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Photoprotective function of photorespiration in *Reaumuria soongorica* during different levels of drought stress in natural high irradiance

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Abstract

Diurnal patterns of gas exchange and chlorophyll (Chl) fluorescence parameters of photosystem 2 (PS2) as well as H_2O_2 content were analyzed in *Reaumuria soongorica* (Pall.) Maxim., a perennial semi-shrub. The rate of photorespiration was estimated by combined measurement of gas exchange and Chl fluorescence. The rate of photorespiration increased with the increasing drought stress (DS). The ratio of carboxylation electron flow to oxygenation electron flow (J_c/J_o) and the maximal photochemical efficiency of PS2 (variable to maximum fluorescence ratio, F_v/F_m) decreased with the increasing DS. F_v/F_m in isonicotinic acid hydrazide (INH)-sprayed plants was lower than that in normal plants under moderate DS, but no significant difference was observed under severe DS. H_2O_2 content in INH-sprayed plants was significantly lower than that in normal plants under severe DS. Taken together, photorespiration *in R. soongorica* consumed excess electrons and protected photosynthetic apparatus under moderate DS, whereas it accelerated H_2O_2 accumulation markedly and induced the leaf abscission under severe DS.

Additional key words: chlorophyll fluorescence; electron flow; gas exchange; hydrogen peroxide; intercellular CO_2 concentration; isonicotinic acid hydrazide; leaf abscission; leaf temperature; photoinhibition; stomatal conductance.

Introduction

Photosynthesis is mainly limited by restricted CO_2 influx (Valentini *et al.* 1995) and reduced intercellular CO_2 concentrations (C_i) (Kaiser 1987, Cornic and Briantais 1991, Quick *et al.* 1992) through stomatal closure under early to moderate drought stress (DS). Low C_i occurring under stomatal closure may cause photoinhibition, even at low photosynthetic photon flux density (PPFD) (Roland *et al.* 2006). The high irradiance and temperature in concomitance with drought can lead to increase of excessive photon energy and decrease of photochemical efficiency, and then damage of photosynthetic apparatus under severe DS (Guan *et al.* 2004).

In order to protect the photosynthetic apparatus against photodamage, excess photon energy might be consumed by photorespiration in C_3 plants and thermal energy dissipation of absorbed photons is associated with the formation of zeaxanthin (Roland *et al.* 2006). Osmond and Björkman (1972) proposed that photorespiration might be an important photoprotective mechanism. However, due to the high rates of photorespiratory CO_2 release, photorespiration is a wasteful process imposing a strong carbon drain on plants (Wingler *et al.* 2000). This great controversy about the photoprotective function of photorespiration exists for many years (Osmond and Björkman 1972). On the one hand, photorespiration can protect the photosynthetic apparatus against photodamage (Osmond and Björkman 1972, Katona *et al.* 1992, Park *et al.* 1996, Osmond *et al.* 1997), and the photoprotective function of photorespiration could be particularly important under high PPFD in DS-leaves (Osmond and Grace 1995, Kozaki and Takeka 1996, Wingler *et al.* 1999, Haupt-Herting and Fock 2000, Guan *et al.* 2004, Streb *et al.* 2005). On the other hand, some researchers (Brestic *et al.* 1995, Meng *et al.* 1999, Nogués and Alegre 2002) suggest that photorespiration does not play significant role in protection of photosynthetic apparatus against photodamage.

