## Title

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# ACTION SPECTRUM AND QUANTUM REQUIREMENTS FOR THE PHOTOREDUCTION OF CYTOCHROME c WITH SPINACH CHLOROPLASTS*

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ABSTRACT: The photoreduction of cytochrome c in the presence of intact chloroplasts occurs with a high quantum efficiency, using reduced trimethyl-p-benzoquinone ($TMQH_2$) as reductant and in the presence of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU). This reaction has a requirement of 2 quanta absorbed per electron transferred to cytochrome c for exciting light in the wavelength region from 620 to 680 mμ; the quantum requirement then falls to 1 quantum per electron at wavelengths greater than 700 mμ. These results confirm the conclusion of Vernon and Shaw (1965) that this redox reaction is mediated by chloroplast pigment system I in the presence of DCMU. The quantum requirement of unity observed at long wavelengths shows that the reaction probably occurs with the maximum efficiency obtainable.

The evaluation of the action spectrum for cytochrome c reduction together with that for the chloroplast Hill reaction, photocatalyzed by pigment system II (Sauer and Park, 1965), strongly suggests that there is no appreciable transfer of electronic excitation energy between the two pigment systems in spinach chloroplasts. The two light reactions apparently interact only at the chemical level of photosynthetic electron transport. A model is presented which rationalizes this conclusion by the physical separation of the two pigment systems on opposite sides of the chloroplast lamellar unit.

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The recent studies of Vernon and Shaw (1965) demonstrated that the photoreduction of cytochrome c by whole chloroplasts is stimulated by the addition of various hydroquinones, including reduced trimethyl-p-benzoquinone ($TMQH_2$).[1] The stimulation is only partially decreased in the presence of DCMU, a potent inhibitor of oxygen evolution by chloroplasts. This finding suggested to Vernon and Shaw that these hydroquinones serve as electron donors for the long-wavelength pigment system I of chloroplasts.

The present investigation seeks to determine by means of its action spectrum whether this photoreduction is a system I reaction. The evidence strongly suggests that such is the case, and the data are used to derive the spectral absorption of pigment system I. The action spectrum for cytochrome c reduction by chloroplasts is found to be similar to that reported previously for the photoreduction of NADP with $DCPIPH_2$ and ascorbate in the presence of DCMU--a known system I reaction. (Hoch and Martin, 1963; Sauer and Biggins, 1965). Furthermore, the consideration of the action spectrum for cytochrome c reduction together with that for the chloroplast Hill reaction (Sauer and Park, 1965)--a system II reaction--provides strong evidence to support the hypothesis that there is no transfer of electronic excitation energy between the two pigment systems in spinach chloroplasts.

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[1]Abbreviations: $TMQH_2$, reduced trimethyl-p-benzoquinone; NADP ($NADPH_2$), nicotinamide adenine dinucleotide phosphate; DCPIP ($DCPIPH_2$), 2,6-dichlorophenolindophenol; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea.

Materials and Methods

Chloroplasts were prepared either from fully grown commercial spinach leaves or from 6-8 week-old plants grown from seed in a growth chamber, as described previously (Sauer and Park, 1965). Horse heart cytochrome c, obtained from Sigma Chemical Co., St. Louis, was dried under vacuum over $Mg(ClO_4)_2$. Samples of the dried cytochrome were oxidized with ferricyanide and reduced with dithionite, and a $\Delta\varepsilon^{red-ox}_{549.5\ m\mu}$ of $1.9 \times 10^4$ $\ell$-mole$^{-1}$-cm$^{-1}$ was observed. This is in good agreement with values of $1.9\text{-}2.1 \times 10^4$ $\ell$-mole$^{-1}$-cm$^{-1}$ in the literature (Paléus and Nielands, 1950; Massey, 1959). DCMU was obtained from duPont de Nemours, Wilmington.

$TMQH_2$ was prepared by reduction of TMQ (K & K Laboratories, Jamaica, N. Y.) with dithionite in a two-phase reaction mixture of water and toluene. Further purification was achieved by crystallization of the $TMQH_2$ from toluene or diethyl ether followed by sublimation in vacuo. A partial reoxidation to TMQ was observed in air either upon recrystallization or upon solution of the solid $TMQH_2$ in ethanol to prepare the reagent solution. Thus, the reaction mixture contained some TMQ at the start of the photoreaction.

