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Stimulation of Photoreactions of Isolated Chloroplasts by Serum Albumin

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Abstract. **Serum albumin was shown to stimulate markedly various photoreactions in isolated bean and lettuce chloroplasts. The maximal effect was obtained when this compound was present during the homogenization step and continuously in the chloroplast preparation. The "basal" electron transport was enhanced using various acceptors and stimulation was obtained also in the presence of uncouplers. The quantum requirement for ferricyanide reduction was appreciably reduced. Serum albumin increased the rate of cyclic phosphorylation and the ratio of P/e_2 in non-cyclic phosphorylation. The increase in phosphorylation is supposedly due to inhibition of the rate of decay of the high energy non-phosphorylated intermediate, X_E.**

It is postulated that serum albumin affects chloroplast photoreactions by binding endogenously released unsaturated fatty acids.

The rates of electron transport and ATP formation of chloroplasts isolated from various plants differ appreciably (6, 10, 17), possibly because of the release of interfering substances during homogenization. Bean leaves, when homogenized at pH 6.0 release large quantities of linolenic acid, which totally inhibits normal chloroplast photoreactions (16). Although bean chloroplasts isolated at pH 8.0 exhibit Hill reaction and cyclic phosphorylation activities (15, 16), no phosphorylation coupled to non-cyclic electron flow has been reported to date for this preparation. We found that serum albumin markedly stimulated various photoreactions of bean chloroplasts. A stimulatory effect was also obtained with lettuce chloroplasts which were shown to have good activities even in the absence of this additive (9, 20). Serum albumin was added to chloroplast preparations by other workers previously (7, 13, 23), but its mode of action was not studied in detail. Recently and independently it was shown to be very effective in preserving the activity of isolated chloroplasts stored *in vitro* (26).

Materials and Methods

Bean plant var. Brittle wax were grown either in a greenhouse or in a growth room at 25°, illuminated by 250 watt mercury lamps at a distance of 80 cm with a photoperiod of 12 hours, for 2 to 3 weeks. Only the primary leaves were used for preparation of chloroplasts. Ten g of leaves were blended in a Waring Blendor for 15 seconds at 100 volts in 100 ml of medium containing 0.4 M sucrose, 0.01 M NaCl and 0.01 M tris (pH 8.0). The homogenate was filtered through gauze and centrifuged at low speed. The chloroplast pellet was then collected by centrifuging for 7 minutes at 2000 × *g*. It was finally resuspended in the original medium at a concentration of 250 μg chlorophyll/ml. Lettuce chloroplasts were prepared from leaves of *Lactuca sativa* var. romaine, bought at the market. These chloroplasts were prepared essentially as above, but the homogenizing medium contained in addition 50 mM ascorbate. The chloroplast pellet was washed once in the homogenizing medium, or in the homogenizing medium without ascorbate when ferricyanide reduction was measured.

Serum albumin when added, unless specified otherwise, was present in the homogenizing and washing media at a concentration of 1 mg/ml and in the final suspension medium of the chloroplasts at a concentration of 10 mg/ml. Since 0.2 ml of chloroplast (unless stated otherwise) was transferred to a reaction mixture of 3 ml, the concentration of serum albumin in the latter, was about 0.7 mg/ml. Human serum albumin and bovine serum albumin were active approximately to the same extent in stimulating the various photoreactions, but egg albumin was inactive. In the reaction where X_E (12) was measured, only bovine serum albumin was used, because an impurity was present in human serum albumin which caused an increase in radioactive counts when the reaction mixture was transferred in the dark from pH 6.0 to 8.0.

Chlorophyll was determined according to the procedure of Arnon (1). The photoreactions were performed by illuminating the reaction mixtures by two 150 watt bulbs, shielded through a water bath, which provided 6500 foot candles at the level of the tubes.

