Basic Biology Course

6 Photosynthesis

BASIC BIOLOGY COURSE
UNIT 3
REGULATION WITHIN CELLS

BOOK 6

Photosynthesis

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Foreword

This book is part of a Basic Biology Course for undergraduates written by the Inter University Biology Teaching project team at Sussex.

The main aim of the book is to show you how green plants and certain bacteria are able to capture the energy of sunlight and transform it into the reducing power and chemical 'currency' necessary to synthesize sugars. An understanding of this vitally important process is essential for any biologist or biochemist, yet far too often it is neglected in many courses. It is as well to remember that there would be no biology without photosynthesis. In fact, it is only within the last twenty years or so that we have come to understand the major pathways involved. In the next twenty or so years perhaps an even deeper understanding of the process may enable us to increase photosynthetic yield and as a result possibly help solve the world's present problem of insufficient food.

Book 6 is in fact one of five books (Books 5 to 9 inclusive) comprising that part of the course called 'Regulation within Cells' (see outline of course structure at the front of the book). It is advisable (but not essential) that students have read Book 2 (*Electron Microscopy and Cell Structure*). Book 6 in turn provides a valuable follow-up to *Ecological Principles* (Book 4).

Brighton, Sussex, 1974

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6.0. Introduction

6.0.1. Discussion

All forms of life on earth require energy for growth, reproduction and maintenance. Since it is not possible to create or destroy energy, the energy acquired by living organisms must be obtained or transformed from another source of energy (the principle of Conservation of Energy). All plants possessing the green pigment chlorophyll – and these range from algae to trees and shrubs – are able to capture solar energy directly and transform it into essential organic food materials. Certain pigmented bacteria are also capable of photosynthesizing. However, animals and non-photosynthetic plants cannot use sunlight directly as a source of energy, so that they have to obtain their energy either by eating plants, or by eating animals which have previously fed on plants (see Book 4, *Ecological Principles*). Therefore, the ultimate source of all metabolic energy on our planet is the sun, and without photosynthesizing organisms there would be no animals (including Man!). Not only are photosynthetic organisms important for synthesizing complex organic food molecules, but they are also responsible for the production and maintenance of the oxygen in the environment as we know it, since oxygen is only produced naturally as a by-product of photosynthesis.

Solar energy and the energy exchanges (fluxes) which result on earth, are also important for another reason. The presence or absence of life on earth is in a critical balance, directly related to the energy exchanges. Fortunately for us, the flux of energy at the earth's surface is maintained in a near-equilibrium state (with small fluctuations corresponding to warm or glacial periods in geological history). If the rate at which energy enters did not equal the rate at which energy leaves, the earth's temperature would either steadily increase or decrease. Such an event would be disasterous to life, which is restricted to a very narrow temperature range (approximately 50 deg C).

This book, then, is primarily about the capture of light energy and its transformation to chemical energy in the form of living material. However, we should not underestimate either the difficulty of this transformation, or the enormity of scale involved. Each year about 4.2×10^{24} joules of light energy are used to synthesize about 2×10^{11} tonnes/km^2 of organic carbon. The conversion of six moles of carbon dioxide to one mole of glucose requires an enormous input of energy (i.e. 2880 kjoules/mole); add to this the fact that the reaction has gone on for about 3000 million years and you begin to see the enormity of the problem, i.e. the fixation of about 6×10^{20} tonnes of carbon/km^2 over the time period of photosynthetic life on earth.

If the earth's productive surface area be taken as 3.6×10^8 km^2, then the total production of organic carbon reaches the astronomical figure of 2.2×10^{29} tonnes. This is about 40 million times the estimated mass of the earth, which is 5.6×10^{21} tonnes. The cycling of carbon is indeed a fantastic phenomenon!

