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Study of temperature influence on electron transport in higher plants via delayed luminescence method: experiment, theory

D.Z. Badretdinov*, E.A. Baranova, A.K. Kukushkin

Faculty of Physics, Lomonosov Moscow State University, Leninskie Gory, Moscow 119992, Russia

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Abstract

The temperature dependence of steady-state millisecond delayed luminescence (DL) is studied within the temperature range from − 23 to 45 °C in leaf segments of chinese rose (*Hibiscus rosa-sinensis* L.) and bean (*Ficia faba*). To describe the experimental dependence of DL steady-state intensity on temperature theoretically, we suggest the temperature dependences of rate constants in earlier proposed model of photosynthesis. Under these conditions, the temperature dependence of DL steady-state value has the same form as experimental curve.

Keywords: Temperature dependence; Electron transport; Luminescence

1. Introduction

Investigation of DL invokes particular interest because its intensity depends directly on the rate of backward electron transport reactions in the reaction center of photosystem 2. In its turn backward electron transport reactions are determined by quantum efficiency of primary processes of photosynthesis. Investigation of temperature dependence of backward reactions rate is of special significance for understanding the electron transfer mechanisms. It should be noted that in primary photosynthetic processes the electron transfer occurs in the membrane lipid pigment–protein complexes. These complexes have a strictly determined chemical composition and condensed structure. To study and describe the properties of such systems, the methods of condensed matter physics are applied [1].

The DL can be described as light emission by photosynthetic organisms shortly after their illumination, but later than prompt luminescence emission. In a final step, DL is radiated during the same excited P680 (P680*) to P680 transition as prompt luminescence. In case of prompt luminescence P680* is created directly by excitation, while for DL the P680* state results from recombination of products formed in a primary photochemical act. Using the theory of higher plant DL developed during last several years, it is possible to determine such characteristics of primary processes as rate constants for forward and activation energies for backward electron transport reactions in the photosystem (PS) reaction centre (RC), the charge location in the RC and the state of Calvin cycle [2–6]. Earlier, it has been shown that DL is a sensitive test for the state of the photosynthetic system. Even the changes in the rate of transport through the phosphate translocator are clearly manifested in induction kinetics of delayed luminescence [6].

The aim of this work was to investigate theoretically the temperature dependence of delayed luminescence in the temperature range from − 25 to 55 °C. We compared the results of experimental study performed on *Hibiscus rosa-sinensis* and *Ficia faba* leaves and the theoretical description of the experimental curves.

2. Materials and methods

2.1. Description of experiment

DL was induced and registered by home-made setup, based on the Lewis–Kasha-type phosphoroscope. The apparatus as well as the measuring protocol and results are described in details in our previous paper [7].

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* Corresponding author. Tel.: +7-95-939-2973; fax: +7-95-939-1195.
E-mail address: badretdinov@phys.msu.su (D.Z. Badretdinov).

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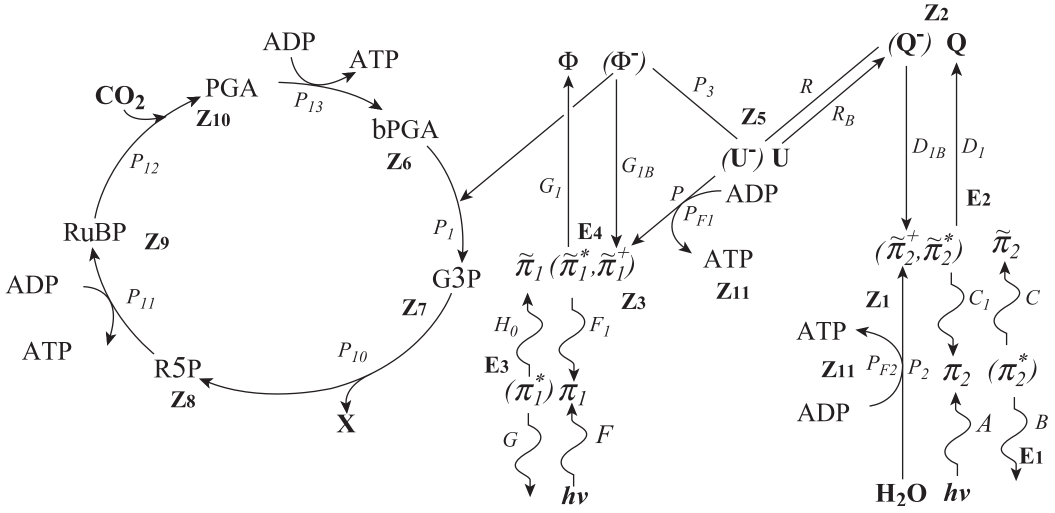

