Plants aren't dumb

Using optimality theory to understand big questions in plant ecophysiology

Nick Smith

Department of Biological Sciences

Texas Tech University

nick.smith@ttu.edu

Acknowledgements

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  - Evan Perkowski (postdoc)
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  - Garrison Garza (PhD)
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- Collaborators around the world
- Funding
  - NSF
  - USDA
  - NPS
  - USGS
  - Schmidt Futures
  - Texas EcoLab

Why do people care about plants?

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Why do people care about plants?

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Why do people care about plants?

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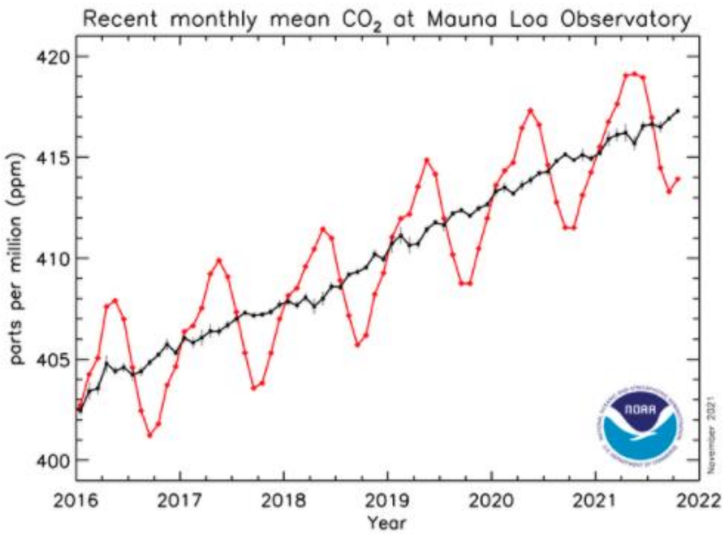
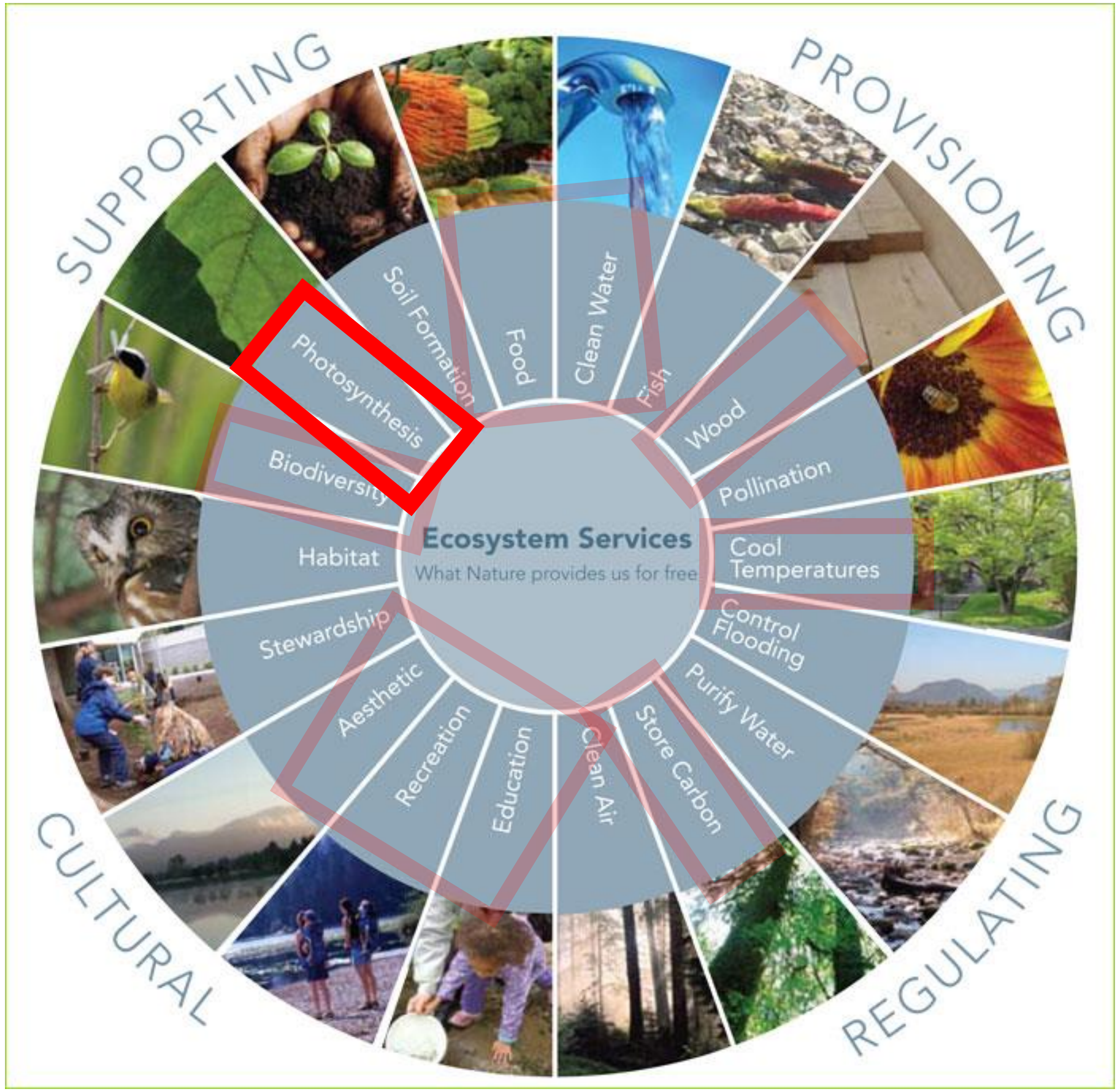


In other words: plants provide ecosystem services

FNAL

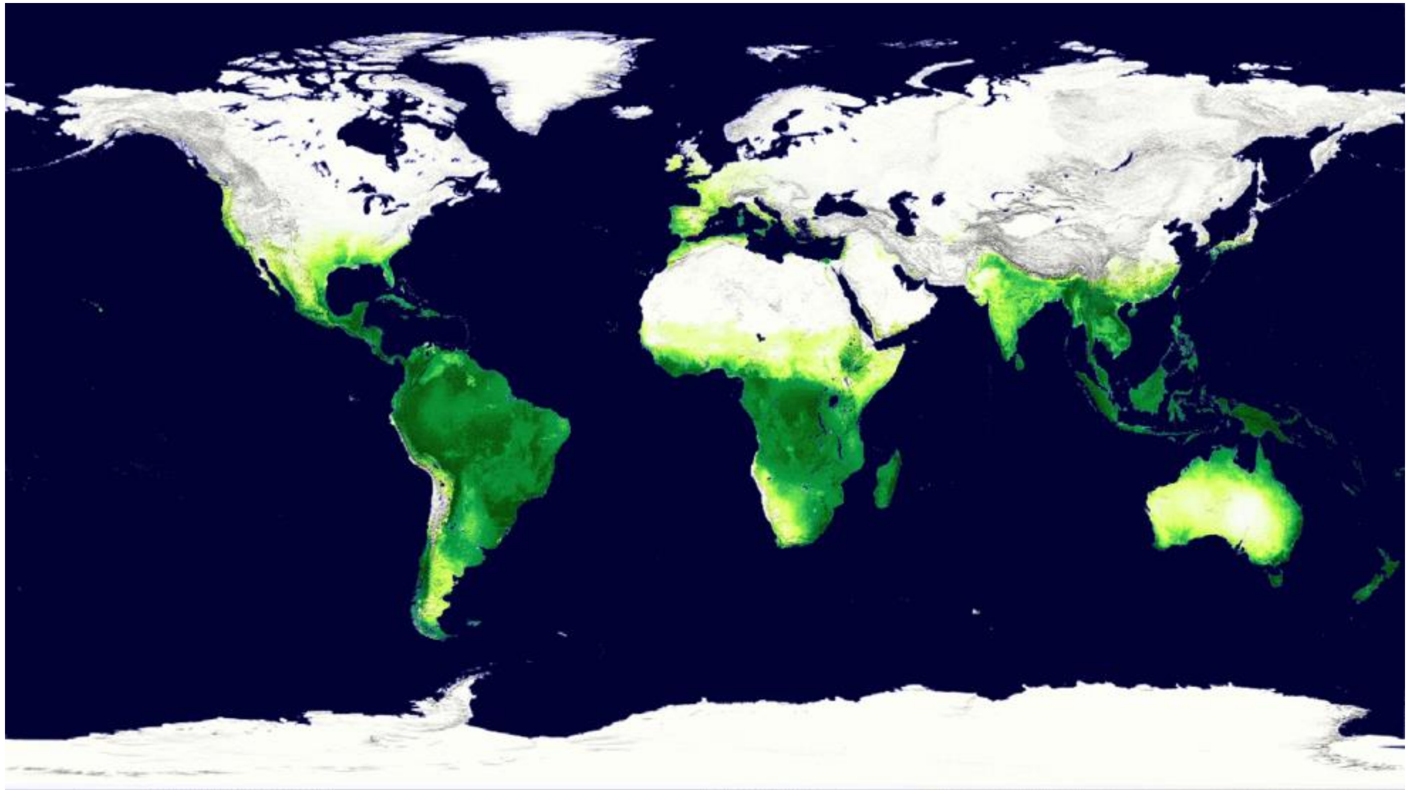
Including photosynthesis



Photosynthesis provides the foundation for other services

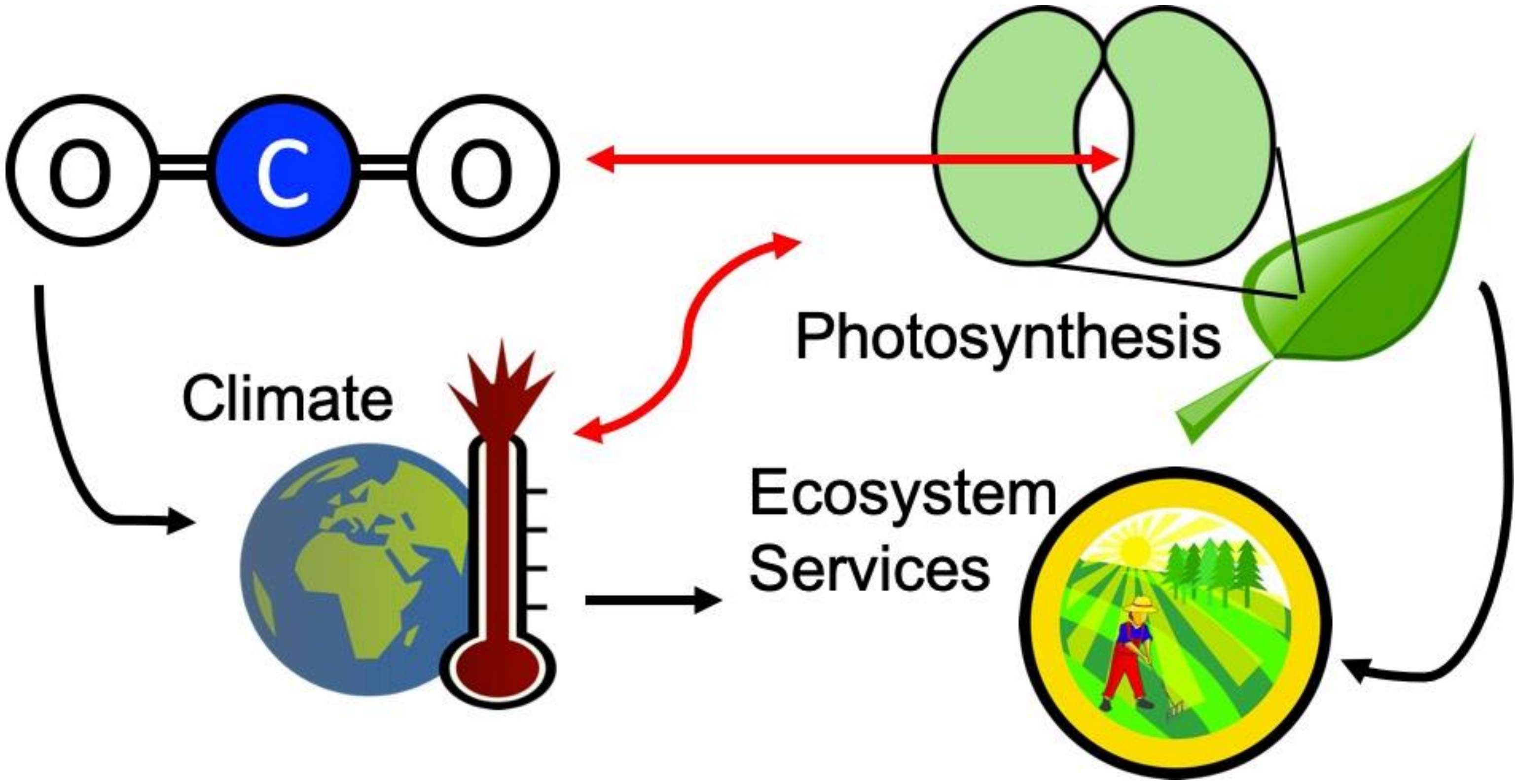
FNAL

Photosynthesis is a dynamic process that is likely to be impacted by global change



MODIS, NASA

Our lab examines photosynthesis as a regulator of global change impacts on ecosystem services



Smith (2024) *Am J Botany*

Photosynthesis is important! An example…

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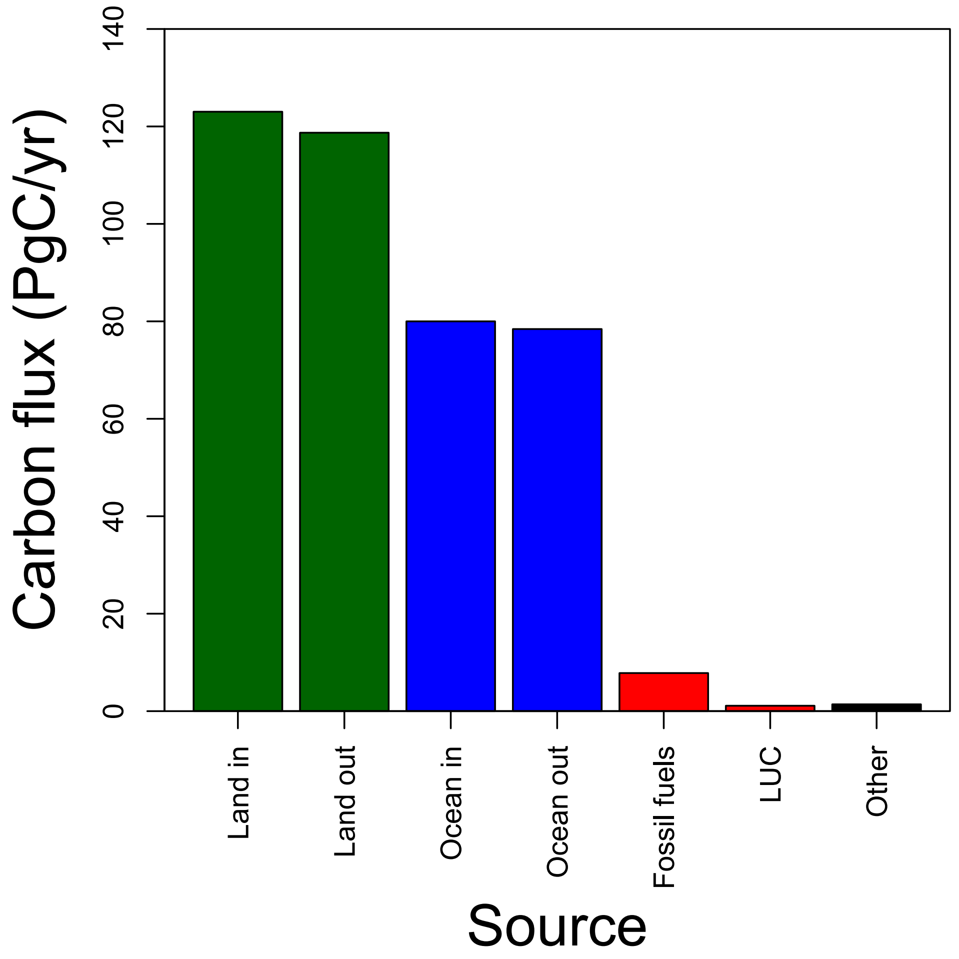
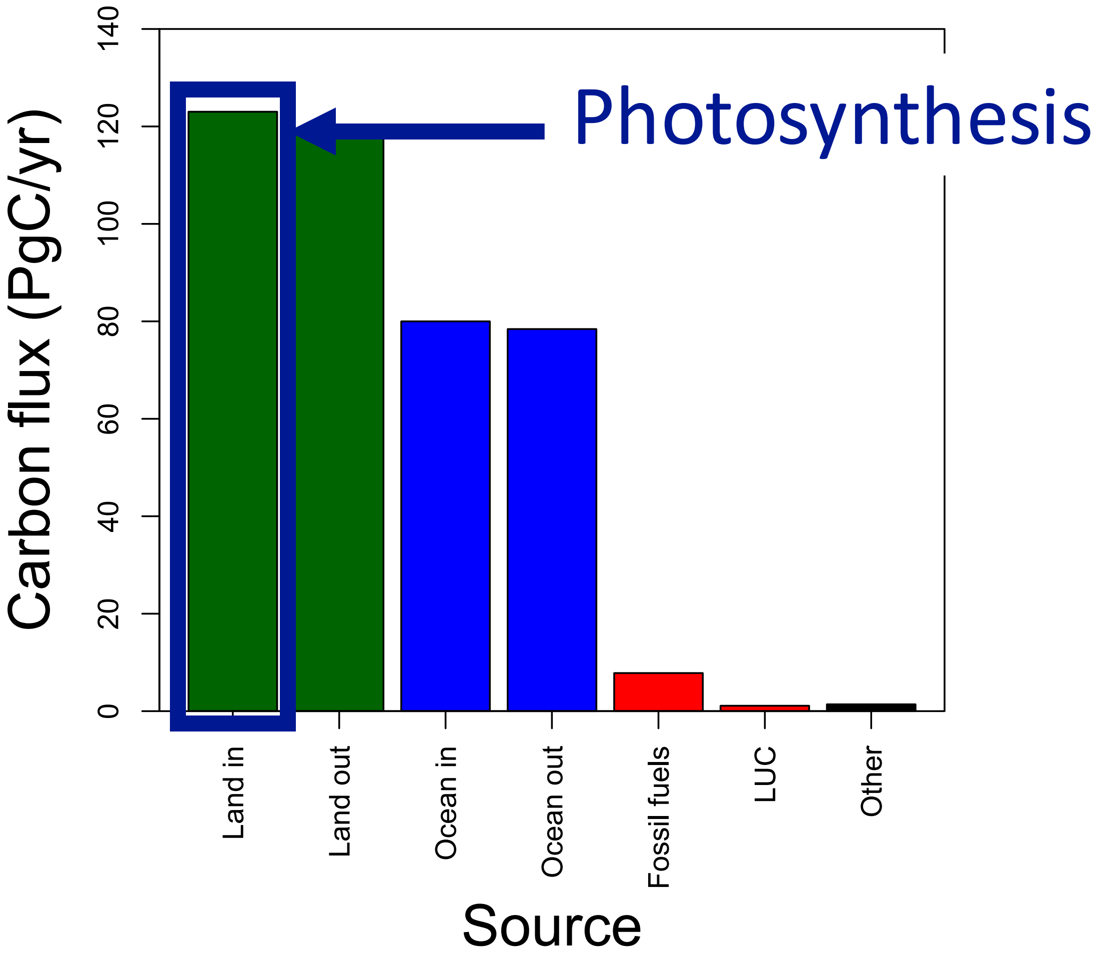


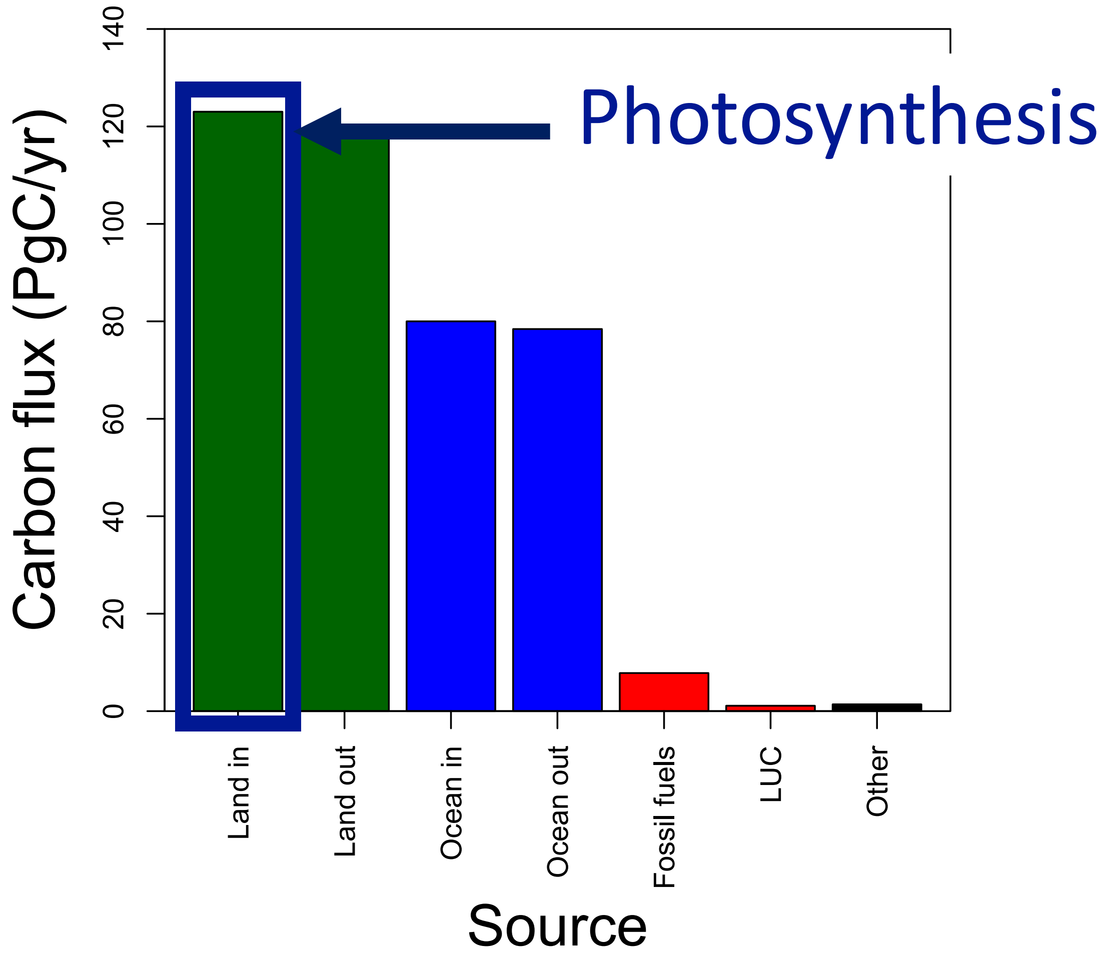
Data from IPCC (2013)

Photosynthesis is important! An example…



Data from IPCC (2013)

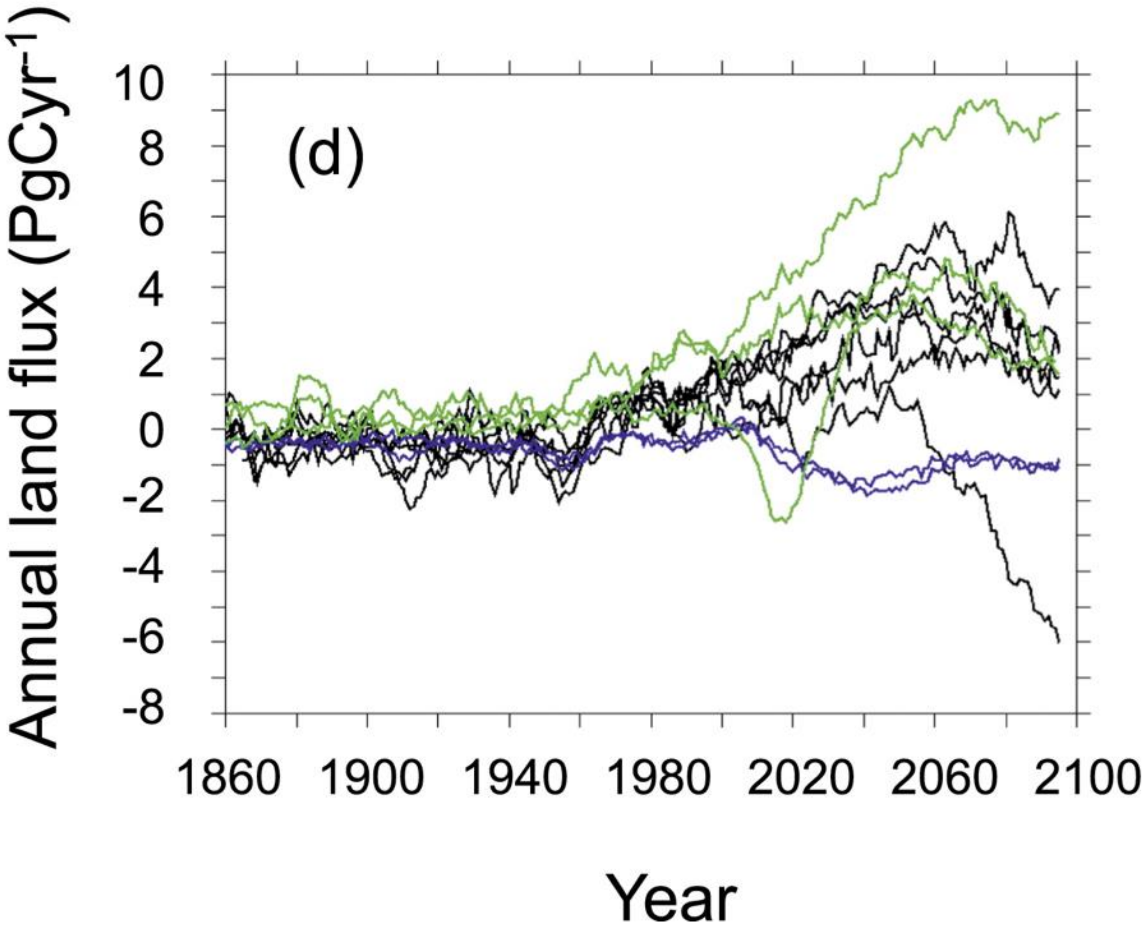
Photosynthesis is important! An example…



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

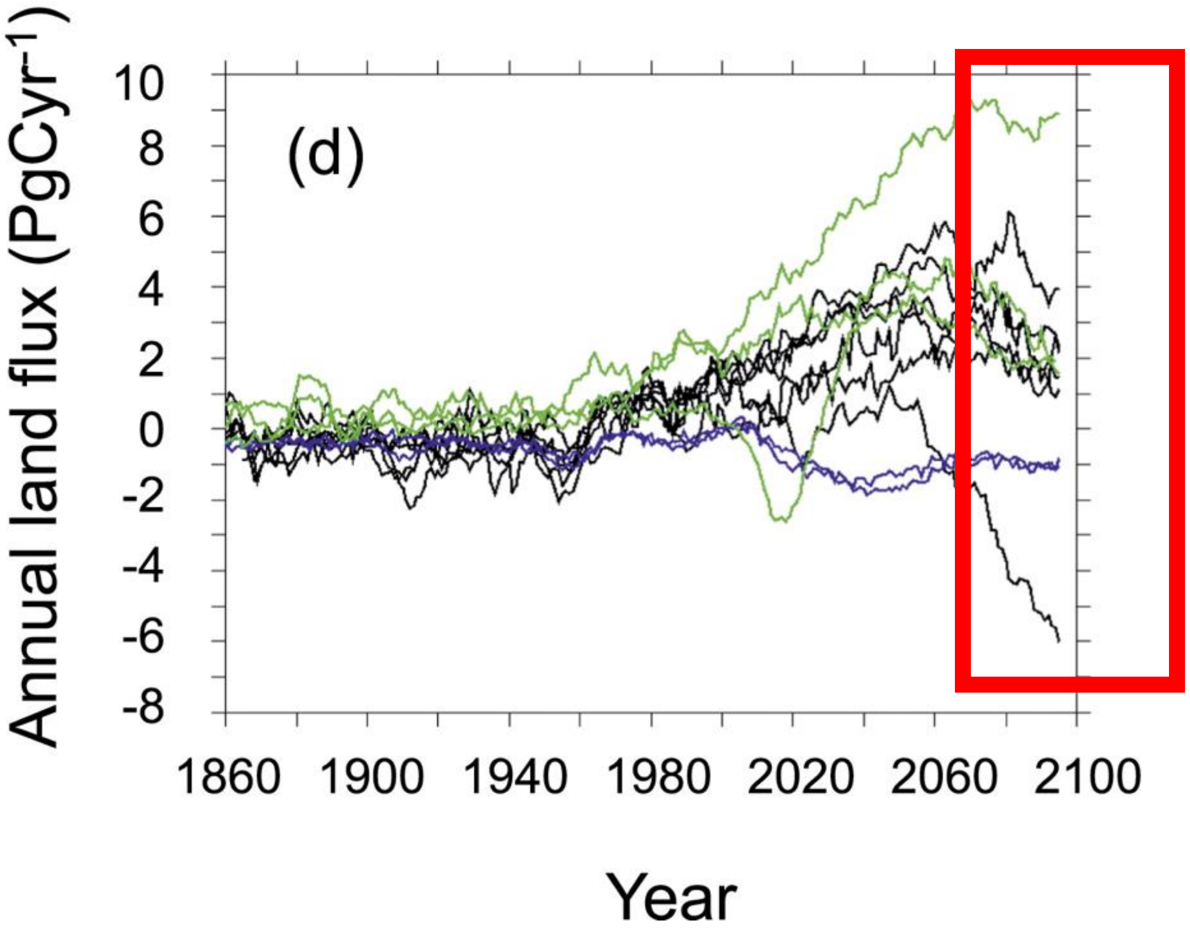
Data from IPCC (2013)

But predictions are uncertain!



