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RESEARCH PAPERS

Effects of Far Red Light on the Induction Changes of Prompt and Delayed Fluorescence and the Redox State of P700 in *Scenedesmus quadricauda*

V. V. Lenbaum, A. A. Bulychev, and D. N. Matorin

Department of Biophysics, Faculty of Biology, Moscow State University, Moscow, 119991 Russia;
e-mail: matorin@biophys.msu.ru

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Abstract—The spectral composition of sunlight in natural aquatic habitats depends on the depth of submergence and the solar time. Changes in the fractional amount of far-red light (FRL) in the total photon flux are associated with the redistribution of light energy absorbed by the two photosystems of photosynthesis. Experiments with a culture of *Scenedesmus quadricauda* revealed the influence of FRL preillumination on photosynthetic electron transport and associated processes in microalgae. The plant efficiency analyzer M-PEA-2 was used to measure simultaneously the induction curves of prompt fluorescence, delayed fluorescence, and the redox transients of chlorophyll P700. The results are discussed in terms of the action of FRL preillumination on cyclic and noncyclic electron flows with account for relocation of the mobile light-harvesting complex of photosystem II during reversible State 1–State 2 transitions. Essential similarities and substantial distinctions have been revealed in the effects of FRL on photosynthetic electron flows in microalgae and higher plant leaves.

Keywords: Scenedesmus quadricauda, chlorophyll fluorescence, photosynthesis, far-red light, regulation

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INTRODUCTION

Photosynthetic electron transport in green plant cells is finely regulated depending on the amount of light energy absorbed and on the plant capacity of using this energy in dark reactions of photosynthesis. Regulatory changes are determined by structural flexibility of thylakoid membranes, existence of alternative electron-transport pathways, and by generation of the electrochemical proton gradient between the lumen and the chloroplast stroma [1–4]. Adjustments in the photosynthetic apparatus and rearrangements of electron-transport pathways may manifest differently in higher plants and green microalgae as representatives of dissimilar taxonomic groups. The role of electrochemical proton gradient ($\Delta\mu_{H^+}$) in regulation of electron-transport pathways can be examined by simultaneous monitoring the redox states of electron carriers in photosystems II and I (PSII and PSI) and membrane energization events during the induction period of photosynthesis.

Abbreviations: DF—delayed chlorophyll fluorescence; FNR—ferredoxin-NADP reductase; FRL—far-red light; P700—the pigment of photosystem I reaction center; PF—prompt fluorescence; PQ—plastoquinone; PSI and PSII—photosystems I and II; Q_A and Q_B—the primary and secondary quinones serving as electron acceptors in PSII.

The currently available modified version of the plant efficiency analyzer, M-PEA-2 enables simultaneous measurements of the induction curves of PSII chlorophyll fluorescence, the redox transients of chlorophyll P700 in PSI reaction centers, and the millisecond component of delayed fluorescence that is sensitive to changes in membrane potential $\Delta\varphi$ and the proton gradient ΔpH [5–8].

Parallel measurements of these parameters with M-PEA-2 in pea leaves revealed differential sensitivity of photosynthetic electron transport to elimination of the electrical and chemical ($\Delta\varphi$ and ΔpH) components of $\Delta\mu_{H^+}$ [8]. Using ionophores as a tool to modify the ionic conductance of thylakoid membrane, we noticed that the rate-limiting steps, acting as a "bottleneck" for electron flow might be replaced with constraints at other locations in the electron transport chain. Infiltration of leaves with valinomycin known to increase ΔpH under concurrent decrease in $\Delta\varphi$ in the induction period seemed to restrict electron transport at the site of plastoquinol oxidation, whereas the protonophore nigericin known to diminish ΔpH eliminated this rate-limiting step and enhanced the sensitivity of electron flow to preillumination with far-red light (FRL) absorbed by PSI only [8]. This was evident from modification of fluorescence induction curves in

infiltrated leaves adapted to darkness or preilluminated with FRL.

The influence of FRL on electron transport and fluorescence induction curves is related to oxidation of the plastoquinone pool. Full oxidation of this pool by FRL eliminates the conditions for cyclic electron flow in the initial period of illumination, thus promoting reduction of electron carriers on the PSI acceptor side, which facilitates the activation of ferredoxin-NADP reductase (FNR) during its recovery from the inactive dark state. One possible mechanism of FRL influence on electron transport consists in reversible transitions of photosynthetic apparatus between States 1 and 2 depending on the redox condition of the plastoquinone pool [9]. Transitions between States 1 and 2 are associated with changes in the cross section of the PSII antenna caused by the imbalance of light energy absorbed by PS I and PSII; these changes are most evident in green microalgae such as *Chlorella* and *Scenedesmus* [9–11]. Therefore, it was important to examine the influence of ionophores and FRL on the induction processes in unicellular green algae representing the essential component of phytocenosis in fresh water ecosystems.

