Plants aren’t dumb

Using optimality theory to understand big questions in plant ecophysiology

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Why do people care about plants?

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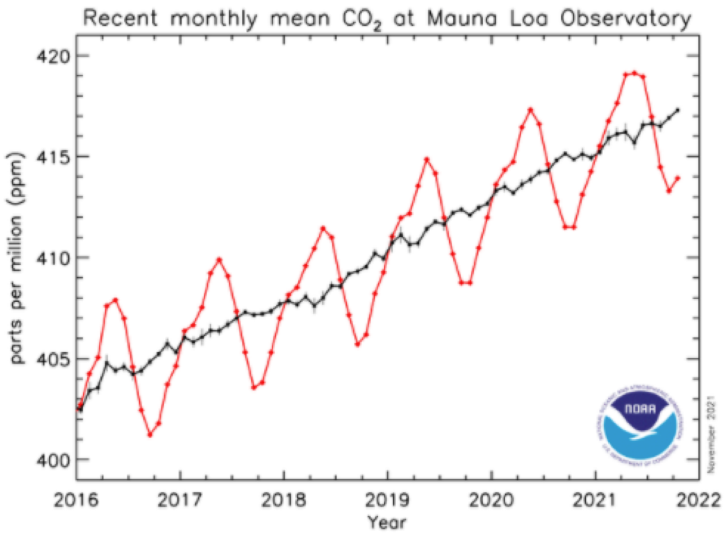


In other words: plants provide ecosystem services

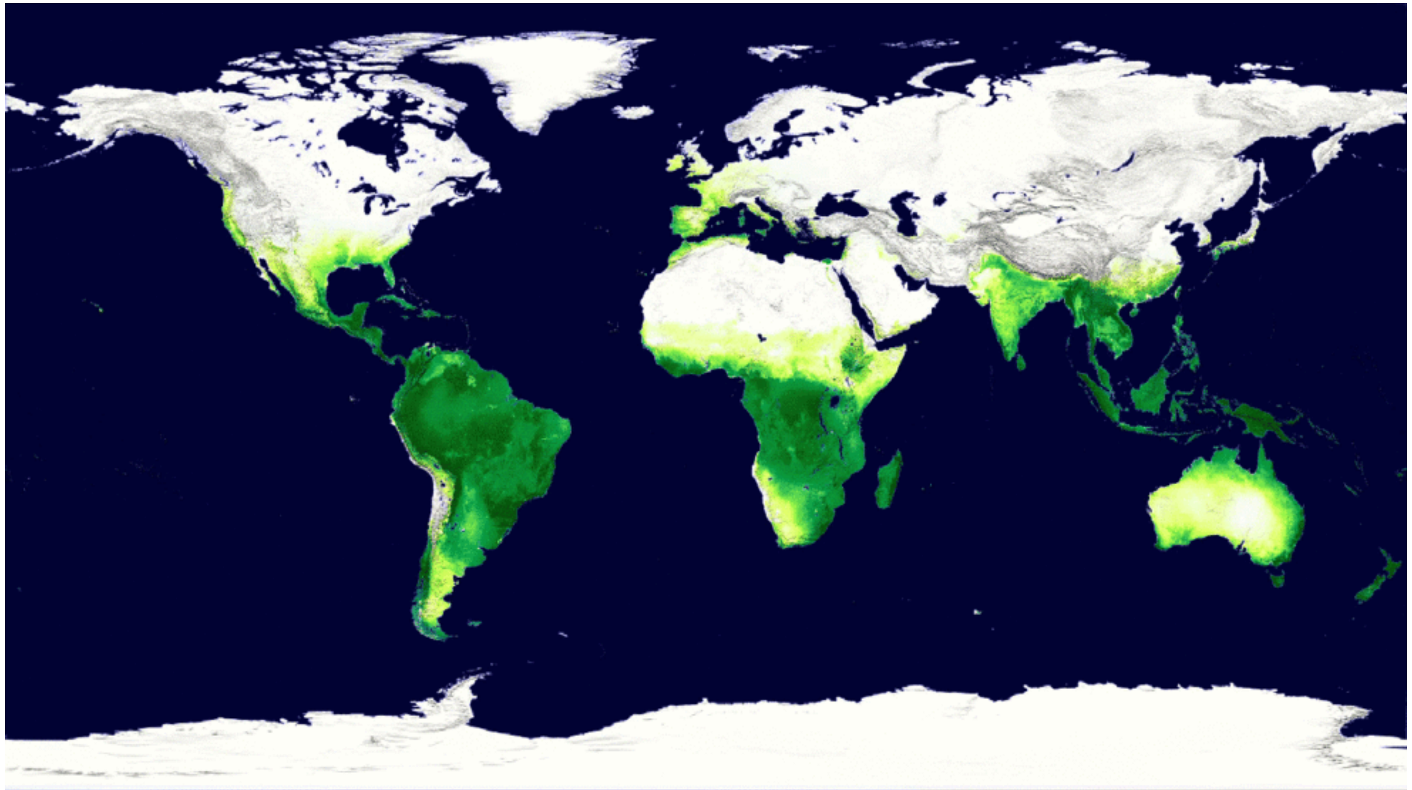
Including photosynthesis

FNAL

Photosynthesis provides the foundation for other services

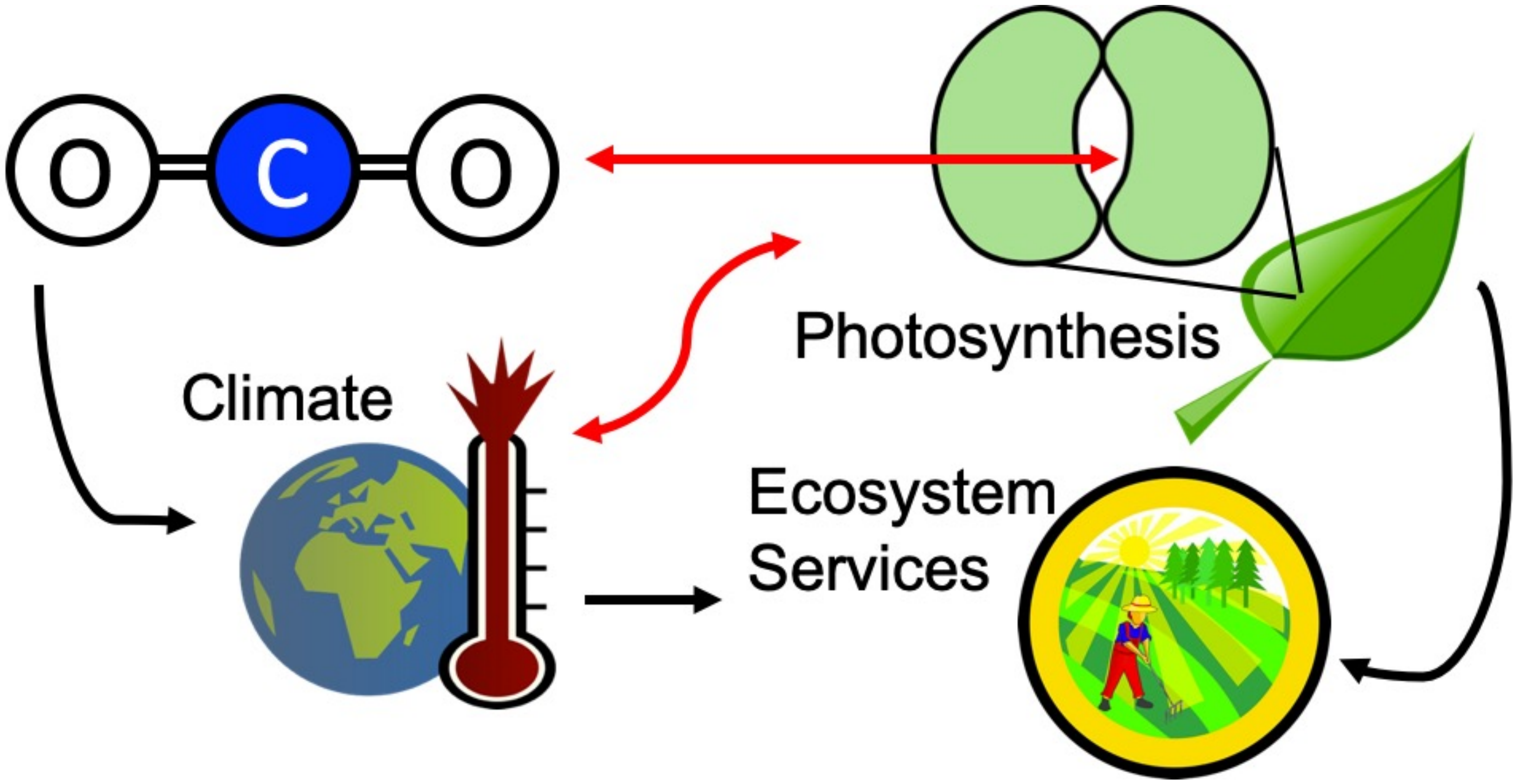
FNAL

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



Photosynthesis is important! An example…

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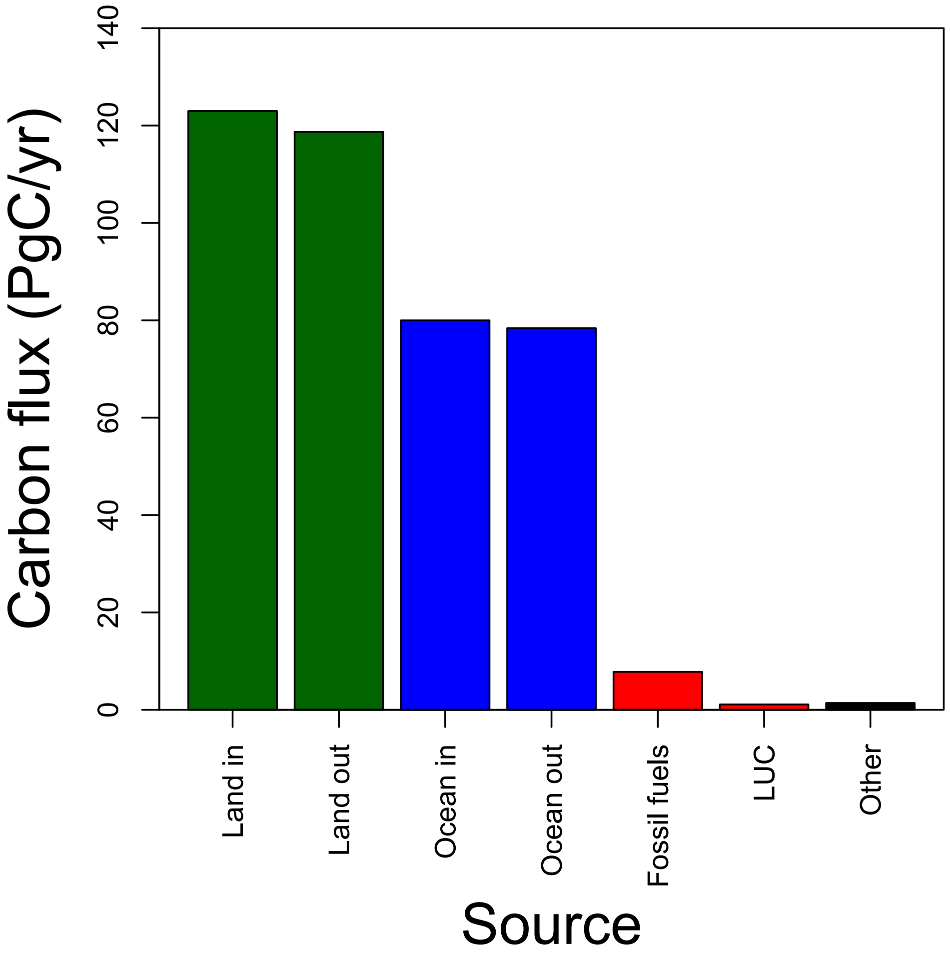
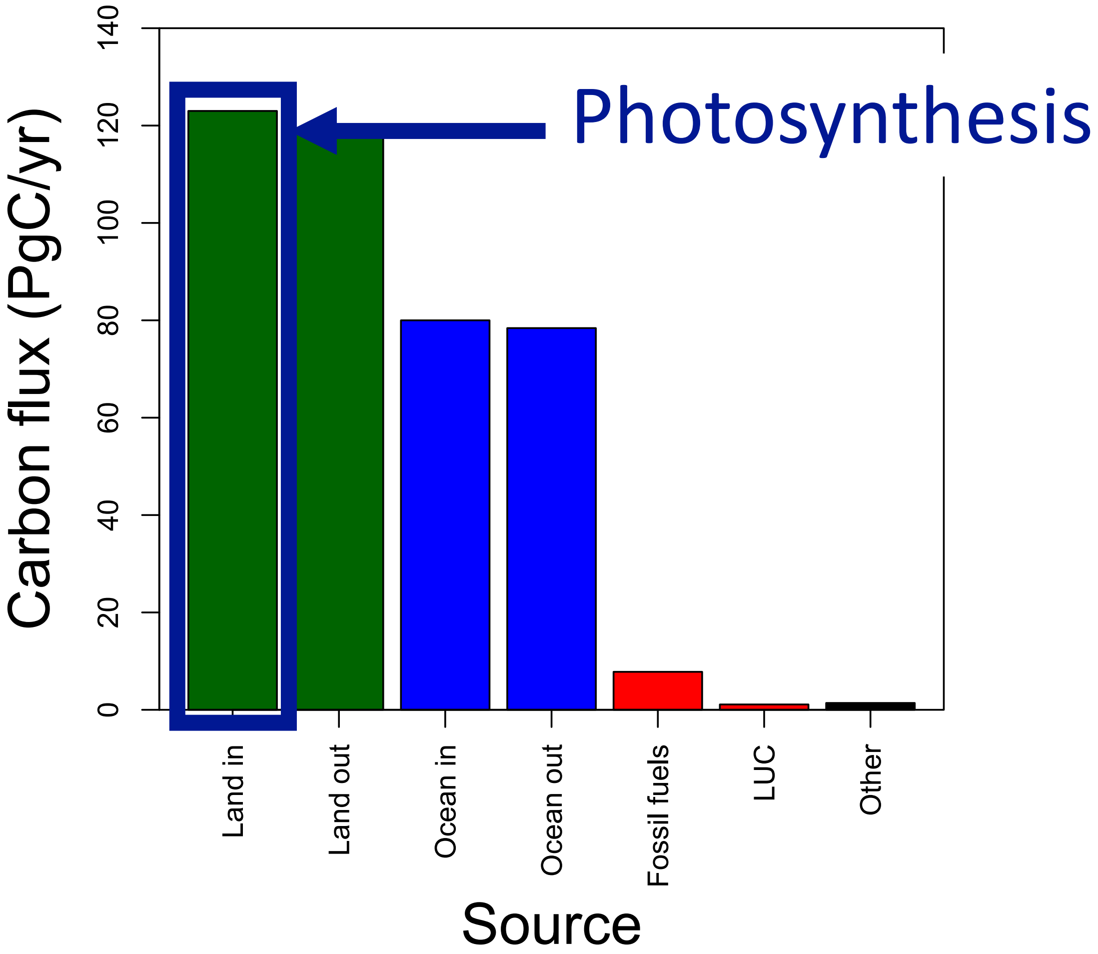


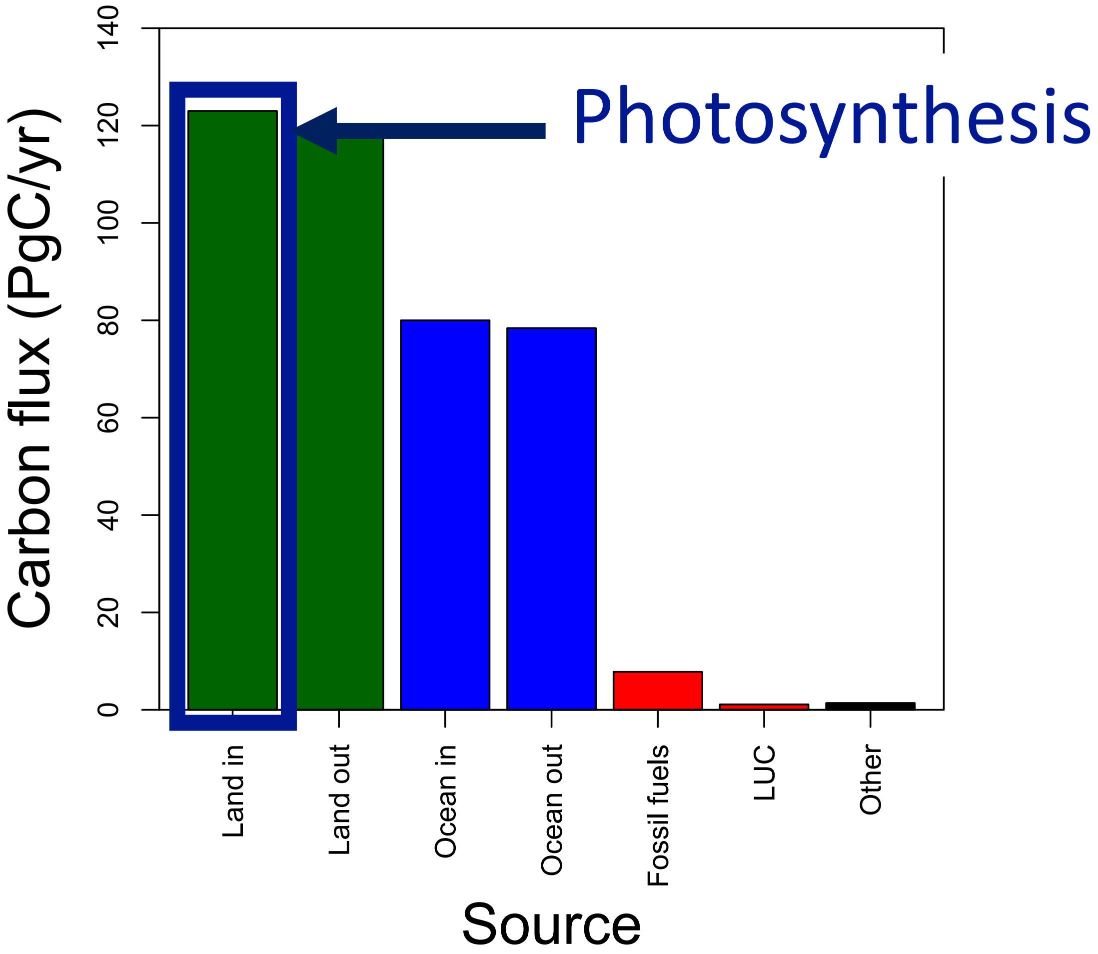
Data from IPCC (2013)

Photosynthesis is important! An example…



Data from IPCC (2013)

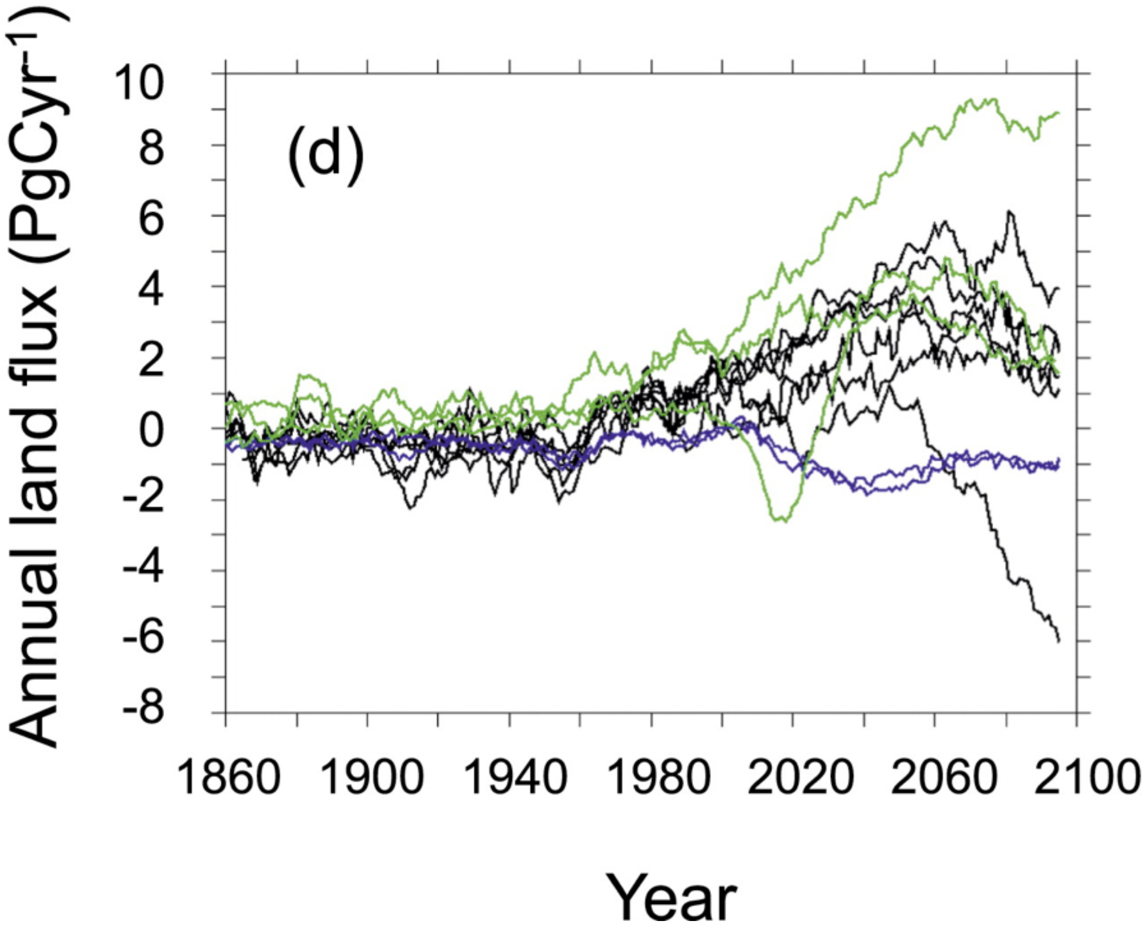
Photosynthesis is important! An example…



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

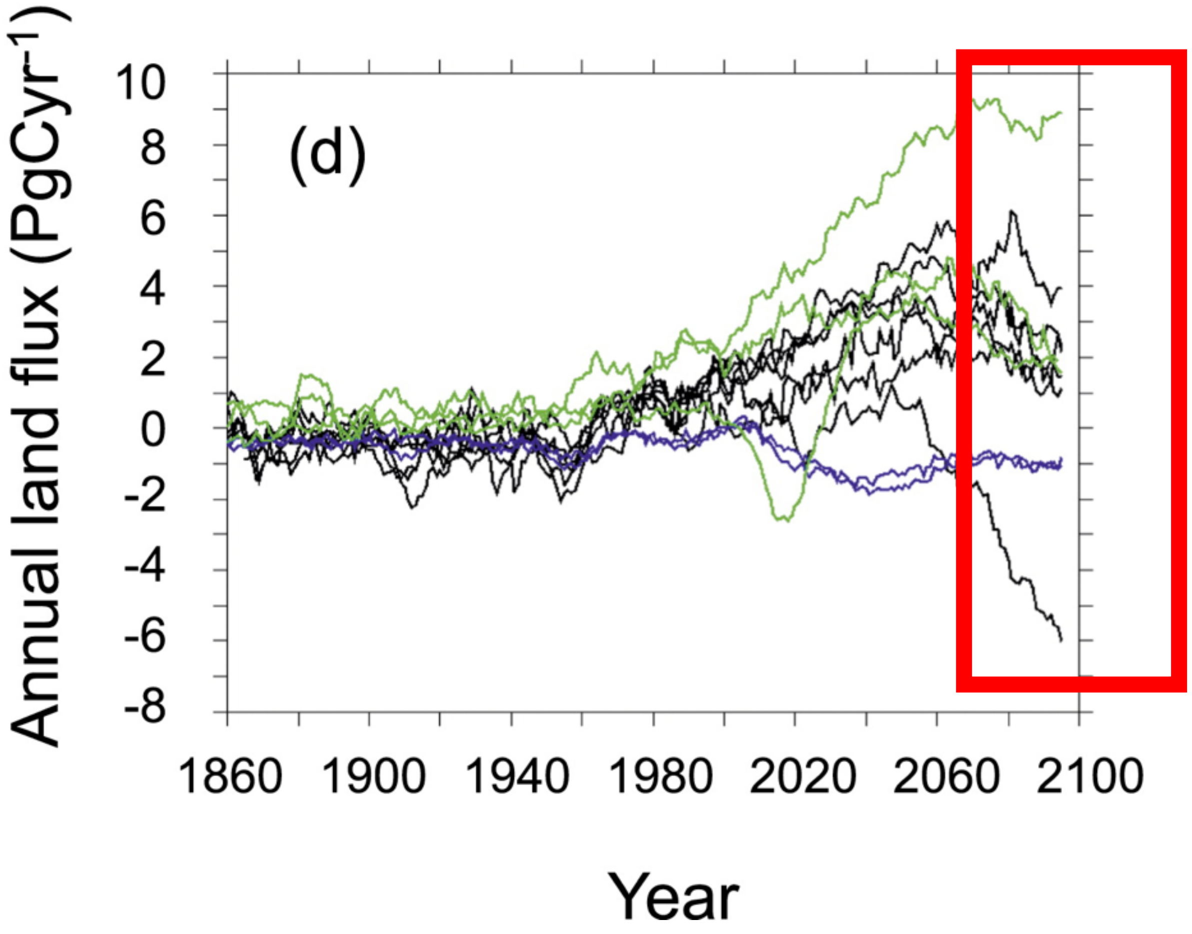
Data from IPCC (2013)

But predictions are uncertain!