Reaction rates were obtained by continuously monitoring the absorbance of the reaction mixture at 549.5 mμ (the α-band maximum for cytochrome c) while the sample was being irradiated from the side with longer-wavelength light. A Cary Model 14 spectrophotometer with a modified Model 1462 scattered-transmission accessory was used, as described by Sauer and Biggins (1965). Exciting light was obtained from a Bausch and Lomb monochromator with supplementary cut-off filters; and light intensity measurements, corrected for reflection losses,

were made using a calibrated photovoltaic cell.

The reaction mixture contained potassium phosphate, pH 7.5, 0.05 M; sucrose, 0.1 M; and the following in μmoles per liter: cytochrome c, 50; $TMQH_2$, 85; and DCMU, 0.9. (The $TMQH_2$ and DCMU were made up in ethanol solutions, which were diluted 100- and 200-fold, respectively, in the reaction mixture.) A sufficient amount of the chloroplast preparation was added in the dark at the start of each measurement to give an absorbance of chlorophyll at 678 mμ of 0.3 to 0.7 for a 1 cm path. It was found that a solution containing cytochrome c and $TMQH_2$ becomes deactivated slowly upon standing in the dark; consequently, a fresh reaction mixture (2 ml) was prepared for each wavelength of exciting light studied. Altogether, seven different chloroplast preparations were used in the study. These generally exhibited no loss in activity for periods up to 5 hours in the dark at 0° C. All measurements were made in air, except where noted, and at room temperature. In no case was the photoreaction carried to more than 15% conversion of the cytochrome c.

Results

The photoreduction was studied as a function of light intensity over a 5- to 30-fold range at each of 24 wavelengths in the region from 620 to 740 mμ. At each wavelength, the calculated quantum requirements were found to increase somewhat with increasing incident light intensity. As in previous studies (Sauer and Biggins, 1965; Sauer and Park, 1965), the measured quantum requirements were extrapolated linearly to zero light intensity. The zero intensity quantum requirements are

summarized as a function of wavelength in Fig. 1 for the two chloroplast preparations studied most extensively. Three other preparations gave results in excellent agreement with these; in the other two there was a partial inactivation of the chloroplasts during the isolation procedure and quantum requirements about twice as large were obtained, but with the same wavelength dependence.

The system usually exhibits a fairly strong back-reaction in the dark following illumination, although for two preparations of chloroplasts it was virtually absent. The rate of the back-reaction, when it occurred, was proportional to the percentage conversion of the cytochrome c, and all photochemical rates reported are corrected for the appropriate interpolated dark reaction. An attempt to reduce this back-reaction by purging the reaction mixture with nitrogen proved unsuccessful; no change in rates of either the back-reaction or the photoreduction was observed.

A reaction mixture in which the chloroplasts had been heated to 65° C for 3 in, conditions known to destroy system I activity (Vernon and Zaugg, 1960; Rumberg and Witt, 1964), exhibited no cytochrome c photoreduction when it was illuminated at 680 mμ. This is taken as an indication that the photoreduction requires the integrity of the chloroplast structure and not just the presence of the pigments.

Methyl amine is known to uncouple the chloroplast Hill reactions from photophosphorylation and to lower the quantum requirements for the Hill reaction at moderate light intensities (Sauer and Park, 1965). In the case of cytochrome c reduction, however, methyl amine (10 $\mu$moles-ml$^{-1}$) had no effect on the rates of either the photoreduction or the back-reaction.

Discussion

On the basis of their observation that the photoreduction of cytochrome c by $TMQH_2$ in the presence of chloroplasts is largely DCMU-insensitive, Vernon and Shaw (1965) proposed that in the presence of DCMU the reaction is catalyzed by pigment system I. The action spectrum presented in Fig. 1 of this paper strongly supports their conclusion. The action spectrum has a fairly constant zero-intensity quantum requirement of 2 quanta absorbed per equivalent of cytochrome c reduced for wavelengths from 620 to 680 mμ. At longer wavelengths there is a decrease in quantum requirement to 1.0 quantum per equivalent at about 710 mμ, which remains constant to 740 mμ. The very high efficiency (low quantum requirement) at wavelengths longer than 700 mμ is a characteristic feature of system I--catalyzed reactions by higher plant chloroplasts. It differs strongly from the action spectrum of the Hill reaction using DCPIP or ferricyanide, where the quantum requirement is 2-3 from 640 to 680 mμ and then increases as much as 10-fold at wavelengths longer than 690 mμ (Sauer and Park, 1965). The action spectrum for cytochrome c reduction by chloroplasts is similar to that for the chloroplast catalyzed photoreduction of NADP by ascorbate coupled with a small amount of $DCPIPH_2$ and in the presence of DCMU (Hoch and Martin, 1963; Sauer and Biggins, 1965). The ascorbate/$DCPIPH_2$ couple provides electrons in lieu of water and does not, apparently, require the participation of pigment system II.

