

Temperature Dependence of Delayed Fluorescence Induction Curve Transients

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Abstract. The temperature dependence of delayed millisecond fluorescence (DF) induction curve transients was investigated. The transients were obtained by keeping intact maize leaf segments in the dark for 30 to 300 s before illumination. The temperature dependence of DF induction revealed abrupt changes in activation energy of the recombination process. Those changes highly overcome the lowest energy barriers for certain types of chemical reactions, implying significant possible alterations in the DF mechanism itself. On the other hand, the particular transients responses expressed some specificities. Both the electrochemical gradient controlled changes, and the temperature induced changes contribute to it.

Key words: Delayed fluorescence — Recombination process — Activation energy — Phase transitions

Introduction

The delayed fluorescence (DF) phenomenon can be described as lighting of green plants, algae and photosynthetic bacteria within the red range of the visible spectrum, shortly upon their illumination, but later than prompt fluorescence emission. In a final step, DF is created by the same $S_1 \rightarrow S_0$ transition as prompt fluorescence (Lang and Lichtenthaler 1991; Krause and Weis 1991). The very different lifetimes clearly indicate two very distinct mechanisms by which photoactive S_1 state of chlorophyll (Chl) is created. The lifetime for prompt fluorescence is 1.5 ns or less (Govindjee et al. 1990; Schmuck et al. 1992). DF lifetimes are expressed in nanoseconds (Sonneveld et al. 1981), microseconds (Holzapfel and Haug 1974; Haveman and Lavorel 1975), milliseconds (Barber and Neumann 1974; Hipkins

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and Barber 1974), and seconds (Rutherford and Inoue 1984). In the case of prompt fluorescence, the S_1 state is created by a direct conversion. In the case of DF, the S_1 state is created through recombination of products formed in a primary photochemical act (Govindjee and Papageorgiou 1971; Papageorgiou 1975; Jursinic 1986). So, unlike prompt fluorescence which doesn't need more than one single Chl molecule to be emitted, the entire entity of the photosynthetic apparatus is necessary for DF emission.

The delayed fluorescence induction curve reflects processes occurring after irradiation of dark adapted photosynthetic object. Most DF induction curves have been recorded under millisecond working regime of a rotating disc with intermittent illumination. One cycle consisted of a few milliseconds of light period, and consecutive few milliseconds of darkness, in which DF is recorded (Vučinić 1983; Marković et al. 1987). The overall shape of the DF induction curve is highly dependent on the length of the dark period, preceding irradiation (Dzhibladze et al. 1988; Bukhov et al. 1989). If the preceding dark period (τ) is longer than 30 and shorter than 300 s, DF induction curve shows at least three maxima, close to 5, 15, and 300 s (Radenović et al. 1985). Veselovsky and Veselova (1990) made a step forward in explaining the DF induction curve transients, by putting DF induction curve on the same time scale with temporal variation of prompt fluorescence during continuous illumination of the photosynthetic apparatus (Kautzky effect), and with oxygen evolution changes. The comparison revealed strong correlation of the transients with the electrochemical gradient (ECG) formed across thylakoid membranes upon illumination (Veselovsky and Veselova 1990). The other comparison aspects, not directly related to this work, have been presented in detail in our review paper (Radenović et al. 1994).

While the temperature dependence of the DF steady state level has been relatively well investigated (Veselova et al. 1973; Vučinić et al. 1982; Marković et al. 1987; Ortoidze et al. 1987; Veselovsky and Veselova 1990; Marković et al. 1993), there are only a few reports on T-dependence of DF induction curve transients, though not the ones we deal with (Ono and Murata 1977, Grigorev et al. 1989). This report is aimed at exploring how temperature affects the dynamics of a resolved DF induction curve.

Materials and Methods

Four different genotypes of maize plants were used. The leaf segments (2 cm²) were cut under water, placed on a temperature controlled plate inside a home made Becquerel phosphoroscope; they were adapted to the temperature of the plate and darkness (τ periods from 30 to 240 s). The DF intensity was measured in the dark periods of intermittently illuminated leaves, using the phosphoroscope and a 150 W quartz-halogen lamp. One cycle consisted of 2 ms of light and 8 ms of darkness. Delayed fluorescence was registered from the 3rd to 7th ms of the dark period, using a cooled home-made photomultiplier. The kinetics of DF was monitored using a storage oscilloscope with a millisecond scale, and a recorder with

a seconds scale. Details of the experimental set up can be found elsewhere (Vučinić 1983). The temperature dependences between 5 °C and 55 °C were investigated (i.e. in the whole physiological range), for τ periods ranging from 30 to 240 s.