Friedlingstein et al. (2014)

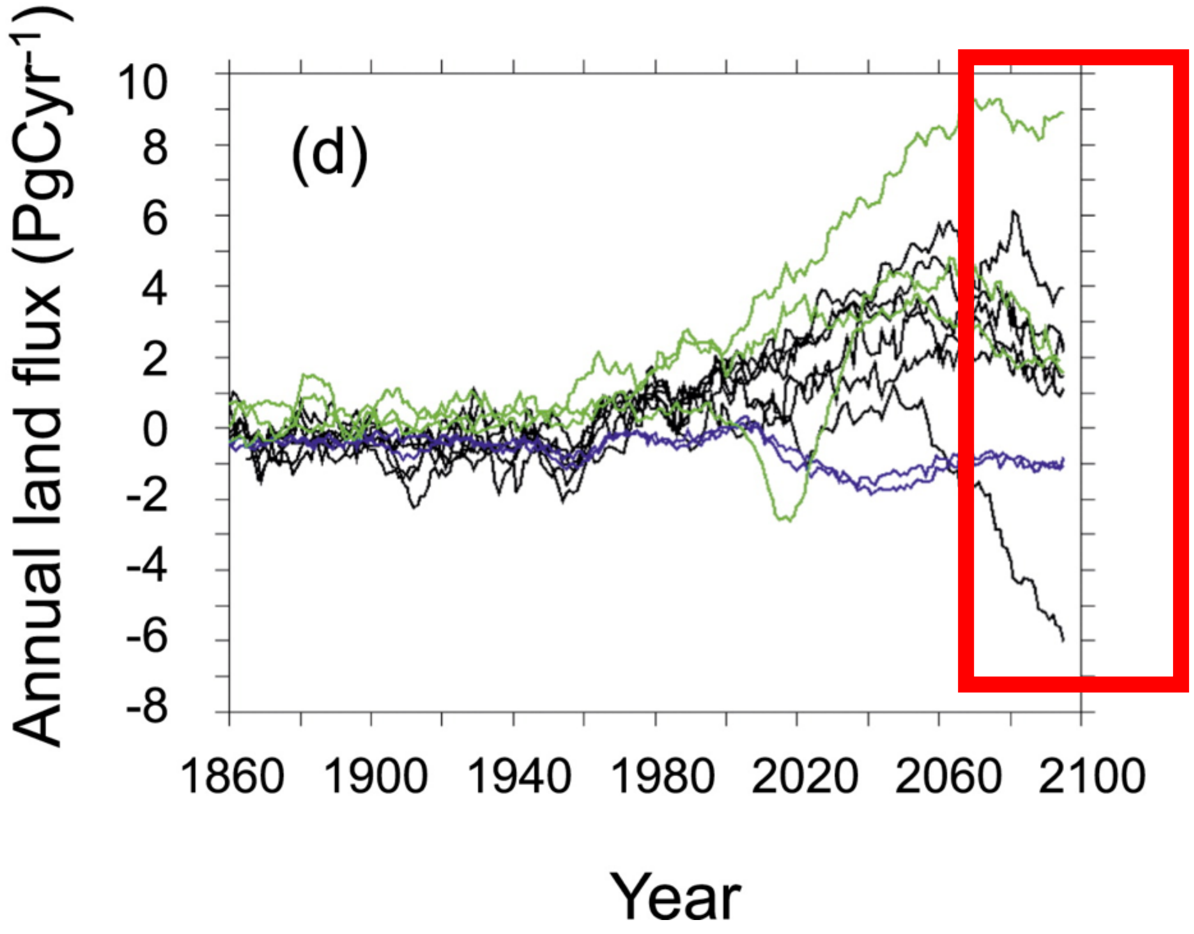
But predictions are uncertain!



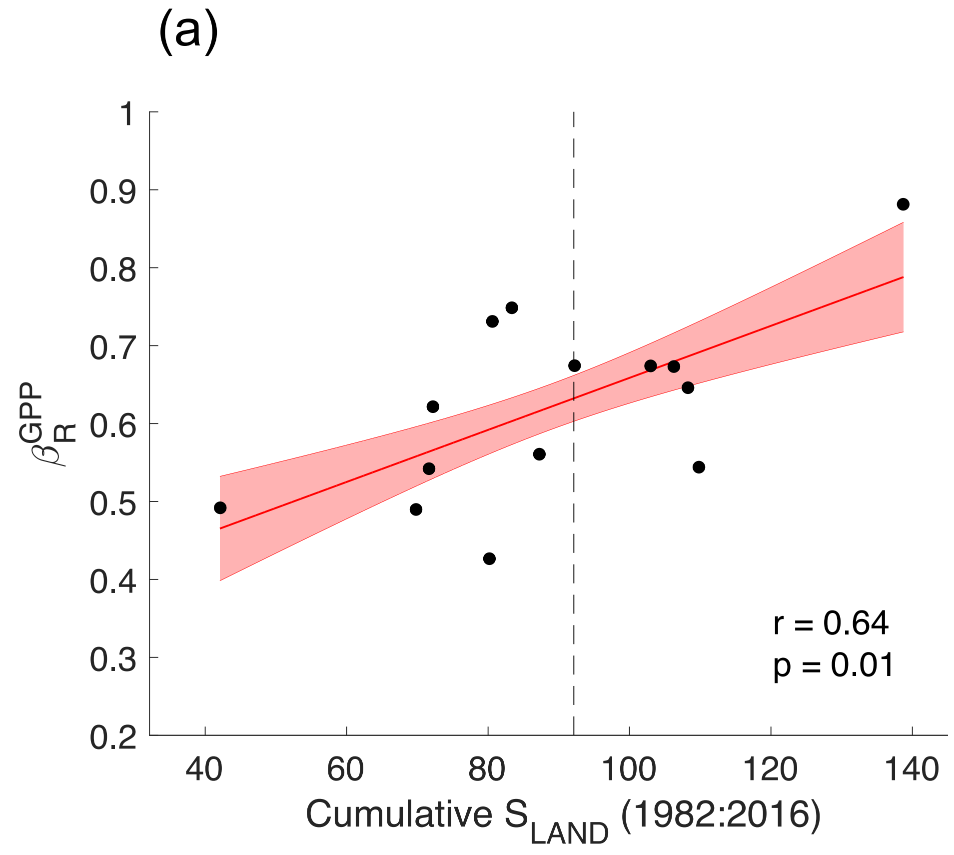
Future model uncertainty (14 Pg) > current fossil fuel emissions (9.5 Pg)

Friedlingstein et al. (2014)

This uncertainty is driven by uncertainty in photosynthesis



Friedlingstein et al. (2014)



Keenan et al. (in prep)

Why the uncertainty? Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

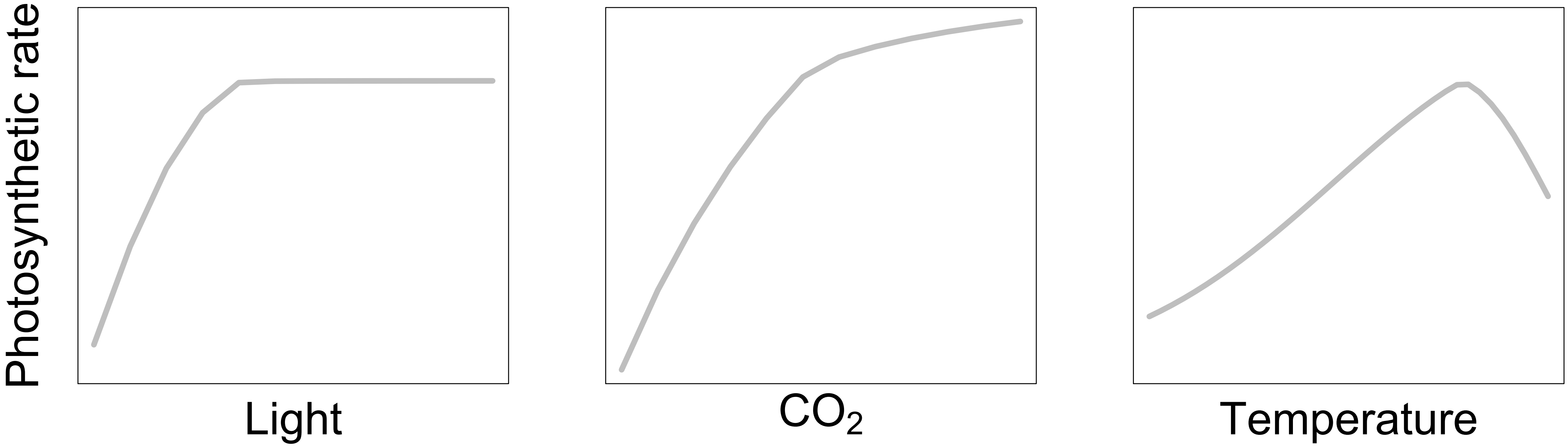
Planta

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

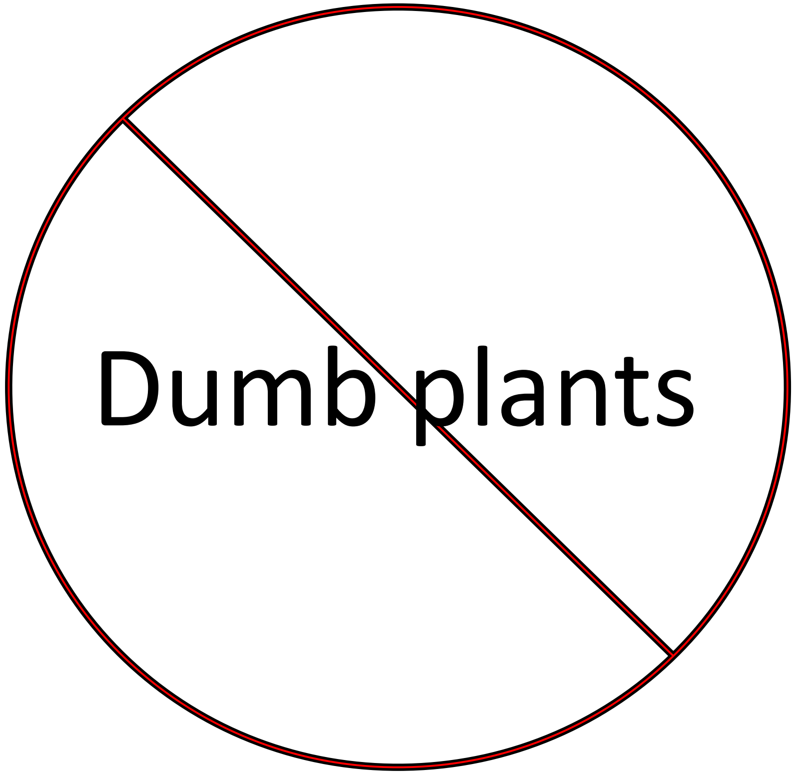
G.D. Farquhar[1], S. von Caemmerer[1], and J.A. Berry[2]

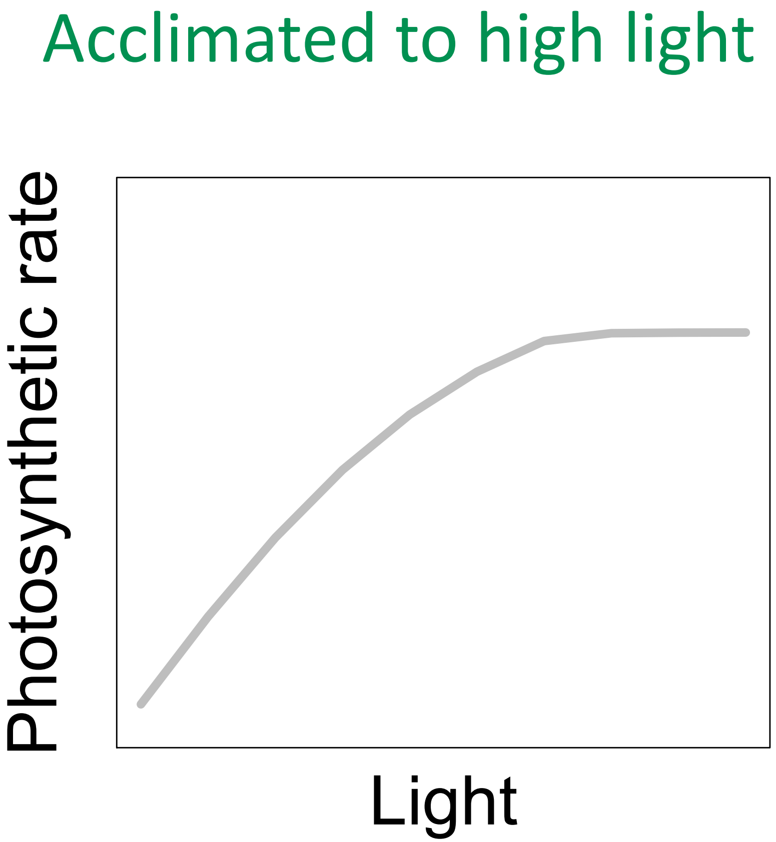
[1] Department of Environmental Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City ACT 2601, Australia and
[2] Carnegie Institution of Washington, Department of Plant Biology, Stanford, Cal. 94305, USA

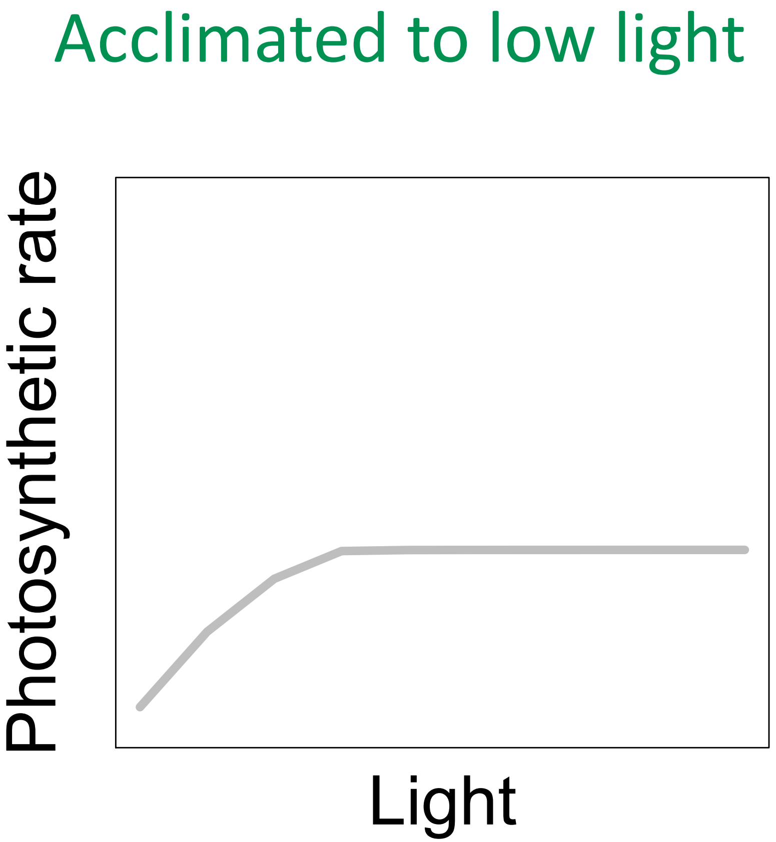
These produce short term responses that match data



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


Dumb plants


Acclimated to high light
Photosynthetic rate
Light


Acclimated to low light
Photosynthetic rate
Light

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)

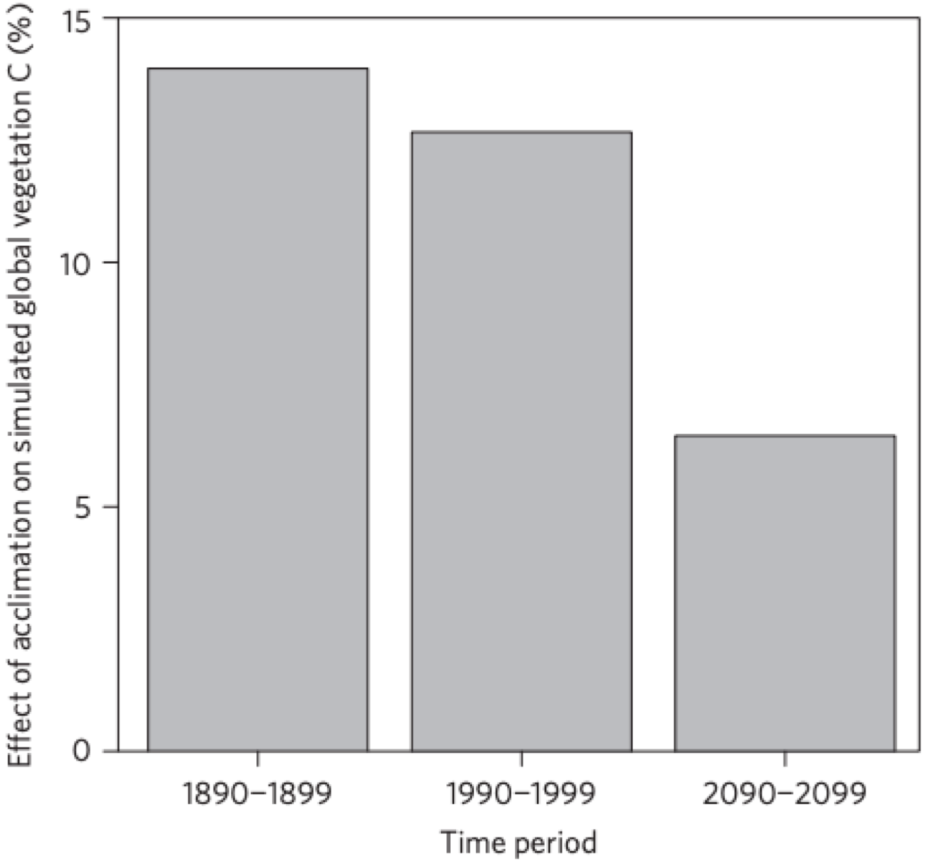
Ann. Rev. Plant Physiol. 1980. 31:491–543

PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

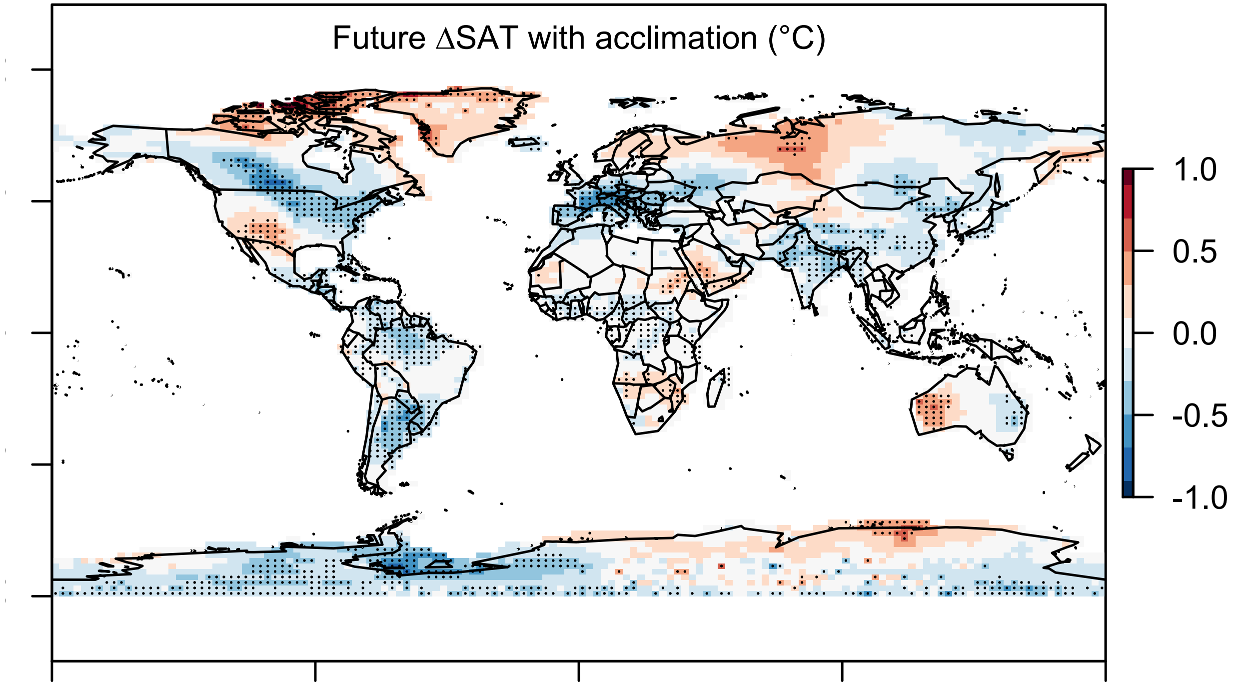
Joseph Berry and Olle Björkman[1]

…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*

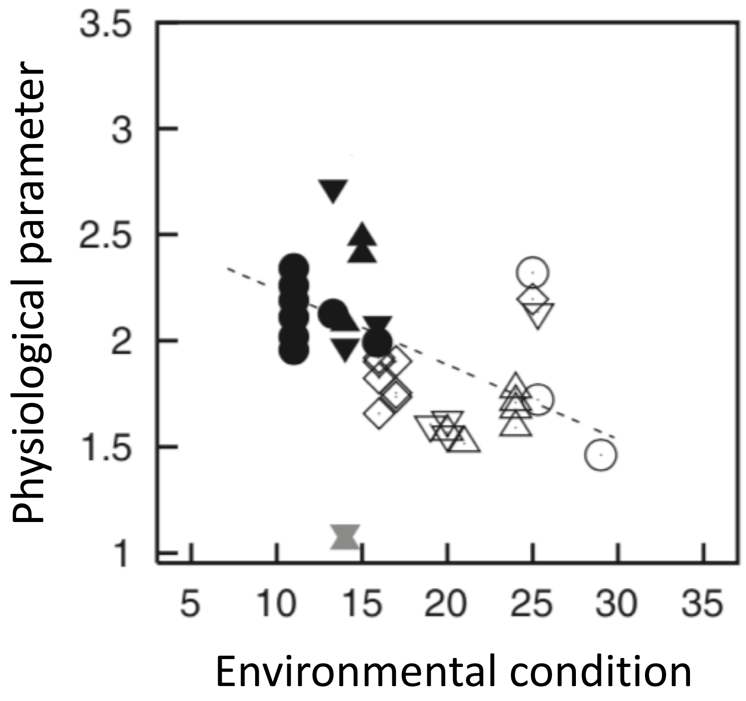
Smith et al. (2017) *JAMES*

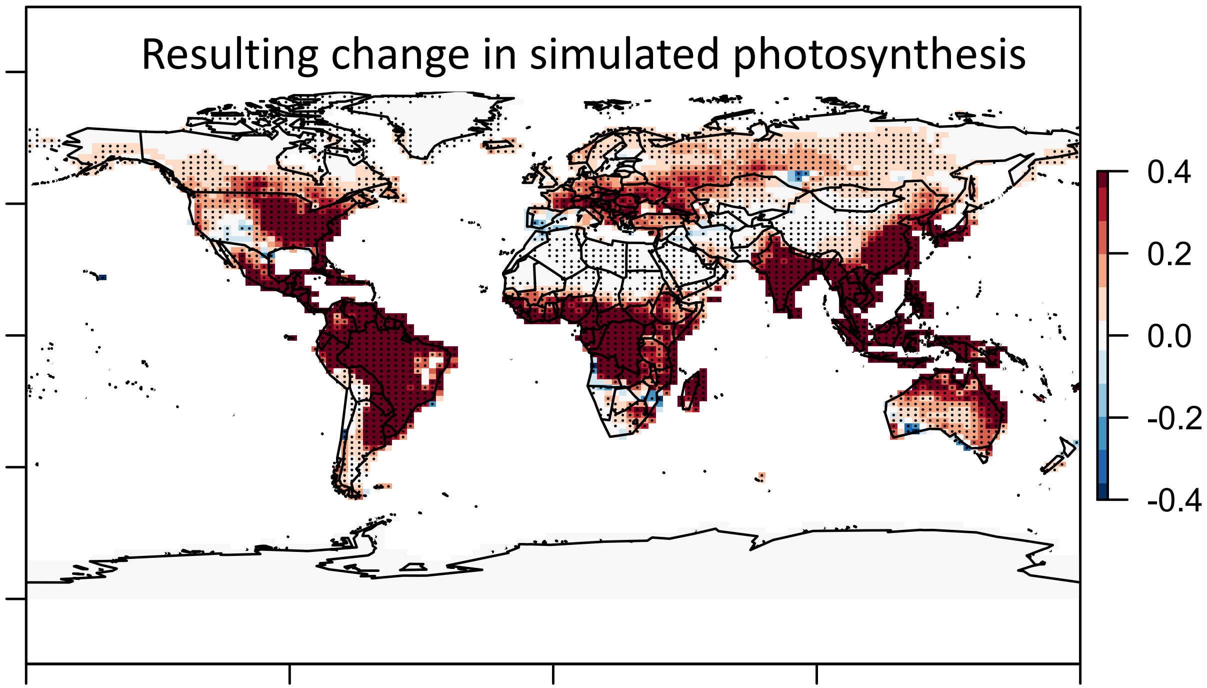
Unfortunately,
no theoretical model for photosynthetic acclimation exists

Lack of theory results in…

Lack of theory results in…

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



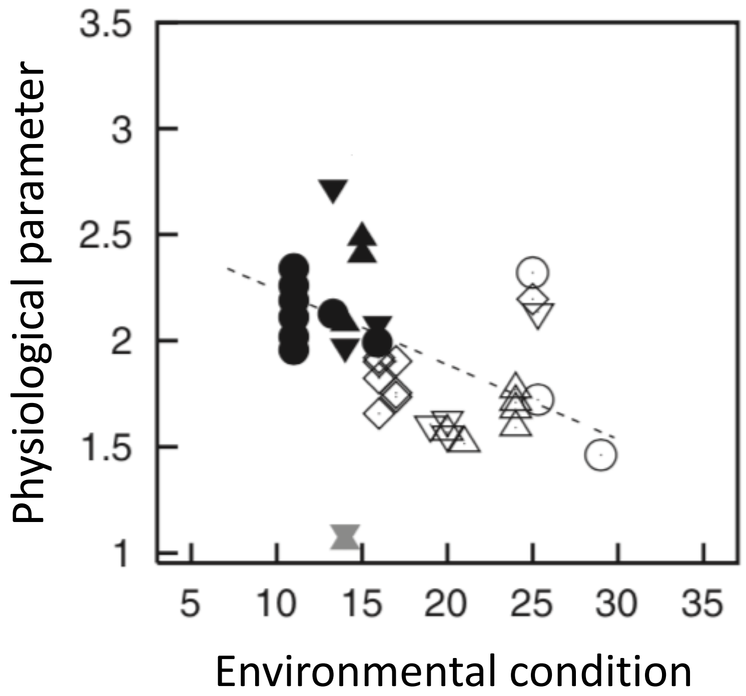


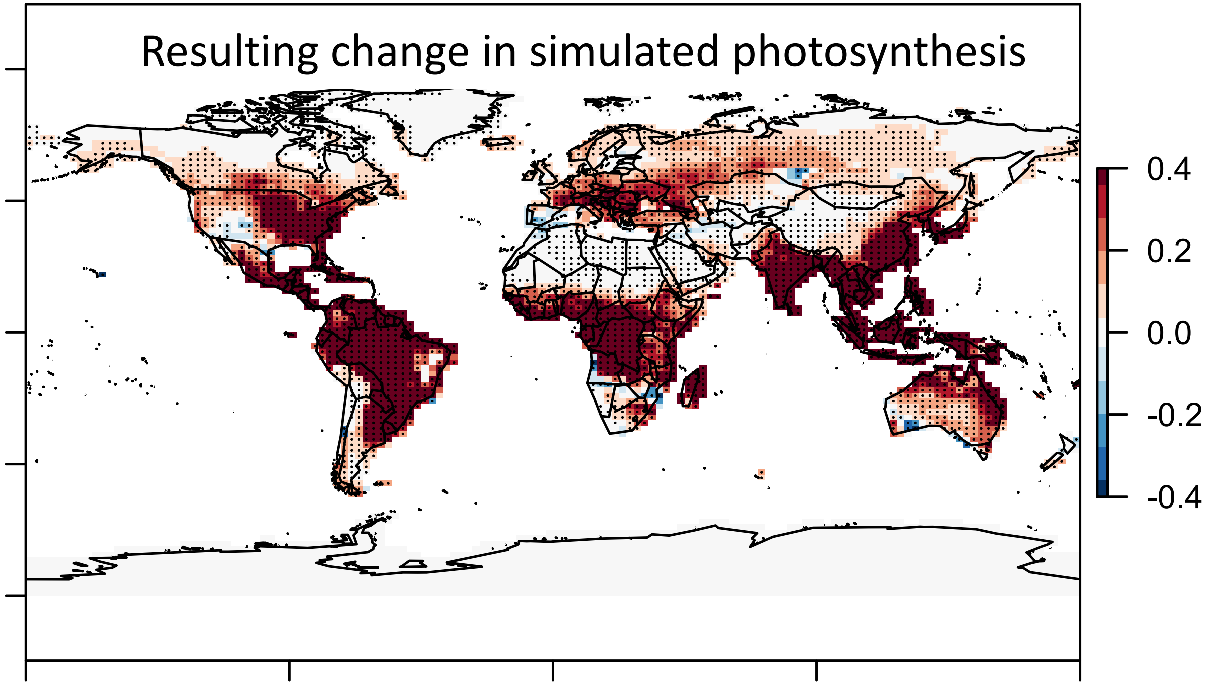
Kattge and Knorr (2007) *PC&E*

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*

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)

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)

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}

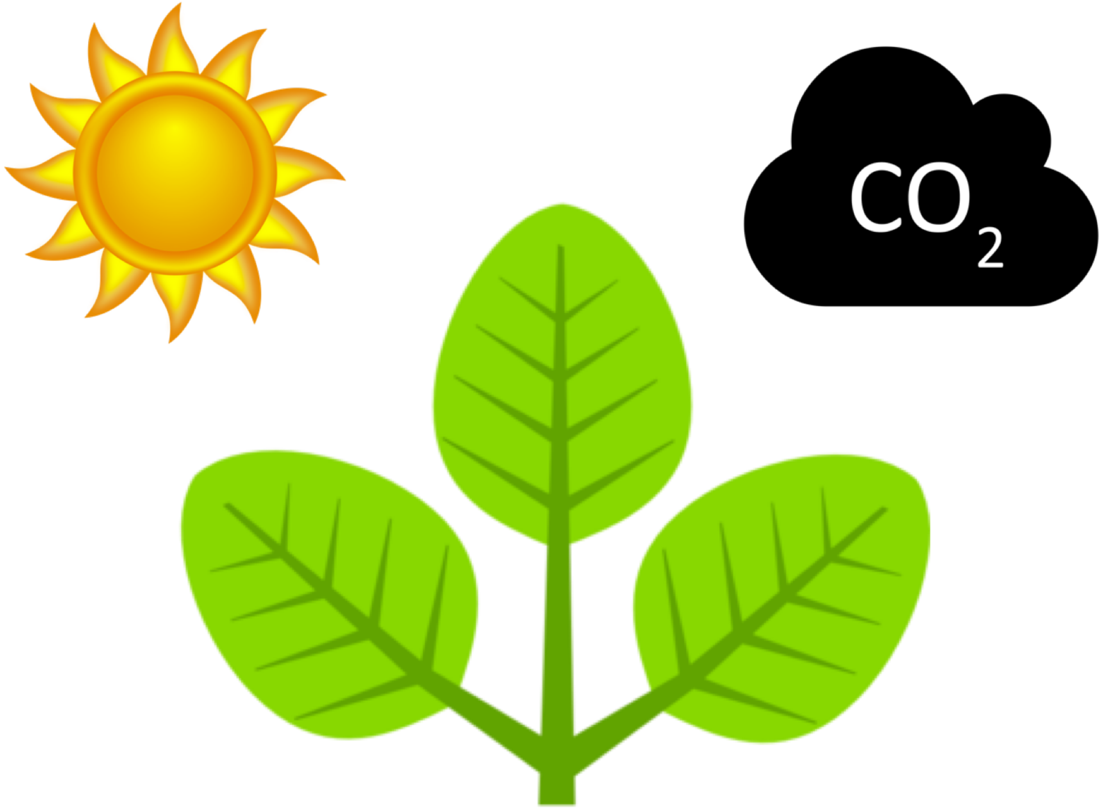
[TALK TO ME LATER ABOUT THIS IF YOU ARE INTERESTED]

Prentice et al. (2014); Wang et al. (2017); Smith et al. (2019)

Optimal photosynthesis

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

Biochemistry optimization

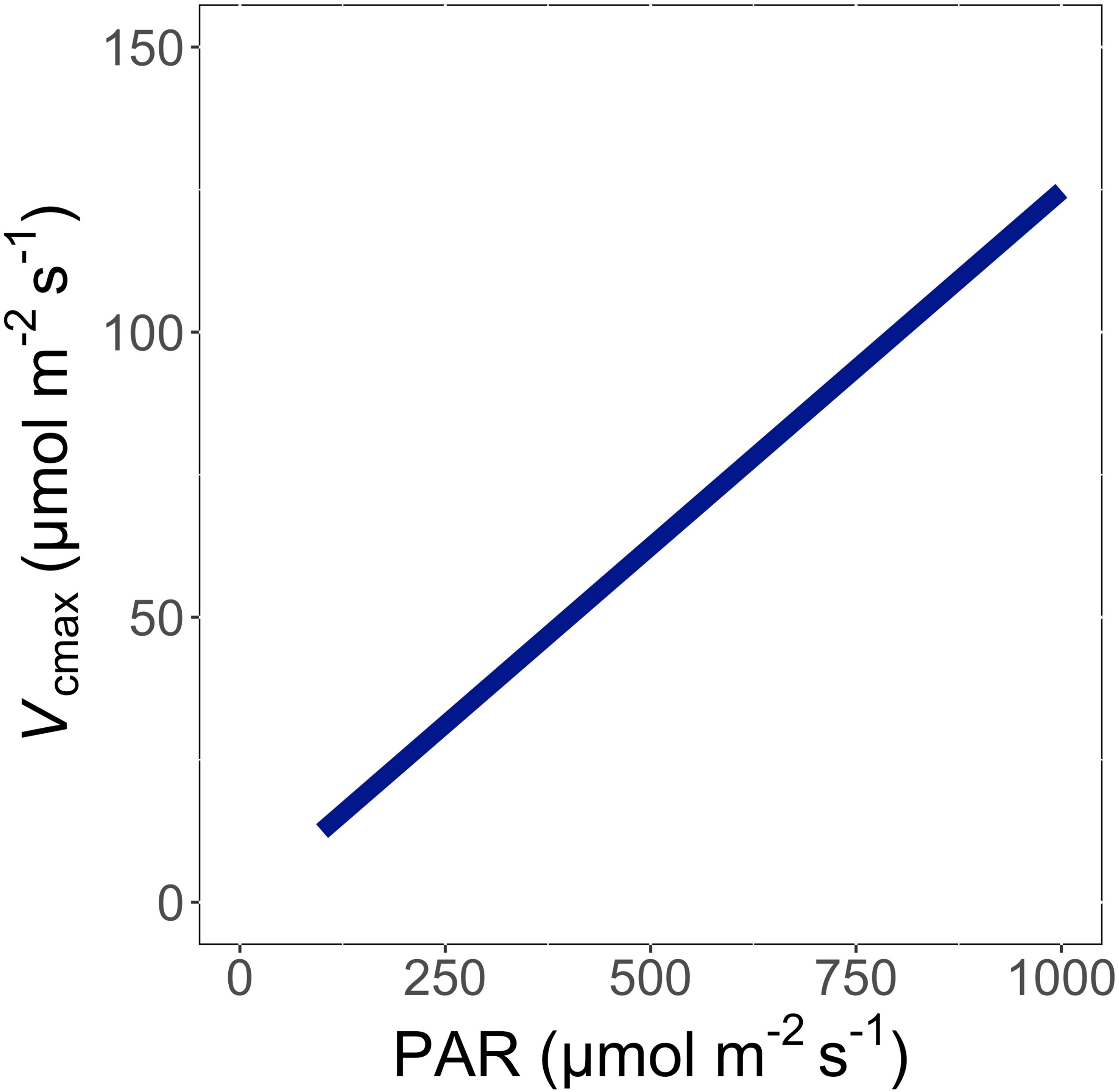


Plant biochemistry setup will aim for equal limitation by all factors

[TALK TO ME LATER ABOUT THE MATHS]

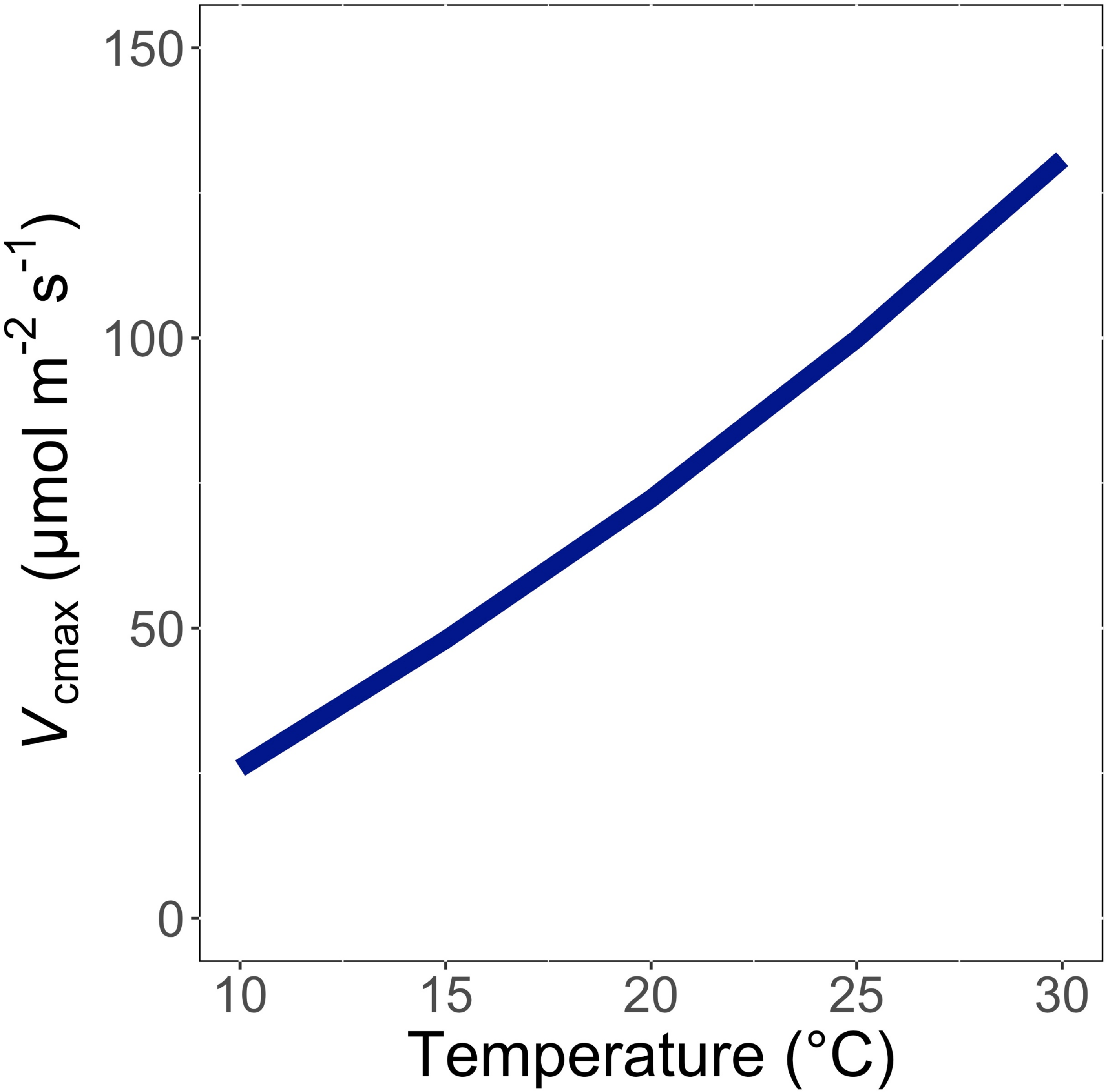
Biochemistry trait

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



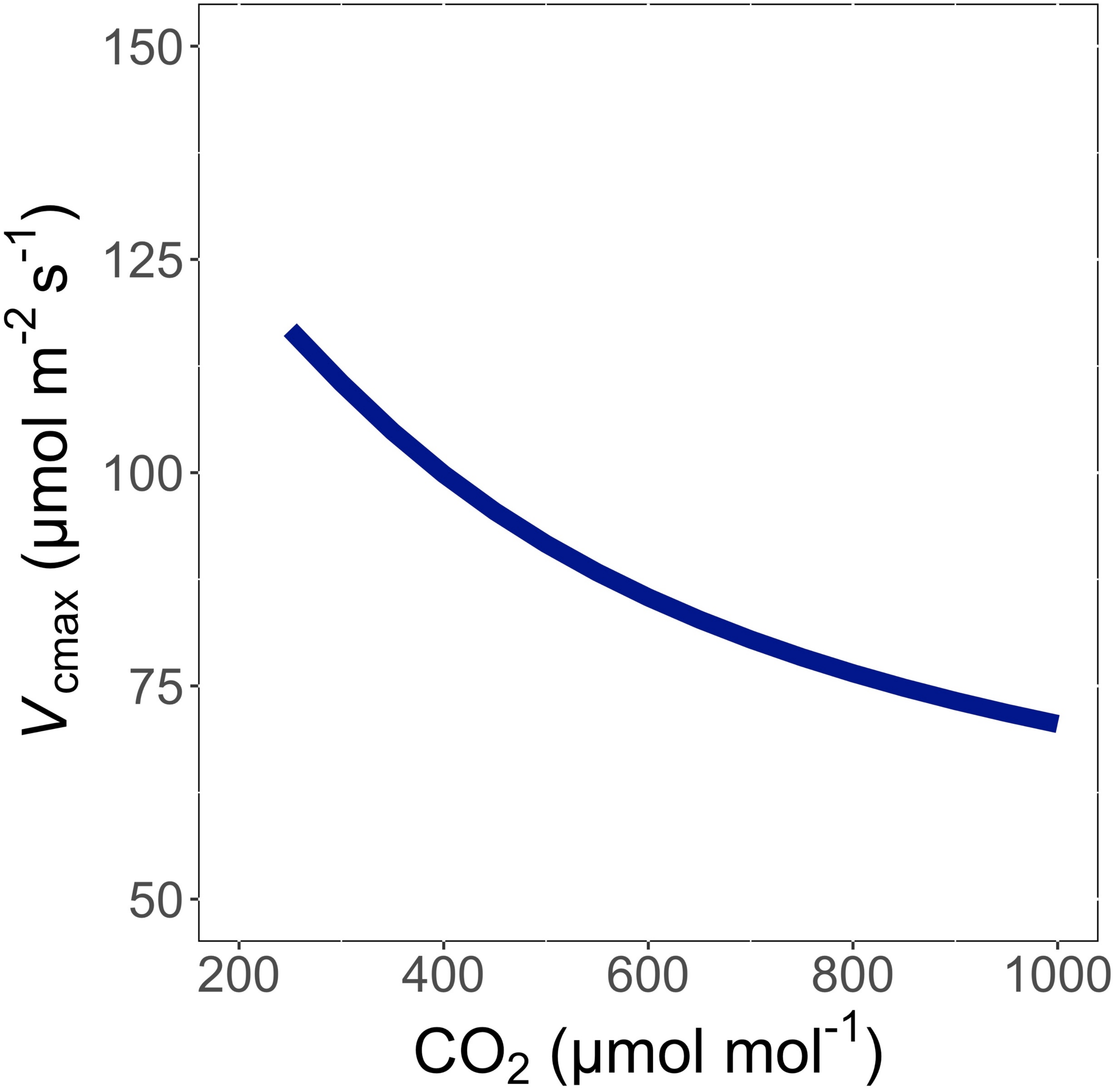
V_{cmax} increases with light because of greater electron transport

