Lecture 7:
Leaf Energy Balance, Photosynthesis and Respiration Models

Dennis Baldocchi
ESPM 228
Leaf Energy Balance

\[ R \downarrow \quad L \downarrow \quad R \uparrow \quad L \uparrow \quad \lambda E \]

- \( R \): is shortwave solar energy, W m\(^{-2}\)
- \( L \): is Longwave, terrestrial energy, W m\(^{-2}\)
- \( \lambda E \): Latent Heat Flux Density, W m\(^{-2}\)
- \( H \): Sensible Heat Flux Density, W m\(^{-2}\)
Net Radiation Balance of a Leaf

\[ R_n = R_B - R_A - L_B - L_A = H + \lambda E \]

- \( R \): Shortwave solar energy, W m\(^{-2}\)
- \( L \): Longwave, terrestrial energy, W m\(^{-2}\)
- \( \lambda E \): Latent Heat Flux Density, W m\(^{-2}\)
- \( H \): Sensible Heat Flux Density, W m\(^{-2}\)
Leaf Energy Balance, Wet, Transpiring Leaf

\[ R_n = H + \lambda E \]

Net Radiation is balanced by the sum of Sensible and Latent Heat exchange

\[ Q = (1 - \rho)R_B + \varepsilon L_B = \varepsilon \sigma T_i^4 + H + \lambda E \]
Leaf resistance/conductance for water vapor, $g_w$

$$r_a + r_s = \frac{1}{g_{av}} + \frac{1}{g_s} = \frac{g_{av} + g_s}{g_{av}g_s} = \frac{1}{g_w}$$

- Boundary layer resistance, $r_a$
- Stomatal resistance, $r_s$  
  \[ r, \text{s/m} \]
- Boundary layer conductance, $g_{av}$ 
  \[ g, \text{m/s} \]
- Stomatal conductance, $g_s$
Various Forms of resistance Equations for LE

\[ \dot{E} = \frac{(m_v / m_a) \lambda \rho \alpha g_w (e_s(T) - e_a)}{P} \]

\[ = \frac{(m_v / m_a) \lambda \rho \alpha (e_s(T) - e_a)}{P \left( g_{sv} + g_s \right)} \]

\[ = \frac{(m_v / m_a) \lambda \rho \alpha (e_s(T) - e_a)}{P(r_s + r_a)} \]
Linearize with 1st order Taylor’s Expansion Series

\[ f(x) \sim f(x_0) + (x - x_0) \frac{df}{dx} \]

\[ \varepsilon \sigma T_l^4 = \varepsilon \sigma T_a^4 + 4 \varepsilon \sigma T_a^3 (T_l - T_a) \]
Linearize the Saturation Vapor Pressure function

\[ e_s(T_i) = e_s(T_a) + e_s'(T_i - T_a) \]

\[ e_s'(T) = \frac{d e_s(T)}{d T} \]

\[ e_s(T_i) = e_s(T_a) + e_s'(T_i - T_a) + \frac{e_s''}{2}(T_i - T_a)^2 \]

\[ e_s''(T) = \frac{d^2 e_s(T)}{d T^2} \]
Derivation

1: Leaf Energy Balance

\[ R_n = H + \lambda E \]

2: Resistance
Equations for H
and \( \lambda E \)

\[ \lambda E = \frac{(m_1 / m_2) \lambda \rho_s g_a (e_s(T_s) - e_v)}{P} \]
\[ H = \rho_s C_p (T_i - T_a) g_a \]

3: Linearize \( T^4 \) and \( e_s(T) \)

\[ e_s(T_i) - e_v = D + e_s'(T_i - T_a) \frac{\lambda E \cdot P}{\rho_s \lambda (m_1 / m_2) g_a} \]
\[ \varepsilon \alpha T_i^4 = \varepsilon \alpha T_a^4 + 4 \varepsilon \alpha T_a^3 (T_i - T_a) \]
Shake and Bake:
Substitute and Manipulate

\[ e_c(T_f) - e_a = D + e^*(T_f - T_i) = \frac{\lambda E \cdot P}{\rho_w} \cdot \frac{\lambda (m_c/m_i) g_w}{P} \]

\[ \lambda E = \rho_w (m_c/m_i) \lambda g_w (D + e^*(T_f - T_i)) \]

\[ T_f - T_i = \Delta T = \frac{\lambda E v}{s \rho_w C_p g_w} - \frac{D}{s} \]

\[ \lambda E = R_u - (\frac{\lambda E v}{s \rho_w C_p g_w} - \frac{D}{s}) \rho_w C_p g_s \]

\[ \lambda E (1 + \frac{\rho_h}{s g_w}) = R_u + \frac{D \rho_w C_p g_s}{s} \]

\[ \lambda E = \frac{s R_u + D \rho_w C_p g_h}{(s + \gamma \frac{g_h}{g_w})} \]