Results and Discussion

A typical three-dimensional DF induction curve is shown in Fig. 1: the transients *B*, *C*, *D* and *E* are indicated above the maximums. The stationary level of DF was established after 2–3 minutes, at room temperature (Dzhanumov et al. 1986; Klimov 1988). The influence of temperature on *B*, *C*, and *D* maxima, and on the steady-state level *E*, is shown in Fig. 2(a–h). Arrhenius plot, $\ln I = f(T^{-1})$, can reveal temperatures at which thylakoid membranes undergo phase transitions.

The application of the Arrhenius plot should have, as a necessary condition, a constant concentration of the radical pairs. It is known that energy transfer inside antennas is temperature independent at higher temperatures (Saray and Yomosa 1981). Since it is a main process preceding the primary photochemical act, one may take the concentration of created radical pairs to be temperature independent in the same T-range. What temperature rise actually does is acceleration of the reversed process, i.e. the radical pairs recombination. However, the acceleration rise is not homogeneous. Changes in temperature induce structural changes in thylakoids, and any other biomembranes. Such changes are seen at Arrhenius plots

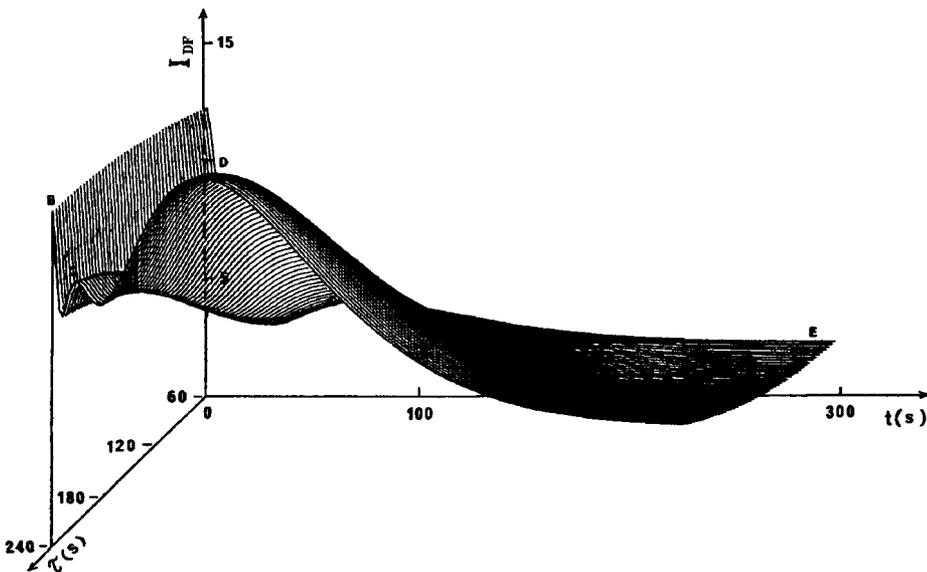


Figure 1. Three-dimensional plot of delayed fluorescence (DF) induction curve resolution, recorded from an intact maize leaf segment, at 32 °C, following various preceding darkness periods (τ). Peaks of the resolved transients are marked *B*, *C*, *D* and *E*.

