

Effect of Drought Stress on Leaf Gas Exchange, Chlorophyll Content and Dry Matter Allocation of *Phragmites australis* in the Heihe River Basin

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***Phragmites australis* is considered the dominant species of wetlands, especially in Northwest China. It plays a very important role in wetland regulation, but little is known about its photosynthetic capacity. Here, we investigated gas exchange parameters, chlorophyll content and dry matter allocation under different watering regimes along the West Lake Wetland of the Hexi Corridor in China. Drought stress significantly decreased P_N , E , g_s , chlorophyll content (Chl a, Chl b, Chl (a + b), Chl a/b) and augmented C_i , but it also decreased the root, shoot, leaf and total dry matter of *P. australis*. According to Farquhar and Sharkey (1982), there are both stomatal and nonstomatal limitations to photosynthesis. Stomatal limitation dominates when water stress first occurs, whereas nonstomatal limitation dominates during severe drought. Drought stress lowered Chl a, Chl b, and Chl (a + b), and also the Chl a/b ratio, showing that water stress seriously damages the PSII reaction center in *P. australis*. Water stress also lowered relative water content (RWC) and water use efficiency (WUE) at 75% water treatment, indicating that *P. australis* was sensitive under drought stress. The threshold for *P. australis* at which seedling growth was reduced or even terminated was a decline in RWC to less than 57.58%.**

Key Words: chlorophyll content, drought stress, dry matter, leaf gas exchange, *Phragmites australis*

Abbreviations: C_i – intercellular CO₂ concentration, CK – control, DS – drought stress, E – transpiration rate, FC – field water capacity, g_s – stomatal conductance, L_s – stomatal limitation value, P_N – photosynthetic rate, PSII – photosynthetic system II, RWC – relative water content, WUE – water use efficiency

INTRODUCTION

Water is an important resource for plants, and a plant's water content is often the decisive factor in controlling the strength of its life activities (Zhang et al. 2011). In arid and semi-arid areas, drought stress is one of the most important abiotic factors affecting crop growth and crop yield (Li et al. 2009). Water deficit is often a key factor limiting plant growth, productivity and survival, and it often adversely affects agroforestry practices in arid and semi-arid areas (Sánchez-Rodríguez et al. 2010; Guo et al. 2016). For most plants, water deficit leads to stomatal closure and reduced photosynthesis. Furthermore, prolonged drought can limit plant growth and biomass production, alter biomass allocation, and even cause plant

death (Yin et al. 2005; Yang et al. 2013). Huang et al. (2007) and Pireivatlou et al. (2008) reported that water deficit has an inhibitory effect on root and shoot growth in wheat, and can significantly reduce its biomass, yield and harvest index. When water-limited, the stem height, total leaf area, total dry weight and specific leaf area of wheat plants have been observed to decrease (Wang et al. 2007). Under drought conditions, the chloroplast stroma ion concentration increases due to cell and chloroplast water loss. The photosynthetic rate decreases because the chloroplast's carbon-fixing enzyme activity and photosynthetic phosphorylation of metabolic pathways change. Accumulation of plant dry matter also changes (Carter et al. 1997). Drought stress may reduce leaf area and chlorophyll content, inhibit the photosynthetic rate and destroy the photosynthetic system II (PSII) (Zhang et

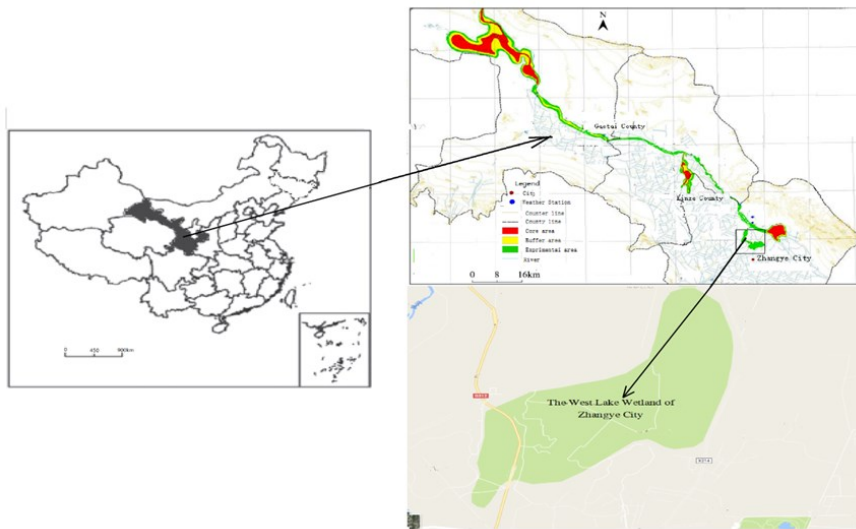


Fig. 1. Map of the study site (cited from Bai et al. 2017; Li et al. 2017).

