Using eco-evolutionary optimality principles to understand and predict photosynthetic acclimation

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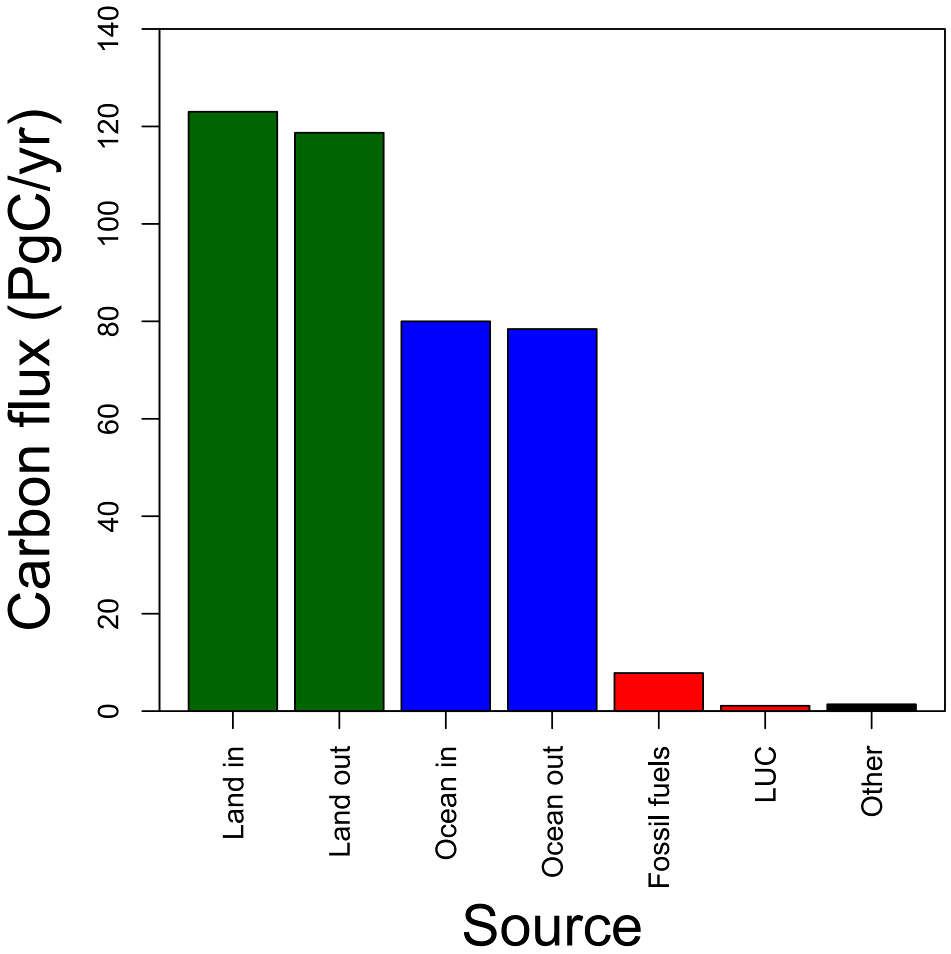
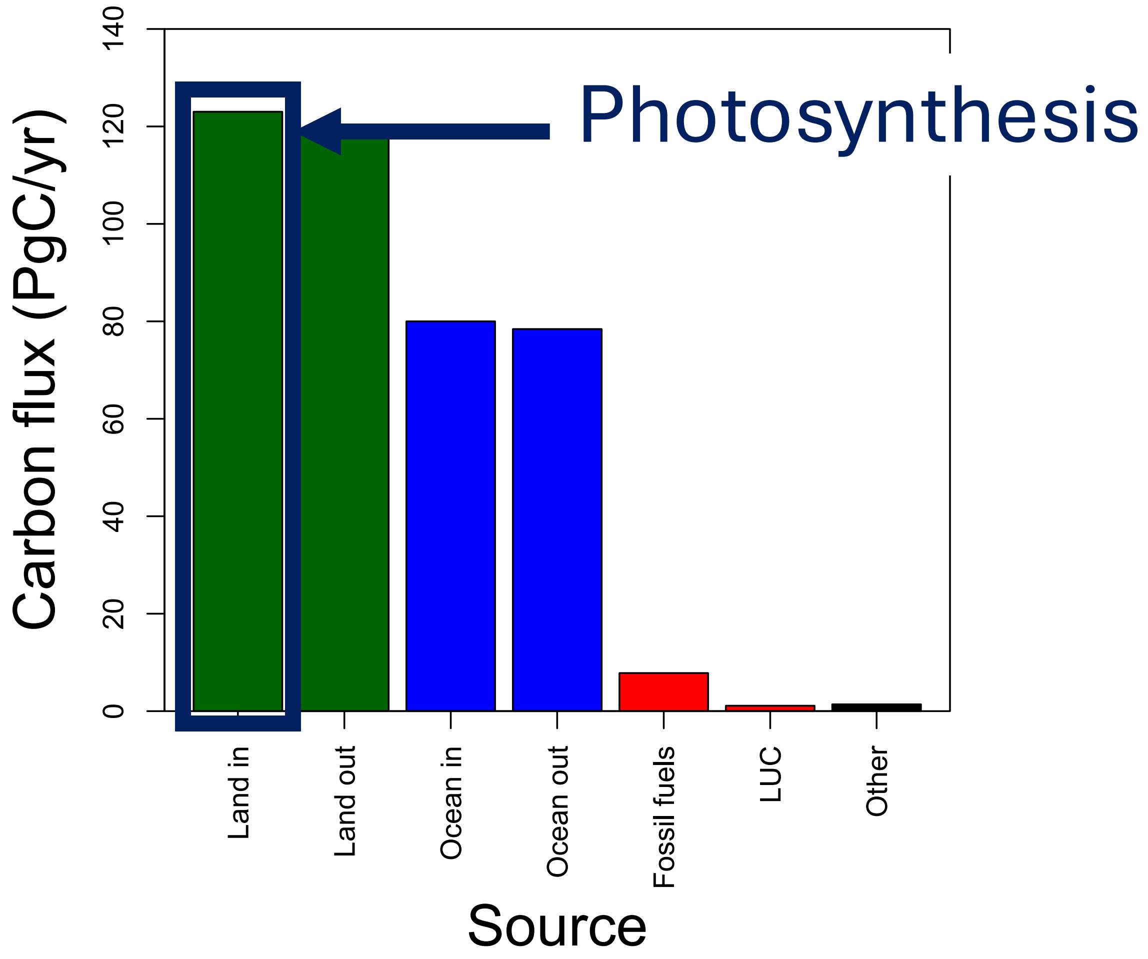
Photosynthesis is a key component of the global carbon cycle



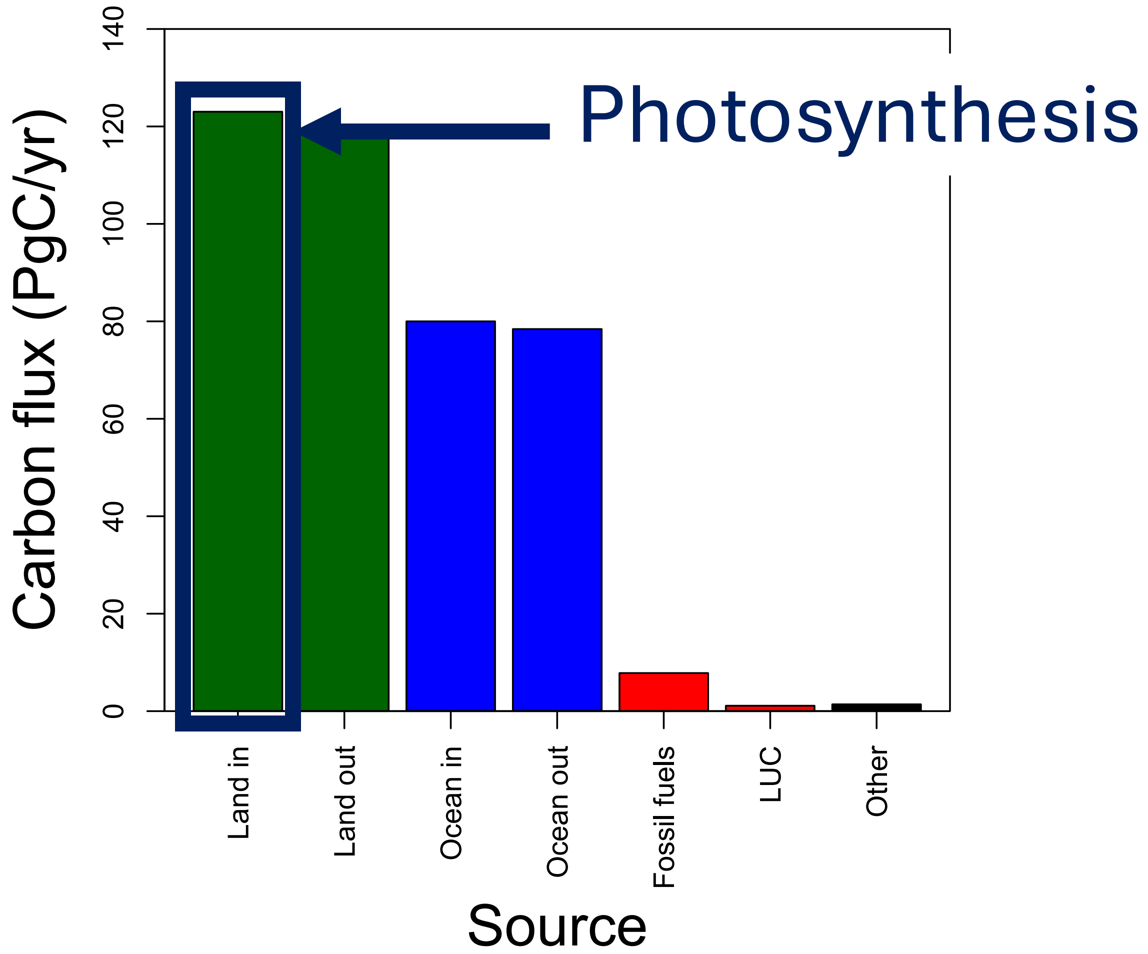
Data from IPCC (2013)

Photosynthesis is a key component of the global carbon cycle



Data from IPCC (2013)

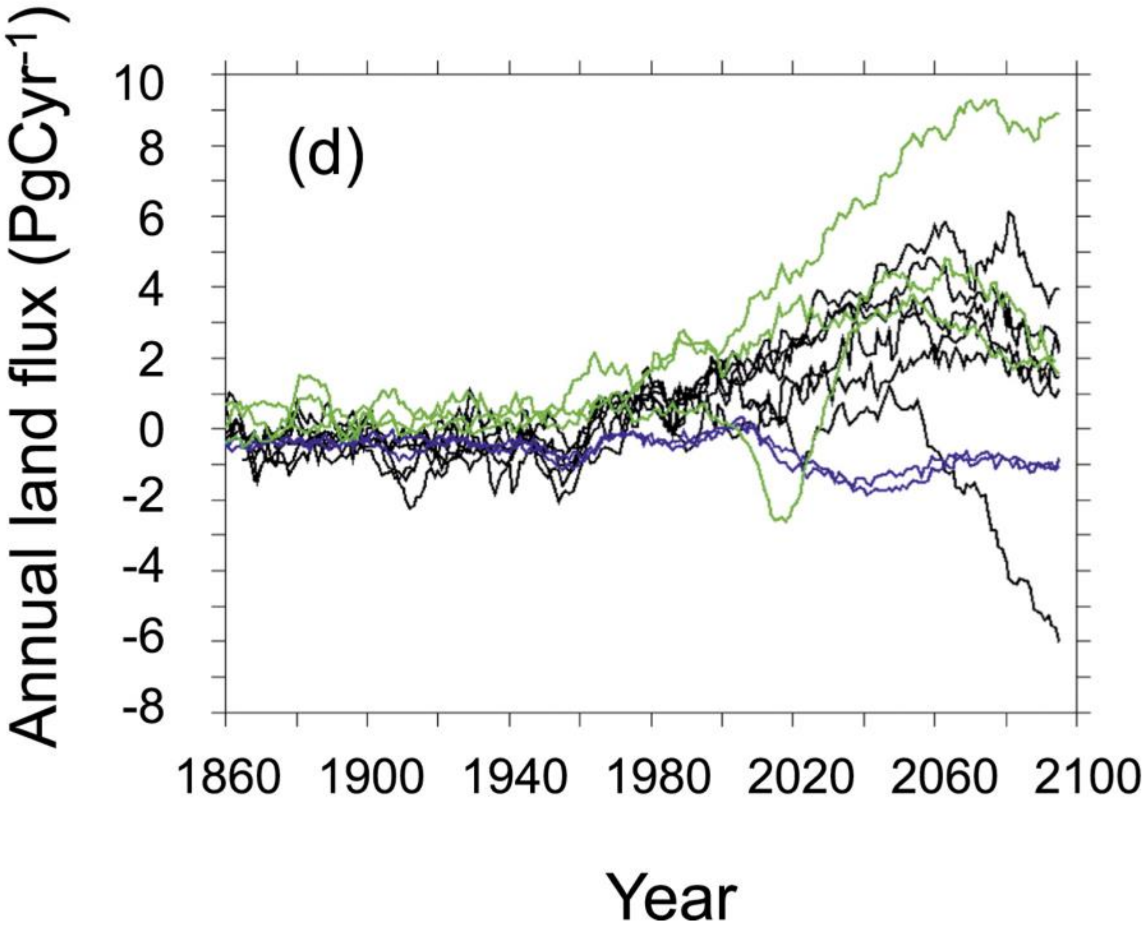
Photosynthesis is a key component of the global carbon cycle



A small percentage change in photosynthesis can have large consequences for climate

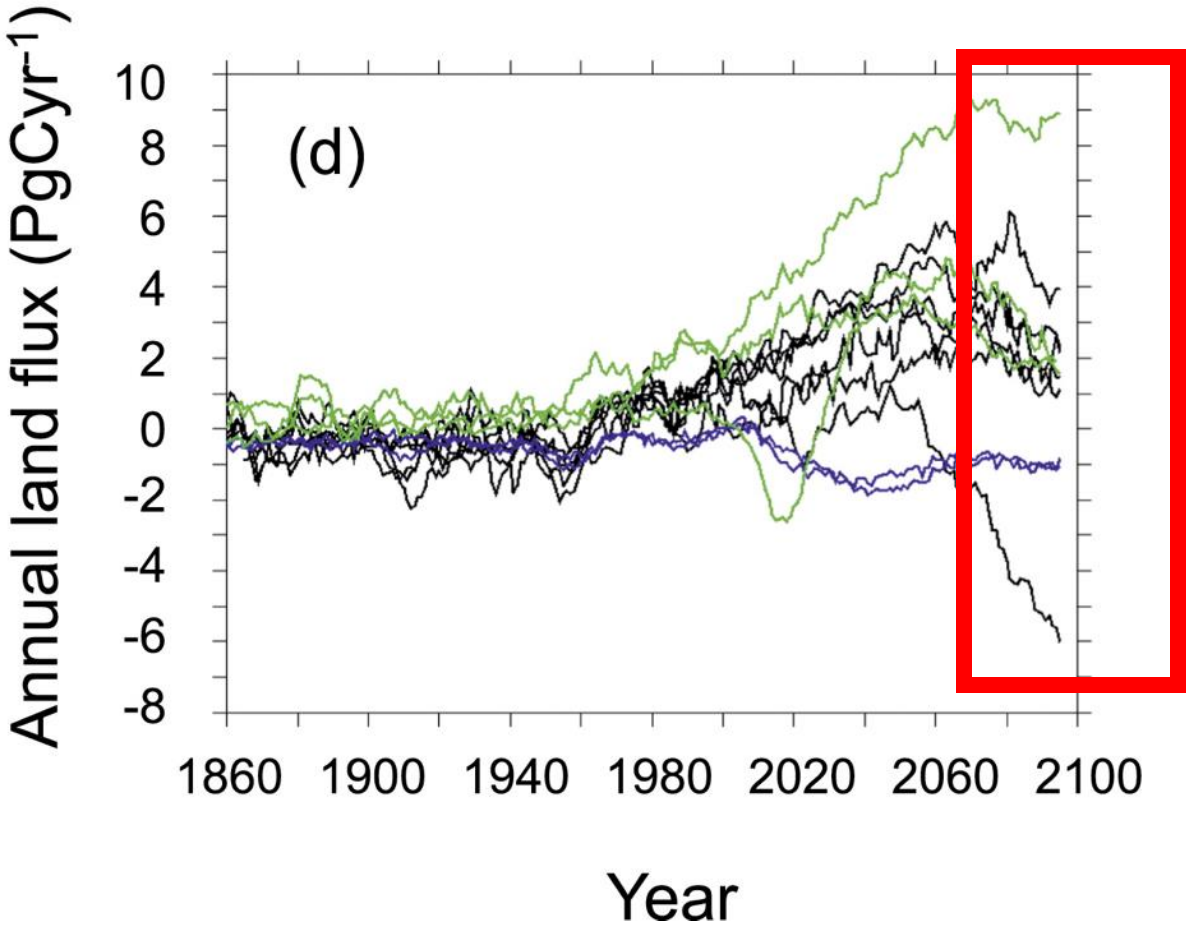
Data from IPCC (2013)

But predictions are uncertain!



