Soil water stress impacts on the stomatal limitation of photosynthesis: a meta-analysis

Aliénor Lavergne¹,*
Heather Graven¹, Iain Colin Prentice²
& David Sandoval², Vincent Hare³

¹ Carbon Cycle Research Group, Department of Physics, Imperial College London (UK)
² Prentice’s Climate Group, Department of Life Sciences, Imperial College London (UK)
³ Stable Light Isotope Laboratory, University of Cape Town (South Africa)

* a.lavergne@imperial.ac.uk
Coupling carbon and water cycles

- Atmospheric aridity and drought impacting physiological function in plant leaves

- However, their relative contributions on changes in ratio of leaf-internal \((c_i)\) to ambient \((c_a)\) partial pressure of CO\(_2\) (also known as \(\chi\)) still difficult to disentangle

> Many stomatal models predicting \(\chi\) include the effect of only one of these drivers

\(\chi\) = index of adjustments in both leaf stomatal conductance and photosynthetic rate to environmental conditions

- Key variable for the study of carbon uptake
- Provides insight into (intrinsic) WUE

\[\text{WUE} = \frac{\text{CO}_2}{\text{H}_2\text{O}}\]
**Least-cost optimality hypothesis:** leaves minimize the summed unit costs of transpiration ($a_E$) and carboxylation ($b_V$):

$$a_E \frac{\partial (E/A)}{\partial \chi} + b_V \frac{\partial (V_{cmax}/A)}{\partial \chi} = 0$$

$\chi$ depends on temperature, vapor pressure, atmospheric CO2 and atmospheric pressure (indexed by elevation)

$E$: transpiration (mol m$^{-2}$ s$^{-1}$), $A$: net assimilation rate (µmol m$^{-2}$ s$^{-1}$)

$V_{cmax}$: photosynthetic capacity (µmol m$^{-2}$ s$^{-1}$)

$D$: leaf-to-air vapour pressure deficit (Pa)

$\eta^*$: viscosity of water relative to its value at 25°C (unitless)

$K$: effective Michaelis constant for Rubisco-limited photosynthesis (Pa)

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

$\beta = \text{ratio of } b_V \text{ and } (a_E/\eta^*)$
Broadly constant $\chi$ over long timescales after integrating environmental effects

Implications for iWUE:
1. increase in iWUE with rising $c_a$ can be offset by increasing mean $T$ and decreasing VPD
2. for the same increase in $CO_2$, iWUE increase with decreasing $P_{atm}$ (increasing elevation)

> 100 $\delta^{13}C_{\text{tree-ring}}$ chronologies

Lavergne et al. (2020) *New Phytol.*
But LC model does not predict how dry soils with reduced soil water availability further influence χ.

→ overestimation of χ under dry conditions and underestimation of χ under moist conditions (Lavergne et al. 2020 New Phytol.)

* AET/PET = ratio of actual to potential evapotranspiration
We hypothesize that:
1. $\beta_{\text{angio}} > \beta_{\text{gymno}} (\chi_{\text{angio}} > \chi_{\text{gymno}})$ due to higher sapwood permeability in angiosperms
2. $\beta$ decrease with reduction in soil moisture due to changes in whole plant hydraulic conductivity $\rightarrow$ decrease of $\chi$

Questions

1) Is there any difference in the response of $\beta$ to soil water between angiosperms and gymnosperms? \textit{s10}
2) Can $\beta$ be predicted from soil moisture data? \textit{s11}
3) Does the inclusion of $\beta$ as a function of soil moisture improve $\chi$ predictions compared to those from the original LC model? \textit{s12-s13}

Lavergne et al. (submitted)
1. Compiling stable carbon isotopes ($\delta^{13}C_{\text{plant}}$) data

- **plant level**: tree-rings $\delta^{13}C_{\text{TR}}$ at 75 sites from Lavergne et al. (2020) *New Phytol.*

* $\text{AET/PET} = \text{ratio of actual to potential evapotranspiration}$


\[ \chi = \frac{c_i}{c_a} = \frac{\Gamma^*}{c_a} + \left(1 - \frac{\Gamma^*}{c_a}\right) \frac{\xi}{\xi + \sqrt{D}} \]  

(1)

\[ \xi = \frac{\sqrt{\beta K + \Gamma^*}}{1.6 \eta^*} \]  

(2)

Expected $\beta$

\[ \beta = 1.6 \eta^* D \frac{\left(\chi_{iso} - \frac{\Gamma^*}{c_a}\right)^2}{(1 - \chi_{iso})^2(K + \Gamma^*)} \]

