed in the above-mentioned quadrats. Where required, the seedlings were thinned to maintain only ten seedlings for standardization in each quadrat. To alleviate transplanting stress, the transplants were watered with fresh water every two days for a week (He et al., 2012b). After one growing season, in September 2018, we counted the number of plants, the number of inflorescences and measured the maximum plant height in each quadrat. In the end, we measured both above- and below- ground dried biomass.

To take into account of the impact of LC on soil salinity, moisture and hardness, the values of each of these parameters were also determined. Topsoil cores, 5.05 cm in diameter and 5.00 cm in depth, were collected at the center of every transplanting quadrat to measure soil salinity and moisture content (8 replicates per lateral transect of each elevational marsh zone). These soil cores were brought to the laboratory, we measured the soil moisture referred to He et al. (2012b). Soil salinity of these samples was measured by the soil rehydration method (Pennings et al., 2003), using a salinometer (3010M, Jenco, California, USA). Soil hardness of these quadrats was also measured with a soil penetrometer (TYD-1, Zhejiang, China). Lastly, a detailed distribution of elevation over the study area was also mapped using the digital elevation model developed earlier of our study (Xie et al., 2021) based on the elevations of 200 control points measured using a GPS device (4600LS, Trimble GPS, California, USA).

2.4. Statistical Analysis

To relate the differences in LC values at the experimental sites to the distance gradient — the transects progressively farther from the tidal channels — in the three elevational marsh zones (i.e., low, middle, and high marshes), we used general linear models (GLMs) with post-hoc tests, because the data could not be transformed to satisfy the assumptions required by the analysis of variance (ANOVA). However, differences in the expansion range of *S. alterniflora* were examined by one-way ANOVA with Tukey's post-hoc multiple tests after testing the normality and the homogeneity of variance. Analogously, one-way ANOVAs (Tukey's HSD tests) were also conducted to compare the differences between the physical forms of stress (soil salinity, moisture, and hardness) as reflected on the survival and growth of the seedlings transplanted progressively far-

