Delayed Fluorescence Induction Transients: Mathematical Modelling Based on the Chosen Kinetic Models

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Abstract. The paper deals with mathematical modelling of the transients obtained by fitting of delayed fluorescence (DF) induction trace The transients are in certain, doubtless connection with electrochemical gradient (ECG) formed across thylakoid membranes upon illumination The fitting of the C and D transients by using consecutive model for first-order reactions (A $\rightarrow$ B $\rightarrow$ C) showed that they might play a role of the intermediate (B), according to scheme down bellow

$$(\text{“A}_1\text{ state”})_{\text{ECG}} \xrightarrow{k_1(C\text{ transient})} C\text{ transient} \xrightarrow{k_2(C\text{ transient})} \text{Products}$$

$$(\text{“A}_2\text{ state”})_{\text{ECG}} \xrightarrow{k_1(D\text{ transient})} D\text{ transient} \xrightarrow{k_2(D\text{ transient})} \text{Products}$$

The two ECG controlled “states” (A_1& A_2) are not the same, which does not exclude some sort of proportionality On the other hand, the E band, contributing mainly to the stationary level of DF induction trace, may be fitted by parallel model of at least two first-order reactions

Key words: Delayed fluorescence — Induction transients — Kinetics modelling — Consecutive and parallel mechanisms

Abbreviations: DF, delayed fluorescence, ECG, electrochemical gradient, τ, period of preceding darkness

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Introduction

Delayed fluorescence (DF) phenomenon can be described as lighting of green plants, algae and photosynthetic bacteria in red range of visible spectrum, immediately upon their illumination. In a final step DF is created by the same $S_1 \rightarrow S_0$ transition as prompt fluorescence (Krause and Weis 1991; Lang and Lichtenthaler 1991). But the very different lifetimes, of 1.5 ns or less for prompt fluorescence (Govindjee et al. 1990; Schmuck et al. 1992), compared to nanoseconds (Sonneveld et al. 1981), over microseconds (Holzapfel and Haug 1974; Haveman and Lavorel 1975) and milliseconds (Barber and Neumann 1974; Hipkins and Barber 1974) to seconds range (Rutherford and Inoue 1984) for DF, clearly indicate two very distinct mechanisms by which photoactive S_1 state of chlorophyll (Chl) is created. In the case of prompt fluorescence, the S_1 state is created in a 10^{-12}–10^{-14} s period by internal conversion, following light absorption. In DF case 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 photosynthetic apparatus is necessary for DF emission.

Delayed fluorescence induction trace reflects processes and phenomena occuring when photosynthetic object is being kept in dark for a while, and then illuminated, i.e. in a transition period, from "dark" to "light" regime. Most of DF induction traces were recorded under millisecond working regime of a rotating disc, with intermittent illumination, consisting of a few milliseconds of light period, and consecutive few milliseconds of darkness in which DF is being recorded (Vučinić 1983; Marković et al. 1987). The overall shape of DF induction trace is highly dependent on the length of the dark period preceding illumination (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 trace is splitted into at least three transients (Radenović et al. 1985). The clear distinct appearance times of their maximums ($t_B = 5 \pm 0.5$ s; $t_C = 15 \pm 5$ s, and $t_D = 300 \pm 60$ s) suggest that their origins are in various processes ocurring during the dark/light transition period. Veselovsky and Veselova (1990) made a step forward in explaining DF induction trace transients by putting DF induction trace on the same time scale with temporal variation of prompt fluorescence during continuous illumination of photosynthetic apparatus (Kautzky effect), and with oxygen evolution changes. The Kautzky effect has been thoroughly investigated and it is reasonably well understood (Govindjee and Papageorgiou 1971; Papageorgiou 1975; Lichtenthaler and Rinderle 1988; Lichtenthaler 1992). The comparison revealed correlation of the B and C transients with electrochemical gradient (ECG) formed across thylakoid membranes upon illumination (Veselovsky and Veselova 1990). In this paper we present further study of correlation between DF induction trace transients and ECG, using mathematical modelling based on chosen kinetic models. Mathematical modelling has already been employed in elucidating some theoretical models concerning dark and light processes of photosynthesis (Karavaev and Kukushkin 1993), as well as the induction

of millisecond DF itself (Kukushkin and Soldatova 1996). However, in the latter case, the proposed model appeared to be more widely applied, dealing *not* with the particular DF transients, but with the effect of photosynthesis "dark phase" phenomena (photorespiration, carbon reduction cycle) on DF induction process.

