Plant Ecophysionlogy

Weston Anderson

March 1, 2017

Contents

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.
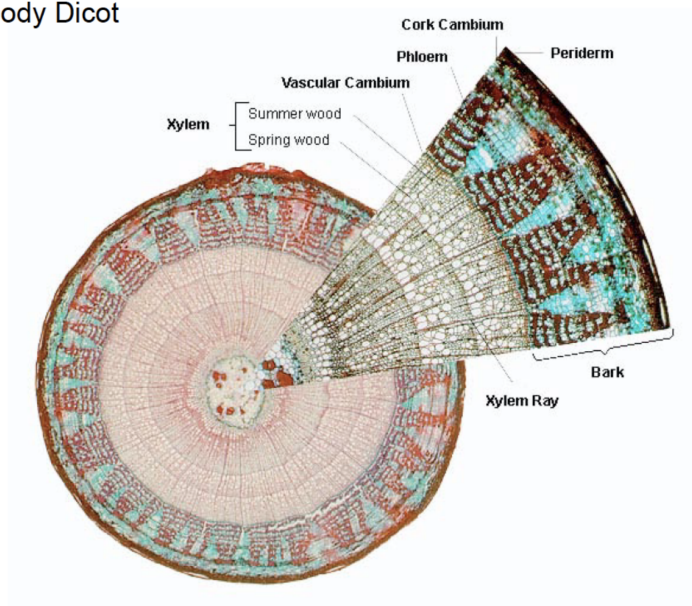

Figure 1: Credit: Kevin Griffin, Lecture 3, 2015, Plant Ecophysiology

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 stoichometry of photosynthesis as:

$$6CO_2 + 6H_2O <-> C_6H_{12}O_6 + 6O_2$$
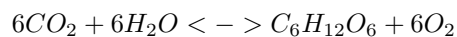
which takes as an input sunlight for energy. This equation reflects both the light and dark reactions. The light reactions take in sunlight and H_2O, splits the H_2O to use the e^- to convert $NADP^+$ to NADPH and produces ATP and O_2. The Calvin cycle (dark reactions) then use the ATP exported by the 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 O_2 and produces CO_2
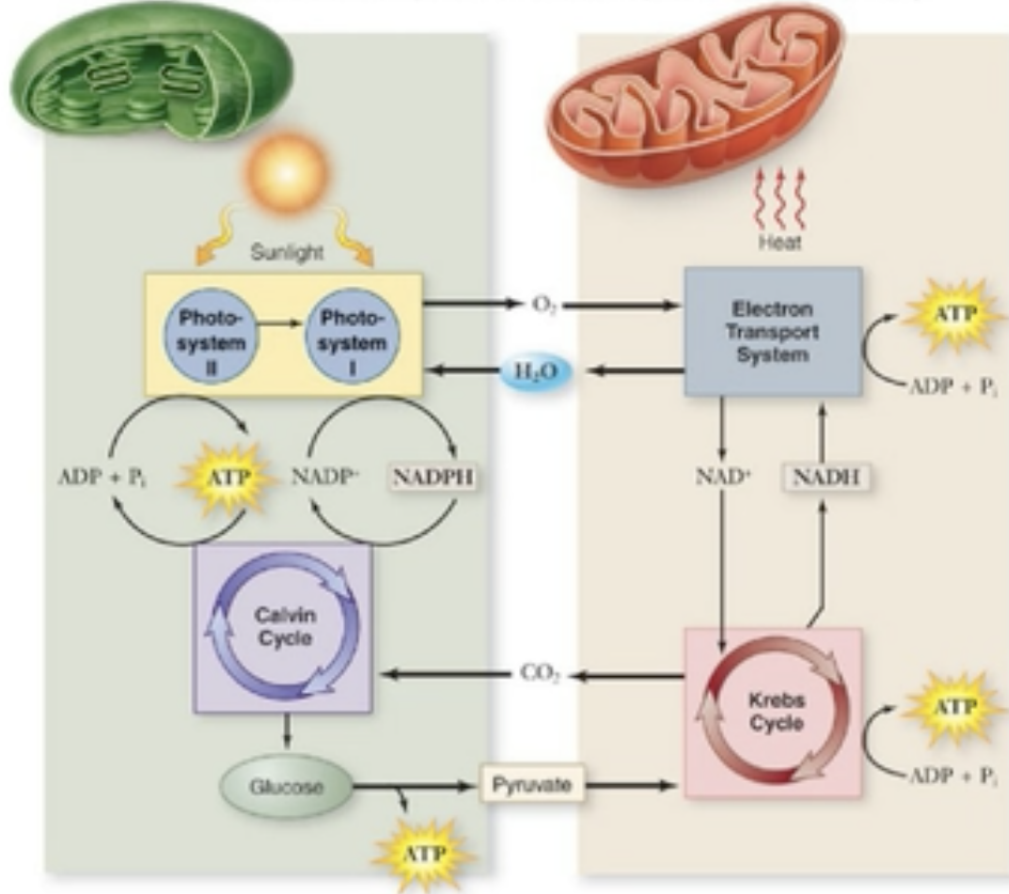
Figure 2: Credit: Kevin Griffin, Lecture 2, 2015, Plant Ecophysiology

