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Photosynthetic responses of *Populus przewalski* subjected to drought stress

C.Y. YIN[*,***], F. BERNINGER[**], and C.Y. LI[*,+]

Chengdu Institute of Biology, Chinese Academy of Sciences, P.O.Box 416, Chengdu 610041, P. R. China[*]
Département des sciences biologiques, Cp 8888 succ centre ville, Université du Québec à Montréal,
Montréal (QC) H3C 3P8, Canada[**]
Graduate School of the Chinese Academy of Sciences, Beijing 100039, P. R. China[***]

Abstract

Cuttings of *P. przewalski* were exposed to two different watering regimes which were watered to 100 and 25 % of field capacity (WW and WS, respectively). Drought stress not only significantly decreased net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), efficiency of photosystem 2 (PS2) (F_v/F_m and yield), and increased intrinsic water use efficiency (WUE_i) under controlled optimal conditions, but also altered the diurnal changes of gas exchange, chlorophyll fluorescence, and WUE_i. On the other hand, WS also affected the P_N-photosynthetically active radiation (PAR) response curve. Under drought stress, P_N peak appeared earlier (at about 10:30 of local time) than under WW condition (at about 12:30). At midday, there was a depression in P_N for WS plants, but not for WW plants, and it could be caused by the whole microclimate, especially high temperature, low relative humidity, and high PAR. There were stomatal and non-stomatal limitations to photosynthesis. Stomatal limitation dominated in the morning, and low P_N at midday was caused by both stomatal and non-stomatal limitations, whereas non-stomatal limitation dominated in the afternoon. In addition, drought stress also increased compensation irradiance and dark respiration rate, and decreased saturation irradiance and maximum net photosynthetic rate. Thus drought stress decreased plant assimilation and increased dissimilation through affected gas exchange, the diurnal pattern of gas exchange, and photosynthesis-PAR response curve, thereby reducing plant growth and productivity.

Additional key words: chlorophyll fluorescence; dark respiration rate; diurnal changes; gas exchange; intercellular CO_2 concentration; stomatal conductance; water use efficiency.

Introduction

Drought stress is an important environmental factor inhibiting plant growth and productivity (Li *et al.* 2000, Li and Wang 2003, Yin *et al.* 2005a, Zhang *et al.* 2005). Changes in plant productivity due to changes in gas exchange, especially net photosynthetic rate (P_N), have received much attention (Thiec and Manninen 2003). Although many studies proved that gas exchange decreased under drought stress (Li 2000, Yin *et al.* 2004, Zhang *et al.* 2004), daily or longer time gas exchange rate measurements provide a better estimate of photosynthetic productivity than a single instantaneous measurement (Christy and Porter 1982, Peterson and Zelitch 1982) because they account for changes in photosynthetic production occurring as a result of genotypic and environmental factors (Wells *et al.* 1986, Nogués *et al.* 2001). Drought decreases photosynthesis; many previous studies proved that stomatal closure is the dominant factor limiting gas exchange (*e.g.* Davies and Gowing 1999, Schultz 2003, Yin *et al.* 2005b), while others argued that water deficit has been attributed to both stomatal and non-stomatal limitations, and non-stomatal limitation may be attributed to the reduced RuBP regeneration, reduced

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[+] Author for correspondence; fax: +86-28-85222753, e-mail: licy@cib.ac.cn, chunyang.li@helsinki.fi

Abbreviations: C_a– ambient CO_2 concentration; C_i– intercellular CO_2 concentration; Chl – chlorophyll; E – transpiration rate; F_v/F_m – the intrinsic (or maximum) efficiency of PS2; g_s – stomatal conductance; I_c– compensation irradiance; I_s – saturation irradiance; Ls – stomatal limitation value; P_{max} – maximum net photosynthetic rate; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; q_N – non-photochemical quenching coefficient; R_D – dark respiration rate; RH – relative humidity; T – temperature; WS – water-stressed treatment; WUE_i – intrinsic water use efficiency; WW – well-watered treatment; Ψ – effective quantum yield of PS2; Φ – apparent quantum yield.

