

Plants aren't dumb

Using optimality theory to understand big
questions in plant ecophysiology

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Why do people care about plants?

Why do people care about plants?



Why do people care about plants?



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Why do people care about plants?



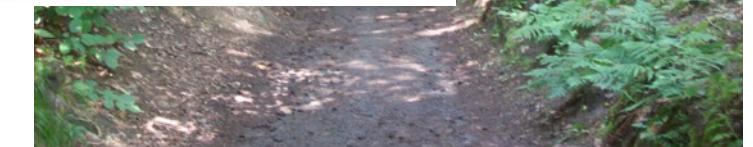
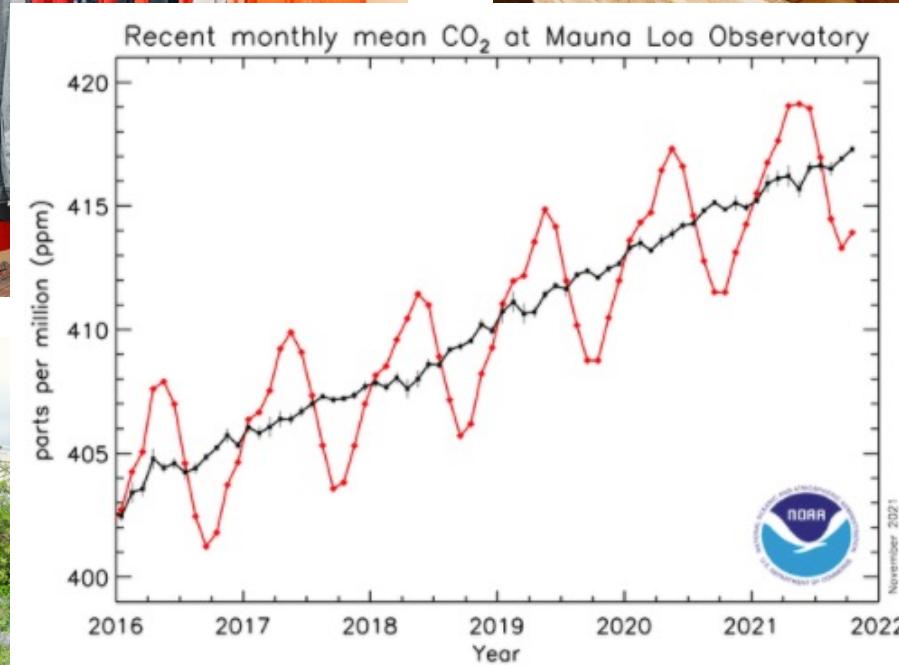
Why do people care about plants?



Why do people care about plants?



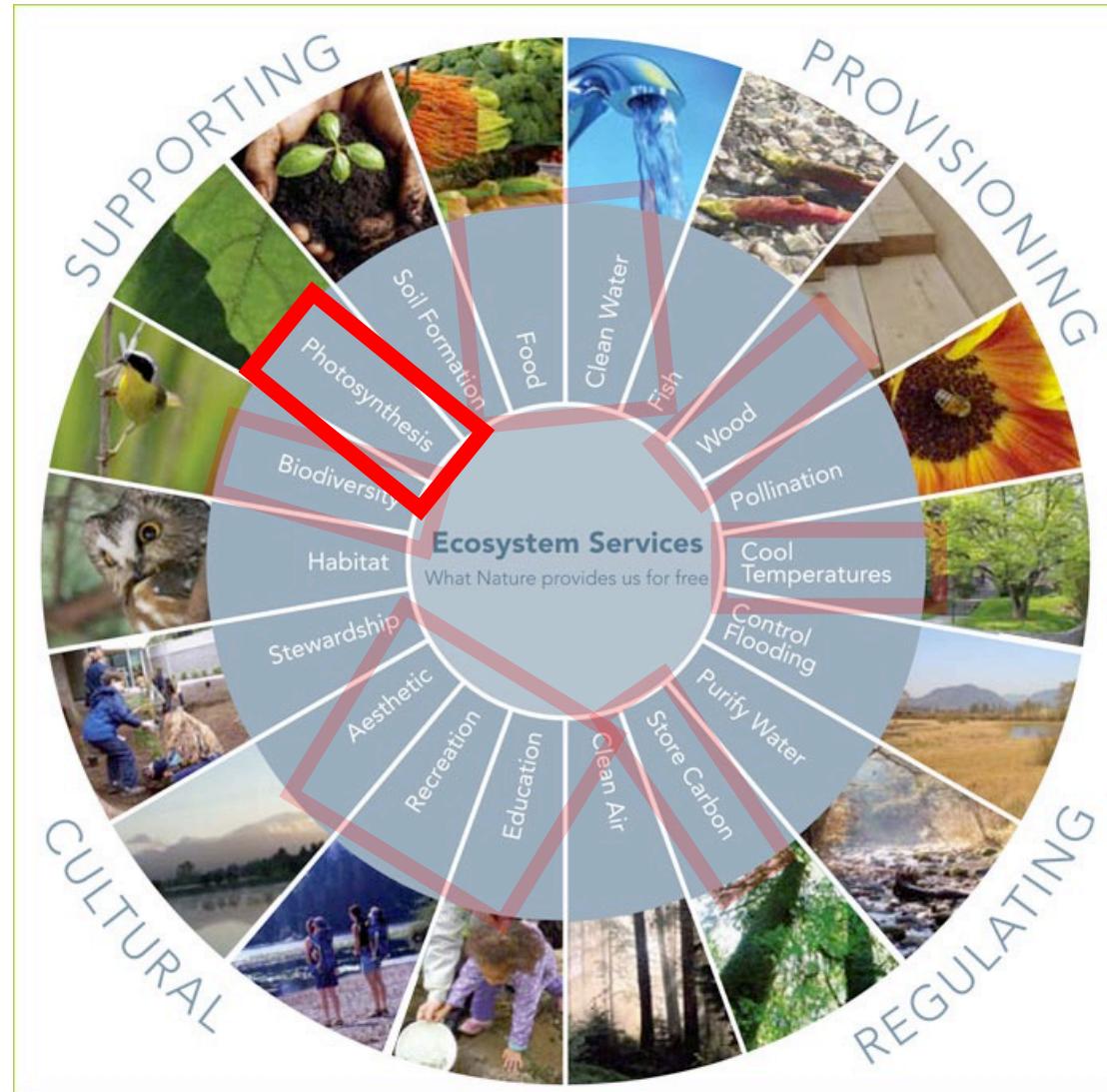
Why do people care about plants?



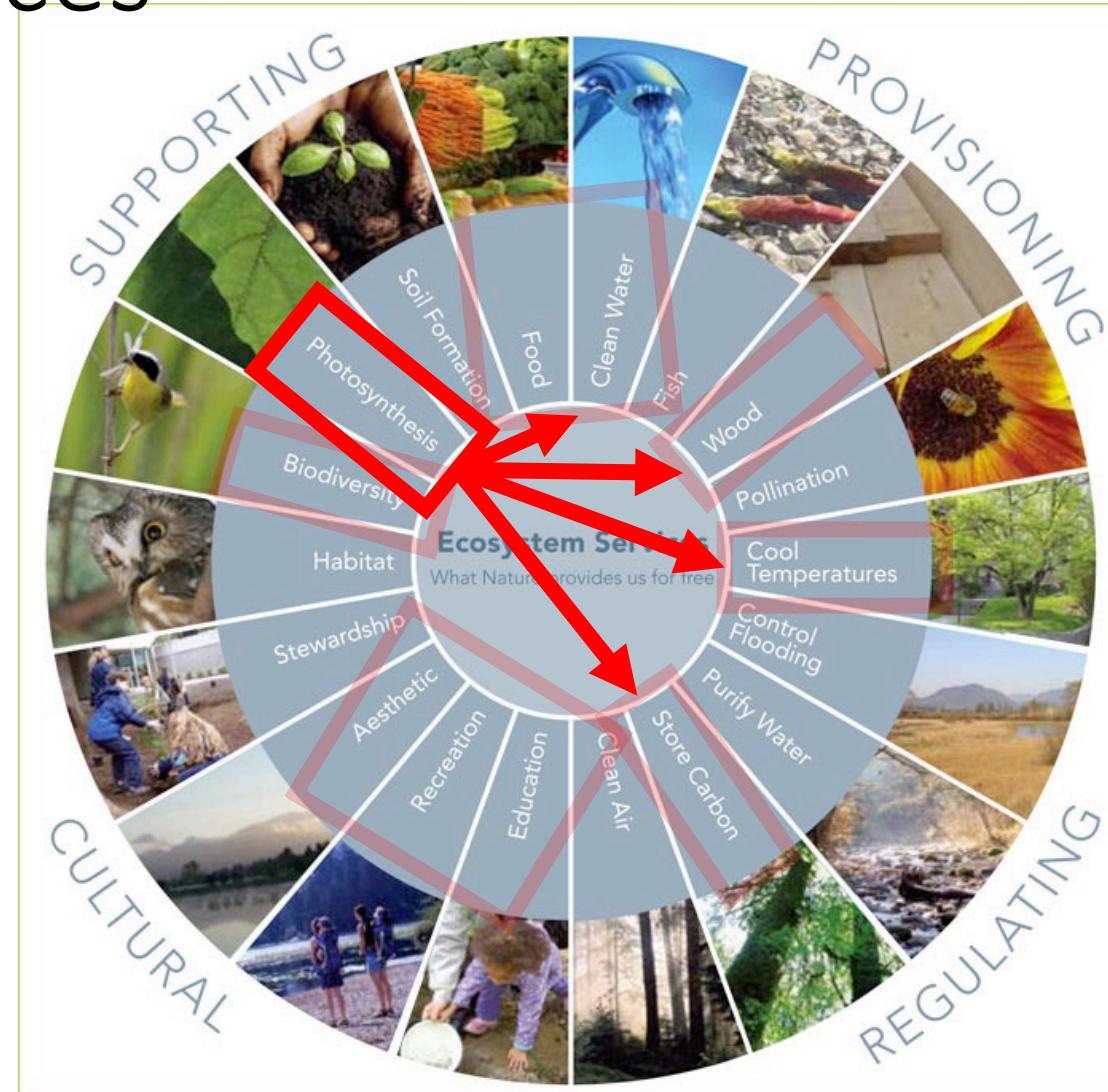
In other words: plants provide ecosystem services



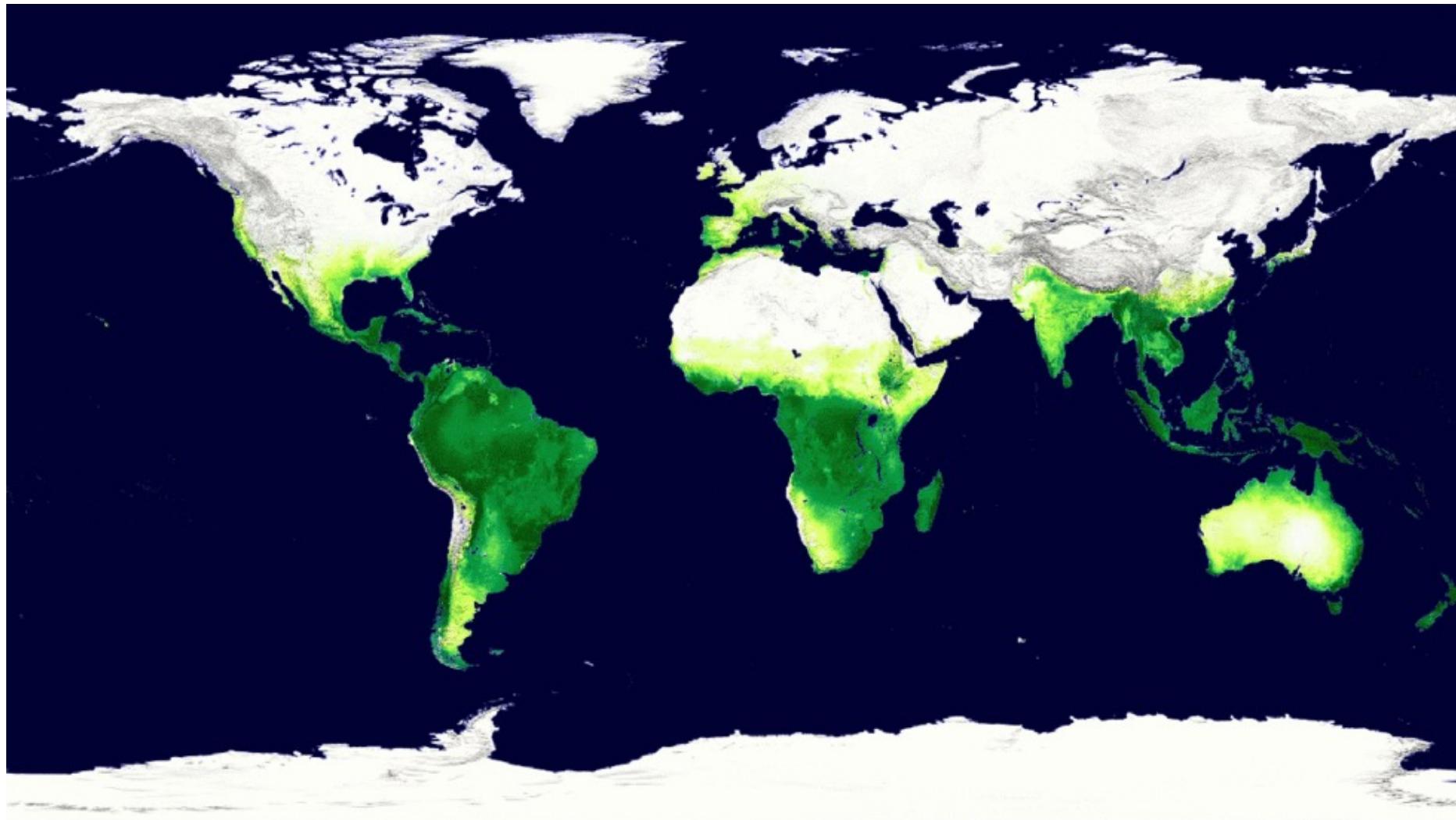
Including photosynthesis



Photosynthesis provides the foundation for other services

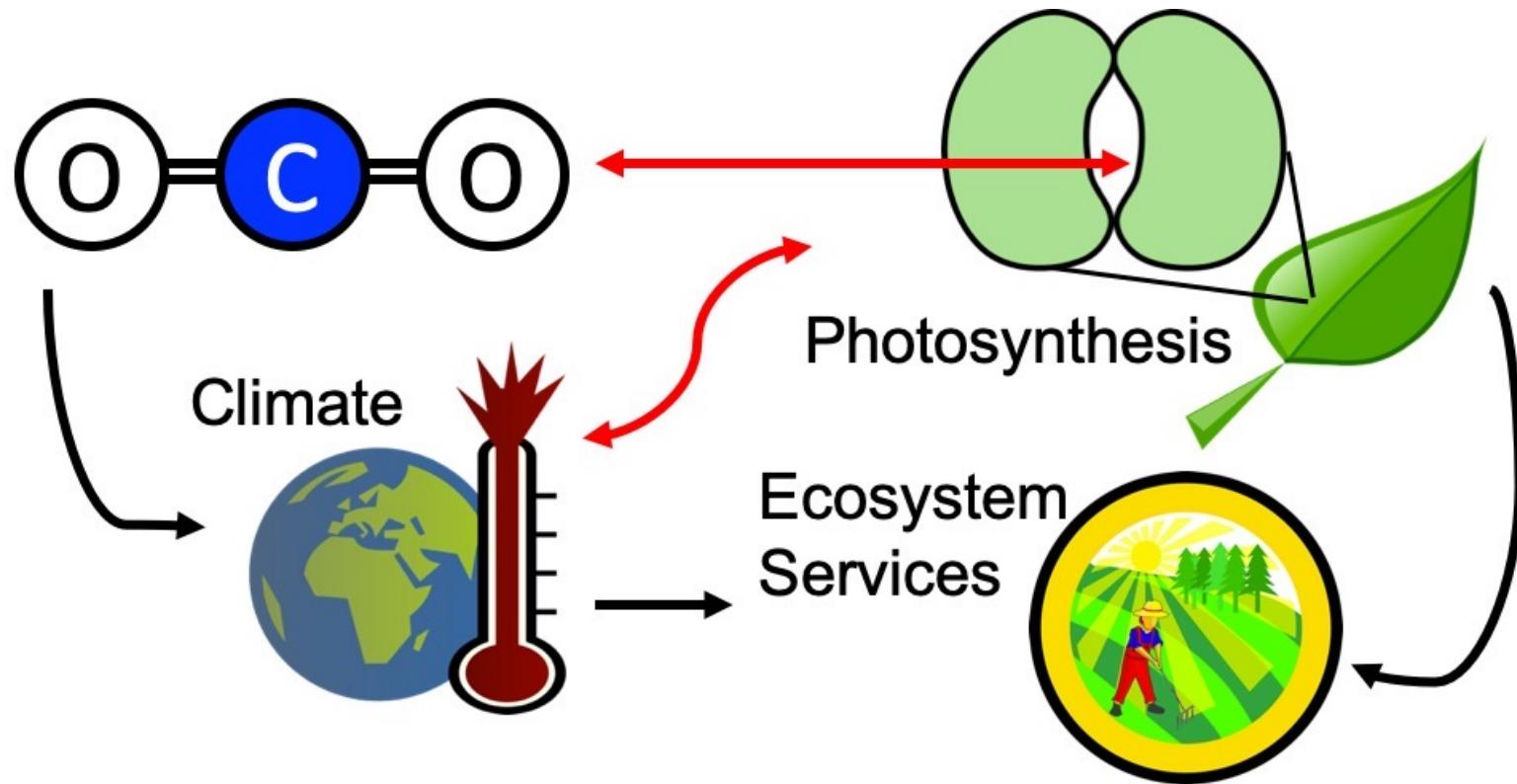


Photosynthesis is a dynamic process



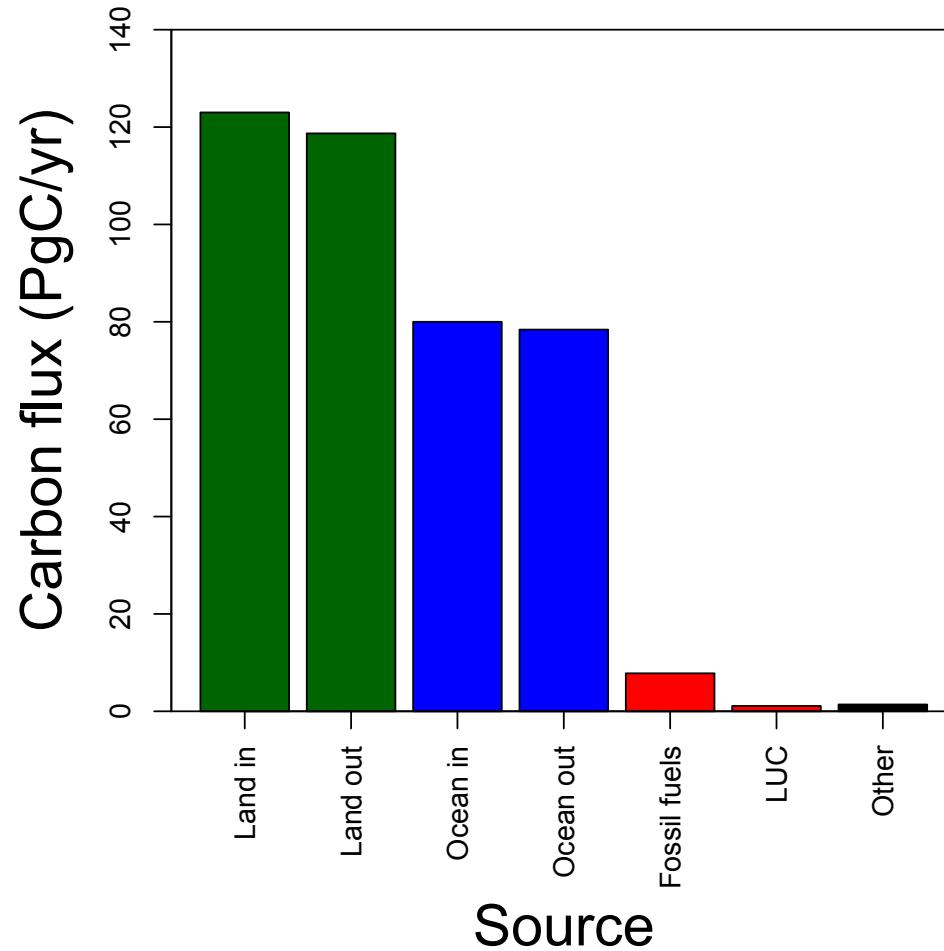
MODIS, NASA

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

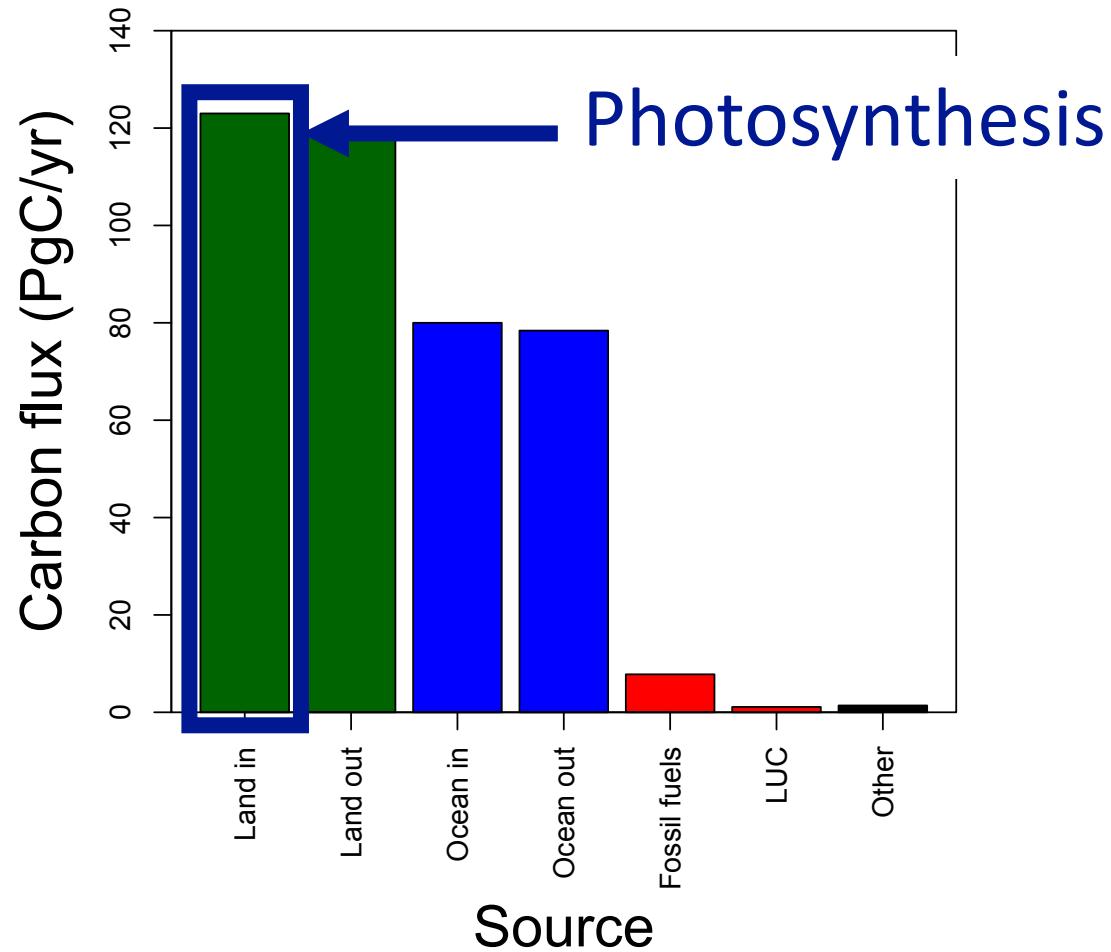


Photosynthesis is important! An example...

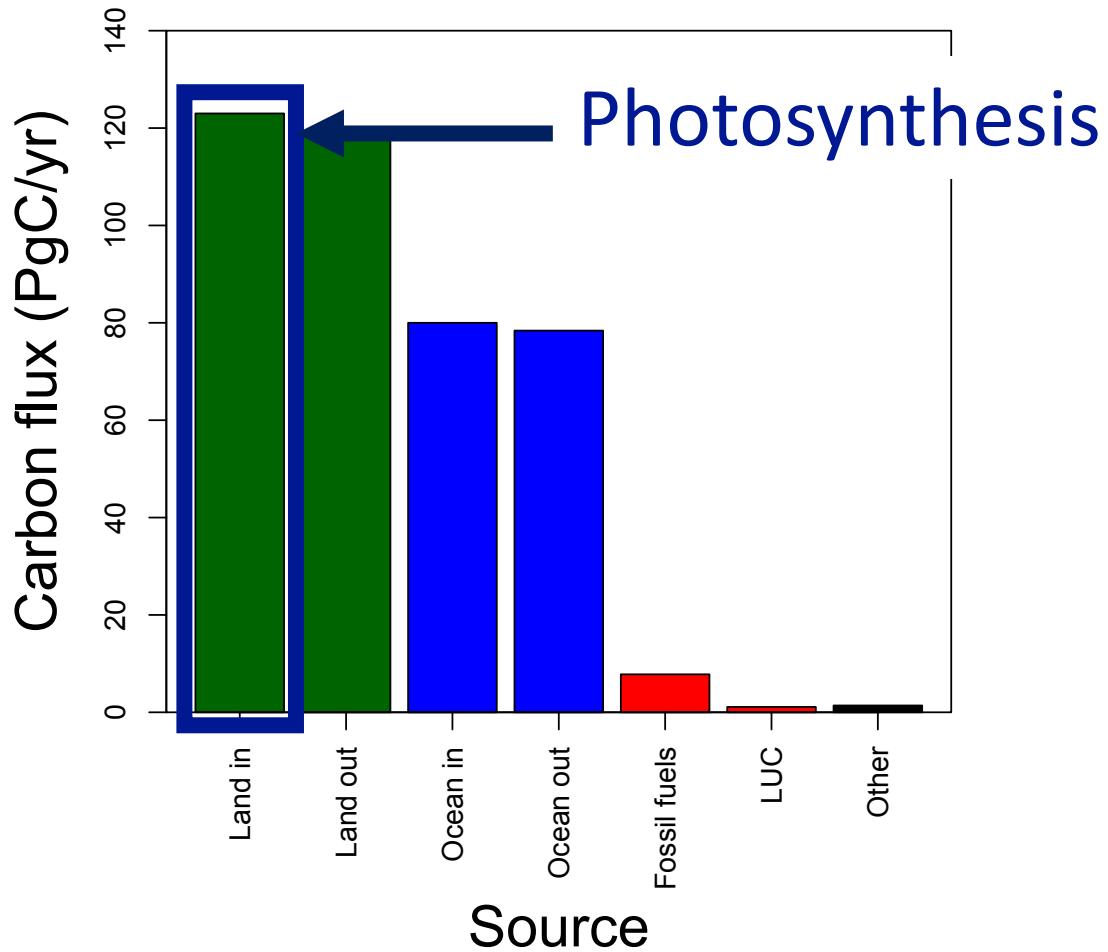
Photosynthesis is important! An example...



Photosynthesis is important! An example...

