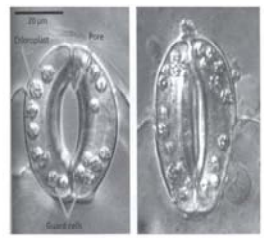
Stomatal Conductance, part 1

- Concepts
  - Stomatal anatomy and mechanics
- Environmental Biology
  - Response of stomata to environmental and physiological forcings
    - light
    - CO_2
    - photosynthesis
    - leaf nitrogen
    - plant functional relations



The stomata are the biological pores through which trace gases pass between vegetation and the atmosphere. If we are to understand biometeorology we must have a deep understanding and appreciation for stomata

Stomata

I stand upon a hill so green,
And spy upon a leaf;
Its occupied with chlorophyll, beyond the mind's belief;
Micro-chasms everywhere,
Stomatal holes of hell;
Expiring vapor,
For the carbon they inhale

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Gotta mix some arts with the sciences. Here is a poem I wrote for a scaling article, after getting dissatisfied with so many articles sounding so similar.

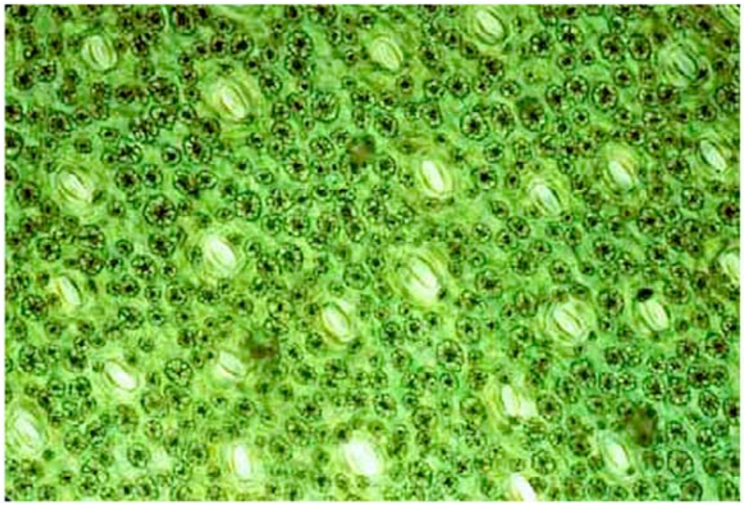
http://images.fineartamerica.com/images-medium-large-5/2-stomata-on-epidermis-of-rose-leaf-power-and-syred.jpg

On campus we want our students to gain capacities in being: 1) literate (to communicate, think critically, express your ideas clearly and accept feedback), 2) numerate (to compute, grapple with data and turn it into information and knowledge), 3) creative (to build, design, fabricate; it can be music, writings, apps, models) and 4) investigative (use the scientific method to discover new things and information). Hopefully, through this class you are getting a chance to balance these pillars of your education.

Stomatal Features and Terminology

- Amphistomatous
  - Stomata on both sides of leaves
- Hypostomatous
  - Stomata on the under side of leaves
- Fractional area of Leaf
  - 0.5 to 5%
- C_3 plants
  - Elliptically shaped stomata
- C_4 plants
  - Dumbbell shaped stomata

Key features and attributes of stomata. They differ on different plants



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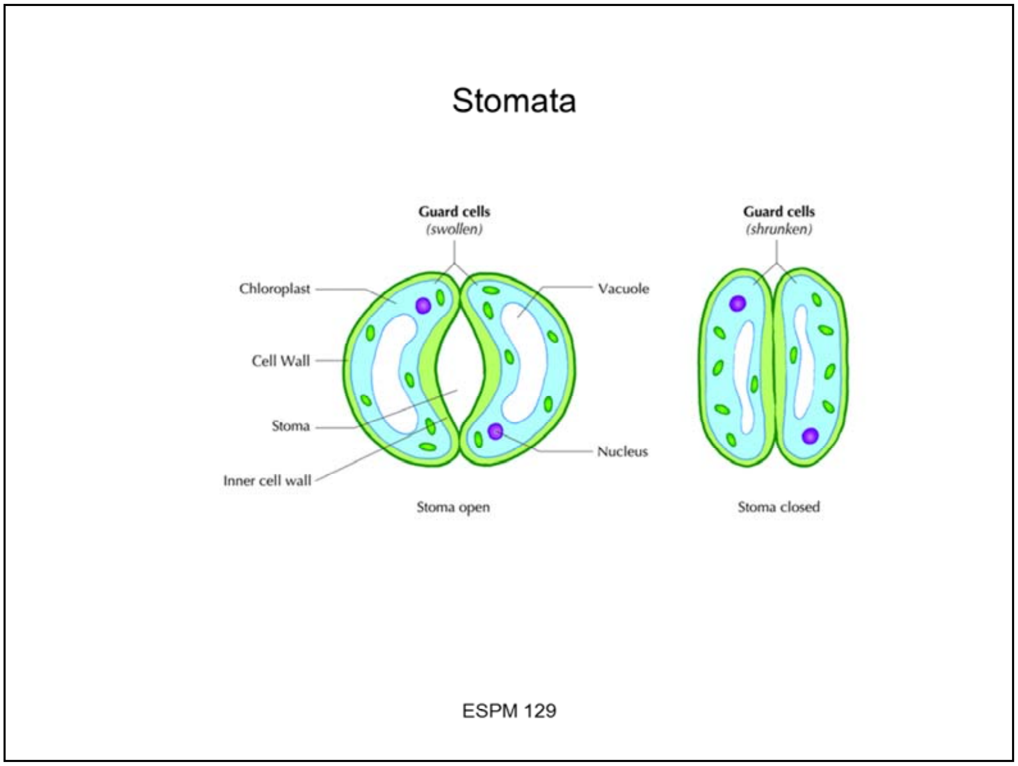
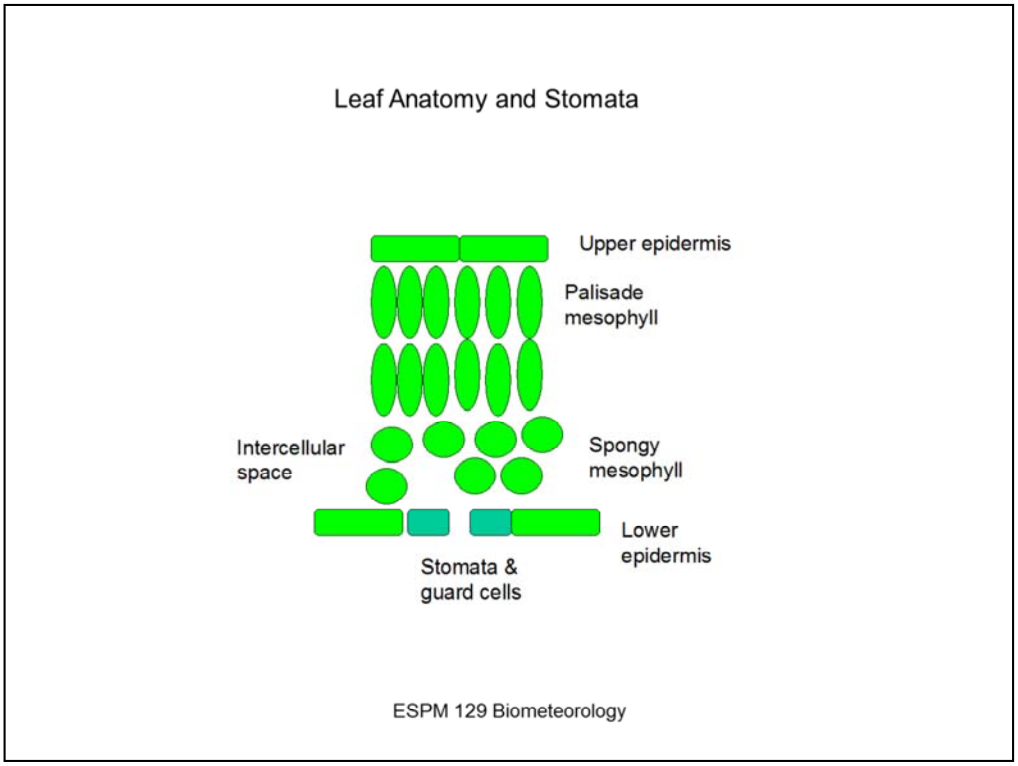
https://plantstomata.files.wordpress.com/2015/03/15consolea-epi-peel-4-inch.jpg