This study aimed at analysis of simultaneously measured induction curves of prompt and delayed fluorescence and the redox transients of chlorophyll P700 in the microalga *Scenedesmus quadricauda* after the treatment of cells with ionophores affecting the proportion of $\Delta\varphi$ and ΔpH in the electrochemical proton gradient at thylakoid membranes; we also investigated the above characteristics as a function of preillumination with far red light that selectively excites PSI. The results demonstrate an important role of electrochemical processes in regulation of photosynthetic electron transport in unicellular algae and unveil certain distinctions of ΔpH influence on electron transport and associated processes in unicellular algae and higher plant leaves.

MATERIALS AND METHODS

Unicellular freshwater alga *Scenedesmus quadricauda* was cultured on a half-strength Tamiya nutrient solution at 24 ± 2°C under permanent illumination at a photon flux density of 30 μE/(m^2 s) and constant stirring.

The induction curves of prompt chlorophyll fluorescence (PF), delayed fluorescence (DF), and oxidation–reduction conversions of P700 were measured by means of Multi-function Plant Efficiency Analyser M-PEA-2 (Hansatech, United Kingdom) designed for simultaneous recording of all three parameters.

The prompt and delayed fluorescence were monitored under intermittent actinic red light (photon flux density 1000 μE/(m^2 s), peak emission at 627 nm) with short intervening dark intervals whose duration sufficed for DF measurements. The kinetics of fluorescence induction was recorded with the maximal resolution of 0.01 ms; reliable changes of P700 redox state were observed from 0.7 ms after the onset of actinic illumination [5, 6]; the total recording length was 60 s. The DF kinetics reflects changes in emission intensity on a time scale 0.1–0.9 ms in the intervals between actinic light pulses. Characteristics and the protocol of measurements with an M-PEA-2 instrument have been described in detail previously [5, 6].

Prior to measurements the algal samples were concentrated on a membrane filter and kept in darkness for 10 min in wet condition. This procedure of sample preparation was considered as the control treatment. It should be noted that M-PEA-2 analyzer is optimized for measurements with plant leaves. However, because of high density of immobilized algal cells sedimented on filters, the signal-to-noise ratio in the records was as high as in measurements with leaves. The average chlorophyll content in cells pelleted on filters was ~400 mg/m^2, which is comparable to its content in leaves of vascular plants (about 500 mg/m^2). Control measurements of *S. quadricauda* fluorescence with an Aqua-Pen fluorometer (Photon Systems Instruments, Czechia) using cell suspensions have shown that the procedure of concentrating samples on filters had no influence on cell physiological condition [12, 13].

In order to study the influence of long-wavelength red light (FRL) on the culture of *S. quadricauda* alga, the filter with pelleted cells was illuminated for 1 min by red light at PFD of 1000 μE/(m^2 s) and transferred to darkness for 2 min. Next, the sample on the filter was preilluminated with FRL (wavelength 735 ± 15 nm) for 30 s at PFD of 300 μE/(m^2 s) and was allowed to stay in darkness for 30 s, after which it was exposed to actinic red light for 1 min. The results of measurements were recorded for the period of illumination with actinic red light.

In experiments with valinomycin and nigericin, the algal culture was incubated for 5 min in the presence of these ionophores dissolved at a nominal concentration of 10^{-5} M. It should be noted that K^+ concentration in the culture medium was about 30 mM, which is sufficient for the ionophorous activity of valinomycin. We used valinomycin from Calbiochem (United States) and nigericin from Sigma (United States).

Figures represent the induction kinetics of PF, DF, and oxidoreduction transients of P700 recorded after switching on the actinic red light. The induction curves of chlorophyll fluorescence were normalized to the level O (F_o); i.e. the F_t/F_o data were plotted as a function of time.

The induction changes of P700 redox state (ΔA_{820} signals) were plotted as I/I_o ratio characterizing the absorbance of $P700^+$ at 820 nm [5], where I_o and I are intensities of modulated light (λ = 820 nm) incident on the detector at the time point of 0.7 ms and any instant t from the onset of actinic light, respectively. The decrease of this ratio (negative shift of I/I_o) designates the oxidation of P700.

Data in figures are the results of representative experiments performed at least in triplicate.

