Plants aren’t dumb

Using optimality theory to understand big questions in plant ecophysiology

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Acknowledgements

- Current lab members
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  - Brad Posch (postdoc)
  - Evan Perkowski (PhD student)
  - Zinny Ezekannagha (PhD student)
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  - Lizz Waring (postdoc; now Asst. Prof at Northeastern State U)
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  - USGS
  - Schmidt Futures

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Why do people care about plants?

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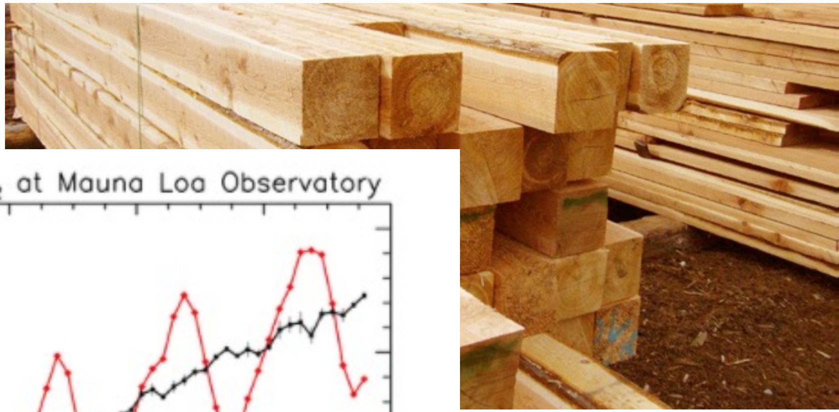

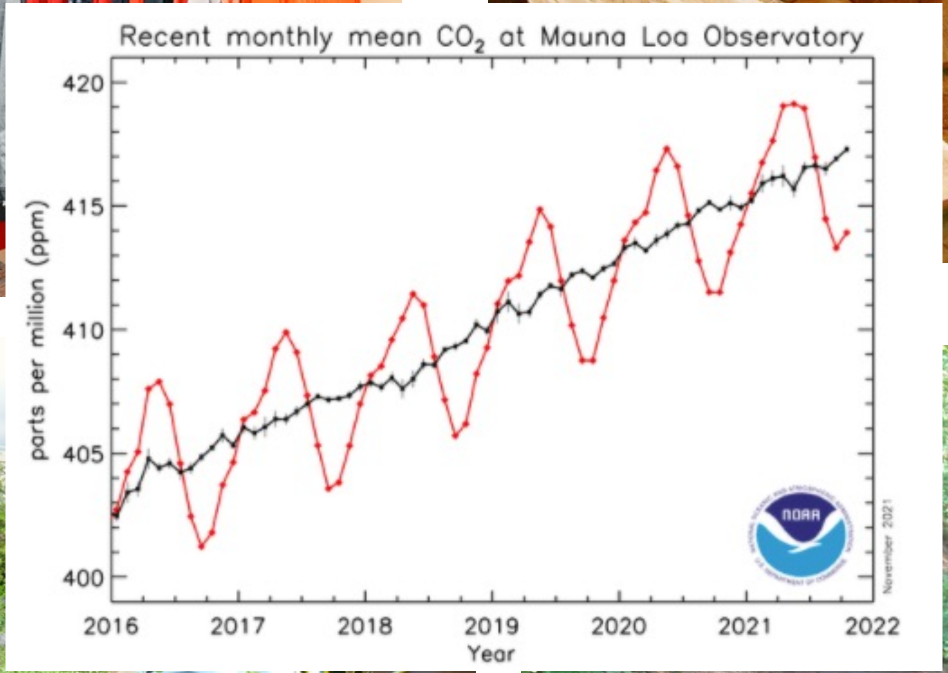

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In other words: plants provide ecosystem services

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Including photosynthesis

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Photosynthesis provides the foundation for other services

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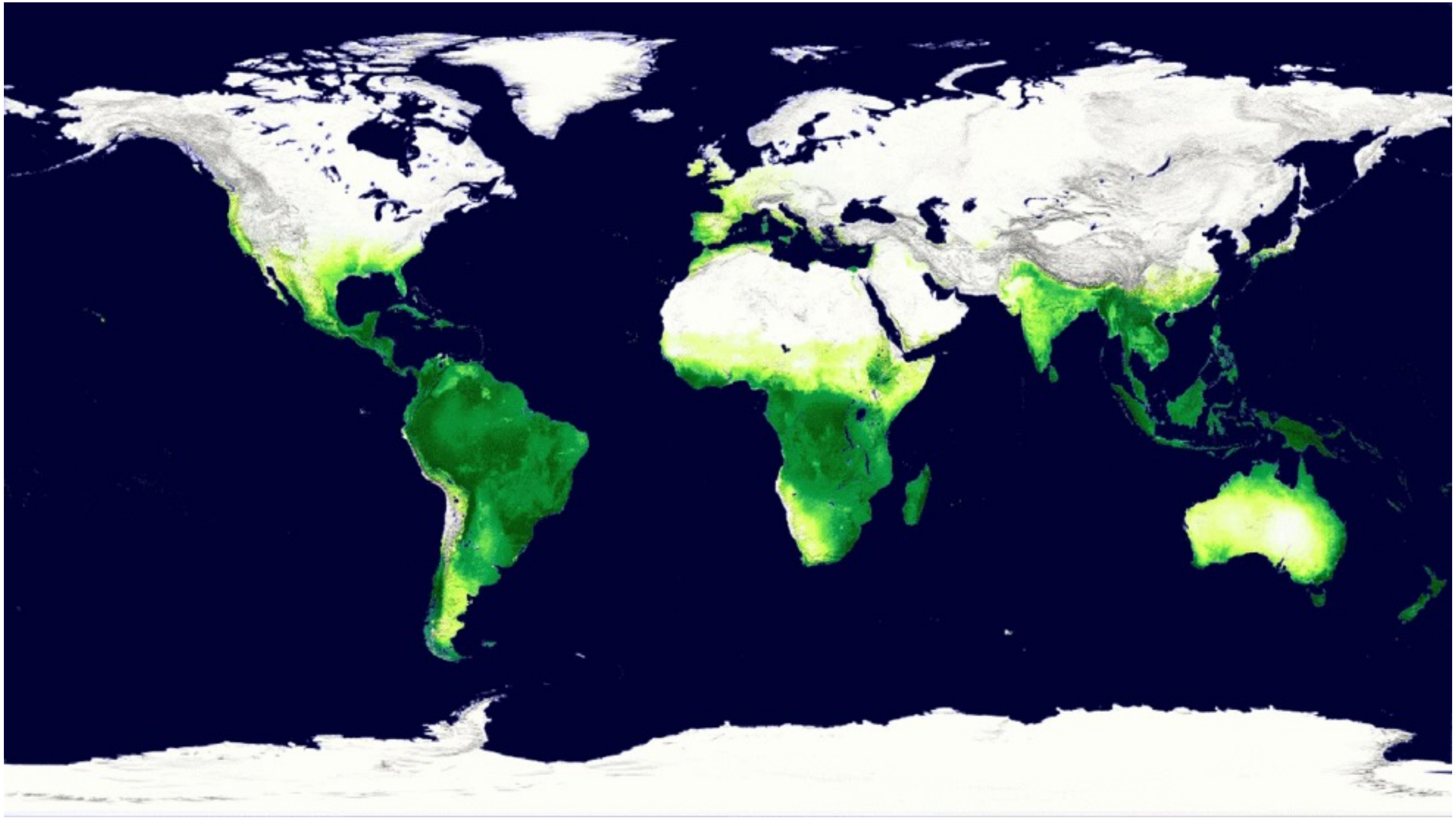
Photosynthesis is a dynamic process



MODIS, NASA

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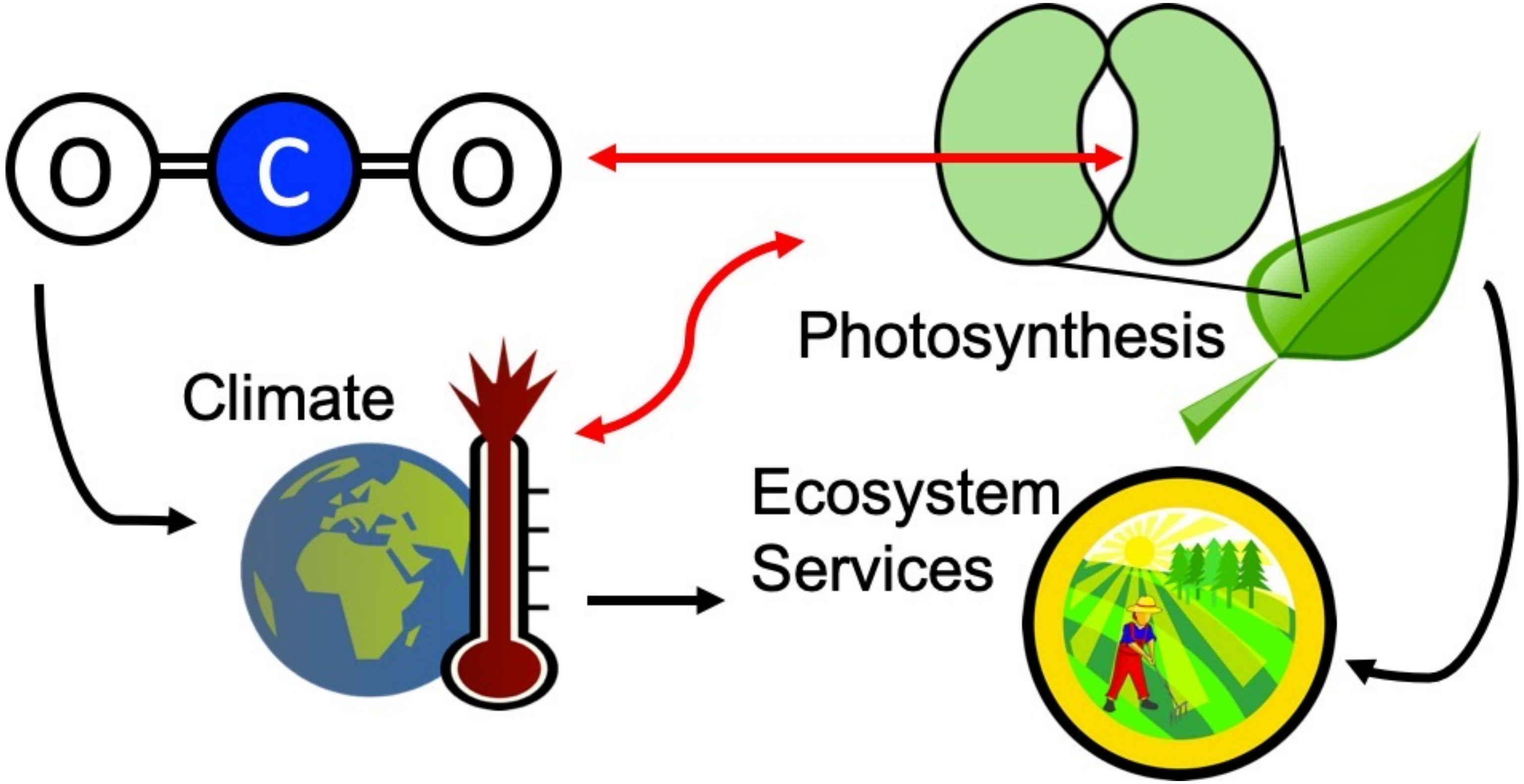
Our lab examines photosynthesis as a regulator of global change impacts on ecosystem services



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Photosynthesis is important! An example…

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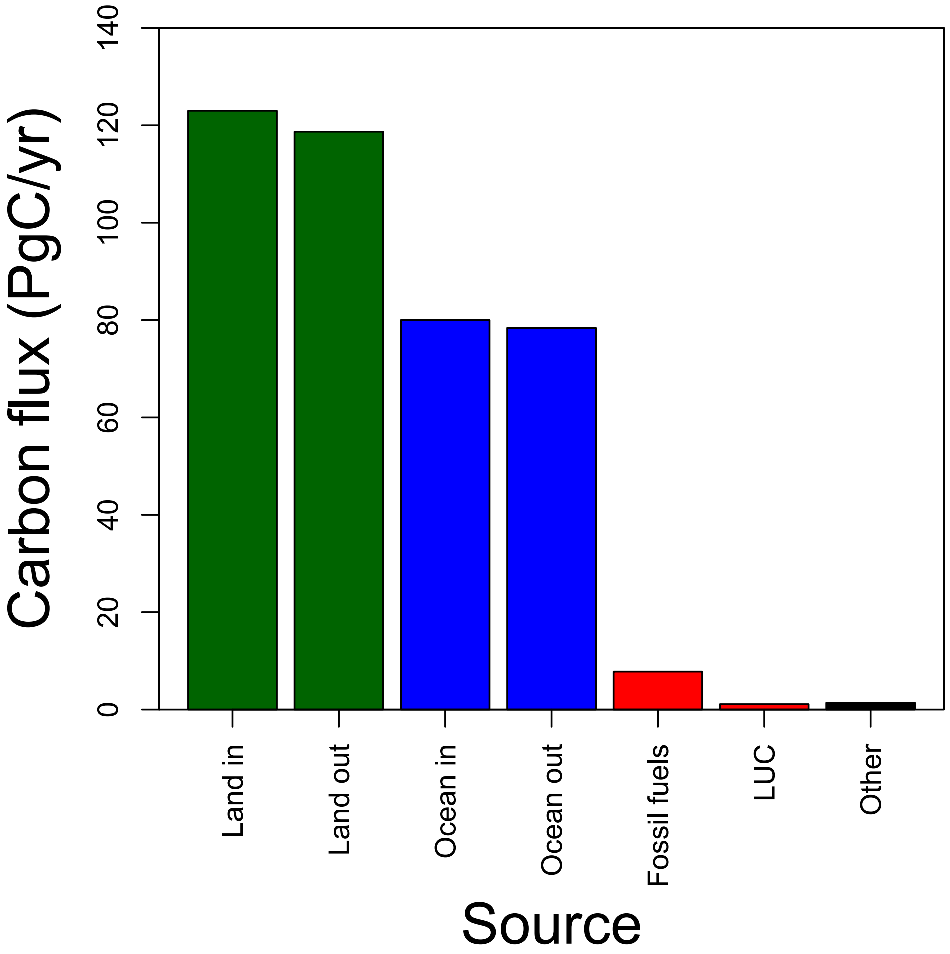
Photosynthesis is important! An example…



Data from IPCC (2013)

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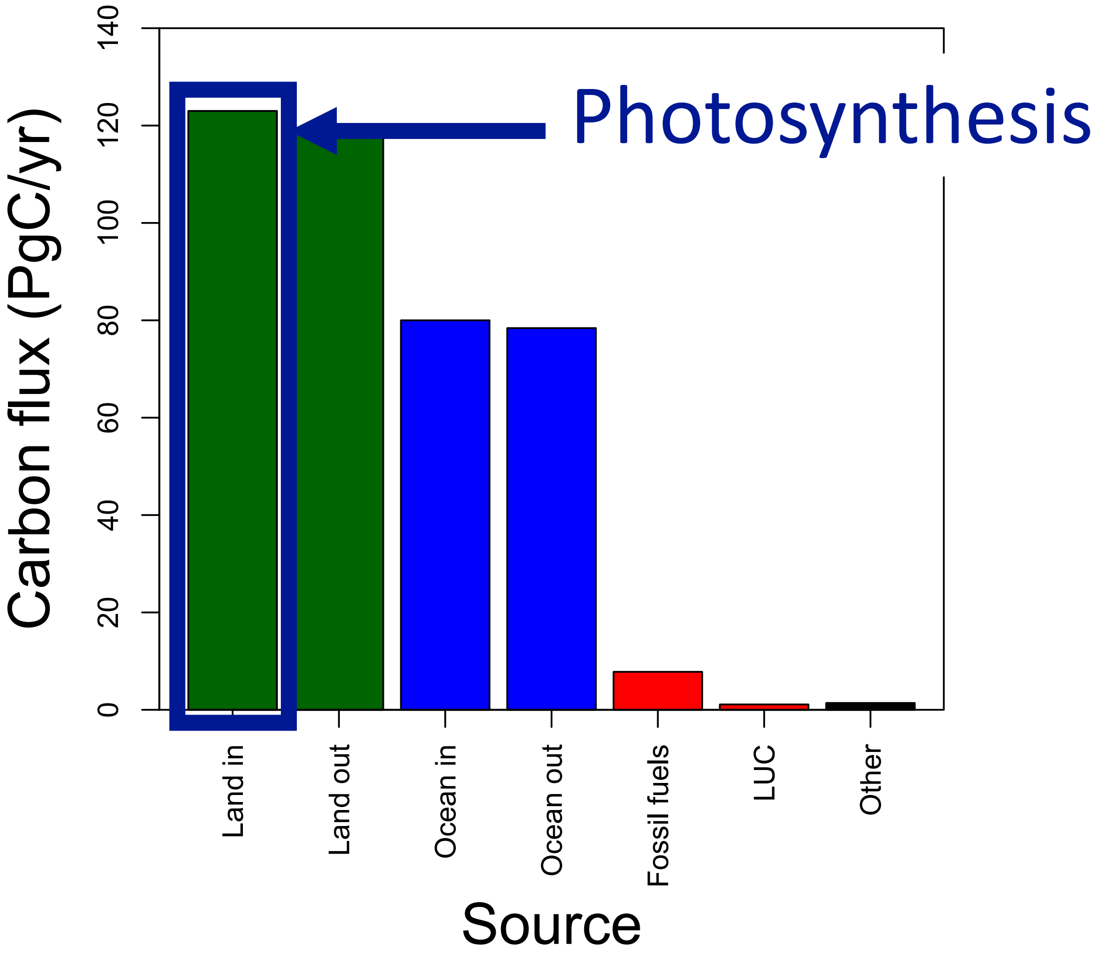
Photosynthesis is important! An example…



Data from IPCC (2013)

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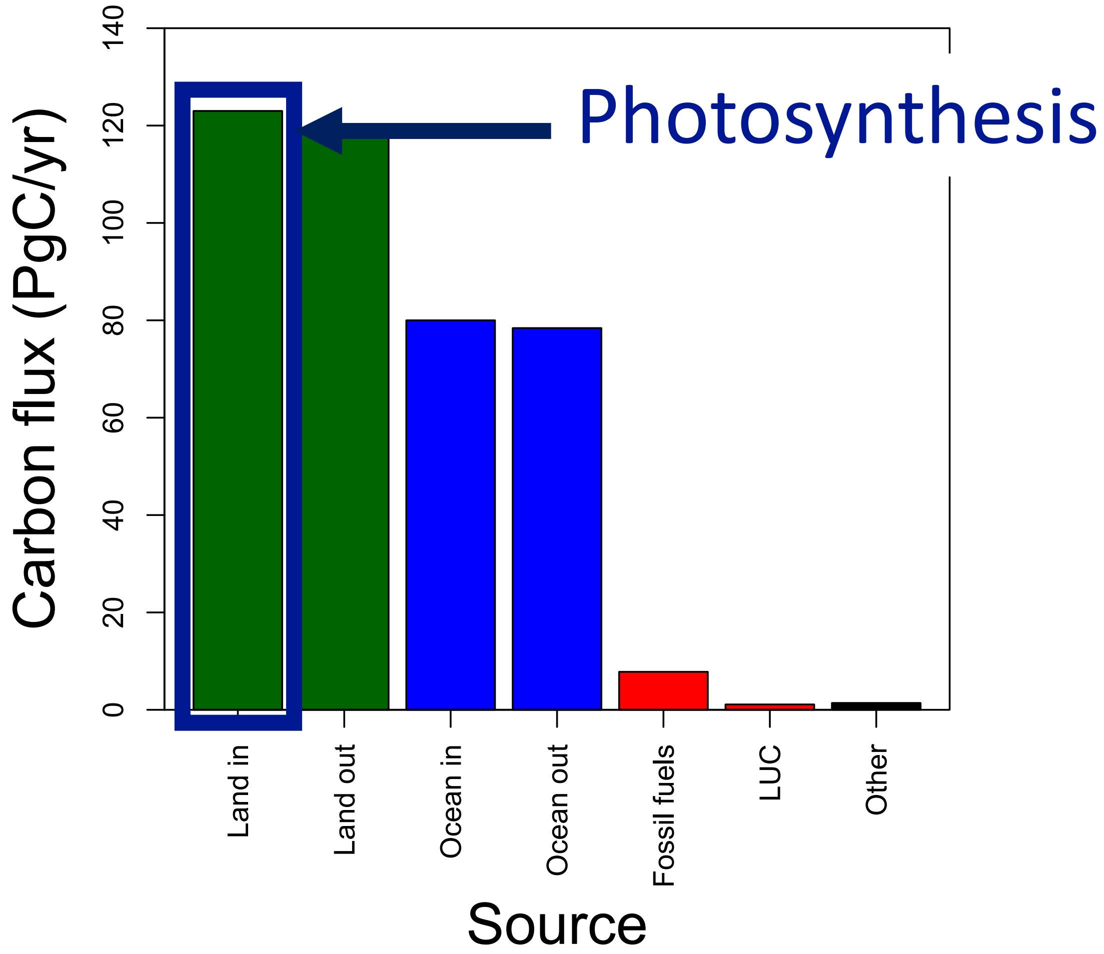
Photosynthesis is important! An example…



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

Data from IPCC (2013)

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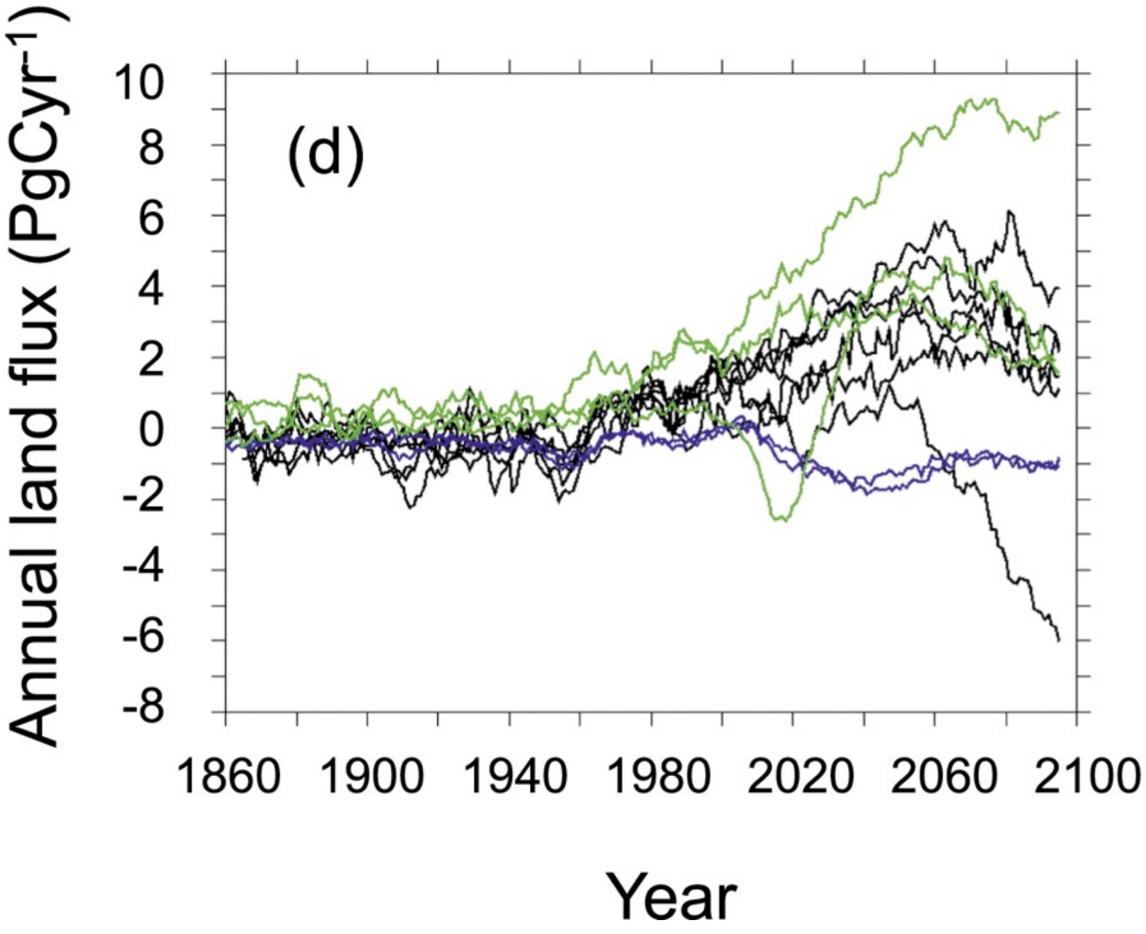
But predictions are uncertain!