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amount of functional ribulose-1,5-bisphosphate carboxylase/oxygenase, and/or other metabolic responses (Panković *et al.* 1999).

The photosynthetic apparatus and particularly photosystem 2 (PS2) is sensitive to various environmental stresses. Damage to PS2 is often the first manifestation of stress in a leaf (Maxwell and Johnson 2000). Fluorescence can provide insights into the ability of a plant to tolerate those environmental stresses and into the extent to which those stresses have damaged the photosynthetic apparatus (Fracheboud *et al.* 1999, Maxwell and Johnson 2000). Many previous studies used a sustained decrease in the efficiency of excitation capture of open PS2 in dark adapted leaves (F_v/F_m) and yield of energy conversion in light adapted leaves (photosynthetic yield) as reliable indicators of photoinhibition of plants in response to stresses (Seaton and Walker 1990, Wagner and Dreyer 1997, Wang and Kellomäki 1997, Lu and Zhang 1998).

A better understanding of the mechanisms that enable plants to adapt to water stress and maintain growth, development, and productivity during stress periods would help in breeding for drought resistance. In this study, we employed *Populus przewalski* as model plant to study the photosynthetic response to drought stress. The goal was to determine which microclimatological and physiological factors limit carbon gain in *P. przewalski* under drought. The specific aims of this study were: (*1*) to compare gas exchange, chlorophyll (Chl) fluorescence, and water use efficiency (WUE) under controlled optimal conditions; (*2*) to compare daily means and diurnal patterns of leaf-level P_N, transpiration rate (E), stomatal conductance (g_s), and WUE; (*3*) to compare P_N-photosynthetically active radiation (PAR) response curves of *P. przewalski* between well-watered (WW) and water-stressed (WS) conditions.

Materials and methods

Plants and experimental design: Cuttings of *P. przewalski* which were collected from 30 trees in their natural habitants in Northwest Sichuan, Southwest China, were pricked in March 2004. After sprouting and growing for about one month, forty healthy cuttings of uniform height (about 20 cm) were chosen and transferred to 5 000-cm^3 plastic pots filled with homogenized soil and grown in a naturally lit greenhouse under the semi-controlled environment (only shelter from rainfall) with day temperature of 12–31 °C, night temperature of 9–15 °C, and the relative humidity (RH) of 35–85 % at Maoxian Field Ecological Station. The treatments were started on May 1, and plants were harvested on September 20, 2004.

Two watering treatments of 100 (WW) or 25 (WS) % field capacity were used. Twenty cuttings were exposed to each watering treatment. In the WW treatment, the pots were weighed every second day and re-watered to field capacity by replacing the amount of water transpired. In the WS treatment, the pots were watered to 25 % of field capacity by watering every second day. An empirical relationship between seedling fresh mass Y [g] and seedling height X [cm]: $Y = 0.975 + 0.112\ X$ ($r^2 = 0.968$, $p<0.001$) (Li *et al.* 2004) was used to correct pot water for changes in plant biomass. Evaporation from the soil surface was prevented by enclosing all pots in plastic bags sealed at the base of the stem of each cutting. A total of 12 g slow release fertilizer (13 % N, 10 % P, and 14 % K) was added to each pot during the experiment.

Gas exchange and chlorophyll (Chl) fluorescence under controlled optimal conditions: During drought period, gas exchange measurements were taken on fully expanded, exposed leaves under controlled optimal conditions using an open system, with a portable photosynthesis measurement system (*CI-301PS*, *CID*, USA). The measurements were made of 3 cuttings per treatment, and 5 times per cutting. PAR was maintained at 1 400 µmol m^{-2} s^{-1} using the *CI-301* artificial light source, and temperature was maintained at 28–30 °C with an RH of 36–55 % inside the leaf chamber during measurement. These measurements were completed in one day from 08:00 to 11:30 and from 15:00 to 17:30. Intrinsic water use efficiency (WUE_i) was calculated by dividing P_N by g_s.

