Trait-based adaptability of Phragmites australis to the effects of soil water and salinity in the Yellow River Delta

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Abstract

Phragmites australis is the dominant species in the Yellow River Delta and plays an important role in wetland ecosystems. Ecological responses of the P. australis community to soil properties were investigated in 96 areas along the coastal-inland regions in the Yellow River Delta of China. The aim was to evaluate the relationship between phenotypic variation and environmental factors, reveal which functional traits could well respond to changes in electrical conductivity and soil water content, and the ecological strategies of P. australis. Within the range of soil water content (9.39–36.92%) and electrical conductivity (0.14–13.29 ms/cm), the results showed that the effects of soil water content and salinity were not equally important for the characterization of the morphological and physiological variability, and that plant functional traits including leaf traits and stem traits responded more strongly to soil salinity than soil water content. Our results suggested that salinity leads to reduced average height, specific leaf area, leaf area, and base stem diameter, but increased leaf water content and leaf thickness. The relationships between functional traits and electrical conductivity were generally linear and logarithmic. The coefficients of variation of morphological traits showed more phenotypic plasticity than the physiological traits. Salinity also led to the stress tolerator/competitor-stress tolerator (S/CS) strategies of P. australis; with the decrease of environmental stress, the main strategy gradually moved to the competitor (C) strategy, making P. australis the dominant species in the Yellow River Delta. KEYWORDS: Soil water content, Electrical conductivity, Functional traits, Plasticity, Life strategies.

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Abstract

Phragmites australis is the dominant species in the Yellow River Delta and plays an important role in wetland ecosystems. Ecological responses of the *P. australis* community to soil properties were investigated in 96 areas along the coastal-inland regions in the Yellow River Delta of China. The aim was to evaluate the relationship between phenotypic variation and environmental factors, reveal which functional traits could well respond to changes in electrical conductivity and soil water content, and the ecological strategies of *P. australis* . Within the range of soil water content (9.39–36.92%) and electrical conductivity (0.14–13.29 ms/cm), the results showed that the effects of soil water content and salinity were not equally important for the characterization of the morphological and physiological variability, and that plant functional traits including leaf traits and stem traits responded more strongly to soil salinity than soil water content. Our results suggested that salinity leads to reduced average height, specific leaf area, leaf area, and base stem diameter, but increased leaf water content and leaf thickness. The relationships between functional traits and electrical conductivity were generally linear and logarithmic. The coefficients of variation of morphological traits showed more phenotypic plasticity than the physiological traits. Salinity also led to the stress tolerator/competitor-stress tolerator (S/CS) strategies of *P. australis* ; with the decrease of environmental stress, the main strategy gradually moved to the competitor (C) strategy, making *P. australis* the dominant species in the Yellow River Delta.

KEYWORDS: Soil water content, Electrical conductivity, Functional traits, Plasticity, Life strategies.

INTRODUCTION

Plant functional traits could be divided as different types as traits of groups of plants that reflect similar responses to environmental factors or exert similar effects on community dynamic processes based on plant morphology and physiology (Duckworth et al., 2000; Guo et al., 2017). Morphological and physiological features that could reflect plant ecological strategies (Spasojevic et al., 2014; Chai et al., 2016). Owing to the adaptability and plasticity to environmental gradients, individual plants have highly variable traits. The variation in plant functional traits determines the feedback of plants in response to various environmental factors (Li et al., 2014; Guan et al., 2017). Functional traits can be used to quantify a wide range of natural and anthropogenic disturbances (Wang et al., 2015; Chai et al., 2016).

Numerous studies have reported the relationships among plant communities and other environmental factors such as salinity in various habitats (Wang et al., 2012; González-Alcaraz et al., 2014, McCoy-Sulentic et al., 2017). These studies have greatly contributed to our understanding of soil–plant interactions that benefit wetland ecosystem restoration. Plant growth is highly dependent on soil water content. Many researchers have reported that community structure (Pérez-Ramos et al., 2012), species composition (Li et al., 2008), and vegetation growth (Yu et al., 2014; Gong et al., 2014) could be affected by soil water content. Salinity is one of the major environmental factors limiting plant growth and productivity (Sdouga et al., 2019). Salinity also affects multiple trait strategy-dimensions, causes consequences for ecosystem functions (De Battisti et al., 2020), and leads to environmental filtering that drives plant community assembly processes (Yi et al., 2020). Plants adapt to heterogeneous habitats through plasticity in growth strategies and functional traits, as well as the optimal allocation and trade-offs of various traits (Mason et al., 2013; Donovan et al., 2014; Guan et al., 2017). Plant functional traits have been useful in answering many important ecological questions at a range of scales (Mason et al., 2013; Pérez-Harguindeguy et al., 2013), providing a tool for determining the feedback of plants under stressful conditions.

Competitor, stress tolerator, ruderal (CSR) theory is a prominent strategy scheme advanced by Grime (1977) and reviewed by Grime & Pierce (2012), in which the three principal strategies represent viable trait combinations. They have also been used to investigate and interpret community processes, such as succession and the relationship between species richness and productivity (Caccianiga et al., 2006; Cerabolini et al., 2016). Three core leaf functional traits, specific leaf area (SLA), leaf dry matter content (LDMC), and leaf area (LA), were used as criteria to determine the ecological strategies of the individual or population of the plant being studied. The plant CSR strategy taxonomy goes beyond the previous research that focused on analyzing plant ecological strategies solely by using CSR strategies or functional trait pedigree (Pierce et al., 2017; Xu et al., 2019).