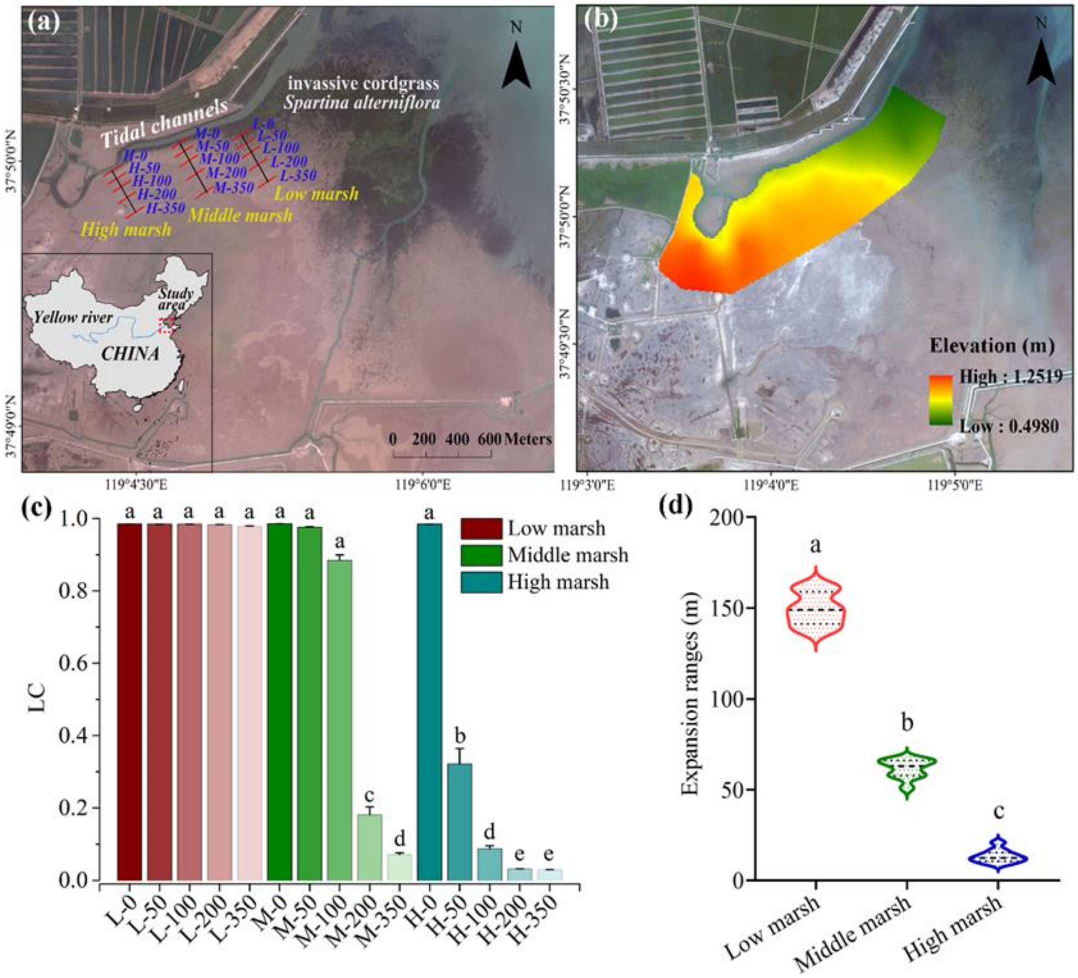

Figure 2. Study area, lateral hydrological connectivity, and expanding area under *Spartina alterniflora*. (a) Study area and design of field experiments. In each elevational zone (low, middle, and high marshes), five parallel transects (red lines), each progressively farther from *Spartina alterniflora* expansion belt (0, 50, 100, 200, and 350 m away), were planted with *S. alterniflora* seedlings. (b) Distribution of elevation zones based on digital elevation models. The elevations refer to ellipsoid height (i.e., elevation relative to the Reference Ellipsoidal Surface). (c) Lateral hydrological connectivity in five transects at three elevations. Data are mean ± SE ($n = 8$), and significant differences ($P < 0.05$, tested by GLMs) are shown by different lowercase letters. (d) Lateral expansion ranges of *S. alterniflora* in three elevational marsh zones; significant differences ($P < 0.05$, tested by one-way ANOVA with Tukey's HSD test, $n = 10$ replicates) are shown by different lowercase letters.

ther within each elevational marsh zone. To examine the effect of LC between the tidal channels and adjacent marsh flats on lateral expansion of *S. alterniflora*, GLMs with post hoc tests were also used for comparing the survival and growth of the plants as reflected in number of surviving plants, the number of inflorescences, maximum plant height, and dry biomass. We used Poisson distribution for the number of plants and number of inflorescences, and the Gaussian distribution for maximum plant height and dry biomass. The relationship among the above-mentioned performances of *S. alterniflora* and LC were analyzed using one-variable linear regression models, which were also used for testing the relationships between LC and the three forms of habitat physical stress. All statistical analyses were conducted in R 4.0.4 (R Core Team 2020).

3. Results

3.1. Distribution of Lateral Hydrological Connectivity and *S. alterniflora* Expansion

The lateral hydrological connectivity (i.e., LC) of the experimental sites, namely the transects progressively farther away from tidal channels, was significantly affected by both the marsh zone and lateral distance from the tidal channel ($P < 0.001$; Figure 2c; Table S1). In the longitudinal gradient, the average LC of the low marshes or that of the middle marshes was much higher than that of the high marshes (0.98 ± 0.0 for low marsh vs. 0.61 ± 0.07 for middle marsh vs. 0.29 ± 0.06 for high marsh; mean ± SE). Along the lateral increased distance gradient of marsh flats adjacent to the tidal channels, the pattern of the dis-

