PHOTOSYNTHETICA 33 (2): 217-226, 1997

Competition between the photosynthetic and the (chloro)respiratory electron transport chains in cyanobacteria, green algae and higher plants. Effect of heat stress

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Abstract

By measuring the effect of cyanide on the flash-induced redox reactions of the cytochrome (cyt) b_6/f complex we carried out a comparative study in order to characterize the interaction between the photosynthetic and the respiratory electron transport systems in cyanobacterial (*Synechococcus sp.* PCC 6301) and green algal (*Chlamydomonas reinhardtii*) cells, and in tobacco (*Nicotiana tabacum* L. cv. Petit Havana SR1) protoplasts. We found that the addition of 1 mM KCN resulted in a significant acceleration of the rereduction-rate of cyt f^+. This enhancement of the activity of the cyt b_6/f complex apparently occurred with the same mechanism in prokaryotes and eukaryotes, and its dependence on the concentration of KCN in eukaryotes ruled out an origin in mitorespiration, superoxide dismutase and plastocyanin, strongly suggesting that a cyanide-sensitive terminal oxidase, a putative component of chlororespiration, competes with photosystem 1 (PS1) for electrons from the plastoquionone (PQ) pool. Concerning the physiological role of the competition between the (chloro)respiratory and the photosynthetic electron transport systems, our data obtained with cyanobacterial and algal cells incubated at elevated temperatures (30-50 °C) showed that the respiratory control over photosynthesis became significant in cells exposed to heat-stress.

Additional key words: *Chlamydomonas*; chloroplast; KCN; *Nicotiana*; photosystem 1; protoplast; *Synechococcus*; temperature.

Received 14 November 1995, *accepted* 25 May 1996.

Abbreviations: cyt, cytochrome; ΔA_{515}, flash-induced electrochromic absorbance changes; PQ, plastoquinone; PS, photosystem.

Acknowledgement: This work was supported by grants from the Hungarian Research Fund, OTKA III/2999 and T017827.

Introduction

Most photosynthetic bacteria develop on the same membrane both respiratory and photosynthetic electron transport systems which intimately interact with each other (Vermeglio and Joliot 1984, Richaud *et al.* 1986). In purple bacteria due to branching around the cyt *b/c* complex the two electron transport systems compete with each other for electrons from the ubiquinone pool (Venturoli *et al.* 1987).

In isolated heterocysts of the cyanobacterium *Anabaena* the flash-induced cyt b_6/f turnover is suppressed entirely at high O_2 concentration but can be restored upon the addition of the respiratory inhibitor KCN which blocks the cyt aa_3-type terminal oxidase (Houchins and Hind 1983). In PS2-containing cyanobacteria cyt b_6/f has been suggested to participate both in respiration and photosynthesis (Peschek 1983, Schubert *et al.* 1995; for review see Scherer 1990).

Existence of a respiratory chain in chloroplasts (chlororespiration) has been shown first in unicellular green algae, *Chlorella* and *Chlamydomonas* (Bennoun 1982). Based on the observed regulation of the redox state of the PQ molecules it is suggested that the branching of the two electron transport chains can be found around the PQ pool.

The operation of the chlororespiratory electron transport in different algal strains has been substantiated by several lines of evidence (Caron *et al.* 1987, Büchel and Wilhelm 1990, Wilhelm and Duval 1990). Earlier, in *Chlorella*, Diner and Mauzerall (1973) observed that the redox state of the PQ pool changed not only in the light but also in the dark. Godde and Trebst (1980) have shown that chloroplast membranes isolated from *Chlamydomonas* are capable to oxidize NADH, suggesting that NADH-dehydrogenase operates in chloroplasts. Sequences coding for proteins homologous to components of the mitochondrial NADH dehydrogenase have been found in tobacco chloroplasts (Shinozaki *et al.* 1986). Molecular biological and immunological evidence for the existence of NADH-dehydrogenase in chloroplasts have been presented by Fearnley *et al.* (1989) and Berger *et al.* (1993), respectively. Peltier and Thibault (1988) observed a weak oxygen uptake in a mutant deficient in PS1, which was sensitive to KCN and rotenone.