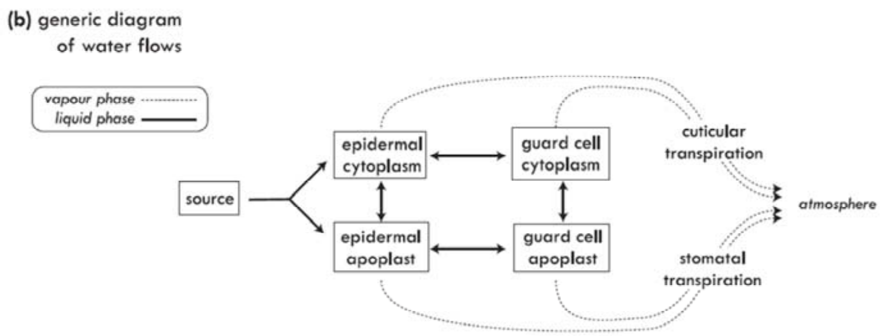


http://everythingmaths.co.za/science/lifesciences/grade-10/05-support-and-transport-systems-in-plants/images/400ba40c937bce0d2766684aa3882c16.png

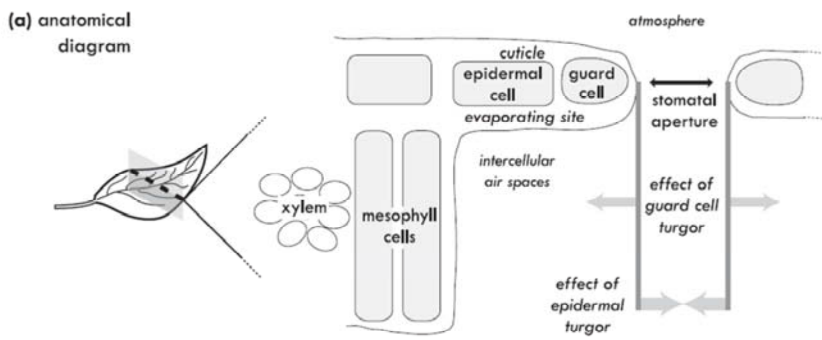
Stomata are active pores on leaves that open to allow carbon dioxide to diffuse into the leaf for photosynthesis and close to inhibit the loss of water vapor from the leaf. Optimization theories by Farquhar/Cowan, Katul et al and Medlyn et al have been informative to show that stomata open and close to minimize the amount of water used per unit carbon gained



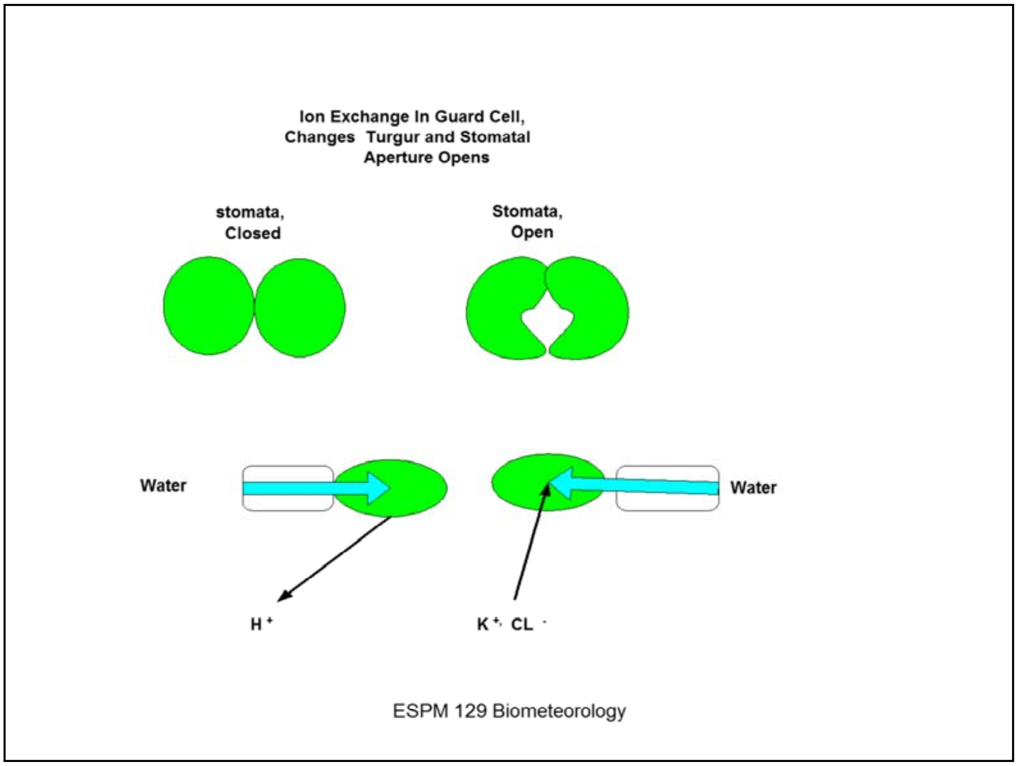
Cross section of a leaf. Of note is the epidermis and cuticle, the spongy and palisade mesophyll, intercellular space and the guard cells that define the stomata