Materials and Methods

Two different genotypes of maize plants (*Zea mays* L.) have been used in these experiments. The leaf segments (2 cm^2) were cut under water and placed on a temperature controlled plate inside a phosphoroscope. They were adapted to the temperature of the plate (two different temperatures: 22 and 32°C) and darkness (two different periods, τ = 210 and 240 s), and then delayed fluorescence emission was recorded. The DF intensity was measured in the dark period of intermittently illuminated leaves, using a Becquerel phosphoroscope and a 150 W quarz-halogen lamp. One cycle consisted of 2 ms of light and 8 ms of darkness. Delayed fluorescence was recorded from the 3^{rd} to 7^{th} ms of the dark period, using a cooled photomultiplier. The signal from the multiplier was registered on a storage oscilloscope for the fastest processes, while the slower variation of DF was recorded on a chart. The few minutes recording produced DF induction trace, with faster transients in the first 2 minutes and slower changes afterwards (Figs. 1, 2). Details of the experimental setup can be found elsewhere (Vučinić 1983).

Mathematical modelling

Theoretical basis for decomposition of DF induction signal came from kinetic model of two consecutive first-order reactions, which could explain mutual behaviour of the C and D transients, and from kinetic model of two parallel first-order reactions, which could fit the stationary level behaviour. The very beginning part of the induction signal, belonging to millisecond A transient, and to B transient, was not analysed for technical reasons.

Concentration changes of participants involved in a chain of two consecutive first-order reactions:

$$\mathrm{A} \xrightarrow{k_1} \mathrm{B} \xrightarrow{k_2} \mathrm{C} \tag{1}$$

are being expressed by formula:

$$(\mathrm{B}) = [k_1(\mathrm{A}_0)/(k_2 - k_1)] \cdot [\exp(-k_1 t) - \exp(-k_2 t)] \tag{2}$$

and:

$$(\mathrm{C}) = (\mathrm{A}_0)\{1 + 1/(k_1 - k_2) \cdot [k_2 \exp(-k_1 t) - k_1 \exp(-k_2 t)]\} \tag{3}$$

where k_1 and k_2 represent two first-order rate constants, (A_0) is initial concentration of the primary reactant A.

Concentration changes of participant M, involved in two parallel first order reactions:

$$\begin{aligned} \mathrm{M} &\xrightarrow{q_1} \mathrm{N} \\ \mathrm{M} &\xrightarrow{q_2} \mathrm{P} \end{aligned} \tag{4}$$

can be expressed as

$$(\mathrm{M}) = (\mathrm{M}_0)\exp(-k_3 t) \tag{5}$$

where (M) and (M_0) are time-dependent and initial concentration of the reactant M, respectively, and $k_3 = q_1 + q_2$, the sum of the two first-order rate constants

Decomposition of DF induction trace was performed using nonlinear fitting procedure for transients C, D and E, simultaneously The following analytical expression was fitted to each set of experimental data

$$\begin{aligned} y(I_{\mathrm{DF}}) = {} & A_C[\exp(-k_{1C}t) - \exp(-k_{2C}t)] + A_D[\exp(-k_{1D}t) - \exp(-k_{2D}t)] + \\ & + A_E[1 - \exp(-k_3 t)] \end{aligned} \tag{6}$$

where subscripts C, D and E – assigned to corresponding rate constants and pre exponential factors – define transients C, D and E, respectively (which sum is equal to overall induction DF signal) For a particular experimental series of data, optimal values for the set of 8 parameters ($A_C, k_{1C}, k_{2C}, A_D, k_{1D}, k_{2D}, A_E, k_3$) were calculated using Nead-Melder simplex algorithm supplied with MATLAB for Windows, Version 4 2c Optimal parameter values correspond to the minimum value of

$$\chi^2 = \sum_{i=1}^{N} [y_i - y(t_i, A_C, k_{1C}, k_{2C}, A_D, k_{1D}, k_{2D}, A_E, k_3)]^2 \tag{7}$$

in the 8-dimensional parametric space (N is the number of experimental data pairs y_i, t_i) Theoretically, each local minimum corresponds to one of the solutions of the system of 8 equations

$$\begin{aligned} \partial\chi^2/\partial A_C &= 0 \\ \partial\chi^2/\partial k_{1C} &= 0 \end{aligned} \tag{8}$$

