Lecture 30, Stomatal Conductance, Part 3, theory

- Phenomenological Stomatal Conductance Models
  - The multiplicative model of PG Jarvis
  - Transpiration Conductance Theories of Mott and Parkhurst, Monteith
- Coupled Photosynthesis-Stomatal Conductance Models
  - Norman/Wong, stomata operate to keep ci/Ca constant
  - Ball Berry Algorithm
  - Pieruschka and Berry, PNAS 2010
  - Leuning
- Optimal Carbon Gain for Water Use Models
  - Cowan/Farquhar theory
  - Optimal use of water with time, Makela, Farquhar
- Coupled Soil Moisture Models
  - Tardieu et al. (ABA)
  - Williams and Tuzet et al models (link to Soil water potential)

Mathematical Representation: Model Algorithms

1. Empirical, Regression Based
   1. Multiplicative
   2. Additive
2. Mechanistic/Diagnostic
3. Prognostic

$$f(t,x,y) = af(t) \cdot bf(x) \cdot cf(y)$$

$$f(t,x,y) = af(t) + bf(x) + cf(y)$$

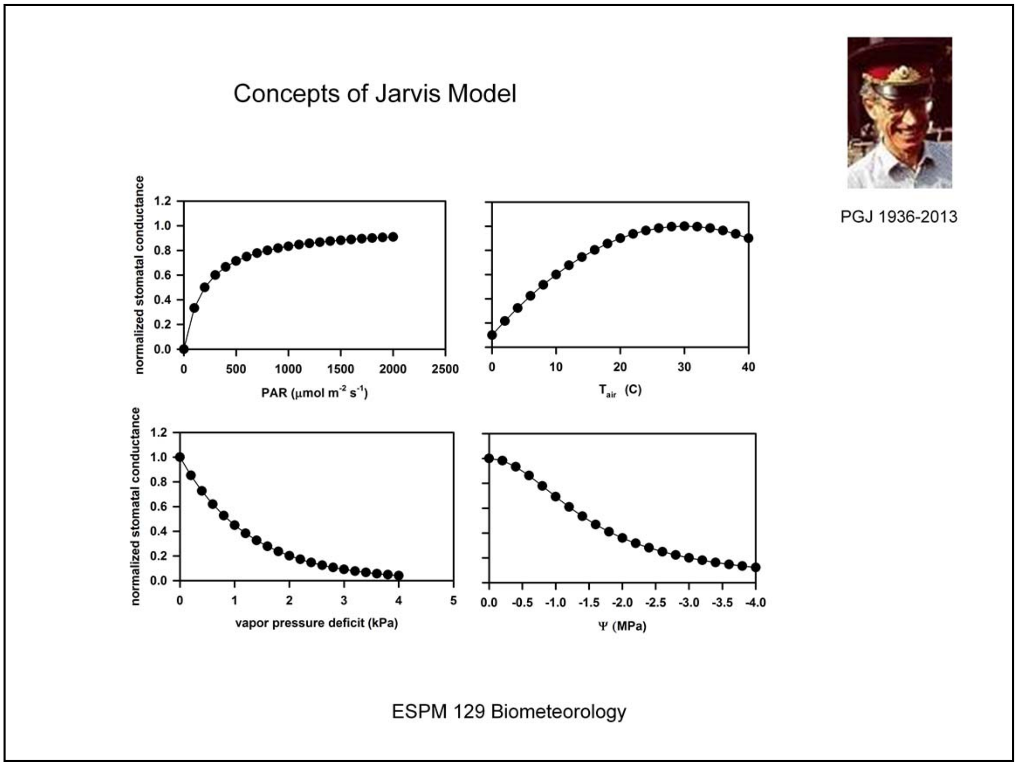
$$Rn = H + \lambda E + G$$

$$\frac{dc}{dt} = f(c,t)$$

Models come in many shapes and forms. They can be empirical, diagnostic and prognostic