ESPM 129 Biometeorology

11
Analytical Solution to Surface Energy Balance

$$a\lambda E^2 + b\lambda E + c = 0$$

Quadratic Eq

$$y = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

Coefficient:

$$a = \frac{\rho \lambda \varepsilon_m(T)}{2m \varepsilon(T) \frac{d^2 \varepsilon}{dT^2}}$$

$$b = -2 \gamma - \alpha T_\text{eq} + \frac{\rho \lambda \varepsilon_m(T)}{m \frac{d \varepsilon}{dT}} + 4 \alpha \varepsilon(T)$$

$$c = \frac{\rho \lambda \varepsilon_m(T)}{2m \varepsilon(T) \frac{d^2 \varepsilon}{dT^2}} \left(2 \gamma - 2 \alpha \varepsilon(T) + 4 \alpha \varepsilon(T) \right)$$

LE Penman Flux, simplified

0 100 200 300 400 500 600

LE quadratic (W/m²)

0 100 200 300 400 500 600

LE quadratic (W/m²)
Here we look at model computations of latent heat exchange, which is the evaporation rate (E) times the latent heat of evaporation, vs the humidity deficit between the leaf and air, so we compute $\Delta h$ as a function of the leaf temperature, Tsfc. These calculations are based on a coupled model that considers leaf energy balance and coupling between stomatal conductance and photosynthesis.

For low humidity deficits, an increase in this difference drives the potential for evaporation and rates of evaporation INCREASE. This is what one would expect simply looking at the Ohms Law analog for evaporation. But real evaporation is more complex. There are other biophysical factors that act to restrict evaporation as humidity deficits get greater and greater.

At intermediate humidity deficits a peak rate in evaporation is reached and then evaporation rates DECREASE with additional increases in humidity deficits. Why?


As we will see below, stomatal conductance is also a function of humidity deficits, which impacts further changes in evaporation as the air dries.

And what is neglected in this simple scheme and model are feedbacks between the humidification of the atmosphere and its further impact on evaporation. Think is a still air with little mixing, evaporation causes the humidity of the air to increase, decreasing humidity deficits and acting to retard further changes in evaporation.
Together we can see that LE is low at highest stomatal conductances because humidity deficits are smallest and LE is low at lowest stomatal conductances because they restrict water loss. LE is optimal at intermediate humidity deficits and stomatal conductances.

These results may seem counter intuitive, but this is why we need theory and models to understand and explain the complex behavior we observe in nature. The problem I see and have is that too often this problem is tackled with over simplified models that do not consider the interactions and feedbacks (whether negative or feedforward) that we see here.
Part of the explanation for LE decreasing with increasing vapor pressure deficit, a stronger potential driver of evaporation, is because stomata conductance also decrease with increasing humidity deficits. This is because guard cells will lose water too, become flaccid and close in dry air.
Photosynthesis: A balance between Supply and Demand

- Biochemical limitation: carboxylation rate
  - Light limitation
  - Enzyme limitation
- Physical limitation: delivery of CO₂ to leaf
  - Diffusion through Leaf Boundary Layer
  - Diffusion through Stomatal Pores
  - Potential Gradient between free Atmosphere and substomatal Cavity

ESPM 111 Ecosystem Ecology
The enzyme ribulose-1,5-bisphosphate carboxylase (rubisco) catalyzes the addition of gaseous carbon dioxide to ribulose-1,5-bisphosphate (RuBP). Product of the reaction are two molecules of 3-phosphoglyceric acid.

\[
C_5O_3H_8(PO_4^{2-})_2 + CO_2 \rightarrow 2 C_3O_3H_4PO_4^{2-}
\]
Using Solar Energy for Life

Light ('Hill') Z Reactions:
PS II and Ps I

- Visible solar energy (400 to 700 nm) is absorbed by pigments.
- This energy is converted into high energy compounds, ATP and NADPH, by photosystems II and I (PS II and I).
  - Photosystem II uses 680 nm energy to generate ATP (non-cyclic electron transport).
  - PS I uses 700 nm solar energy to generate NADPH (cyclic electron transport).
  - Excess energy is lost as heat or fluorescence.
- 8 Photons per CO₂ molecule fixed.