Friedlingstein et al. (2014) *J Climate*

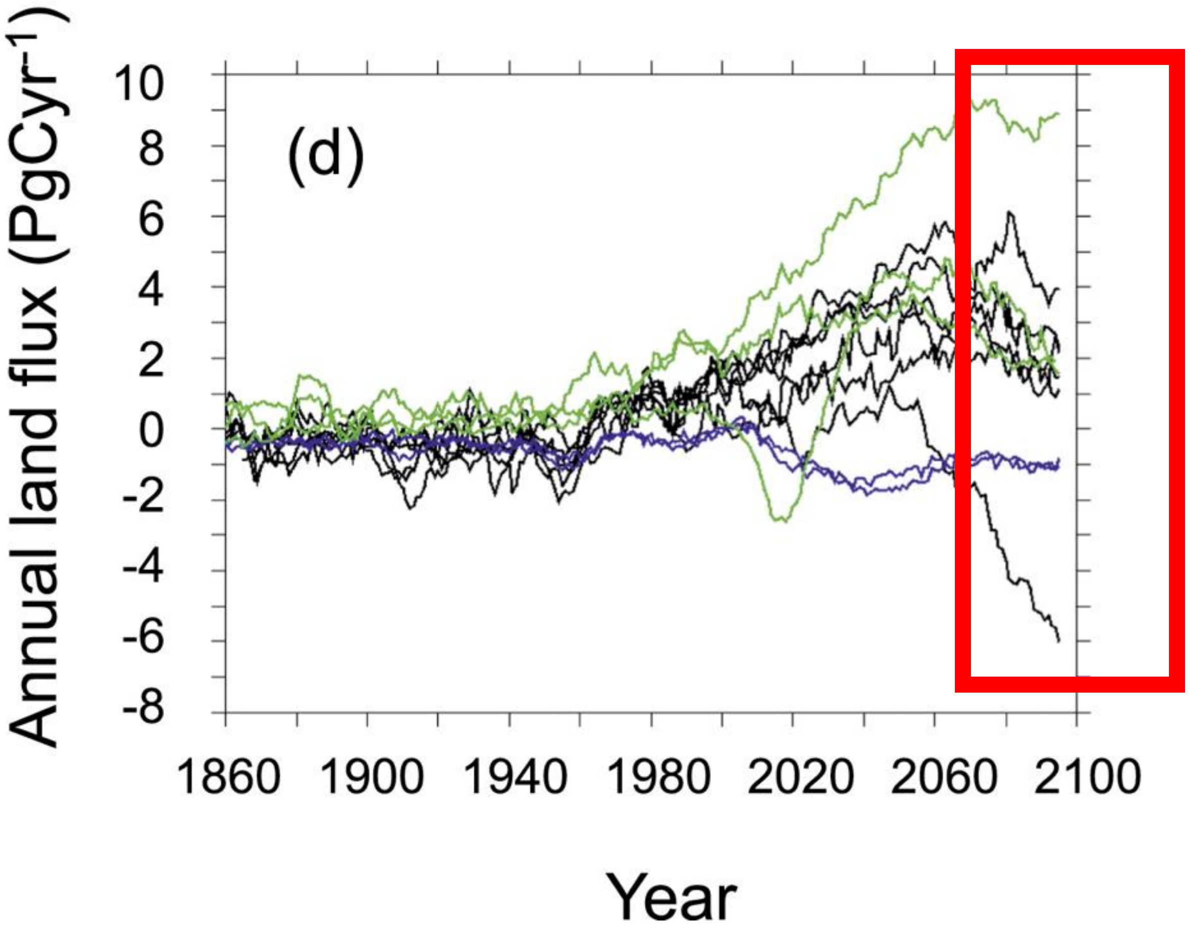
But predictions are uncertain!

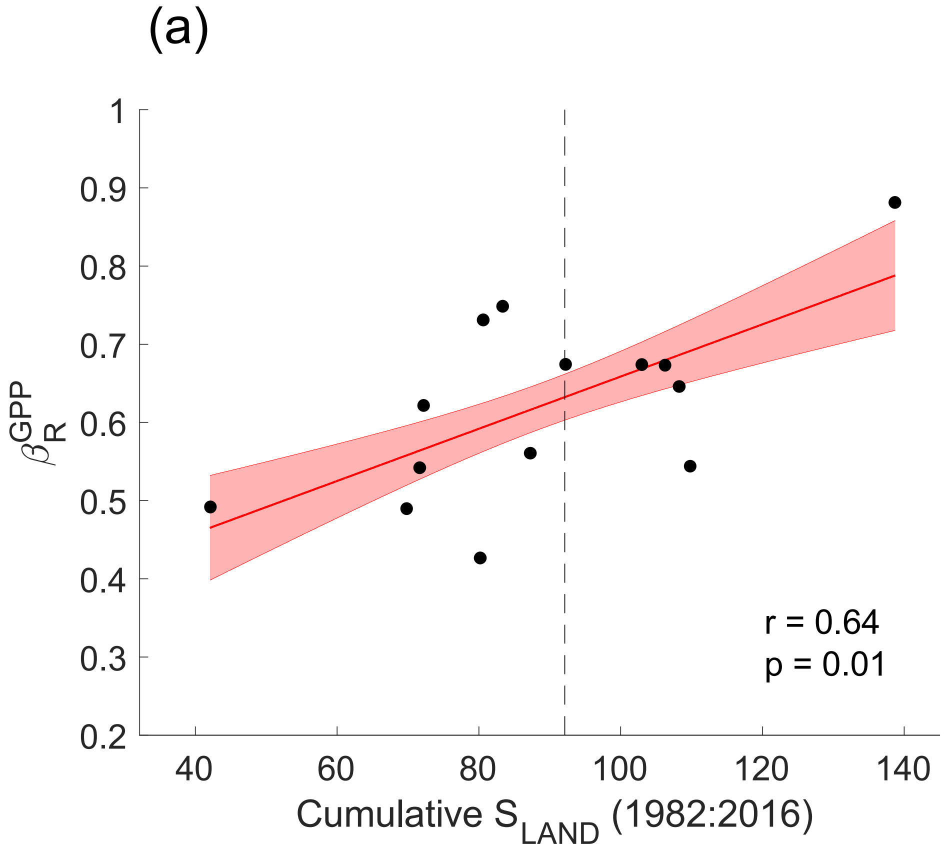


Future model uncertainty (14 Pg) > current fossil fuel emissions (9.5 Pg)

Friedlingstein et al. (2014) *J Climate*

This uncertainty is driven by uncertainty in photosynthesis





Friedlingstein et al. (2014) *J Climate*

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

Why the uncertainty? Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

Planta

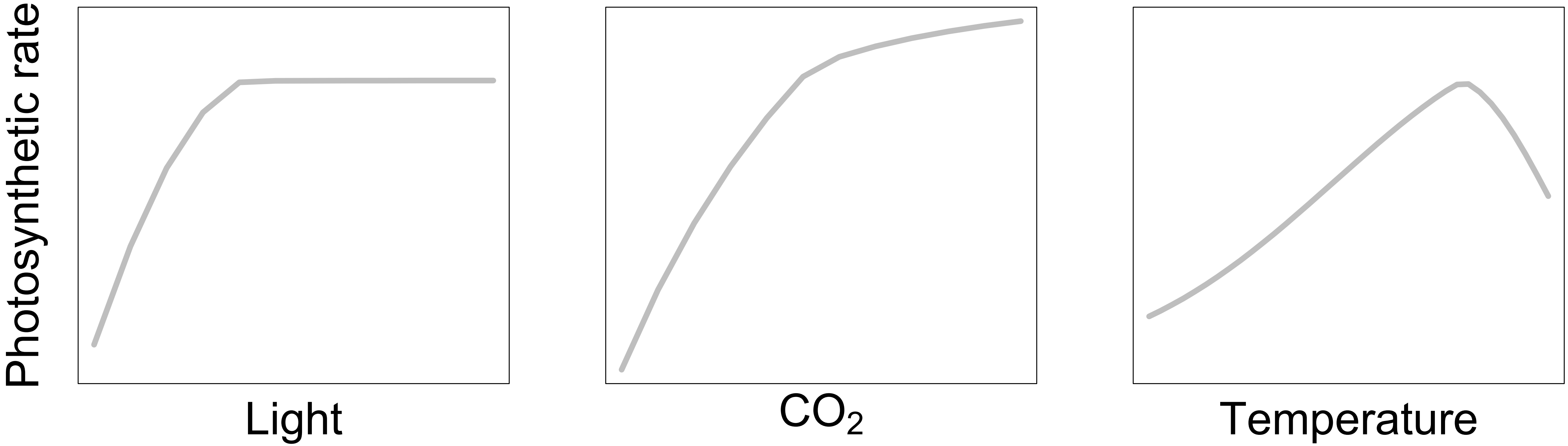
A Biochemical Model of Photosynthetic CO_2 Assimilation in Leaves of C_3 Species

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

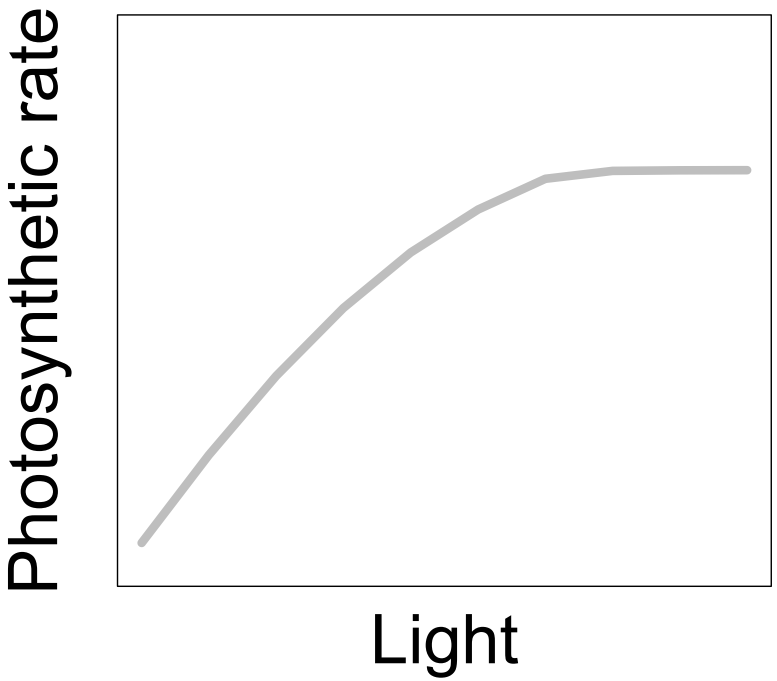


Why the uncertainty? Long-term responses differ from short-term responses due to acclimation

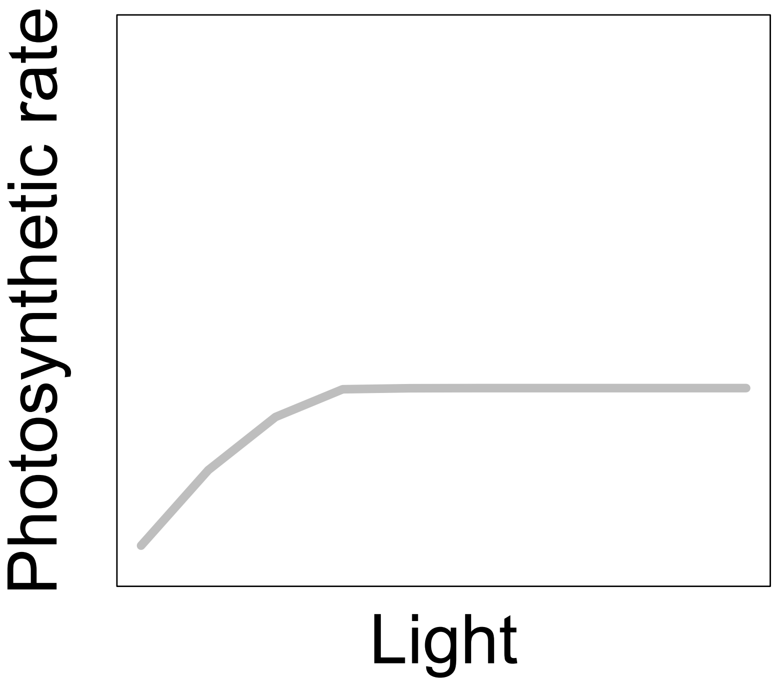
Dumb plants

Acclimation: an example

Acclimated to high light

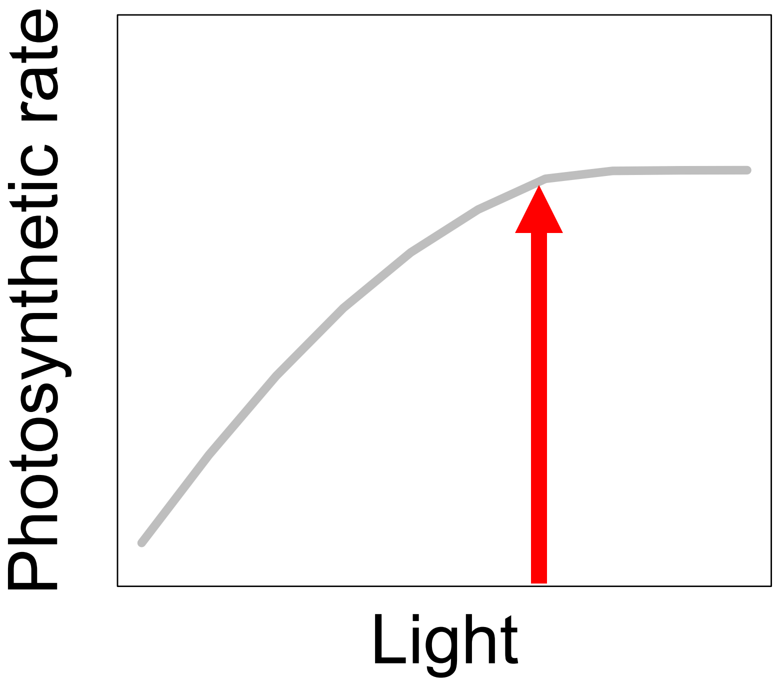


Acclimated to low light

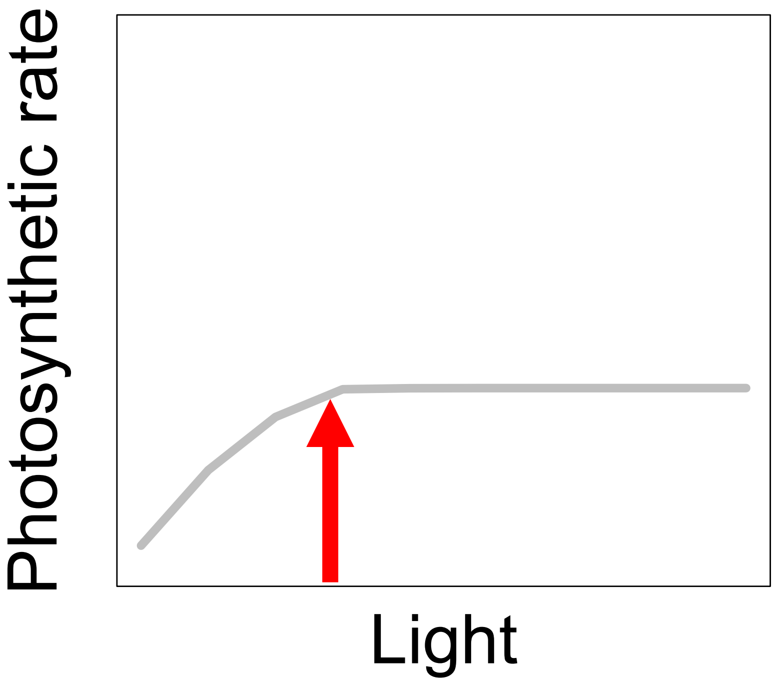


Acclimation: an example

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)

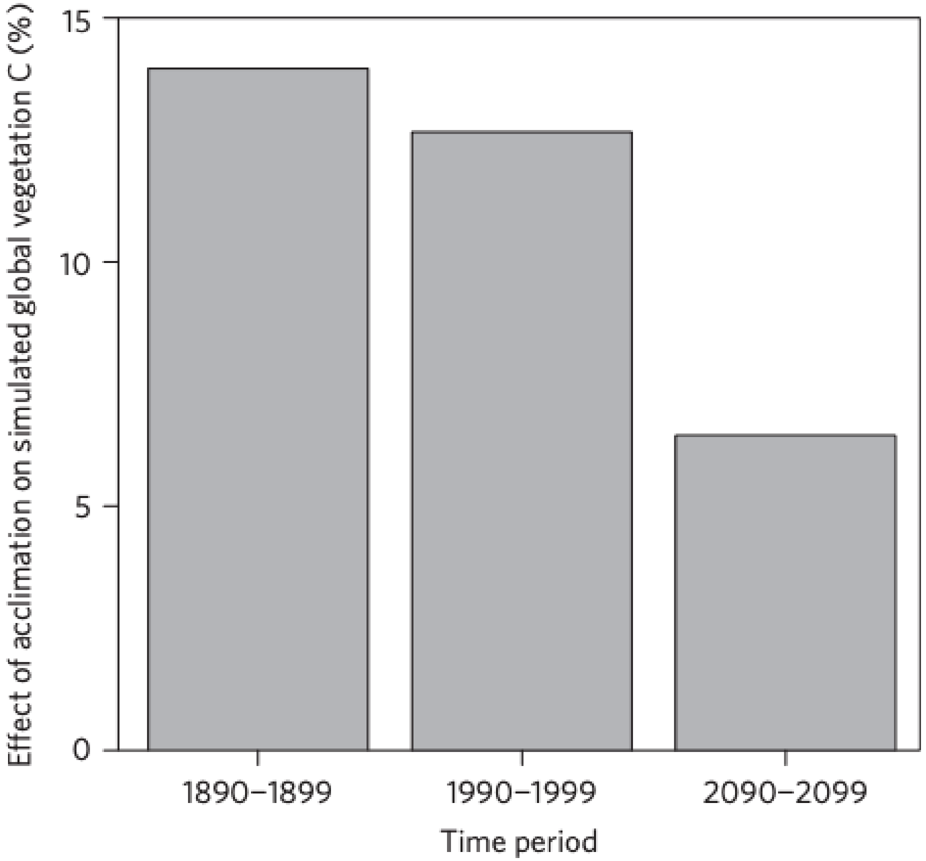
Ann. Rev. Plant Physiol. 1980. 31:491–543

PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

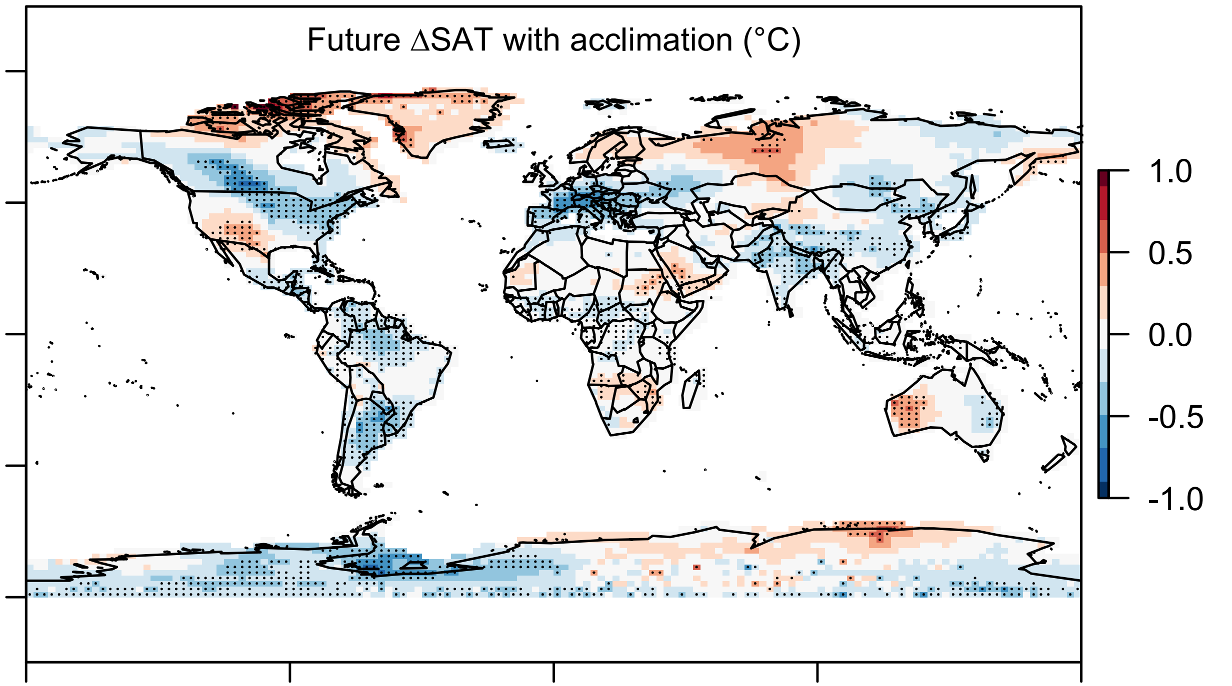
Joseph Berry and Olle Björkman[1]

