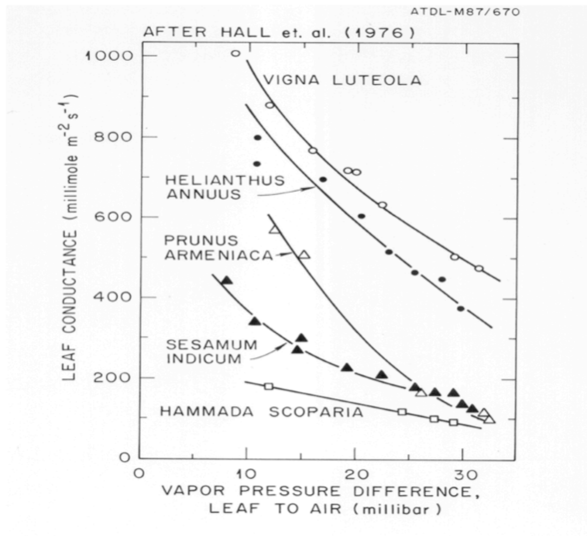
Stomatal Conductance, part 2

- Environmental Biology, Continued
  - Response of stomata to environmental and physiological forcings
    - humidity deficits
    - temperature
  - relation to hydraulic conductance
  - soil moisture
- Diurnal variations of stomata
  - ample soil moisture
  - soil moisture deficits

Stomatal conductance has a strong dependence upon humidity deficits

Stomatal Conductance and Humidity Deficits, Data



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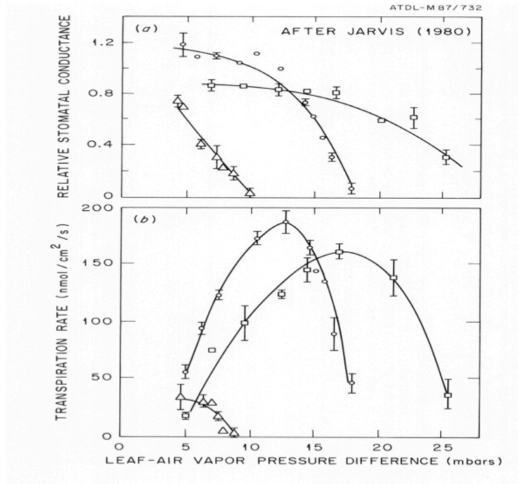
There is no universal function between stomatal conductance and humidity deficits. Some plants are more sensitive than others

Hall et al 1976.

Stomatal Conductance and Humidity Deficits, Data



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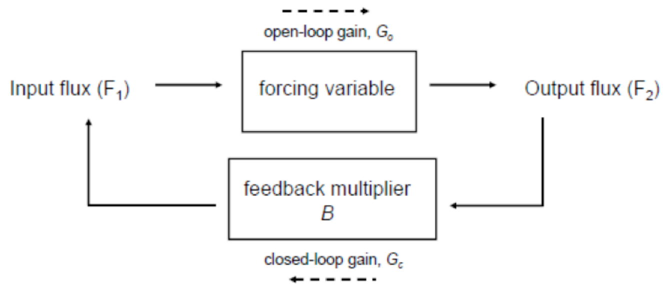
Other data show complex interactions between humidity deficits, transpiration and stomatal conductance…leading others to consider feedback and feedforward response.

Feed Forward, rather than Feedback, Operations Explains the Decline in Evaporation with Increasing Humidity Deficits

- Feedback occurs when a change in the rate of transpiration causes a change in leaf conductance which in turn affects the transpiration rate.
- Feedforward occurs when the imposed change in the environmental factors affecting transpiration rate causes a change in the conductance independent of the resulting change in the transpiration rate.