al. 2011). Li et al. (2007) found that Chl a and Chl b contents decreased under drought stress in several different lawn cultivars. Wu et al. (2008) also reported that drought stress lowered the Chl a, Chl b and Car contents in *Sophora davidii* seedlings. Meanwhile, the decline in photosynthesis caused by drought stress is one of the main reasons for crop yield reduction. Thus, in arid and semi-arid areas, water is considered the most important factor that limits plant growth.

The inland Heihe river basin (N 38°–42°, E 98°–101° 30') is located in the arid and semi-arid region of Northwest China, which is in the center of the Hexi Corridor in Gansu, China. It is the second largest inland river basin in China, covering more than 14.29 × 10⁴ km². Of this, the wetland is about 8000 km², with 30,000 hm² or 17.6% of the total wetland covered by *P. australis* wetland (Zhang et al. 2016). *P. australis* is one of the most important indicator plants in wetland ecosystems and is considered one of the most productive plants. Its growth trend directly affects the health of wetland ecosystems. *P. australis* is also the dominant species of the Heihe wetland. Due to the ecological and economic value of *P. australis*, some scholars have carried out extensive research focusing on the effects of either water and/or salinity stress on its acclimation (Hootsmans and Wiegman. 1998). However, there exists little information regarding the physiological responses of *P. australis* to the effects of soil water stress.

The main objective of this study is to explore the response of photosynthetic parameters, chlorophyll content and dry matter allocation to soil water stress. This will help us understand the physiological responses of *P. australis* to water conditions. The objectives of this paper are as

follows: 1) understand the adaptive mechanism of *P. communis* to drought stress, 2) provide a theoretical explanation for the self-sustenance of *P. australis* in the face of adversity and propose new data-supported methods for the restoration and protection of the Heihe wetland, and finally 3) determine the changes in various physiological indices for *P. australis* under water stress, scientifically describe the water requirement characteristics, calculate the ecological water demand threshold of *P. australis*, protect the plants during wetland construction and provide a scientific basis for the impending

construction of ecological barriers in the Hexi Corridor.

MATERIALS AND METHODS

Site Description and Sampling

The study area is located in the West Lake Wetland of Zhangye City (100°21'E – 100°22'E, 39°01'N – 39°02'N, 1439 – 1496 m AMSL) in Gansu Province, China. The climate is a continental environment with a mean rainfall of only 129 mm. The annual mean evaporation is 2047 mm. The annual mean temperature is 7 °C (Bai et al. 2017). The specific location of the study area is shown in Figure 1 (map of the study site is cited from Bai et al. 2017; Li et al. 2017).

The experiment was carried out in the West Lake Wetland of Zhangye City to determine the effects of water stress on gas exchange, chlorophyll content and dry matter allocation in *P. australis*. On April 11, 2016, we collected about 15 mL of *P. australis* seed from the wetland. The seeds were planted in plastic pots (50 cm in diameter and 45 cm in height) in the wetland soil. The experiment layout included control (CK) and drought-stress (DS) groups. Each treatment contained 10 pots. Then each pot was weighed and the soil water content was measured via a drying method. In order to ensure all treatment pots had precisely the right amount of water, we used a dropper to water the *P. australis* plants. When the plants had grown to an approximate height of 250 cm, all plastic pots were moved to a mobile rain shelter. From July 12 to July 22, 2016, the DS plants were subjected to water stress. The CK plants were grown under the rain

Table 1. Change in field water capacity (FC) and relative moisture content (RWC) for leaves under control (CK) and drought stress (DS) at different treatment days. Data is shown as the mean \pm SE.

