BULG. J. PLANT PHYSIOL., 1995, 21(2–3), 51–70

RESPONSES OF PHOTOSYNTHESIS TO STRESS AND PLANT GROWTH REGULATORS

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Summary. In this paper the response of photosynthesis to stress independently or in combination with other stresses is considered. Some mechanisms by means of photosynthetic apparatus is acclimated to respective stress and enhanced its thermotolerance as well as the role of some heat shock proteins (HSP70, HSP21) and plant growth regulators (polyamines ABA) are also discussed.

Key words: photosynthesis, stress, acclimation, HSPs, plant growth regulators

Introduction

The process of photosynthesis integrates photochemical reactions which proceed at a rate independent of temperature (i. e. Q_{10}=1) with the thermosensitive, enzyme catalized reactions which typically exhibit a Q_{10} of about 2.0 (Hunner, 1995). During exposure to changing environmental conditions photosynthesized organisms must maintain a balance between energy supply through photochemistry and energy consumption through photosynthetic carbon reduction. Sudden imbalances in the energy budget are dampened by regulating PS2 photochemical efficiency through photosynthetic control (Foyer et al., 1990).

In green plants photosynthesis is among the first processes being affected by elevated temperatures (Alexandrov, 1975; Björkman, 1975; Berry and Björkman, 1980; Yordanov, 1992). The damage due to heat stress (HS) includes a wide range of structural and functional changes. The results from *in vivo* and *in vitro* studies showed that the primary target of high temperature stress (HTS) involves the PS2 reaction center (PS2 RC) with reduced water oxidizing activity being the major injury. When temperature rises above 35 °C, the PS2 core complex, as well as part of LHC2 migrate lateraly from the integral spaces in the stroma lamellae where PS1 is mainly

located. These thylakoid membrane structural rearrangements are completely reversible when the temperature decreases. It is believed that their physiological role is to protect PS2 from overexcitation under high irradiances. At higher temperature more extensive breakdown of PS2 occurs, leading to a separation of the PS2 core from the main LHC2, a general destacking of the thylakoid membranes and the phase separation of non bilayer forming lipid components (Leach at al., 1985). These latter changes are accompanied by a dramatic loss of PS2 electron transfer activity, which in turn, is reflected in major changes in photochemistry and fluorescence yield of chlorophyll *a* (Chl. a) associated with PS2 (Schreiber and Armond, 1978).

It is believed that thermal denaturation of PS2 is linked to major physical changes occurring in the lipid matrix of thylakoid membranes during heating which are likely to alter lipid protein interactions (Gounaris et al., 1984; Havaux, 1992) and hence cause conformational changes in thylakoid proteins.

The surface charge of the thylakoid membrane is the major property determining its stability (Träuble and Eibl, 1974, Sackman, 1983). If the charge density on the membrane surface increases, the electrostatic repulsion between equally charged molecules grows as well. As a consequence, lipids become more disordered which could lead to protein lateral diffusion in the membrane plane, accompanied by decrease in its stability, making it more sensitive to heat damage (Barber, 1981; Goltsev et al., 1987). Direct result of heat inactivation is also a release of functional manganese ions from the PS2 complex (Nash et al., 1985; Mamedov et al., 1993).

The heat stress induced hyperfluidization of thylakoid membranes which affects lipid protein interaction and causes various perturbations (phase transitions of lipids as well as conformational changes and destructive processes in the thylakoid membrane) (TM) and altering their major function. The oxygen-evolving complex activity, energy migration, electrochromic shift of pigment absorption at 515 nm (an indicator for membrane potential), electron transport and photophosphorylation are among the first to be affected and injured (Junge, 1977; Schreiber and Berry, 1977; Berry and Björkman, 1980; Yordanov and Weis, 1984; Yordanov et al., 1987). The breakdown of O_2 evolution has been associated with damage of PS2 (Al-Khatib and Paulsen, 1989; Havaux et al., 1991). Simultaneously the biosynthesis and radiant energy activation of Rubisco decreases (Süss and Yordanov, 1986; Santarius et al., 1991).

