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ON SUBCELLULAR ELECTRON TRANSPORT PHOSPHORYLATION SYSTEMS*†

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Abstract—Adenosine triphosphate is known to be a universal carrier of chemical energy between the energy-yielding and energy-requiring processes of living cells. In chlorophyll-containing organisms, such as green plants and photosynthetic bacteria, light induces a phosphorylation of adenosine diphosphate to adenosine triphosphate. The fact that this formation of adenosine triphosphate in the chloroplasts of the plants and the chromatophores of the bacteria is linked to electron transport invites comparison with oxidative phosphorylation in mitochondria. The biochemical mechanisms of oxidative and light-induced phosphorylation are discussed. New evidence is given for certain similarities and some differences between the mechanisms of electron transport phosphorylation in the various systems. The electron transport and phosphorylation reactions involved are not yet completely understood. It appears useful to base any working hypothesis for the investigation of electron transport phosphorylation in various sub-cellular systems on the established occurrence of similarities. Methods applied and results obtained with any of the three well-defined sub-cellular electron transport phosphorylation systems appear to become increasingly valuable when the other ones are being investigated.

INTRODUCTION

ABOUT a half century ago, there existed a rather common opinion, that the phenomenon of life constitutes a revolution against the second law of thermodynamics. This law states that the total amount of entropy in Nature is increasing, or, in other words, that organization goes towards a minimum. Today it is generally recognized that the revolution was only fictional. Life is a "steady state" system and, both when taken as a whole and when it is represented in a single organism, it does not have the properties of a closed system in equilibrium where the basic laws of thermodynamics apply. Life as we define it today ultimately depends on the radiation which the earth is receiving from the sun. Chlorophyll-containing organisms in the reactions of photosynthesis use energy from this radiation to build complicated organic molecules, where part of the energy consumed for their biosynthesis is conserved. Thus the utilizable energy content of these molecules is much higher than that of their primary building stones, water and carbon dioxide. In the reactions where the organic molecules are built, an essential role is played by adenosine triphosphate (ATP).

All available evidence indicates that ATP is the universal, primary carrier of chemical energy between the energy-yielding and energy-requiring processes of living

* "Electron transport phosphorylation" will be used throughout to denote phosphorylation linked to electron (or hydrogen) transport along a chain of electron carriers.

† Abbreviations used in this paper are: ADP, adenosine diphosphate; ATP, adenosine triphosphate; DPN, diphosphopyridine nucleotide; DPNH, reduced diphosphopyridine nucleotide; TPN, triphosphopyridine nucleotide; TPNH, reduced triphosphopyridine nucleotide; FMN, flavin mononucleotide; FAD, flavinadenine dinucleotide; HOQNO, 2-*n*-heptyl-4-hydroxyquinoline-N-oxide.

cells. Thus, as soon as the light quanta from the radiation of the sun have given away their energy to the chlorophyll-containing organism in a photophysical or photochemical reaction, this energy must be transferred through a suitable metabolic system to ATP in order to be useful to the organism. As early as 1943 Ruben[1] suggested that coupled oxido-reduction following the photochemical reaction could convert radiant energy to "high energy phosphate donors".

Recent research has shown that an ATP-generating system, closely linked to the photophysical or photochemical reaction, indeed exists. The formation of ATP is linked to electron transport. The process was found in 1954 by Arnon *et al.*[2] in isolated spinach chloroplasts and by Frenkel[3] in extracts of photosynthetic bacteria. It was given the name photosynthetic[2] or light-induced[3] phosphorylation.

Both in bacteria and in plants the system for light-induced phosphorylation is localized in sub-cellular, chlorophyll-containing structures: chromatophores in bacteria and chloroplasts in plants. Both in bacteria[4] and in plants[5] adenosine diphosphate (ADP) is phosphorylated to ATP in the energy-trapping reactions. This resembles oxidative phosphorylation of mitochondria. How close this resemblance appears to be and what similarities and differences the bacterial and the plant systems for light-induced phosphorylation show, when compared with each other, will be the subject of this lecture.

