Towards a universal model for ecosystem-atmosphere carbon and water exchanges

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**CO₂ seasonal cycle:**

*models differ, none are right*

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**Graph Notes:**
- **Axes:**
  - X-axis: Absolute CO₂ amplitude 2009–2010 (ppm)
  - Y-axis: Relative change in CO₂ amplitude [5861–0910] (%)

**Models:**
- GTEC
- LPJ
- ORCHIDEE
- SiB3
- SiBCASA
- VEGAS
- VISIT
- BIOME
- CLM4
- CLM4VIC
- DLEM
- ISAM
- TEM6
- Observed
- CMIP5 models

**References:**
- Graven et al. (2013)
  - *Science*
- R Thomas *et al.*
  - (in revision) *GRL*
Why do we need a universal model?

- Current models have too many parameters, and *still* fail key benchmark tests
- New theory and observations on plants and ecosystems support a different model structure:
  - *fewer (not more!) PFTs*
  - *fewer parameters*
  - *universal principles*
- Simpler models embodying clear hypotheses are more useful for science and prediction
Evolutionary optimality: a basis for theory in ecosystem science

• The “missing law” of biology in Earth System models
• Natural selection is ubiquitous and extremely effective
  “Nothing in biology makes any sense except in the light of evolution” – T. Dobzhansky
• Explicit hypotheses can be quantitatively tested
Acclimation: bridging time scales

- Variation of parameters over days, weeks and months
- Variation of parameters across environments
- Short-term response ≠ longer-term response (fundamental, and generally ignored)
  - example: plant respiration – almost flat response to temperature
  - may be the cause of the seasonal cycle problem?
  - also applies to photosynthesis
What acclimation is

- Optimization of a phenotypically plastic trait
What acclimation is not

- An effect that *goes away* (cf. “downregulation” in response to enhanced CO$_2$: $V_{cmax}$ declines, $A_{net}$ increases ...)
- An idiosyncratic effect, making modelling even more complex
  - *it makes modelling simpler, by predicting universal relationships!*
Predictability of the $c_i : c_a$ ratio ($\chi$)

The “exchange rate” between CO$_2$ and water

- Least-cost hypothesis: minimize $a(E/A) + b(V_{cmax}/A)$
- This results in:
  \begin{equation}
  \chi_{opt} = \Gamma^*/c_a + (1 - \Gamma^*/c_a). \xi/(\xi + \sqrt{D})
  \end{equation}
  where:
  \begin{align*}
  \xi &= \sqrt{b(K + \Gamma^*)/1.6a} \\
  K &= K_C (1 + O/K_O)
  \end{align*}

\begin{align*}
  a &= r_s h^2 \rho_s \eta / 2(\Delta \psi) k_s \rho_w \\
  b &= \text{constant}
  \end{align*}

H Wang et al. Nature Plants (in revision)

bioRxiv  [http://dx.doi.org/10.1101/040246]
\[
\ln \frac{\chi}{1-\chi} \text{ versus environmental predictors (from global } \delta^{13}\text{C data: } > 3500 \text{ measurements)}
\]

<table>
<thead>
<tr>
<th>Predicted</th>
<th>Fitted</th>
</tr>
</thead>
<tbody>
<tr>
<td>temperature (K)</td>
<td>0.054</td>
</tr>
<tr>
<td>(\ln \text{ vpd} )</td>
<td>−0.5</td>
</tr>
<tr>
<td>elevation (km)</td>
<td>−0.08</td>
</tr>
</tbody>
</table>

\[R^2 = 0.39\]
partial residual plots

(note dependence of elevation effect on relative humidity)
Observed $\chi$

Predicted $\chi$

- Evergreen broadleaf tree
- Deciduous broadleaf tree
- Evergreen needleleaf tree
- Deciduous needleleaf tree
- Savanna tree
- Shrub
- C3 grass
A universal relationship

- Plant Functional Types have different $c_i:c_a$ ratios because they live in different climates.
A universal relationship

- PFTs have different $c_i:c_a$ ratios because they live in different climates.
- Duh.
Predictability of carbon fixation capacity

The activity of the CO$_2$-fixing enzyme, Rubisco

- Predictions: $V_{cmax}$ acclimates so as to make use of the available PAR (not less or more)
  - increases in proportion to PAR
  - increases weakly with temperature; less steeply than enzyme kinetics
  - value at standard temperature (e.g. 25°C) declines with temperature
HF Togashi et al.  
*Functional Plant Ecology*  
(in revision) 

