Simulating photosynthetic acclimation using least-cost optimality

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Photosynthetic 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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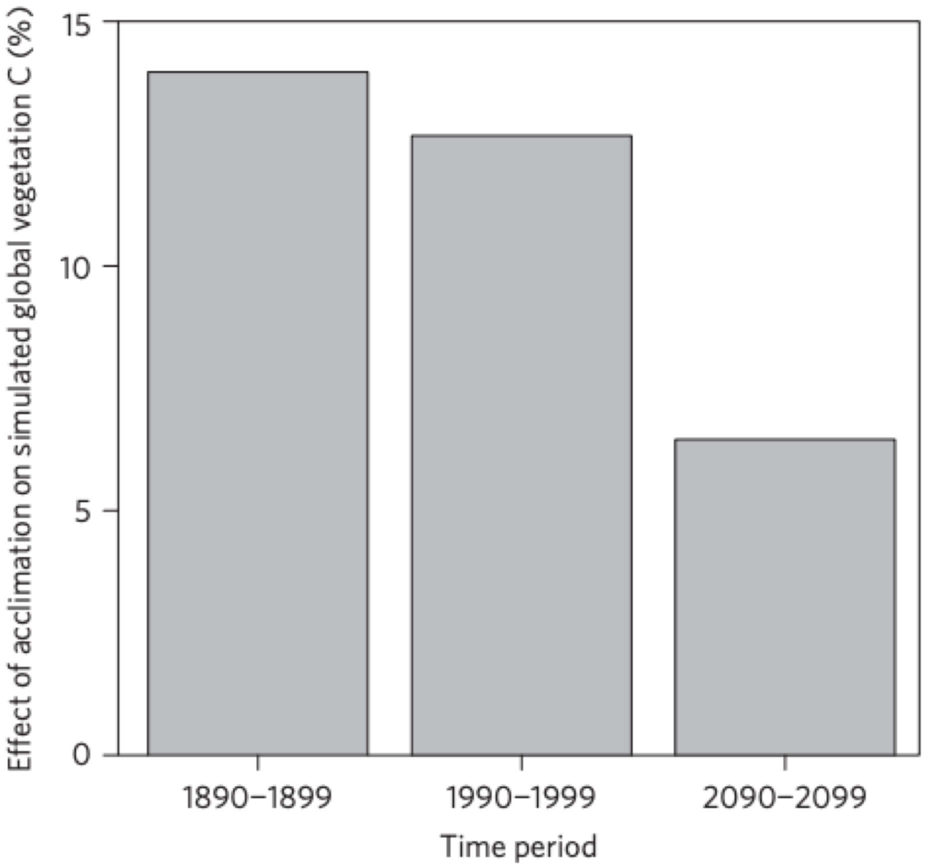
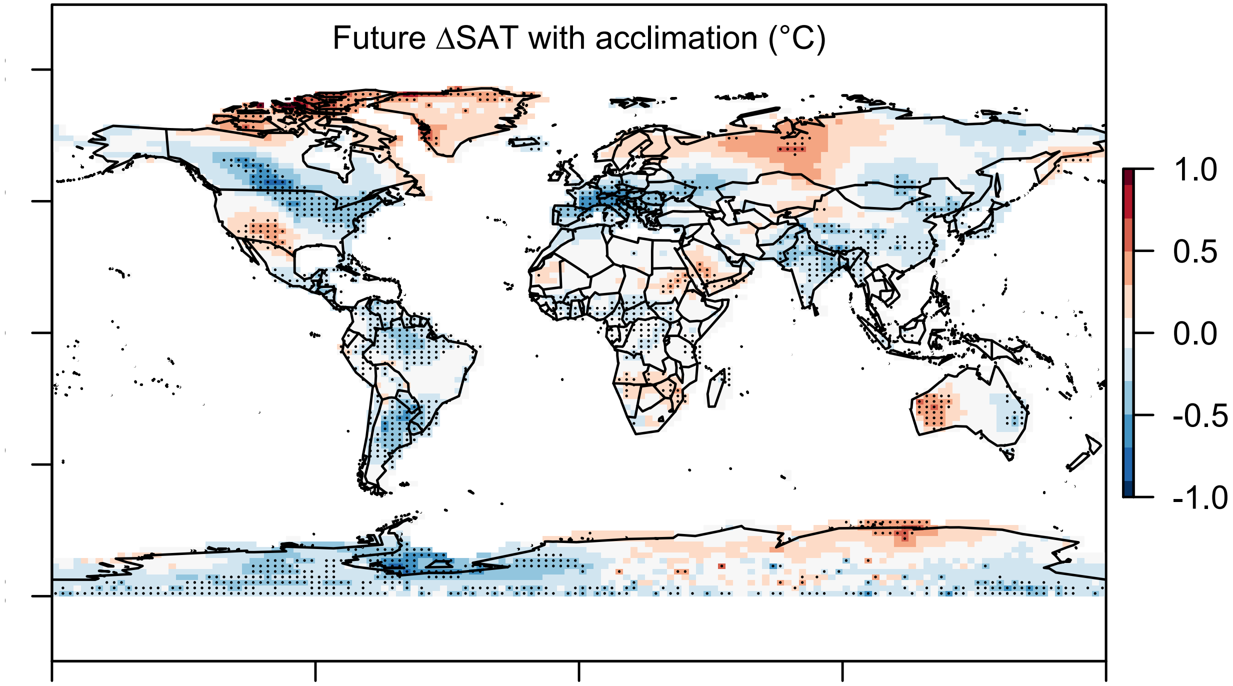
…and can possibly impact carbon cycling and climate

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 problem:

No theoretical model for photosynthetic acclimation exists

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So, we developed a mechanistic model of photosynthetic acclimation

Based on **least cost optimization** and the **first principles** of plant physiological theory

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Least cost theory

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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Optimal photosynthesis

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

OTPIMAL CONDUCTANCE IS NOW INCLUDED IN MANY MODELS
e.g., Prentice et al. (2014), Medlyn et al. (2011)