Treatment Day [d]	Field Water Capacity (FC) [%]		RWC (%)	
	CK	DS	CK	DS
0d	100	100	85.83 \pm 1.13a	89.80 \pm 1.97a
1d	100	95	84.49 \pm 3.24a	84.51 \pm 1.94ab
2d	100	90	85.52 \pm 3.31a	85.17 \pm 1.15b
3d	100	85	84.07 \pm 1.14a	78.07 \pm 1.86c
4d	100	80	85.57 \pm 1.27a	69.99 \pm 1.95d
5d	100	75	86.31 \pm 0.71a	57.58 \pm 0.92e
Rewatering	100	100	84.02 \pm 1.05a	59.64 \pm 1.35e

Values denoted by different letters differ significantly at $P < 0.05$ according to Duncan's multiple range tests.

shelter, with a regular watering regimen. The DS pots were not watered to allow natural consumption of the soil moisture. After 5 d of treatment, all plants were watered daily, with a regimen identical to the control. At 0, 1, 2, 3, 4, 5 and 6 d of treatment, the photosynthetic parameters, Chl content and dry matter allocation were measured in both the CK and DS treatments.

Relative Water Content (RWC) of Leaves

Relative water content (RWC) was determined gravimetrically for each leaf at pre-dawn. Three fully expanded compound leaves were selected per seedling. They were placed in dishes containing wet filter paper and weighed immediately, to determine their fresh weight (FW). Turgid weight (TW) was determined after leaves were floated in distilled water in a dark, closed container at 4°C for 24 h. Dry weight (DW) was determined for the same leaves after oven-drying for 48 h at 70°C. RWC was calculated as follows: $RWC (\%) = [(FW - DW) / (TW - DW)] \times 100$. (Li et al. 2009)

Gas Exchange Calculations

At 0, 1, 2, 3, 4, 5 and 6 d of treatment, the net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s) and intercellular CO₂ concentration (C_i) were measured for *P. australis* leaves from 9:30 to 10:30 AM using a CIRAS-2 portable photosynthesis system. The measurements were conducted on the uppermost, fully expanded healthy leaves of three different plants per treatment. Uniform conditions were maintained during the measurements (30°C, approximately 420 $\mu\text{mol mol}^{-1}$ of CO₂ concentration, 2.5 cm² of leaf area and 1000 $\mu\text{mol m}^{-2}$

s⁻¹ of PAR provided by a LED fixed light source). The ratio of P_N to E was calculated to determine instantaneous water use efficiency (WUE). The stomatal limitation value (L_s) was calculated using the formula: $L_s = 1 - C_i/C_a$ (Yin et al. 2005).

Chl Content Determination

At 0, 1, 2, 3, 4, 5 and 6 d of treatment, we collected 0.1 g of fresh leaf mass to determine the Chl content. Leaves were ground in 80% acetone to extract both Chl a and Chl b. Pigment quantities were calculated according to Lichtenthaler (1987).

Dry Matter Determination

After the photosynthetic activity and quality parameters were determined, all leaves were harvested. We separated the biomass into roots, stems and leaves. These samples were placed in an oven at 60°C for 48 h. After drying, the dry weight recorded content and dry matter allocation were measured for the CK and DS groups. The total plant dry matter is the sum of the root, stem and dry leaf matter (Guo et al. 2016).

Data Analysis

All experiments were conducted using a randomized complete block design replicated three or five times. All data was subjected to one-way analysis of variance (ANOVA). Least significant difference (LSD) multiple comparison tests were used to separate significant differences among all treatments at the 0.05 level. Standard error (SE) was calculated and is shown in the figures and tables. All statistical analyses were performed using SPSS software (standard released version 18.0 for Windows, SPSS, United States), and graphs were generated using the Origin 8.0 software (United States).

RESULTS

Relative Water Content (RWC) of Leaves

For the CK treatment, there was no significant difference in RWC from beginning to end (Table 1). However, the RWC declined significantly during the DS treatment. The RWC of the DS treatment group was reduced significantly in the 75% FC and rewatering compared with 100% FC at 0 d and 95% FC after 1 d of treatment, respectively. The RWC of the seedlings undergoing DS

Table 2. Effect of control (CK) and drought stress (DS) on the chlorophyll (Chl) a, Chl b, Chl (a + b), and Chl a/b of *Phragmites australis* seedlings. Data is shown as mean \pm SE.