The quantum requirements for the cytochrome c - $TMQH_2$ reaction are uniformly lower than those observed previously for NADP reduction using ascorbate/$DCPIPH_2$, and we feel that the former are more representative of the

optimum photochemical potentiality of pigment system I. On the basis of the best evidence available from the literature it seems that the cytochrome c - $TMQH_2$ photoreduction is an energy-storing reaction which requires more than just a suitable catalyst in order to proceed. E' for ferro-ferricytochrome c is +0.26 v from pH 2 to 7.8 (Rockey and Ball, 1950), whereas E° for $TMQH_2$-TMQ is 0.527 v. (Clark, 1960). At pH 7.5, where the present measurements were carried out, $E°_{pH\ 7.5}$ is calculated to be -0.18 v for the $TMQH_2$ - ferricytochrome reaction. Thus, the position of equilibrium lies in the direction of reactants and an appreciable extent of reaction of $TMQH_2$ with ferricytochrome can occur only by means of energy provided by the chloroplast light reactions. As a consequence, this photoreaction cannot be a photo-catalyzed chain reaction, and it must obey the Einstein law of photo-chemical equivalence. The cause of the higher quantum requirements of Sauer and Biggins (1965) for NADP reduction is unknown, but some contributing factors can be postulated. It is possible that a cyclic as well as a non-cyclic pathway exists for electron transport between NADP and the $DCPIPH_2$/ascorbate couple. In the cyclic pathway, $NADPH_2$ would react with DCPIP/dehydroascorbate to complete the cycle and the net reduction of NADP would consequently be decreased. This would serve to increase the observed quantum requirement from that resulting from the non-cyclic pathway alone. It has been reported that ferredoxin, which is an essential cofactor for the NADP photoreduction by chloroplasts, can mediate cyclic photosynthetic electron transport (Tagawa, Tsujimoto and Arnon, 1963; Arnon, Tsujimoto and McSwain, 1964). Other factors which are possible causes of the lower efficiency of this photoreaction are the different source of spinach used by Sauer and

Biggins, the difficulty in characterizing accurately the chloroplast ferredoxin/ferredoxin-NADP reductase preparation (PPNR), and the unexplored effects associated with the uncoupling of photophosphorylation from the NADP reduction.

The presence of a cyclic pathway seems to us to be the most likely explanation; however, further studies are required to clarify this question.

Fig. 2 shows activation spectra obtained by the technique of Sauer and Park (1965) of multiplying the observed zero-intensity quantum yields (reciprocal of the quantum requirement) at each wavelength by the normalized total absorbance of spinach chloroplasts. The activation spectra obtained in this way represent the absorption spectra of the "active pigments"; i.e., that portion of the total pigments responsible for the sensitization of the particular photoreaction being studied. The experimental points (○) and the dashed curve through them summarize the results of this study on the cytochrome c - $TMQH_2$ reaction. The activation spectrum for the Hill reaction using DCPIP (Sauer and Park, 1965) is also presented in Fig. 2 for comparison (△, solid curve). The differences between these two activation spectra are most pronounced at wavelengths longer than 680 mμ, where the former spectrum is virtually identical with the normalized absorption spectrum (topmost curve in Fig. 2) and the latter activation spectrum is nearly zero. In addition, the maximum of the cytochrome c - $TMQH_2$ activation spectrum (system I) occurs at about 680 mμ, whereas the maximum of the DCPIP Hill reaction activation spectrum (system II) is nearer 675 mμ. The differences in the region of maximal chlorophyll b absorption (ca. 650 mμ) are slight. It

would be hazardous to assign chlorophyll b primarily to pigment system II on the basis of the evidence of Fig. 2.