6.0.2. Overview

In preceding books you were introduced to:

(1) a variety of different cells as seen under the light microscope;

(2) the fine-structure of cells as revealed by electron microscopy;

(3) films showing the behaviour of certain living cells in culture;
(4) data showing the dependence of an organism on its environment;
and
(5) data illustrating the degree of tolerance or intolerance which an organism shows with respect to changes in environmental conditions.

In the books concerned with 'Regulation within Cells', we shall:
(1) examine additional evidence for the function of organelles;
(2) examine the inter-relationships which exist between the various inclusions of the cell.

6.0.3. Preknowledge requirements

To be able to recognize the cell organelles and their fine-structure as revealed by electron microscopy (Book 2). The organelles include nucleus, mitochondria, ribosomes, chloroplasts, Golgi bodies or dictyosomes and endoplasmic reticulum. To know that chlorophyll is uniquely associated with chloroplasts (Books 1 and 4) and that oxygen is consumed during respiration, but evolved during photosynthesis.

Elementary chemical knowledge of electrons and protons; isotopes; oxidation and reduction; SI units, i.e. joules, nanometres (nm), micrometres (μm). Knowledge that wavelengths of light are expressed in nm, blue light being of short wavelength and red light of long wavelength. Chromatography.

6.0.4. Objectives

At the end of this book, you should be able to:
(1) Explain absorption spectra and redox potentials.
(2) Explain in outline how ATP and NADPH are synthesized in the light-dependent reaction from energy generated by electrons in the photolysis of water.
(3) Explain in outline how and where ATP and NADPH are used in the fixation of carbon dioxide.
(4) Present evidence supporting a light-dependent and a light-independent phase in photosynthesis.
(5) Present evidence to show where the light-dependent and light-independent reactions occur in the chloroplast.
(6) State how plant and animal cells store molecules such as starch, fat and glycogen respectively.
(7) Correctly interpret reported, graphical or numerical data related to photosynthesis.

6.0.5. Instructions on working through programmed sections

In the programmed sections, questions and answers are arranged sequentially down the page. You are provided with a masking card and a student response booklet. Most of the book is programmed except the Introduction and Appendices. Cover each page in turn, and move the masking card down to reveal two thin lines.

This marks the end of the first question on that page. Record your answer to the question under the appropriate section heading in the response booklet provided. Then *check* your answer with the answer given. If your answer is correct, move the masking card down the page to the next double line and so on. If any of your answers are incorrect retrace your steps and try to find out why you answered incorrectly. If you are still unable to understand the point of a given question, make a note of it and consult your tutor.
The single thick line

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is a demarcation between one frame and the next.
A bold double line indicates a convenient stopping point in the programme, since it is unlikely that you will have time to read through the whole book in one session.

6.1. Photosynthesis

6.1.1. Large molecules as energy stores and the relationship between autotrophs and heterotrophs

1 Let us begin by recalling some important information already introduced in earlier books of this course.
Book 2 (*Electron Microscopy and Cell Structure*) introduced you to a variety of plant and animal cells. Virtually all living cells are seen to possess at least one nucleus, a bounding plasma membrane, internal cytomembranes such as the endoplasmic reticulum, discrete membrane-bound organelles such as mitochondria and Golgi bodies, and organelles such as ribosomes, which are normally associated with cytomembranes. Uniquely, however, the cells of green plants possess membrane-bound organelles called plastids. These plastids develop into complex chloroplasts in photosynthesizing cells, which thus possess the capability of synthesizing sugars in the presence of sunlight. Book 4 (*Ecological Principles*) nevertheless showed how dependent autotrophic organisms are on their environment for certain raw materials.
What are these raw materials?

Water, a source of inorganic carbon and nitrogen, and mineral salts containing important trace elements (e.g. S, Fe, Mg, Mn, Na, K, etc.).

---

2 In a previous book (Book 5, *Cell Membranes*) we were primarily concerned with the way in which these raw materials get into (and out of) cells via the plasma membrane. You will possibly recall that only certain chemical substances can penetrate the plasma membrane, which is selectively permeable (few cells exhibit phagocytosis).
What properties of the various chemical substances required by cells normally govern their entry into the cell?

