# $CO_2$ and carbon uptake by land ecosystems – towards a synthesis of theory, observations and models

**Iain Colin Prentice**

*AXA Professor of Biosphere and Climate Impacts, Imperial College London*

*Honorary Professor in Ecology and Evolution, Macquarie University*

*Foreign Expert, Department of Earth System Science, Tsinghua University*

including unpublished results by:

**Manuela Balzarolo** (*CREAF, Barcelona*)

**César Terrer Moreno** (*CREAF, Barcelona*)

**Beni Stocker** (*CFEAF, Barcelona*)

**Han Wang** (*Tsinghua University*)

# We need OBSERVATIONS

# We need MODELS

- To scale up from leaves to ecosystems
- And from ecosystems to the world
- To establish consistency among different space and time scales of observation

- ....and to make future projections!

# We need THEORY
# (a set of mathematical statements that can be tested)

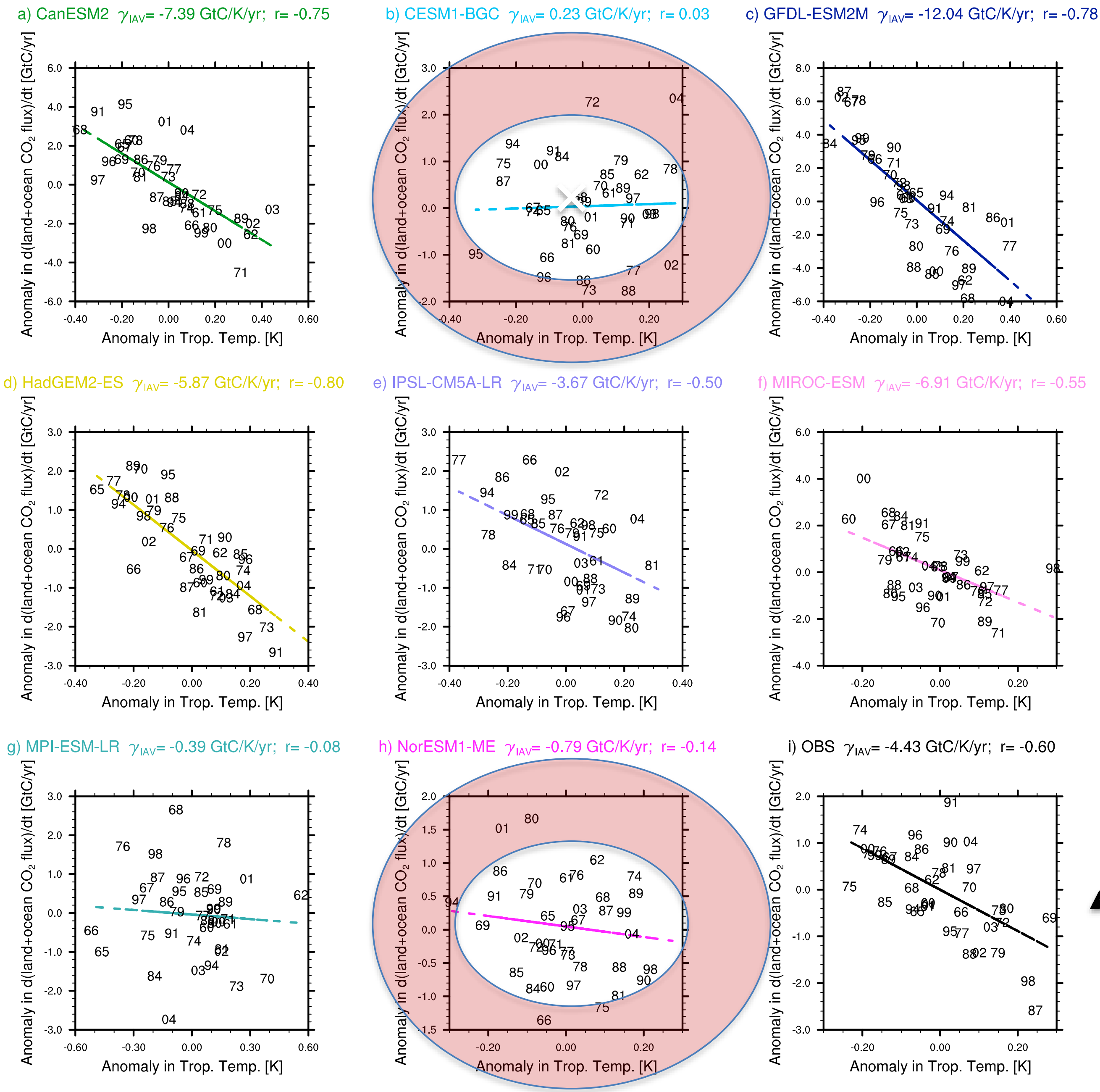
- To interpret observations, including experiments
- To provide a clear and consistent basis for models

# Ecosystem science HAS NO THEORY

It has MYTHS instead... For example, these incorrect statements:

- Photosynthetic capacity is controlled by nitrogen
- NPP/GPP decreases with temperature
- Liebig's "law" – GPP is controlled by the most limiting resource (or even, the most limiting "factor")
- Nitrogen isotope discrimination depends on the "openness" of the nitrogen cycle
- The world is getting dryer
- "Greening" of dry environments will saturate as $CO_2$ increases
- Wildfire frequency increases with population density
- etc., etc.

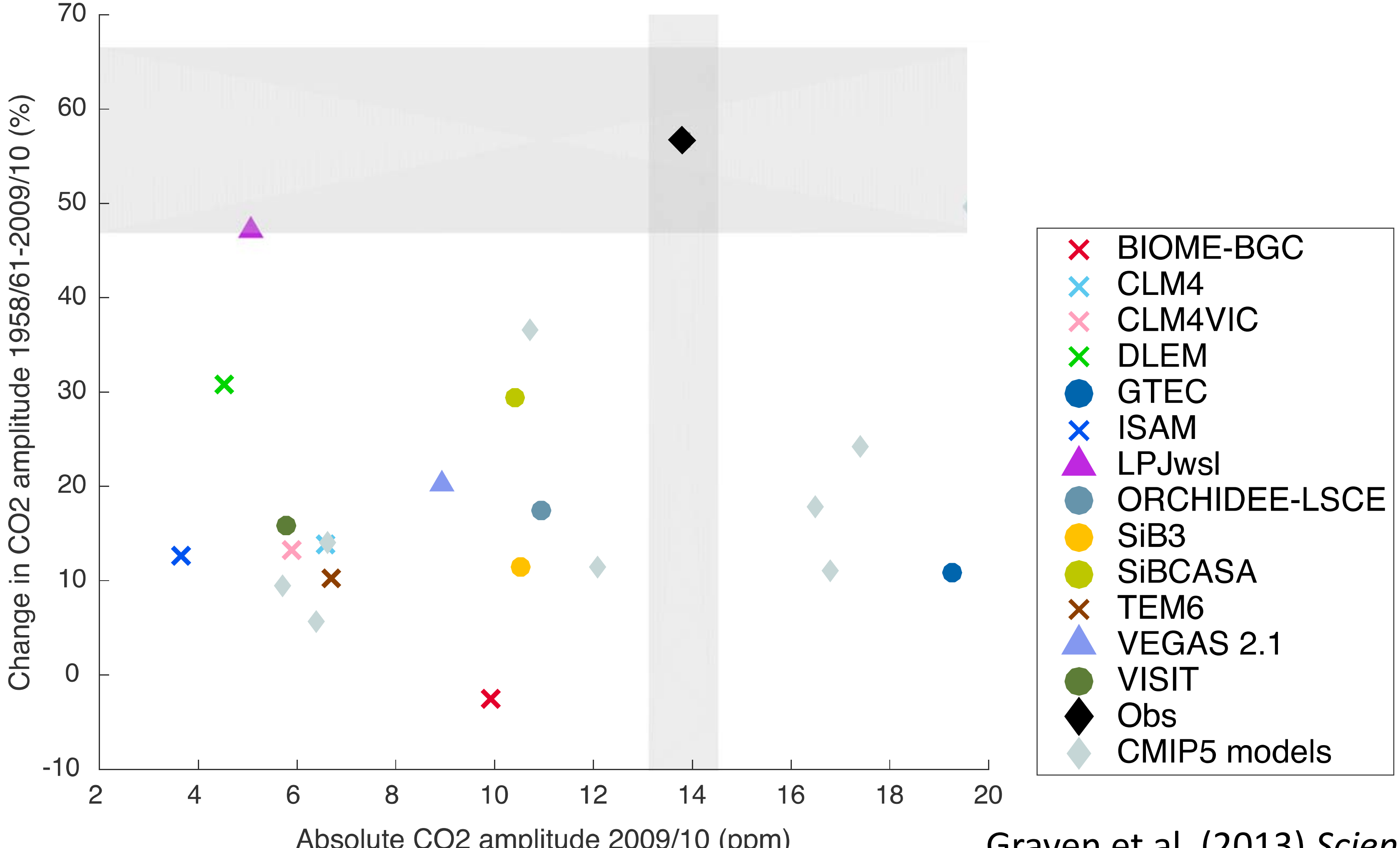
# $CO_2$ uptake and tropical temperatures (in CMIP5 models)




**OBSERVATIONS**

Wenzel *et al.* (2014) *JGR*

# $CO_2$ seasonal cycle high in the northern atmosphere (in CMIP5 and MsTMIP ensembles)




Graven et al. (2013) *Science*
Thomas *et al.* (2016) *GRL*

# Time for a new approach!

- We now live in a data-rich world....
- How about **using data** in the development of theory and models?
- But what principles should guide theory development?

