PHOTOSYNTHETICA 14 (4): 512–516, 1980

Analysis of Action Spectra of Photosynthesis*

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Abstract

Using the established non-linear relation between irradiance and photosynthetic rate (ZEYNALOV 1977), the action spectra of photosynthesis and the spectral dependence of quantum efficiency were analysed. Both the "red drop" and fall of quantum efficiency in the region between 500 nm and 670 nm were a direct consequence of the non-linear character of "light curves" of photosynthesis at low irradiances.

The study of action spectra of photochemical reactions allows one to clarify the participation of different pigments in the primary photochemical act. In complicated systems such as photosynthesizing plants, the role of individual pigments can be different. For this reason, the action spectra of photosynthesis in higher plants and algae as well as in photosynthesizing bacteria have been the subject of many investigations (*cf.* RABINOWITCH 1951).

In our previous papers (ZEYNALOV and MASLENKOVA 1978, ZEYNALOV 1979) it was shown that the quantum efficiency of photosynthetic process depends, in a very complicated way, on the wavelength of radiation because of the non-linear character of light curves of photosynthesis observed at low irradiances. In particular, it was shown that the highest quantum efficiency would be observed at the absorption maxima of the suspensions and it would decrease in the regions of lower absorbances. This conclusion is independent of the way by which the quantum efficiency is determined — by equalizing the number of incident quanta or by equalizing the rate of photosynthetic process (the rate of oxygen evolution). The cause for this more complicated dependence of quantum efficiency on wavelength of exciting radiation is concealed in the non-equal distribution of absorbed quanta in different sublayers of the photosynthesizing systems investigated.

The aim of the present study was to examine some logical consequences of the principle of the non-additiveness in the action of radiant energy in photosynthesis (ZEYNALOV 1977) on the character of action spectra and quantum efficiency of the process.

Photosynthesis Research **21**: 45–50, 1989.

Regular paper

Effect of abscisic acid on the photosynthetic oxygen evolution in barley chloroplasts

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Received 4 June 1988; accepted in revised form 21 September 1988

Key words: abscisic acid, chloroplasts, electron transport, the Kok model, oxygen evolution, photosystem II, S states

Abstract

In vivo effect of abscisic acid (ABA) on photosynthetic oxygen evolution was investigated in barley chloroplasts. The most important kinetic parameters of O_2-producing reactions were changed. The results show inhibition of the O_2-flash yields at ABA concentrations of 10 μmol/l and 100 μmol/l and an increase in the degree of damping of the oscillations. ABA has a marked effect on the distribution of the oxygen-evolving centers in S_0 and S_1 states and on sum of the centers (S_0 + S_1) estimated according to the Kok model. In addition, the amplitude and the shape of the initial oxygen burst under continuous illumination are also significantly altered. At a concentration of 100 μmol/l, ABA strongly inhibits Hill reaction activity measured by DCPIP reduction. The results cannot be explained by the hypothesis of socalled "stomata effect". On the other hand, no effects were observed on the investigated parameters in experiments involving ABA applied in vitro to isolated chloroplasts. It is hypothesized that ABA disrupts the granal chloroplasts structure and raises the degree of participation of the cooperative mechanism of O_2-evolution connected with the functioning of PS II_β centers in the stroma situated thylakoids.

PHOTOSYNTHETICA 14 (4): 506–511, 1980

Red Drop of Quantum Efficiency and Emerson's Second Effect as Direct Consequences of the Principle of Non-additive Action of Light in Photosynthesis*

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Abstract

The spectral dependence of the enhancement and the action spectra of oxygen evolution in the green unicellular algae *Chlorella pyrenoidosa* CHICK and *Scenedesmus acutus* (MEYEN.) CHOD. have been investigated with and without compensation of the initial non-linear part of the "light curves". The enhancement effect was independent of the wavelength of the exciting monochromatic beams but depended on their intensities and effects. The action spectra of the oxygen evolution, recorded after compensation of the initial non-linear part of the "light curves", showed better coincidence with the absorption spectra than those recorded without background light. The results affirm our previous statement (ZEINALOV 1977b) that the "red drop" of the quantum efficiency and enhancement effect (EMERSON's second effect) are the direct consequence of the non-linearity of the photosynthetic "light curves" at low irradiances.

Kinetic analysis of the results obtained in flash experiments showed that the dependence of the rate of oxygen evolution on irradiance is non-linear at low irradiances. This theoretical prediction was experimentally confirmed which permitted us to formulate the principle of non-additive action of radiant energy in photosynthesis (ZEYNALOV 1977a). According to this principle the simultaneous action of two radiant beams, even at one and the same wavelength, is not equal to the sum of the effects, obtained during their independent actions. In 1957, EMERSON succeeded in showing non-additive action of radiant beams of different wavelengths. In the course of twenty years this so-called "enhancement effect" (EMERSON's second effect) was accepted as the strongest argument in favour of the concept of the two photochemical systems participating in the light phase of photosynthesis. This "enhancement effect" falls within the range of our principle. Therefore, it is important to know about the possibility of a complete explanation of EMERSON's enhancement effect through the indicated principle. In other words, it is possible to consider the "enhancement effect" as a direct consequence of the principle of the non-additive action of radiation in photosynthesis, or as a separate effect whose explanation requires the postulation of two independent photochemical systems operating in the light phase.

In the present paper we offer new results which confirm our assertion that the red drop of quantum efficiency and EMERSON's second effect are direct consequences of the principle of the non-additive action of radiation in photosynthesis.

Plant Physiol. (1990) 93, 1316–1320
0032-0889/90/93/1316/05/$01.00/0

Received for publication October 30, 1989
Accepted January 24, 1990

Oxygen-Evolving Activity of Thylakoids from Barley Plants Cultivated on Different Concentrations of Jasmonic Acid[1]

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ABSTRACT

The kinetics characteristics of oxygen evolution in thylakoids prepared from barley (*Horeum vulgare*) seedlings grown in the presence of different jasmonic acid (JA) concentrations were studied. In comparison to control preparations, 100 micromolar JA-treated samples show an inhibition of the Hill activity (46%) and of O_2-flash yields to above 70%. A damping in the oscillations of O_2 yields, induced by a flash train, increases with increasing growth regulator concentration. After these treatments, the value of the total number of oxygen-evolving centers ($S_0 + S_1$), estimated according to the Kok scheme, shows a considerable decrease. In 100 micromolar JA-treated preparations, the turnover half-time of S_i-states increases and the stability of the S_2- and S_3-states decreases.