(i) Molecular size,
(ii) lipid solubility,
(iii) charge and hydration state.

---

3 Although all these factors are important, we can as a general rule say that chemical substances of high molecular weight do NOT penetrate the cell membrane. However, we do know that large molecules such as proteins, lipids and polysaccharides are found within cells.
How do they get there?

They are synthesized within each cell from smaller components.

---

4 We also need to ask why such large molecules are necessary. There appear to be four main functions which they can serve:

(1) Structural, as in the proteins and lipids of membranes (Book 5);
(2) as energy stores such as fats and polysaccharides (Book 8);
(3) as catalysts or enzymes (proteins) (Book 7);
(4) for the storage and transmission of information (the nucleic acids DNA and RNA) (Book 9).

In a previous book (Book 5) we discussed the structural features of cell membranes in some detail. In this book, we are primarily concerned with energy acquisition, transformation and storage in the form of large molecules.

The advantages of using *large molecules as energy stores* may not seem obvious at first. To convert a monosaccharide such as glucose into a polysaccharide requires a lot of energy and not all of this energy can be recovered when the polysaccharide is reconverted to a monosaccharide. Why, then, doesn't the cell use glucose as an energy store? Can you think of any advantages of storing energy in the form of polysaccharides? (You should be able to think of at least TWO.)

---

(1) Polysaccharides are insoluble whereas glucose, being soluble, can diffuse out of the cell.
(2) A very high concentration of glucose would lead to osmotic diffusion of water into the cell, and the expansion and eventual collapse of the cell membrane.
(3) To maintain better control over the storage and retrieval of energy. (Packaging may be costly but it is also convenient. Do you keep your course notes on individual scraps of paper or in a book or file!)

---

5 Energy may be defined as the capacity to do work. For the living organism to maintain its vital functions under a variety of environmental conditions and metabolic demands, the ability to store a supply of potential energy which can be 'tapped' when required to do various kinds of physiological work is obviously important.

In storing energy in the form of polysaccharides rather than monosaccharides an organism is:

(*a*) Converting the system as a whole to a (higher/lower) ____?____ energy state;

and (*b*) increasing the (orderliness/randomness) ____?____ of the system.

---

higher; orderliness

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6 One well-known principle of thermodynamics states that all systems whether living or non-living tend toward their lowest possible energy states (i.e. water flows downhill). This state is frequently referred to as ground state.

What does this imply for the problem of maintaining a dynamic chemical system in a higher energy state (i.e. higher than the ground state)?

(Monosaccharides and polysaccharides are interconvertible in most living cells.)

Energy is required merely to maintain the *status quo*.
(To get water from an underground reservoir into a storage tank above ground, the engineer uses a pump. The pump performs work and expends energy in maintaining the head of water, but once the fuel supply to the pump ceases or the pump itself breaks down, the water cannot be raised to the new level. The same principle applies to living systems; once the energy input system breaks down, death ensues.)

---

7 Another formulation of this principle states that all systems tend to a state of maximum disorder. The technical term for disorder is *entropy*, and most natural irreversible processes are associated with increases in entropy. For example, mixing hot water with cold water to get warm water is a(n) (reversible/irreversible) ____________ process which causes a(n) (decrease/increase) ____________ in entropy.

---

irreversible; increase

---

8 To convert warm water back to hot water and cold water requires energy, which is why refrigerators need a supply of gas or electricity. So what is necessary for maintaining a dynamic living system in a state of order?

An energy input

---

9 For what two reasons, apart from movement, growth, reproduction and temperature maintenance do living systems require energy?

(i) To maintain a higher energy state (i.e. maintain the work potential);
(ii) to maintain a state of order.

