

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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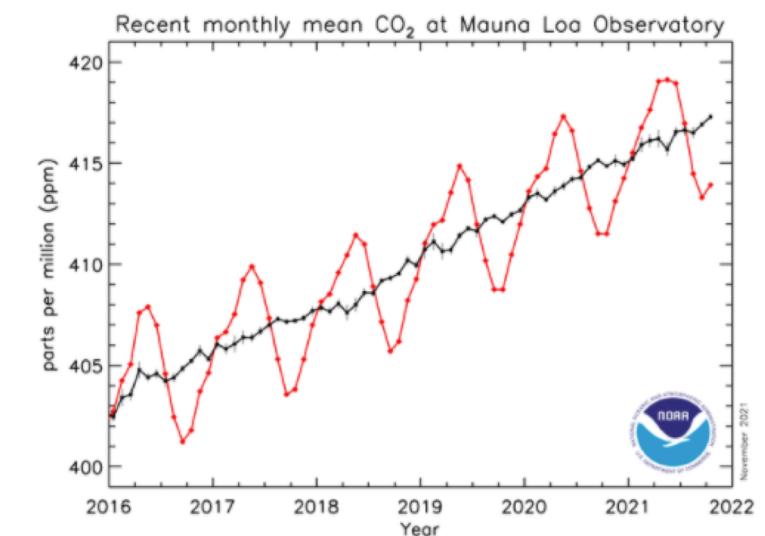
Why do people care about plants?



Why do people care about plants?



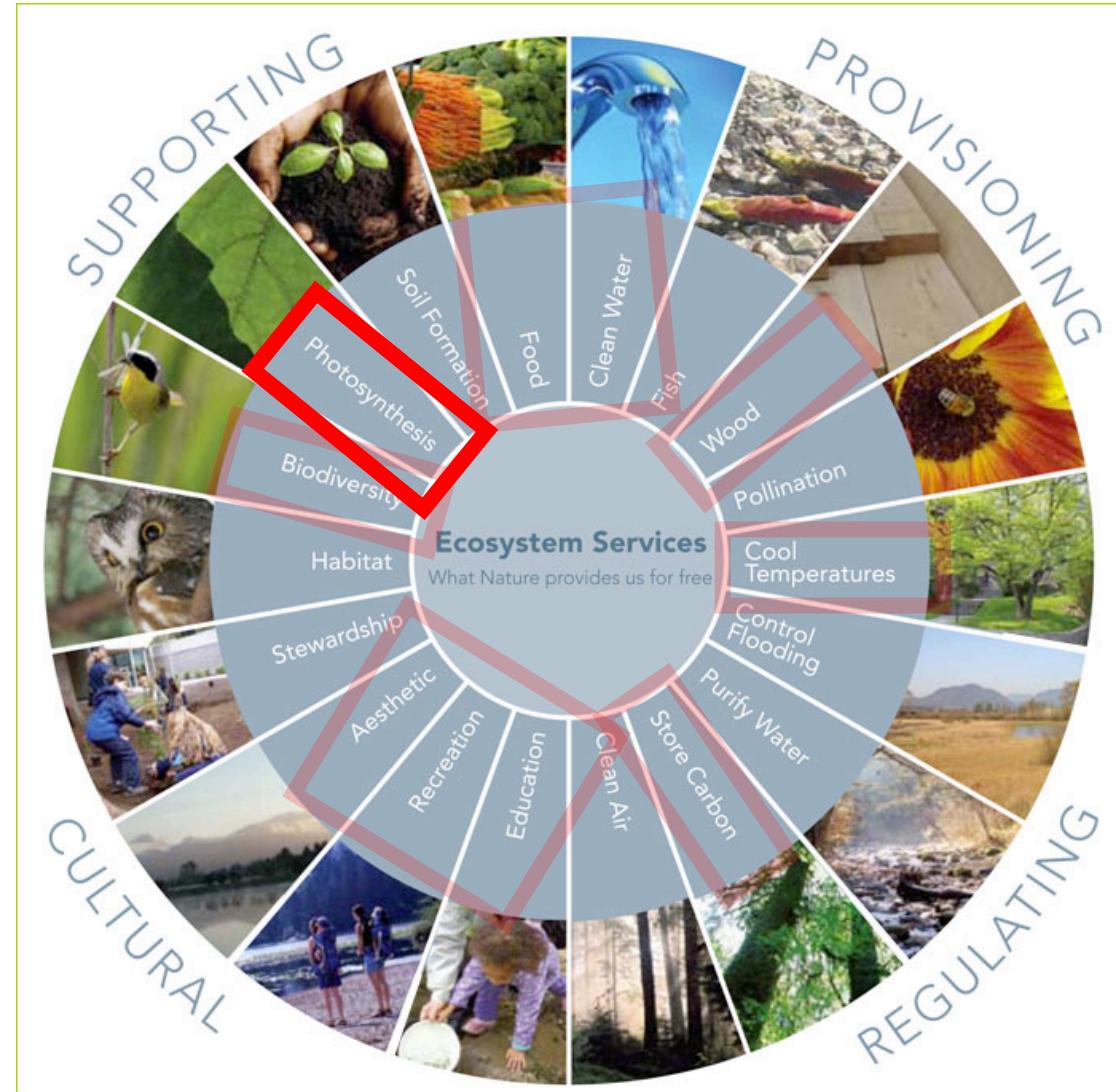
Why do people care about plants?



In other words: plants provide ecosystem services



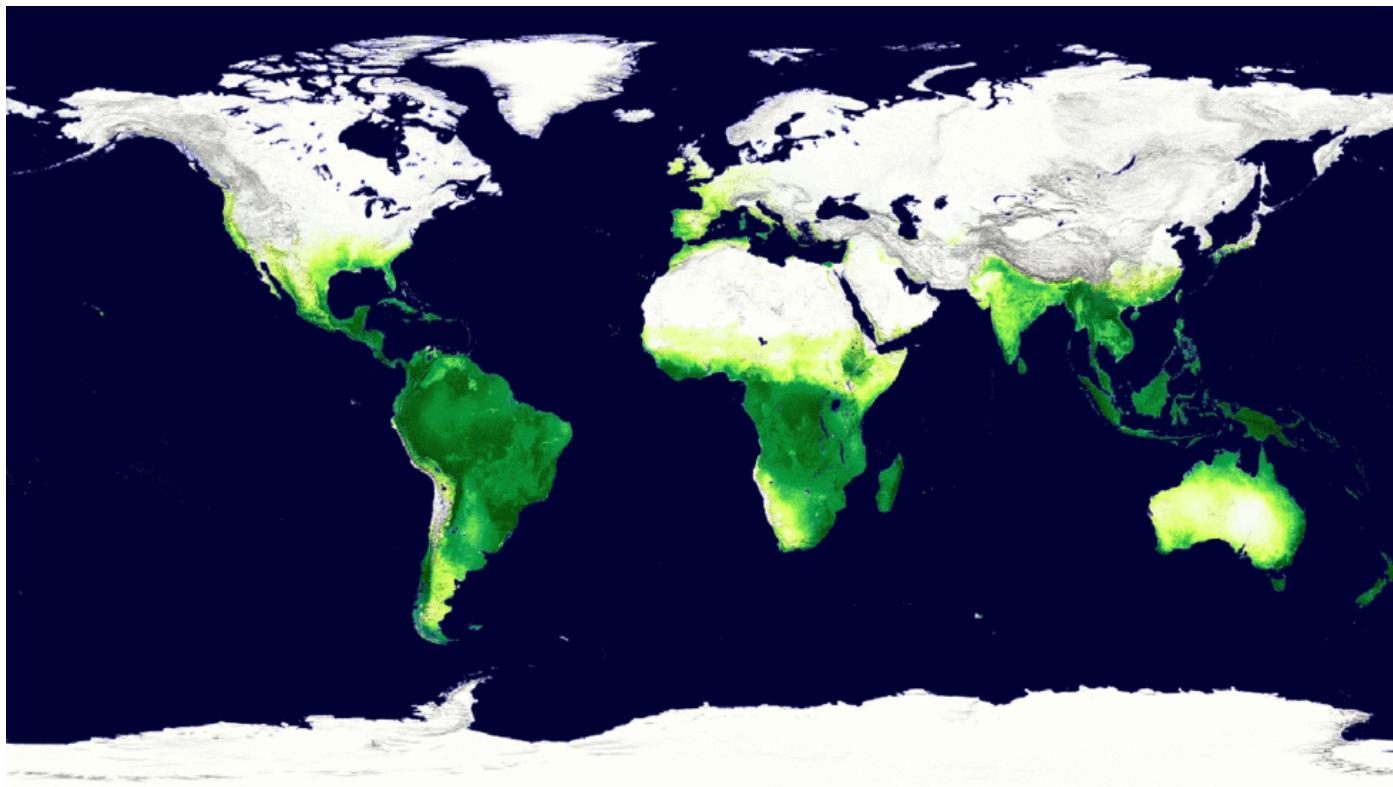
Including photosynthesis



Photosynthesis provides the foundation for other services

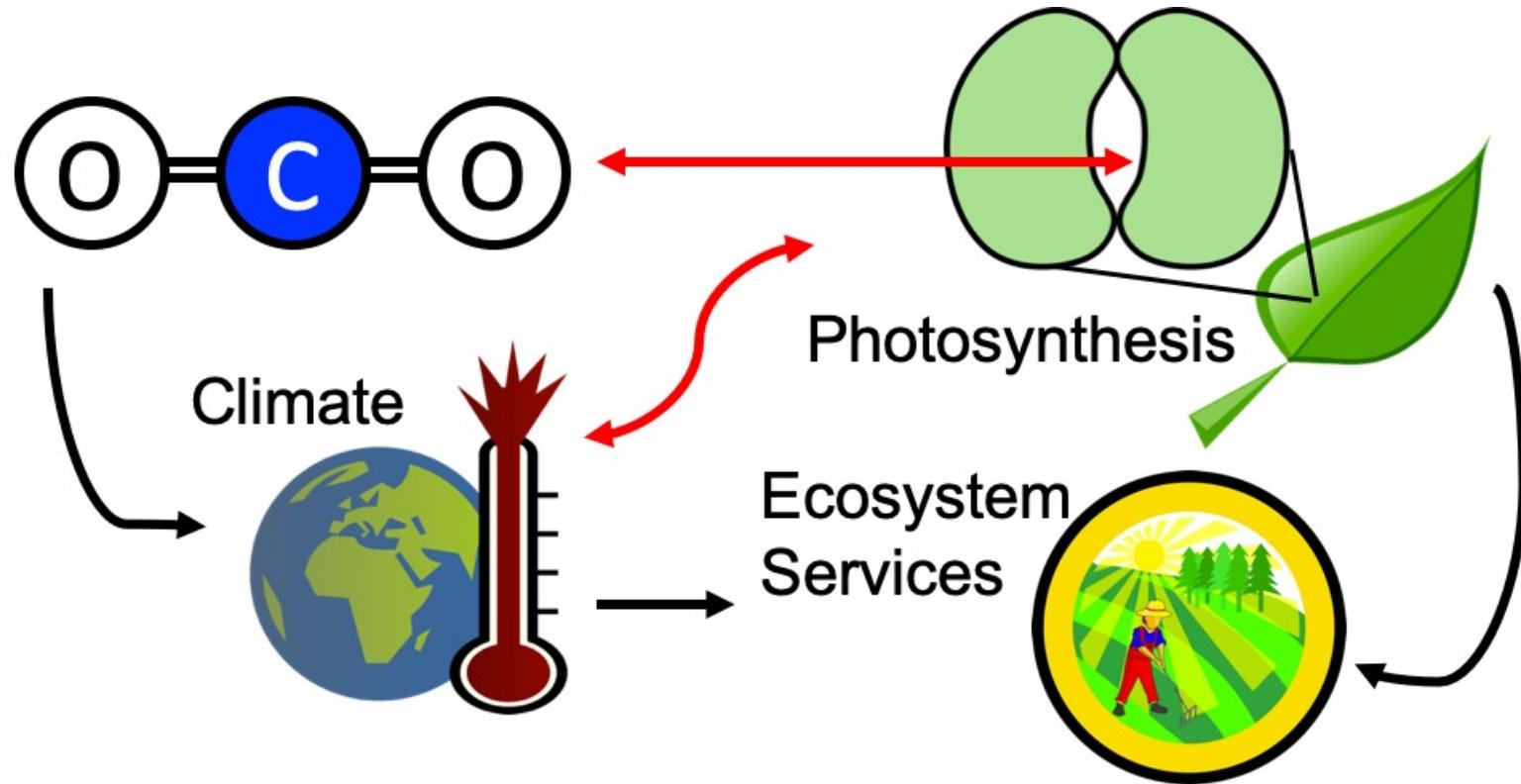


Photosynthesis is a dynamic process that is likely to be impacted by global change



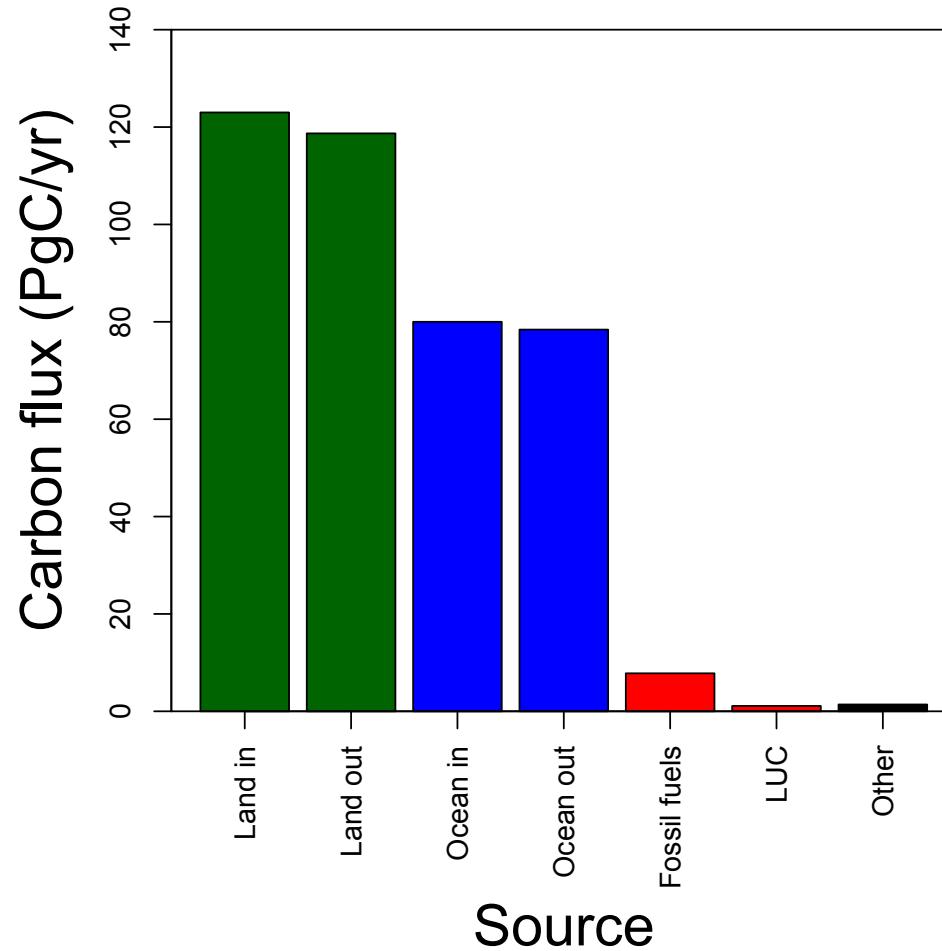
MODIS, NASA

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



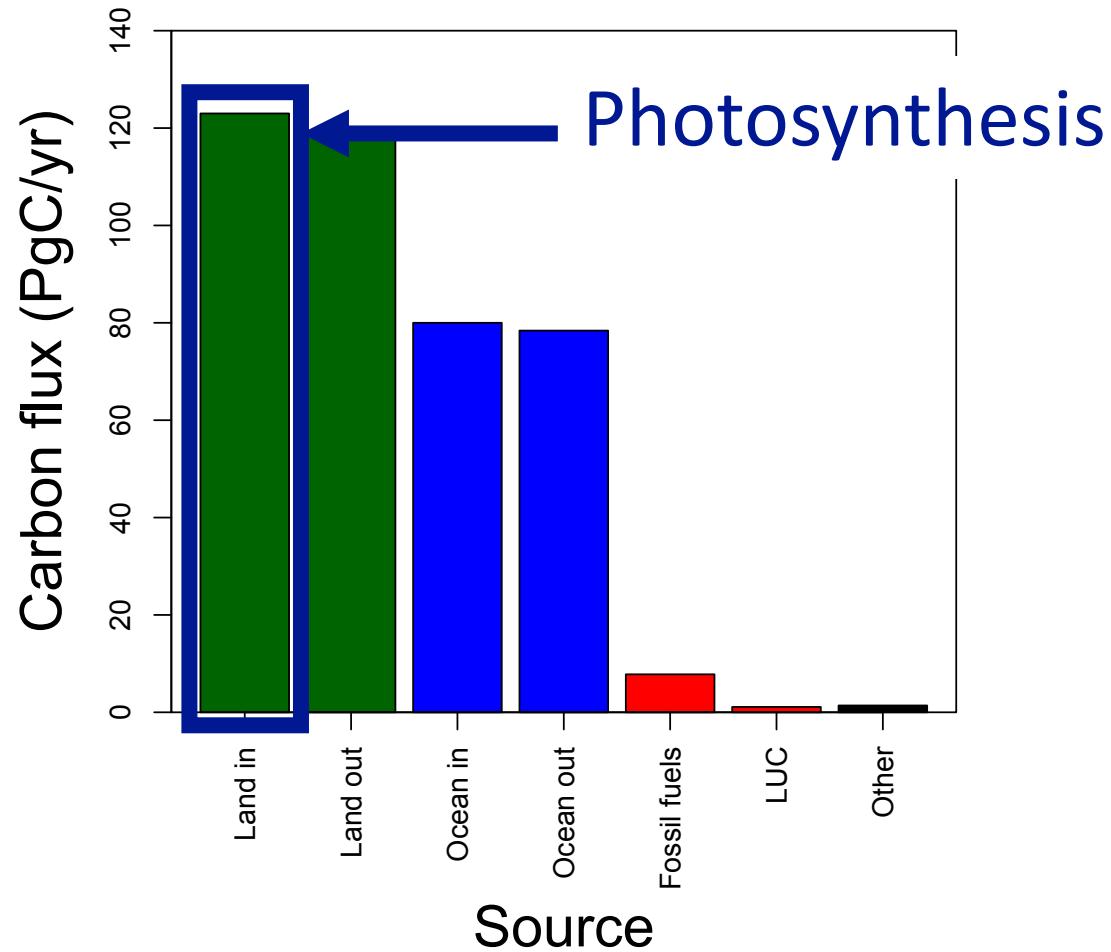
Photosynthesis is important! An example...

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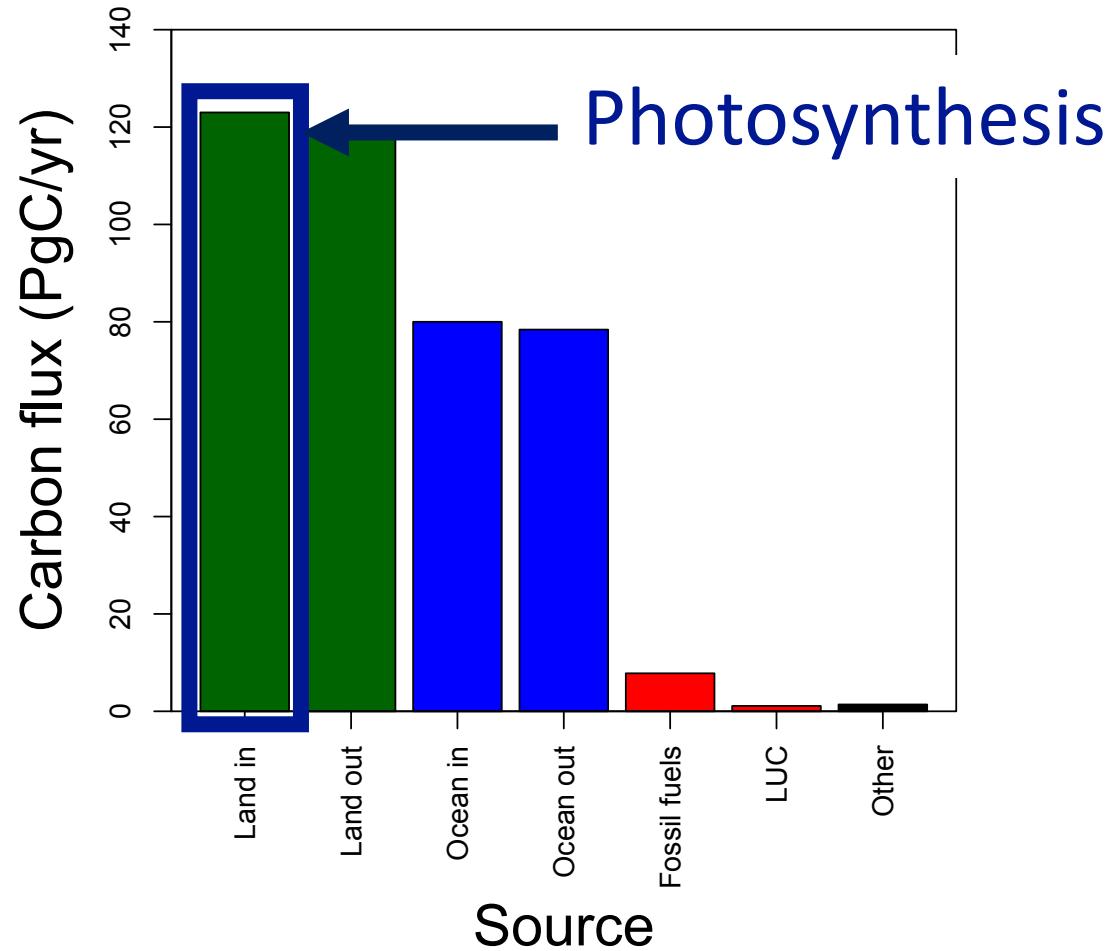


Data from IPCC (2013)

Photosynthesis is important! An example...