# Natural selection => optimality

*"Nothing in biology makes any sense except in the light of evolution"*
*"The unity of life is no less remarkable than its diversity"*
(Dobzhansky, 1973)

# Successful theoretical predictions of traits and rates for plants and ecosystems (1)

- Isoprene emission: Morfopoulos *et al.* (2014) *New Phytologist*
- $c_i$:$c_a$ ratio: Prentice *et* al. (2014) *Ecology Letters*, and Wang *et al.* (2017) *Nature Plants*
- Elevation effects : Wang *et al.* (2017) *New Phytologist*
- Leaf nitrogen: Dong *et al.* (2017) *Biogeosciences*
- $V_{cmax}$: Togashi *et* al. (2018) Biogeosciences, and Smith *et al.* (2018) *Ecology Letters*
- $J_{max}$:$V_{cmax}$ ratio: Wang *et al.* (2017) *Nature Plants*
- Multiple leaf traits: Bloomfield *et al.* (2019) *New Phytologist*
- GPP: Wang *et al.* (2017) *Nature Plants*

# Successful theoretical predictions of traits and rates for plants and ecosystems (2)

- $R_{dark}$: H Wang *et al.* (submitted)
- Recent GPP trends: Cai *et al.* (in prep.)
- Elevation trends in leaf traits, GPP and NPP: Y Peng *et al.* (in prep.)
- Leaf-to-air $\Delta T$: A Kamolphat *et al.* (in prep.)
- Leaf mass-per-area and lifespan: H Wang & IC Prentice (in prep.)

# Photosynthetic physiology

The **FvCB model**:

$$A = \min\{A_C, A_J\} - R_{dark} \text{ where:}$$

$$A_C = \mathbf{V_{cmax}} (\mathbf{c_i} - \Gamma^*)/(\mathbf{c_i} + K)$$

$$A_J \approx \varphi_0 I_{abs} (\mathbf{c_i} - \Gamma^*)/(\mathbf{c_i} + 2\Gamma^*) \text{ at low light...}$$

...asymptotic approach to $\mathbf{J_{max}}$ / 4 at high light

$$R_{dark} = 0.015\, \mathbf{V_{cmax}} \text{ at } 25^\circ\text{C}$$

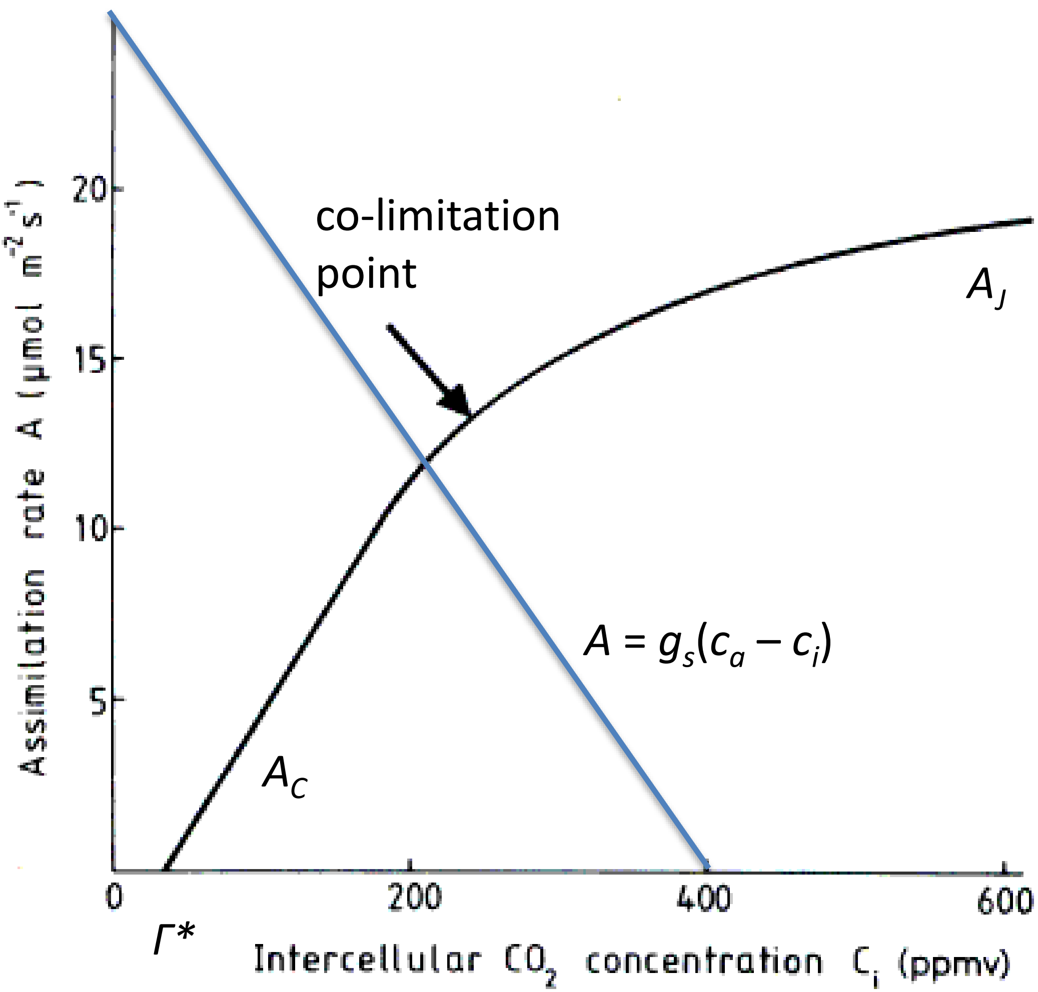
**Diffusion equations** for photosynthesis ($A$) and transpiration ($E$):

$A = \mathbf{g_s} (c_a - \mathbf{c_i})$ — $\mathbf{g_s}$ is stomatal conductance to $CO_2$

$E = 1.6\, \mathbf{g_s}\, D$ — $D$ is vapour pressure deficit

**Green** symbols are **unknown** quantities, **controlled by plants**!

# The $A$-$c_i$ curve



# What controls the $c_i$:$c_a$ ratio ($\chi$)?

- Nearly constant with $c_a$ and $I_{abs}$
- Declines with *D*
- “Empirical” equations used in models:

| | | |
|---|---|---|
| **Ball-Berry** | $\chi \approx 1 - 1/\boldsymbol{m}h$ | (*h* is relative humidity) |
| **Leuning** | $\chi \approx \boldsymbol{f_0}\,(1 - D/\boldsymbol{D_{00}})$ | |

# An alternative, theoretical approach

- Plants must transport water, in order to take up $CO_2$
- Minimize the cost function $\boldsymbol{a}\,(E/A) + \boldsymbol{b}\,(V_{cmax}/A)$
- Take derivative wrt $\chi$ and equate to zero =>

$$\chi = \gamma + (1 - \gamma)\,\xi/(\xi + \sqrt{D})$$

$$\approx \xi/(\xi + \sqrt{D})$$

where:

