How to be a *plant

*photosynthetic, multicellular, terrestrial
Plants are multicellular, terrestrial and photosynthetic

**Multicellular:** Different cells can have various functions, but they must integrate their activities.

**Terrestrial:** Plant ancestors were aquatic, but terrestrial plants have to cope with very dry air.

**Photosynthetic:** Plants and many other organisms can convert solar energy to chemical energy.

Human physiology centers on systems

- **Respiratory system**: Gas exchange
- **Digestive system**: Water and Nutrient uptake
- **Circulatory system**: Nutrient transport
- **Nervous system**: Perception, control
- **Skeletal system**: Support
Plant physiology: Same functions, more broadly distributed

Gas exchange takes place through thousands of stomata.

Energy assimilation takes place throughout photosynthetic tissues.

Nutrients are transported from cell to cell and through vascular tissues.

Perception (of light, pathogens etc.) occurs through receptors and other sensors found in most cells.

Water and nutrient uptake take place across the root (and sometimes shoot) surfaces.

Signals to control and coordinate plant functions move from cell to cell and through vascular tissues.

Support comes from cell walls and hydrostatic pressure.
What are plants? Plants are photosynthetic eukaryotes.

(Circles not drawn to scale)

ALL LIFE

PHOTOSYNTHETIC ORGANISMS

CYANOBACTERIA + “DESCENDANTS”

EUKARYOTES WITH CYANOBACTERIA-DERIVED CHLOROPLASTS

GREEN ALGAE AND DESCENDANTS

PLANTS

- Cyanobacteria
- Diatoms
- Green sulfur bacteria
- Purple sulfur bacteria
- Other bacteria
- Brown algae
- Red algae
- Green algae and descendants

Non-photosynthetic bacteria

Archaea

Fungi

Animals

You are here
Plants descended from a eukaryotic ancestor + a cyanobacteria

Photosynthesis evolved in bacteria. All photosynthetic eukaryotes acquired this ability through endosymbiosis of photosynthetic bacteria.

Therefore, some “plant” genes (those derived from the ancestral bacteria) are more like bacterial genes than the genes of other eukaryotes.

Two endosymbiotic organelles – mitochondria and plastids

Family tree: Plants and green algae

Green algae are photosynthetic eukaryotes, but not all plants

**Chlorophytes**

*Ostreococcus tauri*

*Volvox spp*

*Chlamydomonas reinhardtii*

**Charophytes**

*Spirogyra spp*

*Chara braunii*

Image credits: [JGI](#); Spike Walker Wellcome Images; Jaspar Nance; Show_ryu
Bryophytes are “non-vascular” plants

Liverworts (~7000 – 8500 species)  Mosses (~10,000 – 17,000 species)  Hornworts (~200 species)

Tracheophytes are vascular plants

- Lycophytes (~ 1200 species)
- Ferns (~ 13,000 species)
- Gymnosperms (~ 1000 species)
- Angiosperms (~ 350,000 species)

Photos by Tom Donald
Introduction to bioenergetics

Photo credit: Tom Donald
Energy is never gained or lost, just transferred to other forms

Chemical energy transferred to potential energy by muscles

Potential energy transferred to kinetic energy

Kinetic energy transferred to heat
Energy exists in many forms and can be interconverted between them.
Chemical energy can be stored in bonds and as reducing power

A carbohydrate like starch has energy stored in its bonds.

Energy is released when the bonds are broken.

More energy is released when the carbon in the sugar is oxidized.

Starch – a polymer made of sugar

Energy released

$O_2$  $CO_2$
Energy can be stored or released via the redox state of an element.

Higher energy, reduced form:
- Carbohydrates: $\text{C}_6\text{H}_{12}\text{O}_6$, $\text{CH}_2\text{O}$
- Ammonium: $\text{NH}_4^+$
- Iron (II)

Lower energy, oxidized form:
- Carbon Dioxide: $\text{CO}_2$
- Nitrate, nitrite: $\text{NO}_3^-$, $\text{NO}_2^-$
- Iron (III)

Oxidation involves the removal of electrons, and requires an electron acceptor. Energy input required.

