The economics of leaf-gas exchange in a fluctuating environment and their up-scaling to the canopy level

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Introduction

Jan Baptist van Helmont coined the word ‘gas’ in the 17th century and noted that ‘gas sylvestre’ (carbon dioxide) is given off by burning charcoal.

He also investigated water uptake by a willow tree, thereby pioneering some of the earliest experiments on gas transfer (after the seminal work of Edme Mariotte around 1660).

Introduction

Centuries later, van Helmont’s activities converged into a modern-day story:

Atmospheric CO_2 (c_a) is rising largely due to fossil fuel combustion, and the *ability of terrestrial plants to uptake CO_2 is currently a leading mitigation strategy to offset this rise*.

Stomata and the global climate system

- Global climate models predict future acceleration of continental scale runoff primarily because plant stomata open less as CO_2 concentrations increase thereby reducing transpiration rates (Betts *et al.*, 2007; Gedney *et al.*, 2006).

- Reduced stomatal conductance is also predicted to lead to saturation of CO_2 uptake by plants, contributing to acceleration of global warming (Cox *et al.*, 2000).

Betts RA, Boucher O, Collins M, et al. 2007, Nature, 448: 1037–1041; Cox PM, Betts RA, Jones CD, et al., 2000, Nature, 408: 453–457; Gedney N, Cox PM, Betts RA, et al., 2006, Nature 439: 835–838.

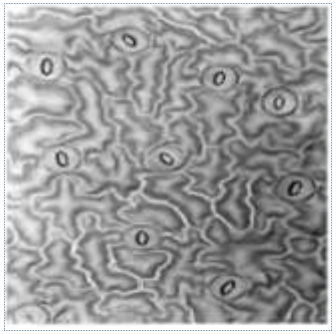
Objective

- A theory explaining the differential sensitivity of stomata to changing environmental conditions at the ecosystem scale must be identified.

Outline

- Part 1: Review fundamentals of photosynthesis and gas exchange at the leaf scale.
- Part 2: Introduce the economics of leaf-gas exchange – and explore modifications due to soil moisture stress, elevated CO_2, and elevated temperature.
- Part 3: Up-scale leaf-level processes to the ecosystem (via canopy closure models of biologically active scalars and turbulence theories).

Stomata (10 μm)



Ecosystem (1 km)

Photosynthesis: Biochemical Models

$$CO_2 + H_2O + light \rightarrow CH_2O + O_2$$

- Leaf photosynthesis to be minimum of 3 rates:

$$f_c = \min \begin{cases} J_E & \text{Light-limited} \\ J_c & \text{Rubisco-limited} \\ J_s & \text{Sucrose-limited} \end{cases}$$

Farquhar Photosynthesis Model

$$J_E = \frac{\alpha_p e_m PAR\ \ C_i - \Gamma^*}{C_i + 2\Gamma^*}$$

$$J_c = \frac{V_m (C_i - \Gamma^*)}{C_i + K_c \left(1 + \frac{C_{oa}}{K_o}\right)}$$

$$J_s = \frac{1}{2} V_m$$

Canonical Form

$$f_c = \frac{\alpha_1\ \ C_i - \Gamma^*}{C_i + \alpha_2}$$

Leaf equations for CO2 and the closure problem

$$f_c = \frac{\alpha_1 \;\; C_i - \Gamma^*}{C_i + \alpha_2}$$

Biochemical Demand

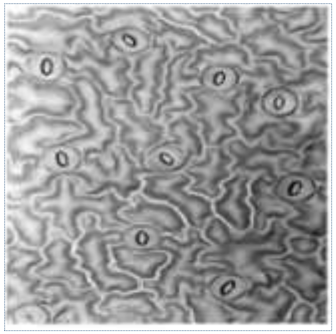
Atmospheric supply (Fickian)

$$f_c = g_s(C_a - C_i)$$

2 equations,

3 unknowns: f_c, g_s, C_i

The ‘closure’ models: General considerations



- Approaches to ‘*close*’ this problem assume an empirical relationship between g_s and some environmental stimuli.

Earliest empirical approach (Jarvis, 1976)

$$\frac{g_s}{g_{s,\max}} = f_1(PAR)\, f_2(D)\, f_3(\psi_l)\, f_4(c_a)\, f_5(T_a)$$

No synergistic interactions – all variables are ‘external’ to the leaf

Jarvis, P., 1976, Philosophical Transactions of the Royal Society of London, Series B. Biological Sciences 273: 593–610.

Closure models: contemporary empirical formulations

Two well-known formulations that fit a wide range of data:

'Ball-Berry' (Collatz *et al.*, 1991)

$$g_1 = \frac{m_1}{c_a} f_c RH + b_1;$$

Leuning (1995)

$$g_2 = \frac{m_2}{c_a} f_c \left(1 + \frac{D}{D_o}\right)^{-1} + b_1$$

The Ball-Berry model was used to allow two-way interactions between the biosphere and atmosphere in climate models (Sellers et al., 1996).

Collatz GJ et al. 1991, Agricultural and Forest Meteorology 54: 107–136; Leuning R. 1995, Plant, Cell & Environment 18: 339–355; Sellers PJ et al. 1996; Science 271: 1402–1406.