$$\gamma = \Gamma^*/c_a \qquad (\approx 0.1)$$

$$\xi = \sqrt{(bK/1.6a)}$$

$$K = K_C\,(1 + O/K_O)$$

***b*/*a*** is roughly constant (at any given temperature)....

Prentice *et al.* (2014) *Ecology Letters*

# Consequences of the theory

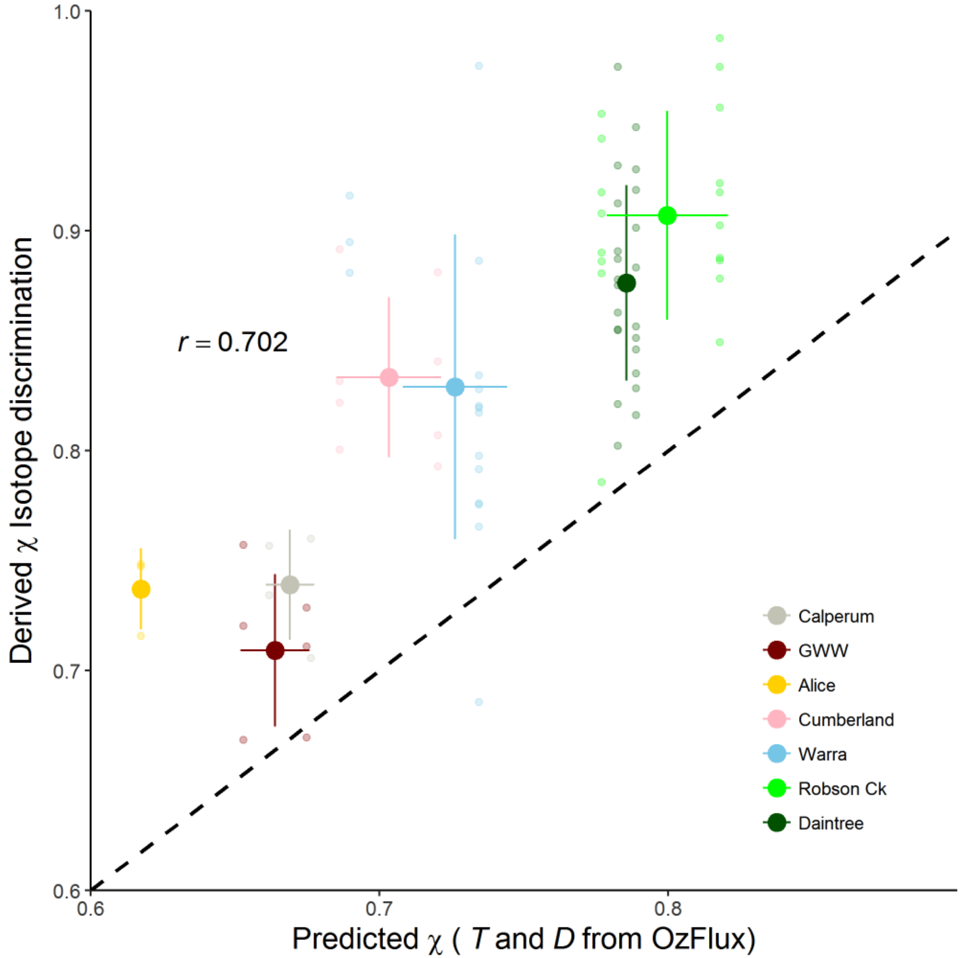
- Environmental responses:
  - χ increases with temperature ($K_c$, $K_o$, $\eta$)
  - χ decreases with vapour pressure deficit ($D$)
  - χ decreases with elevation ($O$, $D$)
- All correct
- Some were known, but not understood properly

# Quantitative effects: Predictions *versus* data (leaf $\delta^{13}C$)

| | predicted (by theory) | fitted (by regression) |
|---|---|---|
| temperature (K) | 0.054 | 0.052 ± 0.006 |
| ln vpd | –0.5 | –0.55 ± 0.06 |
| elevation (km) | –0.08 | –0.11 ± 0.03 |

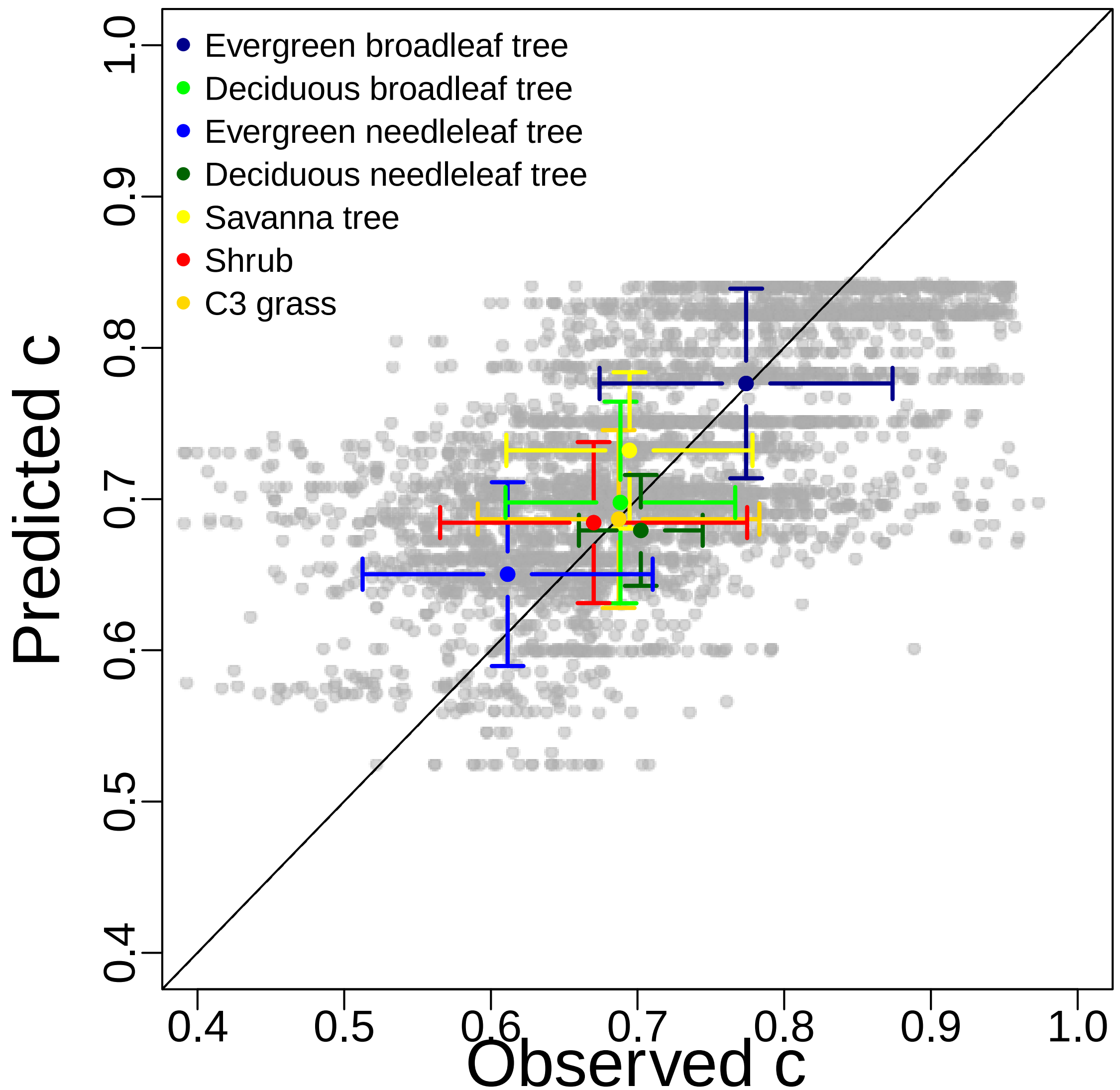
Wang *et al.* (2017) *Nature Plants*

# $\chi$ around Australia




Bloomfield *et al.* (2019) *New Phytologist*

# χ worldwide




Wang *et al.* (2017)
*Nature Plants*

# What controls $V_{cmax}$?

"Co-ordination hypothesis": $V_{cmax}$ is set to just use available light

- not more, not less...
- **co-limitation** by $V_{cmax}$ and light under average daytime conditions
- not a new idea, but its profound implications for modelling have been largely missed

# Regulation of $V_{cmax}$ according to the co-ordination hypothesis

Predictions:

1) $V_{cmax}$ increases **in proportion** to light
   (not a saturating response, as in most models)
2) $V_{cmax}$ increases **weakly** with temperature
   (less steeply than enzyme kinetics, as used in most models)