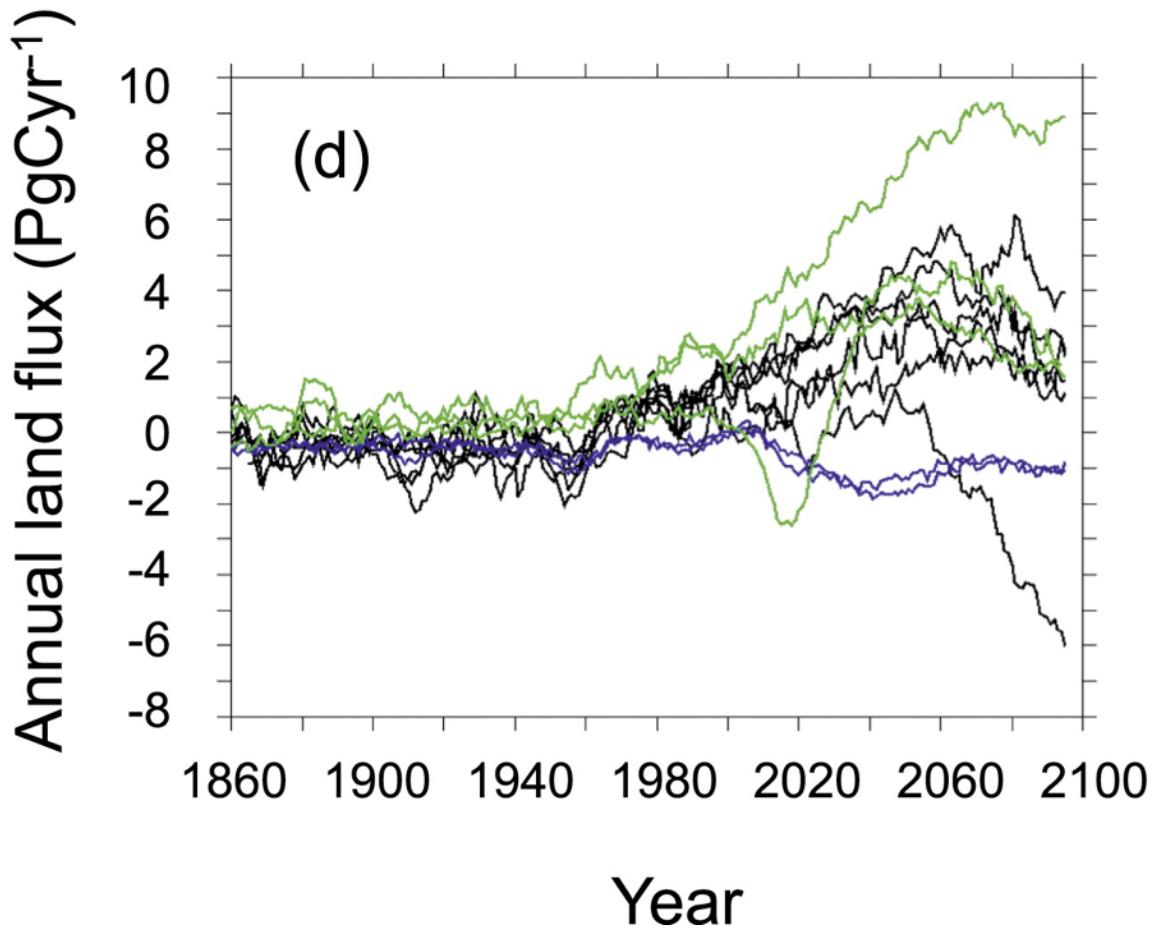


Photosynthesis is important! An example...

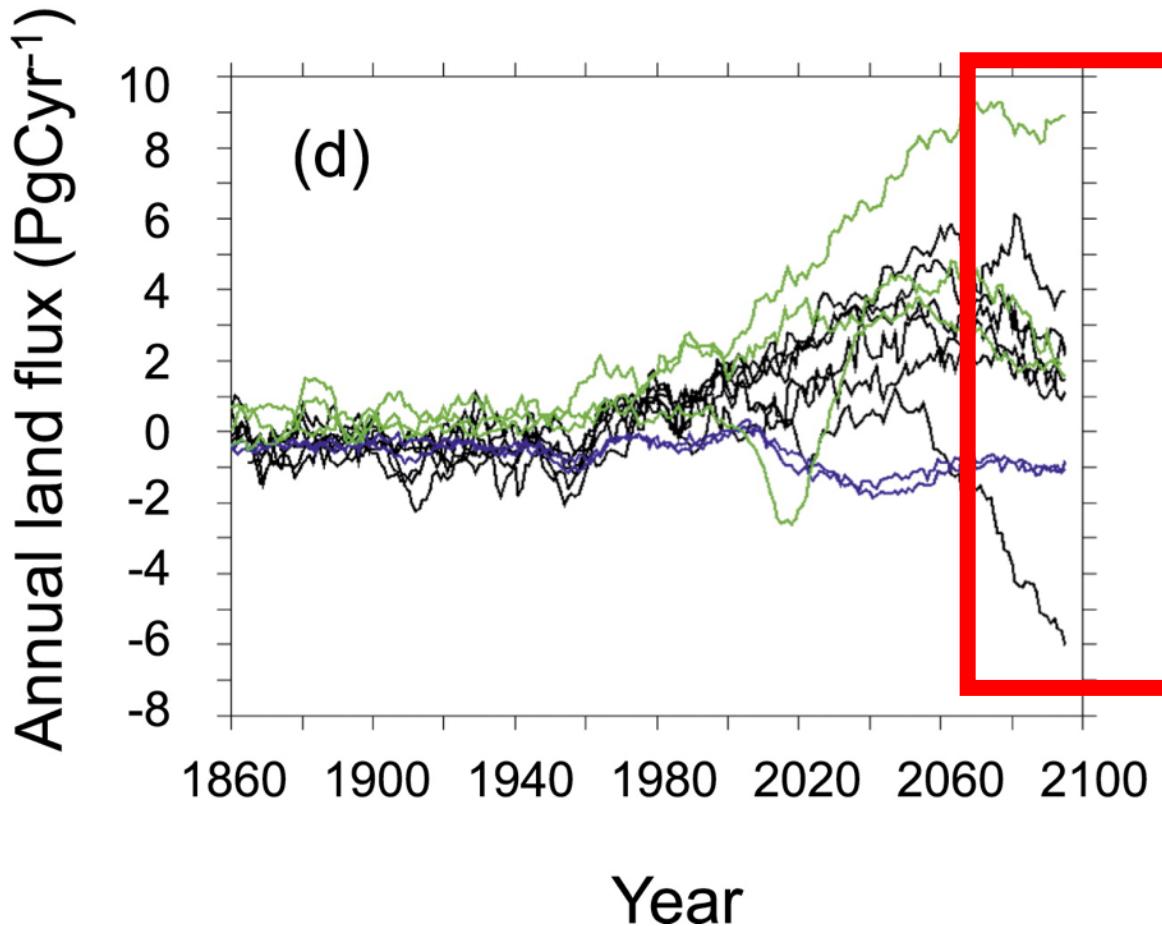


A small percentage change in photosynthesis can have large consequences for climate

But predictions are uncertain!

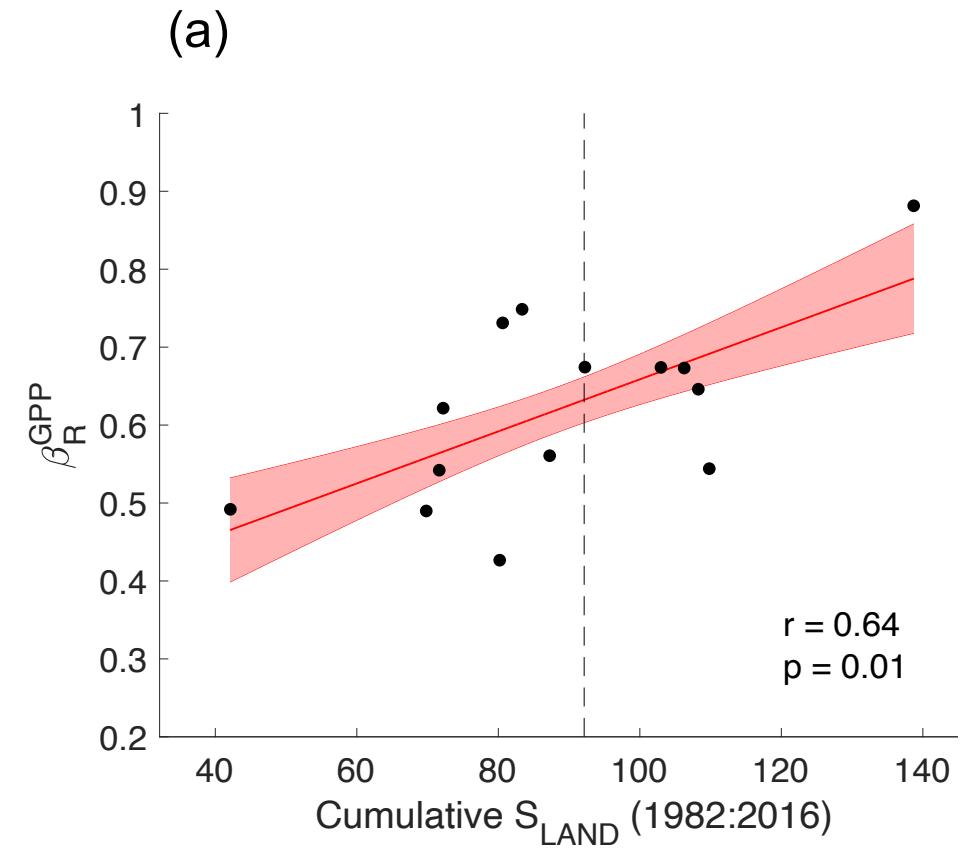
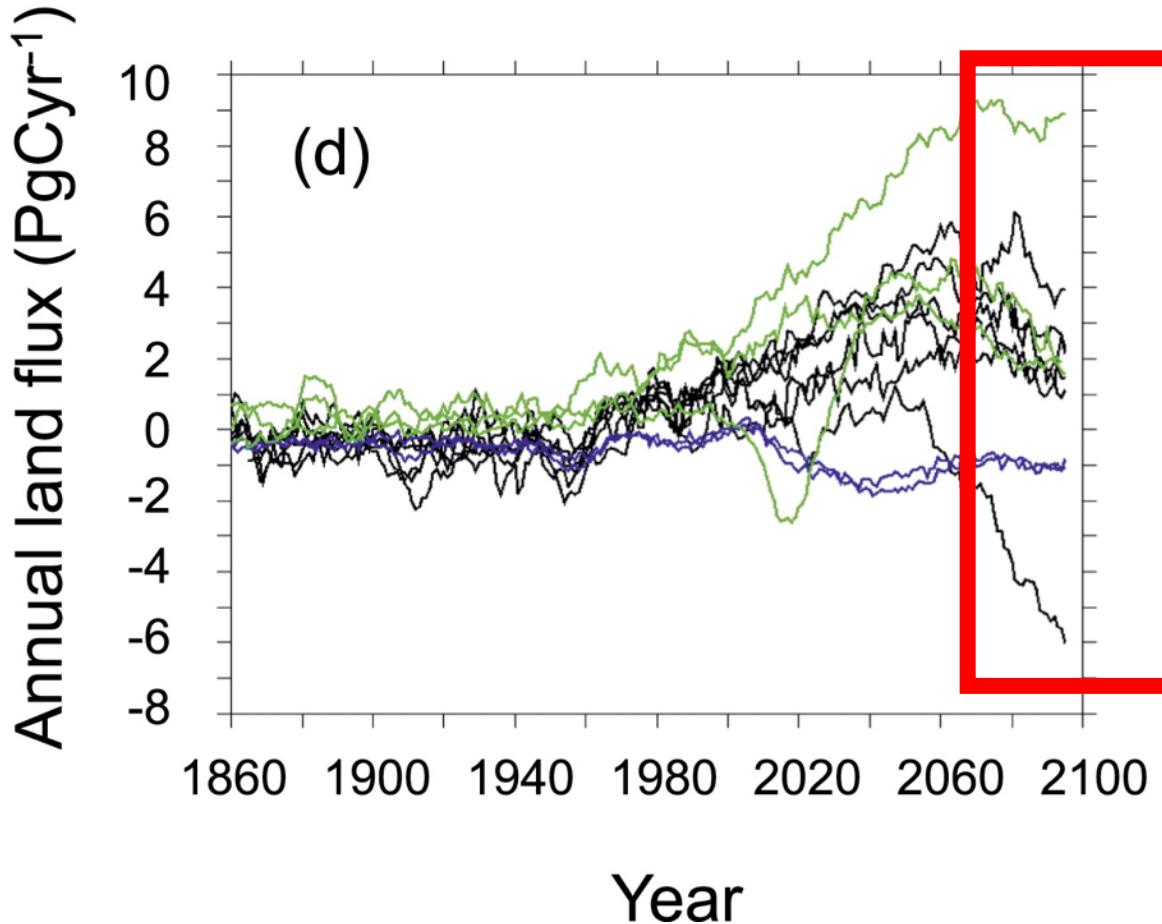


But predictions are uncertain!



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

This uncertainty is driven by uncertainty in photosynthesis



Why the uncertainty? Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

Planta
© by Springer-Verlag 1980

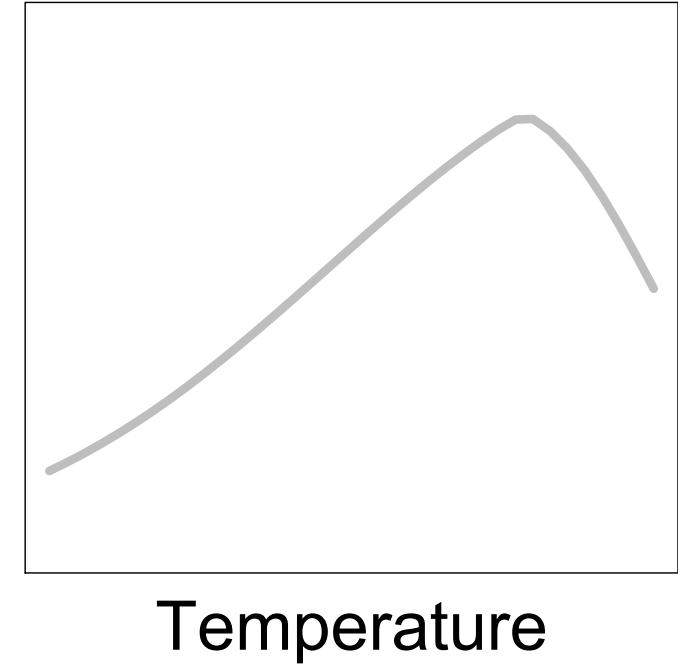
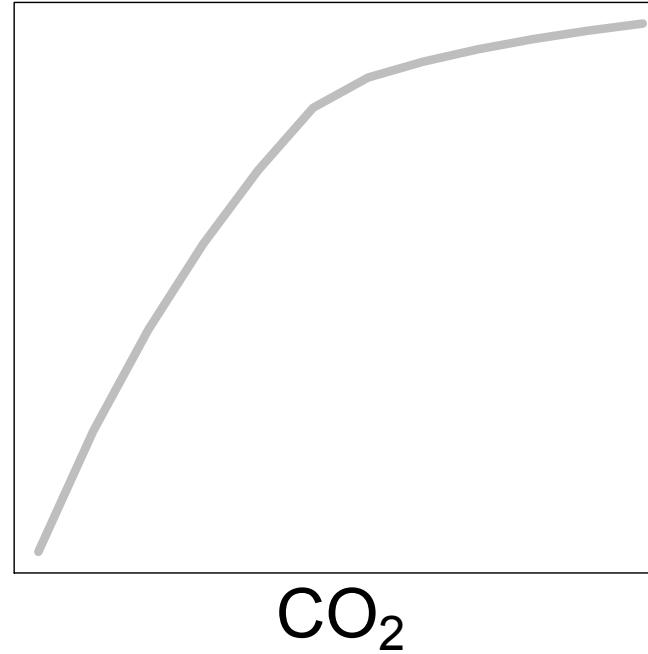
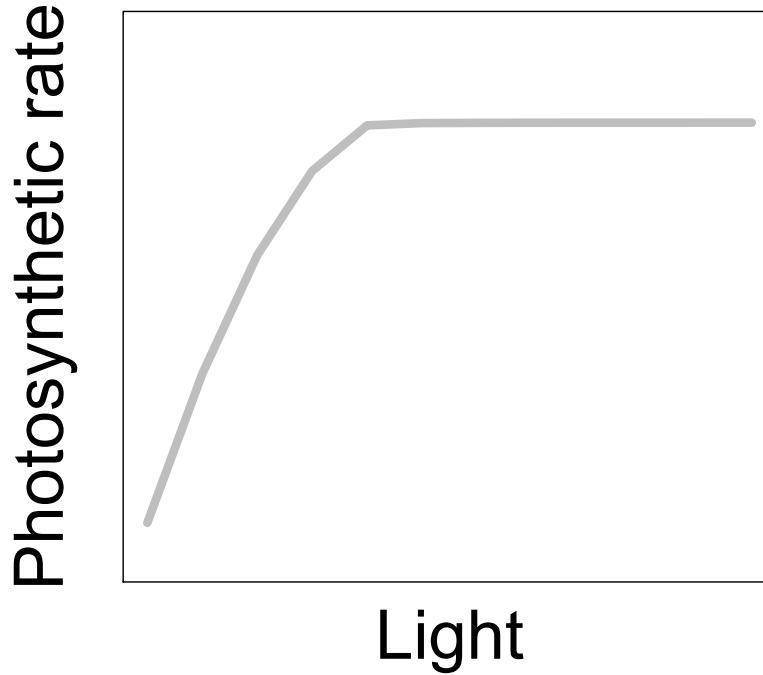
A Biochemical Model of Photosynthetic CO₂ Assimilation in Leaves of C₃ Species

G.D. Farquhar¹, S. von Caemmerer¹, and J.A. Berry²

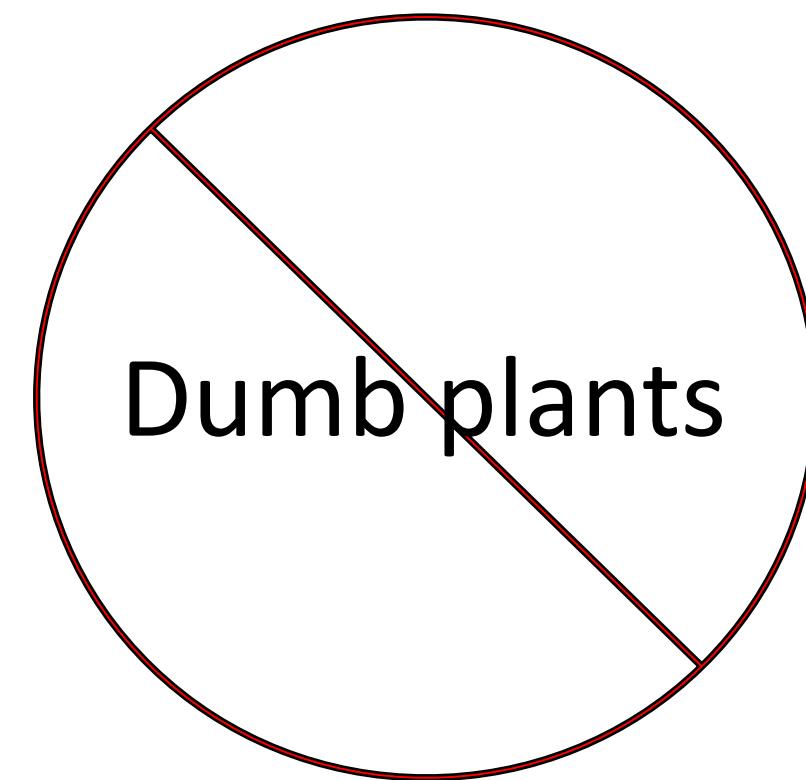
¹ Department of Environmental Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City ACT 2601, Australia and

² Carnegie Institution of Washington, Department of Plant Biology, Stanford, Cal. 94305, USA

These produce short term responses that match data



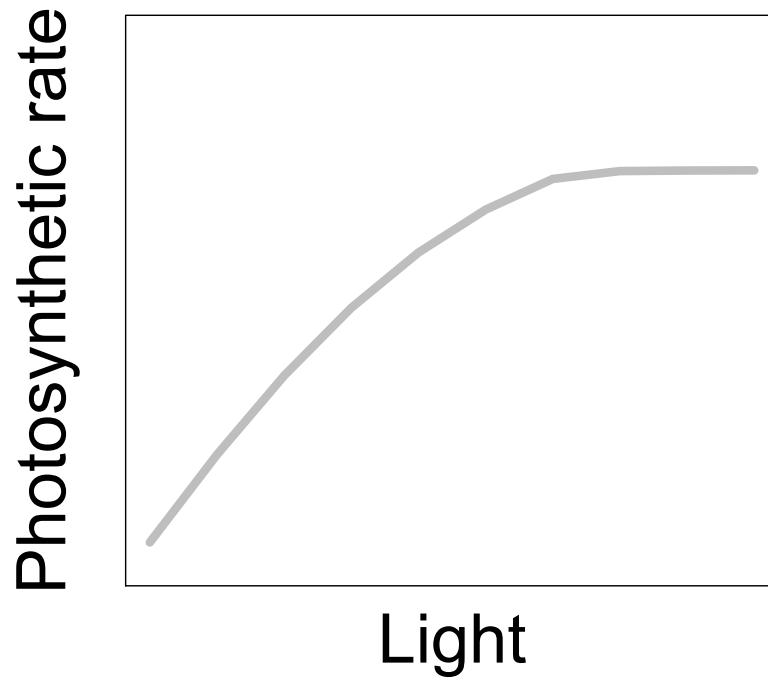
Why the uncertainty? Long-term responses differ from short-term responses due to acclimation



