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Plastoquinones are effectively reduced by ferredoxin:NADP$^+$ oxidoreductase in the presence of sodium cholate micelles Significance for cyclic electron transport and chlororespiration

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Abstract

The effect of sodium cholate and other detergents (Triton X-100, sodium dodecyl sulphate, octyl glucoside, myristyltrimethylammonium bromide) on the reduction of plastoquinones (PQ) with a different length of the side-chain by spinach ferredoxin:NADP$^+$ oxidoreductase (FNR) in the presence of NADPH has been studied. Both NADPH oxidation and oxygen uptake due to plastosemiquinone autoxidation were highly stimulated only in the presence of sodium cholate among the used detergents. Sodium cholate at the concentration of 20 mM was found to be the most effective on both PQ-4 and PQ-9-mediated oxygen uptake. The FNR-dependent reduction of plastoquinones incorporated into sodium cholate micelles was stimulated by spinach ferredoxin but inhibited by Mg^{2+} ions. It was concluded that the structure of sodium cholate micelles facilitates contact of plastoquinone molecules with the enzyme and creates favourable conditions for the reaction similar to those found in thylakoid membranes for PQ-9 reduction. The obtained results were discussed in terms of the function of FNR as a ferredoxin:plastoquinone reductase both in cyclic electron transport and chlororespiration.
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Keywords: Ferredoxin-NADP$^+$ oxidoreductase; Plastoquinone; Chlororespiration; Sodium cholate; Micelles

1. Introduction

Ferredoxin:NADP$^+$ oxidoreductase (EC 1.18.1.2) catalyzes reduction of NADP$^+$ in stroma of chloroplasts and this reaction is the last step of the linear photosynthetic electron transport chain (for review see Arakaki et al., 1997). However, the role of FNR in the cyclic electron transport around photosystem I and chlororespiration has not been elucidated (Moss and Bendall, 1984; Hosler and Yocum, 1985; Bendall and Manasse, 1995; Arakaki et al., 1997; Więckowski and Bojko, 1997; Hoefnagel et al., 1988; Peltier and Cournac, 2002). It has been suggested that the reduction of plastoquinone pool is catalyzed by a NAD(P)H dehydrogenase [NAD(P)H:plastoquinone reductase] (Guedeney et al., 1995, 1996; Endo et al., 1997; Corneille et al., 1998), cytochrome b_6–f complex (Clark et al., 1984; Zhang et al., 2001), cytochrome b_{559} of photosystem II (Kruk and Strzałka, 1999) FNR (Böhme, 1977; Shahak, 1981) or by a hypothetical ferredoxin : plastoquinone reductase (FQR) (Moss and Bendall, 1984; Bendall and Manasse, 1995; Endo et al., 1997). The results obtained previously by our group indicate that FNR may be engaged in this process. We have found that the isolated FNR is able to reduce directly many prenylquinones (Bojko and Więckowski, 1999) and that the quinone-binding site at the enzyme molecule corresponds to the DCPIP-binding site and this site differs from those involved in ferredoxin oxidation or NADP$^+$ reduction (Chang et al., 1991; Bojko and Więckowski, 2001) . The isolated FNR was shown to reduce effectively short-chain

Abbreviations: ApoFd, apoferredoxin; FNR, ferredoxin:NADP$^+$ oxidoreductase; Fd, ferredoxin; FQR, ferredoxin:plastoquinone reductase; PQ, plastoquinone; NADP$^+$, β-nicotinamide adenine dinucleotide phosphate; CMC, critical micelle concentration; CHAPS, 3[(3-cholamidopropyl) dimethylammonio]-1-propane sulphonate; MTAB, myristyltrimethylammonium bromide; OG, octyl glucoside; SDS, sodium dodecylsulphate; DCPIP, 2,6-dichlorophenolindophenol.

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prenylquinones, such as dibromothymoquinone, PQ-2, decyl-PQ and decyl-UQ (Nielsen et al., 1995; Bojko and Więckowski, 1999). However, plastoquinone-9 (PQ-9), which constitutes the plastoquinone pool in thylakoid membranes, was poorly reducible by the FNR-NADPH system. Probably, the high hydrophobicity of PQ-9 molecules makes impossible the interaction of their reducible head groups with the appropriate binding site at the FNR, or PQ-9 molecules form micelles that create unfavourable conditions for their reduction in the aqueous medium.

