Dissipation of excess energy in Mehler-peroxidase reaction in *Rumex* leaves during salt shock

H.-X. CHEN[*], H.-Y. GAO[*,+], S.-Z. AN[**], and W.-J. LI[**]

Department of Plant Sciences, Shandong Agricultural University, Taian, Shandong, 271018, P.R. China[*]
Department of Grassland Sciences, Xinjiang Agricultural University, Urumqi, Xinjiang, 830052, P.R. China[**]

Abstract

By measurement of gas exchange and chlorophyll fluorescence, the effects of salt shock on photosynthesis and the mechanisms to protect photosynthetic machinery against photodamage during salt shock were investigated in leaves of *Rumex* seedlings. Salt shock induced significant decrease in photosynthesis both in 21 and 2 % O_2. In 21 % O_2, quantum yield of photosystem 2 (PS2) electron transport (Φ_{PS2}) decreased slightly and q_P remained constant, suggesting that the excitation pressure on PS2 did not increase during salt shock. In 2 % O_2, however, both Φ_{PS2} and q_P decreased significantly, suggesting that the excitation pressure on PS2 increased during salt shock. NPQ increased slightly in 21 % O_2 whereas it increased significantly in 2 % O_2. The data demonstrated that during salt shock a considerable electron flow was allocated to oxygen reduction in the Mehler-peroxidase reaction (MPR). Under high irradiance and in the presence of saturating CO_2, the susceptibility of PS2 to photoinhibition in salt-shocked leaves was increased when the electron flow to oxygen in MPR was inhibited in 2 % O_2. Hence, MPR is important in photoprotection of *Rumex* seedlings during salt shock.

Additional key words: chlorophyll fluorescence; NaCl; net photosynthetic rate; non-photochemical quenching; oxygen concentration; quantum yield of photosystem 2; stomatal conductance.

Introduction

Cultivated plants frequently cope with stress caused by salt accumulation in the soil or by irrigation with saline water. High exogenous salt concentrations result in ion toxicity and osmotic stress. Under salt stress, photosynthetic capacity is typically declined. So far its underlying mechanism is not well understood. Some studies showed that salt stress inhibited PS2 activity, whereas some other studies stated that the decreased photosynthetic activity was due to decreased conductance to CO_2 diffusion in the mesophyll (Brugnoli and Lauteri 1991, Bethke and Drew 1992).

The decrease in photosynthesis will inevitably result in accumulation of excess photon energy. If not dissipated safely, the excess energy will cause damages of photosynthetic apparatus (Demmig-Adams and Adams 1992). During the course of evolution, plants have developed a number of protective mechanisms to reduce the photodamage. One mechanism is called thermal energy dissipation, which involves the release of photon energy as heat within the antenna pigments (Krause *et al*. 1982). Thermal energy dissipation can be measured by non-photochemical quenching of chlorophyll fluorescence (NPQ). *In vivo*, at least three components can be resolved by analyzing dark relaxation kinetics (Krause and Weis 1991). Another mechanism is the alternative electron transport which can consume the excess electrons. The reduction of oxygen in the Mehler-peroxidase reaction (MPR) has received particular attention. The MPR consists of the Mehler reaction, which is the photoreduction of oxygen by photosystem 1 (PS1) to a superoxide anion radical, followed by the dismutation of this radical by superoxide dismutase to hydrogen peroxide and oxygen. Hydrogen

