ENVIRONMENTAL FACTORS AFFECTING THE HEAT STABILITY OF THE PHOTOSYNTHETIC APPARATUS

Dóra Szopkó & Sándor Dulai

Eszterházy Károly University, Institute of Biology, Department of Botany and Plant Physiology, H-3300 Eger, Leányka str. 6, Hungary;
*E-mail: szopko.dora@uni-eszterhazy.hu

Abstract: Owing to greenhouse effect and severe dry periods in the agricultural fields, cultivated plants are increasingly exposed to the adverse impact of several abiotic stresses. Therefore, an increasing emphasis should be placed on how multiple stresses affect the physiological processes in plants and how plants respond to the coexistence of combined stress factors. Simultaneous environmental factors may elicit a response different from that given to a single factor, resulting in intensification, overlapping or antagonistic effects. Although the rate of photosynthesis is significantly reduced by salinity and decreased water availability, the thermotolerance of the photosynthetic apparatus may be altered by salt and drought preconditioning. In this short review, we focused on the individual effect of heat stress and the influence of dehydration and NaCl treatment on the heat tolerance of plants. According to our present knowledge, the thermostability of the photosynthetic apparatus may usually be improved by pretreatment of drought or NaCl. At the same time, several different mechanisms in the background of the higher thermostability are hypothesized. These possible drought- and salt-induced processes are also summarized by this review article.

Keywords: acclimation, heat stress, multiple stresses, photosynthesis, thermotolerance

INTRODUCTION

The effects of high temperature on photosynthetic processes
Increase in ambient temperature may cause a disruption in the cellular homeostasis exerting an inhibitory effect on growth, development and reproduction ability of plants. Heat stress alone but mainly combined with another abiotic stress factor (e.g. drought, high light intensity) negatively affects the success of agricultural production worldwide (Mittler et al. 2012) in
connection with the prominent sensitivity of photosynthesis to stressful environment (Ashraf and Harris 2013). The optimum temperature for photosynthesis is in the range of 15-35 °C in plants of temperate regions. Above or below the optimum temperature, the structure and the operation of photosynthetic apparatus could be damaged (Wang et al. 2018). The degree of the damage is significantly affected by the temperature at which the plant has grown and the acclimatization and genetic properties of the plant species. The decreased capacity of photosynthesis may be manifested in the limitation of CO₂ assimilation and alterations of photosynthetic electron transport and photophosphorylation (Berry and Björkman 1980, Sharkey 2005). Although, there is a controversy in the literature (Law and Crafts-Brandner 1999), the temperature optimum and thermostability of the enzymes involved in CO₂ fixation in most cases exceed that temperature where photosynthesis is already significantly reduced, therefore the inhibited photosynthesis could primarily be associated with thermo-induced changes in the electron transport processes in the thylakoid lamellae of chloroplast (Berry and Björkmann 1980). In parallel with the slow heating, the strength of the hydrophilic and electrostatic interactions is weakened among the polar groups of proteins in the aqueous phase of the membranes, thereby modification in the structure of the membranes could be observed. Therefore, the strength of hydrophilic interactions are the most sensitive to heat resulting the physical dissociation of the light harvesting complexes (LHClI) from the PSII cores (CCII) (Schreiber and Berry 1977, Gounaris et al. 1984) and desintegration of the chloroplast grana and the conversion of PSII centers from α into β (Gounaris et al. 1984). This lateral reorganization of thylakoids is accompanied by other denaturation phenomena at more severe heat stress, such as the inactivation of oxygen-evolving complexes (OEC), caused by the dissociation of manganese ions and external proteins (Nash et al. 1985, Enami et al. 1994). The temperature at which the denaturation of PSII takes place is directly influenced by its lipid environment and by the fluidity of the thylakoids (Berry and Björkman 1980, Raison et al. 1982, Kunst et al. 1989). Parallel with these denaturation events, a similar decline of linear electron transport and photophosphorylation may be detected. The impaired photophosphorylation is partly attributable to the increase in the permeability of thylakoid lamellae, which forms a
barrier to photophosphorylation by reducing the proton motive force (Havaux et al. 1996).

Under natural conditions, heat stress usually occurs in the presence of light. Positive correlation between thermostability of photosynthetic apparatus and light intensity have been found by Molnár et al. (1998). Their results indicated that the light-dependent energization of the thylakoid membranes could play a considerable role in the thermostability of the photosynthetic apparatus. It was also demonstrated that the xanthophyll cycle is induced by high leaf temperature even under low light intensity (Molnár et al. 1998) by increasing the transthylakoid proton gradient ($\Delta p$H). The enhancement of cyclic electron flow around PSI (CEF) may also contribute to the increase in the $\Delta p$H under heat stress (Bukhov et al. 1999) contributing to the protonation of the LHCII and the accumulation of zeaxanthin. As indicated by Havaux et al. (1996) and Lavaud and Kroth (2006) zeaxanthin maintains the stability of the thylakoid and promotes the induction of non-photochemical quenching (NPQ) (Kiss et al. 2008). The development of the light energy-dependent component of the NPQ requires a conformational change in the antenna system of PSII associated with zeaxanthin accumulation (Jahns and Holzwarth 2012), which ultimately results in aggregated LHCII (Horton et al. 1991). A linear correlation between the formation of heat-induced LHCII aggregation and NPQ was demonstrated by Tang et al. (2007). Thus, the changes in conformation of PSII can improve the thermostability of chloroplasts against high light intensity and heat stress by the thermal dissipation of excess excitation energy. Zeaxanthin is not only a determinant factor in the induction of NPQ but also contributes to avoiding photooxidative damage due to its non-enzymatic antioxidant activity by reducing lipid peroxidation (Johnson et al. 2007).

