

Article

Inundation Depth Shape Phenotypic Variability of *Phragmites australis* in Liaohe Estuary Wetland, Northeast China

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Abstract: Inundation shifts plant growth, species diversity and ecosystem stability, but it remains unclear how inundation depth shapes the phenotypic variability of clonal plants in an estuary wetland. To reveal the response of clonal plant populations to inundation depth, we calculated the variation of *Phragmites australis* using shoot height, leaf length, leaf width, leaf biomass and panicle length in the Liaohe estuary wetland. Reproductive allocation was defined by the ratio of panicle length to shoot height. Linear regression showed that shoot height, leaf length, leaf width, leaf biomass and panicle length were negatively correlated with inundation depth, while the ratio of panicle length to shoot height was negatively correlated with inundation depth ($p < 0.0001$). Based on data regarding the statistical differences of plant phenotypic traits among *P. australis*, we recognized populations had generated variation differentiation. Compared with other functional traits, the coefficient of variation of leaf-related traits were at a high level. Therefore, leaf parameters would be the most suitable, and they increased the area and weight to support the action of plants during floods. Multivariate statistical analysis suggested that *P. australis* populations in the Liaohe estuary wetland were divided into two phenotypic clusters, consistent with geographical distance and morphological similarity. Our results provide a novel perspective on the ecological strategy of cloned plants under inundation change and offer theories for the conservation and restoration of estuarine wetland ecosystems.

Keywords: estuary wetland; *Phragmites australis*; inundation; phenotypic variability; reproductive allocation



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1. Introduction

Coastal wetland ecosystems are extremely vulnerable to global climate change, especially sea level rise [1,2]. Global sea level will continue to rise at a speed of 4–9 mm and 10–20 mm per year under the RCP2.6 and RCP8.5 scenarios [3], consequently, 20–78% of the world's wetlands will be submerged, including coastal wetlands [4,5]. Different inundation depths can affect plant growth, reproduction and biomass allocation by altering sediment and water quality, and they have an important impact on the species diversity and ecosystem stability [6–8]. Understanding vegetation response to inundation depth in an estuarine wetland is of great significance for predicting ecological restoration and sustainable development of estuarine wetlands in the future.

Inundation depth can directly affect the physiological process of plants and profoundly change the ecological strategy of individual plants. Plants can adjust their phenotypic and physiological characteristics to adapt to the environment through native adaptation and phenotypic plasticity according to environmental heterogeneity [9,10]. The former refers to the phenotypic differentiation that can be inherited from generation to generation under environmental pressure, and the latter involves phenotypic changes of different individuals of the same genotype under the influence of different habitats and environmental conditions [11,12]; this phenotypic differentiation is usually not passed on to the next

generation in a short time [13]. There have been numerous research methods to describe the ecological strategies of plants, such as stress tolerance [14,15], leaf economic spectrum (LES) [16] and reproductive strategies [17,18]. The most obvious behavior of reproductive strategies is plants give priority to reproductive growth when the environment becomes extreme [19]. LES suggested the plants could adopt acquisitive strategies that could allocate more resources to leaf economic traits under abundant resource availability, or they could resort to conservative strategies that could spread their growth efforts among small leaves to maximize adaptability under serious disturbance [20,21]. However, there are few reports on plant physiological strategies under the disturbance of inundation depth currently at a population level [22].

Phragmites australis (Cav.) Trin. ex Steud. is a significant ecological species widely distributed in wetlands, grasslands and other ecosystems [23]. From the perspective of evolution, *Phragmites australis* (a eurytopic species) has produced a variety of phenotypes to accept heterogeneous habitats [24]. Phenotypic variation among *Phragmites australis* populations will stimulate their multiple potentials in response to selection pressure in different environments [25]. *Phragmites australis* provides ideal experimental materials to study phenotypic variation under the condition of habitat heterogeneity [26]. As a pseudohalophyte, *P. australis* can grow in inland arid areas with saline-alkali soil [26,27] and in coastal wetlands where fresh water and salt water intersect [28,29]. Water level is an important factor in a coastal wetland ecosystem. For example, inundation experiments significantly reduced the aboveground biomass of *P. australis* in coastal wetland, while *Spartina alterniflora* still had high aboveground biomass even under the highest inundation depth [30]. Inundation depth determines the plant height and biomass and has a significant impact on the composition and metabolism of estuarine wetland vegetation [31,32]. Moreover, high inundation depth hinders the leaf growth, photosynthesis and total biomass of *P. australis* [33,34]. To survive under inundation, *P. australis* tends to allocate more nutrients to reproductive organs to ensure the population's survival [35,36]. However, little information is known about how inundation depth affects the interspecific variation of *P. australis* populations.

