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Original Research

Spatial Expansion Strategy of the Clonal Modules for *Phragmites australis* and Response to Environmental Factors in an Inland River Wetland

Liang Jiao*, Xuerui Liu, Shengjie Wang, Xiaogang Dong, Fang Li, Cunlin Xin**

College of Geography and Environmental Science, Northwest Normal University, Lanzhou, China

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Abstract

The different spatial expansion strategies of clonal plants are the result of their adaptations to extreme heterogeneous environments. In this paper, the spatial expansion strategy and the adaptive responses of *Phragmites australis* to environmental factors were analyzed by comparing clonal modules along degradation gradients (from wetland ecosystem to desert ecosystem). The results show that:

1) With the deterioration of the environmental conditions, the clonal modules (rhizome internode length, spacer length, primary rhizome length and branch angle) showed a trend of first increasing and then decreasing, but the ramet number showed a trend of decreasing first and then increasing, which turned the survival strategy from "Phalanx" (with cluster distribution and showing the invasion attitude) to "Guerilla" (with discrete distribution and showing the evasive attitude) and then back to Phalanx in the process of space expansion.

2) The clonal modules were significantly different in the heterogeneous environment, and were shown the co-development and trade-off relationships ($P<0.05$).

3) Soil water content, bulk density, pH value and salinity were the main driving forces – especially soil water content, bulk density and pH values in the middle and deep layers and the soil salinity of each layer were the most important environmental factors.

The space expansion strategies of *Phragmites australis* in an extreme environment complemented the theories of traditional cloning plant ecology. And there was important guiding significance for the management and restoration of the degradation wetlands in arid and semi-arid regions to clarified environmental driving forces of clonal plants in inland river wetlands.

Keywords: *phragmites australis*, clonal modules, spatial expansion strategy, environmental stress, inland river wetland

*e-mail: jianliang@nwnu.edu.cn
**e-mail: xincunling@163.com

Introduction

Clonal plants can produce new genetically identical individuals with their "maternal" individuals through vegetative propagation under natural habitat conditions [1-3]. Cloned plants have strong environmental adaptability and widely exist in natural ecosystems due to the characteristics of life infinity, spatial mobility, reproductive diversity, and resource sharing, etc. In particular, they occupy an advantageous position and play a pivotal ecological role in grassland, tundra, wetlands, waters and other ecological systems [4-8]. Studies on the morphological, physiological and ecological characteristics of clonal growth have been systematically compared [9-12]. In particular, the research has been more focused on the integration and plasticity of clonal plants [13-14], the trade-off between clonal growth and sexual reproduction [15-16], the sharing mechanism of resources [17-18], and characteristics of life history and discussion of cloning diversity [19-21]. However, analysis of the spatial expansion strategy and driving force from the perspective of clonal modules were relatively scarce in the extremely arid inland river wetlands with fragile and sensitive ecological systems.

Spatial expansion is a strategy of resource allocation trade-offs in clonal plants [22]. Traditional studies suggest that "Phalanx" and "Guerilla" are two clonal growth architectures that have different resource allocation approaches to a heterogeneous environment [23-24]. Phalanx could enhance the competitiveness of clonal plants through cluster distribution of modules, showing the invasion attitude with short spacers, small branch angles and more ramet number. But Guerrilla could increase foraging opportunities through cloning their roots, showing the evasive attitude with long spacers, large branch angles and few ramets number [25]. For example, the spatial distribution pattern of Phalanx is shown in the cloned plants of *Amphibromus scabrivalvis* in the southeastern United States, *Elymus repens* in southeastern France, and *Stipagrostis pennata* in northwestern China [26-28]. The spatial growth strategies of Guerrilla are shown in the cloned plants of *Leymus chinensis* in northeastern China, and *Leymus secalinus* and *Psammochloa villosa* in northwestern China [29-31]. Meanwhile, there was the complexity of spatial expansion in response to the environmental gradient due to the heterogeneity of the environment and the variability survival strategies of plants with more in-depth study the clonal architecture that has gradually changed from Phalanx to Guerrilla [24]. For example, from woodland habitats to grassland and sandy habitats, the cloned plants adopted the intense foraging strategy of Phalanx to Guerrilla with change of spacer length, internode length and branching angle [32]. Research of the clonal plant growth in heterogeneous environments could characterize the strategies of the selective survival pattern [8].