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Optimal photosynthesis

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

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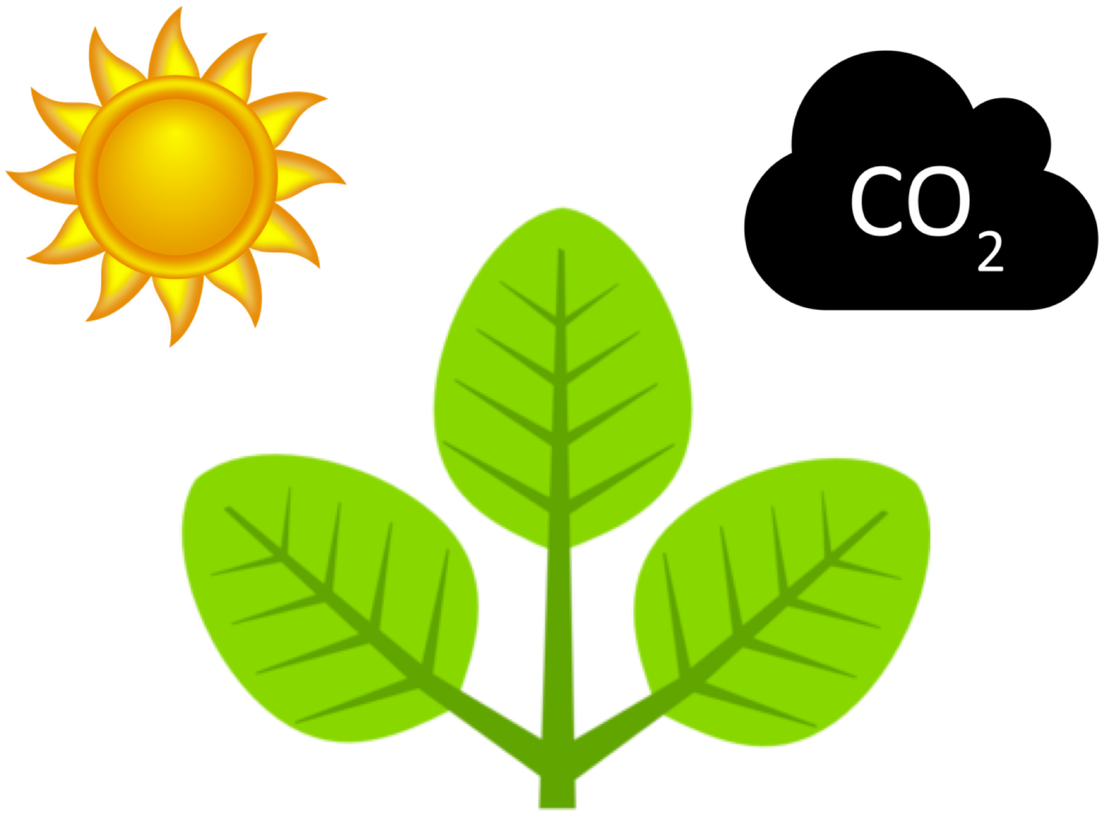
Biochemistry optimization: Coordination hypothesis



Optimal setup = equal limitation by all factors

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Optimally:
electron transport-limited (A_j) = Rubisco-limited (A_c)

$$A_j = A_c$$

Smith et al. (2019)

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Optimally:
electron transport-limited (A_j) = Rubisco-limited (A_c)

$$A_j = A_c$$
$$A_j = f\{J_{max}, \text{light}, \text{T}, CO_2\}$$
$$A_c = f\{V_{cmax}, \text{T}, CO_2\}$$

Smith et al. (2019)

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Optimally (C_4):
A_j = Rubisco-limited A_c = PEP-limited (A_p)

$$A_j = A_c = A_p$$

$$A_j = f\{J_{max}, \text{light}, \text{T}, CO_2\}$$

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

$$A_p = f\{V_{pmax}, \text{T}, CO_2\}$$

Smith et al. (2019)

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Can rearrange the formulas to solve for acclimated traits

V_{cmax}

J_{max}

V_{pmax}

Smith et al. (2019)

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$$\left.\begin{array}{l} V_{\mathrm{cmax}} \\ J_{\mathrm{max}} \\ V_{\mathrm{pmax}} \end{array}\right. = f\{\textit{average env. conditions}\}$$

Smith et al. (2019)

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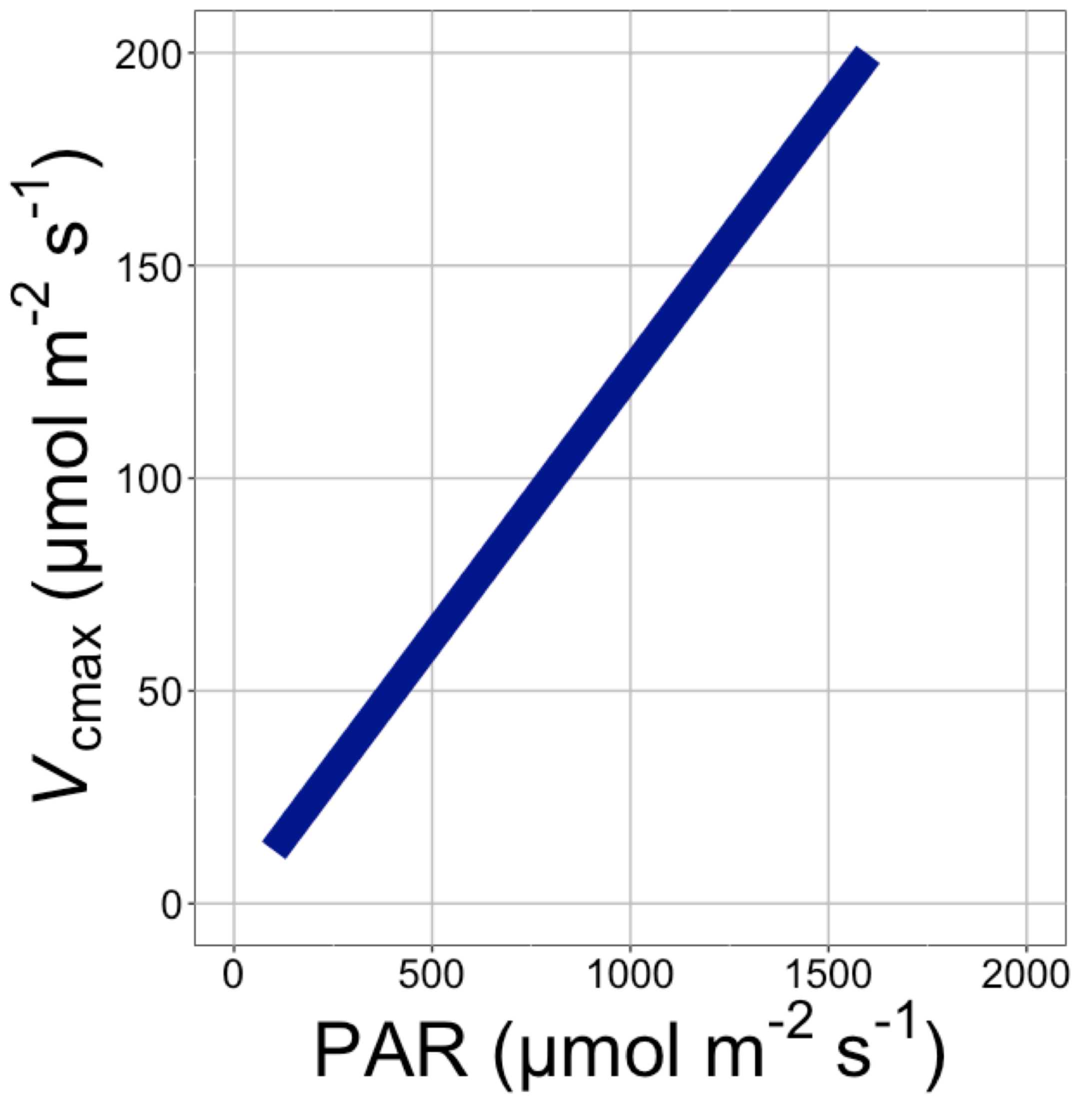

V_{cmax} increases with light because of greater electron transport

Smith et al. (2019)