Great Western Woodlands, Australia
traits *versus* growth temperature

<table>
<thead>
<tr>
<th></th>
<th>predicted</th>
<th>fitted</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\ln V_{cmax}$</td>
<td>0.049*</td>
<td>0.033 ± 0.016</td>
</tr>
<tr>
<td>$\ln J_{max}$</td>
<td>0.024</td>
<td>0.025 ± 0.011</td>
</tr>
<tr>
<td>$\ln R_{dark}$</td>
<td>0.049</td>
<td>0.051 ± 0.016</td>
</tr>
</tbody>
</table>

*slope from Rubisco kinetics is 0.089*
More (true) predictions

- higher $V_{cmax}$ (and leaf N) in dry environments
- higher $V_{cmax}$ (and leaf N) at high elevations
- lower $V_{cmax}$ (and leaf N) at elevated CO$_2$: ‘down-regulation’
Predictability of leaf N content ($\ln N_{area}$)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Predicted</th>
<th>Fitted</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\chi$ (from $\delta^{13}$C)</td>
<td>$-0.62$</td>
<td>$-0.61 \pm 0.25$</td>
</tr>
<tr>
<td>$\ln$ PAR</td>
<td>$1$</td>
<td>$0.87 \pm 0.10$</td>
</tr>
<tr>
<td>mean annual $T$</td>
<td>$-0.048$</td>
<td>$-0.047 \pm 0.007$</td>
</tr>
</tbody>
</table>

N Dong et al. *Global Ecology and Biogeography* (in revision)

N-S Australia transect
partial residual plots

N Dong et al. Global Ecology and Biogeography (in revision)

N-S Australia transect
Predictability of the $J_{\text{max}}:V_{c\text{max}}$ ratio

Ratio of investments in electron transport and carboxylation

- $J_{\text{max}}$ has a cost
- That’s why the response of $J$ to PAR is not linear
- Prediction based on the Smith formula for $J$:
  - the ratio $J_{\text{max}}/V_{c\text{max}}$ has an optimum,
  
  \[
  J_{\text{max}} = 4 \ k \ V_{c\text{max}} \quad \text{where}
  \]
  \[
  k^3 = (1/c^*) (c_i - \Gamma^*)(c_i + 2\Gamma^*)^2/(c_i + K)^3 \quad \text{and}
  \]
  \[
  c^* \approx 0.41 \ (\text{from experimental data})
  \]
\[ \frac{J_{\text{max}}}{V_{c_{\text{max}}}} \] depends on growth temperature

H Wang et al. (unpublished results)
Predictability of GPP

*Photosynthesis on a large scale*

- A further consequence of the theory:
  - $GPP$ is proportional to absorbed PAR (Monteith 1977)
- This is the foundation of LUE models!
- So now we can *predict* GPP, knowing $a/b$ and $c^*$:
  - Need satellite data on green vegetation cover (fAPAR)
  - Don’t need PFTs, or any PFT-specific functions
  - Can predict environmental effects on LUE from first principles (including $CO_2$ effects)
The universal GPP model

\[ A_J = \varphi_0 I_{abs} m \sqrt{1 - \left( \frac{c^*}{m} \right)^\frac{2}{3}} \]

where

\[ m = \frac{c_a - \Gamma^*}{c_a + 2\Gamma^* + 3\Gamma^*} \sqrt{\frac{1.6D\eta^*}{\beta(K + \Gamma^*)}} \]

\[ \varphi_0 = 0.093 \]
\[ c^* = 0.41 \]
\[ \beta = b/a \text{ at } 25^\circ C = 240 \]
Global data-model comparison of monthly GPP

$r = 0.7418$
RMSE = 69.442
**DK–Sor (Deciduous Broadleaf Forests)**

![Graph](image1)

**US–Bar (Deciduous Broadleaf Forests)**

![Graph](image2)
**CZ–BK1 (Evergreen Needleleaf Forests)**

- **GPP [gC/m²/day]**
- **GPP values:**
  - **Observed mGPP (gC/m²/month):**
  - **Modeled mGPP (gC/m²/month):**
  - **RMSE:**
    - 22.9
    - 26.1
- **RMSE values:**

