Photosynthetic acclimation through the lens of optimality

Nick Smith

Texas Tech University

nick.smith@ttu.edu; @nick_greg_smith

Lizz Waring
TTU

Helen Scott
TTU

Trevor Keenan
Berkeley Lab

Wang Han
Tsinghua U.

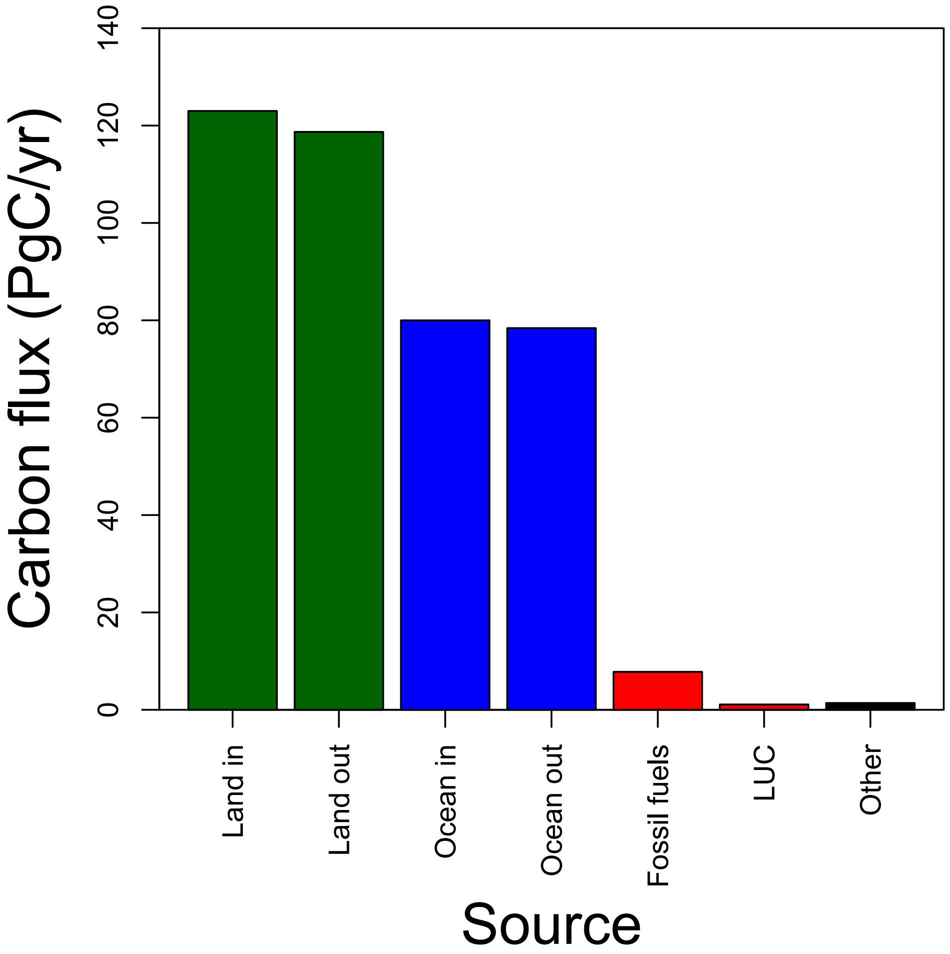
Colin Prentice
Imperial College

nick.smith@ttu.edu; @nick_greg_smith

Photosynthesis is important!

nick.smith@ttu.edu; @nick_greg_smith

Photosynthesis is important!



Data from IPCC (2013)

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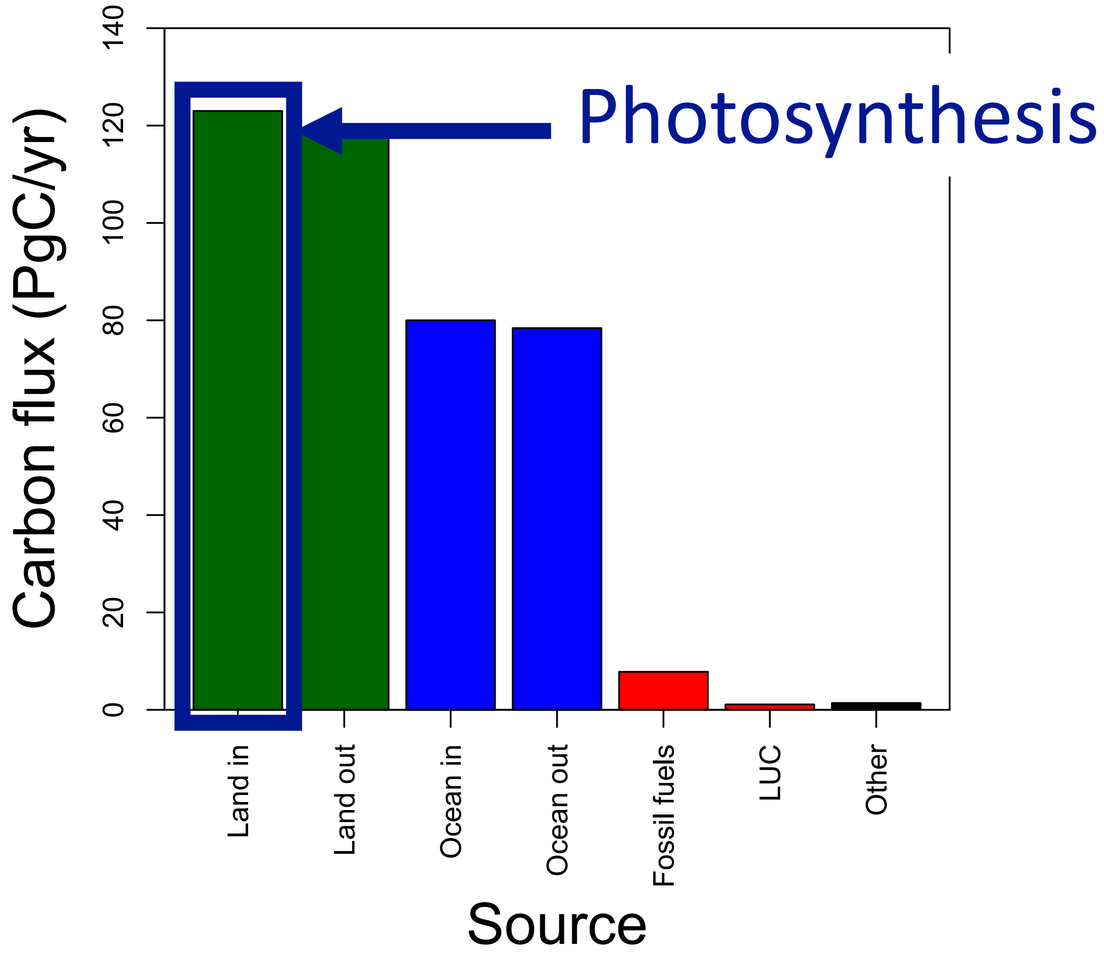
Photosynthesis is important!



Data from IPCC (2013)

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Theoretical models for photosynthesis exist

Planta 149, 78–90 (1980)

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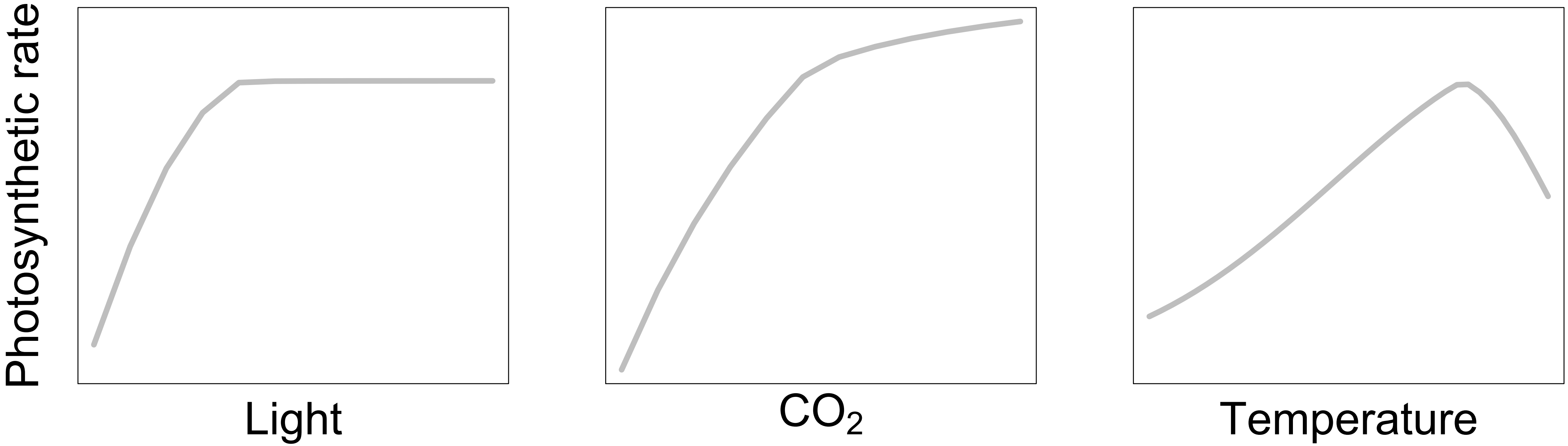
A Biochemical Model of Photosynthetic CO_2 Assimilation in Leaves of C_3 Species

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

nick.smith@ttu.edu; @nick_greg_smith

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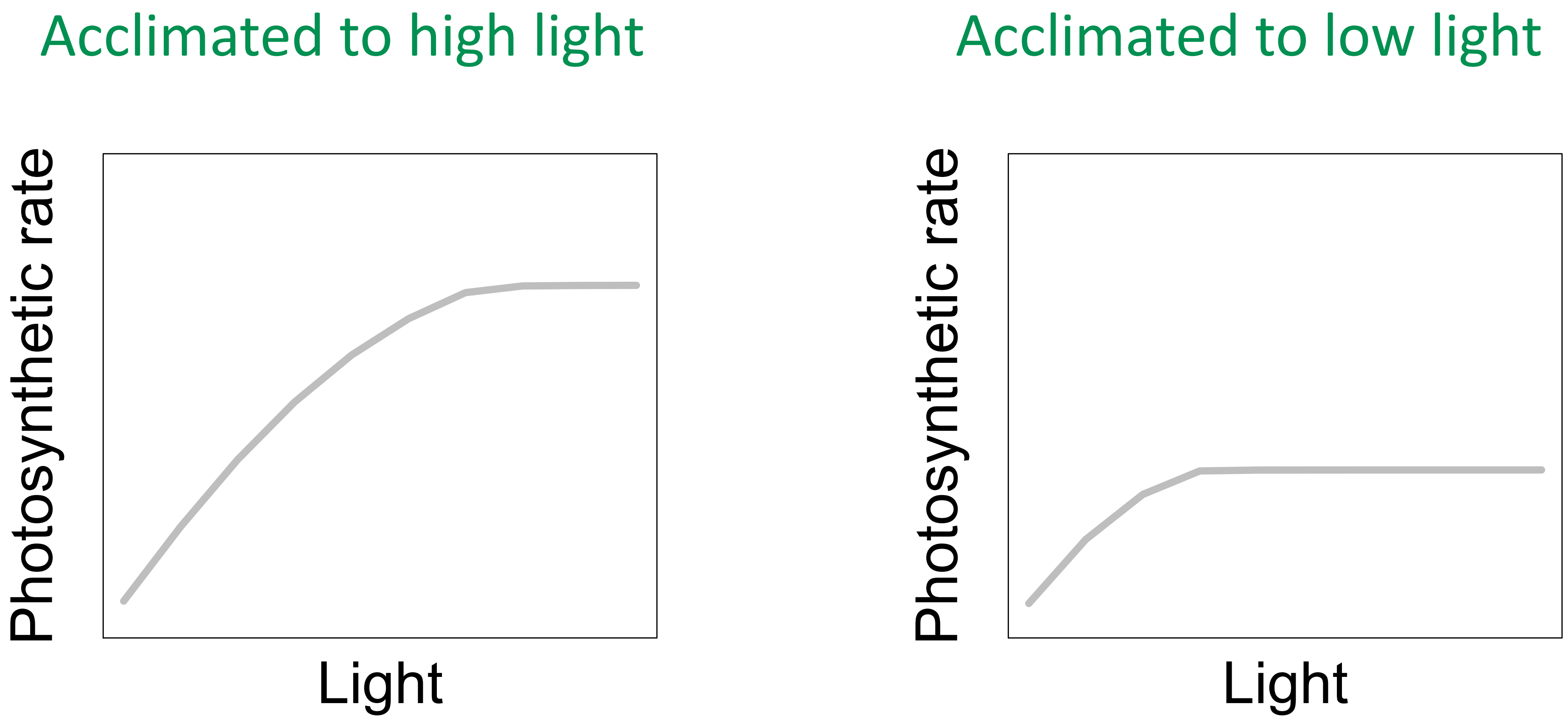
Long-term responses can differ from short-term responses due to acclimation



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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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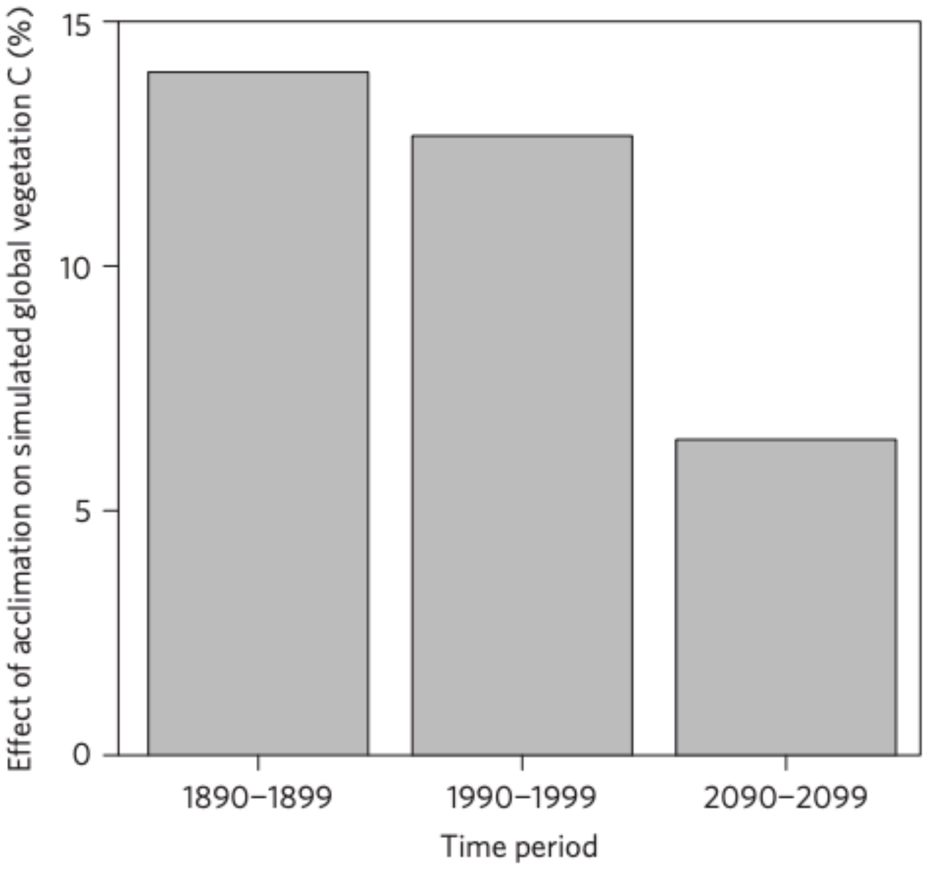
PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

Joseph Berry and Olle Björkman[1]