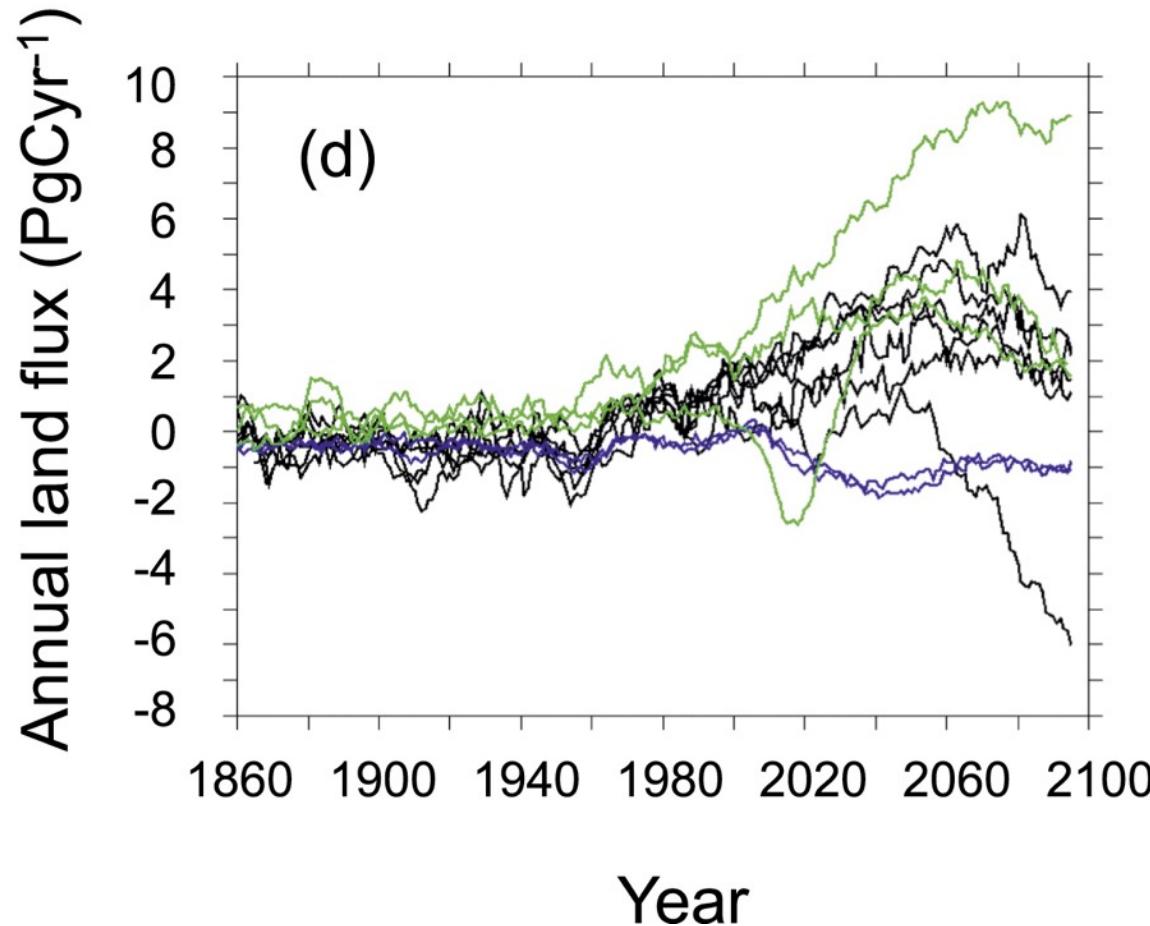


Photosynthesis is important! An example...

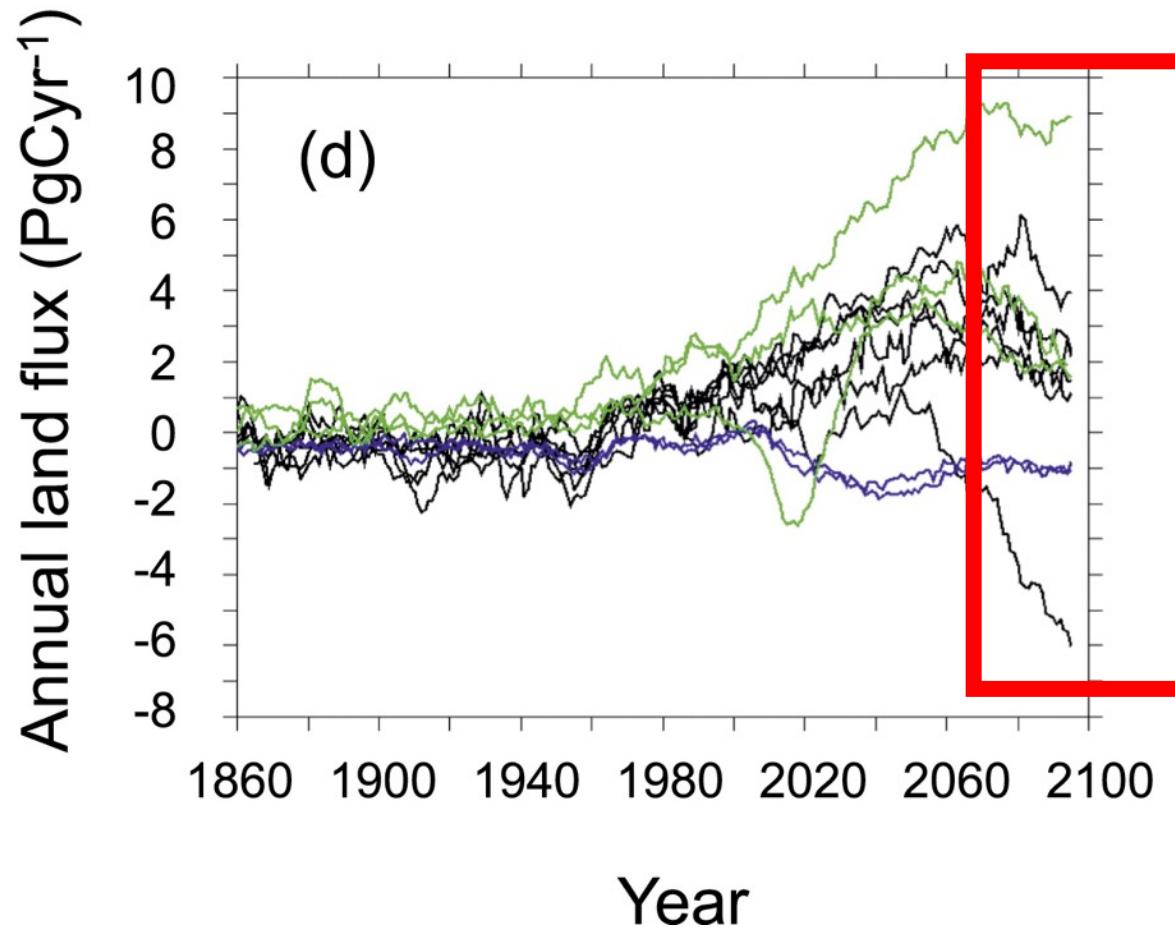


A small percentage change in photosynthesis can have large consequences for climate

But predictions are uncertain!

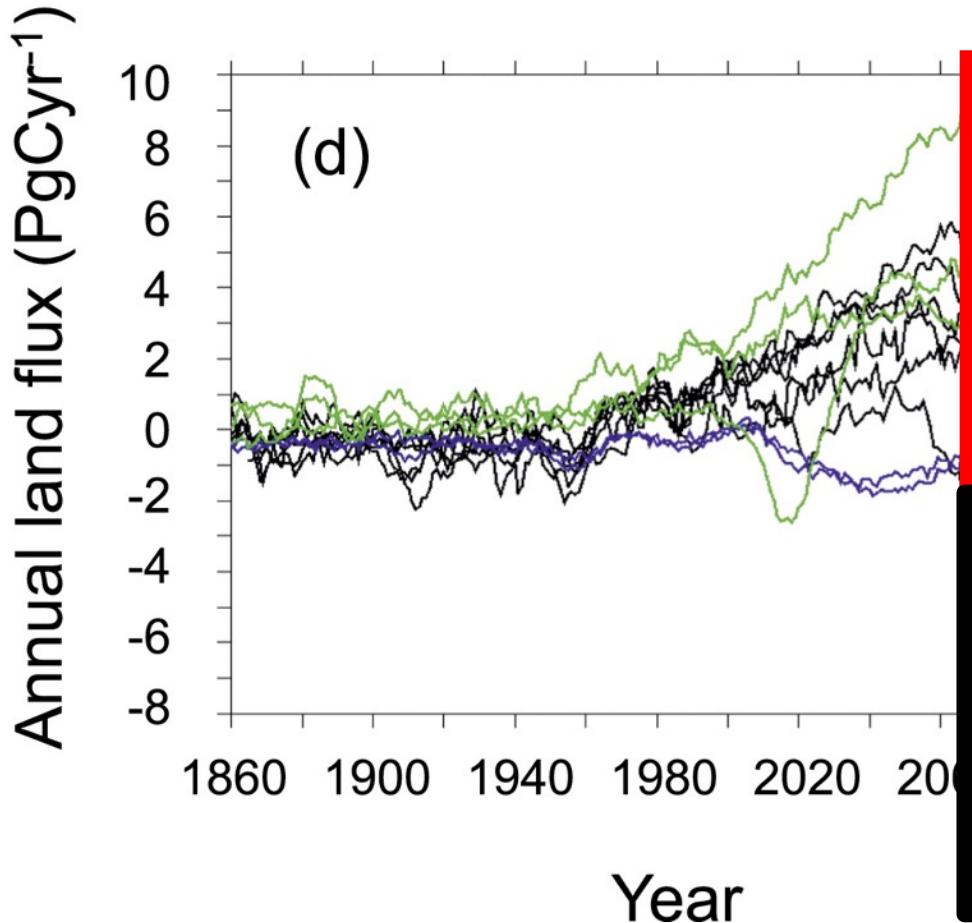


But predictions are uncertain!



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

This uncertainty is driven by uncertainty in photosynthesis

**Article**

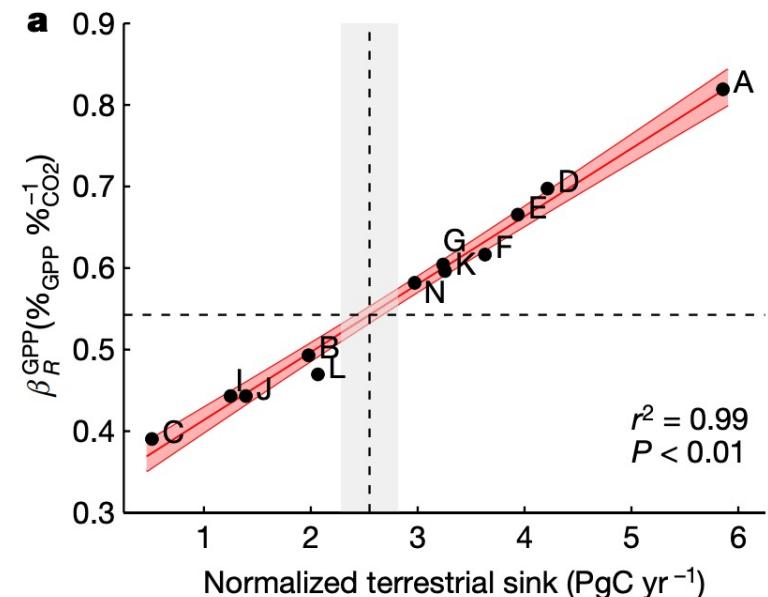
A constraint on historic growth in global photosynthesis due to increasing CO_2

<https://doi.org/10.1038/s41586-021-04096-9>

Received: 9 July 2020

Accepted: 5 October 2021

T. F. Keenan^{1,2}✉, X. Luo^{1,2,3}, M. G. De Kauwe^{4,5,6}, B. E. Medlyn⁷, I. C. Prentice^{8,9,10},
B. D. Stocker^{11,12}, N. G. Smith¹³, C. Terrer¹⁴, H. Wang¹⁰, Y. Zhang^{1,2,15} & S. Zhou^{1,2,16,17,18,19}



Why the uncertainty? Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

Planta
© by Springer-Verlag 1980

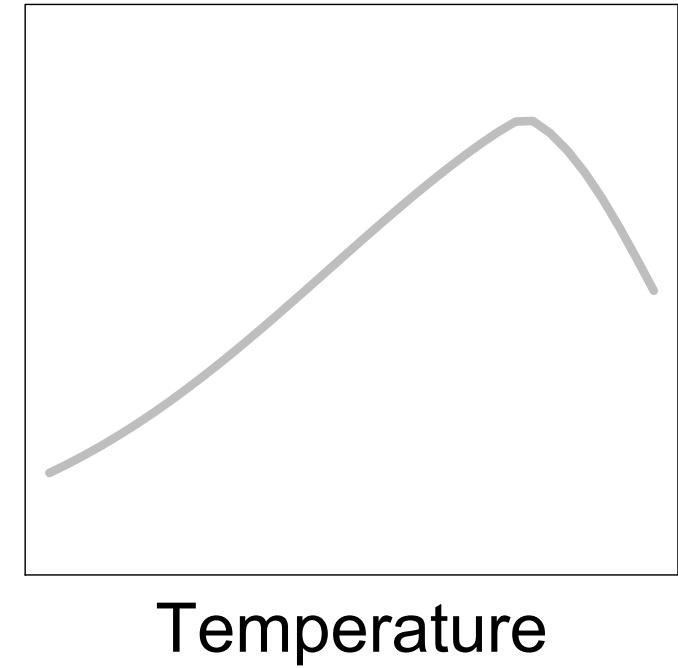
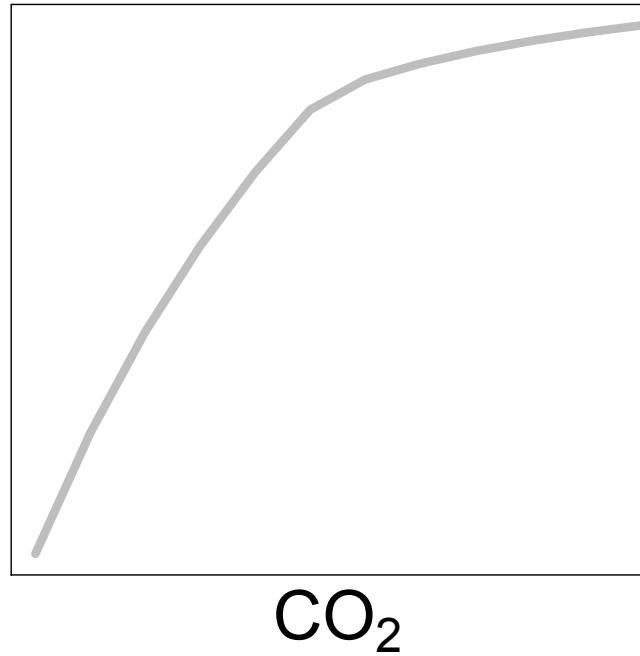
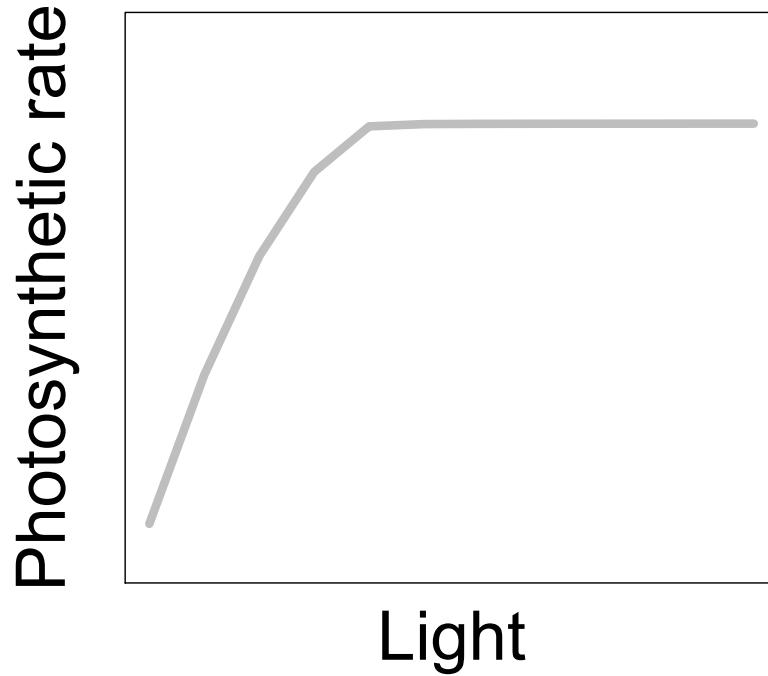
A Biochemical Model of Photosynthetic CO₂ Assimilation in Leaves of C₃ Species

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

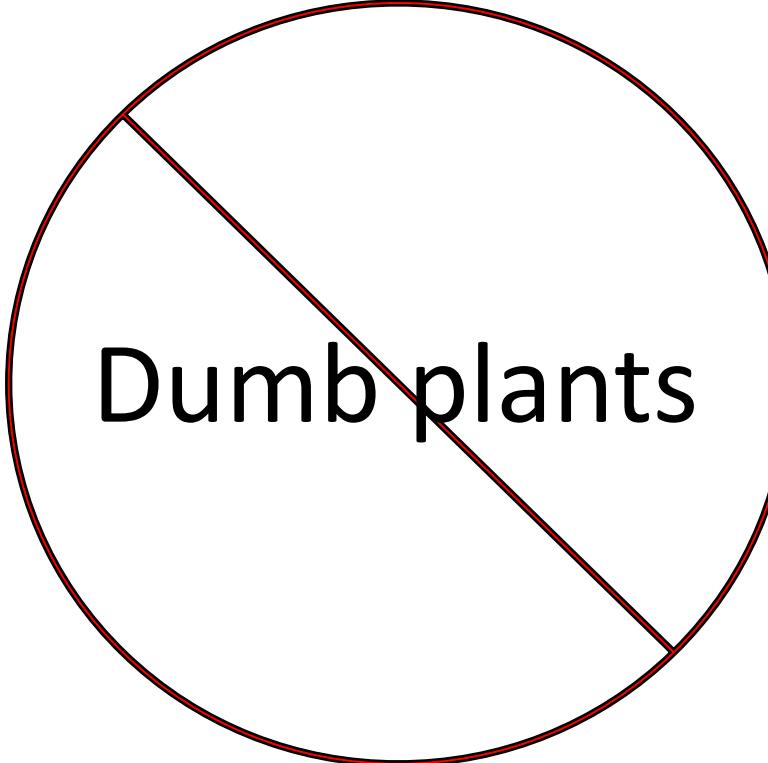
¹ Department of Environmental Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City ACT 2601, Australia and

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

These produce short term responses that match data

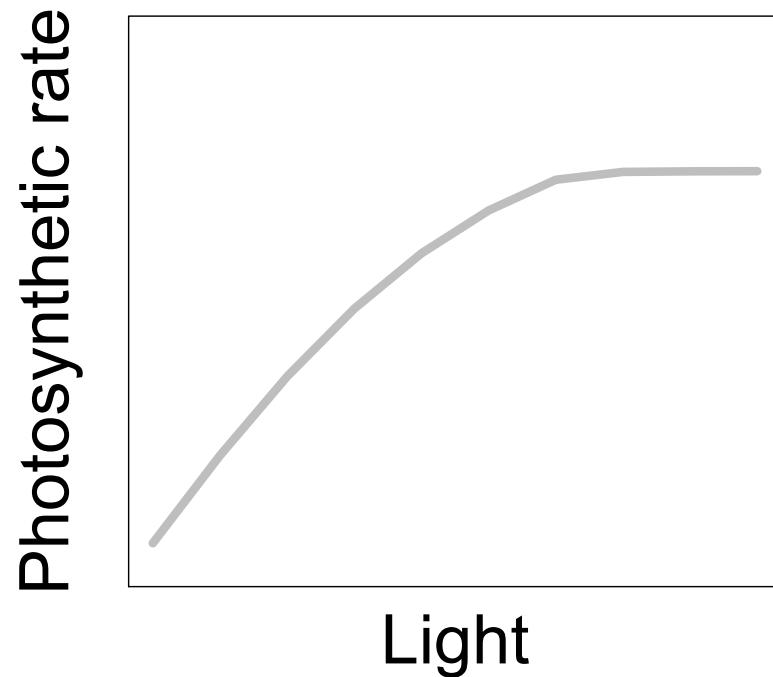


Why the uncertainty? Long-term responses differ from short-term responses due to acclimation

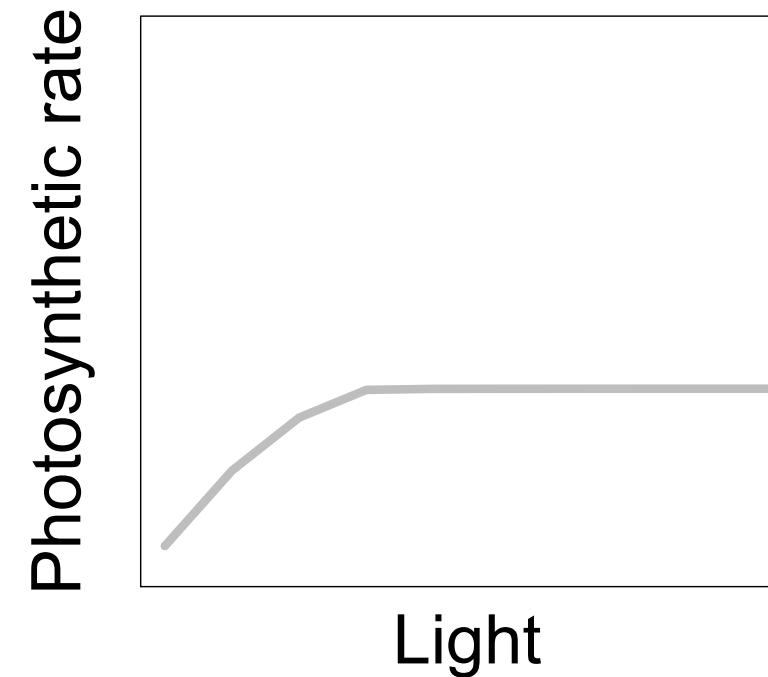


Dumb plants

Acclimated to high light



Acclimated to low light



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

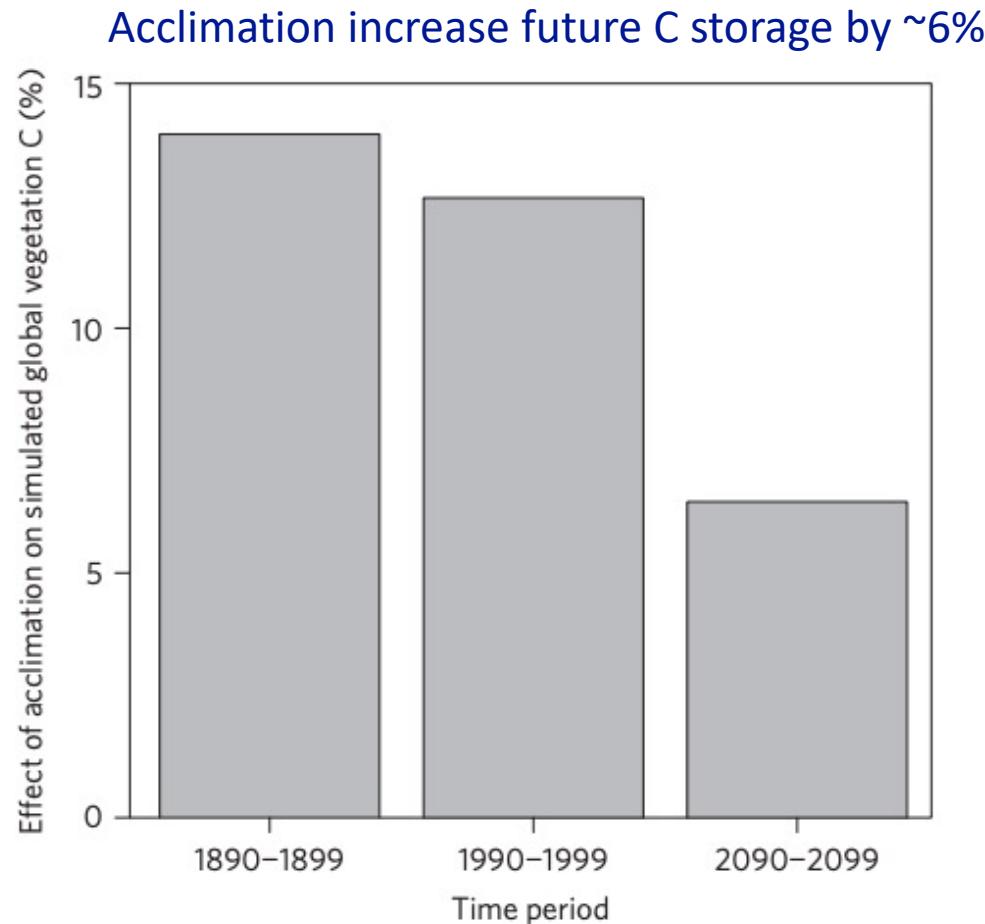
Temperature: Berry & Björkman (1980)

Ann. Rev. Plant Physiol. 1980. 31:491–543
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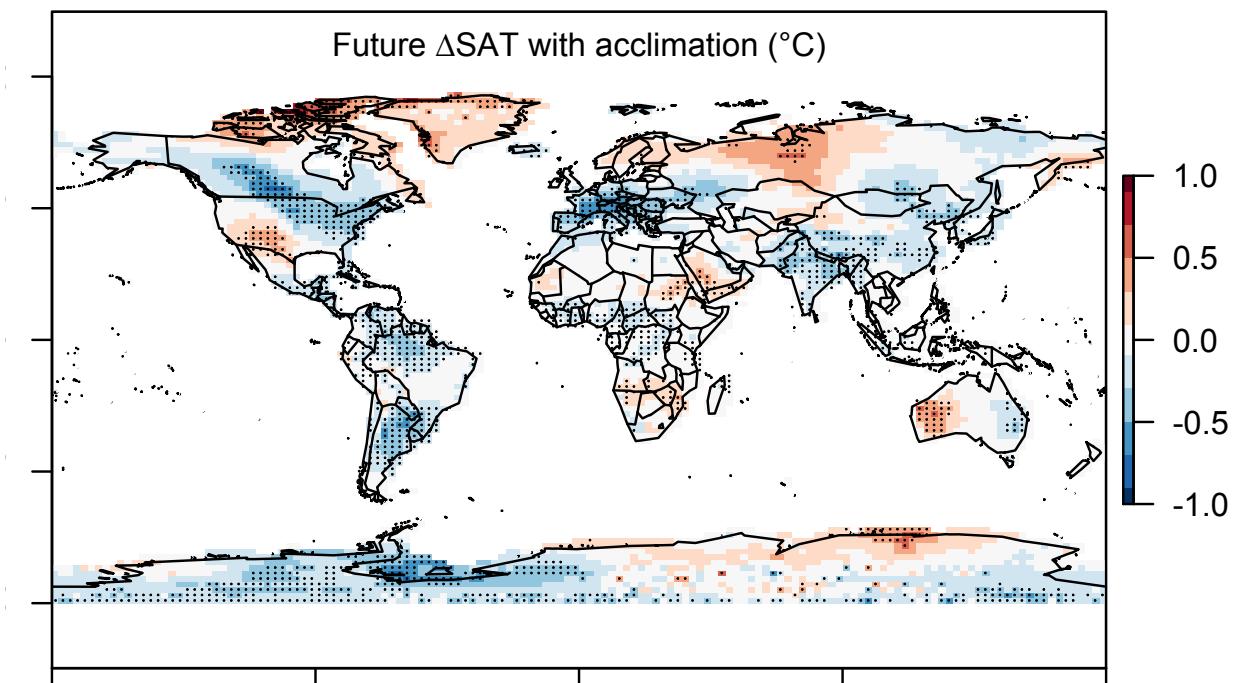
PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

Joseph Berry and Olle Björkman¹

...and can impact carbon cycling and climate



Acclimation alters future temperature by >1°C

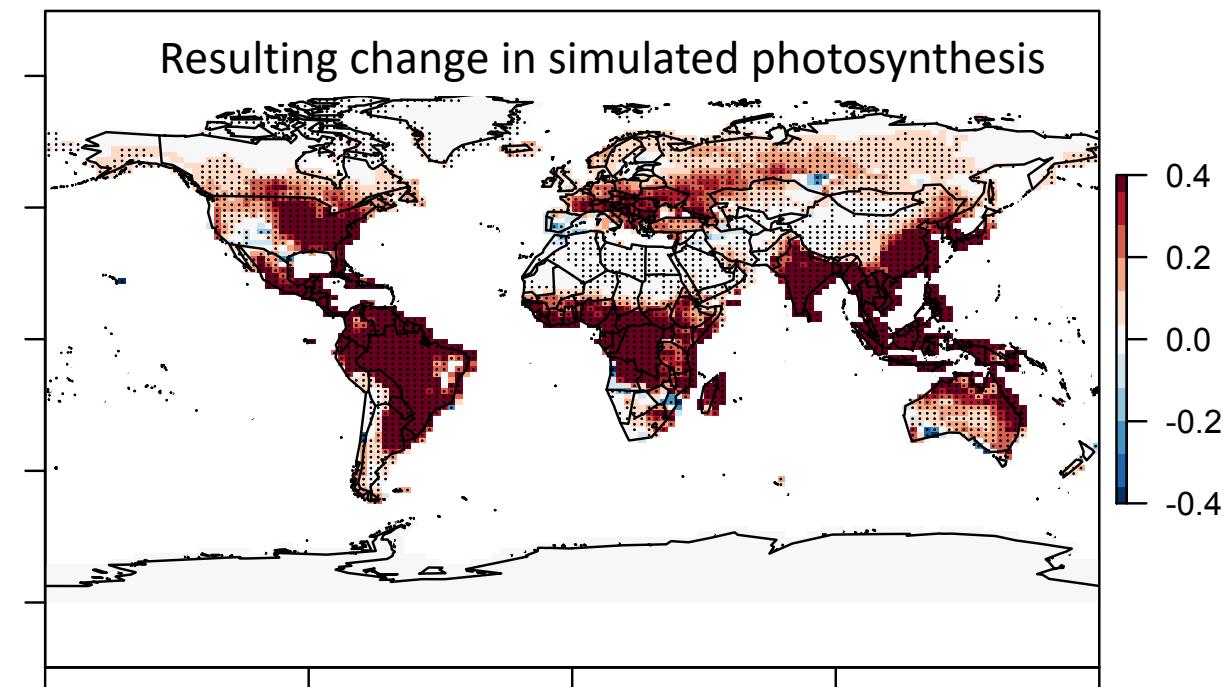
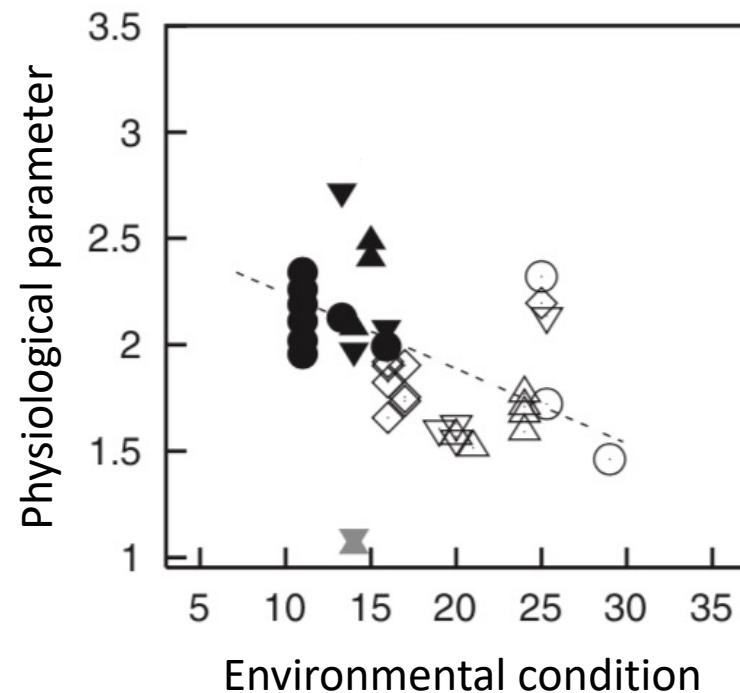


Unfortunately,
no theoretical model for
photosynthetic acclimation exists

Lack of theory results in...

