

Suaeda salsa in Relation to Hydrological Connectivity: From the View of Plant Trait Networks

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ABSTRACT. How plant traits respond to environment changes has been given more concerns worldwide. However, it is hard to reveal the integrative responses of plants only based on independent plant traits without considering the close links among plant traits. Plant trait network (PTN) is emerging as a new way to study how plant traits adapt to changing environment and to find out the key plant trait. We collected soil and plant samples from five sampling zones in *Suaeda salsa* wetlands of the Yellow River Delta in China to construct hydrological connectivity index (HCI) by principal component analysis of eight indicators. PTNs were estimated by network analysis of nine plant traits. The results showed that five study areas had significant different HCIs. The PTNs showed the max tightness in areas with medium HCI and the complexity of PTNs decreased with the rise of HCI. Generally, PTNs exhibited the best performance in the areas with medium HCI in which were the most appropriate for plants to grow. Plant aboveground biomass was the central trait PTNs since it had a high degree as well as betweenness centrality. The findings indicate that *Suaeda salsa* takes different growth strategies under different hydrological connectivity conditions. *Suaeda salsa* enhanced the connections of different traits in areas which were the best for plants to grow while *Suaeda salsa* formed different groups of function modules in areas where hydrological connectivity was weak. This study may give new sights on how plant response to the change of hydrological connectivity.

Keywords: hydrological connectivity, plant trait networks, coastal wetlands, Yellow River Delta, *Suaeda salsa*

1. Introduction

Wetlands are one of the most important ecosystems on the earth. It can regulate water resources, adjust microclimate, purify polluted water and produce food and resource for human beings, and these functions are largely dominated by wetland hydrology (Mitsch et al., 2015). Changes in hydrology will greatly influence the ecological processes of wetlands and further affect the growth and distribution pattern of wetland plants (Keesstra et al., 2018; Wang et al., 2021). Therefore, it is of great importance that better understanding the correlations between wetland plants and the hydrological indicators for wetland restoration and management.

Hydrological connectivity has become an increasingly popular term to measure water and sediment dynamics (Keesstra et al., 2018), contributing to characterizing the spatial variability of runoff (Ali and Roy, 2009). Different indexes have been developed to quantify hydrological connectivity based on hydrolo-

gical indicators like water level, average flux, and the number of connecting days (McDonough et al., 2015). The integral connectivity scale length (ICSL) developed by soil moisture was used to characterize the hydrological connectivity (Ali and Roy, 2010). The flow path length (FL) based on topography could capture the connectivity structure at plot and watershed scales, which could well explain the response of surface runoff (Mayor et al., 2008). The topographic over field capacity index (TOFCI) was constructed based on both soil moisture and topography to distinguish different hydrological characteristics among different types of wetlands (Liu et al., 2019). However, these indexes only represent the structure of hydrological connectivity without considering the relationships among plants, soil, and water. Comparatively, an integrated hydrological connectivity index was constructed through principal component analysis based on sediments, organic matter, benthic organisms, aquatic vegetation, and other indicators, which has been used to study how the lateral hydrological connectivity of the river in the floodplain affected invertebrate diversity (Paillex et al., 2007).

Hydrological connectivity regulates plant growth, survival, and biomass of wetland vegetation through hydrological processes such as the water level and flooding duration of wetlands (Kozłowski, 1997). Generally, the anaerobic environment caused by flooding is not appropriate for plants growing.

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Plants in seasonal flooding wetlands have higher biomass than those in perennial flooding wetlands (Briggs and Knapp, 1995). Perennial plants also exhibit fewer branches in wetlands with longer flooding duration (Hutchinson et al., 2020). However, a longer flooding duration is more conducive to the colonization of salt marsh vegetation (Xie et al., 2021). Meanwhile, plant aboveground biomass and the decomposition of plant litters in salt marshes can be greatly affected by hydrological connectivity (Yin et al., 2020a, 2020b). Liu et al. (2020) also observed that plant biomass and coverage had significant positive correlations with hydrological connectivity. The modification of micro-topography to enhance lateral hydrological connectivity could increase soil water content and reduce soil salinity, thereby promoting the emergence and growth of salt marsh plant seedlings (Wang et al., 2021). Plant seedlings can succeed in colonizing by delaying the growing stage to adapt to changes in hydrology (Maxwell et al., 2016). Moreover, many plants can improve their own plasticity, including adjusting the morphology of roots, buds, and leaves, elongating branches, and increasing the porosity of roots to adapt to the increasing flooding frequencies (Garssen et al., 2015). To adapt to changes in the hydrological cycles, plants can also change total biomass and their allocations in the aboveground and underground organs (Howard and Rafferty, 2006). Additionally, the deep-rooted plants can adjust stomata, root depth, and xylem anatomical characteristics to maximize resource absorption and increase productivity due to hydrological fluctuations (Hultine et al., 2020).

