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Photosynthesis, transpiration, and water use efficiency of *Caragana microphylla, C. intermedia,* and *C. korshinskii*

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Abstract

In the order *C. microphylla – C. intermedia – C. korshinskii*, compensation irradiance, saturation irradiance, and optimum temperature for photosynthesis increased, net photosynthetic rate (P_N) at low irradiance and low temperature decreased, optimum air humidity decreased, and P_N at low air humidity increased. Daily cumulative value of P_N increased while daily cumulative value of transpiration (E) decreased, and hence water use efficiency (WUE = P_N/E) increased. Diurnal course of P_N of *C. microphylla* was a double-peak curve, but the second peak in the curves of *C. intermedia* and *C. korshinskii* was not visible. These physiological characteristics are biological basis for the geographical distribution of these three *Caragana* species, and are in relation to water conditions of their habitats and distinctiveness in leaf hair of plant.

Additional key words: geographic distribution; growth and development; morphological structure; physio-ecological adaptation; water deficit; water regime.

Introduction

Caragana microphylla, C. intermedia, and *C. korshinskii* are drought resistant plants (Xu *et al.* 1998). They are useful species in sand dune fixation and water conservation (Hansson *et al.* 1995, Ren *et al.* 2002). Due to their environmental benefit and economic value, much research has been done on their use. *C. microphylla, C. intermedia,* and *C. korshinskii* are closely-related species, once taxonomically classified as one species. Zhao (1991) and Zhou (1996) established that *C. microphylla* stretches its distribution eastwards in Mongolia plateau, *C. intermedia* exists in the middle part, and *C. korshinskii* is stretched westwards in the plateau. The three species form a geographical vicarious distribution in Mongolia plateau. One of the climate characteristics of Mongolia plateau is that solar radiation and air temperature increase while precipitation decreases gradually from the east to the west. Nine moisture types have been identified in this gradient: humid, sub-humid (partial humid), sub-humid (partial arid), semi-arid (partial humid), semi-arid (partial arid), dry, very dry, intensively dry, and extremely dry (Yang *et al.* 1987). The combination of irradiance, temperature, and humidity is the determining factor for plant distribution. Because *C. microphylla, C. intermedia,* and *C. korshinskii* were able to form a geographical vicarious distribution in such a vast region which varies much in climate, the vegetation type was probably determined by their adaptability to environment, especially to irradiance, temperature, and humidity.

The adaptation of plants to environment is determined by their genetic potential, but both photon energy and water metabolism are ready-to-observe indicators. If a plant is not able to utilize photon energy efficiently for its carbon exchange and growth, it will not survive. On the other hand, if a plant cannot use water efficiently or if the amount of water in its habitat is less than its requirements, the plant is not able to exist. There are some reports on the photosynthesis and water regime of *Caragana* species (Wang B.X. *et al.* 1996, Wang M.B. *et al.* 1996, Yang *et al.* 1997, Zhang *et al.* 1998, Xiao and Zhou 2001, Tang *et al.* 2001), but there exists no document about the association between the characteristics of photosynthesis and water regime with the geographical vicarious distribution. The purpose of our research was to compare characteristics of photosynthesis and water regime of the mentioned three *Caragana* species in Inner Mongolia plateau and in this way understand adaptation mechanism of plant to its habitat, and to discuss the relation of photosynthesis and water regime characteristics to morphological structure and growth and development.