Feedback



$$F_2 = F_1 G_o + F_2 G_o B$$

$$F_2 = \frac{F_1 G_o}{1 - G_o B}$$

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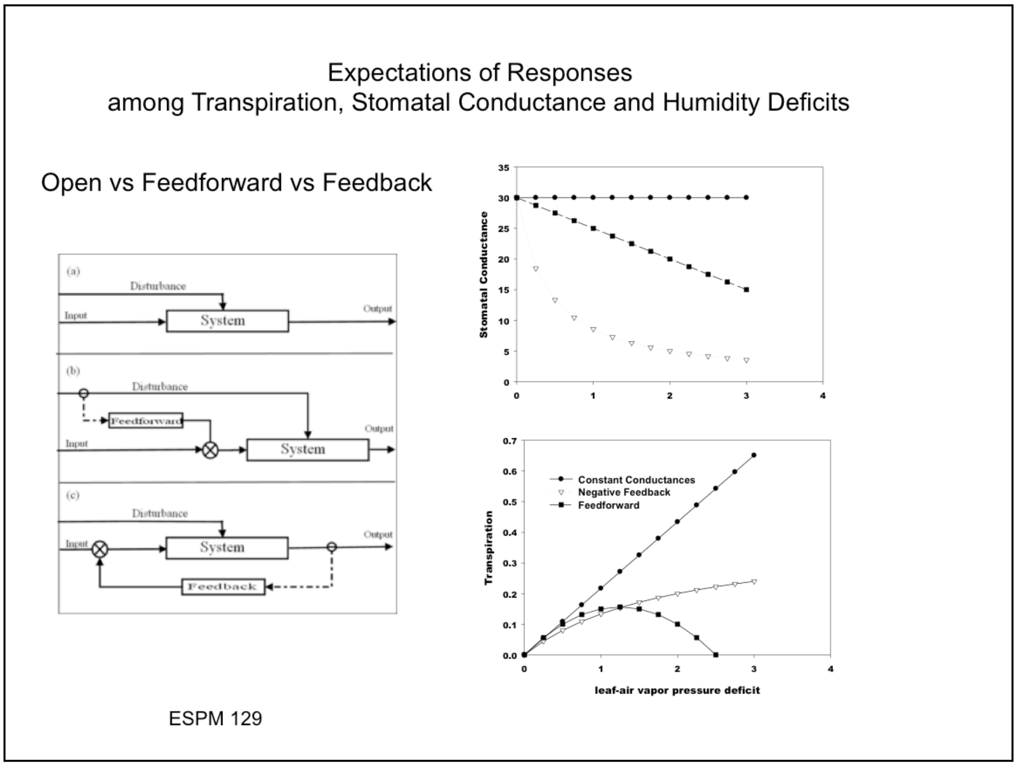
Monson and Baldocchi



Feedbacks, negative and feedforward, help explain the observations in data.

Simplest case, stomata are constant and transpiration increases with humidity deficits. The other extreme is that stomatal conductance closes non linearly with humidity deficits, reaching an asymptotic decline. Then one would expect a diminishing returns behavior. But it seems that stomata operate with a feedforward behavior, leading to a parabolic behavior in transpiration with increasing humidity deficits. This behavior is best described with the model that couples transpiration, leaf energy balance, photosynthesis and stomatal conductance.

https://upload.wikimedia.org/wikipedia/en/thumb/c/c7/Control_Systems.png/450px-Control_Systems.png

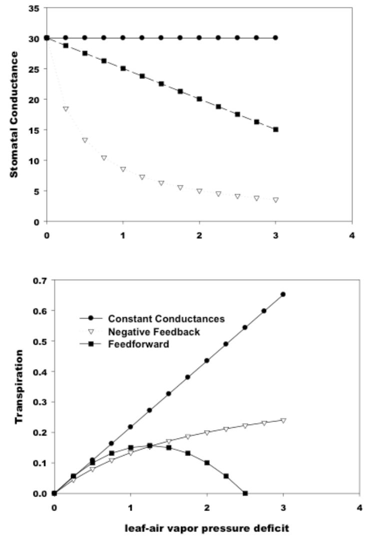
Farquhar 1979 discusses the role of feedforward and feedback effects on the coupling between humidity deficits, stomatal conductance and transpiration

feedforward. The distinction between feedback and feedforward is made clear in Fig. 1. In both cases a change A(Aw) in the humidity difference, Aw, between the inside of the leaf and the ambient air is the perturbation from outside the system. Feedback occurs (Fig. *la)* when a change, AE, in the rate of transpiration causes a change, Ag, in leaf conductance which in turn affects the transpiration rate. Feedforward

Which Behavior Does the Previous Data Support?

