Clonal Growth and Sexual Reproduction Characteristics and Influencing Factors of *Scirpus validus* in Yunnan Plateau Lakes (Postprint)

Authors: Zhao Piao, Liu Zhenya, Wang Na, Niu Mengying, Ai Jing, Xiao Derong, Wang Xing

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Abstract

The response of plant growth and reproduction to future climate change has received widespread attention. To understand the spatial distribution pattern characteristics of clonal growth and sexual reproduction parameters of emergent macrophytes and the influence pathways of environmental factors on plant reproduction, this study utilized the three-dimensional topography of the Yunnan Plateau and employed a space-for-time approach to investigate the geographic variation and changing patterns of clonal growth and sexual reproduction of Schoenoplectus tabernaemontani, a common emergent macrophyte in six lakes, as well as its response to environmental changes. The results showed that: (1) Clonal growth parameters such as density, plant height, and basal diameter of S. tabernaemontani, as well as reproductive parameters including seed set rate, spike biomass, spike biomass investment ratio, seed yield, and number of viable seeds exhibited significant differences across different geographic spaces ($P < 0.05$), whereas aboveground biomass showed no significant difference. (2) Parameters including density, plant height, seed set rate, spike biomass, and spike biomass investment ratio of S. tabernaemontani demonstrated significant zonal distribution characteristics along latitude, longitude, and altitude gradients. Specifically, density increased with increasing latitude and altitude but decreased with increasing longitude; conversely, plant height, seed set rate, spike biomass, and spike biomass investment ratio decreased with increasing latitude and altitude but gradually increased with increasing longitude. (3) Mean temperatures of warm and cold months, soil total nitrogen, and soil total phosphorus were identified as key factors influencing clonal growth (density, plant height) of S. tabernaemontani, with mean temperature of warm months having the greatest impact; mean annual precipitation and soil organic carbon were key factors affecting sexual reproduction, with mean annual precipitation exerting the strongest influence. The study further demonstrated that climatic

factors (mean temperature of warm months, mean temperature of cold months, and mean annual precipitation) are the primary determinants influencing the growth and reproduction of S. tabernaemontani in the littoral zones of lakes on the Yunnan Plateau.

Full Text

Clonal Growth and Sexual Reproduction Characteristics and Influencing Factors of *Schoenoplectus tabernaemontani* in Yunnan Plateau Lakes

ZHAO Piao[12], LIU Zhenya[12], WANG Na[12], NIU Mengying[3], AI Jing[4], XIAO Derong[56], WANG Hang[12*]

[1]Yunnan Key Laboratory of Plateau Wetland Conservation, Restoration and Ecological Services, Southwest Forestry University, Kunming 650224, China
[2]National Plateau Wetlands Research Center/College of Wetlands, Southwest Forestry University, Kunming 650224, China
[3]College of Life Sciences, Southwest Forestry University, Kunming 650224, China
[4]Sugarcane Research Institute of Yunnan Academy of Agricultural Sciences, Kaiyuan 661600, Yunnan, China
[5]College of Life and Environmental Sciences, Wenzhou University, Wenzhou 325035, Zhejiang, China
[6]National and Local Joint Engineering Research Center of Ecological Treatment Technology for Urban Water Pollution, Wenzhou University, Wenzhou 325035, Zhejiang, China

Abstract: The response of plant growth and reproduction to future climate change has attracted widespread attention. To understand the spatial distribution patterns of clonal growth and sexual reproduction parameters in emergent plants and the pathways through which environmental factors influence plant reproduction, this study utilized the three-dimensional topography of the Yunnan Plateau to investigate geographical variations in clonal growth and sexual reproduction of the common emergent plant *Schoenoplectus tabernaemontani* across six lakes, employing a space-for-time substitution approach. The results showed that: (1) Clonal growth parameters including density, plant height, and basal diameter, as well as reproductive parameters such as seed setting ratio, spike biomass, spike investment ratio, seed production, and number of active seeds differed significantly across geographic space ($P < 0.05$), whereas aboveground biomass showed no significant differences. (2) Parameters including density, plant height, seed setting ratio, spike biomass, and spike investment ratio exhibited significant zonal distribution patterns along latitude, longitude, and altitude gradients. Specifically, density increased with increasing latitude and altitude but decreased with increasing longitude; conversely, plant height, seed setting ratio, spike biomass, and spike investment ratio decreased with increasing latitude and altitude but increased gradually with increasing longitude. (3)

Mean temperatures of warm and cold months, soil total nitrogen, and soil total phosphorus were key factors affecting clonal growth (density and height), with warm month mean temperature having the greatest influence. Mean annual precipitation and soil organic carbon were key factors affecting sexual reproduction, with mean annual precipitation having the greatest influence. The study further demonstrated that climatic factors (warm month mean temperature, cold month mean temperature, and mean annual precipitation) are the primary drivers of growth and reproduction in the littoral zone emergent plant *S. tabernaemontani* in Yunnan Plateau lakes.

