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Effects of drought stress on growth and chlorophyll fluorescence of *Lycium ruthenicum* Murr. seedlings

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Abstract

The present study aimed to determine effects of drought stress on *Lycium ruthenicum* Murr. seedlings. Our results showed that mild drought stress was beneficial to growth of *L. ruthenicum* seedlings. Their height, basal diameter, crown, leaf number, stem dry mass, leaf and root dry mass increased gradually when the soil water content declined from 34.7 to 21.2%. However, with further decrease of the soil water content, the growth of *L. ruthenicum* seedlings was limited. After 28 d of treatment, the seedlings were apparently vulnerable to drought stress, which resulted in significant leaf shedding and slow growth. However, growth was restored after rehydration. Drought treatments led to a decrease in contents of chlorophyll (Chl) *a*, *b*, and Chl (*a*+*b*) and increase in the Chl *a*/*b* ratio. After rewatering, the Chl content recovered to the content of the control plants. Under drought stress, minimal fluorescence and nonphotochemical quenching coefficient increased, thereby indicating that *L. ruthenicum* seedlings could protect PSII reaction centres from damage. Maximum fluorescence, maximum quantum yield, actual quantum yield of PSII photochemistry, and photochemical quenching decreased, which suggested that drought stress impacted the openness of PSII reaction centres. A comparison of these responses might help identify the drought tolerance mechanisms of *L. ruthenicum*. This could be the reference for the planting location and irrigation arrangements during the growing period of *L. ruthenicum*.

Additional key words: drought tolerance; dry mass; photosynthesis; relative water content.

Introduction

Drought stress is a key factor that limits plant survival and growth, thereby adversely affecting vegetative restoration in arid and semiarid regions (Li *et al.* 2009). Severe drought stress affects plant morphological structure, photosynthesis, growth, and metabolism (Thimmanaik *et al.* 2002). Only plants that adapt to drought can survive in this environment (An *et al.* 2011). Prolonged drought restricts plant growth and dry mass production, which may even lead to plant death (Rodiyati *et al.* 2005). Photosynthesis is exceptionally sensitive to drought stress, because it can cause the closure of stomata and reduce mesophyll conductance, thereby limiting the CO_2 availability (Flexas *et al.* 2008). During drought stress, plants resist drought *via* different protective strategies or by repairing in order to relieve the damage caused by drought (Cooper *et al.* 2002). Therefore, the response and adaptation of plant photosynthetic characteristics and the dry mass allocation to drought stress have become more important for plant adaptation to drought.

Lycium ruthenicum Murr. of the Solanaceae family is a wild plant in the northwest of China and is an important part of local plant communities in desert-zone vegetation (Lu *et al.* 2009). Its special physiological characteristics of drought and salt resistance make it an ideal plant for preventing soil desertification and alleviation of soil salinity and alkalinity, which are very important for the ecosystem and agriculture in such a eco-fragile region (Zhang *et al.* 2007, Zheng *et al.* 2011).

Lycium fruits contain polysaccharides and proteins, which have been recorded in the Tibetan medical classic "Jing Zhu Ben Cao" as a traditional herb (Zheng *et al.* 2011). Although the beneficial effects presented by *L. ruthenicum* were obvious, scholars have seldom systematically studied its effects to the best of our knowledge.

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Abbreviations: Chl – chlorophyll; CK – control; DAT – days of treatment; DM – dry mass; DS – drought stress; F_0 – minimal fluorescence; F_m – maximum fluorescence; F_v/F_m – the maximum quantum yield of PSII; q_N – the nonphotochemical quenching; q_P – the photochemical quenching; R:S – the root to shoot ratio; RWC – relative water content; Φ_{PSII} – the quantum yield of PSII.