---

10 In what form can energy be acquired by living systems?

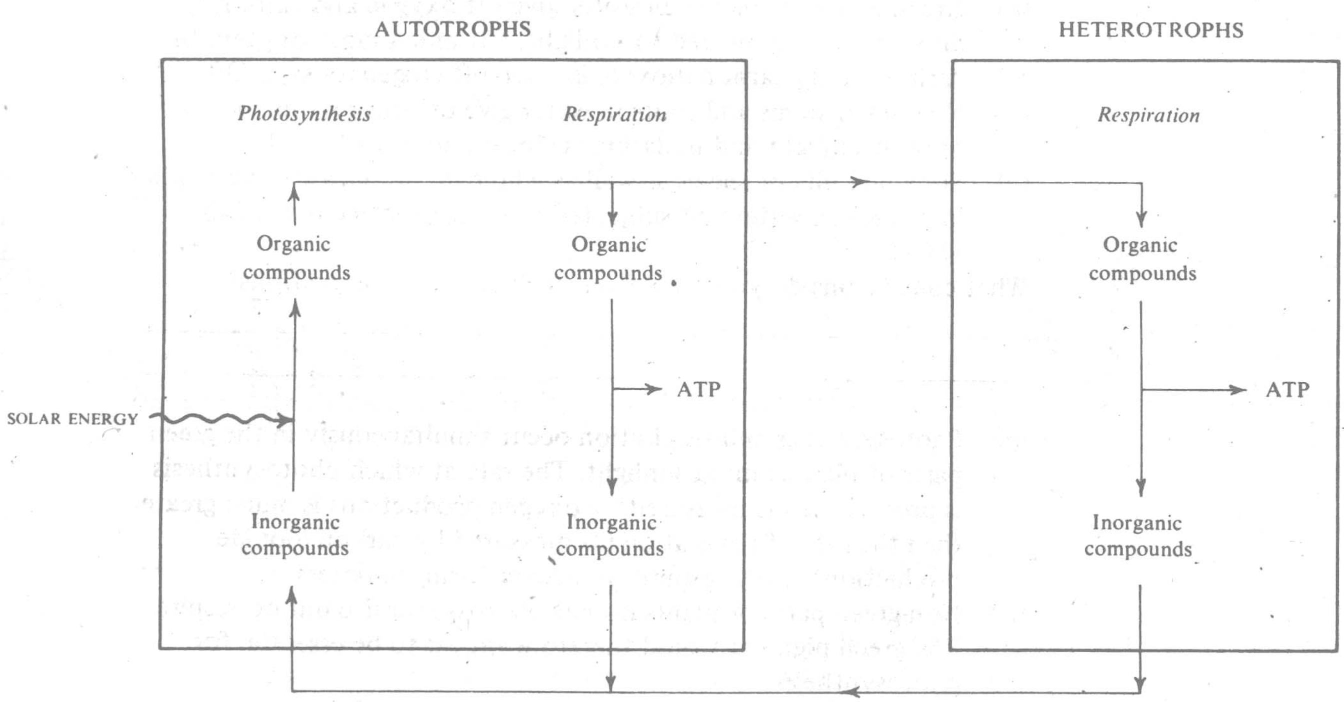
(i) From solar or light energy (green plants);
(ii) from food or chemical energy (plants and animals).

---

11 Review

The mechanisms whereby molecules such as glucose enter the cell and serve as an energy source have already been discussed in Book 5. In a later book (Book 11), the digestion and adsorption of food will be discussed. Here, we shall concentrate on the mechanisms by which certain cells are able to use light as an alternative energy source.

At this stage, however, we should remind you of the overall relationship which exists between autotrophs (photosynthetic plants and bacteria) on the one hand and heterotrophs (non-photosynthetic plants and animals) on the other (Book 4). The situation is summarized below:



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12 Although light is one form of energy which can be utilized by green plants, it might be appropriate at this stage to examine the various forms of energy and ask which is most 'useful' in cellular systems and why.

