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Thermally-induced delayed luminescence from PS I in membranes of thermophilic cyanobacteria

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In our previous investigation on thermophilic cyanobacteria temperature was found to stimulate delayed luminescence (DL) from PS I associated with charge recombination (Biol. Membr. 5 (1988) 1289–1296 (in Russian)). In the following paper the half-time of luminescence decay ($\tau_{1/2}$) is shown to be 6 ms at 66–78°C. This value coincides in order of magnitude with the $\tau_{1/2}$ values for higher plants, suggestive of a similar mechanism behind. PS I luminescence is inhomogeneous in thermophiles. In the presence of DCIP-H_2 the amplitude of the main band at 78°C shows a sharp rise and an additional more thermolabile band appears at 66–78°C. The splitting of the PS I peak is probably caused by a charge in the steady-state distribution of charges between the secondary acceptors. The abstraction of oxygen leads to marked changes in the profiles of the temperature dependence curves and to a rise in the DL intensity. Along with these changes the photodynamic destruction of chlorophyll decreases, electron transport becomes more stable and degree of reversibility of thermally-activated delayed luminescence increases. Besides oxygen, delayed luminescence is quenched with high efficiency by halogen ions (Cl^-, Br^-, I^-) and NO_3^- ions. The findings suggest at least two processes behind the thermal stimulation effect: the temperature-induced increase in the charge recombination rate and the heat-induced impairment of the mechanism responsible for the quenching of excited states of chlorophyll of the PS I reaction center. The latter process is presumably dominant.

Introduction

In higher plants and algae, millisecond delayed luminescence emitted by PS I is associated with backward electron transfer from the complex of iron-sulfur centers P430 [1–4]. Its efficiency is very low, as compared with that of PS II. Being as low as 1% of total chlorophyll luminescence [2], studies of PS I luminescence are difficult to conduct on non-fractionated photosynthetic membranes and intact cells. This is one of the reasons why conceptions on electron transfers at the site of secondary acceptors of PS I [5,6] are rather vague at the moment. Reliable probing of PS I delayed luminescence (DL) has been made with isolated PS I pigment–protein complexes [2]. Recent investigations have shown that applied electric field induces PS I delayed luminescence [4,7–9]. The induction is due to the increased yield of singlet excited states of reaction center chlorophyll in the course of charge recombination. A kinetic analysis of the total electrically induced luminescence of chlorophyll in the presence of ferricyanide and tetraphenylboron makes it possible to differentiate PS I and PS II delayed luminescence [4]. A thermal stimulation of millisecond PS I delayed luminescence was detected by us in experiments with isolated membranes and intact cells of thermophilic cyanobacteria [10]. The thermogram of PS I delayed luminescence has a peak which is shifted by 20–25°C toward higher temperatures relative to the band of PS II delayed luminescence. Perhaps it is due to the high thermal resistance of the photosynthetic apparatus of thermophils, that a simple separation of the PS I and PS II delayed luminescence bands becomes possible. This is especially true for PS I, the photochemical activity of which persists at temperatures above 80°C [11].

In the following work we are making a more detailed investigation of the temperature-induced stimulation of PS I delayed luminescence mechanism in

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Abbreviations: PS I, Photosystem I; LDAO, lauryldimethyl-amine *N*-oxide; DCIP, 2,6-dichlorophenolindophenol; Hepes, 4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid.

membranes of the cyanobacterium *Synechococcus elongatus*.

Materials and Methods

Growth conditions for *S. elongatus* culture, isolation procedure for photosynthetic membranes. PS II particles and PS I-enriched membrane fragments, their functional and spectral properties were described elsewhere [10,12,13]. The preparations were stored at 77 K in a buffer containing 15 mM Hepes–NaOH (pH 7.5), 10 mM $MgCl_2$, 25% glycerol (chlorophyll concentration, 1.5–2.0 mg/ml).