…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*

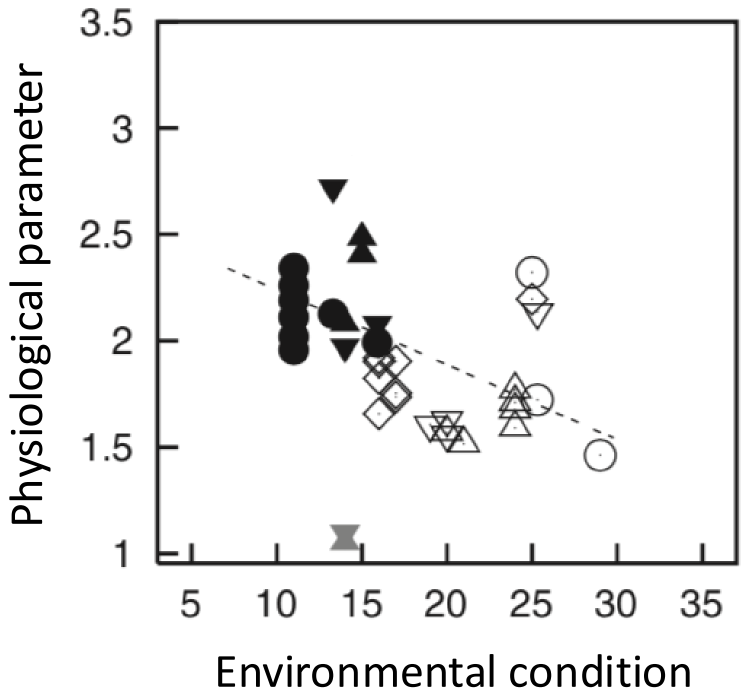
Smith et al. (2017) *JAMES*

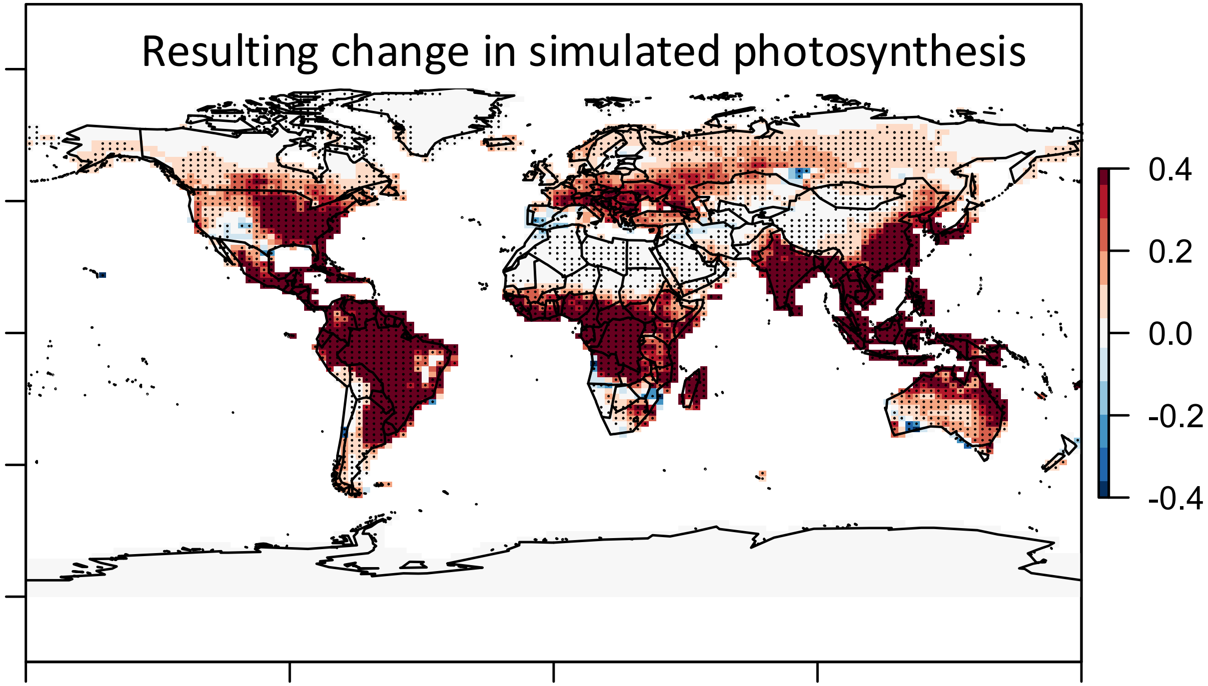
Unfortunately,
no theoretical model for photosynthetic acclimation exists

Lack of theory results in…

Lack of theory results in…

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



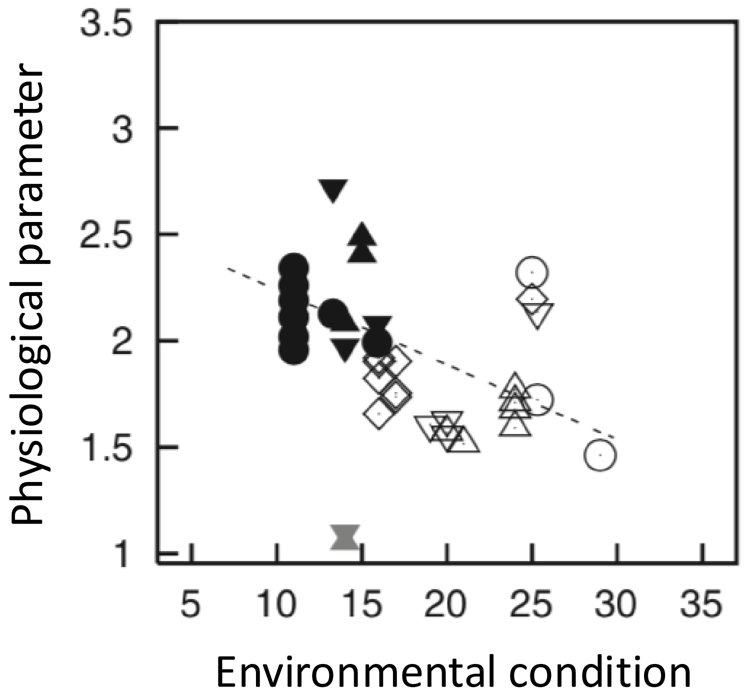


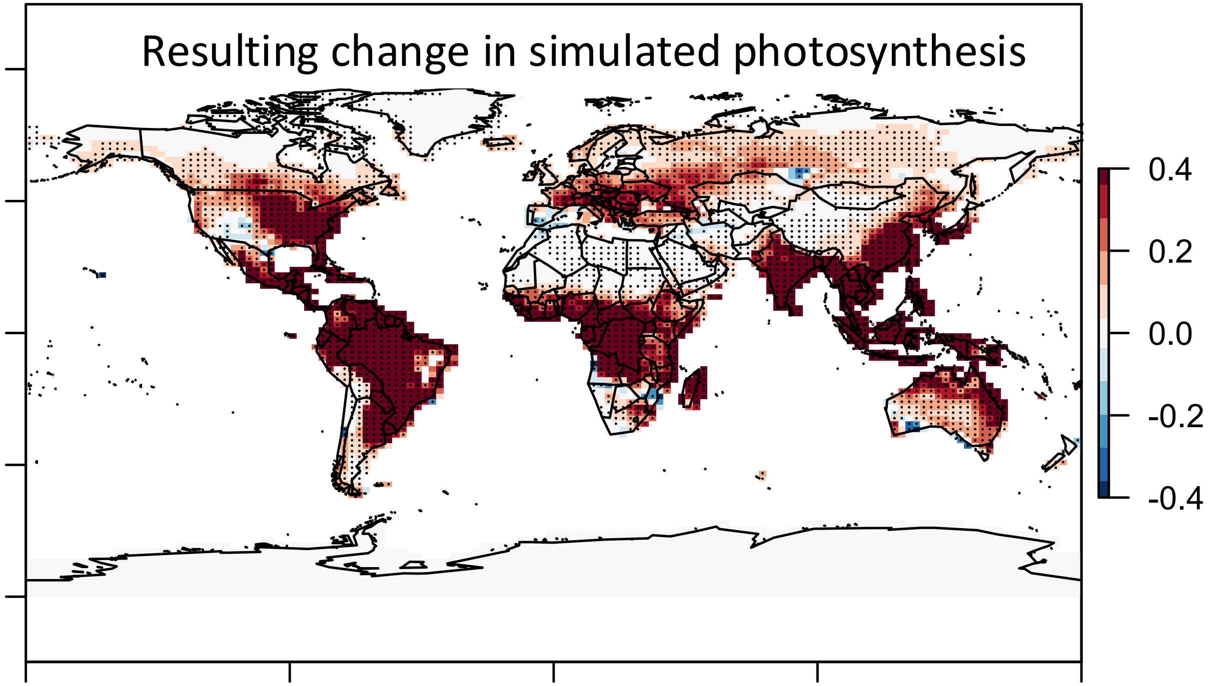
Kattge and Knorr (2007) *PC&E*

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*

La

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![Global Change Biology]

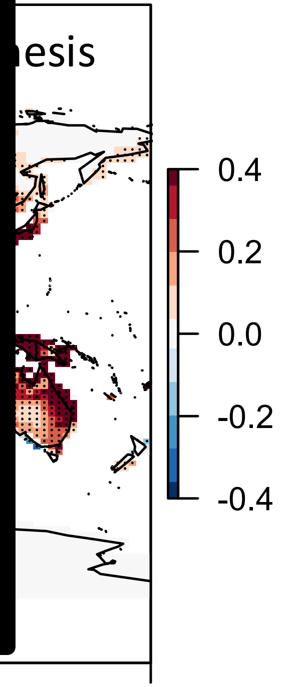
REPORT | Open Access

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

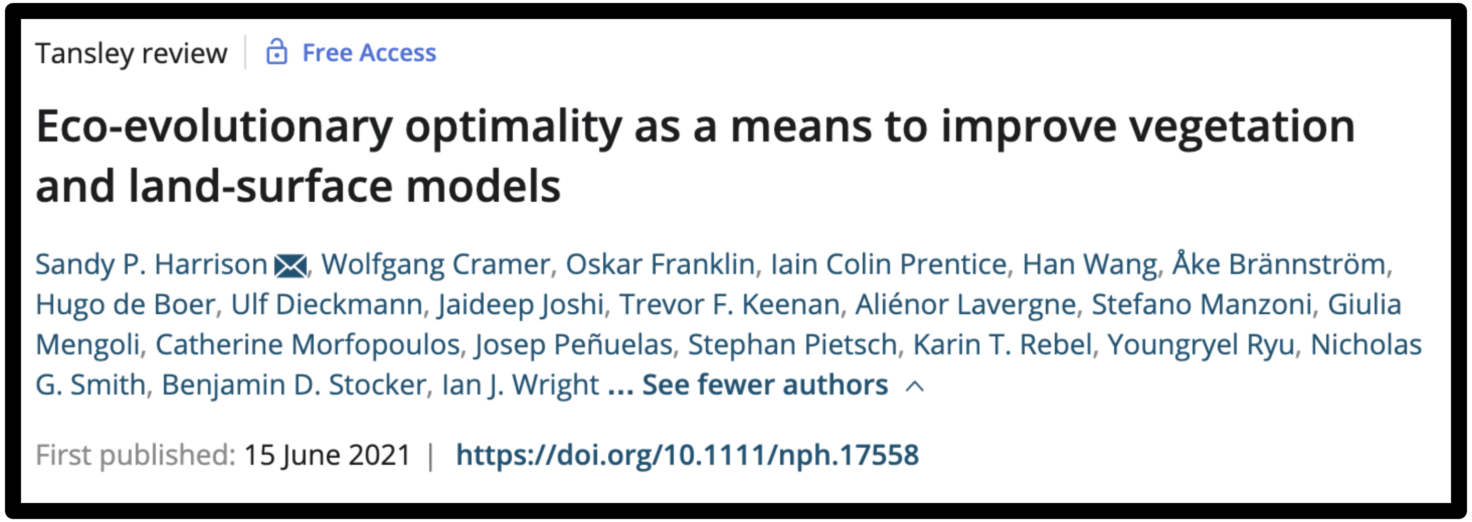


Environmental condition

Kyker-Snowman,... Smith 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,...Smith 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}

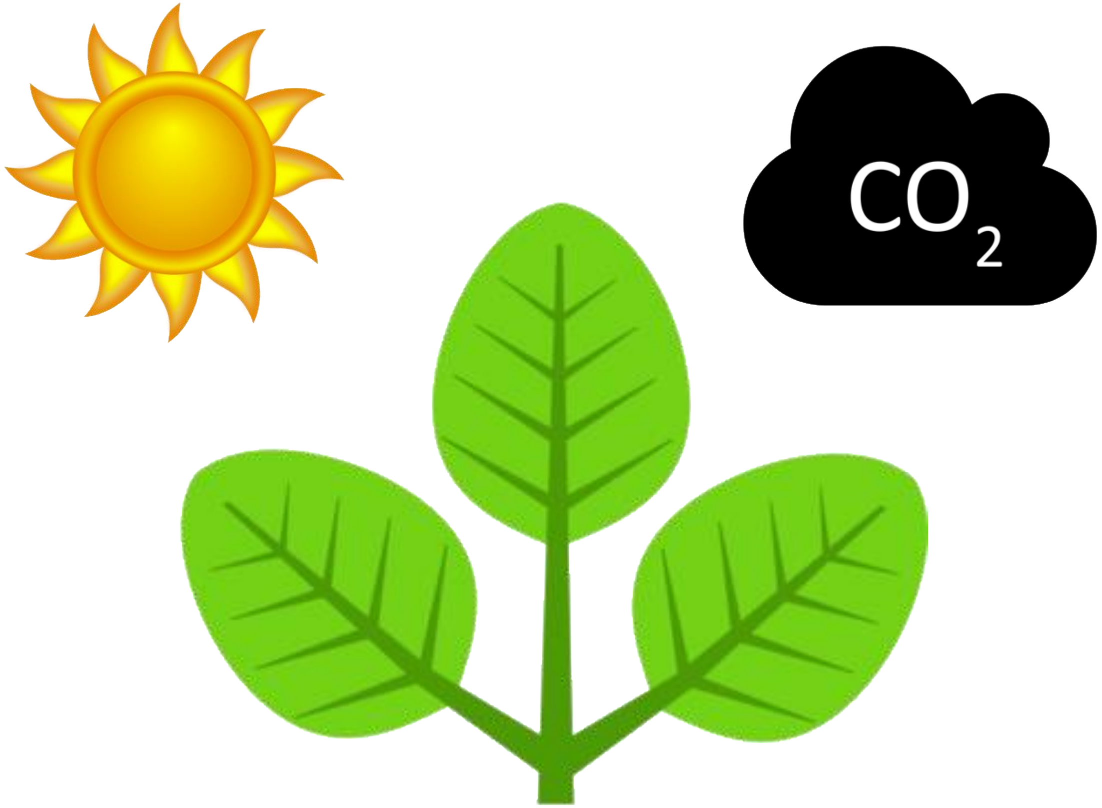
[TALK TO ME LATER ABOUT THIS IF YOU ARE INTERESTED]

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

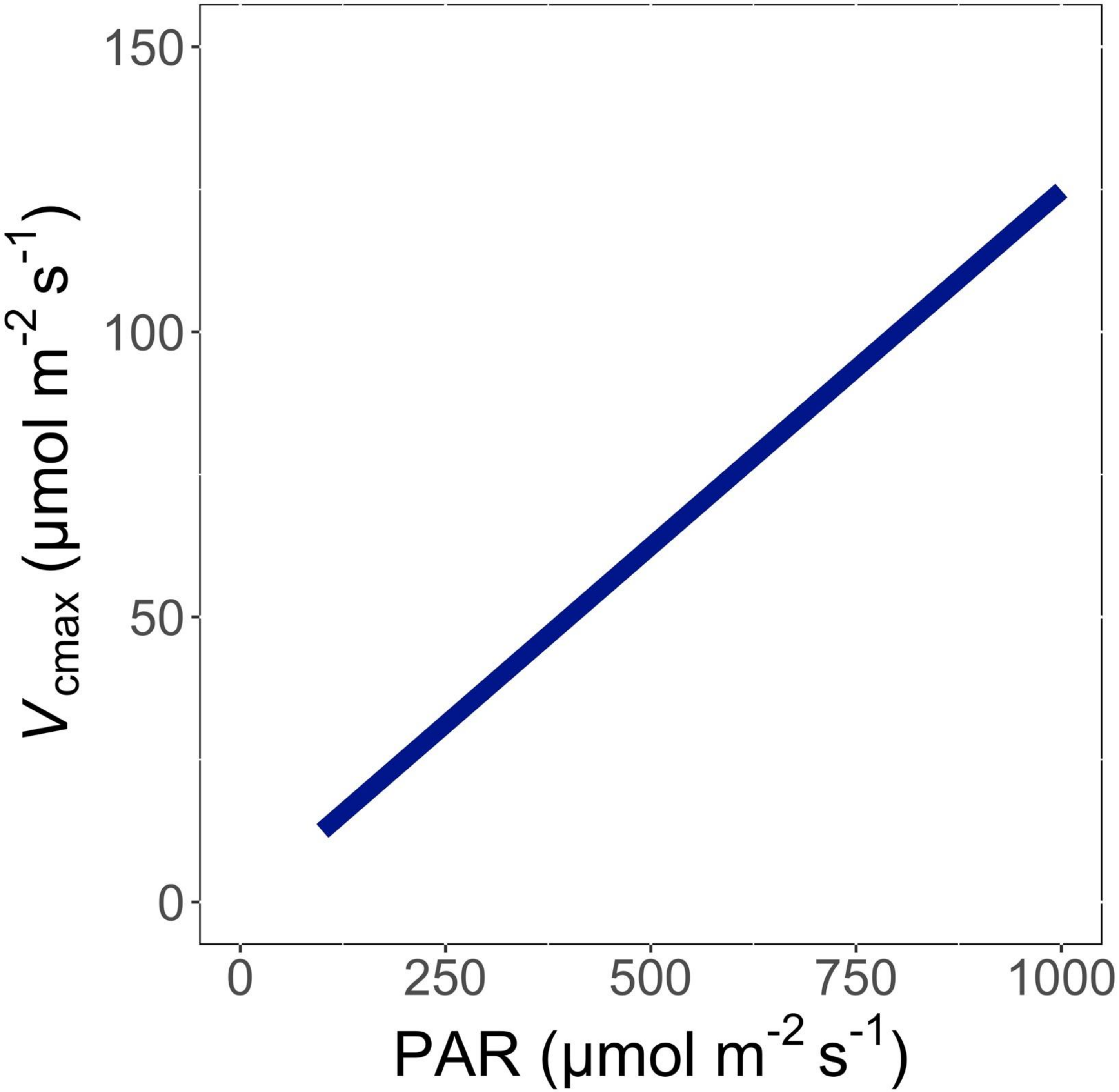


Plant biochemistry setup will aim for equal limitation by all factors

[TALK TO ME LATER ABOUT THE MATHS]

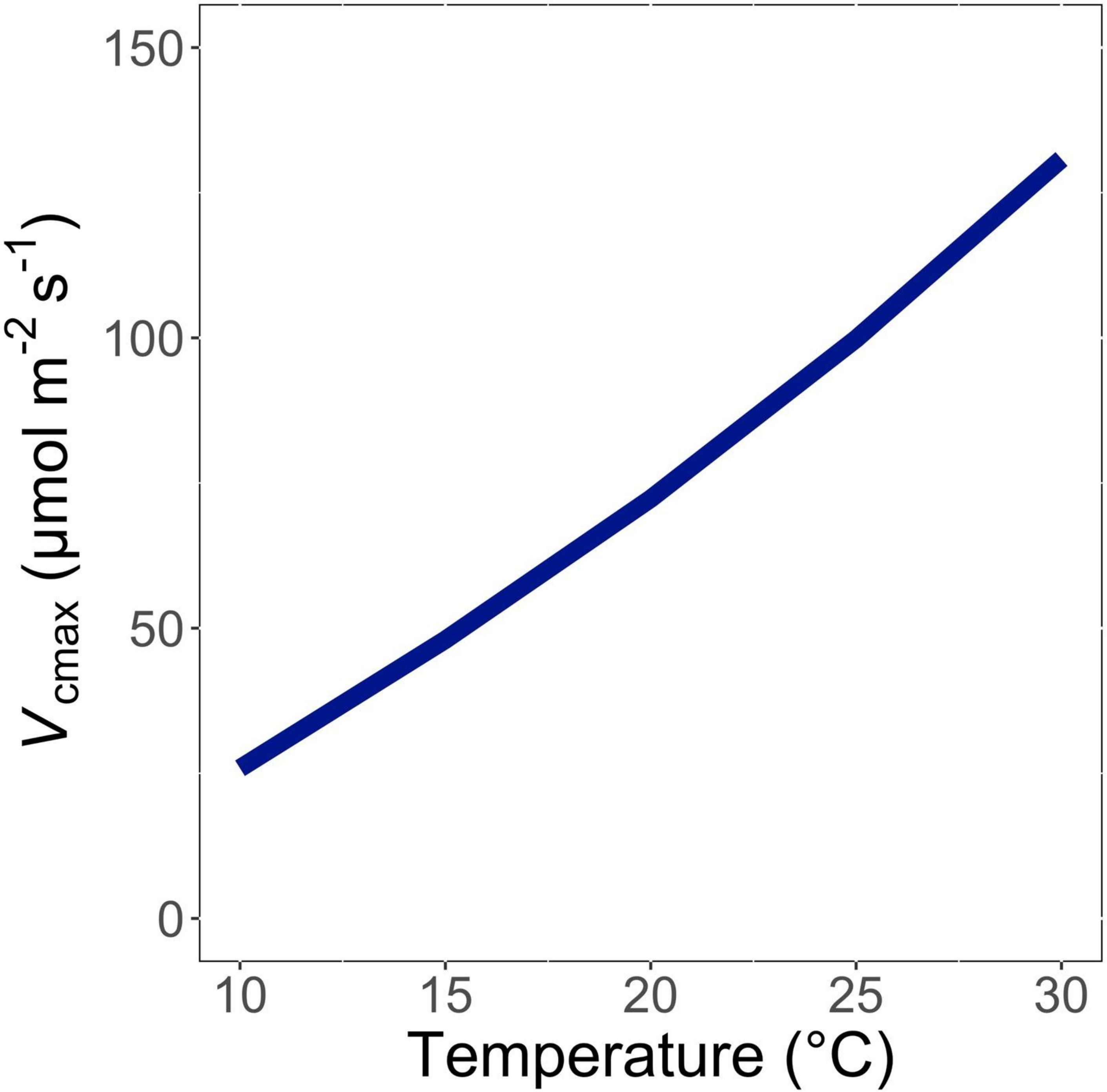
Biochemistry trait

The maximum rate of Rubisco carboxylation (V_{cmax})



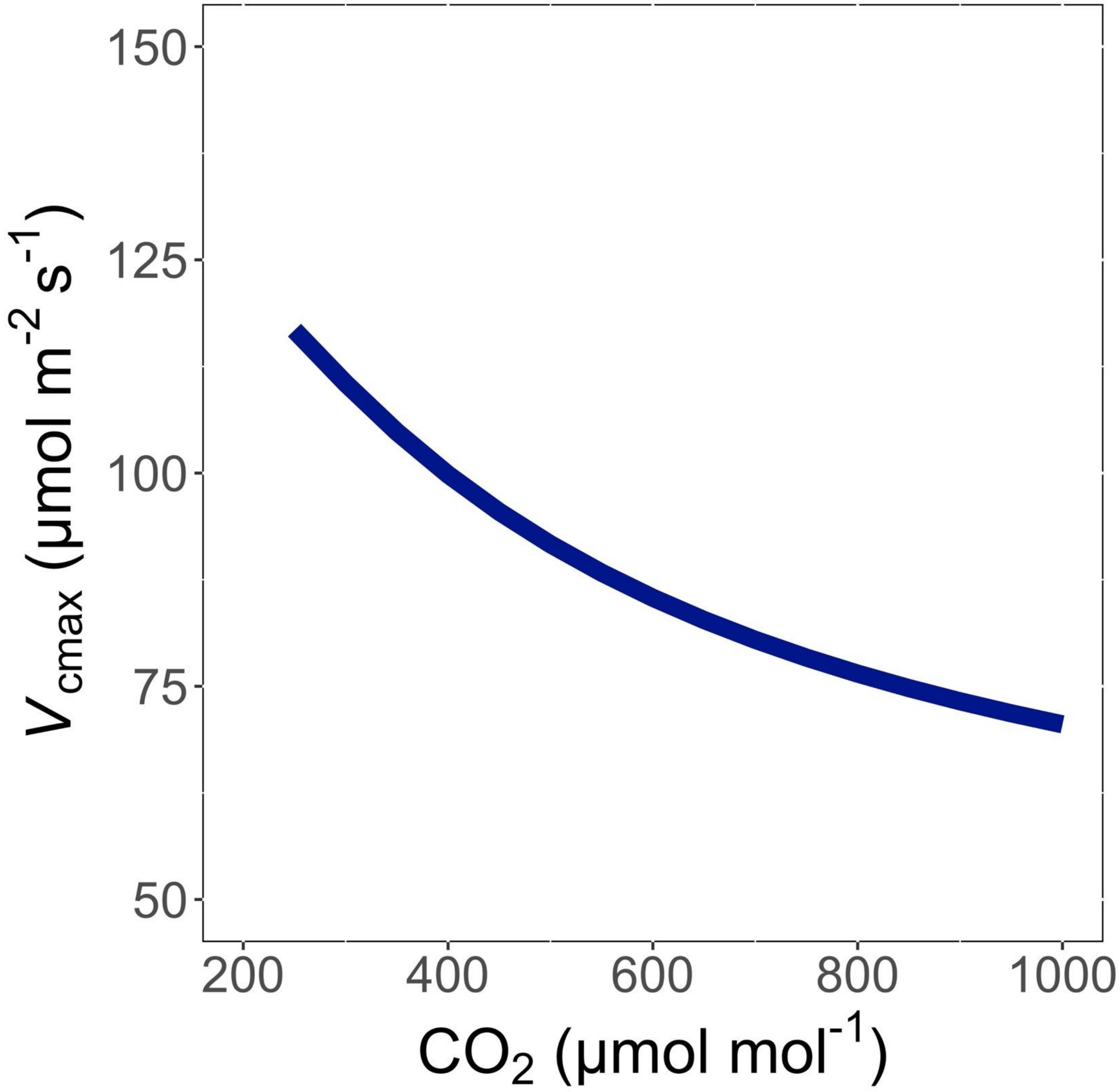
V_{cmax} increases with light because of greater electron transport

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



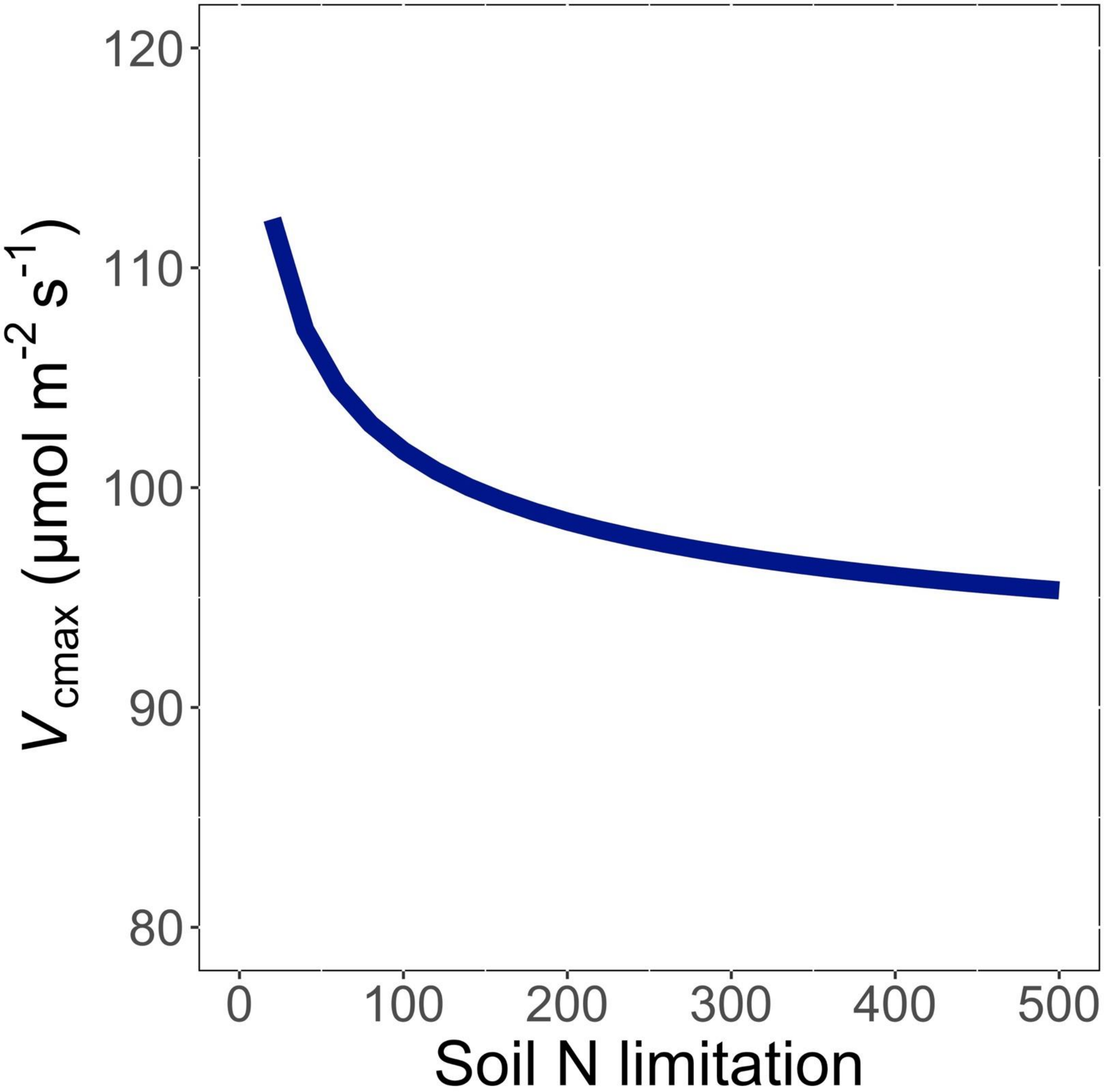
V_{cmax} increases with temperature because of greater electron transport and photorespiration