With these questions in mind, which of the following statements do you consider to be false and which true?

(*a*) Chemical energy is easily stored and readily converted into other forms of energy.

(*b*) Heat energy is easily stored and therefore suited to living systems.

(*c*) Electrical energy is easily stored and can therefore be transferred between cells and within cells.

(*d*) Light energy is difficult to store and must therefore be trapped and converted to chemical energy if it is to be of use to living systems.

(*a*) and (*d*) are TRUE
(*b*) and (*c*) are FALSE

It may be said that chemical energy is the most 'useful' form of energy in living systems because (i) it can be converted into other forms of energy fairly readily (e.g. heat, light, electrical, mechanical etc.), (ii) its energy can be released in small, carefully controlled amounts, and (iii) it can be readily transferred between cells and within cells.

---

13 With the information in frame 11 in mind, examine the following pieces of experimental evidence:

(*a*) Green leaves and stems in water give off oxygen and carbon dioxide when subjected to sunlight, but much more oxygen. In darkness only carbon dioxide is given off (Ingenhousz, 1730–99).

(*b*) Non-green stems and roots in water give off carbon dioxide only, both in sunlight and in darkness (Ingenhousz, 1739–99).

(*c*) Shredded bits of leaves as well as whole leaves release oxygen when immersed in water and subjected to sunlight (Senebier, 1742–1809).

What conclusions do you draw from each of these observations?

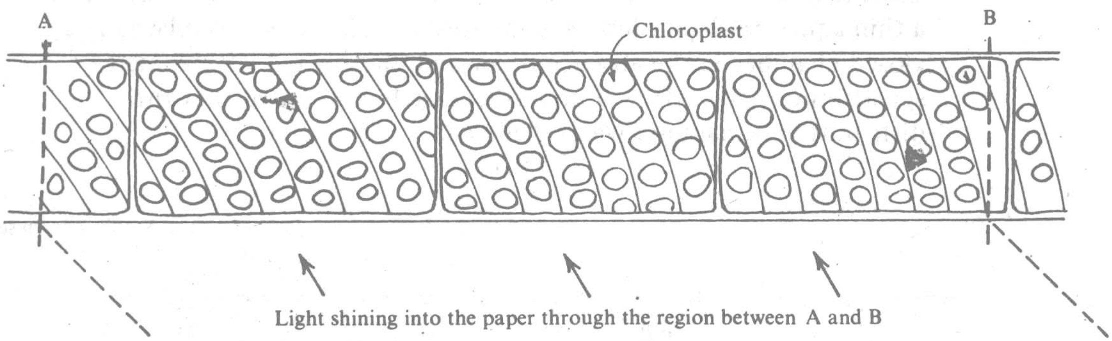
(*a*) Photosynthesis and respiration occur simultaneously in the green parts of plants during sunlight. The rate at which photosynthesis is proceeding (as measured by oxygen production) is much greater than the rate of respiration (as measured by carbon dioxide production). Only respiration occurs during darkness.

(*b*) Non-green parts of plants do not photosynthesize but do respire. The green pigment would therefore appear to be essential for photosynthesis.

(*c*) Photosynthesis is not just performed by the leaf as a single organ, but some smaller unit. This smaller unit may be the single cell or the chloroplast which is the only organelle containing the green pigment chlorophyll (a deduction made from Books 1 and 4).

---

14 In 1882, Engelmann carried out an ingenious experiment with a plant called *Cladophora*. *Cladophora* is a simple alga (see Glossary) consisting of a chain of regular cylindrical cells. Each cell is approximately 80–100 μm in length and the chloroplasts fill the cells uniformly. So, if you transmitted white light through the cells between the areas marked A and B below, what changes (if any) in oxygen production might you expect to occur along this length of the chain of cells?



O_2 production should be uniform between A and B and fall off rapidly outside this region. (This is the special advantage of using *Cladophora*.)

