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Caragana korshinskii seedlings maintain positive photosynthesis during short-term, severe drought stress

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Abstract

Seedling performance may determine plant distribution, especially in water-limited environments. Plants of *Caragana korshinskii* commonly grow in arid and semiarid areas in northwestern China, and endure water shortage in various ways, but little is known about their performance when water shortage occurs at early growth stages. The water relations, photosynthetic activity, chlorophyll (Chl) content and proline accumulation were determined in 1-year-old seedlings growing in a 1:1 mixture of Loess soil and Perlite and subjected to (*1*) a water deficit for 20 days and (*2*) kept adequately watered throughout. The water deficit induced low (–6.1 MPa) predawn leaf water potentials (LWP), but did not induce any leaf abscission. Stomatal conductance (g_s), leaf transpiration rate (*E*), and net photosynthetic rate (P_N) decreased immediately following the imposition of the water deficit, while the maximal photochemical efficiency of photosystem II (PSII) (F_v/F_m) and the effective quantum yield of PSII (Φ_{PSII}) decreased 15 days later. An early and rapid decrease in g_s, reduced *E*, increased Chl (*a+b*) loss, increased the apparent rate of photochemical transport of electrons through PSII (ETR)/P_N, as well as a gradual increase in non-photochemical quenching of fluorescence (NPQ) and proline may have contributed to preventing Φ_{PSII} from photodamage. *C. korshinskii* seedlings used a stress-tolerance strategy, with leaf maintenance providing a clear selective advantage, considering the occasional rainfall events during the growing season.

Additional key words: chlorophyll fluorescence; photochemical efficiency; photosynthesis; proline; water deficit; water relations.

Introduction

Water stress is the main environmental factor limiting plant growth and yield worldwide, especially in the context of future climate scenarios, threatening the generation and sustainability of forests (Boyer 1982, Varela *et al.* 2010). Within limits, plants adapt to water stress through physiological and morphological adaptations (Niinemets 2001, Balaguer *et al.* 2002, Georgieva *et al.* 2007). Reducing stomatal conductance is one of the main physiological characteristics of plant response to water deficits (Balaguer *et al.* 2002, Kitao *et al.* 2003, Georgieva *et al.* 2007). Maintenance of turgor by osmotic adjustment, which results from the accumulation of solutes, such as sugars, organic acids, and proline (Turner and Jones 1980), has been shown to be another physiological characteristic by which plants adapt to water deficits (Turner and Jones 1980). Under morphological

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Abbreviations: Chl – chlorophyll; DAW – days after water was withheld; *E* – transpiration rate; ETR – apparent rate of photochemical transport of electrons through PSII; F_0, F_m – minimal and maximal fluorescence; F_s, F_m' – steady-state fluorescence and maximal fluorescence yield of irradiated leaf; F_v/F_m – maximal photochemical efficiency of PSII; FC – field capacity; g_s – stomatal conductance; NPQ – nonphotochemical quenching of fluorescence; LWP – leaf water potential; PAR – photosynthetically active radiation; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PSII – photosystem II; SWC – soil water content; WUE – water-use efficiency; WW – well watered; WS – water-stressed; Φ_{PSII} – effective quantum yield of PSII.

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responses, plants can increase biomass allocation to the roots to increase water uptake (Palta and Watt 2009), and shed leaves to reduce the water requirements and maintain high water potentials (Morgan *et al.* 1977, Nilsen and Muller 1981, Mahouachi *et al.* 2006).

C. korshinskii is a winter-deciduous shrub, commonly found in desert and semi-desert zones and the Loess Plateau of northwestern China, where it has important ecological and economic value, including playing a key role in the succession from shifting sands to sandy grassland, thereby helping to restore degraded land and serving as a supplemental forage for livestock (Ma *et al.* 2008, Fang *et al.* 2008). As a result, it is chosen as one of the key species for revegetation of these areas. The adult plants of *C. korshinskii* have a deep root system, which can extend over 6 m in depth (Niu *et al.* 2003, Liu *et al.* 2003, Cheng *et al.* 2009), and absorb water from deep soil layers, thereby enabling it to survive in extremely dry regions, even where annual rainfall is only about 100 mm (Ma *et al.* 2004, Fang *et al.* 2006). Field research in this area has shown that P_N, and E of adult plants of *C. korshinskii* were more than 18 μmol m^{-2} s^{-1} and 5 mmol m^{-2} s^{-1}, respectively (Ma *et al.* 2004, 2008), almost equal to those of well watered plants in a pot experiment (Song *et al.* 2008). However, as seedlings have shallower root systems than adult *C. korshinskii*, the question is how seedlings survive periods of water shortage during the summer.