P700 content was 8 mol for a PS I preparation, and 1 mol for a PS II preparation, per 1000 mol of chlorophyll. The rate of O_2 evolution by PS II particles was 650 μmol O_2/mg Chl per (the acceptors used were 1 mM *p*-benzoquinone, 2 mM potassium ferricyanide). For experiments with the PS II particles a storage buffer was used. For the PS I preparations, the rate of oxygen uptake was 180 μmol O_2/mg Chl per h in the presence of reduced dichlorophenolindophenol ($4 \cdot 10^{-5}$ M DCIP, 1 mM sodium ascorbate) and methylviologen (0.1 mM). 15 mM Hepes–NaOH buffer (pH 7.5) was used in experiments with photosynthetic membranes and PS I-enriched fragments. Additions used are given in the legends to the figures and in the table (see Results).

A Clark electrode was used to measure the rate of change of O_2 concentration at 20°C. Chlorophyll *a* and P700 contents were determined as in Ref. 12. A Specord UV-VIS spectrophotometer (Germany) was employed to measure absorption spectra.

A cylindrical phosphoroscope was used to record the millisecond delayed luminescence component. The time between excitation and recording was 1.2 ms. The recording time and the excitation time were 1.9 ms. Luminescence decay was measured on a disc phosphoroscope with an excitation time of 6 ms, a delay of 3 ms between excitation and recording, a recording time of 15 ms and 7 ms between recording and subsequent excitation. While heating the sample, chlorophyll-delayed luminescence was excited with light from a halogen lamp with a red light filter placed ahead. The irradiance was 30 mW/cm^2. Luminescence was recorded on a photomultiplier (spectral sensitivity, 400–850 nm) coupled to an X–Y plotter, or an oscilloscope. Sample temperature, with the sample held in a thermostat, was monitored with a thermocouple to an accuracy of ± 1 C°. Heating rate was 4 C°/min. The rate of cooling was changed in the range 10–40 C°/min. A backing pump, with 10^{-1} atm vacuum built up for 5 min, was used to degas the samples.

Chemical compounds used in the experiments were lysozyme and Hepes-NaOH (Serva, Germany), LDAO (Onix, USA). Other reactants were Soviet-made with approved internationally-accepted quality.

Results

Presented in Fig. 1 (curve 1) is a typical temperature dependence of steady-state delayed luminescence for *S. elongatus* membranes suspended in Hepes-NaOH buffer (pH 7.5). A low-temperature delayed luminescence band with a peak at 45°C and a high-temperature band peak at 78°C, arising from PS II and PS I chlorophyll, respectively [10], are evident. Similar bands can be recorded separately for isolated PS II particles (Fig. 1, curve 3) and for PS I-enriched particles (Fig. 1, curve 2).

Under aerobic conditions the membrane preparation heated to 90°C was found to lose the ability to emit luminescence. The loss is irreversible. A partial recovery of the PS I delayed luminescence band was observed only after heating to temperatures below 78°C. As seen from Fig. 2, the patterns of the DL rise following the heating from 63 to 73°C (curve 1) and the luminescence decay following the subsequent cooling of the sample (curve 2) completely coincide. The coincidence does not depend on the cooling rate and persists with a 10-fold increase of it, as compared with the heating rate. The temperature dependence of delayed luminescence measured during the repeated heating of the cooled samples contains no PS II band and has a lower amplitude of the peak of the PS I band (Fig. 2, curve 3), the position of the peak being unchanged. Along with a change in luminescence intensity after heating, the rate of PS I-driven electron transport decreases too (Fig. 2, curve 4) and a bleaching of the chlorophyll absorption band occurs (Fig. 3, curves 1, 2).