Friedlingstein et al. (2014)

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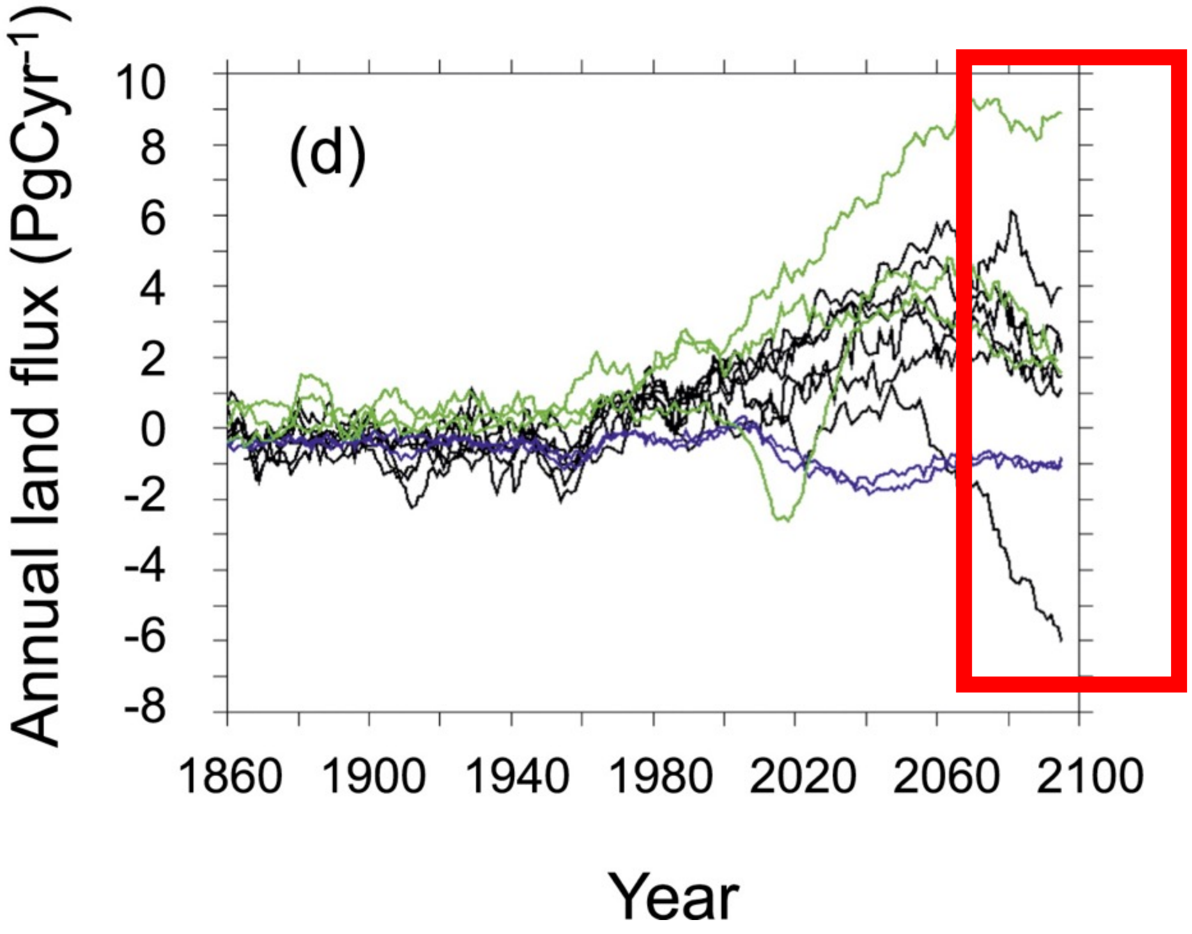
But predictions are uncertain!



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

Friedlingstein et al. (2014)

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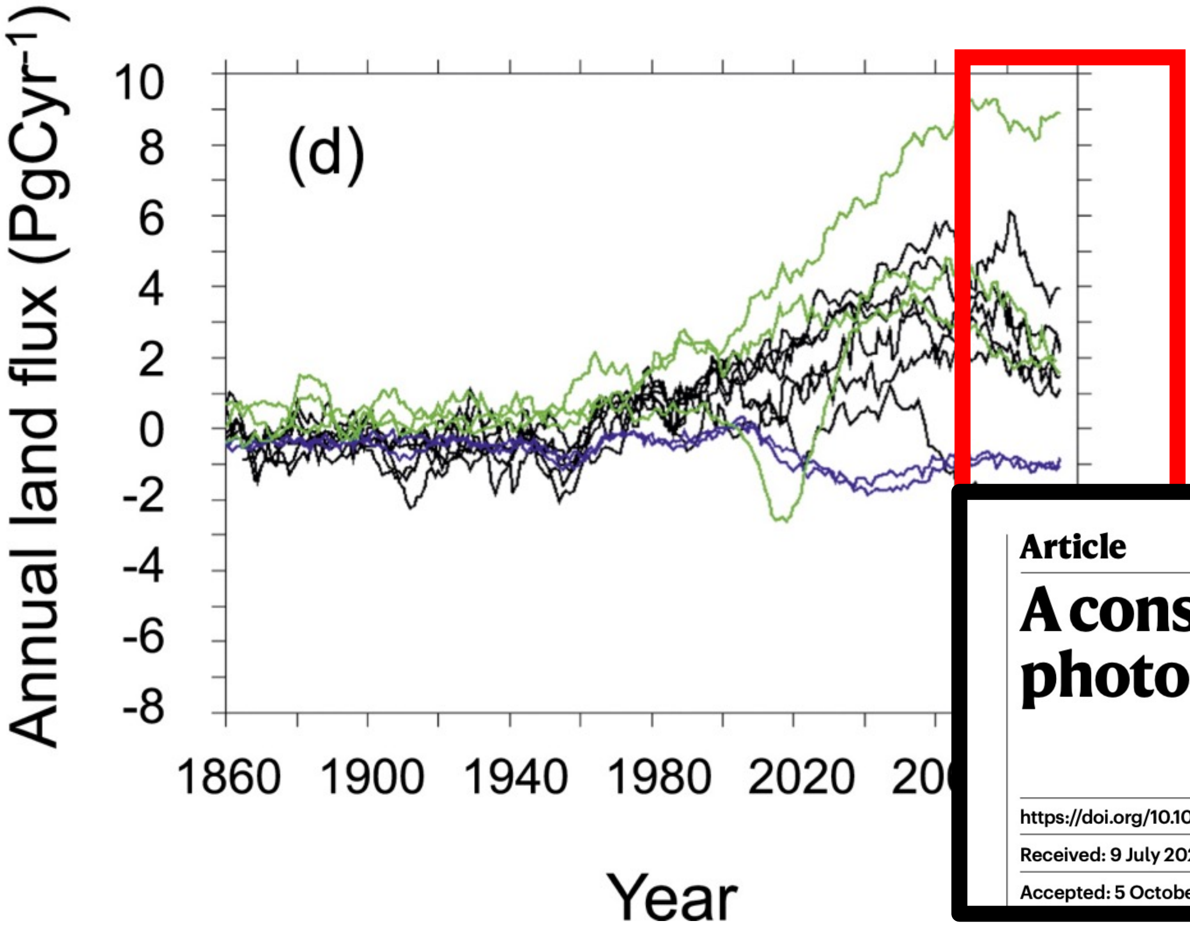
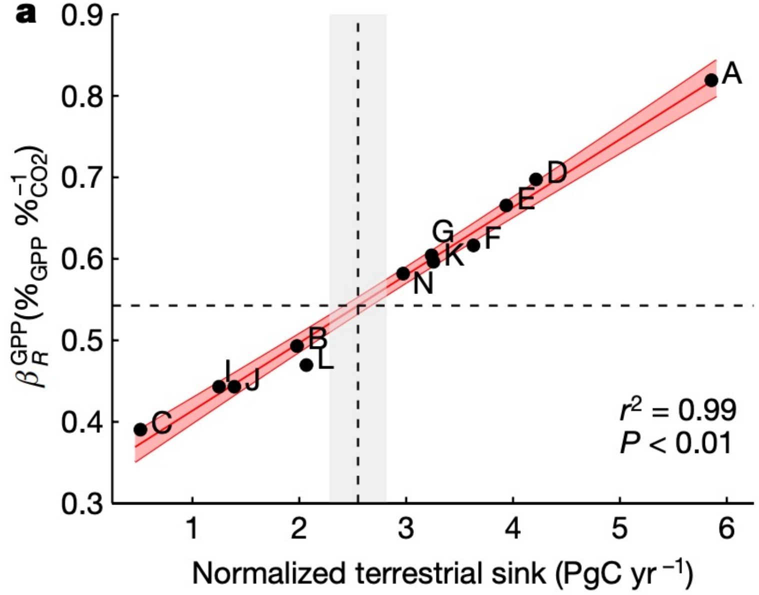
This uncertainty is driven by uncertainty in photosynthesis



Friedlingstein et al. (2014)



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. Medlyn[7], I. C. Prentice[8,9,10], B. D. Stocker[11,12], N. G. Smith[13], C. Terrer[14], H. Wang[10], Y. Zhang[1,2,15] & S. Zhou[1,2,16,17,18,19]

Keenan et al. (2021)

Why the uncertainty? Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

Planta
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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

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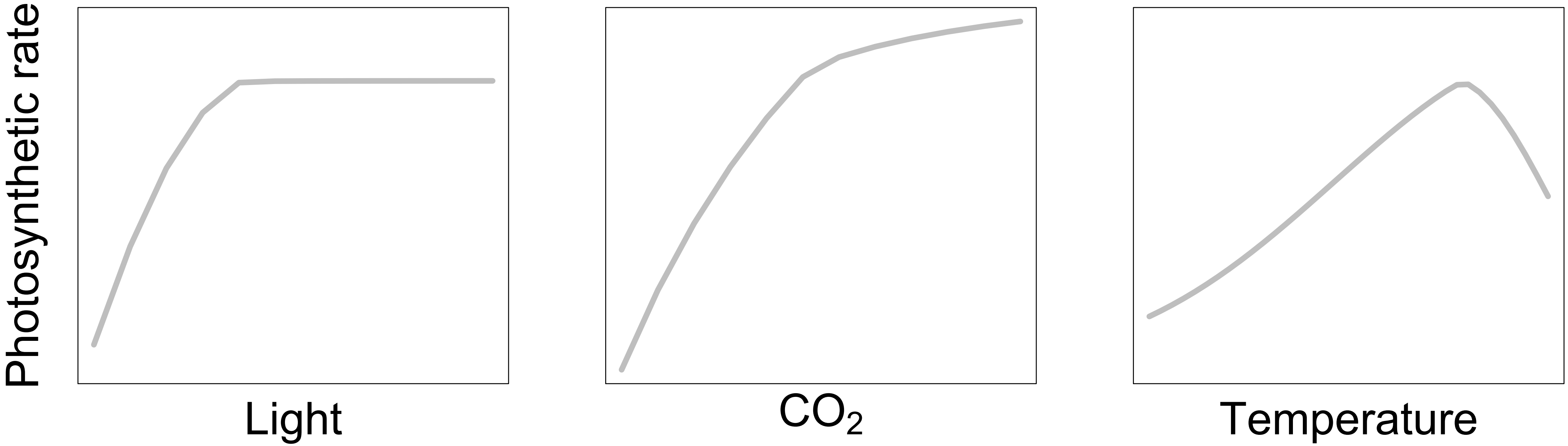
These produce short term responses that match data



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

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Dumb plants

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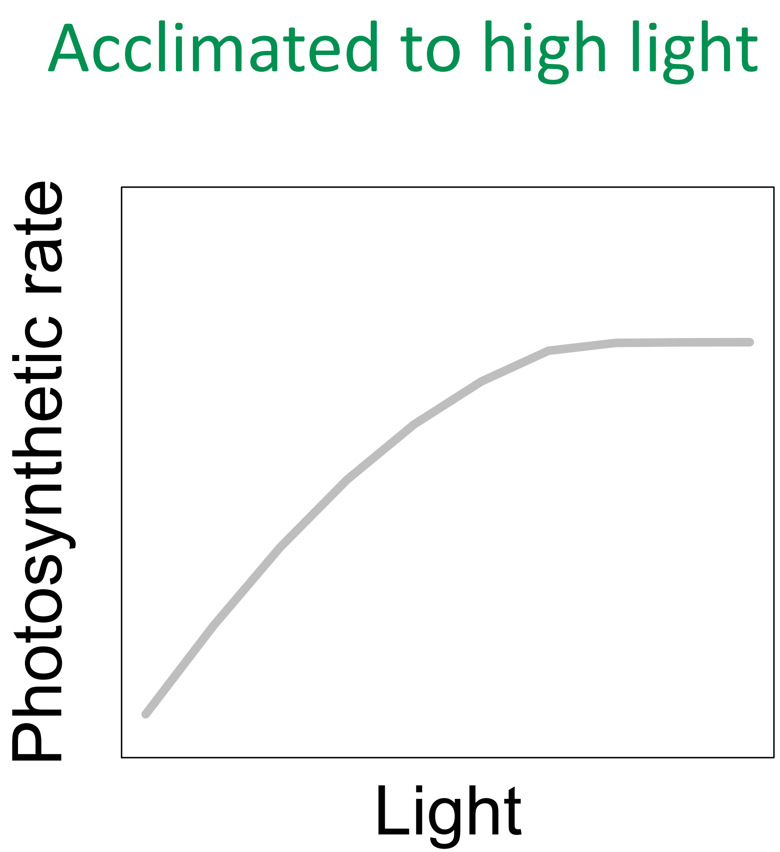

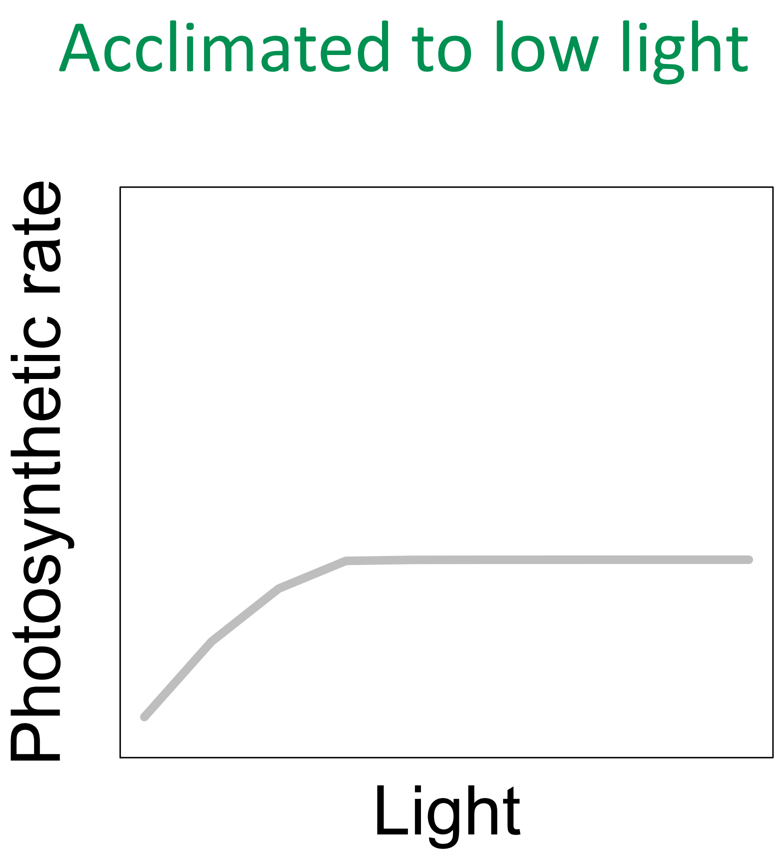

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Acclimation is ubiquitous and well known…

CO_2: Bazzaz (1990)

Annu. Rev. Ecol. Syst. 1990. 21:167–96
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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
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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 Björkman[1]

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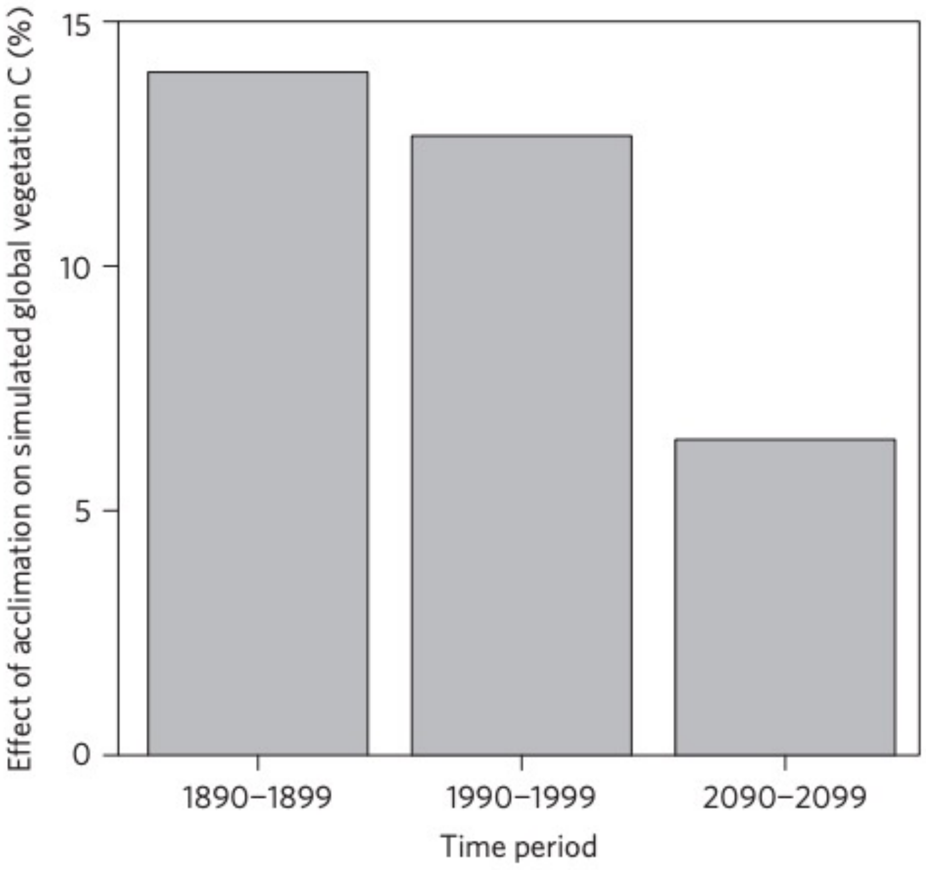
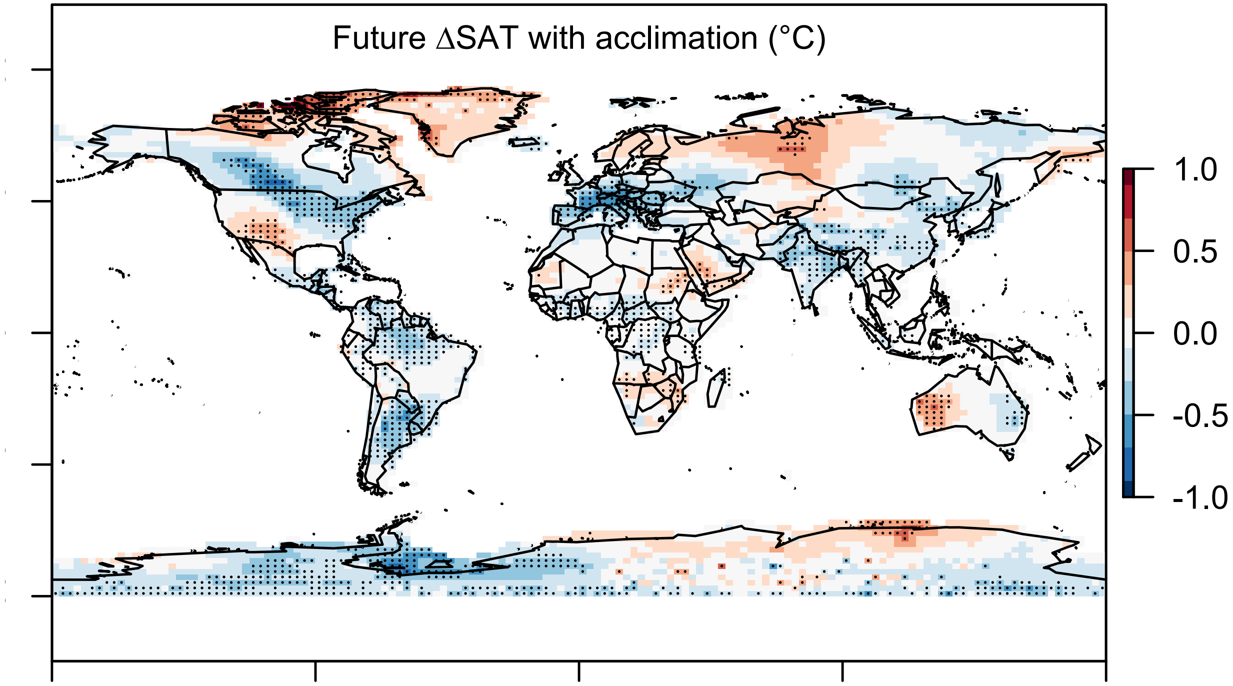
…and can impact carbon cycling and climate

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*

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Unfortunately,
no theoretical model for
photosynthetic acclimation exists

Lack of theory results in…

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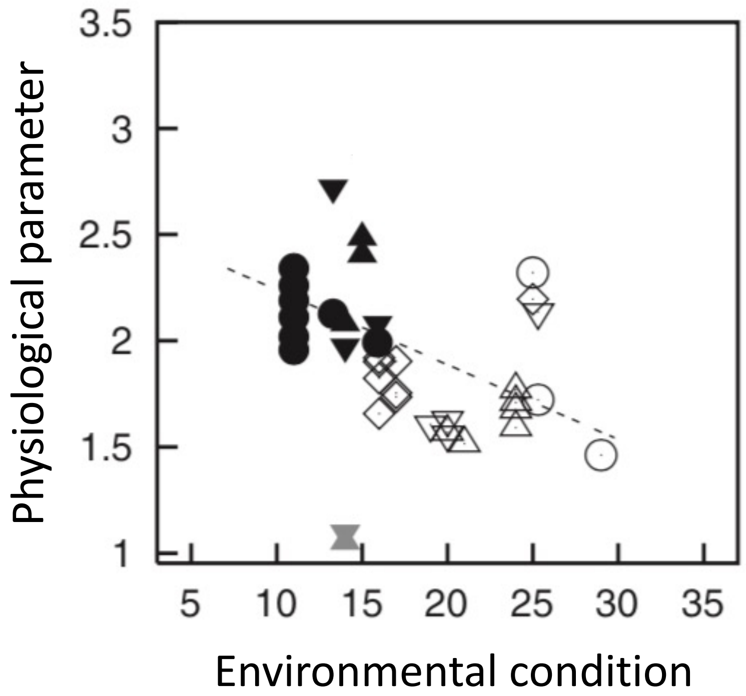
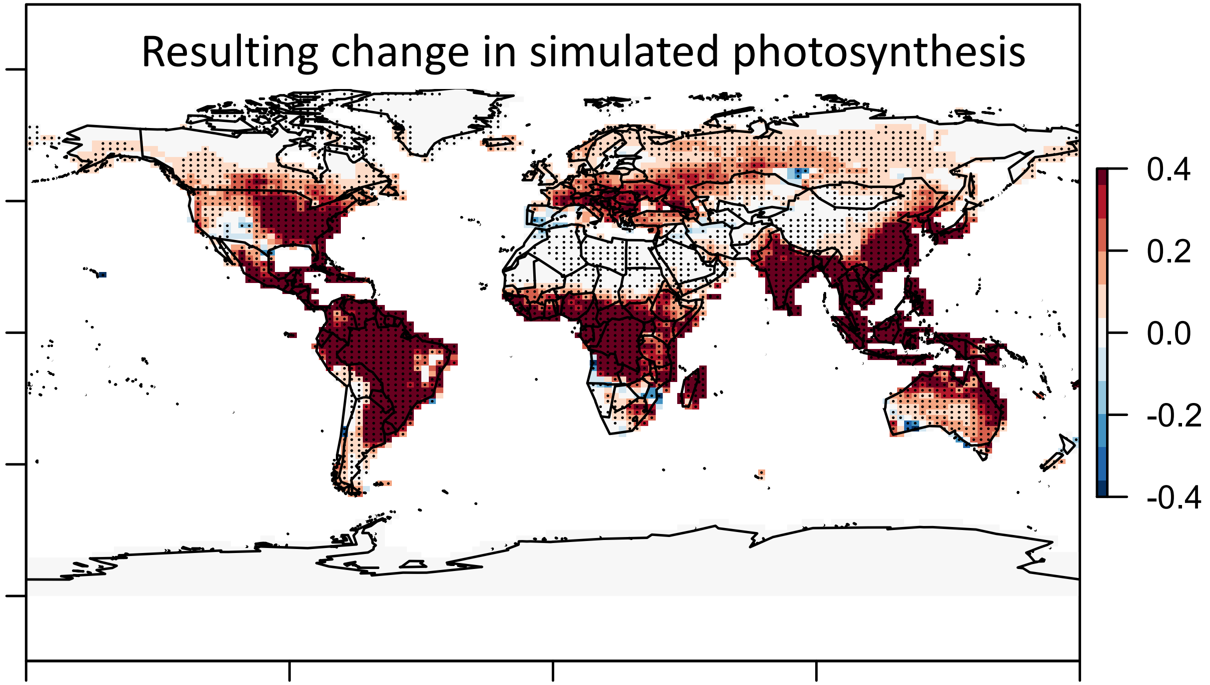
Lack of theory results in…