Friedlingstein et al. (2014) *J Climate*

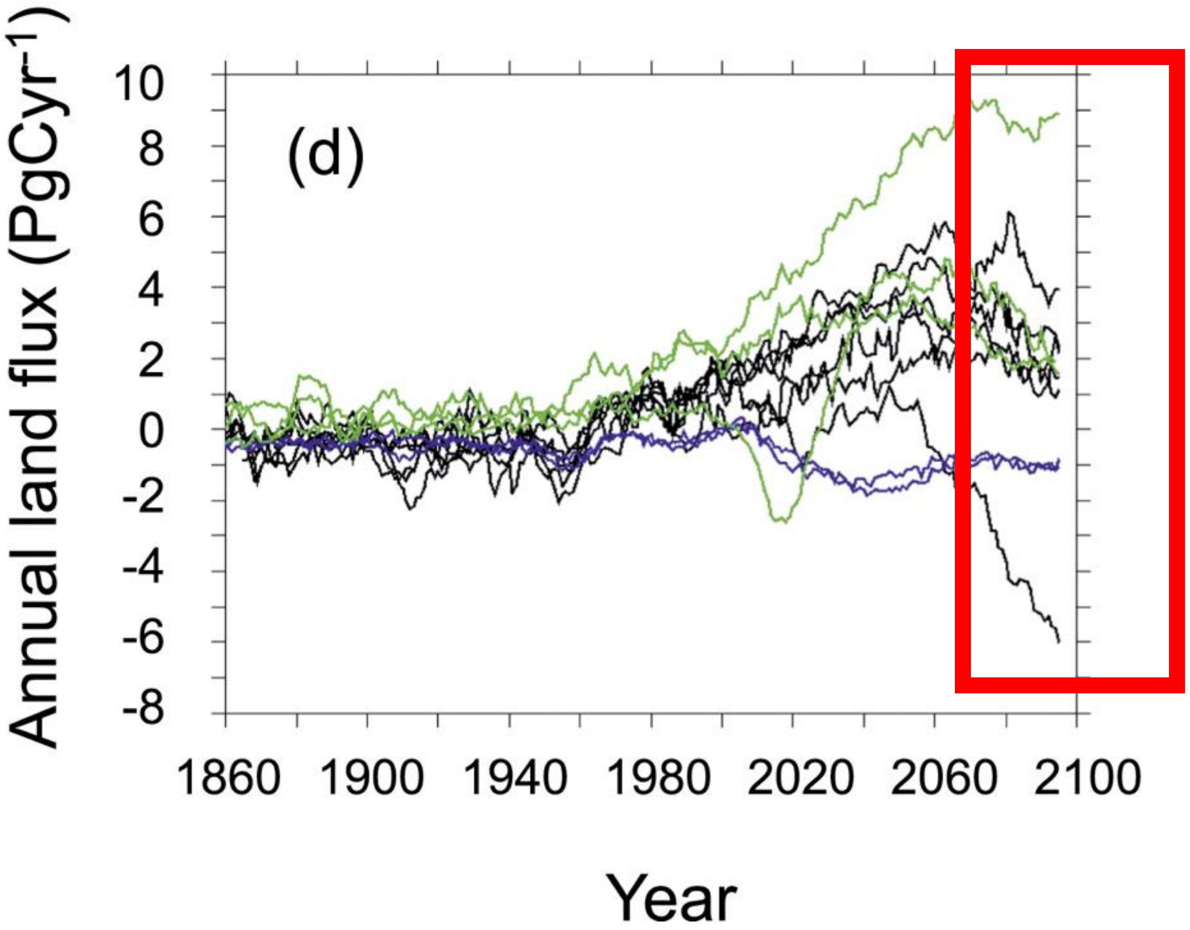
But predictions are uncertain!



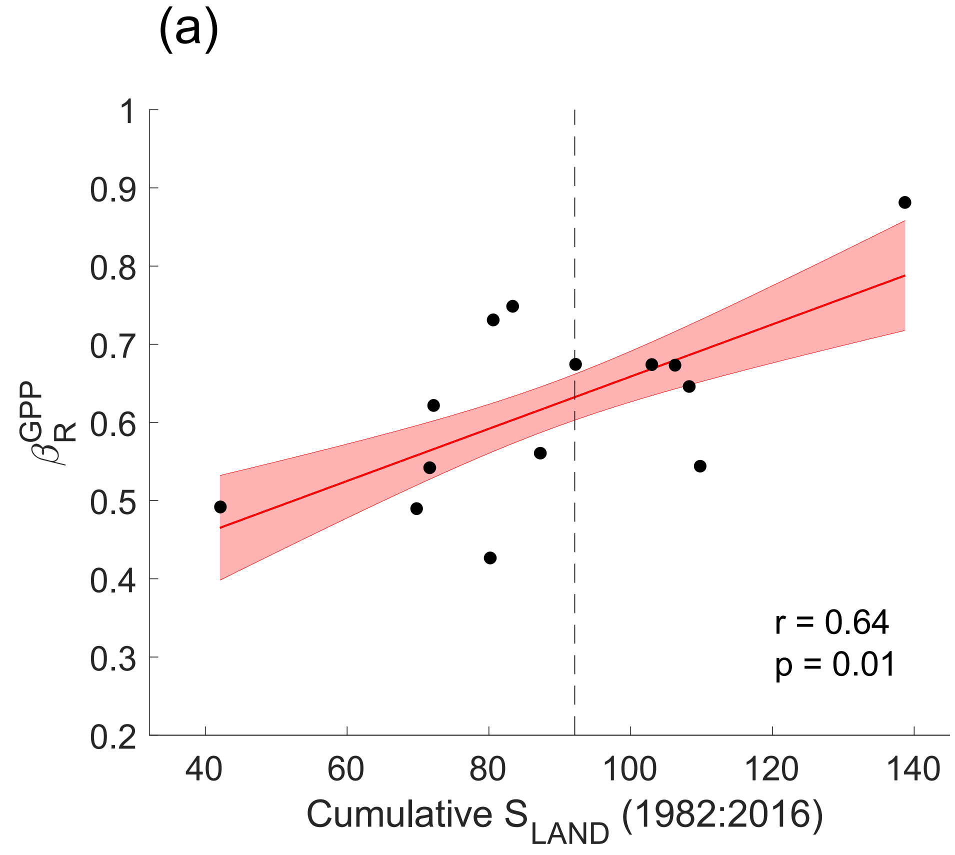
Future model uncertainty (14 Pg) > current fossil fuel emissions (9.5 Pg)

Friedlingstein et al. (2014) *J Climate*

This uncertainty is driven by uncertainty in photosynthesis



Friedlingstein et al. (2014) *J Climate*



Keenan et al. (2023) *Nature Climate Change*

Why the uncertainty? Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

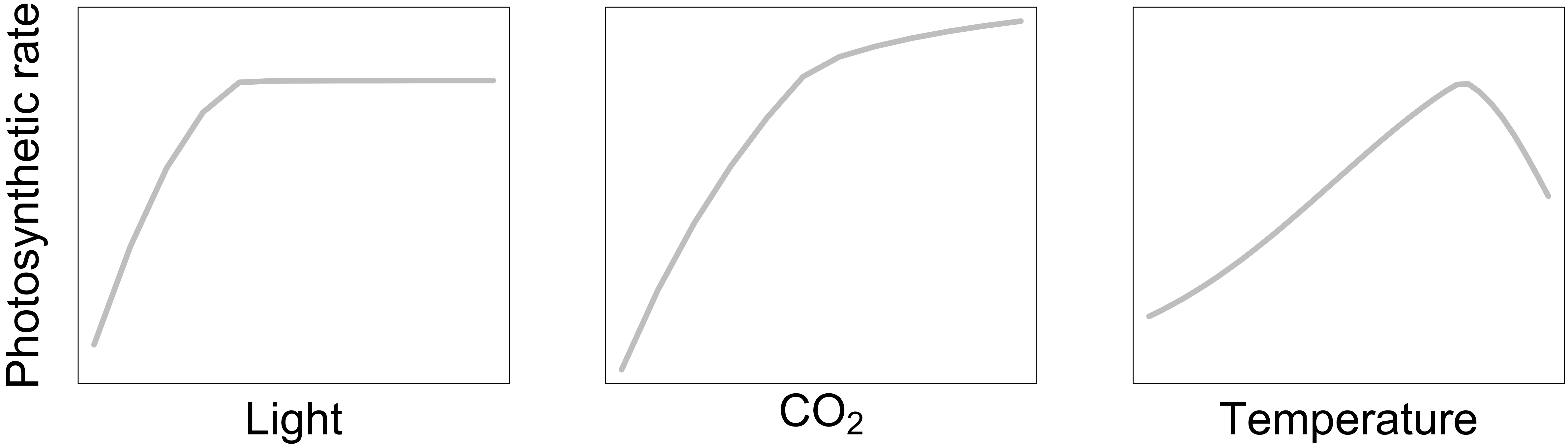
Planta

A Biochemical Model of Photosynthetic CO_2 Assimilation in Leaves of C_3 Species

G.D. Farquhar[1], S. von Caemmerer[1], and J.A. Berry[2]

[1] Department of Environmental Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City ACT 2601, Australia and
[2] Carnegie Institution of Washington, Department of Plant Biology, Stanford, Cal. 94305, USA

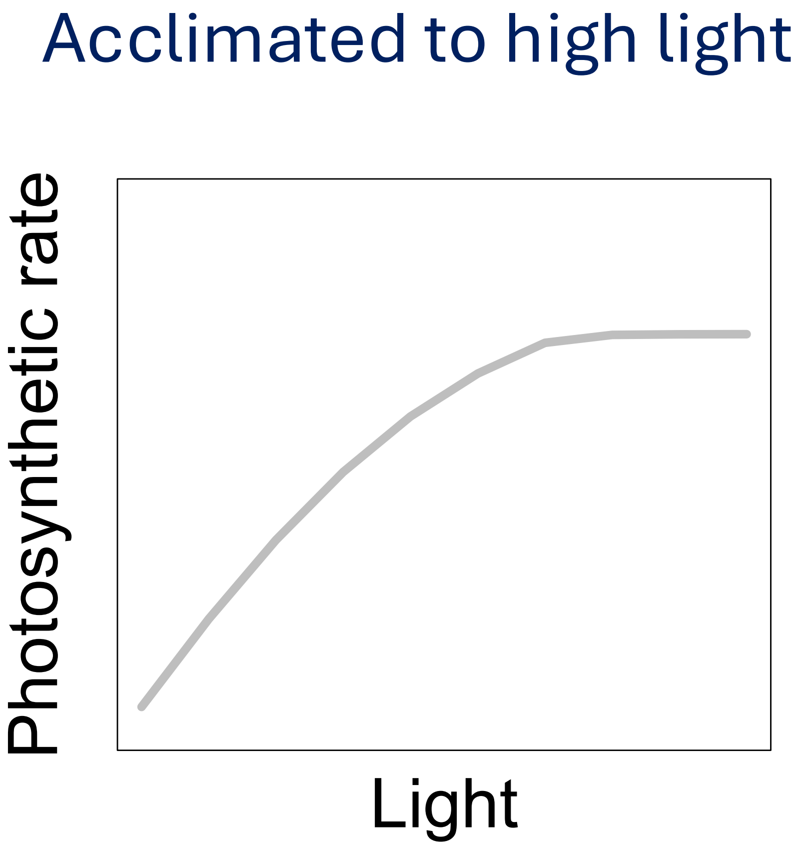
These produce short term responses that match data

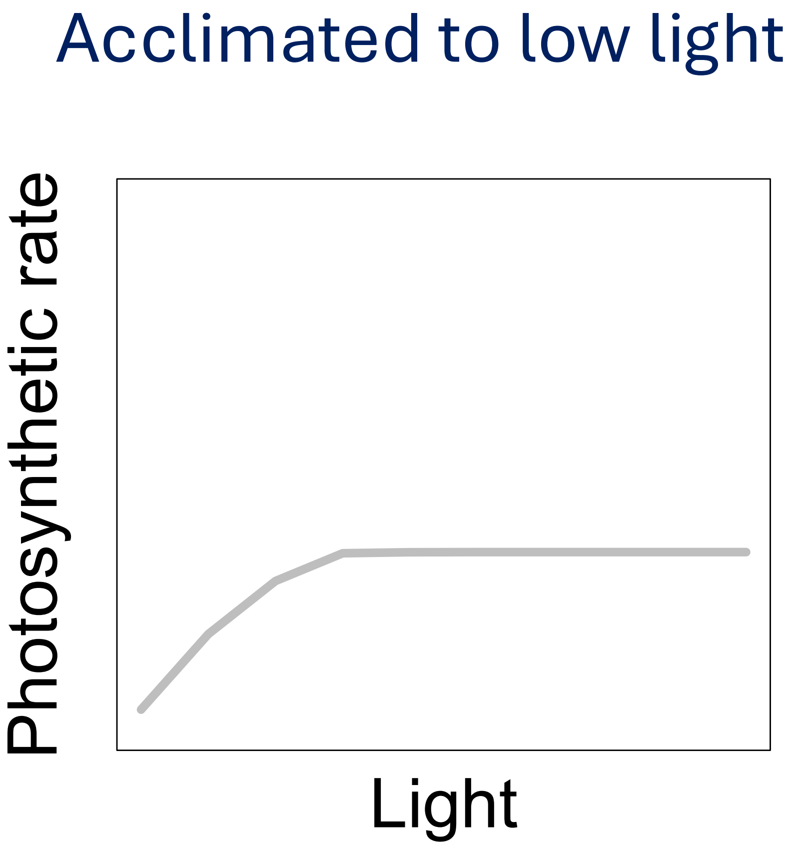


Why the uncertainty? Long-term responses differ from short-term responses due to acclimation

Dumb plants

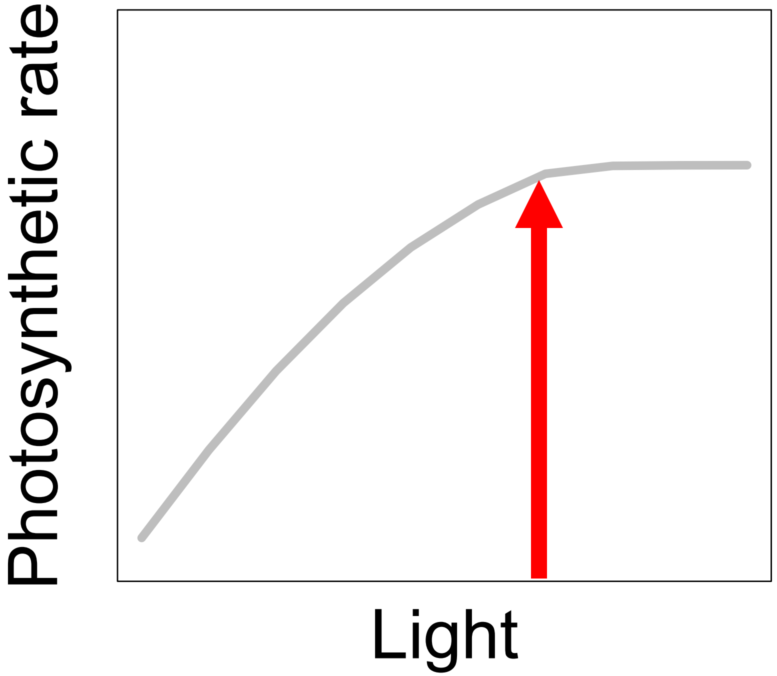
Acclimation: an example



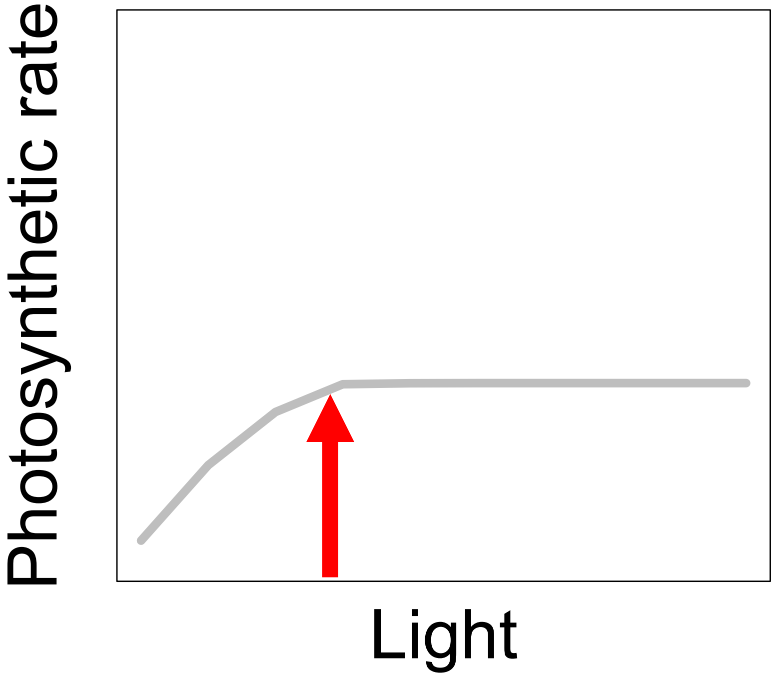


Acclimation: an example

Acclimated to high light



Acclimated to low light



Photosynthesis peaks a light level close to the level the leaf is acclimated to

Acclimation is ubiquitous and well known…

CO_2: Bazzaz (1990)

Annu. Rev. Ecol. Syst. 1990. 21:167–96

THE RESPONSE OF NATURAL ECOSYSTEMS TO THE RISING GLOBAL CO_2 LEVELS

F. A. Bazzaz

Light: Boardman (1977)

Ann. Rev. Plant Physiol. 1977. 28:355–77

COMPARATIVE PHOTOSYNTHESIS OF SUN AND SHADE PLANTS

N. K. Boardman
Division of Plant Industry, CSIRO, Canberra City, A.C.T. 2601, Australia

Temperature: Berry & Björkman (1980)

