Factors limiting photosynthetic recovery in sweet pepper leaves after short-term chilling stress under low irradiance

X.-G. LI[*,**], X.-M. WANG[***], Q.-W. MENG[*,+], and Q. ZOU[*]

College of Life Sciences, Shandong Agricultural University, Tai'an, Shandong, 271018, P. R. China[*]
High-Tech Research Center, Crop Institute, Shandong Academy of Agricultural Sciences, Ji'nan, Shandong, 250100, P. R. China[**]
College of Population, Resources and Environment, Shandong Normal University, Ji'nan, Shandong, 250014, P. R. China[***]

Abstract

The effects of chilling treatment (4 °C) under low irradiance, LI (100 μmol m^{-2} s^{-1}) and in the dark on subsequent recovery of photosynthesis in chilling-sensitive sweet pepper leaves were investigated by comparing the ratio of quantum yields of photosystem (PS) 2 and CO_2 assimilation, Φ_{PS2}/Φ_{CO2}, measured in normal air (21 % O_2, NA) and low O_2-air (2% O_2, LOA), and by analyzing chlorophyll (Chl) *a* fluorescence parameters. Chilling treatment in the dark had little effect on F_v/F_m and Φ_{PS2}/Φ_{CO2}, but it caused the decrease of net photosynthetic rate (P_N) under saturating irradiance after 6-h chilling treatment, indicating that short-term chilling alone did not induce PS2 photoinhibition. Furthermore, photorespiration and Mehler reaction also did not obviously change during subsequent recovery after chilling stress in the dark. During chilling treatment under LI, there were obvious changes in F_v/F_m and Φ_{PS2}/Φ_{CO2}, determined in NA or LOA. F_v/F_m could recover fully in 4 h at 25 °C, and Φ_{PS2}/Φ_{CO2} increased at the end of the treatment, as determined in both NA and LOA. During subsequent recovery, Φ_{PS2}/Φ_{CO2} in LOA decreased faster than in NA. Thus the Mehler reaction might play an important role during chilling treatment under LI, and photorespiration was an important process during the subsequent recovery. The recovery of P_N under saturating irradiance determined in NA and LOA took about 50 h, implying that there were some factors besides CO_2 assimilation limiting the recovery of photosynthesis. From the progress of reduced P700 and the increase of the Mehler reaction during chilling under LI we propose that active oxygen species were the factors inducing PS1 photoinhibition, which prevented the recovery of photosynthesis in optimal conditions because of the slow recovery of the oxidizable P700.

Additional key words: *Capsicum*; chilling; chlorophyll fluorescence; Mehler reaction; P700; photoinhibition; photorespiration; photosystem 2.

Introduction

Many tropical and subtropical plants are sensitive to chilling. Chilling stress leads to a marked reduction of photosynthesis (Wise and Naylor 1987). Chilling under irradiation is harmful to plants, because CO_2 assimilation is retarded to a larger extent than energy absorption and electron flow, and the balance between energy absorption and utilization is disturbed (Wise 1995, Huner *et al.* 1998). The effects of chilling stress on photosynthesis mostly come from the results of chilling treatment accompanied by strong irradiance, and photosystem (PS) 2 reaction centres are commonly damaged, inducing extreme PS2 photoinhibition (Martin *et al.* 1981, Eamus 1987, Aro *et al.* 1993, Barber 1995). In contrast, in chilling-sensitive plants such as cucumber and tomato, PS1 rather than PS2 was proposed to be the primary target for photoinhibition both *in vitro* (Baba *et al.* 1995, 1996, Tjus *et al.* 1998) and *in vivo* (Havaux and Davaud 1994, Terashima *et al.* 1994, Sonoike *et al.* 1995) during chilling stress under

Received 1 December 2003, *accepted* 13 April 2004.
[+]Author for correspondence; fax: +86 538 8226399, e-mail: qwmeng@sdau.edu.cn
Abbreviations: F_v/F_m – maximal photochemical efficiency of PS2; LOA – low O_2 air (2 % O_2); NA – normal air (21 % O_2); P700 – reaction centre chlorophyll of PS1; PFD – photon flux density; P_N – net photosynthetic rate; PS – photosystem; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; Φ_{CO2} – quantum efficiency of CO_2 assimilation; Φ_{PS2} – relative quantum efficiency of PS2 electron transport.
Acknowledgement: This research was supported by the State Key Basic Research and Development Plan of China (G1998010100), the Natural Science Foundation of China (30370854).

