Plants aren’t dumb

Using optimality theory to understand big questions in plant ecophysiology

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Acknowledgements

- Smith Ecophysiology Lab
  - Lizz Waring (now AProf at Northeastern State U)
  - Helen Scott (now in industry)
  - Evan Perkowski (PhD student)
  - Risa McNellis (MS Student)
- Next Generation Ecosystem Modeling Group
  - Colin Prentice (Imperial College)
  - Trevor Keenan (UC Berkeley)
  - Wang Han (Tsinghua U)
  - Beni Stocker (ETH Zurich)

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Photosynthesis is important!

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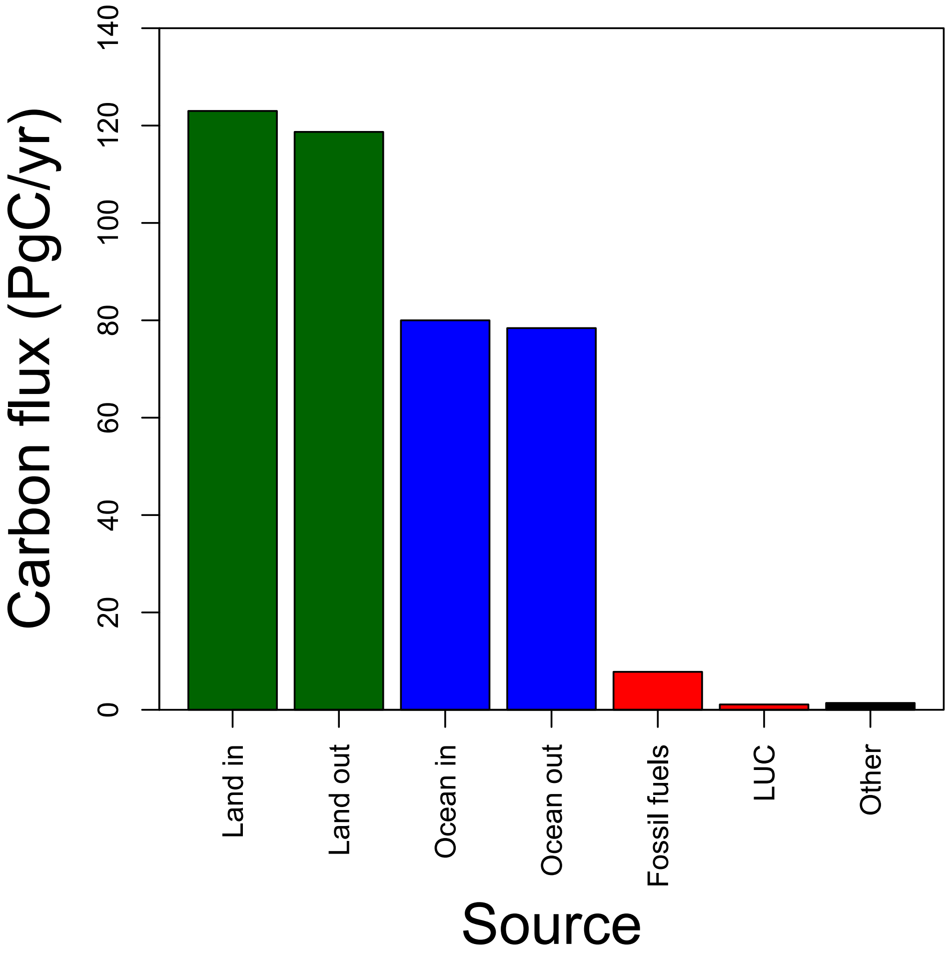
Photosynthesis is important!



Data from IPCC (2013)

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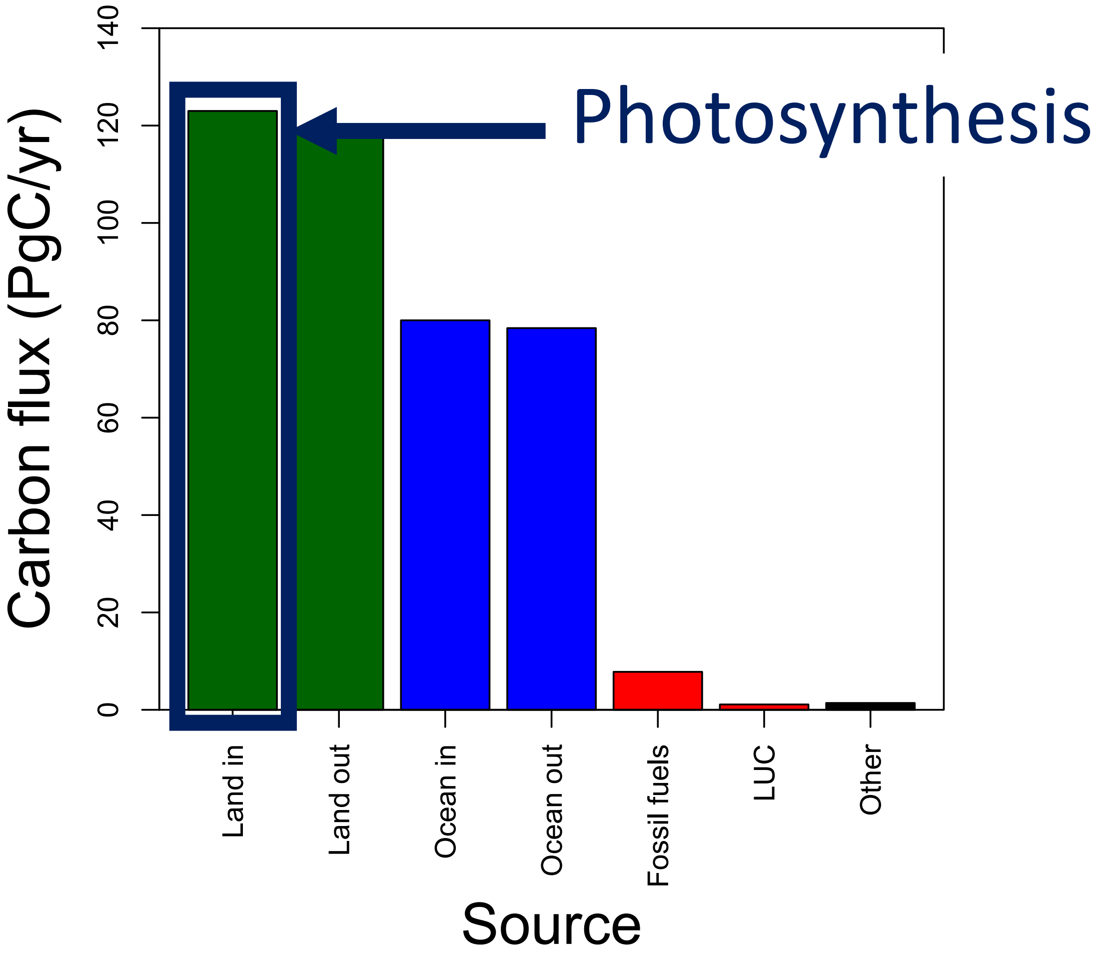
Photosynthesis is important!



Data from IPCC (2013)

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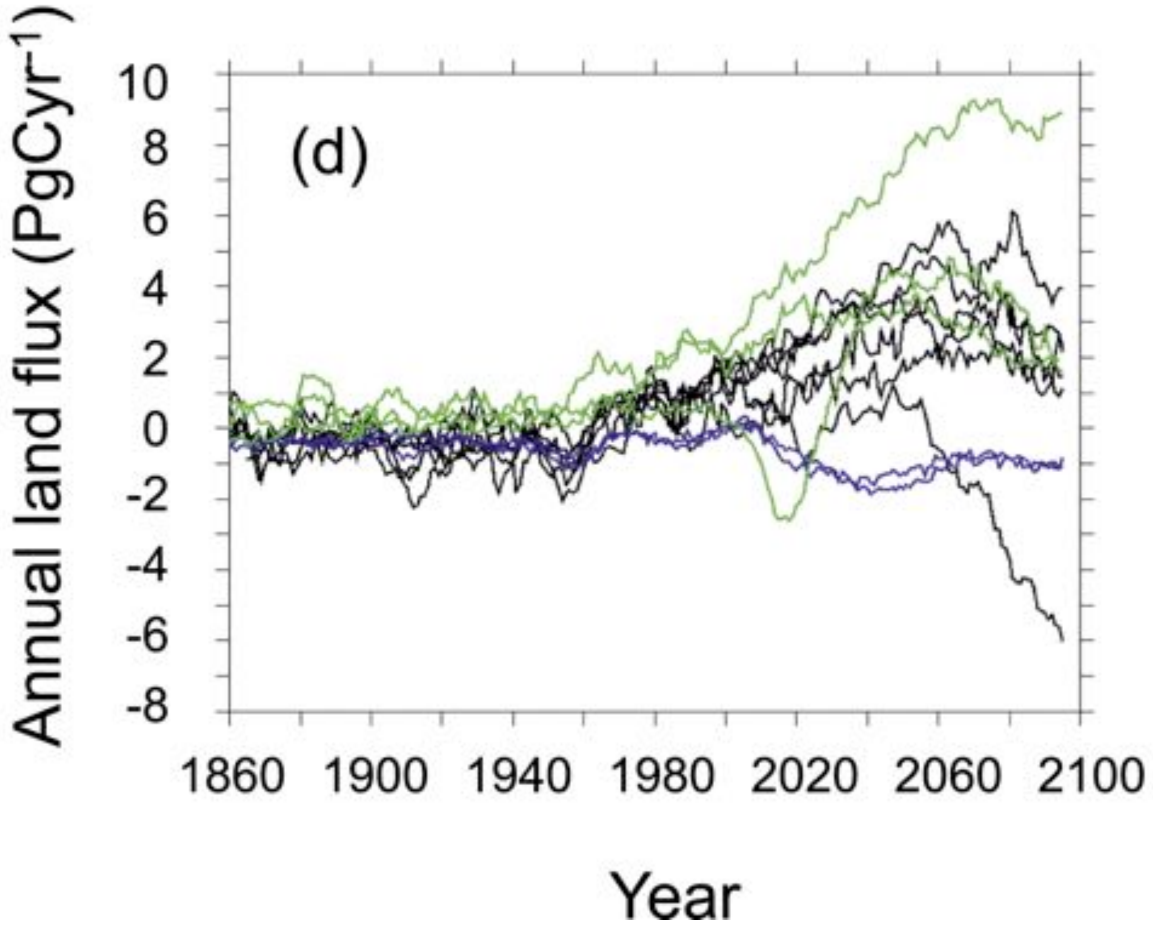
But predictions are uncertain!



Friedlingstein et al. (2014)

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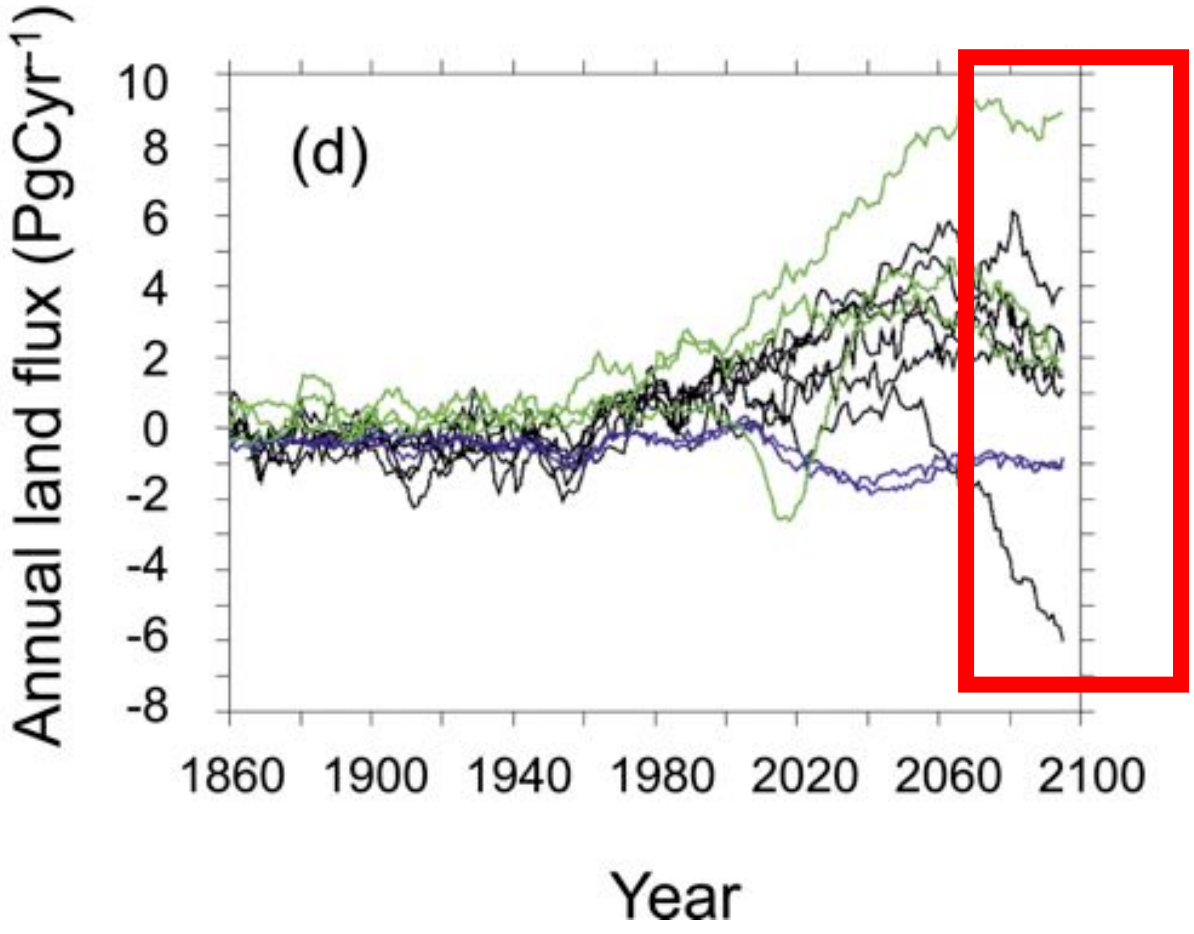
But predictions are uncertain!



Model uncertainty > fossil fuel emissions

Friedlingstein et al. (2014)

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Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

Planta

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

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

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

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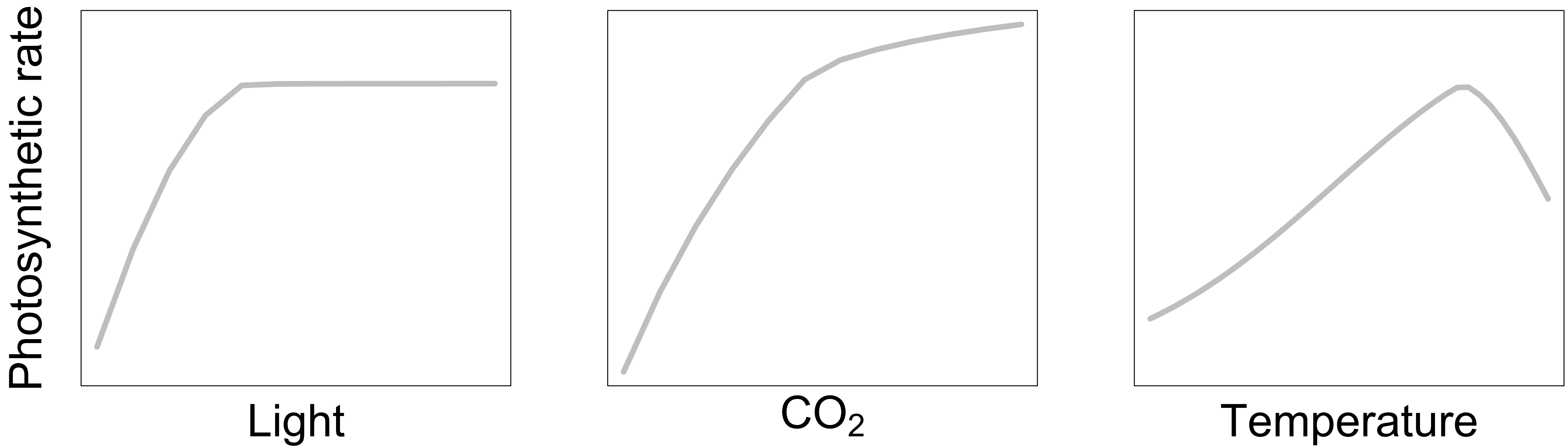
These produce short term responses that match data



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Long-term responses can differ from short-term responses due to acclimation

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Long-term responses can differ from short-term responses due to acclimation

~~Dumb plants~~

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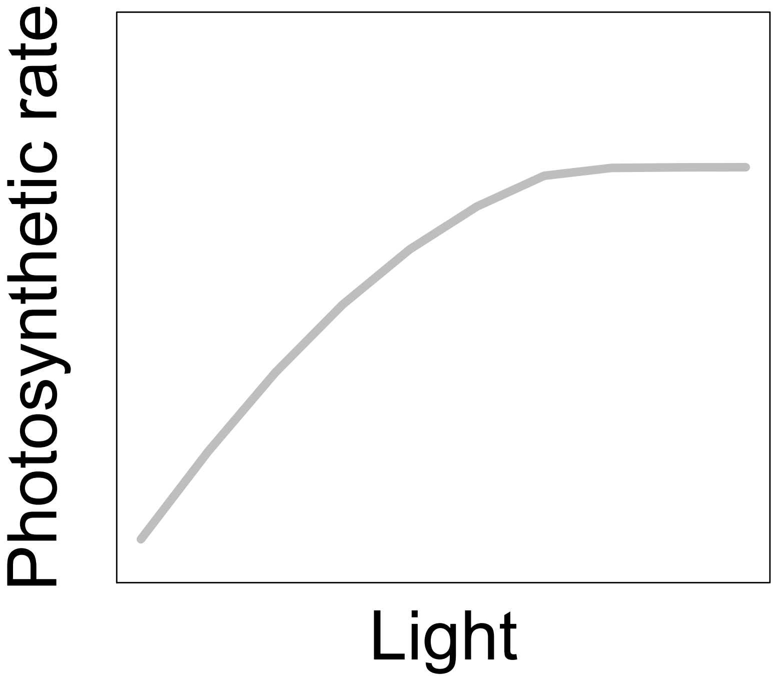
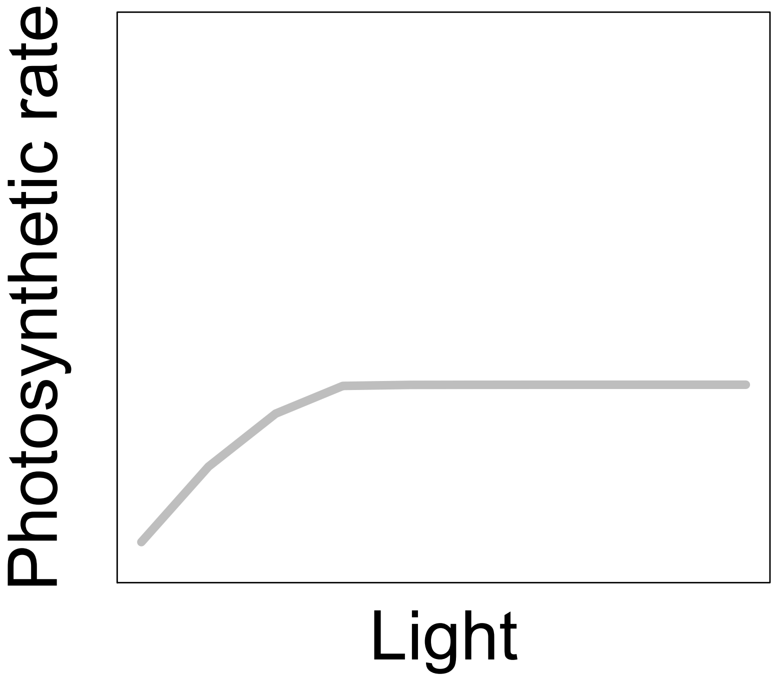
Long-term responses can differ from short-term responses due to acclimation

Acclimated to high light



Acclimated to low light



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Acclimation is ubiquitous and well known...

CO_2: Bazzaz (1990)

Annu. Rev. Ecol. Syst. 1990. 21:167–96

THE RESPONSE OF NATURAL ECOSYSTEMS TO THE RISING GLOBAL CO_2 LEVELS

F. A. Bazzaz

Light: Boardman (1977)

Ann. Rev. Plant Physiol. 1977. 28:355–77

COMPARATIVE PHOTOSYNTHESIS OF SUN AND SHADE PLANTS

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

Temperature: Berry & Björkman (1980)

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

PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

Joseph Berry and Olle Björkman[1]

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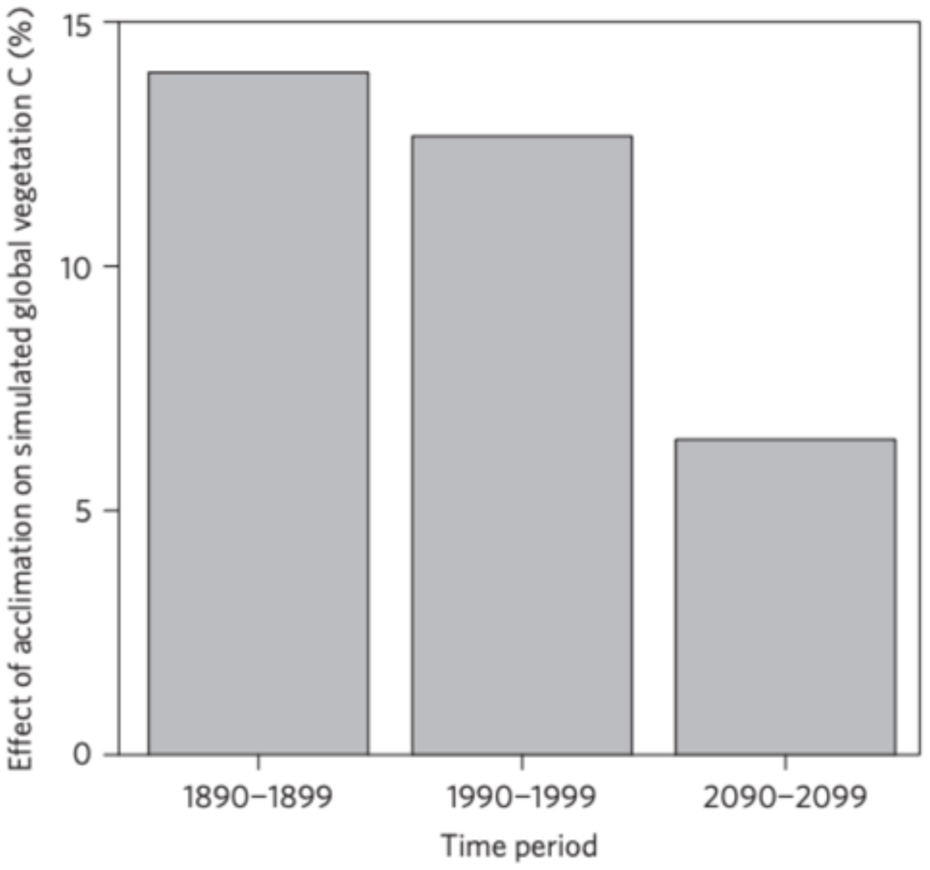
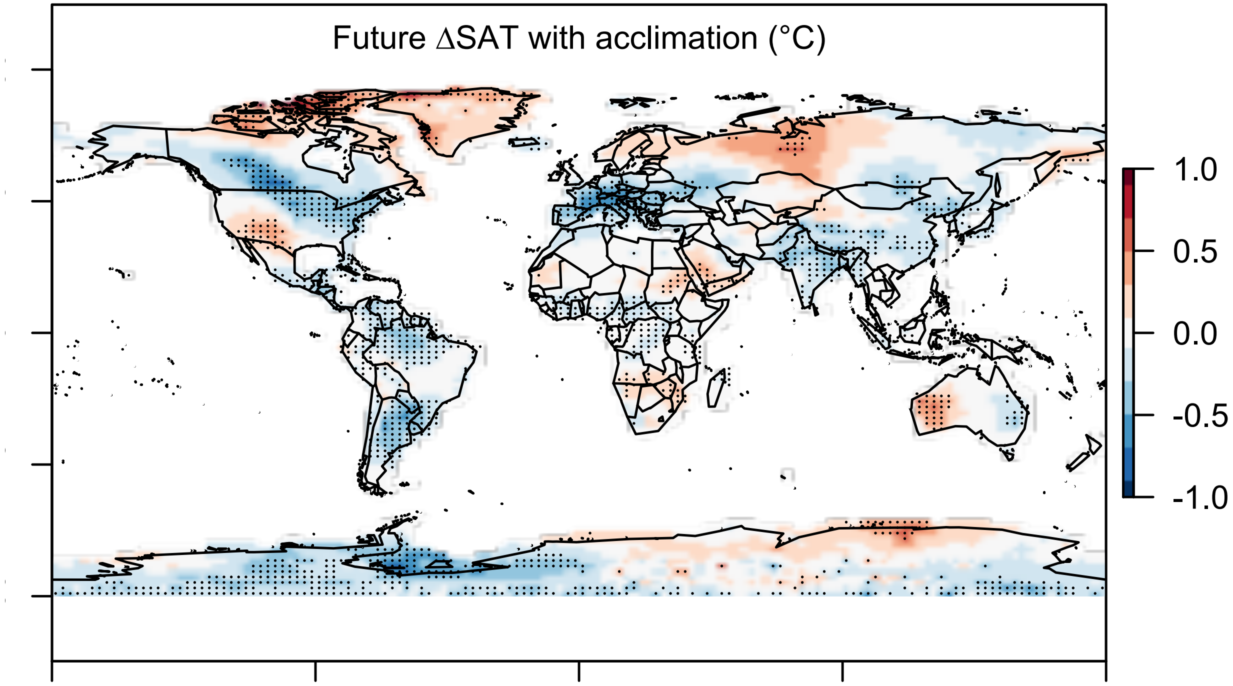
…and can possibly impact carbon cycling and climate

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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Here's the rub:

No theoretical model for photosynthetic acclimation exists

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Lack of theory results in...