In *Chlamydomonas,* the inhibition of mitorespiration by myxothiazol at the site of cyt b/c_1 complex led to the slow reduction of PQ and an increase in the rate of back reaction. In contrast, a decrease in oxygen concentration affecting only slightly the rate of back reaction induced a fast reduction of PQ, suggesting that the chloroplast oxidase has lower affinity for oxygen than the mitochondrial oxidases. The large variations in the rate of back reaction result from changes in the electrochemical gradient built up across the thylakoid membranes, which indicates the existence of a new gradient generator (Bennoun 1994).

In higher plants, evidence for the activity of chlororespiration was obtained by measuring fluorescence characteristics and by showing that the flash-induced activities of cyt b_6/f and PS1 were enhanced by KCN (Garab *et al.* 1989). Experiments indicated the existence of a competition between chlororespiration and photosynthesis, and a branching around the cyt b_6/f complex. By measuring fluorescence yield, Harris and Heber (1993) showed that the reduced plastoquinone could be reoxidized by O_2. Recently, by measuring O_2-uptake, further experimental evidence has been presented by Gruszecki *et al.* (1994) for the existence of chlororespiration in tobacco. However, no biochemical evidence is available on the existence of a terminal oxidase in chloroplasts. The presence of a cyt aa_3-type oxidase in the envelope membrane of tobacco and spinach chloroplasts has been ruled out (F. Lajkó and G. Garab, unpublished).

Earlier we have pointed out (Garab *et al.* 1989) that the competiton between PS1 and the putative terminal oxidase of the chlororespiratory chain for electrons from the PQ pool closely resembles the competition between PS1 and the respiratory terminal oxidase observed in cyanobacterial systems (Houchins and Hind 1983, Peschek 1983, Scherer 1990). However, systematic investigations which would permit direct comparison of values are scarce. In this work, we measured the flash-induced absorbance changes of the activity of the cyt b_6/f complex in cyanobacterial and green algal cells and in tobacco protoplasts, and showed that competition between photosynthesis and (chloro)respiration occurred essentially with the same mechanism in eukaryotic and prokaryotic cells. Further, we showed that heat-stress enhanced the respiratory suppression of the photosynthetic electron transport both in cyanobacterial and green algal cells.

Materials and methods

Plants: *Synechococcus sp. PCC 6301* cyanobacteria were grown under 40 W m^{-2} continuous irradiation at 39 °C in a medium of Allen (1968), supplied with a stream of 5 % CO_2 in sterile air. Cells were harvested by centrifugation at room temperature (4000 × *g*, 10 min), and resuspended in the culture-medium.

Chlamydomonas reinhardtii cell-wall-less green algae were grown phototrophically under 40 W m^{-2} irradiation in TAP-medium (Gorman and Levine 1965). Algae were harvested by low speed centrifugation (1500 × *g*, 10 min). (For comparison, pilot experiments were carried out in *Chlorella* cells, which gave similar results as *Chlamydomonas*.)

Protoplasts were isolated from tobacco (*Nicotiana tabacum* L. cv. Petit Havana SR1) leaves as described by Garab *et al.* (1989).

Isolation of thylakoid membranes: Intact chloroplasts were isolated from tobacco leaves grown in the greenhouse (Garab *et al.* 1988). Thylakoid membranes were prepared from intact chloroplasts by osmotic shock (30 s) in 3 mM $MgCl_2$ solution. The reaction buffer for thylakoid membranes contained 0.35 M sorbitol, 5 mM $MgCl_2$ and 20 mM N-[2-hydroxy-1,1-bis(hydroxymethyl)ethyl]glycine (tricine); pH 7.7.