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Some studies have been recently conducted on the seed germination for this species under drought and salt stress (Chen *et al*. 2010, He *et al*. 2011, Wang *et al*. 2012, Han *et al*. 2014). Given the overexploitation and deterioration of its habitat as well as artificial destructiom, the number of populations and individuals of *L. ruthenicum* has considerably dropped in recent decades to the point where the species is currently considered to be threatened in China and has been listed among the important wild plants for conservation (Liu *et al*. 2012). In this rigorous situation, the effective management and protection of *L. ruthenicum* is a major task for reasonable management. According to the present investigation along the middle and lower basin of the Heihe River, the plant have the rich-fruiting and high seed hermination rate of *L. ruthenicum*. However, we could rarely observe the seedlings in their natural habitat. We speculate that drought limits seedling emergence, development, and establishment. However, drought tolerance and its underlying mechanism in *L. ruthenicum* seedlings have not been investigated prior to this study. Whether *L. ruthenicum* seedlings could adapt to drought stress by adjusting its dry mass allocation and photosynthesis it stays to be determined. The plants were subjected to drought stress in order to clarify the mechanism by which *L. ruthenicum* seedlings adapt to drought environments.

The present study aimed to determine the effect of drought stress and rewatering on the growth, Chl content, and Chl fluorescence of *L. ruthenicum* seedlings. The study could help improve the cultivation and maximization of *L. ruthenicum* growth and production in the northwest of China.

Materials and methods

Habitat conditions and plant material: The study site was located in the agronomy practice base of Hexi University, Zhangye City (37°28′N, 97°20′E) in Gansu Province, China. The climate is a continental environment with a mean rainfall of 113–120 mm. The annual mean evaporation is 2291 mm. The annual mean temperature is 6°C. *L. ruthenicum* seeds were harvested in September 2013 from the Ganzhou region (38°32′N, 100°6′E) in Gansu Province, China. Seeds were stored at 4°C until the beginning of the experiment.

Stress treatments: Before sowing, the seeds were surface sterilised with 2% potassium permanganate solution. Five seeds were sown per pot (23 cm in diameter and 20 cm in height) in 40 pots on 10 March 2014. Each pot contained a mixture of soil, sand, and humus (1:2:1) in the same amounts. The pots were initially well watered to ensure seed germination. When 2–3 true leaves were present, the seedlings were thinned to three plants per pot. Stress treatment was initiated on 27 June 2014. The experiment layout included control (CK) and drought-treated (DS) groups. The CK group included 20 pots. The CK plants were grown under normal watering conditions. The DS group contained 20 pots. All pots were watered until the soil reached the maximum water-holding capacity, after which the pots were not watered for the succeeding days to allow natural consumption of the soil moisture. After 28 d of treatment, plants were rewatered daily to 80% of the holding capacity for 7 d. At 0, 7, 14, 21, 28, and 35 d of treatment (DAT), the growth parameters, dry mass, fluorescence parameters, and Chl content were measured in the CK and DS groups. Soil moisture was measured with a soil moisture measuring instrument (*TDR300*, *SPECTRUM,* USA). All plastic pots were placed to a mobile rain shelter during the period of DS in order to avoid natural rainfall.

Growth parameters: At 0, 7, 14, 21, 28, and 35 DAT, the plant height, basal diameter and crown and leaf number were recorded for the CK and DS groups, respectively. The plant height was determined with a tape measure from the base of the stem to the terminal bud. The basal diameter was measured by a Vernier calliper at the base of stem. The crown was determined with a tape measure from east and west to south and north.

At 0, 7, 14, 21, 28, and 35 DAT, three seedlings of the same size were harvested from the CK and DS groups, respectively. Each plant was separated into the roots, stems, and leaves. These samples were placed in an oven at 60°C for 48 h before the dry mass (DM) of each seedling component was measured. The root and shoot ratio (R:S) was calculated from the abovementioned shoot and root DM. The total plant DM is the sum of the root, stem, and leaf DMs. The leaf DM ratio is calculated from the leaf DM and total DM. The stem DM ratio is calculated from the stem DM and total DM. The root DM ratio is calculated from the root DM and total DM.

Chl content determination: After the photosynthetic activity and quality parameters were determined, all leaves were harvested. 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).