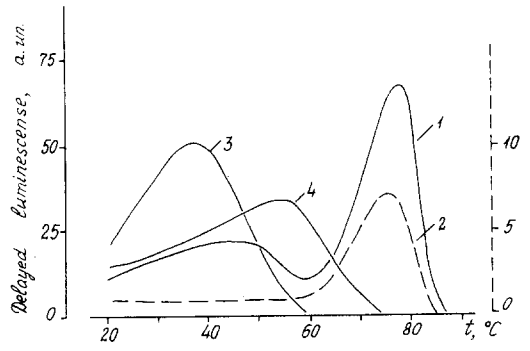

Fig. 1. The temperature dependence of chlorophyll delayed luminescence from intact membranes (1), PS I-enriched membrane fragments (2) and PS II particles (3, 4) of *S. elongatus* thermophilic cyanobacteria under aerobic (1–3) and anaerobic (4) conditions. Ordinate, right scale: the temperature dependence of the PS I preparation. Chlorophyll concentration 12 μg/ml in intact membranes and PS I particles and 3 μg/ml in PS II particles.

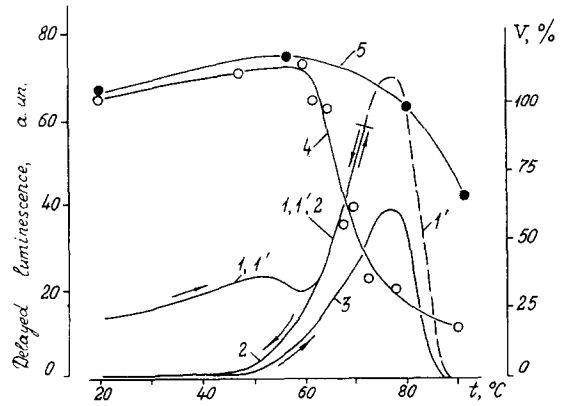

Fig. 2. The temperature dependence of delayed luminescence for *S. elongatus* membranes on heating (1, 1*), cooling (2) and reheating (3), and thermal reheating (3), and thermal resistance of PS I electrons transfer chain (4, 5) under aerobic (4) and anaerobic (5) conditions. Thermograms 1 and 2 were measured for a single membrane preparation heated to 73°C. Arrows, direction of temperature change. For the PS I electron transfer chain, thermal resistance was estimated from the change of oxygen uptake rate (V) at 20°C in the presence of DCIP ($4 \cdot 10^{-5}$ M), sodium ascorbate (1 mM) and methylviologen (0.1 mM) after heating to different temperatures under similar measurement conditions. $V = 100\%$ was taken for oxygen uptake rate at 20°C (180 μmol O_2 /mg Chl per h).

Fig. 4 shows the decay kinetics of PS I delayed luminescence at 78°C 3–18 ms after the cessation of light. The curve was measured on a disc phosphoroscope. As seen, the half-time of the decay ($\tau_{1/2}$) is 6 ms. The temperature dependences were monitored on a cylindrical phosphoroscope which has a higher resolution time (see Materials and Methods). The shorter-lived millisecond components will therefore contribute to the luminescence. After keeping the heated (to

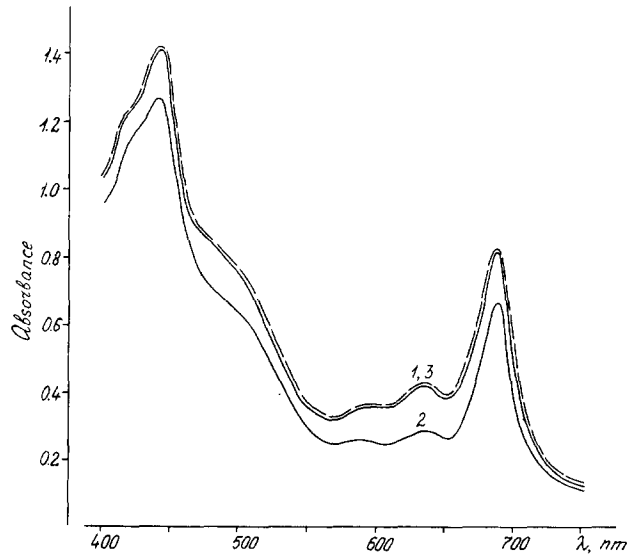

Fig. 3. The absorption spectra of *S. elongatus* membranes (1–3) at room temperature (1) and after preheating to 90°C under aerobic (2) and anaerobic (3) conditions. Heating conditions were the same as for temperature dependence measurements.

