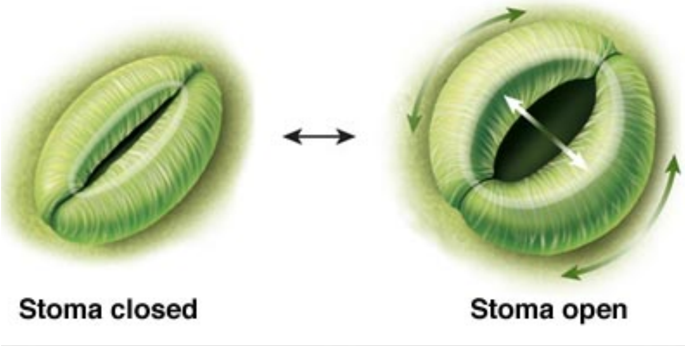
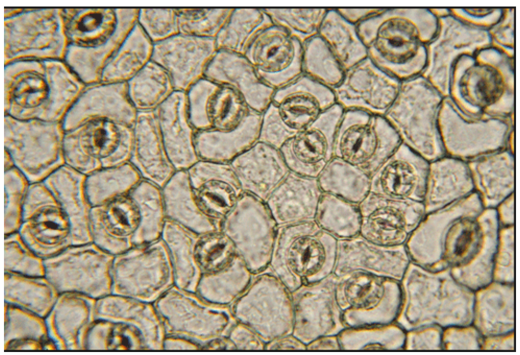
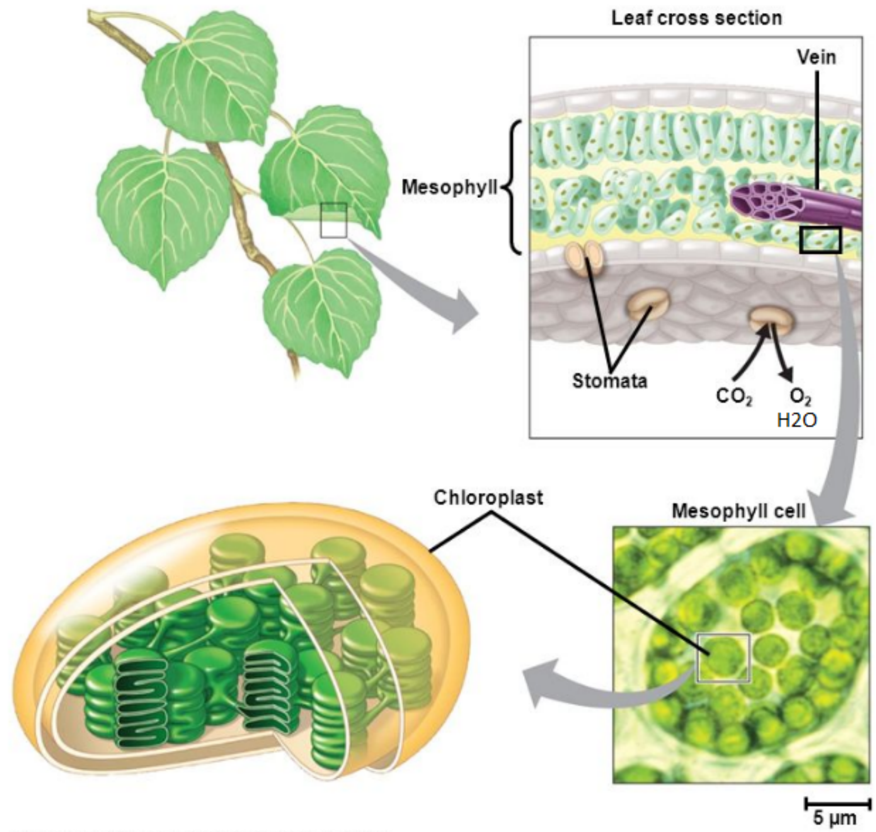
The ever-evolving suite of approaches for modeling stomatal conductance

K. Novick, Flux Course 10, July 11, 2017





Stomatal conductance (g_s) describes the “openness” of plant stoma



CO_2 travels through the stomates and the mesophyll before reaching chloroplasts in mesophyll cells.

Understanding and modeling the functioning of stomates has been an active research topic for decades. Why?

It's necessary to provide closure for the Farquhar model

The Farquhar Model (as expressed by Long & Bernacchi 2003):

$$A_c = \frac{V_{c,\max} C_i}{C_i + K_c(1 + O/K_o)}$$

$$A_p = \frac{J C_i}{4.5 C_i + 10.5\Gamma^*}$$

$$A_J = \frac{3V_{\text{tpu}}}{\left(1 - \frac{\Gamma^*}{C_i}\right)}$$

One equation, two unknowns (A, C_i)

From Fickian Diffusion, we have:

$$A = 0.6\, g_s (c_a - c_i)$$

Two equations, three unknowns (A, C_i, g_s)

If g_s is modeled or measured, we have closure.