Chloroplast photochemical activity decreases after HS (Sabat et al., 1991; Havaux, 1993; Havaux and Gruszecki, 1993) but light can modify the heat stability of the photosynthetic apparatus. In isolated chloroplasts incubated at high temperatures, light can produce an injurious effect on the electron transport chain. In wheat plants thermal injury of *in vivo* photosynthesis was strongly aggravated by bright light. But evidence is accumulated that rather than causes injury, light can alleviate the heat induced inhibition of leaf or chloroplast photosynthesis (Schreiber and Berry, 1977; Kislyuk, 1979; Weis, 1981, 1982a,b; Havaux and Strasser, 1990; Havaux et al., 1991). On Fig. 1 photosynthetic O_2 evolution (A) and maximal Fv (B) in pea leaves pretreated for

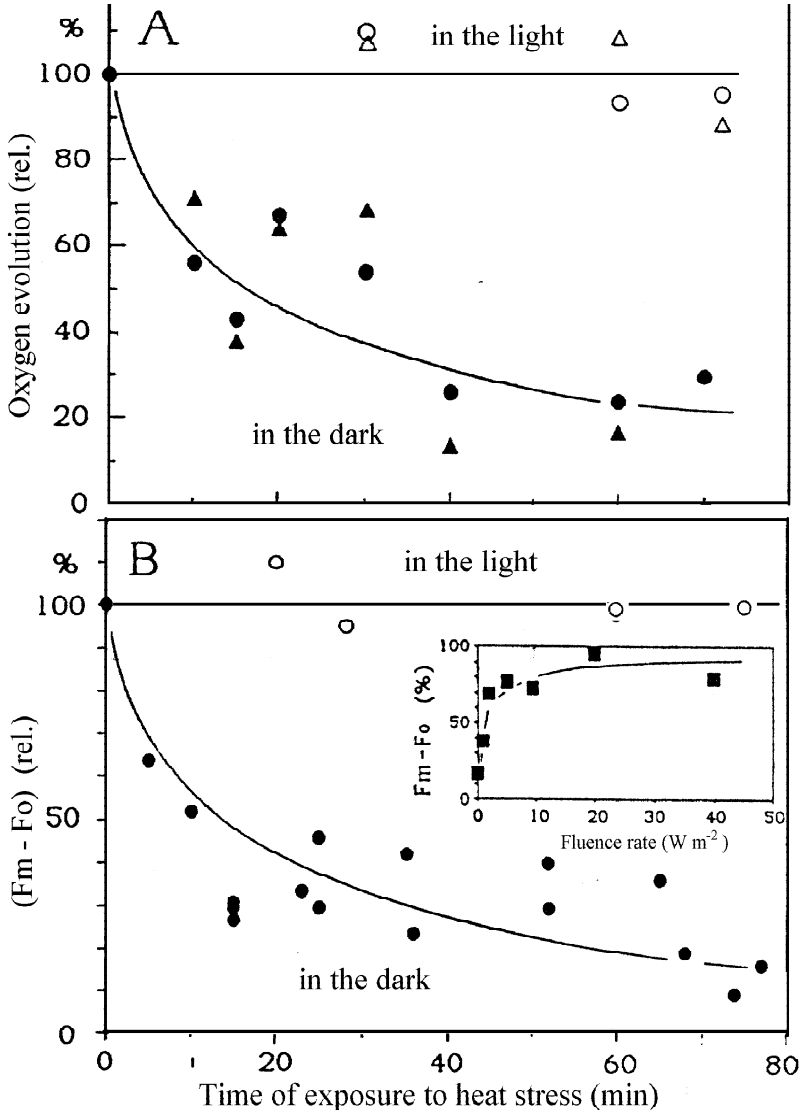

Fig. 1. Photosynthetic oxygen evolution (A) and amplitude (F_m–F_0) of maximal variable chlorophyll fluorescence (B) in pea leaves pretreated for various times at a high themperature of 40±0.5°C in the dark (*closed symbols*) or in the light (*open symbols*). Oxygen exchanges were monitored at 22°C in leaves illuminated with a 300 or 600 nm light of saturating (500W.m^{-2}, ∘ and •) or limiting (6W.m^{-2}, ∆ and ▲) irradiance (according to Havaux et al., 1991)

various time at 40 °C in the dark (close symbols) or in the light (30 W.m^{-2}, open symbols) are shown. It can be seen that HS in the dark causes a drastic inhibition of both

the rate of oxygen production and maximal variable fluorescence. In contrast, when the leaves were exposed to HT in the presence of light no inhibition of oxygen evolution and fluorescence was detected, clearly showing the protective nature of light against heat injury of these processes (Havaux and Strasser, 1990; Havaux, 1992).