The aim of the present investigation was to find experimental condition where the isolated FNR would catalyze efficiently reduction of plastoquinones, including PQ-9. We focused our attention on FNR-NADPH-dependent reduction of short and long side-chain in the presence of different detergents being over their critical micelle concentration (CMC). It can be supposed that incorporation of plastoquinone molecules into detergents micelles should facilitate interaction of quinone head groups with the binding site at the FNR molecule and this should enhance PQ-9 reduction by the enzyme. The obtained results were discussed in terms of the function of FNR as FQR both in cyclic electron transport around photosystem I and chlororespiration.

2. Results and discussion

Fig. 1 shows that along with the increase in the length of the PQ side chain, a decrease of the oxygen uptake rate takes place in the absence of detergents. Among the detergents tested, only sodium cholate stimulated the oxygen uptake in the presence of PQ-2, PQ-3, PQ-4 and PQ-9, while the other detergents showed rather inhibitory effects on the investigated reaction. In the case of PQ-1, stimulation of the reaction by sodium cholate was not observed due to good solubility of PQ-1 in water that already saturates the reaction. Sodium cholate enhanced the rates of PQ-2, PQ-3, PQ-4 and PQ-9 catalyzed oxygen uptake by approximately three-, ten-, ten- and sixfold, respectively, although the absolute values of oxygen consumption decreased with the increase of the length of the side-chain of the quinones tested both in the control and in the cholate-treated samples. Apparently, cholate specifically dissolves water-insoluble PQ-2–PQ-9 homologues increasing the concentration of free plastoquinones available for the reduction by FNR. In the presence of OG and Triton X-100, the investigated reaction was inhibited by 30–70% and 80–90%, respectively. The reaction was almost completely inhibited in the presence of 15 mM SDS or 15 mM MTAB (data not shown). Similar results were obtained when NADPH oxidation was followed spectrophotometrically during the reaction (Fig. 2). The NADPH oxidation rates correlate well with the oxygen consumption rates for short-chain plastoquinones, indicating that under aerobic conditions all electrons from NADPH are transferred to molecular oxygen via plastosemiquinone radical due to its spontaneous autoxidation according to the following reactions:

$$\mathrm{NADPH + FMN + H^+ \rightarrow\ NADP^+ + FMNH_2} \quad \text{(FMN moiety in FNR is a two-electron acceptor)} \tag{1}$$

$$\mathrm{FMNH_2 + 2PQ\ \rightarrow\ FMN + 2H^+ + 2\ PQ^{-\bullet}} \tag{2}$$

$$\mathrm{PQ^{-\bullet} +\ O_2\ \rightarrow\ PQ + O_2^{-\bullet}} \tag{3}$$

$$\mathrm{2O_2^{-\bullet} +\ 2H^+\ \rightarrow\ H_2O_2 + O_2} \tag{4}$$

Under anaerobic conditions, autoxidation of the plastosemiquinone radical is not possible and it undergoes dismutation to plastoquinone and plastohydroquinone:

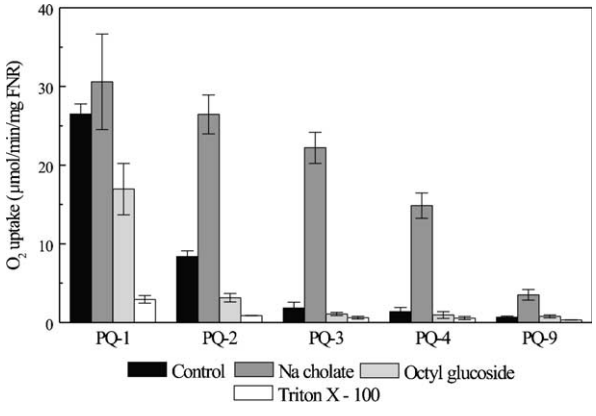

Fig. 1. Effect of sodium cholate (15 mM), OG (25 mM) and Triton X-100 (15 mM) on the oxygen uptake, mediated by enzymatically reduced PQ-1, PQ-2, PQ-3, PQ-4 and PQ-9. The reaction mixture contained 20 μM PQ-n, 60 nM FNR, 0.2 mM NADPH, 1 mM Na_2EDTA and 1 mM $MgCl_2$ in 40 mM Tris buffer (pH 7.7). Mean values and standard deviations from 3–4 repetitions are shown.

