C1.3 Photosynthesis

Interaction and interdependence—Molecules

Standard level and higher level: 3 hours

Additional higher level: 3 hours

Guiding questions

• How is energy from sunlight absorbed and used in photosynthesis?

• How do abiotic factors interact with photosynthesis?

Recommended prior learning: C1.2 Cell respiration

SL and HL

C1.3.1—Transformation of light energy to chemical energy when carbon compounds are produced in photosynthesis
This energy transformation supplies most of the chemical energy needed for life processes in ecosystems.
Photosynthesis is the conversion of light energy into chemical energy, which is essential to life on earth. Not only does it produce energy-rich carbohydrates but oxygen as well, both of which have been crucial to the establishment of complex ecosystems.

C1.3.2—Conversion of carbon dioxide to glucose in photosynthesis using hydrogen obtained by splitting water
Students should be able to write a simple word equation for photosynthesis, with glucose as the product.
$\text{Water} + \text{carbon dioxide} \xrightarrow{\text{light}} \text{glucose} + \text{oxygen}$ Photosynthesis is composed of light-dependent and light-independent reactions. **Light dependent reactions** occur in the thylakoids of chloroplasts where light energy is used to split water in a process called **photolysis** (“photo” meaning light and “lysis” meaning breaking down). This assists in converting light energy into chemical energy. **Light independent reactions** occur in the stroma of chloroplasts where the chemical energy generated from the light dependent stages is used to fuel the production of glucose from carbon dioxide.

C1.3.3—Oxygen as a by-product of photosynthesis in plants, algae and cyanobacteria
Students should know the simple word equation for photosynthesis. They should know that the oxygen produced by photosynthesis comes from the splitting of water.
In plants, algae, and cyanobacteria, oxygen is a by-product of photosynthesis which results from the photolysis of water.

C1.3.5—Absorption of specific wavelengths of light by photosynthetic pigments
Include excitation of electrons within a pigment molecule, transformation of light energy to chemical energy and the reason that only some wavelengths are absorbed. Students should be familiar with absorption spectra. Include both wavelengths and colors of light in the horizontal axis of absorption spectra.
A **photon** is a type of electromagnetic radiation that can be seen by humans as visible light. The higher the energy of a photon, the shorter its wavelength, and vice versa. When electrons within a pigment molecule like chlorophyll absorb a photon, they become excited/filled with energy and aid in the transformation of light energy to chemical energy. The amount of energy/wavelength absorbed depends on the chemical identity of the pigment molecule.

C1.3.4—Separation and identification of photosynthetic pigments by chromatography
Application of skills: Students should be able to calculate R_f values from the results of chromatographic separation of photosynthetic pigments and identify them by color and by values. Thin-layer chromatography or paper chromatography can be used.

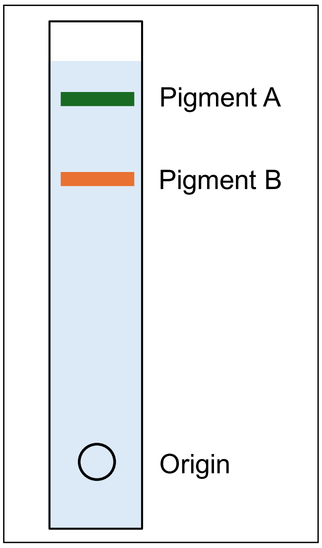

Figure 1: paper chromatography.

$$R_f \text{ value} = \frac{\text{distance travelled by the pigment (solute)}}{\text{distance travelled by the solvent}}$$

C1.3.6—Similarities and differences of absorption and action spectra

Application of skills: Students should be able to determine rates of photosynthesis from data for oxygen production and carbon dioxide consumption for varying wavelengths. They should also be able to plot this data to make an action spectrum.

Absorption spectra are graphs depicting the wavelengths absorbed by a chemical substance, like chlorophyll. The x-axis represents the wavelengths in nanometers and the y-axis shows the amount of light absorbed from 0-100% or arbitrary units (au).