Received 18 November 2003, *accepted* 23 February 2004.
[+]Author for correspondence: fax: +86 538 8249608, e-mail: gaohy@sdau.edu.cn
Abbreviations: AOS – active oxygen species; F_m – maximal fluorescence in dark adapted state; F_m' – maximal fluorescence in light adapted state; F_s – steady state fluorescence; F_v/F_m – maximal efficiency of PS2 photochemistry; F_v'/F_m' – efficiency of excitation energy capture by open PS2 reaction centres; F_0 – minimal fluorescence; MPR – Mehler-peroxidase reaction; NPQ – non-photochemical quenching; NRD – non-radiative energy dissipation; PCO – photorespiratory carbon oxidation cycle; PCR – photosynthetic carbon reduction cycle; PPFD – photosynthetic photon flux density; q_E – energy-dependent quenching; q_P – photochemical quenching; Φ_{PS2} – quantum yield of PS2 electron transport.
Acknowledgements: We are grateful to the China National Nature Science Foundation (39870604) and State Key Basic Research and Development Plan of China (1998010100) for their financial support of this study

peroxide is then reduced by ascorbate peroxidase (APX) to water, followed by the regeneration of ascorbate by direct reduction of monodehydroascorbate reductase. MPR results in electron flow from PS2 to PS1 (Asada 1999, Makino *et al*. 2002). Therefore, MPR consumes excess electrons and protects against photodamage (Osmond and Grace 1995, Li *et al.* 2003). In addition, MPR contributes to the acidification of intra-thylakoids, which in turn promotes non-radiative dissipation of excess energy. In intact chloroplasts, MPR is important for q_E (Schreiber and Neubauer 1990, Neubauer and Yamamoto 1992). However, some recent studies show that MPR does not support a significant flow of electron transport in a number of species such as grape (Flexas *et al*. 1999), tobacco (Ruuska *et al*. 2000), and tomato (Haupt-Herting and Fock 2002). By contrast, evidence for a significant electron flow in MPR is lacking. Moreover, it is not known whether or not MPR can protect photosynthetic apparatus against damage, because the reduction of molecular oxygen results in the formation of harmful radical species (Asada and Takahashi 1987) and the resulting damage to PS1 and PS2 may far outweigh any potential benefit (Clarke and Johnson 2001).

Most of previous studies on the effects of salt stress on photosynthesis and PS2 photochemistry were performed on salt adapted plants (Morales *et al.* 1992, Sharma and Hall 1992). However, less information is available about the initial responses when plants are subjected to salt shock. These rapid responses may be critically important since they may determine whether or not the plant will survive the rapid environmental changes. Salt shock generally results in dramatic decrease in photosynthesis and as a result, much excess excitation energy will be produced in the chlorophyll antennae. The objective of this study is to examine: (*1*) how the excess photon energy was dissipated; (*2*) whether or not MPR plays an important role in dissipation of excess energy.

To address these questions, seedlings of *Rumex* plants were used. *Rumex*, a hybrid of *Rumex patientia×R. tianschaious*, is a salt-tolerant fodder crop with a high content of leaf protein. In northwest of China, this crop is used in the reclamation of dry and saline soil. The study on this plant may contribute to the understanding of adaptation of plants to salt stress.

Materials and methods

Plants: Field-grown seedlings of *Rumex* were transplanted to pots (15 cm both in diameter and in height) containing 1/2 Hoagland nutrient solution. The solution in the pots was refreshed twice every week. The seedlings experienced natural sunlight (0–1 000 μmol m^{-2} s^{-1}) and temperature (20–28 °C). One week later when the seedlings were acclimated to the transition, the latest fully expanded leaves were used in the experiment.

Salt shock: Attached leaves of *Rumex* seedlings were irradiated by a PPFD of 600 μmol m^{-2} s^{-1}. After steady-state photosynthesis was reached, the Hoagland solution was rapidly replaced by 200 mM NaCl.

Photoinhibitory treatment and recovery: One hour after salt shock, leaves were irradiated to induce photoinhibition by a high PPFD of 1 600 μmol m^{-2} s^{-1} in 21 % oxygen and 2 % oxygen in air (oxygen balanced by N_2). To suppress photorespiration, both treatments were made in the presence of saturating CO_2 (5 000 μmol mol^{-1}). Photoinhibition was assessed by decrease in the ratio of variable fluorescence to maximal fluorescence (F_v/F_m). F_v/F_m was measured 15 min after the leaf was kept in the dark. After photoinhibitory treatment, the leaves were placed at a PPFD of about 20 μmol m^{-2} s^{-1} for recovery.