Selecting different patterns of space expansion were an important adaptive strategy for clonal plants to effectively utilize heterogeneous resources with improved survival rates and growth competitiveness, and it is also the result of the interaction between the biological characteristics of clonal plant population and environmental factors [33-35]. Environmental factors (water, salt, pH, nutritional conditions, and so on) are essential for the growth and spatial expansion of clonal plants in habitats with different resource levels [36-39]. Water use efficiency affects the morphological construction of plant leaves. When a habitat has insufficient soil water, *Phragmites australis* reduces transpiration by reducing its leaf number, leaf length and leaf width, and it prevents the loss of water in the body [40-41]. Salinity, as an important constraint factor for the growth of wetland vegetation, has restrained the growth of *Phragmites australis* in the Yellow River Delta [42-43]. Alkaline soil limited plant growth, showing sparser density and lower height for *Leymus chinensis* as a rhizome clone [44]. Environmental heterogeneity greatly intensifies the survival pressure on plants. However, different plants might have formed the optimal spatial expansion strategy in order to adapt to environmental changes and resist the selection pressure brought by environmental heterogeneity in the long course of evolutionary life history [2, 45]. So the studies on the behavior selection of habitats in heterogeneous environments are important to reveal the ecological adaptation strategies of clonal plants [8].

Most studied areas of clonal plants have focused on the coastal wetlands [46], deltaic wetlands [47], and dry area wetlands [48]. However, there were rare studies on the inland river wetlands in the arid and semi-arid regions with fragility and sensitivity of the ecological environment. Specifically, the Xihu wetland of Dunhuang, as a key belt of the earth's ecological system and typical representative of the inland river wetlands, is related to the ecological security of the entire Dunhuang oasis and plays an important role in protecting the ecological balance of western China [49]. Meanwhile, the stability of the wetland ecosystem in Xihu worsened, supporting the evidence that the area had decreased by approximately 40% in past decades due to intensive human activities [50]. *Phragmites australis* of a typical rhizome clone is the main build-group species and often forms a single optimal community of the Xihu wetland in Dunhuang [51-52]. Its widespread and highly social economic ecological value makes the domestic and foreign scholars develop a great amount of research [53-55]. However, little research has been done on the ecological adaptation mechanism for *Phragmites australis* in an inland river wetland. Therefore, we analyzed the spatial expansion strategy and environmental driving factors using the clonal plant *Phragmites australis* under different degraded gradients in the Xihu wetland in Dunhuang. The purposes of this study were 1) to compare the module differences under different degradation environment gradients and explore

the spatial expansion strategy in a heterogeneous environment and 2) to analyze the co-evolutionary relationships among the various clonal modules and clarify the main driving forces for spatial expansion.

Materials and Methods

Study Area and Sample Plots

The study area is located in the Xihu National Nature Reserve in Gansu, China with a total area of 6.6×10^5 hm² (Fig. 1), which ranges from 39º45′ N to 40º36′ N in latitude, from 92º45′ E to 93º50′ E in longitude, and from 820 to 2359 m in altitude, The study area is a typical continental-arid climate, showing a 9.9ºC annual temperature, 39.00 mm average precipitation, 2505.1 mm average evaporation, >16 drying degree, and 2.2 m/s annual average wind speed. Climate change has characteristics of it being rainy and hot during the same period, and precipitation is mainly concentrated during April to September [49-50]. The terrain is high in the south and low in the north, and the middle is the impact plain, which is surrounded by desert and the Gobi [56]. Due to the distribution of large perennial or seasonal wetlands in the area, natural soil dominated by swamp soil was formed, and swampy vegetation communities were developed. The dominant plants are *Phragmites australis*, *Alhagi sparsifolia*, *Glycyrrhiza uralensis*, *Halostach-ys caspica*, *Apocynum venetum*, and so o and so on [49].

Experimental Methods

In mid-July 2017, field surveys were conducted in the inland river wetlands in northwestern China by simultaneous investigation of plants and soil. Three parallel transects were set from the inside to the outside along the direction from wetland to desert with a 4,000m interval of each sample line. Five sampling gradients were set at the same distance of 2,000 m on each sampling line based on plant community characteristics: no degradation (density 90.36% and coverage 90.73%), mild degradation (density 70.78% and coverage 72.89%), moderate degradation (density 51.00% and coverage 53.38%), severe degradation (density 29.86% and coverage 30.29%), and extreme degradation (density12.83% and coverage 13.33%) (Table 1). Three samples were randomly set as 5 m × 5 m in each degradation gradient. A total of 45 survey squares were collected.

Based on an understanding of the characteristics and diversity of the sample community, it was decided that the experiment should be carried out with the clone ramets of *Phragmites australis* as the sampling unit. Under the premise of no disturbance, three *Phragmites australis* were randomly selected on each degradation gradient. All parts of the selected plants aboveground and underground were harvested according to the clonal modules collection method of full digging using "tracking and digging" based on the direction of the rhizomes in every plot [25]. The plant materials were divided into panicles, leaves, stems, horizontal rhizomes and buds with scissors, and the small environmental factors such as altitude, latitude and longitude, geography and geomorphology of each sampling site was recorded. All samples were uniformly numbered and immediately kept in a freezer (0-4ºC).