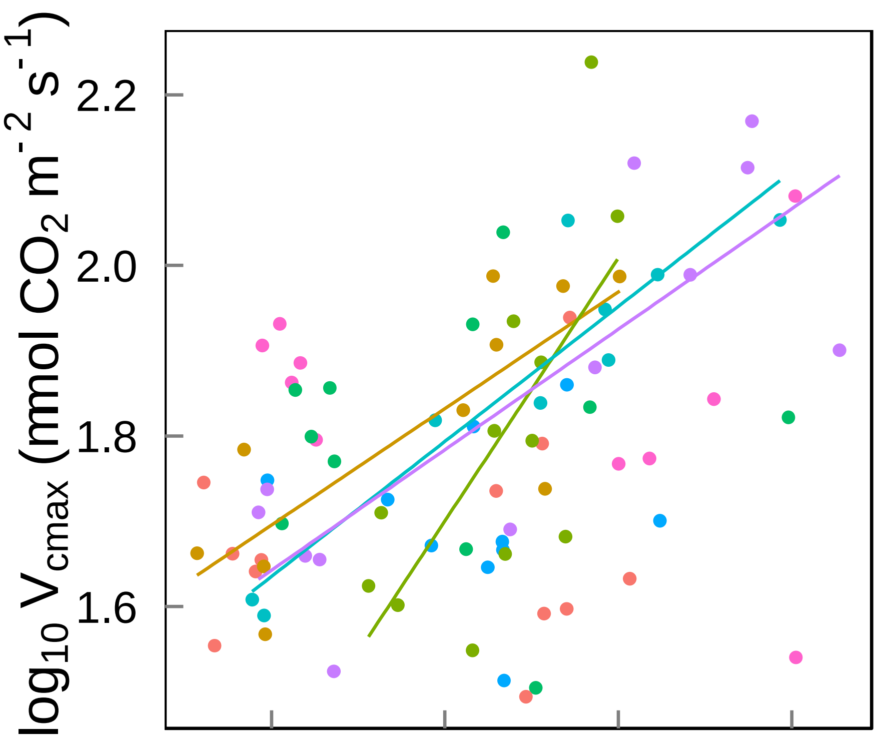
# Some additional correct predictions

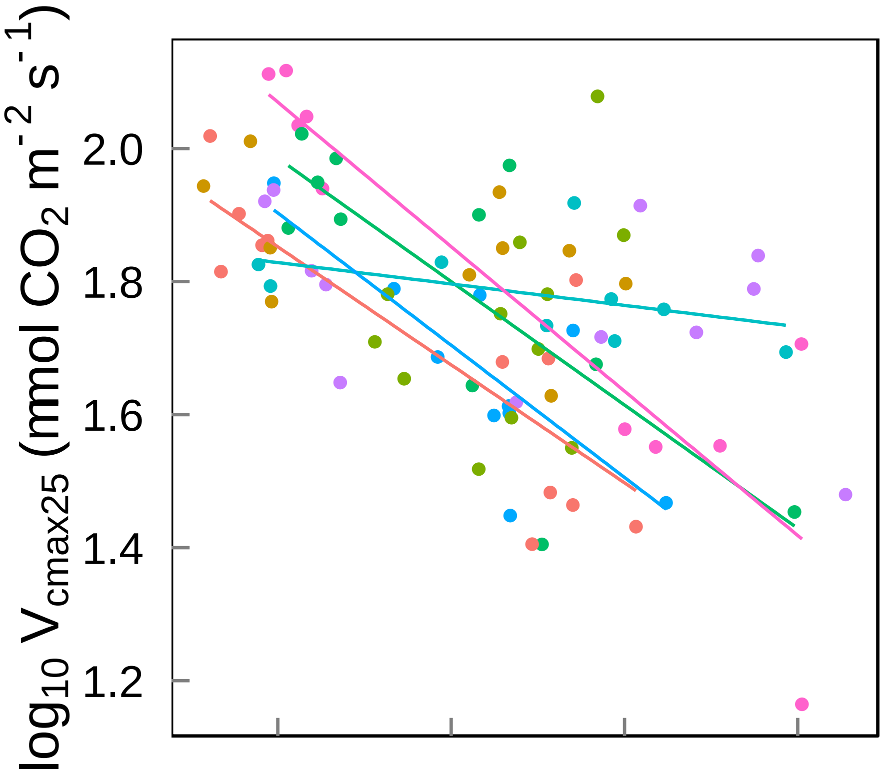
- high $V_{cmax}$ in dry environments
- high $V_{cmax}$ at high elevations
- reduced $V_{cmax}$ at elevated $CO_2$

=> these statements *also apply to leaf N...*

Wang *et al.* (2017) *New Phytologist*

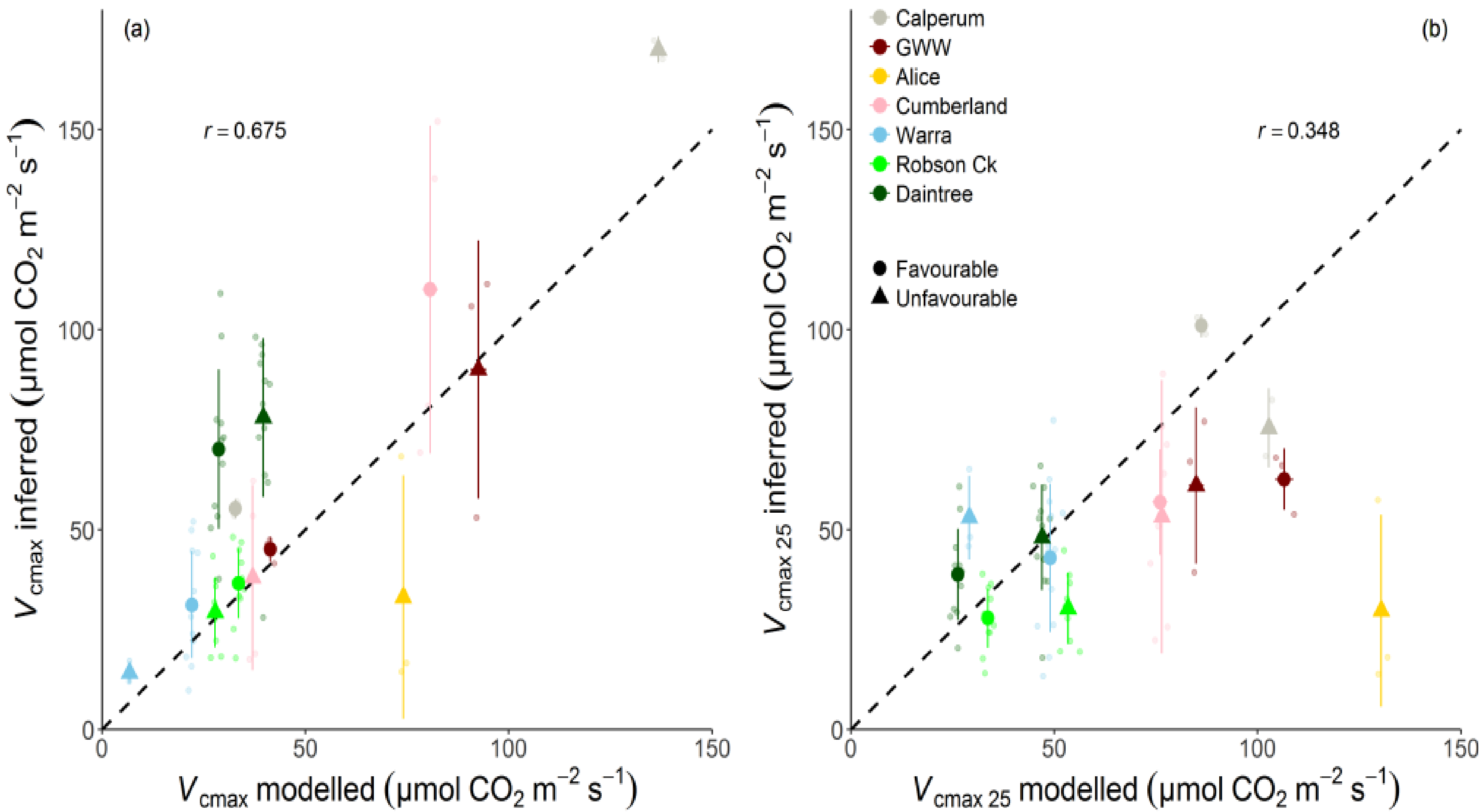
# Seasonal acclimation of $V_{cmax}$ (repeat measurements on the same plants: Great Western Woodlands, Australia)