PHOTOSYNTHETICA 25(4): 557–565, 1991

Effect of Specific Extrinsic Polypeptide Release on Delayed Light Emission and Oxygen Evolving Patterns in Photosystem 2 Particles*

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Abstract

The kinetics of flash-induced oxygen evolution and delayed light emission (DLE) were investigated in oxygen evolving photosystem 2 (PS2) particles, depleted of the peripheral membrane proteins of water oxidizing system. In the preparations depleted of the 24×10^3 and 16×10^3 polypeptides by washing with 1 M NaCl, approximately 55 % of the centres were still operative and no significant changes in either the misses and double hits parameters, S-state turnover time and stability of the centres were observed. DLE kinetics confirmed that the PS2 donor side was not affected. Urea plus NaCl washing released the 33×10^3 peripheral protein in parallel with significant changes in DLE kinetics, reflecting an inhibition on the PS2 donor side and a delayed recombination of separated $P_{680}^{+}Q^{-}$ charges. The depleted membranes showed a considerable depression of the O_2 flash yields. The biphasic kinetics of the deactivation reactions of the S_2 and S_3 oxidized states were delayed (the absence of the $33 \times \times 10^3$ protein increases the stability of the states). The 33×10^3 polypeptide is essential for preservation of the oxygen evolving capacity of the PS2 complexes.

J. Plant Physiol. Vol. 142. pp. 629–634 (1993)

Adaptation to Salinity as Monitored by PSII Oxygen Evolving Reactions in Barley Thylakoids

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Received April 23, 1993 · Accepted July 19, 1993

Summary

The effects of NaCl salinity and Abscisic acid pretreatment on the polypeptide composition, photochemical activity and kinetic characteristics of oxygen evolving reactions in isolated thylakoids from barley (*Hordeum vulgare* L., var. *Alfa*) seedlings were studied.

It was shown that thylakoids isolated from plants previously subjected to a prolonged NaCl treatment were more resistant to high concentration of NaCl after *in vitro* incubation. Pretreatment with ABA 3 days before salinization diminished the inhibitory effect of the NaCl. Both ABA and NaCl treatment lead to an increase in the internal ABA level in the plant leaves. ABA seems to play a specific role in this adaptive process, promoting some structural changes in the chloroplast membranes, which in turn reflect on the oxygen evolving mechanisms. The obtained results are discussed in terms of an effect of salinity and ABA treatment leading to an increased participation of the stroma situated photosystem II centers, possessing higher resistance to damaging factors.

Key words: Hordeum vulgare (L.), Chlorophyll fluorescence, NaCl-salinity, NaCl-stress-induced polypeptides, Oxygen evolution.

Abbreviations: ABA = abscisic acid; BSA = bovine serum albumin; JA = jasmonic acid; DCPIP = 2,6-dichlorophenol-indophenol; DPC = diphenylcarbazide; PSII = photosystem II; S-states = oxidation states of the water splitting enzyme; F_0 = initial (dark) fluorescence level; F_{max} = maximum fluorescence level; F_v = variable fluorescence ($F_v = F_{max} - F_0$).

J Plant Growth Regul (1995) 14:211–218

Journal of
Plant
Growth
Regulation

Involvement of Abscisic Acid in Photosynthetic Process in *Hordeum vulgare* L. during Salinity Stress

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Received June 28, 1995; accepted November 9, 1995

Abstract. In *Hordeum vulgare* L. plants, NaCl stress imposed through the root medium for a period of 8 days decreased the rate of CO_2 assimilation, the chlorophyll and protein leaf content, and the activity of ribulose-1,5-bisphosphate carboxylase. The activity of phosphoenolpyruvate carboxylase was twofold over the control. Pretreatment with abscisic acid (ABA) for 3 days before salinization diminished the inhibitory effect of NaCl on the rate of CO_2 fixation. The leaf Na^+ and Cl^- content decreased in ABA-pretreated plants. Both ABA and NaCl treatments led to an increase in the endogenous level of ABA in the plant leaves. Patterns of total proteins extracted from the leaves of control or ABA- and salt-treated plants were compared. Both ABA and NaCl induced marked quantitative and qualitative changes in the polypeptide profiles concerning mainly the proteins with approximately equal mobility. The results are discussed in terms of a possible role of ABA in increasing the salt tolerance when ABA is applied to the plants for a short period before exposure to salinity stress, thus improving the invulnerability to unfavorable conditions.

Plant Physiol. (1992) 98, 700–707
0032-0889/92/98/0700/08/$01.00/0

Received for publication December 4, 1990
Accepted August 14, 1991

Changes in the Polypeptide Patterns of Barley Seedlings Exposed to Jasmonic Acid and Salinity[1]

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ABSTRACT

Soluble and thylakoid membrane proteins of jasmonic acid (JA)-treated and salt-stressed barley (*Hordeum vulgare* L.) seedlings were investigated using 15% sodium dodecyl sulfate-polyacrylamide slab gel electrophoresis. High JA concentrations induced marked quantitative and qualitative changes in polypeptide profiles concerning mainly the proteins with approximately equal mobility, as in NaCl-stressed plants. The most obvious increase in thylakoid polypeptide band intensity was at 55 to 57 kilodaltons (kD). The relative share of some polypeptides with apparent molecular masses above 66 kD and of polypeptides with lower molecular masses in the region of 20.5 to 15 kD was enhanced. At the same time, one new band at 31 to 31.5 kD was well expressed at 25 and 250 micromolar JA concentrations and became discernible in the 100 micromolar NaCl-treated plants. The intensity of some polypeptides of soluble proteins (molecular masses of 60, 47, 37, 30, and 23.4 kD) increased with increasing JA concentration, whereas the intensities of other polypeptide bands (55, 21.4, and 15 kD) decreased. Enhanced levels of 60-, 47-, 34-, and 30-kD polypeptides and reduced levels of 55- and 15-kD polypeptides were present in NaCl-treated plants. The appearance of one new polypeptide, of 25.1 kD, was observed only in NaCl-treated plants. At 100 millimolar NaCl, an eightfold increase in proline content was observed while at 250 micromolar JA, the proline content was threefold over the control. It is hypothesized that exogenously applied jasmonates act as stress agents. As such, they provoke alterations in the proline content and they can modulate typical stress responses by induction of stress proteins.