RESULTS

Induction Changes in the State of Two Photosystems and the Electrochemical Proton Gradient in S. quadricauda Cells after FRL Preillumination

Figure 1 shows the induction curves of PF, DF, and the redox conversions of P700 under control conditions and after preliminary illumination with FRL. In cells of the microalga, like in higher plant leaves, the induction curves of PF comprise several components, termed O–J–I–P transitions (Fig. 1a). These components reflect the stepwise decrease in photochemical quenching and development of non-photochemical fluorescence quenching in PSII [14]. The stage O–J is determined by the photoinduced reduction of Q_A, whereas the J–I–P transients reflect subsequent accumulation of reduced Q_A caused by slowing down of Q_A^- reoxidation upon the reduction of Q_B and the quinone pool. The levels O and P on the kinetic curve correspond to the values of F_o and F_m [15].

The induction changes of P700 redox state after switching on the light comprise the initial peak of oxidation, subsequent reduction of $P700^+$ by electrons arriving to PSI from PSII after filling the pool of intersystem carriers, and the second wave of P700 oxidation caused by the withdrawal of electrons from the acceptor side of PSI during FNR photoactivation (Fig. 1c).

The induction kinetics of the millisecond component of DF originating from recombination of separated charges (Fig. 1b) is indicative of the electrochemical proton gradient and contains two distinct peaks [16, 17]. The first peak developing in ~10 ms from the onset of illumination is related to the electrical component ($\Delta\varphi$) of the electrochemical proton gradient across the thylakoid membranes and the second peak occurring in the time scale of 1–2 s from the beginning of illumination is determined by its chemical component (ΔpH).

As can be seen from the induction curve of PF (Fig. 1a), the level J was achieved faster in cells preilluminated with FRL than in dark-adapted (control) samples, indicating the accelerated reduction of the primary quinone acceptor Q_A. The Q_A reduction might be speeded because the plastoquinone oxidation by PSI during FRL irradiation is accompanied by dephosphorylation of the mobile part of light-harvesting complex (LHC) and its repositioning from PSI to PSII (State 2–State 1 transition) [9, 11], which increases the absorption cross section of PSII and the frequency of PSII excitations. It can be also seen in Fig. 1a that FRL preillumination led to lowering of the P level in the induction curve of PF.

In the induction curve of DF under control conditions (Fig. 1b), the DF maximum associated with generation of electric potential $\Delta\varphi$ was notably higher than the peak associated with ΔpH formation. After preillumination with FRL, the DL peak at 10–100 ms was substantially lowered, indicating the decrease in electrical component of $\Delta\mu_{H^+}$ on thylakoid membranes. Full oxidation of the plastoquinone pool by preillumination with FRL was reported to inhibit electrogenesis [18] and cyclic electron flow [19] in higher plant chloroplasts in response to subsequent action of FRL. With this in mind, we assume that FRL preillumination of algae may have similar effects on electrogenesis and cyclic electron transport in the initial period of irradiation with red light. The second peak of DF in algae preexposed to FRL developed earlier (by about 300 ms) than in dark-adapted preparations, which indicates a faster generation of ΔpH after the action of FRL.

Under control conditions, the redox transients of PSI reaction center chlorophyll (Fig. 1c) comprised fast oxidation of P700 (1–10 ms), its subsequent reduction (20–200 ms), and the secondary oxidation ($t > 300$ ms); the latter stage reflects acceleration of linear electron flow upon light-induced activation of FNR [20–22]. After preliminary exposure of algae to FRL, the oxidation of P700 in the time range 1–10 ms started earlier than after dark adaptation. The early onset of P700 oxidation is presumably due to the lack of reduced intersystem electron carriers after FRL preillumination.

In addition, the second wave of P700 oxidation in FRL-preilluminated cells appeared earlier and developed faster than in dark-adapted algae, which indicates the earlier activation of electron transport on the acceptor side of PSI. The parallel shifts of P700 secondary oxidation and the second peak of DF after exposure to FRL (Figs. 1b, 1c) point to the relationship between these processes, in line with the supposed activation of FNR upon light-induced alkalinization of the chloroplast stroma [21, 23].

In order to clarify the mechanism of FRL action, we applied the ionophores nigericin and valinomycin acting differentially on the electrical and chemical components of $\Delta\mu_{H^+}$ in thylakoids, thus alleviating or enhancing the ΔpH-dependent constraints of electron flow at the cytochrome b_6f level.