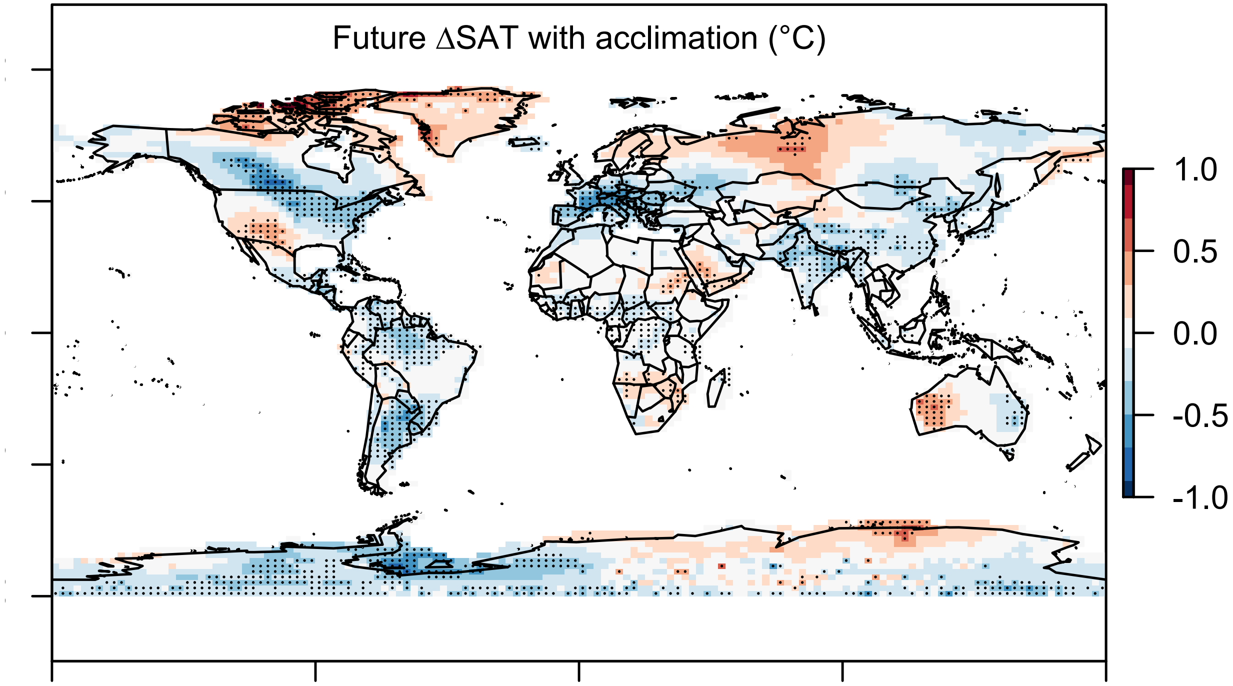
nick.smith@ttu.edu; @nick_greg_smith

…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*

nick.smith@ttu.edu; @nick_greg_smith

But no theoretical model for photosynthetic acclimation exists

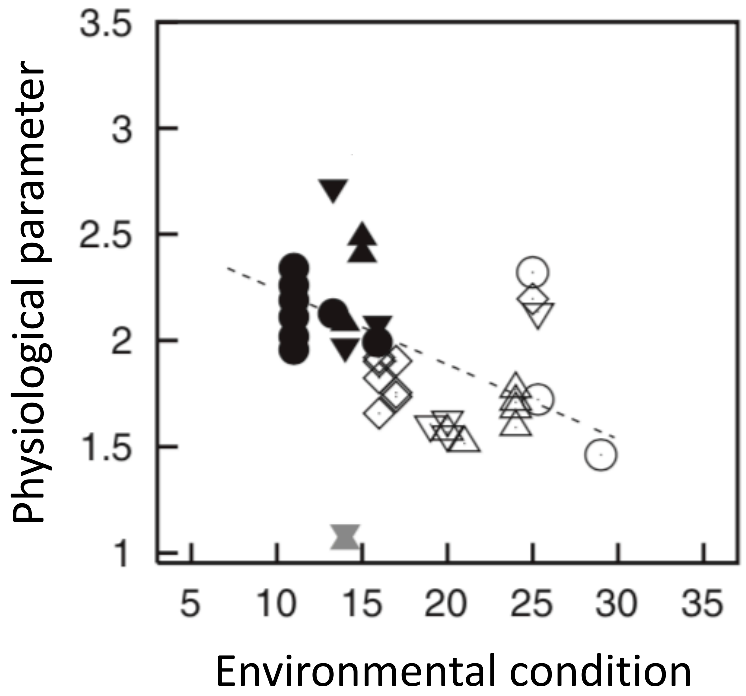
nick.smith@ttu.edu; @nick_greg_smith

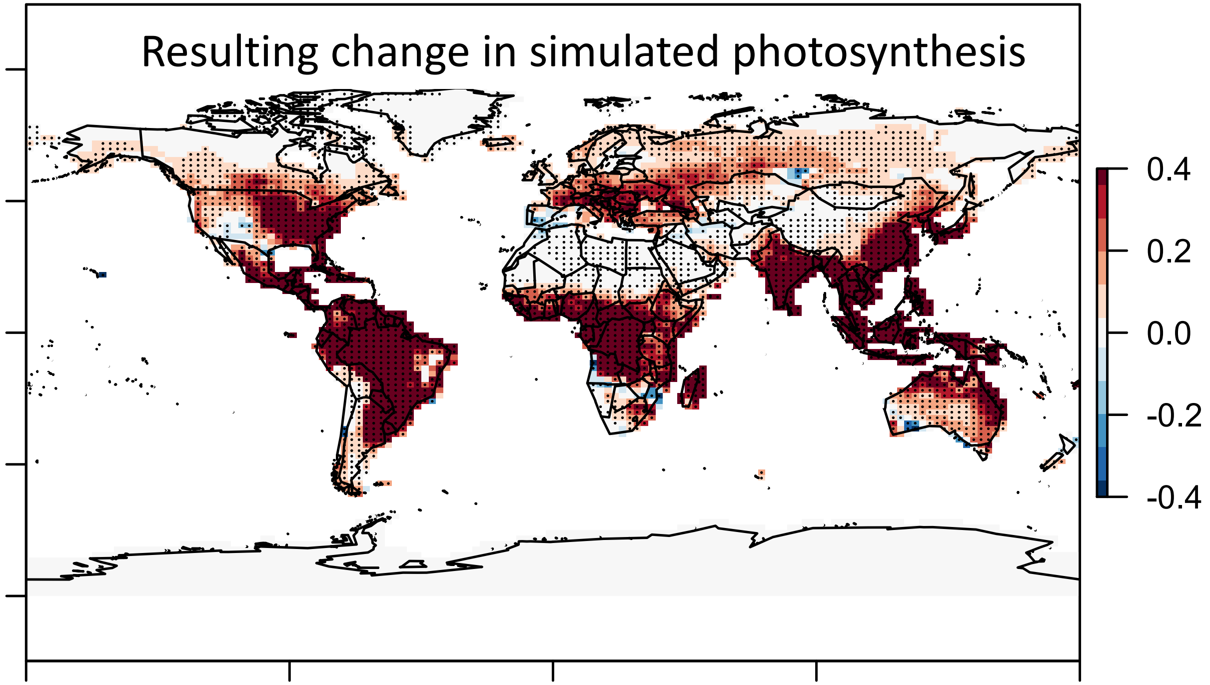
Lack of theory results in…

nick.smith@ttu.edu; @nick_greg_smith

Lack of theory results in…

- Unreliable future predictions (overparameterization, tuning)





Kattge and Knorr (2007) *PC&E*

Smith et al. (2017) *JAMES*

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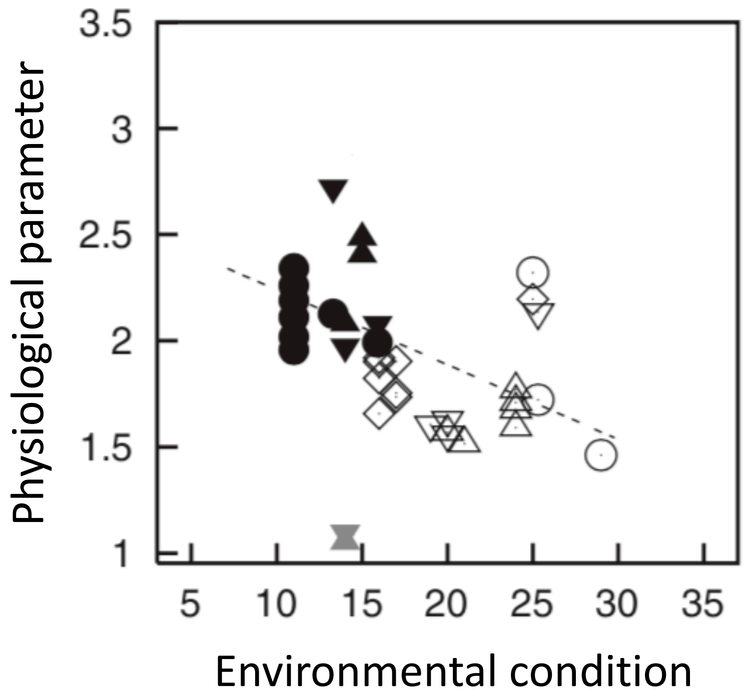
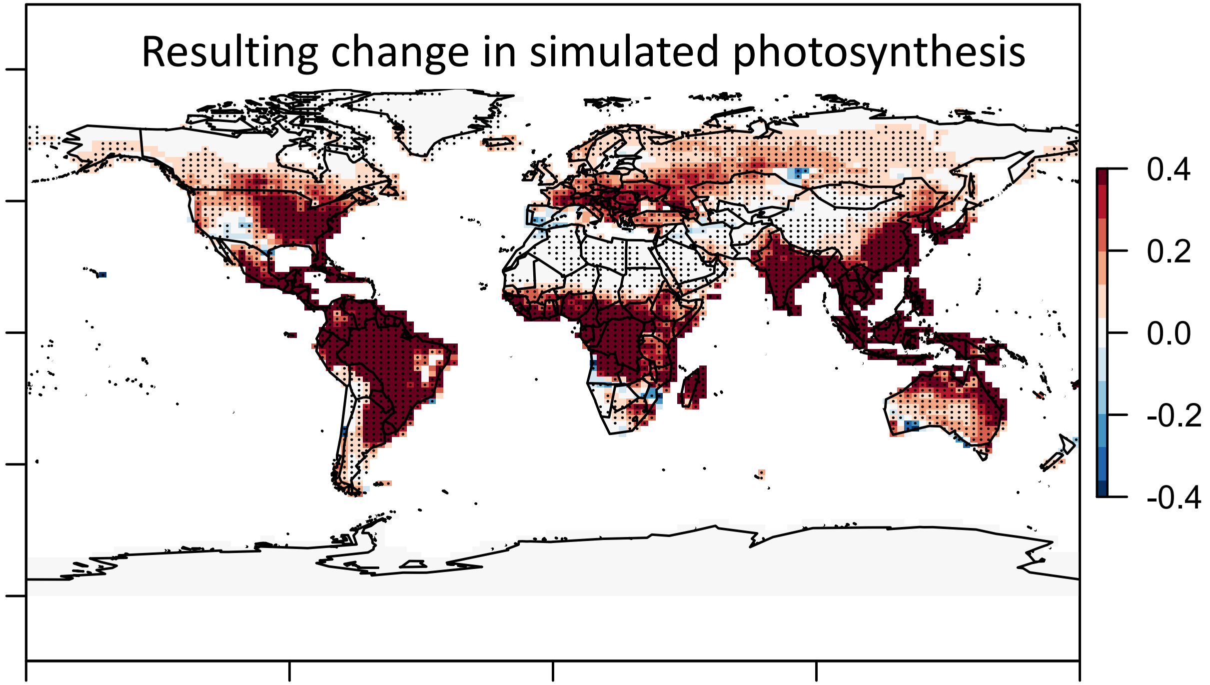
Lack of theory results in…

- Inability to test mechanisms





Kattge and Knorr (2007) *PC&E*

Smith et al. (2017) *JAMES*

nick.smith@ttu.edu; @nick_greg_smith

Our Goal: Develop a mechanistic model of photosynthetic acclimation based on optimization and the first principles of plant physiological theory

nick.smith@ttu.edu; @nick_greg_smith

Optimization: Least cost hypothesis

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

Wright et al. (2003) *American Naturalist*

nick.smith@ttu.edu; @nick_greg_smith

Optimal photosynthesis

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

nick.smith@ttu.edu; @nick_greg_smith

Optimal photosynthesis

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

Must predict optimal rates of both

nick.smith@ttu.edu; @nick_greg_smith

Optimal photosynthesis

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

nature plants
LETTERS
DOI: 10.1038/s41477-017-0006-8

Towards a universal model for carbon dioxide uptake by plants

Han Wang[1,2,3]*, I. Colin Prentice[1,2,4], Trevor F. Keenan[2,5], Tyler W. Davis[4,6], Ian J. Wright[2], William K. Cornwell[7], Bradley J. Evans[2,8] and Changhui Peng[1,9]*

ECOLOGY LETTERS
Ecology Letters, (2014) **17**: 82–91 doi: 10.1111/ele.12211
LETTER

Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology

I. Colin Prentice,[1,2]* Ning Dong,[1] Sean M. Gleason,[1] Vincent Maire[1] and Ian J. Wright[1]

Abstract
A novel framework is presented for the analysis of ecophysiological field measurements and modelling. The hypothesis '*leaves minimise the summed unit costs of transpiration and carboxylation*' predicts leaf-internal/ambient CO_2 ratios (c_i/c_a) and slopes of maximum carboxylation rate (V_{cmax}) or leaf nitrogen (N_{area}) *vs.* stomatal conductance. Analysis of data on woody species from con-

Optimal photosynthesis

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

Biochemistry optimization: Coordination hypothesis

Photosynthesis may be limited by **Rubisco carboxylation rate** or **electron transport rate to regenerate Rubisco**

Biochemistry optimization: Coordination hypothesis

Photosynthesis may be limited by **Rubisco carboxylation rate** or **electron transport rate to regenerate Rubisco**

