Stomatal Physics

Kathryn Sweet[1], Keith A. Mott[2], David Peak[1]

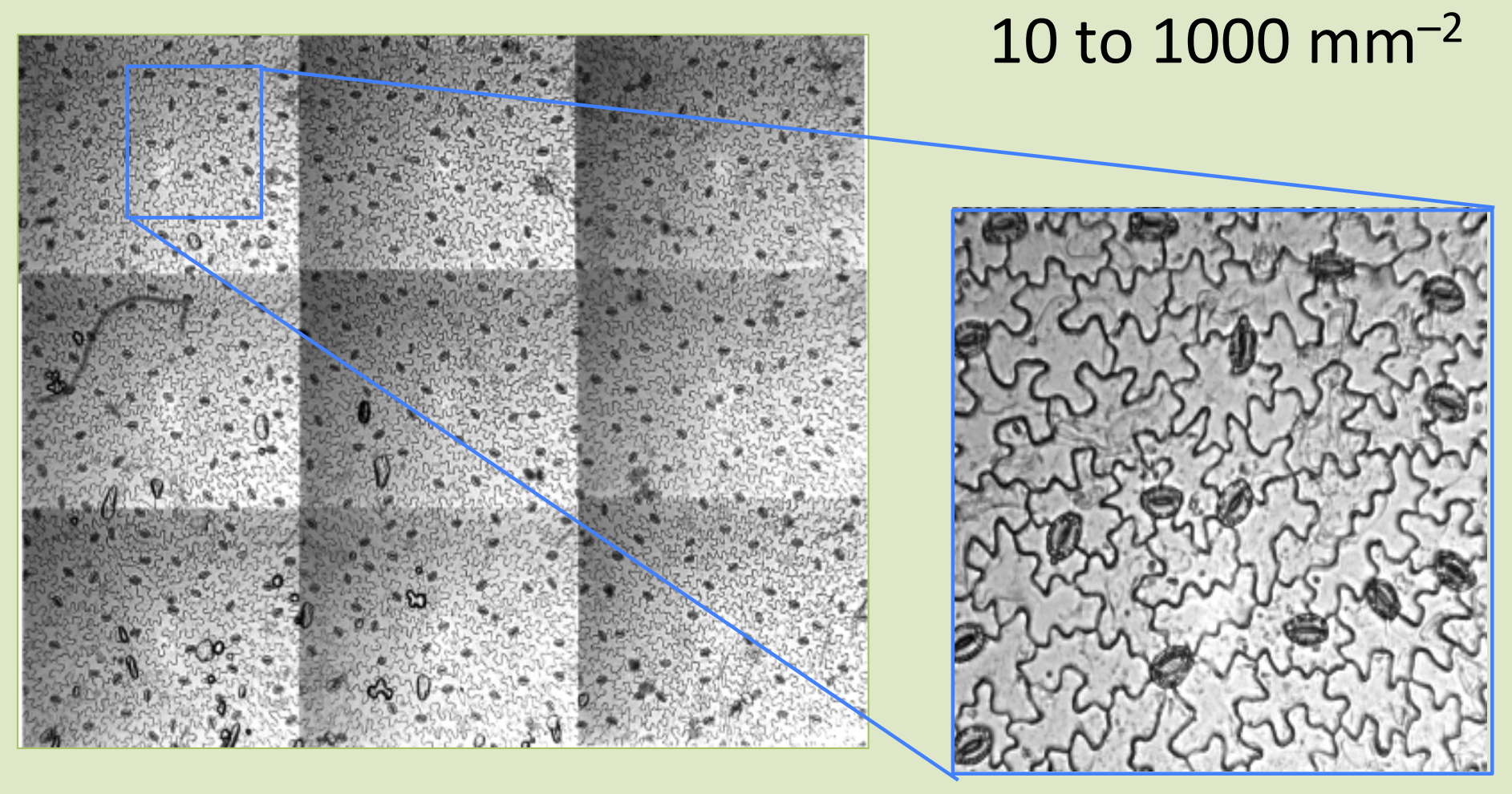
1 Physics Department, 2 Biology Department, Utah State University, Logan, UT 84322