Treatment Day [d]	Chl a [mg g^{-1}]		Chl b [mg g^{-1}]		Chl a+b [mg g^{-1}]		Chl a/b	
	CK	DS	CK	DS	CK	DS	CK	DS
0d	7.19 \pm 0.54 ^a	6.62 \pm 0.32 ^a	2.04 \pm 0.20 ^a	1.70 \pm 0.08 ^a	9.22 \pm 0.65 ^a	8.32 \pm 0.41 ^a	3.52 \pm 0.07 ^b	3.90 \pm 0.05 ^a
1d	6.38 \pm 1.01 ^a	6.14 \pm 0.50 ^a	1.66 \pm 0.13 ^a	1.57 \pm 0.25 ^{ab}	9.25 \pm 1.25 ^a	7.71 \pm 0.74 ^a	3.83 \pm 0.08 ^b	4.04 \pm 0.41 ^a
2d	7.58 \pm 0.70 ^a	5.86 \pm 0.09 ^a	1.66 \pm 0.19 ^a	1.51 \pm 0.18 ^{ab}	8.05 \pm 0.73 ^a	7.36 \pm 0.24 ^a	4.57 \pm 0.40 ^a	4.00 \pm 0.40 ^a
3d	6.36 \pm 0.34 ^a	5.53 \pm 0.30 ^a	1.65 \pm 0.12 ^a	1.49 \pm 0.12 ^{ab}	8.02 \pm 0.39 ^a	7.02 \pm 0.42 ^a	3.85 \pm 0.12 ^b	3.74 \pm 0.16 ^a
4d	7.41 \pm 0.76 ^a	4.38 \pm 0.63 ^b	1.85 \pm 0.27 ^a	1.16 \pm 0.17 ^b	9.16 \pm 0.91 ^a	5.54 \pm 0.79 ^b	3.93 \pm 0.15 ^b	3.78 \pm 0.16 ^a
5d	7.50 \pm 0.23 ^a	0.56 \pm 0.17 ^c	1.91 \pm 0.09 ^a	0.21 \pm 0.04 ^c	9.41 \pm 0.28 ^a	0.77 \pm 0.21 ^c	3.93 \pm 0.03 ^b	2.60 \pm 0.36 ^b
Rewatering	7.38 \pm 0.64 ^a	0.53 \pm 0.06 ^c	2.05 \pm 0.26 ^a	0.20 \pm 0.01 ^c	9.43 \pm 0.77 ^a	0.73 \pm 0.07 ^c	3.59 \pm 0.05 ^b	2.63 \pm 0.23 ^b

Values denoted by different letters differ significantly at $P < 0.05$ according to Duncan's multiple range tests.

treatment was lowered 36% and 34% at the 75% FC and rewatering regimes, respectively, compared with 100% FC. However, there were no significant differences between 75% FC and rewatering under the DS treatment.

Diurnal Variation in Leaf Gas Exchange

Gas exchange parameters differed between the CK and DS treatments (Fig. 2). For the CK treatment, the gas exchange parameters remained constant. For the DS treatment, water stress ranging from 90% to 75% FC resulted in significant decreases in the majority gas exchange parameter (Fig. 2). Under the DS treatment, the P_N tended to decrease with increasing water stress intervals. It was significantly higher in the control than in the water stress treatments (Fig. 2a). The changes in both g_s and WUE under drought treatment were similar to the P_N trend (Fig. 2b, 2e). E and L_s changed similarly, first gradually increasing to a peak of about 90% for the DS treatment, and then decreasing until rewatering (Fig. 2c, 2f). The changes in C_i were the opposite of those in L_s (Fig. 2d) in the DS treatments. All gas exchange parameters differed statistically between the control and drought treatments ($p < 0.05$, Fig. 2).

Photosynthetic Pigment Content

Photosynthetic pigment content was altered significantly in response to the DS treatment (Table 2). All drought stress treatments lowered Chl a compared with the 0 d (100% FC) treatment, but chlorophyll decreased sharply for the 75% FC and rewatering treatments. The rewatering treatment had the lowest Chl a content, followed by the 75% FC treatment. The Chl a of the DS treatment was 91.5% and 92.0% lower than 100% FC in the 75% FC and rewatering regimes, respectively. The

75% and 80% FC treatments had lower Chl a/b compared with the other treatments. The 75% and 80% FC treatments also had lower Chl b and Chl (a + b) contents, showing a similar trend to Chl a. The chlorophyll content parameters remained constant for the *P. australis* seedlings in the CK treatment.

Dry Matter Allocation

Dry matter allocation was altered significantly in the water stress treatments (Fig. 3). Water stress caused a decrease in root, stem, leaf and total dry matter compared with the CK treatment. The leaves of *P. australis* were greatly and significantly affected by water stress ($P < 0.01$). The DS treatment resulted in the lowest dry matter allocation.