Optimally, plants will coordinate their biochemistry to be equally limited by both rates

nick.smith@ttu.edu; @nick_greg_smith

Coordination of photosynthesis

Optimally…

$$A_c = A_j$$

Carboxylation-limited photosynthesis

Electron transport-limited photosynthesis

nick.smith@ttu.edu; @nick_greg_smith

Coordination of photosynthesis

$$A_c = f\{V_{cmax}, T, CO_2\}$$

Carboxylation-limited photosynthesis

$$A_j = f\{light, T, CO_2\}$$

Electron transport-limited photosynthesis

Farquhar, von Caemmer, & Berry (1980) *Planta*

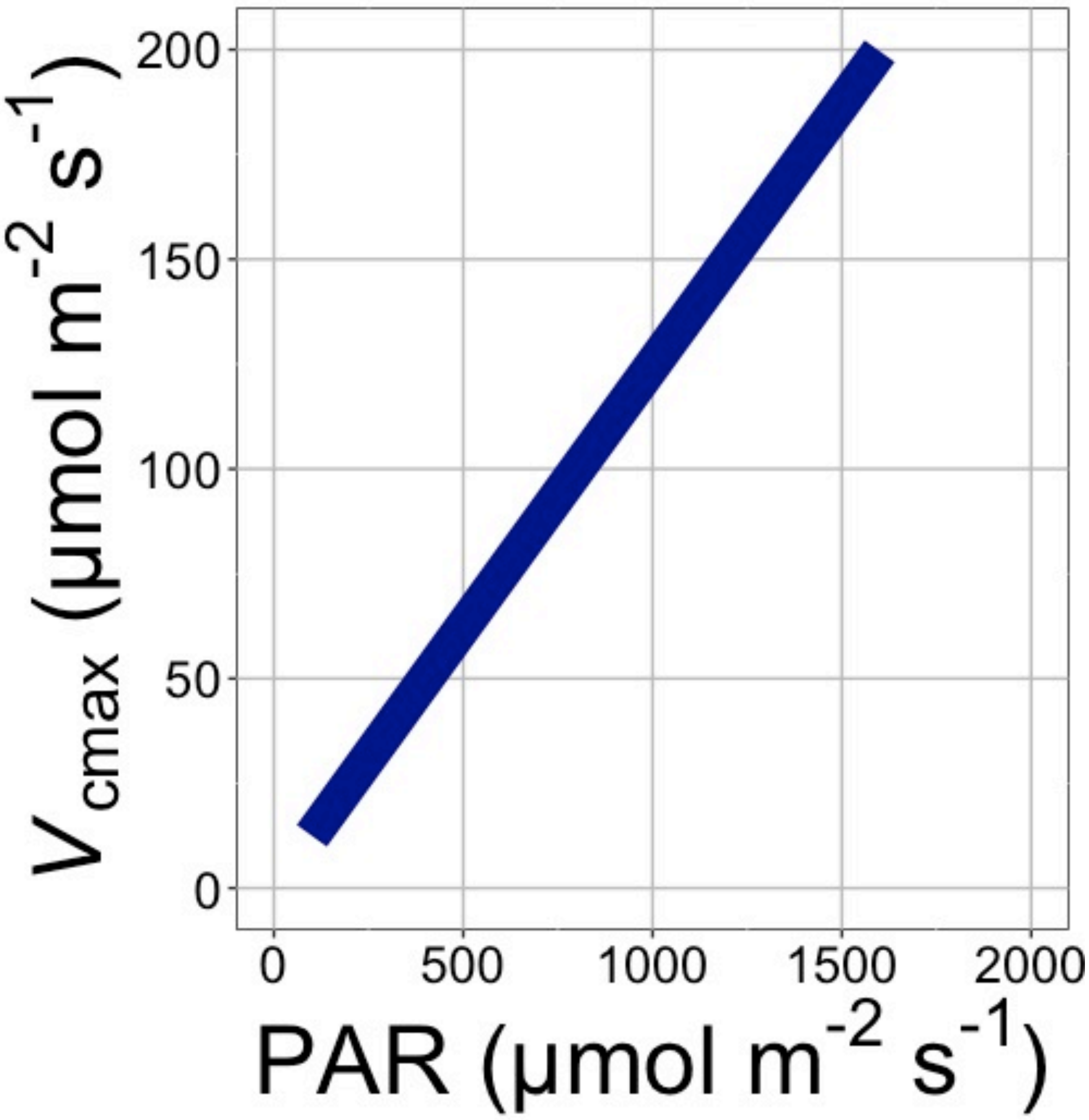
nick.smith@ttu.edu; @nick_greg_smith

Rearrange to solve for measurable traits

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

Smith et al. (2019) *Ecology Letters*

nick.smith@ttu.edu; @nick_greg_smith



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

Smith et al. (2019) *Ecology Letters*

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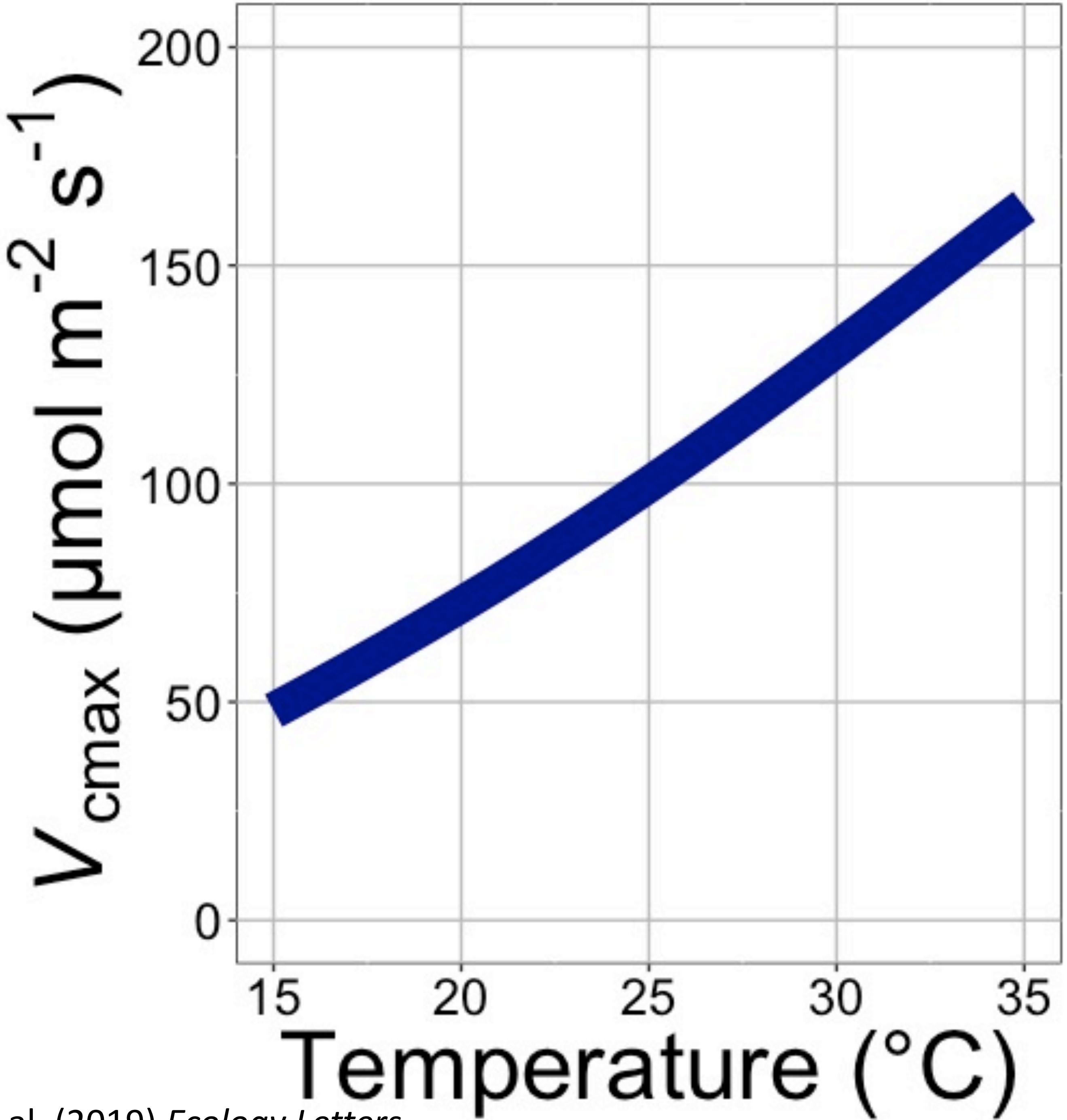

V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019) *Ecology Letters*

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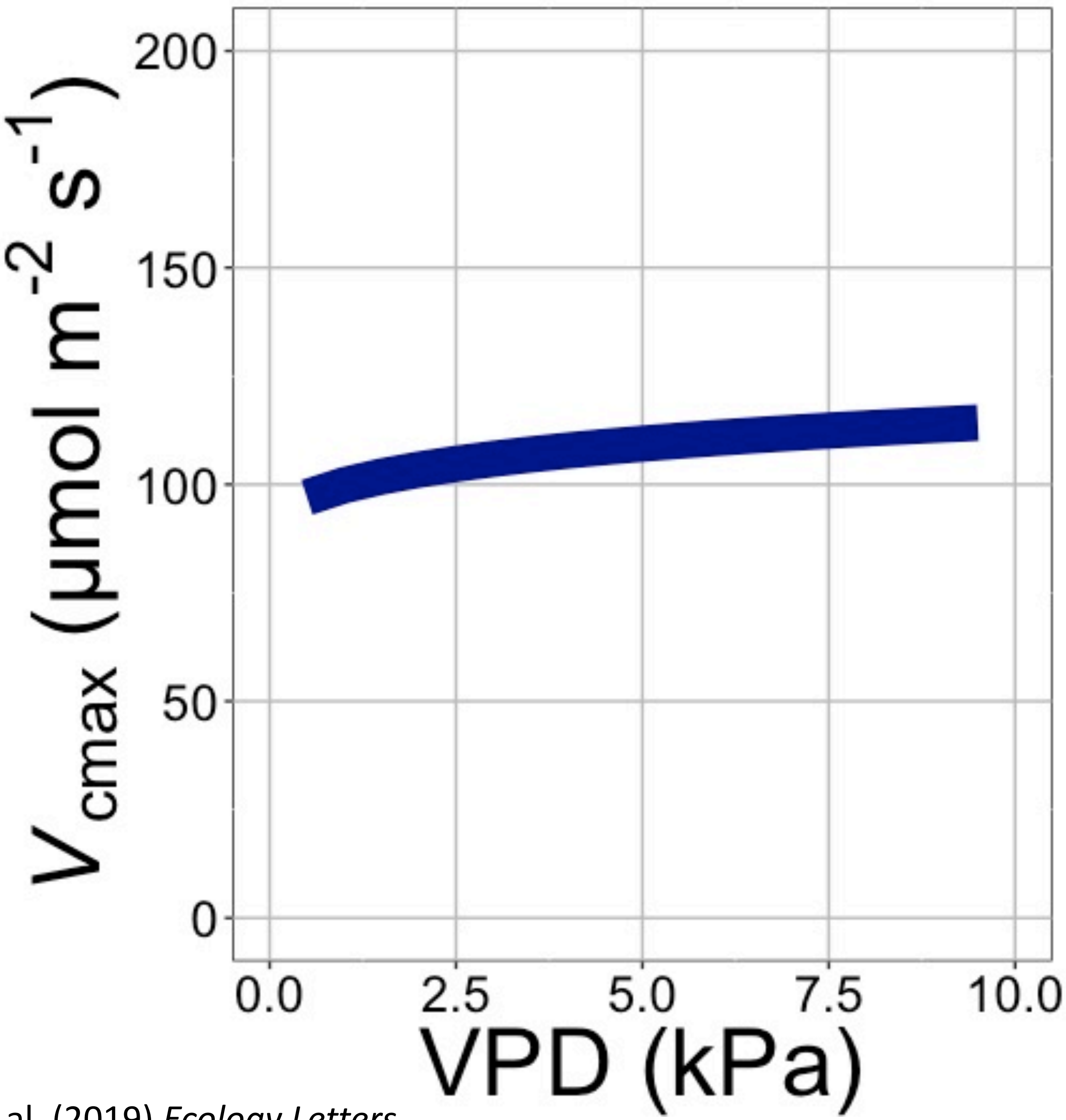

Smith et al. (2019) *Ecology Letters*

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

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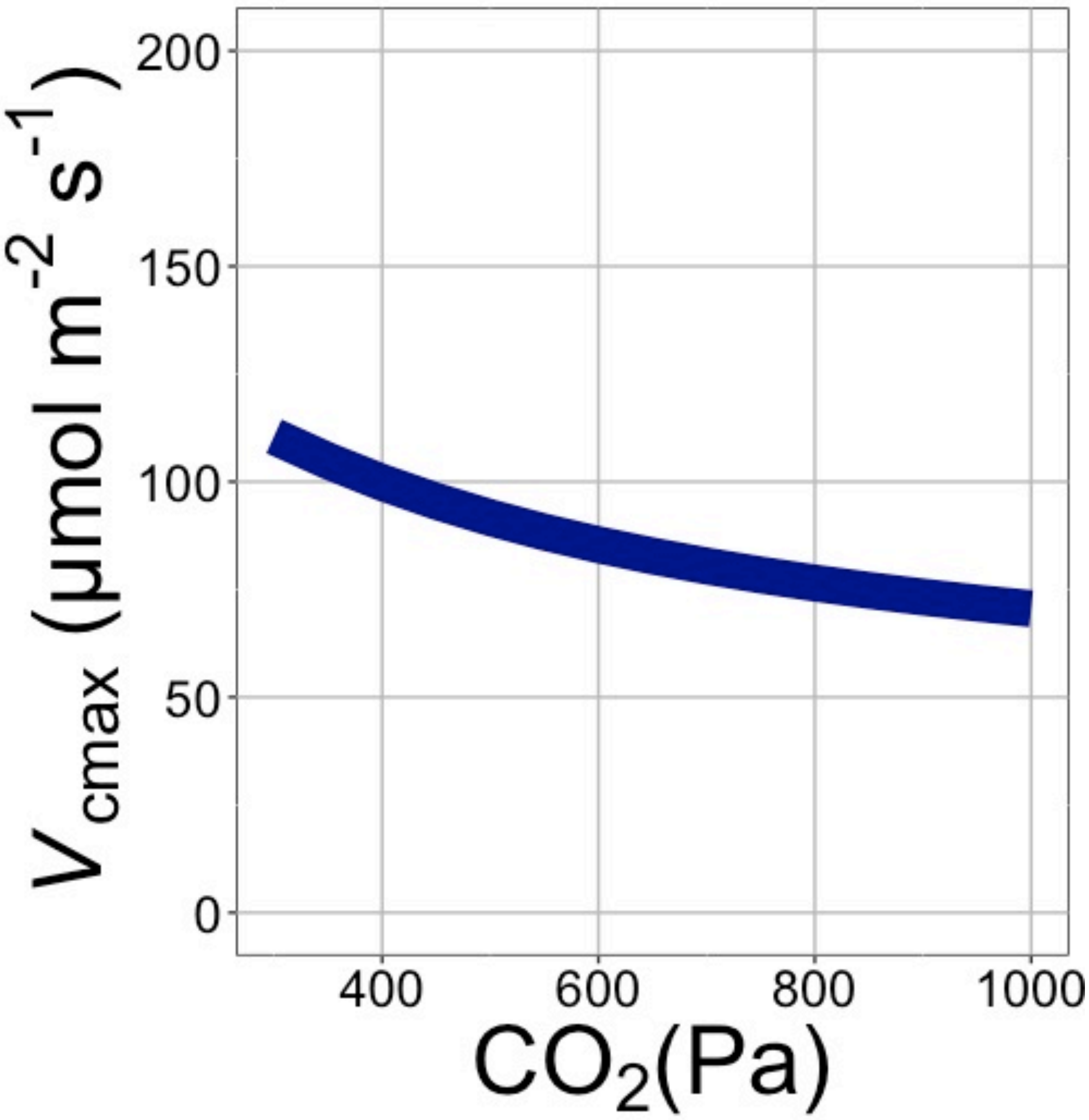

