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PHOTOCHEMICAL ENERGY CONVERSION BY MEMBRANE-BOUND PHOTOREDOX SYSTEMS

Progress Report

for the Period July 1, 1989 to March 1, 1992

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INTRODUCTION

Most of our effort during the past grant period has been directed towards investigating electron transfer processes involving redox proteins at lipid bilayer/aqueous interfaces. This theme, as was noted in our previous three year renewal proposal, is consistent with our goal of developing biomimetic solar energy conversion systems which utilize the unique properties of biological electron transfer molecules. Thus, small redox proteins such as cytochrome c, plastocyanin and ferredoxin function in biological photosynthesis as mediators of electron flow between the photochemical systems localized in the membrane, and more complex soluble or membrane-bound redox proteins which are designed to carry out specific biological tasks such as transbilayer proton gradient formation, dinitrogen fixation, ATP synthesis, dihydrogen synthesis, generation of strong reductants, etc. In these studies, we have utilized two principal experimental techniques, laser flash photolysis and cyclic voltammetry, both of which permit direct measurements of electron transfer processes.

All previous agreement requirements have been complied with. The Principal Investigator (G. Tollin) has devoted approximately 20% of his time during the academic year, and 50% of his time during the summer, to this project. This level of effort will continue during the remainder of the current term.

Fourteen full-length papers have been published, are in press, or have been submitted as a consequence of work done during this grant period (see listing below). Reprints and preprints are attached to this Report. We believe that we have made extraordinary progress over the past three years in developing biomimetic systems for photochemical energy

storage. Especially noteworthy are the following accomplishments: **i. we have achieved efficient photoinduced transbilayer electron transport from reduced cytochrome in the inner aqueous compartment of vesicles to oxidized ferredoxin in the outer aqueous phase, thereby storing approximately 0.7 V in the products; this is a close analog of the electron transport process which occurs in green plant Photosystem I; ii. we have devised a system utilizing a small organic molecule (EDTA) as a sacrificial donor in a two-photoreaction process which results in transbilayer electron transport to ferredoxin; this mimics the two light reactions in photosynthesis and generates a strong reductant; iii. using sulfonated hydroquinones and quinones as electron donors and acceptors, we have accomplished the photogeneration of a pH gradient across a bilayer membrane; such transbilayer pH gradient formation is a key energy storage process in biology; iv. we have developed a novel method of modifying the surface of a metal electrode (using a lipid bilayer) which dramatically improves electrochemical coupling to redox proteins, thus providing a possible new approach to the conversion of photon energy into electrical energy.** A more detailed description of the scientific progress made during this grant period follows.

SUMMARY OF SCIENTIFIC PROGRESS

1- Chlorophyll photosensitized reduction of cytochrome c and cytochrome c oxidase

In previous studies supported by DOE utilizing chlorophyll-containing lipid bilayer vesicles (Senthilathipan & Tollin, Photochem. Photobiol. 43, 545, 1986; Fang & Tollin, Photochem. Photobiol. 47, 741, 1988; 47, 751, 1988), we showed that the heme protein cytochrome c, located in the outer aqueous compartment, could be reduced by an electron

originating in the triplet state of chlorophyll dissolved in the bilayer, either directly by electrostatically binding the cytochrome to the bilayer surface, or indirectly via a quinone mediator. We have now extended this work in two ways: i. **we have improved the efficiency of cytochrome c reduction by approximately a factor of two by using pairs of quinones as mediators** (Chamupathi & Tollin, 1990; ref. 1); ii. **we have coupled chlorophyll-photosensitized cytochrome c reduction to the reduction of membrane-bound cytochrome c oxidase** (Chamupathi et al., 1990; ref. 2), the latter being one of the major energy-transducing proteins in biology.