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



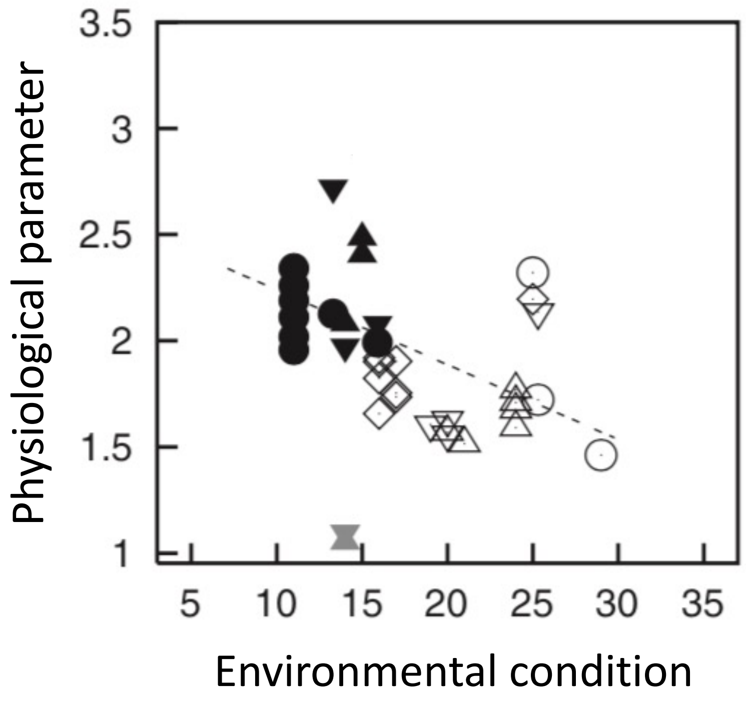


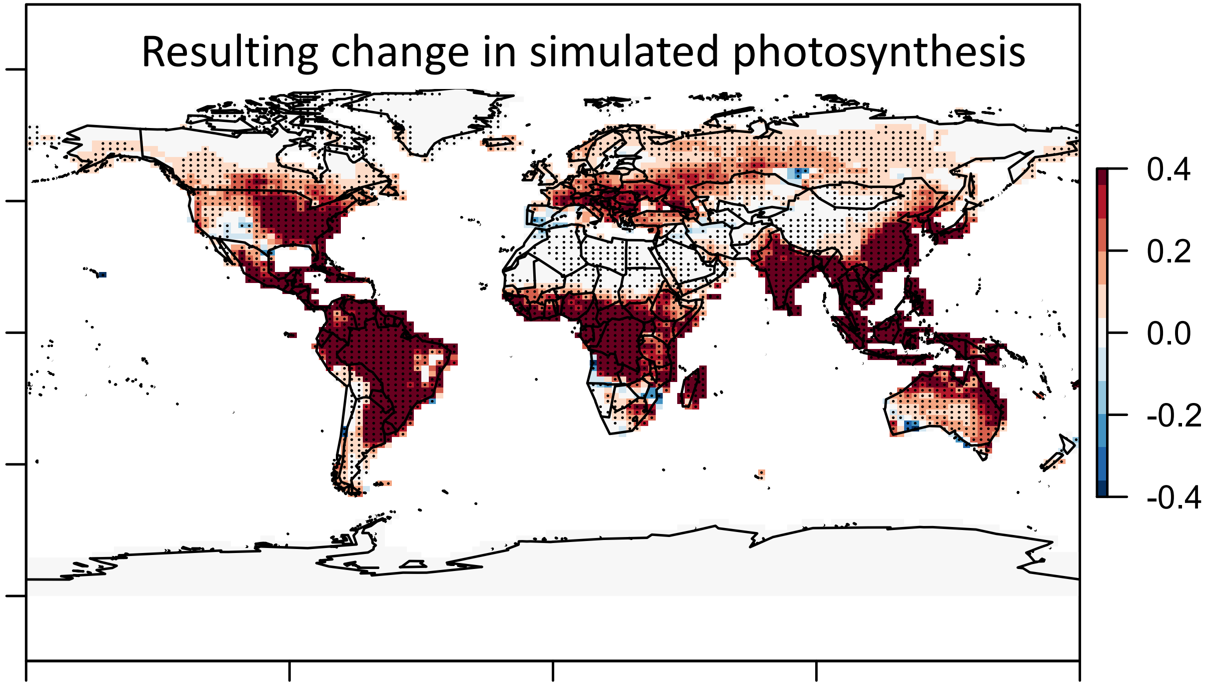
Kattge and Knorr (2007) *PC&E*

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*

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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

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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)

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Optimal photosynthesis

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

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Optimal photosynthesis

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

Must predict optimal rates of both

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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)

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Optimal photosynthesis

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

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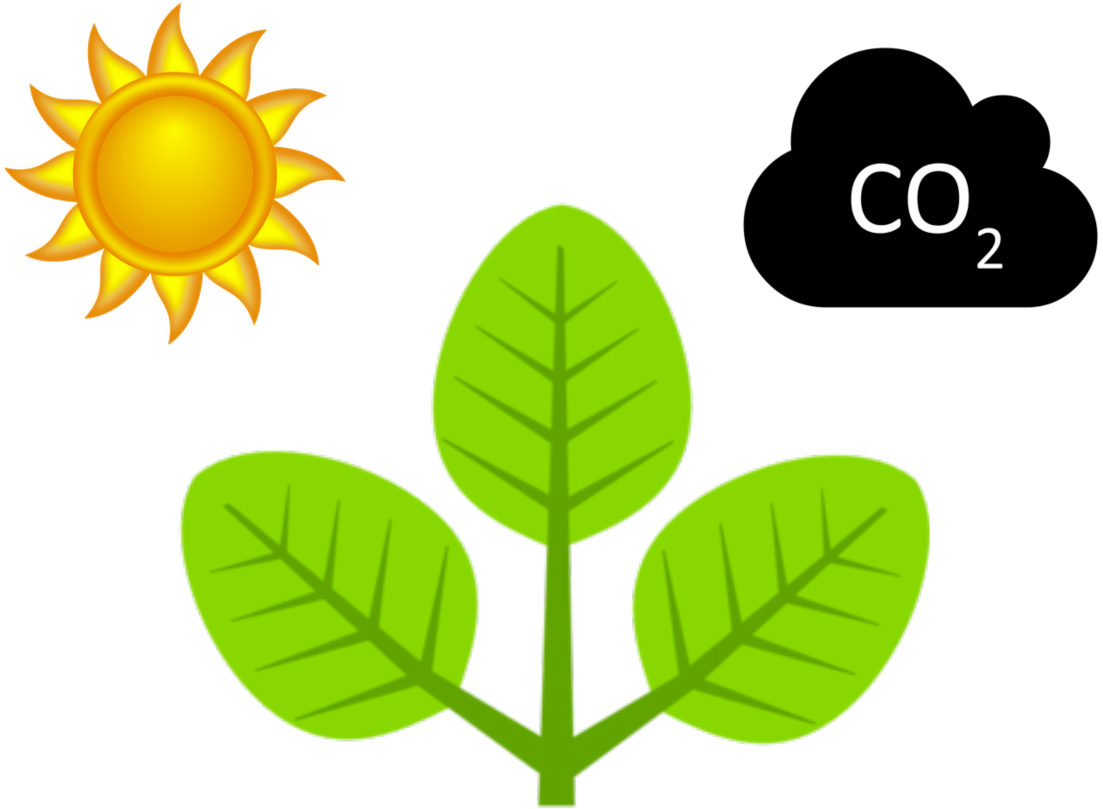
Biochemistry optimization



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})

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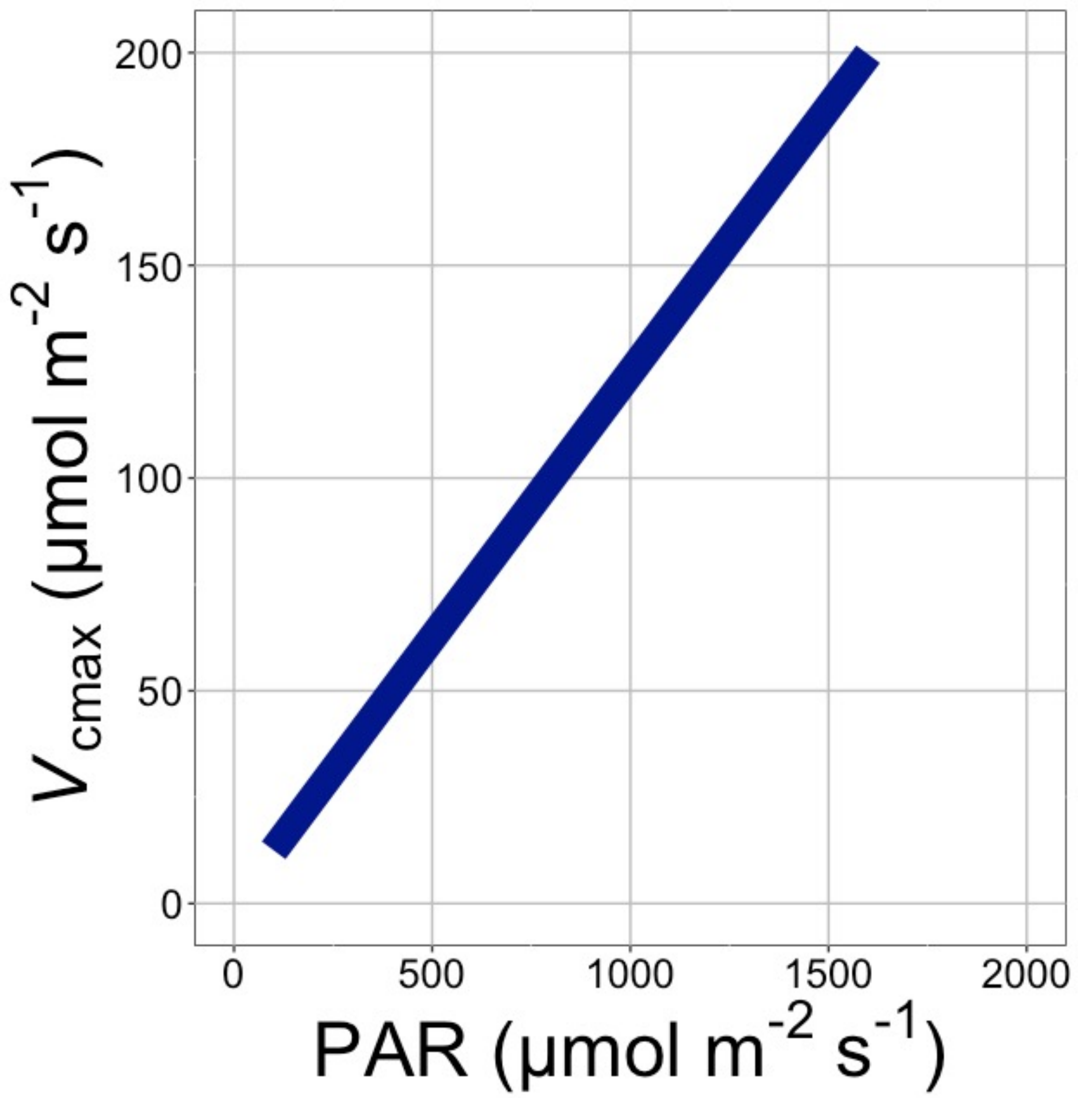

V_{cmax} increases with light because of greater electron transport

Smith et al. (2019)

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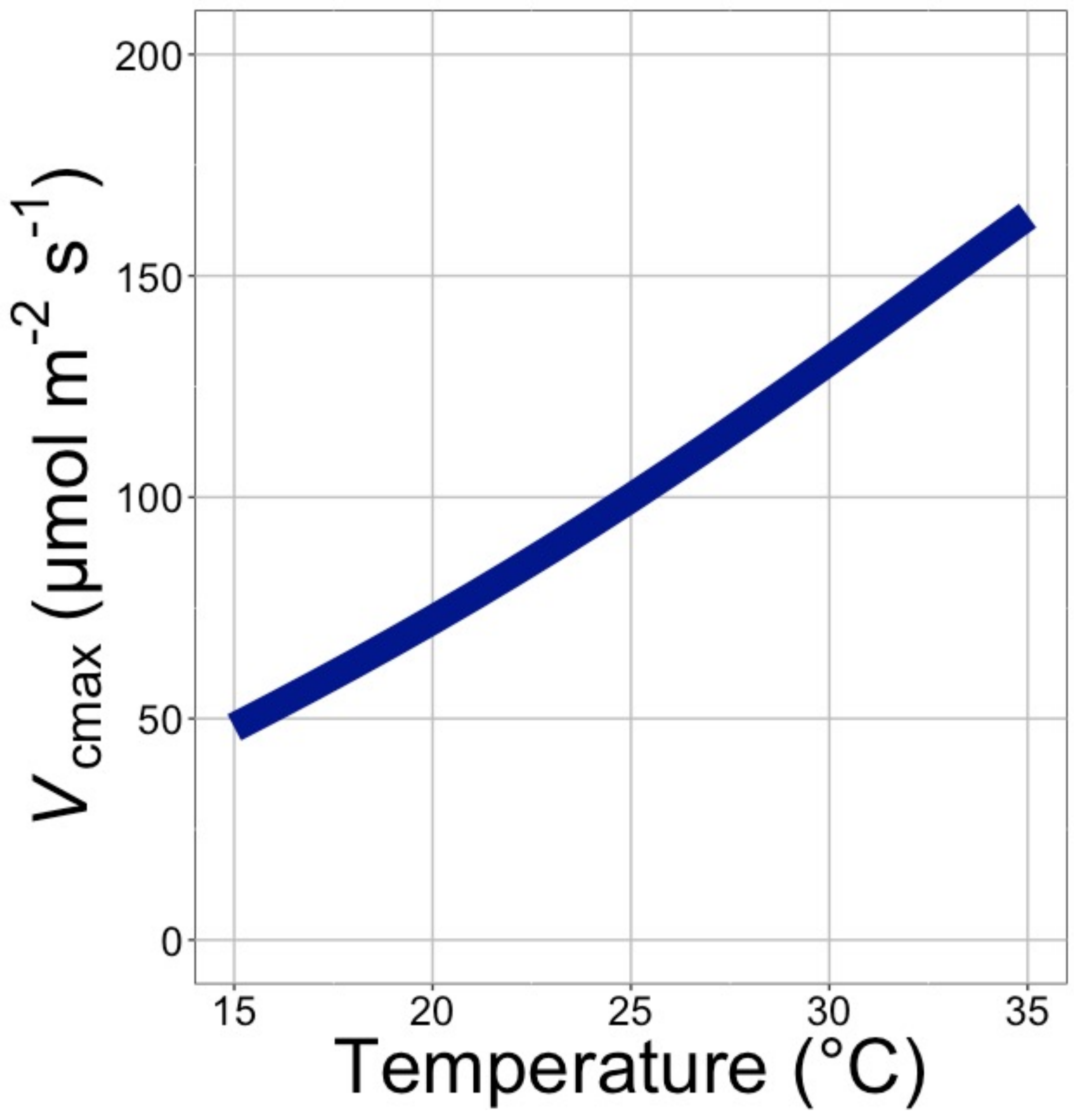

V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019)

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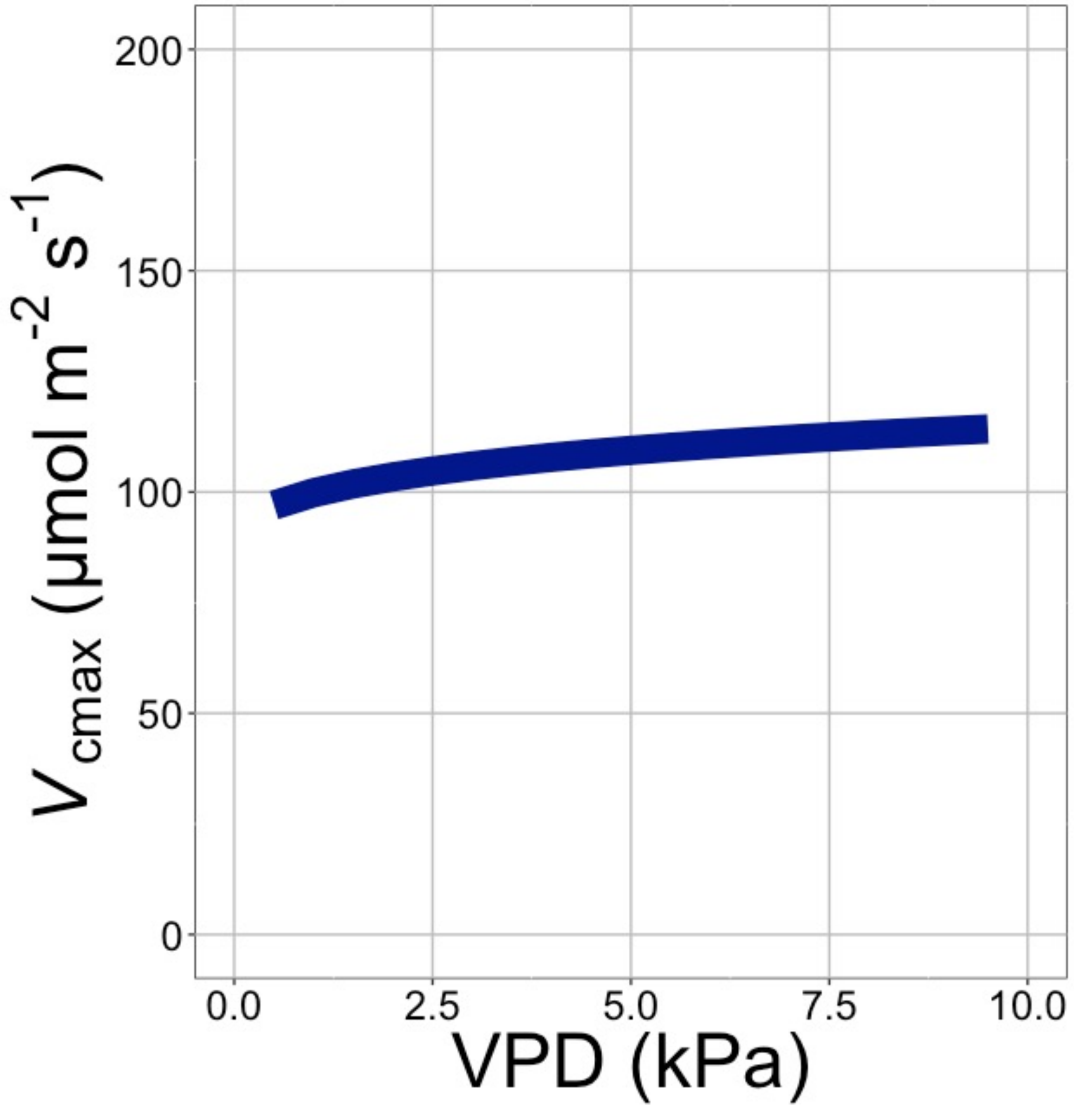

V_{cmax} increases with VPD because of lower stomatal conductance

Smith et al. (2019)

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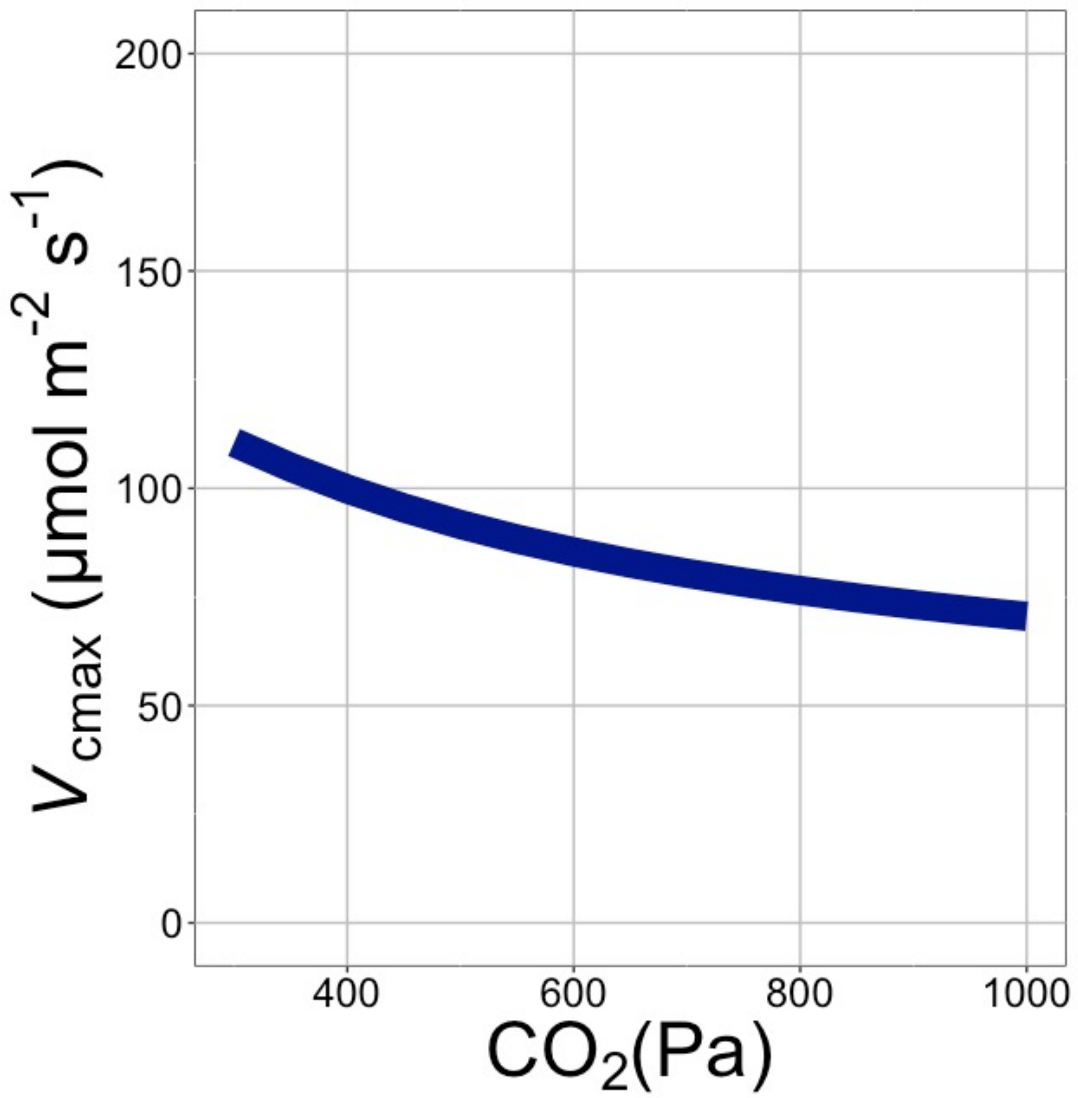

V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf

Smith et al. (2019)

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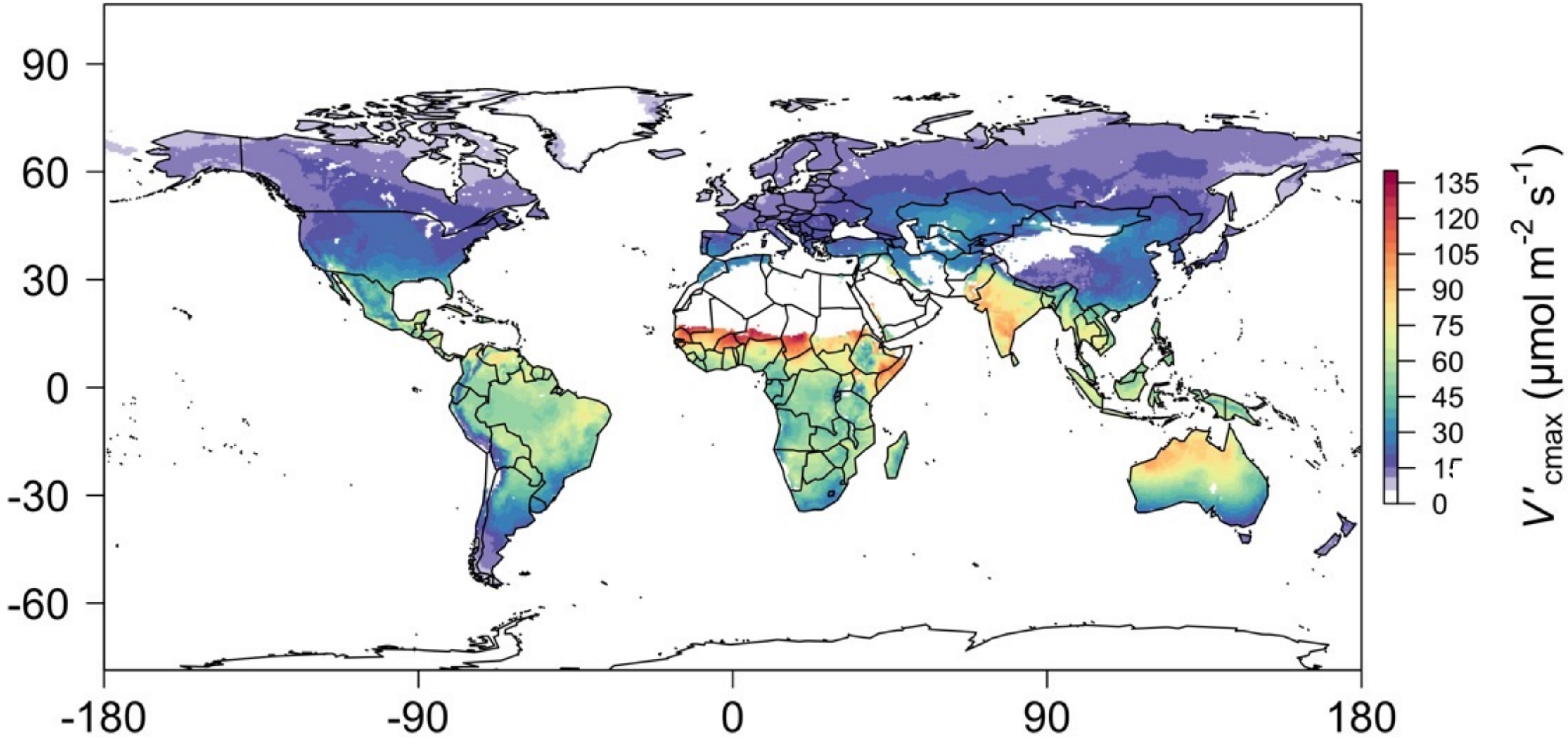
We can predict optimal traits in different environments



Smith et al. (2019)

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Ok, great, but now what?

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

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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 C_4 photosynthesis an advantage over C_3 photosynthesis?

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Question 1: Is photosynthesis optimized to the environment?