Pop quiz: How do we measure g_s using a *LI-6400?*

Answer: From Transpiration

$$\text{Transpiration} = T_r = g_s(e_a - e_{\text{leaf}}) \approx g_s VPD$$

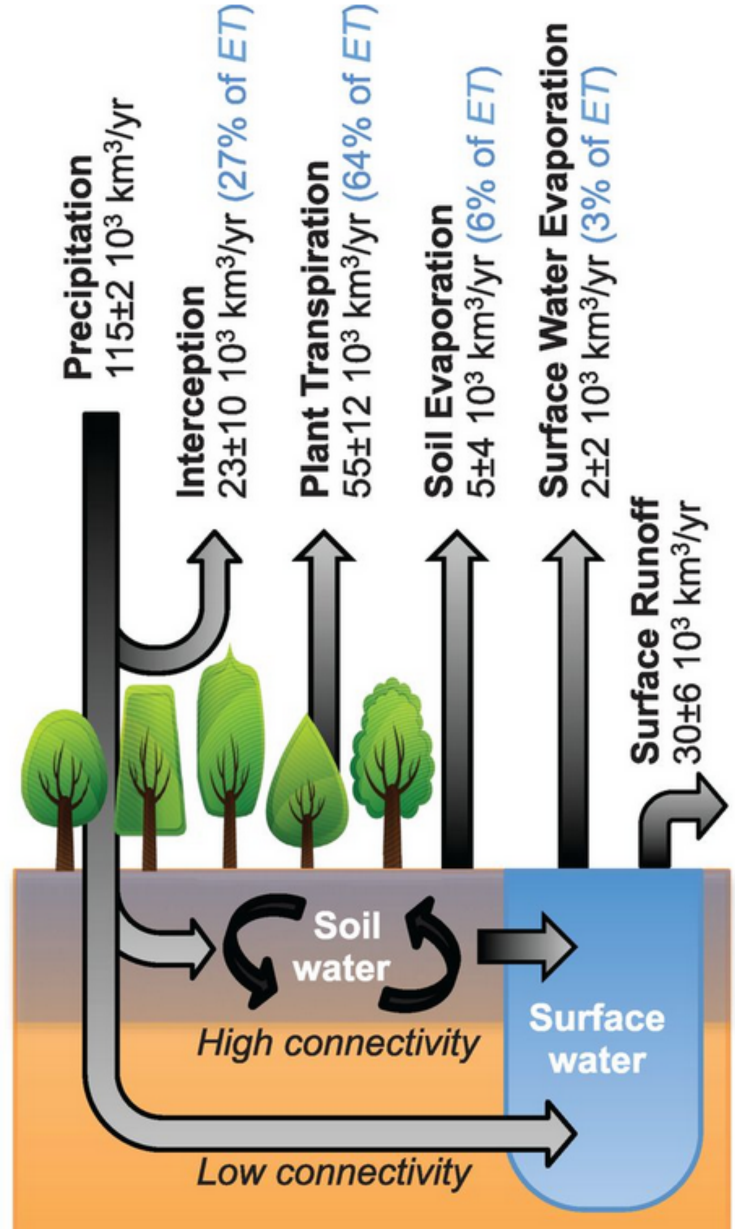
e_a = vapor pressure in air

e_i = vapor pressure in the leaf

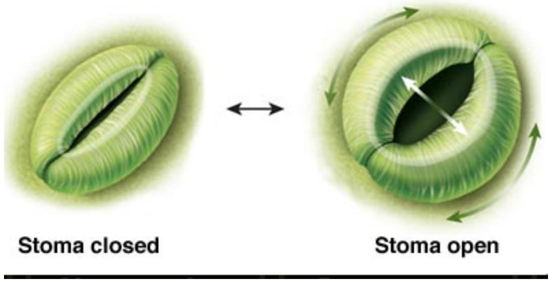
Understanding and modeling the functioning of stomates has been an active research topic for decades. Why?

Stomatal conductance drives tranpsiration– a key hydrologic cycle flux

Evapotranspiration is a cooling process – how plants use water can exert strong control on local temperature



From Good et al. *Science*, 2015



Discussion Topic: What factors determine stomatal conductance? *Think about meteorological and biological factors, and drivers that can change rapidly or slowly.*

Meteorological:

Soil moisture
Vapor pressure deficit (VPD)

Stomates close when water is limiting

Temperature
Light
CO_2

Stomatal functioning is linked to photosynthesis

Structure/Physiological:
LAI (determines canopy-level G_s)

Canopy height (g_s *decreases with* h)
Xylem Conductivity (K)
Xylem vulnerability to cavitation

Plant hydraulics

hy·drau·lics
/hīˈdrôliks/

noun

1. the branch of science and technology concerned with the conveyance of liquids through pipes and channels, especially as a source of mechanical force or control.

What is Vapor Pressure Deficit?
(Usually represented as VPD or *D*)

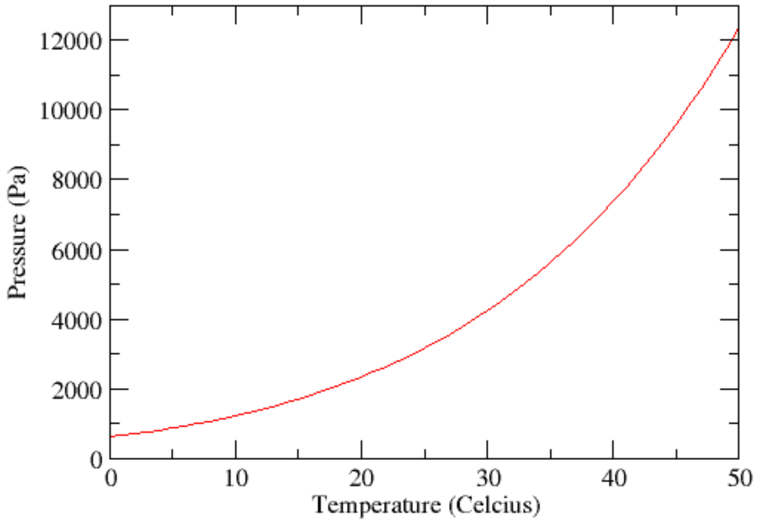
Think of it as how much room there is in the atmosphere for more water vapor

When RH = 100%, VPD = 0 kPa. As humidity declines, VPD increases.