Recording absorbance changes: Flash-induced absorbance transients at 515 nm due to electrochromic absorbance shift (ΔA_{515}) and transients due to redox changes of cyt b_6/f complex between 540 and 572 nm were recorded as described by Barabás *et al.* (1985). The frequency of the exciting flashes was 1 s^{-1}. 30-50 kinetic traces were averaged in the multichannel signal averager.

Density of samples for measuring flash-induced absorbance transients was adjusted to $A_{680nm-750nm} = 0.5$. Unless otherwise indicated, all measurements were carried out at room temperature.

Absorbance changes of 1 mM ferricyanide at 420 nm induced by continuous saturating irradiation, characteristic of the rate of linear electron transport, were measured in a suspension of thylakoid membranes in the presence of 5 mM NH_4Cl. The measurements were carried out in a *Shimadzu UV3000* spectrophotometer equipped with a side-irradiation attachment.

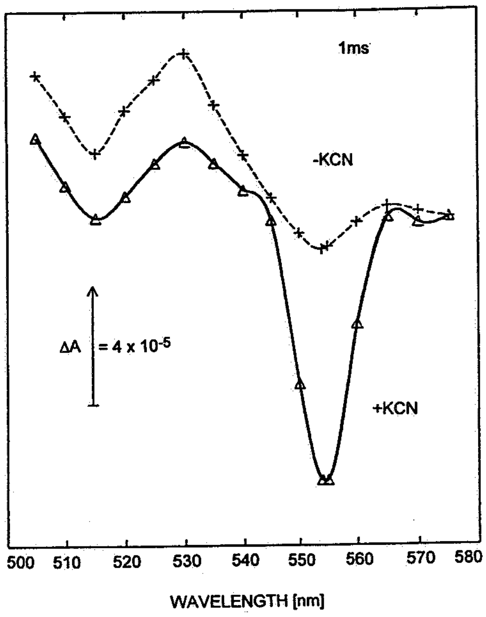

Fig. 1. Transient absorbance spectra at 1 ms after the exciting flash in *Synechococcus sp.* PCC 6301 in the presence (+KCN) and absence (-KCN) of 1 mM cyanide. (For further details see Materials and methods.)

Uptake of O_2: Mitorespiratory O_2-uptake was determined with a Clark-type oxygen electrode in the presence of 5 mM salicyl-hydroxamic acid (SHAM). The superoxide-dismutase activity of thylakoid membranes was also measured with a Clark-type electrode (Lajkó *et al.* 1990): the rate of irradiation-induced O_2-uptake was determined in the presence of 40 μM DCPIP, 2 mM Na-ascorbate, 100 μM methyl viologen, 0.8 mM NaN_3, 16 μM DCMU, and 5 mM NH_4Cl; the chlorophyll content was adjusted to 15 g m^{-3} and the activity of superoxide-dismutase was calculated according to the scheme presented by Allen and Holmes (1986).

Results and discussion

Competition between the respiratory and the photosynthetic electron transport systems: As shown in Fig. 1, in unicellular cyanobacterium cyanide enhances the flash-induced turnover of the cyt b_6/f complex, an effect clearly discernible between 540 and 570 nm. This enhancement closely resembles that in heterocysts of *Anabaena*. In heterocysts, the respiratory terminal oxidase competes very efficiently for electrons from the PQ pool, and as a consequence, under repetitive flash excitation the activity of the cyt b_6/f is almost fully suppressed and could only be restored by inhibiting cyt aa_3 with KCN (Houchins and Hind 1983).