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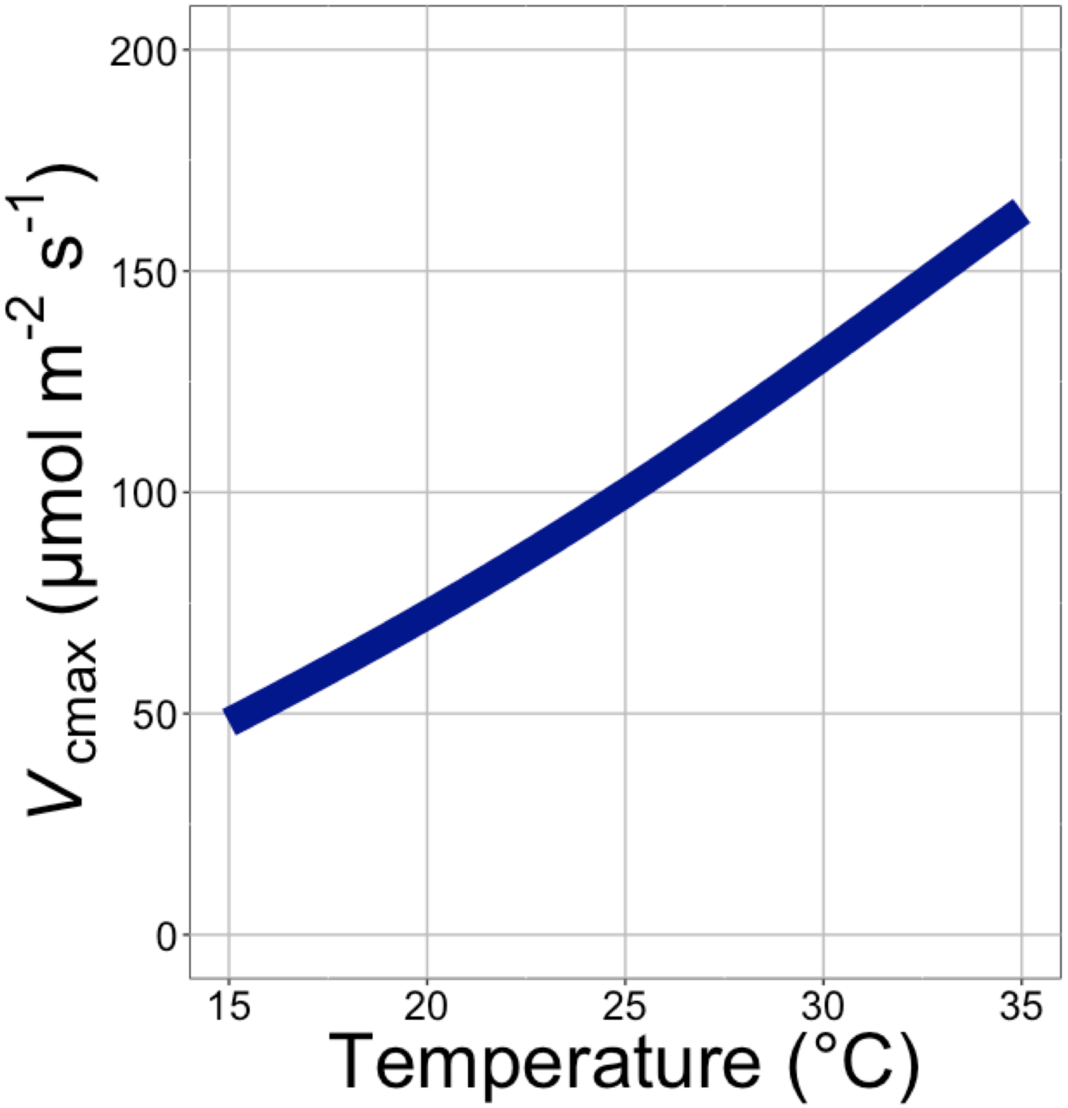

V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019)

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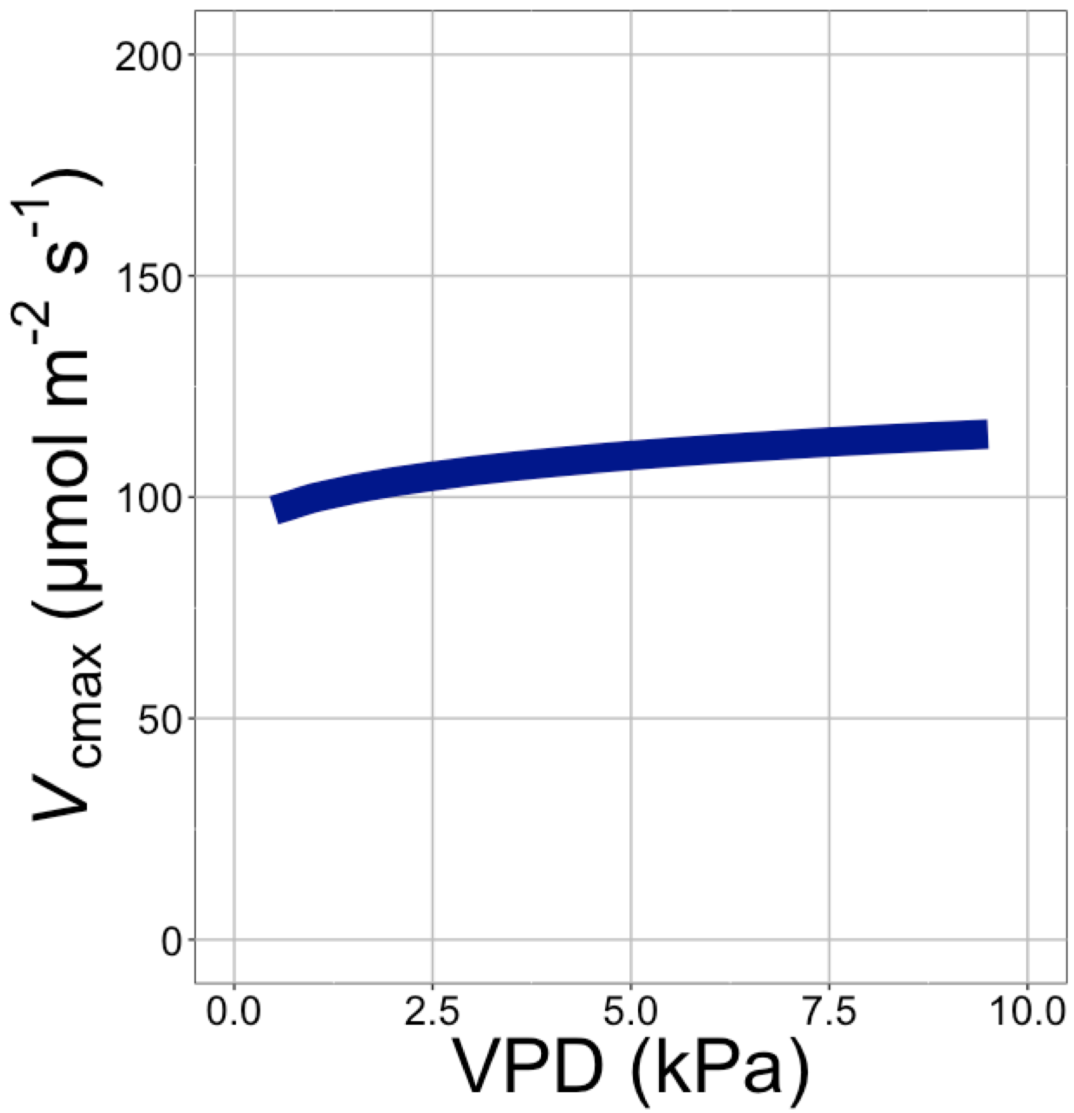

V_{cmax} increases with VPD because of lower stomatal conductance

Smith et al. (2019)

