

# 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](mailto:nick.smith@ttu.edu)

# Why do people care about plants?

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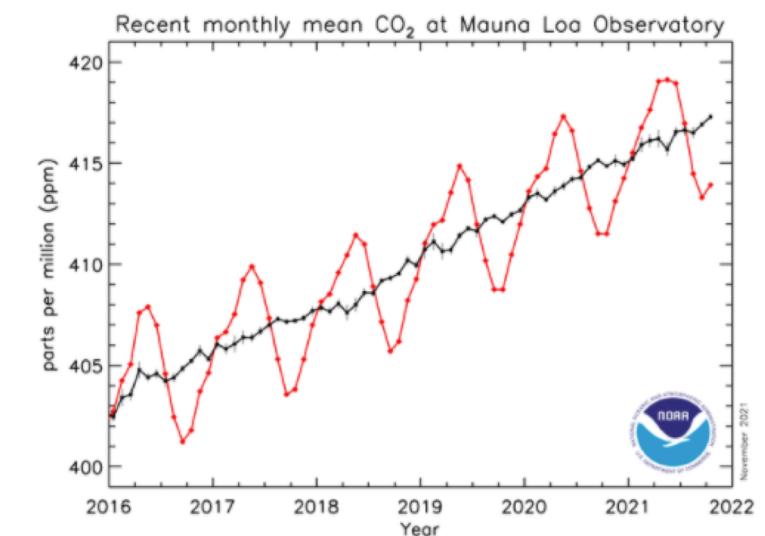
# Why do people care about plants?



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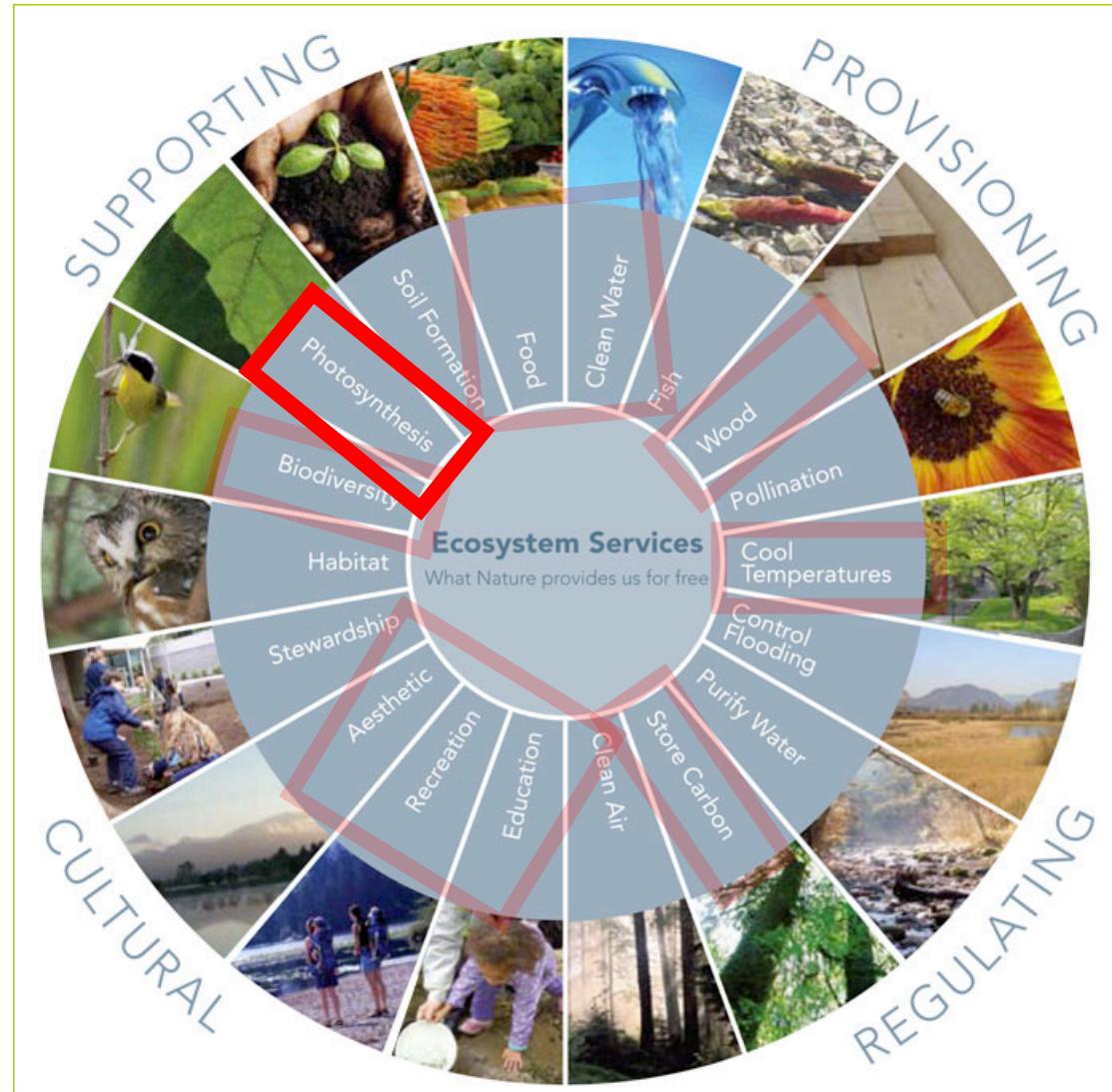
# Why do people care about plants?



# In other words: plants provide ecosystem services



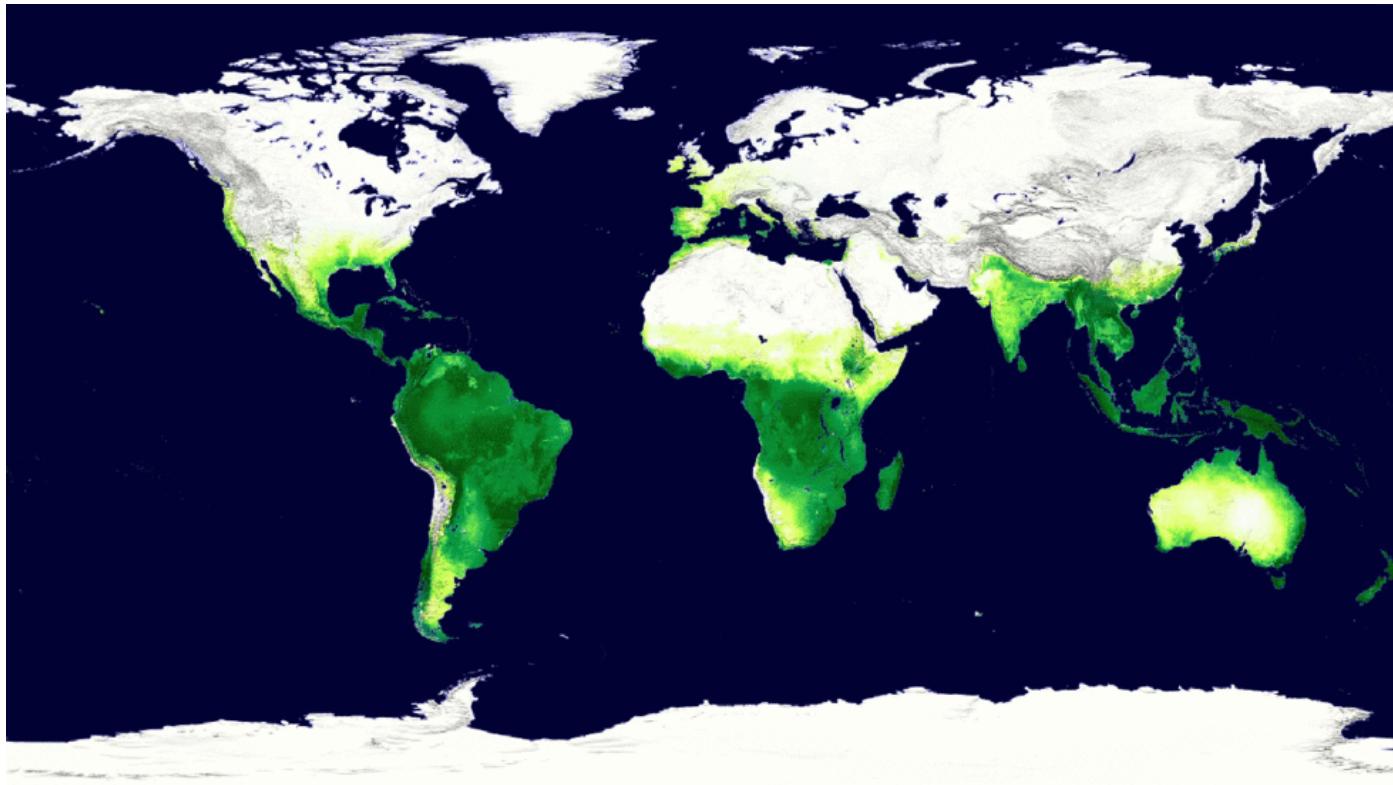
# Including photosynthesis



# Photosynthesis provides the foundation for other services

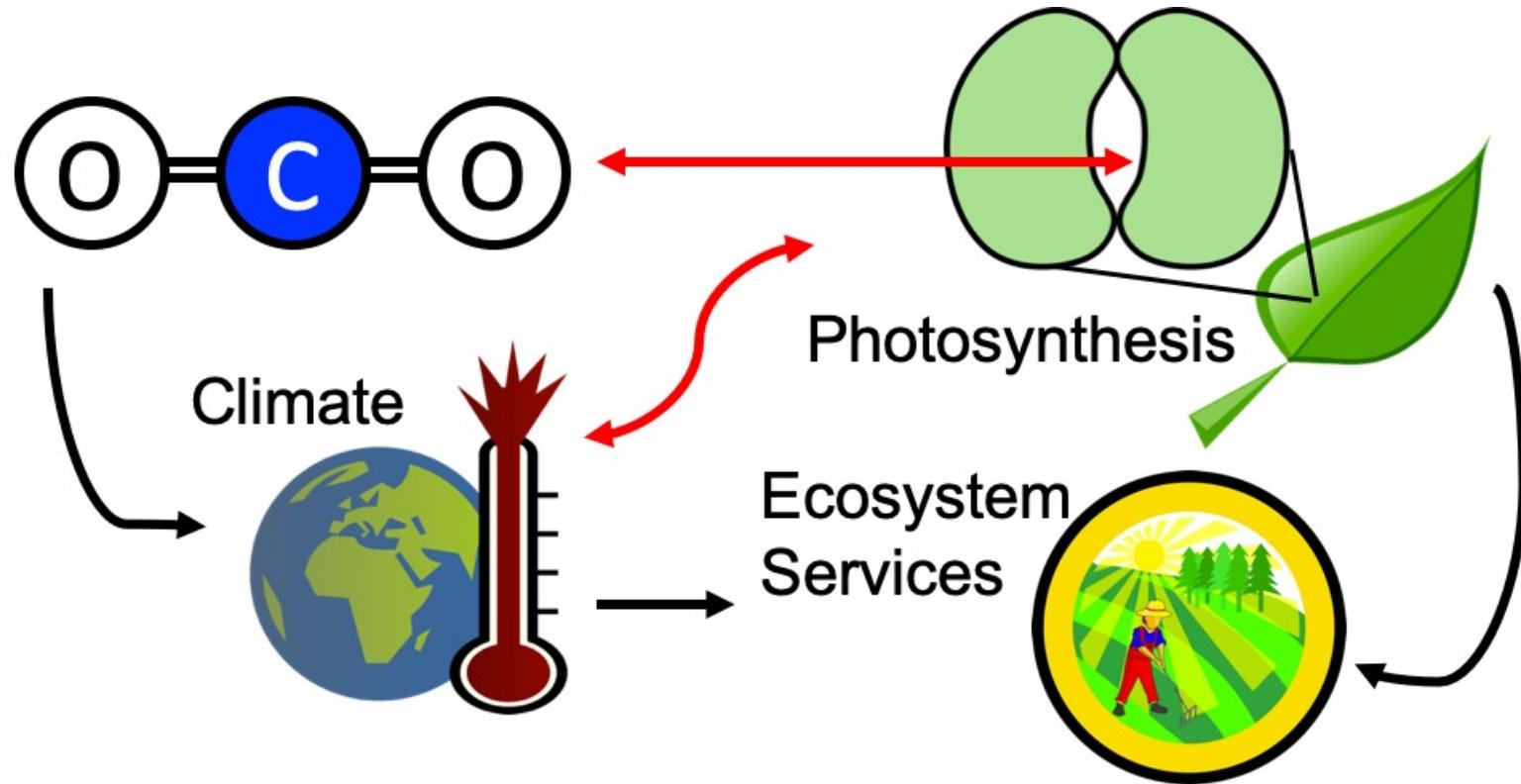


Photosynthesis is a dynamic process that is likely to be impacted by global change



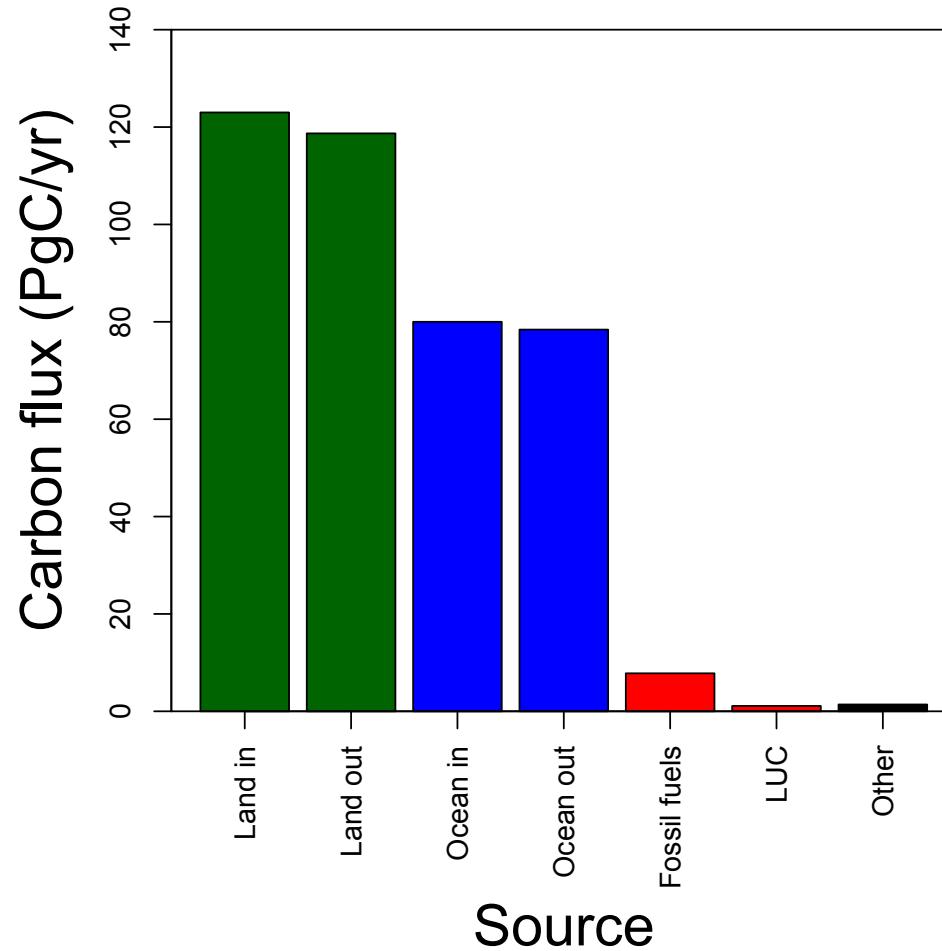
MODIS, NASA

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



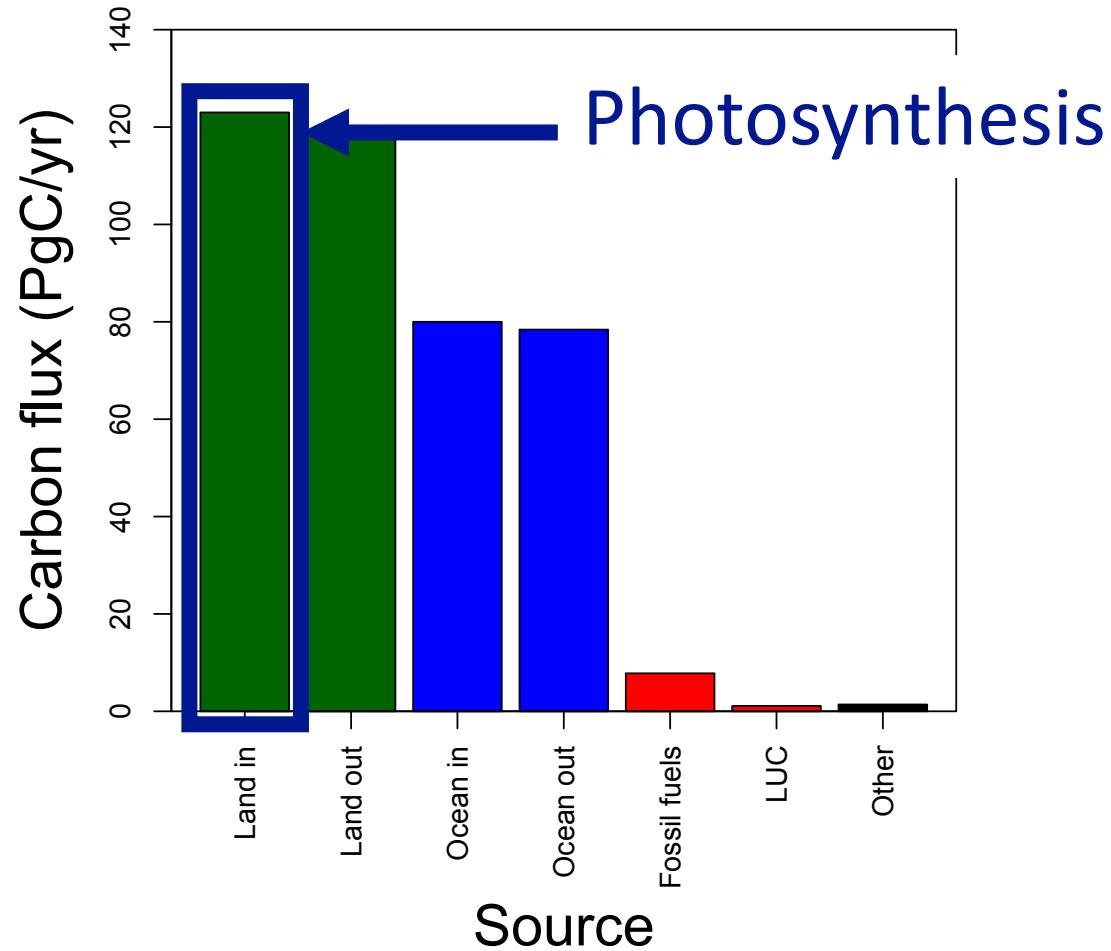
Photosynthesis is important! An example...

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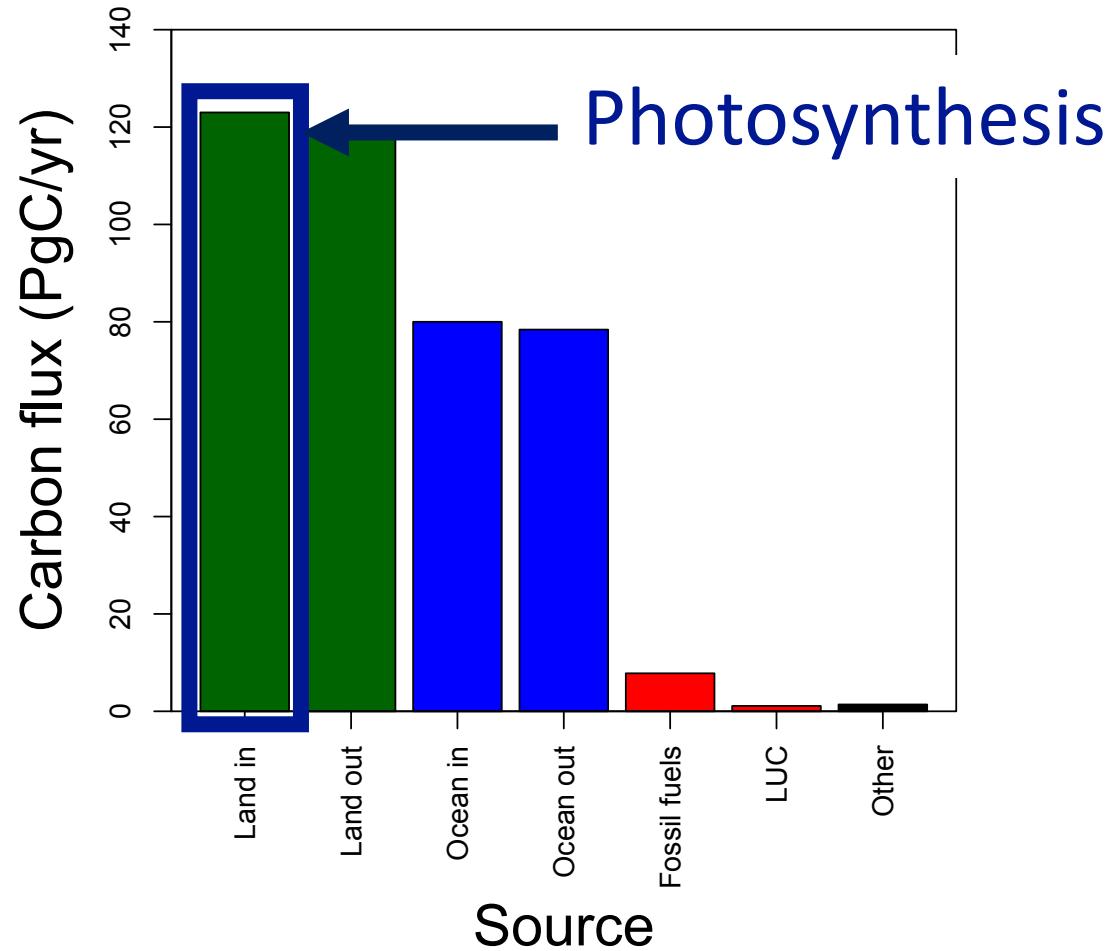


Data from IPCC (2013)

