Photosynthetic Water Use Efficiency

Fundamental plant problem: **Stomata**: pathway for diffusion of CO$_2$ into leaves is the same as the pathway for diffusion of H$_2$O out.

A plant’s success in dealing with water loss and CO$_2$ uptake is measured as its **Photosynthetic Water Use Efficiency (WUE)**.

Photosynthetic Water Use Efficiency

- WUE = amount CO$_2$ fixed by photosynthesis per amount H$_2$O lost by transpiration.
  
  \[(WUE = \frac{\text{CO}_2 \text{ fixed}}{\text{H}_2\text{O transpired}})\]

Is it better to have a high or low WUE?

Two major innovations that have increased WUE involve the evolution of **new photosynthetic pathways**.

To understand these, first review the ancestral **C3 photosynthetic pathway**. (Chapter 8)

Photosynthesis

2 major components:

1. **Light reactions** – where light is ‘harvested’
2. **Dark reactions** – where CO$_2$ is fixed into sugars
Photosynthesis has two major components:

1. **the light-harvesting reactions** (the "light reactions"): 
   - Light energy is absorbed by **chlorophyll** and accessory pigments.

2. **the CO2-fixation reactions** (also known as the "dark reactions"): 
   - Occur in the **stroma** ("soupy" matrix outside thylakoids).
   - CO2 is "fixed" (or chemically bound).

**C3 Photosynthesis**

- **The primary reaction by which CO2 is fixed** in most plants is:
  
  \[ \text{ribose bisphosphate} + \text{CO}_2 \rightarrow 2 \text{3-phosphoglycerate} \]  
  
  \[(C5) \rightarrow (C3)\]

- This is called **C3 photosynthesis** because the primary fixation product is 3-phosphoglycerate (C3).

**C3 Photosynthesis**

- **Enzyme** ribulose bisphosphate carboxylase (or RuBP carboxylase) also known as **Rubisco**.

- **Rubisco** often accounts for more than 50% of the soluble protein in leaves, and thus may be the most abundant protein in nature.
One problem with C3 photosynthesis is that **Rubisco can add O₂ to RuBP** instead of CO₂. (it can catalyze the reaction in reverse)

**Photorespiration** actually releases rather than fixes CO₂, thus *reducing* carbon fixation.

Relative concentrations of CO₂ and O₂ determines balance between C-fixation and photorespiration.

*When it's hot & dry - stomata close*

Effects on CO₂ and O₂ rel. concentrations?

Favoring?

### Photosynthesis (Water Use Efficiency)

Two major innovations that have increased WUE involve the evolution of new photosynthetic pathways:

1. C4 Photosynthesis
2. CAM Photosynthesis

### Plan A: C4 photosynthesis

- In some plants, the primary fixation product of photosynthesis is oxaloacetate (which has 4 carbons).

- These are **"C4 plants"**, CO₂ is fixed when:

  \[
  \text{phosphoenol pyruvate + CO}_2 \rightarrow \text{oxaloacetate (C4)}
  \]

- Catalyzed by the enzyme phosphoenol pyruvate carboxylase (or **PEP carboxylase**).

### C4 photosynthesis – increases WUE

PEP carboxylase has **two key properties**:

- It doesn't do photorespiration.
- It can fix CO₂ at very low concentrations.

E.g. of C4 plants: many tropical grasses including corn, sugar cane, sorghum, and millet.
An additional feature of C4 photosynthesis: separation parts of dark reactions in space

An additional feature of C4 photosynthesis –
- C4 photosynthesis, uses both C4 and C3 pathways.
- In C4 plants there is a spatial separation – Rubisco only has access to CO₂ in bundle sheath cells

C4 photosynthesis – increases WUE
- C4 plants occur in hot, dry environments, where photosynthetic water-use efficiency is at a premium.
- C4 evolved about 15mya when CO₂ levels dropped.

C4 photosynthesis – increases WUE
- Because of the 2 key properties of PEP carboxylase:
  C4 plants can maintain high rates of photosynthesis with less stomatal opening than C3 plants.
- Water-use efficiency?
  C4 plants >> C3 plants (3x higher)

RuBisCO
(Ribulose-1,5-bisphosphate carboxylase/oxygenase)

What is the ‘problem’ most plants experience in hot dry conditions?
- ribulose bisphosphate + CO₂ → Carbon Fixation
- ribulose bisphosphate + O₂ → Photorespiration
C3 vs C4 photosynthetic plants

What enzyme is used to fix CO2 in C3? In C4?

\[
\text{ribulose bisphosphate} + \text{CO}_2 \rightarrow 2 \text{ 3-phosphoglycerate} \quad \text{(C3)}
\]

\[
\text{phosphoenol pyruvate} + \text{CO}_2 \rightarrow \text{oxaloacetate} \quad \text{(C4)}
\]

Difference between RUBISO and PEP carboxylase?

Plan B: Crassulacean Acid Metabolism (CAM)

- CAM photosynthesis, like C4 photosynthesis, uses both C4 and C3 pathways.
- CAM plants there is a temporal separation

Crassulacean Acid Metabolism

- In all CAM species the stomata open during the night and close during the day.

**At Night:** CO2 is fixed by PEP carboxylase into oxaloacetate (same as C3 or C4 plants?).

- stored in large vacuoles.

**During the day:** (stomata are closed)

- The released CO2 is fixed by Rubisco via a pathway similar to that in C3 plants.