Smith et al. (2019); Smith and Keenan (2020)



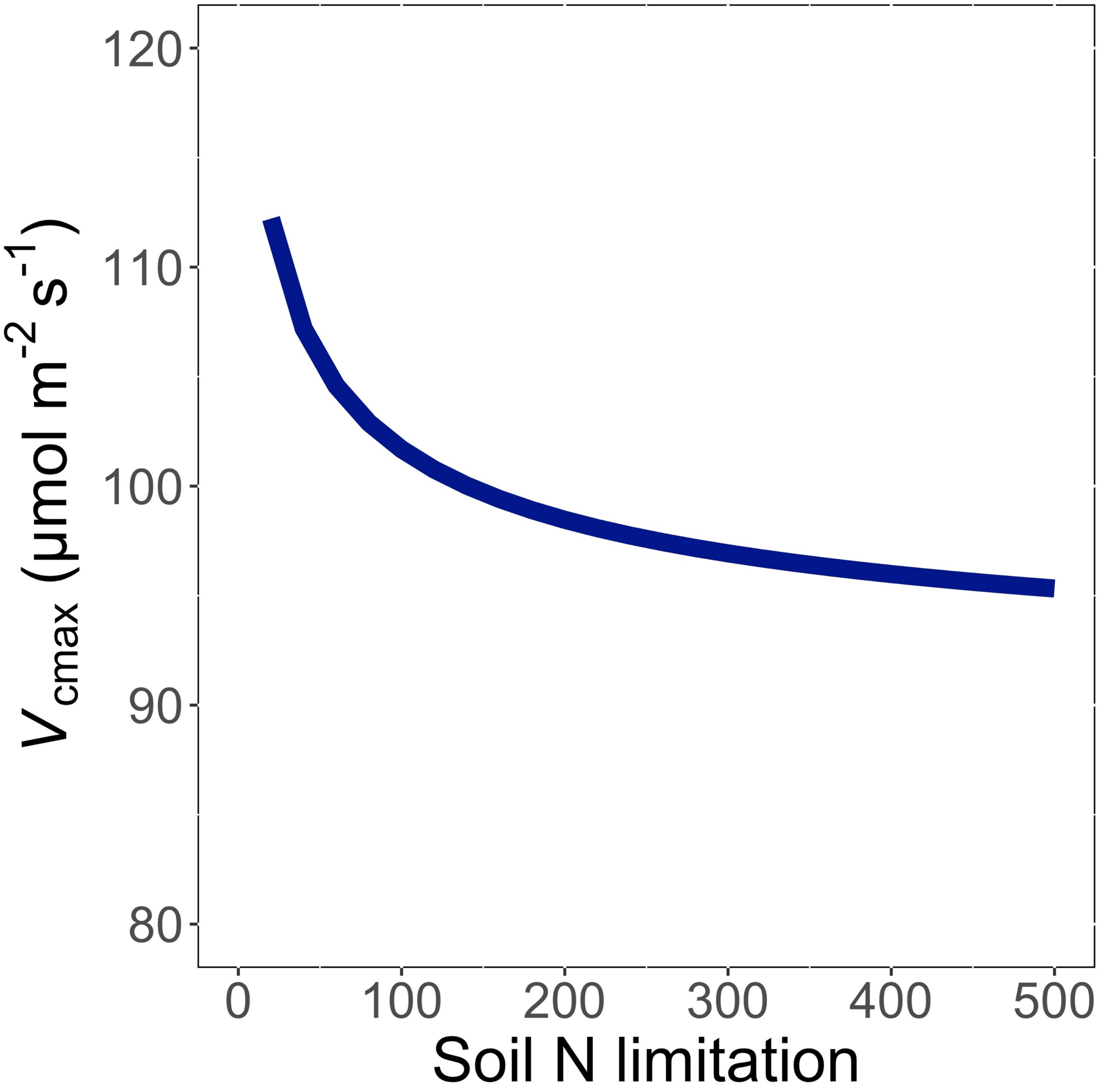
V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019); Smith and Keenan (2020)



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

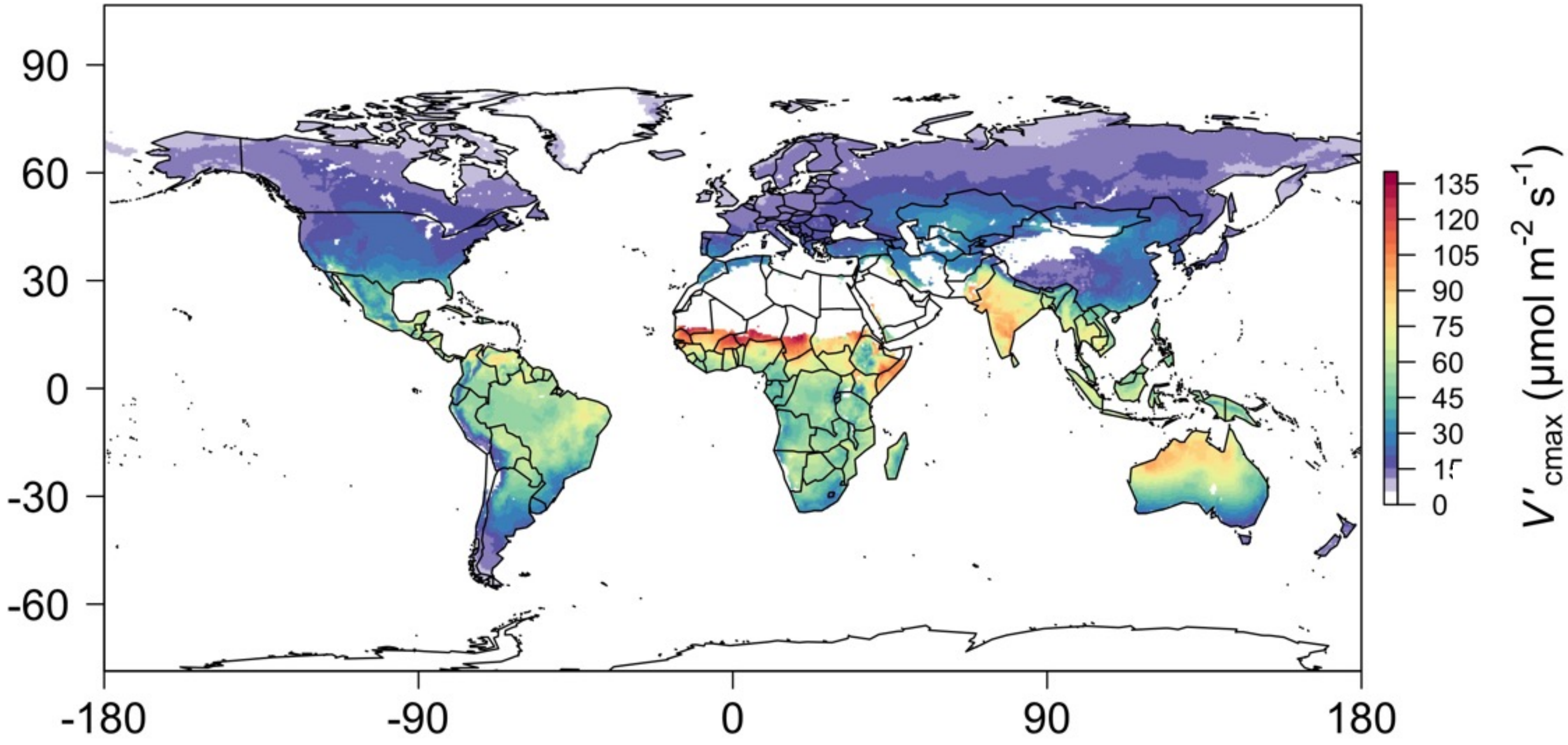
Smith et al. (2019); Smith and Keenan (2020)



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

Smith et al. (2019); Smith and Keenan (2020)

We can predict optimal traits in different environments



Smith et al. (2019)

Ok, great, but now what?

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

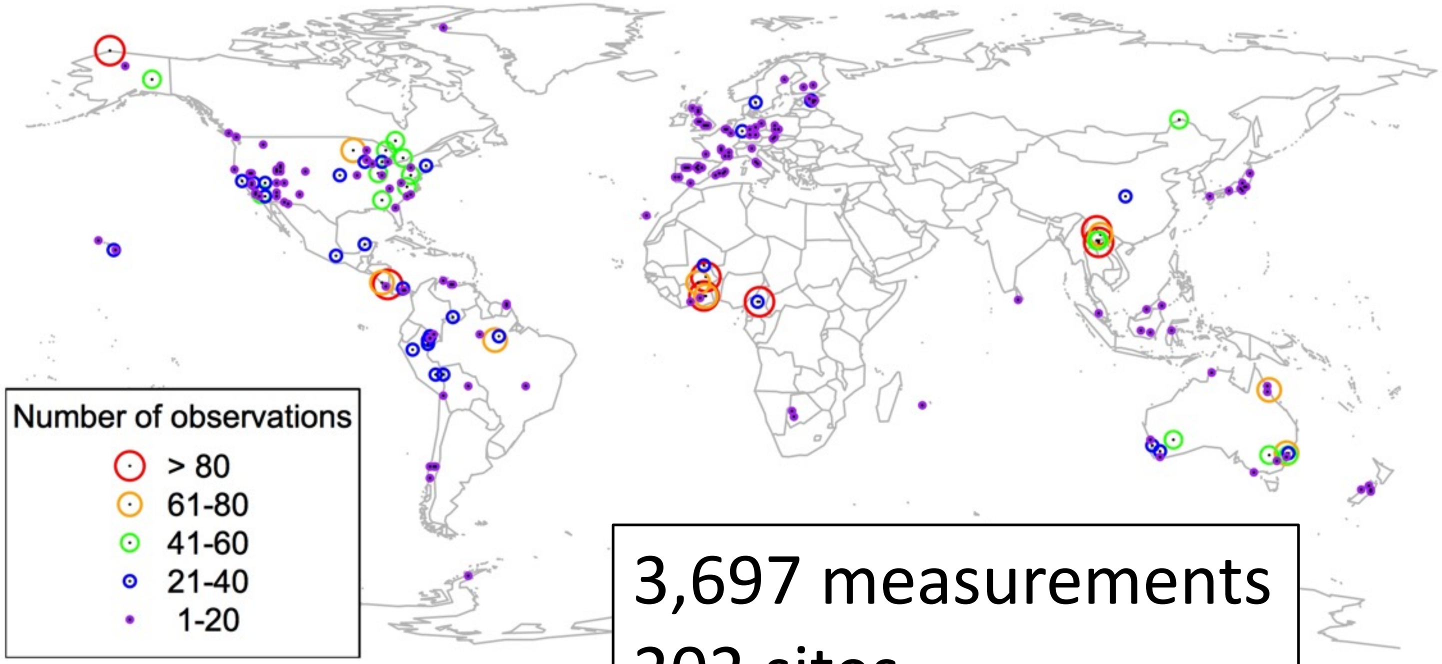
Let’s tackle some big questions in plant ecophysiology!

Big questions

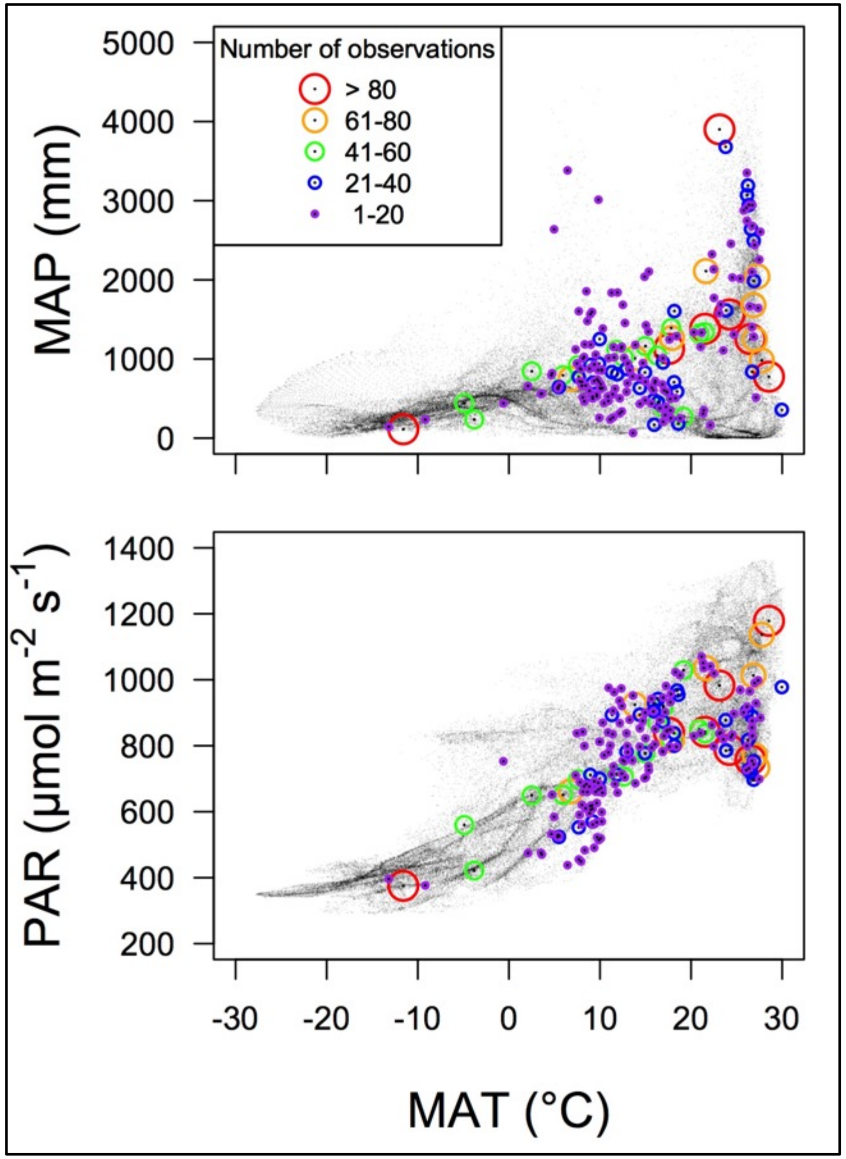
1. Is photosynthesis optimized to the environment?
2. How do plants acclimate to soil nitrogen?
3. What does acclimation mean for future terrestrial biogeochemical cycling?
4. When is C_4 photosynthesis an advantage over C_3 photosynthesis?

Question 1: Is photosynthesis optimized to the environment?

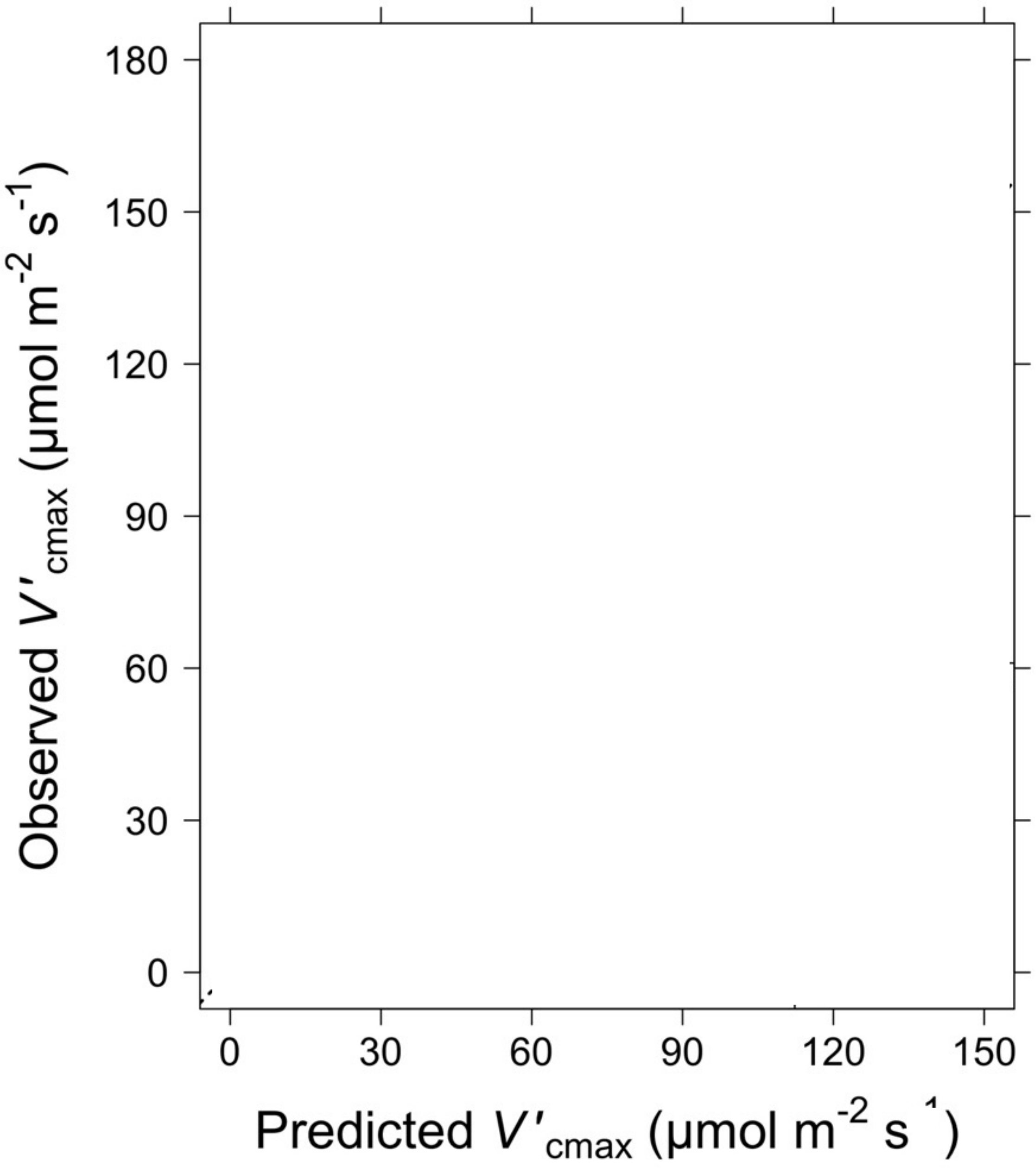
Global V_{cmax} dataset



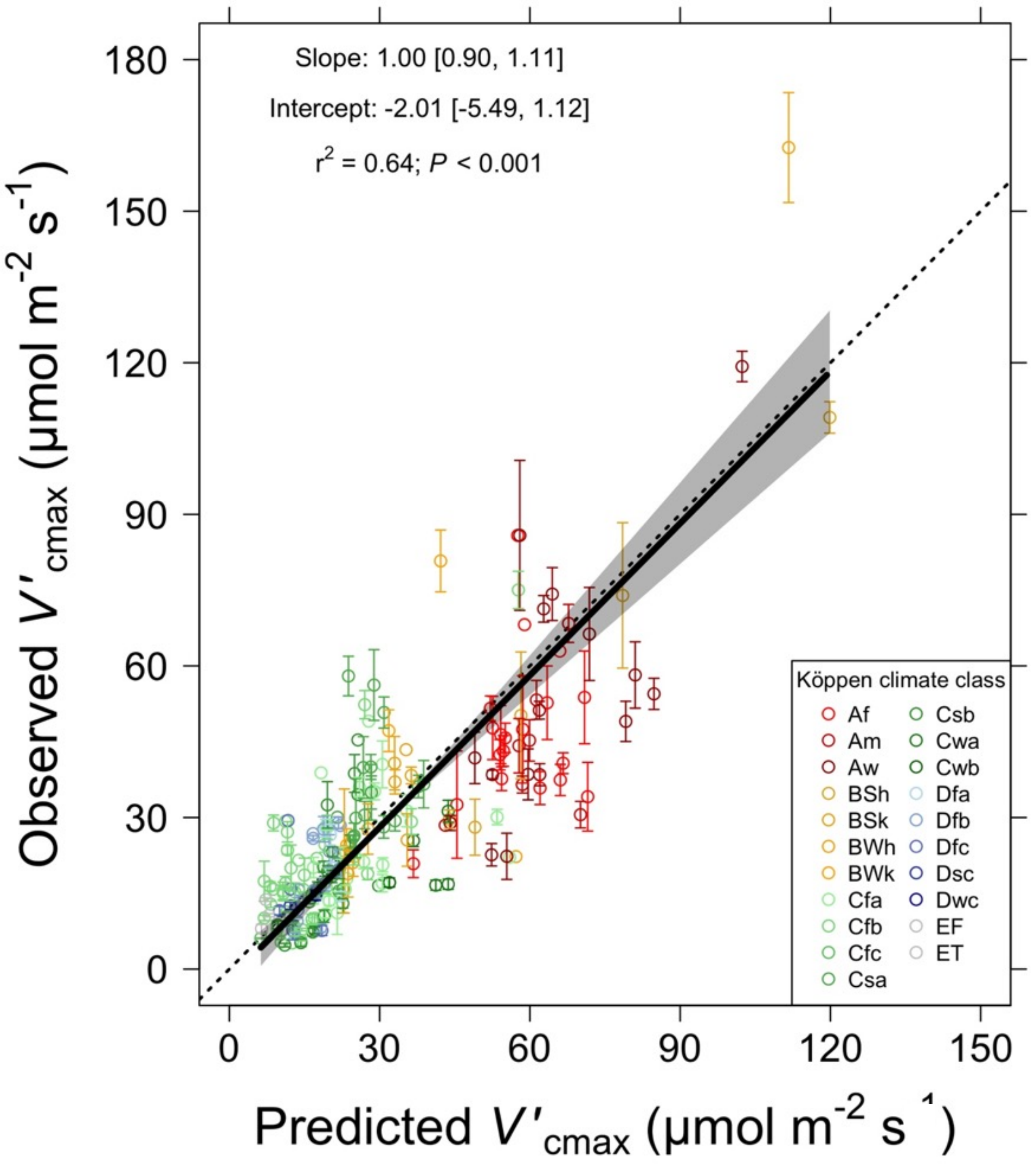
3,697 measurements
202 sites
> 600 genera