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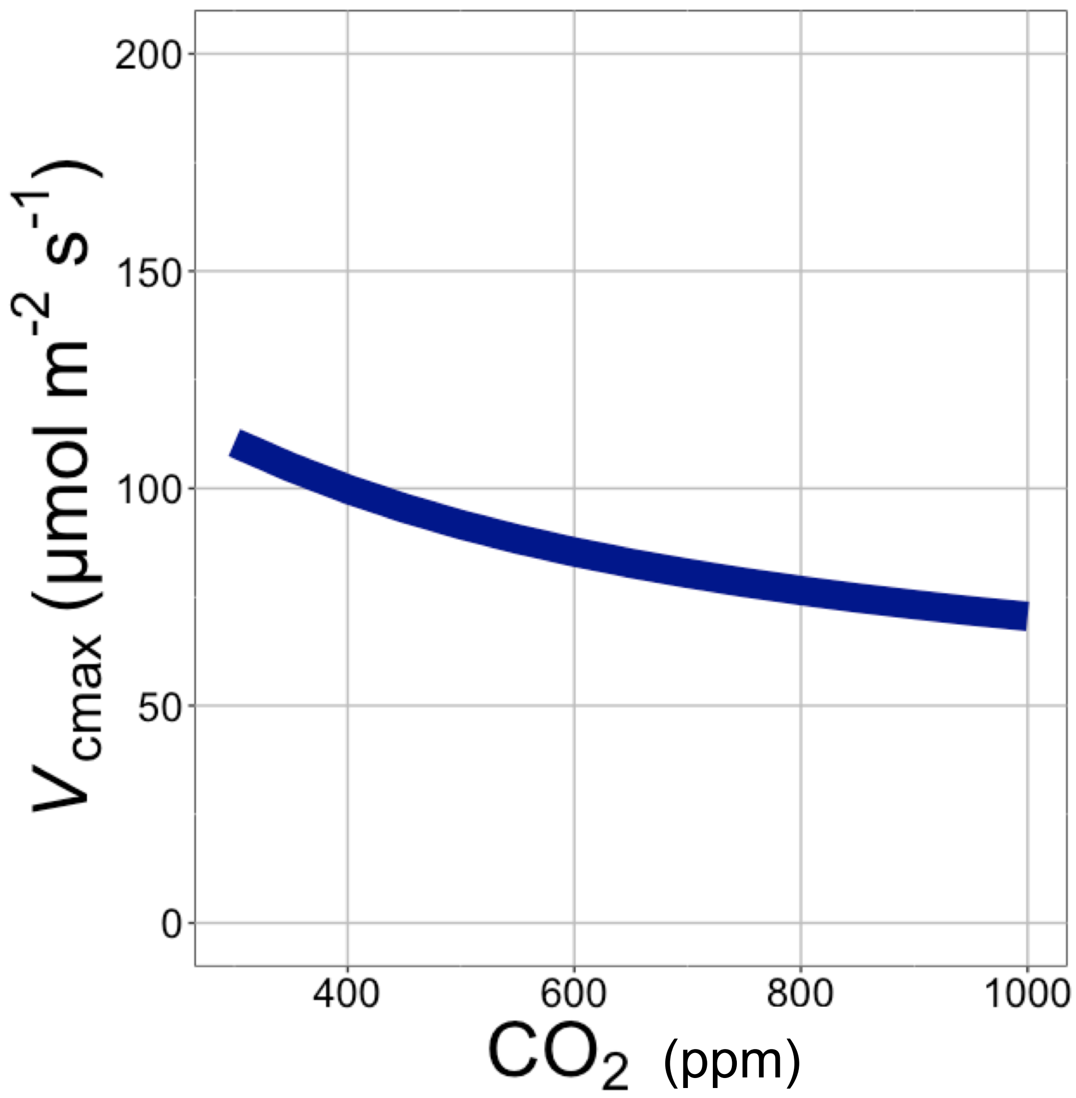

V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf

Smith et al. (2019)

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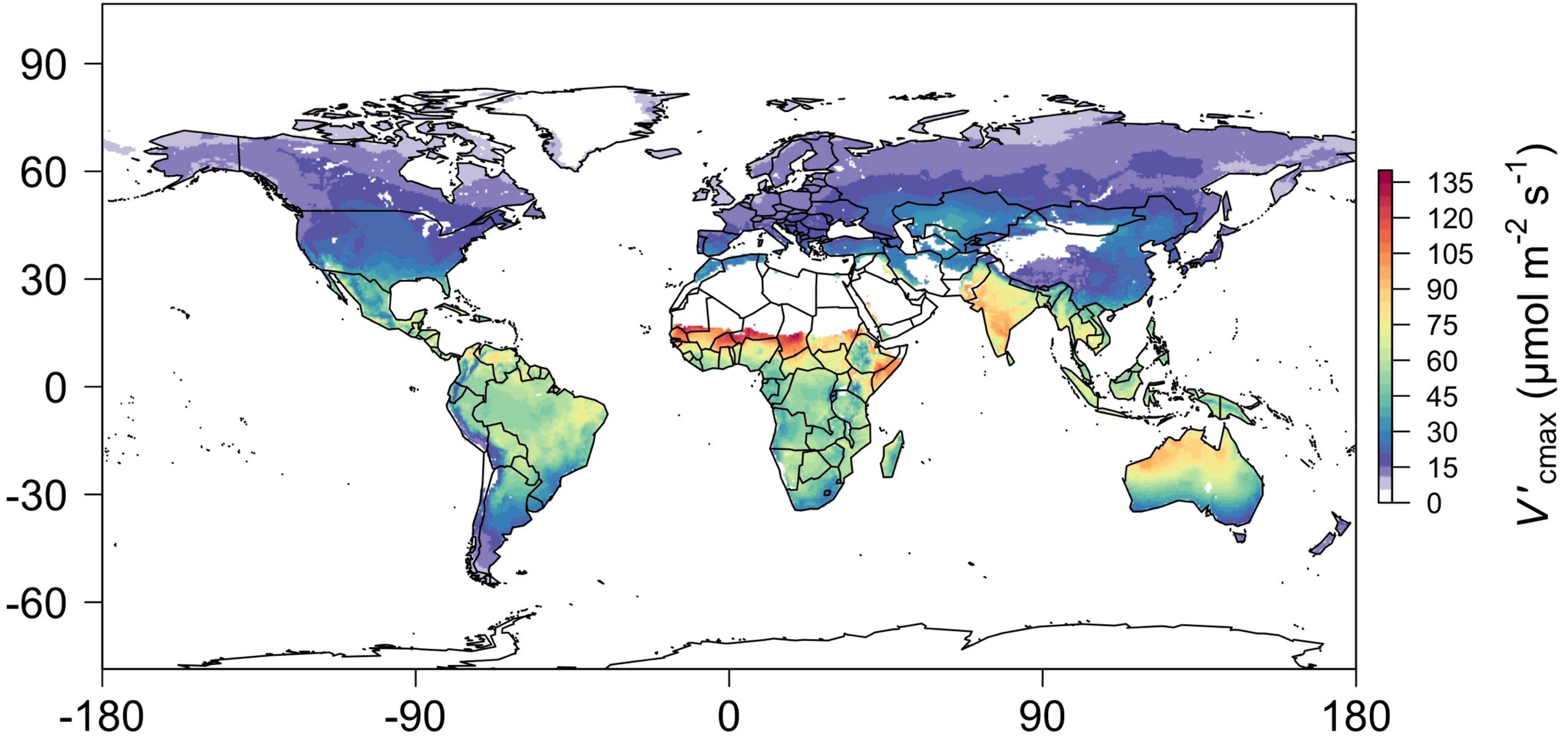
Global, optimally acclimated traits!