Keywords: emergent plant; lakeside zone; reproductive strategy; climate change; plateau lakes

Introduction

Plant growth and reproduction are essential pathways for population maintenance and dispersal, and are highly sensitive to environmental changes that subsequently affect ecosystem structure and function (Sherry et al., 2007). The response of plant growth and reproduction to future climate change has garnered extensive attention (Roa-Fuentes et al., 2012; Wang et al., 2018b). Littoral zone plants in plateau lakes are particularly sensitive to climate change (Liu et al., 2017), making it crucial to investigate how these plants respond to environmental factors to scientifically assess potential impacts of future climate change on plateau lake ecosystems.

Topographic factors (latitude, longitude, altitude), climate (precipitation, temperature), and soil nutrients all influence plant growth and reproduction (Gao & Liu, 2018; Gong et al., 2019; Zhang et al., 2019). Altitude is a dominant factor affecting plant growth and reproduction (Körner, 2007), with plant phenology (Walker et al., 2014) and leaf functional traits (Jiang & Ma, 2015) closely related to elevation. As altitude increases, plant biomass increases (Li, 2015) while plant height decreases (Mao et al., 2018; Liu et al., 2016) and individual size becomes smaller (Méndez & Traveset, 2003), accompanied by increased reproductive investment (Fabbro & Körner, 2004). Beyond altitude, plant height shows a hump-shaped relationship with latitude, peaking at mid-latitudes (Liu et al., 2016), though some studies indicate plant height decreases with increasing latitude (Moles et al., 2009). Due to geographic variation, plant habitats differ substantially. Previous research shows that temperature increases can either promote (Day et al., 2008; Li et al., 2014), inhibit (De et al., 2008; Kreyling et al., 2008), or have no significant effect (Dukes et al., 2005; Bloor et al., 2010) on clonal growth, while clearly promoting sexual reproduction (Wang et al., 2018a; Xiao et al., 2019). Increased precipitation can cause stomatal closure and reduced photosynthetic rates, inhibiting clonal growth (Körner, 2007), though other studies suggest precipitation increases can promote clonal growth (Roa-Fuentes et al., 2012). Enhanced soil nutrients can promote individual plant growth (Nasto et al., 2019) and increase seed yield (Wang et al., 2021). Generally, plant growth and reproduction are influenced by climatic factors at large scales (Svenning & Sandel, 2013) and by altitude gradients at regional scales such as mountains (Tang & Fang, 2004). In low-altitude areas, soil nutrients more significantly affect plant growth and reproduction, whereas temperature becomes more important at high altitudes (Sang, 2009). Thus, studying plant growth and reproductive strategies in response to environmental change represents a hot topic in ecological research, though current findings remain uncertain.

Yunnan Province features extremely complex and diverse topography, with the Hengduan Mountains in the northwest and the Yunnan-Guizhou Plateau in the east, exhibiting a maximum vertical elevation difference of 6,663.6 m. The spatial variation in environmental factors such as topography, climate, and soil is pronounced, creating unique geological, vegetation, and three-dimensional climate characteristics (Yang & Li, 2010). As critical components of the ecological barrier in the Yunnan Plateau, lakes exhibit typical "mountain-littoral-basin" ecological features, playing irreplaceable roles in biodiversity conservation and endemism while being highly sensitive to environmental change (Xiao et al., 2019). Emergent plants are important components of littoral zones in Yunnan Plateau lakes, forming the foundation of plateau lake ecological structure and function. *Schoenoplectus tabernaemontani* is a common species distributed across six plateau lakes including Napahai, Luguhu, Lashihai, Dianchi, Qiluhu, and Yilonghu (Yang & Li, 2010), with clonal growth and sexual reproduction serving as important pathways for maintaining population spatial distribution and dispersal. Therefore, studying how *S. tabernaemontani* responds to environmental factors across different geographic spaces can effectively illustrate adaptation strategies of littoral zone emergent plants to future climate change.

This study utilized the three-dimensional topography and unique climate of Yunnan to select six different plateau lakes, using the common emergent plant *S. tabernaemontani* as a research focus. We examined differences in clonal growth parameters (density, height, basal diameter, above-ground biomass) and sexual reproduction parameters (seed setting ratio, spike biomass, spike investment ratio, seed yield per unit area, number of active seeds per unit area) across different regions, and analyzed correlations between environmental factors (geographic location, climate, soil, and water) and plant growth and reproduction indicators. The study aimed to address three scientific questions: (1) Do growth and reproduction characteristics of the plateau lake emergent plant *S. tabernaemontani* show geographic distribution differences? (2) Do these characteristics exhibit latitudinal, longitudinal, and altitudinal zonation patterns? (3) What impacts do environmental changes resulting from geographic spatial differences have on plant clonal growth and sexual reproduction, and what is the magnitude of these impacts? Answering these questions will lay a foundation for understanding the response mechanisms of plateau lakes to future climate change.

