Photorespiration and photoprotection of grapevine (*Vitis vinifera* L. cv. Cabernet Sauvignon) under water stress

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Abstract

In order to investigate the photoprotective function of photorespiration in grapevine under water stress, potted grapevines (*Vitis vinifera* L. cv. Cabernet Sauvignon) were randomly divided into three uniform groups for well-watered [watered every morning to keep the relative water content (RWC) of soil over 70 %], water-stress adapted (drought-adapted at 30 % relative soil water content for 30 days), and water stress without adaptation treatment (water-stressed to 30 % relative soil water content for 3 days). Net assimilation rate (A_N), stomatal conductance (g_s), substomatal CO_2 concentration (C_i), transpiration rate (E), actual photochemical efficiency of PSII (Φ_{PSII}), and maximum photochemical efficiency of PSII (F_v/F_m) were recorded by combining measurements of gas exchange and chlorophyll fluorescence. Gross photorespiration (P_r), photosynthetic electron partitioning (J_C/J_T), photochemical quenching coefficient (q_P), and non-photochemical quenching (NPQ) were also calculated. The ratio of net assimilation rate to transpiration rate (A_N/E) was used as an indicator of water use efficiency (WUE). A_N, apparent P_r, Φ_{PSII}, F_v/F_m, q_P, and g_s decreased, NPQ increased, and gross P_r sustained at a high level under water stress. This suggests that both photorespiration and energy dissipation play important roles in protecting photosynthetic apparatus against photoinhibition. C_i in water-stressed plants without adaptation treatment increased, which indicates the leaves suffered a non-stomatal limitation, while the water-stress adaped plants only suffered a stomatal limitation indicated by low C_i.

Additional keywords: grapevine, photoprotection, photorespiration, water stress.

Introduction

Photoinhibition usually occurs under adversed conditions, such as high irradiance, high temperature and water stress. Two types of photoinhibition have been distinguished (Osmond 1994), one is dynamic photoinhibition, a short-term down regulation of photosynthesis mainly related to several photoprotective mechanisms, the other is chronic photoinhibition, a long-lasting mechanism understood as photodamage, related to the loss of functionality of PSII units.

Many photoprotective mechanisms were confirmed related to dynamic photoinhibition including xanthophyll cycle-dependent energy dissipation (Demmig-Adams and Adams 1992), Mehler reaction (Flexas 1999) and photorespiration (Osmond and Björkman 1972).

However, the photoprotective function of photorespiration under adverse environment conditions has been considered controversy. Photorespiration was believed to protect the photosynthetic apparatus in following ways. First, photorespiration acts as an alternate sink of excessive excitation energy and protect photosynthetic

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Abbreviations: A_N – net assimilation rate; apparent P_r – photorespiration rate measured by low O_2 method; C_i – substomatal CO_2 concentration; E – transpiration rate; ETR – electron transport rate; F_m – maximum fluorescence in dark; F_m' – maximum fluorescence in light; F_0 – minimal fluorescence; F_0' – instantaneous fluorescence; F_s – steady-state fluorescence; F_v/F_m – maximum photochemical efficiency of PSII; gross P_r – photorespiration rate estimated by combined measurement of gas exchange parameters and chlorophyll fluorescence parameters; g_s – stomatal conductance; J_C – electron flow to carboxylation; J_C/J_T – photosynthetic electron partitioning; J_O – electron flow to oxygenation; J_T – total electron transport; NADP – nicotinamide adenine dinucleotide phosphate; NPQ – non-photochemical quenching; P_r – photorespiration; PS – photosystem; Φ_{PSII} – actual photochemical efficiency of PSII; Q_A – primary quinone electron acceptor; q_P – photochemical quenching coefficient; R_D – mitochondrial respiration during the day; RWC – relative water content; WUE – water use efficiency.
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apparatus from photoinhibition (Osmond and Björkman 1972). Second, photorespiration can prevent the excessive reduction of primary quinone electron acceptor between PSII and PSI, thereby helps to sustain the balance of electron transport system and PSI-dependent cyclic electron transport (Katona *et al.* 1992). The third, photorespiration can provide electron acceptor $NADP^+$ to photoreaction and provide phosphorus to photophosphorylation, thus facilitating the light energy utilization and release the photoinhibition (Gao *et al*. 1989). Takeba and Kozaki (1998) suggested that photorespiration plus recycling of O_2 and CO_2 may be able to sustain most of ETR at CO_2 compensation point, which is enough to protect PSII at low to moderate light level. Tsonev *et al*. (2003) reported that F_v/F_m and Φ_{PSII} decreased when photorespiration was inhibited under low O_2 condition. By inhibition the photorespiration with isonicotinic acid hydrazide, Bai *et al*. (2008) verified the photoprotective function of photorespiration in moderate water stressed *Reaumuria soongorica*. The fact that mutants with reduced activities of photorespiratory enzymes are more prone to water stress and photoinhibition also supports the photoprotective function of photorespiration (Kozaki and Takeka 1996; Wingler *et al*. 1999).

