PHOTOSYNTHETICA 44 (2): 174-180, 2006

Photosynthesis and non-photochemical excitation quenching components of chlorophyll excitation in maize and field bean during chilling at different photon flux density

J. KOŚCIELNIAK* and J. BIESAGA-KOŚCIELNIAK**

*Department of Plant Physiology, Agricultural University, Podluzna 3, 30-239 Krakow, Poland**
*Institute of Plant Physiology, Polish Academy of Sciences, Niezapominajek 21, 30-239 Krakow, Poland***

Abstract

The influence of chilling (8 °C, 5 d) at two photon flux densities [PFD, L = 200 and H = 500 μmol(photon) m^{-2} s^{-1}] on the gas exchange and chlorophyll fluorescence was investigated in chilling-tolerant and chilling-sensitive maize hybrids (*Zea mays* L., K383×K130, K185×K217) and one cultivar of field bean (*Vicia faba* L. *minor*, cv. Nadwiślański). The net photosynthetic rate (P_N) for the both studied plant species was inhibited at 8 °C. P_N of both maize hybrids additionally decreased during chilling. Changes in the quantum efficiency of PS2 electron transport (Φ_{PS2}) as a response to chilling and PFD were similar to P_N. Measurements of Φ_{PS2}/Φ_{CO2} ratio showed that in field bean seedlings strong alternative photochemical sinks of energy did not appear during chilling. However, the high increment in Φ_{PS2}/Φ_{CO2} for maize hybrids can indicate reactions associated with chill damage generation. At 8 °C the non-photochemical quenching (NPQ) increased in all plants with chilling duration and PFD. The appearance of protective ($q_{I,p}$) and damage ($q_{I,d}$) components of q_I and a decrease in q_E (energy dependent quenching) took place. NPQ components of field bean and maize hybrids differed from each other. The amount of protective NPQ ($q_E + q_{I,p}$) components as part of total NPQ was higher in field bean than in maize hybrids at both PFD. On 5th day of chilling, the sum of q_E and $q_{I,p}$ was 26.7 % of NPQ in tolerant maize hybrids and 17.6 % of NPQ in the sensitive one (averages for both PFD). The increased PFD inhibited the ability of all plants to perform protective dissipation of absorbed energy. The understanding of the genotypic variation of NPQ components in maize may have implications for the future selection of plants with a high chilling tolerance.

Additional key words: chlorophyll fluorescence; photochemical and non-photochemical quenching, photoinhibition; photosystem 2; *Vicia*; *Zea*.

Introduction

Photosynthesis is the most important photochemical sink for energy absorbed by leaves. Because of strong CO_2 assimilation inhibition in maize evoked by chilling (Farage and Long 1987, Greer and Hardacre 1989), the maize photosynthetic apparatus is liable to damages. A decrease in the photochemical use of radiation absorbed by pigments can lead to the production of potentially dangerous reactive oxygen species, ROS (Baker 1994). Non-photochemical processes, which help to dissipate the excess of absorbed energy, include two very important components: energy dependent one (q_E) and photoinhibitory quenching (q_I) (van Wijk and van Hasselt 1993a, Ting and Owens 1994, Ruban and Horton 1995). q_E magnitude is regulated by pH gradient across the thylakoid membrane and by inter-conversion of pigments in the xanthophyll cycle (Owens *et al*. 1993, Ting and Owens 1994, Ruban and Horton 1995). q_I component contains photoprotective ($q_{I,p}$) and damage ($q_{I,d}$) sub-components of photoinhibitory quenching (Ting and Owens 1994). An appearance of damage sub-component of q_I is connected

Received 17 May 2005, *accepted* 7 November 2005.
*Fax: +48 12 4251844; e-mail: jan_kosc@poczta.onet.pl

Abbreviations: C_i = intercellular CO_2 concentration; F_0, F_m = minimum and maximum fluorescence yield in dark adapted plants, respectively; F_s, F_0', F_m' = actual, minimum, and maximum fluorescence yield in light-adapted plants, respectively; $F_v = F_m - F_0$; $F_v' = F_m' - F_0'$; F_v'/F_m' = efficiency of excitation energy capture by open PS2 reaction centres; g_s = stomatal conductance; H and L = high and low photon flux densities [200 and 500 μmol(photon) m^{-2} s^{-1}] during chilling; NPQ = non-photochemical quenching of chlorophyll fluorescence; P_N = net photosynthetic rate; PAR = photosynthetically active radiation; PFD = photon flux density; PS2 = photosystem 2; q_p = photochemical fluorescence quenching; q_E = energy dependent quenching; q_I = component of NPQ associated with photoinhibition of photosynthesis ($q_{I,d}$) and processes protecting against PS2 photoinhibition ($q_{I,p}$); S_{SE} = standard error of the mean; Φ_{CO2} = quantum efficiency of CO_2 assimilation; Φ_{PS2} = quantum efficiency of PS2 electron transport.

with the photoinhibition of PS2 reaction centres (Krause 1994).

