

CALTECH

JPL Center for Climate Sciences

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# Terrestrial land surfaces- *a pot pourri*

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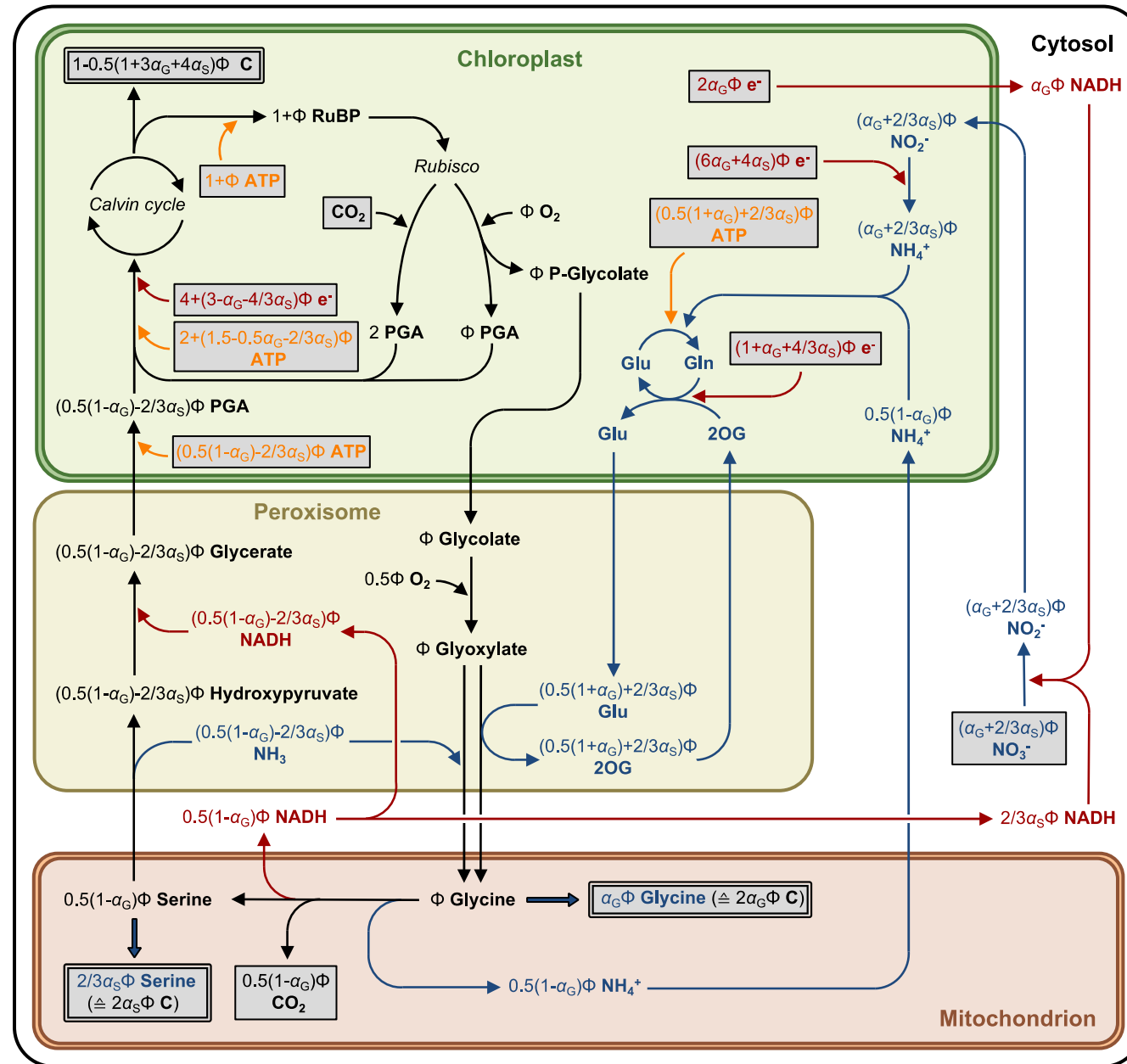
- Timescale is a key issue
- In short term (few years) we can ignore shifts in ecosystems, assume annually recurring photosynthetic surfaces, calculate fluxes and ignore growth
- In longer term there will be differences among species/genotypes in responses to increased  $[\text{CO}_2]$ , and to changing climate, in growth and reproduction

# Short term

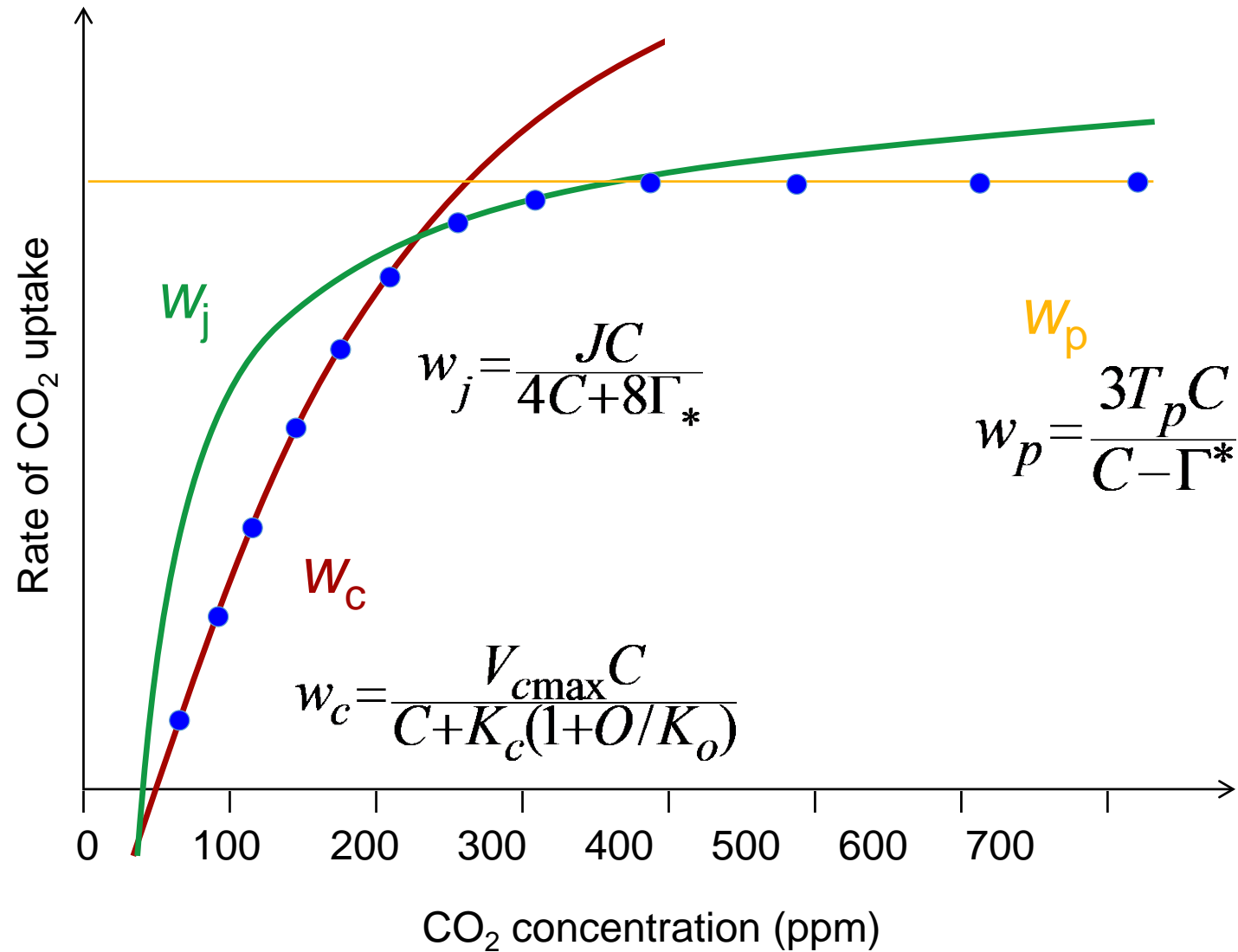
- More details than in present models
- Eg introducing interaction between C and N budgets

# Carbon vs. nitrogen metabolism

Busch,  
Sage &  
Farquhar.  
*Nature  
Plants*  
2017



# CO<sub>2</sub> assimilation model (FvCB model)



# FvCB photosynthesis model v2.0

Glycine export

$$A = V_c - 0.5(1 - \alpha_G)V_o - R_d$$

Not a constant!

$$A = \min\{w_c, w_j, w_p\} \left( 1 - \frac{(1 - \alpha_G)\Gamma^*}{C} \right) - R_d$$