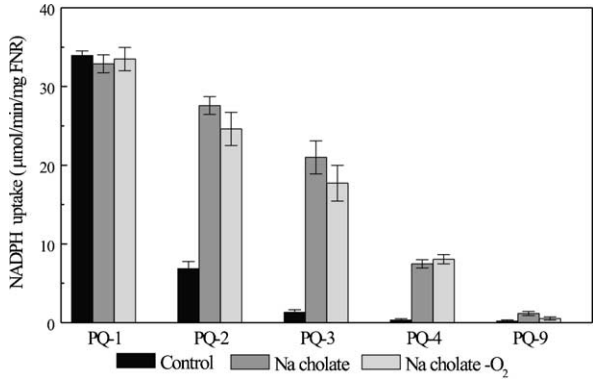

Fig. 2. Effect of sodium cholate (15 mM) and anaerobic conditions on initial rates of NADPH uptake in the presence of PQ-1, PQ-2, PQ-3, PQ-4 and PQ-9. The reaction mixture contained 20 μM PQ-n, 60 nM FNR, 0.2 mM NADPH, 1 mM Na_2EDTA and 1 mM $MgCl_2$ in 40 mM Tris buffer (pH 7.7). Anaerobic conditions were obtained as described in Experimental. Mean values and standard deviations from 3–4 repetitions are shown.

$$2\ PQ^{-\bullet} + 2H^{+} \rightarrow PQ + PQH_2 \quad (5)$$

Similar initial rates of NADPH oxidation both in the presence and absence of oxygen (Figs. 2 and 3) suggest that PQ reduction is a one-electron reaction regardless of the availability of oxygen. The fast decrease of the initial reaction rate under anaerobic conditions is due to the lowering of substrate (PQ) concentration because of its irreversible reduction to the hydroquinone form [reactions (2) and (5)]. On the other hand, under aerobic conditions, there occurs fast substrate regeneration due to semiquinone reoxidation [reaction (3)] and the initial reaction rate decreases considerably slower (Fig. 3).

The results of the effect of ionic detergents on PQ-4-mediated NADPH oxidation (Table 1) indicate that these detergents were without any effect (CHAPS) or inhibited (SDS, MTAB) the studied reaction. The effect of sodium cholate on PQ-4 mediated NADPH oxidation was enhanced by about 20% when Fd or apoFd (Fd with the removed Fe–S center) was added to the reaction mixture (Table 1). Anaerobic conditions did not change the stimulatory effect of Fd on the reaction. This indicates that stimulation of NADPH oxidation by

Table 1
Effect of various detergents, Fd and $MgCl_2$ on the oxidation rate of NADPH in 40 mM Tris buffer (pH 7.7)[a]

Sample	NADPH oxidation rate (μmol/min/mg FNR)
Control	0.186±0.045
+ sodium cholate	0.227±0.041
+ Fd	0.590±0.087
+ PQ-4	0.323±0.009
+ PQ-4 + CHAPS	0.336±0.127
+ PQ-4 + SDS	0.227±0.018
+ PQ-4 + MTAB	0.032±0.002
+ PQ-4 + Fd	0.700±0.009
+ PQ-4 + sodium cholate	7.48±0.52
+ PQ-4 + Fd + sodium cholate	9.14±1.13
+ PQ-4 + Fd + sodium cholate - O_2	8.42±1.29
+ PQ-4 + apoFd + sodium cholate	9.54±0.88
+ PQ-4 + sodium cholate + $MgCl_2$	1.76±0.59
+ PQ-4 + sodium cholate + $MgCl_2$ + Fd	1.97±0.69

[a] The reaction mixute contained 0.2 mM NADPH, 60 nM FNR and additionally 20 μM PQ-4, 15 mM detergent, 60 nM Fd, 60 nM apoFd or 30 mM $MgCl_2$ where indicated. Anaerobic conditions ($-O_2$) were obtained as described in Experimental. Mean values and standard deviations are from 3–4 repetitions.