1.1 Study Area

This study selected six lakes as research sites: Napahai, Luguhu, Lashihai, Dianchi, Qiluhu, and Yilonghu. Napahai, Luguhu, and Lashihai are located in the northwestern Yunnan Plateau, representing hotspots for biodiversity and endemism conservation in this region, with Napahai and Lashihai designated as internationally important wetlands. Dianchi, Qiluhu, and Yilonghu are situated in the central Yunnan Plateau, serving as ecological barriers for sustainable socio-economic development of the central Yunnan urban agglomeration and representing key areas for aquatic ecological security and biodiversity conservation. The six lakes span substantial topographic differences, with geographic locations ranging from 99.66–102.77°E and 23.67–27.85°N, altitudes between 1,412–3,260 m, longitudinal and latitudinal spans of 3.11° and 4.18° respectively, and an elevation difference of 1,848 m. Due to differences in geographic location, the lakes exhibit distinct environmental conditions.

1.2 Sample Collection

During August–October 2020, we established 3–6 1 m × 1 m quadrats in typical *S. tabernaemontani* distribution areas in the littoral zones of Napahai, Luguhu, Lashihai, Dianchi, Qiluhu, and Yilonghu. Specifically, we established 6 quadrats in Napahai, 4 in Luguhu, 3 in Lashihai, 3 in Dianchi, 3 in Qiluhu, and 4 in Yilonghu, totaling 23 quadrats. In the field, we measured total plant number and spike number in each quadrat, and selected 10 mature spiked plants to measure plant height and basal diameter using a vernier caliper with 0.01 mm precision. Spiked plants were clipped and brought back to the laboratory for measurement of spike morphology, biomass, and seed activity parameters. Using the harvest method, we collected above-ground plants from 25 cm × 25 cm subplots within each quadrat for determination of above-ground biomass. GPS was used to record latitude, longitude, and altitude of each quadrat. Surface soil samples (0–10 cm) were collected from each quadrat using a depth peat corer (Eijkelkamp, Netherlands), sealed in ziplock bags, and brought back to the laboratory for physicochemical analysis. Water samples were also collected in 500 mL plastic bottles for laboratory analysis of relevant physicochemical indicators.

1.3.1 Determination of Above-Ground Biomass and Sexual Reproduction Indicators

Using the oven-drying method, harvested plant samples were dried at 65 °C to constant weight for above-ground biomass determination. In the laboratory, spike length of 10 *S. tabernaemontani* plants from each quadrat was measured with a 0.1 cm precision ruler, and the number of spikelets and seeds per spike were recorded. Seed setting ratio was calculated as (number of fruiting plants/total number of plants) × 100%, and seed yield as (seeds/m^2 = average seeds per plant × fruiting plants per m^2). After air-drying the bagged plants, spike biomass and plant biomass were measured separately to calculate the sexual reproduction biomass investment ratio: spike investment ratio = (spike biomass/plant biomass) × 100%. Finally, seeds from each quadrat were mixed thoroughly, and 200 seeds per quadrat were selected in three replicates. After physical removal of seed coats, seeds were longitudinally sectioned along the embryo side with a scalpel and stained in 1% tetrazolium phosphate buffer at (30 ± 1) °C for 24 h. Seed viability was observed under 10× magnification based on staining patterns. Seeds with main embryo structures stained bright red, or with only the radicle tip 2/3 unstained while other parts stained normally, were considered viable. Active seed number per unit area was calculated as: active seeds = seed yield × (stained seeds/total stained seeds × 100%).

1.3.2 Determination of Soil and Water Environmental Indicators

Soil organic carbon (SOC) content was determined using the acid washing method (Tang et al., 2018). Soil total nitrogen (STN) and total phosphorus (STP) were measured using H_2SO_4-H_2O_2 digestion. Water total nitrogen (WTN) and total phosphorus (WTP) were analyzed using a continuous flow analyzer (SEAL Analytical AA3, Germany). Climate parameters including mean annual temperature (MAT), maximum temperature of the warmest month (WMT), minimum temperature of the coldest month (CMT), and mean annual precipitation (MAP) were obtained from global grid data (precision: 0.16° × 0.16°; http://www.paleo.bris.ac.uk/) for each sampling site. Environmental parameters of soil and water at the littoral zones of each lake are presented in Table 1.

Table 1 Characteristics of geographic, climatic, soil, and water factors at each sampling site

Sampling site	Geographic location	Climate factor	Soil factor	Water factor
	Longitude (°E)	Latitude (°N)	Altitude (m)	WMT (°C)
Napahai	99.66	27.85	3260	11.6e

Note: Different lowercase letters within the same column indicate significant differences (P < 0.05).