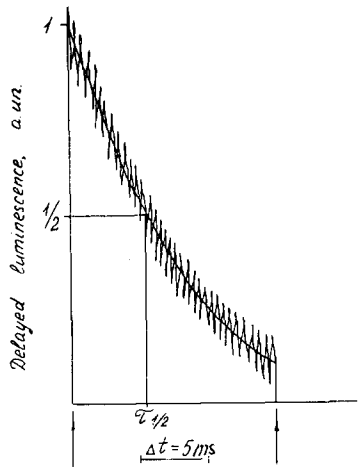

Fig. 4. Decay kinetics of delayed luminescence of *S. elongatus* membranes at 78°C measured in the time range 3–18 ms after cessation of exciting light. Arrows, light on (upward) and off (downward). For recording method, see Materials and Methods.

75–78°C) membrane preparation in the dark for a short time (20 s), one observed the induction of delayed luminescence following the turn-on of exciting light (Fig. 5, curve 1). The induction kinetics contain an unresolvable fast rise phase and a slow decay phase in the second time domain. In the presence of reduced DCIP, the slow induction phase disappears and the steady-state level of luminescence increases sharply (Fig. 5, curve 2).

The addition of reduced DCIP also causes a marked increase in intensity, and a change in the shape of the peak of PS I delayed luminescence (Fig. 6, curves 1a,b). A pronounced shoulder appears at 66–72°C in the temperature curve. A similar change in the behavior patterns of the thermograms was observed for the PS I-enriched membrane preparation (Fig. 6, curve 2a,b). In both situations, the delayed luminescence was quenched with micromolar concentrations of methylviologen (data not shown).

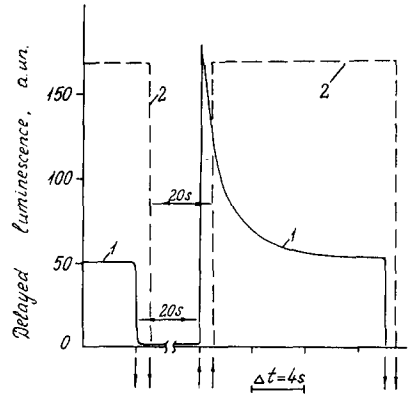

Fig. 5. Kinetics of delayed luminescence decay to the steady-state level after dark incubation (20 s) at 78°C in the presence (1) and absence (2) of DCIP for *S. elongatus* membranes. Arrows, light on and off. Concentrations: DCIP, 40 μM; sodium ascorbate, 1 mM.

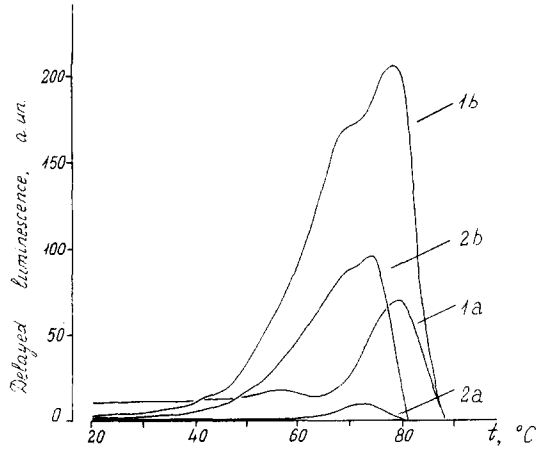

Fig. 6. Temperature dependence of delayed luminescence from membranes (1a, b) and PS I preparation (2a, b) of *S. elongatus* in the presence (1a, 2a) and absence (1b, 2b) of reduced DCIP. Concentrations of DCIP and sodium ascorbate were as in Fig. 5.

