# Antagonistic Effects of α-Tocopherol and α-Tocoquinone in the Regulation of Cyclic Electron Transport around Photosystem II

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α-Tocoquinone (α-TQ) and α-tocopherol (α-TOC) which cannot substitute for plastoquinone-9 (PQ-A) as an electron acceptor from photosystem II (PS II), influence the oxygen evolution activity of thylakoid membranes under continuous illumination. In the presence of the herbicide DCMU and the protonophore FCCP which stimulate cyclic electron transport around PS II, α-TQ decreased oxygen evolution whereas α-TOC enhanced it. The effects are attributed to a stimulation or an inhibition of cyclic electron transport around PS II by α-TQ and α-TOC, respectively. Results of flash light experiments on PS II preparations show that both α-TQ and α-TOC increased the d-parameter which describes the transition probability from the $S_3$- to the $S_0$-state of the oxygen-evolving complex, although to a smaller extent when PQ-A is added alone to the preparations. The initial S-state distribution in dark-adapted samples was changed only upon PQ-A addition and influenced neither by α-TQ nor by α-TOC supplementation. These effects indicate different kinds of interaction of PQ-A, α-TQ and α-TOC with the PS II components. α-TQ increased and α-TOC decreased the "total miss" parameter both in the presence or absence of PQ-A. A possible site of interaction of α-TQ and α-TOC with the cyclic electron transport around PS II is suggested.

## Introduction

According to a generally accepted view cyclic electron flow around photosystem II (PS II) is part of a defense mechanism which protects the photosynthetic apparatus from damage caused by over-excitation under strong light conditions (Thompson and Brudvig, 1988; Whitmarsh and Pakrasi, 1996). Although there is a large body of evidence for the operation of such a cyclic electron transport, its molecular mechanism is still not understood. On the basis of results we obtained by measuring the relative activity of cyclic and linear electron flow, when applying light absorbed by different photosynthetic pigments, we postulated the participation of carotenoids and in particular that of β-carotene of the PS II reaction center in this process (Gruszecki *et al.*, 1995, 1996). We also found that the relative activity of cyclic and vectorial electron flow depended not only on the light quality (i.e. the relative degree of excitation of chlorophyll and carotenoid pigments), but also upon the presence of quinones (Gruszecki *et al.* 1995), the involvement of which was also postulated by other authors (McNamara and Gounaris, 1992; Satoh *et al.*, 1990; Sinclair and Kelley 1992; Tsujimoto and Arnon, 1985).

The thylakoid membrane contains different kinds of quinones. The most abundant species is plastoquinone-9 (PQ-A), the function of which is well characterized and which operates as the primary ($Q_A$) and secondary ($Q_B$) electron acceptor of PS II, and also as a hydrogen carrier across the

*Abbreviations:* BL, Blue light; RL, Red light; WL, White light; α-TQ, α-Tocoquinone; α-TOC, α-Tocopherol; PQ-A, Plastoquinone-A; DBMIB, 2,5-dibromomethyl-6-isopropyl-*p*-benzoquinone; DCMU, 3-(3,4-dichlorophenyl)-N,N'-dimethylurea; FCCP, Carbonylcyanide-p-trifluoromethoxy-phenyl-hydrazone; PS I, Photosystem I; PS II, Photosystem II; TLC, Thin layer chromatography; $Q_A$, the first quinone acceptor in the reaction center of photosystem II; $Q_B$, the second quinone electron acceptor in the reaction center of photosystem II; Hepes, N-[2-hydroxyethyl]piperazine-N'-[2-ethanesulfonic acid].

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thylakoid membrane (PQ-pool) (Rich and Moss, 1987). There are also reports suggesting that PQ-A is involved in cyclic electron transport around PS I (for review, see Więckowski and Bojko, 1997).