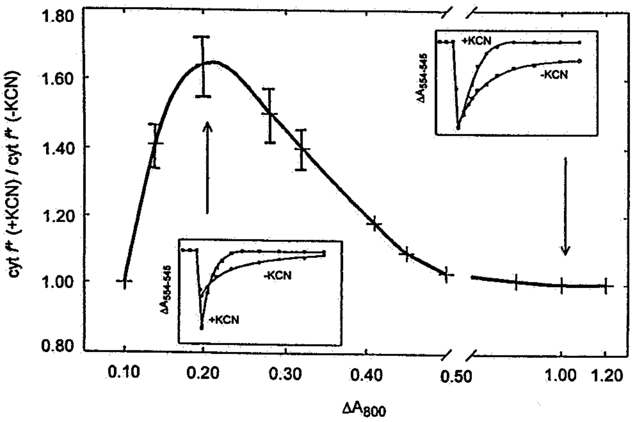

Fig. 2. Enhancement of the flash-induced oxidation of cyt *f* by 1 mM KCN as a function of turbidity (A_{800}) of the culture of *Synechococcus sp.* PCC 6301 during the exponential growth period. *Insets*: typical kinetic traces of $\Delta A_{554\text{-}545}$.

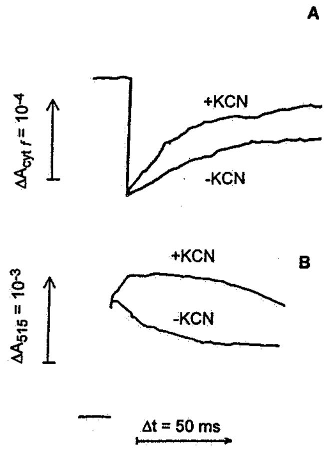

Fig. 3. Effect of 1 mM KCN on the kinetics of the flash-induced absorbance changes $A_{\mathrm{cyt}\,f}$ (*A*) and ΔA_{515} (*B*) in *Chlamydomonas reinhardtii*. $\Delta A_{\mathrm{cyt}\,f}$ was determined from the transients at 554, 545 and 515 nm as described by Bouges-Bocquet (1977).

In *Synechochoccus*, upon an excitation with repetitive flashes the cyanide-induced enhancement of the activity of cyt b_6/f activity depended largely on the age of the culture (Fig. 2). The enhancement of the turnover was high in the early stages of the exponential growth and gradually declined with the aging of the culture during the exponential growth phase. We did not find correlation between this big variation of the cyanide-induced enhancement of the turnover of the cyt b_6/f and the overall rate of respiration of cells (results not shown). However, KCN accelerated the rereduction of cyt f^+, even when it did not affect the extent of its flash-induced turnover.

In green algae, enhancement of the oxidation of cyt f by KCN could hardly be observed. However, KCN induced a significant acceleration of the rereduction cyt f^+. This could be demonstrated both directly by measuring the kinetics of the absorbance changes of cyt f, and indirectly, by measuring the kinetics of ΔA_{515} (Fig. 3). KCN enhanced the decay rate of the absorbance change due to cyt f^+ (Fig. 3*A*) and the amplitude of the slow rise of ΔA_{515} (Fig. 3*B*). The slow rise of ΔA_{515} has been shown to be given rise by an electrochromic activity of the cyt b_6/f complex (for review see, *e.g.*, Cramer *et al.* 1987), although non-electrogenic events also contribute to this kinetic component (Ooms *et al.* 1989).