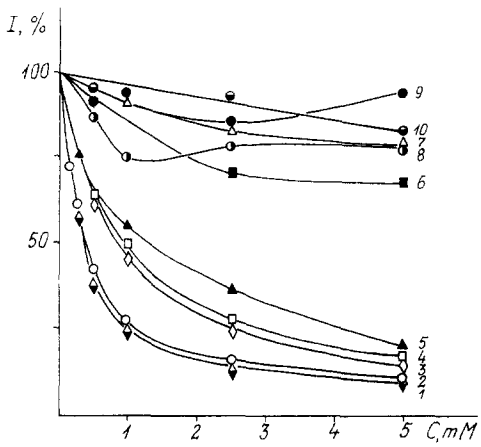

Fig. 8. Effects of different concentrations of salts on the amplitude of the delayed luminescence peak for PS I particles from *S. elongatus*: 1, NaBr; 2, $MgCl_2$; 3, NaI; 4, NaCl; 5, $NaNO_3$; 6, K,Na-phosphate buffer (pH 7.5); 7, sodium citrate; 8, $MgSO_4$; 9, Na_2SO_4; 10, NaF. The peak amplitude in the absence of additions was taken as $I = 100\%$.

It should be noted that the $\tau_{1/2}$ values appear to be the same for the luminescence decay at the inflexion point ($T = 66°C$) on the temperature curve (Fig. 6) and at the peak temperature (78°C) (data not presented).

Oxygen produces a significant effect on the temperature course. As seen from Fig. 7 (curve 2), the abstraction of oxygen from the membrane suspension causes a sharp increase in the intensity of PS I luminescence. Under these conditions, the temperature-induced quenching of delayed luminescence commences only after a fairly long (more the 5 min) heating at the ultimate temperature (90°C). In the absence of oxygen, the electron transport chain exhibits a higher thermal resistance (Fig. 2, curves 4, 5). For example, the reduction of methylviologen after the preliminary heating to 90°C is inhibited by approx. 85% under aerobic conditions and by 40% under anaerobic ones. Moreover, there is no chlorophyll bleaching under anaerobic conditions (Fig. 3).

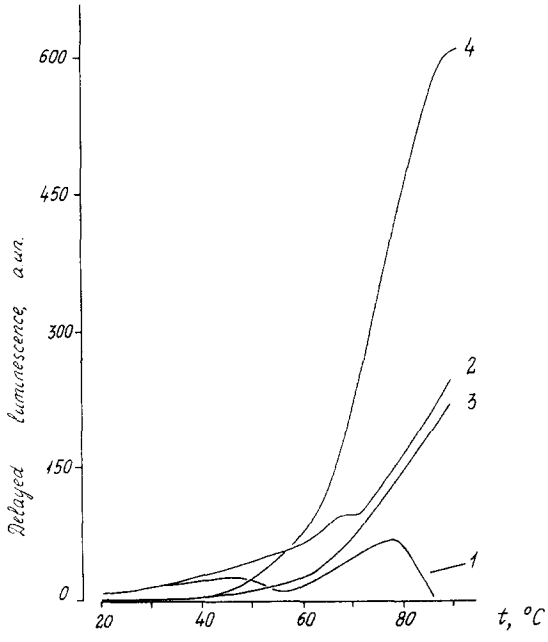

Fig. 7. The temperature dependence of delayed luminescence from *S. elongatus* membranes. 1, aerobic conditions; 2–4, anaerobic conditions in the absence (2) and presence (4) of reduced DCIP, and after preheating to 90°C in the absence of reduced DCIP (3). Thermograms 2 and 3 were measured for a single membrane preparation. Concentrations of DCIP and sodium ascorbate were as in Fig. 5.