irradiation. Some reports suggested that the primary target of chilling stress was the thylakoid membrane (Kratsch and Wise 2000) or some enzymes involved in the Calvin cycle (Krause 1994, Kingston-Smith *et al.* 1997, Huner *et al.* 1998). This implies that the effects of chilling stress on photosynthetic organelles were related to many factors. It is difficult to deduce which factor alone caused the decline of photosynthesis upon exposure to chilling. After chilling stress, factors limiting photosynthetic recovery under optimal conditions might exactly reflect the damage site and the damage extent in chloroplast.

On one hand, plants can use oxygen as a terminal electron acceptor in both photorespiration and in Mehler reaction to protect the chloroplasts from photodamage (Osmond and Grace 1995, Li *et al.* 2003). On the other hand, the production of active oxygen species might be related to injury during chilling under irradiance (Terashima *et al.* 1998, Aroca *et al.* 2001, Li *et al.* 2003). Active oxygen species are produced during chilling stress because enzyme activity in the Calvin cycle is slowed down, and the $NADP^+$ supplement to accept electrons from the electron transport chain is restricted, leading to excess energy absorption by oxygen. There are three main approaches to diminish photooxidation during chilling stress: avoiding production of active oxygen species by diminishing electron transport, dissipating excess energy as heat *via* violaxanthin de-epoxidation (Liu *et al.* 2001), and scavenging active oxygen species (Wise 1995).

Although there have been several attempts to compare the chilling effect under irradiation with the chilling effect in the dark (Peeler and Naylor 1988), in most cases chilling treatment has been applied either in the dark or under strong irradiance. The aim of this study was to elucidate factors limiting the subsequent recovery of photosynthesis in chilling-sensitive sweet pepper after short-term chilling treatment under a weak irradiance of 100 μmol m^{-2} s^{-1} photon flux density (PFD) compared with dark treatment. After chilling treatment under irradiance, the oxidizable P700 required a long time to recover. The Mehler reaction and photorespiration seemed to have different roles in different stages.

Materials and methods

Plants: Sweet pepper (*Capsicum annuum* L., line 156) plants were grown at 25–30/15–20 °C (day/night) under 14-h photoperiod (300–400 μmol m^{-2} s^{-1} PFD) in a greenhouse. Seeds were first germinated between moistened filter paper at 25 ºC for 3 d. Sprouted burgeons were then planted in 13.5 cm-diameter plastic pots (one plant per pot) filled with sterilized soil. When the fifth leaf was fully developed, the plants were used for the experiment.

Chilling treatment in the dark was applied by incubating the plants in a growth chamber maintained at 4 °C for the desired time. For the chilling stress under irradiation, fluorescent lamps provided 100 μmol m^{-2} s^{-1} PFD (LI) at 4 ºC. Values of PFD were measured at leaf level using the photometer *Li-188B* (*Li-Cor*, USA). Attached leaves were used to monitor the subsequent recovery.

Chlorophyll (Chl) fluorescence and photosynthesis: Recovery of photosynthetic parameters after 6-h chilling treatment was monitored at 25 °C under irradiance of 100 μmol m^{-2} s^{-1}. Before determination, photosynthesis of the chilling-treated plants was induced by LI at 25 °C for about 30 min, and then induced by irradiance of 400 μmol m^{-2} s^{-1} PFD for 15 min. Chl fluorescence and net photosynthetic rate (P_N) were measured simultaneously using a pulse-amplitude modulated fluorometer *FMS2* (*Hansatech*, England) and a portable CO_2 analyzer *CIRAS-1* (*PP System*, England). Minimum florescence (F_0) was recorded after dark adaptation for more than 2 h. Maximum fluorescence (F_m) was obtained by applying a 0.8-s saturating pulse (6 000 μmol m^{-2} s^{-1} PFD). The maximum quantum yield of PS2 photochemistry was calculated as $F_v/F_m = (F_m - F_0)/F_m$. The relative quantum efficiency of PS2 electron transport (Φ_{PS2}) and the quantum efficiency of CO_2 assimilation (Φ_{CO2}) were measured according to the methods of Genty *et al.* (1989) and Fryer *et al.* (1998).