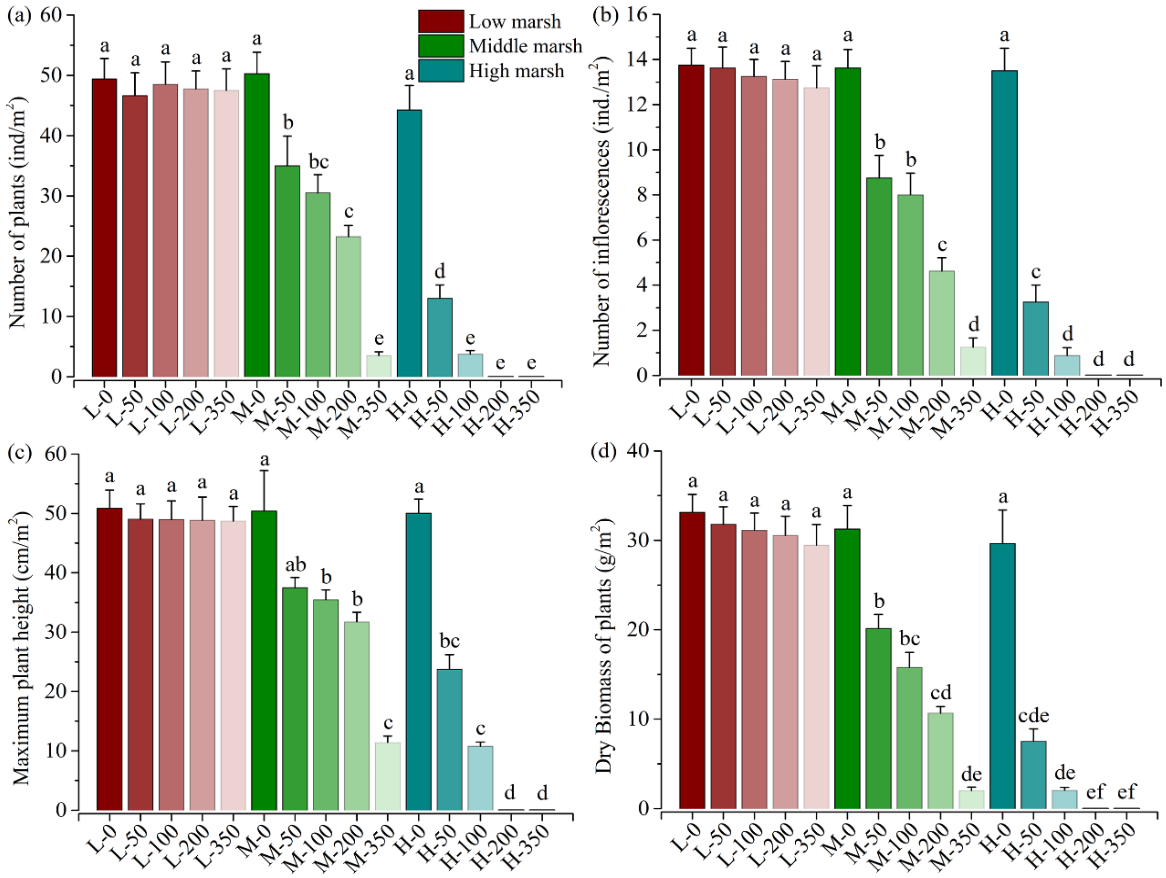

Figure 3. Survival and growth performances of *S. alterniflora*. (a) Number of plants, (b) number of inflorescences, (c) maximum plant height, and (d) dry biomass of plants per quadrat (m^2) grown along five parallel transects progressively farther from *S. alterniflora* expansion belt (i.e., 0, 50, 100, 200, and 350 m away) in three elevational marsh zones (low, middle, and high marshes); data are mean ± SE (n = 8) and significant differences (P < 0.05, tested by GLMs) are shown by different lowercase letters.

tribution of LC varied across the three elevational marsh zones (i.e., low, middle, and high marsh): in the low marshes, the distance had no effect on LC (P > 0.05; Figure 2(c)) whereas in the middle marshes and high marshes, LC decreased markedly with distance from the tidal channels (P < 0.001; Figure 2(c); Table S1).

The lateral expansion range of *S. alterniflora* decreased significantly with increasing elevation in the longitudinal gradient from low marshes to high marshes (Figure 2(d)). Specifically, the expansion belt of *S. alterniflora* was the widest in the tidal channel margins of low marshes, intermediate in the middle marshes, and the narrowest in the high marsh (149.4 ± 2.9 m in low marsh vs. 61.6 ± 1.6 m in middle marsh vs. 13.4 ± 1.1 m in high marsh; mean ± SE; Figure 2(d)).

3.2. Survival and Growth Performances of Transplanted *S. alterniflora*

The results from field transplanting experiments showed that both survival and growth of *S. alterniflora* growing from sexual seedlings were significantly influenced by the interaction between longitudinal elevational marsh zone and lateral distance from the tidal channels (P < 0.001; Table S2). All the plant parameters related to fitness (i.e., number of plants, number of inflorescences, maximum plant height and total dry biomass) were higher in the low marshes and substantially decreased with the longitudinal elevation gradient from low marshes to high marshes (P < 0.001; Figure 3). In the lateral increased distance gradient, the above-mentioned fitness parameters were also higher in plants closer to tidal channels (i.e., in microhabitats with higher LC), and decreased in plants progressively farther from the tidal channels — a pattern recorded in all the three elevational marsh zones (Figure 3). In the low marshes, in which the LC was generally higher, lateral distance had no significant effect on any of the parameters, whereas at the middle and high marshes, the values of all the parameters decreased considerably as the lateral distance increased (P < 0.001; Figure 3).