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

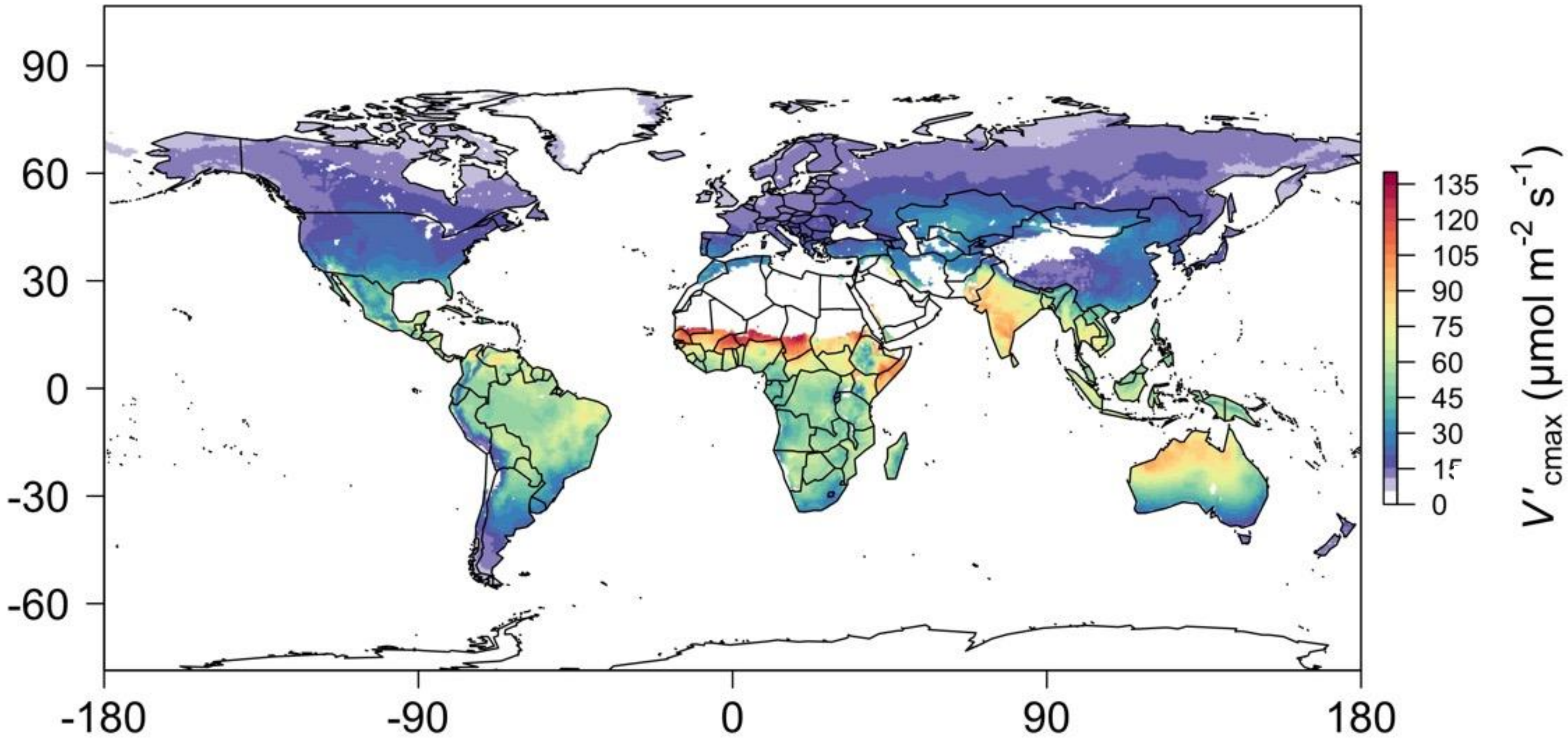
Smith et al. (2019) *Ecol Letters*; Smith and Keenan (2020) *Glob Change Biology*



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) *Ecology Letters*

Ok, great, but now what?

We can use the theory as a null model to explore acclimation mechanisms

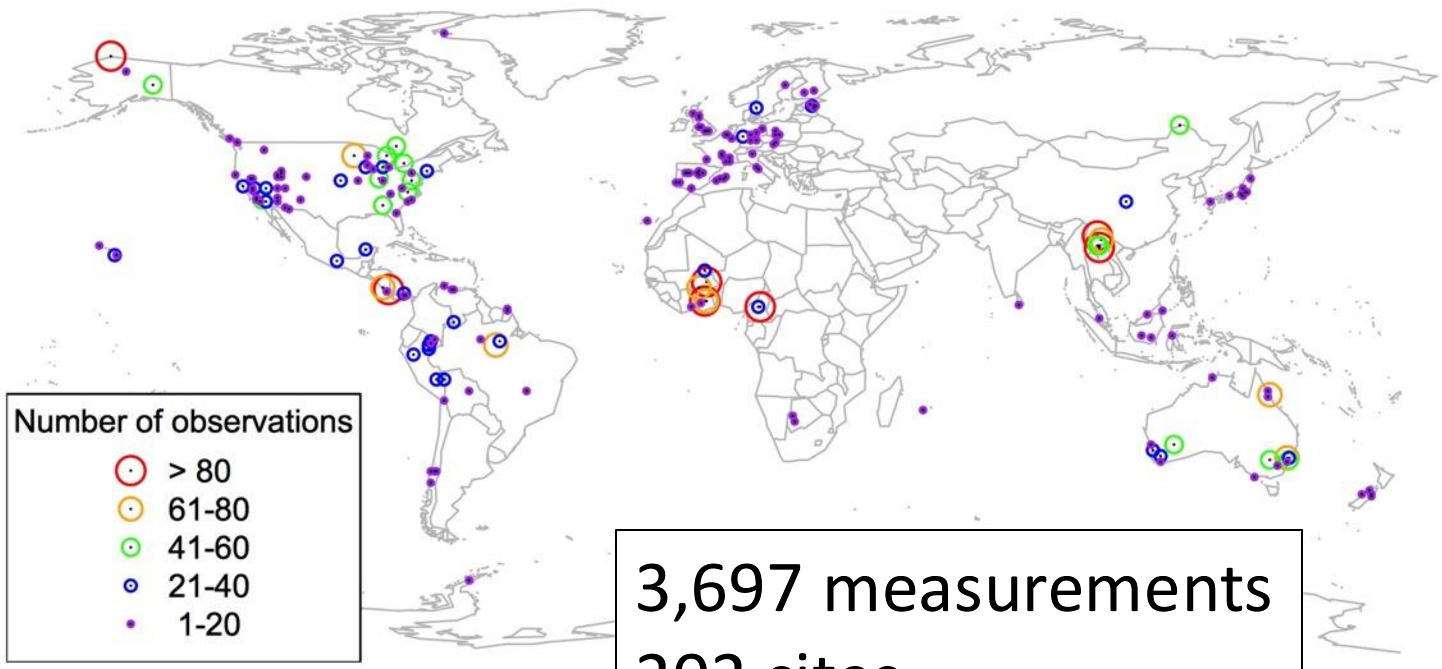
Let’s tackle some big questions in plant ecophysiology!

Big questions

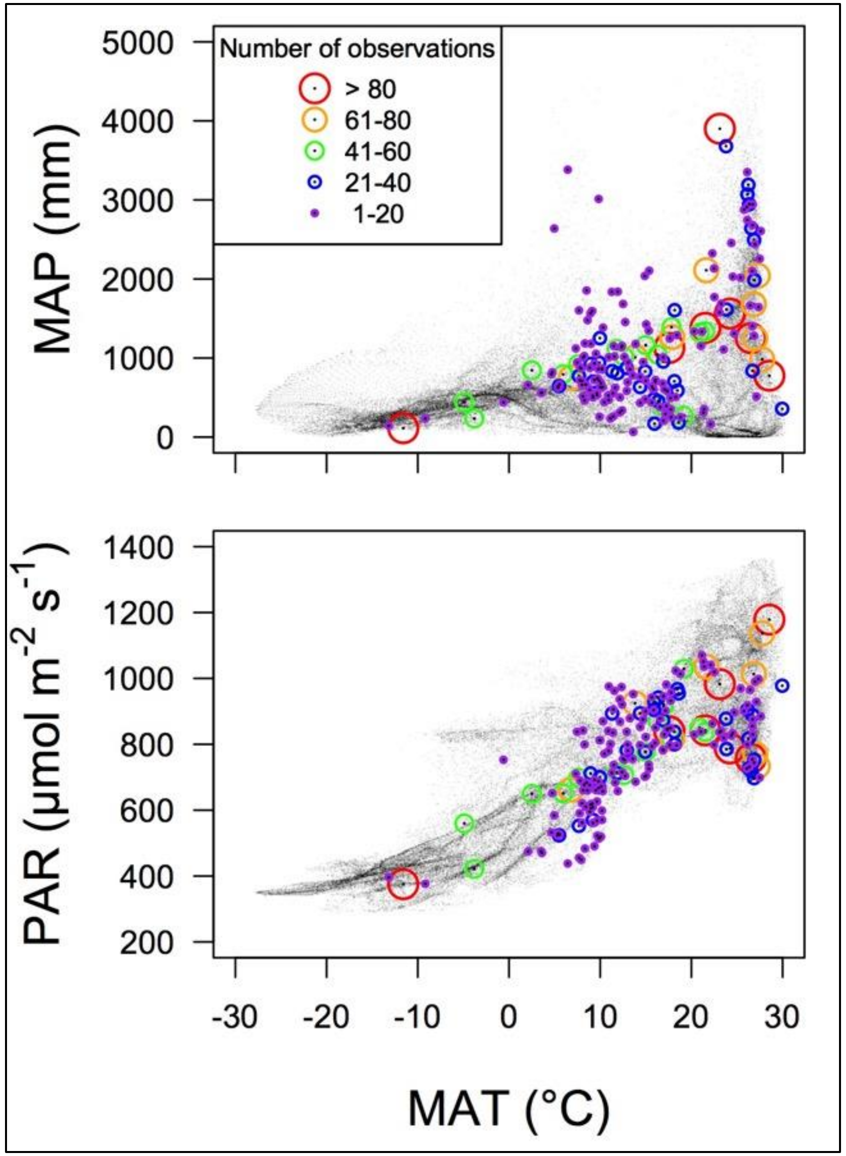
1. Is photosynthesis optimized to the environment?
2. How do plants acclimate to soil nitrogen?
3. What does acclimation mean for future terrestrial biogeochemical cycling?
4. When is C_4 photosynthesis an advantage over C_3 photosynthesis?

Question 1: Is photosynthesis optimized to the environment?

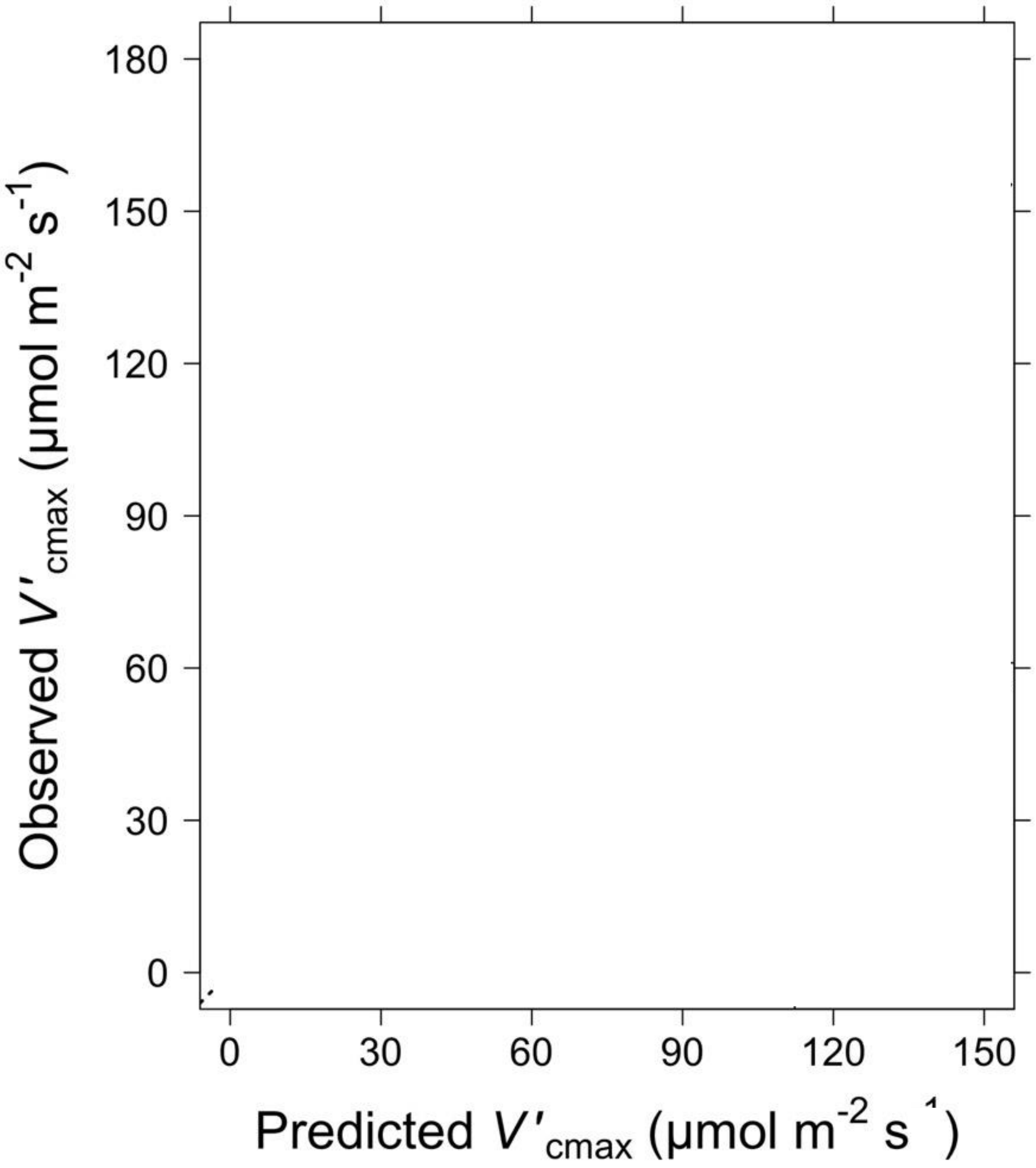
Global V_{cmax} dataset



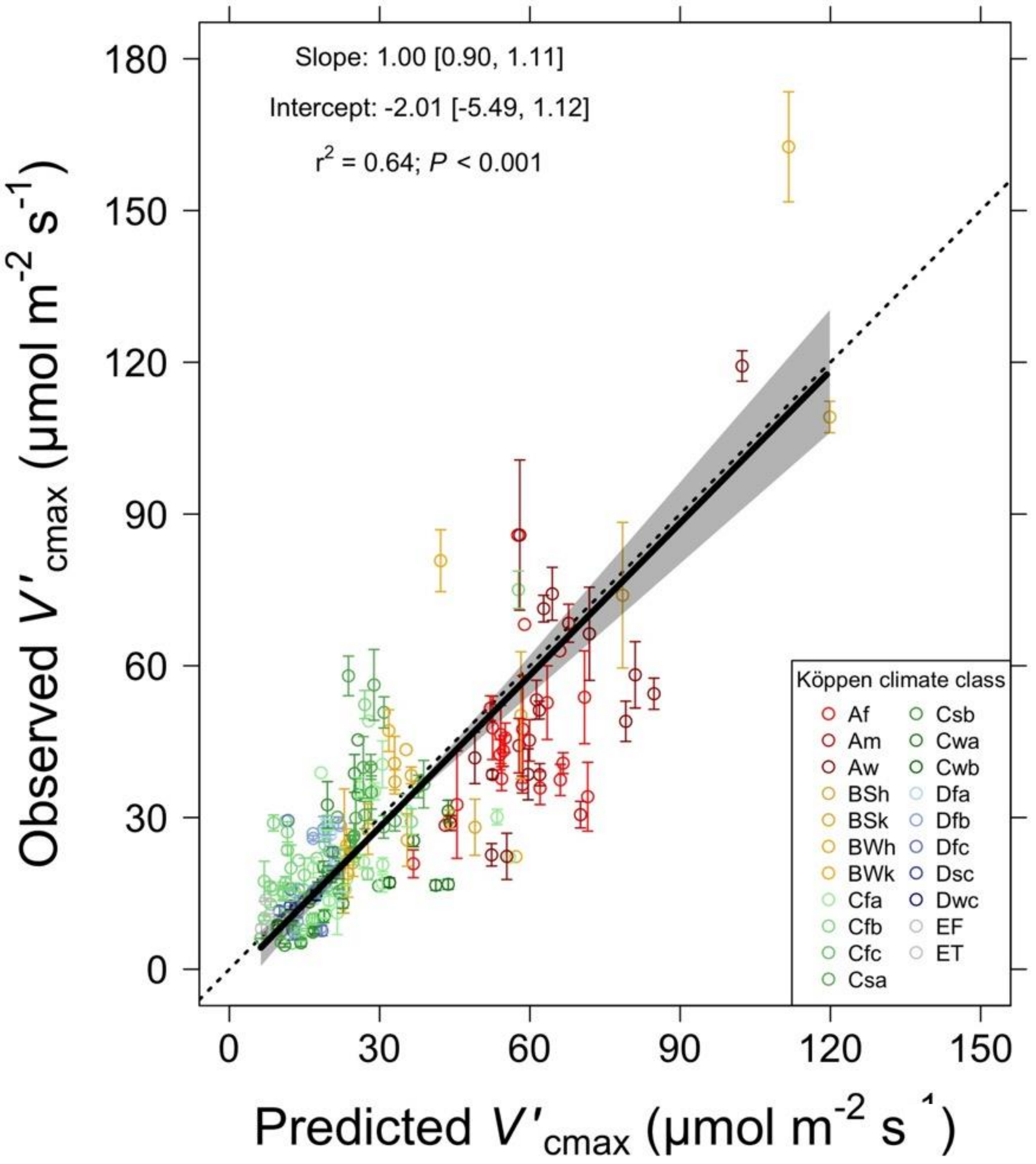
3,697 measurements
202 sites
> 600 genera



Smith et al. (2019) *Ecol Letters*



Smith et al. (2019) *Ecol Letters*



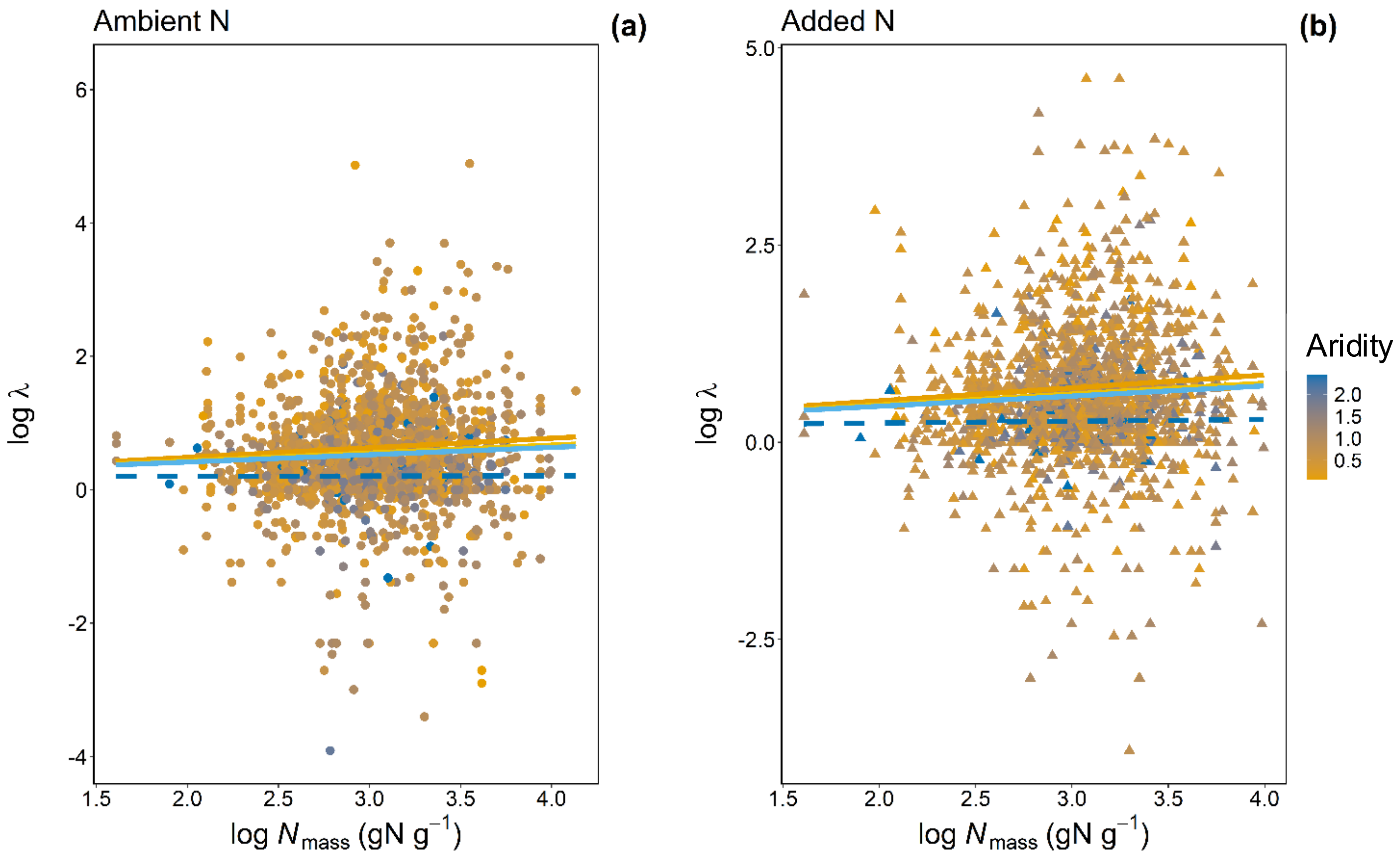
Optimal V_{cmax} is similar to observed values

Smith et al. (2019) *Ecol Letters*

Question 1: Is photosynthesis optimized to the environment?

YES! Photosynthesis acclimates spatially as expected from optimization

Looking forward: using theory to understand larger scale consequences of acclimation



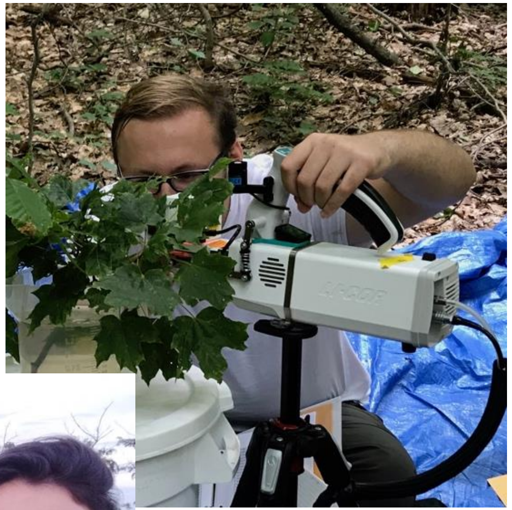
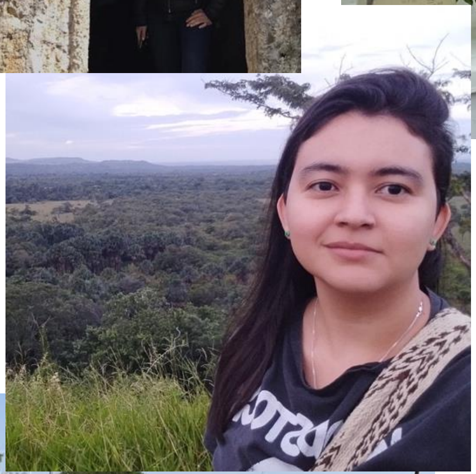
As predicted from theory, increased leaf N confers greater species population growth in dry sites and this is enhanced by eutrophication.

Cheaib,… and Smith (in prep)

Question 2: How do plants acclimate to soil nitrogen?

The lab has examined soil nitrogen impacts in many contexts

- Observational gradient studies
  - Paillassa et al. (2020) *New Phyt*, Cheaib et al. (2025) *New Phyt*, Perkowski and Smith (in review), Cheaib, et al. (in prep)
- Greenhouse soil manipulation studies
  - Perkowski et al. (2021) *J Exp Botany*, Waring et al. (2023) *J Exp Botany*, Perkowski et al. (2025) *J Exp Botany*
- Field soil manipulation studies
  - Cheaib et al. (2025) *Ecol Letters,* Perkowski et al. (in review), Beltran Triana et al. (in prep)

What have we learned?