V_{cmax} decreases with CO_2 because of lower c_i

Smith et al. (2019) *Ecology Letters*

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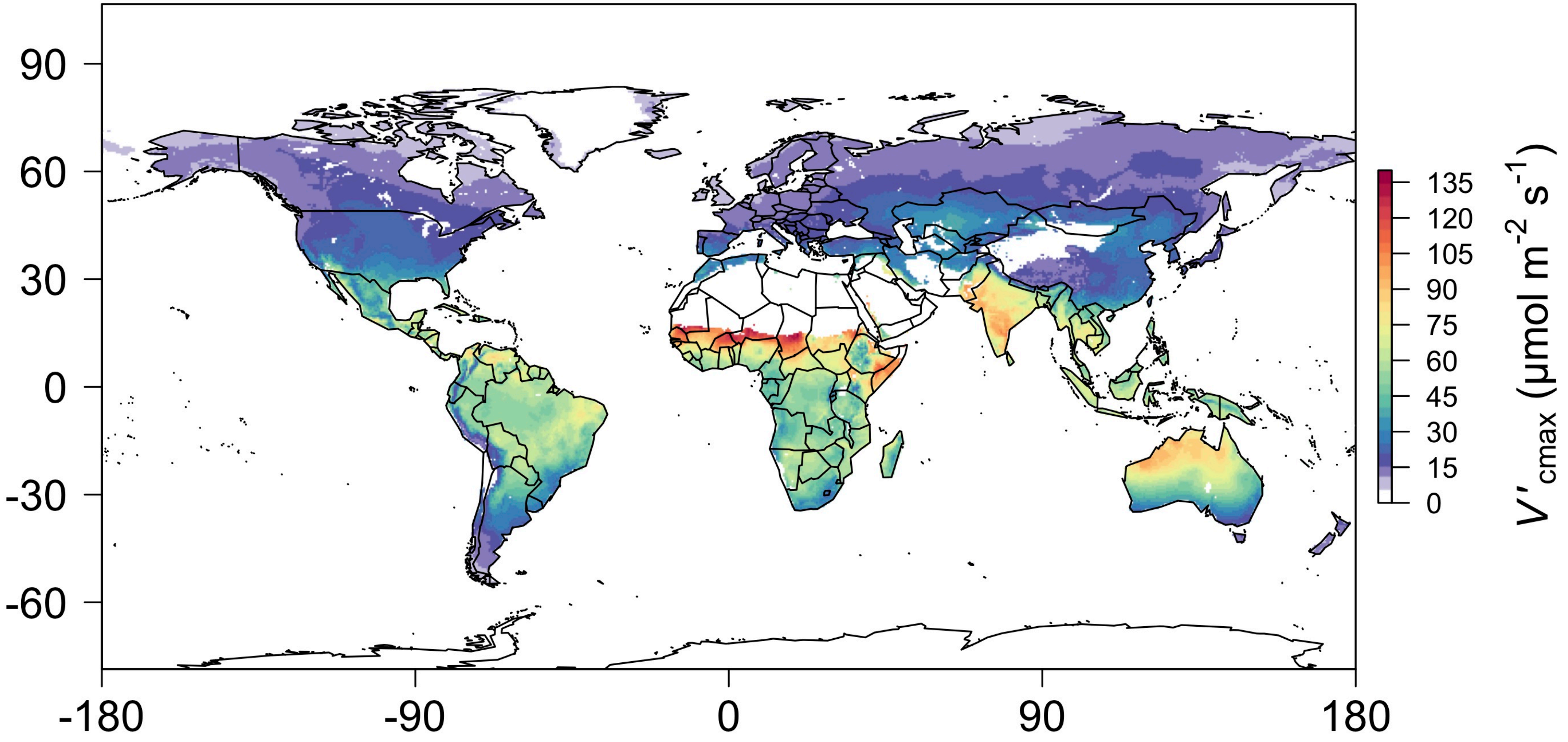
We can predict optimal V_{cmax}



Smith et al. (2019) *Ecology Letters*

nick.smith@ttu.edu; @nick_greg_smith

Ok, great, but now what?

nick.smith@ttu.edu; @nick_greg_smith

Let’s tackle some big questions in plant ecophysiology!

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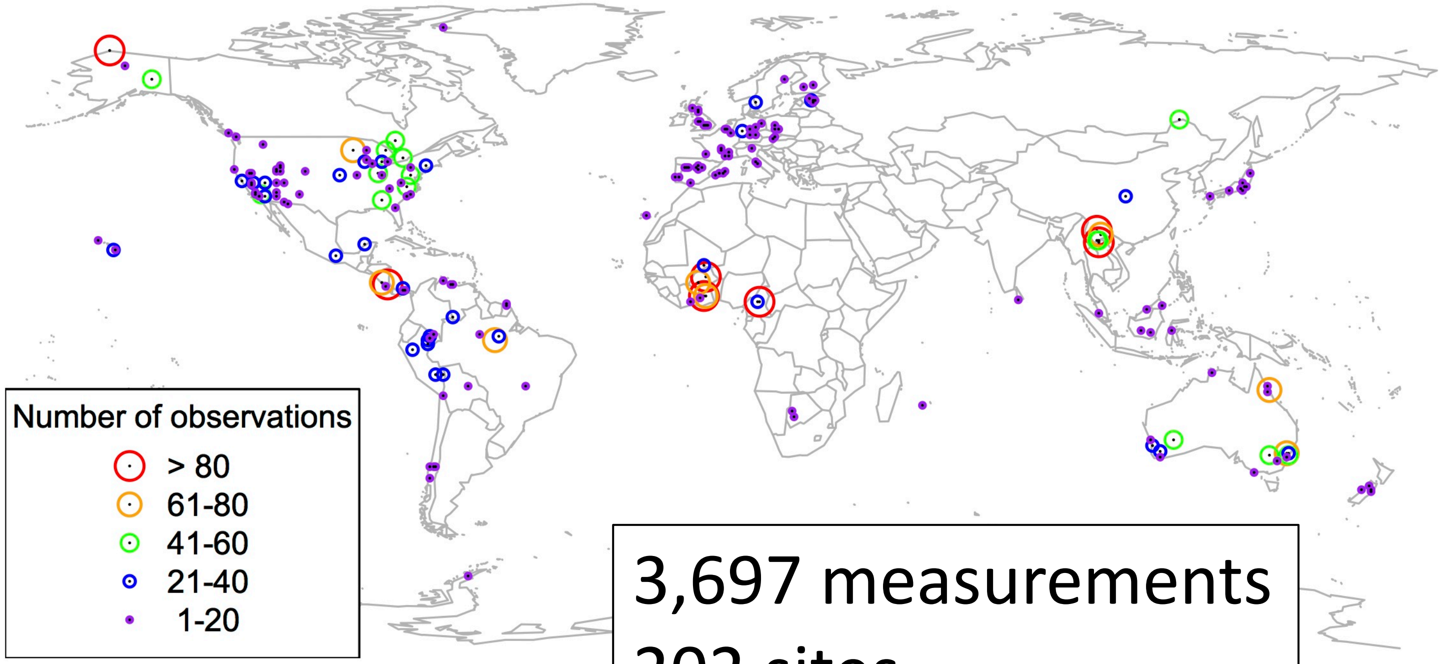
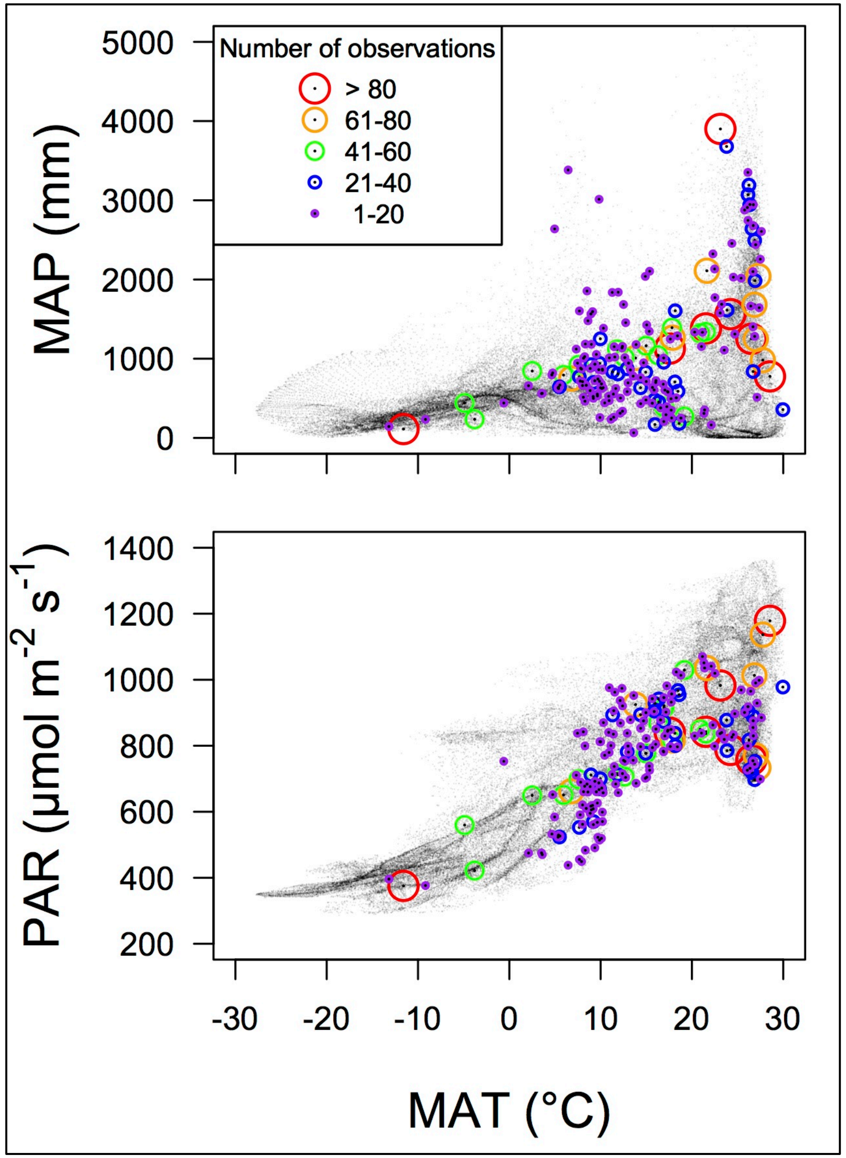
Question 1: Is photosynthesis optimized to the environment?

nick.smith@ttu.edu; @nick_greg_smith

Global V_{cmax} dataset



3,697 measurements
202 sites
> 600 genera



Smith et al. (2019) *Ecology Letters*

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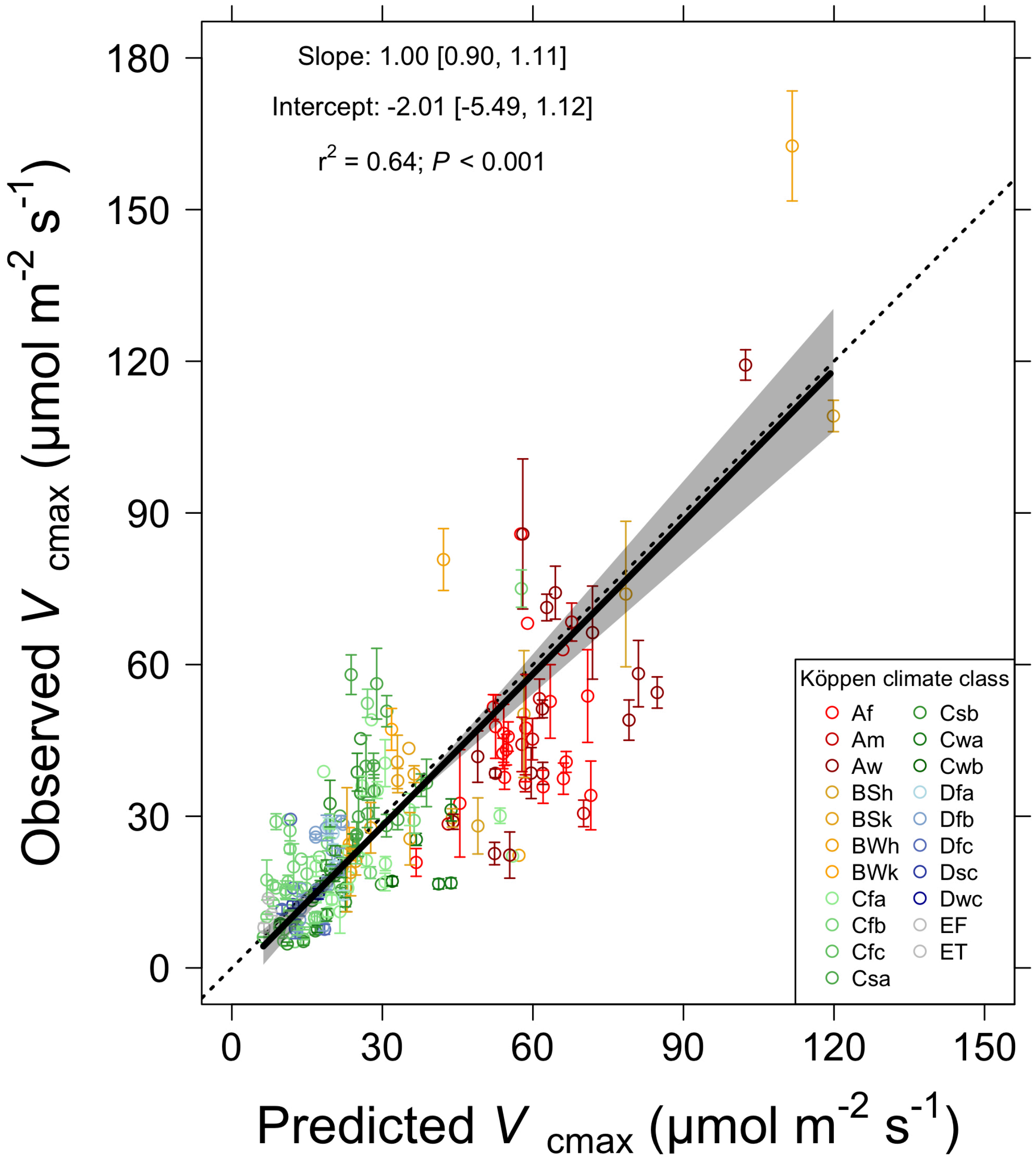

Smith et al. (2019) *Ecology Letters*

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Question 1: Is photosynthesis optimized to the environment?

YES! Photosynthesis acclimates spatially as expected from optimization

nick.smith@ttu.edu; @nick_greg_smith

Question 2: How will photosynthesis acclimate to future conditions?

nick.smith@ttu.edu; @nick_greg_smith

Photosynthetic traits change with temperature and CO_2 in ways expected from optimization

Smith and Keenan (in prep)

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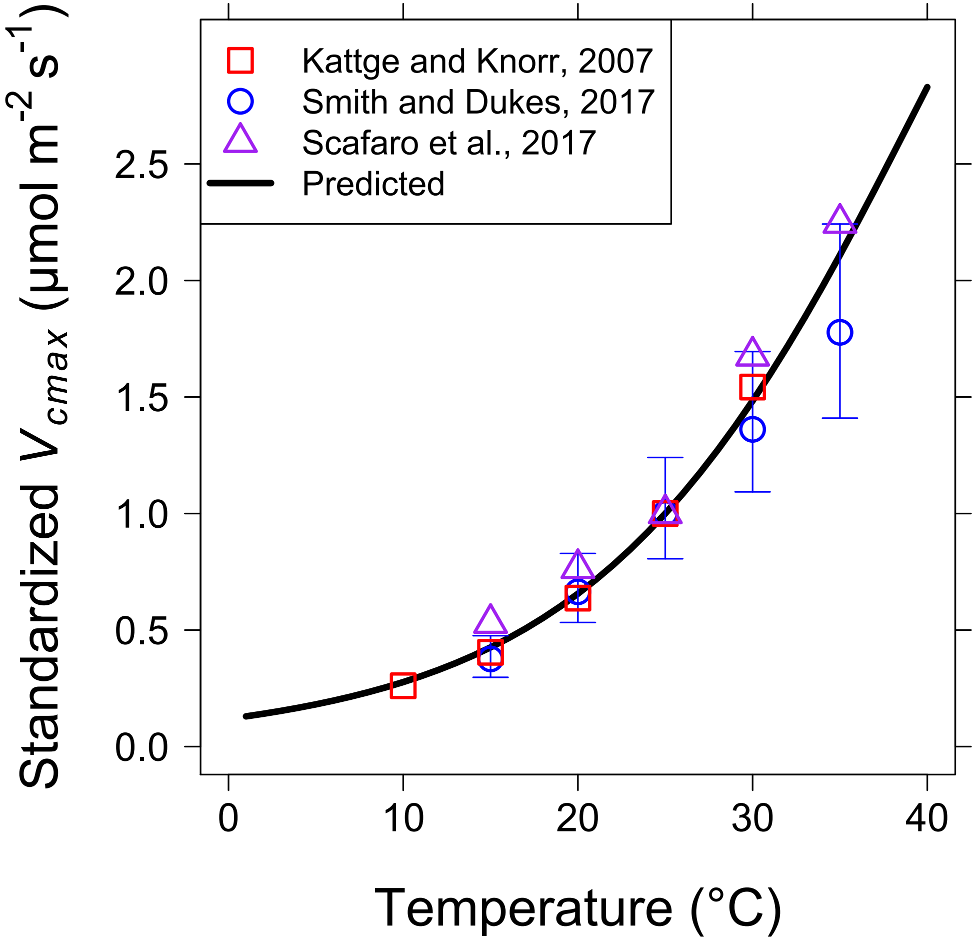
Photosynthetic traits change with temperature and CO_2 in ways expected from optimization