1.4 Data Processing

SPSS 19.0 software was used for one-way ANOVA on growth and reproduction indicators including density, height, basal diameter, above-ground biomass, seed setting ratio, spike biomass, spike investment ratio, seed yield per unit area, and active seed number per unit area across different regions, with significance level set at $\alpha = 0.05$. Pearson correlation analysis was employed to examine relationships between *S. tabernaemontani* growth and reproduction indicators and climatic, soil, and hydrological factors. Stepwise regression analysis was further used to screen key factors affecting growth and reproduction characteristics. Path analysis of key influencing factors was conducted using the Agricolae package in R 4.01 software to investigate pathways and contribution rates of these factors to plant growth and reproduction.

Results

2.1 Spatial Differences in Growth and Reproduction

Except for above-ground biomass, *S. tabernaemontani* growth and reproduction parameters differed significantly across geographic space ($P < 0.05$). Density was highest in Napahai (853 ± 99 plants $\cdot$ m^{-2}) and lowest in Dianchi (256 ± 43 plants $\cdot$ m^{-2}), with significant differences among sampling sites ($P < 0.05$). Plant height was highest in Yilonghu (209 ± 28 cm) and lowest in Napahai (128 ± 5 cm), showing highly significant differences among sites ($P < 0.001$). Basal diameter was greatest in Yilonghu (13.3 ± 0.5 mm) and smallest in Lashihai (6.4 ± 1.4 mm), with highly significant differences ($P < 0.001$). Seed setting ratio peaked in Yilonghu ($71\% \pm 6\%$) and was lowest in Napahai ($35\% \pm 6\%$), with highly significant differences ($P < 0.01$). Spike biomass was highest in Yilonghu (457 ± 390 g $\cdot$ m^{-2}) and lowest in Lashihai (46 ± 17 g $\cdot$ m^{-2}), with significant differences ($P < 0.05$). Spike investment ratio was greatest in Yilonghu ($13.9\% \pm 3.9\%$) and lowest in Napahai ($2.2\% \pm 1.3\%$), with highly significant differences ($P < 0.001$). Seed yield per unit area was highest in Luguhu ($18.0 \times 10^4 \pm 6.6 \times 10^4$ seeds $\cdot$ m^{-2}) and lowest in Dianchi ($3.8 \times 10^4 \pm 0.6 \times 10^4$ seeds $\cdot$ m^{-2}), with significant differences ($P < 0.05$). Active seed number per unit area was highest in Luguhu ($16.0 \times 10^4 \pm 7.1 \times 10^4$ seeds $\cdot$ m^{-2}) and lowest in Dianchi ($2.7 \times 10^4 \pm 0.3 \times 10^4$ seeds $\cdot$ m^{-2}), showing highly significant differences ($P < 0.01$).

Table 2 Clonal growth and sexual reproduction parameters of *Schoenoplectus tabernaemontani* in different Yunnan Plateau lakes

Parameter	Napahai	Luguhu	Lashihai	Dianchi	Qiluhu	Yilonghu	F value
Density (plant $\cdot$ m^{-2})	853 ± 99a	748 ± 233ab	453 ± 24bc	256 ± 43c	581 ± 266b	540 ± 237b	6.101**
Height (cm)	128 ± 5b	206 ± 15a	135 ± 19b	155 ± 32b	199 ± 32a	209 ± 28a	12.488***
Diameter (mm)	11.7 ± 1.0a	11.4 ± 1.4a	6.4 ± 1.4c	9.4 ± 1.6b	13.2 ± 0.9a	13.3 ± 0.5a	17.470***

Parameter	Napahai	Luguhu	Lashihai	Dianchi	Qiluhu	Yilonghu	F value
Above-ground biomass ($g \cdot m^{-2}$)	2786 ± 972a	3069 ± 1195a	690 ± 175b	1976 ± 1204a	2769 ± 502a	2960 ± 1657a	2.786
Seed setting ratio (%)	35 ± 6c	54 ± 16b	48 ± 8bc	58 ± 6ab	56 ± 1ab	71 ± 6a	7.631**
Spike biomass ($g \cdot m^{-2}$)	127 ± 64b	50 ± 22b	46 ± 17b	54 ± 22b	220 ± 94ab	457 ± 390a	3.544*
Spike investment ratio (%)	2.2 ± 1.3c	4.0 ± 0.4c	6.7 ± 1.6bc	3.0 ± 1.4c	7.8 ± 2.4b	13.9 ± 3.9a	17.686***
Seed production (10^4 seeds $\cdot m^{-2}$)	7.0 ± 1.7b	18.0 ± 6.6a	10.0 ± 0.9b	3.8 ± 0.6b	11.0 ± 8.7ab	13.0 ± 6.0ab	4.086*
Active seed (10^4 seeds $\cdot m^{-2}$)	1.8 ± 0.9b	16.0 ± 7.1a	9.0 ± 1.0ab	2.7 ± 0.3b	9.5 ± 7.3ab	11.0 ± 5.3a	6.012**