The Liaohe estuary wetland is one of the three estuaries in China, located on the alluvial plain of the Liaohe Delta near Bohai Sea. Therefore, *P. australis* and *Suaeda salsa* in the Liaohe estuary wetland have created considerable ecological services and values. About 74% of rainfall in the Liaohe estuary wetland is concentrated from June to September, and different inundation depths prevented vegetation respiration and photosynthetic physiology [30,37]. Previous studies have documented the response of *P. australis* to inundation depths in terms of morphological traits indicators [38,39]. However, this research reported few traits related to reproduction, such as the ratio of panicle length to shoot height, i.e., the reproductive distribution ratio.

The previous studies reported that *P. australis* represented apparent variation in morphology and growth, e.g., shoot height, shoot biomass and stem diameter [40,41]. However, possible inundation variation of morphological and functional traits, which is critical to resource allocation and climate change, has not been fully researched. Consequently, we investigated five different habitats of *P. australis* populations in the Liaohe estuary wetland and evaluated the relative contribution of environmental change in driving the traits variability among *P. australis* populations. Our results contribute to revealing the evolutionary mechanism of clonal plants under inundation and provide theories for conservation and instauration of estuarine wetland ecosystems. We hypothesized that (1) plants will allocate more growth resources to reproductive organs under flooding conditions, (2) the primary source of functional traits variation among *P. australis* populations will be vegetative growth organs, and (3) inundation at different depths will significantly change the functional traits of *P. australis* populations in the Liaohe estuary wetland.

2. Material and Methods

2.1. Study Area

The study area is located in Liaohekou Wetland National Nature Reserve (121°28′–121°59′ E, 40°45′–41°06′ N), Liaoning Province, northeast of China, with area of 8×10^4 hm² and altitude of 3.5 m (Figure 1). It is a typical salt marsh estuary wetland in the north temperate zone and is characterized by a warm temperate and monsoon climate. The annual average temperature is 9.3 °C, the annual average precipitation is 564.5 mm, and the annual average evaporation is about 1439 mm. According to statistical data of Liujianfang hydrological station of Liaohe river, the average annual runoff is 4.691 billion cubic meters, and the average sediment concentration is 3.4 kg per cubic meter. The vegetation is dominated by halophytes and hygrophytes with tolerance to inundation, cold and salt, including *Phragmites australis*, *Lagedium sibiricum*, *Cirsium setosum*, *Suaeda salsa*, *Scirpus planiculmis*, *Typha angustifolia* etc.

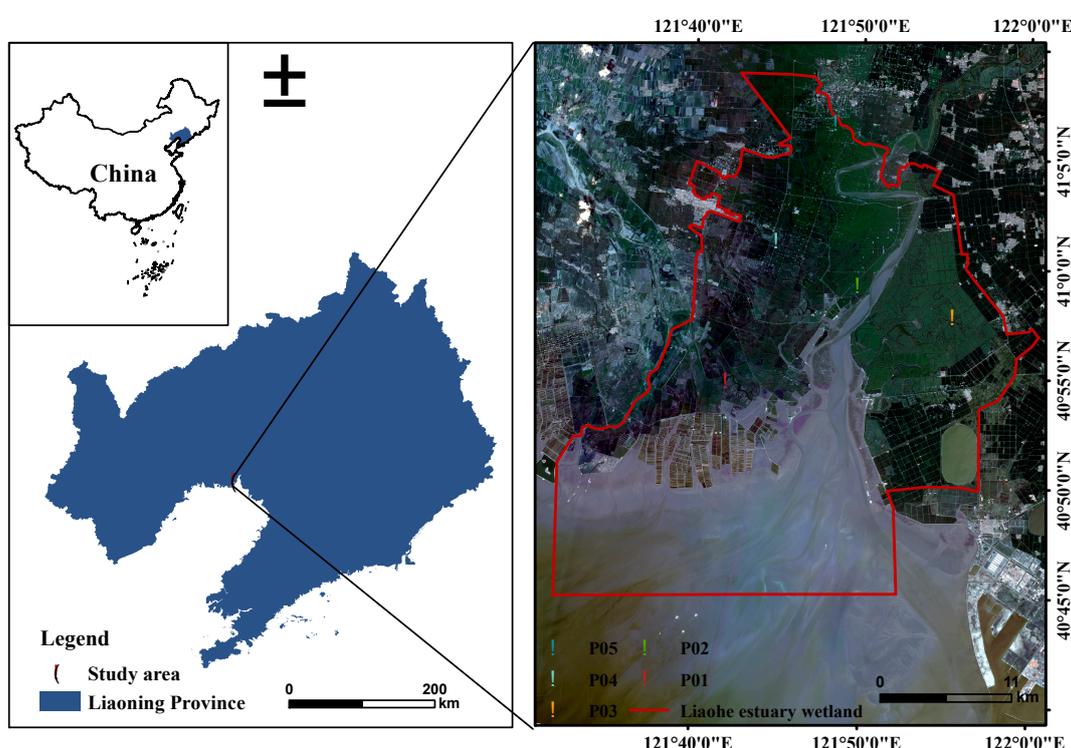


Figure 1. Study area and sampling site distribution.