One could divide the items to be compared into three categories: structure of the particles, mechanism of the electron transport, and mechanism of the phosphorylation reactions. Only the two first groups will be dealt with in some detail, as knowledge about the third is still very limited. The reason why light-induced phosphorylation in plant chloroplasts and bacterial chromatophores will be compared with oxidative phosphorylation in animal mitochondria, and not in plant mitochondria or bacterial structures, is that most of the available information about mitochondria and oxidative phosphorylation has been obtained with animal material. Functional properties of the systems for light-induced phosphorylation will be represented by those from the best known sources in this respect: the photosynthetic bacterium *Rhodospirillum rubrum* in the case of bacteria and spinach in the case of plants.

SUB-CELLULAR STRUCTURES FOR ELECTRON TRANSPORT PHOSPHORYLATION

Three different sub-cellular sites for electron transport phosphorylation, namely, animal mitchondria, plant chloroplasts and bacterial chromatophores, will be briefly described and compared. Our knowledge about them is derived mainly from electron microscopic and biochemical studies.

Animal mitochondria are usually somewhat elongated *in vivo*. A normal size of liver and heart muscle mitochondria is approximately 0·5 by 2 μ. They are surrounded by a double membrane[6] and reveal more or less densely packed, parallel internal double membrane structures.[6, 7] Each double-membrane is considered to consist of two protein layers and a lipid layer. The electron transport chain is intimately connected with the membranes. The electron carriers appear to be oriented in the membranes and arranged in functionally suitable "assemblies"[8] or a network of "sub-units".[9] From the mitochondria it has been possible to isolate components of the electron transport chain as free coenzymes, as proteins and as lipoproteins. Oxidative phosphorylation has been obtained in suspensions of sub-mitochondrial particles (from

isolated mitochondria) but not in solution. The phosphorylating sub-mitochondrial fragments described by Cooper *et al.*[10] were reported to have a particle weight of 50 million.

Plant chloroplasts are lamellar bodies of varying size and shape. They can be several microns in diameter. In higher plants the lamellae are differentiated into the non-pigmented stroma lamellae and the more or less cylindrical, pigmented, chlorophyll-containing grana lamellae. The lamellar bodies appear to consist of alternating lipophilic (lipid-containing) and hydrophilic (protein-containing) layers of a double membrane[11] nature. The lipid- and protein-containing layers have been proposed to be separated by monomolecular films of chlorophyll molecules, with their lipophilic phytol chain reaching into the lipid layer.[12] The chlorophyll content of chloroplasts on a dry weight basis is 5–6 per cent. A minimal functional sub-unit in the chloroplast has been suggested.[13] It would contain 100–300 chlorophyll molecules. Two compounds capable of undergoing oxidation and reduction which are found in chloroplasts, and to which an electron transport function has been ascribed, have been quantitatively determined in relation to chlorophyll. They are vitamin K_1 and cytochrome *f*. The ratio of chlorophyll to vitamin K_1 is roughly 250[14, 15] and chlorophyll to cytochrome *f* about 170, according to a recent estimation.[16] Thus a possibility exists that every proposed photosynthetic sub-unit of the chloroplast is structurally and functionally related to a single electron transport chain.

Bacterial chromatophores are comparatively small organelles. Those of *Rhodospirillum rubrum* have an estimated diameter of 400 Å and a tentative "molecular weight" of 30 million.[17] A single cell is reported to contain about 5000–6000 chromatophores which seem to be evenly distributed throughout the cell. It is still a matter of disagreement whether the bacterial photosynthetic apparatus contains lamellar structures[18, 19] or not.[20] According to Newton and Newton[21] *Chromatium* chromatophores contain 200 molecules of chlorophyll–chromatophore, and the ratio chlorophyll–carotenoid–cytochromes is 10 : 5 : 1. The figure 200 invites comparison with the figures 100–300 in the postulated chloroplast sub-unit.

