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Energy Reception and Transfer in Photosynthesis*

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THE article by Lehninger (p. 136) presents a detailed and excellent description of how a cell can obtain energy by the combustion of carbohydrate. This article describes the reverse process, namely, how the green cells of plants are able to transform electromagnetic energy into chemical energy—by the absorption of carbon dioxide and water, which are the end products of the animal cell, and by the absorption of light—and how they produce the foodstuffs which are the beginning of the process of combustion. Figure 1 illustrates diagrammatically the content of this article.

The starting points in this case are carbon dioxide and water which contain the elements carbon, hydrogen, and oxygen in their lowest energy forms with respect to biological processes. The chemical energy which is accumulated is represented here (Fig. 1) in the form of oxygen (molecular oxygen), on the one hand, and a carbohydrate, on the other. The process itself has been divided, both theoretically and physically, into two rather easily separable stages. The first of these is the absorption of light by chlorophyll or by some related pigments and the subsequent separation of water into a reducing agent, here represented by [H], and some oxidizing fragment not specifically designated here but presumably one of the *A*, *B*, *C*, series. The oxidizing agent, or the primary oxidant, ultimately becomes molecular oxygen. In the second stage, the reducing agent is used to reduce carbon dioxide to the level of carbohydrate and other plant materials.

In order to see how the energy of light actually is accumulated in chemical form, it seems wise to describe what is known about the sequence from carbon dioxide to carbohydrate, and to determine at what point in that sequence the energy ultimately derived from the light enters, and from that point on to recognize and to define the problem of the primary quantum conversion into its first recognizable chemical form. Consider first in some detail what is known about the path of carbon so that one can define more precisely into what sort of energy the light must be converted in order to carry out that process.

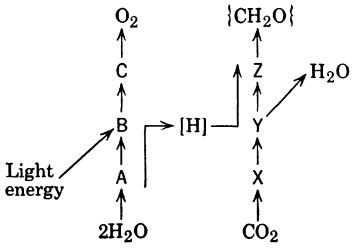

FIG. 1. Elementary photosynthesis scheme.

With the availability of radiocarbon (carbon-14) from the nuclear reactors some 15 years ago, it became possible for our laboratory to trace this sequence in some detail. The plant material used in most of the experiments was the unicellular green alga, *Chlorella*, and occasionally the alga, *Scenedesmus*; higher plants as well as separated photosynthetic material were used also. Figure 2 shows a photomicrograph of the algae cells commonly used; these are the *Chlorella* cells and the green stuff contained in a cup-shaped chloroplast can be seen. It is illustrated well by one of the cells in the upper right-hand corner.

The steps taken to trace the carbon sequence are as follows. The first operation constitutes a selection of cultures, which are grown in 200-cc flasks, and are transferred later into much larger continuous one-liter culture flasks. These are called shake-flask cultures in which algae can be maintained for years at a time.

The most recent type of culture device that is used in our laboratory is a continuous tube culture in which the density of the cells is monitored by a photoelectric cell which controls the automatic feeding of the medium, so that the cells are maintained in a steady state of growth.

The algal sample then is harvested and is used for the feeding of radiocarbon which is done in a special "hot box." In this box, the cells are placed in a little vessel (lollipop) between lights and are adapted with the concentration of normal carbon dioxide of interest. Radioactive carbon dioxide then is administered to the

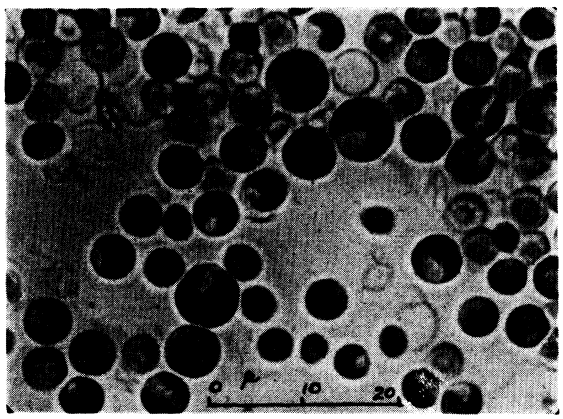

FIG. 2. Photomicrograph of *Chlorella* cells.

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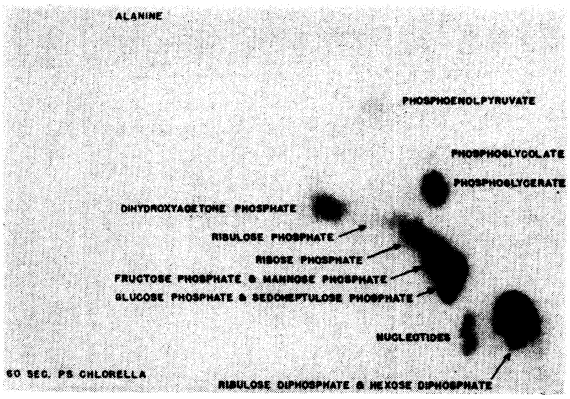


FIG. 3. Chromatogram of extract from algae, indicating uptake of radiocarbon during photosynthesis (60 sec).

adapted cells for a suitable length of time in order to trace the paths taken by the carbon atoms. The radioactive carbon usually is injected in the form of a solution of sodium bicarbonate. It is kept in contact with the cells for a specified period of time after which the cells are killed by a variety of methods; for example, the cells may be dropped into methanol at room temperature. The cell extract then is analyzed by the method of paper chromatography for the radioactive compounds which it may contain. In order to achieve this analysis, the extracts must be concentrated and a vacuum evaporator is used in a routine fashion to reduce the volume from 200 cc, or a liter, down to a cubic centimeter or so.

From this concentrated extract, an aliquot is taken and placed on the corner of a piece of filter paper for chromatographic separation. Prior to chromatography, the radioactivity of the origin is counted in a quantitative way. The filter paper then is hung in a box, in a trough in which a solvent is placed which passes over the filter paper and spreads the compounds down the side of the paper according to their relative solubilities in the solvent. The most soluble run the most rapidly. This procedure results in a set of spots along the side of the filter paper, depending upon the properties of the compound being analyzed. Some of these compounds overlap each other in one solvent system. The paper

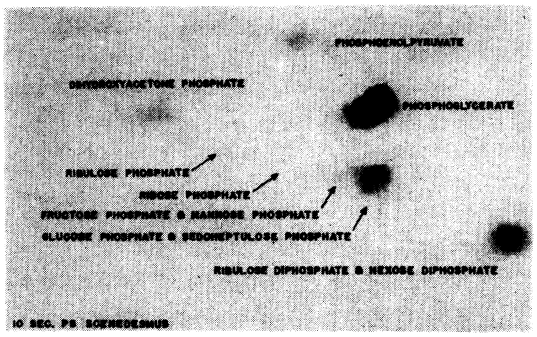


FIG. 4. Chromatogram of extract from algae, indicating uptake of radiocarbon during photosynthesis (10 sec).

then is removed from the box and dried overnight. The paper is rotated 90° and placed in another trough, in another box, with another solvent. The starting point is now a whole series of spots along the top edge of the paper. Another solvent is put in the trough and it spreads those spots out again in a similar operation. After this operation is completed, the paper is dried for a second time. The next problem is to locate the radioactive materials on the paper.

