Driving Forces Analysis of Non-structural Carbohydrates for *Phragmites australis* in Different Habitats of Inland River Wetland

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**Abstract:** Habitat variation in non-structural carbohydrates (NSC) reflects the resource allocation trade-offs for clonal plants, and its driving force analysis embodies the ecological adaptation strategy of clonal plants to heterogeneous environments. In this paper, the reed (*Phragmites australis*) in the northwestern inland wetlands of China, as a typical example of clonal plants, was used as the research object. The content and distribution of NSC in reeds and their response characteristics to soil environmental factors were compared under three different environmental gradients with wet, salt marsh and desert habitats. The results showed: (1) the content of NSC and starch gradually increased and the content of soluble sugar gradually decreased from wetland to desert habitats, and the ratio of soluble sugar to starch increased significantly ($p < 0.05$), which demonstrated that reeds converted more NSC into starch to adapt to harsh environments as the environment changed. (2) Reeds tended to invest more NSC in underground architectures to achieve survival and growth with the increase in environmental stress, providing the evidence that NSC were transferred from leaf to rhizome, and root, stem and rhizome received more soluble sugar investment. The ratio of soluble sugar to starch of reed stem and rhizome increased significantly with the increasing content of soluble sugar and the decreasing content of starch, and more starch was converted into soluble sugar to resist the harsh environment. (3) Soil water, soil bulk density and salinity were the main driving forces for the NSC content and the distribution characteristics of reeds using the relative importance analysis. The study results clarified the habitat variation law, and the main environmental driving forces of NSC for reeds in inland river wetlands, which provided the significant references for enriching the ecology research theory of clonal plants and protection measures in the fragile and sensitive wetlands in arid regions.

**Keywords:** *Phragmites australis*; clonal architecture; water and salt stress; inland salt marsh wetlands; ecological adaptation; non-structural carbohydrates

1. **Introduction**

Non-structural carbohydrates (NSC), synthesized by plant photosynthesis, are not only an essential energy supply for plant growth and metabolism, but also a major contributor to plant structure construction [1]. NSC can be divided into soluble sugars used to maintain the osmotic pressure of cells and starch used for material storage according to their functions [2]. There is a mutual conversion relationship between soluble sugar and starch under certain conditions. NSC is an indicator for evaluating the level of plant-available substances and the balance between carbon source and carbon sink [3]. Meanwhile, the allocation principle of its composition is also an important index to evaluate
the ecological adaptation strategies of plants to heterogeneous environments. In addition, NSC research can reveal the plant's stress resistance mechanism and provide strategies for the protection of inland river wetlands.

The content and distribution patterns of NSC in plants were limited by environmental factors [4]. Soil water and nutritional stress will affect the changes in NSC and component content, which greatly affects the growth trend and the physiological and ecological adaptability of plants. Starch was converted into soluble sugar for Leucaena leucocephala, Pterocarpus soyauxii and Semen sianum of Nigeria in the dry season, and the excess soluble sugar was converted into starch and stored after the drought stress disappeared [5]. The starch content of Pinus sylvestris and Picea abies increased, and the soluble sugar and NSC content of Laurus nobilis in southern Italy gradually decreased under the conditions of water stress [6,7]. The NSC in plants showed different distribution trade-offs under heterogeneous habitats, which might be the mechanisms and strategies employed in order to adapt to different environments. Meanwhile, the response mechanisms of NSC metabolism for different plant types to environmental stress are not completely clear [8]. At present, most research on the relationship between NSC and environmental factors have focused on alpine woody plants [9,10], and there is still a lack of research on herbaceous plants in inland river wetlands. Studying results on the accumulation law of NSC in the inland river wetlands, herbs will helpful to understand the carbon balance of plants at some level and provide important clues to reveal the adaptation mechanism of plants to a specific habitat.