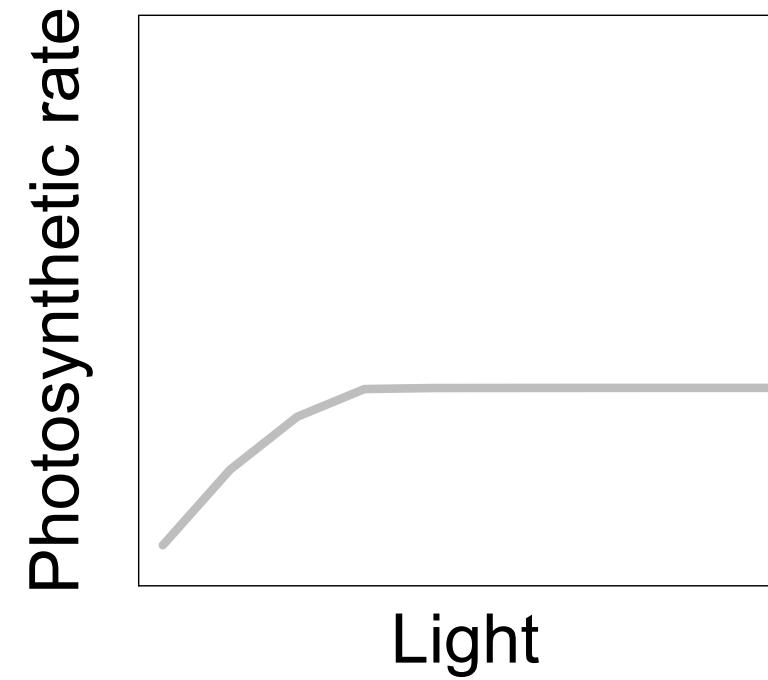
Dumb plants

Acclimation: an example

Acclimated to high light

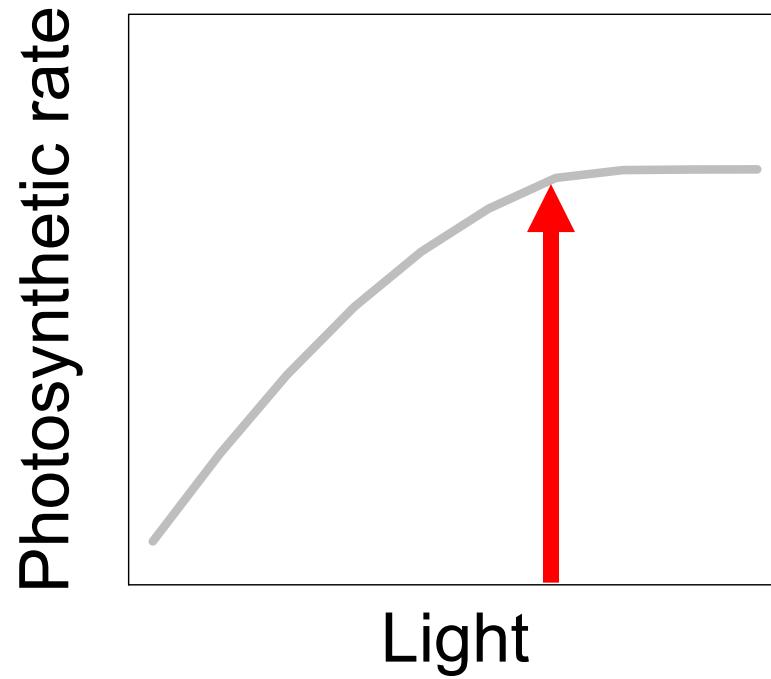


Acclimated to low light

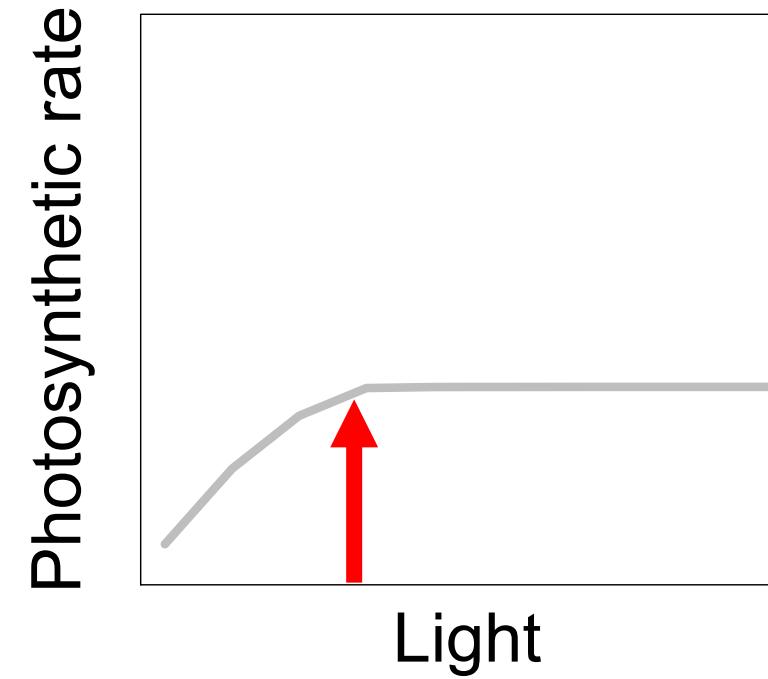


Acclimation: an example

Acclimated to high light



Acclimated to low light



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

Acclimation is ubiquitous and well known...

CO₂: Bazzaz (1990)

Ann. Rev. Ecol. Syst. 1990, 21:167–96
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THE RESPONSE OF NATURAL ECOSYSTEMS TO THE RISING GLOBAL CO₂ LEVELS

F. A. Bazzaz

Light: Boardman (1977)

Ann. Rev. Plant Physiol. 1977, 28:355–77
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COMPARATIVE PHOTOSYNTHESIS OF SUN AND SHADE PLANTS

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

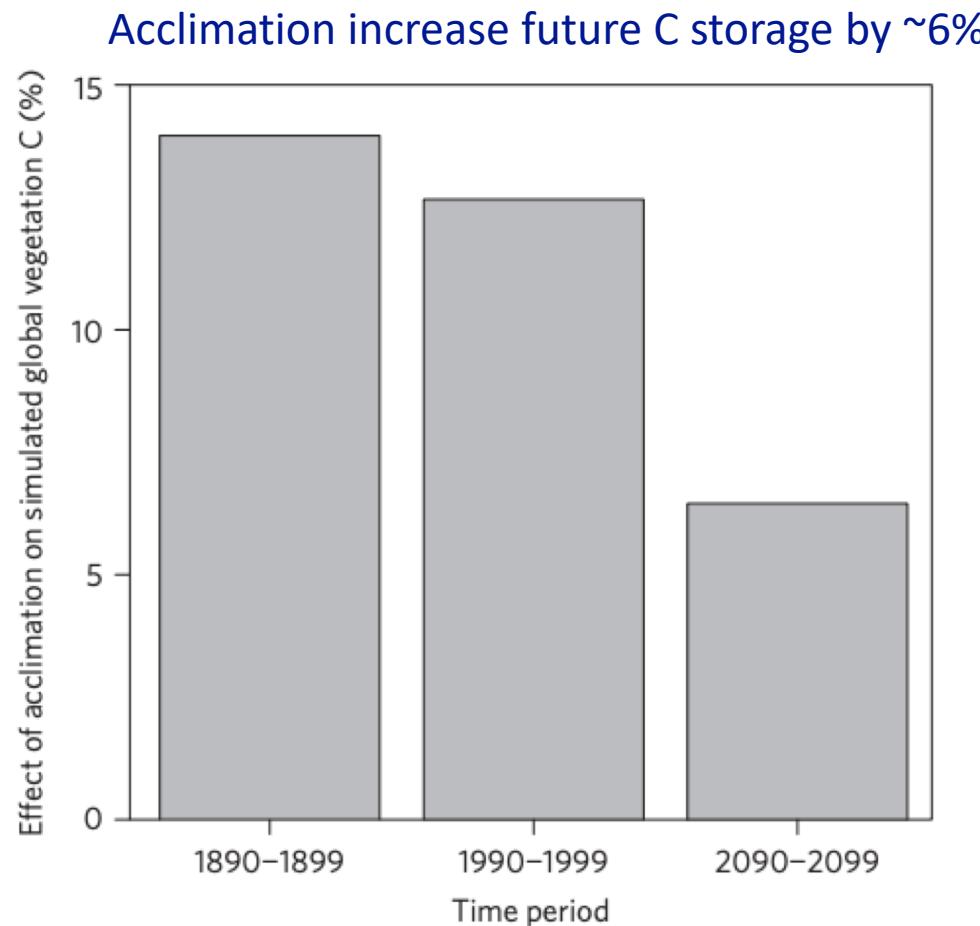
Temperature: Berry & Björkman (1980)

Ann. Rev. Plant Physiol. 1980, 31:491–543
Copyright © 1980 by Annual Reviews Inc. All rights reserved

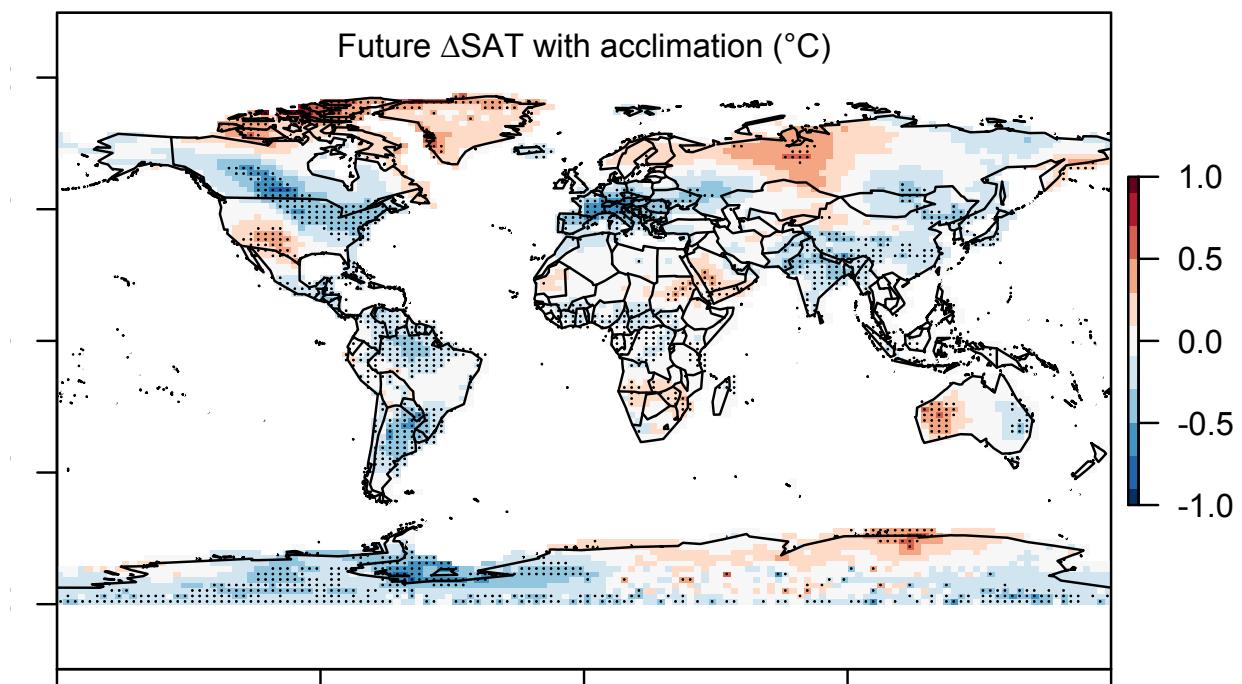
PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

Joseph Berry and Olle Björkman¹

...and can impact carbon cycling and climate



Acclimation alters future temperature by >1°C

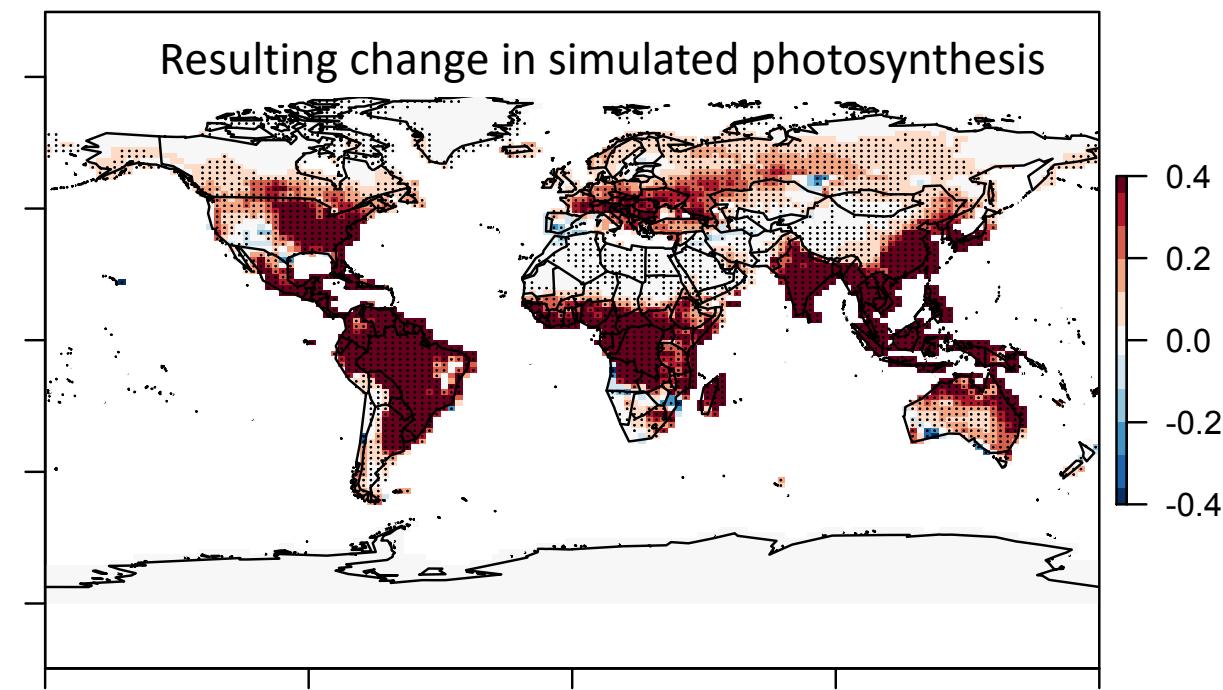
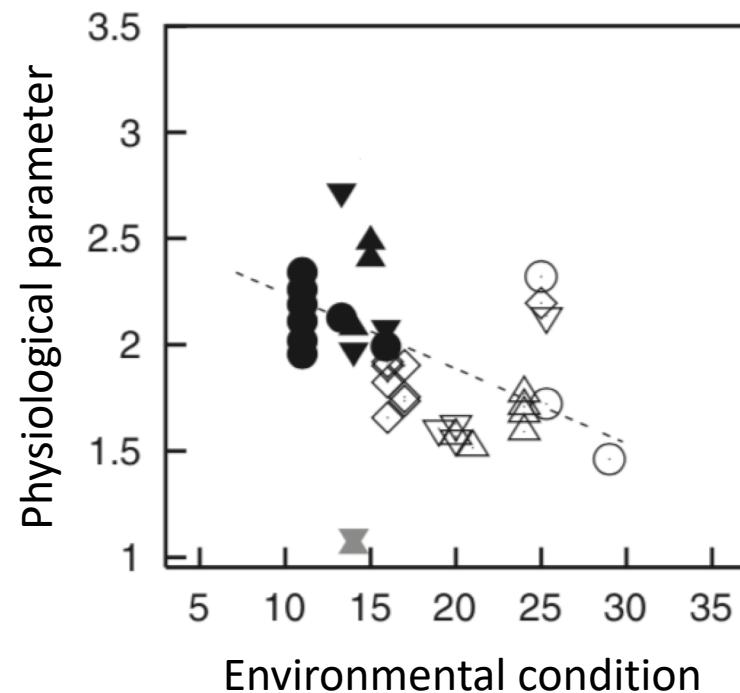


Unfortunately,
no theoretical model for
photosynthetic acclimation exists

Lack of theory results in...

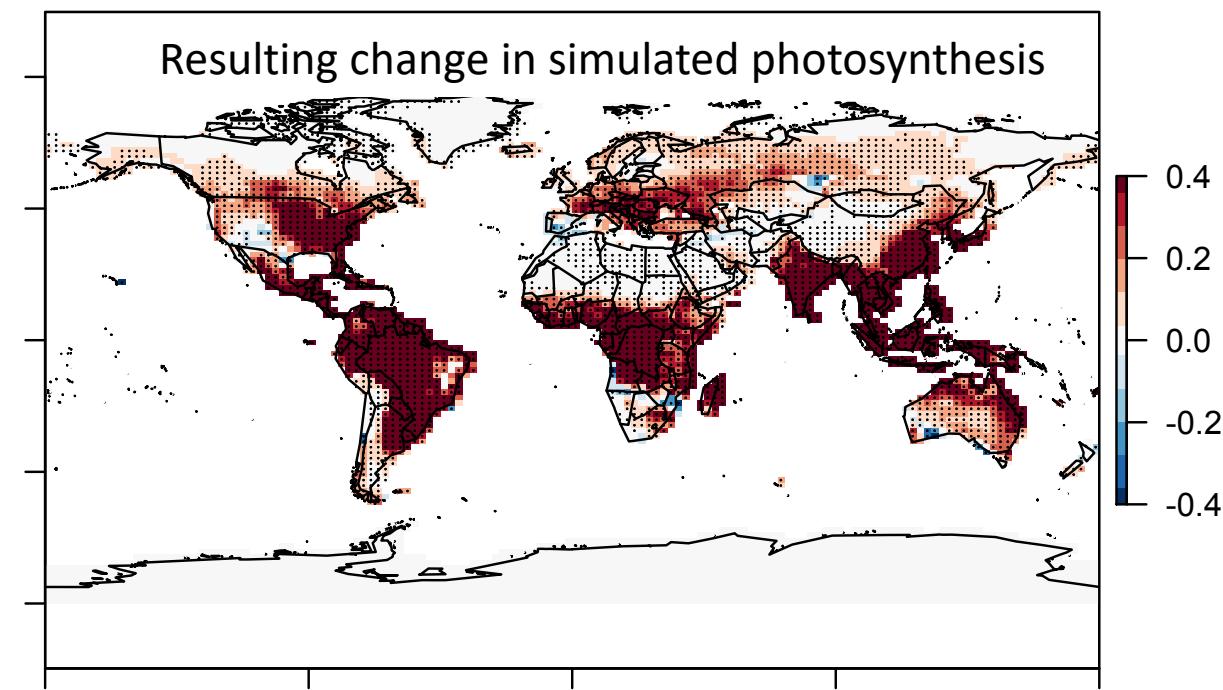
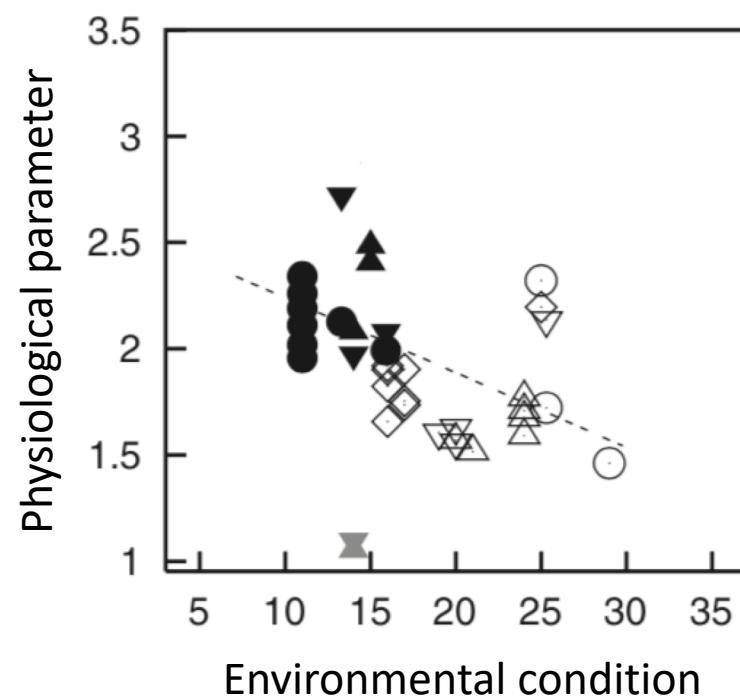
Lack of theory results in...

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



Lack of theory results in...