Buckley, 2005



Buckley, 2005, New Phytologist



Guard cells and subsidiary cells. Movement of cations and anions in an out of the guard cell change its osmotic water potential. Differences in water potential drive movement of water in and out of the guard cell. Movement in, increase turgor. This causes the cell to bulge and because of microfibriles, it bends and forms a pore. Movement of water out of the guard cell causes it to be flaccid and close.

Stomata, Feedback and Feed Forward Loops

- A decrease of CO_2 in the intercellular air space, via Ps, and guard cells enables K+ to move into the guard cell and open the stomates.
  - This allows CO_2 to diffuse into the leaf for photosynthesis.
  - In converse, stomata close when exposed to elevated CO_2 levels
- If too much transpiration occurs (eg due to low humidity or a high radiation load) a direct feed-forward effect occurs by altering the turgor of the guard cells, causing stomatal to close.
- When soils dry, roots and leaves produce ABA
  - This forces a closing of stomata, to conserve water.

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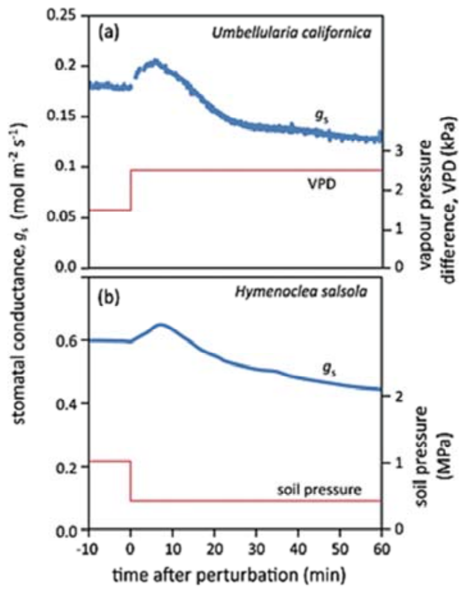
Jones, 1992

Theories Need to Explain Transience in Stomatal Response to Humidity



Plant, Cell & Environment
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http://onlinelibrary.wiley.com/doi/10.1111/pce.12651/full#pce12651-fig-0001

Stomatal responses are similar whether leaf water status is altered via evaporative demand (a) or water supply (b). Data in (b) are reproduced with permission from Comstock and Mencuccini (); raw data in (a) are unpublished data from the author's laboratory.

Why is there Transient Stomatal Opening with Dry Air?

Given that stomatal aperture is controlled by turgor pressure in stomatal guard cells, one might naïvely predict that stomata should close when leaf turgor is reduced by water loss following exposure to dry air.

However, this ignores the countervailing effect of turgor in the surrounding epidermal cells, which affects aperture in the opposite manner as guard cell turgor.

In angiosperms, those cells have a mechanical advantage over guard cells – that is, equal declines in turgor in both epidermal and guard cells cause stomata to open rather than close (Franks *et al*. **1998**).

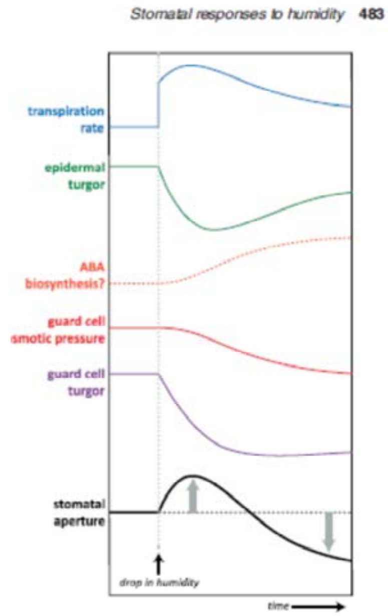
This causes angiosperm stomata to open transiently before closing in dry air

From Buckley 2016 PCE

Mechanism of stomatal responses to humidity according to the hydroactive feedback hypothesis.

Increased water loss initially reduces epidermal and guard cell turgor by similar amounts, causing transient stomatal opening.

Reduced water status then causes biosynthesis of abscisic acid (ABA), which induces solute loss from guard cells, amplifying their turgor loss and causing stomatal closure.



Buckley 2016 PCE

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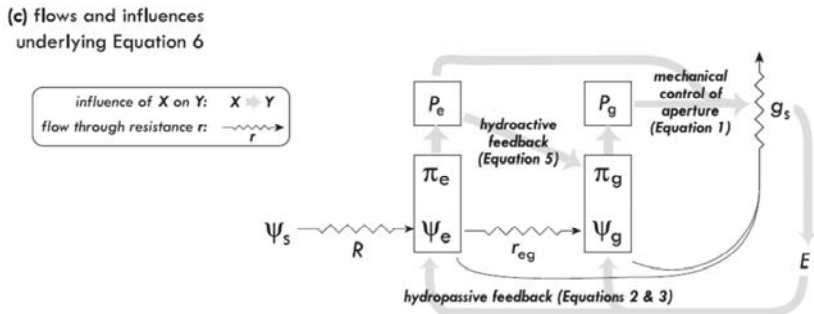
New findings by McAdams and Brodribb on denovo production of ABA refines Buckley theory

Mechanism of stomatal responses to humidity according to the hydroactive feedback hypothesis. Increased water loss initially reduces epidermal and guard cell turgor by similar amounts, causing transient stomatal opening. Reduced water status then causes biosynthesis of abscisic acid (ABA), which induces solute loss from guard cells, amplifying their turgor loss and causing stomatal closure.

