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INDEPENDENT EFFECTS OF MAGNESIUM IONS ON ENERGY-TRANSFER PROCESSES IN CHLOROPLASTS

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The effect of removal of Mg^{2+} on the fluorescence properties of LHCP-PS-II has been examined by different methods: (a) by titration with the artificial quenchers of chlorophyll fluorescence, *m*-dinitrobenzene and DBMIB (2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone); (b) as a function of wavelengths absorbed preferentially by LHCP, compared with wavelengths relatively enriched in PS II absorbed light; (c) by measurement of the fluorescence induction parameters as a function of the Mg^{2+} concentration or the excitation wavelength (i.e., light absorbed preferentially by LHCP or relatively enriched in PS II absorbed wavelengths). The following conclusions are drawn. (a) In the presence of magnesium ions, energy-transfer coupling between LHCP and PS II is tight, which argues against the idea of a weakly coupled population of LHCP molecules. (b) On lowering the Mg^{2+} concentration of a chloroplast suspension: (1) the increased spillover of energy to PS-I involves virtually all LHCP-PS-II entities and not just a part, which is strongly quenched; (2) there is a decrease in LHCP-PS-II energy-transfer coupling and this occurs only at low Mg^{2+} concentrations (below 0.5 mM). This process therefore seems distinct from the spillover interaction; (3) the rate constant for energy transfer to PS-II reaction centers decreases and this seems independent of the decreased LHCP-PS-II energy coupling.

Introduction

It was originally suggested by Murata [1] that divalent cation removal from chloroplasts increases exciton transfer from PS II-LHCP to PS I (spillover). This hypothesis has gained widespread acceptance (see review by Williams [2]) and further experimental support [2–8]. However, it is not known whether all LHCP-PS II complexes are able to transfer energy to PS I at low divalent cation concentrations or whether only a part of the LHCP- PS II population is involved in this interaction. This problem is addressed here by titration of the F_m fluorescence with artificial quenchers of chlorophyll fluorescence at different Mg^{2+} concentrations. It is demonstrated that all or almost all LHCP-PS II units transfer energy to PS I at low divalent cation concentrations.

A number of authors have suggested that divalent cations also control the tightness of exciton transfer coupling between LHCP and the PS II complex [5,9–11]. In fact, the suggestion has been made [9] that this may be the principal effect of

Abbreviations: LHCP, light-harvesting chlorophyll *a*/*b* protein; PS II, the Photosystem II core complex; PS I, Photosystem I; F_m, maximum fluorescence (all traps closed); F_0, non-variable fluorescence (all traps open). F_v, variable fluorescence ($F_m - F_0$); DCMU, 3-(3′,4′-dichlorophenyl)-1,1-dimethylurea; DBMIB, dibromothymoquinone.

divalent cations, with an increased spillover flux to PS I at low divalent cation concentrations being due to the decreased LHCP-PS II coupling. An attempt is made here to investigate a possible relation between the changes in spillover and LHCP-PS II coupling. By analysing the effect of different concentrations of magnesium ions on F_m when the excitation light was preferentially absorbed by LHCP or by both LHCP and PS II, it is demonstrated that the loosening of LHCP-PS II coupling becomes significant only at low Mg^{2+} concentrations (below 0.5 mM), whereas considerable spillover-induced quenching occurs as the Mg^{2+} concentration is lowered from 2.5 to 0.5 mM. Thus, the two processes do not appear to be mechanistically related.

There is considerable confusion in the literature concerning the effect of divalent cations on the F_0 fluorescence. When chloroplasts suspended in the absence of divalent cations are compared with those suspended at saturating concentrations, most authors report little or no change in F_0 [1,9,12–18]. The absence of F_0 changes is surprising, since a spillover type explanation predicts significant decreases in F_0 upon cation removal (for an F_m decline of about 50% the F_0 should decrease by about 15–20%). Such decreases have been observed by several authors [3,19,20]. This problem has been investigated here by analysing the F_0 and F_m levels at different concentrations of magnesium ions. It is found that upon lowering the Mg^{2+} concentration from 2.5 to 0.5 mM the F_0 increases, subsequently to decline at lower concentrations. It is suggested that removal of Mg^{2+} decreases the rate constant for exciton trapping by reaction centres in a manner distinct from the decreased LHCP-PS II coupling. The common failure to observe significant F_0 decreases on divalent cation removal is thus explained as due to a superimposed F_0 increase caused by decreased reaction centre exciton trapping.