Chl fluorescence measurements were taken on the same leaves using a modulated fluorometer (*PAM 2100*, *Walz*, Effeltrich, Germany) as described by Brugnoli and Björkman (1992). The leaves were pre-darkened at least for 30 min before measuring. The intensity of the saturation pulses to determine the maximal fluorescence emission in the presence (F_m') and in the absence (F_m) of quenching on the upper surface of the leaf was 4 000 µmol m^{-2} s^{-1}, 0.8 s, whereas the “actinic light” was 600 µmol m^{-2} s^{-1}. The parameters were determined accoring to Rosenqvist and van Kooten (2003).

Diurnal changes of gas exchange and Chl fluorescence: P_N, transpiration rate (E), g_s, intercellular CO_2 concentration (C_i), air temperature (T), RH, ambient CO_2 concentration (C_a), and PAR were measured at the end of August under natural conditions using a portable photosynthesis measurement system (*CI-301PS*, *CID*, USA). The stomatal limitation value (L_s) was then calculated using the following formula: $L_s = 1 - C_i/C_a$ according to Berry and Downton (1982). In addition, before measuring Chl fluorescence the sampled leaves were pre-darkened for *ca*. 15 min.

P_N-PAR response curve: All measurements were made under uniform conditions (18–20 ºC, 330–350 mmol m^{-3} CO_2, and 71–75 % RH). Responses to PAR were measured at 0, 50, 100, 200, 300, 400, 600, 800, 1 000, 1 200, 1 400, 1 600, 1 800, and 2 000 µmol m^{-2} s^{-1}. P_N in the dark (PAR = 0 µmol m^{-2} s^{-1} for at least 5 min) were used as a measure of R_D [µmol(CO_2) m^{-2} s^{-1}]. Regressions of irradiance and P_N over the range of 0–200 µmol m^{-2} s^{-1} PAR were used to determine compensation irradiance, I_c [µmol m^{-2} s^{-1}], the amount of PAR where photosynthetic activity balances respiratory activity, and apparent quantum yield, Φ [µmol(CO_2) µmol^{-1}(photon)]. Φ (based on incident PAR) was calculated as the slope, and lc as the x-intercept of these regressions (Björkman 1981). PAR response curves were generated by plotting P_N as a function of PAR. These curves were fitted to a model of the form using the non-linear regression of *SPSS* software:

$$P_N = P_{max}\,[1 - e^{-(\Phi\,PAR/P_{max})}] - R_D$$

(for definitions see Bassman and Zwier 1991). Maximum net photosynthetic rate (P_{max}) and saturation irradiance, I_s (when P_N fails to increase with increasing irradiance) were estimated.

Statistical analysis: Effect of watering regimes was assessed by one-way ANOVA and means were compared by Duncan test. P_N-PAR response curves were fitted using linear regression and non-linear regression. All statistical analyses were done with the *SPSS 11.5 for Windows* statistical software package.

Results

Gas exchange and Chl fluorescence under controlled optimal conditions: Under these conditions, drought significantly affected P_N, E, g_s, the intrinsic (or maximum) efficiency (F_v/F_m), and Ψ that were significantly decreased, while WUE_i and non-photochemical quenching coefficient (q_N) were significantly increased in comparison with WW (Table 1).

Table 1. Gas exchange and chlorophyll fluorescence under controlled optimal conditions (means ± SE). E, transpiration rate; F_v/F_m, the intrinsic (or maximum) efficiency of PS2; g_s, stomatal conductance; P_N, net photosynthetic rate; q_N, non-photochemical quenching coefficient; WS, water-stressed treatment; WUE_i, intrinsic water use efficiency; WW, well-watered treatment; Ψ, the effective quantum yield of PS2.