PSI is less susceptible to heat stress than PSII since the inhibition of PSI is not yet detectable at temperatures that trigger the complete inactivation of PSII (Havaux 1996). The heat sensitivity of PSII is closely related to the thermolability of OEC at the donor side of PSII (Yamane et al. 1998, Wang et al. 2010). The loss of OEC activity is mainly due to the detachment of the manganese-stabilizing extrinsic protein from PSII (Enami et al. 1994) and the release of manganese ions (Nash et al. 1985). In addition to changes affecting the donor side, the acceptor side of
PSII may also be limited due to a disruption of the electron transfer between the primary (QA) and the secondary (QB) acceptor plastoquinone of PSII resulting in the accumulation of reduced QA (Kouril et al. 2004). The electron flow from the stroma to the reaction center of PSII may be observed in heat-treated samples under dark conditions, which reduces the optimal quantum efficiency of PSII through the damage of D1 protein (Marutani et al. 2012). In the presence of light, excitation energy may be transmitted to PSI instead of PSII by the so-called state 1 – state 2 transition NPQ process in which phosphorylated LHCII acts as the light-collecting antenna of PSI (Haldrup et al. 2001). State transition contributes to preventing the over-reduction of the acceptor side of PSII and photodamage in PSII under excess light energy by increasing CEF and NPQ (Takahashi et al. 2009). Essemine et al. (2017) showed that thermal damages in PSII could be avoided by CEF in rice which might be facilitated by light-induced state transition (Lemeille and Rochaix 2010). At the same time, state transitions may be induced in the dark under moderately elevated temperature due to increased chlororespiration resulting in the migration of phosphorylated LHCII from the grana to the stroma region by the activated chloroplast thylakoid protein kinase (STN7) (Havaux 1996, Nellaepalli et al. 2011). In addition, increased CEF can also contribute to the maintenance of ATP homeostasis to indirectly prevent irreversible damages to the photosynthetic apparatus (Sharkey and Zhang 2010).

The thermal sensitivity of PSII can be characterized by the determination of critical temperature for photochemical damage (Tc) based on minimum chlorophyll fluorescence (F0) and steady-state fluorescence (F5) vs. temperature (T) curves (Schreiber and Berry 1977, Molnár et al. 1998, Hill et al. 2009) (Figure 1).

The value of Tc is influenced by the fluidity of thylakoid membrane (Havaux and Gruszecki 1993), therefore Tc can be used as an indicator of the thermostolerance of the photosynthetic apparatus in connection with the integrity of thylakoid lamellaes (Hill et al. 2009).
Figure 1. An example of $F_0$ vs. $T$ curve where the temperature was increased at a rate of 1 °C min⁻¹ (Hill et al. 2009). The critical temperature for photochemical damage ($T_c$) was defined as the interception of regression lines fitted to fluorescence data.

In addition, $T_c$ may also indicate the critical temperature where the quantum efficiency of CO₂ fixation is impaired by heat treatment (Schreiber and Bilger 1987). Rising in $F_c$ can be caused by the detachment of LHCII from the PSII core complex (Yamane et al. 1997) and/or by the accumulation of the reduced QA. The latter is connected to the reversed electron donation between QA and QB or the impaired electron transport capacity from QA to QB due to the damaged D1 protein (Gilmore et al. 1996, Kouril et al. 2004). At a temperature above $T_c$, reversible or even irreversible degradation of thylakoid membranes occurs (Hill et al. 2009) leading to increased membrane permeability and decreased ΔpH which causes a reduction in NPQ.

In addition to the dysfunction in photosynthetic electron transport, heat stress also results in decreased chlorophyll content (Feng et al. 2014), deactivated Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) (Sharkey 2005) and denaturated Rubisco activase (Feller et al. 1998). The reduction in chlorophyll content may be attributed to the disturbance of chlorophyll synthesis or a
considerable degradation or both of them (Ashraf and Harris 2013). It has been also observed that the inactivated OEC and the insufficient electron transport around PSII significantly inhibited the rate of ribulose-1,5-bisphosphate (RuBP) regeneration (Wise et al. 2004, Wang et al. 2018). In addition to high light intensity, increased temperature is also conducive to intense photorespiration even under moderate and constant light intensity (Peterhansel et al. 2010). The heat-induced photorespiration is due to the oxygenation of RuBP over carboxylation by Rubisco because the affinity of Rubisco for O$_2$ and the concentration ratio of O$_2$ to CO$_2$ are increased in the stroma by heating event (Hall and Keys 1983).

**Changes in the photosynthetic processes due to temperature acclimation**

Plant can adapt to the adverse effects of supra-optimal temperature through long-term and short-term acclimation processes. These mechanisms are manifested in many metabolic processes, including photosynthesis, and affect both the lipid composition and the structure of proteins. The long-term acclimation to high temperature occurs in a range from some days to weeks thus it can only be suitable for defending from the effects of the seasonal temperature changes. This phenomenon is accompanied by reduced fluidity of thylakoid membranes (Dulai et al. 1998), with decreasing unsaturation of fatty acids of polar lipids (Berry and Björkmann 1980). A higher ratio of saturated fatty acid reduces the thermal sensitivity of PSII by rigidizing the membrane (Kunst et al. 1989), which forms an important part of the long-term acclimatization processes in plants suffering from heat stress. Other factors such as genetically-determined or environmental-induced differences in homologous proteins may also affect the thermostability of the photosynthetic apparatus. Adaptation of plants to elevated temperature entails reduced flexibility of the proteins through changes in intramolecular binding regardless of whether the proteins had high or low thermostability initially. In the long term, the efficient functioning of photosynthesis at high temperatures also depends on the presence of the heat stable protein synthesis system in the chloroplasts that enables heat-damaged proteins to be replaced or repaired (Berry and Björkmann 1980). Experimental evidences have suggested the
prominent sensitivity of the reaction center D1 protein to strong light and heat stress (Komayama et al. 2007, Khatoon et al. 2009). Komayama et al. (2007) described two processes in connection with the turnover of heat-damaged D1 protein: dephosphorylation of the D1 protein in the stroma, and aggregation of the phosphorylated D1 protein with nearby polypeptides. These processes may be essential for the maintaining the activity of PSII under heat treatment. One of the most effective protection against high temperature stress can be provided by heat shock proteins (HSPs) contributing to the refolding of proteins, preventing of the aggregation of denaturated proteins and protecting PSII at supra-optimal temperatures (Al-Whaibi 2011). In chloroplasts, the 21-kDa HSP (Hsp21) may mostly contribute to the stabilization of the thylakoid membrane during thermal fluctuations by directly interacting with the membrane-bound PSII subunits such as D1 and D2 proteins (Chen et al. 2016). Several studies have shown that hydrophobic isoprene could also protect photosynthesis under heat and oxidative stress conditions (Sharkey and Singsaas 1995, Loreto and Schnitzler 2010) by improving integrity of the thylakoid membrane and quenching reactive oxygen species when temperature exceeded the optimum level (Sharkey and Yeh 2001, Velikova et al. 2011). It was suggested that the protective role of isoprene is based on its ability to make stable interactions between proteins and lipids in the membrane (Sharkey and Yeh 2001).