One additional curve, representing the sum of the system I and system II activation spectra, is presented in Fig. 2. This synthesized spectrum is seen to be very similar, both in shape and magnitude, to the observed absorption spectrum, giving strong confirmation to the proposal of Sauer and Park (1965) that the activation spectra are really the absorption spectra of the respective pigment systems, and that the sum of the activation spectra is simply the overall measured absorption spectrum. This would not necessarily be the case if there were appreciable transfer of electronic excitation energy from one pigment system to the other. To the extent that this occurs in any wavelength region, each photoreaction can utilize quanta absorbed by both pigment systems and its potential efficiency would be raised. When the activation spectra for a system I and for a system II reaction are then added, one would anticipate the possibility that the sum would be appreciably greater than the absorption spectrum, particularly in the wavelength region from 620 to 685 mμ where both systems appear to absorb comparably.

An alternative method of analyzing the results is presented in Table I, where quantum yields for the cytochrome c reduction and for the DCPIP-Hill reaction are tabulated at the various wavelengths of exciting light. In the last column of Table I are given values for the sum of the quantum yields for the system I and system II reactions at each wavelength. If electronic energy transfer were possible between the two pigment systems, the sum of quantum yields for their respective reactions could be as high as 2 at some wavelengths. If no electronic

energy transfer is possible, then the sum cannot be greater than 1.0 at any wavelength. The data in the last column of Table I are quite clear on this point. The values observed are all 1.0 ± 0.1 in the wavelength region from 620 to 740 mμ, with the exception of the region around the absorption maximum at 678 mμ, where the sum falls to 0.83. (We now have evidence that the low values in this region result from the monochromator band halfwidth of 10 mμ used routinely in these and the previous studies. In this particular region of the spectrum, the sample is appreciably more transparent to light in the wings of the band of wavelengths incident on it than to those near the center. Consequently, the fraction of light absorbed by the sample tends to be overestimated somewhat in our calculations. The correction is not larger than that required to bring the quantum yield sum to a value of 1.0, however.)

It might be argued that one or the other, or both, reactions are proceeding well below optimal efficiencies and that energy transfer aids in bringing the yields up to the levels observed. The finding that the sum of quantum yields is within about 10% of unity over such a wide wavelength range would then be a fortuity defying any simple explanation. We have every reason to believe that the cytochrome c - $TMQH_2$ reaction is, in fact, operating at optimum efficiency, since only one absorbed quantum is required for each electron transferred at wavelengths longer than 700 mμ. It is not easy to postulate a simple mechanism whereby this intrinsic quantum yield is then reduced to 0.5 at shorter wavelengths, at the same time permitting efficient electronic energy transfer to occur. The authors believe that the simplest explanation lies in the postulate that electronic energy transfer can occur

only within each pigment system and not between them, and that the coupling of the two pigment systems occurs only at the chemical level.

This postulate is not one which is necessarily obvious a priori. It is known that electronic excitation can be transferred over fairly large distances (30-40 Å) between molecules of chlorophyll a in solution (Watson and Livingstone, 1950; Weber, 1960). There is no good reason to believe that such processes would not be possible in vivo as well. It may be that the absorption and emission oscillators of the pigment molecules of the two pigment systems in vivo are oriented unfavorably with respect to one another, in such a manner that radiative transfer has a low probability. This proposal seems unlikely in view of the failure to observe any strong orientation of the bulk of the pigment molecules in chloroplasts or active lamellar fragments isolated from them, using the tests of fluorescence polarization (Arnold and Meek, 1956; Goedheer, 1957), or dichroism (Goedheer, 1955; 1957; Olsen, Butler and Jennings, 1962; Sauer and Calvin, 1962; Sauer, 1965). A much simpler explanation is that the two pigment systems are physically separated in vivo by a distance greater than 30-40 Å, and that the medium separating them is one which does not especially facilitate the transfer of electronic excitation energy, particularly for those excited states produced by the absorption of wavelengths longer than 600 mμ.