The clonal plant is capable of producing offspring with the same genotype as the mother plant through asexual reproduction under natural conditions [11]. Clonal plants show differences from non-clonal plant in many aspects, such as their own growth, metabolism and reproduction with the resource integration, foraging behavior, and morphological plasticity. These unique functions improve the environmental adaptability of clonal plant populations, showing more effective nutrient absorption and space usage [12]. As an important part of the natural ecosystem, clonal plants exist widely and occupy the dominant position of most ecosystems, which has an important impact on species diversity, community succession, ecosystem stability and diversity [13,14]. However, current research on the allocation strategy and environmental adaptability of cloned plant NSC is relatively scarce. The NSC of the whole plant (individual level) can reflect the overall carbon supply, and it is an important parameter for comparing species growth and adaptive capacity under different species or different environmental conditions. The NSC and its components of Phylostachys glauca had different trends in three different soil environments of northwestern China, showing that the soluble sugar concentration gradually increased, and the NSC and starch concentrations decreased and then increased with the increase in environmental stress [15]. However, the starch and NSC did not change significantly in different habitats of Syntrichia caninervis in the Gurbantungut Desert [16]. Therefore, the physiological and ecological mechanisms of different plants adapting to adversity are different. In addition, the differences in the physiological functions and metabolic capabilities of various plant components can also reflect the NSC allocation strategy in plants and their adaptation mechanism under environmental stress [17]. The NSC content in the roots of Vicia unijuga and Allium atrosanguineum increased with environmental stress in southeastern Tibet, China [18]. However, the NSC of thick roots of Caryopteris mongolica in Beijing, China were reduced in moderate and severe environmental stress [19]. Therefore, studying the changes in NSC content and the distribution of clonal plants from both of the level perspectives of the whole plant and artifacts is conducive to grasping the carbon balance mechanism and understanding the physiological and metabolic processes of clonal plants and their environmental response strategies.

Wetland, called “the kidney of the earth” due to its functions of purifying natural water, maintaining water and soil, adjusting regional climate conditions, maintaining ecological balance and species diversity is one of the three major systems of the earth [20]. In particular, the special soil formation process of inland river wetlands determines the spatial heterogeneity and the high sensitivity of ecosystems [21]. In recent years, the degradation of inland river wetlands was severe due to human activities and regional climate change. Reed (Phragmites australis) is a typical rhizome clonal plant and is widely distributed in inland river wetlands, which could form the large-scale single-dominant species
communities in areas with perennial seasonal water accumulation and short-term water accumulation. On the other hand, reed can reduce the biodiversity of the invaded area, such as coastal, lake and river wetlands, cause changes in the structure and function of the ecosystem and eventually lead to the degradation of the ecosystem. A lot of research on reeds has focused on their physiological and biochemical characteristics [22], the response of biological characteristics to environmental factors [23], the trade-off between clonal growth and sexual reproduction [24,25], population ecosystem function and economic value [26], etc. However, studies on the analysis of NSC allocation strategies and the driving forces of reeds based on the characteristics of clonal plant in different habitats in inland river wetlands with fragile ecosystems are currently lacking. Meanwhile, research on the NSC habitat variation and the driving forces of reeds in inland river wetlands could lay a solid foundation for wetland ecosystem functions under heterogeneous environmental conditions, provide a method and basis for predicting the impact of future global changes on wetland ecosystems and play an important role in maintaining the stability and function of wetland ecosystems. Therefore, we selected reeds under different environmental gradients in the inland river wetlands to: (1) explore the response rules of NSC for reeds to different environmental gradients, (2) analyze the distribution trade-offs of NSC in various clonal modules for reeds in different habitats and (3) clarify the main environmental driving forces of NSC allocation for reeds in different habitats.

2. Materials and Methods

2.1. Study Area

The study areas are located in the Dunhuang Yangguan National Nature Reserve in northwestern China (93°53′–94°17′ E, 39°39′–40°05′ N) with flat terrain and an elevation of 1150–1500 m, and are surrounded by the Gobi desert in the hinterland of the inland, as shown in Figure 1. It belongs to a typical continental arid climate, accompanied by a large daily temperature difference. The annual mean temperature is 9.3 °C and the frost-free period is 145 days. Soil types are mainly meadow soil, marsh soil and saline soil. The vegetation is dominated by Phragmites australis, accompanied by Lemus secalinus, Lycium ruthenicum, Triglochin palustre, Salicornia europaea, Glycyrrhiza uralensis, Apocynum venetum, Salicornia europaea and other plants.