In order to analyze change in photorespiration during the recovery period, P_N was measured both in normal air (NA) and in 2 % O_2 air (LOA) according to Farquhar and Sharkey (1982).

P700 *in vivo*: The absorption change around 820 nm due to P700 oxidation *in vivo* was measured using a pulse-modulated system (*PAM 101/102*; *Walz*, Effeltrich, Germany) (Endo *et al.* 1999).

Results

Effect of chilling on PS2 photoinhibition: F_v/F_m in sweet pepper leaves decreased gradually during 6 h of chilling treatment under LI and recovered completely within 4 h when plants were transferred to optimal conditions (25 °C and 100 μmol m^{-2} s^{-1} PFD) (Fig. 1), which indicated that short-term chilling under LI did not cause severe PS2 photoinhibition. F_v/F_m of sweet pepper treated at 4 °C in the dark did not show much change, which implied that low temperatures *per se* did not deteriorate PS2.

Effect of chilling on oxidizable P700: The redox state of P700 can be reflected by absorbance at 820 nm (Endo *et al.* 1999, Eichelmann and Laisk 2000). During chilling under LI, the amount of oxidizable P700 in sweet pepper leaves was obviously affected (Fig. 2). At the end of the 6-h chilling, the oxidizable P700 content decreased by about 59 %. The oxidizable P700 took about 50 h to recover completely under optimal conditions. However, chilling in the dark had little effect on oxidizable P700 and its recovery (Fig. 2).

Recovery of photosynthesis after chilling: P_N decreased obviously after 6 h of chilling treatment under LI, and its recovery took about 50 h (Fig. 3*B*). However, P_N decreased less after chilling in the dark than under LI; its recovery only took about 8 h (Fig. 4*B*). This implies that chilling stress might inhibit the activity of some enzymes involved in the Calvin cycle (Krause 1994, Leegood and Edwards 1996, Huner *et al.* 1998), and these enzymes required about 8 h to recover their activity. In addition, after chilling treatment under LI there might be some other factors limiting the recovery of photosynthesis besides enzyme activity since photosynthesis requires a long time to recover.

Change of Mehler reaction and photorespiration: In order to study the changes of Mehler reaction and photo-

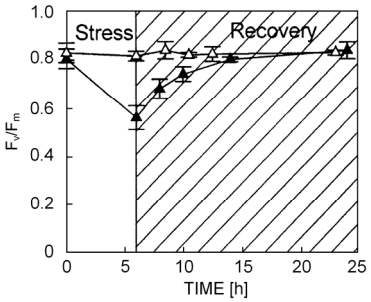

Fig. 1. Responses of F_v/F_m to chilling treatment and subsequent recovery. Subsequent recovery was conducted under 25 °C and 100 μmol m^{-2} s^{-1} PFD. ▲, chilling treatment under low irradiance; Δ, chilling treatment in the dark. Means ± SD of 5 measurements on separate leaves.

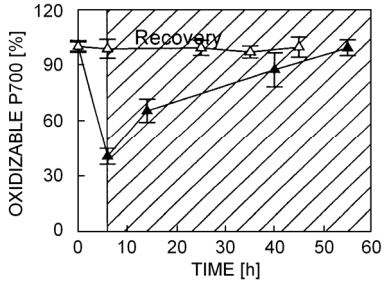

Fig. 2. Effect of chilling treatment (4 °C) under an irradiance of 100 μmol m^{-2} s^{-1} on the amount of oxidizable P700 in sweet pepper leaves. ▲, chilling treatment under irradiance; Δ, chilling treatment in the dark. Leaves were dark adapted for 15 min prior to measurement. Means ± SD of 3 measurements on separ ate leaves.