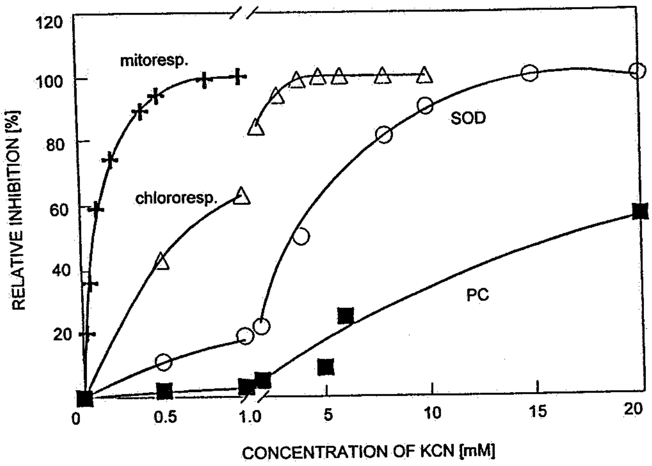

Fig. 4. Dependence of the inhibition of the activity of mitorespiration, chlororespiration, superoxide dismutase (SOD) and plastocyanin (PC) on the concentration of KCN. The rate of mitorespiration of tobacco protoplasts, and the activity of SOD in isolated chloroplasts were determined in a Clark-type electrode (see Materials and methods). The activity of chlororespiration in tobacco protoplasts was determined from the cyanide-dependent kinetic variations of ΔA_{515}, as described in the text. Effect of KCN on plastocyanin was determined by measuring the rate of electron transport of tobacco thylakoid membranes in the presence of 1 mM ferricyanide and 5 mM NH_4Cl.

In higher plants, competition between PS1 and chlororespiration has earlier been demonstrated *via* measuring the cyanide-induced enhancement of the activity of cyt b_6/f complex (Garab *et al.* 1989: Figs. 4 and 1).

Based on these results we conclude that competition between the activity of the photosynthetic electron transport and the (chloro)respiratory oxidase is manifested with essentially the same molecular mechanism in cyanobacteria, green algae and higher plants. The flash-induced activity of cyt b_6/f seems to be a good indicator for testing the competition between (chloro)respiration and photosynthesis.

Effects of cyanide: In order to substantiate that cyanide inhibits the activity of the putative terminal oxidase of the chlororespiratory electron transport careful experiments were performed in which different effects of KCN could clearly be discriminated. In Fig. 4 we show that, indeed, the concentration of KCN which was effective for the inhibition of chlororespiration ($I_{50} \approx 700$ μM, measured as enhancement of the slow rise of ΔA_{515}) was more than an order of magnitude higher than that required for the inhibition of mitorespiration ($I_{50} \approx 50$ μM). This is in agreement with the results obtained in *Xanthophyceae* (Büchel and Garab 1995). Further, the cyanide concentrations which blocked chlororespiration were essentially ineffective both in the inhibition of the superoxide-dismutase ($I_{50} \approx 5$ mM) and the plastocyanin ($I_{50} \approx 25$ mM).

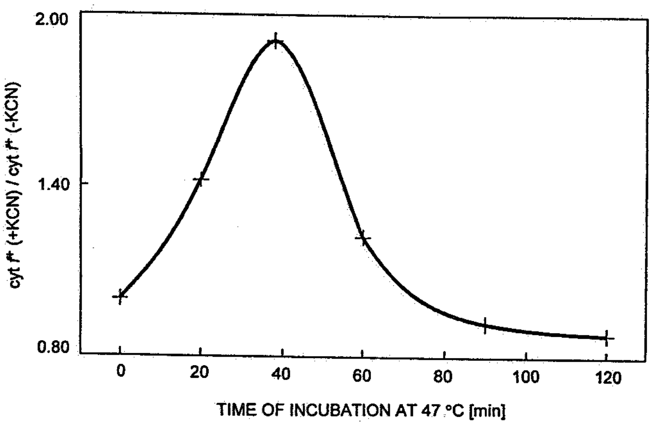

Fig. 5. Cyanide-induced enhancement of the flash-induced cyt *f* oxidation, as a function of incubation time of *Synechococcus sp.* PCC 6301 cells at 47 °C. (The concentration of KCN was 1 mM.)

Effect of heat-stress in cyanobacterial and green algal cells: In cyanobacteria, we observed that the suppression of the photosynthetic activity by respiration, which competed with photosynthesis, became profound when the cells were incubated at temperatures 5-10 °C higher than the temperature of cultivation (results not shown). Also the cyanide-enhancement of the flash-induced turnover of cyt *f* depended on the time of incubation rather than on the temperature of measurements. As shown in Fig. 5, the cyanide-induced enhancement of the activity of cyt b_6/f under repetitive flash excitation gradually increased with short (< 40 min) incubation at 47 °C of the 38 °C grown cells. These results show that cells exposed to heat-stress (cf. Borbély and Surányi 1988, Lehel *et al.* 1993) respond with respiratory suppression of their photosynthetic electron transport system; specifically of the cyt b_6/f complex. This cyanide-sensitive respiratory suppression of the activity of cyt b_6/f gradually decreased with prolonged incubations, which probably could be attributed to adaptation of cells to higher temperature.