The differentiation of NPQ components is possible on the basis of the speed of their relaxation in the dark (Krause and Weis 1991, van Wijk and van Hasselt 1993a,b, Leitsch *et al*. 1994, Melkonian *et al*. 2004). q_E relaxes much more rapidly than $q_{I,p}$ and $q_{I,d}$. $q_{I,d}$ is irreversible in the dark, requiring the irradiance dependent chloroplast protein synthesis to repair damaged PS2 reaction centres complex (Krause and Weis 1991, Leitsch *et al*. 1994).

In usually short experiments, plants are able to regulate NPQ assuring a dissipation of excess absorbed PFD, which can not be used in photochemical processes (Laisk *et al*. 1977, van Wijk and van Hasselt 1993a, Melkonian *et al*. 2004). However, under strong stress this regulation disappears in several species (Laisk *et al*. 1997). It is not clear whether the differentiation of protective components NPQ (q_E and $q_{I,p}$) appears in different maize genotypes during long chilling periods and whether it is correlated with tolerance for low temperatures.

The aim of this work was to find changes in NPQ components for two maize hybrids with different sensitivity to chilling during vegetation for a long period (5 d) at low temperature and at low and high PFD irradiation. As a reference, we used plants of field bean known as resistant to chilling.

Materials and methods

Plants and growth conditions: We used two hybrids of maize (*Zea mays* L., K383×K130, K185×K217) of different chilling tolerance and one cultivar of field bean (*Vicia faba* L. *minor,* cv. Nadwiślański). Plants were grown in growth rooms in pots (5 000 cm^3) filled with a mixture of clay, peat, and sand (3 : 2 : 1, v/v/v) at a 16-h photoperiod, PFD of 350 µmol(photon) m^{-2} s^{-1} (provided by high pressure sodium lamps, *Philips SON-T AGRO*, 400 W) and at 50–60 % of air humidity. During germination (5 d) constant temperature of 20 °C was kept and after emergence the temperature was 20/17 °C (day/night). After 12 d, 4 leaves were visible for maize and 3 leaves for field bean. Then the vegetation temperature was lowered to 8 °C (day/night, 5 d). At that time two PFD were kept: 200±30 and 500±35 µmol(photon) m^{-2} s^{-1} (on level of upper leaves). After 0, 3, and 5 d, we transferred some of the plants to 20/17 °C (day/night, 3 d) to make observations of necrotic leaf injuries caused by chilling. Seedlings were watered and fertilized with half-strength Hoagland nutrient solution as required. All measurements were made in nine replicates on the 3rd leaf (maize) and on leaflet of the 3rd leaf (field bean).

Gas exchange: Net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) in plants were measured by an infrared gas analyser (*Ciras-1*, *PP Systems*, Hitchin Herts, UK) with a Parkinson leaf chamber (*PLC6*) controlling automatically the measurement conditions. The irradiation system (*PP Systems*, Hitchin Herts, UK) consisted of 3 halogen lamps (3×20 W). The flow rate of air with constant CO_2 concentration [400 µmol(CO_2) mol^{-1}(air)] through the assimilation chamber was 350 cm^3 min^{-1}. Studies of the gas exchange were performed at vegetation temperature, directly before chilling (20 °C), and also after 3 and 5 d at 8 °C (the leaf temperature) at two PFD: 200±3 and 500±4 µmol(photon) m^{-2} s^{-1}. Gas exchange parameters were calculated according to the equations of Parkinson *et al*. (1980).