Rubisco – limited

$$w_c = \frac{V_{c\max} C}{C + K_c (1 + O / K_o)}$$

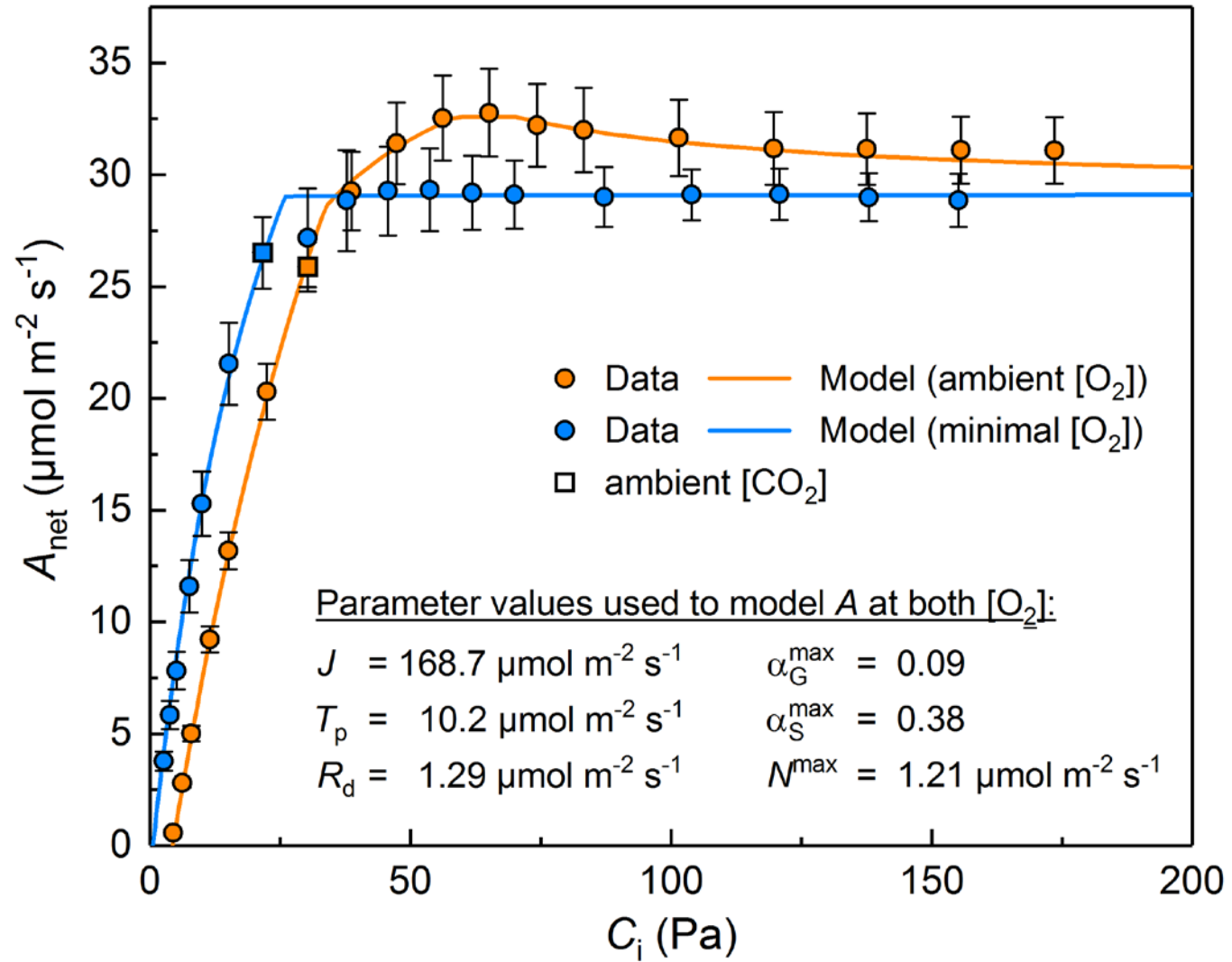
Electron transport  
limited

$$w_j = \frac{J C}{4C + (8 + 16\alpha_G + 6\alpha_S)\Gamma^*}$$

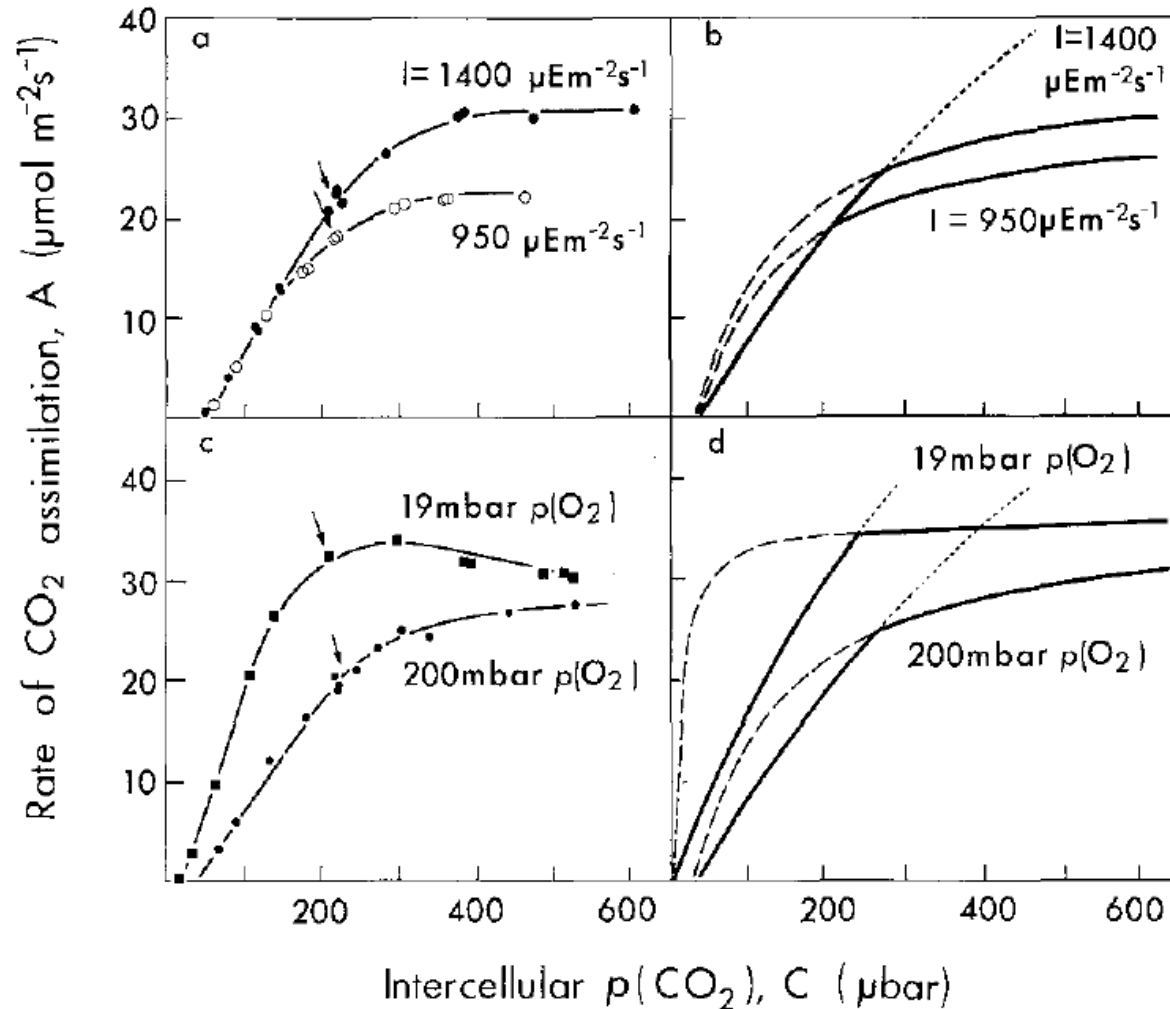
TPU– limited

$$w_p = \frac{3T_p C}{C - (1 + 3(\alpha_G + \alpha_S))\Gamma^*}$$

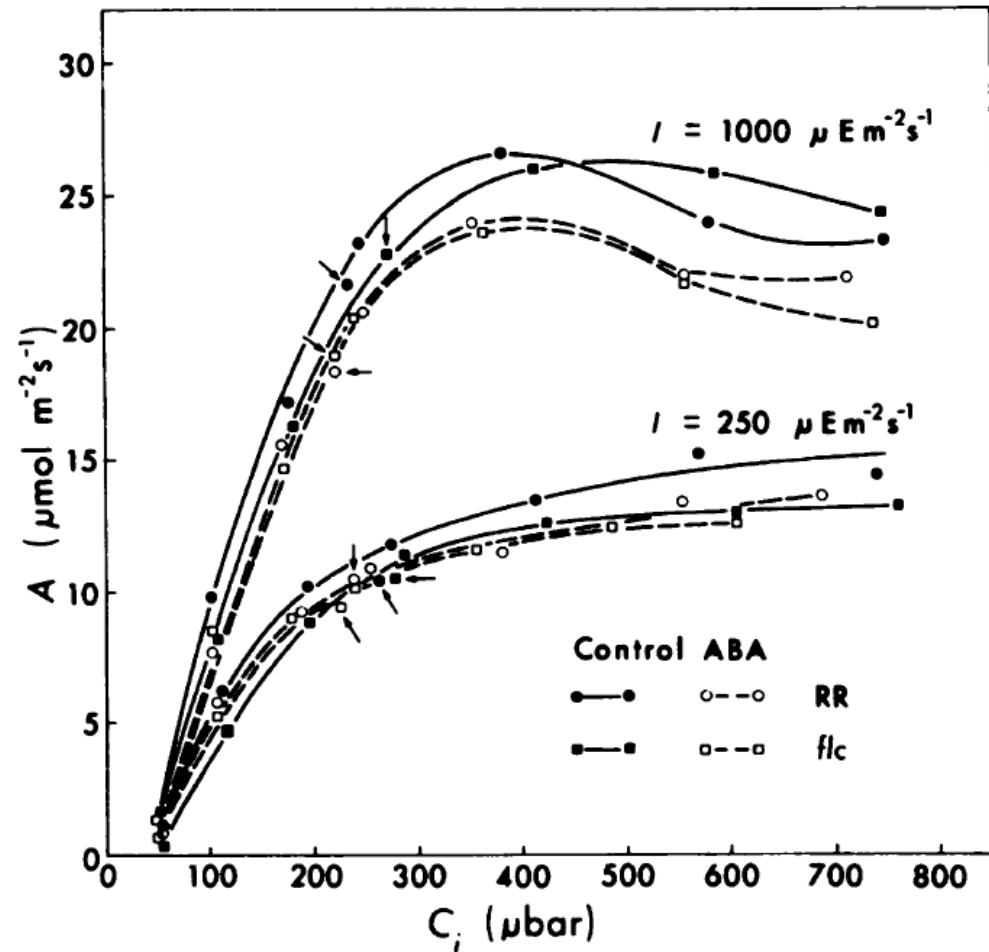
# Effect of $\alpha$ on $A/C_i$ curve



# von Caemmerer & Farquhar 1981



# Bradford, Sharkey & Farquhar 1983



# Short term

- More details than in present models
- Eg introducing interaction between C and N budgets, including better treatment of limitations of triose phosphate utilization
- Eg introducing better link between photosynthesis and respiration. Farquhar GD, Busch F (2017) Changes in the chloroplastic CO<sub>2</sub> concentration explain much of the observed Kok effect: a model. **New Phytologist** 214:570-584.