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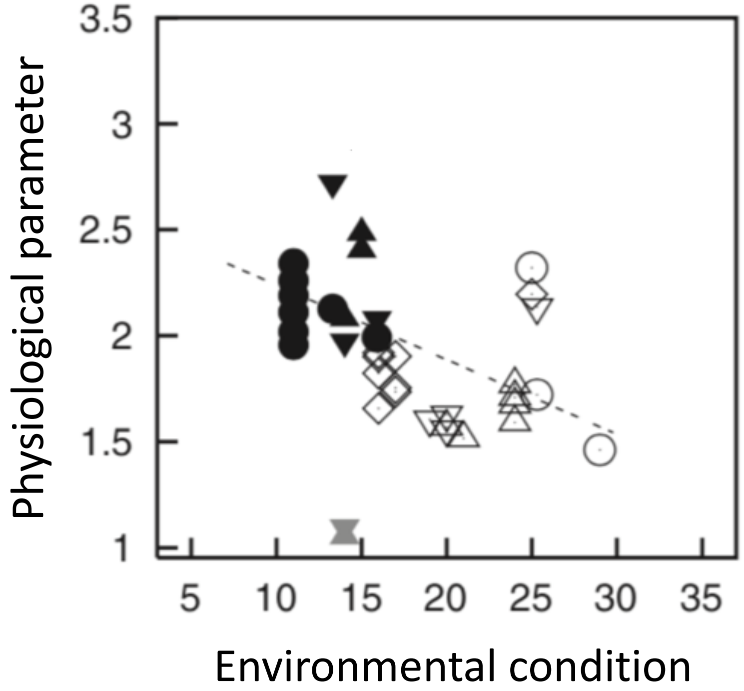
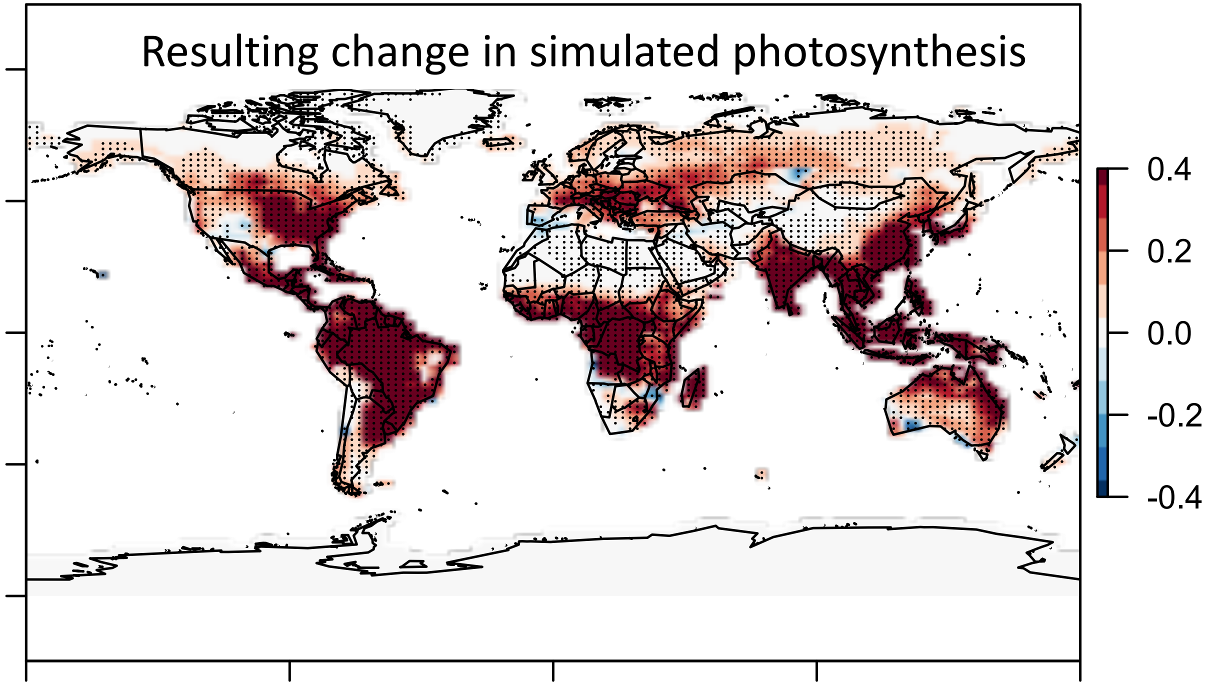
Lack of theory results in…

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





Kattge and Knorr (2007) *PC&E*

Smith et al. (2017) *JAMES*

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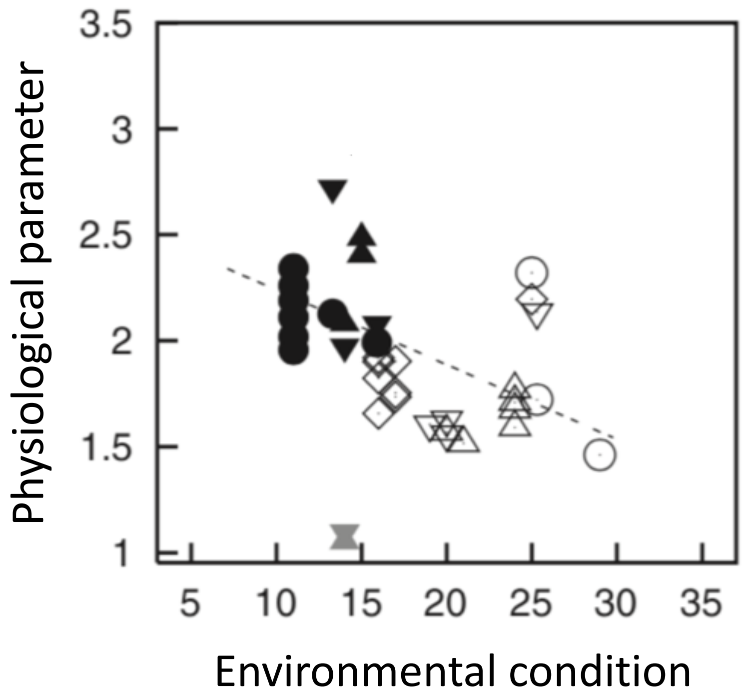
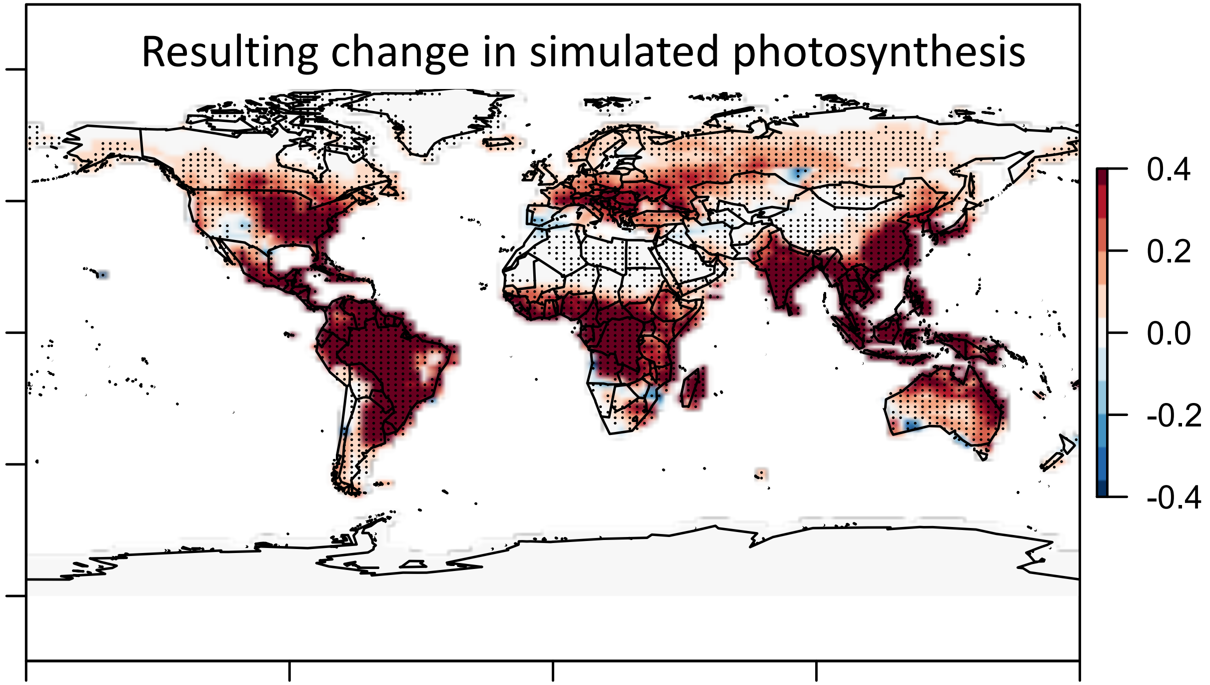
Lack of theory results in…

- 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

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Optimization: Least cost hypothesis

Maintain fastest rate of photosynthesis at the lowest cost (water and nutrient use)

Wright et al. (2003) *American Naturalist*

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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}

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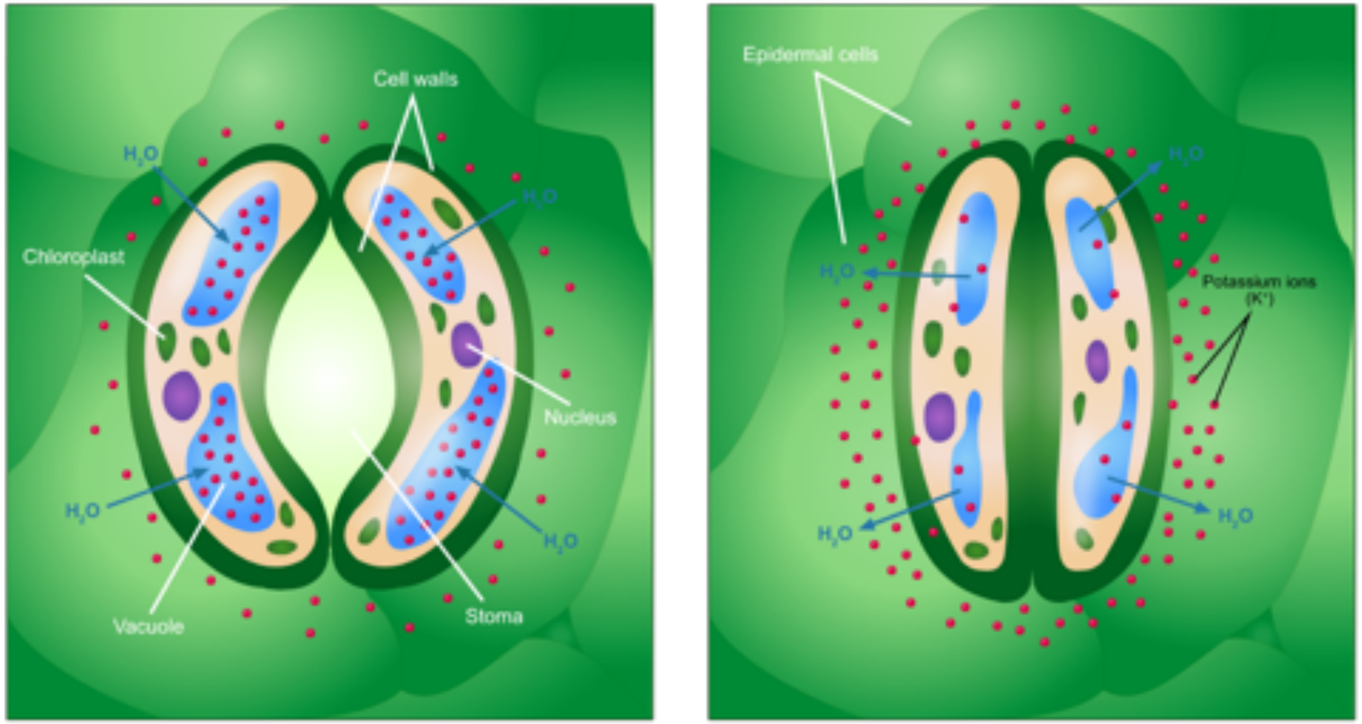

Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux

Closed stomata:

Benefits

- Low water outflux

Costs

- Low CO_2 influx

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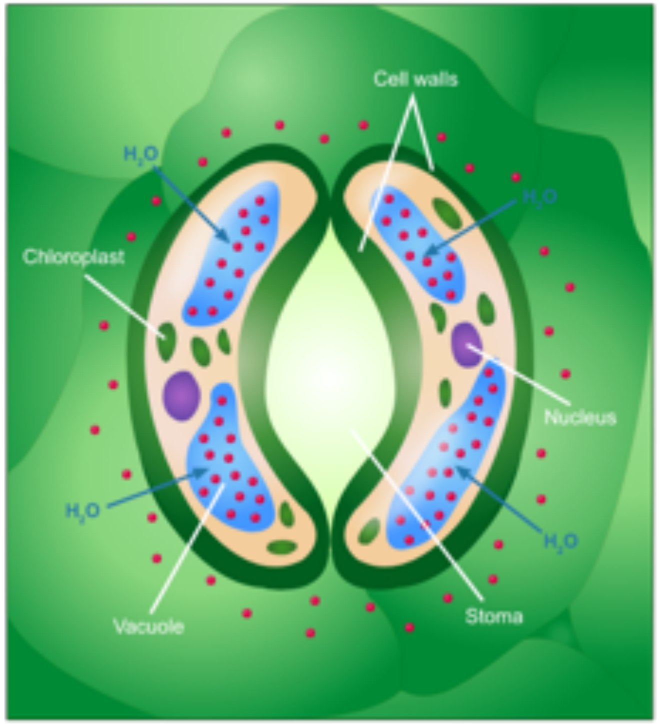

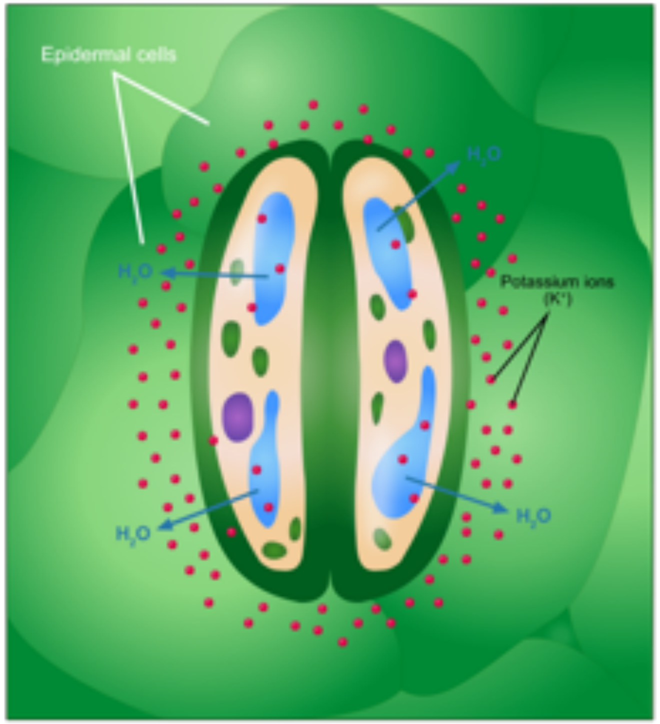

Open stomata:

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
  - Rubisco proxy is V_{cmax}

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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$$C_i/C_a = f\{\text{temperature},\ CO_2,\ \text{vapor pressure deficit}\}$$

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

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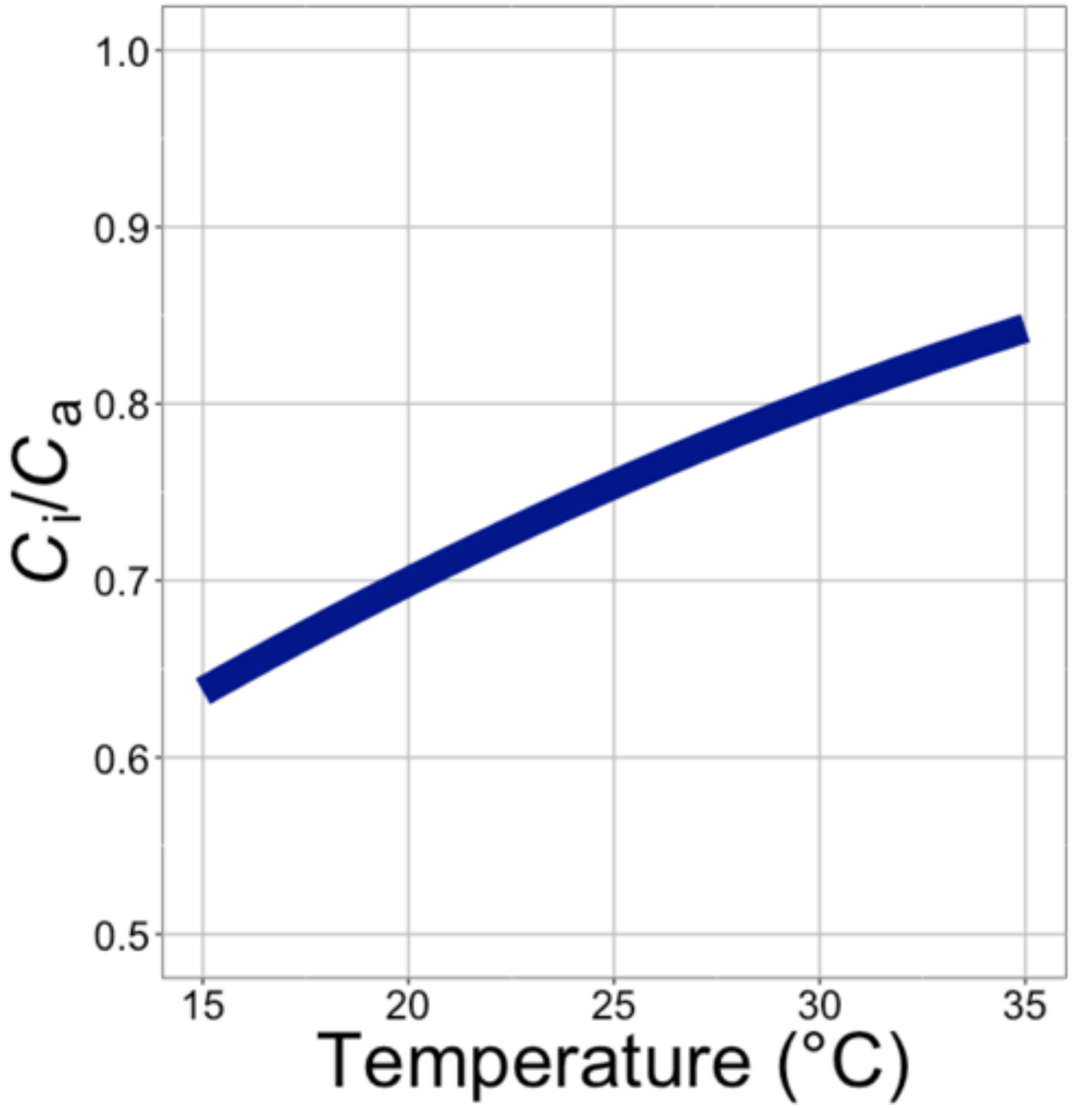

C_i/C_a increases with temperature because of greater photorespiration

Smith et al. (2019)