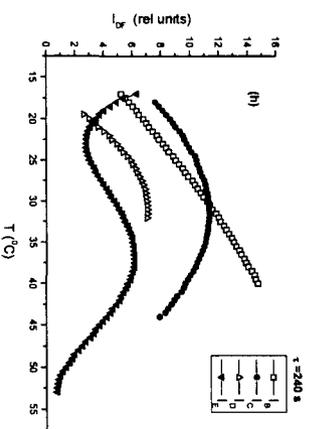
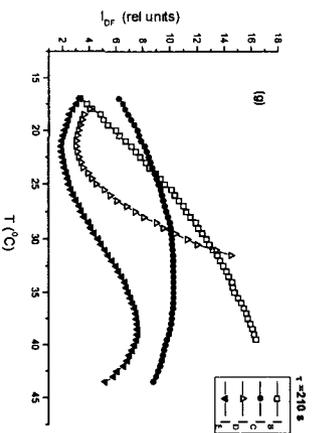
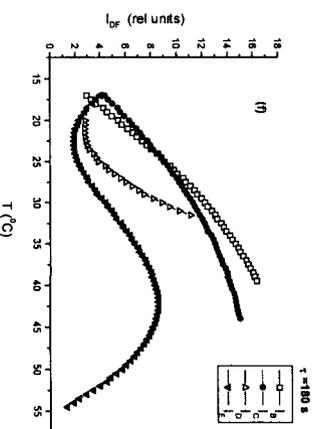
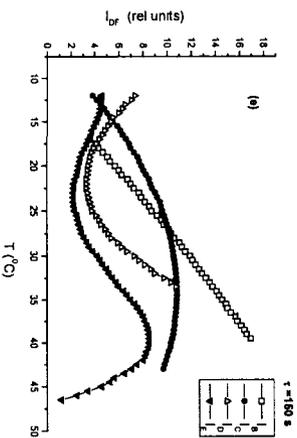
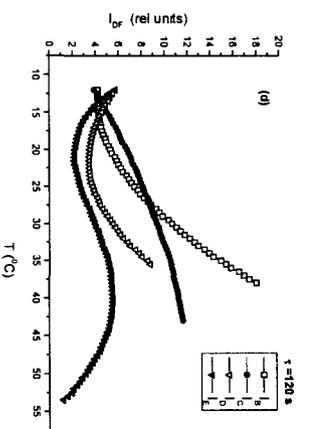
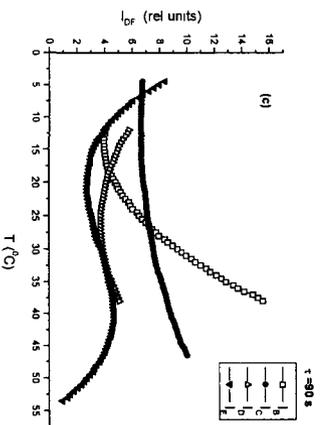
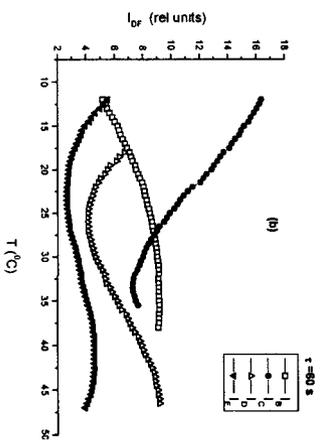
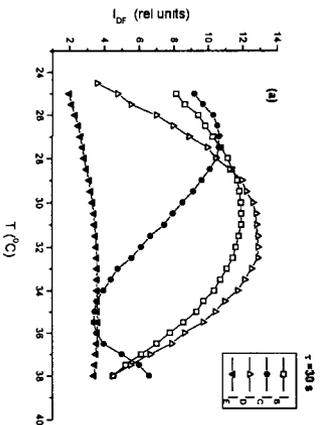


Figure 2(a-h). Temperature dependences of the maxima of the transients, *B*, *C*, *D*, and *E* (conventionally: the thermal curves, TCs), recorded in the 10–50°C interval, from an intact maize leaf segment. The transients were obtained by resolution of DF induction curve (such as shown in Fig. 1), following various preceding darkness period intervals (τ) ranging from 30 s (*a*) to 240 s (*h*).

of related processes as “break” points, indicating the occurrence of phase transitions (Lyons and Raison 1970; Raison and Chapman 1976). Activation energy of the recombination process (E_a) does change at these phase transition temperatures (T_{ph}) (Marković et al. 1987, 1993).

The Arrhenius formula has an inherent limitation of being used for T-plot of photosynthetic processes (including DF) since it is primarily used in homogeneous media. On the other hand, thylakoids with their luminal and stromal surrounding environment make the medium clearly heterogeneous. Still, Arrhenius plot has been used in a number of reports dealing with various photosynthetic processes (Shneyour et al. 1973; Berry and Bjorkman 1980; Raison and Orr 1986), including DF (Jursinic and Govindjee 1972, 1977; Ono and Murata 1977). The T_{ph} values are however in good agreement with those obtained by applying Arrhenius plot on the data got by the other biophysical methods. For example, Vučinić et al. (1982) found T_{ph} values of 12, 20 and 30°C for DCMU-infiltrated maize leaf segments. The T_{ph} values were in good correlation with those found from Arrhenius plot of ESR probe incorporated inside thylakoid membranes (Nešić et al. 1982). Terzaghi et al. (1989) have found the same T_{ph} values from two Arrhenius plots: one for DF, and the other one for *trans*-parinaric acid incorporated in the leaf liposomes. So, Arrhenius plot might be considered as a reliable “tool” to study T-effects on thylakoids in investigated T-region. DF itself is a sensitive, natural, internal probe to study thylakoid membranes (Melcarek and Brown 1977; Vučinić et al. 1982). Going towards the extremes of the physiological T-range for leaves (45–50°C), another limitation may appear. PSII donor side inactivation within the 43–47°C region for leaves (Bukhov et al. 1987) may affect the concentrations of the radical pairs.