Smith et al. (2019)

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Important note: least-cost optimality model adds no free parameters to Farquhar et al. (1980) and Von Caemmerer (2000) models **and dynamically predicts most**

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Important note: adds acclimation, while reducing parametric uncertainty

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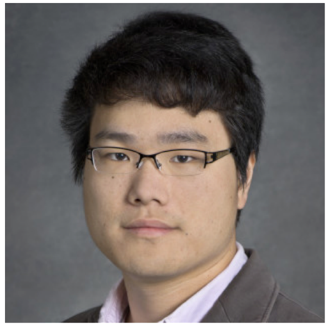
Let’s run a model out into the future!



E3SM Energy Exascale Earth System Model

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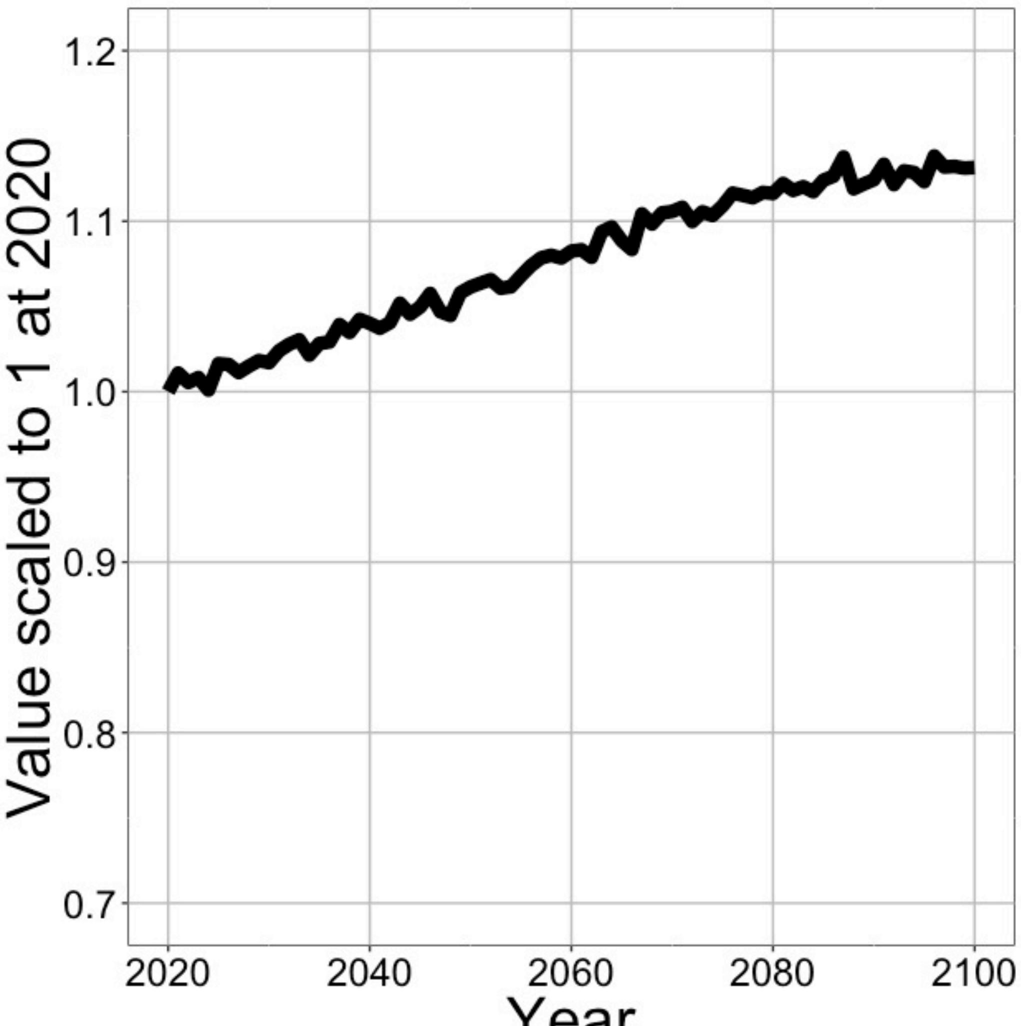
Photosynthesis increases in future



Net Photosynthesis

Smith et al. (in prep)

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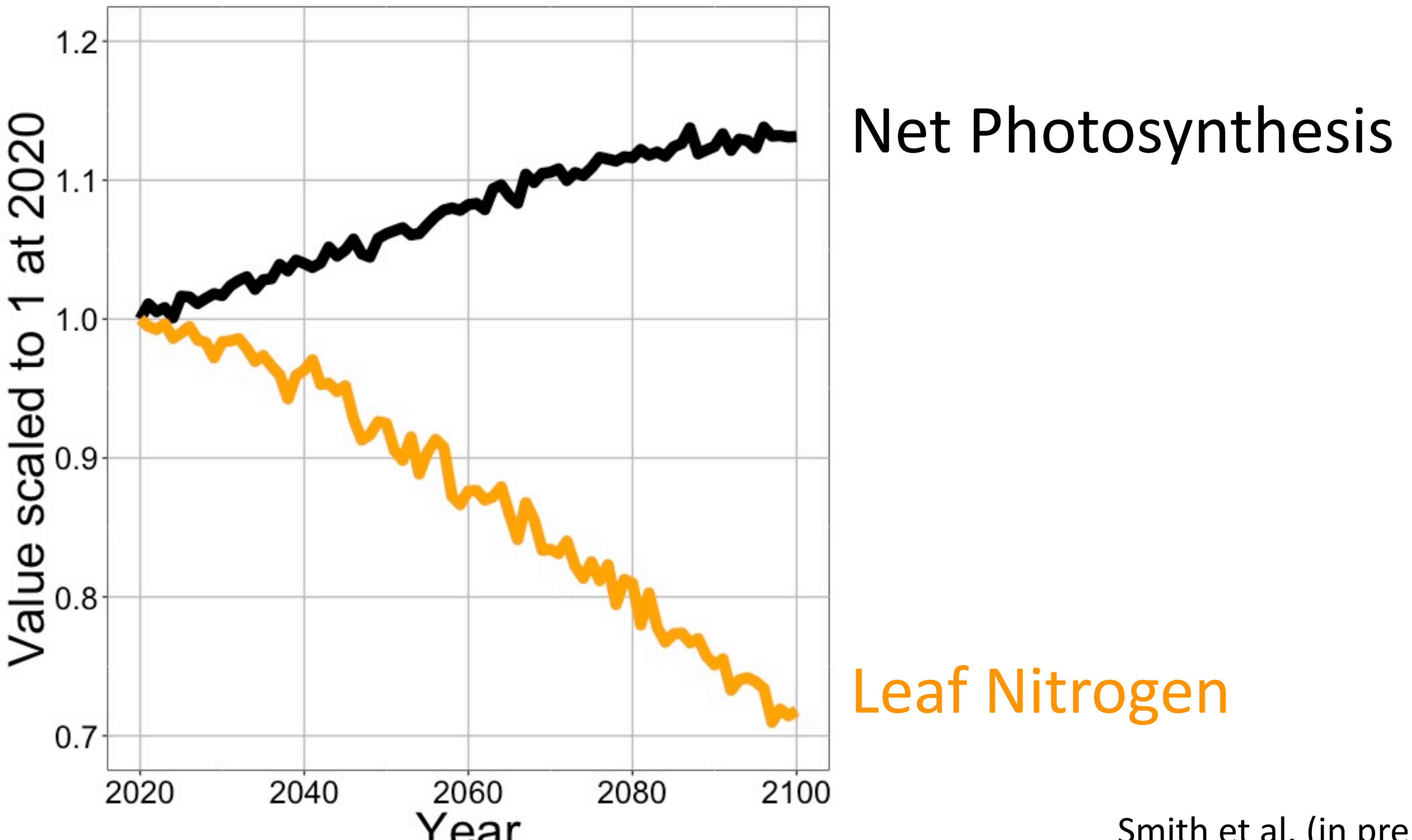
Photosynthesis increases in future
(at lower nutrient use)