The coordinates of the material with respect to the origin constitute a physical property which is useful in the identification of the compound being analyzed. The compounds are not colored, and the only property that can be used to locate them is their radioactivity. This is done by placing the paper in contact with a sheet of photographic single-coat blue-sensitive x-ray film which becomes exposed by the radioactivity on the paper. Wherever there is a radioactive spot on the paper, there appears an exposed area on the film after a suitable period of time. For quantitative work, the film, covered

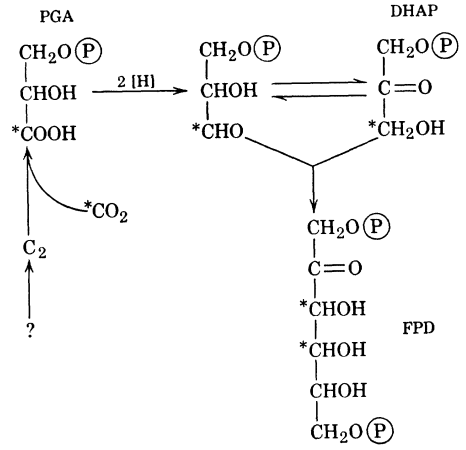


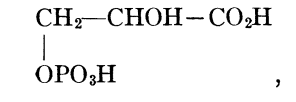
FIG. 5. Path of carbon from CO_2 to hexose during photosynthesis.

by the paper, is placed on an x-ray viewer. The paper is explored with a Geiger counter. The compound can be identified then by its coordinates, and its amount can be determined by the amount of radioactivity found in the spot. A greater or lesser degree of resolution depends upon the nature of the solvent systems used and upon the time used for the chromatography.

Figure 3 shows a chromatograph picture of the extract of a 60-sec illumination of *Chlorella*. One can see that a 60-sec illumination is much too long to find the earliest compounds into which the carbon enters in the course of its conversion from carbon dioxide to carbohydrate. Figure 4 shows a chromatogram of a shorter illumination (10 sec). Here, one compound, phosphoglyceric acid, dominates the scene. Our laboratory has been able to get the same type of sequence of events with isolated chloroplasts plus a number of cofactors. The phosphoglycerate appears no matter how the chloroplasts or the algae are killed: whether they are

killed hot or cold, whether they are killed in alcohol, acetone, etc.

This, then, is an initial clue that the first isolable stable compound obtainable by these methods, or at least identifiable by these methods, is phosphoglyceric acid:



a three-carbon compound containing a low-energy phosphate group.

The next problem is to determine which of these carbon atoms is radioactive. This has been done by chemical-degradation methods. By taking the compound (phosphoglyceric acid) apart, one carbon atom at a time, it was found that the carboxyl group became radioactive first and the other two later. From this, together with the degradation of sugar molecules that came out in the same experiment, our laboratory was able to determine how the sugar molecule was constructed.

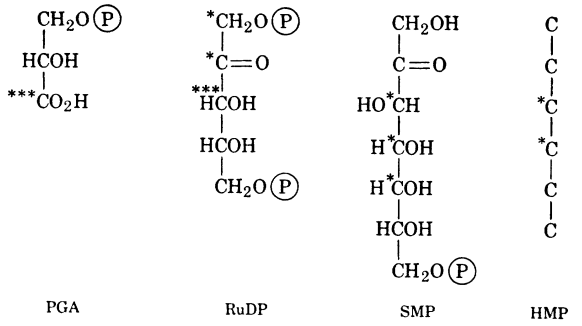


FIG. 6. Distribution of radioactive carbon in certain sugars.

Figure 5 shows what was supposed to have occurred. The phosphoglyceric acid is shown as PGA. By reduction, this goes to triose phosphate. If the ketose phosphate is isomerized, and then combined with the isomer, a hexose diphosphate can be formed with the radioactive carbon atoms in the middle of the molecule. In this manner, the six-carbon molecule can be formed, but one does not know the origin of the three-carbon compound. Although two-carbon-containing molecules have not been found, Fig. 6 illustrates some findings of our laboratory.

In addition to the PGA, there is a five-carbon-atom compound, a sugar (ribulose diphosphate), a seven-carbon-atom sugar (sedoheptulose diphosphate), and, of course, the six-carbon-atom sugars. The stars on Fig. 6 indicate some idea of the way in which the radioactivity is distributed in these various sugar compounds. The heptose and the pentose can be made from the hexose, as shown in Figs. 7 and 8.

Figure 7 illustrates the method by which the heptose may be produced. From one molecule of hexose and one

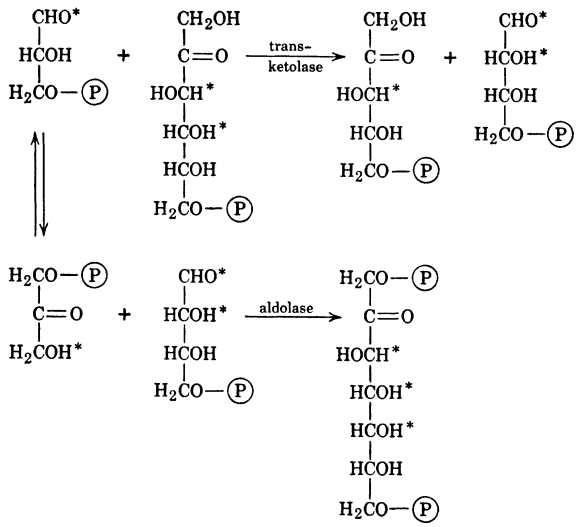


FIG. 7. Formation of a heptose from triose and hexose.

molecule of triose (taking off the top two carbon atoms of the hexose), a pentose and tetrose can be formed; the tetrose is labeled in the top two carbon atoms. The tetrose then can combine with a triose to make a heptose with the proper distribution of radioactive carbon.