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Ferricyanide reduction was measured by loss of absorbance at 420 nm of the deproteinized solution or by continuous recording in a Cary 14 spectrophotometer as described in legend of figure 1. DCPIP[2] reduction was followed by measuring the decrease in OD at 620 nm using a spectronic-20 spectrophotometer. NADP reduction was performed as following: the reduction was stopped by adding KOH to a final concentration of 0.25 M and the suspension was left for 10 minutes at room temperature. A predetermined amount of tris-HCl was added to bring the pH of the reaction mixture to pH 8.0 to 8.5. The suspension was centrifuged and a sample of the supernatant was placed in a cuvette containing 0.3 µmole of benzyl viologen and 45 µmoles tris (pH 7.8) in a total volume of 3.0 ml. The OD at 340 nm was measured, a saturating amount of NADPH diaphorase was added and the OD measured again after 10 minutes. The amount of NADPH was calculated from the difference in OD (M. Avron, personal communication). Ferredoxin was prepared from mangold leaves following the procedure of Hill and Bendall (11) up to and including the column fractionation on DEAE-cellulose. Phosphorylation was measured by following incorporation of ^{32}P into ATP (2).

Human serum albumin (Cohn's fraction V) was purchased from Magen David Adom, Plasma fractionation and drying plant, Jaffa, Israel. All other reagents were of analytical grade.

[2] Abbreviations: DCPIP, 2,6-dichlorophenolindophenol; tricine, tris (hydroxymethyl)methylglycine; PMS, phenazine methosulfate; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; FCCP, carbonyl cyanide *p*-trifluoromethyloxyphenylhydrazone.

Results

Serum albumin stimulated markedly the Hill reaction with DCPIP between pH 6.5 to 9.5. At pH 8.0, the stimulation was about 2-fold, and it was even more between pH 8.5 to 9.5 (both in tris and in tricine buffer) since in this range the rate of reduction of the control declined rapidly, whereas the rate of reduction in the presence of serum albumin was hardly affected. Serum albumin increased the uncoupled rate of DCPIP reduction in the presence of NH_4Cl, atebrin and FCCP (table I). FCCP at 2 µM was somewhat inhibitory in the control but it increased the rate of electron flow in the presence of serum albumin.

The stimulation of electron flow described so far was obtained at saturating light intensities. However, serum albumin stimulated electron transport markedly at low light intensities as well, reducing the quantum requirement for ferricyanide reduction with 640 nm exciting light from 8 to 4.5 (fig 1).

Table I. *Effect of Serum Albumin on the Rate of Reduction of DCPIP in the Presence of Uncouplers*

The reaction mixture contained in a total volume of 5 ml the following in µmoles: tris 100, pH 7.0; $MgCl_2$ 10 and DCPIP 0.125. It also contained bean chloroplasts equivalent to 30 µg chlorophyll. Serum albumin where indicated was added as described in Methods. Illumination was carried on for 1 minute.

Addition	DCPIP Reduction			
	— Serum albumin		+ Serum albumin	
	µmoles reduced/mg chlorophyll•hr	% Of control	µmoles reduced/mg chlorophyll•hr	% Of control
None	186	100	214	100
NH_4Cl, 2 mM	260	140	406	190
Atebrin, 50 µM	286	154	360	169
FCCP, 2 µM	140	75	300	140

Table II. *Effect of Serum Albumin on Electron Transport and Phosphorylation with Ferricyanide*

The reaction mixture contained the following in µmoles: buffer 100; NaCl 70; $MgCl_2$ 10; ferricyanide 1.8; P_i 10 and ADP 3, in a total volume of 3.0 ml. In addition, bean chloroplasts equivalent to 50 µg chlorophyll and ^{32}P 10^6 cpm. Illumination was performed for 3 minutes. Serum albumin was added as described in Methods.