The soil sampling point corresponded to the plant sampling point. Within the five degraded gradient samples, the soil samples in 0-100 cm were taken by the layered method of every 10 cm. The surface layer soil, middle layer soil and deep layer soil were mixed soils at 0-30 cm, 30-60 cm and 60-100 cm, respectively. After debris removal, air drying, grinding and screening, soil water content was measured by the

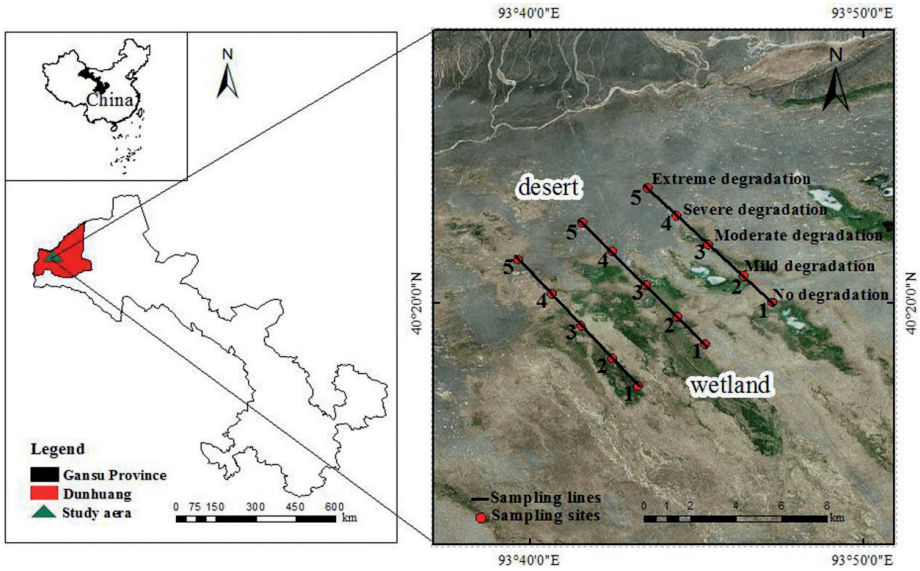

Fig. 1. Study area and sampling point distribution.

drying weighing method, the soil bulk density was measured by ring shear testing (50 cm^3), salt content was determined by the electrical conductivity method [57], and the pH value of soil was determined by a PHS-SD pH instrument.

Data Processing

The data conformed to the normal distribution ($P<0.05$) and can be used directly in the data measured by correlation analysis using Kolmogorov-Smirnov in SPSS 19.0 software. The variances of clonal modules in different degradation gradients were analyzed by ANOVA, and significance was tested by least-significant difference (LSD) using SPSS 19.0 software, and the co-evolution of the clonal modules through the method of space instead of time were analyzed by Pearson correlation method. Pearson correlation coefficient (R) was calculated as shown in formula (1):

$$R = \frac{\sum_{i=0}^{n}\left(x_i-\bar{x}\right)\left(y_i-\bar{y}\right)}{\sqrt{\sum_{i=0}^{n}\left(x_i-\bar{x}\right)^2\left(y_i-\bar{y}\right)^2}} \quad (1)$$

…where n is the sample number, and x_i and y_i are the variable values of two variables respectively.

Redundancy analysis (RDA) is widely used in the study of the relationship between the biological and environmental factors with a multi-variable direct gradient analysis method and the expansion of the multiple linear regressions. Meanwhile, RDA can get the numerical matrix and the eigenvalue decomposition for the characterization of clonal modules index and soil environmental factors reflected in the relationship between axes with the linear relationship between two variables set model. Therefore, the relationship between the clonal modules and major environmental factors were analyzed by RDA using CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA) [58-59]. The charts were produced by Microsoft Excel 2013 and Origin10.4.

Results and Discussion

Characteristic Analysis of Community and Soil Environmental Factors

This study clearly demonstrates that the decreasing trends of density, coverage, frequency and species composition of *Phragmites australis* with the deepening of degradations (Table 1). And the performance was to form no degradation to extreme degradation (density: 90.36% > 70.78% > 51.00% > 29.86% > 12.83%, Coverage: 90.73% > 72.89% > 53.38% > 30.29% > 13.33%, Frequency: 88.64% > 75.00% > 58.13% > 35.00% > 17.50%). However, the average depth of rhizomes had an increasing trend with the deepening of degradations, showing extreme degeneration (126.87 cm) > severe degeneration (112.60 cm) > moderate degeneration (90.30 cm) > mild degeneration (70.11 cm) > no degradation (56.06 cm).

The characteristics of the soil environmental factors under five degradation gradients from no degradation to extreme degradation were analyzed in the Xihu Wetland in Dunhuang (Table 2). The average soil water content under the five degraded gradient soils (0-100 cm; no degradation, mild degradation, moderate degradation, severe degradation and extreme degradation) gradually decreased by 21.16%, 30.19%, 26.68%, 14.58%, and 7.59%, respectively. Soil bulk density and soil salt content had an increasing trend, showing extreme degradation (1.23 g/cm^3) > severe degradation (1.18 g/cm^3) > no degradation (1.14 g/cm^3) > moderate degradation (1.11 g/cm^3) > mild degradation (0.89 g/cm^3) and showing extreme degeneration (0.79%) > severe degeneration (0.77%) > moderate degeneration (0.60%)

Table 1. Differences in community characteristics and average depths of rhizomes for *Phragmites australis* under different degradation gradients.

