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Ecophysiological responses of *Caragana korshinskii* Kom. under extreme drought stress: Leaf abscission and stem survives

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Abstract

Caragana korshinskii Kom. is a perennial xerophytic shrub, well known for its ability to resist drought. In order to study ecophysiological responses of *C. korshinskii* under extreme drought stress and subsequent rehydration, diurnal patterns of gas exchange and chlorophyll (Chl) fluorescence parameters of photosystem II as well as Chl content were analyzed. Plant responses to extreme drought included (*1*) leaf abscission and using stem for photosynthesis, (*2*) improved instantaneous water-use efficiency, (*3*) decreased photosynthetic rate and partly closed stomata owing to leaf abscission and low water status, (*4*) decreased maximum photochemical efficiency of photosystem II (PSII) (variable to maximum fluorescence ratio, F_v/F_m), quantum efficiency of noncyclic electron transport of PSII, and Chl *a* and Chl *b*. Four days after rehydration, new leaves budded from stems. In the rewatered plants, the chloroplast function was restored, the gas exchange and Chl fluorescence returned to a similar level as control plant. The above result indicated that maintaining an active stem system after leaf abscission during extreme drought stress may be the foundation which engenders these mechanisms rapid regrowth for *C. korshinskii* in arid environment.

Additional key words: chlorophyll content; chlorophyll fluorescence; fluorescence quenching; photosynthesis; stress response.

Introduction

Plant water deficit disturbs internal physiological processes (Guo *et al.* 2003). Photosynthesis is exceptionally sensitive to water stress (Chaitanya *et al.* 2003), and it is known to be limited not only by decreased stomatal conductance but also by damage at the chloroplast level under severe stress (Boyer *et al.* 1997, Lawlor 2002). In general, a plant requires either a protection against the stresses, repair of the resulting damage or a combination of the two ones (Cooper and Farrant 2002). Many authors considered that plant resistance to summer drought should rely on a combination of morphological and physiological traits, such as a deep root system (Qian *et al.* 1997), the ability to reduce leaf transpiration rates (Maroco *et al.* 1997), high use efficiency of resource pulses, large pool sizes of osmoprotectants, and a high dehydration tolerance (Balaguer *et al.* 2002). Several studies have focused on the photoprotective mechanism of the plant under strong light and drought stress in recent years (Bai *et al.* 2008, Donald 2001).

Caragana korshinskii Kom. is a long-lived shrub which is widely distributed in desert and semidesert zones in the Loess Plateau in northwestern China (Xia *et al.* 2006). It has important ecological and economic value in this area, including a key role in vegetation succession from shifting dune to sandy grassland, helping to restore degraded land by fixing atmospheric nitrogen,

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Abbreviations: C_i – intercellular CO_2 concentration; Chl – chlorophyll; DAW – day after water was withheld; DAR – day after rehydration; DS – drought stress; E – transpiration rate; F_0 – minimum fluorescence of the dark-adapted state; F_m – maximum fluorescence of the light-adapted state; F_m' – maximum fluoresence yield of the dark-adapted state; F_s – steady-state fluoresence; F_v/F_m – maximum photochemical efficiency of photosystem II; FWC – field water capacity; g_s – stomatal conductance; NPQ – nonphotochemical quenching of fluorescence; PPFD – photosynthetic photon flux density; P_N – net photosynthetic rate; PSII – photosystem II; RWC – relative water content; SWC – soil water content; T_{leaf} – leaf temperature; WW – well watered; WUE – instantaneous water-use efficiency; Φ_{PSII} – quantum efficiency of noncyclic electric transport of PSII.

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forming shrub shelterbelt for crops and artificial grassland (Zhang 1994, Zheng *et al.* 2004). When *C. korshinskii* is subjected to drought stress, leaves are wilted and die completely, and the plant does not grow, but plants are able to recover and develop new leaves upon rainfall (Xu *et al.* 2008). Studies on *C. korshinskii* have mainly focused on its taxonomy, community distribution, biological and ecological characteristics, and species diversity (Zhang *et al.* 2009, Cheng *et al.* 2009), and its adaptive strategies to drought stress (Ma *et al.* 2004). The main objective of the present study was to assess the ecophysiological responses of *C. korshinskii* during progressive soil drought and rehydration. We hoped that the variation in response to drought stress at the level of the individual plant would help to improve our understanding of its adaptation to extreme conditions in these arid and semiarid areas.

