

Water relations, hydraulic conductance, and vessel features of three *Caragana* species of the Inner Mongolia Plateau of China

Jing LI, Yu-Bao GAO*, Zhi-Rong ZHENG, and Zeng-Lu GAO

College of Life Science, Nankai University, Tianjin 300071, P. R. China

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ABSTRACT. From early May to late September 2005, diurnal and seasonal changes in water relations, hydraulic conductance, vessel features, photosynthesis (*DCA*), transpiration (*DCE*), and water use efficiency (*WUE*) were studied in the field for three *Caragana* species—*C. microphylla* Lam, *C. davazamcii* Sancz and *C. korshinskii* Kom—growing in different habitats in the Inner Mongolia Plateau of China. The three species were generally exposed to severe environmental drought during most of the growing period. Among them, *C. korshinskii* had the largest vessels and specific hydraulic conductivity (K_s) in one-year-old twigs while the lowest were recorded in *C. microphylla*. All three species had the highest K_s in the summer and the lowest in the spring. For the three species, the best leaf water status occurred in the autumn indicated by the largest diurnal mean leaf water potential (Ψ_L) and the lowest leaf relative water deficit (*RWD*) while the severest leaf water stresses occurred in the spring. *Caragana microphylla* had larger Ψ_L than the other two species, and the lowest Ψ_L as well as the largest *RWD* occurred in *C. korshinskii*. The lowest *RWD* were found in *C. davazamcii*. The three species had the largest *DCA* and *DCE* in the autumn while the lowest values occurred in the spring for *C. microphylla* and *C. davazamcii*. *Caragana korshinskii* had the lowest *DCA* and *DCE* in the summer, which resulted in a decrease in soil water loss. Leaf stomatal conductance (g_s) and transpiration rate (E) were found to be correlated to hydraulic conductance in soil-leaf continuum (G_t) more closely than K_s in one-year-old twigs. Generally, the seasonal changes in G_t were in accordance with those of *DCA* and *DCE*, with the exception of *C. davazamcii*, which had the largest G_t in the spring. Among the three species, *C. davazamcii* had the highest values of seasonal mean *DCE* and G_t , and the lowest drought resistance during the growing period, which was in line the higher soil water content in its habitat. In the spring, despite the high soil water content, *C. microphylla* had the greatest resistance to the leaf water deficit raised by the low G_t . In the autumn, the greatest drought resistance occurred in *C. korshinskii*, which was exposed to the severest water stress due to low soil water content. By analyses of seasonal changes of K_s and G_t as well as their relationships with leaf gas exchange, G_t was approved to be more important than specific subportions (one-year-old twigs in this study) in terms of leaf water supply.

Keywords: *Caragana davazamcii*; *Caragana korshinskii*; *Caragan microphylla*; Diurnal and seasonal change; Growth rhythm; Hydraulic conductance; Leaf gas exchange; Vessel size.

INTRODUCTION

Numerous studies have been done on plant water relations over a long time period (Kramer, 1983; Zimmermann, 1983; Holbrook and Putz, 1996; Donovan et al., 2001), and it is widely recognized that plants can regulate their transpiration by decreasing stomata conductance in response to water deficit (Sperry, 2000). In addition to the traditional theory that the signals of chemicals like abscissic acid (ABA) (Ackerson and Radin, 1983; Zhang and Davies, 1987, 1990; Tardieu and Davies, 1992) can drive stomatal regulation, hydraulic signals

are being recognized as another mechanism (Fuchs and Livingston, 1996; Meinzer et al., 1995, 1997; Borghetti et al., 1998; Tausend et al., 2000).

There is substantial evidence that stomatal behavior is positively correlated with hydraulic conductance of the soil-leaf continuum (G_t) in diverse plant species and growth forms (Meinzer et al., 1990; Sperry and Pockman, 1993; Irvine et al., 1998; Bond and Kavanagh, 1999; Sohan et al., 1999; Comstock, 2000; Sperry, 2000; Hubbard et al., 2001). Such a close relationship between vapor and liquid phase conductance results from an active response of stomata to G_t . When G_t was experimentally increased by partial defoliation or shading, stomatal conductance (g_s) and transpiration of the untreated foliage

*Corresponding author: E-mail: ybgao@nankai.edu.cn; Tel: 022-23508249.

increased (Tschaplinski and Blake, 1989; Ovaska et al., 1992; Pataki et al., 1998). When G_t was decreased by root pruning, stem notching, or freeze thawing, g_s decreased (Hammel, 1967; Meinzer and Grantz, 1990; Sperry et al., 1993). Such close coordination between leaf gas exchange and liquid phase conductance can dampen variation of daily leaf water potential under a wide range of conditions (Mernzer et al., 1992; Sperry et al., 1993; Sperry, 2000).

For trees and shrubs, most of the hydraulic pathway is composed of xylem, which contains vessels or tracheids. The properties of vessels or tracheids strongly influence water transport efficiency. Numerous studies have demonstrated the great reduction in hydraulic conductance raised by xylem embolism. At the same time, a decrease in leaf gas exchange was observed in many species (Sperry et al., 1998; Nardini and Salleo, 2000; Pockman and Sperry, 2000; Sperry, 2000; Jordi et al., 2002). Since the transpiration stream also flows in extra-xylem pathways in the root and leaf, where embolism does not occur, the changes in root and leaf tissues during water stress can have important consequences for a plant's G_t (Sperry, 2000). Telling which subportions are primarily responsible for the hydraulic resistance is difficult. Generally, stomatal behavior has been found to be more correlated with total resistance than with the resistance of any specific subportion of the pathway (Comstock, 2000).