As an example of the difference in size between chloroplasts of algae and higher plants and bacterial chromatophores, *Euglena* chloroplasts are from two to three times the size of the whole bacterium *Rhodospirillum rubrum*. As Kamen and Newton[22] have pointed out, one may regard a photosynthetic bacterium as analogous to a chloroplast and the chromatophores as analogous to the chloroplast grana. A chromatophore may perhaps also be compared with the postulated sub-unit of the grana membranes.

In summary, the comparison between the structures of mitochondria, chloroplasts and chromatophores shows certain similarities. Present knowledge allows only a dim perception of the details of the various structures. In the search for common denominators one should not neglect the major functional difference between chloroplasts and chromatophores, which transform light energy to chemical energy, and mitochondria, where respiration and oxidative phosphorylation seem to be the main function. In a symposium such as this, however, one may perhaps be allowed to speculate about why electron transport phosphorylation is confined to particles. Oriented double membranes which provide both hydrophilic and lipophilic phases dominate the pictures of mitochondria and chloroplasts, and have been suggested to occur in the chromatophores also. As will be discussed below, both hydrophilic and lipophilic compounds seem to take part in electron transport phosphorylation. Consequently

the phase boundary between the lipophilic and hydrophilic phase can be assumed to contain the electron transport phosphorylation system. The reason why particles are necessary may be that they can provide this boundary between two phases. Assuming that great boundary surface means great capacity for electron transport phosphorylation, one finds that the achitecture of the particles is remarkably rational.

ELECTRON TRANSPORT AND PHOSPHORYLATION

Oxidative phosphorylation in animal mitochondria

An outline of what is known at present about electron transport and oxidative phosphorylation in animal mitochondria will now be given. It is not possible here to follow in any detail the fascinating development of the concept of an electron transport chain for the respiration of the cell. The picture of a chain emerged mainly through the investigations of Keilin and Warburg and their co-workers in the nineteen twenties and thirties. Warburg[23] wrote in 1934 about the function of such a chain: "Es liegt nahe anzunehmen, dass die Aufteilung der Energie der Atmung in kleinere Teile günstig ist für das, was die Natur mit der Atmung bezweckt: die Verwandlung chemischer Energie in Arbeit". Today one would change the six last words to "synthesis of ATP, where chemical energy is preserved".

There are still different opinions about details of the respiratory chain in oxidative phosphorylation. Each year new information is added. Fig. 1 may be said to represent my concept of it today. It is based mainly on the schemes of Slater[24] and of Chance and Williams[25] and on recent results published by Hatefi[26].

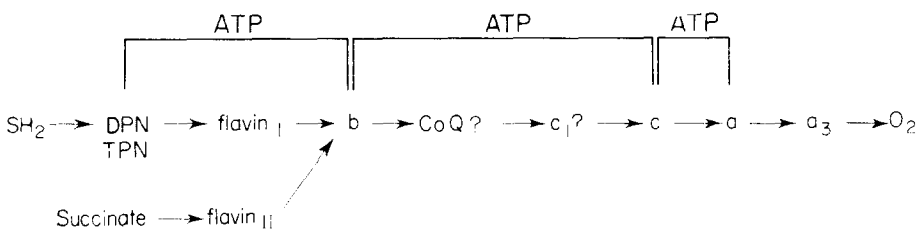


FIG. 1. Respiratory chain and regions of phosphorylation in animal mitochondria. Abbreviations: SH_2 = substrate, *b*, c_1 etc., = cytochrome *b*, cytochrome c_1, etc.