# Longer term

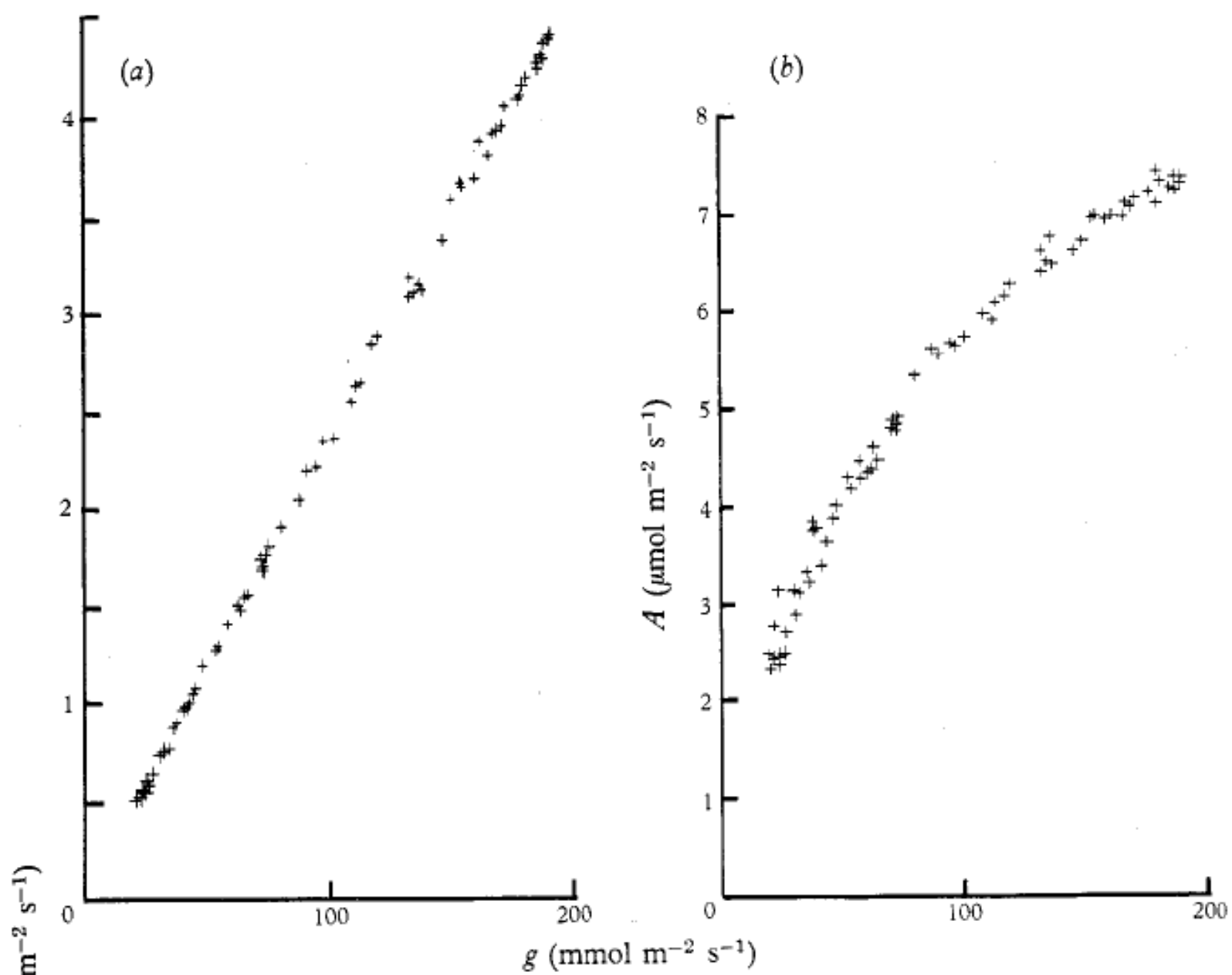
- Establish linkage between photosynthesis and growth
- Between growth and reproduction etc

# Water/carbon trade-off

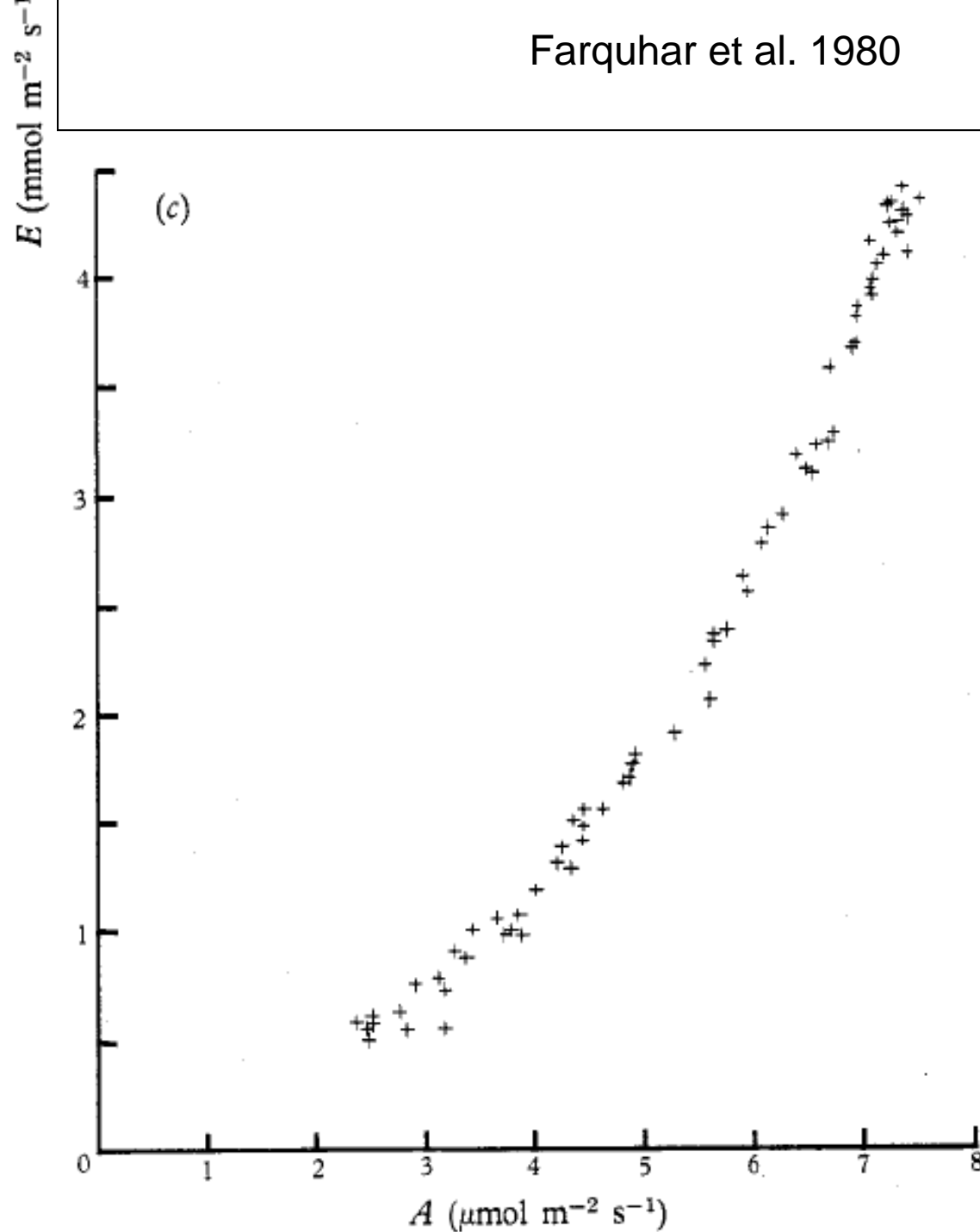


# Optimal water use by plants

- Transpiration causes tension in the water in the plant and draws water in from the soil. This is why we need to water plants. Typically, say, 300 H<sub>2</sub>O/CO<sub>2</sub>.
- Water is the greatest single limitation on plant growth
- How should plants control the apertures of the stomata to assimilate the greatest amount of carbon dioxide for a given total water loss, over a day, say?
- We treat transpiration as an expenditure and CO<sub>2</sub> assimilation as a purchase (Farquhar 1973)



Farquhar et al 1980



**Fig. 1.** Leaf transpiration rate,  $E$ , (a) and rate of  $\text{CO}_2$  uptake  $A$ , (b) versus conductance,  $g$ , during the course of spontaneous stomatal oscillations in *N. glauca* in July 1978. Under the same conditions, (c) relates  $E$  to  $A$ . The slope of this curve represents  $\partial E/\partial A$ .