Closure models: optimization theories

- Stomatal conductance as a “compromise between the need to provide a passage for assimilation and the prevention of excessive transpiration”(Cowan and Troughton, 1971).

- Stomatal conductance is “the control variable to maximize the leaf net C gain, constrained by a given water availability” (Cowan, 1986).

Cowan, I. R. and J. H. Troughton, 1971, Planta 97: 325-336. Cowan, I. (1986) Economics of carbon fixation in higher plants. On the Economy of Plant Form and Function (ed. T.J. Givnish), pp. 133–170. Cambridge University Press, Cambridge;

Optimization model

John
Dalton

Define the short-term flux rates of CO2 and H2O:

$$\text{Carbon Gain} \quad = \quad f_c$$

$$\boxed{\text{Water Loss} \quad = \quad f_e \approx a\, g_s\, D}$$

OBJECTIVE FUNCTION (Givnish and Vermeij, 1976; Cowan and Farquhar, 1977)

Lagrange Multiplier

$$f(g_s) = f_c(g_s) - \lambda f_e(g_s)$$

Stomata close when water flux is large consistent with findings from the *Helox* experiments in Mott and Parkhurst (1991).

Cowan, I., Farquhar, G.D., 1977. in Symposia of the Society of Experimental Biology. Cambridge University Press, pp. 471–505;
Givnish TJ, Vermeij GJ. 1976. Sizes and shapes of liane leaves. The American Naturalist 110: 743–778.
Mott KA, Parkhurst DF. 1991. Plant, Cell & Environment 14: 509–515

Optimization theories:

Express the Fickian diffusion formulation and the Farquhar photosynthesis model as a function of stomatal conductance (g) using (Katul et al., 2010):

$$\frac{c_i}{c_a} = \frac{1}{2} + \frac{-a_1 - a_2 g + \sqrt{(a_1 + (a_2 - c_a)g)^2 + 4g(a_1 c_p + a_2 c_a g)}}{2 g c_a}$$

$$f_c = \frac{1}{2} \boxed{a_1 + (a_2 + c_a)g} - \boxed{\sqrt{(a_1 + g(a_2 - c_a))^2 + 4g(a_1 c_p + a_2 c_a g)}}$$

Linear in g

Non-linear in g – convexity admits optimum

Katul, G.G., et al. 2010, *Annals of Botany*, 105(3):431-442

Optimization models:

- Maximization is achieved at short time scales when

$$\frac{\partial}{\partial g}\left(f_c(g)-\lambda f_e(g)\right)=0$$

- When the condition $\left|\dfrac{\partial\lambda}{\lambda}\right| << \left|\dfrac{\partial f_e}{f_e}\right|$ then

$$g=\frac{-a_1(a_2-c_a+2c_p)}{(a_2+c_a)^2}+\frac{\sqrt{aD\lambda a_1^2(c_a-c_p)(a_2+c_p)(a_2+c_a-2aD\lambda)^2(a_2+c_a-aD\lambda)}}{aD\lambda(a_2+c_a)^2(a_2+c_a-aD\lambda)}$$

This is a general solution for the optimization problem that takes into account all non-linearities in the f_c-c_i curve as well as light and Rubisco limitations on photosynthesis (Katul et al., 2010).

Recovering the canonical form of empirical models from optimization theories

- The photosynthesis model may be simplified as (Hari et al., 1986; Lloyd, 1991)

$$f_c = \frac{a_1}{a_2 + c_i}\, c_i - \cancel{c_p}$$

$$\boxed{a_2 + c_i = a_2 + (c_i / c_a)\, c_a = a_2 + s c_a}$$

Hari P et al., 1986. Tree Physiology 2: 169–176; Lloyd, J. 1991, Australian Journal of Plant Physiology, 18, 649–660.

Optimization models (linear form)

- Upon differentiating *f(*g_s*)* w.r.t g_s and setting it to zero (Hari et al., 1986; Lloyd, 1991; Katul et al., 2009):

$$g_s = \frac{a_1}{a_2 + s c_a}\left(-1 + \sqrt{\frac{c_a}{a\lambda D}}\right)$$

$$\frac{f_c}{c_a} = \frac{a_1}{a_2 + s c_a}\left(1 - \sqrt{\frac{a\lambda D}{c_a}}\right)$$

$$\boxed{\frac{c_i}{c_a} = 1 - \left(\frac{a\lambda}{c_a}\right)^{1/2} D^{1/2}}$$

Practical result – it allows the inference of the Lagrange multiplier from stable isotopes (e.g. [BASIN (Biosphere–Atmosphere Stable Isotope Network); http://basinisotopes.org/]])