Our strategy for improving the quantum yield of cytochrome c reduction was to enhance the efficiency of electron flow from the membrane interior (where the chlorophyll is located) to the outer aqueous phase (where the cytochrome is located). We accomplished this by utilizing a **lipophilic** quinone as the **primary** electron acceptor from triplet chlorophyll within the bilayer, and a **hydrophilic** quinone in the aqueous phase as a **secondary** acceptor from the reduced primary acceptor quinone, which then served as the direct mediator of electron flow to the cytochrome. This allowed us to achieve more effective charge separation across the membrane-water interface. Overall, our measurements showed that approximately 40% of the chlorophyll triplet molecules generated by the laser flash were converted into separated products (i.e. chlorophyll cation radical in the membrane and reduced cytochrome in the aqueous phase). Inasmuch as the cytochrome and the hydrophilic quinone in these experiments were present **only** in the outer aqueous compartment, those triplets formed in the inner monolayer of the vesicle did not participate in the electron transfer events leading to cytochrome reduction. **Thus, the actual efficiency was probably closer to 100%.** Although

reverse electron transfer (i.e. cytochrome reoxidation and chlorophyll cation radical reduction) did eventually occur, the rate of this process was quite slow (**halftime 140 ms**), allowing ample time for additional reactions involving the products of energy storage to proceed (for example, cytochrome oxidase reduction; see below). **It should also be noted that this strategy of using lipophilic/hydrophilic mediator pairs is not specific for cytochrome reduction, and thus represents a general method for enhancing the efficiency of electron flow from a membrane interior to an aqueous compartment.** Indeed, it is utilized in vivo during natural photosynthesis for precisely this same purpose!

In order to accomplish the construction of an effective light-driven electron transport chain in an artificial membrane which resulted in the deposition of electrons into a **membrane-bound energy-transducing redox protein**, analogous to events occurring during natural photosynthesis, we incorporated cytochrome c oxidase into chlorophyll-containing lipid bilayer vesicles which were capable of reducing cytochrome c in the aqueous phase via a quinone mediator. Using time-resolved laser spectroscopy, we clearly showed that sequential electron transfer occurred from triplet chlorophyll to cytochrome oxidase, with intermediate electron flow through the quinone and the cytochrome (i.e. **a four component electron transfer chain**). The overall yield, based on the quenching of the chlorophyll triplet state population, was 14% (again, however, we note that only the outer membrane surface was involved). Back electron transfer regenerating starting materials was exceedingly slow in this system (**halftime 1 s**). Although we did not carry this experiment further to show that proton gradient formation and ATP synthesis could be accomplished with this system, there is no reason to believe that this could not be done, given the appropriate experimental

protocol. Indeed, such processes have been reconstituted in lipid bilayer vesicles in other laboratories (cf. for example, Prochaska & Wilson, Arch. Biochem. Biophys. 290, 179 (1991)). **We therefore feel that these results are of considerable significance for the future development of effective biomimetic solar energy conversion strategies.**

2- Chlorophyll photosensitized vectorial electron transfer across a lipid bilayer from reduced cytochrome to oxidized ferredoxin

One of the key energy storage events in natural photosynthesis is the light-induced separation of redox equivalents across a hydrophobic barrier provided by a lipid bilayer membrane. In green plants, this involves the oxidation of either reduced cytochrome or reduced plastocyanin (the latter is a copper protein) on one side of the membrane, and reduction of the soluble iron-sulfur protein ferredoxin on the other side. During the current grant period, we have accomplished this in our chlorophyll-vesicle systems (Zhao & Tollin, 1991a; ref. 4). This involved incorporating reduced cytochrome c in the inner aqueous compartment of negatively charged vesicles, oxidized ferredoxin in the outer aqueous phase, and using the low potential positively charged viologen analog propylene diquat as a mediator between triplet chlorophyll and ferredoxin. Using both steady-state and laser flash methods, **we demonstrated that illumination of chlorophyll results in ferredoxin reduction and cytochrome oxidation.** The overall yield, based on triplet chlorophyll quenched, was 11%. This was limited by three factors: i. an opposing transmembrane potential which was established upon addition of the highly negatively charged ferredoxin to the outer compartment, and which was enhanced upon electron flow from inside to outside; ii. the build-up of oxidized cytochrome in the inner compartment, which functioned as an electron