The responses of vegetation configuration to the hydrological gradients have also been getting attention. Cook and Hauer (2007) compared differences in groundwater connectivity, near-surface soil moisture, geomorphology, water chemistry, and other indicators in an intermontane depressional wetland, and found that the connected wetlands had higher net primary productivity than the isolated wetlands with different plant community composition. The hydrologic vegetation gradient (HVG) developed for lateral hydrological connectivity in a headwater catchment indicated that the spatial organization of vegetation within catchments could effectively represent the level of dependency of ecosystems along hydrologic flowpaths (Hwang et al., 2012). Among some hillslopes, hydrological connectivity was subject to the balance between evapotranspiration and lateral redistribution of soil water, which decreased with increasing vegetation densities (Emanuel et al., 2014). In the areas with weak hydrological connectivity, a high interspecific competitive relationship was found between two plant species to respond to environmental stress (Liu et al., 2020).

Plant trait networks (PTNs) have emerged as an effective way to capture and visualize the associations among plant traits comprehensively. PTNs can be applied to characterize individuals of a species or communities of many species and highlight the multivariate responses and adaptive mechanisms of plants to the environment (He et al., 2020). It can also help to find the key traits or trait combinations that influence the fitness or other functions of plant communities. Besides, it can reflect changes of trait modules across the environments. For example, leaf economics and hydraulic traits were decoupled in tropical-

subtropical forests, while a stable correlation between two suites of traits was found on the Loess Plateau where is lack of water (Li et al., 2015; Yin et al., 2018). The correlation between leaf economics and hydraulic traits might be a type of adaptation mechanism in arid conditions.

Generally, previous studies have focused on a single or several traits adjusting to the change of hydrological connectivity, and presented that hydrological connectivity can greatly influence plant traits (e.g., plant biomass, root: shoot ratio, and specific leaf area) (Boldrin et al., 2017; Yin et al., 2020) and thus affecting ecological functions in relation to different traits of living plants (Fu et al., 2009). However, little information is available on how plant traits as a whole comprehensively respond to the changes in hydrological connectivity. Therefore, the performance of PTNs for a single plant species or communities might need further exploration since the newly developed PTNs methodology has mainly been used to study a large-scale vegetation response to the environment.

The primary objectives of this work were: (1) to construct a hydrological connectivity index in five *Suaeda salsa* salt marshes with different hydrological conditions in the Yellow River Delta based on principal component analysis of eight indicators including soil properties, crab density, and seed mobility and testify HCI with flooding frequency and flooding time; (2) to develop PTNs of *Suaeda salsa* in each of the five salt marshes using plant traits and identify key traits and clusters of PTNs through network analysis; (3) to analyze the tightness and complexity using morphology parameters; (4) to explore the relationships between hydrological connectivity and PTNs of *Suaeda salsa* using regression analysis. We hypothesized that there exists a nonlinear relationship between PTNs of *Suaeda salsa* and hydrological connectivity, and PTNs will be tightest under moderate hydrological connectivity, while loose and simple PTNs would occur in the areas with strong or weak hydrological connectivity. The findings can contribute to *Suaeda salsa* conservation and restoration in coastal salt marshes by manipulating hydrological connectivity strength.

2. Materials and Methods

2.1. Experimental Design

2.1.1. Study Area

The Yellow River Delta (YRD; 37°35' ~ 38°12' N, 118°33' ~ 119°20' E) is located in Dongying City, Shandong Province, with the area of 1530 km² (Cui et al., 2009). Perennial wetlands and seasonal wetlands account for 63.06 and 36.94% in the YRD, respectively. The annual average temperature is 12.1 °C and the frost-free period lasts 196 days. The annual average evaporation is 1962 mm and the annual average rainfall is 551.6 mm, which is mainly concentrated in summer. Along a typical tidal creek near an artificial river, we set 5 study areas according to the HCI values calculated by Yin et al. (2020a) based on eight indicators, including LON1 (3.062), LON2 (0.881), and LON3 (-0.737) are parallel to the tidal creek, while LAT1 (0.881), LAT2 (-1.158), and LAT3 (-2.049) are perpendicular to the tidal creek (see details in Yin et al., 2020b).

LON2 and LAT1 are the same sampling plot and every plot is 100 m away from each other.

2.1.2. Sample Collection and Data Analysis

Soil samples with three replicates were collected in each sampling plot in October 2018 and brought to the lab. Soil samples were air-dried for two or three weeks and coarse plant litters and stones were removed. All the air-dried samples were passed through a 2 mm sieve. One part of the sieved soils was used to determine soil salinity, and the remaining samples were further ground and sieved through a 0.149 mm sieve to determine soil chemical properties.

Salinity was measured by the salt meter (Sartorius, Germany; soil: water = 1: 5); total carbon (TC) and total nitrogen (TN) were determined on an elemental analyzer (Vario EL, Germany); total phosphorus (TP) was determined by the Inductively Coupled Plasma-Atomic Emission Spectroscopy (ICP/AES). Four pieces of plaster (5 × 5 × 15 cm) were placed in each plot in June 2018 and recollected in August 2018 to test hydrodynamic characteristics (HC) by measuring the loss of plaster. A kind of groove was placed in each plot in June 2018, and the sediments in it were collected in October 2018 to test the sediment deposition (SD) by measuring the mass of air-dried sediments. Crab density (CD) was acquired by randomly throwing quadrat (50 × 50 cm) and counting the crab holes (> 10 mm). Seed mobility (SM) was calculated by dividing seed flux by *Suaeda salsa* density. Additionally, flooding frequency and flooding time were obtained using Odyssey hydrological gauge placed in each plot to verify the effectiveness of hydrological connectivity index.