New Phytologist

Tansley review | Open Access

Empirical evidence and theoretical understanding of ecosystem carbon and nitrogen cycle interactions

Benjamin D. Stocker, Ning Dong, Evan A. Perkowski, Pascal D. Schneider, Huiying Xu, Hugo J. de Boer, Karin T. Rebel, Nicholas G. Smith, Kevin Van Sundert, Han Wang, Sarah E. Jones ... **See all authors**

First published: 23 October 2024 | **https://doi.org/10.1111/nph.20178** | Citations: 1

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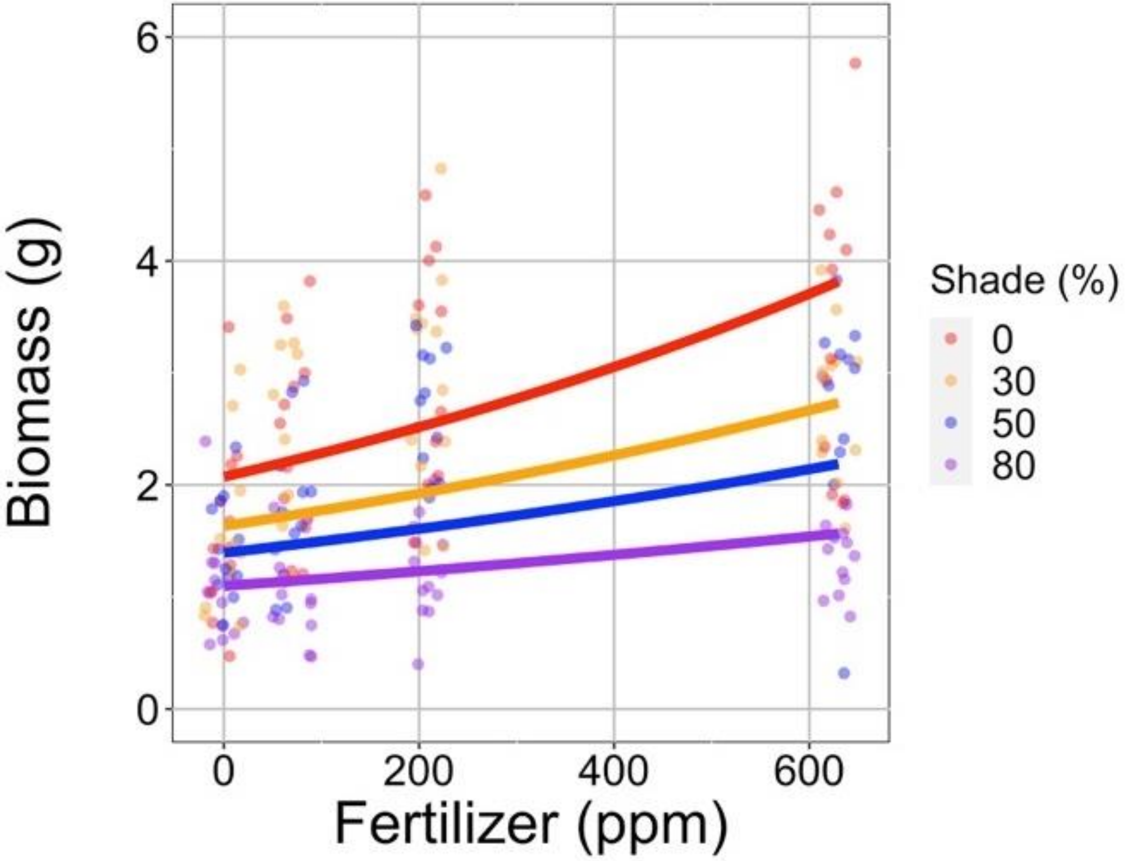
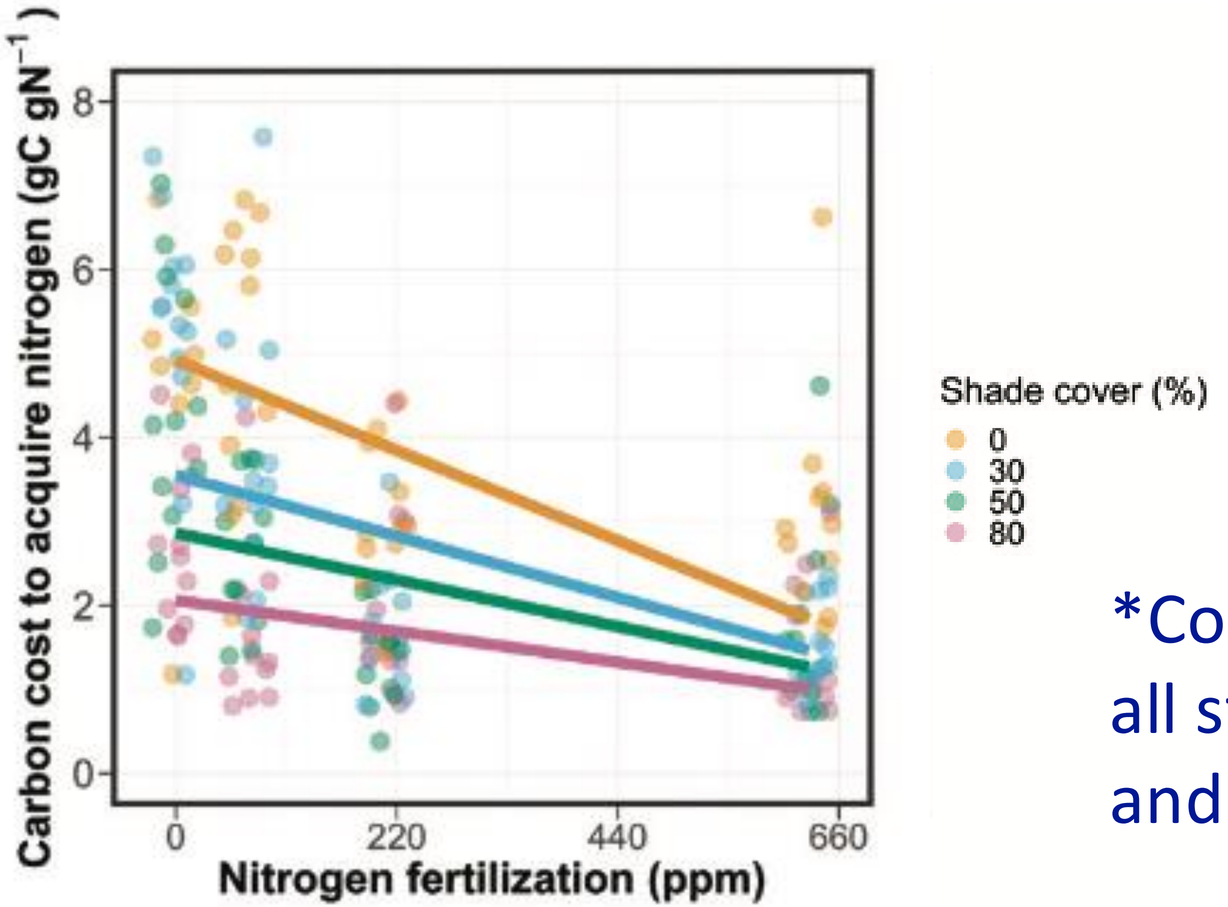
Stocker,…Smith et al. (2025) *New Phyt*

Result 1: Growth increases with increasing soil N



Waring, Perkowski, and Smith (2023) *J Exp Botany*

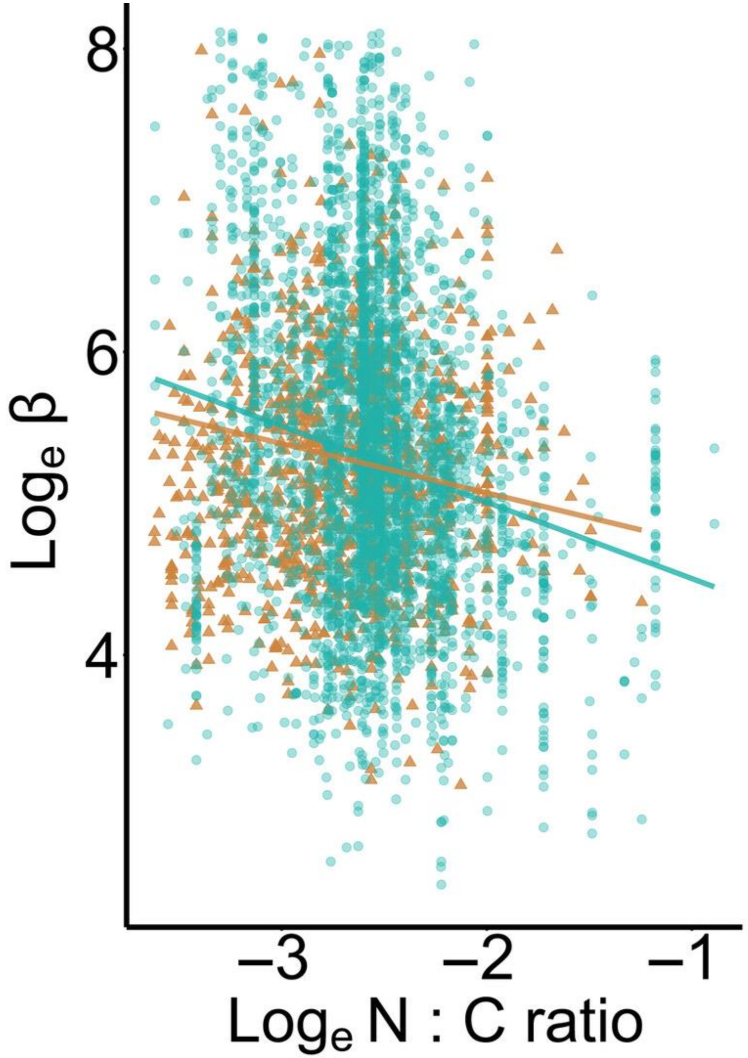
Result 2: C cost to acquire N decreases with increasing soil N

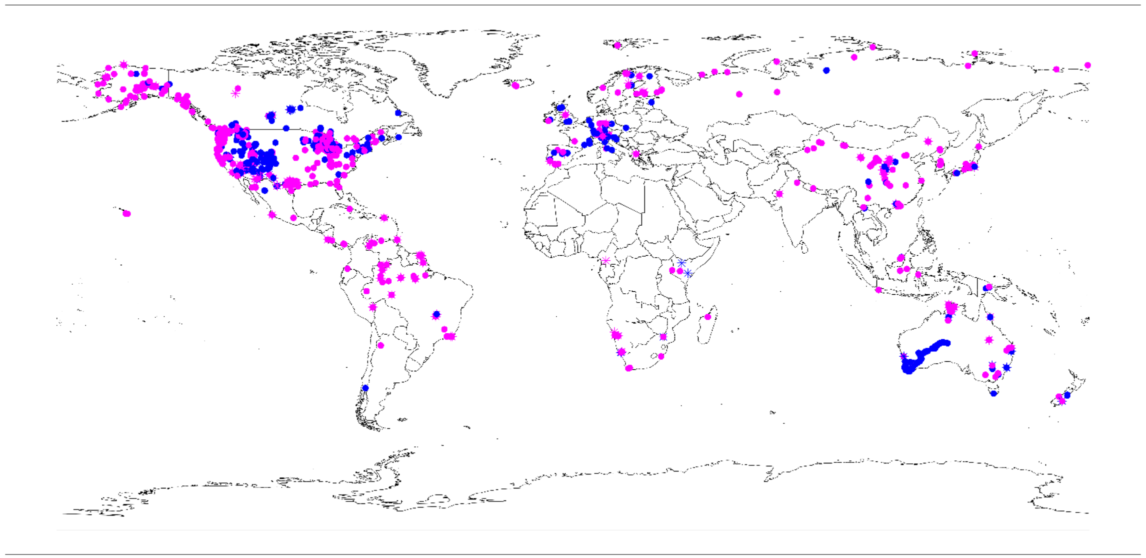


*Consistent across all studies at leaf and plant level

Perkowski, Waring, and Smith (2021) *J Exp Botany*

Result 2: C cost to acquire N decreases with increasing soil N

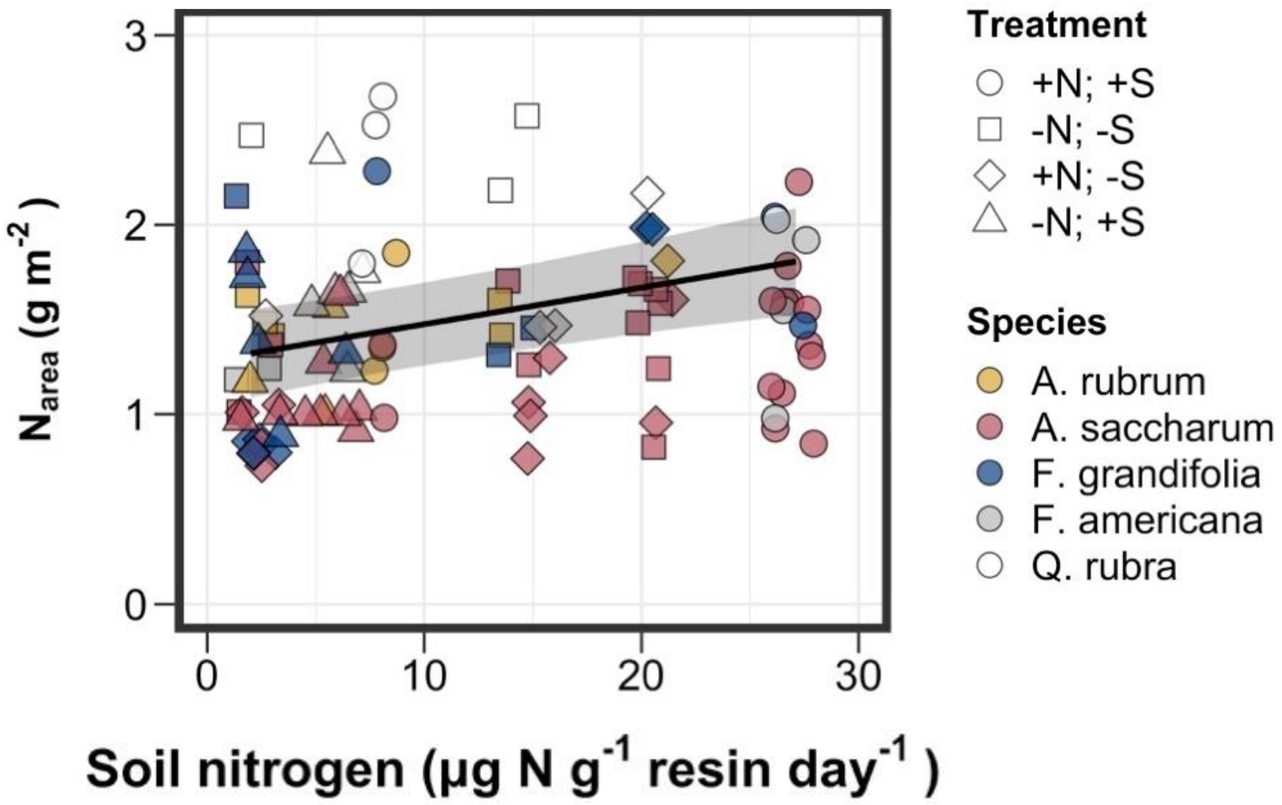




*Consistent across all studies at leaf and plant level

Cheaib, Chieppa, Perskowski, and Smith (2025) *New Phytologist*

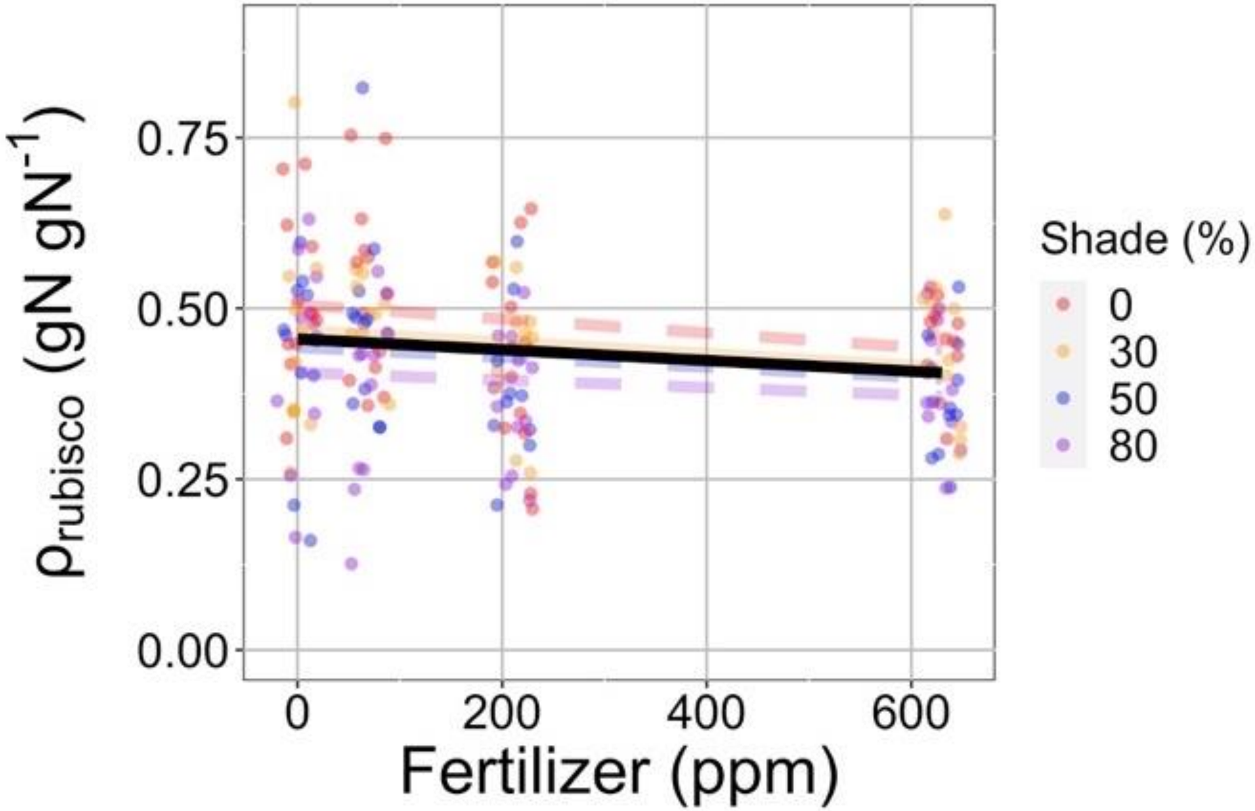
Result 3: Tissue N increases with increasing soil N



*Consistent across all studies

Perkowski,… and Smith (in review)

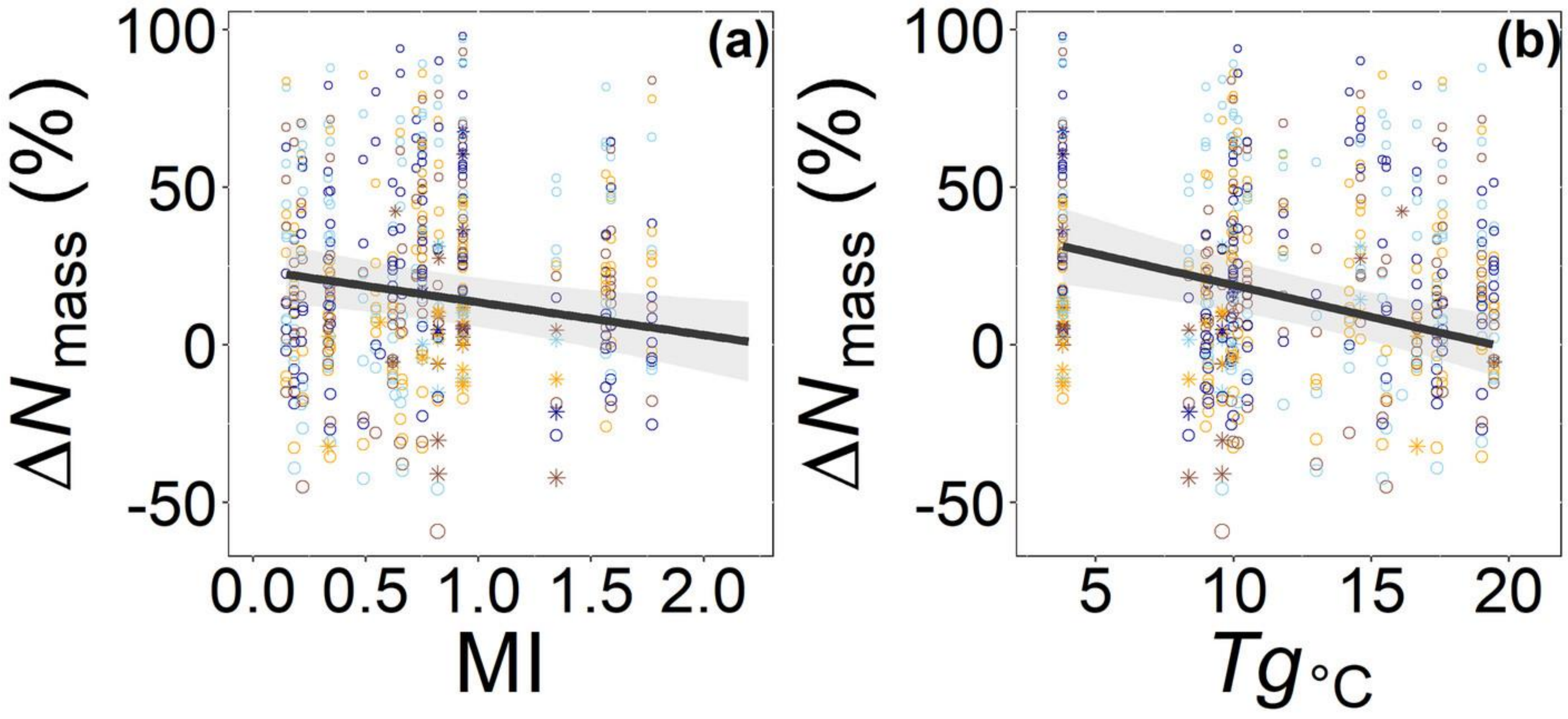
Result 4: Relative leaf N allocation to photosynthesis decreases with increasing soil N



*Consistent across multiple species, metrics, and growth conditions

Waring, Perkowski, and Smith (2023) *J Exp Botany*

Result 5: Response to soil N is dependent on N demand

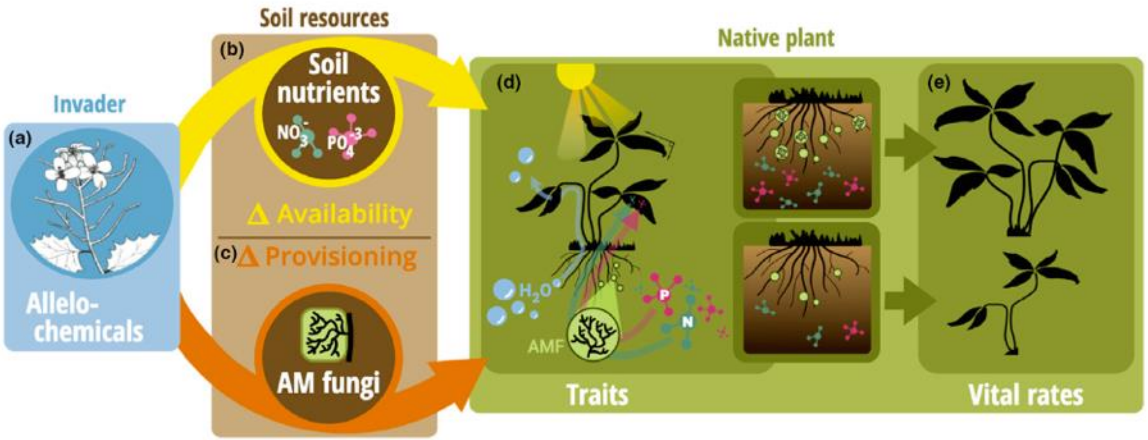


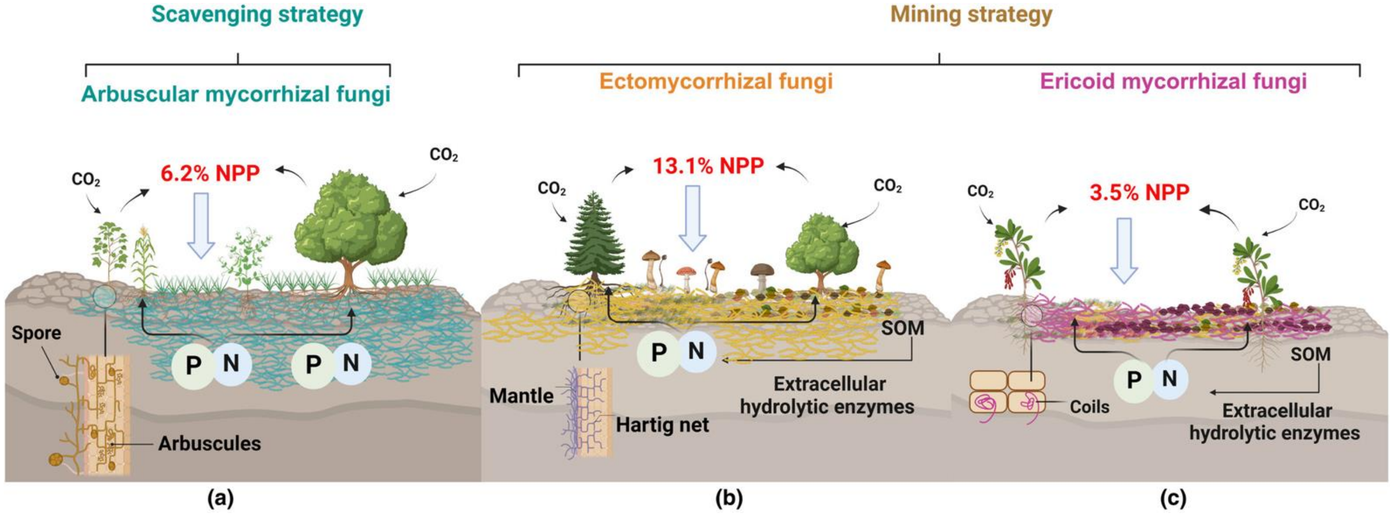
Cheaib,… and Smith (2025) *New Phyt*

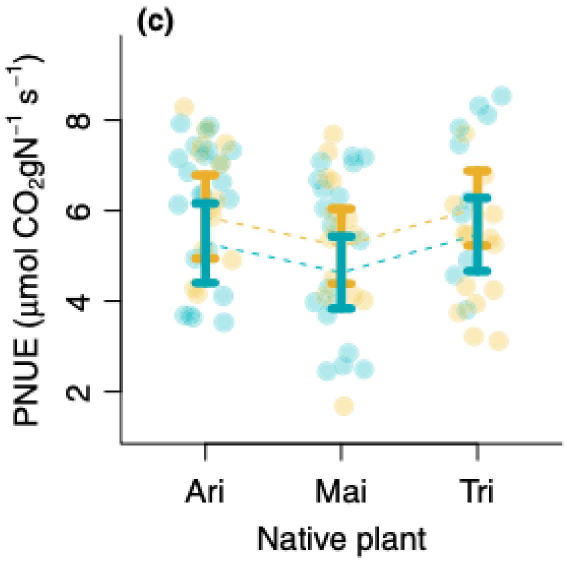
Question 2: How do plants acclimate to soil nitrogen?