Figure 8 shows the way in which the pentose is put together, by combination of a heptose and a triose, in the same kind of reaction (the transketolase reaction) leading to two different pentoses which are in equilibrium with each other. This analysis does not distinguish between the two pentoses. All of these rearrangements are done at the sugar level; triose, tetrose, pentose, hexose, and heptose are all at the same redox level. They are all of them very nearly at the same energy level and there is thus practically no energy required for these rearrangements. However, no experiments of this type gave the desired information—namely, the origin of the three-carbon piece in the first place. This awaited a quite different kind of experiment, an experiment in which a steady state first was established in the organism, after which some environmental variable was changed suddenly. The transients that resulted from changing some of these variables were examined.

Figure 9 shows the results of such an experiment. A steady state is established by feeding the radiocarbon

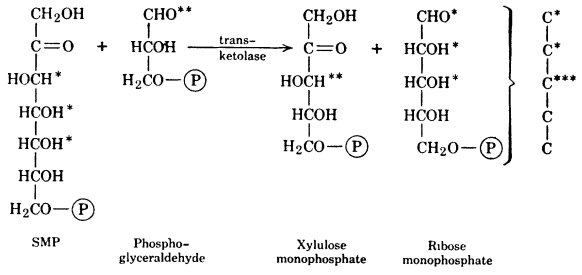


FIG. 8. Proposed scheme for labeling of pentose.

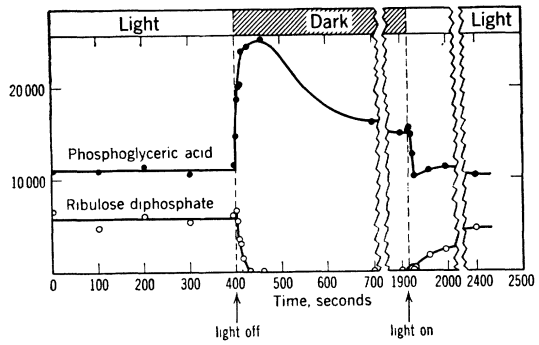


FIG. 9. Light-dark changes in concentrations of phosphoglyceric acid and ribulose diphosphate.

long enough to the plant to saturate the phosphoglyceric acid and the other compound mentioned. The lights are turned off suddenly, and the transient ensues. The phosphoglyceric acid rises suddenly and the ribulose diphosphate falls precipitously. This complementary behavior is the clue needed for the relationship between ribulose diphosphate and phosphoglyceric acid. It seemed as though the ribulose diphosphate was disappearing by combining with the carbon dioxide (that is, five carbons plus one, making a total of six carbon atoms) to produce two molecules of phosphoglyceric acid. If this is the case, then the relationships of the various compounds can be shown diagrammatically, as in Fig. 10.

In Fig. 10, the ribulose diphosphate combines with carbon dioxide to form phosphoglyceric acid which is reduced by light to triose, triose then going through this series of sugar rearrangements (shown in Figs. 6, 7, and 8) back again to the pentose. Turning the light off stops this reaction. When the reduction reaction is stopped, phosphoglyceric acid builds up and the ribulose diphosphate disappears. Figure 10 simply expresses in a scheme what the transient experiment revealed.

But this scheme (Fig. 10) predicts another type of transient. If the light is kept on and the CO_2 stopped, there should be a different kind of transient; namely, the ribulose diphosphate should build up suddenly and the amount of the phosphoglyceric acid should fall. This experiment has been accomplished with considerable difficulty. The results are shown in Fig. 11.

Figure 11 shows the steady state for ribulose diphosphate and the steady state for phosphoglyceric acid with the CO_2 at a concentration of 1%. At the vertical line, the CO_2 concentration is shifted from 1 to 0.003% by turning

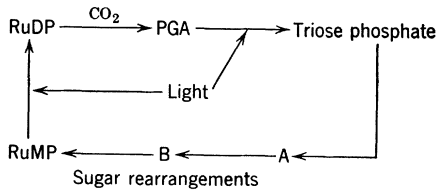


FIG. 10. Formation of PGA from RuDP.

the stopcocks. Under those circumstances, the predicted changes were observed, at least in the initial phase of the transient. The amount of phosphoglyceric acid fell and the amount of ribulose diphosphate rose. There is a number of kinetic oscillations here which are reminiscent of the kinds of oscillations one gets in circuitry, and possibly they are analogous. One or two attempts were made to reproduce these oscillations by putting first-order rate constants into the various reactions that are involved here and then running them through a digital computer. This kind of oscillation can be obtained but this work has not been pursued yet beyond the elementary stage of the first kind of transient. This kind of study will lead to much more-detailed knowledge of the mechanism of cellular response to changes in external or internal environments. It is a very simple system to use and one which is amenable to complete analysis, both experimentally in terms of the compounds

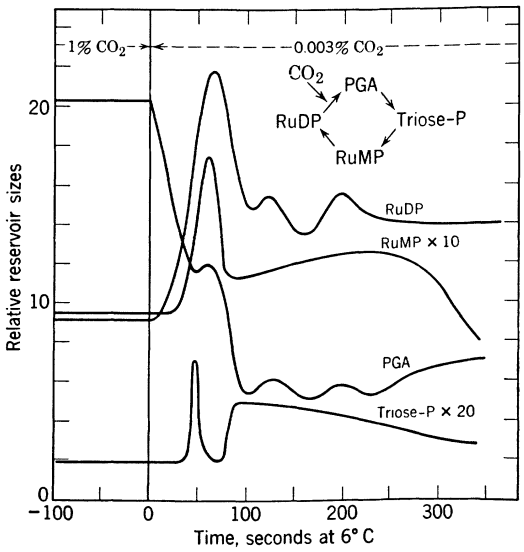


FIG. 11. Transients in the regenerative cycle.

involved and theoretically in terms of the simple kinetics involved.

Figure 12 shows the completed photosynthetic cycle in which there are put together all of the rearrangements of hexose and triose through heptose and pentose, back again to the ribulose diphosphate which then picks up carbon dioxide to make two molecules of phosphoglyceric acid.