Note: Different lowercase letters in the same row indicate significant differences (P < 0.05). indicates P < 0.05; ** indicates P < 0.01; *** indicates P < 0.001.*

2.2 Spatial Distribution Patterns of Growth and Reproduction

S. tabernaemontani growth and reproduction indicators showed regular patterns along geographic gradients (Fig. 1). Plant density decreased with increasing longitude (Fig. 1A), while plant height, seed setting ratio, spike biomass, and spike investment ratio increased with longitude (Fig. 1D, G, J, M). Density increased with increasing latitude (Fig. 1B), whereas plant height, seed setting ratio, spike biomass, and spike investment ratio decreased with latitude (Fig. 1E, H, K, N). Similarly, density increased with altitude (Fig. 1C), while plant height, seed setting ratio, spike biomass, and spike investment ratio decreased with altitude (Fig. 1F, I, L, O).

Figure 1 Changes in growth and reproduction of *Schoenoplectus tabernaemon-*

tani in lakes along geographic gradients on the Yunnan Plateau. * indicates P < 0.05; ** indicates P < 0.01; *** indicates P < 0.001.

2.3 Factors Influencing Growth and Reproduction and Their Pathways

Plant density showed extremely significant positive correlations with above-ground biomass and seed yield (P < 0.01). Plant height was significantly positively correlated with spike biomass, seed yield, and active seed number (P < 0.05) and extremely significantly positively correlated with spike investment ratio (P < 0.01). Basal diameter was significantly positively correlated with spike biomass (P < 0.05). Above-ground biomass was extremely significantly positively correlated with spike biomass and seed yield (P < 0.01) and significantly positively correlated with active seed number (P < 0.05) (Table 3).

Table 3 Pearson correlations between growth and reproduction indexes of *Schoenoplectus tabernaemontani*

Plant parameter	Density	Height	Diameter	Above-ground biomass	Seed setting ratio	Spike biomass	Spike investment ratio	Seed production	Active seed
Density	1	0.640**	0.507*	0.546**					
Height		1	0.518*	0.545**	0.526**	0.802**	0.435*	0.427*	
Diameter			1	0.637**	0.470*	0.571**	0.511*		
Above-ground biomass				1	0.602**	0.533**	0.563**	0.555**	
Seed setting ratio					1	0.571**	0.846**	0.447*	0.508*
Spike biomass						1	0.846**	0.563**	0.555**
Spike investment ratio							1	0.447*	0.508*
Seed production								1	0.961**
Active seed									1

Note: indicates P < 0.05; ** indicates P < 0.01.*

Growth and reproduction indicators showed significant correlations with regional climate and soil factors but not with lake water factors (Table 4). Density was extremely significantly negatively correlated with mean annual temperature, warm month mean temperature, cold month mean temperature, and mean annual precipitation (P < 0.01), extremely significantly positively correlated with soil total nitrogen (P < 0.01), and significantly positively correlated with soil total phosphorus (P < 0.05). Plant height was extremely significantly positively correlated with mean annual temperature, warm month mean temperature, cold month mean temperature, and mean annual precipitation (P < 0.01). Basal diameter and above-ground biomass showed no significant correlations with environmental factors (P > 0.05). Seed setting ratio was extremely significantly positively correlated with mean annual temperature, warm month mean temperature, cold month mean temperature, and mean annual precipitation (P < 0.01), and extremely significantly negatively correlated with soil total nitrogen (P < 0.01). Spike biomass and spike investment ratio were significantly positively correlated with mean annual temperature, warm month mean temperature, cold month mean temperature, and mean annual precipitation (P < 0.05). Seed yield and active seed number per unit area showed no significant correlations with environmental factors (P > 0.05).

Table 4 Pearson correlations between growth and reproduction indexes of *Schoenoplectus tabernaemontani* and climate, soil, and water factors

Plant parameter	Climate factor	Soil factor	Water factor
	MAT	WMT	CMT
Density	-0.572**	-0.571**	-0.578**
Height	0.613**	0.624**	0.598**
Diameter			
Above-ground biomass			
Seed setting ratio	0.794**	0.799**	0.795**
Spike biomass	0.536**	0.538**	0.531**
Spike investment ratio	0.758**	0.758**	0.758**
Seed production			
Active seed			

As shown in Fig. 2, warm month mean temperature, cold month mean temperature, soil total nitrogen, and soil total phosphorus were key factors affecting clonal growth. Soil total nitrogen was the primary factor influencing density, with a path coefficient of 0.59 and contribution of 35%. Warm month mean temperature, cold month mean temperature, and soil total phosphorus were the main factors affecting plant height, with path coefficients of 0.74, -0.67, and 0.04 respectively, contributing over 90% to height variation (Fig. 2A). Soil organic carbon and mean annual precipitation were key factors affecting sexual reproduction parameters. Mean annual precipitation directly influenced seed setting ratio, spike biomass, and spike investment ratio, with path coefficients of 0.81, 0.56, and 0.82 respectively. Soil organic carbon directly affected spike investment ratio with a path coefficient of 0.32. Mean annual precipitation contributed 66% and 31% to seed setting ratio and spike biomass respectively, while mean annual precipitation and soil organic carbon together contributed 78% to spike investment ratio (Fig. 2B).