- Inability to test mechanisms



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](#) ^

Optimization: Least cost theory

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

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$



Must predict optimal rates of both

Optimal photosynthesis

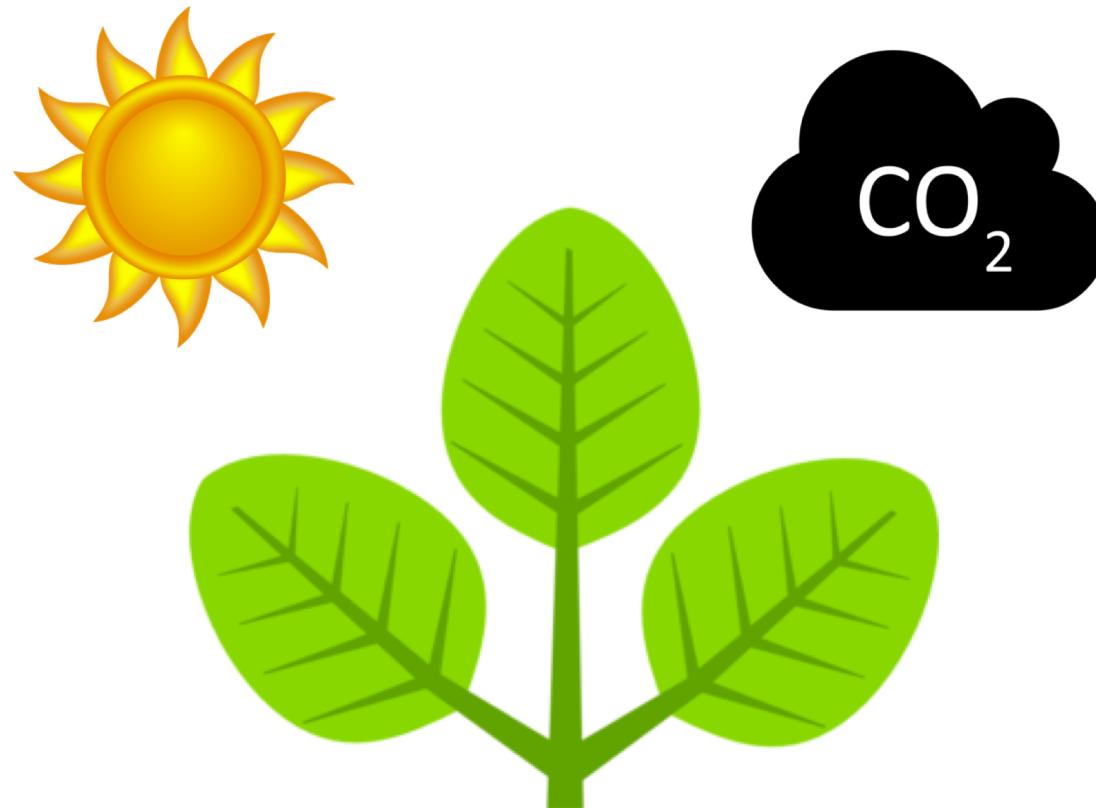
Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$

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

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
photosynthetic biochemistry}

Biochemistry optimization

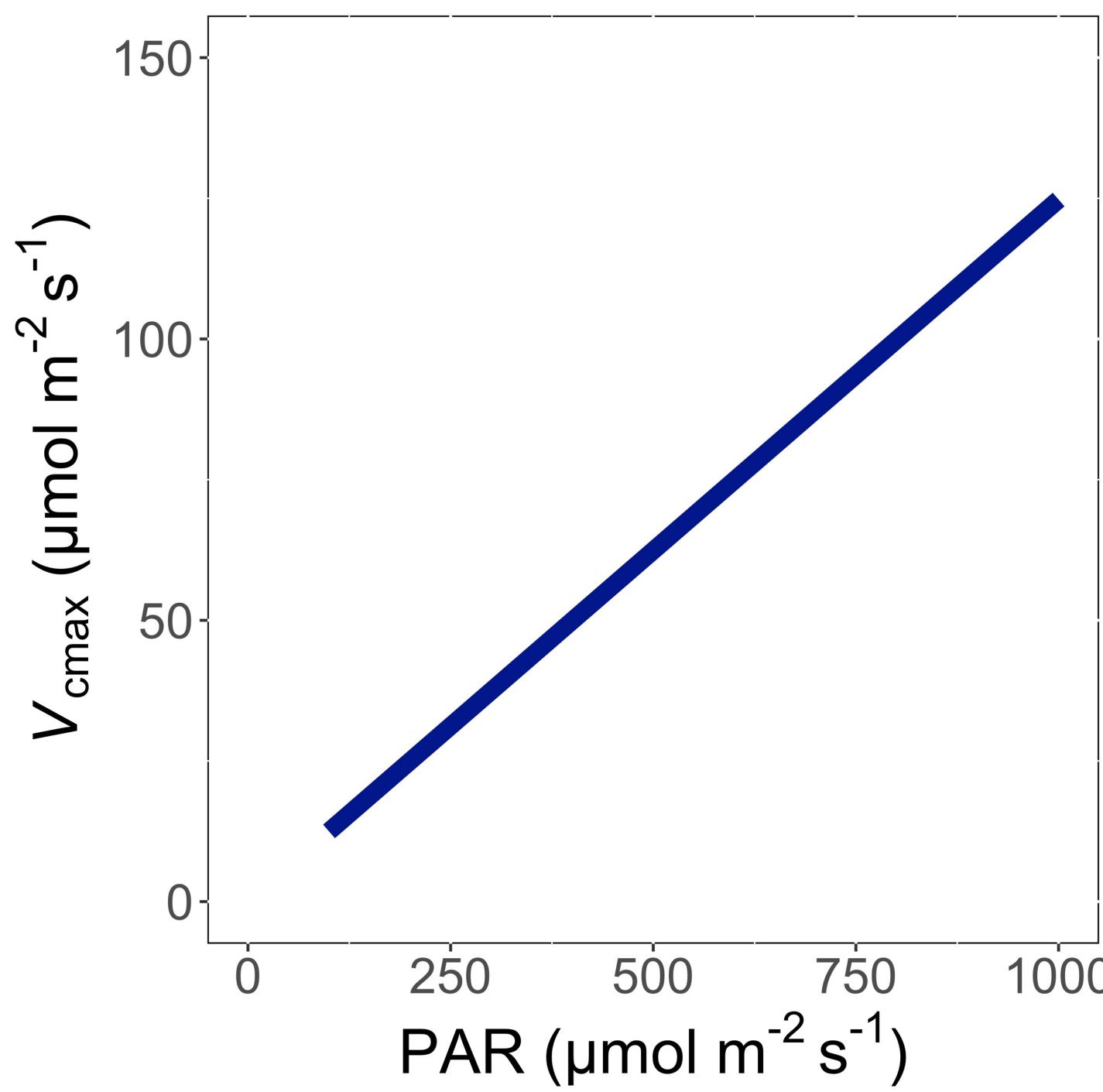


Plant
biochemistry
setup will aim for
equal limitation
by all factors

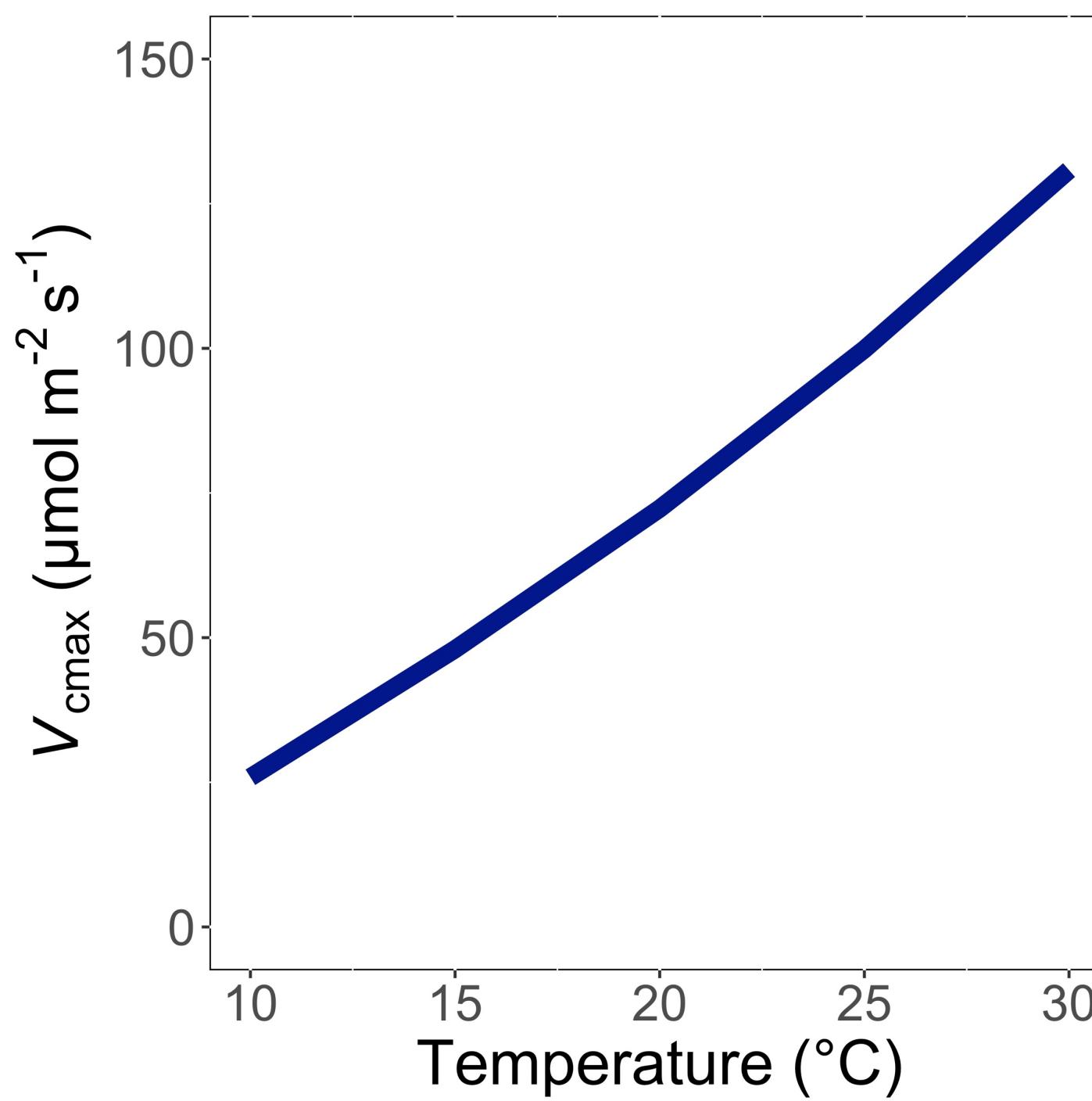
[TALK TO ME LATER ABOUT THE MATHS]

Biochemistry trait

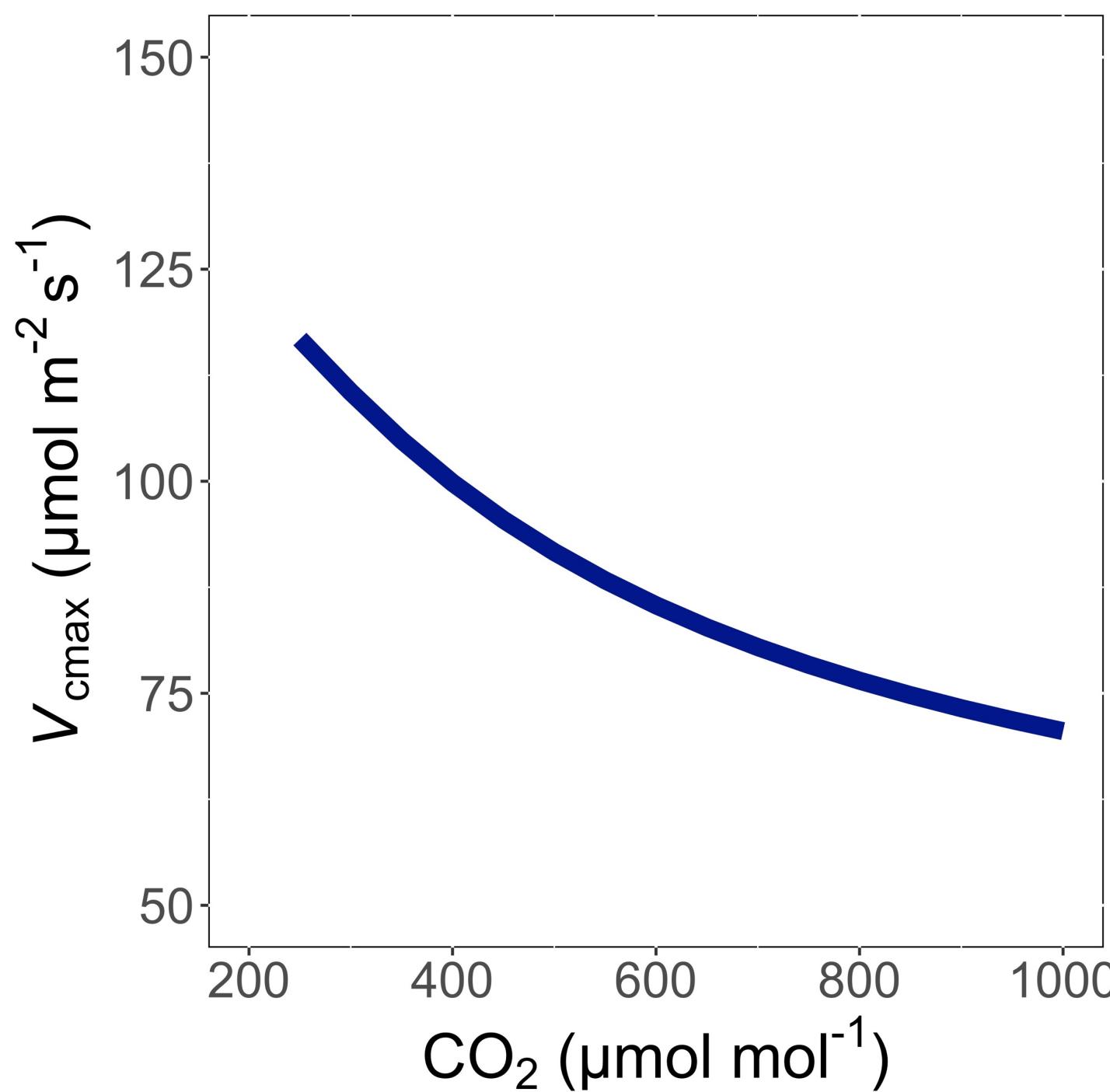
The maximum rate of Rubisco carboxylation (V_{cmax})



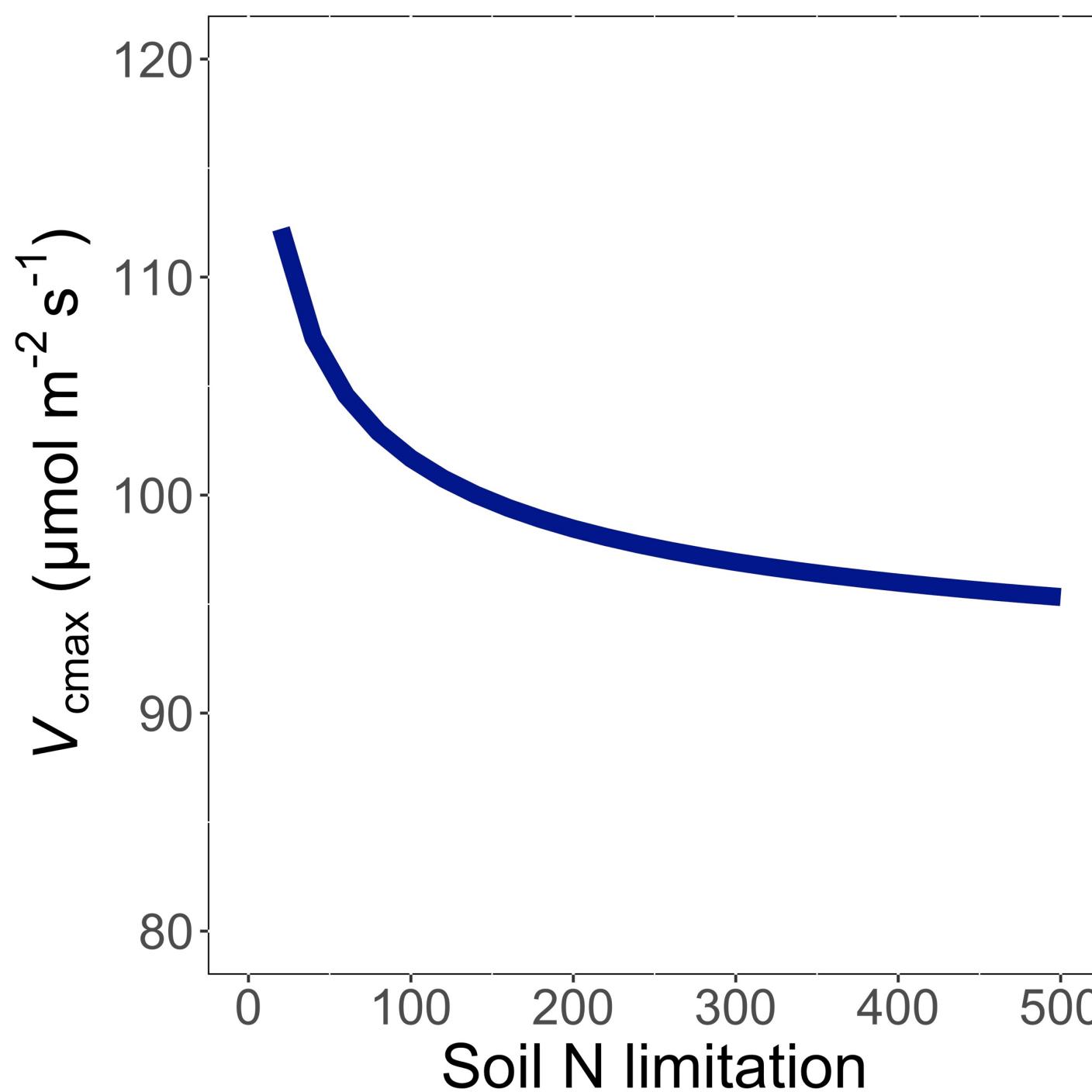
$V_{c\max}$ increases
with light because
of greater electron
transport



$V_{c\max}$ increases
with temperature
because of greater
electron transport
and
photorespiration

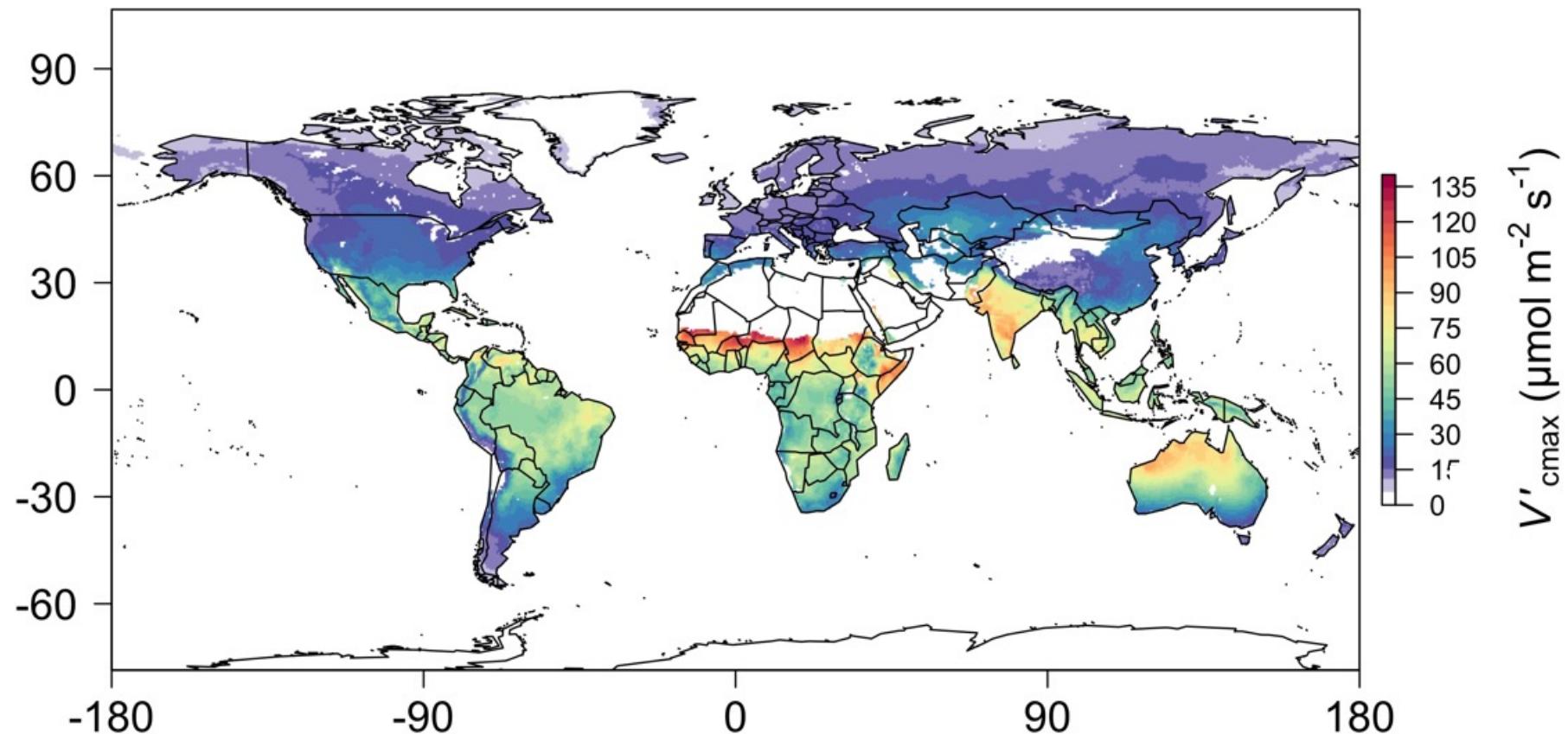


V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf and less photorespiration



$V_{c\max}$ decreases
with soil N
limitation because
Rubisco requires a
lot of N

We can predict optimal traits in different environments



Ok, great, but now what?

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

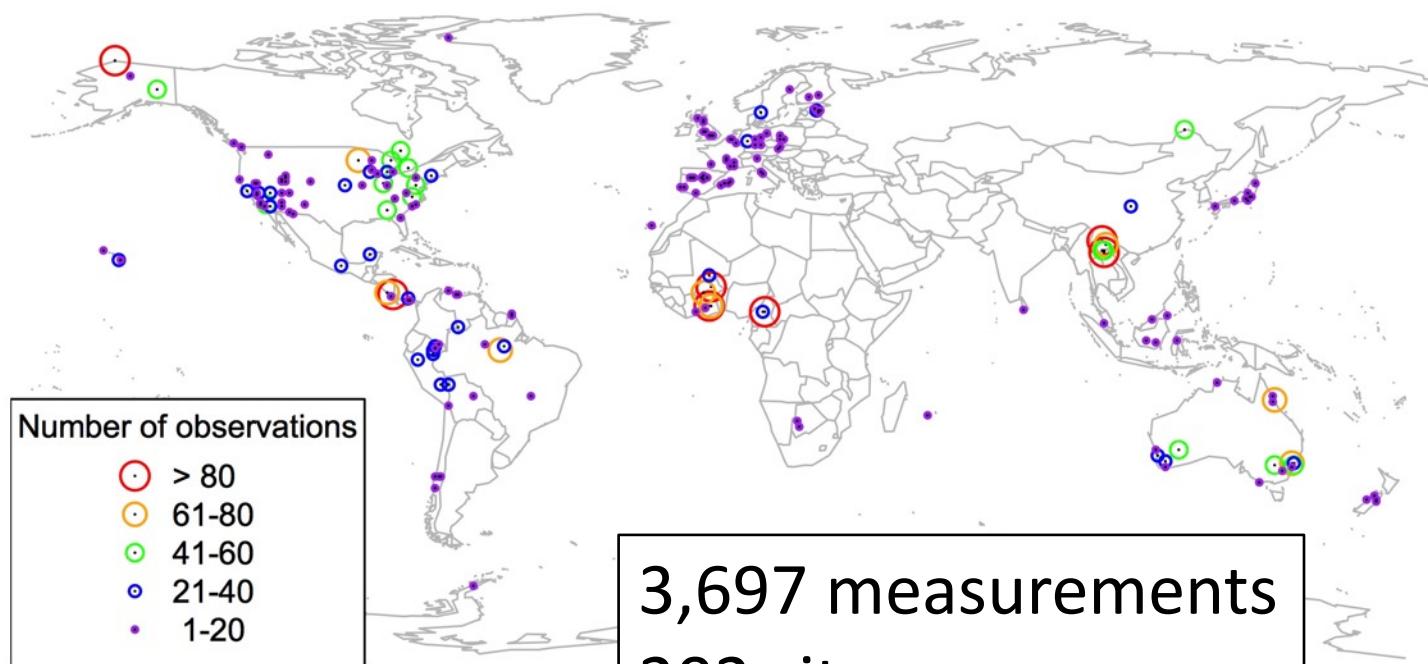
Let's tackle some big questions in
plant ecophysiology!