Degradation gradients	Density (%)	Coverage (%)	Frequency (%)	Dominant species	Species composition	Rhizomes average depth (cm)
No degradation	90.36±1.24^a	90.73±1.19^a	88.64±1.92^a	*Phragmites australis*	*Halogeton arachnoideus. Alhagi sparsifolia. Stipa capillata. Phragmites australis*	56.06±2.339^e
Mild degeneration	70.78±1.45^b	72.89±1.60^b	75.00±1.44^b	*Phragmites australis*	*Glycyrrhiza uralensis. Alhagi sparsifolia. Phragmites australis*	70.11±1.773^d
Moderate degradation	51.00±1.85^c	53.38±2.04^c	58.13±1.88^c	*Phragmites australis*	*Apocynum venetum. Alhagi sparsifolia. Phragmites australis*	90.30±2.141^c
Severe degeneration	29.86±2.39^d	30.29±2.46^d	35.00±2.43^d	*Phragmites australis*	*Apocynum venetum. Alhagi sparsifolia. Phragmites australis*	112.60±3.179^b
Extreme degeneration	12.83±1.30^e	13.33±1.17^e	17.50±1.12^e	*Phragmites australis*	*Phragmites australis*	126.87±4.692^a

Different lowercase letters from peers indicate significant differences between environmental gradients ($P<0.05$)

Table 2. Average characteristic values (0-100 cm) of soil environmental factors under different degradation gradients (Mean±SE).

(0-100 cm) Average	No degradation	Mild degeneration	Moderate degradation	Severe degeneration	Extreme degeneration
Soil water content (%)	21.16±1.00^{b}	30.19±1.36^{a}	26.68±0.71^{a}	14.58±1.12^{c}	7.59±1.91^{d}
Soil bulk density(g/cm^3)	1.14±0.04^{a}	0.89±0.09^{bc}	1.11±0.05^{ac}	1.18±0.03^{a}	1.23±0.06^{a}
Soil pH value	8.62±0.04^{a}	8.34±0.09^{bc}	7.96±0.04^{c}	8.25±0.09^{bc}	8.74±0.07^{a}
Soil salinity (%)	0.14±0.08^{b}	0.59±0.27^{ab}	0.60±0.12^{ab}	0.77±0.20^{a}	0.79±0.32^{a}

Different lowercase letters from peers indicate significant differences between environmental gradients (P<0.05)

> mild degeneration (0.59%) > no degradation (0.14%). However, the pH value of the soil showed a decreasing trend first and then an increasing trend, at 8.62, 8.34, 7.96, 8.25 and 8.74 for no degradation, mild degradation, moderate degradation, severe degradation and extreme degradation, respectively, and these values demonstrated weak alkaline content. However, there were some exceptions in our study regions, suggesting that the soil-water content at the no-degradation level was lower than that at the mild degradation gradient, but the soil bulk density was higher than the mild degradation. The reason for these results is that the soil water content shows the characteristics of seasonal change due to being mainly influenced by groundwater. The soil-water content of the samples showed a decreasing trend at the end of summer and early autumn and downward with groundwater depth under no degradation gradients.

Characteristic Differences of Clonal Modules

Clonal plants tend to have plasticity corresponding to the different environment and resource conditions. With an increase in environmental stress, the clonal modules (plant height, stem diameter, bud number, rhizome internode length, spacer length, primary rhizome length and branch angle) showed a trend of increasing first and then decreasing, and the ramet number showed a trend of decreasing first and then increasing (Fig. 2). From a statistical perspective, the characteristics of the clonal modules were significantly different under moderate degradation than other degradation gradients, such as rhizome internode length, spacer length, primary rhizome length, branch angle and ramet number (P<0.05).

Correlation of Clonal Modules

There were also close relationships between spatial expansion clonal modules (Table 2). Plant height was highly positively correlated with stem diameter (R = 0.662, P<0.01), while the ramets number was significantly positively correlated with the spacer length (R = 0.362, P<0.01). Bud number was significantly positively correlated with rhizome internodes length,