Induction Changes in Two Photosystems and Electrochemical Proton Gradient upon the Diminished ΔpH

Nigericin, the protonophorous uncoupler of electron transport and phosphorylation decreases ΔpH by inducing the H^+/K^+ transmembrane exchange [24]. The diminished ΔpH in thylakoids prevents the retardation of electron transport at the cytochrome b_6f

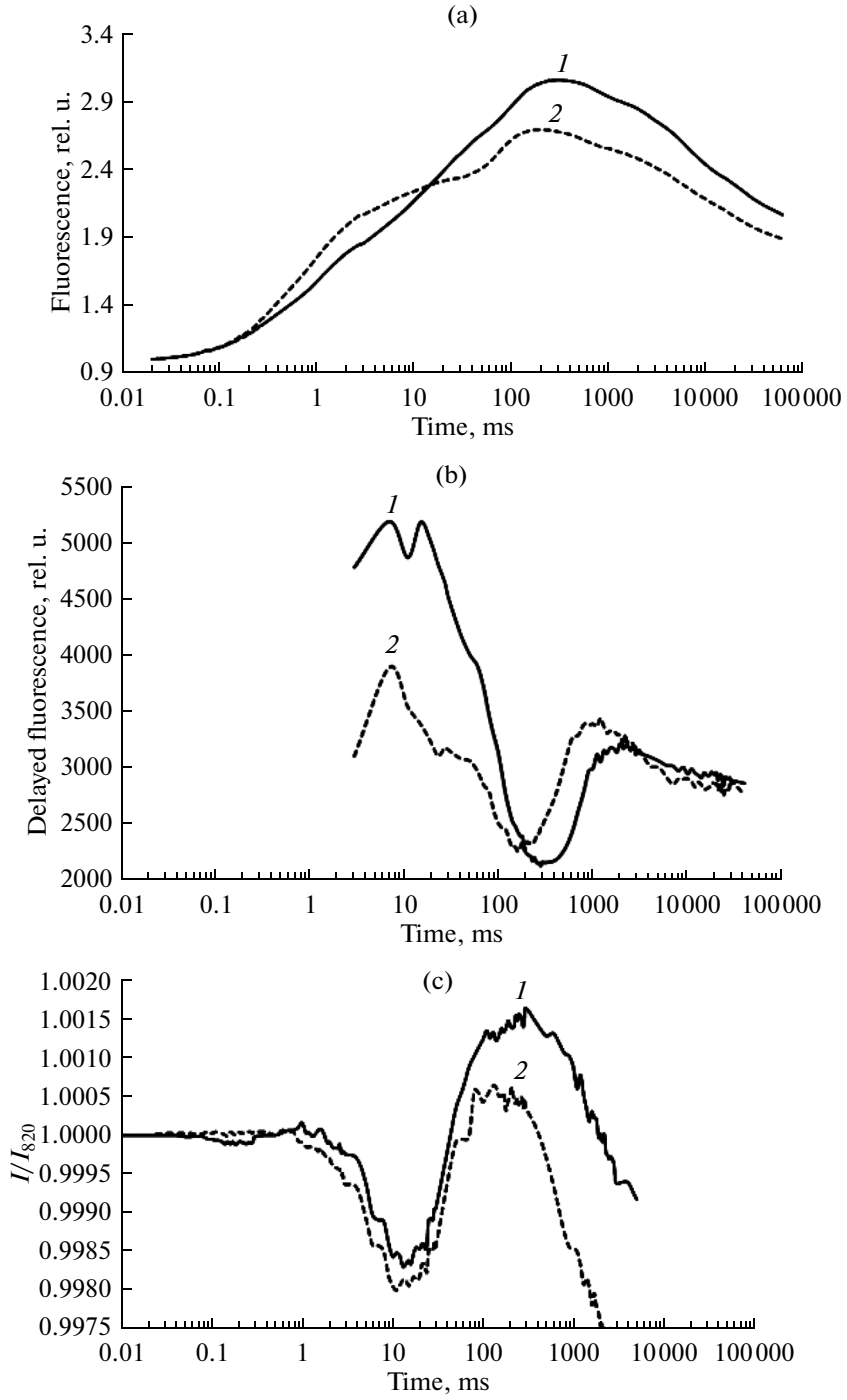

Fig. 1. Induction curves of (a) prompt fluorescence, (b) delayed fluorescence, and (c) absorbance changes at 820 nm in the culture of *S. quadricauda* algae that were adapted to darkness (curves *1*, control) and preilluminated by far-red light with peak emission at 730 nm (curves *2*, FRL).