![Figure 1. Study areas and sampling point distribution.](image-url)

The total annual runoff of the Dunhuang Yangguan National Nature Reserve is $9.9 \times 10^8 \text{ m}^3$, and the total surface runoff length is 146.38 km. The annual total precipitation is 39.9 mm, but the
annual evaporation is 2465 mm. There are about 200 springs and three main water systems—Xitugou, Wowa Pool and Shanshuigou—formed from east to west in the reserve. The main water source of plants is the ice–snow meltwater from Altun Mountain, which is gathered in river valleys and recharged in the form of long underground flows.

2.2. Research Methods

2.2.1. Sample Collection

In May (early growth season), July (mid-growth season) and September (later growth season) of 2018, three parallel internal sampling lines were set up from the wetland to the desert in the Dunhuang Yangguan National Nature Reserve wetlands. Three different habitats were divided for each sampling line based on the distance from the reservoir (500 m, 1500 m, 2500 m), which were represented by wet habitat (density: 90.36–92.55%, coverage: 90.73–93.00%), salt marsh habitat (density: 51.00–52.65%, coverage: 53.38–55.00%) and desert habitat (density: 12.83–15.26%, coverage: 13.33–16.45%). In addition, three 5 m × 5 m squares were randomly set on the ground in three different habitats, and the latitude, longitude and altitude information of each square were recorded [27].

Based on the characteristics of the clonal plant community, three complete reeds were randomly selected with generally consistent good growth in each plot. Taking the clone ramets as the sampling unit, all of the ground and underground parts of the plant were harvested through the “full digging method” for the root system to conduct “tracking and digging” sampling [28,29]. In order to prevent enzyme activity in the sample, the sample was placed at 105 °C for 30 min, and then the whole reed was cut into clonal modules, such as leaves, stems, roots and rhizomes. All clonal module samples were numbered, dried at 80 °C, ground and sifted using a 100-mesh screen.

Soil samples were obtained by the ring knife method and the sampling depth was from 0 cm to 100 cm. The samples were taken every 10 cm with a mix 0–30 cm of soil as surface soil, a mix of 30–60 cm of soil as middle soil and a mix 60–100 cm of soil as deep soil, and the sampling was repeated three times. The collected soil samples were decontaminated, air-dried, ground, and sieved for later use.

2.2.2. Sample Analysis Method

Reed samples (leaf, stem, rhizome and root) were each weighed 0.1 g, and the soluble sugar and starch concentrations were determined by the Anthrone–sulfonic acid method. The NSC concentration was the sum of the soluble sugar and starch concentrations [30–32], and the NSC and its component concentrations were expressed as percentages. The calculation formula is:

\[ SS = \frac{C \cdot VT1}{V1 \cdot W} \]  \hspace{1cm} (1)

\[ S = \frac{C \cdot VT2}{V1 \cdot W} \]  \hspace{1cm} (2)

In the formula, \( SS \) (%) is the content of soluble sugar, \( S \) (%) is the content of starch, \( C \) is the value (ug) displayed by the photometer, \( VT1 \) (mL) is the volume of the extraction solution (ethanol extraction), \( VT2 \) (mL) is the volume of the extraction solution (perchloric acid extraction), and \( V1 \) (mL) is the volume of the sample solution, \( W \) (g) is the weight of the selected clone member.

The soil water content was measured by the oven drying method, the soil bulk density was measured by the cutting ring method, the pH of soil was measured with a PHS-SD pH meter (Beijing Tongde Venture Technology Co., Ltd., Beijing, China) and the soil salinity was measured by the electrical conductivity method.
2.2.3. Data Processing

The one-way ANOVA method and the least significant difference method (LSD) were used to test for the significance of reed NSC and its components in different habitats based on two dimensions of plant and component in SPSS 22.0. The data used were the average of the NSC and its component concentration in May, July and September. All data are expressed as the mean ± SE. The correlations between the reed NSC and soil environmental factors were characterized by relative importance analysis, which was implemented by the Relaimpo package in R. The calculation formula for the contribution of different explanatory variables to the variance of the explained variables is as follows:

$$R^2(\gamma) = \frac{\sum_{j=1}^{j} b_j \text{Cov}(x_j, \gamma)}{\text{Var}(\gamma)} = 1 - \frac{\text{Cov}(e, \gamma)}{\text{Var}(\gamma)}$$

In the formula, $x_j$ represents soil environmental factor (explanatory variable), $\gamma$ represents reed NSC and $j$ represents sample number. All drawings were performed using Origin 8.0 software (Origin Lab Inc., Northampton, MA, USA).

