Plant Ecophysiology
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1 Introduction
This is a summary of notes, primarily from Kevin Griffin’s Plant Ecophysiology course at Columbia. It’s mostly not my own material but is a helpful way for me to organize my own notes on plants. It may be less applicable for redistributing until I’ve produced more of my own content.
2 Plant physiology

2.1 Cellular Organelles

Vocabulary

- **Nucleus** - holds the genetic materials of the plant
- **Vacuole** - The vacuole is water filled and used for storage
- **Golgi apparatus** - cellular processing and cell wall formation
- **Mitochondria** - used in respiration
- **Chloroplasts** - Photosynthesis happens inside the chloroplasts. Has two cell walls. Membranes inside are thylakoids

2.2 Plant parts

More vocabulary

- **Stomata** - pores in the epidermis of the leaves, which are composed of two guard cells that can swell shut or open to allow for the exchange of $CO_2$ and water between the outside atmosphere and the leaf
- **Xylem** - thick secondary walls of the plant that conduct water and ions. Dead at functional maturity
- **Phloem** - Transports sucrose and is living at functional maturity.

![Woody Dicot Diagram](image)

Figure 1: Credit: Kevin Griffin, Lecture 3, 2015, Plant Ecophysiology
2.3 Plant types

Vocabulary about categorizing plants

Gymnosperms - seed-producing plants (conifers)

Angiosperms - are also seed-producing plants, but in addition they have flowers, endosperm within the seeds and have fruits that contain the seeds

3 Photosynthesis and Respiration

We can generally write the stoichiometry of photosynthesis as:

\[ 6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow C_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 \]

which takes as an input sunlight for energy. This equation reflects both the light and dark reactions. The light reactions take in sunlight and \( \text{H}_2\text{O} \), splits the \( \text{H}_2\text{O} \) to use the \( e^- \) to convert \( \text{NADP}^+ \) to \( \text{NADPH} \) and produces \( \text{ATP} \) and \( \text{O}_2 \). The Calvin cycle (dark reactions) then use the \( \text{ATP} \) exported by the light reactions to produce sugars needed in the plant. Note that Rubisco, an important enzyme in the photosynthetic pathway, comes into play in the Calvin cycle.

3.1 cell cycle

Photosynthesis occurs simultaneously with respiration. The figure below demonstrates how the outputs of photosynthesis are used as the inputs for respiration. Respiration takes in \( \text{O}_2 \) and produces \( \text{CO}_2 \)
Photosynthesis takes in sunlight, $H_2O$ and $CO_2$ and produces oxygen and pyruvate. The light reactions happen in the chloroplasts, on the surface of the thylakoid membranes. The Calvin cycle on the above diagram is often referred to as the 'dark reactions' because it does not require sunlight, which means they are occurring at all times (even in the daylight). The Calvin cycle takes in NADPH, $CO_2$ and ATP and turns it into sugar (glucose). The respiration cycle (the Krebs cycle) takes in the pyruvate and produces $CO_2$. 
3.2 light reactions

The sunlight absorbed in photosynthesis isn’t uniform across the spectrum. Photosynthesis absorbs in the spectrum of 400 to 700 nm (roughly visible), but with two absorption peaks at 420 (Chl A and Chl B) and 670 nm (Chl A more than Chl B). So why do we use red lights, which is longer wavelength and therefore lower energy, as grow lights? For photosynthesis it’s the number of packets of light that are absorbed rather than the total energy that matters, and it turns out that long wavelength light makes photosynthesis more efficient. When photosynthesis takes in blue light, which is higher energy, the plant must first dissipate excess energy until it reaches the precise wavelength that can be absorbed by the photosystem.

3.3 dark reactions

A key enzyme in the dark reactions is an enzyme called ribulose biphosphate carboxylase oxygenase (Rubisco). Rubisco as an enzyme is Nitrogen intensive, which is why leaf level nitrogen is so important for plants and why we have Nitrogen fertilizer. So (the dark reaction of) photosynthesis needs Rubisco, which needs Nitrogen.

So as a final summary of the light reactions and the dark reactions, see the below figure.