The Arrhenius plot of the transient *C* for $\tau = 90$ and 120 s is shown in Fig. 3. The least squares method was employed to find the break points, and to calculate activation energies for DF emission (E_a). The E_a values calculated for all the transients (in kJ/mol), and all τ periods, are given in Table 1.¹ The corresponding temperatures of phase transitions (T_{ph} , in °C) are given in Table 2.

The temperature dependencies of the *B*, *C*, *D* and *E* transients maximal intensities shown in Fig. 2(a-h), are conventionally called the transients' *thermal curves* (TCs). Most TCs were recorded in T-intervals between 10°C and 50–55°C in these experiments. TC for $\tau = 30$ s was recorded in the 24–40°C range. It is interesting to see how the TCs shapes were affected by the τ period.

¹ The calculated E_a values are presented in simple numbers; the range of the E_a values makes the use of decimal numbers quite inappropriate.

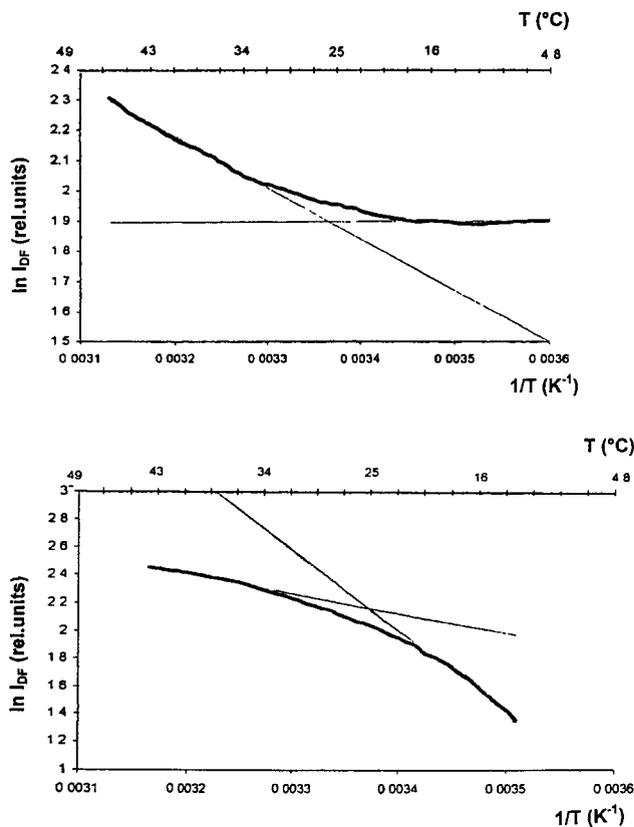


Figure 3. Arrhenius plots of the *C* transient thermal curves (such as given in Fig. 2a–h), for the preceding darkness periods of 90 s (top) and 120 s (bottom).

For all the TCs, τ period of 30–90 s appears to be a kind of an “adaptation response”. Namely, for all the three transients (*B*, *C* and *D*), the TCs shapes pass three phases. Then, at $\tau = 90$ s they reach a shape that is mostly repeated (with certain modifications) for all the other τ periods (120–240 s). For $\tau = 30$ s (Fig. 2a), the “initial phase” is of parabolic type, the “second phase”, $\tau = 60$ s (Fig. 2b), is pretty opposite to it, and the “third one”, $\tau = 120$ –240 s, looks quite stable (Fig. 2d–h). So, it really seems that $\tau = 90$ s (Fig. 2c) represents the point from which the thermal curves take a kind of a defined behaviour.