In this study, the leaf gas exchange, leaf water status, and hydraulic conductance of three *Caragana* species were investigated during different periods of a growing season. The three species, *Caragana microphylla* Lam, *C. davazamcii* Sancz, and *C. korshinskii* Kom, grow in different habitats of China's Inner Mongolia Plateau. Their close interspecific relationships have been proved by morphology, physiology, and molecular biology, and some taxonomists even regarded them as one species (Wang et al., 1994; Wei et al., 1999; Ma et al., 2003a, 2003b; Zhao, 2005). All three *Caragana* species have been shown to adapt well to drought conditions (Li and Zhang, 1996; Xiao and Zhou, 2001; Zhou et al., 2001).

The aims of this study were: (1) to learn the relationship between leaf gas exchange and hydraulic conductance

from two levels, i.e. G_t and the hydraulic conductivity of a specific subportion of the pathway (K_s); (2) to investigate the anatomical fundamentals of K_s adopted in the present study; (3) to understand the growth strategies by which the three *Caragana* species survive unfavorable environments in terms of their seasonal variations in photosynthesis, transpiration, and hydraulic conductance.

MATERIALS AND METHODS

Study site and plant materials

The three study sites were located in the Inner Mongolia Plateau of China, which has a temperate continental climate, with distinct dry (October to April) and rather wet seasons (July to September). The growing period for most plants is from late April to early September.

The shrubs of *C. microphylla* were investigated at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) (43.95°N, 116.07°E, 1,100 m above sea level) in the central part of a typical steppe in Xilingol Plateau. The average annual precipitation is 350 mm, and the average annual temperature is 0.20°C (from 1961 to 2000). Studies on *C. davazamcii* were carried out at the Huangfuchuan Station of the Inner Mongolia Hydrology Research Institute (IMHS) in Zhungeer Banner (39.45°N, 111.07°E, 1,130 m above sea level) in the eastern part of a warm-temperate steppe in Ordos Plateau. The average annual precipitation is 369 mm. The average annual temperature is 6.20°C (from 1953 to 1990), and the soil is of a chestnut type. Studies on *C. korshinskii* were conducted at the Ordos Sandland Ecological Station (OSES) in Yijinhuole Banner (39.21°N, 109.49°E, 1,300 m above sea level) in the central part of a warm-temperate steppe in Ordos Plateau. The annual precipitation is 360 mm. The average annual temperature is 6.30°C (from 1960 to 2000), and the maximum temperature in summer can be as high as 40°C. The soil is of an aeolian sand type. As shown in Table 1, the climatic factors of the three sites varied to a large extent during the growing period, and the precipitation of IMGERS was significantly lower than that of the other two sites (Table 1).

Table 1. Environmental factors recorded in the three study sites in the growing period of 2005.

Environmental factor	Study site	April	May	June	July	August	September	October
Total precipitation in a month (mm)	IMGERS	0.6	15.6	25.7	37.3	11.2	18.0	2.7
	IMHS	16.4	61.4	48.3	82.6	53.0	43.1	2.6
	OSES	4.7	76.3	27.3	73.9	105.3	17.8	8.2
Monthly mean air temperature (°C)	IMGERS	5.9	12.4	19.6	22.0	21.1	14.5	6.2
	IMHS	11.4	17.4	23.4	24.7	21.7	17.1	8.8
	OSES	10.5	16.2	22.6	23.5	20.2	15.7	7.3
Monthly mean atmospheric relative humidity (%)	IMGERS	30.0	38.0	46.0	61.0	53.0	46.0	42.0
	IMHS	30.0	40.0	43.0	53.0	66.0	63.0	51.0
	OSES	24.0	38.0	34.0	50.0	64.0	59.0	50.0

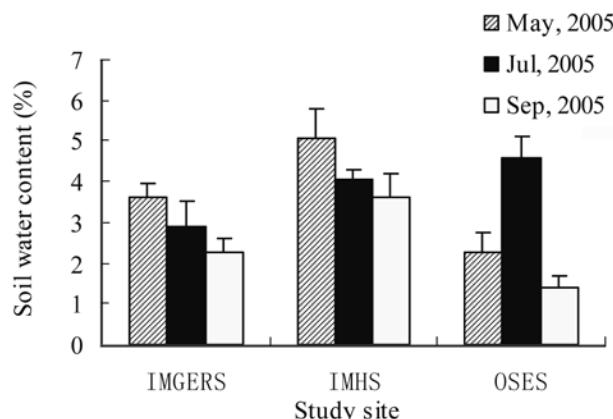


Figure 1. Soil water content of the three study sites during different seasons. Means are given \pm SD ($n=27$).

Since most of the root systems were located at a soil depth of 10–100 cm in the soil (Niu et al., 2003), we collected the soil samples from depths of 30 cm, 60 cm and 100 cm and measured the water contents separately. The mean values were taken as the final soil water content.

Generally, the study sites at IMGERS and IMHS had same seasonal tendency, i.e. spring>summer>autumn (Figure 1). However, the greatest soil water content of OSES occurred in the summer (4.50%), and the smallest values were observed in the autumn (1.40%). Of the three sites, IMHS had the highest soil water content, except in the summer. The study site at OSES had the highest soil water content in the summer, but the lowest values in the spring and autumn.

From each study site, samples were taken of ten healthy adult shrubs for the investigation of plant water relations. Four of them were labeled for the examination of hydraulic architecture and xylem anatomy. Some quantitative characteristics of *Caragana* plants are shown in Table 2. *Caragana korshinskii* shrub covered the smallest area and had the greatest height among the three species. The shrub area of *C. microphylla* was significantly larger than that of the other two species, and its height was a little greater than that of *C. davazamcii*. The highest shrub density was found in *C. davazamcii*, and the lowest in *C. korshinskii*. All the *Caragana* shrubs are more than ten years old.