DISCUSSION

The leaf relative water content (RWC) is considered a reliable indicator for defining the sensitivity of plants to dehydration (Guo et al. 2016). Water-stressed plants maximize the water potential gradient by reducing RWC to increase water uptake from the soil. The RWC of plants commonly reaches 50% to 60% and occasionally $< 50\%$ during severe drought (Li et al. 2009). Our results indicated that high values of RWC are found in well-irrigated plants (Table 1). For the CK treatment, RWC did not differ significantly between 100% FC and rewatering (Table 1). But the DS treatment did affect RWC significantly. The RWC was found to decrease with increased water stress. The RWC decreased sharply in the 57.58% and rewatering treatments. The RWC of the DS treatment seedlings was 36% and 34% lower than the 100% FC for the 75% FC and rewatering regimes,

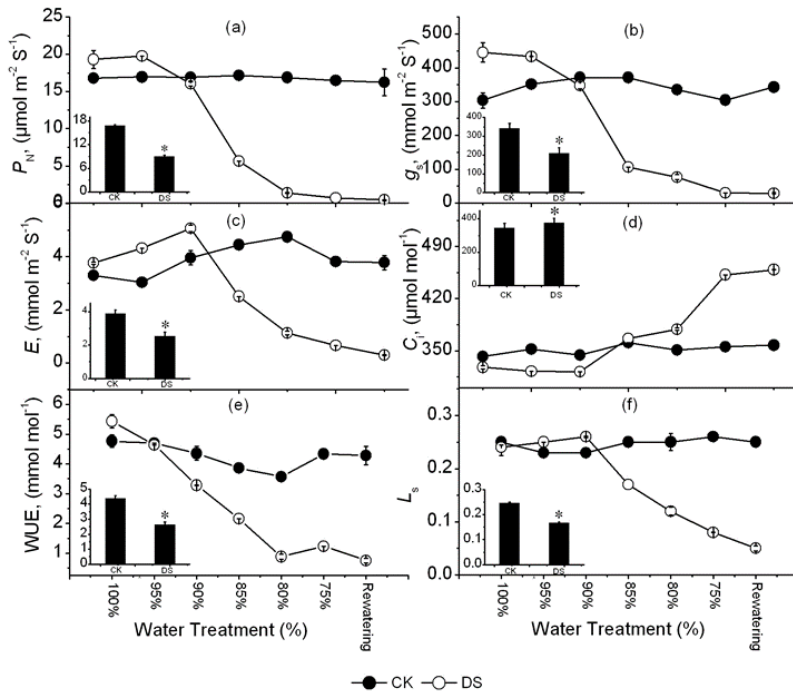


Fig. 2. Diurnal changes of photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), water use efficiency (WUE), intercellular CO_2 concentration (C_i) and stomatal limitation value (L_s) of *Phragmites australis* leaves under control (CK) and drought (DS) conditions. An asterisk(*) in insets indicates a significant difference in diurnal means between drought and control conditions at $P < 0.05$. Mean \pm SE ($n = 3$).

respectively. Similarly, Tambussi et al. (2000) reported that RWC decreases in cultivars of wheat under water stress. Drought-tolerant plant species maintain high RWC compared with drought-sensitive sugarcane cultivars (Tahar et al. 2010). We concluded that a decline in leaf relative moisture content to less than 57.58% RWC was the threshold at which seedling growth was reduced or even terminated. The RWC of *P. australis* did not recover at the end of the water recovery period. This result suggests that this plant is weakly adapted to drought environments. Intriguingly, we also found that the overground leaves and stems of *P. australis* died at the 57.58% RWC threshold, but the subsurface roots survived. Future studies are needed to determine the moisture threshold for the subsurface roots of *P. australis*.