α-TQ is a widespread prenylquinone which is present in the thylakoid membrane at about 10% of the PQ-A amount (Kruk and Strzałka, 1995). The light dependent changes in the redox state of α-TQ (Dilley and Crane, 1963, 1964) might suggest its participation in photosynthetic electron transport. However, its site of redox changes is unknown. α-TQ was shown to restore even at very low concentrations (Henninger and Crane, 1963) cytochrome *c* photoreduction in the presence of ferredoxin-NADPH oxidoreductase. These facts may indicate that the site of its redox change is located in the region of photosystem I (PS I). On the other hand *Anacystis nidulans* (Omata and Murata, 1984) and a *Scenedesmus obliquus* mutant (Bishop and Wong, 1974) which both lack α-TQ and α-TOC, show absence of the high-potential form of cytochrome *b*-559 (Cyt *b*-559 HP) which is generally accepted as a component participating in cyclic electron flow around PS II (Arnon and Tang, 1988). This may point to a relationship between α-TQ, α-TOC and the Cyt *b*-559-mediated cyclic electron flow. It was also suggested that the reduced form of α-TQ plays a role as a membrane-bound antioxidant (Bindoli *et al.*, 1985; Mukai *et al.*, 1993; Kruk *et al.*, 1994, 1997) comparable to α-TOC, the function of which in the antioxidative defence mechanisms in membranes is well established (Machlin, 1980). Apart from its antioxidative function α-TOC, similarly to the discussed above quinones, may also participate in electron transfer reactions connected with PS II (Barr and Crane, 1977; Michalski and Kaniuga, 1981). Its interaction with Cyt *b*-559 may be also possible for the same reasons as for α-TQ. There are reports that α-TOC restores the activity of heptane-extracted PS I-particles, however, only at very high non-physiological concentrations (Baszyński, 1974; Baszyński and Tukendorf, 1975).

The data on possible interaction of chloroplast prenylquinones with Cyt *b*-559 is mainly limited to PQ-A. Such an interaction is derived from restoration of the high-potential form of Cyt *b*-559 by PQ-A (Cox and Bendall, 1974), by the reoxidation of the PQ-pool by protonophores such as carbonylcyanide-*p*-trifluoromethoxyphenylhydrazone (FCCP) which stimulates electron transport (McCauley *et al.*, 1987), and by an inhibition of high potential Cyt *b*-559 photoreduction by DCMU (Samson and Fork, 1991), this, however, at higher concentrations than those required for the inhibition of PQ-A-reduction at the $Q_B$-site.

It was also found that β-carotene was necessary for the reoxidation of the photoreduced high-potential Cyt *b*-559 by the reaction center of PS II, as the result of the operation of cyclic electron transport (Cox and Bendall, 1974). This is in agreement with our recent proposal (Gruszecki *et al*, 1995; Strzałka *et al.*, 1996) on the involvement of the β-carotene molecule of the PS II reaction center in this process.

To investigate the influence of different prenyl-lipids on the cyclic electron transport around PS II we have measured the restoration of oxygen evolution efficiency by α-TQ and α-TOC added separately or in combination with PQ-A and β-carotene, to petroleum ether-extracted thylakoid membranes and to lyophilized or fresh PS II-particles. The restoration efficiency was also measured in the presence of DCMU-concentrations which partially inhibited linear electron transport, and also upon addition of FCCP. Both these treatments stimulated the cyclic component of PS II-mediated electron transport, therefore the effect of investigated prenyl-lipids should be even more pronounced.

## Material and Methods

PQ-A was isolated from lyophilized maple leaves (*Acer pseudoplatanus* L.) by petroleum ether (b.p. 40–60 °C) extraction, column chromatography on silica gel (Merck) in benzene/heptane (85:15, v/v) or benzene followed by thin layer chromatography (TLC) on silica gel plates (Merck) in benzene/heptane (60:40, v/v). α-TOC was from Merck and α-TQ was obtained as described by Kruk (1988). β-carotene was a research gift from Hoffmann-LaRoche (Basel, Switzerland) and it was additionally purified by LC in hexane/chloroform (1:1, v/v), FCCP was purchased from Serva. Concentrations of the investigated prenyl-lipids were determined spectrophotometrically. The molar absorption coefficient for PQ-A at 255 nm in absolute ethanol was 17940 (Kruk *et al.*, 1992). The coefficients used for the α-TOC (mea-

sured at 292 nm) and α-TQ (measured at 268 nm) determination were 3260 and 18830, respectively.

Thylakoid and PS II-particles from *Nicotiana tabacum* var. John William's Broadleaf were prepared according to the method described by Berthold *et al.* (1981) and suspended in 25 mM Hepes buffer, pH 7.5 at a chlorophyll concentration of 250 μg /ml. For extraction-reconstitution experiments the thylakoid suspension was lyophilized and extracted 3 times for one hour with petroleum ether (5 ml/mg chl) under continuous shaking. Petroleum ether-extracted membranes were reconstituted by the addition of hexane solutions of β-carotene, α-TOC and the quinones in various combinations and evaporation of the solvent in a nitrogen stream. Subsequently the samples were dried under vacuum to remove traces of the solvent and were then suspended in Hepes buffer and adjusted to the original chlorophyll concentration (250 μg/ml).