![Photo of a diagram](image)

Figure 3: Credit: Kevin Griffin, Lecture 3, 2015, Plant Ecophysiology

3.4 sensitivity to temperature

Photosynthesis is sensitive to both the concentration of $CO_2$ in the atmosphere, and to temperature. Before we get started let’s distinguish between gross pho-
tosynthesis (C fixed) and net photosynthesis (C fixed - C lost). Carbon is lost, for example, by formation of CO\textsubscript{2} during respiration. As temperature rises both gross photosynthesis and respiration increase such that at some point net photosynthesis begins to decrease when gross photosynthesis levels out but respiration continues to increase (see below figure). This decline in photosynthesis doesn’t involve damage to the photosynthetic apparatus.

Figure 4: Credit: http://ib.berkeley.edu/courses/ib151/IB151Lecture6.pdf

At higher temperatures (35-40 °C), however, the photosynthetic apparatus does become damaged. At this temperature, proteins can denature and membranes can begin to deform. We can see this in the below figure, in which quantum yield (CO\textsubscript{2} fixed / photons absorbed) drops off, fluorescence (an indicator
of stress) increases, the electron transport in photosystem 1 (PS1) continues to function but photosystem 2 (PS2) shuts down as it is damaged. The temperature at which plants experience lethal temperatures depends on the temperatures in which they are evolved (or developed) to grow.

Photosynthesis responds to variations in heat differently at different timescales (adaptation vs. acclimation). At short timescales (acclimation), photosynthesis becomes more efficient up to about 26°C, after which it becomes less efficient.
(but, as mentioned above, extreme heat still eventually damages the plant cell structure). At longer timescales, plants may adapt (at least to some extent) as the below figure demonstrates.

![Temperature Acclimation of photosynthesis](image)

Figure 6: Credit: Kevin Griffin, Lecture 3, 2015, Plant Ecophysiology

### 3.5 modeling photosynthesis

When we begin considering photosynthesis, we often express it in the following terms

\[
A = g_s \times (C_a - C_i)
\]

Where \( A \) is the assimilation rate, or the rate of carbon fixation, \( g_s \) is the stomatal conductance, relating to the passage of water and \( CO_2 \) through the stomata of the plant, \( C_a \) is the concentration of carbon in the atmosphere and \( C_i \) is the intercellular concentration of carbon in the leaf.

Both \( C_3 \) and \( C_4 \) plants use photosynthesis to convert sunlight and \( CO_2 \) into energy, but they evolved at different times (under different conditions) and so the enzymes and leaf structure they use to do so is not identical. \( C_3 \) plants can be thought of as cool season plants that benefit from higher atmospheric \( CO_2 \), while \( C_4 \) plants may be thought of as warm season plants that can thrive at low concentrations of atmospheric \( CO_2 \).
3.6 $C_3$ plants

$C_3$ plants fix $CO_2$ using an enzyme called ribulose biphosphate carboxylase in the chloroplast. The photosynthesis of $C_3$ plants becomes less efficient as temperature increases.

3.7 $C_4$ plants

$C_4$ plants first convert $CO_2$ to oxaloacetate, then the photosynthesis process continues as it would in $C_3$ plants. The benefit of this form of photosynthesis is that little $CO_2$ is lost to photorespiration, meaning that the process is effective for low-$CO_2$ environments. By this same token, $C_4$ plants lose less water in the course of fixing carbon than do $C_3$ plants. It’s thought that $C_4$ plants first evolved when $CO_2$ reached 120 ppm (much lower than present-day 400 ppm).
3.8 CAM plants

CAM is a version of photosynthesis present in desert plants. CAM acts to minimize photorespiration because it decouples the light and dark reactions so that plants can open their stomates at night so as to reduce water loss during the day without wasting too much energy to photorespiration.

4 Plant water relations

Plants regulate water fluxes through their roots (intake) and the stomata on their leaves (loss). Opening and closing stomata takes energy because to open the plant pumps K into the guard cells.

4.1 Types of water modulation

Plants fall into two categories in regard to their water exchange with the atmosphere. They are either:

Isohydric plants reduce stomatal conductance (close stomata) as soil water potential decreases and VPD rises. These plants try to hold their leaf water potential relatively constant throughout the day, despite changing ‘pulls’ from the atmosphere by investing energy into stomatal regulation.