Feedforward

Feedback



$$g_l = e - f\Delta e_l$$

$$E = e\Delta e_l - f(\Delta e_l)^2$$

$$E = g_s(\Delta e_l)\cdot \Delta e_l$$

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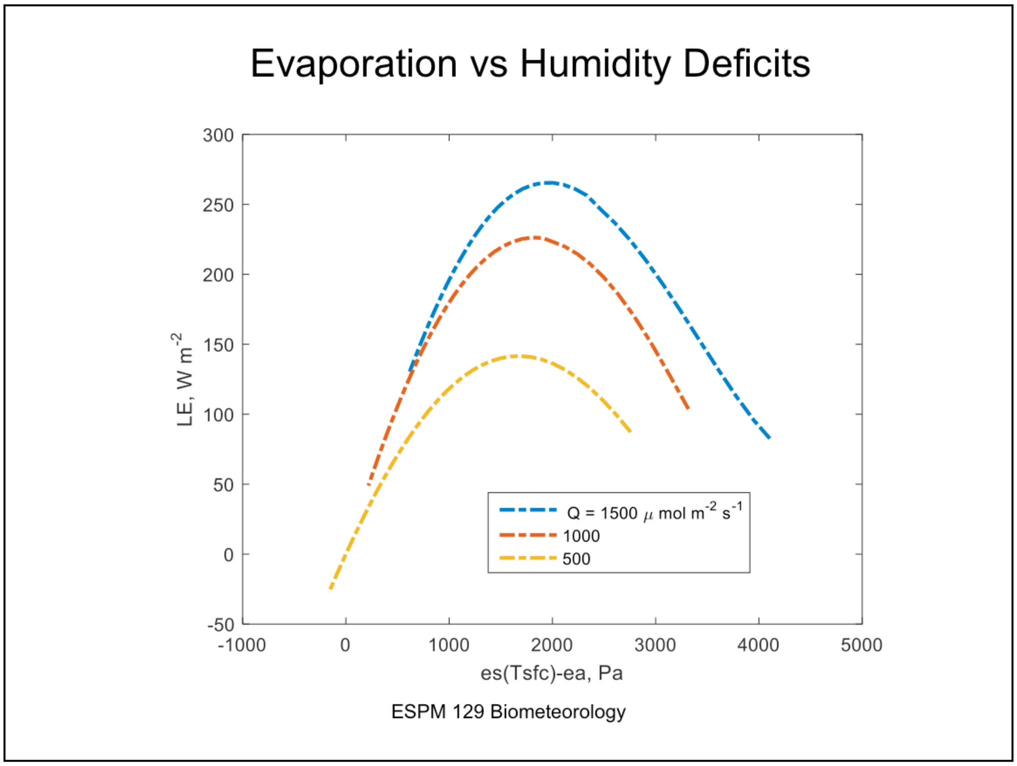
Farquhar and Jones are among those arguing in terms of feedforward rather than feedback effects on stomata, humidity and transpiration.

Wikipedia

Feed-forward is a term describing an element or pathway within a control system which passes a controlling signal from a source in its external environment, often a command signal from an external operator, to a load elsewhere in its external environment. A control system which has only feed-forward behavior responds to its control signal in a pre-defined way without responding to how the load reacts; it is in contrast with a system that also has feedback, which adjusts the output to take account of how it affects the load, and how the load itself may vary unpredictably; the load is considered to belong to the external environment of the system.