Model Pitfalls

- Garbage In = Garbage Out
- Watch out for Non-Linearities
  - Apply at Proper Time-Step and Space-Scale
- Validate, Validate, Validate
- Don't Parameterize Model Algorithms with the Same data used to Validate
- Equifinality, a combination of parameters yield the same answer
  - An appeal to Multiple Constraints
- Avoid Auto-Correlation, y =f(y)
- Avoid Extrapolating Empirical Regression models beyond the range of the dataset
- Use Mechanistic and Prognostic Models to predict the future and to upscale information
- Closure: Equal number of Equations and Unknowns is needed



One of the first models on stomatal conductance that was widely used. The ideas was to use boundary line analysis of multifactorial measurements of stomatal conductance. It then produced response functions in terms of light, temperature, humidity deficits, soil moisture and carbon dioxide. I applied it in 1980s to assess the deposition of pollutants like ozone and sulfur dioxide to plant canopies. Others we quick to use it in land surface energy balance models.

Jarvis, P. G. 1976. Interpretation of Variations in Leaf Water Potential and Stomatal Conductance Found in Canopies in Field. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **273**:593-610.

Example of Boundary Line Analysis of the Jarvis-Reed Model

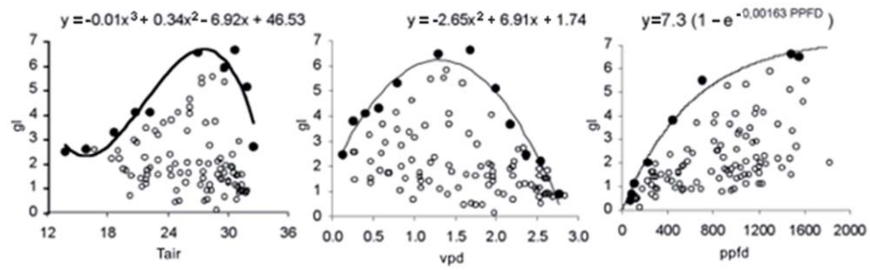


Figure 4. Scatter diagrams of the measurements of leaf diffusive conductance plotted against air temperature, air vapor pressure deficit and photosynthetic photon flux density, with the hypothetical boundary line fitted for each environmental variable.

http://dx.doi.org/10.1590/S1677-04202004000100008

Jarvis Model

$$g_s = g(I_p) \cdot f(T_a) \cdot f(D) \cdot f(\psi) \cdot f(C)$$

$$g(I_p) = \frac{g_{\max} I_p}{I_p + \beta} \qquad g(I_p) = 1 - exp(-kI_p)$$

$$f(T_a) = \left(\frac{T_a - T_h}{T_o - T_l}\right) / \left(\frac{T_h - T_a}{T_h - T_o}\right)^{\frac{T_h - T_o}{T_o - T_l}} \qquad f(T_a) = 1 - k(T - T_{max})^2$$

$$f(D) = 1 - kD \qquad f(D) = exp(-kD)$$

$$f(\psi) = (1 + (\frac{\psi}{\psi_{1/2}})^n)^{-1}$$

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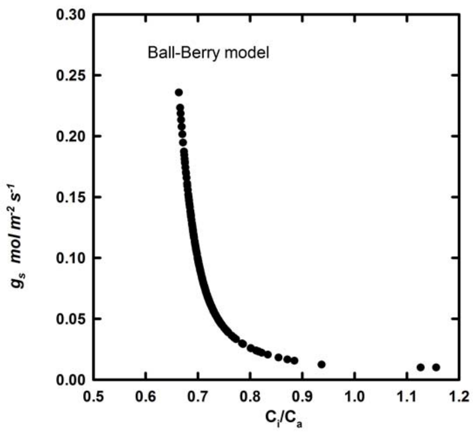
This is a multiplicative model, using functions forms for the other dependent variables.

Ci/Ca is constant
Ci/Ca=0.7, C3
Ci/Ca=0.4, C4

$$A / C_a = g_s (1 - C_i / C_a)$$



Baldocchi, 1994 Tree Physiology

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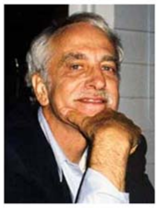
Wong et al showed in the 80's that stomata open and close to keep Ci/Ca conservative and near 0.7 for C3 leaves. This was the start of thinking that we have to couple stomatal conductance with photosynthesis. These are computations I produced with a coupled leaf photosynthesis-stomatal conductance model

Baldocchi, D. D. 1994. An analytical solution for coupled leaf photosynthesis and stomatal conductance models. Tree Physiology **14**:1069-1079.

ls. Before the years of Ball Berry, John Norman, a mentor, argued that Ci/Ca is constant and solve for gs.