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Materials and methods

From 2001 to 2003, we collected plant materials and carried out field investigations from the east to the west in eight sites (see Table 1). Three typical plots were chosen in each site, and the water content of soil samples from depths of 30, 60, and 100 cm was measured separately. We investigated 30 shrubs in each plot. The diurnal courses of net photosynthetic rate (P_N) and transpiration rate (E) were recorded with a *CI-301* CO_2 gas analyzer (*CID Co*., Washington, USA). Mature leaf samples (3~4 g) were taken from 07:00 to 18:00 at an interval of 3 h during a day to determine their water content and leaf water deficit [leaf water deficit = 1 – water content/saturated water content]. The diurnal courses of P_N and E were examined from 07:00 to 19:00 at an interval of two hours during a day, and in each cycle 60 measures were taken. At the same time, changes of photosynthetically active radiation (PAR), air temperature, leaf temperature, air humidity, and CO_2 concentration were recorded automatically with the *CI-301* CO_2 gas analyzer. Diurnal courses of P_N and E were obtained from the average of all plots of all sites where these species were found. Regression equations were obtained using SPSS from P_N with the corresponding PAR, air temperature, or air relative humidity. From these regression equations, compensation irradiance (I_c), saturation irradiance (I_{sat}), optimum temperature, and optimum air humidity were calculated. P_N was calculated for PAR of 500 µmol m^{-2} s^{-1}, air temperature of 20 °C, and relative air humidity of 30 %, to find plant responses to low irradiance, low temperature, and low relative air humidity. Daily cumulative values of P_N and E were calculated by multiplying the values per second by 7 200. WUE was calculated from daily values as P_N/E. The radiation use efficiency (RUE) was calculated as P_N/PAR.

Table 1. Environmental data for the main investigation sites. Xiwuzhumuqin is called Xiwu for short, and Daerhanmaomingan is called Damao for short.

Site	Species	Longit. [°E]	Latit. [°N]	Altitude [m]	Annual precipitation [mm]	Annual average temperature [°C]	Sun time [h]	Soil water content [%] 30 cm	60 cm	100 cm	Mean
Xiwu	*C. microphylla*	117.60	44.58	995.9	340	1.47	2870	4.87	3.04	4.35	4.09
Xilinhaote	*C. microphylla*	116.07	43.95	989.5	281	2.35	2932	3.91	3.95	3.23	3.70
Abaga	*C. microphylla*	114.95	44.02	1126.1	245	1.20	3047	4.09	2.90	2.27	3.09
Suniteyou	*C. microphylla*	112.90	42.40	1150.8	211	4.93	3167	3.21	2.26	1.74	2.40
Damao	*C. intermedia*	110.43	41.70	1376.6	256	4.01	3061	2.41	2.25	1.83	2.16
Walatezhong	*C. intermedia*	108.52	41.57	1288.0	199	5.07	3168	1.25	2.42	2.86	2.18
Hangjinhou	*C. korshinskii*	107.50	41.25	1284.8	150	5.82	3179	1.36	1.93	3.02	2.10
Alashanzuo	*C. korshinskii*	105.66	38.84	1561.0	110	7.80	3200	1.98	1.66	1.55	1.73

Results

Responses of P_N to PAR: I_c and I_{sat} of *C. microphylla* were lower than those of *C. intermedia,* and the latter were lower than those of *C. korshinskii*. At PAR = 500 µmol m^{-2} s^{-1}, the order of P_N was *C. microphylla*>*C. intermedia*>*C. korshinskii* (Table 2).

Responses of P_N to temperature: The optimum temperatures for P_N of *C. microphylla, C. intermedia,* and *C. korshinskii* were 26.0, 33.3, and 36.0 °C, respectively. At 20 °C, P_N of *C. microphylla, C. intermedia,* and *C. korshinskii* were 11.26, 4.42, and 0.40 µmol(CO_2) m^{-2} s^{-1}, respectively (Table 3). P_N at high temperature increased, and at low temperature decreased in the same order as response to PAR.

Responses of P_N to relative air humidity: The optimum air humidity for P_N decreased gradually in the same order as shown above, and P_N at low air humidity (30 %) increased gradually. This suggests that the order of the drought adaptability is *C. korshinskii*>*C.intermedia*> *C. microphylla* (Table 4).

Diurnal courses of P_N: The diurnal course of P_N of *C. microphylla* was a double-peak curve, but the second peak in the curves of *C. intermedia* and *C. korshinskii* was not obvious. In the forenoon, P_N of *C. korshinskii* was higher than that of *C. intermedia*, and the latter was higher than that of *C. microphylla.* However, they were similar in the afternoon (Fig. 1). The accumulation of assimilates in *C. korshinskii* plants mainly occurred in the forenoon whereas in *C. microphylla*, the accumulation of assimilates in the afternoon contributed much to the total production. The differences in diurnal courses of P_N among *C. microphylla, C. intermedia,* and *C. korshinskii* plants were related to water status of the plants. In arid Inner Mongolia plateau, higher P_N in the forenoon might be a strategy of plant adaptation to arid and hot environment. The order of the daily cumulative values of P_N was

C. korshinskii>*C. intermedia*>*C. microphylla* (Table 5). The higher RUE of *C. intermedia* than that of *C. microphylla* was another proof for *C. intermedia* photosynthetic ability: it was greater than that of *C. microphylla*, but RUE of *C. intermedia* was higher than that of *C. korshinskii* probably due to water restriction (Table 5).