(*1*) After 2-min incubation in darkness; (*2*) in 25 s after preliminary 30-sec illumination with FRL at a photon flux density of 300 μE/(m^2 s). The intensity of actinic red light was 1000 μE/(m^2 s). All parameters were measured simultaneously using M-PEA-2 photosynthetic efficiency analyzer.

complex, thus eliminating the rate-limiting step for the outflow of electrons from PSII. Figure 2 shows the induction changes of PF, DF, and P700 redox state in the algae treated with nigericin. In the presence of nigericin the level P was substantially lower than in untreated algae under similar conditions. The ratio F_t/F_o at the peak of fluorescence was higher than 3.0 in control samples (dark-adapted cells in the absence of ionophores), whereas it was about 2.5 after the treatment with nigericin (Fig. 2a). Preillumination with

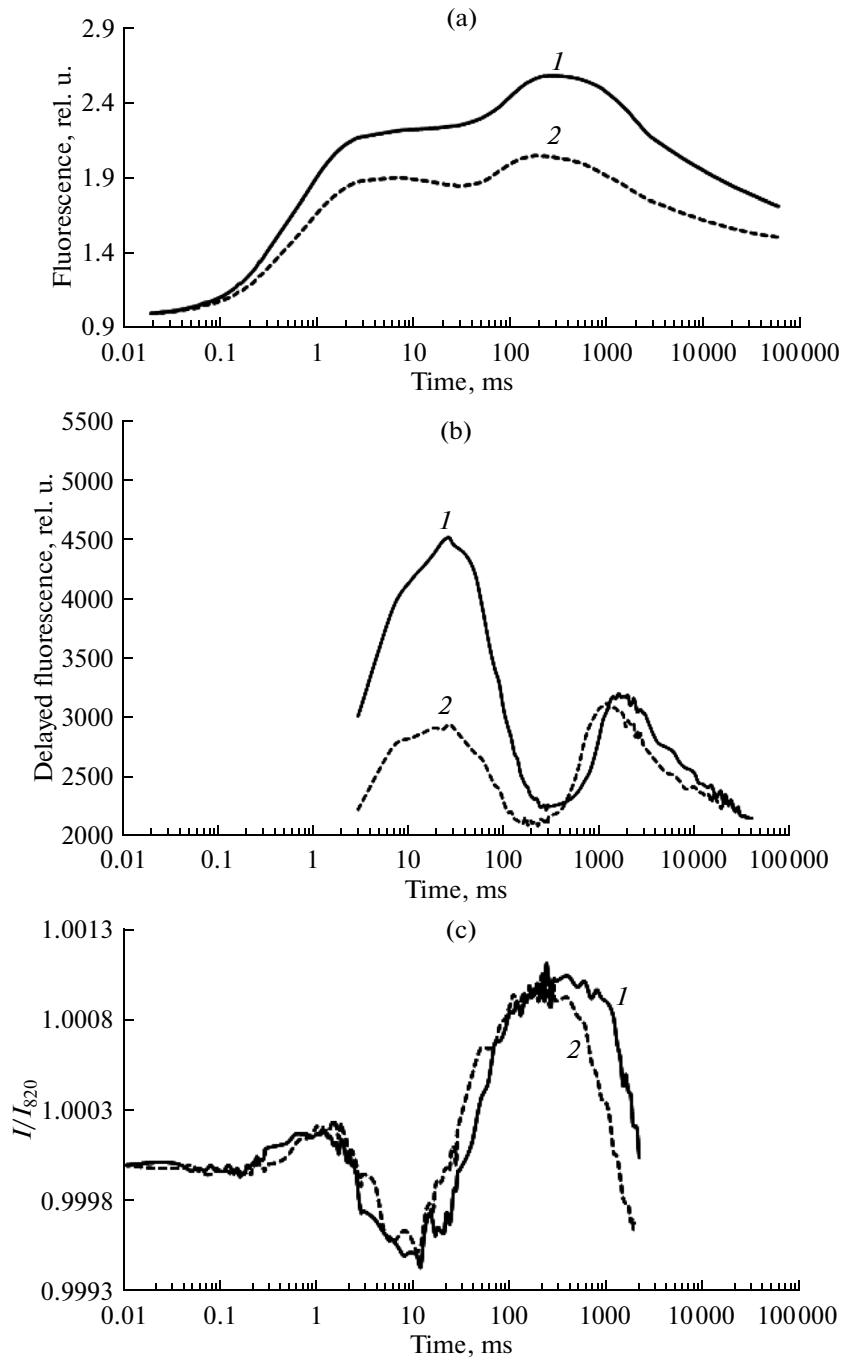

Fig. 2. Induction curves of (a) prompt fluorescence, (b) delayed fluorescence, and (c) absorbance changes at 820 nm in the culture of *S. quadricauda* algae that were treated with 10 μM nigericin and adapted to darkness (curves *1*, nigericin) and in the same samples in 25 s after 30-s preillumination with FRL at a photon flux density of 300 μE/(m^2 s) (curves *2*, nigericin + FRL). The intensity of actinic red light was 1000 μE/(m^2 s). All parameters were measured simultaneously using M-PEA-2 analyzer.