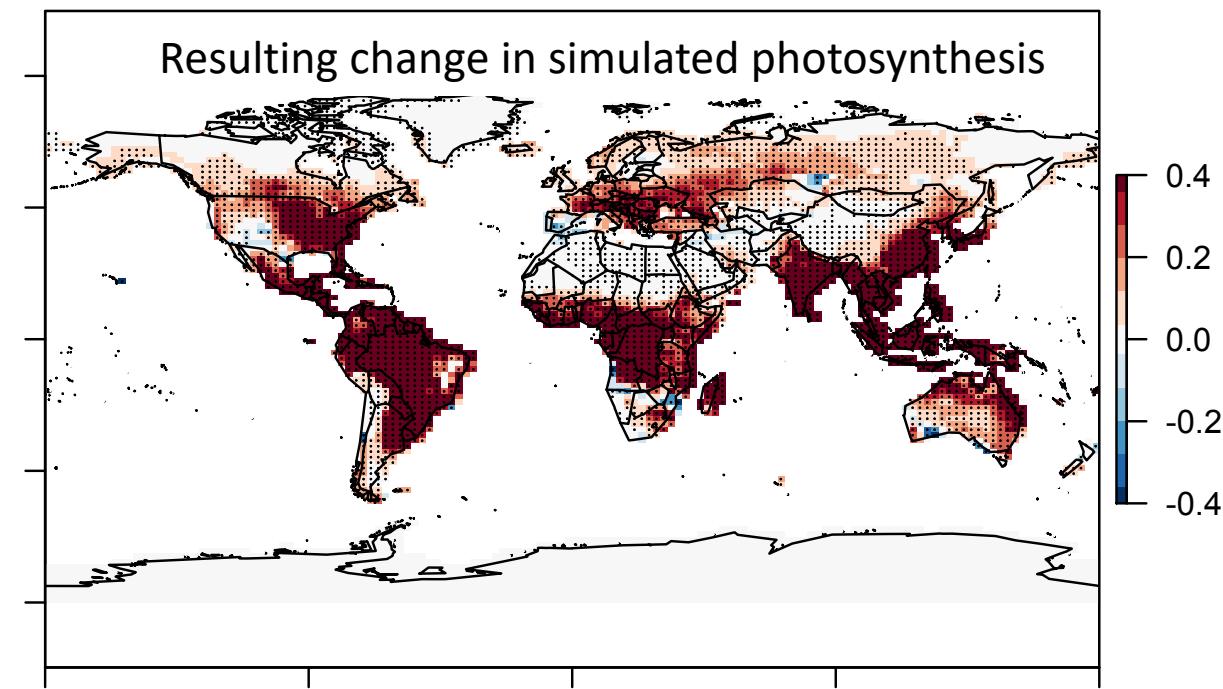
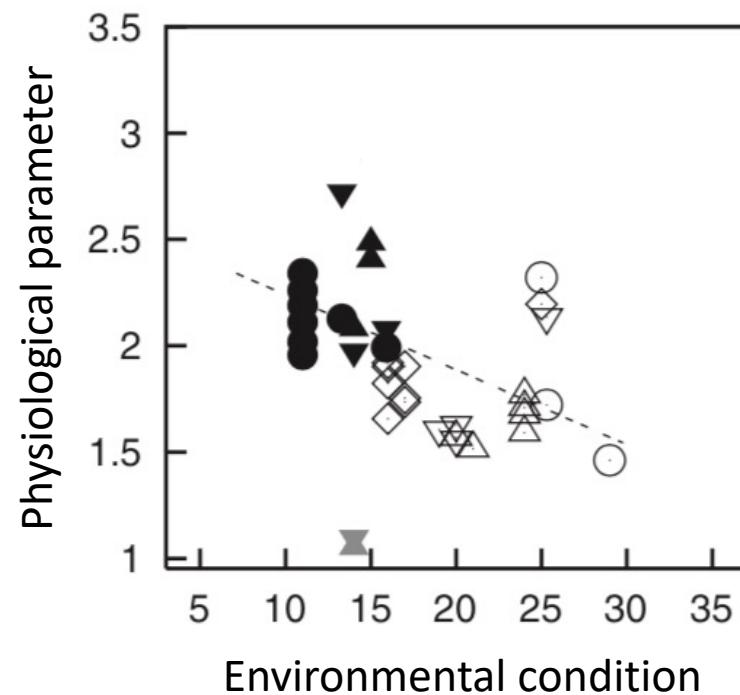
Lack of theory results in...

- 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

Optimization: Least cost theory

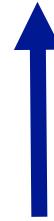
Optimally, plants will maintain
fastest rate of photosynthesis at
the lowest summed resource
cost (water and nutrient use)

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

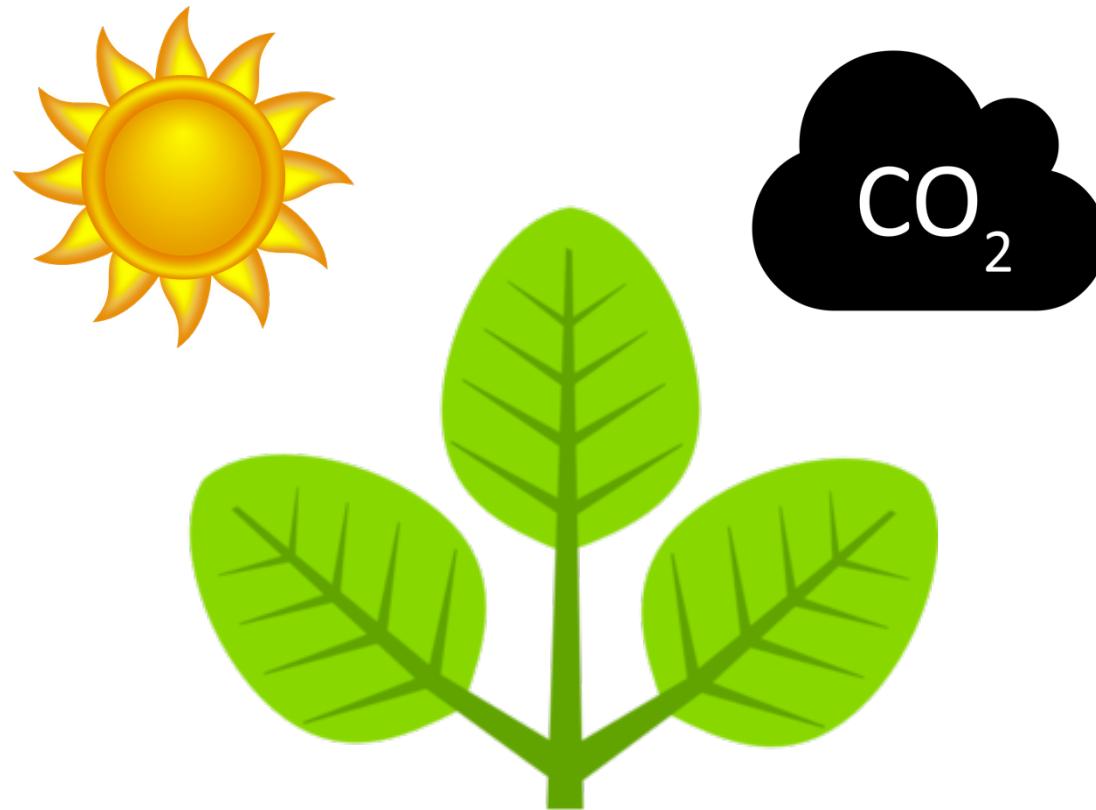
Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$

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

Optimal photosynthesis

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

Biochemistry optimization

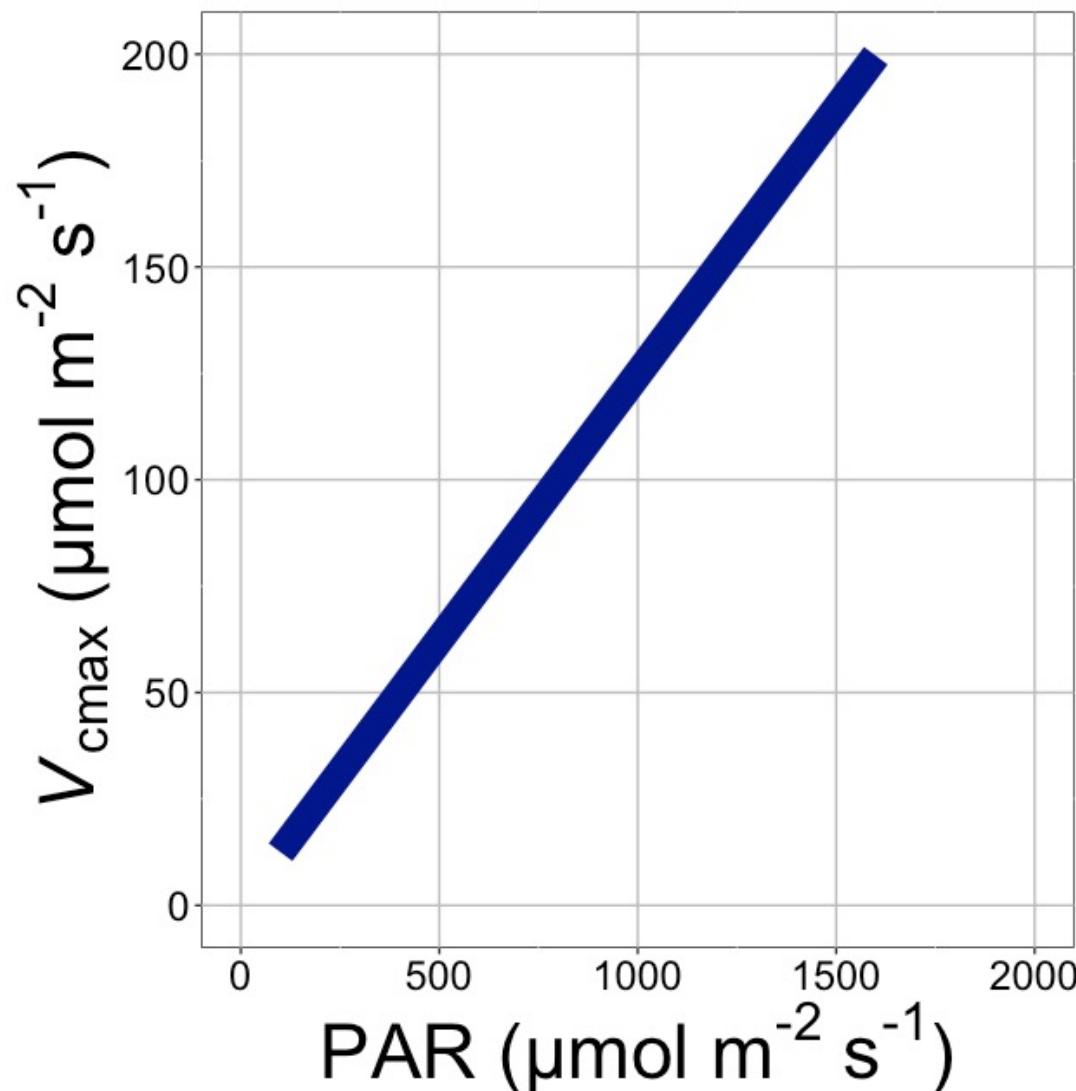


Plant
biochemistry
setup will aim for
equal limitation
by all factors

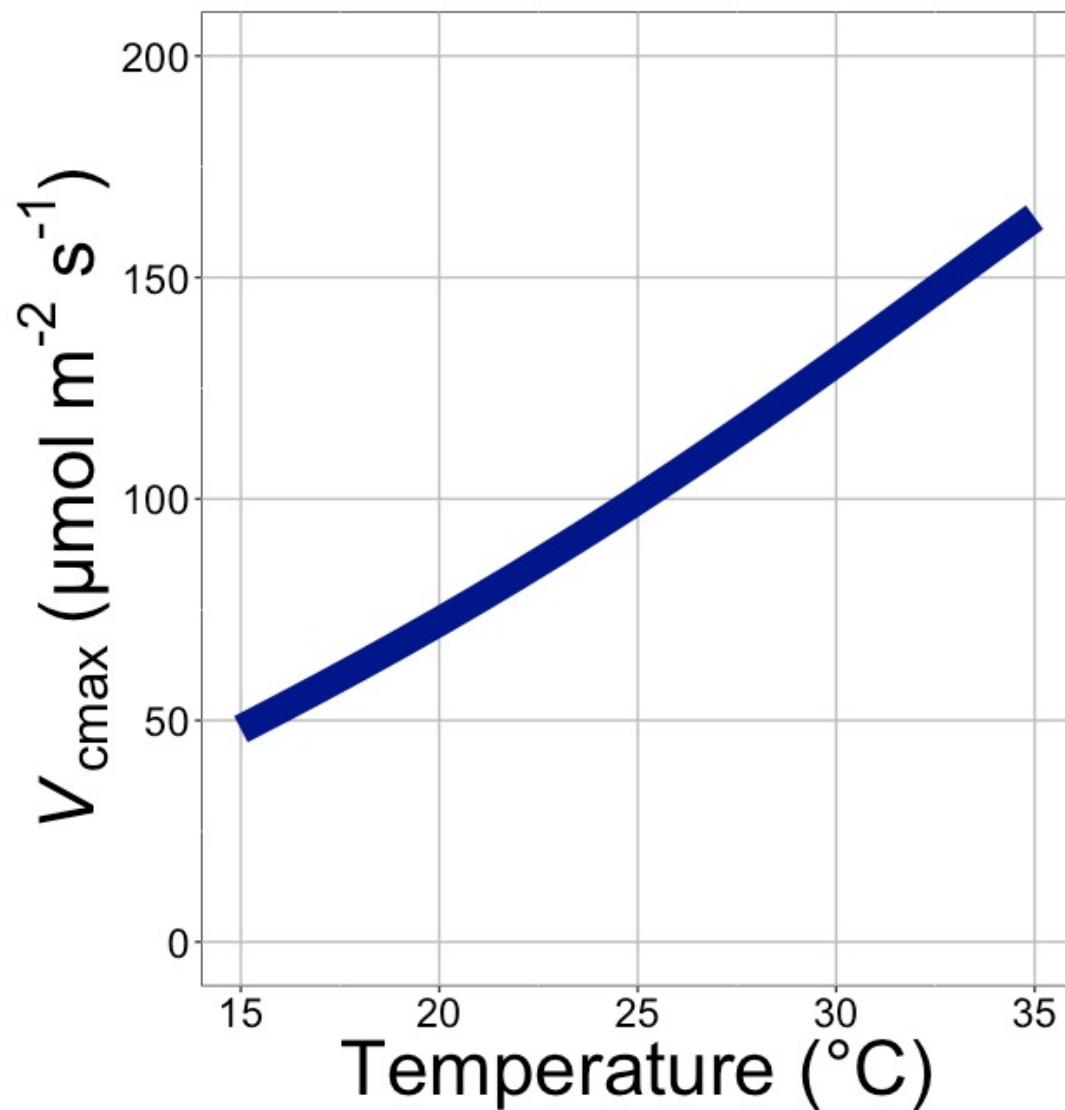
[TALK TO ME LATER ABOUT THE MATHS]

Biochemistry trait

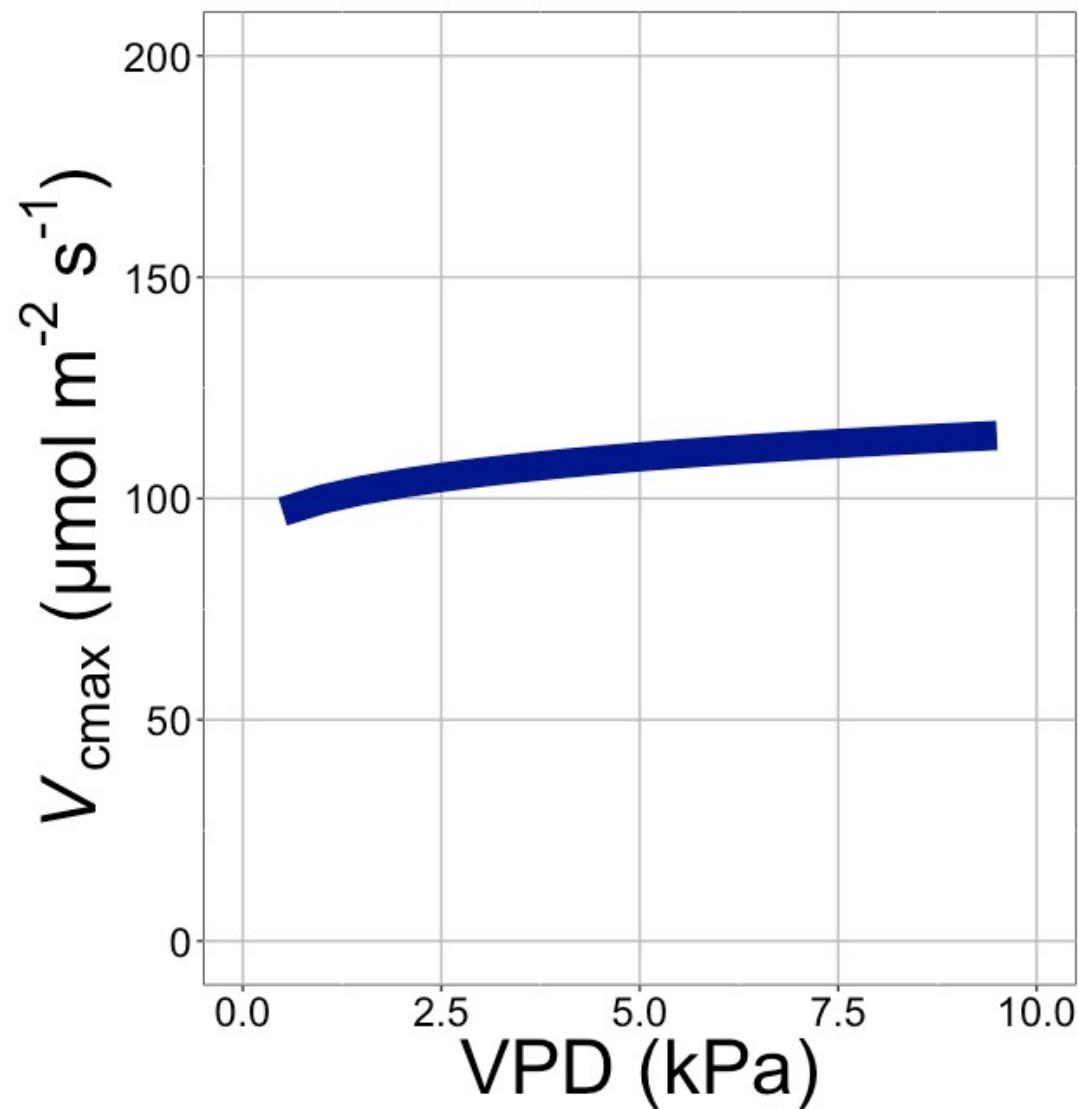
The maximum rate of Rubisco carboxylation (V_{cmax})



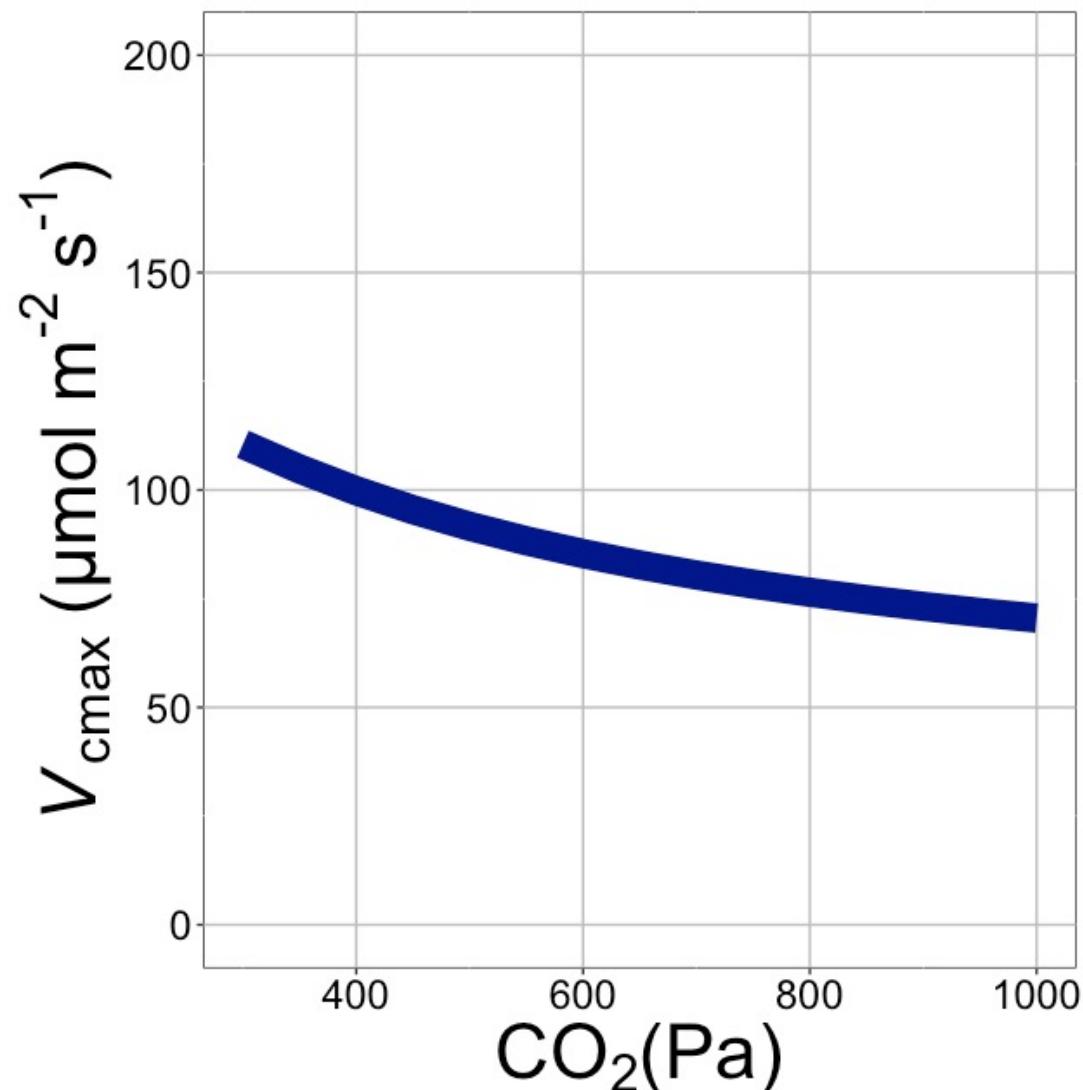
$V_{c\text{max}}$ increases
with light because
of greater electron
transport