# Simplest economic model

(Cowan & Farquhar 1977)

- Optimal solution is to shift temporal pattern of expenditure of water around until no more C could be obtained for a given total amount of water spent over the day.
- At this optimum trajectory the effect of increasing expenditure ( $\delta E$ ) at one point of time (which requires  $-\delta E$  at some other time) always gives the same increase in A [ $= \delta E/\lambda$ ] (and the same loss at the other time):  $\partial E/\partial A = \lambda$

**Always buy more carbon if the price is less than  $\lambda$  mol water per mol C**

# Same argument for spatial variation

- If the return on expending a marginal increase ( $\delta E$  is  $\delta A = \delta E/\lambda$ ) at one part of a leaf then it should be the same for the rest of the leaf, and for all other leaves

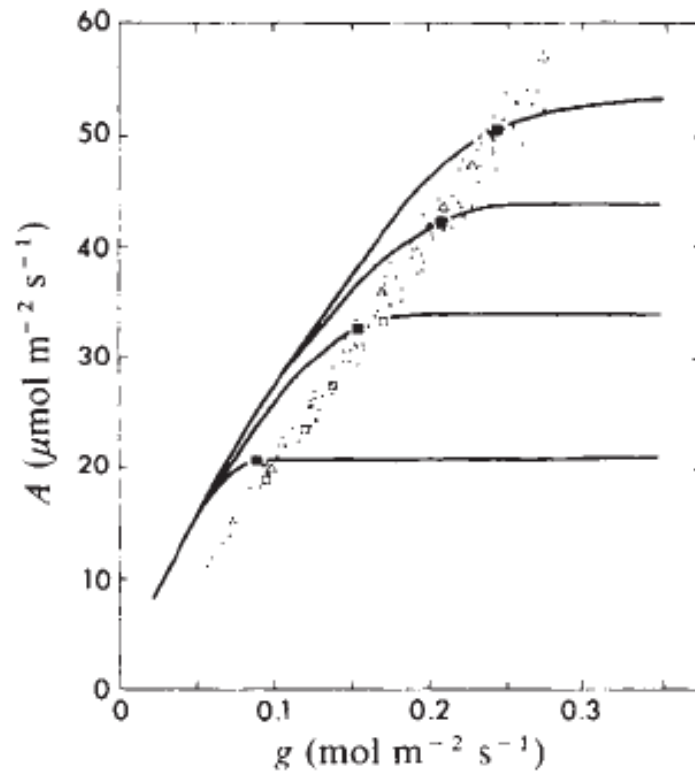
**Always buy more carbon if the price is less than  $\lambda$  mol water per mol C**

**Note that in dry places water is more valuable than in moist places and so  $\lambda$  is often smaller in magnitude in dry conditions.**

# How well do plants follow the economic ideal of $\partial E / \partial A = \lambda$ ?

- Stomata open in the light and close in the dark
- Stomata close with increasing leaf-to-air vapour pressure difference
- But stomata do not open if  $[\text{CO}_2]$  increases
- Leaves with large photosynthetic capacity (e.g. large nitrogen content) have large stomatal conductance

# Amazing correlation between stomatal conductance and photosynthesis at constant temperature and humidity

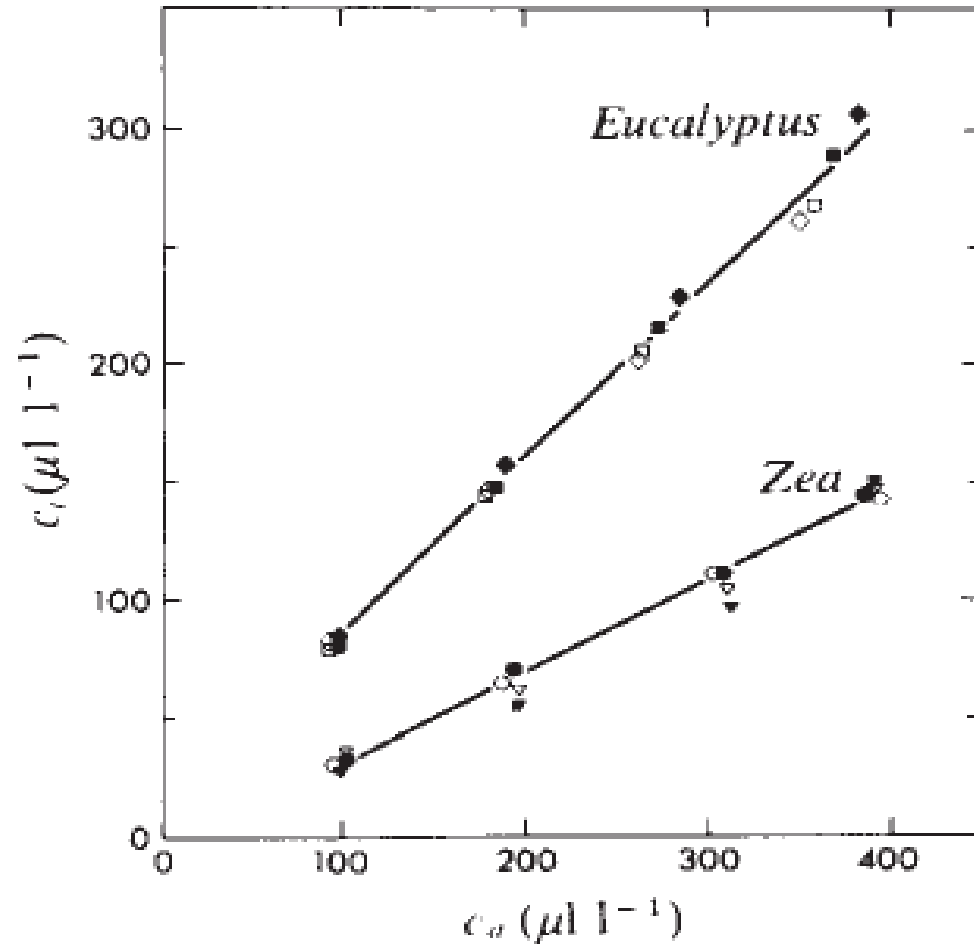


Data from *Zea mays*  
Wong, Cowan & Farquhar Nature 1979

# Variation in photosynthetic capacity

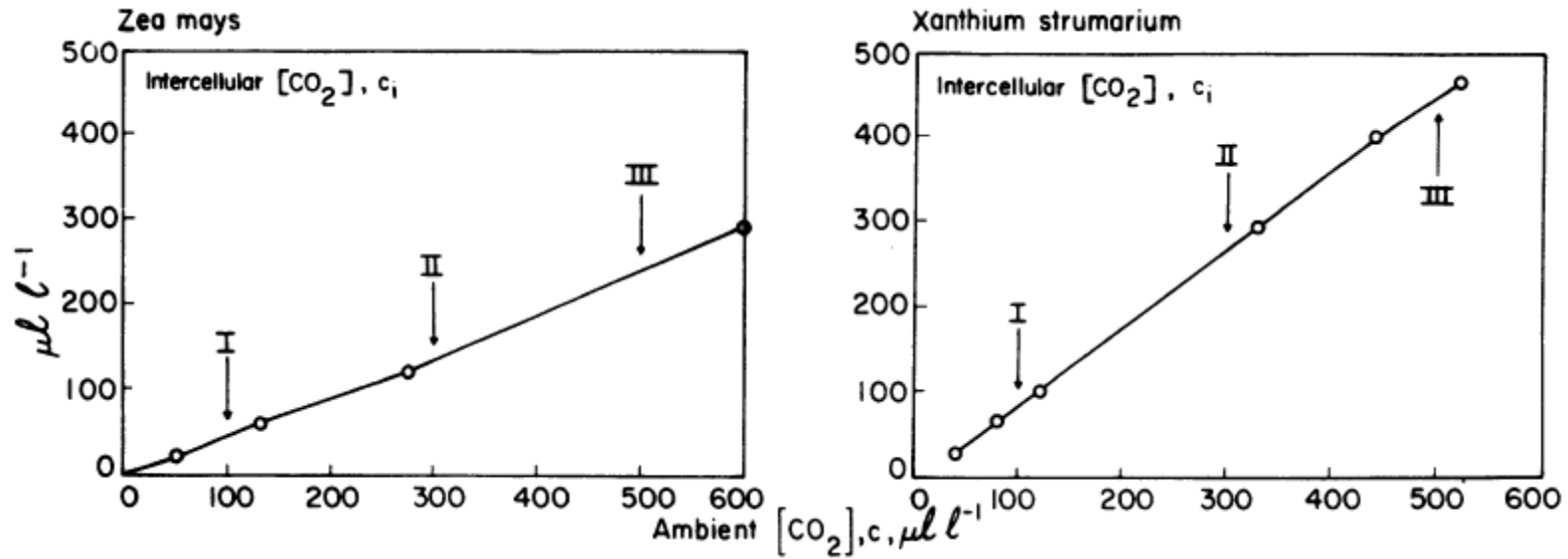
- Individual data (dots) in previous slide show the relationship between assimilation rate,  $A$ , and stomatal conductance,  $g$ , when photosynthetic capacity is the source of variation between leaves. ie  $A \propto g$ . But we know that  $A = g(c_a - c_i)$ , so this means that at a particular  $c_a$ , for well-watered plants at constant humidity,  $c_a - c_i$  is  $\sim$ constant.