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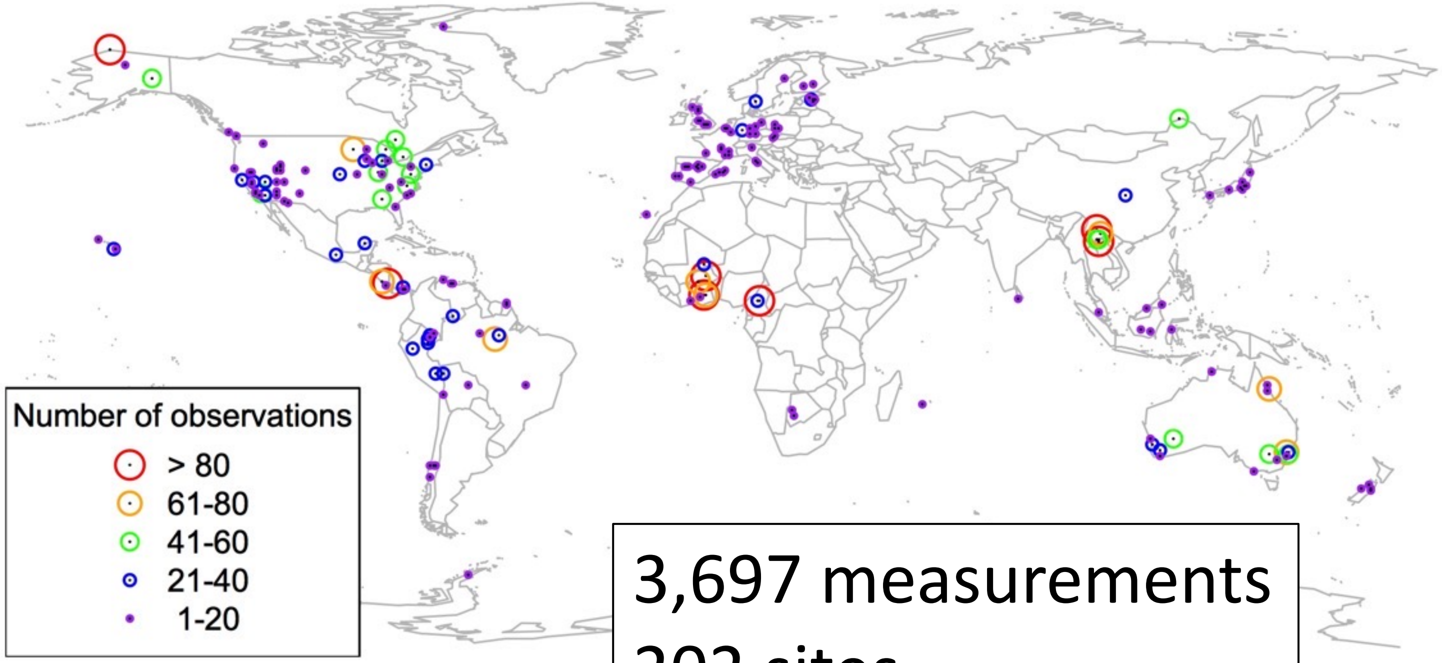
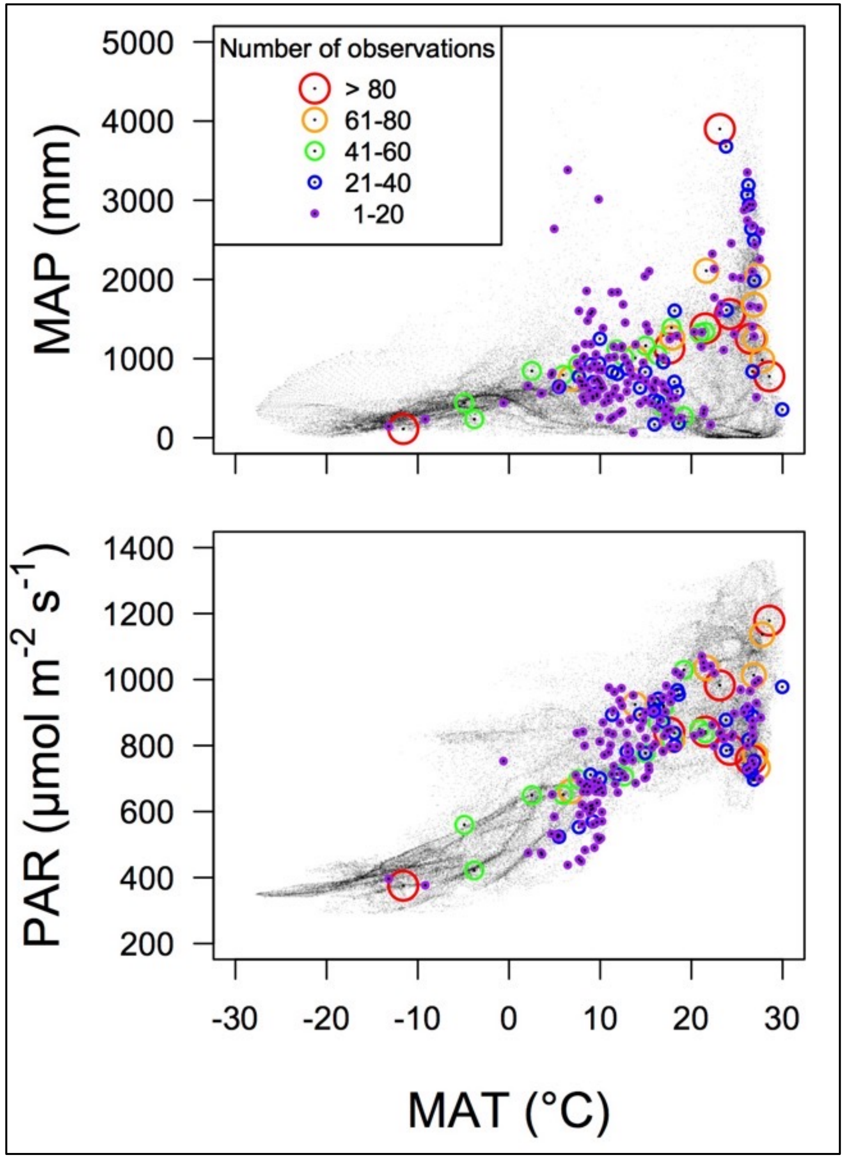
Global V_{cmax} dataset



3,697 measurements
202 sites
> 600 genera



Smith et al. (2019)

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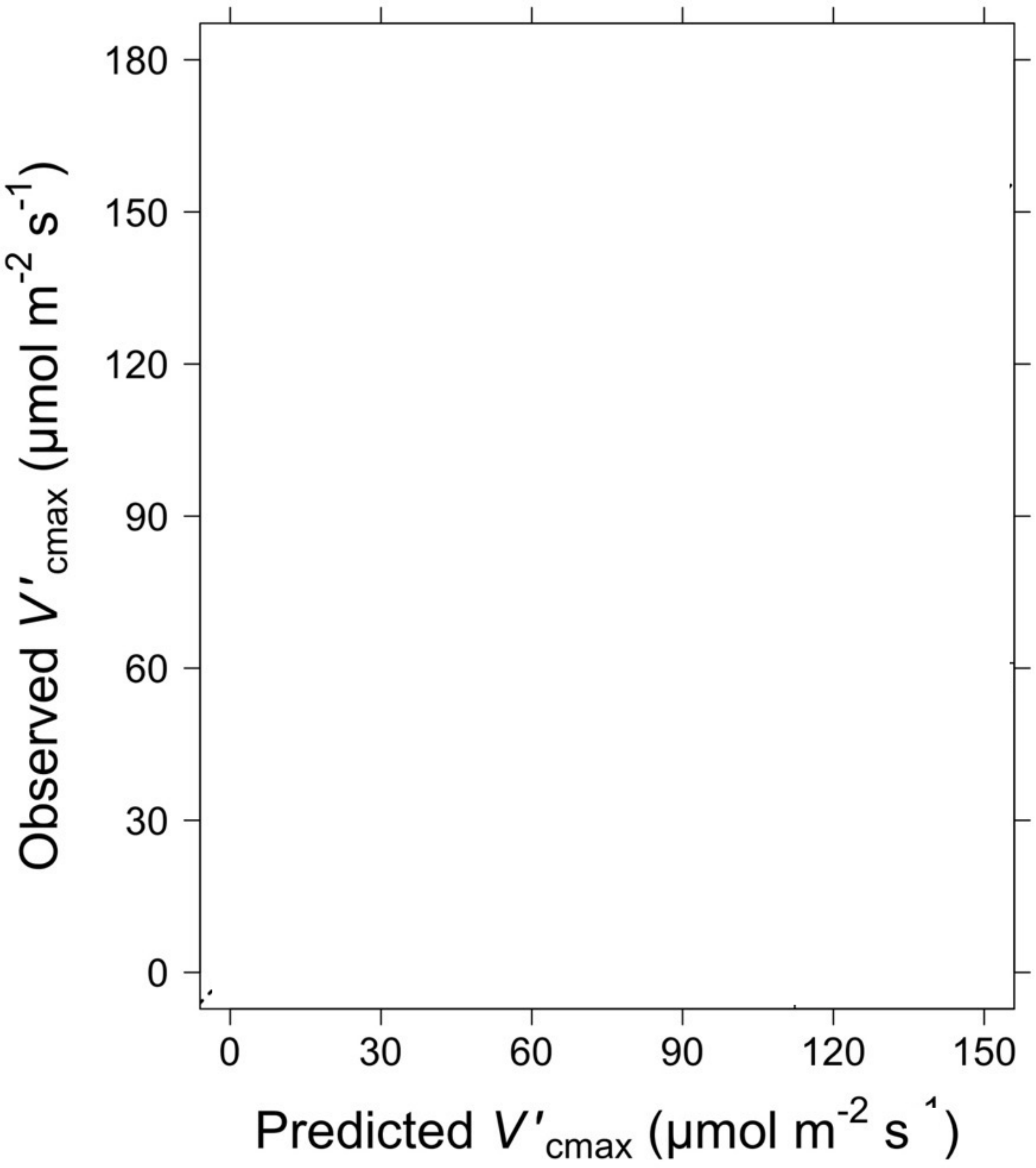

Smith et al. (2019)

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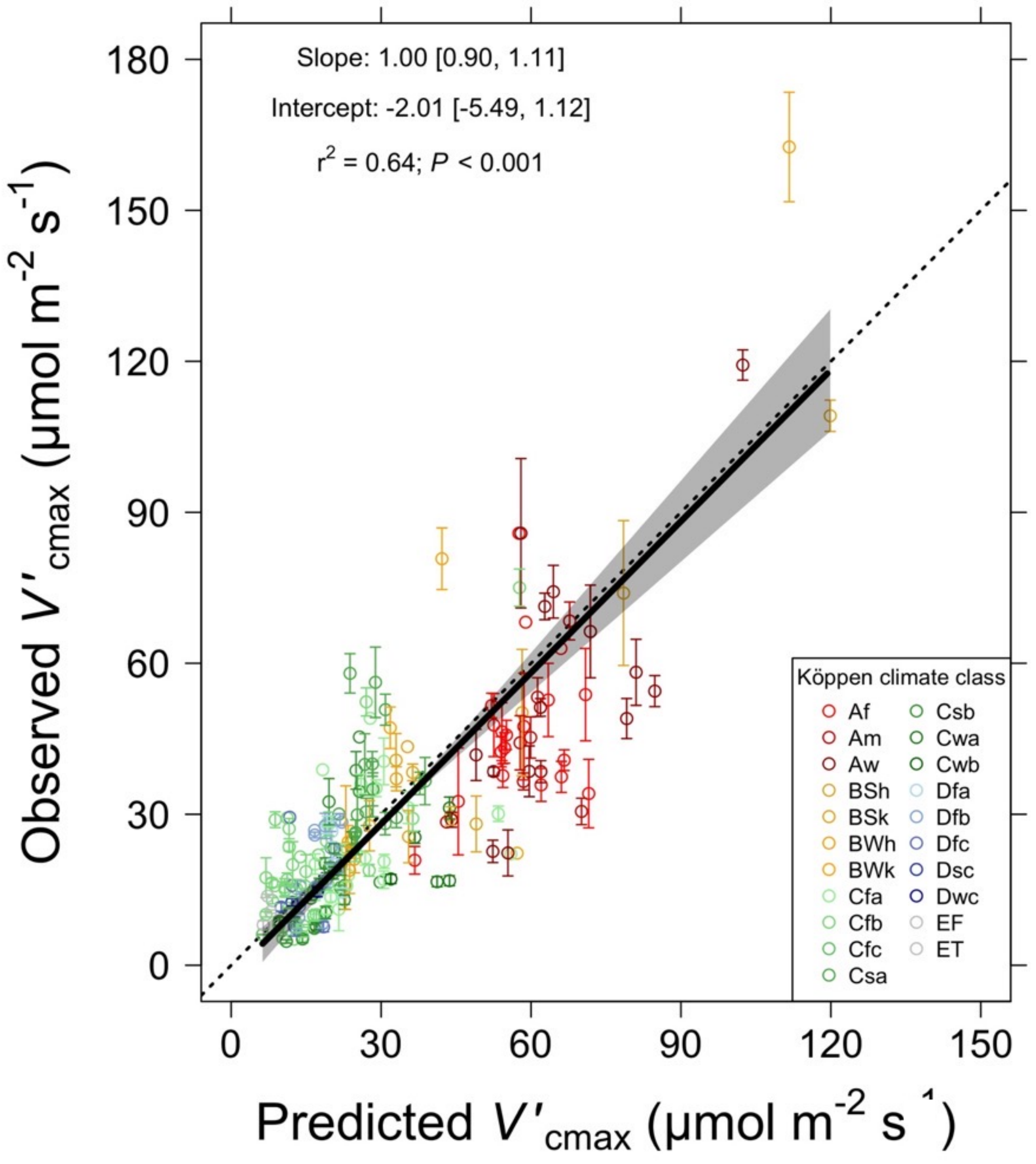

Optimal V_{cmax} is similar to observed values

Smith et al. (2019)

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Question 1: Is photosynthesis optimized to the environment?

YES! Photosynthesis acclimates spatially as expected from optimization

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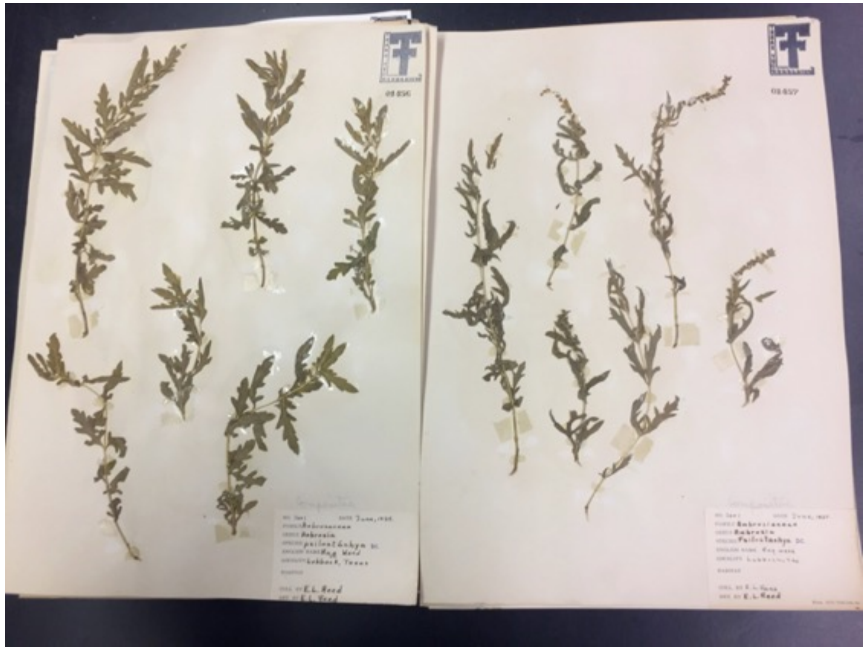
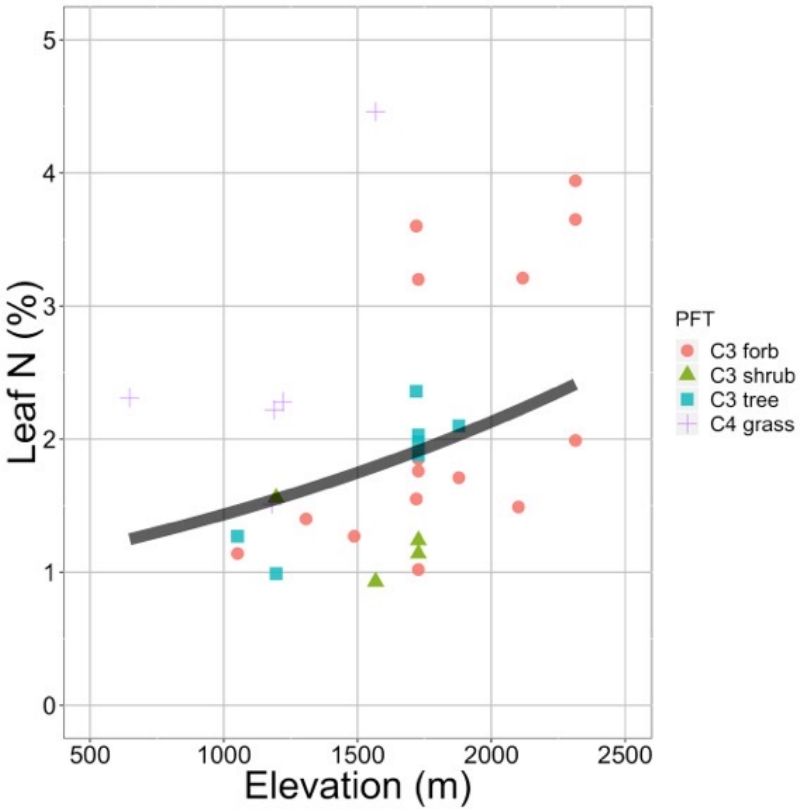
Looking forward: herbarium specimens to examine acclimation over space and time





E.L. Reed Herbarium
Texas Tech University

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

Villeda et al. (in prep)

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Question 2: Does photosynthesis acclimate to soil nutrients?

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From the least cost hypothesis…

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

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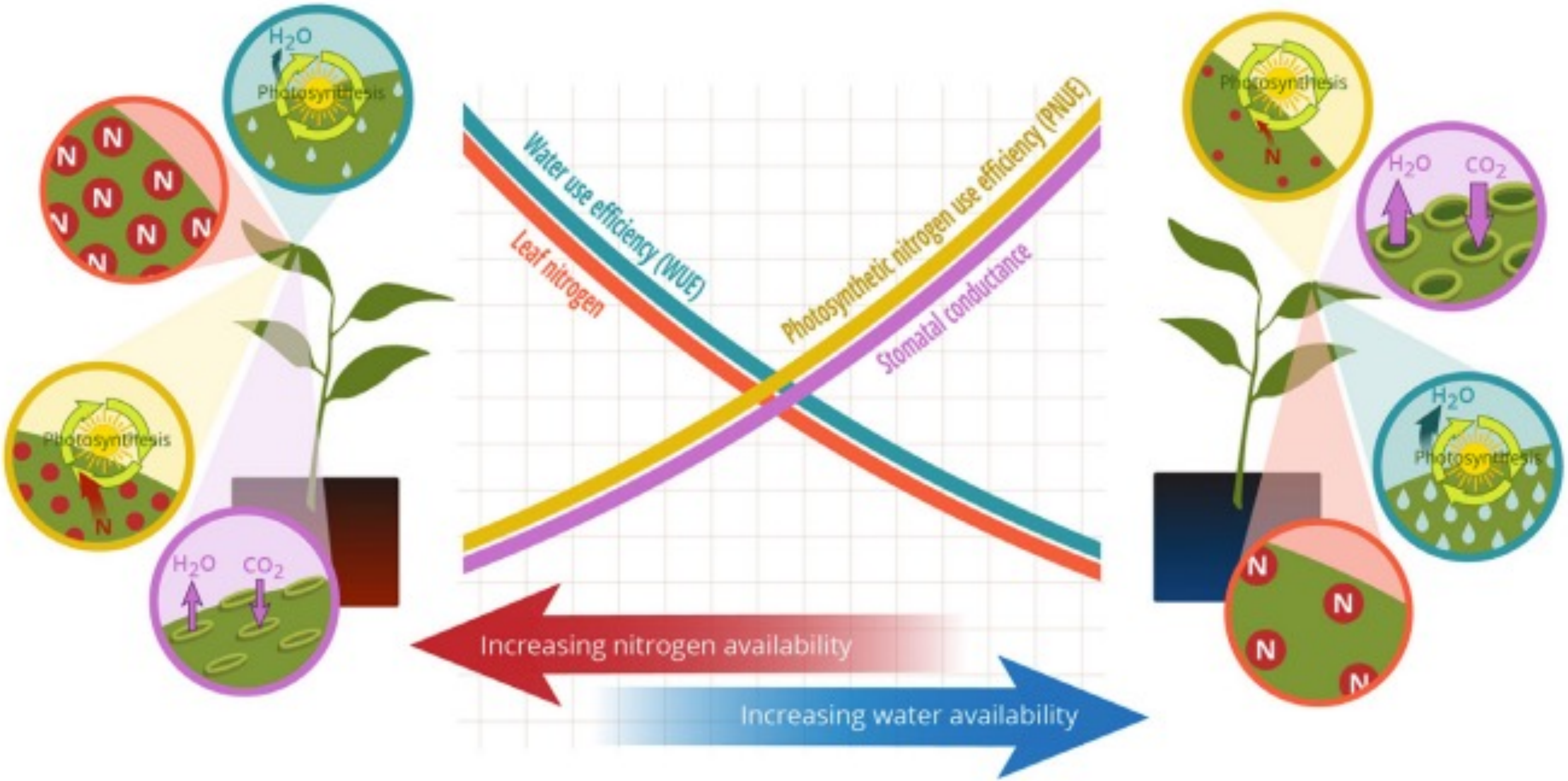
From the least cost hypothesis…



Bialic-Murphy et al. (2021)

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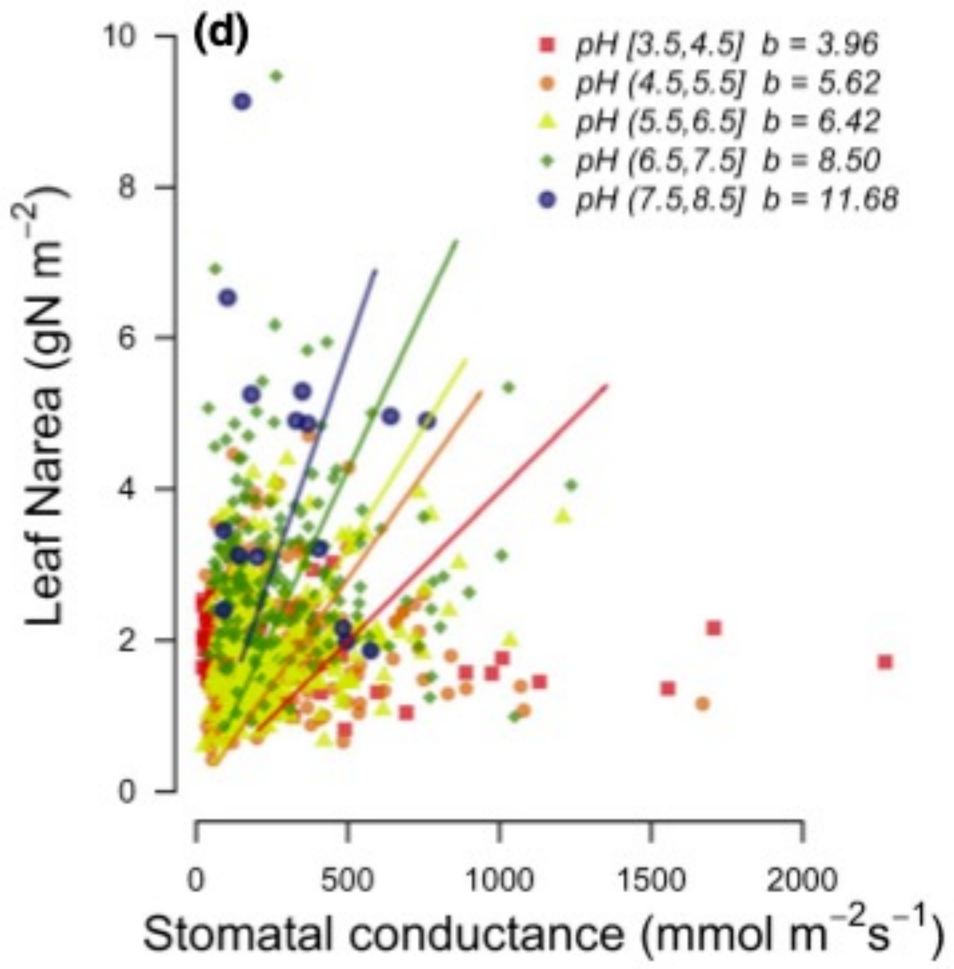
Observations show support for least cost



Paillassa et al. (2020)