In trying to visualize this particular step, a proposed mechanism for this reaction is shown in Fig. 13. Here, the ribulose diphosphate is written as the ene-diol, combining with bicarbonate ion to form an intermediate, hypothetical up to this point, an α-hydroxy-β-keto acid, which then is hydrolyzed to give two molecules of phosphoglyceric acid. This α-hydroxy-β-keto acid, according to our chemical knowledge, would be very unstable either to decarboxylation, in which case it would

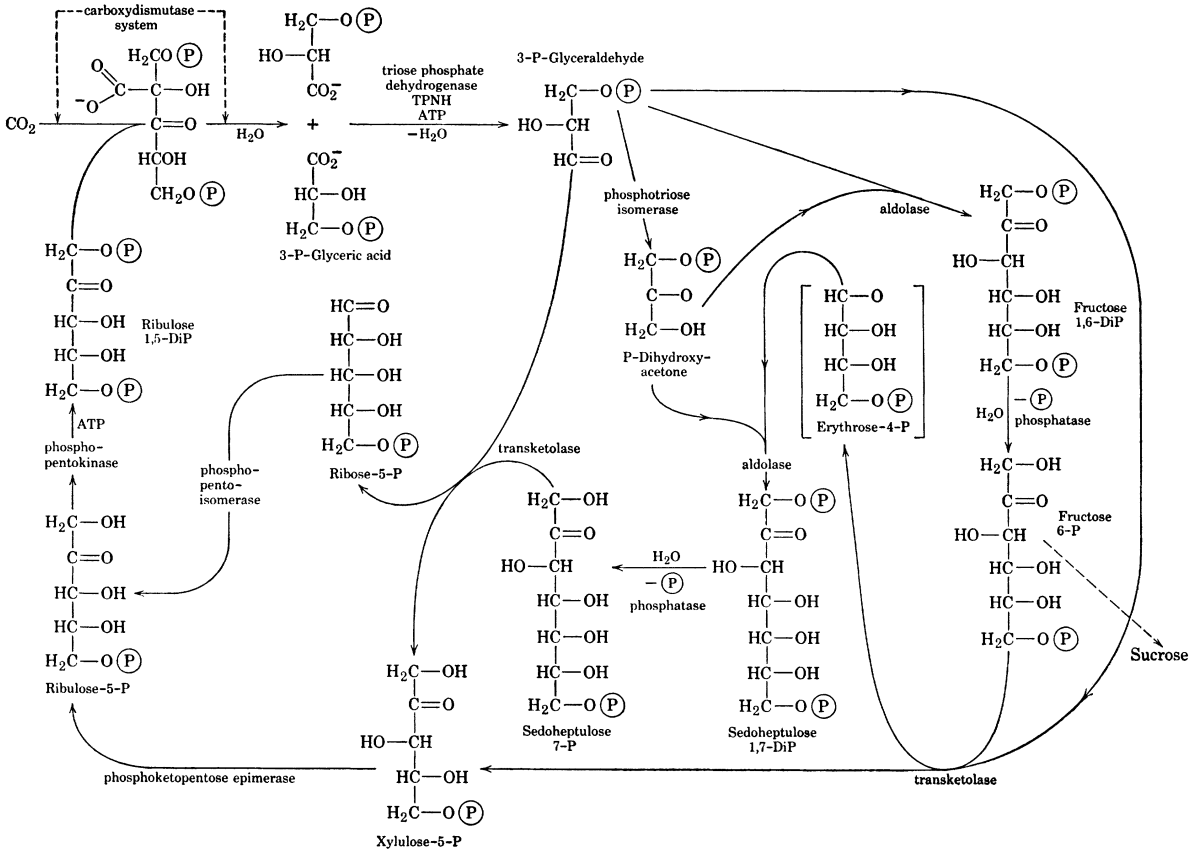


FIG. 12. The photosynthetic carbon cycle.

lead back to ribulose diphosphate, or to hydrolysis, in which case it would lead the other way. Fortunately, in our laboratory, a close relative of this intermediate, and probably some of the compound itself, has been found.[1] On theoretical grounds, it was decided that one might expect a compound of this sort to appear down in the diphosphate area of the chromatogram. Figure 14 shows that chromatogram which ran in a solvent for 48 hr in both coordinates. What was originally a single spot, which is dominantly ribulose diphosphate, now breaks up into at least three spots. The principal spot is the ribulose diphosphate; another one is hexose diphosphate and heptose diphosphate; and the last spot turned out to be a keto-acid diphosphate. It is not the β-keto-acid but rather the γ-keto-acid diphosphate which apparently is an artifact of the method of killing, but it does come from the β-keto-acid diphosphate which is still a labeled compound and does show its presence in small amounts.

In Fig. 15, one sees the diphosphate plus some dephosphorylated compounds, particularly the γ-keto-acid

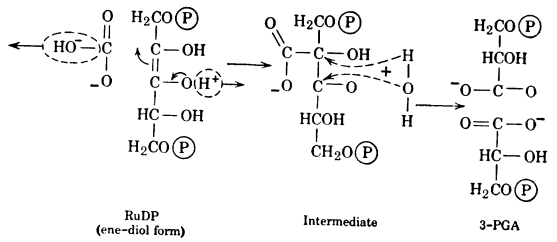


FIG. 13. Mechanism of carboxylation reaction.

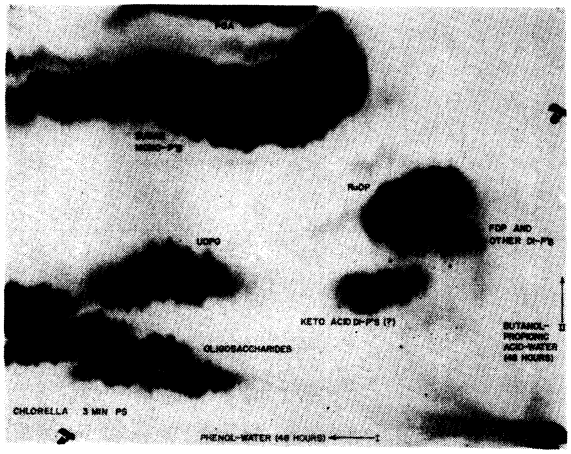


FIG. 14. Chromatogram of extract of *Chorella* after three minutes of photosynthesis in the presence of radiocarbon. The solvents were allowed to run for 48 hr in each dimension.

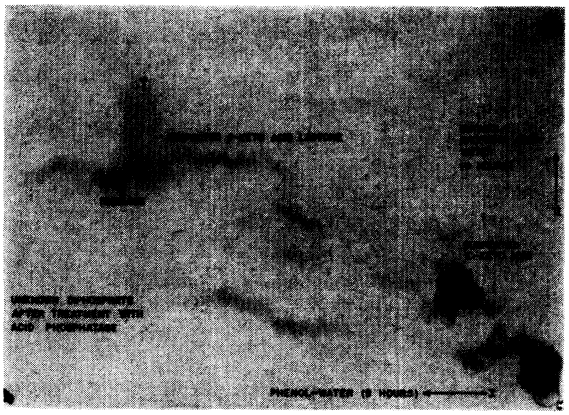


FIG. 15. Unknown sugar phosphate after treatment with acid phosphatase.