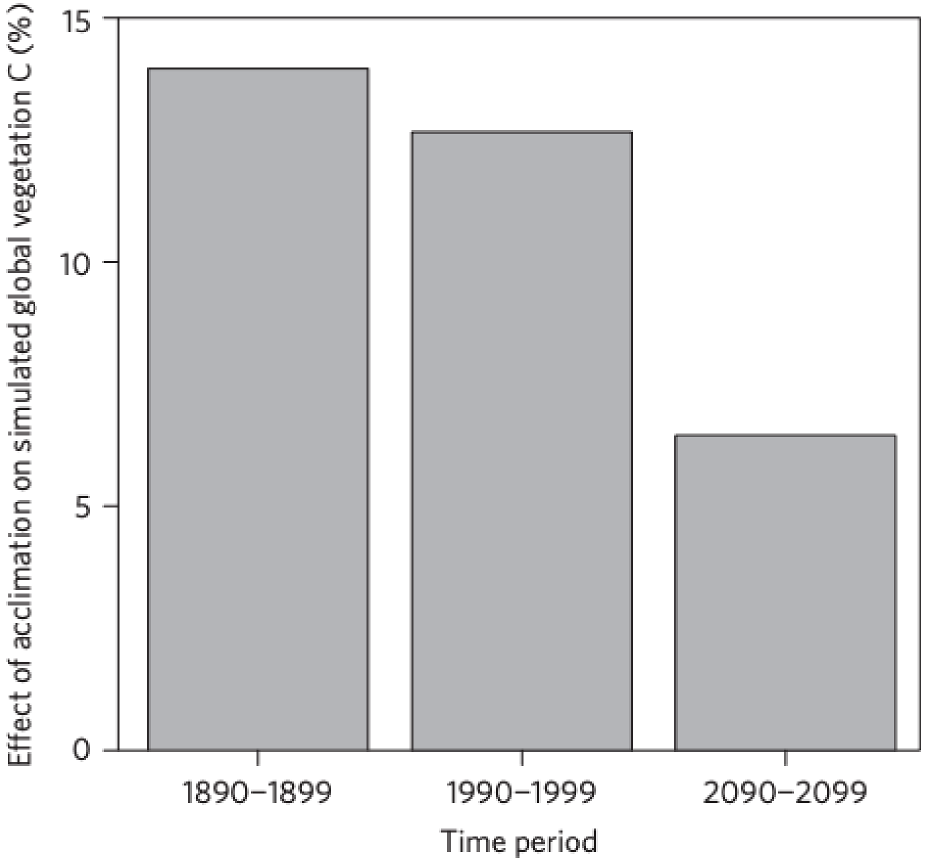
Ann. Rev. Plant Physiol. 1980. 31:491–543

PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

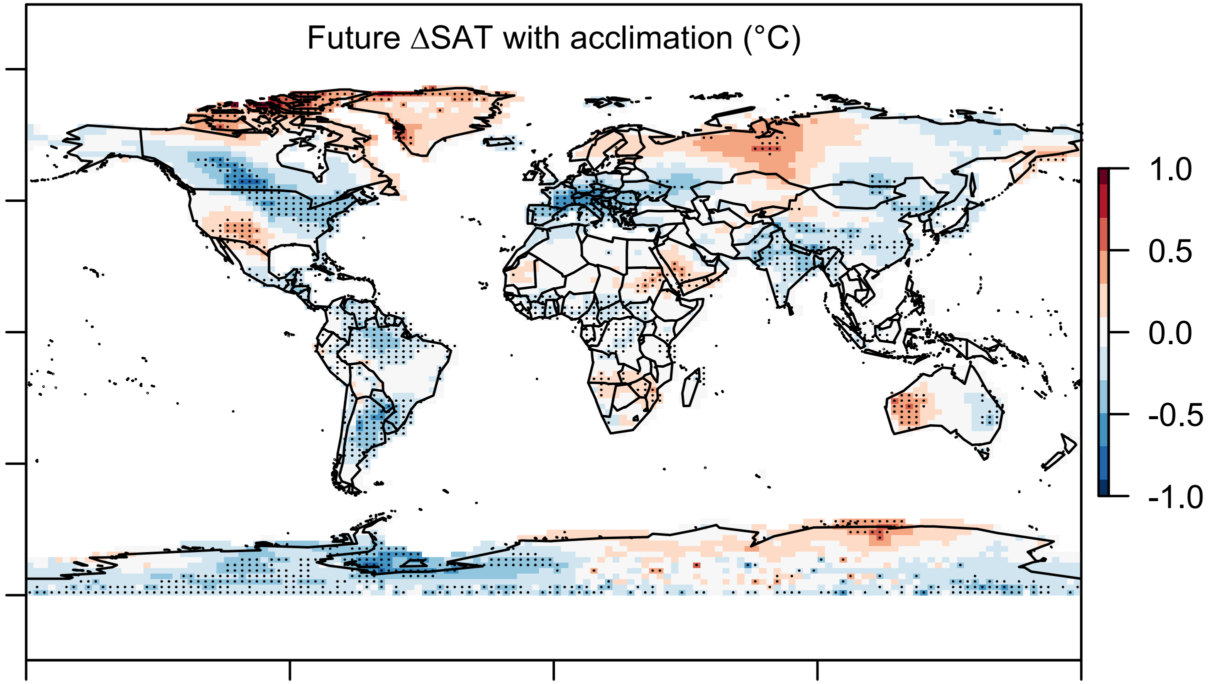
Joseph Berry and Olle Björkman[1]

…and can impact carbon cycling and climate

Acclimation increase future C storage by ~6%



Acclimation alters future temperature by >1°C



Smith et al. (2017) *Nature Climate Change*

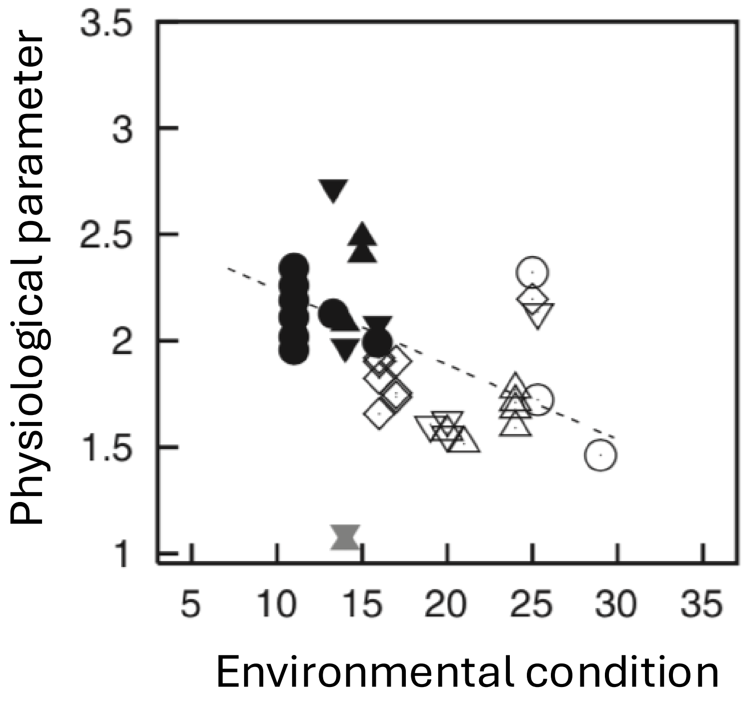
Smith et al. (2017) *JAMES*

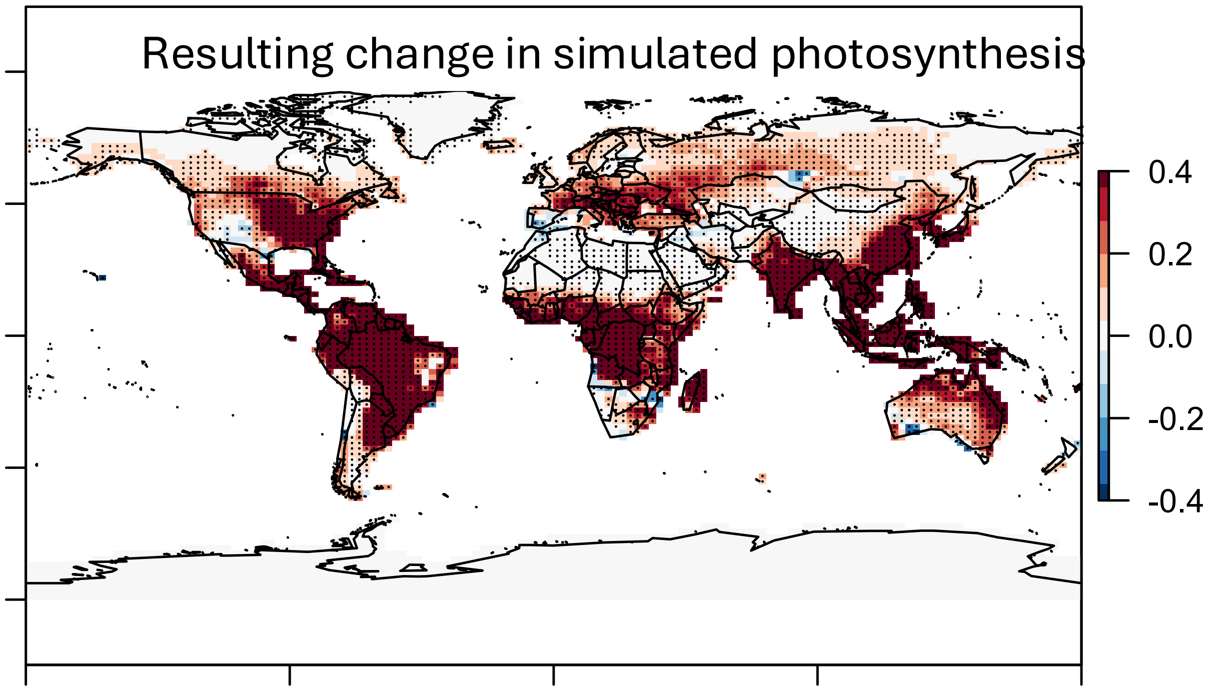
Unfortunately,
no theoretical model for
photosynthetic acclimation exists

Lack of theory results in…

Lack of theory results in…

- Unreliable future predictions (overparameterization, tuning)
  - Reliance on statistical models



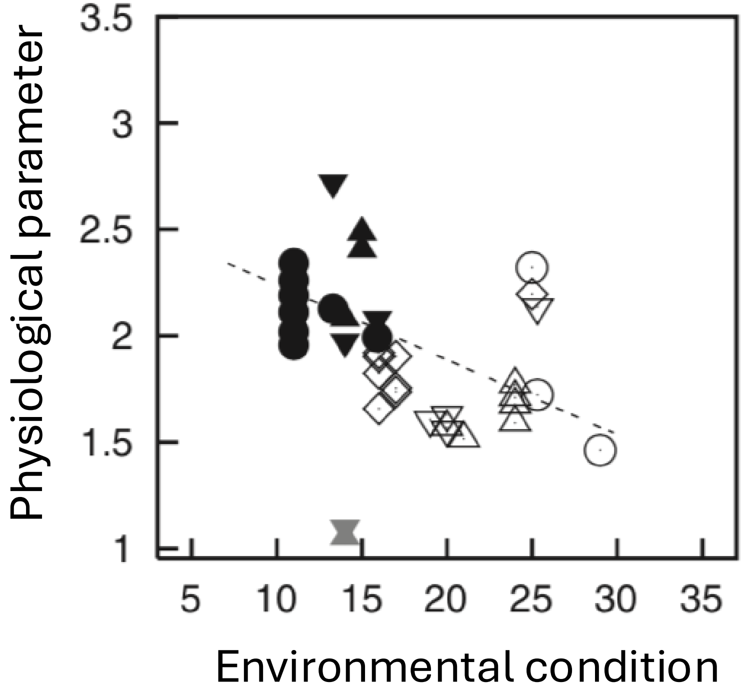


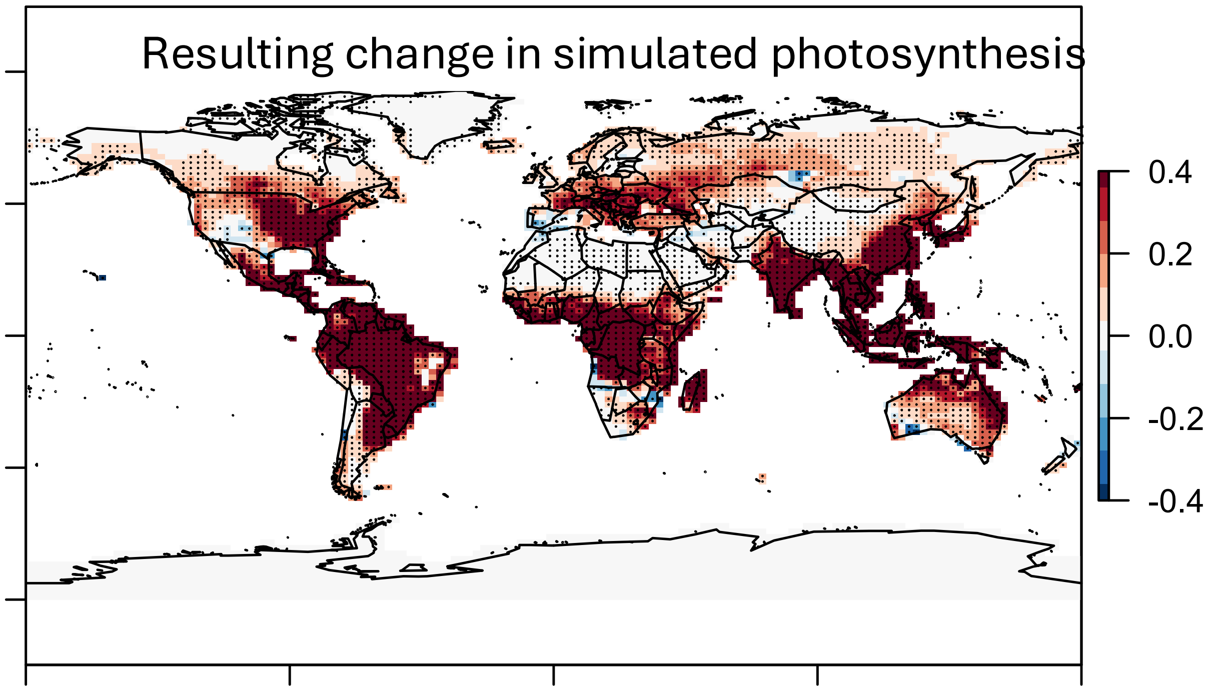
Kattge and Knorr (2007) *PC&E*

Smith et al. (2017) *JAMES*

Lack of theory results in…

- Inability to test mechanisms





Kattge and Knorr (2007) *PC&E*

Smith et al. (2017) *JAMES*

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Global Change Biology

REPORT | Open Access

Increasing the spatial and temporal impact of ecological research: A roadmap for integrating a novel terrestrial process into an Earth system model

Emily Kyker-Snowman, Danica L. Lombardozzi, Gordon B. Bonan, Susan J. Cheng, Jeffrey S. Dukes, Serita D. Frey, Elin M. Jacobs, Risa McNellis, Joshua M. Rady, Nicholas G. Smith ... See all authors

First published: 20 September 2021 | https://doi.org/10.1111/gcb.15894 | Citations: 27

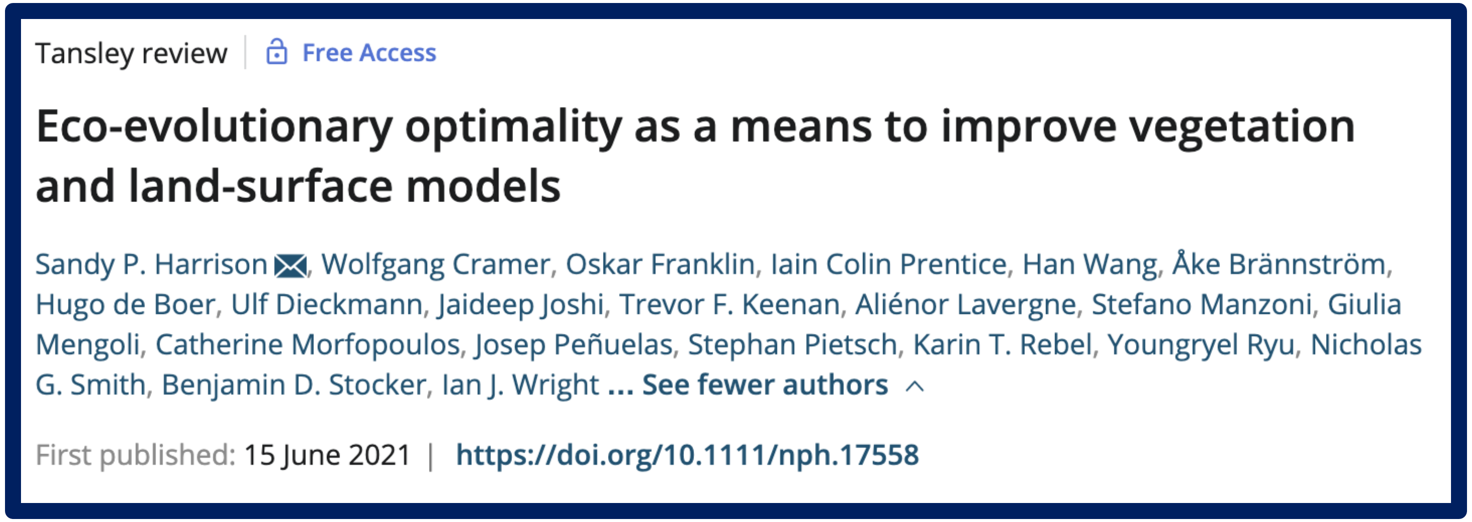
See also commentary on this article by Moore, 28, 343–345

Environmental condition

Kyker-Snowman et al. (2022) *Glob Change Biol*

So, we developed a mechanistic model of photosynthetic acclimation

Based on **optimization** and the **first principles** of plant physiological theory


Tansley review | Free Access

Eco-evolutionary optimality as a means to improve vegetation and land-surface models

Sandy P. Harrison, Wolfgang Cramer, Oskar Franklin, Iain Colin Prentice, Han Wang, Åke Brännström, Hugo de Boer, Ulf Dieckmann, Jaideep Joshi, Trevor F. Keenan, Aliénor Lavergne, Stefano Manzoni, Giulia Mengoli, Catherine Morfopoulos, Josep Peñuelas, Stephan Pietsch, Karin T. Rebel, Youngryel Ryu, Nicholas G. Smith, Benjamin D. Stocker, Ian J. Wright ... See fewer authors

First published: 15 June 2021 | https://doi.org/10.1111/nph.17558

Harrison et al. (2021) *New Phyt*

Optimization: Least cost theory

Optimally, plants will maintain fastest rate of photosynthesis at the lowest summed resource cost (water and nutrient use)