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

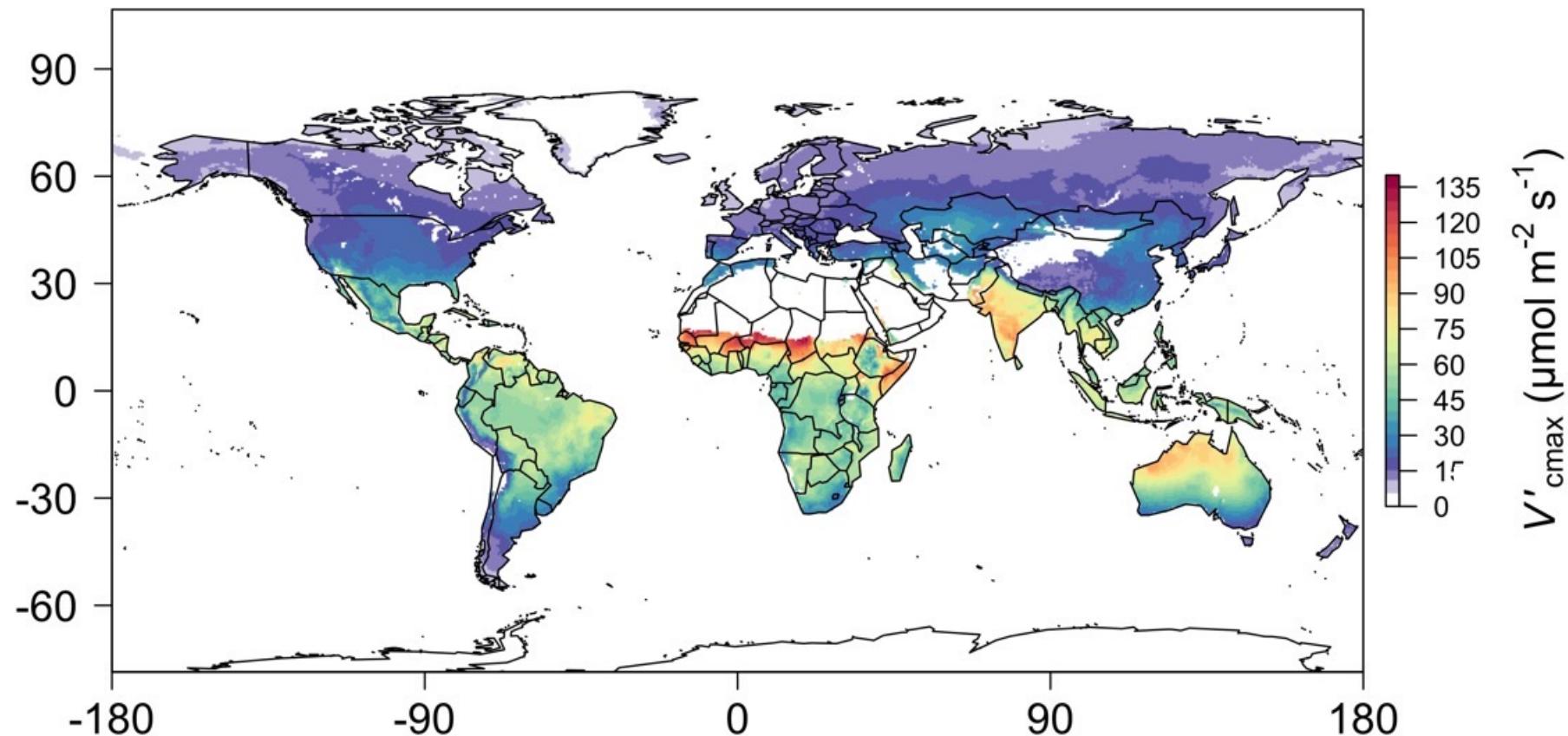


$V_{c\max}$ increases
with VPD because
of lower stomatal
conductance



$V_{c\max}$ decreases
with CO_2 because
of greater CO_2 in
the leaf

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

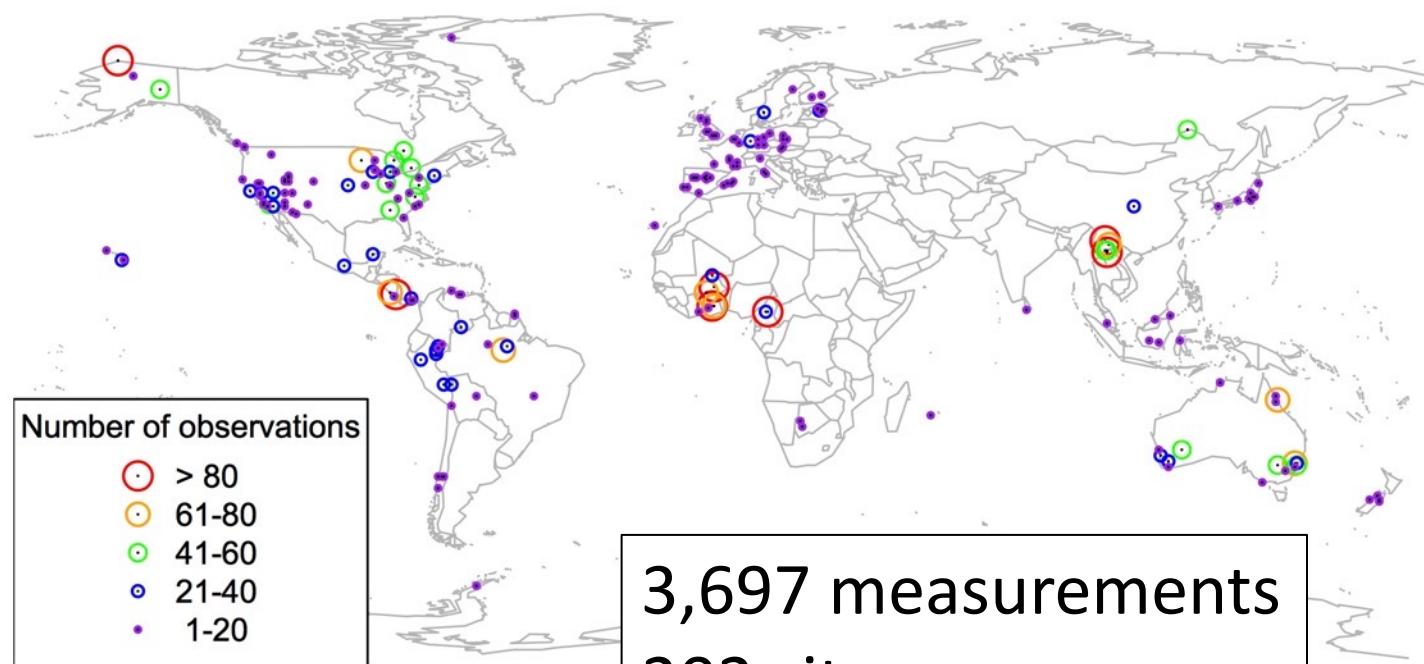
Let's tackle some big questions in
plant ecophysiology!

Big questions

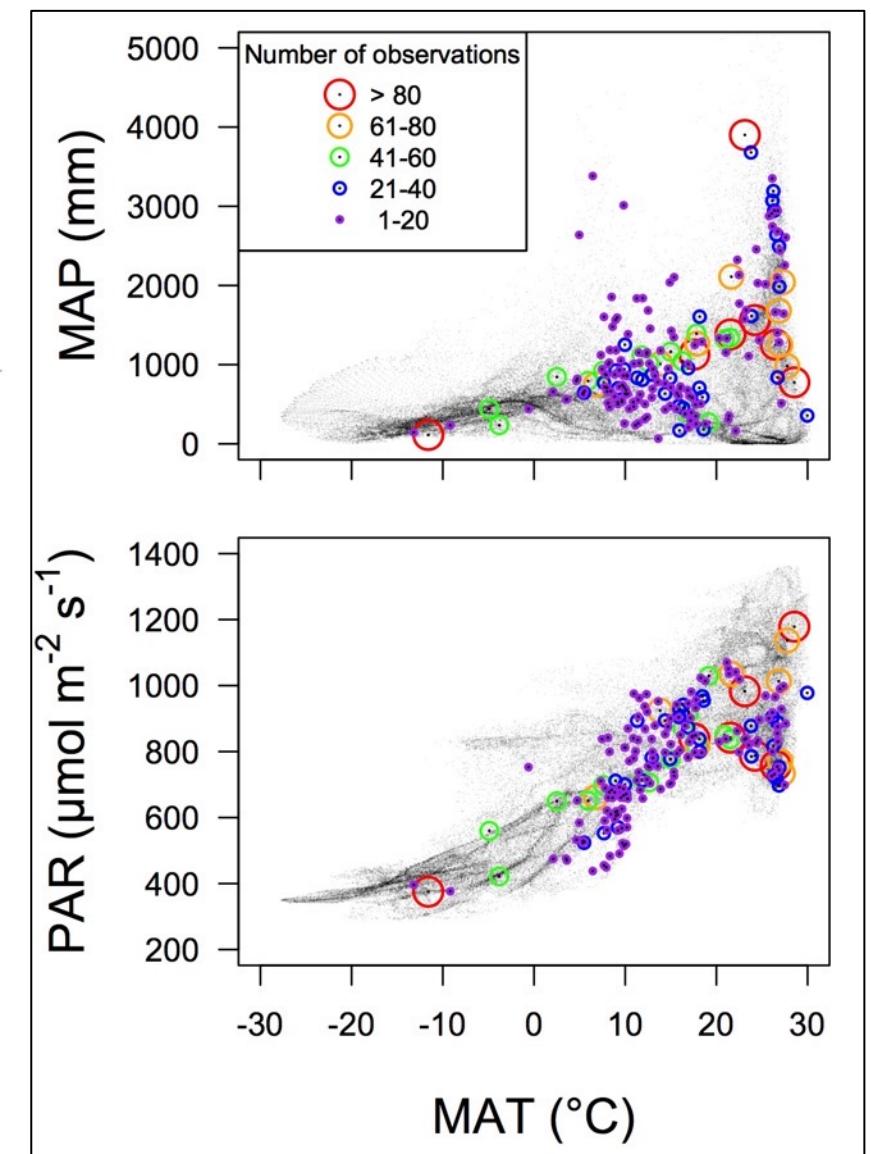
1. Is photosynthesis optimized to the environment?
2. Does photosynthesis acclimate to soil nutrients?
3. What does acclimation mean for future terrestrial biogeochemical cycling?
4. When is C₄ photosynthesis an advantage over C₃ photosynthesis?

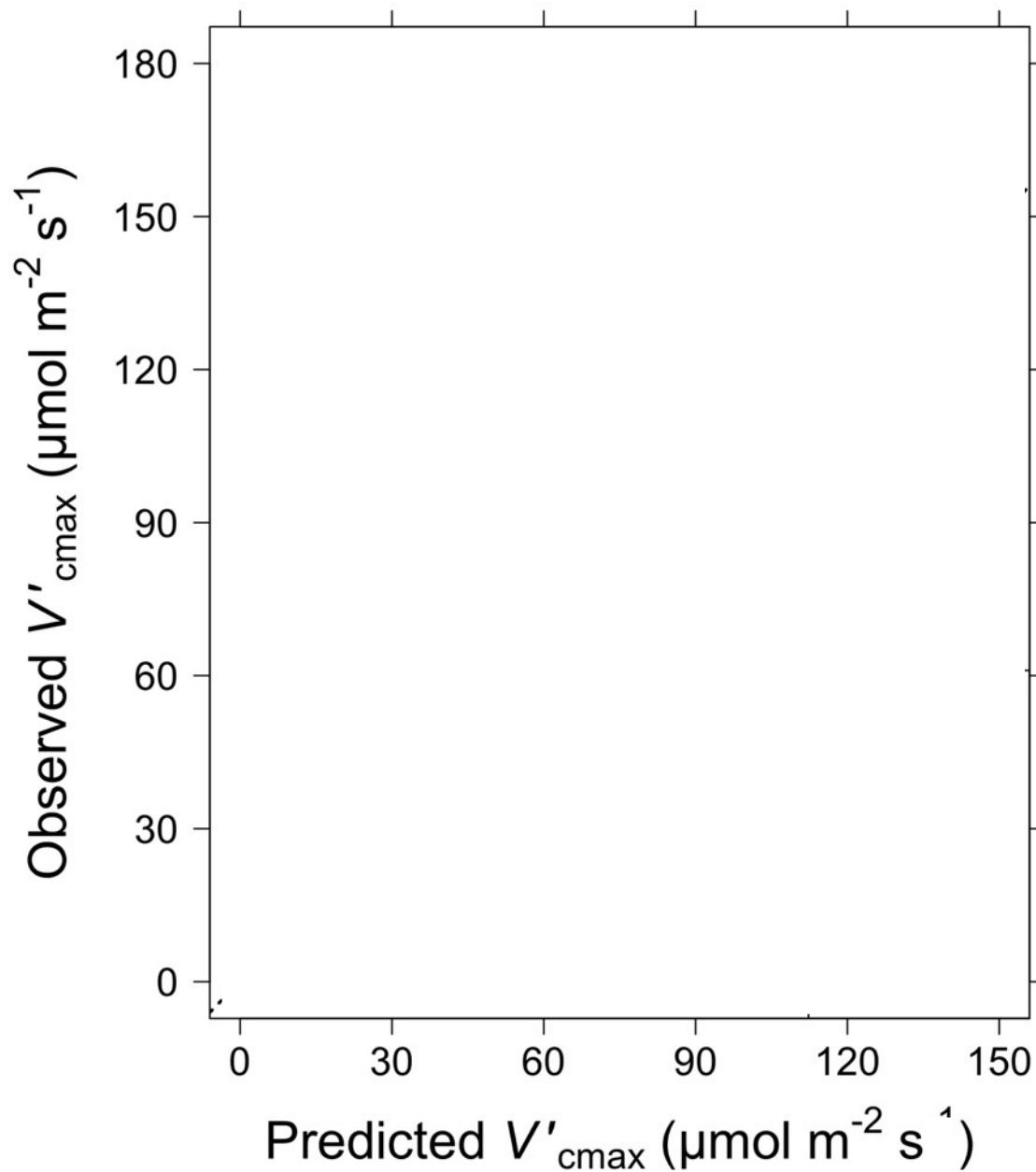
Question 1: Is photosynthesis
optimized to the environment?

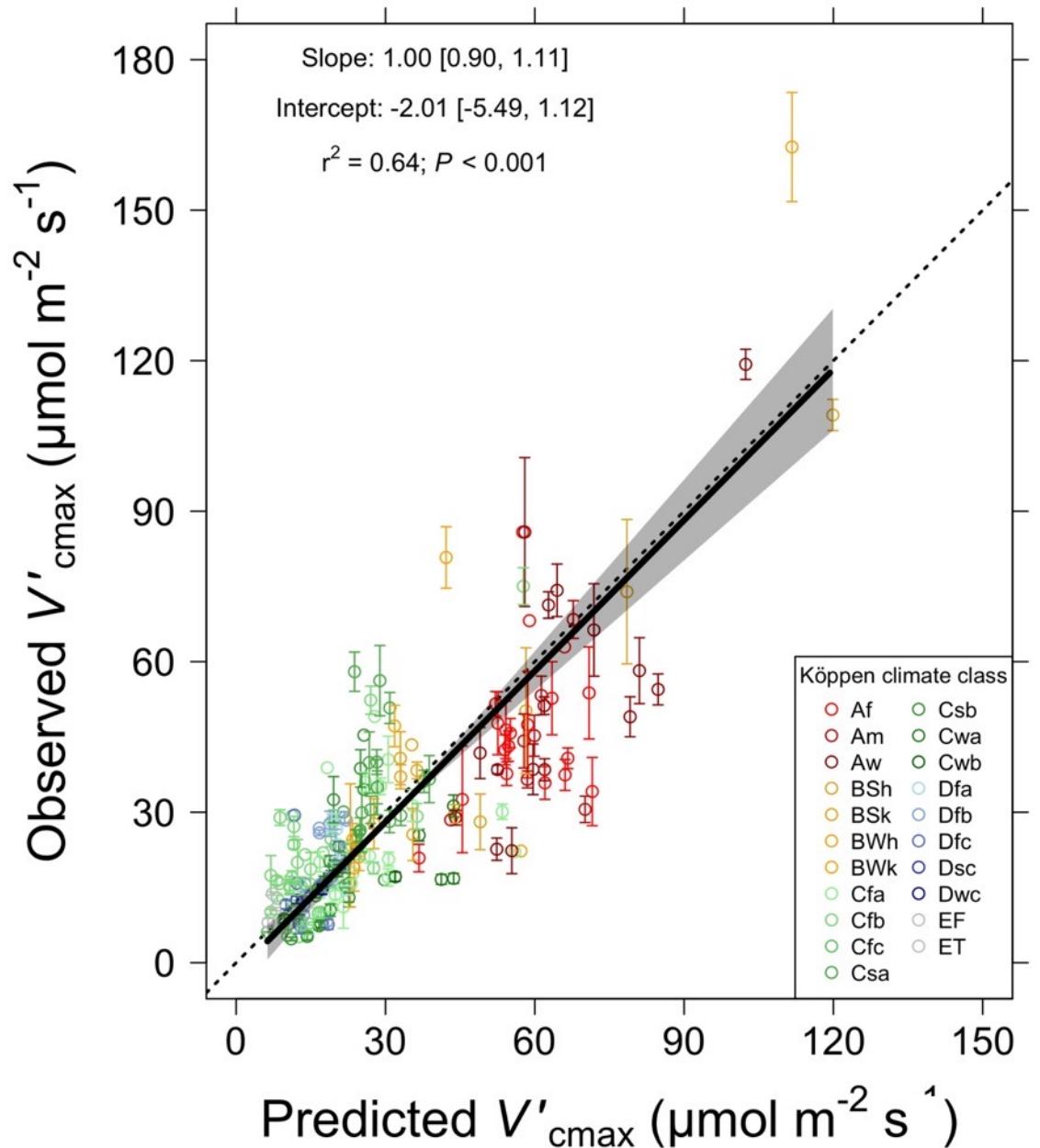
Global V_{cmax} dataset



3,697 measurements
202 sites
> 600 genera





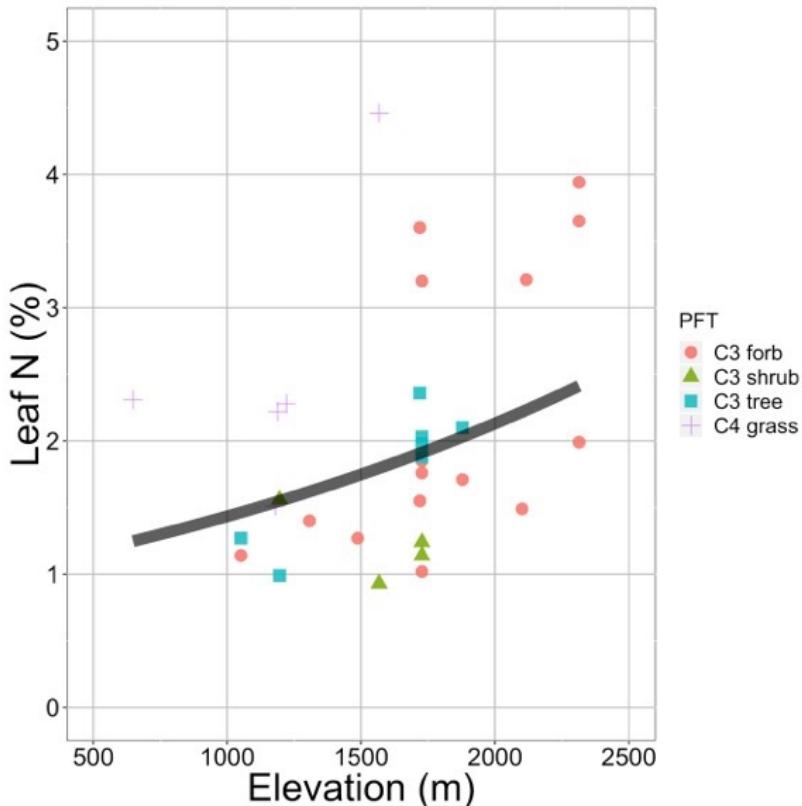
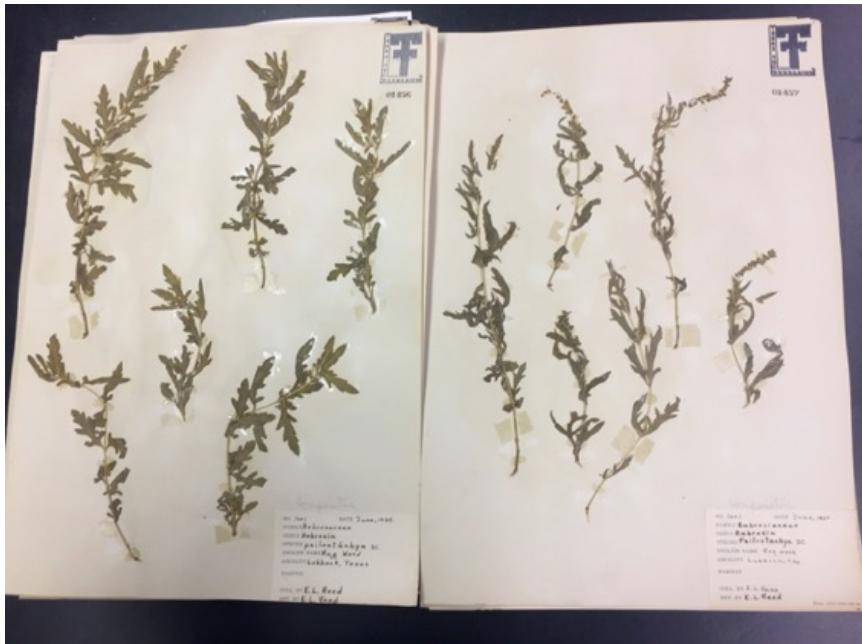


Optimal V'_{cmax} is
similar to
observed
values

Question 1: Is photosynthesis optimized to the environment?

YES! Photosynthesis acclimates spatially as expected from optimization

Looking forward: herbarium specimens to examine acclimation over space and time



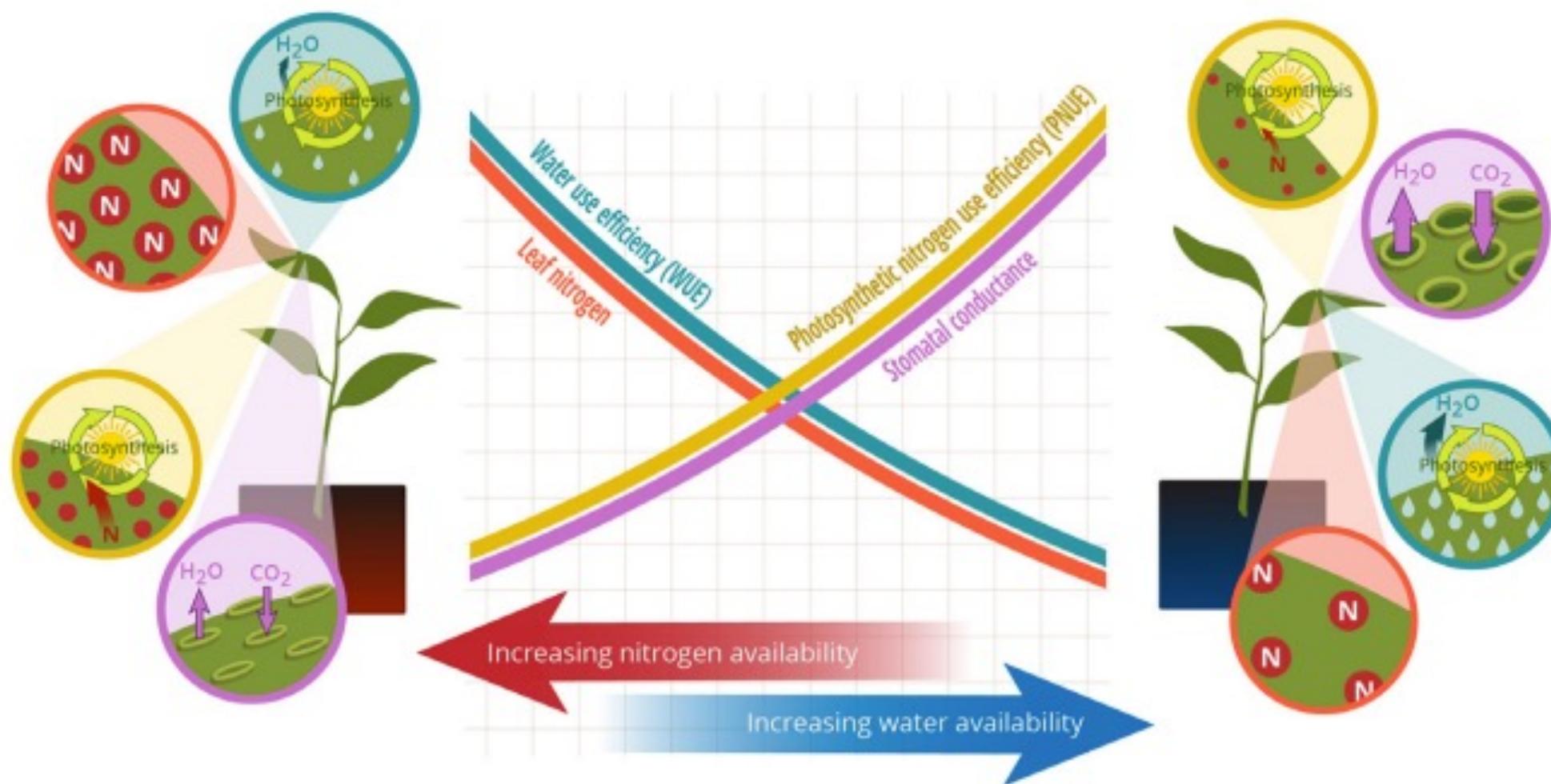
Plants increased leaf N investment with elevation. This response was predicted by acclimation theory.

Question 2: Does photosynthesis
acclimate to soil nutrients?

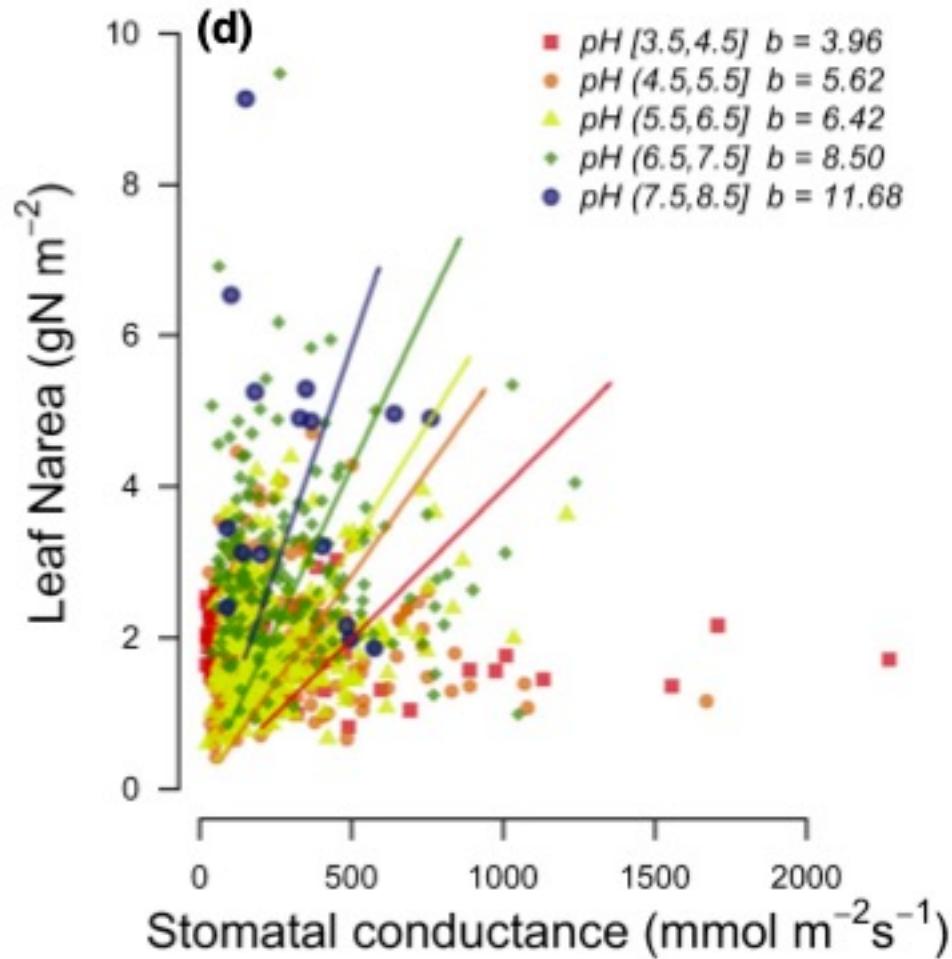
From the least cost hypothesis...

