Photosynthesis is two sets of connected reactions

Photosynthesis is the process by which plants and other organisms convert light energy into chemical energy. It involves two main sets of connected reactions:

1. **Light reactions:** These reactions take place in the thylakoid membranes and involve the capture of light energy.
   - **Photon capture:** Chlorophyll molecules absorb light energy, leading to the excitation of electrons.
   - **Photochemistry:** The excited electrons are transferred to an electron acceptor, often water, leading to the production of oxygen and protons.

2. **Carbon-fixing reactions:** Also known as the Calvin cycle, these reactions take place in the chloroplast stroma and involve the conversion of CO2 into glucose.
   - **Carbon fixation:** The enzyme RuBisCO catalyzes the attachment of CO2 to a 5-carbon sugar, forming a 6-carbon compound that is then split into two 3-carbon molecules.
   - **Reduction of CO2:** NADPH and ATP provide the energy to convert these 3-carbon molecules into glucose and other organic compounds.

The light reactions provide the energy and reducing power (NADPH) needed for the carbon-fixing reactions to proceed.
The Plant Cell, November 2015 © 2015
The American Society of Plant Biologists

Oxygenic photosynthesis requires TWO photosystems.

PSI & PSI are connected by an electron transport chain.

This diagram is known as a Z-scheme.

 PSI can function without PSII, but it doesn’t produce oxygen or NADPH.

The photosystems are embedded in thylakoid membranes.

Electrical and H+ gradients drive ATP synthesis.

Products of the light-dependent reactions drive carbon fixation.

Lesson outline

Evolution and diversity of photosynthesis

Evolution and diversity of photosynthesis

There are two types of reaction centers, Type I & Type II. Each type is found in various photosynthetic bacteria. Both types are found in cyanobacteria and eukaryotes.

Lesson outline

Photosynthesis overview

Evolution and diversity of photosynthesis

The light reaction curve and quantum efficiency

Photosynthesis, light and dark reactions

Structure and function of photosynthetic complexes

Pathways of electron transport

Photosynthesis, light and dark reactions

Photosynthesis and energy conversion

Artificial photosynthesis

Photosynthesis, fungi and animals.
**Light and pigments**

- Light that hits a leaf is mainly light in the visible spectrum (400 – 700 nm).
- The earth’s atmosphere transmits a range of different wavelengths, but much of the very short wavelength light is absorbed by Earth’s atmosphere. The sun emits light at a frequency (ν) of 3 x 10^8 m/sec.
- Frequency (ν) is inversely proportional to wavelength (λ).
- Energy is proportional to frequency: E = hν.
- Small changes in side chains are the basis for different subsets of accessory pigments.

**Accessory pigments are in antenna complexes next to reaction centers**

- Accessory pigments transfer light energy to the reaction center.
- Antenna complexes function as a sunscreen for the leaf.

**Absorbance spectrum of photosynthesis in a green plant**

- Photosynthetic pigments absorb light at different wavelengths.
- The photosynthetic reaction spectrum shows the rate of photosynthesis that occurs when a single wavelength of light shines on a plant.
- All chlorophyll-based photosynthesis systems use chlorophyll as the primary pigment.
- Different antenna systems are responsible for different wavelengths of light absorbed by the leaf.

**Chlorophyll biosynthesis**

- Bacteriochlorophylls are related but have different absorption spectra.
- Chlorophyll biosynthesis involves the conversion of chlorophyllide to chlorophyll a.
- Chlorophyll a is a green leaf pigment containing a phytol tail.
- Protochlorophyllide is a precursor.

**Pigments are characterized by networks of double bonds**

- All pigments are derivatives of a tetrapyrrole ring with double bonds.
- Bacteriochlorophylls are found in cyanobacteria and non-green algae, and Chlorophylls are found in all green plants.

**Light and pigments**

- Light travels at a fixed speed, c = 3 x 10^8 m/sec (3 x 10^10 cm/sec) in a vacuum.
- Frequency (ν) is inversely proportional to wavelength (λ).
- Energy is proportional to frequency: E = hν.
- Light and pigments function in different ways across the range of different wavelengths as a function of their accessory pigments.

**Lesson outline**

- Photosynthesis overview
- Evolution and diversity of photosynthesis
- Photosynthetic pathways
- Photosynthesis overview
- The light reaction curve and quantum efficiency
- Photosynthetic pigments
- Structure and function of photosynthetic complexes
- Photosynthesis in photosynthetic eukaryotes
- Photosynthesis in plants: the very short wavelength light is absorbed by Earth’s atmosphere.
In plants, plastids divide by fission and differentiate.