Energy released.
Campfire: Oxidation of carbon with energy released as heat and light

High-energy reduced carbon in wood

Energy is released as heat and light

Low energy oxidized carbon in carbon dioxide

The non-carbon elements in wood contribute to ash

Oxygen is required for a fire to burn. Oxygen is the electron acceptor in the oxidation reaction

\[
\text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{O}_2 \rightarrow 6 \text{CO}_2 + 6 \text{H}_2\text{O}
\]
Biological metabolism: Controlled release and recapture of energy

High-energy reduced carbon in food

Energy is captured for later use

ATP (adenosine triphosphate)

Low energy oxidized carbon in carbon dioxide

Metabolism

(Specifically, oxidative phosphorylation)

Oxygen is required to efficiently extract energy from carbohydrates. (Oxygen is the electron acceptor in the oxidation reaction)

\[
C_6H_{12}O_6 + 6 O_2 \rightarrow 6 CO_2 + 6 H_2O
\]
Analogy: Hydroelectricity is produced by the controlled release and capture of kinetic energy from falling water

Kinetic energy in the moving water turns the turbine to generate electricity (electromagnetic energy)

The energy of a natural waterfall is transferred to the rocks below it

Adapted from TXU Corp; Poco a poco
Cellular energy currencies, ATP and NAD(P)H

ATP (Adenosine triphosphate) stores energy in a high-energy bond.

NADPH (nicotinamide adenine dinucleotide phosphate) stores reducing power and electrons.

H₂O + energy → ATP

ATP → ADP + H⁺ + 2e⁻
Introduction to photosynthesis

Ultrastructure of a chloroplast showing thylakoid membrane stacks

ATP synthase (yellow) embedded in thylakoid membranes (green)

PSII supercomplexes in thylakoid membranes


Energy enters the biosphere mainly through photosynthesis by plants.

Some energy is introduced by the action of chemotrophs.

Burning buried sunshine*

One gallon of gasoline comes from ~89 metric tons (~180,000 pounds) of ancient lycophytes and ferns that dominated the earth 300 million years ago, but mostly have been supplanted by seed plants.

Fossil fuel reserves are estimated to be about 5,000 gigatons (Gt) of carbon, accumulated over millions of years.

89 metric tons of gold is worth $4 billion ($4 x 10⁹).

89 metric tons is about 89 elephants.

—I get 500 meters per ton

In plants, photosynthesis captures light energy as reduced carbon.

Energy input from sunlight:
- Low energy, oxidized carbon in carbon dioxide.

Oxygen is released as a byproduct:
- \[ 6 \text{ CO}_2 + 6 \text{ H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{ O}_2 \]

High energy, reduced carbon:
- The first step is the capture of light energy as ATP and reducing power, NADPH.
- The second step is the transfer of energy and reducing power from ATP and NADPH to CO\(_2\), to produce high-energy, reduced sugars.
Photosynthesis is two sets of connected reactions

- **The LIGHT-HARVESTING reactions** take place in the chloroplast membranes
  - $2 \text{H}_2\text{O} \rightarrow \text{O}_2 + 2 \text{H}^+$
  - $\text{ADP} + \text{H}^+ \rightarrow \text{ATP}$

- **The CARBON-FIXING reactions** take place in the chloroplast stroma
  - $\text{CO}_2 + \text{ADP} + \text{H}^+ \rightarrow \text{H}_2\text{O} + \text{ATP}$

Light harvesting reactions produce \( \text{O}_2 \), ATP and NADPH

The reactions require several large multi-protein complexes: two light harvesting photosystems (PSI and PSII), a cytochrome \( b_6f \) complex, and an ATP synthase.

Chlorophyll captures light energy to initiate the light harvesting reactions

Porphyrin ring captures photons

Hydrophobic tail anchors chlorophyll in membrane

Photon capture by chlorophyll excites the chlorophyll (Chl*). Chl* loses an electron (e\textsuperscript{-}) and relaxes back to its unexcited state

Oxidized Chl is reduced by stripping an electron from water, releasing oxygen and protons

Plants have two photosystems that work together.

In photosystem II, water is split to release oxygen:

\[ 2 \text{H}_2\text{O} \rightarrow 4 \text{H}^+ + \text{O}_2 \]

Electrons are passed from PSII to PSI and eventually to NADP\(^+\), producing NADPH.

Protons accumulate in the thylakoid lumen.

Electrons are passed from PSII to PSI and eventually to NADP\(^+\), producing NADPH.
A proton gradient drives ATP synthesis

Proton gradient from high (in) to low (out)

Through the Calvin-Benson cycle, ATP and NADPH are used to fix CO$_2$.

Each CO$_2$ fixed requires 3 ATP and 2 NADPH.