# Photosynthesis is important! An example...

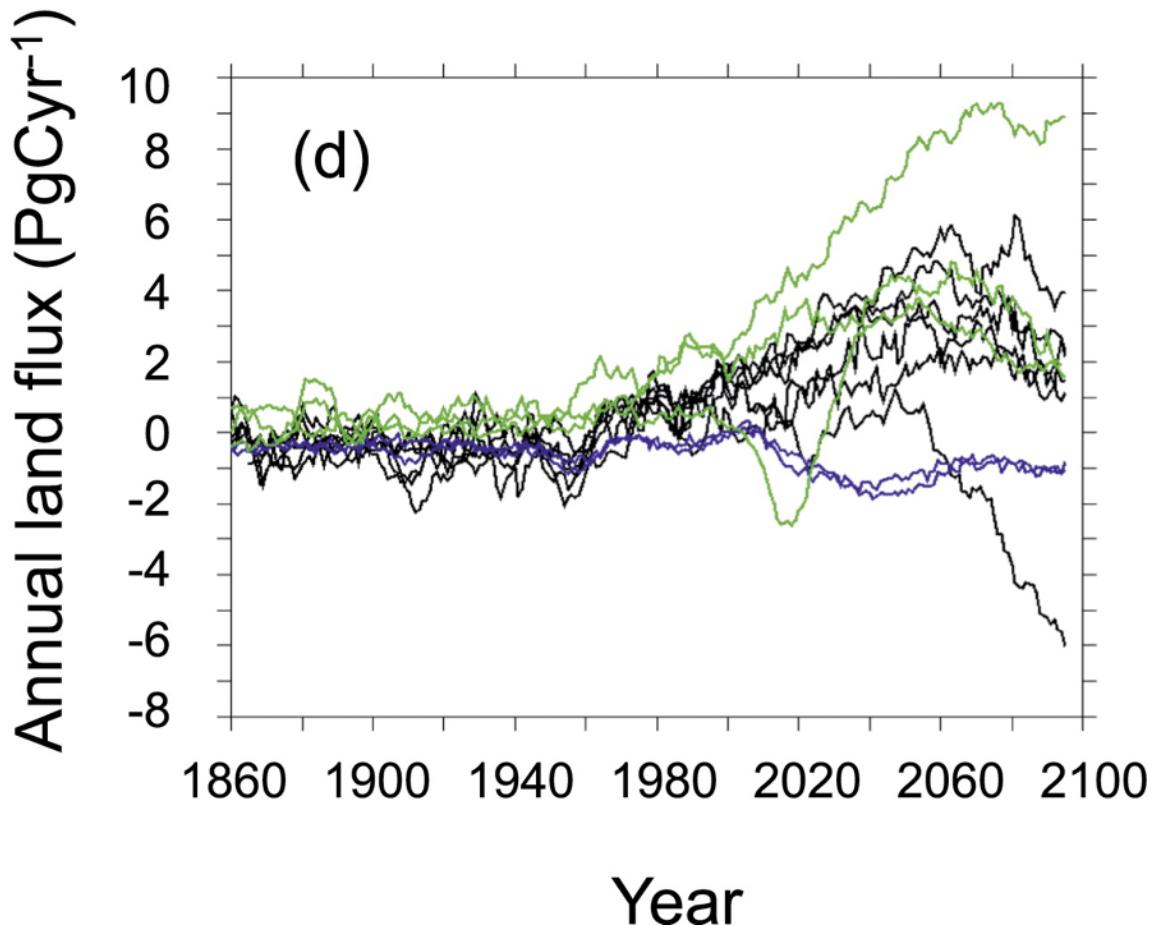


# Photosynthesis is important! An example...

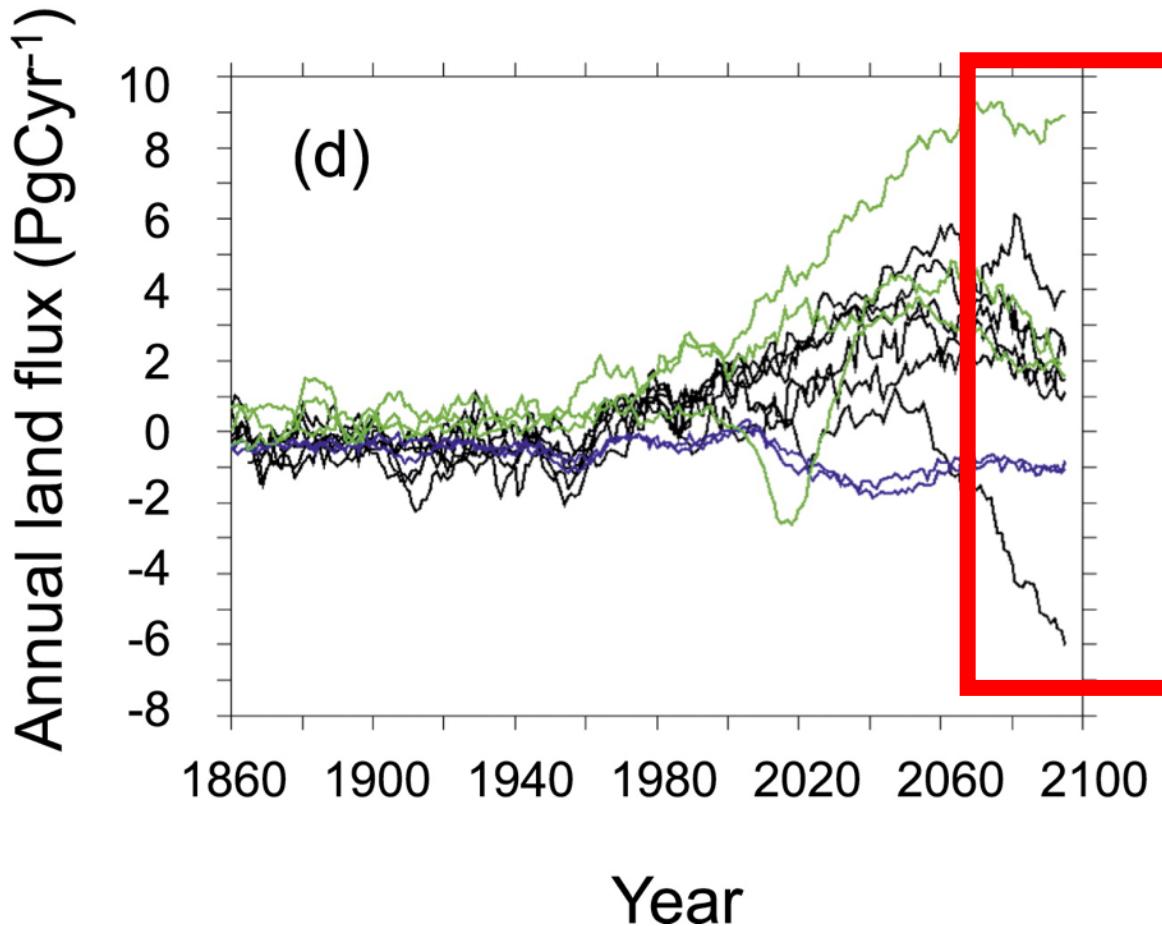


A small percentage change in photosynthesis can have large consequences for climate

# But predictions are uncertain!

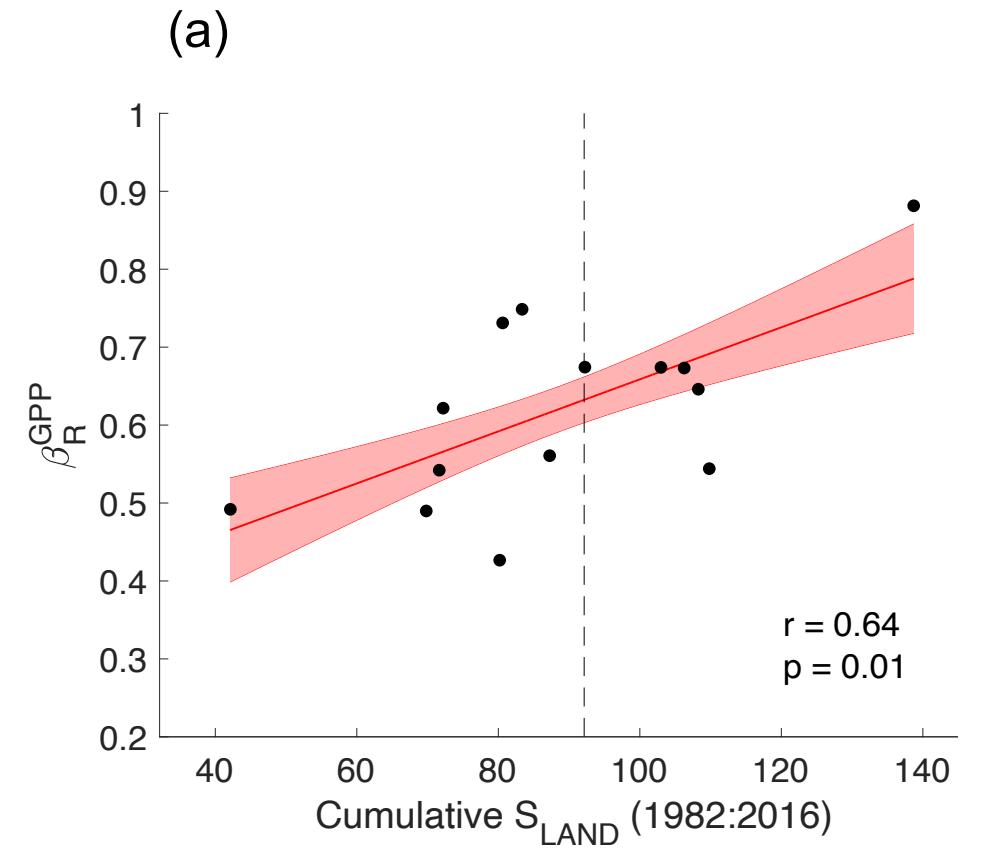
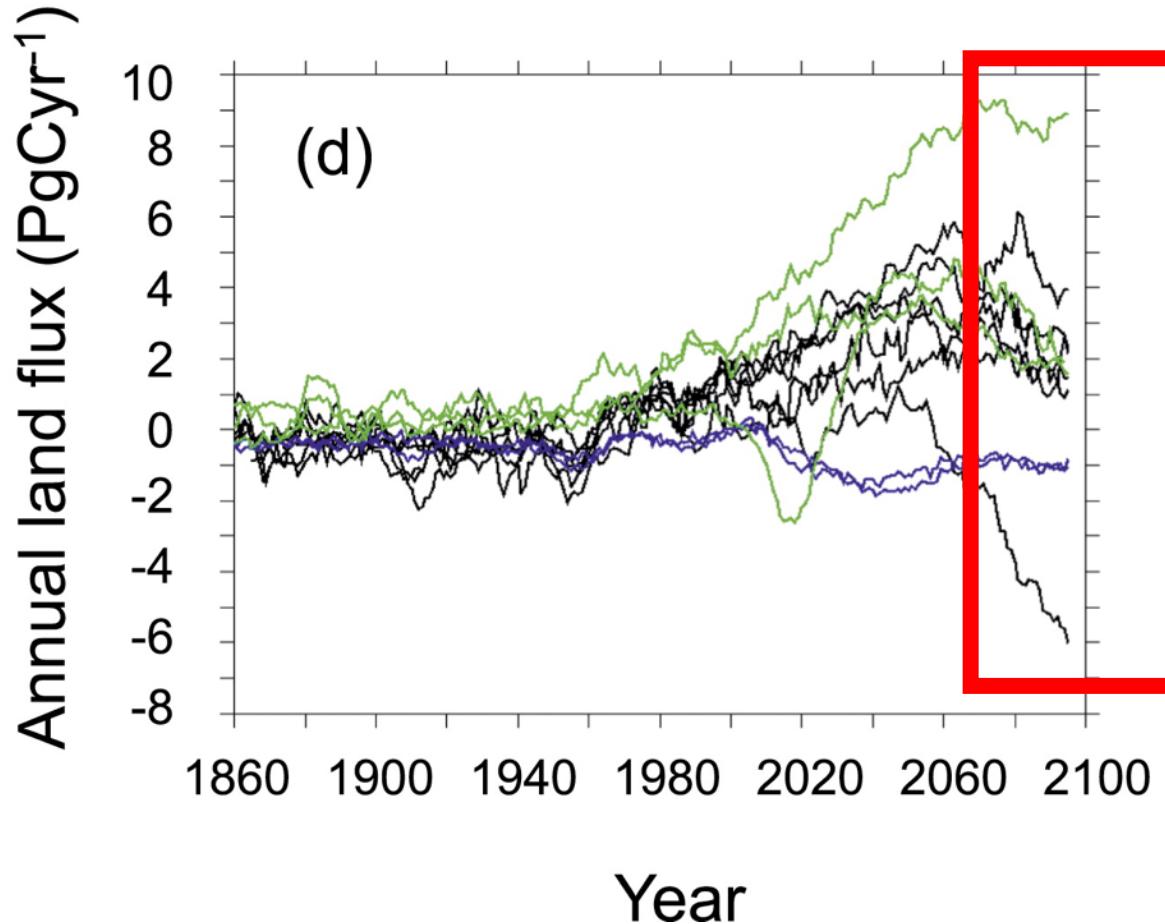


# But predictions are uncertain!



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

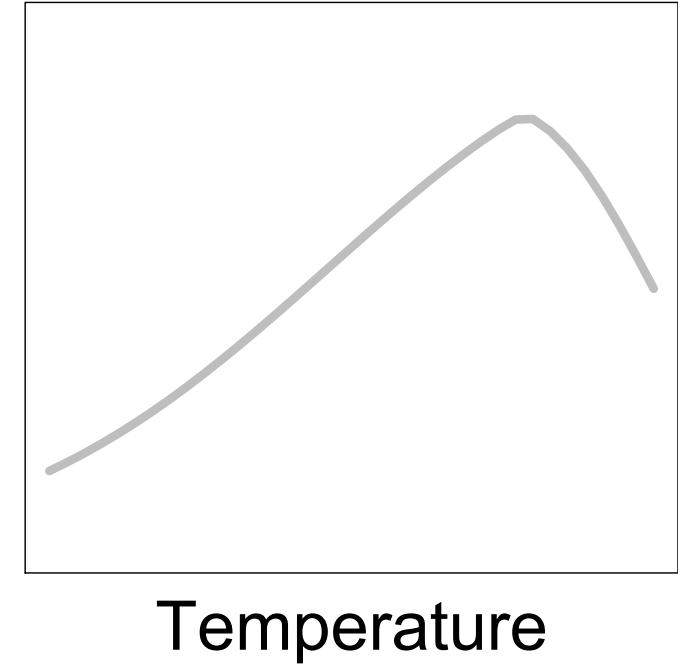
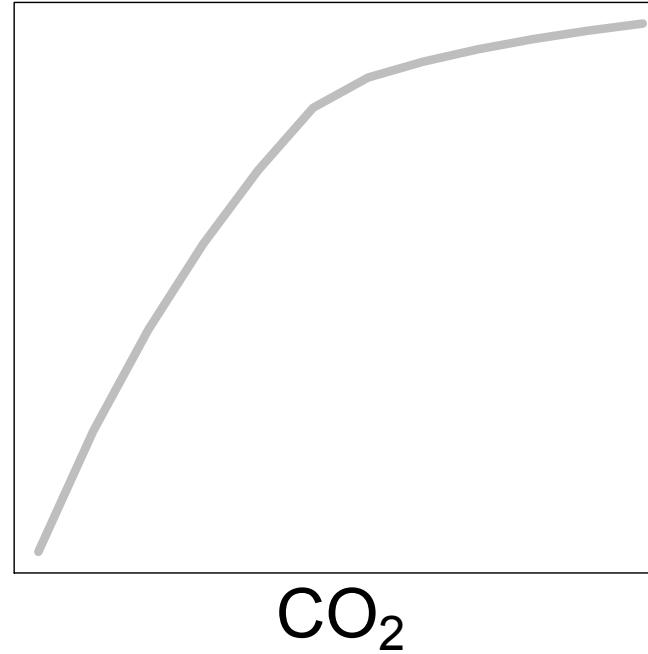
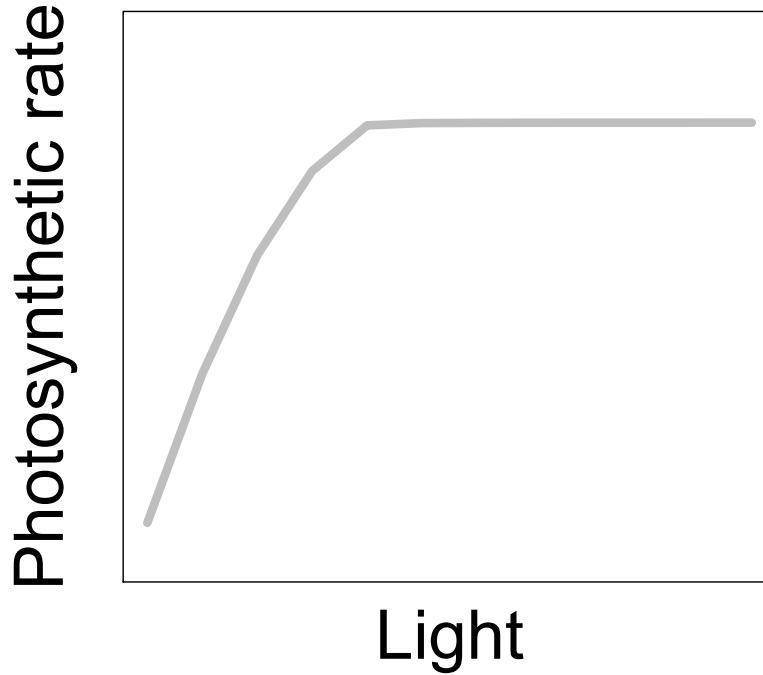
## A Biochemical Model of Photosynthetic CO<sub>2</sub> Assimilation in Leaves of C<sub>3</sub> Species

G.D. Farquhar<sup>1</sup>, S. von Caemmerer<sup>1</sup>, and J.A. Berry<sup>2</sup>

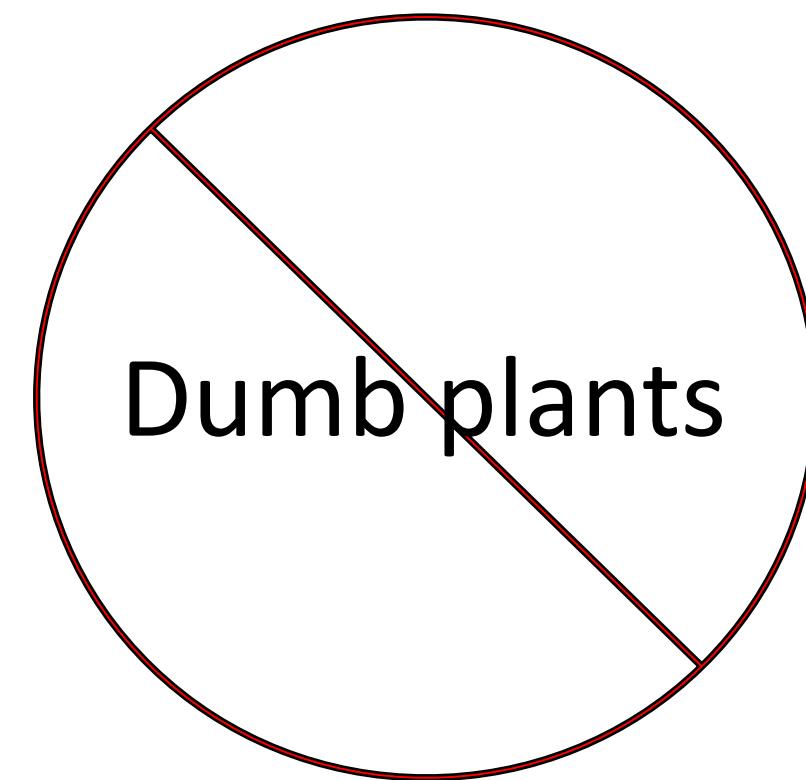
<sup>1</sup> Department of Environmental Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City ACT 2601, Australia and

<sup>2</sup> Carnegie Institution of Washington, Department of Plant Biology, Stanford, Cal. 94305, USA

These produce short term responses that match data



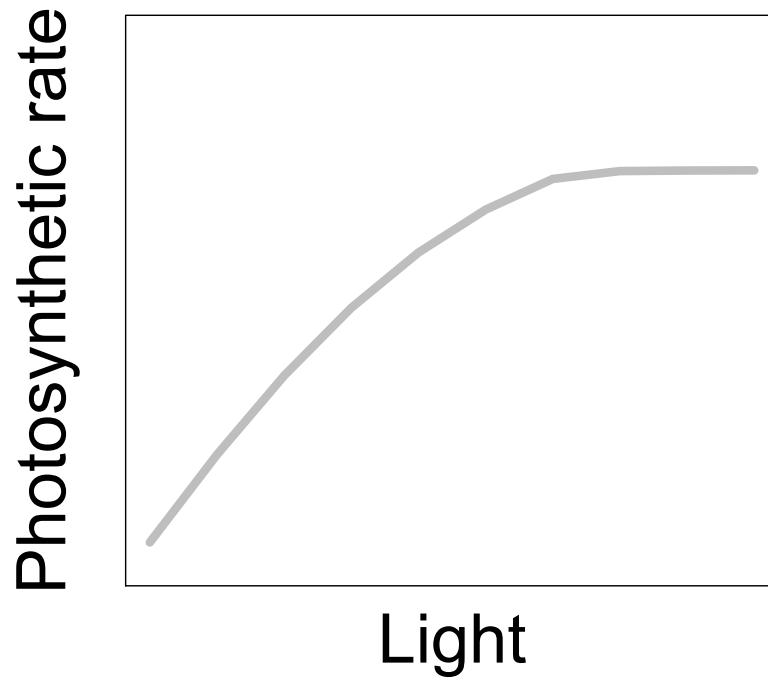
Why the uncertainty? Long-term responses differ from short-term responses due to acclimation