Added nutrients will not increase photosynthesis
because light limitation will kick in

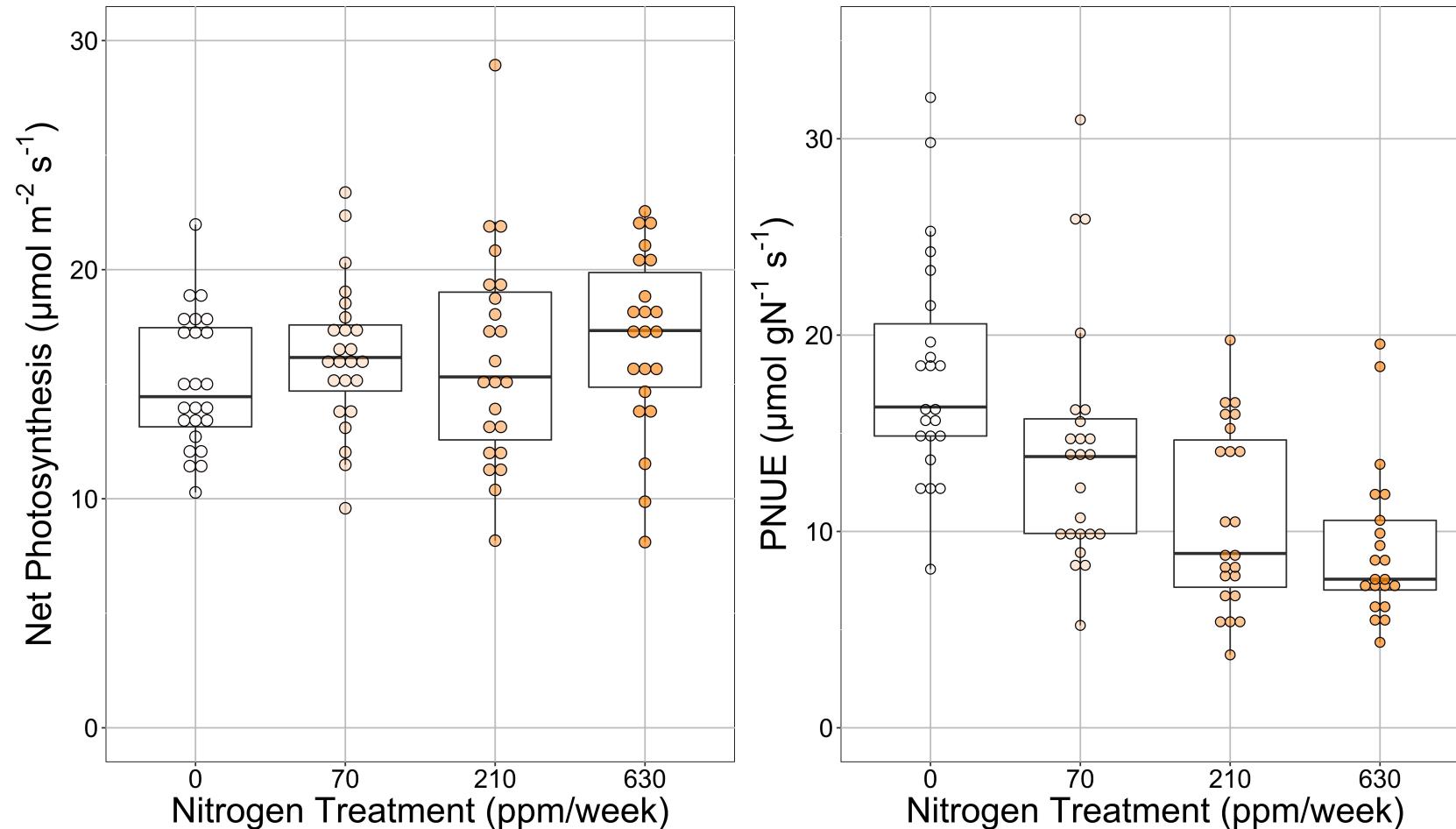
From the least cost hypothesis...



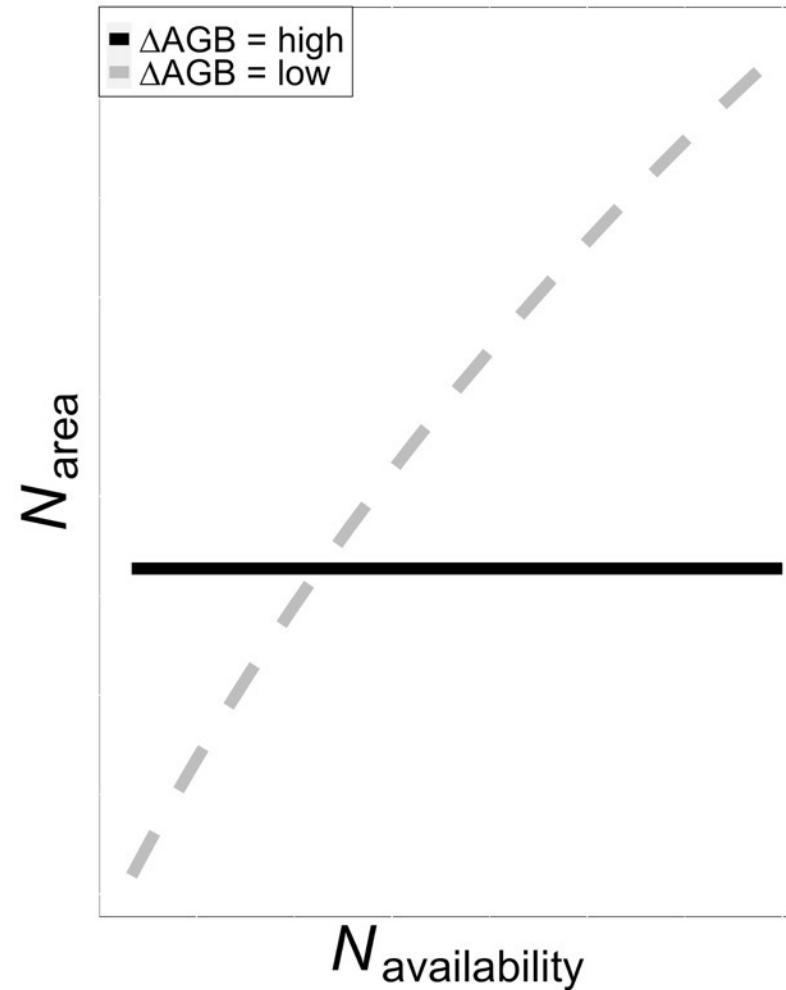
Observations show support for least cost



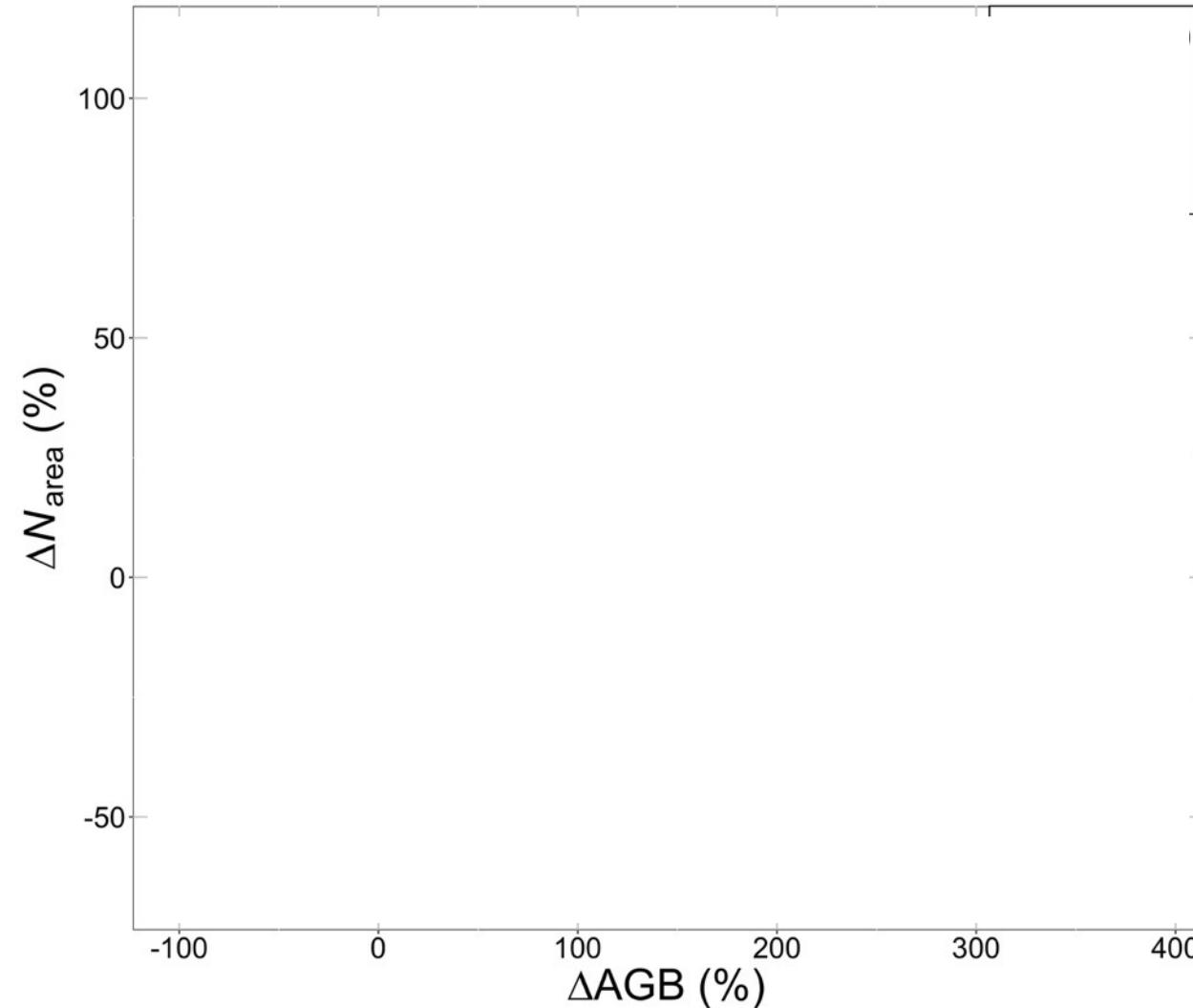
As do greenhouse experiments



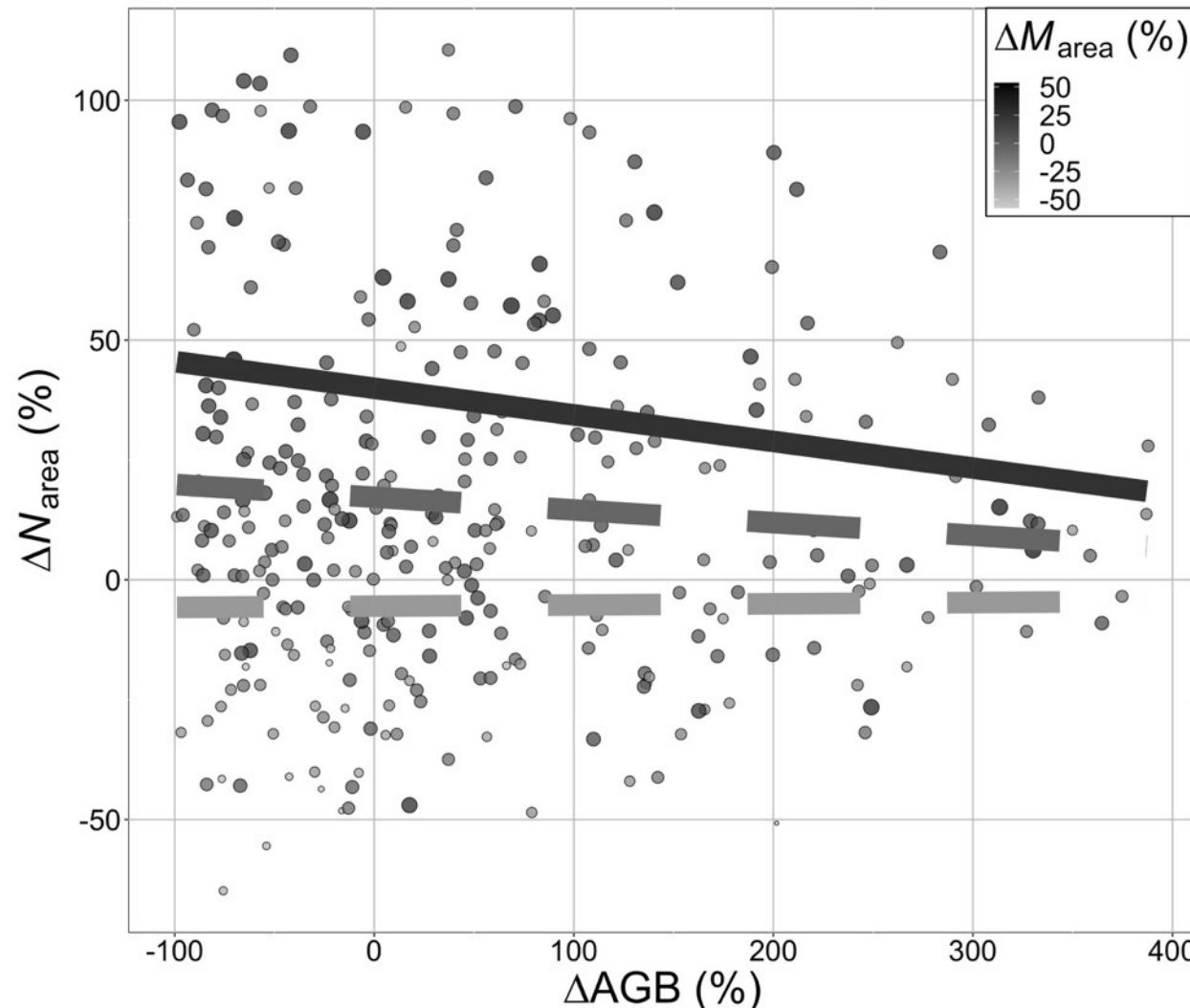
Is plant allocation to leaf N dependent on allocation to biomass?



Is plant allocation to leaf N dependent on allocation to biomass?



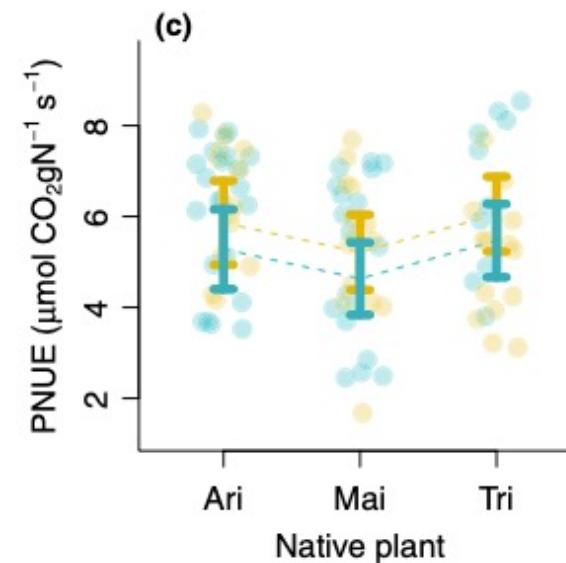
To see a leaf N response to soil N there must be (1) added investment to leaves and (2) small investment to biomass



Question 2: Does photosynthesis
acclimate to soil nutrients?

Yes, although this is dependent on
whole-plant allocation decisions

Looking forward: impact of allelopathic invaders on leaf economics



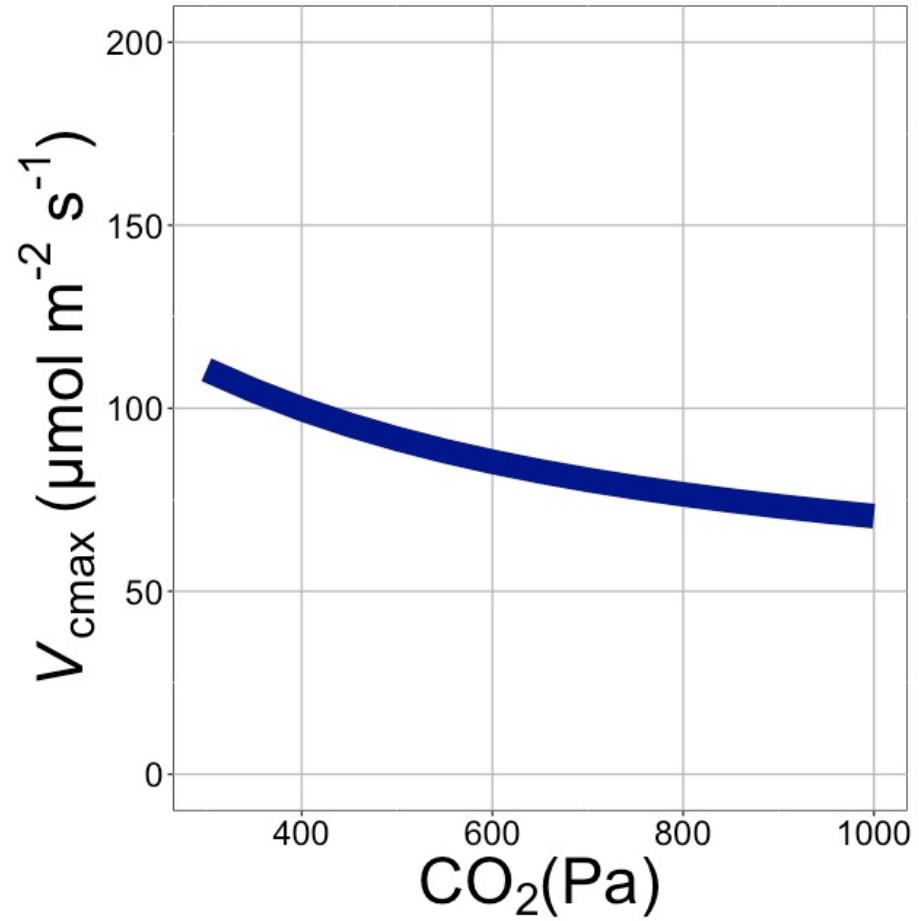
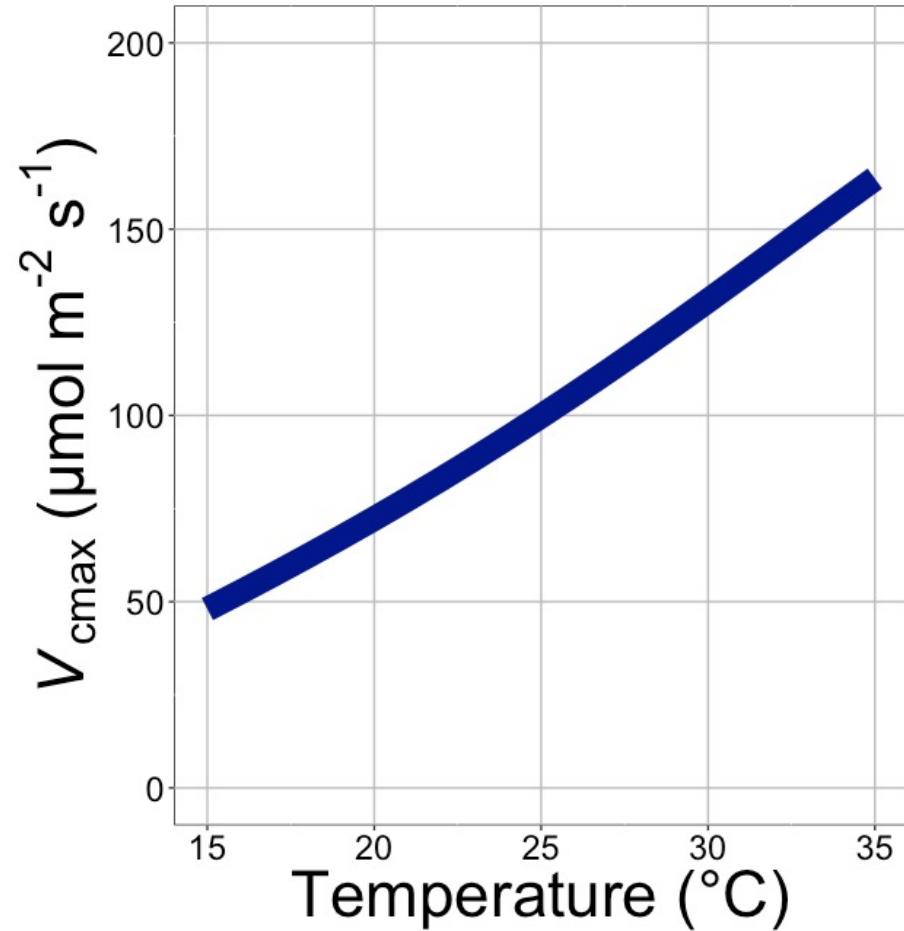
Allelopathic invasion (gold) increased photosynthetic N use efficiency of native plants. This response was predicted by acclimation theory.

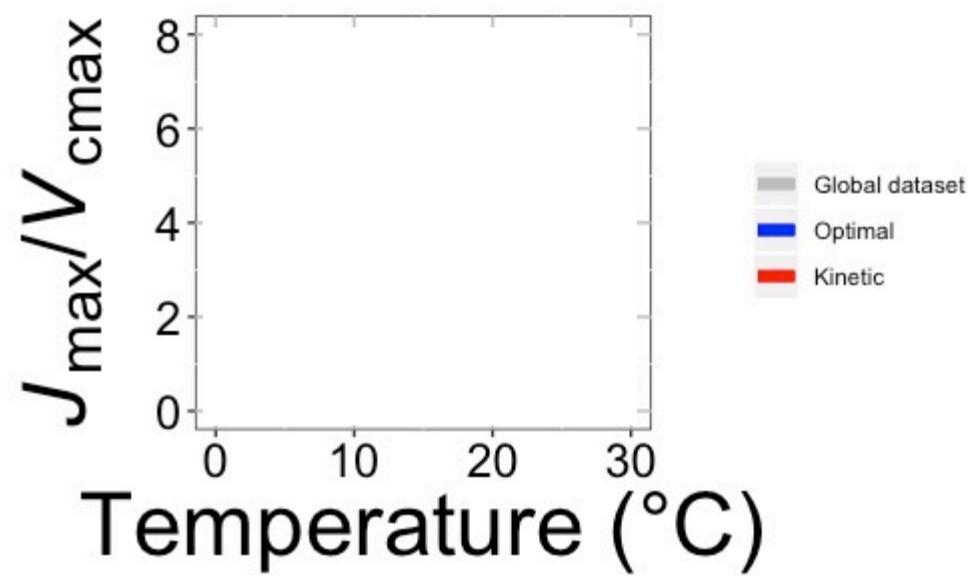
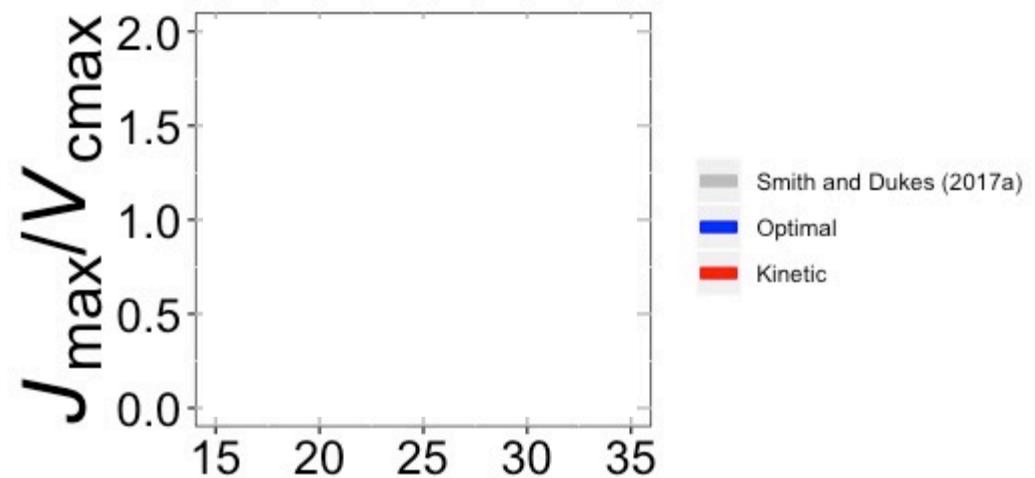
Question 3: What does acclimation mean for future terrestrial biogeochemical cycling?