In the case of thylakoid membranes the amounts of β-carotene and PQ-A, added back to the dried samples, corresponded to 57 and 200 nmol/mg chlorophyll which is approximately two times the amount found *in vivo*. The amount of the other prenyl-lipids namely α-TOC and α-TQ, which were added together with β-carotene and PQ-A corresponded to 25% of the amount of PQ-A. β-carotene was added to each reconstituted sample because it was found to be necessary for an optimal restoration of the oxygen evolving activity in extracted chloroplasts (Cox and Bendall, 1974). Lyophilized PS II-particles were suspended in 50 mM Hepes buffer pH 6.5, containing 2.5 mM $CaCl_2$ and 0.4 M sucrose. The investigated prenyl-lipids (PQ-A, α-TOC, α-TQ) were added as ethanolic solutions to lyophilized samples, resuspended in buffer or to fresh PS II samples containing 10 μg of chlorophyll, yielding a final chlorophyll/prenyl-lipid molar ratio of 5.

The extraction-reconstitution experiments were carried out with 10 individual thylakoid and PS II-preparations. Activity differences between preparations were below 10%. The data given represent experimental series within the same preparation.

Amperometric measurements of oxygen evolution were carried out with the bare platinum electrode described by Schmid and Thibault (1979). Continuous light experiments were performed using red light (36.5 μE $m^{-2}$ $s^{-1}$) which was provided by a halogen projector lamp equipped with a 630 nm cut-off filter combined with 1% $CuSO_4$ solution. In flash light experiments the flashes of 5 μs halfwidth were generated by a Stroboscope 1539A (General Radio, Concord, Mass., USA). Oxygen evolution as consequence of a train of flashes was measured in sequences of 15 white (2.1 μE $m^{-2}$ per flash), blue (1.25 μE $m^{-2}$) or red (1.1 μE $m^{-2}$) light flashes spaced 300 ms apart. The number of photons per flash was calculated by measuring the photon flux of 180 flashes and subsequent division by 180. Blue light flashes were obtained using a BG12 broadband filter and red flashes using a 630 nm cut-off filter.

## Results and Discussion

### *Continuous light experiments*

A non-extracted sample treated with DBMIB, an inhibitor blocking electron transport between PS II and the cytochrome *b/f* complex, was only slightly less active in oxygen production than the untreated control (see legend to Table I), indicating that in our system the oxygen evolution mea-

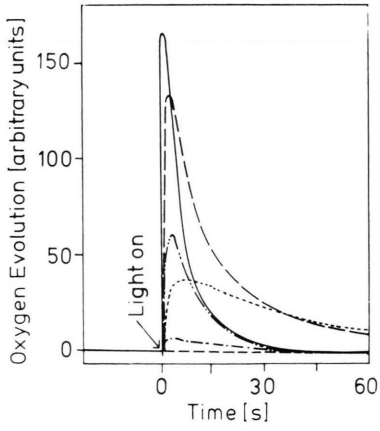


Fig. 1

Fig. 1. Oxygen evolution activity (rate) of unextracted thylakoids (——), as well as of the the thylakoids extracted and reconstituted with PQ-A (– – –), PQ-A + 5 μM FCCP (– ·· – ·· –), PQ-A + 0.25 μM DCMU (.....) PQ-A + 0.25 μM DCMU and 2.5 μM FCCP (– · – · –) and PQ-A + 0.25 μM DCMU and 5 μM FCCP (– – – – – –) under continuous illumination with red light (36.5 μE $m^{-2}$ $s^{-1}$). Red light was given as a light pulse of 60 sec. β-carotene was added to all reconstituted samples. The time dependence of the rate shows that all samples are acceptor limited. The control activity of unextracted thylakoids corresponds to 130 μmol $O_2$ · mg $Chl^{-1}$ · $h^{-1}$.

sured is limited mainly by electron transport reactions associated with photosystem II. PQ-A or PQ-A in combination with α-TQ or α-TOC, when added to the petroleum ether-extracted thylakoids restored significantly their oxygen evolving activity (Fig. 1, Table I). This restoration ranged from 81% (thylakoids reconstituted with PQ-A only) to 72% (thylakoids reconstituted with PQ-A + α-TQ) of their original activity. This indicates a good effectiveness of the reconstitution procedure and points to a preservation of structural integrity of thylakoid membranes after such a treatment. Reconstitution with α-TQ or α-TOC only, without concomitant addition of PQ-A, resulted in membranes ineffective in oxygen evolution, which confirms our findings (not shown here) that these two prenyl-lipids cannot act as electron acceptors in Hill reaction (Kruk *et al.*, 1997).