Hydro-Active feedback

- It is argued that a metabolically mediated feedback response of stomatal guard cells to the water status in their immediate vicinity ('hydro-active local feedback')remains the best explanation for many well-known features of hydraulically related stomatal behaviour, such as transient 'wrong-way' responses and the equivalence of hydraulic supply and demand as stomatal effectors,
  - Buckley, 2005 New Phytologist

Hydro-Active-Negative Feedback Hypothesis



Pe: turgor Pressure Epidermis
Pg: turgor Pressure Guard Cell
π: osmotic pressure
Ψ: water potential

Buckley, 2005, New Phytologist

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the hydroactive feedback hypothesis (HFH), holds that guard cell osmotic pressure is actively regulated

in response to leaf water potential or turgor, rather than humidity or transpiration rate per se. Because the change in

water status precedes and induces the active response, the latter lags behind the former, producing the transient opening

characteristic of stomatal responses to short-term hydraulic perturbations (Buckley, 2016 PCE).

Root-derived ABA signals cannot provide the missing signal, because they generally do not reach guard

cells quickly enough to explain humidity responses and also because any fundamental role for root signals in stomatal

function is questioned by the fact that stomata behave normally in shoots grafted onto rootstock that cannot produce ABA

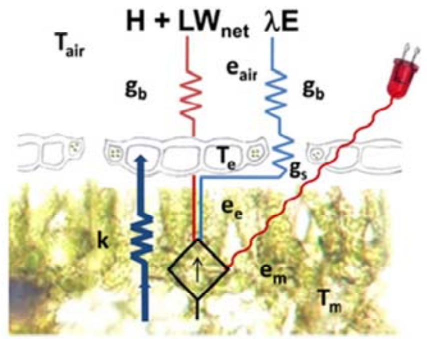
(e.g. Holbrook et al. 2002).

New Findings, Refine HFH Theory

- McAdam et al. (2015) fill this gap and complete the HFH by unequivocally demonstrating a viable mechanism for hydroactive feedback: rapid, de novo synthesis of ABA within the leaf following exposure to dry air.

Control of Transpiration/Stomata by Radiation

the steady-state water potential of the epidermis in the intact leaf is controlled by the difference between the radiation-controlled rate of water vapor production in the leaf interior and the rate of transpiration.
Any difference between these two potentially large fluxes is made up by evaporation from (or condensation on) the epidermis, causing its water potential to pivot around this balance point.



Pieruschka and Berry 2010 PNAS

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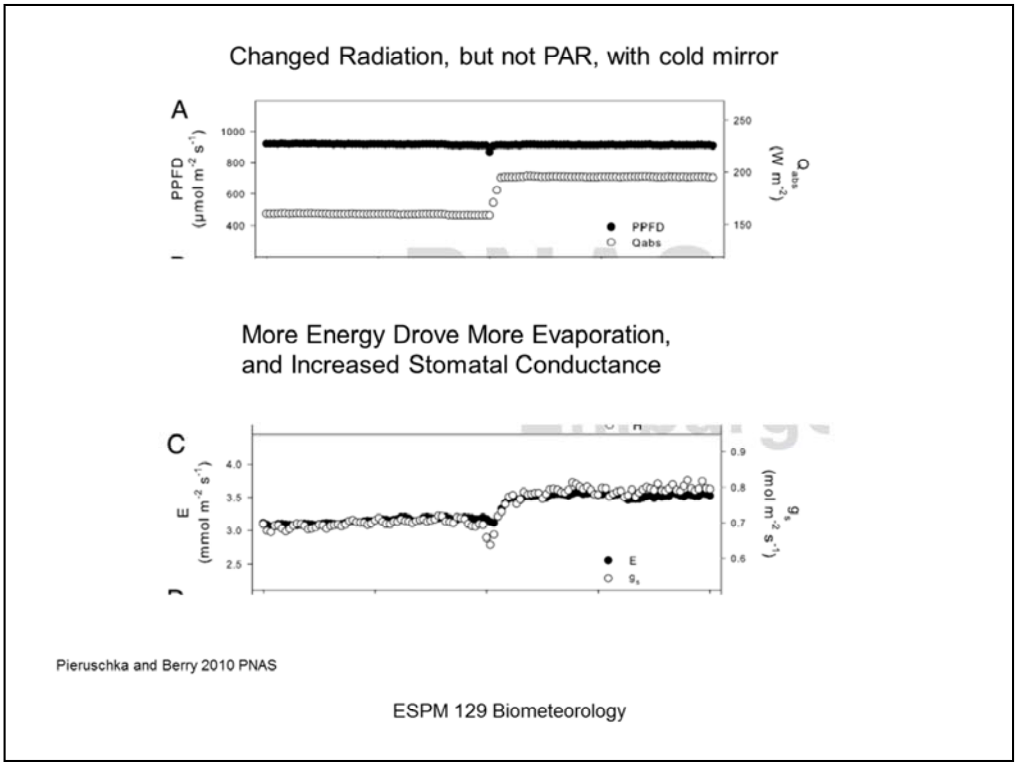
Towards a New Synthesis.. What drives stomata? Is it environmental variables like light, temperature, humidity differences or the Flux of water?

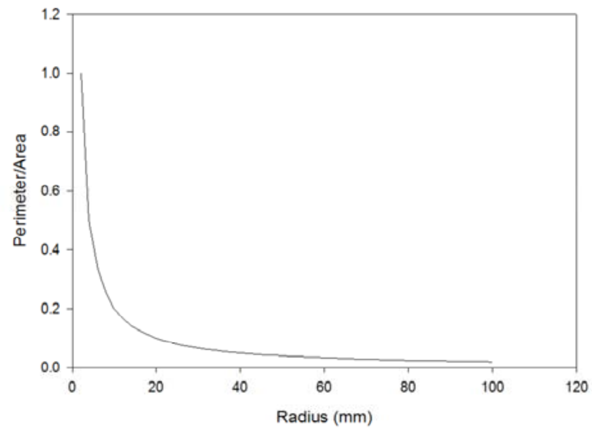


Pieruschuka and Berry performed some clever work by changing the IR flux with a cold mirror and not sunlight. This change in energy changed leaf evaporation and stomatal conductance. This elegant experiment confirms some earlier contentions by Monteith and others that stomatal conductance better scaled with Transpiration than environmental variables

Pore Paradox

- if you have a wet surface and dry a quarter of it, you would expect the evaporation rate to reduce by a fourth.
  - Following this logic one would expect the evaporation rate to decrease by 99% if only 1% of the surface was wet (or had evaporating pores, like stomata).
- This linear effect is not observed in nature.
  - When the holes are arranged in the manner and spacing of a leaf we only observe a 50% reduction in evaporation, as compared to a wet surface!!
  - Why??