The studies were carried out in May (early spring), July (mid-summer), and September (early autumn) of 2005, which covered most of the growing period of the three

Caragana species. In each season, diurnal changes in transpiration, leaf water potential, leaf water deficit, and hydraulic architecture in each species were followed for three or more sunny days. Measurements were made at intervals of 2 h, from 6:00 to 20:00 during those days.

Photosynthetic rate, water relations and soil water content

Leaf photosynthetic rate (A), leaf transpiration rate (E) and stomata conductance (g_s) were recorded with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, Nebraska, USA) operating in an open flow mode. The diurnal cumulative values of net photosynthesis (DCA) and transpiration (DCE) (from 6:00 to 18:00) were calculated following the two formulae (Ma et al., 2004b): (a) $DCA = \Sigma$ net photosynthetic rate \times 7200; (b) $DCE = \Sigma$ transpiration rate \times 7200. The water use efficiency (WUE) was obtained following the formula: $WUE = DCA / DCE$.

Leaf relative water deficit (RWD) was measured following Stocker's method (Liu, 1983). Leaf samples (4–6 g) were taken, and their fresh weight (W_f) was determined. After soaking them in water for 24 h, the saturated weight of leaf was measured (W_{sat}). Leaf dry weight (W_d) was determined by oven-drying the sample (60°C for 48 h). The leaf water deficit was calculated from the formula: $RWD = (W_{sat} - W_f) / (W_{sat} - W_d) \times 100\%$.

Leaf water potential, Ψ_L , was measured with a water potential system (Psypyro, Wescor, Amer). Predawn Ψ_L (6:00) was used to estimate soil water potential (Ψ_{soil}) (Tardieu and Simonneau, 1998; Tausend et al., 2000). The seasonal variations of soil water content were recorded. 30–40 soil samples (30–50 g each) were collected, and the fresh weight of soil samples was measured. After being dried in an oven (105°C for 24 h), the dry weight of the soil was determined, and the soil water content was calculated.

Hydraulic conductance

Four one-year-old twigs were sampled from the labeled shrubs every 2 h, and were taken to the laboratory immediately. Segments of 5 cm in length and 3 mm in diameter were obtained by re-cutting the twigs under water. Meanwhile the segment length (L) was measured accurately, and the leaves from the twigs were collected to measure leaf dry weight. The segments were placed in a conductivity apparatus (Sperry and Tyree, 1988), which permitted the measurement of the flow rate of solution

Table 2. Quantitative characteristics of three *Caragana* shrubs in different habitats.

Species	Density (plant/100 m ²)	Shrub height (cm)	Shrub area (m ²)	Age of plant (years)
<i>C. microphylla</i>	19	90.79 ^b	2.025 ^a	10–15
<i>C. davazamcii</i>	34	79.70 ^b	1.193 ^b	15
<i>C. korshinskii</i>	13	168.6 ^a	0.967 ^b	10

Same letter denotes non-significant difference while different letter denotes a significant difference ($\alpha=0.05$).

(w , g min⁻¹) in response to the pressure difference (ΔP , MPa). In this study, specific hydraulic conductivity, K_s , was adopted to describe the hydraulic architecture of one-year-old twigs: $K_s = w L / (\Delta P \times A_w)$, where A_w is a cross-sectional area of wood (Zotz et al., 1997a, 1997b).

Leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t) was determined as:

$G_t = E / \Delta \Psi$, where $\Delta \Psi$ is the difference between soil water potential (Ψ_{soil}) and leaf water potential (Ψ_L) at a given time (Borghetti et al., 1998; Sperry, 2000; Tausend et al., 2000).

Anatomical analysis

The segments (about 3 mm in diameter) of one-year-old twigs used in the experiments on hydraulic architecture were collected and stored with FAA solution (formal-acetic-alcohol fixative) until sectioning. Sections 10 µm thick were obtained with a rotary microtome, and stained with safranin and fast green FCF. Quantitative data were analyzed with Microscopic Image Analysis.

Because a small number of large conduits contributes much more to conductivity than do many small ones, we employed the statistic D_{95} according to the method introduced by Tyree et al. (1994). D_{100} is the mean diameter of all vessels, and D_{95} is the mean diameter of vessels responsible for about 95% of the total stem conductance. All vessels in one sample were categorized into small, medium and large size classes according to the method of Gorsuch et al. (2001). Vessels in the small size class contributed <1% to total flow. Medium-sized vessels contributed between 1 and 2% to total flow while large vessels contrib-

uted >2% to total flow.

Statistical analysis

The comparisons of parameters among species or seasons were made using a one-way ANOVA followed by a significant difference test (at $P < 0.05$). Relationships between G_t and leaf gas exchange of three *Caragana* species were determined with SPSS software 11.0.

RESULTS

Vessel features and hydraulic architectures of one-year-old twigs

In general, the D_{100} and D_{95} of *C. microphylla* were significantly lower than those of the other two species, and the largest D_{100} and D_{95} were found in *C. korshinskii* (Table 3). Though the greatest contribution to water transport was from the large size vessels of all three species, the contribution from large vessels of *C. microphylla* was much higher than that of the other two species. Vessel density differed significantly among species (Table 3). The species with the narrowest vessels, *C. microphylla*, had the highest vessel density. *C. korshinskii* had a little higher vessel density than *C. davazamcii*.