For every 3 CO$_2$ fixed, one GAP is produced for biosynthesis and energy.
Some plants have additional, CO$_2$-concentrating steps

Because Rubisco has an oxygenase as well as a carboxylase activity, some plants concentrate CO$_2$ to promote the carboxylation reaction.
Fixed carbon has many fates

- Some of the fixed carbon is oxidized in the mitochondria to produce ATP, and released as CO$_2$.
- Some is used for biosynthesis of other compounds.
- Some is transported to growing tissues, or stored as starch or oil in seeds.
- Some is transported to the roots and used for growth, stored, used to support nutrient uptake, or exuded into the soil.
Summary: Plants are photosynthetic eukaryotes

- Plants convert light energy to chemical energy
- Photosynthesis evolved in bacteria, and takes place in the descendants of endosymbiotic photosynthetic bacteria
- Through photosynthesis, plants and algae are responsible for the transfer of most of the energy that enters the biosphere

\[ 6 \text{CO}_2 + 6 \text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{O}_2 \]
Plants are assembled from cells

The plasma membrane is a barrier that lets cells maintain a different internal environment from their surroundings.

A “typical” plant cell
Systems move towards uniformity, unless energy is expended

Dispersed, equally distributed

Nonuniform distribution,

Energy

Equilibrium

Disequilibrium – stored energy

Cells expend energy to maintain an internal environment that is distinct from the external environment
Cells are surrounded by a semi-permeable plasma membrane

The membrane is permeable to water and gases, but impermeable to ions and larger molecules.

Photo credit: Wenche Eikrem and Jahn Throndsen, University of Oslo
Proteins in the plasma and vacuolar membranes move molecules

These transporters bring in needed ions and other compounds, and export unwanted molecules. The transporters are also needed to regulate the cell’s osmotic potential.

Membrane proteins form pores, channels or pumps for ion transport.

The complex protein structures are usually drawn in simplified forms.

Ion transport across a membrane usually directly or indirectly requires energy.
Plant cells move water by osmosis and pressure

Cell showing the cytoplasm pull away from the cell wall as it loses volume (plasmolysis)

Water moves across a semipermeable membrane into a compartment containing salt.

The water flows inwards until the force of the pressure inside balances the osmotic driving force.

The osmotic potential of pure water is 0. The addition of solutes lowers the water potential. Water moves towards a region with a lower water potential.
Osmotic forces drive the movement of water into and out of cells

Cells have a lower osmotic potential than pure water, (because of the salts and proteins in them), so water moves into them

An animal cell might burst

Salt water has a lower osmotic potential than cells, so water flows outwards

Fresh water

Plant cell walls prevent them from bursting

Osmotic potential is written as $\Psi_\pi$ and measured in MegaPascals (MPa)
For seawater, $\Psi_\pi$ is about -2.5 MPa, and for a typical cell, $\Psi_\pi$ is about -0.8 MPa
Water can be moved by tension (pulling) or pressure (pushing)

Pulling up the plunger causes the pressure inside the barrel to be lower than atmospheric. Water from the beaker moves towards the region of lower pressure, into the barrel.

Pushing down the plunger causes the pressure inside the barrel to be higher than atmospheric. Water from the barrel moves out, towards the region of lower pressure.
Pressure can be positive or negative

Pressure washer 15 MPa

Household water pressure 0.3 MPa

Car tire pressure 0.25 MPa

Pressure required to blow up a balloon 0.01 MPa

Vacuum cleaner -0.02 MPa (household)
-0.1 MPa (commercial)
Laboratory vacuum -0.01 MPa

Inside typical plant cell 0.5 – 1.5 MPa

Inside xylem: From +1 MPa to -3 MPa or lower

Human blood pressure < 0.02 MPa

Human blood pressure

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The water potential equation incorporates osmotic and pressure potentials.

The water potential ($\Psi_w$) is the sum of the pressure potential ($\Psi_p$) and the osmotic potential ($\Psi_\pi$).

$$\Psi_w = \Psi_p + \Psi_\pi$$

Water flows from higher to lower water potential.
Water moves towards lower water potential

Initial conditions:

\[
\begin{align*}
\Psi_{\pi} &= 0 \\
+ \Psi_p &= 0 \\
\therefore \Psi_w &= 0
\end{align*}
\]

Water moves towards lower water potential

Final conditions:

\[
\begin{align*}
\Psi_{\pi} &= 0 \\
+ \Psi_p &= 0 \\
\therefore \Psi_w &= 0
\end{align*}
\]

Water is at equilibrium
Plant cell walls are flexible, strong, and complex

The primary cell wall is thin and somewhat flexible.