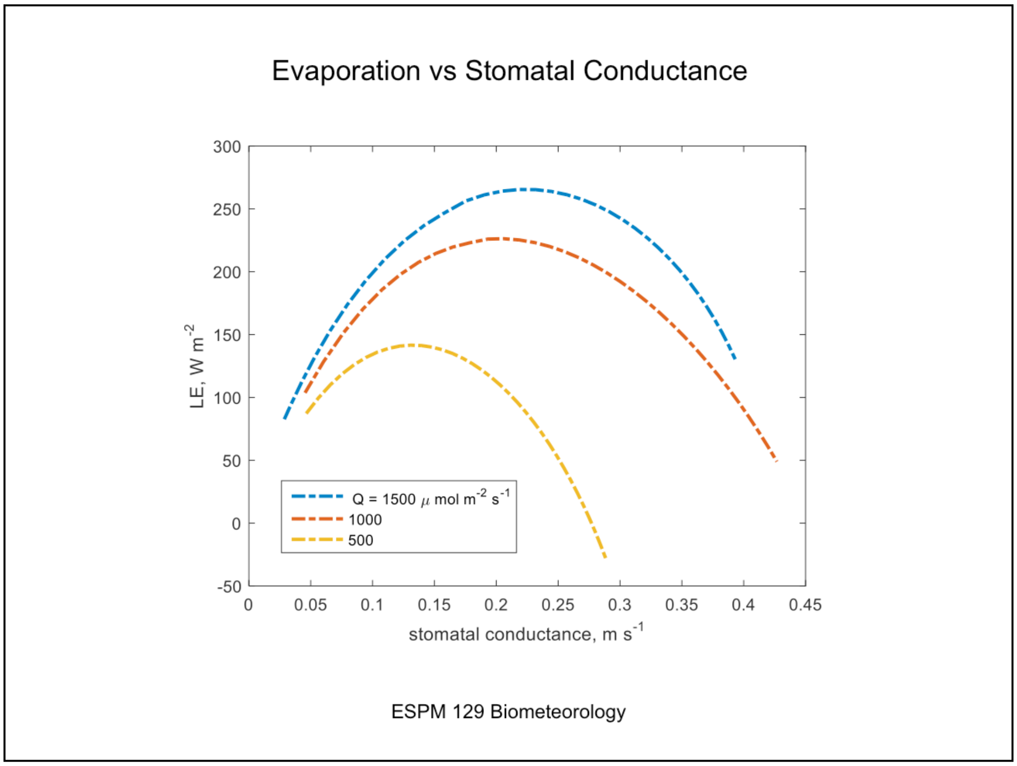
Here we look at model computations of latent heat exchange, which is the evaporation rate (E) times the latent heat of evaporation, vs the humidity deficit between the leaf and air, so we compute es(T) as a function of the leaf temperature, Tsfc. These calculations are based on a coupled model that considers leaf energy balance and coupling between stomatal conductance and photosynthesis.

For low humidity deficits, an increase in this difference drives the potential for evaporation and rates of evaporation INCREASE. This is what one would expect simply looking at the Ohms Law analog for evaporation. But real evaporation is more complex. There are other biophysical factors that act to restrict evaporation as humidity deficits get greater and greater.

At intermediate humidity deficits a peak rate in evaporation is reached and then evaporation rates DECREASE with additional increases in humidity deficits. Why?