Fifteen quadrats (50 × 50 cm) were chosen in each plot, and the density was recorded in September 2018. In total 120 samples were selected from each plot to measure the height, width, number of branches, leaf dry mass, and leaf area. Plant height, width, and base diameter were measured by a ruler. Leaf dry mass was obtained by an electronic balance. Leaf area was measured by a scanner and a leaf area meter. The specific leaf area (SLA) was calculated by dividing the leaf area by its dry mass. The aboveground and underground parts of *Suaeda salsa* samples were collected, separated and weighted respectively before and after drying at 60 °C for 6 to 8 hrs in an oven.

2.2. Construction of PTNs

Data on *Suaeda salsa* traits were imported into R. The “corr.test” in the package “psych” was used to calculate the correlation coefficient R , the significance level p between the traits and to generate traits correlation matrix. The insignificance ($p > 0.05$) or combinations with too low correlation coefficients ($|R| < 0.6$) were ignored to avoid fake correlations between traits. Gephi 0.9.2 was used to make the correlation matrix into plant trait networks. The layout “Fruchterman Reingold” was used to calculate network parameters and node parameters.

Morphology parameters can describe the tightness and complexity of a PTN. Tightness parameters include edge density (ED), diameter (D), and average path length (AL); com-

plexity parameters include average clustering coefficient (AC) and modularity (Q). Node parameters can describe the role that a trait plays in a PTN including degree (k) and betweenness centrality (BC). The detailed equations and ecological descriptions have been provided by He et al. (2020). Briefly, these parameters can be calculated as follows:

$$ED = \frac{2L}{n(n-1)} \quad (1)$$

$$D = \max\{d_{ij}\} (i \neq j) \quad (2)$$

$$AL = \frac{1}{n(n-1)} \sum_{i \neq j} d_{ij} \quad (3)$$

$$AC = \frac{1}{n} \sum_{i=1}^n \frac{2l_i}{t_i(t_i-1)} \quad (4)$$

$$Q = \frac{1}{2m} \sum \left[\left(A_{ij} - \frac{K_i \times k_j}{2m} \right) \delta(c_i, c_j) \right] \quad (5)$$

$$K_i = \sum_{j \neq i} a_{ij} \quad (6)$$

$$BC_i = \sum_{jk} \sigma(j, i, k) \quad (7)$$

where L is the number of connected edges in a network; n is the number of nodes; d_{ij} is the shortest distance between nodes v_i and v_j ; l_i is the number of edges among neighbors of the node; t_i is the number of neighbors of the node; m is the number of edges; A_{ij} is the element of the A adjacency matrix in row i and column j ; k_{ij} is the degree of i / j ; c_{ij} is the component of i / j , the sum encompasses all i and j pairs of vertices; $\delta(x, y)$ is 1 if $x = y$ or it is 0; a_{ij} is the strength of the relationship between nodes v_i and v_j ; $\sigma(j, i, k)$ refers to the number of the shortest path between nodes v_j and v_k passed through the node v_i .

2.3. Data Analysis

Linear regression analysis was used to verify the correlation between the HCIs and hydrological indicators. All the analysis and calculation were performed in R. The “aov” and “Tukey HSD” in the package “stats” in R. were applied for ANOVA test to identify the correlations between parameters of PTNs and HCIs; the “lm” in the package “stat” was used for regression analysis; the package “ggplot2” in R. was used to export graphs.

3. Results

3.1. Relationships between HCIs and Hydrological Conditions

The HCI was developed based on eight HCI indicators including salinity, TN (total nitrogen), TC (total carbon), TP (to-

tal phosphorus), CD (crab density), SD (sediment deposition), HC (hydrodynamic condition), and SM (seed mobility) by PCA (Yin et al., 2020b). PCA showed that PC1 and PC2 were appropriate for constructing the HCI and the cumulative explained variance proportion reached 93.29% (Yin et al., 2020b). In the current study, significant positive correlations could be observed between HCI values and hydrological indicators such as flooding frequency ($p < 0.05$) and flooding time ($p < 0.05$) (Figure 1). This indicated that the constructed HCI could accurately represent the hydrological connectivity in the study area.

3.2. PTNs Characteristics of *Suaeda salsa*

Figure 2 showed the PTNs of *Suaeda salsa* in each sampling zone, and the parameters of PTNs were listed in Table 1. All plant traits were categorized into 3 groups: plant physiology cluster (i.e., aboveground dry mass (UG) and belowground dry mass (BG)), plant morphology cluster (i.e., height of aboveground part (Height), width of canopy (Width), base diameter (Crude), and number of branches (Branch)), and leaf cluster (i.e., leaf area (Area), leaf dry mass (Blade), and SLA).