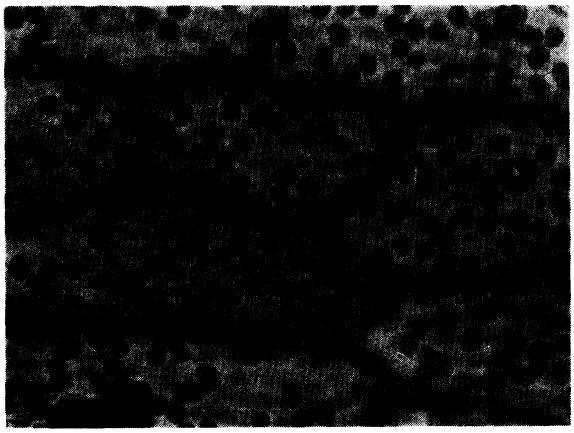


FIG. 17. Photomicrograph of chloroplasts from liverwort.

diphosphate. And here is seen a trace of the β-keto acid in its lactone form because it is stabilized as a lactone, enough to catch it on a chromatogram. Racker[2] has carried out this whole sequence (Fig. 12) by collecting all of the enzymes that were indicated in that figure. By putting in the suitable substrates, ribulose and carbon dioxide, he was able to pull out glucose phosphate from the CO_2. The immediate sources of energy are the two compounds adenosine triphosphate (ATP) and reduced pyridine nucleotide (TPNH). Figure 16 shows the needed relationships.

Figure 16 shows the photosynthetic carbon cycle in a simplified form. Carbon dioxide enters to make the β-keto acid which then goes to the phosphoglyceric acid. The only points of entry of energy into this system, as it is written now, are where there is a need for ATP and for reduced pyridine nucleotide. (These are the points of entry of energy into this wheel.) These points are the gears which drive the cycle in a forward direction.

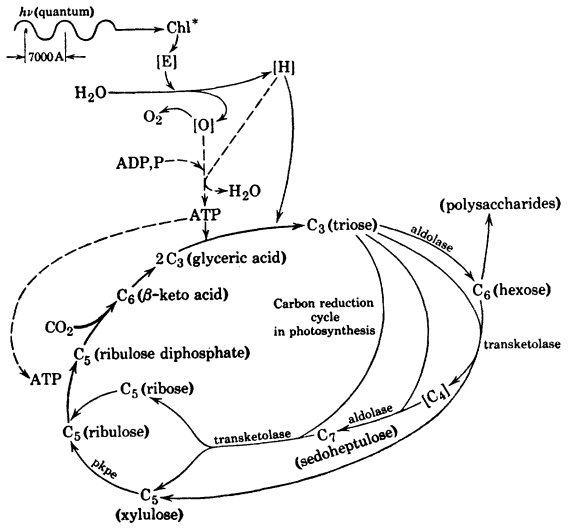


FIG. 16. Suggested cyclic scheme for relationships in photosynthesis.

Clearly the ATP and the TPNH (energy sources for the photosynthetic cycle) must come ultimately from the light. The remainder of this paper is devoted to this problem.

How does the light, which is absorbed by the chlorophyll, produce these two substances (ATP and TPNH) which are known to be required for carbon reduction? Before going into the details of a possible answer, consider some pictures of the apparatus which does it. Figure 17 shows a photomicrograph of liverwort tissue; one can see the cells, the cell walls, and the chloroplasts in which the chlorophyll is distributed very nicely inside the cells. Figure 18 shows isolated chloroplasts from spinach. (These are bigger chloroplasts and they have been isolated in sucrose solution.) All of this carbon reduction, oxygen evolution, phosphate production can be done with these chloroplasts removed from their natural habitat inside a cell. However, in order for that to be possible at anything approaching the rates at which it occurs in the living cell, one must add cofactors, some of which are heat stable, some of which are heat labile, and some of which are unknown but which are obtained out of the sap of the cells. In any case, this whole process can be done outside the cell.

Figure 19, from the work of Steinman and Sjöstrand,[3] shows an electron micrograph of a chloroplast. The picture on the right is shown at a higher magnification. The outstanding features of the chloroplast structures are lamellae, discussed in the following.

For some twenty years, it has been possible to carry out the photochemical evolution of oxygen by isolated chloroplasts using a suitable hydrogen acceptor such as ferrocyanide or quinone. This is called the Hill reaction. In the last five years, by preparing the chloroplasts in a manner which presumably does not destroy a chloroplast membrane or perhaps precipitates enzymes from the cytoplasm onto the chloroplast (i.e., preparing the chloroplasts in salt or sugar solutions), our laboratory has been able to carry out two other reactions with the chloroplasts. These reactions are the reduction of CO_2

as well as the evolution of oxygen, and, finally, the production of ATP by illumination of the chloroplasts. These three reactions, carbon-dioxide reduction (or, one step further back, the production of reduced pyridine nucleotide rather than CO_2 reduction), ATP production, and oxygen production are the three processes that one now can accomplish with the chloroplasts. The reduction of CO_2 requires two of the items and the evolution of oxygen may or may not require ATP.

How many of these things can be done simultaneously by the chloroplasts? In a recent conference,[4] it became evident that all of the pair combinations of these processes (i.e., CO_2 reduction, ATP production, and oxygen production) could be demonstrated.

It has been demonstrated that one could make one mole of pyridine nucleotide for every atom of oxygen produced. Simultaneously, one can demonstrate the production of one mole of ATP for every equivalent of reduced pyridine nucleotide produced. (One can demonstrate now that one mole of ATP is created for every equivalent of oxygen produced simultaneously.) This is something beyond the oxidative phosphorylation about which Lehninger writes (p. 136); that is, the oxidative phosphorylation would be the production of ATP by a recombination of TPNH and intermediate oxidant. It now appears that all three of these things can be reproduced equivalently at the same time.

The apparatus which does this in the plant has been shown in three magnifications—the whole chloroplasts in the cells, the chloroplasts outside the cells, and, finally, the lamellar structure of the chloroplasts as seen by electron microscopy. Studies of this lamellar structure have resulted in a particular conclusion which is sufficiently general to be stated; namely, the chloroplast lamellae seem to be (no matter what plant cell is investigated) disk-like in character; they seem to be connected at the edges to form a hollow disk—this is the lamella. The lamellae are quite long, about 2000 A

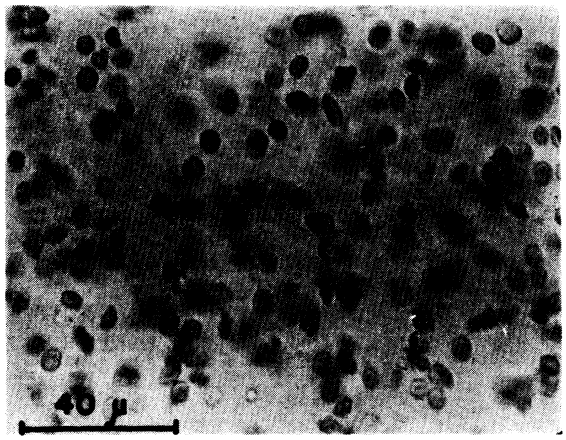


FIG. 18. Photomicrograph of spinach chloroplasts.

in spinach chloroplasts. The lamellae do not appear in the chloroplast in the absence of chlorophyll or protochlorophyll. If, in some way, one prevents either the formation of protochlorophyll or of chlorophyll, one prevents the appearance of well-developed lamellae. Protochlorophyll alone will induce in cells which are normally capable of making them structures which look like these lamellae.