Some researchers argued that photorespiration is not a major factor in protecting photosynthetic apparatus from photoinhibition. Brestic *et al*. (1995) found that Φ_{PSII} was not affected when the O_2 concentration was decreased from 21 % to 2 % at compensation point of CO_2 on well watered and water stressed leaves. Therefore, most of the excess excited energy was dissipated through antenna pigments and only a small portion through photorespiration. Nogués and Alogre (2002) suggested that photorespiration cannot act as an alternate electron sink to protect the photosynthetic apparatus because the oxygenation decreased along with the carboxylation of RuBP in response to water stress.

The purpose of this experiment is to investigate the photoprotective function of photorespiration in grapevine under water stress, and determine the effects of water stress adaptation on photosynthesis.

Material and methods

Plant material and experimental design: The experiment was carried out from March to June 2006, in the Viticulture and Enology Research Center at California State University, Fresno, USA. Two–year–old grapevines (*Vitis vinifera* L. cv. Cabernet Sauvignon) were planted in two-gallon plastic pots (21.6 cm high and 22.9 cm in diameter at the top) filled with 1:1 peat moss/perlite mixture. Vines were divided into three groups for different treatments. Vines in treatment I were watered every morning to keep the RWC of soil over 70 % (well watered). Vines in treatment II were drought adapted at 30 % relative soil water content for 30 days (water stress adapted). Vines in treatment III were well watered as in treatment I and then water stressed to 30 % relative soil water content 3 days before the measurement (water stress without adaptation).

Gas exchange measurements were made two times per day (from 9:00 to 11:00 in the morning and from 13:30 to 15:30 in the afternoon) on south-facing mature leaves by using *CIRAS-2* portable photosynthesis system (*PP systems*, Hoddesdon, UK) at 350 cm^3 m^{-3} CO_2 and 21 % O_2 or 2 % O_2 air conditions (to inhibit the apparent P_r) for A_N, E, g_s, C_i. In order to maintain a uniform illumination intensity, 1500 μmol(photon) m^{-2} s^{-1} artificial light source was used during the measurement according to the natural illumination intensity measurement. After each measurement, the artificial light source was turned off and cuvette was covered with black cloth for 3 minutes, and then the R_D (mitochondrial respiration during the day) was recorded.

Chlorophyll fluorescence measurements were performed on the same leaves used for gas exchange determinations, using *FMS-2* portable pulse modulated fluorometer (*Hansatech*, Kings Lynn, UK). The fibre optic of *FMS-2* was inserted into the artificial light source of the *CIRAS-2* and maintained at an angle of 45º. Steady-state fluorescence (F_s) was recorded during illumination. Maximal fluorescence (F_m') was recorded after a saturating flash (approx. 5 000 μmol(photon) m^{-2} s^{-1}). After switch off the actinic light, a black cloth was placed over the leaf and a 3–s pluse of weak far-red light was applied to give instantaneous fluorescence (F_0'). F_v/F_m was measured on leaves that have been dark adapted for 20 min. Predawn F_v/F_m was also recorded before dawn.

Calculations: Apparent P_r was estimated by subtracting A_N under 21 % O_2 from that under 2 % O_2. Φ_{PSII} (actual photochemical efficiency of PSII) was estimated as $\Phi_{PSII} = (F_m' - F_s)/F_m'$ (Genty *et al*. 1989). Total electron transport (J_T) was estimated as: $J_T = PPFD \times \Phi_{PSII} \times 0.5 \times 0.84$ (Krall and Edwards 1992). Electron flow to carboxylation (J_C) and gross photorespiration (P_r) were estimated by combined measurements of gas exchange and fluorescence as: $J_C = 1/3[J_T + 8(A_N + R_D)]$, $P_r = 1/12[J_T - 4(A_N + R_D)]$ (Valentini *et al*. 1995). Photochemical quenching coefficient (q_P) was calculated as: $q_P = (F_m' - F_s)/(F_m' - F_0')$. The non-photochemical quenching (NPQ) was estimated as: $NPQ = (F_m/F_m') - 1$ (Bilger & Björkman 1990).