Treatment	P_N [µmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	g_s [mmol m^{-2} s^{-1}]	WUE_i [µmol $mmol^{-1}$]	F_v/F_m	Ψ	q_N
WW	6.07 ± 0.29	3.96 ± 0.06	636.29 ± 17.58	0.01 ± 0.00	0.76 ± 0.00	0.55 ± 0.01	0.01 ± 0.01
WS	1.56 ± 0.28	1.00 ± 0.10	53.29 ± 6.96	0.03 ± 0.01	0.65 ± 0.01	0.47 ± 0.01	0.16 ± 0.04
p	0.000	0.000	0.000	0.000	0.000	0.000	0.004

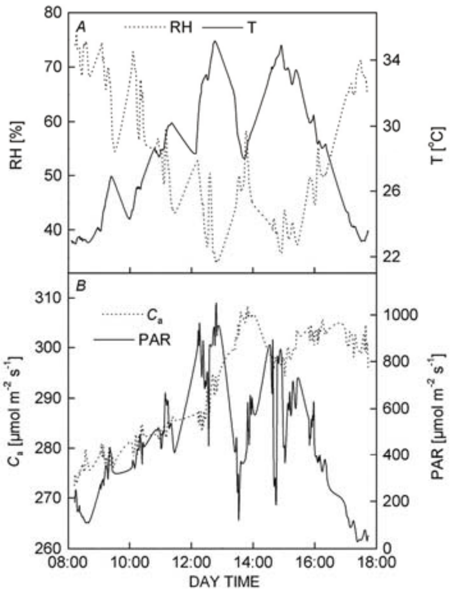

Fig. 1. Diurnal fluctuations of (*A*) temperature (T) and relative humidity (RH), and (*B*) photosynthetically active radiation (PAR) and ambient CO_2 concentration (C_a).

Diurnal changes of gas exchange and Chl fluorescence under natural conditions: The measured parameters changed with daytime (Fig. 1*A*,*B*) and fluctuations of environment (Figs. 2*A*–*F* and 3*A*,*B*). F_v/F_m decreased with the increase of PAR under both WW and WS treatments. Its lowest value was found at about 14:00 (local time), in particular under WS. There was significant difference in F_v/F_m between the WW and WS treatments, it increased with the decreasing of PAR (Fig. 3*A*). In addition, q_N of WS treatment was significantly higher than that of WW treatment at 14:00 (Fig. 3*B*).

P_N of WW plants was significantly higher than that of WS plants, and the former showed P_N peak at about 12:30, while the latter at about 10:30 (Fig. 2*A*). Both E and g_s of WW plants were significantly higher than those of WS plants during diurnal change (Fig. 2*B*,*C*). C_i was relatively steady under WW treatment while it was changed under WS treatment (Fig. 2*D*). Diurnal changes of L_s and WUE_i were very similar. L_s and WUE_i of WS plants were higher than that of WW plants before 12:30, while this trend was vague in afternoon (Fig. 2*E*,*F*).

Photosynthesis-PAR response curve: Water stress also affected R_D, I_c, I_s, Φ, and P_{max}. R_D (it was about 0.53 μmol m^{-2} s^{-1} for WW and 0.99 μmol m^{-2} s^{-1} for WS) and I_c (31.77 μmol m^{-2} s^{-1} for WW and 61.36 μmol m^{-2} s^{-1} for WS) were significantly increased while Φ (0.0168 μmol m^{-2} s^{-1} for WW and 0.0161 μmol m^{-2} s^{-1} for WS), I_s (1 400 μmol m^{-2} s^{-1} for WW and 1 200 μmol m^{-2} s^{-1} for WS), and P_{max} (11.50 μmol m^{-2} s^{-1} for WW and 4.80 μmol m^{-2} s^{-1} for WS) were significantly decreased (Figs. 4 and 5).

Discussion

Generally, P_N, E, and g_s of WW plants were significantly higher than those of WS plants, and P_N of WW plants showed peak at about 12:30 while P_N of WS plants at about 10:30. Compared with WW plants, C_i of WS plants showed more alterations. The stomatal factor-limited P_N is associated with decreased C_i caused by decreasing g_s (Jones 1992). Diurnal changes of L_s and WUE_i were very similar, because of their independent linkages to C_i/C_a