Chl fluorescence was determined for a fully expanded leaf with a pulse modulation fluorometer (*FMS-2*, *Hansatech*, United Kingdom) following the procedure described by van Kooten and Snel (1990). The selected leaves of the CK and DS groups were placed in the dark for 20 min before the Chl fluorescence was measured at 0, 7, 14, 21, 28, and 35 DAT, respectively. Minimal fluorescence (F_0) and maximum fluorescence (F_m) were measured by applying a low-intensity red-measuring light source and a saturating light pulse (0.8 s) of 6,000 μmol(photon) $m^{-2} s^{-1}$. After the dark measurement, the leaf was continuously illuminated with actinic light to obtain the steady-state Chl fluorescence (F_s). Saturating pulses (0.8 s) of white light [6,000 μmol(photon) m^{-2} s^{-1}] were applied to determine the maximum fluorescence in the light-adapted state (F_m'). The maximum quantum yield of PSII (F_v/F_m) and the quantum yield of PSII (Φ_{PSII}) were calculated with a *FMS-2* instrument. The photochemical quenching (q_P) and nonphotochemical quenching (q_N) were calculated according to the following equations:

$$q_P = (F_m' - F_s)/(F_m' - F_0)$$

$$q_N = (F_m - F_m')/F_m'$$

Statistical analysis was performed with the *SPSS 18.0* statistical software package for *Windows*. All data were subjected to one-way analysis of variance (*ANOVA*). LSD multiple comparison tests were used to separate significant differences among all treatments at the 0.05 level. Standard error (SE) was calculated and shown in the figures and tables.

Results

Soil water content and relative water content (RWC): Under DS treatment, the soil water content significantly declined (Table 1). After rewatering, the soil water content significantly increased in the DS group by 139.8%. No significant differences in the leaf RWC were noted for the CK group. However, the RWC of the DS group was significantly reduced from 21 DAT (Table 1). The RWC of the DS-treated seedlings was 40 and 64% lower after 21 and 28 DAT, respectively, compared to the start of the treatment. The RWC of the DS-treated seedlings significantly increased by 86% after rewatering compared with the values after 28 DAT of DS treatment (Table 1).

Growth: The height, basal diameter, crown number, and leaf number of *L. ruthenicum* seedlings exhibited continuous growth until the end of the experiment under the CK treatment (Fig. 1). By contrast, these parameters first increased and then decreased under the DS treatment. After 7 DAT of withholding water from the plants, all these parameters reached the maximum values, and the stressed plants had higher values of these parameters than the CK plants. An increase by 6.3, 4.5, 4.8, and 2.7% was observed in the height, basal diameter, crown number, and leaf number of DS-treated seedlings compared with the CK, respectively. However, seedling growth was inhibited under further DS treatment. After 21 DAT, the height, basal diameter, crown number, and leaf number of *L. ruthenicum* seedlings were significantly greater in the CK group than the that of the DS group. However, the height, basal diameter, crown number, and leaf number were recovered after rewatering.

Dry mass allocation: The DM allocation of the DS seedlings was significantly different from that of the CK plants (Table 2). In the CK, the stem, leaf and root DM increased with time. However, the stem, leaf and root DM followed a similar trend under the DS treatment (Fig. 1, Table 2). After 7 DAT, the stem, leaf and root DM of seedlings in the DS group reached the maximum values and increased by 20.7, 5.6, and 1.0% compared with the CK treatment, respectively. After rewatering, the stem, leaf and root DM of the DS seedlings increased compared with the values after 28 DAT. The R:S of the CK and DS seedlings increased with time. After rewatering, the R:S of the CK seedlings decreased compared with the values of DS-treated seedlings after 28 DAT. The total DM of *L. ruthenicum* seedlings first increased and then decreased under DS (Fig. 2*A*). However, the total DM increased with time in the CK treatment. After 14, 21, and 28 DAT, the total DM of the DS-treated seedlings decreased by 40.0, 75.9, and 86.5% compared with the CK treatment, respectively. Under DS, the percentage of stem DM and root DM increased (Fig. 2*B,D*), whereas the percentage of leaf DM decreased with decreasing soil water content (Fig. 2*C*).

Chl content: Photosynthetic pigment contents exhibited a significant response to DS (Table 3). In the CK, Chl *a*, Chl *b*, Chl (*a*+*b*), and Chl *a*/*b* remained constant. However, Chl *a*, Chl *b*, and Chl (*a*+*b*) significantly decreased and then increased after rewatering under the DS treatment. The Chl *a*/*b* value in the DS treatment increased with experiment duration and recovered after rewatering for 7 d.