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 oxyganase (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.

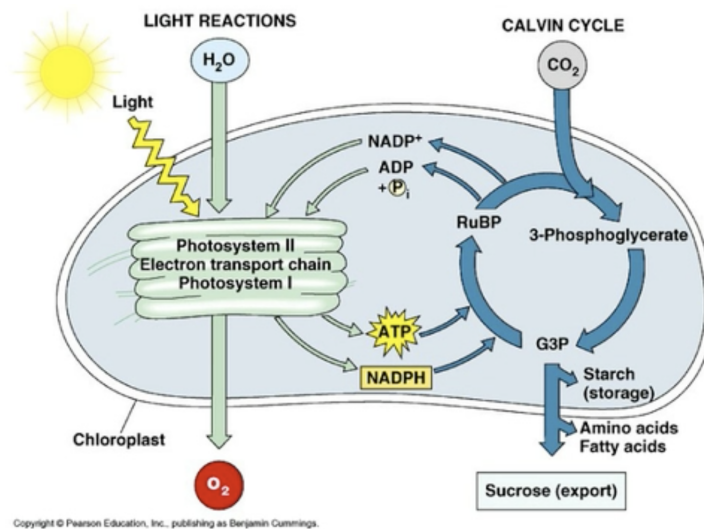   So as a final summary of the light reactions and the dark reactions, see the below figure.

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, fore example, by formation of CO_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.
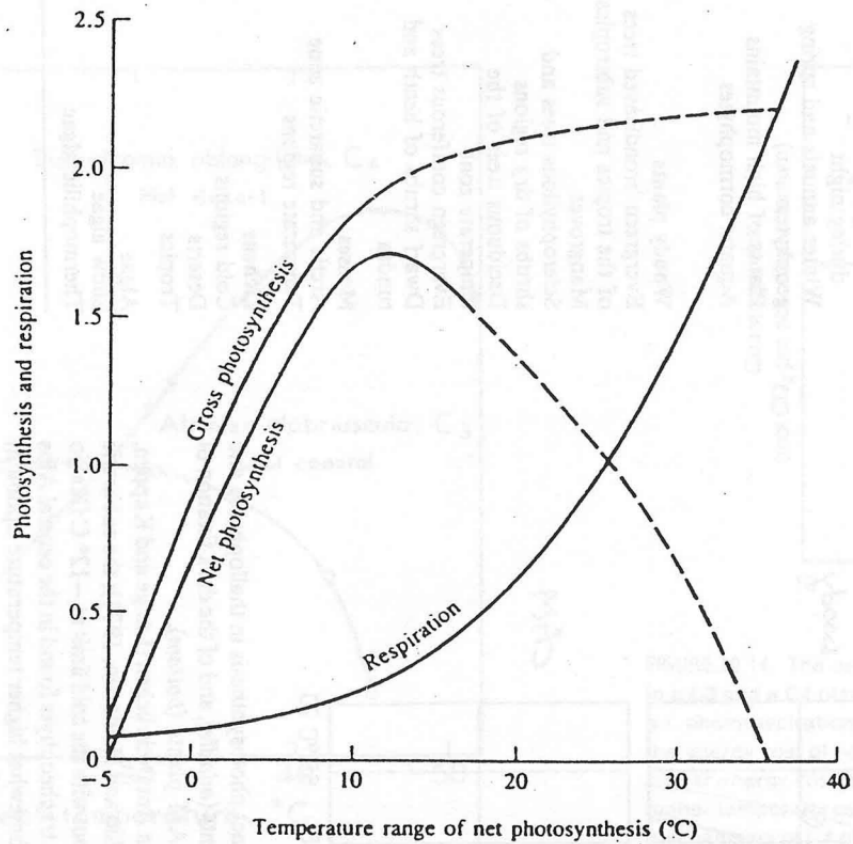
Figure 5.12 Effects of temperature on photosynthesis, respiration, and net or apparent photosynthesis of Swiss stone pine seedlings. Solid lines are from actual measurements; broken lines are estimated. (After Tranquillini, 1955; from Kramer and Kozlowski, 1979, by permission of Academic Press.)

