





## Article

# Effects of Phenotypic Plasticity and Genetic Variation on Plant Growth and Litter Decomposition in a Widespread Wetland Grass

Wei Wei <sup>1,†</sup>, Qishen Wen <sup>1,†</sup>, Hong Zhu <sup>1</sup>, Huijia Song <sup>2,\*</sup>, Xiya Zhang <sup>1</sup>, Wenyi Sheng <sup>1</sup>, Liujuan Xie <sup>3</sup>, Xiao Guo <sup>4</sup> , Yaolin Guo <sup>5</sup> , Siyuan Ye <sup>3</sup>, Yuzhi Wang <sup>1</sup>, Lele Liu <sup>1</sup>  and Weihua Guo <sup>1,\*</sup> 

<sup>1</sup> Qingdao Key Laboratory of Ecological Protection and Restoration, Ministry of Natural Resources Key Laboratory of Ecological Prewarning, Protection and Restoration of Bohai Sea, School of Life Sciences, Shandong University, 72 Binhai Road, Qingdao 266237, China; weiv@mail.sdu.edu.cn (W.W.); wqshakurei@gmail.com (Q.W.); 202332502@mail.sdu.edu.cn (H.Z.); 17853728970@163.com (X.Z.); shwy@sdu.edu.cn (W.S.); wangyuzhi@sdu.edu.cn (Y.W.); liulele@sdu.edu.cn (L.L.)

<sup>2</sup> Natural History Museum of China, 126 Tianqiao South Street, Beijing 100050, China

<sup>3</sup> Key Laboratory of Coastal Wetland Biogeosciences, Qingdao Institute of Marine Geology, China Geological Survey, Qingdao 266000, China; xielujuan1102@163.com (L.X.); siyuanye@hotmail.com (S.Y.)

<sup>4</sup> College of Landscape Architecture and Forestry, Qingdao Agricultural University, 700 Changcheng Road, Qingdao 266109, China; guoxiao018@163.com

<sup>5</sup> School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, USA; yaolinguo22@gmail.com

\* Correspondence: songhuijia@nnhm.org.cn (H.S.); guowh@email.sdu.edu.cn (W.G.)

† These authors contributed equally to this work.

**Abstract:** Wetlands are crucial ecosystems that provide a wide range of ecological services, such as water purification, flood control, and carbon sequestration, where the diversity of wetland plants is fundamental to maintaining these functions. *Phragmites australis* is a globally widespread wetland grass with a high genetic diversity, exhibiting strong intraspecific variation across environmental gradients. While both phenotypic plasticity and genetic variation are recognized drivers of plant adaptation, their relative importance in mediating the growth and decomposition traits of wetland plants remains debated. Here, we surveyed the growth and litter traits of two lineages (haplotypes) of *P. australis* in two common gardens in eastern China. The leaf litter of *P. australis* was also collected from the field in two provinces where the two common gardens are located. Microcosm experiments were carried out to explore the litter decomposition ability. We found that the common garden (growth environment) significantly affected the growth performance (shoot diameter and height), leaf litter stoichiometric traits (contents of N and P), and the leaf decomposition over 180 days. The N content in the leaf litter from the higher-latitude province of Liaoning was greater than that from the lower-latitude province of Shandong, regardless of whether it was collected from the field or the common garden. The litter N and P contents were the key factors affecting the decomposition during the 180-day experiment. However, we did not find the effects of lineage (genetic variation) on the variation of these traits. The climatic factors of the genotype origin were significantly correlated with the growth traits but not the litter traits or decomposition rates. The findings indicate that *P. australis* in eastern temperate China primarily adapts through phenotypic plasticity rather than genetic variation, which is crucial for wetland resilience in a changing climate. This study underscores the pivotal role of environmental factors and phenotypic plasticity in *P. australis* growth and decomposition, suggesting that conservation efforts should prioritize the local environment over genetic variation for effective wetland management.



Academic Editor: Hana Čížková

Received: 11 March 2025

Revised: 10 April 2025

Accepted: 15 April 2025

Published: 17 April 2025

**Citation:** Wei, W.; Wen, Q.; Zhu, H.; Song, H.; Zhang, X.; Sheng, W.; Xie, L.; Guo, X.; Guo, Y.; Ye, S.; et al. Effects of Phenotypic Plasticity and Genetic Variation on Plant Growth and Litter Decomposition in a Widespread Wetland Grass. *Diversity* **2025**, *17*, 282. <https://doi.org/10.3390/d17040282>

**Copyright:** © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

**Keywords:** *Phragmites australis*; functional traits; litter decomposition; stoichiometric characteristics; intraspecific variation; adaptive strategies

## 1. Introduction

Wetlands provide numerous ecosystem services, ranging from nutrient retention and floodwater storage to climate regulation and biodiversity conservation [1]. Wetlands play a very essential role in biogeochemical cycling. Their high productivity, combined with hypoxic and moist environments, enables wetlands to accumulate large amounts of soil organic carbon [2,3]. The carbon sink capacity of wetlands is variable and sensitive, depending on their age, type, and environmental conditions such as climate and location [4,5]. Wetlands in high-latitude regions typically have strong carbon storage capacity due to their low-temperature environments. However, rising temperatures and altered precipitation patterns caused by climate change may weaken their carbon sink functions. In contrast, wetlands in low-latitude regions are more likely to be carbon sources due to the high temperatures and complex precipitation patterns. Climate change further exacerbates their potential for carbon emissions, reducing their carbon sequestration capacity [4]. Plants are the fundamental components of wetlands, especially large wetland plants. They are not only the primary producers in the wetland ecosystem but also the key contributors of these essential functions [6–8]. Many of these dominant plants are widely distributed. Simultaneously, many wetland plants establish mono-dominant communities, significantly influencing the community structure and ecosystem function.

The common reed, *Phragmites australis* (Cav.) Trin. Ex Steud., is a critical species in wetland ecosystems, often forming extensive mono-dominant stands that dominate large areas [9,10]. The pronounced phenotypic plasticity and genetic variability exhibited by *P. australis* endow it with the capacity to adapt to both short-term and long-term environmental changes, thus rendering it a suitable model species for investigating the mechanisms underlying the plant responses to environmental gradients [9,11]. These traits not only enable it to thrive in diverse conditions but also contribute to its significant role in the wetland carbon cycle. *Phragmites australis* exhibits strong carbon sequestration abilities [7] and actively participates in the carbon cycle of wetlands [12]. The intraspecific variation within *P. australis* significantly influences its ecological strategies and resilience levels, thereby affecting wetlands' overall functions [13,14]. There are significant differences in the carbon sequestration capacity of wetlands dominated by *P. australis* across different environments [15]. Latitude can alter the functional traits of *P. australis* [13,16] and the rate of litter decomposition [17], thereby affecting its carbon sequestration capacity.