Reduction in N uptake costs results in bigger plants with more leaf N, particularly where demand is high. However, more leaf N =/= more photosynthesis.

Looking forward: impact of soil resource acquisition strategies on leaf economics



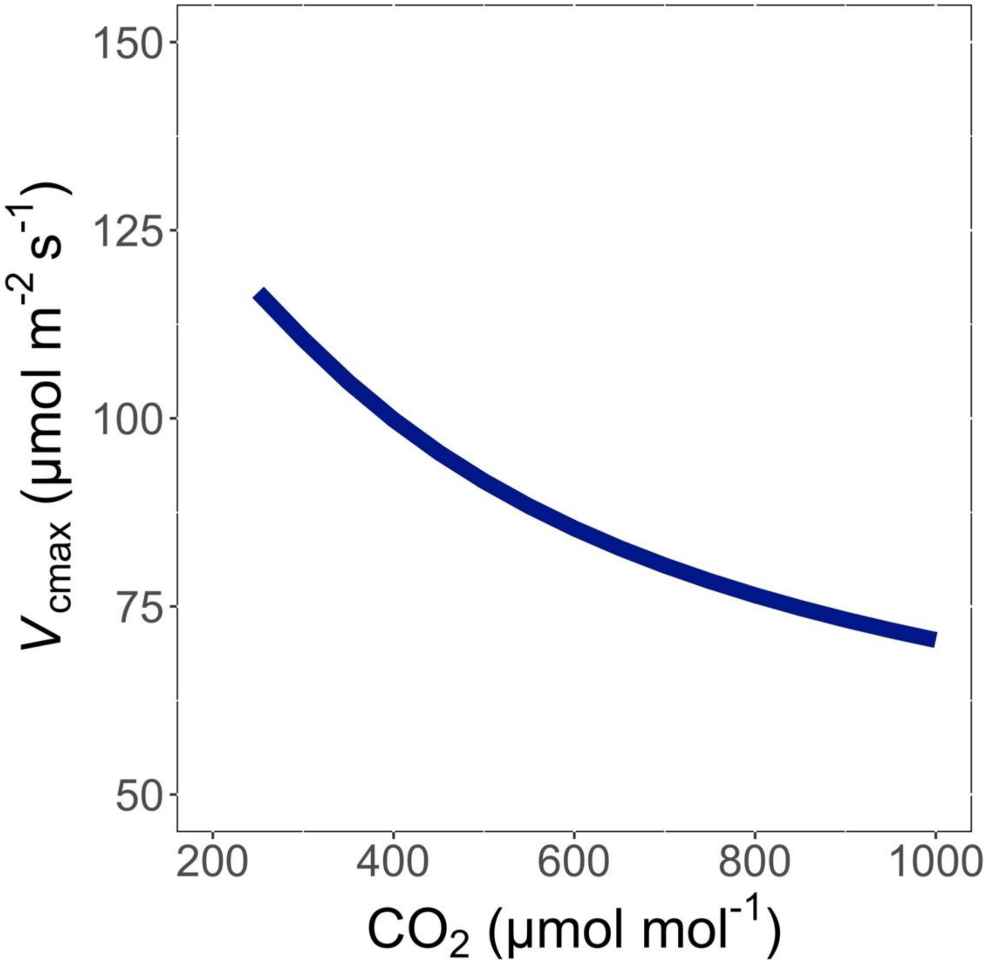




Bialic-Murphy, Smith et al. (2021) *Ecology Letters*
Cheaib, Chieppa, Perkowski, and Smith (2025) *New Phytologist*

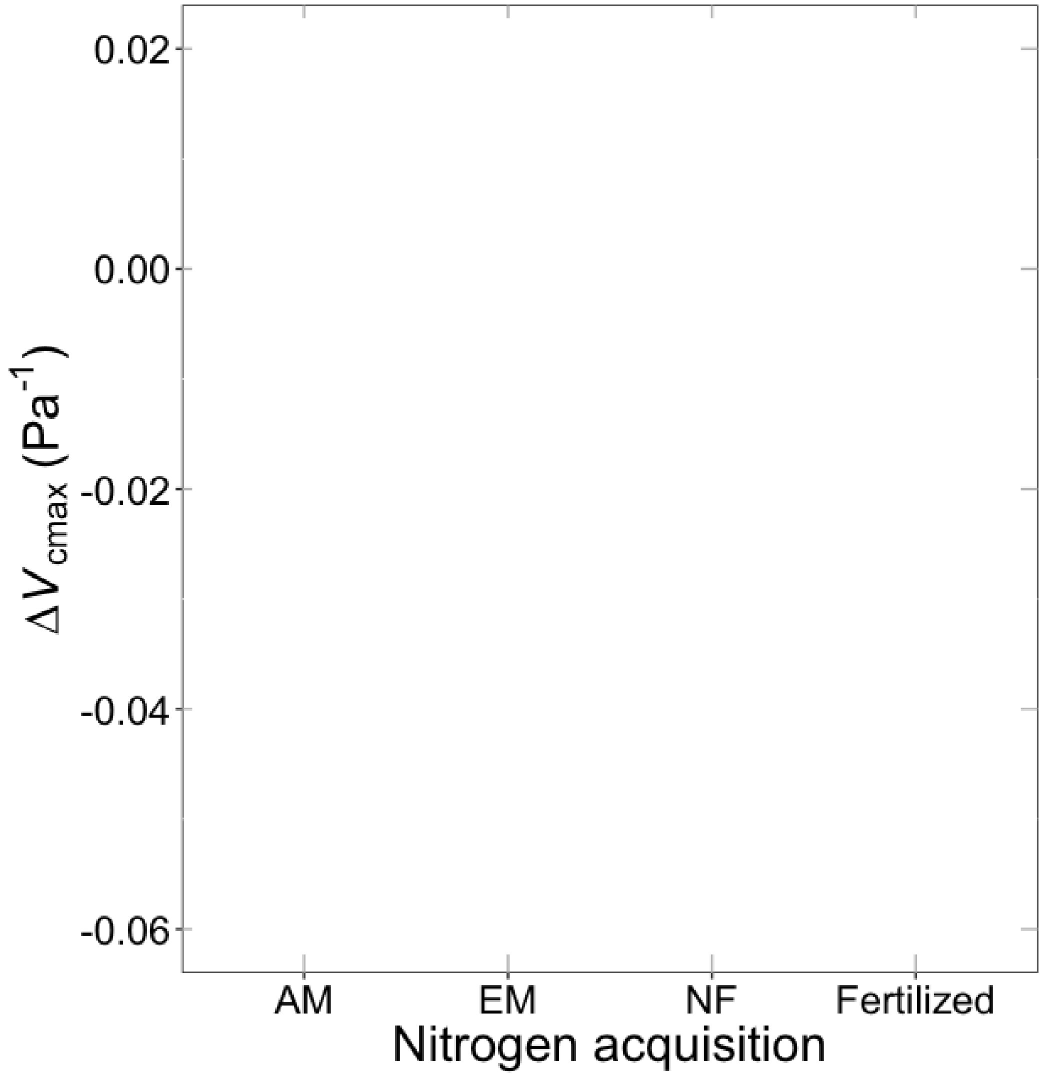
Question 3: What does acclimation mean for future terrestrial biogeochemical cycling?

Expected future responses

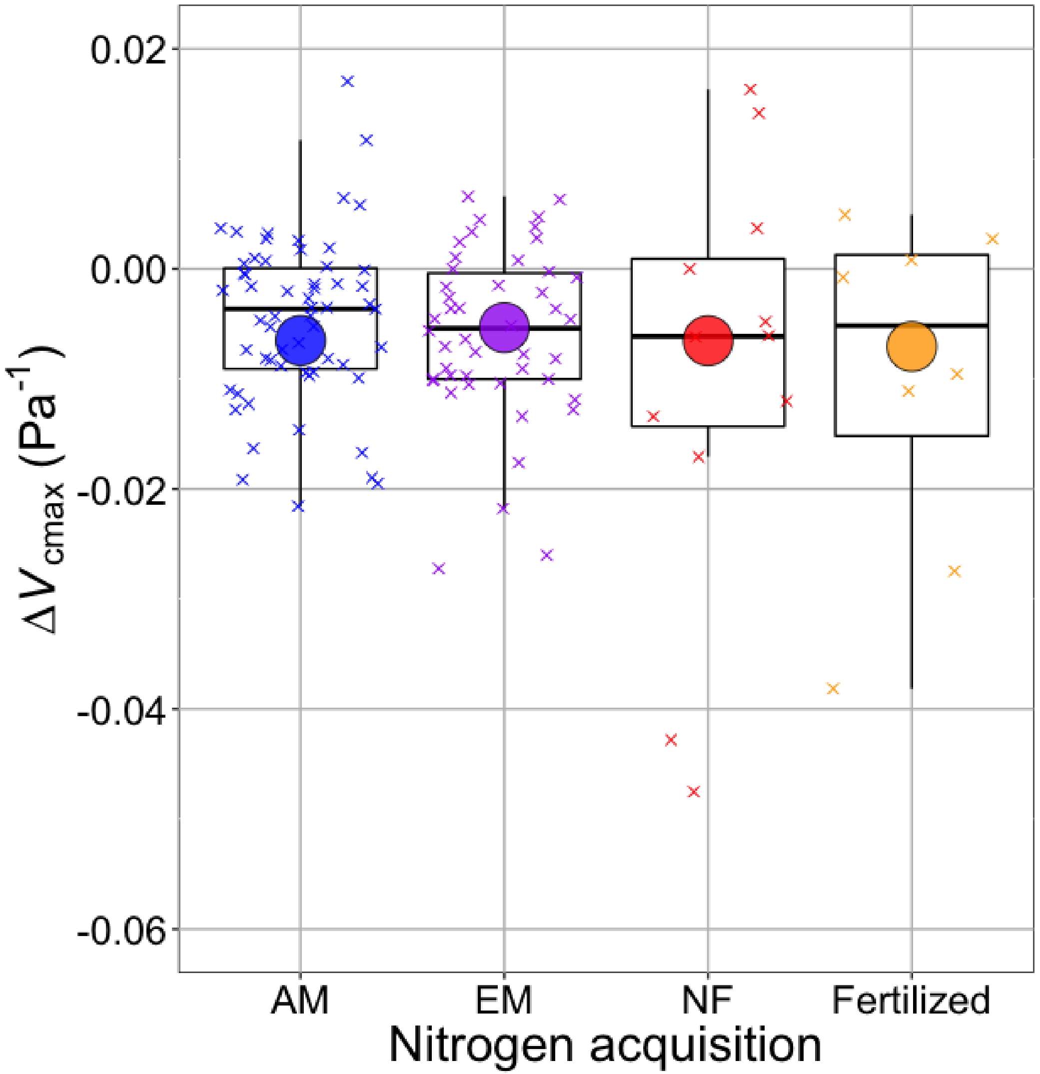


V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf and less photorespiration

Smith et al. (2019) *Ecol Letters*



Smith and Keenan (2020) *Glob Change Biol*



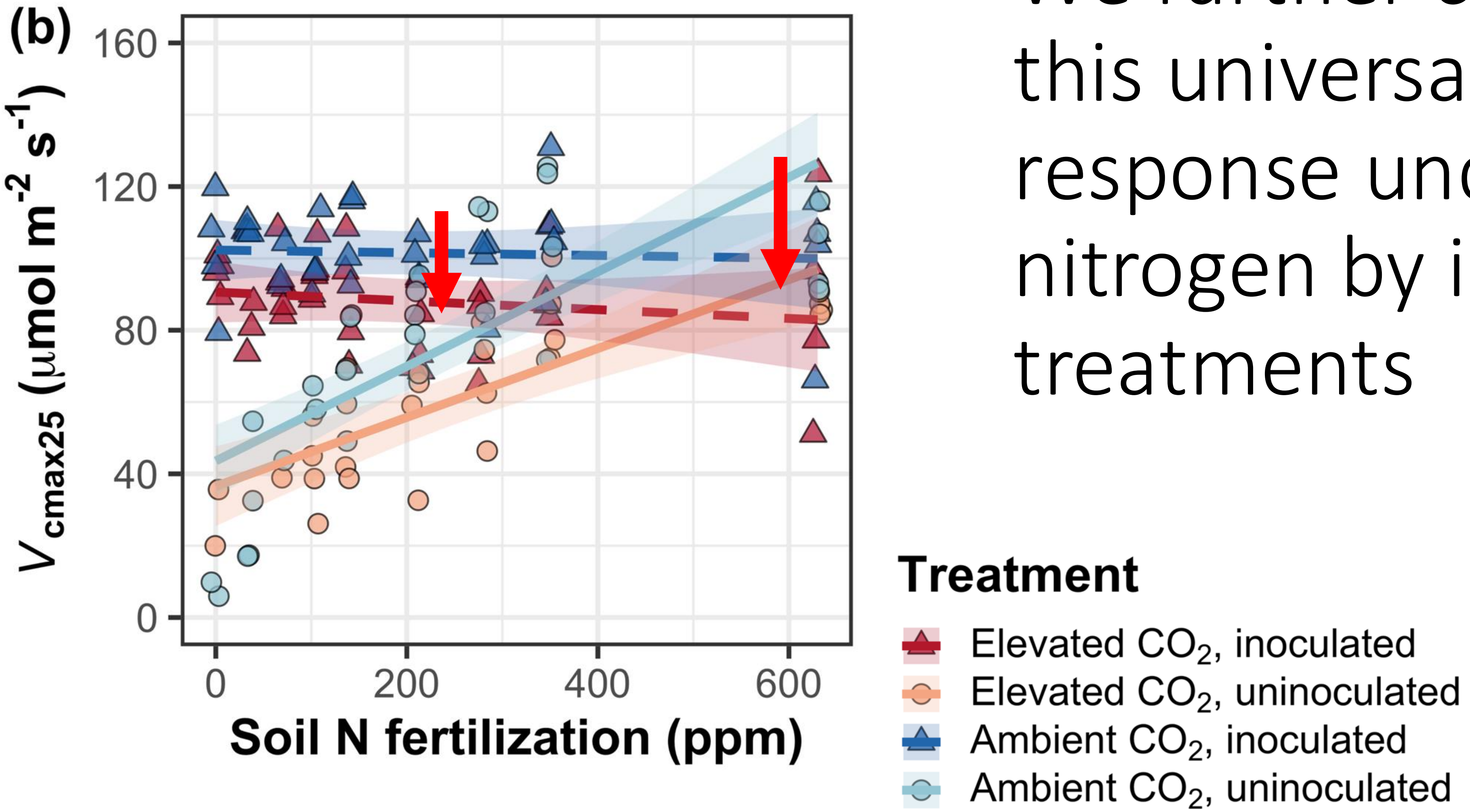
V_{cmax} changes with CO_2 in ways expected from optimization

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

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

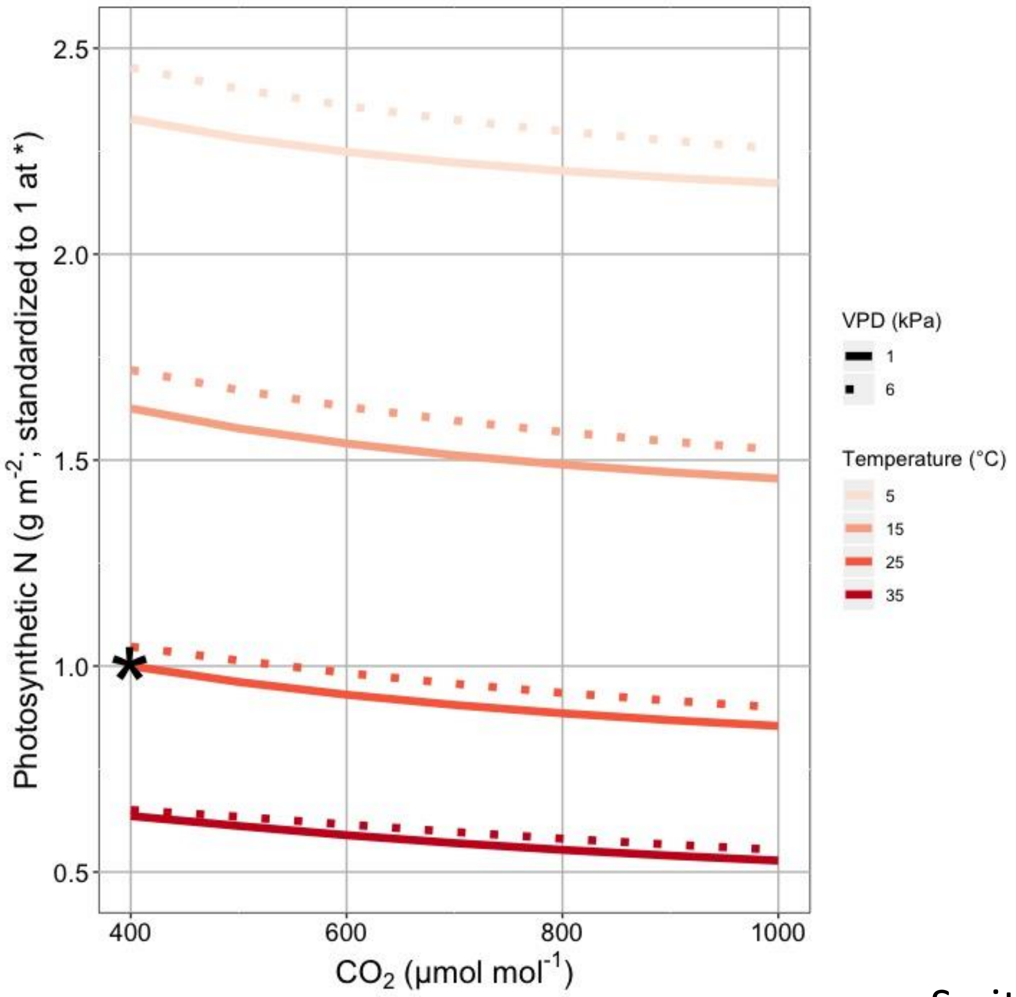
Smith and Keenan (2020) *Glob Change Biol*

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

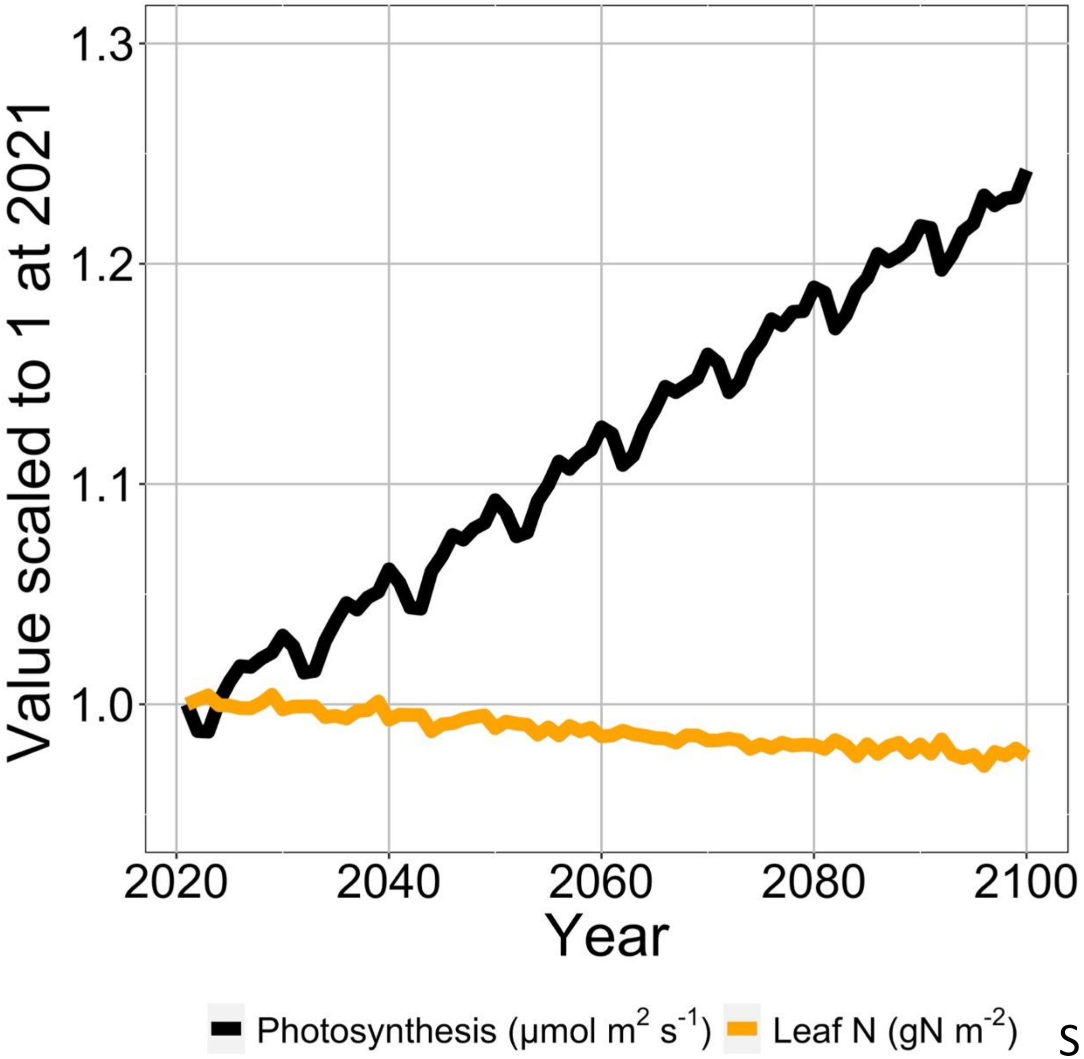


Smith and Keenan (2020) *Glob Change Biol*

Let's run a model out into the future!