Wright et al. (2003) *Am Naturalist*

Optimal photosynthesis

Photosynthesis = *f*{stomatal conductance,
photosynthetic biochemistry}

Optimal photosynthesis

Photosynthesis = f{stomatal conductance,
photosynthetic biochemistry}

Must predict optimal rates of both

Optimal photosynthesis

Photosynthesis = *f*{**stomatal conductance**,
photosynthetic biochemistry}

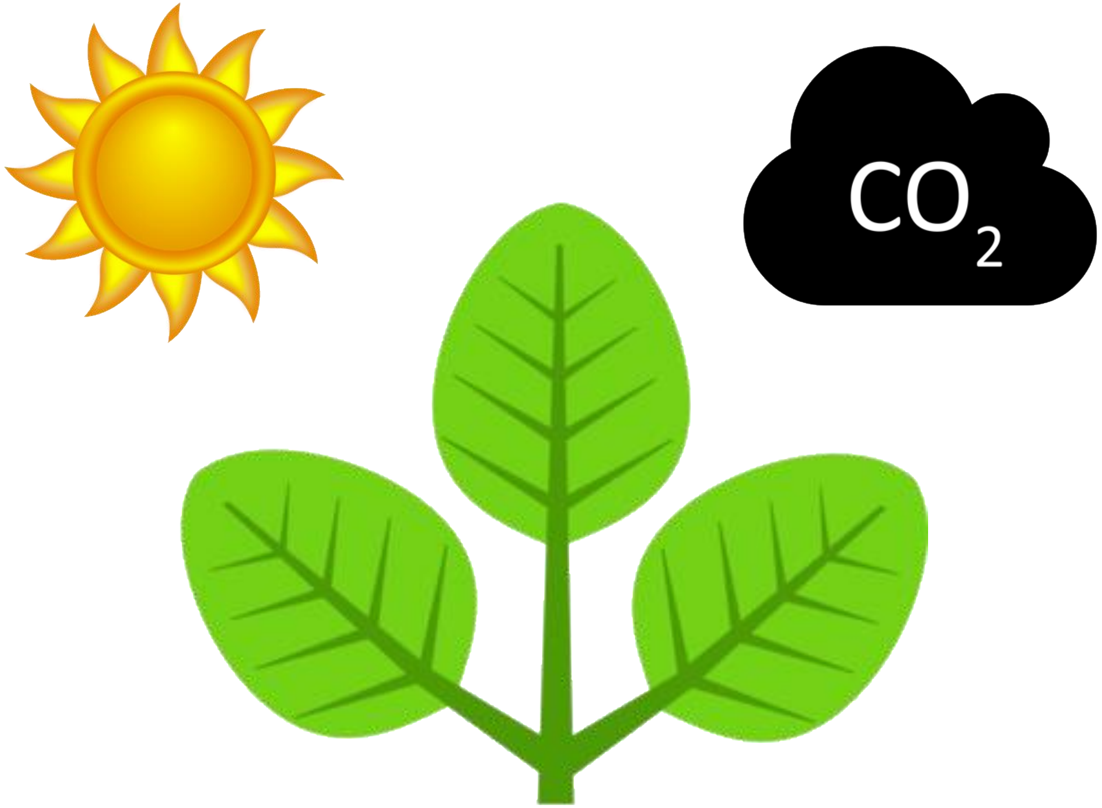
[TALK TO ME LATER ABOUT THIS IF YOU ARE INTERESTED]

Prentice et al. (2014) *Ecol Letters*; Wang et al. (2017) *Nature Plants*; Smith et al. (2019) *Ecol Letters*; Smith and Keenan (2020) *Glob Change Biol*

Optimal photosynthesis

Photosynthesis = *f*{stomatal conductance,
photosynthetic biochemistry}

Biochemistry optimization



Plant biochemistry setup will aim for equal limitation by all factors

[TALK TO ME LATER ABOUT THE MATHS]

Optimally:
electron transport-limited (A_j) = Rubisco-limited (A_c)

$$A_j = A_c$$

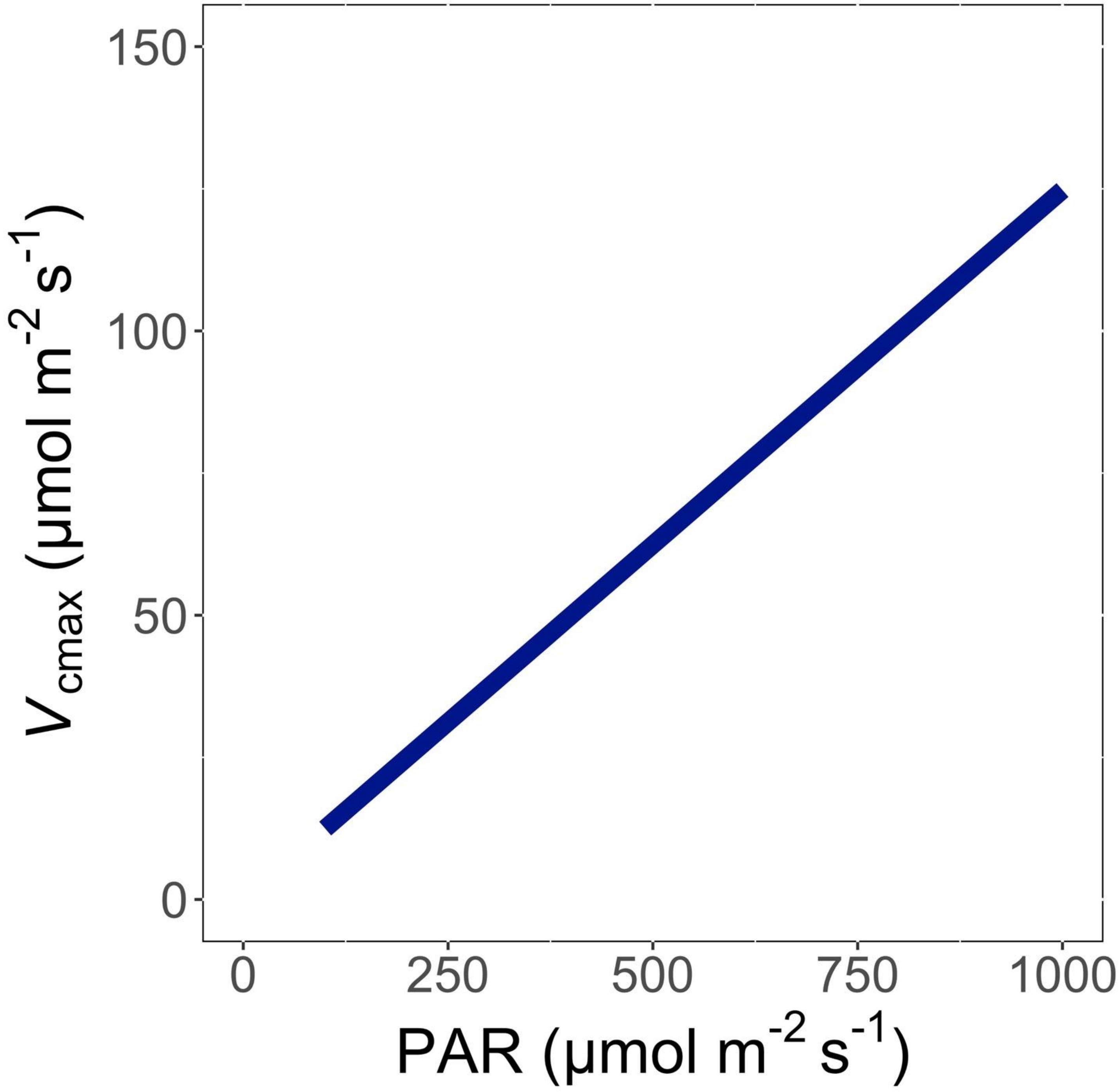
$$A_j = f\{\text{light, T, CO}_2\}$$

$$A_c = f\{V_{cmax}\text{, T, CO}_2\}$$

Smith et al. (2019) *Ecol Letters*

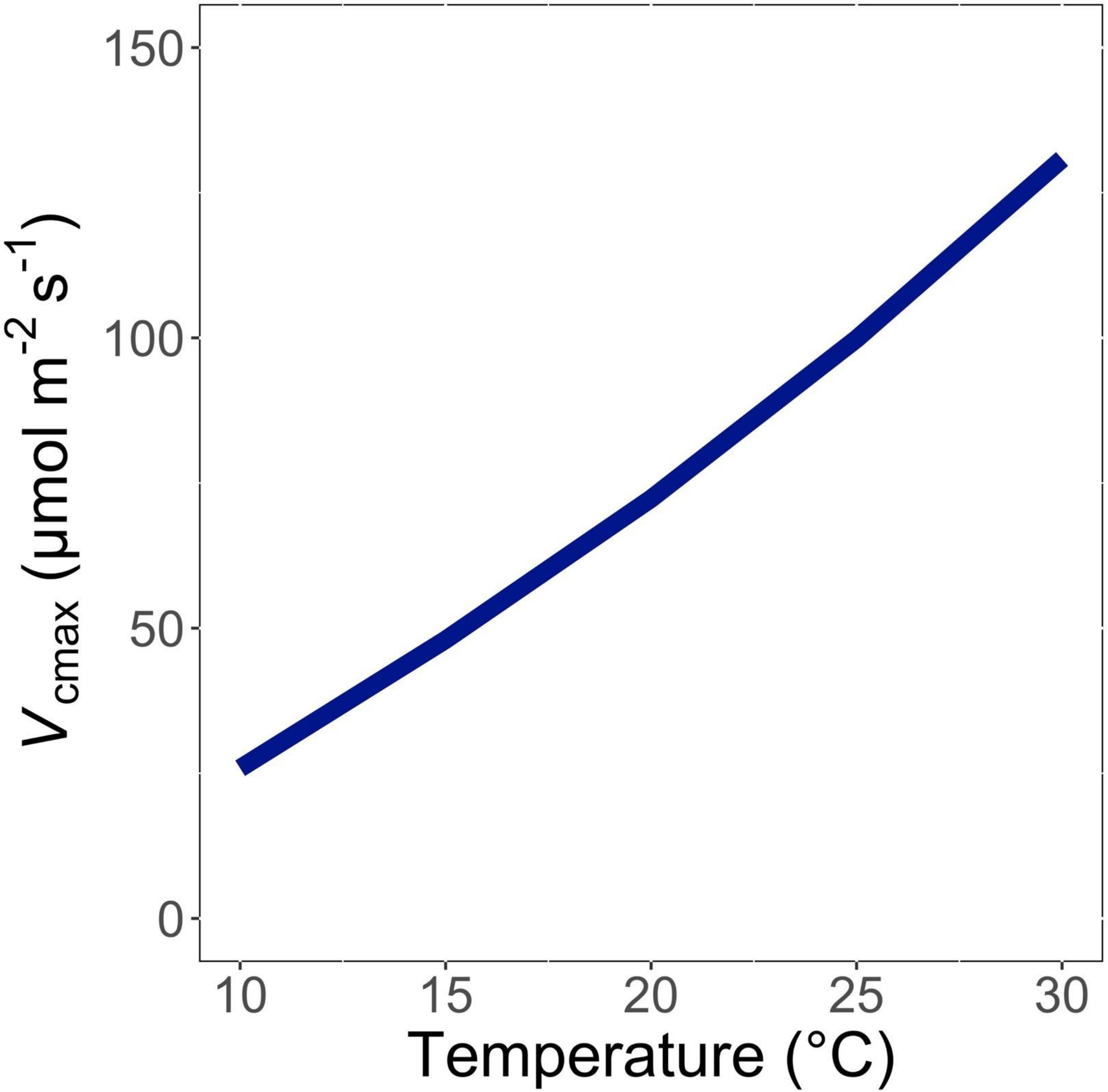
$$V_{cmax} = f\,\{\text{light, T, } CO_2\}$$

Smith et al. (2019) *Ecol Letters*



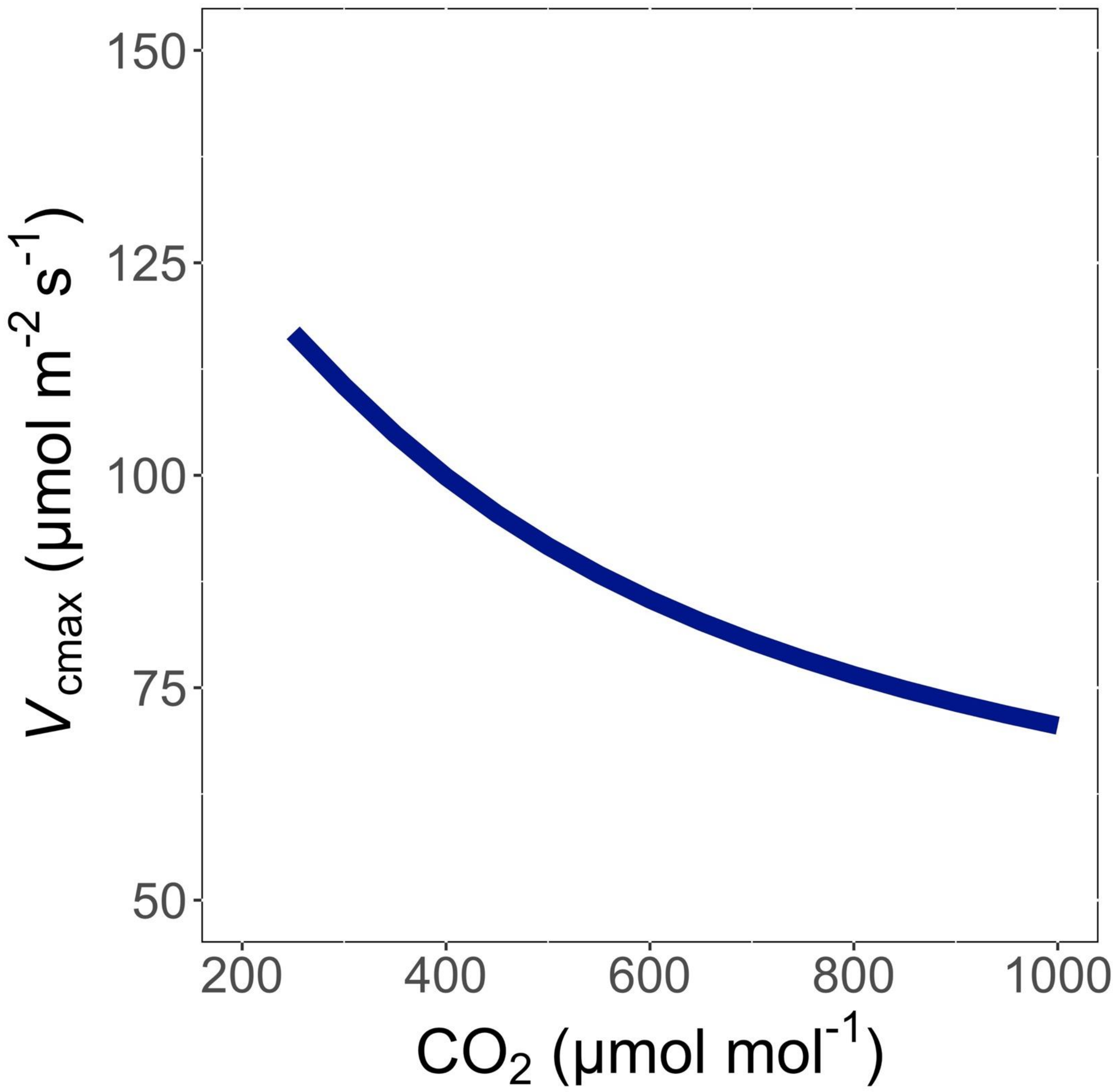
V_{cmax} increases with light because of greater electron transport

Smith et al. (2019) *Ecol Letters*; Smith and Keenan (2020) *Glob Change Biology*



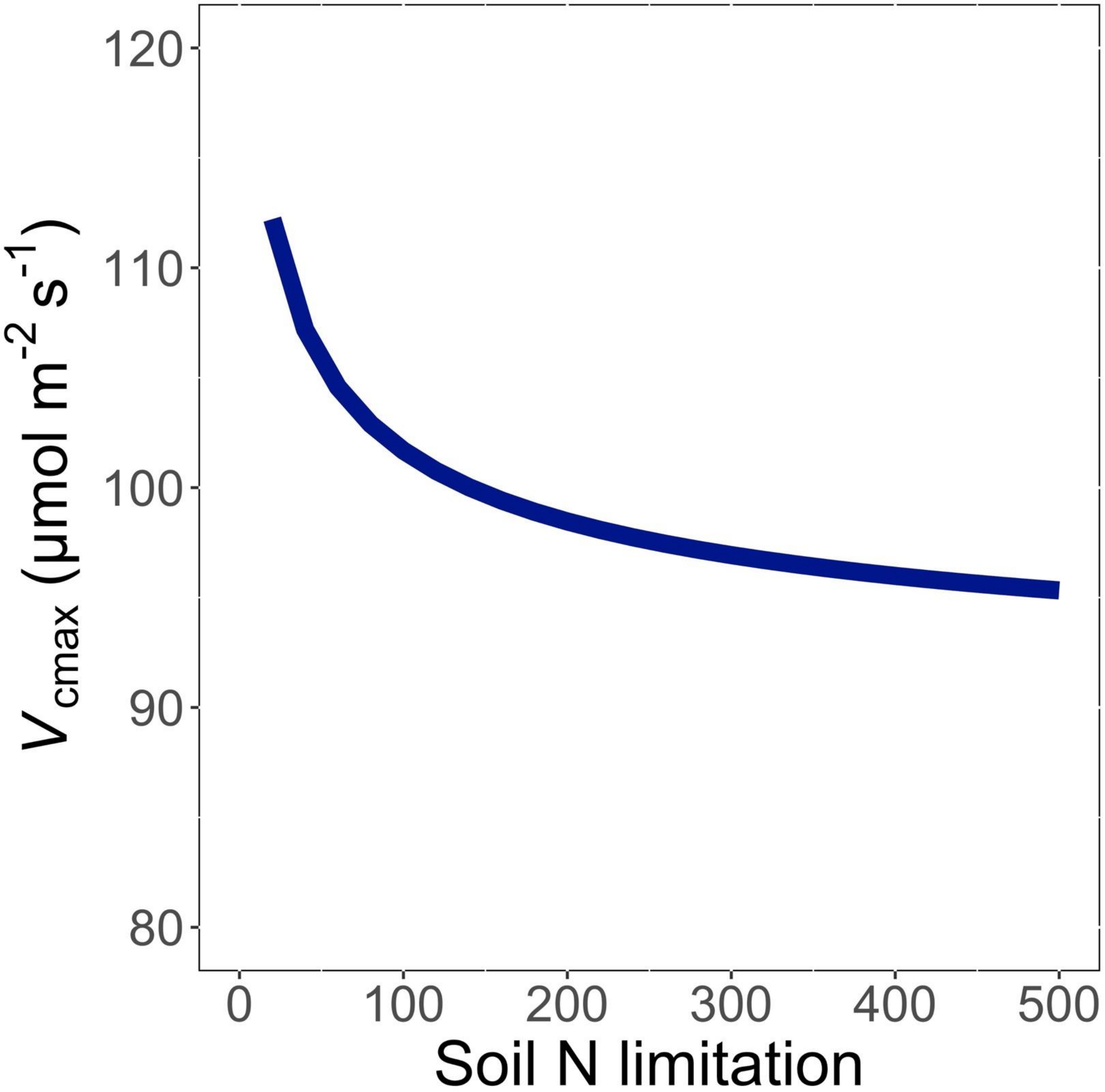
V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019) *Ecol Letters*; Smith and Keenan (2020) *Glob Change Biology*