Anisohydric plants do not tend to dilate stomata as much in response to VPD, such that the leaf loses more water at mid-day. These plants expend less energy by not regulating their leaf water potential, but run the risk of VPD-induced cell damage.

These two types of plants lose the same water when they are not water stressed, but Anisohydric plants tend to experience much greater stress during times of drought / at midday. The benefit of being anisohydric (at least in theory) is that you continue to assimilate C via photosynthesis during times of drought.

Species can also adapt to dry conditions by growing their roots out towards water sources (such as deep tap roots), which is an adaptation mechanism known as hydrotrophism.

4.2 Theories of water movement

There are five general theories about how water moved through the xylem:

1. Water is pumped up the xylem. But at functional maturity the xylem is composed of only dead cell walls. So they cannot pump water.

2. Water moves up xylem elements via capillary action. But capillary action is not strong enough to bring water to the top of the plant. We would need unrealistically small xylem cell diameters to move the water to the top of a tree (particularly a red wood). The space between cell walls could, but would then be unable to move water at the rate required.
3. Water is pushed up through the xylem elements by atmospheric pressure. This could be true up to about 10.3 m (assuming a capped tube). But because stomata are open a model of a capped tube is unrealistic. Without the cap, water cannot move very far above the ground.

4. Water is pushed up through the xylem by root pressure (Gutation). The idea is roots pull in water, creating water pressure at the bottom of the plant, so that there is a pressure gradient from the bottom of the plant to the top of the plant. This does happen, and what we often think of as morning dew on plant leaves is actually xylem sap pushed out through the plant leaf. But this can transfer water only about 10m (as with capillary action) and could not transfer water to the top of a redwood, so at least in those plants there must be another means of moving water up to the top of plants.

5. Water is pulled up through the xylem by evaporation (cohesion/tension). The theory here is that water is 'pulled' from the leaf by atmospheric VPD. The atmospheric force, exerted on the first molecule of water exposed to the atmosphere, is transferred as tension down through the plant towards the roots by the bonds between water molecules throughout the xylem. The continuity of the water 'chain' is crucial for this theory. If the column of water is broken, then the tension is released.

4.3 Cavitation and embolisms

Cavitation is a process in which the force created by atmospheric VPD (i.e. 'pull' of the atmosphere on water in xylem) exceeds the plants ability to supply water. Because the atmosphere is pulling water out of the plant faster than the plant can supply it, an air bubble forms (an 'embolism'), which stops flow of water up the xylem (b/c we need a continuous chain of water molecules for that to happen). Here gutation (i.e. plant roots osmotically pulling in water to create a pressure gradient) may be an important process in smaller plants (which have larger diameter cells in the xylem) for dissolving that air bubble back into solution in the xylem water, thus repairing the damage to the water pathway.

To avoid cavitation, the xylem form tend to be overlapping in sections so that it allows the transference of water, but would confine an embolism (bubble) to a single chamber, which can then either be circumvented or repaired.

During extreme droughts, anisohydric plants undergo more cavitation (somewhat offset by woodier xylems that are more resistant to cavitation) while isohydric plants tend to 'starve' due to lack of photosynthesis because their stomates are closed to avoid cavitation.
5 Plant response to $CO_2$

Plants adjust on both short and long timescales to changing concentrations of $CO_2$ in the atmosphere. These changes could be elastic changes, such as keeping stomata closed longer due to an ability to accumulate more carbon in a shorter time with a higher $C_a - C_i$ gradient, increasing production of carbohydrates in response to more available carbon etc. Or they could be inelastic, such as changes in gene transcription.

![Diagram](image)

Figure 8: Credit: Kevin Griffin, Lecture 4, 2015, Plant Ecophysiology
5.1 $CO_2$ fertilization

$CO_2$ fertilization refers to the phenomena of plants growing more efficiently under higher concentrations of atmospheric $CO_2$. This can be explained by considering that plants exchange $CO_2$ and $H_2O$ with the atmosphere when they open their stomata. If the concentration of $CO_2$ is higher in the atmosphere, then they will be able to keep their stomata closed more often in order to retain $H_2O$. The $CO_2$ fertilization effect is therefore expected to be larger in drier environments, and may be nonexistent in wet environments where plants aren’t $H_2O$ limited.