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_2 fixed / photons absorbed) drops off, fluorescence (an indicator

6

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.
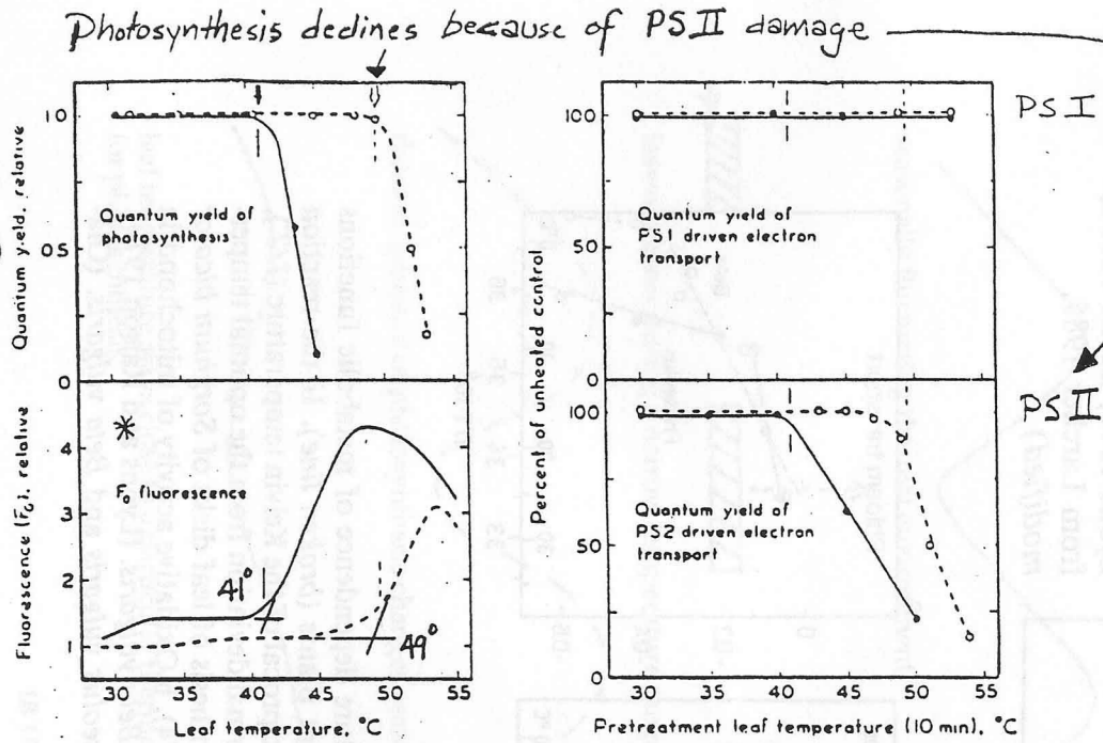

Figure 15.4. Effect of leaf temperature on the quantum yield for CO_2 uptake by intact leaves of *Atriplex sabulosa* (●—●) and *Tidestromia oblongifolia* (○--○) (*top left*), and of pretreating illuminated detached leaves for 10 min at different temperatures on the quantum yields for photosystem 1 (PS1)- and photosystem 2 (PS2)-driven electron transport by chloroplasts isolated from these leaves (*top and bottom right*, respectively). Redrawn from Ref. 7. Also shown is the effect of leaf temperature on the fluorescence yield of detached leaves (*bottom left*). Redrawn from Ref. 10. Solid and open arrows and solid and dashed vertical lines denote the temperatures at which time-dependent inactivation of photosynthesis sets in in *A. sabulosa* and *T. oblongifolia*, respectively.