Chlorophyll *a* fluorescence was measured by means of a pulse amplitude modulation fluorometer (*FMS2*, *Hansatech*). The source of the modulation beam (duration pulses 1.8 µs, 2.3 kHz) was the amber LED [peak wavelength 594 nm, PFD *ca*. 0.05 µmol(photon) m^{-2} s^{-1}]. Actinic and pulse irradiations were provided by a halogen lamp (20 W). The signal detector was a *PIN* photodiode with a long-pass filter (>700 nm), the sampling rate was 10–20 kHz (depending upon the instrument mode). Fluorescence parameters (F_m, F_0, *etc*.) were calculated automatically with the standard for the fluorometer procedures. The efficiency of excitation energy capture by open PS2 reaction centres (F_v'/F_m'), the photochemical quenching (q_p), and the quantum yield of electron transport at PS2 (Φ_{PS2}) were determined (Genty *et al*. 1989). NPQ parameters were calculated as energy-dependent quenching (q_E), the protective ($q_{I,p}$) and damage ($q_{I,d}$) sub-components of photoinhibitory quenching (q_I). These components of NPQ were separated on the basis of differences in relaxation times in the dark (Krause and Weis 1991, van Wijk and van Hasselt 1993a,b, Leitsch *et al*. 1994, Melkonian *et al*. 2004). The contribution of q_E was determined following 15 min of dark relaxation, $q_{I,p}$ was measured as the difference in NPQ between a 15 min and a 2 h dark relaxation (Demmig and Björkman 1987, Hodges *et al*. 1989, Walters and Horton 1991, van Wijk and van Hasselt 1993a, Leitsch *et al*. 1994, Melkonian *et al*. 2004). Listed relaxation periods were the same as applied for bean plant at 6.5 °C by Melkonian *et al*. (2004). They are longer than the ones used at high temperature because of slower relaxation processes during chilling than under normal conditions (Adams *et al*. 1990, van Wijk and van Hasselt 1993b). This method does not allow for perfect differentiation between q_E and $q_{I,p}$ (van Wijk and van Hasselt 1993b). Values of q_E can include a quenching component related to the light state transition (q_T) (Walters and Horton 1991). However, q_T under conditions that provoke strong photoinhibition was omitted because of its low value (Krause and Weis 1991).

The fluorescence parameters (q_E, q_I, and NPQ_{TOT}) were scaled to pre-treatment F_v (F_v^p) on order to compare directly these parameters (see Melkonian *et al*. 2004). Values of NPQ_{TOT} components were calculated according to Ting and Owens (1994) and Melkonian *et al*. (2004), who introduced or applied the technique allowing for a direct comparison of q_E and q_I of samples differing in F_v/F_m:

$$q_I = [F_v^p - F_v^t (F_0^p/F_0^t)]/F_v^p,$$
$$q_E = [(F_m^t - F_m^{'t}) F_0^p/F_0^t]/F_v^p$$

Superscript ^{p} denotes pre-chill samples ($NPQ_{TOT} = 0$), while ^{t} means treated samples ($NPQ_{TOT}>0$). The damage + protective sub-component of q_I were studied after 2 h, and a damage sub-component of q_I after 15 min in the darkness. On this basis, $NPQ_{TOT} = q_E + q_{I,p} + q_{I,d}$. Analyses were performed directly after gas exchange measurements. We removed leaves from the assimilation chamber and placed the fluorescent measurement clips on the leaf surface, precisely in the middle of the parts of leaves, which were used for gas exchange rate measurements. Leaves (without being removed from plants) were put into a container with constant concentration of CO_2 [400 μmol(CO_2) mol^{-1}(air)] and at ambient temperature. Measurements of F_s and F_m' were carried out after 15 min in the "actinic light" with the same irradiance as it was used in gas exchange measurements. F_0' was measured after turning off the "actinic light" by immediate irradiation of the leaf for 3 s by a far red emitting diode (peak wavelength 735 nm, with about 15 W m^{-2}). Measurements in the dark (F_0, F_m) were done after 15 min and 2 h. The saturating pulses (F_m, F_m') had an irradiance of about 5 800 μmol(photon) m^{-2} s^{-1} and lasted 0.9 s. For fluorescence and gas exchange measurements, we applied the protocol by Melkonian *et al.* (2004).

Leaf absorbance (reflectance and transmittance) were measured by means of a *LiCor 1800* spectroradiometer with a *LiCor* integrating sphere (*LiCor*, Lincoln, NE, USA). PAR absorbance (400–700 nm) was calculated based on difference between incident, transmitted, and reflected radiation.

Assessment of necrotic injuries of leaves: During the recovery period (3 d), 20/17 °C (day/night), a photoperiod of 15 h [350 μmol(photon) m^{-2} s^{-1}] and the relative air humidity of 50–60 % were kept. After the recovery period, a visual assessment of necrotic injuries of the third leaves according to an eight-grade scale in the percentage of injured leaf area (0, 5, 15, 25, 35, 50, 75, and 100 %) was made.