2.2. Collection and Measurement of Samples

Five different habitat populations were collected during the end of August 2021 in Liaohe estuary wetland. We investigated 20 undamaged and matured plants of each *P. australis* population and recorded the habitat information and coexistence of plant species. The distance between five *P. australis* populations was more than 10 km, and between sampled plants, it was at least 10 m. We recorded the corresponding geographical coordinates of each sampled plant with a GPS and measured the inundation depths of each sampled plant under range of 40 cm using DF-YWY portable levellogger (Oriental Xinhong Technology Co., Ltd., Beijing, China). Inundation depth greater than or equal to 80 cm was testified to reduce the aboveground biomass of *P. australis* plants [30].

Plant organs (stems, leaves and flowers) are particularly sensitive to environmental changes, and these traits are critical to plant growth, development and reproduction [42]. Shoot height and biomass traits determine the mechanical support and resource acquisition of plants; leaf traits reflect plant ecological strategies to obtain effective light and water; flowering phenology affects plant reproduction [27]. As a consequence, we measured 5 phenotypic traits: shoot height (SH), leaf length (LL), leaf width (LW), leaf biomass (LB)

and panicle length (PL). We cut the reed plants close to the ground, then placed them on horizontal ground, measured SH from shoot base to panicle top and measured PL from panicle stem node to panicle top with a tape. Finally, we collected the largest leaf of each plant, marked number and transported them to the laboratory. We fixed the leaf on the table with tape, measured LL from the end to the tip of leaf with a ruler and recorded the widest part of leaf as LW. Subsequently, we put the largest leaf of each plant into an oven (105 °C, 24 h), and recorded its dry weight as leaf biomass with precise analytical balance. We used the ratio of panicle length to shoot height to present the resource trade-off strategy in annuals. Leaves of each plant were pressed and placed in paper envelopes and deposited in the laboratory.

2.3. Data Processing and Statistics

Based on Shapiro-Wilk test of normality and Levene statistic of homogeneity of variance in SPSS 22.0 (IBM, New York, NY, USA), diversity of population traits was examined using One-way ANOVA. Traits mean and Tukey test were carried out multiple comparisons to test the significant differences among populations. The coefficient of variation (CV) was calculated to describe the dispersion between population functional traits under various inundation depths. Boxplots were processed by OriginPro2020b.

Spearman correlation coefficient verified the relationship between shoot height, leaf length, leaf width, leaf biomass and panicle length to avoid redundant correlation. Principal component analysis (PCA) calculated the contribution rates of all individuals and phenotypic traits. Scatter plot with PC1 as the X axis and PC2 as the Y axis showed all individuals and trait characteristics. To clearly present the differentiation differences among populations, five phenotypic traits were classified by cluster analysis with unweighted pair-group method with arithmetic mean (UPGMA). Similarity among *P. australis* populations is defined by Euclidean distance method. The distance between samples *a* ($x_{i1}, x_{i2}, \dots, x_{i5}$) and *b* ($x_{j1}, x_{j2}, \dots, x_{j5}$) is recorded formula as follows:

$$d_{ij} = \sqrt{\sum_{k=1}^n (x_{ik} - x_{jk})^2}$$

where *k* is count number, and *n* is a vector dimension. Trait means were brought into formula to calculate the distance between populations, combining the nearest populations into an OUT (Operational Taxonomic Unit) and finally generating a dendrogram. Principal component and hierarchical clustering were analyzed by Origin (OriginLab Corporation, Northampton, MA, USA).

Based on independence test, normality test and variance homogeneity test, we carried out a general linear regression with Origin to analyze the relationships between *P. australis* population traits and inundation depths and calculated the slope, R^2 , and *P* of each model.

3. Results

3.1. Comparison of *P. australis* Functional Traits

The inundation depth of *P. australis* population P05 (the inland river in Dongguo Town) in the artificial irrigation zone is 36.18 ± 7.79 cm. The reed population (P04) is an oil field that was abandoned several years ago due to the cessation of production with at least five plant species. Sites P02, P03 and P04 had slightly higher inundation depth (Table 1). The lowest inundation depth of P01 in an intertidal zone with *Suaeda salsa* invasion is 11.44 ± 3.87 cm (Table 1). However, all sites had significant differences in flooding depth (Table 1, $p < 0.001$).

Table 1. The habitat information of *Phragmites australis* populations in Liaohe estuary wetland.