This study aimed to examine the responses of 1-year-old seedlings of *C. korshinskii* to water shortage during the summer growing season. The water relations, CO_2 assimilation rate, fluorescence activity, leaf Chl content and proline changes were measured to better understand the mechanisms of drought survival of seedlings in a desert environment.

Materials and methods

Site and plant material: The study was conducted at Yuzhong, Gansu province (35°57′ N, 104°09′E; 1,750 m a. s. l.; mean annual temperature 7.1°C; mean growing-season temperature 13°C) between 10 and 30 June 2009, the driest period during the growing season. In February 2008, seeds of *C. korshinskii* were placed in Petri dishes lined with wet filter paper to germinate. After germination, three seedlings were transferred into each plastic pot, 27 cm high and 17 cm in diameter, containing 3.6 kg of a 1:1 mixture of sieved Loess soil and Perlite with a dry bulk density of 0.63 g cm^{-3} and a field capacity (FC) of 34.7% after saturation with water and allowed to drain for 48 h. One month after sowing, seedlings were thinned to one per pot. Plants received ample water and were grown in a naturally-lit glasshouse with a roof that was closed manually at night and on rainy days, but open when not raining. During the growing season, the relative humidity was about 58% and the midday mean photosynthetically active radiation (PAR) was more than 1,100 μmol m^{-2} s^{-1}. In the study, only seedlings measuring about 50 cm in height and with a single stem were used.

Treatments: Ninety pots were used and on 10 June 2009 randomly designated to one of the two treatments: well watered (WW) control and water-stressed (WS), 45 pots per treatment. The pots were covered with a small quantity (*ca.* 2 cm) of Perlite to minimize soil evaporation. The WW plants were watered every day to maintain the soil near 80% FC by replacing the water lost through transpiration daily, calculated after weighing 5–10 randomly-selected pots on an electronic balance (*JM-B10001T, Guangzheng Medical Instrument Co.*, Shanghai, China). The WS treatment was imposed by withholding water for 20 days from 10 June.

Measurements: We photographed each plant at the start and the end of the experiment to determine whether leaves had been shed in the two treatments and noted whether any leaves were on the ground during the treatment period.

At 0, 3, 5, 7, 10, 12, 15, 18, and 20 days after water was withheld (DAW), LWP of upper fully-expanded leaves was measured at 04:30–05:30 h using a pressure chamber (*Model 1000, PMS Instrument Company*, Albany, OR, USA) and following the precautions recommended by Turner (1988). The proximal three pairs of leaflets at the base of the midrib of pinnately-compound leaf were removed and then the midrib of the leaf was inserted into the pressure chamber. Five leaves from five seedlings in different pots were measured in each treatment at each sampling time. After the measurement of LWP, the soil water content (SWC) was measured gravimetrically by weighing the same pots.

Between 09:00–11:00 h, similar leaves to those measured for LWP were used to measure leaf gas exchange and Chl fluorescence on the same seedlings on the same day (five different seedlings each treatment at each sampling time). P_N, E, and g_s were measured using a portable open gas-exchange system (*LI-6400, LiCor*, Lincoln, NE, USA) with photosynthetic photon flux density (PPFD) of 1,200 μmol m^{-2} s^{-1} provided by a LED source, and leaf temperature of 25°C. After measurement, the part of the leaf inserted into the cuvette was cut and the area of leaf inside the cuvette measured with a *WinRHIZO* scanner (*WinRHIZO Root Analysis, Regent Instruments*, Quebec, Canada), in order to calculate P_N, E, and g_s per unit leaf area. The instantaneous water-use efficiency (WUE) was defined as the ratio of photosynthesis to transpiration (P_N/E).