V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf and less photorespiration

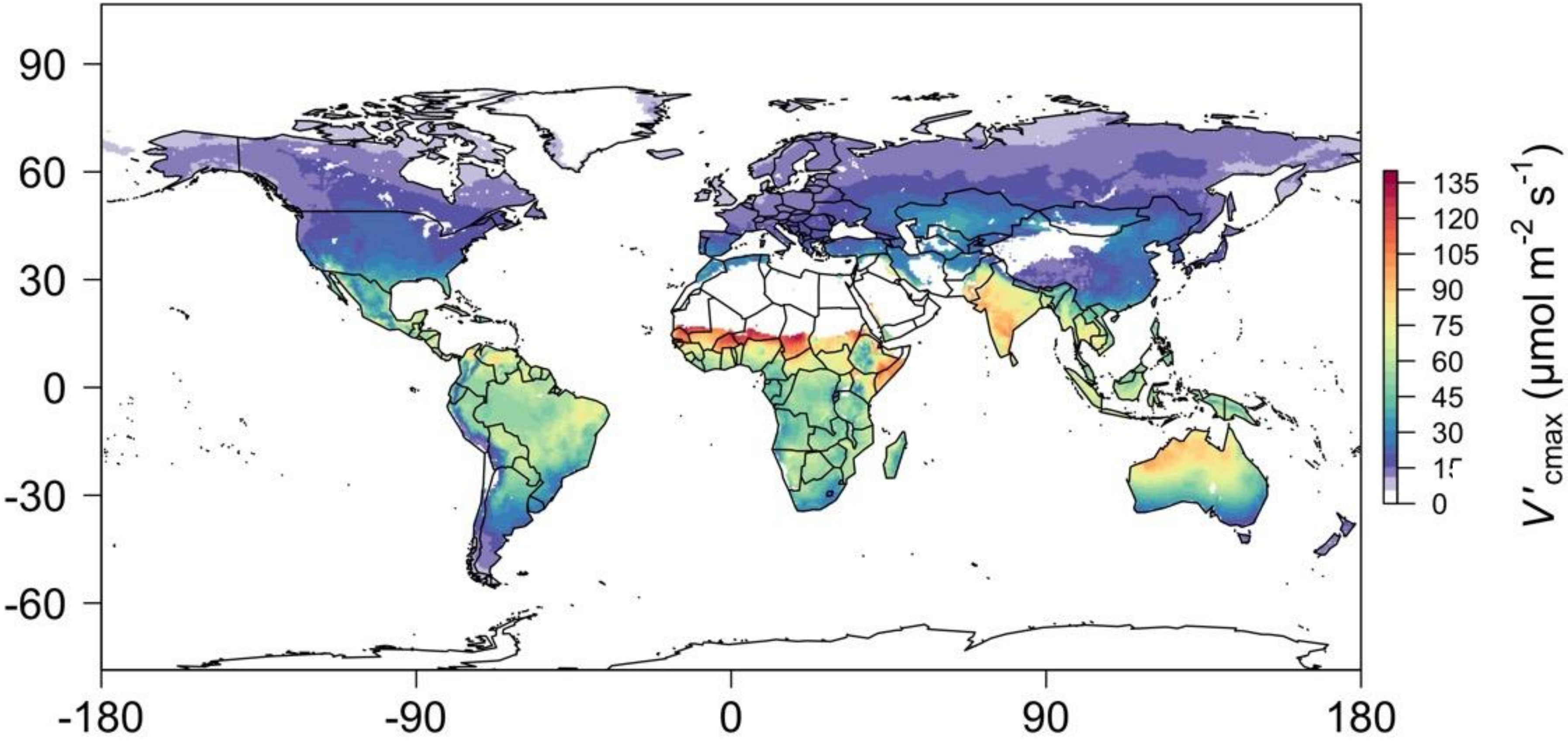
Smith et al. (2019) *Ecol Letters*; Smith and Keenan (2020) *Glob Change Biology*



V_{cmax} decreases with soil N limitation because Rubisco requires a lot of N

Smith et al. (2019) *Ecol Letters*; Smith and Keenan (2020) *Glob Change Biology*

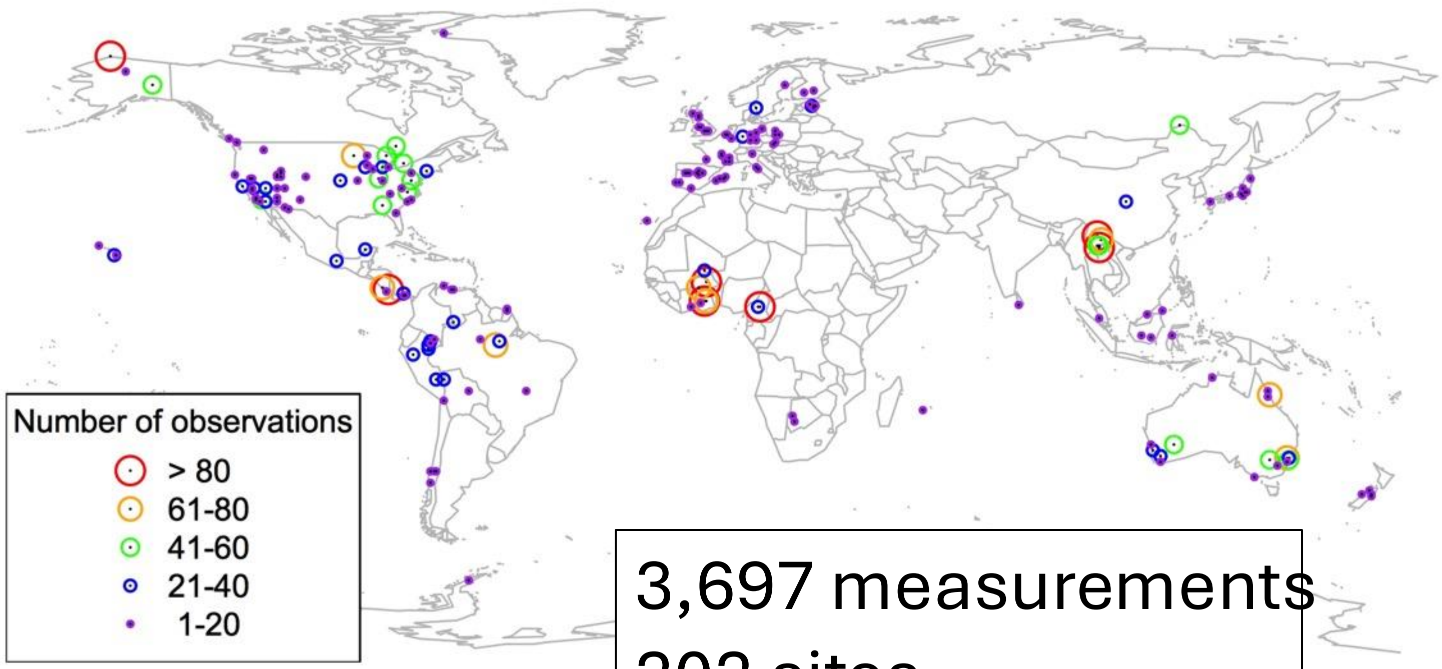
We can predict optimal traits in different environments



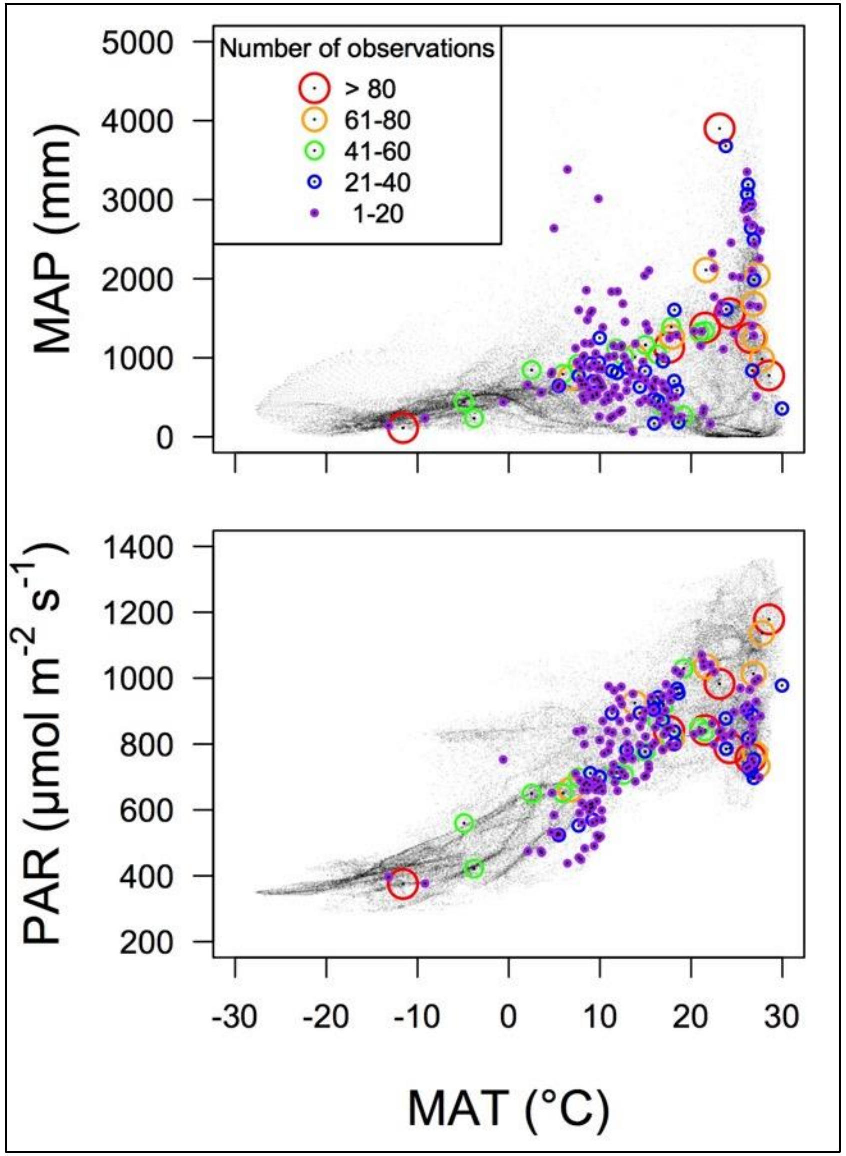
Smith et al. (2019) *Ecol Letters*

Ok great, but does it work?

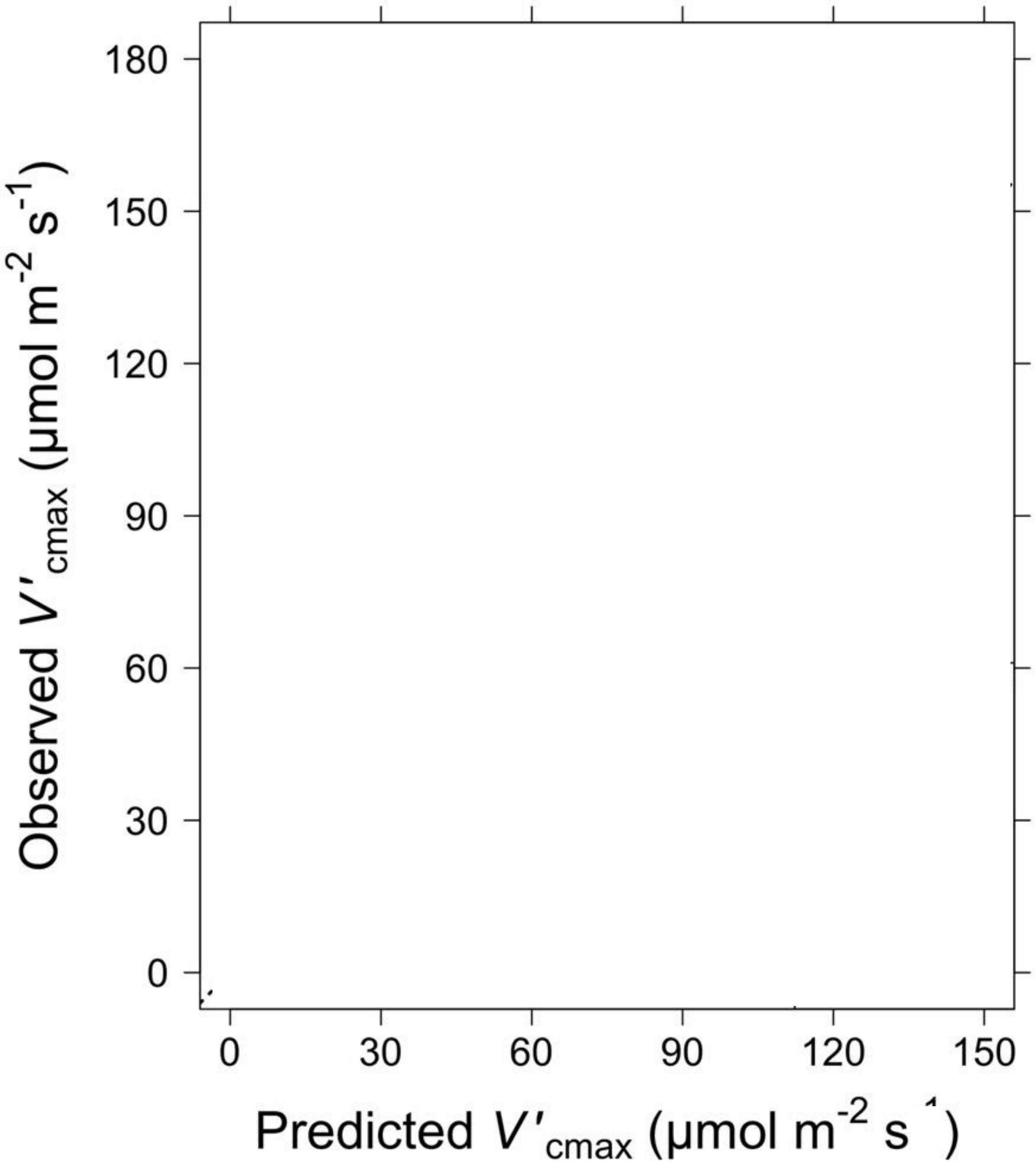
Global V_{cmax} dataset



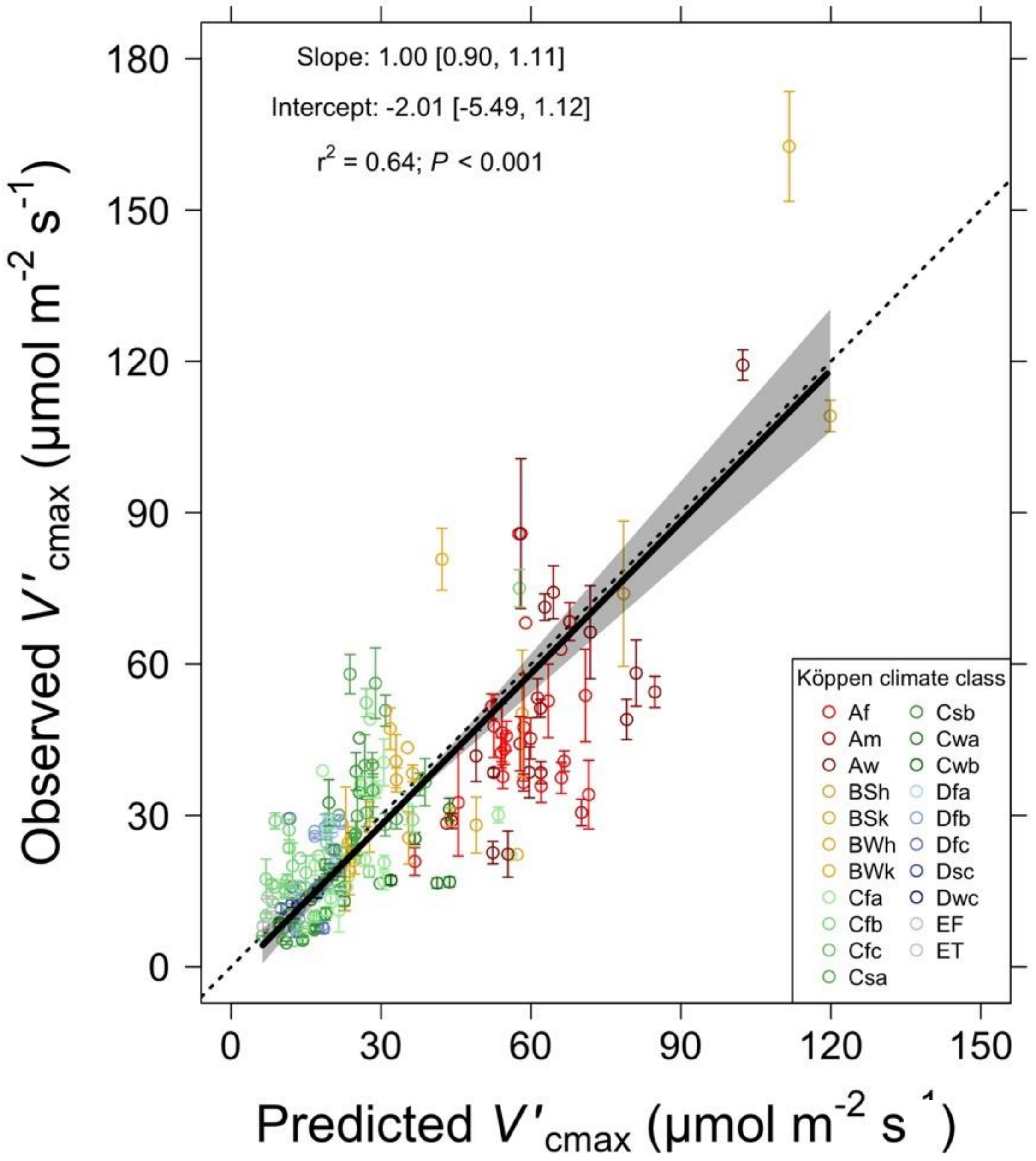
3,697 measurements
202 sites
> 600 genera