Materials and methods

Experimental site and water-stress treatments: The experiment was conducted at the biological station, Lanzhou University (36°01′N, 104°09′E), where the mean annual temperature is 5–9°C and the mean annual precipitation is 324 mm. Three seeds of *C. korshinskii* were sown in each of 60 pots (25 cm in diameter and 30 cm deep) which were buried 30 cm deep in soil with a piece of plastic under the pot's bottom in the spring of 2005. The soil in pots contained 0.132% of nitrogen and 1.54% of soil organic matter. After the emergence of seedlings, the plants were thinned to one per pot. Plants received natural rain from spring of 2005 to 14 May 2006. On 14 May 2006, plants were well watered. Twenty pots were selected for drought treatment. Drought stress (DS) was imposed by withholding water and covering plants with a polyvinyl chloride sheet when it rained over 53 d (DAW) until all leaves abscised in the 20 pots. Thereafter, plants were watered once a week for the next 41 d. The well watered (WW) control plants of the experimental design were normally watered and kept its soil relative water more than 85%.

Soil and leaf relative water content (RWC): Samples for leaf RWC analysis were taken 9 times from the 20 study plants. Mature leaves or young stems were collected from at least 10 plants. The leaves or stems (about 0.5 g fresh mass, FM) were cut and weighed immediately to obtain FM, and then placed in a 25-mL beaker, filled with water, and left overnight in the dark. They were then reweighed to obtain the turgid fresh mass (TM) in the next morning and dry mass (DM) after oven-drying at 80°C for 24 h. The RWC of the leaves could be calculated as $\mathrm{RWC} = [(\mathrm{FM} - \mathrm{DM})/(\mathrm{TM} - \mathrm{DM})] \times 100$.

Soil samples were collected from 0–10 and 10–25 cm depths at each pot using steel cylinder 1.2 cm in diameter and 5 cm in length. Roots and stones were removed manually from the samples. The soil samples were weighed to obtain FM, and then dried at 105–110°C for 72 h and weighed to obtain DM, and the soil water content was calculated as $\mathrm{SWC} = (\mathrm{FM} - \mathrm{DM})/\mathrm{DM} \times 100$. In order to measure the field water capacity (FWC), soil samples were collected from 0–10 and 10–25 cm depths at each pot using aluminum cylinders with a volume of 100 cm^3 (5.03 cm internal diameter, 5 cm height). The bottom of each core was covered with filter paper and placed in a tray of water until the noncapillary and capillary porosity of the soil was fully saturated with water (about 12 h). Then, the core was placed in a dry tray for 24 h to remove water and was weighed to obtain M1. Finally the core was oven-dried at 105–110°C for 72 h and weighed to obtain M2. Field water capacity was calculated as $\mathrm{FWC} = (\mathrm{M1} - \mathrm{M2})/(\mathrm{M2} - \mathrm{M3}) \times 100$, where M3 was a mass of aluminum cylinder. Soil RWC was calculated as $\mathrm{SWC}/\mathrm{FWC} \times 100$ (Zhang *et al.* 1999).

Photosynthesis and Chl fluorescence: Similar mature leaves and young stems were selected to measure leaf and stem diurnal gas exchange and Chl fluorescence on the same plants on the same day (5 different plants for each treatment at each sampling time), net photosynthetic rate (P_N), intercellular CO_2 concentration (C_i), stomatal conductance (g_s), and transpiration rate (E) were measured using a portable open gas-exchange system (*Li-6400, Licor*, Lincoln, NE, USA) with needle leaf chamber, the CO_2 concentration is about 340 μmol mol^{-1}, the length of each treatment is about 10 min. After measurement, the parts of the leaf and stem were cut and the area of leaf and stem measured with portable area meter (*Li-3000C, Licor*, Lincoln, NE, USA), in order to calculate P_N, E, and g_s per unit leaf and stem area. The instantaneous water-use efficiency (WUE) was defined as the ratio of net photosynthetic rate to transpiration rate (P_N/E). The conditions in the measuring chamber (irradiance, temperature, air humidity) were those shown in Table 1.

