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## Community Classification and Spatial Distribution Patterns of Salt Marsh Wetland Plants in Response to Soil Moisture and Salinity: Post-print

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### Abstract

Investigating the response of spatial distribution patterns of inland salt marsh wetland plant communities to soil water-salt conditions will enhance understanding of their environmental plasticity mechanisms. This study employs TWINSpan and CCA methods to examine the relationship between spatial distribution patterns of plant communities and major environmental factors in the Xiaosugan Lake inland salt marsh wetland. The results indicate that vegetation in Xiaosugan Lake can be classified into six community types: *Phragmites australis* + *Leymus secalinus*, *Leymus secalinus*, *Sophora alopecuroides* + *Thermopsis lanceolata*, *Saussurea salsa* + *Leymus secalinus*, *Triglochin palustre* + *Triglochin maritimum*, and *Kobresia capillifolia* + *Carex altaica*. Each plant community exhibits significant spatial differentiation by adapting to the migration patterns of soil water and salt within its respective area. Soil water content, soil Ca<sup>2+</sup>, Cl<sup>-</sup>, and groundwater depth exert the most significant influence on plant community distribution patterns. The distribution pattern of inland salt marsh wetland plant communities and their relationship with soil water-salt factors represent the result of long-term adaptation of wetland plants to special habitats, reflecting the strong tolerance and ecological adaptability of salt marsh wetland plants.

## Full Text

# Community Classification and Spatial Distribution Patterns of Salt Marsh Wetland Plants in Response to Soil Moisture and Salinity

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## Abstract

Investigating the response of spatial distribution patterns of inland salt marsh wetland plant communities to soil moisture and salinity contributes to a deeper understanding of the environmental plasticity mechanisms governing these communities. This study employs TWINSpan and CCA methods to examine the relationship between spatial distribution patterns and key environmental factors in the inland salt marsh wetland of Xiaosugan Lake. The results reveal six distinct plant community types: *Phragmites australis* + *Leymus secalinus*, *Leymus secalinus*, *Sophora alopecuroides* + *Thermopsis lanceolata*, *Saussurea salsa* + *Leymus secalinus*, *Triglochin palustre* + *Triglochin maritimum*, and *Kobresia capillifolia* + *Carex altaica*. Each community exhibits significant spatial differentiation by adapting to local soil water and salt migration patterns. Soil moisture content, soil  $\text{Ca}^{2+}$ ,  $\text{Cl}^{-}$ , and groundwater depth emerge as the most influential factors shaping plant community distribution. The observed distribution patterns and their relationships with soil moisture and salinity factors reflect long-term adaptation of wetland plants to specialized habitats, demonstrating strong tolerance and ecological adaptability in salt marsh vegetation.

**Keywords:** Xiaosugan Lake; salt marsh wetland; plant community; soil water and salt; Gansu

## Introduction

Wetlands are transitional ecosystems that develop at the interface between aquatic and terrestrial environments, characterized by unique eco-hydrological processes [1] and playing crucial roles in maintaining ecosystem functions and regional ecological security [2]. Inland salt marsh wetlands represent marsh ecosystems that are waterlogged or seasonally inundated under arid climates, with saline soils and halophytic vegetation. The spatial distribution patterns of wetland plant communities are intimately linked not only to the biological characteristics of plant populations but also to water-salt migration patterns and spatiotemporal variations in groundwater levels [3-4]. As a vital component of salt marsh ecosystems, vegetation structure and functional traits reflect resource niches and their interrelationships at both intra- and interspecific levels.

Quantitative relationships between vegetation communities and environmental factors collectively demonstrate the ecological adaptability and environmental plasticity mechanisms of plant populations and communities [5-7].

Inland salt marsh wetlands feature alkaline surface water and high soil salt content, with soluble salts accumulating in surface layers. Vegetation communities are typically dominated by few species and exhibit distinct zonation patterns. Topography, surface water conditions, spatial heterogeneity of surface soil salinity, and hydrological conditions of connected lakes and rivers collectively determine plant distribution and vegetation zonation patterns [8-9]. Therefore, investigating the spatial distribution patterns of inland salt marsh vegetation and their relationships with soil moisture and salinity factors is essential for understanding ecological adaptation and stability maintenance mechanisms in wetland plant communities.