In green algae, the enhancement of cyt b_6/f activity, measured by the enhancement of the slow rise of ΔA_{515}, was also sensitive to elevated temperatures (Fig. 6). However, this sensitivity was fully reversible after short (<10 min) incubation periods. The temperature-dependence of the cyanide-induced enhancement of the slow rise of ΔA_{515} strongly indicates that the enhancement has a threshold temperature. (However, this threshold temperature varied from batch to batch, and significant cyanide-enhancements of the slow rise of ΔA_{515} and the rate of rereduction of cyt f^+ were often observed at room temperature - cf. Fig. 3.)

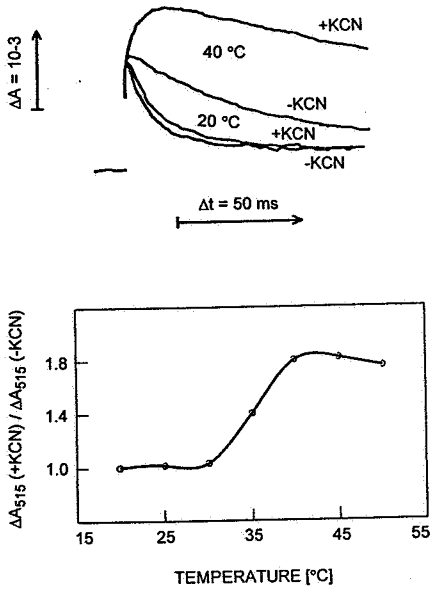

Fig. 6. Typical kinetic traces of the flash-induced electrochromic absorbance changes, ΔA_{515}, of *Chlamydomonas reinhardtii* cells measured at 40 and 20 °C in the absence and presence of 1 mM KCN (*top*), and typical cyanide-induced enhancement of the slow rise of ΔA_{515} as a function of temperature (*bottom*). (The enhancement was measured as the difference between the amplitudes of ΔA_{515} at 10 ms in the presence and absence of KCN.)

Based on the above results, it can be concluded that both in the cyanobacterial and green algal cells heat-stress induces significant enhancements of the (chloro)respiratory electron transport, which in turn suppresses the activity of the photosynthetic electron transport.

Environmental and developmental conditions have earlier been proposed to influence the chlororespiratory activity: electron transport components of photosynthesis and chlororespiration are regulated by the availability of nitrogen (Peltier and Schmidt 1991) and depend on the developmental stage of leaves (Garab *et al.* 1989). Thus, the respiration in prokaryotes and chlororespiration in eukaryotes are capable to significantly regulate the photosynthetic electron transport. This suggests that the interaction between the respiratory electron transport and the photosynthetic electron transport has a physiological function to fine-tune the operation of the redox chains under various conditions deviating from those to which the cells are "normally" exposed.

References

Allen, J.F., Holmes, N.G.: Electron transport and redox titration. - In: Hipkins, M.F., Baker, N.R. (ed.): Photosynthesis Energy Transduction. Pp. 103-141. IRL Press, Oxford - Washington 1986.

Allen, M.M.: Simple conditions for growth of unicellular blue-green algae on plates. - J. Phycol. **4**: 1-4, 1968.

Barabás, K., Zimányi, L., Garab, G.: Kinetics of the flash-induced electrochromic absorbance change in the presence of background illumination. Turnover rate of the electron transport. I. Isolated intact chloroplasts. - J. Bioenerg. Biomembr. **17**: 349-364, 1985.