For all PTNs, UG (aboveground dry mass) had the highest average Degree (6.67), by the following were Crude (base diameter) and Branch (number of branches) (Degree = 6.33). Leaf traits all had lower Degree than other traits. Blade (leaf dry mass) had the highest average BC (0.67) and by the following was UG (BC = 0.625). Plant height, leaf area and SLA had the lowest average BC (0) (Table 2).

Among all sampling zones, the highest ED appeared in LAT2 (0.694), indicating that the connectivity among all traits of plants was highest in LAT2. In contrast, the lowest ED was in PTN from LAT3 zone (0.500). Some sampling zones exhibited the same D (2). The lowest D value (1) occurred in LAT2 zone, which meant that LAT2 zone had the tightest plant trait network compared with other sampling zones. The lowest and highest AL values were observed in LAT2 zone (1.000) and LAT3 zone (1.308), respectively. In contrary, AC showed the

highest value in LAT2 (0.800) and the lowest value in LAT3 (0.537). As for Q value, the lowest value (0.096) appeared in LON2 and LAT1 zones, and the highest Q values (0.190) in LAT3 zone.

3.3. Relationships among PTN Parameters of *Suaeda salsa* and HCI

As shown in Figure 3, the medium-HCI zones usually had the highest or lowest PTN parameters. A steep rise before a gradual decline in AC value was observed with increasing HCI values, while AC values peaked when HCI was -1.158 at LAT2. A similar trend was found for ED values. Comparatively, AL value exhibited a sharp decline before a steep rise, and declined to a low point when HCI value was -1.158. Q value exhibited a steady decline with increasing HCI values ($p < 0.01$) and reached a low point when HCI value was -1.158.

In the longitude direction, the HCI values showed a gradual decrease from LON1 zone to LON3 zone. ED and Q values exhibited a decrease before an increase. AL and AC values showed a decrease and an increase, respectively. Similarly, in the latitude direction, a decrease in the HCI values was also observed from LAT1 zone to LAT2 zone. Q values showed an increase, ED and AC values firstly increased and then decreased, whereas a decrease before an increase in AL and D values were observed.

Figure 4 shows the relationships between HCI indicators and PTN parameters. As for most of PTN parameters, there were no significant relationships with HCI indicators. In most cases, a medium level of HCI indicator usually contributed to higher or lower PTN parameters though no significant relationship was observed between them. However, AL values exhibited a polynomial relationship with HCI values, with the lowest AL value at a medium level of hydrological condition ($p < 0.05$). Comparatively, Q values showed a linear increase with increasing salinities ($p < 0.05$), whereas an exponential decrease with increasing HCI values ($p < 0.05$).

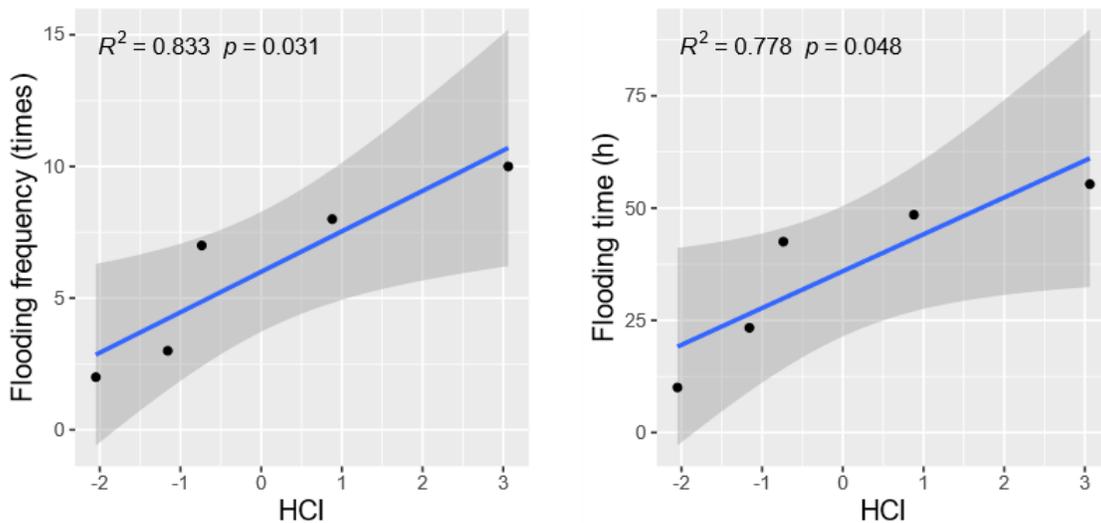


Figure 1. Linear regression analysis between HCI and hydrological indicators.