**Succulents** (water storing plants), e.g., cacti, pineapple, Spanish moss, agaves.

**Water-use efficiency?**

- CAM >> C4 >> C3
- Yet closing stomata during the day severely reduces their ability to take in CO2.
- Thus they are slow growers.
Summary

• **Fundamental problem** especially in hot dry places:
  the pathway for diffusion of CO₂ in is the same as
  the pathway for diffusion of H₂O out

• C₄ and CAM Photosynthesis: both use the more
  efficient C₄ carbon fixation. Enzyme is?

**Difference between the 2 adaptations?**

- **C₄** –
  - safe place (bundle sheaths).
- **CAM** –
  - safe time (when stomata are closed).

Translocation of Substances in the Phloem

• Photosynthesis in the chloroplasts produces
  sugars

• Send it from the leaf through the **phloem** to
  where its needed:
  Growing tips of shoots and roots, fruits, seeds,
  and storage parenchyma in stems or roots.

Translocation of Substances in the Phloem

• Sucrose goes from **source** to **sink**.

• **Source**: sites of photosynthesis or storage
  sites.

• **Sinks**: are any plant parts unable meet
  their own nutritional needs
  (storage sites can be sinks when importing
  and sources when exporting)

The pressure-flow model explains phloem
  transport

Sucrose pumped into sieve tubes at the source.
This creates **osmotic pressure** $\Psi_s$ pulls in
water - creating **turgor**.

Turgor pressure $\Psi_p$ builds up

Water moves because of
build up of $\Psi_p$ –
pushes water thru
phloem

The pressure-flow model explains phloem
transport

Sucrose: unloaded at the
sink and facilitates
water movement out
of the sieve tube.

**Active transport** is
involved with loading
and unloading sieve
tubes.

Transport in Xylem vs. Phloem?

1. Water and minerals are **pulled** through the
  xylem without expending energy.

2. Energy is expended to **push** substances
   through the phloem.
Plant Nutrition

- Most plants are autotrophs: they make energy from compounds using solar power, CO2 and water.
- However, they do need a number other nutrients:
  - Nitrogen (N) for proteins and DNA
  - Phosphorus (P) for ATP
  - Potassium (K) for stomatal opening.
  - Other essential elements

Plant Nutrition

- Nutrients are derived from rock, except for N.
- Plants get most of these (including N) from the local soil.
- Roots "forage" for water and nutrients

Plants limited by nitrogen.
- There is almost always a growth response to added N.
- N is in chlorophyll and Rubisco.
- (There are charts of nutrient deficiencies that are handy to have if you like growing plants (e.g., Table 37.2 in your text)).

Plants and Soils

Particle size: sand, silt, clay; small, smaller, smallest.
- Sandy: plenty of air space, but low in water and nutrients.
- Clayey: plenty of nutrients and water, but low in air (roots need O2).
- Loamy (=mixture of sand, silt, and clay): has good levels of air, water and nutrients.

Clay is critical to plant nutrition
- Many nutrients are positively charged in soil: K+, Mg2+, Ca2+
- Clay particles have negative charges on the outside and attract and hold these + nutrients.
- Ion exchange: Plants release protons (H+) which trade places with the + nutrients, bringing them into solution which can be absorbed.

Negatively charged ions are more readily leached away: NO3-, SO4-, H2PO4-.
- Organic matter is a reservoir of N which slowly releases it during decomposition.
Fertilizer
Under intensive agriculture, plants need nutrient supplements. **Organic fertilizers** (like rotted manure) release nutrients more slowly.
- result in less runoff, which is damaging to waterways.
- Organic matter improves soil structure.

Fertilizer
Under intensive agriculture, plants need nutrient supplements. **Inorganic fertilizers** — instant fix, precisely formulated.
- Leaching and runoff damaging.
- takes much energy to manufacture (the biggest energy input into intensive agriculture).

Humus
Humus = Dark colored organic material 
a product of decomposition - leaf litter, feces, and other stuff (like dead animals and fungi).
- Humus is rich in nutrients, especially N.

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Nitrogen Fixation
- 78% of the atmosphere is nitrogen (N₂)
- **Very stable** and unreactive → triple bond
- A few species of *bacteria* can break it with the enzyme *nitrogenase* and a lot of ATP.

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Nitrogen is fixed by Bacteria
(and factories!)
- *Cyanobacteria* — mostly aquatic
- Most nitrogen fixation on land is done by bacteria that live symbiotically in plant roots.
- Some *lichens* have *symbiotic cyanobacteria*.

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Nitrogen is fixed by Bacteria
- *Rhizobium* (a bacteria) is the root symbiont of *legumes* (one of the largest flowering plant families):
  - Peas, soybeans, clover, mesquite, palo verde
Some Plants are Parasites or Predators

- Unhappy with the lifestyle we’ve been looking at, some plants “eat food”.
- This either replaces or supplements photosynthesis.

(1) Parasites form absorptive organs which invade a host plant and connect to its vascular tissue.
- They take water and nutrients and photosynthate.
- Some partial parasites only supplement their own photosynthesis.

Some Plants are Parasites or Predators

(2) Carnivorous plants, the stuff of science fiction.
- 450 species known.
- Capture and digest insects (not humans).
- Boggy regions have acidic soil which slows the breakdown of organic matter.
- Carnivorous plants supplement their nitrogen supply.