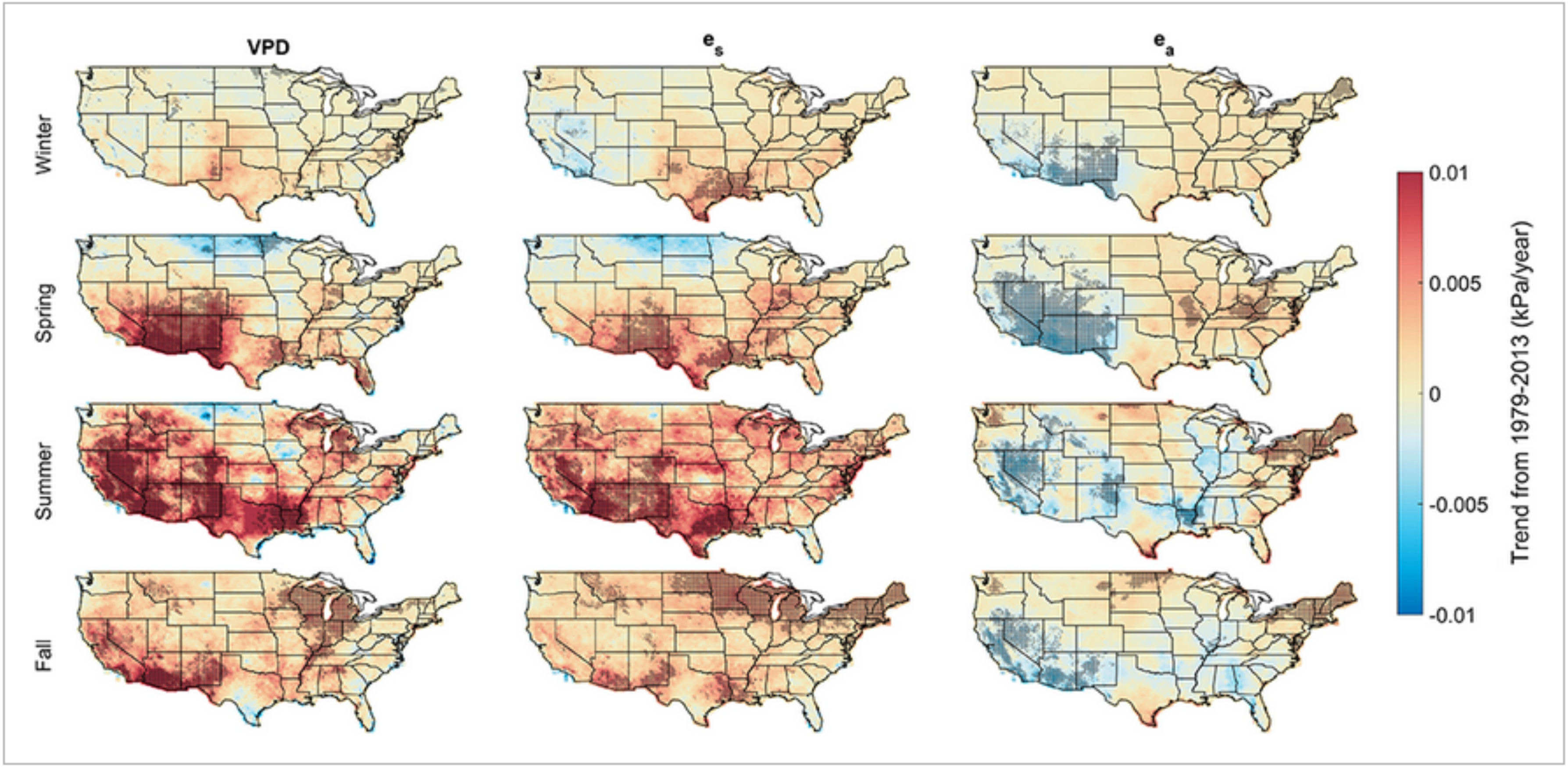
It is the difference between the saturation vapor pressure (e_s) and the actual vapor pressure deficit (e_a). VPD = $e_s - e_a$.

The saturation vapor pressure is exponentially related to temperature.

$$e_s = \exp\left(\frac{17.27T}{T + 237.3}\right)$$

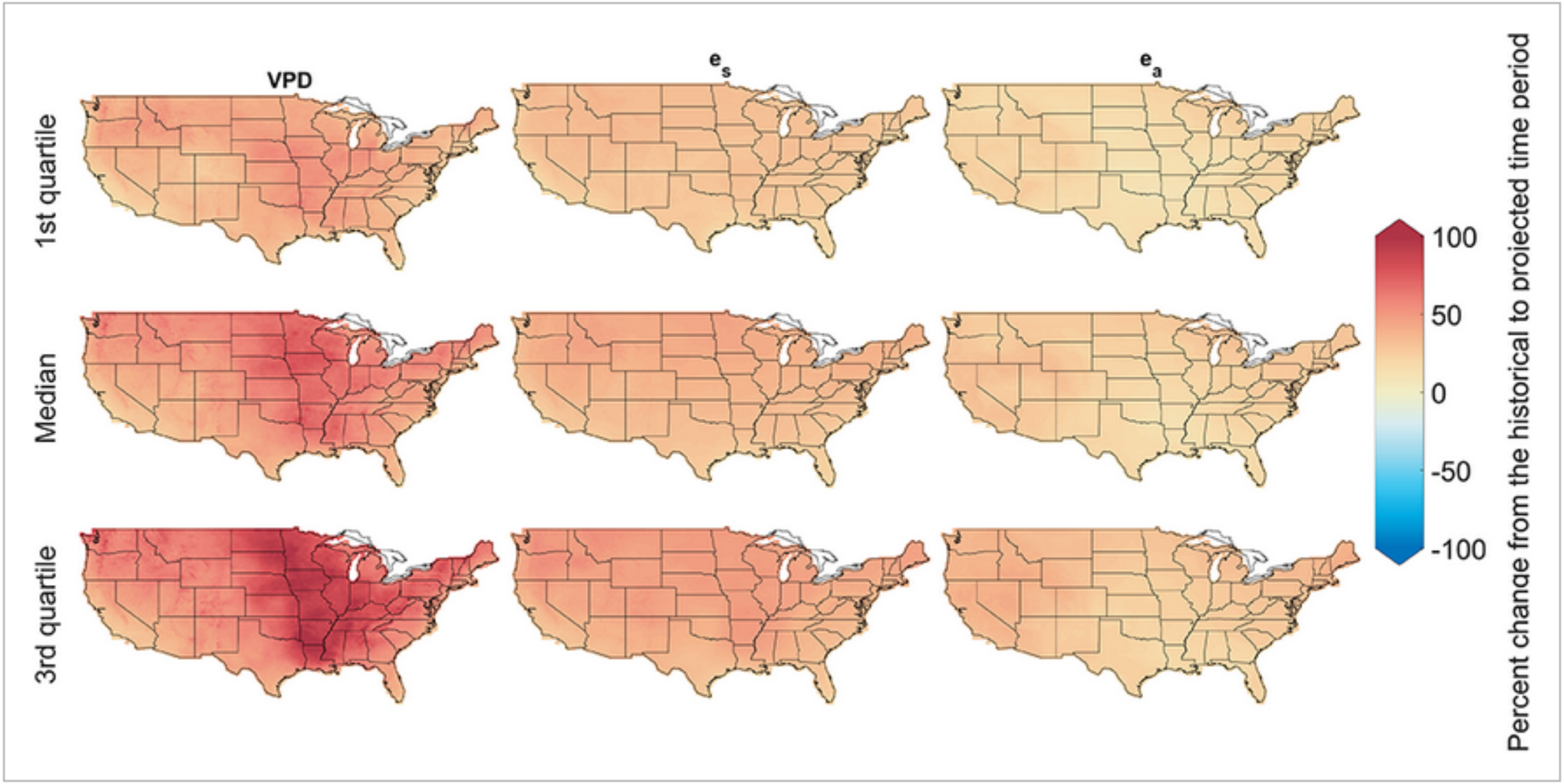


Historically, It's been rising in many places, especially during the summer…



Ficklin & Novick 2017

And is projected to rise nearly universally in the future



Comparing historic (1979-2013) to future (2065-2099) VPD, Ficklin & Novick 2017

Some widely used models for g_s

Ball-Berry Model (see Collatz et al. 1991):

$$g_s = m\frac{A \cdot RH}{c_s} + b$$

c_s is CO_2 concentration at the leaf surface, c_s ~ c_a if leaf boundary layer conductance is high

Leuning model (Leuning, 1995)

$$g_s = \frac{m_2 A}{c_s - \Gamma}\left(1 + \frac{D}{D_o}\right)^{-1} + b_2$$

Γ is the CO_2 compensation point. M_2, D_o, and b_s are constants

What's missing from these models?