Phragmites australis , a widespread species occurring in both freshwater and brackish habits, has strong environmental adaptability and phenotypic plasticity (Yang et al., 2014). The broad range of adaptions to soil water content and salinity has led to the successful growth of *P. australis* in high-salinity areas (Burdick et al., 2001; Achenbach et al., 2013; Guo et al., 2018). A field investigation was carried out in the Yellow River Delta in order to reveal the responses of community characteristics and functional traits of *P. australis* to soil water content and salinity. Here, we hypothesized that (1) the effects of soil water content and salinity were not equally important in characterizing the morphological and physiological variability; and (2) the differences in morphological traits, physiological traits, adaptive mechanisms, and ecological strategies of*P. australis* in response to environmental stress were dominated by functional traits.

MATERIALS AND METHODS

Study region and sampling sites

The study site was located in the Yellow River Delta (36°55'–38deg16'N, 117deg31'–119deg18'E) in Dongying, Shandong Province, northern China. The Yellow River Delta is one of the fastest-growing estuarine wetlands in the world (Cui et al., 2011). The mean annual precipitation in the study area is approximately 628.6 mm and the mean annual temperature is about 11.9degC (Zhou et al., 2020). The region is simultaneously influenced by river water, ground water, and seawater, and is characterized by strong temporal and spatial heterogeneity of soil water and salinity gradients (Zhou et al., 2020). To describe and characterize the patterns and processes influencing the *P. australis* communities, 96 quadrats (1 x1 m) selected at random were investigated along the coastal-inland regions (37deg43'–38deg05'N, 118deg41'–119deg13'E) under different gradients of soil water content and electrical conductivity in the Yellow River Delta in 2013. Samples were chosen in terms of typical *P. australis* communities with little human disturbance, but with significant differences in soil water content and salinity gradient (Figure 1).

Figure 1. Distribution patterns of soil water content and electrical conductivity for 96 different samples.

Measurements of soil properties and functional traits

Soil layer samples were obtained at a depth of 0–20 cm to measure soil water content (SWC) and electrical conductivity (EC). SWC was measured by drying soil samples at 105degC to constant weight.

Soil water content (SWC) = (wet soil weight - dry soil weight) x100% / dry weight of soil

EC was measured by taking 10 g grated dried soil sample and placing it in an Erlenmeyer flask. Water and soil were mixed in a volume ratio of 1: 2.5 and a magnetic stirrer was used to dissolve the salt for about 40 min. A conductivity meter (DDS12A, LIDA, China) was used to measure the EC in the upper suspension.

For each sample, 10 functional traits were measured including average height, number of plants, soil plant analysis development (SPAD) values, leaf water content, specific leaf area, leaf area, leaf thickness, pitch number, internode height, and shoot basal diameter. Leaf thickness was measured by a micrometer caliper at the widest point while avoiding the midrib. The base stem diameter was determined using a vernier caliper. SPAD values were determined using a chlorophyll meter (SPAD-502PLUS, Konica Minolta, Japan). The fresh mass of leaves (LFM) was weighed and then oven-dried at 80degC for 48 h, after which the dry mass of leaves (LDM) was weighed. Leaf area (LA) was analyzed using a broadleaf analysis system (WinFolia pro LM2400P, Regent) through scanning with a Canon scanner (Canon 2000). Specific leaf area was calculated using the following equation:

SLA=LA/LDM, (1)

where SLA (cm^2/g) was the specific leaf area, LA was the leaf area (cm^2), and LDM (g) was the dry mass of the leaf. Leaf water content was calculated using the following equation:

LWC= (LFM-LDM)/LFM=1-(LDM/LFM), (2)

where LWC (g/g) was leaf water content, LFM (g) was the fresh mass of the leaf, and LDM (g) was the dry mass of the leaf.

We used LA, LDMC, and SLA to assign combinations of leaf traits to CSR strategies under different salt conditions (Pierce et al., 2017).

Data analysis

One-way analysis of variance was conducted to identify differences in environmental traits and functional traits. The normality was tested prior to one-way analysis. A logarithmic transformation was necessary to meet the statistical requirement because the data were not normally distributed. Redundancy analysis (RDA), a multivariate direct gradient analysis method, was performed using the Canoco 5.0 software to elucidate the relationship between functional traits and soil environmental factors based on standardized data. The primary statistical analyses, functional traits relationship, partial correlation and curve estimation were performed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA). The CSR model was calculated by the globally calibrated CSR analysis tool 'StrateFy' and the picture was output by R (R Development Core Team 2013). Figures were plotted using Origin Pro 8.0 (Originlab Co., Northampton, MA, USA).

RESULTS

3.1 Trade-off among *P. australis* traits

The *P. australis* height traits had obvious positive correlations with the growth traits of leaf and stem, such as SLA (P<0.01), leaf area (P<0.01), pitch number (P<0.01), internode height (P<0.01), and shoot basal diameter (P<0.01). The SPAD and leaf thickness had significant negative correlations with other traits (Table 1).

Table 1. Trade-off among *P. australis* traits.