Chl *a* fluorescence measurement was made with a pulse-modulated fluorescence monitor system (*FMS-2, Hansatech*, Kings Lynn, UK). Leaf and stem samples were dark-adapted for 30 min, then exposed to a weak modulated irradiance (<0.1 μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) to assess the minimum fluorescence (F_0). A 600-ms saturation flash of light [>7,000 μmol(quantum) $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$] was given to assess the maximum fluorescence (F_m) and F_v/F_m. Then the leaves and stems were continuously irradiated with actinic light (1,200 μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) in order to measure the steady-state fluorescence (F_s) and maximum fluorescence yield (F_m') of irradiated leaves and stems. Measurements of F_m and F_0 were taken to calculate maximal photochemical efficiency of PSII (F_v/F_m) [$F_v/F_m = (F_m - F_0)/F_m$]. Those F_m values used to calculate diurnal nonphotochemical quenching of fluorescence (NPQ) [NPQ =

$(F_m - F_m')/F_m']$. Variation in quantum efficiency of noncyclic electric transport of PSII (Φ_{PSII}) [$\Phi_{PSII} = (F_m' - F_s)/F_m'$] between treatments was calculated according to Genty *et al.* (1989).

Pigments were extracted in the leaves and stems according to the method of Cooper and Farrant (2002) and the absorbance spectra of the extract solution were measured at 647, 663, and 470 nm, respectively. Chl content was calculated according to the method of Sims and Gamon (2002).

Statistical analysis: Data management and statistical analyses were performed using *SPSS 10.0* software (*SPSS for Windows, Version 10.0*, Chicago, IL, USA). Means were expressed with their standard deviation (means ± SD) and compared by *ANOVA* using the LSD test at the 0.05 significance level.

Results

Leaf, stem, and soil water status: In WW plants, leaf RWC was about 85–89% and stem RWC was about 65–68%. There were no significant differences in water status in WW plants during experiment time (P=0.003, data not shown). Comparing to WW plants, leaf and soil water contents showed large differences during DS and rehydration. Soil RWC decreased from 87% to 4% at 0–10 cm and from 91% to 13% at 10–25 cm (Fig. 1*A*) while leaf RWC decreased from 83% to 70% and stem RWC from 65% to 10% during DS (Fig. 1*C*). Unlike the rapid decrease of SWC, leaf water content decreased slowly over 42 d during DS, from that day on, plant leaves became yellow and died at 53 DAW and all leaves abscised. Rehydration induced a rapid recovery of SWC, but stem RWC did not recover until new leaves budded (Fig. 1*B*,*D*).

Gas exchange in leaf and stem: Fig. 2 shows the effect of dehydration and rehydration on P_N, WUE, g_s, and C_i of leaf and stem in *C. korshinskii*. There was no significant difference of P_N, g_s, and C_i between WW plant and plant of 3 DAW ($P \geq 0.12$). P_N in leaf maintained a high level with the maximum around 20 μmol m^{-2} s^{-1} at 3 DAW. P_N, g_s, and C_i showed bimodal behavior in control plant and plant of 3 DAW. The first peak was at midmorning, while the second peak was at 15:00 h. This indicated that *C. korshinskii* has a midday depression in photosynthesis under normal water conditions. Comparing to the value of midmorning, at noon, under saturating PPFD, high T_{leaf} and low air relative humidity (Table 1), P_N, g_s and C_i declined ($P<0.01$) (Fig. 2*A*,*C*,*E*). The maximum values of P_N, g_s, and C_i in control plant were 22 μmol m^{-2} s^{-1}, 790 mmol(H_2O) m^{-2} s^{-1} and 380 μmol(CO_2) mol^{-1}(air), respectively. However, after 42 d of DS, the maximum values of P_N, g_s, and C_i decreased about 15%, 10%, and 35%, respectively, and the second peak disappeared. 53 DAW, plant leaves abscised, and stem had weak gas exchange. There was no significant difference of WUE between WW plant and plant of 3 DAW ($P \geq 0.18$). The maximum values of WUE appeared at sunrise and then declined the whole day during drought stress. 42 DAW, WUE increased ($P<0.01$) (Fig. 2*G*).

After 3-d rehydration, P_N, g_s, C_i, and WUE in stem increased. Comparing to the value in stem 53 DAW, the maximum values of P_N, g_s, C_i, and WUE increased about 80%, 40%, 25%, and 22%, respectively (Fig. 2*B*,*D*,*F*,*H*).