FRL in the presence of the ionophore led to even stronger decrease in F_t/F_o ratio at the peak of fluorescence induction (down to 2.0–2.3), as well as at all stages of O–J–I–P transients. The decrease in fluorescence level during O–J–I–P transients after preillumination with FRL in the presence of nigericin was previously observed with infiltrated pea leaves [8]. This decrease was interpreted as being due to accelerated outflow of electrons from PSII to PSI under conditions when electron transport at the level of cytochrome b_6f complex remains unconstrained owing to dissipation of ΔpH. Under high rate of linear electron flow, the complete Q_A reduction is hardly attained [20, 25]. Comparison of Figs. 1a and 2a indicates that non-

cyclic electron flow in nigericin-treated algae preexposed to FRL proceeds faster than in untreated FRL-preilluminated cells.

The presence of nigericin in cell samples did not prevent fluorescence quenching in the time range from 1 s to tens of seconds. In this respect *S. quadricauda* algae differ from higher plant leaves, where fluorescence quenching in the same time scale was completely removed under the action of this protonophore [8]. This observation suggests different origins of nonphotochemical quenching at the P–T stage in leaves and microalgae. It is possible that the P–T fluorescence quenching in *S. quadricauda* reflects the decrease in the PSII antenna size under intense red light during transition of photosynthetic apparatus from State 1 to State 2.

As shown in Fig. 2b, preillumination with FRL in the presence of nigericin was followed by lowering of the first maximum in the induction curve of the DF millisecond component. This reduction points to weakening of $\Delta\mu_{H^+}$ electric component after the action of FRL, which might be caused by inhibition of cyclic electron flow in the initial period of illumination. In cells treated with nigericin, the inhibition of $\Delta\varphi$-dependent component of DF after FRL preillumination was expressed stronger than in untreated control cells.

Preillumination with FRL in the absence of ionophores accelerated the appearance of P700 secondary oxidation associated with FNR activation (Fig. 1c), whereas this effect was less pronounced in the presence of nigericin (Fig. 2c). This result is conceivable, provided that nigericin prevents the light-induced alkalinization of stromal pH known to be involved in FNR activation [23]. In the kinetic curves of DF, the front of the ΔpH-indicating wave showed no significant shift after FRL preillumination (Fig. 2b), unlike such shifts in Figs. 1b and 3b. This observation is also consistent with the ionophorous mechanism of nigericin action.

Induction Changes in Two Photosystems and Electrochemical Proton Gradient as Affected by Valinomycin

The ionophore valinomycin in the presence of potassium ions is known to diminish $\Delta\varphi$ at the thylakoid membrane, thus promoting light-dependent entry of protons into the lumen [24, 26]. The increase in ΔpH imposes additional constraint on linear electron flow at the level of cytochrome b_6f complex. Figure 3 shows the induction changes of PF, DF, and redox state of P700 in the algae treated with valinomycin.

The effects of far-red preillumination on the induction kinetics of PF were similar in the absence (Fig. 1a) and in the presence of valinomycin (Fig. 3a).

As shown in Fig. 3b, the treatment of cells with valinomycin substantially lowered the first peak of the DF millisecond component. At the same time, the inhibitory action of far-red preillumination on this stage of the DF induction curve was abolished. This results confirms the decrease in $\Delta\varphi$ at the thylakoid membrane in the presence of valinomycin. When the photogeneration of $\Delta\varphi$ was suppressed by the ionophore, preillumination with FRL had no additional inhibitory influence on $\Delta\varphi$ and $\Delta\varphi$-dependent stages of the DF induction.

The kinetic curves of P700 redox conversions (Fig. 3c) show that the second wave of P700 oxidation in the presence of valinomycin started earlier in FRL-preilluminated cells than in the dark-adapted algae, like it occurred in untreated cells (in the absence of ionophores). At the same time, the stages of primary oxidation and reduction of P700 were independent of preillumination with FRL.

DISCUSSION

The results demonstrate an important role of electrochemical membrane processes in regulation of photosynthetic electron transport in microalgae and provide further evidence for regulatory influence of FRL revealed earlier with higher plant leaves [8]. Although the induction curves for the examined parameters in *S. quadricauda* and pea leaves were principally similar under conditions of dark adaptation, preillumination with FRL, and treatments with ionophores, substantial distinctions have been revealed in experiments with microalgae.