3.3. *S. alterniflora* Performances as Affected by Lateral Hydrological Connectivity

In overall marsh flats adjacent to the tidal channels, all the four survival and growth parameters of *S. alterniflora* trans-

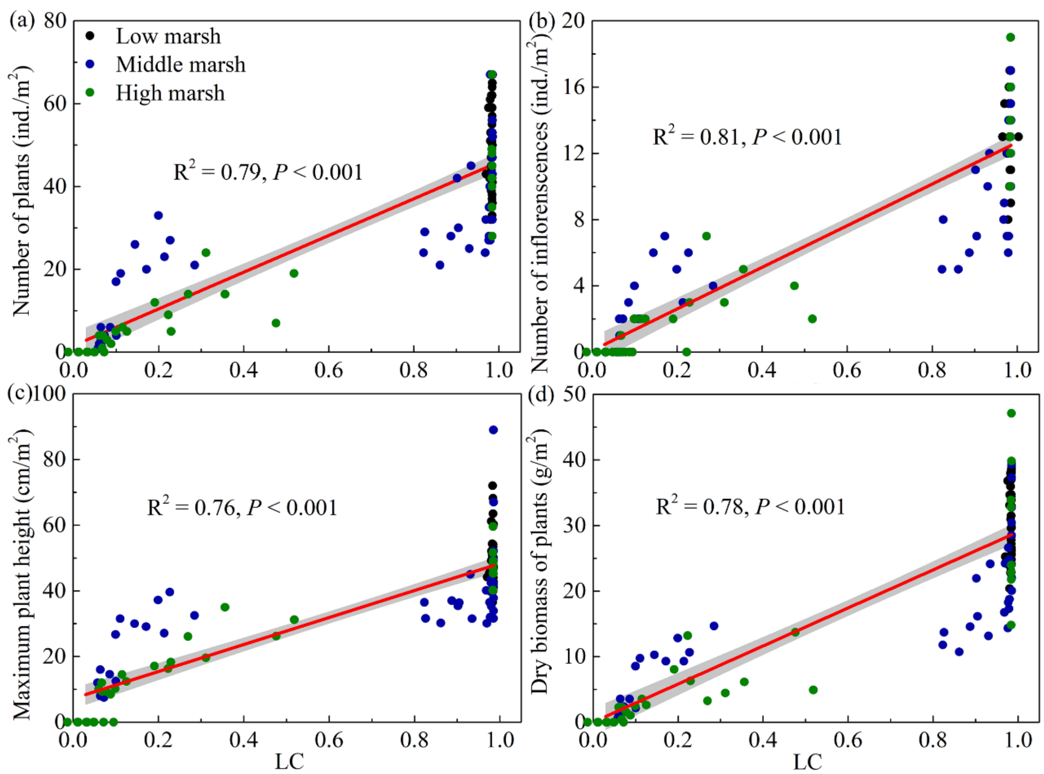

Figure 4. Relationships between lateral hydrological connectivity (i.e., LC) and survival and growth parameters of *S. alterniflora*. (a) number of plants that survived, (b) number of inflorescences, (c) maximum plant height, and (d) dry biomass of plants per quadrat (m^2) growing from transplanted sexual seedlings. Red lines show linear fitting lines and gray bands are 95% confidence intervals. Results of linear regression models are shown as correlation coefficients (R^2) and *P* values.

plants that we recorded (i.e., the number of plants, number of inflorescences, maximum plant height and plant dry biomass) were significantly and positively correlated to the LC between tidal channels and adjacent tidal flats. The coefficient of correlation (i.e., R^2) between LC and the number of plants that survived was 0.79 ($P < 0.001$, Figure 4(a)); that between LC and number of inflorescences was 0.81 ($P < 0.001$, Figure 4(b)); that between LC and maximum plant height was 0.76 ($P < 0.001$, Figure 4(c)); and that between LC and plant dry biomass was 0.78 ($P < 0.001$, Figure 4(d)), respectively.