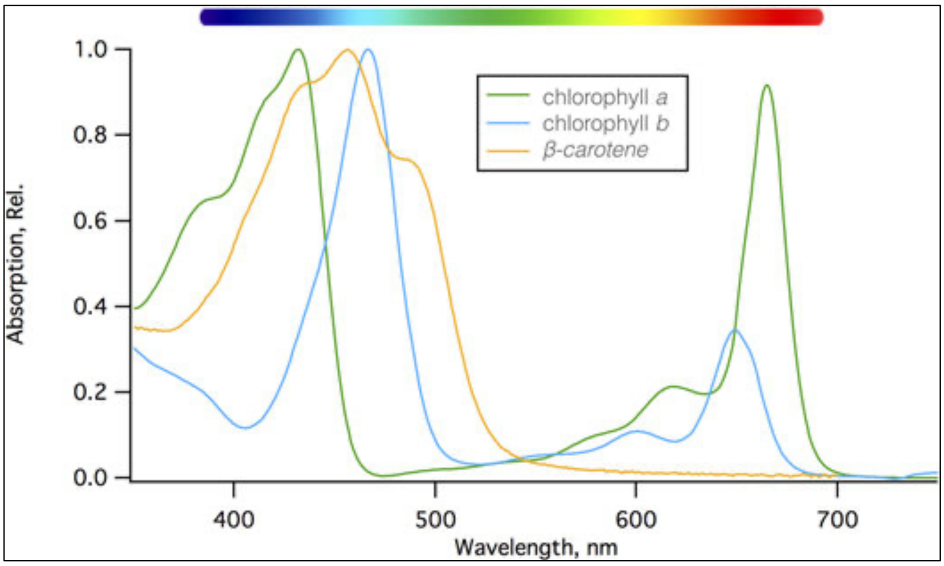

Figure 2: absorption spectra of the major types of chlorophylls and carotenoids (Johnson).

Action spectra are graphs depicting rate of photosynthesis (y-axis) plotted against wavelengths of visible light (x-axis).

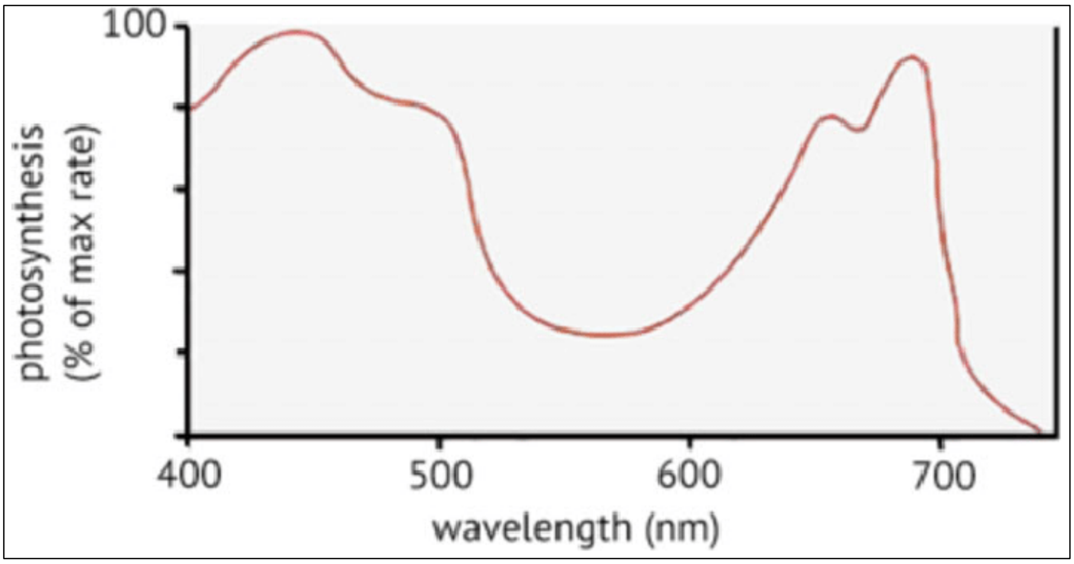

Figure 3: action spectrum of photosynthesis (Hamblin).

