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Magnetic-field effects on primary reactions in Photosystem I

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Abstract

Magnetic-field effects on primary reactions of Photosystem I have been studied by measuring changes of the fluorescence yield in preparations isolated from the cyanobacterium *Synechococcus elongatus*. Photoaccumulation of the reduced phylloquinone A_1 in the presence of dithionite under anaerobic conditions led to an increase of chlorophyll fluorescence yield and appearance of magnetic field effects. A magnetic field effect has been found which is characterized by half-saturation values of the order of ~ 25 G. Addition of salts of monovalent and divalent cations to the suspension significantly modified the profile of the magnetic field dependence. The modification of the magnetic field effect by salts is ascribed to conformational changes in the Photosystem I reaction centre that affect the dipolar and/ or spin exchange coupling in the radical pair $P_{700}^{+\cdot}A_0^{-\cdot}$. Injection of neutral red into suspensions of samples containing reaction centres in the state $P_{700}A_0A_1^{red}$ gives rise to light induced fluorescence quenching and disappearance of the magnetic field effect. Subsequent incubation in the dark restored the high fluorescence yield and the magnetic field effect. It is inferred that under these conditions the Photosystem I reaction centres are photoaccumulated in the redox state $P_{700}A_0^{-\cdot}A_1^{red}$ where the anion radical $A_0^{-\cdot}$ acts as fluorescence quencher.

Keywords: Reaction center; Magnetic field effect; Radical pair; Photosystem I

1. Introduction

Successful crystallization and X-ray structure analysis [1] of Photosystem I (PS I) from *Synechococcus elongatus* offers the possibility for a better understanding of structure-function relations in this integral membrane complex. Of special interest is the mechanism of the primary charge separation and recombination processes between the photoactive pigment, P_{700}, and the acceptor A_0 and subsequent electron transfer form $A_0^{-\cdot}$ to A_1 within the reaction centre (RC). The acceptor components A_0 and A_1 were substantiated as to be a chlorophyll (*Chl*)-*a* monomer and phylloquinone, respectively [2,3]. One way for detailed functional analyses of recombination processes is provided by the high degree of correlation in the motion of the unpaired electron spins in the primary radical pair (PRP) $P_{700}^{+\cdot}A_0^{-\cdot}$ [4–6] and by the influence of external magnetic fields on this motion [7,8]. To study the recombination properties of the primary radical pair it is useful to block the electron transfer from the reduced primary acceptor to the secondary acceptor either by removal or prior reduction of secondary acceptor. Under these conditions the PRP lifetime increases by two to three orders of magnitude and becomes determined by the processes of back electron transfer. The reaction time of charge recombination is sufficiently long for coherent electron spin motion between the nearly degenerate singlet and triplet electron spin states due to magnetic interactions such as nuclear hyperfine and electronic Zeeman interactions [4–8]. These events lead to formation of both, singlet and triplet state of the primary donor. An external magnetic field affects the electron spin motion by removing the triplet states of the PRP from the resonance with singlet state and causes measurable effects on the quantum yield formation of the singlet and triplet states of the primary donor (so-called MARY effect) [8]. The effects of external magnetic fields on these primary

Abbreviations: RC, reaction centre; PS I, Photosystem I; P_{700}, primary donor in PS I; A_0, primary acceptor in PS I; *Pheo*, primary acceptor in PS II; A_1, secondary acceptor in PS I; Q_A, secondary acceptor in PS II; *Chl*, chlorophyll; MARY, magnetic field dependence of the reaction yield; PRP, primary radical pair

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reactions have been extensively studied in RCs of purple bacteria (for reviews on experimental results and their interpretation, see Ref. 7 and 8) and Photosystem II (PS II) [9–16], whereas only a few studies on such effects have been reported for Photosystem I (PS I) [17–19]. The observed MARY effect and theoretical simulations for the PRP spin dynamics in photosynthetic purple bacteria [7,8] and PS II [9–16] led to the conclusion that the spin exchange coupling between the primary radicals is small, i.e. less than 10 G. In contrast to RCs of photosynthetic purple bacteria, the sign change for the profile of the MARY curve was observed for PS I enriched particles within the magnetic field domain 0–200 G [17,18]. A theoretical consideration led to the conclusion that $P_{700}^{+\cdot}$ and $A_0^{-\cdot}$ exhibit a strong spin exchange coupling (60–100 G) [20]. On the other hand, the MARY profile of PS I reported by Sonneveld et al. [19] did not show any spin-exchange coupling. Therefore, taking into account (i) the above mentioned contradiction in the experimental results and (ii) similarities in the structure of the PS I and purple bacteria RCs [1,3], it seemed worthwile reinvestigating magnetic field effects in PS I.