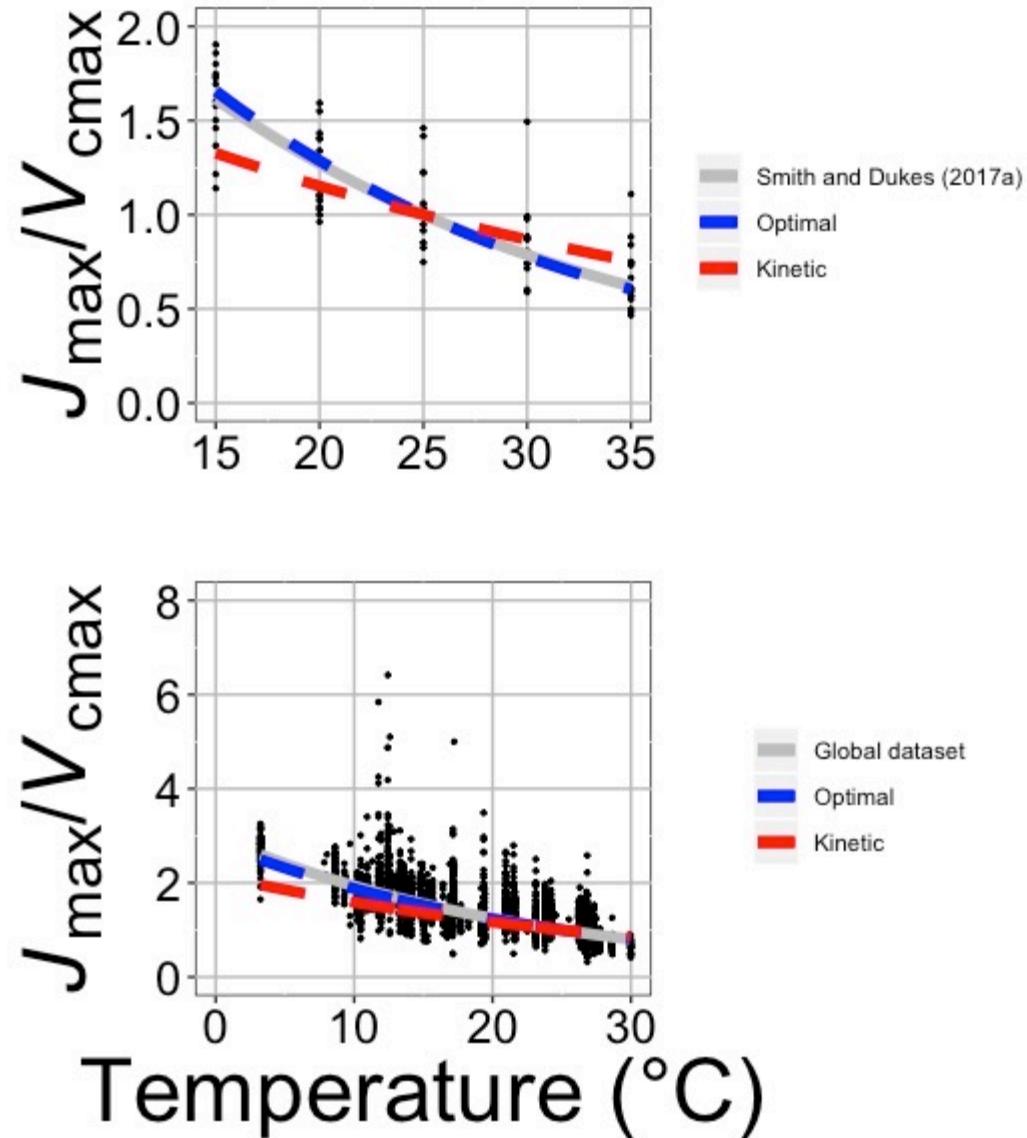


Energy Exascale
Earth System Model

Expected future responses



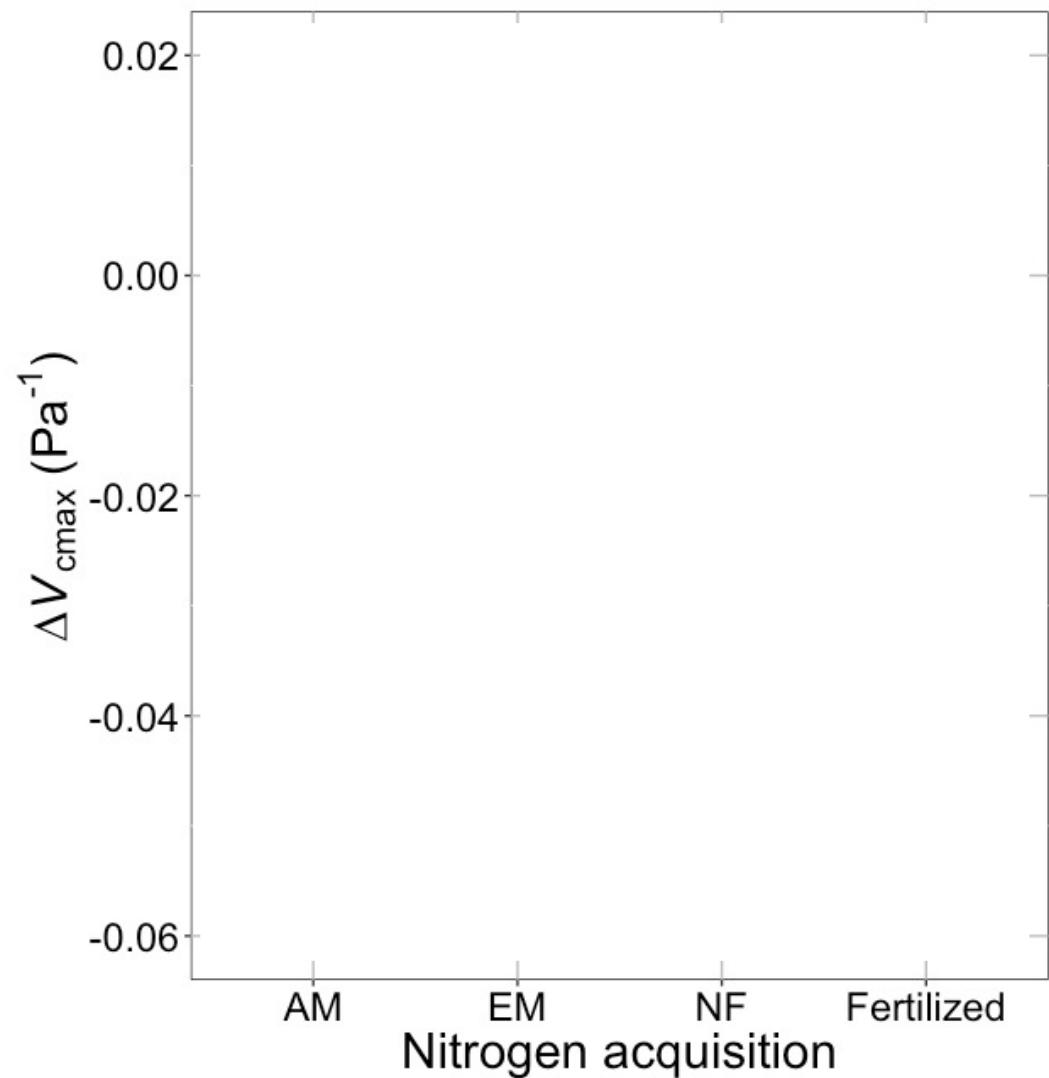


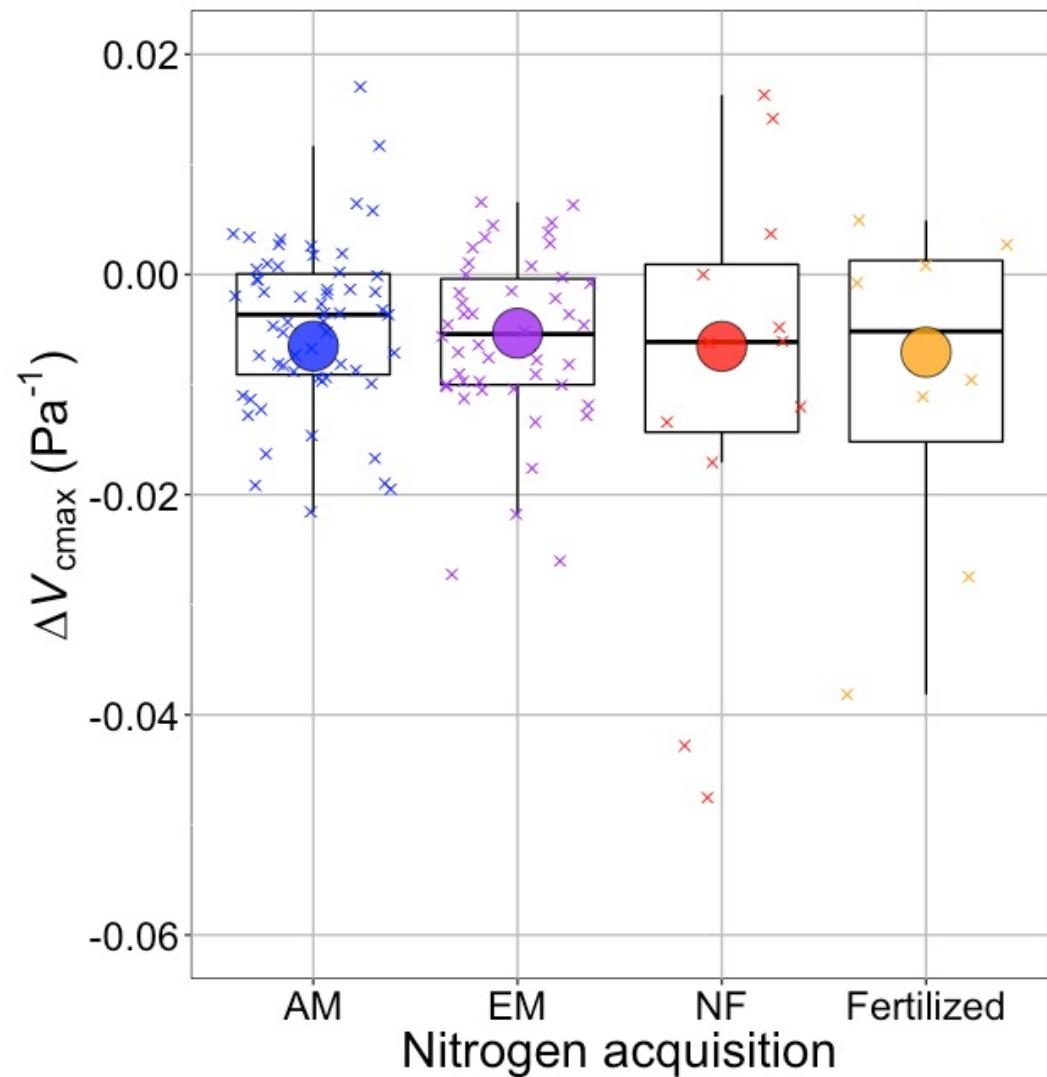


Photosynthetic traits change with temperature in ways expected from optimization

Data = $-0.051 \text{ } ^{\circ}\text{C}^{-1}$

Predicted = $-0.048 \text{ } ^{\circ}\text{C}^{-1}$

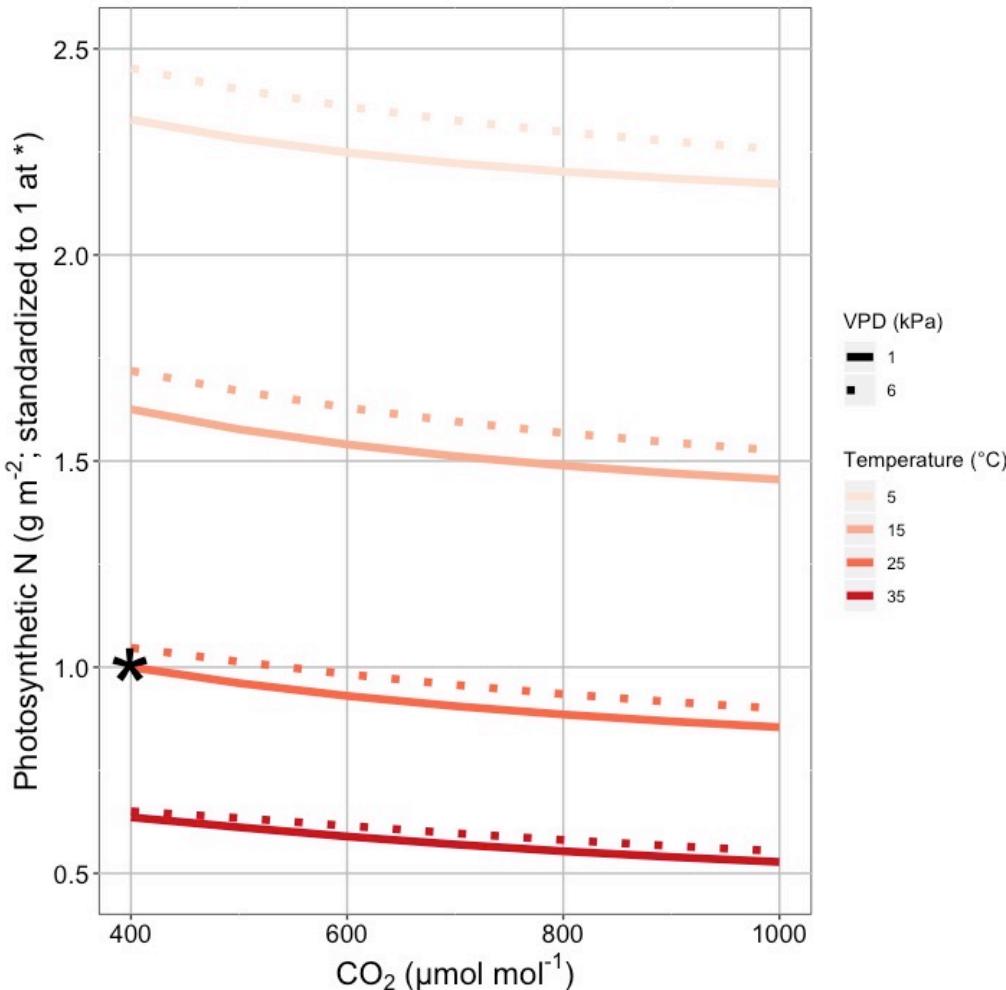




V_{cmax} changes with CO_2 in ways expected from optimization

Boxes = data = -0.0063 Pa^{-1}
Circles = predicted = -0.0066 Pa^{-1}

This generally suggests lower nitrogen demand under warmer, high CO₂ conditions

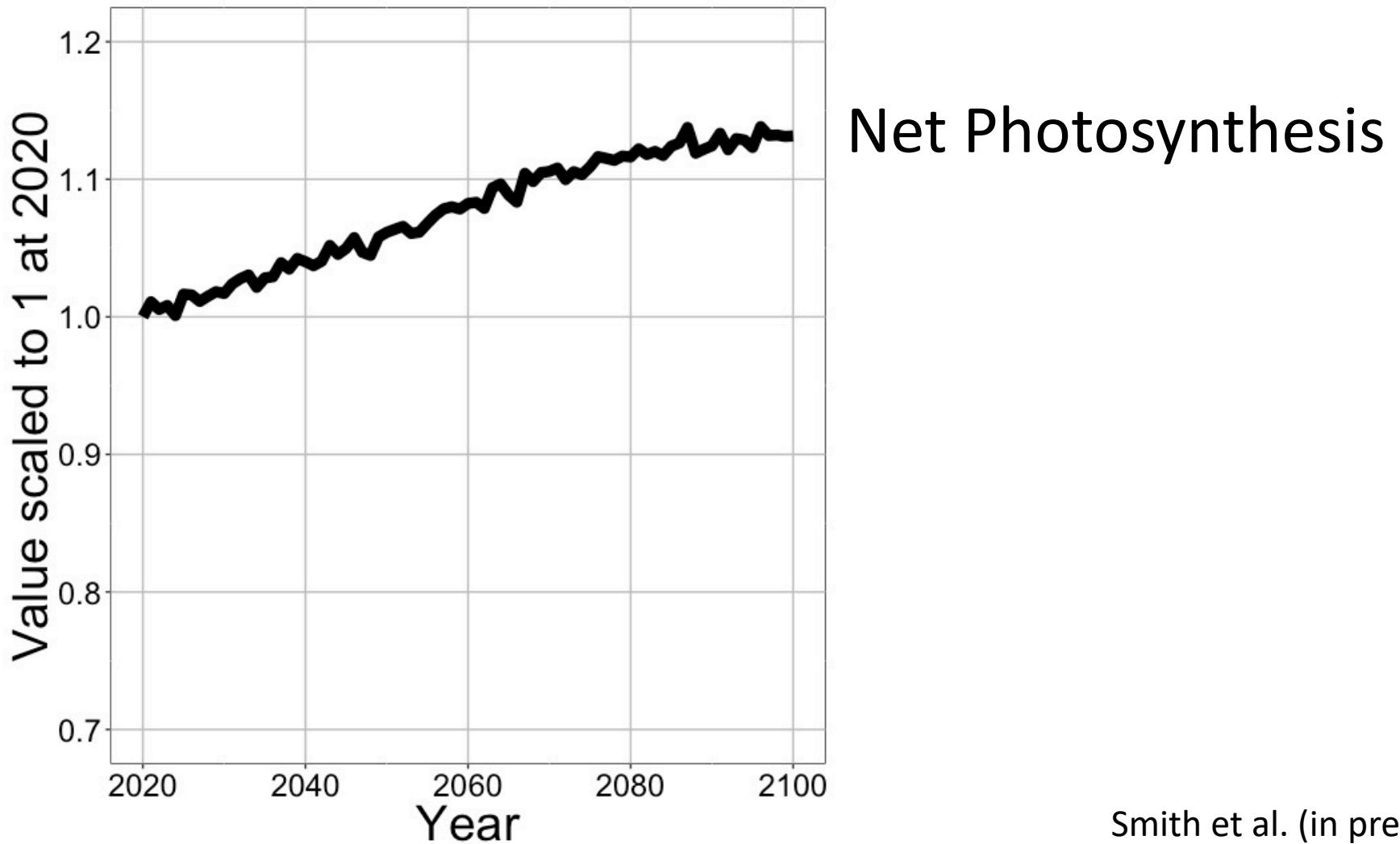


Let's run a model out into the future!

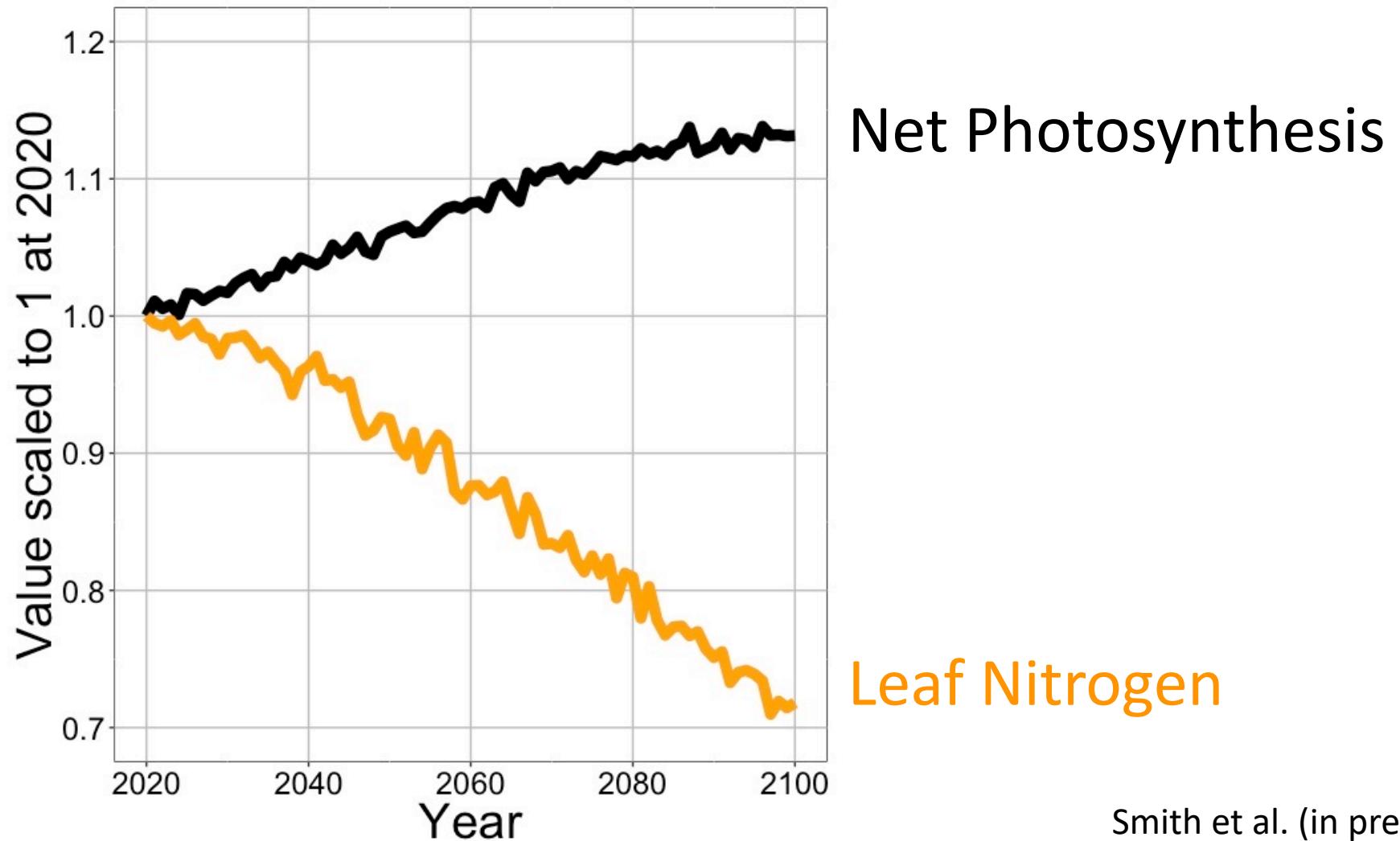


Energy Exascale
Earth System Model

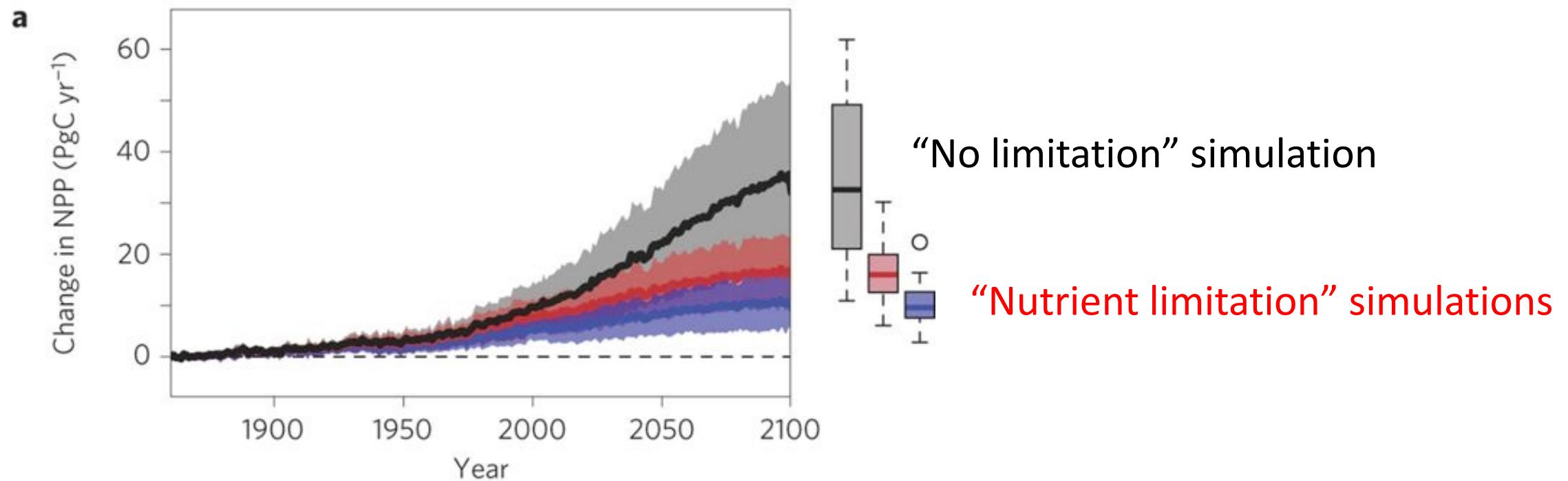
Photosynthesis increases in future



Photosynthesis increases in future (at lower nutrient use)



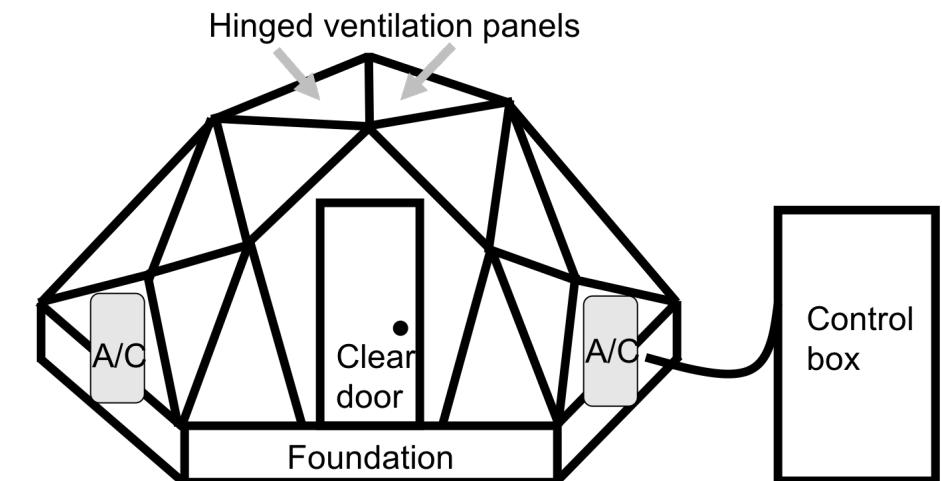
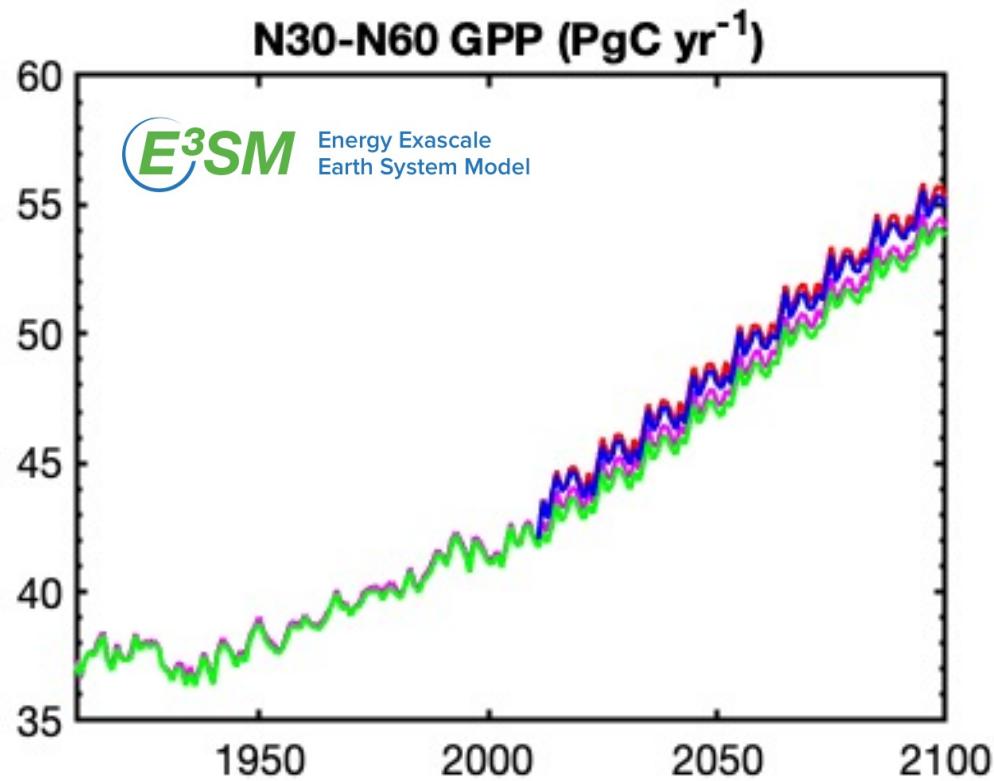
Need to rethink nutrient limitation in models?



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

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

Looking forward: role of acclimation on future ecosystem feedbacks



Coupled model-data experiments

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...

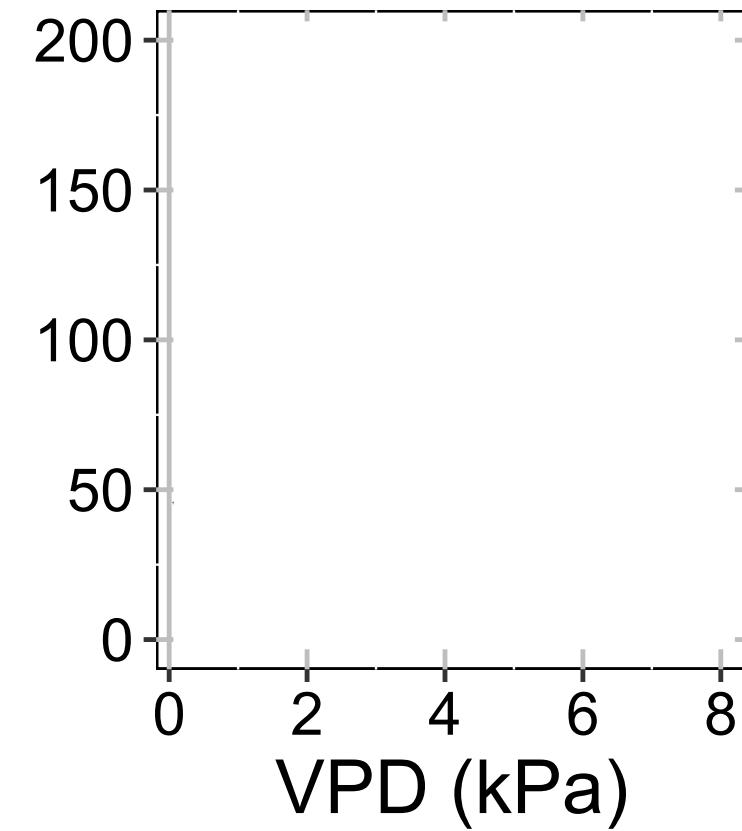
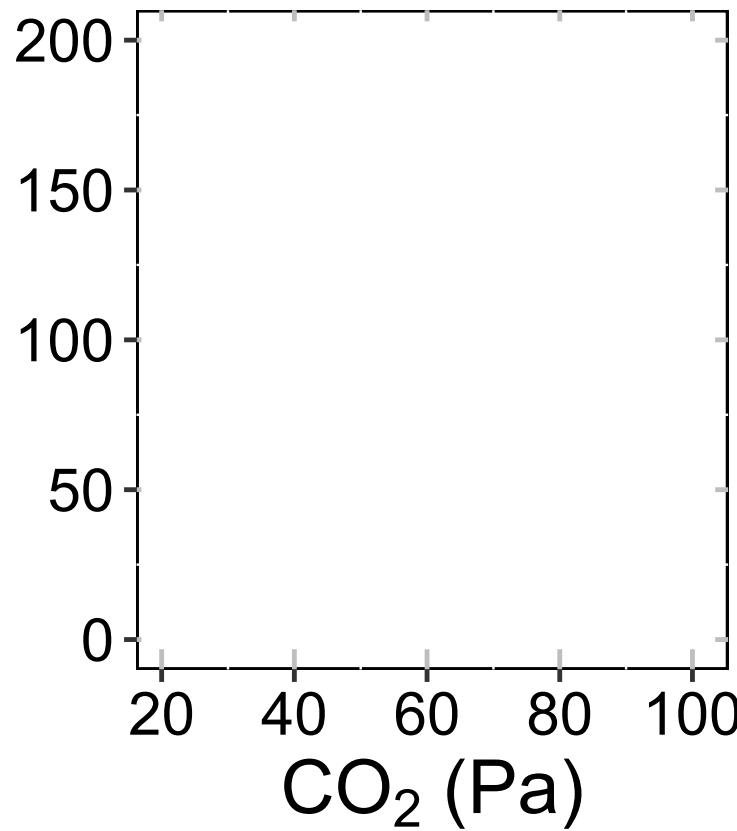
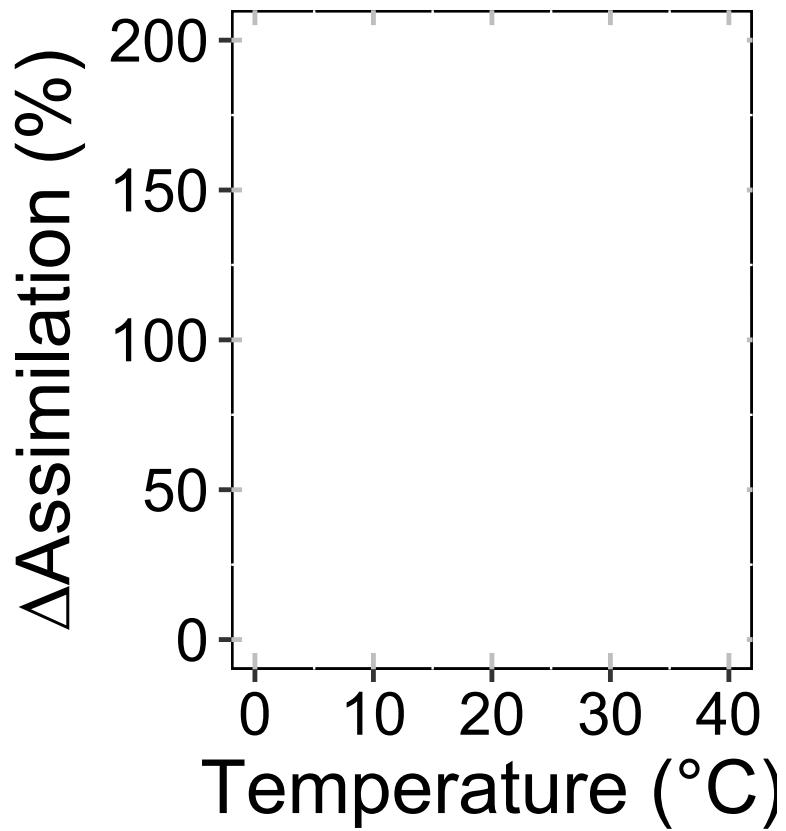
- No photorespiration
- An additional limitation (PEP carboxylation)

