## 1.018 – 7.30J

## Handout:

Adapted from: LECTURES IN BIOLOGY S.E. Luria, 1975 (MIT Professor, Nobel Laureate 1969)

[Note: This account of photosynthesis is over 35 years old. Certainly, much more is known about the structure of the photosynthetic apparatus and its underlying biophysics than is portrayed here. But this account summarizes the important features in a simple and elegant way. Luria was a master at doing this, and it has stood the test of time. P.C.]

Photosynthesis is a remarkable process, which green plants, algae, and some bacteria use to convert the carbon of  $CO_2$  to organic matter. Photosynthesis operates by fixing  $CO_2$  through a cycle of reactions called the Calvin cycle after an American biochemist (no relation of the 16th century Protestant reformer). This cycle has many instructive features.



Each circlet means one or more carbon compounds (Figure represents 6 runnings of the cycle)

The cycle takes in six molecules of  $CO_2$  one at a time and through a series of steps converts them into one molecule of glucose. The important points are:

(1) Carbon enters only as  $CO_2$  and exits only as sugar.

(2) To convert 6 moles of  $CO_2$  to one mole of sugar  $C_6H_{12}O_6$  the cycle uses 18 moles of ATP, converting it to ADP and P<sub>i</sub>. This makes sense: when a cell burns sugar to form  $CO_2$  in glycolysis and the Krebs cycle, it releases energy and stores some of it in the form of ATP. So, to make sugar from  $CO_2$ , there is need to use some ATP.

## **OVERVIEW OF PHOTOSYNTHESIS**

(3) Just as glycolysis and the Krebs cycle release electrons to NAD<sup>+</sup>, the reverse process of making sugar from  $CO_2$  requires electrons. In other words, to reduce  $CO_2$  to sugar one needs a source of *reducing power*. The cycle provides it in the form of NADPH (the relative of NADH). Twelve moles of NADPH are needed for every mole of sugar made; therefore the entire reaction should be written

 $6CO_2 + 12H_2O + 18ATP + 12NADPH + 12 H^+ \rightarrow$ 

glucose-6-P +  $6O_2$  + 18ADP + 12NADP<sup>+</sup> + 17P<sub>i</sub> +  $6H_2O$ 

NADPH is not a specialty of photosynthesis: it is used by most cells as the favorite electron donor for biosynthetic purposes.

[The Calvin cycle is used not only for photosynthesis but for all organisms that must make their organic carbon from carbon dioxide. Some important groups of bacteria, for example, oxidize  $H_2$ , or  $H_2S$ , or S, or even CO (the exhaust gas) and use the electrons from these compounds to get NADH or NADPH and to store energy as ATP made through an electron transport system. They use CO<sub>2</sub> for carbon source, fixing it by the Calvin cycle. This, however, contributes very little to the overall CO<sub>2</sub> fixation on earth.]

Note that in the equation of photosynthesis I have thrown in  $H_2O$  and  $O_2$  and have left out light. The Calvin cycle constitutes the so-called *dark reaction* of photosynthesis. What does light do? It provides the energy needed to make ATP and NADPH by the *light-reaction* part of the process.

In plant cells this takes place in a complex apparatus

## called chloroplast.

Chloroplasts contain pigments that absorb specific wavelengths of light and convert it into chemical energy.



Plants are green because the chloroplast pigments, chlorophyll and carotenoids, absorb the red light. In the chloroplasts the molecules of chlorophyll and carotenoid are present in membrane sacs, called thylakoids, which are stacked in the so-called grana. The arrangement is such that the excitations produced in the pigment molecules by the quanta of light are transferred to a special group of chlorophyll molecules (pigment system I or PSI) which act like a condenser accumulating excitation energy. Then electrons are pulled out and transferred to molecules of ferredoxin: a small protein that is literally loaded with iron atoms. The iron atoms of ferredoxin that receive electrons from chlorophyll are then in the reduced Fe<sup>++</sup> state and are powerful donors of electrons.



These electrons can then be used in a variety of ways. Some are returned to chlorophyll through a series of reactions that produce a substantial amount of ATP. Other electrons from reduced ferredoxin are side-tracked to produce NADPH.

At this point we may have generated all the ATP and NADPH we need to fix CO<sub>2</sub> to form sugar in the Calvin cycle. Naively, we might believe that everything is settled. But once more the first law of Luria raises its ugly head. When electrons are taken from reduced ferredoxin to make NADPH, they cannot be returned to chlorophyll. To regenerate chlorophyll we need a replenishing trick. In plant cells, the trick is to use a second set of pigment molecules, PSII, which when excited by light also release electrons like PSI. These electrons are transferred to the chlorophyll molecules of PSI. But the difference is that the chlorophyll molecules of PSII can regain their electrons from water, releasing oxygen: This is why plant photosynthesis generates  $O_2$ . This reaction is the source of all the oxygen in the atmosphere. The cells are happy, having balanced their equation, and we can take a deep breath. (Note that  $H_2O$  cannot provide electrons directly to PSI.)

Experiments with  $H_2$  <sup>18</sup>O have shown that all oxygen atoms come from water, not from CO<sub>2</sub>. The action spectrum, that is, the relative efficiency of various wavelengths, for plant photosynthesis looks like this:



There are two absorption maxima, one in the red at about 680 nm, the other in the blue at about 450 nm. The red maximum is also the one that is efficient for photosynthesis. Chlorophyll, a green substance, has a porphyrin ring similar to the ones present in the heme of the cytochromes, which are yellow to red.

Plants are not the only organisms that carry out photosynthesis: some bacteria do it too, but they do not generate  $O_2$  because they take electrons from substances like  $H_2S$  or organic compounds rather than from water.

Since photosynthetic bacteria do not produce oxygen, their photosynthesis is inhibited by air. If you look at a pond in the summer, you find green algae spread on the surface of the water. The photosynthetic bacteria locate themselves below the algae, where there is little oxygen left. The light that reaches them has passed through a layer of algae, but they can still use it. The bacterial pigments prefer the longer wavelengths of light, which are not absorbed by algae.

How efficient is photosynthesis? In most plants 1 to 3 percent of the energy absorbed as light is converted into sugar. In sugar cane the yield can be as high as 8 percent: this is why sugar cane is such a fantastically good crop.

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 $2 \text{ H}_2\text{O} \rightarrow \text{O}_2 + 4 \text{ H}^+ + 4 \text{ e}^-$ 

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