Figure 2 Relational graphs of path analysis linking growth and reproductive characteristics of *Schoenoplectus tabernaemontani* with key factors in Yunnan Plateau lakes. Figure A shows influencing factors and pathways for growth characteristics; Figure B shows influencing factors and pathways for sexual reproduction characteristics. Standardized path coefficients are shown beside arrows, red numbers indicate explanatory degrees, solid lines represent positive relationships, and dashed lines represent negative relationships. * indicates $P < 0.05$; ** indicates $P < 0.01$; *** indicates $P < 0.001$. D = Density; H = Height; SSR = Seed setting ratio; SB = Spike biomass; SIR = Spike investment ratio; STP = Soil total phosphorus; STN = Soil total nitrogen; WMT = Maximum temperature of the warmest month; CMT = Minimum temperature of the coldest month; MAP = Mean annual precipitation; SOC = Soil organic carbon.

Discussion and Conclusions

Plant growth and reproductive traits reflect strategies for resource utilization and adaptation (Chen et al., 2014). This study found substantial spatial differences in clonal growth (except above-ground biomass) and sexual reproduction parameters of *S. tabernaemontani*, representing the combined effects of climate, soil, and water factors in their respective lakes and reflecting plant responses to different environmental conditions. These results align with previous studies on growth traits of *Xanthoceras sorbifolium* and seed reproduction of *S. tabernaemontani* (Zhang et al., 2019; Wang et al., 2018b). However, the lack of significant differences in above-ground biomass across sites suggests that littoral zone plant biomass is not affected by geographic environmental conditions, consistent with the law of constant final yield.

Changes in plant traits such as height represent long-term adaptation to climatic conditions (Wright et al., 2005). This study found that *S. tabernaemontani* in northwestern Yunnan had smaller individuals, with sexual reproduction characteristics showing significant latitudinal and altitudinal zonation patterns closely related to water-heat conditions. Typically, low temperatures at high latitudes and altitudes inhibit root water and nutrient uptake, while high UV radiation reduces resource use efficiency, limiting plant growth (He et al., 2002; Peñuelas et al., 2009; Körner, 2006). From central to northwestern Yunnan, spike growth parameters gradually decreased. In high-altitude, high-latitude areas, low temperatures shorten the growing season and reduce carbon accumulation, causing plants to decrease biomass production in all parts (Méndez & Traveset, 2003; Wang et al., 2018b). Consequently, energy allocated to seed reproduction decreases with increasing altitude and latitude, leading to reduced spike growth and seed yield. This may be the primary reason for the zonal distribution patterns of *S. tabernaemontani* growth and reproduction characteristics along latitude, longitude, and altitude gradients.

Clonal growth and sexual reproduction are two important aspects of plant life history strategies. Relationships among different traits under varying environmental conditions reflect functional linkages. This study found close relationships between clonal growth and sexual reproduction in *S. tabernaemontani*. Sexual reproduction characteristics showed strong dependence on individual plant size. Plant height and basal diameter are closely related to light capture capacity, resistance to mechanical damage, and support capacity for reproductive organs. Taller plants can extend to obtain more light but have weaker resistance to mechanical damage, while larger basal diameters enhance mechanical resistance and support thicker vascular structures (Sun et al., 2016), promoting both growth and sexual reproduction. Studies have also shown that larger individual plants produce more seeds and greater total seed weight (Susko & Lovett-Doust, 1998), as larger individuals acquire more total resources and can allocate more to sexual reproduction.

Plant height in this study was closely related to temperature factors, indicating that clonal growth of *S. tabernaemontani* is primarily temperature-driven. Elevated temperatures can enhance photosynthetic efficiency, inhibit respiration, and promote growth. Higher temperatures also extend the growing season, accelerate organic matter decomposition and soil mineralization, and improve nutrient use efficiency (Yang et al., 2010), thereby promoting vegetative growth and carbon accumulation (Day et al., 2008). These findings align with studies on rhizome length changes under warming conditions (Li et al., 2014). Research using OTC warming techniques on the arctic species *Carex bigelowii* also demonstrated that temperature increases enhance plant height (Stenström et al., 1997). However, some studies have found inhibitory effects of temperature increases on clonal growth (De et al., 2008), possibly due to negative effects of intense resource competition under abiotic stress conditions. Additionally, this study found that *S. tabernaemontani* in lakes with higher precipitation showed greater sexual reproduction investment, while water nitrogen and phosphorus content had no significant effects, suggesting that abundant precipitation can promote sexual reproduction in emergent plants, likely related to effects of precipitation on flooding conditions in littoral zones. Given the special habitat of emergent plants, water—one of the three key elements of wetland ecosystems—includes both quantity and quality aspects. For Yunnan Plateau lakes, runoff is primarily supplied by precipitation (Yang & Li, 2010). The flowering and fruiting period of *S. tabernaemontani* is June–September, coinciding with Yunnan's rainy season (May–October), which shows a decreasing trend from south to north (with increasing latitude) (Yan et al., 2018), altering littoral zone water levels. Previous studies have shown that zero ground water level is unfavorable for *S. tabernaemontani* growth (Zhao et al., 2015), and that *Typha* shows increased sexual reproduction proportion with increasing water depth within 0–