Sites	Habitat	Depth (cm)	Coexistence of Plant Species
P01	The intertidal zone with <i>Suaeda salsa</i> invasion	11.44 ± 3.87 ^d	<i>Suaeda salsa</i> , <i>Scirpus planiculmis</i>
P02	The intertidal zone near the Liaohe River	22.90 ± 9.16 ^c	<i>Suaeda salsa</i> , <i>Scirpus planiculmis</i> , <i>Cirsium setosum</i> , <i>Suaeda glauca</i>
P03	The supralittoral zone closed to paddy field	30.56 ± 8.55 ^{ab}	<i>Suaeda salsa</i> , <i>Scirpus planiculmis</i> , <i>Cirsium setosum</i> , <i>Suaeda glauca</i> , <i>Lagedium sibiricum</i> , <i>Glycine soja</i>
P04	Abandoned oil field after stoppage	25.40 ± 8.38 ^{bc}	<i>Cirsium setosum</i> , <i>Suaeda glauca</i> , <i>Lagedium sibiricum</i> , <i>Glycine soja</i> , <i>Kochia scoparia</i> , <i>Kochia scoparia</i> , <i>Chenopodium Acuminatum</i> ,
P05	The inland river zone in Dongguo Town	36.18 ± 7.79 ^a	<i>Cynanchum chinense</i> , <i>Imperata cylindrica</i> , <i>Polygonum sibiricum</i> , <i>Artemisia Annuua</i> , <i>Calamagrostis epigeios</i>

Different letters (^{a-d}) indicated significant differences among the flooding depth ($p < 0.001$).

The variation analysis of phenotypic traits among *P. australis* populations presented that shoot height, leaf length, leaf width, leaf biomass and panicle length had significant differences (Figure 2). The shoot height (315.66 ± 39.69 cm), leaf length (63.81 ± 10.89 cm), leaf biomass (0.96 ± 0.10 g) and panicle length (27.92 ± 2.93 cm) were largest in the deepest inundation depth (P05) but lowest (0.45 ± 0.05 cm, 111.19 ± 29.90 cm, 0.45 ± 0.05 g, 16.62 ± 1.81 cm) in the shallowest inundation depth (P01) (Figure 2, Table 2). The ratio of panicle length to plant height ranged from 0.16 ± 0.04 (P01, shallowest inundation) to 0.09 ± 0.01 (P05, deepest inundation) (Figure 2, Table 2).

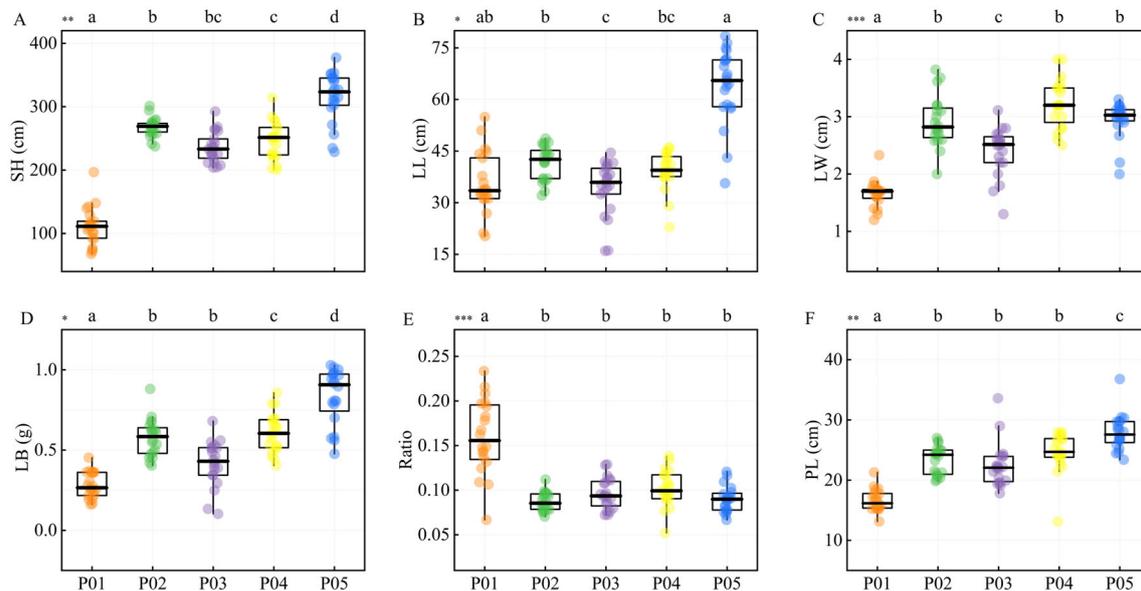


Figure 2. Plant functional traits (A), shoot height; (B), leaf length; (C), leaf width; (D), leaf biomass; (E), the ratio of panicle length to shoot height; (F), panicle length) of different *Phragmites australis* populations. Different letters represent significant differences. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 2. Variance analysis of functional traits among the *Phragmites australis* populations (M \pm SD).