Relative importance analysis can be used in the study of the relationship between organisms and the environment. This method can determine the degree of contribution of different explanatory variables to the determination coefficient $R^2$ in linear regression [33]. In our manuscript, relative importance analysis could quantitatively reflect the relationship between NSC and its components of reed and soil environmental factors. Therefore, the relative importance analysis method was used to analyze the response of the NSC to reed and soil environmental factors (soil bulk density, soil water, soil salinity and soil pH).

3. Results

3.1. Characteristics of the Soil Environmental Factors in Different Habitats

Soil water content showed a gradual decrease trend from wetland to desert habitats, as shown in Figure 2, which specifically reflected the wet (20.34 ± 0.56%) > salt marsh (13.20 ± 0.77%) > desert (4.11 ± 0.23%). Soil salinity, soil bulk density and soil pH showed a gradual increase trend from wetland to desert habitats, showing that the specific performance was desert habitat (salt 1.76 ± 0.10%, bulk density 1.34 ± 0.02 g/cm$^3$ and pH 8.10 ± 0.20) > salt marsh habitat (salt 1.63 ± 0.11%, bulk density 1.21 ± 0.06 g/cm$^3$ and pH 8.29 ± 0.06) > wet habitat (salinity 1.38 ± 0.10%, bulk density 1.20 ± 0.07 g/cm$^3$ and pH 8.46 ± 0.09).
3.2. Spatial Differences of Reed NSC and Its Components

In three habitats, the NSC and starch contents of reeds showed the same regularity from wetland to desert habitats, as shown in Figure 3. The concentrations of NSC and starch gradually decreased, and the specific manifestations were wet habitats (NSC 18.25 ± 0.30% and starch 12.32 ± 0.22%) > salt marsh habitat (NSC 16.83 ± 0.28% and starch 10.29 ± 0.39%) > desert habitat (NSC 15.58 ± 0.21% and starch 8.50 ± 0.36%). The soluble sugar content showed a gradually increasing trend, showing 5.94 ± 0.62% in the wet habitat, 6.54 ± 0.25% in the salt marsh habitat and 7.08 ± 0.45% in the desert habitat.

Figure 3. Comparison of NSC and their component (soluble sugar and starch) contents in *Phragmites communis* from different habitats (Error bars represent standard deviation; different lowercase letters indicate significance among different habitats at *p* < 0.05 level).

NSC contents of the leaf, stem and root modules for reeds showed the continuous decreasing trends from the wet to desert habitats, as shown in Table 1. Meanwhile, the results also showed that reeds tend to invest more NSC in underground parts with the increase in environmental stress. The soluble sugar contents of reed leaf and root modules showed gradually decreasing trends, and those of the reed stem and rhizome modules showed gradually increasing trends with the increase in environmental stress, as shown in Table 2. In addition, the starch contents of the leaf, stem and rhizome modules showed gradually decreasing trends, and the starch contents of root showed a gradually increasing trend with the increase in environmental stress, which suggests that reeds convert more NSC into starch to be stored in their roots in response to environmental stress increases, as shown in Table 3.

Table 1. Comparison of NSC content in clonal modules of *Phragmites communis* in different habitats.

| Habitat | Leafs | Stems | Rhizomes | Roots |
|---------|-------|-------|----------|-------|
| Wetland | 20.50 ± 0.47<sup>a</sup> | 19.11 ± 0.66<sup>a</sup> | 18.82 ± 0.70<sup>a</sup> | 14.59 ± 1.46<sup>a</sup> |
| Salt marsh | 15.79 ± 0.29<sup>b</sup> | 18.44 ± 0.53<sup>a</sup> | 19.84 ± 0.38<sup>a</sup> | 13.26 ± 0.50<sup>a</sup> |
| Desert | 12.79 ± 0.36<sup>c</sup> | 17.78 ± 0.48<sup>a</sup> | 19.31 ± 0.45<sup>a</sup> | 12.44 ± 0.95<sup>a</sup> |

Note: Different lowercase letters indicate significant differences between environmental gradients (*p* < 0.05).