Figure 5: Credit: http://ib.berkeley.edu/courses/ib151/IB151Lecture6.pdf

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.
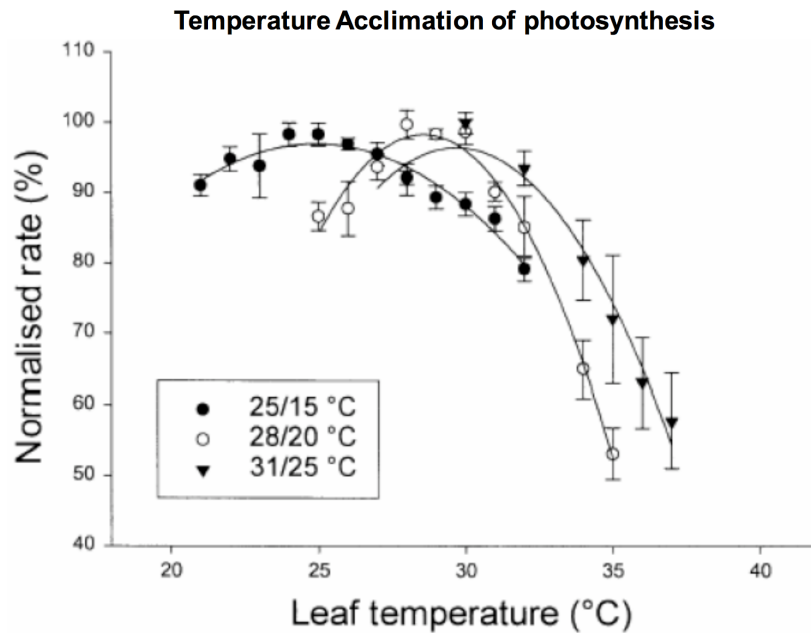

Figure 6: Credit: Kevin Griffin, Lecture 3, 2015, Plant Ecophysiology

3.5   modeling photosynthesis

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

$$A = g_s * (C_a - C_i)$$

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.

8

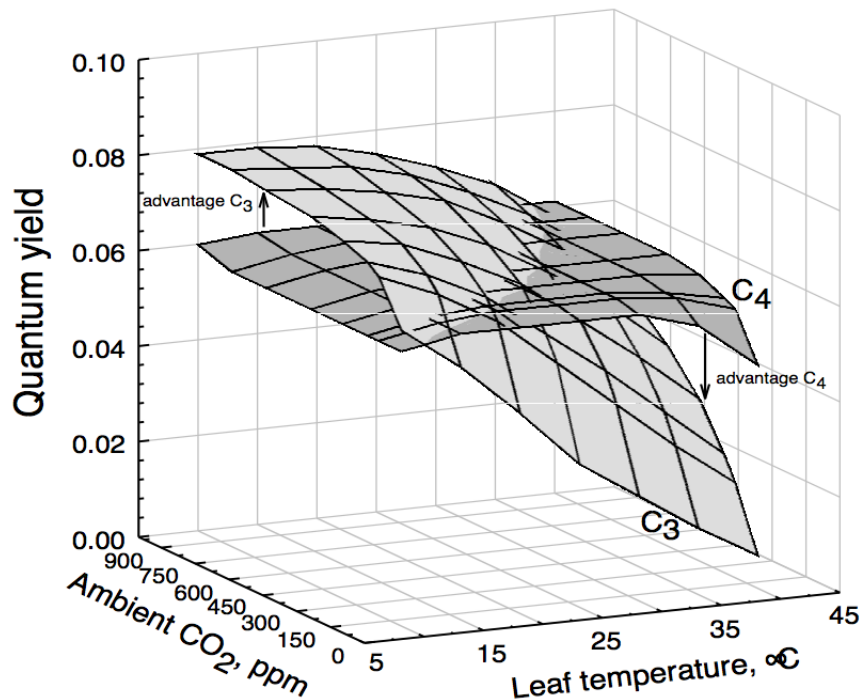# Light Use Efficiency of C₃ (Soy) *versus* C₄ (Corn)