# What about when $c_a$ varies?



Wong, Cowan & Farquhar Nature 1979

# And earlier



Farquhar, Dubbe, Raschke Plant Physiol 1978

# Relative constancy of $c_i/c_a$ for particular mode of photosynthesis

- These experiments showed that  $c_a - c_i$  is  $\sim$ constant because  $c_i/c_a \sim$ constant.
- Expressed differently  $g = A/(c_a - c_i) = A/[c_a(1 - c_i/c_a)]$  at a particular humidity etc.
- ie  $g \propto A/c_a$
- This is the basis for a very successful model of stomatal behaviour

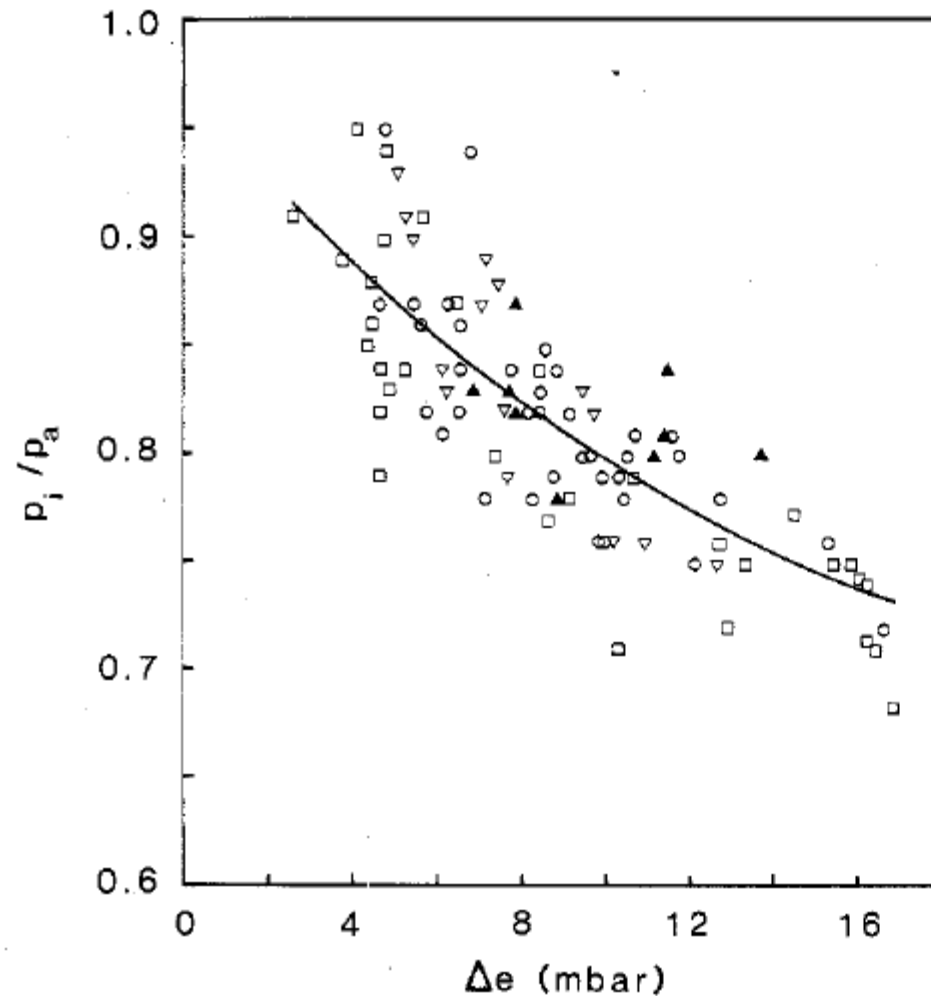
# Ball Berry model of stomatal conductance

- Ball, Berry & Woodrow (1987) suggested the following empirical expression for  $g_s$ :

$$g_s = g_0 + g_1 (A h_r / C_a),$$

where  $g_0$  and  $g_1$  are fitted parameters,  $A$  is net assimilation rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $h_r$  is relative humidity at the leaf surface (dimensionless) and  $C_a$  is atmospheric  $\text{CO}_2$  concentration at the leaf surface ( $\mu\text{mol mol}^{-1}$ ).

Returning to  $g=A/(c_a-c_i)=A/[c_a(1-c_i/c_a)]$



$$c_i/c_a = p_i/p_a$$

**Fig. 8.** Ratio of mean intercellular partial pressure of CO<sub>2</sub> and ambient pressure of CO<sub>2</sub>,  $p_i/p_a$ , as a function of vapour pressure difference between leaf and air,  $\Delta e$ . Symbols represent different leaf temperatures during measurements:  $\blacktriangle$ ,  $< 17^\circ$ ;  $\nabla$ ,  $17-20^\circ$ ;  $\square$ ,  $20-23^\circ$ ;  $\circ$ ,  $> 23^\circ\text{C}$ .

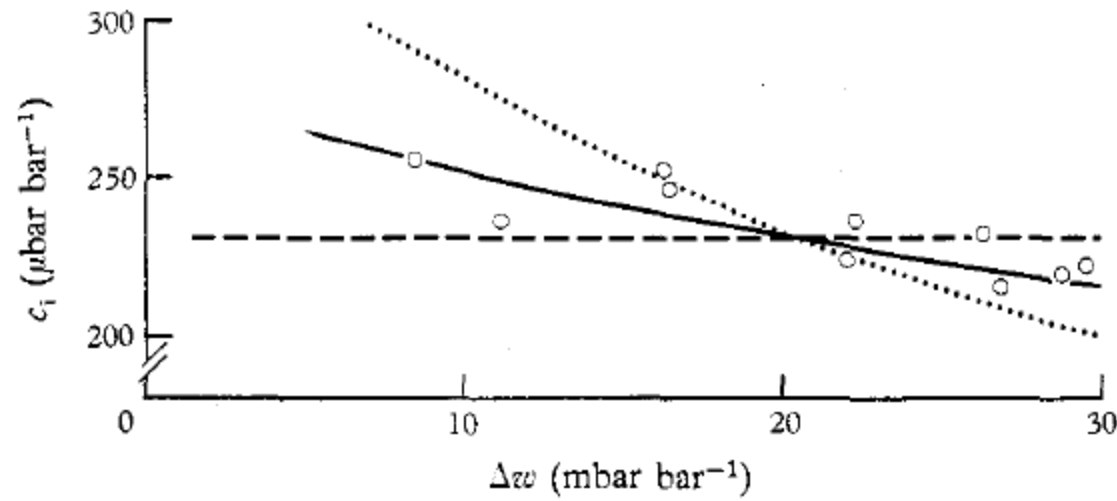
$$p_i/p_a = 0.96 - 0.0194\Delta e + 3.282 \times 10^{-4}\Delta e^2, r^2 = 0.64.$$

Wong & Dunin AJPP 1987  
Small stand of Eucalypt &  
Acacia trees in a large gas  
exchange system

# What does $\partial E/\partial A = \lambda$ say about $1 - c_i/c_a$ ?

- Farquhar Thesis 1973
- Cowan 1977
- Cowan & Farquhar 1977
- Farquhar, Schulze & Küppers 1980
- Hari et al. (1986)
- Farquhar, Lloyd, Taylor, Flanagan, Syvertsen, Hubick, Wong, Ehleringer  
*Nature* 1993
- Lloyd & Farquhar 1994

# (Early) Experiment



$c_1$  ( $231 \mu\text{bar bar}^{-1}$ ). An explanation of the derivation of these curves is given in Appendix 3.

- ..... Constant  $E$ .
- Constant  $\partial E/\partial A$ .
- - - - Constant  $A$ .

Farquhar, Schulze, Küppers AJPP 1980  
*Nicotiana glauca*

# Simple Theory

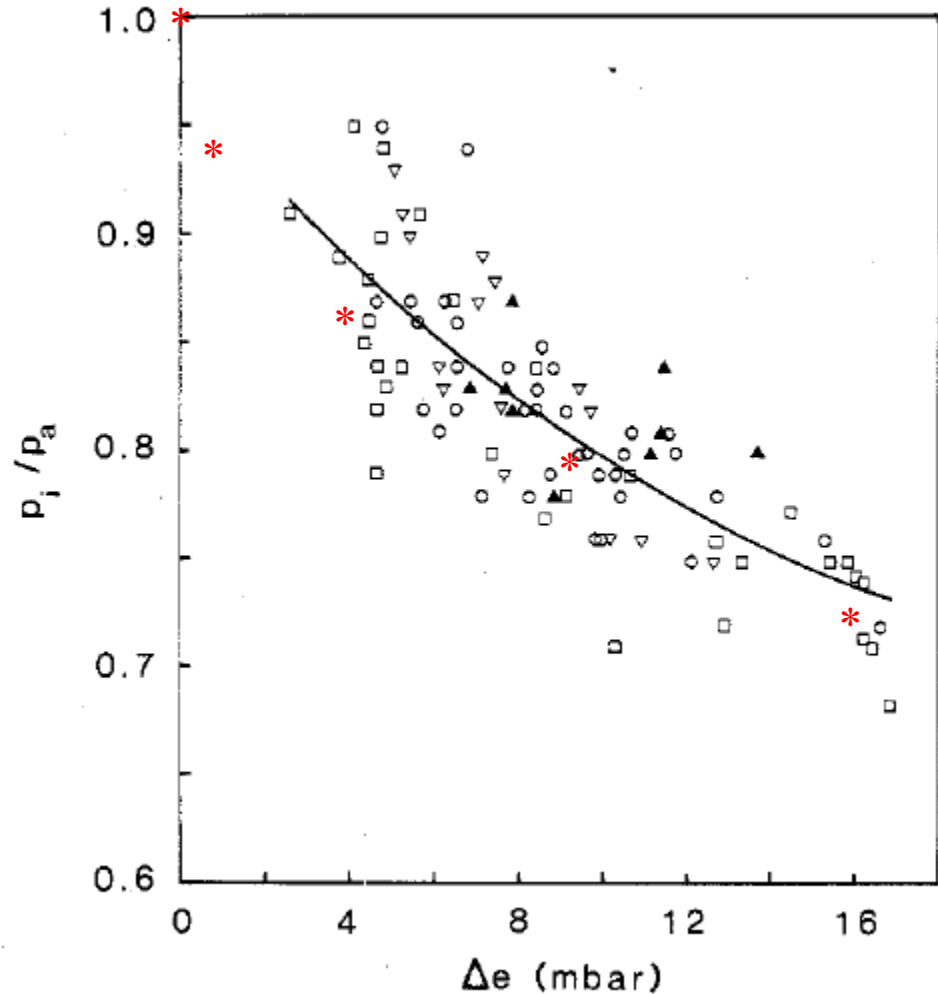
- $\partial E/\partial A = \lambda \rightarrow 1 - c_i/c_a \propto \sqrt{\Delta w}$ ,