Materials and Methods

Chloroplasts were extracted from freshly harvested spinach or barley leaves by blending in a solution containing 30 mM Tricine (pH 8)/0.4 mM sucrose/10 mM NaCl/2.5 mM $MgCl_2$. After filtering through eight layers of cheese cloth, they were pelleted by a brief centrifugation at $1500 \times g$ and resuspended for 3 min in the above medium minus sucrose at the desired $MgCl_2$ concentration. An equal volume of the sucrose-containing medium was then added, maintaining unchanged the $MgCl_2$ concentration, and the chloroplasts were pelleted at $1500 \times g$. They were subsequently resuspended in the sucrose-containing medium at the required $MgCl_2$ concentration and stored in ice for about 1 h before starting the experiment. The basic reaction medium employed the same components as were present in the storage medium minus sucrose.

Fluorescence induction experiments at 20 °C were performed utilising the assembly previously described [17]. The chloroplasts were illuminated with a light of approx. $2 \cdot 10^6$ J · m^2 · s^{-1} intensity (Corning 4-96 filter). Fluorescence emission was measured at 691 or 659 nm (Baltzers interference filters; half band width, 10 nm). DCMU (20 μM) was always present unless otherwise indicated.

Titrations of the maximal fluorescence of the chloroplasts with DBMIB and *m*-dinitrobenzene were performed as previously described [21].

Results

Energy-transfer coupling between PS II and LHCP

The problem of energy-transfer coupling between LHCP and PS II may be formally approached in terms of the bipartite and tripartite photosystem models of Butler and colleagues [4,22]. In the case of a tight exciton-transfer coupling, the LHCP-PS II association may be analysed in terms of the bipartite model. In the case of a weak coupling or a part of the LHCP not being associated with PS II, the tripartite formalism should be used. In this context, fluorescence experiments have been performed utilising light preferentially absorbed by LHCP (475 nm) or absorbed more equally by both LHCP and PS II (435 nm).

We estimate, by analysis of the fluorescence excitation spectra of the chlorina barley mutant which lacks LHCP [23] and its parental wild type, that at 475 nm the cross section of LHCP is approx. 3.5–4 times greater than that of PS II with respect to the situation at 435 nm. We have reasoned that if LHCP is weakly coupled to PS II or if a population of LHCP is physically separated from the LHCP-PS II units (and not quenched by

some endogenous quenching process), as implied by Kyle et al. [24], it should be possible to detect a lower F_m/F_0 ratio exciting with 475 nm than with 435 nm. This simple reasoning is born out by simulations we have performed using the tripartite model of Butler and colleagues [9,22] and assuming different values for the rate constants involved in exciton transfer between LHCP and PS II (Jennings, R.C., unpublished data). In the experiments reported in Table I, no such difference was observed, and we therefore conclude that it seems unlikely that a fraction of loosely coupled or uncoupled LHCP existed at these cation concentrations in these chloroplasts. It should be mentioned that we also obtained similar results when the fluorescence emission was monitored at other wavelengths (677 and 691 nm).

Both Loos [10] and Wong and Govindjee [5] have shown that upon removal of Mg^{2+} from the suspension medium fluorescence quenching is greater when the excitation light is enriched in wavelengths absorbed by LHCP. In Fig. 1 this result is confirmed, and it is further demonstrated that this effect occurs only at concentrations of Mg^{2+} below 0.5 mM. Between 2.5 and 0.5 mM $MgCl_2$, the quenching is equal for both 475 and 435 nm.

A comment on the sensitivity of this method is required. The maximum F_{m475}/F_{m435} ratio change reported in Fig. 1 is from 1 to 0.92 on Mg^{2+} removal. Elsewhere we demonstrate that changes from 1 to between 0.98 and 0.97 (after membrane phosphorylation [25]) are easily detectable. Thus the method is capable of detecting even smaller changes and is probably applicable for ratio decreases greater than from 1 to around 0.99.

TABLE I

THE F_m/F_0 RATIOS FOR CHLOROPLASTS INCUBATED WITH 2.5 mM AND 0.5 mM $MgCl_2$ AND EXCITING WITH EITHER 475 nm OR 435 nm LIGHT (HALF BAND WIDTH, 8 nm)

The emission wavelength was 659 nm (half band width, 10 nm). The F_0 value was determined in the absence of DCMU, which was subsequently added for the F_m measurement.