Smith et al. (2019)



Smith et al. (2019)



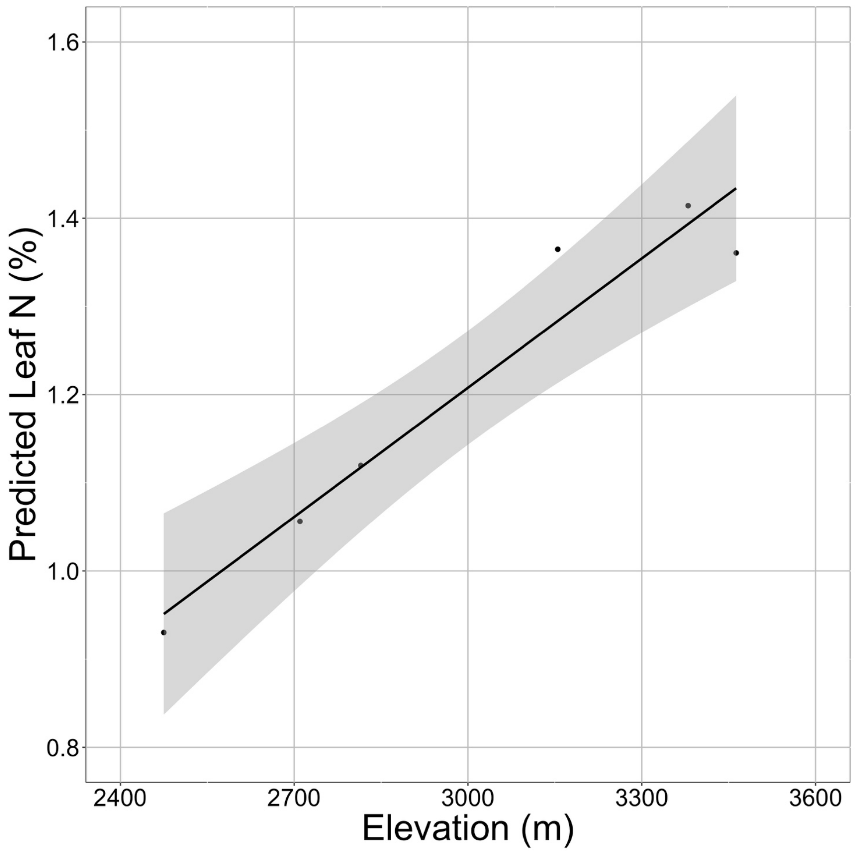
Optimal V_{cmax} is similar to observed values

Smith et al. (2019)

Question 1: Is photosynthesis optimized to the environment?

YES! Photosynthesis acclimates spatially as expected from optimization

Looking forward: larger scale impacts of acclimation



ROCKY MOUNTAIN BIOLOGICAL LABORATORY

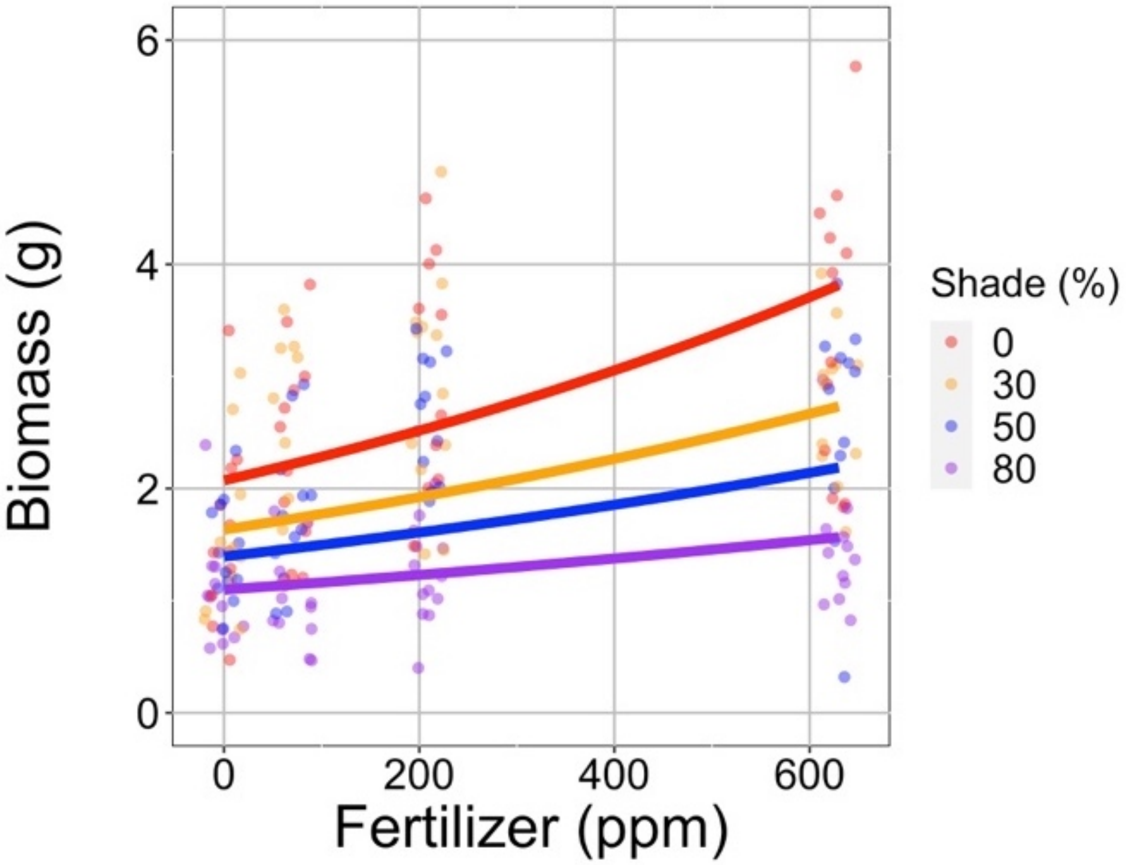
Question 2: How do plants acclimate to soil nitrogen?

The lab has examined soil nitrogen impacts in many contexts

- Observational gradient studies
  - Paillassa et al. (2020), Perkowski and Smith (in prep)
- Greenhouse soil manipulation studies
  - Perkowski et al. (2021), Waring et al. (in review)
- Field soil manipulation studies
  - Perkowski et al. (in prep), Smith et al. (in prep)

What have we learned?

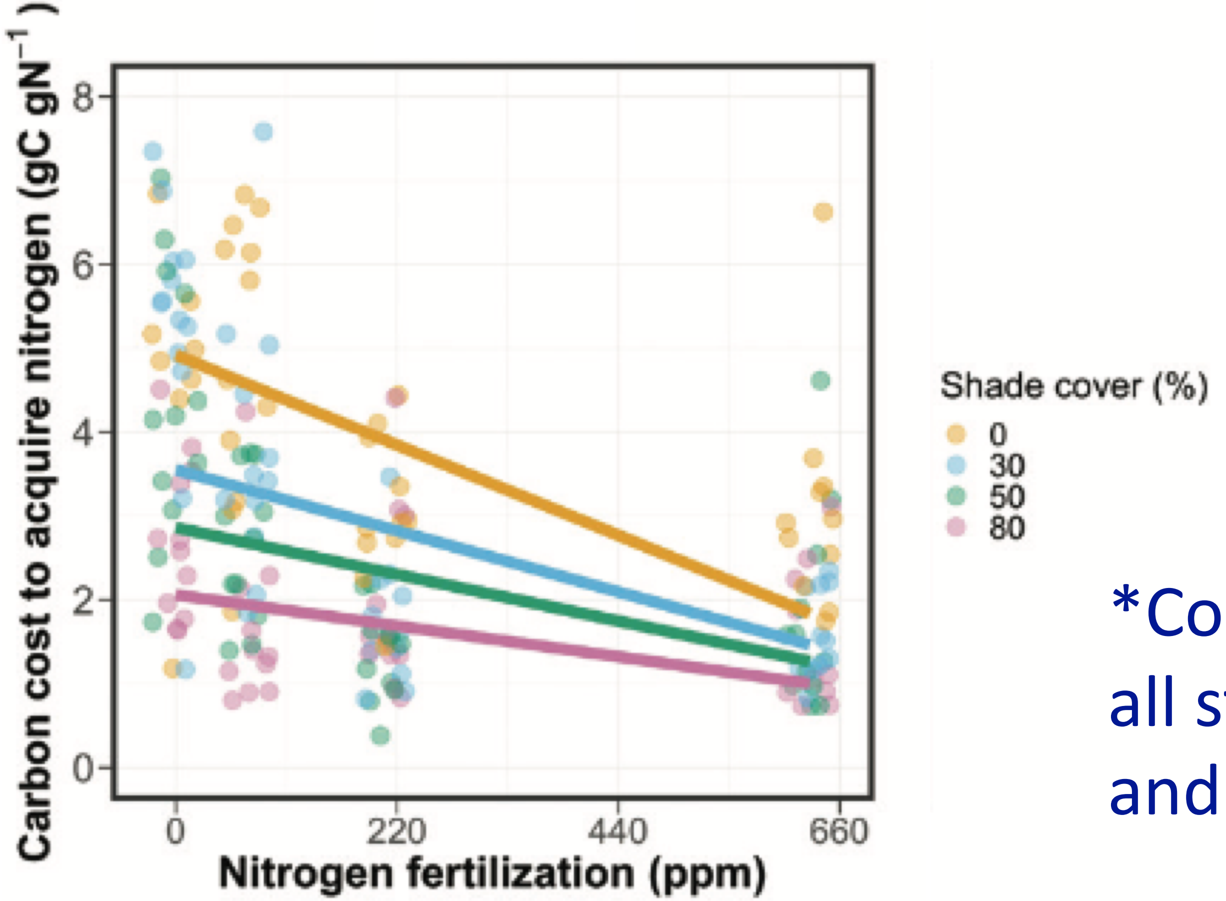
Result 1: Growth increases with increasing soil N



*Consistent across all studies

Waring, Perkowski, and Smith (in review)

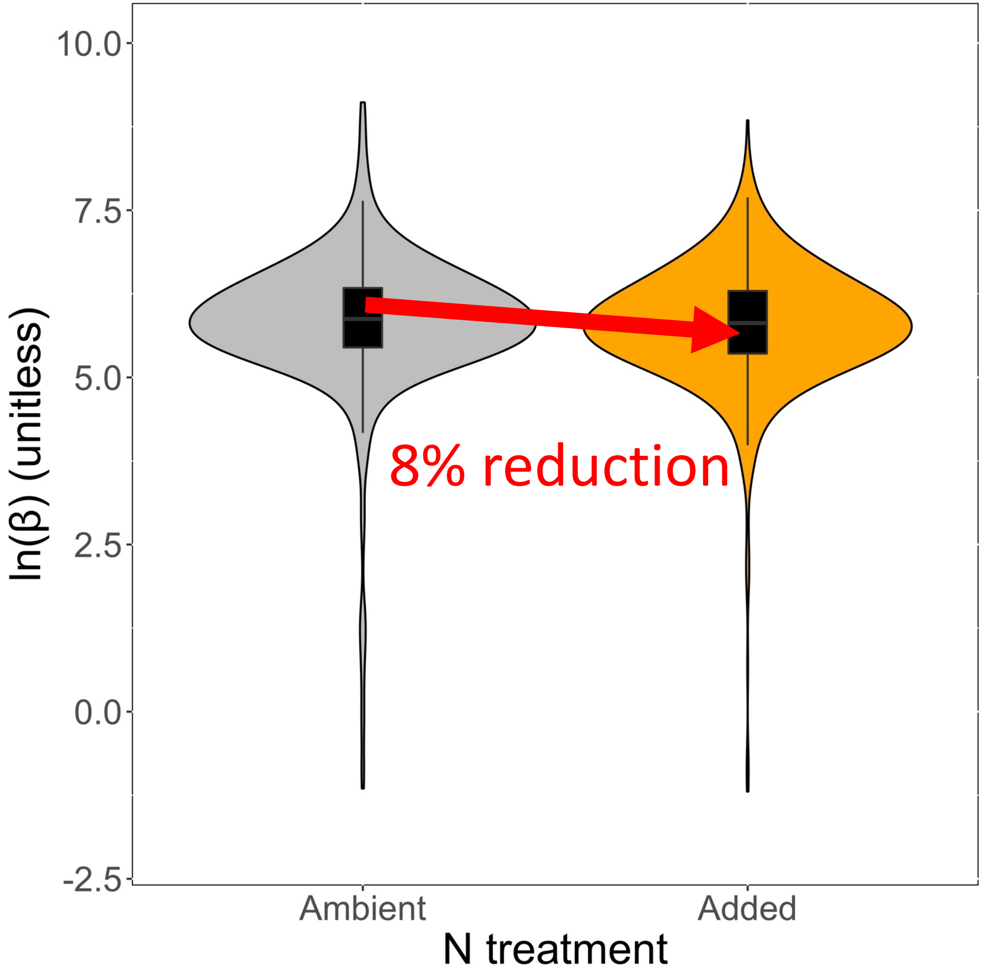
Result 2: C cost to acquire N decreases with increasing soil N



*Consistent across all studies at leaf and plant level

Perkowski et al. (2021)

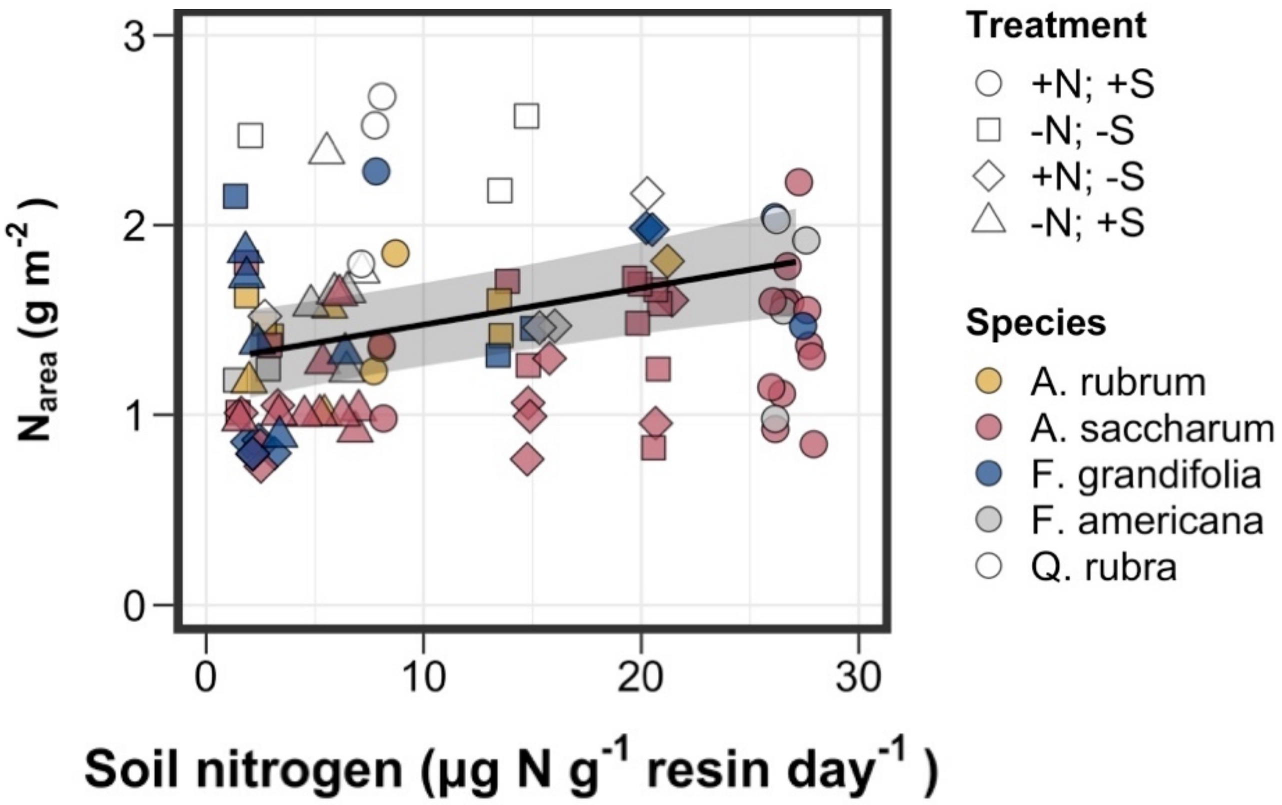
Result 2: C cost to acquire N decreases with increasing soil N



*Consistent across all studies at leaf and plant level

Smith et al. (in prep)

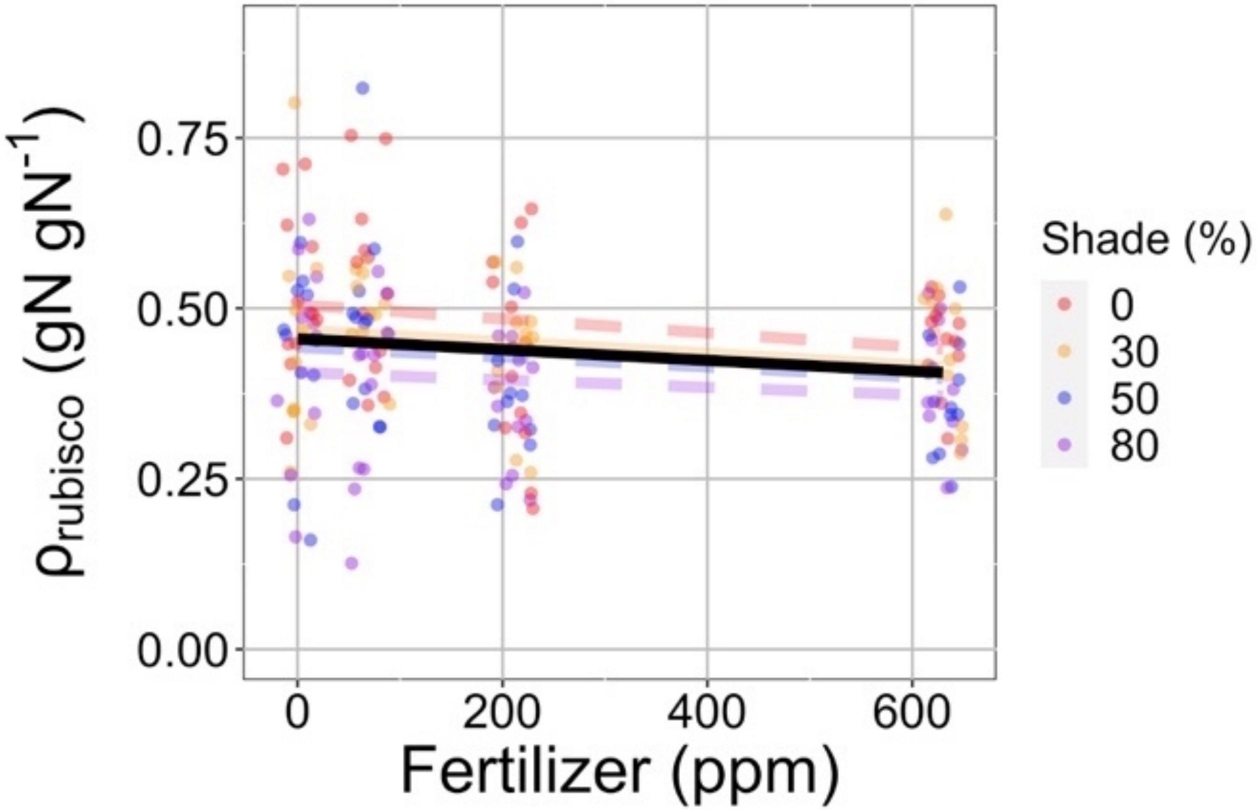
Result 3: Tissue N increases with increasing soil N



*Consistent across all studies

Perkowski et al. (in prep)