acceptor from triplet chlorophyll and thus acted to inhibit electron flow from inside to outside, as well as to limit the reducing equivalents which could be deposited in ferredoxin to one-half of the added cytochrome; iii. the rather poor chlorophyll triplet quenching ability of propylene diquat. The first two of these limitations have been overcome by subsequent work done during the present grant period; the third is an objective of the next grant period (see Proposed Research below). The limitation imposed by the transmembrane potential was mitigated by the addition of the ionophore valinomycin plus potassium ion into the system (Zhao & Tollin, 1991b; ref. 5). This served to neutralize the opposing transmembrane potential by allowing potassium ion to flow through the bilayer, and **increased the overall yield by a factor of two.** The limitation involving oxidized cytochrome generation was overcome by the **incorporation of a second photosystem into the inner compartment** (Zhao & Tollin, manuscripts submitted, 1991a,b; ref. 13,14). This second photoreaction involved a flavin analog (FMN) plus a sacrificial electron donor (EDTA), which upon blue light excitation generated a strong reductant (the flavin semiquinone) as a result of triplet quenching by EDTA. The flavin semiquinone then served to reduce oxidized cytochrome c formed in the inner compartment via electron transfer to chlorophyll cation radical. This prevented the inhibition of electron flow caused by the accumulation of the oxidized cytochrome. As a consequence of this, the limiting factor in the generation of reducing power was no longer the amount of cytochrome which could be incorporated into the inner compartment, but rather the amount of EDTA which could be so incorporated. Inasmuch as the latter molecule is smaller and more soluble than cytochrome c, we were able to

increase the reducing capacity of the system sufficiently so that **all of the ferredoxin added to the outer compartment could be photoreduced under steady-state illumination with white light.** This system has several interesting features with regard to solar energy conversion: **it permits the storage across the bilayer of an appreciable amount of electromagnetic energy (approximately 0.7 V); it utilizes a small organic molecule (EDTA) as a sacrificial electron donor for the generation of a strong reductant (reduced ferredoxin), which can be coupled to dinitrogen fixation or dihydrogen production via the appropriate enzymes; it utilizes two photoreactions, as does natural photosynthesis. We thus believe this constitutes a major achievement in the development of biomimetic solar conversion systems!**

3- Photochemical generation of transbilayer proton gradients in chlorophyll-vesicle systems

Another key event in natural photosynthesis is the generation of a **transmembrane proton gradient coupled to photochemical electron transfer.** This is used in vivo for the synthesis of ATP, as well to drive other energy-requiring processes such as ion transport. **We have now achieved this biomimetically in our chlorophyll-vesicle systems** (Zhao & Tollin, manuscript in press; ref. 10). Our strategy involved the asymmetric placement of sulfonated quinones and hydroquinones into the two aqueous phases of a bilayer vesicle system. Using both laser flash and steady-state methods, we demonstrated that illumination generated the chlorophyll triplet, which reduced the quinone at the outer membrane-water interface forming the quinone anion radical and the chlorophyll cation radical. Hole migration across the bilayer allowed the chlorophyll cation radical to move to the inner surface, where it was then reduced by the hydroquinone forming the hydroquinone cation radical in the aqueous phase and regenerating chlorophyll in the membrane. The overall

efficiency of this vectorial electron flow across the bilayer was 39%, based on chlorophyll triplet quenching. The following quinone radical disproportionation reactions were then responsible for generating a proton gradient across the bilayer:

$$2Q^{\cdot-} + 2H^+ \longrightarrow Q + H_2Q \qquad \text{(outside; net uptake of } H^+\text{)}$$

$$\left.\begin{array}{l} H_2Q^{+\cdot} \longrightarrow Q^{\cdot-} + 2\,H^+ \\ 2Q^{\cdot-} + 2H^+ \longrightarrow Q + H_2Q \end{array}\right\} \text{(inside; net release of } H^+\text{)}$$