Measurement of gas exchange was carried out by a portable photosynthesis system *CIRAS-1* (*PP Systems*, UK). Net photosynthetic rate (P_N) and stomatal conductance (g_s) were determined at a CO_2 concentration of 380 μmol mol^{-1}, temperature of about 25 °C, and a PPFD of 600 μmol m^{-2} s^{-1}.

Chlorophyll (Chl) fluorescence was measured with a portable pulse modulated fluorometer (*FMS2*, *Hansatech,* UK) in combination with *CIRAS-1* photosynthesis system. The optic detecting head of the *FMS-2* was placed in the automatic cuvette of *CIRAS-1* with an angle of 45°. Measurement of Chl fluorescence was performed simultaneously with the measurement of gas exchange.

The minimal fluorescence (F_0) with all PS2 reaction centres open was determined at a modulated irradiance which was low enough not to induce any significant variable fluorescence. The maximal fluorescence (F_m) with all reaction centres closed was determined by a 0.8 s saturating irradiance of about 7 000 μmol m^{-2} s^{-1} on dark-adapted leaf. The leaf was then irradiance-adapted by actinic radiation of 600 μmol m^{-2} s^{-1}. After the leaf reached steady state photosynthesis, parameters of gas exchange and fluorescence were recorded. At intervals the steady-state fluorescence (F_s) was recorded and a second 0.8 s saturating PPFD of about 7 000 μmol m^{-2} s^{-1} was given to determine the maximal fluorescence (F_m') in the light-adapted state. The actinic radiation was then turned off for 3 s to determine the minimal fluorescence in the light-adapted state (F_0'). The following fluorescence parameters were calculated: (*1*) q_P, the photochemical quenching coefficient, $q_P = (F_m' - F_s)/(F_m' - F_0')$; (*2*) F_v'/F_m', the efficiency of excitation energy capture by open PS2 reaction centres, $F_v'/F_m' = (F_m' - F_0')/F_m'$; (*3*) Φ_{PS2}, quantum yield of PS2 electron transport in the light-adapted state, $\Phi_{PS2} = (F_m' - F_s)/F_m'$ (Genty *et al*. 1989); (*4*) NPQ, non-photochemical quenching, $NPQ = (F_m - F_m')/F_m'$.

Electron transport rate through PS2 (J_f) was estimated from the fluorescence data according to the following equation:

$$J_f = PPFD \times \Phi_{PS2} \times \alpha,$$

where Φ_{PS2} is the quantum yield of PS2 electron transport (Genty *et al*. 1989), and α is a constant that depends on the molar ratio of PS2/PS1 and the efficiency of absorption of photons by the leaves. α was determined according to Miyake and Yokota (2000). In *Rumex* leaves, α was determined to be 0.38.

The rate of electron transport required to maintain the photosynthetic carbon reduction cycle (PCR) and photorespiratory carbon oxidation cycle (PCO) was calculated from gas exchange according to Caemmerer and Farquhar (1981):

$$J_g = (P_N + R_D)\,(4\,C_c + 8\,\Gamma)/(C_c - \Gamma)$$

where R_D is rate of mitochondrial respiration in the light, C_c is the pressure of CO_2 at site of carboxylation, and Γ is the partial pressure of CO_2 at which the rate of carboxylation of RuBP equals to the rate of photorespiratory evolution of CO_2. R_D and Γ were determined according to the methods of Brooks and Farquhar (1985). C_c was determined by equation: $C_c = C_i - P_N/g_m$, where g_m is mesophyll conductance to CO_2 determined according to Harley *et al*. (1992). In *Rumex* leaves, Γ was determined to be 4.32 Pa and g_m was 0.86 mol m^{-2} s^{-1}. The rate of alternative electron transport was calculated from the following equation:

$$J_a = J_f - J_g$$

Results

In the first 27 min, both P_N and g_s remained constant, indicating that photosynthesis had reached steady state. Upon transferring the roots of *Rumex* seedlings to solution of 200 mM NaCl (27 min after start of experiment), P_N increased immediately and reached the maximal rate 18 min after the start of salt shock (Fig. 1*A*). This increase was thereafter followed by a rapid decrease, and 70 min after the start of salt shock P_N reached its minimum, which accounted for 33.3 % of the original value. Subsequently, P_N recovered to 5.5 μmol m^{-2} s^{-1}. The response of g_s was similar to that of P_N (Fig. 2*A*). Salt shock also caused decrease in Φ_{PS2} (Fig. 1*B*). Comparing the change in Φ_{PS2} with that in P_N showed that the former was not as pronounced as the latter. Hence other electron transport rather than PRC was operating during salt shock. Such electron flow was regarded as the alternative electron transport.

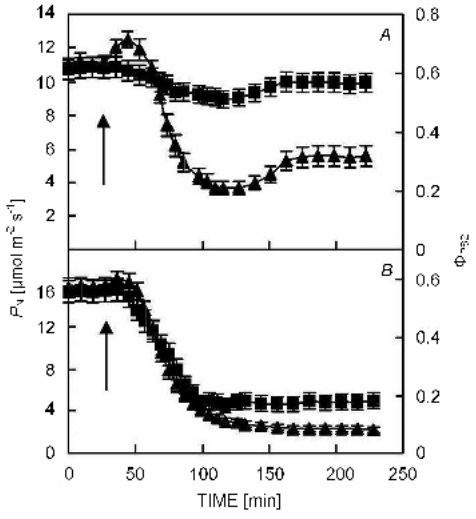

Fig. 1. Time-course of the changes in leaves of *Rumex* seedlings of net photosynthetic rate, P_N (▲) and quantum yield of PS2 electron transport, Φ_{PS2} (■) in response to salt shock in 21 % oxygen (*A*) and 2 % oxygen (*B*). Leaves were irradiated by a PFD of 600 μmol m^{-2} s^{-1}. When leaves reached steady-state photosynthesis, P_N and chlorophyll fluorescence were recorded. Roots of *Rumex* seedlings were transferred to 200 mM NaCl solution after 27 min as the *arrows* indicate. Means ± SE of three replicates.

Time courses of changes in P_N, g_s, and Φ_{PS2} in response to salt shock were further investigated in 2 % oxygen (Figs. 1 and 2*A*). P_N and g_s exhibited similar responses to salt shock, which consisted of three distinct phases. The first phase, characterized by rapid increase in P_N or g_s, was followed by a second phase in which both P_N and g_s decreased dramatically, and then in the third phase they remained unchanged. Φ_{PS2} also decreased dramatically when P_N began to decrease. In 2 % oxygen the decrease in Φ_{PS2} was much more marked than that in 21 % oxygen, suggesting that the alternative electron transport during salt shock depended on oxygen concentration.

Since Φ_{PS2} is determined by the product of q_P and F_v'/F_m', we further investigated the responses of q_P and F_v'/F_m' to salt shock to distinguish which was the determining one (Fig. 2*B,C*). In 21 % oxygen, no change in q_P was observed during salt shock, whereas F_v'/F_m' decreased significantly under salt shock. These results suggested that the change of Φ_{PS2} was due to that of F_v'/F_m'. In 2 % oxygen, however, both q_P and F_v'/F_m' decreased dramatically under salt shock. Obviously, the changes in Φ_{PS2} in 2 % oxygen were due to the changes of both q_P and F_v'/F_m'. Also the time courses of NPQ were modified by salt shock (Fig. 2*D*). In 21 % oxygen, NPQ increased slightly during period in which P_N decreased dramatically and then it decreased to a steady level. In 2 % oxygen, NPQ increased significantly and then remained high.