Traits	P01	P02	P03	P04	P05	F
Shoot height (cm)	111.19 \pm 29.90	267.91 \pm 14.81	235.65 \pm 24.01	245.93 \pm 29.76	315.66 \pm 39.69	145.66 ***
Leaf length (cm)	35.79 \pm 8.78	41.66 \pm 4.99	34.23 \pm 7.95	39.43 \pm 5.61	63.81 \pm 10.89	47.93 ***
Leaf width (cm)	1.65 \pm 0.23	2.91 \pm 0.44	2.39 \pm 0.43	3.22 \pm 0.42	2.95 \pm 0.32	52.98 ***
Leaf biomass (g)	0.45 \pm 0.05	0.66 \pm 0.10	0.69 \pm 0.13	0.86 \pm 0.05	0.96 \pm 0.10	91.72 ***
Ratio	0.16 \pm 0.04	0.09 \pm 0.01	0.10 \pm 0.02	0.10 \pm 0.02	0.09 \pm 0.01	32.29 ***
Panicle length (cm)	16.62 \pm 1.81	23.30 \pm 2.34	22.45 \pm 3.62	24.62 \pm 3.33	27.92 \pm 2.93	40.84 ***

M—arithmetic mean; SD—standard deviation. *** $p < 0.001$.

3.2. Variation Analysis of Functional Traits

The coefficient of variation described the dispersion of traits. The larger the coefficient of variation, the higher the dispersion of traits, i.e., the greater the phenotypic variation. The coefficient of variation analysis of phenotypic traits presented that the mean coefficient of variation is 0.19 among reed natural populations, with a range of 0.12–0.34. The coefficient of variation of shoot height and leaf length was the highest (Table 3, $CV_{SH} = 0.27$, $CV_{LL} = 0.25$ in P01 population) but lowest (Table 3, $CV_{SH} = 0.05$, $CV_{LL} = 0.12$ in P02 population). The variation coefficient of leaf width and panicle length of population P03 was highest (Table 3, $CV_{LW} = 0.18$, $CV_{PL} = 0.16$ in P03 population) but lowest (Table 3, $CV_{LW} = 0.10$, $CV_{PL} = 0.10$ in P05 population).

Table 3. Variation coefficient of functional traits among the *Phragmites australis* populations.

Site	CV_{SH}	CV_{LL}	CV_{LW}	CV_{LB}	CV_R	CV_{PL}	Mean
P01	0.27	0.25	0.14	0.11	0.25	0.11	0.19
P02	0.05	0.12	0.15	0.15	0.11	0.10	0.11
P03	0.10	0.23	0.18	0.19	0.20	0.16	0.18
P04	0.12	0.14	0.13	0.06	0.20	0.14	0.13
P05	0.13	0.17	0.11	0.10	0.11	0.10	0.12
Mean	0.13	0.18	0.14	0.34	0.22	0.12	0.19

CV_{SH} —the coefficient of variation of shoot height, CV_{LL} —the coefficient of variation of leaf length, CV_{LW} —the coefficient of variation of leaf width, CV_{LB} —the coefficient of variation of leaf biomass, CV_R —the coefficient of variation of the ratio of panicle length to shoot height, CV_{PL} —the coefficient of variation of panicle length.

3.3. Correlation between Traits and Inundation Depth

The general linear regression of all sites presented that inundation depth was positively correlated with shoot height, leaf length, leaf width, leaf biomass and panicle length but negatively correlated with the ratio of panicle length to shoot height (Figure 3).

According to the Spearman correlation analysis among traits (Figure 4B), shoot height was positively correlated with leaf length ($r = 0.65$, $p < 0.001$), leaf width ($r = 0.58$, $p < 0.001$), leaf biomass ($r = 0.63$, $p < 0.001$) and panicle length ($r = 0.64$, $p < 0.001$). Panicle length was positively correlated with leaf length ($r = 0.67$, $p < 0.001$), leaf width ($r = 0.53$, $p < 0.001$) and leaf biomass ($r = 0.71$, $p < 0.001$). The ratio of panicle length to shoot height was negatively correlated with shoot height, leaf length, leaf width and leaf biomass ($p < 0.001$).