where  $\Delta w = \Delta e/P$

- $1 - c_i/c_a \propto \sqrt{\Delta w}$  gives better fit than  $1 - c_i/c_a \propto 1/h_r$

according to Medlyn et al. (GCB 2011) who tested a related form

Try  $1 - c_i/c_a \propto \sqrt{\Delta w}$



Try  $1 - c_i/c_a = 0.07 \sqrt{\Delta w(\text{mb}/b)}$

$\Delta w = 0, 1, 4, 9, 16$

$c_i/c_a = 1, .93, .86, .79, .72$

For  $\Delta w = 20 \text{mb}$ ,  $c_i/c_a = 0.69$

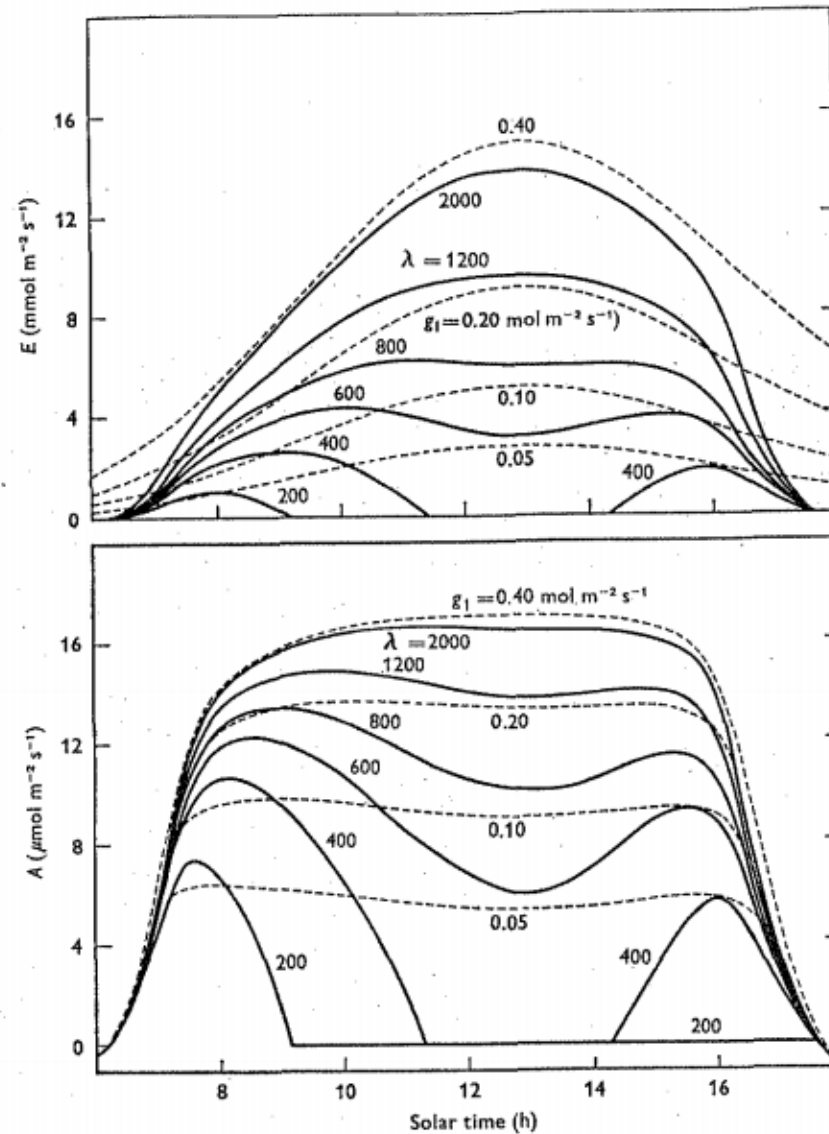
# Suggestion for empirical fit

- For C<sub>3</sub> species

- $$g_{H_2O} = \frac{1.6 A}{c_a 0.07 \sqrt{(10^3 \Delta w)}}$$

- 1.6 converts from CO<sub>2</sub> to water vapour
- 0.07 is a fitting factor that will vary with soil water content, and with species (ie with  $\lambda$ )
- For C<sub>4</sub> species the 0.07 could change to, say, 0.14

$$\partial E / \partial A = [\partial E / \partial g_s] / [\partial A / \partial g_s] = \lambda$$



Cowan & Farquhar 1977

# Returning to $\partial E/\partial A=\lambda$

## What about periods longer than a day?

- If the plant knew exactly when the next rain was coming it should choose the constant value  $\lambda$  that  $\partial E/\partial A$  should equal, such that it would almost run out of water as the next rain arrived.
- But plants don't usually know. They can however adapt to a particular environment: soil water holding capacity and statistics of rainfall.
- Between saturating rain events  $\lambda$  should decrease with time, with the time constant being the average time between events (Cowan; Mäkelä; Farquhar et al. unpub)

## Unpredictable water supply, constant demand

Assume that every rainfall event saturates the soil and that the probability of rainfall in any given time interval is constant, with the average time between rainfall events being  $\tau$ .

Then the probability of rain occurring on any given day is equal to  $(1/\tau)$ , so that the probability of *no* rain occurring equals  $(1-1/\tau)$ .

The probability of no rain occurring for two consecutive days equals  $(1-1/\tau)^2$ ; for three days,  $(1-1/\tau)^3$ ; and so on, for  $n$  days,  $(1-1/\tau)^n$ . Note that  $(1-1/\tau)^n \approx e^{-n/\tau}$

$$\begin{aligned} \text{Exp} \left[ \int_0^{T_D} A(t) dt \right] &= \int_0^{\infty} e^{-t/\tau} A(t) dt \\ &= \int_0^{\infty} e^{-t/\tau} A(g(t)) dt \end{aligned}$$

$$\frac{\partial}{\partial g} \left( e^{-t/\tau} A(g) - \frac{E(g)}{\lambda_0} \right) - \frac{d}{dt} \left( \frac{\partial}{\partial g} \left( e^{-t/\tau} A(g) - \frac{E(g)}{\lambda_0} \right) \right) = 0$$

$$\frac{\partial E}{\partial A} = \frac{\partial E}{\partial A}(t) = \lambda_0 e^{-t/\tau}$$

# Emerging analytical features

- During a rain-free period  $\lambda$  decreases and so  $g$  decreases, becoming zero after sufficient time
- Soil water content  $W$  decreases and an analytical relationship can be formed between  $g$  and  $W$
- Arrange the value of  $\lambda$  at full soil wetting (zero deficit),  $\lambda_o$ , such that no soil water is left when  $g$  reaches zero
- Mechanistically this optimisation could be achieved by soil moisture control of  $\lambda$

# Soil moisture control of $\lambda$

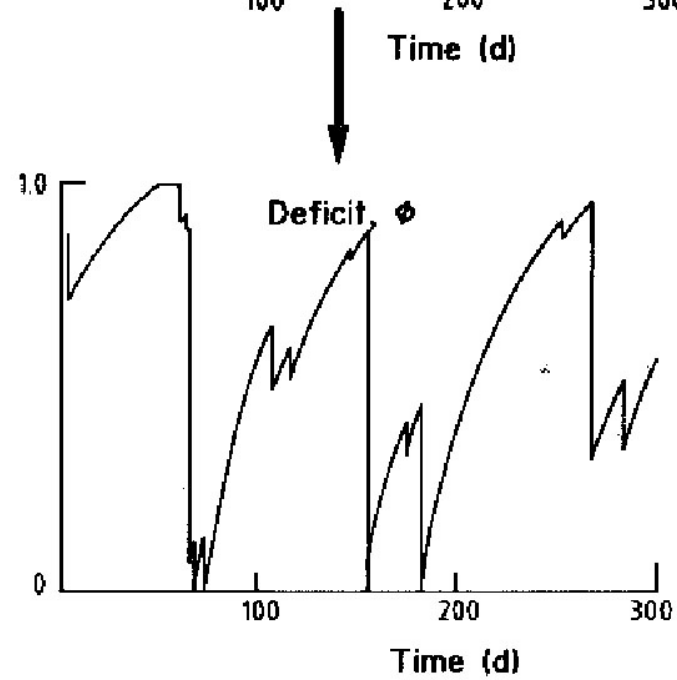
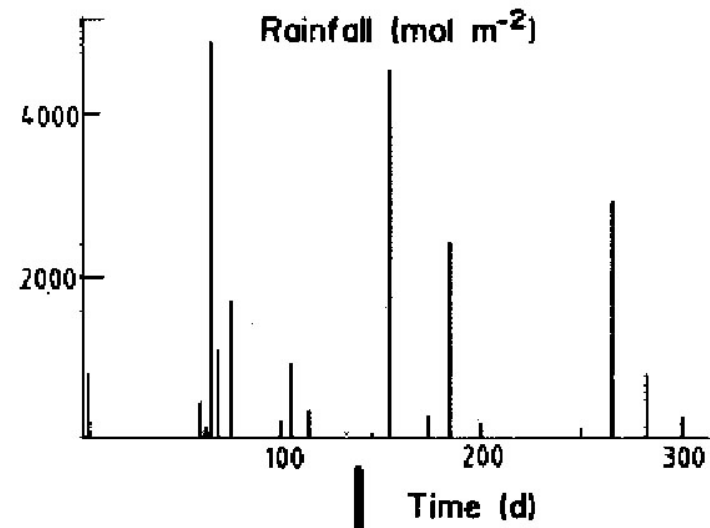
$$W(t) = 3.2 \tau D \left( g - k \ln \left[ 1 + \frac{g}{k} \right] \right)$$