The addition of FCCP which is known to stimulate cyclic electron transport around PS II by promoting the reoxidation of high-potential Cyt *b*-559 (Barabas *et al.*, 1993), lowered pronouncedly (50–65%) oxygen evolution in red light-illuminated samples.

Cyclic electron transport is supposed to occur under conditions when linear electron transport from water to $NADP^+$ is saturated by high light intensity. In order to simulate such a situation, we partially inhibited linear electron flow by DCMU and then studied the effectiveness of reconstitution with different prenyl-lipids. As it can be seen in Table I under DCMU treatment the efficiency of oxygen evolution decreased to a similar level in the samples reconstituted with PQ-A or PQ-A + α-TOC, however, the decrease was more pronounced in the sample reconstituted with PQ-A + α-TQ. This suggests that α-TQ, in contrast to PQ-A and α-TOC may lower oxygen evolution by stimulating cyclic electron transport. The stimulatory effect of α-TQ on cyclic electron flow (a decrease in oxygen evolution) was also found in the case of thylakoids treated with DCMU + 2.5 μM FCCP. In addition, reoxidation of reduced α-TQ may also contribute to some extent to a lowering of net oxygen evolution (Bojko and Więckowski, 1995; Więckowski and Bojko, 1996).

On the other hand, membranes reconstituted with α-TOC showed under these conditions a higher oxygen evolving activity than the other two variants, which may indicate that the prenyl-lipid inhibits to a certain extent the FCCP-induced cyclic electron flow leading to the consequence that more electrons are turned into the linear path. This effect of α-TOC, manifested as an increased

Table I. Relative oxygen evolution activities in control thylakoids (unextracted) of tobacco *Nicotiana tabacum* and preparations extracted and reconstituted with β-carotene, PQ-A and other prenyl-lipids (Q) at the molar ratio of PQ-A / Q = 4 in dependence on the addition of DCMU and FCCP.

| Sample extracted and reconstituted with | Relative oxygen evolution [mV] | | | | |
|---|---|---|---|---|---|
| | No addition | + 5 μM FCCP | + 0.25 μM DCMU | + 0.25 μM DCMU + 2.5 μM FCCP | 0.25 μM DCMU + 5 μM FCCP |
| Control (unextracted) | 165 | 58 | – | – | – |
| β-Carotene + PQ-A | 134 | 61 | 39 | 8 | 0 |
| β-Carotene + α-tocoquinone | 0 | – | – | – | – |
| β-Carotene + α-tocopherol | 0 | – | – | – | – |
| β-Carotene + PQA + α-tocoquinone | 119 | – | 19 | 3 | 0 |
| β-Carotene + PQA + α-tocopherol | 122 | – | 44 | 13 | 8 |

Illumination with continuous red light (36.5 μE $m^{-2}$ $s^{-1}$). For other experimental details see Material and Methods. Maximal error level below 10%. The value for oxygen evolution for the non-extracted sample in the presence of 5 μM DBMIB was 143 mV which corresponds to 130 μmol $O_2$ evolved · mg $Chl^{-1}$ · $h^{-1}$.

oxygen evolution, can also be seen when the concentration of FCCP is raised to 5 μM. In such conditions there was no oxygen evolving activity in all experimental variants studied except for the PQ-A + α-TOC reconstituted membranes (Table I), where significant $O_2$ evolution was still occurring.

*Flash light experiments*

From the results presented above it can be concluded that α-TQ and α-TOC seem to exert an antagonistic effect on oxygen evolution which may be related to their different influence on cyclic electron transport around PS II. To get a better insight into this phenomenon we have studied the effect of PQ-A, α-TQ and α-TOC on oxygen evolution under single-turnover light flashes of white light (WL), blue light (BL) and red light (RL) in isolated PS II particles. Typical patterns of oxygen evolution for selected experimental variants are shown in Figs. 2 and 3. The data obtained were analyzed using the heterogeneous five state-model described by Burda and Schmid (1996). In the calculations double hits were neglected. Calculated parameters such as the S-state distribution, miss frequency (α) and the efficiency for the transition of $S_3 \rightarrow S_4 \rightarrow S_0$ (parameter d) for PS II-particles reconstituted with different prenyl-lipids and illuminated with WL, BL and RL are shown in Tables II and III.