As shown in Table 4, all the three species had the greatest K_s in the summer, and the lowest values occurred in the spring. In the summer, *C. korshinskii* had significantly greater K_s than the other two species. In the spring and autumn, *C. davazamcii* and *C. korshinskii* had similar K_s values, and these exceeded that of *C. microphylla*.

Table 3. Vessel size and density in one-year-old twigs of three *Caragana* species. Data are means ± SD. Vessel density of each species was determined on four segments, and vessel width was determined on 50 vessels per segment.

Species	Diameter range (µm)	Vessel element size		Water transport contribution of three size classes (%)			Vessel density (no./mm ²)	
		D_{100} (µm)	D_{95} (µm)					
				Large	Medium	Small		
<i>C. microphylla</i>	4.93~49.28	13.50 ± 7.73 ^b	23.84 ± 7.56 ^{bc}	69.05	15.24	15.71	1109.52	
<i>C. davazamcii</i>	5.64~60.63	19.09 ± 8.93 ^{ab}	26.77 ± 7.33 ^b	46.97	24.71	28.32	836.17	
<i>C. korshinskii</i>	5.66~60.67	21.01 ± 12.08 ^a	35.66 ± 9.23 ^a	49.56	19.84	31.60	951.27	

Same letter denotes non-significant difference while different letter denotes a significant difference among the three species ($\alpha = 0.05$).

Table 4. Diurnal mean values of K_s of one-year-old twigs for the three *Caragana* species during the growing period.

	<i>C. microphylla</i>	<i>C. davazamcii</i>	<i>C. korshinskii</i>
Spring	0.409 ^b	1.209 ^a	1.267 ^a
Summer	1.168 ^c	2.078 ^b	4.129 ^a
Autumn	0.708 ^b	1.562 ^a	1.501 ^a

Same letter denotes non-significant difference while different letter denotes a significant difference among the three species ($\alpha = 0.05$).

Leaf water status and gas exchange

As shown in Figure 2, there was no difference in diurnal or seasonal patterns of Ψ_L for the three species. The highest diurnal Ψ_L occurred in the morning and evening, and the lowest values occurred at midday. The mean Ψ_L of the three species varied with seasons: spring < summer < autumn. Though the lowest diurnal mean Ψ_L occurred in the spring, the lowest values of $\Psi_{L\min}$ (diurnal minimum of Ψ_L) were always observed in the summer. The diurnal patterns of RWD were the inverse of those of Ψ_L . All three species had the greatest RWD in the spring, and the lowest in the autumn. Among the three species, *C. korshinskii* had the lowest Ψ_L and highest RWD; the highest Ψ_L and lowest RWD occurred in *C. davazamcii*.

In the spring and summer, all three species had the greatest E in the morning (between 8 a.m. and 10 a.m.). In the autumn, the diurnal greatest E occurred at midday. Meanwhile, an abnormal high was observed in *C. korshinskii* in the early morning, when the photon flux density was relatively low. With the exception of *C. microphylla*, which had the greatest E in the summer, both *C. davazamcii* and *C. korshinskii* had the greatest E in the autumn. The lowest E occurred in the spring for *C. microphylla* and *C. davazamcii* but in the summer for *C. korshinskii*. Among the three species, the sequence of E in the spring was *C. davazamcii* > *C. korshinskii* > *C. microphylla*. In the summer and autumn, the sequence was *C. microphylla* > *C. davazamcii* > *C. korshinskii* (Figure 3). As for g_s , the diurnal and seasonal patterns generally were the same as those of E among the three species. In the spring, *C. davazamcii* had higher g_s than the other two species, and the lowest values occurred in *C. microphylla*. *Caragana korshinskii* had the lowest g_s in the summer and the highest g_s in the autumn. The values of *C. microphylla* were higher than those of *C. davazamcii* in the summer, but in the autumn, the two species had a similar g_s .

A significant positive dependence of g_s and E on G_t was found in all three species throughout the growing period. Figure 4A shows the exponential correlations between g_s and G_t ($r^2 > 0.45$, $P < 0.005$). The optimal models of E on G_t were power functions as shown in Figure 4B ($r^2 > 0.50$, $P < 0.005$). The dependence of g_s and E on G_t was different among the three species. Under the same G_t , *C. microphylla* had higher g_s and E than the other two species. In contrast with the dependence of leaf gas exchange on G_t , little or no dependence of g_s or E on K_s of one-year-old twigs was obtained for each species ($r^2 < 0.20$, $P > 0.05$).

As shown in Table 5, each *Caragana* species showed rather different DCA, DCE, WUE, $\Delta\Psi$ and G_t during the whole growing period. Interspecific differences were also recorded during the same season.

In *C. microphylla*, the lowest values of DCA and DCE occurred in the spring, together with the lowest G_t . However, the species had the highest WUE in the spring. In the summer, though the $\Delta\Psi$ decreased a little, the G_t was much higher than in the spring, and the DCA had roughly doubled. The DCE had increased even more, directly re-

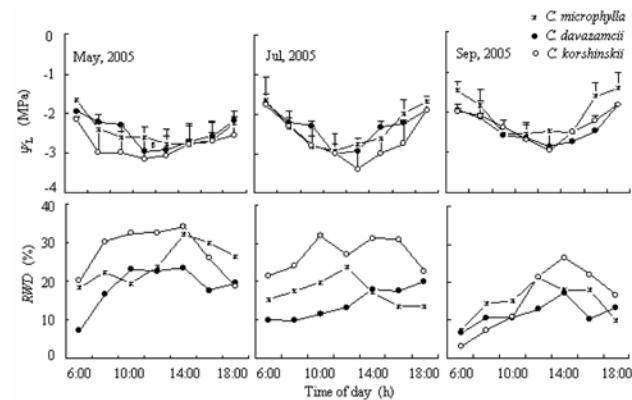


Figure 2. Diurnal and seasonal changes of leaf water potential (Ψ_L) and relative water deficit (RWD) of three *Caragana* species.

