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Effects of water stress and rewatering on growth and photosynthetic parameters of *Typha orientalis* Presl in coexistence conditions

Binbin Huang[a,*], Jie Tu[a], Kumud Acharya[b], Denghua Yan[c]

[a]*JiangXi Engineering Research Centre of Water Engineering Safety and Resources Efficient Utilization, Nanchang Institute of Technology, Nanchang, China, emails: wanilyzxh@163.com (B.B. Huang), tujie8058@163.com (J. Tu)*
[b]*Desert Research Institute, Las Vegas, USA, email: Kumud.Acharya@dri.edu*
[c]*Water Resources Department, China Institute of Water Resources and Hydropower Research, Beijing, China, email: denghuay@gmail.com*

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ABSTRACT

Water stress and interspecific interaction will change the growth characteristics and photosynthetic parameters of wetland plants. The net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), water use efficiency (WUE), plant height (PH), biomass of *Typha orientalis* Presl were analyzed by pot experiments. Pot experiments were conducted utilizing the plant species, *Typha orientalis* Presl alone, and *Typha orientalis* Presl along with *Phragmites australis* coexisting under the same water stress and water abundant conditions. Water stress was divided into four scenarios as W1i, W2i, W3i and W4i that ranged from mild to severe stress. In addition, the control experiment (CKi) was also conducted. The results showed that Pn, Gs, Tr, WUE, PH and biomass were reduced with the increase in severity of water stress. There were large differences in WUE among water stress treatments at the end of the experiment. The trend showed that W2i > W3i > W1i > CKi, while there was a decrease under W4i's scenario. Therefore, the data suggested that a moderate increase in water stress could increase WUE. The growth and photosynthetic parameters of *Typha orientalis* Presl recovered after rewatering, but not under CKi's scenario. The threshold soil moisture for *Typha orientalis* Presl was approximately 30% below, which demonstrated that recovery could be difficult even after rewatering. Coexistence with *Phragmites australis* had significant effects on the growth of *Typha orientalis* Presl and photosynthetic parameters. It was negative for biomass of *Typha orientalis* Presl, and positive for shoot heights in the same water stress treatments. The photosynthetic parameters were higher than single species in coexistence conditions.

Keywords: Water stress; Rewatering; Coexistence; *Typha orientalis* Presl; Growth characteristics; Photosynthetic parameters

1. Introduction

Water availability is one of the most important environmental factors affecting wetland plants [1]. Studies have shown that water availability and duration play a key role in wetland plant distribution, growth and development [2], morphological characteristics, population density and productivity. For example, the depth of water affects transpiration, photosynthesis, leaf area index, plant height and biomass of *Phragmites australis* [3]. The water depth has a positive effect on the average plant height of *Carex lasiocarpa* [4,5]. Therefore, the study of changes in the interaction between different species under different water stress conditions is the basis for studying the response of wetland plants to water stress.

* Corresponding author.

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Typha orientalis Presl and *Phragmites australis* are the two dominant emergent plants in the Baiyangdian wetland area. These plants grow in shallow wetlands, and are mainly distributed in the North, Northeast and South of China. They play an important role in the purification of water quality and provide habitats for animals [6–9]. Drought directly affects the growth and distribution of *Typha orientalis* Presl. Researchers have studied the biological characteristics of *Typha orientalis* Presl since the 1980s [10]. The plant has a notable medicinal value, and can also be used to purify untreated sewage to a certain extent [11,12]. Recently, researchers have studied the growth and physiological characteristics of *Typha orientalis* Presl under environmental stresses such as salinity and temperature. Su's research shows that the content of sucrose, proline and malondialdehyde increased under salt stress. Similarly, superoxide dismutase, peroxidase and catalase were significantly higher and the superoxide anion (O_2^-) was lower under salt stress [13]. Yuan et al. [14] studied the morphological characteristics and biomass changes of *Typha orientalis* Presl under different water level gradients. Wu et al. [15] studied the growth of the *Typha orientalis* Presl community in Hongze Lake wetland area under drought conditions, and the change characteristics of morphological, biomass, chlorophyll content and chlorophyll fluorescence parameters of *Typha orientalis* Presl under different soil water contents. Yuan et al. [16] studied the growth parameters and photosynthetic parameters under water stress and water abundant conditions using *Typha orientalis* Presl and the pot experiment method. Li et al. [17] studied the effect of plant coexistence on wetland plants in the depth gradient on the distribution and growth changes in the Hangzhou Bay wetland area. The past research mainly focused on the effect of environmental stress on the growth characteristics of *Typha orientalis* Presl. There are few studies on the effects of water stress and rewatering on the growth characteristics of *Typha orientalis* Presl in coexistence conditions.