**Quantum Yield: Moles CO₂ fixed or O₂ produced per moles photons**

- **In this study, the quantum yield of CO₂ fixed per photosynthetically active radiation (PAR)**

**Lesson outline**

- Photosynthesis overview
- Evolution and diversity of photosynthetic organisms
- Light and Pigments
- Plastids and chloroplasts
- Structure and function of photosynthetic complexes
- Pathways of electron transport
- Pathways of carbon assimilation and ATP generation
- Bioenergetics of photosynthesis
- Artificial photosynthesis
- Photosynthetic fungi and animals

**Plastids and chloroplasts: Essential organelles for most plant cells**

- **In plants, plastids divide by fission and differentiate.**

**Chlamydomonas cells have a single large chloroplast**

- **Light induces conversion from etioplast to chloroplast.**

---

**Figure 1:** The light response curve and quantum efficiency

- **Why does the rate of CO₂ consumption level off at higher light intensities?**

**Quantifying photosynthesis: The light response curve**

- **At low light intensities, photosynthesis is light limited, so as more photons are absorbed more CO₂ is fixed.**

**Quantum Yield: Moles CO₂ fixed or O₂ produced per moles photons**

- **In this study, the quantum yield of CO₂ fixed per photosynthetically active radiation (PAR).**

**Lesson outline**

- Photosynthesis overview
- Evolution and diversity of photosynthetic organisms
- Light and Pigments
- Plastids and chloroplasts
- Structure and function of photosynthetic complexes
- Pathways of electron transport
- Pathways of carbon assimilation and ATP generation
- Bioenergetics of photosynthesis
- Artificial photosynthesis
- Photosynthetic fungi and animals

**Plastids and chloroplasts: Essential organelles for most plant cells**

- **In plants, plastids divide by fission and differentiate.**

**Chlamydomonas cells have a single large chloroplast**

- **Light induces conversion from etioplast to chloroplast.**
Land plants have distinctive grana stacks in the thylakoids

- Membranes of the margins are non-appressed (gray) and those within the appressed regions are appressed (red).
- Different complexes are found in appressed vs non-appressed regions of the thylakoids.

Appressed and non-appressed thylakoids have different functions

- PSII is mainly found in appressed regions.
- ATP synthase and PSI in non-appressed regions of the thylakoids.

Summary: Light, pigments, quantum efficiency and chloroplasts

- The first step of photosynthesis is light capture by pigments in thylakoid membranes of chloroplasts.

Lesson outline

- Photosynthesis overview
- Evolution and diversity of photosynthesis
- Light and pigments
- Photosynthetic fungi and animals

Structure and function of photosynthetic complexes

- Photosystem II (PSII) and Photosystem I (PSI)
- Cytochrome (Cyt) b6f complex
- ATP synthase

Linear electron transport involves three complexes, PSII, Cyt b6f & PSI

- H2O → O2
- e → PSI - Cyt b6f complex - PSII
- NADP+ → NADPH

Structure and function of Photosystem II – LHCII complex

- PSII is a multifunctional complex that functions as a dimer.
- The antenna complex is a disk-shaped arrangement of LHCCI (LHCII).
- The oxygen-evolving complex (OEC) is located in the center of the LHCII dimer.

Conserved cores, variable light harvesting structures

- Conserved light harvesting complexes (LHCII) are found in all plants.
- Photoproteins (CP43, CP47) and LHCII are found in all photosynthetic organisms.

Proteins in PSII can be characterized by SGC, SDS-PAGE and EM

- Protein complexes can be separated by SDS-PAGE and EM imaging.
- Structural analysis of PSII complexes is performed using advanced electron microscopy techniques.
The oxygen-evolving complex (OEC) resides on PSII luminal surface

The OEC’s catalytic center core is an inorganic Fe4CaO5 cluster which performs the highly exothermic reaction of splitting water into two electrons and four protons from water to form oxygen.

Proteins’ roles are to orient and position pigment molecules

Numerous proteins/molecules are held in other small compartments.

Electron transfer in PSII

Electrons move from luminal to stromal side.

Plastoquinone/plastoquinol is a carrier of electrons and protons

Plastoquinone (PQ) at the QB site is reduced to PQH2; then oxidized to plastoquinone (PQ).

The Q cycle and Cytochrome b6f complex

Electrons are transferred from PSII through Cyt b6f and ultimately passed to plastoquinone (PQ). This is coupled with the production of four protons from water.

Cyt b6f structure (from cyanobacteria)

Electrons are transferred from PSII through Cyt b6f and ultimately passed to plastoquinone (PQ). This is coupled with the production of four protons from water.