Smith et al. (in prep)

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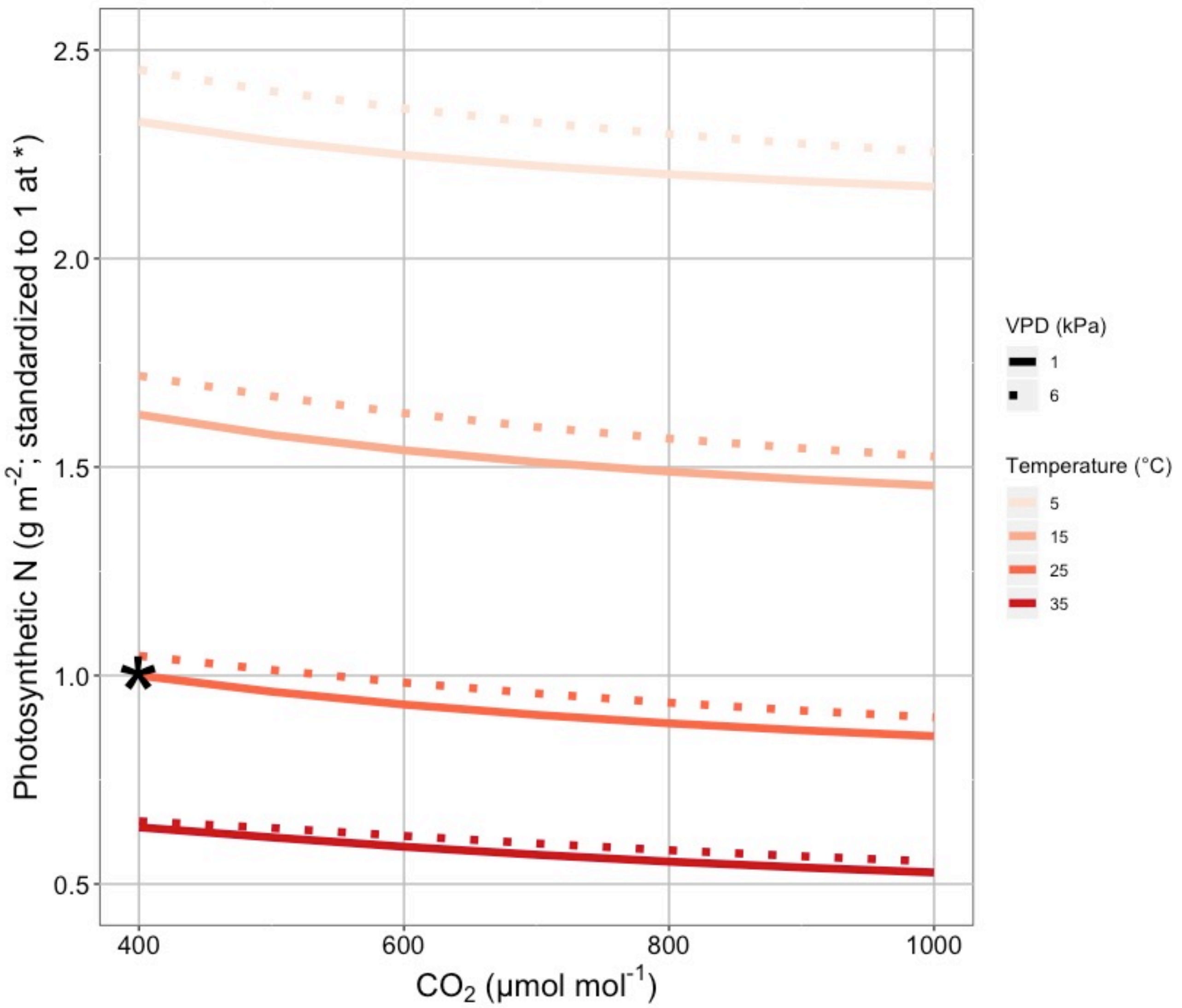
Leaf N declines due to warming and eCO_2



Smith & Keenan (in review)

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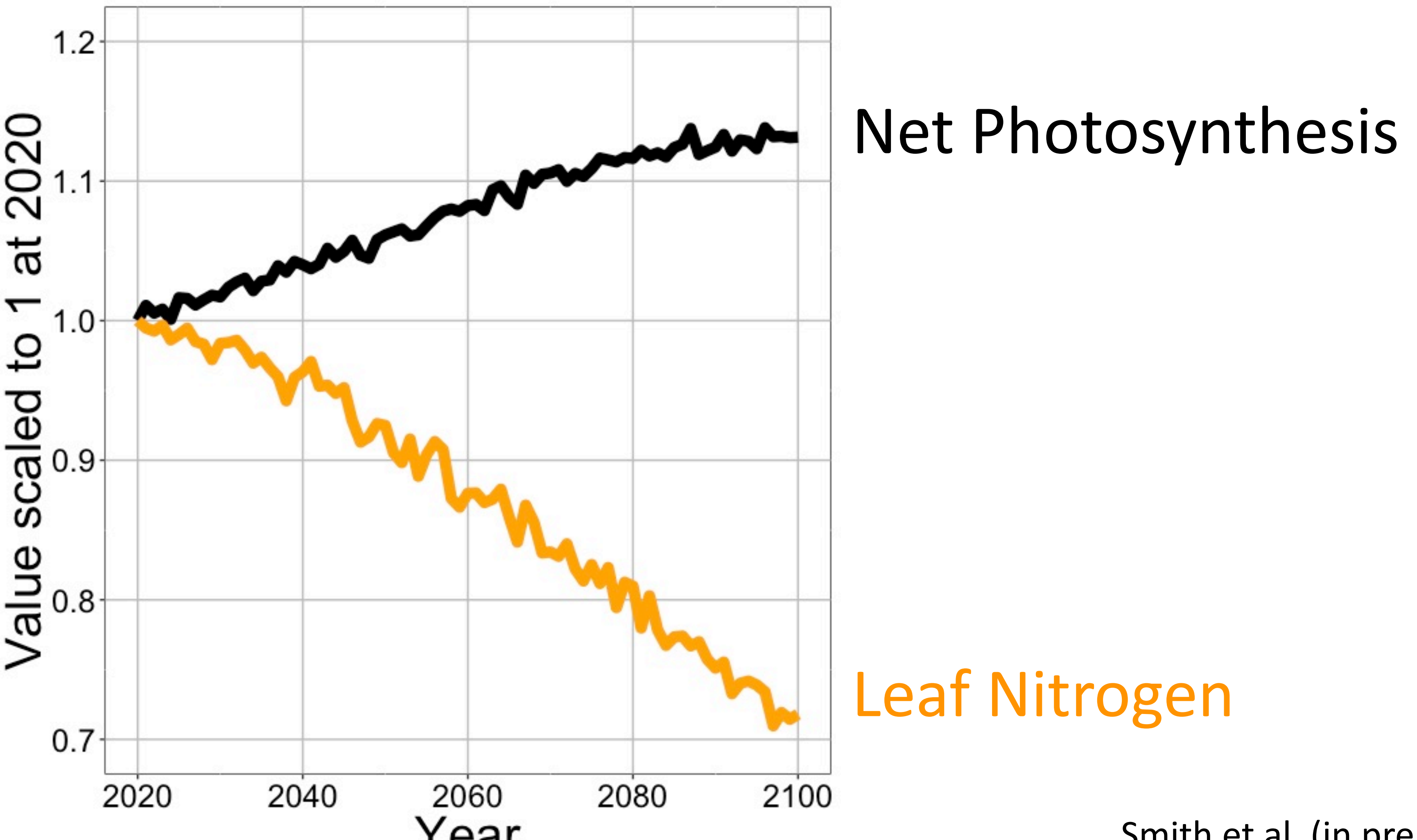