Table 2. Comparison of soluble sugar content in clonal modules of *Phragmites communis* in different habitats.

| Habitat | Leafs | Stems | Rhizomes | Roots |
|---------|-------|-------|----------|-------|
| Wetland | 8.22 ± 0.22<sup>a</sup> | 5.04 ± 0.19<sup>b</sup> | 4.34 ± 0.31<sup>c</sup> | 6.14 ± 0.40<sup>a</sup> |
| Salt marsh | 6.83 ± 0.63<sup>b</sup> | 6.48 ± 0.29<sup>b</sup> | 8.22 ± 0.25<sup>b</sup> | 4.64 ± 0.31<sup>b</sup> |
| Desert | 6.09 ± 0.17<sup>b</sup> | 8.45 ± 0.31<sup>a</sup> | 10.19 ± 0.31<sup>a</sup> | 3.62 ± 0.32<sup>c</sup> |

Note: Different lowercase letters indicate significant differences between environmental gradients (*p* < 0.05).
Table 3. Comparison of starch content in clonal modules of *Phragmites communis* in different habitats.

| Habitat     | Leafs    | Stems    | Rhizomes | Roots    |
|-------------|----------|----------|----------|----------|
| Wetland     | 12.28 ± 0.57 a | 14.07 ± 0.92 a | 14.48 ± 0.74 a | 8.44 ± 0.13 a |
| Salt marsh  | 8.96 ± 0.46 b | 11.96 ± 0.47 b | 11.62 ± 0.27 b | 8.62 ± 0.13 a |
| Desert      | 6.70 ± 0.63 c | 9.34 ± 0.36 c | 9.13 ± 0.32 c | 8.82 ± 0.86 a |

Note: Different lowercase letters indicate significant differences between environmental gradients (*p* < 0.05).

3.3. Spatial Differences in the Ratio of Soluble Sugar and Starch in Reeds

Figure 4 showed that the ratio of soluble sugar and starch for the entire reed plant increased significantly (*p* < 0.05) from wetland to desert habitats, which was specifically manifested in desert (0.83) > salt marsh (0.63) > wet (0.48). In addition, soluble sugar/starch for the leaf, stem and rhizome modules were all increasing trends, but the ratio of soluble sugar and starch for root module was a gradually downward trend along the environmental gradient.

![Figure 4. Comparison of soluble sugar and starch ratios of *Phragmites communis* in different habitats](image)

Histograms represent the soluble sugar to starch ratio of the whole plant, and the alphabets indicate significance among different habitats at *p* < 0.05 level. Error bars represent standard deviation.

3.4. Relative Importance of Soil Environmental Factors to Reed NSC and Its Components in Different Habitats

In the wet habitat, soil bulk density and water had the greatest influence on the reed NSC, starch, soluble sugar and soluble sugar/starch, showing that the relative importance of soil bulk density was 48%, 49%, 53% and 53% and that relative importance of soil water was 34%, 34%, 33% and 33%, respectively, as shown in Figure 5. However, soil pH and salt had little effect on the NSC, starch, soluble sugar and soluble sugar/starch of reeds. In the salt marsh habitat, the relative importance of the reed NSC, starch, soluble sugar, and the ratio of soluble sugar to starch was sorted soil salt > water > pH > bulk density. Among them, the relative importance of soil salt to NSC, starch, soluble sugar and soluble sugar/starch was 36%, and pH and bulk density was 31%, 25%, and 8%, while the importance of bulk density was only 29%, 23%, and 10%, respectively. In desert habitats, soil water was the main limiting factor to reed NSC, starch, soluble sugar and soluble sugar/starch, supporting evidence that the relative importance was 65%, 62%, 62% and 65%. Soil salt was the second most important limiting factor to reed NSC, starch, soluble sugar and soluble sugar/starch, showing that the relative importance was 65%, 62%, 62% and 65%, respectively. However, soil pH and bulk density had little effect on NSC, starch, soluble sugar and soluble sugar/starch of reeds.
4. Discussion