Allen and Martin, 2007 Nature

simplify
Photosynthesis is a function of the rate of carboxylation when ribulose bisphosphate (RuBP) is saturated, and the carboxylation rate when RuBP regeneration is limited by electron transport.
The enzyme ribulose-1,5-bisphosphate carboxylase (rubisco) catalyzes the addition of gaseous carbon dioxide to ribulose-1,5-bisphosphate (RuBP). Product of the reaction are two molecules of 3-phosphoglyceric acid.

\[ \text{C}_5\text{O}_3\text{H}_8(\text{PO}_4^{2-})_2 + \text{CO}_2 \rightarrow 2 \text{C}_3\text{O}_3\text{H}_4\text{PO}_4^{2-} \]
Network for CO2 Diffusion into a Leaf

Flexas et al 2007 PCE
Gaastra’s (1958) Resistance model for Photosynthesis

\[ A = \frac{(C_a - C_i)}{r_{\text{leaf}} + r_{\text{mesophyll}} + r_{\text{chloroplast}}} \]
Michaelis-Menten Type Models for Photosynthesis

\[ P = \frac{P_{\text{max}}}{1 + \frac{K}{C}} = \frac{C \cdot P_{\text{max}}}{C + K} \]

K is the C at \( \frac{1}{2} P_{\text{max}} \)
Simple Light Model for Photosynthesis

\[ P = \frac{\alpha \cdot I \cdot P_{\text{max}}}{\alpha \cdot I + P_{\text{max}}} \]

\[ P = \frac{1}{2\theta} \left\{ \alpha \cdot I + P_{\text{max}} - \left[ \left( \alpha \cdot I + P_{\text{max}} \right)^2 - 4\theta \alpha \cdot I \cdot P_{\text{max}} \right]^{1/2} \right\} \]
Photosynthesis is a Balance between Metabolic Demand and Diffusive Supply

Get slides from Jessica Ci vs Cc etc
In this case we assume that the rate of uptake, \( v \), is positive, causing us to put a negative sign for the supply term.

\[
\begin{align*}
\nu &= \frac{v_{\text{max}} C}{K + C} = -\frac{C_a - C}{r} \\
\text{Eliminate } C, \text{ and substitute } C &= C_a - r

\nu^2 + \nu \left(\frac{K + C_a}{r} + v_{\text{max}}\right) - \frac{v_{\text{max}} C_a}{r} = 0
\end{align*}
\]

Solve with Quadratic Equation

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and Biomet
Farquhar-von Caemmerer-Berry Model (1980, Planta)

\[ A = V_c - 0.5 V_o - R_d \]

A, assimilation rate  
\( V_c \), rate Velocity for Carboxylation  
\( V_o \), Rate Velocity for Oxygenation,  
e.g. photorespiration  
\( R_d \) is dark Respiration
\[ V_c - 0.5V_o = V_c(1 - \frac{\Gamma^*}{C_c}) = \min\{W_c, W_j, W_p J(1 - \frac{\Gamma^*}{C_c})\} \]

- **\(W_c\)**, the rate of carboxylation when ribulose bisphosphate carboxylase/oxygenase (RuBisco) is saturated.
- **\(W_p\)**, the carboxylation rate when RuBP regeneration is limited by electron transport.
- **\(W_j\)**, carboxylation rate with triose phosphate utilization.
$W_d$: demand limited by RUBISCO saturation

$W_l$: demand limited by RuBP regeneration by electron transport

[RUBISCO-Limited (sufficient CO2, not enough photons to regenerate RuBP)]

[Electron-Transport Limited (sufficient CO2, not enough photons to regenerate RuBP)]

Carboxylation rate (fimol m$^{-2}$ s$^{-1}$)