Smith et al. (in prep)

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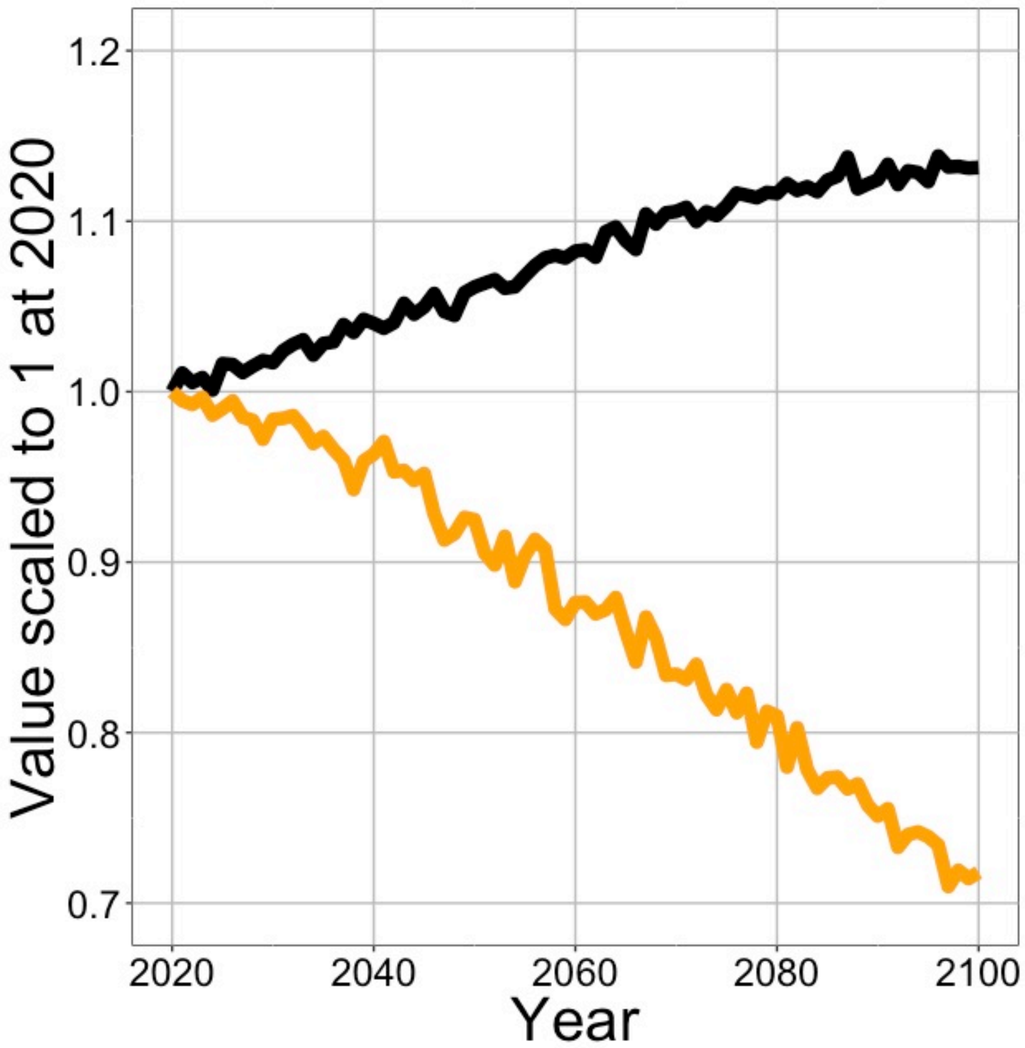
Photosynthesis increases in future
(at lower nutrient use)

Base ELM shows <5% change in leaf N



Net Photosynthesis

Leaf Nitrogen

Smith et al. (in prep)

What does this all mean and is it real?

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A typical LSM photosynthesis scheme

Climate

↓

Soil N → Leaf N → Photosynthesis

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Least cost optimality model

Climate

$\downarrow$

Photosynthesis

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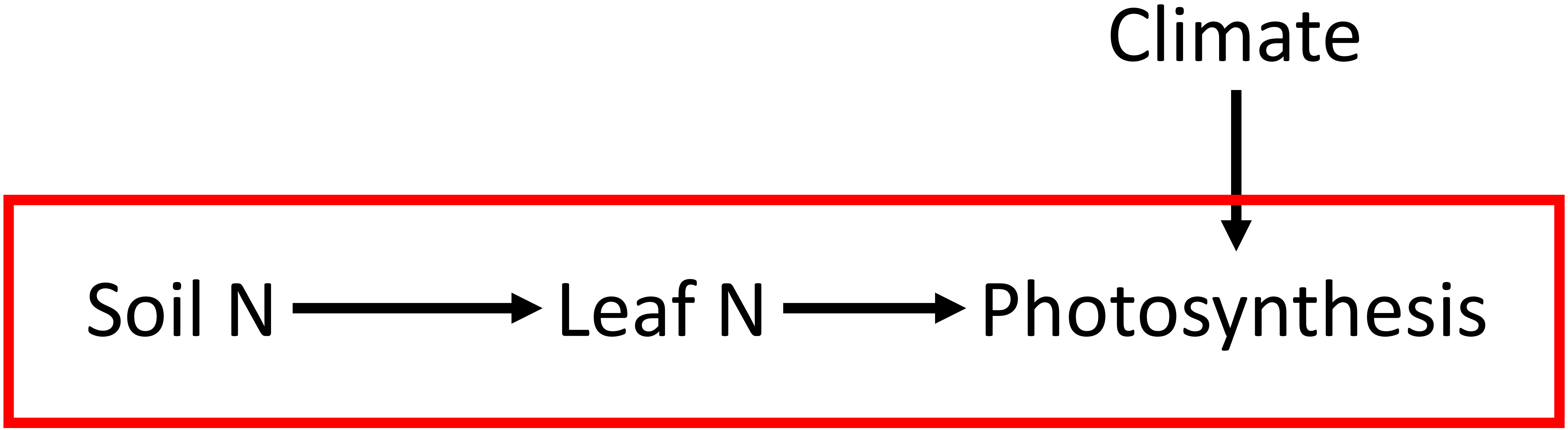
Let’s check this assumption



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Does leaf N respond to soil N?