The possible function of this lamellar structure of the chloroplasts is discussed now. The basic problem of photosynthesis can be reduced to the problem of converting a 35- to 40-kcal quantum of energy into some chemical potential. In order to do this, one presumably has to find a reaction, which will take up 35 kcal at one time. The products of this reaction must not back-react. The 35 kcal are a great driving force for the back-reaction, so there must be some mechanism provided in the apparatus to prevent it.

There are a number of other difficult requirements which must be fulfilled in this quantum-conversion process with respect to the time constants involved. For

FIG. 19. Ultrastructure of chloroplasts [from E. Steinman and F. S. Sjöstrand, Exptl. Cell Research 8, 15 (1955)].

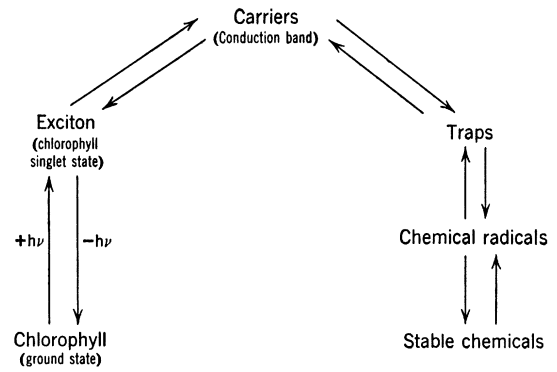


FIG. 20. Hypothetical scheme for light-energy utilization on chloroplasts.

example, following the absorption of the quantum, there must be a very efficient way in which the excited state of chlorophyll can be converted very quickly into a long-lived chemical potential because of the efficiency of the over-all process, regardless of whether one believes the maximum efficiency to be 30 or 60%.

There are a number of approaches to this problem which are based upon ordinary statistical solution photochemistry. In the past, I have looked for reactions unique to chlorophyll that might conceivably be used to store this 35 kcal of energy, such as reduction of chlorophyll to bacteriochlorophyll (that is, adding two more hydrogens to the chlorophyll molecule). Perhaps the process can be accomplished in the reverse manner, taking off two hydrogens from the chlorophyll molecule, making protochlorophyll, and hanging the hydrogen atoms onto something else. These are possible reactions of chlorophyll.

As a matter of fact, our laboratory demonstrated both of these reactions some years ago. More recently, and more elegantly, they have been demonstrated by Krasnovskii[5] in systems that are more nearly related to those which one finds in the living organism.

As a result of a variety of requirements, as a result of the recognition of this highly organized apparatus in which chlorophyll occurs in the chloroplast, and as a result of the failure to solve the problem with solution photochemistry, our group has turned to the notions of cooperative phenomena of organized systems such as those which are represented by barrier-layer cells in physics. Our group is trying to visualize how a lamellar structure such as this conceivably might be an unsymmetrical layer in which one could generate, by the absorption of light, an oxidant and a reductant, on opposite sides of the layer, so that they could not back-react easily and could persist for a long period of time. These substances (reductant and oxidant) should live long enough, by chemical standards, to be taken up efficiently, on the one hand, by electron acceptors to go on to make the reduced pyridine nucleotide, and, on the other hand, by electron donors to make molecular oxygen. I should like to present a proposal which fulfills all of the necessary requirements of the molecular interactions together with the need for conductivity (electrical conductivity) in certain parts of the lamellae and the consequent separation of charges.

The basic proposal is given in Fig. 20 which suggests how these lamellae achieve this energy conversion. Chlorophyll in the ground state absorbs light which brings it to its lowest singlet excited state. The excited state can move around among the chlorophyll molecules by resonance transfer (exciton migration) until a point is reached where ionization occurs. Then charge separation can take place. The exciton can be visualized as a charge-pair which cannot move separately—a positive charge and a negative charge which must move together. When a suitable point in the chlorophyll lattice is reached where the charges can be uncoupled so that they can move separately, there is a conduction band. The electrons can move in one direction and the holes, or positive charges, in another. The electrons and holes move around until they find suitable places of lower potential energy into which they fall, and there sit for times sufficiently long so that suitable chemicals can come up and take off electrons, on the one hand, and the positive holes, on the other. This leads to chemical reactions which then produce stable chemicals such as a pyridine nucleotide and perhaps hydrogen peroxide, or something else of that sort, ultimately going on to the final products.

With this concept, consider how the structure of the lamella may be interpreted in terms of the molecular constitution. It is suggested that this layer is made up of at least four components [Fig. 21(b)]. The protein enzymes involved in carbon-dioxide reduction are on the outside of the disk. The protein enzymes on the inside of the disk are involved in oxygen evolution. The separation of the two processes (carbon-dioxide reduction and oxygen evolution) is achieved by a layer of chlorophyll packed in the characteristic aromatic way. This is a very characteristic pattern of packing. The aromatic rings do not pile flat on themselves; they lie at an angle, approximately 45° to the stacking axis. This type of packing is suggested for chlorophyll.

Figure 21(a) represents chlorophyll molecules tipped this way. Packed between them are carotenoids and the phospholipids. The proposal is that, after absorption, the exciton can migrate around among a few of these chlorophyll molecules to find a suitable point of ionization where the electrons may move in one direction and the positive holes in the other. Thus, one side leads to oxygen production, and the other to the reduction of carbon.