Phragmites australis and *Typha orientalis* Presl often coexist in the same habitat and distribution of the two species causing them to overlap. In this study, we observed and recorded the effects of water stress and rewatering on the growth and photosynthetic parameters of *Typha orientalis* Presl under the condition of coexistence by pot experiment, and it revealed the response mechanism and threshold of the water content of *Typha orientalis* Presl under the coexistence condition. This study can provide a theoretical basis for calculating and regulating water resources in the Baiyangdian wetland area.

2. Methodology

2.1. Study site

The study focused on the Baiyangdian wetland area. It is located in central Hebei Province, close to Beijing and Tianjin regions, as shown in Fig. 1. Baiyangdian wetland is the largest freshwater wetland in the North China Plain, and plays an important role in maintaining ecological balance and biodiversity of the area, conserving the water source, regulating the regional climate and flood detention. However, due to the increased priority of the local government on water resources development and utilization in the upper reaches of wetlands in recent decades, inflows for this wetland have been reduced, resulting in a shrinking wetland area and deterioration of water quality [6,7]. Therefore, it is important to understand the resiliency of the wetlands under water stress conditions.

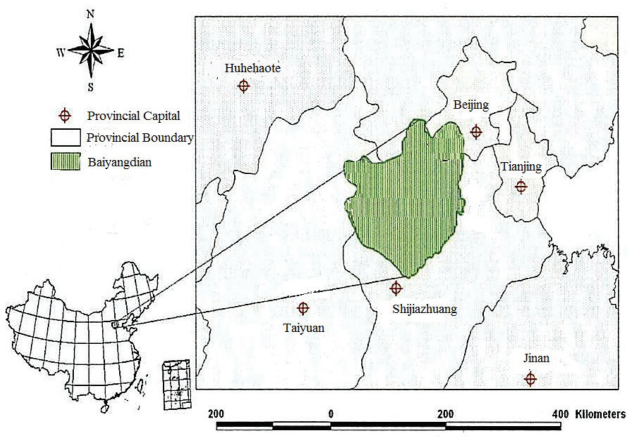

Fig. 1. Geographical location diagram of Baiyangdian.

2.2. Experimental design

Experiments were conducted in 100 cm × 80 cm × 70 cm polyethylene containers. There were a total of 48 containers. The experimental containers were filled with soil, up to 40 cm in depth. The soil bulk density was 1.1 g/cm^3, and the saturated water content was 42% after filling. The experiments were conducted in the science and technology flower greenhouses of Beijing Forestry University. Soil and plants used for the experiments were collected at the Baiyangdian wetland area.

Based on Yuan's research, the optimal water levels were maintained at 30 cm for both CK1 and CK2 scenarios [14]. CK1 was the single plant population and CK2 was the coexistence population. There were four kinds of water stress treatments: mild drought (W1i), moderate drought (W2i), drought (W3i) and severe drought (W4i), $i = 1, 2$. The purpose of the rewatering experiment was to restore the soil moisture content to the optimal water treatment scenario. The water depth and soil moisture content under various conditions are shown in Table 1.

The experiments began on May 15, 2016, and rewatering occurred on July 30, 2016. In order to study the recovery of *Typha orientalis* Presl after different levels of drought, we rewatered the W2i, W3i and W4i treatment scenarios about 2 months after the experiments began.

Approximately 10 cm tall, 150 *Typha orientalis* Presl and *Phragmites australis* seedlings were brought from the Baiyangdian wetland area and kept in the greenhouse prior to the experiments. There were five *Typha orientalis* Presl and *Phragmites australis* seedlings in each experimental container. The containers were maintained at up to saturated conditions for a month to ensure the plant seedlings survival. The soil moisture content was measured every 3–4 d. The plants' characteristics (net photosynthetic rate, stomatal conductance, transpiration rate, etc.) data were collected every 7 d during the experiments.

2.2.1. Determination of leaf physiological parameters

The leaf physiological parameters were obtained by measuring the fourth leaf from the centre of the stem to the outside using Li-6400XT portable photosynthesis machine. The parameters were measured at 8:30 am–11:30 am. The light intensity in the greenhouse was 800 μmol m^{-2} s^{-1} and the atmospheric CO_2 concentration was 490 ± 10 μmol mol^{-1}. The light intensity was controlled by Li-6400XT red and blue light source.