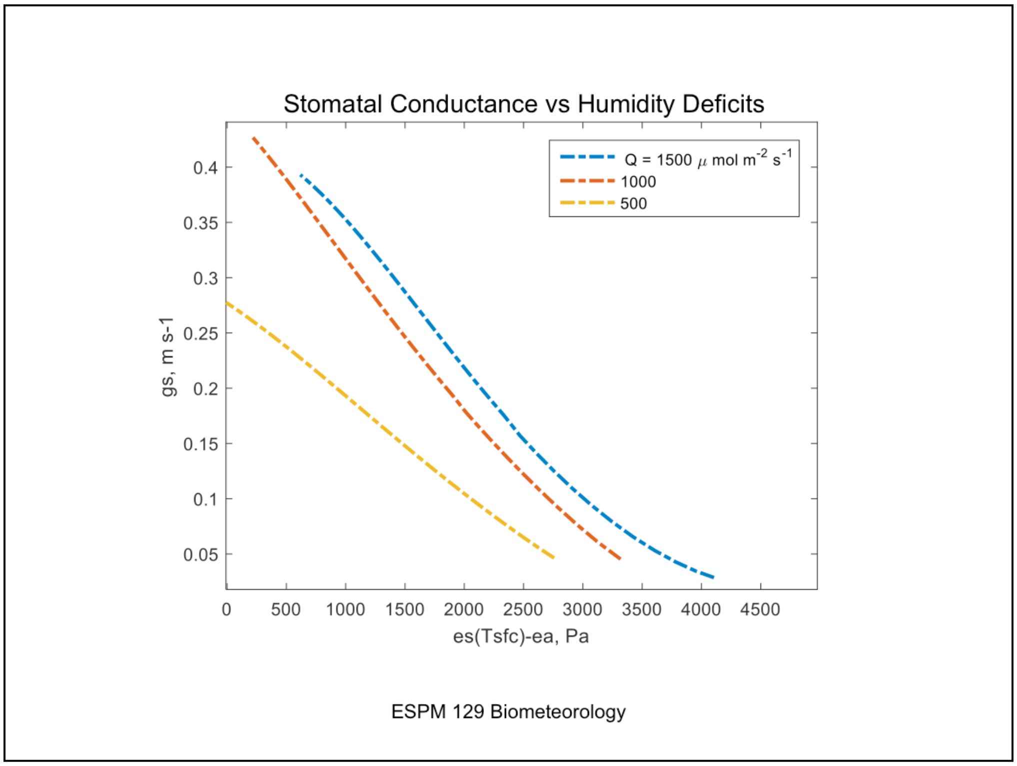
Leaves experience a Feedforward effects between Evaporation and humidity deficits. Farquhar, G.D., 1978. Feedforward Responses of Stomata to Humidity. Australian Journal of Plant Physiology, 5(6): 787-800.

As we will see below, stomatal conductance is also a function of humidity deficits,

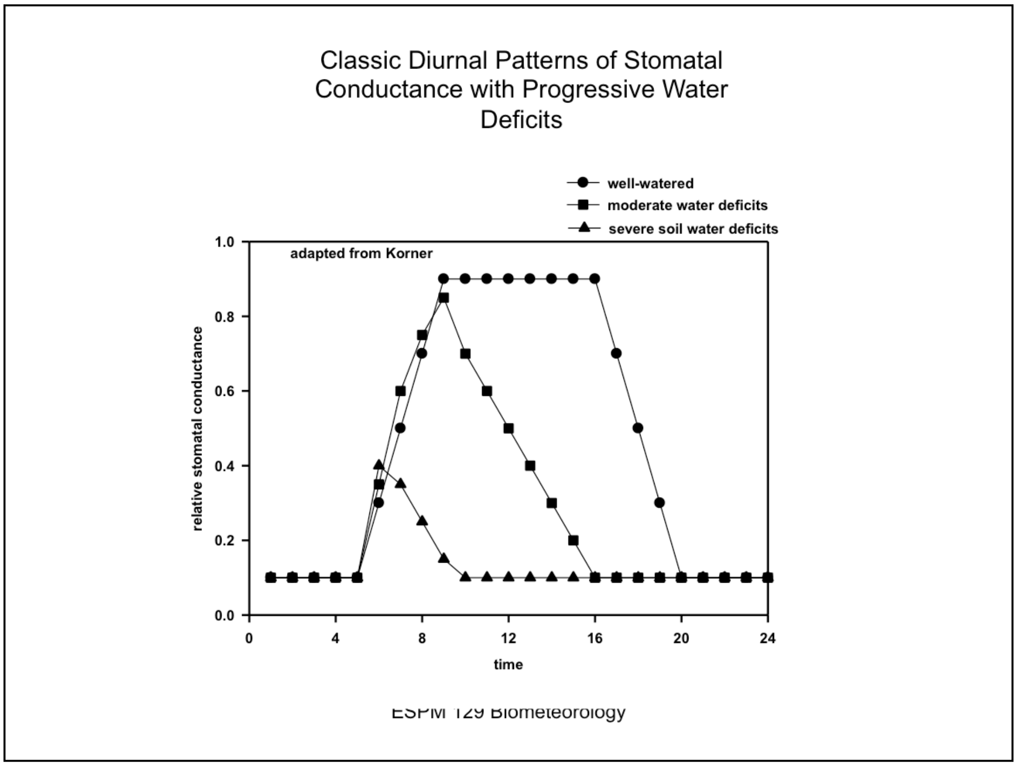


Together we can see that LE is low at highest stomatal conductances because humidity deficits are smallest and LE is low at lowest stomatal conductances because they restrict water loss. LE is optimal at intermediate humidity deficits and stomatal conductances.