2. Materials and methods

Trimeric form of PS I was isolated from membranes of *Synechococcus elongatus* as described earlier [1]. They were kept in a solution containing 30 mg/ml protein, 100 mM $MgSO_4$, 5 mM 2-(*N*-morpholino)ethanesulphonic acid (MES), pH 6.4, 0.02% w/w β-dodecyl-maltoside at 6–8°C until needed [1]. The preparations had a P_{700} to *Chl* ratio of 1:90 that was determined as described earlier [21] by using a molar extinction coefficient for P_{700} of 64 mM^{-1} cm^{-1}. The suspension of PS I particles was diluted with 0.2 M glycine-NaOH (pH 8.4 or 10.2) to the final *Chl* concentration of ~ 3 μg/ml. In order to lower the redox potential of the sample oxygen was removed by preincubation in the dark for at least 5 min with 5 mM glucose, 0.1 mg ml^{-1} catalase and 0.1 mg ml^{-1} glucose oxidase [22–24] at 12°C, and ~ 200 μg/ml sodium dithionite was also added.

Chlorophyll fluorescence was excited by broad-band (400–600 nm) light from a 30 W projector lamp after transmission through a filter combination of 5 mm C3C-21 and 2 mm C3C-25 (LOMO, Sankt-Petersburg). The intensity of this beam was ~ 40 μJ cm^{-2} s^{-1}. Fluorescence was monitored at the right angle to the direction of the exciting beam with a photomultiplier screened by a cut-off 2 mm KC-19 filter ($\lambda > 680$ nm, LOMO) or/and an interference filter. The photomultiplier output was amplified by a home-built amplifier, digitized at a rate 10 μs/12 bit and transferred to an IBM compatible personal computer. The magnetic field strength was swept by a home-built 600 W ramp generator. The ramp pulse duration and the delay time between the ramp pulses were adjusted to ~ 0.2 s and ~ 0.8 s, respectively. All MARY measurements were done at 12°C.

3. Results and discussion

It is well established that photoaccumulation of Q_A^{red} in the RCs of purple bacteria and PS II of green plants is accompanied by a 2–6-fold increase of (bacterio) *Chl* fluorescence [25] and also gives rise to magnetic field-induced enhancement of its yield [7–9]. On the other hand, in preparations enriched with PS I only a very small light-induced increase of the fluorescence yield has been observed under strong reductive conditions [26,27]. However, Ikegami [28] observed a considerable increase of the fluorescence yield after incubation in the presence of dithionite of ether extracted particles highly enriched in P_{700} (P_{700}/Chl ratio, 1:6–9). A relatively strong light induced fluorescence increase has been also found by Telfer et al. [29] in PS I-enriched particles (P_{700}/Chl ratio, 1:30–50) in the presence of sodium dithionite.

Fig. 1 shows fluorescence induction curves of PS I particles. Illumination in the presence of ~ 1 mg/ml sodium ascorbate under anaerobic conditions caused an instantaneous rise of the fluorescence to a level that will be