Hydraulics
Soil moisture (comes in empirically through a parameter that can reduce *A*)
Also, RH/VPD sensitivity is highly empirical

The evidence is mounting that Ball-Berry and Leuning Type models do not perform particularly well during drought conditions. Their theoretical basis is also questioned.

Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum

G. B. Bonan[1], M. Williams[2], R. A. Fisher[1], and K. W. Oleson[1]

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[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK

The performance of the SPA stomatal model was … significantly better than the CLM Ball–Berry model **when there was soil moisture stress.**

Global Change Biology (2011) 17, 2134–2144, doi: 10.1111/j.1365-2486.2010.02375.x

Reconciling the optimal and empirical approaches to modelling stomatal conductance

BELINDA E. MEDLYN*, REMKO A. DUURSMA†, DEREK EAMUS‡, DAVID S. ELLSWORTH†, I. COLIN PRENTICE*, CRAIG V. M. BARTON§, KRISTINE Y. CROUS¶, PAOLO DE ANGELIS‖, MICHAEL FREEMAN** and LISA WINGATE††

[B]ecause these stomatal conductance models are **empirical, their parameters have no meaning attached….acclimation and adaptation**

Review New Phytologist

Tansley review

What plant hydraulics can tell us about responses to climate-change droughts

Author for correspondence:

John S. Sperry and David M. Love

Empirical functions … lack the predictive power of a physically constrained equation... As a result, **capturing the drought response has proven difficult** for ecosystem models.

Research New Phytologist

Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought

Thomas L. Powell[1], David R. Galbraith[2,3], Bradley O. Christoffersen[4], Anna Harper[5,6], Hewlley M. A. Imbuzeiro[7], Lucy Rowland[8], Samuel Almeida[9], Paulo M. Brando[10], Antonio Carlos Lola da Costa[11], Marcos Heil Costa[7], Naomi M. Levine[1], Yadvinder Malhi[3], Scott R. Saleska[4], Eleneide Sotta[12], Mathew Williams[8], Patrick Meir[8] and Paul R. Moorcroft[1]

Model predictions agreed with the observed C fluxes in the control plots of both experiments, **but poorly replicated the responses to the drought** treatments.

Stomatal Function across Temporal and Spatial Scales: Deep-Time Trends, Land-Atmosphere Coupling and Global Models[1][OPEN]

Peter J. Franks*, Joseph A. Berry, Danica L. Lombardozzi, and Gordon B. Bonan

Less is known about how to represent stomatal closure in dry soils…there is considerable **ongoing model development to implement** … the effects of **plant hydraulic** stress on stomata

Two active paths towards next generation models for stomatal conductance:

Plant Hydraulics

Stomatal Optimization Theory

A Plant Hydraulics View of stomatal function

An Ohm's law analogy for plant water flow through a plant

$$\mathrm{T} = g_s \cdot VPD = K(\Psi_S - \Psi_L - pgh)$$

$$g_s = \frac{K(\Psi_S - \Psi_L - pgh)}{VPD}$$

T = transpiration

g_s = stomatal conductance

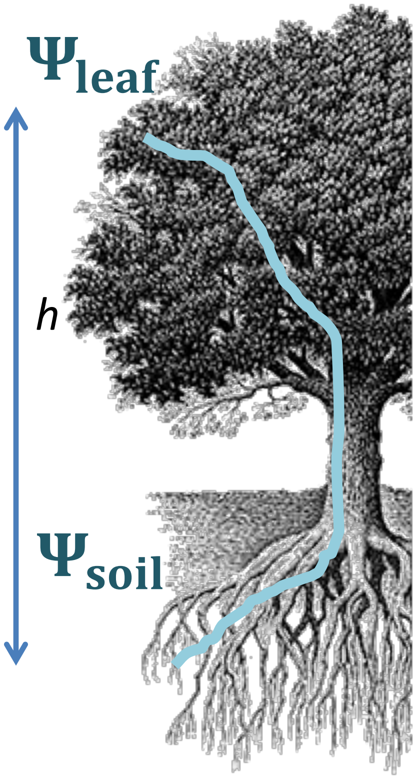
Ψ_s = soil water potential

Ψ_L = leaf water potential

K = hydraulic conductivity

VPD = vapor pressure deficit

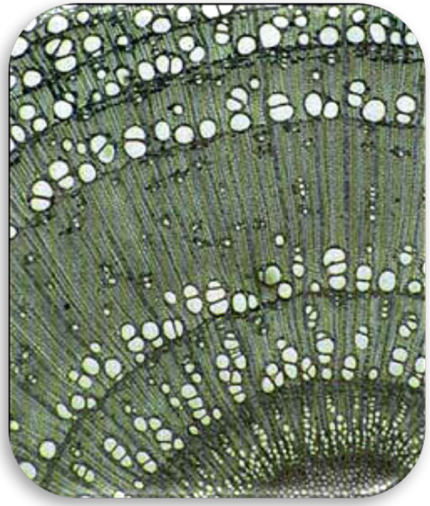
Stomatal conductance depends on both soil water status and VPD!