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www.publish.csiro.au/journals/fpb
Functional Plant Biology, 2003, **30**, 515–524

Response of *chlorina* barley mutants to heat stress under low and high light

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Abstract. Barley plants (*Hordeum vulgare* L.) of wild type and two *chlorina* mutants, *chlorina 126* and *chlorina* f_2, were subjected to 42°C for 5 h at light intensities of 100 and 1000 μmol photons m^{-2} s^{-1}. The exposure of plants to heat stress at a light intensity of 100 μmol m^{-2} s^{-1} induced enormous proline accumulation, indicating that the effect of heat stress was stronger when it was combined with low light intensity. The functional activity of PSII, O_2 evolution and flash-induced thermoluminescence B-band amplitude were strongly reduced when plants were exposed to heat at low light intensity. The results clearly showed that high light intensity had a protective effect on photosynthetic activity when barley plants were treated with high temperature. Comparison of the thermosensitivity of wild type plants and *chlorina* mutants revealed that O_2 evolution in *chlorina 126* and, especially, in *chlorina* f_2 was more sensitive to heat than in wild type.

Thermoluminescence Study of Photosystem II Activity in *Haberlea rhodopensis* and Spinach Leaves During Desiccation

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Received: October 30, 2003; Accepted: February 25, 2004

Abstract: Thermoluminescence glow curve parameters were used to access the functional features of PS II in the Balkan endemic *Haberlea rhodopensis*. This representative of the higher desiccation-tolerant plants is unique for the European flora. An unusual high temperature of TL emission from *Haberlea* leaves after excitation by one flash at 5 °C was observed. The position of the main TL B band ($S_2Q_B^-$) was at 45–47 °C, while this temperature was 30–32 °C in drought-sensitive mesophytic spinach. Consistent with the up-shift in TL emission, the lifetime of the S_2 state was also increased, showing a stabilization of charge storage in PS II complex in this resurrection plant. In addition, a part of PS II centres was less susceptible to DCMU. We consider the observed unusual TL characteristics of *Haberlea rhodopensis* reflect some structural modifications in PS II (especially in D1 protein), which could be related to the desiccation tolerance of this plant. This suggestion was supported by the different manner in which dehydration affected the TL properties in desiccation-tolerant *Haberlea* and desiccation-sensitive spinach plants.

Photosynthesis Research (2005) 85: 191–203

Regular paper

Comparative study on the changes in photosynthetic activity of the homoiochlorophyllous desiccation-tolerant *Haberlea rhodopensis* and desiccation-sensitive spinach leaves during desiccation and rehydration

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Received 18 November 2004; accepted in revised form 14 February 2005

Key words: chlorophyll fluorescence, desiccation tolerant plant, drought stress, photosynthesis, thermoluminescence

Abstract

The functional peculiarities and responses of the photosynthetic system in the flowering homoiochlorophyllous desiccation-tolerant (HDT) *Haberlea rhodopensis* and the non-desiccation-tolerant spinach were compared during desiccation and rehydration. Increasing rate of water loss clearly modifies the kinetic parameters of fluorescence induction, thermoluminescence emission, far-red induced P700 oxidation and oxygen evolution in the leaves of both species. The values of these parameters returned nearly to the control level after 24 h rehydration only of the leaves of HDT plant. PS II was converted in a non-functional state in desiccated spinach in accordance with the changes in membrane permeability, malondialdehyde, proline and H_2O_2 contents. Moreover, our data showed a strong reduction of the total number of PS II centers in *Haberlea* without any changes in the energetics of the charge recombination. We consider this observation, together with the previously reported unusually high temperature of B-band ($S_2Q_B^-$) emission of *Haberlea* to reflect some specific adaptive characteristics of the photosynthetic system. As far as we know this is the first time when such adaptive characteristics and mechanism of the photosynthetic system of a flowering HDT higher plant is described. These features of *Haberlea* can explain the fast recovery of its photosynthesis after desiccation, which enable this HDT plant to rapidly take advantage of frequent changes in water availability.

Planta (2007) 225:955–964
DOI 10.1007/s00425-006-0396-8

ORIGINAL ARTICLE

Photosynthetic activity of homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and rehydration

Katya Georgieva · Zoltan Szigeti · Eva Sarvari · Laszlo Gaspar · Liliana Maslenkova · Violeta Peeva · Evelin Peli · Zoltan Tuba

Received: 12 June 2006 / Accepted: 22 August 2006 / Published online: 16 September 2006

Abstract The functional state of the photosynthetic apparatus of flowering homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and subsequent rehydration was investigated in order to characterize some of the mechanisms by which resurrection plants survive drought stress. The changes in the CO_2 assimilation rate, chlorophyll fluorescence parameters, thermoluminescence, fluorescence imaging and electrophoretic characteristics of the chloroplast proteins were measured in control, moderately dehydrated (50% water content), desiccated (5% water content) and rehydrated plants. During the first phase of desiccation the net CO_2 assimilation decline was influenced by stomatal closure. Further lowering of net CO_2 assimilation was caused by both the decrease in stomatal conductance and in the photochemical activity of photosystem II. Severe dehydration caused inhibition of quantum yield of PSII electron transport, disappearance of thermoluminescence B band and mainly charge recombination related to $S_2Q_A^-$ takes place. The blue and green fluorescence emission in desiccated leaves strongly increased. It could be suggested that unchanged chlorophyll content and amounts of chlorophyll–proteins, reversible modifications in PSII electron transport and enhanced probability for non-radiative energy dissipation as well as increased polyphenolic synthesis during desiccation of *Haberlea* contribute to drought resistance and fast recovery after rehydration.