The saturation pulse method was used for determinations of all the fluorescence parameters with a portable fluorometer *(FMS-2, Hansatech*, Kings Lynn, UK). Briefly, leaf samples were dark-adapted for 1 h, then exposed to a weak modulated irradiance (<0.1 µmol m^{-2} s^{-1}) to asses the minimum fluorescence (F_0). A 600-ms saturation flash of light (>7,000 µmol quanta m^{-2} s^{-1}) was given to assess the maximum fluorescence (F_m) and F_v/F_m. Then the leaves were continuously irradiated with actinic light (1,200 µmol m^{-2} s^{-1}) in order to measure the steady-state fluorescence (F_s) and maximum fluorescence yield (F_m') of irradiated leaves. Measurements of F_m and F_0 were taken to calculate F_v/F_m [$F_v/F_m = (F_m - F_0)/F_m$]. These F_m values were also used to calculate NPQ [NPQ = ($F_m - F_m'$)/F_m']. Variation in Φ_{PSII} [$\Phi_{PSII} = (F_m' - F_s)/F_m'$] between treatments was calculated according to Genty *et al.* (1989). ETR was then calculated as: ETR = 0.84 × PPFD × Φ_{PSII} × 0.5. Then ETR/P_N was calculated.

After measurements, the seedlings in the five replicate pots per treatment at each sampling time were harvested. After leaf areas were measured with the WinRHIZO scanner (*WinRHIZO Root Analysis, Regent Instruments*, Quebec, Canada), about 0.2 g of leaf tissue was used to measure Chl content, and some remaining leaves, 'thin roots' (diameter < 1 mm), and 'medium roots' (diameter between 1 and 5 mm) were used to measure the proline content.

Analyses of Chl and proline content: Chl *a* and Chl *b* were extracted from leaf disks with 80% acetone. The pigment content was determined spectrophotometrically according to Lichtenthaler (1987) and the data were expressed per unit leaf area. Free proline content was determined according to Sofo *et al.* (2004). A 5.0 ml aliquot of 3% (w/v) sulfosalicylic acid was added to 0.5 g of powder and boiled in a water bath at 100°C for 0.5 h in glass tubes covered at the top. The mixture was centrifuged at 2,000 × *g* for 300 s at 25°C. A 0.2 ml aliquot of extract was mixed with 0.4 ml distilled water and 2.0 ml of reagent mixture (30 ml glacial acetic acid, 20 ml distilled water and 0.5 g of nihydrin), and boiled at 100°C for 1 h. After cooling the reaction mixture, 6.0 ml toluene were added. The chromophore containing toluene was separated and absorbance at 520 nm was read, using toluene as a blank. Proline concentration, in µmol g^{-1}(DM), was calculated using L-proline for the standard curve.

Statistical analysis: The data of SWC, LWP, Chl (*a*+*b*), P_N, g_s, E, WUE, F_v/F_m, Φ_{PSII}, ETR/ P_N, NPQ, and leaf and root proline concentration were compared using *t*-test (*SPSS 15.0*, Chicago, IL, USA). *Levene*'s test was used to verify the assumption of homogeneity of variance. If variances were heterogeneous, data were log transformed or square-root transformed.

Results

SWC and LWP: The SWC in the WW pots varied between 79% and 82% FC during the experiment, but after water was withheld the SWC decreased progressively in WS treatment to reach 44% FC by 5 DAW and 16% FC by 12 DAW. Subsequently SWC decreased slowly to reach 7.0% FC by 20 DAW (Fig. 1*A*). Predawn LWP in WW seedlings ranged from –0.5 to –0.6 MPa during the experiment, and in WS seedlings, the predawn LWP did not decrease significantly for the first 5 DAW and then decreased steadily from –0.5 MPa at 5 DAW to –6.1 MPa at 18 DAW. LWP in WS seedlings was not measured at 20 DAW (Fig. 1*B*).

Leaf maintenance and Chl content: No leaf abscission was observed during the experiment in the WS and WW seedlings. Total Chl (*a*+*b*) expressed per unit leaf area was similar in the WS and WW seedlings for the first 5 DAW, and then decreased steadily to 24 µg cm^{-2} in WS seedlings, 57% of that in WW seedlings, by 20 DAW (Fig. 1*C*).