$[MgCl_2]$ (mM)	475 nm	435 nm
2.5	4.48	4.46
0.5	2.90	2.91

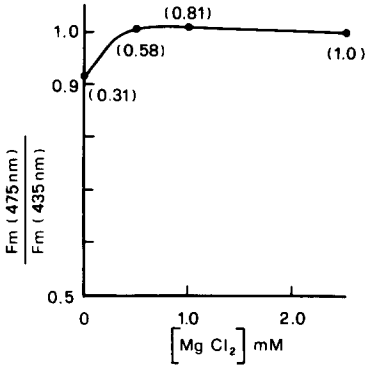

Fig. 1. The effect of different concentrations of magnesium ions on the F_m fluorescence measured with either 475 or 435 nm excitation light. Fluorescence was measured at 691 nm and excited at 475 nm or 435 nm (half band width, 12 nm). The numbers in parentheses represent the relative fluorescence values measured with the 435 nm excitation light.

In order to explain the greater quenching observed with 475 nm excitation light, two hypothe-

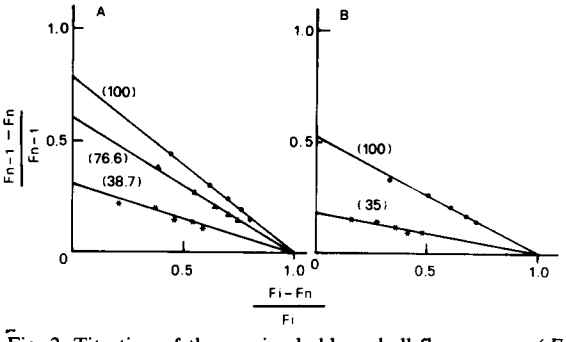

Fig. 2. Titration of the maximal chlorophyll fluorescence (F_m) with the artificial fluorescence quenchers DBMIB (A) and *m*-dinitrobenzene (B) at different concentrations of Mg^{2+}. Each titration consisted of five consecutive additions of either DBMIB (0.6 μM) or *m*-dinitrobenzene (125 μM). The concentrations of $MgCl_2$ are 2.5 mM (●), 0.5 mM (▲), 0 (★). Chlorophyll was 4 μg/ml. F_i, initial fluorescence, before quencher addition; F_n, fluorescence after n additions of quencher; F_{n-1}, fluorescence after $n-1$ additions of quencher. Numbers on the various curves are the fluorescence emission values in arbitrary units. The symbols represent the data points, whereas the straight lines are the theoretical plots assuming homogeneous quenching, standardised to the $[MgCl_2] = 2.5$ mM titration. Each data point is the average of five separate titrations, each titration performed with three different chloroplast preparations.

ses have been entertained. (1) The quencher (presumably PS I, via spillover) interacts predominantly with LHCP with no decrease in the rate constants for energy-transfer coupling between LHCP and PS II. Mathematical simulation using the tripartite model of Butler and Strasser (Ref. 22 and unpublished data) suggests that this can explain the effect only in the case of a fairly weak coupling between LHCP and PS II (or when some LHCP is detected from PS II). We estimate that in order for the LHCP-PS II coupling to be sufficiently weak to permit the successful application of such a hypothesis that the F_m/F_0 ratio measured exciting with 435 nm light would be at least 5–15% greater than that measured using 475 nm. Since no difference in this ratio was observed (Table I), this hypothesis is discarded. (2) The removal of magnesium ions leads to decreased energy-transfer coupling between LHCP and PS II (i.e., decreased average values for the rate constants for energy transfer between these two complexes) and the fluorescence quencher (PS I) acts principally at the level of LHCP. This hypothesis is supported by simulation studies using the tripartite model (Ref. 22 and unpublished data). The data would therefore indicate that on reducing the concentration of Mg^{2+} below 2.5 mM the LHCP-PS II complex is initially quenched (presumably via 'spillover') though exciton energy coupling remains high. Additionally, this latter parameter decreases at concentrations of Mg^{2+} below 0.5 mM. Thus the influence of magnesium ions on spillover-induced quenching and LHCP-PS II coupling seems to be two distinct phenomena. A similar conclusion has been published recently by Telfer et al. [8] based on a different experimental approach, after this paper was submitted for publication.