- $\lambda \approx \lambda_{\text{minimum}} (1 + W / (0.32 D \tau k))$
- where  $\lambda_{\text{minimum}}$  is the value of  $\lambda$  when stomata are closed,  $W$  is soil water content,  $D$  is VPD,  $\tau$  is average time between rainfalls, and  $k$  is carboxylation efficiency

# Improving the statistics

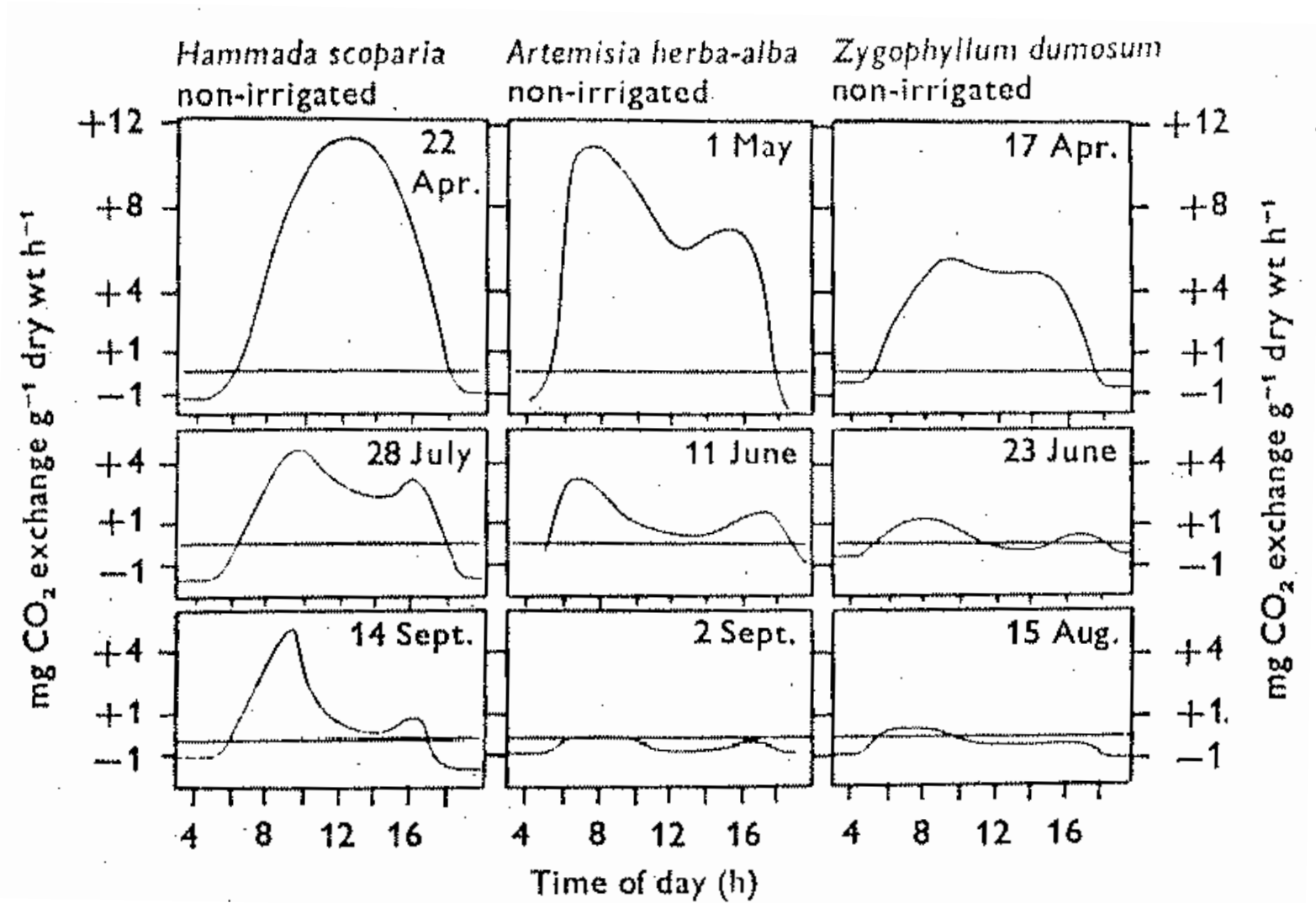
- Like Cowan (1982) and Makela et al. (1996) we assumed a Poisson process, with random saturating rainfalls.
- In practice not all rainfall events saturate the soil. Cowan (1986) introduced constant probability of rainfall (Poisson as above) but with the probability of a rainfall being greater than a certain amount taken as decreasing exponentially with the amount.

I. R. COWAN (1986)



# Returning to $\partial E/\partial A=\lambda$

## Observations



Lange et al 1975, and Cowan & Farquhar 1977

# Effective water use vs efficient water use

- Optimal water use means keeping  $\partial E/\partial A$  constant over a day, and having it decline as soil water content decreases.
- In an environment with frequent rain and deep soil this means large  $\partial E/\partial A$  and hence large  $A$ ,  $E$ ,  $g$  & large intercellular  $[CO_2]$ . ie effectiveness here  $\rightarrow$  low transpiration efficiency ( $A/E$ ).
- With infrequent rain and thin soil, effectiveness  $\rightarrow$  small  $\partial E/\partial A$ , low  $C_i$  & high transpiration efficiency.

**we can use stable carbon isotope composition to recognise such differences across genotypes**

**Combining carbon isotope  
discrimination,  $\Delta$ , with  $\partial E/\partial A = \lambda$**

$b$ =discrimination by Rubisco

$a$ =discrimination during diffusion

$\Gamma$ =CO<sub>2</sub> compensation point

$\rho = \lambda / \lambda_{\min}$

$$\Delta = b - (b - a)(1 - \Gamma / c_a)\rho^{-1/2}$$

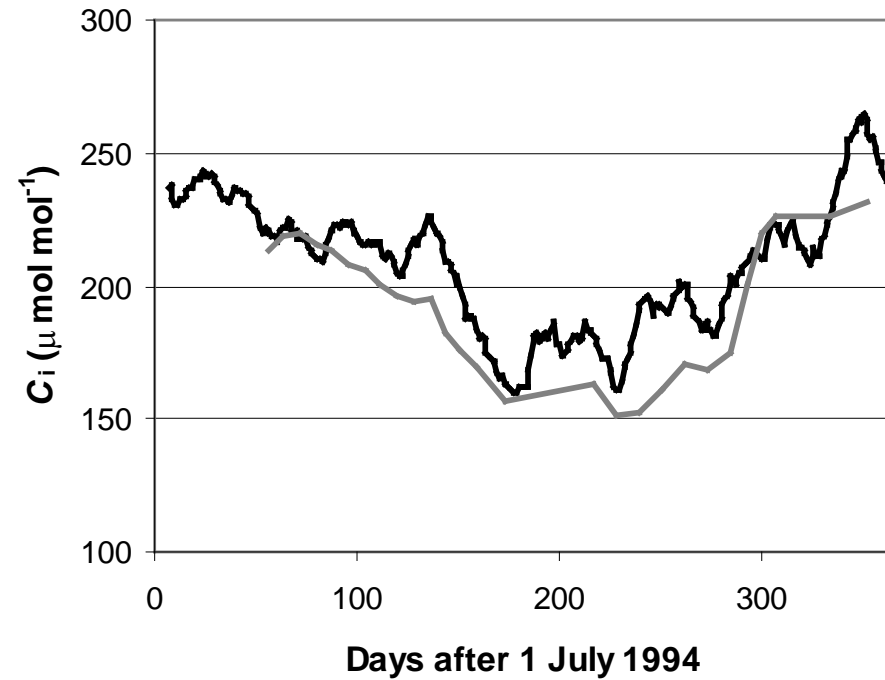
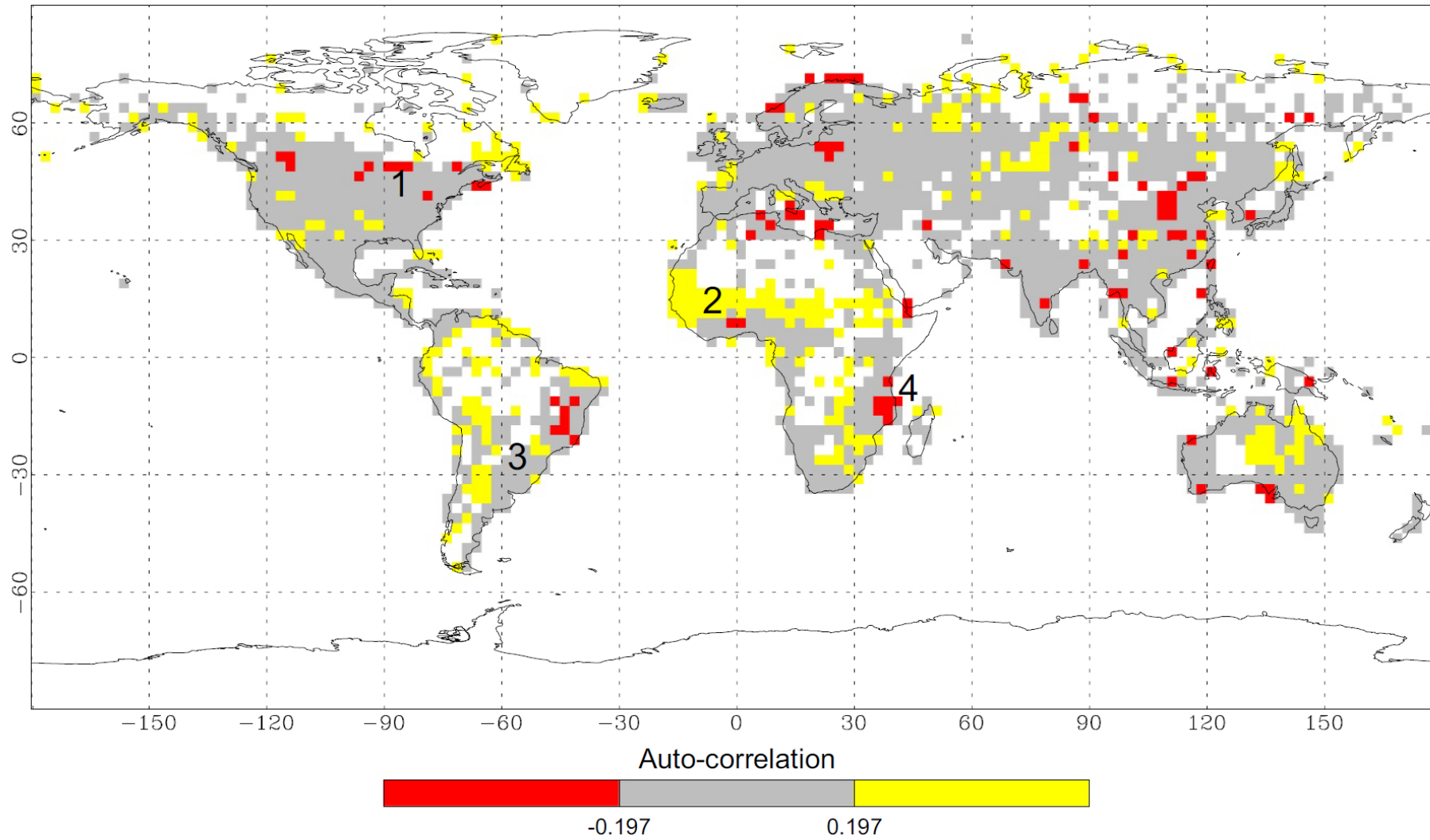