The indicator dye, bromcresol purple, was used in both steady-state and laser flash experiments to observe the pH changes produced in this system. Quantitation of these pH effects led to the conclusion that a single laser flash caused a proton concentration decrease of 0.2 μM in the outer compartment, and the release of an equal quantity of protons in the inner compartment (note that because the volume of the inner phase is only 1/1000 that of the outer phase, the H^+ concentration change was correspondingly larger, i.e. $\approx$ 200 μM). Thus, **a large pH gradient was produced across the bilayer.** Although, in our experiments, we did not utilize this photogenerated pH gradient for any practical purposes, it seems clear that this could be done. **Again we conclude that these results have important implications for the future design of solar conversion systems, and perhaps other technologies as well.**

Use of lipid bilayers as electrode coatings to facilitate redox protein electrochemistry

Facile electron exchange between redox proteins and electrode surfaces has long been a difficult problem in electrochemistry, and much effort has been expended on developing various methods of electrode surface modification to improve the efficiency of this process. During the current grant period, we have combined our extensive experience with electron transfer reactions of redox proteins located at lipid bilayer-aqueous interfaces, with the development in Tien's laboratory (Tien & Salamon, Bioelectrochem. Bioenerg. 22, 211, 1989; Martynski & Tien, Bioelectrochem. Bioenerg. 25, 317, 1991) of a method for coating metal surfaces with lipid bilayers, to **develop a novel approach to electrode surface modification which allows direct electrochemical reactions involving redox proteins to occur with high efficiency, as well as providing a support for incorporating small molecule electron mediators which can assist in the effective coupling of the electrode surface to the redox protein** (Salamon & Tollin, 1991a,b; Salamon & Tollin, manuscripts in press; refs. 6,7,8,11). We have utilized this approach to carry out cyclic voltammetry measurements with cytochrome c, ferredoxin, and plastocyanin which have demonstrated quite clearly that lipid bilayer-modified electrodes have electrochemical properties which are as good as or better than those obtained using other methods of electrode surface modification. By varying the lipid concentration in the bilayer, the bilayer surface charge and the ionic strength of the medium, we were able to show that attractive electrostatic interactions, as well as hydrophobic forces, are involved in the membrane-protein interactions which allow the occurrence of facile electron transfer with the electrode surface. Variation of these parameters allows us to tailor the properties of the electrode surface to match the particular

protein which is under investigation. Thus, negatively charged proteins can be made to interact with a positively charged membrane surface, etc. This is an extremely important feature of this methodology, inasmuch as **it permits the construction of electrode surfaces which display specificity in their ability to interact with redox proteins. We believe that this new approach to redox protein electrochemistry will be useful in coupling photochemical energy storage in redox proteins (as in the results described above) to the generation of electrical potentials in an external circuit.** We are presently working towards this end (see Proposed Research).

5- NMR studies of protein-membrane interactions

This was one of the areas in which we proposed to work during the current grant period, as a means of obtaining structural information about protein-bilayer interactions. We have indeed attempted to carry out several NMR experiments utilizing the copper protein plastocyanin. Thus far, none of these has proven successful. We first attempted to detect paramagnetic shifts of the ^{31}P NMR signals of phospholipids upon binding oxidized plastocyanin to the membrane. This was unsuccessful. On the basis of control experiments with simple copper chelates, we concluded that the distance between the paramagnetic copper ion which is bound within the plastocyanin molecule and the phosphorous atoms of the lipid headgroup was too large for such effects to be observed. Our next approach was to use 2-D proton NMR to detect structural changes in reduced (diamagnetic) plastocyanin upon binding of the (negatively charged) protein to micelles formed from deuterated positively charged lipids (dodecyltrimethylammonium ions). Although we were successful in obtaining well-resolved 2-D NMR spectra (NOE's) from plastocyanin solutions, we found

that the positively charged micelles caused plastocyanin to denature. We are presently attempting to continue this work using a neutral lipid (dodecylphosphorylcholine) as the micelle-forming entity (we have shown that plastocyanin also binds to neutral lipids via hydrophobic interactions). In preliminary experiments, we have verified that this neutral lipid does not cause plastocyanin to denature, and the appropriate NMR experiments are now in progress.