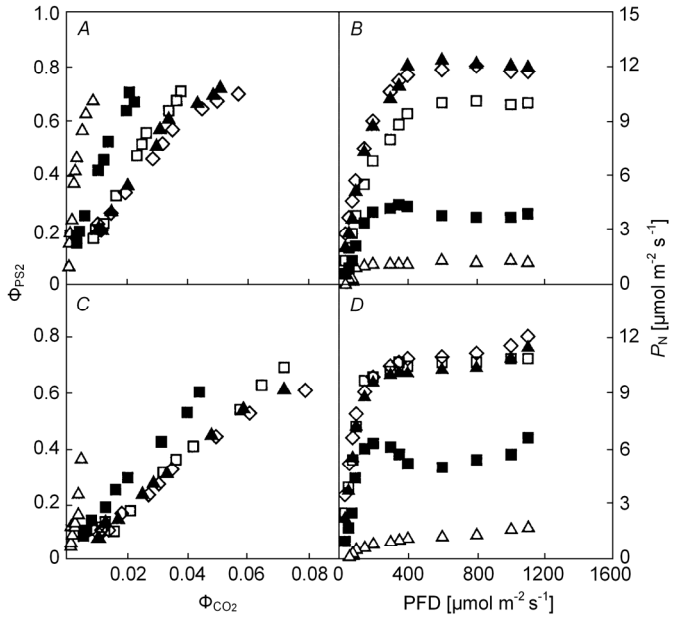

Fig. 3. Responses of the relationship between Φ_{PS2} and Φ_{CO2} and P_N–PFD curves to chilling treatment under irradiance and subsequent recovery. Both chlorophyll *a* and P_N were measured under 25 °C. Subsequent recovery was conducted at 25 °C under 100 μmol m^{-2} s^{-1} PFD. (*A*) The relationship between Φ_{PS2} and Φ_{CO2} determined in NA. (*B*) P_N–PFD curves determined in NA. (*C*) The relationship between Φ_{PS2} and Φ_{CO2} determined in LOA. (*D*) P_N–PFD curves determined in LOA. ▲, CK; Δ, post-treatment; ■, recovery for 8 h; □, recovery for 32 h; ◊, recovery for 49 h.

respiration during the subsequent recovery, Φ_{PS2}/Φ_{CO2} was measured in normal air (21 % O_2, NA) and in low oxygen air (2 % O_2, LOA). After chilling under LI, Φ_{PS2}/Φ_{CO2} measured in both NA and LOA increased significantly after chilling stress under LI (Fig. 3*A,C*). However, the complete recovery of the ratio in LOA took more than 8 h, which was shorter than in NA, where it required about 50 h. The difference in ratio between NA and LOA did not change obviously during chilling under irradiation (Fig. 3*A,C*), but it increased greatly in the first 8 h of subsequent recovery, and it took less than 40 h to recover completely. In contrast, chilling treatment in the dark induced no change of Φ_{PS2}/Φ_{CO2} determined in NA and LOA, even during subsequent recovery (Fig. 4*A,C*). After chilling treatment in the dark, the response curve of P_N to PFD recovered completely in 8 h (Fig. 4*B,D*).

Discussion

Photoinhibition of PS1 and PS2 under chilling stress: Upon exposure to chilling temperature, LI induced slight PS2 photoinhibition of sweet pepper without damage to PS2 reaction centres (Li *et al.* 2003) (Fig. 1).

In cucumber leaves, PS2 is less sensitive to chilling under LI than under high irradiance (Terashima *et al.* 1994, 1998, Li *et al.* 2003). Chilling treatment under LI caused an accumulation of reducing power on the acceptor side of PS1 (Havaux and Davaud 1994, Terashima *et al.* 1994, Sonoike 1996, Li *et al.* 2003) in sweet pepper leaves (Fig. 2). Since CO_2 assimilation was inhibited (Fig. 3*B*), the limited electron acceptors caused the increase of stromal over-reduction, which would contribute to the accumulation of active oxygen species and electron recombination of P700 (Li *et al.* 2003). Under optimal conditions, slower recovery of oxidizable P700, which required about 50 h, suggests that stromal over-reduction was not the main factor limiting its recovery, and PS1 might be severely damaged. This could be related to the damage of FeS centres as has been suggested by Sonoike *et al.* (1995), Sonoike (1996), and Tjus *et al.* (1998).