**RU–Zot (Evergreen Needleleaf Forests)**

- **GPP [gC/m²/day]**
- **GPP values:**
  - **Observed mGPP (gC/m²/month):**
  - **Modeled mGPP (gC/m²/month):**
  - **RMSE:**
    - 22.9
    - 26.1
    - 22.9
BE–Vie (Mixed Forests)  

Year

GPP [gC/m²/day]

observed mGPP (gC/m²/month)

modeled mGPP (gC/m²/month)

RMSE = 29.8
RMSE = 54.2
RMSE = 52.8

US–Syv (Mixed Forests)  

Year

GPP [gC/m²/day]

observed mGPP (gC/m²/month)

modeled mGPP (gC/m²/month)

RMSE = 62.8
RMSE = 61.7
RMSE = 45.2
US-Ton (Woody Savannas)

ES-LMa (Savannas)

GPP [gC/m²/day] vs Year

observed mGPP (gC/m²/month) vs modeled mGPP (gC/m²/month)

RMSE = 17
RMSE = 19.6
RMSE = 33.6

RMSE = 27.8
RMSE = 24.6
RMSE = 24.1

RMSE = 33.6
RMSE = 19.6
RMSE = 17
Predictability of CO$_2$ effects

Comparison with Ainsworth & Long (2005) meta-analysis of FACE experiments ($\approx$ 200 ppm CO$_2$ enhancement):

<table>
<thead>
<tr>
<th>Metric</th>
<th>Meta-analysis</th>
<th>Predicted</th>
</tr>
</thead>
<tbody>
<tr>
<td>LUE</td>
<td>12.2 ± 9 %</td>
<td>15.2 %</td>
</tr>
<tr>
<td>WUE</td>
<td>54.3 ± 17 %</td>
<td>55 %</td>
</tr>
<tr>
<td>$J_{\text{max}}/V_{\text{cmax}}$</td>
<td>5.2 ± 2.8 %</td>
<td>9.8 %</td>
</tr>
<tr>
<td>$g_s$</td>
<td>-20 ± 3 %</td>
<td>15 %</td>
</tr>
</tbody>
</table>
Allocation: from GPP to biomass production

- Maintenance of functional and stoichiometric balance ≠ fixed allocation fractions
- Key to C-N cycle coupling: optimal allocation
Components of SOFUN

**P-model**
Wang et al., 2014 BG

**DyN-LPJ**
Xu-Ri & Prentice, 2008

**LPJ/new**
sensu Manzoni et al., 2008

B. Stocker et al., unpublished
Stoichiometric balance

The graph shows the relationship between the allocation fraction to leaves and the labile N (gN m\(^{-2}\)) and labile C (gC m\(^{-2}\)). The optimum allocation fraction is indicated by a vertical line.
SwissFACE (Lüscher et al, 2004 GCB)

- temperate grassland
- factorial CO₂ x N-fertilization experiment
- modelled with daily climate and CO₂, actual N-fertilization and harvest
- no parameter tuning to fit the results
Swiss FACE: harvested biomass

![Graph showing harvested biomass from 1993 to 2002 with different treatments: low CO2, low N; high CO2, low N; low CO2, high N; high CO2, high N. The graph compares the harvested biomass per year and treatment, with error bars indicating variability.](image-url)
Swiss FACE: LAI

- low CO2, low N
- high CO2, low N
- low CO2, high N
- high CO2, high N


LAI values range from 0 to 7.
Swiss FACE: root mass

![Graph showing root mass over years with different CO2 and N conditions.]

- **low CO2, low N**: Green line and bars
- **low CO2, high N**: Red line and bars
- **high CO2, low N**: Orange line and bars
- **high CO2, high N**: Purple line and bars

The graph illustrates the root mass over years from 1993 to 2001, with variations in CO2 and N levels showing different trends and values.
Why do some N-limited ecosystems respond/not respond to enhanced CO$_2$?

It’s the mycorrhizae, stupid!

Terrer et al. (2016) Science
It’s the mycorrhizae, stupid!

Terrer et al. (2016) Science
Conclusions

- GPP can be predicted from fAPAR with a single, universal equation.
- \( E = 1.6 g_s D \), where \( g_s = (A/c_a)/(1 – \chi) \)... ➢ *transpiration is predictable in the same way.*
- \( \text{CO}_2 \) effects can be predicted with the same equation.
- The next big challenge is to ‘close the loop’ between GPP and fAPAR, requiring a comprehensive treatment of allocation.