Plant Growth

- **Definition:**
  - Size increase by cell division and enlargement, including synthesis of new cellular material and organization of subcellular organelles.

Growth and Development

- **Growth**
  - Irreversible change in Mass

- **Development**
  - Irreversible change in State
    - Embryogenesis
    - Juvenile
    - Adult Vegetative
    - Adult Reproductive
Growth

- Components
- 1. Cell Division
- 2. Cell Enlargement

MEASURING GROWTH

- Increase in fresh weight
- Increase in dry weight
- Volume
- Length
- Height
- Surface area
HOW PLANTS GROW

- Meristems
  - Dicots
    - Apical meristems - vegetative buds
      - shoot tips
      - axils of leaves
    - Cells divide/redive by mitosis/cytokinesis
    - Cell division/elongation causes shoot growth
    - Similar meristematic cells at root tips

HOW PLANTS GROW

- Meristems (cont)
  - Secondary growth in woody perennials
    - Increase in diameter
      - due to meristematic regions
    - vascular cambium
      - xylem to inside, phloem to outside
    - cork cambium
      - external to vascular cambium
      - produces cork in the bark layer
Cell Division

- **Meristematic Cells (Stem Cells)**
- **Primary**
  - Shoot Apical Meristem (SAM)
  - Root Apical Meristem (RAM)
- **Secondary**
  - Axillary Buds
  - Vascular Cambium
  - Cork Cambium
  - Pericycle (root)

Cell Enlargement

- Adjacent to Meristems
- **Internode** growth - Shoot
- **Zone of Elongation** - Root
- **Turgor Pressure**
  - H₂O Uptake
  - Cell Wall Loosening
  - new cell walls
Types of Growth

1. **Determinant**
   - Terminal shoot apex flowers

2. **Indeterminant**
   - Axillary buds flower
   - Terminal buds vegetative

3. **Monocarpic**
   - Flower once then die

4. **Polycarpic**
   - Flower repeatedly over several seasons

---

Types of Growth

5. **Annual**
   - Monocarpic
   - Flower in one season and then die

6. **Biennial**
   - Monocarpic
   - Flower in second season and then die
Types of Growth

7. Herbaceous Perennial
- Polycarpic
- Determinant
  Flower early and then go dormant
  Flower Bulbs
- Indeterminant
  Flower throughout season
- Shoot dies in Fall

8. Woody Perennial
- Polycarpic
- Indeterminant
  flower only once per year
- Biennial Bearing
  flower and set fruit every other year
- Mast Flowering
  more prolific in some years than in others
ENVI RONMENTAL FACTORS INFLUENCING PLANT GROWTH

- Light
- Temperature
- Water
- Gases

PLANT GROWTH REGULATORS

3. Hormone
   - a. Substance that acts in very low concentration (micro-molar or less)
   - b. Produced in one part of plant and act in another (translocatable)
   - c. Has the same response in many different plant species
PLANT GROWTH REGULATORS

- 1. Auxins
- 2. Cytokinins
- 3. Gibberellins
- 4. Abscisic Acid
- 5. Ethylene

Natural Auxin

- 1. Endogenous
- Indole Acetic Acid

![Indole-3-acetic acid (IAA)](image)
**Synthetic Auxins**

- **2,4-Dichlorophenoxyacetic acid (2,4-D)**
- **2-Methoxy-3, 6-dichlorobenzoic acid (dicamba)**

**Auxin**

- **Synthesis**
  - a. Young developing leaves
  - b. Terminal buds, growing axillary buds
  - c. coleoptile tips
- **Transport**
  - **Basipetal**
    - away from tip
**Auxin Polar Transport**

**Auxin Action**

- **Mechanism of Action**
  - a. Bind Receptor Protein Plasma membrane
  - b. **Transport** into cell
  - c. Activate ATPase in Plasma membrane
  - d. H+ ion extrusion
  - e. acidify cell wall
  - f. break **hemicellulose-pectin** bonds
  - g. cellulose **microfibrils** slide apart
  - h. cell enlarges
**Auxin Cell Wall Loosening**

- Hemicelluloses
- Cellulose microfibril
- Pectins
- Rhamnogalacturonan I
- Structural protein