Buffer	Serum albumin	Ferricyanide reduction	ATP Formation	P/e_2
		µmoles per mg chlorophyll per hr		
Tris, pH 8.0	—	224	32	0.29
	+	356	128	0.72
Tricine, pH 8.6	—	266	81	0.61
	+	480	212	0.88
Glycylglycine, pH 8.6	—	248	84	0.68
	+	505	248	0.98

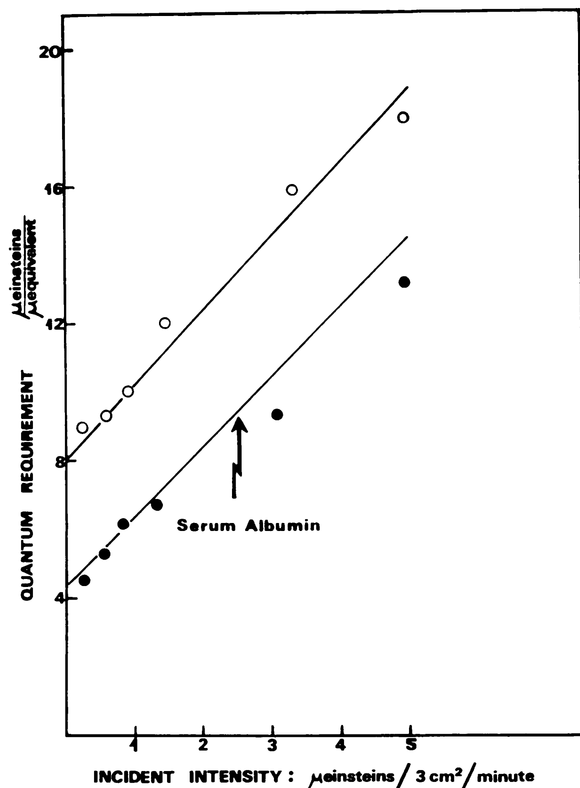

FIG. 1. The effect of serum albumin on ferricyanide reduction at 640 nm. The reaction mixture contained in 3.0 ml the following in µmoles: tricine 300 pH 8.3; NaCl 120 and ferricyanide 1. Lettuce chloroplast equivalent to 50 µg chlorophyll. Serum albumin added, as described in Methods. Ferricyanide reduction was measured by decrease in OD at 420 nm by continuous recording in a Cary 14 spectrophotometer. In the latter the actinic beam was provided by a 300 watt slide projector at a right angle to the measuring beam and passed through an interference filter with a half band width of 30 nm. The phototube was protected from the actinic beam by 2 blue filters (Corning No. 496 and No. 7-59). The maximal incident light intensity used was 1.5 × 10^5 erg cm^{-2} sec^{-1}, it was measured by an YSI Kettering wavelength independent Radiometer (model 65). The absorption of the chloroplast suspension was measured in an integrating (Ulbricht) sphere built by Dr. S. Malkin. ○ - control; ● - plus serum albumin.

This stimulation was obtained with lettuce chloroplasts which, unlike bean chloroplasts, show good rates of photoreactions even without serum albumin.

Serum albumin also enhanced the rate of electron transport in the presence of phosphorylating reagents (table II). The stimulations obtained were 59 % in tris buffer and 100 % in glycylglycine buffer. It should be noted, however, that the stimulation of ATP formation during ferricyanide reduction was greater than the stimulation of electron transport, resulting in a significant increase in P/e_2 (see Good *et al.* (8) for use of the notation P/e_2 in preference to P/2e). Similar results were obtained in NADP photoreduction and its coupled ATP formation (table III), but the relative effect of albumin in this reaction was even more striking.

The results of table IV show that serum albumin stimulated ATP formation with various cofactors considerably, both in bean chloroplasts and in lettuce