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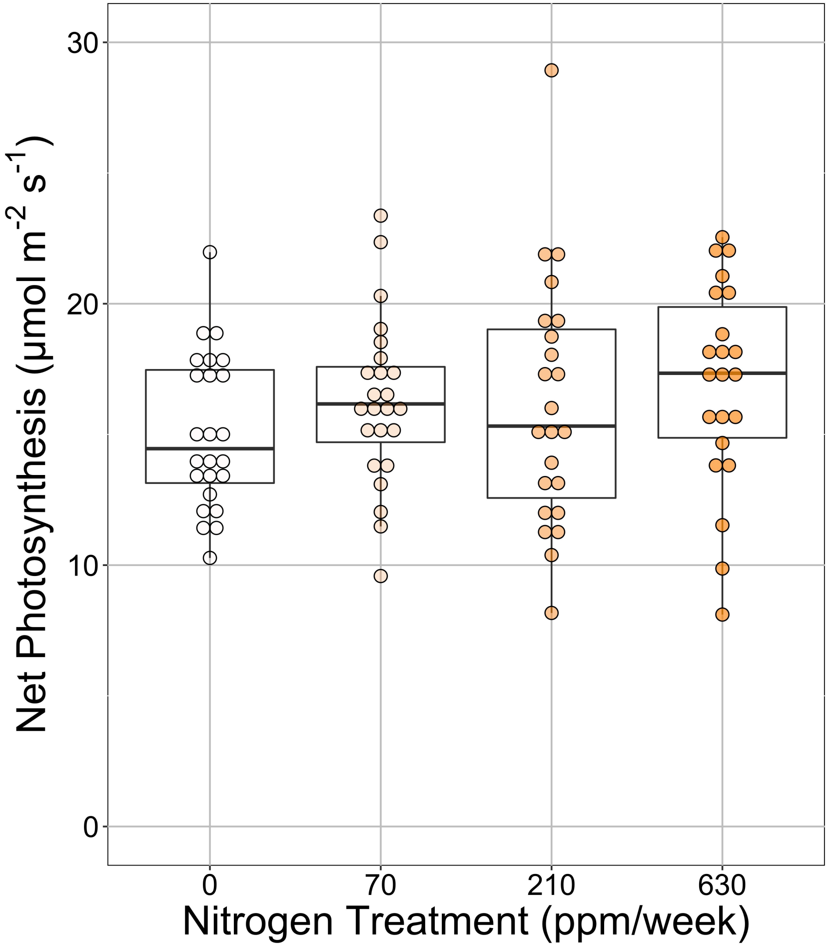
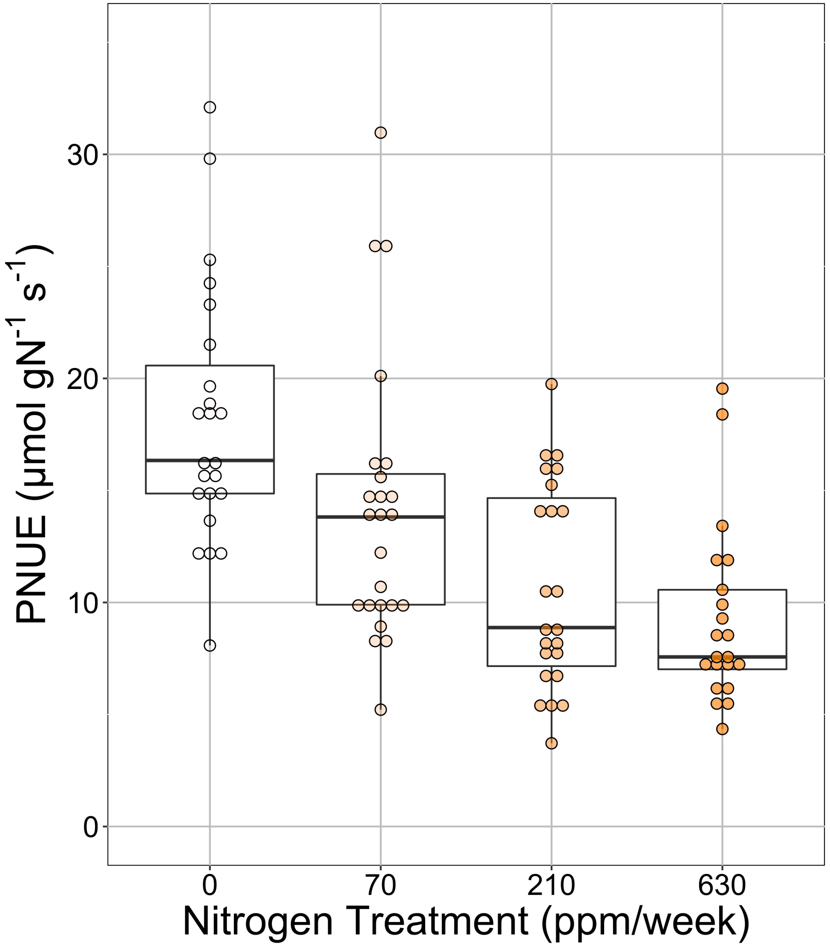
As do greenhouse experiments





Waring and Smith (in prep)

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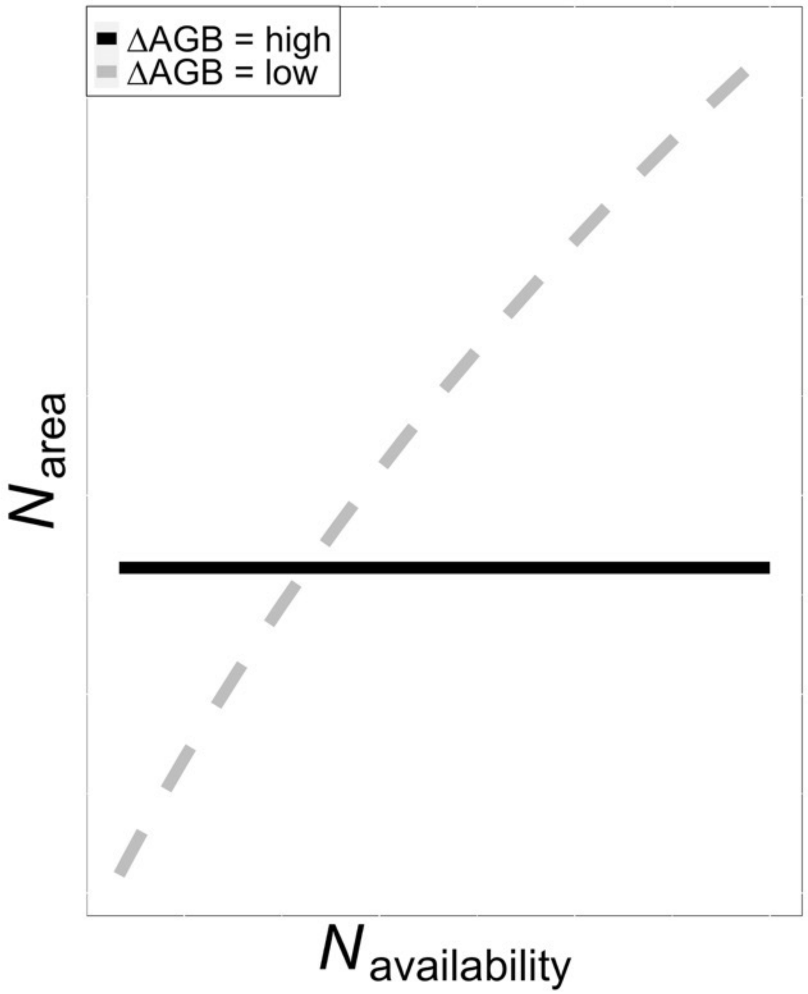
Is plant allocation to leaf N dependent on allocation to biomass?



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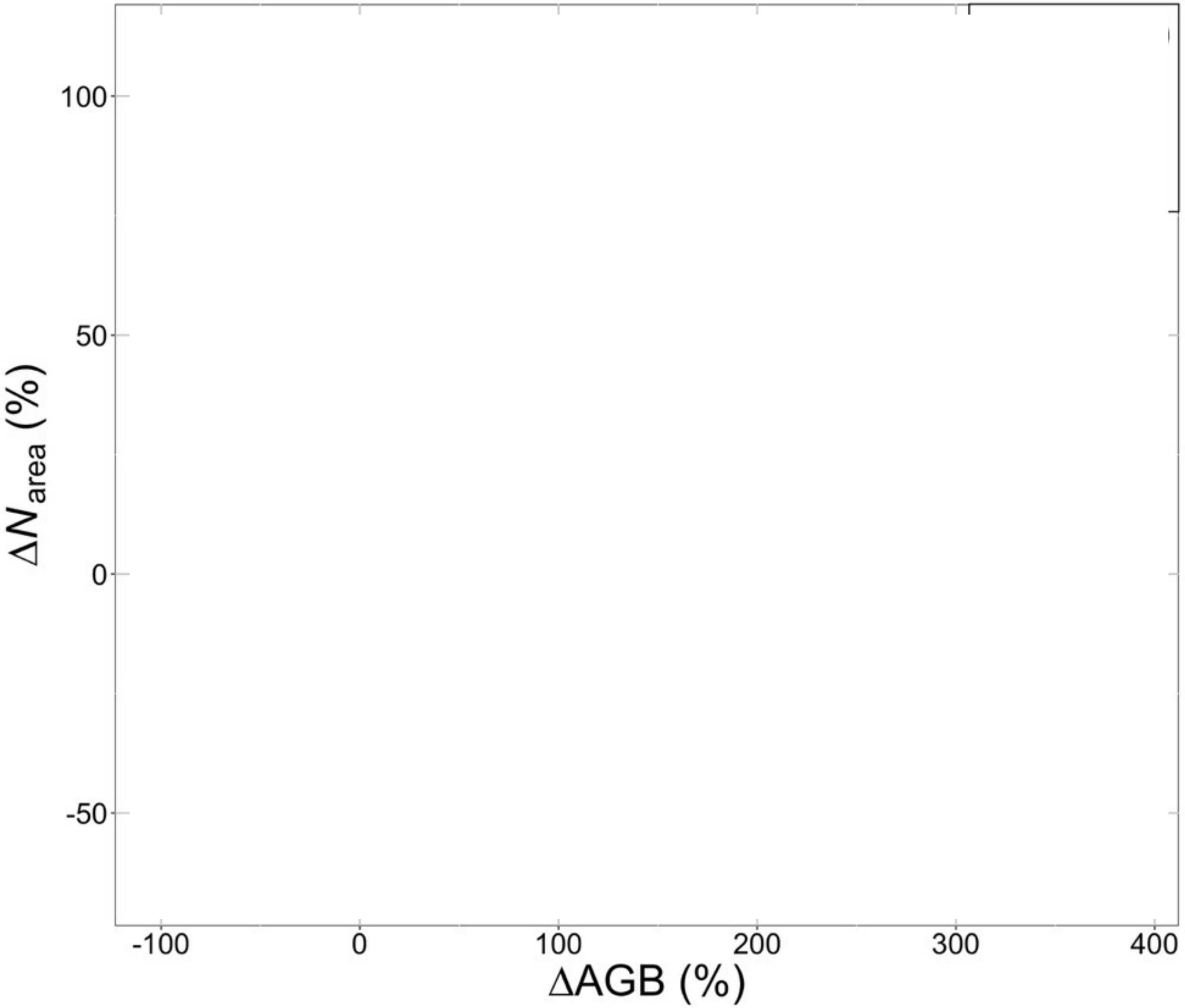
Is plant allocation to leaf N dependent on allocation to biomass?



nutrient network

Smith et al. (in prep)

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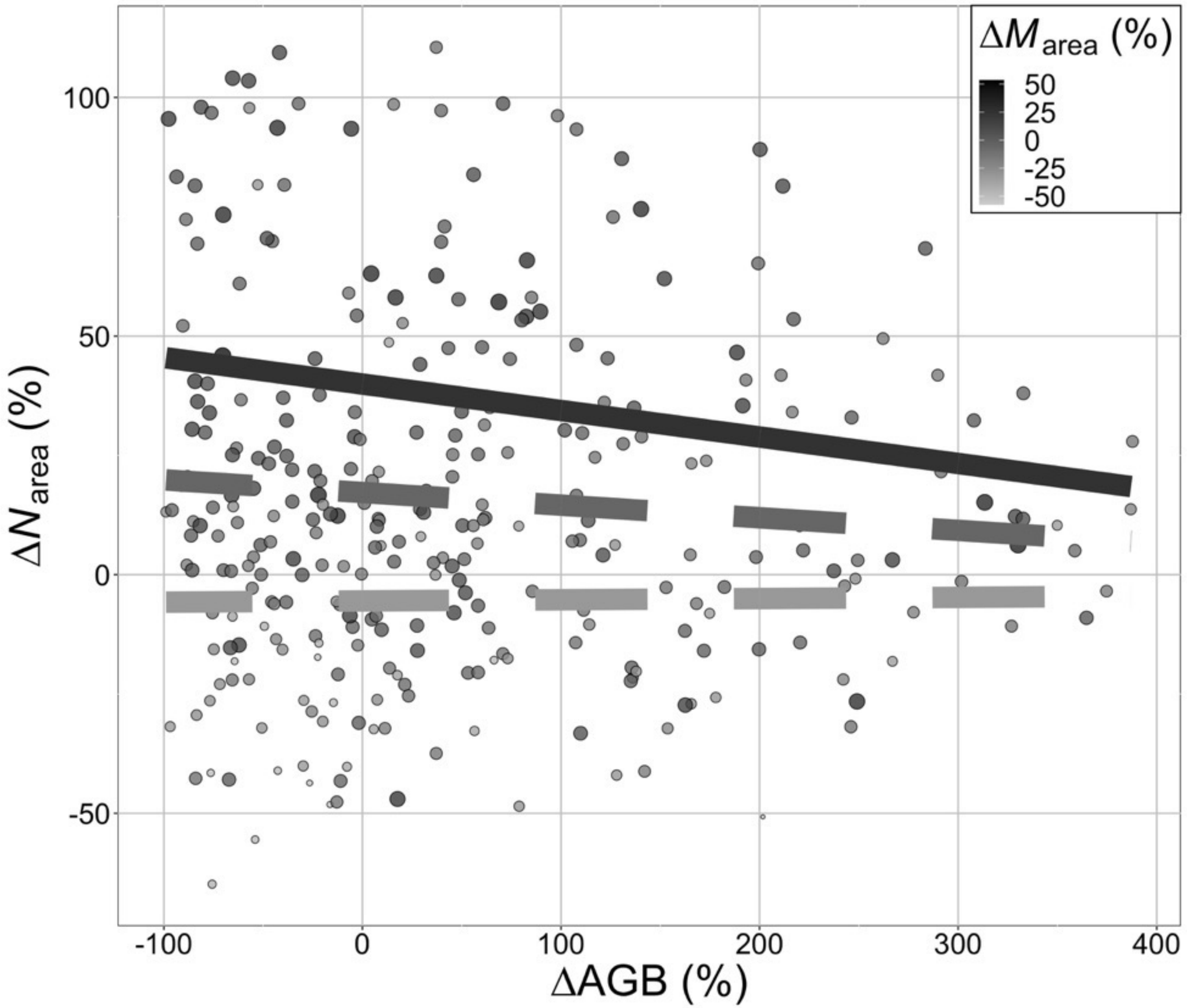
To see a leaf N response to soil N there must be (1) added investment to leaves and (2) small investment to biomass



nutrient network

Smith et al. (in prep)

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Question 2: Does photosynthesis acclimate to soil nutrients?

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

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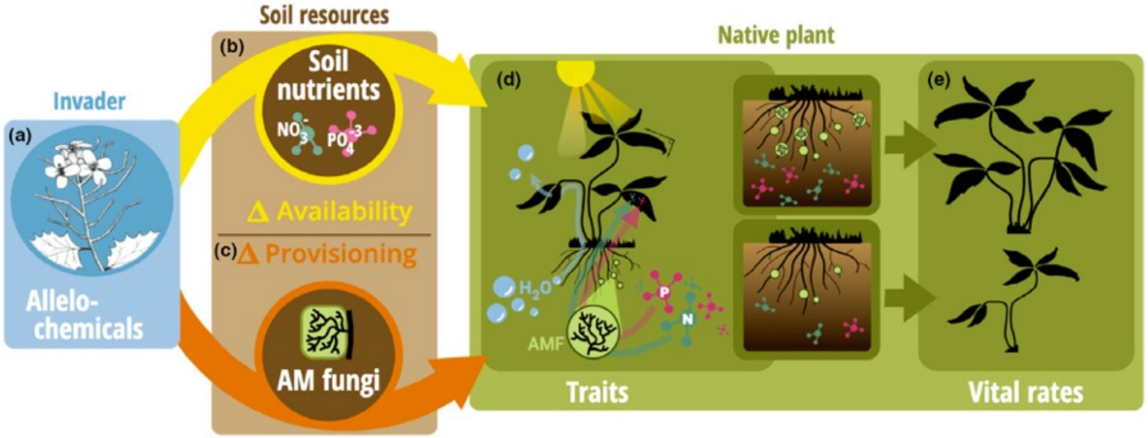
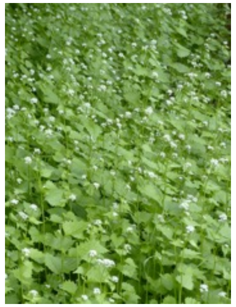
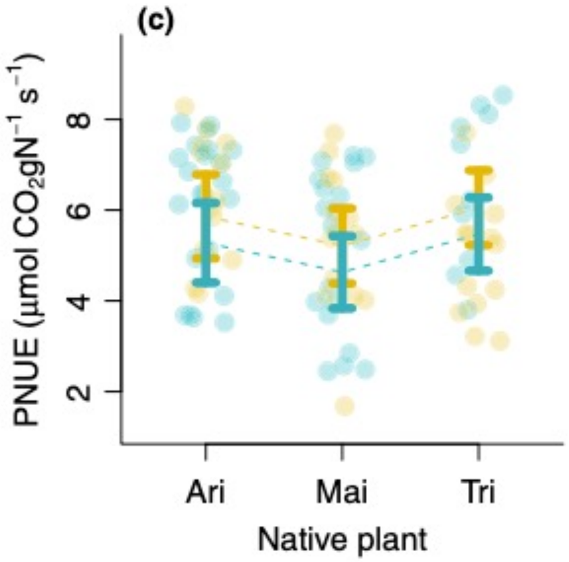
Looking forward: impact of allelopathic invaders on leaf economics







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

Bialic-Murphy et al. (2021)

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

E3SM Energy Exascale Earth System Model

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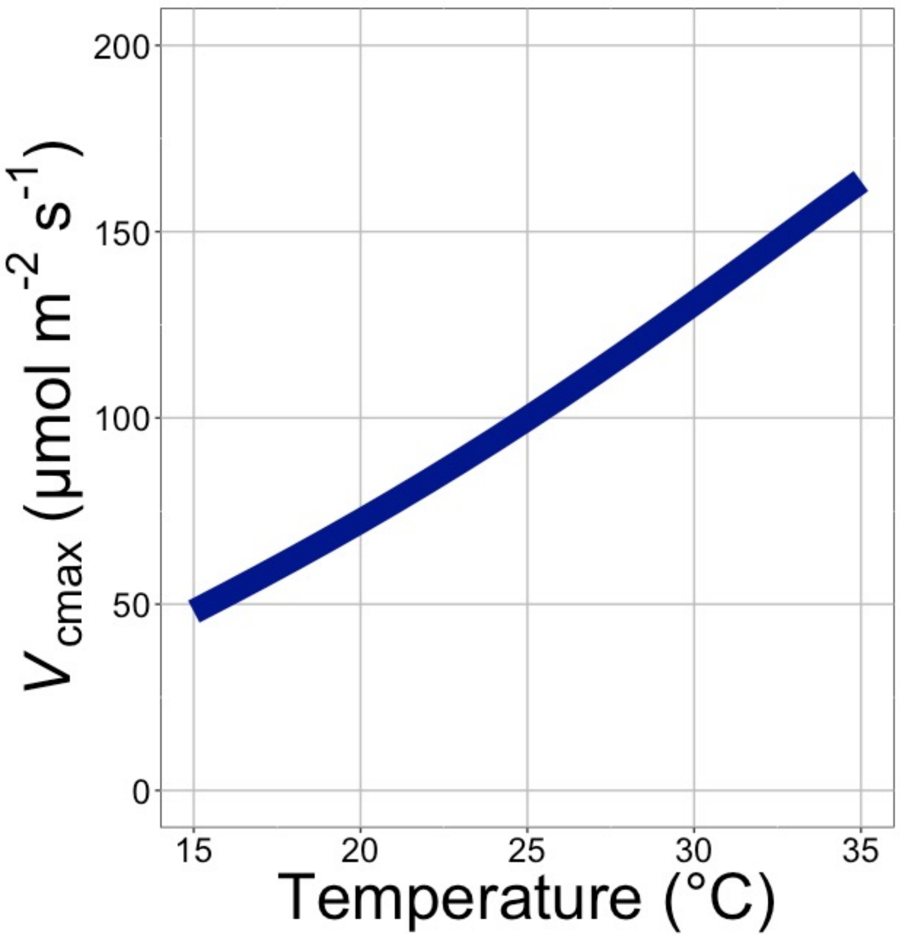
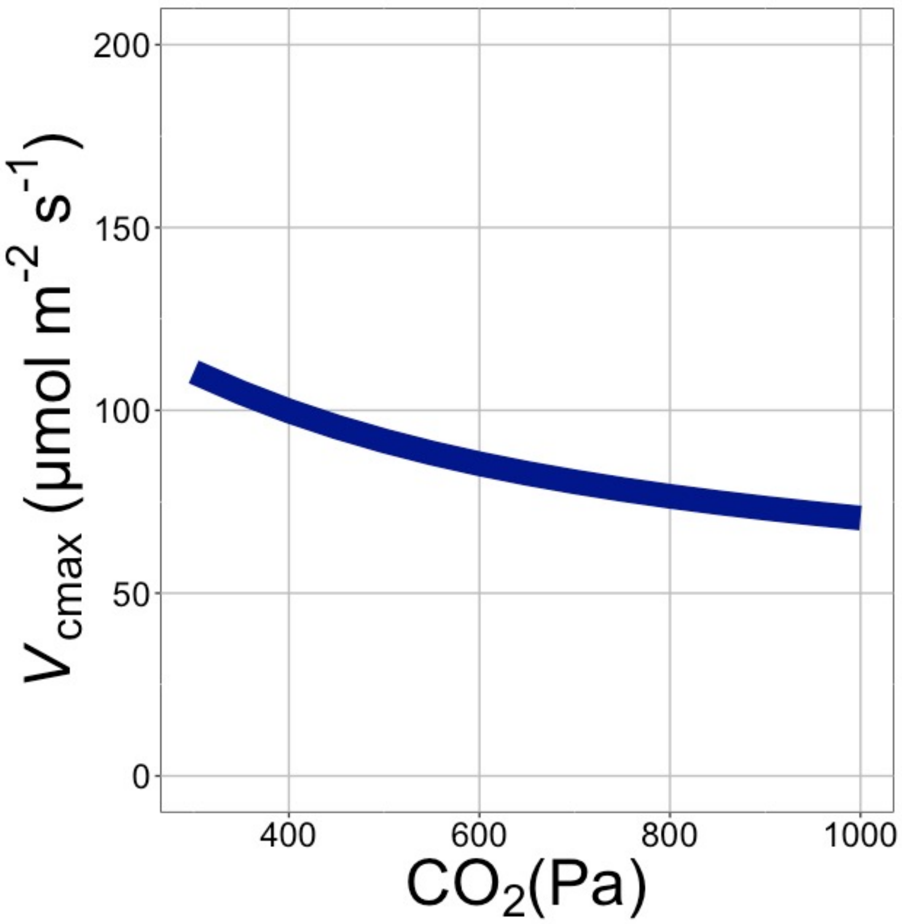
Expected future responses