	H (cm)	Nu	SPAD	LWC (%)	SLA	LA (cm^2)	LT (cm)	Lpnu	Lpih (cm)	BSD (c
H (cm)										
Nu	-0.05									
SPAD	**-0.286****	-0.128								
LWC (%)	0.069	0.165	0.168							
SLA	**0.261***	-0.002	**-0.225***	**-0.375****						
LA (cm^2)	**0.498****	-0.089	0.006	0.000	0.037					
LT (cm)	**-0.366****	-0.055	**0.253***	-0.085	**-0.475****	-0.148				
Lpnu	**0.680****	-0.105	-0.177	0.162	0.116	**0.247***	**-0.318****			
Lpih (cm)	**0.852****	-0.001	**-0.253***	-0.09	**0.261***	**0.528****	-0.196	**0.277****		
BSD (cm)	**0.555****	-0.18	**-0.252***	**-0.246***	**0.225***	**0.385****	-0.143	**0.446****	**0.456****	

Pearson correlation coefficients are shown in the table.*, $P < 0.05$; **, $P < 0.01$. Abbreviations: H, average height; Nu, number of plants; SPAD, SPAD values; LWC, leaf water content; SLA, specific leaf area; LA, leaf area; LT, leaf thickness; Lpnu, pitch number; Lpih; internode height; and BSD, shoot basal diameter.

3.2 Response of functional traits to environmental variables

Partial correlations were conducted to determine the relationships between environmental variables and functional traits (Table 2). The results indicated that functional traits could better respond to changes in electrical conductivity than soil water content. The average height, specific leaf area, leaf area, pitch number, internode height, and base stem diameter were significantly negatively correlated with electrical conductivity ($P<0.01$), while significantly positive relationships were only discovered between soil water content and leaf water content, and between electrical conductivity and leaf water content and leaf thickness ($P<0.05$). When compared with plant traits and leaf traits, the relationship between stem traits and environmental variables was much closer.

Table2. Partial correlation coefficient matrix between environmental variables and selected functional traits (plant traits, leaf traits, and stem traits) of *P. australis* .

Index	Index	SWC	SWC	EC	EC
		r	P	r	P
Plant traits	Average height	0.204	0.060	**-0.563*****	0.000
	Number of plants	0.019	0.862	0.014	0.901
Leaf traits	SPAD values	-0.123	0.259	0.063	0.564
	Leaf water content	**0.238***	0.027	**0.228***	0.035
	Specific leaf area	0.088	0.423	**-0.442*****	0.000
	Leaf area	-0.068	0.532 9	**-0.619*****	0.000
	Leaf thickness	-0.047	0.668	**0.232***	0.031
Stem traits	Pitch number	0.142	0.193	**-0.349****	0.001
	Internode height	0.075	0.494	**-0.524*****	0.000
	Base stem diameter	0.072	0.510	**-0.290****	0.007

Asterisks indicate a significant correlation between environmental variables and functional traits (2-tailed) ($^{*}P<0.05$;$^{**}P<0.01$;$^{***}P<0.001$). Abbreviations: SWC, soil water content; EC, electrical conductivity.

Significant regression relationships were only observed between functional traits and electrical conductivity, and these relationships were generally linear and logarithmic (Figure 2). For whole-plant traits variables, significantly logarithmic relationships were only found between the electrical conductivity and average height ($P<0.001$) of *P. australis* . For leaf traits, significant correlations were discovered in the relationship between electrical conductivity and leaf water content ($P<0.05$), specific leaf area ($P<0.01$), leaf area ($P<0.001$), and leaf thickness ($P<0.01$). For stem traits, significant correlations were observed between electrical conductivity and all selected stem traits, including pitch number ($P<0.001$), internode height ($P<0.001$), and base stem diameter ($P<0.01$). Moreover, positive relationships between electrical conductivity with leaf water content and leaf thickness were discovered.