2.2.2. Determination of plant height and biomass

The plant height was obtained by measuring the vertical distance from the fourth leaf, leaves to the soil. We collected the stems and leaves above the ground of the plants after the experiment and measured the biomass by electronic balance.

2.2.3. Index calculation

2.2.3.1. Water use efficiency Water use efficiency is a comprehensive index of photosynthesis, transpiration rate and suitability for the evaluation of plant growth. It reflects the ability of the fixation of CO_2 or dry matter produced by per water consumption. The ratio of net photosynthetic rate to transpiration rate is usually used to represent water use efficiency as follows:

$$\text{WUS} = \text{Pn}/\text{Tr} \quad (1)$$

where WUS is the water use efficiency, Pn is the net photosynthetic efficiency and Tr is the transpiration rate.

2.2.3.2. Relative moisture content Relative water content has many ways of expression. It is expressed by fresh weight and dry weight in this research as follows:

Table 1
Water stress under different scenarios

Scenarios	Water treatment	Number of samples
CK1	Flooded 30 cm	3
CK2	Flooded 30 cm	3
W11 (Signal population)	Flooded 10 cm	3
W12 (Coexistence)	Flooded 10 cm	3
W21 (Signal population)	Up to 30%–40% of saturated moisture	6
W22 (Coexistence)	Up to 30%–40% of saturated moisture	6
W31 (Signal population)	Up to 20%–30% of saturated moisture	6
W32 (Coexistence)	Up to 20%–30% of saturated moisture	6
W41 (Signal population)	Up to 10%–20% of saturated moisture	6
W42 (Coexistence)	Up to 10%–20% of saturated moisture	6

$$\text{RWC} = (F - D)/F \quad (2)$$

where RWC is the relative water content, F is the fresh weight of the plant and D is the plant dry weight.

2.3. Data processing

The data were analyzed by one-way ANOVA and Duncan method. SPSS19.0 was used for the data analysis. The effect of the water depth and species coexistence and rewatering of *Typha orientalis* Presl was analyzed by multi-way ANOVA method.

3. Results

3.1. Effects of water stress and rewatering on growth characteristics

3.1.1. Individual Typha orientalis Presl plants

The plant height decreased with the increase in severity of water stress, it was 97.2%, 88.3%, 74.9% and 65.6% compared with the CK1 scenario, as shown in Fig. 2. After rewatering, the plant height increased, but none of them reached to the

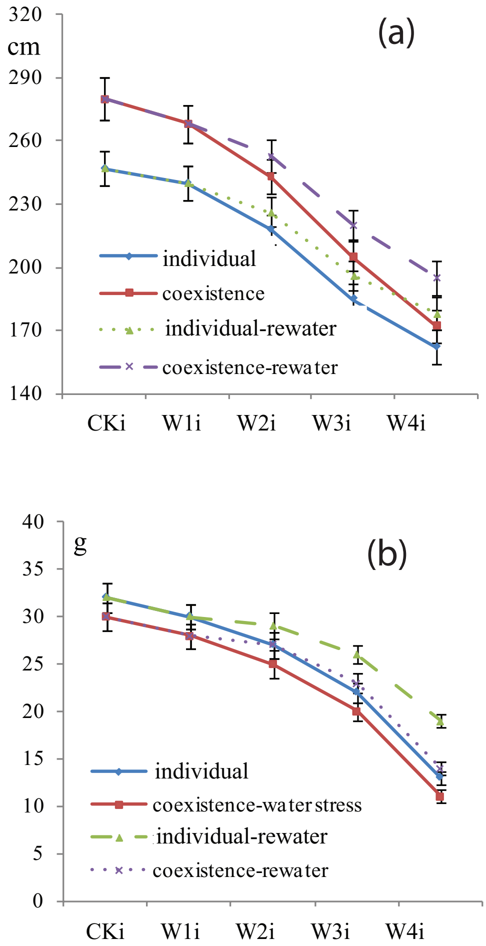

Fig. 2. Impact of stressed rewatering on (a) shoot heights and (b) biomass.

height of the CK1 scenario. At the end of the experiment, the plant height of W21, W31 and W41 scenarios increased by 3.7%, 5.9% and 9.9%, respectively. The more severe the water stress, the higher the plant height after rewatering.