Intraspecific variation arises from two primary sources: genetic adaptation and phenotypic plasticity [13]. Genetic adaptation might result in long-term differentiation among populations, while plasticity enables rapid trait adjustment within a population under varying conditions. Genetic adaptation involves the rapid selection of adaptive genotypes, often driven by high levels of genetic diversity [18–20]. Meanwhile, phenotypic plasticity, which refers to the ability of a single genome to produce multiple phenotypes, enables plants to maintain fitness components without solely relying on evolutionary adaptation in certain scenarios [21,22]. This capacity for phenotypic variation is particularly relevant when examining the intraspecific diversity of plants such as *P. australis*. In temperate China, *P. australis* comprises two relatively independent lineages, haplotype O and haplotype P, which differ in ploidy levels and morphological traits [23]. These genetic differences influence their growth rates and litter quality, which in turn affect their decomposition rates and carbon cycling. This unique system provides an ideal framework for investigating

the roles of genetic and environmental factors in intraspecific variation, as well as their influence on plant growth and function [13].

Plant growth is influenced by varying environmental conditions, and plants ensure their survival and reproduction success by adapting their leaf traits, growth rates, and biomass allocation in response to environmental changes [24]. Some variation is driven by genetic adaptation, with intraspecific differences often correlating with latitude-related factors such as temperature and water availability [12,18]. Additionally, phenotypic plasticity, particularly in leaf traits and growth rates, plays a significant role in plant growth [11,22]. These mechanisms not only provide a buffer against rapid environmental changes but also facilitate rapid adaptation, thereby promoting the development of ecological strategies [25]. Populations have evolved various strategies to cope with environmental factors, such as the leaf economic spectrum and CSR strategies [26,27]. The potential for evolutionary responses is likely to play a critical role in shaping population dynamics and adaptive strategies. As a dominant primary producer, the growth of *P. australis* is essential for carbon deposition and the overall health of wetland ecosystems.

Litter decomposition provides the energy for microbial growth, and alters the microbial activity, microbial abundances, and carbon cycling [28]. The carbon pool in wetlands comprises two main components: the vegetation biomass carbon pool and the sediment organic carbon pool. The plant litter input is an important driver of soil and/or sediment organic carbon turnover [29]. Studies have shown that higher species and genetic diversity can negatively impact plant litter decomposition [30]. Changes in plant diversity, including genetic diversity, can alter the litter decomposition rates and, consequently, affect the carbon sink of wetland ecosystems [31,32]. Previous studies have shown that *P. australis* influences decomposition rates compared to other wetland species. For example, its decomposition rate is faster than that of *Triarrhena lutarioriparia* but slower than that of *Carex cinerascens* [33]. Additionally, the decomposition rate of *P. australis* is positively correlated with the initial nitrogen content and negatively correlated with the C/N ratio [34]. These findings highlight the importance of *P. australis* in nutrient cycling within wetland ecosystems. However, there is a lack of integrated studies on both plant growth and decomposition under common garden conditions across different lineages. Our study aims to fill this gap by examining these processes in two distinct lineages of *Phragmites australis* under controlled conditions [35,36].

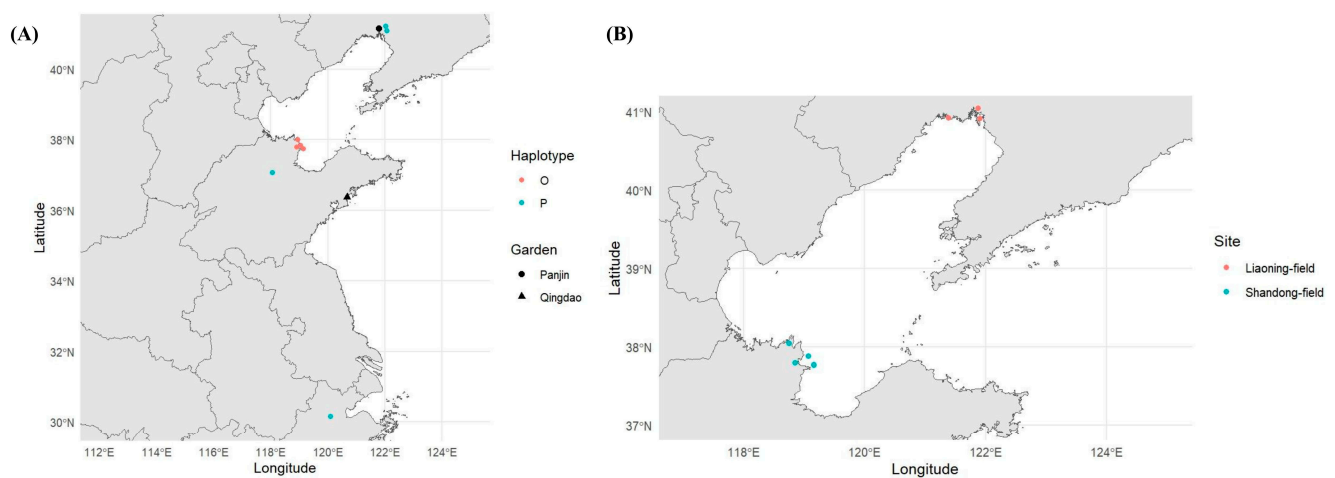
In the present study, we therefore sampled *P. australis* from the Liaohe Wetland and the Yellow River Delta, and planted in common gardens located in Panjin and Qingdao. We hypothesized that different lineages of *P. australis* would exhibit significant variations in litter decomposition and plant growth, driven by both phenotypic plasticity and genetic adaptation. Our study aims to test these hypotheses by comparing these traits across lineages under the common garden conditions. We anticipate that our findings will elucidate the mechanisms underlying the observed variations, thereby enhancing our understanding of the carbon and nutrient cycling in wetland ecosystems. Specifically, by identifying the relative contributions of phenotypic plasticity and genetic adaptation, our results will provide actionable insights for the effective management of wetland resources. Additionally, the knowledge gained will support evidence-based conservation strategies and contribute to the sustainable development of wetland ecosystems.

## 2. Materials and Methods

### 2.1. Common Garden Experiment

Common gardens were established at Shandong University in Qingdao (36.36° N, 120.69° E) and at the Wetland Scientific Research Institute in Panjin (41.22° N, 121.3° E) (Figure 1A) [11]. The common garden in Qingdao has an average annual precipitation of

662.1 mm and an average annual temperature of 12.7 °C, while the common garden in Panjin has an average annual precipitation of 650 mm and an average annual temperature of 10.5 °C. To capture a representative genetic variation found in temperate China wetlands, we selected nine genotypes of *P. australis*, encompassing tetraploid haplotype O (YRD3, YRD4, YRD5, YRD9) and octoploid haplotype P (CN2014, CN2019, CN2021, CN2024, CN2026). In February 2023, the rhizomes from these nine genotypes were transplanted into pots in two common gardens. Each pot (0.4 m in diameter and 0.5 m in height) was filled with a substrate composed of 50% peat soil and 50% quartz sand (particle size: 0~2 mm). Pots were spatially arranged with 1 m intervals and buried to ensure uniformity in the soil surface levels. Manual weeding and pest control were carried out, and the plants were irrigated with municipal water to maintain the optimal moisture. Drainage holes in each pot facilitated the removal of excess water.