Table 1. Changes in soil water content and leaf relative water content (RWC) under control (CK) and drought stress (DS). Data were shown as means ± SE. *Different letters* in the table indicate significant differences between treatments at P<0.05.

Treatment time [d]	Soil water content [%]		RWC [%]	
	CK	DS	CK	DS
0	33.90 ± 1.24^a	34.70 ± 0.66^a	0.75 ± 0.02^a	0.77 ± 0.04^a
7	32.96 ± 0.91^a	21.18 ± 0.55^b	0.77 ± 0.02^a	0.76 ± 0.06^a
14	32.20 ± 1.63^a	13.82 ± 0.78^c	0.73 ± 0.03^a	0.70 ± 0.03^a
21	35.35 ± 4.15^a	8.73 ± 0.18^d	0.72 ± 0.06^a	0.46 ± 0.03^b
28	35.33 ± 2.84^a	7.89 ± 0.27^d	0.72 ± 0.04^a	0.28 ± 0.02^c
Rewatering	33.78 ± 0.69^a	18.92 ± 0.89^e	0.73 ± 0.05^a	0.52 ± 0.04^d

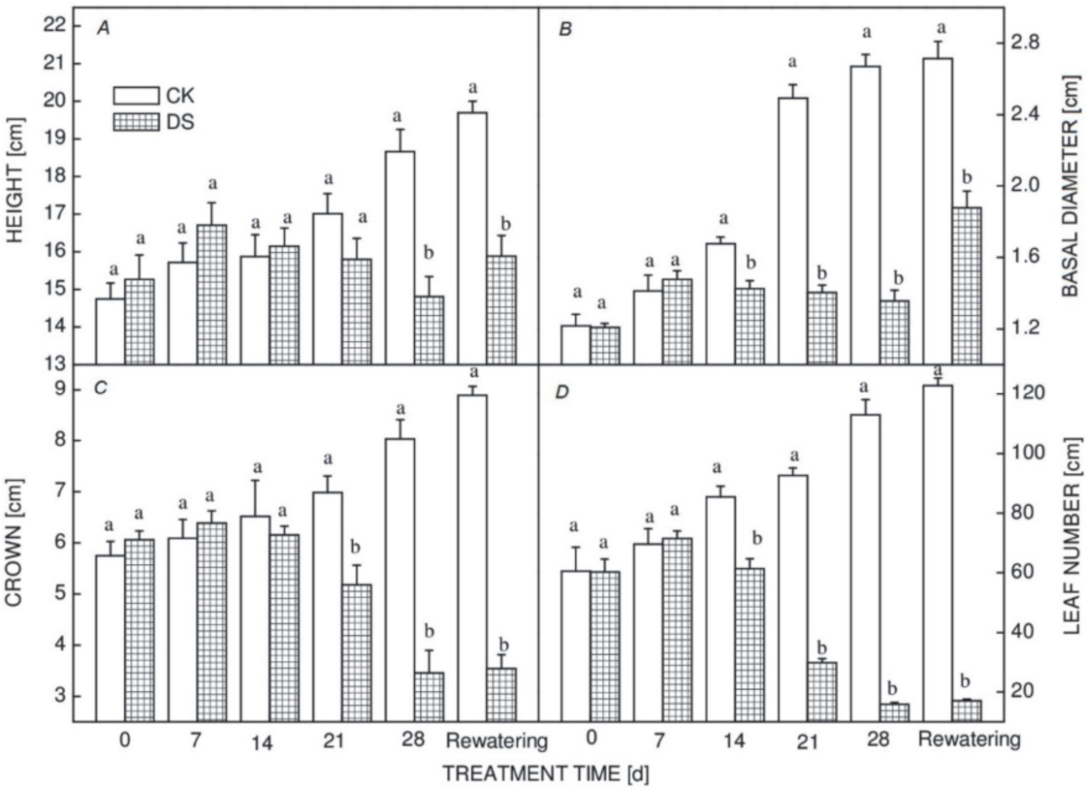

Fig. 1. Effect of drought stress (DS) on seedling the height (*A*), the basal diameter (*B*), crown (*C*), and the leaf number (*D*) of *Lycium ruthenicum* Murr. Each value represents the mean ± SE of at least three independent experiments. *Different letters* denote significant differences ($P<0.05$). CK – control.