The biomass of *Typha orientalis* Presl was decreased with the increase in severity of water stress. The biomass under W11's scenario was lower than that of CK1's scenario, and the dry weight of W41's scenario was the smallest at 13.2 g. It was 59.4% lower than that of CK1's scenario. After rewatering, the biomass of *Typha orientalis* Presl had a certain degree increase, but did not reach the CK1's scenario. The rewatering treatment increased the biomass of *Typha orientalis* Presl by 7.4%, 18.2% and 46.2%, respectively. The more severe the water stress, the greater increase of biomass after rewatering.

3.1.2. Coexisting population

The changes rule of plant height and biomass of *Typha orientalis* Presl in the coexisting scenario were similar to the single scenario.

The plant height of *Typha orientalis* Presl was 11.7%, 11.3%, 10.8% and 6.8% higher than the single population under coexistence conditions, and the increase proportion of plant height was gradually reduced with the increase in severity of water stress compared with the single population. After rewatering, plant height increased 4.2%, 7.3% and 13.4%, respectively, and was higher than the level in the single *Typha orientalis* Presl population.

The biomass of *Typha orientalis* Presl was decreased with the increase in severity of water stress. The biomass in the coexisting scenario was less than the single population condition 6.7%, 7.4%, 9.2% and 15.3%, respectively, under the same water stress conditions. After rewatering, the biomass increased 8%, 15% and 27.3%, respectively, which were higher than those of the single *Typha orientalis* Presl population.

3.2. Effects of water stress rewatering on net photosynthetic rate and stomatal conductance

3.2.1. Individual Typha orientalis Presl population

The net photosynthetic rate of the single population was decreased with the severity of water stress, as shown in Fig. 3. The net photosynthetic rate of *Typha orientalis* Presl was only 8.7 μmol m^{-2} s^{-1} after the experiment under the W41 scenario. It was only 30% of CK1's scenario. The net photosynthetic rate of *Typha orientalis* Presl was increased 12.4%, 7.9% and 40%, respectively, compared with the corresponding water stress after the rewatering under W21, W31 and W41 scenarios.

The stomatal conductance of the individual population was decreased with the severity of water stress, and it was 68.9%, 57.5%, 42.6% and 36.8% of CK1's scenario under water stress. After rewatering, the stomatal conductance showed an upward trend, and W21, W31 and W41 scenarios were increased by 33.7%, 17.3% and 1.9%, respectively. The recovery ability of W41's scenario was the weakest.

3.2.2. Coexisting population

The changes found in the rules of net photosynthesis rate and stomatal conductance *Typha orientalis* Presl were similar to the single population under water stress.

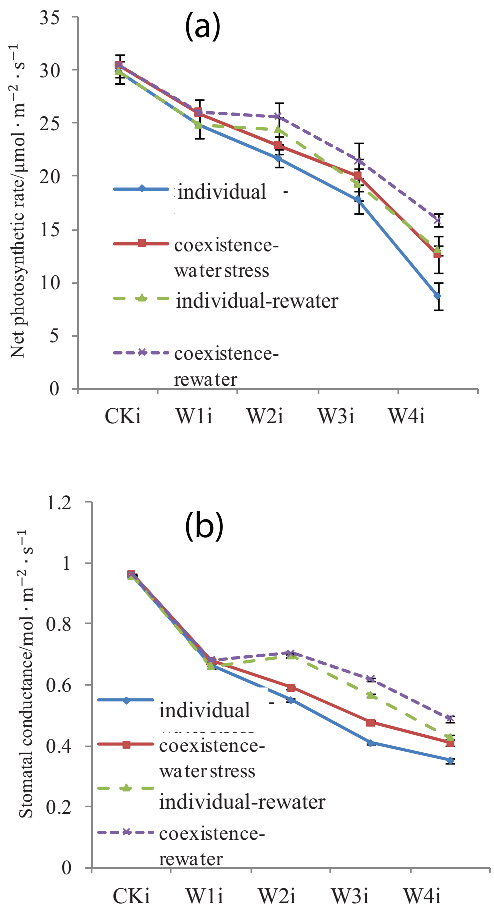

Fig. 3. Impact of water stress rewatering on (a) net photosynthetic rate and (b) stomatal conductance.

The net photosynthetic rate of *Typha orientalis* Presl was higher than that of the single population under coexistence condition, 4.9%, 5.8%, 12.9% and 45.1%, respectively. The increase ratio of net photosynthetic rate was gradually increased with the increase in severity of water stress. The net photosynthetic rate increased 11.6%, 6.7% and 25.7% after rewatering, which was higher than that under the individual *Typha orientalis* Presl population.