For $\tau = 90$ –120 s (Fig. 2c–d), TC of the *B* transient rose in T-interval of 10–40°C. But the rise was not continuous. A break point (T_{ph}) was detected at temperatures of 19.5 and 17.9°C (Table 2), leading to the corresponding jumps of E_a values, from 4 to 52, and from 5 to 53 kJ/mol (Table 1). Such a sharp rise may suggest a change in the DF mechanism itself, which is opposite to basic conclusions from our previous work (with the steady state level, the *E* component):

Table 1. Activation energies, E_a , for DF induction curve processes, belonging to the resolved transients *B*, *C*, *D* and *E* (Fig. 1), for different preceding darkness periods (τ).

Period of preceding darkness (τ , s)	Activation energy, E_a (kJ/mol)									
	Transient <i>B</i>		Transient <i>C</i>		Transient <i>D</i>		Transient <i>E</i>			
30	65	-199	84	-171	348	267	-290	99	-21	
60	33	2	-33	24	-23	-65	40	-62	32	-56
90	4	52	0	14		-28	28	-57	26	-229
120	5	53	48	12		-61	64	-90	54	-141
150	93	30	69	-15		-69	94	-62	93	-598
180	135	26	75	15		-4	116	-145	106	-368
210	122	22	34	-17		-63	132	-109	93	-104
240	54	22	30	-30		144	13	-134	74	-176

The E_a values were calculated from the Arrhenius plots (see Fig. 3), from the straight lines slopes (drawn using the least squares method).

Table 2. Phase transitions temperatures (T_{ph}) relating to DF induction curves processes belonging to the transients *B*, *C*, *D*, and *E*, for different preceding darkness periods (τ).

Period of preceding darkness (τ , s)	Phase transitions temperatures, T_{ph} ($^{\circ}\text{C}$)									
	Transient <i>B</i>		Transient <i>C</i>		Transient <i>D</i>		Transient <i>E</i>			
30	33.3 \pm 0.2	28.5 \pm 0.2	35.6 \pm 0.2	31.6 \pm 0.2	30.8 \pm 0.2					
60	23.4 \pm 0.3	17.4 \pm 0.3	32.7 \pm 0.3	25.4 \pm 0.3	22.0 \pm 0.3	42.6 \pm 0.3				
90	19.5 \pm 0.2		25.8 \pm 0.3	26.5 \pm 0.2	20.5 \pm 0.4	48.6 \pm 0.4				
120	17.9 \pm 0.2		25.0 \pm 0.5	22.5 \pm 0.2	21.0 \pm 0.4	44.6 \pm 0.4				
150	24.7 \pm 0.4		26.3 \pm 0.4	22.6 \pm 0.2	25.0 \pm 0.3	43.6 \pm 0.3				
180	24.0 \pm 0.3		26.3 \pm 0.3	23.1 \pm 0.2	23.8 \pm 0.5	48.5 \pm 0.5				
210	24.3 \pm 0.3		31.0 \pm 0.4	22.0 \pm 0.2	22.2 \pm 0.3	38.5 \pm 0.3				
240	26.1 \pm 0.3		32.0 \pm 0.4	23.8 \pm 0.2	22.8 \pm 0.5	41.6 \pm 0.5				

T_{ph} values were obtained from the Arrhenius plots (see Fig. 3), using the least squares method.

temperature increases the activation energy for DF emission, but does not affect the mechanism itself (Marković et al. 1993). Intriguingly, the behaviour for the rest of the τ periods (150–240 s) does not relativize such a possible strong conclusion. The break point appears to be at 24 $^{\circ}\text{C}$ (26 $^{\circ}\text{C}$, for $\tau = 240$ s, Table 2). However, relationships between the E_a values are at least 3 or more. The least difference between E_1 and E_2 (the E_a values before, and after the break) is 63 kJ/mol – for $\tau = 150$ s. The biggest one, for $\tau = 180$ s, is 109 kJ/mol (Table 1). For these τ periods (150–240 s, Fig. 2e–h), $E_1 \gg E_2$. This is totally opposite compared to τ periods of 90 and 120 s ($E_1 \ll E_2$ Fig. 2c–d).

The C transient expressed a rather close behaviour compared to B transient. For $\tau = 90$ s, $E_1 \ll E_2$ (0 vs. 14 kJ/mol – Table 1), and then *vice versa* for the remaining τ periods (Table 1). Interestingly, after the break point (25–26°C, for τ periods of 120, 150 and 180 s, and 31–32°C, for τ periods of 210 and 240 s – Table 2), E_2 becomes negative (Fig. 2e, g–h), i.e. a further increase in temperature leads to a decrease in DF intensity.