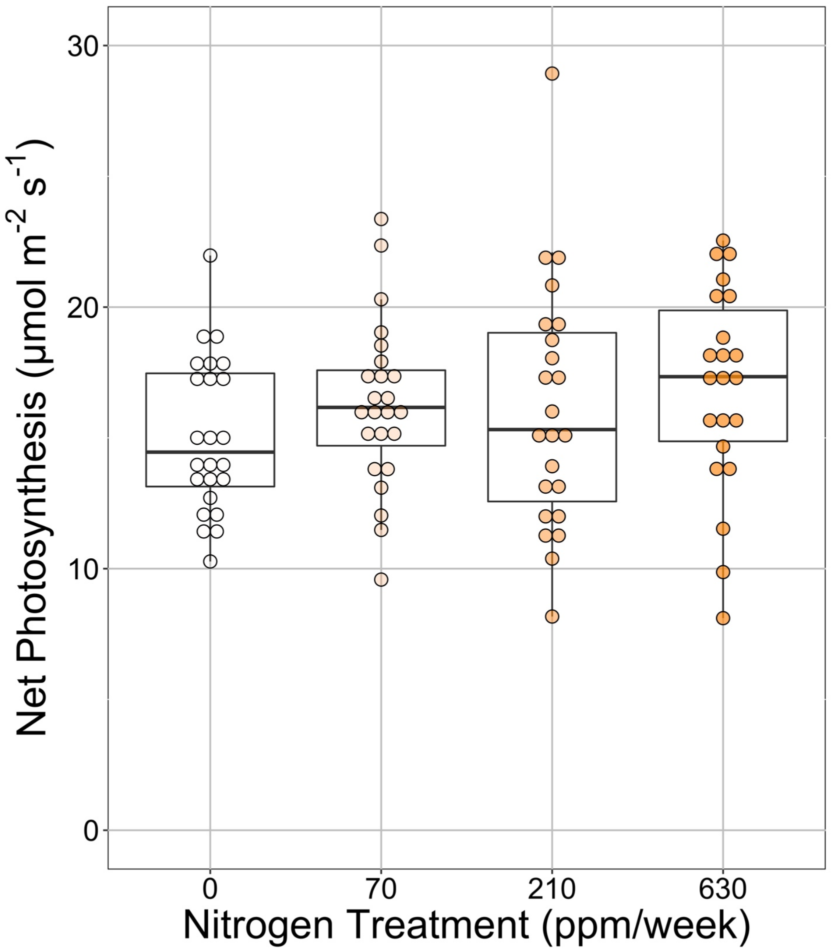
Result 4: Relative leaf N allocation to photosynthesis decreases with increasing soil N



*Consistent across multiple species, metrics, and growth conditions

Waring, Perkowski, and Smith (in review)

Result 5: Little to no change in per-leaf-area photosynthesis

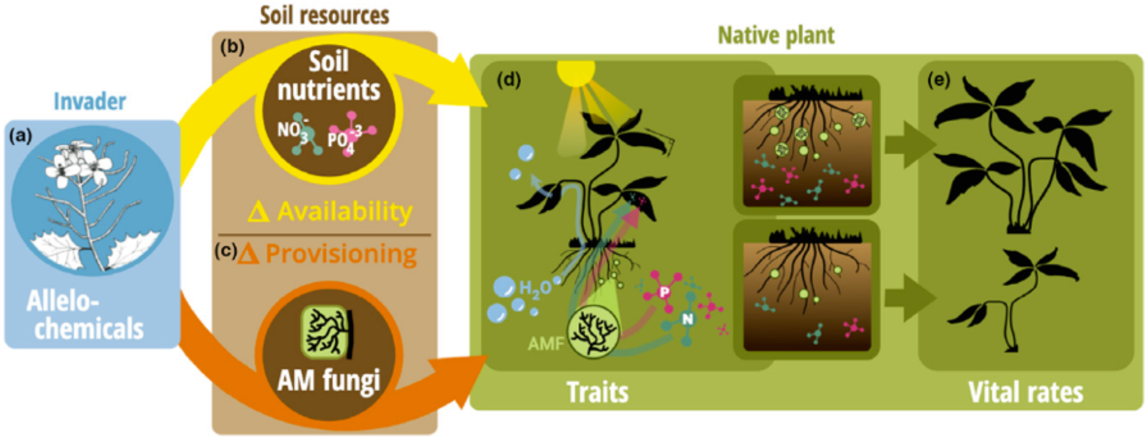


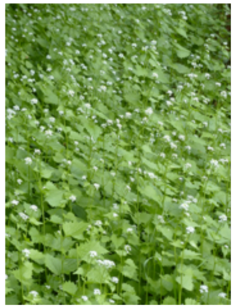
Waring, Perkowski, and Smith (in review)

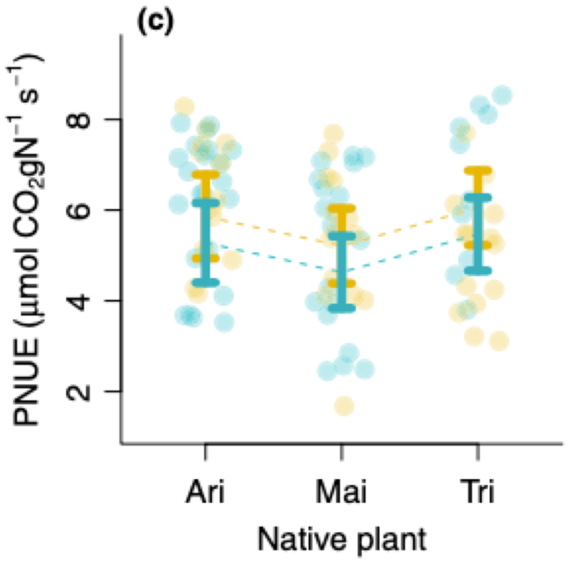
Question 2: How do plants acclimate to soil nitrogen?

Reduction in N uptake costs results in bigger plants with more leaf N, but little change in per-leaf-area photosynthesis

Looking forward: impact of allelopathic invaders on leaf economics





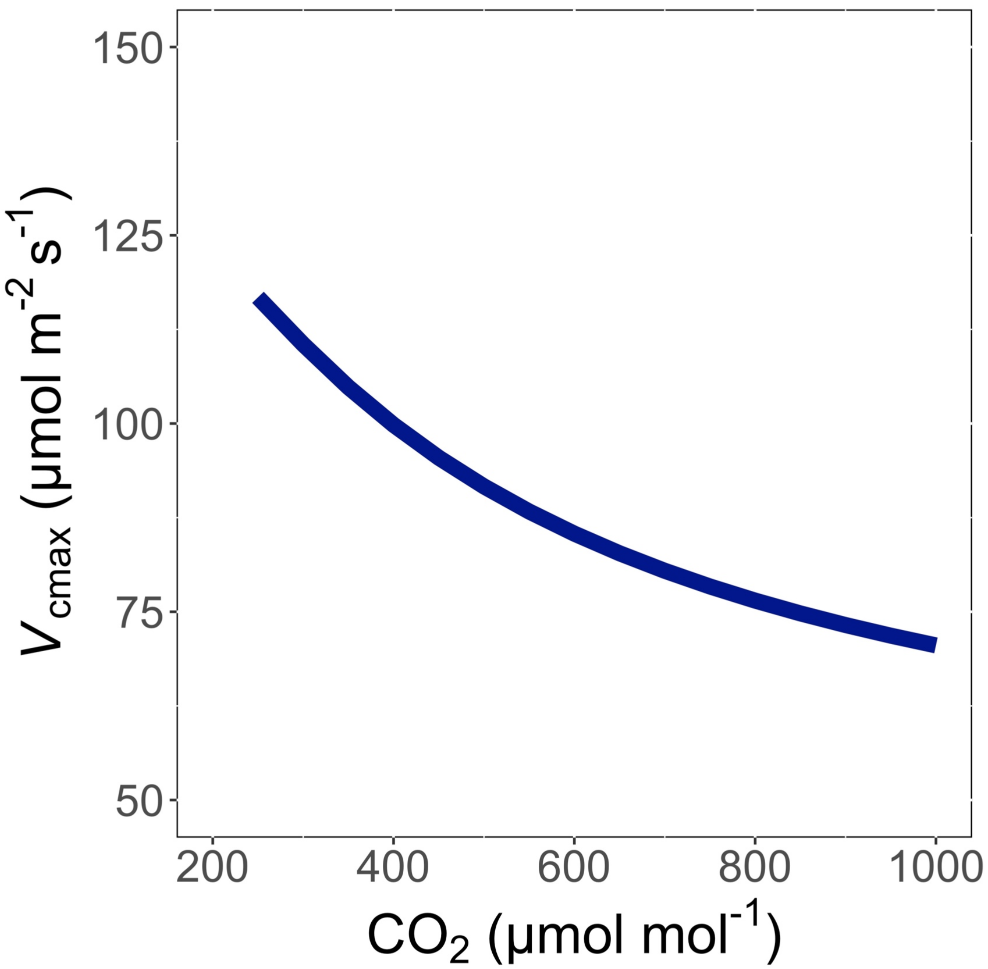


Allelopathic invasion (gold) increased photosynthetic N use efficiency of native plants. This response was predicted by acclimation theory.

Bialic-Murphy et al. (2021)

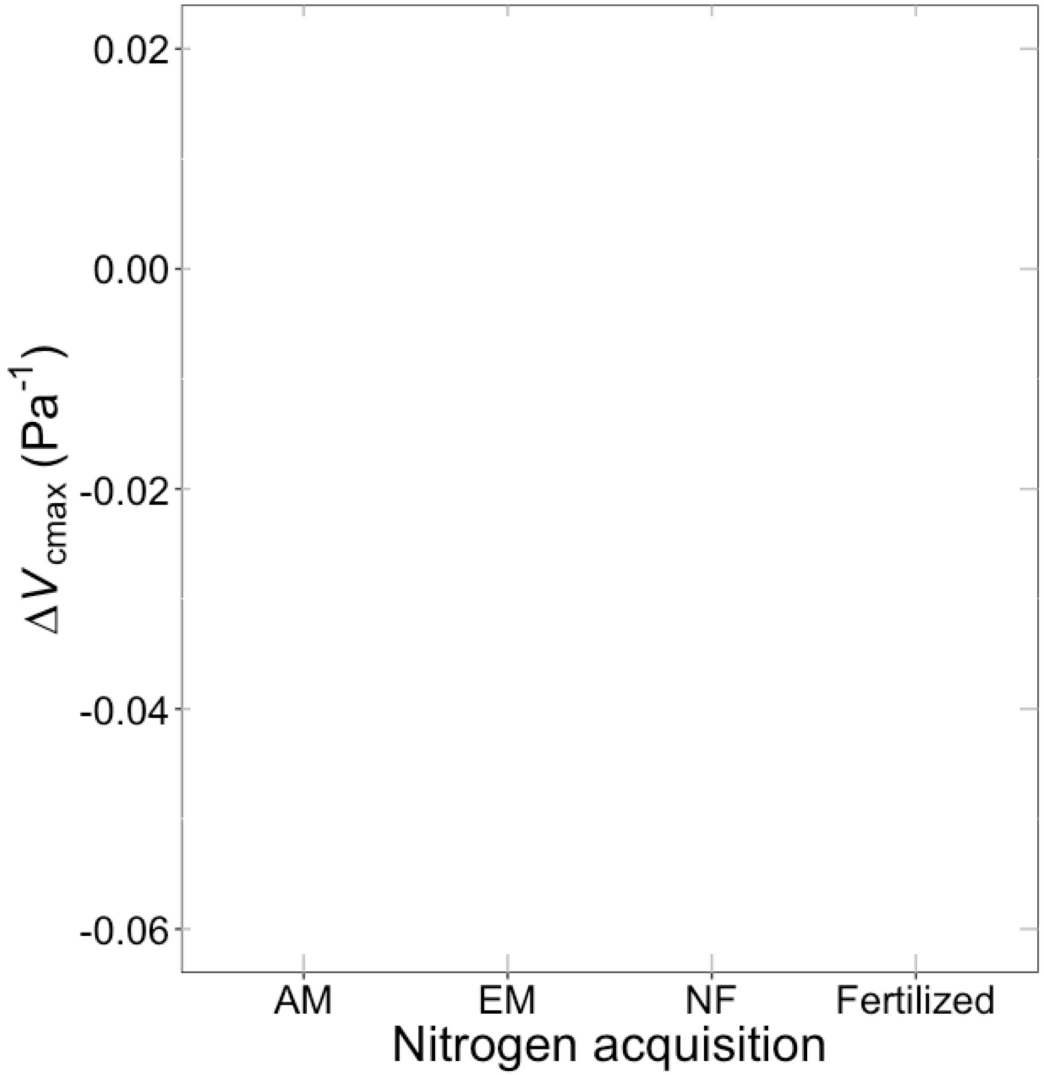
Question 3: What does acclimation mean for future terrestrial biogeochemical cycling?

Expected future responses

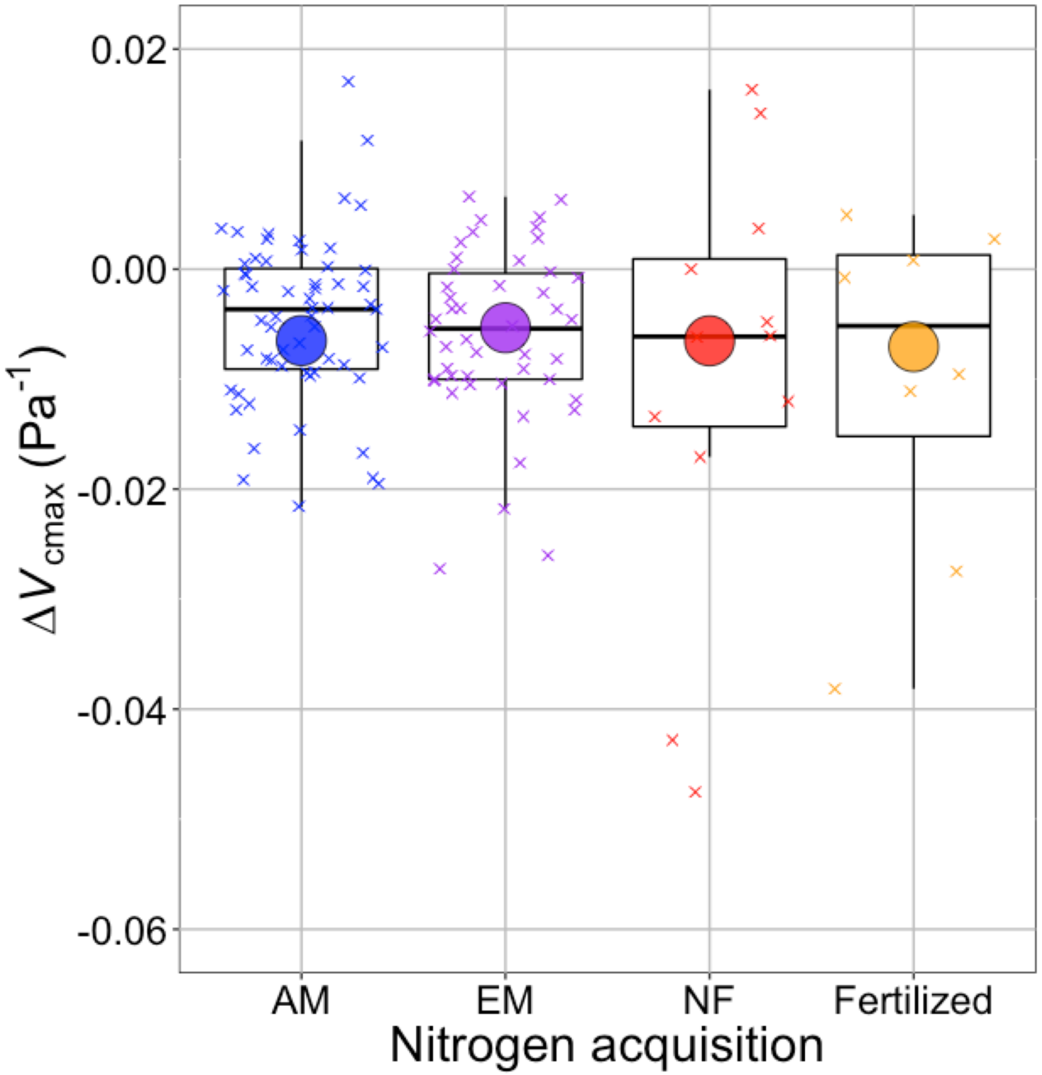


V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf and less photorespiration

Smith et al. (2019)



Smith and Keenan (2020)



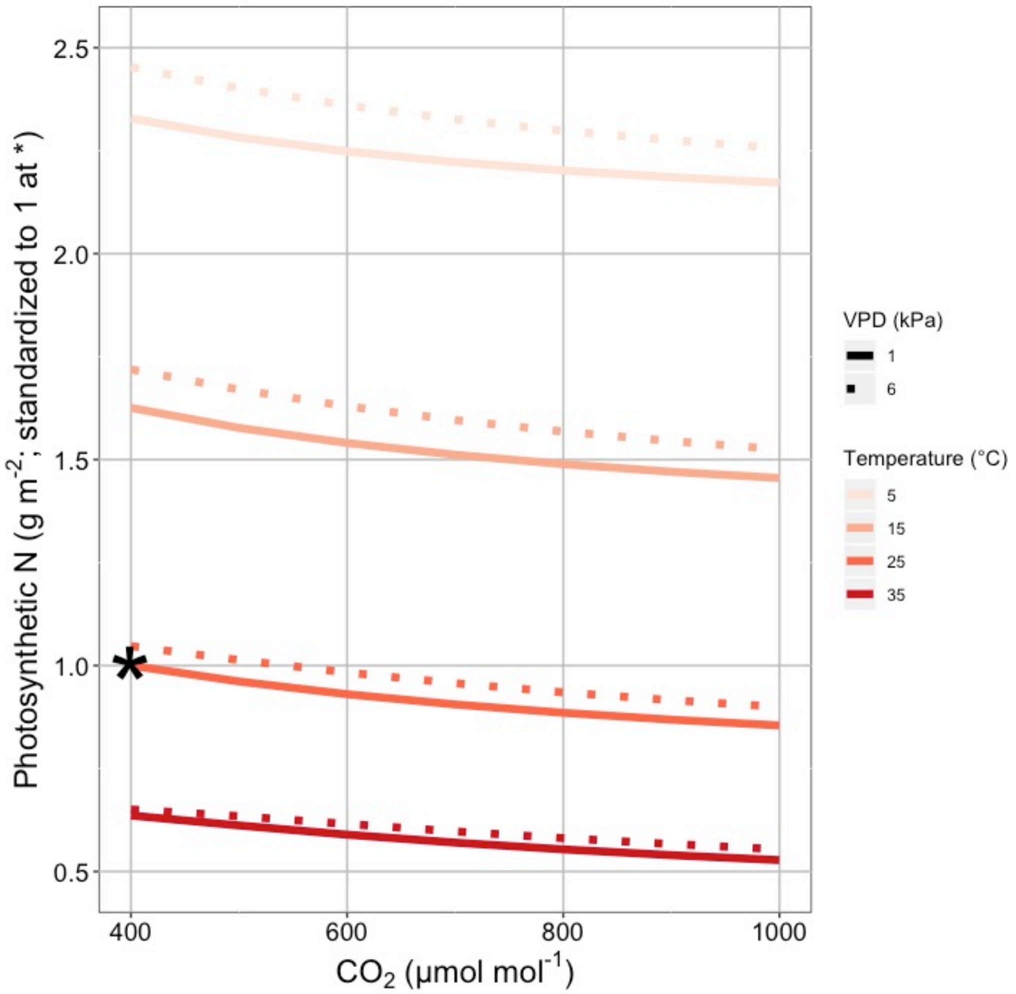
V_{cmax} changes with CO_2 in ways expected from optimization

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

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

Smith and Keenan (2020)

This generally suggests lower nitrogen demand under future conditions

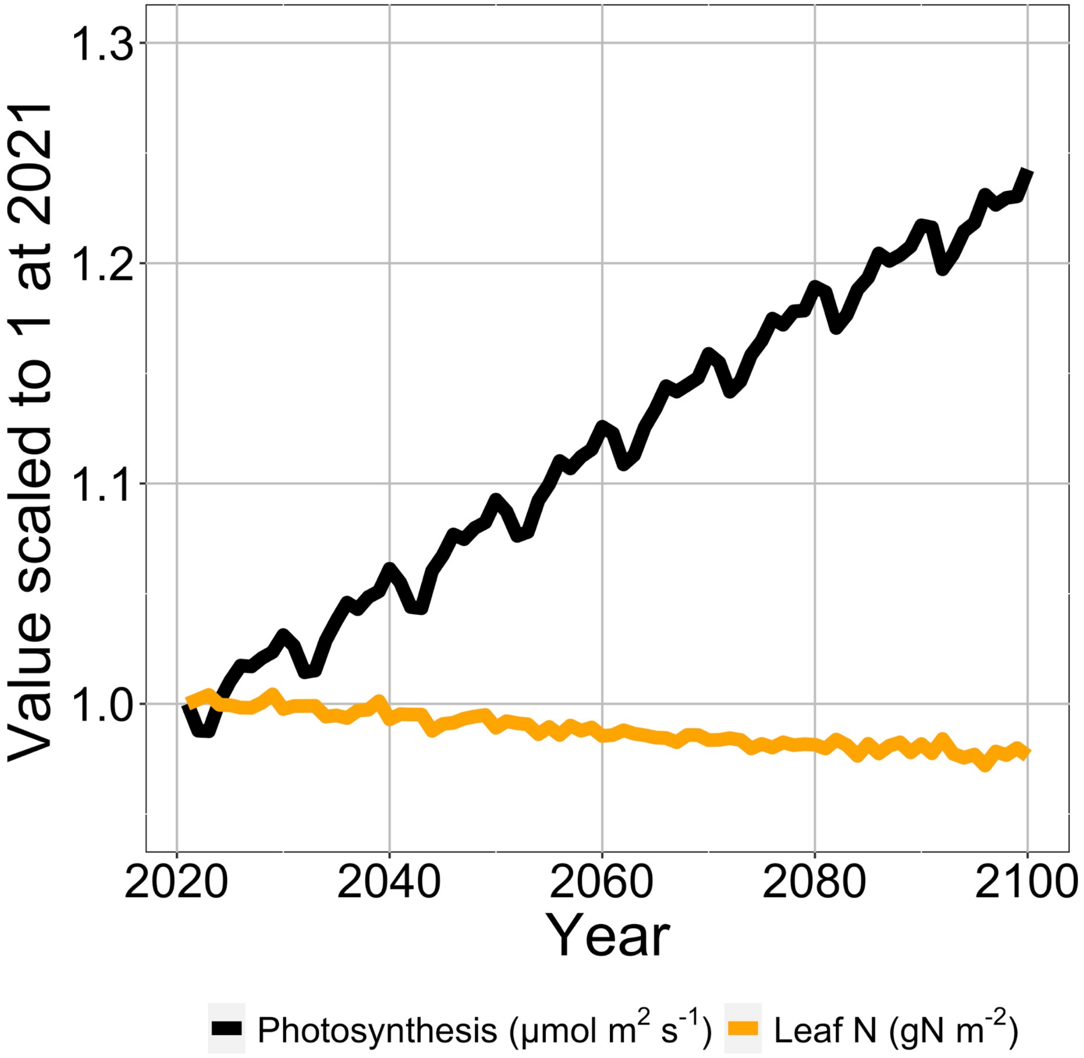


Smith and Keenan (2020)

Let's run a model out into the future!