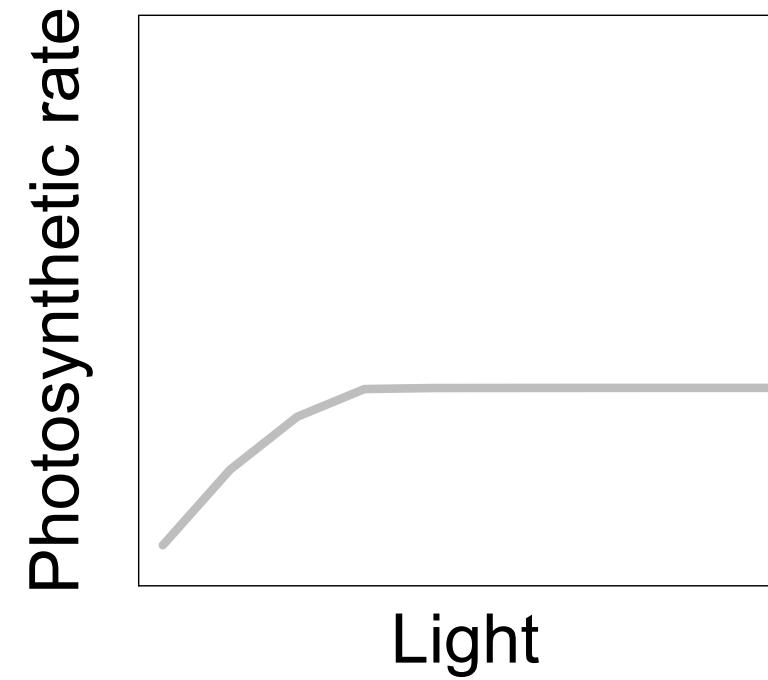
Dumb plants

# Acclimation: an example

Acclimated to high light

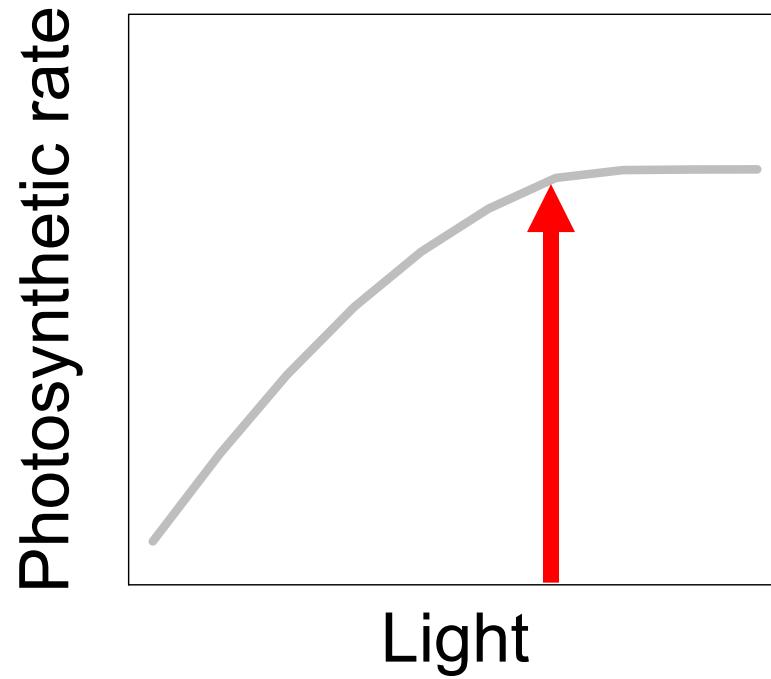


Acclimated to low light

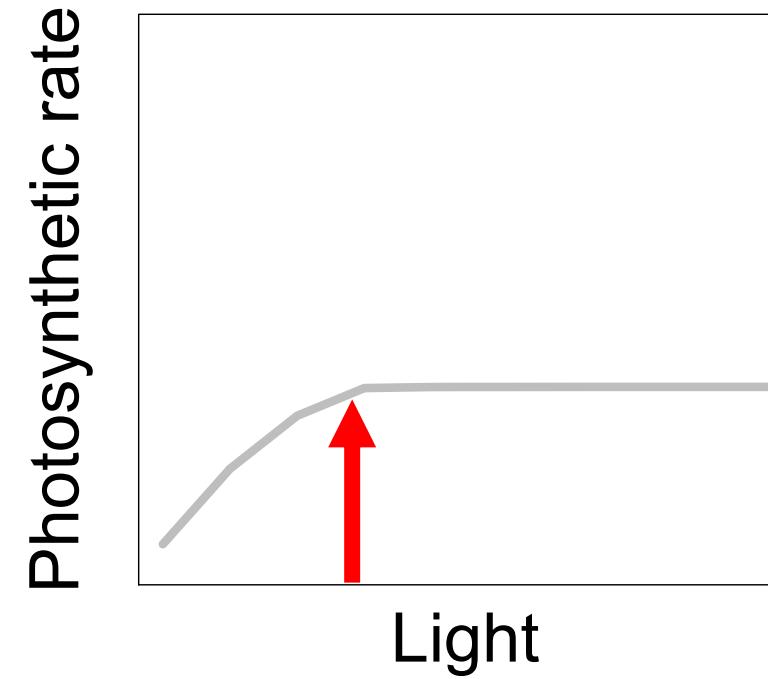


# Acclimation: an example

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...

CO<sub>2</sub>: Bazzaz (1990)

*Ann. Rev. Ecol. Syst.* 1990, 21:167–96  
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THE RESPONSE OF NATURAL ECOSYSTEMS TO THE RISING GLOBAL CO<sub>2</sub> 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

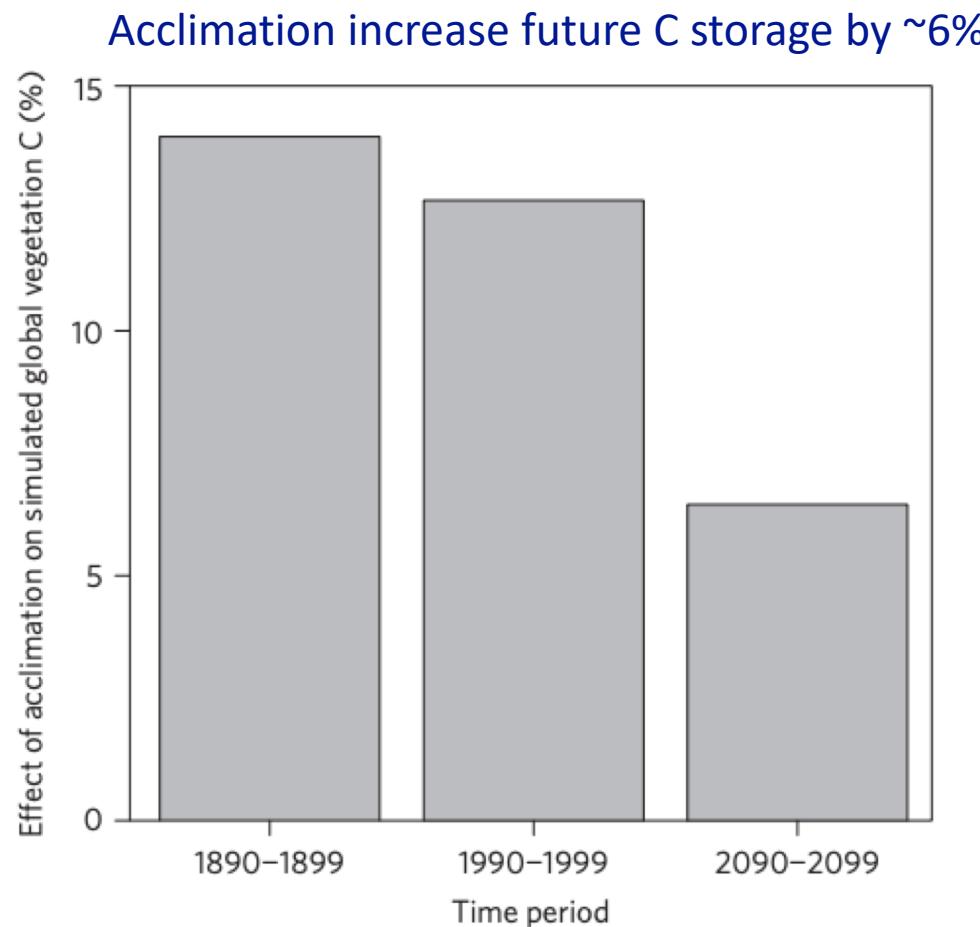
Temperature: Berry & Björkman (1980)

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

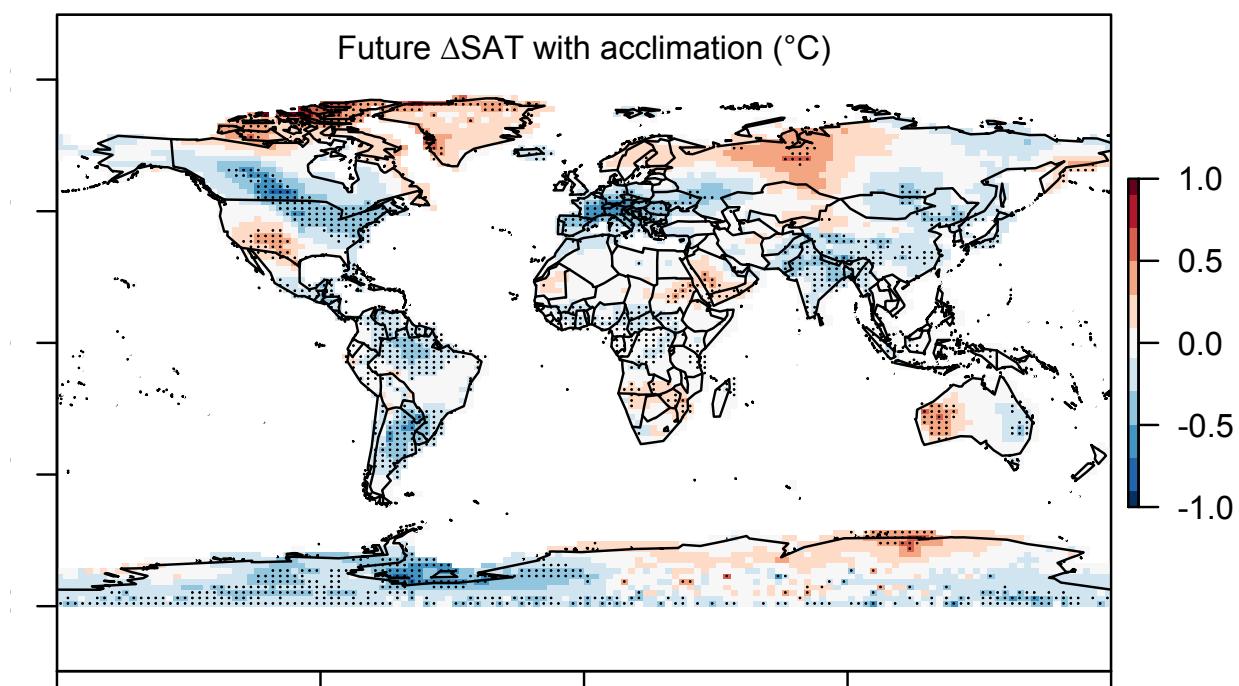
PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

Joseph Berry and Olle Björkman<sup>1</sup>

# ...and can impact carbon cycling and climate



Acclimation alters future temperature by >1°C

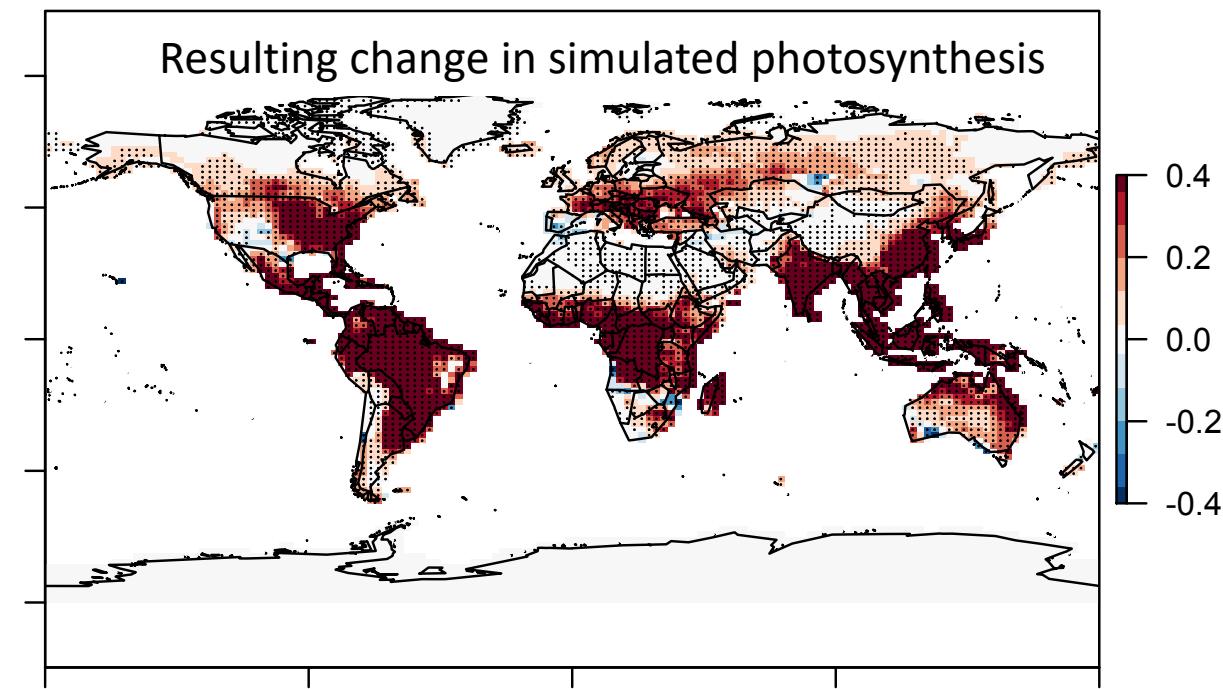
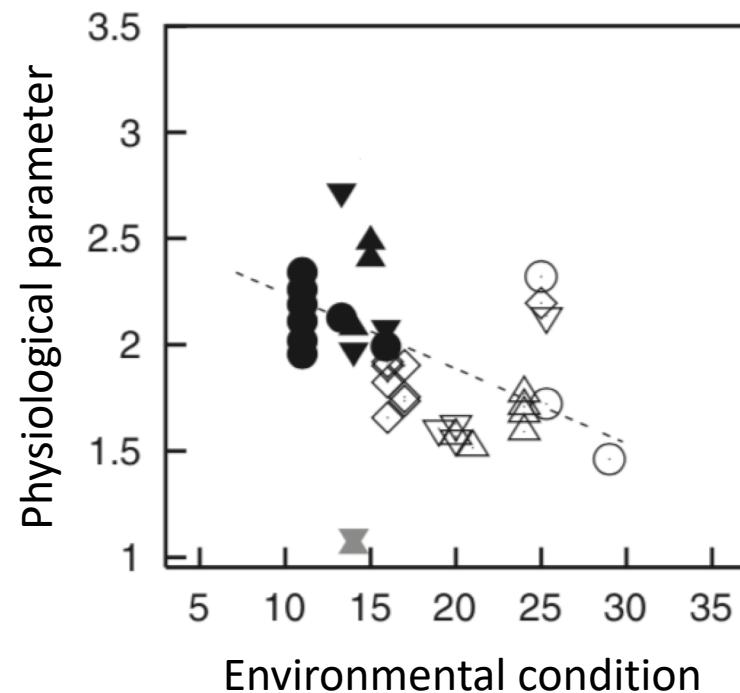


Unfortunately,  
no theoretical model for  
photosynthetic acclimation exists

Lack of theory results in...

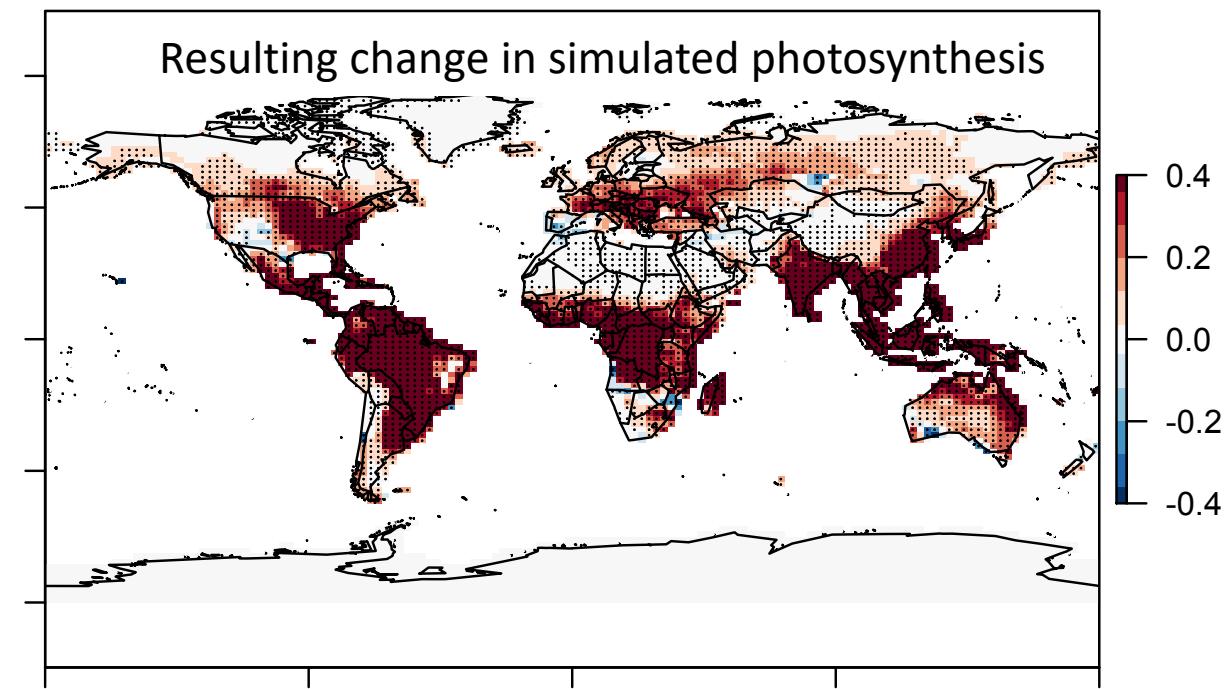
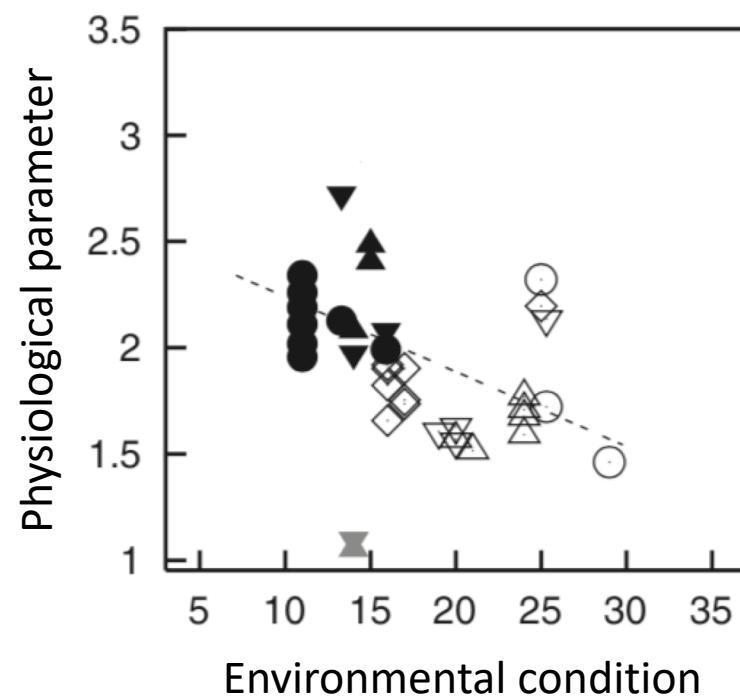
# Lack of theory results in...