In Figs 1 and 2 experimental data are presented as crosses, while componental transients C, D and E, obtained by fitting, as well as their sum (corresponding to Eq (6)), are shown as continual curves

Results

The typical DF induction traces are shown in Figs 1 and 2 the transients C, D and E are indicated under the trace The program algorithm itself selects the final transient shapes, based on chosen *initial* parameter values (A, k_1, k_2), for deliberately chosen tolerance of fitting (10^{-10}) At the end of the variable part of the trace, a stationary level is established after 2–3 minutes at room temperature (Dzhanumov et al 1986, Klimov 1988)

An important agreement exists today about close correlation between origin of the B, C and D transients and the electrochemical gradient (ECG) formed across thylakoids' membranes upon illumination It has been proved experimentally that

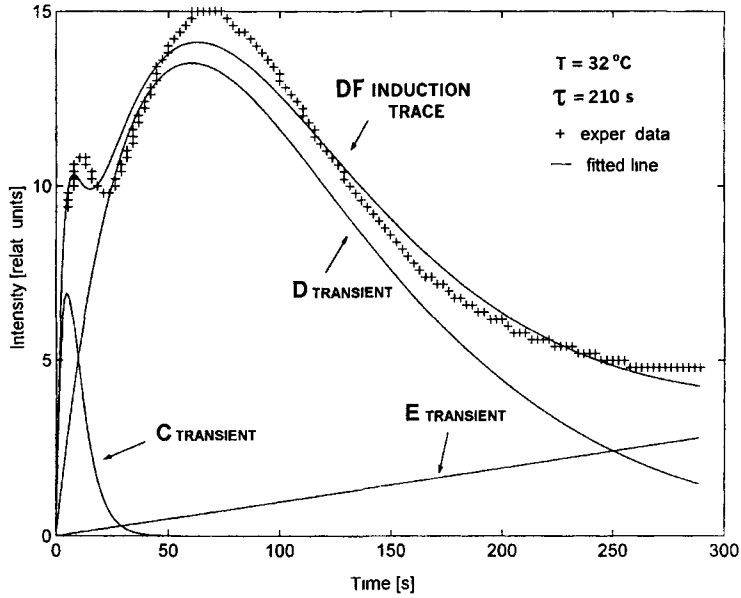

Figure 1. Delayed fluorescence induction trace and the transients C, D and E,obtained as a result of the experimental data (+ + + +) fitting, according to Eq (6), the first member describes the transient C, the second one the transient D, and the third one the transient E The trace was obtained as described in experimental part Temperature of the leaf segment was 32 °C, and the preceding dark period (τ) was 210 s The appertaining parameters for transient C, rate constants $k_{1C} = 0\ 205\ s^{-1}$ and $k_{2C} = 0\ 208\ s^{-1}$, and pre-exponential factor $A_C = 1\ 32 \times 10^3$, for transient D, rate constants $k_{1D} = k_{2D} = 0\ 017\ s^{-1}$, and pre-exponential factor $A_D = 1\ 85 \times 10^4$, for transient E, rate constant $k_3 = 3\ 07 \times 10^{-6}\ s^{-1}$, and pre-exponential factor $A_E = 3\ 16 \times 10^3$ Tolerance of fitting 10^{-10} $\chi^2 = \sum_{i=1}^{132}[y_i - y(t_i, A_C, k_{1C}, k_{2C}, A_D, k_{1D}, k_{2D}, A_E, k_3)]^2 = 35\ 402$, $\chi^2/132 = 0\ 268$, and C $[y_i, y(t_i, \quad)] = 0\ 988$ (correlation coefficient between experimental and fitted data)

millisecond DF emission (the same lifetime as the one described in this paper), exponentially depends on ECG (Crofts et al 1971; Lavorel et al. 1982).

In addition, Veselovsky and Veselova (1990) offered a broader explanation about the ECG influence on the C and D transients behaviour. In their interpretation, the C transient is controlled by electrical ($\Delta\psi$) component of ECG, and the D transient through ΔpH induced microstructural changes. Indeed, the behaviour of the B and D transients in the presence of uncouplers (dissipating ECG) confirmed such conclusions (Wraight and Crofts 1971; Itoh and Murata 1973; Lavorel 1975). The transient C has the similar character, since its behaviour is sensitive to the presence of uncoupler valynomicine (Veselovsky and Veselova 1990).

