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Photoinhibition of *Suaeda salsa* to chilling stress is related to energy dissipation and water-water cycle

N. SUI

Key Laboratory of Plant Stress Research, College of Life Science, Shandong Normal University, Jinan 250014, China

Abstract

To investigate the photoprotection of energy dissipation and water-water cycle, a C_3 euhalophytic herb, *Suaeda salsa* L., was exposed either to chilling temperature (4°C) accompanied by moderate irradiance (600 μmol m^{-2} s^{-1}) (CM) and/or to chilling temperature (4°C) accompanied by low irradiance (100 μmol m^{-2} s^{-1}) (CL). During chilling stress, both the maximal photochemical efficiency of PSII (F_v/F_m) and the oxidizable P700 decreased in *S. salsa* leaves either under CM or CL, which indicated the severe photoinhibition. Relative to F_v/F_m, the oxidizable P700 decreased markedly under CL, which indicated that PSI was more sensitive to CL treatment than PSII. Initial fluorescence, number of closed PSII centers, and nonphotochemical quenching increased under CM, but more markedly under CL in *S. salsa* leaves. Activity of superoxide dismutase and ascorbate peroxidase was higher under CM than that under CL. The production of reactive oxygen species (ROS) decreased first and then increased under both treatments, but the content of $O_2^{\cdot -}$ and H_2O_2 was higher under CL than that under CM after 12 h of chilling stress. These results suggested that photoinhibition in *S. salsa* might be related to the accumulation of reactive oxygen species (ROS) induced by excess energy. The water-water cycle could not dissipate energy efficiently under CL, which caused the great accumulation of ROS.

Additional key words: antioxidant enzyme; chlorophyll fluorescence;halophyte; photosystem I; photosystem II.

Introduction

Low temperature is an abiotic factor limiting the growth and distribution of plants. The combination of low temperature with irradiance has the potential to induce chronic photoinhibition of PSII. This is partly because lower temperature generally reduces the rates of biological reactions, particularly carbon dioxide reduction and photorespiration, and therefore limits the sinks for the absorbed excitation energy (Allen and Ort 2001, Takami *et al.* 2013). Chloroplast membrane is the primary site to be damaged under chilling stress (Kratsch and Wise 2000). Since Lyons and Raison (1970) considered that chilling could impair membrane permeability by the transition of membrane lipids from a liquid-crystalline phase to a gel phase, many experiments have suggested that chilling tolerance is related to the composition and structure of plant membrane lipids (Somerville 1995, Nishida and Murata 1996, Murata and Los 1997). It has been reported that chilling temperature decreased CO_2 assimilation by decreasing the activity of some enzymes and caused the accumulation of excessive reducing power at PSI. PSI photoinhibition was the main factor limiting the subsequent recovery of photosynthesis after chilling stress (Li *et al.* 2004a).

In the long-term evolution of plants, many protective mechanisms were formed to adapt to all kinds of stress. Thermal energy dissipation in the light-harvesting antenna complexes of PSII, measured as nonphotochemical quenching (NPQ), protects the photosynthetic apparatus

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E-mail: suina800101@163.com
Abbreviations: APX – ascorbate peroxidase; AsA – ascorbic acid; Chl – chlorophyll; CL – chilling temperature (4°C) accompanied by low irradiance (100 μmol m^{-2} s^{-1}) ; CM – chilling temperature (4°C) accompanied by moderate irradiance (600 μmol m^{-2} s^{-1}); F_0 – minimal fluorescence yield of the dark-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_s – steady-state fluorescence yield; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; NPQ – nonphotochemical quenching; Q_A – primary quinone electron acceptor of PSII; q_p – photochemical quenching; RC – reaction centre; ROS – reactive oxygen species; SOD – superoxide dismutase; Φ_{PSII} – effective quantum yield of PSII photochemistry.
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from inactivation and damage caused by excessive excitation energy (Horton *et al.* 1994). At chilling temperature under low irradiance, NPQ might be an efficient pathway for plants to alleviate PSII photoinhibition (Xu *et al.* 1999a, Liu *et al.* 2001).