Statistical analysis: Analysis of variance (one-way *ANOVA*) was performed to test significant variations in response to different treatments. In order to evaluate significant differences, the *LSD*-test (Least Significant

Difference) was used on a significance level of $p<0.05$. Student's *t*-test was used to analyse whether differences between treatments were significant. Data are the means±standard error (SE) of five replications ($n = 5$).

Results and discussion

Photosynthesis and photorespiration: A_N of all the three treatments was higher in the morning than in the afternoon. A_N was lower under water stress in both morning and afternoon (Fig. 1*A,B*). A_N of well watered plants increased under 2 % O_2 in the morning but not in the afternoon. A_N of water stressed plants only increased slightly under 2 % O_2.

Since 2 % O_2 reduces the intercellular O_2 concentration and photorespiration, the difference between A_N under 2 % O_2 and 21 % O_2 can be considered as apparent P_r (Sharkey 1988), while the photorespiration calculated from electron transport partitioning can be considered as gross P_r (Valentini *et al*. 1995). We found that gross P_r of well watered plants was much lower under 2 % O_2 than under 21 % O_2, while that of water stressed plants showed no difference. Water stress adapted plants expressed a similar trend as well watered plants.

Since a great part of the CO_2 released by photorespiration can be re-used in carbon assimilation, it is difficult to obtain an accurate measure of the P_r (Gerbaud and André 1987; Loreto *et al*. 1999). Two methods are typically used to estimating P_r, one is by subtracting A_N under ambient O_2 condition from that under low O_2 condition, which was called apparent P_r. There are three defects in this method. The first is that low O_2 concentration might result in a reduced substrate concentration for RuBP carboxylation/oxygenation and a decrease in total electron transport through PSII, and in sequence underestimate the photorespiration by reduction of the total amount of photorespiration and photosynthesis. Second, photorespiration was greatly reduced but not eliminated under low O_2 condition, which leads to underestimation of photorespiration. Finally, as this method does not take the recycling between photosynthesis and photorespiration into account (Loreto *et al*. 1999), it underestimates the photorespiration rate, especially under water-stress conditions because low g_s blocks the gas exchange between cell and atmosphere (Sharkey 1988).

The alternative method is to combine measurements of gas exchange and chlorophyll fluorescence. Gross P_r is estimated as the difference between total electron transport and electron transport consumed by carboxylation and oxygenation. However, other electron sinks such as the Mehler reaction and the water-water cycle are not taken into account in this method (Valentini *et al*. 1995), which leads to an overestimation of P_r. By comparing these two methods, we found that gross P_r was two times higher under normal condition, and several times higher than apparent P_r under adverse environment conditions such as water stress, high temperature, and high irradiance. Considering the increase of recycling between photorespiration and photosynthesis, the true value of photorespiration should be much closer to gross P_r. Photorespiration was not reduced under water stress; it still plays an important role in protecting grapevine leaves from photoinhibition under water stress.

Photorespiration protects photosynthetic apparatus from photoinhibition by consuming excess excitation energy (Flexas *et al*. 1999). The photoprotective function