In our earlier report on DF induction trace kinetic behaviour (Radenovic et al. 1985) we have shown that dependence of the C and D transients maximums on

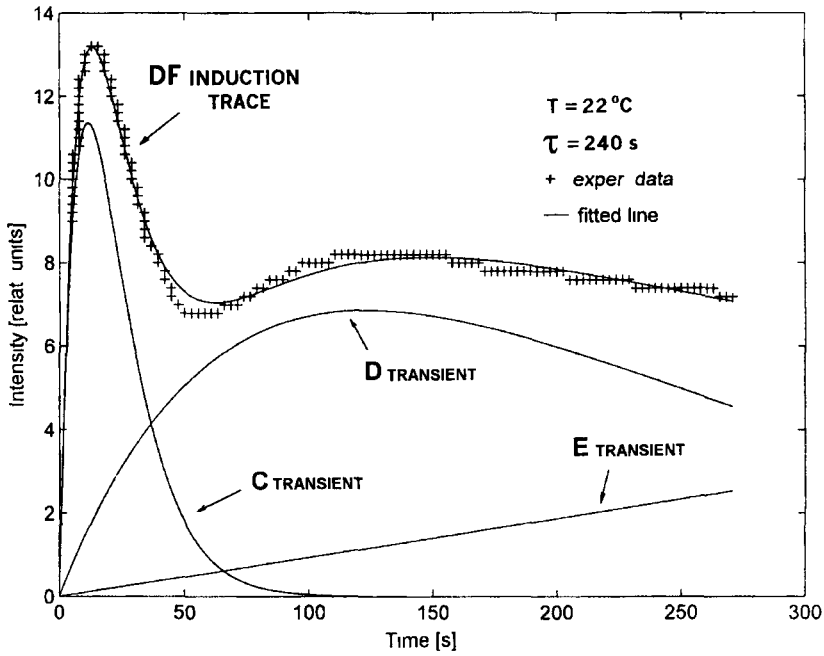

Figure 2. Delayed fluorescence induction trace and the transients C, D and E, obtained as a result of the experimental data (+ + + +) fitting, according to Eq (6), the first member describes the transient C, the second one the transient D, and the third one the transient E The trace was obtained as described in experimental part Temperature of the leaf segment was 22 °C, and the preceding dark period (τ) was 240 s The appertaining parameters for transient C, rate constants $k_{1C} = k_{2C} = 0\ 086\ s^{-1}$, and pre-exponential factor $A_C = 3\ 57 \times 10^4$, for transient D, rate constants $k_{1D} = k_{2D} = 0\ 008\ s^{-1}$, and pre-exponential factor $A_D = 1\ 36 \times 10^4$, for transient E, rate constant $k_3 = 3\ 01 \times 10^{-7}\ s^{-1}$, and pre-exponential factor $A_E = 3\ 11 \times 10^4$ Tolerance of fitting 10^{-10} $\chi^2 = \sum_{i=1}^{139}[y_i - y(t_i, A_C, k_{1C}, k_{2C}, A_D, k_{1D}, k_{2D}, A_E, k_3)]^2 = 10\ 063$, $\chi^2/139 = 0\ 072$, and C $[y_i, y(t_i, \quad)] = 0\ 988$ (correlation coefficient between experimental and fitted data)

the length of the preceding dark period (τ) may be expressed by two first-order consecutive reactions, having different rate constants. That was an evidence that their origins are in different processes ocurring during dark/light transition period. One of the consequences of keeping photosynthetic object (in this case, the leaf segment) in dark is "disenergization" of thylakoids' membranes, i.e. dissipation (disappearance) of ECG (Evans and Crofts 1973; Morita et al. 1981). Since the preceding dark period (τ) is the quantitative measure of ECG dissipation, we found it reasonable to try to apply a kinetic model for consecutive first-order reactions on the whole temporal behaviour of the C and D transients (rise, maximum and decline). Precisely, the goal was to check out how well the C and D transients

(obtained by application of Eq. (6) on the experimental DF induction traces – Figs. 1, 2) fit the model of two consecutive first-order reactions.