C1.3.7—Techniques for varying concentrations of carbon dioxide, light intensity or temperature experimentally to investigate the effects of limiting factors on the rate of photosynthesis

Application of skills: Students should be able to suggest hypotheses for the effects of these limiting factors and to test these through experimentation.

Carbon dioxide: increasing CO_2 concentration increases the rate of photosynthesis until another limiting factor becomes short in supply. CO_2 levels can be varied through several methods:

- Using aquatic photoautotrophs and dissolving different amounts of sodium bicarbonate
- In a sealed chamber, CO_2 injectors can vary gas concentrations with a sensor to help in monitoring

Light intensity: increasing light intensity increases the rate of photosynthesis until another limiting factor becomes short in supply.

- Adjusting distance of photoautotroph from light source
- Adjusting light source intensity then measuring light intensity using a **lux meter**

Temperature: increasing temperature increases rate of photosynthesis up until the optimum temperature is reached in which any further increase causes denaturation of enzymes like rubisco, decreasing the rate of photosynthesis.

- Using a water bath and monitoring using thermometer
- Changing temperature of the atmosphere through air conditioning or enclosed chamber

C1.3.8—Carbon dioxide enrichment experiments as a means of predicting future rates of photosynthesis and plant growth

Include enclosed greenhouse experiments and free-air carbon dioxide enrichment experiments (FACE).

With the rise in CO_2 levels since the industrial revolution, it is important to also understand how this might not only affect photoautotrophs but the ecosystems in which they exist in as well. Although there is a lot of research regarding the effects of CO_2 on plants, most of these studies have been done in very controlled labs and greenhouses. While this has allowed us to better understand the physiology of plants, it provides little insight into how these environmental factors influence ecosystems as a whole.

Free-Air Carbon Dioxide Enrichment (**FACE**) experiments enable the study of increased CO_2 concentrations on plants and ecosystems under natural (free-air) conditions without confinement or enclosure (not within a greenhouse or lab, where plant competition and other ecological mechanisms are not considered). This is done through installing CO_2 blowers/injectors in certain areas of an ecosystem and relying on wind to disperse the gas in order to raise the levels of CO_2 and observe its effects. Some hypotheses around these experiments include:

- Increases in CO_2 will increase crop yield (result: FACE experiments showed smaller increases in crop growth than expected)
- Different types of plants will respond more to increased CO_2 than others (result: FACE experiments showed that trees were more responsive than grasses)

Since FACE experiments take years to complete, there is still a lot of data needed before predicting future rates of photosynthesis and plant/ecosystem growth with sufficient certainty.

NOS: Hypotheses are provisional explanations that require repeated testing. During scientific research, hypotheses can either be based on theories and then tested in an experiment or be based on evidence from an experiment already carried out. Students can decide in this case whether to suggest hypotheses for the effects of limiting factors on photosynthesis before or after performing their experiments. Students should be able to identify the dependent and independent variable in an experiment.

An **independent variable** is the variable being manipulated/changed in an experiment so as to explore its effects; it is the 'cause'.

A **dependent variable** is the variable being measured/observed in an experiment; it is the 'effect'.

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NOS: Finding methods for careful control of variables is part of experimental design. This may be easier in the laboratory but some experiments can only be done in the field. Field experiments include those performed in natural ecosystems. Students should be able to identify a controlled variable in an experiment.

Controlled variables remain unchanged/fixed during an experiment to reach valid and precise conclusions.

Aspect	Lab experiments	Field experiments
Controlling variables	Easier and more precise	Harder and less precise
Reproducibility	High due to standardized equipment and conditions	Low due to variable natural conditions
Ecological applicability	Less ecologically relevant	More ecologically relevant

Additional higher level

C1.3.9—Photosystems as arrays of pigment molecules that can generate and emit excited electrons
Students should know that photosystems are always located in membranes and that they occur in cyanobacteria and in the chloroplasts of photosynthetic eukaryotes. Photosystems should be described as molecular arrays of chlorophyll and accessory pigments with a special chlorophyll as the reaction center from which an excited electron is emitted.