0.5 m (Sorrell et al., 2012). This study also found that soil nutrient content importantly affected plant growth and reproduction, with soil nitrogen having greater influence on clonal growth because plants primarily obtain nutrients from soil. Nitrogen promotes cell division and expansion, increasing leaf area for photosynthesis and thus promoting clonal growth, consistent with studies on soil nutrient effects on plant growth (Nasto et al., 2019). Path analysis revealed that the contribution to plant clonal growth and sexual reproduction characteristics followed the pattern: climatic factors > soil factors > water factors. This indicates that in Yunnan Plateau lakes, regional climatic factors (warm month mean temperature, cold month mean temperature, and mean annual precipitation) are the primary environmental factors affecting growth and reproduction of littoral zone plant *S. tabernaemontani*, while soil nutrients have significant effects. The influence of aquatic environmental factors on plateau lake plant reproduction characteristics under future environmental changes requires further investigation.

References

Bloor JMG, Pichon P, Falcimagne R, et al., 2010. Effects of warming, summer drought, and CO_2 enrichment on aboveground biomass production, flowering phenology, and community structure in an upland grassland ecosystem. *Ecosystems*, 13(6): 888-900.

Chen YB, Wang CS, Gao WT, et al., 2014. Study on phenology and growth rhythm of *Aconitum kusnezoffii*. *Journal of Jilin Agricultural Science and Technology University*, 23(2): 4-6.

Day TA, Ruhland CT, Xiong FS, 2008. Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra. *Global Change Biology*, 14(8): 1825-1837.

De BHJ, Lemmens C, Zavalloni C, et al., 2008. Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences*, 5(2): 585-594.

Dukes JS, Chiariello NR, Cleland EE, et al., 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS Biology*, 3(10): e319.

Fabbro T, Körner C, 2004. Altitudinal differences in flower traits and reproductive allocation. *Flora*, 199(1): 70-81.

Gao J, Liu YH, 2018. Climate stability is more important than water-energy variables in shaping the elevational variation in species richness. *Ecology and Evolution*, 8(14): 6872-6879.

Gong HD, Yu T, Zhang X, et al., 2019. Effects of boundary constraints and climatic factors on plant diversity along an altitudinal gradient. *Global Ecology and Conservation*, 19: e00671.

He YY, Häder DP, 2002. UV-B-induced formation of reactive oxygen species and oxidative damage of the cyanobacterium *Anabaena* sp.: protective effects of ascorbic acid and N-acetyl-L-cysteine. *Journal of Photochemistry and Photobiology B: Biology*, 66(2): 115–124.

Jiang ZH, Ma KM, 2015. Environmental filtering drives herb community composition and functional trait changes across an elevational gradient. *Plant Ecology and Evolution*, 148(3): 301–310.

Körner C, 2006. Significance of temperature in plant life. In: *Plant Growth and Climate Change*. Oxford: Blackwell Publishing: 1–16.

Körner C, 2007. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, 22(11): 569–574.

Kreyling J, Beierkuhnlein C, Elmer M, et al., 2008. Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. *Plant and Soil*, 308(1): 175–188.

Li Z, Lin J, Zhang T, et al., 2014. Effects of summer nocturnal warming on biomass production of *Leymus chinensis* in the Songnen Grassland of China: from bud bank and photosynthetic compensation. *Journal of Agronomy and Crop Science*, 200(1): 66–76.

Li YF, 2015. Effects of water levels on the growth and reproductive characteristics of dominant plants in the Dongting Lake wetlands. Master' s thesis. Changsha: Central South University of Forestry and Technology.

Liu WL, Yang J, Sun J, et al., 2016. Species turnover of wetland vegetation in northeastern China: disentangling relative effects of geographic distance, climate, and hydro-geomorphology. *Flora*, 220: 1–7.

Liu ZY, Zhang XN, Li LP, et al., 2017. Influence of simulated warming on light and CO_2 utilization capacities of lakeside dominant plants in a typical plateau wetland in northwestern Yunnan. *Acta Ecologica Sinica*, 37(23): 7821–7832.

Mao LF, Chen SB, Zhang JL, et al., 2018. Altitudinal patterns of maximum plant height on the Tibetan Plateau. *Journal of Plant Ecology*, 11(1): 85–91.