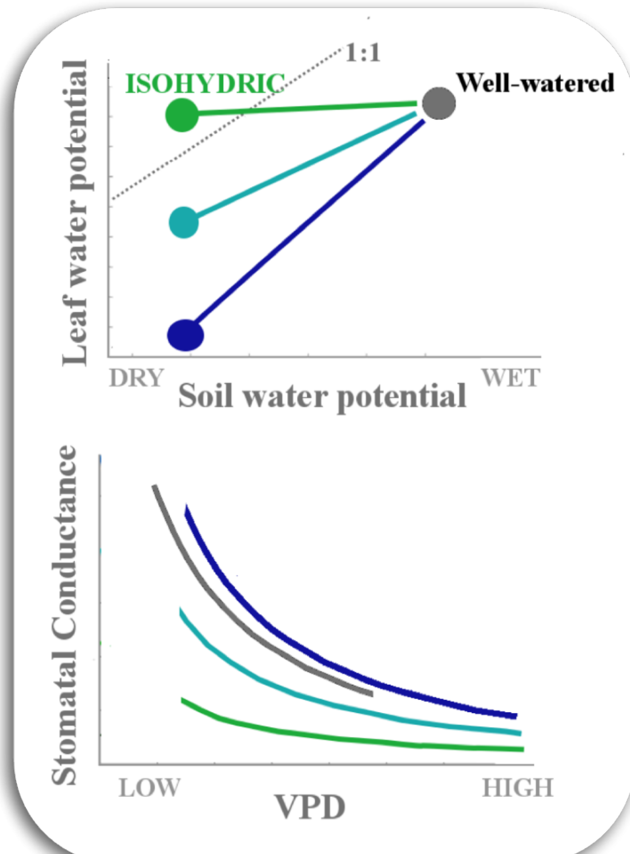
As soil dries, or D increases, Ψ_L must decrease (become more negative) to sustain g_s.

$$g_s = \frac{K(\Psi_S - \Psi_L - pgh)}{VPD}$$

This is a dangerous operation for the tree!



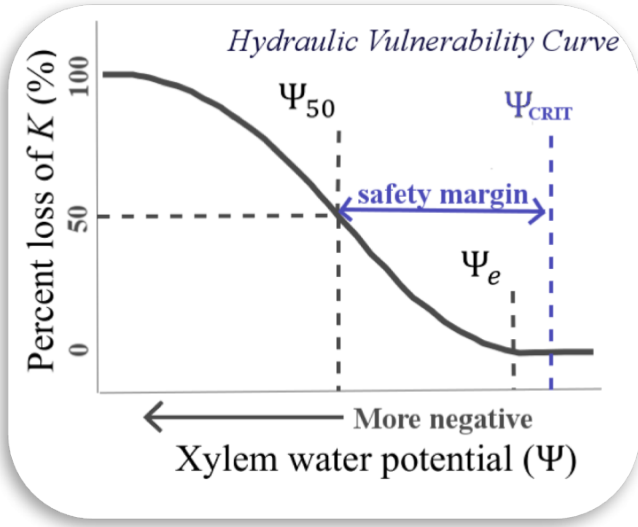
http://nhm.ac.uk/resources-rx/images

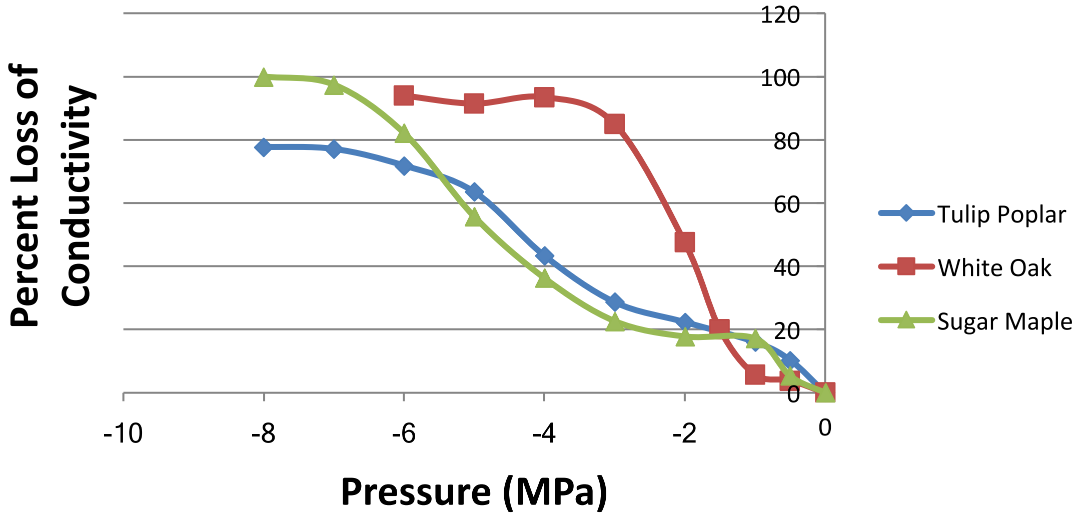


Isohydric trees maintain relatively constant leaf water potential…conductance declines rapidly

Anisohydric trees allow leaf water potential to fall…incurring risk of cavitation

Generally believed that degree of isohydricity is linked to xylem vulnerability





Generally, it is believed that plants **with more vulnerable xylem are more isohydric**

Consider a prototypical isohydric species (Pinyon pine) and anisohydric species (Juniper) growing in the American Southwest:

Isohydric Pinyon pine is associated with **more vulnerable xylem** and **smaller safety margins** when compared to **anisohydric** Juniper

McDowell et al. (2008), Plaut et al. (2012)

But there is emerging evidence that this is not the case in some wetter climates.

$$g_s = \frac{K(\Psi_S - \Psi_L - pgh)}{VPD}$$

Using a hydraulic model requires:

- Soil water potential (can be modeled, with great uncertainty, from soil moisture)
- VPD
- Canopy height
- Hydraulic conductivity: $K = \frac{k_S A_S}{A_L h}$
- k_s = instrinsic conductivity…decreases if cavitation occurs
- A_s:A_L = ratio of sapwood to leaf area

- Leaf water potential Ψ_L (could be presumed as a function of Ψ_S reflecting the degree of isohydricity, see also Sperry & Love 2015)

- Vulnerability curves (to determine loss of k_s)

What’s missing?

photosynthesis

Stomatal optimization models assume that plants have evolved to maximize carbon uptake while minimizing water loss.

$$F = A - \mathrm{mWUE} \times T_r$$

Farquhar model for A
Diffusion analogies for A and T_r

$$F = f(g_s)$$

Optimal g_s is the g_s when $dF/dg_s = 0$.