C_4 versus C_3 optimization

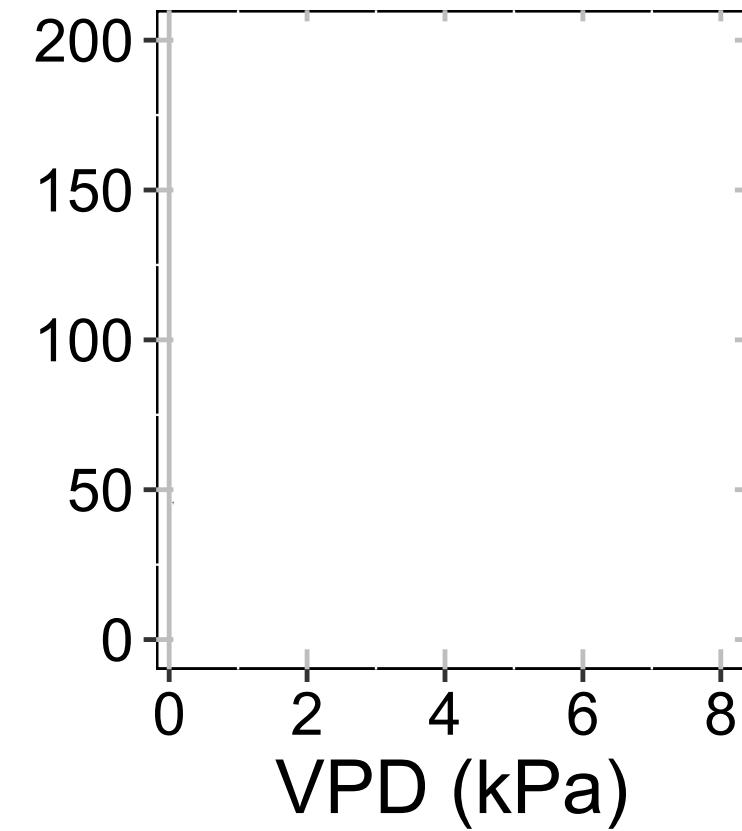
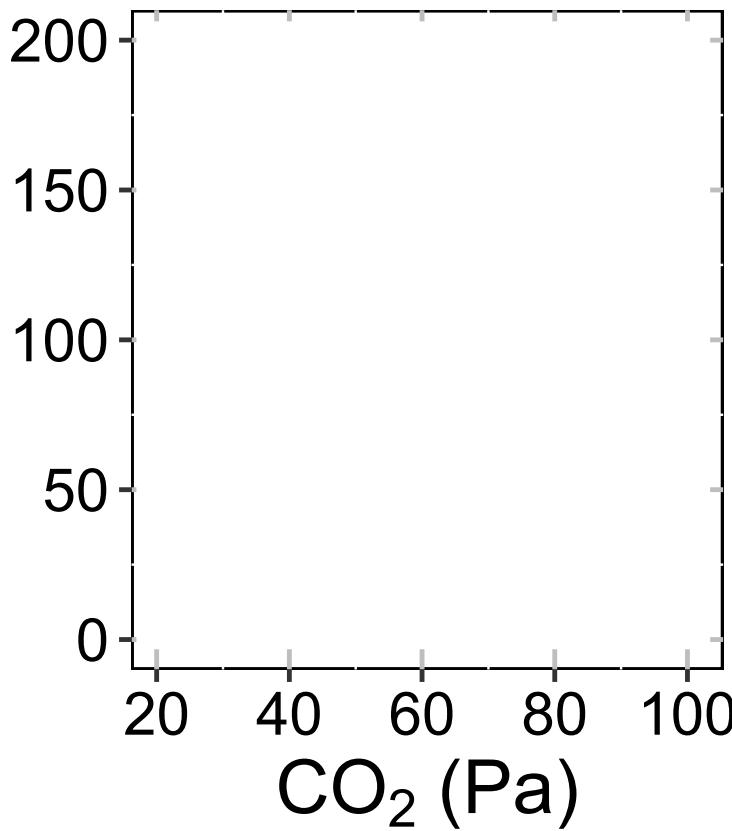
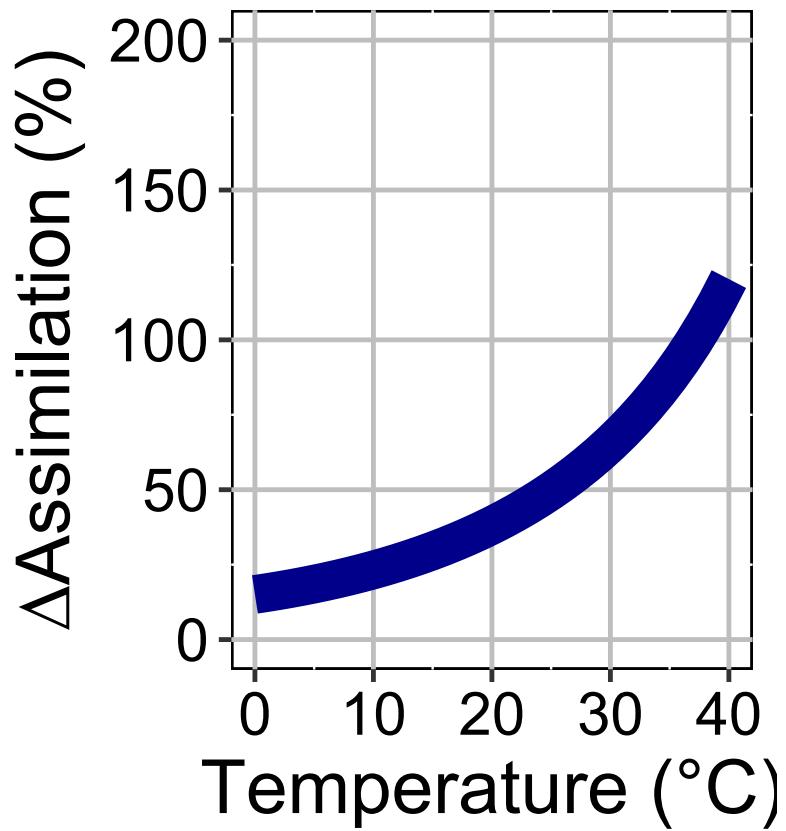
C_4 photosynthesis has...

- **No photorespiration**
- An additional limitation (**PEP carboxylation**)

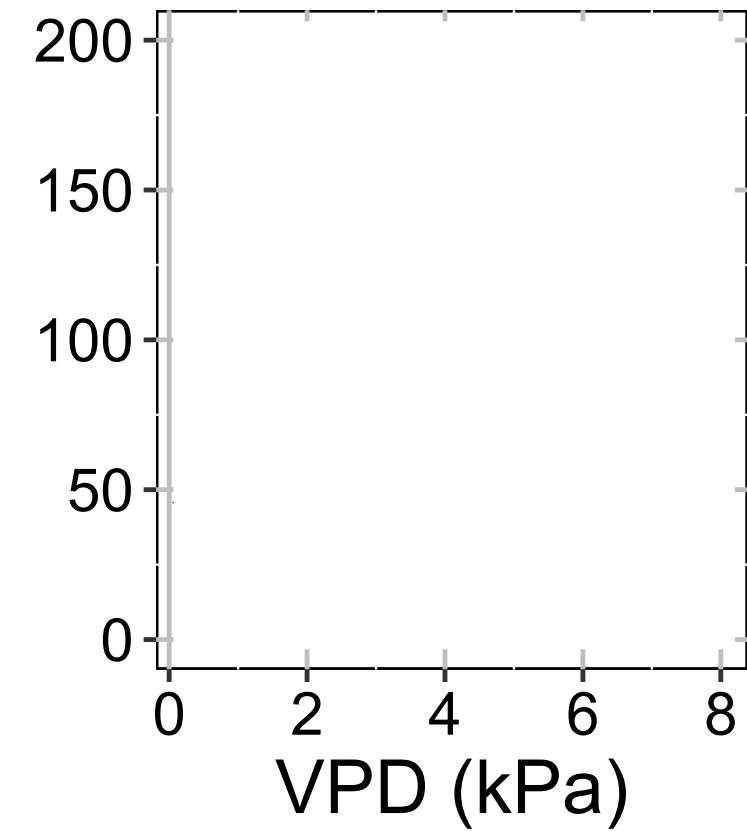
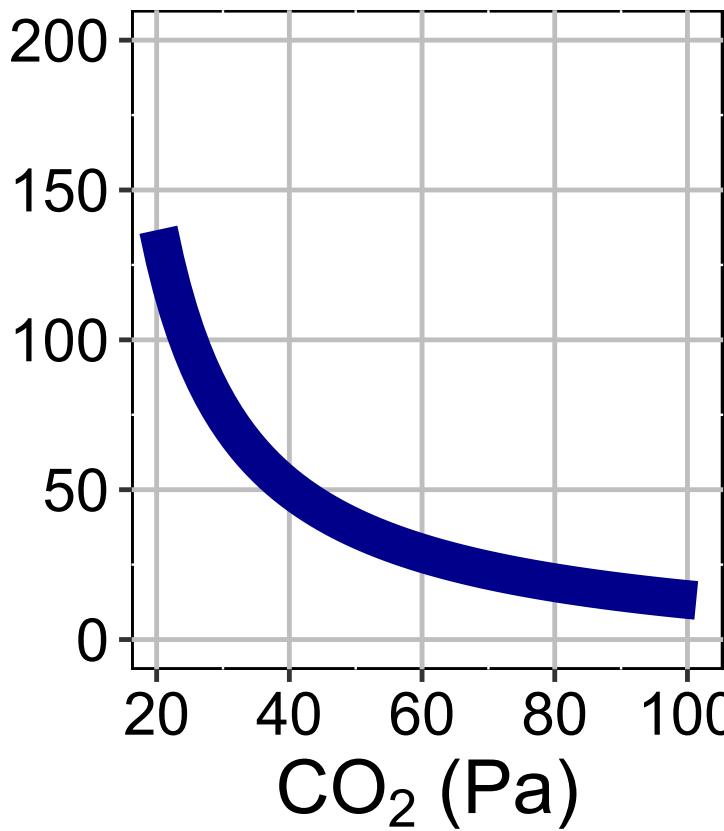
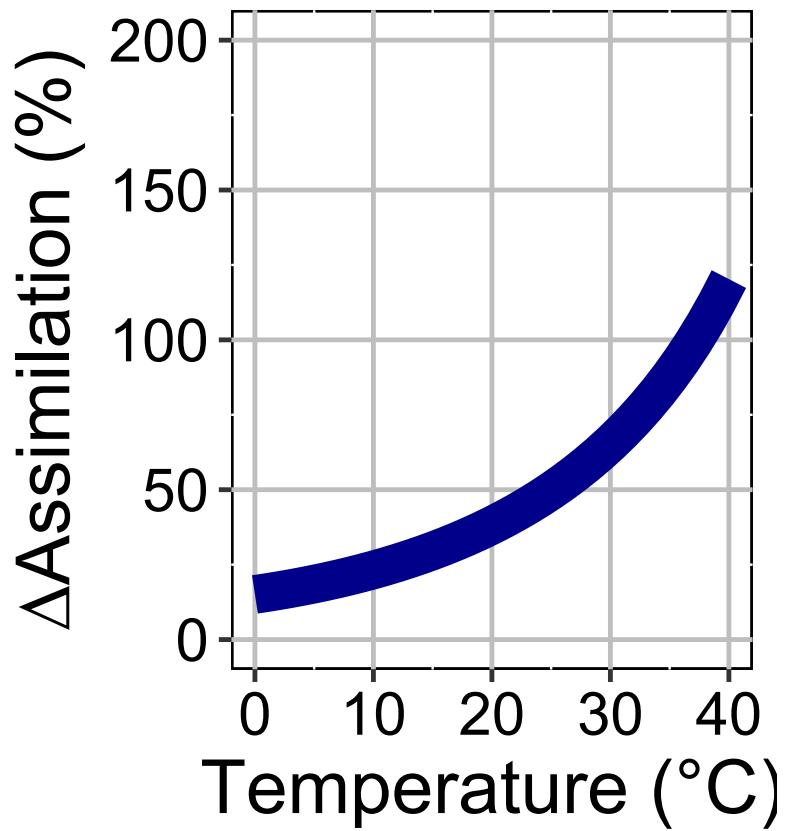
Relative advantage of C₄ physiology



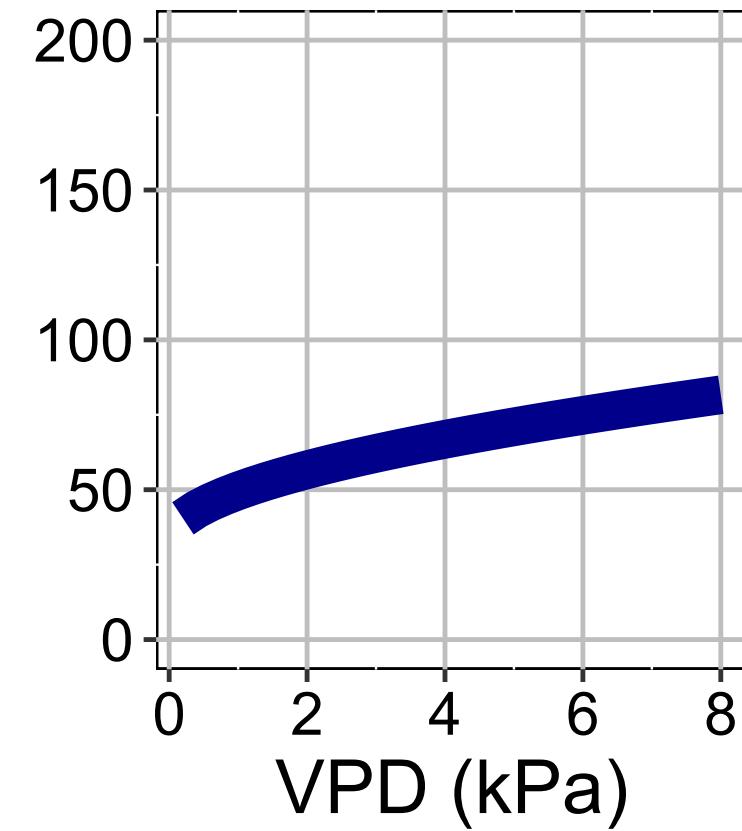
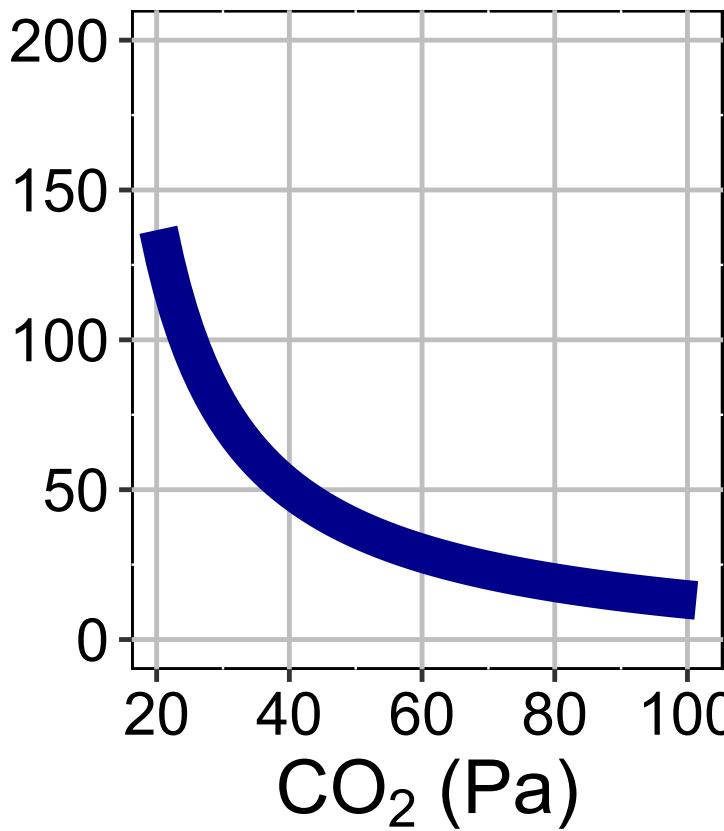
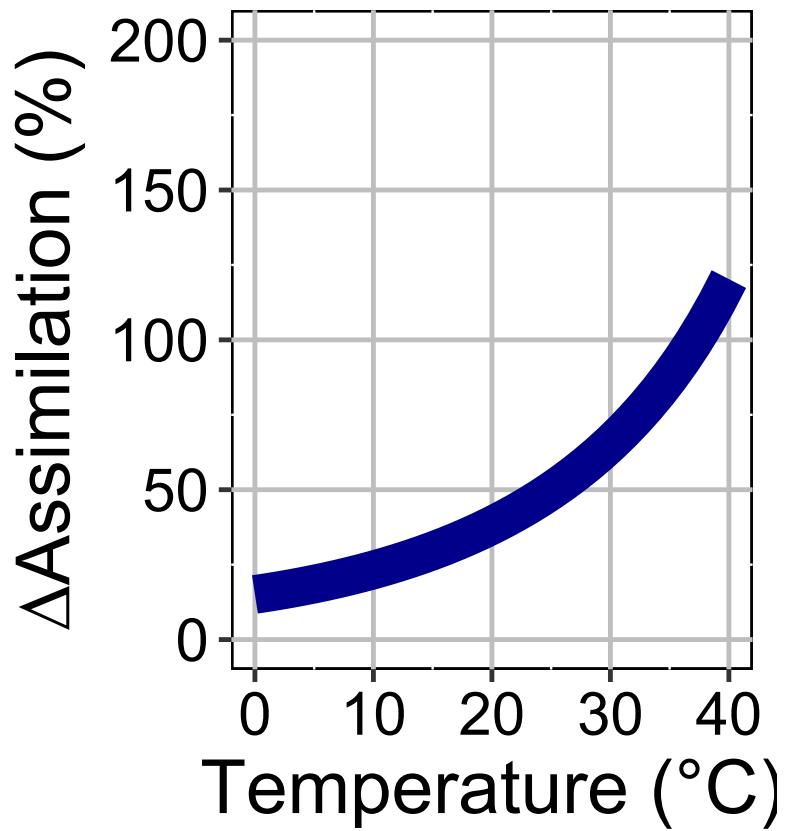
Relative advantage of C₄ physiology

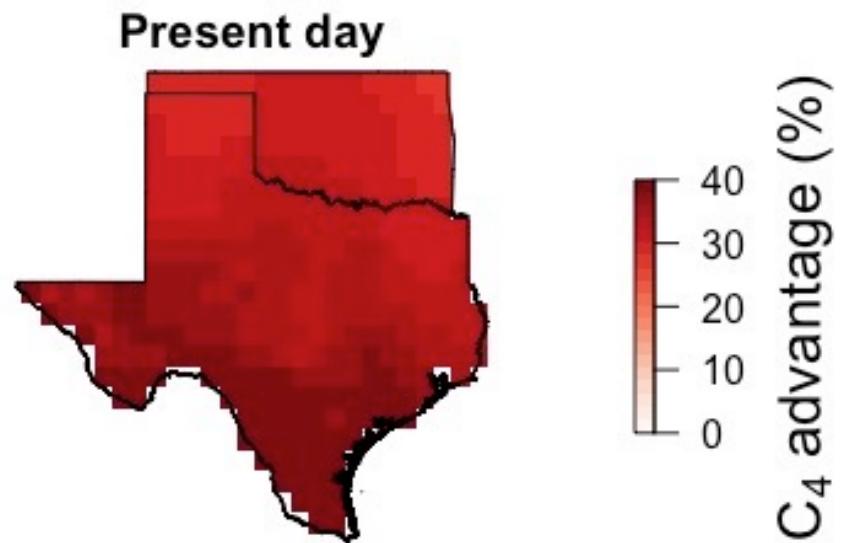


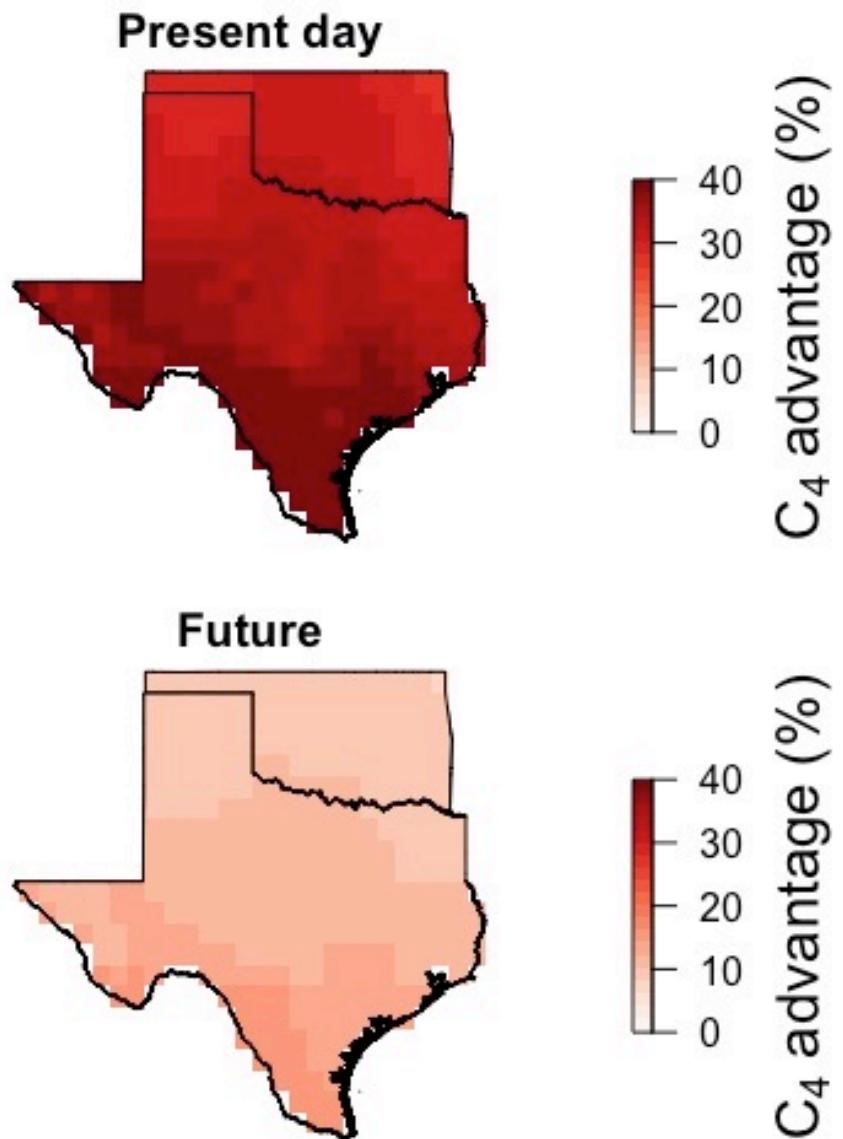
Relative advantage of C₄ physiology



Relative advantage of C₄ physiology







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

C₄ is better in hot, dry, low CO₂ environments

Looking forward: model-data comparisons for C_4 plants



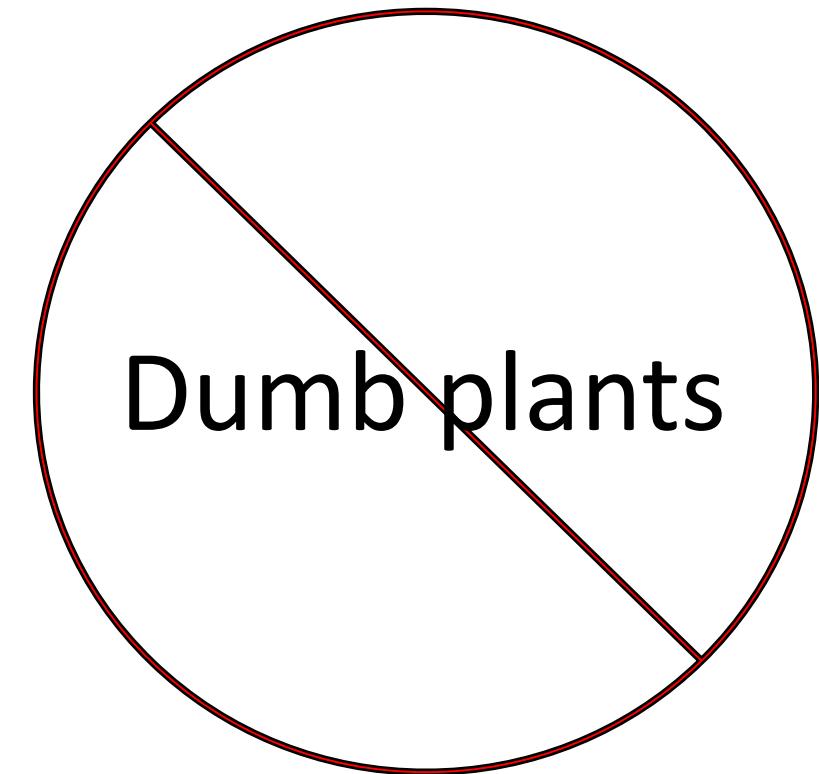
Powell Center



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



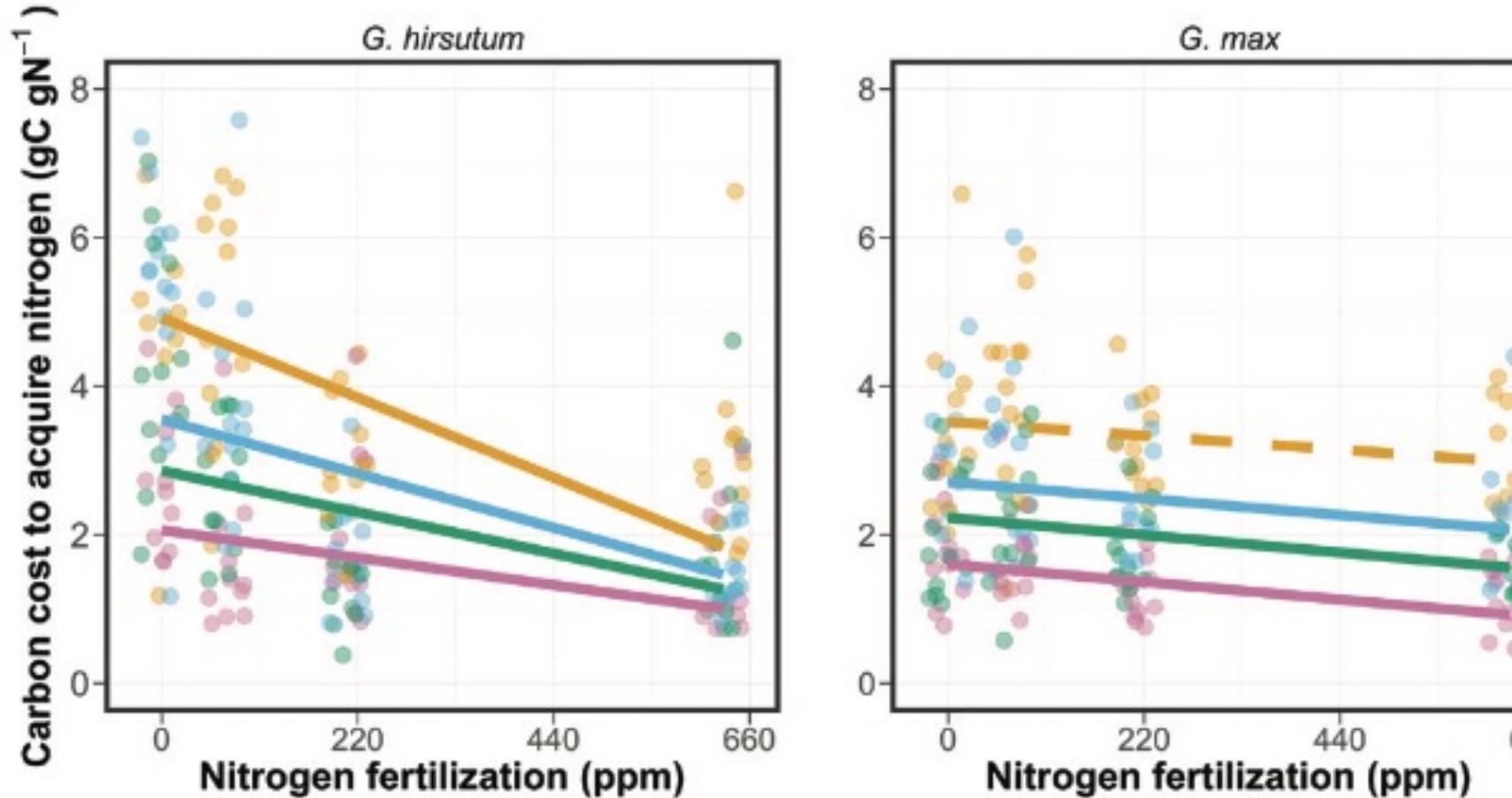
Presentation available at:

www.github.com/SmithEcophysLab/seminar/2021_michigan



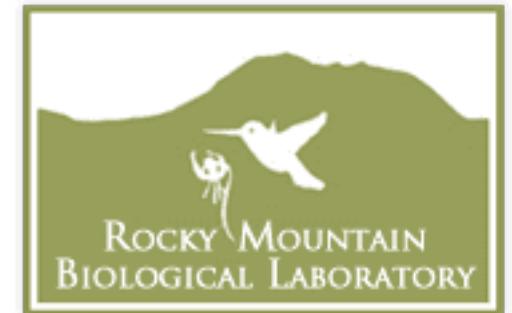
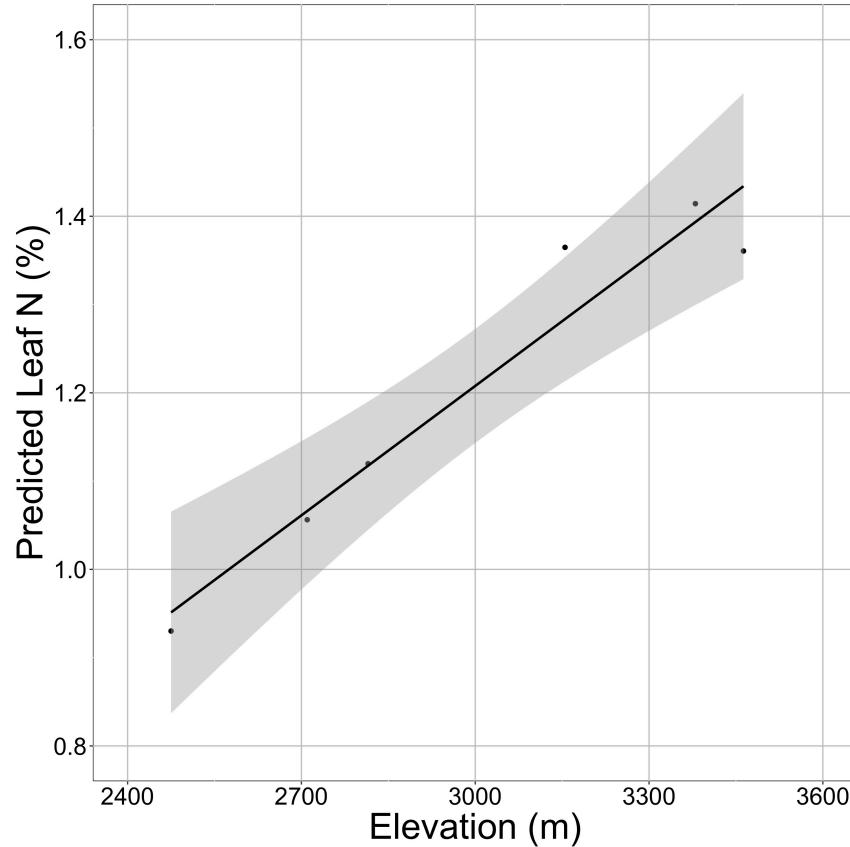
Thanks!

Looking forward: symbioses as modifiers of plant economies under variable conditions



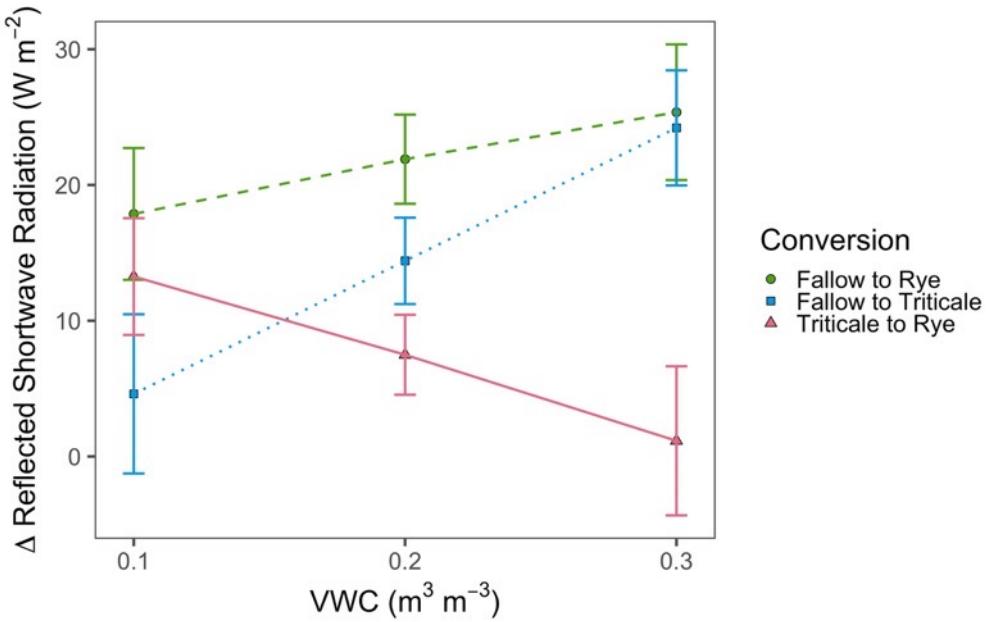
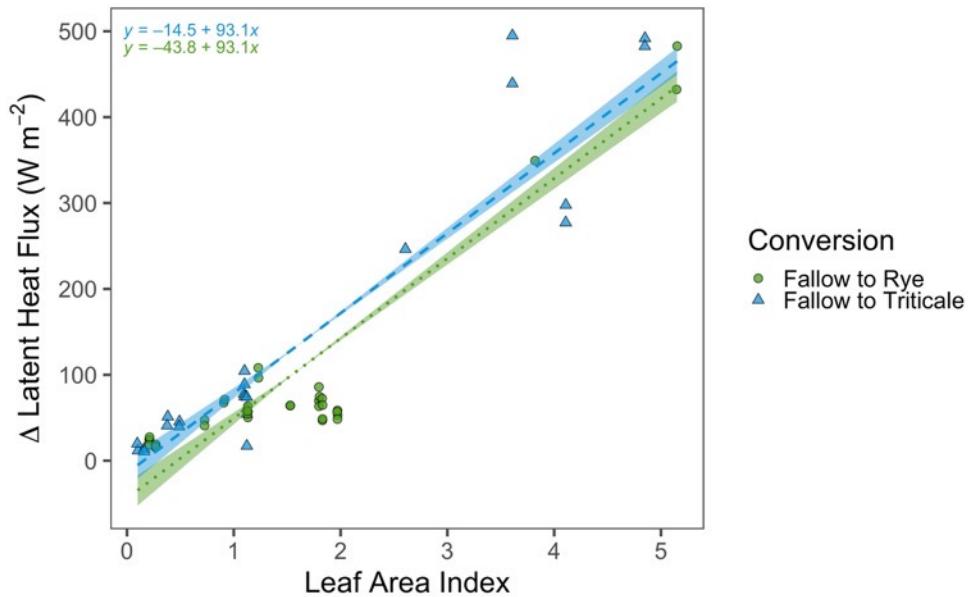
Soybean (right panel)
economics are much
less responsive to soil
nitrogen than cotton
(left panel)

Looking forward: more acclimation predictions in more places to examine larger scale impacts

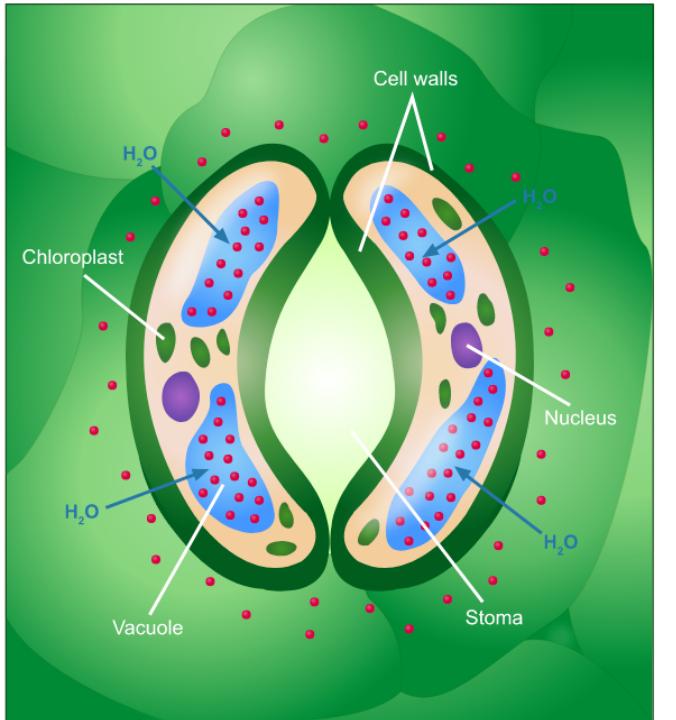


Looking forward: other ongoing and future research

Land management modifications of plant-atmosphere feedbacks



Cover crop implementation increases latent heat flux (left) and albedo (right) as compared to fallow fields.



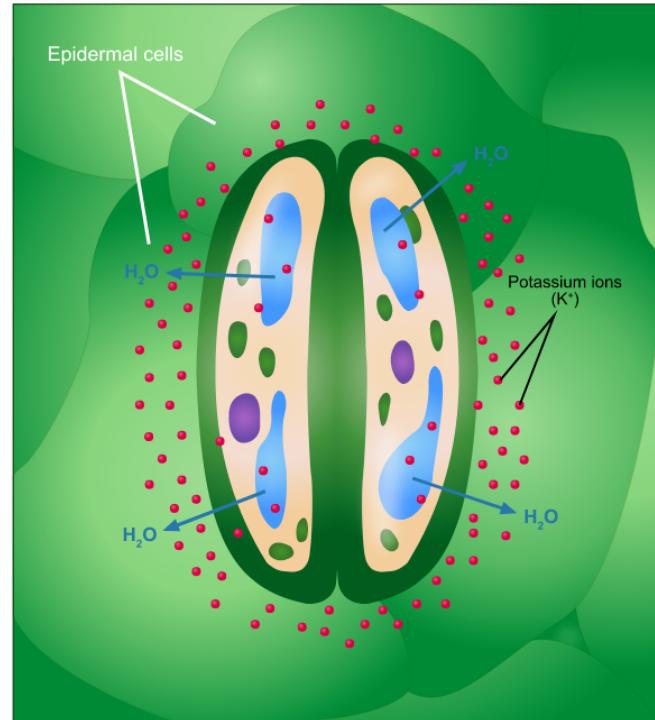
Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux



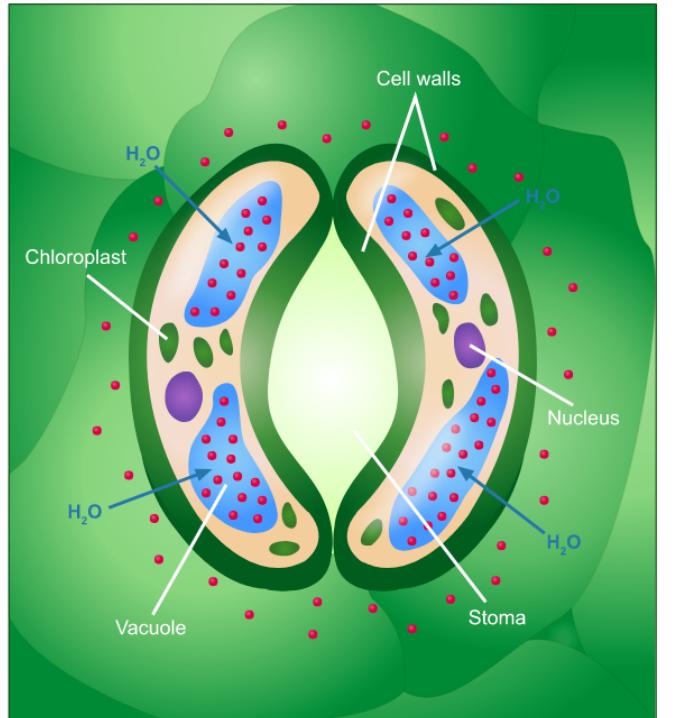
Closed stomata:

Benefits

- Low water outflux

Costs

- Low CO_2 influx



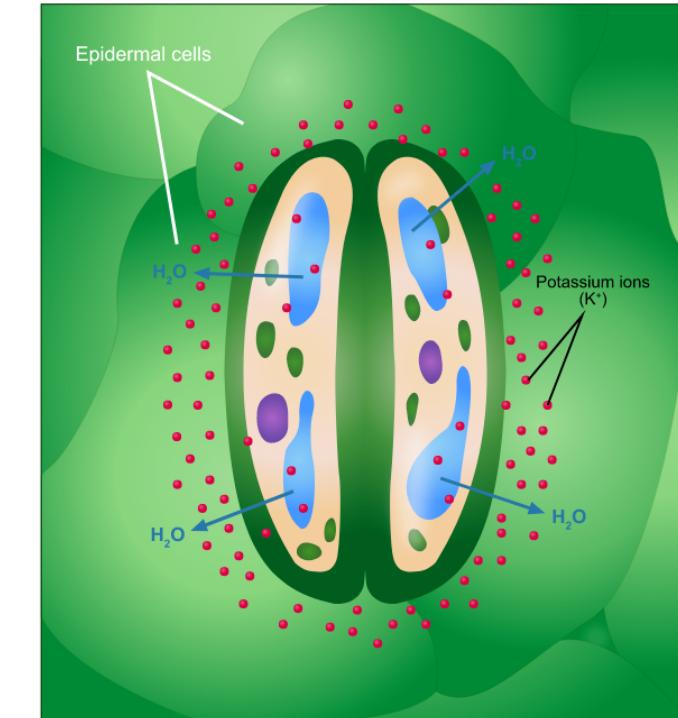
Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux



Closed stomata:

Benefits

- Low water outflux

Costs

- Low CO_2 influx
- Must maintain high amount of Rubisco to do photosynthesis

Optimal stomatal conductance

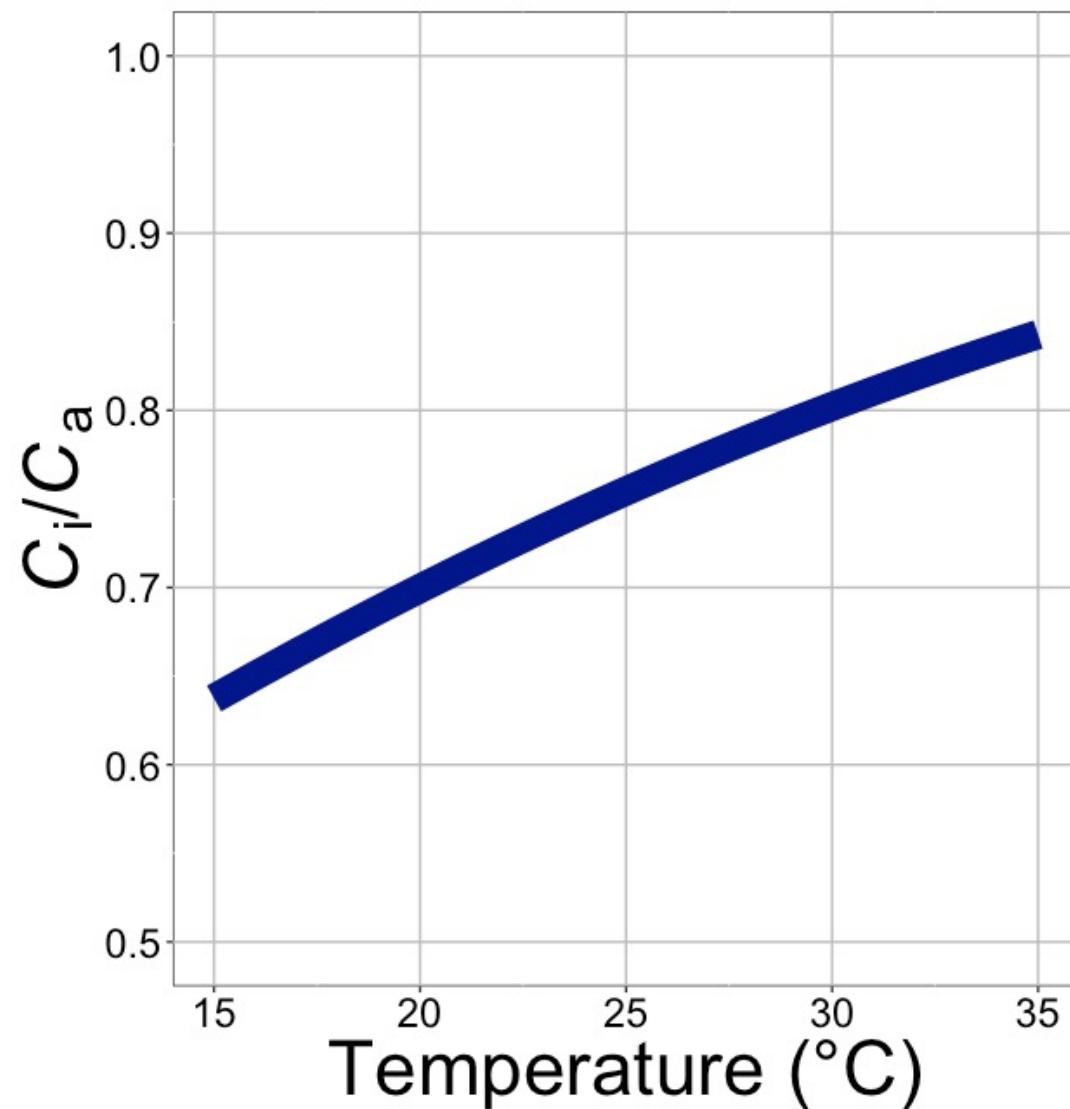
Optimal conductance maximizes photosynthesis
at least water loss and nutrient use

- Water loss is from transpiration
- Nutrient use is nutrients used to maintain Rubisco

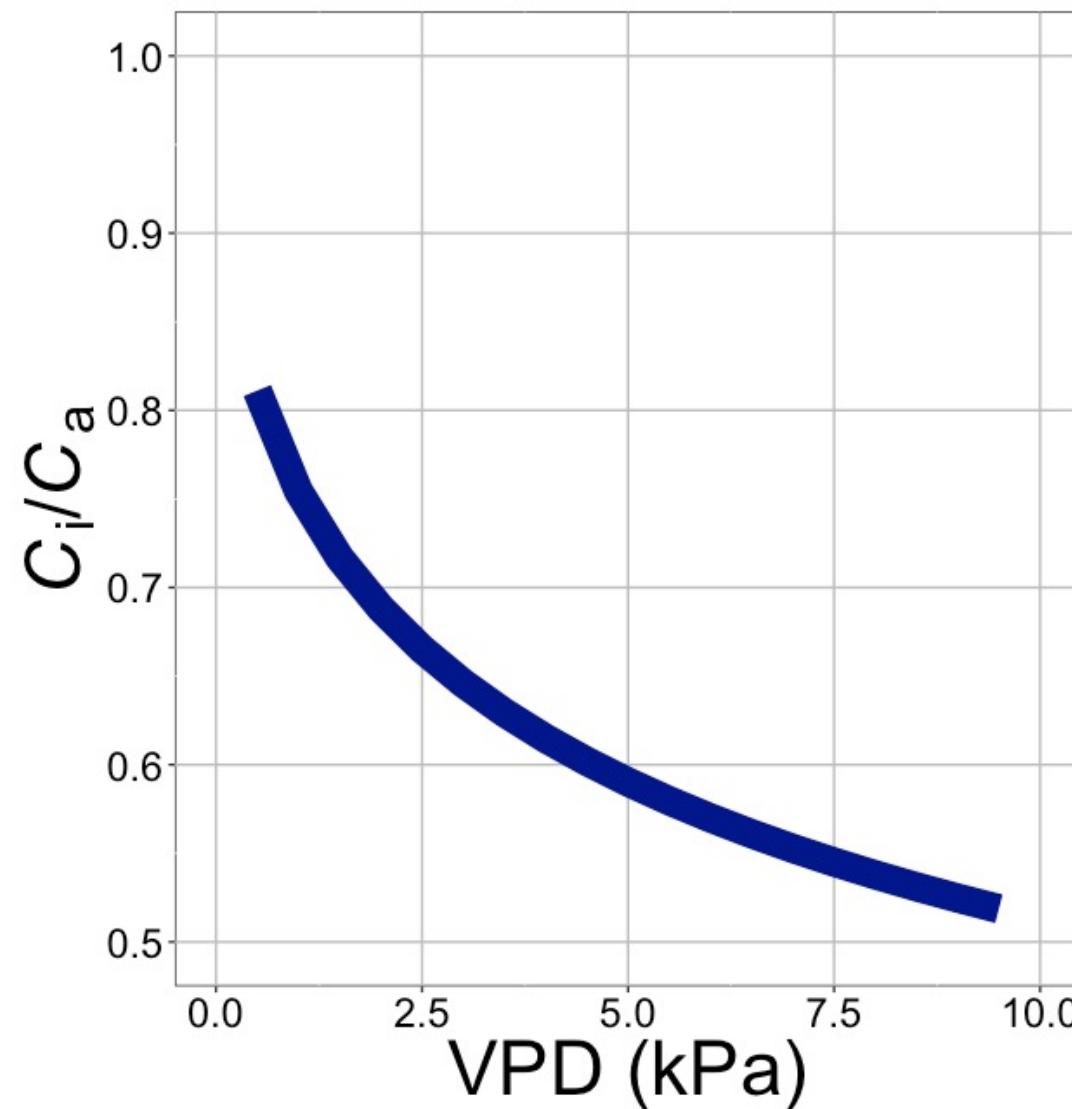
[TALK TO ME LATER ABOUT THE MATHS]

Stomatal conductance trait

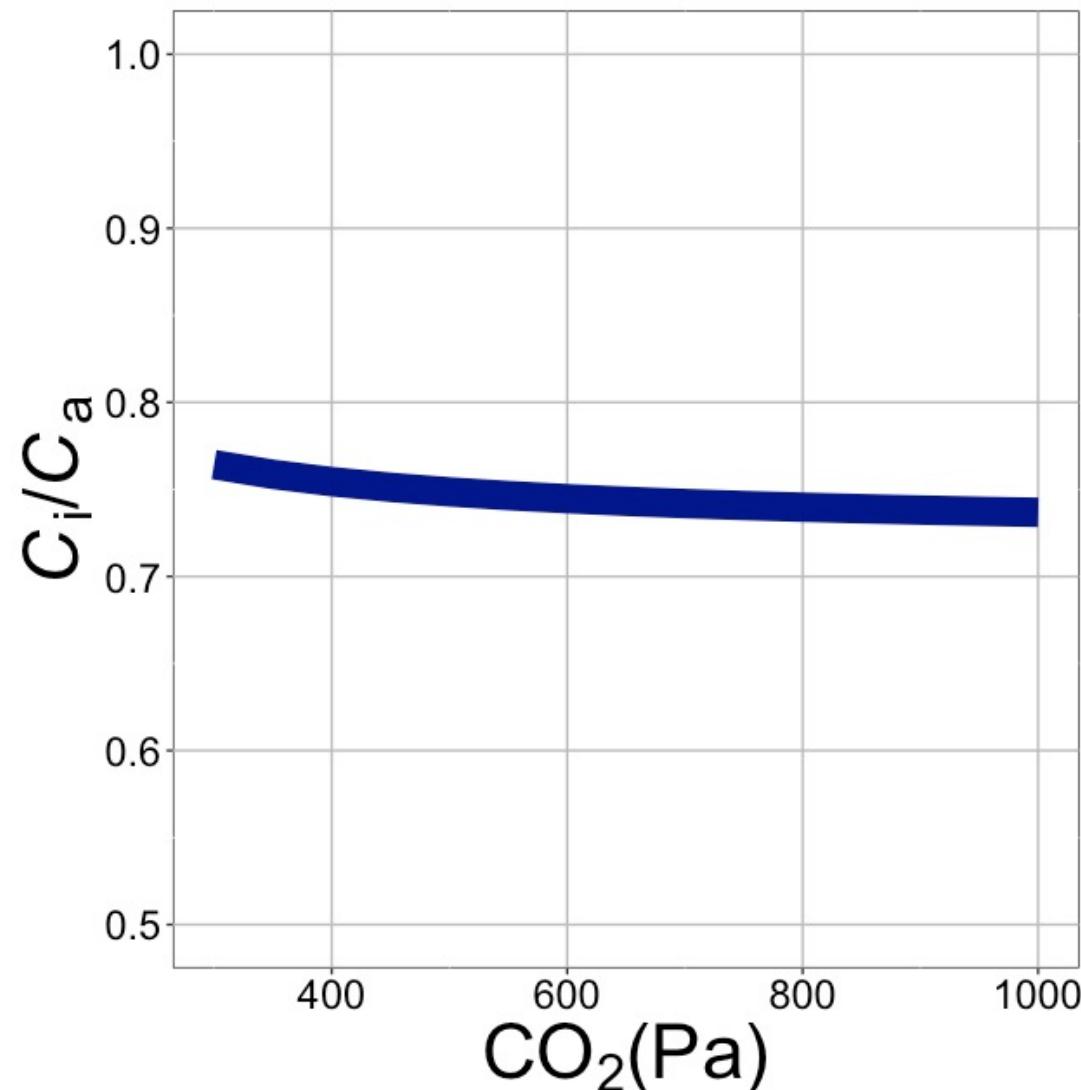
The ratio of CO₂ in the leaf to CO₂ outside of the leaf (C_i/C_a)



C_i/C_a increases
with temperature
because of greater
photorespiration



C_i/C_a decreases
with VPD to avoid
water loss



C_i/C_a decreases
with CO_2 because
of lower openness
needed to satisfy
Rubisco