Keywords Blue-green fluorescence · Chlorophyll fluorescence · Chlorophyll–proteins · Desiccation tolerant plant · Photosynthesis · Thermoluminescence

Abbreviations

Ca	Ambient air CO_2 concentration
Chl	Chlorophyll
Ci	Intercellular CO_2 concentration
F_v/F_m	Maximal quantum efficiency of photosystem II in the dark adapted state
gs	Stomatal conductance
LHCI	Light harvesting complex I

PHOTOSYNTHETICA 30 (1): 35-44, 1994

Irradiance dependence and action spectra of photosynthesis I. Theoretical consideration

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Abstract

Analysis of the photosynthetic irradiance curves (IC), and action and quantum efficiency spectra on the basis of the model of Kok *et al.* (1970) showed that under a low irradiance all IC, irrespective of sample absorbances, had non-linear (exponential) parts. Under a high irradiance, the IC (especially those of higher situated sublayers) showed "saturation", which was expressed as a decrease in the decline of the curves. The IC non-linearity was reflected in the shape of the photosynthetic action spectra (AS). Under a low irradiance, the AS showed a decrease (drop) in the spectral regions with low absorbances, *i.e.* between 500 and 650 nm, as well as above 690 nm (Emerson's "red drop effect"). On the contrary, under higher irradiances an increase in quantum efficiency (QE) in the same regions was well-expressed. When IC were non-linear, exact estimation of the photosynthetic AS and QE was much complicated and respective results should be accepted with a fair approach to accuracy.

Plant Physiology and Biochemistry 47 (2009) 224–231

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Exogenous treatment with salicylic acid attenuates cadmium toxicity in pea seedlings

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ARTICLE INFO

Article history:
Received 29 October 2008
Accepted 9 November 2008
Available online 18 November 2008

Key words:
Antioxidants
Cadmium
Fatty acids
Photosynthesis
Pisum sativum L.
Salicylic acid
Thermoluminescence

ABSTRACT

The present study investigated the possible mediatory role of salicylic acid (SA) in protecting plants from cadmium (Cd) toxicity. The exposure of pea plants to increasing Cd concentrations (0.5, 1.0, 2.0 and 5.0 μM) during early stages of their establishment, caused a gradual decrease in shoot and root fresh weight accumulation, the rate of CO_2 fixation and the activity of ribulose-1,5-bisphosphate carboxylase (RuBPC, E.C. 4.1.1.39), the effect being most expressed at higher Cd concentrations. In vivo the excess of Cd-induced alterations in the redox cycling of oxygen-evolving centers and the assimilatory capacity of the pea leaves as revealed by changes in thermoluminescence emission after flash illumination. The levels of some important parameters associated with oxidative stress, namely lipid peroxidation, electrolyte leakage and proline production were increased. Seed pretreatment with SA alleviated the negative effect of Cd on growth, photosynthesis, carboxylation reactions, thermoluminescence characteristics and chlorophyll content, and led to decrease in oxidative injuries caused by Cd. The data suggest that the beneficial effect of SA during an earlier growth period could be related to avoidance of cumulative damage upon exposure to cadmium thus reducing the negative consequences of oxidative stress caused by heavy metal toxicity. In addition, the observed high endogenous levels of SA after treatment with Cd suggests that SA may act directly as an antioxidant to scavenge the reactive oxygen species and/or indirectly modulate redox balance through activation of antioxidant responses.

Taken together these evidences could explain at some extend the protective role of SA on photochemical activity of chloroplast membranes and photosynthetic carboxylation reactions in Cd-stressed pea plants.

Plant Physiology Preview. Published on August 1, 2011, as DOI:10.1104/pp.111.182519

Running head: Isoprene and thermal resistance of leaves

Increased thermostability of thylakoid membranes in isoprene-emitting leaves probed with three biophysical techniques[1]

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Abstract

Three biophysical approaches were used to get insight into increased thermostability of thylakoid membranes in isoprene-emitting plants. Arabidopsis plants genetically modified to make isoprene and *Platanus orientalis* leaves, in which isoprene emission was chemically inhibited, were used. *First*, in the circular dichroism spectrum the transition temperature of the main band at 694 nm was higher in the presence of isoprene, indicating that the heat stability of chiral macrodomains of chloroplast membranes, and specifically the stability of ordered arrays of LHCII-PSII in the stacked region of the thylakoid grana, was improved in the presence of isoprene. *Second*, the decay of electrochromic absorbance changes resulting from the electric field component of the proton motive force (ΔA_{515}) was evaluated following single-turnover saturating flashes. The decay of ΔA_{515} was faster in the absence of isoprene when leaves of Arabidopsis and Platanus were exposed to high temperature, indicating that isoprene protects the thylakoid membranes against leakiness at elevated temperature. *Finally*, thermoluminescence measurements revealed that $S_2Q_B^-$ charge recombination was shifted to higher temperature in Arabidopsis and Platanus plants in the presence of isoprene indicating higher activation energy for $S_2Q_B^-$ redox pair, which enables isoprene-emitting plants to perform efficient primary photochemistry of PSII even at higher temperatures. The data provide biophysical evidence that isoprene improves the integrity and functionality of the thylakoid membranes at high temperature. These results contribute to our understanding of isoprene mechanism of action in plant protection against environmental stresses.

BULG. J. PLANT PHYSIOL., 1995, 21(1), 3–11

EFFECT OF SOME ARTIFICIAL ELECTRON DONORS AND ACCEPTORS ON THE FUNCTIONING OF THE PHOTOSYNTHETIC OXYGEN EVOLVING SYSTEM

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Received April 6, 1995

Summary. Use of isolated pea chloroplasts and excitation with short saturating flashes showed that after addition of the reducing (ascorbate+DCPIP) couple the deactivation rate of S_2- and S_3 oxidised states decreased while in the presence of PBQ a significant increase was observed. The effect of these two reagent types on S_i states distribution and on the values of "misses" and "double hits" parameters are also presented. The observed increase of "misses" in the presence of (ascorbate + DCPIP) and a decrease in the presence of PBQ are discussed in relation with changes in the deactivation rate constants of the different S_i states.