Supported through
NSF Grant IOS-1122003

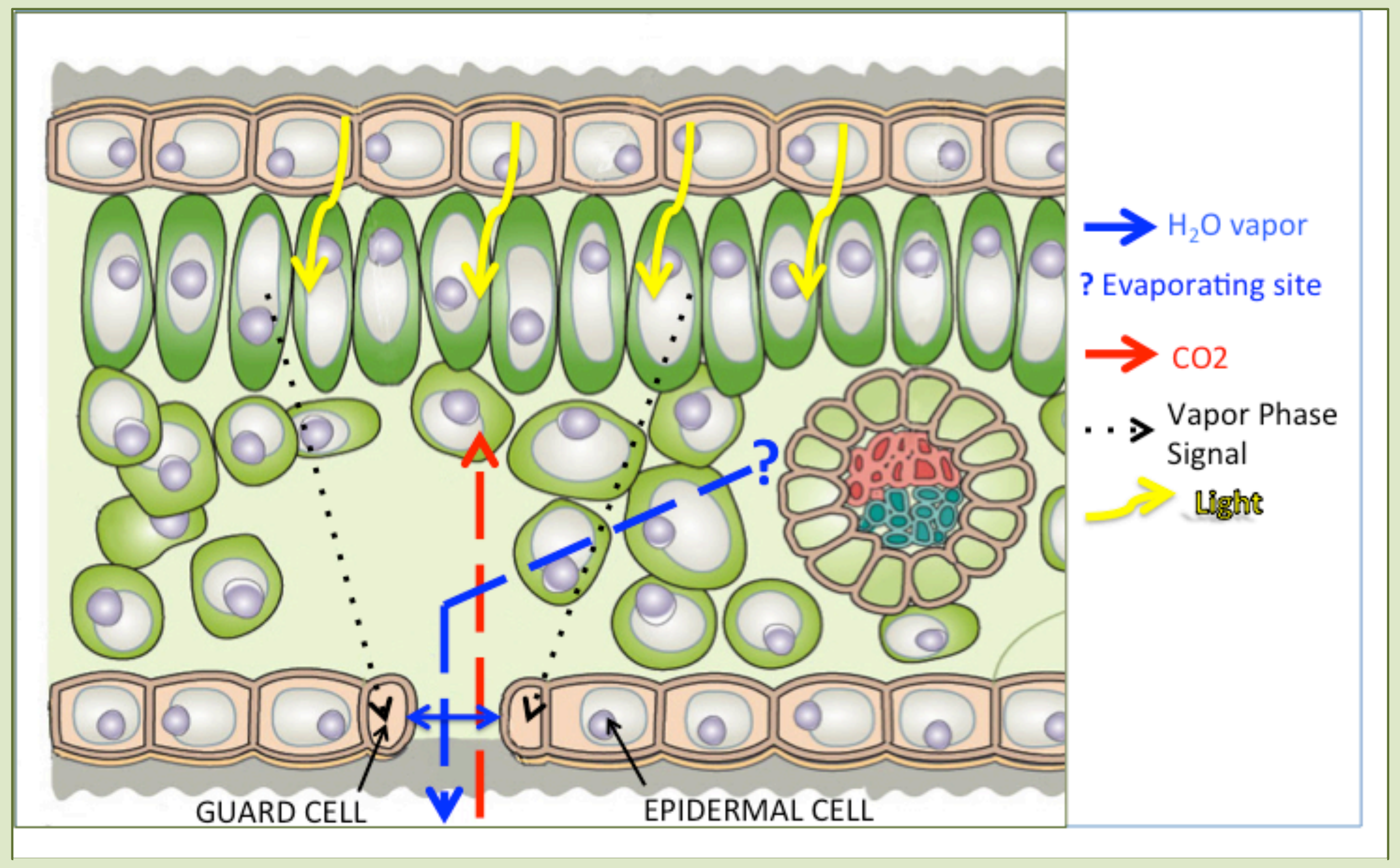
Background

- Stomata, microscopic pores on a leaf's surface, regulate the diffusion of CO2 from, and the diffusion of water vapor to, the air.
- Stomata are responsible for fixing essentially all carbon in the biosphere and generating over 90% of the water vapor in the atmosphere over landmasses.
- Exactly how stomata respond to temperature, light intensity, and ambient CO2 and humidity, is still a matter of active debate.
- Most research probing this question focuses on identifying and unraveling complicated biochemistry. Recent investigations in our laboratory, however, indicate that much of stomatal behavior can be understood in terms of a simple vapor phase physical model.

10 to 1000 mm^{-2}



Bean-shaped "guard" cell pairs form stomatal pores on the surface of a leaf surrounded by jig-saw-puzzle-shaped epidermal cells



Schematic of the interior of a leaf: Leaves evaporate water to regulate their temperature and take in CO2 for use in photosynthesis through stomatal pores on the leaf's surface. The interior of a leaf is roughly 50% humid air.

Motivation

1. Isolated stomata (removed from mesophyll cells in leaf interior) respond to air humidity just as they do in intact leaves.[1]
2. Isolated stomata don't respond to light and CO2, but when brought close to, but not in contact with, mesophyll cells they do.[2]
3. Isolated stomata respond to vapor phase ions.[3]

Physics

VAPOR PHASE MODEL OF STOMATAL CONDUCTANCE

$$g_S = \frac{g_{S0} - \theta \dfrac{\Delta w}{w_L}}{1 + Z\Delta w}$$

g_S = stomatal conductance (aperture)
g_{S0} = conductance at 100% external humidity
w_L = saturated water vapor (WV) concentration inside the leaf
$\Delta w = w_L - w_a$, where w_a is the WV concentration in the outside air
Θ = humidity sensitivity due to resistance to WV diffusion from inside the leaf to the air
Z = humidity sensitivity due to resistance to heat transport inside the leaf

MECHANICS

$$g_S = \chi(P_g - mP_e)$$

- Stomatal aperture is proportional to the difference in turgor pressures in guard (P_g) and surrounding epidermal (P_e) cells.
- Larger epidermal cells have a mechanical advantage (m).