Titration studies with quenchers of chlorophyll fluorescence

The data, presented in the first subsection of the Results, suggest that the quenching of F_m due to removal of Mg^{2+} involves two distinct processes, i.e., a quenching interaction (with PS I) with little or no significant change in LHCP-PS II exciton transfer coupling down to 0.5 mM $MgCl_2$ followed by a decrease in the latter parameter together with preferential quenching of LHCP at concentrations below 0.5 mM. It is of interest to know whether the quenching interaction involves all or only a fraction of the LHCP-PS II units. Thus, titration experiments with two different quenchers of chlorophyll fluorescence (DMBIB or *m*-dinitrobenzene) were performed and the data plotted as the $(F_{n-1} - F_n)/F_{n-1}$ vs. $(F_i - F_n)/F_i$ graph (Fig. 2). We have demonstrated [21] using the bipartite model formalism and a homogeneous quenching interaction with added quencher (i.e., all LHCP-PS II fluorescing units are approximately equally quenched rather than just a fraction of them being more strongly quenched) that such a plot yields a straight line which extrapolates to 1 on the $(F_i - F_n)/F_i$ axis. If this titration is then performed at different levels of homogeneous background quenching, the ratio of the intercepts on the $(F_{n-1} - F_n)/F_{n-1}$ axis should equal the ratio of the F_m values prior to addition of added quencher. It can be demonstrated that a similar situation holds also when one considers the more complicated tripartite model (see Appendix). However, if only a fraction of the LHCP-PS II units were to be quenched (heterogeneous quenching), macroscopic deviations from the above described titration behaviour wich artificial quenchers are to be expected (see Appendix).

In Fig. 2, it can be seen that titrating the F_m fluorescence with both DBMIB and *m*-dinitrobenzene, the experimental data very closely approximate the theoretical expectations, assuming homogeneous background quenching. This is interpreted to indicate that approximately all LHCP-PS II units are quenched by PS I upon lowering the concentration of Mg^{2+} below saturating levels. In the case of some LHCP becoming fucntionally detached from PS II traps in the absence of magnesium ions, these data indicate that quenching by PS I involves both the detached LHCP as well as the remaining LHCP-PS II entities.

The rate constant for energy transfer to PS II traps

The data in this first subsection suggest that between 2.5 and 0.5 mM $MgCl_2$ LHCP and PS II can be considered to form a single energy-transfer entity which may be analysed in terms similar to those of the bipartite model of Butler and Kitajima [4]. Below 0.5 mM $MgCl_2$ the tripartite model is

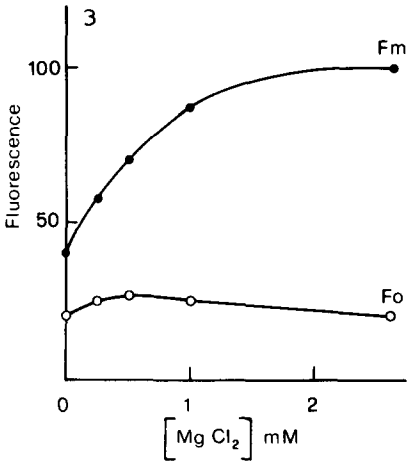

Fig. 3. Titration of the F_m and F_0 fluorescence induction parameters with $MgCl_2$. Similar results were obtained when the F_0 values were determined in the absence of DCMU, which was subsequently added to permit the F_m determination. Each data point is the average of twelve separate determinations, repeated with three different chloroplast preparations.

required. The familiar fluorescence induction parameters for Mg ion concentrations between 2.5 and 0.5 mM (Fig. 3) have therefore been analysed according to a bipartite type formalism, for which one can write:

$$F_m = \frac{k_F}{k_F + k_X + k_{T21} + k_{T'}\psi_d} \quad (1)$$

$$F_0 = \frac{k_F}{k_F + k_X + k_{T21} + k_T} \quad (2)$$

$$F_v/F_m = \frac{k_T - k_{T'}\psi_d}{k_F + k_X + k_{T21} + k_T} \quad (3)$$

where k_F, k_{T21}, k_T, $k_{T'}$, and k_X are respectively the rate constants for fluorescence, spillover, energy transfer to open PS II traps, energy transfer to closed PS II traps, and other processes that compete for LHCP-PS II excitons. ψ_d is the probability for non-radiative decay at the closed reaction centre [4].