Ball-Berry-Collatz Model



$$g_s = \frac{m\ A\ rh}{C_s} + g_0$$

A: photosynthesis
Rh: relative humidity
Cs: CO2 at leaf surface

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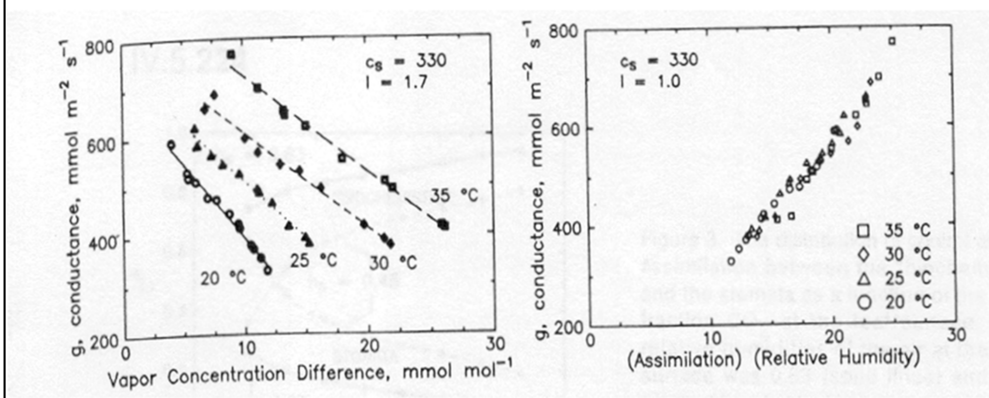
By the 1990s some of us (Piers Sellers, moi) were having problems utilizing the Jarvis models in our canopy energy balance models. It was too sensitive to positive feedbacks and the stomata tended to slam shut. At a key workshop in Penn State in 1989, Tim Ball, Joe Berry and Jim Collatz reported on a new way to compute stomatal conductance, as a function of leaf photosynthesis. This introduced a new degree of complication, the computation of photosynthesis, but it produced better and more stable values of stomatal conductance. Plus with the publication of the Farquhar-von Caemmerer-Berry photosynthesis model, we were half the way there.