A model for pigment ordering within the chloroplast, consistent both with the requirement of separated pigment systems and with the current picture of chloroplast lamellar structure, especially as elucidated by the electron microscope studies of Park and coworkers

(Park and Pon, 1961; 1963; Park and Biggins, 1964; Park, 1965), is shown in Fig. 3. The model consists of a lamellar array of the order 100 Å thick made up of a planar assembly of quantasome particles, with the molecules of the two pigment systems imbedded on opposite faces of the planar array and separated by a matrix containing protein and colorless lipid. Separations of at least 30-40 Å would be perfectly feasible in such a model. The intervening lipoprotein matrix would contain many of the intermediate cofactors (cytochromes, quinones, plastocyanin, phosphorylation sites, etc.) which couple the two pigment systems at the chemical level. If adjacent lamellae are in an anti-parallel arrangement, indicated in the model and strongly suggested by the electron microscopic studies, then the model has the additional advantage of providing for the physical separation of the powerful reductants (chloroplast ferredoxin, $NADPH_2$) normally produced by pigment system I reactions and the powerful oxidants (molecular oxygen, etc.) which are products of pigment system II reactions. Any direct coupling between these products by what would be a highly exothermic dark reaction would constitute a dissipative process which would sericusly reduce the efficiency of photosynthetic energy conversion.

Other models are possible. For example, if the respective pigment systems were always separately located on quantasomes in different regions of the lamellar array, which is consistent with the views of Olson, Butler and Jennings (1961) and of Gross, Becker and Shefner (1964), the requisite separation in space would be accomplished. We know of no compelling evidence, either morphological or photochemical, in support of this hypothesis. On the other hand, it seems to make the problem of chemical

communication between the two pigment systems that much more difficult.

The anti-parallel lamellar hypothesis illustrated in Fig. 3, where the pigment systems are on opposite sides of the same quantasomes and the central region provides the principal pathway of chemical communication between them, appeals to us as being simple conceptually and compatible with the notion of the chloroplast as an array of photosynthetic units roughly the size of quantasomes.

Acknowledgments

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TABLE I: Quantum Yields for Cytochrome c Reduction by $TMQH_2$ and for the DCPIP Hill Reaction of Spinach Chloroplasts at Various Wavelengths

| Wavelength (mμ) | Quantum Yields (equivalents/einstein absorbed) | | |
|---|---|---|---|
| | $\phi_{Cyt}$ | $\phi_{DCPIP}$[a] | $\phi_{Cyt} + \phi_{DCPIP}$ |
| 622 | 0.50 | | |
| 630 | 0.50 | | |
| 635 | 0.50 | 0.44 | 0.94 |
| 639 | 0.50 | 0.49 | 0.99 |
| 642 | 0.50 | 0.50 | 1.00 |
| 648 | 0.50 | 0.51 | 1.01 |
| 650 | 0.49 | 0.52 | 1.01 |
| 653 | 0.49 | 0.51 | 1.00 |
| 660 | 0.48 | 0.48 | 0.96 |
| 666 | 0.48 | 0.42 | 0.90 |
| 670 | 0.47 | 0.39 | 0.86 |
| 675 | 0.46 | 0.38 | 0.84 |
| 678 | 0.46 | 0.37 | 0.83 |
| 680 | 0.48 | 0.36 | 0.84 |
| 683 | 0.53 | | |
| 685 | 0.58 | 0.30 | 0.88 |
| 690 | 0.72 | 0.26 | 0.98 |
| 695 | 0.83 | 0.18 | 1.01 |
| 700 | 0.88 | 0.13 | 1.01 |
| 704 | 0.94 | | |
| 710 | 1.00 | 0.08 | 1.08 |

(Continued)

TABLE I (Continued)

| Wavelength (mμ) | Quantum Yields (equivalents/einstein absorbed) | | |
|---|---|---|---|
| | $\phi_{Cyt}$ | $\phi_{DCPIP}$[a] | $\phi_{Cyt} + \phi_{DCPIP}$ |
| 720 | 1.00 | 0.08 | 1.08 |
| 730 | 1.00 | 0.04 | 1.04 |
| 740 | 1.00 | | |

[a] Data taken from the results of Sauer and Park (1965).

## Legends for Figures

Figure 1: Action spectrum for the reduction of cytochrome c by $TMQH_2$ using spinach chloroplasts (2 different preparations). The quantum requirements are values obtained from extrapolations to zero light intensity at each wavelength.