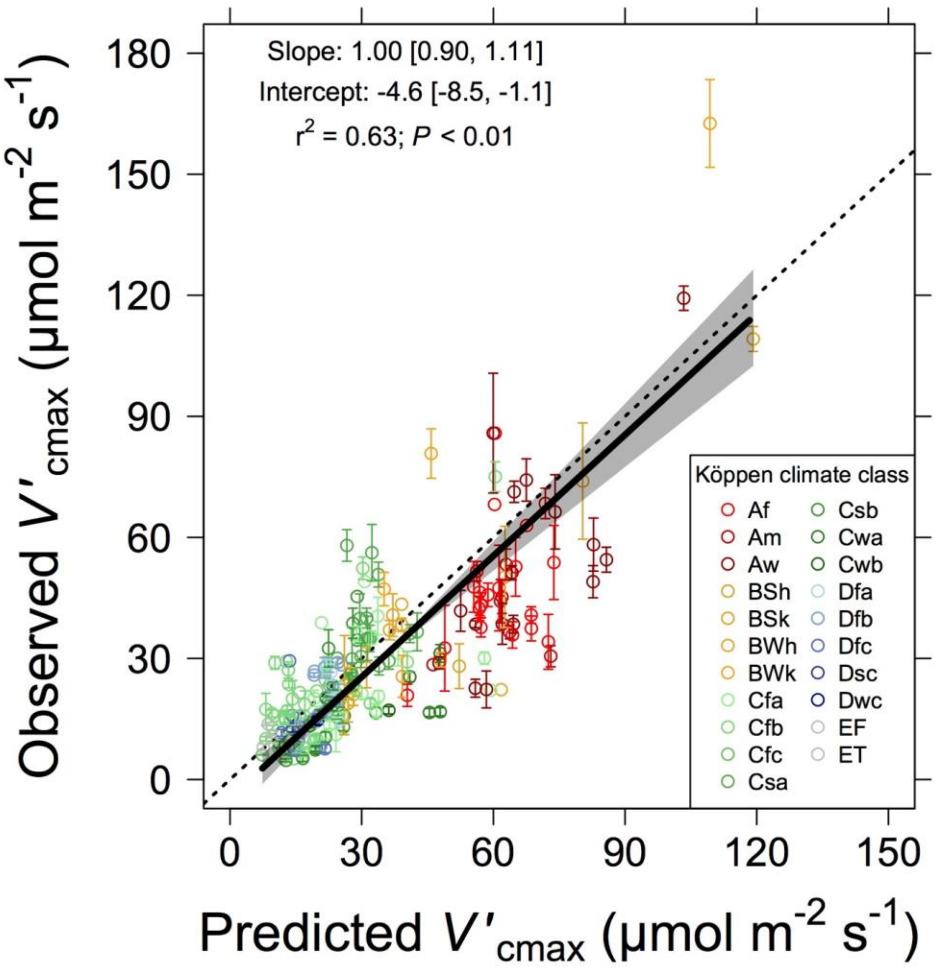

Togashi *et al.* (2018) *Biogeosciences*

# $V_{cmax}$ around Australia




Bloomfield *et al.* (2019) *New Phytologist*

# $V_{cmax}$ worldwide



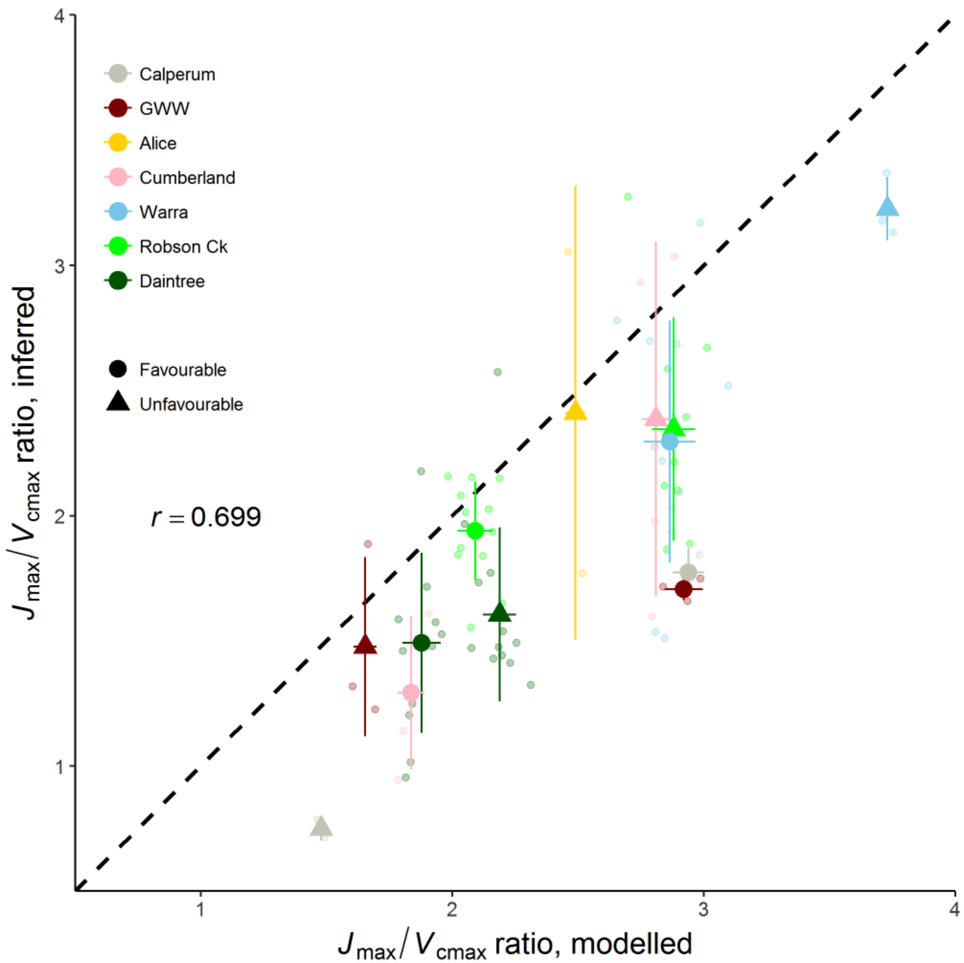

Smith *et al.* (2018)
*Ecology Letters*

# What controls $J_{max}$?

An extension: maximize the **benefit** (added photosynthesis) **minus cost** of an increment in $J_{max}$

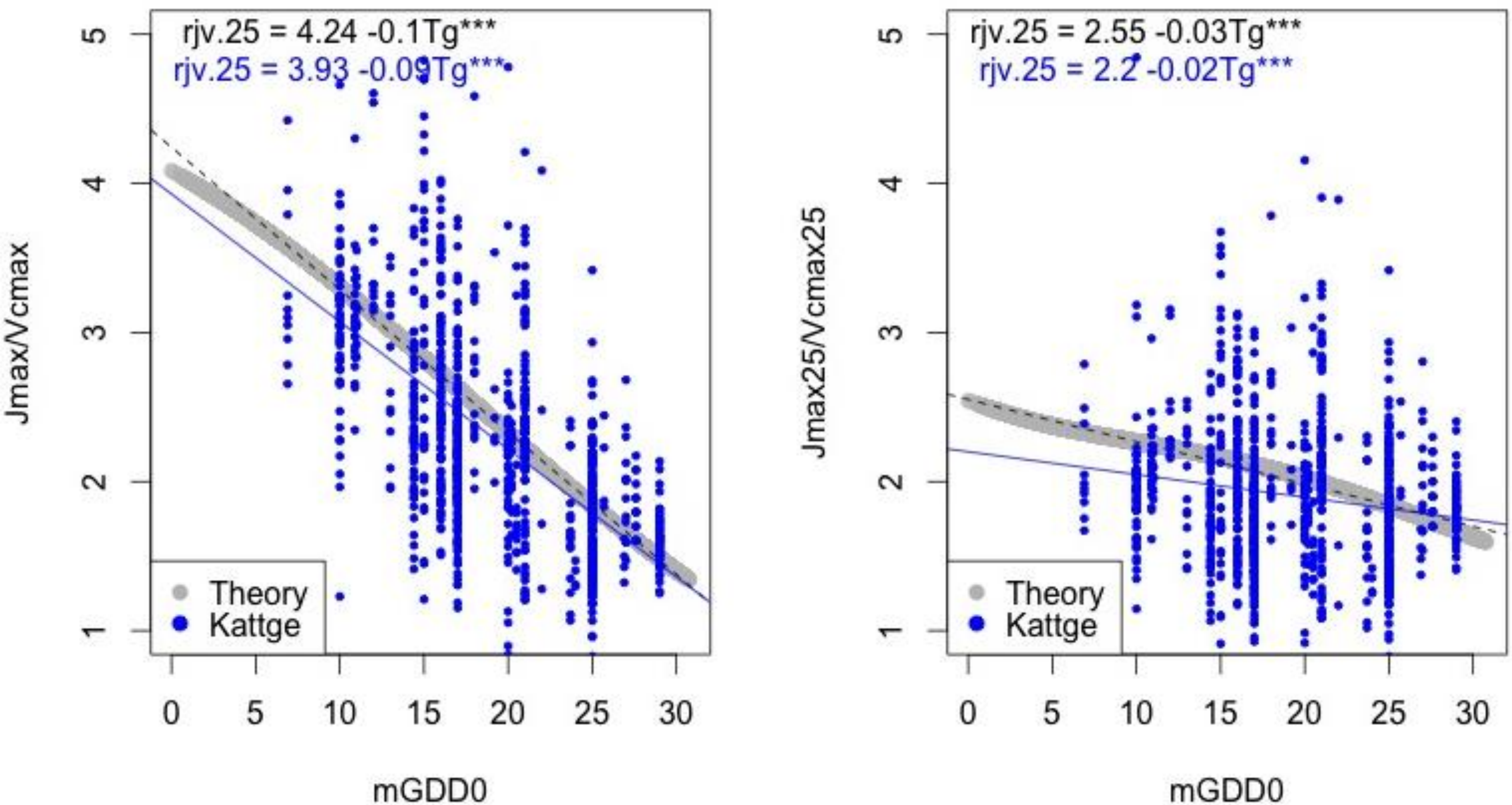
- predicts a conservative *ratio* of $J_{max}$ to $V_{cmax}$
- ratio declines steeply with growth temperature