Table 2. Relationship between PAR and net photosynthetic rate (P_N) of *C. microphylla, C. intermedia*, and *C. korshinskii* plants. y = P_N; x = PAR.

Species	Regression equation	Compensation irradiance [μmol m^{-2} s^{-1}]	Saturation irradiance [μmol m^{-2} s^{-1}]	P_N at PAR of 500 μmol m^{-2} s^{-1} [μmol(CO$_2$) m^{-2} s^{-1}]
C. microphylla	$y = -1.3444\times10^{-5} x^2 + 0.029552 x - 5.174$	192	1099	6.24
C. intermedia	$y = -1.9969\times10^{-5} x^2 + 0.052097 x - 17.243$	389	1304	3.81
C. korshinskii	$y = -7.937\times10^{-6} x^2 + 0.028491 x - 11.435$	460	1795	0.83

Table 3. Relationship between air temperature and net photosynthetic rate (P_N) of *C. microphylla, C. intermedia,* and *C. korshinskii* plants. y = P_N; x = air temperature.

Species	Regression equation	Optimum temperature [ºC]	P_N at 20 ºC [μmol(CO$_2$) m^{-2} s^{-1}]
C. microphylla	$y = -0.0251 x^2 + 1.3277 x - 5.259$	26.0	11.26
C. intermedia	$y = -0.0783 x^2 + 5.2118 x - 68.500$	33.3	4.42
C. korshinskii	$y = -0.0534 x^2 + 3.8466 x - 55.174$	36.0	0.40

Table 4. Relationship between air relative humidity and net photosynthetic rate (P_N) of *C. microphylla, C. intermedia*, and *C. korshinskii* plants. y = P_N; x = relative air humidity.

Species	Regression equation	Optimum air humidity [%]	P_N at 30 % air humidity [μmol(CO$_2$) m^{-2} s^{-1}]
C. microphylla	$y = 0.0016 x^2 + 0.048 x + 1.7456$	100	4.63
C. intermedia	$y = -0.0035 x^2 + 0.6313 x - 10.449$	90	5.34
C. korshinskii	$y = -0.0046 x^2 + 0.5578 x - 1.9245$	61	10.67

Table 5. Daily cumulative values of net photosynthetic rate (P_N) and transpiration rate (E), and radiation use efficiency (RUE) and water use efficiency (WUE) of *C. microphylla, C. intermedia*, and *C. korshinskii* plants. Means of 4 sites for *C. microphylla,* 2 sites for *C. intermedia,* and 2 sites for *C. korshinskii. Different letters in the right column* denote a significant difference (α = 0.05 by the Duncan`s method).

Species	P_N [mmol(CO$_2$) m^{-2} d^{-1}]	RUE [mmol(CO$_2$) mol^{-1}(proton)]	E [mol(H$_2$O) m^{-2} d^{-1}]	WUE [mmol(CO$_2$) mol^{-1}(H$_2$O)]
C. microphylla	426.23a	7.23a	356.22a	1.20a
C. intermedia	501.79b	8.94c	344.82a	1.46b
C. korshinskii	512.73b	7.81b	232.24b	2.21c

***E* and WUE**: Maximal *E* decreased in the order *C. microphylla*–*C. intermedia*–*C. korshinskii*, and the time when this occurred during day came earlier in this order (Fig. 1). The differences in diurnal course of *E* in these species were related to their water status. The daily cumulative value of *E* decreased in the same order (Table 5). The lower maximum values of *E* and daily cumulative values of *E* endowed plants with better adaptation to the arid and hot environments. The WUE increased gradually in the same order as *E* decreased (Table 5). The increase of WUE is an important character for plants to adapt to drought that resulted from ecological evolution over a long period of time.