Photosystems are protein complexes embedded within thylakoidal membranes that aid in the conversion of light energy to chemical energy and are composed of two main components:

- **Antenna complex**: consists of several light-harvesting protein complexes that contain **accessory pigments** (**chlorophyll a**, **chlorophyll b**, **carotenoids**). These pigments protect the **special chlorophylls** in the reaction center from oxidation by absorbing sunlight and transfer this light energy between pigments within the antenna until reaching the reaction center. Thus, the antenna complex acts as a funnel by harnessing and directing light energy to a site where it can be effectively used.
- **Reaction center**: a protein complex that contains a special *pair* of chlorophyll molecules whose electrons, once excited by energy passed from accessory pigments, are immediately transferred to carriers in the **Electron Transport Chain** (**ETC**).

There are two types of photosystems (named according to the order in which they were discovered and not in the order of electron transfer) in thylakoids which have the same structure but differ on the basis of what they oxidize and reduce.

- **Photosystem II** (PSII) is the first one involved in electron transfer which oxidizes water (photolysis) and reduces an electron-carrier molecule (plastoquinone, PQ).
- **Photosystem I** (PSI) is the second photosystem involved in electron transfer which oxidizes an electron-carrier molecule (plastocyanin, PC) and reduces $NADP^+$.

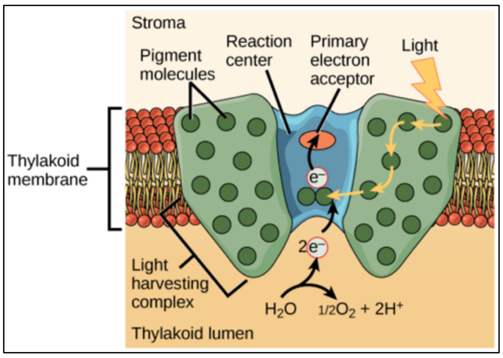

Figure 4: structure of a photosystem (Ann Clark).

C1.3.10—Advantages of the structured array of different types of pigment molecules in a photosystem
Students should appreciate that a single molecule of chlorophyll or any other pigment would not be able to perform any part of photosynthesis.

A **pigment** is a molecule whose electrons selectively absorb some wavelengths and reflect others. The reflected wavelengths that aren't absorbed mix together to form the pigment's color. There are several advantages of the structured array of different types of pigment molecules in a photosystem:

- The diversity of pigments broadens the range of wavelengths that can be absorbed by a photosystem, so collectively a greater amount of sunlight can be captured
- Some of the pigments help protect against photodamage by dissipating excess energy as heat
- The proximity of pigments to other ones in the antenna complex facilitates efficient and effective transfer of energy

C1.3.11—Generation of oxygen by the photolysis of water in photosystem II

Emphasize that the protons and electrons generated by photolysis are used in photosynthesis but oxygen is a waste product. The advent of oxygen generation by photolysis had immense consequences for living organisms and geological processes on Earth.

When the special chlorophylls in PSII lose their two electrons to an electron carrier (plastoquinone), they become a strong oxidizing agent. This causes the photolysis of water according to the following equation:

$$2H_2O \rightarrow O_2 + 4H^+ + 4e^-$$

The protons produced contribute to the proton gradient during chemiosmosis.

The electrons produced compensate for those lost from the special chlorophylls, 2 for each molecule within the pair.

The oxygen generated is a waste product and leaves the plant through the stomata. The production of oxygen billions of years ago had immense consequences for living organisms and geological processes on Earth. Photoautotrophs first evolved inside oceans, so oxygen in water reacted with dissolved iron to produce iron oxide, which precipitated and formed **banded iron formations** (rocks). Once iron and other elements in the ocean were oxidized, oxygen started to accumulate in the atmosphere, leading to the **Great Oxidation Event** and the evolution of aerobic respiration.

C1.3.12—ATP production by chemiosmosis in thylakoids

Include the proton gradient, ATP synthase, and proton pumping by the chain of electron carriers. Students should know that electrons are sourced, either from photosystem I in cyclic photophosphorylation or from photosystem II in non-cyclic photophosphorylation, and then used in ATP production.