Photosynthesis and electron transport in PSII: P_N, g_s, and E in the WW seedlings varied from 16–19 µmol m^{-2} s^{-1}, 0.21–0.25 mol m^{-2} s^{-1}, and 4.0–4.6 mmol m^{-2} s^{-1}, respectively, during the experiment. However, in the WS seedlings, P_N, g_s, and E decreased by 20–40% in the first 5 DAW as SWC decreased from 80% to 44% FC, but

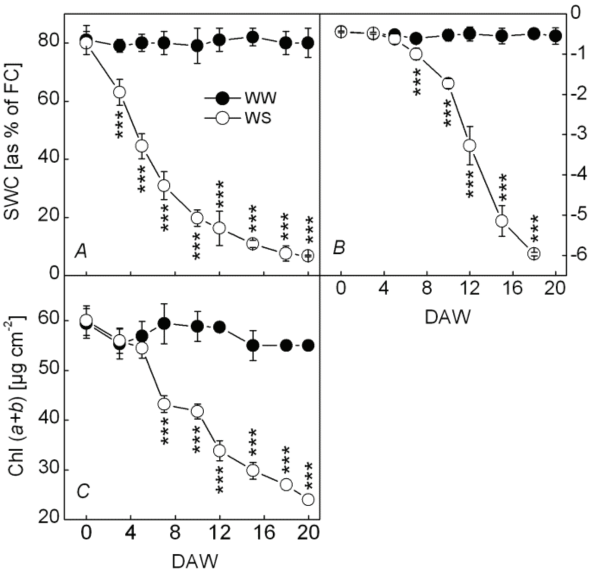

Fig. 1. Change with days after water was withheld (DAW) in the water-stressed treatment on soil water content [SWC, % of field capacity (FC)] (*A*), predawn leaf water potential (LWP) (*B*), and chlorophyll content per unit area [Chl (*a*+*b*)] (*C*) of *C. korshinskii* seedlings in the water-stressed (WS) and well watered (WW) treatments. Values are means ± SE (n = 5). Significant differences between WW and WS treatments on a particular date are indicated as *<0.05, **<0.01, and ***<0.001.

before the predawn LWP decreased significantly, and continued to decrease to reach 0.1 µmol $m^{-2} s^{-1}$, 0.01 mol $m^{-2} s^{-1}$, and 0.24 mmol $m^{-2} s^{-1}$, respectively, by 20 DAW. Note that after 20 days without water P_N, g_s, and E were still positive despite a predawn LWP of below –6.1 MPa (Fig. 2*A*,*B*,*C*). There was a positive correlation between P_N and g_s when LWP decreased below –1.0 MPa (r^2 = 0.95, p<0.01). The instantaneous WUE increased in the WS seedlings from 0 to 10 DAW, decreased thereafter and was lower than that in WW seedlings by 18 DAW (Fig. 2*D*). F_v/F_m was similar between the two treatments from 0 to 12 DAW as LWP in WS seedlings decreased from –0.5 to –3.3 MPa. Thereafter, it decreased in WS seedlings to 78% of that in WW seedlings by 20 DAW (Fig. 3*A*). Φ_{PSII} followed a similar pattern as F_v/F_m, but decreased more dramatically from 12 DAW (Fig. 3*B*). ETR/P_N was higher in WS seedlings than in WW seedlings 12 DAW and the largest differences were more than five times higher by 15 DAW (Fig. 3*C*). The thermal energy dissipation, expressed as NPQ, increased steady from 3 DAW and was twice as high in WS than in WW seedlings by 20 DAW when LWP decreased below –6.1 MPa (Fig. 3*D*).

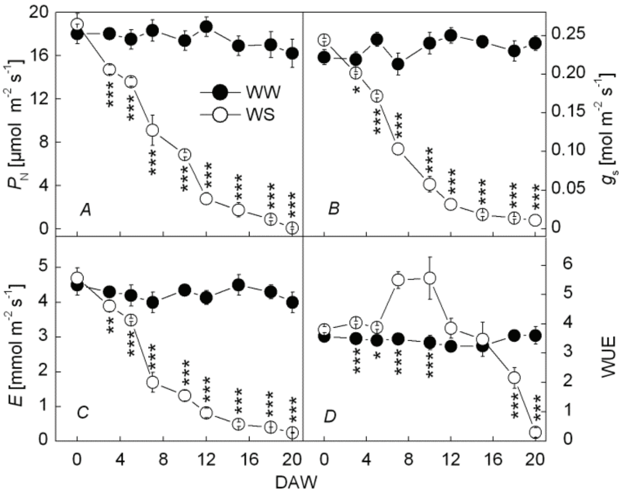

Fig. 2. Change with days after water was withheld (DAW) in the water-stressed treatment on leaf net photosynthetic rate (P_N)(*A*), stomatal conductance (g_s) (*B*), transpiration rate (*E*) (*C*), and instantaneous water-use efficiency (WUE) (*D*) in *C. korshinskii* seedlings in the water-stressed (WS) and well watered (WW) treatments. Values are means ± SE (n = 5). Significant differences between WW and WS treatments on a particular date are indicated as *<0.05, **<0.01, and ***<0.001.