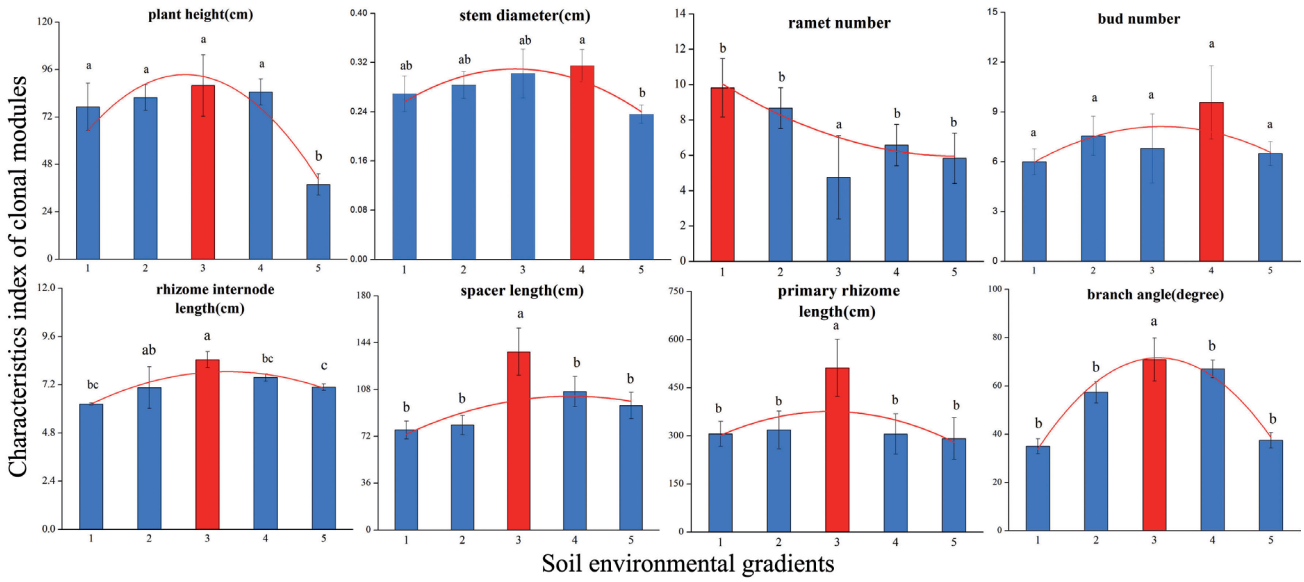

Fig. 2. Characteristics index of clonal modules under different degraded gradients (mean±SE); different lowercase letters indicate significant differences between different degradation gradients (P<0.05): 1) no degradation, 2) mild degeneration, 3) moderate degradation, 4) severe degeneration, and 5) extreme degeneration.

Table 3. The correlation between clonal modules.

	Plant height	Stem diameter	Ramet number	Bud number	Rhizome internode length	Spacer length	Primary rhizome length	Branch angle
Plant height	1	0.662**	-0.171	-0.044	0.253	0.008	0.266	0.218
Stem diameter		1	-0.045	-0.007	0.173	-0.205	-0.068	0.052
Ramet number			1	0.244	0.065	0.362**	0.198	0.103
Bud number				1	0.555**	0.491**	0.293	0.346*
Rhizome internode length					1	0.421**	0.576**	0.559**
Spacer length						1	0.819**	0.478**
Primary rhizome length							1	0.680**
Branch angle								1

* Significant at the 95 % confidence level.
** Significant at the 99 % confidence level

spacer length, and branch angle (P<0.05). The rhizome internode length, spacer length, primary rhizome length and branch angle were significantly positively correlated (P<0.01). The correlation results showed a good correlation for the growth indexes of the plant height and stem diameter, while the other clonal space expansion modules had better correlation.

Response of Clonal Modules to Environmental Factors

Soil water content, bulk density, pH and salinity content are extremely important for the clonal traits of *Phragmites australis*. Fig. 3 accumulatively explained 98.4% of the species-environmental relationships. Soil water content was significantly positively correlated with a (plant height), b (stem diameter), c (ramet number), e (rhizome internode length), f (spacer length), g (primary rhizome length), and h (branch angle) (P<0.05). Soil bulk density and a (plant height), b (stem diameter), c (ramet number), e (rhizome internode length), f (spacer length), g (primary rhizome length), and h (branch angle) have a significant negative correlation (P<0.05). Soil pH and a (plant height), b (stem diameter), e (rhizome internode length), f (spacer length), g (primary rhizome length), and h (branch angle) were extremely significantly negatively correlated (P<0.01). Soil salinity and a (plant height), b (stem diameter), and d (bud number) were significantly negatively correlated (P<0.01), and e (rhizome internode length), f (spacer length), g (primary rhizome length), and h (branch angle) were significantly positively correlated (P<0.01).