6- Miscellaneous

By invitation, a review of chlorophyll photochemistry in microheterogeneous media was written (Tollin, 1991; ref. 3) for the volume "Chlorophylls", edited by H. Scheer. This covered work done in micelles, planar lipid bilayers, lipid bilayer vesicles, microemulsions and several miscellaneous heterogeneous systems, and focussed particularly on processes relevant to energy conversion and storage.

An invitation was also received to contribute an article to "The Spectrum", which is the scientific newsletter of the Center for Photochemical Sciences at Bowling Green State University. A copy of the submitted article is appended to this report. Although, strictly speaking, this does not constitute a publication (and hence is not included in the listing below), it does provide a convenient summary of our point of view and some of our recent progress, and thus may be of use to DOE and the reviewers of this proposal. Its publication in the newsletter should considerably increase the breadth of the audience which is aware of our work.

During the present grant period we have utilized our DOE-purchased laser photolysis equipment, as well as the experience we have obtained during our DOE-funded research

with photoinduced electron transfer processes involving redox proteins, to carry out studies of the oxidation of reduced plastocyanin and cytochrome c, and the reduction of oxidized ferredoxin, by membrane preparations isolated from spinach chloroplasts (Hervas et al., manuscript in press; Hervas et al., manuscript submitted; refs. 9,12). These studies were stimulated by a visit to my laboratory of two scientists from the University of Sevilla in Spain, who had experience with steady-state kinetic measurements of these reactions. Inasmuch as the results are not within the scientific framework of our DOE grant, I will not summarize them here. However, since we acknowledged DOE support for this work, I am appending copies of the manuscripts to this Progress Report and including the references in the publication list.

In the previous review of this grant, I was criticized for not involving graduate students in this research program, and relying solely on postdoctoral students. As can be noted, this situation has not changed during the current grant period, although in one of our publications (ref. 2) an undergraduate student (D.M. Moezzi) participated as a significant contributor. It is also fair to say that it is unlikely that this will change significantly in the near future. There are two principal reasons for this: i. there is a clear shortage of graduate students in biochemistry; ii. it is difficult to obtain biochemistry graduate students who are interested in pursuing research in biomimetic solar energy conversion. Although, in principle, I have access to chemistry graduate students as a consequence of having a joint appointment in the Department of Chemistry, in practice it is exceedingly rare at this university for such students to opt to work for a faculty member whose principal appointment and physical location is in the Department of Biochemistry (in fact, it has never

happened!). In contrast to this, I continue to receive many inquiries from individuals, whose backgrounds are mainly in chemistry or biophysics, for postdoctoral positions in my laboratory to work in this area.

PUBLICATIONS DURING GRANT PERIOD

1- Chamupathi, V.G. & Tollin, G. Photochem. Photobiol. 51, 611-619 (1990).

2- Chamupathi, V.G., Moezzi, D.M. & Tollin, G. Photochem. Photobiol. 52, 883-891 (1990).

3- Tollin, G., in Chlorophylls, H. Scheer, ed., pp. 317-337, CRC Press, Boca Raton, 1991.

4- Zhao, Z.-G. & Tollin, G. Photochem. Photobiol. 54, 113-122 (1991a).

5- Zhao, Z.-G. & Tollin, G. Photochem. Photobiol., 54, 827-831 (1991b).

6- Salamon, Z. & Tollin, G. Bioelectrochem. Bioenerg. 25, 447-454 (1991a).

7- Salamon, Z. & Tollin, G. Bioelectrochem. Bioenerg. 26, 321-334 (1991b).

8- Salamon, Z. & Tollin, G. Bioelectrochem. Bioenerg., in press.

9- Hervas, M., De la Rosa, M. & Tollin, G. Eur. J. Biochem., in press.