4.1. Distribution Trade-Offs of NSC and Components in Phragmites australis in Different Habitats

The variation of NSC content in plants can not only reflect the physiological activity, but also reflect the ecological response to environmental changes. Our studies found that the NSC of reeds were significantly different in different habitats (p < 0.05), and the NSC contents in reeds showed a downward trend, as reeds tend to invest more NSC in underground components to achieve survival and growth, as shown in Figure 3 and Table 1. These research results exactly concurred with reeds and Spartina alterniflora in the Chongming Dongtan Wetland in Shanghai, China, Periploca sepium in the Loess Hilly Region and Vaccinium myrtillus in Friuli Venezia Giulia, Italy, which showed that the plants could balance consumption and benefit by controlling NSC investment to maximize the efficiency of resource acquisition and utilization [34–36]. This shows that, as the habitat changes, the carbon assimilation rate of reed was gradually lower than the carbon consumption rate, supporting the evidence that reeds reduced the NSC content of leaves through the NSC redistribution process and allocate limited NSC to roots, as shown in Figure 3 and Table 1. The purpose of the transformation of NSC content between the clone modules to maintain the resources of these non-photosynthetic organs, is to increase root vitality and promote root growth into deeper soil to obtain more nutrients to adapt to the harsh external environmental conditions. The sexual reproduction of reeds was greatly restricted due to environmental stress and clonal propagation that depended on the rhizomes selected. At the same time, in order to escape plaques with poor resource levels and transfer to better-quality plaques, more NSC were invested on the rhizome modules and the best life history countermeasures were formed by the trade-off between growth and reproduction [37].

Among the components of NSC, soluble sugar plays an important role in plant osmotic regulation and signal transduction and, while starch is an important energy storage substance in plants as an important role against adversity [38,39], soluble sugar can be converted to starch under certain conditions. Some studies had found that the soluble sugar content and the ratio of soluble sugar to starch of Jatropha curcas and Mediterranean beech increased under environmental stress [40,41]. Meanwhile, our study results also indicated that reeds could perform adaptive countermeasures to save energy and maintain normal physiological metabolism in adverse environments through the break-down of starch to increase soluble sugar in order to maintain the cell’s vitality and water balance to adjust osmotic potential and ensure respiration. There was a similar result on the dynamic changes of the content of NSC and its components in Robinia pseudoacacia under stressful environments [42]. This showed that the survival of reeds under adverse conditions not only depended on the total NSC but also a sufficiently high ratio of soluble sugar to starch. Therefore, the mutual conversion mechanism of soluble sugar and starch played an important role in maintaining the sustainability of clonal plants.
in inland river wetlands against environmental stress. During the transition from wet habitats to desert habitats, the ratio of soluble sugar to starch content of reed leaves, stems and rhizome components increased, and soluble sugars were transferred from leaves and root components to stems and rhizome components. The stems and rhizome modules reduced starch content, as shown in Tables 1–3 and Figure 3. The stem had the ability to regulate the osmotic potential of soluble sugar to create a transport channel between leaves and roots. The role of rhizome as an important vegetative reproductive organ is closely related to clonal propagation. Meanwhile, studies have shown that if the plant’s storage material is mainly distributed in the roots, this indicates that the plant has strong anti-interference abilities through synthesized defensive compounds to buffer environmental stress [43,44]. The ratio of soluble sugar to starch of reed leaves, stems, and rhizome gradually increased from wetland to desert habitat also confirmed these results, as shown in Figure 4. The different distribution mechanisms of soluble sugar and starch among the modules of clonal plants are an adaptive response to environmental conditions, which means that the more difficult and the harsher the habitat conditions for plant growth, the more obvious and active the plant protection strategy.

4.2. Distribution Driving Forces of NSC and Components for Phragmites australis in Different Habitats

The soil environment, as the main nutrient source for vegetation in the ecosystem, plays an important role in plant growth and development, community structure and ecosystem stability [45]. Especially, soil water, bulk density, pH and salinity are the main driving forces affecting clonal plants in inland river wetlands. The relative importance analysis showed that the main driving force affecting reed NSC changed from soil bulk density to soil salinity with habitat changes from wetland to salt marsh, while soil water became a direct driving force in reed NSC in desert habitats, as shown in Figure 5.