Diurnal changes of leaf water deficit (LWD): After sunrise, LWD increased because more water was lost by transpiration than taken in by root. Leaf water deficit declined in the order *C. korshinskii*–*C. intermedia*–*C. microphylla*. The changes of leaf water deficit were correlated with the water conditions of habitat, and this might be an important cause for the changes of diurnal curves of P_N and *E* mentioned above.

Discussion

Relation of P_N and water regime characteristics of *Caragana* species to their distribution: Drought may depress P_N by stomatal limitation or non-stomatal limitation (*e.g.* damage of the membrane structure of photosynthesis system) and by affecting the transport of photosynthates out of leaf (Chaves 1991, Gabriel 2000). Strong radiation and high temperature reduce P_N by decreasing stomatal conductance (Farquhar and Sharkey 1982), depressing RuBP carboxylase activity (Kobza and Edwards 1987), destroying the photosynthetic system (Gounaris *et al.* 1984, Baker 1991), and increasing respiration rate (Jia *et al.* 2001). Plants usually adapt to irradiance, temperature, and humidity (Johnson 1996, Ueda *et al.* 2000). Berry and Björkman (1980) and Boardman (1977) pointed out that the plants which were native to and grown in low temperature and low irradiance environments generally exhibited optimum P_N at lower temperature and had lower I_c and maximum P_N than the plants which were native to and grown in high temperature and high irradiance environments and exhibited higher P_N at low temperature and low irradiance. Sheu and Lin (1999) suggested that *Schima superba* incubated at higher temperature had higher optimum temperature for photosynthesis. Different plants differently react to water stress (Mireia and Ralph 1998). The photosynthetic system of the plant, which originated in arid tropical environment, is better adapted to drought than that of the plant, which originated in other places (Fausto *et al.* 1997). There are so far few reports on the adaptation of *C. microphylla*, *C. intermedia,* and *C. korshinskii* to the gradients of irradiance, temperature, and moisture. In the present study we found that the adaptability of photosynthetic system to high irradiance, high temperature, and arid environment increased gradually from *C. microphylla* to *C. intermedia* and then to *C. korshinskii*, and adaptation ability to low irradiance, lower temperature, and higher humidity gradually decreased. The daily cumulative value of P_N increased gradually, while the daily cumulative value of E gradually decreased, and as a result WUE increased significantly. The tested *Caragana* species took the strategy of depressing transpiration and increasing photosynthesis to economize water use. These photosynthetic characteristics were adaptable to irradiance, temperature, and humidity of their own habitat. These intrinsic characteristics were formed by plants during long time adaptation to "native" environment. Li and Zhang (1996) studied anatomical structure and found that the drought resistance order of the plants was *C. microphylla*<*C. intermedia*< *C. korshinskii,* which showed adaptation to the "native" environment. Undoubtedly, variation in these ecological adaptations has a genetic basis. It may be a basis for the geographical distribution of these *Caragana* species.

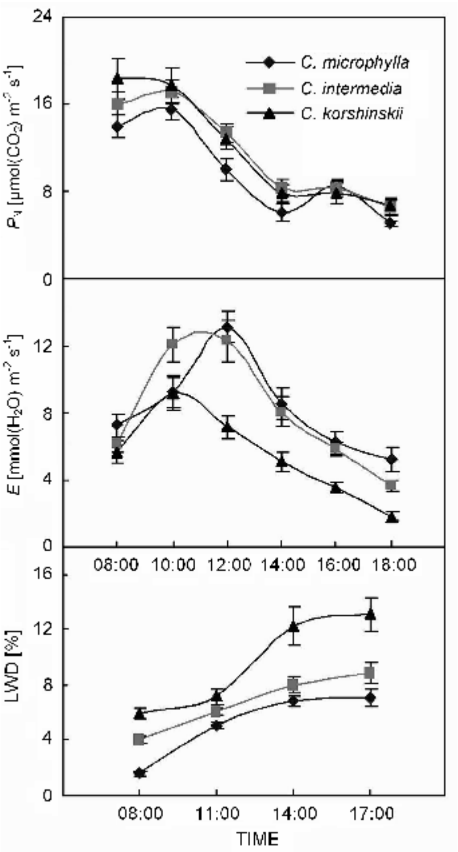

Fig. 1. Diurnal changes of net photosynthetic rate (P_N), transpiration rate (E), and leaf water deficit (LWD) of *C. microphylla, C. intermedia*, and *C. korshinskii* plants. Means of 4 sites for *C. microphylla,* 2 sites for *C. intermedia*, and 2 sites for *C. korshinskii.*