The stomatal conductance of *Typha orientalis* Presl decreased with the severity of water stress. Under the same water stress, the stomatal conductance in the coexistence was 3.1%, 7.5%, 17.1% and 16.2% higher than individual population, respectively. After rewatering, the stomatal conductance increased 18.9%, 28.8% and 19.3%, which were higher than individual *Typha orientalis* Presl population.

3.3. Effects of water stress rewatering on transpiration rate and water use efficiency of leaves

3.3.1. Individual Typha orientalis Presl population

The transpiration rate of the individual population was decreased with the increase in severity of water stress, as shown in Fig. 4. It was only 7.9 mmol m^{-2} s^{-1} under W41 scenario, only 40% of the CK1 scenario. After rewatering, the transpiration

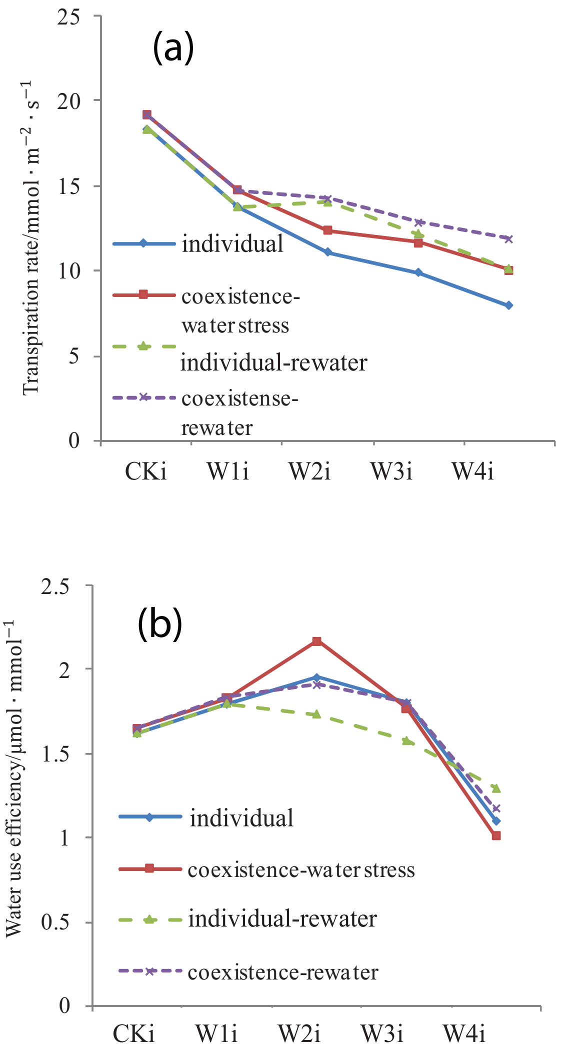

Fig. 4. Impact of stress rewatering on (a) transpiration rate and (b) water use efficiency.

rate increased by 26.8%, 23.5% and 27.8% under the W21, W31 and W41 scenarios.

With the increase in severity of water stress, the water use efficiency of individual population increased at first, followed by a decrease. The highest water use efficiency was W21's scenario, which was 1.96 μmol $mmol^{-1}$. The water use efficiency was reduced by 11.3% and 12.7% under W21 and W31 scenarios, but the water use efficiency increased by 17.3% under W41's scenario.

3.3.2. Coexisting population

The changes of the transpiration rate and the water use efficiency of *Typha orientalis* Presl were similar to those of the individual population under the same water stress conditions.

The transpiration rate of *Typha orientalis* Presl was 6.9%, 11.6%, 18.1% and 26.9% higher than that of individual population under the coexistence condition. The proportion of the transpiration rate increased with the increase in severity of water stress. It was 14.9%, 9.7% and 18.1%, respectively, which were lower than the individual *Typha orientalis* Presl population after rewatering.

The water use efficiency increased first, and then decreased with the increase in severity of water stress, and the highest water use efficiency was found in the W22 scenario, which was at 2.17 μmol $mmol^{-1}$. The water use efficiency was reduced by 11.9% in the W22 scenario, while it increased by 1.7% and 15.8% under the W32 and W42 scenarios.

3.4. Results of multivariate analysis of variance

The results of multivariate analysis of variance showed that the effects of water stress and rewatering on the morphology and photosynthetic parameters were significant ($p < 0.01$), as shown in Table 2. The effect of interspecies had a significant influence on the plant height and biomass of *Typha orientalis* Presl ($p < 0.01$), and also had a significant effect on the photosynthetic parameters ($p < 0.05$).