The TC behaviour of the D transient, however, differs significantly from those of the transients B and C . Starting from the “reference τ point” (90 s – Fig. 2c), a distinguished behaviour could be seen: a decline in the maximum (between 10–15°C and 22–23°C), and a rise afterwards. The rise however grows with the prolongation of the τ period (Fig. 2c–g), from 28 kJ/mol ($\tau = 90$ s), to 132 kJ/mol ($\tau = 210$ s) – (Table 1) ($\tau = 240$ s is an exception – Fig. 2h). So, the E_a rise was almost fivefold, lifting and lifting barrier for DF emission. The total ΔE change ($E_2 - E_1$) ranges from 56 kJ/mol ($\tau = 90$ s), to 195 kJ/mol ($\tau = 210$ s) (Table 1). That is common with the B & C TCs behaviour: the E_a change highly exceeds the lowest barriers for chemical reactions, implying possible alterations in the DF mechanism itself.

Finally, the E transient (steady-state level) expresses a behaviour that was already seen in our former reports (Marković et al. 1987, 1993). The intensity decreases starting from 10°C, until the break point of about 22°C (for almost all τ periods in the range of 60–240 s). Then, the rise takes place ending with a collapse point, “oscillating” rather irregularly, in the 38–48°C range (Table 2). The E_a values also increase after the break, from 26 kJ/mol ($\tau = 90$ s) to 106 kJ/mol ($\tau = 180$ s), and then decline slightly (93 and 74 kJ/mol, for $\tau = 210$ and 240 s, respectively – Table 1). So, as for the D transient, the barrier for the recombination process became fourfold, starting from $\tau = 90$ s, and ending at $\tau = 180$ s.

To summarize, one may generally conclude that there are three kinds of consequences derived from these investigations:

- 1) There undoubtedly is a relationship between the period of preceding darkness (τ), and the T-action. Though it is premature to speculate on its nature it is probably not wrong to presume that such a relationship is related to ECG formation and dissipation.

- 2) Activation energies for DF emission became augmented severalfold, with an increase of the τ period (usually starting from $\tau = 90$ s). The fact doubtlessly indicates a sharp increase of a barrier, needed to be overcome in the recombination process. That was seen with all the transients. Such a degree of a coherence was not seen with the T_{ph} values. For each particular transient they “oscillate” rather irregularly, and one would say, independently, in relation to the τ periods. Most frequently, the break point is in the 22–26°C range, but with certain significant variations. For the E transient only (steady-state level), the next break point after the rise (the “collapse point”) is in the 41–48°C range, which was already seen in our earlier works (Marković et al. 1987; 1993). Since temperature produces structural changes in thylakoid membranes, one may suggest that “pre-changes” (i.e. changes influenced by a prolongation of the τ period) are also of a structural nature. The

pre-changes and the T-induced changes would then work together in rising the activation barrier for DF emission.² Because the τ -period directly affects dissipation of ECG, it is logical to presume that the pre-changes are ECG controlled. This is a reasonable speculation based on the transients T-response only. The lack of direct experimental evidence – direct measurements of ECG reestablishment (after a particular τ period) in the same T-range – can not deny the logic. Briefly, one deals with double, but simultaneous responses of thylakoid membranes: the first one is related to ECG dissipation and consecutive reestablishment after irradiation, and the second one is to the simultaneous T-action.

3) The transients' particular responses (starting from “standardized changes” at $\tau = 90$ s) indicate variations in the thylakoids general response, described under items 1) and 2). Namely, the *B&C* TCs behave one way, the *D* transient TC the other way. In the T-range of 10(15)–25°C the *B&C* maxima increase, while that of the *D* transient decreases. So, despite the general consensus that the transients are ECG dependent (see review of Veselovsky and Veselova 1990), the ways they depend on it may evidently vary. So far, we can only notice this fact, but in the view of the lack of other experimental details we can not speculate about the meaning.

In conclusion, it is necessary to underline that direct experiments are needed to get more basic support to conclusions given under 1), 2) and 3). They should connect ECG creation and dissipation with T-induced structural changes. Still, it is useful to emphasize the necessity of such investigations.

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² Evidently the pre-changes are dependent on the length of the τ -period (otherwise, thylakoid membranes would react uniformly on T-action in the same T-interval – speaking in E_a and T_{ph} terms of the investigated transients).

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