$[\text{CO}_2]$ (ppm)
If $W_c$ is minimal, then:

$$W_c = \frac{V_{C_{\text{max}}} C_c}{C_c + K_c (1 + \frac{O_3 I}{K_o})}$$

$$V_c - 0.5V_o = W_c (1 - \frac{\Gamma^*}{C_c}) = \frac{V_{C_{\text{max}}} (C_c - \Gamma^*)}{C_c + K_c (1 + \frac{O_3 I}{K_o})}$$

If $W_j$ is minimal, then

$$W_j = \frac{JC_c}{4C_c + 8\Gamma^*}$$

$$V_c - 0.5V_o = W_j (1 - \frac{\Gamma^*}{C_c}) = \frac{J(C_c - \Gamma^*)}{4C_c + 8\Gamma^*}$$

If $W_p$ is minimal, then

$$W_p = \frac{3V_{\text{num}}}{1 - \frac{\Gamma^*}{C_c}}$$

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The electron quantum yield is 4 times greater than the CO₂ quantum yield because from the Redox equation for CO₂ fixation it takes 4 electrons for each CO₂ molecule fixed.
Potential rate of electron transport:
Rectangular Hyperbola

\[ J = \frac{Q_2 + J_{\text{max}} - \sqrt{(Q_2 + J_{\text{max}})^2 - 4\theta_{\text{psII}} Q_2 J_{\text{max}}}}{2\theta_{\text{psII}}} \]  
(\text{\(\mu\)mol m}^{-2}\text{ s}^{-1}).

\[ Q_2 = I\alpha \phi_{\text{psII},\text{max}} \beta \]

\[ \phi_{\text{psII},\text{max}} \text{ Max quantum yield of ps II} \]
\[ \phi_{e^-} = 4\phi_{\text{CO}_2} \]
\[ \beta \text{ Fraction of light reaching psII (0.5)} \]

Von Caemmerer, 2000
### Analytical Equation for Leaf Photosynthesis

**Table 1** List of equations and unknowns for solving coupled photosynthesis-stomatal conductance model (after Baldocchi, 1994)

<table>
<thead>
<tr>
<th>Unknowns</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_t$</td>
<td>$C_t = \frac{A}{g_s}$</td>
</tr>
<tr>
<td>$C_r$</td>
<td>$C_r = \frac{A}{g_t}$</td>
</tr>
<tr>
<td>$g_d$</td>
<td>$g_d = \frac{m A r h}{C_r} + g_0$</td>
</tr>
<tr>
<td>$A - R_d$</td>
<td>$V_* - 0.5 V_* = \min[W_* W_4 \left(1 - \frac{\sum}{C_t}\right)$</td>
</tr>
<tr>
<td>$W_r$, $W_c$</td>
<td>$a C_t - \frac{ad}{e C_t + b}$</td>
</tr>
</tbody>
</table>

Baldocchi 1994 Tree Physiology

ESPM 228, Advanced Topics in Micromet and Biomet
Cubic Equation for $A$

$$e\alpha A^3 +$$

$$A^2 (e\beta + b\theta - a\alpha + e\alpha R_d ) +$$

$$A (e\gamma + \frac{b\gamma}{C_a} - a\beta + ad\theta + eR_d\beta + R_d b\theta)$$

$$-a\gamma + \frac{ad\gamma}{C_a} + eR_d\gamma + \frac{R_d b\gamma}{C_a} = 0$$

$$\alpha = 1 + \frac{b}{g_b} - m \cdot rh$$

$$\beta = C_a (g_b \cdot m \cdot rh - 2b - g_b)$$

$$\theta = (g_b \cdot m \cdot rh - b)$$
3 limitations to photosynthesis:
   CO2: controlled by stomatal conductance which is controlled by VPD (radiation, water)
   Rubisco: activity and quantity; affected by adaptation to environment and nutrients and conditions (rubisco downregulation via drought)
   RuBP: how fast RuBP can be regenerated in the cells

On an ACi curve this translates as
   CO2: the slope of the line is symbolic of stomatal conductance because looking at Ci
   Rubisco: Vcmax is the maximum velocity of carboxylation, the reaction regulated by rubisco...the initial slope is symbolic of Vcmax showing how good the
   Rubisco is at assimilating available CO2
   RuBP: Once Rubisco is CO2 saturated, it is then limited by RuBP and this is shown by the maximum of the curve.
Introduce Co-limitation Method of Collatz