During chilling stress, ROS are produced; this is associated with the photoinhibition of PSI (Sonoike 1996, Sonoike *et al.* 1997, Li *et al.* 2003, 2004b; Zhang *et al.* 2011). Thus, another important mechanism is the water-water cycle, which is referred to the reduction of atmospheric O_2 into water in PSI with the electrons generated from water in PSII and without a net change of O_2. It has been proposed to be an effective protection mechanism under environmental stress (Asada 1999). Superoxide dismutase (SOD) can convert $O_2^{\cdot -}$ to H_2O_2 and O_2, and plays a major role in the defense against superoxide-derived oxidative stress in plant cells. Ascorbate peroxidase (APX) reduces H_2O_2 to water with ascorbic acid (AsA) as a specific electron donor and is the most important plant peroxidase in H_2O_2 detoxification in chloroplasts (Foyer and Halliwell 1976, Noctor and Foyer 1998). Since more than 50% of APX in the chloroplasts is thylakoid bound, the transition of membrane lipids from a liquid crystalline phase to a gel phase can affect the activity of thylakoid-bound APX and consequently affect the scavenging of ROS (Sonoike and Terashima 1994).

The Chenopodiaceae, *Suaeda salsa* L., a C_3 euhalophytic herb native to saline soils, has shown high resistance not only to salinity stress but also to photoinhibition, even when treated with salinity as high as 400 mmol L^{-1} NaCl and exposed to full sunlight (Lu *et al.* 2002). But there is little information on the damaging mechanisms of CL treatment to PSII and PSI in this halophyte. In the present study, we used halophyte, *S. salsa*, to investigate the role of energy dissipation and water-water cycle on PSII and PSI under CM and CL. It seemed that the water-water cycle could not dissipate energy efficiently under CL, which caused the accumulation of ROS more than that under CM. Photosystem photoinhibition in *S. salsa* might be related to the accumulation of ROS. Our results showed that the photoinhibition of *Suaeda salsa* during chilling stress was related to energy dissipation and the water-water cycle.

Materials and methods

Plant culture and treatments: Brown seeds of *S. salsa* were collected during November 2011 in saline inland of the Yellow River Delta (37°25′N, 118°58′E) in Shandong province of China. Dry seeds were stored in a refrigerator at –4°C before being used. Seeds were sown in round plastic pots with drainage holes. There were ten seedlings and 1.0 kg river sand in each pot. The plants were grown in a glasshouse under 14 h of light/10 h of dark with natural light. The temperature in the glasshouse was 28 ± 5°C during the day and 20 ± 3°C at night. Nutrient solution was supplied daily, and the volume applied (200 mL per pot) was in excess of the volume required to saturate the sand, so that some of the solution drained out of the pot with each application. After four weeks, the pots were treated at 4°C for 0, 3, 6, 9, and 12 h either under CM [moderate irradiance of 600 μmol(photon) m^{-2} s^{-1}] or under CL [low irradiance of 100 μmol(photon) m^{-2} s^{-1}]. The treated leaves were then frozen in liquid nitrogen and stored at –80°C until further use for the determinations of antioxidant enzyme activities and the content of reactive oxygen species.

Chlorophyll (Chl) fluorescence was measured using a portable fluorometer (*FMS2*, *Hansatech*, King's Lynn, UK) following the protocol described by van Kooten and Snel (1990). Minimal fluorescence (F_0) with all PSII RCs open was determined by modulated light which was low enough not to induce any significant variable fluorescence (F_v). Maximal fluorescence (F_m) with all RCs closed was determined by 0.8 s saturating light of 8,000 μmol(photon) m^{-2} s^{-1} on a dark-adapted leaf (adapted 30 min in darkness). Then the leaf was illuminated by an actinic light of 500 μmol(photon) m^{-2} s^{-1}. Steady-state fluorescence (F_s) was recorded when the leaf reached steady-state photosynthesis. A second 0.8 s saturating light pulse of 8,000 μmol(photon) m^{-2} s^{-1} was given to determine maximal fluorescence in the light-adapted state (F_m'). F_0' is the initial fluorescence in light adapted leaves, which was measured using a 3 s far red light (6 μmol m^{-2} s^{-1} PFD) when actinic light was turned off. Maximal photochemical efficiency (F_v/F_m) of PSII was expressed as: $F_v/F_m = (F_m - F_0)/F_m$. Nonphotochemical quenching (NPQ) and photochemical quenching (q_p) were calculated as $NPQ = F_m/F_m' - 1$ and $q_p = (F_m' - F_s)/(F_m - F_0')$ according to Schreiber *et al.* (1994), respectively. The second leaf from the top was used for the measurement of the Chl fluorescence.