The shoulder in the thermograms at 64–69°C (Fig. 7, curve 2) is related to PS II. It is missing from the temperature curve after the repetitive heating of the membrane preparation (Fig. 7, curve 3) and does not show in the experiments with the PS I-enriched membrane preparation (data not shown). The shift of the PS2 band toward higher temperatures under anaerobic conditions is due to the higher thermal resistance of the membranes. This is evident from the temperature dependence of delayed luminescence for PS II particles (Fig. 1, curves 3, 4). The addition of reduced DCIP to deaerated membrane samples causes a sharper increase in the amplitude of the PS I band (Fig. 7, curve 4).

The effective inhibition of PS I luminescence was caused not only by oxygen but also by halogen ions and NO_3^-. As seen from Fig. 8 (curves 1–5), increasing the concentration of the above ions causes a monotonic decrease of the PS I peak. Among the anions F^-, Cl^-, Br^-, the capacity to quench luminescence increases with atomic weight, the concentration being equal (Fig. 9). The exception is the anion I^-, perhaps due to its chemical instability at high temperatures. The ions of other salts used – K_2HPO_4, NaH_2PO_4, $MgSO_4$, sodium citrate – have a much weaker influence on PS I luminescence (Fig. 8, curves 6–9).

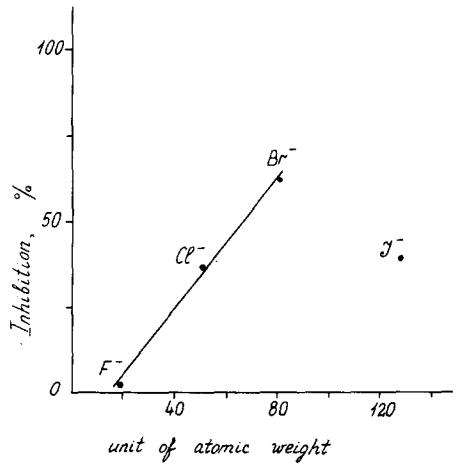

Fig. 9. The degree of inhibition of delayed luminescence from *S. elongatus* membranes at 78°C as a function of atomic weight of the ionic quencher. Concentration: NaF, NaCl, NaBr, 500 μM.

Presented in Fig. 10 are concentration dependences of luminescence quenching by ions, as plotted from the Stern-Volmer equation:

$$\frac{L}{L_Q} = 1 + \tau K_q [Q]$$

where L and L_Q are quantum yields of delayed luminescence in the absence and presence of the quencher Q, τ is the lifetime of luminescence, K_q is the quenching rate constant, [Q] is the concentration of the quencher. The dependence are linear for all ions of the quenchers.

No correlation was found to exist between the effect of ions on delayed luminescence and PS I-driven electron transport. As seen from Table I, the ions of the $MgCl_2$, NaCl and $NaNO_3$ salts, which are efficient inhibitors of delayed luminescence (Fig. 8, curves 2, 4, 5), differ largely in the ability to activate PS I-driven

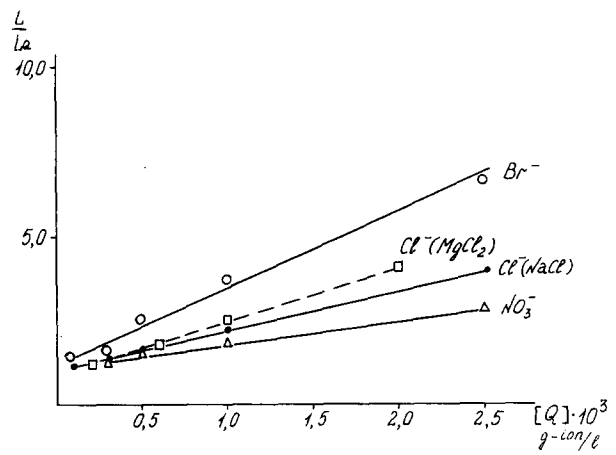

Fig. 10. Stern-Volmer plot of the concentration dependence of inhibition degree of delayed luminescence from *S. elongatus* membranes by anions. L/L_Q, the ratio of the quantum yields of delayed luminescence in the absence and presence of the quencher Q.