Cytoplasm
Vacuole
Plasma membrane

Secondary cell walls form inside of the primary cell wall. Secondary walls are usually rigid and contain lignin, a complex, insoluble polymer.

The cell wall is synthesized outside of the plasma membrane from materials transported outward through the plasma membrane.

Primary cell wall: cellulose, proteins and other components

Plants are multicellular

Advantages:
• Bigger means better able to compete for light, nutrients
• Cells can specialize

Disadvantages:
• Need to move resources and information, coordinate actions

Photo credit: Tom Donald
Multicellular organisms need to transmit materials and information

Metabolic products have to be distributed throughout the body

Information has to be transmitted to integrate activities

Raw materials have to be distributed – diffusion is inadequate for larger organisms
(Most) plant cells are connected by plasmodesmata

Plasmodesmata are plasma-membrane lined, regulated cytoplasmic bridges between plant cells.

Signals, nutrients, ions and water can move to adjacent cells, or longer distances via the phloem.

Guard cells are isolated, without functional plasmodesmata.

Pathogens can spread through the plant through plasmodesmata.

Transport in bryophytes – some specialized transport cells

Bryophytes take up water from the air and substrate

Water moves along external surfaces, within cells, between cells, and through specialized water-conducting cells or hydroids (h)

Hydroids (h) in cross section

Some bryophytes have food-conducting cells or leptoids (l)

The end walls between food-conducting cells can have enlarged plasmodesmata-


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Vascular plants have long-distance transport systems

**XYLEM**
Water moves from the soil to the atmosphere through the hollow dead cells of the xylem

**PHLOEM**
Photosynthetically-produced sugars (and other molecules) move from their *source* to *sinks* (non-photosynthetic tissues) through the phloem
Water uptake and movement in vascular plants

Water moves from the soil, into the outer layers of the root, then into the vascular cylinder and xylem.

In the leaf, water evaporates out of the xylem into the intracellular spaces, and then through the stomata into the atmosphere.

Water is pulled through the hollow xylem by tension developed at evaporative sites in the leaves.
Water movement in the xylem is driven by evaporation.

\[ \Psi_w = -0.2 \, \text{MPa} \]

Water moves from moist soil to the dry atmosphere. The plant simply taps into this force to draw water through its body.

\[ \Psi_w = -15 \text{ to } -100 \, \text{MPa} \]
Water movement in the xylem is driven by evaporation

\[ \Psi_w = -0.2 \text{ MPa} \]

Simple model:
Hollow tube that water evaporates through

Better model:
Hollow tube with a selectivity filter in the roots and a flow regulator at the top

\[ \Psi_w = -15 \text{ to } -100 \text{ MPa} \]

Guard cells
Casparian strip of the endodermis

Xylem cells are highly specialized water-conducting cells

The cells form thickened rings of secondary wall tissue and then die, leaving behind a hollow, reinforced vessel.

Elongation → Secondary wall deposition → Programmed cell death

The structure of xylem cell walls prevents embolisms from spreading.

Because water moves under tension, air bubbles or embolisms can form. The small gaps in the xylem walls permit water but not air bubbles to move through them.

The secondary walls are reinforced by lignin, a water-impermeable polymer.

Lignin-strengthened cell walls are one of the major features that let plants get big.

Bryophytes produce monolignols: UV protection? Defense?

Tracheophytes produce lignin polymer: Structure for xylem, support and strength for size.

Lignified xylem provides structural support for vascular plants

The tallest living trees tower over many familiar monuments

- 115 m Sequoia sempervirens
- 93 m Statue of Liberty
- 65 m Taj Mahal
- 65 m Sydney Opera House
- 111 m St. Paul’s Cathedral
The root endodermis acts as a selectivity filter.

The endodermis produces a water-impermeable layer, the Casparian strip, that provides selectivity.

Photo credit Michael Clayton
The Casparian strip forces water to cross a plasma membrane.

Water can enter the root through the apoplast (cell wall spaces) until it reaches the Casparian strip, which blocks apoplastic water flow.

Water forced to cross a plasma membrane is effectively filtered.

Waxy cuticles prevent water loss; regulated pores allow it

Most plant aerial surfaces are covered by a waxy cuticle. Pores called stomata, usually covered by pairs of guard cells, permit transpiration.

Guard cells change their volume to open and close the pore. Guard cells are sensitive to the atmospheric conditions and the plant’s needs for gas exchange and water conservation.
The companion cell loads the sieve element and provides it with genetic materials, through extensive plasmodesmatal connections.

Functional sieve elements lack nuclei and central vacuoles, facilitating flow.