**Auxin Responses**

- **Cell Enlargement**
  - Shoot Growth
  - Internodes
  - Tubers
  - Bulbs
- **Root Growth**
  - Storage Roots
  - Adventitious Roots
- **Fruit Growth**
  - Strawberry - Receptacle enlargement
- **Apical Dominance**
  - Auxin:Cytokinin Ratio
    - High - Dormant Axillary Buds
    - Low - Axillary Bud Growth
Auxin Agricultural Uses

- Rooting of Cuttings
  - Propagation
  - Greenhouse and Nursery Crops
    - Hormodin, Rootone, etc.
    - Commercial preps of 2,4-D
- Herbicide
  - High Concentration 2,4-D
  - Dicots more sensitive
  - Monocots less sensitive
  - Weed control in cereal crop production
- Prevent Abscission of Leaves and Fruit
  - Older leaves
  - Ripe Fruit
    - Endogenous production of IAA stops
    - Replaced by exogenous NAA

CYTOKI NINS

- Ribosylzeatin (zeatin riboside)
- N\(^6\)-\(\beta\)-Isopentenyl)adenosine ([IP]1P)

\[\text{IPA}\]
Cytokinins

- **Synthesis**
  - Root Apex
- **Transport**
  - Upward in Xylem

Cytokinins

- **Responses**
  - Stimulate Cell Division
  - Apical Dominance
    - High Auxin in Shoot Apex
    - High Cytokinin in Root Apex
  - Gradient Between:
    - High Auxin:Cytokinin
    - Dormant Axillary Buds
  - Low Auxin:Cytokinin
  - Branch Growth
Cytokinins

- **Synthetic Cytokinins**
  - Kinetin
    - DNA degradation
  - Benzyladenine (BA or 6-Benzyl amino purine)
- **Agricultural Uses**
  - Limited
  - Induction of Axillary Buds
    - Roses, Chrysanthemum
  - Micropropagation
    - Shoot proliferation in Tissue Culture

Gibberellins

- Family of more than 130 structures
Gibberellins

Gibberellins

- Inactive
- Active

[Diagram showing the structure of GA1 and GA10 with a reaction involving GA 3β-hydroxylase]

PLANT PHYSIOLOGY, Third Edition, Figure 38 © 2002 Sinauer Associates, Inc.
Gibberellins

- **Synthesis**
- **Tissue Localization**
  - Immature seed embryo, Young Leaves, roots
- **Transport**
  - Phloem

**Responses**
- Cell Elongation
- **Dwarf** cultivars
  - eg. Peas (Little Marvel)
- **Dwarfing rootstocks**
  - apples, pears, peaches
  - height from roots
  - fruit quality from scion
- **Seed Dormancy**
  - High ABA
  - Reversed by GA application
  - Synthesis of GA by embryo
**Gibberellins**

**Agricultural Uses**

- **1. Thompson Seedless Grapes**
  - Principal use
  - Parthenocarpic Fruit

- **2. Seed Germination**
  - Malting Barley
  - Precocious germination

- **3. Male Flower production**
  - Monoecious & Dioecious Plants

- **4. Chilling Requirement**
  - Azaleas
  - Biennials
  - Biennial Bearing
**Ethylene**

- **C₂H₄**
- Gas at room temperature
- **Synthesis**

  \[
  \text{Methionine} \rightarrow \text{SAM} \rightarrow \text{ACC} \rightarrow \text{Ethylene} \rightarrow \text{PG}
  \]

  1. S-Adenosyl Methionine
  2. Amino Cyclo Propane
  3. Polygalacturonase

1. S Adenosyl Methionine
2. Amino Cyclo Propane
3. Polygalacturonase
Ethylene

- **Agricultural Uses**
  - Ethaphon - breaks down to form ethylene
  - **1. Fruit Ripening**
    - Tomato, Banana, Melon, etc.
      - Pick unripe and firm for shipping
      - Spray in store to “ripen”
    - Color development and softening
    - Field Spray
      - Uniform and synchronous ripening
    - Canning Tomatoes
    - Mechanical Harvest

- **2. Floral Development**
  - Bromeliads
    - Pineapple
    - Banana
  - Uniform development of inflorescence

- **3. Sex Expression**
  - Female Flowers
  - Curcubits
  - opposite of GA action