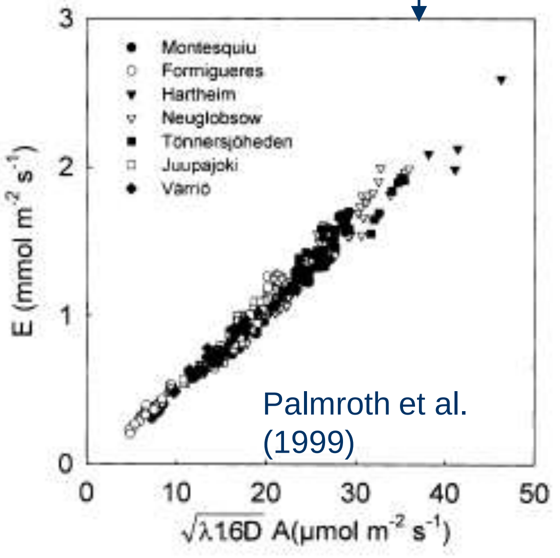
Recovery of empirical models


Scots Pine

- Combine the formulation for conductance and photosynthesis (Katul et al., 2010; Launiainen et al., 2011)

$$g = \frac{f_c}{c_a}\sqrt{\frac{c_a}{a\lambda}}\,D^{-1/2} \qquad \lambda = \lambda_o\left(\frac{c_a}{c_o}\right)$$

$$g_1 = \frac{m_1}{c_a} f_c\,RH + b_1; \qquad g_2 = \frac{m_2}{c_a} f_c\left(1+\frac{D}{D_o}\right)^{-1} + b_1$$

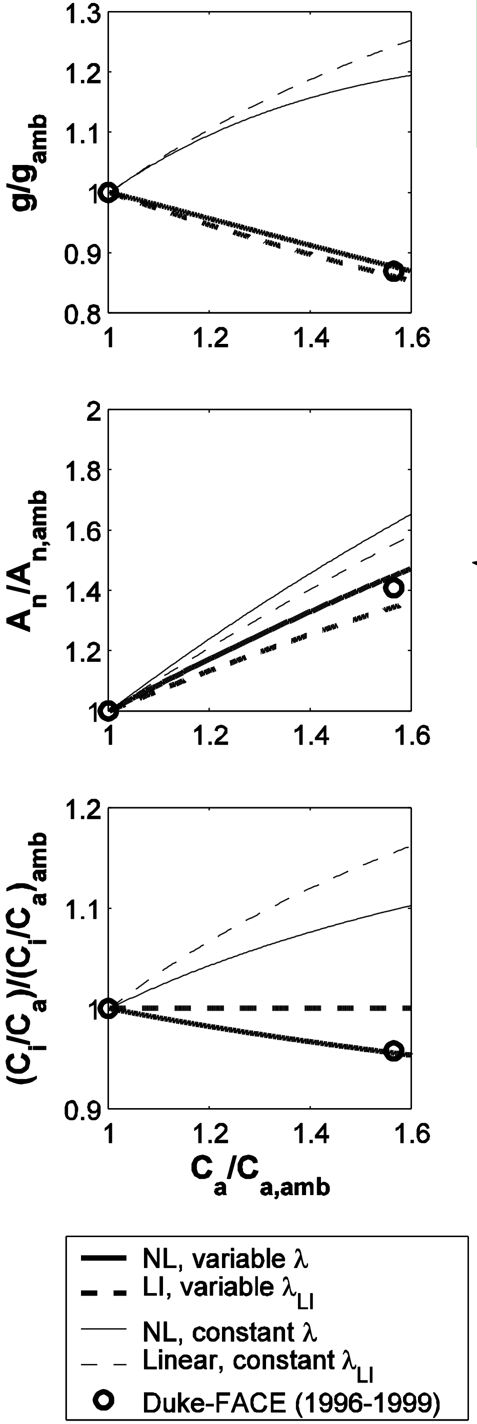


Palmroth et al. (1999)

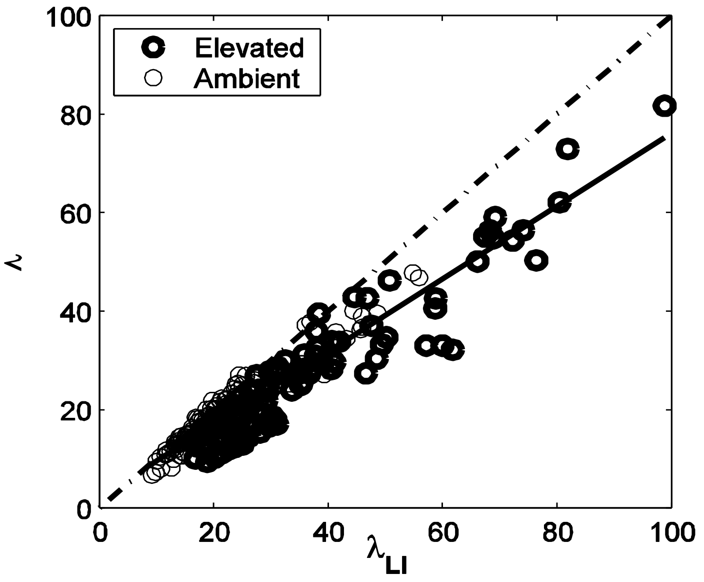
Medlyn et al. (2011) – similar result using a variant on the non-linear light-limitation version of the A-Ci curve. Jointly, these results suggest that g-fc/ca relationship may be robust to the precise shape of the A-Ci.