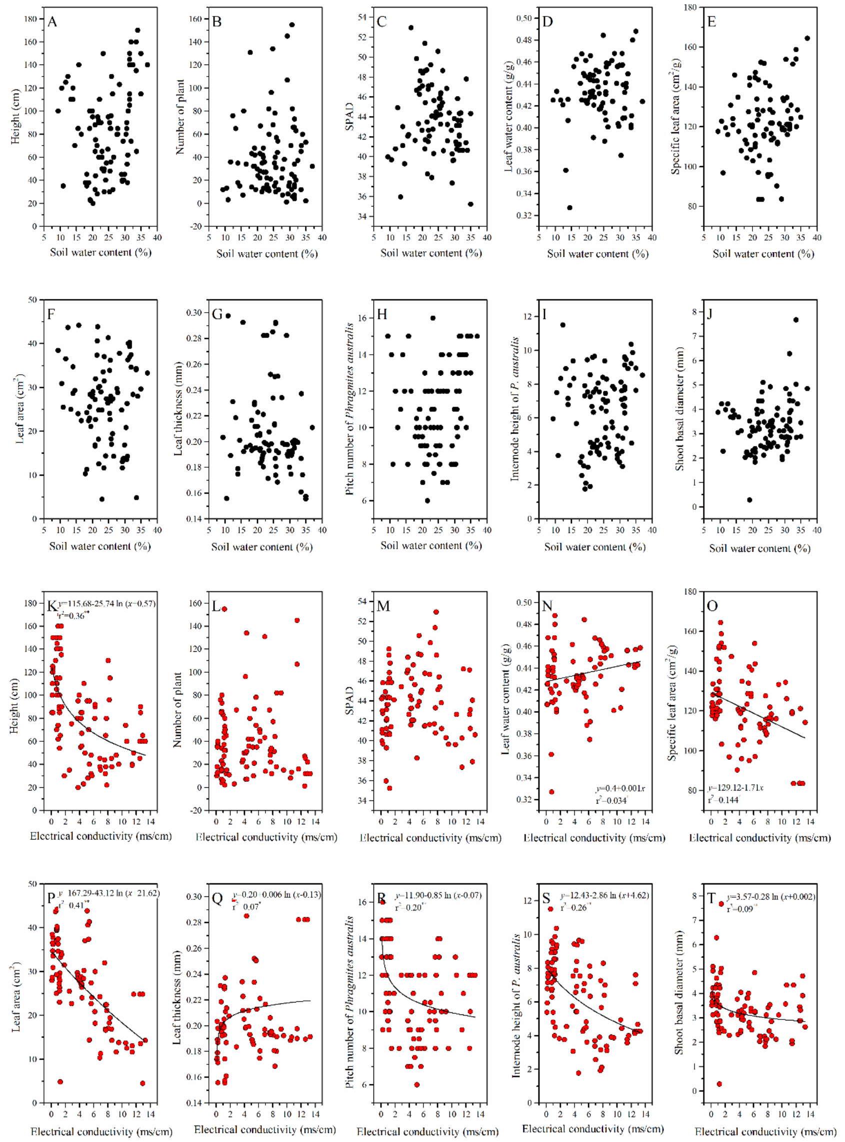

Figure 2. Regression relationship between functional traits of*P. australis* and soil water content.

(A–J), electrical conductivity (K–T). A, K, average shoot height; B, L, number of shoots; C, M, SPAD values; D, N, leaf water content; E, O, specific leaf area; F, P, leaf area; G, Q, leaf thickness; H, R, pitch number; I, S, internode height; and J, T, shoot basal diameter.

3.3 Plant-environment relationships

Redundancy analysis (RDA) was applied to further investigate the contribution of soil water content and electrical conductivity to functional traits of *P. australis* . As shown in Figure 3, selected environmental variables completely explained 15.43% of the variance in functional trait variables (F=7.8, P<0.01). The first axis explained 14.34% in the ordination with electric conductivity. The second axis explained 1.08%, with soil water content. The relationships with electrical conductivity were negative, including SPAD, height, and stem traits, but the functional trait variables had almost no correlation with soil water content. The response of leaf traits to environmental variables were inconsistent. Leaf water content had positive relationships with soil water content and electrical conductivity. Leaf thickness had a strong positive relationship with electrical conductivity, while leaf area and specific leaf area had strong negative correlations with electrical conductivity.

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Figure3. Biplot of environmental factors (soil water content and electrical conductivity) with community characteristics and functional trait variables by redundancy analysis (RDA). Hollow black arrows are soil water content and electrical conductivity; solid blue arrows are functional traits of *P. australis* . Abbreviations: EC, electrical conductivity; SWC, soil water content; H, average height; Nu, number of plants; SPAD, SPAD values; LWC, leaf water content; SLA, specific leaf area; LA, leaf area; LT, leaf thickness; Lpnu, pitch number; Lpih; internode height; and BSD, base stem diameter. Green indicates plant traits including H and Nu; red indicates leaf traits including SPAD, LT, LA, SLA, and LWC; black indicates stem traits including Lpih, Lph, Lpnu, and BSD.

3.4 ***P. australis*** adaptability and plasticity

Environmental factors and selected functional traits of *P. australis* varied greatly (Table 3), indicating the strong phenotypic plasticity and environmental tolerance of *P. australis* . The coefficient of variation of soil water content was larger than 25%, while the electrical conductivity was up to 87%. The amplitude of soil water content (9.39–36.92%) and electrical conductivity (0.14–13.29 ms/cm) indicated the high tolerance of *P. australis* to environmental variables in the Yellow River Delta. The coefficients of variation of leaf traits were lower than 20%, except for the leaf area, while the stem traits were higher than 20%.

Table 3. Statistical characteristics of environmental variables and functional traits for *P. australis.*

Index	Index	Minimum	Maximum	Mean	SD	CV (%)
Environmental variables	Soil water content (%)	9.39	36.92	24.65	6.4	25.95
	Electrical conductivity (ms/cm)	0.14	13.29	4.55	3.9	86.51
Plant traits	Average height (cm)	20	170	82.73	37.67	45.54
	Number of plants	1	352	42.36	44.91	106.01
Leaf traits	SPAD values	22.2	55.53	43.45	4.46	10.25
	Leaf water content (%) (g/g)	32.71	48.82	43.31	0.03	5.96
	Specific leaf area (cm^2/g)	83.46	164.41	121.48	16.88	13.89
	Leaf area (cm^2)	4.46	44.19	26.96	9.68	35.91
	Leaf thickness (cm)	0.16	0.3	0.21	0.03	15.93
Stem traits	Pitch number	6	16	11.14	2.37	21.25
	Internode height (cm)	1.77	11.5	6.34	2.26	35.59
	Base stem diameter (mm)	1.83	7.68	3.33	0.96	28.87

Abbreviations: SD, Standard Deviation; CV, Coefficient of Variation.