These results may seem counter intuitive, but this is why we need theory and models to understand and explain the complex behavior we observe in nature. The problem I see and have is that too often this problem is tackled with over simplified models that do not consider the interactions and feedbacks (whether negative or feedforward) that we see here.

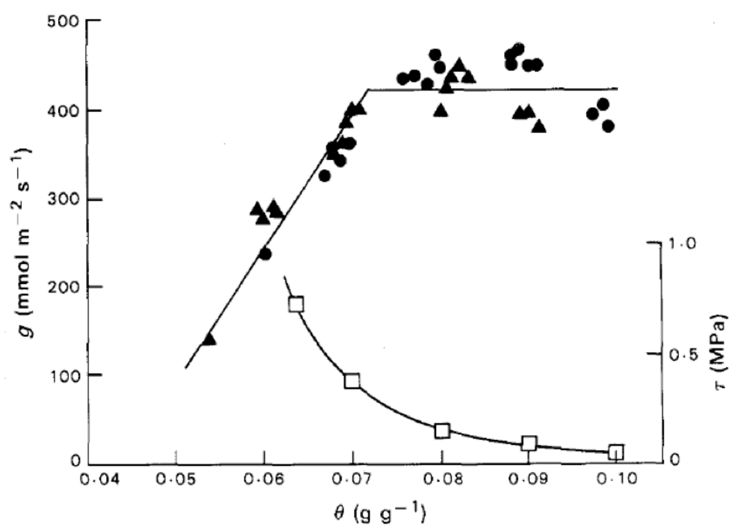


Part of the explanation for LE decreasing with increasing vapor pressure deficit, a stronger potential driver of evaporation, is because stomata conductance also decrease with increasing humidity deficits. This is because guard cells will lose water too, become flaccid and close in dry air.



Soil water deficits have an impact on the value and diel course of stomatal conductance.

Stomatal Conductance and Soil Moisture



Gollan et al 1986, Aust J Plant Physiol

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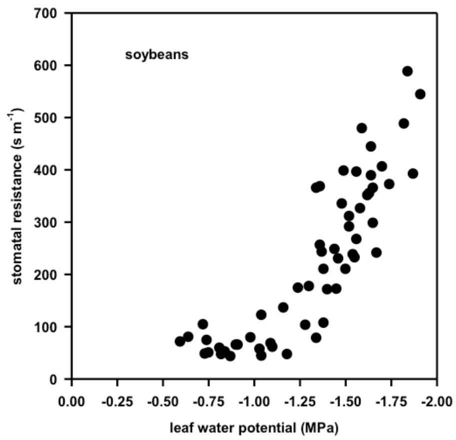
Stomata close with less water in soil. But plants are better measures of the energy that water is held, eg water potential, than moisture content. Available water can differ greatly for sand, clay and loam for the same water content in the soil.

Stomatal Resistance and PreDawn Water Potential: soybeans



Baldocchi, dissertation, 1982

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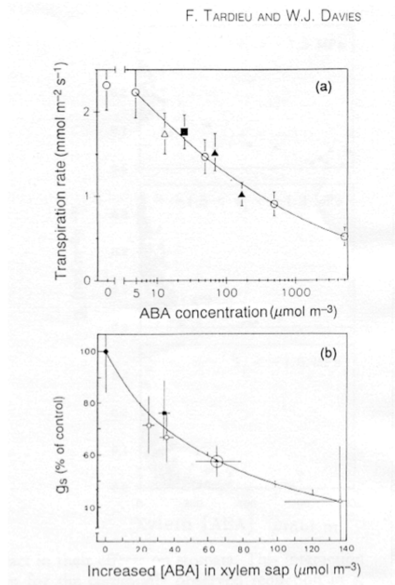
Lots of data, including some from my dissertation, show that stomata stay open until a critical water potential, lik -1.0 to -1.5 Mpa. Then they close, increasing the resistance, or decreasing the conductance.