Discussion

The concentration changes of participants involved in a chain of two consecutive first-order reactions (Eq. 1) are shown by Eqs. (2, 3). For our purpose we will consider initial reactant ("precursor") A as an ECG controlled "state", temporal changes of which may cause possible appearance of DF induction trace transients. The term "state" is being based on all current up-dated knowledge about mechanisms producing DF emission. The two today accepted theories about the origin of DF emission (recombination and radical-pair theory) both imply creation of the chlorophyll S_1 photoactive state as a result of a series of consecutive reverse reactions and processes, with many participants at the donor as well as at the PSII reaction center acceptor side (Jursinic 1986). The initial concentrations, as well as the rate constants for this whole reverse process may only be speculated: the experimental data are not reported yet. Part of the process is doubtlessly ECG controlled, since PSII donor and acceptor side lie on the two sides of thylakoid membrane through which ECG is being established immediately upon illumination. One might take this part of the whole reverse process as a "state" controlled by ECG, which is in certain, doubtless connection with the C and D transients existence (Veselovsky and Veselova 1990, and the references cited therein). If one takes this logic, it is even more logical that the "state" is being dissipated in first-order processes with the "rate constants" k_1 and k_2. Quotation marks have been used because k_1, as well as k_2 are not real rate constants, but rather "pseudo-ones", and most probably, very complex ones.

Figures 1 and 2 show two different DF induction traces, obtained experimentally from two different maize leaf segments. The both curves have been presented as a sum of three transients: C, D and E(according to procedure described in "Materials and Methods"). The last one (without the peak) contributes mainly to the stationary level, established at the end of all DF induction trace changes.

First of all, it is necessary to emphasize that it was *not* possible to fit the experimental data (DF induction traces – Figs. 1, 2) by inserting the Eq. (3) into the overall equation (6). A function defined by Eq. (3) has no extreme values (maxima or minima) for $t > 0$ ($k_1 \neq k_2$), regardless of the values of k_1 and k_2. This is evidently not the case with the shapes of induction traces (Figs. 1, 2). Contrary to this, the insertion of Eq. (2) into Eq. (6) yielded good fitting of the experimental traces (Figs. 1, 2). One may conclude two important things from this fact. Firstly, a consecutive chain, "A state" $\rightarrow$ C transient $\rightarrow$ D transient simply *does not exist.* Its existence might be eventually expected from the chronological point of view (the C transient appears first, and the D transient later – Figs. 1, 2), but, except for this there is no other evidence to support the expectation. Secondly, the ECG controlled "A state" is *not* the same for the C and D transients. Additional proof for the last conclusion came from mutual comparison of k_1 and k_2 pseudo-constants, belonging

to C and D transients, from the same experimental induction trace. From Fig. 1 follows:

$$k_1(C_{\text{transient}})/k_1(D_{\text{transient}}) = 0.205/0.017 \cong 12.3$$
and
$$k_2(C_{\text{transient}})/k_2(D_{\text{transient}}) = 0.208/0.017 \cong 12.5$$

From Fig. 2 follows

$$k_1(C_{\text{transient}})/k_1(D_{\text{transient}}) = 0.086/0.008 \cong 10.6$$
and
$$k_2(C_{\text{transient}})/k_2(D_{\text{transient}}) = 0.086/0.008 \cong 10.6$$

If we presume that ECG controlled "A state" is the same for C and D transients it is then reasonable to expect the corresponding k_1 and k_2 pseudo-constants to be very close. That is evidently *not* the case. But, the fact that the "A state" is not initial common "state" for the C and D transients appearance does not mean that kinetic model for consecutive first-order reactions (represented by Eq (1)) can not be applied any longer. Contrary, k_1/k_2 relationships for C and D transients, taken separately from both Figs. 1 and 2, confirms its validness. From Fig. 1 follows

$$(k_1/k_2)_{C\text{transient}} = 0.205/0.208 \cong 0.99$$
and
$$(k_1/k_2)_{D\text{transient}} = 0.017/0.017 \cong 1$$

From Fig. 2 follows

$$(k_1/k_2)_{C\text{transient}} = 0.086/0.086 \cong 1$$
and
$$(k_1/k_2)_{D\text{transient}} = 0.008/0.008 \cong 1$$