To further understand the relationship of plants and the environment, the correlation coefficients between clonal modules and environmental factors of soil layers were calculated by the redundant analysis (Fig. 4a-d). Clonal modules of a (plant height), b (stem diameter), c (ramet number) and d (bud number) had significant positive correlations with middle layer soil content water (P<0.01), while e (rhizome internode length), f (spacer length), g (primary rhizome length) and h (branch angle) had significant positive correlations with deep layer soil water content (P<0.01) (Fig. 4a). Clonal modules of a (plant height), b (stem diameter) and c (ramet number) had negative correlations with each layer soil bulk density (P<0.05), while e (rhizome internode length), f (spacer length), g (primary rhizome length) and h (branch angle) had significant positive correlations with deep soil bulk density (P<0.05) (Fig. 4b). Clonal modules of a (plant height), b (stem diameter), d (bud number), e (rhizome internode length), f (spacer length), g (primary rhizome length) and h (branch angle) had significant negative correlations with each layer of soil pH values (P < 0.01) (Fig. 4c). Clonal modules of a (plant height) and b (stem diameter) had significant negative

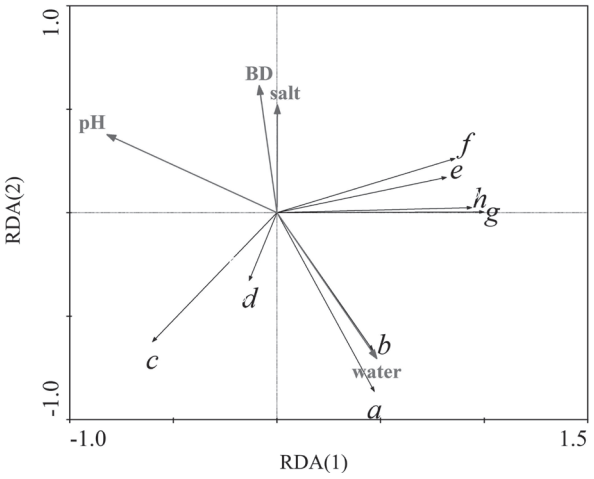

Fig. 3. Redundant analysis of clonal modules and soil environmental factors (0-100 cm). BD: bulk density; a: plant height; b: stem diameter; c: ramet number; d: bud number; e: rhizome internode length; f: spacer length; g: primary rhizome length; and h: branch angle.

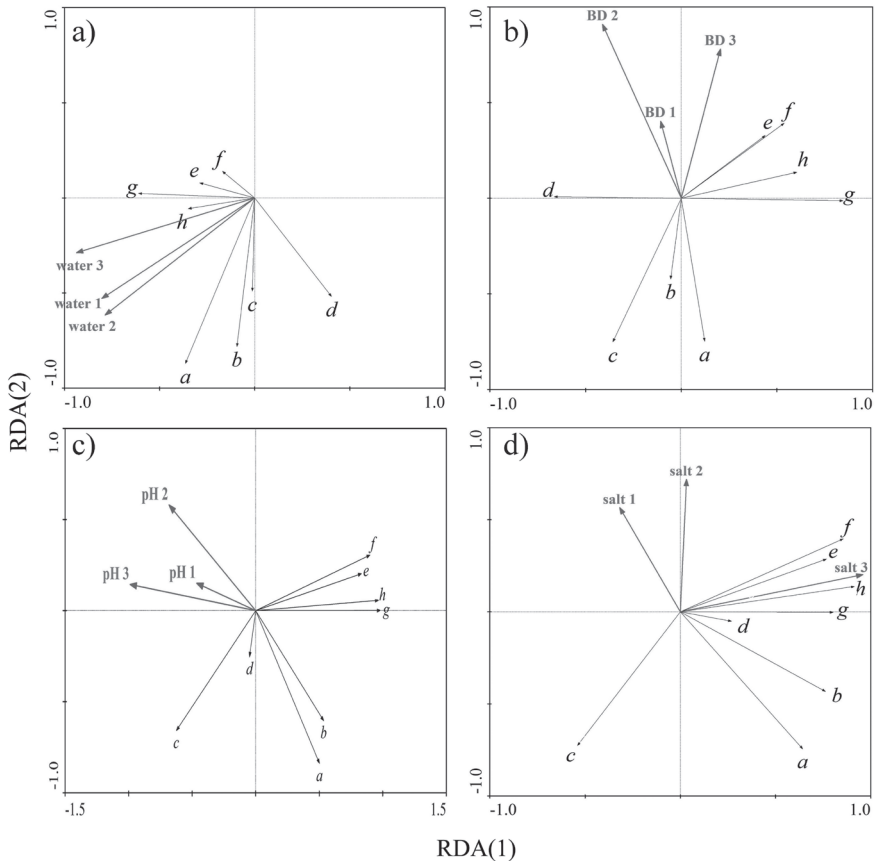

Fig. 4. Redundant analysis of clonal modules and soil water a), BD: bulk density b), pH c), and salt d) of soil layers (0-30 cm, 30-60 cm, and 60-100 cm). a: plant height; b: stem diameter; c: ramet number; d: bud number; e: rhizome internode length; f: spacer length; g: primary rhizome length; h: branch angle. a) Water 1: represents the soil surface layer water; Water 2: represents the soil middle layer water; Water 3: represents soil deep layer water. b) BD 1: represents the soil surface layer bulk density; BD 2: represents the soil middle layer bulk density; BD 3: represents the soil deep layer bulk density. c) pH 1: represents the soil surface layer pH value; pH 2: represents the soil middle layer pH value; pH 3: represents the soil deep layer pH value. d) Salt 1: represents the soil surface layer salt; Salt 2: represents the soil middle layer salt; Salt 3: represents the soil deep layer salt.

correlations with surface and middle layer soil salinity ($P<0.05$), while e (rhizome internode length), f (spacer length), g (primary rhizome length) and h (branch angle) had highly significant positive correlations with deep-layer soil salinity ($P<0.01$) (Fig. 4d).