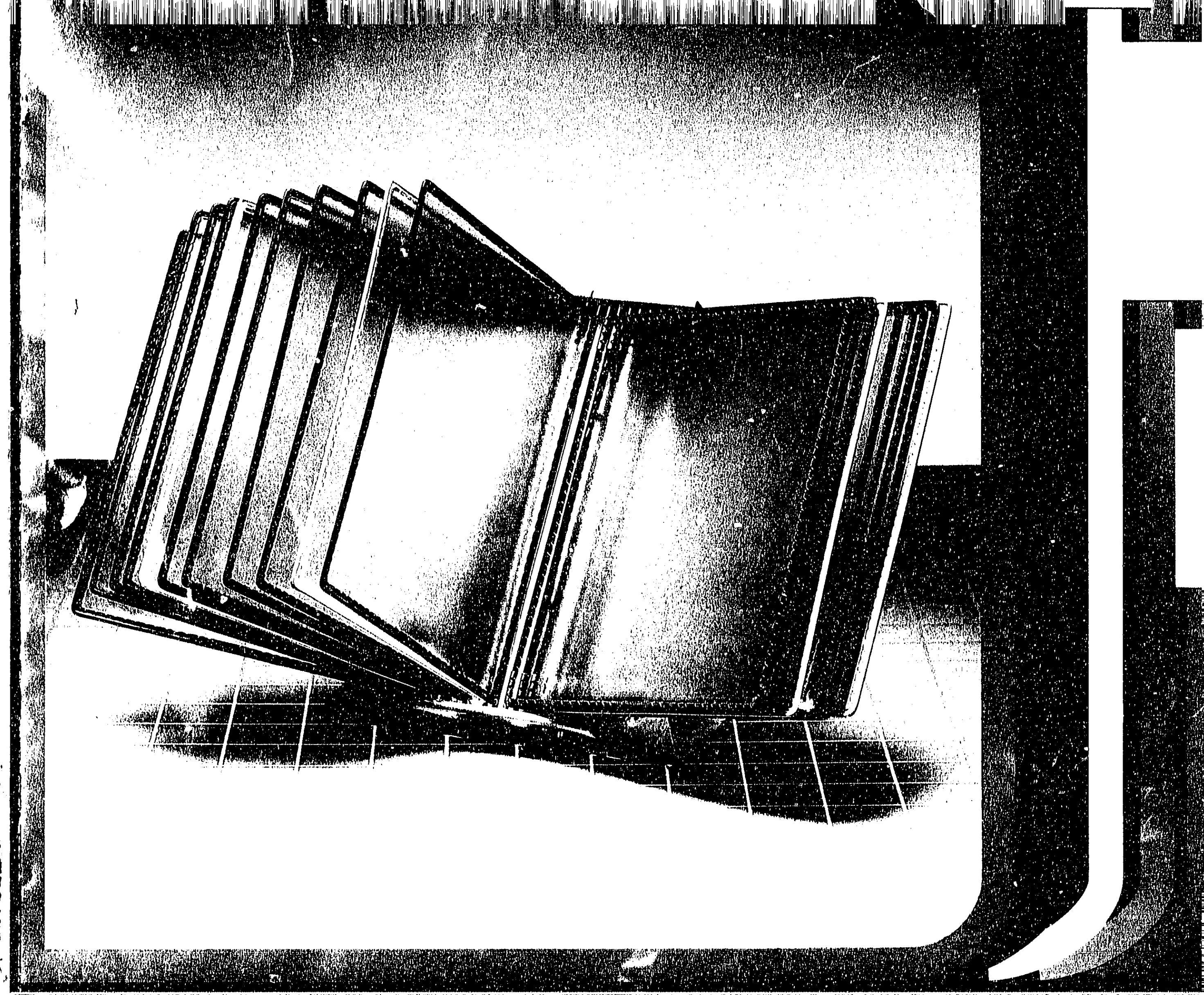
10- Zhao, Z.-G. & Tollin, G. Photochem. Photobiol., in press.

11- Salamon, Z. & Tollin, G. Arch. Biochem. Biophys., in press.

12- Hervas, M., Navarro, J.A. & Tollin, G. Photochem. Photobiol., manuscript submitted.

13- Zhao, Z.-G. & Tollin, G. Photochem. Photobiol. (1991a), manuscript submitted.