Once electrons are transferred from the special chlorophylls to the electron-carrier molecules, they move through the ETC, and their energy is used by cytochrome complexes to pump protons into the thylakoid lumen. Due to the small size of thylakoids, a steep proton gradient is quickly established between the stroma (low H^+ concentration) and the thylakoid lumen (high H^+ concentration). This causes the protons to passively diffuse into the stroma through ATP synthase via chemiosmosis, which generates the ATP necessary to fuel the light-independent reactions later on.

The final electron acceptor in the ETC is PSI, which accepts the now low-energy electrons from plastocyanin into its reaction center. Each of the electrons received are boosted to a high-energy state by light energy funneled through the antenna complex and then used to reduce $NADP^+$ in the stroma. This process is called **noncyclic photophosphorylation**, which produces around 1 ATP molecule per pair of electrons passed to $NADP^+$.

Cyclic photophosphorylation occurs when the cell needs to produce more ATP molecules to power the light-independent reactions. Instead of passing the re-energized electrons to $NADP^+$, PSI passes them back to the cytochrome complexes in order to pump more protons into the thylakoid lumen, thereby increasing the proton gradient that drives ATP synthase to produce more ATP. The cell has mechanisms to regulate how much light energy is converted into high-energy phosphate bonds (ATP) and how much into reducing power (NADPH).

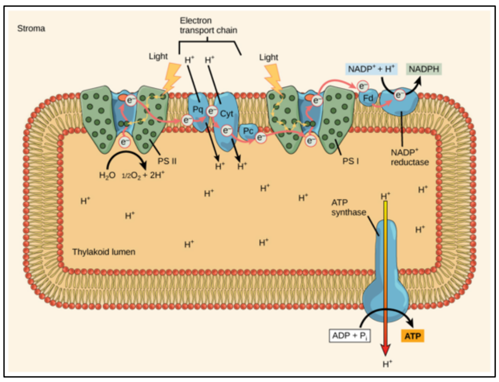

Figure 5: diagram of light-dependent reactions (Ann Clark).

C1.3.13—Reduction of NADP by photosystem I

Students should appreciate that NADP is reduced by accepting two electrons that have come from photosystem I. It also accepts a hydrogen ion that has come from the stroma. The paired terms “NADP and reduced NADP” or “$NADP^+$ and NADPH” should be paired consistently.

NADP (nicotinamide adenine dinucleotide phosphate) is the same as a typical NAD molecule but with an added phosphate group. $NADP^+$ can undergo reduction to gain electrons and a hydrogen ion (NADPH), or oxidation to donate electrons and a proton. **NADP reductase** is an enzyme embedded within the thylakoid membrane that catalyzes the reduction of $NADP^+$ to NADPH. Since a proton is used to reduce $NADP^+$, this decreases the H^+ concentration of the stroma which further increases the steepness of the proton gradient.

C1.3.14—Thylakoids as systems for performing the light-dependent reactions of photosynthesis

Students should appreciate where photolysis of water, synthesis of ATP by chemiosmosis and reduction of NADP occur in a thylakoid.

Thylakoids are membrane-bound compartments within chloroplasts that perform the light-dependent reactions of photosynthesis. A stack of disc-shaped thylakoids is called a **granum** (plural grana), which is connected to other grana via **lamellae** (unstacked stroma thylakoid).

PSII are mainly concentrated in grana and PSI in lamellae. Since lamellae have more access to the stroma than grana, $NADP^+$ reduction is easier in them compared to grana.

C1.3.15—Carbon fixation by Rubisco

Students should know the names of the substrates RuBP and CO_2 and the product glycerate 3-phosphate. They should also know that Rubisco is the most abundant enzyme on Earth and that high concentrations of it are needed in the stroma of chloroplasts because it works relatively slowly and is not effective in low carbon dioxide concentrations.

The **Calvin Cycle** constitutes the light-independent reactions of photosynthesis and involves 3 main steps:

1. Carbon fixation
2. Reduction
3. Regeneration

CO_2 is a non-polar and small molecule that can easily diffuse through stomatal openings into plant cells. This makes it a suitable provider of the carbon atoms needed as backbone for biomolecules like glucose.