In wet habitats, the rank manifest of the relative importance to the spatial change of reed NSC was the soil bulk density > water > salinity > pH, as shown in Figure 5. Soil bulk density directly affected soil porosity aeration and root penetration, and indirectly changed the number and activity of soil microorganisms [46,47]. There was higher soil water and lower soil bulk density in the wetland habitat, which led to the lack of available oxygen in the reed root system and this limited the roots’ abilities to absorb the nutrients and water [48,49]. Reeds adapt to the environment by changing the NSC allocation strategy through the conversion mechanism of sugar and starch. Therefore, reed maintained osmotic pressure by mobilizing soluble sugar to achieve survival and growth.

In the salt marsh habitat, salinity was the most important soil environmental factor directly driving the reed NSC and its components, as shown in Figure 5. Salt stress can induce changes in certain structures and functions in plants, which, in turn, affects the photosynthetic physiological characteristics of plants, breaks the ionic balance in plants, disrupts protein synthesis and inhibits plant growth and reproduction [50]. Non-structural carbohydrates participate in the osmotic regulation of plant cells under stressful conditions. Therefore, plants would accumulate more soluble sugar to increase the osmotic potential of cells in order to improve the water-use efficiency and increase the concentration of cytosol under the condition of salt stress. As the salt concentration increases, plants could achieve ionic balance with the external environment through the efflux and absorption of ions. Plants expelled Na⁺ out of their cells to reduce salt stress. The process of Na⁺ removal required the consumption of more non-structural carbohydrates for energy supply, which led to a reduction in plant NSC content. The change of reed NSC and its components in the salt marsh habitat were the result of environmental stress driving the adaptive evolution of plants, and also reflecting the plant’s ability to adapt to adversity [51].

In the desert habitat, water was the main driving force for the spatial change of NSC and its components in reeds, as shown in Figure 4. Desert plants require significantly more water than plants in other habitats with relatively scarce water resources. Water, as a basic factor limiting plant growth, determines reed survival and growth by affecting the carbon allocation and carbon storage processes of different organs [52]. In desert habitats, the photosynthesis of reeds was significantly inhibited due
to more stomata, and the respiration of reeds was significantly promoted due to the consumption of more NSC to maintain life vitality with the drought stress intensified [53]. The results have confirmed that Bothriochloa ischaemum in the Loess Hilly-Gully region and Caragana microphylla in the southeast of Horqin Sandy Land consumed NSC in response to water pressure [54,55]. At the same time, the plants could adjust the ratio of soluble sugar to starch according to soil water conditions to reduce water potential and maintain cell swelling pressure to achieve the purpose of resisting drought [56,57].

Clonal plants are most susceptible to changes in climate, soil nutrients, surface and ground water in inland river wetlands. The results of the response characteristics of clonal plants to the heterogeneous environments in inland river wetlands could further provide theoretical support for clonal plant ecology. The ecological adaptation strategy of reeds in adversity, based on the trade-offs of NSC also could further provide technical references for the protection and restoration of fragile and sensitive wetland ecosystems in extremely arid regions.

5. Conclusions

Habitat variation analysis of non-structural carbohydrates for Phragmites australis in inland river wetlands showed that the contents of NSC and starch significantly decreased, while the soluble sugar and soluble sugar/starch significantly increased from wetland to desert habitats. NSC tended to invest in underground modules with the increase in environmental stress, confirming that reeds had different adaptation strategies for different environments through changes in the accumulation and distribution of NSC in different clonal modules. These conclusions could provide references for the growth strategy and resource balance of clonal plants in inland river wetlands. At the same time, the level of available resources (soil water, pH, salinity and bulk density) between patches in inland wetland habitats was the main driving force of the allocation and trade-offs of NSC for reeds. Among them, soil bulk density was the most limiting factor of reed NSC in wet habitats, and soil salinity and water were the most important limiting factors for reed NSC in salt marsh habitats and desert habitats, respectively. These conclusions prove that soil environmental factors could drive clonal plants in different habitats by constructing appropriate resource allocation strategies for effective resource acquisition and utilization. These study results could also further reveal the competition mechanism, enrich the competition theory, and provide a theoretical basis for the formulation and application of degraded vegetation restoration in the inland river wetlands of extremely arid regions. In the arid region of northwest China, the investment of NSC in aboveground parts of reeds in salt marsh and desert habitats will increase with the climate changes from warm and dry to warm and wet. Therefore, different dominant management methods should be adopted for ecosystems and clonal plants under the condition changes of the climate warming, humidity and community succession.

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