- 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

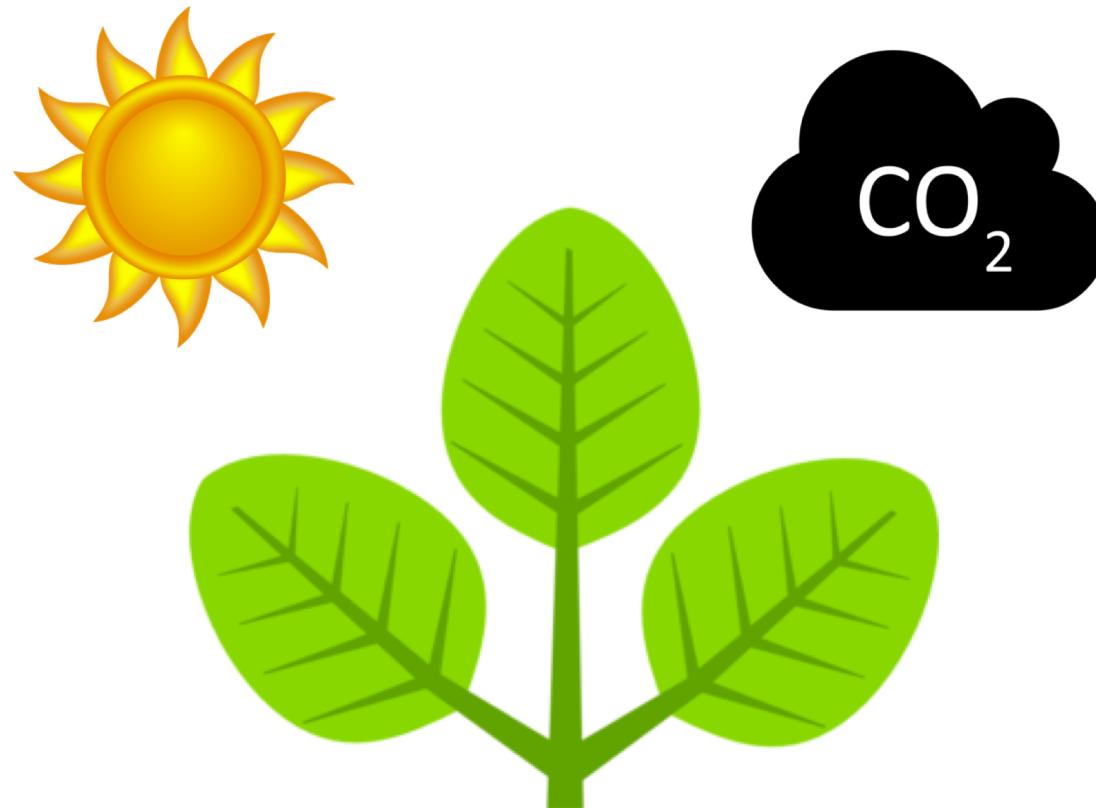
Photosynthesis =  $f\{\text{stomatal conductance,}$   
 $\text{photosynthetic biochemistry}\}$

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

# Optimal photosynthesis

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

# Biochemistry optimization

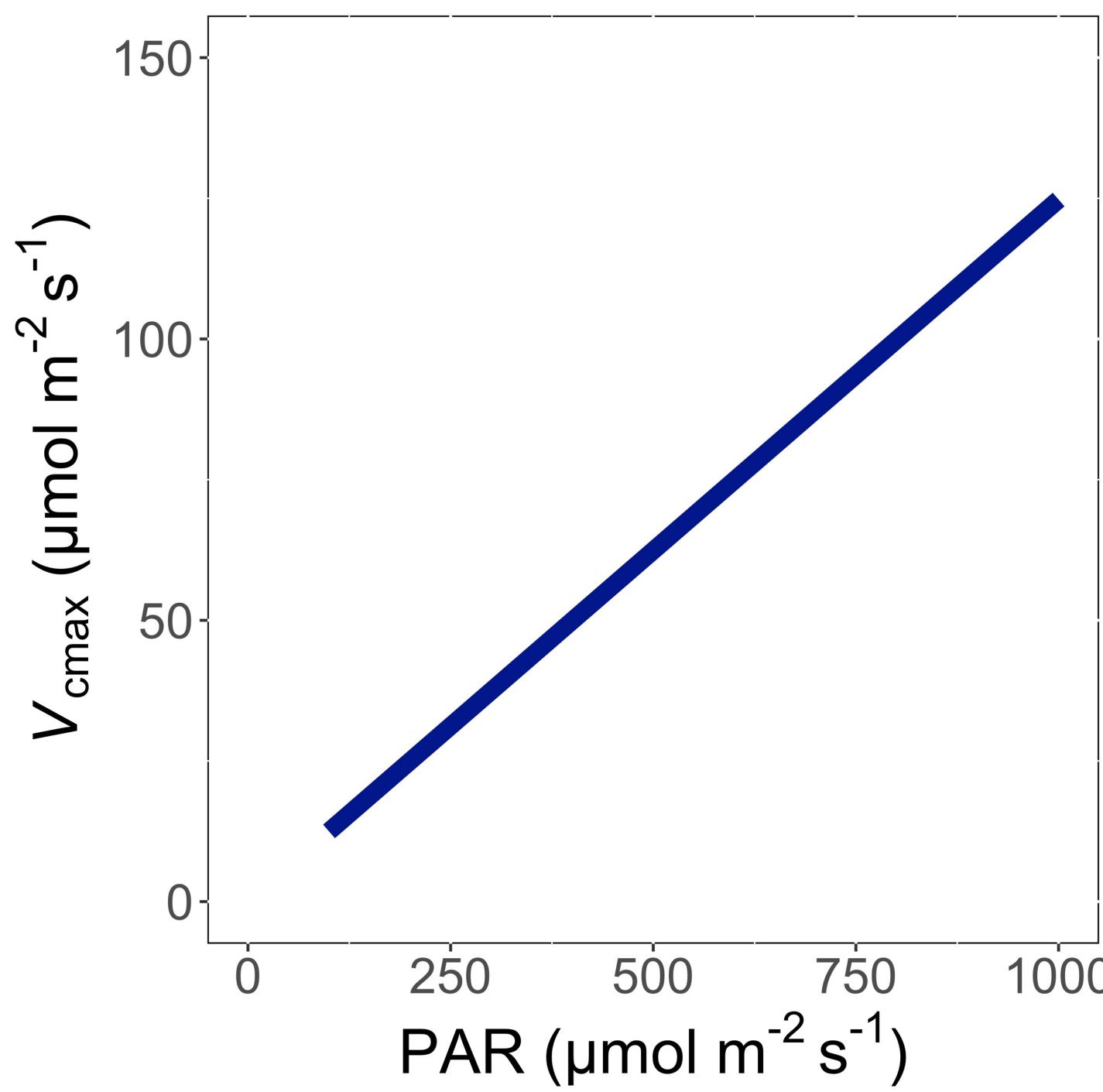


Plant  
biochemistry  
setup will aim for  
equal limitation  
by all factors

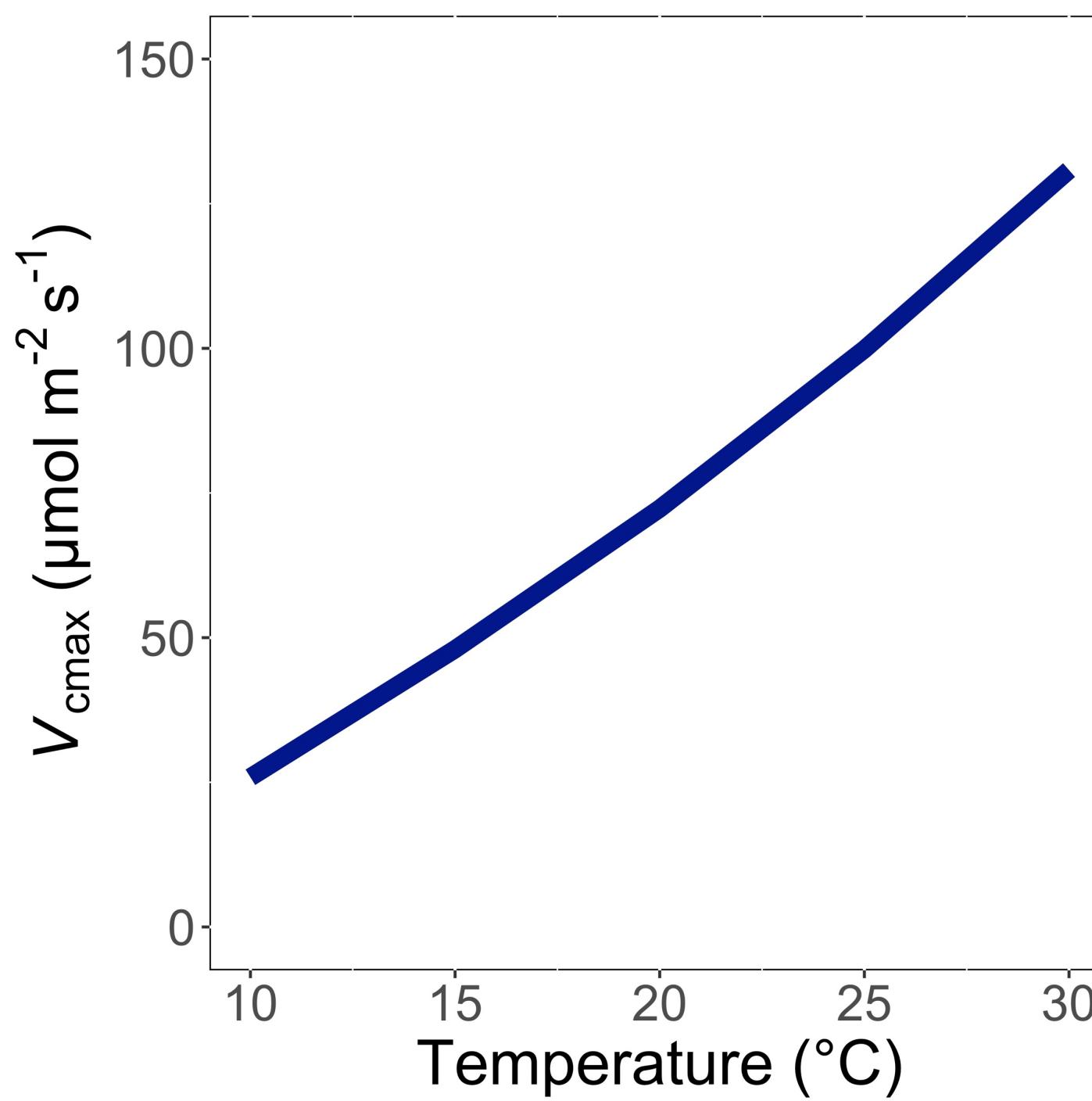
[TALK TO ME LATER ABOUT THE MATHS]

## Biochemistry trait

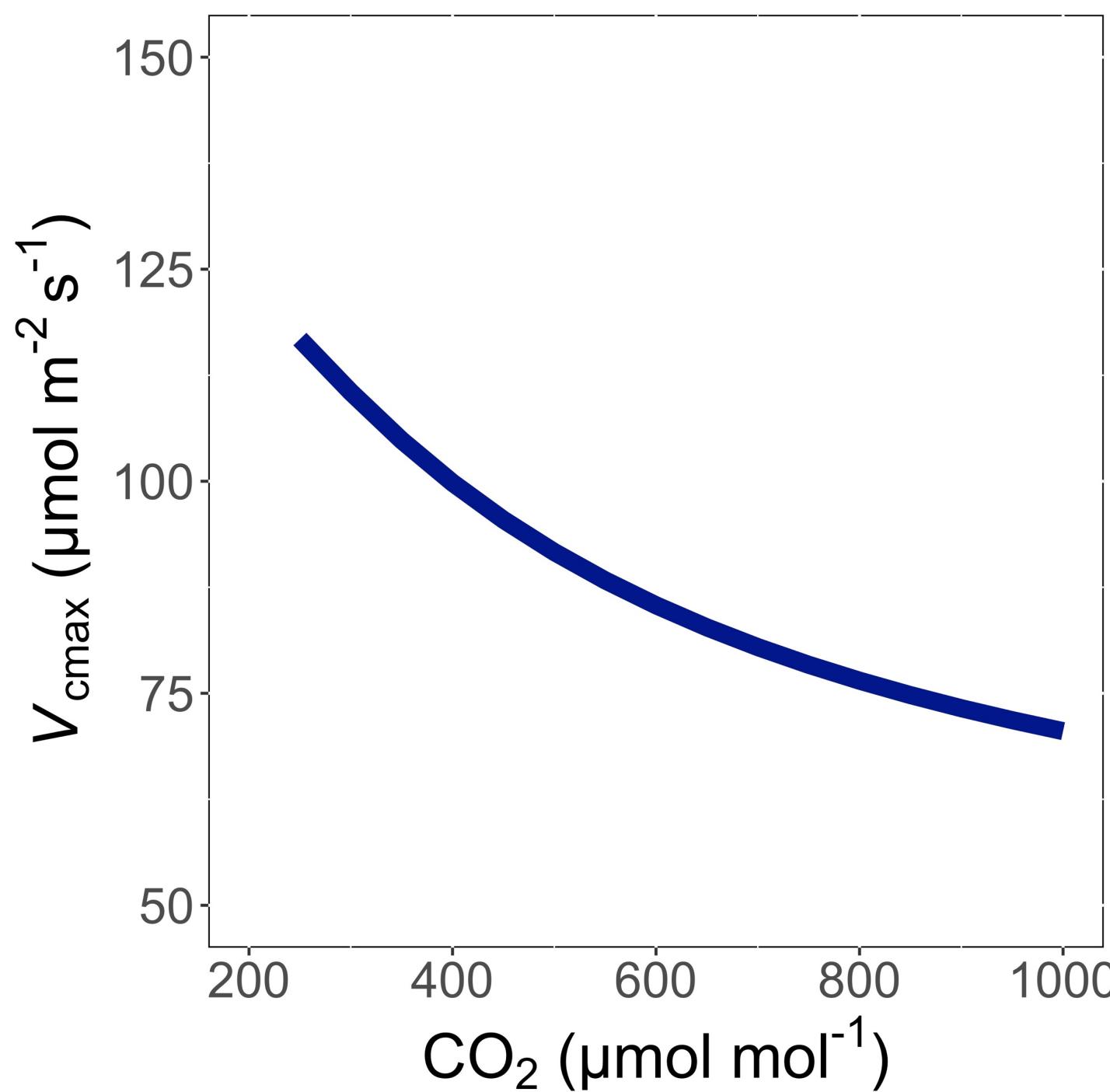
The maximum rate of Rubisco carboxylation ( $V_{cmax}$ )



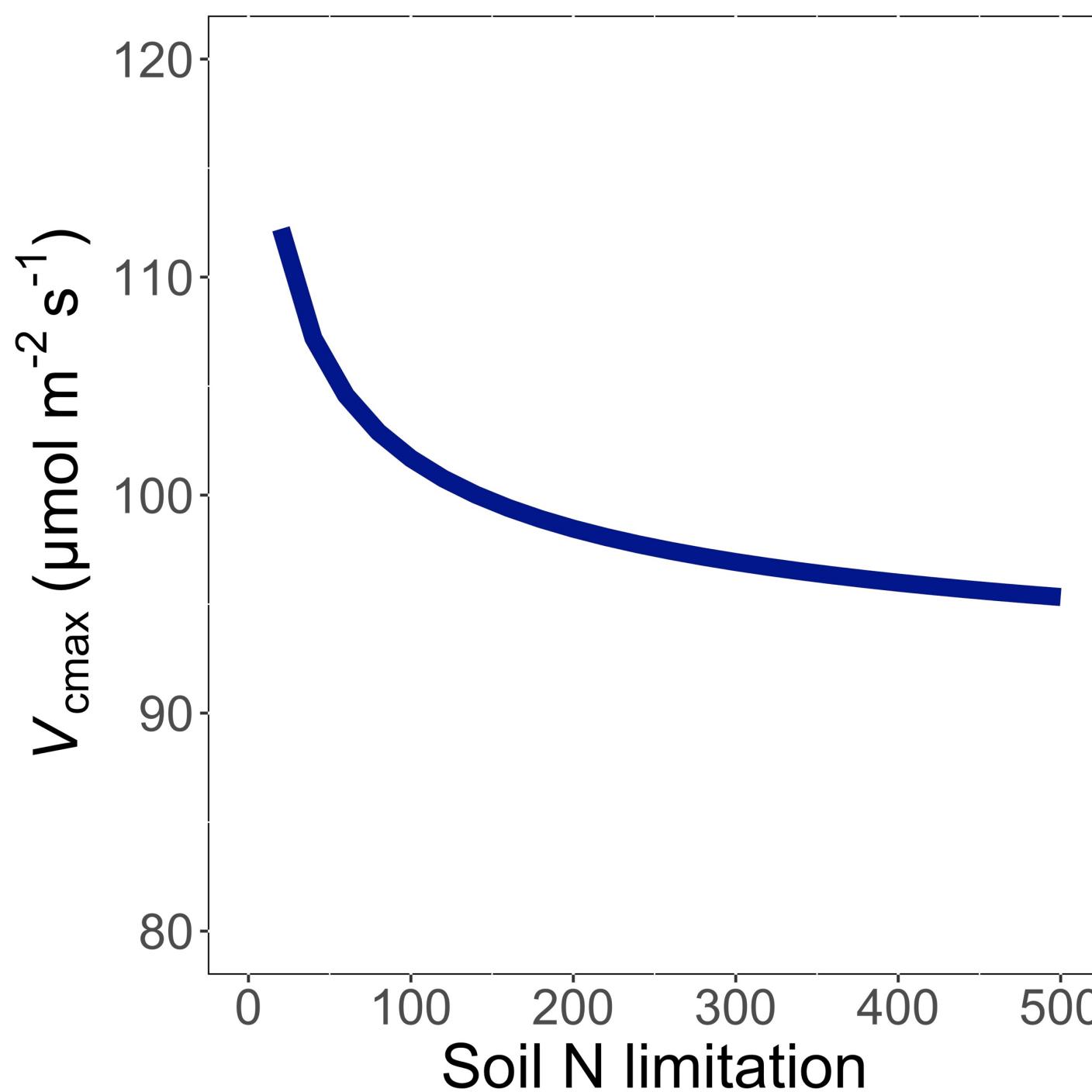
$V_{c\max}$  increases  
with light because  
of greater electron  
transport



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

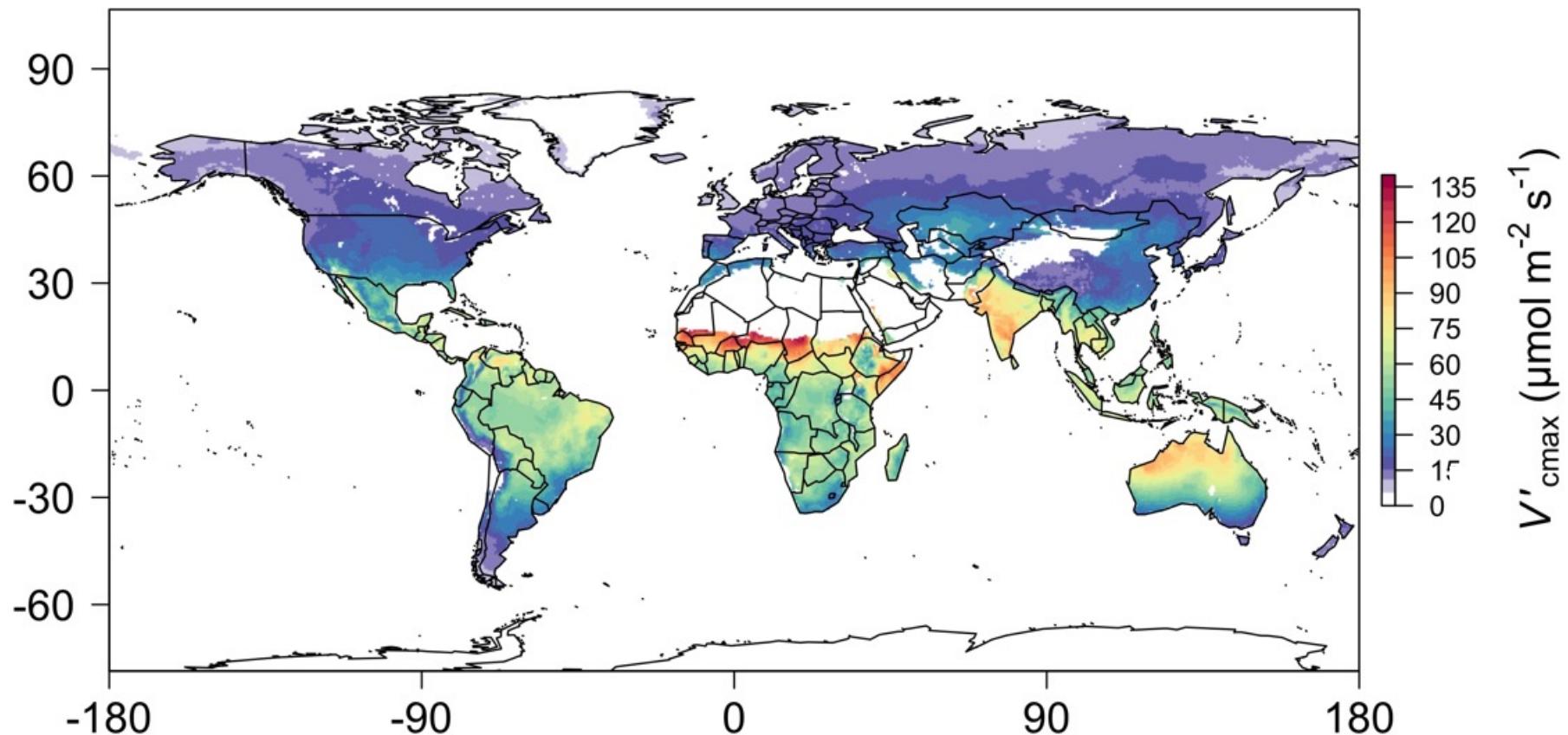


$V_{\text{cmax}}$  decreases with  $\text{CO}_2$  because of greater  $\text{CO}_2$  in the leaf and less photorespiration



$V_{c\max}$  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

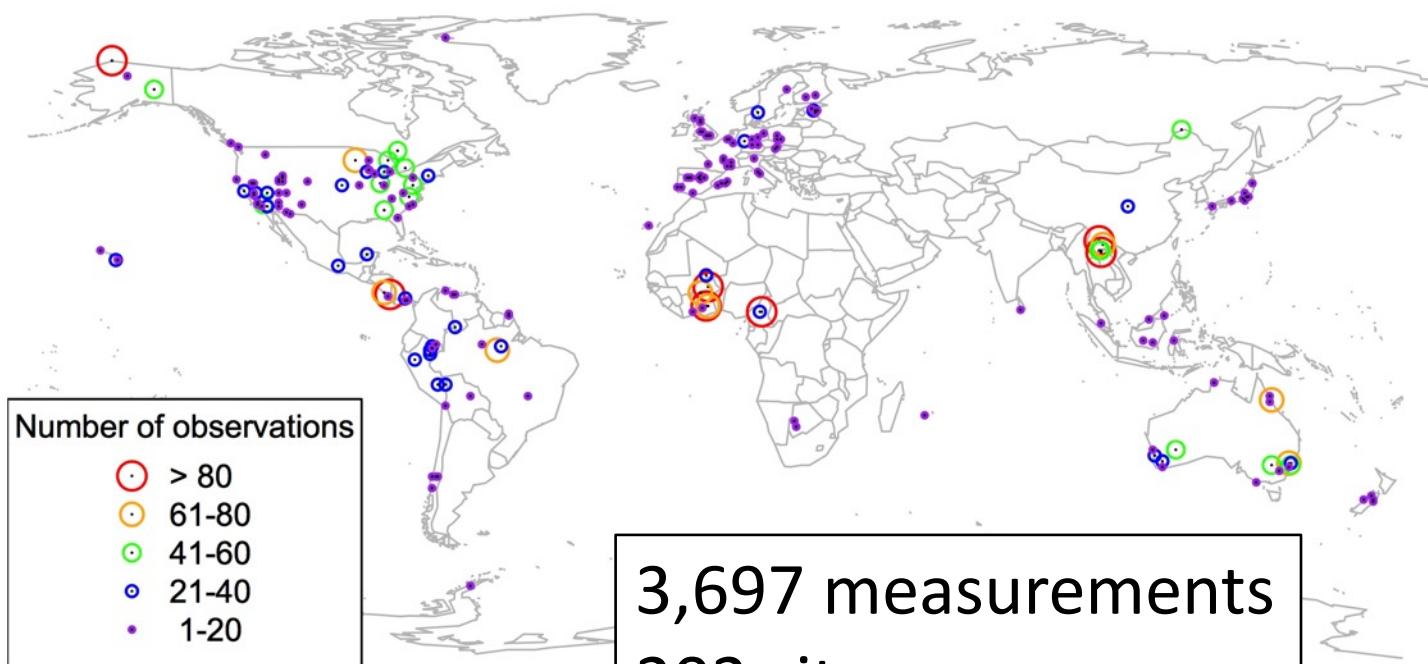
Let's tackle some big questions in  
plant ecophysiology!