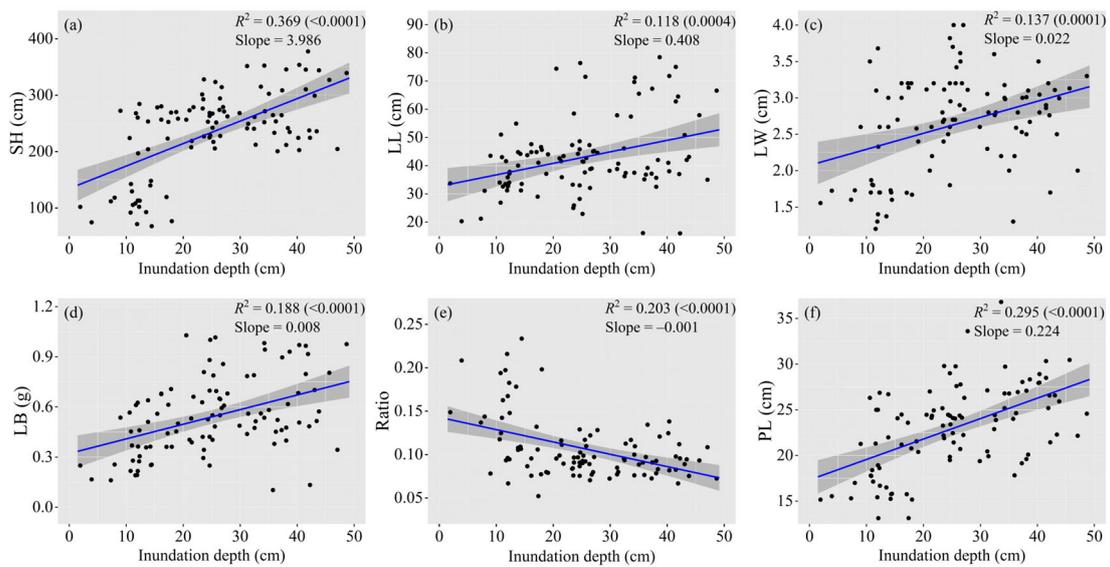


Figure 3. Correlation relationships between functional traits (a), shoot height; (b), leaf length; (c), leaf width; (d), leaf biomass; (e), the ratio of panicle length to shoot height; (f), panicle length and inundation depth among the *Phragmites australis* populations based on general linear models.

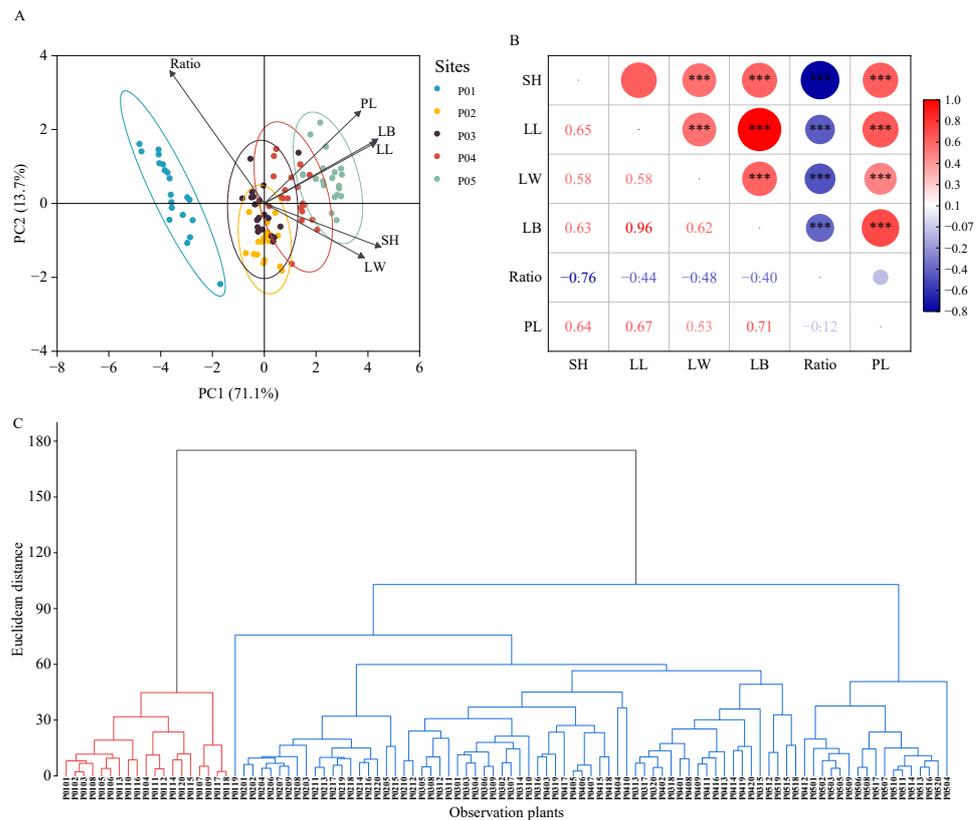


Figure 4. Variation structure of *Phragmites australis* populations based on the functional traits. (A) Principal component analysis. (B) Spearman correlation analysis. (C) Cluster analysis. Plant functional traits: SH—shoot height; LL—leaf length; LW—leaf width; LB—leaf biomass; Ratio—the ratio of panicle length to shoot height; PL—panicle length. *** $p < 0.001$.