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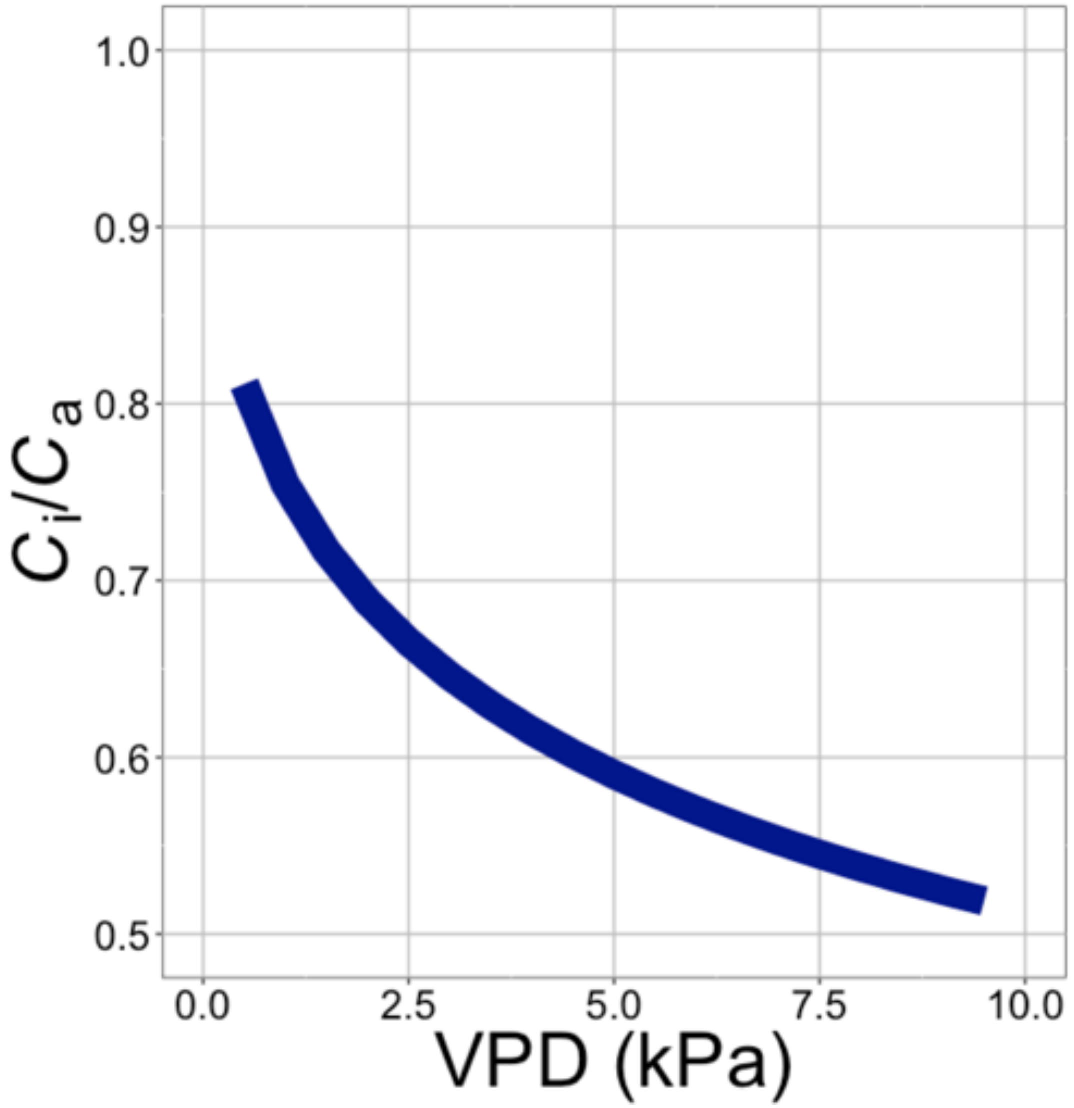

C_i/C_a decreases with VPD because of greater water loss

Smith et al. (2019)

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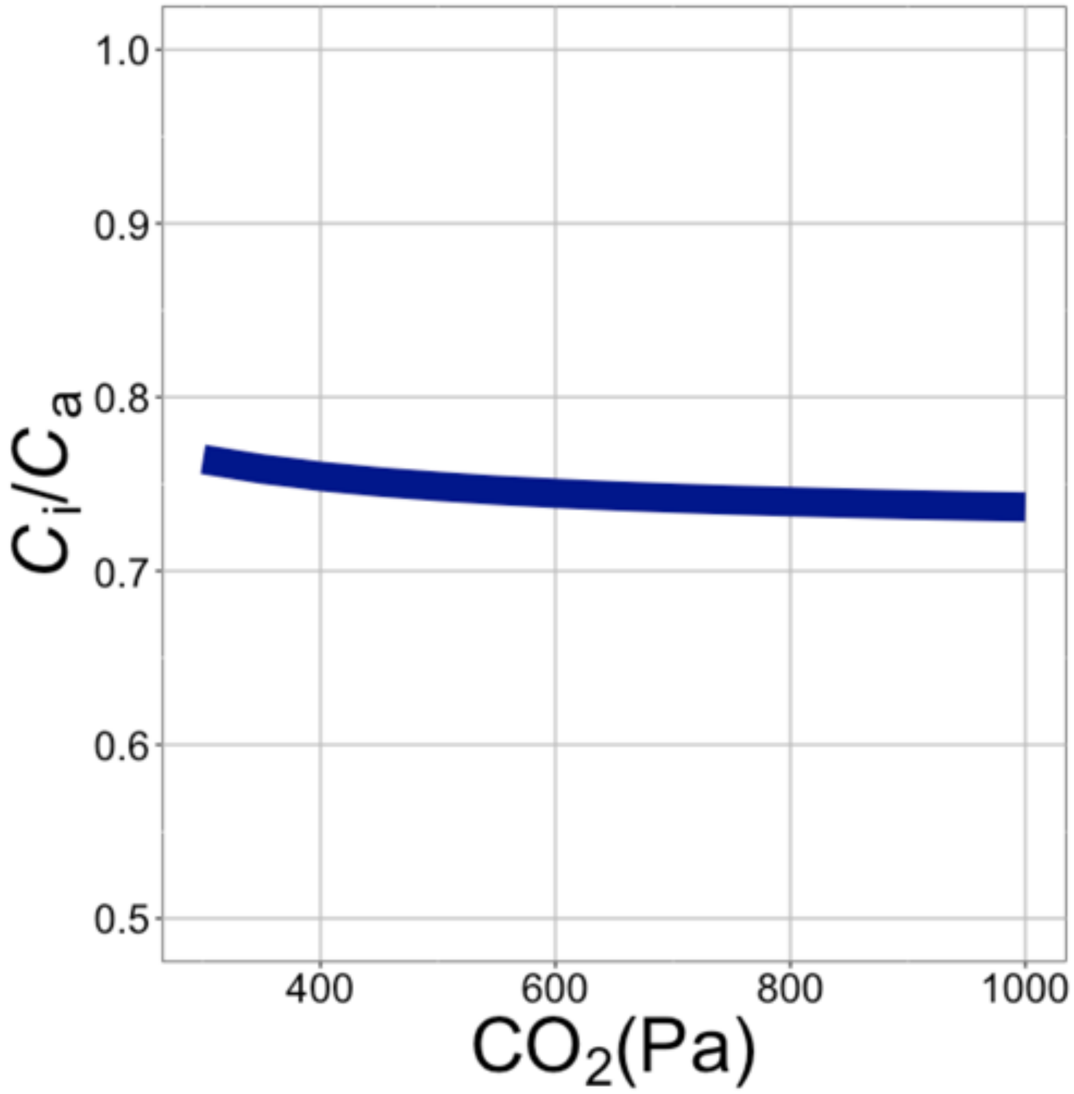

C_i/C_a decreases with CO_2 because of lower openness needed to satisfy Rubisco

Smith et al. (2019)

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Optimal photosynthesis

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

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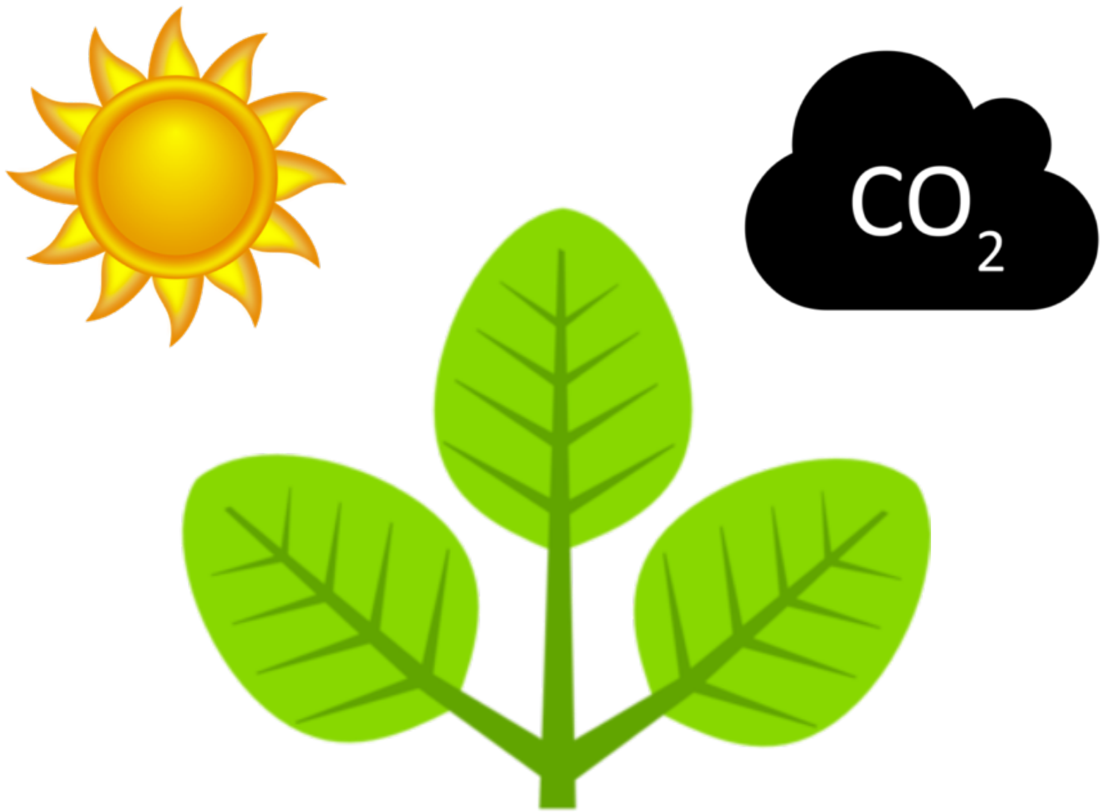
Biochemistry optimization: Coordination hypothesis



Plant biochemistry setup will aim for equal limitation by all factors

Biochemistry trait

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

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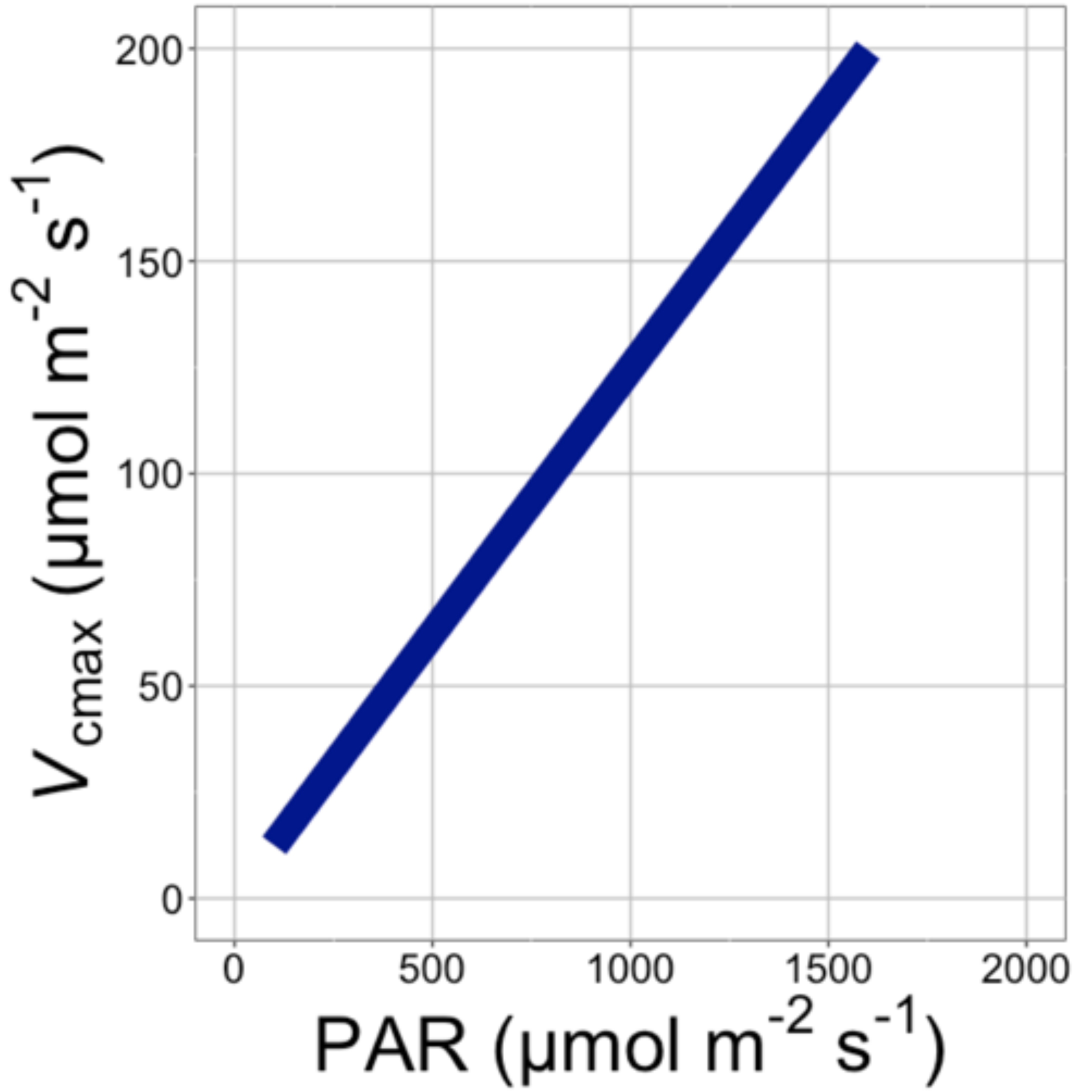
$$V_{cmax} = f\ \{\text{light, T, CO}_2\}$$

Smith et al. (2019)

nick.smith@ttu.edu; @nick_greg_smith



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

Smith et al. (2019)

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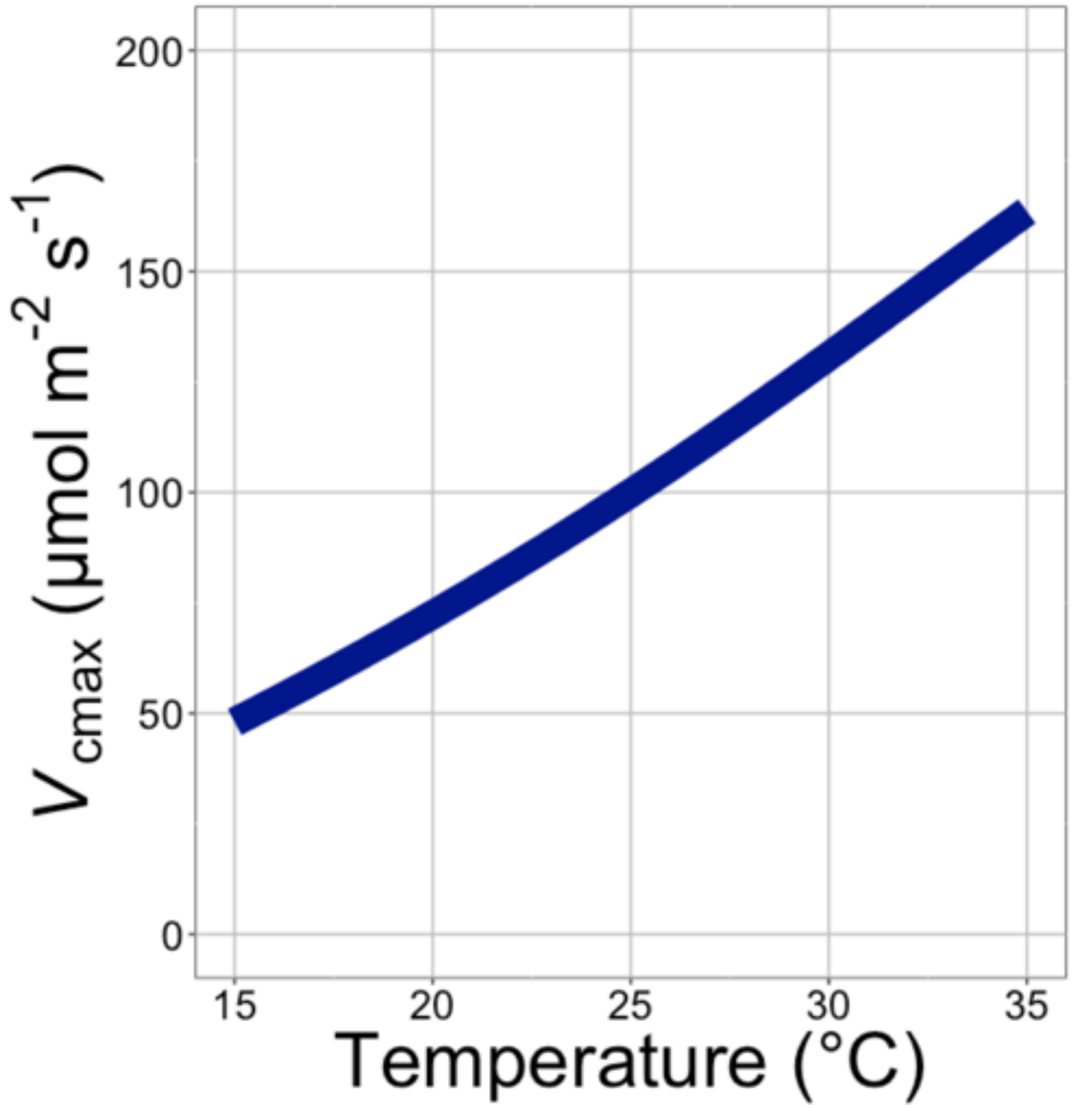

V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019)

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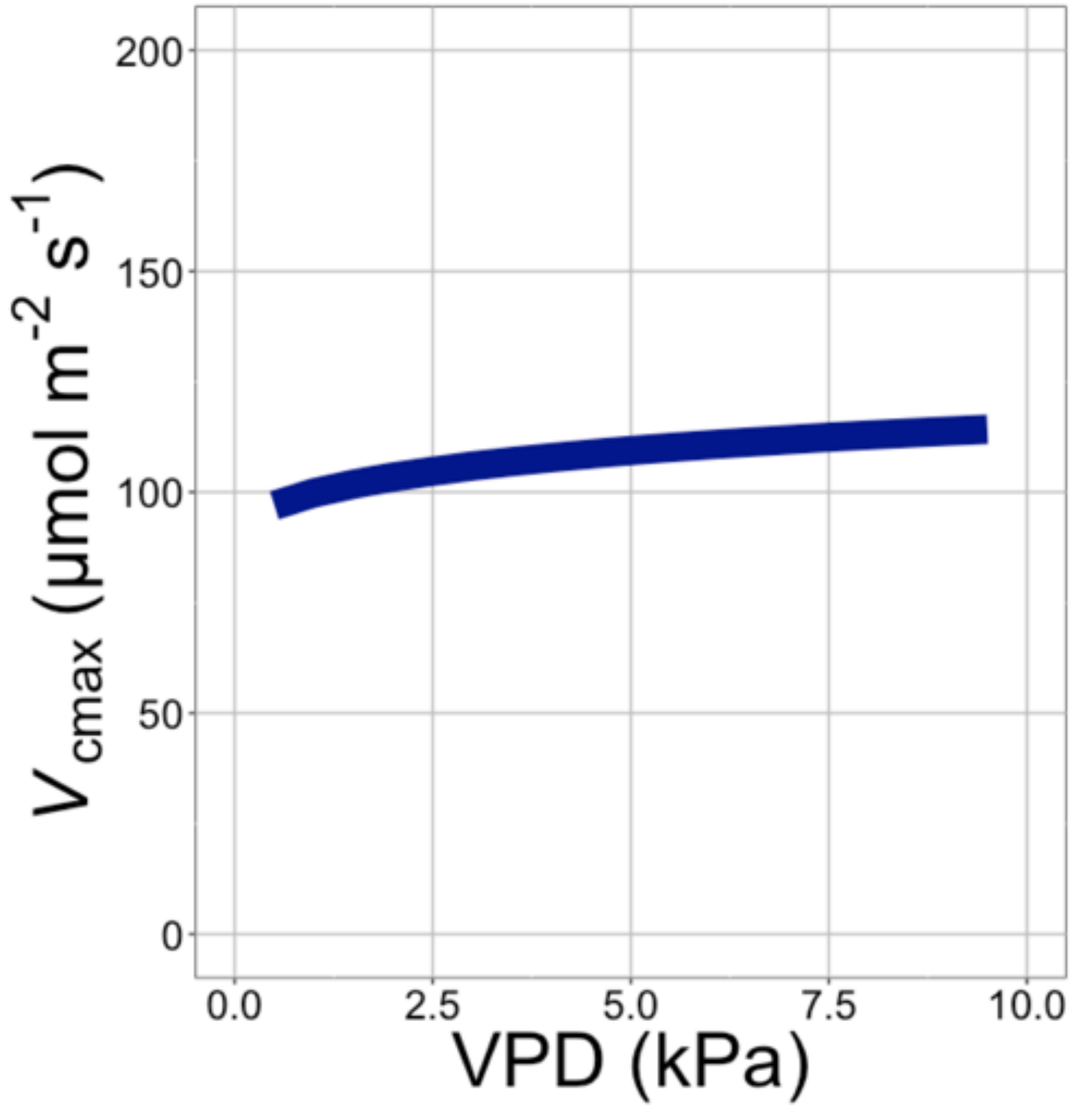

V_{cmax} increases with VPD because of lower stomatal conductance

Smith et al. (2019)

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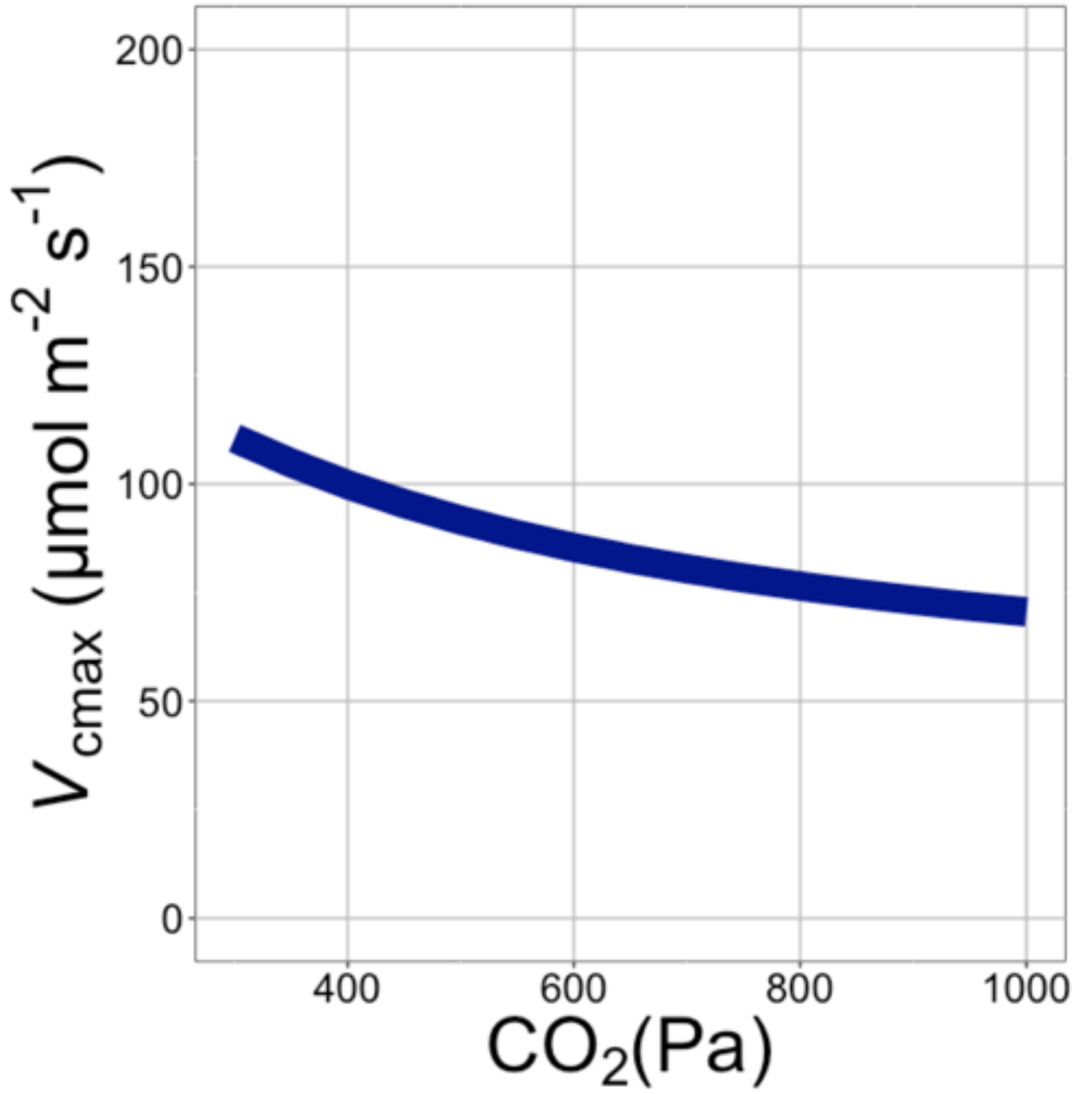