- **4. Degreening of Citrus**
  - Oranges, Lemons, Grapefruit
    - Break down Chlorophyll
  - Leaves Carotenoids
Ethylene

5. Mechanical Harvesting
   - Formation of Abscission Zone
   - Stimulate Fruit Drop
     - Cherries, Walnuts, Pecans

6. Postharvest Shelf Life
   - block ethylene synthesis
     - AgNO3 or Silver Thiosulfate
   - delay senescence
     - Carnations

Abscisic Acid

![Abscisic Acid structure](image)
Abscisic Acid

- Natural Plant **Growth Retardant**
  - Opposes action of GA and Auxin
- **Synthesis**
  - Chloroplasts
  - Breakdown product of Carotenoids

Abscisic Acid

- **Responses**
- **Dormancy Maintenance**
  - high levels in dormant seed and buds
- **Drought Resistance**
  - causes stomatal closure
- **Agricultural Uses**
  - None
Translocation in the Phloem

Patterns of translocation: Source to Sink
Metabolites move from source to sink.

**SOURCE = area of supply**
- exporting organs: mature leaves
- storage organs: seed endosperm, storage root of second growing season beet

**SINK = areas of metabolism (or storage)**
- non-photosynthetic organs and organs that do not produce enough photosynthetic products to support their own growth or storage
- Example: roots, tubers, developing fruits/seeds, immature leaves
Exactly what is transported in phloem?

Sucrose
The sugar that is most important in translocation is sucrose.
Sucrose is a disaccharide, i.e., made up of two sugar molecules – an additional synthesis reaction is required after photosynthesis.

Sucrose - is not a rigid structure, but mobile in itself.

http://www.biologie.uni-hamburg.de/b-online/e16/16h.htm#sucr
Compounds translocated in the phloem

Sucrose
Raffinose
Stachyose
Verbascose

Galactose  Galactose  Galactose  Glucose
Nonreducing sugar  Fructose

Sugar alcohol

Compounds translocated in the phloem

Glutamic acid, an amino acid, and glutamine, its amide, are important nitrogenous compounds in the phloem, in addition to aspartate and asparagine.

Amino acid  Amide

Species with nitrogen-fixing nodules also utilize ureides as transport forms of nitrogen.

Ureides
Primary phloem and primary xylem

Phloem Location

Root Stele  Stem Vascular Bundle  Leaf Midrib

Phloem is always in close proximity to xylem.
Sieve elements are highly specialized for translocation

(A) External view

B) Longitudinal section

- Sieve plate
- Sieve plate pore
- Lateral sieve area

- P-protein
- Sieve tube element
- Modified plastid
- Sieve tube element
- Smooth endoplasmic reticum
- Cytoplasm
- Plasma membrane
- Thickened primary wall
- Sieve plate pore
- Sieve plate

- Companion cell
- Branched plasmodesma
- Vacuole
- Chloroplast
- Nucleus
- Mitochondrion
Three different types of companion cells

Ordinary companion cells
- have chloroplasts
- few plasmodesmata between companion cell and surrounding cells, except for own sieve elements
- symplast of sieve element and its companion cell is relatively isolated from surrounding cells

Transfer cells
- similar to ordinary companion cells
- develop fingerlike wall ingrowths, particularly on walls that face away from sieve element
- wall ingrowths increase surface area of plasma membrane
  (increases potential for solute transfer across membrane)

Intermediary cells
- have numerous plasmodesmata connecting them to bundle sheath cells
- have many small vacuoles
- poorly developed thylakoids and lack of starch grains

Phloem transport
Velocities \(\approx 1 \text{ m hour}^{-1}\), much faster than diffusion

What is the mechanism of phloem transport?
What causes flow?, What's the source of energy?
Physiological process of loading sucrose into the phloem

**Pressure-flow**
Phloem and xylem are coupled in an osmotic system that transports sucrose and circulates water.

Physiological process of unloading sucrose from the phloem into the sink

Sugars are moved from photosynthetic cells and actively (energy) loaded into companion cells.

Fig. 10.14

Small vein

(See part 2)
Sugars are moved from photosynthetic cells and actively (energy) loaded into companion & sieve cells. The concentrating of sugars in sieve cells drives the osmotic uptake of water.