# $J_{max}$:$V_{cmax}$ ratios around Australia




Bloomfield *et al.* 2018 *New Phytologist*

# $J_{max}$:$V_{cmax}$ ratios in experiments



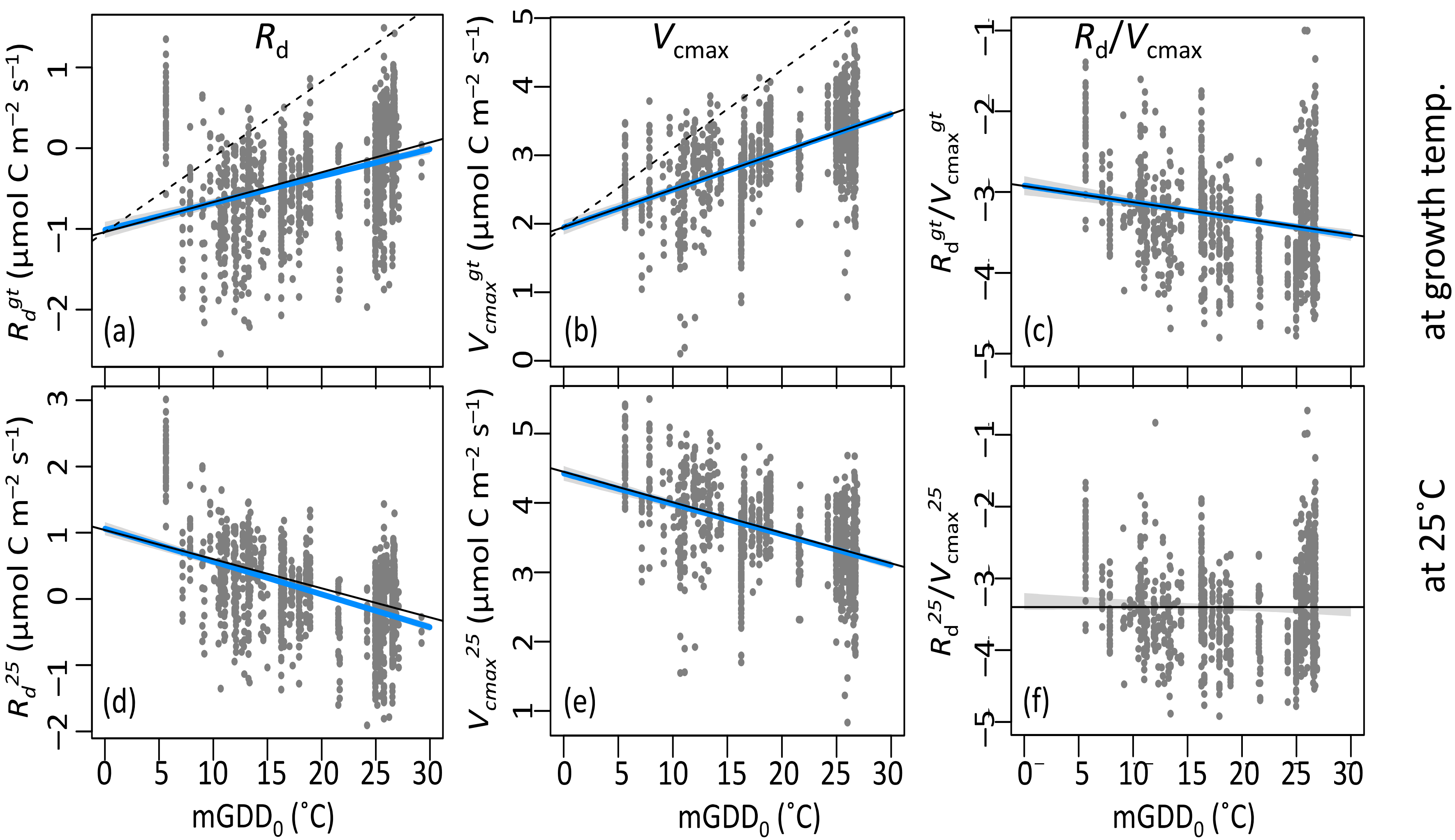

H Wang *et al.* (unpublished results)

# What controls $R_{dark}$?

FvCB model: at constant temperature (e.g. 25˚C), $R_{dark}$ is a **fixed fraction** of $V_{cmax}$

- predicts a conservative *ratio* of $R_{dark}$ to $V_{cmax}$
- the optimal ratio declines slightly with growth temperature

# $R_{dark}$, $V_{cmax}$ and their ratios, worldwide




H Wang *et al.* (submitted)

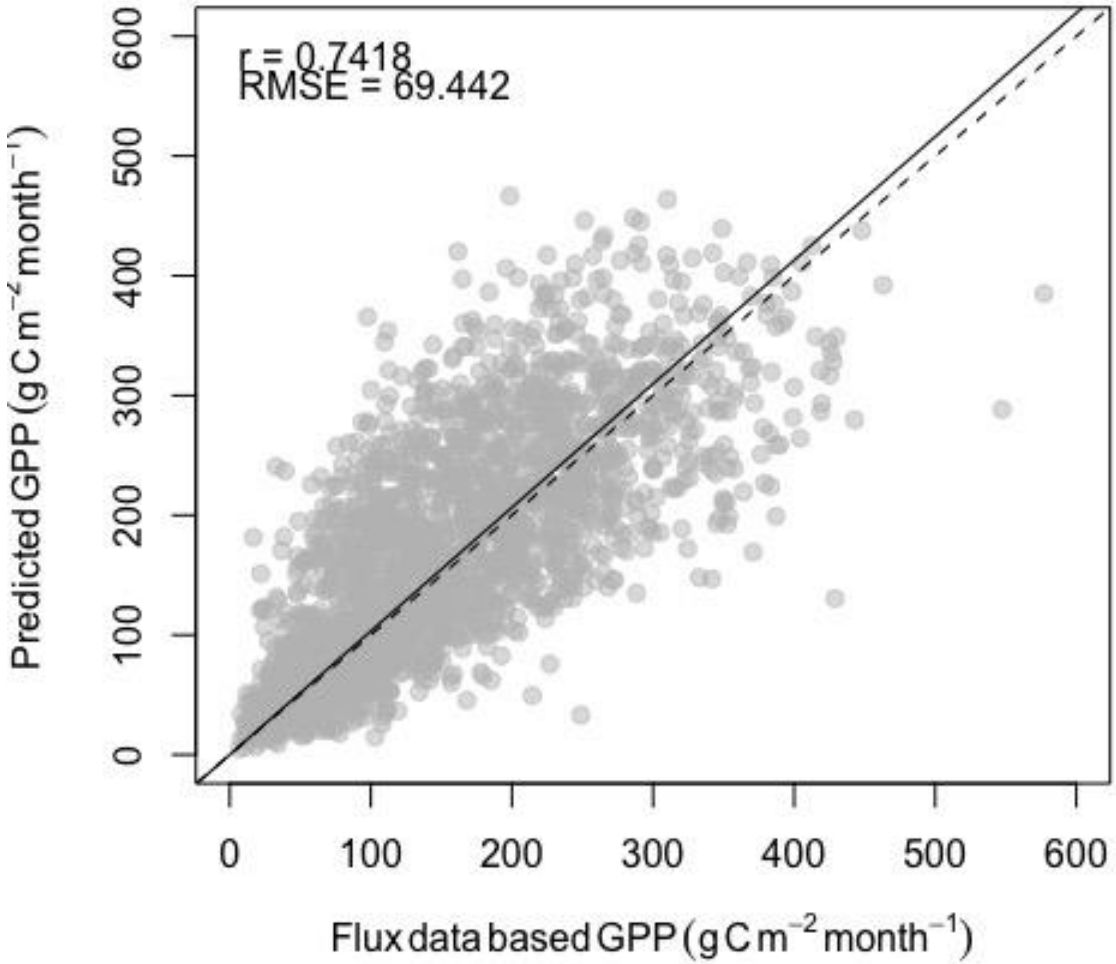
# Leaf N: cause or effect?

- Most models assume $V_{cmax}$, $J_{max}$ and $R_d$ are *controlled* by leaf N.
- They are *correlated* with leaf N.
- An alternative interpretation: $V_{cmax}$ is tightly regulated, and *controls* $J_{max}$, $R_{dark}$ and leaf N.

# Leaf N (ln $N_{area}$) around Australia

| | predicted | fitted |
|---|---|---|
| χ (from $\delta^{13}C$) | –0.62 | –0.61 ± 0.25 |
| ln PPFD | 1 | 0.87 ± 0.10 |
| mean annual T | –0.048 | –0.047 ± 0.007 |

Dong *et al.* (2017) *Biogeosciences*




# Predicting monthly GPP

$$A_J = j_0 I_{abs} m \sqrt{1 - \left(\frac{c^*}{m}\right)^{\frac{2}{3}}}$$

$$m = \frac{c_a - G^*}{c_a + 2G^* + 3G^* \sqrt{\frac{1.6 D h^*}{b\left(K + G^*\right)}}}$$