Data from Ball's Dissertation



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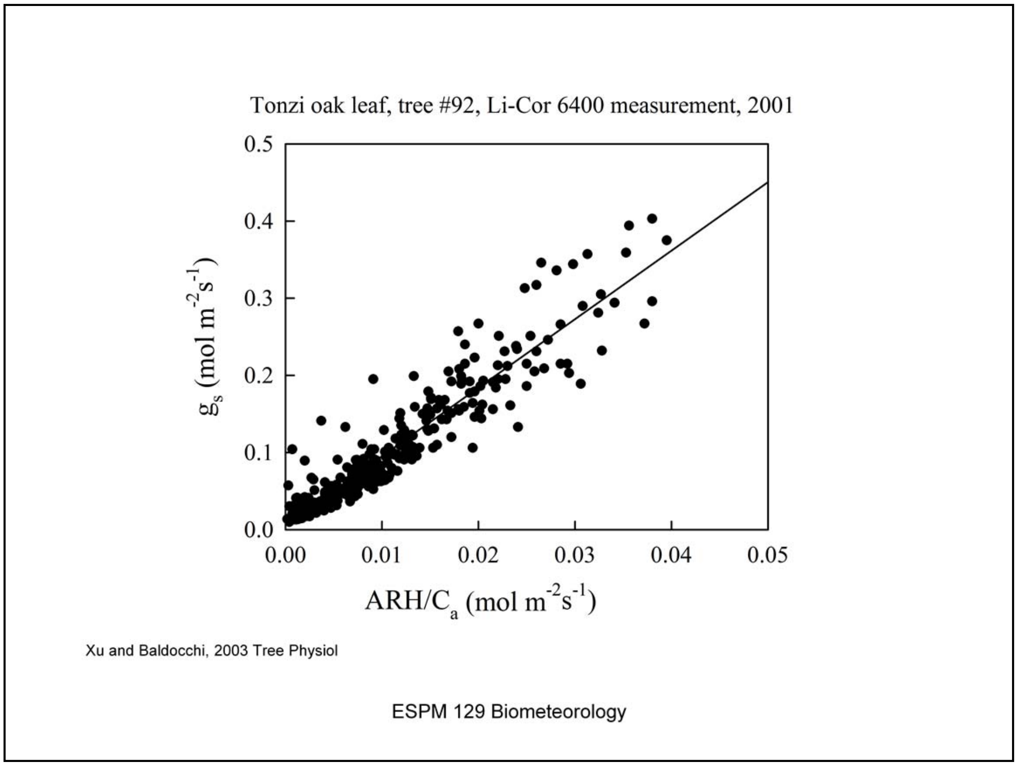
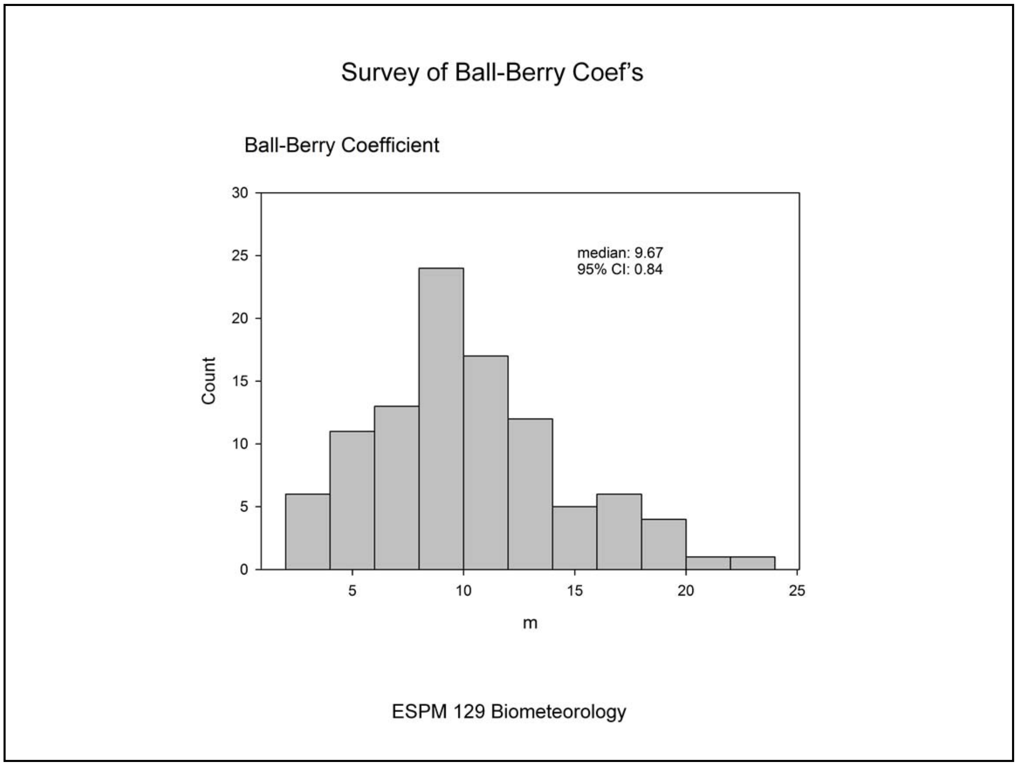
In Ball thesis, he shows with soybeans how all the response functions collapse on a single line when reported as a product of photosynthesis times relative humidity.



Here are tests of the Ball-Berry-Collatz model for oak savanna exposed to a wide range of soil water deficits, temperatures and light.



While the Ball Berry model introduces a new unknown, our survey of the literature shows it is conservative and near 10.