So, the k_1/k_2 relationships are about the same for the both transients, *obtained from two different experiments, from two different leaf segments (and from two different maize genotypes)*. That is certainly not a coincidence. It clearly appears that the consecutive chain (Eq. (1)) is in effect, but the C and D transients can not be linked to its final product (C) but rather to the "intermediate" (B). So, taken just schematically, instead of the first presumed scheme·

$$(\text{“A}_1\text{ state”})_{\text{ECG}} \xrightarrow{k_1} C \text{ transient} \xrightarrow{k_2} D \text{ transient}$$

the other one looks more reasonable:

$$(\text{“A}_1\text{ state”})_{\text{ECG}} \xrightarrow{k_1(C\text{ transient})} C \text{ transient} \xrightarrow{k_2(C\text{ transient})} \text{Products}$$

$$(\text{“A}_2\text{ state”})_{\text{ECG}} \xrightarrow{k_1(D\text{ transient})} D \text{ transient} \xrightarrow{k_2(D\text{ transient})} \text{Products}$$

The last scheme does not mean necessarily any parallelism between the "two A states", but some sort of proportionality can not be neglected The above cited and very constant relationships, $k_1(C_{\text{transient}})/k_1(D_{\text{transient}})$ and $k_2(C_{\text{transient}})/k_2(D_{\text{transient}})$, calculated from the same figures (about 12 3 and 12 5 from Fig 1, and about 10 6 from Fig 2) does not question the proposed scheme The fact that the C constants are much bigger than the D ones simply means that C transient appears earlier, and D transient later, which, of course, cannot be denied (Figs 1, 2)

Speaking about E transient (Figs 1, 2) it is clearly evident even from the shape that the consecutive first-order kinetic model (Eq (1)) cannot be applied any longer This transient appears as a "precursor" of the stationary level, which is believed rather to be a product of a few independent contributions, than a transient itself To check this out we used the simplest kinetic model for parallel processes two first-order parallel reactions (Eq (4)), and corresponding equation (5), included into the overall equation (6) This time, k_3 is pseudo-constant for the same reasons as k_1 and k_2 pseudo-constants (for the C and D transients) The transient shape, though looking as a straight line, is what the algorithm did calculate

One may prove easily that q_1 and q_2 first-order pseudo-constants are different from their "counterparts", the C and D transients' pseudo-constants, k_1 and k_2 (Figs 1, 2)

$$(k_3 = q_1 + q_2)_{E\text{transient}} = 3\,07 \times 10^{-6} \neq (k_1 + k_2)_{C\text{transient}} = 0\,205 + 0\,208 \cong 0\,413$$

and

$$(k_3 = q_1 + q_2)_{E\text{transient}} = 3\,07 \times 10^{-6} \neq (k_1 + k_2)_{D\text{transient}} = 0\,017 + 0\,017 \cong 0\,034$$

The same comparison from Fig 2 yields

$$(k_3 = q_1 + q_2)_{E\text{transient}} = 3\,01 \times 10^{-7} \neq (k_1 + k_2)_{C\text{transient}} = 0\,086 + 0\,086 \cong 0\,172$$

and

$$(k_3 = q_1 + q_2)_{E\text{transient}} = 3\,01 \times 10^{-7} \neq (k_1 + k_2)_{D\text{transient}} = 0\,008 + 0\,008 \cong 0\,016$$

Furthermore, it clearly means that initial "M state" (precursor of the E transient) is different from "A_1 and A_2 states" (precursors of C and D transients) Here, the term "M state" has even more general meaning than in the case of the "A states" As the modelling shows, at least two distinct, parallel, probably ECG dependent processes are responsible for the E transient, and so for the existence of stationary level So far, one might only speculate about any connection between the "A states" and the "M state" But, probably, if the connection exists, it occurs *via* ECG functioning

It is worth underlining again that all the conclusions have been made using two really *different* DF induction traces The differences come not only from various

chosen photosynthetic objects (two different leaf segments from two different maize plants), but from different experimental conditions, too (τ = 210 s, T = 32°C for the first DF induction trace; τ = 240 s, T = 22°C for the second one). So, it really arises that, despite different chosen objects and conditions, not a coincidential, but rather regular behaviour has been reflected, in a sequence of photosynthesis "light phase" connected to ECG.

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