As we have already demonstrated in our previous paper (Gruszecki *et al.*, 1997) flashes of RL (which was found to stimulate cyclic electron transport), increased significantly the proportion of misses in the control sample, so the value of total misses ($\alpha_t$) for this experimental variant was significantly higher than the corresponding values for control samples illuminated with WL- or BL-flashes. This is valid for both fresh and lyophilized PS II-particles reconstituted with PQ-A, α-TQ and

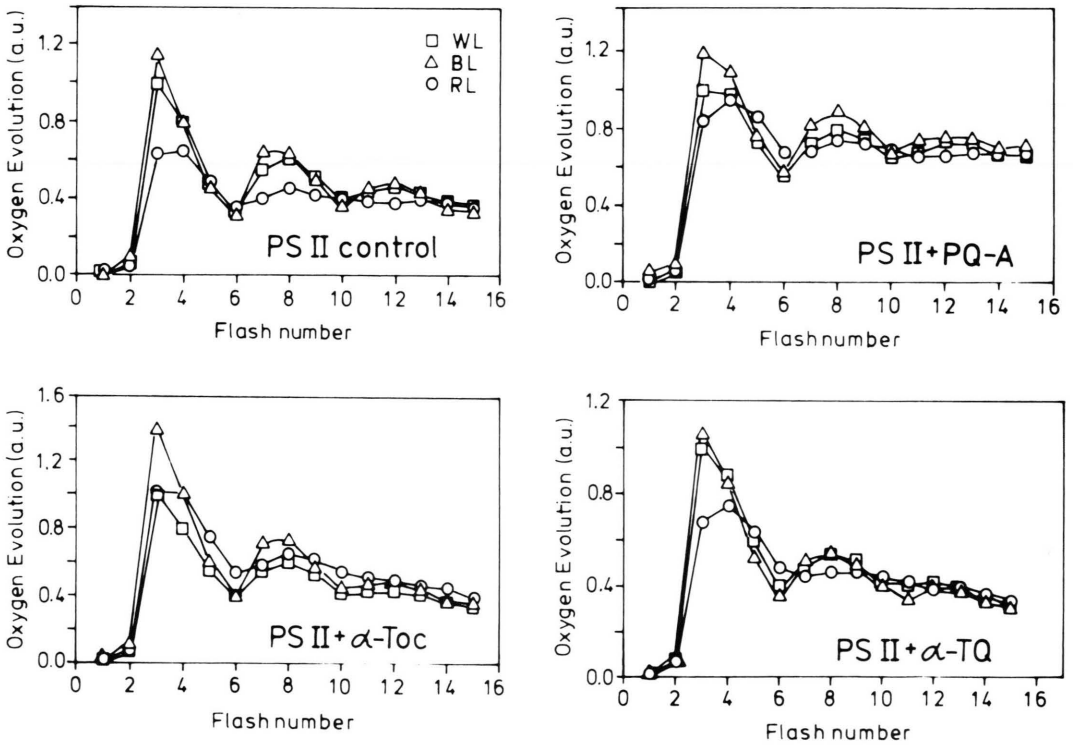


Fig. 2. Flash-induced oxygen yield pattern in lyophilized and resuspended photosystem II particles of tobacco, treated with PQ-A, α-TOC and α-TQ under white light (WL), blue light (BL) and red light (RL) illumination. Oxygen evolution is expressed as the amplitude of the polarographic signal (rel. units) per particle preparation corresponding to 30 μg of chlorophyll deposited on the electrode. All experimental variants are normalized to the amplitude of oxygen evolution at the third flash of white light. The parameters of the mathematical fits corresponding to these patterns are given in Table II.