Launiainen, et al. 2011, *Agricultural and Forest Meteorology*, 151, 1672-1689; Medlyn et al., 2011, Global Change Biology,17, 2134–2144; Palmroth et al., 1999; Oecologia, Vol. 121, No. 3 (1999), pp. 302-309

Elevated CO2
Duke FACE Experiment:



From Katul et al. (2010)

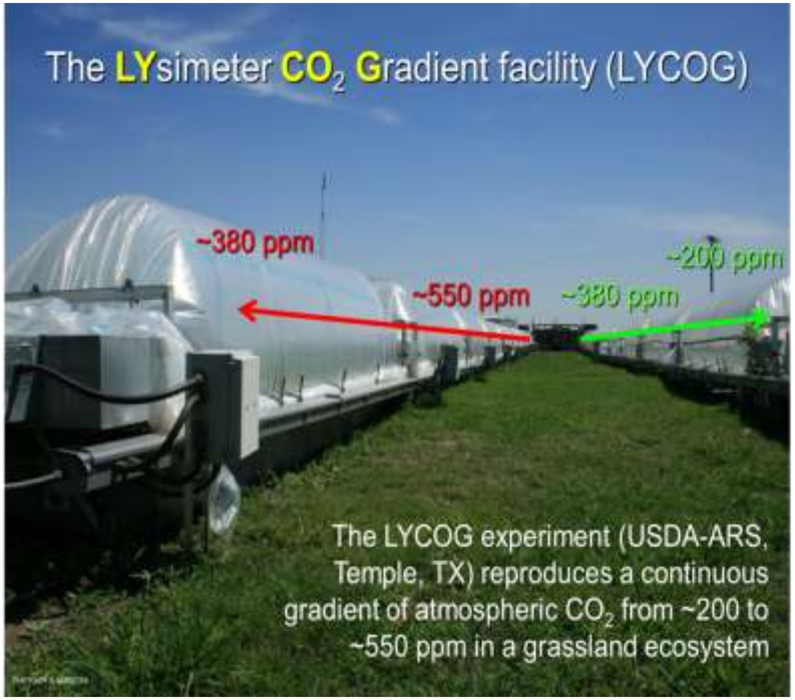


$$\lambda = \lambda_o \left(\frac{c_a}{c_o}\right)$$

Ambient: 380 ppm
Elevated: Ambient + 200 ppm

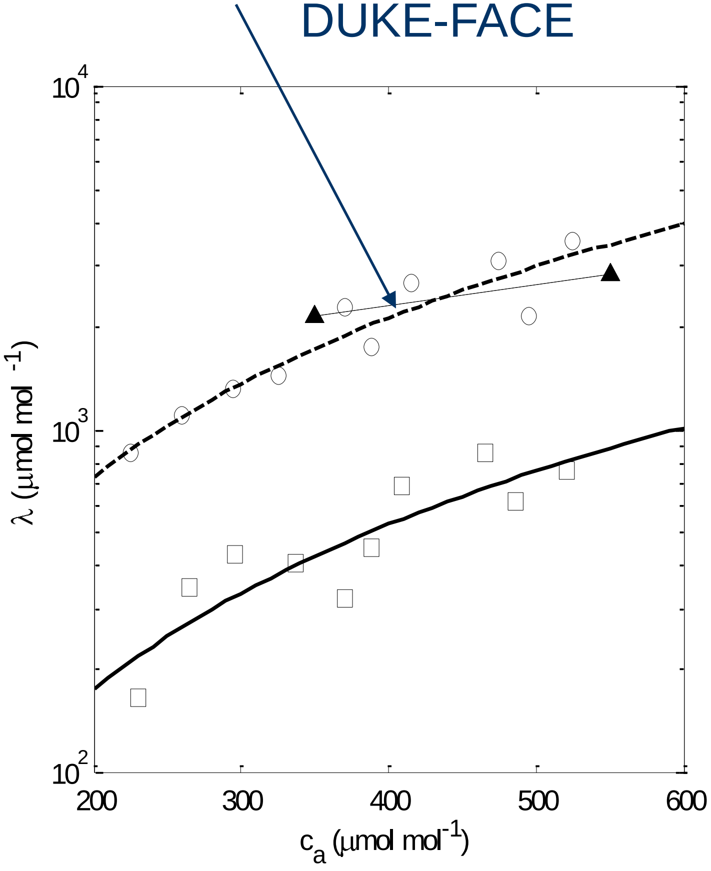
LYCOG Experiment: Grasses

From Manzoni et al. (2011a)



The LYsimeter CO$_2$ Gradient facility (LYCOG)

The LYCOG experiment (USDA-ARS, Temple, TX) reproduces a continuous gradient of atmospheric CO$_2$ from ~200 to ~550 ppm in a grassland ecosystem