# Big questions

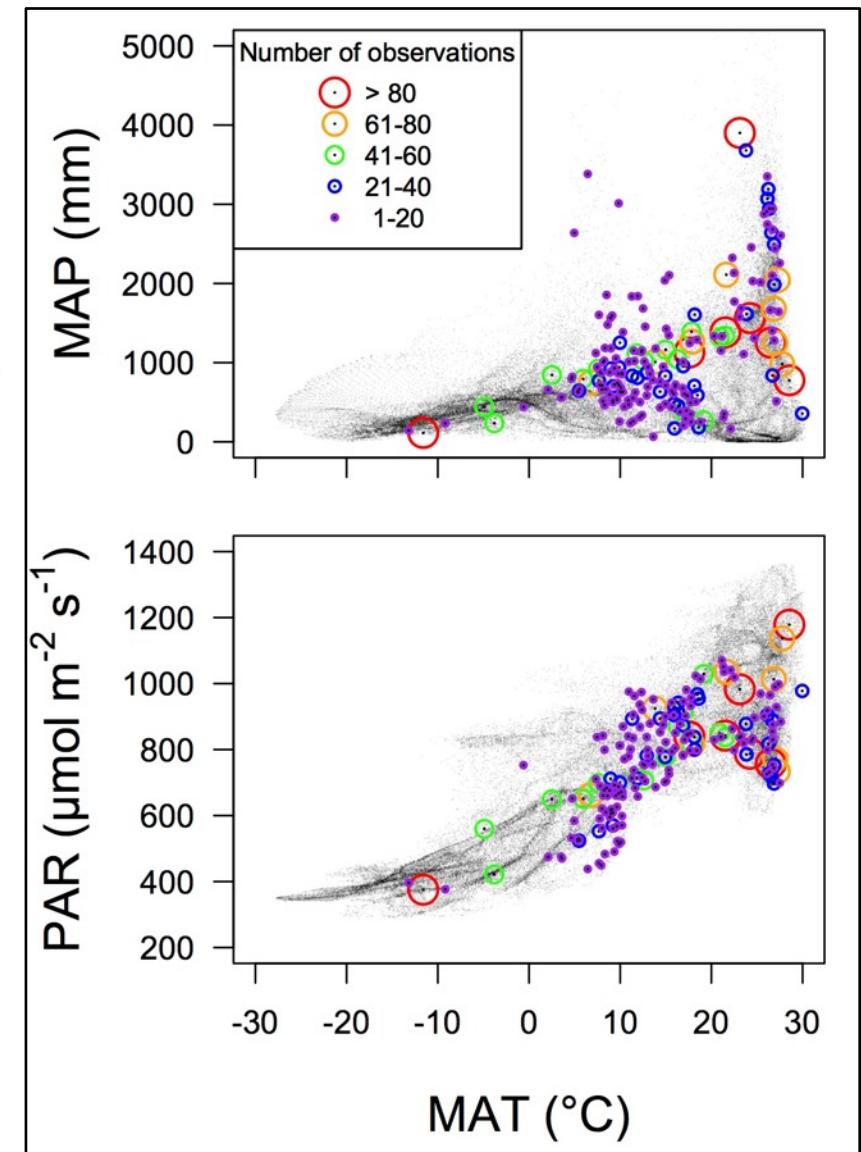
1. Is photosynthesis **optimized** to the environment?
2. How do plants acclimate to **soil nitrogen**?
3. What does acclimation mean for **future** terrestrial biogeochemical cycling?
4. When is **C<sub>4</sub>** photosynthesis an advantage over C<sub>3</sub> photosynthesis?

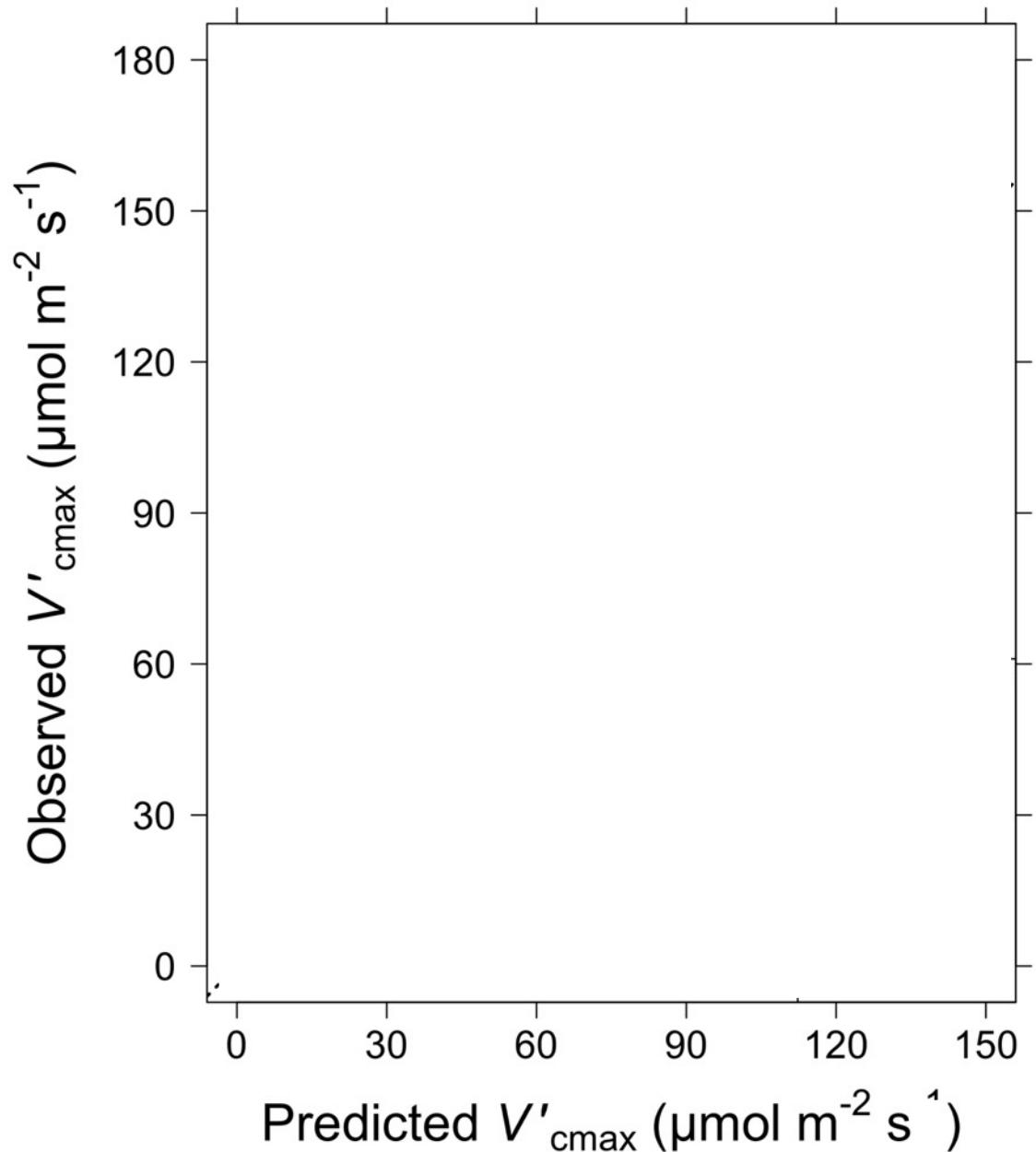
**Question 1:** Is photosynthesis optimized to the environment?

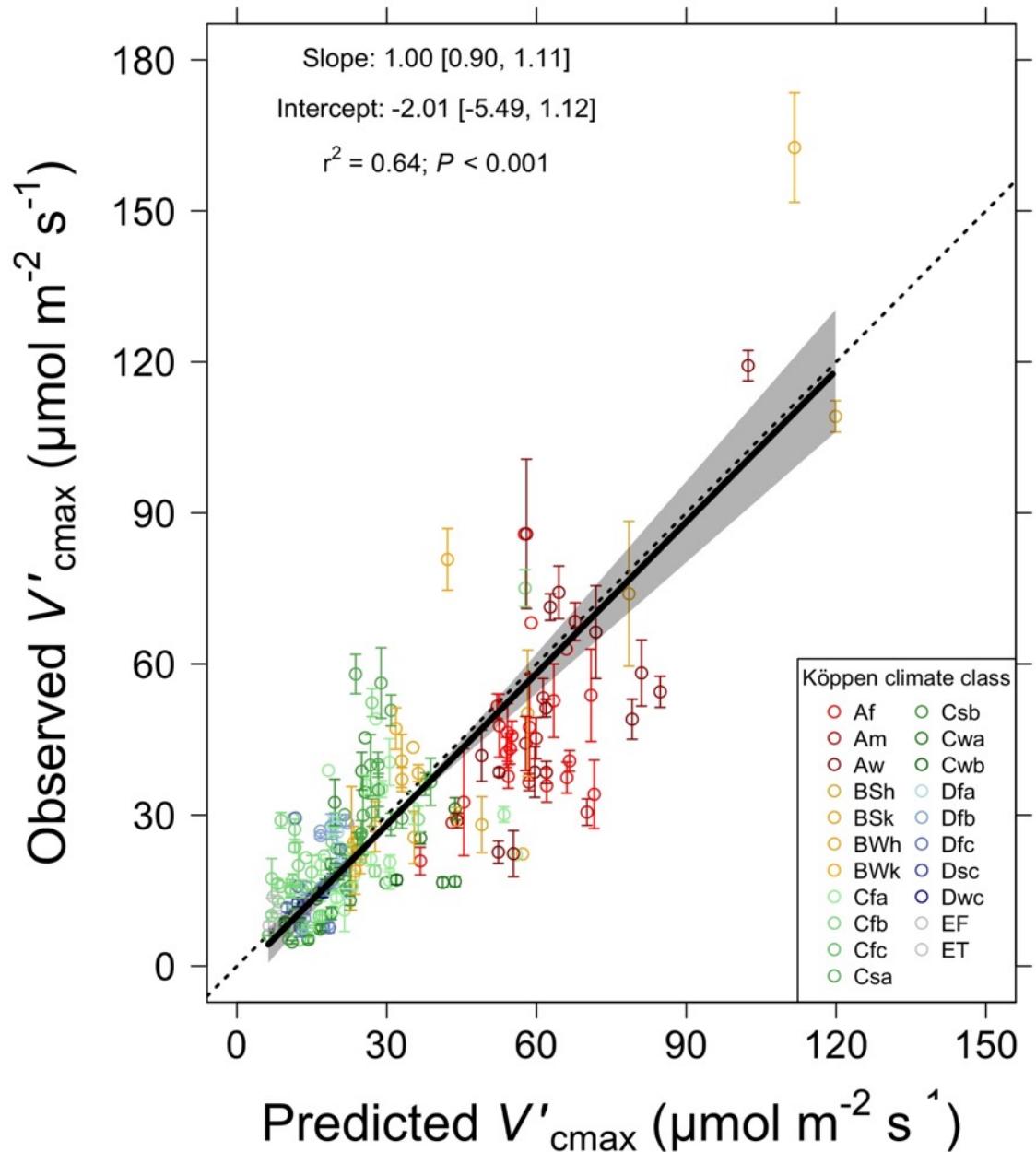
# Global $V_{cmax}$ dataset



3,697 measurements  
202 sites  
> 600 genera







Optimal  $V'_{\text{cmax}}$  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?

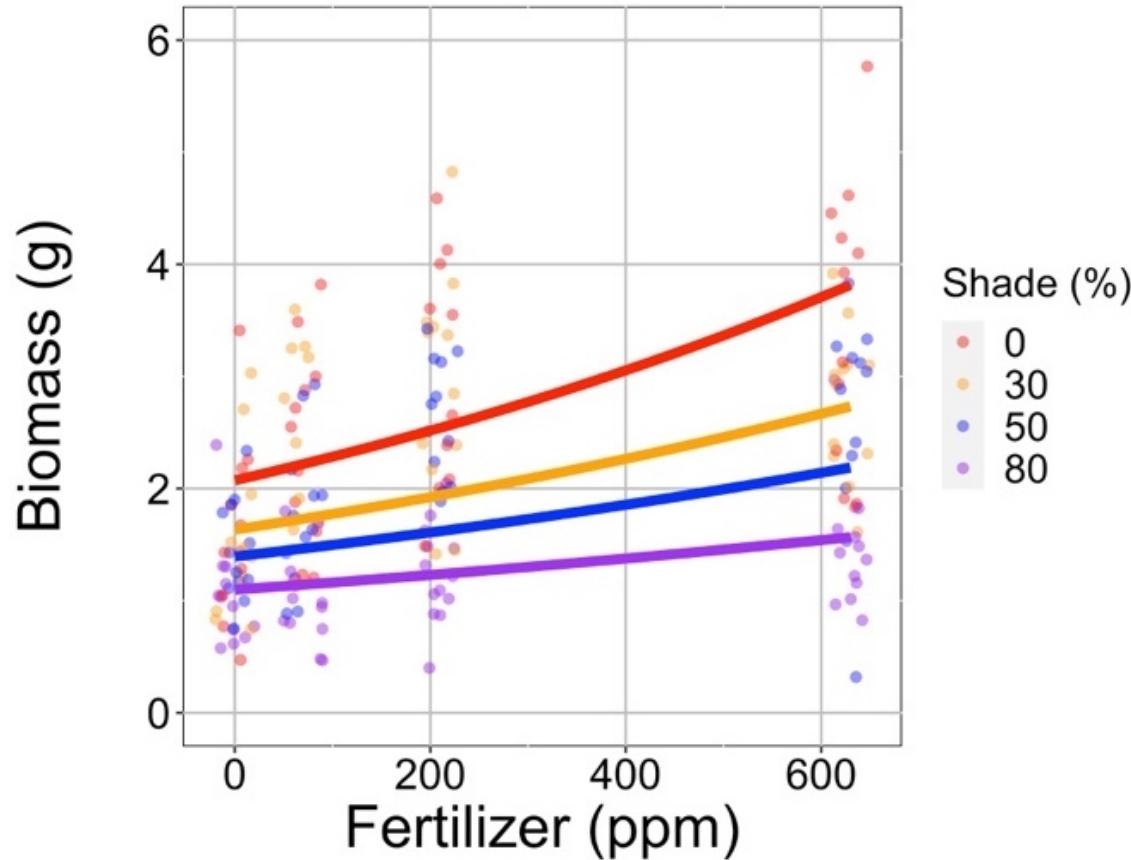
# The lab has examined soil nitrogen impacts in many contexts

- 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)



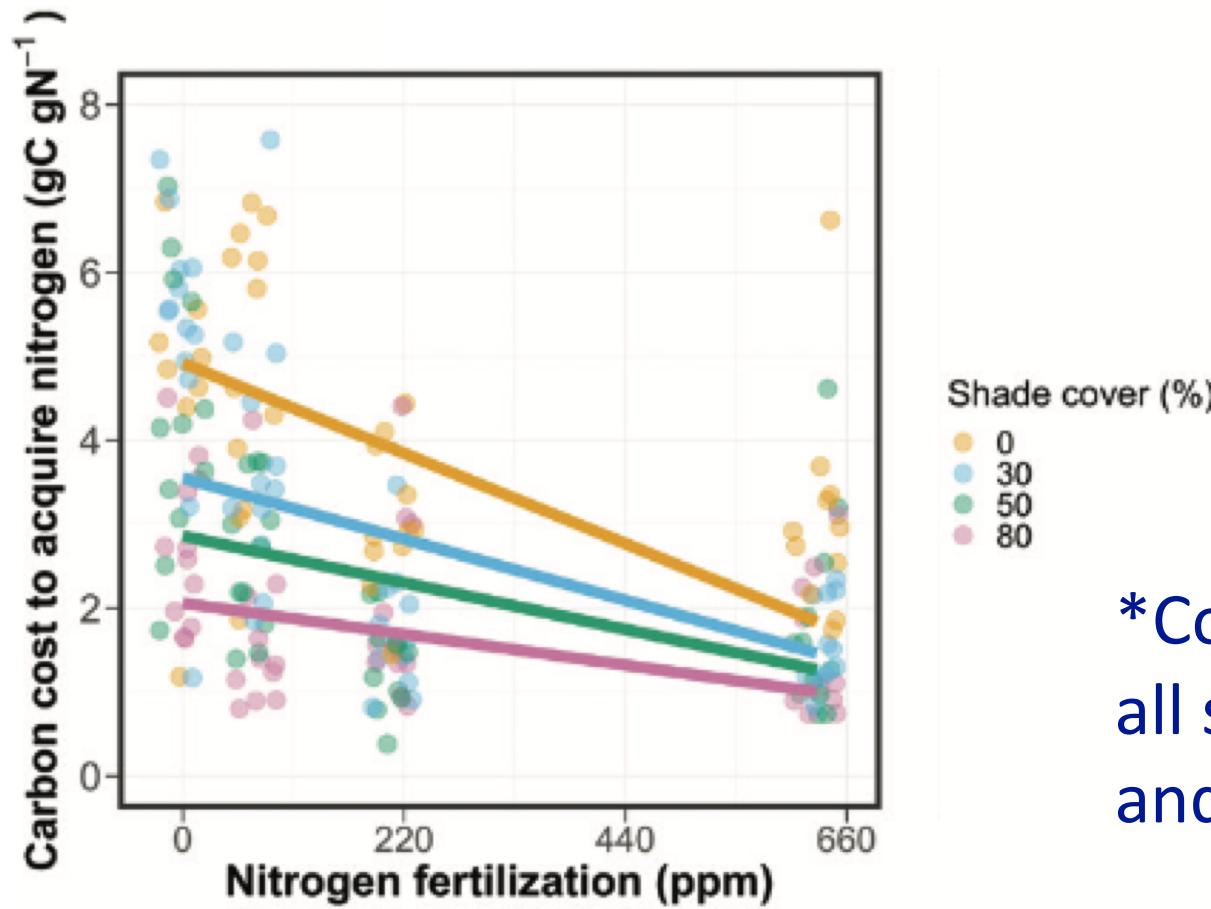
What have we learned?

# Result 1: Growth increases with increasing soil N



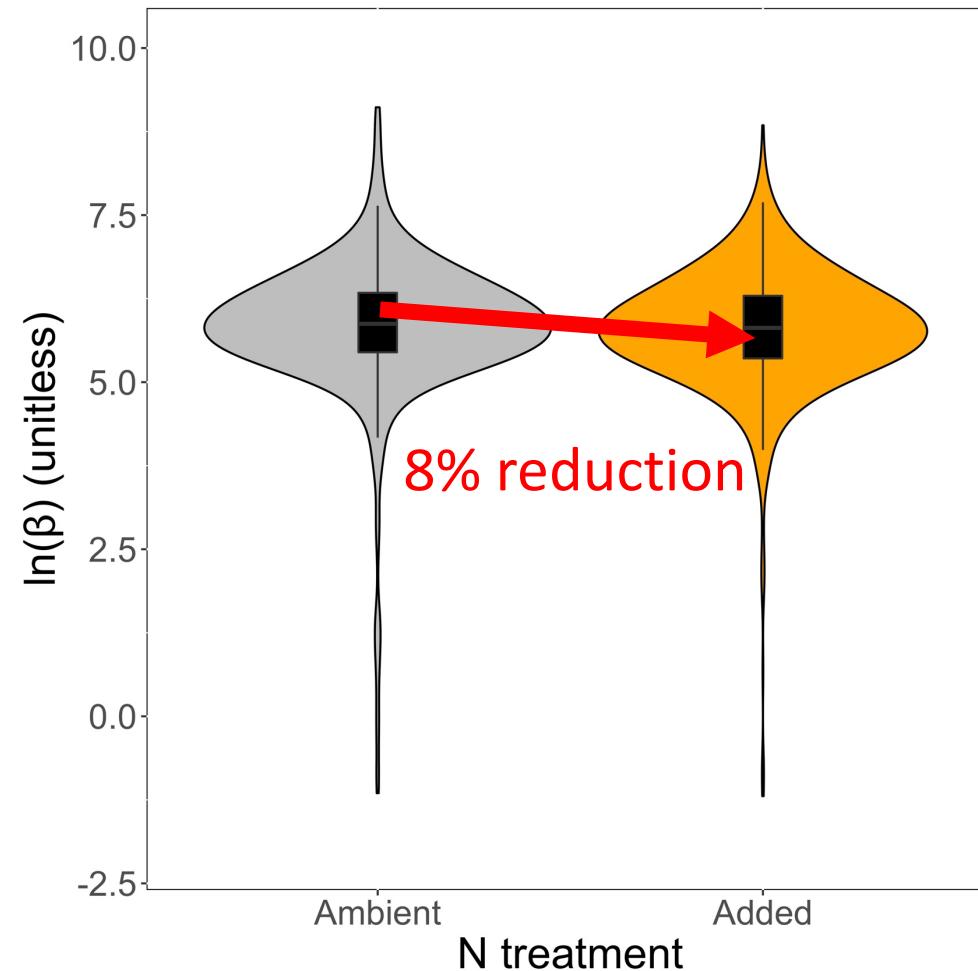
\*Consistent across  
all studies

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



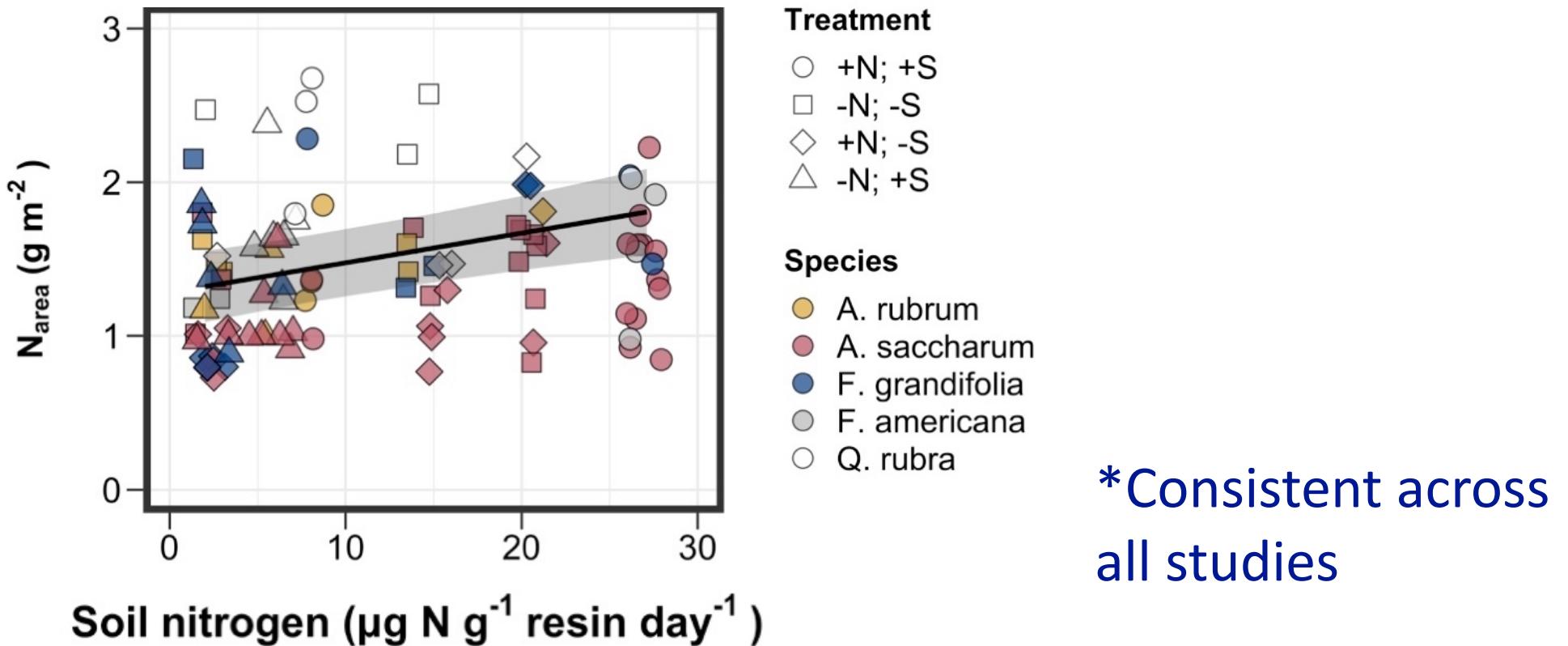
\*Consistent across all studies at leaf and plant level