**Figure 1.** Location of *Phragmites australis* sampling sites. Black dot represents Panjin common garden in Liaoning, and black triangle dot represents Qingdao common garden in Shandong. Colored dots indicate sampling points, with red dots representing haplotype O and green dots representing haplotype P (A). Red dots indicate the location of field sites in Liaoning, and the green dots indicate the location of field sites in Shandong (B).

In October 2023, the functional traits of *P. australis* within the common gardens were determined. To focus on the most competitive individuals, we selected the five tallest plants from each pot. We measured the plant height from the soil surface to the apex using a tape measure and assessed the base diameter with a vernier caliper. The total number of individual plants and inflorescences were counted, and the aboveground biomass was harvested by cutting the stems at the soil level.

## 2.2. Litter Collection

To explore the variations in the stoichiometric characteristics of *P. australis* litter, litter samples in both common gardens and the field were collected. Leaf litter was collected in the Panjin common garden on 14 October 2023 and the Qingdao common garden on 20 November 2023. To focus on the typical litterfall dynamics of *Phragmites australis*, we collected only the leaf blades that had fallen but were still attached to the plant, excluding leaf sheaths and other parts. Wilted litter leaves were collected in kraft paper bags, ensuring that they did not make contact with the ground. Stem litter was collected at the Panjin common garden on 14 October and the Qingdao common garden on 20 November 2023. The five tallest dry plants were selected from each common garden and cut off from the base, with any attached leaves removed.

We also conducted litter collection in the field: the Yellow River Delta Wetland in Dongying City, Shandong Province (118.7~119.2° E, 37.7~38.1° N) and the Liaohe Delta Wetland in Panjin City, Liaoning Province (121.3~121.9° E, 40.9~41.2° N) (Figure 1B). These areas are characterized by a temperate monsoon climate that features distinct seasonal variability and considerable precipitation, providing diverse wetland ecosystems conducive to the growth of *P. australis* [14]. The Yellow River Delta Wetland is known for its complex interactions between natural conditions (e.g., vegetation, soil properties, and hydrology) and anthropogenic activities (e.g., agriculture, road construction, and oil exploration). In contrast, the Liaohe Delta Wetland is characterized by its unique ecological features, such as different soil nutrient compositions and vegetation types. These two wetlands were selected to provide a comparative study of *P. australis* under contrasting environmental pressures and latitudes. Leaf litter was collected in Liaohe Delta on 14 October 2023 and Yellow River Delta area on 21 November 2023. Five samples were collected from each site, and the withered reed leaves of the same year were selected. The collected litter was labeled by lineage, thoroughly washed, and dried in an oven at 65 °C for 72 h before proceeding with the analysis of the litter stoichiometric characteristics and conducting decomposition experiments.

The nitrogen content was analyzed using the Kjeldahl method [37]. Dried litter samples were ground and subjected to sulfuric acid digestion, with the nitrogen concentration quantified using a fully automatic Kjeldahl nitrogen analyzer (K9860, Hanon, Jinan, China). The phosphorus concentration was determined by using a spectrophotometer (UV-9000s, Metash, Shanghai, China) according to the molybdenum blue colorimetric method. The carbon content was assessed via the potassium dichromate titration method, where samples were digested using potassium dichromate and sulfuric acid prior to titration with a standard ferrous sulfate solution.

### 2.3. Decomposition Experiment

For the decomposition assessment, 18 samples from nine genotypes (two lineages: CN and YRD) were selected from the litter of the common gardens. A decomposition experiment was carried out in the greenhouse at Shandong University on 8 May 2024, utilizing three biological replicates for each treatment. Approximately 0.5 g of dry, shredded litter was placed into nylon bags with a 0.5 mm mesh size. Decomposition occurred within plastic containers (height: 15.4 cm, upper diameter: 11.8 cm, lower diameter: 8.0 cm) containing 50 g of soil. The litter bags were buried in the soil, and each container was covered with a lid featuring ventilation holes. To accurately simulate the coastal wetland environment, the soil moisture level was maintained above the soil surface by 1 cm, and the water lost through evaporation was replenished every 2 days. To ensure experimental consistency, the spatial arrangement of microcosm systems was randomized within the greenhouse. Furthermore, the microcosm systems were subjected to weekly random relocation to mitigate positional bias. Field microcosm experiments included five litter samples from both Shandong and Liaoning, resulting in a total of 10 samples and three biological replicates, leading to 30 microcosm systems. After 60 days on 8 July 2024 and 180 days on 8 November 2024, litter bags were retrieved, washed, dried, and weighed to determine the residual mass.

The initial mass of the litter placed in the nylon bags was recorded using an electronic balance. Following the decomposition phase, the litter was washed and dried, and final mass measurements were taken. The litter mass loss and decomposition percentage were calculated based on the initial and final mass.



## 2.4. Statistical Analysis

Data were analyzed using R software (v4.2.2). We used independent samples *t*-tests to detect the differences in *P. australis* traits and litter characteristics across varying environmental conditions. Two-way ANOVA and principal component analysis were employed to discern the factors influencing the variations in *P. australis* traits. We used the Shapiro–Wilk test to assess the normality of the data. For the differences in growth traits and litter chemical traits between two independent groups (e.g., between the Qingdao and Panjin common gardens), Student’s *t*-test was used. For multiple group comparisons (e.g., the differences in litter decomposition rates across different sites), Duncan’s multiple comparison test was employed to analyze the differences among the groups. Significant results were denoted by different lowercase letters ( $p < 0.05$ ). Pearson correlation analysis was conducted to examine the relationships between the growth traits of *P. australis* and associated litter stoichiometric characteristics and decomposition rates.