**Fig. 10.14**

**Fig. 10.16** Phloem loading uses a proton/sucrose symporter.
Pressure-Flow-Hypothesis

*Munch Hypothesis*

**Source**

- High concentration of sucrose, via photosynthesis, 
  - \( \Delta [\text{sucrose}] \) drives diffusion,
- Active \( \text{H}^+\)-ATPase,
  - electrochemical gradient drives symporters,
- \( -\Psi_s \) builds, water enters the cell, \( +\Psi_p \) builds.

**Sink**

- Low concentration of sucrose, 
  - \( \Delta [\text{sucrose}] \) drives diffusion,
- Active \( \text{H}^+\)-ATPase,
  - electrochemical gradient drives antiporters,
  - \( -\Psi_s \) drops, water exits the cell, \( \Psi_p \) drops.

---

Pressure-Flow-Hypothesis

\[ \Psi_p \]

- Notice that the \( \Psi_s \) at the source is more negative than at the sink!

- Why don’t we expect water to flow toward the source?

Water, along with solutes moves down the pressure gradient, not the water potential gradient.
**Phloem unloading**

- **Apoplastic**: three types
- (1) [B] One step, transport from the sieve element-companion cell complex to successive sink cells, occurs in the apoplast.
- Once sugars are taken back into the symplast of adjoining cells transport is symplastic

(A) **Symplastic phloem unloading**

(B) **Apoplastic phloem unloading**

---

**Water Cycling**

- **Apoplastic**: three types
- (1) [B] One step, transport from the sieve element-companion cell complex to successive sink cells, occurs in the apoplast.
- Once sugars are taken back into the symplast of adjoining cells transport is symplastic
The pressure-flow model of phloem translocation

At source end of pathway
- Active transport of sugars into sieve cells
- $\Psi_s$ and $\Psi_w$ decrease
- Water flows into sieve cells and turgor increases

At sink end of pathway
- Unloading of sugars
- $\Psi_s$ and $\Psi_w$ increase
- Water flows out of sieve cells and turgor decreases
Photosynthesis Overview

Energy for all life on Earth ultimately comes from photosynthesis.

\[6\text{CO}_2 + 12\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{H}_2\text{O} + 6\text{O}_2\]

Oxygenic photosynthesis is carried out by:
cyanobacteria, 7 groups of algae,
all land plants

Photosynthesis Overview

Photosynthesis is divided into:

**light-dependent reactions**
- capture energy from sunlight
- make ATP and reduce NADP\(^+\) to NADPH

**carbon fixation reactions**
- use ATP and NADPH to synthesize
  organic molecules from CO\(_2\)
Photosynthesis Overview

Photosynthesis takes place in chloroplasts.

- **thylakoid membrane** – internal membrane arranged in flattened sacs
  - contain **chlorophyll** and other pigments

- **grana** – stacks of thylakoid membranes
- **stroma** – semiliquid substance surrounding thylakoid membranes
Discovery of Photosynthesis

The work of many scientists led to the discovery of how photosynthesis works.

Jan Baptista van Helmont (1580-1644)
Joseph Priestly (1733-1804)
Jan Ingen-Housz (1730-1799)
F. F. Blackman (1866-1947)
Discovery of Photosynthesis

C. B. van Niel, 1930’s
- proposed a general formula:
  \[ \text{CO}_2 + \text{H}_2\text{A} + \text{light energy} \rightarrow \text{CH}_2\text{O} + \text{H}_2\text{O} + 2\text{A} \]
  where \( \text{H}_2\text{A} \) is the electron donor
- van Niel identified water as the source of the \( \text{O}_2 \) released from photosynthesis
- Robin Hill confirmed van Niel’s proposal that energy from the light reactions fuels carbon fixation

Pigments

**photon**: a particle of light
- acts as a discrete bundle of energy
- energy content of a photon is inversely proportional to the wavelength of the light

**photoelectric effect**: removal of an electron from a molecule by light
- occurs when photons transfer energy to electrons
Pigments

**Pigments**: molecules that absorb visible light

Each pigment has a characteristic absorption spectrum, the range and efficiency of photons it is capable of absorbing.
Pigments