3.4. Variation Structure among *P. australis* Populations

Principal component analysis presented that the contribution rate of the X axis was 71.1%, and shoot height, leaf length, leaf width and leaf biomass had major constituents,

which represented the vegetative growth of *P. australis*; the contribution rate of the Y axis was 13.7%, and the panicle length had the main proportion, which embodied the reproductive growth of *P. australis* (Figure 4A). Inundation depth had a great influence on phenotypic traits, and vegetative traits (PC1) were more affected than reproductive traits (PC2) (Figure 4A). Inundation depth had different impacts among five populations. The vegetative traits of the P04 and P05 populations and the reproductive traits of the P01 population were most affected by inundation depth (Figure 4A).

European distance ranged from 11.750 (P03 and P04) to 206.700 (P01 and P05) (Table 4). PCA presented two clusters separated by the first principal component (Figure 4A). Euclidean distance UPGMA cluster also supported the two genetic clusters (Figure 4D). *P. australis* populations in the Liaohe estuary wetland were clustered into a branch from P02 to P05. Among this branch, P05 was significantly different from other populations in morphology, which might be related to its superior water and soil conditions. The phenotypic traits of P01 in the other branch were the most unique, but it could not be regarded as a normal population due to its low flooding and high salt stress.

Table 4. Euclidean distance of functional traits among the *Phragmites australis* populations.

	P01	P02	P03	P04	P05
P01	0				
P02	156.986	0			
P03	124.618	33.120	0		
P04	135.039	22.140	11.750	0	
P05	206.700	52.838	85.478	73.946	0

4. Discussion

Flooding experiments in five riparian areas from Denmark, Germany and Holland presented that winter flooding changed the composition of plant communities and reduced plant species diversity [43]. Plants can adjust specific phenotypic traits to improve ecological adaptability under heterogeneous environments [44]. To avoid the adverse effects of flooding stress, plants have evolved two ecological strategies to deal with it. One is the acquisitive strategy, in which to obtain sunshine, plants extend the buds and leaves for photosynthesis to maintain self-growth; the other is the static strategy, in which a plant slows down growth and retains development with internal energy and nutrition [45,46]. For instance, *Rorippa amphibia* adopted the former strategy with a shallow flooded habitat, while *Rorippa sylvestris* selected the latter strategy, as it occupied deeper and temporarily flooded surroundings [47]. In the coastal wetlands of the USA, Morris reported that *Spartina alterniflora* had a significant parabolic relationship with flooding depth, clearly indicating the optimal growth range [48]. However, in this study, regarded as a flooding-tolerant plant species, *P. australis* grew into the dominant plant in the 0–40 cm inundation depth. It prolonged its shoot height to escape flooding stress and restored the contact area between leaves and the atmosphere for photosynthesis [45]. Compared with the results of the Danube River Delta in Romania, seawater intrusion severely inhibited the density, plant height and biomass of *P. australis* [49], while flooding depth significantly increased shoot height and aboveground biomass of *P. australis* in this study, indicating that *P. australis* chose the acquisitive strategy.

By observing data statistical differences of plant phenotypic traits such as shoot height, leaf length, leaf width and leaf biomass of *P. australis* populations, we recognized phenotypic traits of *P. australis* had generated variation differentiation. Consistent with the previous research results, flooding depth significantly increased reed density and leaf area index above water surface [50], which resulted from the fact that more energy and carbohydrates produced by photosynthesis were provided for plant growth to endure lasting flooding. The variation coefficient of leaf traits among reed populations in the Liaohe estuary wetland was between 13.06% and 25.19%. Considered as one of the momentous plant economic traits, leaves play crucial parts in plant-atmosphere interaction [51],

such as gas exchange, available photosynthetic area and thermoregulation [52–54]. Accordingly, masses of vegetation generated multifarious leaf morphology to survive under various water transpiration rates or stress conditions [55]. Leaf area, petiole length and leaf biomass determined light capture [56] and resulted in high variability [57]. The above viewpoint was also verified by previous research on the leaf trait diversity of other wetland plants, namely *Carex lasiocarpa* [58], *Polygonum hydropiper* [50], *Scirpus planiculmis* [59] and *Bolboschoenus planiculmis* [60]. Generally speaking, reed populations with broad leaves live in wet habitats, while those with narrow leaves live in drought environments.