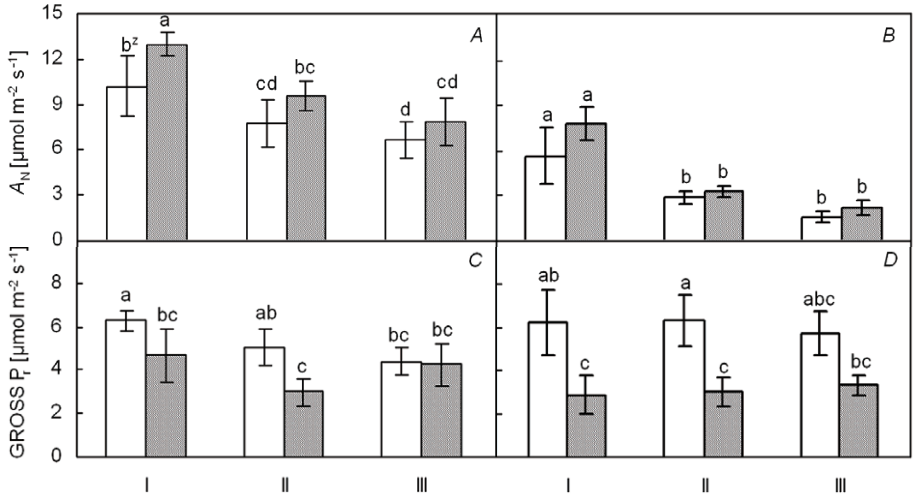

Fig. 1. Net asssimilation (A_N) and gross photorespiration (gross P_r) of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment at 21 % O_2 (blank) and 2 % O_2 (stripe) in the morning (*A,C*) and afternoon (*B,D*). Means ± SE of five replications are shown.
[z] Means for each treatment with different letters are significantly different by Fisher's LSD at p=0.05.

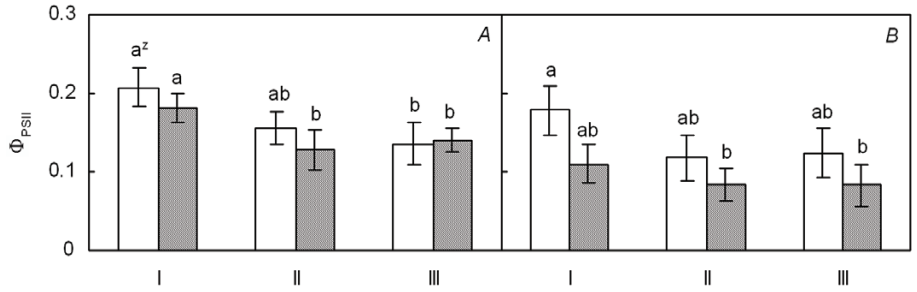

Fig. 2. Actual photochemical efficiency (Φ_{PSII}) of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment at 21 % O_2 (*blank*) and 2 % O_2 (*striped*) in the morning (*A*) and afternoon (*B*). Means ± SE of five replications are shown.
[z] Means for each treatment with different letters are significantly different by Fisher's LSD at $p = 0.05$.

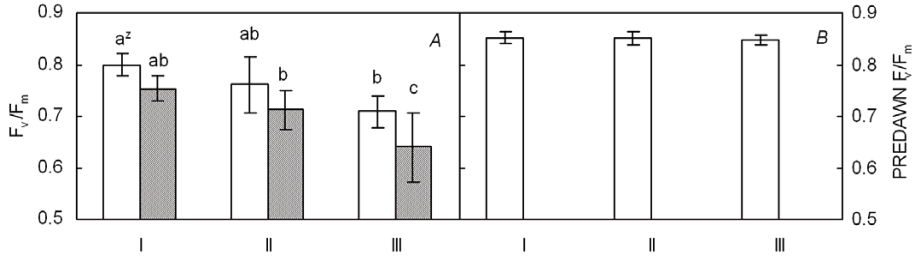

Fig. 3. Maximum photochemical efficiency (F_v/F_m) of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment in the morning (*A, blank*), afternoon (*A, stripe*), and predawn (*B*). Means ± SE of five replications are shown.
[z] Means for each treatment with different letters are significantly different by Fisher's LSD at $p = 0.05$.

of photorespiration in leaves depends on its activity. Streb *et al*. (1998) found that photoprotective function of photorespiration differred among species and varieties. It was also demonstrated that photorespiration increased under moderate water stress and played an important role in photoprotection in several grape varieties, but in some other varieties, photorespiration decreased severely under slight water stress and attributed less to photoprotection (Guan *et al*. 2004). In this experiment, we found that a higher proportion of electron transport was used in oxygenation and less in carboxylation in Cabernet Sauvignon when the vines encountered a combination of water stress, high temperature and high irradiance. This indicates that photorespiration is important in protecting leaves from photoinhibition in this variety.

Φ_{PSII} under water stress: Φ_{PSII} was higher in well watered plants than in water stressed plants (Fig. 2). After water stress adaptation for 30 days, Φ_{PSII} increased slightly. Compared with that in the morning, Φ_{PSII} of all the three treatments decreased in the afternoon.

All the three treatments had lower Φ_{PSII} under 2 % O_2 than 21 % O_2. As O_2 concentration in reference air decreased from 21 % to 2 %, the electron flow consumed by RuBP oxygenation decreased. Even if this decrease is partially compensated by the increase of the electron flow comsumed by RuBP carboxylation, total electron transport still slightly decreased.