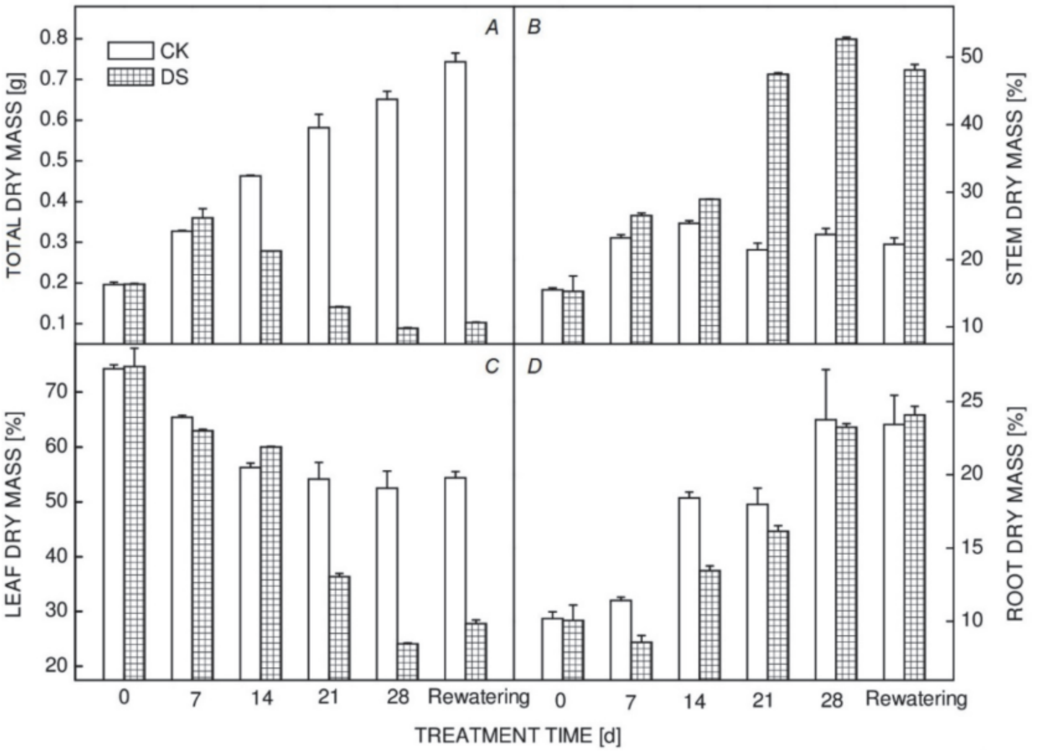

Fig. 2. Variations in the total dry mass (*A*), the percentage of stem dry mass (*B*), leaf dry mass (*C*), and root dry mass (*D*) in *Lycium ruthenicum* Murr. seedlings in dependence on different drought stress (DS) times. Each value represents the mean ± SE of at least three independent experiments. CK – control.

Table 2. Effect of control (CK) and drought stress (DS) on stem dry mass, leaf dry mass, root dry mass, and the root and shoot ratio (R:S) of *Lycium ruthenicum* Murr. seedlings. Data were shown as means ± SE.

Treatment time [d]	Stem dry mass [g]		Leaf dry mass [g]		Root dry mass [g]		R:S	
	CK	DS	CK	DS	CK	DS	CK	DS
0	0.031 ± 0.001	0.03 ± 0.004	0.146 ± 0.003	0.147 ± 0.005	0.020 ± 0.006	0.020 ± 0.002	0.114 ± 0.006	0.112 ± 0.013
7	0.076 ± 0.001	0.096 ± 0.007	0.214 ± 0.002	0.227 ± 0.015	0.037 ± 0.008	0.038 ± 0.008	0.129 ± 0.003	0.118 ± 0.008
14	0.117 ± 0.002	0.081 ± 0.006	0.261 ± 0.004	0.167 ± 0.005	0.085 ± 0.002	0.031 ± 0.002	0.226 ± 0.006	0.124 ± 0.001
21	0.124 ± 0.002	0.067 ± 0.009	0.313 ± 0.003	0.051 ± 0.002	0.105 ± 0.012	0.023 ± 0.008	0.302 ± 0.007	0.193 ± 0.005
28	0.155 ± 0.003	0.046 ± 0.008	0.341 ± 0.013	0.021 ± 0.003	0.156 ± 0.003	0.021 ± 0.002	0.317 ± 0.006	0.303 ± 0.004
Rewatering	0.165 ± 0.003	0.049 ± 0.008	0.404 ± 0.009	0.029 ± 0.004	0.175 ± 0.002	0.025 ± 0.008	0.308 ± 0.003	0.317 ± 0.001