3.5 Ecological strategy of *P. australis* under different environmental factors

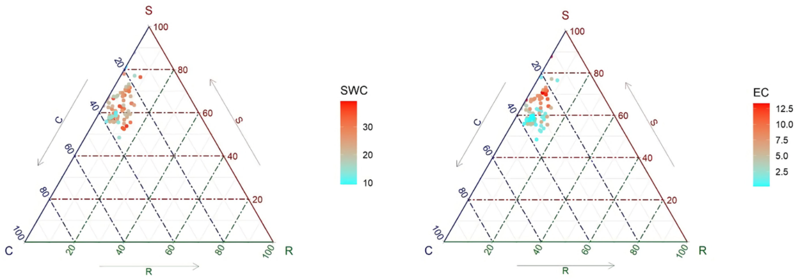

Figure 4 . Ecological strategies of *P. australis* under different environmental conditions based on the 96 areas. Abbreviations: SWC, soil water content; EC, electrical conductivity; C: competitor; S: stress tolerator, R: ruderal.

The ecological strategies of *P. australis* in the Yellow River Delta under different salt and water conditions mainly consisted of stress tolerator/competitor-stress tolerator (S/CS) (57.3%, C: S: R=28.5: 66.7: 4.7), competitor-stress tolerator (CS) (27.1%, C: S: R=36.0: 57.3: 6.7), stress tolerator/ competitor-stress tolerator-ruderal (S/CSR) (11.5%, C: S: R=29.9: 57.8: 12.3), and rarely competitor-stress tolerator/ competitor-stress tolerator-ruderal (CS/CSR) (3.1%) and stress tolerator (S) (1%) (Figure 4). The major strategies consisted of S/CS and CS (84.4%). The three strategies of S/CS-CS-S/CSR formed a S-C trade-off strategy axis with weak R, indicating the competition and stress tolerance in high-salinity areas of the Yellow River Delta. The R strategy was the minor one in the Yellow River Delta, mainly distributed in the low-salinity areas. There were no obvious different strategies of *P. australis* under different soil water contents, while the S strategy was dominant in the Yellow River Delta. However, with the decrease of soil salinity and the increase of soil water content, *P. australis* gradually shifted to the C strategy.

DISCUSSION

4.1 Effects of environmental factors on functional traits of*P. australis*

Phragmites australis is a type of salt-tolerant plant (Mauchamp et al., 2001; Santos et al., 2016); higher salinity inhibits their growth. *Phragmites australis* is more likely to be found in sites of surface ground water discharge and appears to access deeper, less saline water (Burdick et al., 2001; Guo et al., 2018; Veldhuis et al., 2019). Salinity stress results in a clear stunting of plants (Wang et al., 2016) and reduced leaf area expansion (Parida et al., 2005; Gong et al., 2020). As previously reported, the height reduction of *P. australis* growth was a marked feature under salinity stress (Lissner et al., 1997; Guo et al., 2018; Sdouga et al., 2019). Leaf traits are closely related to the growth, ability to utilize resources, and survival strategies of plants under environmental changes (Mason et al., 2013). Specific leaf area associated with allocation strategy tends to scale positively with leaf nitrogen concentration, and negatively with leaf longevity (Pérez-harguindeguy et al., 2013; Spasojevic et al., 2014). Leaf thickness plays a key role in determining the physical strength of leaves, being higher in sunnier, drier, and less fertile habitat, as well as in longer-lived leaves (Wu et al., 2008). Our results clearly verified these conclusions, as indicated by the average height of *P. australis* being negatively correlated with electrical conductivity (Figure 3). Based on our results, salinity affects plant leaves through reduced specific leaf area and leaf area, but increased leaf water content and leaf thickness enhance the ability to resist environmental stress, altering the living strategy from growth to survival.

Stem traits play a vital role in the entire plant life cycle, supporting ground organization, holding water and nutrients, and conducting water and elements (Liu et al., 2015). Based on our results, the stem traits had positive correlations among themselves (Table 1), which were generally linear and logarithmic relationships with electrical conductivity (Figure 3). Under low electrical conductivity, the plant had a relatively high growth rate, with stem elongation, an increased number of sections, and thickened base stem diameter to support more leaves and better compete for resources. Under high-salinity environments, plants changed their growth strategy to thicken and strengthen their structures to preserve internal resources to survive.

The results of the present study verified that the electrical conductivity of environments was the dominating factor controlling the functional properties of *P. australis* in the Yellow River Delta.

Many studies have reported that community structure (Pérez-Ramos et al., 2012), species composition (Li et al., 2008), and vegetation growth (Gong et al., 2014a) were affected by soil water content. Generally, a non-linear relationship with an obvious soil moisture threshold value appeared for most plants (Yu et al., 2012), and plant growth could be limited by both a water deficit and excess soil water. The relationship between soil water content and growth traits was approximately linear in dry habits (Gong et al., 2014b). However, based on our laboratory experiments, *P. australis* has no obvious specific correlation between soil water content and functional traits, except for the leaf water content (Table 1, Figure 3). *P. australis* had a wide range of niche adaptations to water and had high tolerance to both drought and waterlogged conditions; the soil water conditions used in our research were not extreme enough to cause stress. The results indicated a high adaptability to soil water content for the growth of *P. australis* , however, soil water content was not the limiting factor based on the 96 samples in our research.