Water deficit is one of the most important limitations for plant photosynthesis and productivity (Wu et al. 2008). Photosynthesis is exceptionally sensitive to drought stress, because drought can cause stomata to close and reduce mesophyll conductance, thereby limiting CO_2 availability (Flexas et al. 2008). A decline in the photosynthetic rate under water stress conditions could be attributed either to a decrease in stomatal conductance

and/or to non-stomatal limitations (Chartzoulakis et al. 2002). Ramanjulu et al. (1998) and Zhao et al. (2011) found that stomatal limitation plays a major role in how mild drought stress affects the P_N of mulberry and *Lespedeza davurica*. However, the non-stomatal limitation was found to dominate during severe drought. This was evident in our results, too. We found that C_i decreased and that L_s and E decreased from 100% FC to 90% FC, but after 90% FC, the changes observed in C_i , L_s and E were the opposite (Fig. 2c, 2d, 2f). According to Liao and Wang (2014), non-stomatal limitation is the dominating photosynthesis-limiting factor when a decrease in L_s is accompanied by an increase in C_i . Conversely, stomatal limitation dominates when L_s increases and C_i decreases. Thus, the P_N depression of *P. australis* leaves is first caused by stomatal limitation, and then non-stomatal limitation became a bigger factor during severe drought (Fig. 2a). Similar results were observed for other species, such as mulberry (Ramanjulu et al. 1998) and *Lespedeza davurica* (Zhao et al. 2011). Our results also showed that P_N and g_s were constant under well-watered conditions (Fig. 2a, 2b). Under drought conditions, the P_N was significantly inhibited and accompanied by a decrease in g_s and WUE. The WUE is an important index for evaluating the ability of a plant to maintain water equilibrium (Zhang et al. 2016). Some drought-tolerant plants avoid plant damage by enhancing WUE (Zhang et al. 2016; Tahar et al. 2010). In our study, water stress significantly lowered WUE (Fig. 2e). Similar findings were documented for a variety of crop plants such as millet, barley and sorghum (Tahar et al. 2010). Michihiro et al. (1994) pointed out that drought-tolerant plants increased in WUE, while the drought-sensitive plant decreased in WUE. This result further confirmed that *P. australis* is not drought-tolerant.

Chlorophyll content is another factor that affects the photosynthetic process in green plants (Luvaha et al. 2011). Leaf Chl content is one of the most important factors in determining photosynthesis rate, and it is also associated with dry matter production (Dai et al. 2009). Some reports have suggested that reduced rates of photosynthesis may result from reduced Chl content. Our data shows that the Chl a, Chl b and Chl (a+b) were significantly reduced under severe water stress (treatment

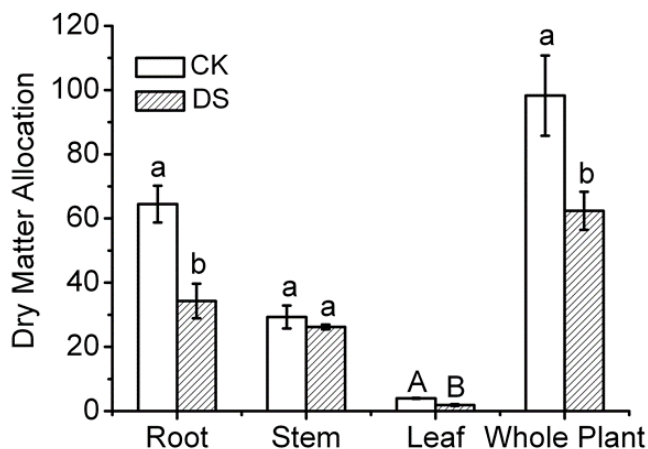


Fig. 3. Root mass, stem mass, leaf mass and whole plant mass of *Phragmites australis* at different water stress treatments [control group (CK) and drought stress (DS) treatments]. Each value represents the mean \pm SE of at least three independent experiments. Different lowercase letters denote a significant difference at $P < 0.05$ and uppercase letters denote a significant difference at $P < 0.01$.

75%) (Table 2). The reduction in Chl a, and a parallel decreasing trend in Chl b, led to a barely decreasing Chl a/b ratio. This decline in the Chl content suggests that water stress greater than 75% water level may seriously impair or totally inactivate the photosynthetic system (Dai et al. 2009). A decline in the Chl a/b ratio suggests that water stress may excite imbalance between PSI and PSII, possibly damaging the photosynthetic apparatus (Zhang et al. 2011). Zhang et al. (2011) observed a similar phenomenon in lilies. After rewatering, the chlorophyll content did not recover, indicating that water stress caused serious damage to the PSII reaction center in *Phragmites australis*. Even when the stressful conditions had subsided, the PSII reaction center remained closed and unable to capture light energy for photochemical reactions. Thus, the photosynthesis was blocked, which led to death for *P. australis*, the destruction of wetland ecosystems, and the loss of function.