In the case of diffusion from a bounded pore its flux density scales with the diameter of the diffusion front, not its cross-sectional area.



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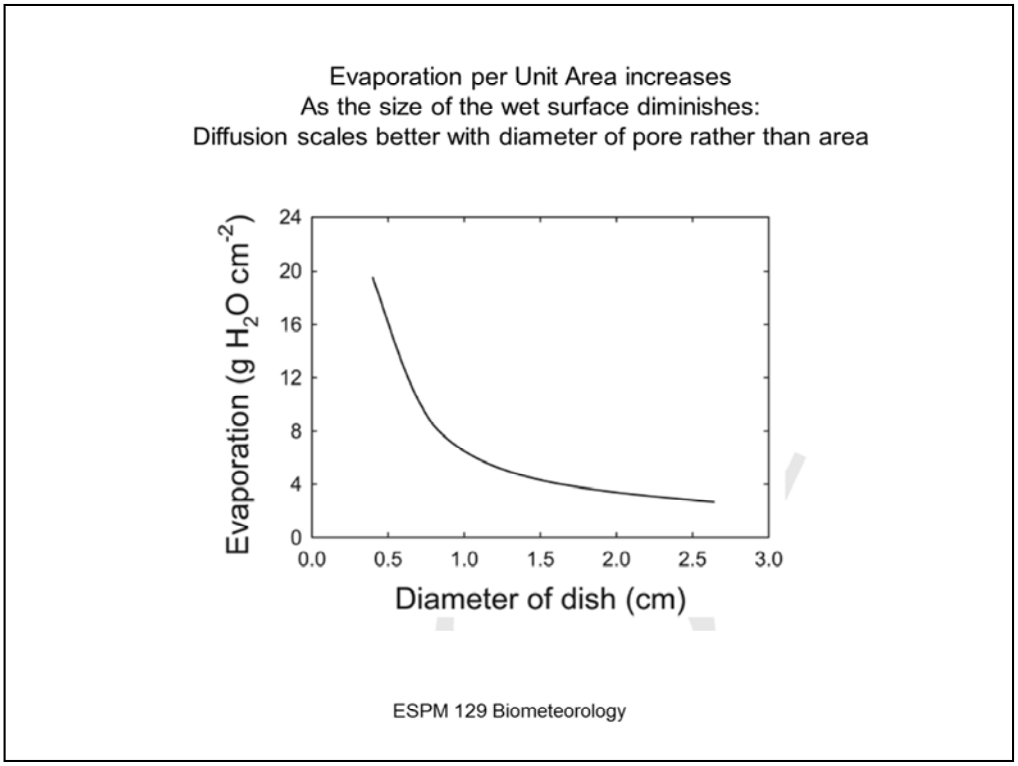
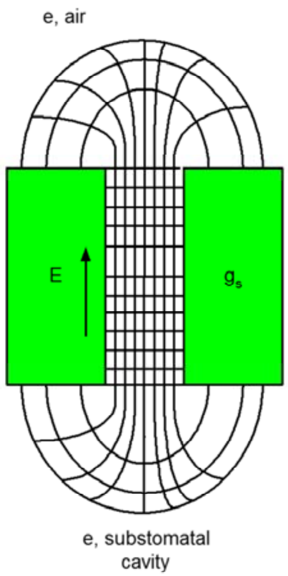


Data from Sayre 1926, figure from Monson and Baldocchi (2014)

Diffusion out of a Leaf is 3D



$$g_s \neq \frac{D_v n a}{z}$$

$$r_s = \frac{l}{n\pi r^2 D} + \frac{1}{4n\pi D}$$

Brown and Escombe, 1900

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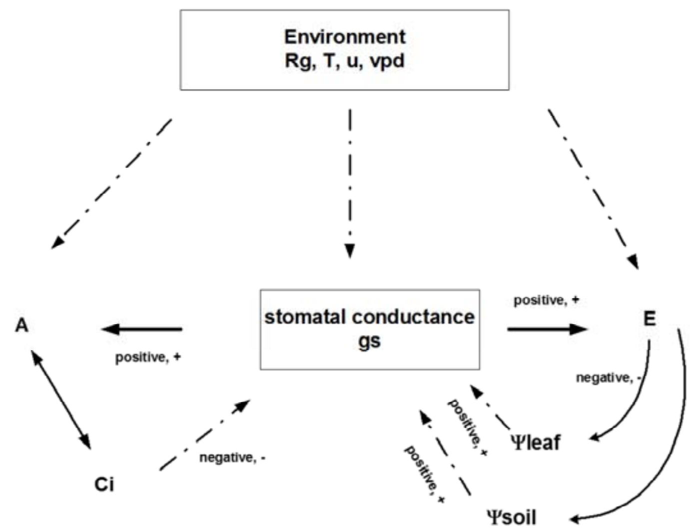
Brown and Escombe argued that diffusion out of a pore is 3 dimensional which augments the transfer