Reaumuria soongorica (Pall.) Maxim, an extreme xeric semi-shrub of Tamaricaceae, is the constructive and dominant species of desert grasslands in China. It is

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Abbreviations: C_i – intercellular CO_2 concentration; DS – drought stress; F_v/F_m – maximal photochemical efficiency of dark-adapted leaves; $\Delta F/F_m'$ – actual photochemical efficiency; g_s – stomatal conductance; INH – isonicotinic acid hydrazide; J_c and J_o – electron flows used for RuBP carboxylation and RuBP oxygenation; J_T – total electron flow; PPFD – photosynthetic photon flux density; P_N – net photosynthetic rate; P_R – photorespiration rate; RuBP – ribulose-1,5-bisphosphate; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase.

exposed to a multiple environmental stresses, including low water availability, extreme temperature fluctuations, high irradiance, and nutrient deprivation. When *R. soongorica* is subjected to desiccation, leaves are wilted and die completely, and then the plant does not grow. But they are still able to recover and develop new leaves upon rainfall (Liu *et al.* 2007). This characteristic may be a strategy to cope with extreme environment stresses.

Many reports have suggested that photorespiration plays the photoprotective function under DS in plants. However, to our knowledge, only few studies elucidate in detail the roles of photorespiration in plants at the different levels of DS. We selected *R. soongorica* to investigate photoprotective function of photorespiration by application of an inhibitor of photorespiration, isonicotinic acid hydrazide (INH, *Sigma*) under different levels of DS.

Materials and methods

Plants and growth: The research was conducted from March to August, 2006 in the Botanical Garden of Lanzhou University. The 2-year-old *R. soongorica* were transplanted from the field to individual 3 000 cm^3 plastic pots with their original soil. The potted plants were transferred to a field tunnel with the same depth as the height of pots. The bottoms of the plastic pots were mulched with plastic to avoid the roots spreading into ground and thereby absorb moisture from it. A rain shed was made over pots and covered with plastic to avoid precipitation. Three different levels of water deficit were set up with 12 pots each, including well-watered conditions (80–85 % of maximum field capacity), moderate DS (40–45 %), and severe DS (below 35 %). Half of plants were sprayed with 10 mM INH in the morning for 3 d before measurement. On the surface of soil for each pot four holes of 1.5-cm diameter and 10-cm depth were made. Water loss during the day was supplied through the holes each evening.

Gas exchange and chlorophyll (Chl) fluorescence measurements: Leaf gas exchange (a gas exchange system *CIRAS-1*; *PP Systems*, UK) and Chl fluorescence (a pulse-modulated fluorescence monitor system *FMS-2*; *Hansatech*, UK) were monitored on the shoots every two hours from predawn to 19:00 in all plants. These parameters were measured, including net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), photosynthetic photon flux density (PPFD), leaf temperature (T_n), actual photochemical efficiency ($\Delta F/F_m'$), and maximal photochemical efficiency (F_v/F_m).

H_2O_2 production: Fresh *R. soongorica* leaves were collected and then stored in liquid nitrogen to investigate H_2O_2 content. The concentration of H_2O_2 in leaves was measured by monitoring the absorbance of the titanium–peroxide complex at 410 nm following the method of Patterson *et al.* (1984). Absorbance values were quantified using a standard curve generated from known concentrations of H_2O_2.

Computation and data analysis: Mitochondrial respiration during the day (R_D) was estimated from net CO_2 assimilation rates measured before dawn (R_N). R_D was extrapolated at different temperatures using a Q_{10} relation (Larcher 1983) as follows:

$$R_D = R_N\, Q_{10}^{(Td - Tn)/10}\ (Q_{10} = 2.2) \qquad (1)$$

where T_n is the leaf temperature at which R_N was measured and T_d is the leaf temperature at which R_D was calculated.

Total electron flow (J_T) was estimated according to the following formula (Krall and Edwards 1992, Galmés *et al.* 2007):

$$J_T = \Delta F/F_m'\ \mathrm{PPFD}\ \alpha f \qquad (2)$$

where α is the ratio of radiation absorbed by leaf as compared to incidence radiation, generally 84 %, and *f* is 0.5 in C_3 plants.