In carbon fixation, the enzyme **Rubisco** catalyzes the reaction between CO_2 molecule and **ribulose bisphosphate** (**RuBP**), a 5C compound with 2 phosphate groups, which produces 2 **glycerate-3-phosphate** (**GP**) molecules.

Rubisco is the most abundant enzyme on earth and found in all three domains of life. It works relatively slowly compared to most enzymes, which according to evidence may be because of the reciprocal relationship between enzyme specificity and activity. Ever since the great oxidation event, the enzyme had to evolve to precisely distinguish between CO_2 and O_2 molecules, which came at the cost of a reduced catalytic rate. The enzyme is also not very effective at low CO_2 concentrations, so high concentrations of Rubisco are needed within the stroma of chloroplasts.

C1.3.16—Synthesis of triose phosphate using reduced NADP and ATP

Students should know that glycerate-3-phosphate (GP) is converted into triose phosphate (TP) using NADPH and ATP.

In the reduction step, the 2 GP molecules are reduced into **triose phosphate** (**TP**), a 3C compound, by hydrolyzing 2 ATP molecules into ADP + Pi and oxidizing 2 NADPH molecules into $NADP^+$.

C1.3.17—Regeneration of RuBP in the Calvin cycle using ATP
Students are not required to know details of the individual reactions, but students should understand that five molecules of triose phosphate are converted to three molecules of RuBP, allowing the Calvin cycle to continue. If glucose is the product of photosynthesis, five-sixths of all the triose phosphate produced must be converted back to RuBP.

In the regeneration step, and for every 3 Calvin cycles, 1 TP molecule is used to make glucose while the other 5 are used to regenerate RuBP to enable sustainable production. 3 ATP molecules are hydrolyzed into 3ADP + 3Pi in this step per 3 molecules of CO_2 fixed.

Since 6 carbon atoms make up the structure of glucose, 6 CO_2 molecules need to be fixed, so 6 Calvin Cycles need to be performed in order to produce 1 glucose molecule.

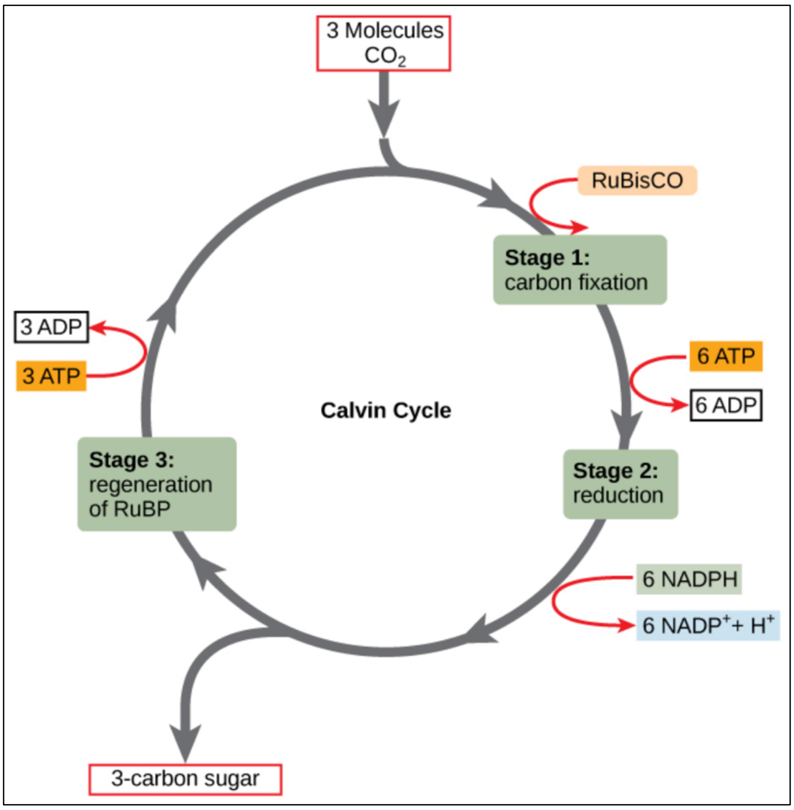

Figure 6: 3 turns of the Calvin cycle (Molnar).