Results

Chilling injuries, gas exchange, and quantum yield of PS2: Leaves of field bean were not damaged by 8 °C as opposed to the maize ones (Fig. 1). The injuries to maize increased with the prolongation of the chilling period and also with an increase in PFD. The genotype K383×K130 was more chill-sensitive. The injuries appeared earlier (3rd day) than in K185×K217 and included larger part of leaf area. After 5 d of vegetation under H, injuries spread over around 54 % of leaf surface in the chill-sensitive hybrid while in the chill-tolerant it reached only to about 37 %. The decreased temperature inhibited P_N in analysed leaves in maize and in field bean (Fig. 2*A*). H combined with chill increased the inhibition of photosynthesis only in maize hybrids. At the same periods of vegetation, P_N of field bean was higher for H. After the transfer of plants into chilling conditions, g_s decreased for all plants, but usually relatively less than P_N (Fig. 2*B*). However, P_N and C_i were linearly related (Fig. 2*C*). Hence, it is less probable that P_N was limited strongly by stomata at low temperature. CO_2 concentration in leaves with low P_N values [less than 8 μmol(CO_2) m^{-2} s^{-1}] decreased by no more than 16 % in relation to CO_2 content in the external air and that is why it did not limit photosynthesis. Decreasing C_i for some plants in the range of 330–250 μmol(CO_2) mol^{-1}(air) did not change P_N. Stomata limitation could be connected only with high P_N at 20 °C when C_i decreased to around 130 μmol(CO_2) mol^{-1}.

Changes in PS2 electron transport (Φ_{PS2}), as a response to chilling and PFD, were similar to those in P_N for maize and field bean (Fig. 3*A*). At the low temperature, slightly higher activity of PS2 electron transport was found for tolerant maize hybrids. The important obstacle for PS2 energy transport at low temperature and at H was connected with a decrease in the number of "open" reaction centres (decrease in q_p) (Fig. 3*B*). That is why q_p and Φ_{PS2} changes were similar.

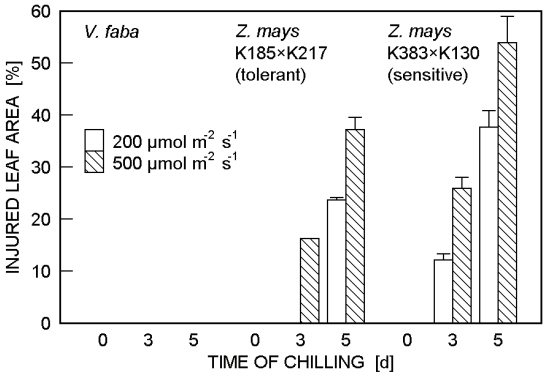

Fig. 1. Necrotic injuries to field bean and two genotypes of maize (chill tolerant and chill sensitive) in relationship with PFD and the time of growth at 8 °C. Injuries were measured after chilling (3 d at 20 °C). Means±SE.

The ratio Φ_{PS2}/Φ_{CO2} indicates how efficiently the PAR is used for carbon fixation, *i.e.* the higher the ratio the lower efficiency of photon energy use (Fig. 3*C*). Φ_{PS2}/Φ_{CO2} values for field bean plants were at all temperatures and irradiations nearly constant. However, in maize hybrids the Φ_{PS2}/Φ_{CO2} increment occurred from about 13.0 at 20 °C to 14.5–15.3 at 8 °C. The highest Φ_{PS2}/Φ_{CO2} increment was after vegetation at H. The increase in Φ_{PS2}/Φ_{CO2} values can indicate the appearance of photochemical sinks not connected with CO_2 assimilation.