Oxidizable P700: Oxidation and reduction of P700 was measured at 820 nm with a *Plant Efficiency Analyzer* (*PEA Senior*, *Hansatech*, King's Lynn, UK) as described by Schansker *et al.* (2003). The oxidizable P700 (expressed as a ratio of continuous light-oxidizable P700 in extracted PSI particles/P700 in chloroplasts) was measured under CM and CL.

Activities of antioxidant enzymes: Superoxide dismutase (SOD, EC 1.15.1.1) assay was performed as described by Giannopolitis and Ries (1977). Leaves (0.5 g) without midrib were thoroughly ground with a cold mortar and pestle in an ice bath. The grinding medium was 4 cm^3 of 0.05 M phosphate buffer (pH 7.8), plus homogenizing glass beads. The homogenate was centrifuged at 3,000 × *g* for 15 min at 0–4°C. The supernatant, hereafter referred to as crude SOD extract, was used for determination. The absorbance at 560 nm of the reaction mixture was determined by using a *UV/Vis* spectrophotometer (*UV-1601*,

Shimadzu, Japan). Enzyme activity was calculated as 50% inhibition expressed in U per mg of total protein.

Ascorbate peroxidase (APX, EC 1.11.1.11) activity was determined by following the decrease of absorbance at 290 nm. The reaction mixture contained 50 mM potassium phosphate buffer (pH 7.0), 0.5 mM ascorbate, 0.2 mM H_2O_2, and the suitable volume of enzyme extract (Jimenez *et al.* 1997). Enzyme activity was calculated per mg of total protein in U which represents the amount of enzyme needed to oxide 1 μmol of AsA within 1 min at room temperature.

$O_2^{\cdot-}$ and H_2O_2: $O_2^{\cdot-}$ was measured according to Wang and Luo (1990). Leaves without midrib were thoroughly ground with a cold mortar and pestle in an ice bath. The grinding medium was 0.05 M phosphate buffer (pH 7.8) with homogenizing glass beads. The homogenate was centrifuged at 5,000 × *g* for 10 min at 0–4°C. The supernatant with phosphate buffer (pH 7.8) and 10 mM hydroxylammonium chloride was incubated at 25ºC for 20 min, then 17 mM *p*-aminobenzenesulfonic acid and 7 mM α-naphthylamine were added, and the mixture was incubated at 25ºC for 20 min. Finally, ethyl ether was added into the mixture and the mixture was centrifuged at 1,500 × *g* for 5 min, the water phase was used to determine the absorbance at 530 nm.

H_2O_2 content was determined according to the Sairam and Srivastava (2002). The concentration of H_2O_2 was estimated by measuring the absorbance of the titanium-hydroperoxide complex and using a standard curve plotted with known concentration of H_2O_2.

Statistical analysis: All measurements were performed five times, and the means and calculated standard deviations (SD) were reported.

Results

Photoinhibition of photosystems under chilling stress: Photoinhibition of PSII was estimated by measuring F_v/F_m. Photoinhibition of PSI was reflected by $P700^+$, which was calculated by the transmission at 820 nm. As shown in Fig. 1, F_v/F_m and the oxidizable P700 decreased in *S. salsa* leaves under CM and CL. But F_v/F_m (Fig. 1*A*) and the oxidizable P700 (Fig. 1*B*) decreased more under CL than CM. Simultaneously, after 12 h of chilling stress, F_v/F_m decreased by 15% under CM and 23.9% under CL. The oxidizable P700 decreased by 19.8% under CM and 45.2% under CL. Relative to F_v/F_m under CL, the oxidizable P700 declined markedly, which indicated that PSI was more sensitive to CL than PSII.