Fully acclimated response

Smith and Keenan (in prep)

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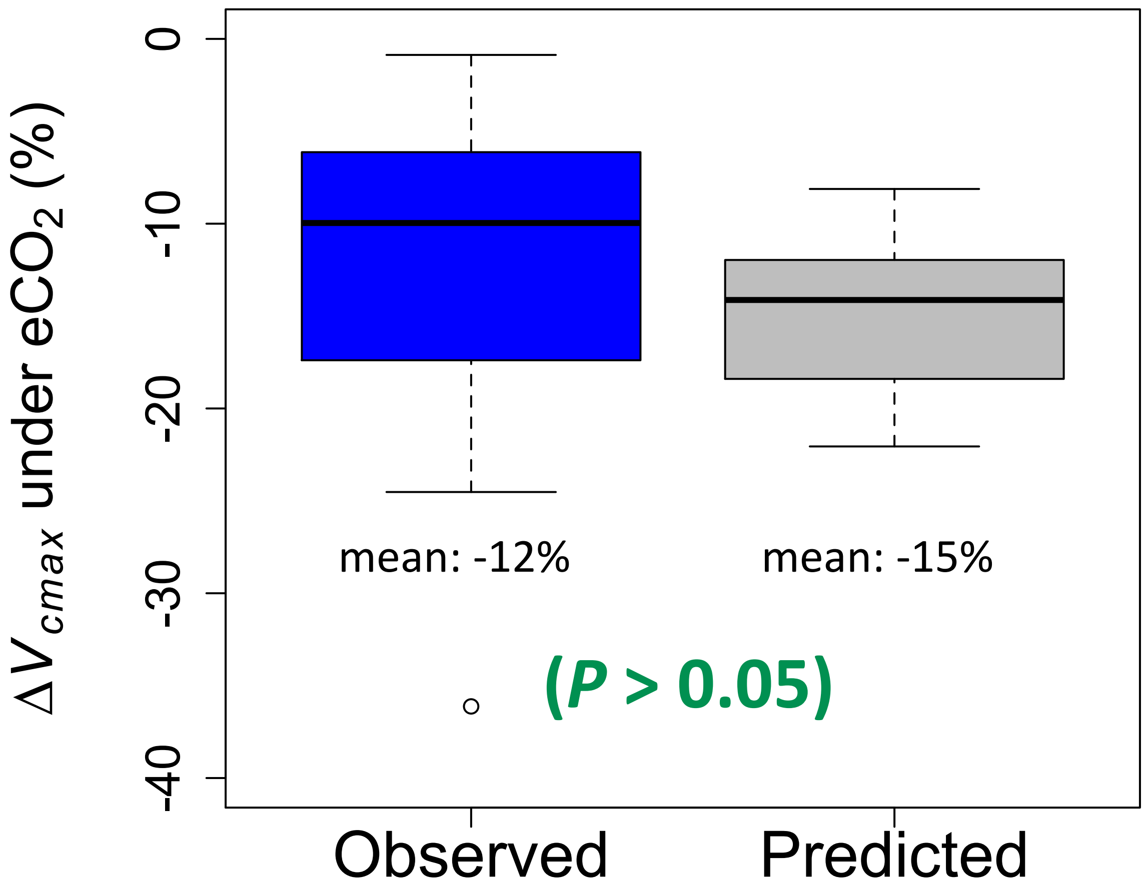
Photosynthetic traits change with temperature and CO_2 in ways expected from optimization



Smith and Keenan (in prep)

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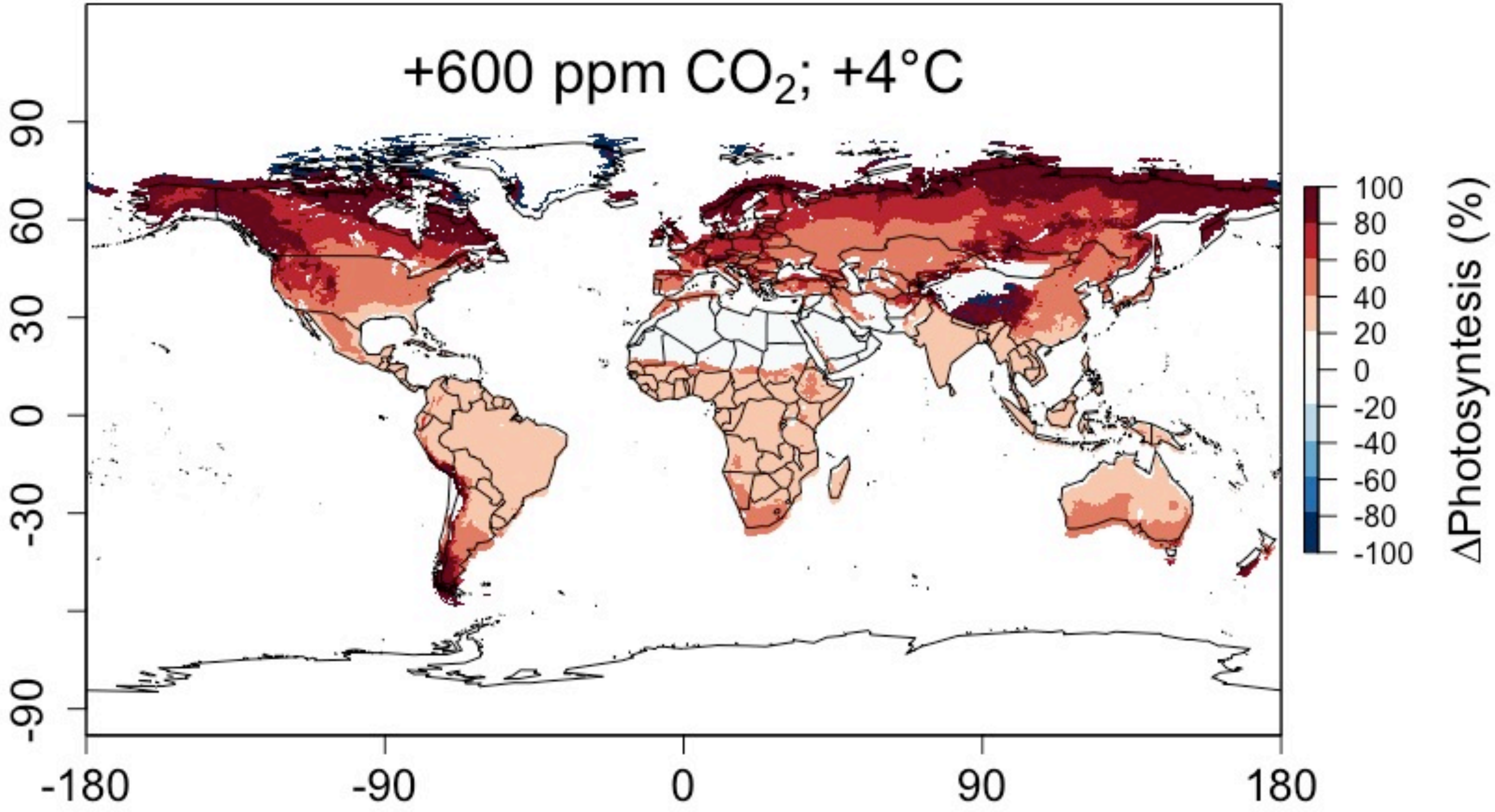
Higher CO_2 and increased temperatures increase future photosynthesis



Smith and Keenan (in prep)

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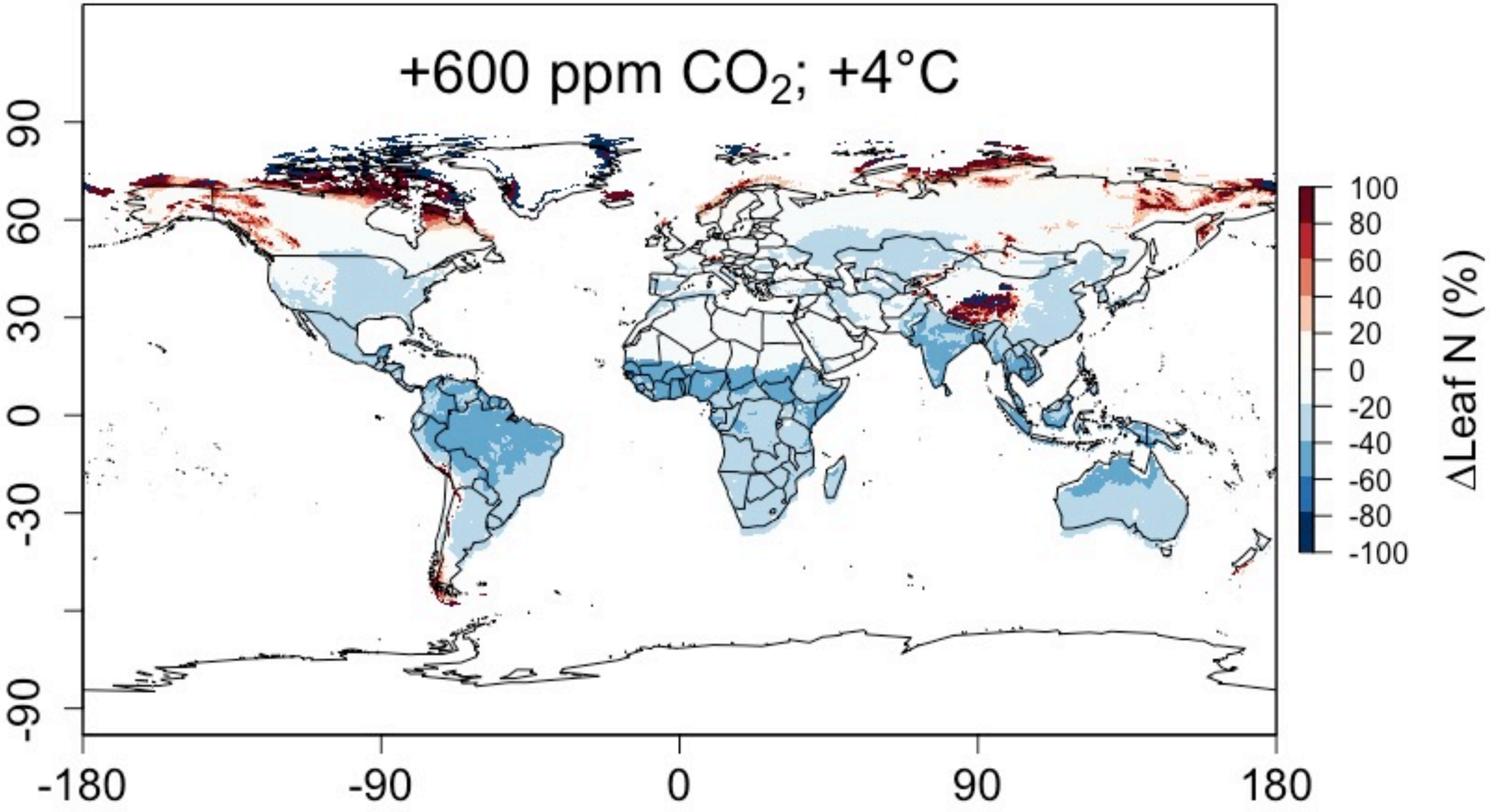
Higher CO_2 and increased temperatures increase future photosynthesis (at lower nutrient use)



Smith and Keenan (in prep)

nick.smith@ttu.edu; @nick_greg_smith

Question 2: How will photosynthesis acclimate to future conditions?

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

nick.smith@ttu.edu; @nick_greg_smith

Question 3: Does photosynthesis respond to nutrient addition?

Lizz Waring
TTU

nick.smith@ttu.edu; @nick_greg_smith

From the least cost hypothesis…

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

nick.smith@ttu.edu; @nick_greg_smith

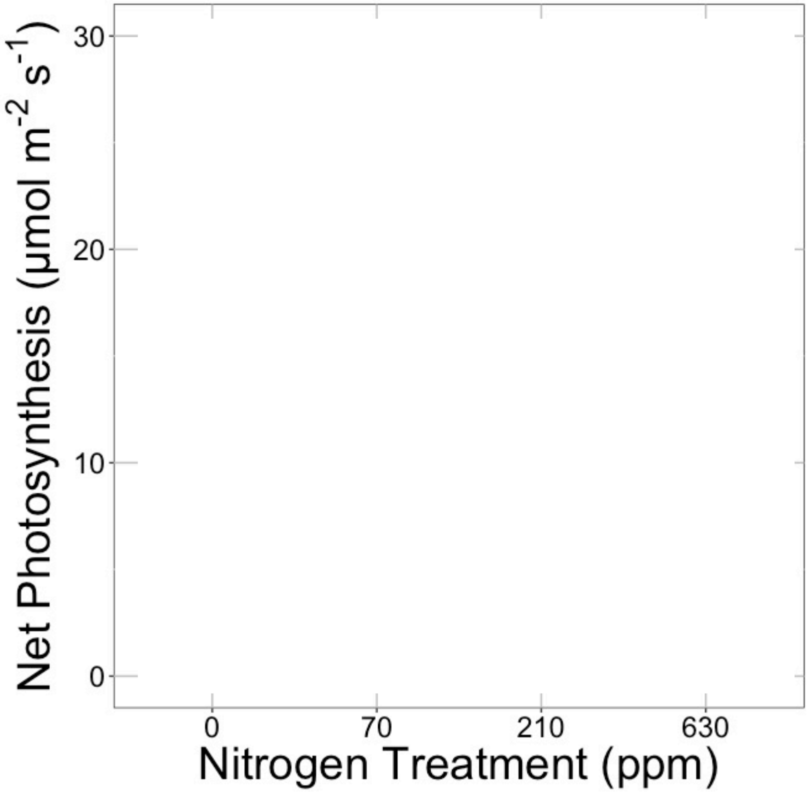
From the least cost hypothesis…

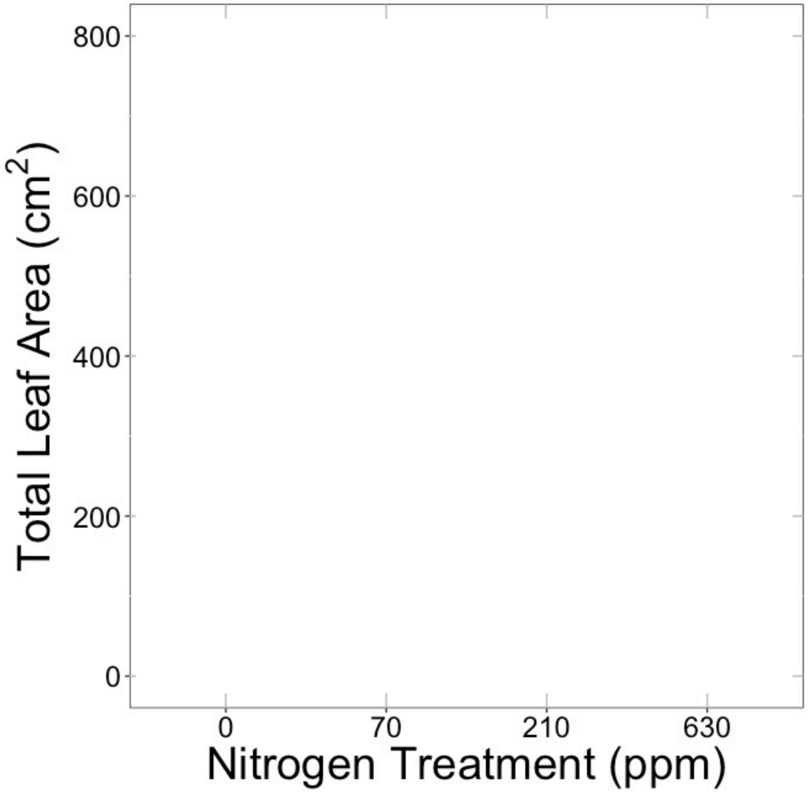
Added nutrients will not increase photosynthesis because light limitation will kick in