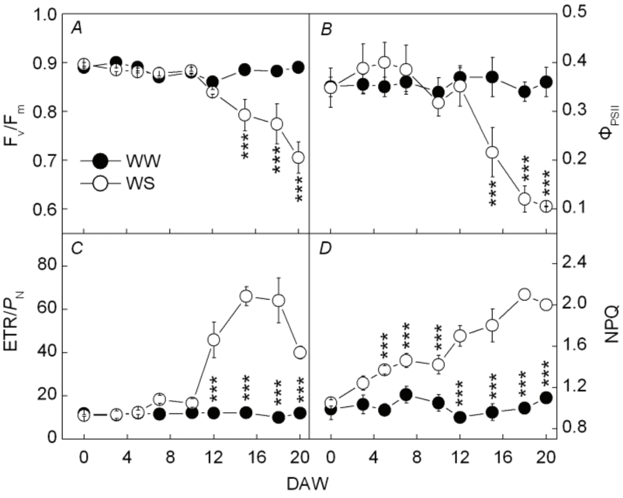

Fig. 3. Change with days after water was withheld (DAW) in the water-stressed treatment on maximal photochemical efficiency of PS II (F_v/F_m) (*A*), effective quantum yield of PSII (Φ_{PSII}) (*B*), apparent rate of photochemical transport of electrons through PSII divided by the photosynthetic rate (ETR/P_N) (*C*) and nonphotochemical quenching of fluorescence (NPQ) (*D*) in *C. korshinskii* seedlings in the water-stressed (WS) and well watered (WW) treatments. Values are means ± SE (n = 5). Significant differences between WW and WS treatments on a particular date are indicated as *<0.05, **<0.01, and ***<0.001.

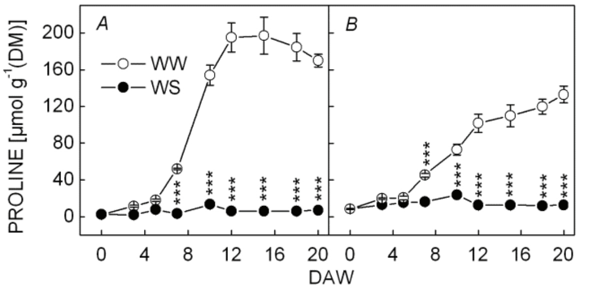

Fig. 4. Proline accumulation with days after water was withheld (DAW) in the water-stressed treatment in leaves (*A*) and roots (*B*) of *C. korshinskii* seedlings in the water-stressed (WS) and well watered (WW) treatments. Values are means ± SE (n = 5). Significant differences between WW and WS seedlings on a particular date are indicated as *<0.05, **<0.01, and ***<0.001.

Proline accumulation: Proline significantly increased in both the leaves and roots in WS seedlings by 7 DAW when LWP decreased to –1.1 MPa (Fig. 4*A*, *B*), reached a maximum by 15 DAW in leaves and continued to rise in roots for all 20 DAW. While the increase in the roots was 10 times that of the WW seedlings, in the leaves the increase was 30 times. There was no significant difference of proline concentration between thin roots (<1 mm diameter) and medium roots (1–5 mm diameter) both in the WS and WW seedlings (date not shown).

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 the present study, initially as SWC decreased, the predawn LWP was unchanged, but then decreased at a rate of 0.3 MPa d^{-1}. Although 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* (Xu *et al.* 2008), the seedlings of *C. korshiskii* did not shed any leaves to reduce evaporative demand even though the LWP of *C. korshiskii* decreased below –6.1 MPa. However, the Chl concentration in the leaves did decrease gradually with declining LWP and the leaves became yellow, but the stomata remained slightly open and net photosynthesis was still positive even when LWP was –6.1 MPa. The results suggest that *C. korshinskii* seedlings have 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 leaf span under water stress in order to take advantage of the occasional rainfall events in the summer.