Feedbacks with Environmental Biology



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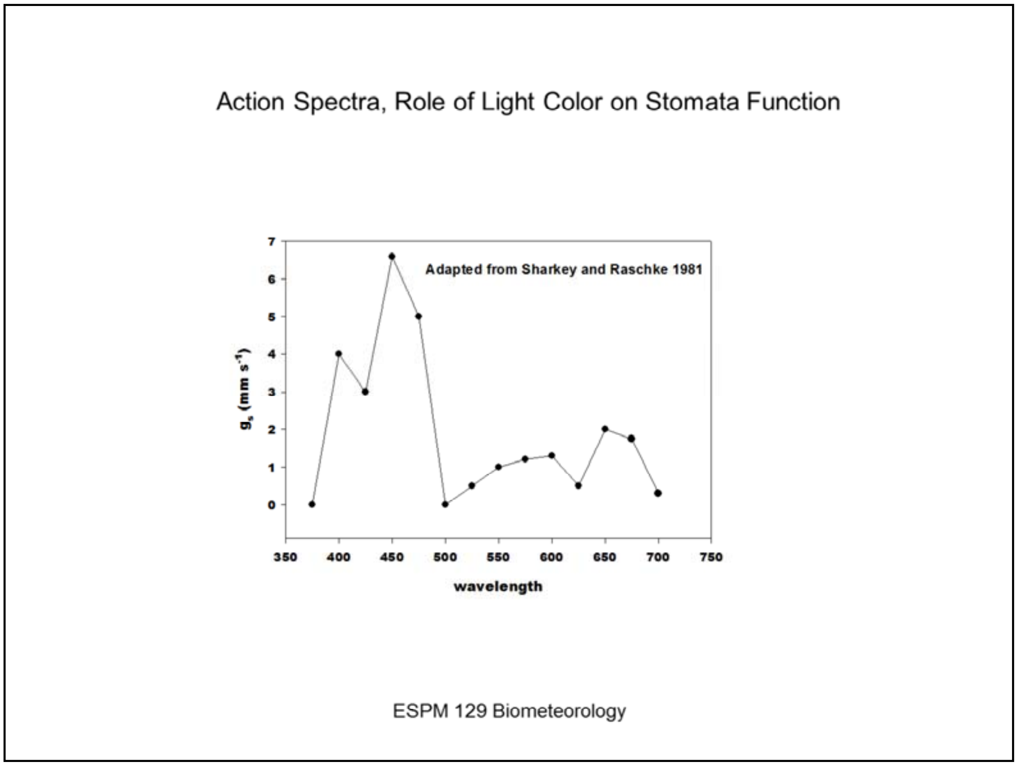
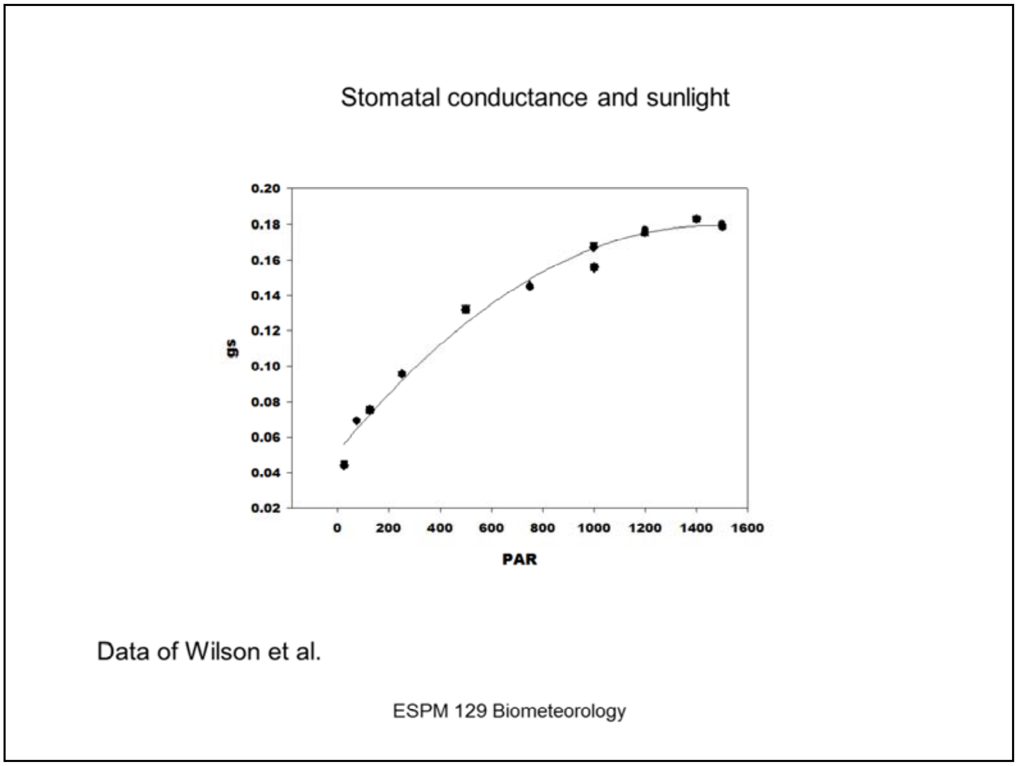
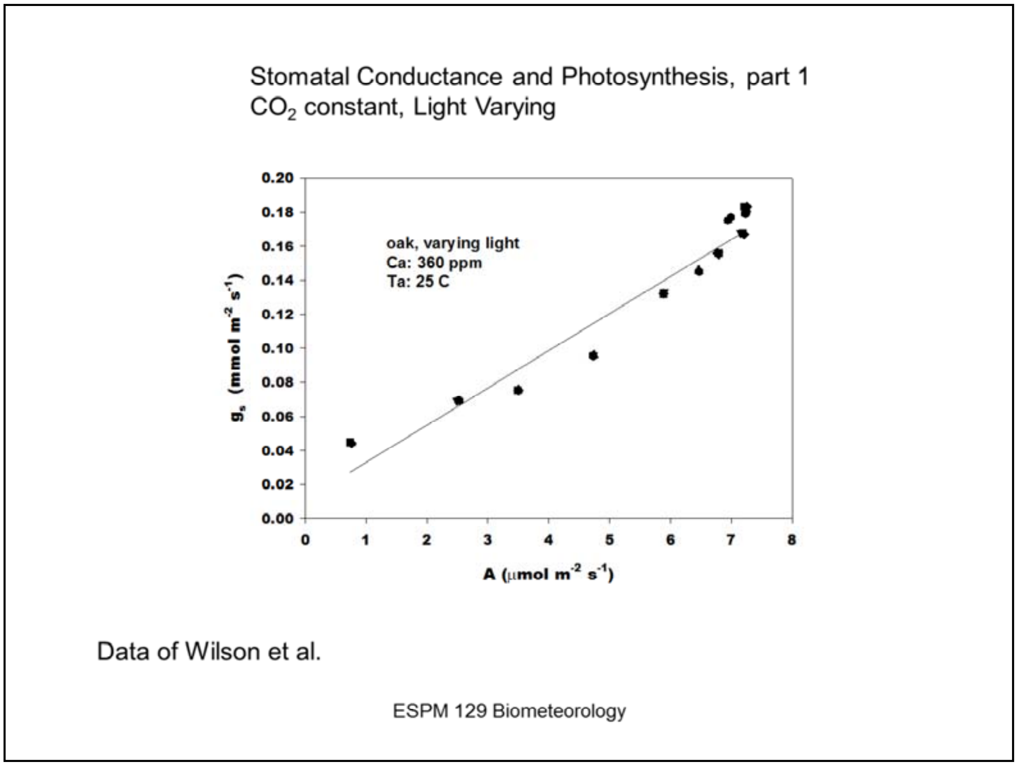


How do stomata respond to environmental drivers? There is a broad band response of stomata to PAR, photosynthetically active radiation. But action spectra shows a preferred response to blue light. Early makes of the LICOR 6400 photosynthesis instrument used LED and was not capable of illuminating the blue light well enough. Recent advances in LEDs, which led to the 2014 Nobel prize in Physics, produced a blue led that was later incorporated into the measurement system and an improvement was made in measuring stomatal conductance with that instrument.