Fig. 1. Scheme showing the reactions included in the theoretical model of photosynthesis. π_1—light harvesting pigment of photosystem (PS) I, π_1^*—excited light harvesting pigment of PS1, $\tilde{\pi}_1$—reaction centre of PS1, $\tilde{\pi}_1^*$—excited reaction centre (RC) of PS1, $\tilde{\pi}_1^+$—oxidized RC of PS1, π_2, π_2^*, $\tilde{\pi}_2$, $\tilde{\pi}_2^*$, $\tilde{\pi}_2^+$—the same for PS2; Q—primary acceptor of PS2, Q^-—reduced primary acceptor of PS2, U—intermediate electron acceptor, U^-—reduced intermediate acceptor, Φ—primary acceptor of PS2, Φ^-—reduced primary acceptor of PS2 united with NADPH; RuBP—ribulose 1,5-bisphosphate, PGA—phosphoglycerate, bPGA—1,3-bisphosphoglycerate, G3P—glyceraldehyde 3-phosphate, R5P—ribulose 5-phosphate, P_i (P_{ext})—internal (external) inorganic phosphate, X—carbon stored inside the chloroplast (starch).

2.2. Description of theoretical model

The scheme of the mathematical model for the primary processes of photosynthesis and Calvin–Benson cycle is shown in Fig. 1. The detailed description of the model and assumptions in use are presented in works [8,9]. The denotes of Fig. 1 describe the meaning of the notations. In this model, the kinetic behavior of components is described by the set of ordinary nonlinear differential equations.

$$\frac{d}{d\tau}z_1 = 10D_1E_0E_2(z_1,z_2)(1-z_2) - D_{1B}E_0z_1z_2 - P_2z_1;$$

$$\frac{d}{d\tau}z_2 = (10D_1E_2(z_1,z_2) + 0.1(U_0/E_0)R_B)(1-z_2) - D_{1B}z_1z_2 - P_{O22}z_2 - R(1-z_5)z_2;$$

$$\frac{d}{d\tau}z_3 = 10G_1E_4(z_3,z_4)(1-z_4) - G_{1B}z_3z_4 - 0.1PU_0z_5z_3;$$

$$\frac{d}{d\tau}z_4 = 10G_1E_4(z_3,z_4)(1-z_4) - G_{1B}z_3z_4 - P_1z_4z_6 - 0.1P_3z_4(1-z_5) - P_{O21}z_4;$$

$$\frac{d}{d\tau}z_5 = ((RE_0/U_0)z_2 + 0.1(P_3/U_0)z_4)(1-z_5) - (0.1R_B(1-z_2) + 0.1Pz_3)z_5;$$

$$\frac{d}{d\tau}z_6 = P_{13}z_{10}z_{11} - P_1z_4z_6;$$

$$\frac{d}{d\tau}z_7 = P_1z_4z_6 - 2P_{10}z_7^2; \quad \frac{d}{d\tau}z_8 = P_{10}z_7^2 - P_{11}z_8z_{11};$$

$$\frac{d}{d\tau}z_9 = P_{11}z_8z_{11} - P_{12}P_{CO2}z_9;$$

$$\frac{d}{d\tau}z_{10} = 2P_{12}P_{CO2}z_9 - P_{13}z_{10}z_{11};$$

$$\frac{d}{d\tau}z_{11} = (P_{F2}P_2z_1 + 0.1P_{F1}PU_0z_5z_3)(a_0 - z(11)) - P_{11}z_8z_{11} - P_{13}z_{10}z_{11};$$

where

$$E_2(z_1,z_2) = \frac{AC(1-z_1) + [0.1B + C(1-z_1)]D_{1B}E_0z_1z_2}{0.1BC_1 + BD_1E_0(1-z_2) + 10D_1E_0C(1-z_1)(1-z_2)};$$

$$E_4(z_3,z_4) = \frac{FH_0(1-z_3) + [0.1G + H_0(1-z_3)]G_{1B}z_3z_4}{0.1F_1G + GG_1(1-z_4) + 10G_1H_0C(1-z_3)(1-z_4)};$$

The expressions for E_1 and E_3 have the following form:

$$E_1 = \frac{A + C_1E_2}{B + 10C(1-z_1)}, \quad E_3 = \frac{F + F_1E_4}{G + 10H_0(1-z_3)};$$

$\tau = 10^3t$, where t is time in seconds.