**chlorophyll a** – primary pigment in plants and cyanobacteria
- absorbs violet-blue and red light

**chlorophyll b** – secondary pigment absorbing light wavelengths that chlorophyll a does not absorb
Pigments

Structure of pigments:

**porphyrin ring**: complex ring structure with alternating double and single bonds
- magnesium ion at the center of the ring

- photons excite electrons in the ring
- electrons are shuttled away from the ring
Pigments

**Accessory pigments**: secondary pigments absorbing light wavelengths other than those absorbed by chlorophyll a

- Increase the range of light wavelengths that can be used in photosynthesis
- Include: chlorophyll b, carotenoids, phycobiloproteins
- Carotenoids also act as antioxidants
A **photosystem** consists of

1. an **antenna complex** of hundreds of accessory pigment molecules
2. a **reaction center** of one or more chlorophyll a molecules

Energy of electrons is transferred through the antenna complex to the reaction center.
Photosystem Organization

At the reaction center, the energy from the antenna complex is transferred to chlorophyll a.
This energy causes an electron from chlorophyll to become excited.
The excited electron is transferred from chlorophyll a to an electron acceptor.
Water donates an electron to chlorophyll a to replace the excited electron.
Light-Dependent Reactions

Light-dependent reactions occur in 4 stages:

1. primary photoevent – a photon of light is captured by a pigment molecule
2. charge separation – energy is transferred to the reaction center; an excited electron is transferred to an acceptor molecule
3. electron transport – electrons move through carriers to reduce NADP*
4. chemiosmosis – produces ATP

In sulfur bacteria, only one photosystem is used for cyclic photophosphorylation

1. an electron joins a proton to produce hydrogen
2. an electron is recycled to chlorophyll -this process drives the chemiosmotic synthesis of ATP
Light-Dependent Reactions

In chloroplasts, two linked photosystems are used in **noncyclic photophosphorylation**

1. **photosystem I**
   - reaction center pigment ($P_{700}$) with a peak absorption at 700nm

2. **photosystem II**
   - reaction center pigment ($P_{680}$) has a peak absorption at 680nm
Light-Dependent Reactions

Photosystem II acts first:
- accessory pigments shuttle energy to the $P_{680}$ reaction center
- excited electrons from $P_{680}$ are transferred to $b_{2-f\text{ complex}}$
- electron lost from $P_{680}$ is replaced by an electron released from the splitting of water

Light-Dependent Reactions

The $b_{2-f\text{ complex}}$ is a series of electron carriers.
- electron carrier molecules are embedded in the thylakoid membrane
- protons are pumped into the thylakoid space to form a proton gradient
Light-Dependent Reactions

Photosystem I
- receives energy from an antenna complex
- energy is shuttled to $P_{700}$ reaction center
- excited electron is transferred to a membrane-bound electron carrier
- electrons are used to reduce NADP$^+$ to NADPH
- electrons lost from $P_{700}$ are replaced from the $b_6$-$f$ complex

ATP is produced via chemiosmosis.
- **ATP synthase** is embedded in the thylakoid membrane
- protons have accumulated in the thylakoid space
- protons move into the stroma only through ATP synthase
- ATP is produced from ADP + P$_i$
Carbon Fixation Reactions

To build carbohydrates, cells need:

1. energy
   - ATP from light-dependent reactions

2. reduction potential
   - NADPH from photosystem I
Carbon Fixation Reactions

**Calvin cycle**
- biochemical pathway that allows for carbon fixation
- occurs in the stroma
- uses ATP and NADPH as energy sources
- incorporates CO$_2$ into organic molecules

---

Carbon Fixation Reactions

**carbon fixation** – the incorporation of CO$_2$ into organic molecules
- occurs in the first step of the Calvin cycle

\[
\text{ribulose-bis-phosphate} + \text{CO}_2 \rightarrow 2(\text{PGA})
\]

5 carbons  →  1 carbon  →  3 carbons

The reaction is catalyzed by **rubisco**.
Carbon Fixation Reactions

The Calvin cycle has 3 phases:
1. carbon fixation
   \[ \text{RuBP} + \text{CO}_2 \rightarrow 2 \text{molecules PGA} \]
2. reduction
   PGA is reduced to G3P
3. regeneration of RuBP
   G3P is used to regenerate RuBP
Carbon Fixation Reactions

Glucose is not a direct product of the Calvin cycle.