Water deficit is often a key factor limiting plant growth, productivity and survival (Li et al. 2009). Many studies have found that prolonged drought can limit plant growth and biomass production, alter the allocation pattern of biomass and even cause plant death (Li et al. 2009). Yin et al. (2005) reported that the shoot height, total biomass, total number of leaves and total leaf area of two sympatric *Populus* species declined significantly under water stress (Yin et al. 2005). In this experiment, root, shoot, leaf and total dry matter accumulation were the greatest observed decreases (Fig. 3). The effects of water stress upon biomass reported here are similar to those reported by others (Pagter et al. 2005). The water stress

had an extremely significant effect on *P. australis* leaves ($P < 0.01$) (Fig. 3). The leaf is the plant organ most responsive to environmental conditions and the reduction of leaf area limits photosynthesis, and further decreases biomass production (Li et al. 2009). Our experiments confirmed that the leaf of *P. australis* seedlings are very sensitive characters to soil drought.

CONCLUSIONS AND RECOMMENDATION

Conclusively, drought stress significantly decreased gas exchange (i.e., P_N , E , g_s , and WUE), photosynthetic pigment content, and Chl a/b ratio, as well as RWC and root, shoot, leaf and total dry matter accumulation. Eventually, drought stress led to the death of *P. australis*. Both stomatal and nonstomatal limitations affected photosynthesis. Stomatal limitation was most dominant in the beginning stages of water stress, but nonstomatal limitation dominated during severe drought. The chlorophyll content was significantly reduced by severe water stress. Even after rewatering, the chlorophyll content did not recover. This revealed that water stress seriously damages the PSII reaction center in *P. australis*. Low RWC and WUE in the 75% water treatment confirmed that *P. australis* is sensitive under drought stress. Meanwhile we identified an RWC threshold of 57.58%, at which the declining RWC correlates with reduced or terminated seedling growth. However, this threshold only holds for the moisture content of overground leaves and stems of *P. australis*. Thus, future efforts may be made to determine the moisture threshold at which the subsurface roots of *P. australis* are harmed.

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REFERENCES CITED

- BAI N, WANG L, KONG DS. 2017. Spatial distribution and chemical properties of marsh wetland soil in the Heihe nature reserve. *Acta Prataculturae Sinica* 26: 15–28. [In Chinese]