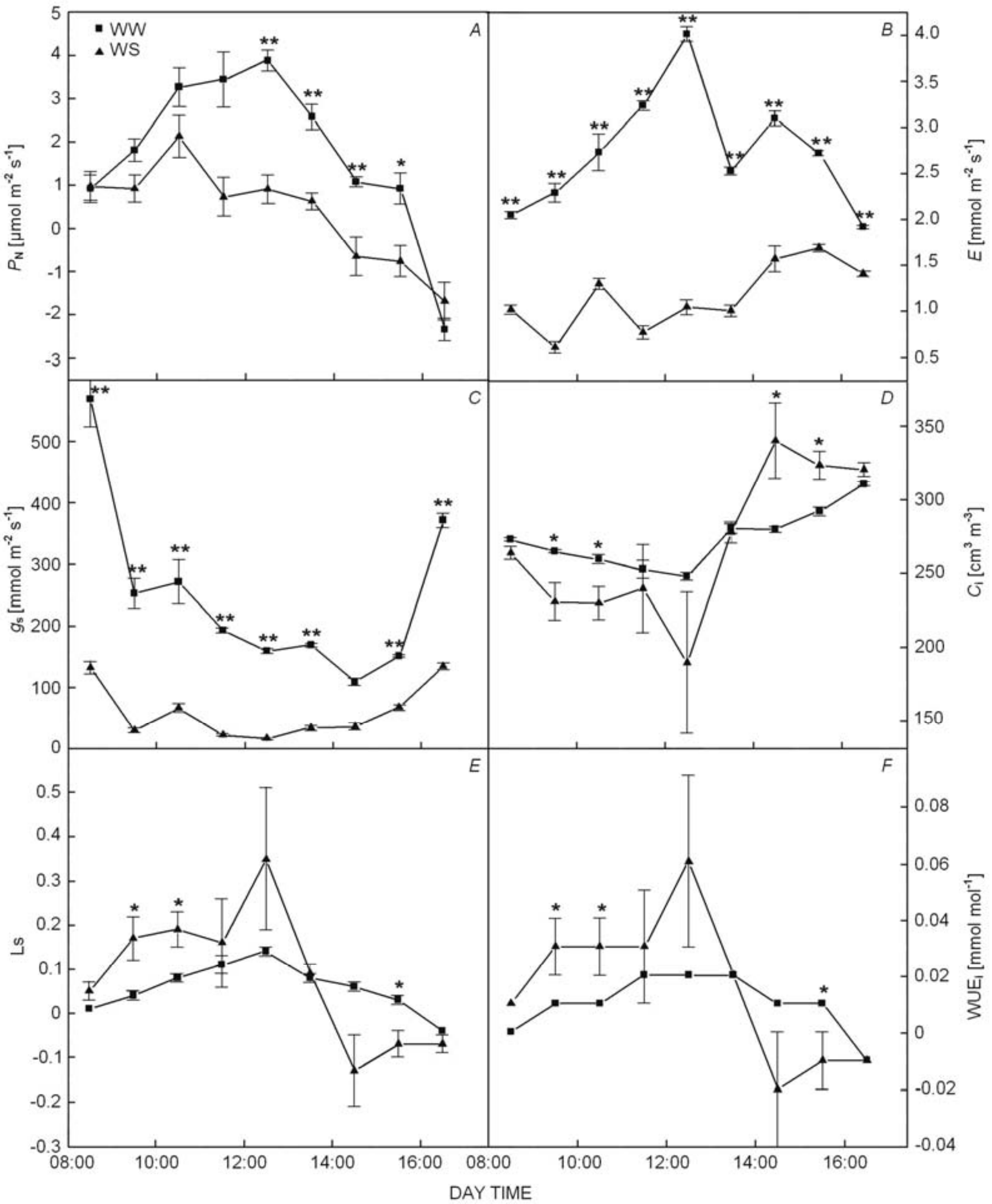

Fig. 2. Diurnal changes of net photosynthetic rate, P_N (*A*), transpiration rate, E (*B*), stomatal conductance, g_s (*C*), intercellular CO_2 concentration, C_i (*D*), L_s (*E*), and water use efficiency, WUE_i (*F*) in poplars under well-watered (WW) and water-stressed (WS) conditions. Means ± SE. $^{**}p< 0.01$, $^{*}p< 0.05$.