Leuning Model

$$g_s = g_0 + \frac{\alpha A}{[(C_s - \Gamma)(1 + \frac{D_s}{D_0})]}$$

D=es(T)(1-rh).

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Around the same era Ray Leuning produced an alternative model that is a function of vapor pressure deficits. He argued that leaves respond to gradients and vpd, not RH. While he is technically correct, we can express RH in terms of D and if we argue from the perspective of parsimony the BB model has fewer unknowns. Yet, the Leuning model is a good model and a popular one.

Leuning, R. 1990. Modeling Stomatal Behavior and Photosynthesis of Eucalyptus-Grandis. Australian Journal of Plant Physiology **17**:159-175.

Mott-Parkhurst Helox Experiment

- Found that the response of stomata to D is actually a response to transpiration.
- HELOX is an inert gas with different diffusivities than air.
- By using HELOX and CO_2 rather than air and CO_2, one is able to alter the molecular diffusivities of CO_2 and H_2O
  - the ratio increased by a factor of 2.3.
- For fixed CO_2 levels, assimilation rates were 27% higher in hypostomatous and 7% higher in amphistomatous leaves.
- Does this suffer from Autocorrelation??
  - Stomatal conductance is inferred from cuvette measurements of transpiration
  - Helox gives independent set of measurements

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There is evidence that stomata respond to transpiration.

Stomatal Conductance scales with evaporation

$$g_s = a - bE$$

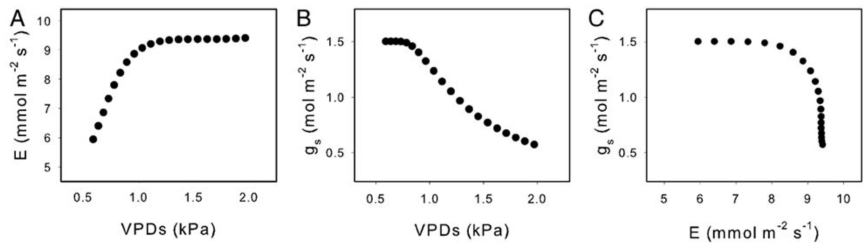
$$\frac{g_s}{g_m} = 1 - \frac{E}{E_m}$$

Pieruschka and Berry Model

$$Q_{\mathrm{abs}} = \mathrm{LW}_{\mathrm{net}} + c_{\mathrm{p}} \times g_{\mathrm{b}}(T_{\mathrm{e}} - T_{\mathrm{air}}) + \lambda \times \frac{g_{\mathrm{t}}(e_{\mathrm{s}} - e_{\mathrm{air}})}{P_{\mathrm{air}}}. \qquad \textbf{[2]}$$

$$Q_{\mathrm{abs}} \cdot m = \lambda \times \frac{g_{\mathrm{t}}(e_{\mathrm{s}} - e_{\mathrm{air}})}{P_{\mathrm{air}}} + \lambda \times k(\Psi_{\mathrm{e}} - \Psi_{\mathrm{m}}). \qquad \textbf{[3]}$$