Limitations of photosynthetic recovery: Some reports showed that the main effect of chilling temperatures on plants was to increase their sensitivity to photoinhibition, primarily due to restricted photosynthetic energy utilization through limiting the activity of the enzymes involved in carbon metabolism (Krause 1994, Leegood and Edwards 1996, Huner *et al.* 1998). Decreases in photosynthesis after chilling under irradiation and in the dark have been attributed to a loss of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity (Kingston-Smith *et al.* 1997). The decrease of P_N after chilling treatment (Fig. 4*B*) implied that some Calvin cycle enzymes might be the primary factors affecting photosynthesis recovery in sweet pepper leaves. These enzymes could completely recover their activity within 8 h under optimal conditions (Fig. 4*B*). These enzymes recovered their activity faster relative to that of P_N *via* chilling treatment under irradiation. This suggests that the recovery of P_N was limited by some other factors besides Calvin cycle enzymes (Fig. 3*B*); the most likely candidate was photoinhibition of PS1 (Fig. 2) (Baba *et al.* 1996, Sonoike 1996, Terashima *et al.* 1998, Tjus *et al.* 1998).

The roles of Mehler reaction and photorespiration: Our results show that the Calvin cycle was inhibited under chilling treatment. This implies that more electrons are transported to some pathways other than those for CO_2 assimilation such as pathways for Mehler reactions and photorespiration.

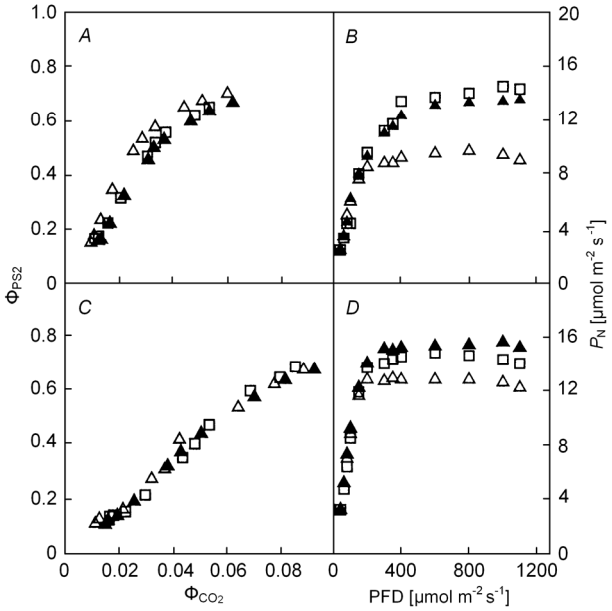

Fig. 4. Responses of the relationship between Φ_{PS2} and Φ_{CO2} and P_N–PFD curves to chilling treatment in the dark and subsequent recovery. Both chlorophyll fluorescence and the photosynthesis rate were measured at 25 °C. Subsequent recovery was conducted at 25 °C and 100 μmol m^{-2} s^{-1} PFD. (*A*) The relationship between Φ_{PS2} and Φ_{CO2} determined in NA. (*B*) P_N–PFD curves determined in NA. (*C*) The relationship between Φ_{PS2} and Φ_{CO2} determined in LOA. (*D*) P_N–PFD curves determined in LOA. ▲, CK; Δ, post-treatment; □, recovery for 8 h.

At the end of chilling treatment under LI, the increase of Φ_{PS2}/Φ_{CO2} in NA (Fig. 3*A*) suggests that Mehler reaction occurred. The Mehler reaction might alleviate the sensitivity to photoinhibition (Savitch *et al.* 2000) during chilling treatment under irradiation, and it had a minor effect on subsequent recovery (Fig. 3*C*). During chilling under irradiation, on one hand, Mehler reaction consumed excess photon energy; on the other hand, the Mehler

reaction might cause accumulation of active oxygen species since the $NADP^+$ supplement to accept electrons from the electron transport chain was restricted. Hence active oxygen species have the potential to damage PS1 and induce PS1 photoinhibition (Fig. 2) (Asada 1996, Terashima *et al.* 1998, Li *et al.* 2003).

Although sweet pepper is a C_3 plant, the protection of photorespiration was ineffective to chill-induced photoinhibition in sweet pepper leaves (Fig. 3*A,C*) during 6-h chilling under LI. This might be related to the concurrent loss of RuBPCO carboxylase activity mirrored by a decline in oxygenase activity and therefore a reduction in the photorespiration sink for electrons (Kozaki and Takeba 1996, Kingston-Smith *et al.* 1997, Osmond and Grace 1997, Streb *et al.* 1998, Allen and Ort 2001). Thus photorespiration might act as an effective electron sink to distribute the electrons flowing to CO_2 during subsequent recovery (Fig. 3*A,C*). In this way, photorespiration could reduce the excited pressure on PS2 and/or PS1 to protect them from photoinhibition or damage.