Big questions

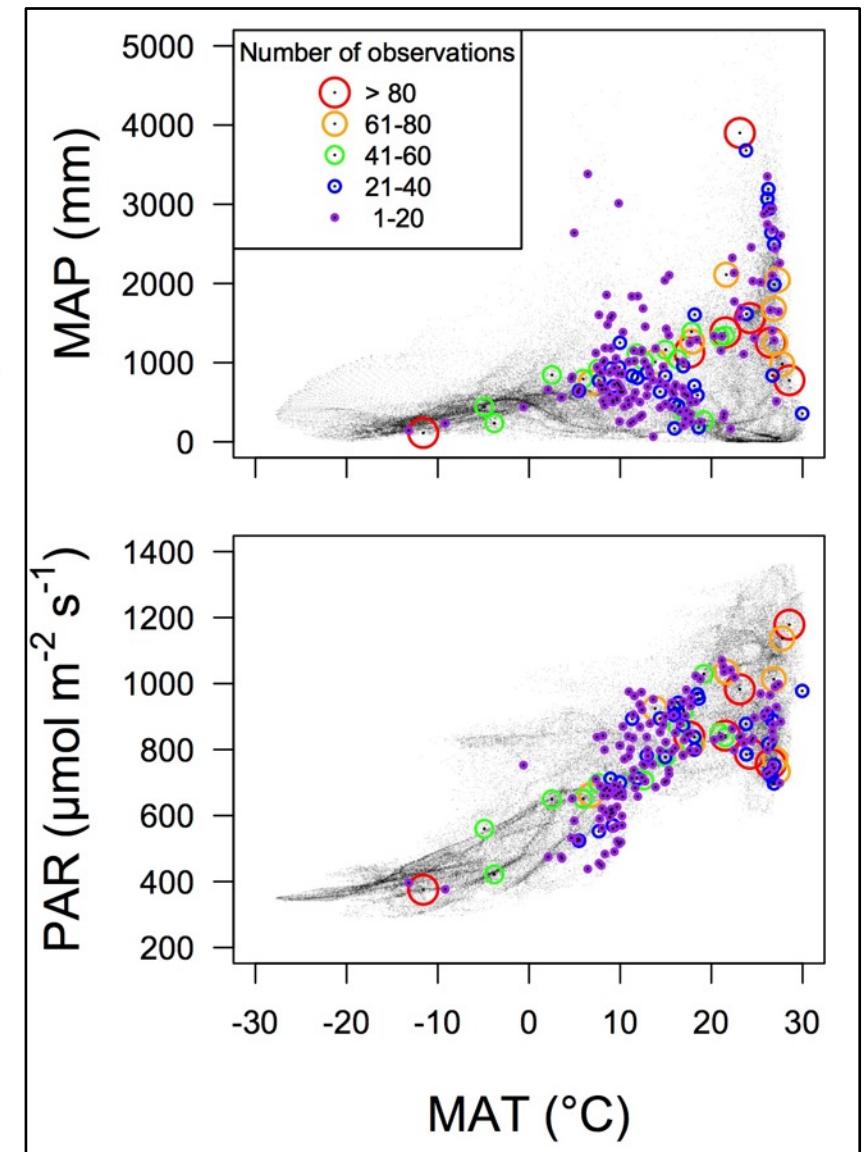
1. Is photosynthesis **optimized** to the environment?
2. How do plants acclimate to **soil nitrogen**?
3. What does acclimation mean for **future** terrestrial biogeochemical cycling?
4. When is **C₄** photosynthesis an advantage over C₃ photosynthesis?

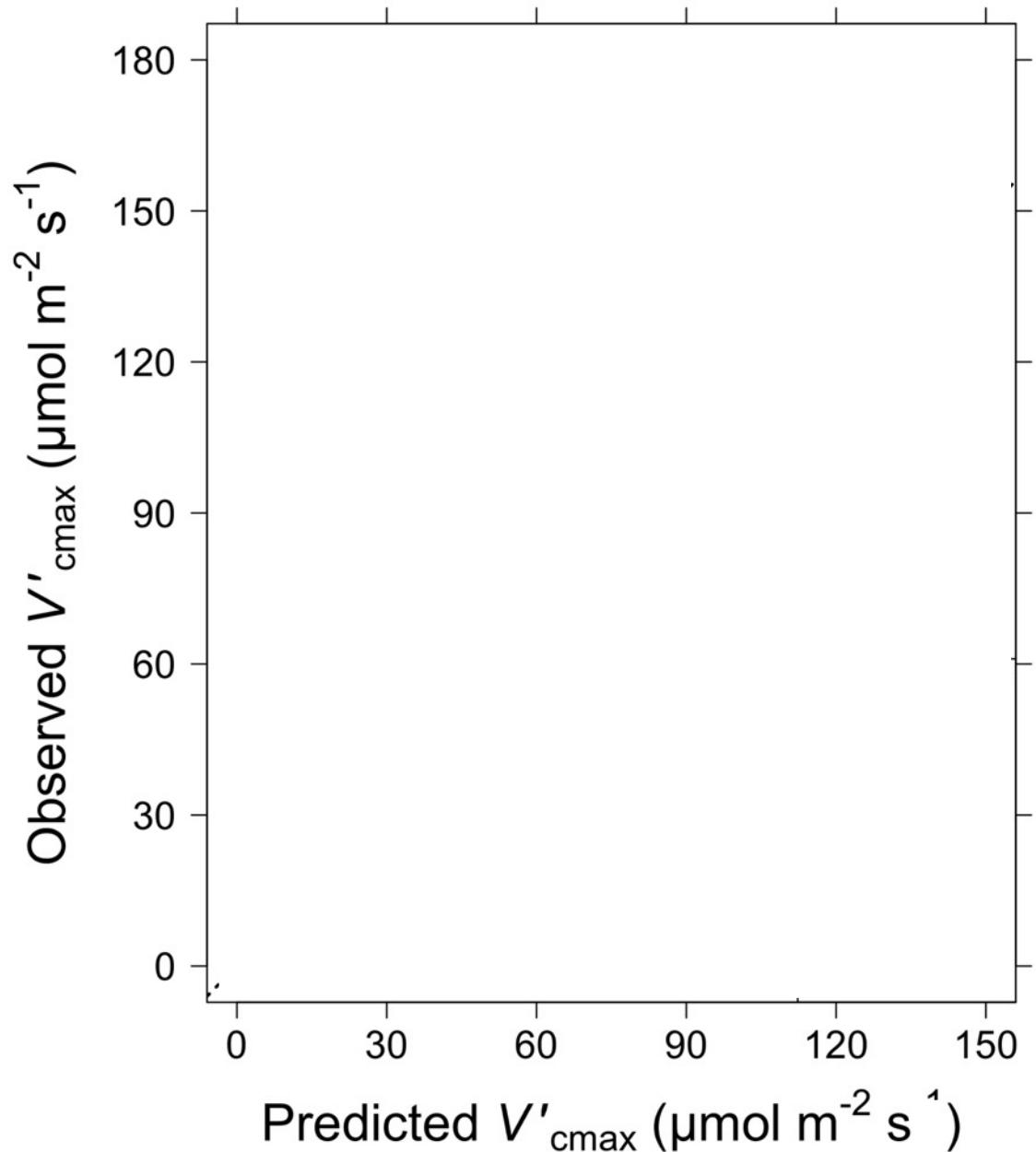
Question 1: Is photosynthesis optimized to the environment?

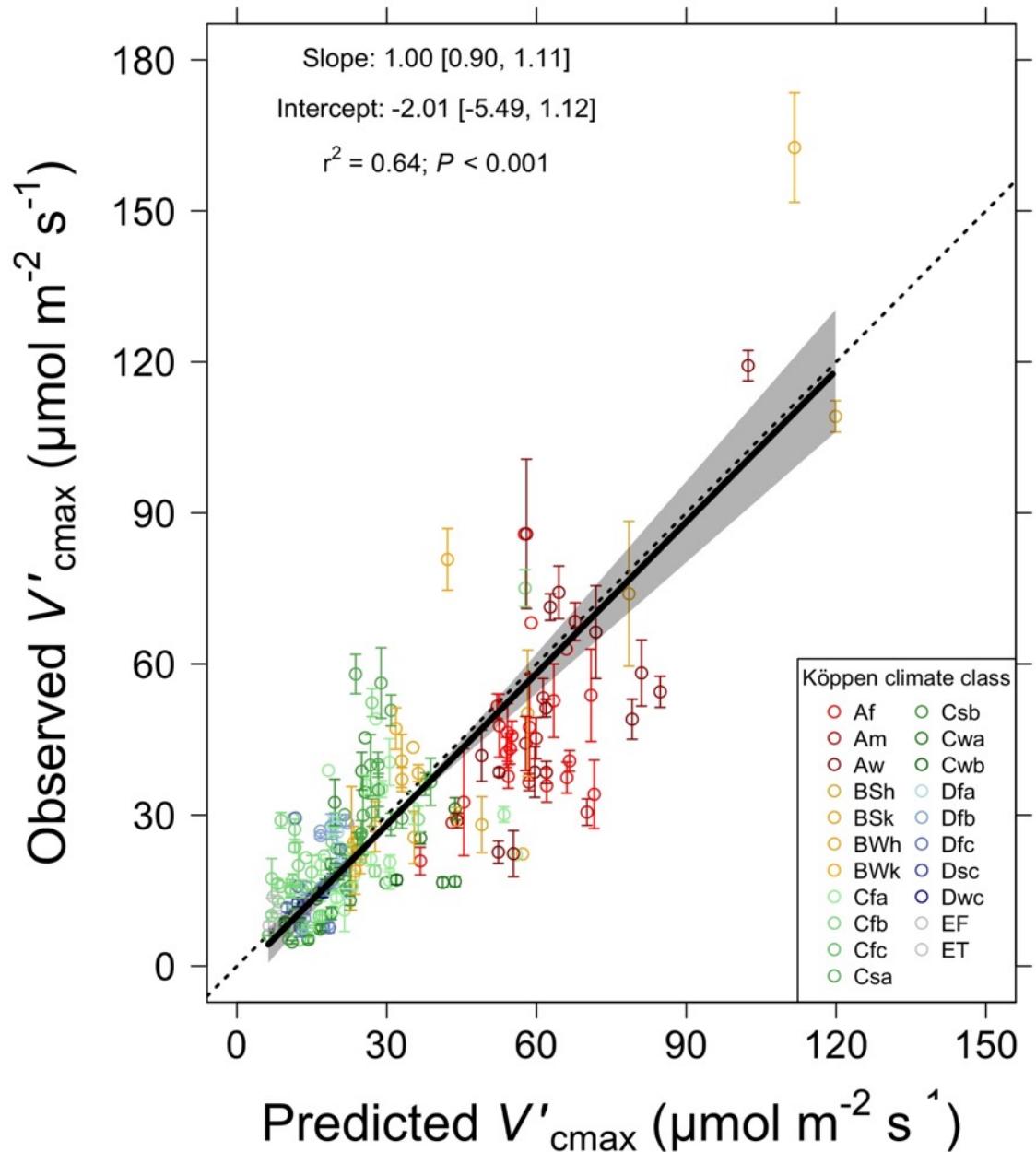
Global V_{cmax} dataset



3,697 measurements
202 sites
> 600 genera







Optimal V'_{cmax} is
similar to
observed
values

Question 1: Is photosynthesis optimized to the environment?

YES! Photosynthesis acclimates spatially as expected from optimization

Question 2: How do plants
acclimate to soil nitrogen?

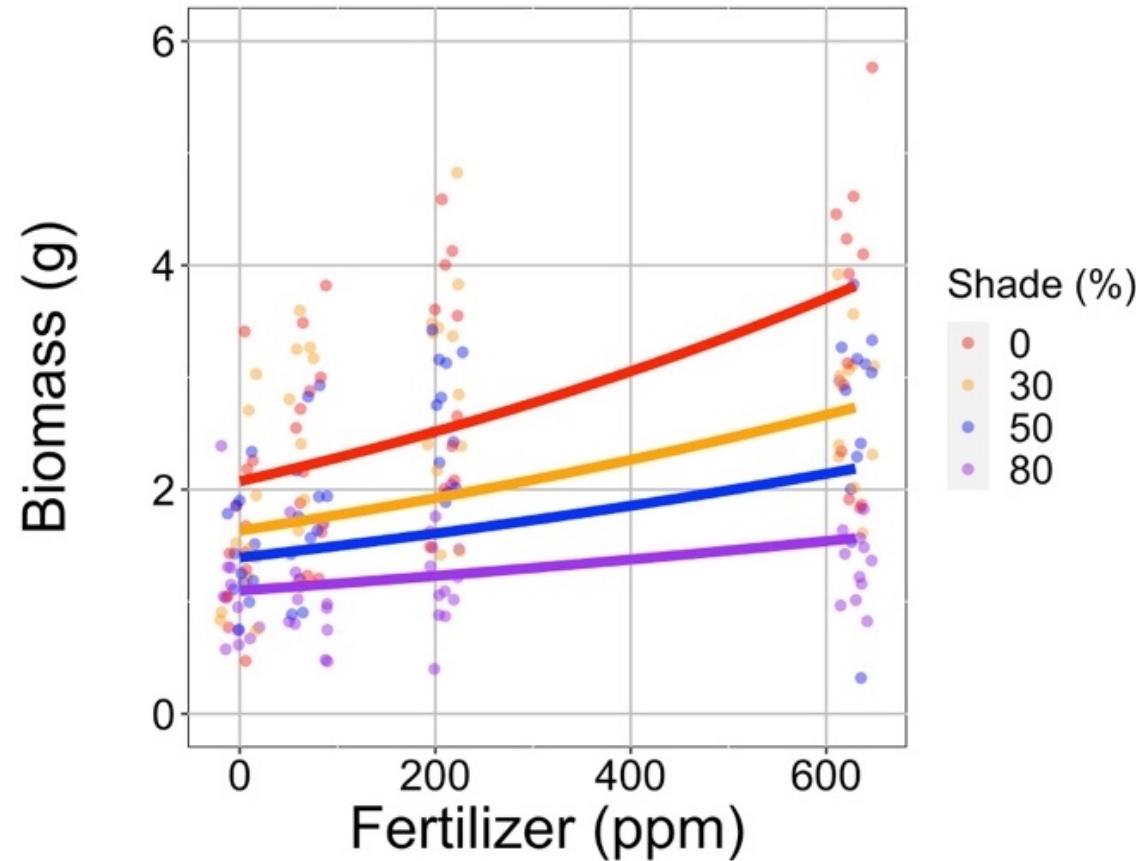
The lab has examined soil nitrogen impacts in many contexts

- 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)



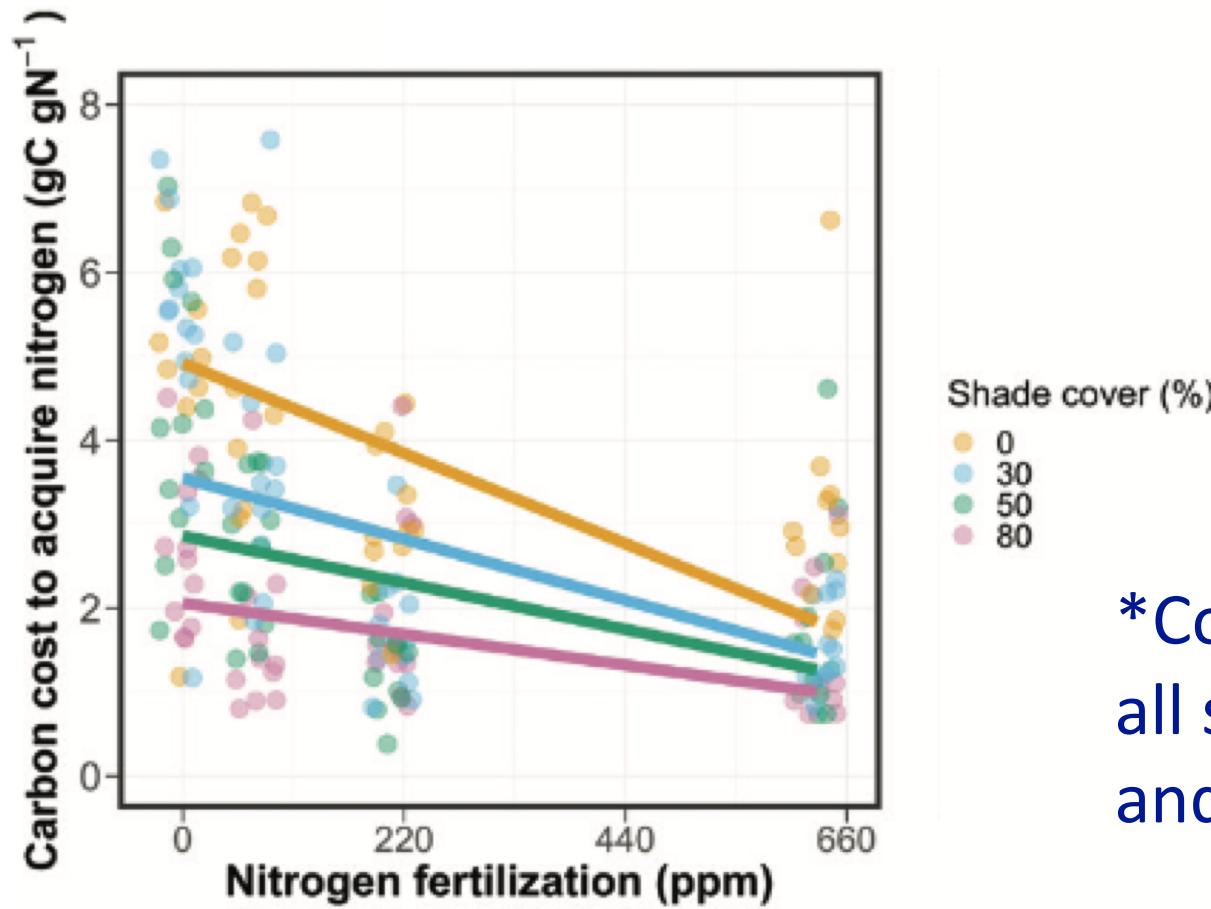
What have we learned?