The variables in the equations are proportional to the concentrations of the corresponding values.

The numerical values of the coefficients chosen were such as to ensure correspondence with the characteristic times of the elementary processes and the rates of the individual stages isolated in the experiment [10].

To obtain the theoretical DL curves in model the excitation by pulsed light was used. For that purpose the model parameters F and A denoting the light intensity absorbed by PS1 and PS2 were made to change periodically. The solution was obtained with help program written on programming language *Delphi 5.0*, which integrated the set of equations using stable predictor–corrector method of Robertson [11].

To describe theoretically the experimental dependence of DL steady-state induction from temperature, we took into account the temperature dependence of constant rate of 12 processes in photosynthesis model [11]. On the basis of the literature data, we suggested the temperature dependence for rate constants R_b, R, P, P_1, $\mathrm{D}{-}_2$, P_{10}, P_{11}, P_{12}, P_{13}, D_{1b}, C and $\tilde{\mathrm{N}}_1$ shown in Fig. 2. For the rate constant of reactions, describing Calvin cycle (P_1, P_{10}, P_{11}, P_{12}, P_{13}), we use the temperature dependence with maximal value near optimal temperature for the plant and small values at low and high temperatures (Fig. 2a) [12–15].

For temperature dependence of P, the rate constant of electron transfer from an intermediate carrier to oxidized reaction center of PS1, we used the data about dependence of diffusion and oxidation processes plastohydroquinone on temperature [16]. The rate constant of this step linearly increases with temperature range from − 10 to 40 °C. Outside of this range we have the rate constant to be fixed (Fig. 2b). There are data about instability of water dissociation complex in literature [17,18]. Under low temperature the rate of water dissociation decreases on freezing. We suppose that in the range from − 10 to + 40 °C the rate of dissociation scarcely vary. (Fig. 3c). The temperature dependences for constants C, C_1 and D_{1b} are similar to the dependence for P_2, they are based on observations of structure modifications in PS2 RC at extreme temperatures. At high temperature, part of reaction centre and antenna complex proteins PS2 leaves the membrane [17,19]. In that case, proteins D1 and D2 undergo structural changes [20], the rate of electron transfer decreases [21,22]. At low temperatures, the processes of charge separation and electron transfer in PS2 take place [23]. The constant R (the rate constant of electron transfer from primary acceptor to intermediate carrier) decreases at the high and low temperature, it results in electron transport decrease in the $\mathrm{Q_A}$–$\mathrm{Q_B}$ region [23–25] (Fig. 2c). Backward constant R_b, by our

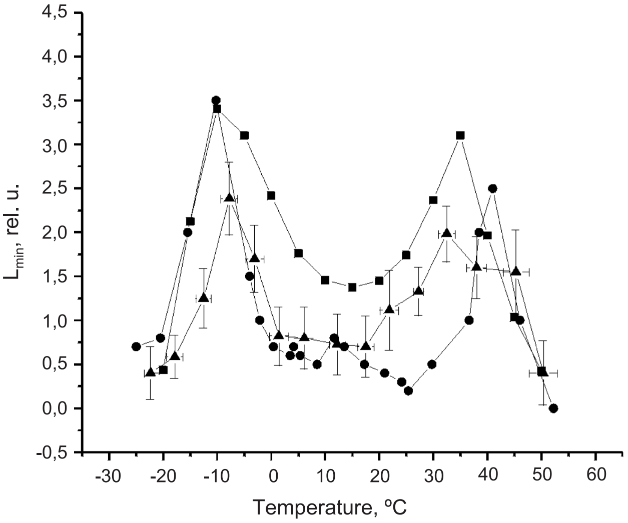

Fig. 3. The temperature dependence of L_{min}, steady-state delayed luminescence intensity. Experimental values measured on the leaf of ▲—*H. rose-sinesis*, ●—*F. faba*, ■—theoretical values.