PSII activities and energy dissipation: As showed in Fig. 2, F_0, $1 - q_p$, and NPQ in *S. salsa* leaves increased under CM, but they also increased markedly under CL. After 12 h chilling stress, F_0 increased by 30.1% under CM and by 42.2% under CL (Fig. 2*A*). $1 - q_p$ increased 2.0 times under CM and 3.7 times under CL (Fig. 2*B*). NPQ increased 4.0 times under CM and 16.5 times under CL (Fig. 2*C*).

SOD and APX activities: Activity of SOD, one of the key enzymes of water-water cycle, increased first and then decreased under CM and CL treatments (Fig. 3*A*). After 12 h of chilling stress, SOD activity was higher under CM than that under CL. The APX activity under CM and CL also increased first and then declined (Fig. 3*B*). But during chilling stress, APX activity was higher under CM than that under CL. At the end of chilling stress, the SOD activity increased by 22.7% of the original value under CM and declined by 19.4% under CL. The APX activity decreased by 11.2% of the original value under CM and by 45.9% under CL.

The contents of $O_2^{\cdot-}$ and H_2O_2: The production of reactive oxygen species ($O_2^{\cdot-}$, H_2O_2) declined first and then increased under both CM and CL treatments (Fig. 3*C*,*D*). At the end of the chilling stress, the $O_2^{\cdot-}$ content was enhanced by 2.4% of the original value under CM and 24.8% under CL. H_2O_2 contents were reduced by 32.4% under CM and elevated by 40.3% under CL.

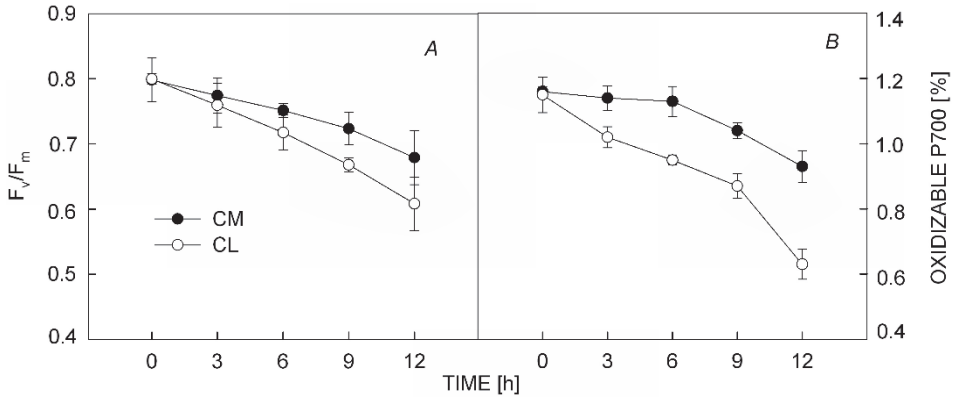

Fig. 1. Effects of chilling stress under moderate (CM) and low irradiation (CL) on the maximal photochemical efficiency of PSII (F_v/F_m) and the oxidizable P700 in *Suaeda salsa* leaves. Each point represents the means ± SD of five measurements on each of five plants.

Discussion

Chilling stress inhibits photosynthesis by the process of photoinhibition (Aro *et al.* 1993, Zhang *et al.* 2011). It results in the scarcity of effective electron acceptors and the accumulation of reducing power on the acceptor side of PSI (Havaux and Davaud 1994, Terashima *et al.* 1994, Sonoike 1996). The activities of PSII and PSI were inhibited significantly in *S. salsa* leaves upon exposure to CL (Fig. 1). PSII is believed to play a key role in leaf photosynthesis in responses to environmental stresses (Baker 1991). Under chilling stress, photosynthetic rate decreased markedly. The lower utilization of light energy results inevitably in an excess of light energy, and consequently PSII becomes over-excited. We demonstrated that PSI was more sensitive to CL than PSII by comparing the ratio of oxidizable P700 and F_v/F_m (Fig. 1). The results showed that 100 μmol m^{-2} s^{-1} PFD was excessive to halophyte *S. salsa* when Calvin cycle was inhibited under low temperature, therefore electrons accumulated in the carriers at the PSI acceptor side. Thus, the significant decrease of the oxidizable P700 could be attributed not only to the limitation of electron acceptors and stromal over-reduction, but probably also to the damage of PSI components (related to the damage of FeS centres) as it has been suggested previously (Inoue *et al.* 1989, Sonoike *et al.* 1995, Sonoike 1996, Tjus *et al.* 1998, Zhang *et al.* 2011).