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

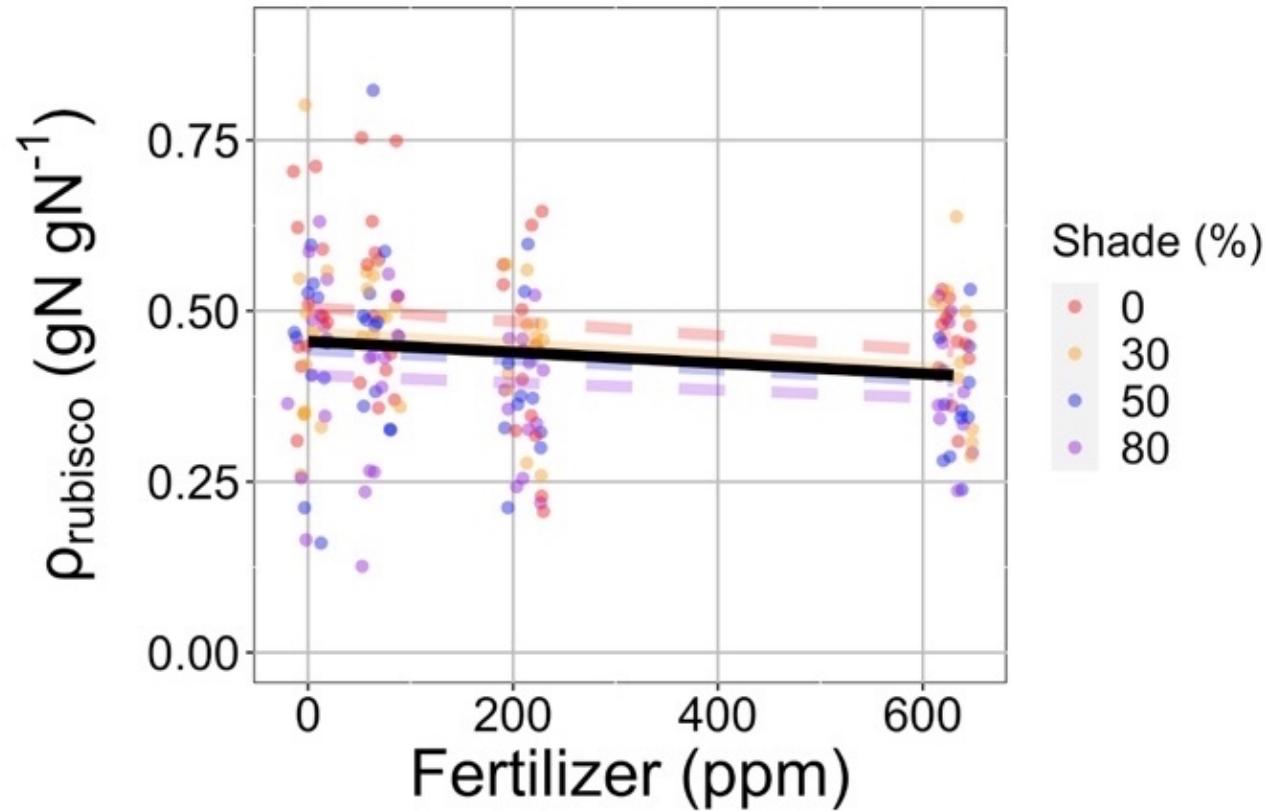


\*Consistent across all studies at leaf and plant level

# Result 3: Tissue N increases with increasing soil N

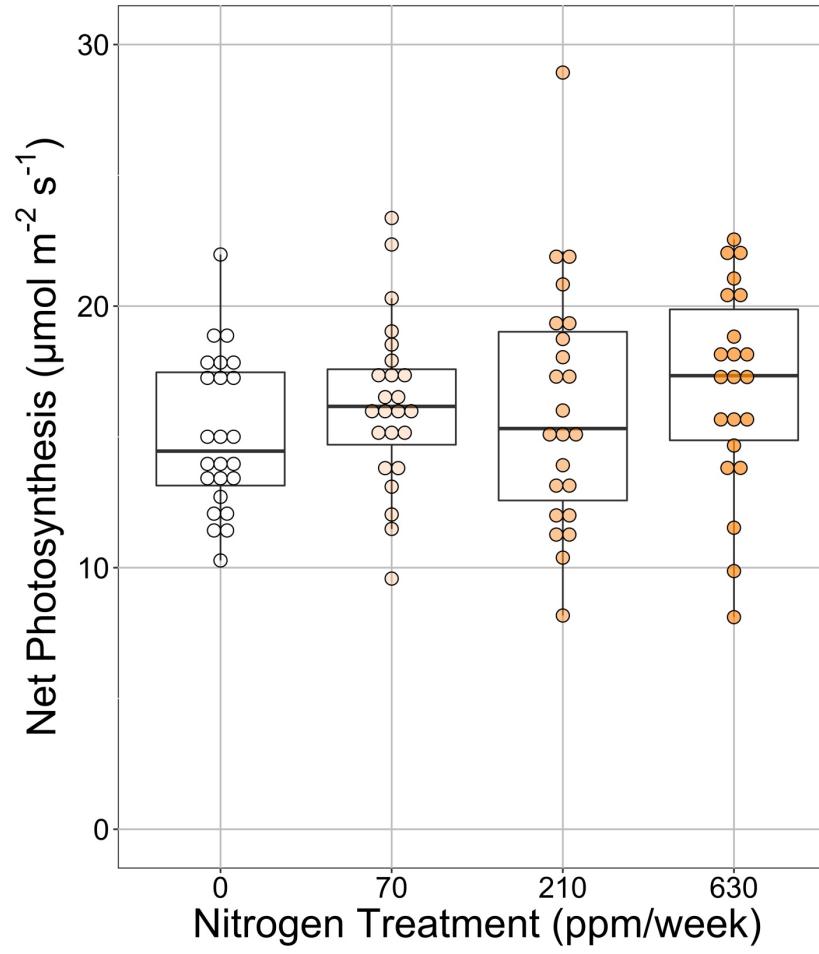


# Result 4: Relative leaf N allocation to photosynthesis decreases with increasing soil N



\*Consistent across multiple species, metrics, and growth conditions

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

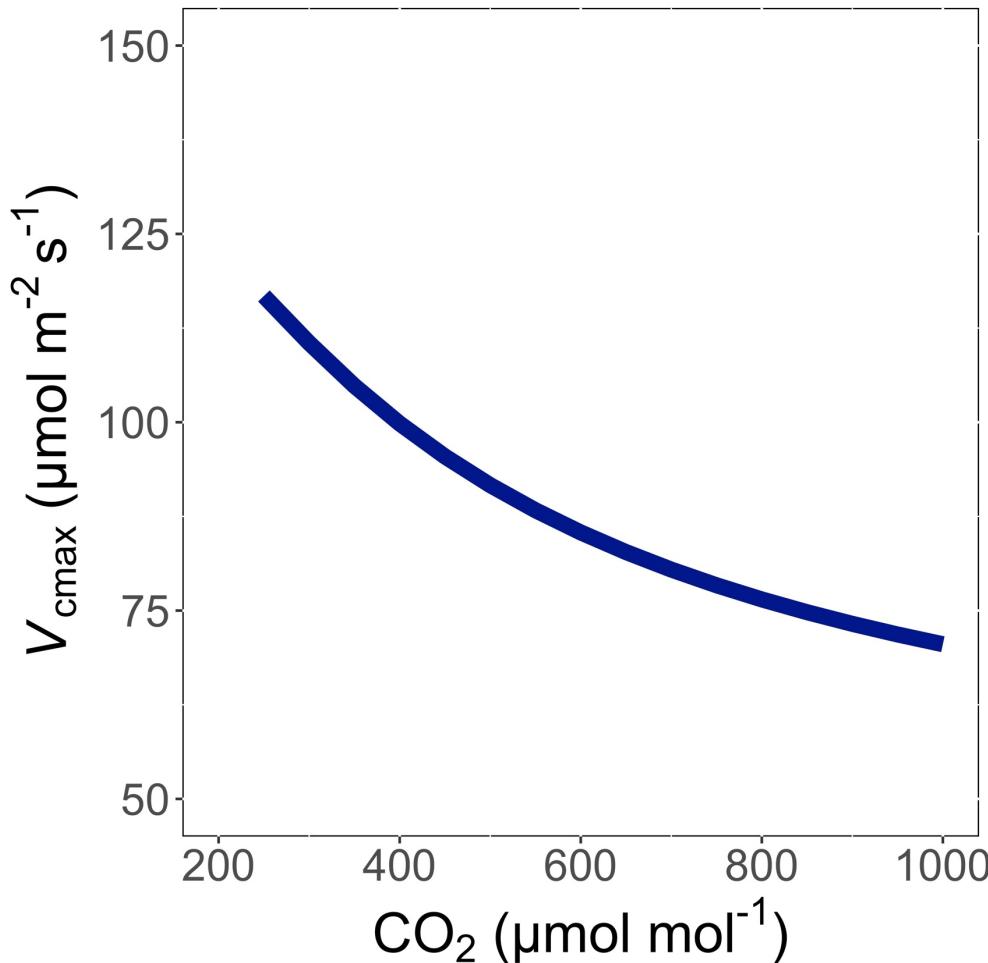


Question 2: How do plants acclimate  
to soil nitrogen?

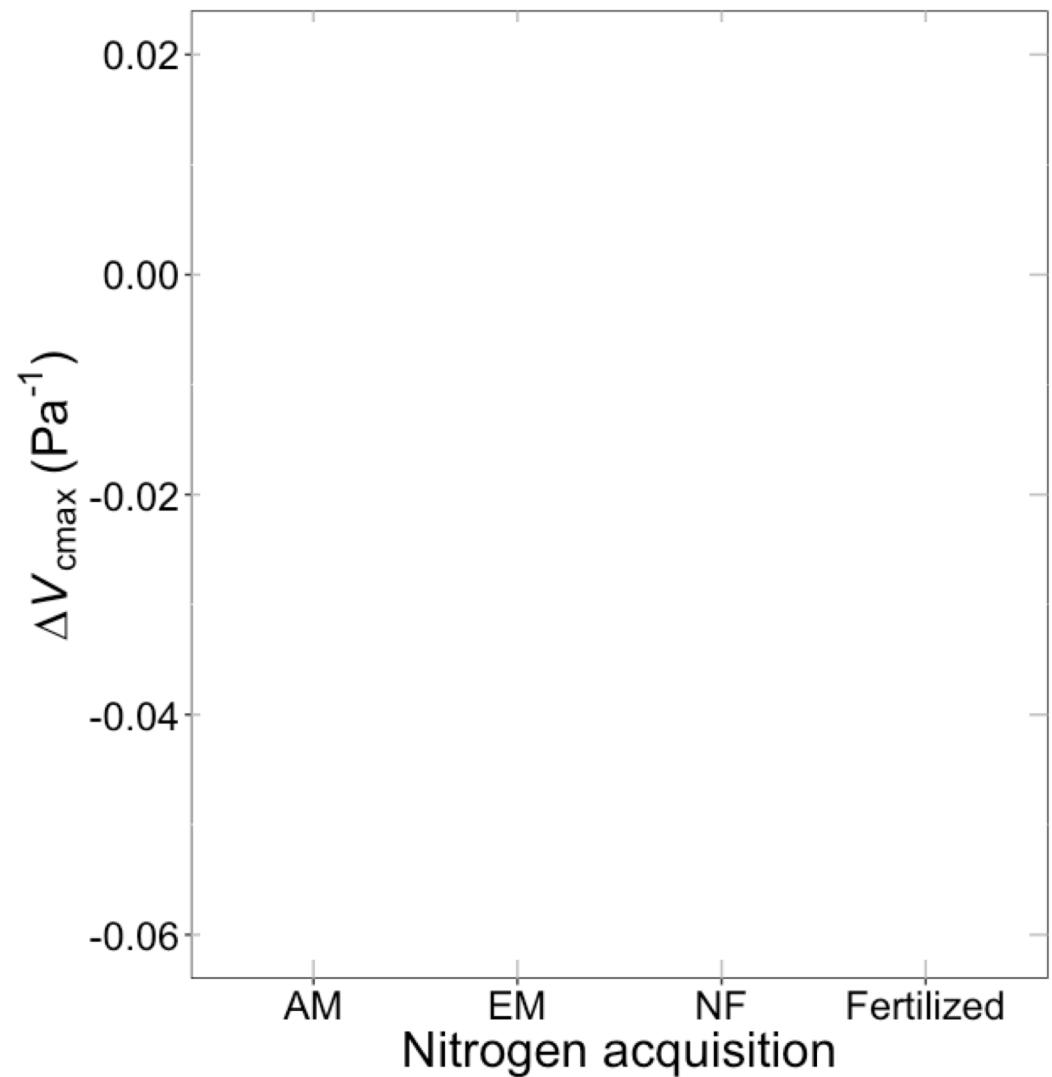
Reduction in N uptake costs results in  
bigger plants with more leaf N, but  
little change in per-leaf-area  
photosynthesis

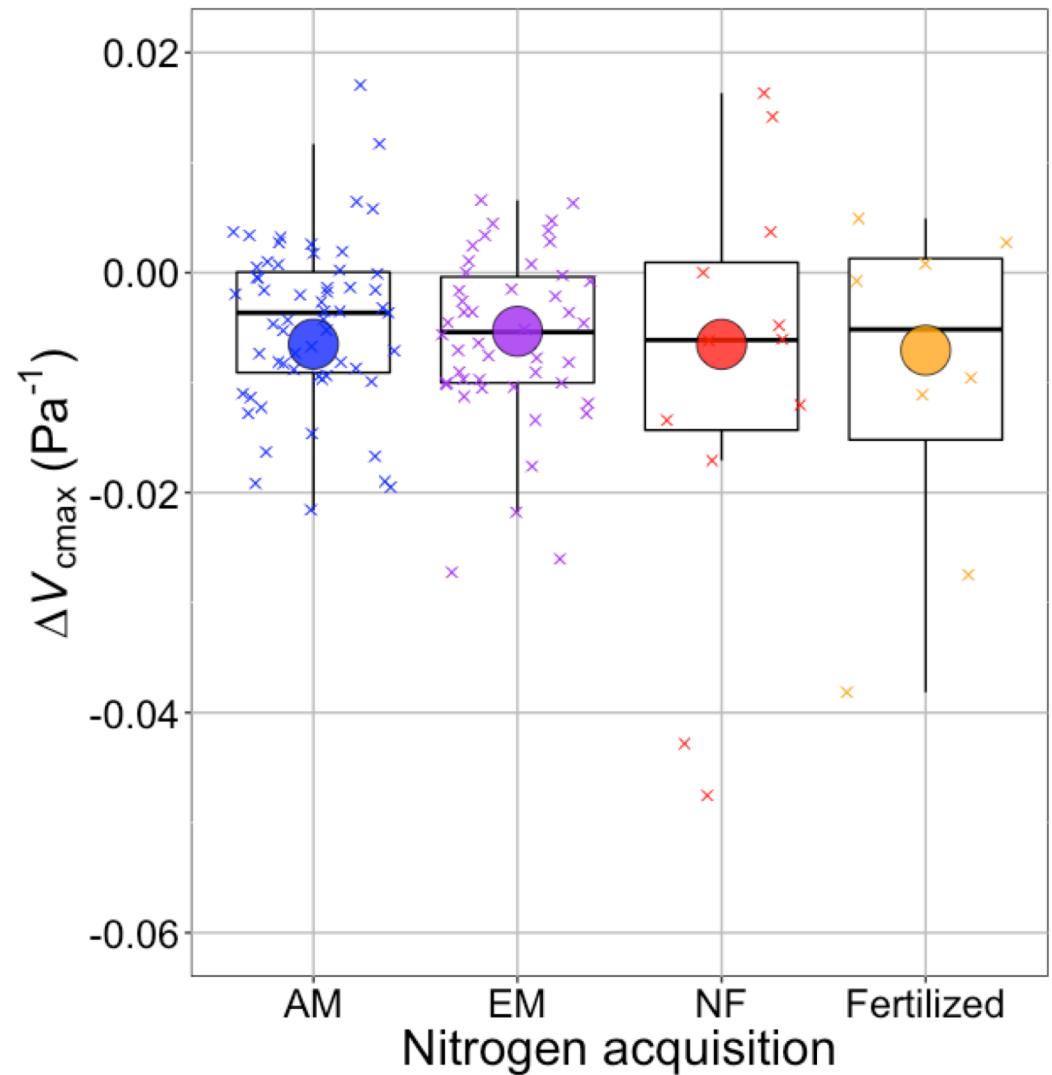
**Question 3:** What does acclimation mean for future terrestrial biogeochemical cycling?