Based on the chlorophyll fluorescence parameters behaviour at HT stress we (Goltsev and Yordanov, non-publ.) try to present in consecutive order the injury to different parts of the photosynthetic machinery (Fig. 2). At high temperature conditions the changes in different parameters of chlorophyll fluorescence induction kinetics are caused by some processes proceeding simultaneously, but dominating at different temperature diapasons. They influenced differently F_v, F_0 and F_m. At mild temperatures 25–40 °C the main influence on fluorescence changes is connected with two processes: enhancing the radiationless deactivation of excited chlorophyll molecules and increasing the excitation energy migration from LHC2 RC2 to RC1. The

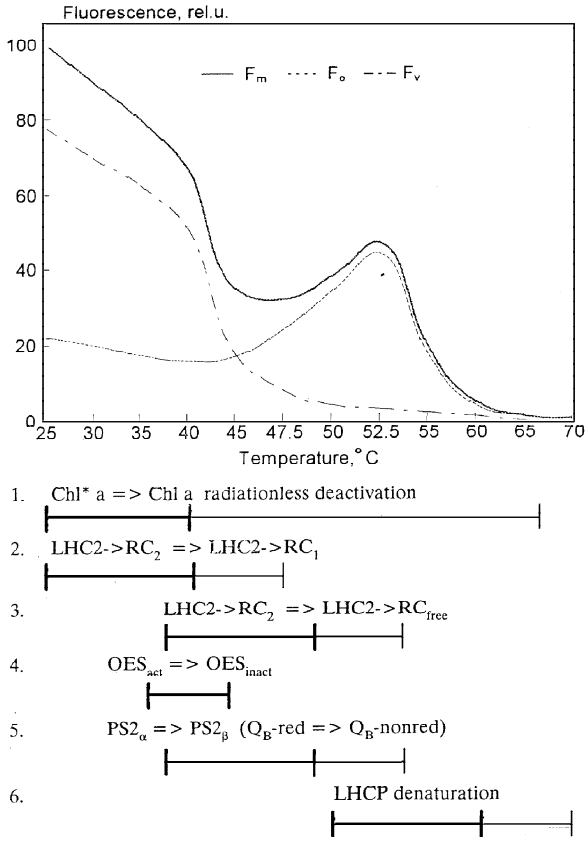

Fig. 2. Conceivable consecution of the reactions leading to the injury to different parts of photosynthetic mashinery

latter leads to an increase in the size of weakly fluorescing PS1. Both processes decreased the quantum efficiency of fluorescence resulting in an amplitude lowering of all three parameters.

More complex is the situation in the 40–47.5 °C range, where besides the above mentioned processes proceed, in addition, at least three other processes, modifying fluorescence quantum yield directly and changing the rate of electron transport around PS2. Part of the LHC2 complexes dissociated from the PS2 core and are in a free state so they could realize chlorophyll excitation only through irradiation or radiationless deactivation, which leads to an increase of F_0 fluorescence. Simultaneously an inactivation of oxygen evolution system occurs which leads to formation of a fluorescence quenching state (e. g. P^{+}_{680}), and causes the sharp drop of F_v in the 40–45 °C range. These temperatures provoke also the changes in the acceptor side of PS2. In this situation a part of PS2α centers is transferred in PS2β Q_B-non reducing ones. At very HT (above 52 °C) a denaturation of protein components of LHCP occurs which changes the surrounding of chlorophyll molecules and increases the access of the molecule quenchers to excited chlorophylls. As a result fluorescence is almost entirely inhibited.

Fortunately, organisms are able to acquire thermotolerance and to survive within a wider temperature interval involving constitutional and facultative changes. The later are transitional phylogenetic modifications that appear in response to different environmental agents.

Acclimation to High Temperature Stress

The role of protein synthesis

Acclimation involves both short-term chemical, molecular and physiological responses and long term physiological structural and morphological modifications (Howarth and Ougham, 1993). In most cases the adaptive mechanisms to different thermal regimes could be considered as compensatory, because they enable plants to buffer the effect of the temperature shift on their metabolic systems (Berry and Raison, 1981). As a result, the amount of specific components compensating the temperature effect on the rate of a given reaction changes.