However, the important question is how leaves adapt to water deficits in species in which leaves do not shed. In all species, regardless of growth form and leaf type, there is a shift from limitations mostly caused by limitation to CO_2 diffusion by stomatal closure at mild-to-moderate water deficits, to a combination of diffusive and biochemical limitations at severe water deficits (Galmés *et al.* 2007). Numerous physiological and developmental mechanisms that allow leaves to adapt to periods of water shortage can be involved during this process. In the present study, $P_{N,}$ g_s, and E of *C. korshinskii* seedlings were about 18 μmol m^{-2} s^{-1}, 0.23 mol m^{-2} s^{-1} and 4.2 mmol m^{-2} s^{-1} at high soil water availability, respectively. These values were similar to those in *C. korshiskii* seedlings observed by Song *et al.* (2008) but were significantly lower than those of other species seedlings growing in a similar habitat such as *Reaumuria soongorica*, *Salsola passerina*, and *Artemisia ordosica* (Song *et al.* 2008). The same result was also found in the field when *C. korshinskii* plants were compared to woody species such as *Tamarix austromongolica*, *Atraphaxis bracteata*, *Zygophyllum xanthoxylon*, *Ammopiptanthus mongolicus*, *Hedysarum scoparium*, *Nitraria tangutorum*, and *Haloxylon ammodendron* (Li *et al.* 2006). 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, even though predawn LWP was unchanged. Roots of *C. korshinskii* seedlings 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*) (Centritto *et al.* 2005, Aganchich *et al.* 2009) and six deciduous tree species (Croker *et al.* 1998). However, under severe water stress (LWP about –6.1 MPa), the stomata were still slightly open, and P_N was still positive, indicating that the seedlings 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* seedlings had a smaller relative decrease under a gradually increasing water deficit compared with other woody species in the same habitat. Whether this is attributed to lower xylem vulnerability to cavitation in *C. korshinskii* plants under severe drought conditions still needs to be resolved. A good relationship between g_s and P_N observed in the present study indicates that stomatal diffusion is the primary factor initially limiting photosynthesis under water stress, and this is a common feature of drought-adapted species (Chaves 1991).

While leaf photosynthesis decreased immediately following the reduction in water supply, it was 12 days and the predawn LWP was below –3.3 MPa before Φ_{PSII} began to decrease slowly. This resulted in an increase in the ratio ETR/P_N, suggesting that severe water stress leads to an increase in the partitioning of electron flow to pathways other than CO_2 assimilation, including photorespiration and the Mehler-peroxidase reaction (Kitao *et al.* 2003, Georgieva *et al.* 2007). Increased allocation of electrons to oxygen under water stress has been suggested as a possible mechanism by which excess photochemical energy can be dissipated and the high quantum yield of PSII electron transport can be maintained, thus protecting PSII from damage (Lu and Zhang 1998). It is likely that increased ETR/P_N would be advantageous in increasing the ability of *C. korshinskii* seedlings to maintain some photosynthetic activity under severe water stress as observed in the present study.

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 temperatures. In addition, NPQ in WS seedlings increased twice compared with the WW ones, 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).

Accumulation of osmotically active solutes is another means of maintaining some photosynthesis under severe stress (Turner and Jones 1980). Although osmotic adjustment was not measured in this study, the dramatic accumulation of proline in both the roots and leaves from 7 DAW may suggest that some degree of osmotic adjustment occurred as proline appears to accumulate in the cytosol to balance the accumulation of sugars and organic acids in the vacuole. This would contribute to the maintenance of turgor, allowing the stomata to remain partially open and CO_2 assimilation to continue at low values of LWP (Yin *et al.* 2005). In addition, proline has a protective action which prevents membrane damage and protein denaturation during severe drought stress, and replenishes the $NADP^+$ supply in altered redox potentials. It has also been proposed that proline can act as an electron acceptor, avoiding damage to photosystems (Hare *et al.* 1998).

Conclusions: Although the *C. korshinskii* seedlings did not shed their leaves when exposed to severe stress, they exhibited a range of drought tolerance strategies to reduce the damaging effect of the water deficit on physiological activity. Withholding water induced a reduction in stomatal conductance and water loss by transpiration. While this reduced the rate of leaf photosynthesis, it allowed conservation of soil water and the maintenance of low, but positive, photosynthesis at extremely low values of predawn LWP (below –6.1 MPa). The water-stressed *C. korshinskii* seedlings also accumulated large amounts of proline in both the leaves and roots to increase their ability to tolerate water stress. At more severe levels of water deficit, increased loss of Chl ($a+b$), higher ETR/P_N, as well as increased NPQ, contributed to protecting Φ_{PSII} from drought-stress-induced damage. These results provide insights into the reasons why *C. korshinskii* seedlings are able to survive and grow in arid and semiarid regions and provide a summer fodder for grazing animals in northwest China.

