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ENVIRONMENTAL FACTORS AFFECTING THE HEAT STABILITY OF THE PHOTOSYNTHETIC APPARATUS

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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 CO_2 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 CO_2 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 (LHCII) 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 (ΔpH). The enhancement of cyclic electron flow around PSI (CEF) may also contribute to the increase in the ΔpH 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 (Q_A) and the secondary (Q_B) acceptor plastoquinone of PSII resulting in the accumulation of reduced Q_A (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 (F_0) and steady-state fluorescence (F_S) *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 thermotolerance of the photosynthetic apparatus in connection with the integrity of thylakoid lamellaes (Hill *et al.* 2009).

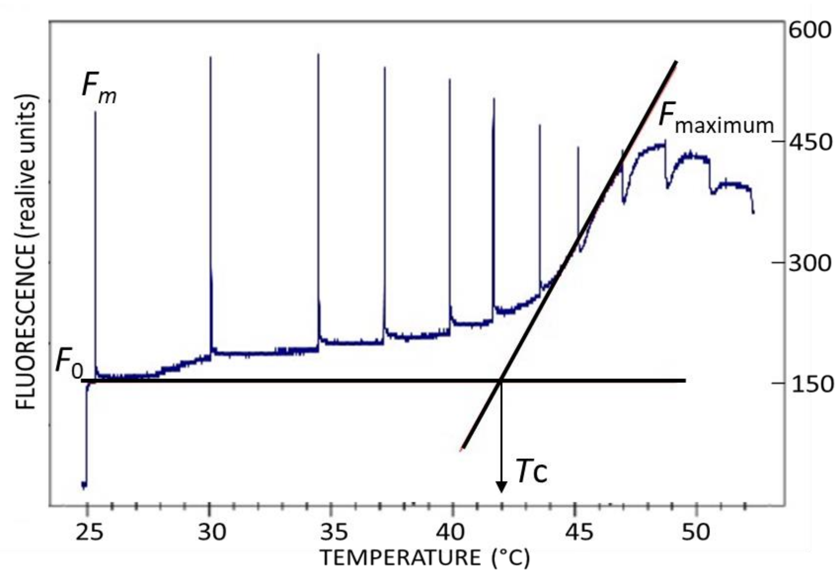

Figure 1. An example of F_0 *vs*. T curve where the temperature was increased at a rate of 1 °C min^{-1} (Hill *et al.* 2009). The critical temperature for photochemical damage (Tc) was defined as the interception of regression lines fitted to fluorescence data.

In addition, Tc may also indicate the critical temperature where the quantum efficiency of CO_2 fixation is impaired by heat treatment (Schreiber and Bilger 1987). Rising in F_o 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 Q_A. The latter is connected to the reversed electron donation between Q_A and Q_B or the impaired electron transport capacity from Q_A to Q_B due to the damaged D1 protein (Gilmore *et al.* 1996, Kouril *et al*. 2004). At a temperature above Tc, 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 (ϕ_{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 stabilty 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 availibility (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.

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