Electron flows used for RuBP carboxylation (J_c), electron flows used for RuBP oxygenation (J_o), and photorespiration rate (P_R) were estimated according to the following formulae (Epron *et al.* 1995, Valentini *et al.* 1995):

$$J_c = \tfrac{1}{3}[J_T + 8(P_N + R_D)] \qquad (3)$$

$$J_o = \tfrac{2}{3}[J_T - 4(P_N + R_D)] \qquad (4)$$

$$P_R = 1/12[J_T - 4(P_N + R_D)] \qquad (5)$$

There were 4–6 repetitions each pot for all measurements. All data analyses were performed by ANOVA using *SPSS* (version *11.5*). Significant differences among three treatments were determined at $p<0.05$, according to least significant difference (LSD) test. All figures were plotted using *Origin* (version *6.1*).

Results and discussion

Photosynthetic characteristics under DS: *R. soongorica* was exposed to multiple environmental stresses, including water deficit, high irradiance, and high air temperature. Maximal irradiance and temperature were about 1 100 $\mu mol\ m^{-2}\ s^{-1}$ and 42 °C in the experiment, respectively (Fig. 1*A*,*B*). g_s and C_i decreased markedly ($p<0.05$) as DS increased (Fig. 1*C*,*D*). P_N declined significantly ($p<0.05$) with the increasing DS (Fig. 1*E*). Diurnal time

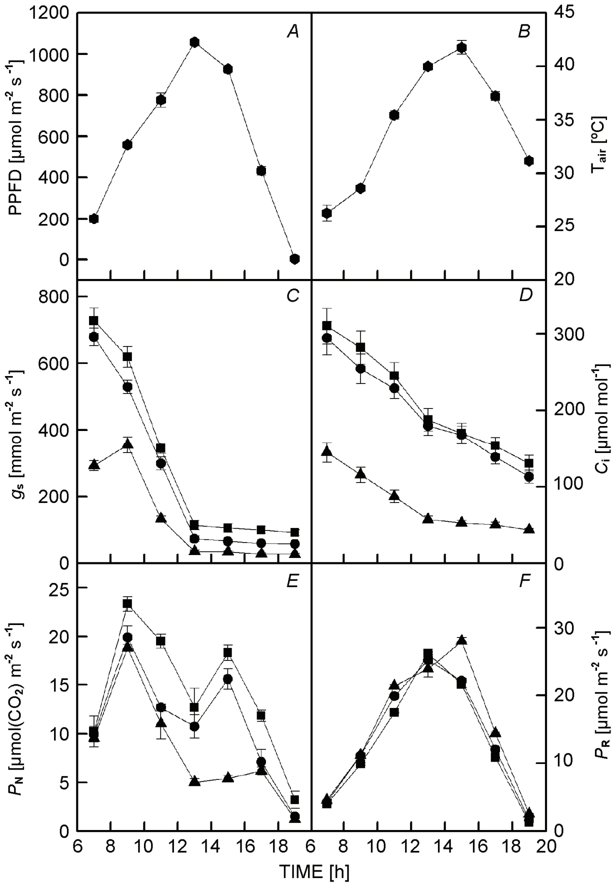

Fig. 1. Diurnal time courses of (*A*) photosynthetic photon flux density (PPFD) and (*B*) air temperature (T_{air}) in experiment field, and (*C*) stomatal conductance (g_s), (*D*) intercellular CO_2 concentration (C_i), (*E*) net photosynthetic rate (P_N), and (*F*) photorespiratory rate (P_R) in *R. soongorica* leaves under different drought stress (DS): well-watered condition (*closed squares*), moderate DS (*closed circles*), and severe DS (*closed triangles*).

courses of P_N of *R. soongorica* displayed typical double-peak curve model, especially under well-watered and moderate DS. However, under severe DS diurnal courses of P_N tended to be a single-peak curve. The photosynthetic performance of *R. soongorica* was consistent with the results of other researchers (Xu *et al.* 2005, Jia *et al.* 2006, Liu *et al.* 2007).

