What controls stomatal resistance? Plants have stomates to keep in balance two competing processes:

- Photosynthesis, which is the good one
- Evaporation, which can be the bad one

Evaporation is a necessary by product of photosynthesis - the plants must allow CO₂ to diffuse into the leaf for photosynthesis, but since the cells must be wet, this inevitably means that water vapor will diffuse out.

The smart thing for plants to do is keep the rate of evaporation to the minimum needed to allow for photosynthesis.

Why would it be stupid for a plant to have it's stomates too far open? Why would it be stupid to have them too far shut?
**Photosynthetic controls on Stomata**

Once cleaned up so the units cancel, the equations describing $H$ as a function of $\Delta T$ and $E$ as a function of $\Delta VP$ can be used to accurately predict a leaf’s exchanges with the atmosphere. These equations are particularly valuable, since they describe in a mechanistic sense what controls $E$ and $H$.

The third equation (for $A$) is somewhat misleading, since it gives the erroneous impression that CO$_2$ exchange is controlled most strongly by the concentration of CO$_2$ inside the leaf and the stomatal resistance. In fact, photosynthesis is controlled by interactions between the weather (light and temperature) and the chloroplast. This rate of photosynthesis then helps control the stomatal resistance in a way that tends to maintain a constant internal CO$_2$ concentration (often at around 220 ppm or ~145 ppm below the atmosphere for C3 plants). The equation for $A$ should then be rearranged to predict stomatal resistance as a function of photosynthesis.
The concentration of CO$_2$ in the leaf is a good measure of whether the plants have enough CO$_2$ for photosynthesis. It turns out that C3 plants need about 220 ppm of CO$_2$ inside their leaves for rapid photosynthesis (ambient CO$_2$ is ~370 ppm). More CO$_2$ does not speed photosynthesis appreciably, less CO$_2$ slows photosynthesis. C3 plants therefore control their stomates to keep the concentration of CO$_2$ inside the leaf at around 220 ppm.

What would happen to a C3 plant that decided to adjust its stomates to control the internal concentration at 100 ppm?

How about a plant that decided to adjust its stomates for 350 ppm?

In practice, photosynthesis is the main thing that controls stomatal aperture.

How should the stomates respond to an increase in photosynthesis?

What should the stomates do at night?
Controls on Photosynthesis
The rate of CO\textsubscript{2} exchange is ultimately set by the rates of CO\textsubscript{2} fixation and production in the leaf’s cells. A leaf’s net CO\textsubscript{2} exchange can be thought of as composed of two components fluxes – respiration and photosynthesis. Leaf respiration continues during daytime, so that the daytime exchange of CO\textsubscript{2} measured with a chamber actually represents the net rate of assimilation, or the difference between gross photosynthesis and respiration.

Temperature and light are the strongest controllers of leaf CO\textsubscript{2} exchange. Under favorable temperatures, leaf photosynthesis shows a saturating relationship.
Temperature also plays an important role in controlling leaf CO$_2$ exchange, provided that there is sufficient light. The relationship between temperature and net CO$_2$ uptake can be best understood by separating CO$_2$ exchange into its component fluxes.
Putting it all together
We now have enough information to begin constructing a conceptual model of how a leaf works. Diagram the mechanistic interactions between these things:

Sunlight
Leaf temperature
Photosynthesis
CO$_2$ inside the leaf
Stomatal resistance
Vapor pressure inside the leaf
Evaporation
We can then take this information a step forward, and use it to predict a leaf’s interaction with the atmosphere in response to a sudden change in light.
We can then take this information a step forward, and use it to predict a leaf’s interaction with the atmosphere over the course of a day.

- **Sunlight**
- **VP inside the leaf**
- **Air T**
- **Transpiration**
- **CO₂ Exchange**
  - Gaining
  - Zero
  - Losing
- **Sensible Heat Flux**
- **Stomates**
  - Wide open
  - Tightly closed
Nitrogen controls on maximum rates of photosynthesis

The photosynthetic rate under optimal conditions (ample light, favorable temperature) varies significantly from species to species. These differences help explain some of the between-species differences in growth rate.