The approach is not new (Cowan & Farquhar 1977, Cowan 1986, Berninger & Hari 1993, Katul et al. 2009, Medlyn et al. 2011, 2012, Bonan et al. 2014, Sperry et al. 2016, Novick et al. 2016)

$$g_s^* \approx g_0 + 1.6\left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a}$$

Global Change Biology

Global Change Biology (2011) 17, 2134–2144, doi: 10.1111/j.1365-2486.2010.02375.x

Reconciling the optimal and empirical approaches to modelling stomatal conductance

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Global Change Biology

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Corrigendum

Reconciling the optimal and empirical approaches to modelling stomatal conductance

Belinda E. Medlyn, Remko A. Duursma, Derek Eamus, David S. Ellsworth, I. Colin Prentice, Craig V. M. Barton, Kristine Y. Crous, Paolo de Angelis, Michael Freeman, Lisa Wingate

First published: 4 October 2012 Full publication history

$$g_s{}^* \approx g_0 + 1.6\left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a}$$

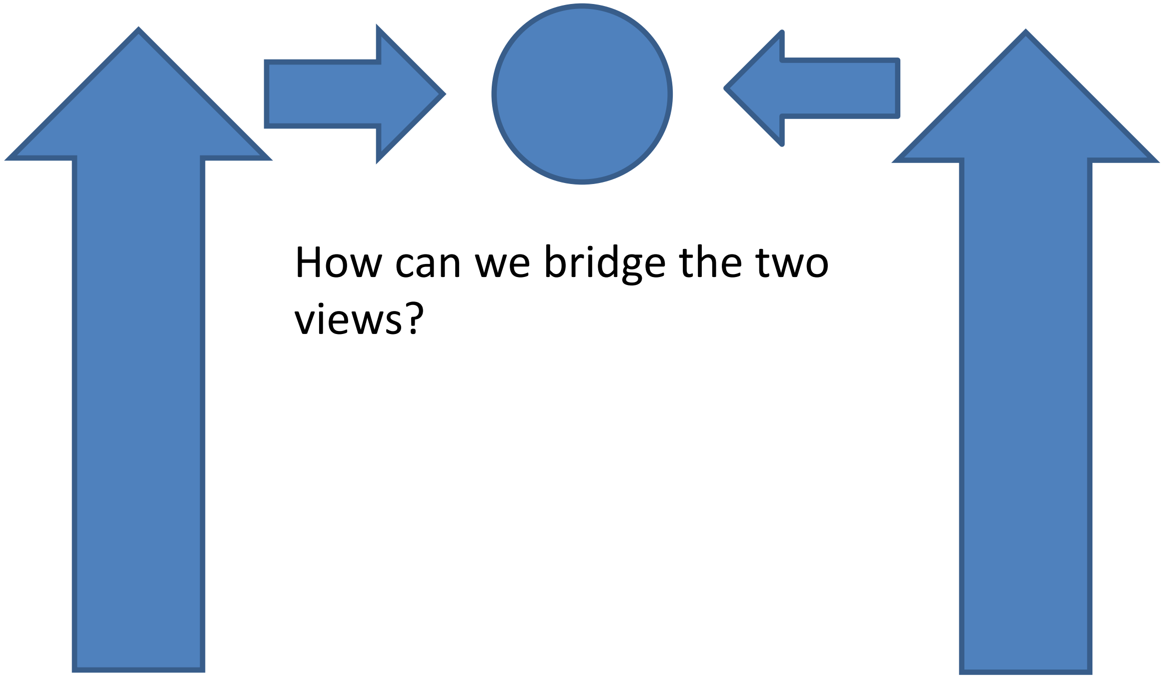
The g_1 parameter is sometimes called the 'marginal water use efficiency.' It is believe to be constant over the course of a day, but to increase as drought develops

Getting the temporal variability of g_1 right is a key challenge in implementing these models

What's missing?

Plant hydraulics
Soil moisture dependence is not explicit
Major advancement is that the vapor pressure dependence is theoretical, not empirical

Two paths towards next generation models for stomatal conductance:



Plant Hydraulics	Stomatal Optimization Theory

Plant Hydraulics

Pros:
- Incorporate structural controls on g_s
- Theoretical approach for modeling soil moisture dependencies

Cons:
- No photosynthesis
- Getting leaf water potential right is hard

Stomatal Optimization Theory

Pros:
- Theoretical formulation for VPD dependency
- Elegant

Cons:
- No hydraulics
- Getting g_1 right is hard

How can we bridge the two views?

Geosci. Model Dev., 7, 2193–2222, 2014
www.geosci-model-dev.net/7/2193/2014/
doi:10.5194/gmd-7-2193-2014

Geoscientific Model Development
Open Access

Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum

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[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK
Correspondence to: G. B. Bonan (bonan@ucar.edu)

Plant, Cell & Environment
Plant, Cell and Environment (2016) **39**, 583–596 doi: 10.1111/pce.12657

Original Article

Drought limitations to leaf-level gas exchange: results from a model linking stomatal optimization and cohesion–tension theory

Kimberly A. Novick[1], Chelcy F. Miniat[2] & James M. Vose[3]

Conductance is estimated from optimality but with the constraint that leaf water potential can not dip below some minimum value

Plant, Cell & Environment
Plant, Cell and Environment (2017) **40**, 816–830 doi: 10.1111/pce.12852

Original Article

Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost

John S. Sperry[1], Martin D. Venturas[1], William R. L. Anderegg[1], Maurizio Mencuccini[2,3], D. Scott Mackay[4], Yujie Wang[1] & David M. Love[1]

The marginal water use efficiency parameter (e.g. g_1) is linked to xylem vulnerability.

So, I need a model of stomatal conductance for my site…which should I choose?

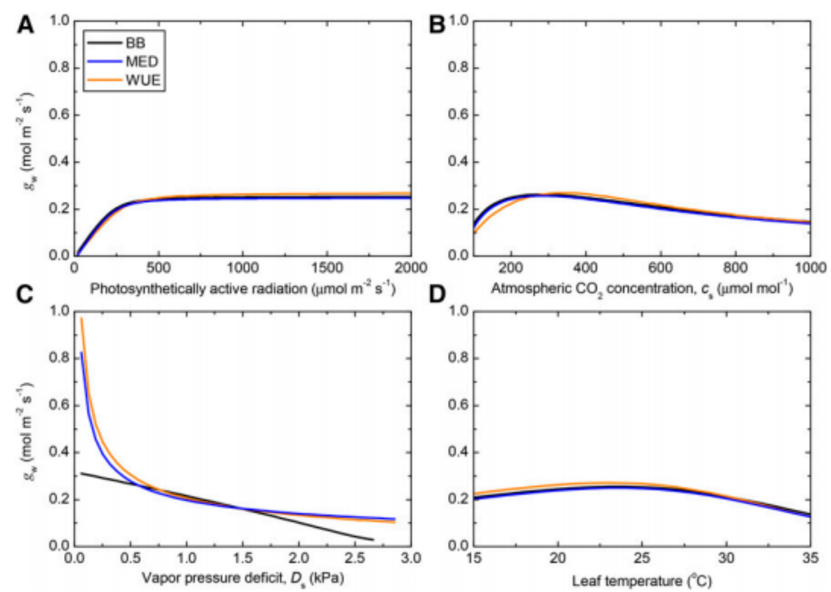
Depends on the application…don't choose one that's 'missing' some key driver from the perspective of your research questions.