Our prior results (Li *et al.* 2003) showed that the reduction of oxidizable P700 is mainly caused by the stromal over-reduction in sweet pepper leaves upon exposure to chilling under LI. During the recovery, with the recovery of RuBP carboxylase activity the activity of RuBP oxygenase might also recover to shunt the electrons which flow to CO_2. Under such conditions, photorespiration rate was high during the primary stage of the recovery. However, when the RuBP carboxylase activity completely recovered, photorespiration declined to its normal rate. The higher activity of photorespiration does not last as long as the photosynthesis recovery. This shows that the main factor limiting the photosynthesis recovery was not photorespiration, but the damage of the PS1 reaction centres. The repair of PS1 reaction centres was a slow process. However, short-term chilling treatment in the dark seems to have little effect on Mehler reaction and photorespiration during both chilling treatment and subsequent recovery.

In conclusion, we propose that CO_2 assimilation was the main limiting factor during subsequent recovery of photosynthesis after chilling in the dark, and PS1 photoinhibition was the main factor limiting the subsequent recovery after chilling treatment under irradiation. It can also be deduced that the Mehler reaction played an important role during chilling under irradiation and photorespiration played an important role during the subsequent recovery.

References

Allen, D.J., Ort, D.R.: Impacts of chilling temperatures on photosynthesis in warm-climate plants. – Trends Plant Sci. **6**: 36-42, 2001.

Aro, E.M., Virgin, I., Andersson, B.: Photoinhibition of photosystem II. Inactivation, protein damage and turnover. – Biochim. biophys. Acta **1143**: 113-134, 1993.

Aroca, R., Irigoyen, J.J., Sanchez-Diaz, A.: Photosynthetic characteristic and protective mechanisms against oxidative stress during chilling and subsequent recovery in two maize varieties differing in chilling sensitivity. – Plant Sci. **161**: 719-726, 2001.

Asada, K.: Radical production and scavenging in the chloroplasts. – In: Baker, N.R. (ed.): Photosynthesis and the Environment. Pp. 123-150. Kluwer Academic Publishers, Dordrecht – Boston – London 1996.

Baba, K., Itoh, S., Hastings, G., Hoshina, S.: Photoinhibition of Photosystem I electron transfer activity in isolated Photosystem I preparations with different chlorophyll contents. – Photosynth. Res. **47**: 121-130, 1996.

Baba, K., Itoh, S., Hoshina, S.: Degradation of photosystem I reaction center proteins during photoinhibition in vitro. – In: Mathis, P. (ed.): Photosynthesis: from Light to Biosphere. Vol. II. Pp. 179-182. Kluwer Academic Publishers, Dordrecht – Boston – London 1995.

Barber, J.: Molecular basis of the vulnerability of photosystem II to damage by light. – Aust. J. Plant Physiol. **22**: 201-208, 1995.

Eamus, D.: Influence of preconditioning upon the changes in leaf conductance and leaf water potential of soybean, induced by chilling, water stress and abscisic acid. – Aust. J. Plant Physiol. **14**: 331-339, 1987.

Eichelmann, H., Laisk, A.: Cooperation of photosystems II and I in leaves as analyzed by simultaneous measurements of chlorophyll fluorescence and transmittance at 800 nm. – Plant Cell Physiol. **41**: 138-147, 2000.

Endo, T., Shikanai, T., Takabayashi, A., Asada, K., Sato, F.: The role of chloroplastic NAD(P)H dehydrogenase in photoprotection. – FEBS Lett. **457**: 5-8, 1999.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – Annu. Rev. Plant Physiol. **33**: 317-345, 1982.

Fryer, M.J., Andrews, J.R., Oxborough, K., Blowers, D.A., Baker, N.R.: Relationship between CO_2 assimilation, photosynthetic electron transport, and active O_2 metabolism in leaves of maize in the field during periods of low temperature. – Plant Physiol. **116**: 571-580, 1998.

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.

Havaux, M., Davaud, A.: Photoinhibition of photosynthesis in chilled potato leaves is not correlated with loss of Photosystem-II activity. Preferential inactivation of Photosystem I. – Photosynth. Res. **40**: 75-92, 1994.