Smith et al. (2019) *Ecol Letters*



Smith et al. (2019) *Ecol Letters*

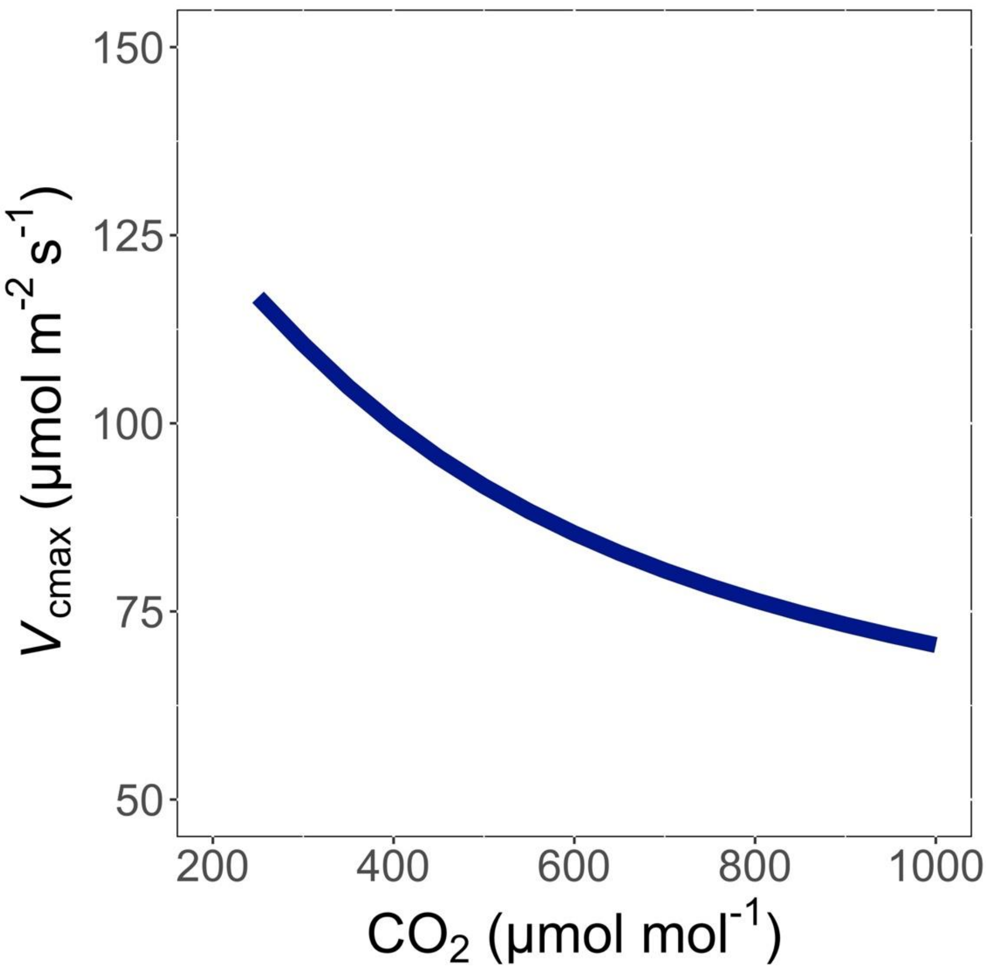


Optimal V_{cmax} is similar to observed values

Smith et al. (2019) *Ecol Letters*

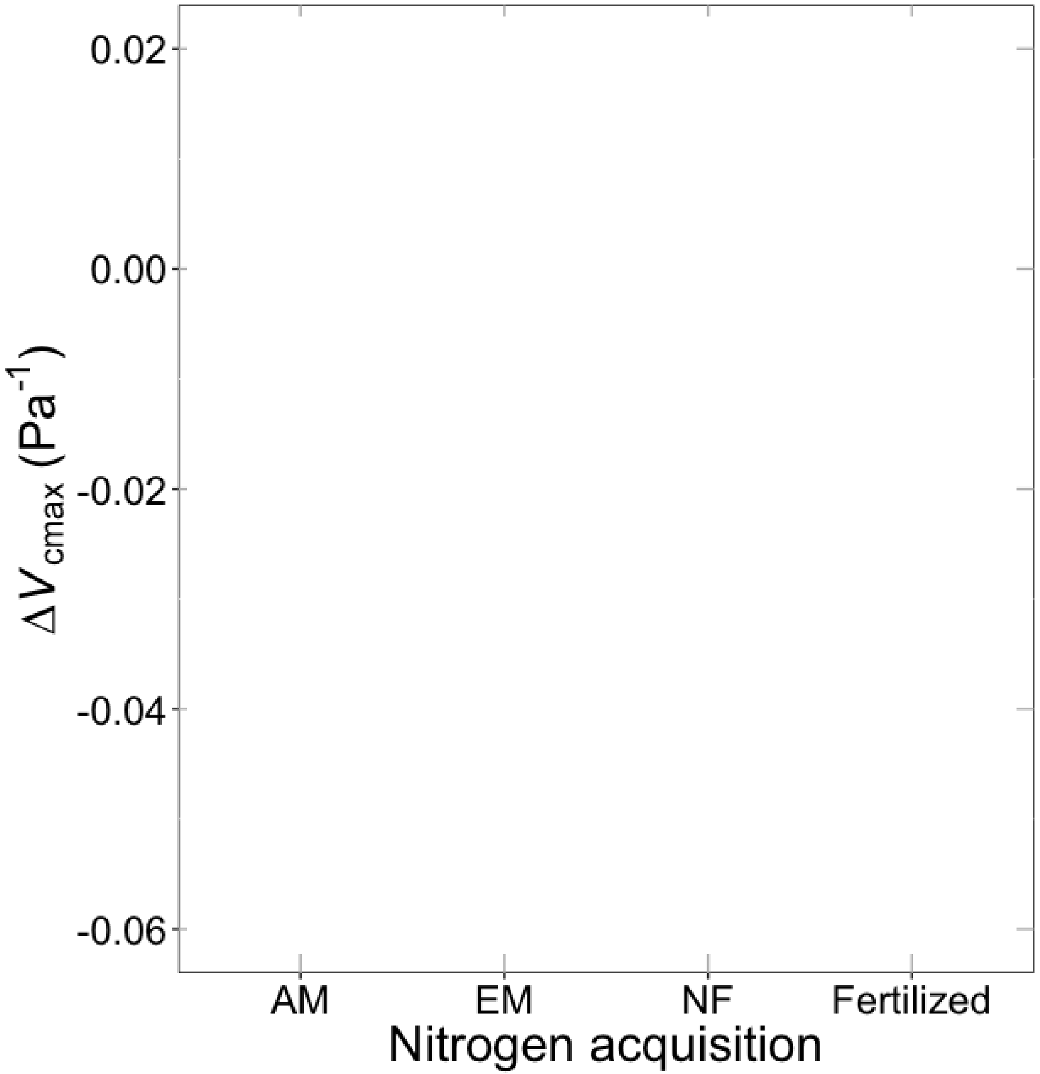
What does acclimation mean for future terrestrial biogeochemical cycling? An Example

Expected future responses

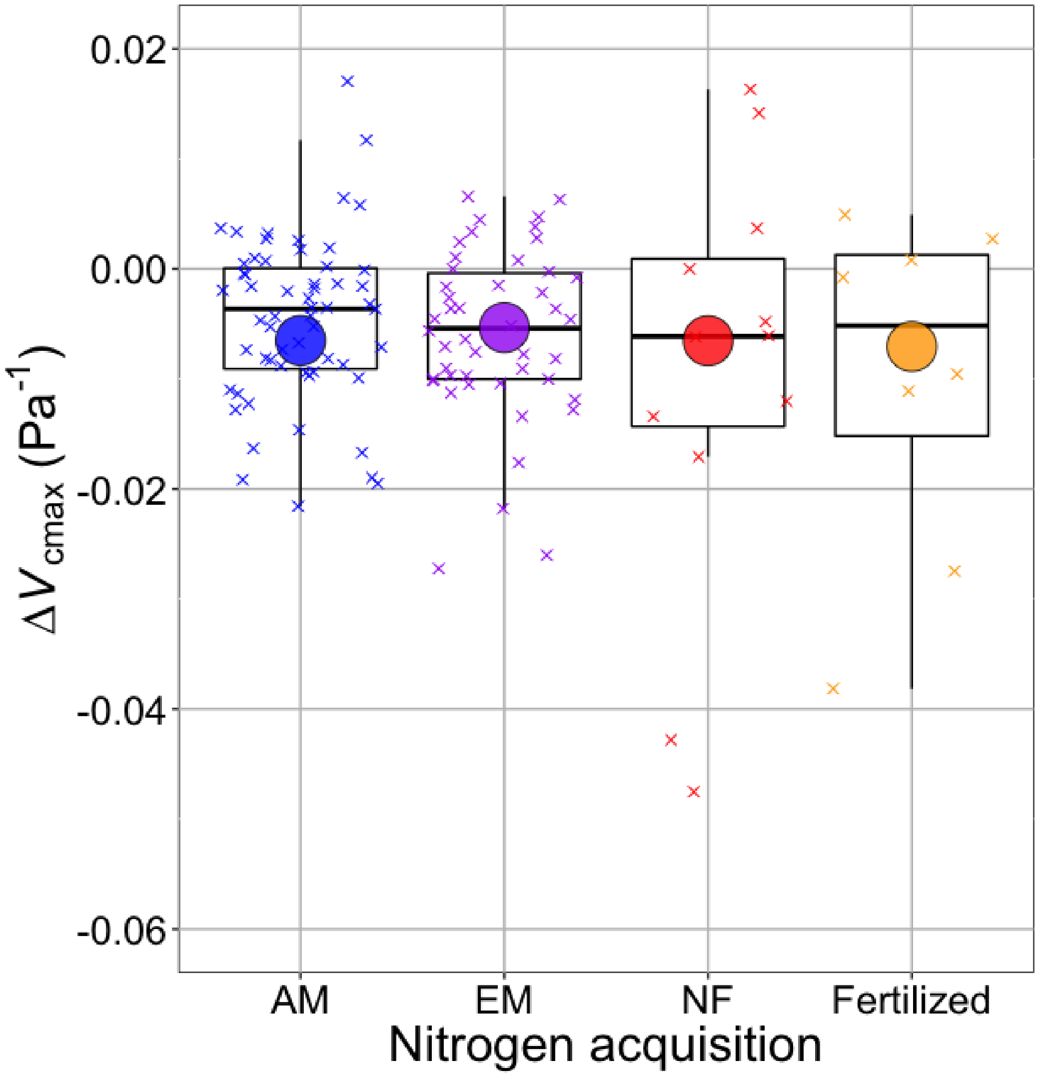


V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf and less photorespiration

Smith et al. (2019) *Ecol Letters*



Smith and Keenan (2020) *Glob Change Biol*

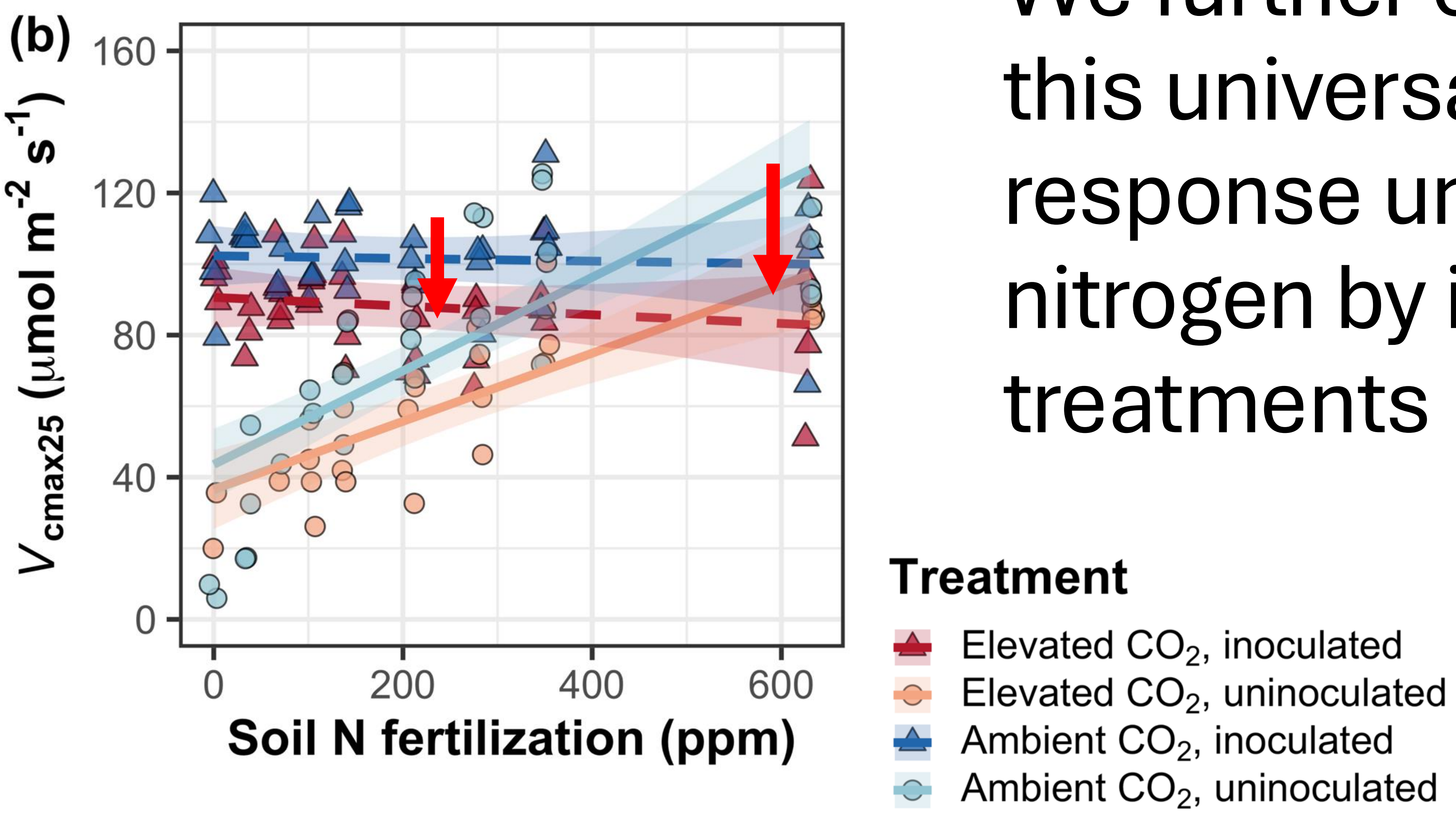


V_{cmax} changes with CO_2 in ways expected from optimization

Boxes = data = -0.0063 Pa^{-1}

Circles = predicted = -0.0066 Pa^{-1}

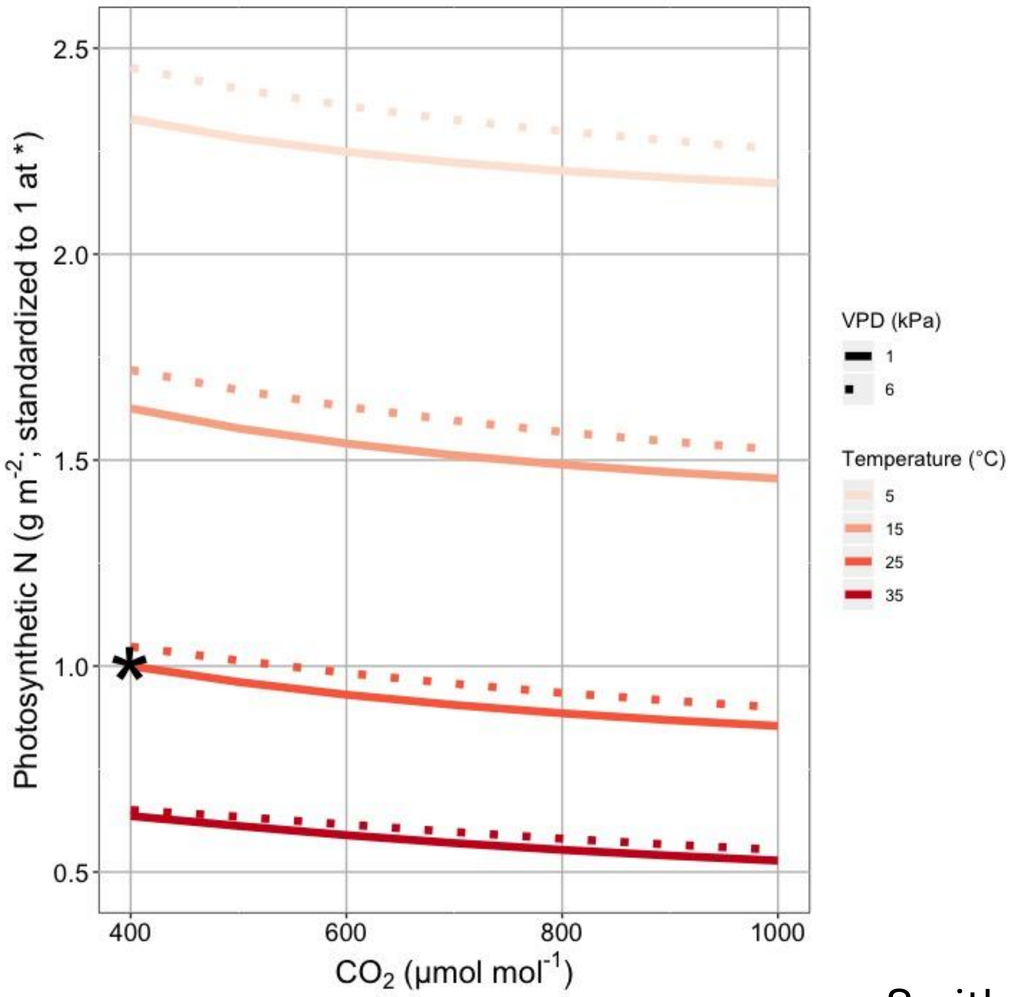
Smith and Keenan (2020) *Glob Change Biol*