- 2 molecules of G3P leave the cycle
- each G3P contains 3 carbons
- 2 G3P are used to produce 1 glucose in reactions in the cytoplasm

Carbon Fixation Reactions

During the Calvin cycle, energy is needed. The energy is supplied from:

- 18 ATP molecules
- 12 NADPH molecules
Carbon Fixation Reactions

The energy cycle:

- photosynthesis uses the products of respiration as starting substrates
- respiration uses the products of photosynthesis as starting substrates
Photorespiration

Rubisco has 2 enzymatic activities:
1. carboxylation – the addition of CO₂ to RuBP
   - favored under normal conditions
2. photorespiration – the oxidation of RuBP by the addition of O₂
   - favored in hot conditions

CO₂ and O₂ compete for the active site on RuBP.
Some plants can avoid photorespiration by using an enzyme other than rubisco. 

- **PEP carboxylase**
  - CO₂ is added to phosphoenolpyruvate (PEP)
  - a 4 carbon compound is produced
  - CO₂ is later released from this 4-carbon compound and used by rubisco in the Calvin cycle

---

**C₄ plants**

- use PEP carboxylase to capture CO₂
- CO₂ is added to PEP in one cell type (mesophyll cell)
- the resulting 4-carbon compound is moved into a bundle sheath cell where the CO₂ is released and used in the Calvin cycle
Photorespiration

**CAM plants**
- CO₂ is captured at night when stomata are open
- PEP carboxylase adds CO₂ to PEP to produce a 4 carbon compound
- this compound releases CO₂ during the day
- CO₂ is then used by rubisco in the Calvin cycle
Photosynthesis

The Source of most Biological Energy
Trapped in Photosynthesis
Energy Converted to Chemical Bonds

**Light:** An Energy Waveform With Particle Properties Too

![Light spectrum diagram](image_url)
**Light**: An Energy Waveform With Particle Properties Too

![Visible Spectrum Diagram](image)

- Wavelength (nm)
  - 400
  - 500
  - 600
  - 700
- Visible Spectrum:
  - 400 nm to 700 nm
  - $10^{-9}$ meter
  - 0.000000001 meter!

---

**Leaf Pigments Absorb Most Colors**

- White Light
- Green is reflected!
Light: An Energy Waveform With Particle Properties Too

Many metric units for different purposes
We will use an easy-to-remember English unit: foot-candle

0 fc = darkness
100 fc = living room
1,000 fc = CT winter day
10,000 fc = June 21, noon, equator, 0 humidity

What wavelengths of light drive photosynthesis?

Action Spectrum

Green light reflected

Some still drives photosynthesis

Visible spectrum

Light beyond 700 nm has insufficient energy to drive photosynthesis
Photosystem II

Light

<table>
<thead>
<tr>
<th>Pigment</th>
<th>Energy Transfer</th>
</tr>
</thead>
<tbody>
<tr>
<td>chlorophyll b</td>
<td>P450</td>
</tr>
<tr>
<td>lutein</td>
<td>P470</td>
</tr>
<tr>
<td>zeaxanthin</td>
<td>P480</td>
</tr>
<tr>
<td>β-carotene</td>
<td>P500</td>
</tr>
<tr>
<td>lycopene</td>
<td>P510</td>
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<tr>
<td>chlorophyll b</td>
<td>P650</td>
</tr>
<tr>
<td>chlorophyll a</td>
<td>P680</td>
</tr>
</tbody>
</table>

In each energy transfer, some energy is lost as heat: 2nd law of thermodynamics.

But enough energy is passed to P680 to eject an electron to the electron transport system.

Photosynthetic pigments are amphipathic.

Lutein
What intensities of light drive photosynthesis?

Photosynthesis

Add to reserve
Grow
Reproduce

Using reserves and may die

0 10 100 1,000 10,000 fc

Reaction Rate

0 100%

Respiration

The example plant shown here “breaks even” at an intensity we have in our homes…a house plant!