Figure 2: Absorption spectra of pigments responsible for cytochrome c reduction by $TMQH_2$ in presence of DCMU (●, and lower dashed curve) and for the DCPIP Hill reaction (▲, and lower solid curve; data from Sauer and Park, 1965) by spinach chloroplasts. Upper solid curve gives the normalized absorption spectrum of spinach chloroplasts, corrected for light scattering (Sauer and Biggins, 1965). Upper dashed curve is the sum at each wavelength of the two lower curves.

Figure 3: A model of a cross-section of the chloroplast lamellar system, showing a proposed physical separation of the two pigment systems and of the products of their photoreactions. Portions of several identical quantasome units are sketched.

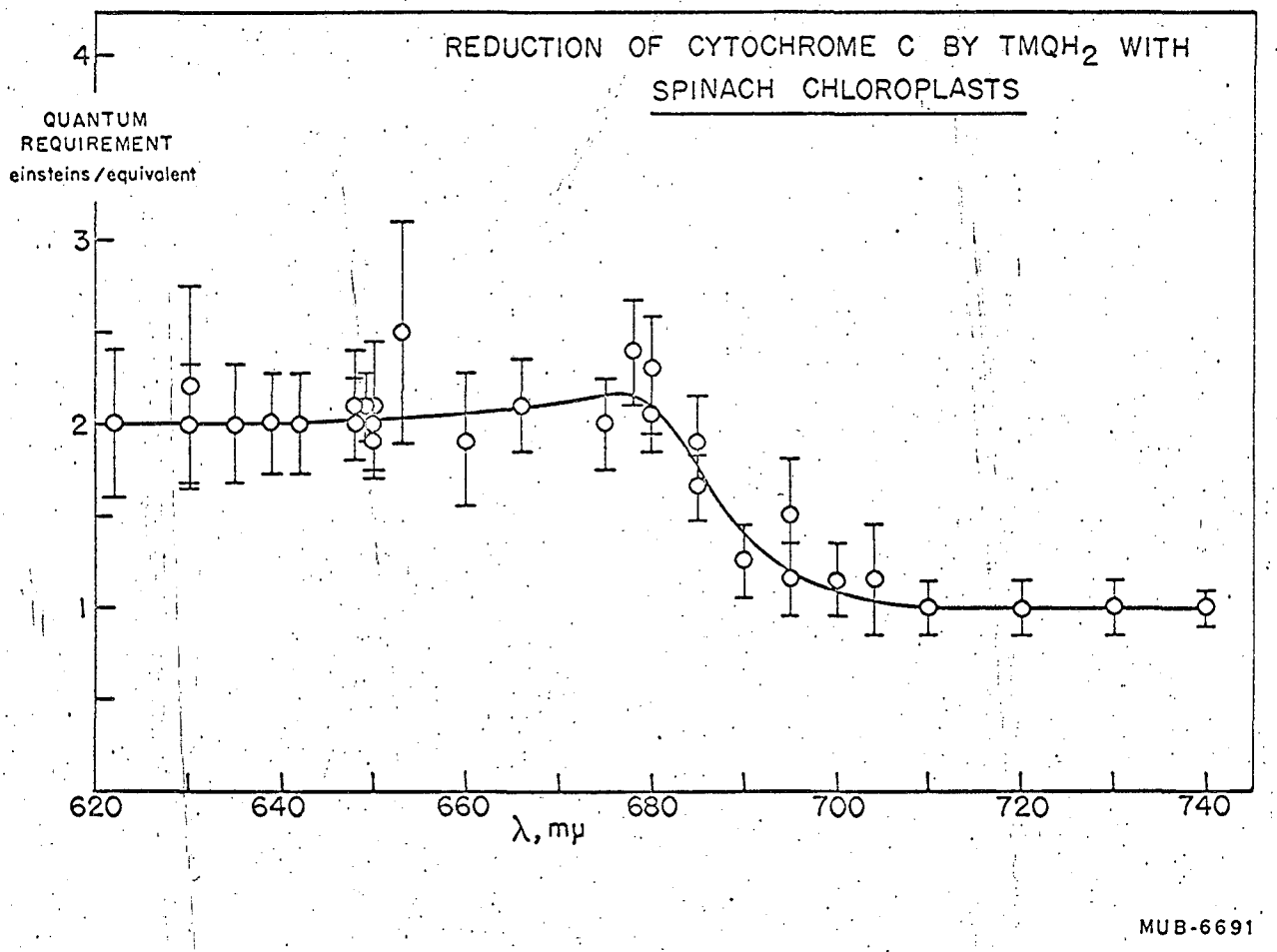
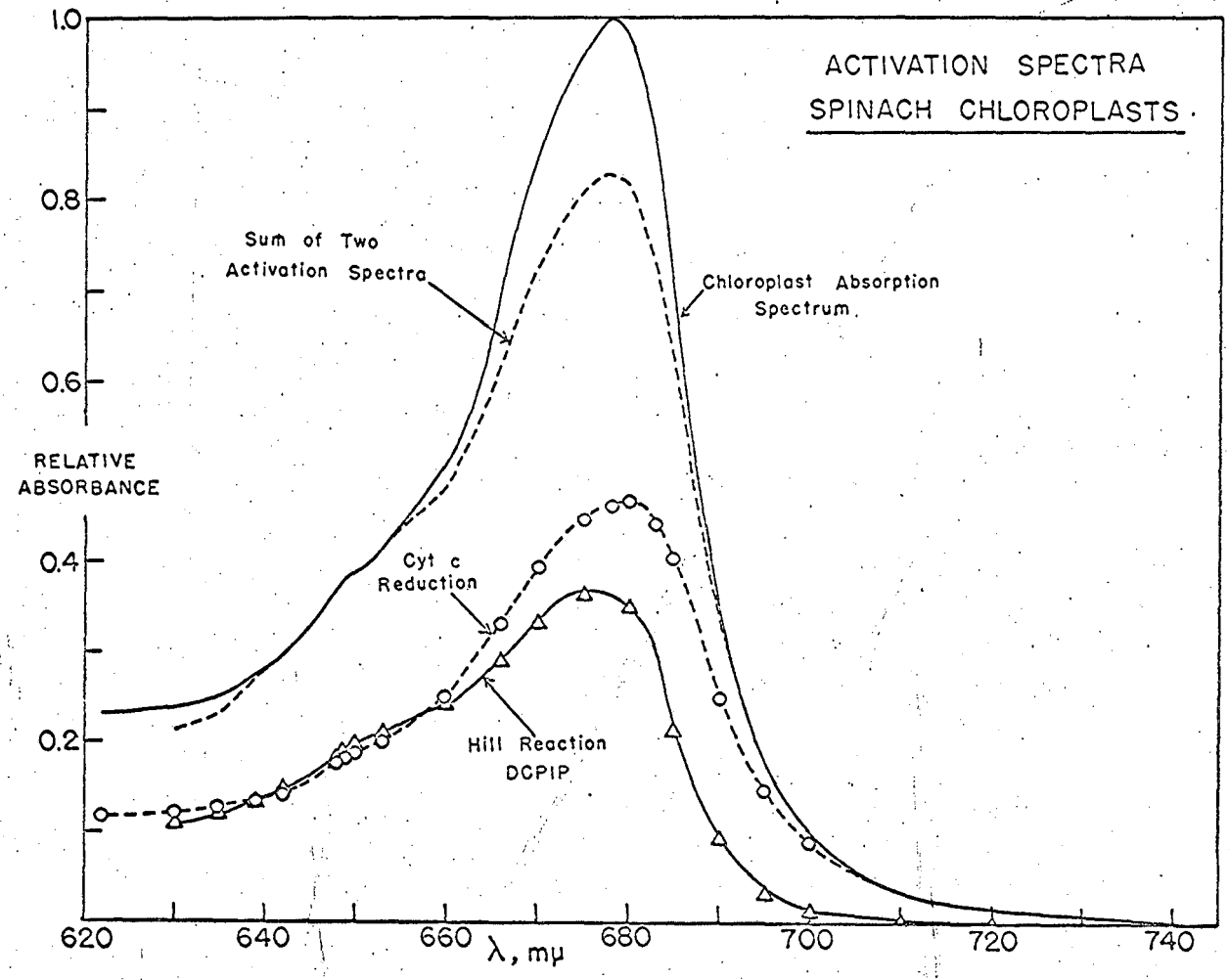

REDUCTION OF CYTOCHROME C BY TMQH2 WITH
SPINACH CHLOROPLASTS
QUANTUM
REQUIREMENT
einsteins/equivalent
4
3
2
1
620
640
660
680
700
720
740
λ, mμ
MUB-6691