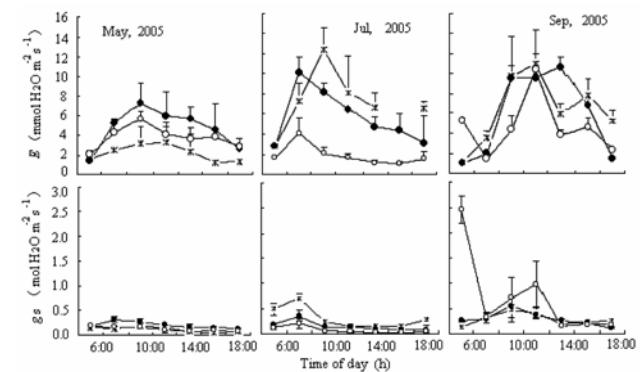


Figure 3. Diurnal patterns of transpiration rate (E) and stomatal conductance (g_s) in different seasons for the three *Caragana* species. Symbols are as in Figure 2.

sulting in a significant decrease in WUE. In the autumn, *C. microphylla* had the highest G_t and lowest $\Delta\Psi$ during the growing period, which resulted overall in a decrease in DCE. Since the DCA was unchanged from the summer, the WUE increased a little in the autumn. The seasonal variation of DCE in *C. davazamcii* was the lowest among the three species. Though the species had the largest G_t in the spring, the lowest $\Delta\Psi$ resulted in the smallest DCE during the growing period. With the increase in $\Delta\Psi$ in the summer, the DCE was higher than in the spring. However, the low DCA resulted in decreased WUE in the summer. The greatest photosynthesis and transpiration occurred in the autumn, when the species had the greatest WUE. Among the three species, *C. korshinskii* had the most significant seasonal variations in photosynthesis and transpiration: its lowest DCA and DCE occurred in the summer, and its highest in the autumn. This was similar to the seasonal patterns of *C. davazamcii*. The highest WUE of *C. korshinskii* occurred in the autumn, when the species had the largest G_t and the lowest $\Delta\Psi$ during the whole growing period.

Comparing all three species, *C. microphylla* had the highest DCA and DCE during most of the growing period; the lowest values were found in *C. korshinskii*. The $\Delta\Psi$ of *C. davazamcii* was the lowest, but the G_t was higher than

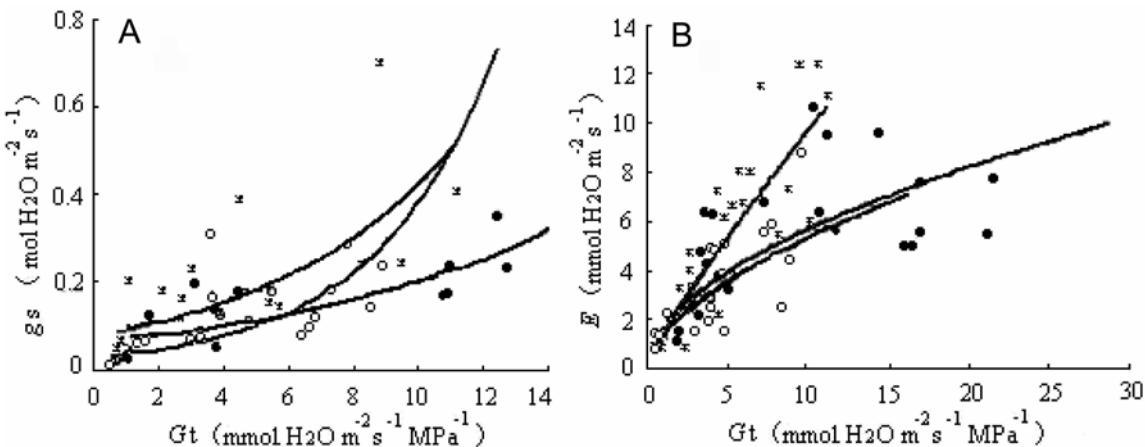


Figure 4. Relationship between g_s and E with G_t of three *Caragana* species during the whole growing period. Solid lines are fitted nonlinear regressions: (A) *C. microphylla* $y=0.0657e^{0.1895x}$, $r^2=0.62$, $P=0.000$, *C. davazamcii* $y=0.0644e^{0.1156x}$, $r^2=0.452$, $P=0.004$ and *C. korshinskii* $y=0.026e^{0.2681x}$, $r^2=0.650$, $P=0.000$ (B) *C. microphylla* $y=1.305x^{0.8364}$, $r^2=0.80$, $P=0.000$, *C. davazamcii* $y=1.681 x^{0.5253}$, $r^2=0.56$, $P=0.000$, and *C. korshinskii* $y=1.3924x^{0.5809}$, $r^2=0.72$, $P=0.000$. Symbols are as in Figure 2.

in the other two species. The $\Delta\Psi$ and G_t of *C. korshinskii* were generally lower than those of *C. microphylla*, but the G_t was higher in the spring. As for WUE, the lowest values of the whole growing period occurred in *C. davazamcii*. In the spring, *C. microphylla* had the highest WUE while *C. korshinskii* had it in the autumn.