From Fig. 3 one can see that upon lowering the concentration of Mg^{2+} below 2.5 mM the F_m decreased monotonically. However, the F_0 increased between 2.5 and 0.5 mM $MgCl_2$ and subsequently declined. This observation is similar to that reported by Hipkins [26] and has also been observed by Vernotte and Briantais (personal communication), but differs from that of Henkin and Sauer [18] and Telfer et al. [8], who failed to observe such an increase in F_0 upon lowering the concentration of Mg^{2+} below saturating levels.

Considering Eqns. 1–3, it is clear that spillover changes alone (or in combination with the $k_{T'}\psi_d$ parameter) cannot explain the marked increase in F_0 on passing from 2.5 mM to 0.5 mM $MgCl_2$. This observation can, however, be explained in terms of a decreased rate constant for energy transfer to open reaction centres (k_T). Numerical solution of Eqns. 1–3, (unpublished data) suggest that on passing from 2.5 mM to 0.5 mM $MgCl_2$ an increased 'spillover' may be accompanied by an approx. 30% decrease in the k_T value. Below 0.5 mM $MgCl_2$, any further increases in the F_0 value are presumably masked by the large increases in 'spillover' which lead to a net lowering of the F_0. We would furthermore point out that the proposed decrease in the k_T value on reducing the concentration of Mg^{2+} seems distinct from the decrease in energy coupling between LHCP and PS II, as this latter seeems to occur largely at Mg ion concentrations below 0.5 mM. Thus, two relatively independent parameters are involved that influence F_0 fluorescence in opposite ways. The relative balance of these two factors in different chloroplast preparations then probably explain the apparently contradictory data in the literature concerning cation effects on F_0 (see Introduction).

Acknowledgements

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Appendix

In order to analyse the effect of titrating the maximum fluorescence emission (F_m) with quenchers of chlorophyll fluorescence, it is convenient to utilise either the bipartite or tripartite models of Butler and Kitajima [4] and Butler and Strasser [22].

The bipartite equation for fluorescence yield is:

$$F_m = \frac{k_F}{k_F + k_X + k_{21} + k_{T'}\psi_d}$$

where k_F, k_{21}, k_T, and k_X are respectively the rate constants for fluorescence, 'spillover', energy transfer to closed PS II traps and all other processes that compete for LHCP-PS II excitons. ψ_d is the probability for non-radiative decay at the closed reaction centre.

The tripartite equation is:

$$\phi_F = \frac{\gamma\psi_{F_3} + \beta\psi_{T_{23}}\psi_{F_3} + \beta\psi_{F_2} + \gamma\psi_{T_{32}}\psi_{F_2}}{1 - \psi_{T_{23}}\psi_{T_{32}}} \qquad \text{(A-1)}$$

where β and γ are the relative optical cross sections of PS II and LHCP, respectively; ψ_{F_2} and ψ_{F_3} are the fluorescence probabilities for PS II and LHCP, respectively; $\psi_{T_{23}}$ and $\psi_{T_{32}}$ are the transfer probabilities from PS II to LHCP and from LHCP to PS II, respectively. These latter terms define the degree of exciton transfer coupling between the two types of complex. All these probabilities are defined as the ratios of the rate constants as explained by Butler and Strasser [22].

In order to carry out numerical simulations using these equations, the following assumptions have been made. The rate constant for fluorescence emission is 50% that of non-radiative dissipative processes within the antenna pigments in the absence of spillover to PS I [27]. The fluorescence yield at the F_m level is in the range 0.1, as is expected from yield and lifetime measurements [3,28]. The F_v/F_m ratio, when β is assumed to equal γ, is 0.8, as is experimentally determined. The difference between F_0 and F_m is due to the conversion of a strong photochemical quenching at the open reaction centre to a weak non-photochemical quenching at the closed reaction centre [4,27]. When 435 nm light is used, $\beta = \gamma = 0.5$. When 475 nm light is used, $\beta = 0.2$ and $\gamma = 0.8$. These changes in the relative absorption cross sections are consistent with the approx. 4-fold increase in the relative optical cross section of LHCP (relative to PS II) at 475 nm with respect to 435 nm, determined here (see Results, first subsection). The assumption of a somewhat lower value for β at 435 nm ($\beta = 0.4$), as suggested by the data of Anderson and colleagues [29,30], does not alter the conclusions reached here. It is the relative values at the two wavelengths that are important. PS I absorption is ignored, since it is not considered to contribute to the fluorescence signal under these conditions. The relative rate constant values used are: for the fluorescence $k_F = 0.02$, for non-radiative dissipative processes in the antenna pigments $k_X = 0.04$, and various values for energy transfer between LHCP and PS II ($k_{T_{32}}$, $k_{T_{23}}$). From the Forster overlap integrals calculated by Shipman and Housman [31] and the absorption profiles of the ioslated LHCP and PS II [29,32], one would expect that the ratio $k_{T_{32}}/k_{T_{23}}$ should be in the range 1–4.