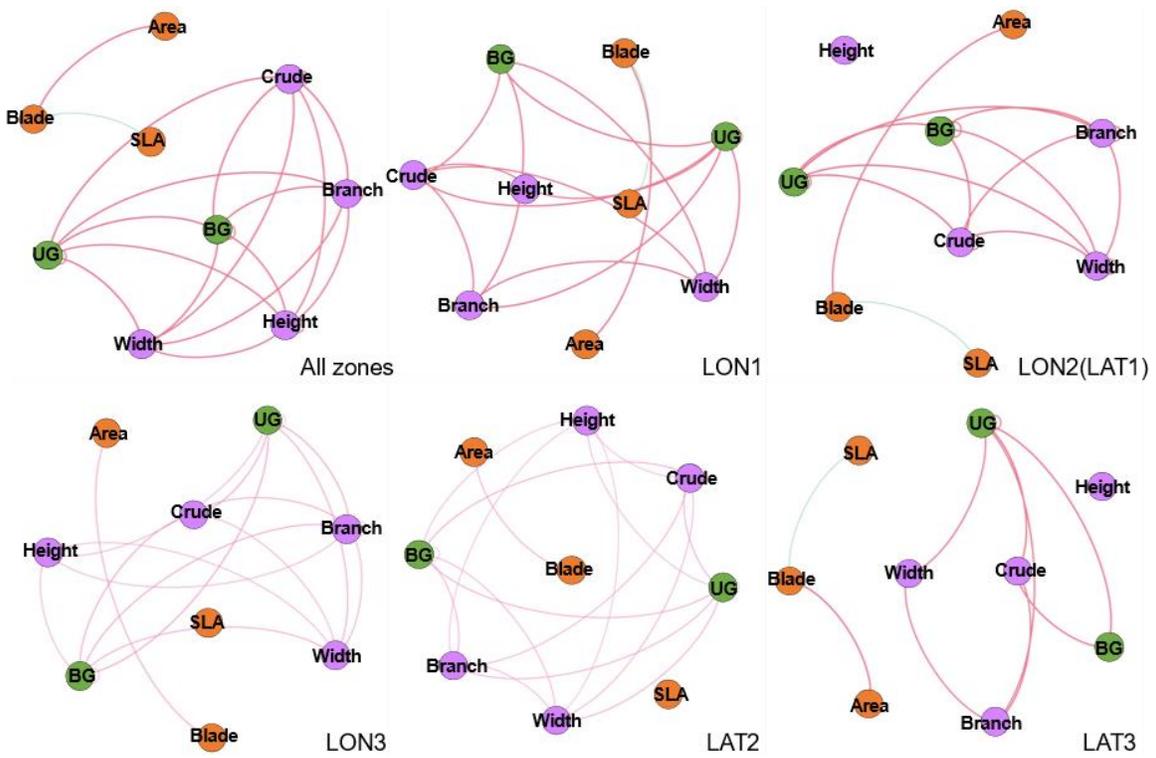


Figure 2. The characteristics of PTNs in five sampling zones (Pink line: positive correlation; Green line: negative correlation; UG: aboveground dry mass; BG: belowground dry mass; Crude: base diameter; Branch: number of branches; Height: height of aboveground part; Width: width of the canopy; Blade: leaf dry mass; Area: leaf area; SLA: specific leaf area).