In addition to the long-term acclimatization, short-term mechanisms also play a prominent role in the emergence of heat resistance by facilitating rapid responses. Havaux and Tardy (1995) have demonstrated the flexibility of thermotolerance of PSII which was reflected in improved thermostability within a few minutes in plants grown at 25 °C. An explanation of this rapid acclimatization to elevated temperature is summarized by Havaux and Tardy (1995, 1996). Their hypothesis is based on the temperature-dependent conversion of the xanthophyll cycle pigments, namely, the violaxanthin convert to zeaxanthin through antheraxanthin by the operation of violaxanthin de-epoxidase (Yamamoto et al. 1967). The phenomenon can occur under light and also under dark conditions and may be triggered off by ascorbate treatment (Havaux and Tardy 1995). Zeaxanthin can provide a protection function against the negative effects of high temperature not only by enhancing the stability of the thylakoid
membrane (Tardy and Havaux 1997) but also by promoting the induction of NPQ (Kiss et al. 2008).

**Impact of water deficit and salt pretreatment on PSII thermostability**

Water deficit and salt stress often occur in combination with heat stress under conditions of high light intensity. These stress factors may limit the processes of the carbon metabolism simultaneously (Dulai et al. 2005). During global climate change, it may become increasingly common for cultivated plants to tolerate the combined effects of the abiotic stress factors (Suzuki et al. 2014). Consequently, the survival and productivity of plants can be determined by their ability to coordinate mechanisms protecting against multiple stresses. The synchronization of regulating/protecting processes largely determines the flexibility of plants’ tolerance under the effects of the combined factors at a given time and place. Accordingly, the improved phenotypic plasticity in the changing environment may be essential for the reserved photosynthesis and growth. Simultaneous environmental factors may elicit a response different from that given to a single factor, resulting in intensification, overlapping or antagonistic effects (Osmond et al. 1986), however these effects strongly depend on the severe of first stress, the species, genotypes and the age of plants. Although the rate of photosynthesis is significantly reduced by high temperatures (Berry and Björkman 1980), the thermostability of the photosynthetic apparatus can be induced by drought and salt preconditioning (Lu and Zhang 1999, Dulai et al. 2006, Yan et al. 2012).

Perhaps the most common combined stress is the drought together with high temperature, which frequently occurs in hot and dry summer periods. Under conditions of water limitation, the significantly decreased transpiration also contributes to the stimulation of heat stress due to the insufficient heat transfer from the leaves (Teskey et al. 2014). However, the drought stress can induce the defence mechanisms in plants against high temperatures as well, which results in an enhanced tolerance to high temperatures (Ahuja et al. 2010). As demonstrated by Dulai et al. (2006) and Ribeiro et al. (2008) drought as a previous stress before heating could increase the thermostability in PSII, which may be reflected in the lower thermal sensitivity of effective
quantum yield of PSII ($\phi_{\text{PSII}}$) (Dulai et al. 2006, Ribeiro et al. 2008). Osmotic stress-induced increase in thermotolerance can be associated with different mechanisms. The improved thermostability of the drought-preconditioned Poa pratensis was attributed to the expression of HSPs, a higher antioxidant activity and changes in lipid composition (Peng et al. 2012). In water-deficient plants, these changes may minimize the damages of proteins and membranes during the heating event. Osmolytes involved in osmotic adjustment in water-stressed plants, such as glycine betaine or proline, may also benefit above the thermal optimum due to their stabilization function in the thylakoid membranes (Rhodes and Hanson 1993). Based on the observation made by Seemann et al. (1986) on desert plants, a common signal can be attributed to the simultaneous development of higher thermostability and osmotic adaptation. Denaturation of PSII at high temperatures also relates to physical changes affecting the lipid matrix of thylakoid membrane, which also modifies the conformation of proteins in thylakoid by altering the interaction between membrane proteins and lipids (Gounaris et al. 1984, Havaux 1992). Accordingly, the modified lipid composition during dehydration can help to strengthen the interaction between PSII proteins and surrounding lipids (Havaux 1992). The quantitative reduction of polyunsaturated fatty acid chain lipids or the increased zeaxanthin content in the membranes of chloroplast may be induced by osmotic stress, thus resulting more rigid thylakoid membrane (Ferrari-Iliou et al. 1984, Demmig et al. 1988, Tardy and Havaux 1997). Zeaxanthin, in addition to supporting the rigidity of thylakoid membrane, also acts as an antioxidant by moderating lipid peroxidation (Johnson et al. 2007). The preservation of the integrity of thylakoid membrane is also necessary for conformational changes that accompany the development of NPQ (Dau 1994), which can improve the thermostability in plants against high light and heat stress by the dissipation of excess absorbed energy. LHCII trimers can be transformed into an aggregated form by the conformational changes, which also require zeaxanthin (Horton et al. 1991, Jahns and Holzwarth 2012).