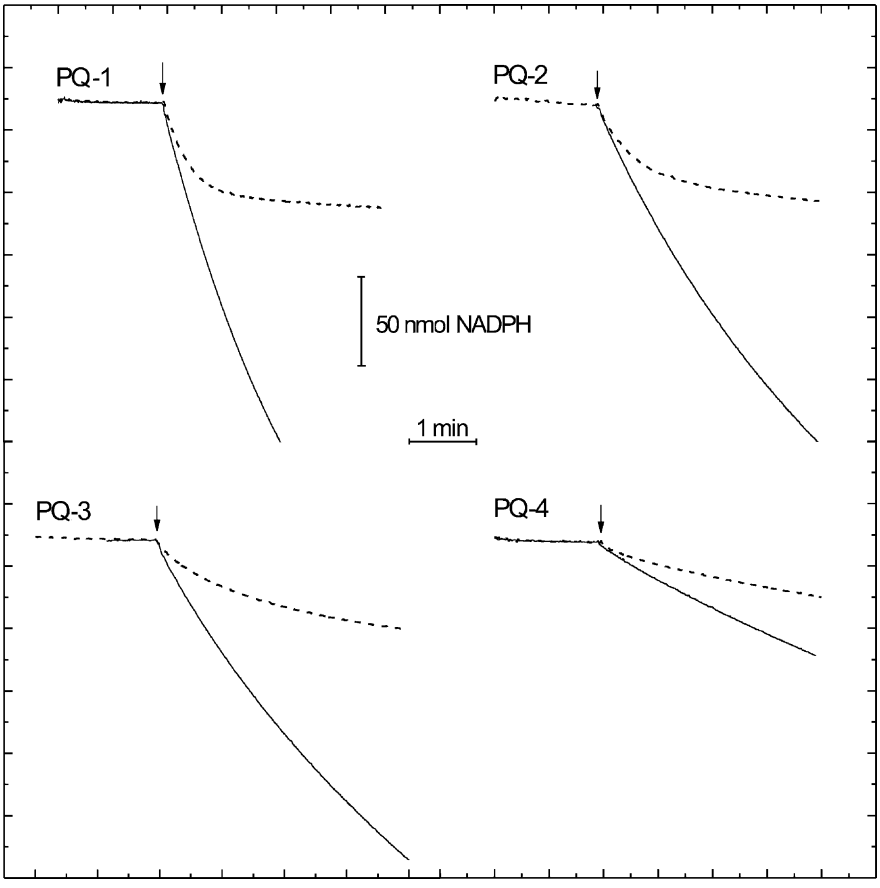

Fig. 3. Time course of NADPH oxidation in the presence of various PQ homologues and 15 mM cholate under aerobic (——) and anaerobic (- - - -) conditions followed at 340 nm. Arrow denotes the addition of FNR. Other details as in Fig. 2.

Fd in the presence of PQ-4 and cholate is not due to Fd autoxidation. Similar effect of Fd was already observed for dibromothymoquinone (Bojko and Więckowski, 1995), PQ-2 and decyl-PQ (Bojko and Więckowski, 1999). We suppose that Fd induces conformation changes of the FNR molecules as it was recently observed (Kurisu et al., 2001) and this favours PQ reduction.

We have also found that $MgCl_2$ decreased the rate of the investigated reaction approximately 4-fold (Table 1). The inhibitory effect of $MgCl_2$ on PQ-4-catalyzed oxygen uptake is probably due to the electrostatic shielding of the cholate carbonyl group by Mg^{2+} ions (Roux and Bloom, 1990; Walter et al., 2000). The presence of $MgCl_2$ probably makes it also difficult to incorporate PQ-4 into cholate micelles.

The obtained results apparently indicate that the NADPH- and FNR-dependent reduction of quinones increased only in the presence of sodium cholate among various detergents tested. This concerns particularly PQ-2, PQ-3, PQ-4 and to a lower extent also PQ-9. The reason why only the cholate is stimulatory among the investigated detergents is probably due to the smallest size of micelles formed by cholate (Table 2). The other detergents studied, form large micelles where PQ molecules are probably deeply embedded and reside far from the water/lipid interface where their reduction by the enzyme is only possible. The micelles formed by CHAPS are also of a small size but in this case probably the steric hindrance of the long side-chain of CHAPS makes it difficult to access the micelles by the enzyme. The presence of the positive charge in the CHAPS molecule did also not facilitate the interaction of FNR with the substrate.