As is seen, pyridine nucleotide accepts hydrogen from the substrates, except from succinate, which directly reduces a flavoprotein, succinic dehydrogenase.[27] DPNH reduces another flavoprotein. TPNH has been reported to become oxidized in phosphorylating mitochondria along two different pathways,[28] over DPN through the action of pyridine nucleotide transhydrogenase and over TPNH-oxidase. The two branches of the respiratory chain join at cytochrome *b* and from here on the electrons flow, as is indicated in Fig. 1, along a single chain to reduce the final acceptor, oxygen. A quinone, coenzyme Q, is reported to be situated between cytochromes *b* and *c*.[26] Vitamin K[29, 30] and vitamin E[31] have been suggested as links in the phosphorylating electron transport chain, but the situation with respect to these agents seems less clear. It may be noted that they both are also quinones. Cytochrome c_1 participates in electron transport in non-phosphorylating mitochondria,[32] but a role for it in oxidative phosphorylation has not been demonstrated.

To sum up, there may be four different types of compounds carrying electrons from substrate to oxygen in animal mitochondria: pyridine nucleotides, flavoproteins, cytochromes and quinones.

Although many attempts have been made during the last ten years to clarify the mechanism of oxidative phosphorylation it is essentially still obscure. Several general or specified mechanisms have been suggested[25, 33–38] but a detailed and comprehensive logical picture is lacking. Thus it may suffice here to mention a few generally accepted facts.

(1) Owing to the flow of two electrons between DPNH and O_2, three molecules of ATP are formed. Two are formed between succinate and O_2, two between DPNH and cytochrome *c* and one between cytochrome *c* and O_2.

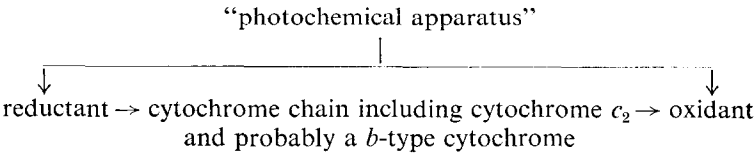
(2) The normal potentials of the redox systems involved are such that the above values are energetically feasible.

(3) When the electrons flow in the electron transport chain from a higher energy level to a lower, they give off potential energy. This energy is utilized to link inorganic phosphate by a "high energy bond" with an intermediate phosphate acceptor. The product reacts with ADP to give ATP.

Light-induced phosphorylation in bacterial chromatophores and plant chloroplasts

Light-induced phosphorylation has been shown to be linked to electron transport, for example by means of its stimulation by electron carriers and inhibition by typical inhibitors of electron transport. In the presence of light, photosynthetic systems are capable of producing a reductant and an oxidant. Light-induced phosphorylation is generally pictured as resulting from the reaction of these with each other over a chain of electron carriers. The concept of an electron transport chain in light-induced phosphorylation immediately suggested the possibility that similiarities existed between this system and that of mitochondrial oxidative phosphorylation. Current views of electron transport in light-induced phosphorylation will now be presented, and after this some of our own results will be demonstrated and discussed.

The result reported by Smith and Baltscheffsky[39] that 2-*n*-heptyl-4-hydroxyquinoline-N-oxide (HOQNO) completely inhibited light-induced phosphorylation in extracts of *Rhodospirillum rubrum* indicated that the process in bacteria was linked to electron transport. The inhibitor is known to block the electron transport in animal mitochondria between cytochrome *b* and cytochrome c_1.[40] The assumption that the site of action is identical or very similar in the bacterial extracts is supported by the finding of Geller[41] that also antimycin A and SN 5949 (a naphthoquinone) which act at the same level as HOQNO in mitochondrial electron transport inhibit the bacterial system. Further support for similarity between the two systems was obtained when Smith and Baltscheffsky,[42] working with both whole cells and extracts of *R. rubrum*, found that HOQNO caused a reduction of a *b*-type cytochrome and an oxidation of cytochrome c_2, as compared with the uninhibited systems. This finding demonstrated participation of cytochromes in the electron transport reactions of light-induced phosphorylation in bacteria. The following scheme was given to account for the results:



Up to now it is the most detailed scheme given for electron transport in light-induced phosphorylation of bacteria. On the basis of the above-mentioned studies, Frenkel has also included cytochrome c_2 in a schematic representation of electron transport in light-induced phosphorylation of *R. rubrum* chromatophores[43] (cf. Frenkel[44]).