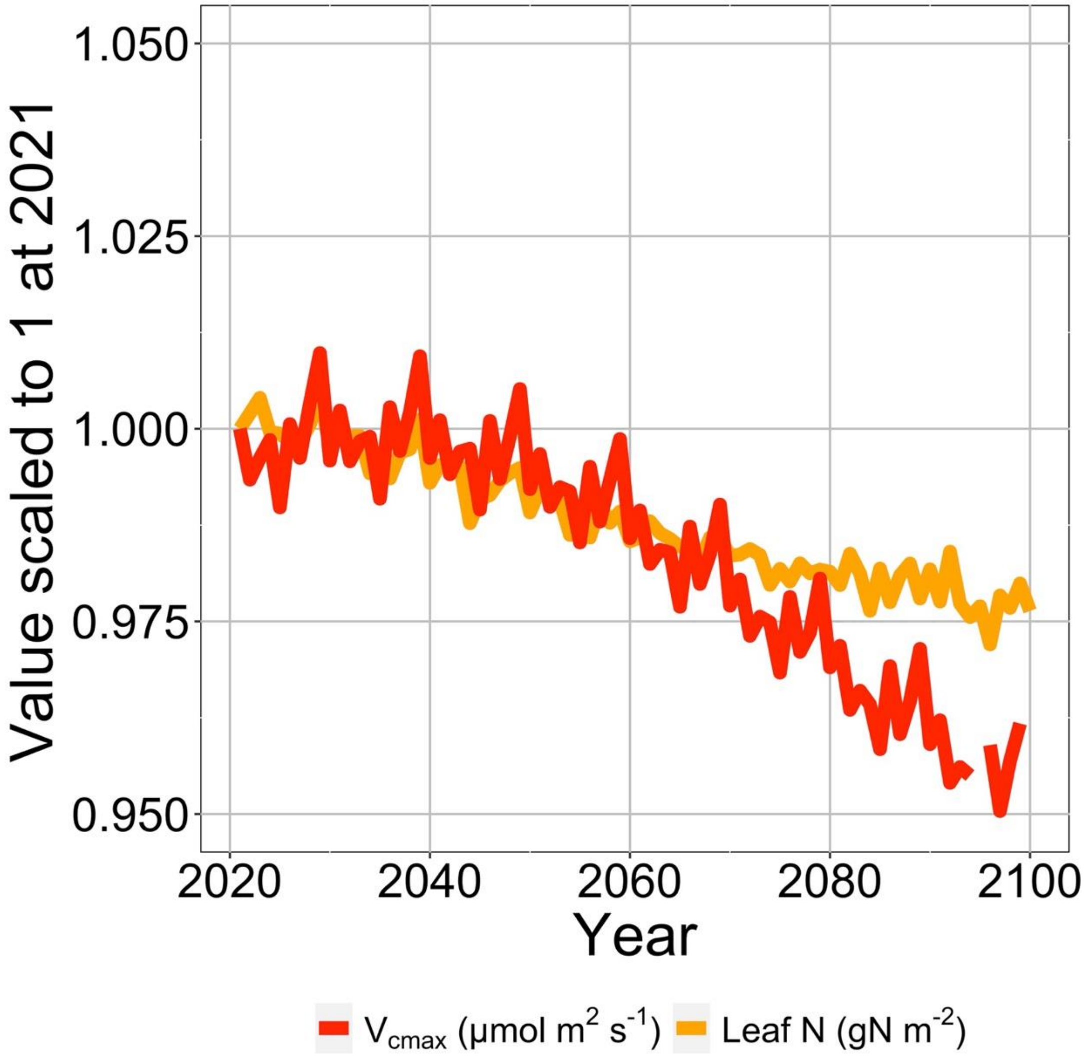
E3SM Energy Exascale Earth System Model

Photosynthesis increases with elevated CO_2 at lower leaf N



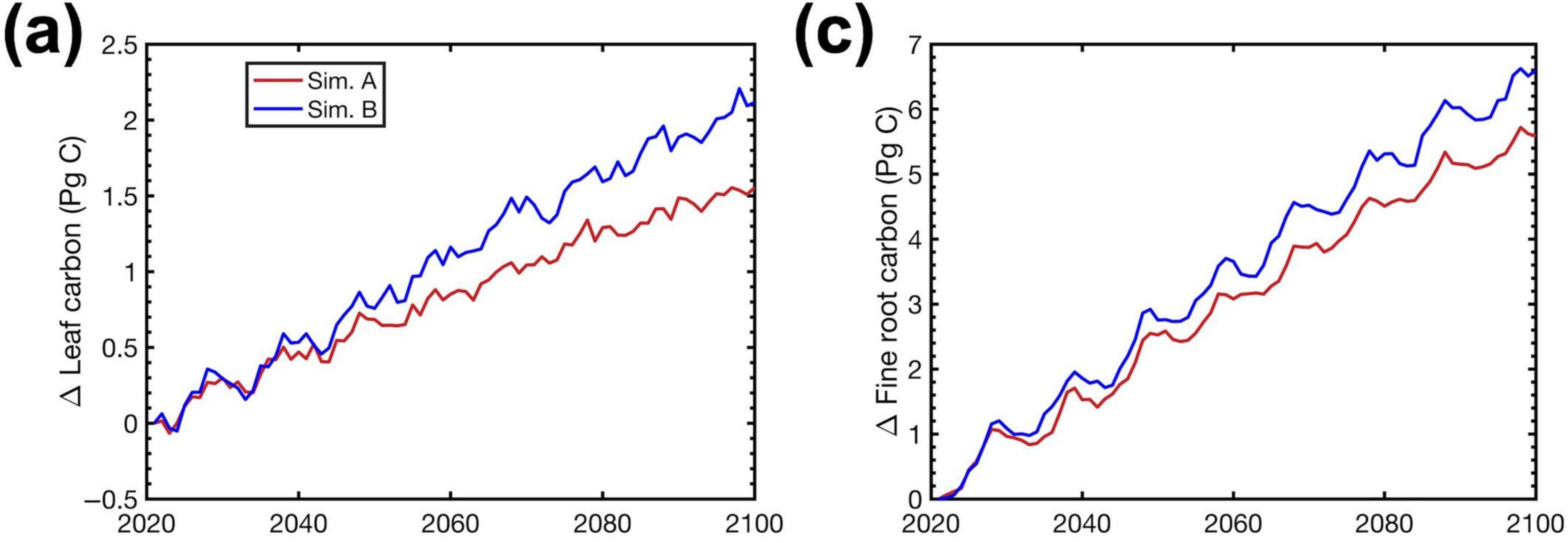
Smith et al. (2024) *Glob Change Biol*

Leaf N reduction is due to a reduction in photosynthetic capacity



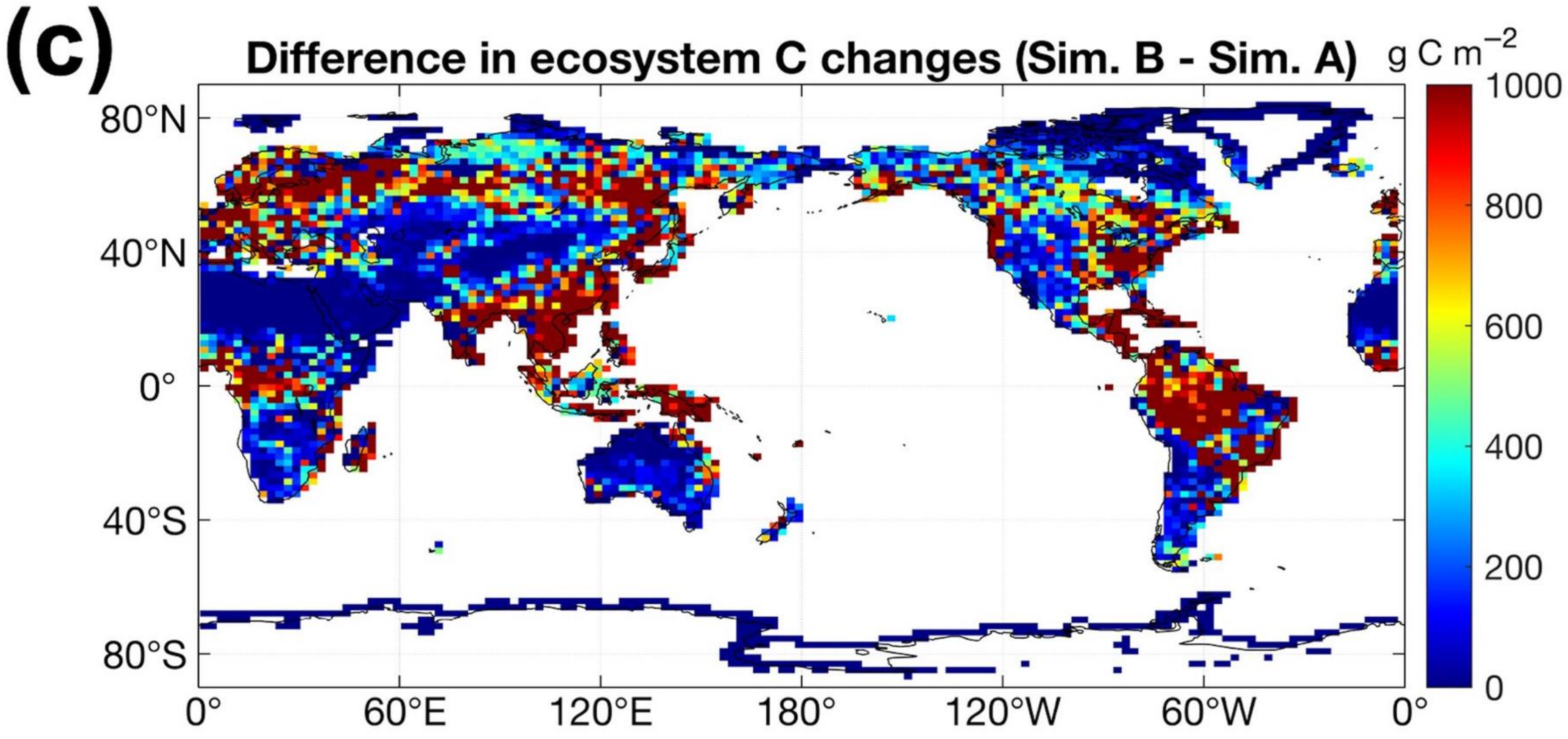
Smith et al. (2024) *Glob Change Biol*

Plants build more leaves and fine roots



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

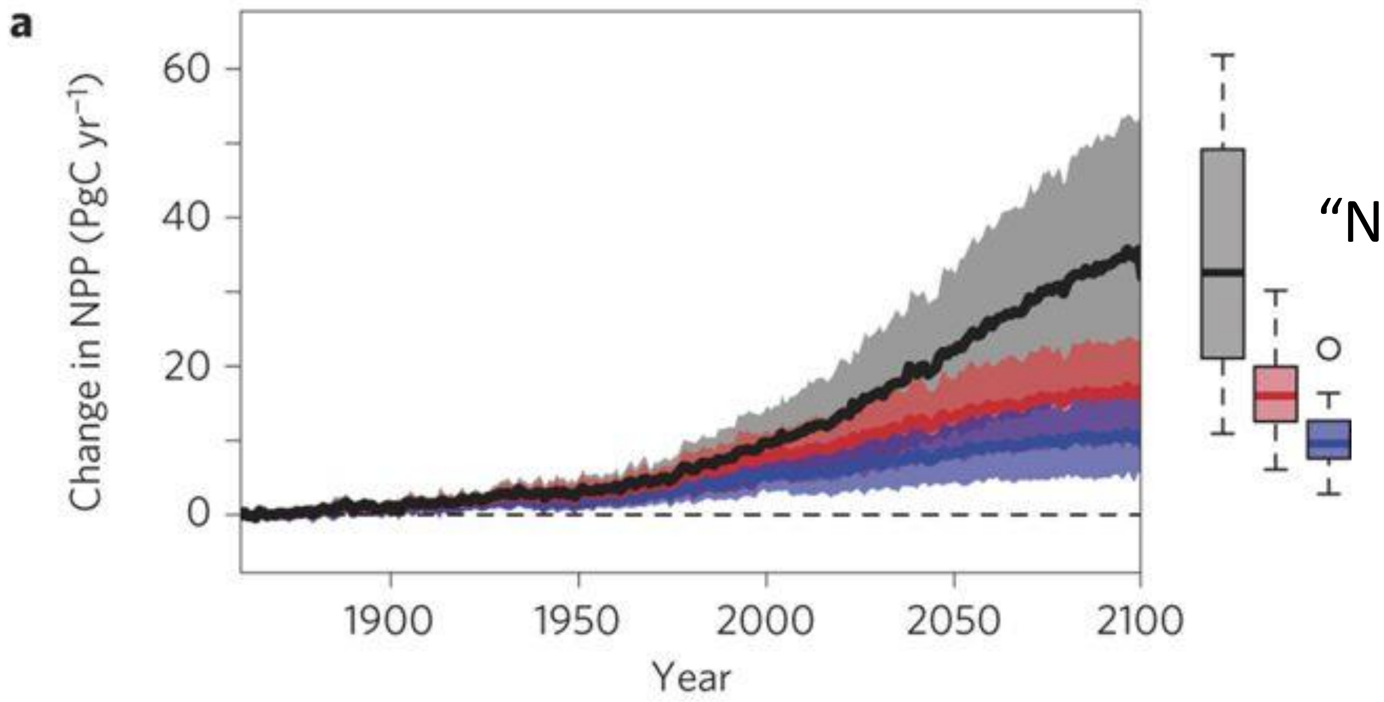
Leaf N savings increases long-term ecosystem carbon stocks



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

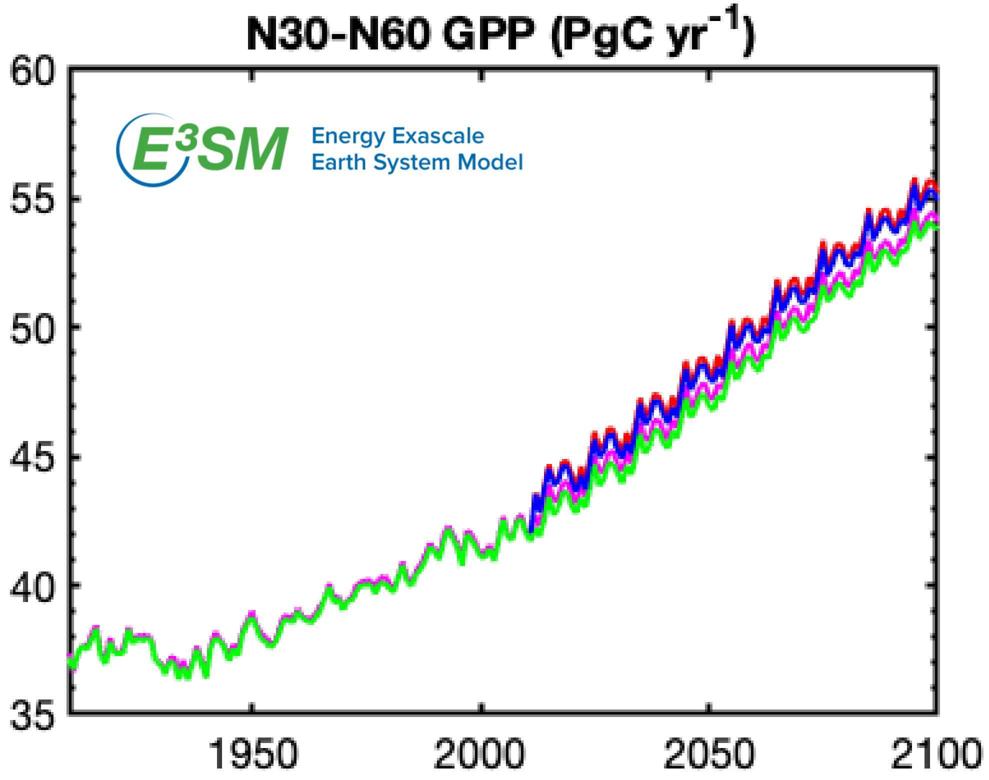
“Nutrient limitation” simulations

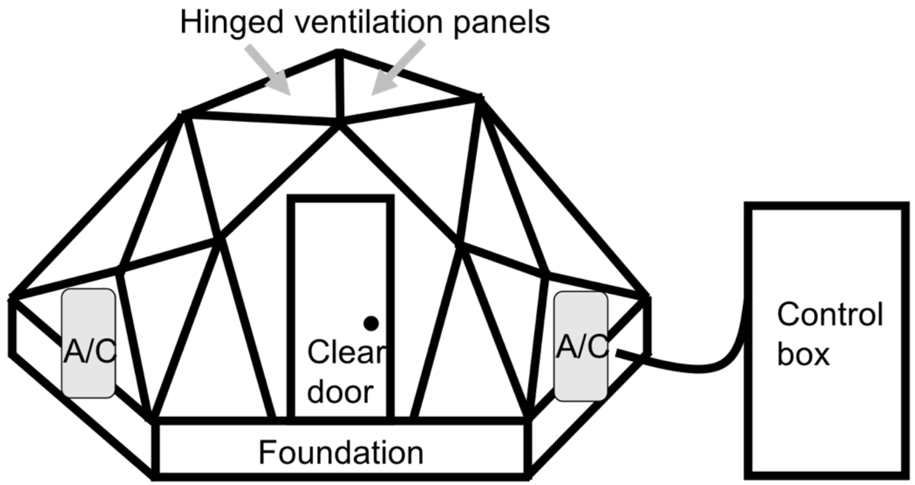
Weider et al. (2015)

Question 3: What does acclimation mean for future terrestrial biogeochemical cycling?

Photosynthesis will increase and per-leaf-area nutrient use will decrease, reducing N limitation and increasing future ecosystem C

Looking forward: role of acclimation on future ecosystem feedbacks to global change





Coupled model-data experiments

Question 4: When is C_4 photosynthesis an advantage over C_3 photosynthesis?

C_3 versus C_4 optimization

C_4 versus C_3 optimization

C_4 photosynthesis has…

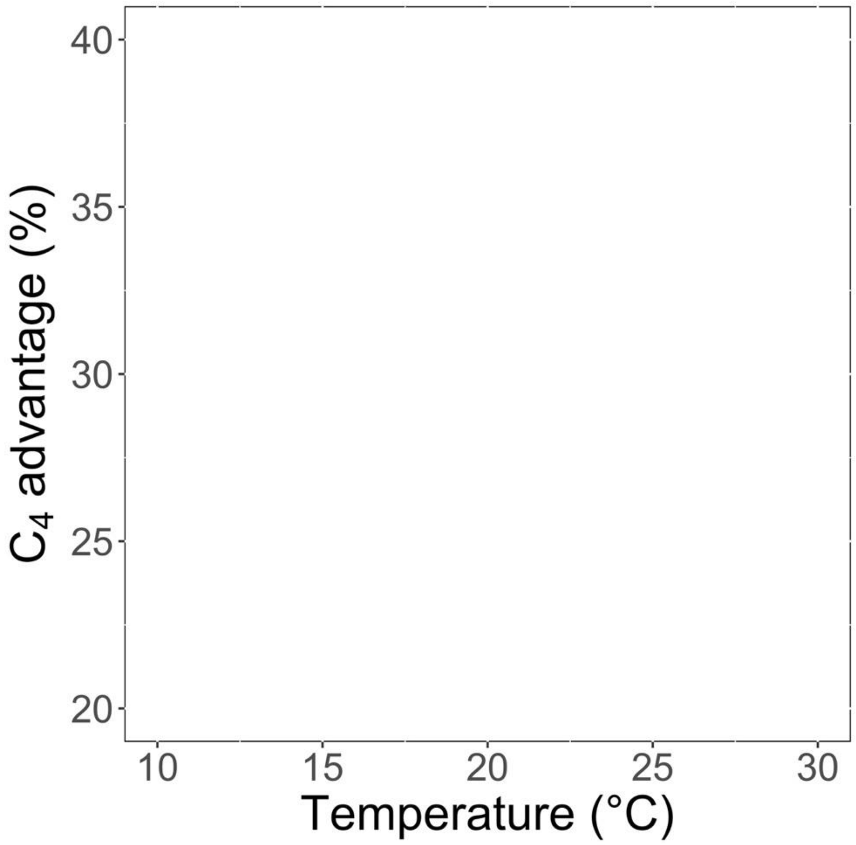
- Little photorespiration
- An additional limitation (PEP carboxylation)

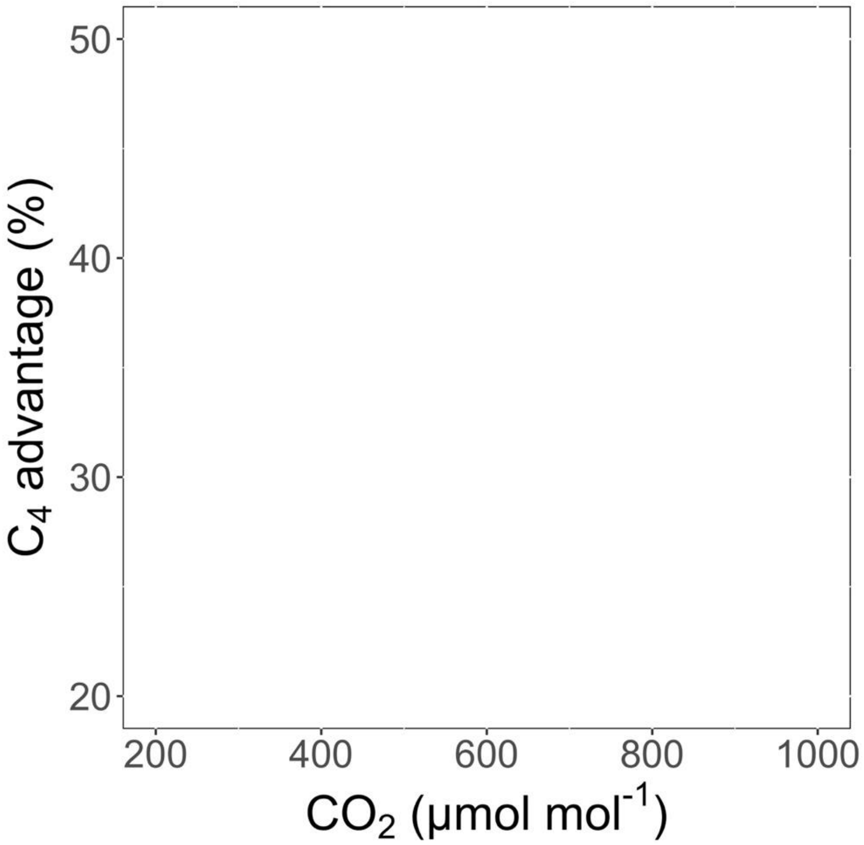
C_4 versus C_3 optimization

C_4 photosynthesis has…

- **Little photorespiration**
- An additional limitation (PEP carboxylation)