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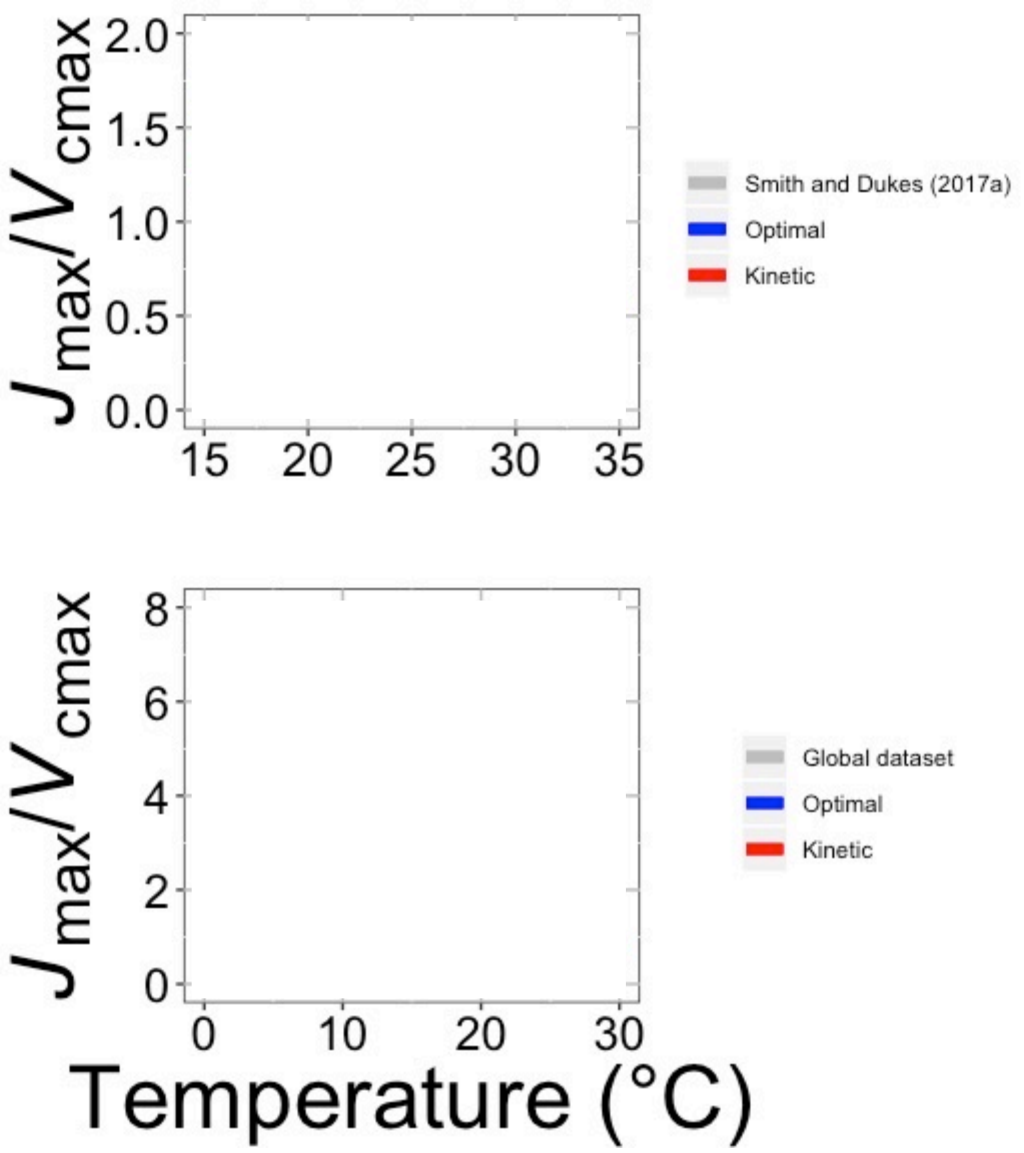
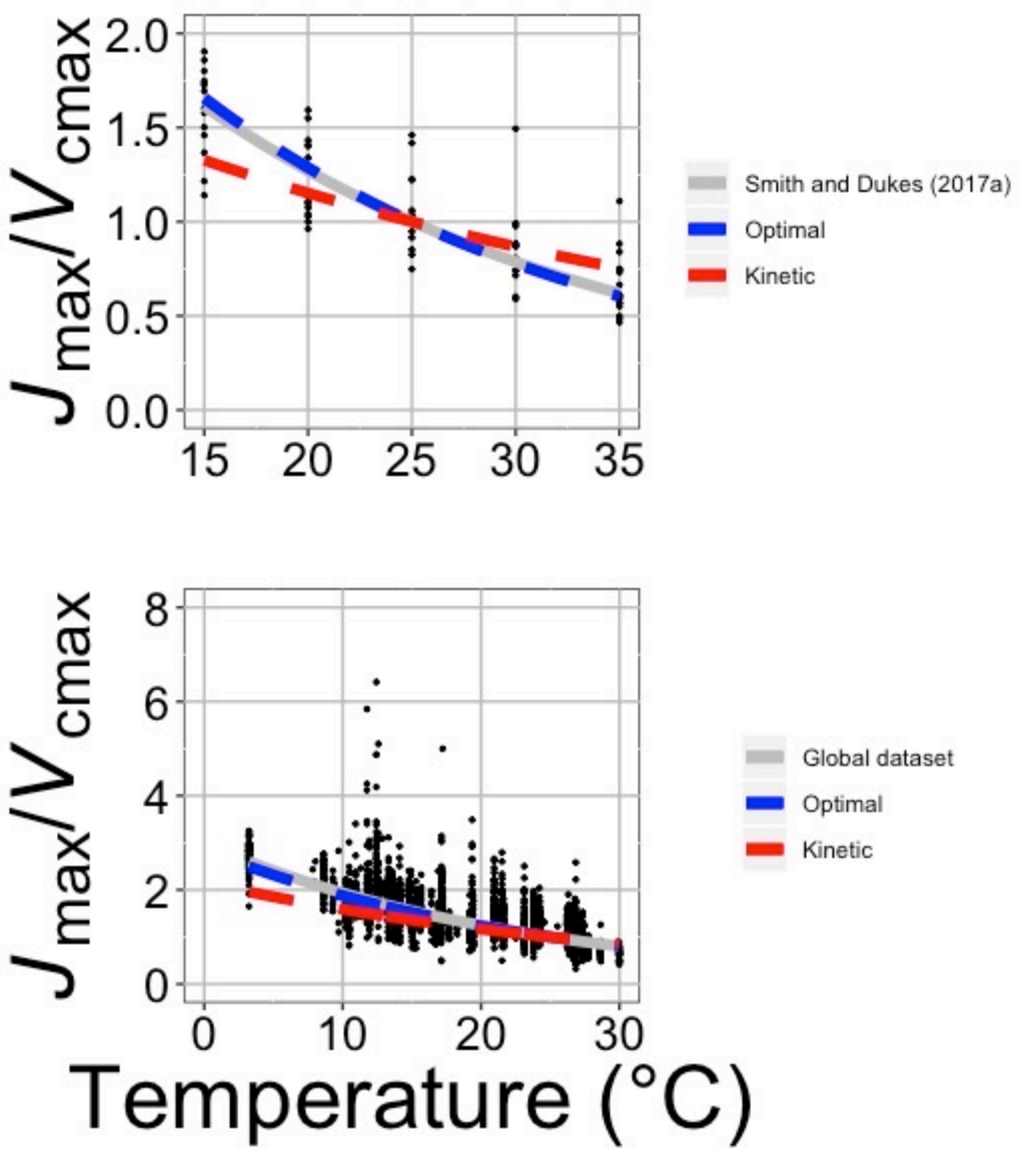


Smith and Keenan (2020)

nick.smith@ttu.edu; @nick_greg_smith

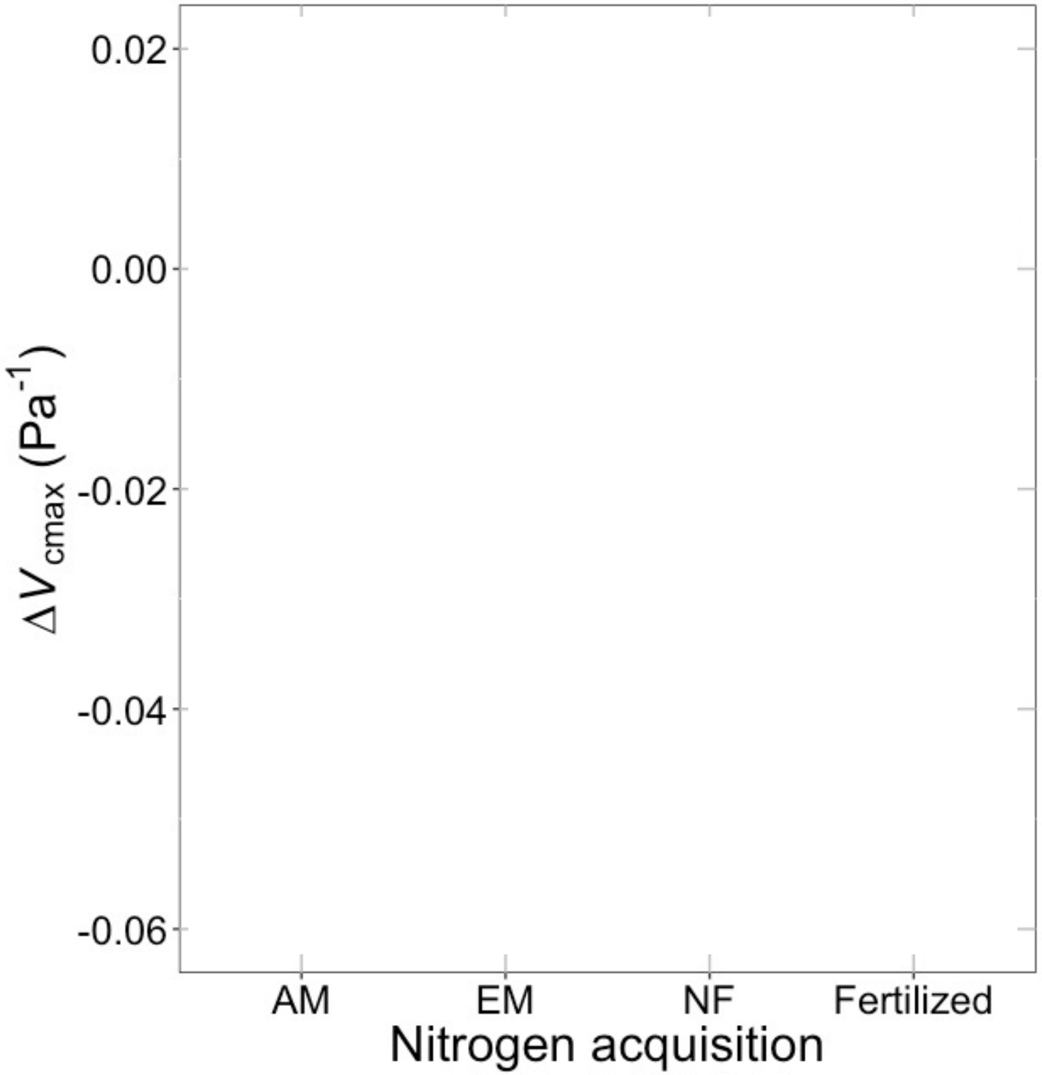


Photosynthetic traits change with temperature in ways expected from optimization

Data = -0.051 °C^{-1}
Predicted = -0.048 °C^{-1}

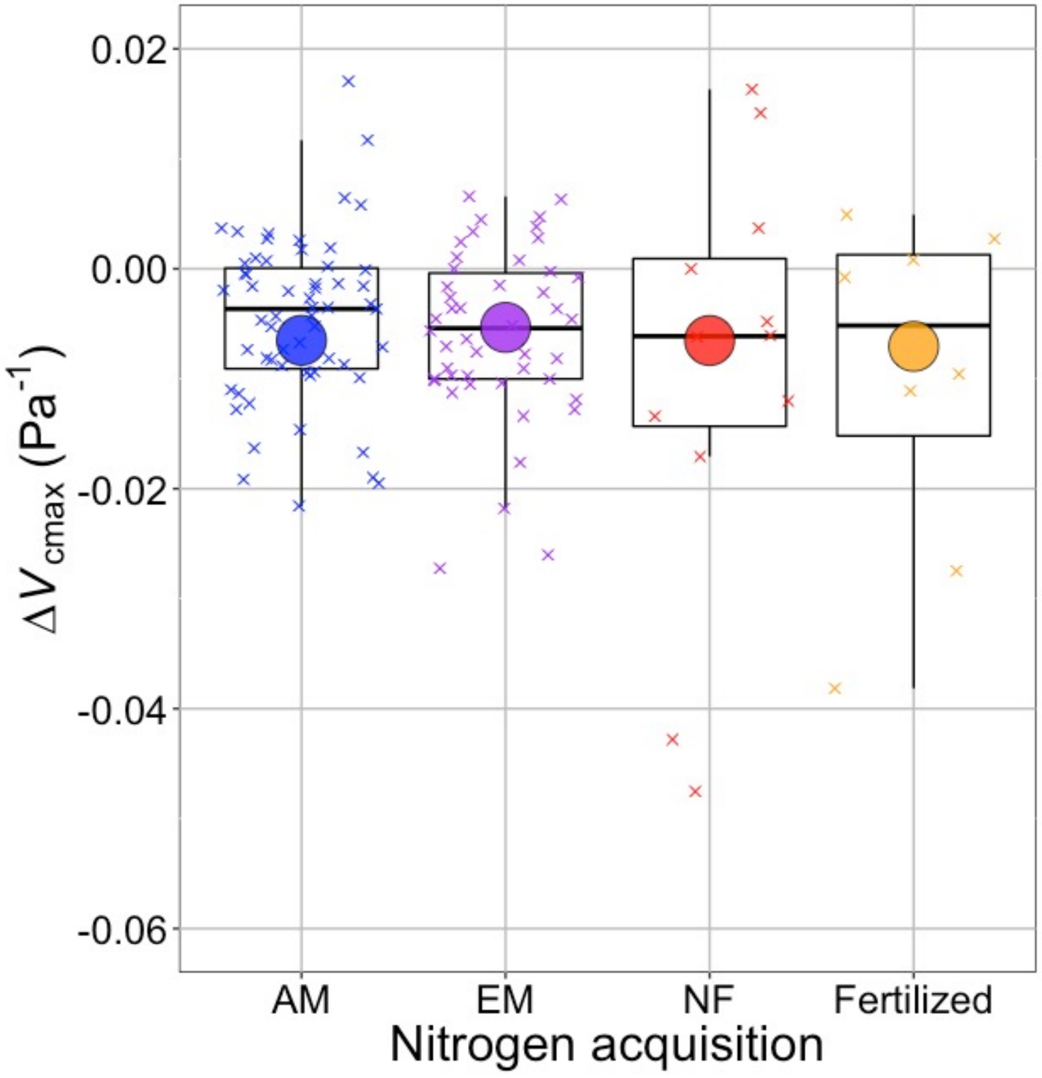
Smith and Keenan (2020)

nick.smith@ttu.edu; @nick_greg_smith



Smith and Keenan (2020)

nick.smith@ttu.edu; @nick_greg_smith



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)

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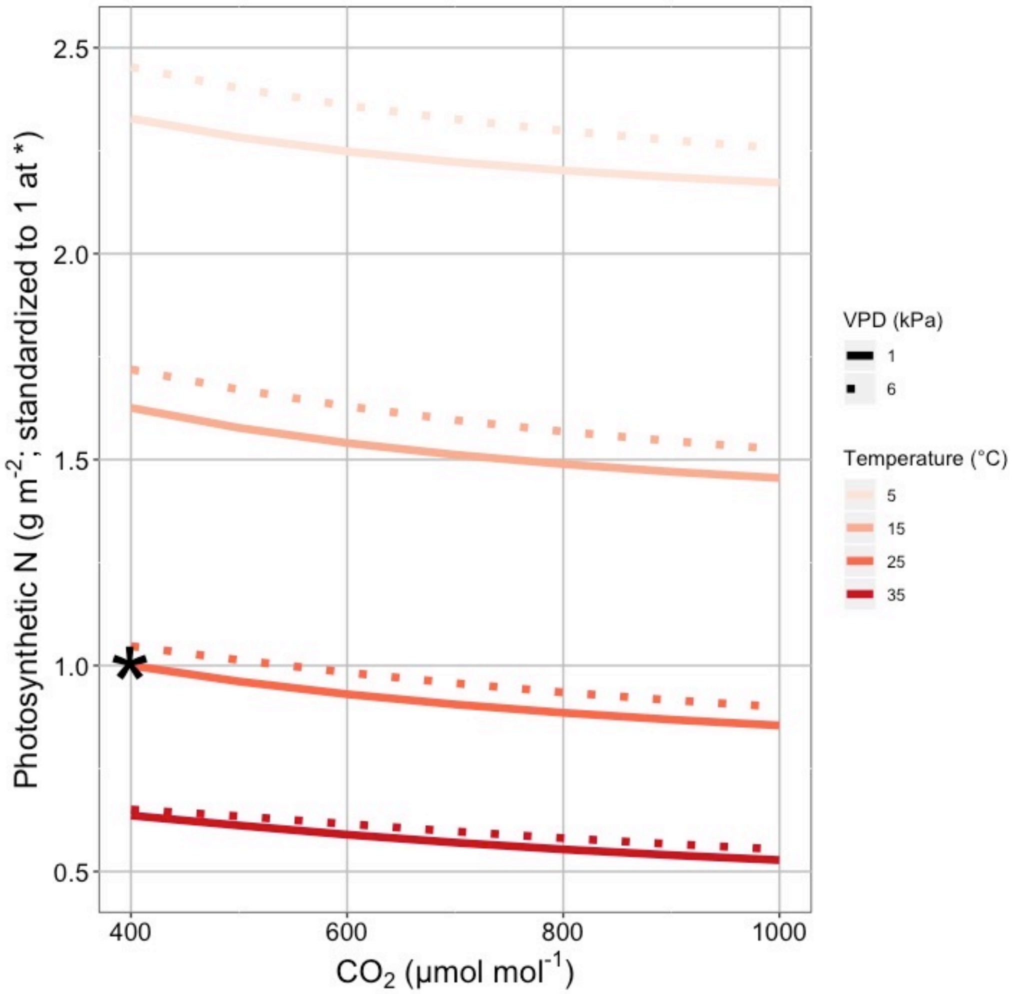
This generally suggests lower nitrogen demand under warmer, high CO_2 conditions



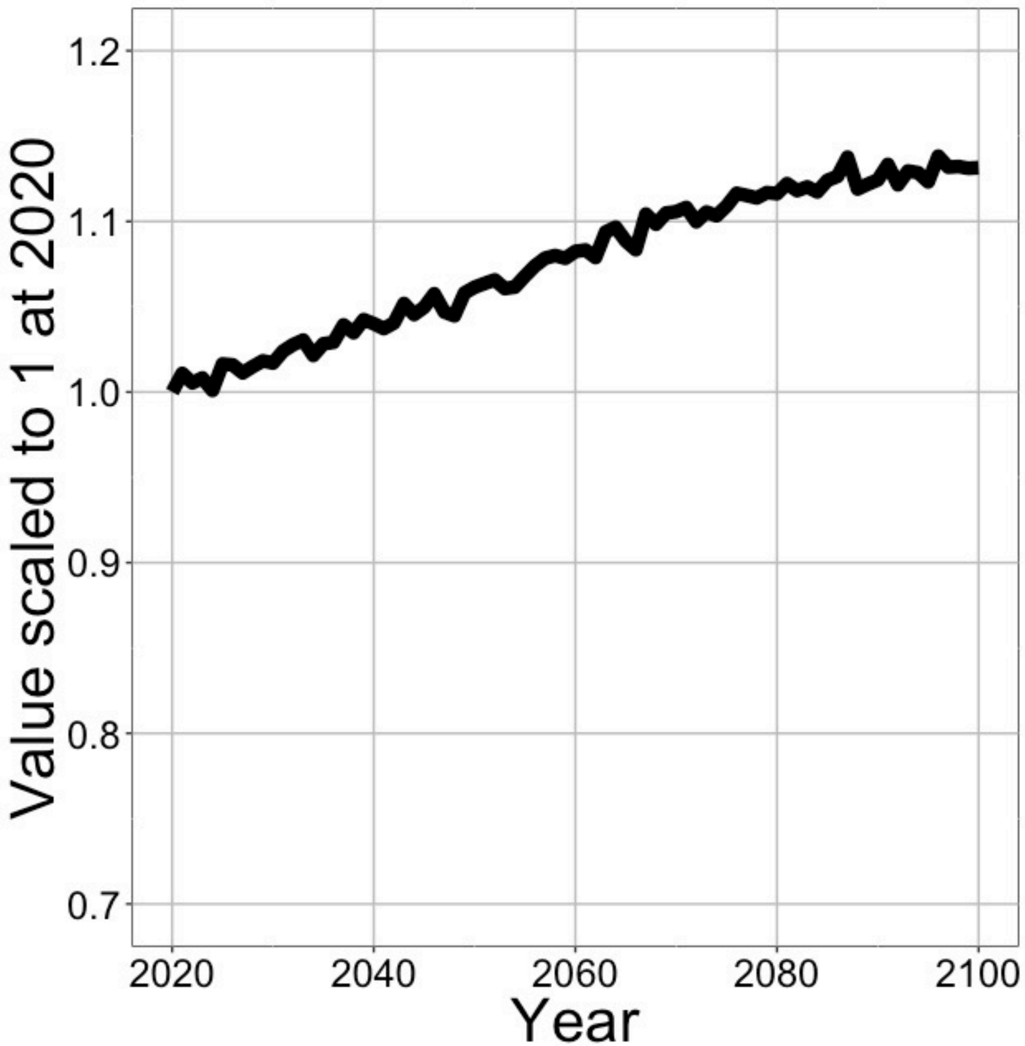
Smith and Keenan (2020)

Let’s run a model out into the future!

E3SM Energy Exascale Earth System Model

nick.smith@ttu.edu; @nick_greg_smith

Photosynthesis increases in future

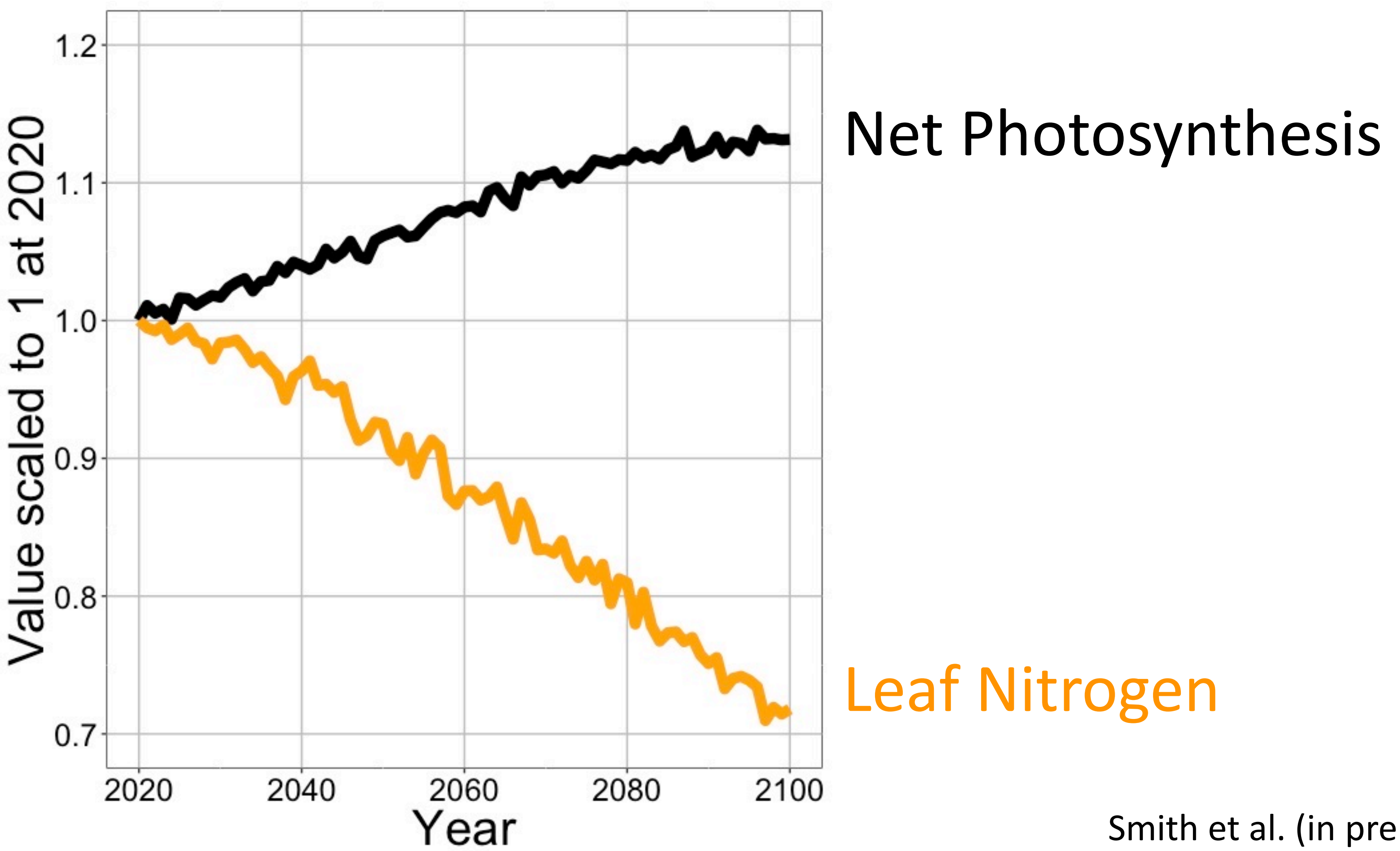


Net Photosynthesis

Smith et al. (in prep)

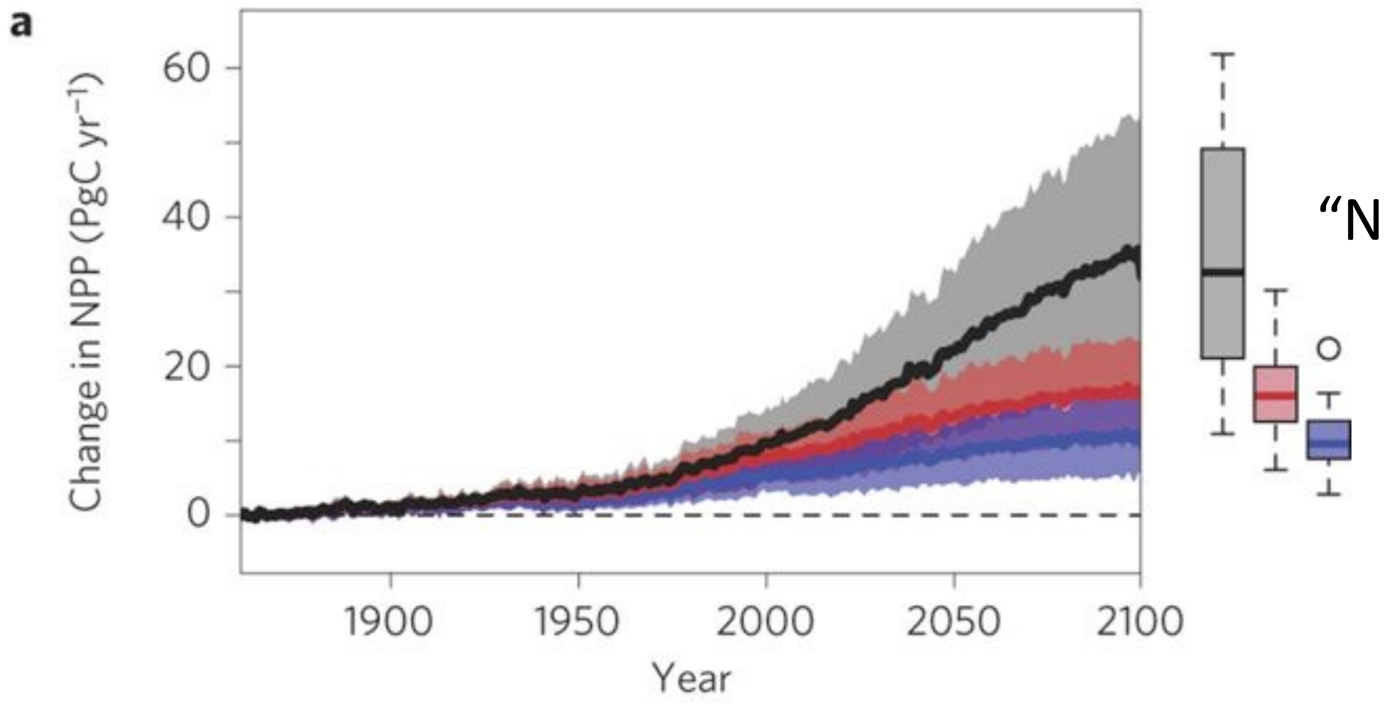
nick.smith@ttu.edu; @nick_greg_smith

Photosynthesis increases in future
(at lower nutrient use)



Smith et al. (in prep)

Need to rethink nutrient limitation in models?