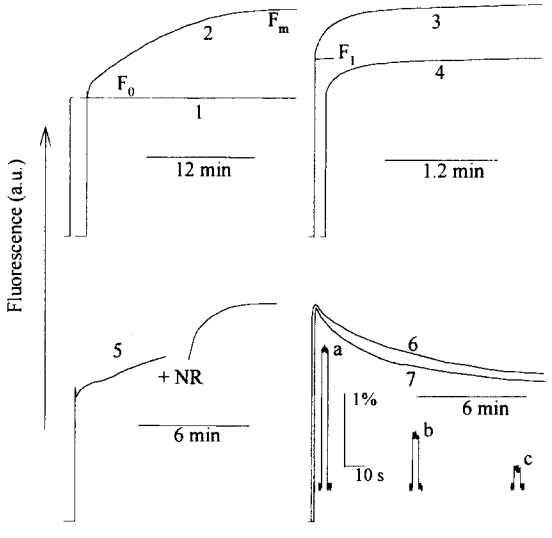

Fig. 1. Time course of the light-induced fluorescence yield changes of PS 1 particles under anaerobic conditions for sample suspension (see Section 2. Trace 1, in the presence of 1 mg/ml sodium ascorbat; trace 2, in the presence of ~ 200 μg/ml sodium dithionite; trace 3, second illumination of the sample dark incubated for 5 min after the first illumination by the exciting light; trace 4, sample as 2 but plus 2 mM NaCl; trace 5, plus 2 μM neutral red as indicated; trace 6, plus 2 μM neutral red which was added when the maximal fluorescence yield had been achieved in the presence of 200 μg/ml sodium dithionite under exciting light illumination; trace 7, second illumination of the sample with 2 μM neutral red and ~ 200 μg/ml sodium dithionite by the exciting light after incubation in the dark for 5 min of preilluminated sample; traces a, b and c, kinetic curves of fluorescence yield changes induced by the magnetic field of 650 G strength measured at the beginning, middle and last part of the fluorescence decline that is shown by the traces 6 and 7.

considered as reference and is therefore for convenience designated as F_0. Prolonged illumination has no influence on the fluorescence (see Fig. 1, trace 1). In agreement with results of Telfer et al. [29], addition of sodium dithionite, and sample illumination with the exciting beam leads at first to an immediate rise of the fluorescence to the level F_0 followed by a slow increase to a maximal level F_m (see Fig. 1, trace 2). After turning off the light beam, the sample was incubated in the dark for at least 5 min and then exposed to a second illumination. As in the case of complete dark adaptation the preilluminated sample exhibits an instantaneous rise but the level F_1 attained is markedly higher than F_0 (see Fig. 1, trace 3). The subsequent rise to the same F_m level is significantly faster than in the former sample. These findings are in correspondence with a previous report by Telfer et al. [29]. Progressively longer incubation in darkness after the first illumination did not influence the typical fluorescence induction curve represented by trace 3 (data not shown). In all cases, the initial level F_1 of the preilluminated samples appears to be always higher than the F_0 level. The reason for this phenomenon is not yet clear.

Incubation of PS I particles with dithionite for about ~ 30 min under anaerobic conditions in darkness before the first illumination does neither change the F_0 level nor the time course of fluorescence induction (see Fig. 1, trace 5). The slow light-induced fluorescence increase in the presence of dithionite under anaerobic conditions can be ascribed to photoaccumulation of the reduced A_1 within RCs [30,31], thereby giving rise to an increased yield of the delayed nanosecond recombination fluorescence [32]. A nanosecond delayed fluorescence has been recently found to arise in membranes of a Photosystem II-depletion mutant of the cyanobacterium *Synechocystis sp.* PCC 6803 after addition of dithionite at pH 10.5 [33]. The fluorescence yield of this mutant strongly increases upon addition of dithionite and exposure to the excitation beam of the fluorometer for a few minutes. Based on the idea of a nanosecond delayed emission arising owing to photoaccumulation of state $P_{700}A_0A_1^{red}$, the light-induced fluorescence increase shown in Fig. 1 is expected to be accompanied by the appearance of a magnetic field effect.

In the absence of dithionite and presence of sodium ascorbate under anaerobic conditions there was neither a light induced increase (see Fig. 1, trace 1) nor a magnetic field-induced change of the fluorescence yield (see Fig. 2, trace 1). However, if samples are suspended in the presence of sodium dithionite under anaerobic conditions, illumination by the excitation beam gives rise to the appearance of variable fluorescence (Fig. 1, trace 2) and of a magnetic field effect (see Fig. 2, trace 2). Progressively longer illumination is accompanied by the increase of both, the fluorescence yield (see Fig. 1, trace 2) and the extent of the magnetic field effect (see Fig. 2, traces 2–6). It appears worth mentioning that the profile of the MARY curves 2–4 in Fig. 2 markedly differs from that presented