What kind of experimental evidence might detect this kind of system? Electrodes cannot be placed on these lamellae; they are too small. But one part of this scheme is susceptible to experimental observation—namely, the trapped holes and trapped electrons. It is expected that

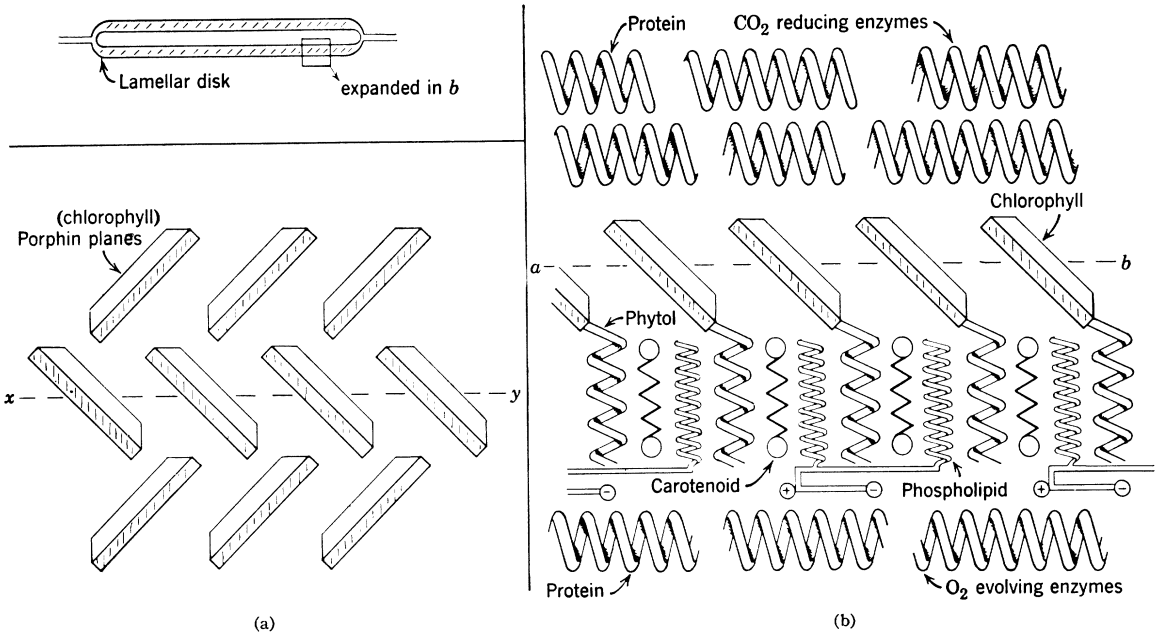


FIG. 21. Schematic representation of possible molecular structure for a lamella.

these trapped electrons are single, trapped electrons and, therefore, are detectable by paramagnetism. Our laboratory set out to search for photoinduced paramagnetism in the chloroplasts. Figure 22 shows the results of that search.[6–8] This is an illustration of electron spin-resonance signals for illuminated whole spinach chloroplasts at 25°C and at −150°C. (Similar signals, at least at room temperature, were reported from the St. Louis laboratory by Townsend.) The fact that one can get the signals at −150°C, either in chloroplasts or in algae, indicates that their production is not an enzymatic process.

The next question that may be asked is: "How fast can the signals be produced at −150°C as compared to 25°C? This is shown in Fig. 23. At 25°C, when the lights are turned on, the signals grow more rapidly than the instrument can follow them. At −150°C, the signals grow equally rapidly. The difference lies in the rate of decay of the signals. They have a complex decay—partly rapid and partly slow. At room temperature, the decay is rather rapid. At −150°C, there may be a rapid decay, but most of it is slow. This at least eliminates the possibility that the signals result from enzymatic formation. The questions remain, could the signal result from a triplet state—that is, a paramagnetic excited chlorophyll—or could the signal be the result of a

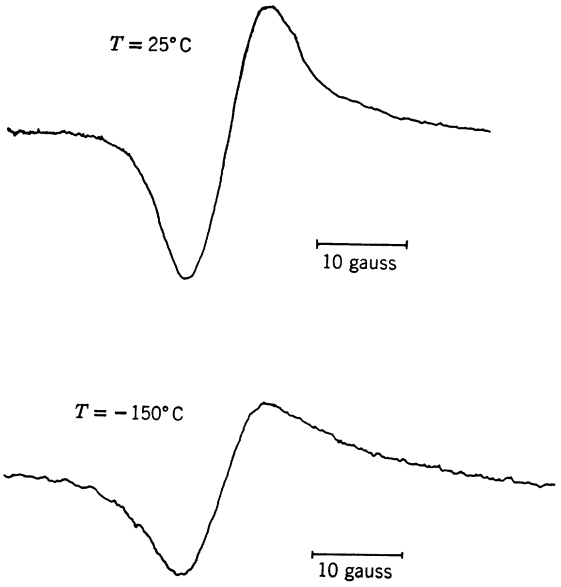


FIG. 22. Light signals from whole spinach chloroplasts.

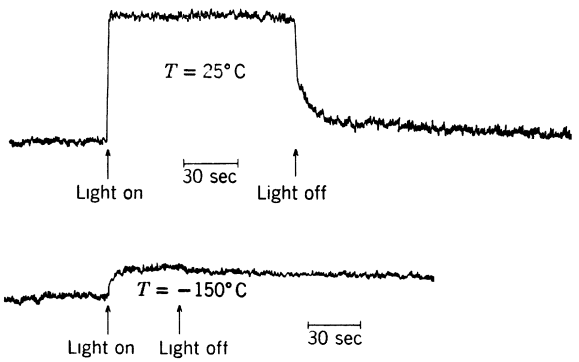


FIG. 23. Signal growth and decay time curves of whole spinach chloroplasts at 25°C and at −150°C.

photodissociation of chlorophyll, or something very closely associated with chlorophyli, to form chemical radicals, which process can take place at −150°C? These questions are discussed in the next article.

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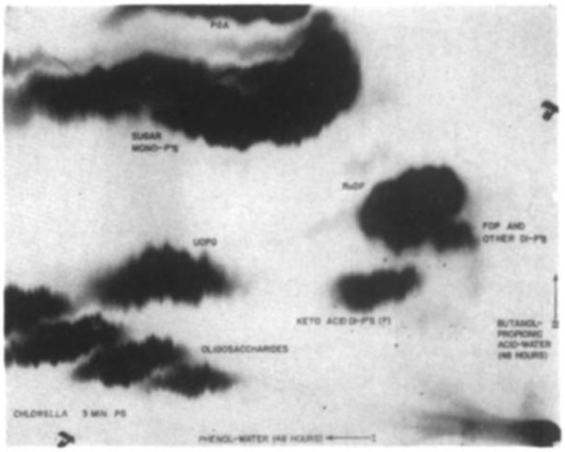

FIG. 14. Chromatogram of extract of *Chorella* after three minutes of photosynthesis in the presence of radiocarbon. The solvents were allowed to run for 48 hr in each dimension.