Figure 7: Credit: Kevin Griffin, Lecture 2, 2015, Plant Ecophysiology

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.
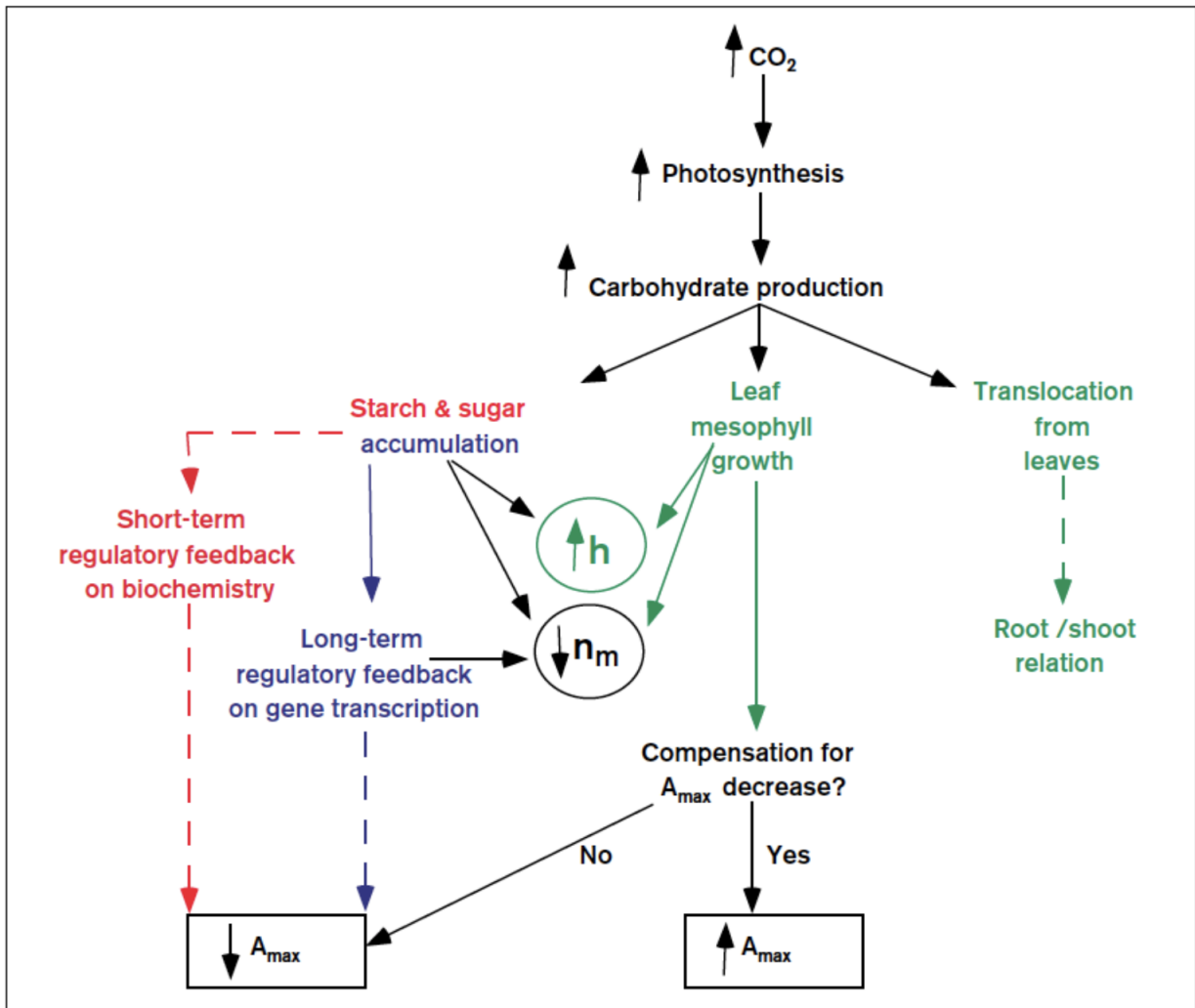

Figure 8: Credit: Kevin Griffin, Lecture 4, 2015, Plant Ecophysiology

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.