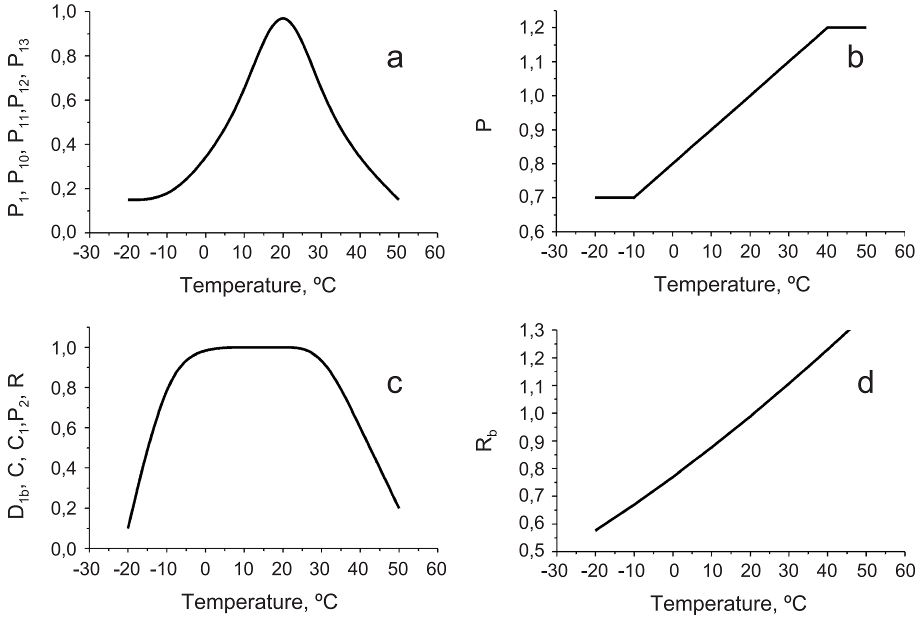

Fig. 2. The temperature dependences of the model rate constants.

hypothesis, depends on temperature according to standard exponential law $R_{\mathrm{b}} = R\exp(-E_{\mathrm{A}}/kT)$ (Fig. 2d) [26].

3. Results and discussion

The temperature dependences for steady-state DL value are given in Fig. 3. This figure shows experimental data obtained on leaf segments of chinese rose (*H. rosa-sinensis*), bean (*F. faba*) and theoretical data.

The existence of two peaks on this temperature dependence can be explained in the following way. At temperatures lower than −23 °Ñ some of the forward electron transport reactions, especially the diffusion, become slower and the backward electron transport is inhibited by low temperatures. As the temperature increases, the forward reactions are still slow, while the rate of backward reactions in the PS2 RC increase as $\exp(-E_{\mathrm{A}}/kT)$ and we have a maximum around −7 °C. With increasing temperature, the forward electron transport overgrows the backward and at physiological temperatures the DL luminescence intensity is lowest, which corresponds to most effective utilization of light energy. At 30–40 °Ñ we suppose that the Calvin cycle activity decreases, causing an increase in backward electron transport and hence in DL intensity. At 45–50 °Ñ destructive changes in the PS2 RC take place, making both forward and backward electron transport in the RC impossible and resulting in the fall of DL intensity. The position of maxima on steady-state DL intensity vs. temperature curve is reported to correlate with heat and cold tolerance of the plant [3].

Theoretical data shown in Fig. 3 were obtained in the following way. Taking into account the earlier described theoretical temperature dependences of the rate constants we calculated DL induction curves for different temperature values. Then we constructed the theoretical dependence of steady-state value of DL induction on temperature. This curve has two maxima and the same form as experimental curve.

4. Conclusions

The temperature dependences for parameters of DL induction curve were obtained adding the temperature dependence for 12 rate constants to the earlier proposed model of photosynthesis. These temperature dependences were proposed on base of literature date about temperature influence on different photosynthesis stages. The theoretical temperature dependence of DL steady-state intensity has the same form as experimental curve.

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