Figure 1. Seasonal course in assimilation-weighted whole-canopy intercellular  $\text{CO}_2$  concentration in a dry-land *Pinus radiata* forest derived from intra-tree-ring measurements of  $\delta^{13}\text{C}$  (grey line), and that simulated using the model of canopy photosynthesis and stomatal conductance based on the optimisation hypothesis (black line, 14-day smoothing applied).

# Rainfall stats on longer time scale

- **Rainfall statistics, stationarity, and climate change**
- **Fubao Sun, Michael L. Roderick, and Graham D. Farquhar**
- **PNAS March 6, 2018**

Estimate of the lag 1 autocorrelation of annual  $P$  (1940–2009; GPCC).



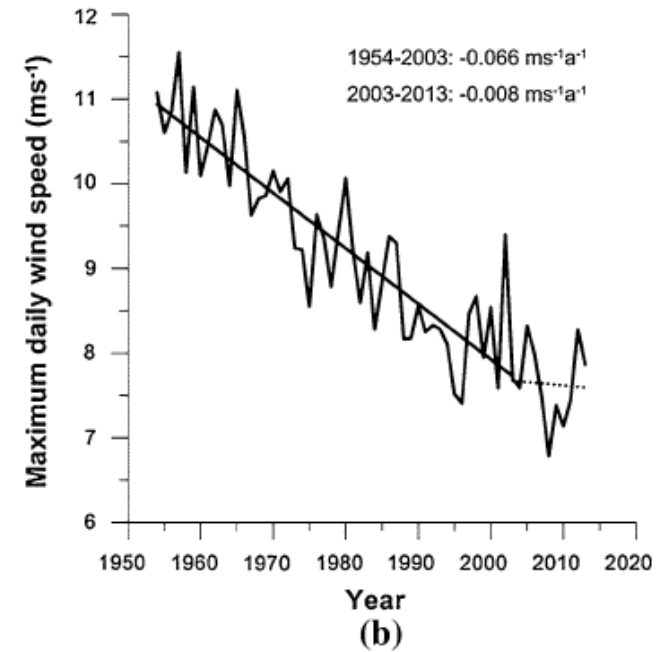
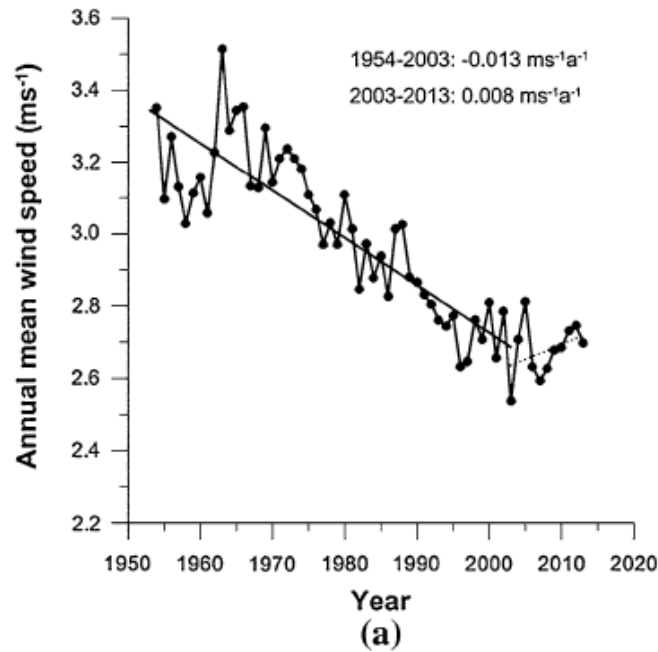


# Windspeed

- Roderick ML, Rotstayn LD, Farquhar GD and Hobbins MT. (2007) On the attribution of changing pan evaporation. **Geophysical Research Letters** VOL. 34, L17403, doi:10.1029/2007GL031166
- Showed that windspeed is declining over land. Eg Australia 1 cm/s per year over the last 30 years means a drop of 0.3 m/s against a mean wind speed of 2 m/s, ie a 15% drop!
- This despite apparent increases of windspeed over oceans

# Declining windspeeds in S Korea

Kim & Paik  
Climate Dynamics  
2015



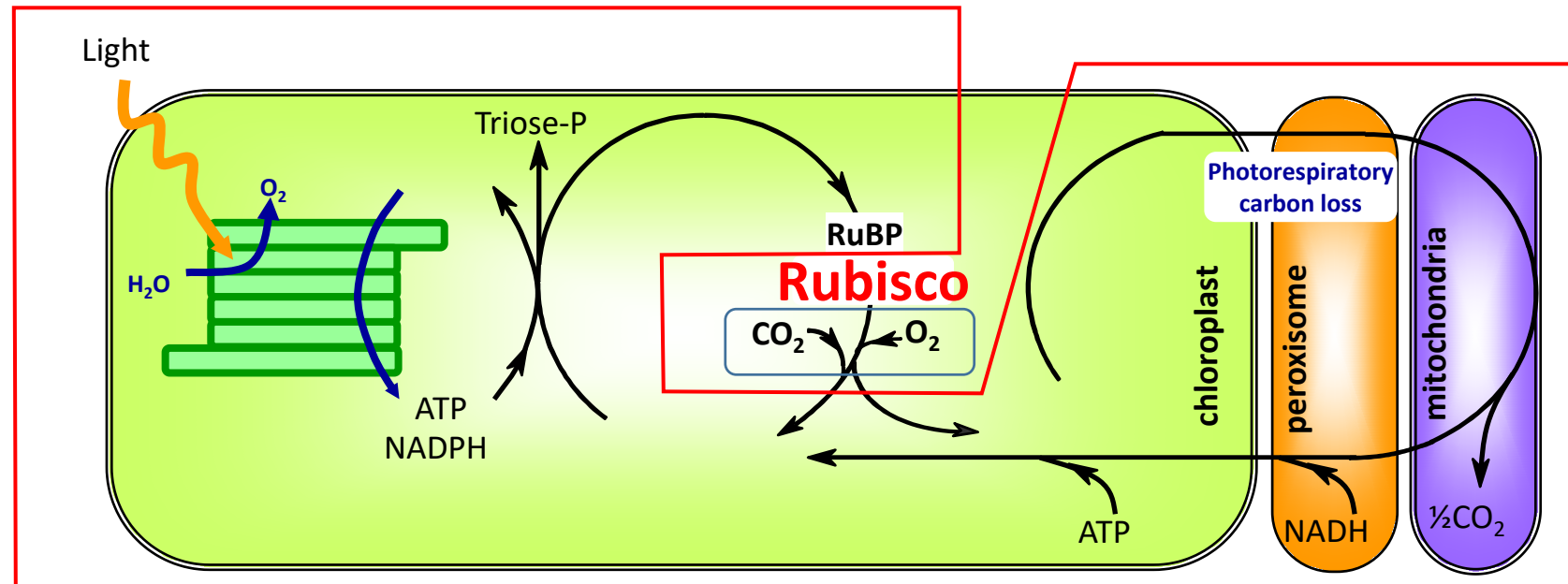
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- Thank you

# Farquhar, von Caemmerer & Berry model of $C_3$ photosynthesis

Simplified all of the biochemistry into two limiting conditions

1. Rubisco activity
2. RuBP supply



Planta 149: 78-90 (1980)