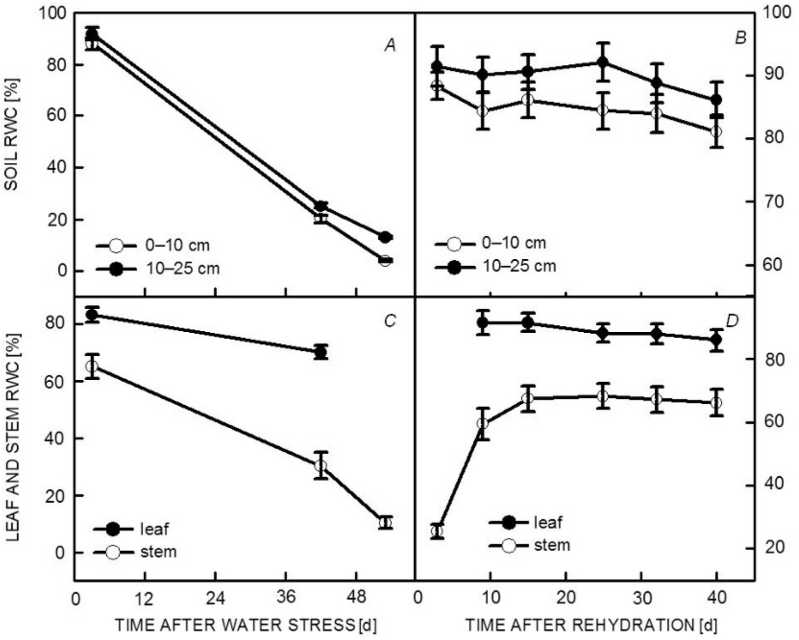

Fig. 1. Changes in soil relative water content (RWC) during dehydration (*A*) and rehydration (*B*), and leaf and stem RWC during dehydration (*C*) and rehydration (*D*). Values are means ± SE (n = 6).