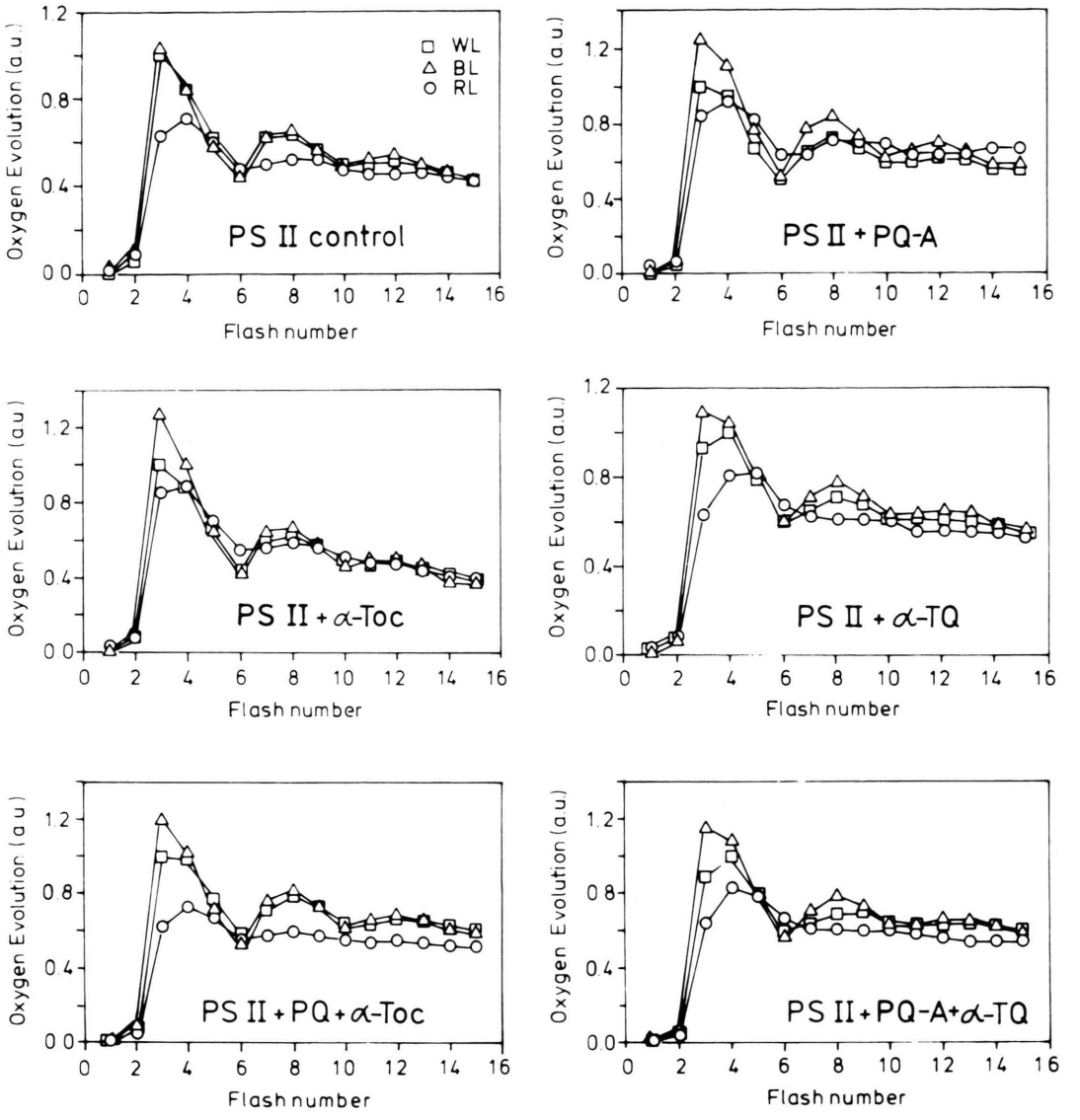


Fig. 3. Flash-induced oxygen yield pattern in fresh photosystem II particles of tobacco, treated with PQ-A, α-TOC and α-TQ or their combinations, under white light (WL), blue light (BL) and red light (RL) illumination. Oxygen evolution is expressed as amplitudes of the polarographic signal (rel. units) per preparation corresponding to 30 μg of total chlorophyll deposited on the electrode. All experimental variants are normalized to the amplitude of oxygen evolution at the third flash of white light. The parameters of the mathematical fits corresponding to these patterns are given in Table III.