We further confirmed this universality of this response under 18 nitrogen by inoculation treatments

Perkowski, Ezekannagha, and Smith (2025) *J Exp Botany*

This generally suggests lower nitrogen demand under future conditions

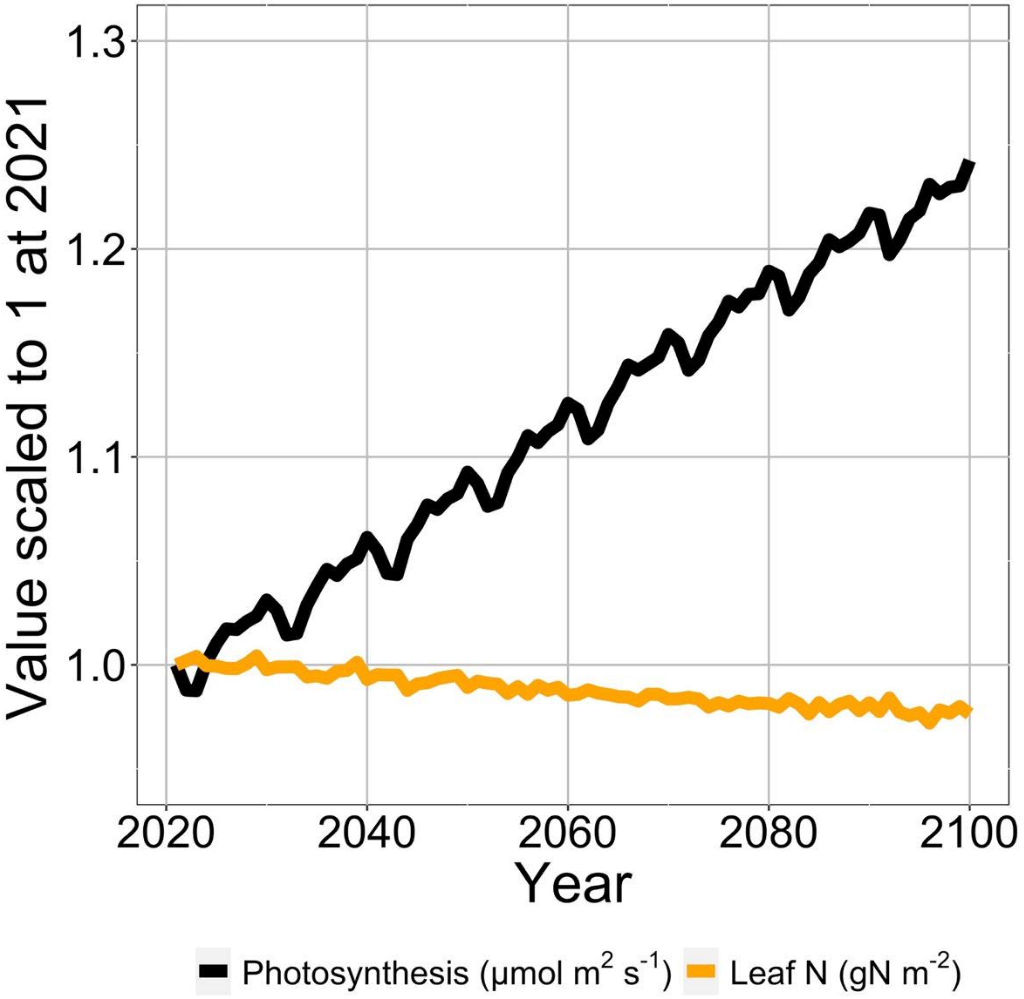


Smith and Keenan (2020) *Glob Change Biol*

Let’s run a model out into the future!

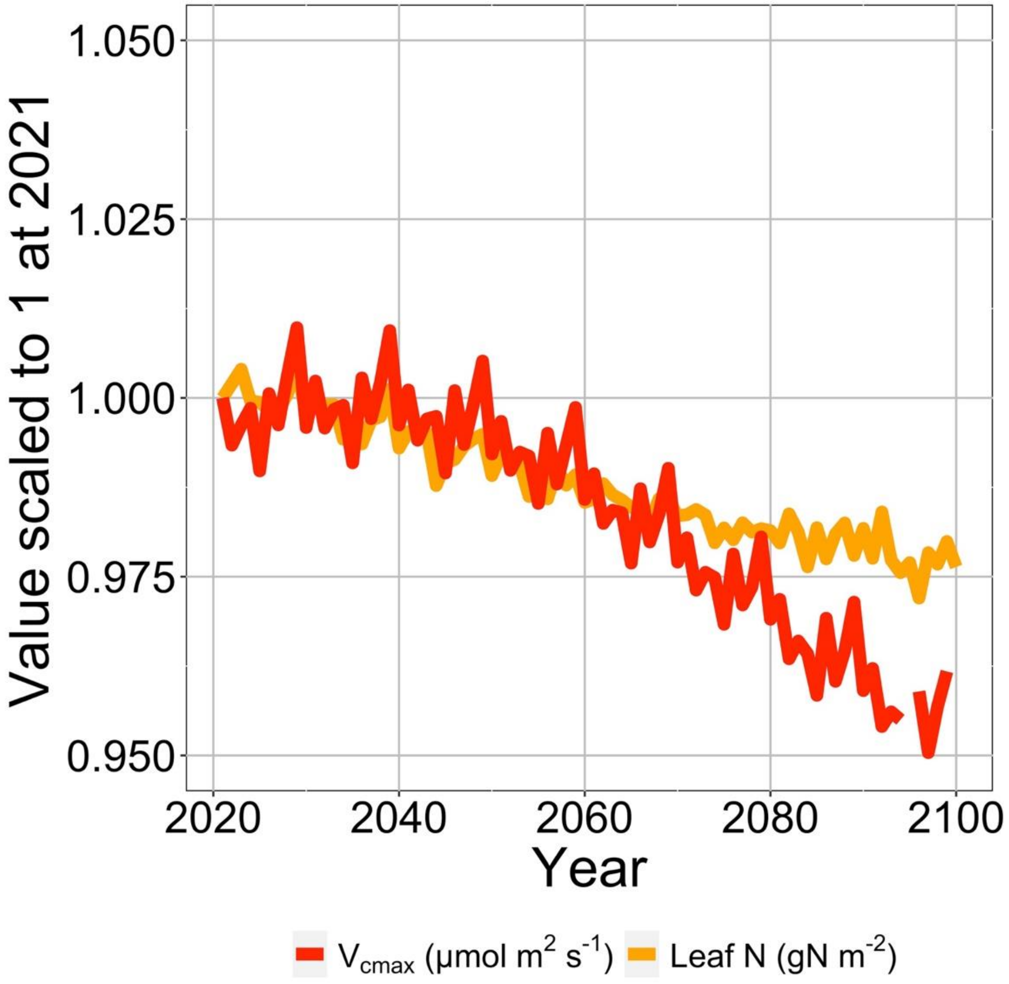
E3SM Energy Exascale Earth System Model

Photosynthesis increases with elevated CO_2 at lower leaf N



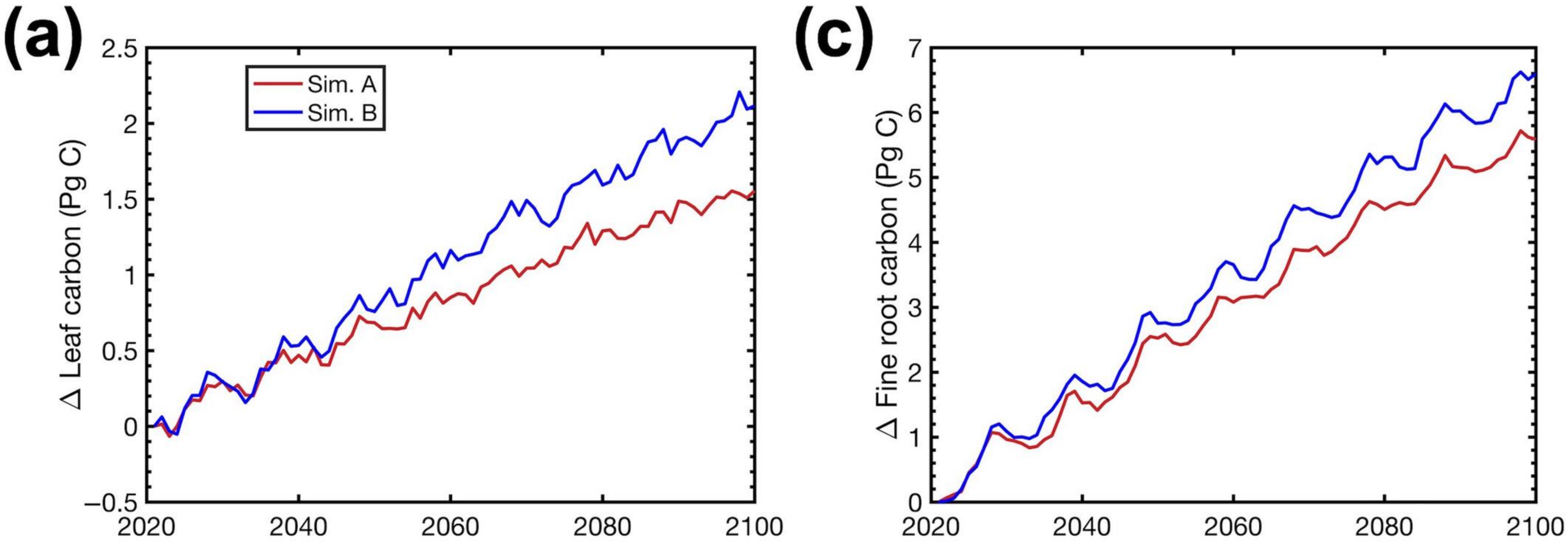
Smith et al. (2024) *Glob Change Biol*

Leaf N reduction is due to a reduction in photosynthetic capacity



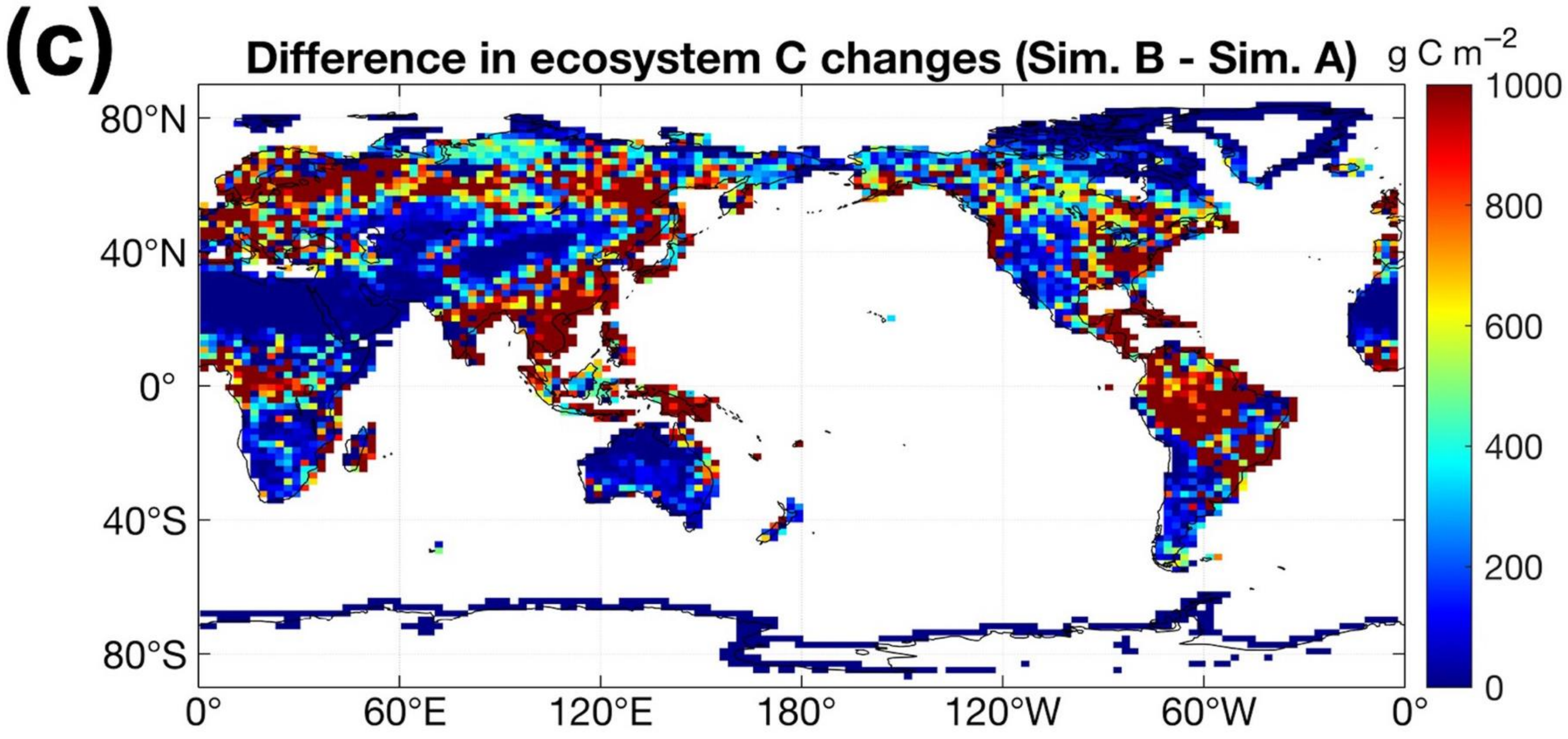
Smith et al. (2024) *Glob Change Biol*

Plants build more leaves and fine roots



Smith et al. (2024) *Glob Change Biol*

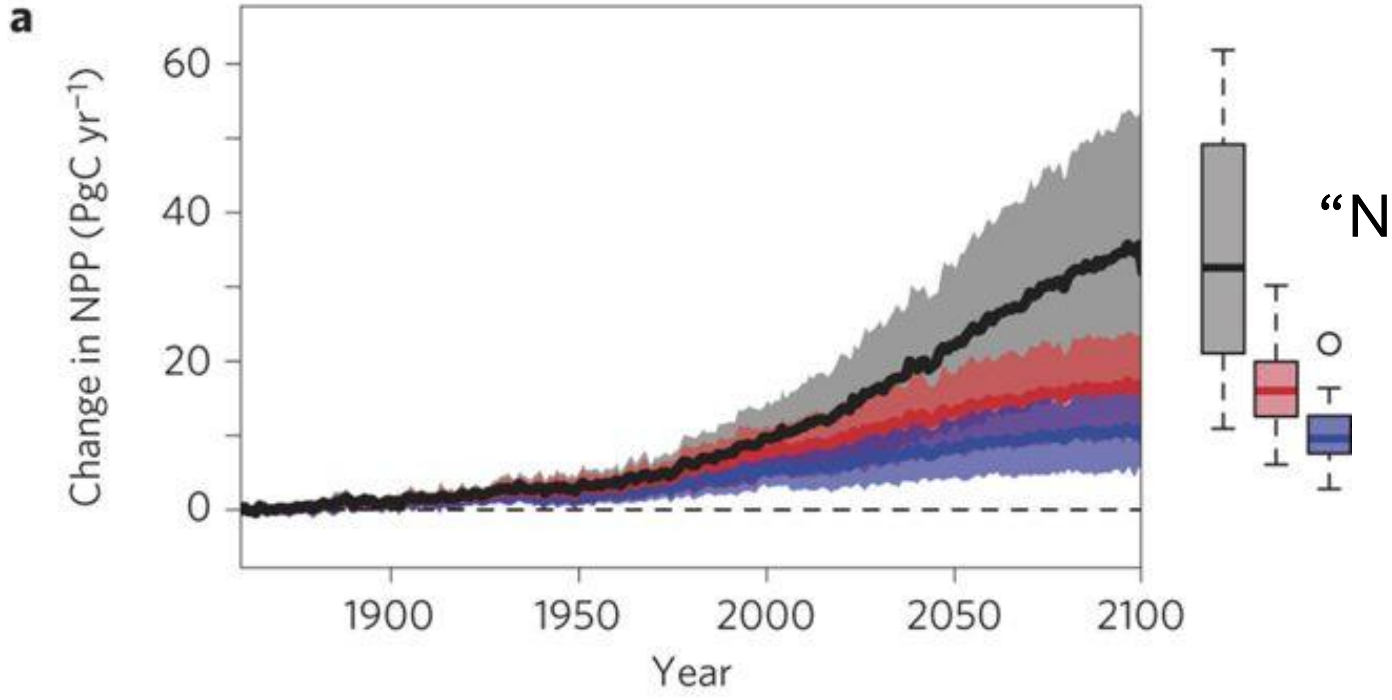
Leaf N savings increases long-term ecosystem carbon stocks



50% increase in ecosystem carbon from CO_2 acclimation

Smith et al. (2024) *Glob Change Biol*

Need to rethink nutrient limitation in models?