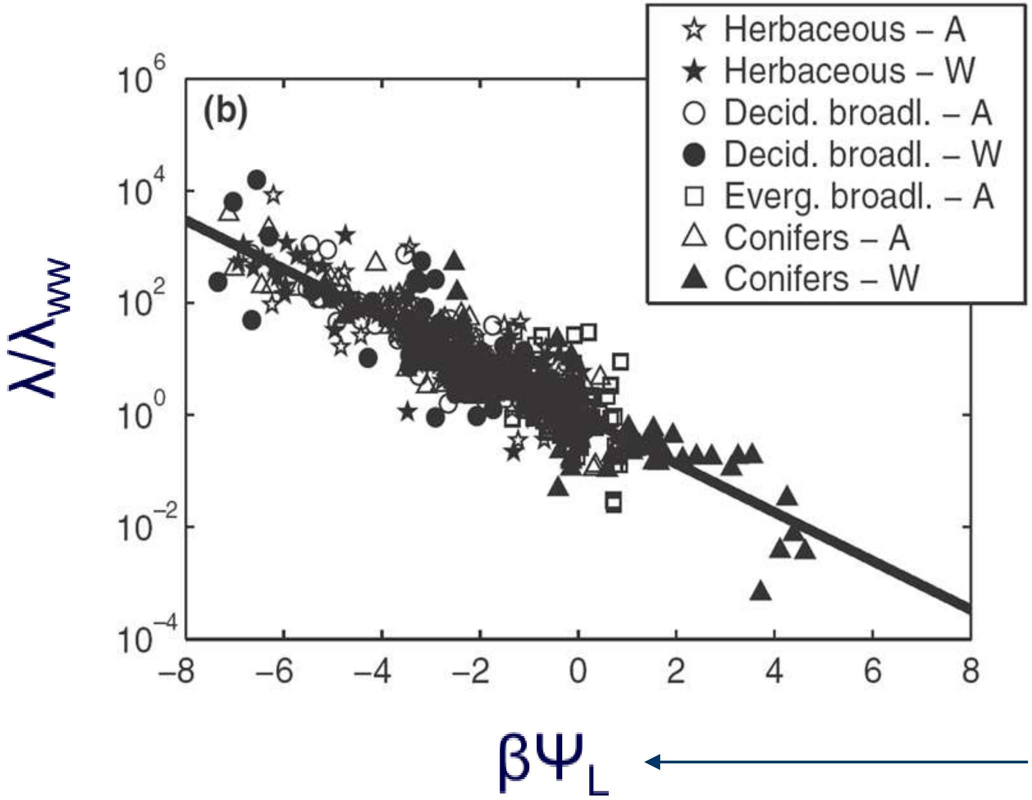


DUKE-FACE

Manzoni, S., 2011a, *Ecological Modeling*, 222, 653-665

Meta-analysis on the effects of droughts (Manzoni et al., 2011b)

λ increases with decreasing water availability

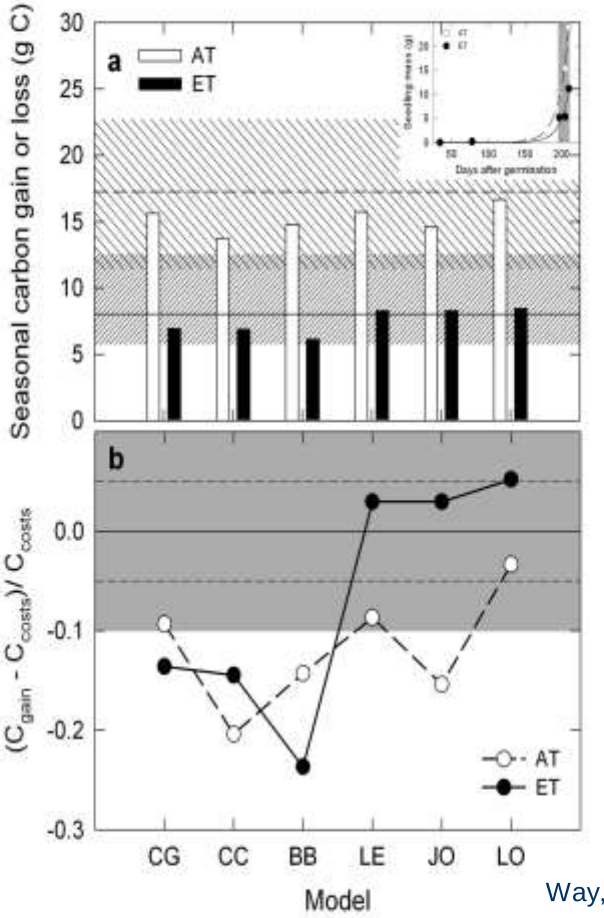


Results consistent with Cowan (1986) and Makela et al. (1996)