The Sugan Lake wetland system comprises a closed intermontane fault basin that maintains a largely pristine ecological sequence. As a nationally protected wetland resource, it holds typical, representative, and specially protected scientific research value in China's northwest desert region. Xiaosugan Lake is a slightly saline lake with an outlet, characterized by low precipitation and high evaporation. Through long-term co-evolution with this environment, wetland plants have developed unique regional adaptations to cold, drought, and salt stress. While extensive research has addressed plant community classification and ordination [10-11] and environmental interpretation of population differentiation [12-13], studies on inland salt marsh wetlands have focused on species composition and diversity [14], water-salt migration patterns [15], and vegetation-groundwater relationships [16]. Research on Sugan Lake wetland plant diversity [17] and natural vegetation responses to groundwater levels [18] has also emerged. However, investigations into how soil anions and cations, surface soil moisture content, and groundwater depth collectively influence plant community spatial distribution patterns and the environmental adaptability of dominant species in Xiaosugan Lake salt marsh wetlands remain limited. This study addresses this gap by applying TWINSPLAN and CCA classification and ordination methods to analyze relationships between plant community distribution and key hydro-saline environmental factors, aiming to clarify vegetation spatial distribution characteristics under water-salt influences and identify the causes of such spatial heterogeneity.

### 1.1 Study Area Description

The study area is located in the Xiaosugan Lake Nature Reserve in Aksai, Gansu Province, within the Huahaizi Plateau Basin among the Altun, Danghe South, Saishiteng, and Tuergendaban mountains on the northern margin of the Qaidam Basin on the Qinghai-Tibet Plateau. Geographically positioned at 39°01'25" - 39°05'32" N, 94°10'33" - 94°14'43" E, with elevations ranging from 2807 to 2908 m, the region experiences a typical inland alpine arid climate. The mean annual temperature is below -0.4°C, with January averaging -14°C and July 13.8°C.

Annual precipitation is 77.6 mm, evaporation reaches 1964.8 mm, sunshine duration ranges 3100–3500 h, aridity index is 30, and frost-free period is approximately 90 days. The Sugan Lake water system belongs to the Qaidam endorheic river system. Soils are primarily meadow soil, meadow swamp soil, and saline soil. Dominant plants include *Phragmites australis*, *Leymus secalinus*, *Sophora alopecuroides*, *Glaux maritima*, *Suaeda glauca*, *Triglochin maritimum*, *Poa pratensis*, *Triglochin palustre*, and *Salicornia europaea*.

## 1.2 Plant Community Survey

Field surveys were conducted during August–September 2018. Based on preliminary vegetation reconnaissance and considering wetland types and plant coverage, we established 45 large quadrats (20 m × 20 m) across the study area [Figure 1: see original paper]. Within each large quadrat, five 1 m × 1 m herbaceous sub-quadrats were selected using the cross-diagonal method, recording plant height, coverage, density, frequency, and aboveground biomass for all species, totaling 225 herbaceous sub-quadrats. Site characteristics were described observationally, and GPS was used to record location data. Wetland types encountered included inland salt marsh, seasonal saline swamp, swamp meadow, freshwater spring, and herbaceous swamp.

## 1.3 Environmental Data Collection

Soil sampling accompanied vegetation surveys. Within each quadrat, five random sampling points were selected to collect 0–20 cm depth soil samples for physicochemical analysis. Soil total salt content was measured using the electrical conductivity method;  $K^+$  and  $Na^+$  by atomic absorption spectrophotometry;  $Ca^{2+}$  and  $Mg^{2+}$  by EDTA titration;  $CO_3^{2-}$  and  $HCO_3^-$  by double indicator-neutralization titration;  $Cl^-$  by  $AgNO_3$  titration; and  $SO_4^{2-}$  by EDTA indirect complexometric titration. Soil moisture content (SMC) was determined using the aluminum box method. Groundwater depth was measured by digging with a shovel until water flow appeared and stabilizing before measurement [19].