CO$_2$ assimilation may show stronger sensitivity to salinity than the operation of the electron transport around PSII (Darkó et al. 2015), thus salt stress finally causes oxidative damage through over-reduction of photosynthesis (Asada 2006, Ashraf and Harris
2013). In salt adapted halophyte plants, enhanced NPQ was observed, which provided effective protection against photoinhibition not only under salt stress but also at high temperatures (Qiu et al. 2003). A linear relationship was found between the aggregated LHCII and NPQ in heat-stressed plants (Tang et al. 2007). Since aggregation was observed at a lower temperature than the decrease in $F_v/F_m$, aggregated LHCII could also play a protective role in thermal stress as well as in the case of salt treatment. Due to salt preconditioning, a less pronounced thermosensitivity of OEC and PSII reaction center in salt-adapted plants have been shown by several studies (Chen et al. 2004, Wen et al. 2005, Yan et al. 2012). Since reduced water-splitting activity is also associated with the detachment of chloride ions under heat conditions (Krishnan and Mohanty 1984, Nash et al. 1985), it is possible that the higher chloride ion content under salt stress may increase the stability of OEC and result in the formation of more thermoresistant PSII. The synthesis of NaCl-induced compatible osmotics can also result in higher thermal resistance. Salt-induced proline accumulation may also contribute to the protection of reaction center, donor and acceptor side of PSII in heat-treated plants due to its membrane stabilizing role (Yan et al. 2012). Similarly to proline, salt-induced betaine and glycine betaine may also play a prominent role in protecting thylakoid membrane components, the stabilization of OEC (Chen and Murata 2008, Tian et al. 2017), and in the prevention of the detachment of external proteins from PSII (Murata et al. 1992). Modification of the lipid composition in the thylakoid membrane could be observed as a result of ionic stress which may also be part of the adaptation processes to salinity (Müller and Santarius 1978). The saturation of fatty acid in the thylakoid membrane can be determinative for avoiding salt stress and preventing the stability of membrane during the heating. Shu et al. (2015) have described an increase in the saturated fatty acid contents of thylakoid membranes under severe ion toxicity caused by NaCl. The higher ratios of the saturated fatty acids to unsaturated fatty acids may be beneficial even at high temperatures due to the reduced membrane fluidity (Raison et al. 1982). Accumulation of raffinose family oligosaccharides, polyols and polyamines may also represent a successful plant response to salinity and decreased water availability (Krasensky and Jonak 2012). Since these
macromolecules have considerable implications for protection of membrane and alleviating oxidative stress (Nishizawa et al. 2008, Krasensky and Jonak 2012) therefore their increased amount in salt-adapted plants could also be advantageous when plants are simultaneously affected by elevated temperature. HSPs also play a prominent role in defense of membranes against the negative effect of abiotic stresses (Al-Whaibi 2011). The increased amount of HSPs may be induced not only by heating, but also by several stress treatments such as salinity and dehydration (Swindell et al. 2007) representing an overlap in the signal transduction pathways induced by different stresses (Krasensky and Jonak 2012).

CONCLUSION

It is now evident that photosynthetic apparatus is harmfully affected by stressful environment such as water deficit, salinity and high temperature having a considerable impact on plant growth and development. The impact of each of these stress factors has been extensively studied but we have a less knowledge about their combined effect on the physiology processes of plants. OEC and cellular membranes especially thylakoid membrane may be disrupted by heat stress resulting in decreased activity of membrane-associated electron carries thereby photosynthesis will be limited. Although salinity and drought are known as a significant inhibitor of photosynthesis, but these stress factors may induce responses in plant cells having a positive effect on the thermotolerance of photosynthetic apparatus. These stress-induced modifications are mainly manifested in more rigid membranes, improved thermal resistance of OEC by compatible solutes and less pronounced lipid peroxidation by quenching reactive oxygen species. Summarizing our present knowledge, we can conclude that responses of plants induced by individual stress could promote plants to acclimatize more successfully to another stress which often appears simultaneously under natural conditions.

Acknowledgement – The first author’s research was supported by the grant EFOP-3.6.1-16-2016-00001 (”Complex improvement of research capacities and services at Eszterházy Károly University”). Sándor Dulai is grateful to TAMOP 4.2.2A-11/1/KONV-2012-0008 project.
REFERENCES

AHUJA, I., DE VOS, R.C.H., BONES, A.M. & HALL, R.D. (2010). Plant molecular stress responses face climate change. *Trends in Plant Science* **15**: 664–674. https://doi.org/10.1016/j.tips.2010.08.002

AL-WHAIBI, M.H. (2011). Plant heat-shock proteins: a mini review. *Journal of King Saud University-Science* **23**: 139–150. https://doi.org/10.1016/j.jsus.2010.06.022

ASADA, K (2006). Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant Physiology* **141**: 391–396. https://doi.org/10.1104/pp.106.082040

ASHRAF, M. & HARRIS, P.J.C. (2013). Photosynthesis under stressful environments: an overview. *Photosynthetica* **51**: 163–190. https://doi.org/10.1007/s11099-013-0021-6

BERRY, J. A. & BJÖRKMAN, O. (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**: 491–543. https://doi.org/10.1146/annurev.pp.31.060180.002423

BUKHOV, N.G., WIESE, C., NEIMANIS, S. & HEBER, U. (1999). Heat sensitivity of chloroplasts and leaves: leakage of protons from thylakoids and reversible activation of cyclic electron transport. *Photosynthesis Research* **59**: 81–93. https://doi.org/10.1023/A:1006149317411

CHEN, T.H.H. & MURATA, N. (2008). Glycinebetaine: an effective protectant against abiotic stress in plants. *Trends in Plant Science* **13**: 499–505. https://doi.org/10.1016/j.tplants.2008.06.007