Collatz uses a quadratic model to compute a dummy variable wp to allow for the transition between wj and wc, when there is colimitation. This is important because if one looks at the light response curves of the current code one see jumps in A at certain Par values.

\[
\theta \ wp^2 \ - \ wp \ (wj + wc) \ + \ wj \ wc = 0
\]

\[
a \ x^2 + b \ x + c = 0
\]

\[
x = \frac{-b \ \pm \ \sqrt{b^2 - 4 \ a \ c}}{2a}
\]

\[
a = 0.98, \quad b = -(wj + wc), \quad c = \text{wj}^*wc;
\]

\[
wp = \text{min}(wp1,wp2);
\]

\[
\beta \ A^2 \ - \ A \ (\text{wp}1) \ + \ \text{lpis} = 0
\]

\[
aa = 0.95, \quad bb = -(wp1 + \text{lwcrease}), \quad cc = \text{wp}^*\text{lwcrease};
\]

\[
\text{Apis} = \text{min}(\text{Apis1},\text{Apis2});
\]
Photosynthetic Compensation Point

The CO2 concentration that promotes \( V_c - 0.5V_o = 0 \)

\[
\frac{V_o}{V_c} = \frac{V_{o,\text{max}}}{V_{c,\text{max}}} \frac{K_c[O_2]}{K_o[CO_2]} = 2 \quad 2V_c = V_o
\]

\[
[CO_2] = \Gamma^* = \frac{0.5 \cdot V_{o,\text{max}} K_c[O_2]}{V_{c,\text{max}} K_o} = \frac{0.5 \cdot O_2}{S}
\]

\( S \) is the Specificity Coefficient
Assessing Model Parameters: Photosynthetic Compensation Point

\[
\frac{V_o}{V_c} = \frac{V_{o,\text{max}}}{V_{c,\text{max}}} \frac{K_c [O_2]}{K_o [CO_2]}
\]

\[
\frac{V_{o,\text{max}}}{V_{c,\text{max}}} = 0.21
\]

Specificity Coefficient

\[
\frac{V_c}{V_o} = \frac{S}{[O_2]} \quad \frac{V_{c,\text{max}}}{V_{o,\text{max}}} = \frac{K_c}{K_o}
\]

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We must assess \( \text{CO}_2 \) and \( \text{O}_2 \) in liquid phase

\[
\frac{V_c}{V_o} = S \frac{[\text{CO}_2]}{[\text{O}_2]} \frac{K_{H,\text{CO}_2}}{K_{H,\text{O}_2}}
\]

\( \tau \), Specificity times Henry's Law for oxygen and \( \text{CO}_2 \) in water

\[
\tau = \frac{K_{H,\text{CO}_2}}{K_{H,\text{O}_2}} S \approx 28.38 \cdot 102.33
\]

\[
\frac{V_c}{V_o} = \tau \frac{[\text{CO}_2]}{[\text{O}_2]}
\]

\[
\Gamma^* = \frac{0.5 \cdot V_{\text{e,max}}}{V_{\text{c,max}}} \frac{K_{H,\text{O}_2}}{K_{H,\text{CO}_2}} \frac{K_{H,\text{O}_2}}{\tau} \]

Get this straight
Henry Law $K_h$’s are $f(T)$, too

\[
K_{H,CO_2}(T) = 78.5 \cdot 10^{-3} - 2.89 \cdot 10^{-3} T + 54.7 \cdot 10^{-6} T^2 - 0.417 \cdot 10^{-8} T^3
\]

\[
K_{H,CO_2}(T) = 2.1 \cdot 10^{-1} - 57.1 \cdot 10^{-6} T + 1.0247 \cdot 10^{-6} T^2 - 7.503 \cdot 10^{-9} T^3
\]
Show specificity factor for Co2/O2 its value and how it varies with temperature. S decreases with T favoring O2 over Co2 and increasing photorespiration...important point to make in how leaves respond to warming or to Co2.
CO₂ Compensation Point

\[ V_c - 0.5V_o - R_d = 0 \]

\[ V_o = 2(V_c - R_d) \]
Leaf Light Response Curve, f(Vcmax)