“No limitation” simulation

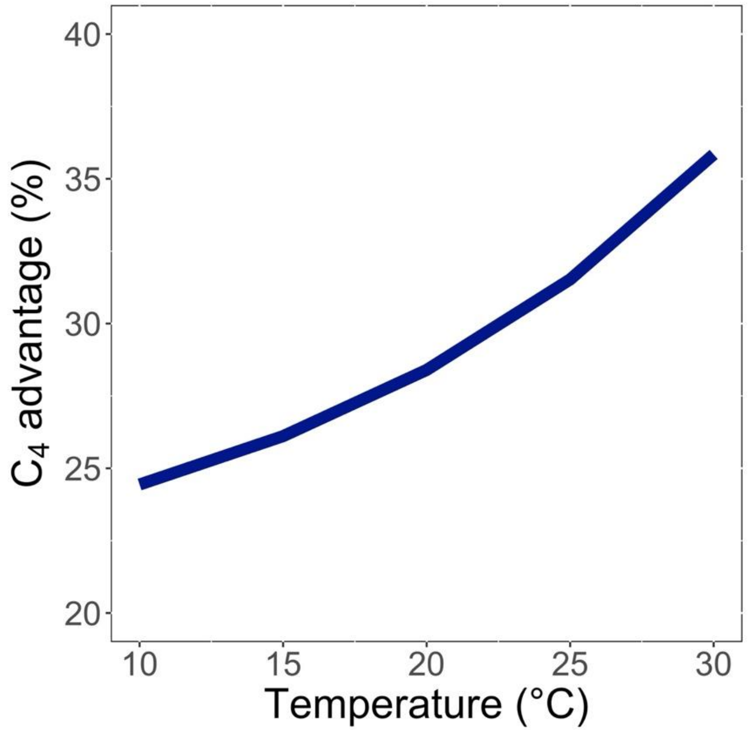
“Nutrient limitation” simulations

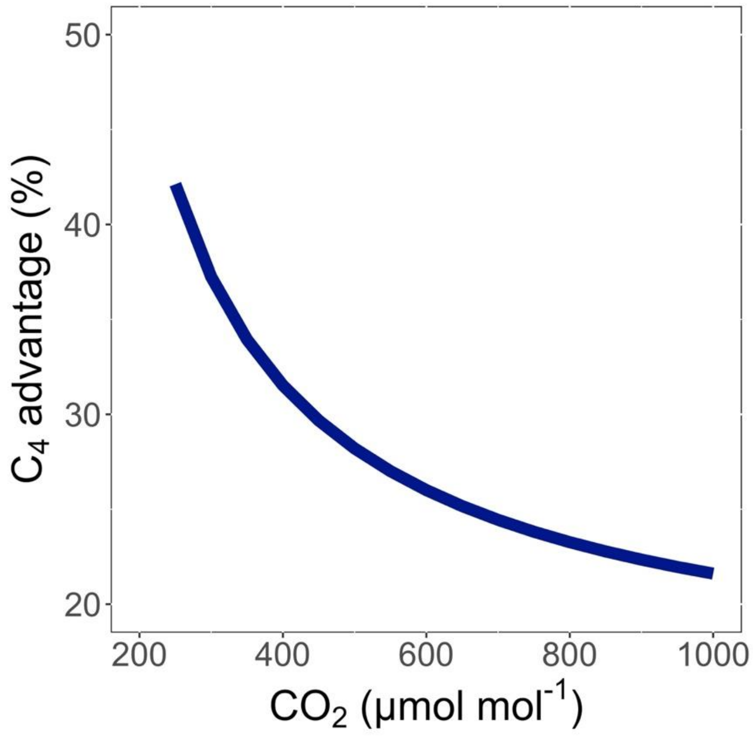
Weider et al. (2015) *Nature Geosci*

Extensions of this approach

Extensions of this approach

- C_4 photosynthesis

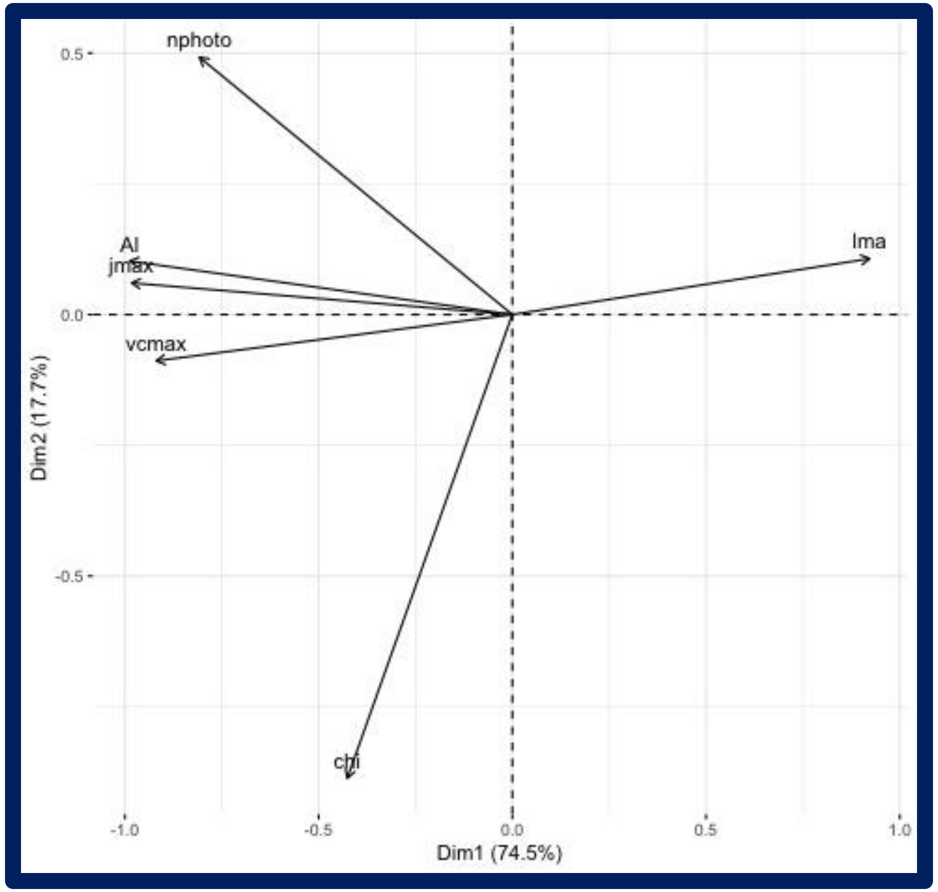




Scott and Smith (2022) *JAMES*

Extensions of this approach

- Other leaf traits



Smith et al. (in prep)

Theory development can help with prediction, but is also a powerful tool to understand mechanism

Acclimation theory has helped us understand…

- Photosynthetic responses to nutrient availability (Waring et al., 2023; Stocker et al., 2025; Perkowski et al., 2025; Cheaib et al., 2025a)
- Plant interactions with microbial symbionts (Perkowski et al., 2025; Cheaib et al., 2025b)
- Photosynthetic trait influences on populations (Cheaib et al., in prep) and communities (Kelley et al., in prep)

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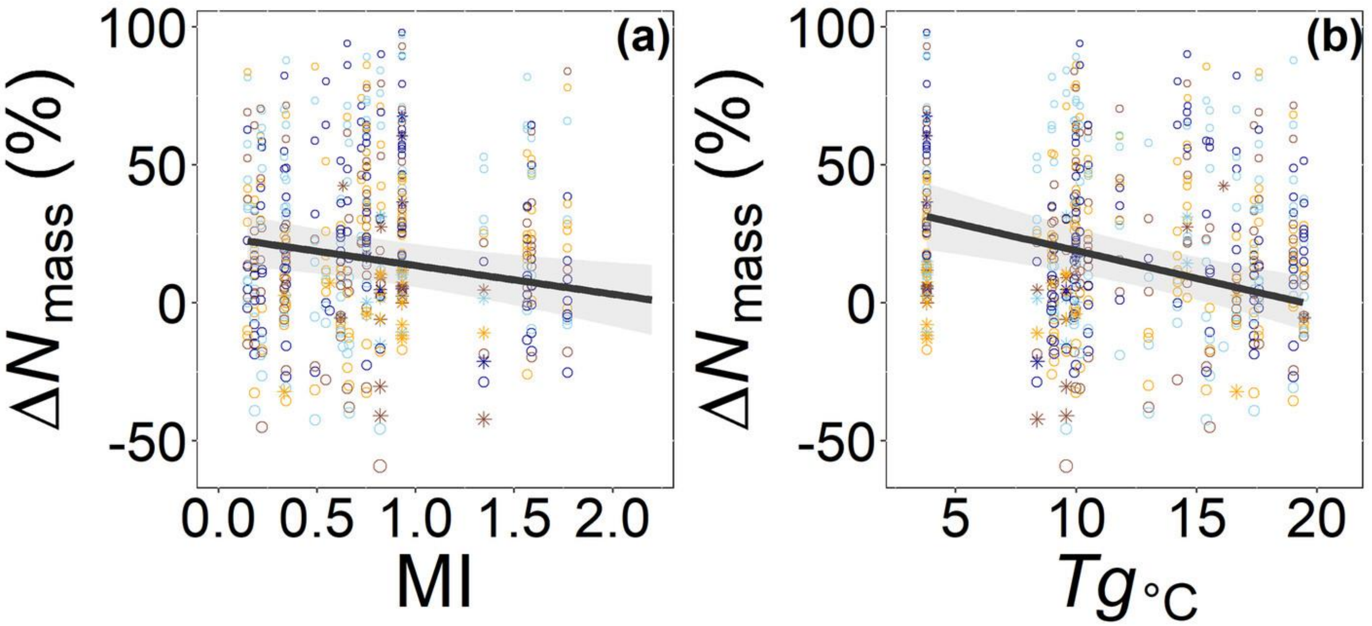
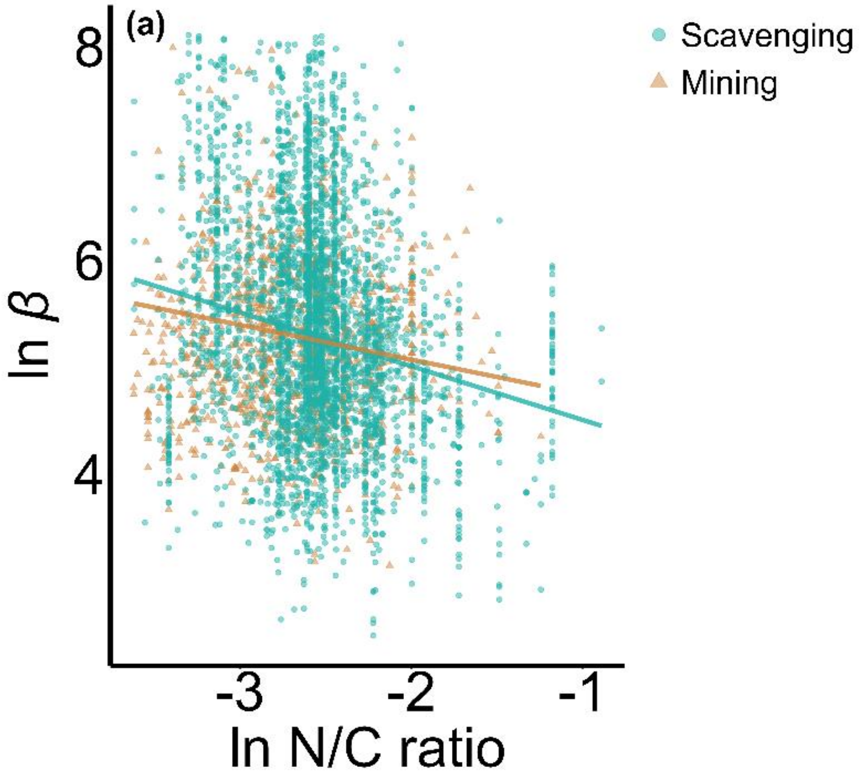


Leaves more responsive to soil N when demand is high (low MI, low T)

Cheaib et al. (2025) *Ecol Letters*

Acclimation theory has helped us understand…

- Plant interactions with microbial symbionts (Perkowski et al., 2025; Cheaib et al., 2025)

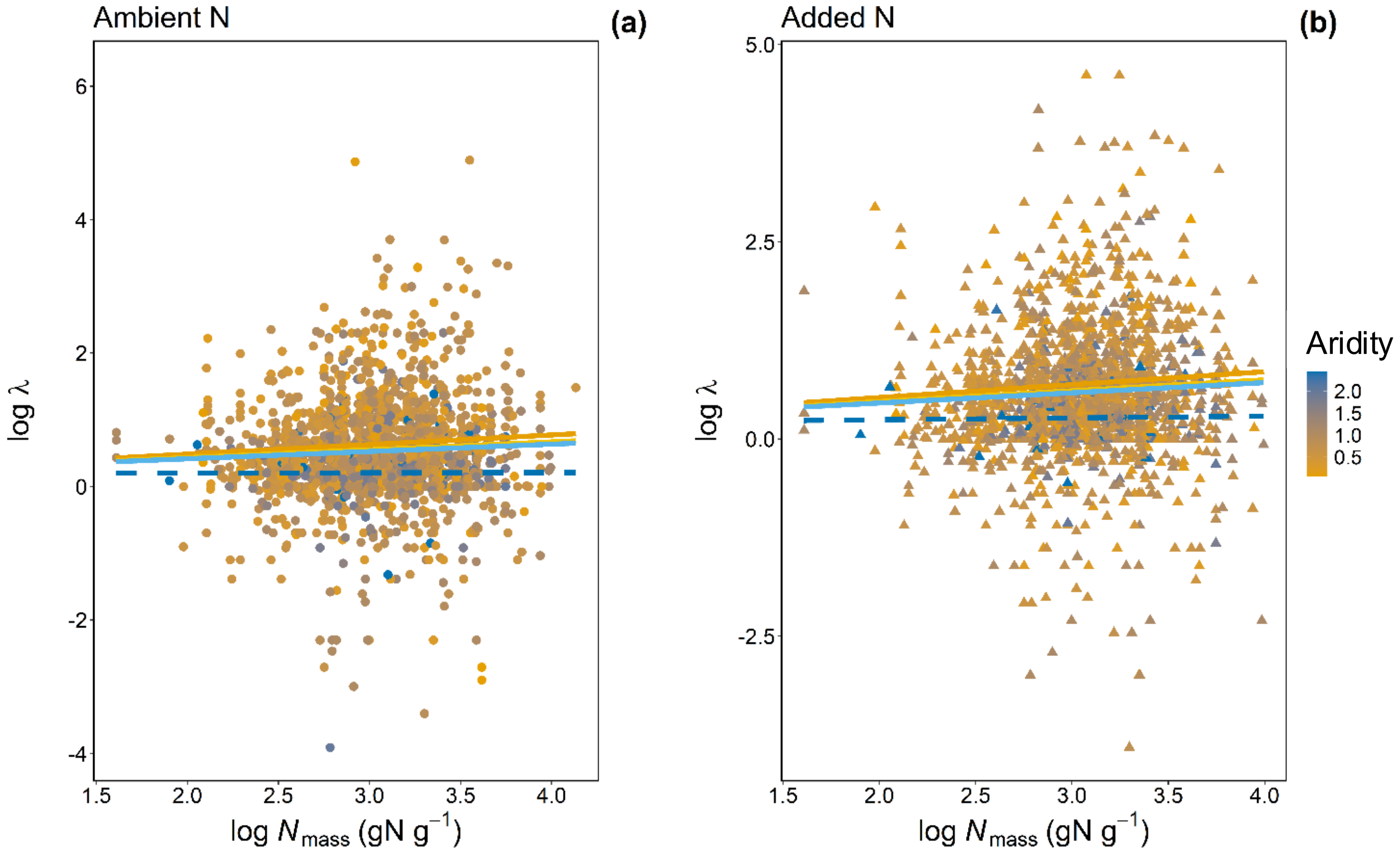


Scavenging strategy (e.g., AMF) is less costly when soil N is high and mining strategy (e.g., EcMF) is less costly when soil N is low

Cheaib et al. (2025) *New Phyt*

Acclimation theory has helped us understand…

- Photosynthetic trait influences on populations (Cheaib et al., in prep) and communities (Kelley et al., in prep)



As predicted from theory, increased leaf N confers greater species population growth in dry sites and this is enhanced by eutrophication.

Cheaib et al. (in prep)

Acknowledgements

- Current and former lab members
  - Alissar Cheaib (postdoc)
  - Evan Perkowski (postdoc)
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  - Daniel Owusu Kwakye (PhD)
  - Garrison Garza (PhD)
  - Clara Drake (MS)
  - Gwen Wattt (MS)
  - Brad Posch (postdoc)
  - Jeff Chieppa (postdoc)
  - Lizz Waring (postdoc)
  - Kieran Carroll (lab manager)
  - Christine Vanginault (MS)
  - Zinny Ezekannagha (MS)
  - Eve Gray (MS)
  - Risa McNellis (MS)
  - Helen Scott (MS)
  - Too many (40+) undergrads to list!

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  - USDA
  - NPS
  - USGS
  - Schmidt Futures
  - Texas EcoLab

Presentation available at:
www.github.com/SmithEcophysLab/seminar/2025_grc

Model code:
www.github.com/SmithEcophysLab/optimal_vcmax_R

Contact: nick.smith@ttu.edu