← Leaf pressure

Manzoni, S., et al. 2011b, *Functional Ecology*, 25, 456-46

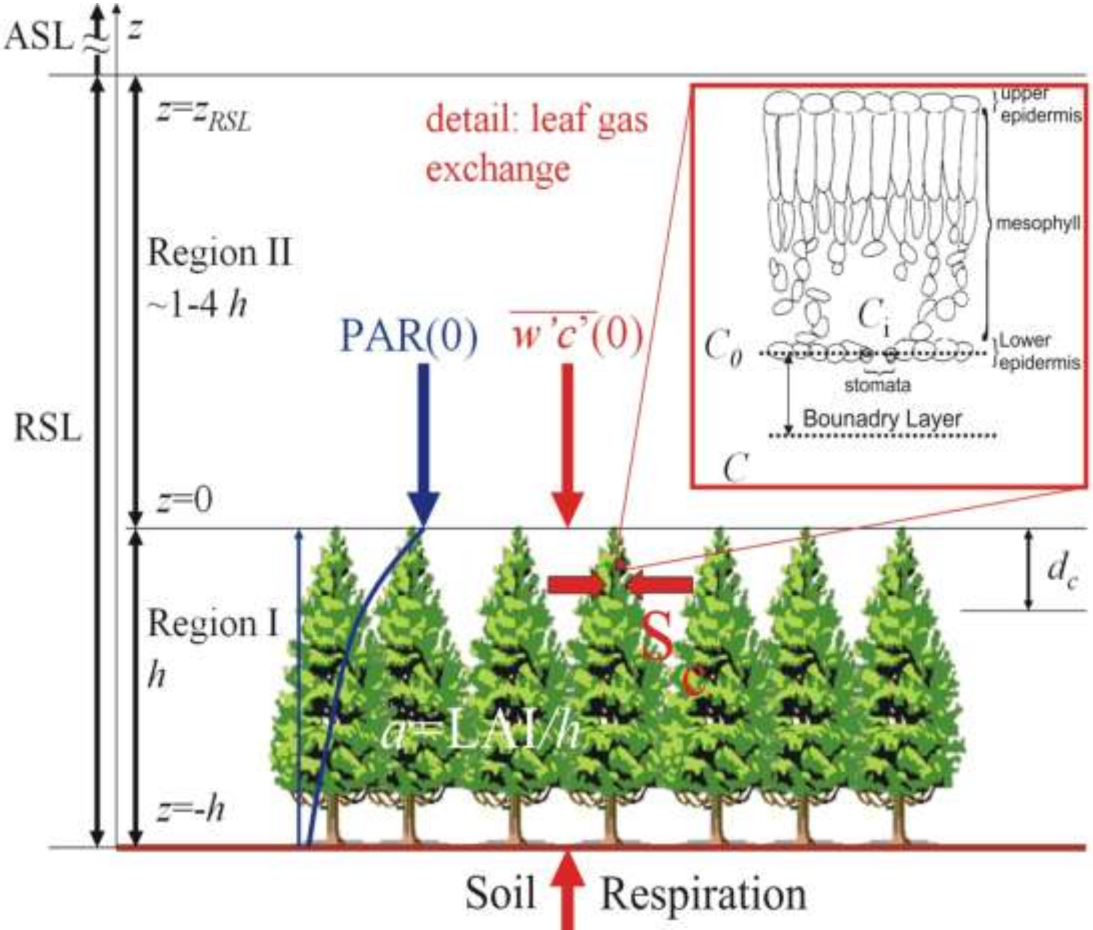
Effect of warming (Spruce) from Way et al. (2011) – long time scales



CG=constant conductance
CC = constant ci/ca
BB = Ball-Berry model
LE = Leuning model
JO = Jarvis-Oren model
LO = Linear optimality

Way, D., et al. 2011, *Journal of Geophysical Researach*, 116, G04031, doi:10.1029/2011JG001808

Up-scaling to the canopy



Focus here is on Region – I but the proposed model considers both regions.

Model formulation (Region – I)

Level of model complexity sought here is commensurate with the analytical model of Harman and Finnigan (2008).

$$\frac{\partial \overline{w'c'}(z)}{\partial z} = S_c(z),$$

Conservation of scalar mass

$$\overline{w'c'}(z) = -K_t(z)\frac{\partial c_a(z)}{\partial z}$$

Gradient-diffusion closure

$$K_t = \left(\frac{1}{S_N}\right) l^2 \left|\frac{\partial U}{\partial z}\right|$$

Leaf area density ↘

$$S_c(z) = a(z)\boxed{g_s(z)c_a(z)\left(\frac{c_i(z)}{c_a(z)} - 1\right)},$$

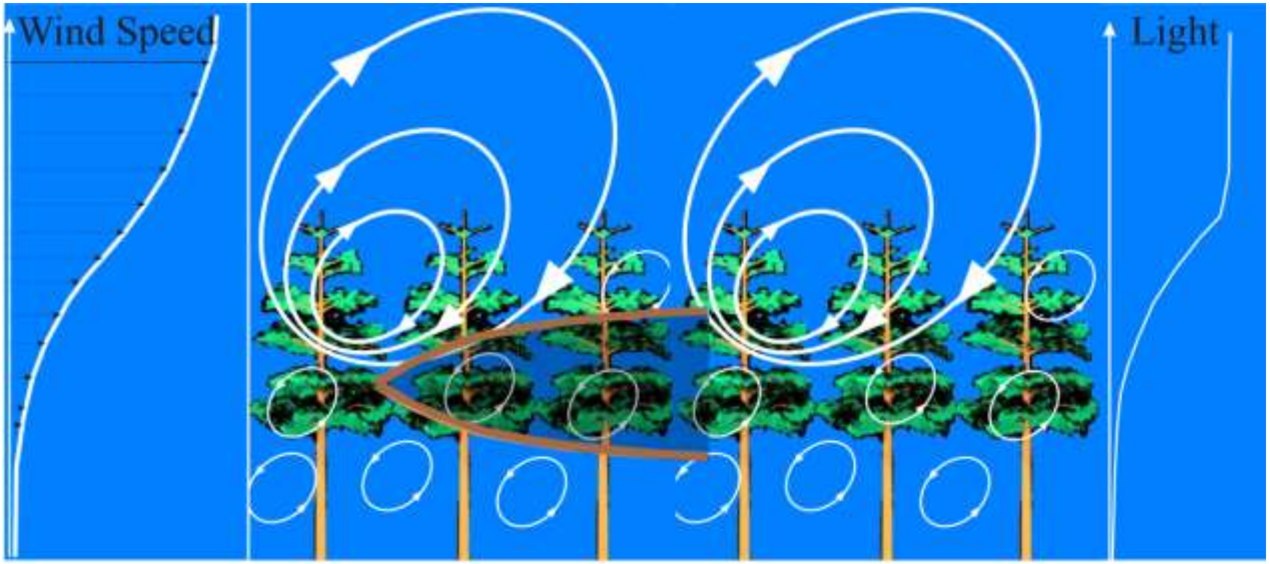
Sink at a give level =
Leaf photosynthetic rate x leaf area density