# Expected future responses



$V_{\text{cmax}}$  decreases with  $\text{CO}_2$  because of greater  $\text{CO}_2$  in the leaf and less photorespiration



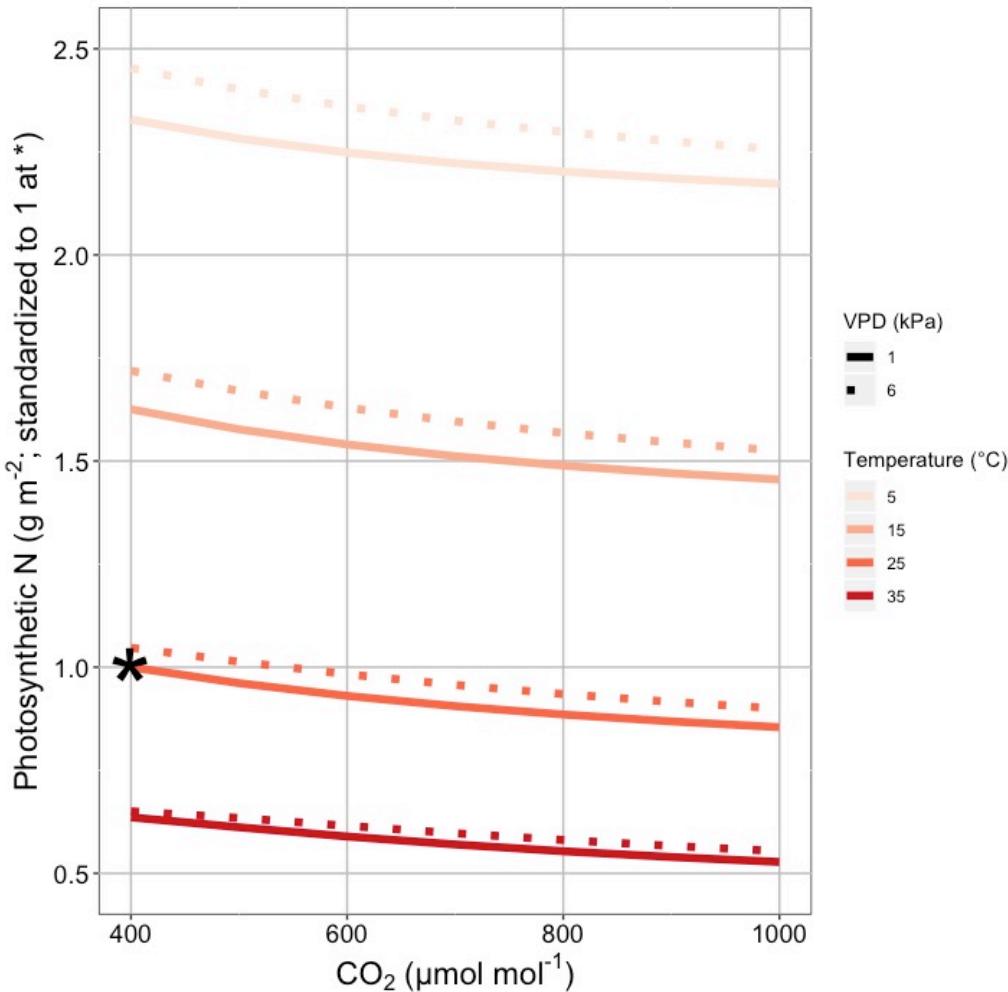


$V_{\text{cmax}}$  changes with CO<sub>2</sub> in ways expected from optimization

Boxes = data = -0.0063 Pa<sup>-1</sup>

Circles = predicted = -0.0066 Pa<sup>-1</sup>

This generally suggests lower nitrogen demand under future conditions

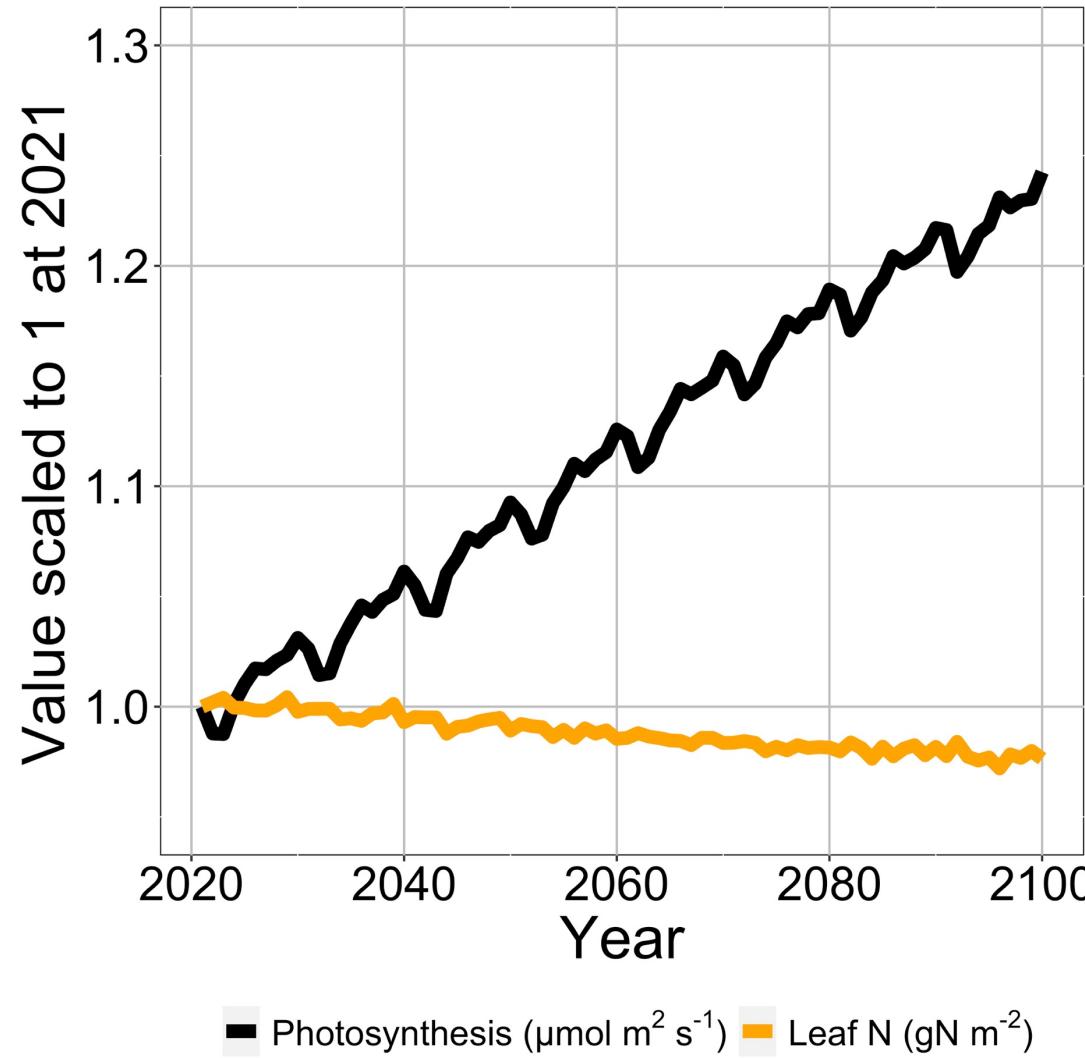


Let's run a model out into the  
future!

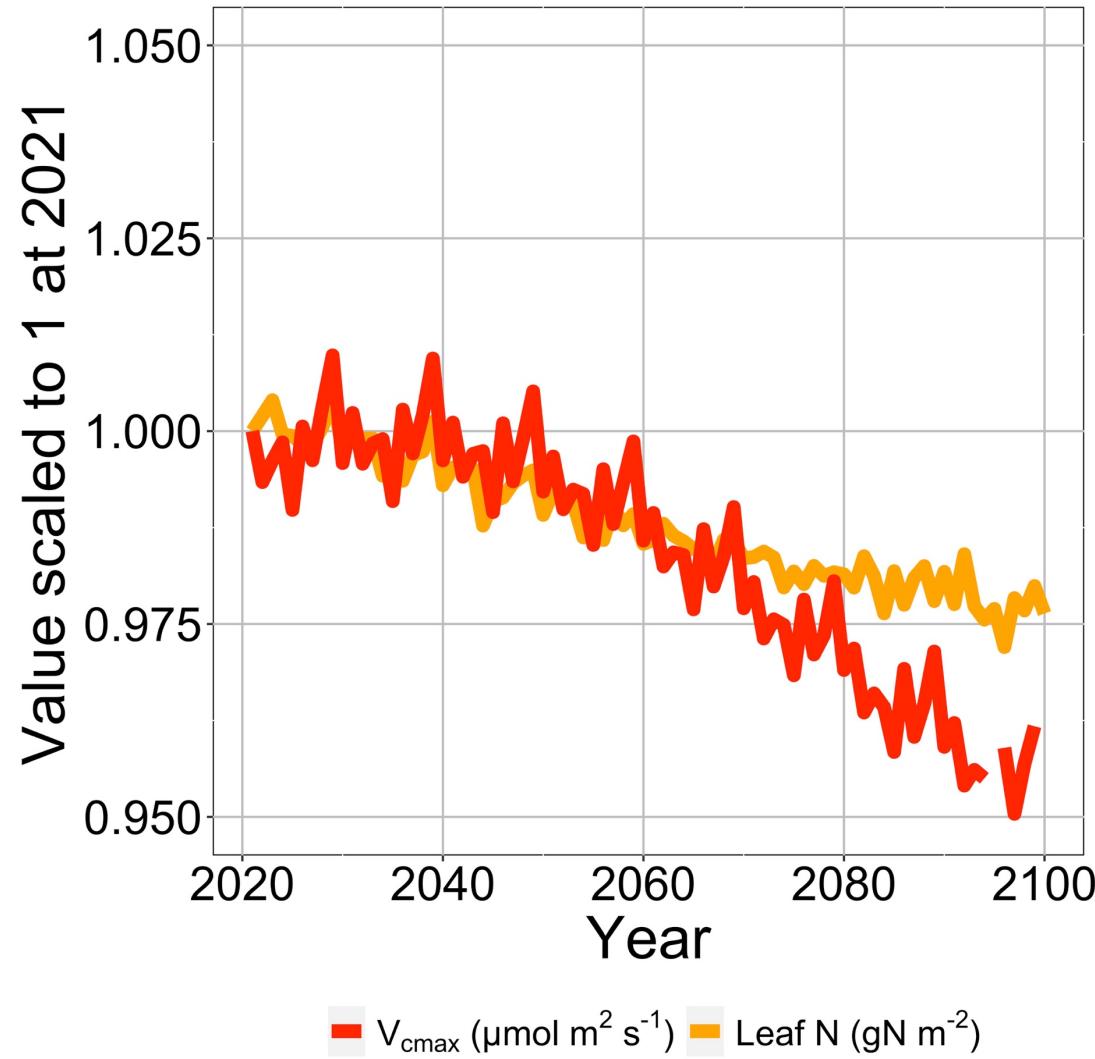


Energy Exascale  
Earth System Model

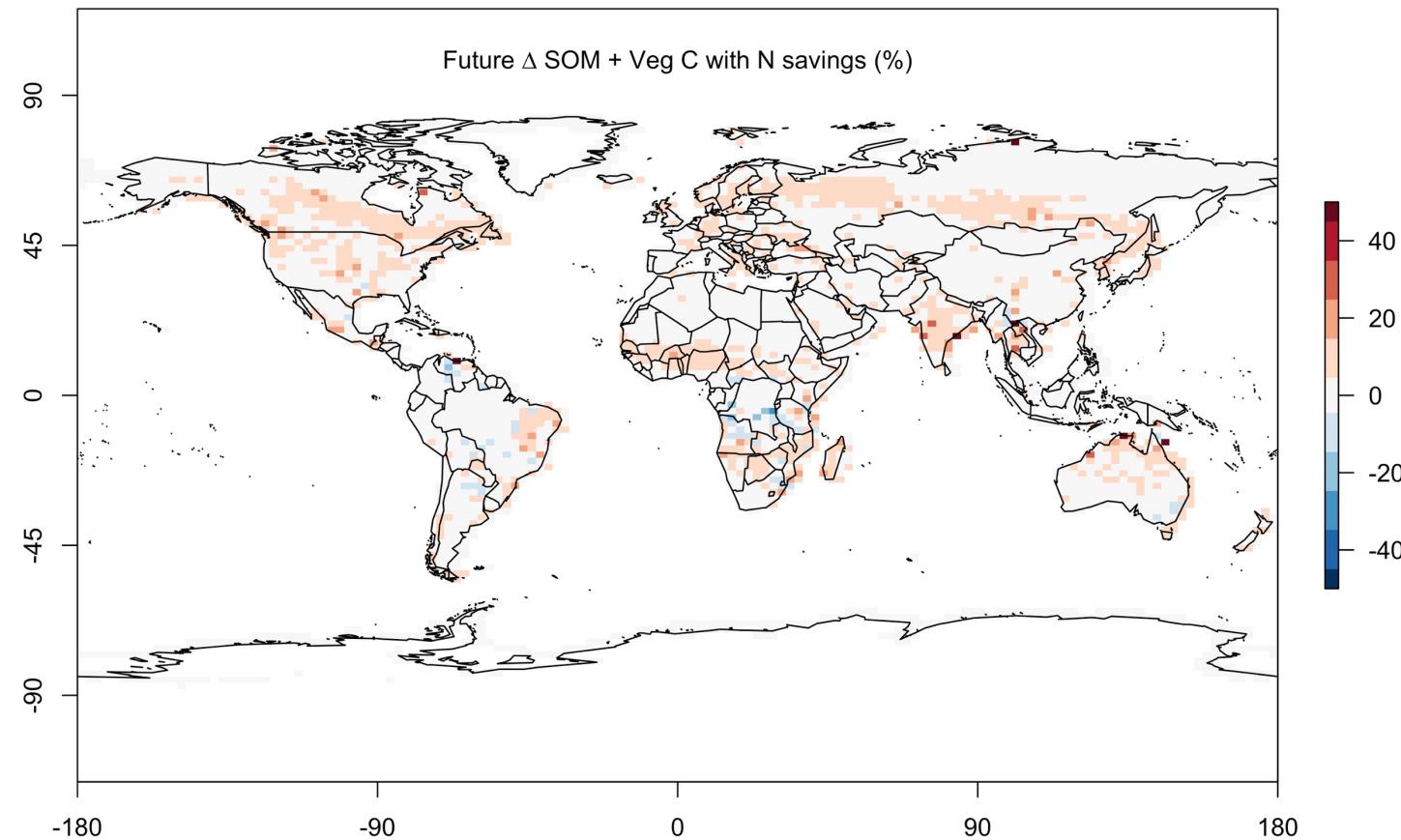
# Photosynthesis increases with elevated CO<sub>2</sub> at lower leaf N



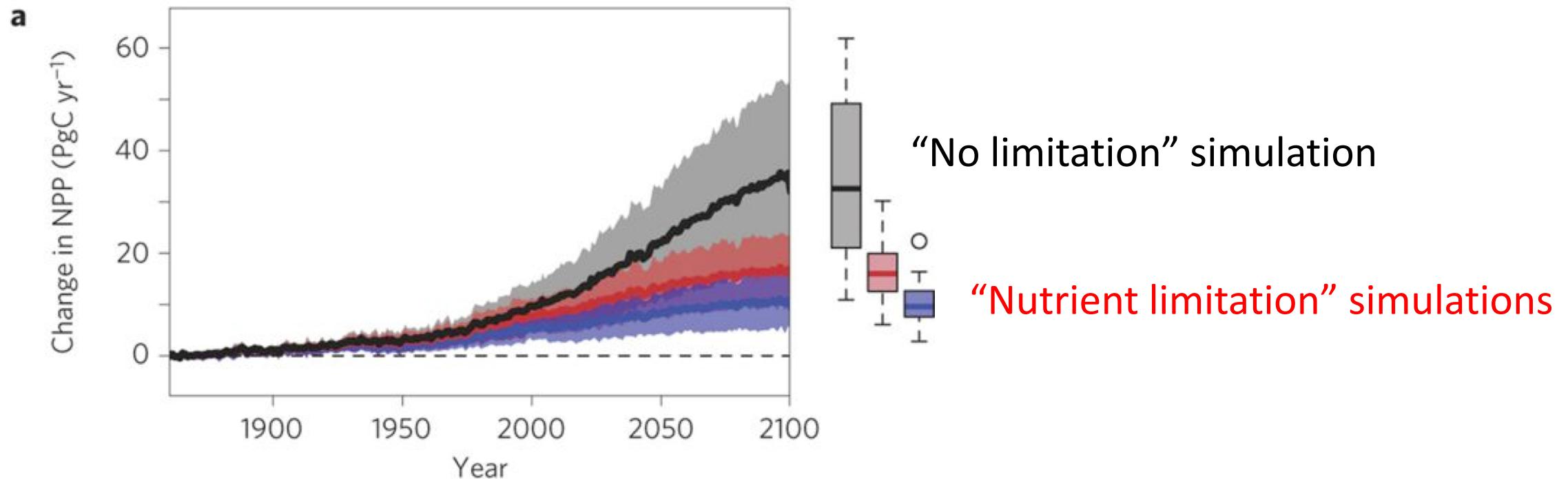
# Leaf N reduction is due to a reduction in photosynthetic capacity



# 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 C<sub>4</sub> photosynthesis an advantage over C<sub>3</sub> photosynthesis?

# $C_3$ versus $C_4$ optimization

# $C_4$ versus $C_3$ optimization

$C_4$  photosynthesis has...

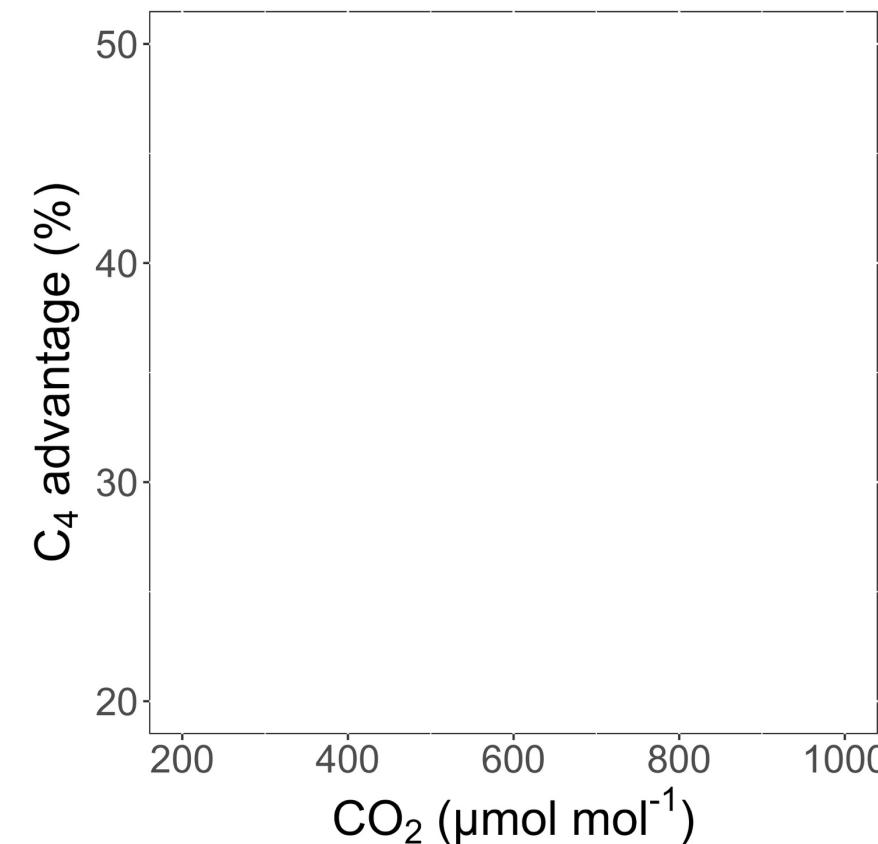
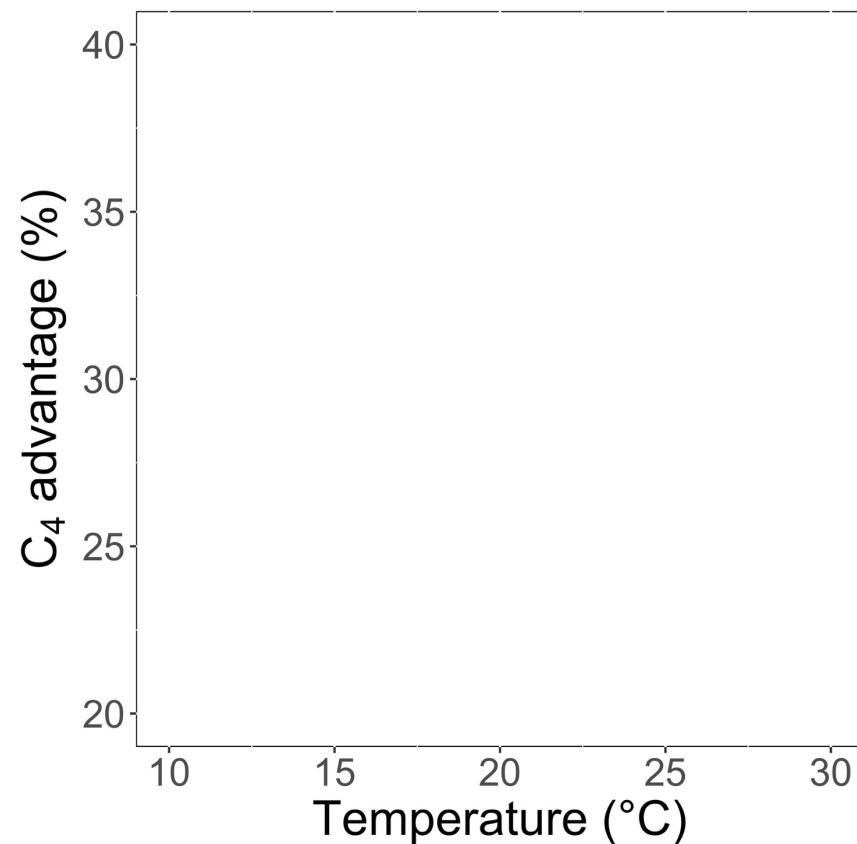
- Little photorespiration
- An additional limitation (**PEP carboxylation**)

# $C_4$ versus $C_3$ optimization

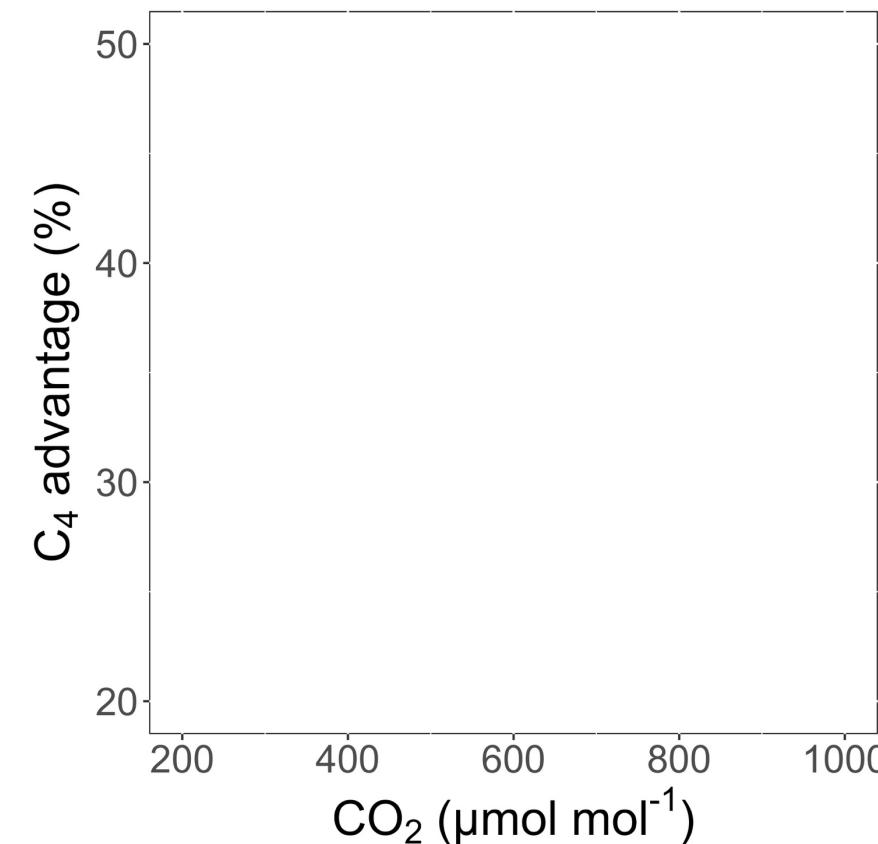
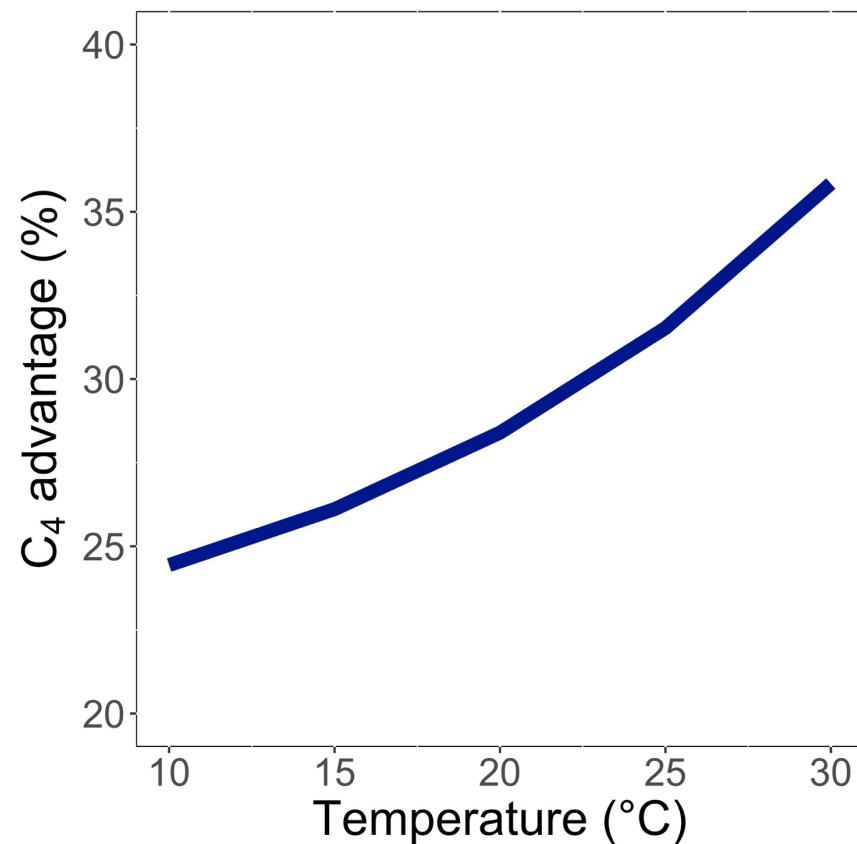
$C_4$  photosynthesis has...