Result 1: Growth increases with increasing soil N



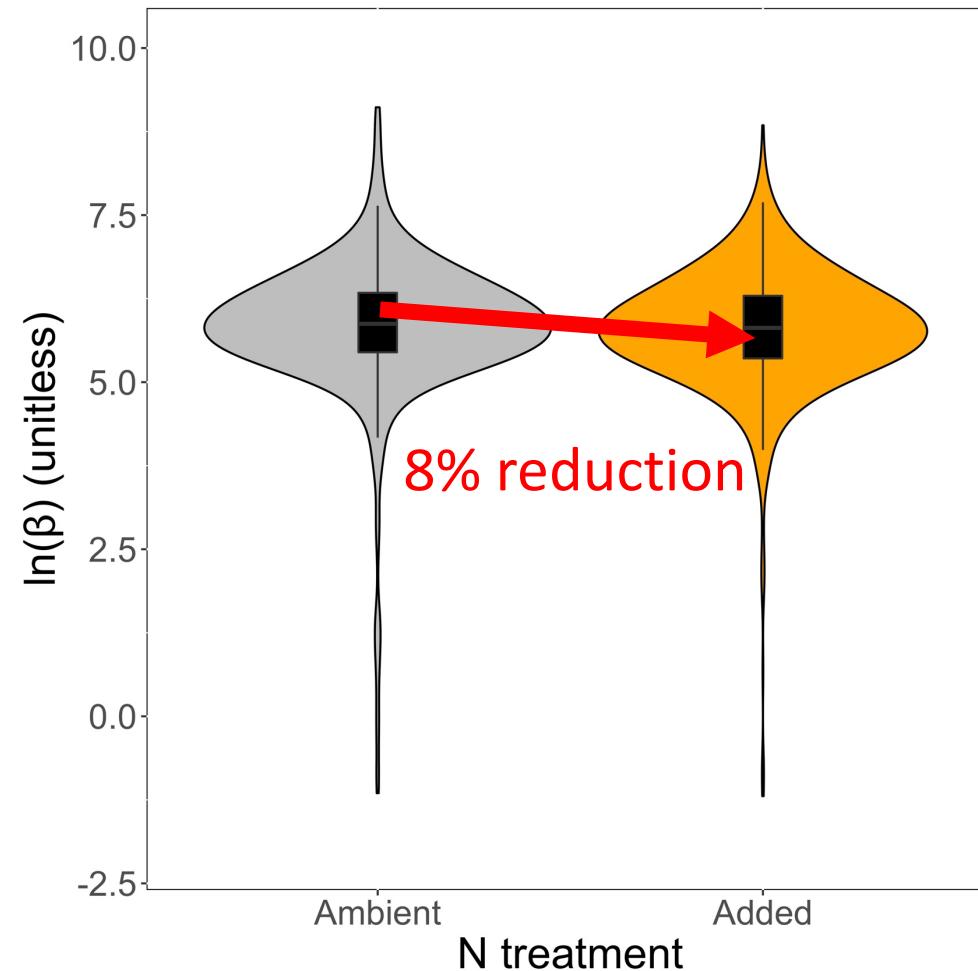
*Consistent across all studies

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



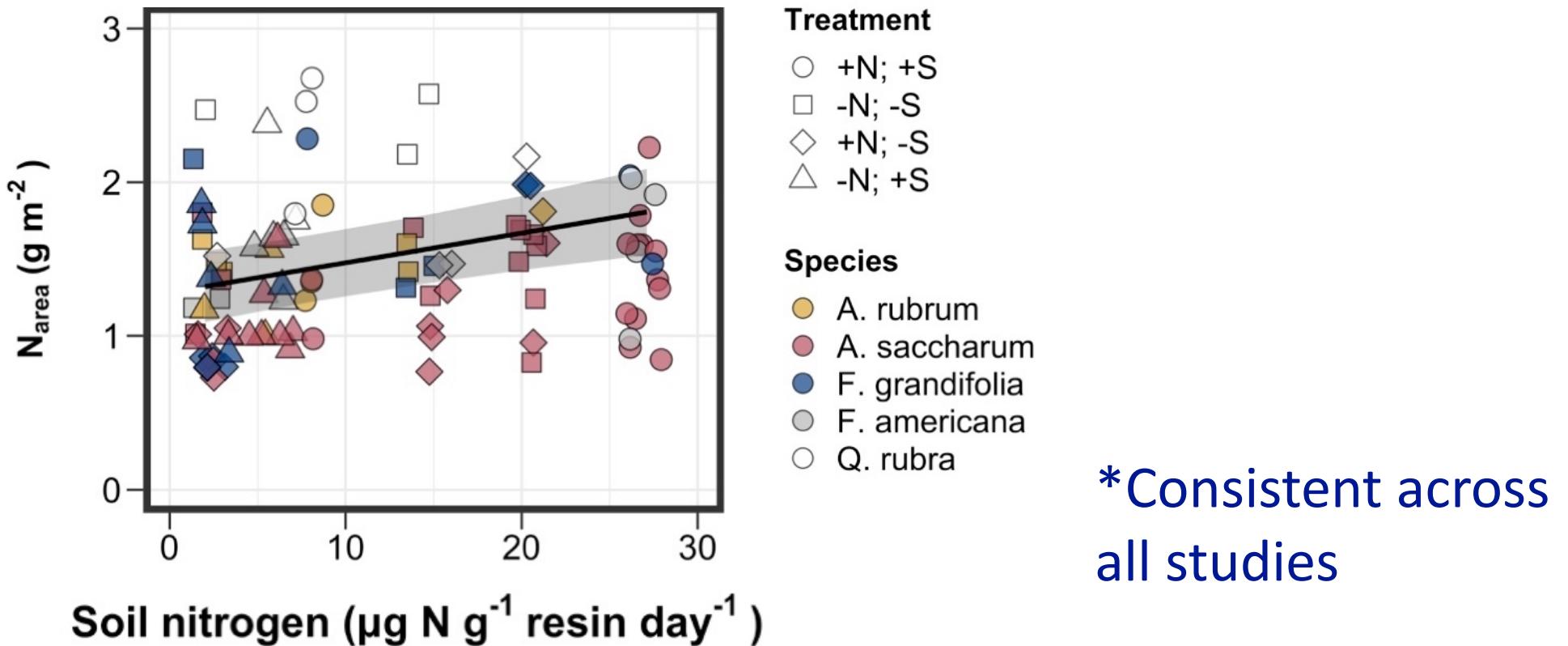
*Consistent across all studies at leaf and plant level

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

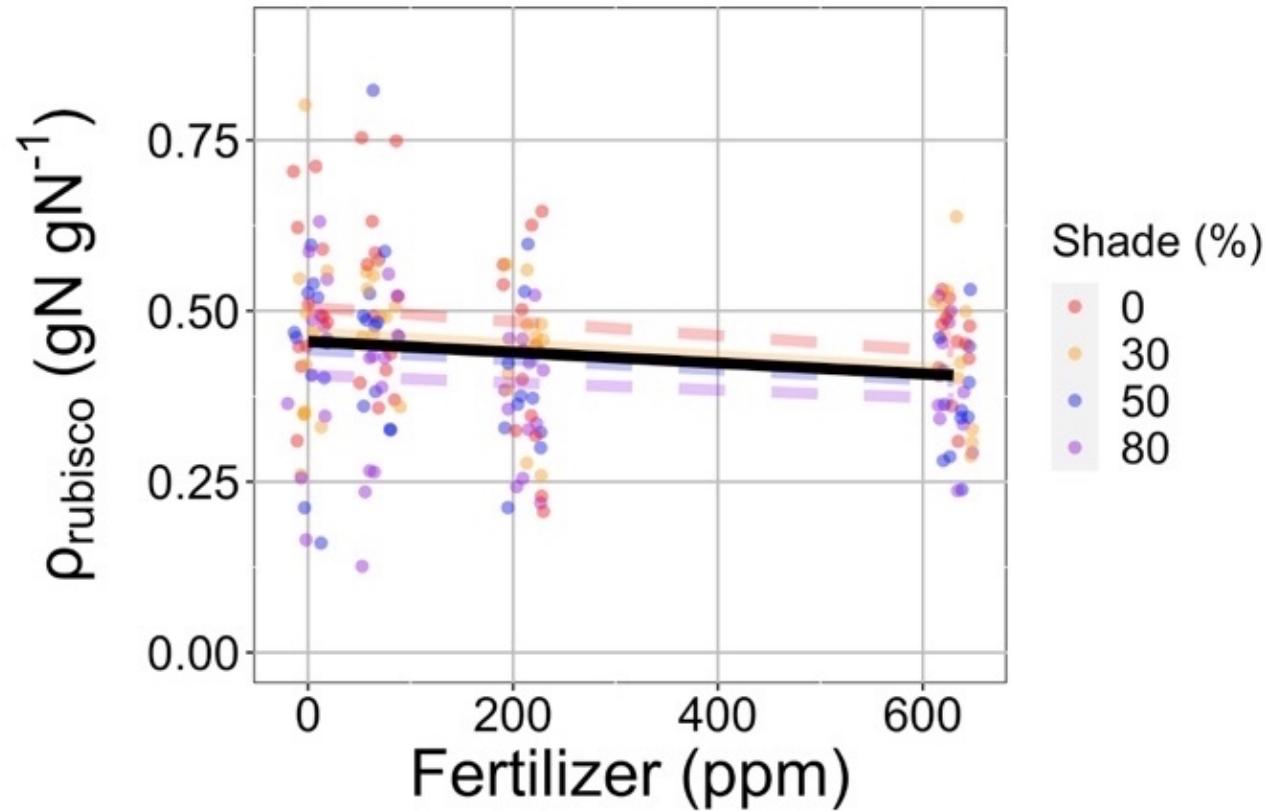


*Consistent across all studies at leaf and plant level

Result 3: Tissue N increases with increasing soil N

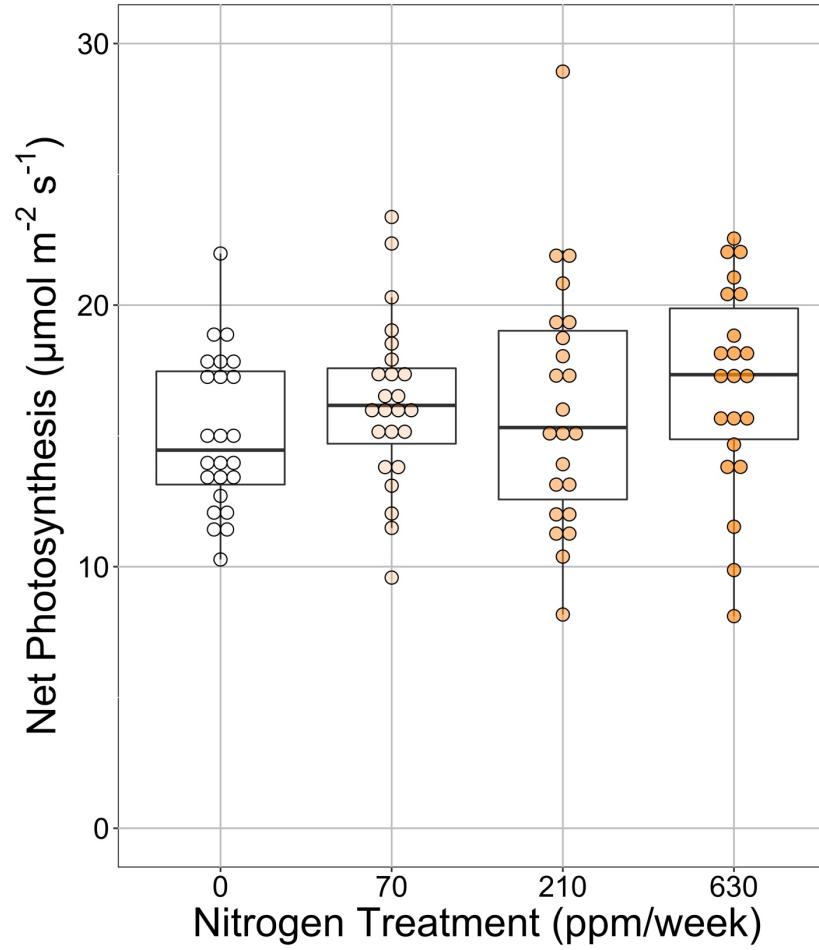


Result 4: Relative leaf N allocation to photosynthesis decreases with increasing soil N



*Consistent across multiple species, metrics, and growth conditions

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

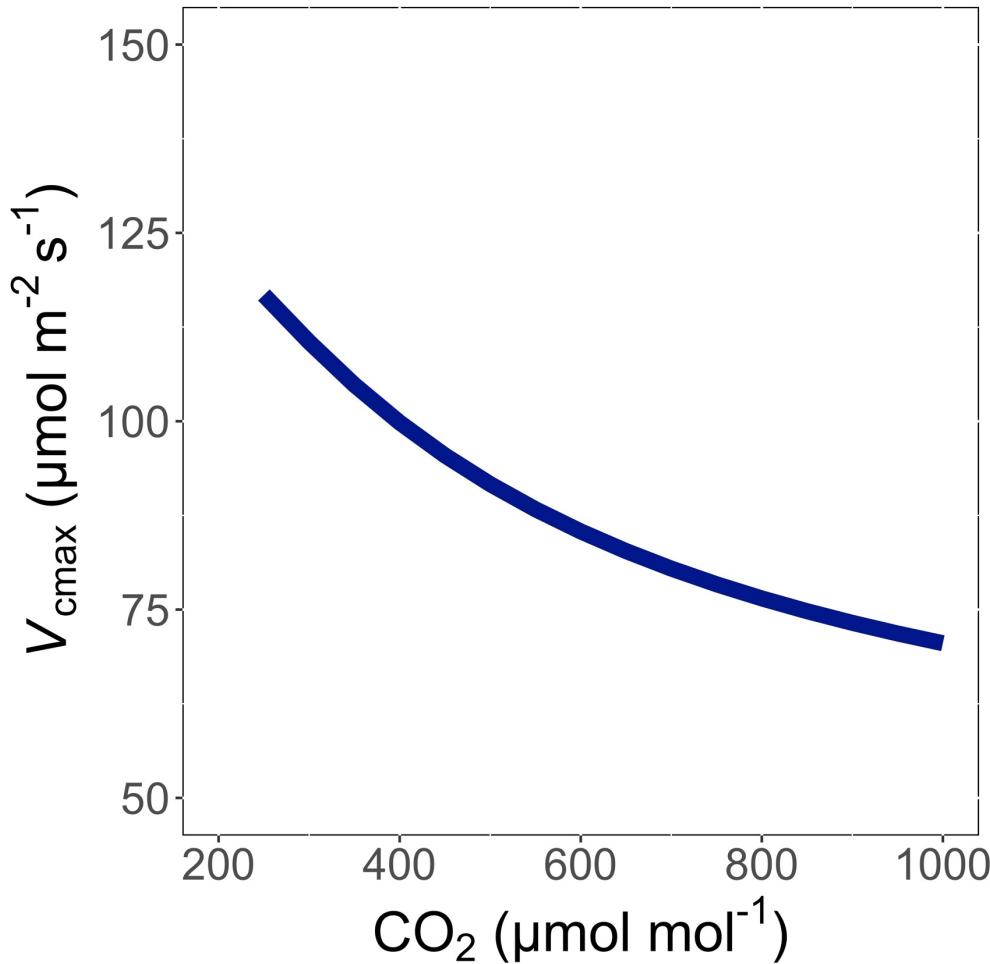


Question 2: How do plants acclimate
to soil nitrogen?

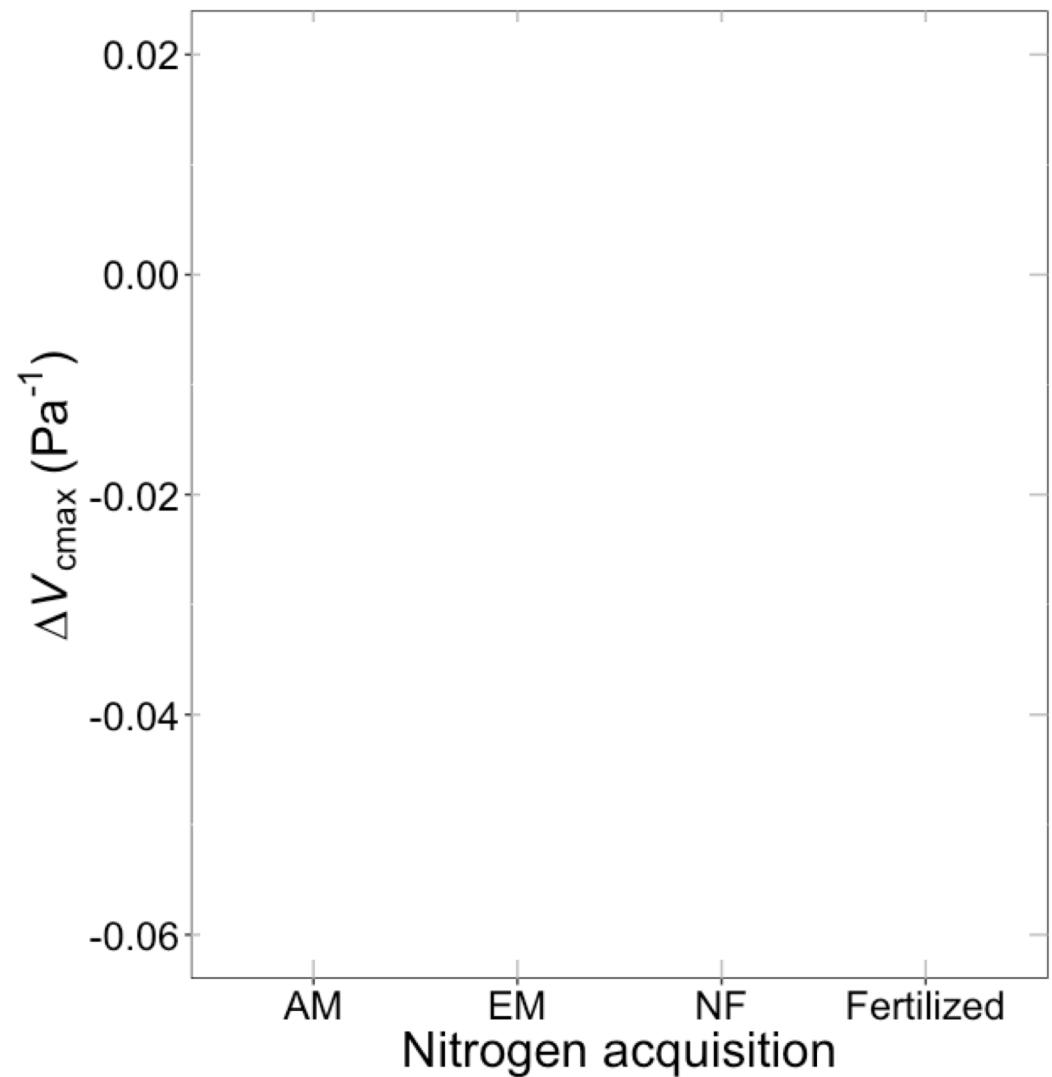
Reduction in N uptake costs results in
bigger plants with more leaf N, but
little change in per-leaf-area
photosynthesis

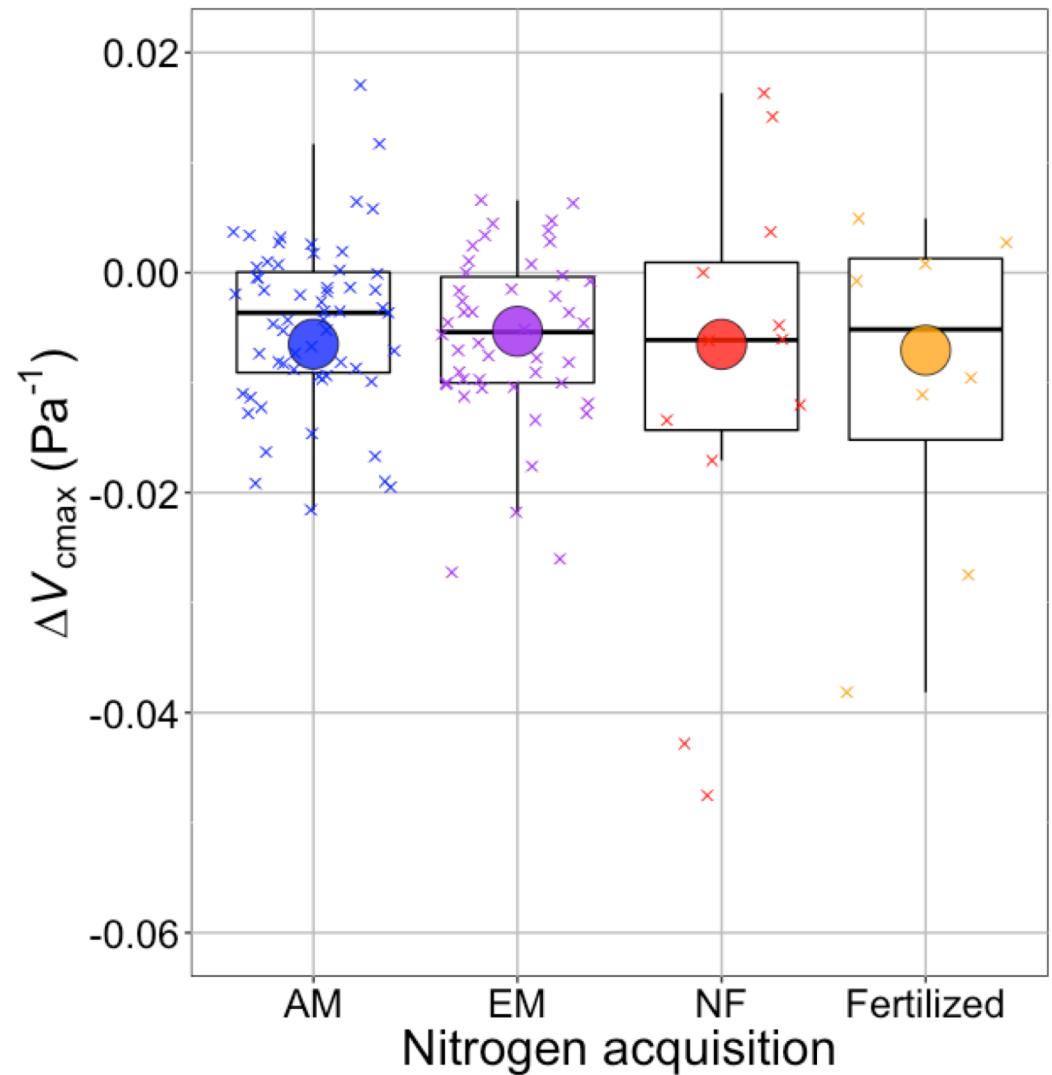
Question 3: What does acclimation mean for future terrestrial biogeochemical cycling?