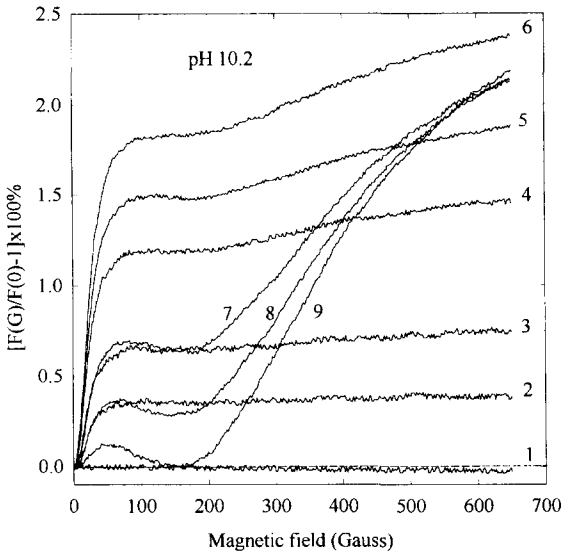

Fig. 2. Magnetic field-induced fluorescence yield changes of PS I particles (MARY curves) under anaerobic conditions (see Section 2 as a function of the magnetic field strength at pH 10.2. The magnetic field sweep rate was 825 G/s. Each trace is the average of 128 sweeps. Trace 1, in the presence of 3 mg/ml sodium ascorbat; trace 2, MARY curve measured immediately after addition of dithionite from a stock solution to the final concentration of ~ 200 μg/ml; traces 3 and 5, MARY curves were measured with a 2 min delay as the traces 2 and 4 had been accumulated (during the time delay the sample was exposed to the exciting light beam); traces 4 and 6, MARY curves measured about 4 and 5 min after measuring the MARY curves 3 and 5; trace 7, MARY curve measured immediately after addition of NaCl from a stock solution to the final concentration of 10 mM; traces 8 and 9; MARY curves measured after about 5 and 10 min delay after accumulation of traces 7 and 8, respectively.

in Refs. [17–19]. The MARY curves 2 and 3 in Fig. 2 clearly show the existence of a magnetic effect that saturates at comparatively low field strength ($G_{0.5} \approx 25$ G). Prolonged exposition of the sample in the excitation beam until reaching the maximum fluorescence level led to the appearance of an additional magnetic effect that saturates at higher field strength (see Fig. 2, traces 4–6). An extension of the illumination up to 2 h did not cause further changes of the MARY curve profile (data are not shown). However, pronounced changes of the MARY curve profile were observed immediately after addition of approx. 10 mM NaCl (final concentration in the suspension) to the sample. The contribution of magnetic field effects saturating at low and high field strength were markedly decreased and increased, respectively. Prolonged incubation of this sample with NaCl led to a further increase of the high-field saturated component (see Fig. 2, traces 7–9). The effect is not ion specific because similar changes in the MARY curve profile have been obtained by addition of $MgSO_4$, $CaCl_2$, $MgCl_2$ or KCl. The salt induced effects could be explained by changes of the rate constants of electron donation to $P_{700}^{+\cdot}$ from the external donors [34,35] that lead to corresponding modifications of the quantum yield of single- and double-reduced A_1 photoaccumulation. In this

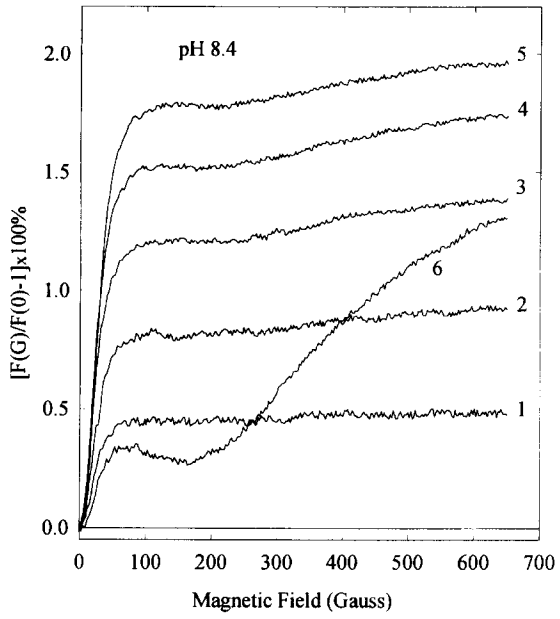

Fig. 3. MARY curves of PS I particles under anaerobic conditions in the presence of ~ 200 μg/ml sodium dithionite at pH 8.5 (each trace is an average of 128 sweeps). Trace 1, MARY curve measured immediately after addition of sodium dithionite; traces 2–5, MARY curves measured with 2 min delay after traces 1–4 were accumulated (during the time delay the sample was exposed to the exciting light beam); trace 6, MARY curve measured immediately after addition of NaCl leading to a final concentration of ~ 10 mM.

case the low- and high-field saturated magnetic effect could be ascribed to PS I reaction centres with the single- and double-reduced A_1.