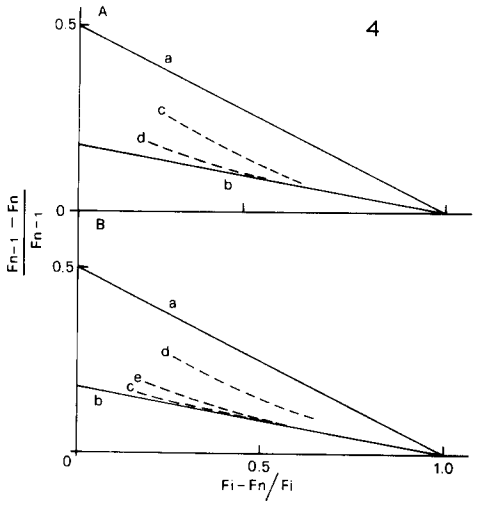

Fig. 4. Simulated titrations of chlorophyll fluorescence with an added fluorescence quencher at different levels of background fluorescence (e.g., for chloroplasts plus or minus magnesium ions) for homogeneous and heterogeneous background quenching. In A, the bipartite model has been used; in B, the tripartite model has been used. In both A and B, the initial fluorescence yield for curve a was 0.1 (at saturating concentrations on magnesium ions) and for the other curves it was 0.036 (in the absence of magnesium ions). (A) Curve a, no background quenching by PS I; curve b, homogeneous background quenching; curve c, heterogeneous background quenching in which 75% of the fluorescing units (LHCP-PS II) were quenched by PS I; curve d, heterogeneous background quenching in which 90% of the fluorescing units were quenched by PS I. (B) Curve a, no background quenching by PS I. The $k_{T_{32}}$ value assumed was greater than 10 ($k_F = 0.02$, $k_X = 0.04$) and the $k_{T_{32}}/k_{T_{23}}$ ratio was 2; curve b, homogeneous background quenching with no change in the $k_{T_{32}}$, $k_{T_{23}}$ values; curve c, homogeneous background quenching with a large decrease in the $k_{T_{32}}$, $k_{T_{23}}$ values (1 and 0.5); curve d, heterogeneous background quenching in which 75% of the fluorescing units were quenched by PS I and in which there was a large decrease in the $k_{T_{32}}$ $k_{T_{23}}$ values (1 and 0.5); curve e, as for curve d, except that 90% of the fluorescing units were quenched. All other assumptions are described in the text. For definition of the various F parameters, see legend to Fig. 2.

On the basis of these assumptions, we have calculated the expected effect of titration with an artificial quencher at different levels of either homogeneous or heterogeneous background quenching, utilising both the bipartite and tripartite models (Fig. 4). In the case of homogeneous quenching (where all the fluorescing bed is considered to be approximately equally quenched by the background quenching process) and when LHCP-PS II energy transfer coupling is high, both models yield straight line double quenching plots which extrapolate to 1 on the $(F_i - F_n)/F_i$ axis irrespective of the level of background quenching. The ratio of the intercepts on the $(F_{n-1} - F_n)/F_{n-1}$ axis in this case is equal to the ratio of the F_i values at the different levels of background quenching (see also Ref. 21). A large decrease in energy-transfer coupling (curve *c*, Fig. 4B) leads to minor deviations from the ideal situation, but which may not be experimentally detectable. However, if the background quenching is heterogeneous (only part of the fluorescing bed is quenched by the background quenching processes), large titration deviations are seen and this is irrespective of the photosystem model used.

We would emphasise that the simulations presented here are intended to have a qualitative character and as such are not dependent on the exact values chosen for the various rate constants. Within the limits imposed by experiental observation, the choice of numerically different values leads to similar conclusions.

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