BULG. J. PLANT PHYSIOL., 1995, 21(1), 29–35

NaCl-INDUCED CHANGES IN OXYGEN EVOLVING ACTIVITY AND THYLAKOID MEMBRANE PATTERNS OF BARLEY PLANTS. ADAPTATION TO SALINITY

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Received April 6, 1995

Summary. The effects of NaCl salinity on photosynthetic oxygen evolving activity and polypeptide membrane profiles were investigated in barley seedlings. High salinity (100 mM NaCl) markedly reduced oxygen evolution in isolated thylakoids from NaCl-treated plants. Lower salt concentrations and stepwise (20–100 mM NaCl) treatment of the seedlings had a lower effect on O_2-producing reactions.

Chloroplasts isolated from prolonged NaCl-treated plants showed enhanced ability to tolerate high (1 M NaCl) concentration after *in vitro* incubation. We consider the observed stabilization in PSII oxygen-evolving activity as a result of adaptation to salinity.

Protein patterns of thylakoid membranes on SDS-PAGE stained with Coomassie revealed that the relative amount of a number of polypeptides were altered when barley plants were grown on NaCl solutions.

The results are discussed as an effect of prolonged NaCl application on the photochemical activity determined by some structural alterations in biomembranes that seems to play a specific role in the adaptive process.

Bulg. J. Plant Physiol., 1995, 21(4), 48–55

EFFECT OF ABSCISIC ACID AND JASMONIC ACID (or JA-Me) ON THE PHOTOSYNTHETIC ELECTRON TRANSPORT AND OXYGEN EVOLVING REACTIONS IN PEA PLANTS

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Acad. M. Popov Institute of Plant Physiology, Acad. G. Bonchev Str., Bl. 21, 1113 Sofia, Bulgaria

Received October 24, 1995

Summary.The effect of prolonged ABA and JA-Me application to the growth medium of pea seedlings on PSII light reactions was assessed by monitoring of Hill reaction activity, fluorescence induction, kinetic behaviour of oxygen evolving PSII centres and polypeptide analysis of thylakoids and purified PSII oxygen evolving complexes (PSII OEC).

Results show the significant inhibitory effect of the two endogenous plant growth regulators on PSII activity and some specific alterations in the structural organization of chloroplast membranes.

Restoration of Hill reaction activity with DPC led to the conclusion that the used phytohormones have a direct effect on the PSII donor side and oxygen evolving enzyme complex itself. In addition, ABA and JA-Me treatment led to an increase in the number of $PSII_\beta$ centres situated in stroma lamellae regions, which are functioning by the cooperative mechanism for O_2 production. The polypeptide composition of grana and stroma lamellae vesicles confirmed this conclusion.

Bulg. J. Plant Physiol., 1996, 22(3–4), 88–94

A COMPUTERISED EQUIPMENT FOR THERMOLUMINESCENCE INVESTIGATIONS

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Received November 5, 1996

Summary. Plant materials (intact leaves, chloroplasts or chloroplast particles) preilluminated at room temperature and rapidly cooled to -196 °C and on raising temperature are capable to emit light quanta (luminescence) the number of which is temperature depending. Such kind of thermoluminescence could be measured as function of temperature, by means of sensitive photo-electron counting technique. In the present work a computerised set for thermoluminescence investigation equipped in our laboratory is described.

Доклади на Българската академия на науките
Comptes rendus de l'Académie bulgare des Sciences

Tome 49, N° 4, 1996

BIOLOGIE
Physiologie des plantes

IMPAIRMENT OF PHOTOSYSTEM II REACTIONS IN COPPER- AND COBALT-TREATED PEA PLANTS AS ASSAYED BY OXYGEN EVOLUTION AND CHLOROPHYLL FLUORESCENCE OF ISOLATED CHLOROPLASTS

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(Submitted by Corresponding Member B. Tenchov on November 10, 1995)

Although the sensitivity of PSII reactions to heavy metal ions, especially under in vitro conditions is documented, there is no general agreement regarding the exact site of action and the underlying mechanisms [1]. Several possible sites of action of Cu ions on PSII have been taken into consideration, such as the oxidizing side (oxygen evolving complex), PSII reaction centre, the acceptor side of PSII at the level of secondary quinone acceptor Qb and at the level of cyt f, and the antenna chl a [2-5]. The effect of Co ions on PSII reactions is much less studied [6-8].

In the present work we have explored the in vivo effect of toxic copper and cobalt concentrations (400 μM and 1000 μM) on PSII light reactions. By monitoring the oxygen evolution during illumination, Hill reaction activity, fluorescence induction and polypeptide analysis of thylakoids we have attempted to localize the side of Cu and Co ions action on PSII reactions.

The results obtained point to the suggestion that the side of Co inhibition is localized mainly on the acceptor part of PSII while the Cu ions affect both the acceptor side of PSII and oxygen evolving enzyme complex. Cu- and Co toxicity lead to some changes in the distribution of the oxygen evolving PSII centres in grana and stroma thylakoid regions and as a consequence to the enhanced participation of the co-operative mechanism for oxygen production. This effect is more pronounced in the case of Cu treatment.

Доклади на Българската академия на науките
Comptes rendus de l'Académie bulgare des Sciences

Tome 49, N° 5, 1996

BIOLOGIE
Physiologie des plantes

STRUCTURAL AND FUNCTIONAL PROPERTIES OF PURIFIED PSII OXYGEN EVOLVING COMPLEXES IN COPPER AND COBALT TREATED PEA PLANTS

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(Submitted by Corresponding Member B. Tenchov on November 28, 1995)

The inhibitory effect of heavy metal ions on photosynthetic electron transport is well established [1], but the possible site of action and the underlying mechanisms remain a subject of controversy [2-6]. Our recent work [7] on in vivo effect of toxic copper and cobalt concentrations on PSII reactions in isolated chloroplasts has shown that possible site of Co inhibition is localized mainly on the acceptor side of PSII while Cu ions affect both the reducing side and oxygen evolving enzyme complex. Moreover, toxic metal concentrations lead to some changes in the distribution of PSII oxygen evolving centers in grana and stroma thylakoid regions namely to an increased participation of PSIIβ centers.

