Modelling historical changes in the water use efficiency of plants and ecosystems with different vegetation models

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Water-use efficiency: A Carbon & Water Balance

Coupling the Carbon & Water Cycles

\[ WUE = \frac{\text{CO}_2}{\text{H}_2\text{O}} \]
Water-use efficiency: A Carbon & Water Balance

\[
WUE \approx \frac{c_a}{1.6 \cdot D} \cdot \left(1 - \frac{c_i}{c_a}\right)
\]

A: photoassimilation rate; E: transpiration; \(c_a\): atmospheric CO2 concentration; \(c_i\): intercellular CO2 concentration; \(D\): vapour pressure deficit
Water-use efficiency: A Carbon & Water Balance

**Ecosystem level**

\[
\text{WUE} = \frac{\text{GPP}}{\text{ET}}
\]

GPP: gross primary production; ET: evapotranspiration
Water-use efficiency: A Carbon & Water Balance

Discrepancies in magnitude of changes in WUE between different types of observations

Underprediction by vegetation models

What are the relative contributions from environmental drivers?

Lavergne et al. (2019) GCB

EC: eddy-covariance flux data
TR: carbon isotopes in tree rings
Coupling the Carbon & Water Cycles

Are the dependencies of WUE on CO₂ and D the same at leaf and ecosystem levels?

→ Contributions from CO₂ (a) and D (b) to WUE

\[
\text{WUE}_T = \frac{c_a}{1.6 \ D} \left( 1 - \frac{c_i}{c_a} \right)
\]

\[
\ln \left\{ 1 + f_{\text{WUE}} \right\} = a \ln \left\{ 1 + f_{c_a} \right\} + b \ln \left\{ 1 + f_D \right\}
\]

Values (mean ± sd) from 31 TR and 28 EC observational series over 1900-2010:

\(a = 1.51 \pm 0.57\)  \(b = -0.72 \pm 0.16\)

Fractional changes

\[
f_X = \frac{X - \overline{X}}{\overline{X}}
\]

Dekker et al. (2016) *ESD*
Driving factors: Indices for Evaluating Models?

→ Testing the performance of different types of vegetation models to predict the environmental dependencies of WUE at the leaf and ecosystem levels

How?

→ Estimation of contributions from CO$_2$ and $D$ on WUE from:

1. independent networks of TR (leaf-level) and EC (ecosystem-level) observations over their common period of records (1991-2014)
2. vegetation model outputs

→ Model-data comparisons
Predicting Vegetation: different Types of Models

- fixed land cover map
- prescribed leaf area index (LAI) → seasonal variations derived from phenology model but no year-to-year variations
- distinction among plant functional types (PFTs): fixed parameters defining behaviour of the vegetation
- ability of plants (within any one PFT) to acclimate or adapt to environmental changes
- stomatal limitation of photosynthesis only driven by environmental variables

Prentice et al. (2014)
Wang et al. (2017)
Stocker et al. (in revision)
Two different model configurations for stomatal limitation of photosynthesis

**Jacobs (1994): JAC**

$$g_s = 1.6RT_{\text{leaf}} \frac{A \beta}{c_a - c_i}$$

$$c_i = (c_a - \Gamma^*) \frac{c_i}{c_a} \left(1 - \frac{D}{D_{\text{crit}}}ight) + \Gamma^*$$

- $\beta$: soil moisture stress factor (unitless)
- $R$: universal gas constant (J K$^{-1}$ mol$^{-1}$)
- $T_{\text{leaf}}$: leaf surface temperature (°K)
- $\Gamma^*$: CO$_2$ photorespiration compensation point (Pa)
- $A$: potential leaf net assimilation rate (µmol mol$^{-1}$)

**Medlynn et al. (2011): MED**

$$g_s \approx g_0 + \left(1 + \frac{g_1}{\sqrt{D}}\right) \frac{A}{c_a}$$

$$c_i = c_a \left(\frac{g_1}{g_1 + \sqrt{D}}\right)$$

- $D$: leaf-to-air vapour pressure deficit (Pa)
- $D_{\text{crit}}$: critical leaf-to-air vapour pressure deficit (Pa)
- $g_1$: sensitivity of $g_s$ to assimilation rate