V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf

Smith et al. (2019)

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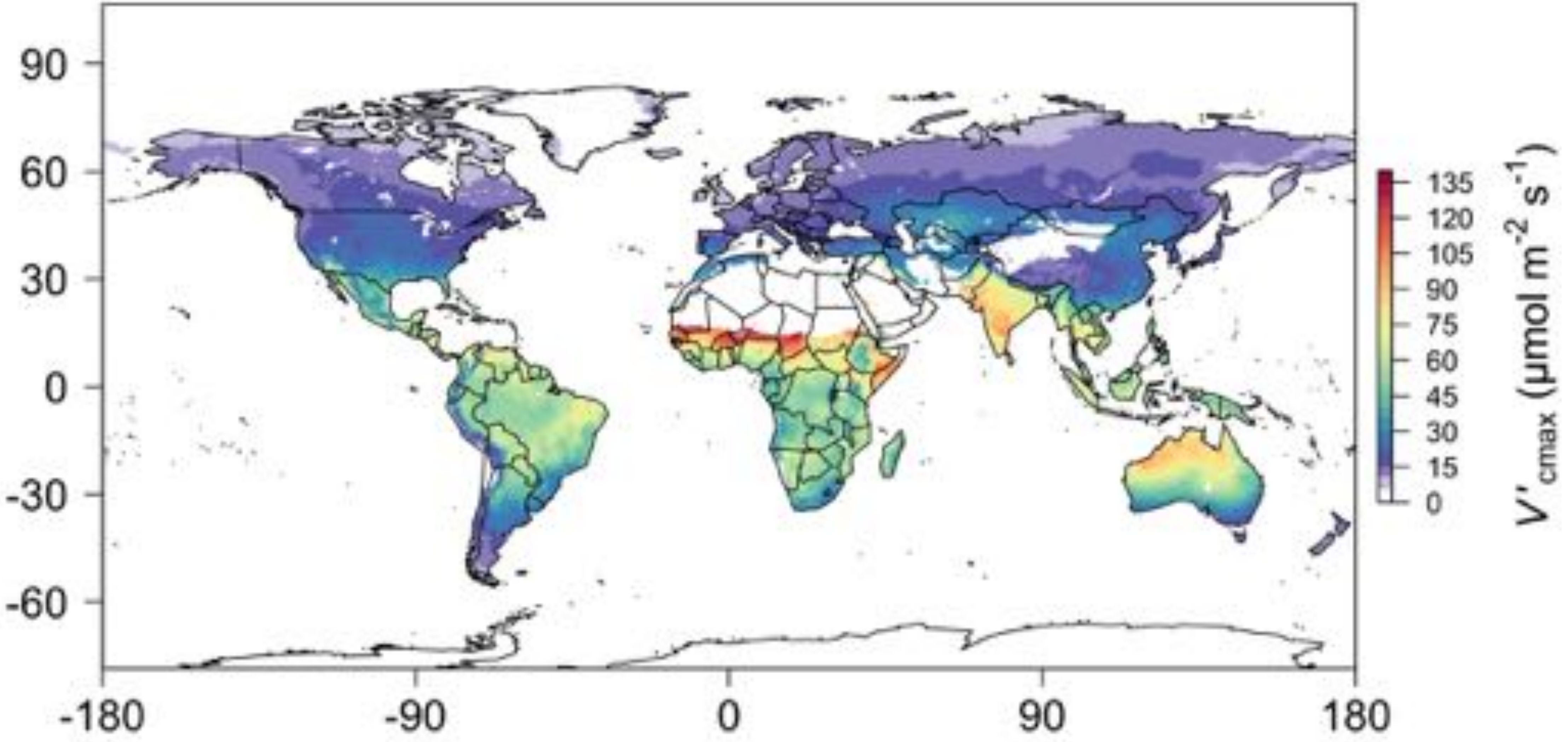
Global, optimally acclimated traits!



Smith et al. (2019)

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Ok, great, but now what?

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Let’s tackle some big questions in plant ecophysiology!

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Question 1: Is photosynthesis optimized to the environment?

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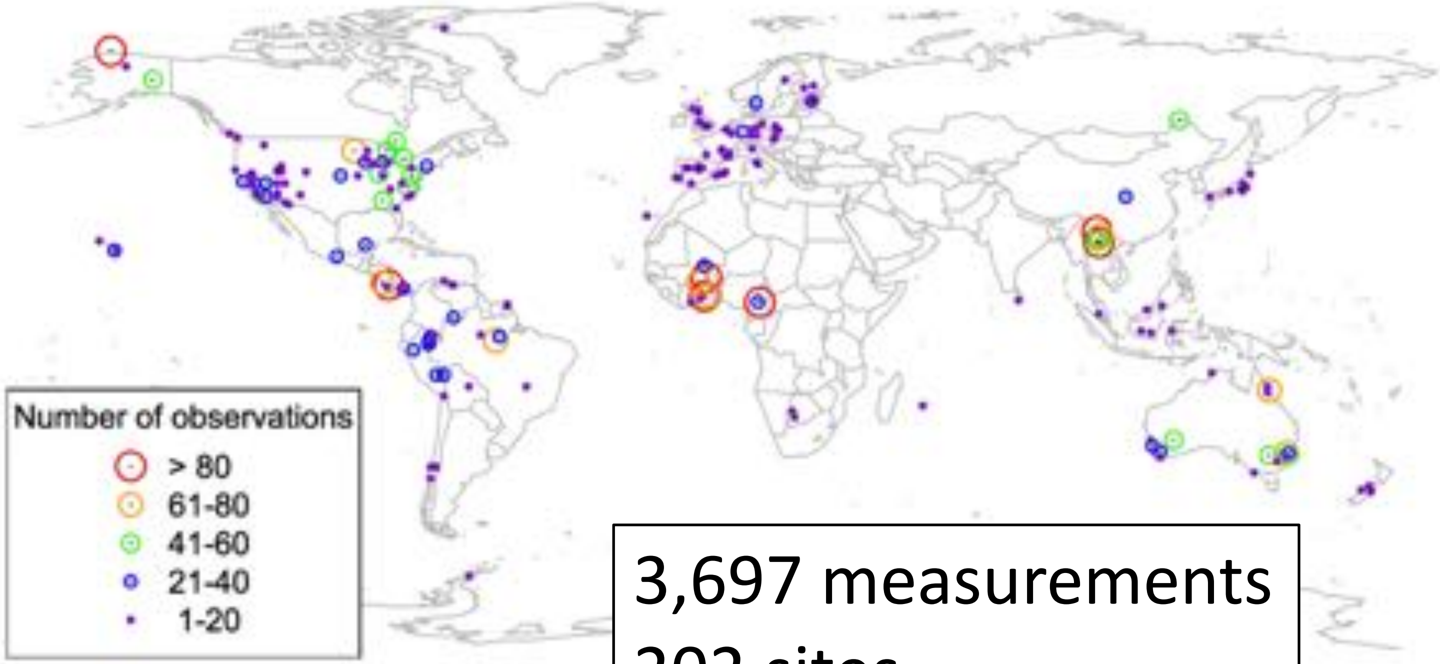
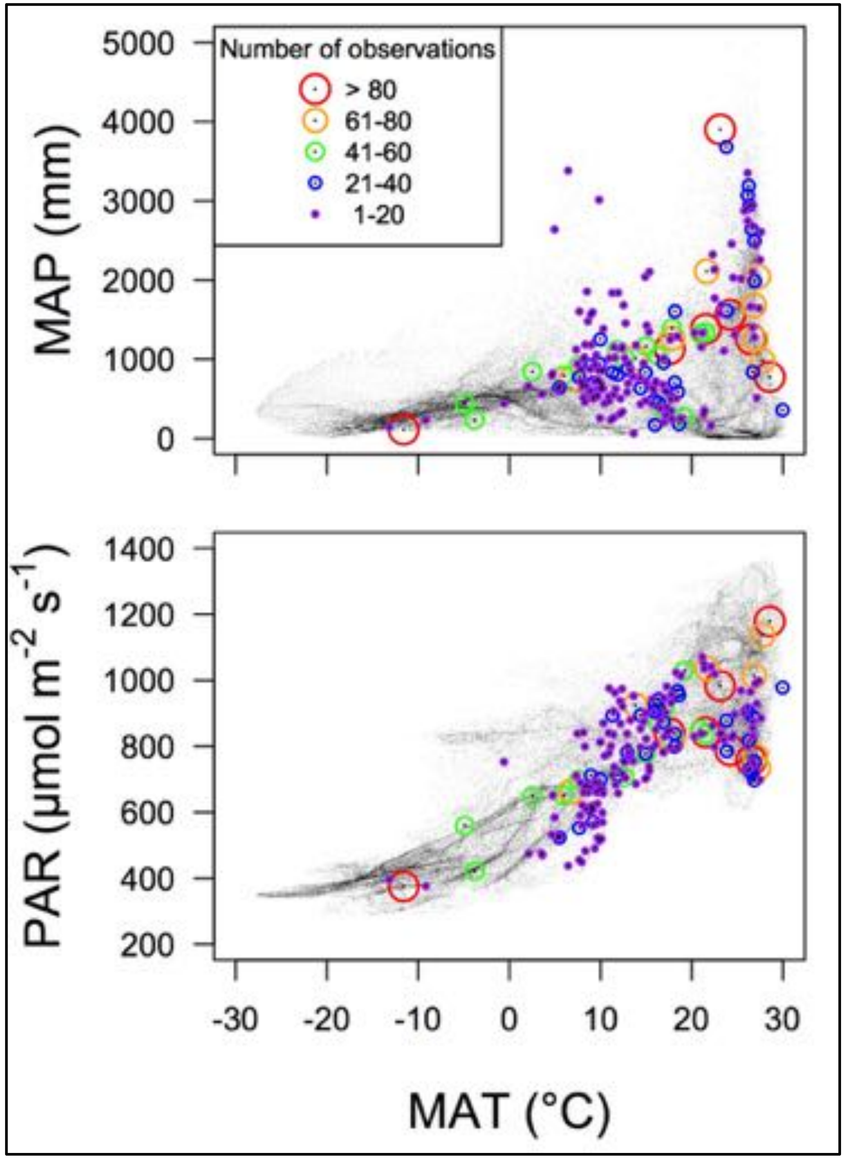
Global V_{cmax} dataset



3,697 measurements
202 sites
> 600 genera



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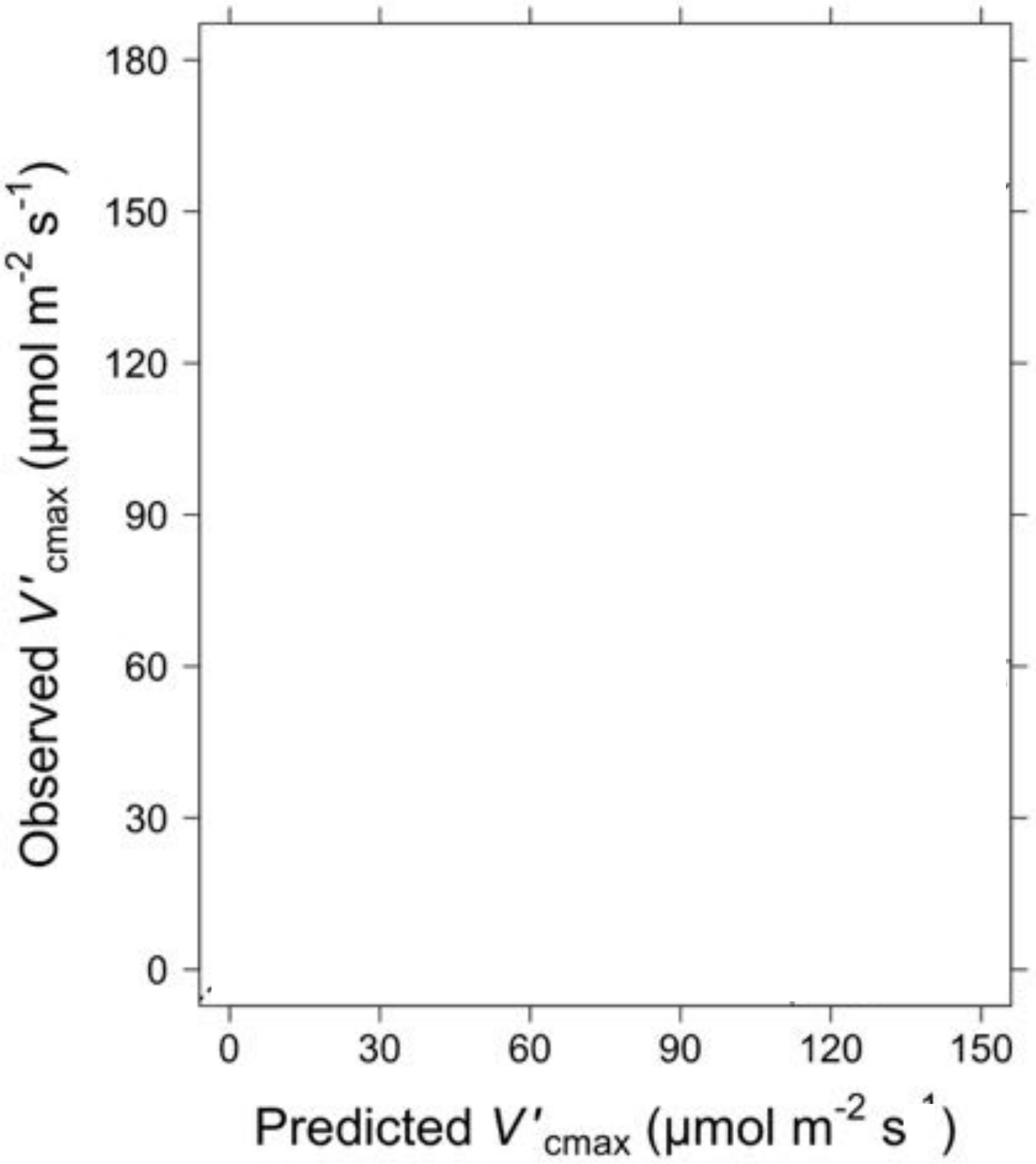

Smith et al. (2019)

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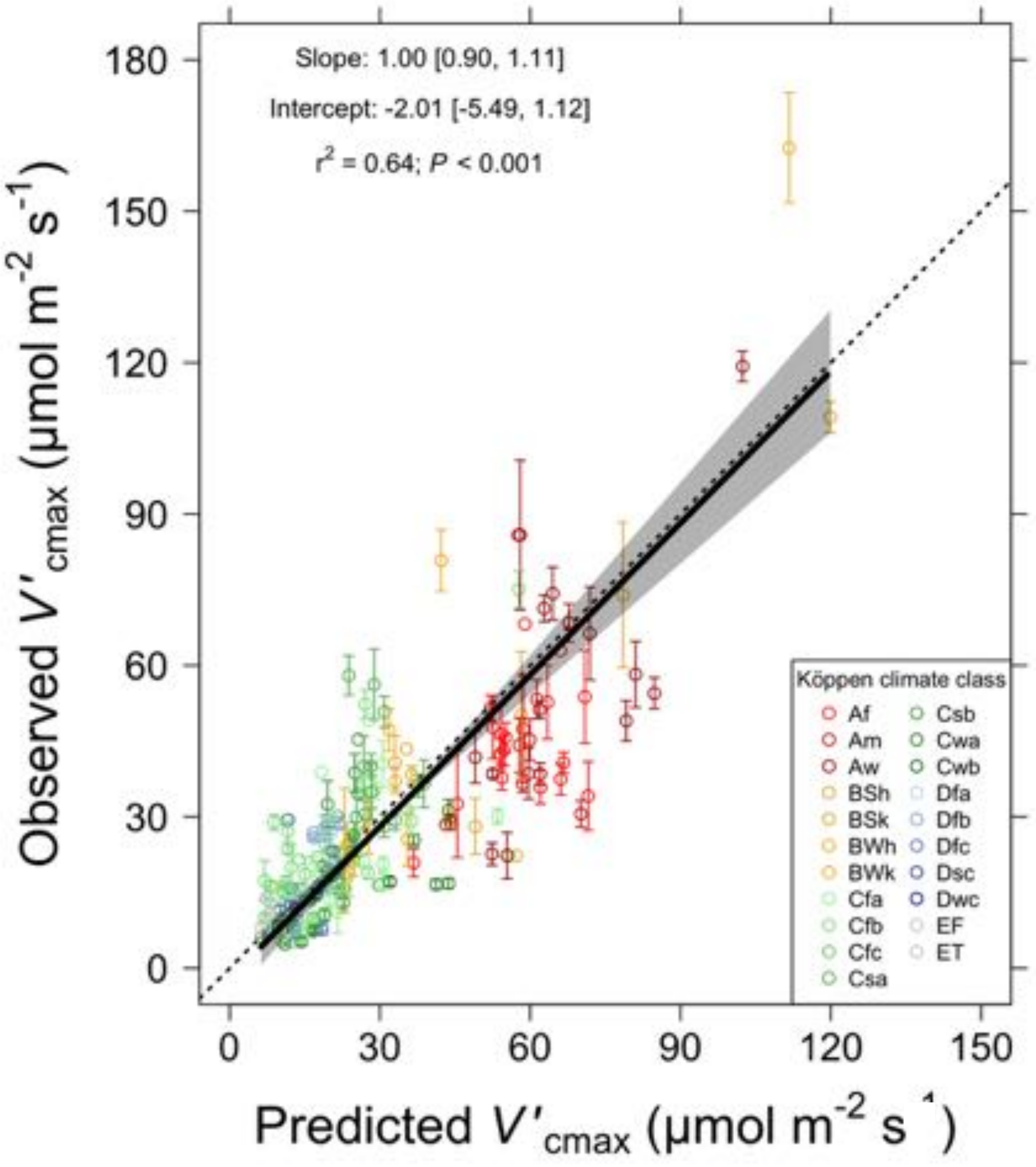

Optimal V_{cmax} is similar to observed values

Smith et al. (2019)

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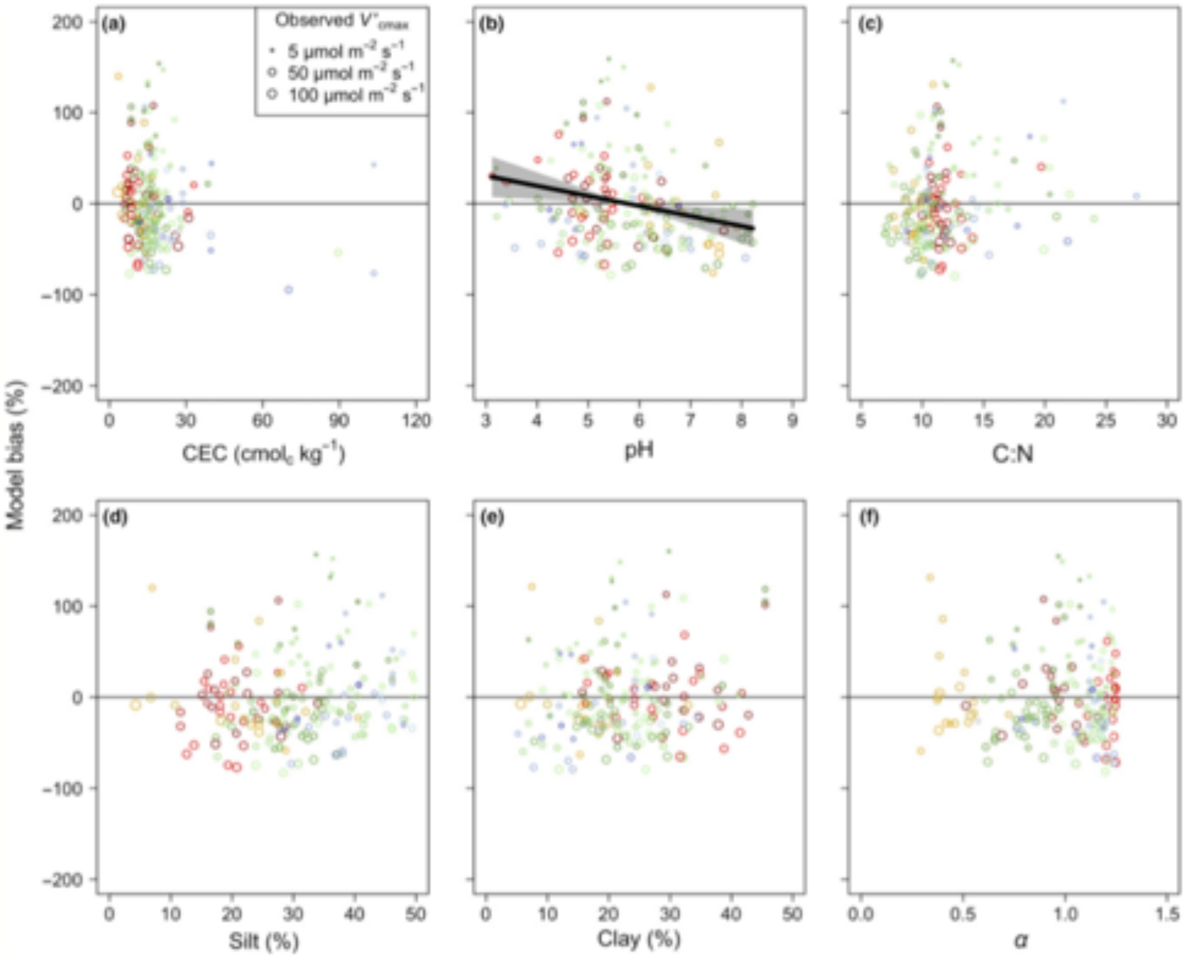
There is little effect of soils on V_{cmax}



Soil increased explained variation from 64% to 68% compared to optimal response alone

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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Question 2: Does photosynthesis respond to soil nutrients?