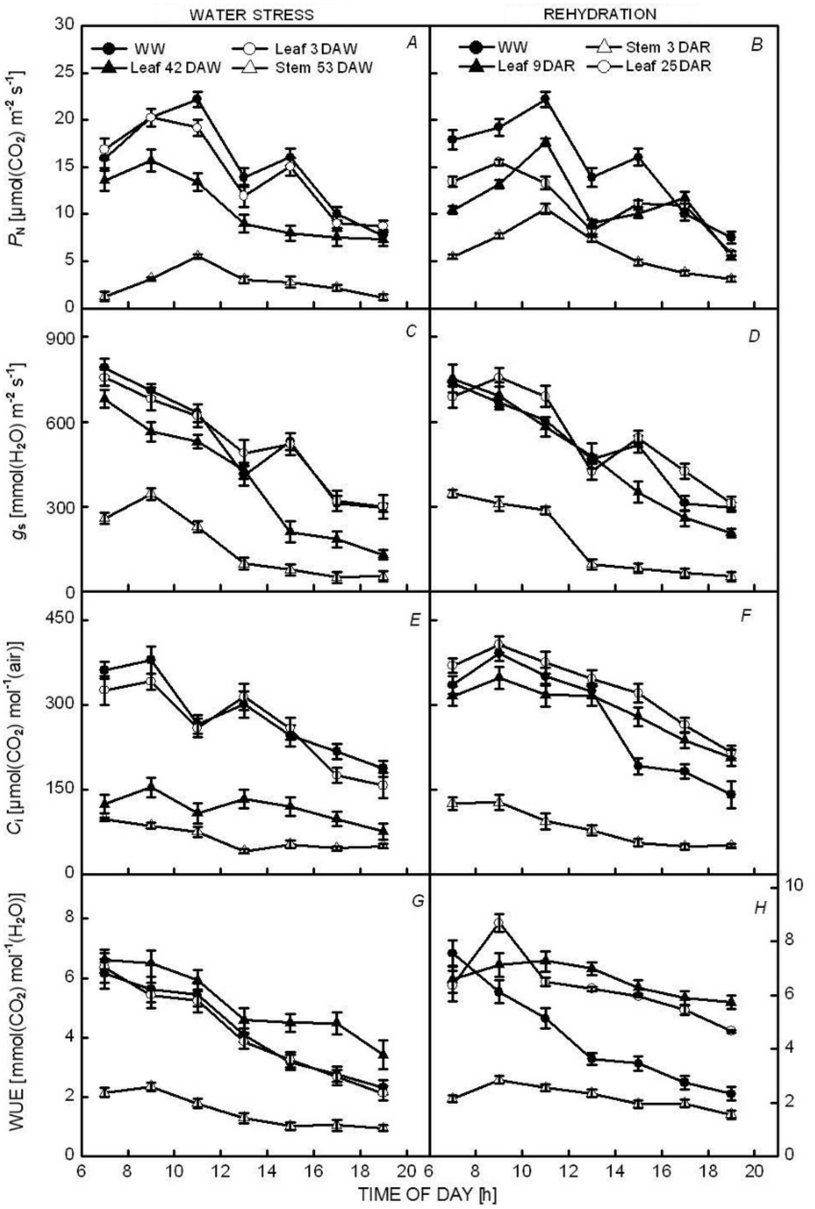

Fig. 2. Diurnal time courses of net photosynthetic rate (P_N) (*A,B*), stomatal conductance (g_s) (*C,D*), intercellular CO$_2$ concentration (C_i) (*E,F*) and instantaneous water-use efficiency (WUE) (*G,H*) in *Caragana korshinskii* leaf in well watered (WW), 3 d after water withholding (DAW) and 42 DAW (*left*) , and stem 53 DAW (*left*) and leaf in WW, stem 3 d after rehydration (DAR), leaf 9 DAR and 25 DAR (*right*) during drought stress and rehydration. Values are means ± SE ($n = 6$).

Table 1. Diurnal variations of photosynthetic photon flux density (PPFD), leaf temperature (T_{leaf}) and air relative humidity (RH) on July 12, 2006 at experimental site. Means ± SD of 9 independent observations. Values within the same row followed by *the same letters* are not significantly different ($P<0.05$).

Parameter	Time of day [h]						
	7:00	9:00	11:00	13:00	15:00	17:00	19:00
PPFD [μmol m^{-2} s^{-1}]	187 ± 16^a	441 ± 7^b	902 ± 19^c	1,253 ± 13^d	941 ± 18^c	818 ± 11^e	427 ± 6^b
T_{leaf} [°C]	14.3 ± 0.32^a	26.4 ± 0.15^b	37.9 ± 0.25^c	40.8 ± 0.26^d	38.2 ± 0.21^c	36.3 ± 0.14^c	35.2 ± 0.4^e
RH [%]	12.7 ± 0.19^a	11.2 ± 0.12^b	10.6 ± 0.18^c	9.1 ± 0.11^d	9.3 ± 0.10^d	9.2 ± 0.14^d	9.7 ± 0.19^e

6 DAR, plant produced new leaves. With those new leaves, P_N, g_s, C_i, and WUE in leaf increased 9 DAR, but lower than control plant ($P<0.005$). Thereafter, there was no significant difference of P_N, g_s, C_i, and WUE between WW plant and plant 25 DAR ($P \geq 0.12$).

Electro transport in PSII: F_v/F_m was similar between WW plant and plant of 3 DAW. Thereafter, it decreased from 0.85 to 0.65 in leaf as soil RWC decreased from 88% to 20% of 42 DAW, and then reached to 0.6 in stem as soil RWC decreased to 4% (Fig. 3*A*). Φ_{PSII} followed a