## 3. Results

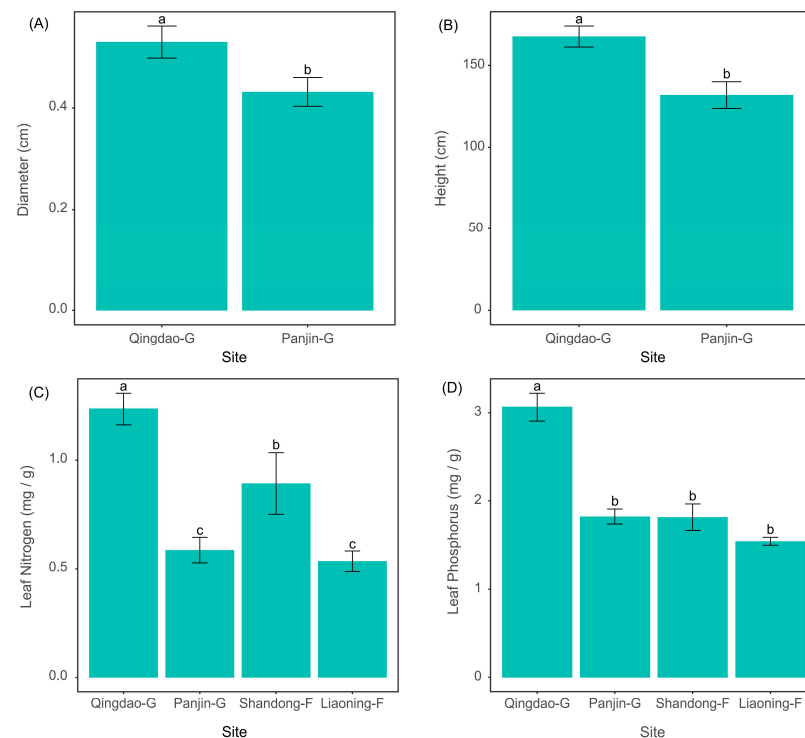
Two-way ANOVA showed no significant differences in the stoichiometric characteristics of the litter and plant growth traits among different *P. australis* lineages. However, significant differences were observed in the plant diameter ( $p = 0.046$ ), height ( $p = 0.004$ ), leaf nitrogen (LN) ( $p < 0.001$ ), leaf phosphorus (LP) ( $p < 0.001$ ), and carbon-to-nitrogen ratio (C/N) ( $p < 0.001$ ), as well as the mass loss ratios (MLRs) of the leaf litter from the 180-day harvest (LeafMLR180) ( $p = 0.026$ ) among *P. australis* in different common gardens (Table 1).

**Table 1.** *F* values of two-way ANOVA of effects of garden, haplotype, and their interactions on growth traits, litter stoichiometric characteristics, and mass loss ratios (MLRs) of *Phragmites australis*. (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ).

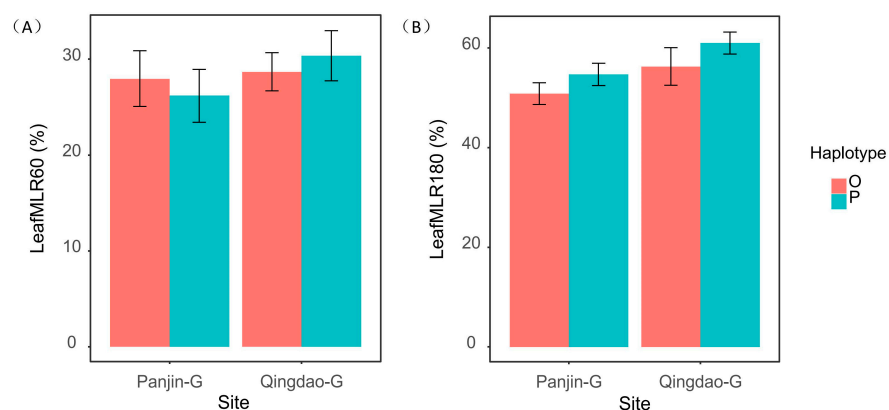
Parameters	<i>F</i> (Garden)	<i>F</i> (Haplotype)	<i>F</i> (Garden × Haplotype)
Diameter	4.867 *	0.445	0.080
Biomass	4.581	0.008	0.440
Height	12.281 **	1.933	1.098
Shoot Density	0.089	0.291	0.659
Leaf Litter N	44.779 ***	0.0000	0.986
Leaf Litter P	46.481 ***	1.174	0.058
Leaf Litter C	1.410	0.908	1.306
Leaf Litter C/N	24.210 ***	0.911	1.674
Leaf Litter N/P	3.769	0.677	0.594
Leaf MLR 60 days	1.004	0.005	0.382
Leaf MLR 180 days	6.302 *	2.836	0.027

For the growth traits, the average base diameter of *P. australis* in the Qingdao common garden was significantly higher than that in the Panjin common garden (Figure 2A). The average height (H) of *P. australis* in the two common gardens showed significant differences, with the *P. australis* in the Qingdao common garden being 27% taller than that in the Panjin common garden (Figure 2B). Compared with the Panjin common garden, the *P. australis* in the Qingdao common garden had a higher biomass and lower density, but there were no significant differences statistically. Significant differences in LN and LP were noted between the two common gardens, and LN was significantly different between the two wild populations. Notably, LP in the Qingdao common garden was significantly higher than that of the wild *P. australis* in Shandong. In contrast, no significant differences were observed among LP and LN between the Panjin common garden and the wild populations in Liaoning (Figure 2C,D). For the litter stoichiometric characteristics, there was no significant difference between the two common gardens and two wild populations.

In the decomposition study of *P. australis* leaf litter, after 60 days of incubation, the mass loss rates were approximately 25% for lineage O and 25% for lineage P in the Qingdao common garden, and about 27% for lineage O and 26% for lineage P in the Panjin common garden (Figure 3A). After 180 days of incubation, the mass loss rates were about 55% for lineage O and 58% for lineage P in the Qingdao common garden, and around 50% for lineage O and 53% for lineage P in the Panjin common garden (Figure 3B). The results indicate that the mass loss rate of leaf litter significantly increased with an extended incubation time, and the mass loss rate of the lineage P was slightly higher than that of the lineage O.

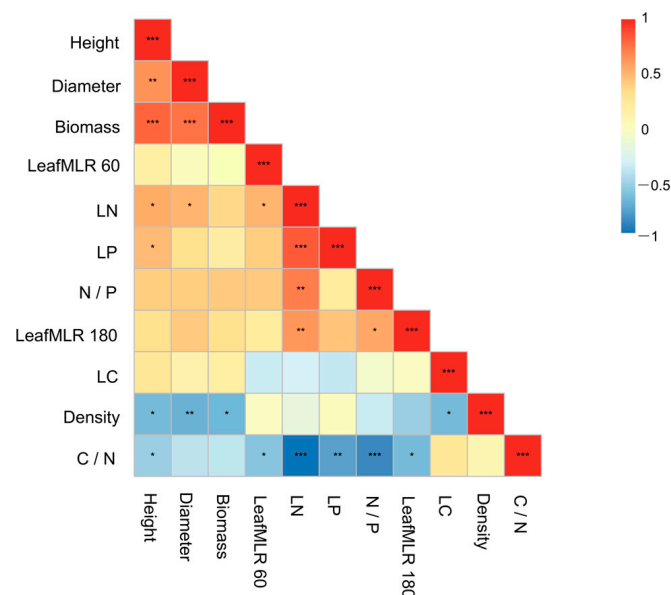


**Figure 2.** Diameter (A), height (B), leaf nitrogen (C), leaf phosphorus (D) of *Phragmites australis* in two common gardens (G) of Qingdao and Panjin and in the field (F) of Shandong and Liaoning (values are means  $\pm$  standard error). Different letters denote significant differences among groups: (A,B) as determined by one-way ANOVA followed by Student's *t*-test ( $p < 0.05$ ); (C,D) as determined by Duncan's multiple range test ( $\alpha = 0.05$ ).