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Temperature Response curve

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[Graph showing temperature response curve with different lines for various units]
## Vcmax Parameters

<table>
<thead>
<tr>
<th></th>
<th>Vcmax@25C</th>
<th>Na</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>μmol m⁻² s⁻¹</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>Tropical Trees (oxisols)</td>
<td>29+/−7.7</td>
<td>2.17+/−0.8</td>
</tr>
<tr>
<td>Tropical Trees (nonoxisols)</td>
<td>41+/−15.1</td>
<td>1.41+/−0.56</td>
</tr>
<tr>
<td>Temperate Broadleaved Evergreen</td>
<td>61.4+/−27.7</td>
<td>1.87+/−0.93</td>
</tr>
<tr>
<td>Temperate Broadleaved Deciduous</td>
<td>57.7+/−21.2</td>
<td>1.74+/−0.71</td>
</tr>
<tr>
<td>Evergreen coniferous</td>
<td>62.5+/−24.7</td>
<td>3.10+/−1.35</td>
</tr>
<tr>
<td>Evergreen deciduous</td>
<td>39.1+/−11.7</td>
<td>1.81+/−0.64</td>
</tr>
<tr>
<td>Evergreen shrubs</td>
<td>61.7+/−24.6</td>
<td>2.03+/−1.05</td>
</tr>
<tr>
<td>Deciduous shrubs</td>
<td>54.0+/−14.5</td>
<td>1.69+/−0.62</td>
</tr>
<tr>
<td>C3 herbaceous</td>
<td>78.2+/−31.1</td>
<td>1.75+/−0.76</td>
</tr>
<tr>
<td>C3 crops</td>
<td>100.7+/−36.6</td>
<td>1.62+/−0.61</td>
</tr>
</tbody>
</table>

Kattge et al. 2009 GCB

ESPM 228, Advanced Topics in Micromet and Biomet
$J_{\text{max}}$ and $V_{c\text{max}}$ scale with one another

Wullschleger, 1993 J Expt Bot

Wullschleger 199 J exp bot
Practical Assessment for Vcmax in sites with many species and spatial variability

Data of KB Wilson

Wright 1996 mountain grassland species

ESPM 228, Advanced Topics in Micromet and Biomet
Seasonality in $V_{cmax}$

Wilson et al. 2001 Tree Physiol

ESPM 228, Advanced Topics in Micromet and Biomet
$V_{\text{cmax}}$ and water deficits

*Quercus douglasii*

Baldocchi and Xu, 2007, Adv Water Resources
Revised T functions by Bernacchi et al.
Made *in vivo* over a wide range of temperature

Exponential function

\[ f(T) = f(T_{298}) \exp(c - \frac{\Delta H_d}{RT}) \]

If T optimum

\[ f(T) = f(T_{298}) \frac{\exp(c - \frac{\Delta H_d}{RT})}{1 + \exp(\Delta s T_K - \frac{\Delta H_d}{RT_K})} \]

\( \Delta H_a \) Enthalpy of activation

\( \Delta H_d \) Enthalpy of deactivation

Bernacchi et al. PCE; 2001, 2003
Revised T functions by Bernacchi et al.
Made in vivo over a wide range of temperature, tobacco

\[ f(T) = f(T_{298}) \exp(c \cdot \frac{\Delta H_{d}}{RT}) \]

<table>
<thead>
<tr>
<th></th>
<th>( f(T_{298}) )</th>
<th>c</th>
<th>( H_a )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( J_{\text{max}} )</td>
<td>1</td>
<td>17.7</td>
<td>43.9</td>
</tr>
<tr>
<td>( V_{\text{e max}} )</td>
<td>1</td>
<td>26.35</td>
<td>65.33</td>
</tr>
<tr>
<td>( V_{\text{t max}} )</td>
<td>1</td>
<td>22.98</td>
<td>60.11</td>
</tr>
<tr>
<td>( \Gamma )</td>
<td>42.75</td>
<td>19.02</td>
<td>37.83</td>
</tr>
<tr>
<td>( K_e )</td>
<td>404.9</td>
<td>38.05</td>
<td>79.43</td>
</tr>
<tr>
<td>( K_d )</td>
<td>278.4</td>
<td>20.3</td>
<td>36.3</td>
</tr>
<tr>
<td>( R_d )</td>
<td>1</td>
<td>18.72</td>
<td>46.39</td>
</tr>
</tbody>
</table>