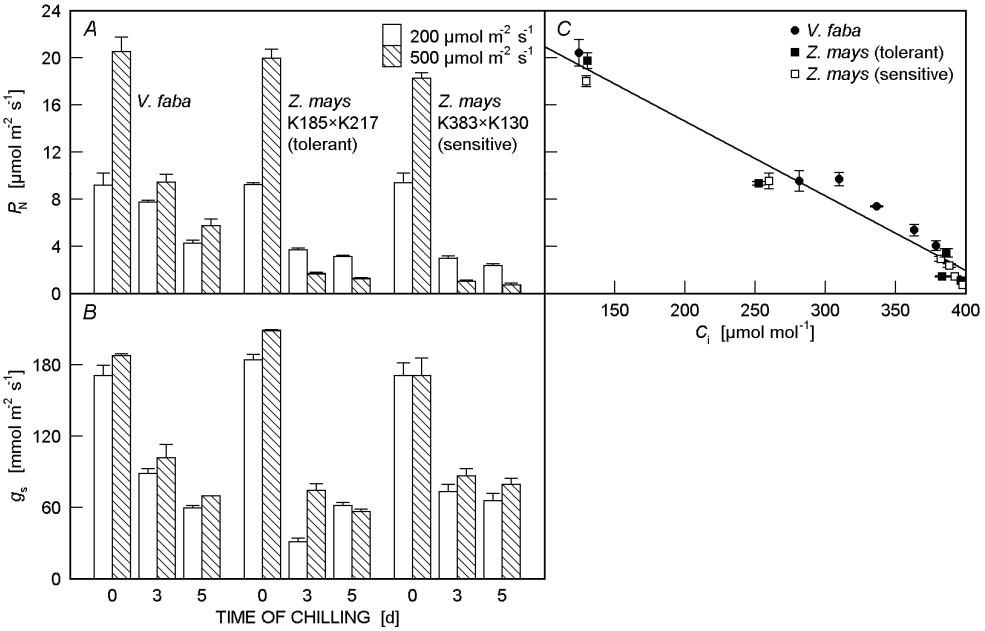

Fig. 2. Net photosynthetic rate, P_N (*A*), stomatal conductance, g_s (*B*), and relationship between P_N and C_i (*C*) in leaves of field bean and two genotypes of maize before chilling (20 °C) and during growth at 8 °C for different PFD. P_N, g_s, and C_i were determined at 200 and 500 µmol(photon) m^{-2} s^{-1} PFD and at temperature of vegetation. Means ± SE.

Components of NPQ: The scaled contributions of $q_{E,}$ $q_{I,p}$, and $q_{I,d}$ into NPQ_{TOT} in relation to irradiation during chilling are shown in Fig. 4*A*. After the transfer of maize and field bean seedlings to 8 °C, NPQ_{TOT} increased strongly despite of q_E decrease with the prolongation of chilling and an increase in PFD. NPQ_{TOT} increment was connected with the appearance of the protective and damage components of q_I. During chilling, strong differences between NPQ_{TOT} components of field bean and maize were visible as well as among hybrids of maize. NPQ_{TOT} (q_E + $q_{I,p}$) protective components of field bean contributed more to NPQ_{TOT} at both PFD than they did in the case of hybrids of maize (Fig. 4*B*). For instance, after 5 d q_E and $q_{I,p}$ sum was 43.5 % of NPQ_{TOT} for field bean and 22.2 % of NPQ_{TOT} for both maize hybrids (mean values for H and L). At the same time, the sum of these quenching components of NPQ_{TOT} (mean values for both PFD) was 26.7 % for the maize tolerant hybrid and only 17.6 % for the sensitive hybrid. The increase in irradiance declined very clearly the ability of all plants to utilize the mechanism of the protective scattering of photon energy.

Discussion

Contrary to maize, field bean did not show necrotic injuries of leaves after vegetation at 8 °C. Plant chilling sensitivity may be caused by an ability of the lipid membrane to change at a low temperature from fluid to solid phase. This results in conformational changes and higher activation energy in membrane-bound enzymes and in dysfunction of membranes (Lyons 1973, Raison 1974). This phase transition of lipids is considered the primary event of chilling injury (Lyons *et al*. 1979).

In this study, after the transfer of seedlings from 20 to 8 °C, the photosynthesis inhibition was stronger for maize than for field bean plants (Fig. 2*A*). The low use of absorbed PAR by the photosynthetic process could provoke, especially in the case of maize, the formation of potentially damaging ROS (Baker 1994). P_N in maize at lowered temperature was smaller at H than at L. The metabolic cause of it could be the increased production of ROS at high PFD at decreased efficiency ROS scavenging systems during chilling, which led to the damage of the photosynthetic apparatus.

A decrease in C_i in leaves of field bean seedlings can induce a decrease in photosynthesis (Lal *et al.* 1996). In

our experiments, a decrease in P_N during chilling could not be ascribed to a g_s increase. P_N of field bean and maize took place at a much higher concentration of CO_2 in leaves than at 20 °C (Fig. 2*C*). A lack of essential stomata limits of photosynthesis in maize during chilling is well-documented (Irigoyen *et al*. 1996, Janda *et al*. 1998, Kościelniak *et al*. 2005).