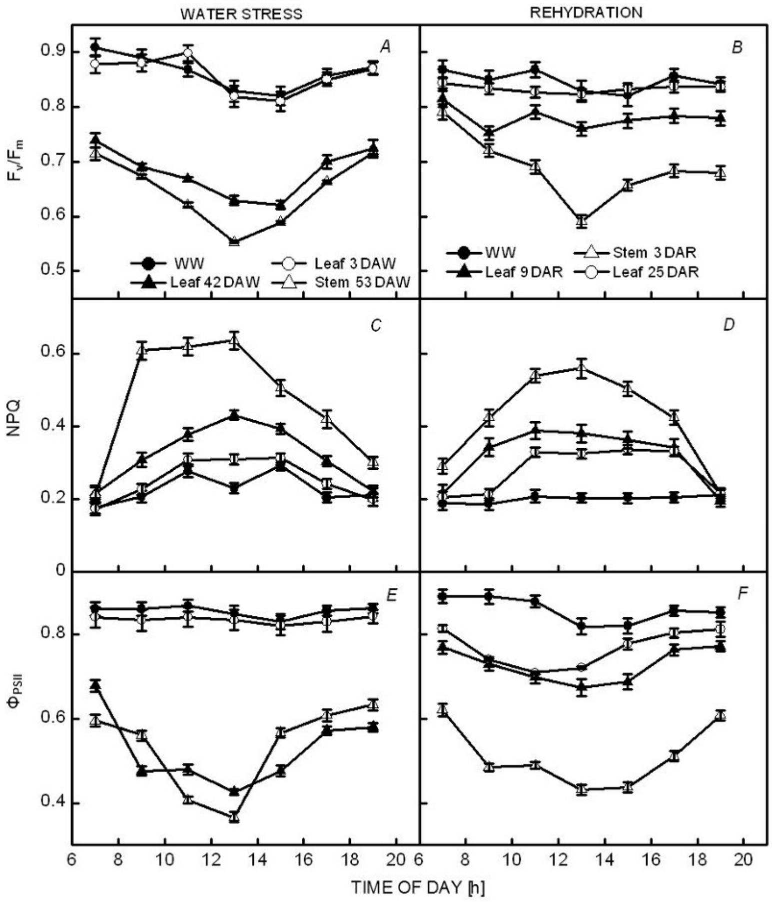

Fig. 3. Diurnal time courses of maximum photochemical efficiency of photosystem II (F_v/F_m) (*A*,*B*), nonphotochemical quenching of fluorescence (NPQ) (*C*,*D*) and quantum efficiency of noncyclic electric transport of PSII (Φ_{PSII}) (*E*,*F*) in *Caragana korshinskii* leaf in well watered (WW), 3 d after water withholding (DAW) and 42 DAW, and stem 53 DAW (*left*) and leaf in WW, stem 3 d after rehydration (DAR), leaf 9 DAR and 25 DAR (*right*) during drought stress and rehydration. Values are means ± SE (*n* = 6).

Table 2. Chlorophyll (Chl) *a* and *b*, Chl (*a*+*b*) contents in *C. korshinskii* leaf and stem during drought stress and rehydration process. Means ± SD of three independent observations. Values within same row followed by the same letter(s) are not significantly different ($P<0.05$).

	Chl content [g kg^{-1}(DM)]	Control					
		3 d	42 d	53 d	3 d	9 d	25 d
Leaf	Chl *a*	1.564 ± 0.014^{a}	1.578 ± 0.019^{a}	1.547 ± 0.017^{a}	1.562 ± 0.021^{a}	1.603 ± 0.034^{a}	1.615 ± 0.037^{a}
	Chl *b*	0.567 ± 0.017^{a}	0.561 ± 0.021^{a}	0.558 ± 0.019^{a}	0.547 ± 0.032^{a}	0.560 ± 0.026^{a}	0.549 ± 0.031^{a}
	Chl (*a*+*b*)	2.131 ± 0.022^{a}	2.139 ± 0.026^{a}	2.097 ± 00.17^{a}	2.119 ± 0.023^{a}	2.147 ± 0.031^{a}	2.164 ± 0.033^{a}
Stem	Chl *a*	0.118 ± 0.004^{a}	0.114 ± 0.005^{a}	0.119 ± 0.001^{a}	0.121 ± 0.006^{a}	0.118 ± 0.001^{a}	0.115 ± 0.005^{a}
	Chl *b*	0.036 ± 0.003^{a}	0.039 ± 0.002^{a}	0.038 ± 0.002^{a}	0.034 ± 0.005^{a}	0.031 ± 0.006^{a}	0.033 ± 0.003^{a}
	Chl (*a*+*b*)	0.141 ± 0.006^{a}	0.142 ± 0.004^{a}	0.146 ± 0.001^{a}	0.151 ± 0.007^{a}	0.145 ± 0.005^{a}	0.149 ± 0.007^{a}
		Drought stress			Rehydration		
		3 d	42 d	53 d	3 d	9 d	25 d
Leaf	Chl *a*	1.572 ± 0.005^{a}	0.975 ± 0.007^{b}			0.849 ± 0.022^{c}	1.508 ± 0.088^{a}
	Chl *b*	0.553 ± 0.017^{a}	0.404 ± 0.003^{b}			0.306 ± 0.025^{c}	0.532 ± 0.036^{a}
	Chl (*a*+*b*)	2.126 ± 0.013^{a}	1.314 ± 0.011^{b}			1.145 ± 0.019^{c}	2.04 ± 0.062^{a}
Stem	Chl *a*	0.115 ± 0.008^{d}	0.098 ± 0.004^{d}	0.085 ± 0.003^{e}	0.084 ± 0.002^{e}	0.094 ± 0.004^{d}	0.118 ± 0.002^{d}
	Chl *b*	0.037 ± 0.002^{d}	0.031 ± 0.001^{d}	0.033 ± 0.008^{d}	0.032 ± 0.003^{d}	0.033 ± 0.004^{d}	0.040 ± 0.006^{d}
	Chl (*a*+*b*)	0.153 ± 0.012^{d}	0.131 ± 0.004^{d}	0.119 ± 0.006^{e}	0.114 ± 0.008^{e}	0.126 ± 0.013^{e}	0.160 ± 0.017^{d}