Lizz Waring
TTU

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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…

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

Optimal response would be to increase leaf area

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But let’s test it experimentally

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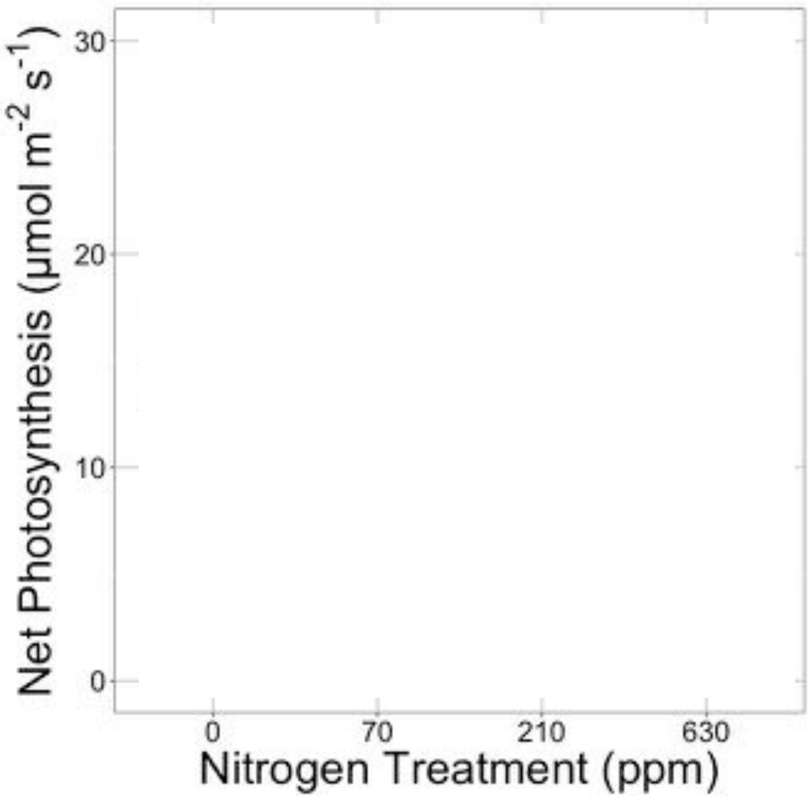

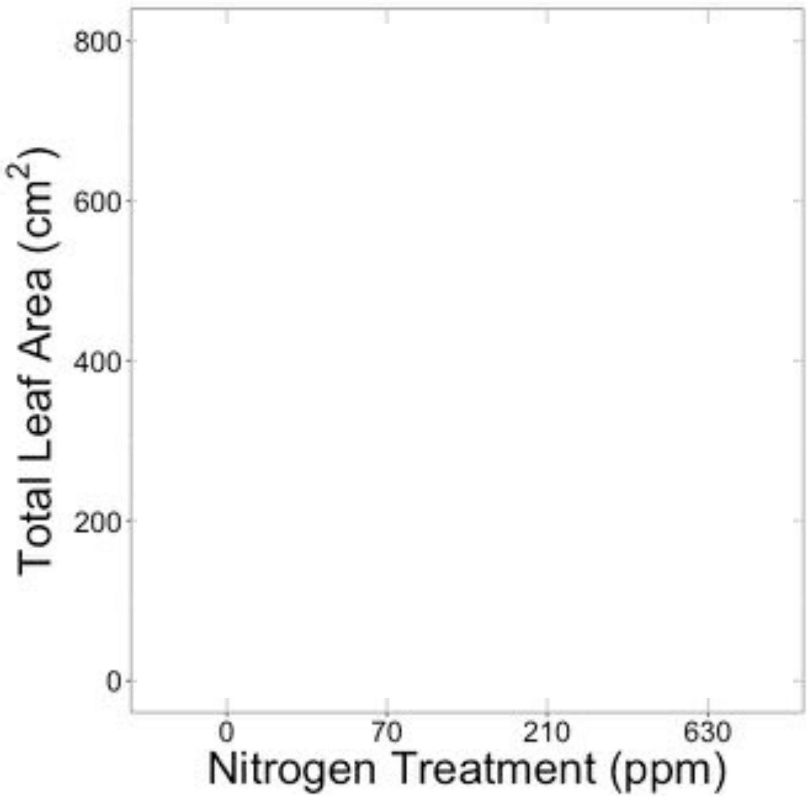

Waring and Smith (in prep)

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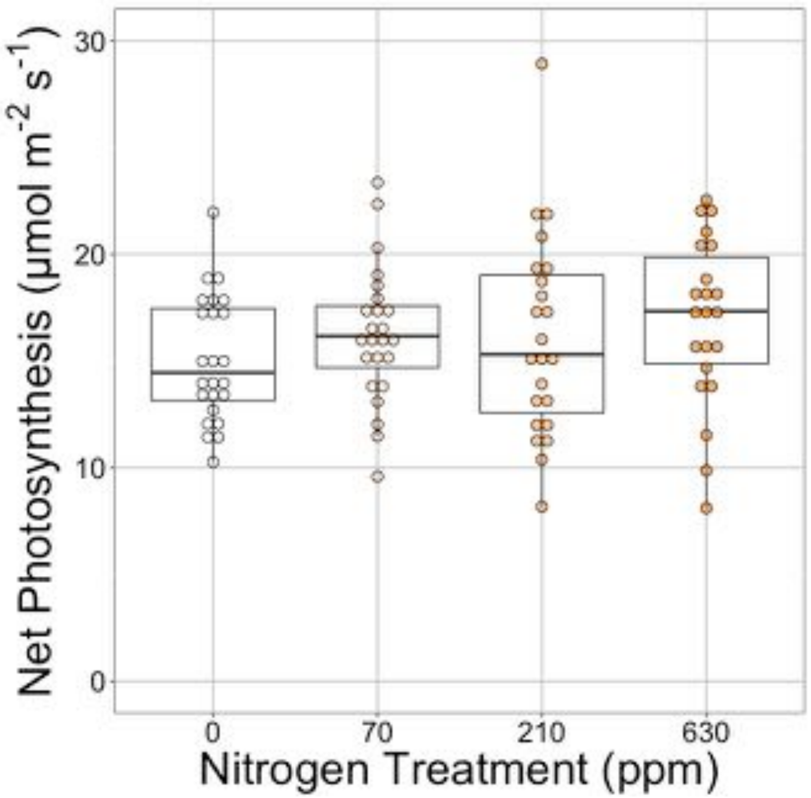
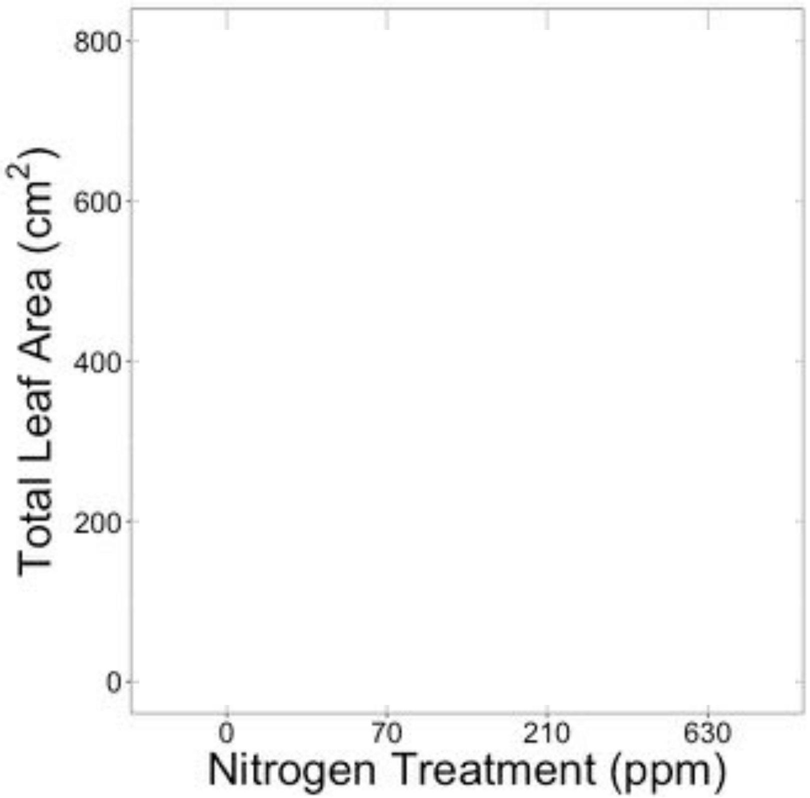
No change (P = 0.42)





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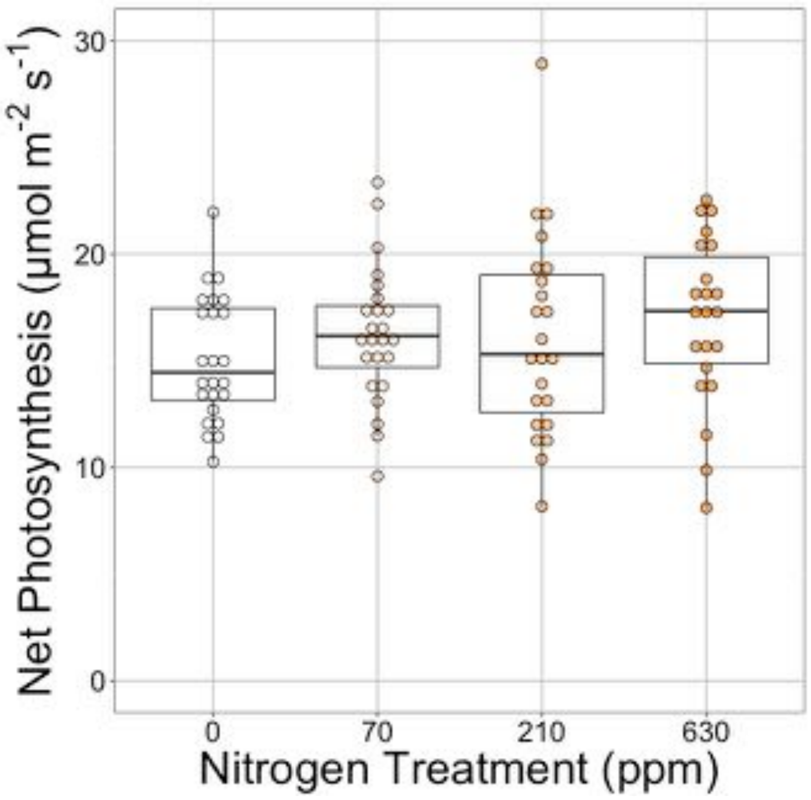
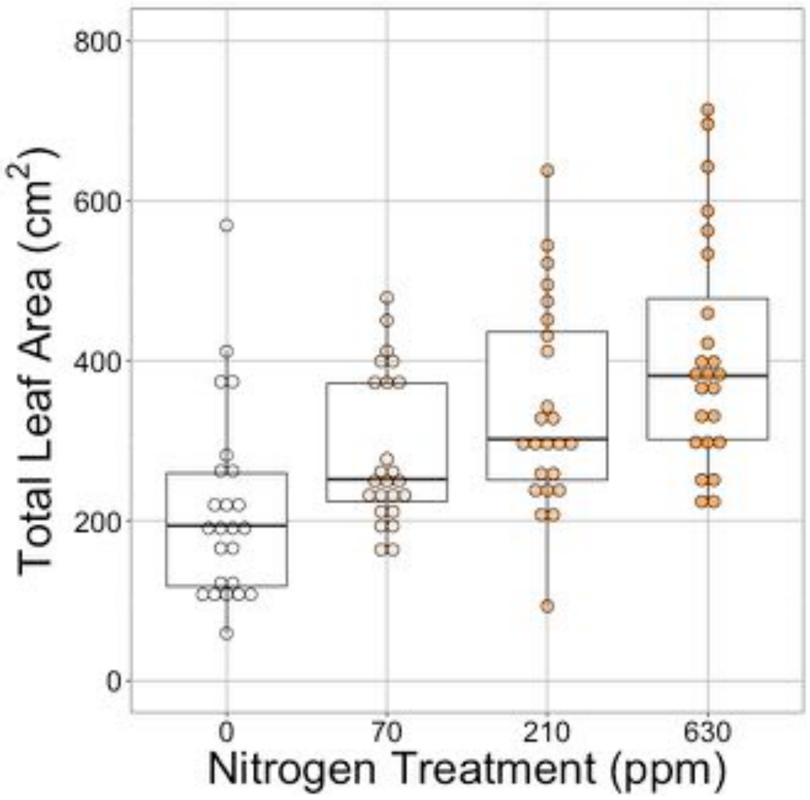
Leaf area, but not photosynthesis increases with N addition

No change (P > 0.05)



91% increase (P < 0.05)



Waring and Smith (in prep)

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But do greenhouse experiments translate to the field?

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nutrient network

Grassland soil nutrient addition network:

1. Leaf area index
2. Per-leaf-area nitrogen (photosynthetic proxy)

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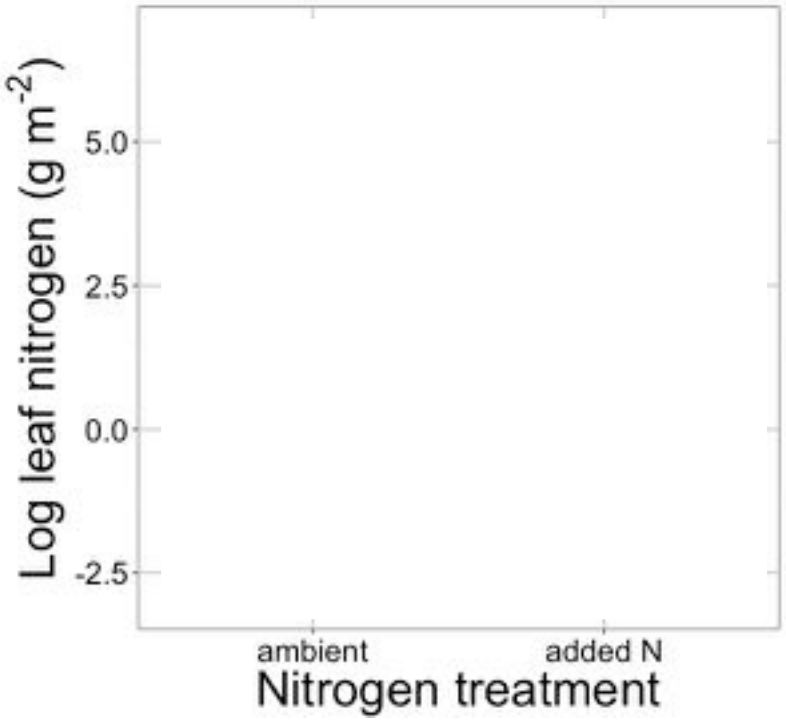

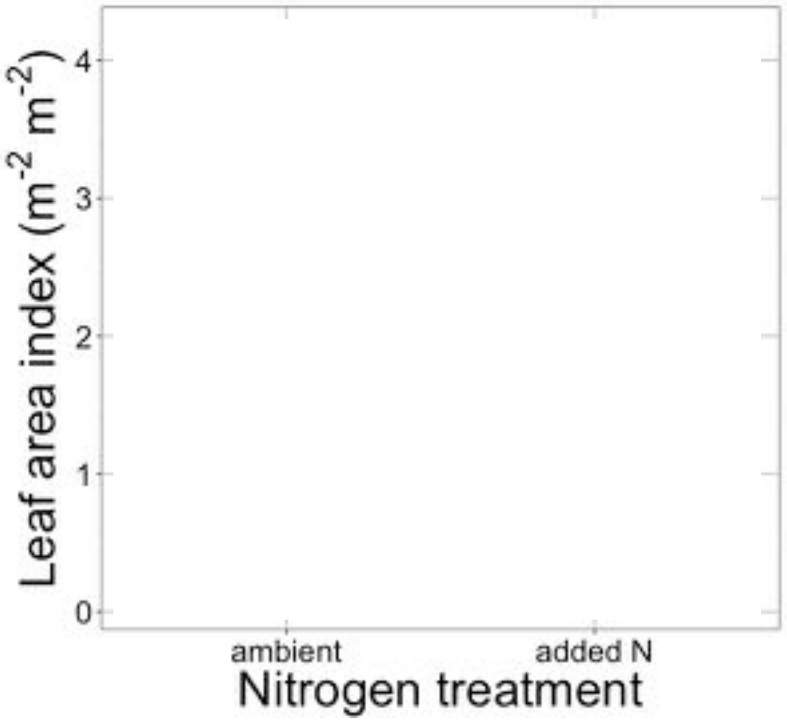

nutrient network

Waring and Smith (in prep)

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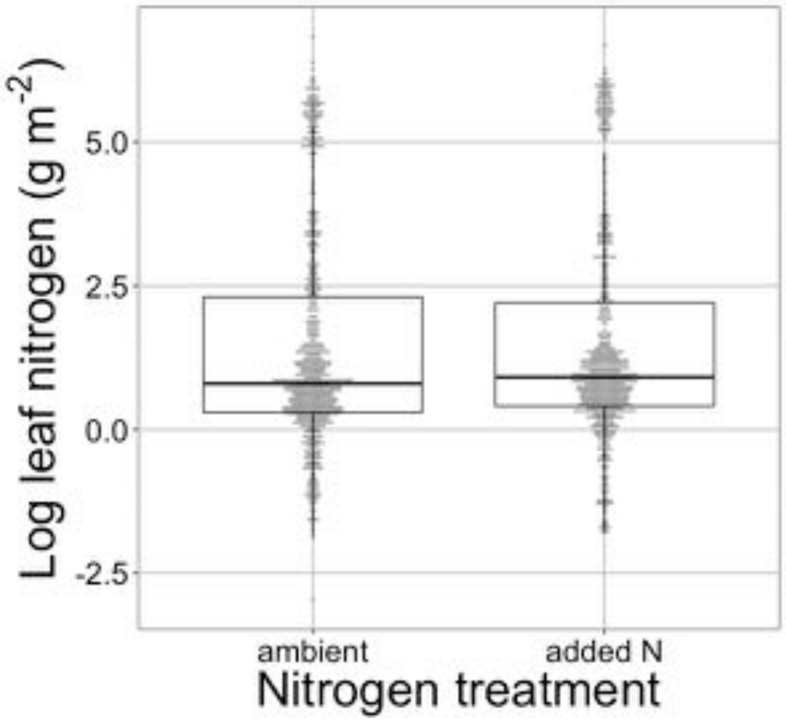
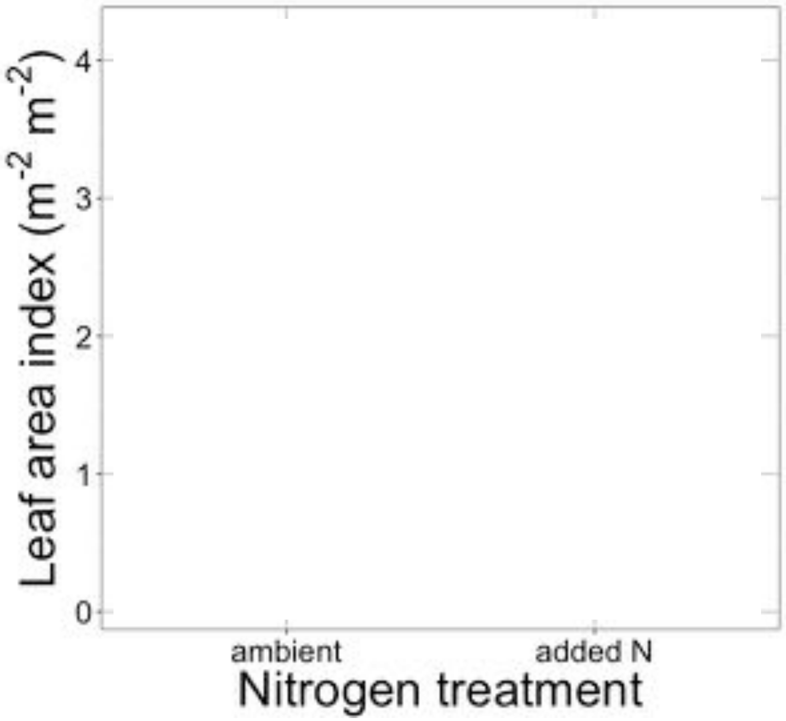
No change (P > 0.05)





nutrient network

Waring and Smith (in prep)

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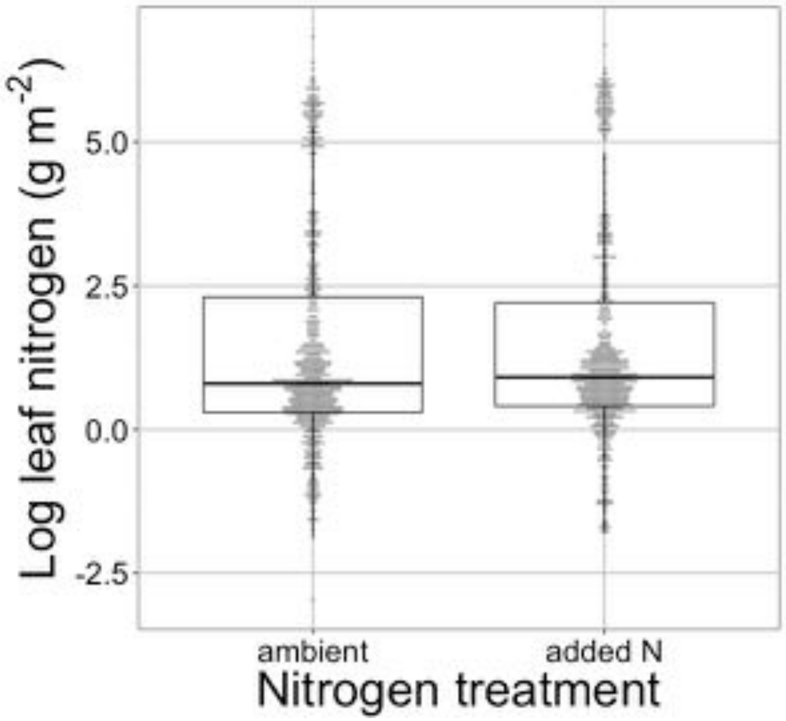
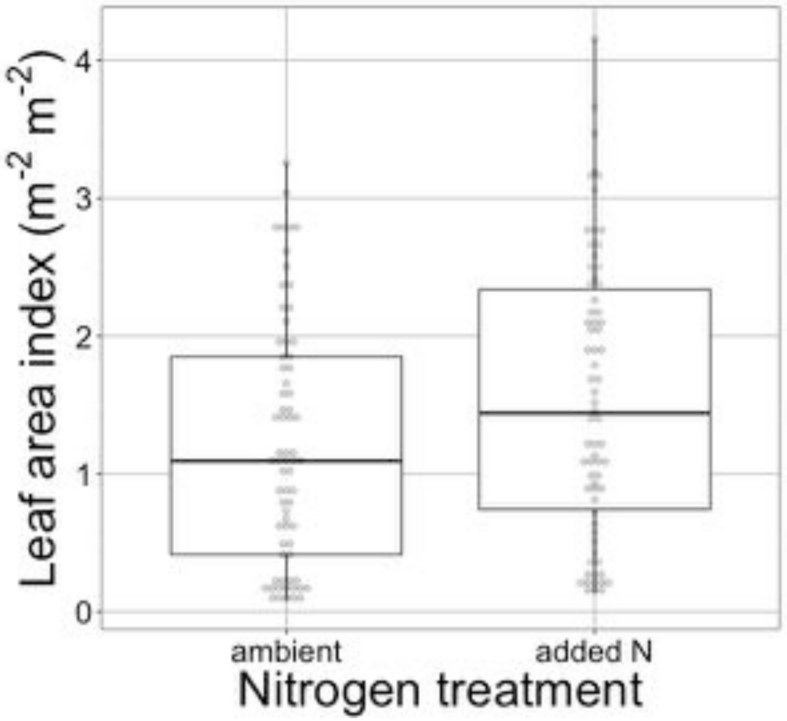
Globally, N addition increases leaf area, not leaf N

No change (P > 0.05)



41% increase (P < 0.05)



nutrient network

Waring and Smith (in prep)

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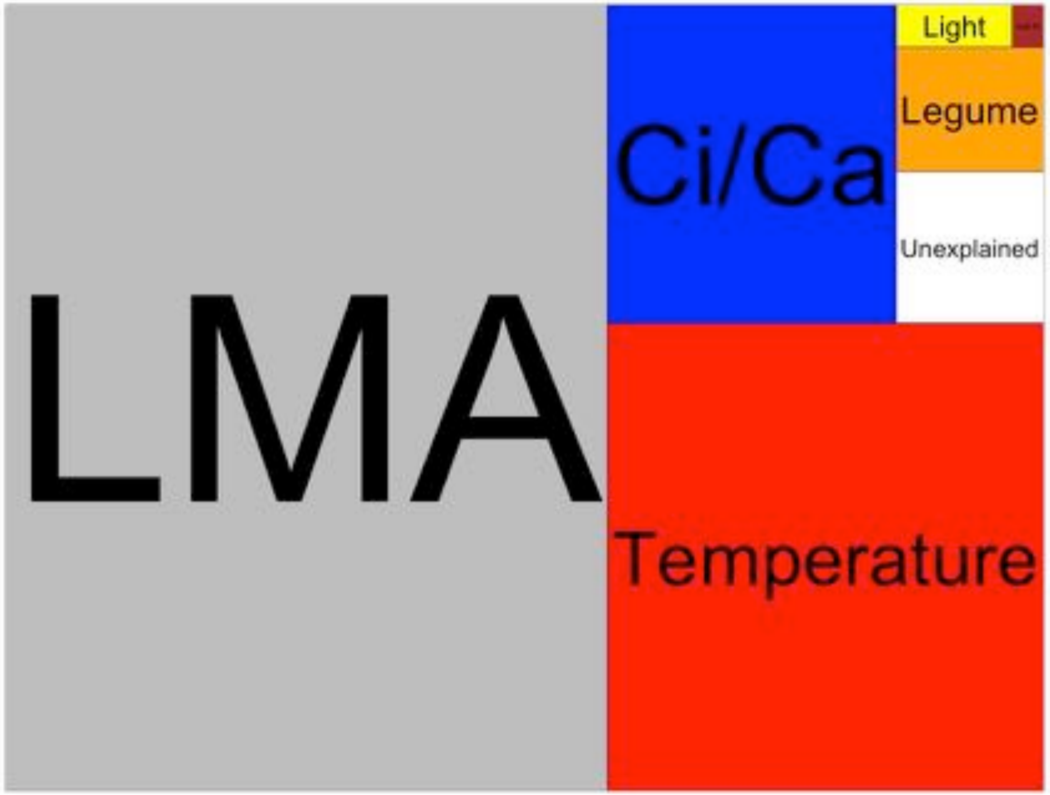
Globally, N addition has no impact on leaf N



Each box is proportional to the variance in leaf N explained by each variable

Waring and Smith (in prep)

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Question 2: Does photosynthesis respond to soil nutrients?