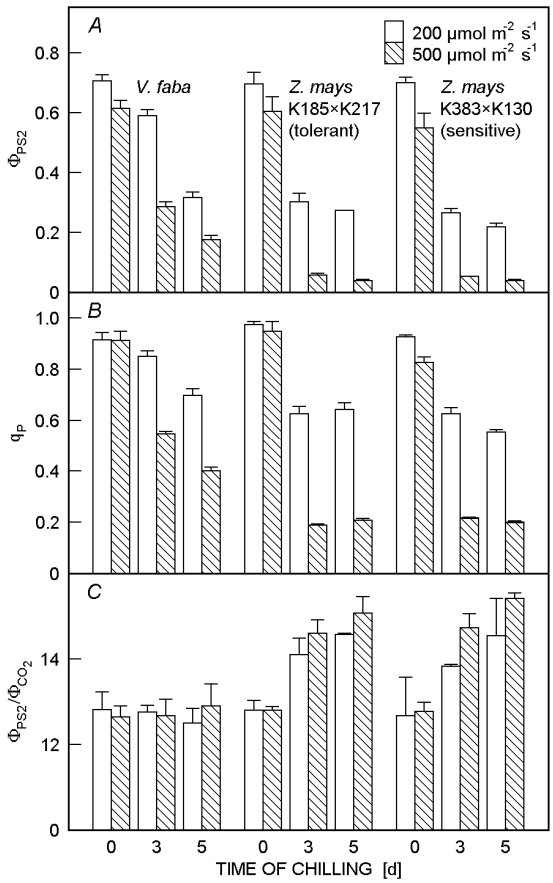

Fig. 3. Quantum efficiency of PS2 electron transport, Φ_{PS2} (*A*), the photochemical excitation quenching (*B*), and Φ_{PS2}/Φ_{CO2} ratio (*C*) in leaves of field bean and two genotypes of maize before chilling and during growth at chilling as in Fig. 2. Means ± SE.

The ratio between the quantum yield of PS2 and CO_2 is an estimate of the relationship between electron transport rate and carbon fixation (Genty *et al*. 1989). Experimentally, Φ_{PS2}/Φ_{CO2} values greater than 8 were obtained for both C_3 and C_4 plants (Edwards and Baker 1993). In C_3 plants, this may indicate that processes other than photosynthesis also use electrons: photorespiration, N assimilation, pseudocyclic electron transport, and reactions connected with an action of stress on plants (Cornic and Briantais 1991, Asada 1999). Directions of changes in P_N and Φ_{PS2} in field bean plants were similar and because of this, the values of Φ_{PS2}/Φ_{CO2} did not considerably depend on temperature and PFD (Fig. 3*C*). This suggests that strong alternative photochemical sinks of energy did not appear in field bean seedlings during chilling. Melkonian *et al*. (2004) obtained similar results while studying CO_2 assimilation and Φ_{PS2} during chilling of bean at 6.5 °C. In C_4 plants photorespiration is negligible, but there is an additional requirement of electrons, mainly because of the high demand for ATP (Krall and Edwards 1990). For maize, Φ_{PS2}/Φ_{CO2} is around 9–12 during chilling (15 °C) (Massacci *et al*. 1995). In our study, Φ_{PS2}/Φ_{CO2} values were higher at H as well as at L, and it could be caused by the use of data related to net photosynthesis and not to gross photosynthesis for calculations. When leaves of maize were stressed by low temperature, carbon photosynthesis metabolism was strongly reduced, and then the absorbed photons might also drive alternative reactions. A similar result of maize study at slightly lowered temperature (16 °C) was obtained by Massacci *et al*. (1995). The excess of energy can generate oxygen radicals. For instance, electrons may be donated to oxygen and form superoxide radicals (Wise 1995).