Bennoun, P.: Evidence for a respiratory chain in the chloroplast. - Proc. nat. Acad. Sci. USA **79**: 4352-4356, 1982.

Bennoun, P.: Chlororespiration revisited: mitochondrial-plastid interactions in *Chlamydomonas*. - Biochim. biophys. Acta **1186**: 59-66, 1994.

Berger, S, Ellersiek, U., Westhoff, P., Steinmüller, K.: Studies on the expression of NDH-H, a subunit of the NAD(P)H-plastoquinone-oxidoreductase of higher-plant chloroplasts. - Planta **190**: 25-31, 1993.

Borbély, G., Surányi, G.: Cyanobacterial heat shock and stress responses. - In: Colowick, S.P., Kaplan, N.O. (ed.): Methods in Enzymology. Vol. 167. Pp. 622-629. Academic Press, New York 1988.

Bouges-Bocquet, B.: Cytochrome *f* and plastocyanin kinetics in *Chlorella pyrenoidosa*. I. Oxidation kinetics after a flash. - Biochim. biophys. Acta **462**: 362-370, 1977.

Büchel, C., Garab, G.: Evidence for the operation of a cyanide-sensitive oxidase in chlororespiration in the thylakoids of the chlorophyll *c*-containing alga *Pleurochloris meiringensis (Xanthophyceae)*. - Planta **197**: 69-75, 1995.

Büchel, C., Wilhelm, C.: Wavelength independent state transitions and light regulated chlororespiration as mechanisms to control the energy status in the chloroplast of *Pleurochloris meiringensis*. - Plant Physiol. Biochem. **28**: 307-314, 1990.

Caron, L., Berkaloff, C., Duval, J.-C., Jupin, H.: Chlorophyll fluorescence transients from the diatom *Pheodactylum tricornutum*: relative rates of cyclic phosphorylation and chlororespiration. - Photosynth. Res. **11**: 131-139, 1987.

Cramer, W.A., Black, M.T., Widger, W.R., Girvin, M.E.: Structure and function of photosynthetic cytochrome b-c_1 and cytochrome b_6-f complexes. - In: Barber, J. (ed.): The Light Reactions. Pp. 447-493. Elsevier Science Publ., Amsterdam - New York - Oxford 1987.

Diner, B., Mauzerall, D.: Feedback controlling oxygen production in a cross-reaction between two photosystems in photosynthesis. - Biochim. biophys. Acta **305**: 329-352, 1973.

Fearnley, I.M., Runswick, M.J., Walker, J.E.: A homologue of the nuclear coded 49 kd subunit of bovine mitochondrial NADH-ubiquinone reductase is coded in chloroplast DNA. - EMBO J. **8**: 665-672, 1989.

Garab, G., Faludi-Daniel, A., Sutherland, J.C., Hind, G.: Macroorganization of chlorophyll *a/b* light-harvesting complex in thylakoids and aggregates: Information from circular differential scattering. - Biochemistry **27**: 2425-2430, 1988.

Garab, G., Lajkó, F., Mustárdy, L., Márton, L.: Respiratory control over photosynthetic electron transport in chloroplasts of higher plant cells: evidence for chlororespiration. - Planta **179**: 349-358, 1989.

Godde, D., Trebst, A.: NADH as electron donor for the photosynthetic membrane of *Chlamydomonas reinhardii*. - Arch. Microbiol. **127**: 245-252, 1980.

Gorman, D.S., Levine, R.P.: Cytochrome *f* and plastocyanin: their sequence in the photosynthetic electron transport chain in *Chlamydomonas reinhardi*. - Proc. nat. Acad. Sci. U.S.A. **54**: 1665-1669, 1965.

Gruszecki, W.I., Bader, K.P., Schmid, G.H.: Light-induced oxygen uptake in tobacco chloroplasts explained in terms of chlororespiratory activity. - Biochim. biophys. Acta **1188**: 335-338, 1994.