No, plants respond to added nutrients by increasing leaf area, not photosynthesis

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Question 3: How will photosynthesis acclimate to future conditions?

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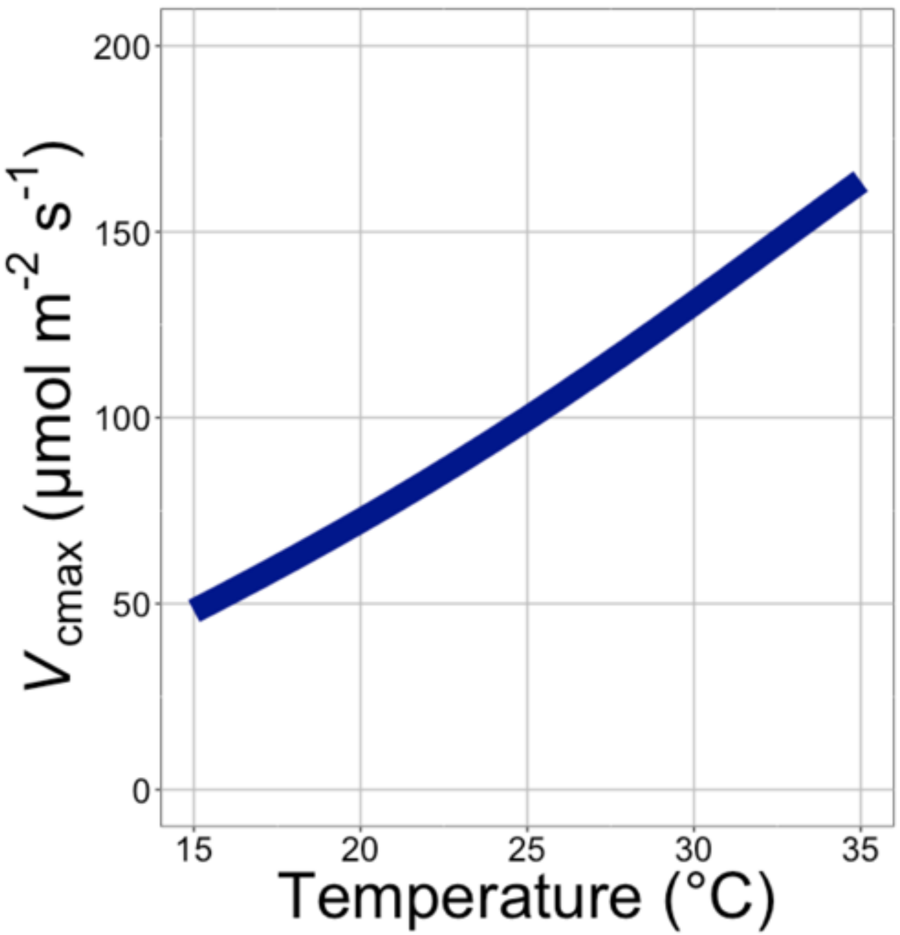
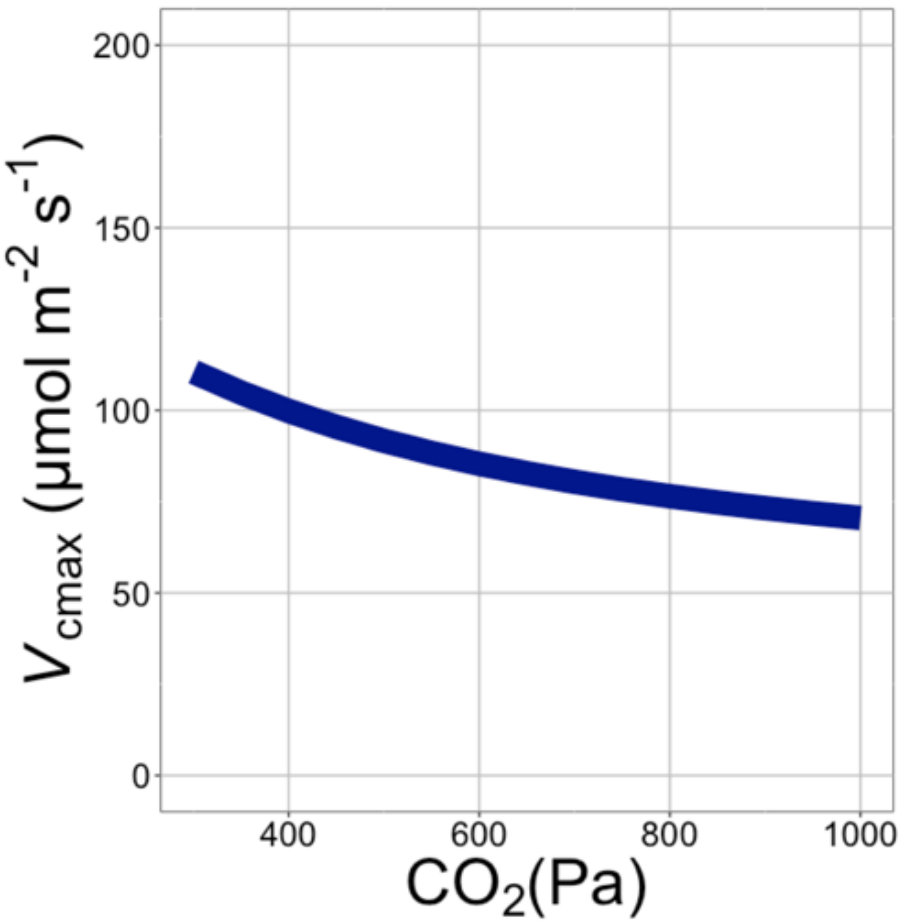
Expected future responses





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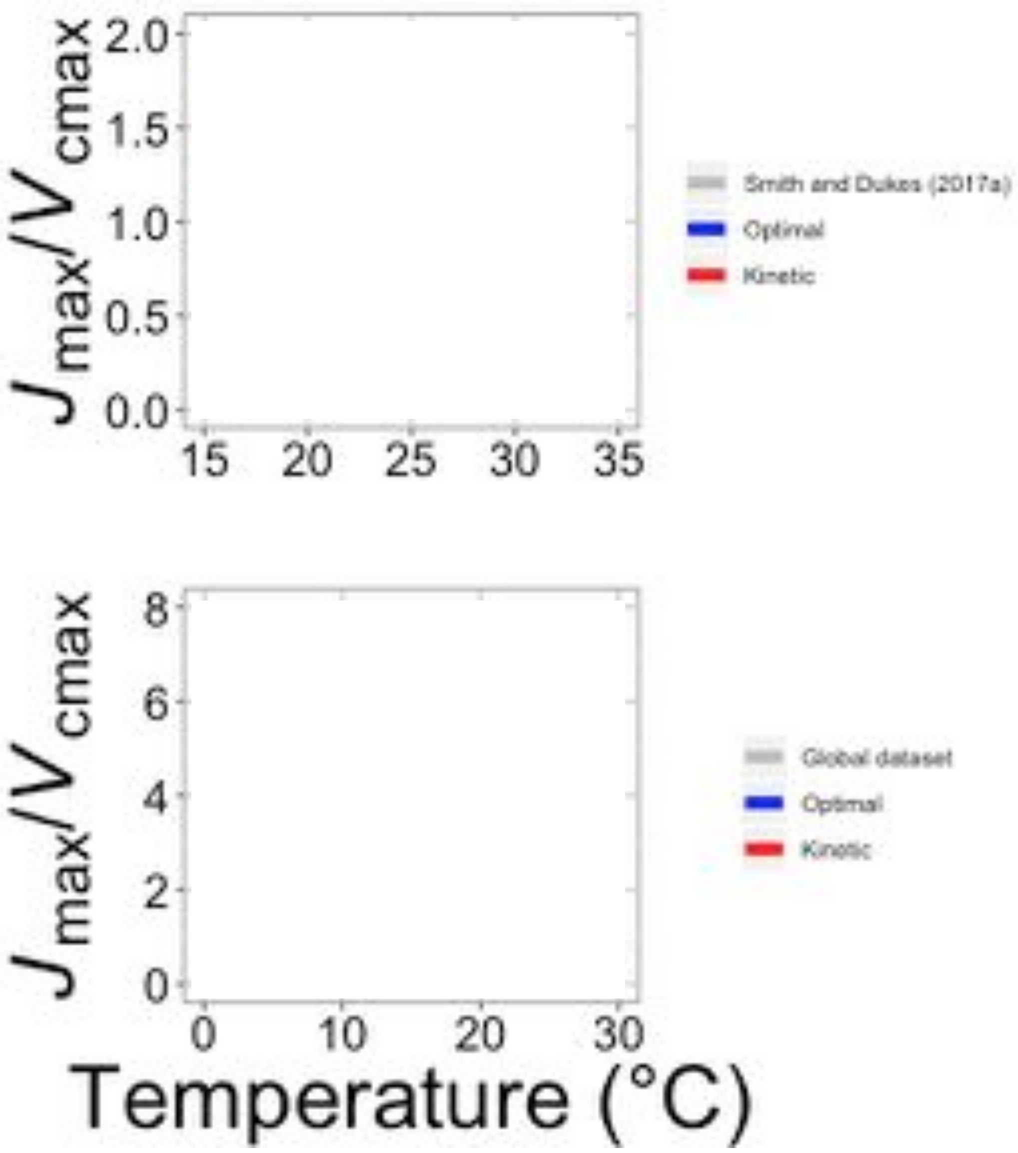
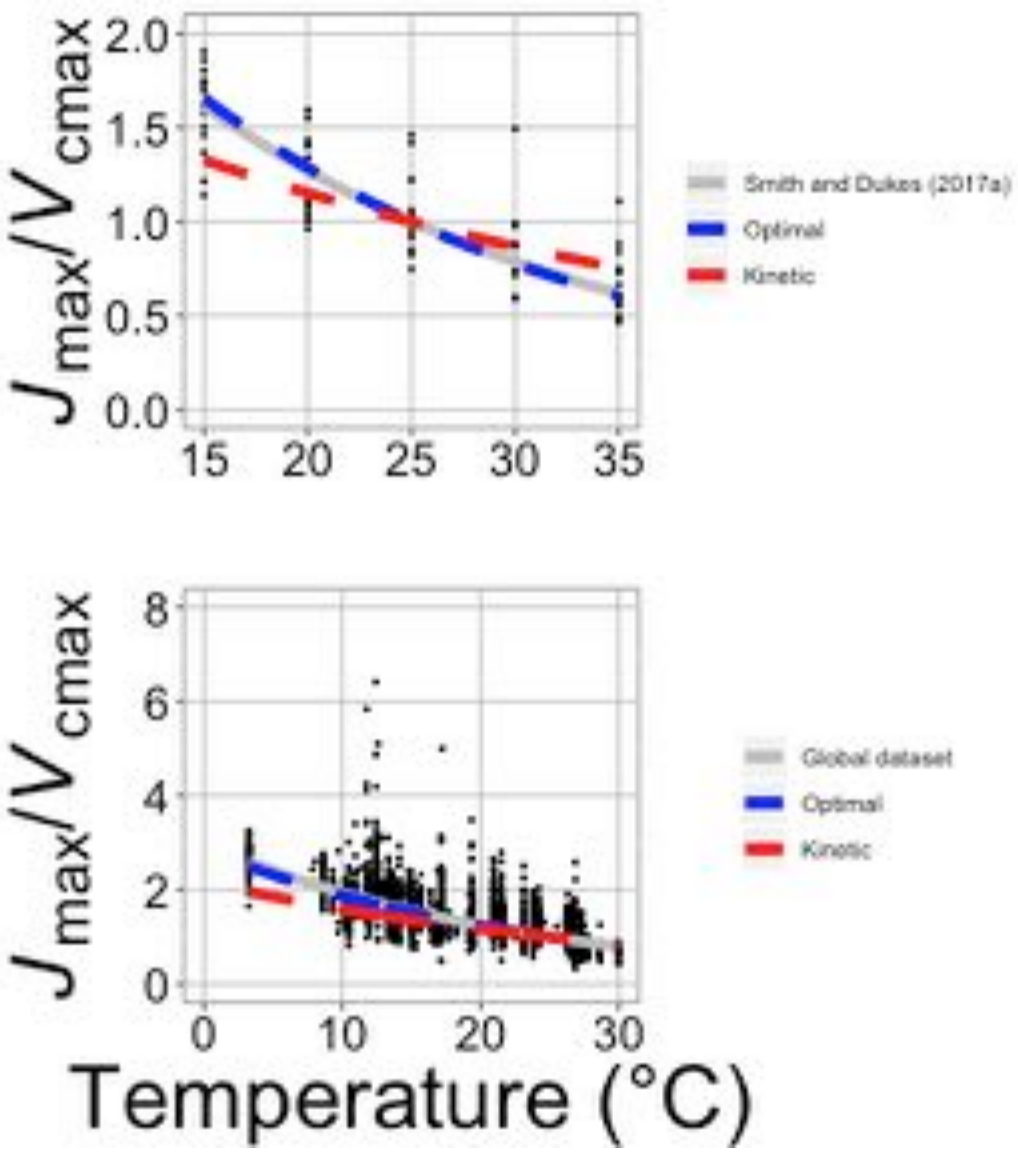


Smith and Keenan (in review)

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 (in review)

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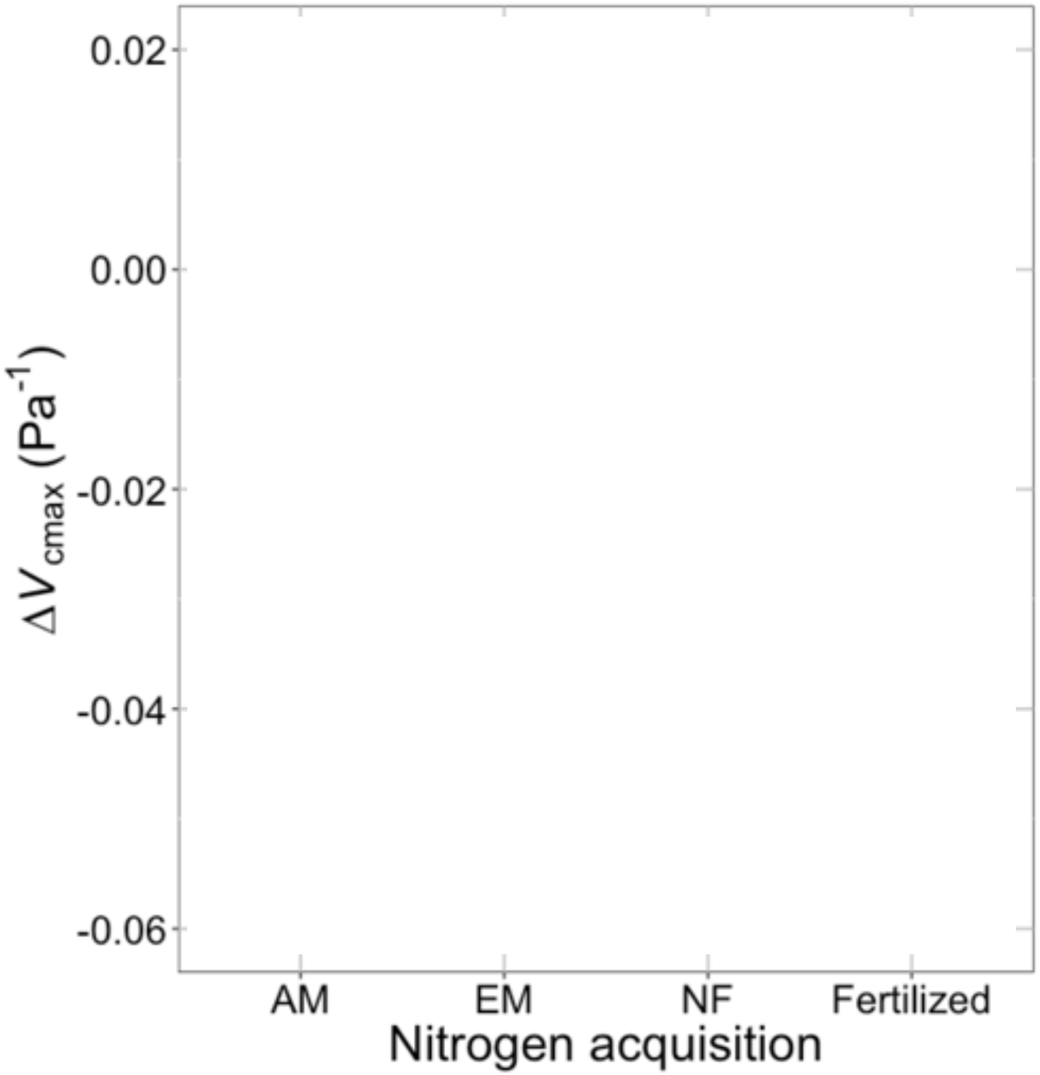

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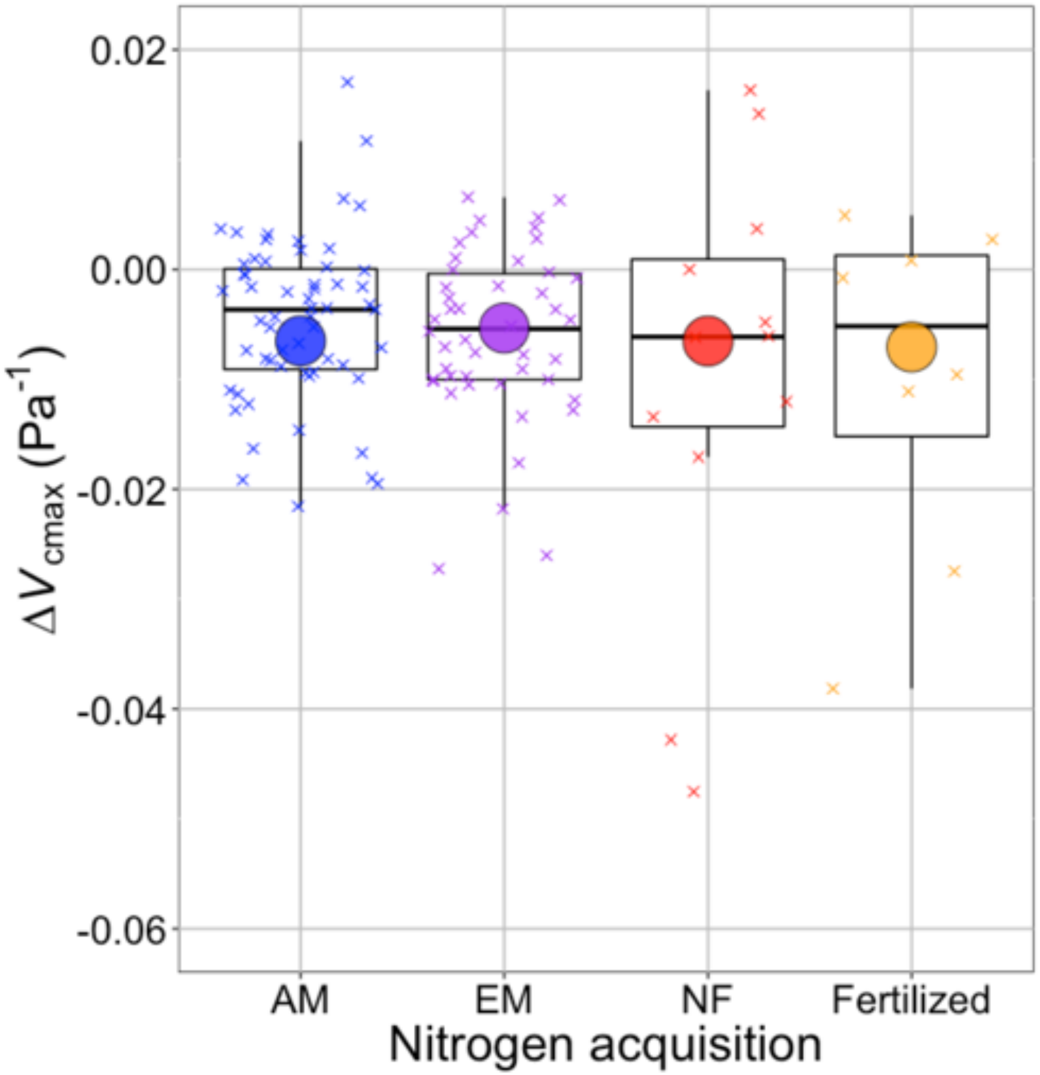


V_{cmax} changes with CO_2 in ways expected from optimization

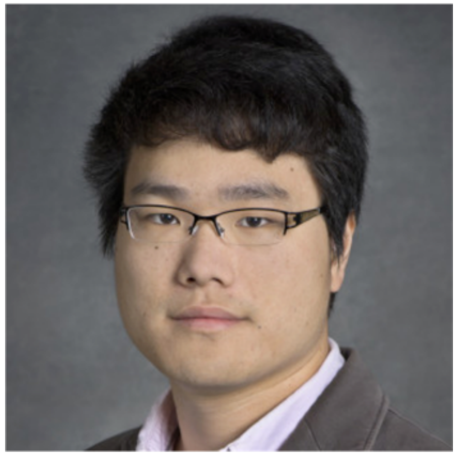
Boxes = data = -0.0063 Pa^{-1}

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

Smith and Keenan (in review)

What does that mean for future projections?