One obvious difference between the induction processes in higher plant leaves and microalgae is that the stage P–S of fluorescence quenching in the induction curve of *S. quadricauda* was insensitive to elimination of ΔpH on thylakoid membranes under the action of nigericin, whereas the P–S fluorescence quenching disappeared in pea leaves infiltrated with this ionophore [8]. Hence, despite the seeming similarity of P–S stages in these materials, the origin of fluorescence quenching in *S. quadricauda* is unrelated to energization of thylakoid membranes (ΔpH formation). It is likely that the slow fluorescence quenching in *S. quadricauda* results from changes of PSII antenna size and the respective redistribution of captured energy between PSII and PSI at high fluence excitation of PSII by red light; i.e., it is caused by the transition of photosynthetic apparatus from State 1 characterized by the increased absorption cross section of PSII to State 2 in which the PSII absorption cross section is lowered. It is known that the transition from State 1 to State 2 is determined by dissociation of a part of LHC from PSII after its phosphorylation by the kinase activated upon the reduction of the plastoquinone pool [1, 9, 11]. Therefore, the decrease in the number of quanta absorbed by PSII should be accompanied by the decrease in PSII fluorescence, irrespective of the presence or absence of ΔpH.

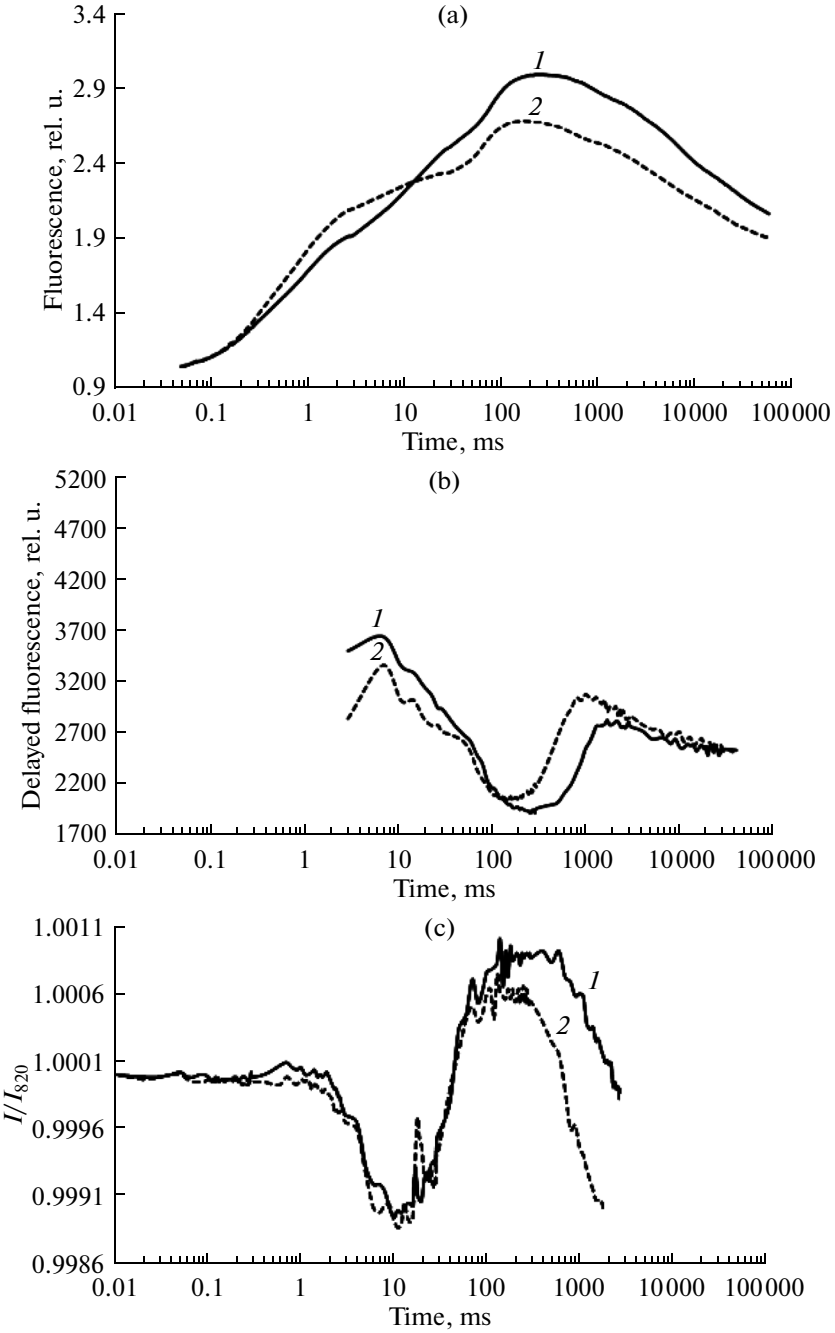

Fig. 3. Induction curves of (a) prompt fluorescence, (b) delayed fluorescence, and (c) absorbance changes at 820 nm in the culture of *S. quadricauda* algae that were treated with 10 μM valinomycin and adapted to darkness (curves *1*, valinomycin) and in the same samples after 25-s preillumination with FRL at a photon flux density of 300 μE/(m^2 s) (curves *2*, valinomycin + FRL). The intensity of actinic red light was 1000 μE/(m^2 s); the intensity of FRL was 300 μE/(m^2 s). All parameters were measured simultaneously using M-PEA-2 photosynthetic efficiency analyzer.