The ends of adjoining sieve elements are connected by pores derived from enlarged plasmodesmata.

Transport in the phloem

1. Sugars are loaded into the phloem by active transport

2. Water moves in by osmosis

3. The fluid moves through the sieve elements under pressure, by bulk flow (like water in a hose)

4. Sugars are released into the sink tissues

5. Water follows by osmosis

From source to sink

Vascular tissues are essential conduits for information flow

Some signals move in the xylem. Signals from drought-stressed roots cause guard cells to close.

In animals, signals moving through the nervous and circulatory systems convey information.

Other xylem-borne signals convey information about nutrient availability and soil-microbes.

The phloem is also responsible for long-distance signaling

Coordination of root and shoot functions:
When leaves are phosphate-limited, a microRNA (miR399) moves through the phloem to the root and promotes phosphate uptake.

Time to reproduce:
Under appropriate day-length conditions (i.e. seasons) the protein FLOWERING LOCUS T (FT) and its orthologs move from leaves to the shoot apex, to promote the transition to reproductive growth.

Opportunities and challenges of the terrestrial environment

>450 million years ago, plants moved onto dry land

The aquatic environment was competitive and filled with herbivores

Initially, land offered less competition and fewer herbivores

However, plants had to overcome significant challenges to adapt to dry land
The terrestrial environment is challenging

Too heavy, dry, hot and cold and bright

Aquatic environment:
- Buoyancy
- Abundant water
- Moderate temperatures
- Filtered light

Terrestrial environment:
- No buoyancy
- Scarce water
- Extreme temperatures
- Excess light including UV
As sessile organisms, plants have to respond and adjust to stress.

Like animals, plants sense and respond to the physical conditions of their environment: temperature, humidity, light intensity.
Obtaining and retaining water is a challenge for terrestrial plants.

Freshwater green algae easily take up water from their aquatic environment.

The water potential of air and soil is usually lower than that of the plant cells. How do terrestrial plants survive?
Desiccation tolerance or avoidance, drought evasion or tolerance

Most bryophytes can tolerate desiccation (drying out extensively)

Some desert plants evade drought. They survive the dry season as seeds, sprouting and flowering in a brief period of rain

Most tracheophytes cannot tolerate desiccation – they die

Some desert plants tolerate dry conditions through adaptations such as deep roots, C₄ photosynthesis, and tiny or absent leaves

Photo credits: Mary Williams; Amrum; Scott Bauer; James Henderson, Golden Delight Honey, Bugwood.org
Desiccation tolerance or desiccation avoidance

Most bryophytes (and a few angiosperms) can tolerate desiccation. The vegetative tissues of most angiosperms cannot tolerate desiccation, but the seeds can.

The cells adjust with external water availability, and can survive desiccation. The cells do not really adjust with external water availability, and die if totally desiccated.

Photo credits: Mel Oliver, IRRI, IRRI
Strategies for desiccation tolerance include stabilization and repair

Craterostigma pumilum, an angiosperm desiccation tolerant “resurrection plant”

Upon desiccation, the leaves curl in, purple anthocyanin photoprotective pigments accumulate, and small molecules that stabilize cell integrity accumulate.

Desiccation affects membranes and walls, which must be rapidly repaired on rehydration.

By contrast, most tracheophytes *avoid* desiccation

Tracheophytes have:
- A waxy cuticle that covers their aerial tissues
- Regulated pores (stomata) for water and gas exchange
- Lignified vascular tissues that conduct water
- Roots specialized for water and nutrient uptake

Plants can survive across most of the earth.
Plants can adapt and acclimate to temperature extremes

Some plants have evolved to tolerate high temperatures

Larrea tridentata, an extremely thermotolerant desert plant

To a certain extent, most plants can acclimate to higher or lower temperatures, by sensing and responding to a change in temperature

How long can bryophytes tolerate extreme cold? 400 years!

Behind a retreating glacier, scientists found viable bryophytes that laid dormant under the ice for ~400 years.

Light is good, but too much light is damaging.

When light is too bright, chloroplasts can move to reduce light incidence.

Vertical orientation minimizes light absorption at midday.

Photoprotective pigments can protect delicate light-harvesting machinery.

SUMMARY

Like animals, plants need energy, water, and the ability to tolerate environmental challenges.

Plants have endosymbiotic photosynthetic organelles that let them produce chemical energy from light.

The two groups of plants, bryophytes and tracheophytes, differ in size, how they move materials, and how they deal with desiccation.
Plants are green, but they aren’t aliens. (They were here first!)