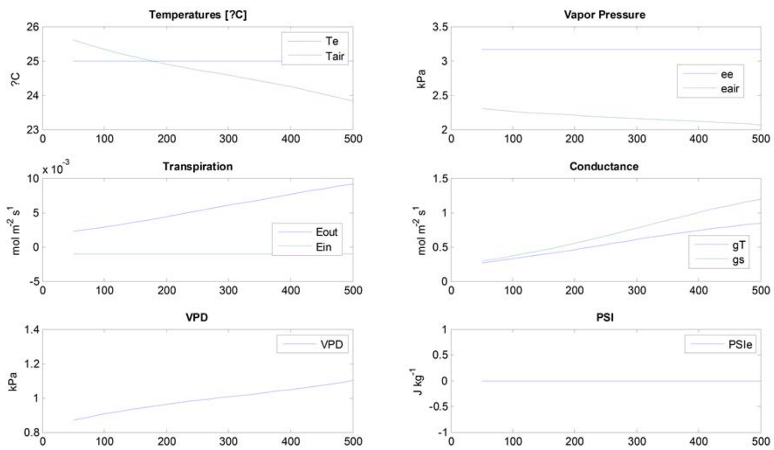
$$m = \Delta/(\Delta + \gamma)$$



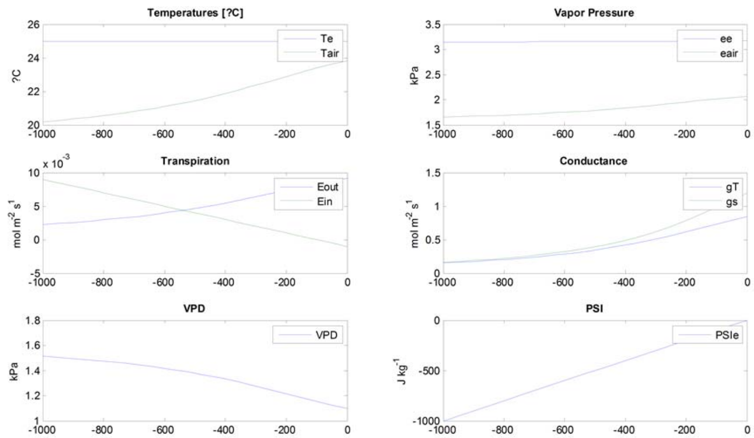
Pieruschka et al. 2010 PNAS ESPM 129 Biometeorology

Pieruschka and Berry followed up on the Mott idea with measurements based on a cold mirror and an energy balance approach

Pieruschka and Berry Model, f(Rabs), absorbed radiation



Pieruschka and Berry Model = f(water potential)



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Farquhar-Cowan Transpiration-Photosynthesis Optimization

$$\int_0^T \int_0^S (E(s,t) - \overline{E}) - \lambda(A(s,t) - \overline{A}) ds dt = \min$$

$$\frac{\partial E / \partial g_s}{\partial A / \partial g_s} = \lambda$$

$$\frac{\partial^2 E}{\partial A^2} > 0$$

Borrow Idea of Economic Minimization and Lagrange Multiplier

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Cowan and Farquhar invoked economic optimization theory.

Predicts Typical Diurnal Behavior

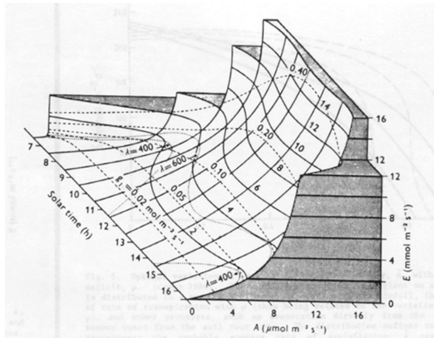

Fig. 4. Rate of transpiration, E, as a function of rate of assimilation, A, and time of day for certain assumed characteristics of leaf metabolism and environment. The magnitudes of E are indicated on the contours of the surface. The broken lines are trajectories on the surface, representing the diurnal variation of E and A for particular constant magnitudes of leaf conductance, $g_\ell (= 1/r_\ell)$. The dotted lines are trajectories for which $\partial E/\partial A = \lambda$ is constant. (Cowan and Farquhar 1977).

Shortcomings:
What value is economizing water if it can be used by its competitors?

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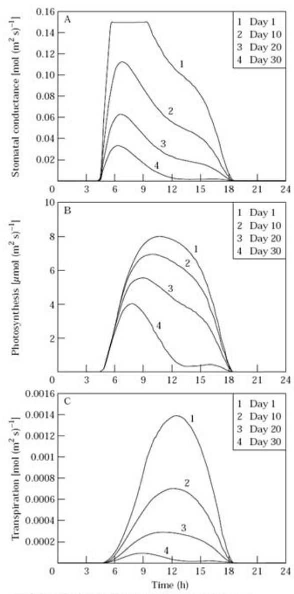
The model produces the type of behavior seen in the field. But it does not prescribe a value for lambda.