Optimal response would be to increase leaf area

nick.smith@ttu.edu; @nick_greg_smith

Leaf area, but not photosynthesis increases with N addition





Waring and Smith (in prep)

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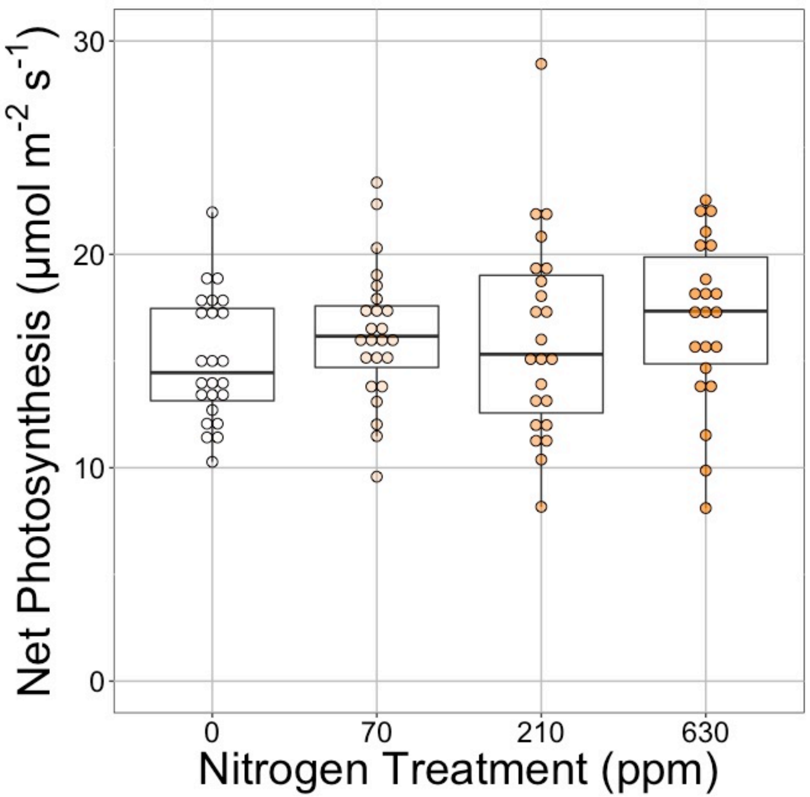

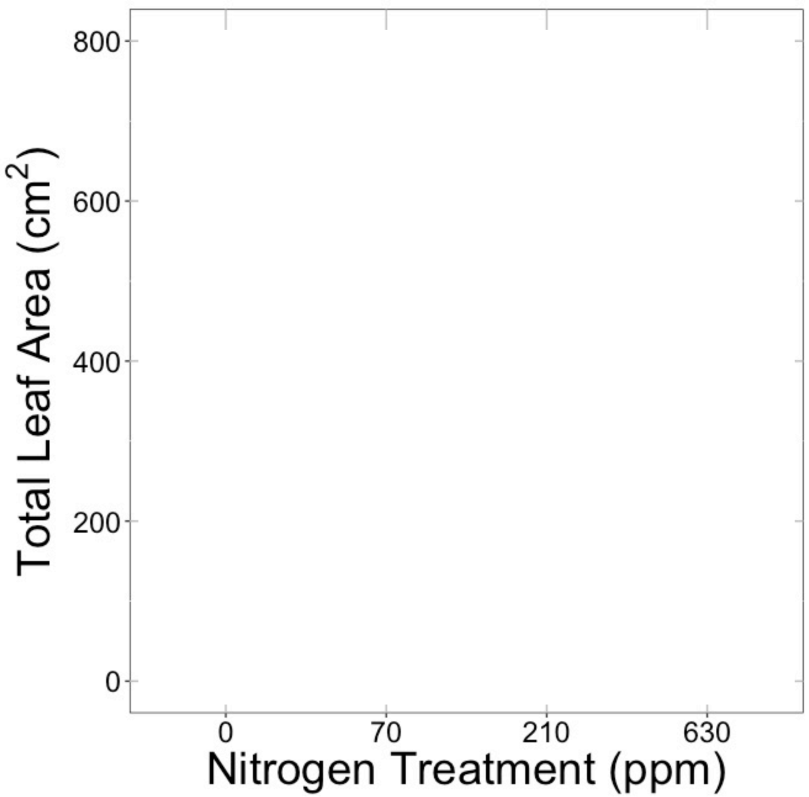

Waring and Smith (in prep)

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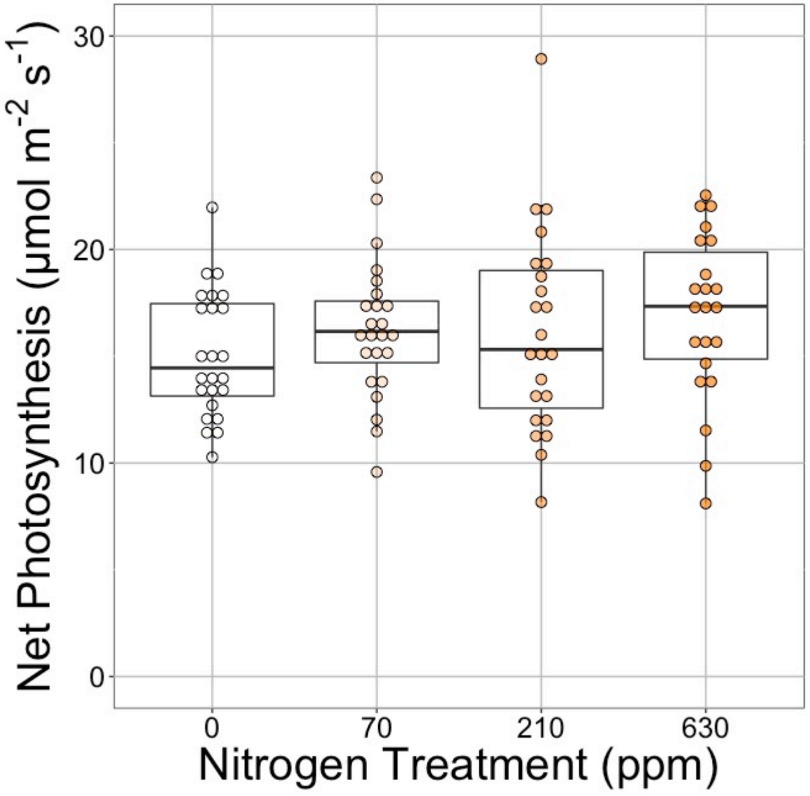
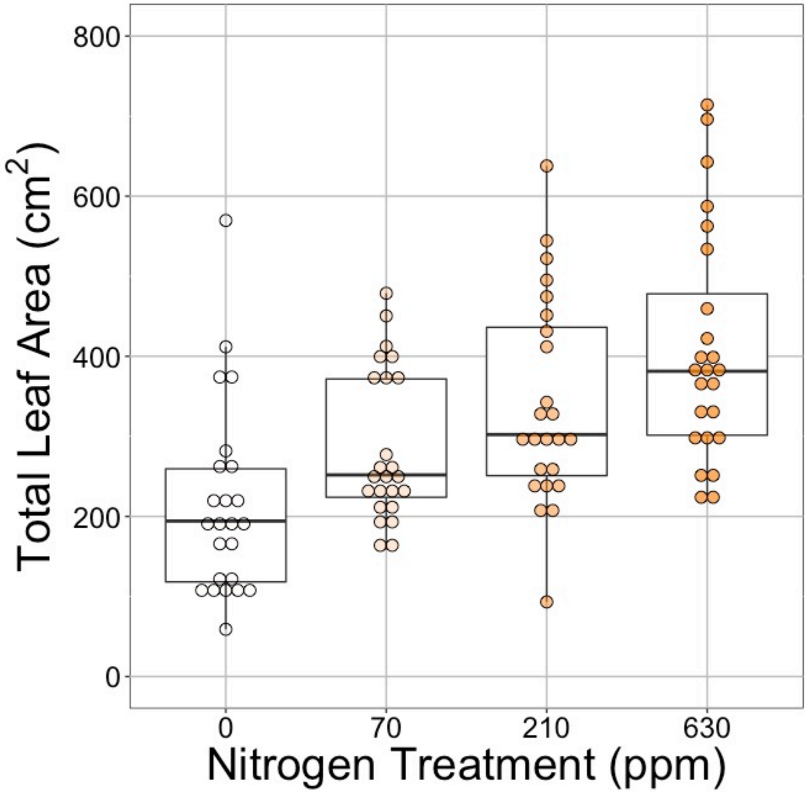
Leaf area, but not photosynthesis increases with N addition





Waring and Smith (in prep)

But do greenhouse experiments translate to the field?

nutrient network

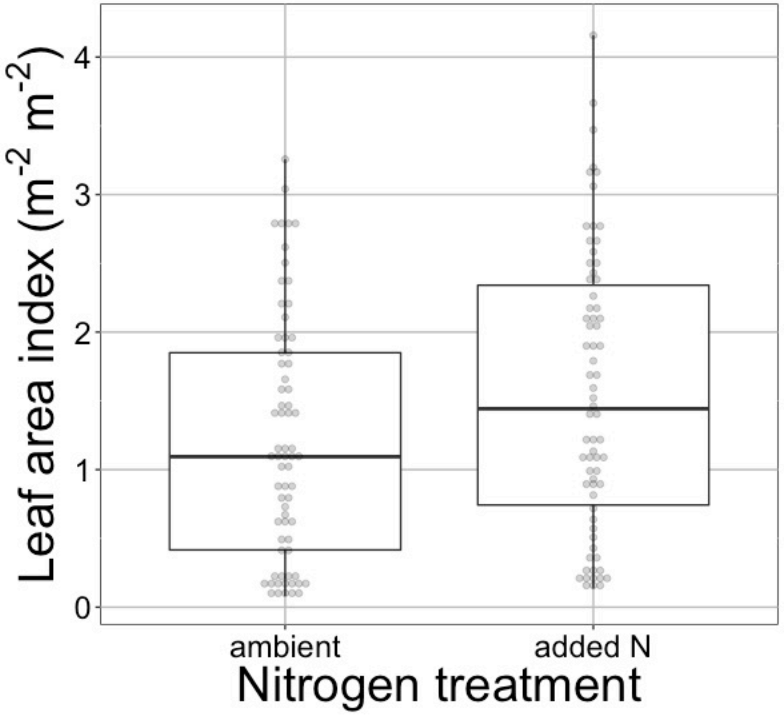
Grassland soil nutrient addition network:

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

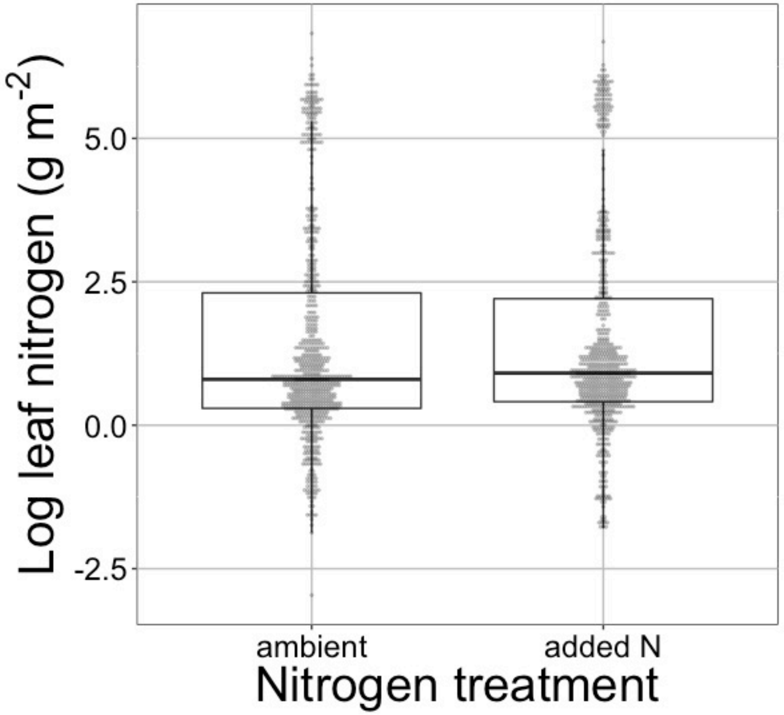
nick.smith@ttu.edu; @nick_greg_smith

Globally, N addition increases leaf area, not leaf N

41% increase (P < 0.05)



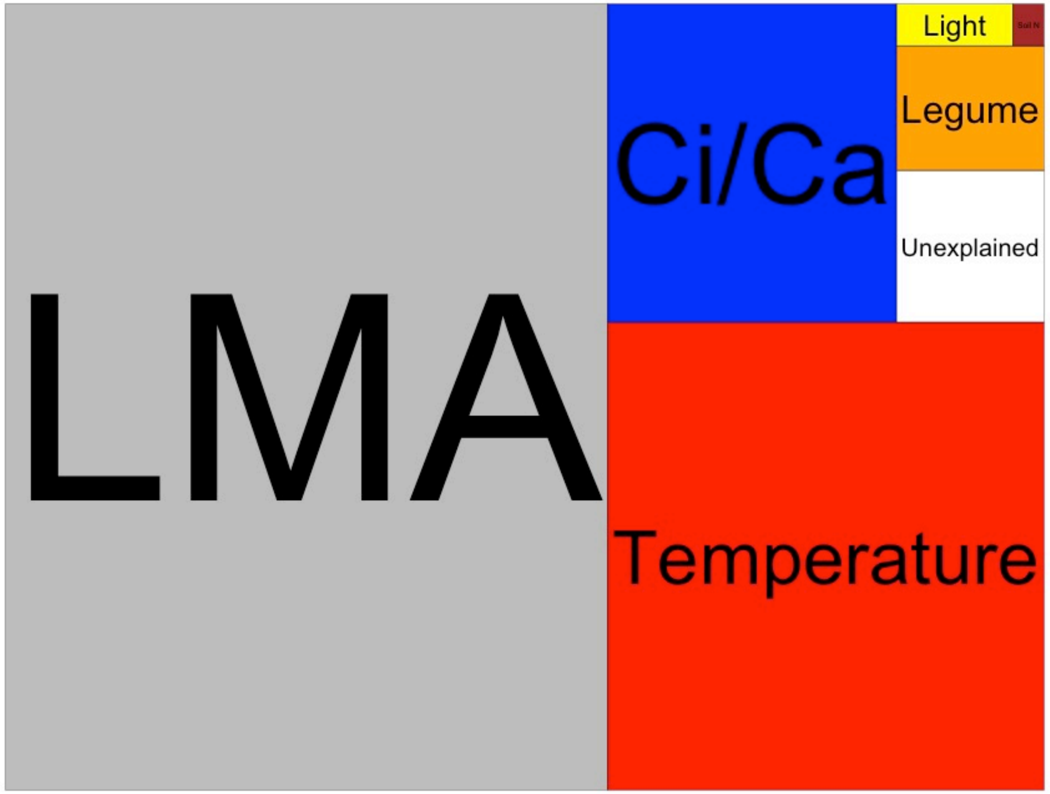
No change (P = 0.42)



Waring and Smith (in prep)

nick.smith@ttu.edu; @nick_greg_smith

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)

nutrient network

nick.smith@ttu.edu; @nick_greg_smith

Question 3: Does photosynthesis respond to nitrogen addition?