It has been reported that under strongly reducing conditions A_1 becomes double-reduced to the quinol by illumination in the presence of redox mediators [31]. In order to avoid double reduction of A_1, experiments were repeated at pH 8.4 and in the absence of redox mediators [30,3]. The data obtained are shown in Fig. 3. A comparison with those depicted in Fig. 2 reveals that a pH decrease does not considerably influence the MARY curve profiles. On the other hand, salt addition at pH 8.4 gives rise to similar changes in the profile of the MARY curves (see Fig. 3) as was observed at pH 10.2 (see Fig. 2). Two conclusions can be gathered from these data: (i) A_1 was photoaccumulated in its reduced states in the absence of redox mediators under anaerobic conditions in the presence of dithionite with efficiencies which seem to be pH independent; and (ii) A_1 was photoaccumulated only in the single-reduced semiquinone form at both pH values and added salts induced conformational changes in the PS I particles. This transition of the conformational state could be independent of pH within the range of pH 8–10 and would be expected to cause a change of the dipolar and/or spin exchange coupling between the primary radicals $P_{700}^{+\cdot}$ and $A_0^{-\cdot}$. The change of these couplings necessarily leads to changes in the MARY curve profile [36,7]. The assumption of salt controlled conformation is further supported by the salt-induced overall fluorescence yield decrease (see Fig. 1 and compare traces 3 and 4), while the ratio of the variable to the initial (F_1) fluorescence remains practically unchanged.

Trace 5 in Fig. 1 shows that in agreement with the observation of Telfer et al. [29] addition of neutral red causes a steep increase of the rate of the dithionite induced fluorescence rise. However, in marked contrast to this behaviour, addition of neutral red to samples that have already achieved the maximum level of light induced fluorescence yield caused a fluorescence yield decrease upon further illumination (see Fig. 1, trace 6): This light-induced fluorescence quenching was reversible. Subsequent dark adaptation of the sample for about 5 min resulted in a fluorescence yield increase back to the original F_m level. A second illumination led again to quenching with a somewhat faster kinetics (see Fig. 1, trace 7). It should be emphasised that photoaccumulation of the reduced primary acceptor in the reaction centres of the purple bacteria [37,10] and PS II [21,38,10,38,40] is accompanied by quenching of (bacterio)*Chl a* fluorescence. Furthermore, it has been shown that photoaccumulation of both reduced bacteriopheophytin *a* in the reaction centres of *Chromatium minutissimum* and *Pheo a* in PS II results in the disappearance of the magnetic field effect and dark reoxidation of the photoreduced primary acceptors is accompanied by the reappearance of the magnetic effect [10]. The results of the present study reveal that basically the same features also arise in PS I: the photoindiced fluorescence yield decrease was accompanied by a decrease of the magnetic field effect signal caused by the application of a magnetic field of 600 G (see Fig. 1, traces a–c, below curves 6 and 7). Therefore, it appears reasonable to assume that addition of neutral red after prior formation of the state $P_{700}A_0A_1^{red}$ in PS I reaction centres can induce photoaccumulation of $A_0^{-\cdot}$. The formation of state $P_{700}A_0^{-\cdot}$ is accompanied by the disappearance of the magnetic field effect. The decrease of fluorescence yield can be explained by excitation energy transfer to the anion radical $A_0^{-\cdot}$ that acts as an efficient quencher [10,39–41].