Several electron carriers have been suggested as physiological co-factors in light-induced phosphorylation of plants. In contrast to the chromatophores of *R. rubrum* where high rates of phosphate esterification have been obtained without addition of external electron carriers, isolated plant chloroplasts have given only extremely low rates of light-induced formation of ATP in the absence of added electron carriers. In the presence of agents such as menadione,[45] FMN[46] or phenazine methosulphate[47] very high rates of phosphorylation have been obtained.[48] When considering electron transport properties in light-induced phosphorylation of isolated spinach chloroplasts it must be kept in mind that the presence of an added carrier may possibly introduce a by-pass for the electrons around a smaller or greater portion of a physiological electron transport chain.

In 1955 Arnon *et al.*[15, 16] found that ascorbate, flavin mononucleotide and menadione stimulated light-induced phosphorylation in isolated spinach chloroplasts. They suggested that the conversion of light energy into the pyrophosphate bond energy of ATP involved an electron transport chain according to the following tentative scheme:

$$\begin{array}{ccccc} 2\,(H) & \longleftarrow & H_2O & \longrightarrow & (O) \\ \downarrow & & & & \uparrow \\ \text{FMN} & \longrightarrow & \text{vitamin K} & \longrightarrow & \text{ascorbate} \end{array}$$

In this scheme, water was photolysed in the Hill reaction[49] to a reductant and an oxidant, the electron transport chain transporting electrons from the former to the latter. Owing to the intensive subsequent research by these and other workers the scheme is today, 4 years later, only of historical interest. It is only possible here briefly to mention some of the important recent developments. Arnon *et al.*[50] have found that the rate of ATP-formation in the presence of light can be stimulated by TPN. Their conclusion that TPN participates in the electron transport of the process is, however, not shared by Wessels.[51] Wessels[52] and Whatley *et al.*[53] agree that flavin mononucleotide and menadione appear to catalyse separate pathways of electron transport in light-induced phosphorylation and that ascorbate may act primarily as a protective agent for the chloroplasts.[51, 53] According to Jagendorf and Avron[47] flavin mononucleotide and menadione as well as phenazine methosulphate may all act by bridging a gap in the electron transport of the chloroplasts, which may have been damaged during their isolation.

In a very recent article on photosynthesis Arnon[54] suggests that ATP can be formed in the presence of light in chloroplasts of green plants along three different pathways: (1) the cyclic electron transport system involving vitamin K and a cytochrome, (2) the cyclic electron transport system involving TPN, flavin mononucleotide and cytochromes, and (3) the "open" non-cyclic mechanism, which transports electrons from chlorophyll to TPN. In (3), molecular oxygen is produced in an equivalent amount to the TPN reduced. In this system or in model experiments, where ferricyanide[55] is substituted for TPN, one molecule of ATP is formed for each two electrons reaching the acceptor. A different sensitivity towards various inhibitors (*o*-phenanthroline,

2 : 4-dinitrophenol) and towards chloride ion has prompted the postulation of the separate electron transport chains.

Practically nothing is known about the mechanism of the phosphorylation reactions in light-induced phosphorylation. Mg^{2+}-ion is a necessary co-factor for the formation of ATP both in chromatophores[4] and chloroplasts.[56] In isolated chloroplasts no ATPase reaction or exchange reaction between ATP and ^{32}P was found by Avron and Jagendorf,[57] who took this as evidence that the last phosphorylation reaction is irreversible. On the other hand, we have shown that a Mg^{2+}-stimulated ATPase activity exists in isolated spinach chloroplasts.[58] Oligomycin A, which appears to act on a phosphate transfer reaction in mitochondrial oxidative phosphorylation,[59] inhibits strongly light-induced phosphorylation in bacterial chromatophores,[60] but