The protein synthesizing system plays a crucial role in plant acclimation processes. It has been hypothesized that particular proteins whose synthesis is induced by stress conditions are critical for the survival in that stress (Schöffl et al., 1988; Scandalios, 1990) Pretreatments which lead to acquisition of thermotolerance are conditions under which heat shock proteins (HSPs) are synthesized (Kimpel and Key, 1985; Kimpel et al., 1990; Nagao et al., 1986). During HS these HSPs could interact with other proteins to prevent their aggregation and facilitate reassemblance of func-

tional structure (Pelham, 1988). These and other correlative data strongly suggest, but still do not demonstrate definitively, that accumulation of HSPs is crucial in protecting from thermal killing (Vierling, 1991). If the growth temperature of plants is increased beyond a particular point, dramatic changes in gene expression and translation occur. Instead of normal pattern a new set of proteins is synthesized from new mRNAs. Munro and Pelham (1985) suggest that it is the level of denatured proteins in the cell which triggers HS response. The authors found support of this suggestion in the behaviour of HS induced HSP70 which is involved in degradation of denatured proteins. According to Pelham (1988) during HS, HSP70 binds to the exposed hydrophobic regions of protein aggregates and facilitates their degradation. Moreover, some authors called free HSP70 "cellular thermometer".

Since it appeared that thermotolerance, in most cases, correlates closely with HSP synthesis it has been hypothesized that the function of at least one HS gene is implicated in causing thermotolerance. The requirements for protein synthesis in the development of thermotolerance has been shown by inhibitor studies. Addition of cycloheximide immediately prior HS blocks both HSP synthesis and the induction of thermotolerance (McAlister and Finkelstein, 1980). The exogenous cytokinin, benzyladenine, which stimulates the protein synthesizing system activity affects resistance positively (Titov et al., 1986).

Accumulating evidence indicates that through the stabilization of proteins in a particular state HSP90, HSP70 and HSP60 facilitate a wider diversity of important processes including protein folding, transport of proteins across membranes and their correct conformation, the assembly of oligomeric proteins and modulation of receptor activities, DNA replication and mRNA turnover (Pelham, 1986; Ellis, 1987; Lindquist and Craig, 1988; Vierling, 1991). All these functions require the alteration or maintenance of specific polypeptide conformation. Based on these activities, HSP90, HSP70 and HSP60 have been termed "molecular chaperones" or polypeptide chain binding proteins (Ellis, 1987; Rothman, 1989; Pelham, 1990). Therefore, chaperone proteins serve multifunctional roles. May be they prevent the formation of incorrect structures or support reconstitution of partially denatured proteins (Ellis, 1990).

The HSP60 in chloroplasts is the Rubisco subunits binding protein also known as chloroplast chaperonin. It is proposed to be involved in assembling the Rubisco holoenzyme (Roy, 1989).

In addition to high molecular weight (HMW) HSPs typical of eucariotes, higher plants and algae also synthesize nucleus encoded low molecular weight (LMW) 17–26 kDa proteins which are localized in chloroplasts (Kloppstech et al., 1985; Süss and Yordanov, 1986; Vierling, 1987; Vierling et al., 1986, 1988). In contrast to HMW HSPs presented both constituively and at elevated temperatures only certain LMW HSPs are present in absence of stress. Some of LMW HSPs have been demonstrated to became associated with photosynthetic membranes, potentially protecting the photosynthetic apparatus from damage at high temperatures (Schuster et al., 1988). The

fact that chloroplast HSPs are found in diverse plant species and that chloroplast HSP mRNA is abundant during stress suggests that those proteins are major components of the HS response. The half-life of chloroplast HSP21 in pea at control temperatures was 52 ± 12 h suggesting that the protein function is critical during recovery, as well as during stress (Chen et al., 1990). There is also an evidence for thermal adaptation dependent regulation of HSP21 synthesis (Lehel et al., 1993).

It was shown that in pea, bean, Chlamidomonas and some other plants HSP21, which is the only heat-induced chloroplast protein, is bound to chloroplast membranes (Glaczinski and Kloppstech, 1988; Adamska and Kloppstech, 1991; Süss and Yordanov – unpubl.). Such a localisation would be in accordance with its probable function against photoinhibition under HS conditions (Adamska and Kloppstech, 1991). In agreement with this interpretation HSP22 in Chlamidomonas was found in the grana thylakoid membrane fraction.