3.4. Habitat Soil Physical Stresses as Affected by Lateral Hydrological Connectivity

In overall marshes, all the three physical forms of stress or soil properties that we examined, namely soil salinity, moisture, and hardness, were markedly affected by LC (Figure 4; Table S3). As the LC increases, soil salinity decreased significantly ($R^2 = 0.78$, $P < 0.001$, Figure 5(a)), as did soil hardness ($R^2 = 0.79$, $P < 0.001$, Figure 5(e)), whereas soil moisture showed a significant negative correlation with LC ($R^2 = 0.65$, $P < 0.001$, Figure 5(c)). Specifically, the impact of lateral distance from the tidal channels on the three parameters varied with longitudinal marsh elevations: in the low marshes, neither soil salinity ($P = 0.12$, Figure 5(b)) nor soil hardness ($P = 0.54$, Figure 5(f)) was impacted by the lateral distance, whereas soil moisture decreased markedly with lateral distance ($P < 0.001$, Figure 4(d)). In the middle and high marshes, both soil salinity ($P < 0.001$, Figure 5(b)) and soil hardness ($P < 0.001$, Figure 5(f)) increased significantly with lateral increased distance, whereas soil moisture decreased significantly with lateral distance ($P < 0.001$, Figure 5(d)). Overall, microhabitats in the marsh flats with higher LC were generally characterized by low soil salinity and soil harness, but high soil moisture (Figure 5).

4. Discussion

Lateral hydrological connectivity (i.e., LC) is being increasingly seen to be fundamentally important to a variety of ecosystem processes including shaping of a habitat's environment, biogeochemical cycles, population establishment, and community dynamics because many materials of vital importance (e.g., sediment, nutrients, and propagules) to these ecological processes are transported by over-surface waters (Racchetti et al., 2011; Reid et al., 2016; Liu et al., 2018; Wang et al., 2021). This study elucidated that higher values of LC between tidal channels and neighboring marsh flats is of benefit for *S. alterniflora* to expand its lateral invasion ranges along the margins of tidal channels, because the higher values of LC could make the physical environments more conducive for the survival and growth of invasive *S. alterniflora*. The results of present study indicate that LC, as an important driving force, could