## 1.4 Data Processing

Species importance in communities was described using importance value (IV), calculated as [20]:

$$IV = (relative\ biomass + relative\ height + relative\ coverage + relative\ density + relative\ frequency) / 5$$

A total of 19 plant species were recorded across 225 herbaceous sub-quadrats. Mean IV values for herbaceous species were calculated for each of the 45 sites, yielding a 45 × 19 site-species matrix. Environmental factors included soil  $Ca^{2+}$ ,  $Mg^{2+}$ ,  $K^+$ ,  $Na^+$ ,  $CO_3^{2-}$ ,  $HCO_3^-$ ,  $SO_4^{2-}$ , total salt content (s), surface soil moisture content (SMC), and groundwater depth (dep), forming a 45 × 11

site-environmental factor matrix. To investigate relationships between wetland vegetation and environmental factors, DCA ordination was first performed. The first axis gradient length of 6.964 ( $>4$ ) indicated that unimodal-based CCA ordination was appropriate for vegetation-environment correlation analysis [21]. To avoid “arch effects” from redundant variables, Monte Carlo tests were applied to screen key environmental factors influencing species distribution [16,22-23] before CCA ordination.

TWINSPAN vegetation classification was performed using Wintwins 2.3 software. DCA ordination, CCA ordination, and Monte Carlo tests were conducted using Canoco for Windows 4.5.

## Results

### 2.1 Plant Community Classification

TWINSPAN hierarchical classification of the 45-site, 19-species importance value matrix [Figure 2: see original paper], combined with actual ecological conditions, identified six community types (I-VI). Communities were named using dominant and indicator species from TWINSPAN classification .

#### 2.2.1 Environmental Factor Screening

In vegetation distribution and environmental interpretation studies, more environmental factors do not necessarily yield more accurate results, as factors may interact and introduce errors [22]. To avoid redundancy effects, Monte Carlo tests were applied to the 11 measured soil water-salt factors for significance testing. Results showed that soil moisture content, groundwater depth, total salt content,  $\text{Ca}^{2+}$ ,  $\text{Cl}^-$ , and  $\text{CO}_3^{2-}$  significantly influenced plant community distribution ( $P < 0.05$ ), while  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{SO}_4^{2-}$ , and  $\text{HCO}_3^-$  showed limited significance ( $P > 0.05$ ). Therefore, soil moisture content, groundwater depth, total salt content,  $\text{Ca}^{2+}$ ,  $\text{Cl}^-$ , and  $\text{CO}_3^{2-}$  were selected as proxy environmental variables. This significance analysis effectively performs forward selection, eliminating irrelevant variable effects on ordination results [23].

#### 2.2.2 Environmental Characteristics of Different Plant Community Types

Environmental factor characteristics of major plant groups in Xiaosugan Lake wetland are presented in . The *Phragmites australis* + *Leymus secalinus* community exhibited relatively high total salt content and the highest mean  $\text{Cl}^-$  content, indicating high chloride salt tolerance and adaptation to  $\text{Cl}^-$ -rich areas. The *Leymus secalinus* community, dominated solely by *Leymus secalinus*, showed the greatest mean groundwater depth, suggesting adaptation to higher elevations. The *Sophora alopecuroides* + *Thermopsis lanceolata* community, associated with salt-tolerant species like *Saussurea salsa* and *Leymus secalinus*, displayed high total soluble salt content and the highest  $\text{Ca}^{2+}$  content among

all communities, indicating high calcium salt tolerance. The *Saussurea salsa* + *Leymus secalinus* community showed lower ion content than the previous two communities but higher than the remaining three, with the greatest species diversity. The *Triglochin palustre* + *Triglochin maritimum* community had higher soil moisture content and was dominated by salt-excreting species like *Glaux maritima*. The *Kobresia capillifolia* + *Carex altaica* community exhibited significantly lower salt ion content than other communities but the highest soil moisture content and shallowest groundwater depth.

### 2.2.3 CCA Ordination Analysis

After removing redundant variables, CCA ordination using the six selected proxy variables revealed that the first two axes explained 65.2% of the total species-environment variance. Since the first three eigenvectors exceeding 40% of total variance indicates satisfactory ordination results [24], only the first two axes were retained to interpret plant-environment relationships.