The direction of F_0 changes depends on the dominant factor between the energy dissipation and the inactivation or damage of PSII. An increase in NPQ could lead to a decrease in F_0 (Ögren and Öquist 1984), while the inactivation or the damage of PSII causes the increase of F_0 (Xu and Wu 1996). We showed that CL treatment damaged PSII reaction centers since F_0 increased greatly during CL (Fig. 2). The extent of PSII photoinhibition is closely correlated with the redox state of Q_A under a range of stress condition (Havaux *et al.* 1991, Li *et al.* 2004b). The relative redox state of Q_A *in vivo* can be estimated as $1 - q_p$ (Qin *et al.* 2011). Result showed that $1 - q_p$ in *S. salsa* leaves increased under both CM and CL, and even more under CL. It suggests that the extent of Q_A reduction was more severe under CL. The xanthophyll cycle-dependent NPQ mechanism constitutes an important protective response to prevent over-reduction of Q_A (Demmig-Adams and Adams 1996). The increase of $1 - q_p$ accompanied by marked increase in NPQ (Fig. 2) suggested that the extent of PSII photoinhibition was closely correlated with the redox state of Q_A (Xu *et al.* 1999).

If excess energy could not be dissipated and CO_2 assimilation was blocked under chilling temperature, PSI RCs were completely reduced to produce triplet P700, which could easily react with O_2 to generate ROS. ROS, such as the superoxide anions ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH^{\cdot}$), are formed in all aerobic cells as byproducts of normal metabolic processes (Asada 1992, Airaki *et al.* 2012), especially under environmental stress, resulting in oxidative damage at the cellular level. Excitation energy that is not used for photochemistry and not dissipated as fluorescence or heat can be transferred to molecular oxygen, creating highly damaging ROS (Apel and Hirt 2004, Foyer *et al.* 1994, Niyogi 1999). On one hand, plants can use O_2 as terminal electron acceptor in both photorespiration and Mehler reaction to protect the chloroplasts from photodamage (Osmond and Grace 1995, Sui *et al.* 2007). On the other hand, the production of ROS might be related to more electrons transported to Mehler reaction caused by the inhibition of the Calvin cycle and photorespiration during chilling stress. Meanwhile, plants contain various nonenzymatic antioxidants, such as ascorbate, glutathione, flavonoids, and carotenoids, and enzymatic antioxidants, such as SOD, APX, and catalase (CAT) (Song *et al.* 2005). Their function is to scavenge properly the toxic ROS and protect the plants from ROS damage (Noctor and Foyer 1998, Song *et al.* 2005,

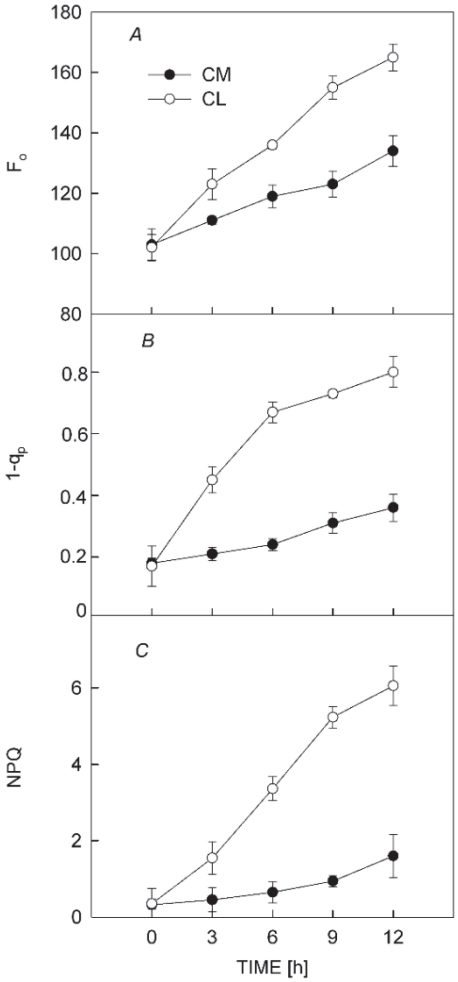

Fig. 2. Changes of minimum fluorescence (F_0), the reduction state of Q_A ($1 - q_p$), and nonphotochemical quenching (NPQ) under moderate (CM) and low irradiation (CL) in *Suaeda salsa* leaves. Each point represents the means ± SD of five measurements on each of five plants.