Bernacchi et al. PCE; 2001, 2003
ESPM 228, Advanced Topics in Micromet and Biomet
Temperature Response Curve

\[ f(T) = \frac{\exp\left(\frac{\Delta H_f}{RT}\right)}{1 + \exp\left(\frac{\Delta H_d}{RT_f}\right)} \]

\[ f(T) = \frac{\exp\left(E_f \cdot \frac{(T_f - T_{op})}{(R \cdot T_f - T_{op})}\right)}{1 + \exp\left(\frac{s \cdot T_f - \Delta H_d}{R \cdot T_f}\right)} \]

\( E_f \) or \( H_f \) activation energy
\( s \): change in entropy
\( \Delta H_d \): change in deactivation enthalpy
\( R \): Universal gas constant
\( T \): temperature, K

Harley and Tenhunen; Bernacchi et al.

ESP228, Advanced Topics in Micromet
and Biomet
Warren and Dreyer 2006 J Expt Bot

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Figure 2. Sample responses of (a) $N_{\text{max}}$ and (b) $\Delta_{\text{max}}$ to leaf temperature. Values are normalized to 1 at 25°C.
$C_i$ does not equal $C_c$ and $g_m$ is not infinite

Warren and Abrams (2006 PCE)

ESPM 228, Advanced Topics in Micromet and Biomet
Mesophyll Conductance is Finite and Not Constant

Flexas et al 2012 Plant Science

ESPM 228, Advanced Topics in Micromet and Biomet
Get this straight. Graphic does not give with concept. Take A-C_i curve assume g_m and compute C_c and V_{cmax}.
Effect of Internal Conductance on Photosynthesis Computations

\[ A \text{ (mmol m}^{-2} \text{s}^{-1}) \]

\[ p_i \text{ (Pa)} \]

\( g_i = \infty \)
\( g_i = \text{high} \)
\( g_i = \text{low} \)

Tholen and Zhu, 2011 Plant Physiology

ESPM 228, Advanced Topics in Micromet and Biomet
Two Methods for assessing $g_m$

• Fluorescence Method

• Isotope Method
Estimating mesophyll conductance with Fluorescence measurements of electron transport, $J$

\[ J_c = (A + R_D) \frac{4C_c + 8\Gamma^*}{C_c - \Gamma^*} \]
\[ C_c = C_i - \frac{A}{g_m} \]
\[ g_m = \frac{A}{C_i - \frac{\Gamma^*(J + 8(A + R_d))}{J - 4(A + R_d)}} \]
Measure Quantum Yield with Fluorescence

\[
\phi_{psII} = \frac{F_m' - F'}{F_m'} = \frac{\Delta F}{F_m'}
\]

- \(F_m\) maximum rate of fluorescence
- \(F\), steady state rate

\[
J_f = \phi_{psII} \cdot Q_p \cdot \alpha \cdot \beta
\]

\[
J_f = \frac{\Delta F}{F_m} \alpha \cdot 0.5 \cdot Q_p
\]

- \(Q_p\), photon flux density
- \(\alpha\), leaf absorptance

*Fig. 2: The kinetics of the decay of fluorescence yield measured 10 ms after a dark-adapted pea leaf is given a saturating, single saturating flash (half-width 3 μs).*

Gonty et al 1990 Pfl Res

ESPM 228, Advanced Topics in Micromet and Biomet
Sequence of a typical fluorescence trace. A measuring light is switched on (↑MB) and the zero fluorescence level is measured (Fo). Application of a saturating flash of light (↑SP) allows measurement of the maximum fluorescence level ($F_{m}^{o}$). A light to drive photosynthesis (↑AL) is then applied. After a period of time, another saturating light flash (↑SP) allows the maximum fluorescence in the light ($F_{m}^{'}$) to be measured. The level of fluorescence immediately before the saturating flash is termed Ft. Turning off the actinic light (AL), typically in the presence of far-red light, allows the zero level fluorescence ‘in the light’ to be estimated.
$J_f$ from fluorescence equals $J_a$ from gas exchange