How LMW HSPs fulfil their protective role is not known. In the laboratory of Kloppstech (Kloppstech at all, 1985; Glaczincki and Kloppstech, 1988; Adamska and Kloppstech, 1991) it was proposed that the chloroplast HSP21 functions to protect or repair PS2 which is one of the most sensitive chloroplast components during stress. On the basis of our data it can be concluded that as a main product of heat acclimation HSP21 may protect also the normal supramolecular organization of "the flexible" enzyme of Benson–Calvin cycle. It is interesting to mention that by isolation HSP21 was always found at the same fraction with pyrophosphate epimerase, transketolase and aldolase.

In spite of the great interest in HSPs it is still not possible to say categorically that their and only their synthesis is responsible for the acquisition of thermotolerance (Howarth and Ougham, 1993). It is also possible that their role is not in the development of thermotolerance, but in the repair of heat induced damages.

The role of lipids in thylakoid membrane thermotolerance acquisition

The possible role of plant lipids, particularly membrane lipids, in high temperature susceptibility and tolerance is also an important problem. The degree of unsaturation of acyl residues of glycerolipids determines the physical characteristics of membranes (Chapmen, 1975; Quinn, 1988; Quinn et al., 1989). Therefore one can be postulated that the degree of fatty acid unsaturation should affect various functions of membrane bound proteins. Glycerolipids of the thylakoid membrane not only serve as a major constituent of the membrane-forming bilayer but they also provide hydrophobic ligands to membraneous proteins (Doyle and Yu, 1985). They play an important role also in maintaining the photosynthetic electron transport machinery.

As Williams (1994) noted the role of lipids in determining the ability of plant to resist thermal stress is not well known. But, a remarkable increase in protein/lipid ratio under acclimation was observed in thylakoids (Vigh et al., 1990). High tempera-

ture acclimation of higher plants is usually, but not always, accompanied by increased lipid saturation (Santarius and Müller, 1979). Many authors (Pearcy, 1978; Raison 1982; Süss and Yordanov, 1986) observed that the rise in growth temperature increases the level of saturated fatty acids in membrane lipids and enhances the heat stability of photosynthesis. Moreover, Thomas et al. (1986) found marked increases in PS2 stability following hydrogenation of the thylakoid membranes of pea chloroplasts. In the same time, Gombos et al. (1991) have reported little or no difference in the thermal stability of a fatty acid desaturase mutant of *Synechoccystis* PCC6803 that was incapable of synthesizing polyenoic lipids and wild-type cells, suggesting that the presence of such lipids plays little part in PS2 ability in cyanobacteria. Moreover, in the recent paper Gombos et al. (1994) demonstrated that in contrast to the previous hypothesis, unsaturation of membrane lipids stabilizes to a small, but distinct extent, photosynthesis of cyanobacteria *Synechocystis* PCC6803 against heat inactivation.

High temperature acclimation involves also adaptive changes in lipid composition. Raison et al. (1982) showed that during heat acclimation the threshold temperature at which fluidity still maintains the native membrane structure and function rises. We have also demonstrated that thermotolerance of the photosynthetic apparatus is influenced by the ratio of the main lipid components of thylakoid membrane i. e. MGDG/DGDG (Süss and Yordanov, 1986). This ratio decreased from 1.3 in control bean plants to 0.9 in heat adapted plants. Moreover, we tentatively identified DGDG with fatty acyl pairing 18:1/16:0 besides those species formed by control plants at 25 °C as being accumulated by heat induction in thylakoid membrane of heat adapted but not in notadapted plants. Therefore, the achieved thermotolerance of the majority of thermosensible light reactions is probably caused by both the lipid induced more stable conformations of membrane connected protein subunits and the adjustment of membrane lipid fluidity.

Low Temperature Stress

The reaction of photosynthetic apparatus to low temperatures as well as to water- and salt stresses shows some similarities to HS response. It is also characterized by alteration in thylakoid membrane electron transfer connected with PS2, the oxygen evolving complex and photophosphorylation (Hällgren and Öquist, 1990). Biomembranes are the main target for attack at low temperature and during freezing. The synthesis of some key proteins required for photosynthesis (components of electron transport chain, Rubisco etc) is specifically susceptible to low temperature stress (Maruyama et al., 1990). The prolonged exposure of leaves to low temperature results in selective inactivation of the oxygen evolving system in cucumber (Kaniuga et al., 1978a,b; Terashima et al., 1989a,b; Shen et al., 1990), bean (Margulies, 1972), tomato (Smillie and Nott, 1979).