Fig. 1




MUB-6692

Fig. 2

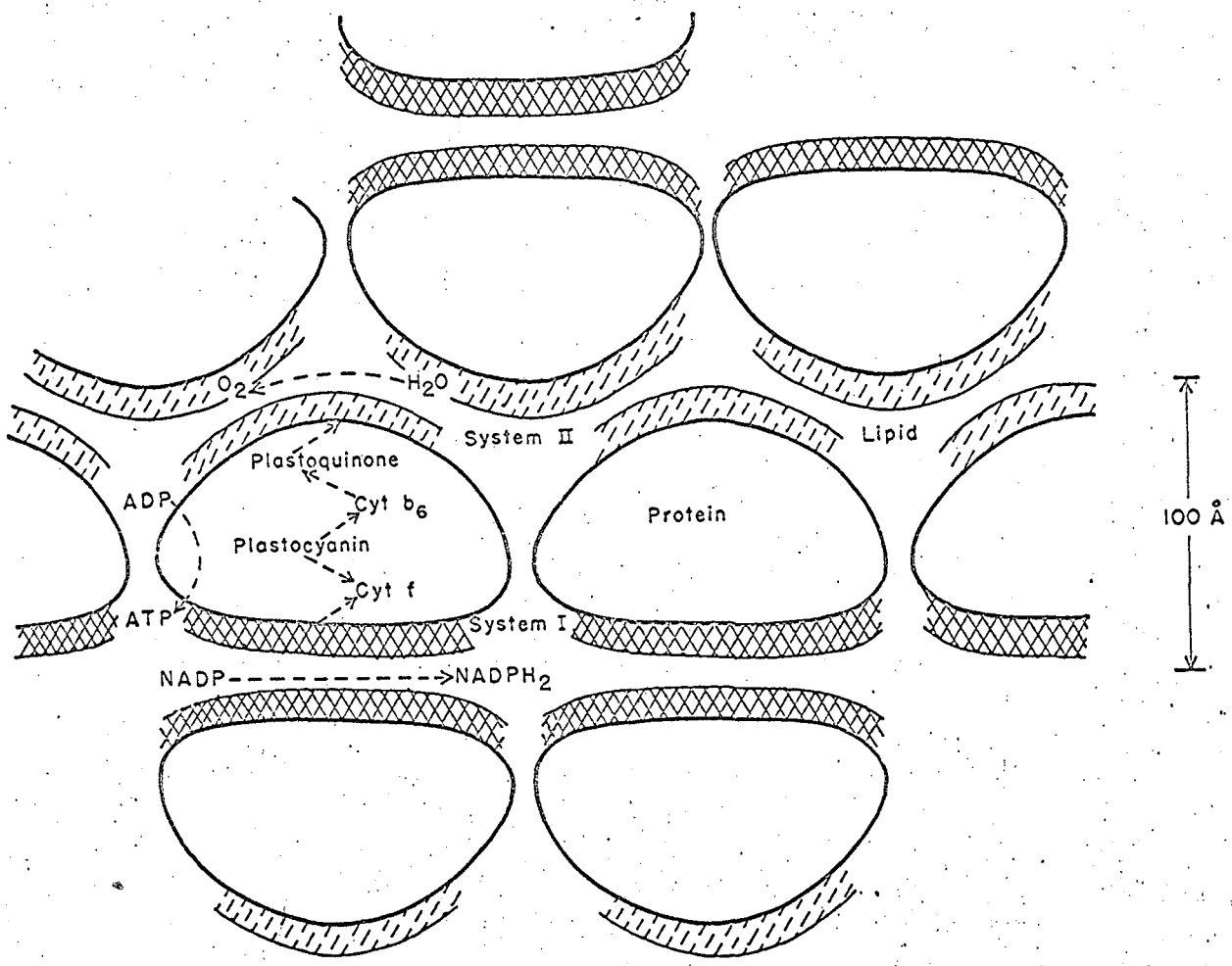

$O_2$
$H_2O$
System II
Lipid
Plastoquinone
ADP
Cyt $b_6$
Protein
Plastocyanin
Cyt f
ATP
System I
NADP
$NADPH_2$
100 Å
MUB-6796

Fig. 3