Table 3. Effect of control (CK) and drought stress (DS) on the chlorophyll (Chl) *a*, Chl *b*, Chl (*a* + *b*), and Chl *a*/*b* of *Lycium ruthenicum* Murr. seedlings. Data were shown as means ± SE. *Different letters* in the table indicate significant differences between treatments at $P<0.05$.

Treatment time [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
0	2.92 ± 0.01^{a}	2.92 ± 0.00^{a}	2.29 ± 0.01^{a}	2.29 ± 0.01^{a}	5.21 ± 0.02^{a}	5.21 ± 0.01^{a}	1.27 ± 0.01^{a}	1.27 ± 0.00^{a}
7	2.90 ± 0.01^{a}	2.83 ± 0.01^{b}	2.32 ± 0.02^{a}	2.23 ± 0.02^{b}	5.22 ± 0.01^{a}	5.06 ± 0.04^{b}	1.25 ± 0.01^{a}	1.27 ± 0.01^{a}
14	2.88 ± 0.01^{a}	2.63 ± 0.01^{c}	2.32 ± 0.01^{a}	2.06 ± 0.01^{c}	5.21 ± 0.01^{a}	4.68 ± 0.01^{c}	1.24 ± 0.00^{b}	1.28 ± 0.00^{a}
21	2.88 ± 0.01^{a}	2.49 ± 0.01^{d}	2.29 ± 0.02^{a}	1.93 ± 0.00^{d}	5.17 ± 0.02^{a}	4.50 ± 0.00^{d}	1.26 ± 0.01^{a}	1.29 ± 0.01^{ab}
28	2.90 ± 0.02^{a}	2.31 ± 0.01^{e}	2.32 ± 0.02^{a}	1.73 ± 0.01^{e}	5.21 ± 0.01^{a}	4.04 ± 0.02^{e}	1.25 ± 0.02^{a}	1.33 ± 0.01^{c}
Rewatering	2.88 ± 0.01^{a}	2.76 ± 0.03^{f}	2.29 ± 0.01^{a}	2.25 ± 0.01^{a}	5.17 ± 0.02^{a}	5.01 ± 0.04^{b}	1.26 ± 0.01^{a}	1.23 ± 0.01^{bd}