Makela Model, Optimizing stomatal conductance and soil moisture

$$\int_0^t E(t)dt < W(0)$$

$$\frac{dW}{dt} = -E(t)$$



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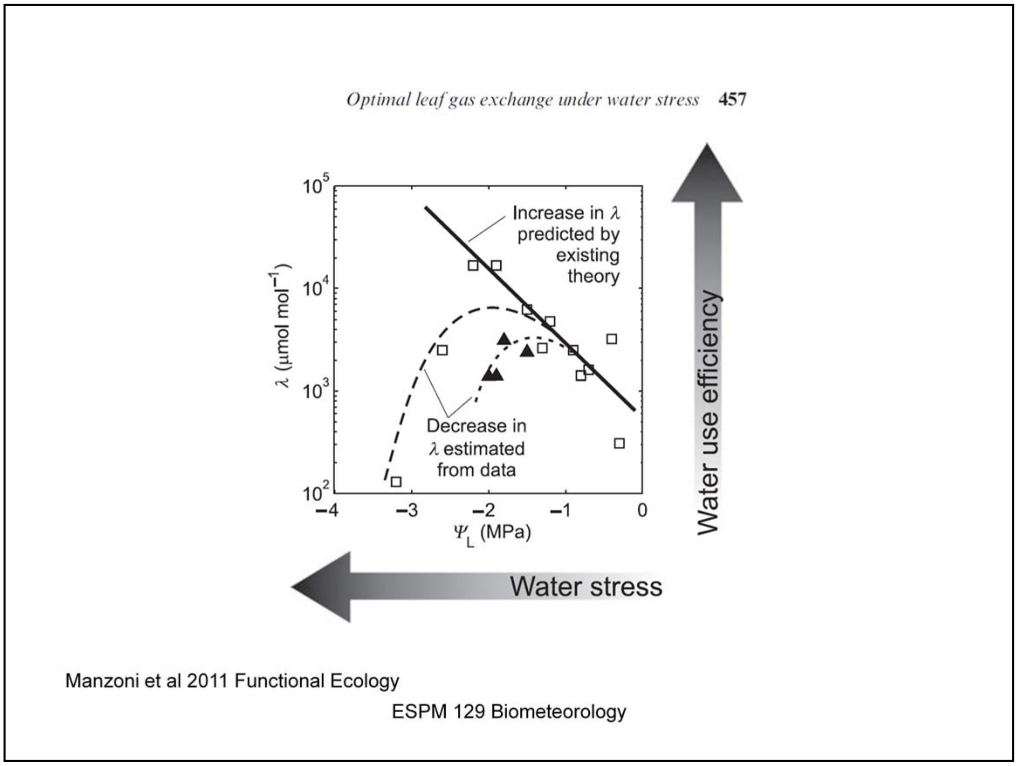
Makela and Hari took the optimization step further and invoked the soil water budget. This idea has been up followed by Manzoni, Katul and colleagues



Manzoni, S., G. Vico, G. Katul, P. A. Fay, W. Polley, S. Palmroth, and A. Porporato. 2011. Optimizing stomatal conductance for maximum carbon gain under water stress: a meta-analysis across plant functional types and climates. Functional Ecology **25**:456-467.

Analytical Equation for the Lagrange Multiplier

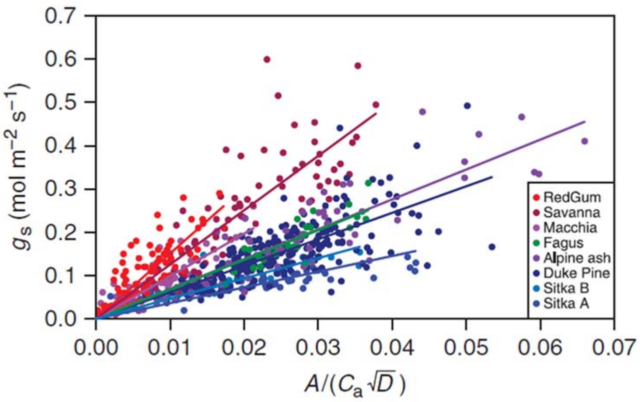
$$\lambda = \frac{(A/g_C)^2(1 + R_d/A)}{aD(c_a + R_d/g_C - \Gamma^*/\eta)} = \mathrm{WUE}^2 \frac{D\left(a + g_{W,0}/g_C\right)^2(1 + R_d/A)}{a(c_a + R_d/g_C - \Gamma^*/\eta)}.$$

A: photosynthesis; Rd: dark respiration; D: vapor pressure deficit
gc: stomatal conductance, gw: boundary layer conductance;
Gamma: CO2 compensation point, Ca: CO2

After Manzoni et al 2010

Katul, G., S. Manzoni, S. Palmroth, and R. Oren. 2010. A stomatal optimization theory to describe the effects of atmospheric CO2 on leaf photosynthesis and transpiration. Annals of Botany **105**:431-442.