Harman and Finnigan, 2008, Boundary-Layer Meteorol. 129:323–351

Light and wind regimes – exponential forms inside the canopy

Harman and Finnigan (2007) $U(z) = U_h \exp(\beta z / l); \quad \beta = u_* / U_h; \quad l:$ mixing length

Siqueira and Katul (2010) $g_s(z) = g_{max} \exp(\beta_e a z); \quad \beta_e:$ light extinction coefficient



Siqueira, M.B., and G.G. Katul, 2010, *Boundary-Layer Meteorology*, 135, 31-50; Harman and Finnigan, 2007, Boundary-Layer Meteorology 123: 339–363.

Stomatal conductance: optimal theory

- Assume light limitation throughout the canopy

$$g_s = \left(\frac{\alpha_1}{\alpha_2 + s\,c_a} \right) \left(-1 + \left(\frac{c_a}{a\lambda D} \right)^{1/2} \right) \qquad \alpha_1 \sim PAR(z)$$

Assume vapor pressure deficit is well-mixed inside the canopy so that

$$\lambda = \lambda_o \left(\frac{c_a}{c_o} \right)$$

$$\frac{c_i}{c_a} = 1 - \left(\frac{a\lambda}{c_a} \right)^{1/2} D^{1/2}$$

only varies with D

Final budget equation for Region I

Variable coefficient

$$\frac{\partial^2 c_a}{\partial z^2} + \frac{\beta}{l}\frac{\partial c_a}{\partial z} + \frac{\beta}{l}\boxed{\frac{LAI}{h}}\frac{(1-c_i/c_a)}{\beta^2}\boxed{\frac{g(z)}{U(z)}}S_N c_a = 0$$

Mixing Length

Leaf area density

Schmidt Number

Boundary conditions: Lower BC is forest floor respiration

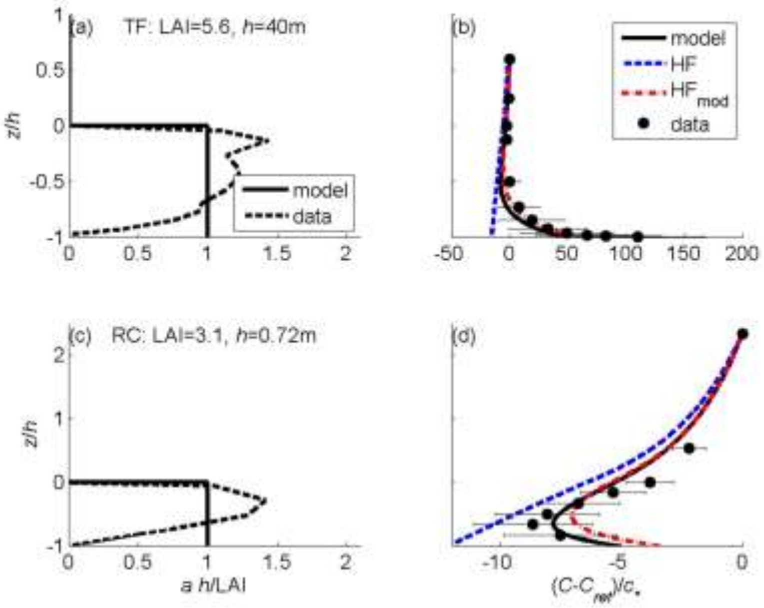
Upper boundary condition: z>>d – specified CO2 concentration for region II

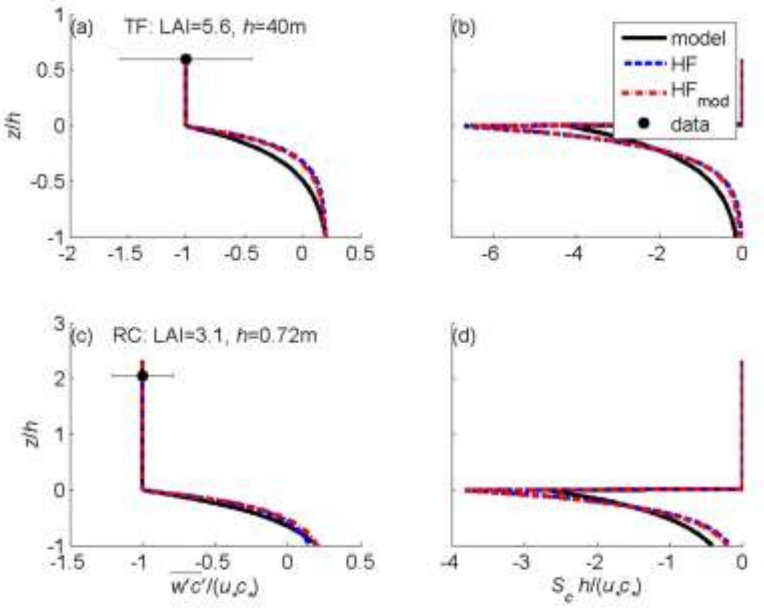
Analytical solution presented in Siqueira and Katul (2010)