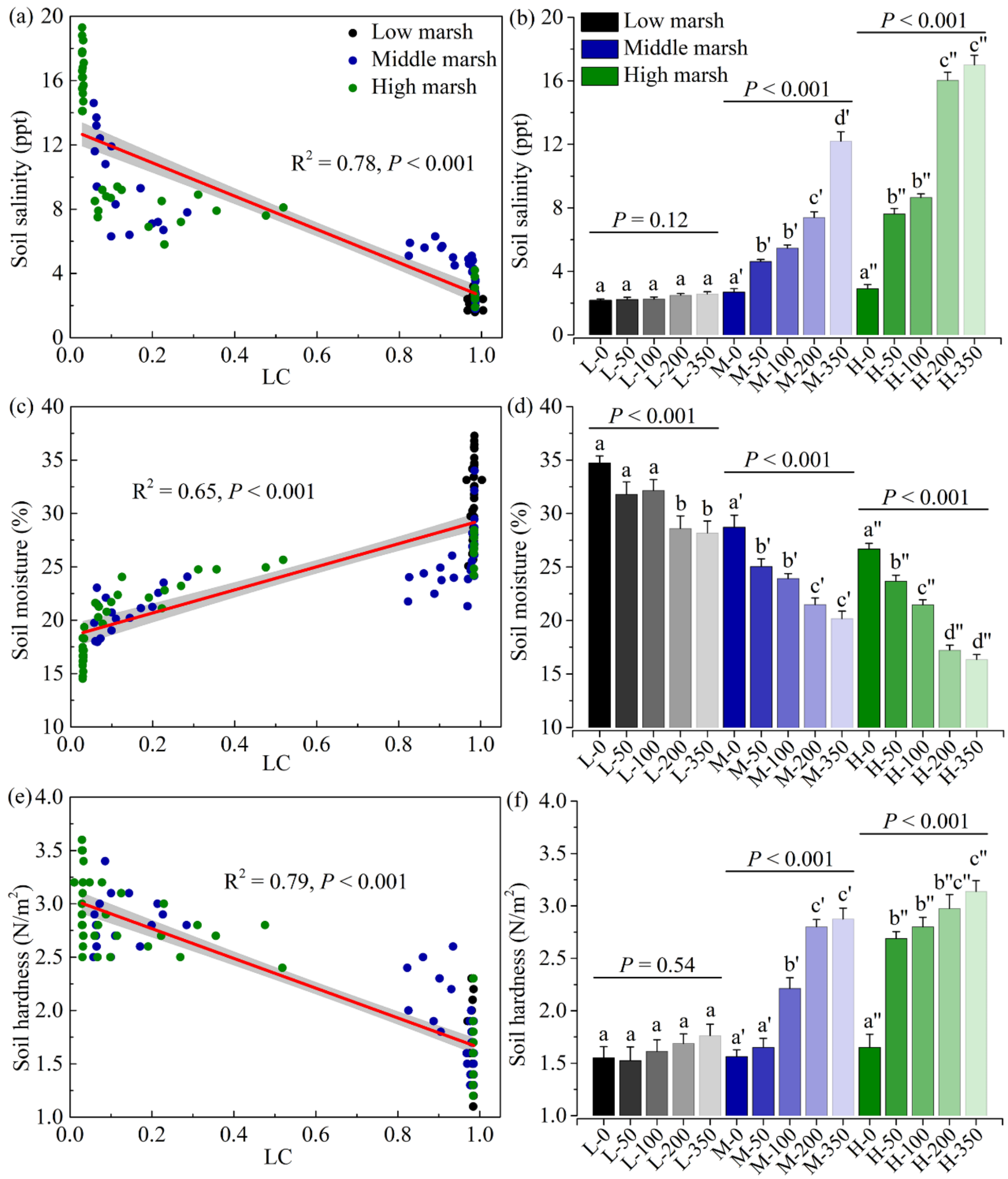

Figure 5. Relationships between three physical properties (forms of stress) of soil and (1) lateral hydrological connectivity (a, c, e) and (2) distance from *Spartina alterniflora* expansion belt (b, d, and f) at different elevational marsh zones. (a) Soil salinity. (c) Soil moisture. (e) Soil hardness. Red lines show linear fitting and grey bands are 95% confidence intervals. (b) Changes in soil salinity with lateral distance. (d) Changes in soil moisture with lateral distance. (f) Changes in soil hardness with lateral distance. Distance from *S. alterniflora* expansion belt: 0, 50, 100, 200, and 350 m. In b, d, and f, significant differences ($P < 0.05$, tested by one-way ANOVA with Tukey's HSD tests) are shown by different lowercase letters; data are mean ± SE ($n = 8$); P values in each elevational marsh zone are given above the bar.

profoundly regulate the range-expansion of invasive plants in tidal channel-salt marsh systems by mediating associated habitat physical stresses.

4.1. Distribution of Lateral Hydrological Connectivity and *S. alterniflora* Expansion Ranges in Tidal Channel-Salt Marsh Systems

Identifying how the LC in salt marshes changes in time and location is particularly helpful in understanding the dynamics of the hydrological process and ecological processes embedded in (Xie et al., 2021). Our results showed that habitat with a lower elevation (i.e., the overall low marsh area in the longitudinal gradient, and habitat near tidal channels in the lateral gradient) was characterized by higher LC irrespective of their lateral distance from tidal channels (see Figure 2(b)). This might be the result of the interaction of marsh elevations and tidal levels. In low marsh, the high homogeneity of mash elevations and tidal levels causes the insignificant differences in the LC variations along the lateral increasing distance gradient. In contrast, high spatial heterogeneity of the marsh topographies is existed in higher elevational marsh zone, which leads to significant differences in the LC changes of both middle and high marshes, with increasing lateral distance from tidal channels (see Figures 2(b) and 2(c)). Previous studies have also demonstrated that geomorphic features such as elevations, slopes and macro-/micro-topographies, could play as essential factors to determine the movement and retention of waters on marsh surface, which may generate potential influences on LC (Jencso et al., 2009; Chirol et al., 2018; Wang et al., 2021).

Our field survey results demonstrated that the lateral spread of *S. alterniflora* was kept in check at sites in the high marshes, which showed lower LC than those in the low and middle marshes (see Figures 2(c) and 2(d)). As many tidal water-mediated materials were transported by over-marsh flows in tidal channel-salt marsh systems, the deficits of propagules/seeds, soil moisture, or some nutrients, and the surplus of soil salinity might be existed in these areas with low LC, and these adverse factors would hamper some important ecological process crucial to plant survival and growth during plant-life history (Rand, 2000; He et al., 2012b; Wang et al., 2021). Therefore, an optimized region that could arrest the lateral expansion of *S. alterniflora* existed in the high and middle marshes, but not in the low marshes, thus resulting in a relatively higher invasion intensity in the low marshes. This observation is consistent with some earlier studies, which concluded that areas that are flooded only inferquently and high-salinity areas, particularly sites farther from tidal channels in the high and middle marshes, can check the progress of *S. alterniflora* and thus remain free from its invasion (Pennings et al., 2005; Qi et al., 2017; Ning et al., 2021).