$\varphi_0$ = 0.085
*from literature*

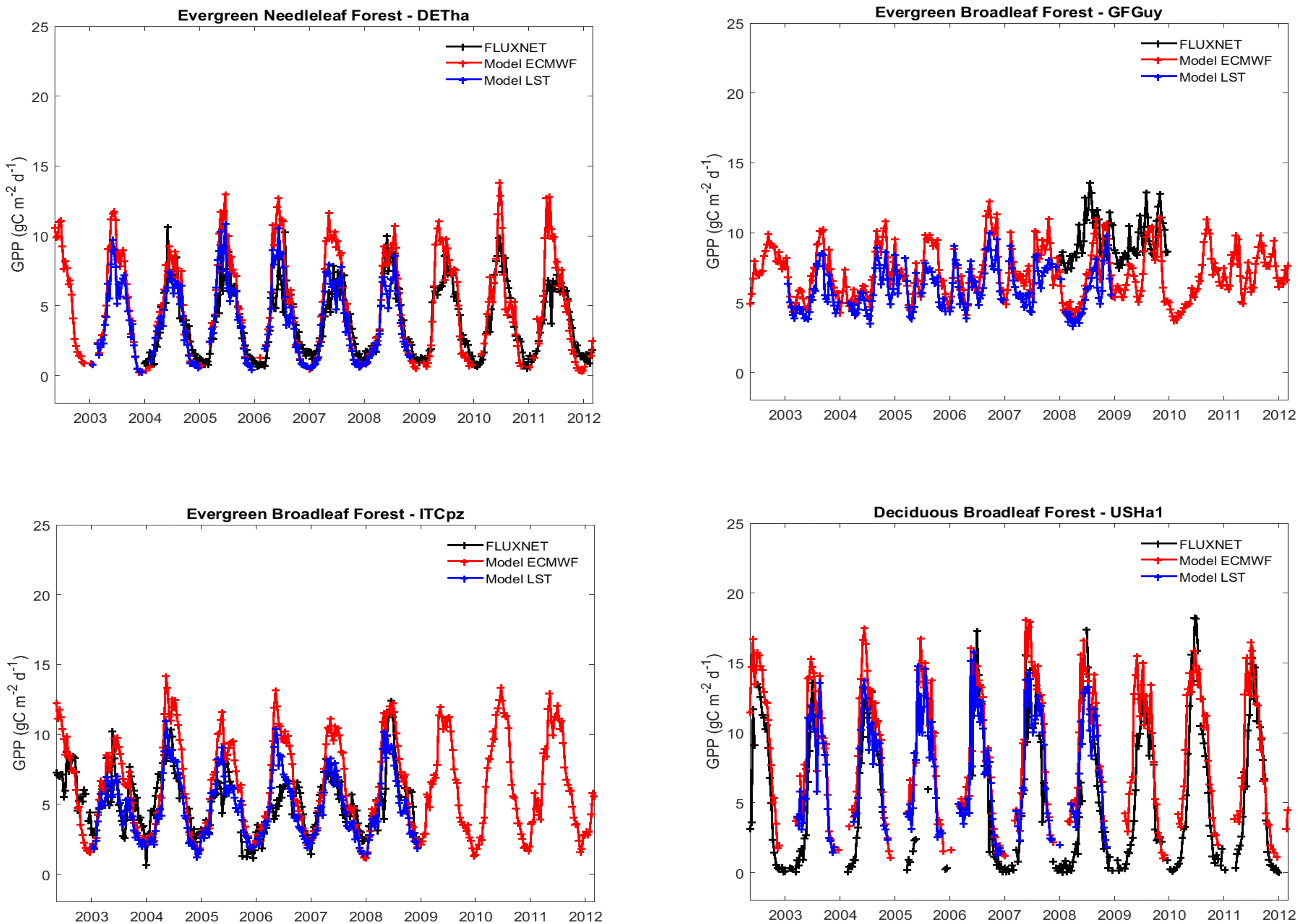
$c^*$ = 0.41
*from experiments*

β = *b*/*a* at 25˚C = 146
*from* $\delta^{13}$*C data*

Wang *et al.* (2017)
*Nature Plants*

Green vegetation cover = **MODIS EVI**
Temperature, vpd, sunshine hours = CRU CL2.0
$CO_2$ = NOAA GlobalView

# TerrA-P validation sites: flux data (black), model (red, blue)




Balzarolo *et al.* (2018)

# Comparison with experimental $CO_2$ effects

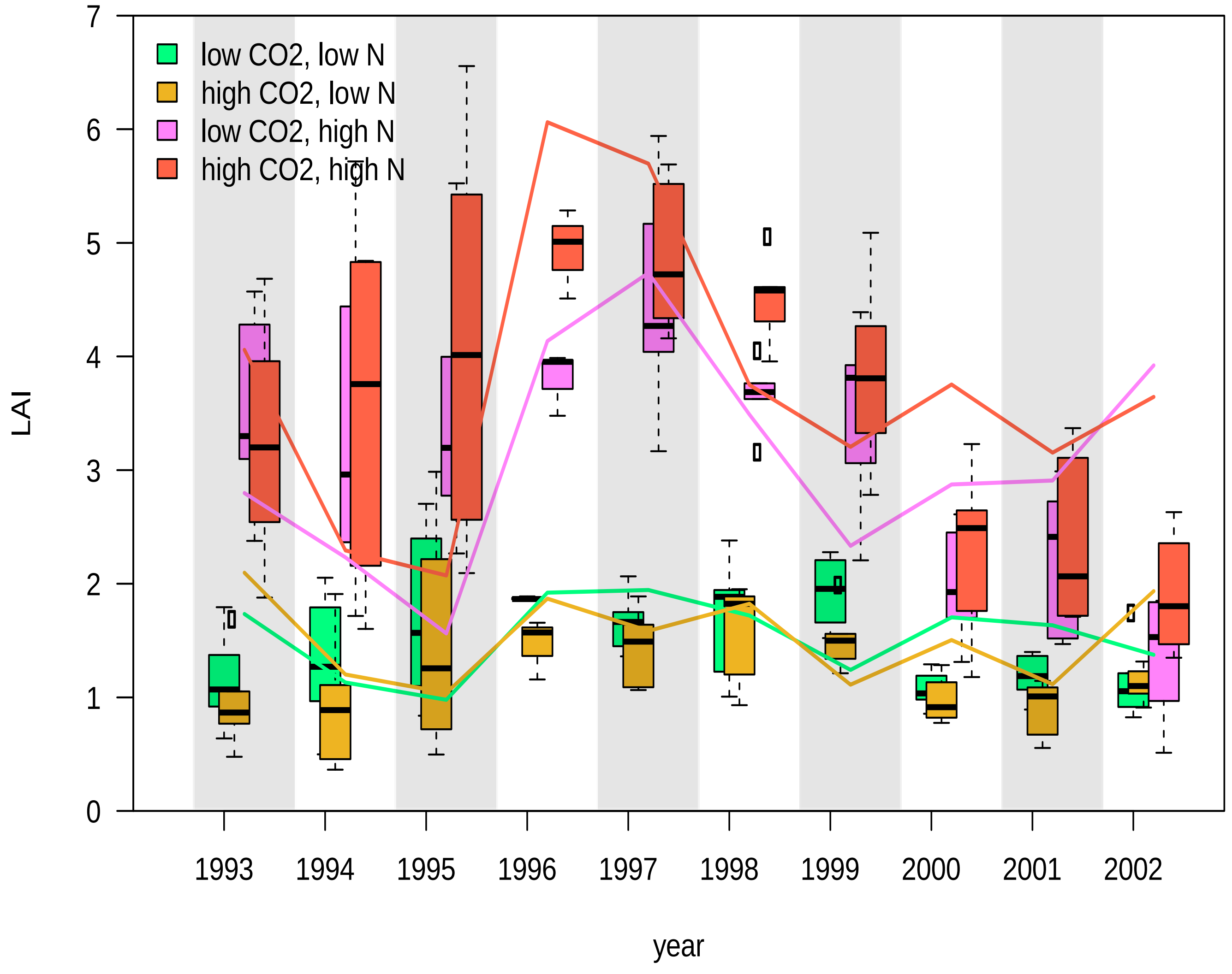
Comparison with Ainsworth & Long's (2005) meta-analysis of FACE experiments (≈ 200 ppm $CO_2$ enhancement):

| | meta-analysis | model |
|---|---|---|
| Light use efficiency | 12.2 ± 9 % | 15.2 % |
| Water use efficiency | 54.3 ± 17 % | 55 % |
| Stomatal conductance | –20.0 ± 3 % | –15.0 % |

Other satellite-based models, e.g. the widely used MODIS GPP, cannot show **any** of these responses.

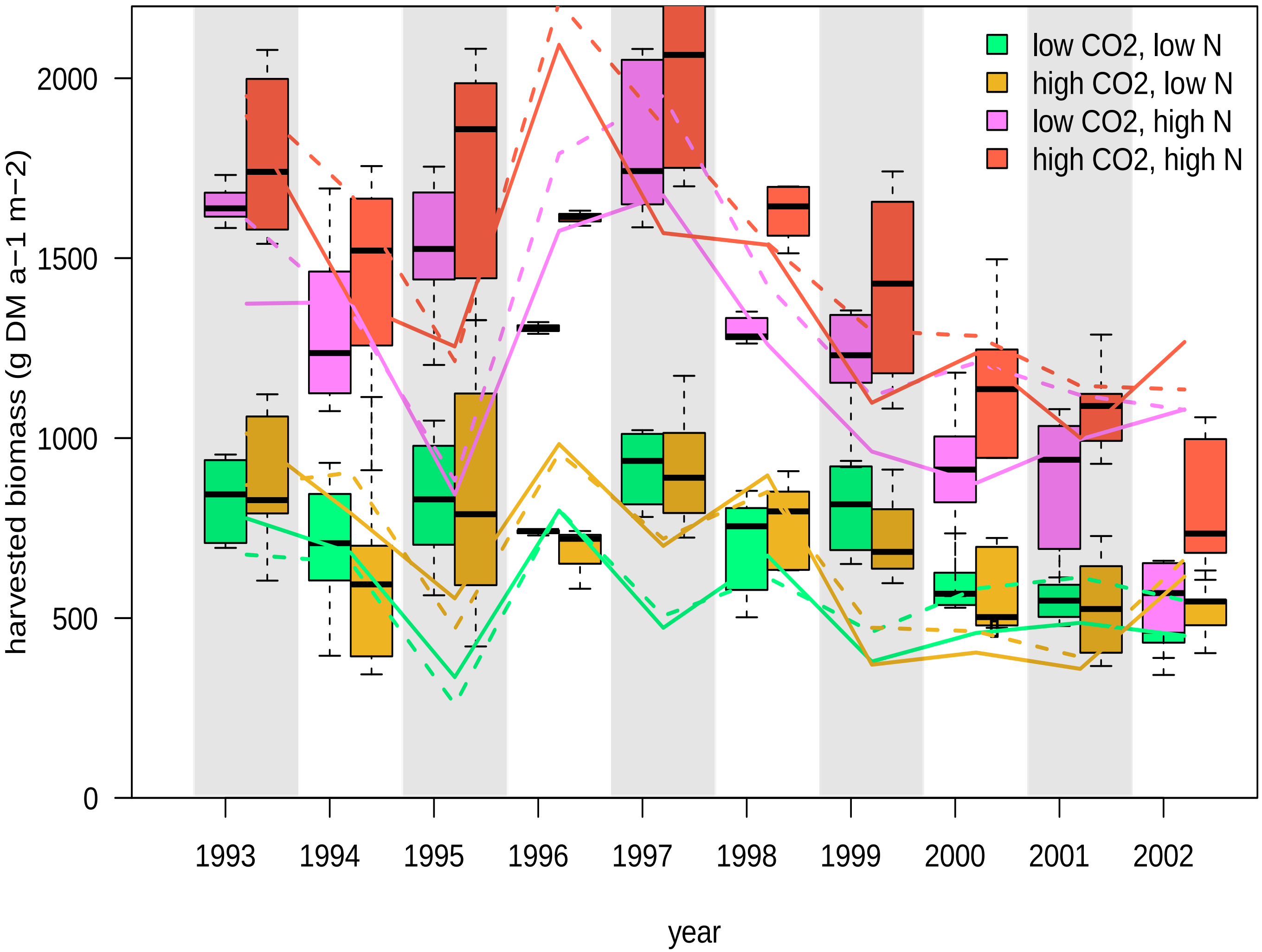
Wang *et al.* (2017) *Nature Plants*

# Swiss FACE: LAI




B Stocker *et al.* (in prep.)