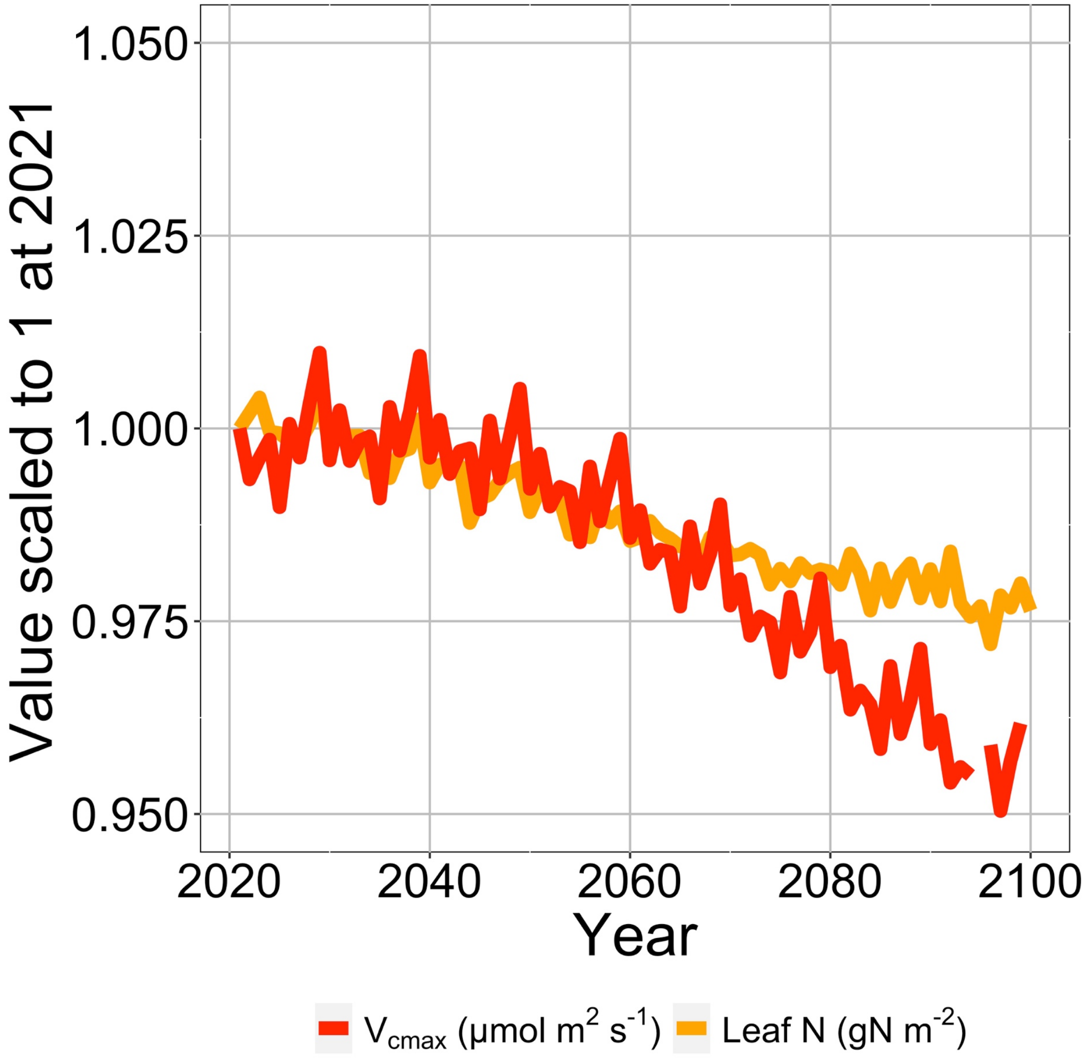
E3SM Energy Exascale Earth System Model

Photosynthesis increases with elevated CO_2 at lower leaf N



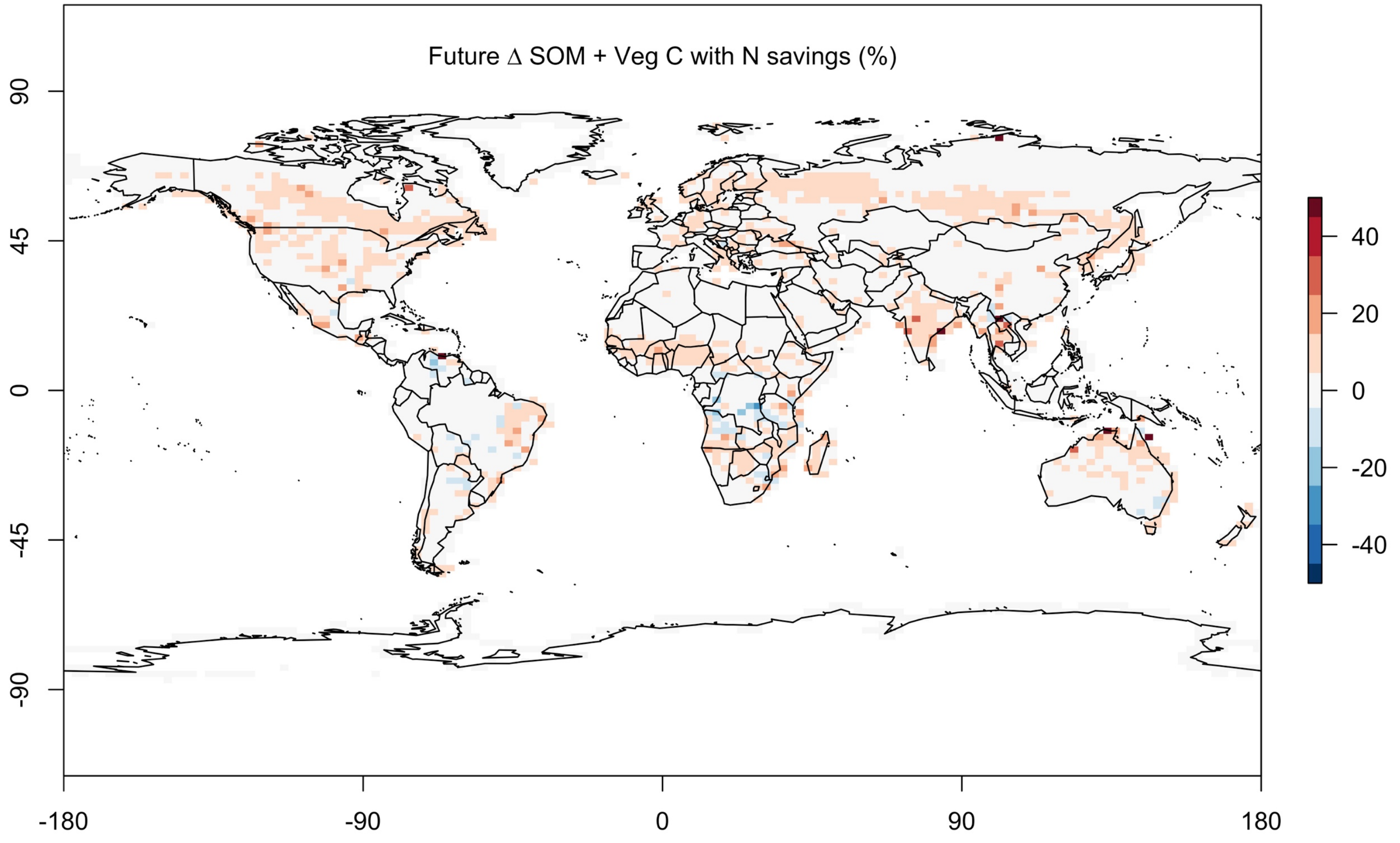
Smith et al. (in prep)

Leaf N reduction is due to a reduction in photosynthetic capacity



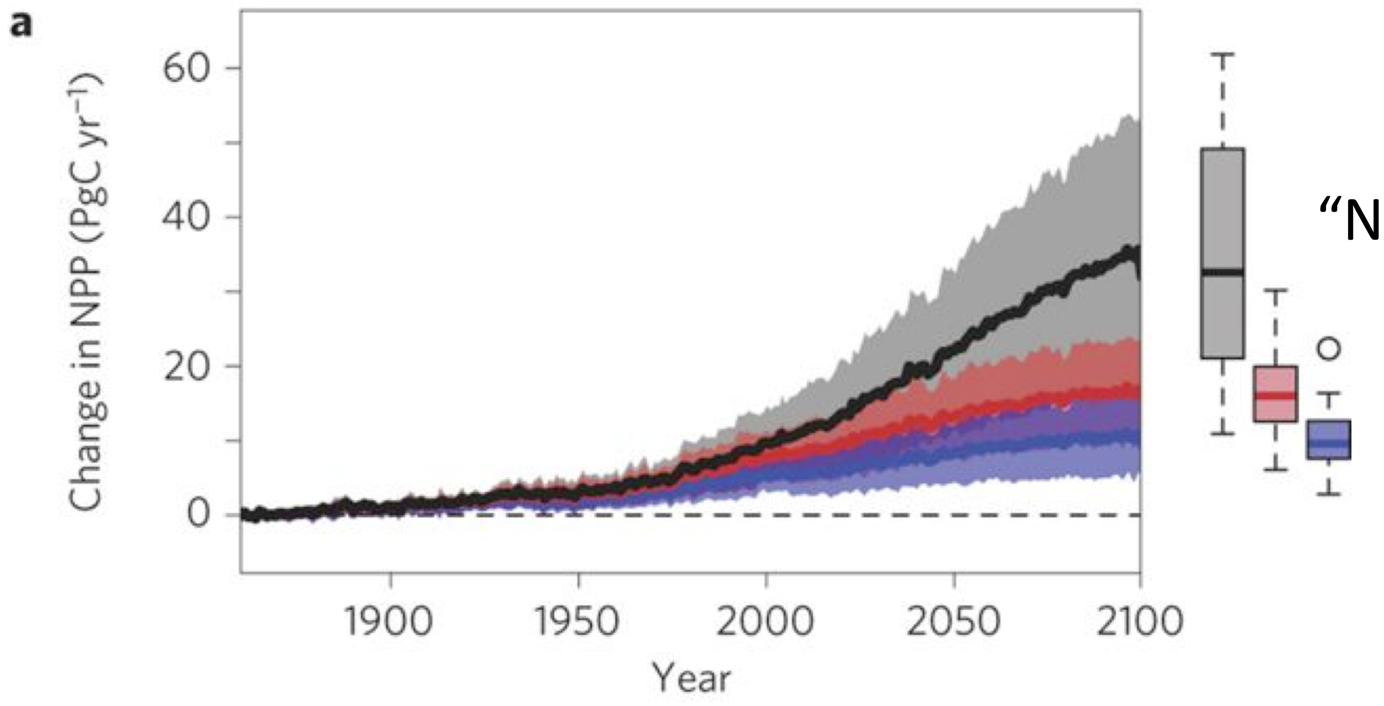
Smith et al. (in prep)

Leaf N savings increases long-term ecosystem carbon stocks



Smith et al. (in prep)

Need to rethink nutrient limitation in models?



“No limitation” simulation

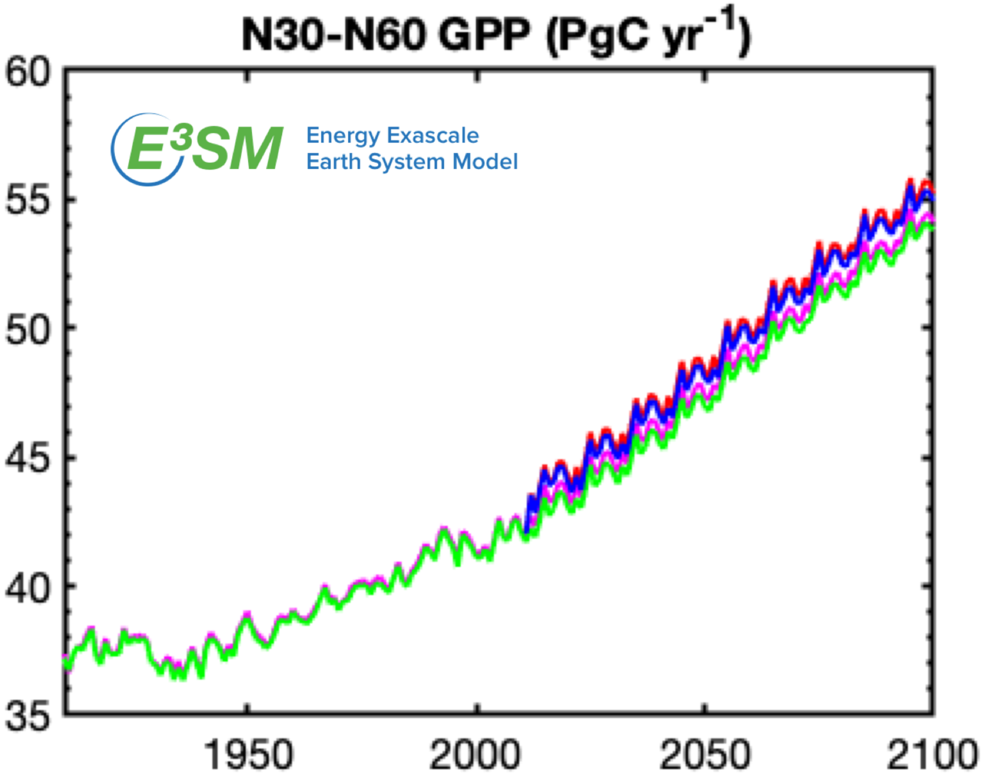
“Nutrient limitation” simulations

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

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



Coupled model-data experiments

SCHMIDT FUTURES

NSF

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…

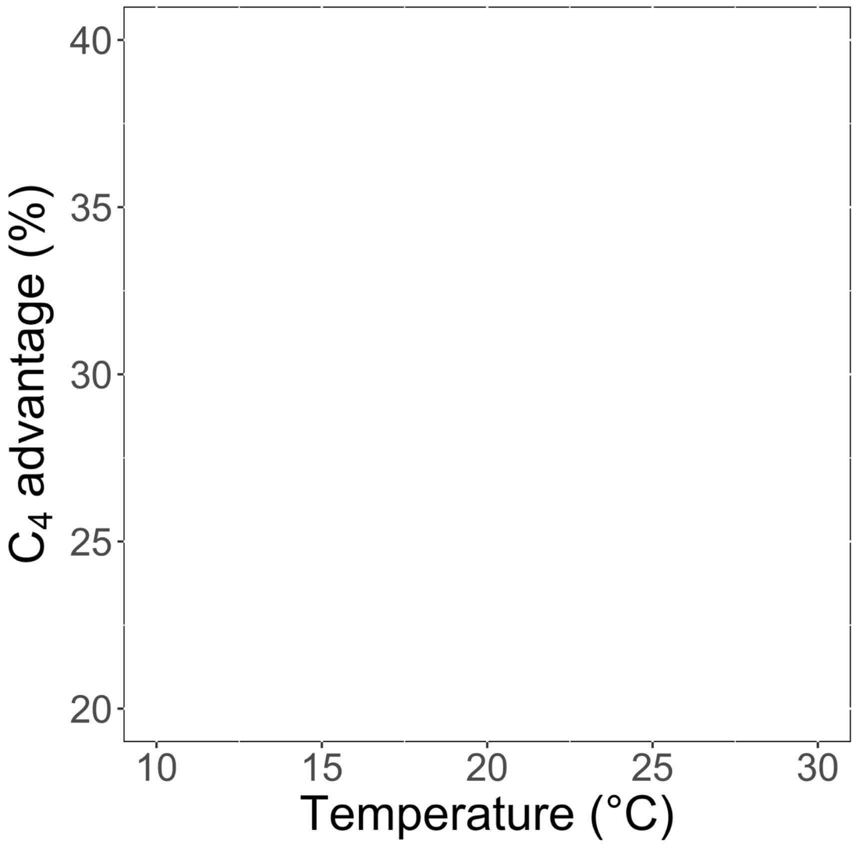
- Little photorespiration
- An additional limitation (PEP carboxylation)

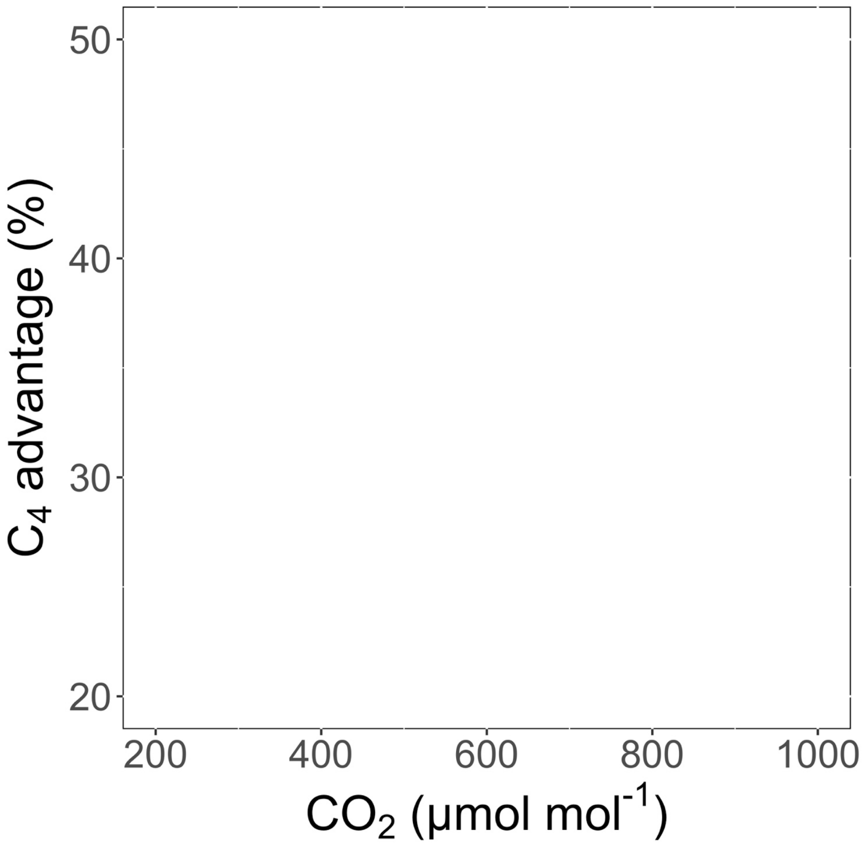
C_4 versus C_3 optimization

C_4 photosynthesis has…

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

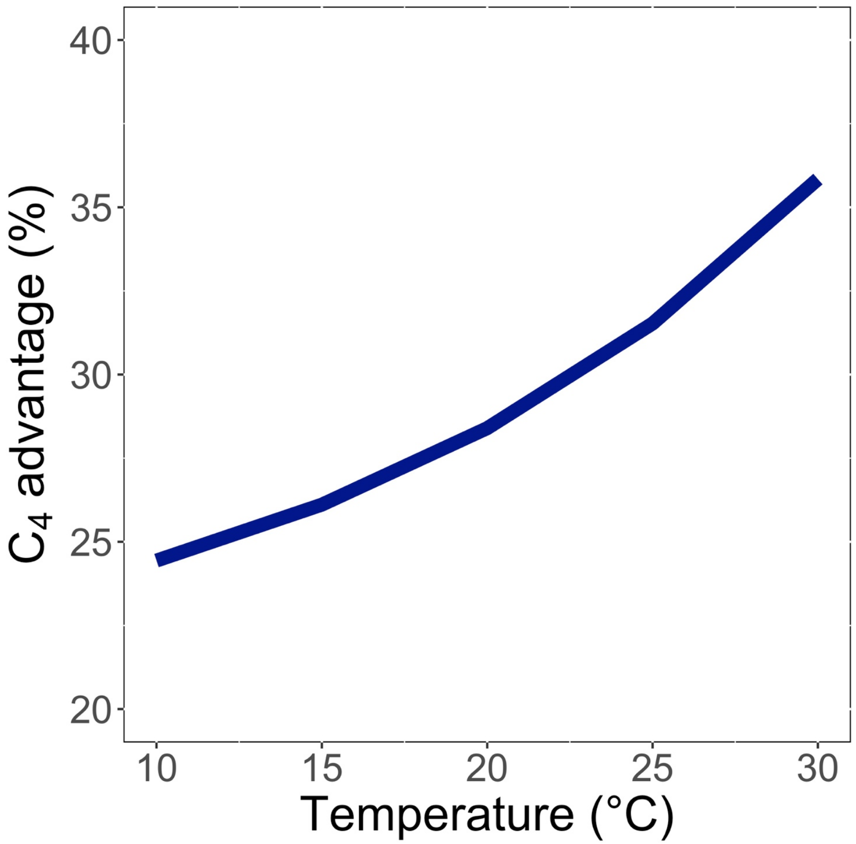
Relative advantage of C_4 physiology

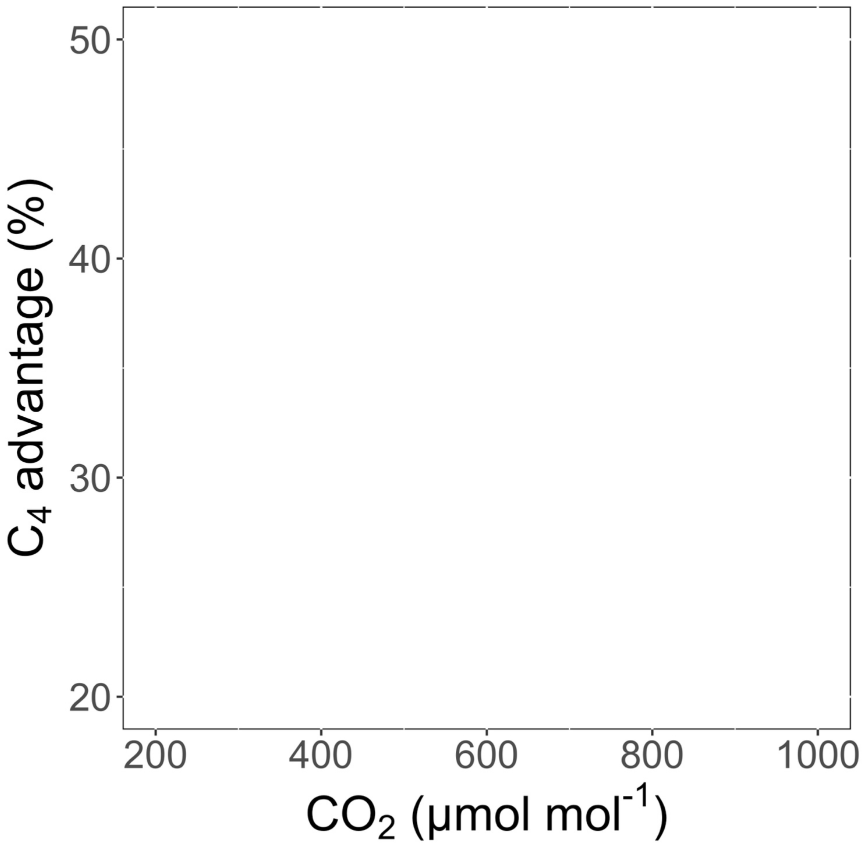




Scott and Smith (2022)