4.2. Potential Mechanisms by which Lateral Hydrological Connectivity Impacts the Range-Expansion of *S. alterniflora*

Physical forms of stress that affect plants, such as tidal regime, salinity and inundation, are the main bottom-up driving factors that affect many important processes in the life history of plants growing on salt marshes, including seedling establishment, plant growth and reproduction, which further significantly determine the plant zonation in salt marshes (Castillo, 2000; Silvestri et al., 2005; Cui et al., 2011; Farina et al., 2018). In general, locations or habitats with high lateral hydrological connectivity (i.e., LC) are characterized by high soil moisture, low soil salinity and hardness - the outcome of frequent tidal activity. In contrast, locations or habitats that are distant from tidal channels (i.e., locations/habitats with low LC) usually are typically dry and highly saline because the soil is subjected to greater heating and soil moisture is subjected to faster evaporation (see Figure 5 and Figure 2(b); He et al., 2012; Ning et al., 2021). The suitability a habitat, as shaped by LC, can favour or inhibit the spread of *S. alterniflora*, which explains why areas with high LC are more prone to invasion by *S. alterniflora*. These results are consistent with the conclusions of previous studies, which reported that *S. alterniflora* performs better when soil salinity is low and inundation frequency is high (Qi et al., 2017; Xue et al., 2018). In addition to soil salinity and moisture, low soil hardness is also generally considered favorable for seedling emergence and establishment of salt marsh plants (Bertness and Ellison, 1987; Wang et al., 2018a). Previous studies have documented that habitats with favourable physical conditions could offer niches or invasion windows for the establishment of seedlings of invasive species, thereby helping them to 'conquer' those novel habitats (Dethier and Hacker, 2005; Vetter et al., 2019; Ning et al., 2020). Therefore, higher values of LC, by alleviating the relevant physical forms of stress — by making soils less saline and less hard and moister — make a habitat favourable and provide such spatial windows for invasion by *S. alterniflora*, which can then expand rapidly along the margins of tidal channels in tidal channel-salt marsh systems.

Besides physical forms of stresses, propagule pressure mediated by LC, as measured from the quantity and quality of seed, also plays important roles in determining successful invasion and rapid spread of invasive plants (Simberloff, 2009; Britton and Gozlan, 2013). Although we did not quantify the relationship between the seed dispersal and LC in the present study, our earlier studies conducted in the same region had shown that the arrival and deposition of *S. alterniflora* seeds (i.e., propagule pressure) decreased as distance from the source of seeds increased, the source areas being close to tidal channels and generally with high LC. Meanwhile, propagule pressure was also observed much greater along the margins of tidal channels in the low marshes than in the middle and high marshes (Ning et al., 2021; Xie et al., 2021). Both field and greenhouse experiments have shown that less saline and more moist habitats are conducive for the germination of *S. alterniflora* seeds (Xiao et al., 2011; Xie et al., 2021). Thus, higher propagule pressure combined with more favorable physical conditions — both mediated by LC — made it easier for *S. alterniflora* to extend its invasion range along the margins of tidal channels, especially in the low and middle marshes which recorded higher values of LC. In addition, high LC could also promote the growth of invasive plants by providing nutrient subsidies and sediments (e.g., nitrogen) with the water flows. Although we did not measure soil nutrients, a previous study revealed that the growth and productivity of invasive *S. alterniflora* has benefited from the coastal eutrophication (Zhao et al., 2015; Xu et al., 2020).

4.3. Implications for Managing *S. alterniflora* Landward Invasion

The results of the present study show the potential ecological effects of LC, which makes the marsh flats adjacent to the tidal channels (i.e., habitats with high LC) more invasible, and thus facilitates *S. alterniflora* to laterally expand it invasion range in tidal channel-salt marsh systems. Now that we know that it is the lateral hydrological connectivity between the tidal channels and neighboring marsh flats that regulate the range-expansion process of *S. alterniflora* along tidal channel margins, through mediating the relevant habitat physical stresses (i.e., soil salinity, moisture and hardness). This invasive mechanism could offer potential implications for managing *S. alterniflora*