CHENG, H.X., LI, W.J., AN, S.Z. & GAO, H.Y. (2004). Characterization of PSII photochemistry and thermostability in salt-treated *Rumex* leaves. *Journal of Plant Physiology* **161**: 257–264. https://doi.org/10.1016/0176-6518(00)00243-2

CHEN, S.T., HE, N.Y., CHEN, J.H. & GUO, F.Q. (2016). Identification of core subunits of photosystem II as action sites of HSP21 that is activated by the GUN5-mediated retrograde pathway in *Arabidopsis*. *The Plant Journal* **38**: 42–49. https://doi.org/10.1111/tjp.13447

DARKÓ, É., JANDA, T., MAJLÁTH, I., SZOPKÓ, D., DULAI, S., MOLNÁR, I., TÜRKÖSI, E. & MOLNÁRLÁNG, M. (2015). Salt stress response of wheat-barley addition lines carrying chromosomes from the winter barley "Manas". *Euphytica* **203**: 491–504. https://doi.org/10.1007/s10681-014-1245-7

DAU, H. (1994). Short-term adaptation of plants to changing light intensities and its relation to photosystem II photochemistry and fluorescence emission. *Journal Photochemistry and Photobiology* **26**: 3–27. https://doi.org/10.1016/1011-1344(94)85032-1

DEMIG, B., WINTER, K., KRÜGER, A. & Czygan, F.C. (1988). Zeaxanthin and the heat dissipation of excess light energy in *Nerium oleander* exposed to a combination of high light and water stress. *Plant Physiology* **87**: 17–24. https://doi.org/10.1104/pp.87.1.17

DULAI, S., MOLNÁR, I. & LEHOCZKI, E. (1998). Effects of growth temperature of 5 and 25 ºC on long-term responses of photosystem II to heat stress in atrazine-resistant and susceptible biotypes of *Erigeron canadensis* (L.). *Australian Journal of Plant Physiology* **25**: 154–143. https://doi.org/10.1071/pp97112
DULAI, S., MOLNÁR, I., PRÓNAY, J., MARSCHALL, M., CSERNÁK, Á., TARNAI, R. & MOLNÁR-LÁNG, M. (2005). Effects of drought on thermal stability of photosynthetic apparatus in bread wheat and Aegilops species originating from various habitats. *Acta Biologica Szegedensis* **49**: 215–217.

DULAI, S., MOLNÁR, I., PRÓNAY, J., CSERNÁK, Á., TARNAI, R. & MOLNÁR-LÁNG, M. (2006). Effects of drought on photosynthetic parameters and heat stability of PSII in wheat and in Aegilops species originating from dry habitats. *Acta Biologica Szegedensis* **50**: 11–17.

ENAMI, I., TOMO, T., KITAMURA, M. & KATOH, S. (1994). Immobilization of the three extrinsic proteins in spinach oxygen evolving Photosystem II membranes: roles of the proteins in stabilization of binding of Mn and Ca\(^{2+}\). *Biochimica et Biophysica Acta* **1185**: 75–80.

https://doi.org/10.1016/0005-2788(94)90195-3

ESSELINE, J., XIAO, Y., QU, M., MI, H. & ZHU, X.G. (2017). Cyclic electron flow may provide some protection against PSII photoinhibition in rice (*Oryza sativa L.*) leaves under heat stress. *Journal of Plant Physiology* **211**: 138–146.

https://doi.org/10.1016/j.jplph.2017.01.007

FELLER, U., CRAFFTS-BRANDNER, S.J. & SALVUCCI, M.E. (1998). Moderately high temperatures inhibit ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase-mediated activation of Rubisco. *Plant Physiology* **116**: 539–546. https://doi.org/10.1104/pp.116.2.539

FENG, B., LIU, P., LI, G., DONG, S.T., WANG, F.H., KONG, L.A. & ZHANG, J.W. (2014). Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. *Journal of Agronomy and Crop Science* **200**: 143–155. https://doi.org/10.1111/jac.12045

FERRARI-ILOU, R., PHAM-TI, A.T., VIEIRA, D.A. & SILVA, J. (1984). Effects of water stress on the lipid and fatty acid composition of cotton (*Gossypium hirsutum*) chloroplasts. *Physiologia Plantarum* **62**: 219–224.

https://doi.org/10.1111/j.1399-3054.1984.tb00374.x

GOULARIS, K., BRAIN, A.R.R., QUINN, P.J. & WILLIAMS, W.P. (1984). Structural reorganisation of chloroplast thylakoid membranes in response to heat-stress. *Biochimica et Biophysica Acta* **766**: 198–208. https://doi.org/10.1016/0005-2728(84)90232-9

GILMORE, A.M., HAZLETT, T.L., DEBRUNNER, P.G. & GOVINDEE (1996). Comparative time-resolved photosystem II chlorophyll a fluorescence analyses reveal distinctive differences between photoinhibitory reaction center damage and xanthophyll cycle-dependent energy dissipation. *Photochemistry and Photobiology* **64**: 552–563. https://doi.org/10.1111/j.1751-1097.1996.tb03105.x

HALDRUP, A., JENSEN, P.E., LUNDE, C. & SCHELLER, H.V. (2001). Balance of power: a view of the mechanism of photosynthetic state transitions. *Trends in Plant Science* **6**: 301–305. https://doi.org/10.1016/S1360-1385(01)01953-7

HALL, N.P. & KEYS, A.J. (1983). Temperature dependence of the enzymic carboxylation and oxygenation of ribulose 1,5-bisphosphate in relation to effects of temperature on photosynthesis. *Plant Physiology* **72**: 945–948. https://doi.org/10.1104/pp.72.4.945

HAVAUX, M. (1992). Stress tolerance of photosystem II in vivo. Antagonistic effects of water, heat, and photoinhibition stresses. *Plant Physiology* **100**: 424–432. https://doi.org/10.1104/pp.100.1.424
HAVAUX, M. (1996). Short-term responses of photosystem I to heat stress: Induction of a PS II-independent electron transport through PSI fed by stromal components. Photosynthesis Research 47: 85–97. https://doi.org/10.1007/BF00017756

HAVAUX, M. & GRUSZECKI, W.I. (1993). Heat- and light-induced chlorophyll a fluorescence changes in potato leaves containing high or low levels of the carotenoid zeaxanthin: indication of regulatory effect of zeaxanthin on thylakoid membrane fluidity. Photochemistry and Photobiology 58: 607–614. https://doi.org/10.1111/j.1751-1097.1993.tb04940.x

HAVAUX, M. & Tardy, F. (1995). Short-term adaptive responses of photosynthesis to elevated temperatures and strong light. In: Mathis, P. (ed.): Photosynthesis: from Light to Biosphere. Kluwer Academic Publishers, Dordrecht, pp. 777–782.