Ball-Berry and Leuning models remain good choices while the community is sorting out the details of the next-generation optimality/hydraulics models.

Also, keep in mind that you can derive an estimate of canopy-scale stomatal conductance from flux tower data by inverting the Penman-Monteith Equation (more on that on Friday).

Franks et al. 2017

Figure 5. Using comparable g_1 and g_{1M} values results in similar outputs for the BB and MED models. Conditions were as in Figure 4, but with g_{1M} = 2.8 $(kPa)^{0.5}$ for MED and λ = 0.714 mmol water μmol^{-1} CO_2 for WUE.



Penman – Monteith (1965): ET from a vegetated surface

$$ET = \frac{\Delta(R_N - G) + c_p \rho_a g_a D}{\lambda \rho_w \left[\Delta + \gamma \left(1 + \frac{g_a}{g_c}\right)\right]}$$

g_a = aerodynamic conductance = $\frac{ku^*}{ln\left(\frac{z-d}{z_h}\right)+\Psi_h}$

g_c = total surface conductance = incorporates soil and plant conductances

D = vapor pressure deficit

$R_N - G$ is the available radiation

Surface conductance is best representative of stomatal conductance when soil evaporation is minimal, and conditions are well mixed.

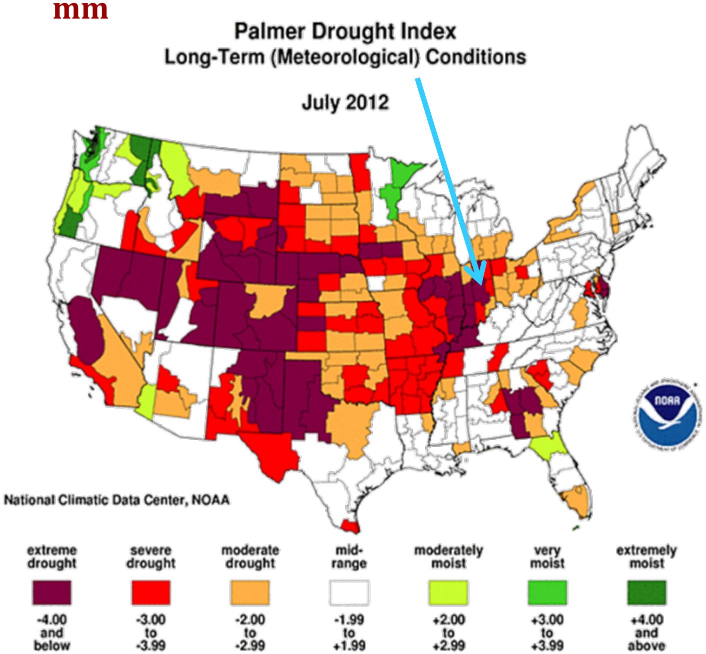
Modeling stomatal conductance during the course of a severe drought event at Morgan Monroe State Forest – a practical exercise