After having been dark-adapted for 20 minutes, F_v/F_m of water-stressed plants was much lower than that of well watered plants in both morning and afternoon, while that of water stress adapted plants was lower than well watered plants and higher than water-stressed plants (Fig. 3*A*). As the index of photodamage state of PSII reaction center, predawn F_v/F_m of all the three treatments sustained high levels with no difference among all the three treatments (Fig. 3*B*). This implied that no chronic photoinhibition occurred under the water stress conditions employed in this experiment.

As compared with the decrease of A_N and apparent P_r, no decreasement was found in gross P_r under water stress. Although Φ_{PSII} and F_v/F_m with dark adaptation for 20 minutes decreased under water stress, predawn F_v/F_m still expressed a high level, which suggested that no photodamage happened under water-stressed plants. As to the electron partitioning, more electrons were consumed by oxygenation and less by carboxylation in the afternoon under water stress. This suggested that photorespiration plays an important role in protecting leaves from photodamage in water stressed Cabernet Sauvignon grape.

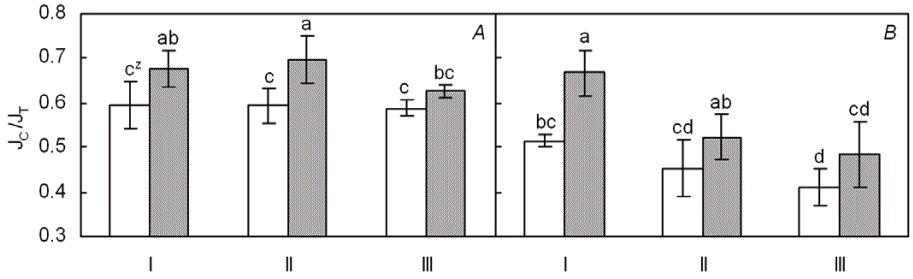

Fig. 4. J_C/J_T of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment at 21 % O_2 (*blank*) and 2 % O_2 (*striped*) in the morning (*A*) and afternoon (*B*). Means ± SE of five replications are shown.
[z] Means for each treatment with different letters are significantly different by Fisher's LSD at $p = 0.05$.

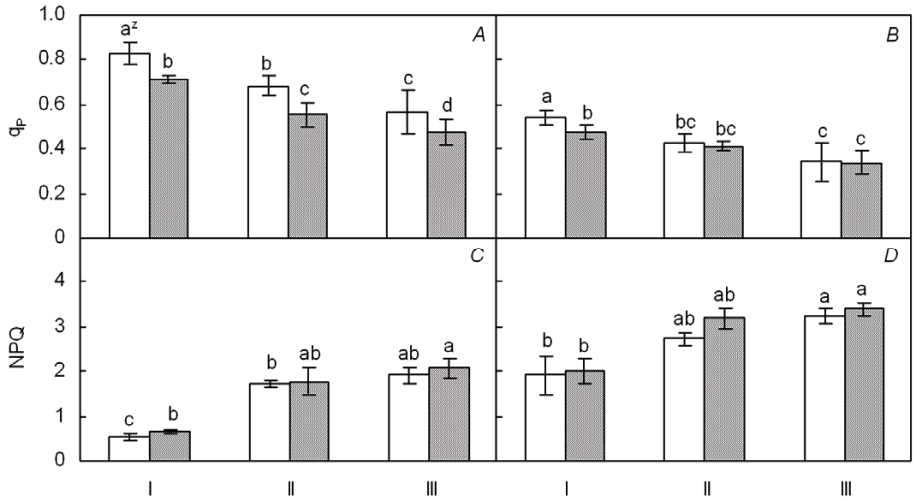

Fig. 5. Photochemical quenching coefficient (q_P) and non-photochemical quenching (NPQ) of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment at 21 % O_2 (*blank*) and 2 % O_2 (*stripe*d) in the morning (*A,C*) and afternoon (*B,D*). Means ± SE of five replications are shown.
[z] Means for each treatment with different letters are significantly different by Fisher's LSD at $p = 0.05$.