- CARTER EB, THEODOROU MK, MORRIS P. 1997. Responses of *Lotus corniculatus* to environmental change. I. Effects of elevated CO₂, temperature and drought on growth and plant development. *New Phytol* 136: 245–253.
- CHARTZOULAKIS K, PATAKAS A, KOFIDI G, BOSABALIDIS A, NASTOU A. 2002. Water stress affects leaf anatomy, gas exchange, water relations and growth of two avocado cultivars. *Sci Hortic* 95: 39–50.
- DAI YJ, SHEN ZG, LIU Y, WANG LL, HANNAWAY D, LU HF. 2009. Effects of shade treatments on the photosynthetic capacity, chlorophyll fluorescence, and chlorophyll content of *Tetrastigma hemsleyanum* Diels et Gilg. *Environ Exp Bot* 65: 177–182.
- FLEXAS J, RIBAS-CARBÓ D, GALMÉS, MEDRANO H. 2008. Mesophyll conductance to CO₂: current knowledge and future prospects. *Plant Cell Environ* 31: 602–621.
- FARQUHAR GD, SHARKEY TS. 1982. Stomatal conductance and photosynthesis. *Ann Rev Plant Physiol* 33: 317–345.
- GUO YY, YU HY, KONG DS, YAN F, ZHANG YJ. 2016. Effects of drought stress on growth and chlorophyll fluorescence of *Lycium ruthenicum* Murr. seedling. *Photosynthetica* 54: 524–531.
- HUANG ML, DENG XP, ZHOU SL, ZHAO YZ. 2007. Grain yield and water use efficiency of diploid, tetraploid and hexaploid wheats. *Acta Ecol Sin* 27: 1113–1121. [In Chinese]
- HOOTSMANS MJM, WIEGMAN F. 1998. Four helophyte species growing under salt stress: their salt of life? *Aquat Bot* 62: 81–94.
- LI YQ, XIA XL, YIN WL. 2007. Effects of water stress on photosynthetic pigments and chlorophyll fluorescence in four turf grasses. *Journal of Henan Agricultural Sciences* 36: 69–72.
- LI FL, BAO WK, WU N. 2009. Effects of water stress on growth, dry matter allocation and water-use efficiency of a leguminous species, *Sophora davidii*. *Agroforest Syst* 77: 193–201.
- LI XY, WEN BL, YANG F, HARTLEY A, LI XJ. 2017. Effects of alternate flooding-drought conditions on degenerated *Phragmites australis* salt marsh in northeast China. *Restor Ecol* 25: 810–819.
- LIAO JX, WANG GX. 2014. Effects of drought stress on leaf gas exchange and chlorophyll fluorescence of *Glycyrrhiza uralensis*. *Russ J Ecol* 45: 532–538.
- LICHTENTHALER HK. 1987. Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. *Methods Enzymol* 148: 350–382.
- LUVAHA E, NETONDO GW, OUMA G. 2011. Effect of water deficit on the growth, gas exchange and chlorophyll content of mango (*Mangifera indica*) rootstock seedlings. *Acta Hortic* 911: 375–382.
- MICHIHIRO W, LUI JCB, GARVALHO GC. 1994. Cultivar difference in leaf photosynthesis and grain yield of wheat under soil water deficit conditions. *Jpn J Crop Sci* 63: 339–344.
- PAGTER M, BRAGATO C, HANS B. 2005. Tolerance and physiological responses of *Phragmites australis* to water deficit. *Aquat Bot* 81: 285–299.
- PIREIVATLOU AS, ALIYEV RT, HAJIEVA SI. 2008. Structural changes of the photosynthetic apparatus, morphological and cultivation responses in different wheat genotypes under drought stress condition. *Abst 11th Int Wheat Genetics Symp* 2008, p. 1–3.
- RAMANJULU S, SREENIVASULU N, SUDHAKAR C. 1998. Effect of water stress on photosynthesis in two mulberry genotypes with different drought tolerance. *Photosynthetica* 35: 279–283.
- SÁNCHEZ-RODRÍGUEZ E, RUBIO-WILHELM M, CERVILLA LM, BLASCO B, RIOS JJ, ROSALES MA, ROMERO L, RUIZ JM. 2010. Genotypic differences in some physiological parameters symptomatic for oxidative stress under moderate drought in tomato plants. *Plant Sci* 178: 30–40.
- TAHAR B, ABDELLAH A, ABDULKHALIQ AAS, ALI MA. 2010. Effect of water stress on growth and water use efficiency (WUE) of some wheat cultivars (*Triticum durum*) grown in Saudi Arabia. *Journal of Taibah University for Science* 3: 39–48.
- TAMBUSSI EA, BARTOLI CG, BELTRANO J, GUIMET JJ, ARAUS JL. 2000. Oxidative damage to thylakoid proteins in winter stressed leaves of wheat. *Physiol Plant* 108: 398–404.
- WANG T, ZHANG X, LI C. 2007. Growth, abscisic acid content, and carbon isotope composition in wheat cultivars grown under different soil moisture. *Biol Plant* 51: 181–184.
- WU FZ, BAO WK, LI FL, WU N. 2008. Effects of water stress and nitrogen supply on leaf gas exchange and fluorescence parameters of *Sophora davidii* seedlings. *Photosynthetica* 46: 40–48.

- YANG ZF, XIE T, LIU Q. 2013. Physiological responses of *Phragmites australis* to the combined effects of water and salinity stress. *Ecohydrology* 7: 420–426.
- YIN CY, WANG X, DUAN BL, LUO JX, LI CY. 2005. Early growth, dry matter allocation and water use efficiency of two sympatric *populus* species as affected by water stress. *Environ Exp Bot* 53: 315–322.
- ZHANG YJ, XIE ZK, WANG YJ, SU PX, AN LP, GAO H. 2011. Effect of water stress on leaf photosynthesis, chlorophyll content, and growth of oriental lily. *Russ J Plant Physiol* 58: 844–850.
- ZHANG HB, MENG HJ, ZHAO WJ, GAO HJ, ZHAO YH. 2016. Vertical distribution characteristic of soil carbon of reed wetland in the middle region of Heihe Basin. *Ecol Sci* 35: 123–127. [In Chinese]
- ZHAO X, DONG KH, ZHANG Y, ZHU HS, YANG WD, YANG MH. 2011. Effects of water stress and rehydration on photosynthetic characteristics of *Lespedeza davurica* (Laxm.) Schindl. *Acta Agrestia Sinica* 19: 584–590. [In Chinese]