similar pattern as F_v/F_m, but decreased more dramatically 42 DAW and 53 DAW (Fig. 3*E*). The thermal energy dissipation expressed as NPQ was similar between WW plant and plant of 3 DAW. Thereafter, it increased steadily 42 DAW and was two time higher in stem of 53 DAW than in leaf of WW plant (Fig. 3*C*). After 3-d rehydration, F_v/F_m and Φ_{PSII} had the same pattern in stem and both higher than that in stem of 53 DAW. 9 DAR,

F_v/F_m and Φ_{PSII} steady increased, but were still lower than those in WW plant. After 3-d rehydration, NPQ decreased and was lower than that in stem of 53 DAW. NPQ decreased and reached as control plant 25 DAR (Fig. 3*D*).

Leaf abscission and Chl content: Leaf abscission was observed in drought-stressed plant after 42-d treatment. At 53 DAW, all leaves abscised. Chl *a* and *b,* and total Chl (*a*+*b*) contents were similar in leaf and stem in WW plant during experimental process and plant of 3 DAW. Dehydration caused significant decrease in Chl *a, b* and Chl (*a*+*b*) in leaf of 42 DAW plant, but did not have an effect on stem; 53 DAW, Chl *a* in stem decreased, 74% of that in control plant. 3 DAR, Chl *a,* Chl *b,* and Chl (*a*+*b*) contents kept constant in stem. Thereafter, Chl *a* in stem and Chl *a, b* in leaf increased steadily during the rehydration period (Table 2).

Discussion

Different water-use strategies in response to drought have been adopted by woody plants to overcome water deficits during dry periods, namely, isohydric control of water potential (avoidance mechanism by stomata closure; Tyree and Sperry 1988, Lo Gullo and Salleo 1988), anisohydric behavior (generally seen as a drought tolerance mechanism in which stomatal closure is less than in isohydric behavior; Lo Gullo and Salleo 1988, McDowell *et al.* 2008), or any of number of intermediate situations (Varela *et al.* 2010). In present study, the fully mature leaves of *C. korshinskii* can lost up to 70% of their water content and shed, but stems can lost up to 90% of their water content and still viable. Upon rehydration, the plants produce new leaves. Leaf abscission is regarded as a good mechanism to avoid drought damage during the periods of low water availability (Nilsen and Muller 1981, Mahouachi *et al.* 2006), as observed in *Gossypium hirsutum* (Morgan *et al.* 1977), *Lotus scoparius* (Nilsen and Muller 1981), *Carica papaya* (Mahouachi *et al.* 2006), *Cordia africana*, *Croton macrostachyus*, *Millettia ferruginea* (Gindaba *et al.* 2004), and *Reaumuria soongorica* (Liu *et al.* 2007, Xu *et al.* 2010). *Reaumuria soongorica* can survive drying to a point when stem relative water content (RWC) no more than 5% of dry mass, but its leaves shed when their RWC is below 45% of dry mass (Xu *et al.* 2010). Those two shrubs have similar strategies under extremely drought stress, such as different limitations. *C. korshinskii* is more sensitive than *R. soongorica* under extreme drought stress. *C. korshinskii* only can survive when stem RWC is no more than 10% of dry mass. These results can explain the distribution area of these two plants. *R. soongorica* is distributed in arid area where the precipitation is about 30–150 mm (Wang *et al.* 2002a), and *C. korshinskii* is distributed in arid area where the precipitation is less than 250 mm (Wang *et al.* 2002b). The results suggest that *C. korshinskii* stem has strong ability to tolerate soil water deficits. In the desert environment, there may be a selective advantage for plants to allocate limited resources to maintain photosynthesis to prolong the life span under water stress in order to take advantage of the occasional rainfall events in the summer.