Table 2
Results of forms and photosynthetic parameters of *Typha orientalis* Presl in coexisting population by multivariate analysis of variance

Forms and photosynthetic parameters	Factors	*F*	*p*	Forms and photosynthetic parameters	Factors	*F*	*p*
	Water stress	5.881	0.001**		Water stress	1.935	0.001**
Height	Interspecies	15.996	0.002**	Stomatal conductance	Interspecies	17.192	0.020*
	Rewatering	7.377	0.002**		Rewatering	5.672	0.000**
	Water stress	54.824	0.001**		Water stress	5.729	0.000**
	Interspecies	22.853	0.000**	Transpiration rate	Interspecies	5.814	0.030*
Biomass	Rewatering	5.833	0.005**		Rewatering	10.918	0.001**
	Water stress	4.768	0.001**		Water stress	4.408	0.001**
Net photosynthetic rate	Interspecies	12.702	0.025*	Water use efficiency	Interspecies	11.222	0.030*
	Rewatering	1.265	0.000**		Rewatering	13.417	0.004**

*Indicates significant difference at the level of $p < 0.05$.
**Indicates significant difference at $p < 0.01$ level.

4. Discussions

4.1. Effects of drought on the growth of Typha orientalis Presl

Photosynthesis is one of the basic physiological processes of plant growth, which is affected by light, temperature, water, fertilizer, carbon dioxide and other factors. Net photosynthetic rate, transpiration rate and plant height will be reduced with the increase in severity of water stress, which indicated that the drought stressed the limit of plant accumulation and affected plant growth [18,19]. At the beginning of the experiment, the plant height and photosynthesis of *Typha orientalis* Presl were close to each other, but at the end of the experiment, the more severe the stress of the drought, the more the restriction on the growth of *Typha orientalis* Presl.

4.2. Effects of rewatering on the growth of Typha orientalis Presl

The results show that rewatering can produce a compensatory effect on plants after moderate drought stress. When rewatering, the structure and physiology are beneficial to the ability of plant growth and yield formation, which is similar to other researchers' conclusions on wheat [20]. The results showed that the net photosynthetic rate was relatively low. Although the growth of *Typha orientalis* Presl had been restored after rewatering, it did not reach the level of CKi's scenario. The reason for the difference may be due to the rewatering time of the experiment in early August. During the period, *Typha orientalis* Presl had mostly stopped growing. The fresh weight in W2i's scenario was more than CKi's scenario, and the dry weight was the same as CKi's scenario, indicating that there was a super-compensation effect on *Typha orientalis* Presl after rewatering. Through analysis of the recovery rate of the net photosynthetic rate and biomass after rewatering, it can be concluded that rewatering could not return the plants to a better condition when the soil water content was less than 30% under drought stress conditions.

Water use efficiency reflects the relationship between plant dry matter accumulation and water loss. Studies have shown that moderate drought can improve plant water use efficiency. At the end of the water stress experiment, W2i's scenario had the highest water use efficiency. In addition, water stress and rewatering improved the water use efficiency of *Typha orientalis* Presl, which was an effective way to reduce the adverse effects of drought on the plant, and also provided the basis for calculating ecological water demand of the wetland plant species.

4.3. Effects of coexisting population on the growth of Typha orientalis Presl

Compared with the individual population, the plant height of the coexisting population was increased, and the biomass was decreased, which indicated that the coexistence of species could affect the plant's individual morphology and spatial distribution. In order to obtain more light resources, the plant height must be higher due to the reduction of light received by the interspecific competition. The reduction of biomass is due to competition leading to the reduction in the availability of resources for each species in coexistence scenarios.

5. Conclusions

Under the influence of drought and water stress; photosynthesis, plant height and biomass of *Typha orientalis* Presl were decreasing with the increase in severity of drought, and moderate drought could improve the water use efficiency.

There was a compensatory effect in the growth of *Typha orientalis* Presl when rewatering, but when the soil moisture content dropped to less than 30%, the effect of rewatering made it extremely difficult to restore the plant to a better state.

Rewatering can improve the water use efficiency of *Typha orientalis* Presl, different recovery degree under different water stress, but the other scenario plants did not recover to CKi scenario levels. After rewatering, it increased the water absorption, but the dry matter quality increased less.

Compared with the individual species, the number of leaves and the biomass of *Typha orientalis* Presl were decreased in coexistence scenarios, but the plant height increased.

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