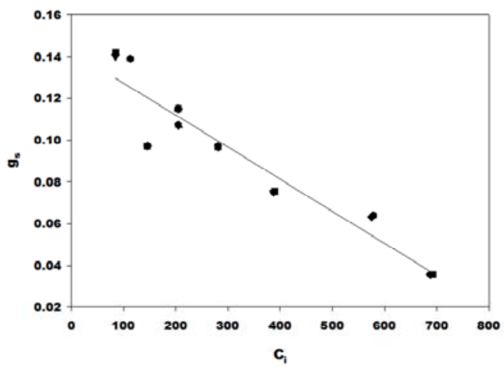


Light response curve we measured for a white oak in Tennessee between stomatal conductance and PAR. It has a saturating response curve like photosynthesis, given steady temperature and CO_2.



Environmental response functions show strong correlations among stomatal conductance and photosynthesis. This later led to a leading model by Ball and Berry. In this case CO2 is constant and light varies.

Stomatal Conductance and Internal CO_2



Data of Wilson et al.

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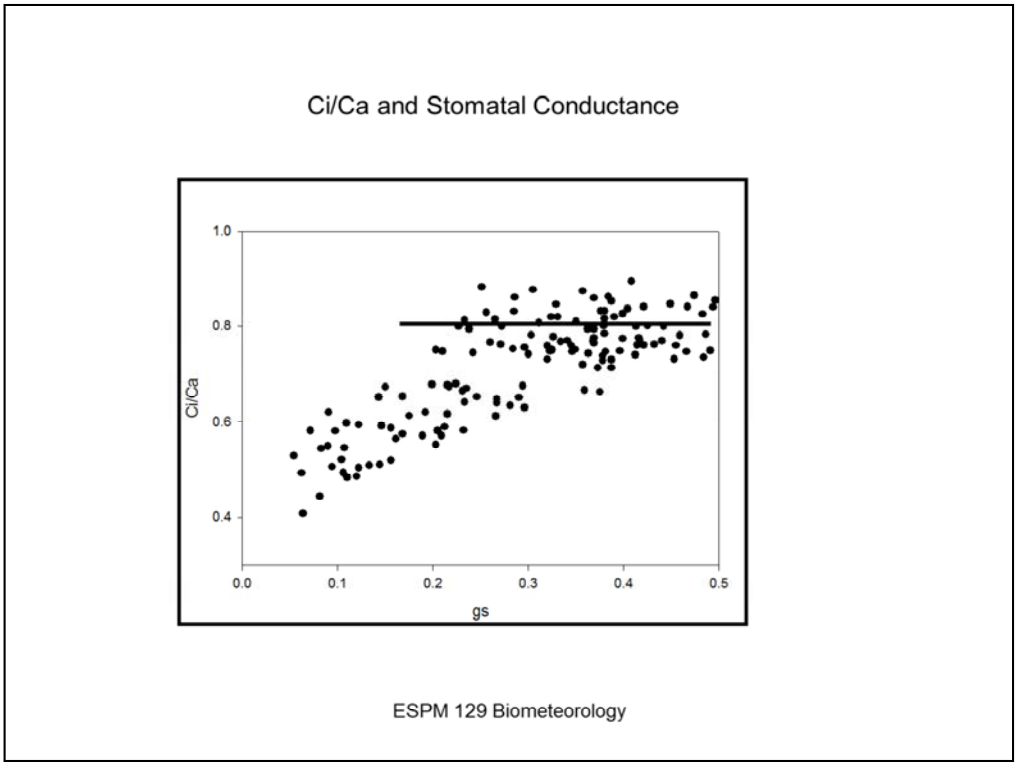
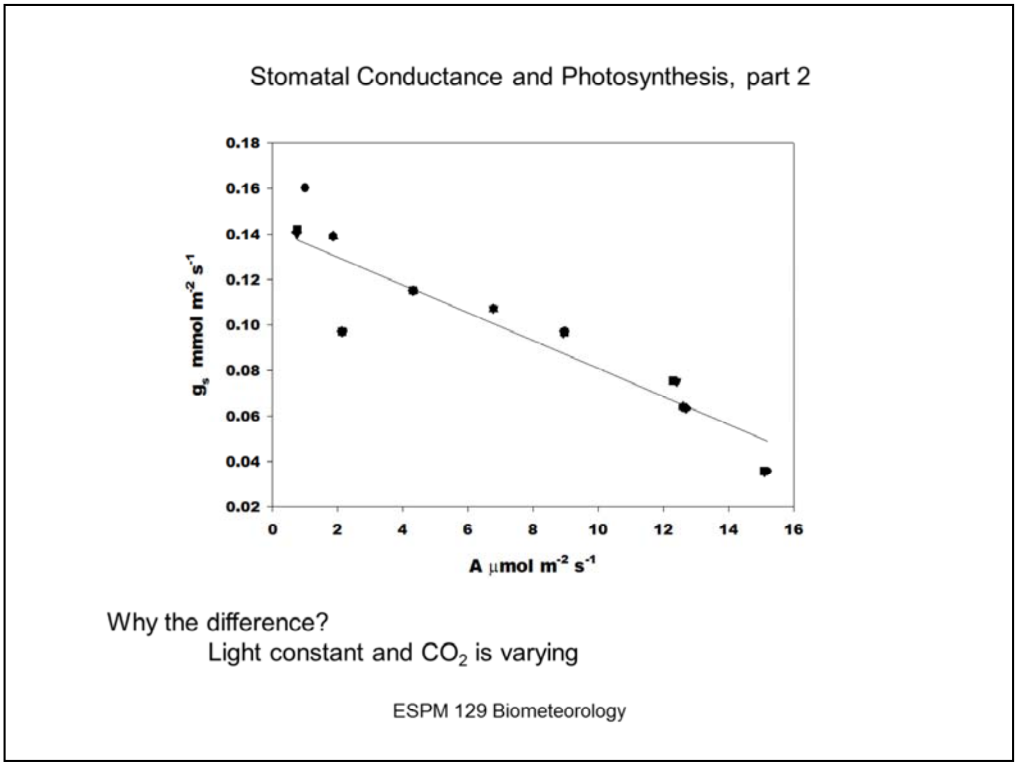
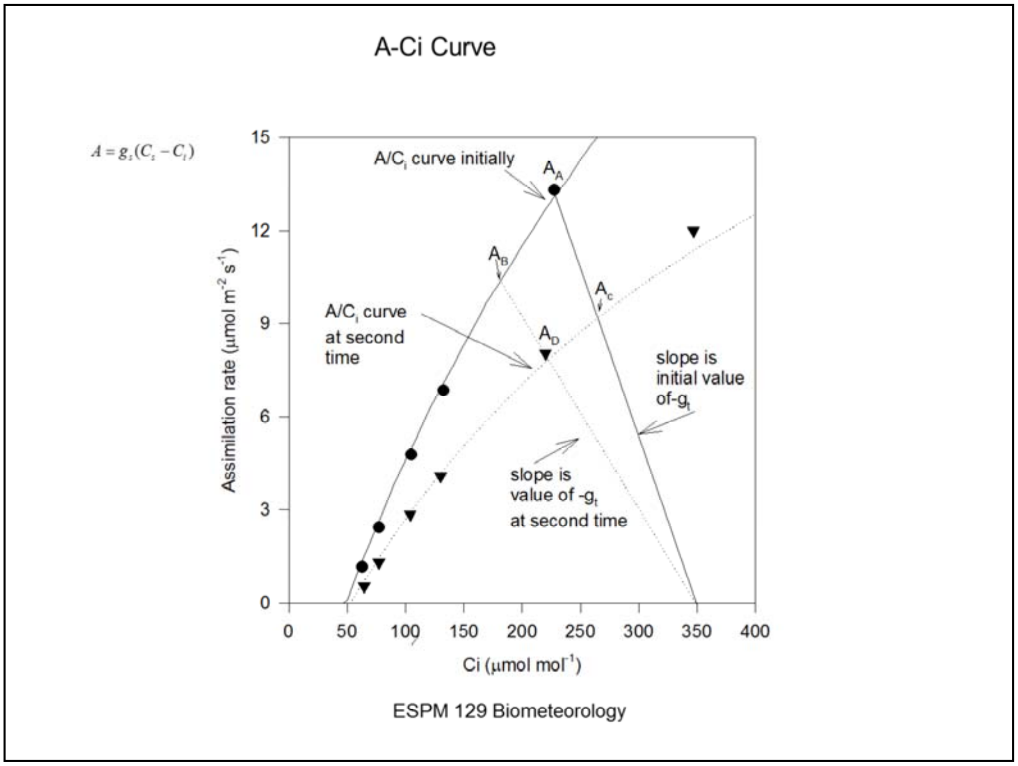
On the other hand there is an inverse relation between stomatal conductance and the CO2 concentration in the intercellular regions of a leaf. If CO2 is high, the stomata don’t need to open so widely and lose more water.