# Swiss FACE: harvested biomass




B Stocker *et al.* (in prep.)

# Have we solved all the problems?

# Have we solved all the problems?

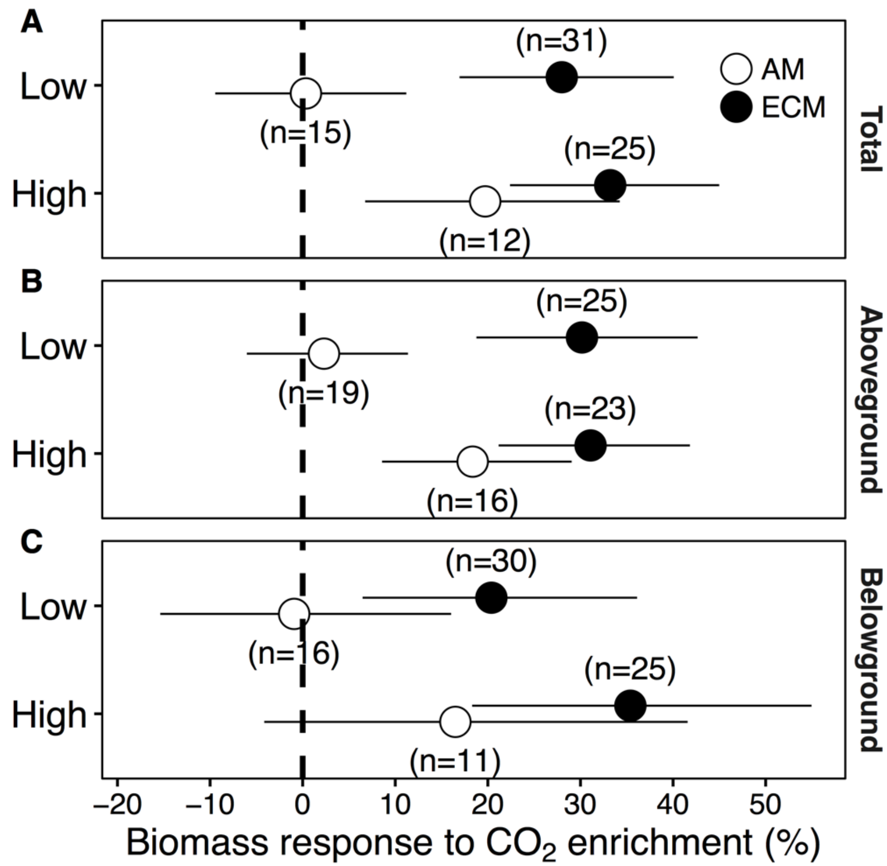
NO

# Some of the outstanding questions

- Why do tree-ring studies not show increased growth?
- How is carbon allocation controlled (to fine roots, leaves and wood)?
- Where is the carbon sink?
- Are there negative consequences of rising $CO_2$ (apart from clmate change) for plants, e.g. reduced nitrate assimilation, increased leaf temperatures?
- Does (or will) N supply limit the $CO_2$ fertilization effect?
- Inconsistent response of plant growth to $CO_2$ and N addition in ecosystem experiments...

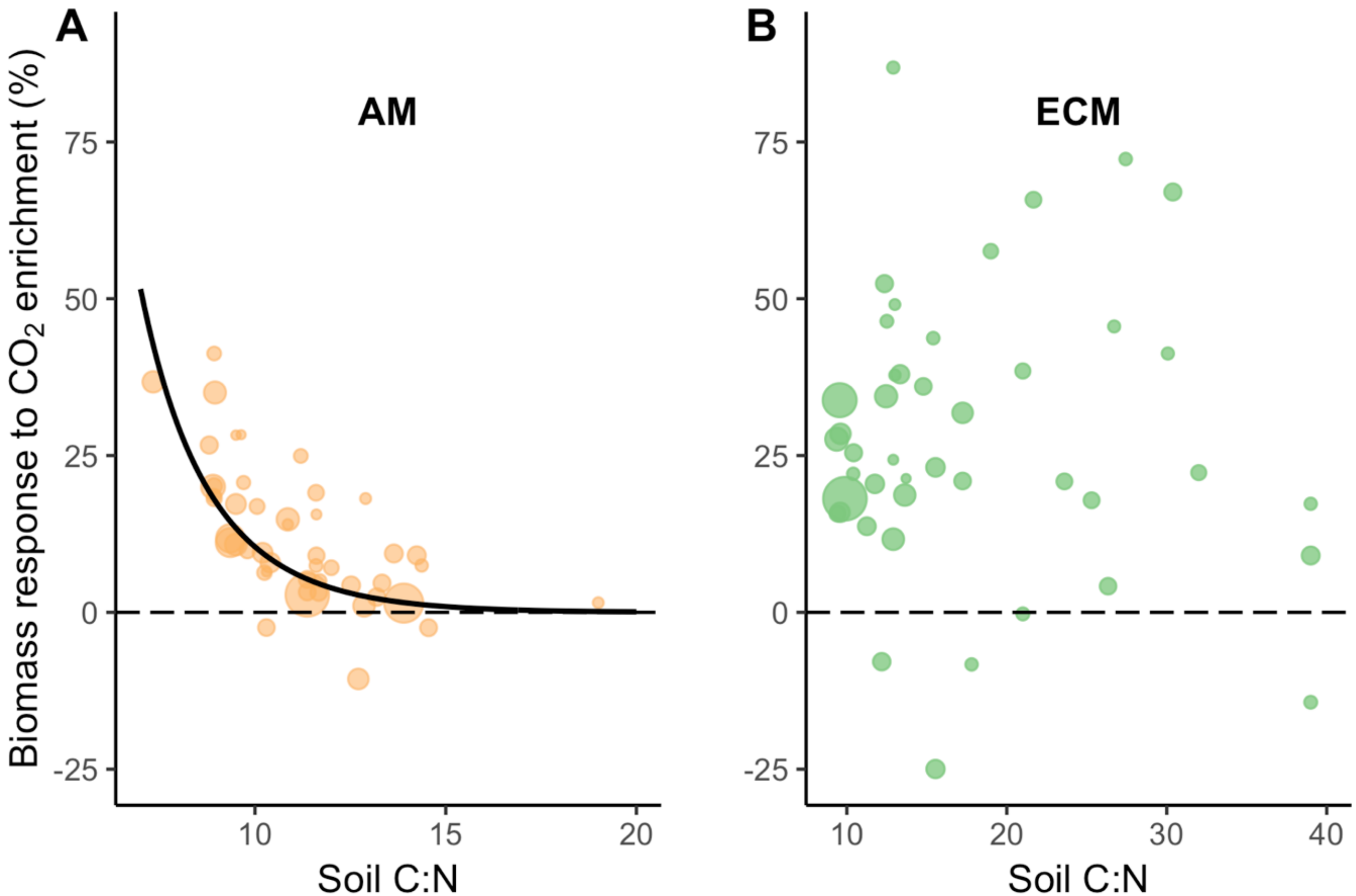
# Mycorrhizae explain varying effects of $CO_2$ on biomass (meta-analysis)

total biomass increase:




Terrer *et al.* (2016) *Science*

# Soil C:N ratio indexes the cost of N acquisition via AM




C Terrer *et al.* (in prep.)

# Conclusions (1)

- One key to theory development is **eco-evolutionary optimality**: the “missing law” of biology for Earth System modelling!
- The other key to theory development is to **proceed hand-in-hand with empirical science**.
- Without well-tested theory, **models should not be trusted**.

# Conclusions (2)

- We have an initial theory for **plant carbon and water exchanges**, with each element tested against observations.
- **Simpler** and **better** (than "state-of-the-art") ecosystem models can be made, based on this theory.
- A great deal of **work remains to be done** to develop theory and soundly based models for:
  - carbon allocation
  - responses to drought
  - nutrient acquisition (incl. exudation)
  - implications of reduced stomatal conductance
  - and much else...