Harris, G.C., Heber, U.: Effects of anaerobiosis on chlorophyll fluorescence yield in spinach

(*Spinacia oleracea*) leaf discs. - Plant Physiol. **101**: 1169-1173, 1993.

Houchins, J.P., Hind, G.: Flash spectroscopic characterization of photosynthetic electron transport in isolated heterocysts. - Arch. Biochem. Biophys. **224**: 272-282, 1983.

Lajkó, F., Kadioglu, A., Garab, G.: Involvement of superoxide dismutase in heat-induced stimulation of photosystem I-mediated oxygen uptake. - Biochim. biophys. Acta **1074**: 696-700, 1990.

Lehel, C., Gombos, Z., Török, Z., Vígh, L.: Growth temperature modulates thermotolerance and heat shock response of cyanobacterium *Synechocystis* PCC 6803. - Plant Physiol. Biochem. **31**: 81-88, 1993.

Ooms, J.J.J., Vredenberg, W.J., Buurmeijer, W.F.: Evidence for an electrogenic and a non-electrogenic component in the slow phase of the P515 response in chloroplasts. - Photosynth. Res. **20**: 119-128, 1989.

Peltier, G., Schmidt, G.W.: Chlororespiration: An adaptation to nitrogen deficiency in *Chlamydomonas reinhardtii*. - Proc. nat. Acad. Sci. USA **88**: 4791-4795, 1991.

Peltier, G., Thibault, P.: Oxygen-exchange studies in *Chlamydomonas* mutants deficient in photosynthetic electron transport: evidence for a Photosystem II-dependent oxygen uptake *in vivo*. - Biochim. biophys. Acta **936**: 319-324, 1988.

Peschek, G.A.: The cytochrome *f-b* electron-transport complex. A common link between photosynthesis and respiration in the cyanobacterium *Anacystis nidulans*. - Biochem. J. **210**: 269-272, 1983.

Richaud, P., Marrs, B.L., Vermeglio, A.: Two modes of interaction between photosynthetic and respiratory electron chains in whole cells of *Rhodopseudomonas capsulata*. - Biochim. biophys. Acta **850**: 256-263, 1986.

Scherer, S.: Do photosynthetic and respiratory electron transport chains share redox proteins? - Trends biochem. Sci. **15**: 458-462, 1990.

Schubert, H., Matthijs, H.C.P., Mur, L.R.: *In vivo* assay of P700 redox changes in the cyanobacterium *Fremyella diplosiphon* and the role of cytochrome *c* oxidase in regulation of photosynthetic electron transfer. - Photosynthetica **31**: 517-527, 1995.

Shinozaki, K., Ohme, M., Tanaka, M., Wakasugi, T., Hayashida, N., Matsubayashi, T., Zaita, N., Chunwongse, J., Obokata, J., Yamaguchi-Shinozaki, K., Ohto, C., Torazawa, K., Meng, B.Y., Sugita, M., Deno, H., Kamogashira, T., Yamada, K., Kusuda, J., Takaiwa, F., Kato, A., Tohdoh, N., Shimada, H., Sugiura, M.: The complete nucleotide sequence of the tobacco chloroplast genome: its gene organization and expression. - EMBO J. **5**: 2043-2049, 1986.

Venturoli, G., Fenoll, C., Zannoni, D.: On the mechanism of respiratory and photosynthetic electron transfer in *Rhodospirillum rubrum*. - Biochim. biophys. Acta **892**: 172-184, 1987.

Vermeglio, A., Joliot, P.: Light-induced absorption changes in intact cells of *Rhodopseudomonas sphaeroides*. Evidence for interaction between photosynthetic and respiratory electron transport chains. - Biochim. biophys. Acta **764**: 226-232, 1984.

Wilhelm, C., Duval, J.C.: Fluorescence induction kinetics as a tool to detect a chlororespiratory activity in the prasinophycean alga, *Mantoniella squamata*. - Biochim. biophys. Acta **1016**: 197-202, 1990.