Discussion

Spatial Expansion Strategies of Clonal Modules for *Phragmites australis* under Different Degradation Environment Gradients

To effectively use habitat resources and better adapt to the environment in the process of natural selection, clonal plants tend to adopt a series of strategies for certain changes in phenotype and physiology to cope with environmental heterogeneity [60-61]. In particular, spatial expansion is the most direct manifestation of these strategies [22, 62-65]. But for many clonal plants that spread vegetatively from attached organs (rhizomes, roots, stem bases), the opportunity for populations to track environmental change through long-distance dispersal will be limited.

Our studies found that the main spatial expansion clonal modules of the rhizome internode length, spacer length, primary rhizome length, and branching angle for *Phragmites australis* gradually increased, and ramet number gradually decreased during the progression from no degeneration gradient to the moderate gradient (Fig. 2). This result indicated that the clonal architecture of *Phragmites australis* tended to "Phalanx" with the increasing ramet number of the shortened rhizome internode lengths and spacer lengths and the smaller branching angles in well-conditioned patches of inland river wetlands. Therefore, more ramets would be placed under the patches of good conditions to easily acquire resources of the entire plant. However, in the relatively poor resource conditions, the rhizome internode length and spacer length of *Phragmites australis* increased, the branch angle increased, the ramet number decreased, and the clone architecture tended to Guerrilla, which helped the plants escape from the poor plaques of the resources and transfer to the better plaques [66-67].

Traditional studies suggest that Phalanx and Guerilla are two different resource allocation strategies for plants dealing with heterogeneous environments [22-23]. For example, clonal plants of *Alhagi sparsifolia* changed from Phalanx to Guerrilla as the effectiveness of soil moisture changed from high to low in northwestern China [68]. Clonal plants of *Lysimachia congestiflora* tended to be Phalanx in its clonal architecture in the open forest habitat and Guerrilla in forest margins and forest habitat in southwestern China [69].

The above conclusion of spatial expansion clonal modules was consistent with the changes in the community characteristics along the degradation gradient, from no degradation to moderate degradation. However, our results on the relationship of spatial expansion and community characteristics also showed differences with the degradation gradient from moderate to extreme degradation (Table 1, Fig. 2). But this is not contradictory. We found that the results were not consistent with traditional studies, suggesting that the clonal architecture of *Phragmites australis* tended to Phalanx with the gradually reducing trends of rhizome internode length, spacer length, rhizome length and branching angle, and increasing trends of ramet number from the moderate degradation gradient to the extreme degradation gradient (Fig. 2). *Phragmites australis* maintained survival by reducing growth investment in the rhizome internode length, spacer length, branch angle and increasing investment in the depth of underground rhizomes for deep water and nutrient resources with stronger resource constraints and worse stress conditions in poorer patches. This result confirmed that the clonal plants could balance resources between acquisition and investment in the process of space expansion [39]. There are substantial potential costs for clonal plants to maintain the connection between plants, the integrated transfer of resources, the generation of new ramets and the supply of energy when clone plants occupy bigger spaces [70-71]. Meanwhile, the depth of the underground root system and rhizomes of *Phragmites australis* spread from the original plant by approximately 50 cm to 120 cm (Table 1). Hence, clonal plants in harsher environmental conditions of inland river wetlands displayed this ecological adaptation strategy in two ways, the continuous increase in modules in the vertical direction and the change in clonal architecture from Guerrilla to Phalanx in the horizontal space in order to obtain more resources and maintain community stability.

In addition, there are co-development relationships between the biological indicators of plants that are interdependent and mutually restrictive, which together determine the plant structure and function [72-74]. Our results confirmed this conclusion, showing significant correlations between clonal modules (Table 3). Meanwhile, the rhizome internode length, spacer length, primary rhizome length and branch angle under different degraded environmental gradients showed the collaborative development relationship with the same growth trend as the environmental changes, while ramet number showed the trade-off relationship with the opposite growth trend (Fig. 2). Therefore, the increasing integration effects among clone network of *Phragmites australis* with increasing heterogeneity. Other results for the clonal plants of *Leymus chinensis* and *Duchesnea indica* had similar conclusions with the same growth trends of the rhizome internode length, spacer length, and branch angle, and the reciprocal relationship between branch intensity and spacer length and ramet number [75-76]. These results showed that clonal plants could directly adjust their morphological plasticity and biomass distribution patterns in order to survive in environmental heterogeneity. Thus, the trade-off of resource allocation between survival modes was an adaptive strategy for clonal plants in various environments [77].