Q cycle and Cytochrome b6f complex

Electrons are transferred from PSII through Cyt b6f and ultimately passed to plastoquinone (PQ). This is coupled with the production of four protons from water.

In plants, LHCII assembles as trimers

In plants, LHCII assembles as trimers.

Plastoquinone is a two-electron carrier that delivers e− to Cyt b6f

Plastoquinone (PQ) is reduced to plastoquinol (PQH2), then oxidized to plastoquinone (PQ). This is coupled with the production of two protons and two electrons.
**Electrons & protons pass through Cyt b6f through the Q cycle**

First half Q cycle

PSI accepts two protons and two electrons from PC. PQ returns to PSI.

Second half Q cycle

Cycle completion

Another PQ delivers two protons to PSI; another electron to Cyt b6. PQ; two electrons to PSI; two protons regenerate PQH2, which cycles again.

**Structure and function of Photosystem I – LHCl complex**

PSI Reaction Center

In plants, PSI is surrounded by a crescent of LHCl complexes.

**PSI is a large multi-protein, multi-pigment complex**

PSI is a complex of 17 protein subunits designated by PsaA and PsaB, and 178 LHC1 protein subunits, totaling 600 protein subunits.

Ferredoxin transfers electrons via ferredoxin:NADP+ reductase (FNR)

**Structure and function of ATP synthase**

ATP synthase is a multi-subunit rotary machine

ATP synthase couples the dissipation of the proton gradient to ATP synthesis.

**Summary: Structure and function of photosynthetic complexes**

The efforts of hundreds of scientists across several decades have revealed detailed structures and mechanisms for each of the unusual, important, and beautiful photosynthetic complexes, containing dozens of proteins and hundreds of pigments and other cofactors.
Lesson outline

- Photosynthesis overview
- Electron and energy flow in photosynthesis
- The light reactions: light harvesting and energy conversion
- The light reactions: electron and energy conversion
- Pathways of electron transport
- Pathways of energy conversion
- Photosynthetic fungi and animals
- Artificial photosynthesis
- Optimizing and improving photosynthesis
- Monitoring light reactions
- Damage avoidance and repair: Acclimations to light
- Pathways of electron transport
- Plastids and chloroplasts

Pathways of electron transport

1. Linear Electron Transport
   - Electrons transferred from NADH to NADP+
   - Electron transport (ET) balances production of ATP and NADPH

2. Cyclic Electron Transport
   - Electrons cycle within the photosynthetic apparatus
   - Synthesis but not NADPH

3. Water-Water Cycle
   - Electrons transferred from NADH to NADP+
   - Generates ATP and NADPH but not NADP+

4. Cycling Electron Transport around Photosystem I (CET)
   - Each 5 photons absorbed by PSII result in 1 ATP and 4 NADPH
   - 14 H+ generated per cycle

5. Calvin-Benson Cycle
   - Net 6 H+ required per cycle
   - 3 ATP generated per cycle

LET: Flow of electrons from H2O to PSII to Cyt b6f to PSI to NADPH

Stoichiometry of electron transport yields

- 1 molecule of ATP requires 5 H+ electrons
- 1 molecule of NADPH requires 2 H+ electrons

In cyclic electron transport, electrons pass from PSI to Cyt b6f

Plastid terminal oxidase oxidizes reduced PQH2 by reducing O2

There are two routes of cyclic electron transport (CET)

The water-water cycle is another form of electron flow

Plastid terminal oxidase oxidizes reduced PQH2 by reducing O2
Flavodiiron proteins provide photoprotection in cyanobacteria