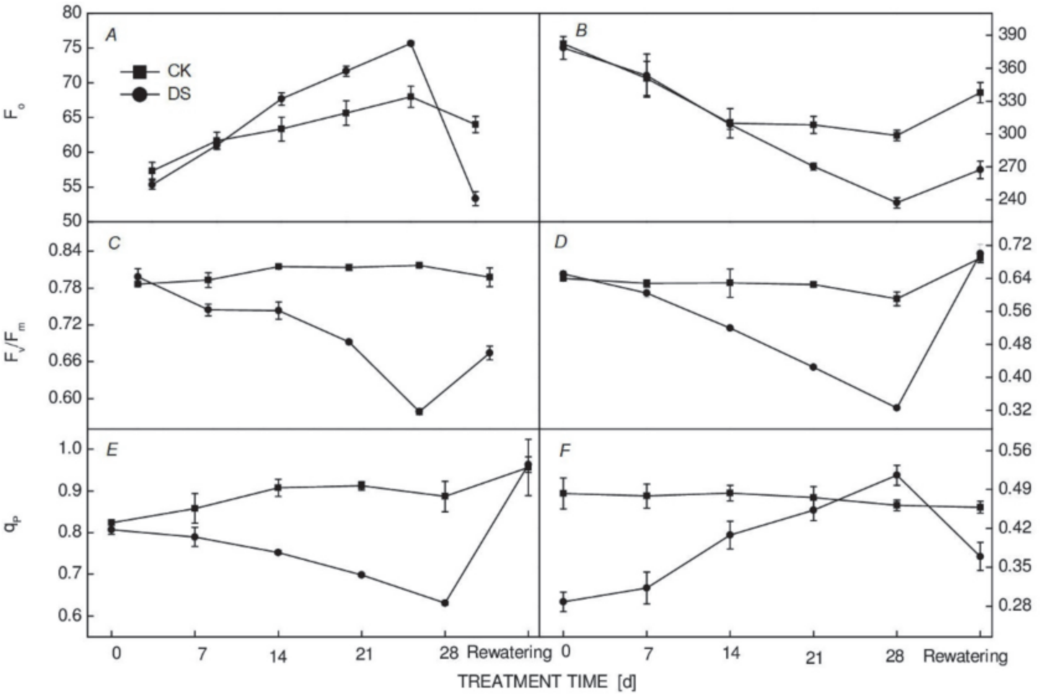

Fig. 3. Changes of the minimal fluorescence (F_0) (*A*), maximum fluorescence (F_m) (*B*), the maximum quantum yield of PSII (F_v/F_m) (*C*), the quantum yield of PSII (Φ_{PSII}) (D), the photochemical quenching (q_P) (*E*), and nonphotochemical quenching (q_N) (*F*) of *Lycium ruthenicum* Murr. seedlings under control (CK) and drought stress (DS). Each value represents the mean ± SE of at least three independent experiments.

Chl fluorescence: The F_0 remained constant in the CK. Under the DS treatment, the F_0 initially increased and then decreased after rewatering. The F_0 values in the two treatment groups were significantly different after 21 DAT (Fig. 3*A*). The F_m initially decreased and then increased in the CK and DS treatment groups. After 14 DAT, the F_m values in the two treatment groups were significantly different. The value of F_v/F_m remained constant in the CK, but decreased under the DS treatment. After 7 DAT, a significant decrease in the F_v/F_m values was observed after DS treatment *vs*. the CK treatment. At the end of the DS period, the F_v/F_m declined by 27.6% as compared with the original level during the initiation of stress. However, the F_v/F_m value was recovered after rewatering for 7 d. The fluorescence parameters of Φ_{PSII} and q_P remained constant in the CK but decreased under the DS treatment. At the end of DS, the Φ_{PSII} and q_P values decreased by 49.8 and 21.8%, respectively. During the 7 d of the recovery period after termination of DS, the Φ_{PSII} and q_P values increased, and the attained values were similar to those of the CK. During DS, the q_N increased by 78.9% from 0 to 28 DAT of treatment. The q_N declined after rewatering for 7 d.

Discussion

The leaf RWC is considered a reliable and widely used indicator for defining the sensitivity of plants to dehydration (Rampino *et al*. 2006, Sánchez-Rodríguez *et al*. 2010). The results of this study indicated that constant DS can impose severe soil water deficit. The RWC, seedling growth, dry mass production and partitioning of *Prunus mongolica* are significantly influenced by the soil water content (Guo *et al*. 2015). By contrast, the seedling growth and dry mass production of *L. ruthenicum* were insensitive to mild DS. In the early stage of stress, the seedling height, base diameter, crown, leaf number, stem dry mass, leaf dry mass and root dry mass increased with increasing stress and reached their maximum after 7 d. The short-term decrease in the soil water content was beneficial to *L. ruthenicum* seedling growth. Similar results have been reported in *Acorus calamus* (Wang *et al*. 2013). With the further decrease of the soil water content, the growth of *L. ruthenicum* seedlings was limited. The growth of different organs and the dry mass allocation was adjusted to adapt to DS, thereby supporting the findings of other studies on other seedlings (Li *et al*. 2009, Wu *et al*. 2008). The present study indicated the absence of mortality during the experiment. However, *L. ruthenicum* seedlings were vulnerable to severe DS conditions because of significant leaf shedding and low growth. Root systems are complex and dynamic structures; water uptake may be limited by the number of roots in a particular soil layer, whereas enhanced root growth can increase drought tolerance (Klepper and Rickman 1990). With the decreasing soil water content, *L. ruthenicum* seedlings relatively increased dry matter allocation to the root; thus, R:S gradually increased. This change is a morphological adaptation in order to reduce water loss. Similar results have been reported in previous studies (Marron *et al*. 2002, Siemens and Zwiazek 2003, Yin *et al*. 2005).