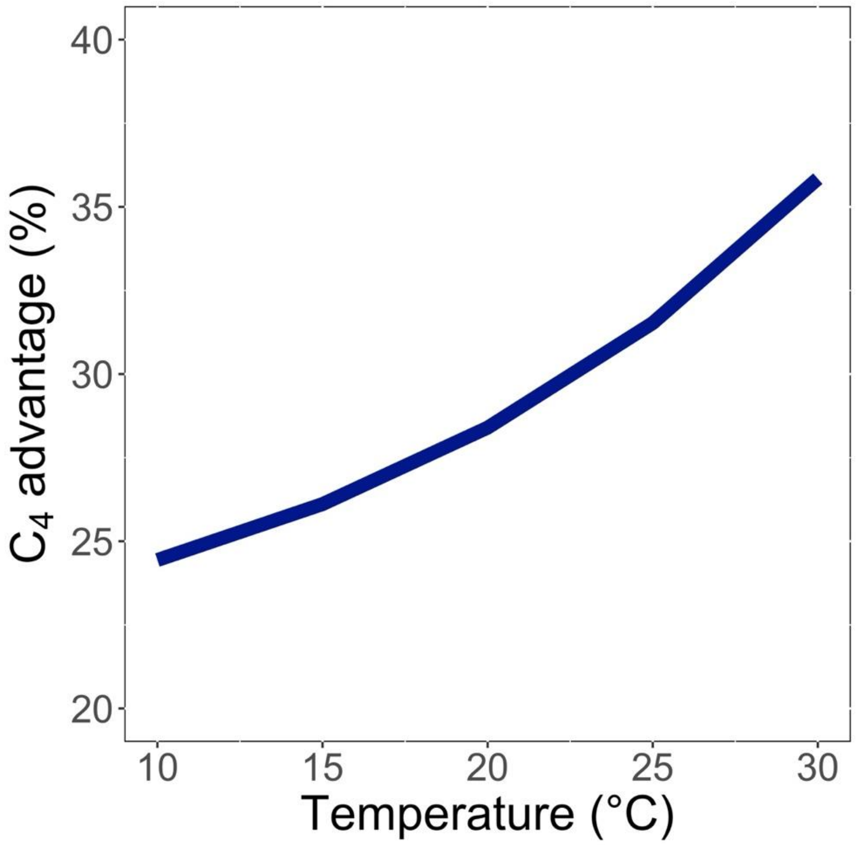
Relative advantage of C_4 physiology

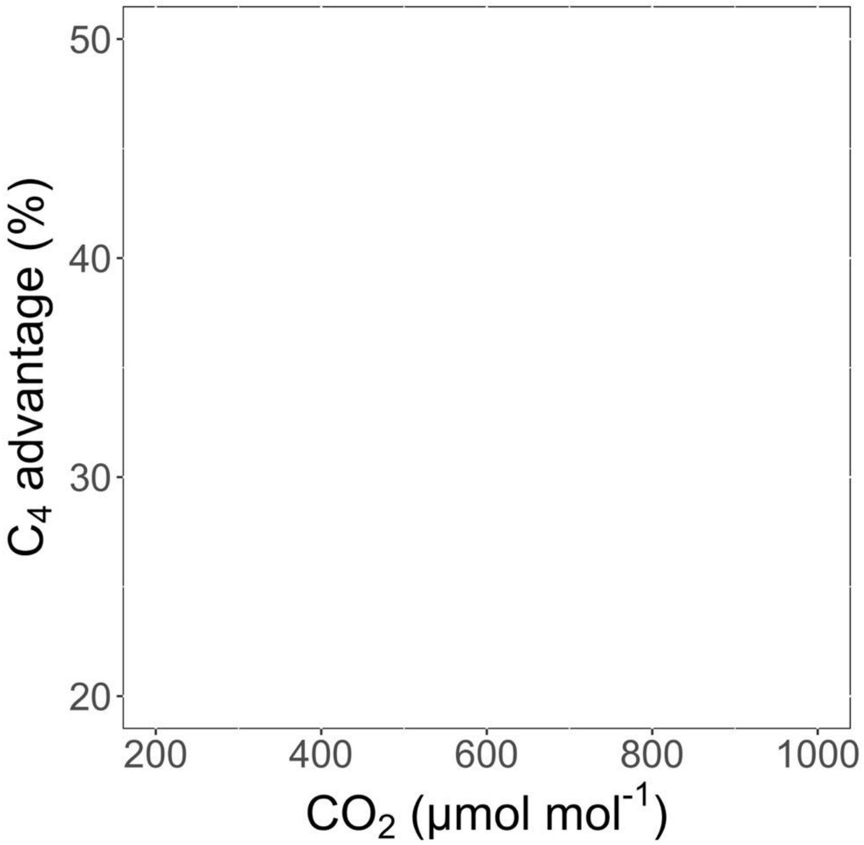




Scott and Smith (2022) *JAMES*

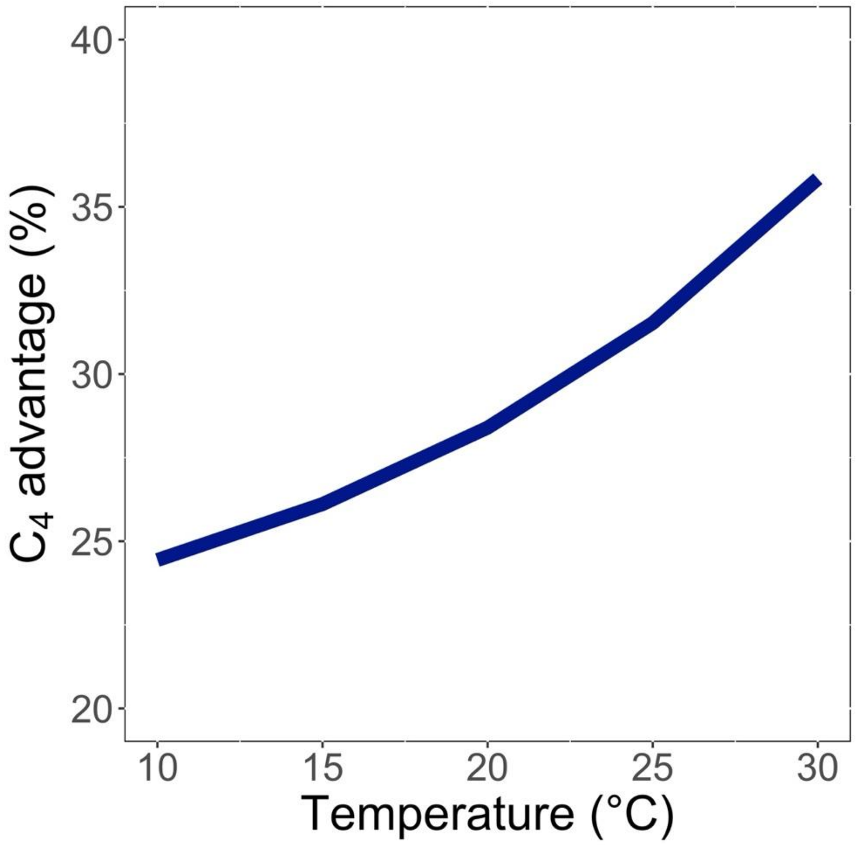
Relative advantage of C_4 physiology

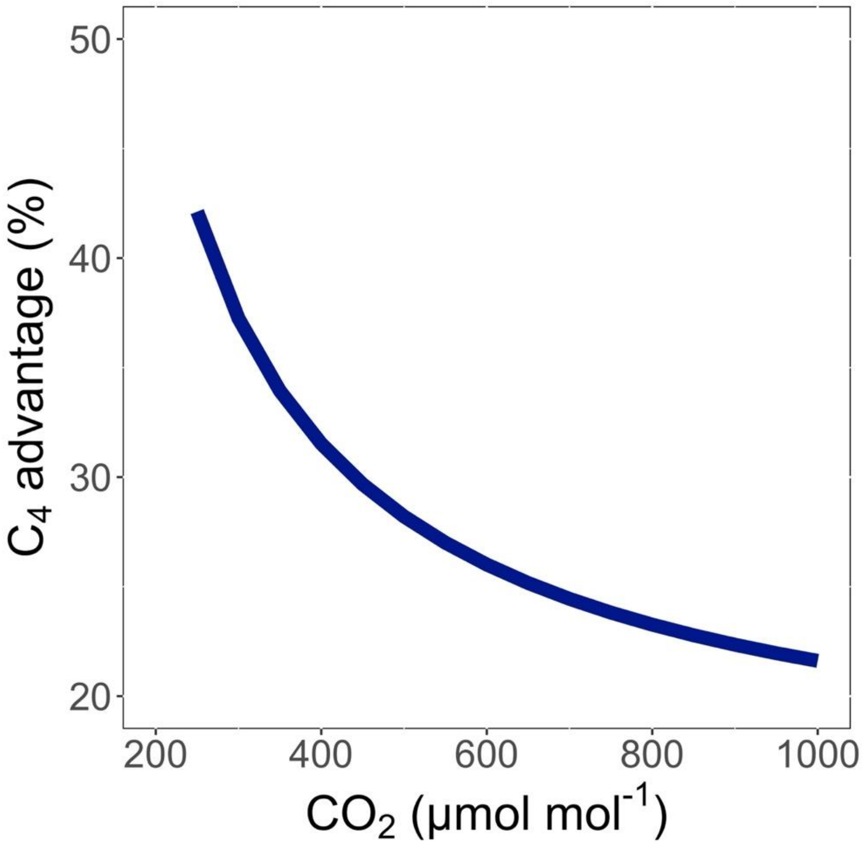




Scott and Smith (2022) *JAMES*

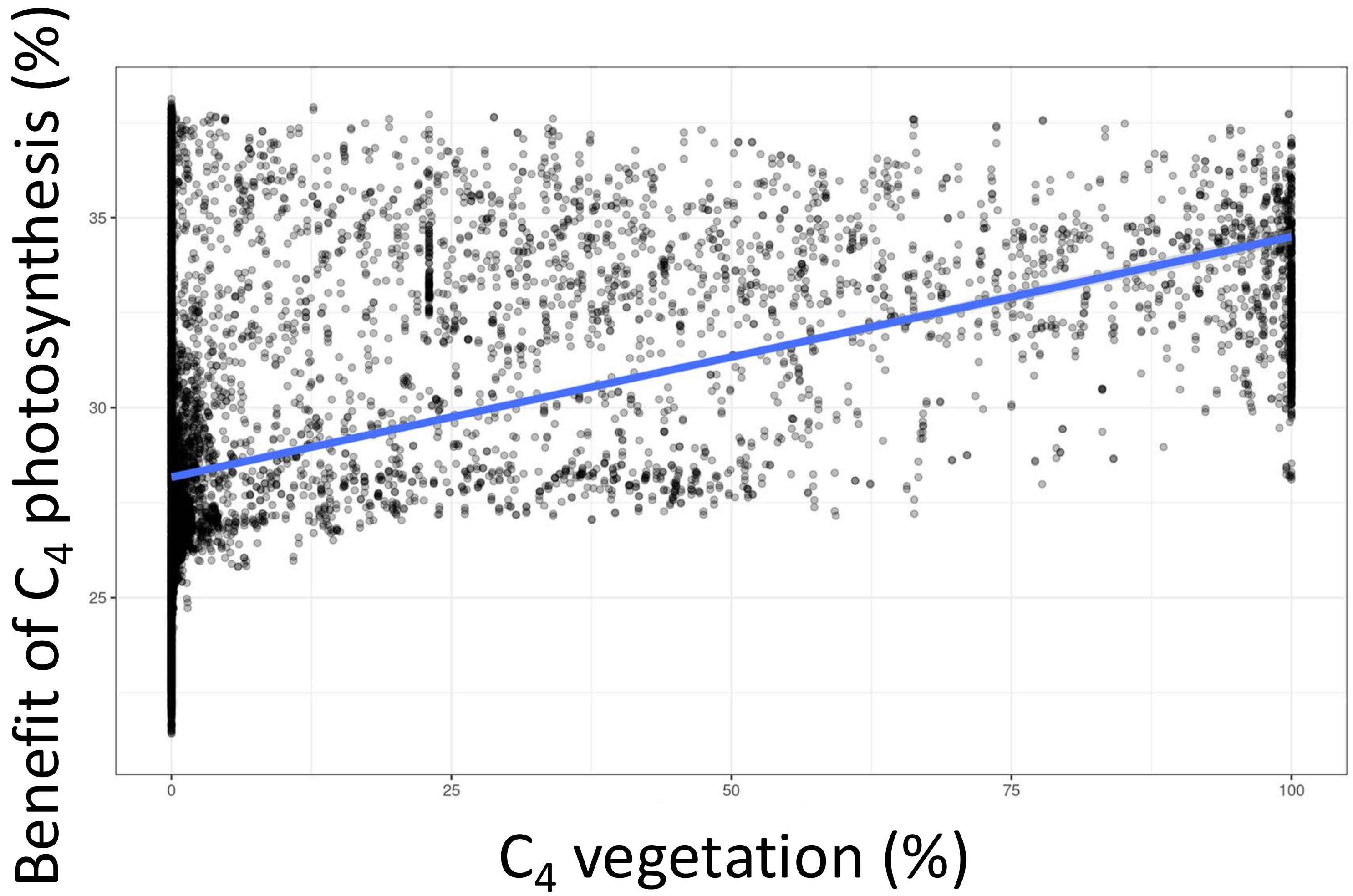
Relative advantage of C_4 physiology



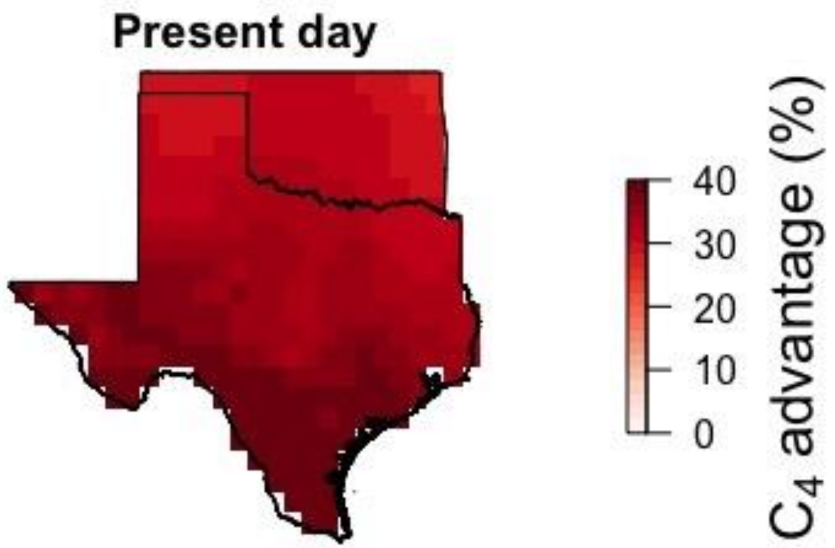


Scott and Smith (2022) *JAMES*

The model seems to work!

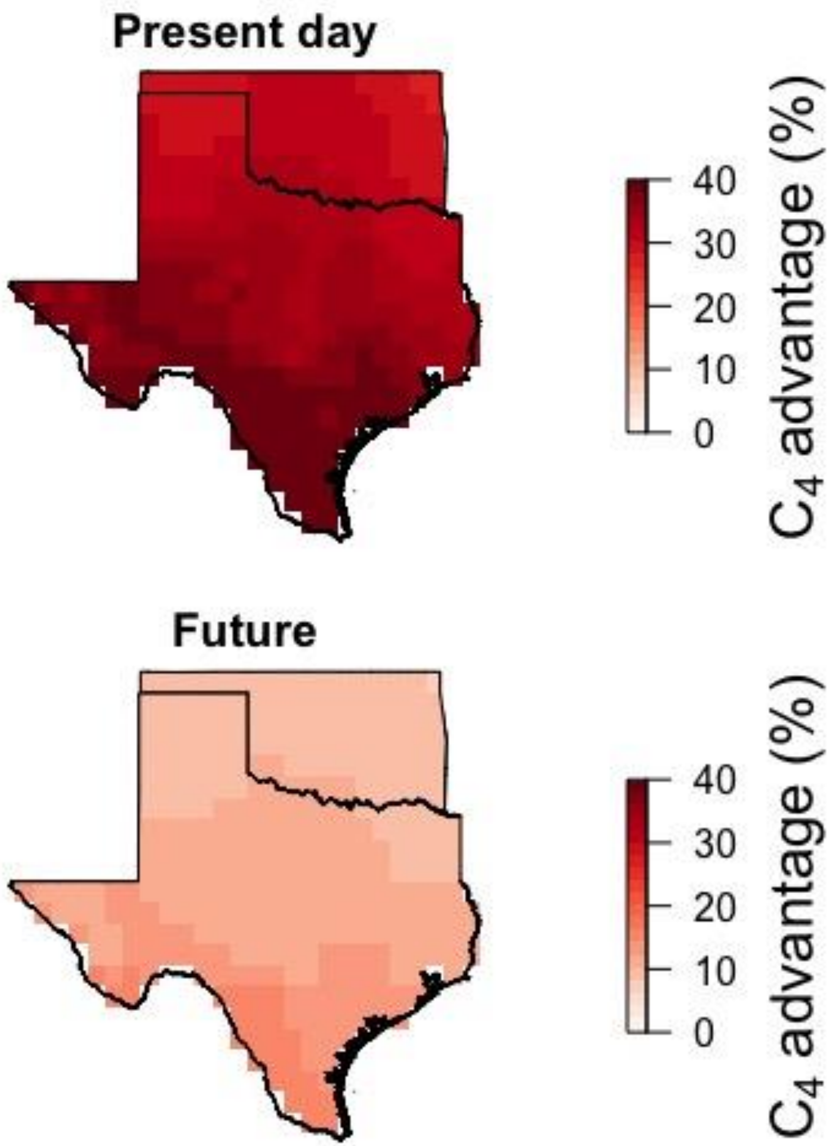


Scott and Smith (2022) *JAMES*



Ansley,… Smith et al. (2023) *Ecosphere*

Relative advantage of C_4 physiology may decrease in the future in the Southern Great Plains



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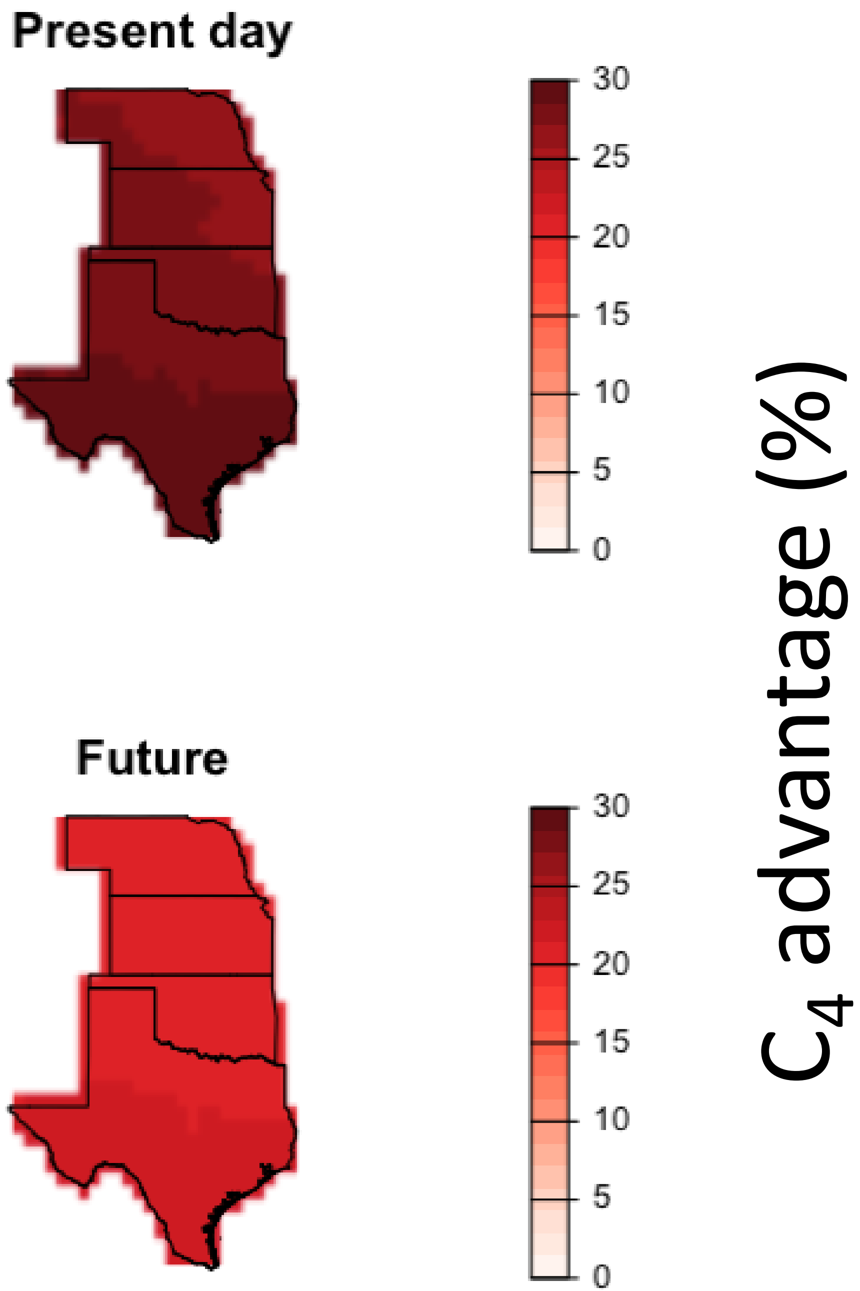
Ansley,… Smith et al. (2023) *Ecosphere*

Similar responses further North

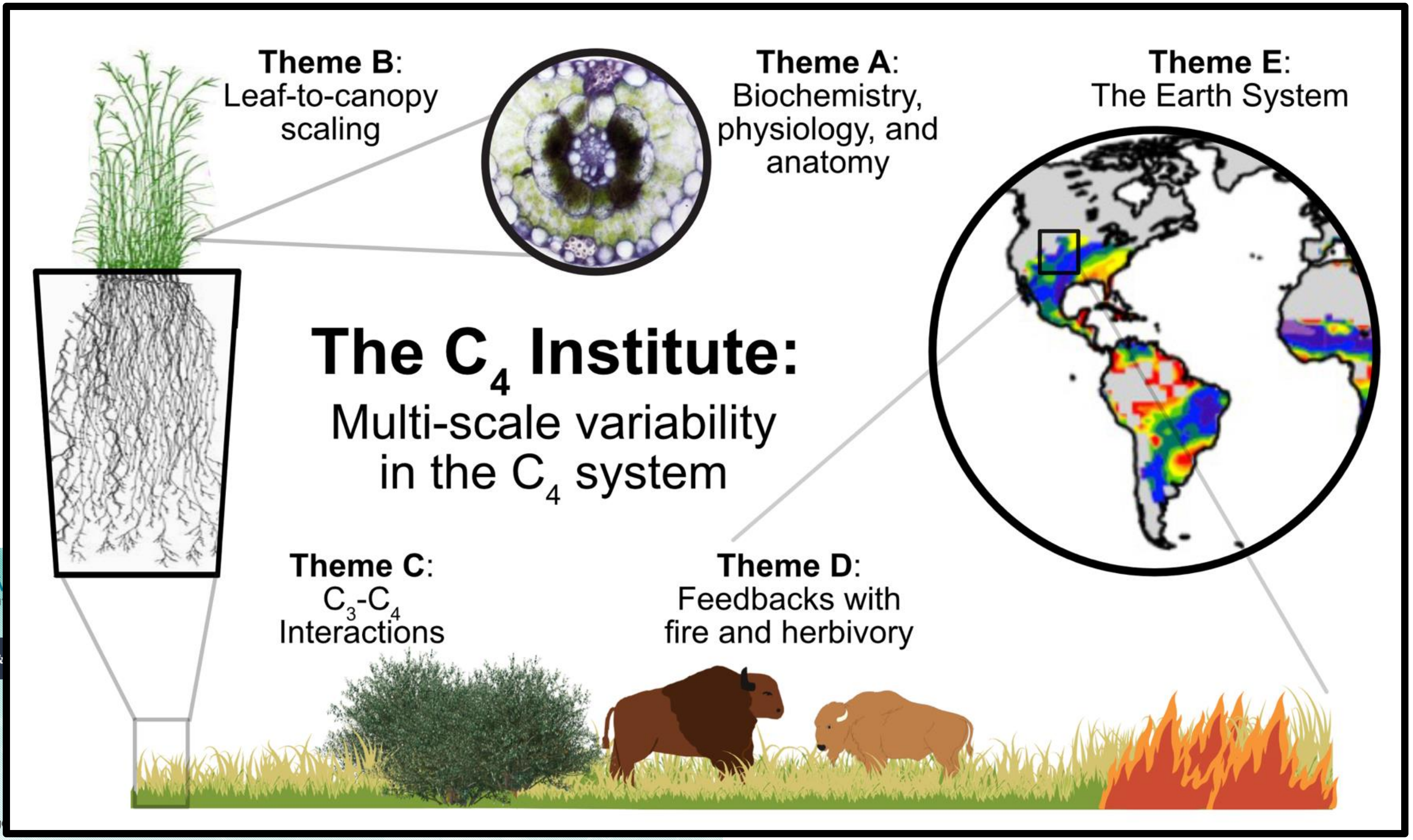


Ansley,… Smith et al. (2023) *Ecosphere*

Question 4: When is C_4 photosynthesis an advantage over C_3 photosynthesis?

C_4 is better in hot, dry, low CO_2 environments

Looking forward: scaling of C_4 biology from cells to biomes



New Phytologist

Tansley review | Free Access

C_4 photosynthesis, trait spectra, and the fast-efficient phenotype

Russell K. Monson, Shuai Li, Elizabeth A. Ainsworth, Yuzhen Fan, John G. Hodge, Alan K. Knapp, Andrew D. B. Leakey, Danica Lombardozzi, Sasha C. Reed, Rowan F. Sage, Melinda D. Smith, Nicholas G. Smith, Christopher J. Still, Danielle A. Way ... See fewer authors

First published: 27 March 2025 | https://doi.org/10.1111/nph.70057

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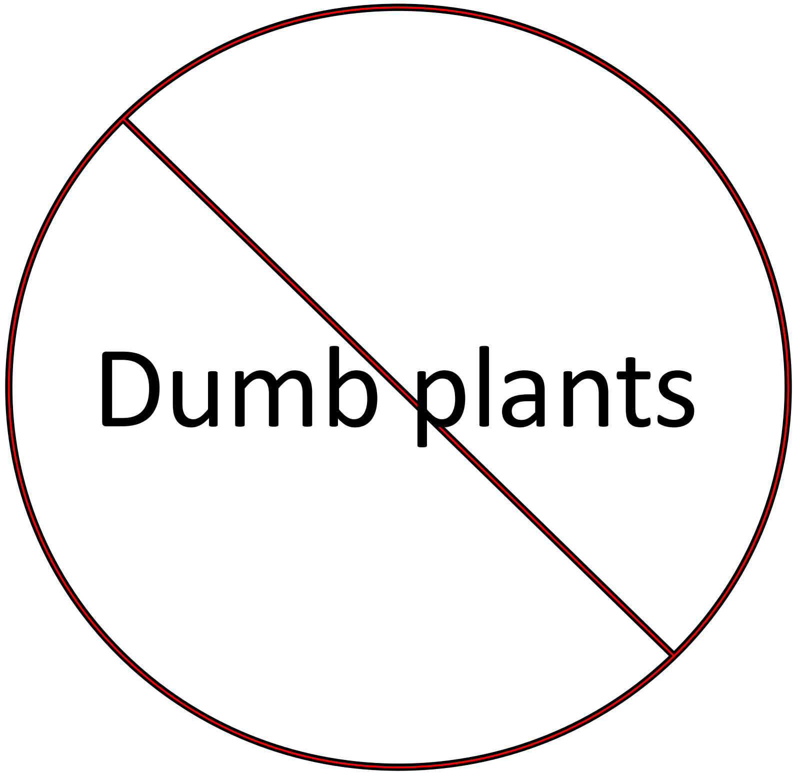
Agency	Agency Tracking Number	Grants.gov Tracking ID	Submitting Institution	Descriptive Title of Project	Status	Status Date	Received Date	Requested Amount
NSF	2525062		Texas Tech University View SAM Legal Business Name	BII: The C4 Institute	Pending	02/19/2025	02/17/2025	$14,981,629

Monson,...Smith et al. (2025) *New Phyt*

Conclusions

Conclusions

- Plants aren't dumb!
  - Assuming plants don't dynamically respond to their environment can lead to poor understanding of ecological functioning from individuals to the Earth system

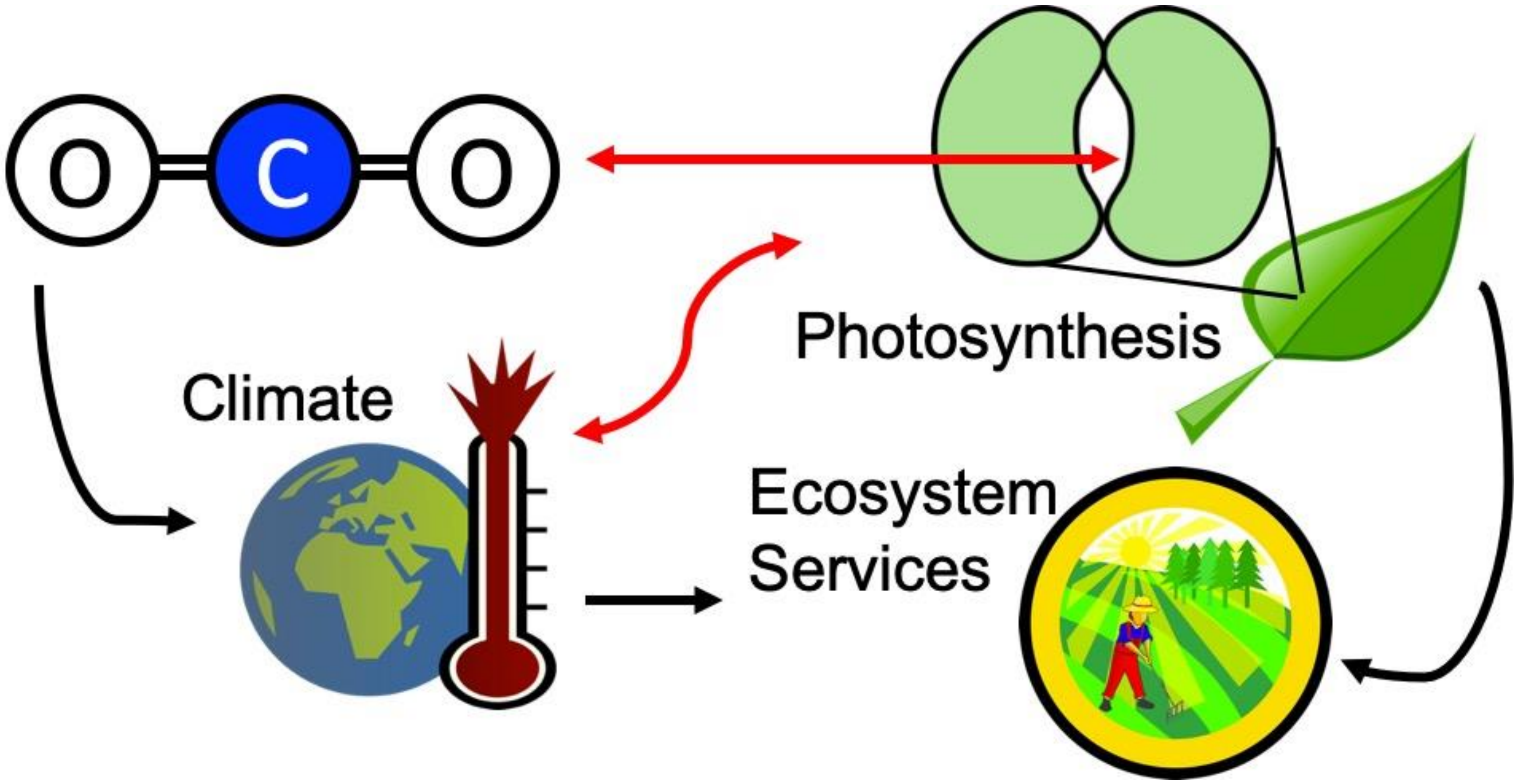


Conclusions

Quantified physiological theory can:

1. Improve mechanistic understanding of physiological processes that underlie higher level responses
2. Produce more reliable future projections

And ultimately lead to a better understanding of how future ecosystem services will be impacts by global change



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

Data and code:
www.github.com/SmithEcophysLab
www.smithecophyslab.com/data

Contact: nick.smith@ttu.edu

Botanical Scaling

Core of ongoing and future projects

IntBio (Funded)
CAREER (Funded)
BII (In Review)

nutrient network

Interdisciplinary Science

Atmo., Physics, Chemistry, Media & Coms

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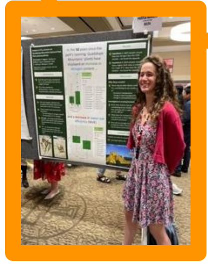
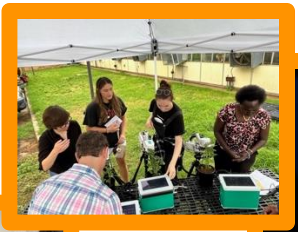
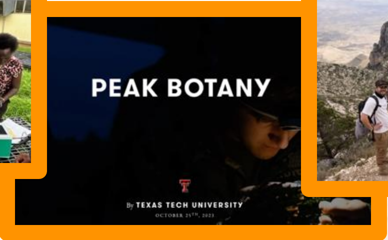
BIOL 1401

Lab Manual
CURE: Plants and Global Change

Nick Smith, PhD
Texas Tech University







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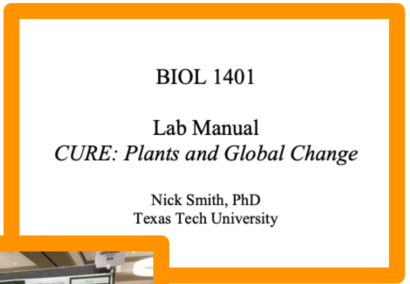
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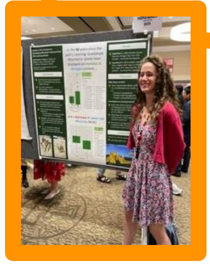

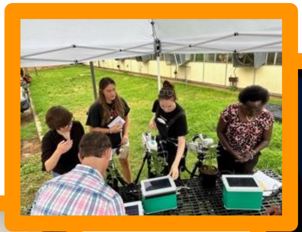

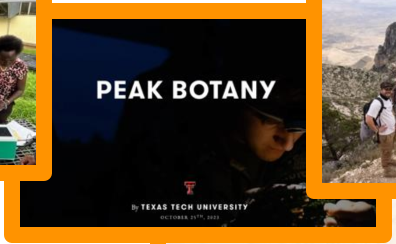

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