Relation of P_N and water regime characteristics of *Caragana* species to water conditions: In arid region, P_N and water regime of plant are determined largely by the water conditions. Zhou *et al.* (2001) introduced *C. microphylla*, which was a dominant shrub in Kerqin sandy grassland with better water conditions, and *C. intermedia*, which was a dominant shrub in Maowusu sandy grassland with bad water conditions, to Tenggeli desert with very bad water conditions, and then compared the diurnal courses of P_N before and after the introduction. They found that after the introduction, P_N values of *C. microphylla* and *C. intermedia* were reduced 11.63 and 4.5 times, respectively. The present study showed that the diurnal course of P_N of *C. microphylla* was a double-peak curve, and the second peak in the curves of *C. intermedia* and *C. korshinskii* was not evident. In *C. microphylla* distribution region (sub-humid to semi-arid) there were high soil water content and air humidity, as well as low temperature and low irradiance. The water deficit caused by transpiration before noon might be compensated for in the afternoon, so P_N possessed the second peak after a "mid-day depression". In contrast, *C. intermedia* was found in dry to very dry regions, and

C. korshinskii was found in intensively to extremely dry regions with low soil water content, low air humidity, high temperature, and high irradiance. Their water deficit was caused by continuous strong transpiration increase during the daytime (Fig. 1). This is why the second peak of P_N was not obvious in the afternoon. In addition, the differences in daily cumulative values of *E*, WUE, and RUE among *C. microphylla*, *C. intermedia*, and *C. korshinskii* (Table 5) were not the only intrinsic characteristics formed by plants during adaptation to "native" environment for a long period of time as mentioned above, but were also related, to some extent, to water regime in the distribution regions during a long or short period of time. This suggested that water conditions were important for the differences in photosynthesis and water regime characteristics among the studied *Caragana* species.

Relation of P_N and water regime characteristics of *Caragana* species to morphological structure, growth, and development: Leaf hair presence is a taxanomic criterion for *C. microphylla, C. intermedia,* and *C. korshinskii*. The leaf of *C. microphylla* is covered by thin short villis, the leaf of *C. intermedia* by silky villis or is hairless on the upper side, and the leaf of *C. korshinskii* by dense silky villis (Fu 1989). The leaf of *C. korshinskii* is covered by dense silky villis, which have strong reflecting ability, and therefore absorb less solar energy; and as a result, the leaf temperature is low. On one hand, the plant can avoid injury caused by strong irradiation and high temperature; on the other hand, it can reduce *E* and improve water conservation. This is one of the causes why *C. korshinskii* has high adaptation ability to intensive PAR and high temperature, and has low *E*. In contrast, leaf of *C. microphylla* is covered by thin short villis that absorb more photons; as a result, *C. microphylla* exhibits higher P_N at low temperature and low irradiance, as well as higher *E*. The characteristics of *C. intermedia* vary between those of *C. microphylla* and *C. korshinskii*. Hence the variations in plant morphological structure are in accordance with physiological adaptation.

The shrub height is another taxonomic criterion: *C. microphylla* 40–70 cm, *C. intermedia* 70–150 cm, and *C. korshinskii* 150–300 cm (Fu 1989). Water is a key factor for plant growth and distribution in Mongolia plateau. The shrub height of *C. korshinskii*, which was found from intensively arid to extremely arid regions, was higher than that of *C. intermedia,* that grows in dry to very dry regions. Shrub height of the latter was higher than that of *C. microphylla,* which grows in sub-humid to semi-arid regions. This paradox may imply a significant difference in metabolism among the three species. Our results showed that the daily cumulative values of P_N and WUE of plants in their distribution region were in the order *C. korshinskii*>*C. intermedia*>*C. microphylla*, which might explain the paradox. And thus growth and development of plants is in close relation to their photosynthesis and water regime.

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