A two-dimensional CCA ordination diagram of plant species and environmental factors was constructed using the first two axes [Figure 3: see original paper]. Environmental factors are represented by arrows; arrow length and angle with ordination axes indicate correlation strength—longer arrows with smaller angles denote stronger correlations, while shorter arrows with larger angles indicate weaker relationships [21].

CCA ordination axes reflect habitat gradient characteristics. The first axis primarily represents a moisture gradient, with soil moisture content showing the longest arrow and smallest angle with Axis 1, indicating the highest correlation ( $r = 0.8147$ , ). Axis 2 correlates most strongly with soil  $\text{Cl}^-$  and  $\text{Ca}^{2+}$  ( $r = 0.7258$  and  $-0.6772$ , respectively, ). Although total salt content (S) has a small angle with Axis 2, its short arrow length indicates weaker correlation than  $\text{Cl}^-$  and  $\text{Ca}^{2+}$ . Soil  $\text{CO}_3^{2-}$  shows the shortest arrow with large angles to both axes, indicating low correlation. Groundwater depth (dep), despite large axis angles, has the longest arrow length, suggesting relatively high correlation with both axes.

Axis 1 essentially reflects the water gradient across plant communities. From left to right, soil moisture content increases while groundwater depth decreases, with community types transitioning from *Sophora alopecuroides* + *Thermopsis lanceolata* and *Saussurea salsa* + *Leymus secalinus* communities to the *Triglochin palustre* + *Triglochin maritimum* community, and finally to the *Kobresia capillifolia* + *Carex altaica* community. This transition along Axis 1 also reflects habitat changes, with wetland types shifting from salt marsh to seasonal saline swamp and finally to freshwater spring. Axis 2 primarily represents key soil ions ( $\text{Cl}^-$  and  $\text{Ca}^{2+}$ ). From bottom to top along Axis 2, communities transition from  $\text{Ca}^{2+}$ -rich *Sophora alopecuroides* + *Thermopsis lanceolata* to *Saussurea salsa* + *Leymus secalinus*, then to *Triglochin palustre* + *Triglochin maritimum* in seasonal saline swamps and *Kobresia capillifolia* + *Carex altaica* at freshwater

springs, and finally to  $\text{Cl}^-$ -rich *Phragmites australis* communities .

## Discussion

Soil moisture and salinity factors in inland salt marsh wetlands typically exhibit relative spatial stability, profoundly influencing plant assemblage patterns and population spatial distribution. Wetland soil and hydrological factors constitute primary drivers of community ecological characteristics, constraining the direction of biological processes [25-26]. The close linkage between wetland plant spatial patterns and soil water-salt distribution characteristics facilitates understanding of environmental plasticity mechanisms in inland salt marsh plant populations.

Differential adaptation to growth conditions among species, combined with environmental and biological characteristics, leads to distinct community composition [27-28]. Xiaosugan Lake inland salt marsh wetland plant communities exhibit relatively simple structure with patchy, discontinuous distribution. Field observations revealed: (1) *Triglochin palustre* + *Triglochin maritimum* and *Kobresia capillifolia* + *Carex altaica* communities primarily occur around freshwater springs, rivers, and lakes, where shallow groundwater depth (<1 m) maintains continuous connection between surface soil water and capillary zones. Persistent saturation facilitates reduction reactions, desalination, and microbial activity, reducing soil salinization and developing swamp meadows dominated by low-stature species like *Kobresia capillifolia*, *Scirpus pumilus*, *Eleocharis interstita*, and *Hippuris vulgaris*. (2) *Sophora alopecuroides* + *Thermopsis lanceolata* and *Saussurea salsa* + *Leymus secalinus* communities occupy salt marshes relatively distant from freshwater sources. During wet seasons, shallow groundwater maintains connected water-capillary zones with smooth flow paths, while high evaporation concentrates surface salts. During dry seasons, deeper groundwater disconnects these zones, transporting and accumulating substantial salts in root and surface layers under intense evaporation, forming extensive salt marshes with high total salt content and halophytic vegetation like *Sophora alopecuroides*, *Saussurea salsa*, *Salicornia europaea*, and *Suaeda glauca*. (3) *Phragmites australis* + *Leymus secalinus* communities occur in low-lying areas around rivers and lakes—salt accumulation centers with relatively high salinity—interspersed with *Leymus secalinus* in salt marshes. *Leymus secalinus* communities are widely distributed across the region (except salt patches, bare land, and lake areas), predominantly on higher terraces. This distribution reflects both poor subsurface drainage with high, mineralized groundwater and short inundation periods, and *Leymus secalinus*'s biological characteristics as a perennial herb with descending rhizomes, erect coarse culms, and broad adaptability to moisture, drought, and cold. The differential distribution patterns represent community reorganization responses to complex environmental conditions, objectively expressing habitat adaptability.