Electron partitioning under water stress: Not only J_T, but also J_C and J_O can be estimated by combined measurements of gas exchange and chlorophyll fluorescence, giving that day respiration under light is the same as the mitochondrial respiration in the dark. We can use the ratio J_C/J_T to express the electron partitioning (Zhang and Dang 2006). Fig. 4 shows that J_C/J_T increased under 2 % O_2 compared with 21 % O_2. In the morning, water stress-adapted plants expressed the highest J_C/J_T ratio while the water-stressed plants the lowest. The J_C/J_T ratio was lower in the afternoon than in the morning. Water-stressed and water stress-adapted plants expressed lower J_C/J_T ratio than well watered plants. This implied that although the excitation energy through PSII reaction center decreased and that dissipated by antenna pigments increased, J_C/J_T still sustained a stable level in the morning under water-stress conditions. In the afternoon, more electron transport was consumed through other pathways, mainly by photorespiration, especially in the water-stressed plants. It seemed that water stress adaptation had no impact on electron partitioning. The J_C/J_T ratio was much higher under 2 % O_2 than 21 % O_2 due to the increase of substomatal $[CO_2]/[O_2]$ ratio. It is quite interesting that the J_C/J_T ratio maintained a very high level in the afternoon in well watered plants. This suggests that the decrease of photosynthesis in well watered plants in the afternoon is mainly attributed to the decrease of C_i. In the water-stressed plants, although the J_C/J_T increased in the afternoon under 2 % O_2, it was still much lower than that in the morning, which means that the stimulation of 2 % O_2 to the carboxylation of RuBP was impaired by water stress. There are two possible explanations for this phenomenon: one is that the 2 % O_2 in reference air led to a greater decrease in C_i *via* low g_s under water stress; the other is that water stress inactivated the enzymes and increased the non-stomatal limitation of photosynthesis.

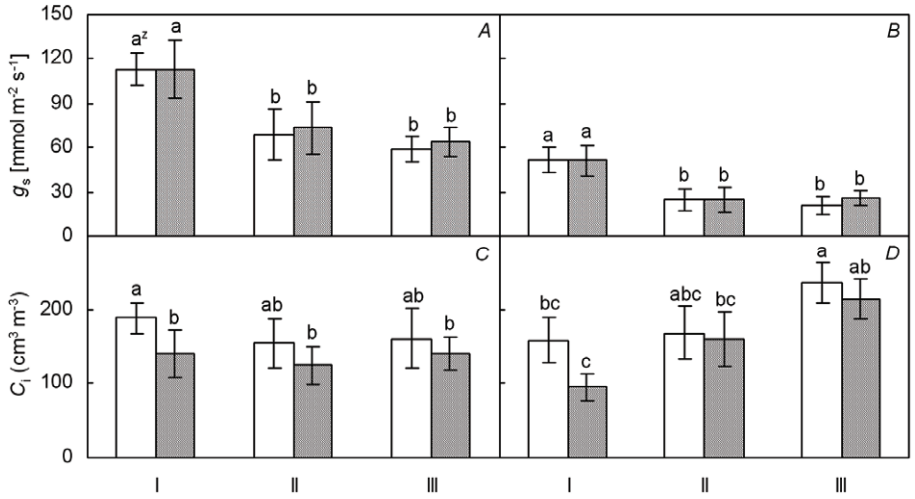

Fig. 6. Stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment at 21 % O_2 (blank) and 2 % O_2 (stripe) in the morning (*A,C*) and afternoon (*B,D*). Means ± SE of five replications are shown.
[z] Means for each treatment with different letters are significantly different by Fisher's LSD at $p = 0.05$.

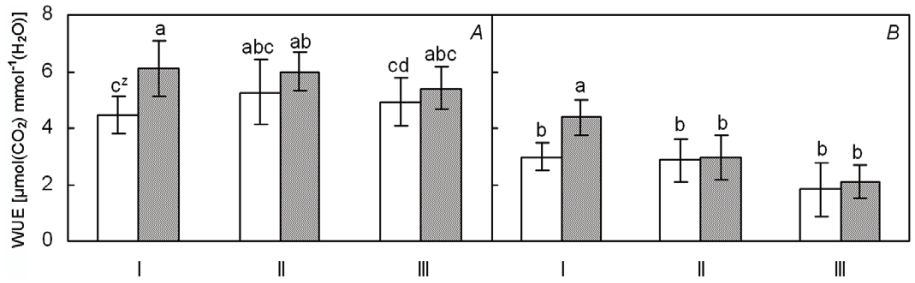

Fig. 7. Water use efficiency (WUE) of potted Cabernet Sauvignon with well watered (I), water stress-adapted (II), and water-stressed without adaptation (III) treatment at 21 % O_2 (*blank*) and 2 % O_2 (*striped*) in the morning (*A*) and afernoon (*B*). Means ± SE of five replications are shown. [z] Means for each treatment with different letters are significantly different by Fisher's LSD at $p = 0.05$ level.