4.2 The plasticity of morphological and physiological traits

Functional traits can be divided into morphological traits and physiological traits (Liu & Ma, 2015). Strong plasticity of variability was observed in whole plant traits, especially in the morphological traits, and coefficient of variation was the accepted method used to standardize variability among traits with fundamentally different units (Acasuso-Rivero et al., 2019). Morphological traits involve the shape and structure of each organ, responses of individuals to environmental changes based on internal genes, and adaptations of plants to environmental heterogeneity (Hu et al., 2008). In our research, the leaf area, stem pitch number, height, and shoot basal diameter were attributed to morphological traits. All these traits had high coefficients of variation, which were higher than 20%, indicating that morphological traits are sensitive under the stress of environmental factors. Higher phenotypic plasticity contributed to *P. australis*being able to adapt to a wide range of niches under salinity stress in the Yellow River Delta.

Physiological traits are related to biochemical processes and reproduction (Zhang & Luo, 2004). Some researchers showed that physiological traits were more susceptible to soil properties with regard to morphological traits (Schneider et al., 2017). Compared with morphological traits, the coefficient of variation values of physiological traits contained the SPAD, leaf thickness, SLA, and leaf water content in our research and were lower than 20%. The lower coefficients of variation indicated relatively lower plasticity and stable intrinsic properties of *P. australis* under various environmental stressors. SLA and leaf thickness, although shown as morphological traits (Smith & Knapp, 2001), were regarded as physiological traits in some research (Zhang & Luo, 2004; Wright et al., 2004). They remain relatively stable under specific environments, and were not only influenced by soil factors, but also influenced by factors including leaf tissue characteristics (such as the epidermis cells and mesophyll cells) and chemical composition.

In the Yellow River Delta, the mode of *P. australis* morphological traits is an integrated system in growth, but physiological traits have different mode to reflect the environmental stress. Grouping plants by functional trait types rather than by organs could help us more accurately understand the process of plant growth and the response to environmental stress. It's worth noting that while plasticity is not equal to fitness (Acasuso-Rivero et al., 2019), the relationship between them is still worth studying in the Yellow River Delta under environmental stress.

4.3 The model of *P. australis* life strategies

The trade-off between growth and survival is the heart of the economic spectrum theory of leaves (Reich, 2014; Díaz et al., 2016). Three core leaf traits, SLA, LDMC, and LA, were used as criteria to determine the ecological strategies of individuals (Pierce et al., 2017). The application of the CSR strategy in community construction has been controversial. Many studies have verified the explanation of CSR strategy classification for community species composition in habitats where species strategy distribution was concentrated (Negreiros et al., 2014, Paula et al., 2015). However, CSR strategies are usually used to research the different species in communities, and there are few studies on the strategies of the same species under different environmental stresses.

According to the top-level succession theory, the plant community in the Yellow River Delta should be in the early stage of succession and salt is a limiting factor for most herbaceous species (Tan et al., 2012). Therefore, the plants with strong salinity stress tolerance under the S/CS strategy have more advantages, and the plants near the S strategy have greater survival opportunities. S is the dominant strategy for*P. australis* in the Yellow River Delta. Plants near the S strategy end have lower LDMC, while plants near the C strategy end have higher SLA traits, representing revenue capacity, than those near the S strategy end. With the decrease of soil salinity and the increase of soil water content, the strategy of *P. australis* in the Yellow River Delta gradually shifted to C. For the C strategy, plant selection and growth are mainly aimed at rapidly occupying resources, and a relatively large SLA is needed to grow rapidly (Xu et al., 2019). Plants under the R strategy are adapted to environments with strong disturbance, tend to invest many resources in reproduction to offset the effects of disturbances on the population, achieve the purpose of survival and continuation of the population (Pierce et al., 2017). In the Yellow River Delta, *P. australis* have a minor ruderal (R) strategy.

As a perennial herb, *P. australis* tends to grow rapidly and spread by underground stems, forming a single community, which is common in the Yellow River Delta. Due to the habits of *P. australis* , the R strategy rarely appears in the Yellow River Delta. There are similar modes of strategies of *P. australis* related to the soil salinity and the soil water content. We believe that environmental factors partly determined the C or S strategy of *P. australis* , while with the decrease of environmental stress, the mainly strategy gradually shifts from S to C. This indicated that *P. australis* has stronger tolerance and competitive ability in the communities from the coastal wetland to inland areas, therefore becoming the dominant species in the Yellow River Delta.

4.4 Summarizes and Perspectives

Gradients of environmental stress and disturbance are important drivers of morphological and physiological variability for *P. australis*in the Yellow River Delta. The response of functional traits to the environment could be summarized as follows: (1) The relationships between functional traits and electrical conductivity were generally linear and logarithmic, indicating that soil salinity was the main factor that influenced the functional traits of *P. australis* in the Yellow River Delta. (2) The plant morphological traits had higher plasticity based on the coefficients of variation, which were much higher than 20%. However, compared with the morphological traits, the coefficients of variation for physiological leaf traits were lower than 20%. This indicated that physiological traits are more stable than morphological traits in response to environmental variables. (3) The variability of strategies for *P. australis* indicated that in the high-salinity area, competition (C) and stress tolerator (CS) were the main strategies that affected the growth and distribution for *P. australis.* With the decrease of environmental stress, the mainly strategy gradually moved from S to C. Further studies, including studies focused on underground traits and genetics, are needed to clearly understand different responses to related ecotypes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest in the publication of this paper.