**Figure 3.** The mass loss ratios of leaf litter from the 60-day harvest (LeafMLR60, A) and the mass loss ratios of leaf litter from the 180-day harvest (LeafMLR180, B) of *Phragmites australis* litter in Qingdao and Panjin common garden (G) (values are mean  $\pm$  standard error).

Pearson correlation analysis revealed a strong correlation between LP and LN, a significant positive correlation between LP and height, and a strong negative correlation with C/N. Additionally, LP showed positive correlations with Leaf Resource (LeafMLR 60 and LeafMLR 180). LN exhibited a significant positive correlation with height and diameter, a strong negative correlation with C/N, and a significant positive correlation with LeafMLR 180. Diameter showed positive correlations with biomass and height, and a significant negative correlation with density. Finally, biomass was significantly positively correlated with height (Figure 4).



**Figure 4.** Pearson correlation analysis between growth traits and stoichiometric characteristics. Average diameter, biomass, density, height; carbon to nitrogen ratio (C/N), percentage of carbon content (LC), nitrogen content (LN), phosphorus content (LP), nitrogen to phosphorus ratio (N/P), the mass loss ratios of leaf litter from the 60-day harvest (LeafMLR60), the mass loss ratios of leaf litter from the 180-day harvest (LeafMLR180) (\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ ).

Pearson correlation analysis revealed correlations between several bioclimatic variables and the growth traits of *P. australis*. Specifically, a significant positive correlation was found between the mean diurnal temperature range and the diameter of *P. australis* ( $p < 0.05$ ). The mean diurnal temperature range and the mean temperature of the wettest quarter were positively correlated with *P. australis* biomass and negatively correlated with *P. australis* density, although these correlations were not statistically significant (Figure S1).

#### 4. Discussion

Phenotypic plasticity is a key mechanism through which *P. australis* adapts to the environmental conditions. In previous studies, it was found that salinization shifts the phenotypic variability and intraspecific variation in the foundation plant species in estuarine wetlands [38]. In our study, the location of the common garden environment significantly influenced the growth performance (shoot diameter and height), leaf litter stoichiometric traits (contents of N and P), and the leaf decomposition in 180 days. *Phragmites australis* of different lineages were found to have a variation in growth traits in the Panjin and Qingdao gardens. *Phragmites australis* adapts to climate factors through phenotypic plasticity and then has possible effects on population functioning [39–41]. *Phragmites australis* showed an increase in plant height and basal diameter with increasing latitude in the common gardens, as found in other studies [11,42]. Plants often face trade-offs between the energy allocation and evolutionary potential. The role of phenotypic plasticity is constrained by



resources, genetic factors, and other limitations, ultimately restricting its effectiveness [25]. Correlation analysis also confirmed the relationship between growth traits and temperature. This adaptability allows organisms to improve their survival and reproductive success under varying environmental conditions. Adaptive plasticity is helpful to the rapid and low-cost adaptive adjustment of plants, thereby enhancing their capacity to sustain fitness across a larger region or a spectrum of conditions.

Genetic variation, including epigenetic variation, serves as a key mechanism of adaptation for many species. Previous studies on *P. australis* showed significant differences between haplotype O and haplotype P in plant functional traits (e.g., specific leaf area and leaf length) [23,40,43], which may affect the decomposition rate of leaf litter. The correlation between species diversity and litter decomposition has been found in other studies, and higher species and genetic diversity had negative effects on plant litter decomposition. The litter mass loss of four-species mixtures was significantly lower compared to that of one-species and two-species mixtures ( $p < 0.05$ ) [30]. Intraspecific variation plays a critical role in maintaining ecosystem function and resilience. This diversity enables populations to adapt to changing environmental conditions, thereby contributing to the health and sustainability of ecosystems. However, the differences in plant growth and litter decomposition between haplotype O and haplotype P were not observed in our study. Plant growth and litter decomposition are affected by many factors, and the samples in our study came from a similar environment or the same ecotype. Natural selection, gene flow, or clone reproduction may lead to a similar genetic background, which in turn affects the phenotype. It is worth noting that conducting the decomposition experiment in natural field settings, rather than in microcosms, might have revealed additional differences that were not detected in our current experimental design. This is because microbial communities in natural soils play a crucial role in the decomposition processes and are influenced by the litter characteristics. Other factors, such as population size, environmental conditions, and the short duration of the research, may have also contributed to an incomplete assessment of the influence of genetic variation. Additionally, local adaptation to regional factors, such as salinity, may have diminished the phenotypic differences among different lineages in this species [14].

Plants employ a variety of growth strategies to optimize their survival and reproduction in diverse environments. These strategies often involve trade-offs between resource allocation to different structures and functions. Some plants exhibit rapid growth and early reproduction (r-strategists) in unstable or disturbed habitats [26,27]. In our study, the diameter of *P. australis* is negatively correlated with density and also shows a correlation with latitude, indicating that intraspecific variation exists in the adaptation strategies of *P. australis*. The adaptation strategy of *P. australis* population is rapid growth and dispersal in cold climates, consistent with r strategists. The litter leaf N content in Qingdao is higher than that in Panjin, a result consistent across both the common garden and field experiments. It has also been found in other studies that the leaf N and P content is correlated with the annual average temperature and precipitation, which may be due to the fact that plants at higher latitudes allocate more energy to their leaves, forming a larger leaf area and increasing the chlorophyll content [44,45]. This is further supported by the significant positive correlation between the leaf N content and leaf area. Evidence suggests that leaves are a stronger sink for N than fine roots, and the N might transfer from high-N to low-N components [46,47]. *Phragmites australis* employs different adaptation strategies to balance the relationship between economic traits. The leaf economics spectrum is also present within the *P. australis* population. Additionally, the correlation of the leaf N and P contents with plant height and basal stem also confirms that the adjustment of leaf traits and growth rate is the main survival strategy for plants to adapt to environmental changes [48].