Huner, N.P.A., Öquist, G., Sarhan, F.: Energy balance and acclimation to light and cold. – Trends Plant Sci. **3**: 224-230, 1998.

Kingston-Smith, A.H., Harbinson, J., William, J., Foyer, C.H.: Effect of chilling on carbon assimilation, enzyme activation, and photosynthetic electron transport in the absence of photoinhibition in maize leaves. – Plant Physiol. **114**: 1039-1046, 1997.

Kozaki, A., Takeba, G.: Photorespiration protects C3 plants from photooxidation. – Nature **384**: 557-560, 1996.

Kratsch, H.A., Wise, R.R.: The ultrastructure of chilling stress. – Plant Cell Environ. **23**: 337-350, 2000.

Krause, G.H.: Photoinhibition induced by low temperatures. –

In: Baker, N.R., Bowyer, J.R. (ed.): Photoinhibition of Photosynthesis: From Molecular Mechanisms to the Field. Pp. 331-348. Bios Scientific Publishers, Oxford 1994.

Leegood, R.C., Edwards, G.E.: Carbon metabolism and photorespiration: temperature dependence in relation to other environmental factors. – In: Baker, N.R. (ed.): Photosynthesis and the Environment. Pp. 191-221. Kluwer Academic Publishers, Dordrecht – Boston – London 1996.

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.

Liu, P., Meng, Q.-W., Zou, Q., Zhao, S.-J., Liu, Q.-Z.: Effects of cold-hardening on chilling-induced photoinhibition of photosynthesis and on xanthophyll cycle pigments in sweet pepper. – Photosynthetica **39**: 467-472, 2001.

Martin, B., Ort, D.R., Boyer, J.S.: Impairment of photosynthesis by chilling-temperatures in tomato. – Plant Physiol. **68**: 329-334, 1981.

Osmond, C.B., Grace, S.G.: Perspectives on photoinhibition and photorespiration in the field: Quintessential inefficiencies of the light and dark reaction of photosynthesis? – J. exp. Bot. **46**: 1351-1362, 1995.

Peeler, T.C., Naylor, A.W.: A comparison of the effects of chilling on thylakoid electron transfer in pea (*Pisum sativum* L.) and cucumber (*Cucumis sativus* L.). – Plant Physiol. **86**: 147-151, 1988.

Savitch, L.V., Massacci, A., Gray, G.R., Huner, N.P.A.: Acclimation to low temperature or high light mitigates sensitivity to photoinhibition: roles of the Calvin cycle and the Mehler reaction. – Aust. J. Plant Physiol. **27**: 253-264, 2000.

Sonoike, K.: Photoinhibition of photosystem I: its physiological significance in the chilling sensitivity of plants. – Plant Cell Physiol. **37**: 239-247, 1996.

Sonoike, K., Terashima, I., Iwaki, M., Itoh, S.: Destruction of photosystem I iron-sulfur centers in leaves of *Cucumis sativus* L. by weak illumination at chilling temperatures. – FEBS Lett. **362**: 235-238, 1995.

Streb, P., Shang, W., Feierabend, J., Bligny, R.: Divergent strategies of photoprotection in high-mountain plants. – Planta **207**: 313-324, 1998.

Terashima, I., Funayama, S., Sonoike, K.: The site of photoinhibition in leaves of *Cucumis sativus* L. at low temperatures is photosystem I, not system II. – Planta **193**: 300-306, 1994.

Terashima, I., Noguchi, K., Itoh-Nemoto, T., Park, Y.M., Kubo, A., Tanaka, K.: The cause of PSI photoinhibition at low temperatures in leaves of *Cucumis sativus*, a chilling-sensitive plant. – Physiol. Plant. **103**: 295-303, 1998.

Tjus, S.E., Møller, B.L., Scheller, H.V.: Photosystem I is an early target of photoinhibiton in barley illuminated at chilling temperatures. – Plant Physiol. **116**: 755-764, 1998.

Wise, R.R.: Chilling-enhanced photooxidation: The production, action and study of reactive oxygen species produced during chilling in the light. – Photosynth. Res. **45**: 79-97, 1995.

Wise, R.R., Naylor, A.W.: Chilling-enhanced photooxidation. Evidence for the role of singlet oxygen and superoxide in the breakown of pigments and endogenous antioxidants. – Plant Physiol. **83**: 278-282, 1987.