Photoinhibition under DS: Photoinhibition occurs when photon energy is in excess of the amount used by photosynthesis, which is characterized by the decline of F_v/F_m and of apparent photosynthetic quantum yield of O_2 evolution or CO_2 uptake (Long *et al.* 1994). Accordingly, the extent of photoinhibition is dependent on the amount of excessive photon energy. In addition, the high irradiance and high temperature often appear simultaneously with drought, so the excessive photon energy may increase under DS. Former reports stated that the decrease of F_v/F_m showed the sensitivity to photoinhibition (Manetas *et al.* 2002, Guan *et al.* 2004). The diurnal courses of F_v/F_m and $\Delta F/F_m'$ in *R. soongorica* are shown in Fig. 2*A*,*B*. With the increasing DS, F_v/F_m and $\Delta F/F_m'$ decreased. Diurnal courses of F_v/F_m and $\Delta F/F_m'$ displayed a significant decrease during the morning and then a increase from 13:00 to late afternoon. F_v/F_m decreased significantly ($p<0.05$) at noon with the increasing DS (Fig. 2*A*). At noon the decrease of $\Delta F/F_m'$ was slight under moderate DS and sharp ($p<0.05$) under severe DS (Fig. 2*B*). Therefore, the decline of F_v/F_m and $\Delta F/F_m'$ implied that drought led to photoinhibition and

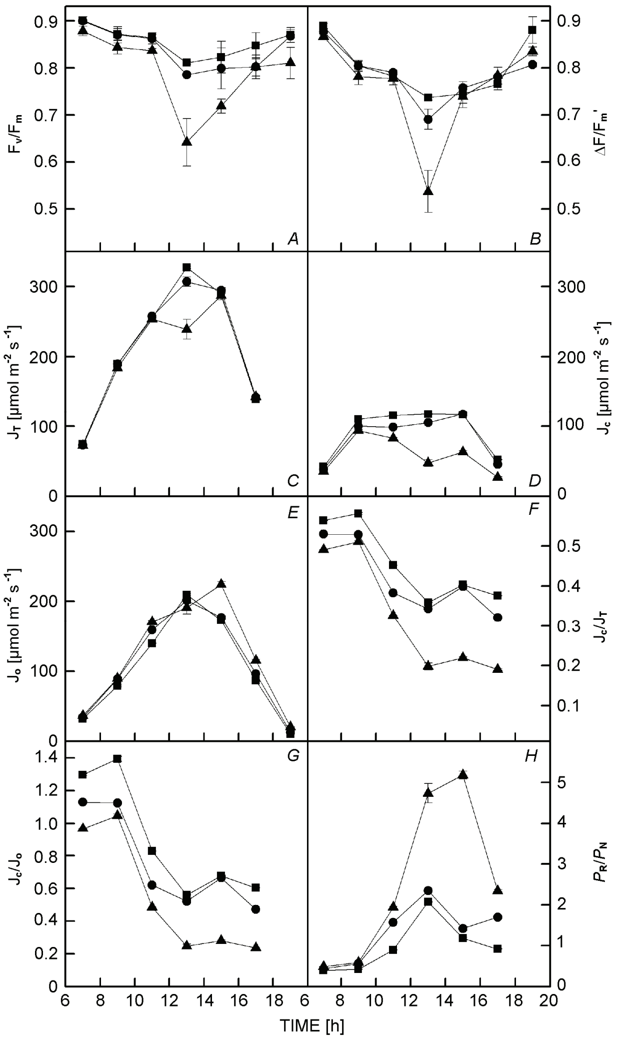

Fig. 2. Diurnal time courses of (*A*) maximum photochemical efficiency of photosystem 2 (F_v/F_m), (*B*) actual photochemical efficiency of photosystem 2 ($\Delta F/F_m'$), (*C*) total electron flow (J_T), (*D*) electron flow used for RuBP carboxylation (J_c), (*E*) electron flows used for RuBP oxygenation (J_o), (*F*) ratio between carboxylation electron flows and total electron flow (J_c/J_T), (*G*) ratio J_c/J_o, and (*H*) ratio between photorespiratory rate and net photosynthetic rate (P_R/P_N) in *R. soongorica* leaves under different drought stress (DS): well-watered condition (*closed squares*), moderate DS (*closed circles*), and severe DS (*closed triangles*).