α-TOC (Tables I and II). However, only in the presence of α-TQ the effect of red light on the increase of the $\alpha_t$ parameter was pronounced, and the most affected transition was the $S_0 \rightarrow S_1$ transition (the $\alpha_0$ value increased greatly). On the other hand, the value of the $\alpha_0$ parameter decreased in RL-illuminated PS II-particles reconstituted with α-TOC + PQ-A, when compared to the sample reconstituted with PQ-A only (Table II). PQ-A was the only prenyl-lipid used which significantly changed the S-state distribution pattern, increasing the proportion of $S_0$ in comparison to the $S_1$ state in both fresh as well as in lyophilized samples. This quinone was also most effective in rising

Table II. Determination of the S-state distribution, the miss frequency (α) and the efficiency of the $S_3 \rightarrow S_4 \rightarrow S_0$ transition (parameter d) for lyophilized and resuspended PS II particles, reconstituted with different prenyl-lipids and illiminated with flashes of white light, blue light and red light. Fitting error below 3%.

| Train of 15 flashes of | S-States | | | | Misses | | | | Total misses | Transition probability $S_3 \rightarrow (S_4) \rightarrow S_0$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | $S_0$ | $S_1$ | $S_2$ | $S_3$ | $\alpha_0$ | $\alpha_1$ | $\alpha_2$ | $\alpha_3$ | $\alpha_t$ | d |
| *Lyophilized PS II* | | | | | | | | | | |
| White light | 0.135 | 0.807 | 0.058 | 0.000 | 0.000 | 0.001 | 0.632 | 0.001 | 0.634 | 0.194 |
| Blue light | 0.128 | 0.786 | 0.090 | 0.004 | 0.000 | 0.000 | 0.556 | 0.000 | 0.556 | 0.108 |
| Red light | 0.137 | 0.825 | 0.048 | 0.011 | 0.001 | 0.035 | 0.706 | 0.136 | 0.878 | 0.114 |
| *Lyophilized PS II + α-TOC* | | | | | | | | | | |
| White light | 0.116 | 0.812 | 0.068 | 0.005 | 0.001 | 0.001 | 0.682 | 0.001 | 0.685 | 0.634 |
| Blue light | 0.119 | 0.805 | 0.073 | 0.003 | 0.000 | 0.000 | 0.597 | 0.000 | .0597 | 0.778 |
| Red light | 0.126 | 0.811 | 0.065 | 0.004 | 0.055 | 0.070 | 0.709 | 0.076 | 0.910 | 0.515 |
| *Lyophilized PS II + α-TQ* | | | | | | | | | | |
| White light | 0.135 | 0.805 | 0.064 | 0.004 | 0.267 | 0.069 | 0.632 | 0.076 | 1.044 | 0.590 |
| Blue light | 0.127 | 0.810 | 0.069 | 0.005 | 0.182 | 0.006 | 0.608 | 0.063 | 0.859 | 0.640 |
| Red light | 0.128 | 0.803 | 0.075 | 0.007 | 0.786 | 0.112 | 0.699 | 0.308 | 1.905 | 0.345 |
| *Lyophilized PS II + PQ-A* | | | | | | | | | | |
| White light | 0.208 | 0.722 | 0.073 | 0.002 | 0.000 | 0.000 | 0.735 | 0.000 | 0.735 | 0.985 |
| Blue light | 0.200 | 0.724 | 0.084 | 0.014 | 0.000 | 0.000 | 0.677 | 0.000 | 0.677 | 0.996 |
| Red light | 0.215 | 0.723 | 0.065 | 0.003 | 0.310 | 0.002 | 0.769 | 0.183 | 1.264 | 0.928 |

the value of d parameter. This parameter was in the range of 0.1–0.3 in control PS II samples which is characterisitc for the system deprived of electron acceptors, which indicates that PS II-particles lost the biggest part of their endogenous PQ-pool during the isolation procedure. Addition of PQ-A increased this parameter to the value of 0.76–0.86 in the case of fresh PS II samples and to the value close to 1 in the case of lyophilized preparations. Interestingly enough, the two remaining prenyl-lipids (α-TQ and α-TOC), although they cannot act as electron acceptors for the linear part of the PS II electron pathway, they also significantly increase the value of the d parameter. Since this rise is not accompanied by an increased oxygen evolution, the α-TQ- and α-TOC-mediated deactivation (discharge) of the $S_3$ state (rise in the d parameter) must proceed via another mechanism than in the case of PQ-A.