Siqueira and Katul, 2010, *Boundary-Layer Meteorology*, 135, 31-50

Comparison with data: Tropical Forest and Rice Canopy

- From Siqueira and Katul (2010)





HF = Harman and Finnigan (2008)

HF_{mod} = Harman and Finnigan (2008) modified for finite canopy effects

Conclusions – 1:

- It was argued that the stomatal optimization principle may be operating on time scales commensurate with opening and closure of stomatal aperture, and each leaf *optimally* and *autonomously* regulates stomatal conductance.

- When such an optimality hypothesis is combined with mass transfer (atmospheric supply) and photosynthesis models (biochemical demand), they can explain the functional forms in empirical models allowing for synergistic interactions (e.g. light-temperature).

$$\frac{g_s}{g_{s,\max}} = f_1(PAR)\, f_2(D)\, f_3(\psi_l)\, f_4(T_a)\, f_5(c_a)$$

Conclusion - 2

- Optimality results are ‘robust’ even if the Lagrange multiplier is not exactly constant provided that:

$$\left|\frac{\partial \lambda}{\lambda}\right| << \left|\frac{\partial f_e}{f_e}\right|$$

Conclusions – 3:

Using basic principles from RANS along with canonical length scales describing vortical motion inside canopies, we were able to resolve two-way interaction between the leaves and their microclimate analytically.

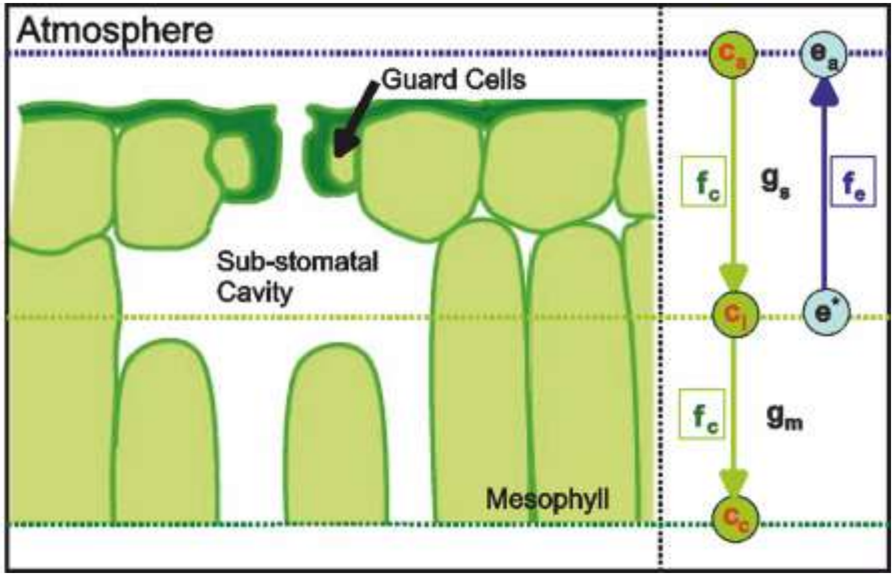
How the canopy attenuates light vis-à-vis momentum is a critical variable in explaining the stationary mean concentration profiles.

Future Directions – Protected Environments

- The area of crops cultivated in extensive screenhouses is rapidly growing, especially in semi-arid and arid regions.
- Water vapor, carbon dioxide, and sensible heat released or taken up by crops within such protected environments can substantially alter the immediate micro-environment, which in turn, affects these fluxes.
- This amplified interaction between plants and their microclimate challenges simple assessments on how partially covering the crop by a screen modifies plant water uptake and photosynthesis.
- Proposed approach here is being explored in screen-houses (Siqueira et al., 2012).

Siqueira, M.B., G.G. Katul, and J. Tanny, 2012, The effect of the screen on the mass, momentum, and energy exchange rates of a uniform crop situated in an extensive screenhouse, *Boundary-Layer Meteorology*, 142, 339-363

Future Directions – Salt/Water Stress (sea level rise and salt contamination)



Revise theories to accommodate water and salt stress under ambient and elevated CO$_{2}$.

Manzoni, S., G. Vico, G.G. Katul, P.A. Fay, H. 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

Volpe, V., S. Manzoni, M. Marani, and G.G. Katul, 2011, Leaf conductance and carbon gain under salt-stressed conditions, *Journal of Geophysical Reasearach*, 116, G04035, doi:10.1029/2011JG001848

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