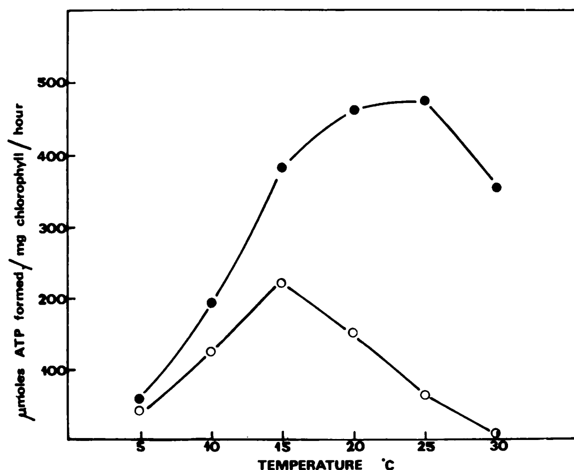

FIG. 2. The effect of serum albumin on cyclic phosphorylation at various temperatures. The reaction mixture contained the following in µmoles in 3 ml: tris 100 at pH 7.8; $MgCl_2$ 10; NaCl 70; ascorbate 30; P_i 10; PMS 0.09 and ADP 3. It also contained bean chloroplasts equivalent to 50 µg chlorophyll and ^{32}P 10^6 cpm. Serum albumin was added where indicated, as described in Methods. Illumination 3 minutes. ○—control; ●—plus serum albumin.

Table III. *Effect of Serum Albumin on NADP Photoreduction and its Coupled ATP Formation*

The reaction mixture contained in µmoles: tris 100, pH 7.8; NaCl 70; $MgCl_2$ 10; NADP 4.5; P_i 10 and ADP 3, in a total volume of 3 ml. In addition, bean chloroplasts equivalent to 50 µg chlorophyll, ^{32}P 10^6 cpm and saturating amounts of ferredoxin. Seventy-five µg protein of partially purified flavoprotein was added as indicated. The flavoprotein was purified, up to the second absorption step on the DEAE column (25). The fraction used contained 0.5 mµmole of flavoprotein per mg protein.

Addition	NADP Photoreduction	ATP Formation + NADP	ATP Formation − NADP	ATP/e_2	Corrected ATP/e_2 [1]
	µmoles per mg chlorophyll per hr				
None	5	2	1	0.4	0.2
Serum albumin	27	62	35	2.3	1.0
Serum albumin and flavoprotein	31	74	34	2.4	1.3

[1] Calculated after subtraction of the amount of ATP formed in the absence of NADP.

Table IV. *Effect of Serum Albumin on ATP Formation in the Presence of Various Cofactors*

The reaction mixture for bean chloroplasts contained the following in μmoles: tris 100, pH 7.8; NaCl 70; $MgCl_2$ 10; P_i 10; ADP 3, and where indicated PMS 0.09; pyocyanine 0.13; FMN 0.12; vitamin K_5 0.15, in a total volume of 3 ml. In addition, chloroplasts equivalent to 50 μg chlorophyll and ^{32}P 10^6 cpm. 30 μmoles ascorbate were added to the PMS and DCPIP reaction mixtures. The latter contained also 0.03 μmole of DCMU. Illumination was carried on for 3 minutes.

The reaction mixture for lettuce chloroplasts contained the following in μmoles: tricine 100 pH 8.5; NaCl 120; $MgCl_2$ 20; P_i 10 and ADP 4 in a total volume of 3 ml. In addition, chloroplasts equivalent to 50 μg chlorophyll and 10^6 cpm of carrier free ^{32}P. Also, where indicated, PMS was added at 50 μM and pyocyanine, FMN, or vitamin K_5 at 0.5 mM. DCPIP at 0.37 mM, ascorbate at 5 mM and in this reaction DCMU was present at 10 μM. Illumination was carried on for 2 minutes.

Serum albumin where indicated was added as described in Methods.

	ATP Formation					
	Bean chloroplasts			Lettuce chloroplasts		
Addition	— Albumin	+ Albumin	% Of Control	— Albumin	+ Albumin	% Of Control
	μmoles per mg chlorophyll per hr			*μmoles per mg chlorophyll per hr*		
None	7	25	355	61	59	97
PMS	387	456	120	915	1610	174
Pyocyanine	95	316	332	920	1350	147
FMN	17	82	484	350	525	150
Vitamin K_5	13	76	585	170	435	256
DCPIP-ascorbate	7	41	585	105	194	185

chloroplasts. The stimulating effect of serum albumin in cyclic phosphorylation with PMS is more pronounced at higher temperatures (fig 2).

ATP formation can be separated into 2 stages: a light stage where a high energy intermediate, X_E, is formed and a dark stage, the synthesis of ATP proper (12). Serum albumin when added in the light stage increased markedly the yield of X_E, but it had no effect when added in the dark stage (table V). The rate of formation of this intermediate is increased and the rate of its dark decay is decreased by serum albumin (fig 3).