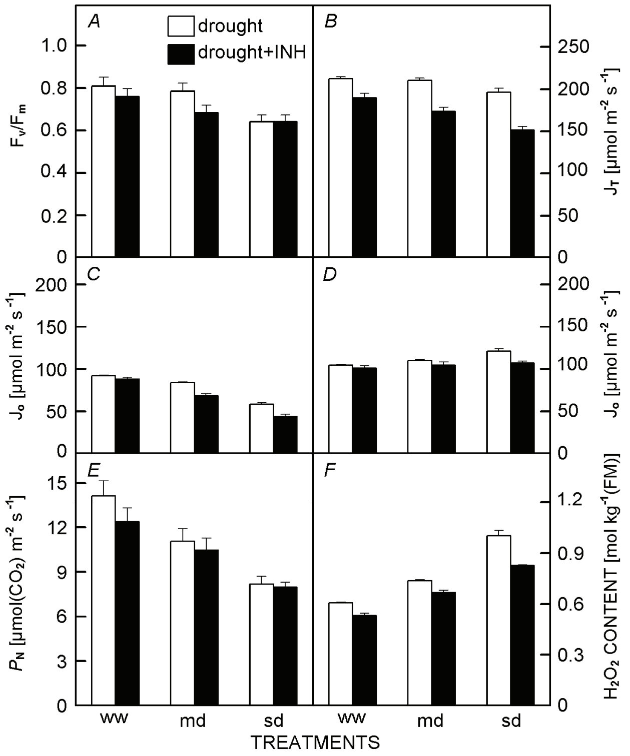

Fig. 3. Effects of INH on (*A*) maximum photochemical efficiency of photosystem 2 (F_v/F_m), (*B*) total electron flows (J_T), (*C*) electron flows used for RuBP carboxylation (J_c), (*D*) electron flows used for RuBP oxygenation (J_o), (*E*) net photosynthetic rate (P_N), and (*F*) H_2O_2 content in *R. soongorica* leaves under different drought stress (DS): ww, well-watered; md, moderate DS; and sd, severe DS.

photodamage of photosynthetic apparatus in leaves of *R. soongorica*.

Photorespiration estimated by combined measurement of gas exchange and Chl fluorescence under DS: The rate of photorespiration in some shrub vegetation in desiccated environment can be estimated by combined measurement of gas exchange and Chl fluorescence (Galmés *et al.* 2007). This holds also for *R. soongorica*. In our study, the total electron flow (J_T) changed diurnally in parallel with irradiance and reached maximum rates of about 327 and 307 μmol m^{-2} s^{-1} at midday under well-watered condition and moderate DS, respectively. Maximum J_T was lower under severe DS than under the other levels in the afternoon (Fig. 2*C*). The carboxylation electron flows (J_c) showed similar diurnal trends under well-watered and moderate DS, which increased first rapidly, then slowly, reached the peak values during the afternoon, and then decreased. Under severe DS, J_c increased, reached the peak value in the morning, and then decreased (Fig. 2*D*). Oxygenative electron flows (J_o) and photorespiration rate (P_R) displayed similar diurnal trends under all treatments, with the peak values occurring in the afternoon. The peak value of J_o and P_R under severe DS was significantly ($p<0.05$) higher than those under the two other levels (Figs. 2*E*, 1*F*).