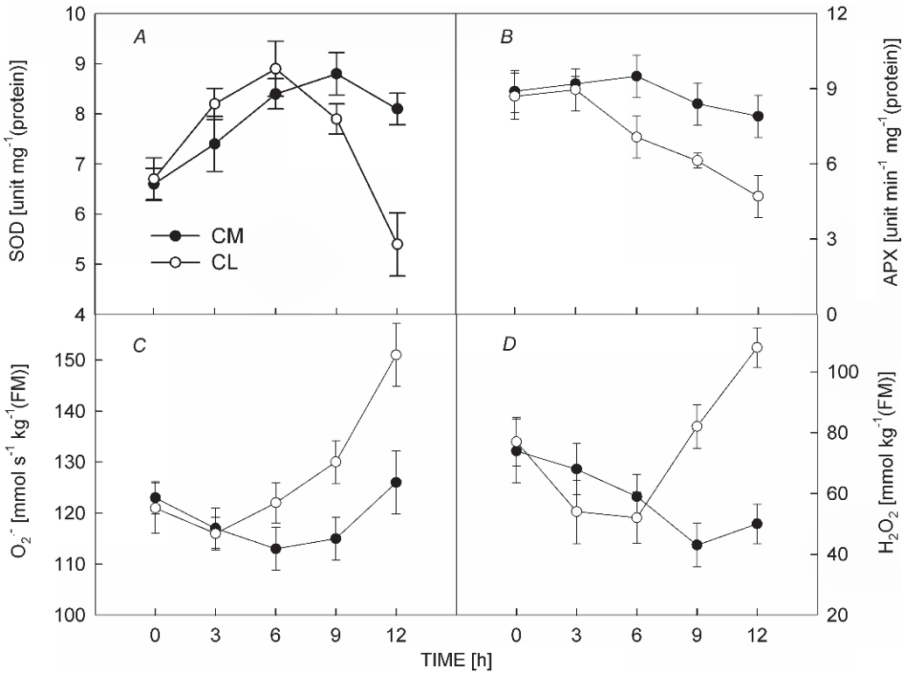

Fig. 3. Changes in superoxide dismutase (SOD) and ascorbate peroxidase (APX) activity, and in superoxide anion radical ($O_2^{\cdot -}$) and H_2O_2 contents under moderate (CM) and low irradiation (CL) in *Suaeda salsa* leaves. Each point represents the means ± SD of five measurements on each of five plants.

Airaki *et al.* 2012). SOD is one of the key enzymes to scavenge ROS produced in active cells. When exposed to CL, water-water cycle seemed not to be affected so much as that under CM (Fig. 3). At low temperature, electron transport chain tends to form $O_2^{\cdot -}$, which could be metabolized by SOD to form H_2O_2. When exposed to chilling stress, the activity of SOD under CM was higher than that under CL (Fig. 3). APX, which eliminates peroxides by converting AsA to dehydroascorbate, is one of the most important enzymes playing a crucial role in eliminating toxic H_2O_2 in plant cells (Foyer *et al.* 1994). APX activity under both CM and CL increased first and then decreased (Fig. 3). But APX activity was higher under CM than that under CL. Consistently, the contents of $O_2^{\cdot -}$ and H_2O_2 were higher under CL than under CM. It seems that $O_2^{\cdot -}$ and H_2O_2 could not be scavenged efficiently under CL owing to the limited SOD and APX activity (Fig. 3). The elevated $O_2^{\cdot -}$ and H_2O_2 contents under CL then probably enhanced the photoinhibition of PSII and PSI (Fig. 1) and decreased the photosynthetic rate.

In conclusion, PSII and PSI was more sensitive to CL than to CM treatment. On the other hand, PSI was more sensitive to CL treatment than PSII. We suggested that the sensitivity of plant to chilling stress depended on the protective mechanisms related both with PSI and PSII, especially, on the energy dissipation and the water-water cycle.

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