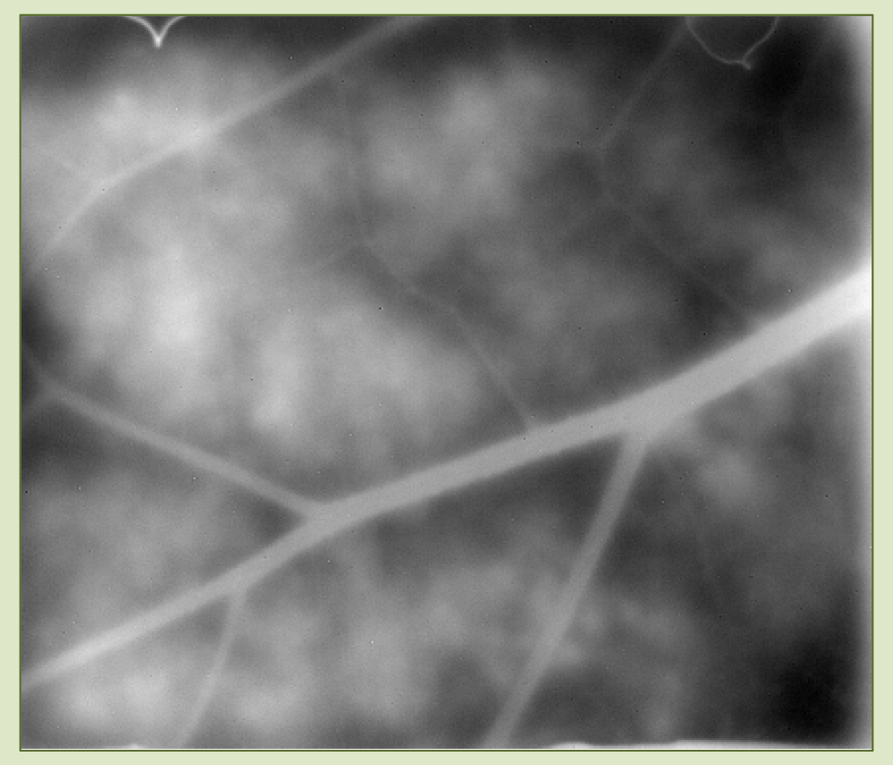
THERMODYNAMICS

- Chemical potential of water, Ψ, determines direction of water transport
  - Liquid Phase $\Psi = P - \pi,\ \pi = cRT$
    - This yields $g_{S0} = \chi(\pi_g - m\pi_e)$
  - Vapor Phase $\Psi = \frac{RT}{v_w}\ln\frac{w}{w_{sat}},\ w_{sat} = w_0 e^{\frac{-T_w}{T}}$
  - Transport of water vapor is fast compared with hydration of guard cells
  - This leads to equilibrium conditions:
    - Liquid phase potential in the epidermis = liquid phase potential at the evaporation site = vapor phase potential immediately outside the evaporation site
    - Vapor phase potential in the stomatal pore = liquid phase potential in the guard cells
  - And a steady state condition:
    - Vapor phase potential in the stomatal pore = (fraction, σ) vapor phase potential in the external air + (fraction, $1-\sigma$) vapor phase potential at the evaporating site
  - Approximations:
    - Liquid phase potential at the evaporation site << RT/v_w
    - Temperature of evaporating site is slightly lower than that of epidermis
      - These yield Z
    - σ is small (< 0.1)
      - This yields θ

References

1. Shope, J.C., et al., Plant, Cell & Environ., DOI: 10.1111/j.1365-3040.2008.01844.x (2008)
2. Mott K.A., et al. Plant, Cell & Environ., DOI: 10.1111/j.1365-3040.2008.01845.x. (2008)
3. Mott, K.A., et al., Plant, Cell & Environ., DOI: 10.1111/pce.12226 (2013)

Experimental Setup



Experimental chamber: Leaves are placed in a gas exchange chamber that regulates and measures environmental conditions. A thermal imaging camera captures temperature (±0.05 °C) images of the leaf (160,000 pixels–roughly one stoma per pixel). See image to the right.