“No limitation” simulation

“Nutrient limitation” simulations

Weider et al. (2015)

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

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

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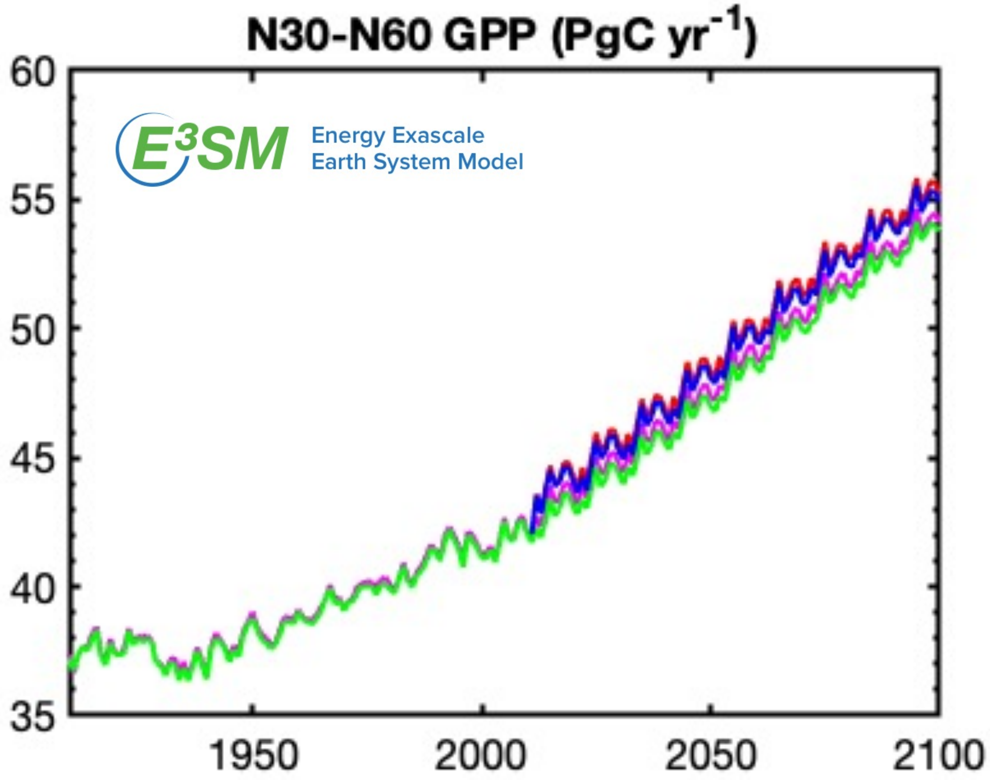
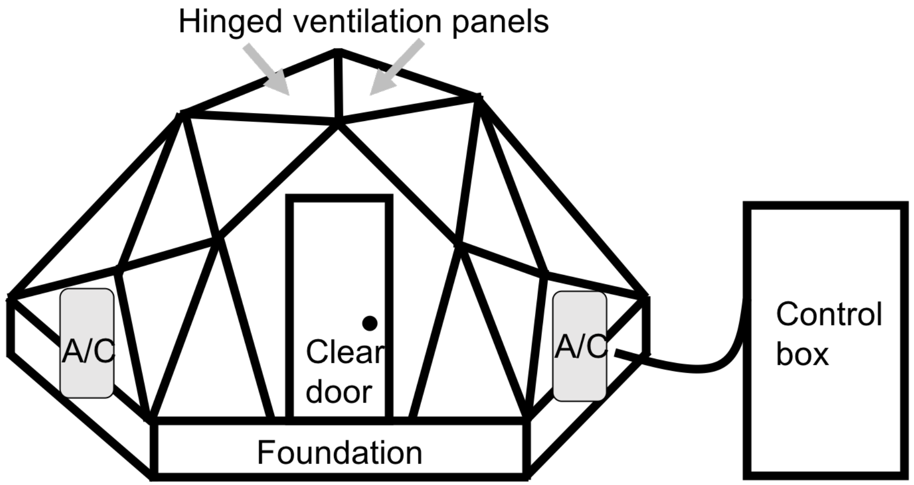
Looking forward: role of acclimation on future ecosystem feedbacks





Coupled model-data experiments

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

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C_3 versus C_4 optimization

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C_4 versus C_3 optimization

C_4 photosynthesis has…

- No photorespiration
- An additional limitation (PEP carboxylation)

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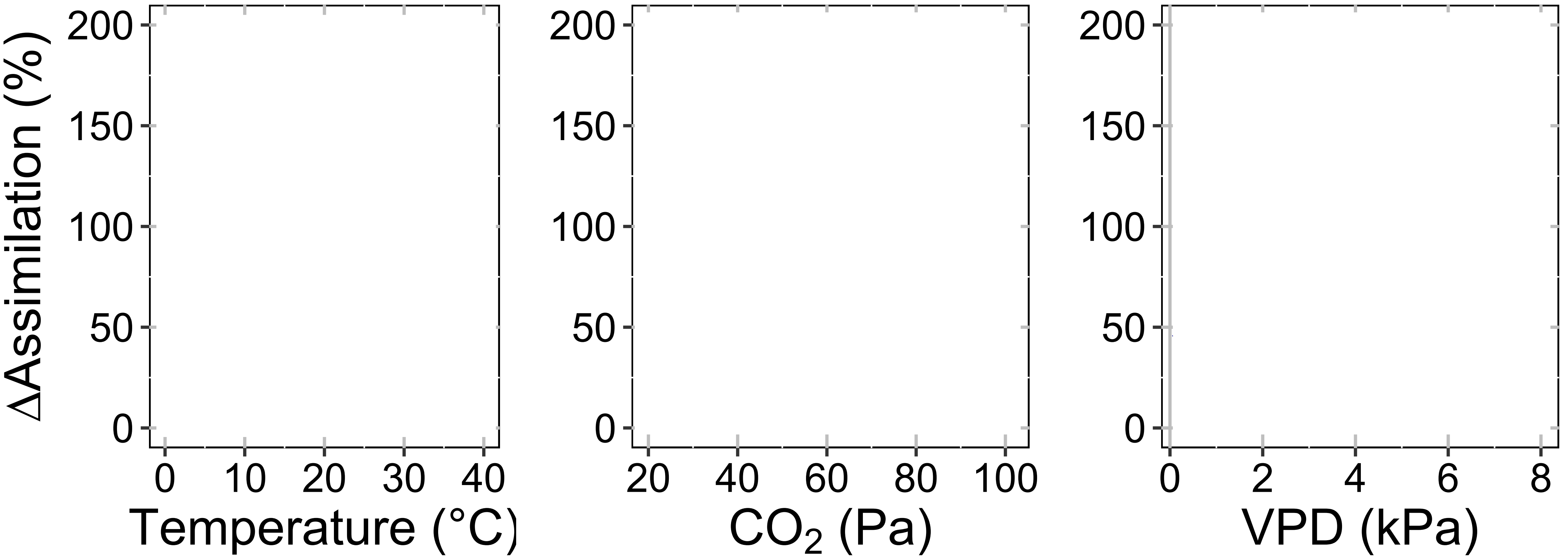
C_4 versus C_3 optimization

C_4 photosynthesis has…

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

nick.smith@ttu.edu; @nick_greg_smith

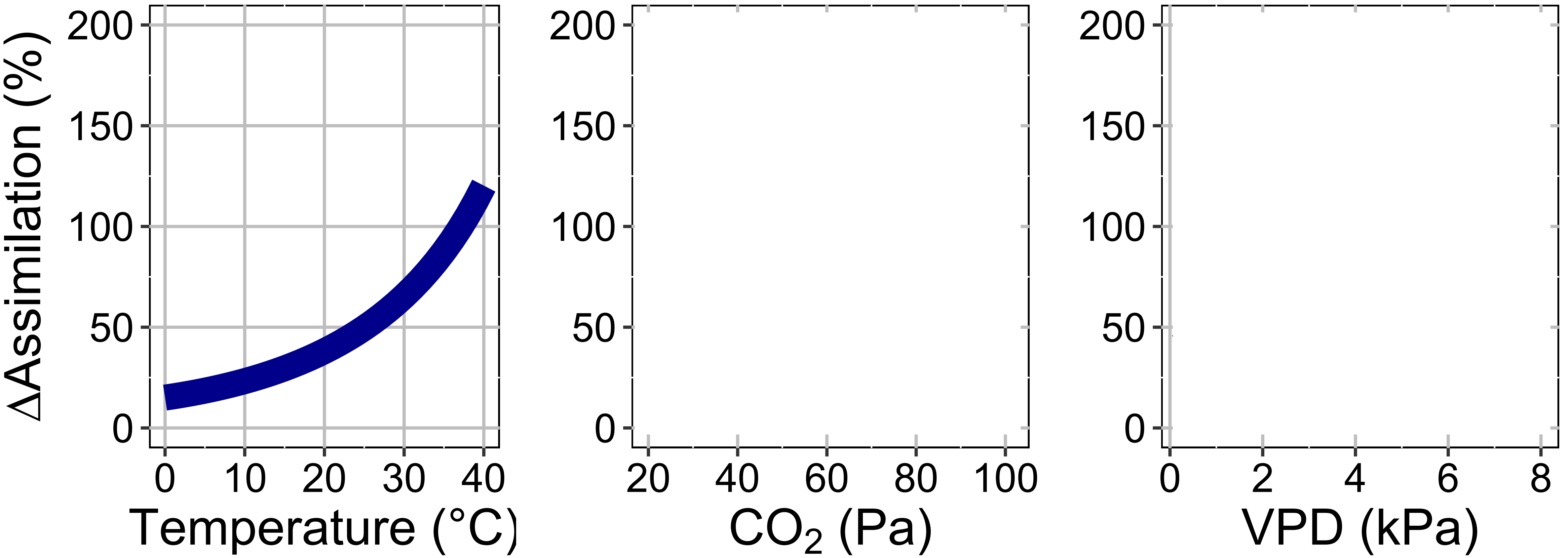
Relative advantage of C_4 physiology



Scott and Smith (in review)

nick.smith@ttu.edu; @nick_greg_smith

Relative advantage of C_4 physiology



Scott and Smith (in review)

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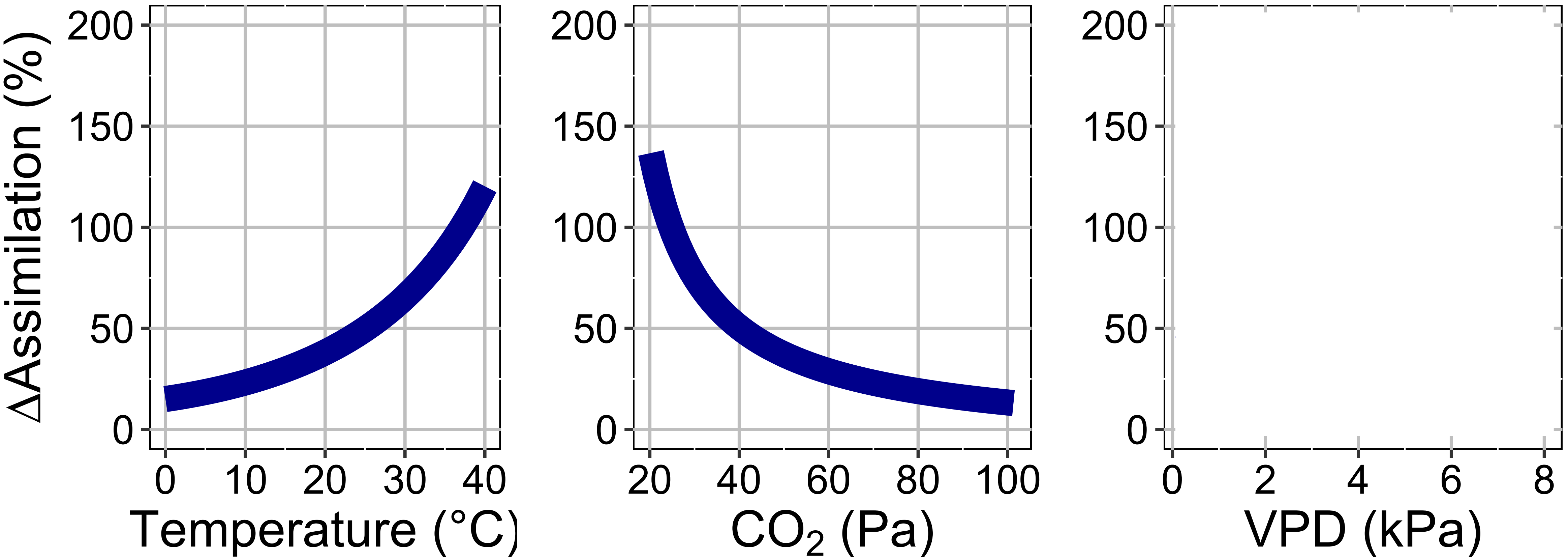
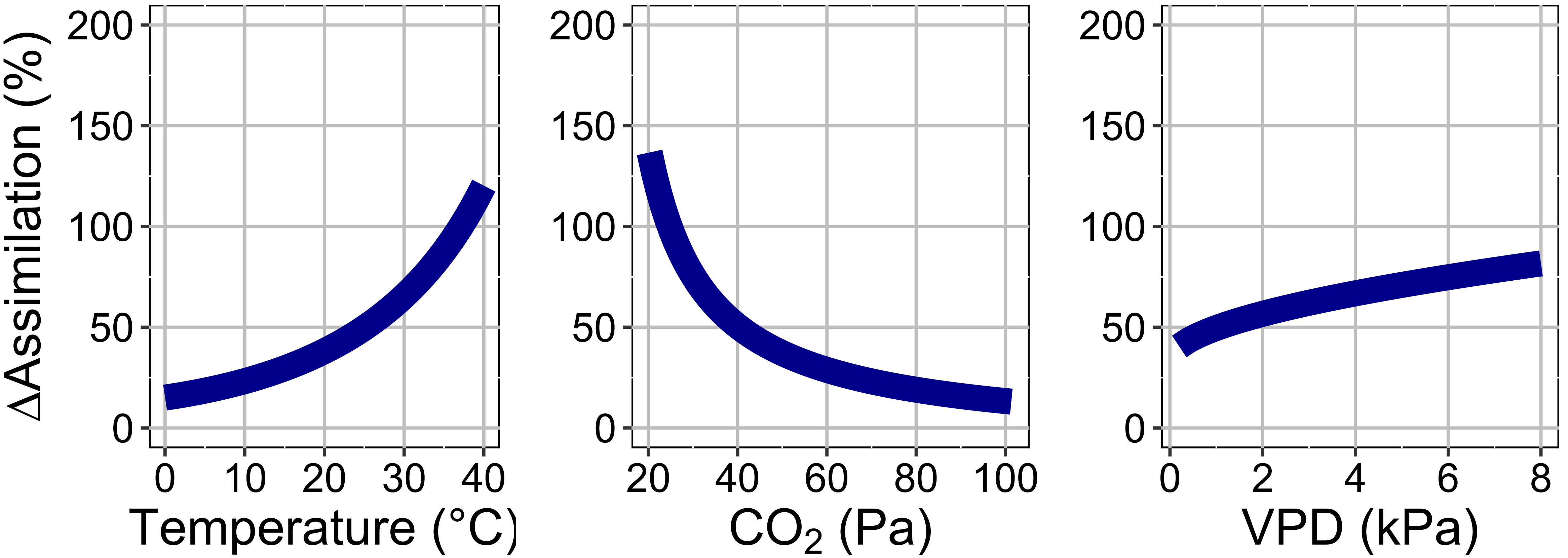
Relative advantage of C_4 physiology



Scott and Smith (in review)

nick.smith@ttu.edu; @nick_greg_smith

Relative advantage of C_4 physiology



Scott and Smith (in review)

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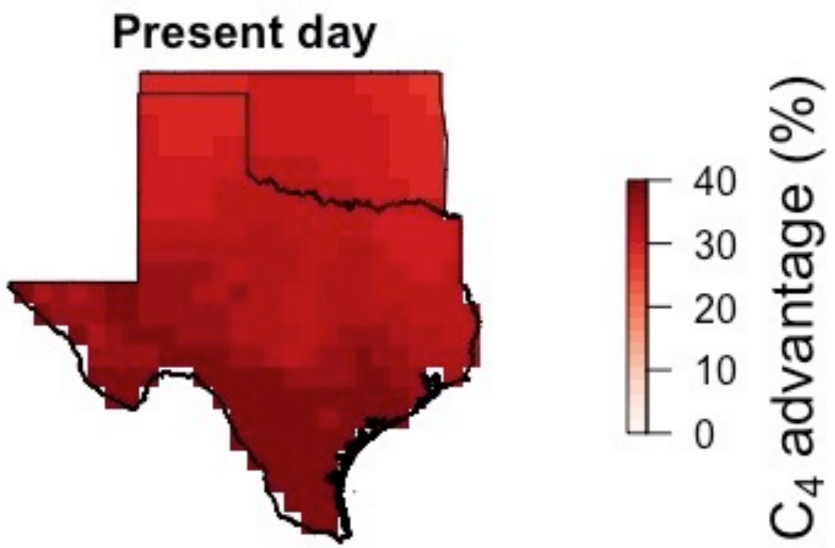
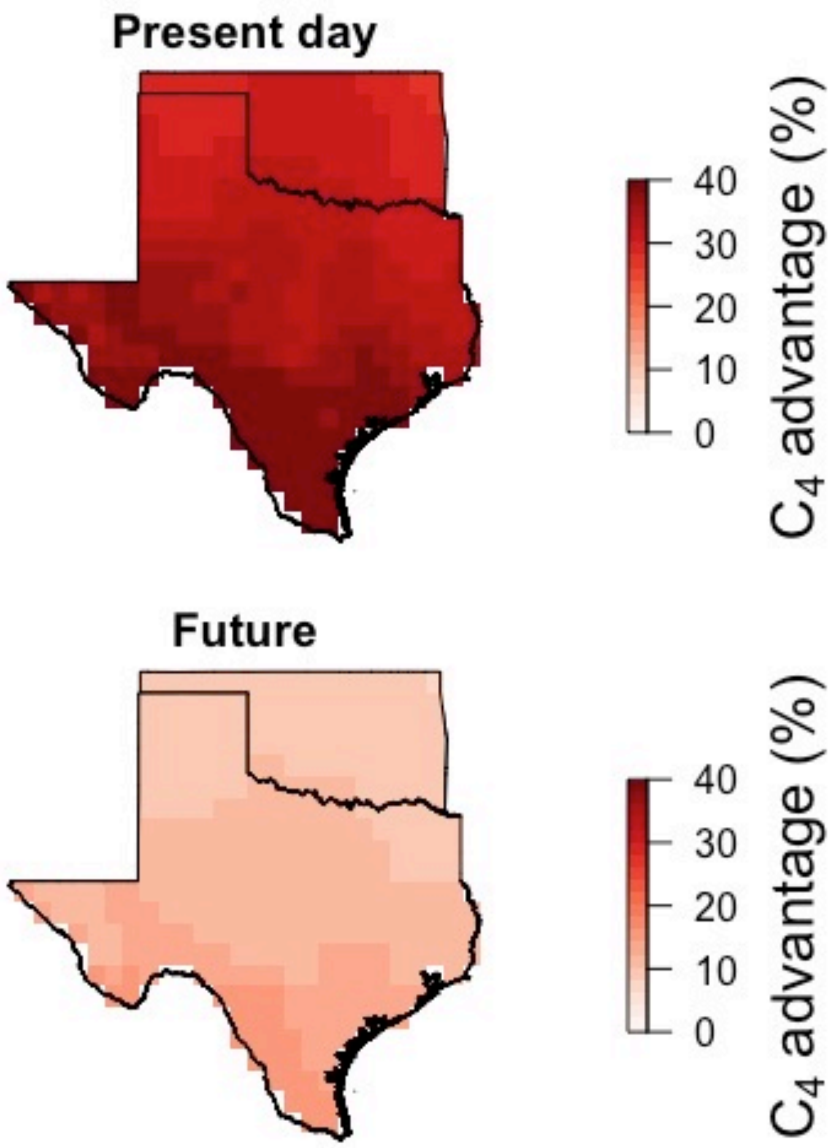


Ansley et al. (in prep)

nick.smith@ttu.edu; @nick_greg_smith



Ansley et al. (in prep)

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

C_4 is better in hot, dry, low CO_2 environments

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Looking forward: model-data comparisons for C_4 plants

Powell Center

USGS
science for a changing world

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Conclusions

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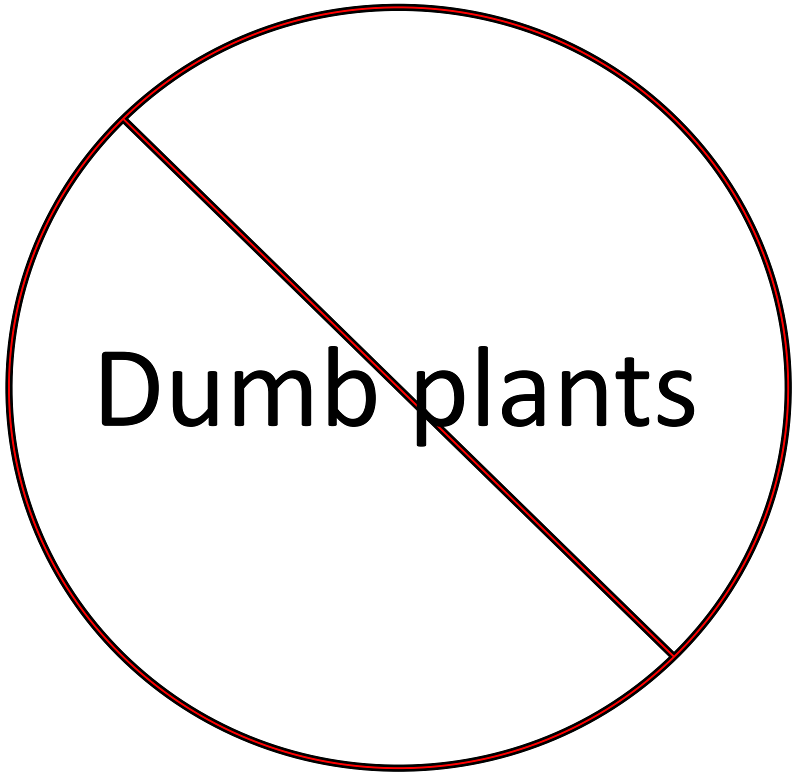
Conclusions

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



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Conclusions

Quantified physiological theory can:

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

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Presentation available at:
www.github.com/SmithEcophysLab/seminar/2021_michigan

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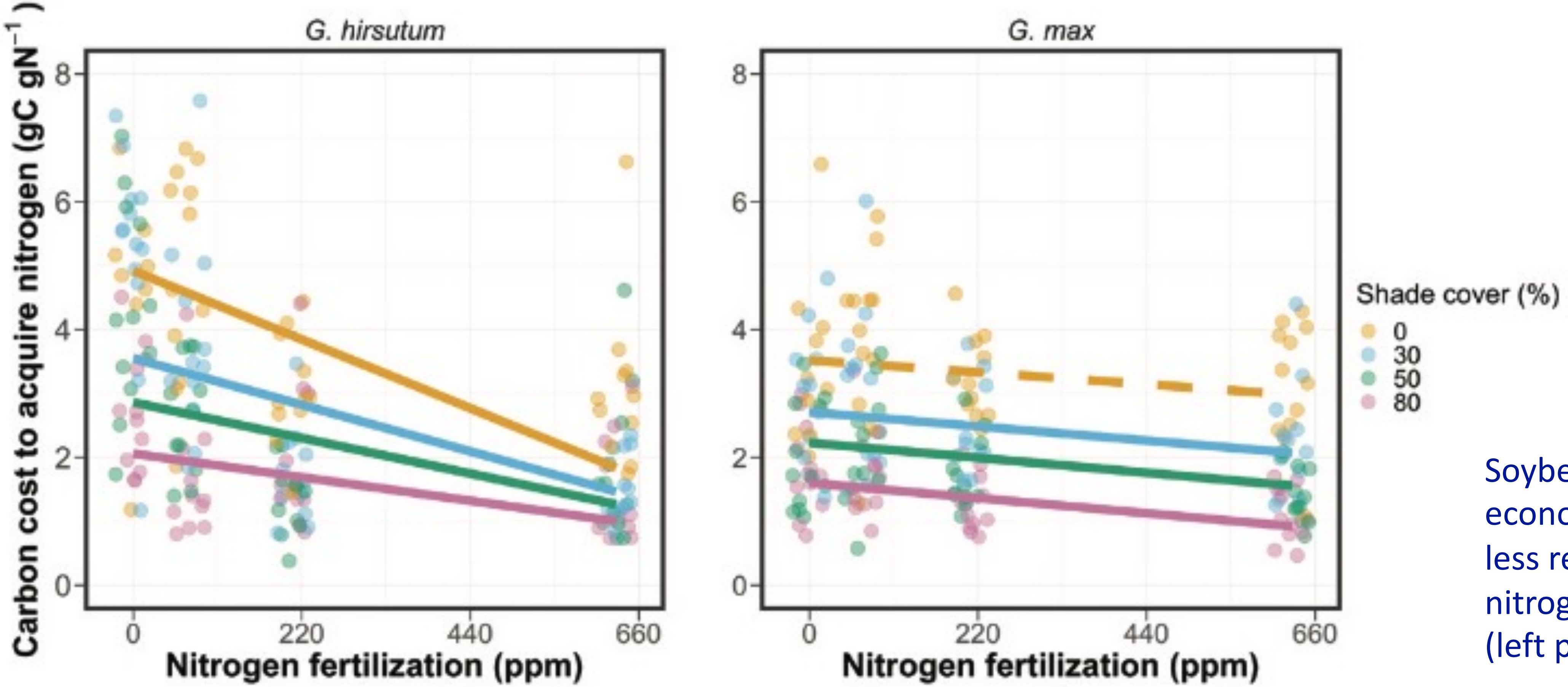
Looking forward: symbioses as modifiers of plant economies under variable conditions