DISCUSSION

Effect of vessel features on hydraulic conductance

According to the Hagen-Poiseuille Law, maximum hydraulic conductivity of xylem (K_h) is linearly proportional to the mean hydraulic diameter of the conduits raised to the fourth power: $K_h \propto d_h^4 \cdot n_c$, where n_c is the number of conduits (Tyree et al., 1994; Jordi et al., 2002). If the xylem area is proportional to d^2 and n_c , maximum specific hydraulic conductivity (K_s) would scale with the square of mean conduit diameter. In this study, *C. korshinskii* had the greatest D_{100} and D_{95} while the lowest D_{100} and D_{95} were obtained in *C. microphylla*. Thus, the expected sequence of maximum K_s of one-year-old twigs was *C. korshinskii* > *C. davazamcii* > *C. microphylla*, which was in accordance with the actual observations of K_s .

Furthermore, the analysis of three size classes helps us understand the seasonal variations in K_s of one-year-old twigs of three *Caragana* species. As shown in Figure 5A, the quantitative proportions of large vessels was no less than 7.50% for all three species, and most of the vessels (>85%) were categorized as small. With regards to water transport contribution, large vessels were responsible for the majority of water transport Figure 5B. Though large vessels are highly efficient for water transport, they are fragile and vulnerable to the embolism caused by water deficit or low temperatures (Tyree et al., 1994). In contrast, small vessels can successfully withstand large amounts of

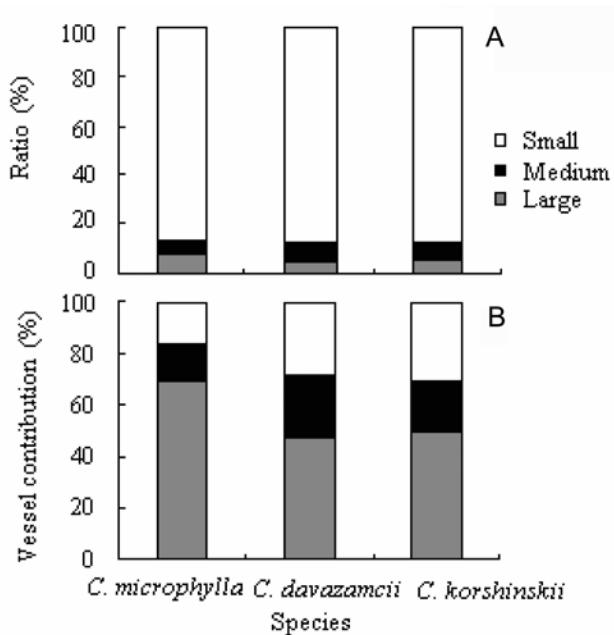


Figure 5. Three vessel size classes (small, medium and large) in xylem. (A) Ratio of vessel number of each size class to total vessel number. (B) Contribution of three vessel size classes to total conductivity in each *Caragana* species.

negative tension in the xylem though they transport water less efficiently. The coexistence of large vessels in small quantities and small vessels in large quantities embodies a strong adaptation to drought in three *Caragana* species.

Relationships of leaf gas exchange and hydraulic conductance

Numerous studies have demonstrated a positive correlation of E and g_s with G_t (Meinzer and Grantz, 1990; Meinzer et al., 1995; Saliendra et al., 1995; Sperry, 2000). When G_t is experimentally increased by partial defoliation

Table 5. Seasonal changes of photosynthesis, transpiration and *WUE* together with $\Delta\Psi$ and G_t of *Caragana microphylla*, *C. davazamcii* and *C. korshinskii* plants.

Parameter	Species	Spring	Summer	Autumn
Diurnal cumulative value of net Photosynthesis (<i>DCA</i>) (mmol CO ₂ m ⁻²)	<i>C. microphylla</i>	446.32 ^b	888.21 ^a	881.43 ^a
	<i>C. davazamcii</i>	583.36 ^b	454.10 ^b	803.33 ^a
	<i>C. korshinskii</i>	483.53 ^b	234.71 ^b	963.54 ^a
Diurnal cumulative value of transpiration (<i>DCE</i>) (mol H ₂ O m ⁻²)	<i>C. microphylla</i>	113.36 ^b	362.82 ^a	318.72 ^a
	<i>C. davazamcii</i>	235.15 ^a	285.43 ^a	293.98 ^a
	<i>C. korshinskii</i>	190.40 ^{ab}	95.53 ^b	233.92 ^a
Water use efficiency (<i>WUE</i>) (mmol CO ₂ mol ⁻¹ H ₂ O)	<i>C. microphylla</i>	4.01 ^a	2.45 ^b	2.77 ^b
	<i>C. davazamcii</i>	2.48 ^a	1.59 ^b	2.73 ^a
	<i>C. korshinskii</i>	2.53 ^b	2.46 ^b	4.12 ^a
Diurnal mean water potential difference between soil to leaf ($\Delta\Psi$) (MPa)	<i>C. microphylla</i>	0.97 ^a	0.92 ^{ab}	0.83 ^b
	<i>C. davazamcii</i>	0.66 ^b	0.80 ^a	0.75 ^a
	<i>C. korshinskii</i>	0.81 ^b	1.09 ^a	0.65 ^c
Diurnal mean hydraulic conductance of soil-leaf continuum (G_t) (mmol H ₂ O m ⁻² s ⁻¹ MPa ⁻¹)	<i>C. microphylla</i>	2.73 ^b	7.95 ^a	8.11 ^a
	<i>C. davazamcii</i>	12.05 ^a	9.56 ^b	9.90 ^b
	<i>C. korshinskii</i>	5.09 ^b	2.61 ^c	7.12 ^a

Different letters denote a significant difference following Duncan's multiple test (a=0.05).

or shading, g_s and E of the untreated foliage increase; when G_t is decreased by stem notching or root pruning, g_s decreases accordingly (Meinzer and Grantz, 1990; Pataki et al., 1998). The results obtained from our experiments on the three *Caragana* species during the entire growing period also demonstrated that both E and g_s were closely related to G_t (Figure 5). Similar positive relationships between E and g_s and G_t in the three species suggest that leaf stomatal behavior and transpiration were limited by G_t over the entire range observed. The regression curves in this study were non-linear, which is similar to what has been observed in some other studies (Sperry and Pockman, 1993; Meinzer et al., 1995). The G_t values of all three *Caragana* species varied greatly with seasons and species. The highest values exceeded 20 mmol H₂O m⁻² s⁻¹ MPa⁻¹, greater than those reported in other studies (Meinzer et al., 1995; Tausend et al., 2000).