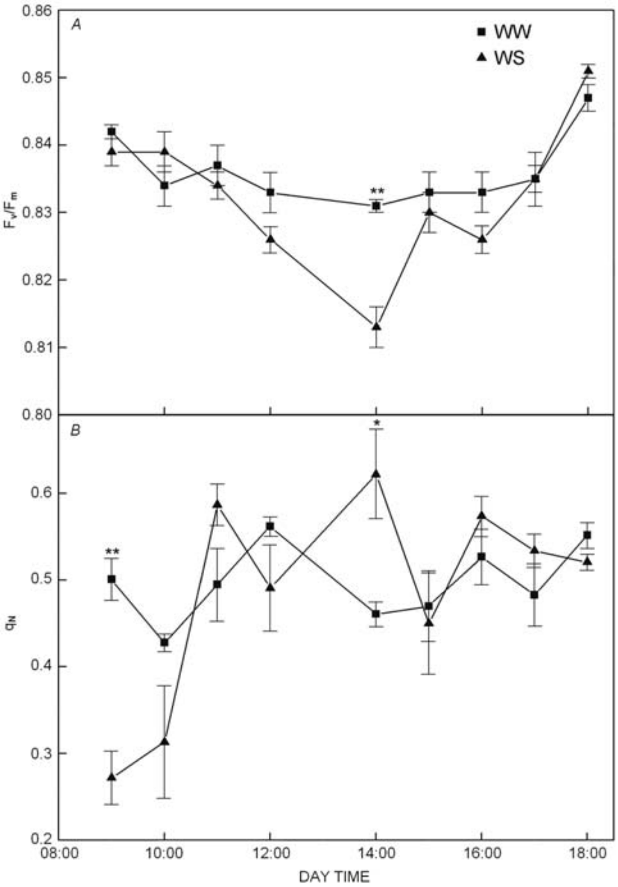

Fig. 3. Diurnal changes of F_v/F_m (*A*) and q_N (*B*) in poplars under well-watered (WW) and water-stressed (WS) conditions. Means ± SE. $^{**}p < 0.01$, $^{*}p < 0.05$.

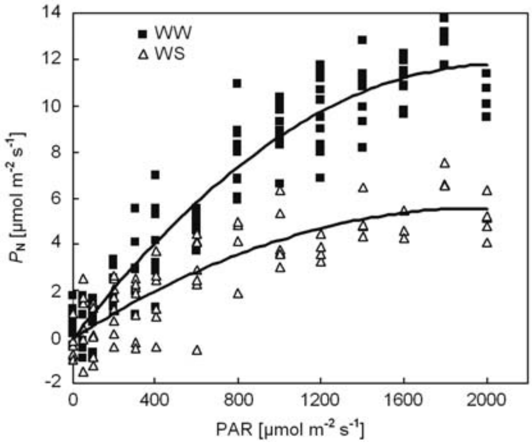

Fig. 4. Photosynthesis-PAR response curves in poplars under well-watered (WW) and water-stressed (WS) conditions.

(Ripullone *et al.* 2004). The L_s and WUE_i of WS plants were higher than those of WW plants mostly before 12:30. R_D and I_c of WS plants significantly increased while Φ, I_s, and P_{max} significantly decreased, and initial slope of photosynthesis-PAR response was reduced. These results were similar to the findings of Colom and Vazzana (2003). Water stress decreased P_N at both saturating and sub-saturating PAR. Increasing of I_c and decreasing of I_s would reduce the time of effective P_N, and increasing of R_D would make plants consume more at night. Therefore, we concluded that assimilation decreased at day and dissimilation increased at night because drought stress reduced plant growth and productivity; perhaps there were other possible factors, *e.g.* increased root exudation *etc*. (Dizengremel and Gérant 1997).