The influence of α-TQ and α-TOC on cyclic electron transport around PS II rises the question about the site of interaction of the two prenyl-lipids with the components of this electron transport system. A reasonable site could be cytochrome *b*-559 where α-TQ and α-TOC might interact with its high potential form.

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Table III. Determination of the S-state distribution, the miss frequency (α) and the efficiency of the $S_3 \rightarrow S_4 \rightarrow S_0$ transition (parameter d) for fresh PS II particles and PS II particles with different prenyl-lipids added and illiminated with white light, blue light and red light flashes. Fitting error below 3%.

| Train of 15 flashes of | S-States | | | | Misses | | | | Total misses | Transition probability $S_3 \rightarrow (S_4) \rightarrow S_0$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | $S_0$ | $S_1$ | $S_2$ | $S_3$ | $\alpha_0$ | $\alpha_1$ | $\alpha_2$ | $\alpha_3$ | $\alpha_t$ | d |
| *Fresh PS II-Particles Control* | | | | | | | | | | |
| White light | 0.135 | 0.754 | 0.103 | 0.002 | 0.003 | 0.000 | 0.726 | 0.000 | 0.729 | 0.283 |
| Blue light | 0.132 | 0.759 | 0.102 | 0.007 | 0.001 | 0.001 | 0.669 | 0.000 | 0.671 | 0.344 |
| Red light | 0.145 | 0.748 | 0.102 | 0.004 | 0.011 | 0.105 | 0.793 | 0.067 | 0.976 | 0.180 |
| *PS II-Particles + α-Tocopherol* | | | | | | | | | | |
| White light | 0.127 | 0.812 | 0.063 | 0.002 | 0.001 | 0.000 | 0.714 | 0.034 | 0.749 | 0.647 |
| Blue light | 0.125 | 0.831 | 0.052 | 0.007 | 0.017 | 0.009 | 0.607 | 0.041 | 0.674 | 0.708 |
| Red light | 0.116 | 0.819 | 0.063 | 0.012 | 0.088 | 0.001 | 0.735 | 0.231 | 1.055 | 0.460 |
| *PS II-Particles + Tocoquinone* | | | | | | | | | | |
| White light | 0.128 | 0.806 | 0.066 | 0.001 | 0.003 | 0.034 | 0.750 | 0.146 | 0.933 | 0.401 |
| Blue light | 0.119 | 0.837 | 0.048 | 0.004 | 0.000 | 0036 | 0.758 | 0.035 | 0.829 | 0.552 |
| Red light | 0.130 | 0.788 | 0.069 | 0.013 | 0.818 | 0.310 | 0.719 | 0.376 | 2.223 | 0.295 |
| *PS II-Particles + Plastoquinone-A* | | | | | | | | | | |
| White light | 0.191 | 0.762 | 0.047 | 0.000 | 0.000 | 0.000 | 0.715 | 0.000 | 0.715 | 0.760 |
| Blue light | 0.185 | 0.757 | 0.053 | 0.006 | 0.000 | 0.000 | 0.666 | 0.000 | 0.666 | 0.829 |
| Red light | 0.168 | 0.781 | 0.060 | 0.010 | 0.131 | 0.135 | 0.797 | 0.007 | 1.070 | 0.863 |
| *PS II-Particles + Plastoquinone-A + α-Tocopherol* | | | | | | | | | | |
| White light | 0.199 | 0.732 | 0.073 | 0.005 | 0.000 | 0.000 | 0.759 | 0.007 | 0.766 | 0.785 |
| Blue light | 0.151 | 0.768 | 0.076 | 0.005 | 0.000 | 0.000 | 0.687 | 0.000 | 0.687 | 0.992 |
| Red light | 0.168 | 0.750 | 0.064 | 0.003 | 0.004 | 0.004 | 0.875 | 0.095 | 0.978 | 0.616 |
| *PS II-Particles + Plastoquinone-A + a-Tocoquinone* | | | | | | | | | | |
| White light | 0.167 | 0.772 | 0.057 | 0.004 | 0.000 | 0.088 | 0.730 | 0.125 | 0.943 | 0.777 |
| Blue light | 0.170 | 0.782 | 0.045 | 0.003 | 0.000 | 0.002 | 0.715 | 0.017 | 0.734 | 0.848 |
| Red light | 0.180 | 0.771 | 0.048 | 0.001 | 0.460 | 0.077 | 0.755 | 0.367 | 1.659 | 0.542 |


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