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

nick.smith@ttu.edu; @nick_greg_smith

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

Helen Scott
TTU

nick.smith@ttu.edu; @nick_greg_smith

C_3 versus C_4 optimization

nick.smith@ttu.edu; @nick_greg_smith

C_4 versus C_3 optimization

C_4 photosynthesis has…

- No photorespiration
- An additional limitation (PEP carboxylation)

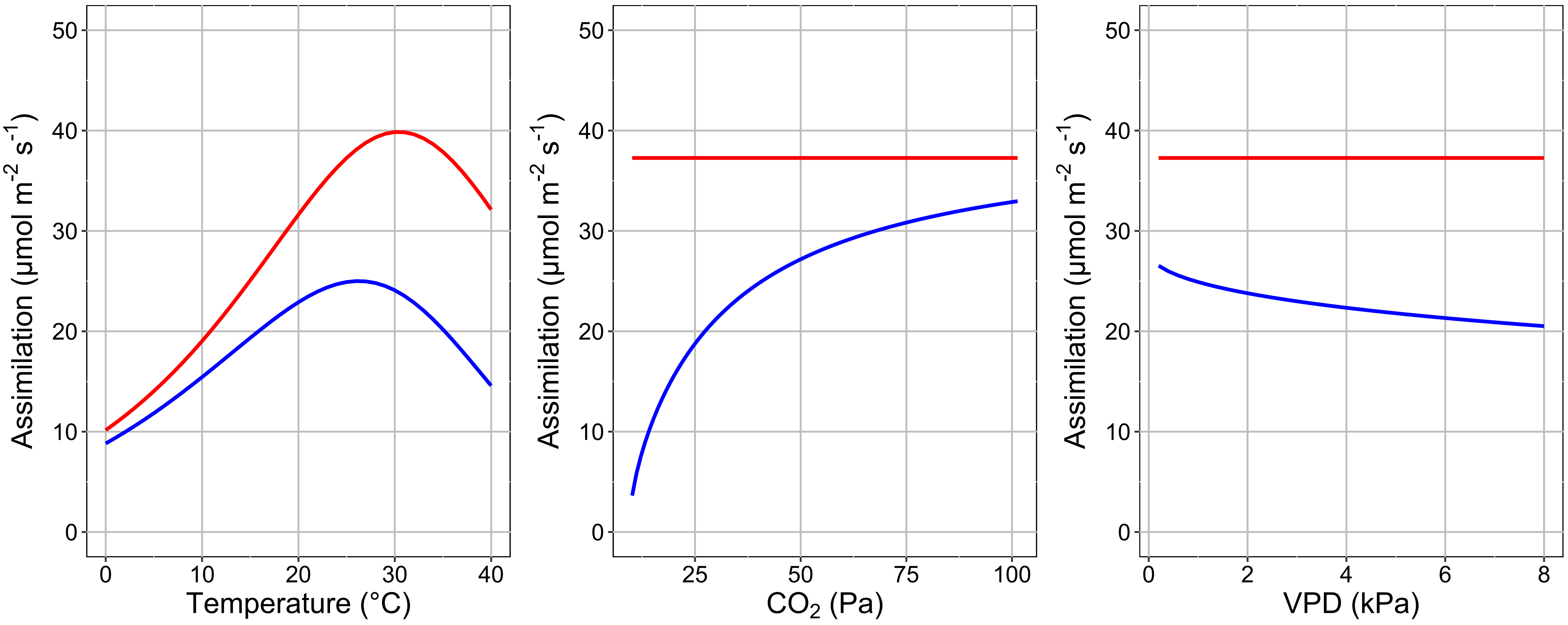
nick.smith@ttu.edu; @nick_greg_smith

C_4 versus C_3 optimization

C_4 photosynthesis has…

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

nick.smith@ttu.edu; @nick_greg_smith



Red = C_4 Blue = C_3

Scott and Smith (in prep)

nick.smith@ttu.edu; @nick_greg_smith

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

C_4 is better in hot, dry, low CO_2 environments

Conclusions

1. We have a theoretical model for photosynthetic acclimation
    - Few empirical parameters
    - Mechanistically based

Conclusions

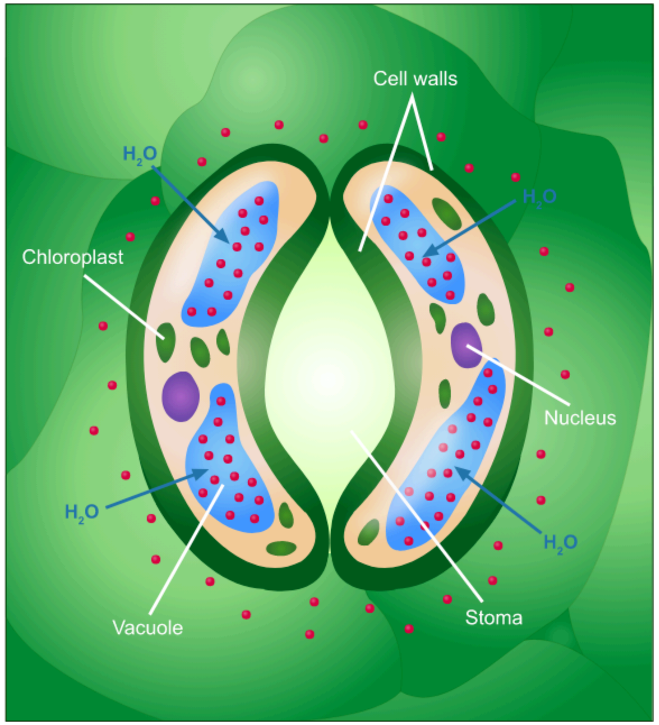
1. We have a theoretical model for photosynthetic acclimation
   - Few empirical parameters
   - Mechanistically based
2. The theory can be useful!
   - Improving the reliability of climate models
   - Acting as a null model for understanding mechanisms

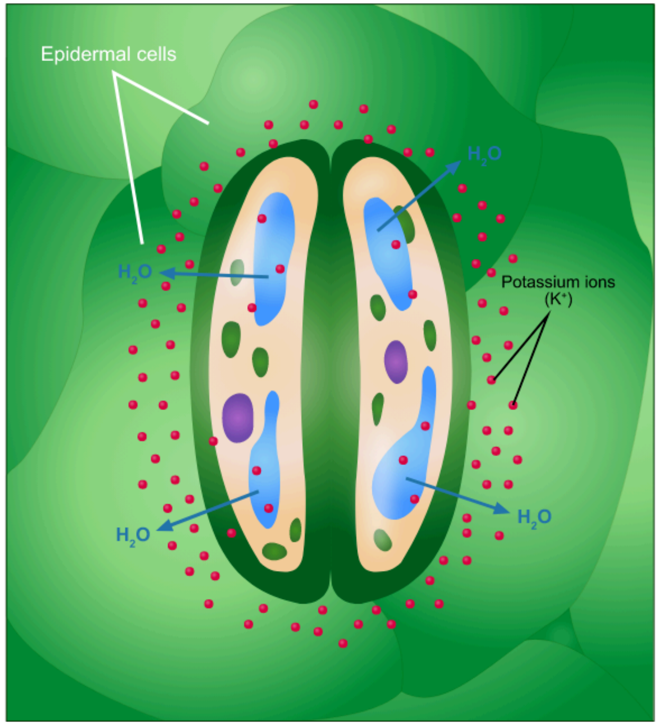
nick.smith@ttu.edu; @nick_greg_smith

Presentation available at:
github.com/SmithEcophysLab/SMB_2019

Thanks!

nick.smith@ttu.edu; @nick_greg_smith





Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux

Closed stomata:

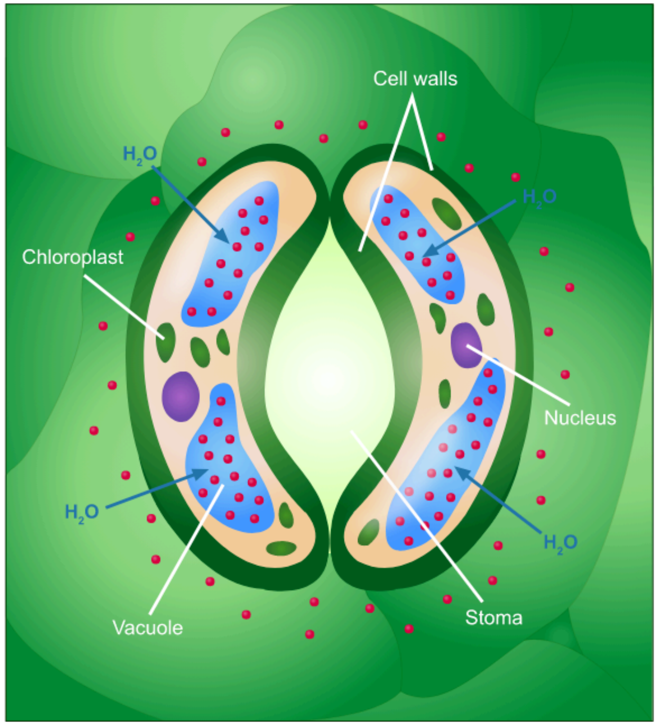
Benefits

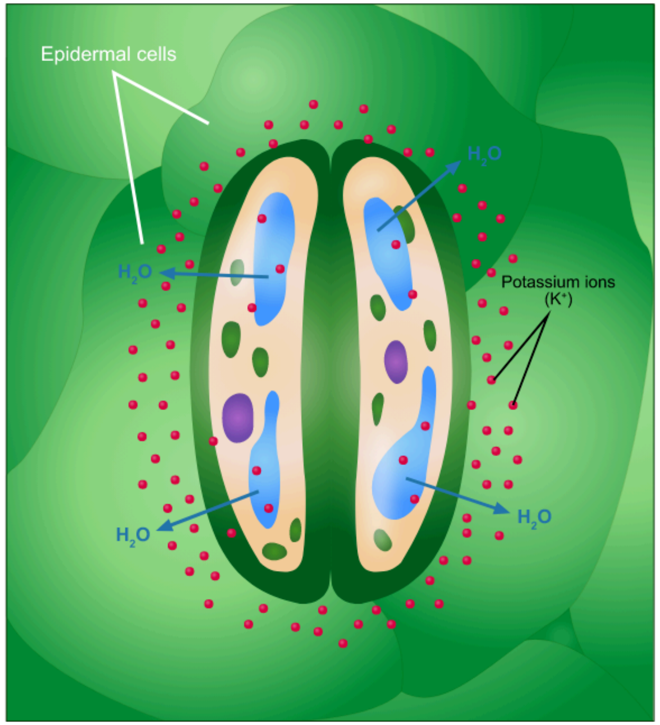
- Low water outflux

Costs

- Low CO_2 influx

nick.smith@ttu.edu; @nick_greg_smith





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

nick.smith@ttu.edu; @nick_greg_smith

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}

nick.smith@ttu.edu; @nick_greg_smith

Stomatal openness determines χ

χ = internal leaf CO_2 / external leaf CO_2

$$\chi = c_i / c_a$$

nick.smith@ttu.edu; @nick_greg_smith

Optimal χ minimizes the costs to maintain transpiration and carboxylation

$$a\frac{\partial\left(\frac{E}{A}\right)}{\partial\chi} + b\frac{\partial\left(\frac{Vcmax}{A}\right)}{\partial\chi} = 0$$

Cost factor for transpiration (E)

Cost factor for Rubisco (V_{cmax})

Prentice et al. (2014) *Ecology Letters*

nick.smith@ttu.edu; @nick_greg_smith

Optimal χ mathmatically

$$\chi = \frac{\Gamma^*}{c_a} + \left(1 - \frac{\Gamma^*}{c_a}\right)\frac{\xi}{\xi + \sqrt{D_g}}$$