C1.3.18—Synthesis of carbohydrates, amino acids and other carbon compounds using the products of the Calvin cycle and mineral nutrients
Students are not required to know details of metabolic pathways, but students should understand that all of the carbon in compounds in photosynthesizing organisms is fixed in the Calvin cycle and that carbon compounds other than glucose are made by metabolic pathways that can be traced back to an intermediate in the cycle.

All of the carbon in compounds in photosynthesizing organisms is fixed in the Calvin cycle. Other carbon compounds, like amino acids and lipids, are made by metabolic pathways that can be traced back to an intermediate in the cycle. For example, amino acids can be synthesized using TP and fatty acids using GP with the addition of phosphates and sulfurs from mineral nutrients like ammonium.

C1.3.19—Interdependence of the light-dependent and light-independent reactions
Students should understand how a lack of light stops light-dependent reactions and how a lack of CO_2 prevents photosystem II from functioning.
The light-dependent and independent reactions are interconnected and interdependent on each other. If the light-dependent reactions do not occur, the Calvin cycle cannot proceed as it has no ATP and NADPH to fuel it, and if the Calvin cycle does not take place, then the light-dependent reactions will not have the biomolecules it needs to function. Lack of CO_2 prevents PSII from functioning, because there is no need to produce more ATP and NADPH if there is no carbon dioxide for the Calvin cycle to fix into carbohydrate.

Linking questions

• What are the consequences of photosynthesis for ecosystems?

• What are the functions of pigments in living organisms?

Review questions

SL and HL

- Identify the reactants and products of photosynthesis. [1]
- State the equation of photosynthesis. [1]
- Outline the reactions within photosynthesis. [2]
- Outline the consequences of constantly increasing light intensity past the saturation point. [2]
- Explain the significance of photosynthesis to life on earth. [3]
- In a chromatography experiment, a student finds that the two pigments have very similar Rf values. Outline three different methods the student can use to
- Outline why changes to the photosynthetic process are necessary for plants living in the desert and taiga biomes. [4]
- Explain the importance of FACE experiments in predicting the effects of climate change on both plants and ecosystems. [4]

Additional higher level

- State why photosystem II does not function when carbon dioxide is missing. [1]
- Suggest why two forms of energy, ATP and NADPH, are needed during the Calvin cycle. [1]
- Outline why carbon dioxide is a good source of carbon in photosynthesis. [2]
- Outline the interdependence of the light-dependent and independent reactions of photosynthesis. [2]
- Explain the role of rubisco in photosynthesis. [3]
- Outline the role of accessory pigments in photosynthesis. [3]
- Explain how the proton gradient across the thylakoid membrane influences the synthesis of ATP during photosynthesis. [3]
- Explain the consequences of releasing oxygen as a by-product of photosynthesis. [3]
- Explain the role of reduced NADP in photosynthesis. [4]
- Describe how a proton gradient is established between the thylakoid lumen and chloroplast stroma. [4]
- Explain the significance of photolysis in photosynthesis. [4]
- Explain the role of ATP in photosynthesis. [4]
- Compare and contrast the two types of photophosphorylation in the light-dependent reactions of photosynthesis. [4]
- Explain the significance of having two variations of the electron transport chain in thylakoids. [4]

- Describe the Calvin cycle. [4]
- Explain how the structure of a chloroplast is adapted to its function. [5]
- Compare and contrast the photosystems involved in photosynthesis. [6]
- Explain how photosystems I and II are adapted to their function. [6]
- Explain how variations in chlorophyll concentrations can affect the absorption spectrum of a leaf, and outline how this might influence a plant's ability to adapt to different light environments. [7]
- Discuss how ATP is produced within chloroplasts. [8]
- Discuss the movement of electrons during the light-dependent and independent reactions of photosynthesis. [8]

References

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