The dynamics of nitrogen and phosphorus nutrients are the main factors influencing the carbon balance and litter decomposition rate in ecosystems. Nitrogen and phosphorus, as key nutrients, affect the carbon cycle. Nitrogen affects photosynthesis and biomass production, thus affecting carbon fixation. Phosphorus is also involved in energy transfer and nucleic acid synthesis, which are very important for the activities of plants and microorganisms [6,49]. The transfer of N is likely associated with the transfer of C. As a primary pathway for soil carbon input, the litter induces an excitation effect, which is linked to the soil nitrogen availability [15,29]. The decomposition rate of leaf litter is positively correlated with the N and P content of leaf litter and negatively correlated with C/N, indicating that a lower C/N of leaf litter facilitates the rapid decomposition of leaf litter. The dynamic change of the nutrient content of carbon, nitrogen, and phosphorus in litter shows a trend of promoting decomposition. Nitrogen and phosphorus in litter limit the decomposition rate of litter and affect the dynamic balance of the carbon cycle in the environment [45,50]. The experimental results also confirmed the coupling effect of nitrogen and phosphorus. Additionally, based on the decomposition ability of leaves, the decomposition ability in gardens is significantly higher than that in the wild. Nitrogen and phosphorus in soil are limiting nutrients for plant growth, and *P. australis* in the wild may be constrained by the nitrogen and phosphorus availability. Litter decomposition is an important process in the cycling of biogeochemical elements and energy flow in wetland ecosystems, serving as a primary mechanism for the carbon pool balance. In future research, we should comprehensively consider the interaction among plant organs, litter, and soil stoichiometric characteristics, as well as the influence of environmental variables (such as climate, soil types and interference factors) on the overall nutrient cycle, and strengthen the fitting of large-scale data models. Thus, the influence of the environment on the stoichiometric characteristics and nutrient migration can be understood more deeply.

## 5. Conclusions

This study demonstrates that environmental factors, rather than genetic variation (lineage), predominantly shape the growth traits, litter stoichiometry, and decomposition dynamics of *P. australis* in eastern temperate China. The growth performance and litter nutrient content (N and P) were significantly influenced by the common garden environment, with the leaf litter from higher-latitude regions exhibiting a consistently higher N content, irrespective of its origin. The litter decomposition rates were strongly driven by the N and P availability, underscoring the role of the nutrient stoichiometry in ecosystem processes. Notably, climatic conditions from the genotype's origin were linked to growth traits, but not to litter traits or decomposition, indicating that *P. australis* may locally adapt genetically for diverse environments without influencing the associated ecological processes of litter decomposition. These findings emphasize the importance of environmental context and plant plasticity in sustaining wetland ecosystem functions. For conservation and management, prioritizing the habitat conditions over genetic diversity may enhance the resilience of *P. australis* populations and wetland ecosystems under global climate change.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d17040282/s1>. Figure S1: Pearson correlation analysis between climate environmental factors and the traits and stoichiometric characteristics of *Phragmites australis*. Diameter, biomass, density, height; carbon-to-nitrogen ratio (C/N), percentage of carbon content in litter (LC), nitrogen content in litter (LN), phosphorus content in litter (LP), nitrogen-to-phosphorus ratio (N/P), the mass loss ratios of leaf litter from the 60-day harvest (LeafMLR60), the mass loss ratios of leaf litter from the 180-day harvest (LeafMLR180). bio1, Annual mean temperature; bio2, Mean diurnal temperature range; bio3, Isothermality; bio4, Temperature seasonality coefficient; bio5, Maximum temperature of warmest month; bio6, Minimum temperature of coldest month; bio7,

Temperature annual range; bio8, Mean temperature of wettest quarter; bio9, Mean temperature of driest quarter; bio10, Mean temperature of warmest quarter; bio11, Mean temperature of coldest quarter; bio12, Annual precipitation; bio13, Precipitation of wettest month; bio14, Precipitation of driest month; bio15, Precipitation seasonality; bio 16, Precipitation of wettest quarter; bio 17, Precipitation of driest quarter; bio 18, Precipitation of warmest quarter; bio 19, Precipitation of coldest quarter (\*,  $p < 0.05$ ).

**Author Contributions:** Conceptualization, H.S., W.G. and L.L.; methodology, W.W., Q.W., H.S. and L.L.; software, W.W., Q.W., L.L. and W.S.; validation, H.Z., W.S. and X.Z.; formal analysis, W.W. and Q.W.; investigation, Q.W., H.Z., X.Z. and L.X.; resources, X.G., Y.G., S.Y. and W.G.; data curation, W.W., Q.W. and L.L.; writing—original draft preparation, W.W., Q.W. and H.S.; writing—review and editing, W.W., H.S., W.S., L.X., Y.W. and L.L.; visualization, W.W.; supervision, X.G., Y.G., S.Y., L.L., Y.W. and W.G.; project administration, H.S., L.L. and W.G.; funding acquisition, X.G. and W.G. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the National Natural Science Foundation of China (grant number: 32301317; 32470388; 32271588; U22A20558), and Shandong Provincial Natural Science Foundation (ZR2024QC197).

**Institutional Review Board Statement:** Not applicable.

**Data Availability Statement:** Data will be made available upon request.

**Conflicts of Interest:** The authors declare no conflicts of interest.

## References

- McLaughlin, D.L.; Cohen, M.J. Realizing Ecosystem Services: Wetland Hydrologic Function along a Gradient of Ecosystem Condition. *Ecol. Appl.* **2013**, *23*, 1619–1631. [\[CrossRef\]](#) [\[PubMed\]](#)
- Means, M.M.; Ahn, C.; Korol, A.R.; Williams, L.D. Carbon Storage Potential by Four Macrophytes as Affected by Planting Diversity in a Created Wetland. *J. Environ. Manag.* **2016**, *165*, 133–139. [\[CrossRef\]](#)
- Ma, S.; Creed, I.F.; Badiou, P. New Perspectives on Temperate Inland Wetlands as Natural Climate Solutions under Different CO<sub>2</sub>-Equivalent Metrics. *NPJ Clim. Atmos. Sci.* **2024**, *7*, 222. [\[CrossRef\]](#)
- Kayranli, B.; Scholz, M.; Mustafa, A.; Hedmark, Å. Carbon Storage and Fluxes within Freshwater Wetlands: A Critical Review. *Wetlands* **2010**, *30*, 111–124. [\[CrossRef\]](#)
- Lu, Q.; Gao, Z.; Zhao, Z.; Ning, J.; Bi, X. Dynamics of Wetlands and Their Effects on Carbon Emissions in China Coastal Region—Case Study in Bohai Economic Rim. *Ocean Coast. Manag.* **2014**, *87*, 61–67.
- Were, D.; Kansime, F.; Fetahi, T.; Hein, T. Soil Organic Carbon Storage in a Tropical Freshwater Wetland: The Influence of Vegetation Type. *Afr. J. Aquat. Sci.* **2021**, *46*, 161–172. [\[CrossRef\]](#)
- Wang, Q.; Xie, H.; Ngo, H.H.; Guo, W.; Zhang, J.; Liu, C.; Liang, S.; Hu, Z.; Yang, Z.; Zhao, C. Microbial Abundance and Community in Subsurface Flow Constructed Wetland Microcosms: Role of Plant Presence. *Environ. Sci. Pollut. Res.* **2016**, *23*, 4036–4045. [\[CrossRef\]](#) [\[PubMed\]](#)
- Zhang, Y.; Ding, W.; Luo, J.; Donnison, A. Changes in Soil Organic Carbon Dynamics in an Eastern Chinese Coastal Wetland Following Invasion by a C4 Plant *Spartina alterniflora*. *Soil Biol. Biochem.* **2010**, *42*, 1712–1720. [\[CrossRef\]](#)
- Eller, F.; Skálová, H.; Caplan, J.S.; Bhattarai, G.P.; Burger, M.K.; Cronin, J.T.; Guo, W.-Y.; Guo, X.; Hazelton, E.L.G.; Kettenring, K.M.; et al. Cosmopolitan Species as Models for Ecophysiological Responses to Global Change: The Common Reed *Phragmites australis*. *Front. Plant Sci.* **2017**, *8*, 1833. [\[CrossRef\]](#)
- Packer, J.G.; Meyerson, L.A.; Skálová, H.; Pyšek, P.; Kueffer, C. Biological Flora of the British Isles: *Phragmites australis*. *J. Ecol.* **2017**, *105*, 1123–1162. [\[CrossRef\]](#)
- Song, H.; Jespersen, E.; Guo, X.; Du, N.; Xie, L.; Pei, L.; Ye, S.; Wang, R.; Brix, H.; Eller, F.; et al. Differences in Relative Air Humidity Affect Responses to Soil Salinity in Freshwater and Salt Marsh Populations of the Dominant Grass Species *Phragmites australis*. *Hydrobiologia* **2021**, *848*, 3353–3369. [\[CrossRef\]](#)
- Maron, J.L.; Elmendorf, S.C.; Vilà, M. Contrasting Plant Physiological Adaptation to Climate in the Native and Introduced Range of *Hypericum Perforatum*. *Evol. Int. J. Org. Evol.* **2007**, *61*, 1912–1924. [\[CrossRef\]](#)
- Ren, L.; Guo, X.; Sorrell, B.K.; Eller, F.; Brix, H. Responses to Cold Temperature Determine Clinal Patterns of Photosynthetic Acclimation of a Cosmopolitan Grass Genus and Challenge the Concept of Quantifying Phenotypic Plasticity. *Funct. Ecol.* **2025**, *39*, 583–595. [\[CrossRef\]](#)