Microenvironments influence plant distribution, growth, and community succession directions, altering community structure and species distribution. Environ-

mental heterogeneity can shift community types [29-30]. The six community types identified in this study align well with CCA ordination patterns [Figure 3: see original paper], revealing vegetation-water-salt relationships and indicating that community composition serves as a habitat indicator [31]. CCA analysis identified soil moisture content and groundwater depth as most strongly correlated with Axis 1, while Axis 2 primarily related to soil salinity, particularly  $\text{Ca}^{2+}$  and  $\text{Cl}^-$ . This pattern arises because: (1) Soil moisture content acts as a critical habitat selection pressure. The Sugan Lake basin is a closed inland basin with scarce precipitation and intense evaporation; limited rainfall infiltrates to combine with groundwater, making groundwater the primary water source for vegetation. Groundwater depth determines water acquisition strategies and constrains soil water-salt dynamics and vegetation recovery [32]. Shallow groundwater allows direct root water uptake, supporting flood-tolerant species like *Kobresia capillifolia*, *Carex altaica*, and *Hippuris vulgaris*. Deeper groundwater transports water to the surface via capillary action, influencing vadose zone moisture and community growth [33]. (2) Calcium stabilizes biological membranes, maintaining selective ion absorption. Under high salinity, appropriate  $\text{Ca}^{2+}$  reduces membrane permeability, preventing  $\text{K}^+$  efflux and  $\text{Na}^+$  influx, thereby enhancing halophyte salt tolerance.  $\text{Cl}^-$  is a crucial inorganic ion in halophyte vacuoles, significantly affecting cellular osmosis. Topography influences salt migration; salts precipitate sequentially by solubility from piedmont to plain to basin center [34]. In alluvial plains distant from the lake, less soluble calcium salts deposit first, supporting *Sophora alopecuroides* + *Thermopsis lanceolata* communities with highest  $\text{Ca}^{2+}$  content. Highly soluble chlorides accumulate in low-lying basin areas, where *Phragmites australis* communities dominate. This demonstrates the ecological adaptability of Xiaosugan Lake inland salt marsh plant community distribution patterns to environmental conditions—an outcome of long-term adaptation to specialized habitats.

## Conclusions

- (1) Xiaosugan Lake wetland plants can be classified into six community types: *Phragmites australis* + *Leymus secalinus*, *Leymus secalinus*, *Sophora alopecuroides* + *Thermopsis lanceolata*, *Saussurea salsa* + *Leymus secalinus*, *Triglochin palustre* + *Triglochin maritimum*, and *Kobresia capillifolia* + *Carex altaica*. Each community displays significant spatial differentiation by adapting to regional soil water-salt migration patterns.
- (2) CCA ordination clearly reflects the ecological significance of axes: Axis 1 represents the moisture gradient, with community transitions along this axis indicating wetland type changes from salt marsh to seasonal saline swamp to freshwater spring; Axis 2 primarily reflects the influence of key soil ions ( $\text{Cl}^-$  and  $\text{Ca}^{2+}$ ) on community distribution. Soil moisture content,  $\text{Cl}^-$ ,  $\text{Ca}^{2+}$ , and groundwater depth emerge as the primary hydro-saline factors influencing spatial distribution of plant communities in Xiaosugan Lake inland salt marsh wetlands.

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