Table V. *Effect of Serum Albumin on the Yield of* X_E

The assay of X_E was performed according to the procedure of Hind and Jagendorf (12). The pellet of bean chloroplasts was washed in sucrose 0.4 M, NaCl 0.01 M. The reaction mixture for the light stage contained in 2.3 ml the following in μmoles: tris-maleate 3 (for each), pH 5.5; NaCl 52; $MgCl_2$ 15 and PMS 0.18. Also, chloroplasts equivalent to 200 μg chlorophyll. The reaction mixture for the dark stage contained in 0.75 ml the following in μmoles: tris 60, pH 7.8; P_i 5 and ADP 0.6. Also 10^6 cpm of carrier free ^{32}P. 1.7 ml of the reaction mixture of the light stage were illuminated for 15 seconds in a syringe at a light intensity of 3000 foot candles and then transferred into the reaction mixture for the dark stage for 30 seconds. The incubation was terminated by addition of 0.3 ml trichloroacetic acid 30 % and a sample was taken for the determination of ATP. Serum albumin was present in the reaction mixture only.

Addition of serum albumin		X_E	
Stage added	mg in reaction mixture	mμmoles ATP formed/mg chlorophyll	% Of control
None	0	24	100
Light	0.33	33	138
Light	1.0	40	166
Light	3.0	40	166
Light	10.0	41	171
Dark	4.5	23	96

Linoleic and linolenic acids at 0.12 mM, when added to the light stage in the 2 stage reaction, using bean chloroplasts, inhibited X_E to the extent of 94 % and 96 % respectively. When added in the dark, the same concentration of fatty acid did not inhibit.

In order to obtain maximal stimulation, serum albumin has to be present during homogenization and continuously in the chloroplast suspension. When present during the photoreaction only, the stimulation is less. This was found to be true, both for lettuce chloroplasts (table VI) and bean chloroplasts (data not shown).

Discussion

Inhibition of chloroplast photoreactions, presumably due to inhibitors released during the isolation of chloroplasts was observed in several plant species (10, 17, 19), including *Phaseolus*. In the latter, photoreactions were strongly inhibited when chloroplasts were isolated at pH 6.0 (16) or when homogenized by mortar and pestle at pH 8.0 (15). It is possible that in bean chloroplasts the inhibitor is linolenic acid, since large amounts of this compound were shown to be present in chloroplast suspension isolated at pH 6.0, and smaller amounts were present even at pH 8.0 (16). Fatty acids

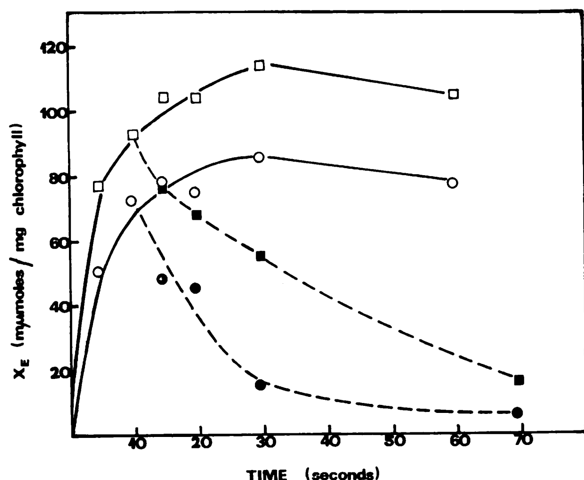

FIG 3. The effect of serum albumin on the rate of formation and decay of X_E. The formation of X_E was measured as described in table V, except that lettuce chloroplasts were used. The decay of X_E was measured following Hind and Jagendorf (12). The reaction mixture was illuminated, then transferred for various time intervals to darkness as indicated, and finally injected into the medium which contained the phosphorylating reagents at pH 7.8. Albumin when present was added as described in Methods, in the homogenizing and suspending media. Circles - no albumin added; squares - plus serum albumin; open symbols - amount of X_E after various time intervals of illumination; closed symbols - amount of X_E after 15 seconds of illumination and various time intervals of dark decay.

were indeed shown to be released enzymically from galactosyl diglycerides in bean leaves (24). When added exogenously, these compounds strongly inhibit ATP formation and electron transport (14, 16). Although several uncouplers were shown at higher concentrations also to inhibit electron transport (3), in some uncouplers these activities overlap to a considerable extent (21, 22). Linolenic acid belongs to this latter group (16).