The second example plant shown here cannot survive in our homes…it is a sun-loving crop plant!
The Light Reactions: An Energy Diagram

The PCR Cycle has Three Phases
Let's Do Some Stoichiometry:

3 ADP

3 ATP

5 x 3 = 15 C

To take off 3 carbons:
sucrose for transport
starch for storage

3 x 5 = 15 C

rubisco
carboxylation

3 CO₂

rubisco
regeneration
complex
shuffling

6 C-C-C-P
3-phosphoglycerate

6 ATP
6 NADPH
6 NADP⁺

To take off 3 carbons:
sucrose for transport
starch for storage

3 ADP

3 ATP

5 x 3 = 15 C

rubisco
carboxylation

3 CO₂

rubisco
regeneration
complex
shuffling

6 C-C-C-P
3-phosphoglycerate

6 ATP
6 NADPH
6 NADP⁺

To take off 3 carbons:
sucrose for transport
starch for storage

sucrose and starch are not 3-carbon compounds!
The PCR Cycle and Light Reactions are interdependent

The PCR Cycle cannot operate in darkness!
“Dark Reactions?”

RuBisCO: an ancient enzyme with a modern problem

RuBP + CO₂ → 2 x P-C-C-C (Phosphoglycerate)
RuBisCO

1% in air
RuBP → P-C-C-C (a Phosphoglycerate) + P-C-C → 2 x CO₂
photorespiration

RuBP + O₂ → P-C-C-C
RuBisCO
20% in air

• Early in evolution of photosynthesis the atmosphere was anaerobic, so RuBisCo evolved without a problem.
• As photosynthesis was successful, competitive inhibition from oxygen was essentially a negative feedback.
• Evolution has not yet replaced RuBisCO.
• But several workarounds have evolved…
**C₄ Photosynthesis:** The first fixation is a 4-carbon compound

**Mesophyll Cell**
- regeneration
- HCO₃⁻
- CO₂
- phosphoenol pyruvate
- carboxylation
- CO₂

**Bundle Sheath Cell**
- PCR cycle
- rubisco
- CO₂
- decarboxylation
- CO₂

The C₄ and C₃ reactions are spatially separated

---

**C₄ Leaves**
- Zea mays
- Flaveria bidentis

**PEPc expression in leaf cs**
- B-Zellen
- M-Zellen

**Rubisco expression in leaf cs**

[http://botlibrary.wisc.edu/images/130/Leaf/Zea_leaf_cross_section/Major_vein_MC.jpg](http://botlibrary.wisc.edu/images/130/Leaf/Zea_leaf_cross_section/Major_vein_MC.jpg)
[http://wings.buffalo.edu/academic/department/fnsm/bio-sci/facultyart.GIFS/Berryart.gif](http://wings.buffalo.edu/academic/department/fnsm/bio-sci/facultyart.GIFS/Berryart.gif)
Zea mays leaf cross section showing classic Kranz anatomy.

These bulliform cells lose water and the leaf rolls...which way?
**C₄ Photosynthesis:** A cycle requiring ATP and NADPH

**Mesophyll Cell**

- P
- CCCOO-
- phosphoenol pyruvate
- CO₂
- HCO₃⁻
- carbonic anhydrase
- pepc
- malate dehydrogenase
- NADH
- NAD⁺
- low pH
- stomata open!
- CO₂

**Bundle Sheath Cell**

- ATP
- ADP
- pyruvate-phosphosphate dikinase
- CCCOO-
- pyruvate
- NADPH
- NAD⁺
- malate dehydrogenase
- malate
- NADPH
- NAD⁺
- high pH
- stomata closed!
- CO₂

The C₄ and C₃ reactions are spatially separated

**CAM Photosynthesis:** Crassulacean Acid Metabolism

**At Night**

- triose phosphate
- phosphoenol pyruvate
- HCO₃⁻
- pepc
- oxaloacetate
- NADH
- NAD⁺
- malic acid
- malate dehydrogenase
- malate
- NADPH
- NAD⁺
- starch
- low pH

**In Daylight**

- PCR cycle
- NADPH
- NAD⁺
- malic enzyme
- malic acid
- stomata closed!
- CO₂

The C₄ and C₃ reactions are temporally separated
Sedum leaf cross-section (a CAM plant) Note the lack of palisade/spongy differentiation

Sedum leaf cross-section (a CAM plant) Note the lack of Kranz anatomy