Warren, 2006 Function Ecol

ESPM 228, Advanced Topics in Micromet and Biomet
$J_{\text{max},c}$ from gas exchange ($J_{\text{max},c}$) vs fluorescence ($J_{\text{max},f}$) Relation is a function of temperature

Bernacchi et al., 2003 PCE
Isotope Method: 
$^{13}\text{CO}_2$ and $^{12}\text{CO}_2$

Assimilation
$\delta^{13}\text{C}_{\text{assimilates}} = -24$ to $-28\%$

Disequilibrium

Respiration = autotrophic + heterotrophic
$\approx -22$ to $-25\%$

atmospheric CO$_2$
$\delta^{13}\text{C}_{\text{air}} = -7.8\%$

Discrimination ($\Delta$)

Courtesy of A. Knohl
\[ \Delta = a + (b - a) \frac{c_i}{c_a} \]

\[ \Delta = a_b \frac{c_a - c_s}{c_a} + a_i \frac{c_i - c_a}{c_a} + a_i \frac{c_i - c_c}{c_a} + b \frac{c_c}{c_a} \]

- \( a \) diffusion from the leaf surface to the substomatal cavity (4.4%)
- \( b \) carboxylation during photosynthesis (28%)
- \( ab \) diffusion through the laminar boundary layer to the stomata (2.9%)
- \( ai \) dissolution of CO\(_2\) into water diffusion of dissolved CO\(_2\) through water (1.8%)

Courtesy of A. Knohl
Estimating $g_m$ from stable isotope measurements

$$\Delta = a_b \frac{p_a - p_x}{p_a} + a_i \frac{p_i - p_x}{p_a} + a_i \frac{p_i - p_x}{p_a}$$

$$+ b_l \frac{p_c}{p_a} - \frac{eR}{k + f}$$

$$\Delta = \frac{R_{air}}{R_{plant}} - 1 \quad R = \frac{^{13}CO_2}{^{12}CO_2}$$

ESP 228, Advanced Topics in Micromet and Biomet
Assessing $g_m$ and $C_c$ from stable isotopes

Case 1: observe $\Delta$:

$$\Delta = a \frac{P_{u} - P_{s}}{P_{a}} + a \frac{P_{s} - P_{i}}{P_{a}} + a_i \frac{P_{i} - P_{c}}{P_{a}} + b \frac{P_{c}}{P_{a}} - \frac{eR}{k + \infty}$$

Case 2: $g_m$ is infinite:

$$\Delta_i = a + (b - a) \frac{P_{i}}{P_{a}}$$

$$\Delta_i = 4.4 \%_0 + 23.1 \%_0 \frac{P_{i}}{P_{a}}$$

ESPM 228, Advanced Topics in Micromet and Biomet
Take differences between isotope fractionation in plant material and assumption that \( g_m \) is infinite

\[
\Delta = a \frac{p_t - p_i}{p_a} + a_i \frac{A}{g_m p_a}
+ b \frac{p_c}{p_a} \frac{eR/k + f\Gamma_z}{p_a}
\]

Simplified with no boundary layer fractionation

\[
\Delta_i = \frac{a(p_a - p_i)}{p_a} + \frac{b p_i}{p_a}
\]

\( g_m \) is infinite

\[
\Delta - \Delta_i = (a_i - b) \frac{A}{g_m p_a} - \frac{eR/k + f\Gamma_z}{p_a}
\]

Difference

ESPM 228, Advanced Topics in Micromet and Biomet
Deduce $g_m$ graphically knowing $A$ and $\Delta_i - \Delta$.

$$\Delta - \Delta_i = (a_i - b) \frac{A}{g_m P_d} - \frac{e R / k}{P_d}$$

$1/g_m$ is related to the slope between $\Delta_i - \Delta$ and $A$.

Von Caemmerer and Evans (1992)
Flexas et al. 2007 PCE
Mesophyll conductance scales with Photosynthesis

Warren, 2006 Function Ecol

ESPM 228, Advanced Topics in Micromet and Biomet
Dark Respiration

\[ R_a = r_b B + r_I I + r_N N + r_T T + r_M M \]

1. \( R_{\text{dark}} = R_{\text{growth}} + R_{\text{main}} = a \ Ps + bW \) (McCree, 1970)