To examine the distribution of photosynthetic electrons during salt shock, we calculated the electron transport rate through PS2 (J_f) and the electron transport rate required to maintain photosynthetic carbon reduction and photorespiration (J_g). The difference of J_f and J_g represented the rate of alternative electron transport (J_a). Both

J_f and J_g decreased gradually upon salt shock (Fig. 3). J_f was significantly higher than J_g during the period of salt shock. J_a increased rapidly and reached its maximum 70 min after the start of salt shock.

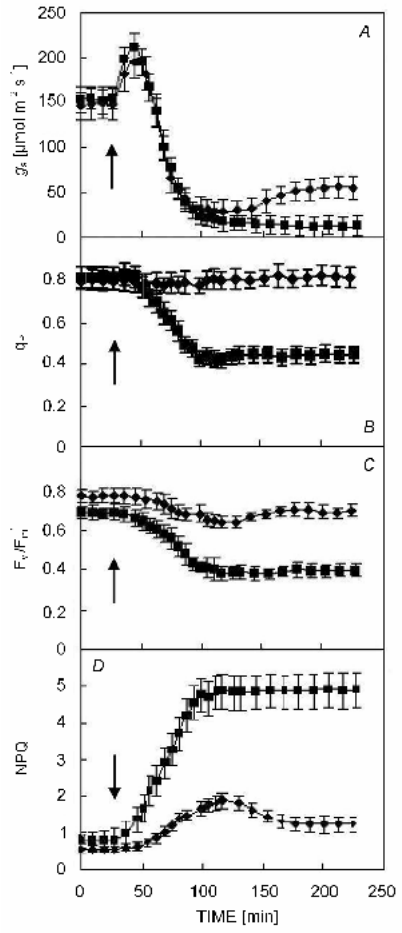

Fig. 2. Time-course of changes in (*A*) stomatal conductance, g_s, (*B*) photochemical quenching, q_P, (*C*) efficiency of excitation energy capture by open PS2 reaction centres, F_v'/F_m', and (D) non-photochemical quenching, NPQ in response to salt shock in 21 % oxygen (♦) and in 2 % oxygen (■) in *Rumex* leaves. Means ± SE of three replicates. The same treatments as in Fig. 1.

Fig. 4 shows the effects of oxygen on the susceptibility of PS2 to photoinhibition. The *Rumex* leaves were irradiated by a high PPFD of 1 600 μmol m^{-2} s^{-1} either in 21 or 2 % oxygen. A significant decrease in F_v/F_m in *Rumex* leaves was observed both in 21 and 2 % oxygen when the *Rumex* leaves were exposed to high irradiance, indicating the occurrence of photoinhibition. However, the decrease in F_v/F_m in 2 % oxygen was more pronounced compared with that in 21 % oxygen. During recovery under dim irradiation, F_v/F_m in 21 % oxygen recovered faster than in 2 % oxygen and it almost recovered within

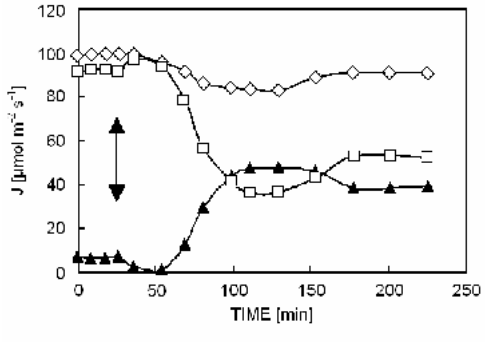

Fig. 3. Time-course of changes in the rate of electron transport from chlorophyll fluorescence (J_f, ◊), gas exchange (J_g, □), and alternative electron flow (J_a, ▲) in leaves of *Rumex* seedlings in response to salt shock. The same treatments as in Fig. 1.