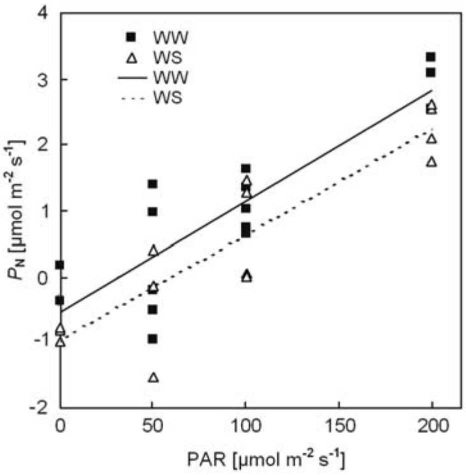

Fig. 5. Dark respiration rate (R_D), compensation irradiance (I_c), and apparent quantum yield (Φ) in poplars under well-watered (WW) and water-stressed (WS) conditions.

The intrinsic efficiency of PS2 (*i.e.* F_v/F_m) of both treatments, in particular of the WS treatment, had the lowest value at the local time of about 14:00, and in one day the only significant difference between the WW and WS treatments was at 14:00. q_N of WS plants was significantly higher than that of WW plants at 14:00. According to Kumar *et al.* (1999), P_N mainly depended on PAR and *E* depended on air temperature. Jiang and Zhu (2001) reported that high T led to the different patterns of gas exchange and the serious depression of P_N. In our study, the results of Figs. 1–3 illustrated that the change of *E* was consistent with the diurnal fluctuation of air T, but the diurnal change of P_N was affected by the whole microclimate, *i.e.* T, RH, PAR, *etc*. Therefore, the midday depression of P_N and g_s of *P. przewalski* seemed to be related to leaf T, low RH, and high irradiance. Increases in C_i found between 12:00 and 14:00 corresponded to the decrease in P_N. Our results are different to the findings of Flexas *et al.* (2001) that F_v/F_m remains unaffected by water stress and reductions in photochemical capacity (photoinhibition) are not responsible for depression of P_N. Thy proved that high heat and radiation loads in canopy leaves reduce PS2 photochemical activity (Gamon and Pearcy 1990, Epron 1997). Restricted CO_2 availability under drought stress could possibly lead to increased susceptibility to photodamage

(Powles 1984), and to a decrease in the amount of radiant energy for its development. Other previous studies showed that photo-damage does not generally occur during water stress under natural conditions (Di Marco *et al.* 1988, Gamon and Pearcy 1990). However, under conditions limiting growth there may be a higher probability for photo-damage when forward PS2 electron transport is blocked (Maxwell *et al.* 1995, Baroli and Melis 1998).

F_v/F_m remained unchanged during one day except for 14:00 regardless of the imposed treatments, confirming an earlier study of Da Matta *et al.* (1997) which reported a high stability of the potential PS2 photochemical efficiency to water deficit in *Coffea robusta*, and suggested photosynthesis decreases are due mainly to stomatal closure (Lima *et al.* 2002). L_s increased all along in morning and then decreased after 12:00, suggesting that stomatal limitation to photosynthesis was dominating in morning but non-stomatal limitation was dominating in afternoon; we thought perhaps after the midday depression of photosynthesis the plant needs longer time to repair itself. Low P_N at midday was the result of both a reduction in the photochemical process and an increase in stomatal limitation (Ishida *et al.* 1999).

In conclusion, drought stress not only significantly decreased gas exchange (*i.e.* P_N, E, and g_s) and efficiency of PS2 (*e.g.* F_v/F_m, and Ψ), and significantly increased WUE_i under controlled optimal conditions, but also altered the diurnal changes of gas change, Chl fluorescence, and WUE_i. On the other hand, drought stress also affected the photosynthesis-PAR response curve. P_N of WS plants peaked earlier (at about 10:30 of local time) than P_N of the WW plants (at about 12:30 of local time). At midday, there was a depression in photosynthesis for WS plants, but not for WW plants, and it could be caused by the whole microclimate, especially high T, low RH, and high PAR. There were stomatal and non-stomatal limitations to photosynthesis. Stomatal limitation was dominating in morning, and low P_N at midday was caused by stomatal and non-stomatal limitation, but non-stomatal limitation was dominating in afternoon. Photosynthesis-PAR response curve showed drought stress increased I_c and R_D, and decreased I_s and P_{max}.

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