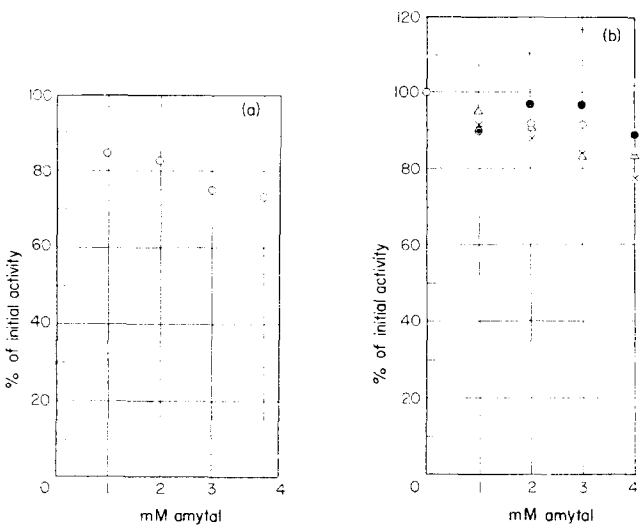


FIG. 2. Effect of amytal on light-induced phosphorylation in chromatophores and chloroplasts. (a) Chromatophores; experimental details as Baltscheffsky[72]. (b) Chloroplasts. The following stimulating agents were used: × = FMN, ○ = FAD, △ = phenazine methosulphate, ● = menadione and + = ascorbate. The phenazine methosulphate and menadione series represent mean values of three and two experiments, respectively. The rate of phosphorylation in the ascorbate series was extremely low. With the exception of the phenazine methosulphate series all tubes contained 30 μmoles of ascorbate. Further experimental details as in Baltscheffsky[61]. Partially reproduced from *Acta Chem. Scand.*[61].

has very little effect in plant chloroplasts.[61] This may indicate that the phosphorylation mechanisms are different in these two systems.

Recently we have obtained some new information about the electron transport in light-induced phosphorylation using certain well-known inhibitors of electron transport in phosphorylating animal mitochondria. The inhibitors employed were amytal, atebrin, antimycin A and HOQNO. In mitochondria, amytal acts between diphosphopyridine nucleotide and flavin,[62, 63] atebrin at the flavin level[64, 65] and antimycin A and HOQNO, as mentioned, between cytochrome *b* and cytochrome c_1.

As is shown in Fig. 2 amytal did not inhibit light-induced phosphorylation in either chromatophores* or chloroplasts. This suggests that photosynthetic systems lack an

* Mrs. M. Baltscheffsky participated in most of the experiments with photosynthetic bacteria.

electron transport step identical with that between DPNH and flavin in phosphorylating mitochondria. Earlier it has been shown that diphosphopyridine nucleotide does not seem to be involved in light-induced phosphorylation of chloroplasts.[50]

Low concentrations of atebrin strongly inhibited light-induced phosphorylation in extracts of *Rhodospirillum rubrum*. This is shown in Fig. 3, where it can also be seen that FAD is capable both of stimulating markedly the light-induced phosphorylation and of counteracting the inhibitory effect of atebrin. The evidence from these three experiments thus indicates that flavin is involved in light-induced phosphorylation in *R. rubrum*. In Fig. 4 it is demonstrated that atebrin also strongly inhibited the chloroplast system, regardless of whether phosphorylation had been initiated by addition of