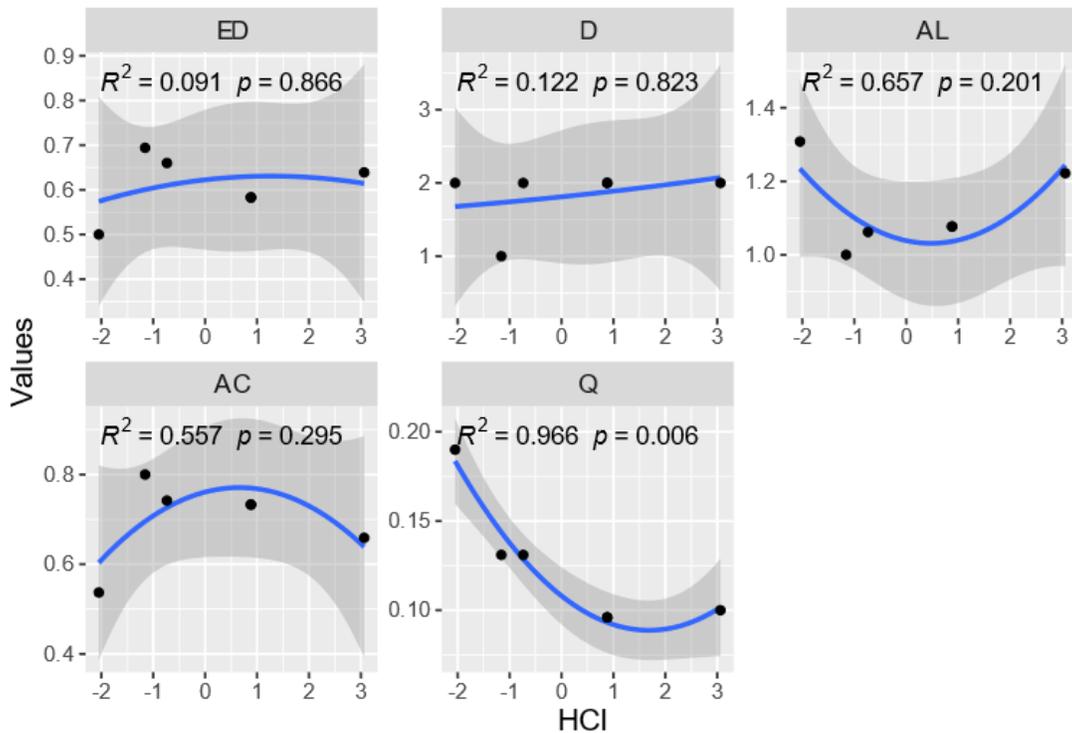


Figure 3. Relationships between HCI and PTN parameters (*ED*: edge density; *D*: diameter; *AL*: average path length; *AC*: average clustering coefficient; *Q*: modularity).

Table 1. PTN Parameters in Different Sampling Zones

Zone	ED	D	AL	AC	Q
LON1	0.639	2	1.222	0.659	0.100
LON2	0.583	2	1.077	0.733	0.096
LON3	0.660	2	1.062	0.742	0.131
LAT1	0.583	2	1.077	0.733	0.096
LAT2	0.694	1	1.000	0.800	0.131
LAT3	0.500	2	1.308	0.537	0.190
All	0.722	2	1.056	0.785	0.078

Notes: ED: edge density; D: diameter; AL: average path length; AC: average clustering coefficient; Q: modularity.

Table 2. Node Parameters of PTNs in Different Sampling Zones

Zone	Trait	Degree	BC	Zone	Trait	Degree	BC
LON1	UG	7	1.5	LON3	Crude	6	0
LON1	Crude	7	1.5	LON3	Height	6	0
LON3	UG	7	0.25	LAT3	Crude	5	0.5
LON3	BG	7	0.25	LAT3	Branch	5	0.5
LON3	Branch	7	0.25	All	Blade	4	1
LON3	Width	7	0.25	LON1	Blade	4	1
All	UG	7	0	LON2	Blade	4	1
All	BG	7	0	LAT3	Blade	4	1
All	Crude	7	0	LON1	Height	4	0
All	Branch	7	0	LAT3	BG	4	0
All	Height	7	0	LAT3	Width	4	0
All	Width	7	0	All	Area	3	0
LAT2	UG	7	0	All	SLA	3	0
LAT2	BG	7	0	LON1	Area	3	0
LAT2	Crude	7	0	LON1	SLA	3	0
LAT2	Branch	7	0	LON2	Area	3	0
LAT2	Height	7	0	LON2	SLA	3	0
LAT2	Width	7	0	LON3	Blade	3	0
LAT3	UG	6	2	LON3	Area	3	0
LON1	BG	6	0	LAT2	Blade	3	0
LON1	Branch	6	0	LAT2	Area	3	0
LON1	Width	6	0	LAT3	Area	3	0
LON2	UG	6	0	LAT3	SLA	3	0
LON2	BG	6	0	LON2	Height	2	0
LON2	Crude	6	0	LON3	SLA	2	0
LON2	Branch	6	0	LAT2	SLA	2	0
LON2	Width	6	0	LAT3	Height	2	0

Notes: BC: betweenness centrality; UG: aboveground dry mass; BG: belowground dry mass; Crude: base diameter; Branch: number of branches; Height: height of aboveground part; Width: width of the canopy; Blade: leaf dry mass; Area: leaf area; SLA: specific leaf area.

4. Discussion

4.1. Key Trait Nodes and Connections of PTNs

In this study, it is hard to define a key trait by analyzing correlations between a single plant trait and a single hydrological indicator since no significant result can be found. However, PTN gives us a new insight about how the relationships among traits are affected by environment change and how to find a key trait through it. For a PTN, the importance of the traits can be assessed by their degree and betweenness central-

ity (He et al., 2020). Traits with high degree and betweenness centrality can be considered as the key traits in a PTN, representing that the traits are of great importance during the plant growth, and these traits might play a central regulatory role in influencing the whole phenotype and coordinating several sub-networks (He et al., 2020). Network analysis showed that the aboveground UG was a hub trait as well as a mediator trait, indicating that other plant traits were closely related to the aboveground biomass.

Kleyer et al. (2019) found that SLA was the hub trait in a trait correlation network based on a compilation of relationships across the literature, but biomass allocation traits and stem specific length were stronger hubs in herbaceous perennial plant networks. However, plant physiology cluster of *Suaeda salsa* in this study had larger number of hub and mediator traits than plant morphology cluster. Leaf cluster was clearly separated from other clusters, indicating that leaf traits were not hub traits and uncorrelated to the plant growth. Therefore, different kinds of plant trait networks may lead to different PTN characteristics. The leaves of *Suaeda salsa* were not flat, so the results of SLA might differ from those of flat leaves, and the difference was reflected in the PTNs. The PTNs with more hub and mediator traits tend to be tighter since shorter connections are included in the PTNs. Previous studies have shown that a high correlation between plant traits indicates a strong competitive ability (Grace, 1990). Thus, *Suaeda salsa* was more competitive in the zones with medium hydrological connectivity in this study. Additionally, previous studies focused on the PTNs of leaf economic traits of perennial woody plants, while this study gave more concerns on plant phenotypic traits of annual herbaceous plants. Leaf economic traits can be used to classify woody and herbaceous vascular plants, and they are also precise enough to distinguish strategies between species within genera and populations (Pierce et al., 2013). Thus, types of plant traits might also affect PTN characteristics.