The greatest G_t generally occurred in the early autumn, when the leaf gas exchange and photosynthesis rate reached the highest level of the whole growing period, with the exception of *C. davazamcii*, which had the greatest G_t in the spring. Meanwhile, the three *Caragana* species had the best leaf water status in the early autumn, indicated by relatively high leaf water potential and the lowest water deficit. *Caragana microphylla* had the lowest diurnal mean value of G_t in the spring, which was in line

with its lowest g_s , E and A . *Caragana korshinskii* had the lowest G_t in the summer, when the lowest leaf gas exchange and A occurred. Among the three species, *C. davazamcii* had a greater G_t than the other two species, but the greatest E occurred in *C. microphylla* due to its high $\Delta\Psi$ and G_t . *Caragana korshinskii* had the least G_t , which was in accordance with its lower g_s and E during most of the growing season.

As for the hydraulic conductance of a specific subportion of the pathway, its influence on leaf gas exchange may be different from G_t . Generally, there were no statistically remarkable correlations in this study between K_s in one-year-old twigs and g_s or E ($r^2 < 0.20$, $P > 0.05$). As for the seasonal changes of K_s , apparent variations were observed for the three *Caragana* species, which can be interpreted as the result of embolism and refilling in the vessels (Tyree and Sperry, 1988). By comparison, *C. korshinskii* had greater K_s than the other two *Caragana* species, especially in the summer. In the autumn, because of the cumulating embolism in the xylem, the decrease in K_s occurred for all three *Caragana* species. In contrast, the highest G_t usually occurred in the autumn, when the E and g_s were the greatest too.

The difference in the response of leaf gas exchange to G_t and K_s of one-year-old twigs can be interpreted from the hydraulic resistance located in the different parts of

the sap flow pathway. Xylem composes most of the water transport pathway. Meanwhile, since the transpiration stream also flows in extra-xylary pathways in root and leaf, where cavitation does not occur, changes of hydraulic resistance in root and leaf tissues during water stress can have important consequences for plants (Sperry, 2000). It is impossible to tell here whether this hydraulic resistance was primarily in root, stem, leaf veins, or symplastic portions to the pathway associated with movement from veins to evaporative sites, which have been identified as sites of unusually high hydraulic resistance in past studies (Zimmermann, 1983; Tyree et al., 1993; Yang and Tyree, 1993). Overall, stomatal behavior was generally much better correlated with total resistance than was any specific subportion of the pathway (Comstock and Ehleringer, 1988; Comstock, 2000).

Specific growth rhythm in relation to hydraulic conductance in plant

For most plants growing in arid and semi-arid areas, water and heat are the most important environmental factors. The former determines their distribution and survival, and the latter determines the length of the growing period. Though *C. microphylla*, *C. davazamcii*, and *C. korshinskii* share a close interspecific relationship, it is hard to find two *Caragana* species in one habitat due to their geographical replacement in the Inner Mongolia Plateau of China. During its long-term adaptation to the specific water and heat conditions of this habitat, a *Caragana* species would have had to develop a particular growth rhythm.

Growing mainly in the east of the Inner Mongolia Plateau, *C. microphylla*'s growing period was about a month shorter than that of the other two species found in the west. Its leaf elongation begins in late May, two weeks later than the other two species, and apparent defoliation occurs usually in mid September. Its shorter growing period required *C. microphylla* to develop a rapid growth strategy, which was demonstrated by the great photosynthesis and transpiration rate observed in the field. To meet the water demands of leaf growth, highly efficient water transport was also necessary. Except for the lower values at the beginning of its growing period due to the severe embolism in its xylem, its G_t value was high at all times. Though the soil water content was much higher in the spring, the transpiration rate in leaves was still lower because of the higher hydraulic resistance from soil to leaves. However, *DCA* and *WUE* also demonstrated its high adaptability to leaf desiccation, which originated from low hydraulic efficiency in the spring. In the summer and autumn, *C. microphylla* had a higher *DCA* and *DCE*, accompanied by its higher G_t .

Among the three species, *C. davazamcii* lived in the most favorable environmental conditions, with a good amount of rainfall and relatively suitable air temperatures and humidity. The growing period started in early May and finished by the end of September. Though its *DCA* and

DCE were not as high as those in *C. microphylla* in the summer and autumn, its seasonal mean values during the growing period were greater. On account of its relatively steady environmental conditions, the seasonal variations in *DCE* and *DCA* were not as dramatic as in the other two species. Reflecting its need to supply a large quantity of water to leaves in the spring during active growth, *C. davazamcii* had the greatest G_t to complement the lower differences in water potential from the soil to the leaves. The highest *DCE* and *DCA* occurred in mid September, when the leaves started to defoliate. G_t also increased accordingly to meet the increased water demand from the leaves. Generally, *C. davazamcii* had the smallest *WUE*, and perhaps the least drought resistance among the three species, which is in line with the better water conditions in its habitat.