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\( \chi \) inferred from \( \delta^{13}C_{plant} \) assuming infinite mesophyll conductance:

\[ \chi_{iso} = \frac{\left(\delta^{13}CO_2 - \left(\delta^{13}C_{plant} - d\right)/1000\right) + f \frac{\Gamma^*}{c_a}}{b - a_s} \]

- \( a_s = 4.4 \)‰ fractionation due to diffusion of CO2 in air
- \( b = 28\)‰ fractionation due to carboxylation
- \( f = 12 \)‰ fractionation due to photorespiration
- \( d = 2.1 \)‰ post-photosynthetic fractionation (for TR only)

\( \Gamma^* \) and \( K \): calculated from temperature and atmospheric pressure using parameter values at 25°C derived from Bernacchi et al. (2001) *Plant, Cell & Env.*

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- CRU climate dataset as input: 0.5 x 0.5 spatial resolution over 1901-2018
- Atmospheric CO2 from SCRIPPS
- \( \delta^{13}CO_2 \) from Graven et al. (2017) *Geosc. Mod. Dev.*
3. Comparing inferred $\beta$ values with soil water data

**soil moisture**  
cci  
$\sim 0.5$ cm soil depth

**ESA CCI v4.4 product** (1979-2018)  

**GLEAM v3.3a product** (1980-2018)  
Martens et al. (2017) *Geosci. Mod. Dev.*

**SPLASH model**  
$1$ m soil depth  
Davis et al. (2017) *Geosc. Mod. Dev.*

v2.0 from Sandoval et al. (in prep)*  
https://github.com/dsval/rsplash

*see Session HS2.2.1 - 5073: https://meetingorganizer.copernicus.org/EGU2020/EGU2020-5073.html
Sensitivity of $\beta$ to soil water: across plant groups

> 4,050 measures over 1980-2018

$\Rightarrow$ Higher sensitivity of $\beta$ to changes in soil water content for angiosperms than for gymnosperms

$\Rightarrow$ Crossover at around $0.35 \pm 0.05 \text{ m}^3 \text{ m}^{-3}$

A: angiosperm
G: gymnosperm
Increase of $\beta$ within bins of soil water Saturation at high soil moisture?

$\beta$ increase relatively linearly over the whole range of soil water conditions

$$\ln \beta = a_\beta \theta + b_\beta$$

$a_\beta = 2.0 \pm 0.1$

$b_\beta = 4.4 \pm 0.1$
Predicting $\beta$ with soil moisture: calibration

Cross-validation tests:
100 training/testing subsets

Bootstrapping (100 replicates)

- Median values for modified model
- Original model

RMSE = root mean square error
$R^2_{adj}$ = adjusted $R^2$

$\rightarrow$ Higher predictive skill for the modified than for the original models
Optimal $\chi$: modified versus original LC model

Soil moisture effect reducing on average predicted $\chi$ values by $1.4 \pm 3.9\%$ over the globe

But higher predicted $\chi$ values in modified than in original model in dense vegetation areas (e.g., boreal or tropical rainforests)
Optimal $\chi$: environmental dependencies

Partial residual regressions of isotope-derived and predicted $\chi$ with environmental drivers

- Good predictions of environmental dependencies from LC model
- Larger effects of temperature and vapor pressure deficit on $\chi$
Towards an improvement of optimal $\chi$ predictions

- Only **partial support for our first hypothesis**: $\beta_{angio} > \beta_{gymno}$ solely under well-watered upper- to mid-soil conditions

- Higher sensitivity of $\beta$ to soil water for angiosperms than for gymnosperms

  → **contrasting trait-based hydraulic strategies** for the two plant vascular groups:
  
  - larger diameter of xylem conduits / narrower hydraulic safety margins / lower water potential for angiosperms than for gymnosperms
  
  **maximizing hydraulic conductance of angiosperms**

- Simple empirical function for $\beta$ to represent $\chi$ responses to soil drought improving predictions by $6.2 \pm 2.4\%$ (mean $\pm$ sd of adjusted $R^2$) over 1980-2018

- **But approach** does not provide insights into underlying processes → need to incorporate plant hydraulics and information about trait-environment dependencies into the model*

*see Jadeep Joshi presentation beyond the ‘$\beta$ approach’ Session BG3.6: https://meetingorganizer.copernicus.org/EGU2020/EGU2020-9687.html
This research is funded by the Marie Skłodowska-Curie project ECAW-ISO
Past, present and future Exchanges of Carbon and Water between the vegetation and the atmosphere: new insights from analysis and modelling of stable carbon ISOtope data

More information:
 a.lavergne@imperial.ac.uk  
github.com/Alielav

Twitter: @AlienorLavergne

http://www.imperial.ac.uk/people/a.lavergne
http://www.sp.ph.ic.ac.uk/~hgraven/people.html
https://prenticeclimategroup.wordpress.com/lab-members/