$$\xi = \sqrt{\beta\frac{K + \Gamma^*}{1.6\eta^*}}$$

Prentice et al. (2014) *Ecology Letters*

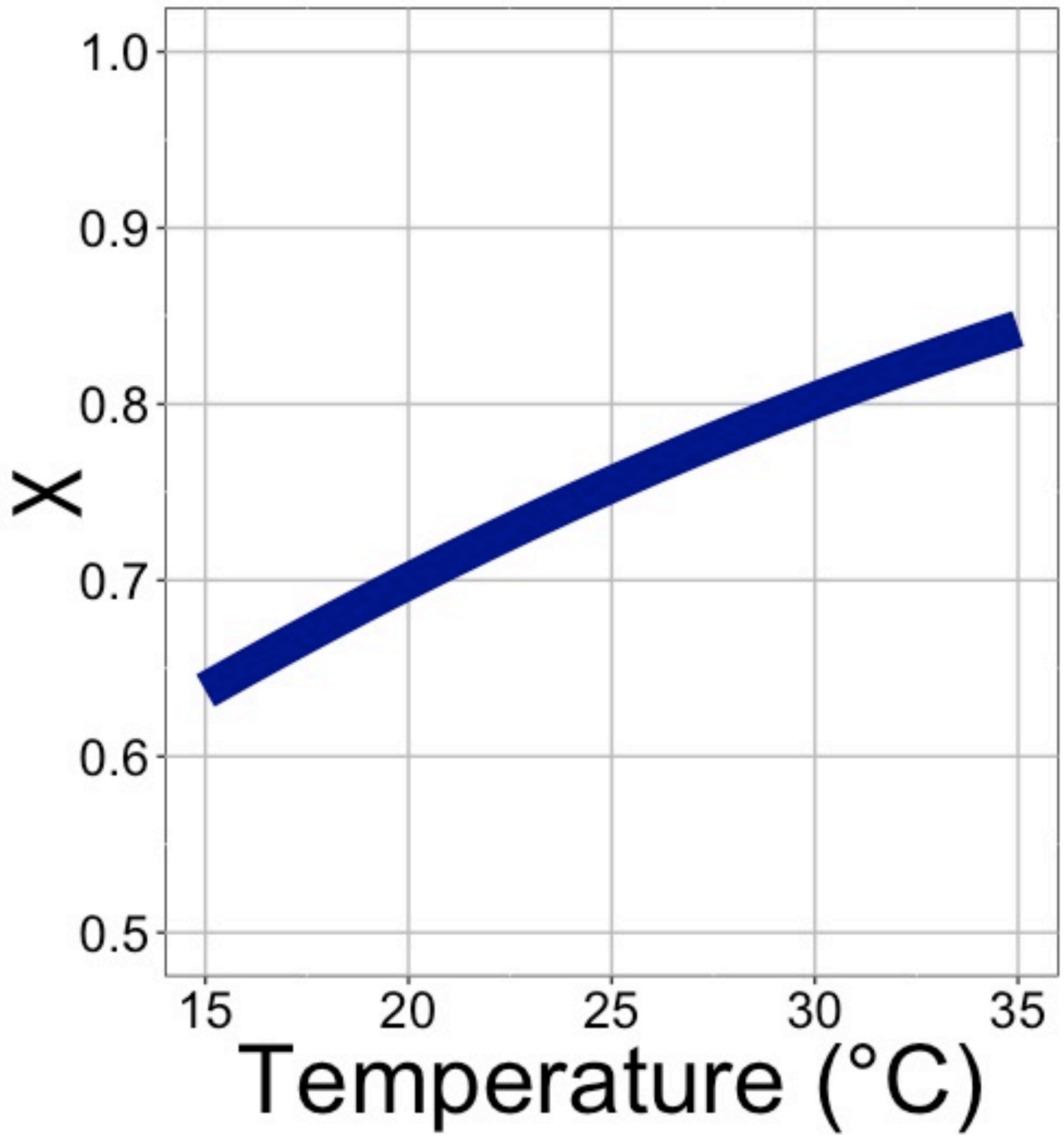
nick.smith@ttu.edu; @nick_greg_smith

Optimal χ is a function of the costs and the environment

$$\chi = f\{\text{temperature}, \\ CO_2, \\ \text{vapor pressure deficit}\}$$

Prentice et al. (2014) *Ecology Letters*; Wang et al. (2017) *Nature Plants*

nick.smith@ttu.edu; @nick_greg_smith



χ increases with temperature because of greater photorespiration

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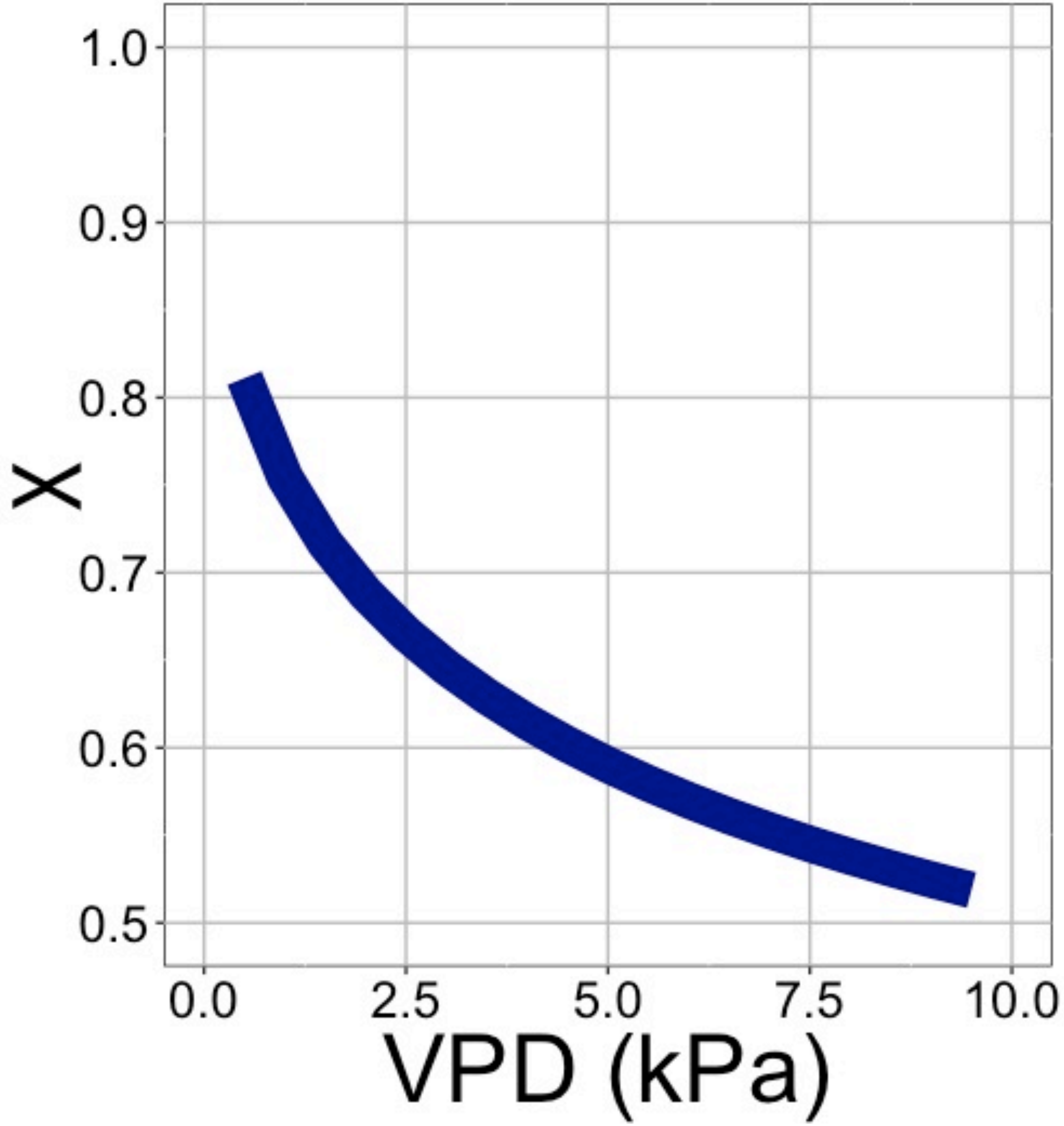
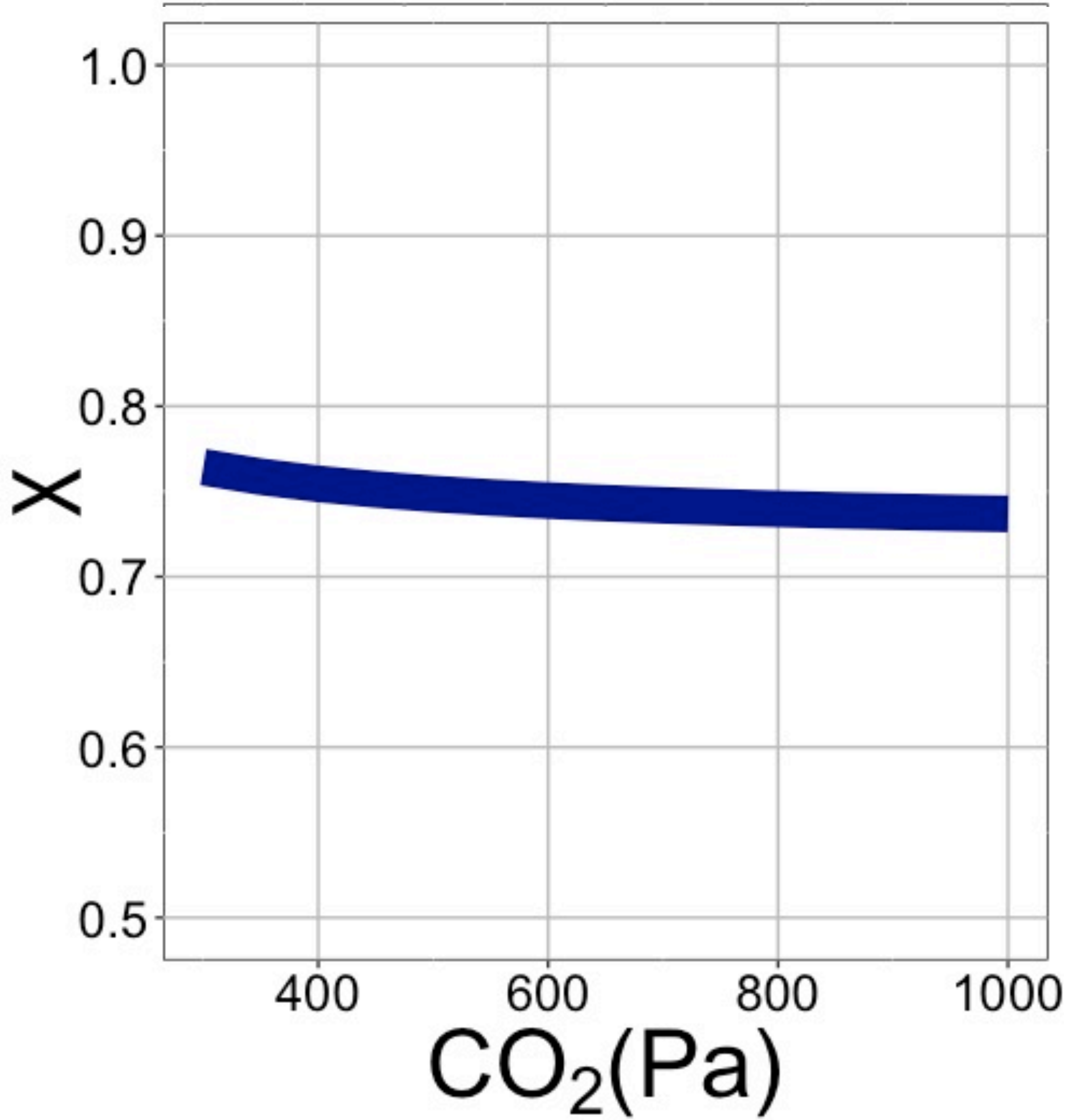


χ decreases with VPD because of greater water loss

nick.smith@ttu.edu; @nick_greg_smith



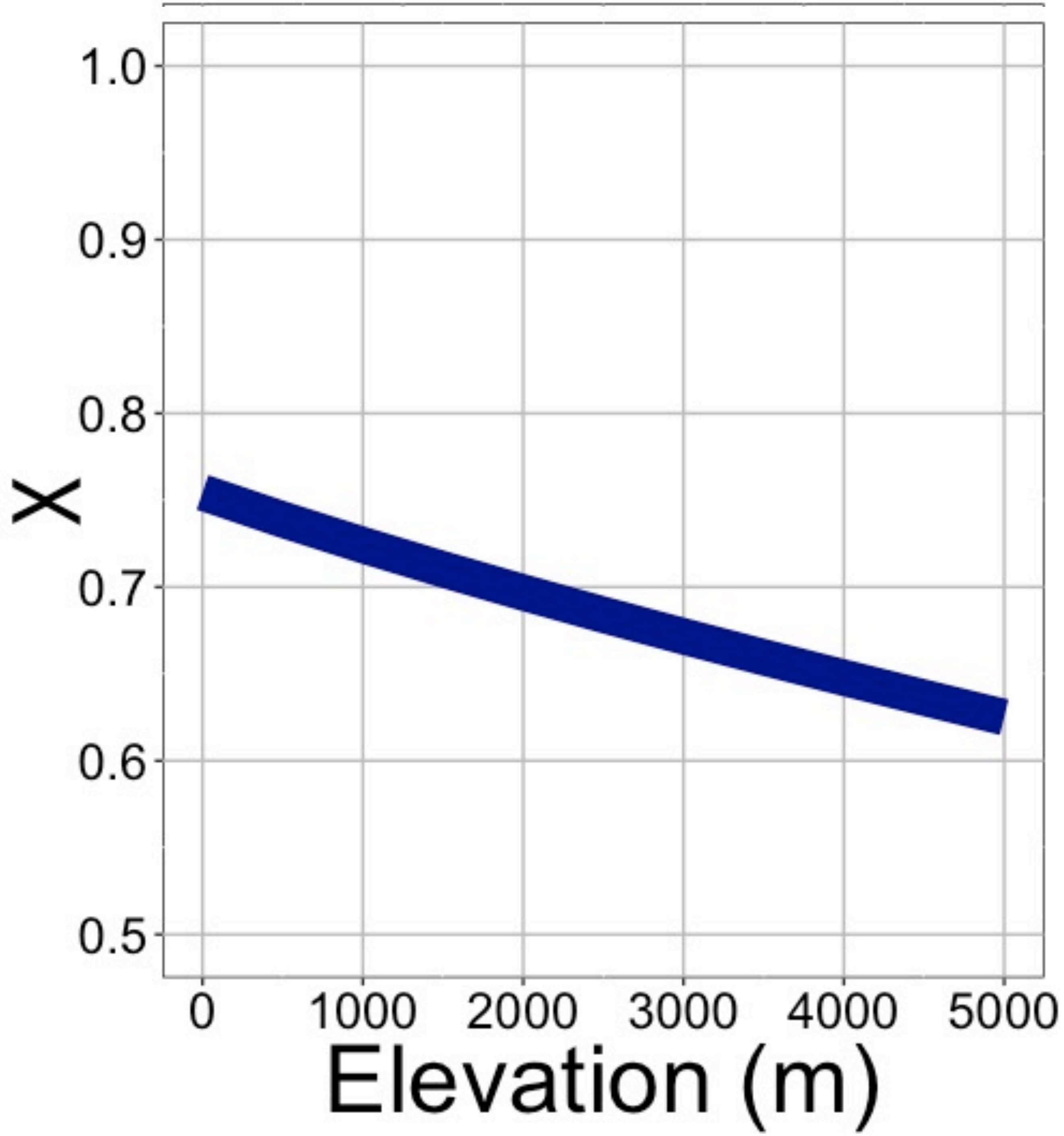
χ decreases with elevation because of lower openness needed to satisfy Rubisco

Globally, χ is optimized

Predictor	Theoretical value	Fitted coefficient
ΔT_g	**0.0545**	0.0515
$\ln D_0$	**−0.5**	−0.5478
z	**−0.0815**	−0.1065
Intercept	**1.189**	1.1680

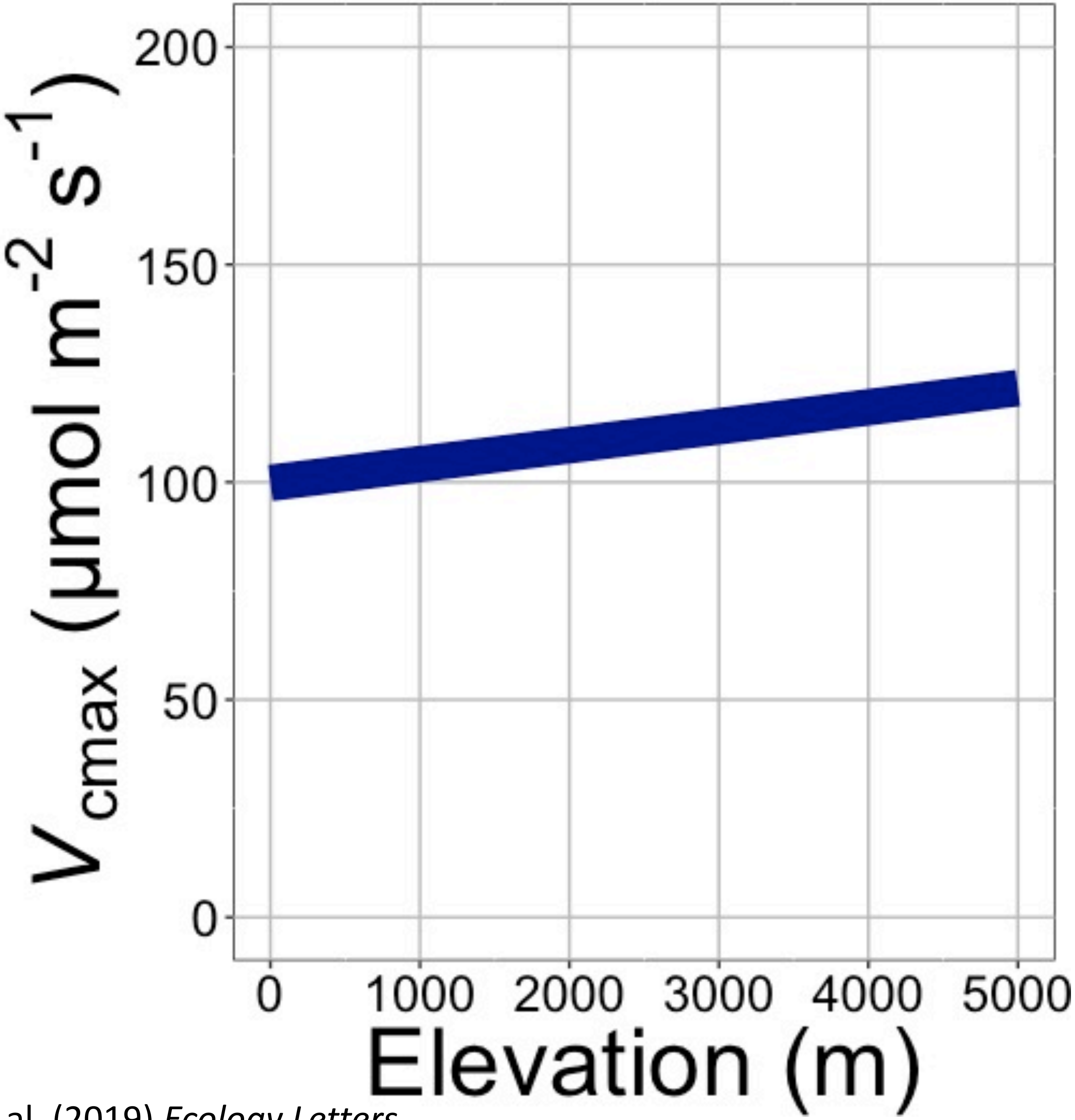
Wang et al. (2017) *Nature Plants*

nick.smith@ttu.edu; @nick_greg_smith



χ decreases with elevation because of greater VPD

nick.smith@ttu.edu; @nick_greg_smith



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

Smith et al. (2019) *Ecology Letters*