14. Sheng, W.; Liu, L.; Wu, Y.; Yin, M.; Yu, Q.; Guo, X.; Song, H.; Guo, W. Exploring Salt Tolerance and Indicator Traits across Four Temperate Lineages of the Common Wetland Plant, *Phragmites australis*. *Sci. Total Environ.* **2024**, *912*, 169100. [[CrossRef](#)] [[PubMed](#)]
15. Silan, G.; Buosi, A.; Bertolini, C.; Sfriso, A. Dynamics and Drivers of Carbon Sequestration and Storage Capacity in *Phragmites australis*-Dominated Wetlands. *Estuar. Coast. Shelf Sci.* **2024**, *298*, 108640. [[CrossRef](#)]
16. Ren, L.; Guo, X.; Liu, S.; Yu, T.; Guo, W.; Wang, R.; Ye, S.; Lambertini, C.; Brix, H.; Eller, F. Intraspecific Variation in *Phragmites australis*: Clinal Adaption of Functional Traits and Phenotypic Plasticity Vary with Latitude of Origin. *J. Ecol.* **2020**, *108*, 2531–2543. [[CrossRef](#)]
17. Zhang, Y.; Pennings, S.C.; Liu, Z.; Li, B.; Wu, J. Consistent Pattern of Higher Lability of Leaves from High Latitudes for Both Native *Phragmites australis* and Exotic *Spartina alterniflora*. *Funct. Ecol.* **2021**, *35*, 2084–2093. [[CrossRef](#)]
18. Ravenscroft, C.H.; Fridley, J.D.; Grime, J.P. Intraspecific Functional Differentiation Suggests Local Adaptation to Long-term Climate Change in a Calcareous Grassland. *J. Ecol.* **2014**, *102*, 65–73. [[CrossRef](#)]
19. Kahl, S.M.; Lenhard, M.; Joshi, J. Compensatory Mechanisms to Climate Change in the Widely Distributed Species *Silene vulgaris*. *J. Ecol.* **2019**, *107*, 1918–1930. [[CrossRef](#)]
20. Sambatti, J.B.M.; Rice, K.J. Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). *Evolution* **2006**, *60*, 696–710.
21. Kawecki, T.J.; Ebert, D. Conceptual Issues in Local Adaptation. *Ecol. Lett.* **2004**, *7*, 1225–1241. [[CrossRef](#)]
22. Cuma Mushagalusa, F.; Bauman, D.; Mujinya Bazirake, B.; Mleci, Y.; Kalenga, M.; Shutcha, M.N.; Meerts, P. Phenotypic Plasticity, Not Ecotype Differentiation, Explains the Broad Ecological Niche of a Tree Species in African Dry Woodlands. *Environ. Exp. Bot.* **2020**, *178*, 104186. [[CrossRef](#)]
23. Liu, L.; Yin, M.; Guo, X.; Wang, J.; Cai, Y.; Wang, C.; Yu, X.; Du, N.; Brix, H.; Eller, F.; et al. Cryptic Lineages and Potential Introgression in a Mixed-ploidy Species (*Phragmites australis*) across Temperate China. *J. Syst. Evol.* **2022**, *60*, 398–410. [[CrossRef](#)]
24. Pastore, M.A. Bringing the Underground to the Surface: Climate Change Stressors Negatively Affect Plant Growth, with Contrasting above and Belowground Physiological Responses. *Plant Cell Environ.* **2022**, *45*, 2267–2270. [[CrossRef](#)]
25. Nicotra, A.B.; Atkin, O.K.; Bonser, S.P.; Davidson, A.M.; Finnegan, E.J.; Mathesius, U.; Poot, P.; Purugganan, M.D.; Richards, C.L.; Valladares, F.; et al. Plant Phenotypic Plasticity in a Changing Climate. *Trends Plant Sci.* **2010**, *15*, 684–692. [[CrossRef](#)]
26. Pierce, S.; Brusa, G.; Vagge, I.; Cerabolini, B.E.L. Allocating CSR Plant Functional Types: The Use of Leaf Economics and Size Traits to Classify Woody and Herbaceous Vascular Plants. *Funct. Ecol.* **2013**, *27*, 1002–1010. [[CrossRef](#)]
27. Zhang, Y.; Meiners, S.J.; Meng, Y.; Yao, Q.; Guo, K.; Guo, W.; Li, S. Temporal Dynamics of Grime's CSR Strategies in Plant Communities during 60 Years of Succession. *Ecol. Lett.* **2024**, *27*, e14446. [[CrossRef](#)]
28. Pei, Z.; Leppert, K.N.; Eichenberg, D.; Bruehlheide, H.; Niklaus, P.A.; Buscot, F.; Gutknecht, J.L.M. Leaf Litter Diversity Alters Microbial Activity, Microbial Abundances, and Nutrient Cycling in a Subtropical Forest Ecosystem. *Biogeochemistry* **2017**, *134*, 163–181. [[CrossRef](#)]
29. Ding, Y.; Wang, D.; Zhao, G.; Chen, S.; Sun, T.; Sun, H.; Wu, C.; Li, Y.; Yu, Z.; Li, Y.; et al. The Contribution of Wetland Plant Litter to Soil Carbon Pool: Decomposition Rates and Priming Effects. *Environ. Res.* **2023**, *224*, 115575. [[CrossRef](#)]
30. Yin, M.; Liu, L.; Wu, Y.; Sheng, W.; Ma, X.; Du, N.; Zhu, P.; Wang, C.; Cui, Z.; Brix, H.; et al. Effects of Litter Species and Genetic Diversity on Plant Litter Decomposition in Coastal Wetland. *Ecol. Indic.* **2022**, *144*, 109439. [[CrossRef](#)]
31. Mori, A.S.; Cornelissen, J.H.C.; Fujii, S.; Okada, K.; Isbell, F. A Meta-Analysis on Decomposition Quantifies Afterlife Effects of Plant Diversity as a Global Change Driver. *Nat. Commun.* **2020**, *11*, 4547. [[CrossRef](#)] [[PubMed](#)]
32. Yan, J.; Zhang, Y.; Crawford, K.M.; Chen, X.; Yu, S.; Wu, J. Plant Genotypic Diversity Effects on Soil Nematodes Vary with Trophic Level. *New Phytol.* **2021**, *229*, 575–584. [[CrossRef](#)] [[PubMed](#)]
33. Xiao, L.; Ma, Y.; Gan, Z.; Cai, R.; Li, Z.; Ge, G.; Wu, L. Influence of soil fauna on the litter decomposition of Lake Poyang Wetland in winter. *J. Lake Sci.* **2020**, *32*, 395–405.
34. Zhang, L.; Zhang, Y.; Zou, J.; Siemann, E. Decomposition of *Phragmites australis* litter retarded by invasive *Solidago canadensis* in mixtures: An antagonistic non-additive effect. *Sci Rep.* **2014**, *4*, 5488. [[CrossRef](#)] [[PubMed](#)]
35. Zhang, G.; Cai, Y.; Luo, H.; Hong, S.; Song, C.; Yan, J.; Fang, H. Effects of Abiotic Factors on Plant Community Composition and Functional Traits in the Liaohe Estuary. *J. Mar. Environ. Eng.* **2024**, *11*, 141–156. [[CrossRef](#)]
36. Liu, L.; Du, N.; Eller, F.; Ye, S.; Li, X.; Wei, J.; Guo, Y.; Brix, H.; Guo, W. Ecological Mechanisms of Carbon Sequestration in Vegetated Coastal Wetland Ecosystem: Exploring the Roles of Biodiversity and Environmental Changes. *J. Mar. Environ. Eng.* **2025**, *12*, 35–47.
37. Brabson, J.A. The Kjeldahl Method for Organic Nitrogen. *J. Assoc. Off. Anal. Chem.* **1966**, *49*, 481. [[CrossRef](#)]
38. Wu, Y.; Liu, L.; Yin, M.; Guo, W. Phylogenetic relationship and soil salinity shape intraspecific trait variability of *Phragmites australis* in the Yellow River Delta. *Front. Mar. Sci.* **2022**, *9*, 980695. [[CrossRef](#)]
39. Clevering, O.A.; Brix, H.; Lukavská, J. Geographic Variation in Growth Responses in *Phragmites australis*. *Aquat. Bot.* **2001**, *69*, 89–108. [[CrossRef](#)]