The maximum rate of leaf photosynthesis is controlled by the amount of photosynthetically-active enzymes within the leaf (most importantly, rubisco). The amount of nitrogen in a rubisco molecule is constant from species to species, and rubisco is the dominant nitrogen-containing molecule within leaves. Consequently, there is a tight relationship between a leaf’s nitrogen content and its maximum rate of photosynthesis.

This relationship is part of the reason plants grow faster in response to nitrogen fertilization.
Regardless of a leaf’s nitrogen content, it still obeys the basic rules we already laid down. If two leaves that differ in nitrogen concentration are exposed to the same weather how would you expect the following things to differ?

Photosynthesis

Internal CO$_2$ concentration

Stomatal resistance

Evaporation

Leaf temperature

Sensible heat flux

The extreme case is represented by some heavily fertilized, well watered crop plants. What could happen to a such a leaf’s $T_{leaf}$ and H under direct sun?
**Water Use Efficiency (WUE)** - Molecules of water lost per molecule of CO\(_2\) taken up.

Up until now we have focused on C\(_3\) photosynthesis, which is the most common type. There are two additional types of photosynthesis that have evolved in part to help plants improve their WUE.

\[
\text{WUE} = \frac{\text{moles CO}_2 \text{ assimilated}}{\text{moles H}_2\text{O evaporated}} = \frac{A}{E}
\]

How could a plant improve its WUE? We can use the equations describing Evaporation and CO\(_2\) uptake to get a sense of the possible approaches.
Plants can improve WUE either by decreasing the CO$_2$-inside or the VP$_{inside}$ during the times when the stomates are open.

**C$_4$ plants** use a biochemical pump to concentrate CO$_2$ within the leaves, allowing high rates of photosynthesis at low CO$_2$-inside. C$_3$ plants typically operate with an internal CO$_2$ concentration of around 220 ppm. This concentration is largely dictated by the kinetic properties of rubisco – 220 ppm represents the lowest concentration that does not substantially limit photosynthesis for most C$_3$ species. In contrast, the initial enzyme involved in C$_4$ photosynthesis has a much higher affinity for CO$_2$ than does rubisco, and so C$_4$ plants can operate at a much lower internal CO$_2$ concentration. C$_4$ metabolism also has advantages over C$_3$ at high temperatures (above $\sim$28$^\circ$C), and C$_4$ plants tend to occur in dry hot areas, especially tropical grasslands.

The best way to decrease the effective VP$_{inside}$ is to open the stomates only during cool periods. **CAM plants** keep their stomata closed during daytime and open them at night when VP$_{inside}$ is low. CAM plants uptake and store CO$_2$ at night, and then to use it during photosynthesis on the next day, avoiding the need to open the stomata for CO$_2$ during daytime. CAM plants may have extremely high WUE, allowing them to survive in severe desert conditions.
Why does leaf gas exchange matter?

Many people feel that access to fresh water is California’s greatest long-term problem. A large fraction of the water used in California currently goes to agriculture. Pressure to allocate less water to agriculture increases dramatically during drought years, and likely will increase dramatically in the future as cities grow. Agriculture is very important to California’s economy and people’s livelihoods, and the diversion of water to cities would be very disruptive. Exactly what will happen is unclear though, since leaf gas exchange may solve the problem.

The concentration of CO$_2$ in the atmosphere has risen by about 80 ppm to 385 ppm over the last 200 years, and will likely continue to rise to about 500 to 700 ppm by 2100.

Most crops grown in California are C$_3$. How will the future rise in CO$_2$ affect the WUE of C$_3$ plants if we assume that VP$_{in}$, VP$_{out}$, and CO$_2$$_{in}$ do not change?