As can be seen from Fig. 4, the optimal sodium cholate concentration for PQ-4 and PQ-9 catalyzed oxygen uptake was about 20 mM. In the presence of 20 mM cholate, the reaction rate for PQ-4 and PQ-9 increased approximately 18-fold and 7-fold, respectively. In the presence of 60 mM cholate, these rates reached only 5-fold (PQ-4) or 1.7-fold (PQ-9) higher values than those in the control. At the cholate concentration of 15 mM, where we observed stimulation of the reaction both for short-chain (PQ-2 to PQ-4) and long-chain (PQ-9) plastoquinones, the aggregation number of the micelles

Table 2
Critical micelle concentration (CMC) and aggregation number of the used detergents[a]

Detergent	CMC (mM)	Aggregation number
Sodium cholate	10	4
CHAPS	3–10	4–14
SDS	1.2–7.1	62–101
Triton X-100	0.25	75–165
OG	19–25	~90
MTAB	4.5	56

[a] Data taken from LeMaire et al. (2000) and Findlay (1989)

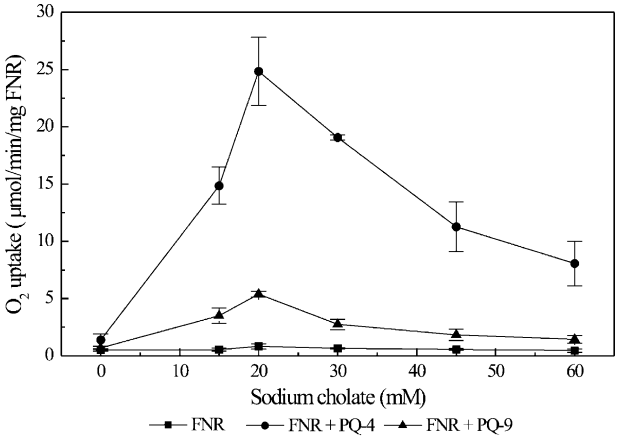

Fig. 4. Effect of sodium cholate concentration on the oxygen uptake, mediated by enzymatically reduced PQ-4 and PQ-9. Other details as in Fig. 1.

is 4 (Small et al., 1969; Sugioka and Moroi, 1998). A molecule of PQ-4 and of the other short-chain homologues would fit into such a micelle easily, since the length of PQ-4 side-chain corresponds approximately to the length of the cholate micelle (Fig. 5a). In the case of PQ-9, two cholate micelles would be necessary to cover the long side-chain of the PQ-9 molecule (Fig. 5b). At higher concentrations (>20 mM), cholate forms micelles with the aggregation number of 8 (Sugioka and Moroi, 1998) and such micelles are

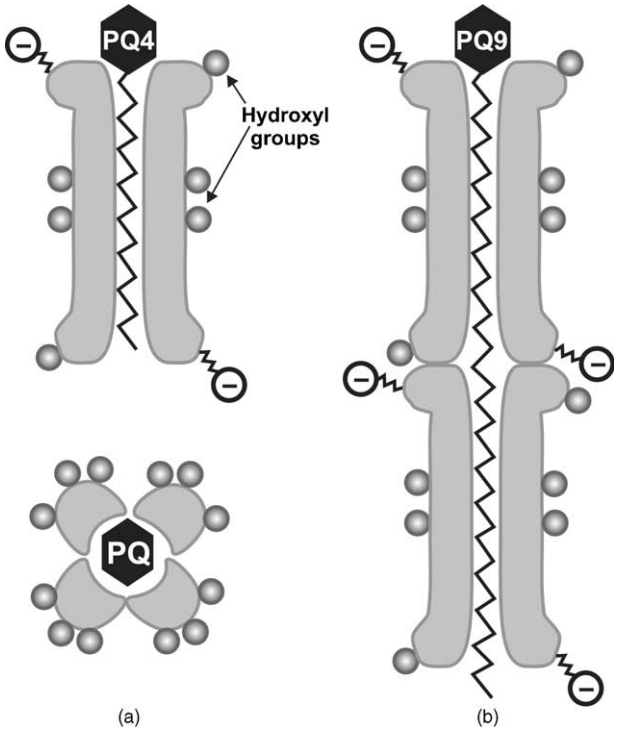

Fig. 5. The proposed molecular structure of PQ-4/cholate mixed micelles (a) and PQ-9/cholate mixed micelles (b). The aggregation numbers of the micelles are 4 (a) and 8 (b) in respect to cholate. Based on Small et al. (1969).

probably necessary to incorporate PQ-9 into cholate micelles even at lower cholate concentration than that of 20 mM. The cholate concentration above 20 mM is probably inhibitory for the oxygen uptake because of the inhibitory effect of the detergent on the enzyme itself at such a detergent concentration. The increase in cholate to phosphatidylcholine ratio in the mixed micelles caused also the decrease of the initial rate of phosphatidylcholine hydrolysis by porcine pancreatic phospholipase A_2 (Gheriani-Gruszka, 1988; Nalbone et al., 1980). A similar effect was also observed when increasing Triton X-100 concentration (Deems et al., 1975). It is likely that higher quinone concentration in the micelle causes unfavourable conditions for the interaction of a quinone head group with the binding site at the FNR molecule.