AUTHOR CONTRIBUTION

Dayou Zhou : Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing-original draft (lead); writing-review and editing (equal).**Yuehan Ni**

: Conceptualization (equal); data curation (equal); formal analysis (equal); methodology (equal); writing-original draft (supporting). **Xiaona Yu** : Conceptualization (equal); formal analysis (equal); data curation (equal); methodology (equal); validation (equal); writing-review and editing (lead). **Kuixuan Lin** : Funding acquisition (equal); investigation (equal); project administration (equal); writing-review and editing (equal). **Ning Du** : Formal analysis (equal); investigation (equal); methodology (equal); writing-review and editing (equal). **Lele Liu** : Formal analysis (equal); methodology (equal); visualization (equal); writing-review and editing (equal). **Xiao Guo** : Formal analysis (equal); methodology (equal); writing-review and editing (equal).**Weihua Guo** : Conceptualization (equal); data curation (equal); funding acquisition (lead); methodology (equal); project administration (lead); writing-original draft (supporting); writing-review and editing (equal). All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Plant functional traits and environmental factors data input files are available at: https://doi.org/10.5061/dryad.x3ffbg7j4.

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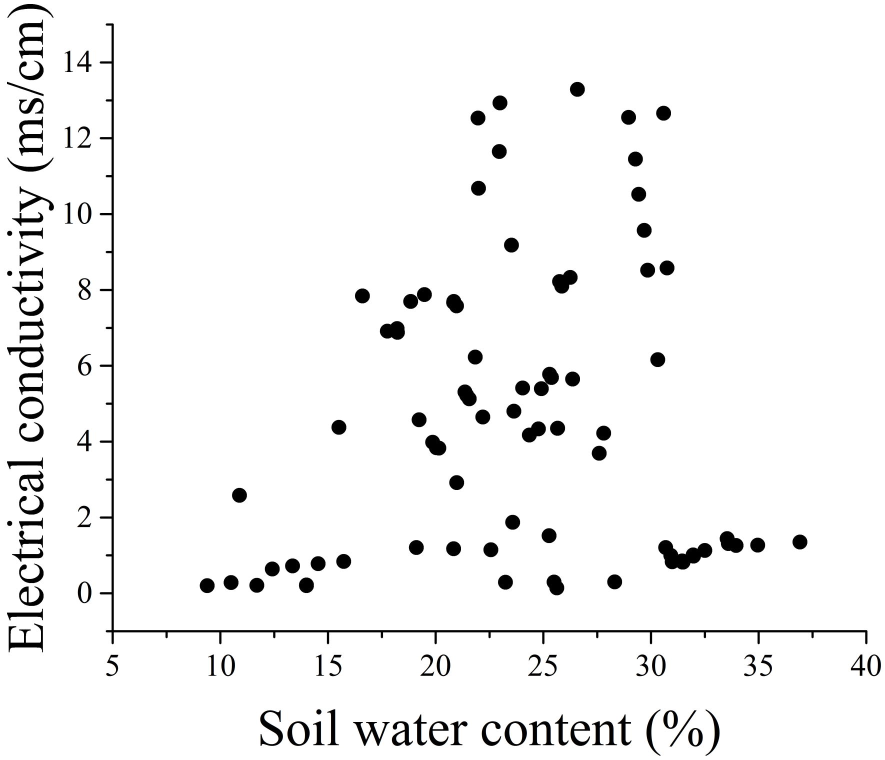
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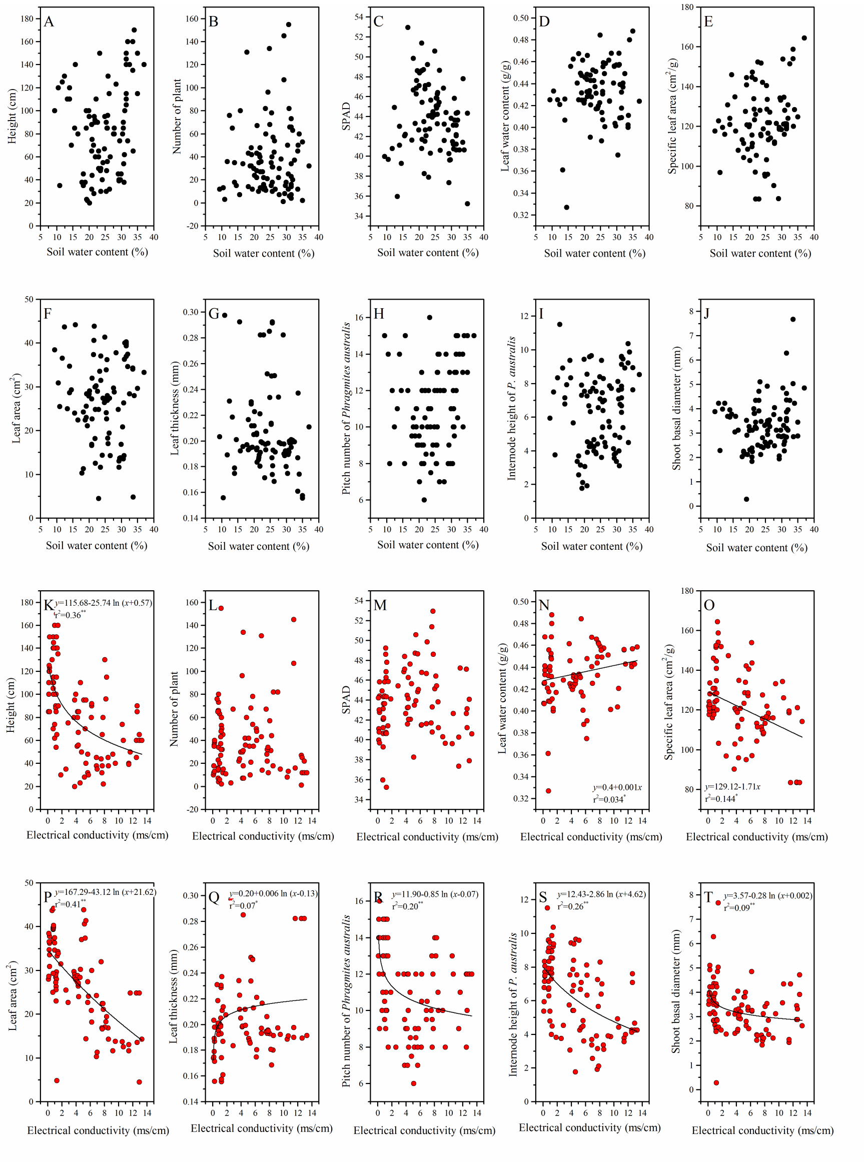