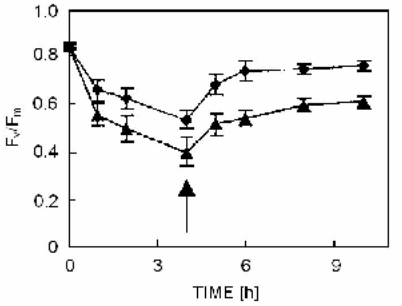

Fig. 4. Changes in the maximal efficiency of PS2 photochemistry (F_v/F_m) in salt-stressed leaves in saturating CO_2 (5 000 μmol mol^{-1}), 21 % oxygen (♦), or 2 % oxygen (▲) during photoinhibitory treatment (1 600 μmol m^{-2} s^{-1}) and subsequent recovery in dim irradiance (20 μmol m^{-2} s^{-1}). *Arrow* shows the end of photoinhibitory treatment and the start of recovery. Means ± SE of four replicates.

6 h. By comparison, F_v/F_m in leaves treated in 2 % oxygen only partially recovered within 6 h. These results demonstrated that under high irradiance photoinhibition was increased when the oxygen concentration was reduced to 2 %. Both photoinhibitory treatments were made in the presence of saturating CO_2. Under these conditions, the photorespiration was largely inhibited and the effect of oxygen concentration on photoinhibition was due to the MPR. Therefore, our results suggest that MPR is important for photoprotection in *Rumex* leaves during salt shock.

Discussion

We found that salt shock resulted in dramatic decrease in P_N, which was accompanied by a parallel decrease in g_s. We also observed that under saturating CO_2, P_N of *Rumex* leaves was not affected by salt shock within the time of investigation (values not shown). These observations suggested that the decrease in P_N was caused by closure of stomata. However, to our surprise, a slight increase in P_N as well as in g_s was observed at the very beginning of salt

shock (Fig. 1). Such phenomenon has not yet been reported and the underlying mechanism was still unclear.

Under normal condition, most of photon energy is used *via* photochemistry and less is dissipated as heat and re-emitted as fluorescence. During salt shock, P_N decreased dramatically (Fig. 1). Such decrease in P_N would potentially result in accumulation of excess energy. The excess energy would over-excite PS2 and thus lead to damages to photosynthetic apparatus (Müller *et al*. 2001). Φ_{PS2} decreased only slightly (Fig. 1*A*), indicating that alternative electron transport was operating under salt shock. In addition, the data demonstrated that such electron flow was dependent on oxygen (Fig. 1). There are two oxygen-dependent processes which can maintain the photosynthetic electron flow: one is photorespiration and the other is oxygen reduction in MPR (Osmond and Grace 1995). The data in Fig. 3 suggest that the alternative electron transport was restricted to MPR. The electron flow in MPR increased as P_N decreased, and reached about 40 % of the total electron flow when P_N decreased to its minimum. Such considerable electron flow in MPR would certainly consume some of the excess electrons and mitigate photoinhibition under high irradiance, as confirmed by much less decrease in F_v/F_m in 21 % oxygen than in 2 % oxygen (Fig. 4). The electron flow to oxygen in MPR was greater than expected from earlier research. Transgenic tobacco with reduced content of ribulose-1,5-bisphosphate carboxylase/oxygenase did not show a significant electron flow allocating to MPR (Ruuska *et al*. 2000). It was thought that the MPR is unlikely to support a significant flow of electron, due to a strong control of MPR in the absence of ATP consumption by PCR and PCO cycles (Badger *et al*. 2000). There is a need to explore why there was a considerable electron flow to oxygen in MPR during salt shock.