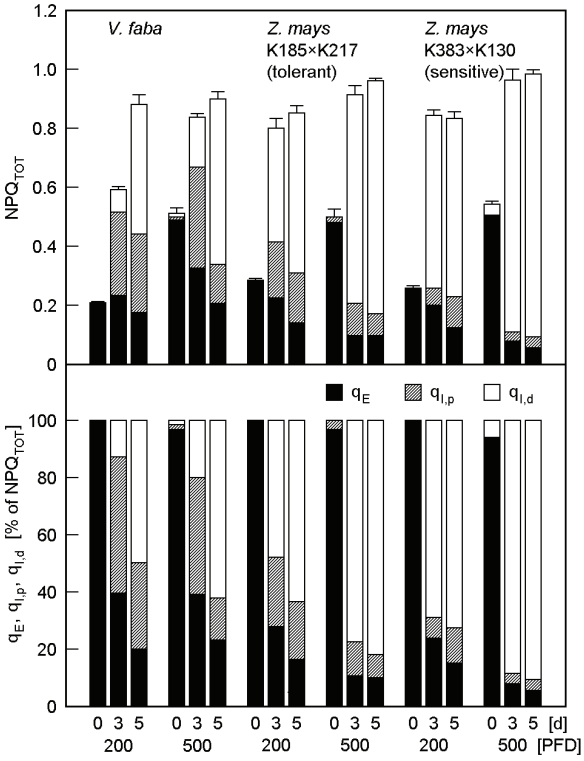

Fig. 4. The components of NPQ_{TOT} (*A* – normalized values, *B* – normalized values in % of NPQ_{TOT}) in leaves of field bean and two genotypes of maize before chilling and during growth at chilling (as in Fig. 2). The subscripts ^{p} and ^{d} of q_I refer to the protective and damaging sub-components of q_I (see the text). Means ± SE. SE concerns NPQ_{TOT}.

Excess of absorbed PFD was stronger dissipated as heat at the time of prolonged chilling (Fig. 4*A*). Then a decrease in q_E was accompanied by the appearance of a second protective component NPQ, $q_{I,p}$. With the prolongation of chilling, the contribution of q_E and $q_{I,p}$ to

NPQ decreased while the sub-component of photoinhibitory quenching increased, similarly to other experiments (van Wijk and van Hasselt 1993a, Melkonian *et al*. 2004). The amount of protective components of NPQ was higher in field bean than in hybrids of maize, what can support a view of an existing ability to co-regulate NPQ and CO_2 assimilation in field bean during chilling. The coordination of both processes disappears under severe stress conditions (Laisk *et al*. 1997). Despite of strong chilling injuries, in the tolerant hybrid of maize the higher amount and greater contribution of protective NPQ components were observed than in seedlings of the sensitive genotype.

Our present results support a view about the resistance of the photosynthetic apparatus of field bean plants to low temperatures. In comparison with maize, field bean seedlings have a higher ability to scatter excess of captured energy and can prevent more effectively PS2 degradation during chilling. The possibility of studying genotypic variations of NPQ components of maize during chilling stress can be applied in future selection of plants with higher tolerance to low temperature.

References

Adams, W.W., III, Demmig-Adams, B., Winter, K.: Relative contributions of zeaxanthin-related and zeaxanthin-unrelated types of 'high-energy-state' quenching of chlorophyll fluorescence in spinach leaves exposed to various environmental conditions. – Plant Physiol. **92**: 302-309, 1990.

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

Baker, N.R.: Chilling stress and photosynthesis. – In: Foyer, C.H., Mullineaux, P.M. (ed.): Causes of Photooxidative Stress and Amelioration of Defense System Plants. Pp. 127-154. CRC Press, Boca Raton 1994.

Cornic, G., Briantais, J.-M.: Partitioning of photosynthetic electron flow between CO_2 and O_2 reduction in a C_3 leaf (*Phaseolus vulgaris* L.) at different CO_2 concentrations and during drought stress. – Planta **183**: 178-184, 1991.

Demmig, B., Björkman, O.: Comparison of the effect of excessive light on chlorophyll fluorescence (77 K) and photon yield of O_2 evolution in leaves of higher plants. – Planta **171**: 171-184, 1987.

Edwards, G.E., Baker, N.R.: Can CO_2 assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? – Photosynth. Res. **37**: 89-102, 1993.

Farage, P.K., Long, S.P.: Damage to maize photosynthesis in the field during periods when chilling is combined with high photon fluxes. – In: Biggins, J. (ed.): Progress in Photosynthesis Research. Vol. 4. Pp. 139-142. Martinus Nijhoff Publ., Dordrecht – Boston – Lancaster 1987.

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.

Greer, D.H., Hardacre, A.K.: Photoinhibition of photosynthesis and its recovery in two maize hybrids varying in low temperature tolerance. – Aust. J. Plant Physiol. **16**: 189-198, 1989.

Hodges, M., Cornic, G., Briantais, J.-M.: Chlorophyll fluorescence from spinach leaves: resolution of non-photochemical quenching. – Biochim. biophys. Acta **974**: 289-293, 1989.

Irigoyen, J.J., De Juan, J.P., Sanchez-Diaz, M.: Drought enhances chilling tolerance in a chilling-sensitive maize (*Zea mays*) variety. – New Phytol. **134**: 53-59, 1996.