4.2. Adaption of *Suaeda salsa* to Different HCI Values

Exploring the relationship between plant traits and growth conditions might help to better understand plant growth strategies and predict the dynamic changes (Adler et al., 2014). Plants can efficiently use resources when traits are highly interdependent with each other (Flores-Moreno et al., 2019). A higher ED value (or lower AL and D values) usually indicates better synergy between plant traits, indicating the plant has a higher resource utilization efficiency or production efficiency. In this study, PTNs changed with increasing hydrological connectivity. PTNs tended to have higher AL and D values at higher or lower levels of HCI, implying looser PTNs. However, if the HCI value was extremely high or low, soil and water conditions would not be suitable for plants to grow. Therefore, within the PTNs, plants increased the coordination between traits, and multiple traits gather into small groups to jointly realize some functions to improve the production efficiency, which could benefit plant growth (Flores-Moreno et al., 2019). Fewer connections between clusters indicate the overall network is looser. If plants adapt to resource scarcity and stress conditions by restricting certain specific traits, these traits will tend to be

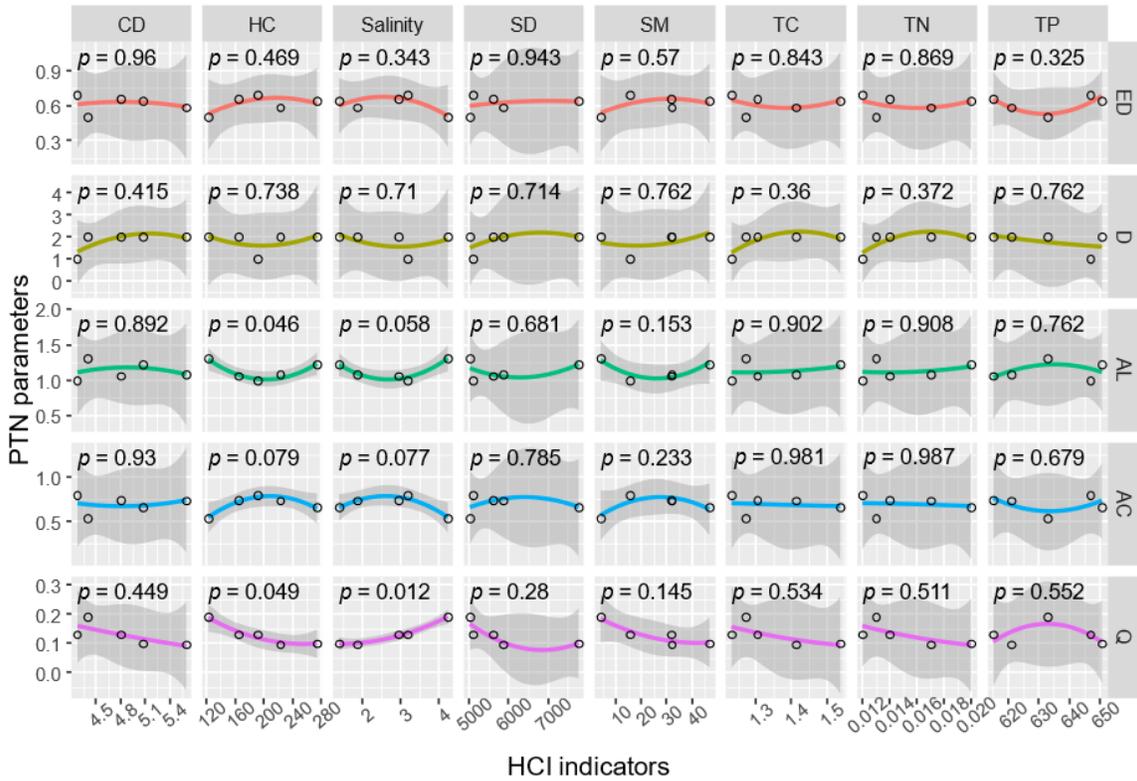


Figure 4. Relationships between HCI indicators and PTN parameters (TN: total nitrogen ($\mu\text{g/g}$); TC: total carbon ($\mu\text{g/g}$); TP: total phosphorus ($\mu\text{g/g}$); CD: crab density ($\text{ind}/0.25\text{m}^2$); SD: sediment deposition (g); HC: hydrodynamic condition (g); SM: seed mobility (%); ED: edge density; D: diameter; AL: average path length; AC: average clustering coefficient; Q: modularity).

irrelevant to the rest of the comprehensive phenotypic traits, resulting in a loose network.