The most particular species is *C. korshinskii*, which grew in the habitat with soil drought and atmospheric drought imposed upon it asynchronously. Since its study site was only about 120 kilometers away from that of *C. davazamcii*, there was not much difference in rainfall. However, the air temperature of the OSER was higher than that in IMHS, which could have been the main cause of low *DCA* and *DCE* of *C. korshinskii* during most of the growing season. Consistent with its lower metabolic rate in the leaves, *C. korshinskii* had the least efficient water transport system, i.e. lower G_t than the other two species. The species entered the growing period in early May, which was about two weeks earlier than *C. microphylla* in IMERS. By late May, the species already had higher G_t due to the refilling of embolized vessels, but the low soil water content limited its rapid growth. In the summer, G_t decreased greatly, which might have acted as a hydraulic signal and resulted in the dramatic decreases in g_s and E . According to observations by Wang et al. (1996), the photosynthesis of *C. korshinskii* is very sensitive to high air temperatures. So in the summer, to avoid the dysfunction of photosynthetic organ and unnecessary water loss, it closes most of its stomata. The decreased E in leaves also saved some soil water under shrubs. When the air temperatures went lower in late summer, *C. korshinskii* recovered its rapid growth, which resulted in continuous water loss till September, when the soil water content was as low as 1.40%. Due to having the highest G_t in the autumn, the species still had the greatest E and A . Furthermore, the calculated *WUE* was as great as 4.12 mmol CO₂·mol⁻¹·H₂O, which demonstrated the high resistance of *C. korshinskii* to soil drought in the autumn.

Conclusions

The three *Caragana* species growing in arid or semi-arid habitats displayed different hydraulic conductance, vessel features, leaf water status, gas exchange, and growth rhythm during an entire growing season in 2005. Overall, *C. korshinskii* had the largest vessels and K_s in one-year-old twigs, and *C. microphylla* had the lowest values, but there were no significant relationships between

leaf gas exchange and K_s . Additionally, the seasonal changes of photosynthesis and transpiration were not in line with K_s . In contrast, the leaf gas exchange (E and g_s) was positively correlated to total hydraulic conductance of the soil/leaf pathway (G_t) for the three *Caragana* species, and the seasonal patterns of G_t were generally in accordance with those of DCA and DCE. That is, the leaf stomatal behavior of one-year-old twigs was governed by G_t rather than K_s . Among the three species, *C. davazamcii* had the best leaf water status and highest G_t , and the least drought resistance during the growing period. *Caragana microphylla* was exposed to the severest leaf water deficit in the spring, which resulted from its lowest G_t . Though the DCA and DCE were lower than those of the other two species, the WUE was the highest. *Caragana korshinskii* had the lowest DCA, DCE and G_t among the three species. In the autumn, *C. korshinskii* had the greatest drought resistance, indicated by a WUE higher than the other two species.

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內蒙古高原三種錦雞兒植物的水分關係、水力傳導和導管特徵

李 晶 高玉葆 鄭志榮 高增璐

中國天津南開大學 生命科學學院

從 2005 年 5 月初到 9 月末，對生長在中國內蒙古高原不同生境下的小葉錦雞兒、中間錦雞兒和檸條錦雞兒進行野外研究，內容包括植物一年生枝條的導管特徵、葉片水分關係的日變化和季節變化、水力傳導、光合作用（DCA）、蒸騰作用（DCE）以及水分利用效率（WUE）的季節變化。三種錦雞兒在生長季大多時期都遭遇嚴重的環境乾旱脅迫。其中，檸條錦雞兒一年生枝條的導管和比導率 (K_s) 都最大，小葉錦雞兒的值最小，三種植物都是在夏季的 K_s 最大，春季 K_s 最小。葉片在秋季的日平均水勢 (Ψ_L) 最大，相對水分虧缺最低 (RWD)，這表明三種錦雞兒都是在秋季的葉水分狀況最好，春季葉片水分脅迫最為嚴重。種間相比，小葉錦雞兒的 Ψ_L 高於另外兩種植物，檸條錦雞兒的 Ψ_L 最低而且 RWD 最大，中間錦雞兒的 RWD 最小。三種錦雞兒植物都是在秋季的 DCA 和 DCE 最大，小葉錦雞兒和中間錦雞兒的最低值出現在春季，檸條錦雞兒的最低值出現在夏季，這也減少了夏季灌叢下土壤水分的喪失。研究發現，與一年生枝條的 K_s 相比，土壤—葉片連續體系的導水率 (G_t) 與葉片氣孔導度 (g_s) 和蒸騰速率 (E) 的關係更為密切。除了中間錦雞兒以外在春季有較高的 G_t 外， G_t 的季節變化總體上與 DCA、DCE 的季節變化一致。比較三種植物，整個生長季中，中間錦雞兒的季節平均 DCE 和 G_t 最大，抗旱性最低，這與其生境具有較高的土壤含水量相符。小葉錦雞兒所在生境雖然春季的土壤含水量較高，但較低的 G_t 仍引起葉片嚴重的水分虧缺，相應地，植物抗旱性也是最大的。秋季檸條錦雞兒生境土壤含水量很低，植物抗旱性也高於兩外兩種錦雞兒。通過分析 K_s 和 G_t 的季節變化以及它們與葉片氣體交換的關係，證實了同特定的分枝部位（本研究中特指一年生枝條）相比， G_t 對於葉片供水更為重要。

關鍵詞：小葉錦雞兒；中間錦雞兒；檸條錦雞兒；導管大小；水力傳導；葉片氣體交換；日變化和季節變化；生長節律。