Additional evidence of State 1–State 2 transitions in *S. quadricauda* comes from the effect of FRL on O–J transient in the induction curves of chlorophyll fluorescence (Fig. 1). The preliminary exposure of algae to FRL, which promotes plastoquinone oxidation and LHC dephosphorylation, should enlarge the PSII antenna size and, accordingly, accelerate the reduction of Q_A under subsequent action of red light. The accelerated O–J rise in the fluorescence induction curve was indeed observed after preillumination with FRL (Fig. 1a).

Considering that the PSII antenna size increases after far-red preillumination, whereas the Δφ-dependent stages in the induction curve of the millisecond

DF component are substantially suppressed after preexposure to FRL (Fig. 1b), one may assume that the electrogenic activity of PSI in *S. quadricauda* is higher than that of PSII. The comparatively low electrogenic activity of PSII cannot be explained by retardation of the photochemical reaction, because the far-red preillumination oxidizes the intersystem electron carriers, thus preventing the possible shortage of electron acceptors for PSII. Probably, the elevated capability of PSI to generate Δφ is caused by its involvement in cyclic electron flow. High electrogenic effect of cyclic electron flow in the presence of exogenous cofactors was earlier shown for higher plant chloroplasts [18]; the highest Δφ values (up to 150 mV) at thylakoid membranes were actually observed under activation of cyclic electron flow.

Preillumination with FRL promotes full oxidation of the PQ pool, which disturbs the operation of cyclic electron flow at short illumination periods (<10 ms) preceding the PQ reduction. The inhibitory influence of FRL preillumination on electrogenic (associated with Δφ generation) cyclic electron flow in the initial period of measurements under red light might account for the drastic decrease in DF intensity in the time range from few milliseconds to one-tenth of a second (Fig. 1b). This explanation is supported by observations that dissipation of Δφ in the presence of valinomycin almost abolished the impact of FRL preillumination on Δφ-dependent component of DF (Fig. 3b), whereas the Δφ generation promoted by the presence of nigericin enhanced the influence of FRL preillumination on the initial stage of the DF induction curve (Fig. 2b).

Thus, the results suggest that preillumination with FRL regulates the pathways of cyclic and linear electron flows; furthermore, the regulatory effect of FRL becomes most evident after elimination of ΔpH-dependent "bottleneck" in the electron transport pathway. The diminished photogeneration of ΔpH in the presence of nigericin was followed by a notably enhanced influence of far-red preillumination on the fluorescence induction curves and the Δφ-dependent component of DF (Figs. 2a, 2b). Similar enhancement of the FRL effect on fluorescence induction curves was observed under diminished ΔpH in infiltrated pea leaves [8]. The sustained decrease of fluorescence in the induction curves after preillumination with FRL in the presence of nigericin (Fig. 2a) indicates the accelerated electron flow along electron-transport chain, at which full reduction of the acceptor Q_A is not achieved. This effect is essentially similar to the fluorescence decrease at the I–P stage in the presence of methyl viologen, an effective electron acceptor from PSI [25].

Consistent effects of FRL and ionophores are also manifested in ΔA_{820} signals and the millisecond component of DF. For example, after preillumination with FRL, the second (ΔpH-dependent) wave of DF and the secondary oxidation of P700 (Figs. 1b, 1c) developed earlier than in dark-adapted cells. This influence of FRL was weakened in the presence of nigericin (Figs. 2b, 2c) known to diminish ΔpH but remained evident in the presence of valinomycin (Figs. 3b, 3c) that suppresses Δφ without hindering ΔpH formation [24]. The earlier formation of ΔpH and the second wave of P700 oxidation are consistent with the notion that photoinduced alkalinization of the stroma stimulates FNR activation [23] resulting in secondary oxidation of P700 [19–21].

Thus, a comparative examination of the effects of FRL preillumination and ionophores on the induction changes of fluorescence, delayed fluorescence, and redox transitions of chlorophyll P700 in algal cells and plant leaves indicates the existence in the electron-transport chain of two steps that restrict the rate of noncyclic electron transport. One of them (at the level of the cytochrome b_6f complex) ensures ΔpH-dependent regulation of electron flow, whereas the other (on the acceptor side of PSI) is sensitive to the action of FRL. The regulatory effect of FRL becomes most evident after elimination of ΔpH-dependent constraints to electron flow. The existence of ΔpH-dependent and FRL-dependent mechanisms of electron transport regulation should be taken into account in the analysis of microalgal photosynthesis under natural environmental conditions.

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