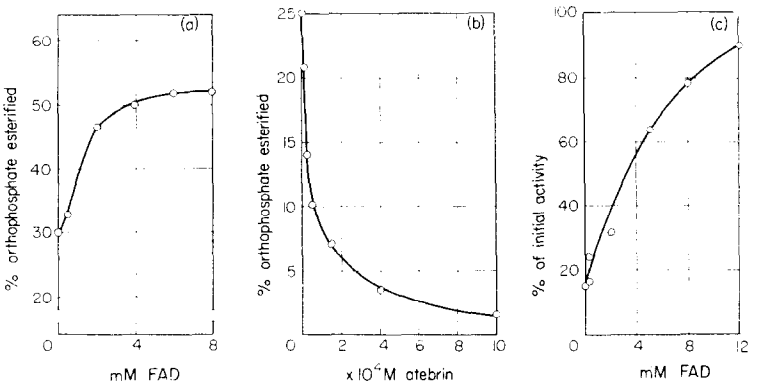


FIG. 3. Evidence for the participation of flavin in light-induced phosphorylation of chromatophores. (a) Stimulation of light-induced phosphorylation by FAD. (b) Inhibition of light-induced phosphorylation by atebrin. (c) Reversal of the inhibitory effect of atebrin on light-induced phosphorylation by FAD. The tubes contained 2×10^{-4} M atebrin. The value of 100 for "per cent of initial activity" corresponds to the value obtained in the absence of atebrin. Experimental details as in Baltscheffsky-[7]. Partially reproduced from *Biochim. Biophys. Acta*[72].

flavin mononucleotide, flavinadenine dinucleotide, menadione, ascorbate or phenazine methosulphate. This indicates that an endogenous flavoprotein must be involved. This possibly is the FAD-containing TPNH-specific diaphorase which has been isolated from chloroplasts by Avron and Jagendorf[66] and can reduce both flavin mononucleotide and menadione. In the chloroplast system no release of the inhibition induced by atebrin was obtained with FAD. On the contrary, it was observed that 2 mM FAD completely inhibited light-induced phosphorylation.[61]

In Fig. 5 it is shown that antimycin A and HOQNO in similar concentrations as those necessary to block mitochondrial respiration[67, 68] gave an inhibition of the bacterial light-induced formation of ATP, whereas in order to obtain inhibition in plant chloroplasts, a roughly thousandfold greater concentration of these inhibitors must be added. Thus, whereas a component of similar nature appears to be acted upon in mitochondria and in chromatophores, the nature of the action of these inhibitors on the chloroplast system is clearly different in some way. From the laboratory of Green [69] evidence has been reported that antimycin A may act upon coenzyme Q in mitochondria. It is interesting in connexion with the inhibitor studies just reported

that coenzyme Q also has been found in *Rhodospirillum rubrum*[70] and that "plastoquinone", a similar but not identical quinone is concentrated in chloroplasts.[61]

The inhibitor studies reported here have supplied evidence for a role of endogenous flavin in light-induced phosphorylation, and flavin is included in the tentative scheme given for the electron transport of this process both in chromatophores and in chloroplasts. As is seen from the schemes, endogenous flavin is assumed to participate in the

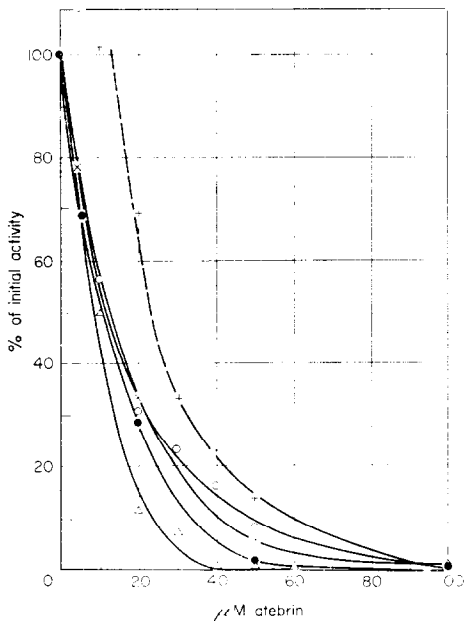


FIG. 4. Effect of atebrin on light-induced phosphorylation in chloroplasts. The following stimulating agents were used: × = FMN, ○ = FAD, △ = phenazine methosulphate, ● = menadione and + = ascorbate. The rate of phosphorylation in the ascorbate series was extremely low. With the exception of the FAD and phenazine methosulphate series all tubes contained 30 μmoles of ascorbate. Experimental details as in Baltscheffsky[61]. Partially reproduced from *Acta Chem. Scand.*[61]

electron transport whichever of the stimulatory agents menadione, flavin mononucleotide or phenazine methosulphate, is used.