The MARY curve profile was shown to depend on the PS I fluorescence wavelength [17]. Fig. 4 shows the MARY curves obtained at different wavelength of the PS I fluorescence (traces 2–6). In order to control the time-dependent salt-induced (see Fig. 2, traces 7–9) profile changes of the MARY curves, the fluorescence was also detected through the cut-off filter at the beginning (trace 1) and end (trace 7) of these measurements. Within the accuracy of the present experiments and a salt-induced large scale time instability of the MARY curve profile (see Fig. 2, traces 7–9) there was no noticeable difference between the MARY curves measured at various wavelength of the *Synechococcus elongatus* PS I fluorescence. Therefore, a spectral sensitivity of the magnetic field effect presented earlier [17] seems to be the result of a long-time adaptation of the PS I particle conformation to a new medium which

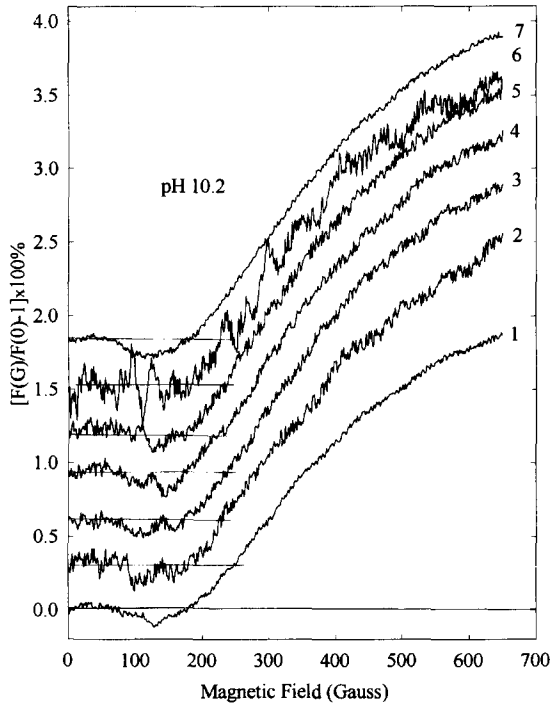

Fig. 4. MARY curves of PS 1 particles under anaerobic conditions in the presence of ~ 200 μg/ml sodium dithionite and ~ 10 mM NaCl at pH 10.2 (traces shown are averages of 128 sweeps). Traces 1 and 7, fluorescence was monitored through the cut off filter (see Section 2; traces 2–6, fluorescence was monitored through the cut off and interference filter with a maximal transmitance at 744, 734, 715, 698 and 684 nm, respectively.

is caused by their transferring from the storage medium to the measuring suspension rather than a spectral representation of various magnetic field-sensitive processes. This assumption is further supported by a long-time instability of the MARY curve profile which is observed for the PS I particles diluted with Tris-HCl buffer (see Fig. 5 and compare traces 2 and 3). I this case the contribution of magnetic field effect saturating at high field strength was markedly higher when compared with the glycine-NaOH buffer (see traces 6 in Fig. 2 and 2 in Fig. 5). Furthermore, in contrast to the solutions with glycine-NaOH buffer added NaCl did not influence the MARY curve profile immediately after its addition. Therefore, an absence [18] and minor contribution [17] of a magnetic effect that saturates at comparatively low field strength seems to be the result of Tris-HCl buffer used in the mentioned experiments.

Triplet-triplet annihilation processes are expected to play an important role for the magnetic effect that saturates at high-field [42,43]. In this case both the magnitude and profile of the magnetic effect is known to be a function of the exciting beam intensity [42–45]. This suggests that in the measured MARY curves the contributions of the components saturating at low- and high-magnetic field, respectively, might be changed owing to a variation of the light intensity. In order to check this idea magnetic effect