He et al. (2020) have shown that the leaf trait network of forest plants could be modified by the environment and presented an obvious latitude pattern, indicating that plants could adjust the leaf trait network to adapt to the environment. Changes in plant traits and the coordination relationship between traits are the basis for species coexistence, especially the synergy between traits helps us understand the self-regulation and adaptation mechanisms of plants to ecological processes (Violle et al., 2012). Under resource-limited conditions (e.g., sunlight, nutrition, or water-limited), the relationships between plant traits tend to be unitary. On the contrary, in a rich-resource environment, plants adopt a different strategy. The traits are divided into several modules to achieve greater diversity and the combination of traits tends to be diversified (Mason and Donovan, 2015). In this study, the PTNs tended to have high modularity in the low HCI level environment, which was inconsistent with the previous studies. The reason might lie in the type of ecosystem. Although plant traits are less effective for predicting how changes in plant species combination influence ecosystem functions in mixed communities, they can be used to predict certain soil properties and ecosystem functions in monocultures (De Long et al., 2019). In forest ecosystems, the impact of climate and environmental variables on seedling emergence and establishment for trees are significant (Petrie et al., 2016). The D, AL,

and AC values of the leaf trait networks show an increasing trend with latitude, and changes in temperature and precipitation are the main factors leading to this pattern (He et al., 2020). However, in wetland ecosystems, water salinity and hydrodynamic conditions can also affect soil nutrients in addition to precipitation and temperature (Poulin et al., 2009; Bai et al., 2012). Changing the microtopography structure to enhance lateral hydrological connectivity can help increase soil water content and reduce soil salinity, thereby affecting the seed germination and colonization of wetland plants, which ultimately gives an impact on the establishment of plant communities (Wang et al., 2021).

The adaption of PTNs to changing HCI values could also be reflected in the change of AC and Q values. In this study, a higher or lower HCI value usually led to a lower AC value and a higher Q value. A lower AC value indicates that the plants tend to form small functional groups to achieve specific functions (He et al., 2020). A higher Q value indicates clearer boundaries of the functional modules, tighter internal connections of the functional modules, and weaker connections between the functional modules, which reveals the functional modules are composed of specific traits and perform specific functions (He et al., 2020). Significant relationships were observed between HCI and Q values and between salinity and Q values ($p < 0.05$). Under the same light and temperature conditions, the differences in water and salt characteristics of the areas with different

hydrological connectivity led to the differences in PTNs. Compared with the zones with medium hydrological connectivity, soil in the zones with weak hydrological connectivity could no longer support the growth of *Suaeda salsa*. Plants had to form specific functional modules to survive in harsh environments. Therefore, PTNs tended to have higher modularity in the zone with low hydrological connectivity.

Compared with low-latitude areas where the temperature is higher, the inner coordination of plant traits in high-latitude areas is promoted, and multiple traits are gathered into small groups to jointly reinforce part of the plant functions, thereby increasing production efficiency (Flores-Moreno et al., 2019). In areas where is lack of rainfall, plant traits also tend to form loose but partly dense PTNs (He et al., 2020). In addition, Manson and Donovan (2015) believed that plant traits formed simple but strong correlations in resource-limited areas. When the resource is highly available, plant traits tend to form multiple trait groups to achieve greater diversification in functions (Mason and Donovan, 2015). The economic and hydraulic traits of leaves show a strong correlation in arid areas (Yin et al., 2018), while they are decoupled in humid areas (Li et al., 2015).

5. Conclusions

In this study, the hydrological connectivity index (HCI) was developed by principal component analysis based on eight indicators including soil properties, crab density, and seed mobility, which had significant relationships with hydrological indicators. Plant trait networks (PTNs) were constructed by nine plant traits for *Suaeda salsa* salt marshes with different HCI values and the key traits, tightness, and complexity of PTNs were identified to reveal the relationships between PTNs and hydrological connectivity. Results showed that plant above-ground biomass was the hub and mediator trait that was closely correlated with other plant traits. HCI values could significantly influence PTN parameters (at least Q value). PTNs tended to be tighter in medium-HCI zones, and they were more complex in low-HCI zones than in high-HCI zones. Among PTN tightness parameters of *Suaeda salsa*, we observed a higher ED , and lower D and AL in the medium-HCI zones. As for PTN complexity parameters of *Suaeda salsa*, a higher AC value in medium-HCI zones and a higher Q value in low-HCI zones were observed. The PTNs of *Suaeda salsa* changed nonlinearly with increasing hydrological connectivity, the medium hydrological connectivity will contribute to tighter and more stable PTNs of *Suaeda salsa*, which supports our hypothesis. The findings of this work reveal that hydrological connectivity can greatly influence the relationships among plant traits of *Suaeda salsa* and contribute to modulating plant growth and ecological restoration in coastal wetlands. However, further studies are still needed to test the fidelity of PTN parameters based on more data on plant traits in the areas along a gradient of hydrological connectivity, since the influencing mechanisms of hydrological connectivity on PTNs still remain unclear.

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