Photoprotective function of photorespiration by consuming excess electrons under moderate DS: F_v/F_m in INH sprayed plants was markedly lower ($p<0.05$) than that of normal plants under moderate DS (Fig. 3*A*). This indicated that photorespiration maintained lower photoinhibition and played an important role in protecting photosynthetic apparatus. J_o in *R. soongorica* increased with the increasing DS (Fig. 3*D*), whereas J_T and J_c decreased (Fig. 3*B*,*C*). J_T, J_c, J_o, and P_N were lower in INH-sprayed plants than in normal plants under moderate DS (Fig. 3*B*,*C*,*D*,*E*), indicating that photorespiration was a key pathway consuming excess electrons.

J_c/J_T, indicating the relative importance of J_c, displayed the diurnal trend with two peak values occurring in the morning and in the afternoon, respectively. J_c/J_T decreased significantly ($p<0.05$) along with the severity of DS (Fig. 2*F*). The decrease of J_c/J_T indicated the importance of oxygenation of RuBP under DS. Moreover, J_c/J_o is a good indicator of the relative rates of carboxylation *versus* oxygenation, and may be directly controlled by the kinetic properties of ribulose-1,5-bisphosphate carboxylase/oxygenase (Valentini *et al.* 1995). In the present study, J_c/J_o showed a similar diurnal trend as J_c/J_T, decreasing markedly ($p<0.05$) with the increasing DS (Fig. 2*G*). The decrease of J_c/J_o in *R. soongarica* indicated that excessive electrons were transported to photorespiratory pathway (*i.e.* photorespiration consumed excessive electrons) and photorespiration had photoprotective function by consuming excessive electrons under moderate DS. Furthermore, P_R/P_N, which indicates the relative role of photorespiration as compared to P_N, increased with the extent of DS. P_R/P_N (Fig. 2*H*) increased markedly ($p<0.05$) under severe DS. The diurnal average of P_R/P_N in *R. soongorica* reached values as high as 1.30 under moderate DS and 0.89 under well-watered condition. The present data are higher than those reported in other plants (Ogren 1984, Gerbaud and Andre 1987, Zelitch 1992, Jacob and Lawlor 1993, Valentini *et al.* 1995). That may be due to the higher temperature during the present experiment. Both the decrease of J_c/J_T and the increase of P_R/P_N in *R. soongorica* further emphasized the importance of photorespiration in the carbon cycle under water stress (Valentini *et al.* 1995).

Leaf abscission caused by producing excess H_2O_2 in photorespiration under severe DS: There was no significant difference of F_v/F_m between the INH-sprayed and normal plants under severe DS (Fig. 3*A*), which suggested that photorespiration in *R. soongorica* had no obvious effect on photoprotection under extremely severe DS. Photorespiration accelerates senescence when the rate of photorespiration becomes too high, for example, when the O_2 concentration is increased above the O_2 compensation concentration (Tolbert *et al.* 1995, Wingler *et al.* 2000). In the present study, both g_s and C_i decreased with the increased DS, especially under severe DS ($p<0.01$) (Fig. 1*C*,*D*). The decreased g_s and C_i could lead to the increased O_2 concentration and high photorespiration, which induced the leaf senescence and abscission under severe DS.

In photorespiration, H_2O_2 is produced by the glycollate oxidase reaction in the peroxisomes. H_2O_2 is a toxic substance in cells and has been commonly used as the inducer for stress-induced premature senescence. In the present study, H_2O_2 content in *R. soongorica* increased markedly with increasing DS. The H_2O_2 content in INH-sprayed plants was lower than that of normal plants under DS, especially under severe DS (Fig. 3*F*). Moreover, superoxide production by the photosynthetic electron transport chain (*via* the Mehler reaction) is exacerbated by drought (Noctor *et al.* 2002). We suggest that, since a lot of H_2O_2 production in photorespiration of *R. soongorica* was not scavenged completely, excess H_2O_2 induces the leaf senescence and abscission under extremely severe DS.

In summary, we found that photorespiration in *R. soongorica* played a protective role by consuming photoinhibition-induced excess electrons under moderate DS. However, under extreme severe DS high photorespiration could increase H_2O_2 accumulation, which resulted in leaf senescence and abscission.

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