Oliver et al. (2018) *Biogeosci.*
Best et al. (2011) *Geosci. Model Dev.*
Clark et al. (2011) *Geosci. Model Dev.*

+ Farquhar-Collatz photosynthesis model
+ canopy $A$ (≈ GPP) estimated with big leaf approach (scaled by LAI using Beer’s law)
P Model: a Simple Optimality model

Least-cost hypothesis (LC):

\[ c_i = c_a \left( \frac{\xi}{\xi + \sqrt{D}} \right) \]
\[ \xi = \sqrt{b} \frac{K}{1.6 \eta^*} \]

\( D \): leaf-to-air vapour pressure deficit (Pa)
\( b \): ratio of dimensionless cost factors for carboxylation and transpiration
\( \eta^* \): viscosity of water relative to its value at 25°C
\( K \): effective Michaelis-Menten coefficient for Rubisco-limited photosynthesis (Pa)

Coordination hypothesis:

\[ GPP = I_{abs} \cdot \phi_0 \cdot m \sqrt{1 - (c^*/m)^{2/3}} \]
\[ m = \frac{c_a - \Gamma^*}{\{c_a + 2\Gamma^* + 3\Gamma^* \sqrt{1.6 \cdot \eta^* \cdot D \cdot b^{-1} (K + \Gamma^*)^{-1}}\}} \]

\( \phi_0 \) is the intrinsic quantum yield (g C / mol)
\( I_{abs} \) is the absorbed photosynthetic photon flux density (PPFD*fAPAR, mol/m²/s)
\( fAPAR \): fraction of absorbed photosynthetically active radiation (unitless)
\( \Gamma^* \) is the photorespiratory compensation point (Pa)
\( c^* \approx 0.41 \) is estimated from observed \( J_{max: Vc_{max}} \) ratios proportional to the unit carbon cost for the maintenance of electron transport capacity

Prentice et al. (2014)
Wang et al. (2017)
Stocker et al. (in revision)

But no explicit prediction of transpiration yet!
**Model-Data approach: Input Data & Parameters**

- WATCH-WFDEI data (Weedon et al. 2014) as input + atmospheric CO2 from Scripps

1. **leaf level**: at > 100 TR sites with carbon isotope data ($\delta^{13}C_{TR}$) compilation from Lavergne et al. (in revision)

2. **ecosystem level**: at 34 EC flux sites with > 6 years of records representing forest ecosystems (FLUXNET dataset)

→ Model-data comparisons over common 1991-2014 period: $c_a$ increase by 43 ppm

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Broadleaf</th>
<th>Needleleaf</th>
<th>References</th>
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<tbody>
<tr>
<td>Jacobs (JAC)</td>
<td>$D_{crit}$ (kg kg$^{-1}$)</td>
<td>0.09</td>
<td>0.06</td>
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<td>Medlyn (MED)</td>
<td>$g_1$ (kPa$^{0.5}$)</td>
<td>3.22</td>
<td>2.22</td>
<td>Oliver et al. (2018)</td>
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<td>Prentice (LC)</td>
<td>$b$ (unitless)</td>
<td>146</td>
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<td>Smith et al. (2019)</td>
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Observed Data: leaf $c_i$, GPP, ET, WUE & eWUE

\[ \frac{c_i}{c_a} = \frac{\left( \delta^{13}CO_2 - (\delta^{13}CTR-d) \right) \cdot a + f \cdot \Gamma^*}{b - a} \]

\[ WUE = \frac{c_a}{1.6 \cdot D \cdot \left( 1 - \frac{c_i}{c_a} \right)} \]

$\delta^{13}CO_2$: stable carbon isotopic composition of atmospheric CO2 (‰)

$\Gamma^*$: CO2 photorespiration compensation point (Pa)