Lots of data show that happy leaves have a operating point where stomata open and close to keep the ratio of the internal CO2 concentration to its atmospheric value near 0.7 (for C3 leaves). Our data supports this for as long as the stomata are relatively open. Closure can cause a drawdown in Ci and reduce this ratio. Isotopic ecohydrologists use measures of the stable isotope content of a leaf, del 13C as a measure of ci/ca and infer stomatal conductance.

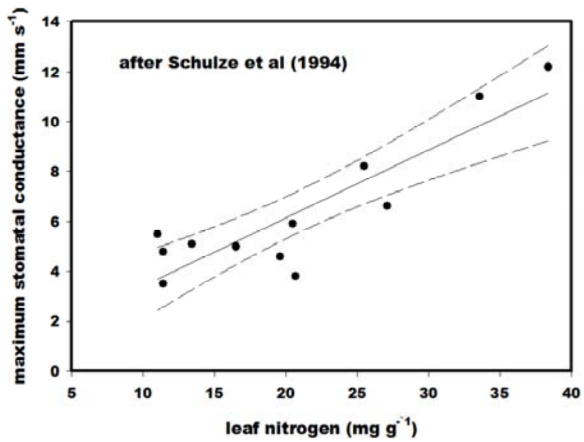


In this instance, if we keep light constant and increase CO2 we will see an increase in photosynthesis, A, but a decrease in stomata conductance. Is something broken?



The A-Ci curve lets us explore how and why stomatal conductance decreases with CO2 and photosynthesis increases. Gs is related to the ratio between A/(Ca-Ci). If this difference is zero, gs goes to infinity. But in practice Ci is about 0.7 Ca for C3 plants so the slope decreases as Ci differs from Ca more and more. We also see a change in slope if photosynthetic capacity decreases. Hence stomatal conductance is less for leaves with lower photosynthetic capacity.

Stomatal Conductance and Leaf Nitrogen



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Photosynthetic capacity scales with leaf nitrogen, so we see an increase in stomatal conductance with more leaf nitrogen

vegetation type	nitrogen content	specific leaf area	max stomatal conductance
	mg/g	m2/kg	mm/s
broadleaved crops	38.4	23.6	12.2
cereals	33.6	25.3	11
deciduous conifers	20.7	11.3	3.8
evergreen conifers	11	4.1	5.5
monsoonal forest	11.4	4.3	3.5
sclerophyllous shrubland	11.4	6.9	4.8
temperate deciduous forest	19.6	11.5	4.6
temperate deciduous fruit trees	23.8	10.1	
temperature broadleaved evergreen	13.4	5.7	5.1
temperate grassland	25.5	16.9	8.2
tropical deciduous forest	27.1	14.1	6.6
tropical plantation	13.6	6.8	
tropical grassland	10.7		
tropical rainforest	16.5	9.9	5
tundra	20.5		5.9

Summary

- Stomata are active pores on leaves that regulate the transfer of carbon dioxide and water vapor between plants and the atmosphere
- Though covering a small fraction of the surface of a leaf, their distribution allows three-dimensional transfer to enhance the area-weighted one-dimensional flux, hence the pore paradox.
- Water vapor, CO_2 and air bump into each other as they pass through the small diameter of the stomatal pore. Hence, ternary diffusion needs to be considered when computing leaf level trace gas fluxes (especially leaf photosynthesis) and properties (C_i) properly.
- a metabolically mediated feedback response of stomatal guard cells to the water status in their immediate vicinity ('hydro-active local feedback') remains the best explanation for many well-known features of hydraulically related stomatal behaviour
- A-Ci curve helps diagnose how stomata respond to environmental drivers like light, CO_2 and leaf nitrogen

extra