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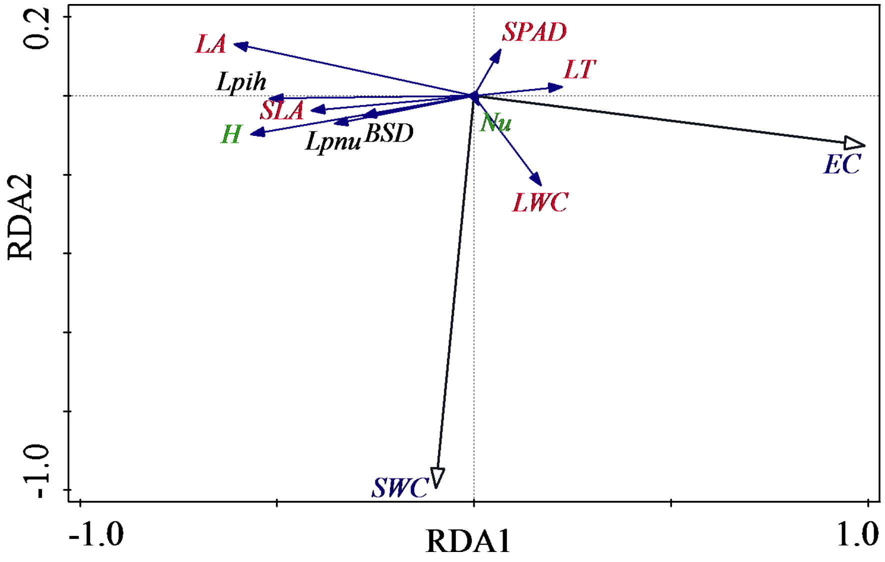
E
Specific leaf area (cm2/g)
Soil water content (%)
F
Leaf area (cm2)
Soil water content (%)
G
Leaf thickness (mm)
Soil water content (%)
H
Pitch number of Phragmites australis
Soil water content (%)
I
Internode height of P. australis
Soil water content (%)
J
Shoot basal diameter (mm)
Soil water content (%)
K
y=115.68-25.74 ln (x+0.57)
r2=0.36**
Height (cm)
Electrical conductivity (ms/cm)
L
Number of plant
Electrical conductivity (ms/cm)
M
SPAD
Electrical conductivity (ms/cm)
N
y=0.4+0.001x
r2=0.034*
Leaf water content (g/g)
Electrical conductivity (ms/cm)
O
y=129.12-1.71x
r2=0.144*
Specific leaf area (cm2/g)
Electrical conductivity (ms/cm)
P
y=167.29-43.12 ln (x+21.62)
r2=0.41**
Leaf area (cm2)
Electrical conductivity (ms/cm)
Q
y=0.20+0.006 ln (x-0.13)
r2=0.07*
Leaf thickness (mm)
Electrical conductivity (ms/cm)
R
y=11.90-0.85 ln (x-0.07)
r2=0.20**
Pitch number of Phragmites australis
Electrical conductivity (ms/cm)
S
y=12.43-2.86 ln (x+4.62)
r2=0.26**
Internode height of P. australis
Electrical conductivity (ms/cm)
T
y=3.57-0.28 ln (x+0.002)
r2=0.09**
Shoot basal diameter (mm)
Electrical conductivity (ms/cm)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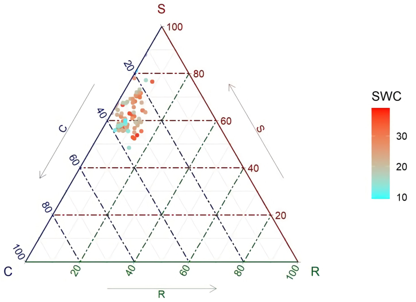
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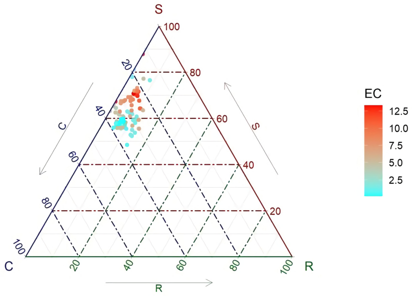
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