$a$: fractionation due to CO2 diffusion in air = 4.4 ‰

$b$: fractionation due to effective Rubisco carboxylation = 30‰

$f$: fractionation due to photorespiration = 8‰

$d$: post-photosynthetic fractionations = 2.1‰

\[ \text{eWUE} = \frac{\text{GPP}}{\text{ET}} = \frac{\text{GPP}}{\text{LE}} \lambda_v \]

$\lambda_v$: latent heat of vaporization (kJ kg$^{-1}$)

LE: latent heat flux (W m$^{-2}$)

- Filtering and processing with R package bigleaf (Knauer et al. 2018 PlosOne)
- Aggregation over summer months (June-August)
**Coupling the Carbon & Water Cycles**

**Vegetation models & Observations**

**Initial Results**

**Conclusion & Perspectives**

**Next steps**

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**TR sites: Measured versus Predicted leaf \( c_i \)**

**Leaf level**

1991-2014

\[
\begin{align*}
\text{(JAC)} & \quad c_i = (c_a - \Gamma^*) \frac{c_i}{g_1 c_a} \left(1 - \frac{D}{D_{crit}}\right) + \Gamma^* \\
\text{(MED)} & \quad c_i = c_a \left(\frac{\xi}{g_1 + \sqrt{D}}\right) \\
\text{(LC)} & \quad c_i = c_a \left(\frac{\xi}{\xi + \sqrt{D}}\right)
\end{align*}
\]

**PFT**

- ENF
- DBF

**TR sites**

Measured versus Predicted leaf \( c_i \)

- \( R^2_{adj} = 0.28 \) (LC)
- \( R^2_{adj} = 0.20 \) (MED)
- \( R^2_{adj} = 0.14 \) (JAC)
**Coupling the Carbon & Water Cycles**

### Initial Results

**Ecosystem level**

1991-2014

**EC sites**: Measured and Predicted GPP & ET

**EC fluxes**

- $R^2_{adj} = 0.29$

**Predictions**

- $R^2_{adj} < 0.01$ (ET)
- $R^2_{adj} = 0.86$ (T)
Drivers: Relative Contributions to WUE: obs

Partial residuals over 1991-2014

Leaf-level

\[
\text{WUE} = \frac{c_a}{1.6 \cdot D} \cdot \left(1 - \frac{c_i}{c_a}\right)
\]

\[
\begin{aligned}
\ln \left(1 + \Delta \text{WUE}/\text{WUE}\right) &= 0.76 \ p < 0.001 \\
\ln \left(1 + \Delta \text{CO}_2/\text{CO}_2\right) \\
\end{aligned}
\]

\[
\begin{aligned}
\ln \left(1 + \Delta \text{D}_g/\text{D}_g\right) &= -0.90 \ p < 0.001 \\
\end{aligned}
\]

Ecosystem-scale

\[
\text{eWUE} = \frac{\text{GPP}}{\text{ET}} = \frac{\text{GPP}}{\text{LE}} \cdot \lambda_v
\]

\[
\begin{aligned}
\ln \left(1 + \Delta \text{WUE}/\text{WUE}\right) &= 0.46 \ p > 0.1 \\
\ln \left(1 + \Delta \text{CO}_2/\text{CO}_2\right) \\
\end{aligned}
\]

\[
\begin{aligned}
\ln \left(1 + \Delta \text{D}_g/\text{D}_g\right) &= -0.22 \ p < 0.001 \\
\end{aligned}
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### Drivers: Relative Contributions to WUE: obs versus simu

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**Drivers:** Using ET flux

**Using ET flux:**

- **CO$_2$:** 0.29, 0.533, 5.3, 6.9, <0.01
- **$D$:** 0.22, 0.009, 93.3, 95.1, <0.01
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<td>$D$</td>
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<td>0.048</td>
<td>&lt;0.001</td>
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<td>SIMU MED</td>
<td>CO$_2$</td>
<td>0.29</td>
<td>0.472</td>
<td>0.533</td>
<td>5.3</td>
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<td>$D$</td>
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<td>CO$_2$</td>
<td>0.27</td>
<td>0.469</td>
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<td>$D$</td>
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<td>0.011</td>
<td>93.8</td>
<td>94.9</td>
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**Using ET flux:**