E3SM Energy Exascale Earth System Model

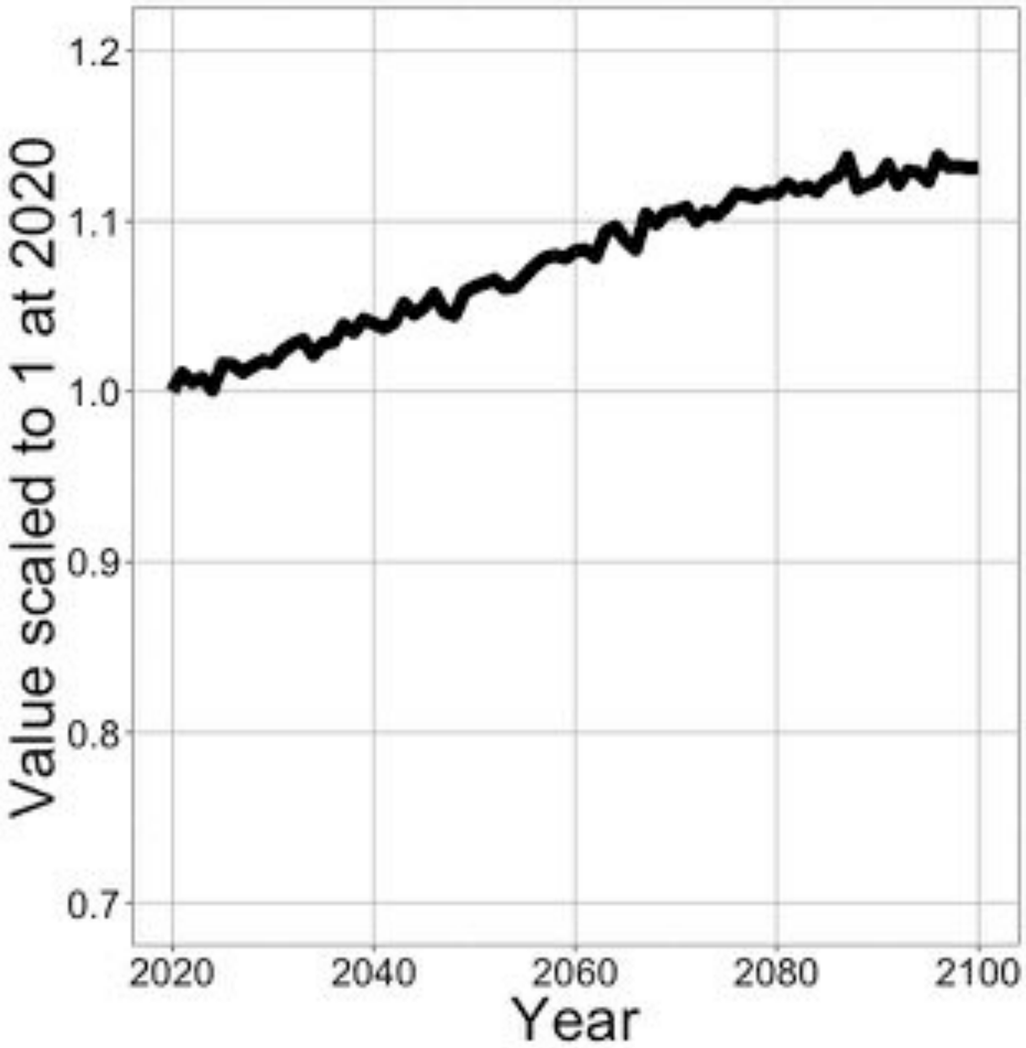


Qing Zhu (LBNL)

Bill Riley (LBNL)

nick.smith@ttu.edu; @nick_greg_smith

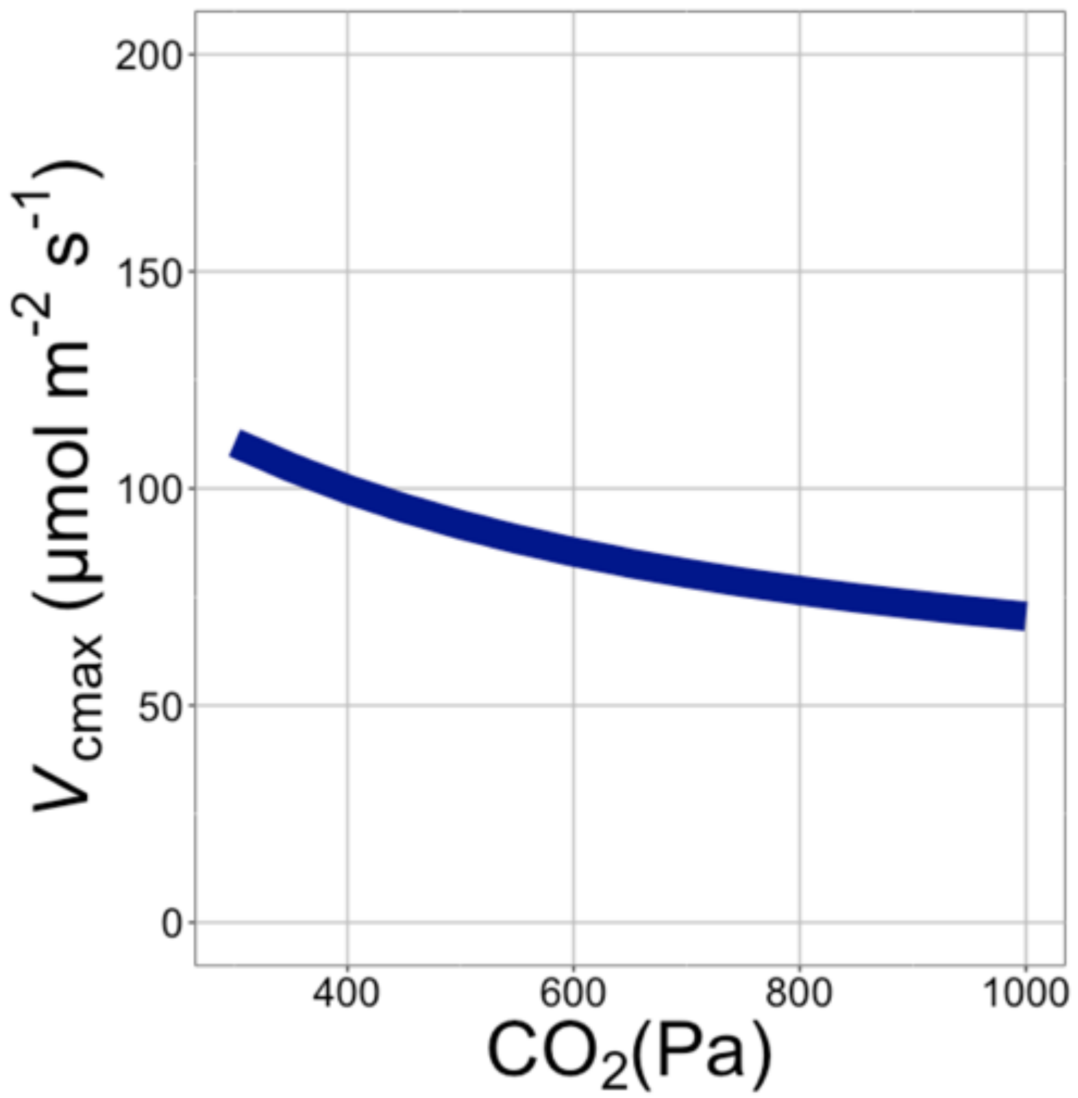
Higher CO_2 and increased temperatures increase future photosynthesis



Net Photosynthesis

Smith et al. (in prep)

nick.smith@ttu.edu; @nick_greg_smith

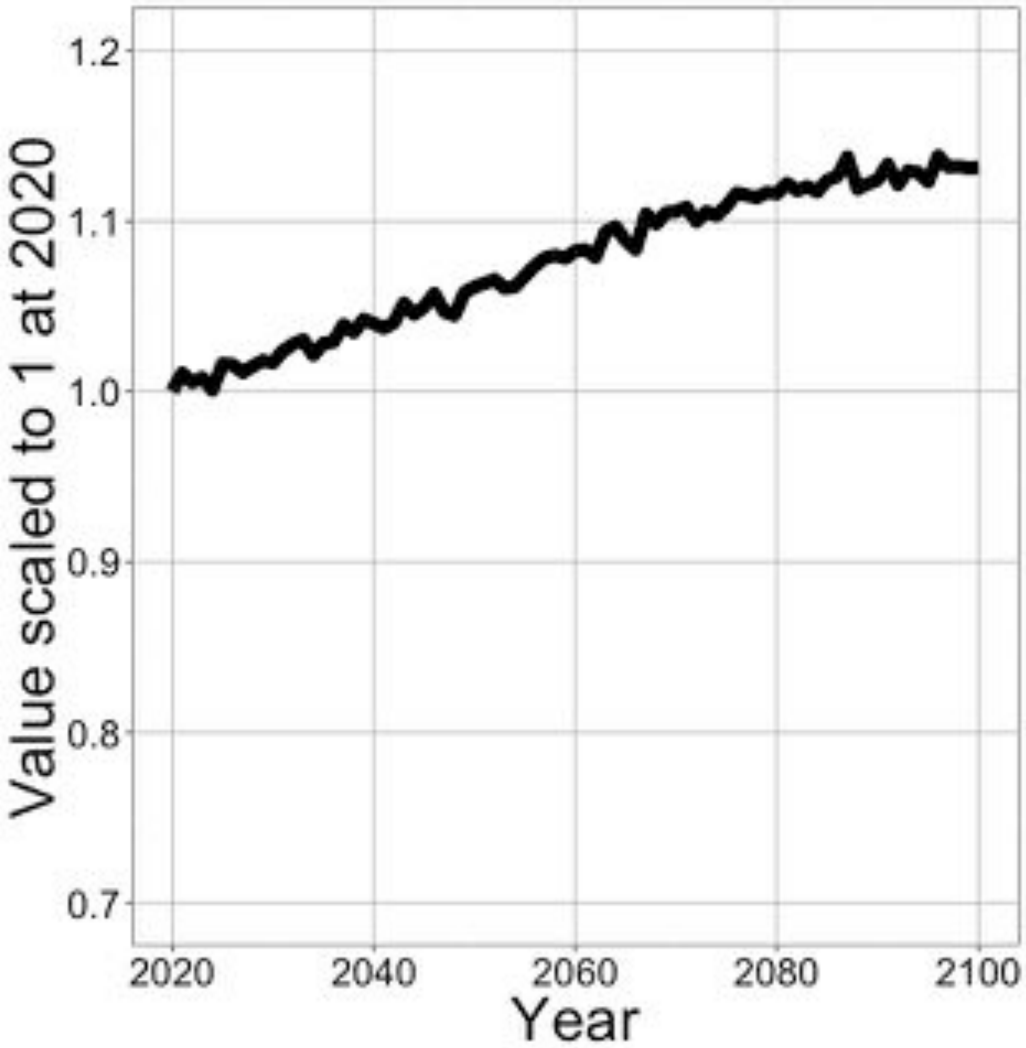


Downregulation under elevated CO_2 would reduce leaf nutrient demand!

Smith et al. (2019)

nick.smith@ttu.edu; @nick_greg_smith

Higher CO_2 and increased temperatures increase future photosynthesis

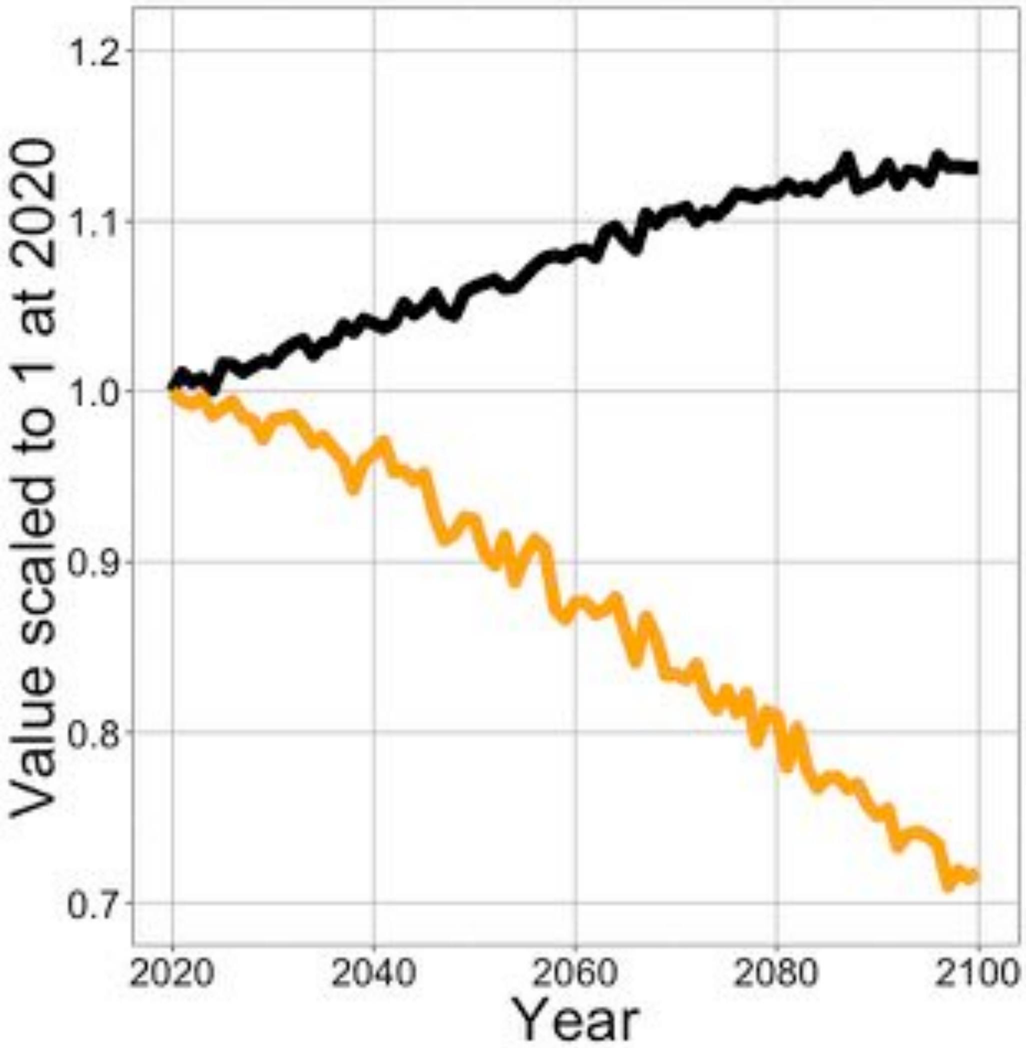


Net Photosynthesis

Smith et al. (in prep)

nick.smith@ttu.edu; @nick_greg_smith

Higher CO_2 and increased temperatures increase future photosynthesis (at lower nutrient use)

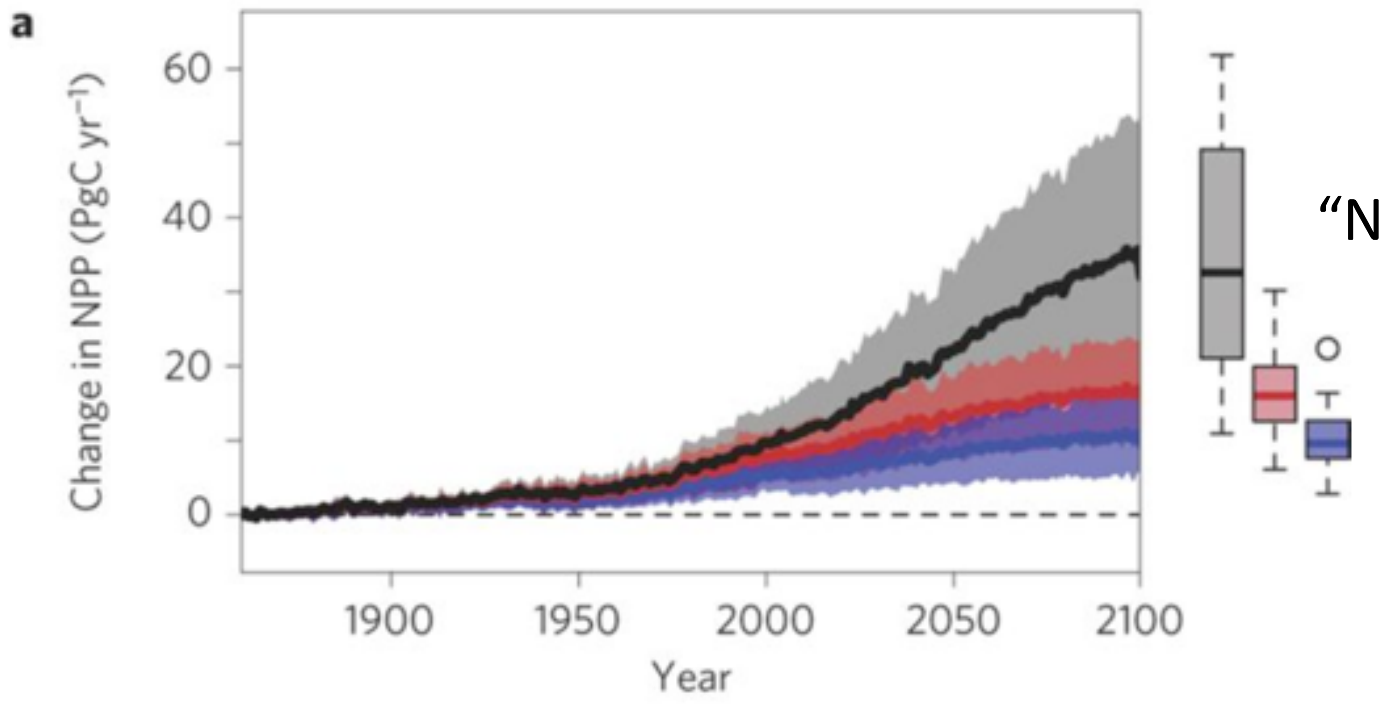


Net Photosynthesis

Leaf Nitrogen

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: How will photosynthesis acclimate to future conditions?

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

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

Helen Scott
TTU

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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)

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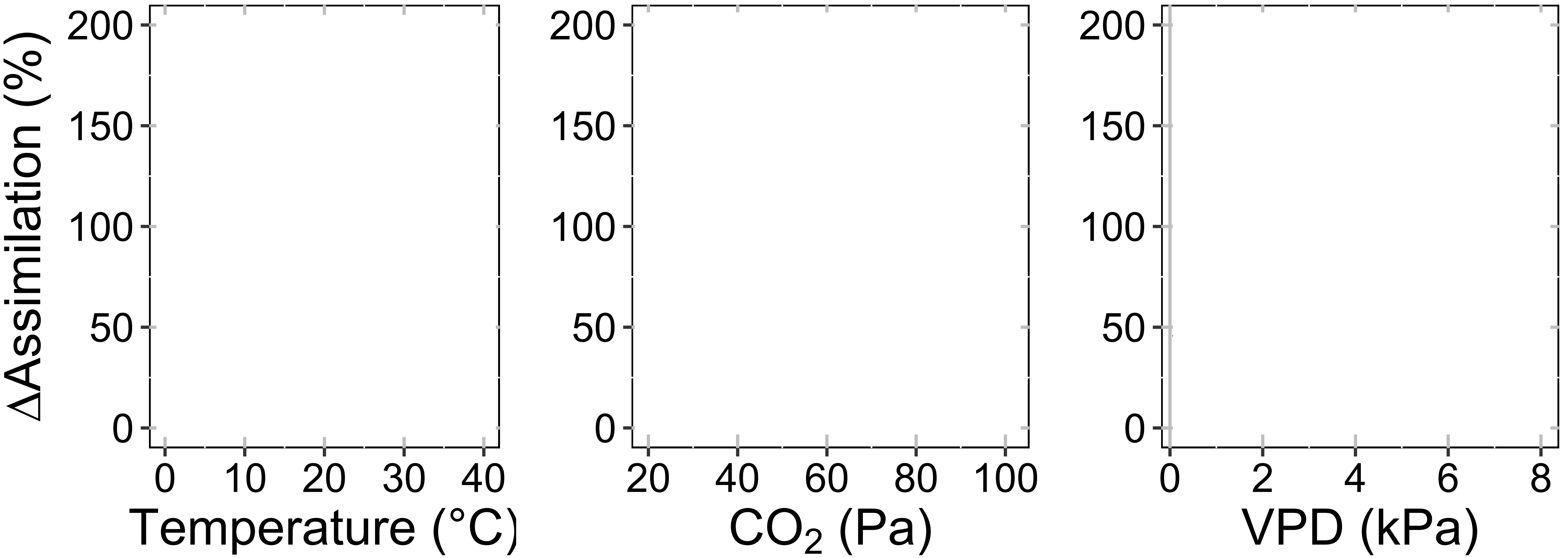
Relative advantage of C_4 physiology



Scott and Smith (in prep)

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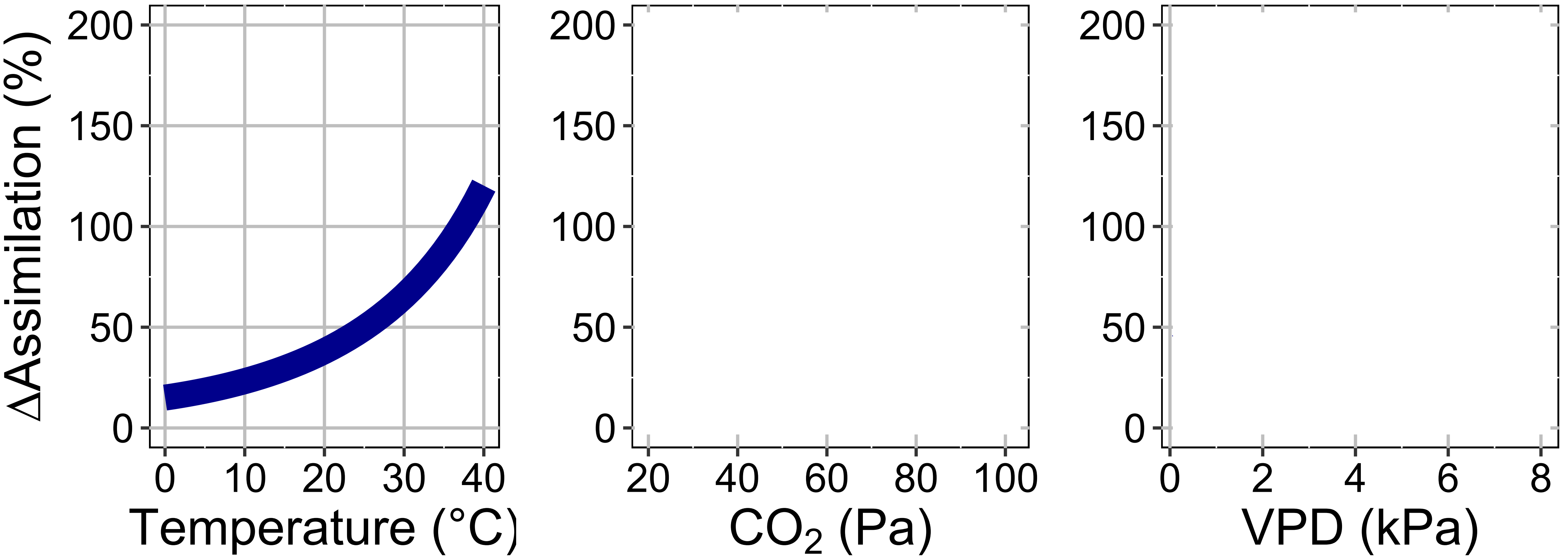
Relative advantage of C_4 physiology