Summary: Variations in photosynthetic electron transport

Lesson outline

Damage avoidance and repair: Acclimations to light stress

Excess excitation energy can lead to photo-oxidative damage

There are protective strategies to avoid high-light induced damage

Movements to optimize light interception

Acclimation via stoichiometric changes in complex abundance

Excess light energy is dissipated via non-photochemical quenching

Flavodiiron proteins provide photoprotection in cyanobacteria

Summary: Variations in photosynthetic electron transport

Lesson outline

Damage avoidance and repair: Acclimations to light stress

Excess excitation energy can lead to photo-oxidative damage

There are protective strategies to avoid high-light induced damage

Movements to optimize light interception

Acclimation via stoichiometric changes in complex abundance

Excess light energy is dissipated via non-photochemical quenching

Flavodiiron proteins provide photoprotection in cyanobacteria

Summary: Variations in photosynthetic electron transport

Lesson outline

Damage avoidance and repair: Acclimations to light stress

Excess excitation energy can lead to photo-oxidative damage

There are protective strategies to avoid high-light induced damage

Movements to optimize light interception

Acclimation via stoichiometric changes in complex abundance

Excess light energy is dissipated via non-photochemical quenching

Flavodiiron proteins provide photoprotection in cyanobacteria

Summary: Variations in photosynthetic electron transport

Lesson outline

Damage avoidance and repair: Acclimations to light stress

Excess excitation energy can lead to photo-oxidative damage

There are protective strategies to avoid high-light induced damage

Movements to optimize light interception

Acclimation via stoichiometric changes in complex abundance

Excess light energy is dissipated via non-photochemical quenching

Flavodiiron proteins provide photoprotection in cyanobacteria

Summary: Variations in photosynthetic electron transport

Lesson outline

Damage avoidance and repair: Acclimations to light stress

Excess excitation energy can lead to photo-oxidative damage

There are protective strategies to avoid high-light induced damage

Movements to optimize light interception

Acclimation via stoichiometric changes in complex abundance

Excess light energy is dissipated via non-photochemical quenching


Zeaxanthin and lutein also have roles as antioxidants and in photoprotection. Proc. Natl. Acad. Sci. USA 94: 14162-14167.

The redox state of PQ pool contributes to state transitions (qT).

The structural changes usually occur from light energy to be dissipated as heat.

Zeaxanthins promote structural changes & heat dissipation.

The D1 protein of Arabidopsis thaliana varieg1 varieg2 is susceptible to photodamage, repair, and when repair exceeds the rate of damage, photosynthesis is inhibited. Photosynthesis is repaired.

Energy-dependent quenching (qE) usually is dominant form of NPQ.

The reaction is reversed by ZE de-epoxidation in monogalactosyldiacylglycerol micelles. Plant Cell Physiol 45: 92-102 by permission of Oxford University Press.
Changes in PSI/PSII stoichiometry

NADP+

The cytochrome


function)

Retrograde signals

Metabolic demand for NADPH and ATP

feed back into light harvesting

The cytochrome

When supply = demand, increase NADPH/ATP levels feedback and increase photosynthesis (light harvesting)

NPQ

phosphorylated proteins

conversion of chlororesin (P) into mesoquinone (P)

photosynthetic control of photoprotective mechanisms

phosphorylated proteins

Metabolic, abscisic acid, drought, cold, pathogen infection and other stress can decrease light harvesting and increase NPQ

Heat, drought, & other stresses affect photosynthetic efficiency

• High temperatures elevate electron transport and create photoinhibitory non-photochemical quenching (NPQ) and thermal dissipation of light energy
• Drought stresses elevate stomatal closure and elevate NADPH & ATP levels
• Cold and pathogen infection affect photosynthesis through increased ROS, nucleotide derivatives and derived from heme biosynthesis

Methods to monitor light reactions

Photosynthesis can be measured by O₂ production and CO₂ consumption

Alternatively, photosynthesis can be measured by chlorophyll fluorescence
• PSI activity can be measured by chlorophyll fluorescence
• PSII activity can be measured by the absorbance change at 980-680 nm
• Translational protein synthesis and photosyntheticbp can be measured by chromatography

Summary of photosynthetic acclimation mechanisms

Although the photosynthetic machinery is susceptible to photoinhibition, the plant also has several strategies to protect itself

Retrograde signaling from plastid to nucleus is critical for homeostasis

Retrograde signals

Retrograde signals activate transcriptional events in the nucleus

Gas exchange

CO₂ in (acquised) can be measured in a closed-chamber system

PPFD

Incident light

Photosynthetic activity (light, dark, NPQ, NADP+ and ATP)

Plantcell.org/cgi/doi/10.1105/tpc.115.tt1015

The Plant Cell, November 2015 © 2015
The American Society of Plant Biologists

www.plantcell.org/cgi/doi/10.1105/tpc.115.tt1015
Reaction centers “close”, maximizing fluorescence after pulse

Light-induced fluorescence is quenched by qP + NPQ

Dissociation of saturating light results in a transient pulse of fluorescence as reaction centers close (become quenched) and light is emitted as fluorescence.

Determining max $F_m$, min $F_o$, and $F_v$

Max $F_m$, variable fluorescence ($F_v$), and min $F_o$ are determined by measuring light after a saturating pulse.

$F_v / F_m$ is an indicator of maximum quantum yield of PSII

The proton-motive force (pmf) is measured by the change in absorbance of a redox indicator when reaction centers are open or closed (6)

Trans-thylakoid pmf can be measured by electrochromic shift

PSI redox status can be determined by 810 nm absorbance

Different NPQ components relax at different rates

A very bright light pulse is given to dark-adapted tissues. The light induces reaction centers “close”, maximizing fluorescence. The proton-motive force is generated, and absorbance spectra can be used to measure the pmf.