HAVAUX, M. & Tardy, F. (1996). Temperature-dependent adjustment of the thermal stability of photosystem II in vivo: possible involvement of xanthophyll-cycle pigments. Planta 198: 324–333. https://doi.org/10.1007/bf0620047

HAVAUX, M., Tardy, F., Ravenel, J., Chanu, D. & Parot, P. (1996). Thylakoid membrane stability to heat stress studied by flash spectroscopic measurements of the electrochromic shift in intact potato leaves: influence of the xanthophyll content. Plant, Cell and Environment 19: 1359–1368. https://doi.org/10.1111/j.1365-3040.1996.tb00014.x

Hill, R., Ulstrup, K.E. & Ralph, P.J. (2009). Temperature induced changes in thylakoid membrane thermostability of cultured, freshly isolated, and expelled zooxanthellae from Scleractinian corals. Bulletin of Marine Science 85: 223–244.

Horton, P., Ruban, A.V., Rees, D., Pascal, A.A., Noctor, G. & Young, A.J. (1991). Control of the light/harvesting function of chloroplast membranes by aggregation of the LHCII chlorophyll protein complex. FEBS Letters 292: 1–4. https://doi.org/10.1016/0014-5793(91)80819-0

Jahns, P. & Holzwarth, A.R. (2012). The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. Biochimica et Biophysica Acta 1817: 182–193. https://doi.org/10.1016/j.bbabio.2011.04.012

Johnson, M.P., Havaux, M., Triantaphylides, C., Ksas, B., Pascal, A.A., Robert, B., Davison, P.A., Ruban, A.V. & Horton, P. (2007). Elevated zeaxanthin bound to oligomeric LHCII enhances the resistance of Arabidopsis to photo-oxidative stress by a lipid-protective, antioxidant mechanism. The Journal of Biological Chemistry 282: 22605–22618. https://doi.org/10.1074/jbc.M702831200

Khatoon, M., Inagawa, K., Pospisil, P., Yamashita, A., Yoshioka, M., Lundin, B., Horie, J., Morita, N., Jajoo, A. & Yamamoto, Y. (2009). Quality Control of Photosystem II thylakoid unstacking is necessary to avoid further damage to the D1 protein and to facilitate D1 degradation under light stress in spinach thylakoids. Journal of Biological Chemistry 284: 25343–25352. https://doi.org/10.1074/jbc.M109.007740

Kiss, A.Z., Ruban, A.V. & Horton, P. (2008). The PsbS protein controls the organization of the photosystem II antenna in higher plant thylakoid membranes. The Journal of Biological Chemistry 283: 3972–3978. https://doi.org/10.1074/jbc.M707410200

Komayama, K., Khatoon, M., Takenaka, D., Horie, J., Yamashita, A., Yoshioka, M., Nakayama, Y., Yoshida, M., Ohira, S., Morita, N., Velitchkova, M., Enami, I. &
Yamamoto, Y. (2007). Quality control of photosystem II: Cleavage and aggregation of heat-damaged D1 protein in spinach thylakoids. *Biochimica et Biophysica Acta Bioenergetics* **1767**: 838–846. https://doi.org/10.1016/j.bbabio.2007.05.001

Kouril, R., Lazar, D., Ilík, P., Skotnica, J., Krchnák, P. & Naus, J. (2004). High temperature-induced chlorophyll fluorescence rise in plants at 40-50°C: experimental and theoretical approach. *Photosynthesis Research* **81**: 49–66. https://doi.org/10.1023/B:PRES.0000028391.70533.eb

Krasensky, J. & Jonak, C. (2012). Drought, salt, and temperature stress-induced metabolic rearrangements and regulatory networks. *Journal of Experimental Botany* **63**(4): 1593–1608. https://doi.org/10.1093/jxb/err460

Krishnan, M. & Mohanty, P. (1984). Reactivation by chloride of Hill activity in heat- and Tris-treated thylakoid membranes from *Beta vulgaris*. *Photosynthesis Research* **5**: 185–198. https://doi.org/10.1007/BF00028531

Kunst, L., Browse, J. & Somerville, C. (1989). Enhanced thermal tolerance in a mutant of *Arabidopsis* deficient in palmitic acid unsaturation. *Plant Physiology* **91**: 401–408. https://doi.org/10.1104/pp.91.1.401

Lavaud, J. & Kroth, P. (2006). In diatoms, the transthylakoid proton gradient regulates the photoprotective non-photochemical fluorescence quenching beyond its control on the xanthophyll cycle. *Plant and Cell Physiology* **47**: 1010–1016. https://doi.org/10.1093/pcp/pcj058

Law, R.D. & Crafts-Brandner, S.J. (1999). Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate Carboxylase/Oxygenase. *Plant Physiology* **120**: 173–182. https://doi.org/10.1104/pp.120.1.173

Lemeille, S. & Rochaix, J.D. (2010). State transitions at the crossroad of thylakoid signalling pathways. *Photosynthesis Research* **106**: 33–46. https://doi.org/10.1007/s11120-010-9538-8

Loreto, F. & Schnitzler, J.P. (2010). Abiotic stresses and induced BVOCs. *Trends in Plant Science* **15**: 154–166. https://doi.org/10.1016/j.tpls.2009.12.006