Reconciling Optimal and Empirical Models



$$g_s^* \approx g_0 + \left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a}.$$

Medlyn et al 2011. Global Change Biology

Medlyn et al show that a simplied form of the optimal model looks a lot like the Ball Berry/Leuning models

Medlyn attempted to reconcile the two approaches and they yield similar functional forms.

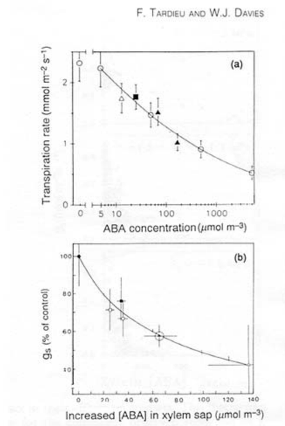
Medlyn, B. E., R. A. Duursma, D. Eamus, D. S. Ellsworth, I. C. Prentice, C. V. M. Barton, K. Y. Crous, P. De Angelis, M. Freeman, and L. Wingate. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. Global Change Biology **17**:2134-2144.

Tardieu ABA theory

$$g_s = g_{s,\min} + \alpha \exp([ABA]\beta \exp(\delta \psi_l)$$

$$J_w = \frac{(\psi_{root} - \psi_{leaf})}{R_{plant}}$$

$$[ABA] = \frac{J_{aba}}{J_w + b} = \frac{a\psi_{root}}{J_w + b}$$



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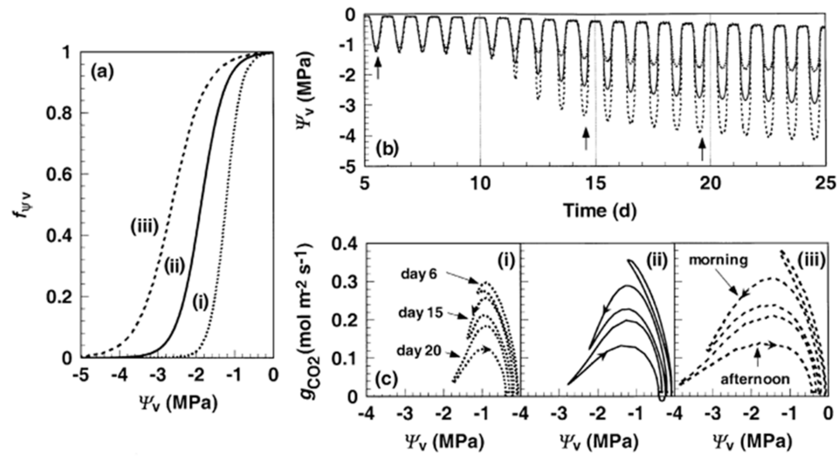
Tardieu attempted to model soil plant leaf water transport and invoke a signal from the hormone ABA

Tuzet et al



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Tuzet et al put all this together for a coupled system

Summary

- Jarvis Model
  - Multiplicative functions of environmental drivers
- Ball-Berry-Collatz + Leuning Models
  - Gs is a function of photosynthesis, relative humidity and CO2
- Mott + Pieruschka et al
  - Consider water balance of Epidermis
- Cowan Farquhar Model
  - Uses economic theory regarding minimizing water used for carbon gained.
- Hari-Makela, Katul-Manzoni, Medlyn Models
  - Considers water balance and water use efficiency
- Tardieu and Davies
  - Considers the role of ABA on stomata
- Tuzet and Leuning
  - Considered coupled plant soil system and feedbacks with water potential.