14- Zhao, Z.-G. & Tollin, G. Photochem. Photobiol. (1991b), manuscript submitted.



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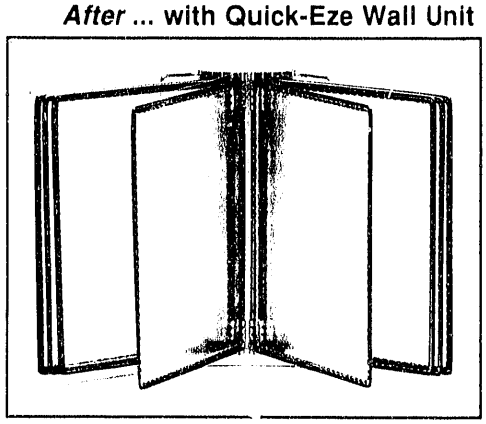

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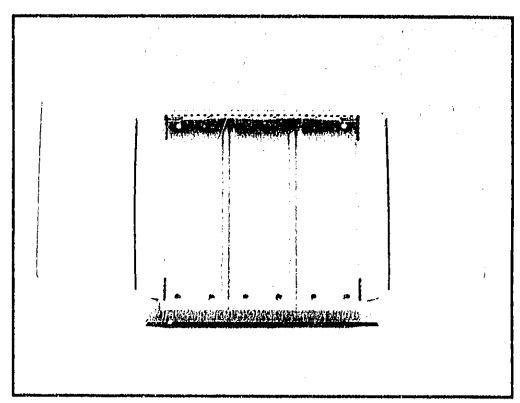

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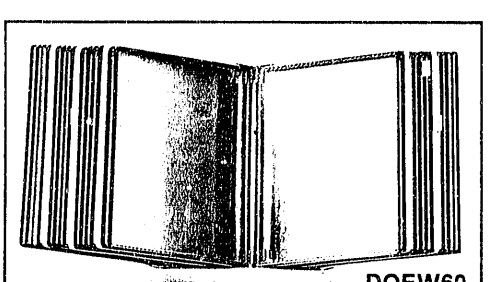

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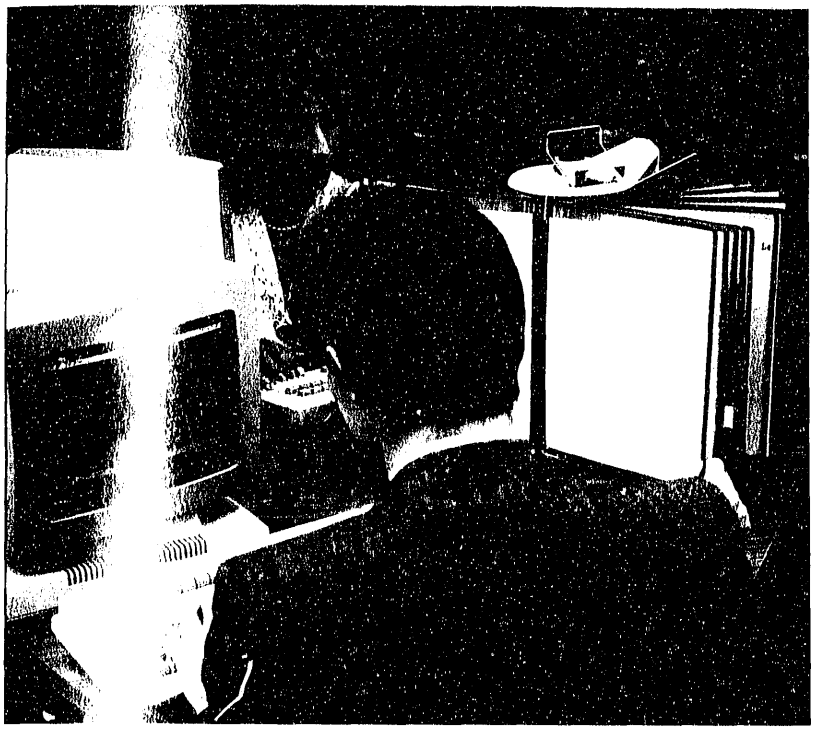