Evidence of ABA Hormone Controlling Stomata and Transpiration Under Water Deficits



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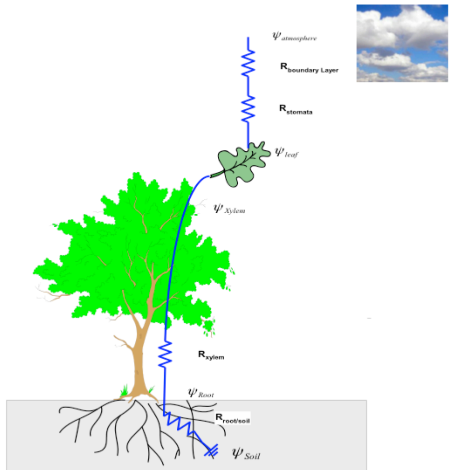
Soil-Plant-Atmosphere Continuum, SPAC



$$E = g_s \Delta e = k_l (\Psi_{soil} - \Psi_{leaf})$$

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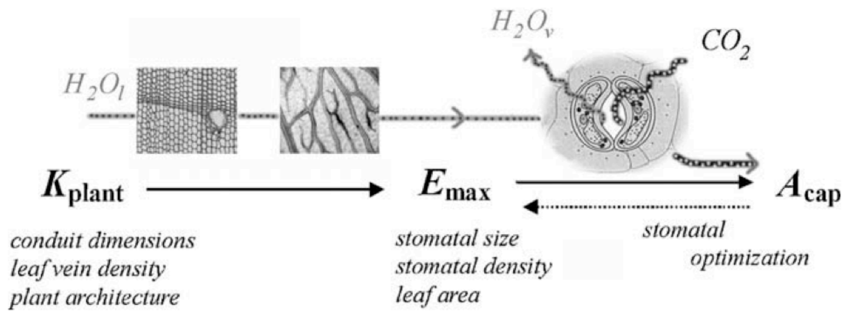
Stomata are coupled to leaves, coupled to xylem, coupled to roots and the soil. So we need to consider the soil-plant-water-atmosphere continuum to understand stomatal behavior during periods of soil moisture deficits.

Links between Plant Hydraulics and Conductance



Brodribb 2009 Plant Science

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Hydraulic Conductance Modulates Stomatal Conductance

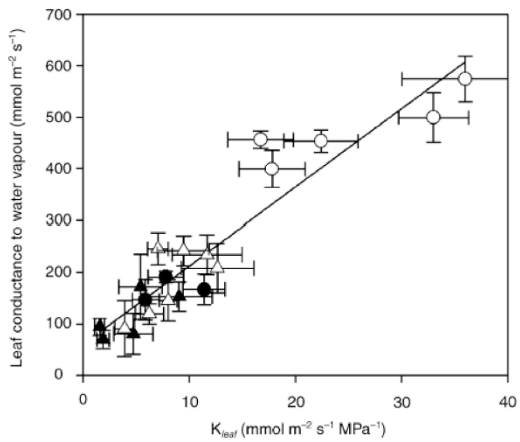
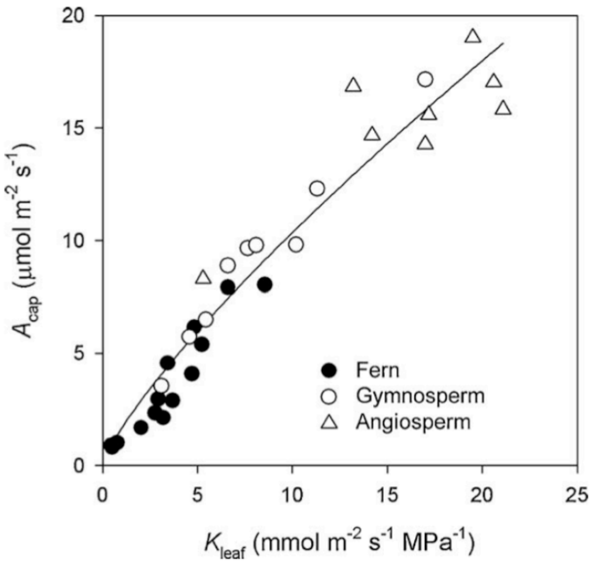