Méndez M, Traveset A, 2003. Sexual allocation in single-flowered hermaphroditic individuals in relation to plant and flower size. *Oecologia*, 137(1): 69–75.

Moles AT, Warton DI, Warman L, et al., 2009. Global patterns in plant height. *Journal of Ecology*, 97(5): 923–932.

Nasto MK, Winter K, Turner BL, et al., 2019. Nutrient acquisition strategies augment growth in tropical N_2-fixing trees in nutrient-poor soil and under elevated CO_2. *Ecology*, 100(4): e02646.

Peñuelas J, Rutishauser T, Filella I, 2009. Phenology feedbacks on climate change. *Science*, 324(5929): 887–888.

Roa-Fuentes LL, Campo J, Parra-Tabla V, 2012. Plant biomass allocation across a precipitation gradient: an approach to seasonally dry tropical forest at Yucatán, Mexico. *Ecosystems*, 15(8): 1234–1244.

Sang WG, 2009. Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research*, 24(2): 303–314.

Sherry RA, Zhou XH, Gu SL, et al., 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences USA*, 104(1): 198–202.

Sorrell BK, Tanner CC, Brix H, 2012. Regression analysis of growth responses to water depth in three wetland plant species. *AoB Plants*, 2012: pls043.

Stenström M, Gugerli F, Henry GHR, 1997. Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. *Global Change Biology*, 3(S1): 44–54.

Sun M, Su T, Zhang SB, et al., 2016. Variations in leaf morphological traits of *Quercus guyavifolia* (Fagaceae) were mainly influenced by water and ultraviolet irradiation at high elevations on the Qinghai-Tibet Plateau, China. *International Journal of Agriculture and Biology*, 18(2): 266–273.

Susko DJ, Lovett-Doust L, 1998. Variable patterns of seed maturation and abortion in *Alliaria petiolata* (Brassicaceae). *Canadian Journal of Botany*, 76(10): 1677–1686.

Svenning JC, Sandel B, 2013. Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100(7): 1266–1286.

Tang WX, Meng FQ, Zhang Y, et al., 2018. Comparison of different soil organic carbon determination methods. *Soils*, 50(3): 552–557.

Tang ZY, Fang JY, 2004. A review on the elevational patterns of plant species diversity. *Biodiversity Science*, 12(1): 20–28.

Walker JJ, De Beurs KM, Wynne RH, 2014. Dryland vegetation phenology across an elevation gradient in Arizona, USA, investigated with fused MODIS and Landsat data. *Remote Sensing of Environment*, 144: 85–97.

Wang Y, Wang WQ, Wang QK, et al., 2021. Effects of soil nutrients on reproductive traits of invasive and native annual Asteraceae plants. *Biodiversity Science*, 29(1): 1–9.

Wang ZB, Sun M, Liu ZY, et al., 2018a. Response of seed reproduction of two dominant lakeside species to experimental warming in a typical plateau wetland in Northwestern Yunnan Plateau. *Chinese Journal of Applied Ecology*, 29(3): 696–704.

Wang ZB, Tian K, Guan DX, et al., 2018b. Responses of seed reproduction traits of a wetland dominant plant *Schoenoplectus tabernaemontani* to environmental changes in Hengduan Mountains. *Journal of Northeast Forestry University*, 46(3): 12–15.

Wright IJ, Reich PB, Cornelissen JHC, et al., 2005. Assessing the generality of global leaf trait relationships. *New Phytologist*, 166(2): 485–496.

Xiao DR, Yan PF, Zhan PF, et al., 2019. Temperature variations in simulated warming alter photosynthesis of two emergent plants in plateau wetlands, China. *Ecosphere*, 10(5): e02729.

Yan HM, Li QQ, Wang DQ, 2018. Temporal and spatial characteristics of rainy season in Yunnan and its relationship with atmospheric circulation. *Journal of Tropical Meteorology*, 34(1): 12–22.

Yang B, Wang JC, Zhang YB, 2010. Effect of long-term warming on growth and biomass allocation of *Abies faxoniana* seedlings. *Acta Ecologica Sinica*, 30(21): 5994–6000.

Yang L, Li H, 2010. *Yunnan Wetlands*. Beijing: China Forestry Press.

Zhang X, He X, Gao J, et al., 2019. Latitudinal and climate effects on key plant traits in Chinese forest ecosystems. *Global Ecology and Conservation*, 17: e00527.

Zhang Y, Ao Y, Liu JF, et al., 2019. Differences in growth characters of *Xanthoceras sorbifolium* from different distribution areas and analysis on its correlation with geographical-climatic factors. *Journal of Plant Resources and Environment*, 28(3): 44–50, 57.

Zhao XJ, Tian K, Yue HT, 2015. Growth stress of *Scirpus tabernaemontani* of dominant plant in plateau wetland lakeshore to water level fluctuating. *Guihaia*, 35(3): 303–308.

Note: Figure translations are in progress. See original paper for figures.