The induced Chl fluorescence as a kinetic parameter is an ideal method to research and explore the effect of DS on plant photosynthesis. Chl fluorescence analysis is becoming an increasingly popular technique to detect photosynthetic physiological conditions and investigate the mechanism of photosynthesis (Maxwell and Johnson 2000, Liu *et al*. 2015). This study showed that the F_0 of *L. ruthenicum* leaves increased, whereas the F_m value decreased during DS. Therefore, the transport of energy, which was absorbed by the PSII antenna pigments, was lost as the fluorescence and heat dissipation increased, whereas the photochemical reactions were conversely reduced. Similar results have been reported in sugar beet seedlings (Li *et al*. 2013) and *Coronnilla varia* (Yang *et al*. 2013). F_v/F_m is a measure of the maximum photochemical efficiency of PSII when all the reaction centres are opened. When plants suffer severe DS, the F_v/F_m declines (Woo *et al*. 2008). Our study showed that DS lowered the F_v/F_m of *L. ruthenicum* seedling. After 7 DAT, the F_v/F_m of the DS group significantly decreased compared with the CK groups, indicating that the original light energy conversion efficiency was reduced, and the potential of active centers was damaged, which suppressed the primary photosynthetic reaction of *L. ruthenicum* seedling. The decreasing F_v/F_m was completely restored after rehydration, which suggested that the inhibition of PSII was reversible under the stress treatment. Φ_{PSII} is positively correlated with PSII activities and can be used to evaluate the transfer rate of photosynthetic PSII to PSI electrons (Krall and Edwards 1992, Martínez-Carrasco *et al*. 2002). This study showed that Φ_{PSII} gradually decreased with increasing DS. Similar results have been reported in sugar beet seedlings (Li *et al*. 2013). The decrease was prominent from 14 DAT onward. The result suggests that the photosynthetic apparatus PSII of *L. ruthenicum* seedling leaves was damaged and lost its heat-dissipation capability. However, the plant can quickly recover after rewatering. The excess energy was effectively dissipated by the increasing q_N to prevent damage on PSII reaction centres (Golding and Johnson 2003, Saglam *et al*. 2011). This study showed that the q_N increased with the decreasing soil water content, suggesting that the excess energy in leaves was dissipated in the form of heat, which effectively reduced the damage to the photosynthetic organs or avoided photochemical inhibition and the degree of openness in the reaction centers. Similar results have been reported in sugar beet (Li *et al*. 2013) and *Coronilla varia* seedlings (Yang *et al*. 2013). The q_N declined after rehydration for seven days, and it did recover to the level in the CK. It indicated that the damaged photosynthetic apparatus can recover within a relatively short time. The q_P indicates the openness of the PSII reaction centres. With the decreasing soil water content, the q_P of *L. ruthenicum* seedlings gradually decreased. This fact confirmed that the excess energy in leaves dissipated in the form of heat, and the openness of the reaction centres decreased.

Lower photosynthetic efficiency was not just due to changes in energy flow through the PSII but due to the decreased pigment content. The current study showed that the lower photosynthetic performance might be associated with the reduced Chl content [Chl *a*, Chl *b*, and Chl (*a*+*b*)] of *L. ruthenicum* seedlings under water stress (Table 3). The increased Chl *a/b* ratio was also observed under water stress in our study (Table 3). It was associated with the decrease in the size of PSII light-harvesting antenna, insuring that the supply of electrons from PSII is sufficient to keep pace with the rate of excitation of PSI (Kitajima and Hogan 2003). After rewatering, the Chl content recover to the control content. It showed that the damage to the PSII reaction centers was rather mild under short period of DS. So, when stress condition ended, the PSII reaction centers could open again and capture the light energy for photochemical reactions.

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