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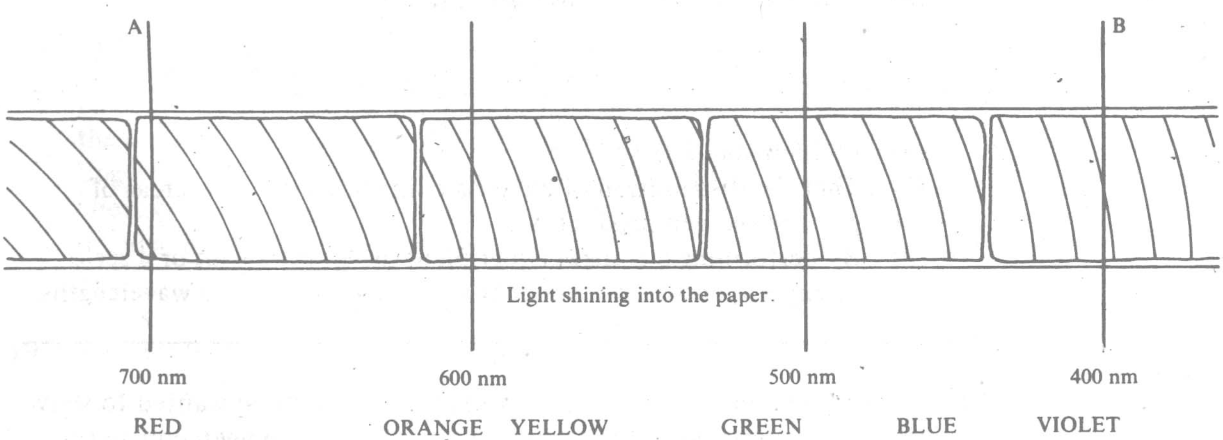
15 Engelmann performed this important control experiment in a slightly modified way and then proceeded with his main experiment, in which he transmitted a microspectrum of light through a small chain of *Cladophora* cells



By this means chloroplasts near position A were only exposed to light of 700 nm wavelength and chloroplasts near position B were only exposed to light of 400 nm wavelength. What do you think was the purpose of this experiment?

To find whether any particular wavelengths of light were absorbed preferentially by chloroplasts.

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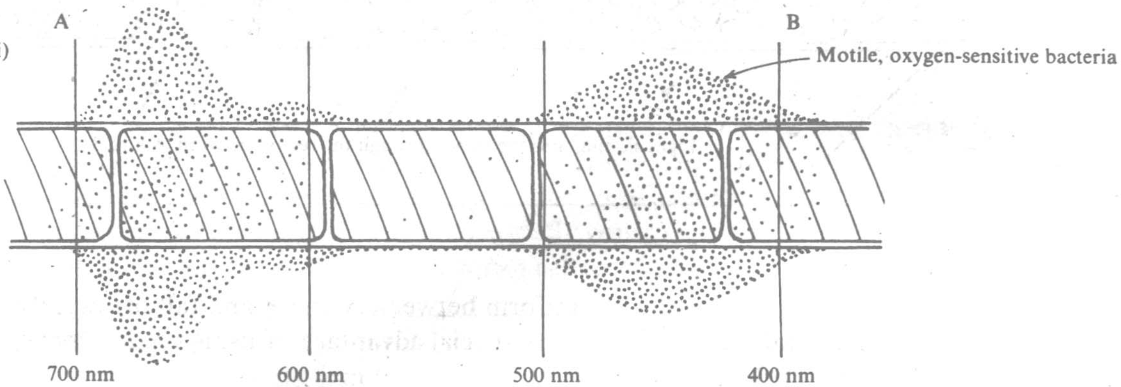
16 In order to do this Engelmann had to devise some means of measuring oxygen production on a purely local basis and hit upon the ingenious idea of using the properties of oxygen sensitive bacteria. These bacteria migrate towards areas where the oxygen concentration is greatest and are much more active in such areas.