Expected future responses



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



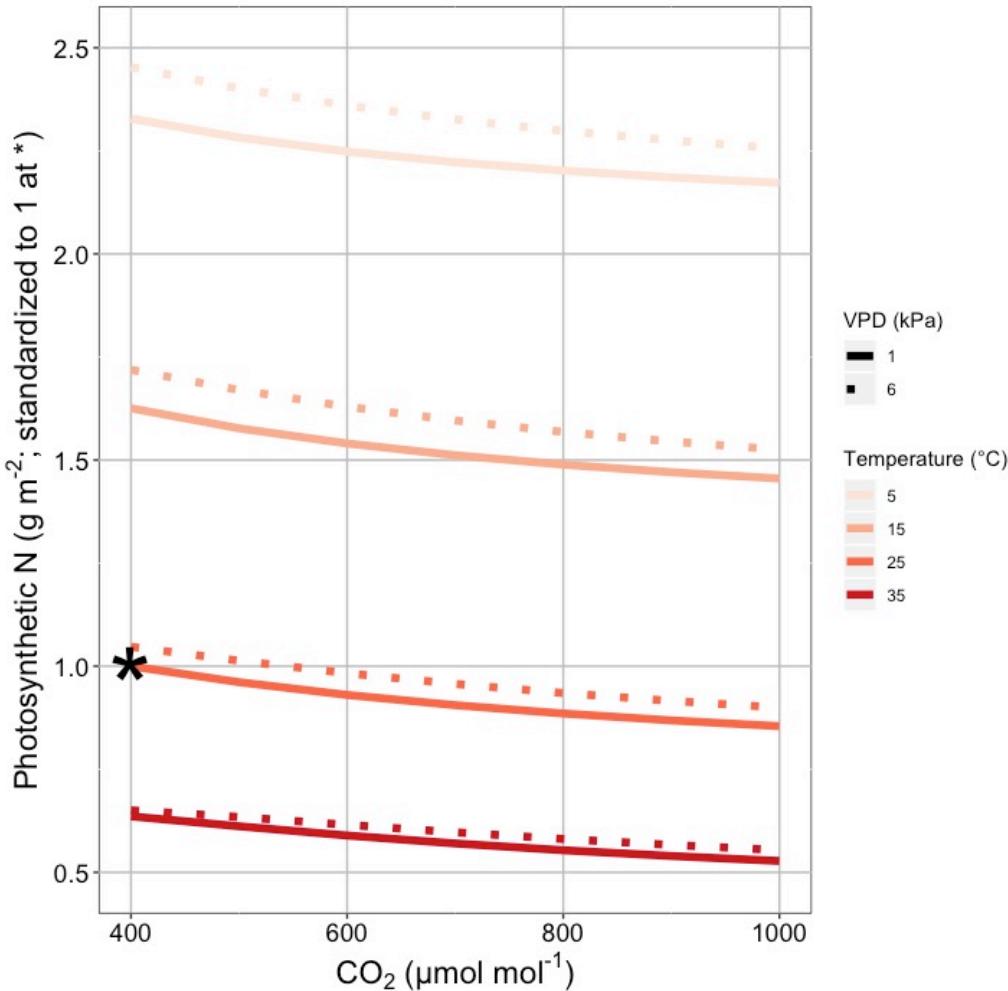


V_{cmax} changes with CO₂ in ways expected from optimization

Boxes = data = -0.0063 Pa⁻¹

Circles = predicted = -0.0066 Pa⁻¹

This generally suggests lower nitrogen demand under future conditions

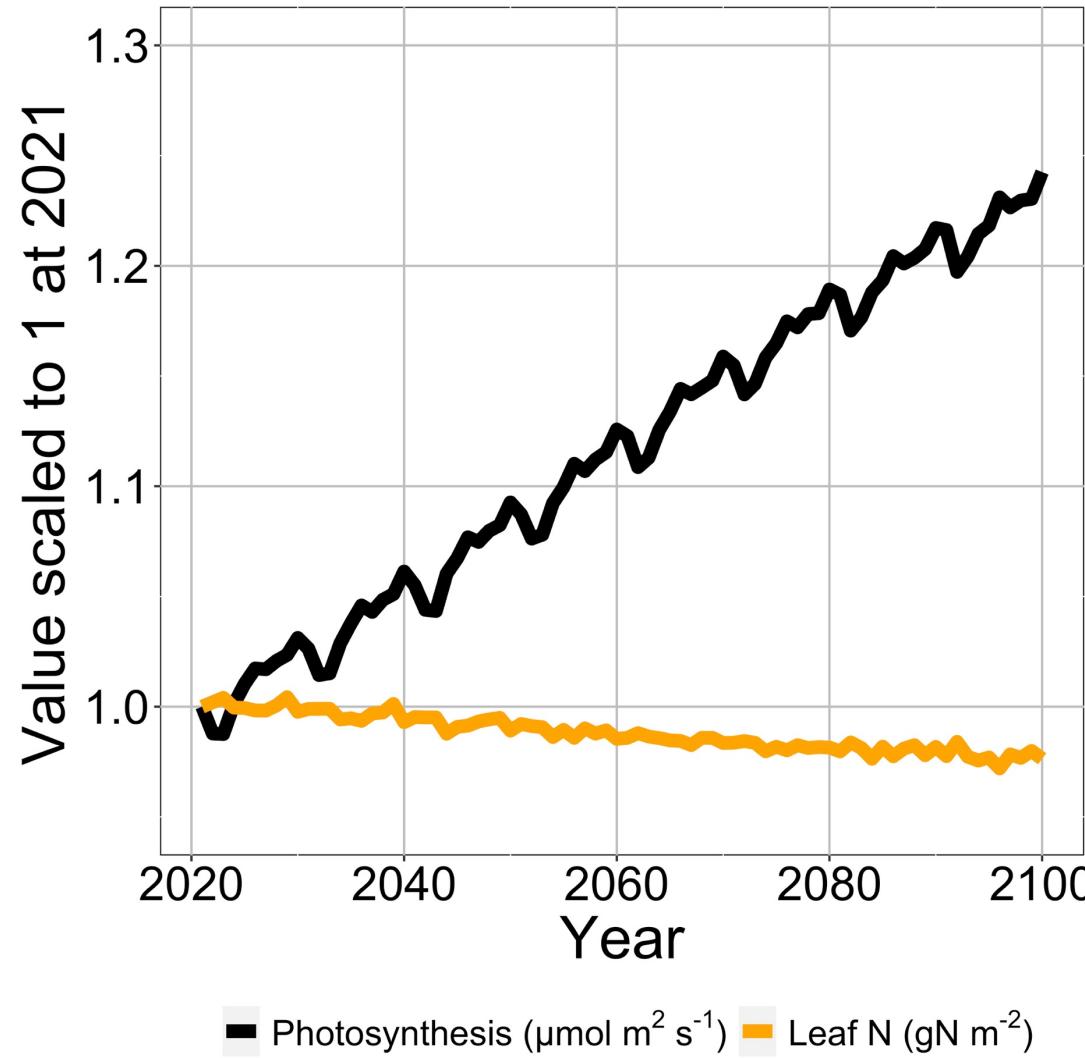


Let's run a model out into the
future!

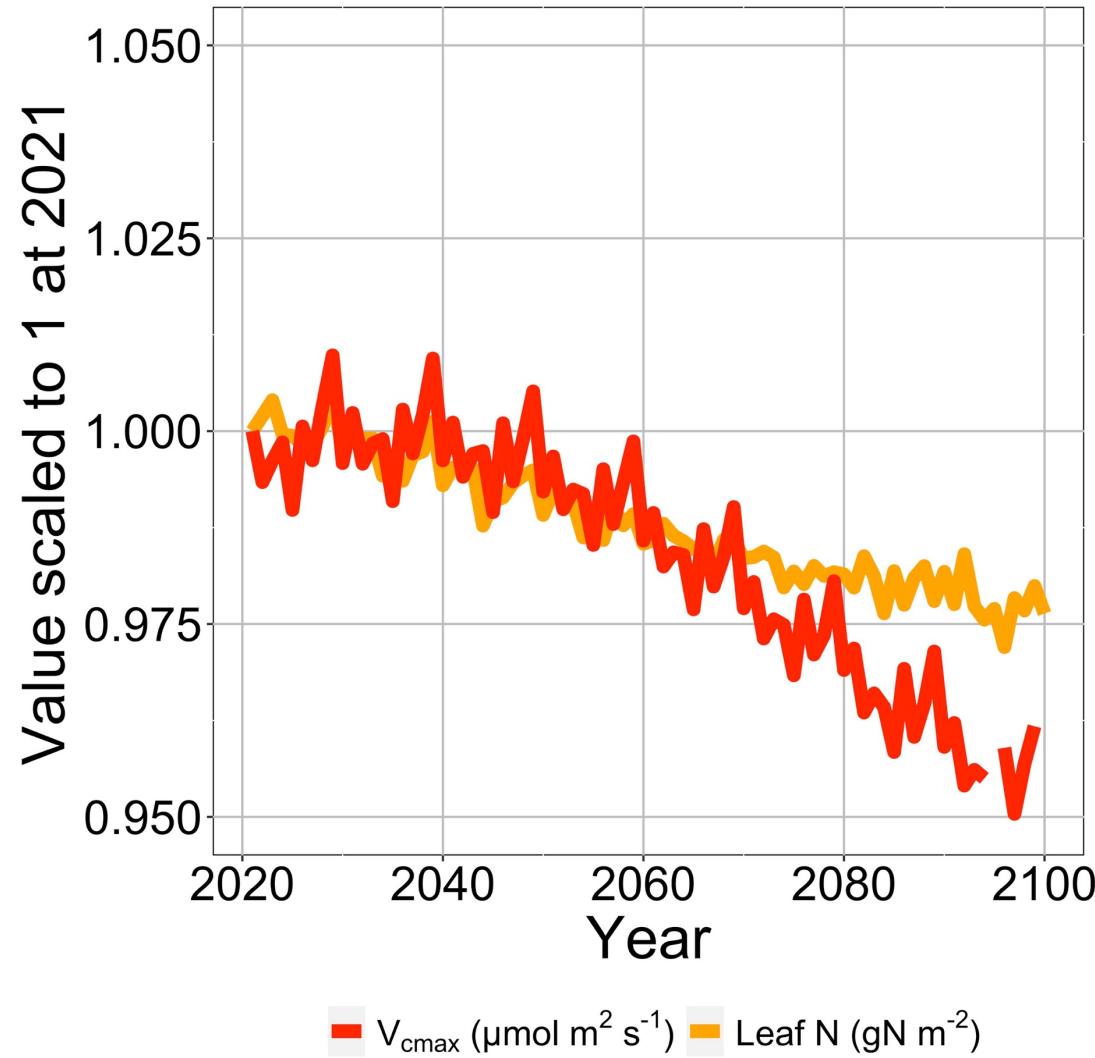


Energy Exascale
Earth System Model

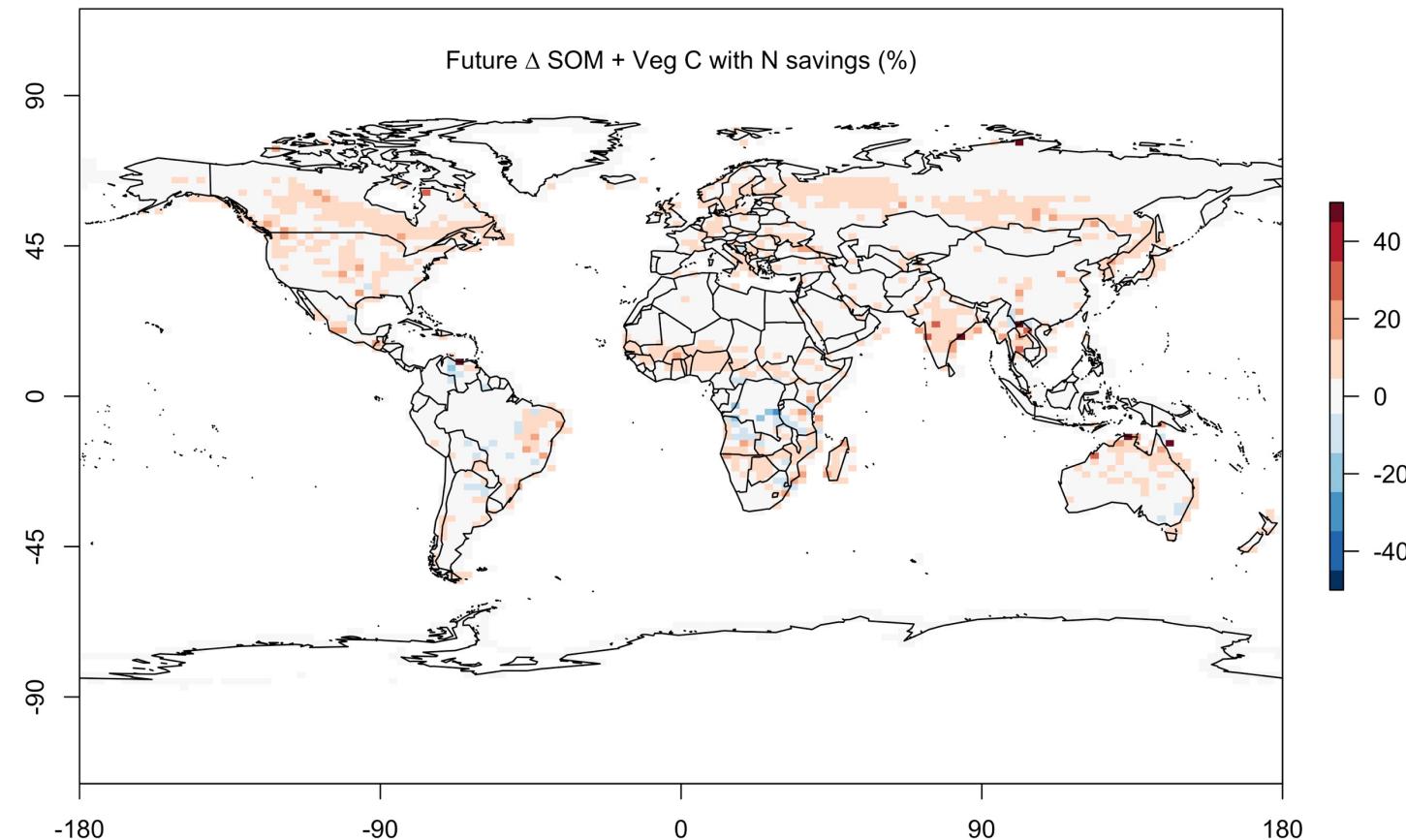
Photosynthesis increases with elevated CO₂ at lower leaf N



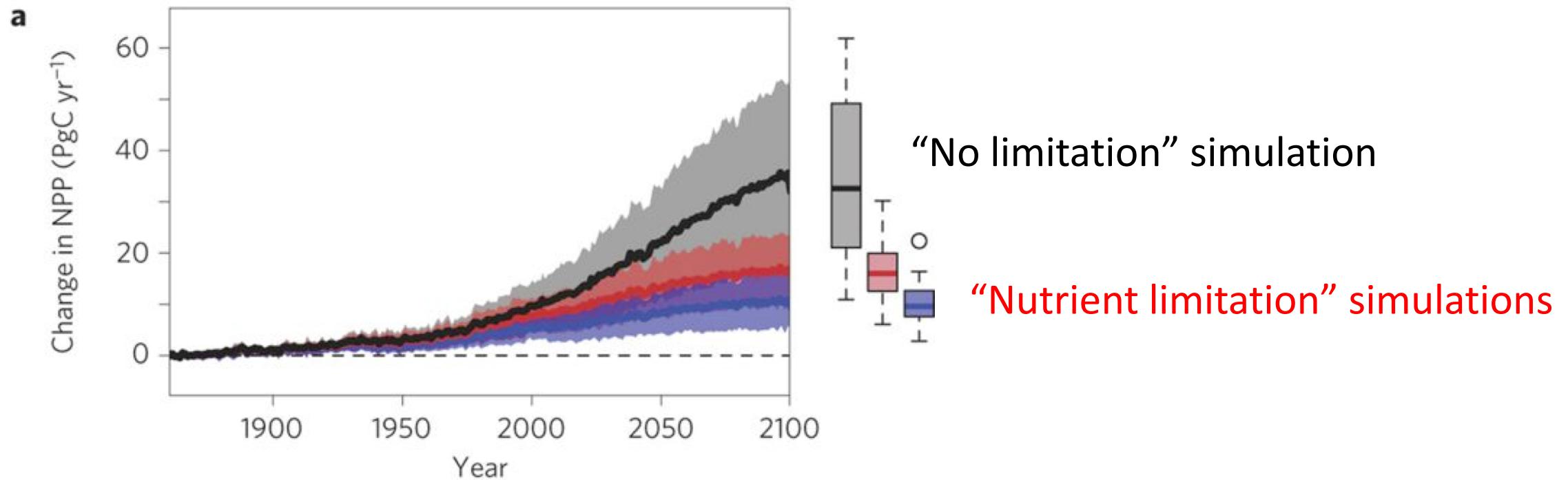
Leaf N reduction is due to a reduction in photosynthetic capacity



Leaf N savings increases long-term ecosystem carbon stocks



Need to rethink nutrient limitation in models?



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

Photosynthesis will increase and per-leaf-area nutrient use will decrease

Question 4: When is C₄ photosynthesis an advantage over C₃ photosynthesis?

C_3 versus C_4 optimization

C_4 versus C_3 optimization

C_4 photosynthesis has...

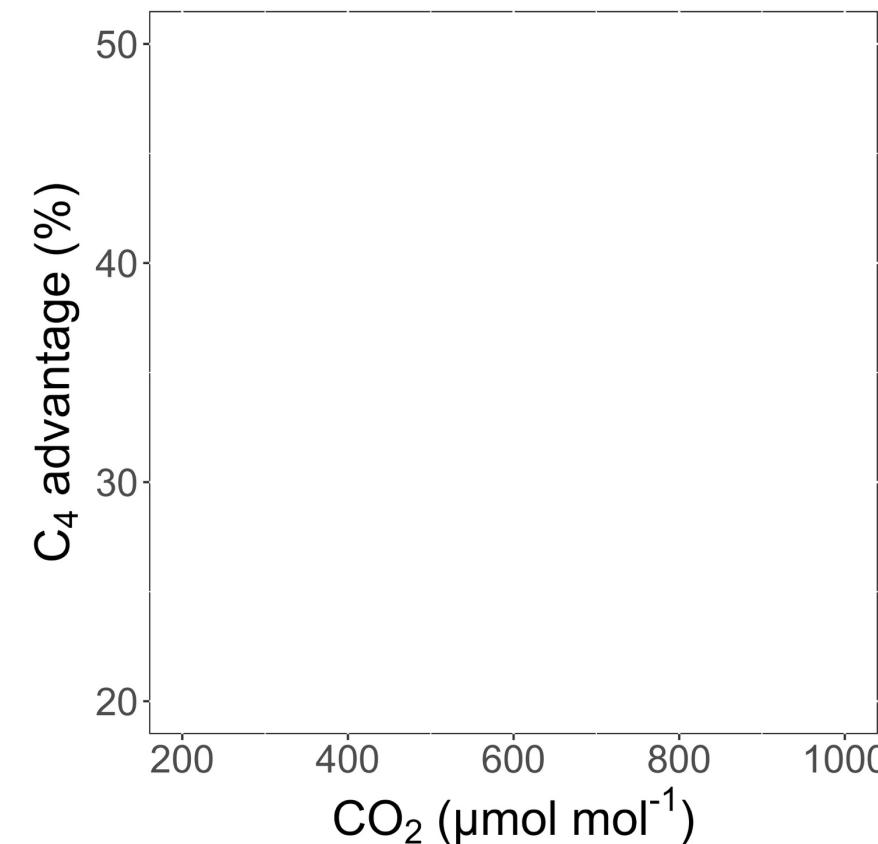
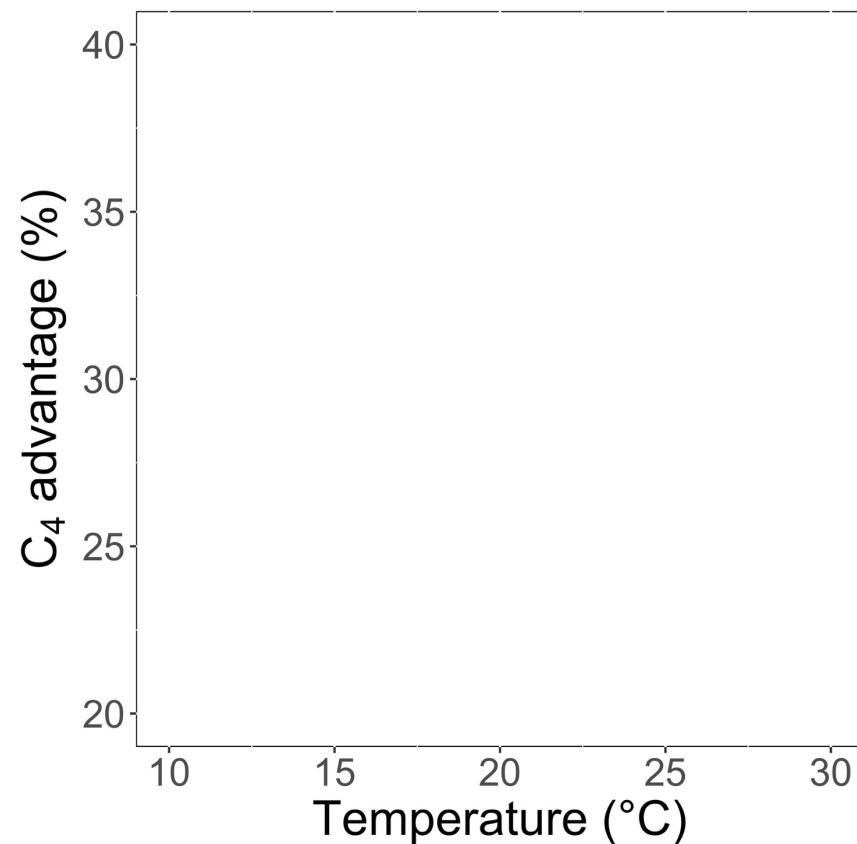
- Little photorespiration
- An additional limitation (**PEP carboxylation**)

C_4 versus C_3 optimization

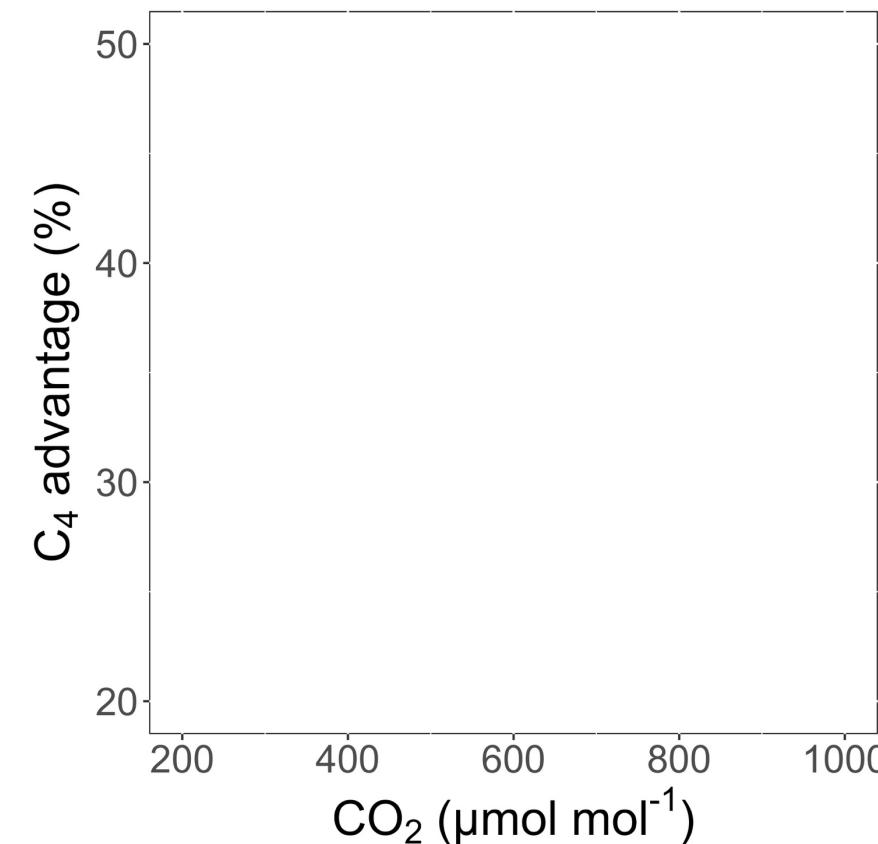
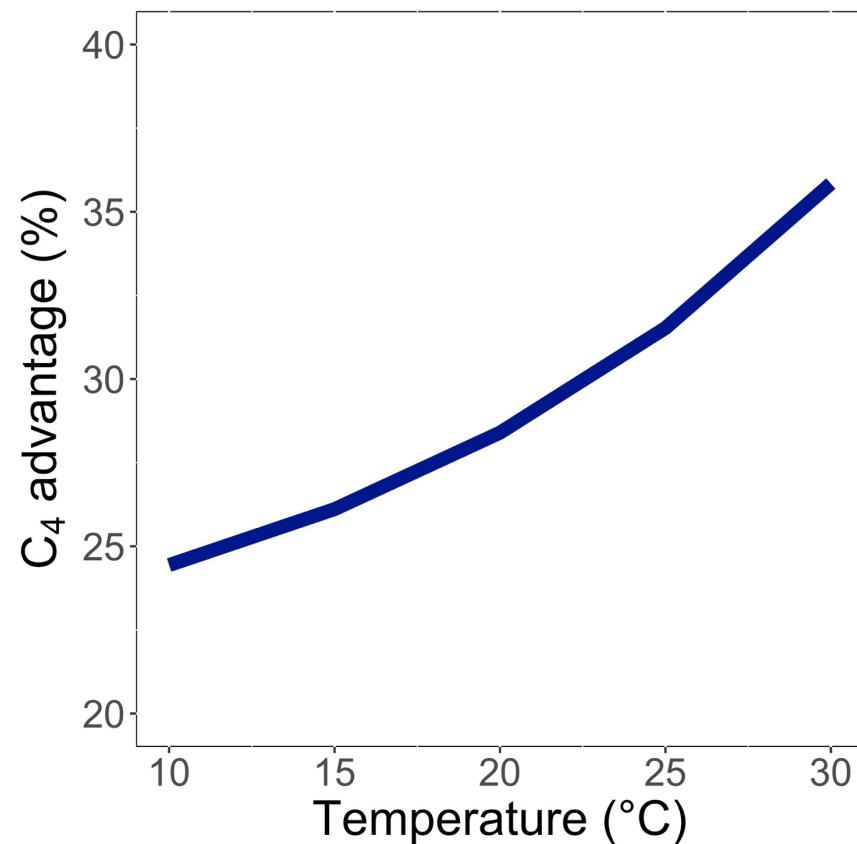
C_4 photosynthesis has...