In an effort to determine in details structural and functional changes in PSII complexes as a result of in vivo heavy metal application to the growth medium we have used purified oxygen evolving particles.

The obtained results show that toxic Cu concentrations have a marked effect on the polypeptide composition of grana thylakoid membranes, especially extrinsic polypeptides of oxygen evolving enzyme complex concomitantly to the changes in electron transport activity and in the sum and kinetic behaviour of effectively working centers. On the contrary, a high concentration of Co ions did not alter the membrane composition, except the amount of the extrinsic 17 kDa polypeptide of the O_2 evolving system which was slightly decreased.

Bulg. J. Plant Physiol., 1999, 25(1–2), 58–64

THERMOLUMINESCENCE AND OXYGEN EVOLUTION IN JA-TREATED BARLEY (*Hordeum vulgare* L.)

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Received 27 July 1999

Summary. The effect of jasmonic acid on PSII reactions was assessed by changes in kinetic characteristics of O_2 evolution and thermoluminesce glow curves in barley leaves and isolated thylakoid membranes. In comparison to the control preparation, JA-treated samples showed reduced efficiency in the utilization of oxidizing equivalents generated at PSII reaction centres and retardation of S-state transitions. S_2 and S_3 states in JA-treated samples were found to be significantly unstabilized.

Доклади на Българската академия на науките
Comptes rendus de l'Académie bulgare des Sciences
Tome 53, No 4, 2000

BIOLOGIE
Physiologie des plantes

STABILIZED S_2 STATE IN LEAVES OF THE DESICCATION TOLERANT RESURRECTION FERN *POLYPODIUM POLYPODIOIDES*[1]

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(*Submitted by Corresponding Member E. Karanov on December 22, 1998*)

Introduction. Water conservation by leaves of the epiphytic fern *Polypodium polypodioides* is very inefficient. As a consequence, the water potential of the leaves follows that of the surrounding air rather closely and, as a result, may be at very low levels for extended period of time. In such a desiccated state, metabolic functions have ceased completely, but they can be resumed very quickly when at high humidity, or during rains, an adequate water status is re-established [1].

It is not well understood which physiological properties allow such a resurrection plant to tolerate the frequent desiccation-rehydration cycles. During our studies of *P. polypodioides* we noticed that thermoluminescence emitted by the chlorophyll of its leaves occurred at an unusually high temperature. With intact, photosynthetically active cells, such a high emission temperature had been reported only for another type of stress-tolerant organisms, namely a thermophilic cyanobacterium or desiccation tolerant lichen [2, 3]. We wondered, therefore, whether the unusual thermoluminescence property of the *P. polypodioides* leaves was related to their desiccation tolerance.

Доклади на Българската академия на науките
Comptes rendus de l'Académie bulgare des Sciences
Tome 53, No 12, 2000

BIOLOGIE
Physiologie des plantes

COMPARATIVE STUDY OF PHOTOSYSTEM II REACTIONS IN CHLOROPLASTS FROM DESICCATION-TOLERANT FERNS *P. POLYPODIOIDES* AND *P. VIRGINIANUM* AND DESICCATION-SENSITIVE SPINACH PLANTS BY THERMOLUMINESCENCE AND OXYGEN EVOLUTION

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(*Submitted by Corresponding Member E. Karanov on May 2, 2000*)

Introduction. The so-called "resurrection" plants represent a unique group of organisms which can withstand extremely high level of desiccation for extended period of time [1]. In such a state metabolic functions have ceased completely, but they can be resumed very quickly when an adequate water status is re-established.

During our studies of the resurrection fern *Polypodium polypodioides* we notice that the thermoluminescence (TL) emitted by the chlorophyll of its leaves occurred at an unusually high temperature [2]. With intact, photosynthetically active cells, such a high emission temperature had been reported only for another type of stress-tolerant organisms, namely a thermophylic cyanobacterium and desiccation tolerant lichen [3,4]. We wondered, therefore, whether the unusual TL property of the *P. polypodioides* leaves was related to their desiccation tolerance.

The experimental evidence presented in this article suggests that the abnormal thermoluminescence can be attributed to a chloroplastic solute which modifies the acceptor site for Q_B on the reducing side of Photosystem II (PSII) in a way that slows the recombination of the $S_2Q_B^-$ charge pair thereby stabilising the S_2 state of oxidant accumulation. While this feature was found to be expressed to a much lesser degree with less desiccation resistant control fern *P. virginianum*, it needs to be explored further whether and how it may be related to desiccation tolerance, and what kind of protection it may provide.

Доклади на Българската академия на науките
Comptes rendus de l'Académie bulgare des Sciences

Tome 49, N° 11-12, 1996

BIOLOGIE

Physiologie des plantes

A METHYL-JASMONATE INDUCED SALINITY TOLERANCE IN BARLEY SEEDLINGS

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(Submitted by Corresponding Member E. Karanov on May 30, 1996)

Plant physiological responses to environmental stress are expressed through many processes and phytohormones play an important role in mediating these responses. Photosynthesis of many plants is known to decrease as a result of NaCl salinity [1]. Analysis of thylakoid structure and function has revealed that photosynthetic membranes are directly affected by salinization [2,3]. Nevertheless, many plant species are capable of adapting to extreme salinity. The increase in salt resistance involves a protection of chloroplast membranes by some structural changes in protein and lipid composition, accumulation of different protector compounds and significant increase in the level of the so-called stress phytohormones, abscisic acid (ABA) and jasmonic acid (JA). Applied exogenously these substances can induce physiological changes identical with plant responses to stress conditions and can facilitate the adaptation to stress [4,5]. The molecular basis of this effect is still obscure.