References

Aganchich, B., Wahbi, S., Loreto, F., Centritto, M.: Partial root zone drying: regulation of photosynthetic limitations and antioxidant enzymatic activities in young olive (*Olea europaea*) saplings. – Tree Physiol. **29**: 685-696, 2009.

Balaguer, L., Pugnaire, F.I., Martínez-Ferri, E., Armas, C., Valladares, F., Manrique, E.: Ecophysiological significance of chlorophyll loss and reduced photochemical efficiency under extreme aridity in *Stipa tenacissima* L. – Plant Soil **240**: 343-352, 2002.

Boyer, J.S.: Plant productivity and environment. – Science **218**: 443-448, 1982.

Centritto, M., Wahbi, S., Serraj, R., Chaves, M.M.: Effects of partial rootzone drying (PRD) on adult olive tree (*Olea europaea*) in field conditions under arid climate: II. Photosynthetic responses. – Agric. Ecosyst. Environ. **106**: 303-311, 2005.

Chaves, M.M.: Effects of water deficits on carbon assimilation. – J. Exp. Bot. **42**: 1-16, 1991.

Cheng, X., Huang, M., Shao, M., Warringon, D.N.: A comparison of fine root distribution and water consumption of mature *Caragana korshinkii* Kom grown in two soils in a semiarid region, China. – Plant Soil. **315**: 149-161, 2009.

Comstock, J.P.: Hydraulic and chemical signalling in the control of stomatal conductance and transpiration. – J. Exp. Bot. **53**: 195-200, 2002.

Croker, J.L.,Witte, W.T., Auge, R.M.: Stomatal sensitivity of six temperate, deciduous tree species to non-hydraulic roottoshoot signalling of partial soil drying. – J. Exp. Bot. **49**: 761-774, 1998.

Fang, X.W., Wang, X.Z., Chen, K., Li, H., Wang, G.: Responses of *Caragana korshinskii* to aboveground partial shoot removal: combining defence and tolerance strategies. – Ann. Bot. **98**: 203-211, 2006.

Fang, X.W., Li, J.H., Xiong, Y.C., Fan, X.W., Li, F.M.: Responses of *Caragana korshinskii* Kom. to shoot removal: mechanisms underlying regrowth. – Ecol. Res. **23**: 863-871, 2008.

Fleck, I., Hogan, K.P., Llorens, L., Abadía, A., Aranda, X.: Photosynthesis and photoprotection in *Quercus ilex* resprouts after fire. – Tree Physiol. **18**: 607-614, 1998.

Galmés, J., Flexas, J., Savé, R., Medrano, H.: Water relations and stomatal characteristics of Mediterranean plants with different growth forms and leaf habits: responses to water stress and recovery. – Plant Soil **290**: 139-155, 2007.

Genty, B., Briantais, J.M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta. **990**: 87-92, 1989.

Georgieva, K., Szigeti, Z., Sarvari, E., Gaspar, L., Maslenkova, L., Peeva, V., Peli, E., Tuba, Z.: Photosynthetic activity of homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and rehydration. – Planta **225**: 955-964, 2007.

Gindaba, J., Rozanov, A., Negash, L.: Response of seedlings of two *Eucalyptus* and three deciduous tree species from Ethiopia to severe water stress. – For. Ecol. Manag. **201**: 119-129, 2004.

Hare, P.D., Cress, W.A., Van Staden, J.: Dissecting the roles of osmolyte accumulation during stress. – Plant Cell Environ. **21**: 535-553, 1998.

Kitao, M., Lei, T.T., Koike, T., Tobita, H., Maruyama, Y.: Higher electron transport rate observed at low intercellular CO_2 concentration in long-term drought-acclimated leaves of Japanese mountain birch (*Betula ermanii*). – Physiol. Plant. **118**: 406-413, 2003.

Li, Q.H., Liu, J.F, Zhang, J.B., Jiang Z.P.: [Photosynthetic and physiological characteristics of eight psammophilic shrub species in northeast Ulanbuh desert during the late growing season.] – Acta Bot. Boreal.-Occident. Sin. **26**: 2318-2323, 2006. [In Chin.]