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

Perkowski et al. (2021)

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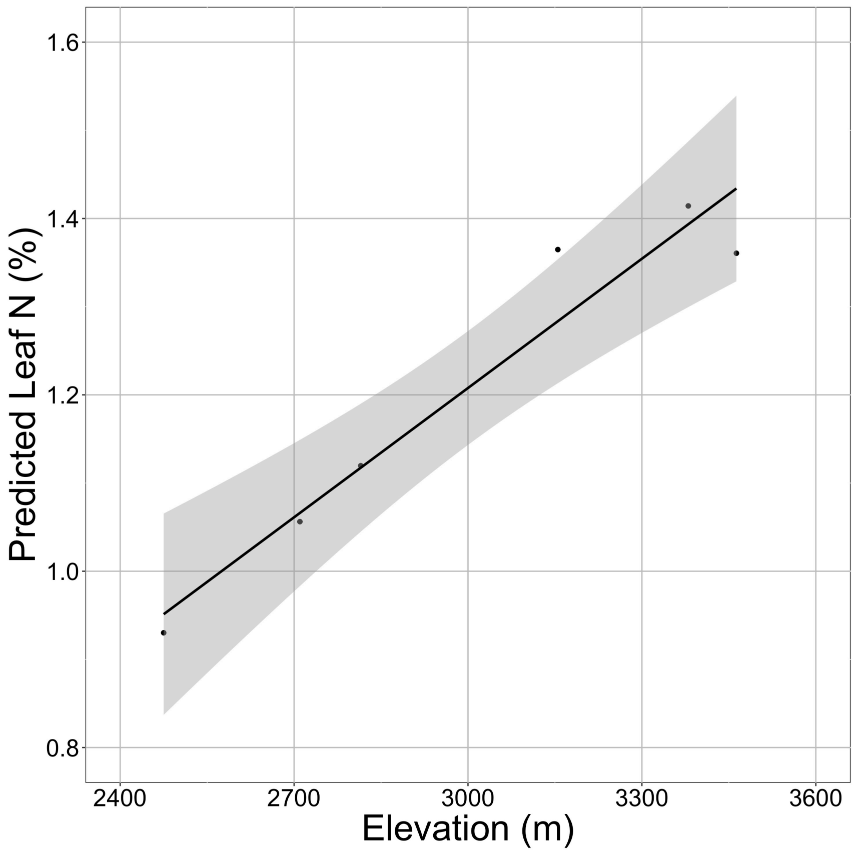
Looking forward: more acclimation predictions in more places to examine larger scale impacts



ROCKY MOUNTAIN BIOLOGICAL LABORATORY

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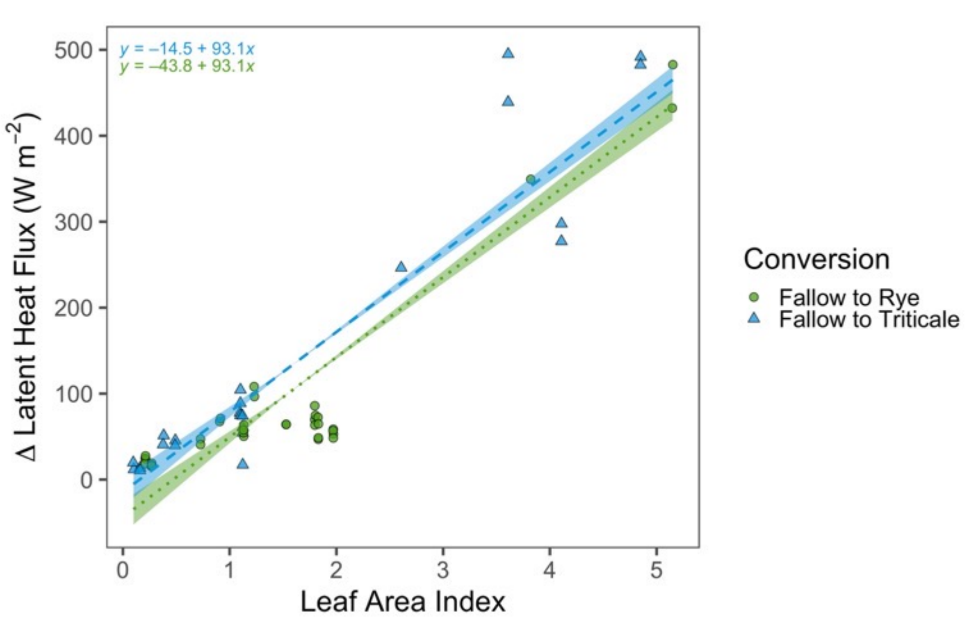
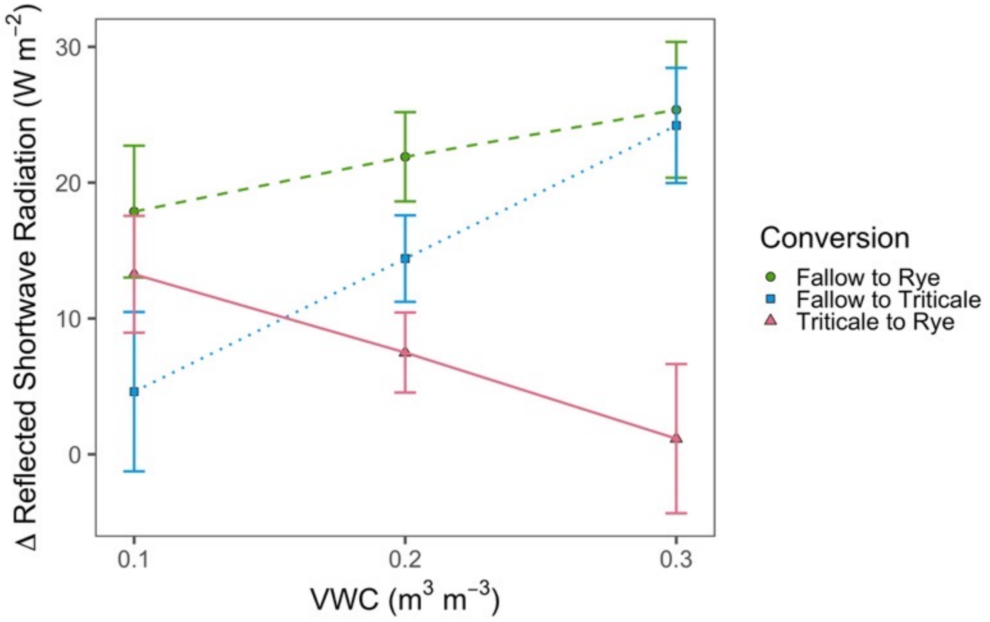
Looking forward: other ongoing and future research

Land management modifications of plant-atmosphere feedbacks





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

McNellis et al. (in review)

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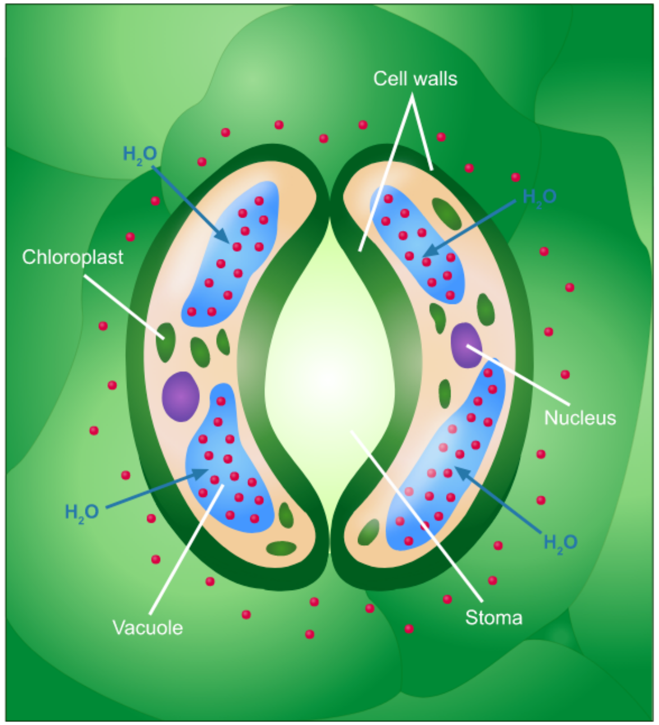

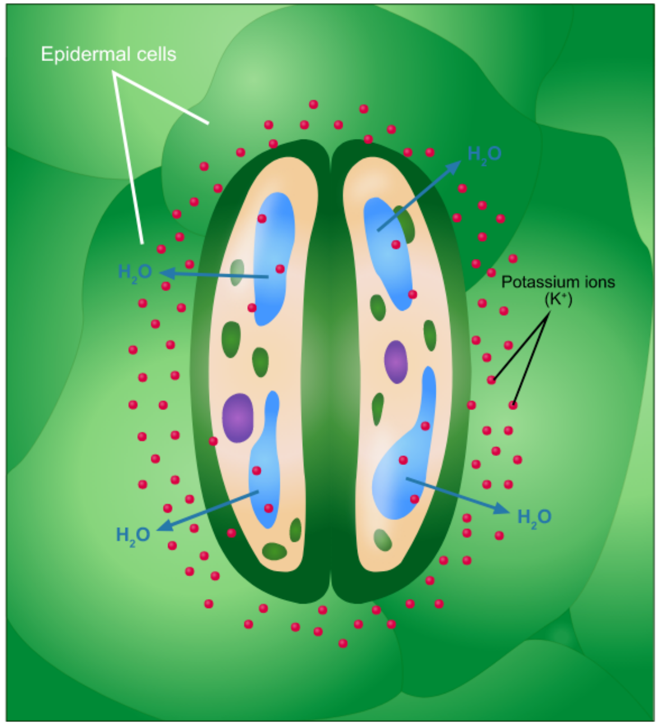

Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux

Closed stomata:

Benefits

- Low water outflux

Costs

- Low CO_2 influx

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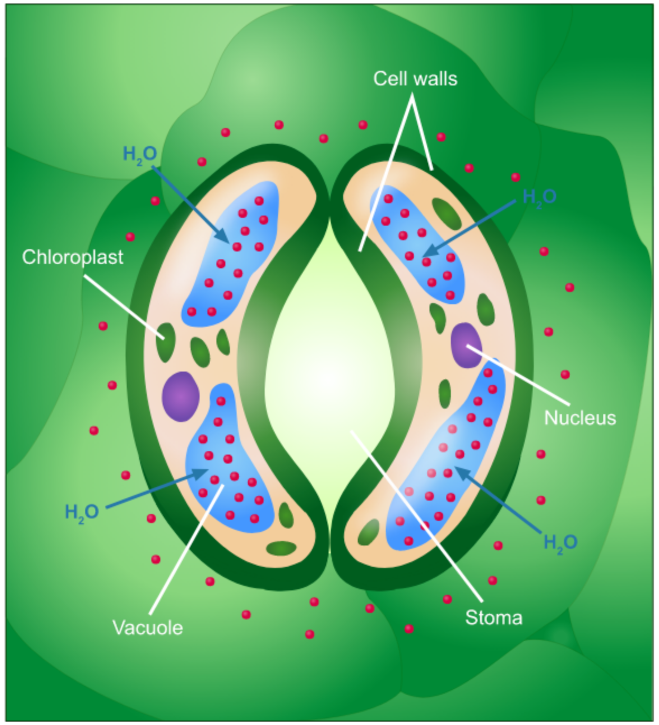

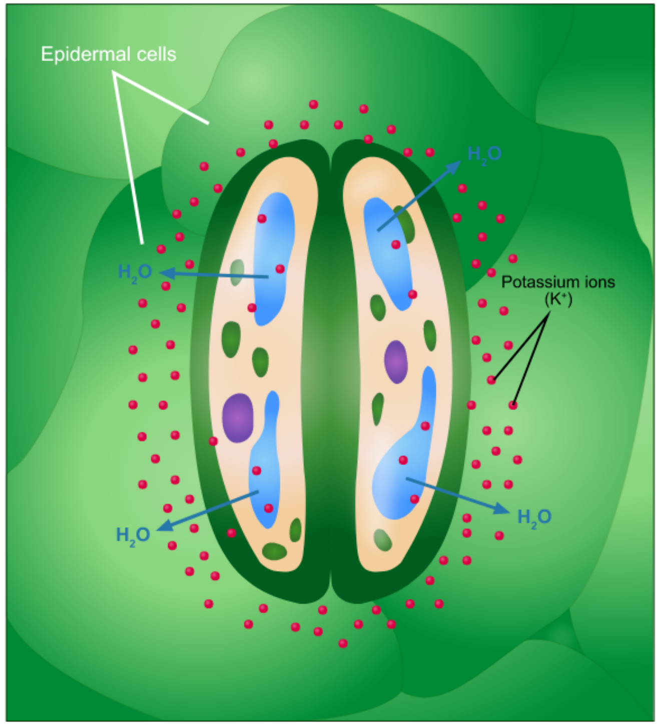

Open stomata:

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

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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 CO_2 in the leaf to CO_2 outside of the leaf (C_i/C_a)

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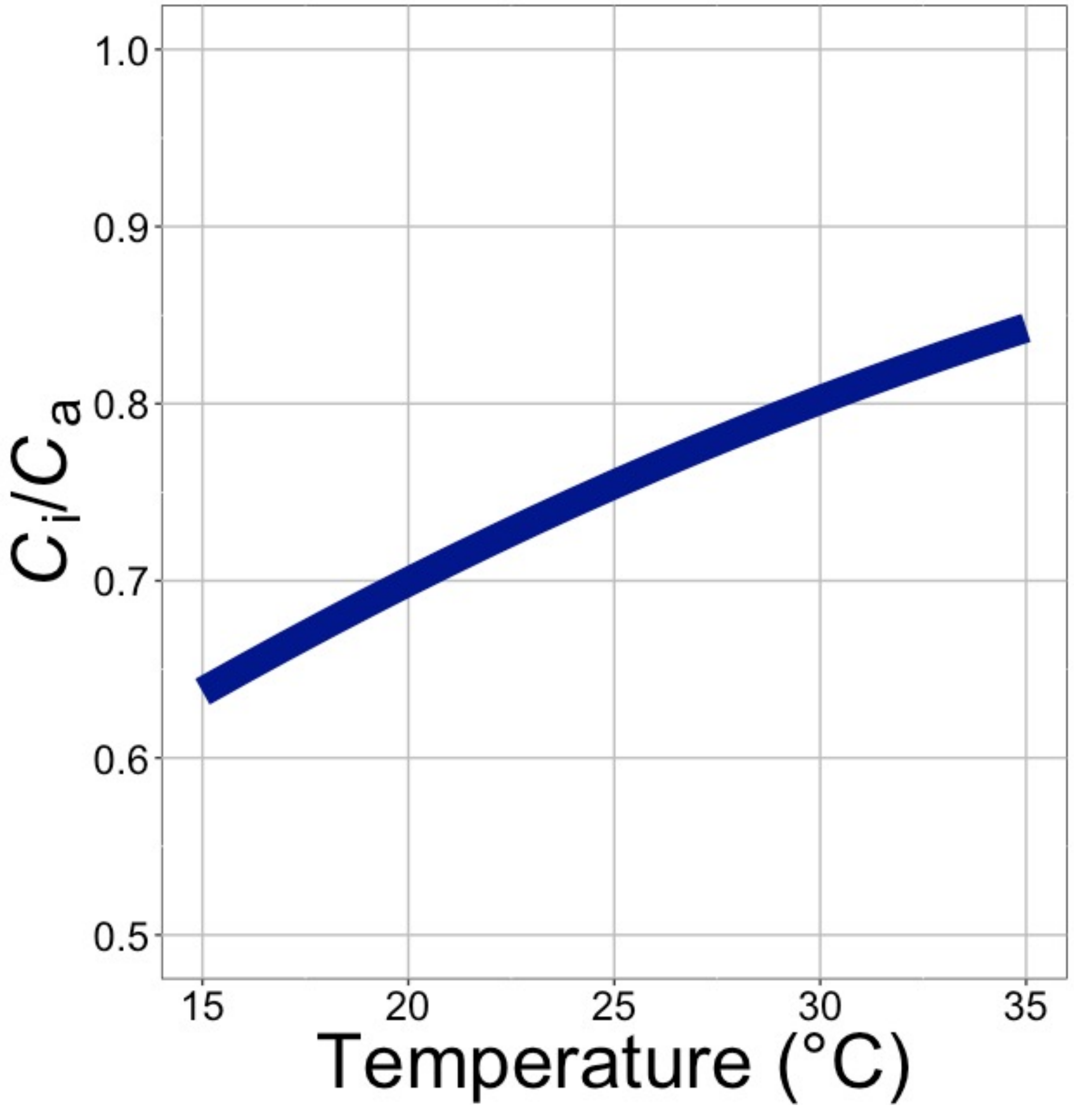

C_i/C_a increases with temperature because of greater photorespiration

Smith et al. (2019)

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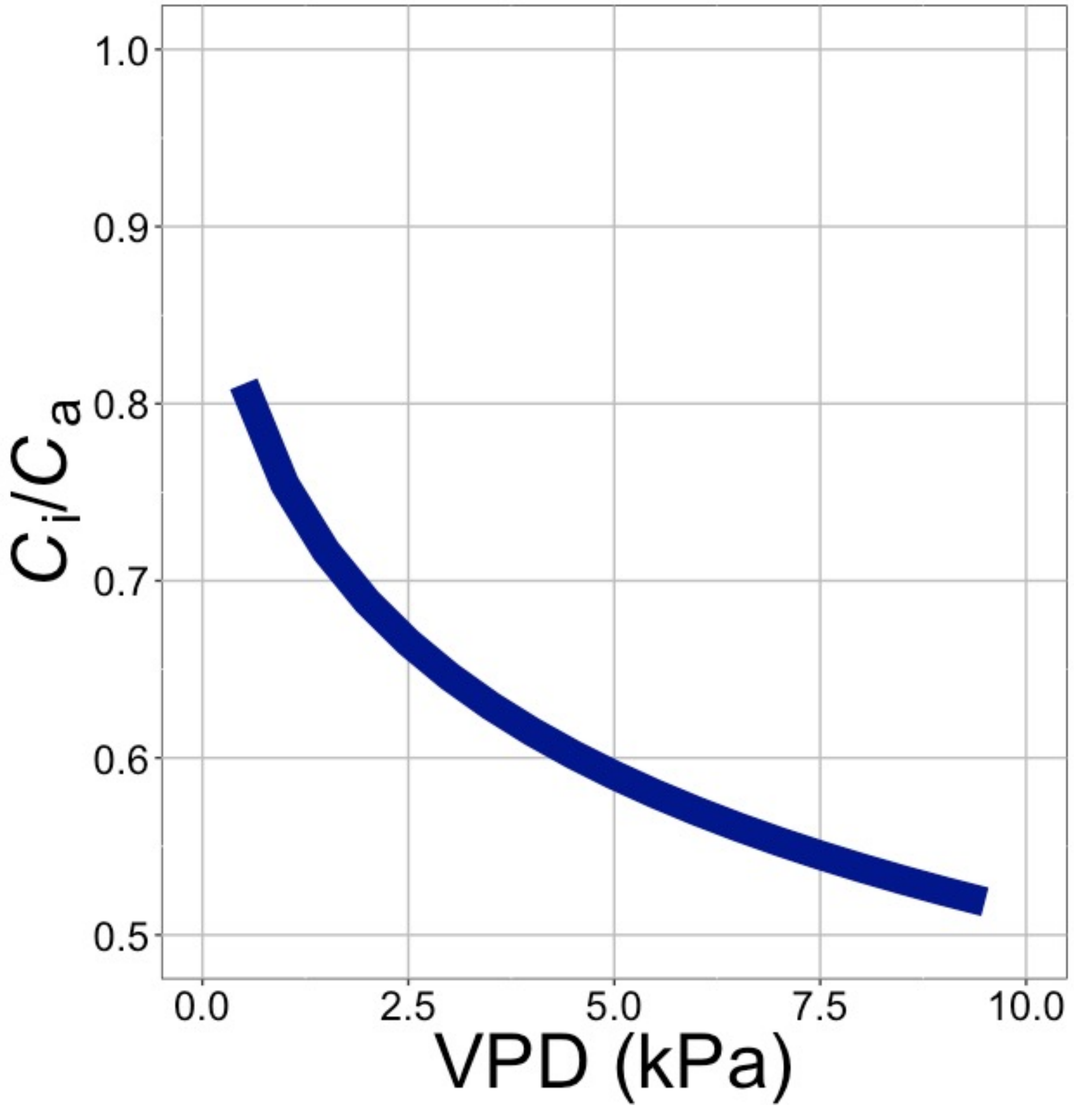
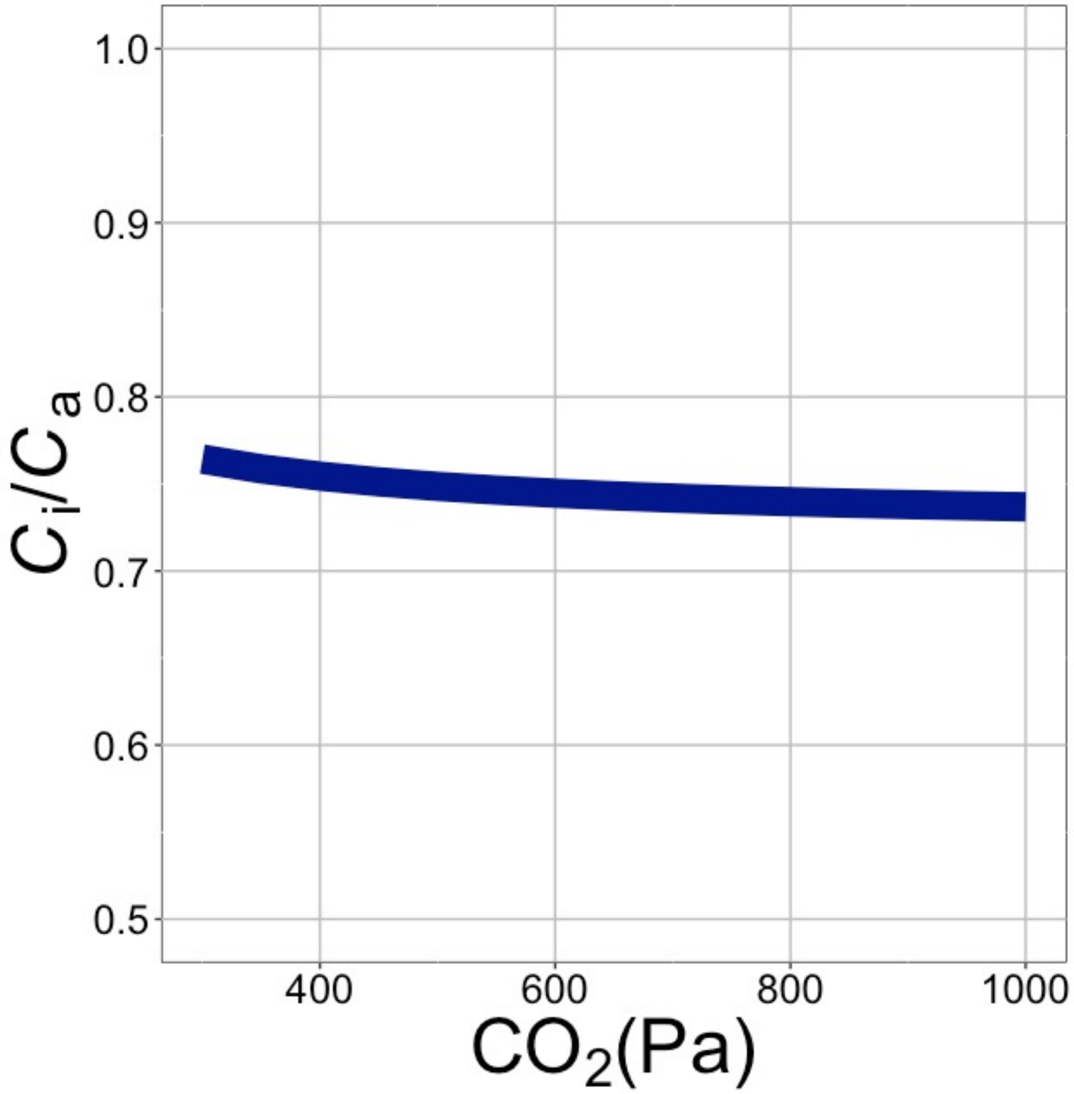


C_i/C_a decreases with VPD to avoid water loss

Smith et al. (2019)

nick.smith@ttu.edu; @nick_greg_smith



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

Smith et al. (2019)