40. Mozdzer, T.J.; Caplan, J.S.; Hager, R.N.; Proffitt, C.E.; Meyerson, L.A. Contrasting Trait Responses to Latitudinal Climate Variation in Two Lineages of an Invasive Grass. *Biol. Invasions* **2016**, *18*, 2649–2660. [[CrossRef](#)]
41. Oostra, V.; Saastamoinen, M.; Zwaan, B.J.; Wheat, C.W. Strong Phenotypic Plasticity Limits Potential for Evolutionary Responses to Climate Change. *Nat. Commun.* **2018**, *9*, 1005. [[CrossRef](#)] [[PubMed](#)]
42. Lissner, J.; Schierup, H.-H.; Comín, F.A.; Astorga, V. Effect of Climate on the Salt Tolerance of Two *Phragmites australis* Populations. *Aquat. Bot.* **1999**, *64*, 317–333. [[CrossRef](#)]
43. Liu, L.; Wang, J.; Ma, X.; Li, M.; Guo, X.; Yin, M.; Cai, Y.; Yu, X.; Du, N.; Wang, R.; et al. Impacts of the Yellow River and Qingtongxia Dams on Genetic Diversity of *Phragmites australis* in Ningxia Plain, China. *Aquat. Bot.* **2021**, *169*, 103341. [[CrossRef](#)]
44. Kattge, J.; Knorr, W.; Raddatz, T.; Wirth, C. Quantifying Photosynthetic Capacity and Its Relationship to Leaf Nitrogen Content for Global-scale Terrestrial Biosphere Models. *Glob. Change Biol.* **2009**, *15*, 976–991. [[CrossRef](#)]
45. He, Y.; Xu, X.; Kueffer, C.; Zhang, X.; Shi, P. Leaf Litter of a Dominant Cushion Plant Shifts Nitrogen Mineralization to Immobilization at High but Not Low Temperature in an Alpine Meadow. *Plant Soil* **2014**, *383*, 415–426. [[CrossRef](#)]
46. Pregitzer, K.S.; Zak, D.R.; Talhelm, A.F.; Burton, A.J.; Eikenberry, J.R. Nitrogen Turnover in the Leaf Litter and Fine Roots of Sugar Maple. *Ecology* **2010**, *91*, 3456–3462. [[CrossRef](#)]
47. Berglund, S.L.; Ågren, G.I.; Ekblad, A. Carbon and Nitrogen Transfer in Leaf Litter Mixtures. *Soil Biol. Biochem.* **2013**, *57*, 341–348. [[CrossRef](#)]
48. Wright, I.J.; Reich, P.B.; Westoby, M. Strategy Shifts in Leaf Physiology, Structure and Nutrient Content between Species of High- and Low-rainfall and High- and Low-nutrient Habitats. *Funct. Ecol.* **2001**, *15*, 423–434. [[CrossRef](#)]
49. Sisto, M.L.D.; Macdougall, A.H. Effect of Terrestrial Nutrient Limitation on the Estimation of the Remaining Carbon budget. *Biogeosciences* **2024**, *21*, 21. [[CrossRef](#)]
50. Uddin, M.N.; Robinson, R.W. Responses of Plant Species Diversity and Soil Physical-Chemical-Microbial Properties to *Phragmites australis* Invasion along a Density Gradient. *Sci. Rep.* **2017**, *7*, 11007. [[CrossRef](#)]

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.