Relative advantage of C_4 physiology





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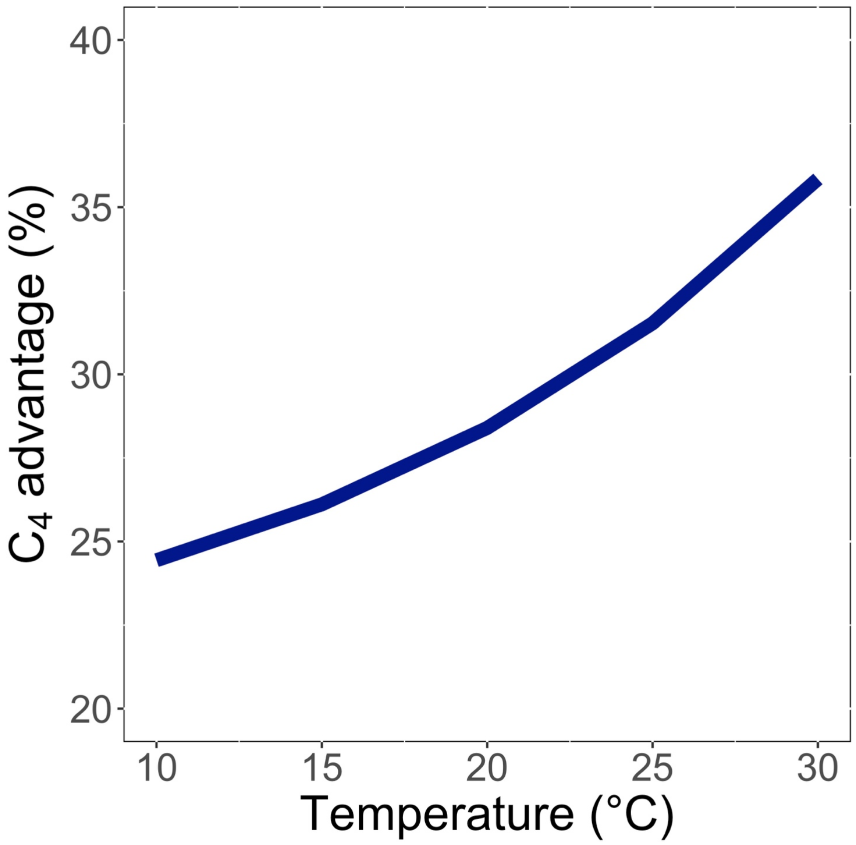
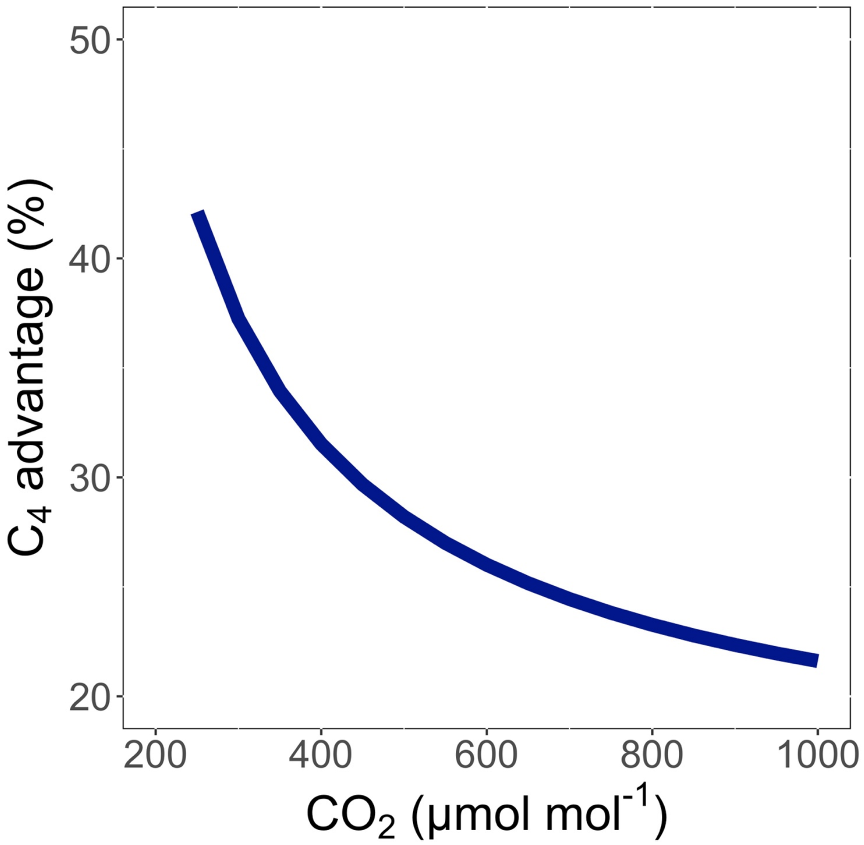
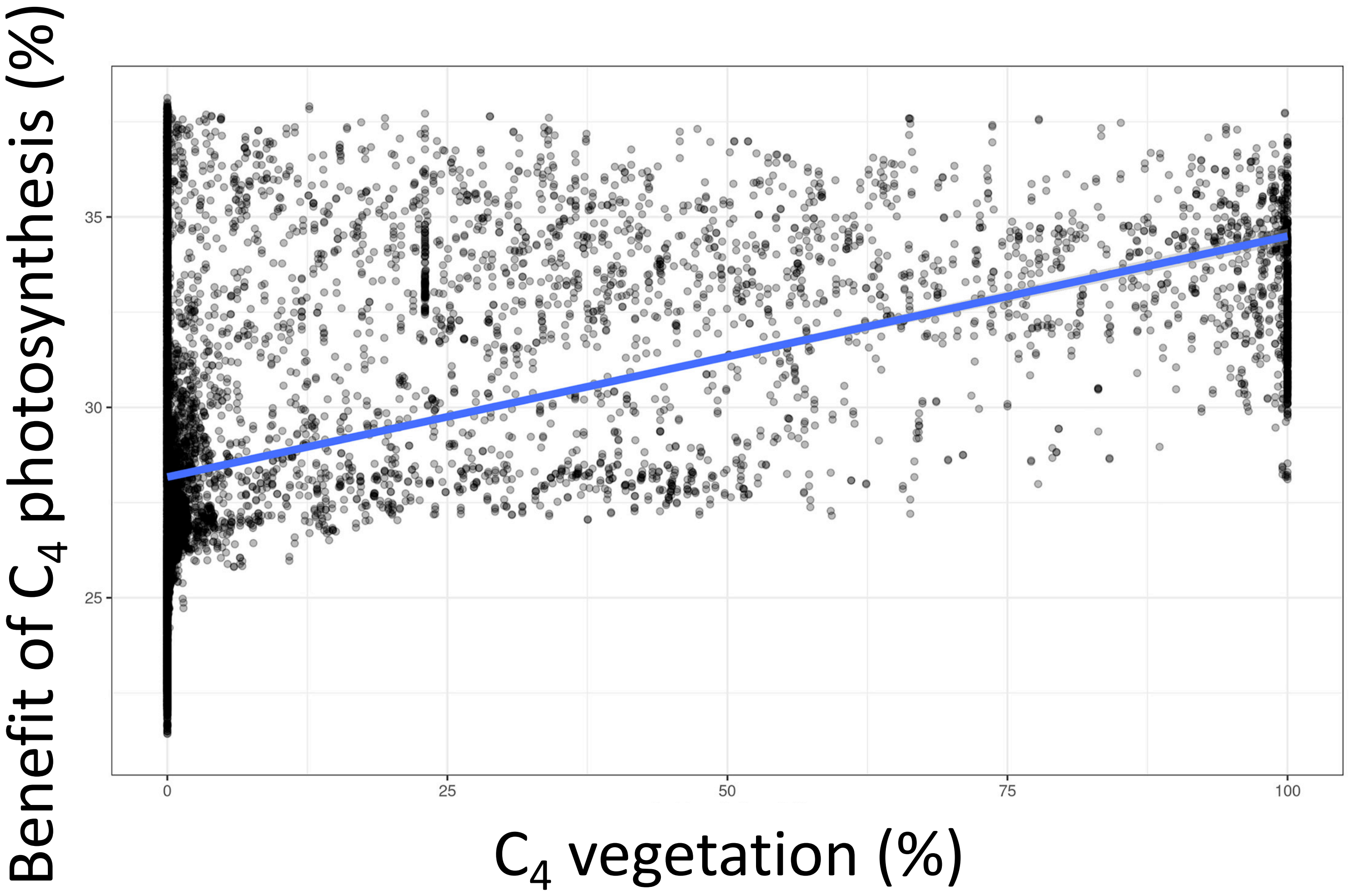
Relative advantage of C_4 physiology



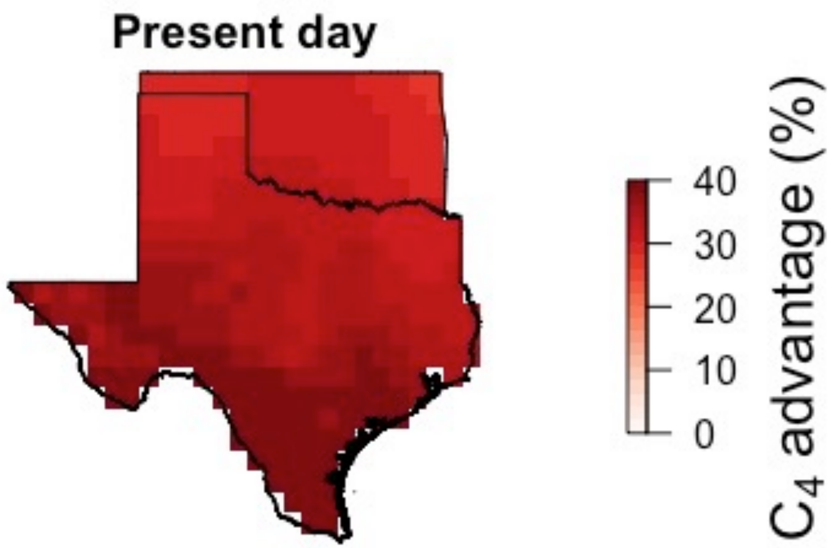


Scott and Smith (2022)

The model seems to work!

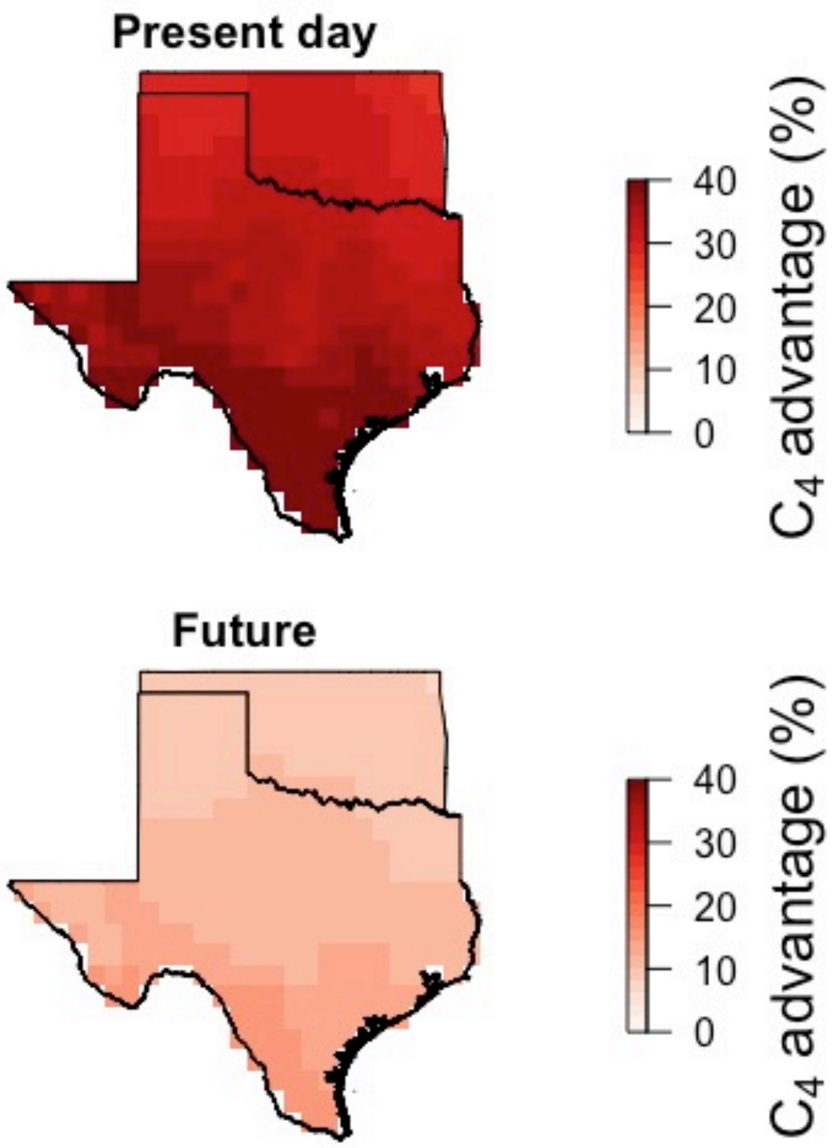


Scott and Smith (2022)



Ansley et al. (in review)

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



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Ansley et al. (in review)

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

C_4 is better in hot, dry, low CO_2 environments

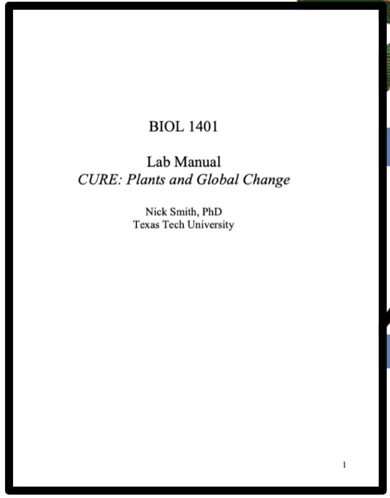
Looking forward: model-data comparisons for C_4 plants

Powell Center

USGS
science for a changing world

Other activities of note

- Role of agricultural land management in determining plant- and ecosystem-scale processes
  - Bell and Smith (2021); McNellis et al. (in prep); Borus et al. (in prep)
- Southern pine beetle impacts on pitch pine
  - Licht and Smith (2020); Licht et al. (in review); Licht et al. (in prep)
- Large-scale phenological observations
  - Gu et al. (2022), He et al. (2021), Wang et al. (2021), Chen et al. (2020)
- 5th National Climate Assessment for Southern Great Plains
  - McPherson et al. (in prep)
- Course-based undergrad research experiences (CUREs)


BIOL 1401

Lab Manual
CURE: Plants and Global Change

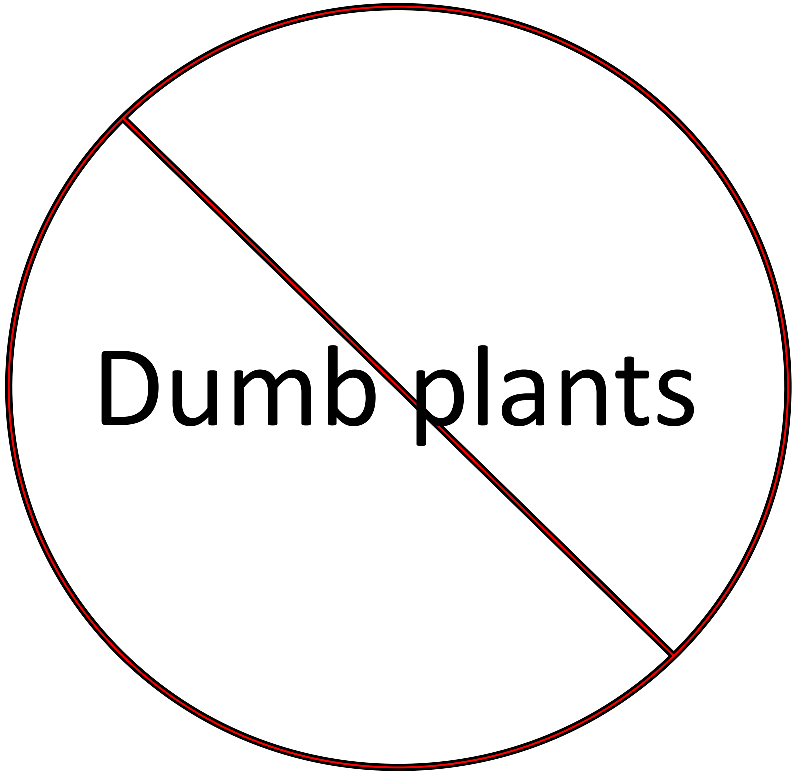
Nick Smith, PhD
Texas Tech University

1

Conclusions

Conclusions

- Plants aren't dumb!
  - Assuming plants don't dynamically respond to their environment can lead to poor understanding of ecosystem functioning

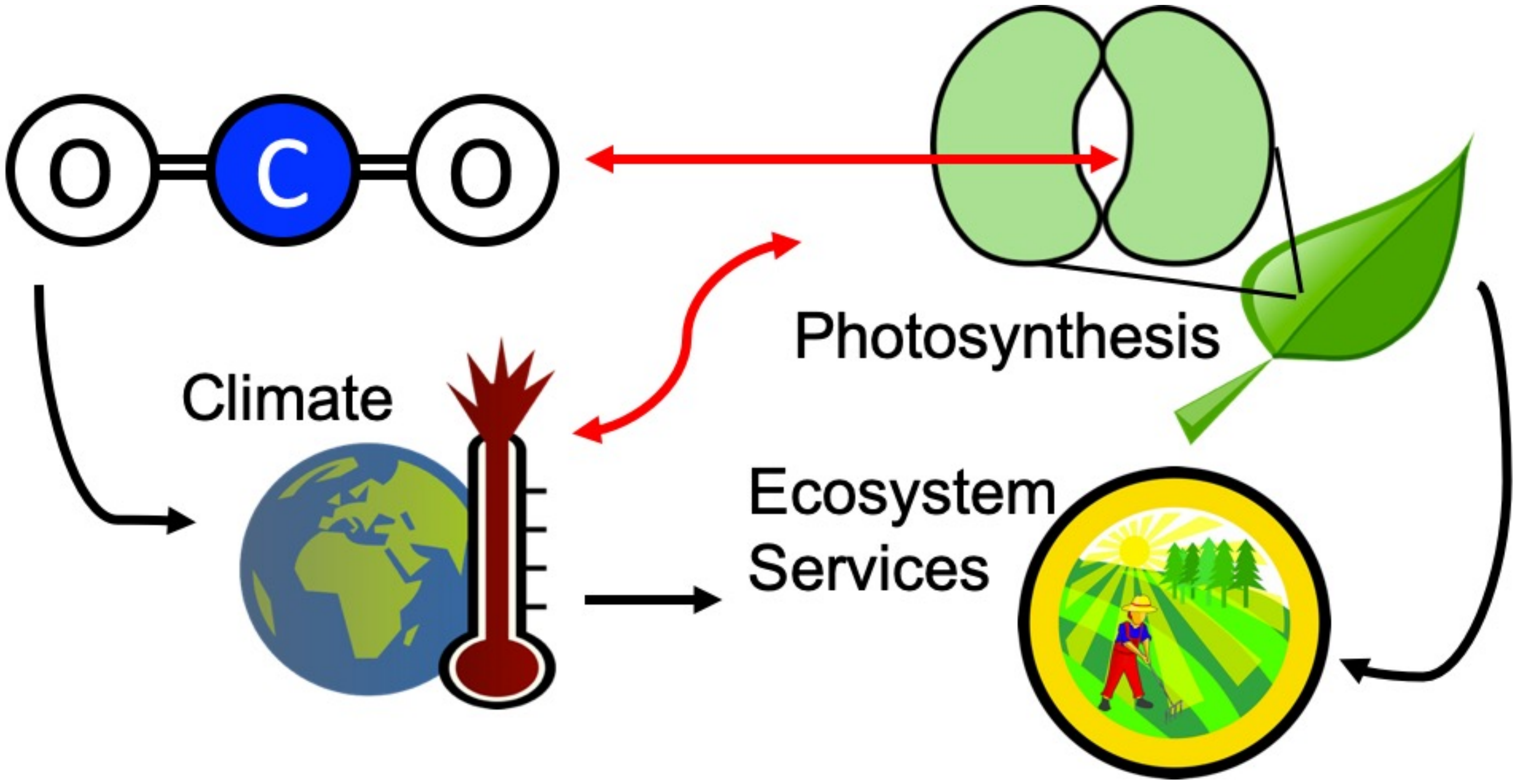


Conclusions

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



Acknowledgements

- Current lab members
  - Brad Posch (postdoc)
  - Evan Perkowski (PhD)
  - Zinny Ezekannagha (PhD)
  - Snehanjana Chatterjee (PhD)
  - Eve Gray (MS)
  - Monika Kelley (MS)
  - Isabella Beltran (MS)
- Former lab members
  - Jeff Chieppa (postdoc; now working in industry)
  - Lizz Waring (postdoc; now Asst. Prof at Northeastern State U)
  - Risa McNellis (MS; now at Plum Island LTER)
  - Helen Scott (MS; now in industry and PhD student at BU)
  - Abigail Bell (BS; now in industry)
  - Jorge Ochoa (BS; now in industry)
  - Too many (34) undergrads to list!
- Collaborators, colleagues, and friends at TTU
- Bio and TTU staff
- Collaborators around the world
- Funding
  - NSF
  - USDA
  - NPS
  - USGS
  - Schmidt Futures
  - Texas EcoLab

Presentation available at:
www.github.com/SmithEcophysLab/seminar/2022_ttu

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