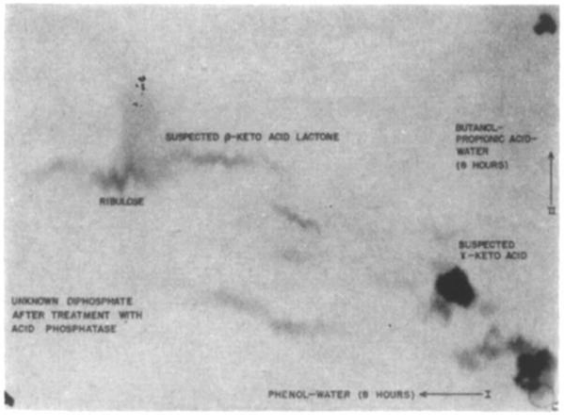

FIG. 15. Unknown sugar phosphate after treatment with acid phosphatase.

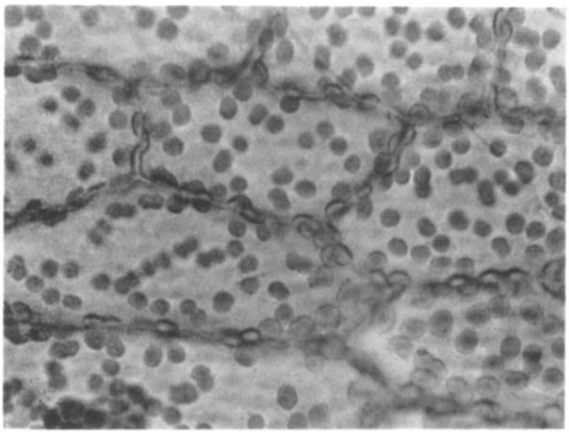

FIG. 17. Photomicrograph of chloroplasts from liverwort.

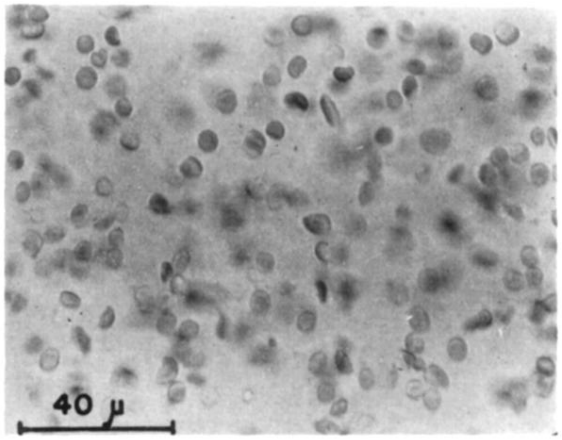

FIG. 18. Photomicrograph of spinach chloroplasts.

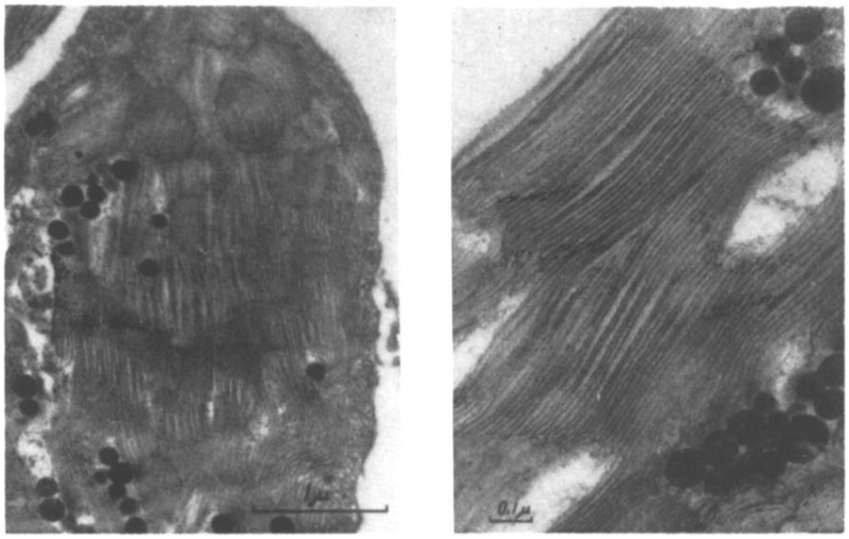

FIG. 19. Ultrastructure of chloroplasts [from E. Steinman and F. S. Sjöstrand, Exptl. Cell Research **8**, 15 (1955)].

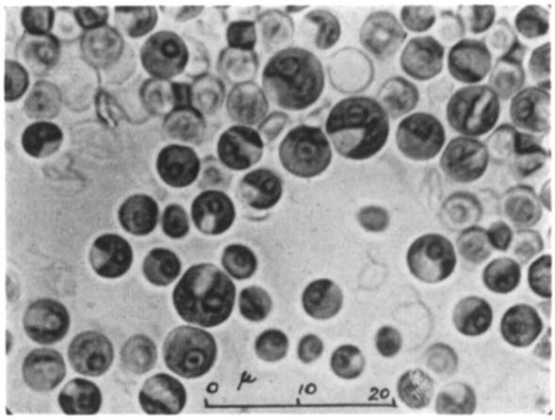

FIG. 2. Photomicrograph of *Chlorella* cells.

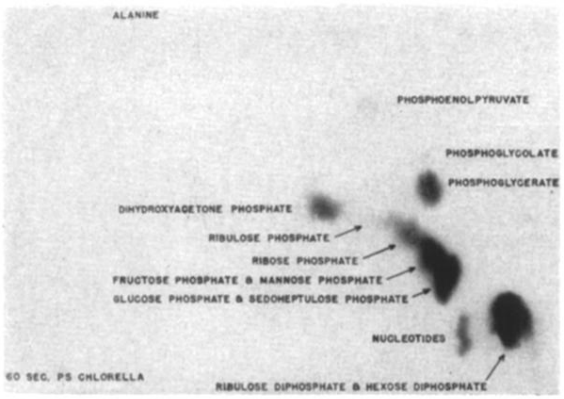

FIG. 3. Chromatogram of extract from algae, indicating uptake of radiocarbon during photosynthesis (60 sec).

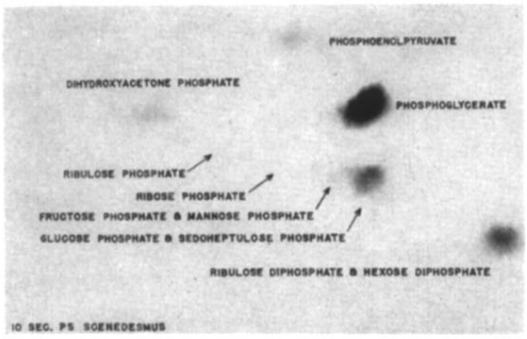

FIG. 4. Chromatogram of extract from algae, indicating uptake of radiocarbon during photosynthesis (10 sec).