It was shown that during cold acclimation newly translatable mRNAs were induced (Guy et al., 1985; Guy, 1990) and new set of proteins were synthesized (Umeura and Yoshida, 1984; Volger and Heber, 1975) i. e. different gene expression occured.

Low temperature and cold acclimation modify PS2 RC and LHCP (Griffith et al., 1984). According to Krupa et al. (1987) the specific changes in lipid composition (decrease in trans hexadecenoic acid and increase in palmatic acid of phosphatidylglycerol in the membrane) account for the structural differences between cold hardened and non hardened LHCP2. However, not all plant species have shown a decrease in trans hexadecenoic acid at low temperatures.

Acclimation of winter rye to cold temperature results in an increased capacity for photosynthetic electron transport (Hunner, 1985), a decrease of the apparent activation energy of recombination (Briantais et al., 1992) and in an increased resistance to low temperature induced photoinhibition (PI) (Lapointe et al., 1991). Cold acclimation caused also changes in the activity and isozyme variations of some enzymes. In cabbage it induced changes in Rubisco, leading to the formation of two distinct forms of two subunits (Shomer-Ilan and Waisel, 1975).

Protective Role of the Xanthophyll Cycle under Stress Condition

In conditions of strong light or combined action of intense light and high or low temperature the carotenoid composition of thylakoid membrane responded rapidly with zeaxanthin (Zx) being formed by violaxanthin (Vx) deepoxidation and recovered to Vx in low light (Yamamoto, 1979; Hager, 1980). It is believed that this reversible formation of Zx in the so called xanthophyll cycle (XC) protected the chloroplasts against harmful effects of excessive light (Demmig-Adams, 1990). As Havaux and Gruszecki (1993) mentioned the mechanism by which Zx could exert its supposed protective role remains however illusive. Its exact physiological function is still not clear, but several proposals suggested that it takes place in thermal dissipation of the excess of radiation energy absorbed by the photosynthetic pigments.

It is shown that energy of the lowest singlet excited state is higher than the energy of Q_y-state of Chl. *a* in the case of Vx but lower in the case of Zx (Frank et al., 1994). A relative position of these levels on energy scale favours a singlet-singlet excitation energy transfer from Vx to Chl. *a* (antenna function) and from Chl. *a* to Zx (chlorophyll excitation photoprotection) (Gruszecki, 1995).

The structural effect of Zx with respect to the thylakoid membrane is important in the physiological response to stress conditions. Havaux and Gruszecki (1993) observed Zx related increase in thermal resistance of PS2. As can be seen from Fig. 3, at the presence of Zx the thermotolerance of Chl. *a* fluorescence of potato leaves increased considerably. The temperature at which thylakoid membrane was irreversibly injured increased with 3–5 °C.

