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.
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.


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.
Key features and attributes of stomata. They differ on different plants.
https://plantstomata.files.wordpress.com/2015/03/15consolea-epi-peel-4-inch.jpg
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, New Phytologist

ESPM 129 Biometry
Guard cells and subsidiary cells. Movement of cations and anions in and 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 CO₂ in the intercellular air space, via Ps, and guard cells enables K+ to move into the guard cell and open the stomates.
  - This allows CO₂ to diffuse into the leaf for photosynthesis.
  - In converse, stomata close when exposed to elevated CO₂ 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.

Jones, 1992
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 naively 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
New findings by McAdams and Brodribb on de novo 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
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.
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??

ESPM 129 Bioremediology
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.
Data from Sayre 1926, figure from Monson and Baldocchi (2014)
Brown and Escombe argued that diffusion out of a pore is 3 dimensional which augments the transfer.
Feedbacks with Environmental Biology

Environment
$R_g, T, u, vpd$

stomatal conductance $gs$

$A$ positive, $+$

$C_l$ negative, $-$

$E$

$E_{leaf}$ positive, $+$

$E_{soil}$ negative, $-$

ESPM 129 Biometry
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 CO2.
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.
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.
Photosynthetic capacity scales with leaf nitrogen, so we see an increase in stomatal conductance with more leaf nitrogen.
<table>
<thead>
<tr>
<th>vegetation type</th>
<th>nitrogen content</th>
<th>specific leaf area</th>
<th>max stomatal conductance</th>
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ESPM 12B Biodiversity
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, CO2 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 (Cl) 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, CO2 and leaf nitrogen.
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