It is likely that serum albumin stimulates the photoreactions by binding free unsaturated fatty acids, since serum albumin is well known to have such an activity (5). Recently, serum albumin was found also to bind phenols (27), which inhibit photoreactions in chloroplasts (20). However, the stimulatory effect of serum albumin was evident also in the presence of ascorbate (table IV) and this compound abolishes the inhibitory effect of endogenous phenols, presumably by maintaining them in the reduced state (J. Neumann, unpublished results).

The release of fatty acids presumably begins during homogenization since the addition of serum albumin at this stage is more effective than if present during the photoreaction only (table VI). Part of the fatty acids are probably bound irreversibly to the chloroplasts and therefore cannot be released when serum albumin is added to the chloroplasts only in the reaction mixture. The decrease in the rate of cyclic phosphorylation with moderate increase of temperature (fig 2), might be due to a faster release of fatty acids at higher temperatures.

The inhibitor, neutralized by serum albumin, seems to affect directly electron transport, since uncoupled electron flow is stimulated markedly by serum albumin (table I), as well as electron flow at low light intensities (fig 1). The fact that the stimulation does not decrease when the light intensity is increased (fig 1) may mean that the inhibitor interferes with a component which, when inactive, blocks the function of an entire photosynthetic unit. The true pH optimum for electron transport seems to be higher than usually reported. Serum albumin abolished the inhibition at high pH not only in the presence of tris which was shown to be inhibitory (28), but in the presence of tricine buffer as well.

ATP formation in the presence of various cofactors is considerably stimulated by serum albumin (table IV). It is not known whether this is due to an increase in the rate of cyclic electron flow, since the latter cannot be assessed. However, from the results of tables II, III, and VI it is obvious that serum albumin increases the rate of ATP formation not only by increasing the rate of noncyclic electron transport, but that it acts also at a site concerned more directly with phosphorylation, increasing the P/e_2 ratio. The marked inhibition of the rate of decay of the high energy intermediate

Table VI. *Sequential Addition of Serum Albumin to Chloroplasts*

The reaction mixture contained in 3.0 ml the following in μmoles: tricine buffer 100, pH 8.6; $MgCl_2$ 10; NaCl 70; ferricyanide 1.8; P_i 10 and ADP 3. Also, lettuce chloroplasts equivalent to 50 μg chlorophyll and ^{32}P 10^6 cpm. Human serum albumin when present during the photoreaction only, was added to a final concentration of 0.5 mg/ml (which was saturating under these conditions), the amount added during homogenization and subsequently to chloroplast suspension as described in Methods. Illumination was carried on for 3 minutes.

Serum albumin present	Ferricyanide reduced	ATP formed	ATP/e_2
	μmoles per mg chlorophyll per hr		
None	250	99	0.79
During photoreaction only	388	190	0.98
During homogenization, in chloroplast resuspending medium and photoreaction	752	447	1.19

X_E (fig 3), may indicate that the integrity of some chloroplast structure required for ATP synthesis is preserved. Serum albumin was indeed shown to affect conformational and or osmotic changes of chloroplasts (18). The inhibition of the yield of X_E by linoleic and linolenic acids when added in the light is probably due to stimulation of decay of the high energy intermediate. The fact that, when added in the dark, fatty acids do not inhibit and serum albumin does not stimulate the yield of X_E, may reflect the high efficiency at which X_E is trapped and converted to ATP in the final steps of phosphorylation.

The effect of serum albumin in increasing the P/e_2 ratio of isolated chloroplasts resembles its action in mitochondria where it was shown to eliminate uncoupling by binding free fatty acids (4).

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