Water is the limiting factor for plants growing in arid and semiarid regions. For desert plants, the compromise that occurs in the nature between restricting water loss through stomata *vs*. maintaining a high-carbon gain depends on stomatal and nonstomatal regulation. In the present study, the change of P_N in *C. korshinskii* during dehydration was in the same direction to C_i and g_s (Fig. 2*A*,*C*,*E*). The criterion for establishing that stomatal responses are dominant in the response of assimilation rate to some perturbation is that C_i should change in the same direction as P_N. If the changes are in the opposite direction, the most important change must have been in the mesophyll cells, caused by nonstomatal factors (Farquhar and Sharkey 1982). In our study, the diurnal course of C_i associated with the diurnal course of P_N under dehydration suggested that stomatal factors were the main cause of the reduction of P_N. In the present study, P_N, g_s, and *E* of *C. korshinskii* were about 20 μmol m^{-2} s^{-1}, 781 mmol m^{-2} s^{-1}, and 4.2 mmol m^{-2} s^{-1} at high soil water availability, respectively. These values were similar to the species growing in a similar habitat such as *Reaumuria soongorica* (Liu *et al.* 2007, Bai *et al.* 2008, Xu *et al.* 2010). These results indicate that *C. korshinskii* tends to conserve soil water rather than use it rapidly when soil water is available. Furthermore, g_s declined to reduce water loss through transpiration, leaves of *C. korshinskii* can "sense" the soil water deficit and use root to shoot signaling (mainly ABA, Comstock 2002) to induce stomata to close against further water loss and irreversible cell dehydration. Similar behavior has also been observed in other woody plants, such as olive (*Olea europaea*) (Aganchich *et al.* 2009) and six deciduous tree species (Croker *et al.* 1998). However, under severe water stress, the stomata were still slightly open, and P_N was still positive, indicating that plant were well adapted to enable metabolism to occur at low water potential. This result was also confirmed by previous observations (Song *et al.* 2008), in which P_N of *C. korshinskii* had a smaller relative decrease under a gradually increasing water deficit compared with other woody species in the same habitat.

F_v/F_m and Φ_{PSII} are important indicators of photosynthetic capacity. Stresses affecting PS are often accompanied by a decline in F_v/F_m which reflects the maximal efficiency of excitation capture of a dark-adapted plant, and is correlated with the number of functional PSII reaction centres (Schiller *et al.* 1999). Significant declines of F_v/F_m were observed in *C. korshinskii* leaves in the dark after dehydration, suggesting that the aximum capacity of the primary reaction of photosynthesis may be impaired. Φ_{PSII} is a parameter closely correlated with the quantum yield of noncyclic electron transport (Genty *et al.* 1989). Values of Φ_{PSII} were near to 0.35 and NPQ was near to 0.65 at the end of desiccation. Similar results has also been observed in *Reaumuria soongorica* (Liu *et al.* 2007, Bai *et al.* 2008). The decrease of F_v/F_m could be induced by the decrease of functional PSII, but also induced by persistent NPQ. NPQ increased during drought stress, indicating that the activity of photoprotective processes such as thermal dissipation at the antenna level increased under water stress (Fleck *et al.* 1998, Balaguer *et al.* 2002), and this was probably as a consequence of the xanthophyll cycle (Fleck *et al.* 1998). The main function of this regulation may be to contribute to maintaining PSII fractionally open even when the stomata are almost closed (Kitao *et al.* 2003).

The leaf of *C. korshinskii* is covered by dense silky villis (Ma *et al.* 2004), which reflect the incoming radiation, enable leaves to absorb less solar energy, and as a result, the plant can avoid injury caused by strong irradiation and high temperature. *C. korshinskii* survives the loss of 89% of its water. During drying about 80% Chl (a+b) is lost and the thylakoid membranes are dismantled accompanying leaf shed. Leaf shedding reduces the surface area exposed to light during severe drought stress. The leaf shed and the loss of Chl in this species may be necessary to prevent excess photon absorption. *C. korshinskii* can survive extreme drought stress through leaf abscission but keeps the stem alive. A previous study (Xu *et al.* 2008) has shown that during drought-stress process, *C. korshinskii* accumulated more carbohydrates, especially the nonstructural ones, in stem, and after rehydration the concentration of carbohydrates in stem declined (Xu *et al.* 2008). We think the high carbohydrate concentration in stem provided fundamental energy for resprouting of new leaves and regrowth (Xu *et al.* 2008). Another study showed that when the shoot of *C. korshinskii* was removed or clipped, plant has responded by drawing upon more carbohydrates from roots, elevated photosynthesis, improved water status, and photosynthate allocation shifted contributing to rapid resprout regrowth. These regrowth mechanisms enable *C. korshinskii* to recover quickly from damage in a disturbed environment (Fang *et al.* 2007). In summary, *C. korshinskii* uses different strategies to cope with different stress.

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