Lu, C. & Zhang, J. (1999). Effects of water stress on PSI photochemistry and its thermostability in wheat plants. *Journal of Experimental Botany* **50**: 1199–1206. https://doi.org/10.1093/jxb/50.336.1199

Marutani, Y., Yamauchi, Y., Kimura, Y., Mizutani, M. & Sugimoto, Y. (2012). Damage to photosystem II due to heat stress without light-driven electron flow: involvement of enhanced introduction of reducing power into thylakoid membranes. *Planta* **236**: 753–761. https://doi.org/10.1007/s00425-012-1647-5

Mittler, R., Finka, A. & Goloubinoff, P. (2012). How do plants feel the heat? *Trends in Biochemical Sciences* **37**: 118–125. https://doi.org/10.1016/j.tibs.2011.11.007

Molnár, I., Csíz, K., Dulai, S., Darkó, É. & Lehoczki, E. (1998). *Light dependence of thermostability of photosynthetic apparatus*. In: Garab, G. (ed.): *Photosynthesis: Mechanisms and Effects*. Kluwer Academic Publishers, Dordrecht/Boston/London, pp. 2241–2244. https://doi.org/10.1007/978-94-011-3953-3_524

Murata, N., Mohanty, P.S., Hayashi, H. & Papageorgiou, G.C. (1992). Glycinebetaine stabilizes the association of extrinsic proteins with the photosynthetic oxygen-
evolving complex. FEBS Letters 296: 187–189. https://doi.org/10.1016/0014-5793(92)80376-R

MÜLLER, M. & SANTARIUS, K.A. (1978). Changes in chloroplast membrane lipids during adaptation of barley to extreme salinity. Plant Physiology 62: 326–329. https://doi.org/10.1104/pp.62.3.326

NASH, D., MIYAO, M. & MURATA, N. (1985). Heat inactivation of oxygen evolution in photosystem II particles and its acceleration by chloride depletion and exogenous manganese. Biochimica et Biophysica Acta 807: 127–133. https://doi.org/10.1016/0005-2728(85)90115-x

NELLAEFPALLI, S., MEKALA, N.R., ZSÍROS, O., MOHANTY, P. & SUBRAMANYAM, R. (2011). Moderate heat stress induces state transitions in Arabidopsis thaliana. Biochimica et Biophysica Acta 1807: 1177–1184. https://doi.org/10.1016/j.bbabio.2011.05.016

NISHIZAWA, A., YABUTA, Y. & SHIGEOKA, S. (2008). Galactinol and raffinose constitute a novel function to protect plants from oxidative damage. Plant Physiology 147: 1251–1263. https://doi.org/10.1104/pp.108.122465

OSMOND, C.B., AUSTIN, M.P., BERRY, J.A., BILLINGS, W.D., BOYER, J.S., DACEY, W.J.H., NOBEL, P.S., SMITH, S.D. & WINTER, E. (1986). Stress physiology and the distribution of plants. BioScience 37: 38–48. https://doi.org/10.2307/1310176

PENG, Y., XU, C., XU, L. & HUANG, B. (2012). Improved heat tolerance through drought preconditioning associated with changes in lipid composition, antioxidant enzymes, and protein expression in kentucky bluegrass. Crop Science 52: 807–817. https://doi.org/10.2135/cropsci2011.06.0327

PETERHANSEL, C., HORST, I., NIessen, M., BLUME, C., KEBEISH, R., KÜRCÜOĞLU, S. & KREUZALER, F. (2010). Photorespiration. The Arabidopsis Book/American Society of Plant Biologists 8: e0130. https://doi.org/10.1199/tab.0130

QIU, N., LU, Q. & LU, C. (2003). Photosynthesis, photosystem II efficiency and the xanthophyll cycle in the salt-adapted halophyte Atriplex centralasiatica. New Phytologist 159: 479–486. https://doi.org/10.1046/j.1469-8137.2003.00825.x

RAISON, J.K., ROBERTS, J.K.M. & BERRY, J.A. (1982). Correlation between the thermal stability of chloroplast (thylakoid) membranes and the composition and fluidity of their polar lipids upon acclimation of the higher plant, Nerium oleander, to growth temperature. Biochimica et Biophysica Acta 688: 218–228. https://doi.org/10.1016/0005-2736(82)90597-1

RHODES, D. & HANSON, A.D. (1993). Quaternary ammonium and tertiary sulfonium compounds in higher plants. Annual Review of Plant Physiology and Plant Molecular Biology 44: 357–384. https://doi.org/10.1146/annurev.pp.44.060193.002041

RIBEIRO, R.V., SANTOS, M.G., MACHADO, E.C. & OLIVEIRA, R.F. (2008). Photochemical heat-shock response in common bean leaves as affected by previous water deficit. Russian Journal of Plant Physiology: a Comprehensive Russian Journal on Modern Phytophysiology 55: 350–358. https://doi.org/10.1134/S1021443708030102

SCHREIBER, U. & BERRY, J.A. (1977). Heat-induced changes of xanthophyll fluorescence in intact leaves correlated with damage of the photosynthetic apparatus. Planta 136: 233–238. https://doi.org/10.1007/BF00385990

105
Schreiber, U. & Bilger, W. (1987). Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. In: Tenhunen, J.D., Cararino, F.M., Lange, O.L. & Oechel, W.D. (eds.): Plant response to stress. Springer-Verlag, New York, pp 27–53. https://doi.org/10.1007/978-3-642-70868-8_2

Seemann, J.R., Downton, W.J.S. & Berry, J.A. (1986). Temperature and leaf osmotic potential as factors in the acclimation of photosynthesis to high-temperature in desert plants. Plant Physiology 80: 926–930. https://doi.org/10.1104/pp.80.4.926

Sharkey, T.D. (2005). Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant Cell and Environment 28: 269–277. https://doi.org/10.1111/j.1365-3040.2005.01324.x