Besides tolerance and leaf economic spectrum, reproductive allocation plays a large part in resource acquisition and population competition. As an adjustment and a response to the ecological environment, multiple reproductive allocation determines a plant's ability to obtain resources [61,62]. Perennial plants ordinarily give priority to sexual reproduction in variable and stressful circumstances [63]. Similar to the results in the northern Mediterranean, long-term and extreme flooding reduced the seed production of *P. australis* [64], reflecting the significant negative correlation between inundation depth and reproductive allocation (Figure 3e). The pattern is advantageous to botanic growth and reproduction due to the reduced air exposure area, oxygen acquisition rate and respiratory consumption [45,46]. In regions with advantageous conditions, *P. australis* rapidly acquires resources and disposes more nutrients for shoot height, aboveground biomass and stem diameter; in regions with disadvantageous conditions, *P. australis* assigns more resources for the formation of panicles instead of stems and leaves [65].

In summary, our results suggested that *P. australis* populations in the Liaohe estuary wetland were divided into two phenotypic clusters, consistent with wild geographical distance and morphological similarity to some extent. An adequate water supply can promote photosynthesis of leaves and nutrient absorption of roots and accelerate plant growth, energy metabolism and nutrient storage [66,67]. Consequently, water level determines the spatial distribution pattern of reed populations in coastal salt marsh wetlands. Based on the response of salt marsh plants to inundation stress, *Phragmites australis*, *Tamarix chinensis* and *Suaeda salsa* had a zonal distribution pattern along groundwater levels and salinity gradients in the Yellow River estuary [68]. Despite the influence of inundation depth, the shoot height and leaf size of the *P. australis* population in the intertidal zone with a *Suaeda salsa* invasion were unexpectedly small. A salinity gradient control experiment could explain this phenomenon, as high salinity reduced the density, shoot height and biomass of *P. australis* populations in the east coast of North America [69]. When observing the phenotypic diversity of population, however, the impact of soil pH and salinity cannot be excluded. For instance, species diffusion patterns presented that low salt and medium salt similarly inhibited growth of reed in the Chesapeake Bay of the United States [70] and Chicago [71], and plants growing in saline soil tend to accumulate salt ions (Na^+ and Cl^-) excessively [72]. Salt will destroy the original osmotic balance of cells, hinder their normal physiological and ecological functions and restrict the growth and reproduction of plants [73].

Interpopulation variability consists of the adaptation process of individuals under heterogeneous environmental pressures [53,74], indicating a close relationship between the phenotypic plasticity of populations and individuals [54,75]. Plant populations with adaptive plasticity generate appropriate functional phenotypes through modification mechanisms and gene expressions to make greater responses to climate change [54,76], as shown in this study, in which the leaf area of *P. australis* populations increased obviously in a moderately flooded habitat. After living in a certain environment for a long time, a species will produce specific phenotypic traits, but its offspring's genetic genes or just some individuals' epigenetic adaptation may have changed, not the population plasticity [77]. Plants allow genotypes to cope with habitat heterogeneity; in this study, although the shoot height and leaves of *P. australis* in an estuary and inland were dominated by heredity, they still adopted a different growth strategy when the environment changed. With extensive ecological scope, *P. australis* populations have low requirements for soil conditions and are

resistant to salt, drought and flood [78]. Considering plasticity and adaptability to local conditions, we predict that *P. australis* species have diversified phenotypic variation under diverse conditions. As a consequence, it can be reasonably assumed that taxonomic groups of *P. australis* populations in this study are actually only a part of intraspecific variability restricted by the local habitat and climatic conditions.

5. Conclusions

In this study, functional traits among *P. australis* populations presented broad variability under inundation stress. Inundation increased the vegetative growth (shoots and leaves) of plants, but plants allocated more resources from shoot height to panicle length with the increase of inundation depth. Meanwhile, compared with other functional traits, leaf parameters (leaf length, leaf width and leaf biomass) well explained the source of variation among *P. australis* populations, as they increased in area and weight as a response to inundation stress. In addition, inundation had statistically significant correlations with phenotypic traits, indicating that geographical distance existed among *P. australis* populations; consequently, phenotypic traits determined two clustering groups of *P. australis* populations in multivariate statistical analysis. Overall, we recognized functional trait variability observed in this study can be attributed to the phenotypic plasticity of the reed population and its individual local adaptability. The study of plant phenotypic variation contributes to the sustainable development, vegetation restoration and ecosystem reconstruction of estuarine wetlands and saline alkali areas with the global sea level rise and ecosystem degradation.

However, this experiment evaluated the adaptability of *P. australis* to an inundation environment with a coefficient of variation, rather than from the perspective of cell structure, to explain the impact of flooding on *P. australis*. Therefore, carrying out research on the *P. australis* genotype would provide us with an accurate understanding of the relationship between plants and the environment.

Author Contributions: F.Z. collected experimental data. P.C. analyzed and wrote the manuscript. F.S. participated in conceptualization, data analysis, and manuscript preparation and review. All authors have read and agreed to the published version of the manuscript.

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