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

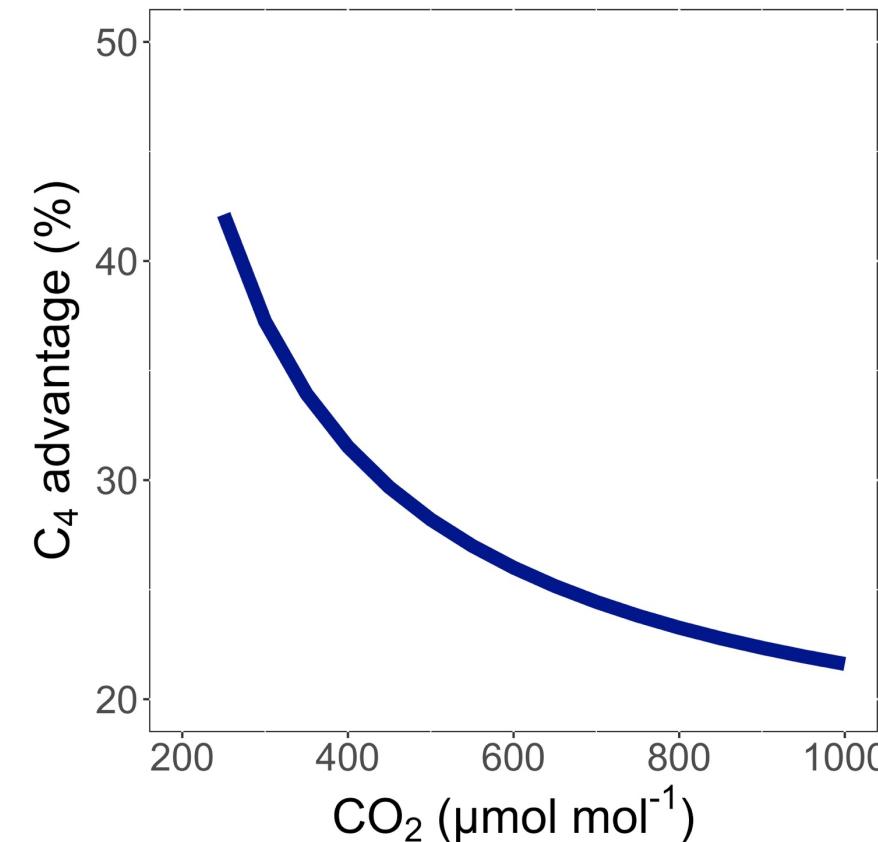
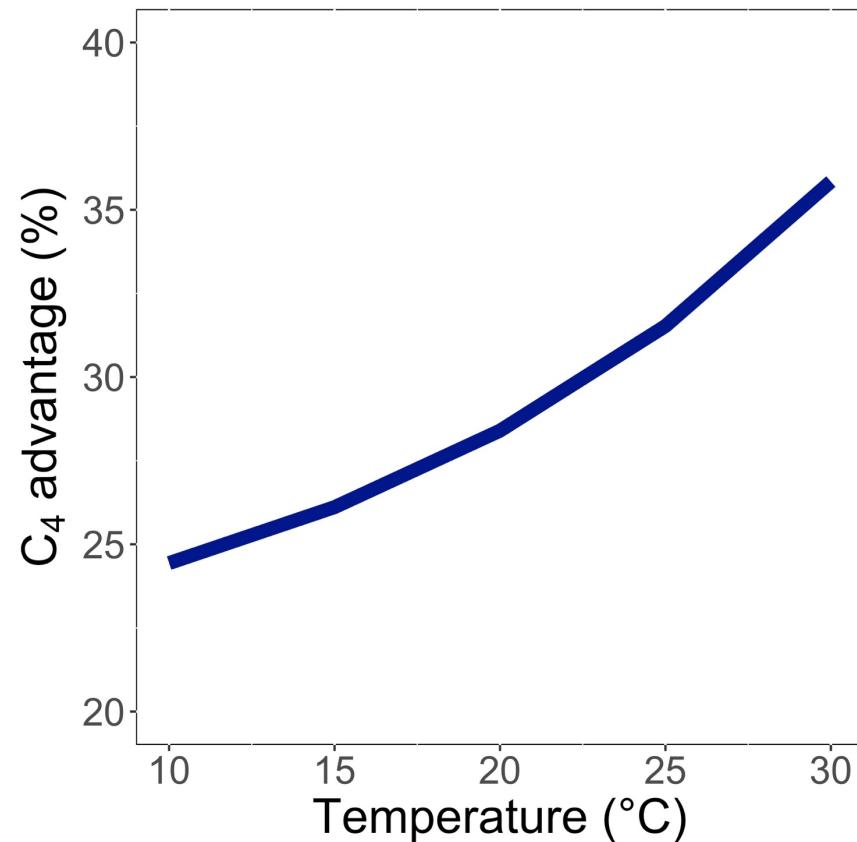
# Relative advantage of C<sub>4</sub> physiology



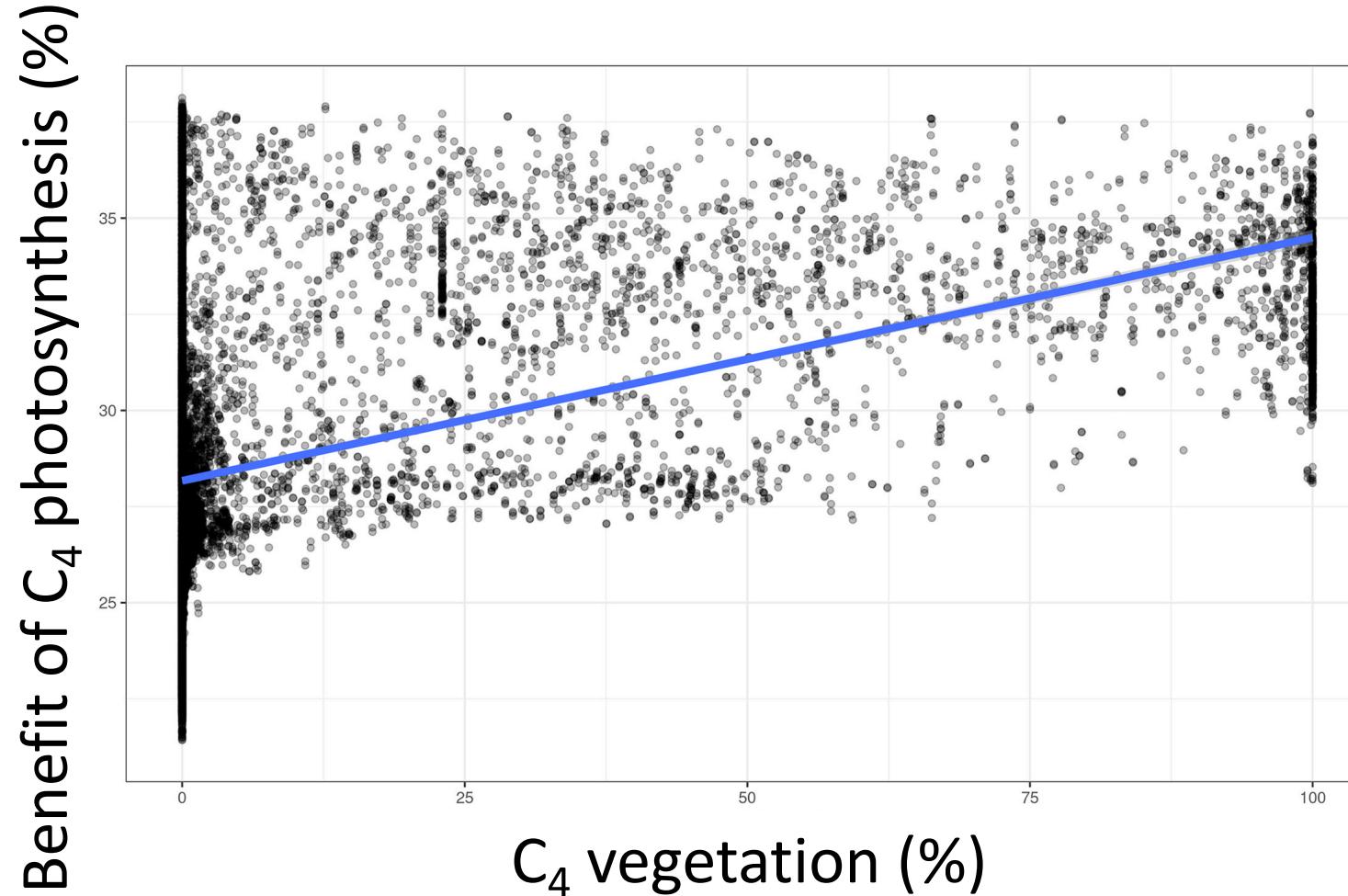
# Relative advantage of C<sub>4</sub> physiology

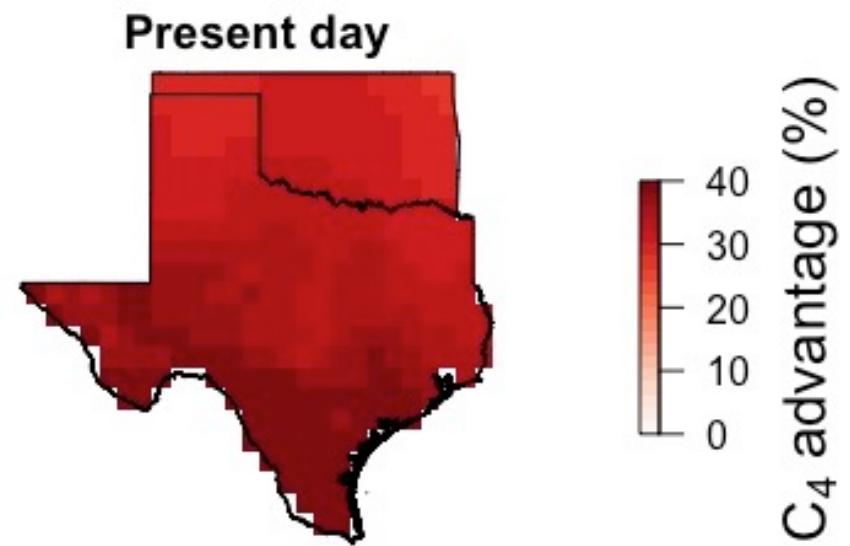


# Relative advantage of C<sub>4</sub> physiology

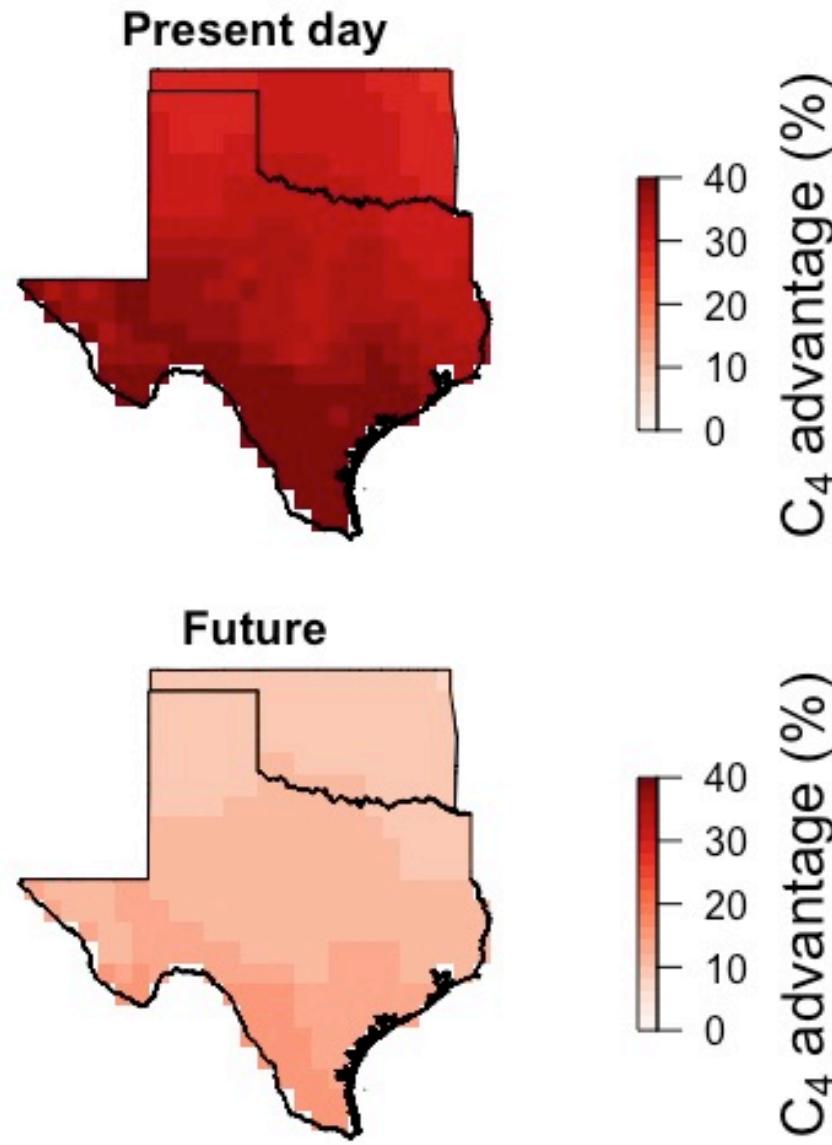


# The model seems to work!





Relative advantage of C<sub>4</sub> physiology may decrease in the future in the Southern Great Plains



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CLIMATE ADAPTATION SCIENCE CENTER

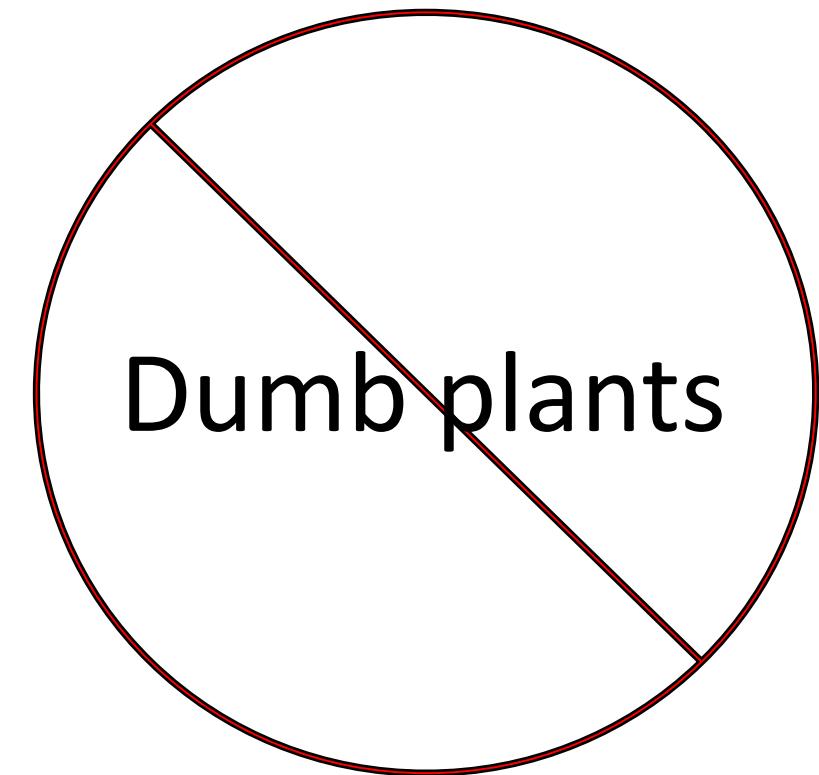
Question 4: When is C<sub>4</sub> photosynthesis an advantage over C<sub>3</sub> photosynthesis?

C<sub>4</sub> is better in hot, dry, low CO<sub>2</sub> environments

# Conclusions

# Conclusions

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



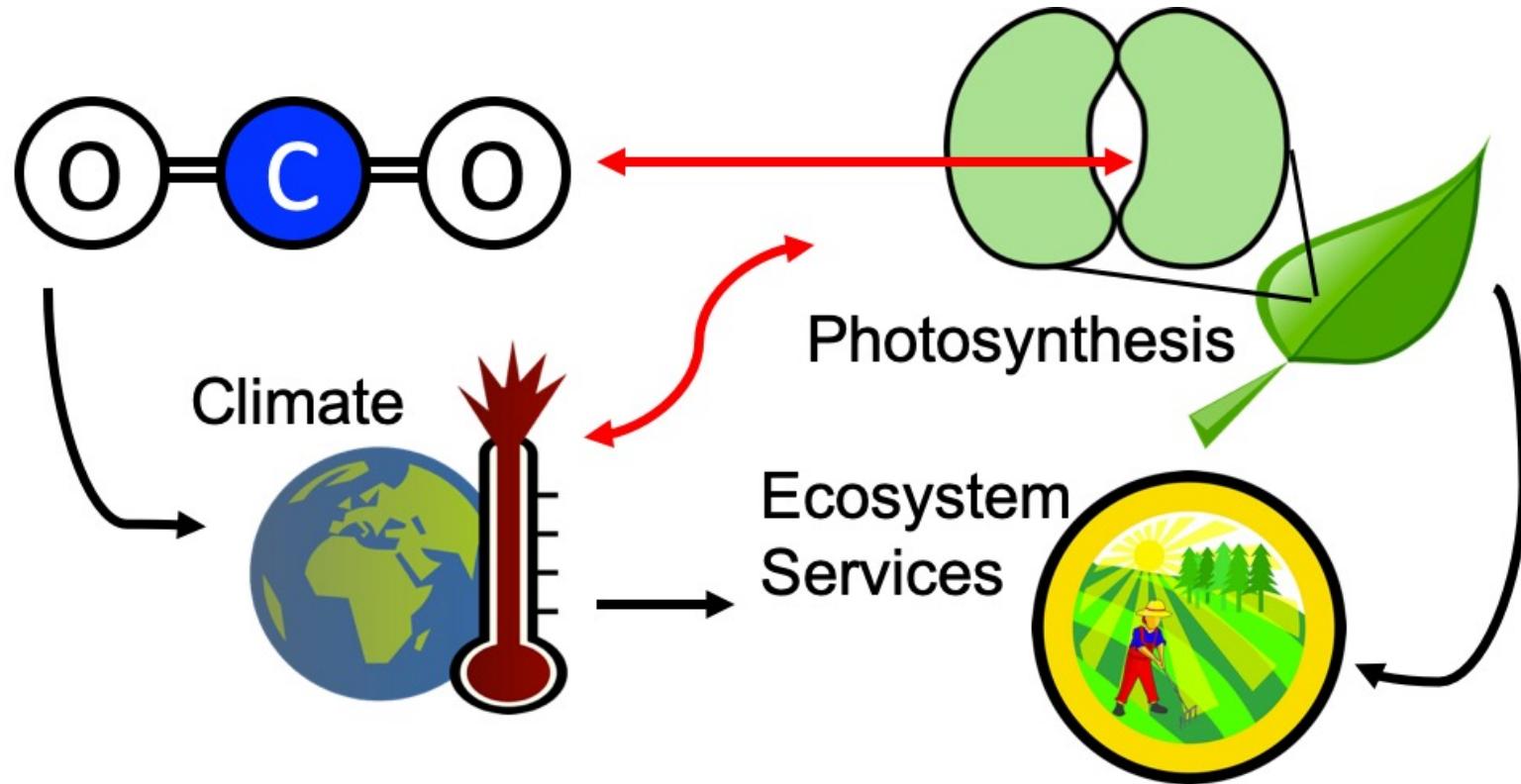
# Conclusions

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
  - Evan Perkowski (PhD)
  - Zinny Ezekannagha (PhD)
  - Snehanjana Chatterjee (PhD)
  - Eve Gray (MS)
  - Monika Kelley (MS)
  - Isabella Beltran (MS)
  - Rafael Freitas (MS)
- Former lab members
  - Jeff Chieppa (postdoc; now working in industry)
  - Lizz Waring (postdoc; now Asst. Prof at Northeastern State U)
  - Brad Posch (postdoc; now at UC Berkeley)
  - 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
- Collaborators around the world
- Funding
  - NSF
  - USDA
  - NPS
  - USGS
  - Schmidt Futures
  - Texas EcoLab



Presentation available at:

[www.github.com/SmithEcophysLab/seminar/2023\\_tsu](https://www.github.com/SmithEcophysLab/seminar/2023_tsu)

Data and code:

[www.github.com/SmithEcophysLab](https://www.github.com/SmithEcophysLab)

[www.smithecophyslab.com/data](https://www.smithecophyslab.com/data)



Thanks!