TABLE I

Effect of different salts on the rate of PS I-driven electron transport

Preparations of PS I suspended in medium containing 15 mM Hepes–NaOH (pH 7.5), 40 μM DCIP, 1 mM sodium ascorbate, 0.1 mM methylviologen.

Salt	[a]	$MgCl_2$ (10 mM)	$MgSO_4$ (10 mM)	NaCl (30 mM)	$NaNO_3$ (30 mM)
V (%)	100	247	245	103	110

[a] $V = 100\%$ was taken for oxygen uptake rate at 20°C (180 μmol O_2/mg Chl per h).

electron transport at 20°C (Table I). The effect of ions is not due to the electrostatic effects. For instance, the ions of $MgSO_4$, in contrast to the ions of $MgCl_2$, have little influence on luminescence (Fig. 8, curves 2, 8).

Discussion

Thermally-induced millisecond delayed luminescence of PS I originates from the recombination reaction [10]. The luminescence is produced only when PS I is photochemically active (Fig. 2). The intensity increases sharply when P700 is reduced (Fig. 6) and is completely abolished upon oxidation of the acceptor pool with methylviologen.

The decay time of PS I luminescence from *S. elongatus* is 6 ms at 78°C (Fig. 4). In higher plants and algae, millisecond delayed luminescence at room temperature is composed of two components, $\tau_{1/2} = 5$–20 ms [2–4] and 70 ms [4], presumably due to backward charge transfer from the iron-sulfur center, F_A and F_B, respectively. As judged from the decay time, the high-temperature delayed luminescence from *S. elongatus* seems very likely to arise from $P700F_A$ charge recombination. The observations suggest a similar origin of the PS I emission in cyanobacteria and higher plants. This conclusion is not, however, unambiguous because the backward transfer of a charge from P430 has a fairly high barrier of activation energy (430–650 mV [3,4]). Hence, $\tau_{1/2}$ of the components has to decrease with increased temperature. Moreover, the thermally-induced luminescence from PS I is probably inhomogeneous and contains at least two components with different thermal resistance. They are distinctly seen in membranes and PS I particles with reduced P700 (Fig. 6). The splitting of the band due to PS I in the presence of reduced DCIP presumably occurs as a result of a change in the steady-state charge distribution between the secondary acceptors, as their electron populations increase.

In the presence of DCIP-H_2, the slow, second-time scale component of luminescence induction disappears (Figs. 4, 5). With a small degree of P700 reduction, the induction kinetics presumably reflect the establishment of equilibrium in the steady-state charge distribution in

the light. Although the data suggest the inhomogeneity of the PS I band in *S. elongatus*, we failed to observe any marked differences in the decay behavior of the low-temperature (66°C) and the high-temperature (78°C) components. Perhaps much overlapping of the bands, or little difference in the lifetimes of the two components at high temperatures, accounts for this.

One phenomenon behind the temperature-induced rise in PS I delayed luminescence is probably the temperature-dependent increase of the recombination rate, which has a high activation energy.

A notable feature that arises in the course of analysis of the reasons for the induction of luminescence by high temperature is that the peak due to PS I becomes pronounced with increasing degradation of PS I, and exhibits a high sensitivity to oxygen. The abstraction of oxygen causes a sharp rise of delayed luminescence. With this, the degree of reversibility of the temperature-induced effect increases (Fig. 7), the thermal resistance of the electron transport chain also increases, and chlorophyll bleaching is completely prevented (Figs. 2, 3). Undoubtedly, the effect of anaerobic conditions is in reducing the oxidative degradation of functionally active components of PS I. However, the effect of oxygen is probably not restricted to this mechanism. The major contribution to oxidative photodynamic destruction of chlorophyll and other pigments comes from interaction with excited states, primarily triplets. Decreasing the oxygen content will therefore result in an increase of chlorophyll triplets in the steady state.