In this study we present some evidences resulting from the analysis of photosystem II reactions in JA pre-treated barley plants that reflect co-adaptive resistance promoting alterations in the chloroplast membrane structure and function. The main finding was that exogenous 25 μM JA application to the growth medium of barley seedlings increased salinity tolerance of the plants.

Доклади на Българската академия на науките
Comptes rendus de l'Académie bulgare des Sciences
Tome 51, No 11–12, 1998

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BIOLOGIE
Physiologie des plantes

SALICYLIC ACID-INDUCED CHANGES IN PHOTOSYSTEM II REACTIONS IN BARLEY PLANTS

L. T. Maslenkova, S. R. Toncheva

(*Submitted by Corresponding Member E. Karanov on October 13, 1997*)

Introduction. Salicylic acid (SA) is widespread phenolic compound and many of its physiological and biochemical effects have been known for a long time. The most important effects of SA are connected with regulation of plant flowering, heat production and disease resistance [1]. It has been shown that exogenous SA application can also induce resistance to pathogens and production of pathogenesis-related (PR) proteins in treated plants. After discovering the role of SA in the flowering of thermogenic plants it have joined the group of endogenous plant regulators [1]. Some observations that SA exerted inhibitory effect on stomata function, chlorophyll content, photosynthetic gas-exchange and the activity of carboxylating enzymes [2] point to a possible regulatory function of salicylic acid connected with photosynthetic reactions. Furthermore, the observations show that the effect of SA on the capacity of the plants for CO_2 fixation is related mainly to non-stomatal (biochemical) factors. One possible way to verify this assumption is to investigate the effect of SA on photochemical activity in chloroplasts isolated from treated plants. The data about changes in electron-transport capacity under SA treatment could also furnish useful infomation about the mechanism of action of this substance. In order to obtain information regarding the effect of SA on the photochemical activity of PSII, we performed analysis of the Hill reaction activity, oxygen flash-yields, TL-glow curves and polypeptide pattern of isolated photosynthetic membranes.

The results obtained demonstrate that SA applied exogenously to the root medium of barley seedlings for 7 days diminished significantly the activity of chloroplast PSII. The inhibitory effect of SA on oxygen evolution correlated to the observed alterations in the membrane polypeptide composition showing a liberation of the 33 kDa peripheral protein. The observations indicated that SA treatment inhibits PSII activity by affecting the redox potential of secondary quinone acceptor Q_B and inhibition of S_3 to S_4 transition of water oxydizing complex.

BULG. J. PLANT PHYSIOL., 1999, 25(1–2), 26–38

ESTIMATION OF THE QUANTUM EFFICIENCY OF PHOTOSYNTHESIS. I. THEORETICAL GROUND AND EXPERIMENTAL APPROACHES

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Received 27 July 1999

Summary. All preceding investigations on the quantum efficiency of photosynthesis, starting with the early experiments of Warburg and Negelein (1922a, b) and Emerson and Lewis (1939, 1941) are performed under low irradiances, even under light compensation point, assuming that the photosynthetic "light curves" are linear and the quantum efficiency of photosynthesis is maximum under these conditions.

However, as it was shown in our investigations (Zeinalov, 1977a, b; Zeinalov and Maslenkova, 1980, 1996) "light curves" of photosynthesis are non-linear or "S"-shaped. In this work a special polarographic oxygen electrode system is described allowing irradiation with background light, and some principal problems existing in the experiments dealing with the maximum value of photosynthetic quantum efficiency are considered.

Key words: Emerson transient effect, oxygen induction phenomena, photosynthsis, quantum efficiency

BULG. J. PLANT PHYSIOL., 2000, 26(1–2), 58–69

ON THE ACTION SPECTRA OF PHOTOSYNTHESIS AND SPECTRAL DEPENDENCE OF THE QUANTUM EFFICIENCY

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Received 27 July 1999

Summary. Analysis of the results obtained during the investigation of the photosynthetic oxygen evolution upon irradiation with short saturating flashes and of the widely accepted Kok's model for the reactions leading to the oxygen production showed that the photosynthetic irradiance should be non-linear (quadratic or higher degree of dependence) under low irradiance. This non-linearity of the irradiance curves leads to several consequences on the action spectra of photosynthesis and particularly on the decrease of the quantum efficiency in the spectrum regions where pigment absorption is lower, as we demonstrated in our earlier investigations (Zeinalov, 1982; Maslenkova et al., 1994).

An attempt for estimating the action spectra and spectral dependence of the quantum efficiency of photosynthesis in *Scenedesmus acutus* is presented using a polarographic oxygen rate electrode and irradiation with two light beams, one of them being continuous and the other one modulated. The obtained results show that after compensation of the initial non-linear part of the irradiance curves in the estimating of the action spectra and quantum efficiency of photosynthesis the values for the investigated parameters in the spectral regions with low absorbances increase significantly.

Key words: action spectra of photosynthesis, "enhancement" effect, irradiance dependence of photosynthesis, quantum efficiency, "red drop" effect

SALICYLIC ACID-INDUCED CHANGES IN PHOTOSYSTEM II REACTIONS IN BARLEY PLANTS

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ABSTRACT

In vivo effect of salicylic acid (SA) on photosynthetic oxygen evolution and thermoluminescence emission curves were investigated in barley (Hordeum vulgare L.).

Increasing concentrations of SA (0.1mM, 0.5mM and 1mM), imposed through the root medium for a period of 7 days have a marked effect on the energetics of the charge recombination of barley leaves and isolated chloroplast. Data showed a reduction of Hill reaction activity and oxygen flash yields in accordance with the changes in membrane permeability and malondialdehyde content. When 7-day old barley seedlings were supplied with SA through the transpiration stream for 24 h no marked changes in photosynthetic reactions were observed.

Possible reasons for the responses of photosynthetic light reactions to SA are discussed.