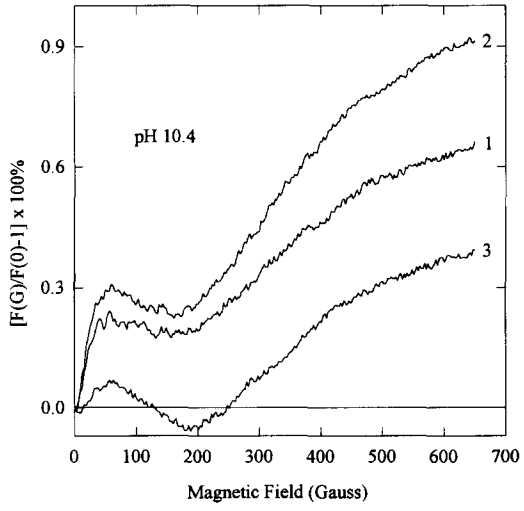

Fig. 5. Magnetic field-induced changes of relative fluorescence yield in PS 1 particles diluted with 30 mM Tris-HCl buffer (pH 10.4) under anaerobic conditions. Trace 1, MARY curve measured with a 4 min delay after addition of dithionite from a stock solution to the final concentration of ~ 200 μg/ml; traces 2 and 3, MARY curves measured after about 15 and 60 min delay after accumulation of trace 1, respectively (during the time delay the sample was exposed to the exciting light beam). Traces shown are averages of 128 sweeps.

profiles were measured at two different light intensities. Fig. 6 depicts the results obtained at a relatively strong (trace 1 and 3) and weak (trance 2 and 4) light intensity in the absence (trace 1 and 2) and presence of NaCl (trace 3 and 4) in the suspension. This data shows that within the accuracy of the present experiments the MARY curve profiles are independent of the intensity of the measuring light.

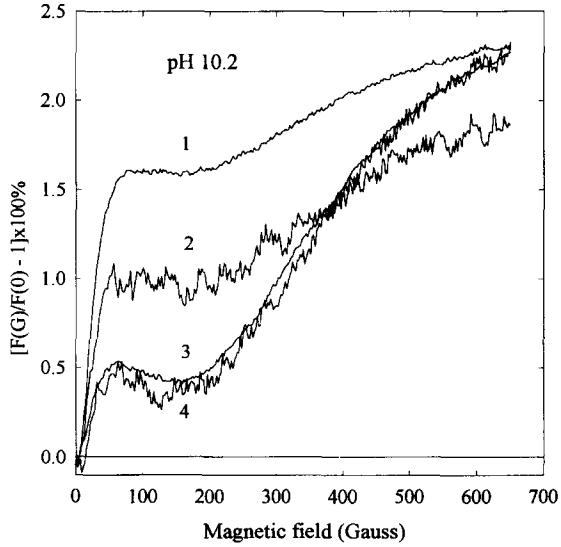

Fig. 6. Magnetic field-induced changes of relative fluorescence yield in PS 1 particles under anaerobic conditions in the presence of ~ 200 μg/ml sodium dithionite at pH 10.2 without NaCl addition (traces 1, 2) and in the presence ~ 10 mM NaCl (traces 3, 4) upon exciting light intensity of 40 J cm^{-2} s^{-1} (1,3) and 5 J cm^{-2} s^{-1} (2, 4). The traces 1(2) and 3(4) are averages of 128 (256) sweeps.

4. Conclusion

The present study shows: (a) under conditions leading to photoaccumulation of PS I reaction centres in state $P_{700}A_0A_1^{red}$ which is accompanied by a fluorescence increase, the fluorescence yield exhibits a pronounced magnetic field dependence; (b) a new magnetic effect has been discovered in PS I preparations suspended in buffers with low salt content. This effect is characterized by a rather low field strength for half saturation ($B_{0.5} \approx 25$ G) that is indication of a very weak dipolar and/or spin exchange coupling within the radical pair $P_{700}^{+\cdot}A_0^{-\cdot}$. Addition of salts of monovalent and divalent cations to the suspension or replacement of the glycine-NaOH by Tris-HCl buffer significantly modified the profile of the magnetic field dependence. These findings indicate that conformational changes of PS I proteins seem to change a distance or angle or both the distance and angle between the primary radicals $P_{700}^{+\cdot}$ and $A_0^{-\cdot}$. The previously described high-saturated magnetic field effect [17,18] is obtained under the same redox conditions if the sample suspensions contain Tris-HCl buffer. Under these conditions the results of the abovementioned reports can be reproduced. And (c) illumination in the presence of neutral red of samples in state $P_{700}A_0A_1^{red}$ lead to quenching of PS I fluorescence and disappearance of the magnetic field effect. In the dark the high fluorescence and the magnetic field effect are restored. These phenomena are ascribed to photoaccumulation of state $P_{700}A_0^{-\cdot}A_1^{red}$ and a strong quenching effect of the *Chl a* anion radical $A_0^{-\cdot}$ that closely resembles that of $Pheo^{-\cdot}$ in PS II.

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