According to the concepts put forth in recent years, the radiative and radiationless recombination of charges involves singlet and triplet states, respectively, of the primary donor. An equilibrium proportion of these states is: $^1P700 : {}^3P700 = 1:3$ [4,14,15]. The increased yield of chlorophyll triplets will cause a shift in equilibrium with the increase in the steady-state concentration of $^1P700$. This will result, in turn, in a luminescence rise.

A similar mechanism presumably makes an essential contribution to the thermal activation of PS I delayed luminescence. The increase in yield of chlorophyll triplets may also be a result of the thermally induced lowering of the efficiency of interaction between chlorophyll and carotenoids, the major quenchers of triplets in the reaction center [14,15].

Evidence for the relation between thermally-induced delayed luminescence and generation of chlorophyll triplets in *S. elongatus* membranes comes from an investigation of the effect of halogen anions and NO_3^- ions on luminescence (Fig. 8). In contrast to the ions of other salts, the above ions cause a sharp drop in delayed luminescence. By illustration, in the presence of 2.5 mM $MgCl_2$ the peak of PS I luminescence decreases by 85% (see Fig. 8). The efficiency of the halogen ions increases with atomic weight (Fig. 9), consistent with the capability to deactivate excited states of dyes by a physical mechanism [16]. A linear pattern of the changes in the luminescence yield – a Stern-Volmer plot (Fig. 10) – gives good reason to believe that the inhibition of radiation is primarily due to the deactivation of chlorophyll triplets of PS I [17]. It should be noted that in native membranes the chlorophyll of the lipid–protein complexes of the antenna and reaction center is in hydrophobic surrounding. Hence, it is less exposed to exogenous charged quenchers. At high temperatures, however, its contribution to chlorophyll deactivation may increase.

Indirect evidence for the proposed mechanism of thermal activation is the reversibility of the temperature effect. Under anaerobic conditions the general pattern of the thermograms recovers even after heating to 90°C (see Fig. 7). The important point is the coincidence of the patterns of the relaxation changes of delayed luminescence caused by cooling over a wide temperature range (63–73°C) and the part of the temperature dependence curve corresponding to heating, the relaxation changes induced by low temperature being independent of the rate of cooling (see Fig. 2). This means that delayed luminescence activation is brought about by processes where equilibrium attained very rapidly. This property is inherent in shallow reversible conformational shifts in the polypeptide segments connecting the carotenoids and chlorophyll.

Two related phenomena may be responsible for the thermal activation of the millisecond delayed luminescence of PS I in thermophilic cyanobacteria: the increased rate of charge separation and decreased efficiency of interaction between carotenoids and chlorophyll. The latter gives rise to an increased yield of singlets of the primary donor via the backward electron transfer reaction. The sharp rise of PS I luminescence under anaerobic conditions and in the absence of triplet-deactivating ions suggests that the latter plays an important role in the thermal induction of delayed luminescence.

The thermal stimulation of delayed luminescence has been observed in higher plants too [3,4,8]. Symons and coworkers [8] observed a 5-fold increase in the field-induced light-dependent luminescence of PS I after a preparation of osmotically disrupted chloroplasts had been heated from 20 to 50°C. The activation of delayed luminescence in this case was, most probably, due to the temperature-induced increase of the rate of the charge recombination reaction. However, from the data reported here one can suppose that with the deficiency of exogenous quenchers of chlorophyll triplets, a significant contribution to activation comes from a heat-induced deterioration of carotenoid–chlorophyll intermolecular interactions in the reaction center.

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