q_P and NPQ: q_P of water-stressed plants was lower than that of well watered plants in both morning and afternoon, which indicates that the excitation pressure of PSII reaction centers was higher in water-stressed plants than that in well watered plants. q_P decreased at 2 % O_2 in well watered plants in both morning and afternoon, indicating that low O_2 led to a higher excitation pressure and an increased risk of photoinhibition. However, low O_2 reference air had no impact on q_P under water stress, mainly because the low g_s depressed the effect of low O_2 in reference air on stomatal O_2 concentration. It is interesting to mention that q_P of water stress-adapted plants in the morning was higher than that of water-stressed plants without adaptation, while this difference disappeared in the afternoon.

As an important photoprotective mechanism, NPQ protects photosynthetic apparatus from photoinhibition by dissipating excitation energy as heat. NPQ was higher in the afternoon than in the morning in all the three treatments (Fig. 5). NPQ in water-stressed plants was much higher than that in well watered plants in both morning and afternoon. Water stress adaptation had no impact on NPQ.

g_s and C_i: Water stress decreased g_s (Fig. 6), and water-stress adaptation had no impact on g_s. Compared with that in the morning, g_s was lower in the afternoon in all the three treatments. As an important indicator of water stress degree, C_i in water-stressed plants was higher in the afternoon than in the morning. The possible explanation could be the patchy stomatal closure caused by water stress (Gunasekera and Berkowith 1992) or the decrease of enzyme activity that retarded the photosynthetic rate even with high C_i. However, A_N expressed no response to O_2 concentration in the afternoon (Fig. 1), which supported the hypothesis that non-stomatal limitation is the main mechanism in inhibition of A_N in the water-stressed plants in the afternoon. The decrease of C_i in water stress-adapted plants in the afternoon implied a release of non-stomatal limitation of photosynthesis. C_i decreased in low O_2 reference air while g_s was not affected.

Although the decrease of photosynthesis is mainly

caused by the decrease of g_s, the decrease in enzyme activity in response to high temperature also contributes to the decrease in photosynthesis. We observed that as the light intensity increased from 1 400 μmol(photon) m^{-2} s^{-1} to 1 500 μmol(photon) m^{-2} s^{-1} at midday, the temperature of both air and leaf increased significantly (the air temperature from 23.6 °C to 30.2 °C, the leaf temperature from 27.9 °C to 34.8 °C). We also found that the photosynthesis showed almost the same values with the morning data in cool afternoon (data not shown), which also suggests the inhibition effect of high temperature on leaf photosynthesis.

Long-term water stress leads to reorganization of antenna pigments and core pigments in PSII (Giardi *et al*. 1996) and higher Rubisco content (Pankovic *et al*. 1999). As a result, water stress-adapted plants sustain higher photosynthesis than plants under water stress without adaptation. We found in this experiment that the non-stomatal limitation of photosynthesis in water-stressed plants was reversed by water-stress adaptation, which suggested that water-stress adaptation increased the resistance of photosynthetic apparatus to water stress.

WUE: The ratio of leaf A_N/E was used as an indicator of WUE, which was higher in the morning than in the afternoon in all the three treatments and was not affected by water stress or water-stress adaptation (Fig. 7). Under 2 % O_2, WUE in all the three treatments increased in the morning. But in the afternoon, WUE in water-stressed treatments showed no response to 2 % O_2. Because of the non-stomatal limitation water-stressed leaves suffered, WUE did not increase significantly under 2 % O_2. Water-stress adaptation increased the photoprotective and alleviated photoinhibition in the morning, avoided the non-stomatal limitation of photosynthesis, but had no impact on WUE.

The data about the effect of water stress and water-stress adaptation on A_N, P_r, photochemical efficiency, and electron partitioning in this experiment suggest that both photorespiration and energy dissipation play important roles in protecting photosynthetic apparatus against photoinhibition under water stress. Water-stress adaptation increased the gross P_r of leaves and alleviated the photoinhibition.

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