Fig. 2 A highly significant linear correlation ($r^2 = 0.87$) between mean leaf hydraulic conductance (± SD; $n = 9$) and stomatal conductance (± SD; $n = 9$) in a sample of tropical (○) and temperate (△) angiosperms, tropical ferns (●), and temperate conifers (▲).

Brodribb et al New Phytol 2005

There is a tight linkage between the hydraulic plumbing of a plant and stomatal conductance



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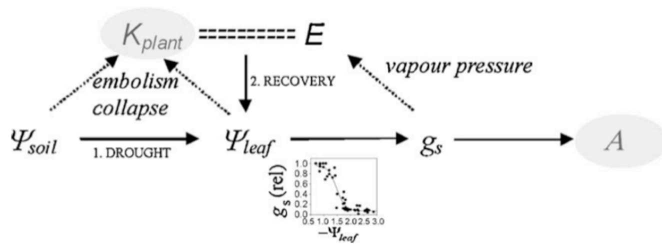
Also a link between conductance and photosynthesis

Drought, Embolism and Stomatal Closure



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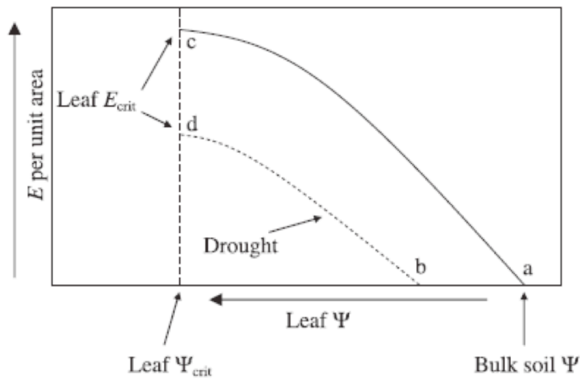
Trees don’t like to have bubbles or embolisms form in their xylem. So as soils dry there can be feedbacks to reduce the hydraulic conductance

Coordinated Changes in Soil-Plant-Water Continuum with Drought



Mild Deficits:
Stomata Operate to prevent
Cavitation and Control Transpiration

Moderate Deficits:
Cavitation Occurs, Xylem Conductance is Lost; peak Transpiration Declines

Severe Deficits:
Hydraulic Failure; Mortality

McDowell et al 2008 New Phytologist

Summary, Key Points

- From an environmental standpoint, stomata open and close with changes in light, temperature, humidity, CO_2, soil moisture, a hormone (ABA) and transpiration. Stomatal conductance scales with photosynthesis and transpiration. As guard cells respond to light, their solute concentration increases. This allows water to enter the guard cell, forcing them to bow and open.
- As guard cells respond to CO_2, there is a solute efflux from the guard cells. This forces the turgor of the guard cells to decrease and the stomata to close.
- Direct effects on stomata occur by high transpiration rates and high humidity deficits. Water loss from the guard cells force them to close.
- Soil moisture deficits trigger the product of ABA, which acts as a signal and causes stomata to close.
- Stomata tend to open and close to maintain Ci/Ca of C3 plants near 0.7 and Ci/Ca of C4 plants near 0.4.
- From a dynamic standpoint, stomatal movement is relatively slow, changing over the course of a half-hour to a change in light. The time response will be faster if a leaf is induced.
- The shape of the diurnal pattern of stomatal conductance is a strong indicator as to whether the plant is suffering from soil water deficits.
- When soil moisture deficits occur, stomatal closure can be patchy.