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

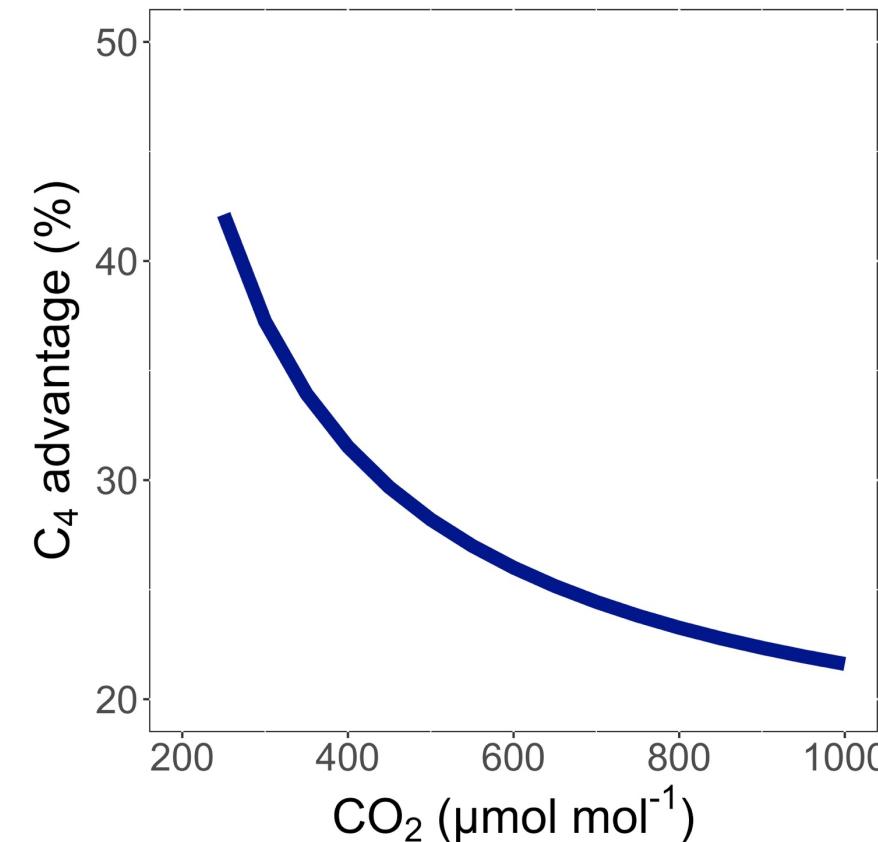
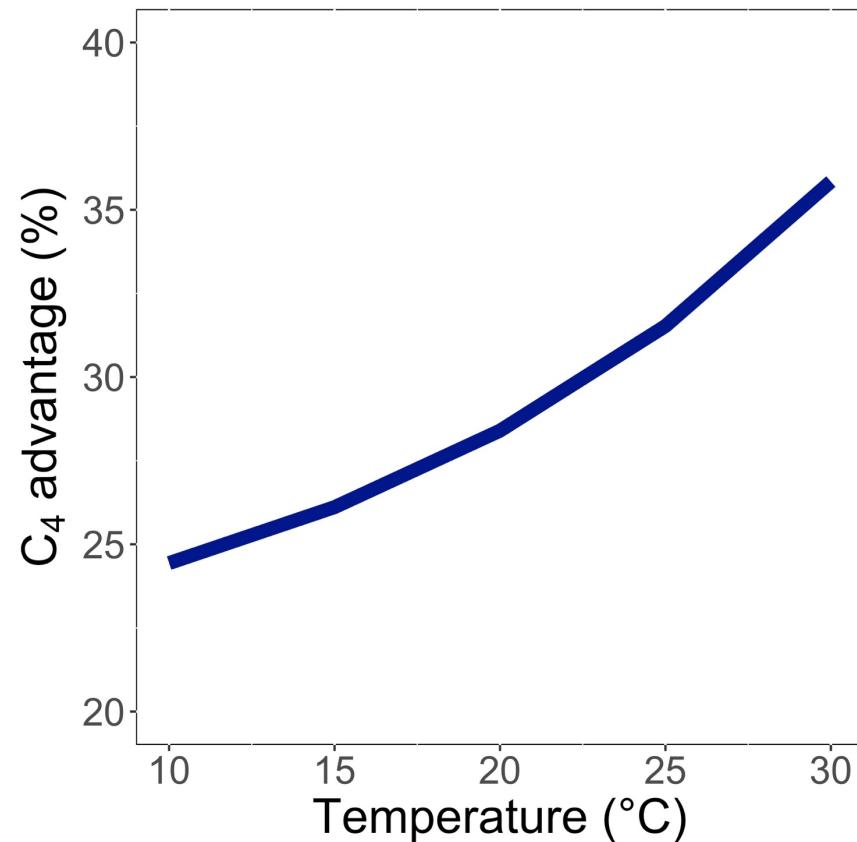
Relative advantage of C₄ physiology



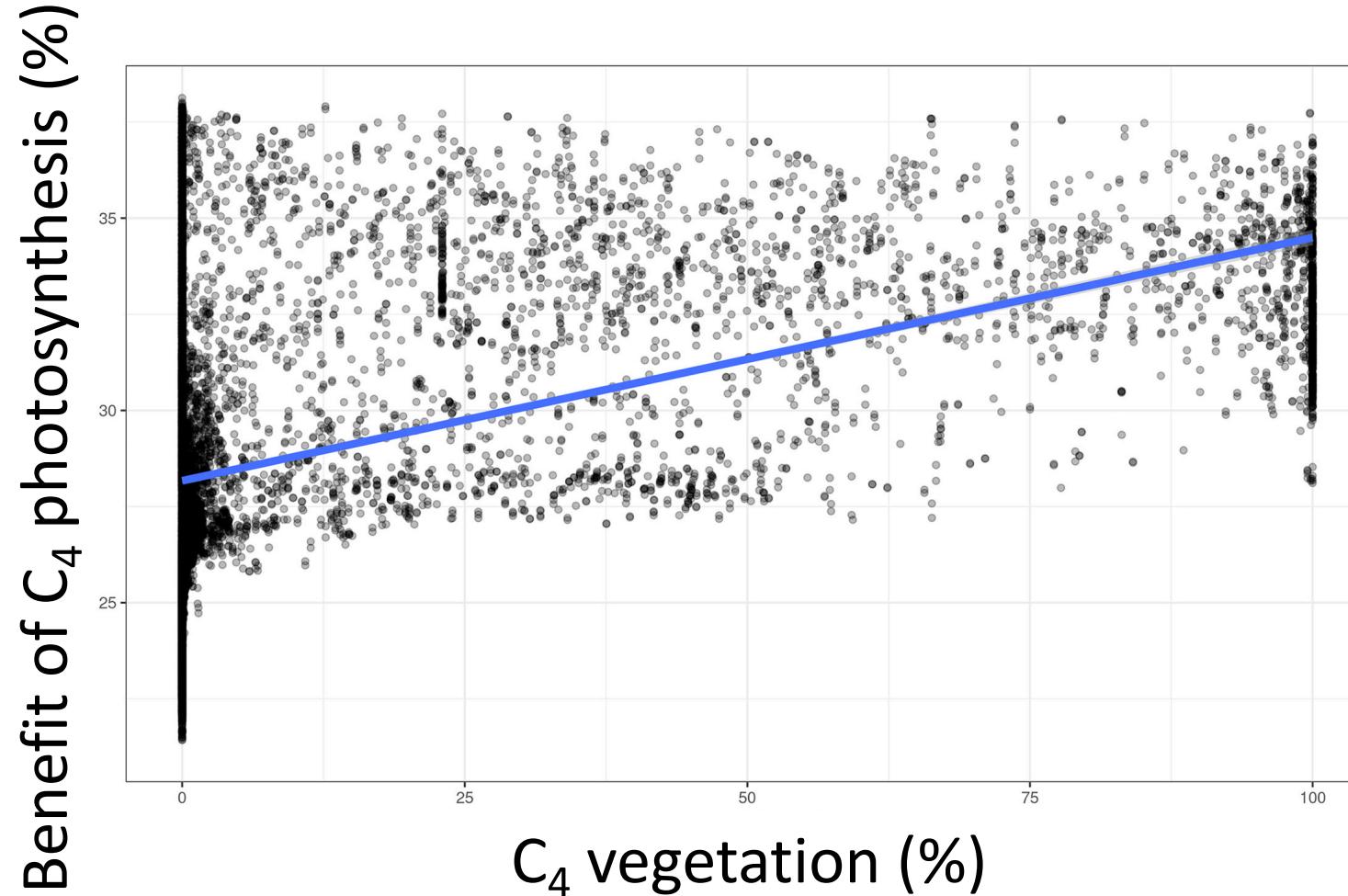
Relative advantage of C₄ physiology

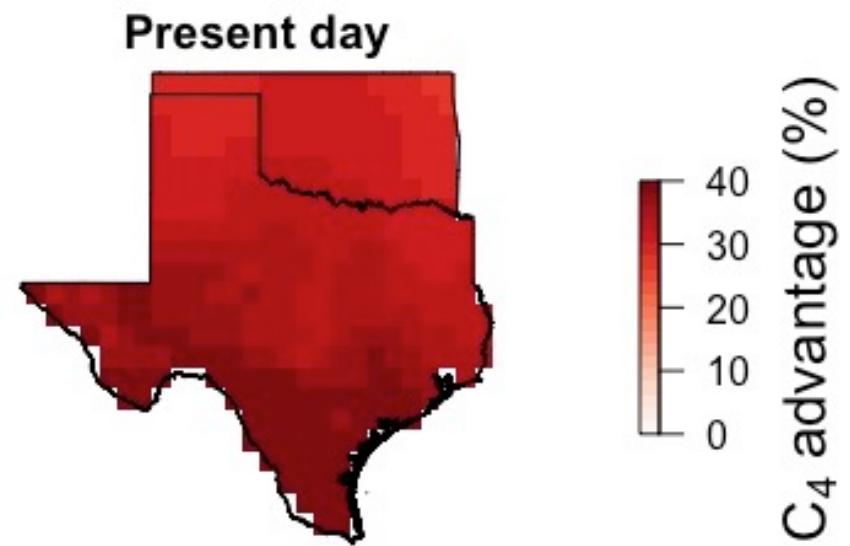


Relative advantage of C₄ physiology



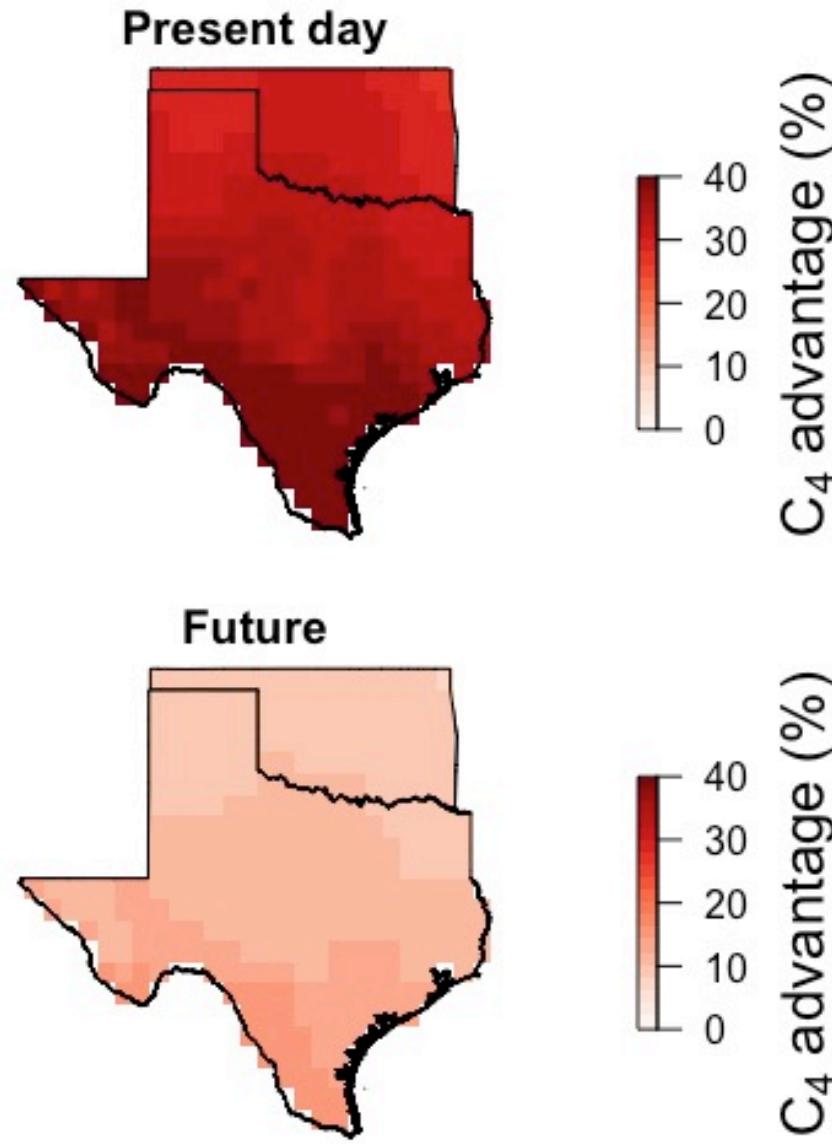
The model seems to work!





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Relative advantage of C₄ physiology may decrease in the future in the Southern Great Plains



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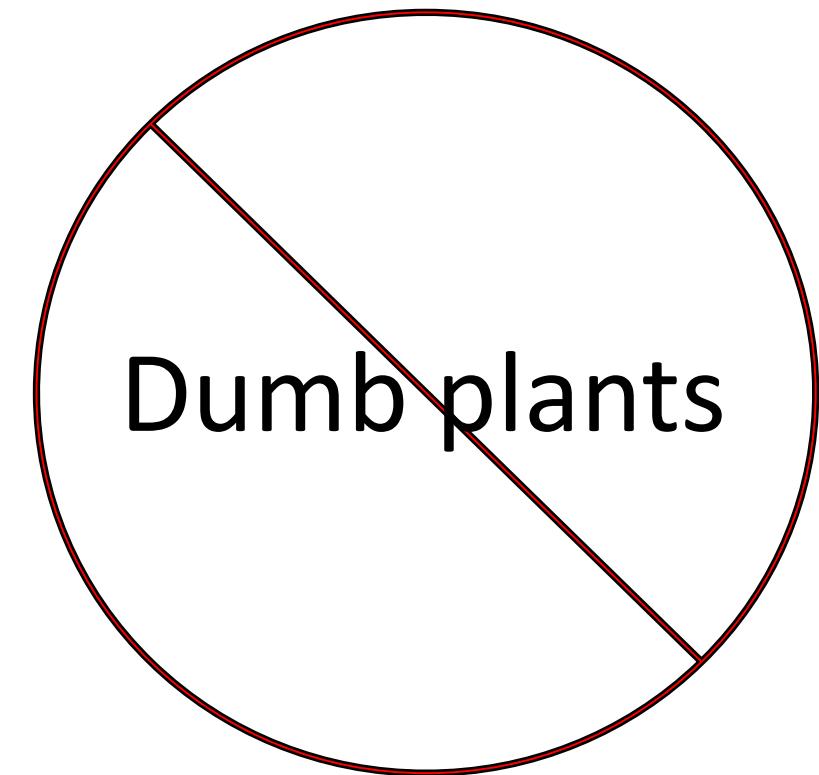
Question 4: When is C₄ photosynthesis an advantage over C₃ photosynthesis?

C₄ is better in hot, dry, low CO₂ environments

Conclusions

Conclusions

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



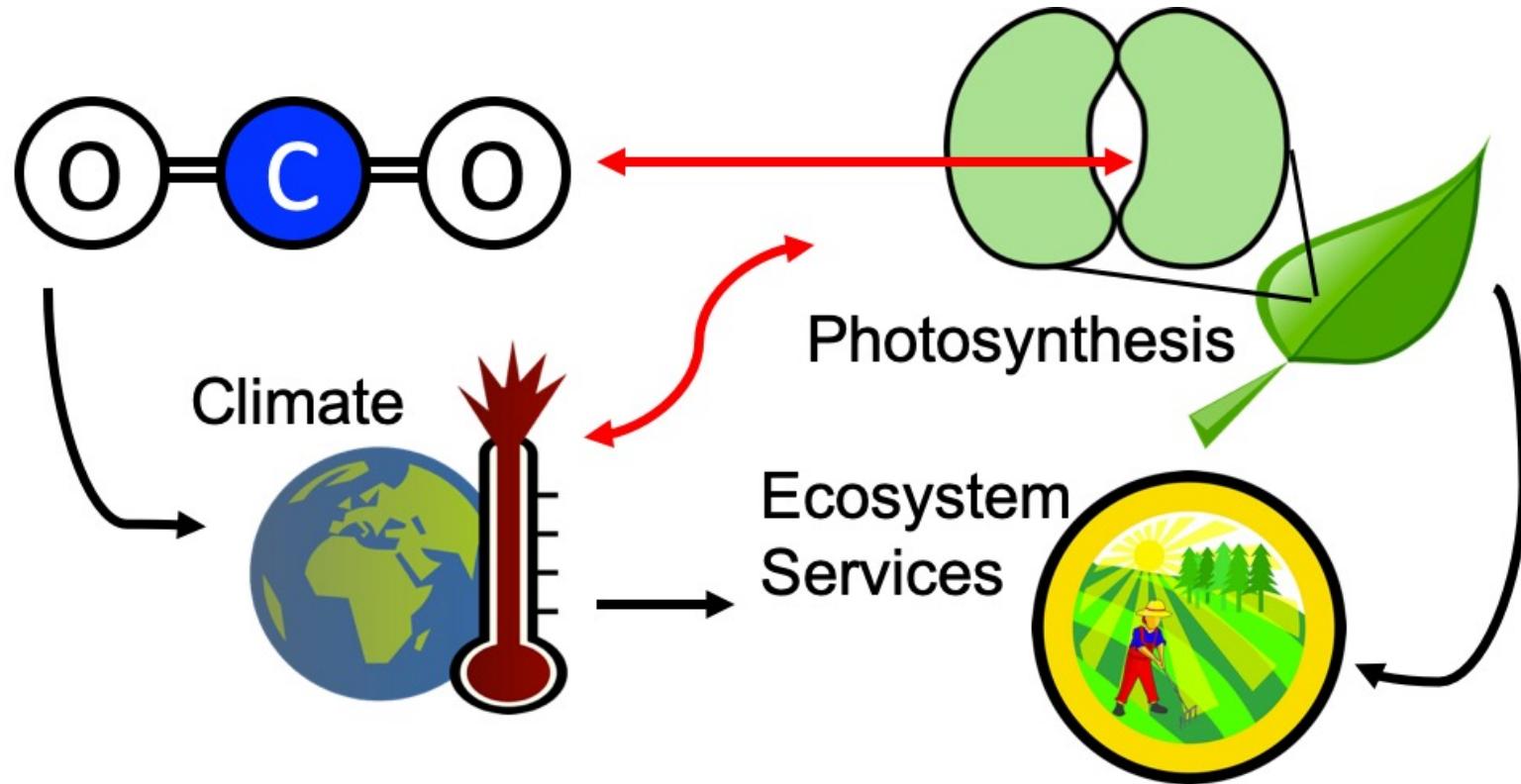
Conclusions

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/2023_tsu

Data and code:

www.github.com/SmithEcophysLab

www.smithecophyslab.com/data



Thanks!