Lichtenthaler, H.K.: Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. – Methods Enzymol. **148**: 350-382, 1987.

Liu, M. Z., Jiang, G. M., Li, Y. G., Niu, S. L., Gao, L. M., Ding

L., Peng Y.: Leaf osmotic potentials of 104 plant species in relation to habitats and plant functional types in Hunshandak Sandland, Inner Mongolia, China. – Trees **17**: 554-560, 2003.

Lo Gullo, M.A., Salleo, S.: Different strategies of drought resistance in three Mediterranean scierophyllous trees growing in the same environmental conditions. – New Phytol. **108**: 267-276, 1988.

Lu, C., Zhang, J.: Effects of water stress on photosynthesis, chlorophyll fluorescence and photoinhibition in wheat plants. – Aust. J. Plant Physiol. **25**: 883-892, 1998.

Ma, C.C., Gao, Y.B., Guo, H.Y., Wang, J.L.: Photosynthesis, transpiration, and water use efficiency of *Caragana microphylla, C. intermedia*, and *C. korshinskii*. – Photosynthetica **42**: 65-70, 2004.

Ma, C.C., Gao, Y.B., Guo, H.Y., Wang, J.L., Wu, J.B., Xu, J.S.: Physiological adaptation of four dominant *Caragana* species in the desert region of the Inner Mongolia Plateau. – J. Arid Environ. **72**: 247-254, 2008.

Mahouachi, J., Socorro, A.R., Talon, M.: Responses of papaya seedling (*Carica papaya* L.) to water stress and re-hydration: growth, photosynthesis and mineral nutrient imbalance. – Plant Soil **281**: 137-146, 2006.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A.: Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? – New Phytol. **178**: 719-739, 2008.

Morgan, P.W., Jordan, W.R., Davenport, T.L., Durham, J.I.: Abscission response to moisture stress, auxin transport inhibitors, and ethephon. – Plant Physiol. **59**: 710-712, 1977.

Niinemets, Ü.: Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. – Ecology **82**: 453-469, 2001.

Nilsen, E.T., Muller, W.H.: Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. – Ecol. Monogr. **51**: 323-341, 1981.

Niu X.W., Ding Y.C., Zhang Q., XU Q.: [Studies on the characteristics of *Caragana* root development and some relevant physiology.] – Acta Bot. Boreal-Occident Sin. **23**: 860-865, 2003. [In Chin.]

Palta, J.A., Watt, M.: Crop roots systems form and function: Improving the capture of water and nutrients with vigorous root systems. – In: Sadras, V., Calderini, D. (ed.): Crop physiology: applications for genetic improvement and agronomy. Pp 309-325. Academic Press, San Diego 2009.

Sofo, A., Dichio, B., Xiloyannis, C., Masia, A.: Lipoxygenase activity and proline accumulation in leaves and roots of olive trees in response to drought stress. – Physiol. Plant **121**: 58-65, 2004.

Song, W.M., Zhou, H.Y., Jia, R.L., Zhao, X., Feng, L., Tan, H.J.: [Response of photosynthesis function and trehalose content of four desert plants to gradual drought stress.] – J. Desert Res. **28**: 449-454, 2008. [In Chin.]

Turner, N.C.: Measurement of plant water status by the pressure chamber technique. – Irrig. Sci. **9**: 289-308, 1988.

Turner, N.C., Jones, M.M.: Turgor maintenance by osmotic adjustment: A review and evaluation. – In: Turner, N.C., Kramer, P.J. (ed.): Adaptation of plants to water and high temperature stress. Pp.87-103. Wiley-Interscience, New York 1980.

Tyree, M., Sperry, J.: Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. – Plant Physiol. **88**: 574-580, 1988.

Varela, S.A., Gyenge, J.E., Fernández, M.E., Schlichter, T.: Seedling drought stress susceptibility in two deciduous *Nothofagus* species of NW Patagonia. – Trees **24**: 443-453, 2010.

Xu, D.H., Li, J.H., Fang, X.W., Wang, G., Su, P.X.: Photosynthetic activity of poikilochlorophyllous desiccation tolerant plant *Reaumuria soongorica* during dehydration and re-hydration. – Photosynthetica **46**: 547-551, 2008.

Yin, C., Peng, Y., Zang, R., Zhu, Y., Li, C.: Adaptive responses of *Populus kangdingensis* to drought stress. – Physiol. Plant **123**: 445-451, 2005.