Electrochromic (ECS) monitors pmf and ATP synthase activity

$F_v / F_m$ is an indicator of maximum quantum yield of PSII

$F_v / F_m$ is an indicator of maximum quantum yield of PSII

The kinetics of ECS can separate activities of different components

electron transport chain

13
Summary: Spectrophotometric measurements of photosynthesis

The light-emitting and absorbing properties of the photosynthetic complexes allow their activities to be monitored with great precision. These methods have been development since before World War II, but chlorophyll fluorescence analysis is now a vital part of modern biotechnology.

Lesson outline

Photosynthesis overview
Evolution and diversity of photosynthesis
Photosynthetic light harvesting
The light response curve and quantum efficiency
Flexibility and adaptability
Structure and function of photosynthetic complexes
Pathways of electron transport
Damage avoidance and repair
Accelerations to light harvesting
Photosynthetic light harvesting, excitation, and photoprotection
Affix photosynthetic
Photosynthetic fungi and animals

Optimizing and improving photosynthesis

Can shading be decreased in field conditions?

In a typical canopy, larger leaves often allow light to reach lower leaves. This is a “nurse canopy” effect where upper leaves block the access to photosynthetic complexes and a zone develops at lower levels that is saturated with light. This allows near light to reach lower leaves for greater photosynthetic efficiency.

Can photoprotection be optimized for less phototoxic damage?

ROS production can induce damage that is metabolically costly to repair. Enhancing photosynthetic pathways can enhance overall resistance and protect productivity of crop plants.

Lesson outline

Photosynthesis overview
Evolution and diversity of photosynthesis
Photosynthetic light harvesting
The light response curve and quantum efficiency
Flexibility and adaptability
Structure and function of photosynthetic complexes
Pathways of electron transport
Damage avoidance and repair
Accelerations to light harvesting
Photosynthetic light harvesting, excitation, and photoprotection
Affix photosynthetic
Photosynthetic fungi and animals
Applying photosynthetic insights towards solar electricity and fuels

The goal of artificial photosynthesis is to develop cheap, scalable ways to make fuels from sunlight (like a leaf).

Developing biomimetic systems for photosynthesis

The four fundamental steps that comprise photosynthesis can be implemented using catalysts:

1. Light harvesting
2. Charge separation
3. Water oxidation
4. Proton reduction

Semiconducting materials can be used as photocatalysts

They can be used together as a PEC device.

Hybrid and bio-inspired systems are being explored for fuel production

A biotechnical chemical cell: Water splitting and proton reducing by the photosynthetic reaction of Barilla IR-1205 H2 in a fermenter.

Bacteriorhodopsin: non-chlorophyll based phototrophic system

As an alternative to chlorophyll based systems, bacteriorhodopsins are being explored for solar-driven chemistry.

Photosynthetic fungi and animals

Photosynthesis is to store sunlight (like a leaf) in fermenters.

Photosynthetic fungi: Lichen

Lichens are terrestrial associations of fungi and green or blue-green algae (e.g., cyanobacteria).

Photosynthetic animals: Reef-building corals

Symbiosis between photosynthetic dinoflagellates and large canals of coral provide the euphycts with reduced sunlight to return for shelter, nutrients, and food.

Lesson outline

- Photosynthesis overview
- Evolution and diversity of photosynthesis
- Light harvesting
- Structure and function of photosynthetic complexes
- Pathways of electron transport
- Storage and/or use of light
- Optimizing and improving photosynthesis
- Artificial photosynthesis
- Photosynthetic fungi and animals
Summary: Light-dependent reactions are billions of years old

Photosynthetic animals: Spotted salamanders

Photosynthetic animals: Plastid-stealing sea slugs

Summary:Photosynthesis research may lead to better crops and fuels

Photosynthesis has to be integrated with stress & development

Summary: Photosynthetic reactions are Variable and responsive

Variable
- light angle, duration
- light intensity, wavelength
- age, demand for photosynthate
- environmental stress
- whole-plant physiology
- chloroplast chemistry
- transthylakoid pH/pmff
- PQ / PQH2
- pmf

Photosynthetic animals:
- Spotted salamanders
- Plastid-stealing sea slugs

Photosynthesis has to be integrated with stress & development:
- Light intensity, wavelength
- Age, demand for photosynthate
- Environmental stress
- Whole-plant physiology
- Chloroplast chemistry
- Transthylakoid pH/pmff
- PQ / PQH2
- PMF

Summary: Photosynthesis research may lead to better crops and fuels