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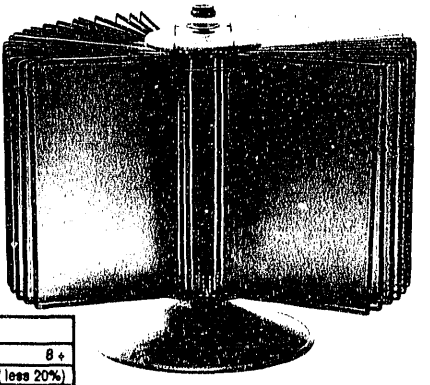

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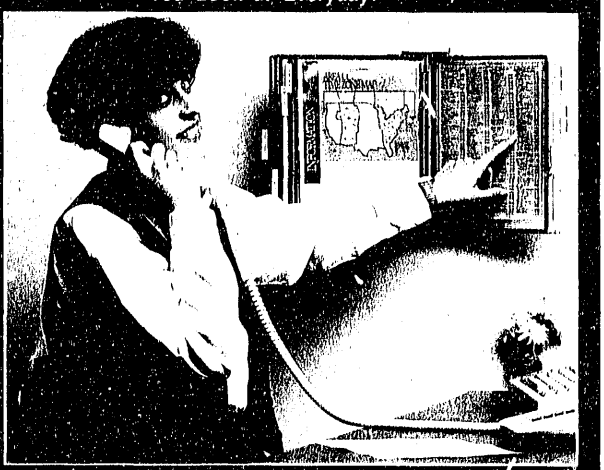

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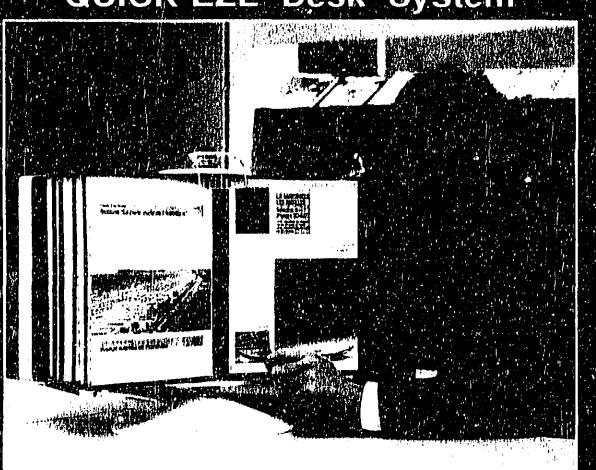

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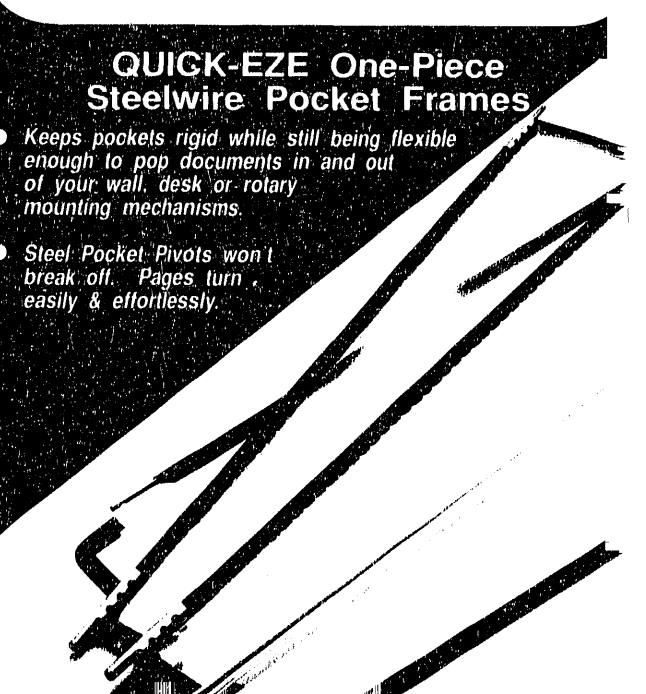

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