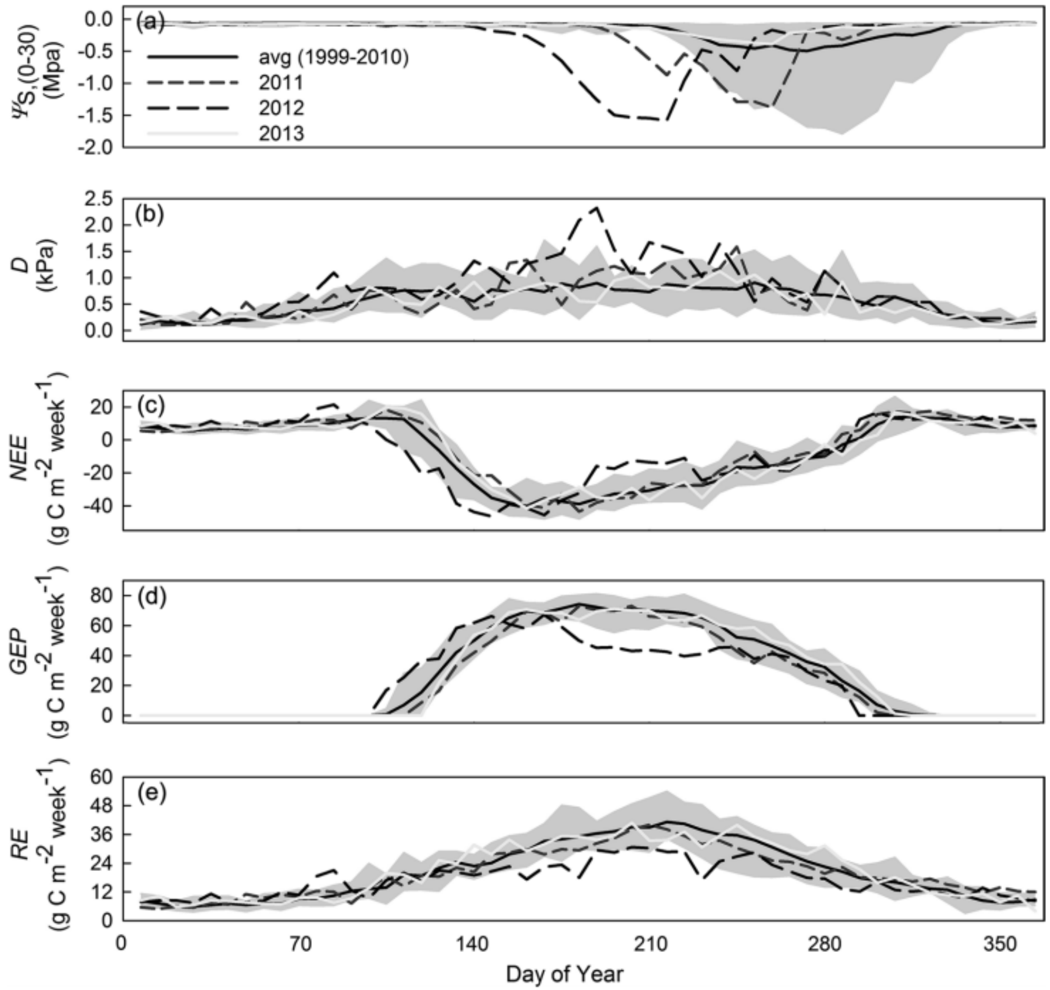
Roman et al. 2015

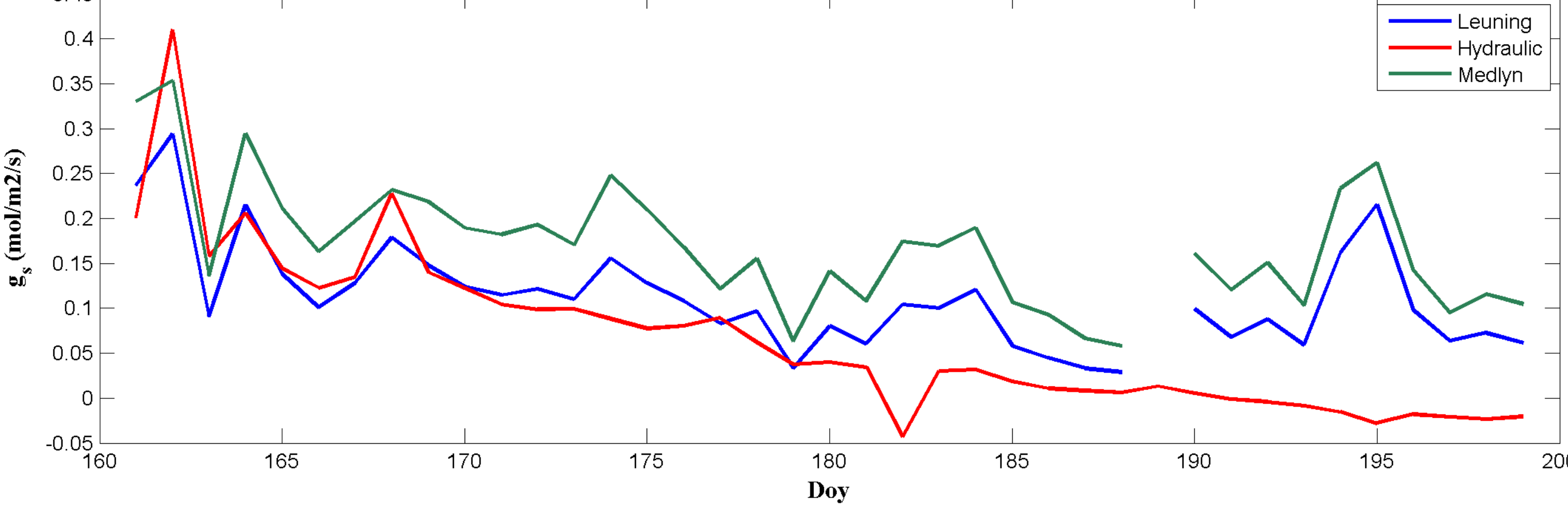
In **Morgan-Monroe State Forest in 2012**:

Long-term mean rainfall for June & July: **243 mm**

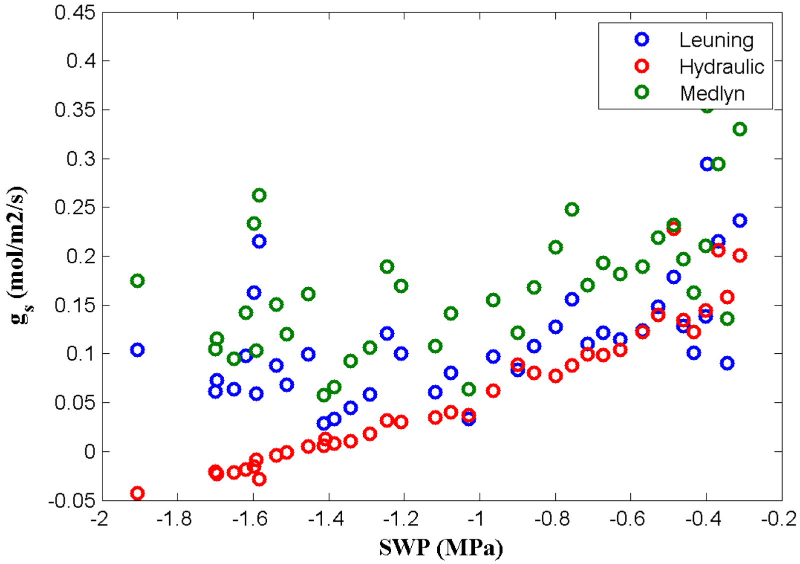
Total Rainfall in June & July of 2012: **23 mm**



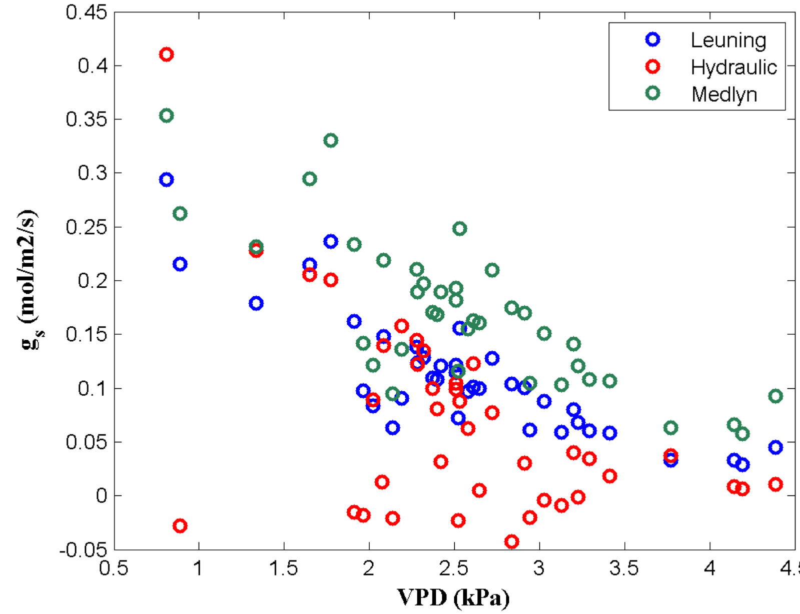




Leuning
Hydraulic
Medlyn
g_s (mol/m2/s)
Doy



Leuning
Hydraulic
Medlyn
g_s (mol/m2/s)
SWP (MPa)



Leuning
Hydraulic
Medlyn
g_s (mol/m2/s)
VPD (kPa)