Engelmann placed his chain of *Cladophora* cells on a microscope slide, together with an even distribution of oxygen-sensitive bacteria in a thin aqueous suspension. The microscope slide was then placed in a closed chamber in the absence of air and illuminated with a microspectrum of light. After 30 minutes, Engelmann noted that the distribution of bacteria was as follows:

(i)



(*a*) What wavelengths of light appear to be mainly responsible for oxygen production in *Cladophora* cells?
(*b*) What assumption about the behaviour of the bacteria is necessary for the above conclusion?
(*c*) How would you test this assumption?

(*a*) 650 nm and 450 nm.
(*b*) That the distribution of bacteria coincides with those areas of greatest oxygen production.
(*c*) By performing a control experiment using white light or a series of experiments using monochromatic light of various wavelengths.

---

17 What other control experiment would be needed if one wanted to show that the bacteria were responding to differences in oxygen concentration rather than directly to different wavelengths of light?

One experiment would be to place the bacteria in a microspectrum of light in the absence of the green plant. If the different wavelengths of light have no effect then the bacteria will be dispersed randomly.

In fact this is what happens.
(NB Other experiments are possible.)

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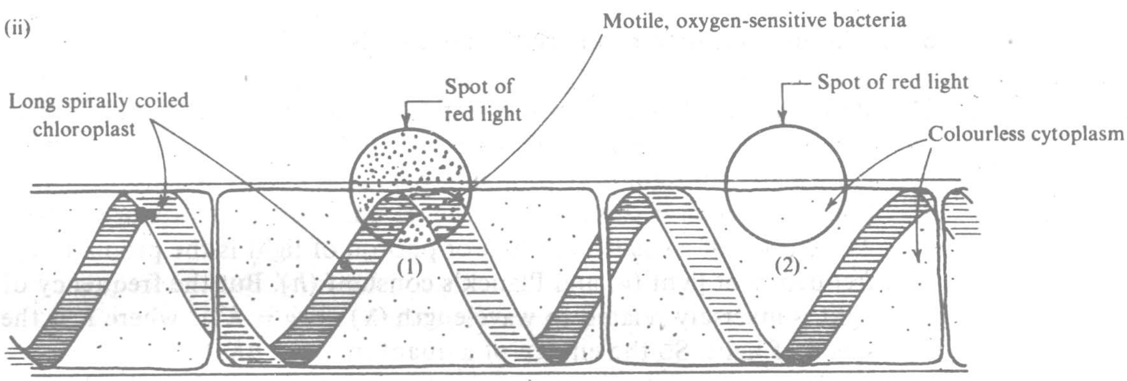
18 Engelmann then conducted further experiments with another fresh-water alga, called *Spirogyra*. Here the cells have a regular shape, but characteristically, the chloroplasts are loosely coiled within the cell, revealing areas of colourless cytoplasm.

Again he placed the cells in water containing motile oxygen-sensitive bacteria, but this time directed light of an effective wavelength (1) on a chloroplast, and (2) on a piece of colourless cytoplasm.
The results are shown below:

(ii)



Do the experiments performed by Engelmann support the claim that photosynthesis takes place exclusively in the chloroplasts of cells? Give your reasons.

They support it but they do not prove it. If oxygen production alone was the only measure of the rate of photosynthesis then the experiments support the claim. However, we do not as yet know about all the reactions involved in this process, and therefore although Engelmann's experiments give strong support to the contention that photosynthesis is associated with the chloroplasts, they do not support the idea that it is exclusively located here.

---

19 What further experimental evidence would be needed to support this claim?

Evidence from isolated intact chloroplasts.
If isolated chloroplasts alone amongst the cell fractions were able to carry out photosynthesis, then this would indicate that chloroplasts are the *exclusive* sites of photosynthesis.
(We shall return to this point later.)

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