Chromatophores

→ flavoprotein → *b*-type cytochrome → coenzyme Q → cytochrome c_2 →

Chloroplasts

→ TPN → flavoprotein → | → ?

menadione
flavin mononucleotide
phenazine methosulphate

In support for the position of flavin in chromatophores in the same chain as the other components may be mentioned the demonstration that the flavinadenine dinucleotide-stimulated part of light-induced phosphorylation was inhibited by low concentrations

of antimycin A and HOQNO.[72] Further support for the position of flavin comes from the finding that phenazine methosulphate, which provides a by-pass for electrons around the site where antimycin A and HOQNO inhibit the light-induced phosphorylation in bacteria[41, 73] has been shown to be an acceptor of electrons from flavoenzyme[74, 75] in a mitochondrial system.

If menadione, flavin mononucleotide and phenazine methosulphate act as stimulating agents for light-induced phosphorylation of isolated chloroplasts by providing a by-pass around some blocked physiological step in the electron transport sequence, it is possible that several of the electron carriers which have been found in chloroplasts

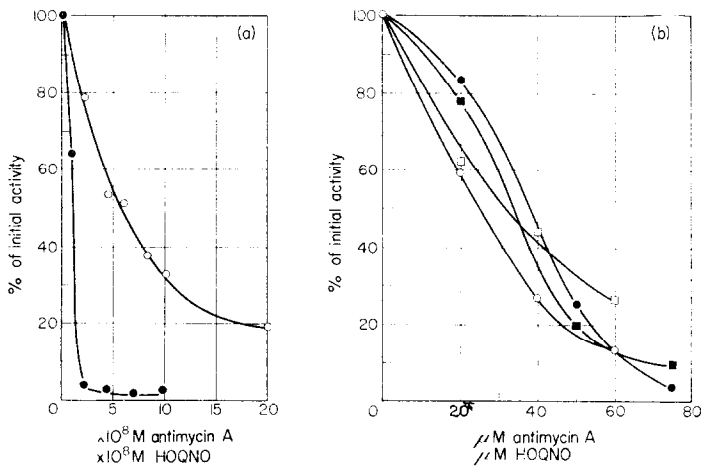


FIG. 5. Effects of antimycin A and HOQNO on light-induced phosphorylation in chromatophores and chloroplasts. (a) Chromatophores: ● = antimycin A, ○ = HOQNO. (b) Chloroplasts. The following stimulating agents were used: ○ and ● = FMN, □ and ■ = phenazine methosulphate. ● and ■ = antimycin A, ○ and □ = HOQNO. Experimental details as in Baltscheffsky[61]. Partially reproduced from *Acta Chem. Scand.*[61]

may be situated in the by-passed portion of the electron transport chain. As an example of a possible similarity between the electron transport in chloroplasts and chromatophores (see above) it may be emphasized that chloroplasts also contain a *b*-type cytochrome (cytochrome b_6[76]), the previously mentioned coenzyme Q-like quinone (plastoquinone[71]) and a spectrally *c*-type cytochrome (cytochrome *f*[77]). One may speculate that an arrangement of individual electron carriers in chloroplasts similar to that suggested above for chromatophores may be possible. From the little information yet available, the redox potentials of the cytochromes[76] would agree with such a sequence; however kinetic data obtained by Chance and Sager[78] do not support it.

Clearly, the mechanisms for electron transport and for formation of ATP in different systems still offer the investigator challenging problems. It is hoped that this presentation has given an impression that interesting similarities have already been found between the different systems for electron transport phosphorylation, and that possibly more similarities are only waiting to be demonstrated. The fact that organelles as different as animal mitochondria, plant chloroplasts, and bacterial chromatophores

have been shown to exhibit several common denominators with respect to their ATP-generating function indicates the usefulness of applying a comparative biochemical approach in this area. Although certain differences have been revealed, and others may be anticipated, it appears fruitful at present to base any working hypothesis for the investigation of electron transport phosphorylation in various subcellular systems on the established occurrence of important similarities.

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