Janda, T., Szalai, G., Ducruet, J.-M., Páldi, E.: Changes in photosynthesis in inbred maize lines with different degrees of chilling tolerance grown at optimum and suboptimum temperatures. – Photosynthetica **35**: 205-212, 1998.

Kościelniak, J., Janowiak, F., Kurczych, Z.: Increase in photosynthesis of maize hybrids (*Zea mays* L.) at suboptimal temperature (15 ºC) by selection of parental lines on the basis of chlorophyll *a* fluorescence measurements. – Photosynthetica **43**: 125-134, 2005.

Krall, J.P., Edwars, G.E.: Quantum yields of photosystem II electron transport and carbon dioxide fixation in C_4 plants. – Aust. J. Plant Physiol. **17**: 579-588, 1990.

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.

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

Laisk, A., Oja, V., Rasulov, B., Eichelmann, H., Sumberg, A.: Quantum yields and rate constants of photochemical and nonphotochemical excitation quenching. Experiment and model. – Plant Physiol. **115**: 803-815, 1997.

Lal, A., Ku, M.S.B., Edwars, G.E.: Analysis of inhibition of photosynthesis due to water stress in the C_3 species *Hordeum vulgare* and *Vicia faba*: Electron transport, CO_2 fixation and carboxylation capacity. – Photosynth. Res. **49**: 57-69, 1996.

Leitsch, J., Schnettger, B., Critchley, C., Krause, G.H.: Two mechanisms of recovery from photoinhibition *in vivo*: Reactivation of photosystem II related and unrelated to D1-protein turnover. – Planta **194**: 15-21, 1994.

Lyons, J.M.: Chilling injury in plants. – Annu. Rev. Plant Physiol. **24**: 445-466, 1973.

Lyons, J.M., Raison, J.K., Steponkus, P.L.: The plant membrane in response to low temperature: an overview. – In: Lyons, J., Graham, M.D., Raison, J.K. (ed.): Low Temperature Stress in Crop Plants. Pp. 1-24. Academic Press, New York 1979.

Massacci, A., Iannelli, M.A., Pietrini, F., Loreto, F.: The effect of growth at low temperature on photosynthetic characteristics and mechanisms of photoprotection of maize leaves. – J. exp. Bot. **46**: 119-127, 1995.

Melkonian, J., Owens, T.G., Wolfe, D.W.: Gas exchange and co-regulation of photochemical and nonphotochemical quenching in bean during chilling at ambient and elevated carbon dioxide. – Photosynth. Res. **79**: 71-82, 2004.

Owens, T.G., Shreve, A.P., Albrecht, A.C.: Dynamics and mechanism of singlet energy transfer between carotenoids and chlorophylls: light harvesting and non-photochemical fluorescence quenching. – In: Murata, N. (ed.): Research in Photosynthesis. Vol. I. Pp. 179-186. Kluwer Academic Publ., Dordrecht – Boston – London 1993.

Parkinson, K.J., Day, W., Leach, J.E.: A portable system for measuring the photosynthesis and transpiration of

graminaceous leaves. – J. exp. Bot. **31**: 1441-1453, 1980.
Raison, J.K.: A biochemical explanation of low-temperature stress in tropical and subtropical plants. – In: Bielski, R.L., Ferguson, A.R., Cresswel, M.M. (ed.): Mechanism of Regulation of Plant Growth. Pp. 487-497. Royal Society of New Zeland, Wellington 1974.
Ruban, A.V., Horton, P.: An investigation of sustained component of nonphotochemical quenching of chlorophyll fluorescence in isolated spinach chloroplasts and leaves of spinach. – Plant Physiol. **108**: 721-726, 1995.
Ting, C.S., Owens, T.G.: The effects of excess irradiance on photosynthesis in the marine diatom *Phaeodactylum tricornutum*. – Plant Physiol. **106**: 763-770, 1994.
van Wijk, K.J., van Hasselt, P.R.: Photoinhibition of photosystem II *in vivo* is preceded by down-regulation through light-induced acidification of the lumen: Consequences for the mechanism of photoinhibition *in vivo*. – Planta **190**: 359-368, 1993a.
van Wijk, K.J., van Hasselt, P.R.: Kinetic resolution of different recovery phases of photoinhibited photosystem II in cold-acclimated and non-acclimated spinach leaves. – Physiol. Plant. **87**: 187-198, 1993b.
Walters, R.G., Horton, P.: Resolution of components of non-photochemical chlorophyll fluorescence quenching in barley leaves. – Photosynth. Res. **27**: 121-133, 1991.
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.