The conclusion of our study is different from that of traditional studies, showing more complex clone architectures for *Phragmites australis* from Phalanx to Guerrilla and then to Phalanx with the change of environmental gradient (from not degraded to extremely degraded) in the special environmental conditions of inland rivers, which suggests that cloned plants had more diverse and complex survival strategies than traditionally understood. This conclusion would enable us to further understand the formation and the environmental adaptation mechanism of the clonal plant community, and is also an important supplement to the ecological theory of clonal plants.

Spatial Expansion Driving Forces of Clonal Modules for *Phragmites australis*

Environmental factors such as soil water content, pH and salt content are the main limiting factors for the survival of clonal plants in inland river wetlands [42, 78-79]. Water is one of the important factors controlling plant growth and reproduction, and the allocation trade-off of water resources is the important mechanism in the process of plant ecological adaptation [80]. Soil water content played a positive role on *Phragmites australis* in the Xihu wetland of Dunhuang (Fig. 3). The soil water content in the middle layer had a significant positive correlation ($P<0.05$) with plant height, stem diameter, ramet number and bud number, and the water content in deep soil had a significant positive correlation ($P<0.05$) with the rhizome internode length, spacer length, primary rhizome length and branch angle (Fig. 4a). The surface soil water content of inland river wetlands is relatively lacking, so the roots of clonal plants are mainly distributed in deep soil layers for absorbing middle and deep layer soil water [77]. The study results on soil water response of the clonal modules for *Spartina alterniflora* and *Duchesnea indica* were consistent with those of our results [68, 75].

Alkaline soils have a significant negative impact on the growth and development of plants [79]. Our results also confirmed that the growth of clonal modules for

Phragmites australis became worse with increasing soil pH value in the middle and deep layer soil (Figs 3, 4c). High alkaline content in soil inhibits plant growth and reproduction through the disintegration of the fine structure of the chloroplasts in the plant, changes in composition and structure of the thylakoid membrane with the hard and dense soil, destruction of the structure of the pellet, reductions in soil porosity, etc. [44, 79, 81-82].

A large number of studies have confirmed that salt stress mainly limits plant growth and development by osmotic stress, disturbance of cell ion balance, and ion toxicity effects [83-88]. The salt content of soil in our study was a limiting effect on the growth index – especially the significant negative correlation between the surface salt and plant height and stem diameter for *Phragmites australis* ($P<0.05$). Moreover, our study also found that salinity promoted the growth of main clonal modules of spatial expansion, showing a significant positive correlation between the salinity in the middle and deep layer soil and the rhizome internode length, the spacer length, the primary rhizome length and the branch angle ($P<0.01$). The main reason for this result was that clonal plants tried to escape the salt stress environment as soon as possible by increasing investments in clonal modules.

Our results demonstrated the complexity of the driving force for the spatial expansion of cloned plants in inland river wetland, showing the synergism of variety soil environmental factors and different responses to soil layers. Meanwhile, there are widely distributed of inland river wetlands in central Asia, Africa and other fragile wetlands in arid and semi-arid regions of the world, which play an important role in ecological healthy development [50-52, 89]. Therefore, our research conclusion provides a valuable case for the restoration of degraded wetlands, suggesting that we should focus on the coordination of environmental factors on plant growth in the process of wetland protection and management.

Conclusions

An analysis of the spatial expansion and environmental driving force of clonal modules in inland river wetlands can clarify the ecological adaptation strategy of clonal plants for *Phragmites australis* under extreme drought conditions. First, the clonal plants growing in the heterogeneous habitats adapted to different environments and obtained the best resource supply through morphological changes and physiological integration. With the worsening of environmental degradation, the spatial expansion architecture of clonal plants for *Phragmites australis* transformed from Phalanx to Guerrilla and then to Phalanx in horizontal space, and increasing investments of modules in the vertical direction. Second, there were the co-development and trade-off evolution patterns of clonal modules, showing the same increasing and decreasing trends with the rhizome internode length, the spacer length, the primary rhizome length, the branch angle and an opposite trend between ramet number and other clonal modules. Finally, the available resource level (soil water content, bulk density, pH value and salinity content) could be identified as the main driving force for the spatial expansion of *Phragmites australis* clonal modules in inland river salt marsh wetlands. In particular, the water content, bulk density and pH value in the middle and deep layer of soil and the soil salinity content in each layer were more direct factors. Clone plants could effectively acquire resources and continue the population by appropriately adjusting clonal modules with community succession. Therefore, different management methods should be adopted based on the different spatial expansion strategies of clonal plants coping with the intensification of drought in inland river wetlands in the future.

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Conflict of Interest

The authors declare no conflict of interest.

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