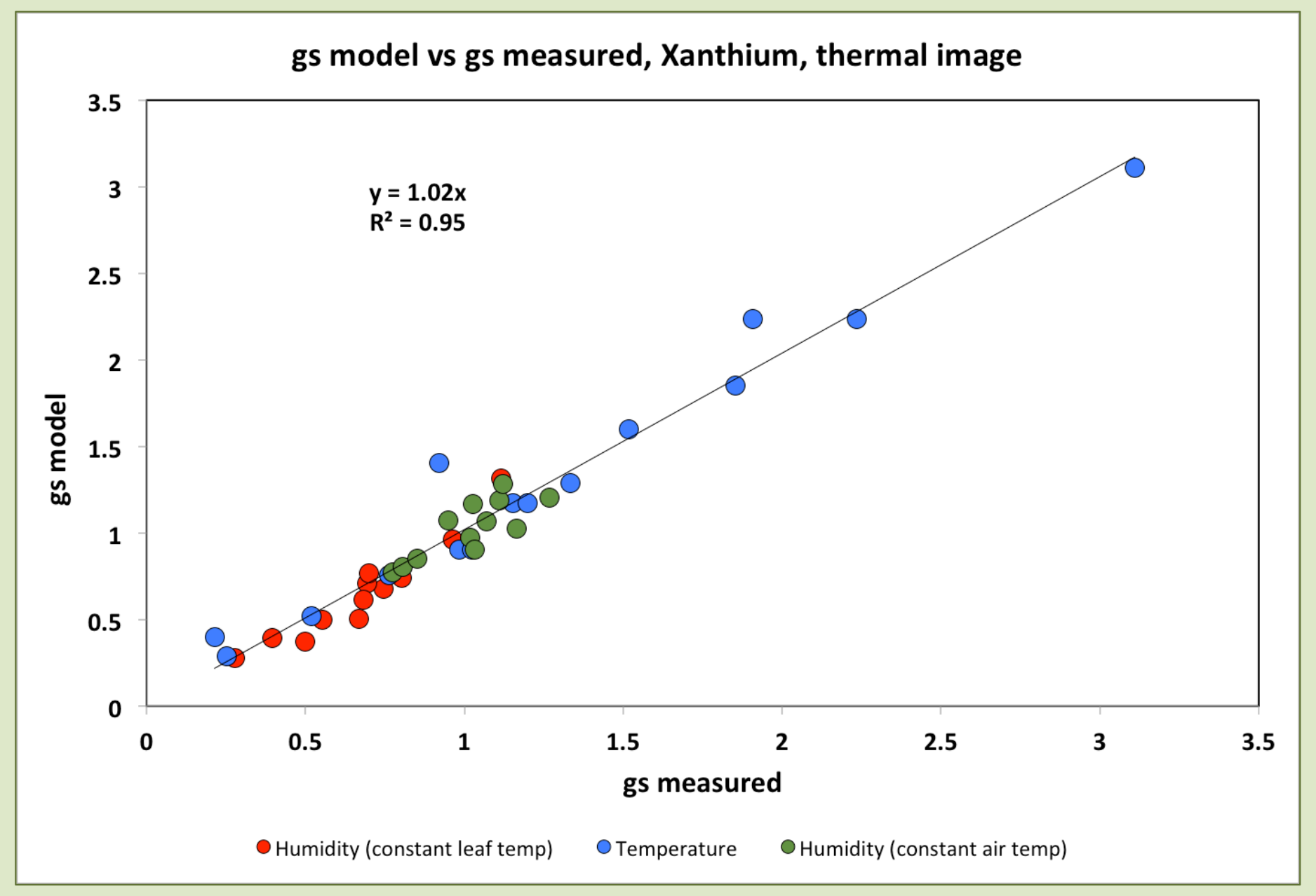
From the non-vein pixel temperatures (veins don't contribute to evaporation) we can calculate an accurate average leaf temperature and an accurate whole leaf conductance.

Leaf heterogeneity: The temperature across a leaf is rarely uniform (see image). Measurements that do not account for this (and cannot adjust for veins) for are unlikely to accurately assess stomatal behavior.

Results

Experiments: with *Xanthium strumarium* (cocklebur), to test the validity of the model.
1. Constant CO2, light, and chamber air humidity constant; vary air temperature between 20 and 33 ^{0}C.
2. Constant CO2, light, and leaf temperature (26^0 C); vary chamber air humidity.
3. Constant CO2, light, and air temperature (26^0 C); vary chamber air humidity.

Results: When fit to the data to the vapor phase model agrees with experimental observation with the same values for Θ and *Z* and same g_{S0} temperature dependence. The figure to the right shows the g_S values predicted by the model vs the g_S values experimentally observed for 39 different conditions across 10 days of experiments.



Conclusion

- Some important aspects of stomatal behavior can be explained through simple mechanics and vapor phase physics. This runs counter to the prevailing tradition in plant physiology that essentially all stomatal behavior is biochemistry.
- Some metabolic component to stomatal response is contained in the temperature dependence of g_{S0}. A more complete understanding of this requires additional experiments varying light and CO2, which we are now conducting.