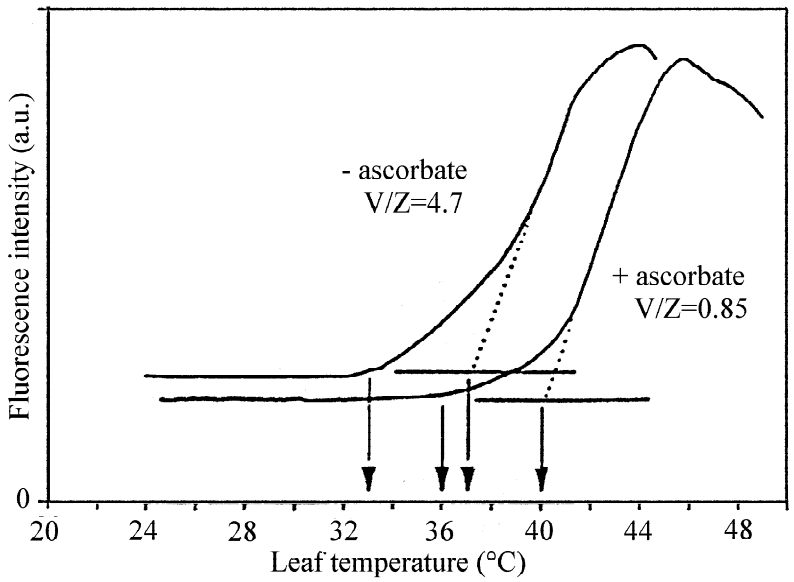

Fig. 3. Temperature dependence of the chlorophill *a* fluorescence intensity (in low exciting light) in potato leaves (cv. Haig) containing high or low levels of zeaxanthin obtained by infiltrting them for 2.5 h in the dark with a buffer with or without 100 mM ascorbate, respectively (according to Havaux and Grzszecki, 1993)

A Zx-induced decrease in lipid fluidity will reduce membrane permeability to small molecules, e. g. oxygen. This effect could be of great importance in respect to the photoprotection of chloroplast membranes as lowered oxygen concentration will decrease destructive reactions involving oxygen, such as lipid peroxidation.

Gruszecki et al. (1995) postulate also a new physiological function of XC, namely the regulation of the cyclic electron transport around PS2. In their model Vx would play a role in controlling excitation energy flow from accessory xanthophyll pigments towards PS2-RC-β-carotene. β-carotene was incorporated in this model to the cyclic electron transfer chain and its excitation state was postulated to stop the possibility of such a transfer. Blue light absorbed and transferred by carotenoids may inhibit cyclic electron transfer around PS2 in the Vx state, but not in Zx state of the photosynthetic apparatus. According to the authors here XC appears to work as a triggering mechanism regulating electron flow around PS2 depending on light conditions.

In nature we usually observe a combined action of different stress factors, which can result in intensification, overlapping or reversal of the stress effect (Osmond et al., 1987). For example water stress markedly modified the responses of PS2 superimposed constraints. Its stability to heat increased strongly in leaves exposed to water stress conditions. Heat treatment (e. g. 42 °C in the dark) which caused complete and irreversible inhibition of PS2 in well watered tomato leaves resulted in a small

and fully reversible reduction of the photochemical efficiency of PS2 in drought stressed leaves. In this case stress induces a shift of more than +5 °C in the resistance of PS2 evaluated on the basis of quantum yield (Havaux, 1992). Increased stability of PS2 to heat by drought stress is of great ecophysiological significance because both stresses are usually combined in the field.

Havaux (1992) proposed several mechanisms concerning water stress protection to PS2 against heat injury. Considering the apparent correlation between heat tolerance of PS2 and chloroplast lipids one can propose that water stress increased the stability of PS2 to heat by strengthening the interaction between PS2 proteins and their lipid environment. This may be achieved via the alteration in lipid composition of the thylakoid membrane. Kaiser (1984) also reported that high osmotic potential partially prevents photosynthesis from inactivation at supraoptimal temperature and suggested that intracellular salt concentration could be an important agent for adaptation to high temperature.

Plant Growth Regulators and Tolerance of Plants to Stress

Plant growth regulators play an important role in plant behaviour, especially in stress conditions. Stress can change the levels of specific hormones or the plants sensitivity to them. As Morgan (1990) mentioned, from the days of Darwin and of Went plant hormones have been viewed as chemical messagers regulating the normal progression of developmental changes, as well as responses to environmental signals. Abscisic acid (ABA), proposed as a common mediator of plant stress responses (Quarrie and Jones, 1977), is associated with cold (Chen et al., 1983), salt (LaRosa et al., 1985), drought (Innes et al., 1984) and heat tolerance (Hiron and Wright, 1973). According to Skriver and Mundy (1990) plant stress can also be induced by exogenous ABA. A family of dehydrins accumulate in a wide range of plant species in response to dehydratation stresses and ABA treatment. A novel property of some ABA-responsive proteins (Jacobsen and Shaw, 1989) and dehydrins (Close et al., 1989) is their resistance to heat induced coagulation. It has been hypothesized (Robertson et al., 1994) that the role of these unique proteins is to function in combination with cell osmolytes, such as sucrose, to prevent denaturation and coagulation of cellular proteins and membrane under stress conditions. Ivanov et al. (1995) showed that exogenous ABA induced in barley seedlings protection of PS2 against photoinhibition and this effect was accompanied by higher photochemical quenching.