Apart from the role as a sink for excess electrons, the MPR was supposed to have an additional role in creating a trans-membrane proton gradient (Schreiber and Neubauer 1990, Neubauer and Yamamoto 1992). In the present study, however, it seemed that MPR did not have such a role. Non-radiative energy dissipation, determined as non-photochemical fluorescence quenching, is closely correlated with trans-membrane proton gradient. A low intra-thylakoid pH is required for the de-epoxidation of violaxanthin to zeaxanthin, which is probably involved in the non-radiative dissipation of excess energy in PS2. Therefore, NPQ can be used as an indicator to reflect the relative changes in ΔpH. If the MPR indeed contributed to generating ΔpH, a higher NPQ could be thus expected. However, we observed in 21 % oxygen that when there was a considerable electron flow, NPQ was much lower than that in 2 % oxygen.

In 21 % oxygen when a large amount of excess electrons was transferred to oxygen in the MPR, q_P remained constant. Thus the excitation pressure over PS2 did not increase although P_N decreased dramatically. In contrast, when the electron flow to oxygen in the MPR was inhibited, although large amount of excess energy was dissipated as heat, the excitation pressure over PS2 still increased significantly as reflected by the decrease in q_P. These results suggested that during salt shock the consumption of electrons in the MPR was preferred to NRD. The operation of MPR would result in formation of active oxygen species (AOS) that are extremely harmful to photosynthetic apparatus. However, plants have evolved a number of scavenging enzymes and antioxidants to cope with AOS (Asada 1999). Under environmental stress, these scavenging enzymes and antioxidants are generally up-regulated, which may bring production of AOS and its quenching into proper balance (Noctor and Foyer 1998, Burritt and Mackenzie 2003).

To summarize, we showed that in *Rumex* leaves during salt shock MPR was enhanced and played an important role in dissipating excess photon energy. However, the enhanced MPR did not contribute to the generation of trans-membrane proton gradient, rather it served as an efficient sink for excess electrons. By draining excess electrons off the electron transport chain, the susceptibility of PS2 to photoinhibition was alleviated. Hence MPR might be important in the adaptation of photosynthetic apparatus to salt shock.

References

Asada, K.: The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons. – Annu. Rev. Plant Physiol. Plant mol. Biol. **50**: 601-639, 1999.

Asada, K., Takahashi, M.: Production and scavenging of active oxygen in photosynthesis. – In: Kyle, D.J., Osmond, C.B., Arntzen, C.J. (ed.): Photoinhibition. Pp. 227-287. Elsevier, Amsterdam – New York – Oxford 1987.

Badger, M.R., Caemmerer, S. von, Ruuska, S., Nakano, H.: Electron flow to oxygen in higher plants and algae: rates and control of direct photoreduction (Mehler reaction) and rubisco oxygenase. – Phil. Trans. roy. Soc. London B **355**: 1433-1446, 2000.

Bethke, P.C., Drew, M.C.: Stomatal and nonstomatal components to inhibition of photosynthesis in leaves of *Capsicum annuum* during progressive exposure to NaCl salinity. – Plant Physiol. **99**: 219-226, 1992.

Brooks, A., Farquhar, G.D.: Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Estimates from gas-exchange measurements on spinach. – Planta **165**: 397-406, 1985.

Brugnoli, E., Lauteri, M.: Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt tolerant (*Gossypium hirsutum* L.) and salt sensitive (*Phaseolus vulgaris* L.) C_3 non-halophytes. – Plant Physiol. **95**: 628-635, 1991.

Burritt, D.J., Mackenzie, S.: Antioxidant metabolism during acclimation of *Begonia×erythrophylla* to high light levels. –

Ann. Bot. **91**: 783-794, 2003.

Caemmerer, S. von, Farquhar, G.D.: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. – Planta **153**: 376-387, 1981.

Clarke, J.E., Johnson, G.N.: *In vivo* temperature dependence of cyclic and pseudocyclic electron transport in barley. – Planta **212**: 808-816, 2001.

Demmig-Adams, B., Adams, W.W., III: Photoprotection and other response of plants to high light stress. – Annu. Rev. Plant Physiol. Plant mol. Biol. **43**: 599-626, 1992.