Scott and Smith (in prep)

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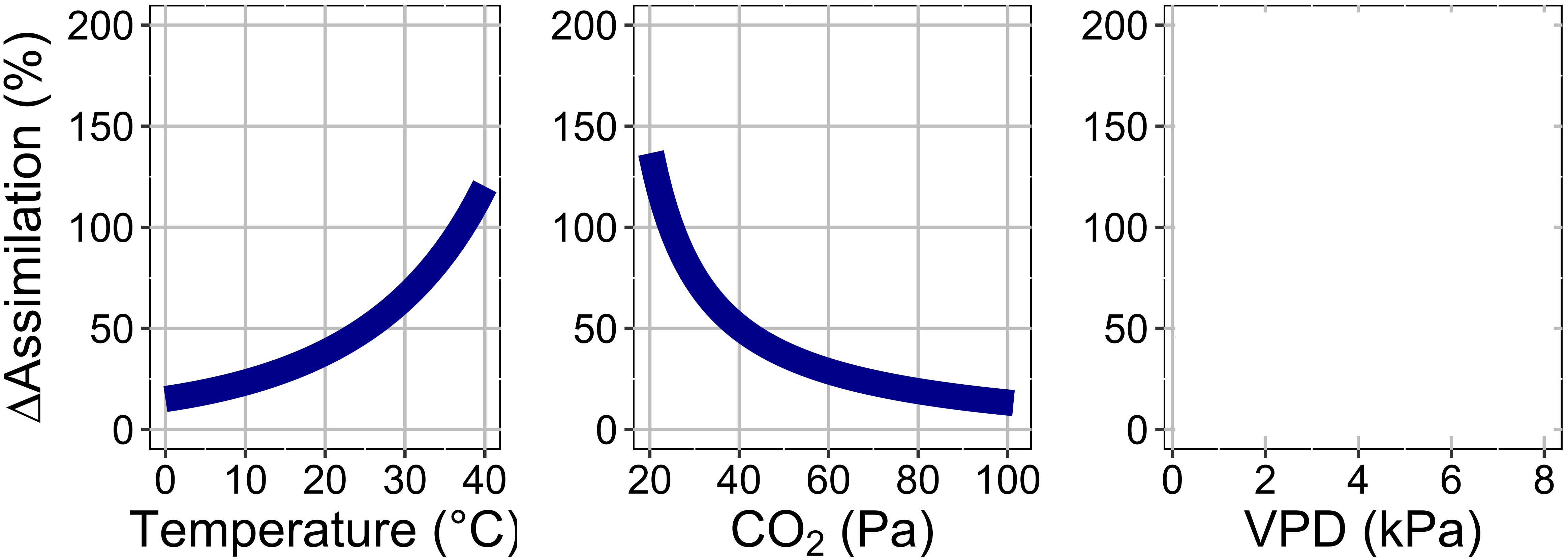
Relative advantage of C_4 physiology



Scott and Smith (in prep)

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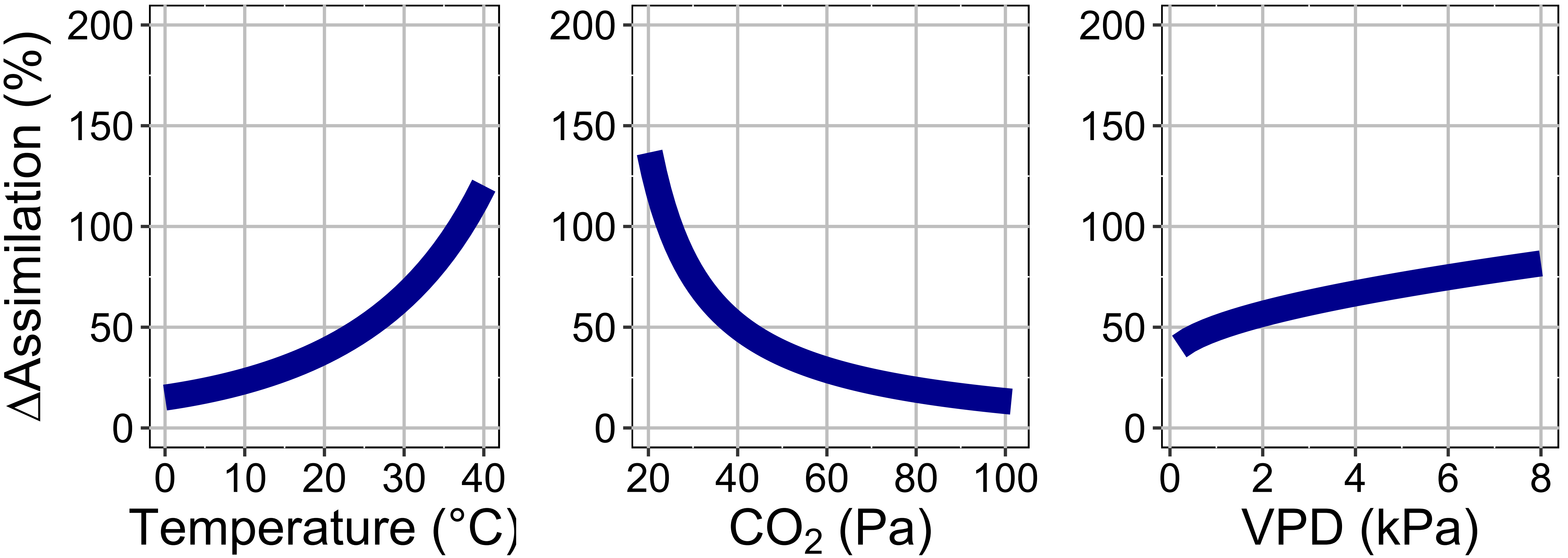
Relative advantage of C_4 physiology



Scott and Smith (in prep)

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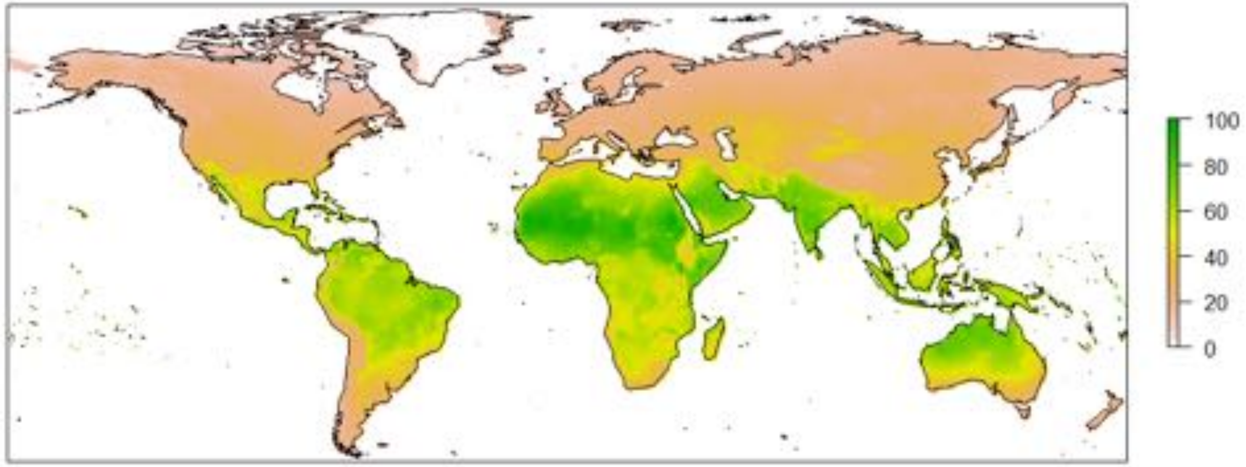
Current relative advantage of C_4 (%)



Scott and Smith (in prep)

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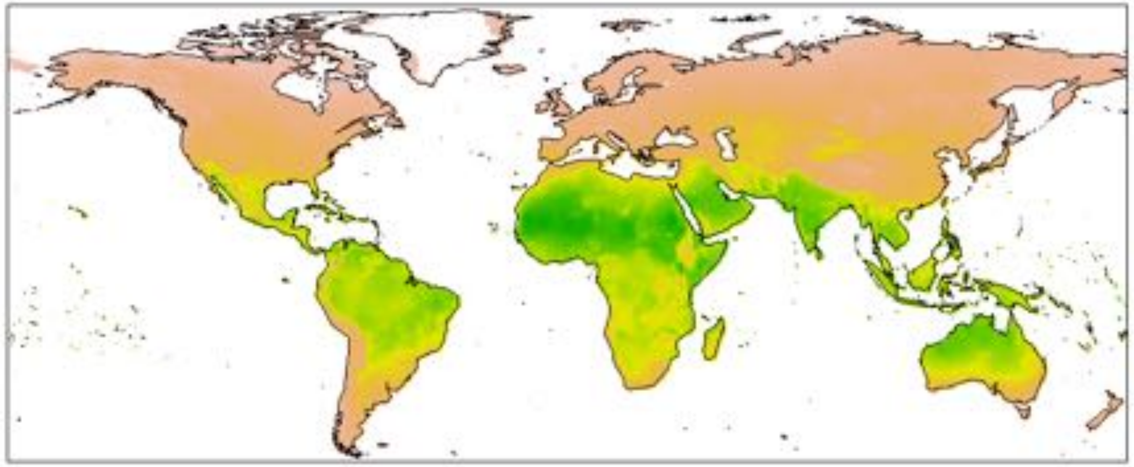
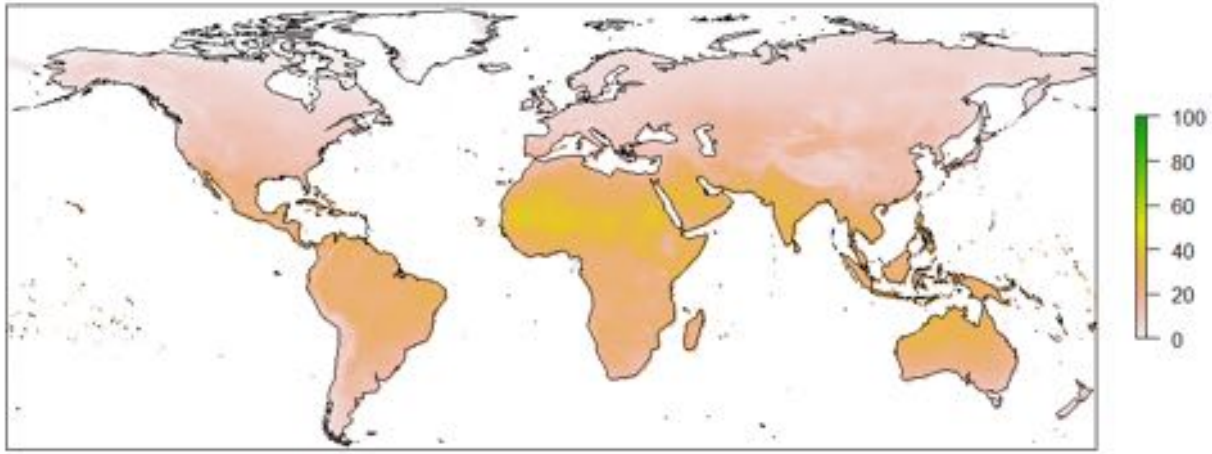
Current relative advantage of C_4 (%)



Future relative advantage of C_4 (%)



Scott and Smith (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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Conclusions

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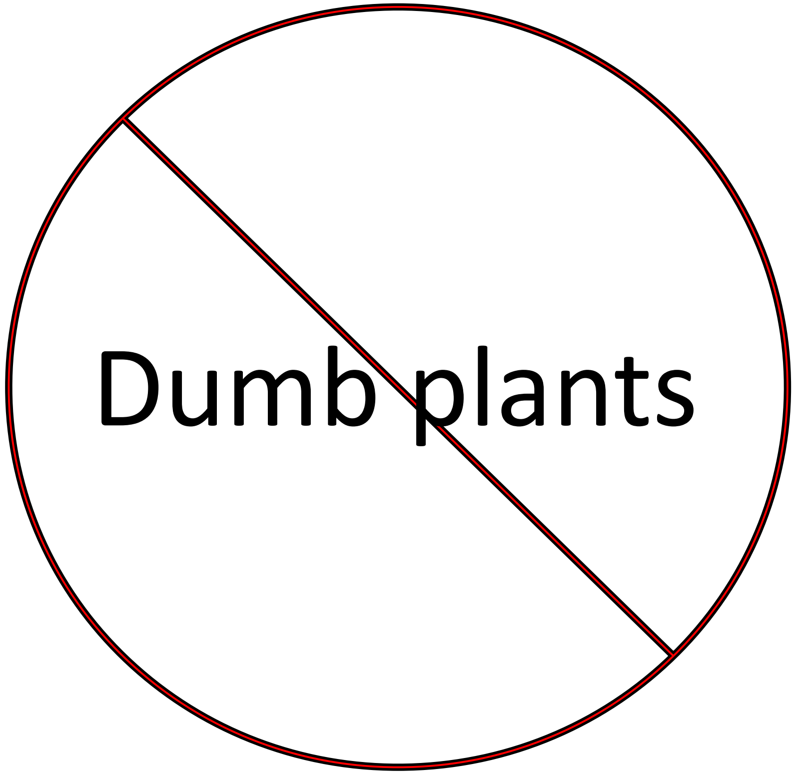
Conclusions

- Plants aren’t dumb!
  - Need to make sure our models allow for adaptive responses



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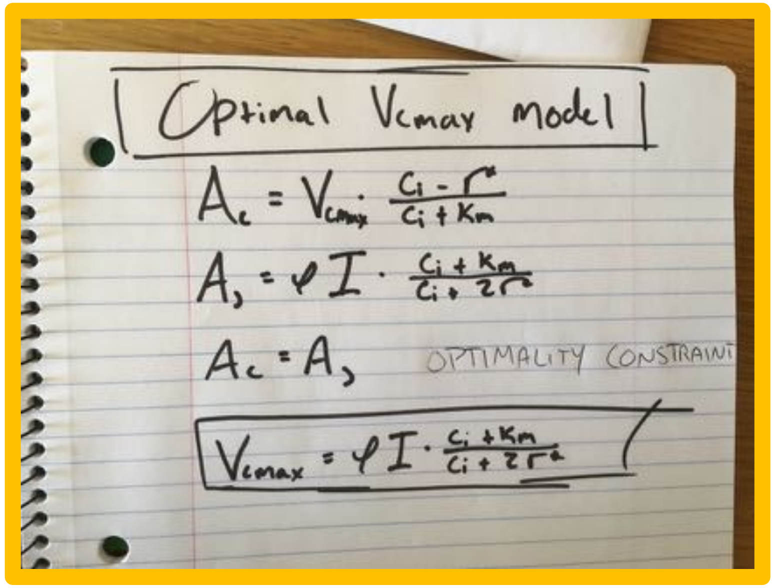
Conclusions

- Theory yields mechanistic insight about acclimation and associated feedbacks



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Conclusions

- Theory yields mechanistic insight about acclimation and associated feedbacks
- We using it to study
  - Plant invasion
  - Mycorrhizal symbioses
  - Agriculture
  - Herbarium specimens

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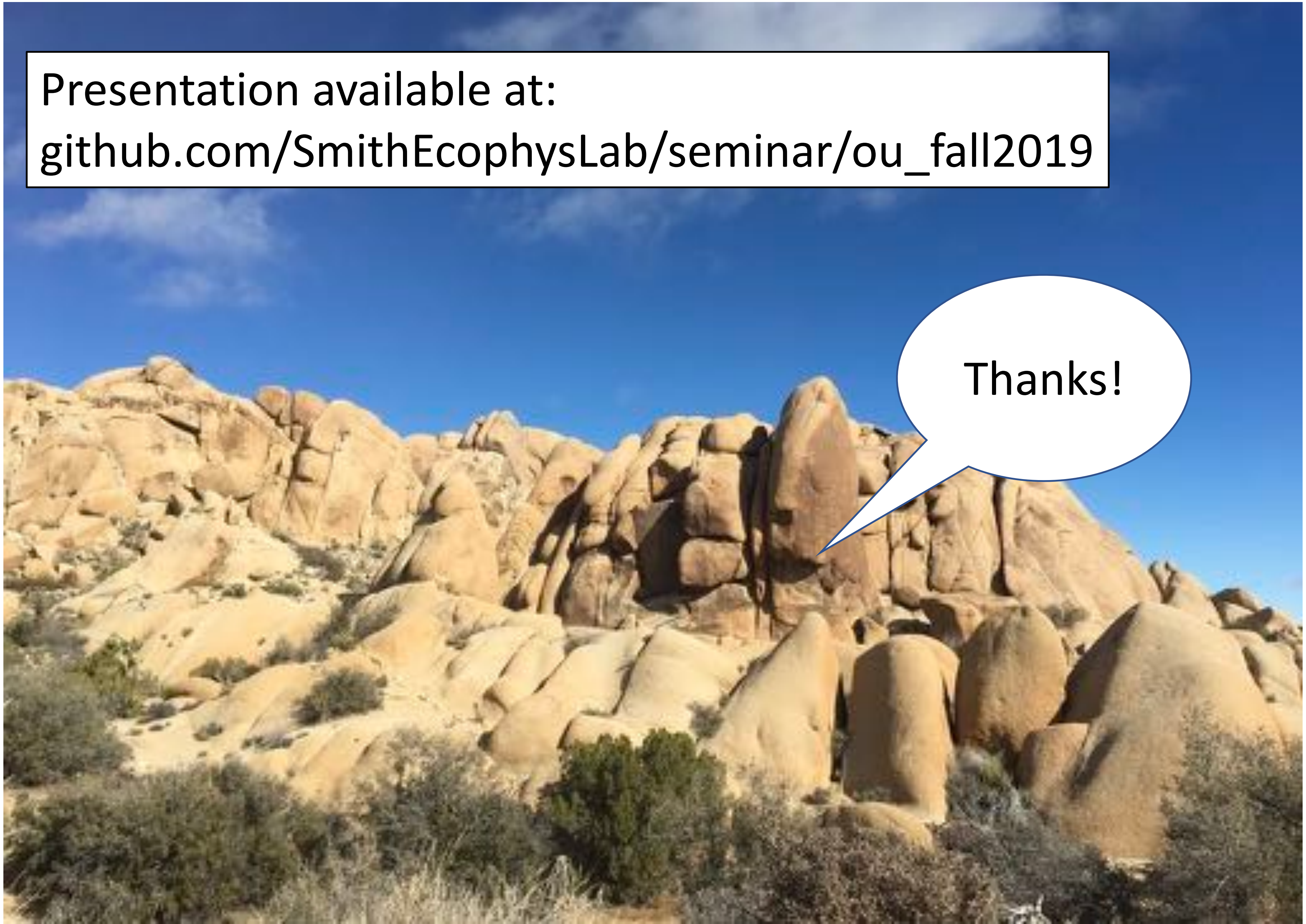

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Global leaf isotope dataset

~4,000 observations
594 sites

Cornwell et al. (2018)

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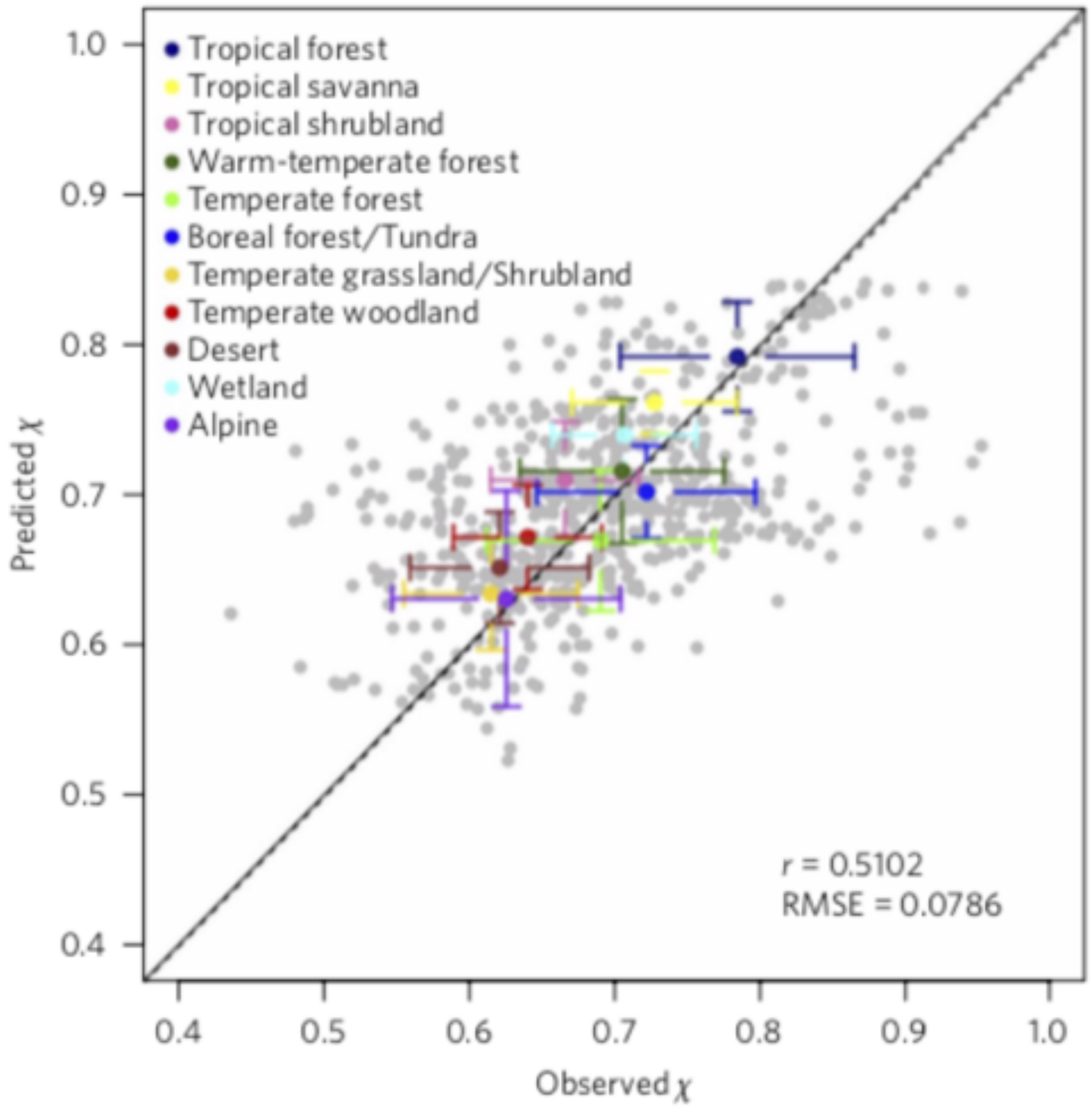

Stomatal conductance is optimized!

Wang et al. (2017)