As with many other stresses growing plants at high temperatures increased their ABA content and often conjugated ABA as well (Daie et al., 1981). It was shown by Robertson et al. (1994) that the bromegrass cell suspension culture in medium containing 75 µM ABA without prior heat treatment had a 87% survival rate, as determined by regrowth analysis following exposure to 42 °C for 120 min. In contrast, less

than 1% of the control cells survived during this heat treatment. It was also shown that sucrose (8%), in combination with responsive to ABA heat stable proteins, is the most effective in conferring heat stability.

As it is known polyamines are an important factor regulating growth, protein biosynthesis as well as stabilizing chloroplast thylakoid membranes and retarding chlorophyll degradation (Cohen et al., 1979; Galston and Kaur-Sawhney, 1982; Smith, 1985; Bagni, 1986). Polyamine metabolism change may play a role in plant adaptation to agents including biological stresses and may serve as a homeostatic buffering mechanism to stabilize cellular pH in stressed plant cells (Slocum et al., 1984; Smith, 1985). Many of the biological functions of polyamins (PAs) appear to be attributed to the cationic nature of these molecules, which are highly protonated at physiological pH. On Tables 1 and 2 the data about the influence of PAs on F_v/F_0 and F_v/F_m ratio in the leaf discs and isolated chloroplasts from control, acclimated and non acclimated bean plants are shown (Yordanov et al., 1990). It could be seen that the treatment of leaf discs with putrescine as well as with spermidine did not change considerably the induction kinetics pattern and the amplitude of the prompt chlorophyll fluorescence at 25°C. Polyamines strongly influenced the fluorescence parameters of isolated chloroplasts. That was especially characteritic for the parameter F_v/F_0. Putrescine increased it with 80% in chloroplasts from control plants. Analogous was the spermidine action increasing the same parameters with 114% in control plants and 54% in non-acclimated ones. The F_v/F_m ratio changed in a similar way.

Table 1. Influence of PAs on the F_v/F_0 and F_v/F_m ratio of chlorophyll fluorescence in leaf discs and isolated chloroplasts from control (C), acclimated (A) and non-acclimated (NA) plants

Variants	Leaf discs				Chloroplasts			
	F_v/F_0		F_v/F_m		F_v/F_0		F_v/F_m	
Put	–	+	–	+	–	+	–	+
C	5.69	5.17	0.85	0.84	1.77	3.19	0.64	0.76
A	4.26	4.30	0.81	0.81	3.86	4.85	0.79	0.83
NA	3.44	3.32	0.78	0.77	1.75	2.85	0.64	0.74
Spd	–	+	–	+	–	+	–	+
C	4.67	4.64	0.82	0.82	1.44	3.10	0.59	0.76
A	4.63	4.78	0.82	0.83	2.78	3.68	0.73	0.78
NA	3.96	4.19	0.80	0.81	1.85	2.85	0.64	0.74

Chloroplasts isolated from the three groups of plants manifested a similar behaviour to temperature inactivation, but for acclimated plants T50 was slightly increased (Table 2). The addition of Put or Spd causes in isolated choroplasts of all three plant groups an increase of T_{50} with 3–5°C.

Table 2. Influence of PAs on T50 of F_v/F_0 ratio in leaf discs and isolated chloroplasts from control (C), acclimated (A) and non-acclimated (NA) plants

Variants	Leaf discs		Chloroplasts		Leaf discs		Chloroplasts	
	–Put	+Put	–Put	+Put	–Spd	+Spd	–Spd	+Spd
C	45.5	45.8	33.3	36.3	47.7	47.0	33.3	37.3
A	47.3	47.5	34.7	37.4	49.5	49.0	35.7	40.1
NA	48.3	48.0	33.7	35.8	50.0	49.0	32.9	36.5

In conclusion, it is necessary to stress that as by HSPs (Vierling, 1991) many correlative data strongly suggest but have still not demonstrated definitively that the levels of some plant hormones are crucial for acclimation, for protection or recovery from strong injurious stress. A wide range of other environmental factors affect plant performance. As Howarth and Ougham noted it is possible that in some cases the synthesis of a protein indicates sensitivity to a stress rather than being part of a tolerance mechanism. Thus, to solve these problems additional investigations on different levels of plant organisation are needed.

***Acknowledgement*:** This work was supported by Grant No.K-408/1994 from the National Science Fund, Bulgaria.

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