Our results demonstrate that FNR can reduce efficiently short-chain plastoquinones and to a smaller extend also PQ-9 in the presence of sodium cholate. The less efficient PQ-9 reduction is probably due to uncomplete dissolvation of PQ-9 aggregates even in the presence of sodium cholate.

We were unable to detect any NADPH- and FNR-dependent reduction of PQ-9 molecules incorporated into liposome membranes prepared from egg yolk lecithin or dipalmitoylphosphatidylcholine according to the method given in Kruk et al. (1993) and Jemioła-Rzemińska et al. (1996) (data not shown). This is probably because of the poor association of FNR with liposome membranes. In vivo, FNR can be both loosely and tightly bound to thylakoid membranes (Matthijs et al., 1986). It is likely that in vivo, the effective reduction of PQ-9 catalyzed by FNR requires the presence of a binding protein that connects FNR with photosystem I (Andersen et al., 1992; Nielsen et al., 1995), with the cytochrome b_6-f complex (Clark et al., 1984; Zhang et al., 2001) and/or with NAD(P)H dehydrogenase complex (Quilles et al., 2000). It is highly probable that a binding protein facilitates contact of the head group of PQ-9 molecules with FNR, and plays similar role like sodium cholate micelles under our experimental conditions.

Although the plastosemiquinone radical is autoxidized under our aerobic experimental conditions, in vivo this reaction probably does not occur, since in the aprotic membrane interior where PQ-9 resides, the lifetime of semiquinone radical is extended and its dismutation probably dominates [reaction (5)] giving plastohydroquinone. It is known that in the aprotic surroundings, semiquinone radicals are stable even in the presence of oxygen.

If we want to estimate the possible significance of the observed FNR-mediated PQ reduction in our experiments for the reduction of the PQ-pool by FNR in vivo, the corresponding reaction rates should be compared. It was found that the rate of O_2 uptake due to chlororespiration is in the range of 2–4% of the maximal rate of O_2 evolution in photosynthesis (Bennoun, 1982; Peltier and Cournac, 2002), which is about 250 μmol O_2 per mg chlorophyll per hour (Bennoun, 1982). Assuming 600 chlorophyll molecules and one FNR molecule per one electron transport chain, it can be calculated that it corresponds to 60 μmol O_2 per min per mg FNR or 30 μmol $NADP^+$ reduced per min per mg FNR in the linear electron transport chain. Comparing these rates with the specific NADPH oxidation rates obtained in our experiments, it can be concluded that the FNR-catalysed PQ-reduction could be responsible for the observed in vivo rates of chlororespiration and the cyclic electron transport and this also indicates that FNR can play the function of FQR in vivo.

3. Experimental

FNR and Fd were isolated from spinach as described previously (Bojko and Więckowski, 1995 and 1999). NADPH oxidation was monitored spectrophotometrically at 340 nm using SLM AMINCO DW2000 spectrophotometer. Oxygen uptake coupled with plastoquinols oxidation was measured with a Clark type oxygen electrode (Hansatech, UK) connected to TZ 4100 recorder (Czech Republic). In order to prepare mixed detergent-quinone micelles, solutions of various detergents were prepared and stirred for about 10 s. Subsequently, ethanol solution of a prenylquinone was added under continuous stirring. Final detergents concentration in solution was above their CMC (Table 2) and final ethanol concentration did not exceed 1% in the reaction medium. Apoferredoxin was prepared as described by Bojko and Więckowski (2001). Anaerobic conditions were obtained using oxygen trap composed of glucose oxidase (50 units/ml = 1.5 mg/ml), catalase (500 units/ml = 23.8 μg/ml) and 5 mM glucose in sealed cuvettes.

Other details are described in the preceding papers (Bojko and Więckowski, 1995, 1999) and in the legends of the figures.

Short-chain plastoquinones were gifts from Dr. H. Koike (Himeji Institute of Technology, Hyogo, Japan) and PQ-9 was obtained as previously described (Kruk, 1988). Sodium cholate, CHAPS, MTAB and NADPH were from Sigma, Triton X-100 was from Serva, OG was purchased from Calbiochem and SDS was from Merck. Tris was obtained from Fluka. Other reagents of analytical grade were from the POCh (Poland).

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