Flexas, J., Badger, M., Chow, W.S., Medrano, H., Osmond, C.B.: Analysis of the relative increase in photosynthetic O_2 uptake when photosynthesis in grapevine leaves is inhibited following low night temperatures and/or water stress. – Plant Physiol. **121**: 675-684, 1999.

Genty, B., Briantais, J.-M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. biophys. Acta **990**: 87-92, 1989.

Harley, P.C., Loreto, F., di Marco, G., Sharkey, T.D.: Theoretical considerations when estimating the mesophyll conductance to CO_2 flux by analysis of the response of photosynthesis to CO_2. – Plant Physiol. **98**: 1429-1436, 1992.

Haupt-Herting, S., Fock, H.P.: Oxygen exchange in relation to carbon assimilation in water-stressed leaves during photosynthesis. – Ann. Bot. **89**: 851-859, 2002.

Krause, G.H., Vernotte, C., Briantais, J.-M.: Photoinduced quenching of chlorophyll fluorescence in intact chloroplast and algae. Resolution into two components. – Biochim. biophys. Acta **679**: 119-124, 1982.

Krause, G.H., Weis, E.: Chlorophyll fluorescence and photosynthesis: the basics. – Annu. Rev. Plant Physiol. Plant mol. Biol. **42**: 313-349, 1991.

Li, X.G., Meng, Q.W., Jiang, G.Q., Zou, Q.: The susceptibility of cucumber and sweet pepper to chilling under low irradiance is related to energy dissipation and water-water cycle. – Photosynthetica **41**: 259-265, 2003.

Makino, A., Miyake, C., Yokota, A.: Physiological function of the water-water cycle (Mehler reaction) and the cyclic electron flow around PSI in rice leaves. – Plant Cell Physiol. **43**: 1017-1026, 2002.

Miyake, C., Yokota, A.: Determination of the rate of photoreduction of O_2 in the water-water cycle in watermelon leaves and enhancement of the rate by limitation of photosynthesis. – Plant Cell Physiol. **41**: 335-342, 2000.

Morales, F., Abadía, A., Gomez-Aparisi, J., Abadía, J.: Effects of combined NaCl and $CaCl_2$ salinity on photosynthetic parameters of barley grown in nutrient solution. – Physiol. Plant. **86**: 419-426, 1992.

Müller, M., Li, X.P., Niyogi, K.K.: Non-photochemical quenching. A response to excess light energy. – Plant Physiol. **125**: 1558-1566, 2001.

Neubauer, C., Yamamoto, H.Y.: Mehler-peroxidase reaction mediates zeaxanthin formation and zeaxanthin-related fluorescence quenching in intact chloroplasts. – Plant Physiol. **99**: 1354-1361, 1992.

Noctor, G., Foyer, C.H.: Ascorbate and glutathione: Keeping active oxygen under control. – Annu. Rev. Plant Physiol. Plant mol. Biol. **49**: 249-279, 1998.

Osmond, C.B., Grace, S.C.: Perspective on photoinhibition and photorespiration in the field: quintessential inefficiencies of the light and dark reactions of photosynthesis. – J. exp. Bot. **46**: 1351-1362, 1995.

Ruuska, S.A., Bagder, M.R., Andrews, T.J., Caemmerer, S. von: Photosynthetic electron sinks in transgenic tobacco with reduced amounts of Rubisco: Evidence for significant Mehler reaction. – J. exp. Bot. **51**: 357-368, 2000.

Schreiber, U., Neubauer, C.: O_2-dependent electron flow, membrane energization and the mechanism of non-photochemical quenching of chlorophyll fluorescence. – Photosynth. Res. **25**: 279-293, 1990.

Sharma, P.K., Hall, D.O.: Changes in carotenoid composition and photosynthesis in sorghum under high light and salt stress. – J. Plant Physiol. **140**: 661-666, 1992.