Sharkey, T.D. & Singh, E.L. (1995). Why plants emit isoprene. Nature 374: 769. https://doi.org/10.1038/374769a0

Sharkey, T.D. & Yeh, S. (2001). Isoprene emission from plants. Annual Review of Plant Physiology and Plant Molecular Biology 52: 407–436. https://doi.org/10.1146/annurev.arplant.52.1.407

Sharkey, T.D. & Zhang, R. (2010). High temperature effects on electron and proton circuits of photosynthesis. Journal of Integrative Plant Biology 52: 712–722. https://doi.org/10.1111/j.1744-7909.2010.00975.x

Shu, S., YUAN, Y., Chen, J., Sun, J., ZHANG, W., TANG, Y., ZHONG, M. & Guo, S. (2015). The role of putrescine in the regulation of proteins and fatty acids of thylakoid membranes under salt stress. Scientific Reports 5: 14390. https://doi.org/10.1038/srep14390

Suzuki, N., Rivero, R.M., Shulaev, V., Blumwald, E. & Mittler, R. (2014). Abiotic and biotic stress combinations. New Phytologist 203: 32–43. https://doi.org/10.1111/nph.12797

Swindell, W.R., Huebner, M. & Weber, A.P. (2007). Transcriptional profiling of Arabidopsis heat shock proteins and transcription factors reveals extensive overlap between heat and non-heat stress response pathways. BMC Genomics 8: 125. https://doi.org/10.1186/1471-2164-8-125

Takahashi, S., Milward, S.E., Fan, D.Y., Chow, W.S. & Badger, M.R. (2009). How does cyclic electron flow alleviate photoinhibition in Arabidopsis? Plant Physiology 149: 1560–1567. https://doi.org/10.1104/pp.108.134122

Tang, Y., Wen, X., Lu, Q., Yang, Z., CHENG, Z. & Lu, C. (2007). Heat stress induces an aggregation of the light-harvesting complex of photosystem II in spinach plants. Plant Physiology 143: 629–638. https://doi.org/10.1104/pp.106.090712

Tardy, F. & Havaux, M. (1997). Thylakoid membrane fluidity and thermostability during the operation of the xanthophyll cycle in higher-plant chloroplasts. Biochimica et Biophysica Acta 1330: 179–193. https://doi.org/10.1016/S0005-2736(97)00168-5

Teskey, R., WERTIN, T., Bauweraerts, I., AMEYE, M., McGuire, M.A. & Steppe, K. (2014). Responses of tree species to heat waves and extreme heat events. Plant, Cell and Environment 38: 1699–1712. https://doi.org/10.1111/pce.12417

Tian, F., Wang, W., Liang, C., Wang, X., Wang, G. & Wang, W. (2017). Overaccumulation of glycine betaine makes the function of the thylakoid
membrane better in wheat under salt stress. *The Crop Journal* **5**: 73–82. https://doi.org/10.1016/j.cj.2016.05.008

**Velikova, V., Várkonyi, Zs., Szabó, M., Maslenkova, L., Nogues, I., Kovács, L., Pevva, V., Busheva, M., Garab, Gy., Sharkey, T.D. & Loreto, F.** (2011). Increased thermostability of thylakoid membranes in isoprene-emitting leaves probed with three biophysical techniques. *Plant Physiology* **157**: 905–916. https://doi.org/10.1104/pp.111.182519

**Wang, G.P., Li, F., Zhang, J., Zhao, M.R., Hui, Z. & Wang, W.** (2010). Overaccumulation of glycine betaine enhances tolerance of the photosynthetic apparatus to drought and heat stress in wheat. *Photosynthetica* **48**: 30–41. https://doi.org/10.1007/s11099-010-0006-7

**Wang, Q.L., Chen, J.H., He, N.Y. & Guo, F.Q.** (2018). Metabolic reprogramming in chloroplasts under heat stress in plants. *International Journal of Molecular Sciences* **19**(3): 849. https://doi.org/10.3390/ijms19030849

**Wen, X.G., Qiu, N.W., Lu, Q.T. & Lu, C.M.** (2005). Enhanced thermotolerance of photosystem II in salt-adapted plants of the halophyte *Artemisia anethifolia*. *Planta* **220**: 486–497. https://doi.org/10.1007/s00425-004-1382-7

**Wise, R.R., Olson, AJ., Schrader, S.M. & Sharkey, T.D.** (2004). Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. *Plant, Cell and Environment* **27**: 717–724. https://doi.org/10.1111/j.1365-3040.2004.01171.x

**Yamamoto, H.Y., Chang, J.L. & Aihara, M.S.** (1967). Light-induced interconversion of violaxanthin and zeaxanthin in New Zealand spinach-leaf segments. *Biochimica et Biophysica Acta* **141**: 342–347. https://doi.org/10.1016/0006-2977(67)90108-0

**Yamane, Y., Kashino, Y., Koike, H. & Satoh, K.** (1997). Increases in the fluorescence F_0 level and reversible inhibition of Photosystem II reaction center by high-temperature treatments in higher plants. *Photosynthesis Research* **52**: 57–64. https://doi.org/10.1023/A:1005884717655

**Yamane, Y., Kashino, Y., Koike, H. & Satoh, K.** (1998). Effects of high temperatures on the photosynthetic systems in spinach: Oxygen-evolving activities, fluorescence characteristics and the denaturation process. *Photosynthesis Research* **57**: 51–59. https://doi.org/10.1023/A:1006019102619

**Yan, K., Chen, P., Shao, H., Zhao, S., Zhang, L., Zhang, L., Xu, G. & Sun, J.** (2012). Responses of photosynthesis and photosystem II to higher temperature and salt stress in Sorghum. *Journal of Agronomy and Crop Science* **198**: 218–226. https://doi.org/10.1111/j.1439-037X.2011.00498.x

(Submitted: 28.06.2018, accepted: 13.09.2018)