- SIMU MED CO$_2$: 0.29, 0.472, 0.533
- SIMU JAC CO$_2$: 0.27, 0.469, 0.561

**Not Using ET flux:**

- SIMU MED CO$_2$: 0.29, 0.472, 0.533
- SIMU JAC CO$_2$: 0.27, 0.469, 0.561
## Drivers: Relative Contributions to WUE: obs versus simu

<table>
<thead>
<tr>
<th>Spatial scale</th>
<th>Type</th>
<th>Driver</th>
<th>Estimate</th>
<th>SE</th>
<th>p value</th>
<th>% of $R^2$ (unique)</th>
<th>% of $R^2$ (unique + common)</th>
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<td>Leaf level</td>
<td>OBS-TR</td>
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<td>Using T flux</td>
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**Notes:**
- **OBS-TR** refers to observations versus truth.
- **SIMULC** refers to simulations with a closed canopy.
- **SIMUMED** refers to simulations with a medium canopy.
- **SIMUJAC** refers to simulations with a jack pine canopy.
- **CO$_2$** refers to carbon dioxide.
- **$D$** refers to a specific driver or variable.
- $R^2$ values indicate the proportion of variance explained by each model.
**Conclusion:** Need to refine processes at ecosystem level

**Leaf level:** all models of stomatal limitation of photosynthesis (i.e. LC, JAC or MED) reproduce reasonably well the relative contributions from $c_a$ and $D$ to changes in leaf WUE.

**Ecosystem level:** JULES tends to assign erroneously a positive influence of $D$ to changes in eWUE when using LE flux, or overestimate the influence of CO2 when using the transpiration flux.

Need to refine processes modelled at the ecosystem level → testing new formulations for GPP and ET against EC flux measurements.

Implementation of transpiration in the P model done by colleagues will allow predictions of eWUE.
**Next steps: Planning**

- **RUNNING LONGER SIMULATIONS WITH JULES TO ASSESS LONG-TERM PREDICTIVE SKILLS**
- **TESTING IMPLEMENTATION OF LC HYPOTHESIS IN JULES AND COMPARING SIMULATIONS WITH CARBON ISOTOPE DATA**
- **IMPLEMENTATION OF CARBON ISOTOPES IN JULES**
- **IMPROVING PREDICTIONS OF T AND GPP IN JULES?**

**Coupling the Carbon & Water Cycles**

- Vegetation models & Observations
- Initial Results
- Conclusions & Perspectives
- Next steps
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More information:
alavergne@imperial.ac.uk

Rebecca Oliver & Lina Mercado for providing the JULES outputs
Iain Colin Prentice & Heather Graven for general discussions
FLUXNET contributors
All colleagues providing carbon isotopes data from tree rings

github.com/Alienlav
bitbucket.org/labprentice
**Input data**
- Atmospheric CO₂, temperature, vapour pressure deficit
- Incoming shortwave radiation, fAPAR
- Elevation

**P model**
- **Least-cost (LC) hypothesis**
  - leaves minimize the summed unit costs of transpiration and carboxylation
- **Coordination hypothesis**
  - photosynthesis equally limited by electron transport and carboxylation under average environmental conditions

**Outputs**
- \( \chi \)
  - Leaf-internal to ambient CO₂ concentrations
- GPP
  - Gross primary production

**Spatial Resolution**
- **Site**
  - (e.g. FLUXNET, tree-ring sites)
- **Region**
  - (e.g. high resolution satellite data)
- **Global**
  - (e.g. MERIS, MODIS, ECMWF)

**Temporal Resolution**
- Half-hourly to daily
- Monthly
- Annual

**Methods**
**P Model: a Simple Optimality model**

- Least-cost (LC) hypothesis
  - Leases minimize the summed unit costs of transpiration and carboxylation
- Coordination hypothesis
  - Photosynthesis equally limited by electron transport and carboxylation under average environmental conditions