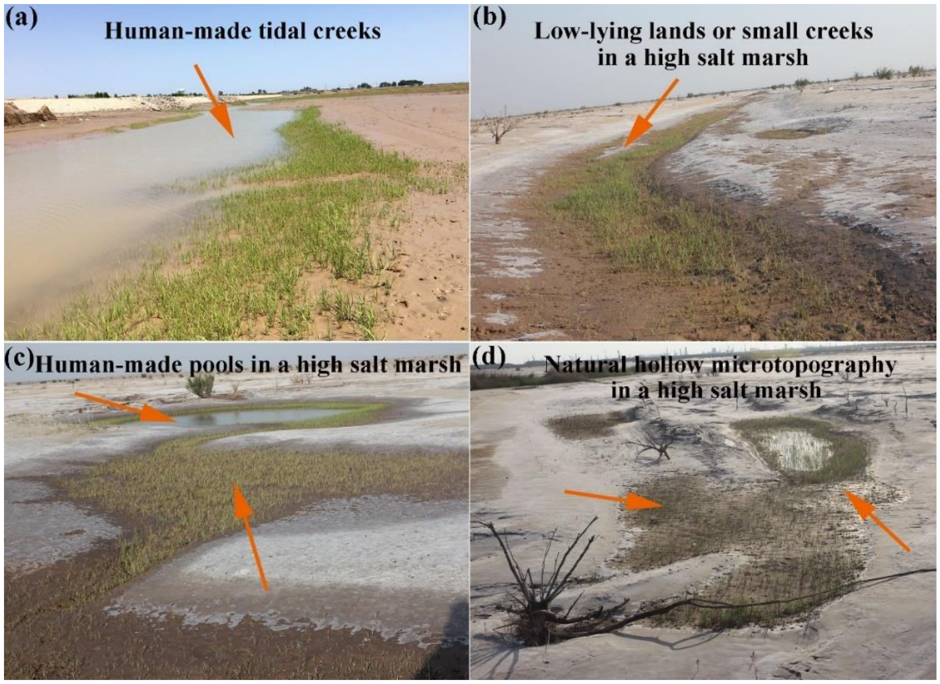

Figure 6. Field photographs showing the enhancement of the hydrological connectivity caused by the human-made constructions (a, c) or nature-formed topographic structures (b, d) such as tidal creeks, pools, low-lying lands and microtopography in salt marsh flats adjacent to the tidal channels. These topographic structures offered windows of opportunity for the establishment and spread of invasive *S. alterniflora* to new areas of salt marshes through sexual reproduction (a ~ d). Photos credit: Z. Ning and C. Chen.

invasion in salt marshes. Firstly, habitats with high LC, such as the natural waterlogged regions near tidal channels, should be monitored more closely for exotic plant invasion because those sits could offer spatial windows of opportunity to *S. alterniflora* to extend landward. Secondly, even in area of high salt marshes that featured with low LC, managers should also watch out for low-lying lands such as human-made tidal creeks, natural pools, small creeks, and sites with hollow micro-topography, because these low-lying sites will show greater LC in future, thereby facilitating the initial establishment of *S. alterniflora* seedlings and then successful invasion by the species (see Figure 6). Earlier studies have also shown how ditches dug in marshlands at higher elevations inevitably increased the risk of invasion by *S. alterniflora* (Ning et al., 2019; Xie et al., 2021). Therefore, anthropogenic disturbances need to be curbed severely, so as to maximally control *S. alterniflora* landward invasion. In addition, other feasible ways of regulating LC (e.g., regulating tidal flows, modifying microgeomorphic features, and filling up human-made ditches) combined with minimizing propagule pressure (e.g., removing the seeds of *S. alterniflora*, uprooting its seedlings, and mowing down the larger plants), will go a long way in curbing the establishment of *S. alterniflora* and its landward spread into tidal channel-salt marsh systems. Most important, considering the relationships among the hydrological connectivity, habitat characteristics, and invasion processes of exotic plant species, will be of great benefit for developing a theoretically and practically feasible framework to further predict and control landward invasion of exotic plants in tidal channel-salt marsh systems.

5. Conclusions

Lateral hydrological connectivity, which represents the hydrological connections between tidal channels and adjacent marsh flats in tidal channel-salt marsh systems, regulates the lateral range-expansion of invasive *S. alterniflora* along the margins of tidal channels by altering/alleviating some physical forms of stress in the habitat. Habitats with greater lateral hydrological connectivity generally have less saline, less hard, and moister soil conditions that are conducive to *S. alterniflora* and allow it to expand; habitats with low lateral hydrological connectivity, on the other hand, repel the lateral expansion of *S. alterniflora*. Moreover, human-made and naturally formed geomorphic structures among salt marshes at higher elevations (e.g., artificial ditches, pools, and hollow microtopographic structures) have the potential to enhance lateral hydrological connectivity over time, thereby making such sites prone to be invaded by *S. alterniflora*. The findings of this study not only highlight lateral hydrological connectivity as a fundamental driving force behind the range-expansion of invasive *S. alterniflora* along the margins of the tidal channels, but also suggest ways to check such landward invasion.

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