GENERAL AND APPLIED PLANT PHYSIOLOGY – 2010, VOLUME 36 (1–2), PP. 87–99

Available online at http://www.bio21.bas.bg/ipp/

SPECIAL ISSUE (PART II) – PROCEEDINGS OF THE XI NATIONAL CONFERENCE ON PLANT PHYSIOLOGY
18–19 November 2009, Sofia, Bulgaria

THERMOLUMINESCENCE FROM PHOTOSYNTHESIZING SYSTEMS AS A METHOD FOR DETECTION OF EARLY PLANT STRESS SYMPTOMS. EFFECT OF DESICCATION ON THERMOLUMINESCENCE EMISSION PARAMETERS IN MESOPHYTIC AND POIKILOHYDRIC PLANTS

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Received: *15 March 2010* Accepted: *23 April 2010*

Summary. The non-invasive optical technique of thermoluminescence (TL) proves to be a simple and valuable procedure in monitoring PSII activity from different photosynthesizing materials, like algae suspension, leaf peaces or isolated thylakoids and oxygen-evolving PSII preparations. The parameters of different bands in TL emission curves are very sensitive to even small changes in the redox potentials of the radical pairs on the donor and acceptor sides of PSII, which makes the obtained information very useful in understanding the mechanisms of injury and preservation of highly sensitive photosynthetic apparatus, namely PSII, in changing environmental conditions. Using TL technique, we observed some peculiarities of PSII redox reactions in resurrection plants, which can reflect specific adaptive characteristics of their photosynthetic system, related to unusual desiccation tolerance of these resurrection plants. In addition to multiple mechanisms for chloroplast integrity preservation, the observed stabilization of charge storage in PSII complex of the resurrection fern *Polypodium polypodioides* L. and the desiccation-tolerant vascular flowering plants *Haberlea rhodopensis* Friv., together with a strong reduction of the total number of PSII centers without any changes in their energetic status, can explain the fast recovery of the photosynthetic activity after desiccation.

SCREENING BY THERMOLUMINESCENCE METHOD THE QUANTITY OF BIOLOGICALLY ACTIVE COMPOUNDS FROM *TRIBULUS TERRESTRIS* PLANTS WITH DIFFERENT ORIGIN

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ABSTRACT

Tribulus terrestris L. (Zygophyllaceae) is an annual prostrate medicinal plant that is widely used for treatment of sexual deficiency, as an affrodiziak. Steriodal saponins and rutin are among the basic compounds responsible for the biological activities of T. terrestris extracts. In the present study a comparative analysis of thermoluminescence (TL) emission parameters and the content of steriodal saponins and rutin from three different origins of Tribulus terrsetris (Turkey, Hungary and Bulgaria) was presented. The plants were cultivated at identical conditions on the field near Sofia and the samples were collected in the stage of full blossoming and seedling. The observed correlation between TL properties of the leaves and the content of the dominating biologically active compounds of the samples - furostanol saponins, can be consider as an possibility TL method to be used for early screening the quality of the herb.

ARTICLE DOI: 10.5504/BBEQ.2011.0028 B&E

THE EFFECT OF THIDIAZURON (DROPP [R]) ON THE GROWTH, PHOTOSTNTHETIC ACTIVITY AND SAPONIN CONTENT OF PUNCTURE VINE (*TRIBULUS TERRESTRIS* L.)

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ABSTRACT

Puncture vine (Tribulus terrestris L., Zygophyllaceae) is an annual prostrate medicinal plant that is widely used in traditional or modern medicine. Steroidal saponins and rutin are among the basic compounds responsible for the biological activities of T. terrestris extracts. The efficiency of exogenous application of thidiazuron (TDZ) (Dropp [R]), a phenylcarbamide type synthetic cytokinine, on the growth and dry matter, on the activity of the photosynthetic apparatus and the saponin content of the above ground biomass of Bulgarian and Turkish varieties of puncture vine were studied. The plants were cultivated at identical conditions in the Experimental field of the Institute of Botany nearby Sofia and were treated with different concentrations of thidiazuron (50, 100 and 150 mg/L) during the stage of plant bud formation. The samples were collected after the stage of seed ripening. Treatment with 50 mg/L TDZ was more efficient in relation to dry matter and saponin content accumulation in the above ground part of the plants. However, the effects differed among the plant varieties. 50 mg/L TDZ was more effective for the furostanol type of saponins in the shoot of the plants from the Bulgarian variety, while spirostanol saponins were more abundant in the plants of Turkish origin. Highly correlative relations between the photosynthetic efficiency of the plant shoots evaluated by the TL method and the dry matter and saponin contents in the plants were found.

Annuaire de l'Université de Sofia "St. Kliment Ohridski"
2002, volume 95, livre 4, pp. 105–112
9ème session scientifique, Sofia '01

EFFECT OF SOME PLANT GROWTH REGULATORS ON THE DEFENSE RESPONSE OF *SCENEDESMUS INCRASSATULUS* INFECTED WITH *PHLYCTIDIUM SCENEDESMI*

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Key words: *Scenedesmus incrassatulus, Phlyctidium scenedesmi*, induced resistance, PGR, ABK, MJ, SA, cytokinins.

Abstract: The effect of plant growth regulators (PGR) abscisic acid (ABA) (10^{-5}M); methyl jasmonate (MJ) (10^{-5} M); salicylic acid (SA) (2.10^{-3} M) and both cytokinins BAP (10^{-5} M) and 4-PU-30 (10^{-5} M) on the host – parasite relationship in the system of microalgal *Scenedesmus incrassatulus* – chytridial parasite *Phlyctidium scenedesmi* was evaluated. It was established that all PGR studied inhibited the process of infection. Cytokinins BAP and 4-PU-30 were most effective. The pretreatment with PGR induced resistance in the host cells. Moreover, the treatment with all PGR under study of both non infected and infected cultures was connected with stimulation of the algal growth and increase of pigment content. Cytokinins BAP and 4-PU-30 stimulated activity of the photosystem II (PSII) whereas ABA, MJ, SA suppressed PSII reactions 10-25 %. The infection of the nonresistant host cultures was associated with loss of nearly all photosynthetic activity whereas during the infection of the PGR pretreated algae their ability to release O_2 was restored. The possible mechanisms of the PGR protector effect against pathogen attack as well as of their role in the resistance induction are discussed.