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

nutrient network

Smith et al. (in prep)

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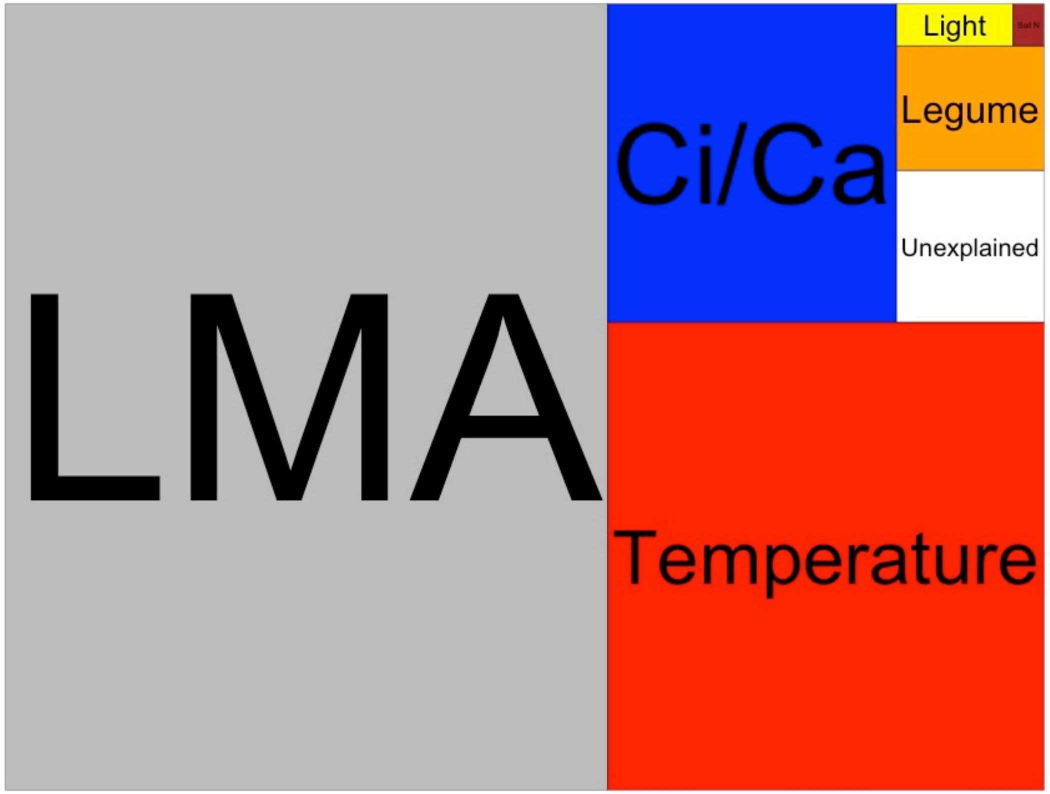
Globally, N addition little impact on leaf N



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

nutrient network

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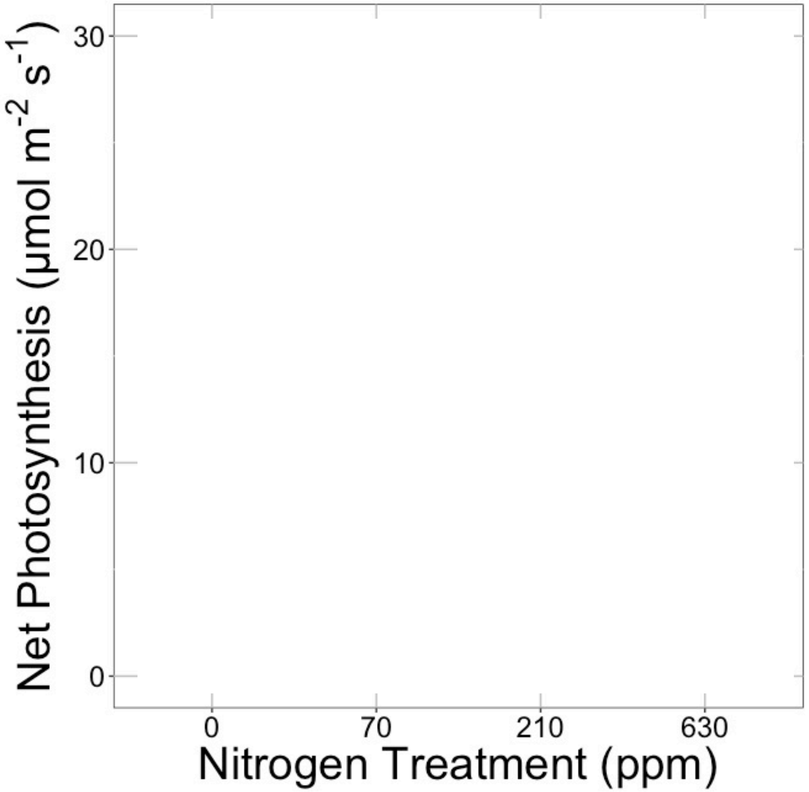

Waring and Smith (in prep)

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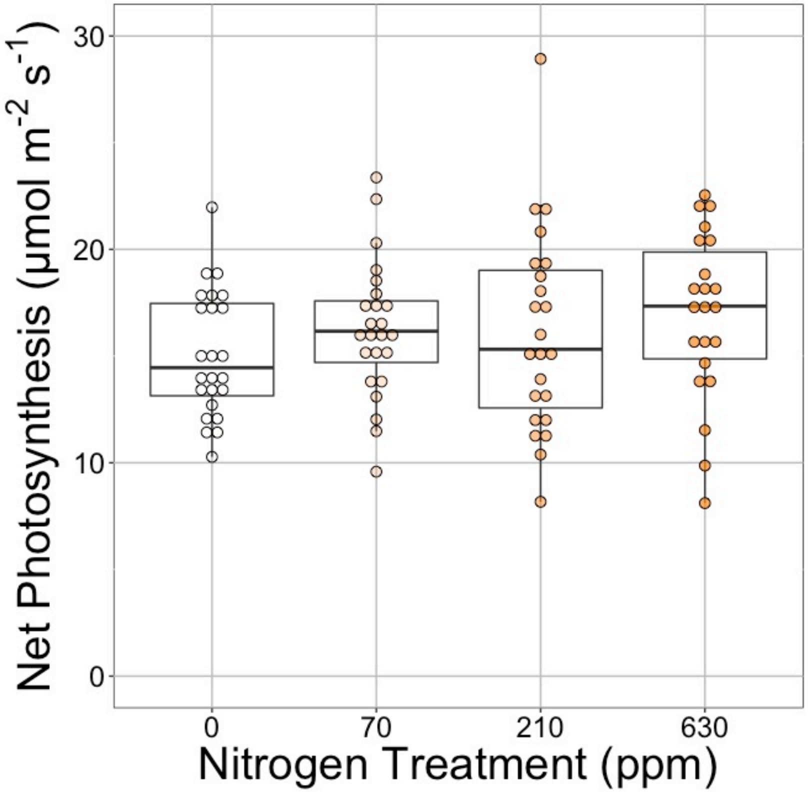
Photosynthesis does not change with soil N

No change (P = 0.42)



Waring and Smith (in prep)

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How does the optimality model do?

Climate

↓

Photosynthesis

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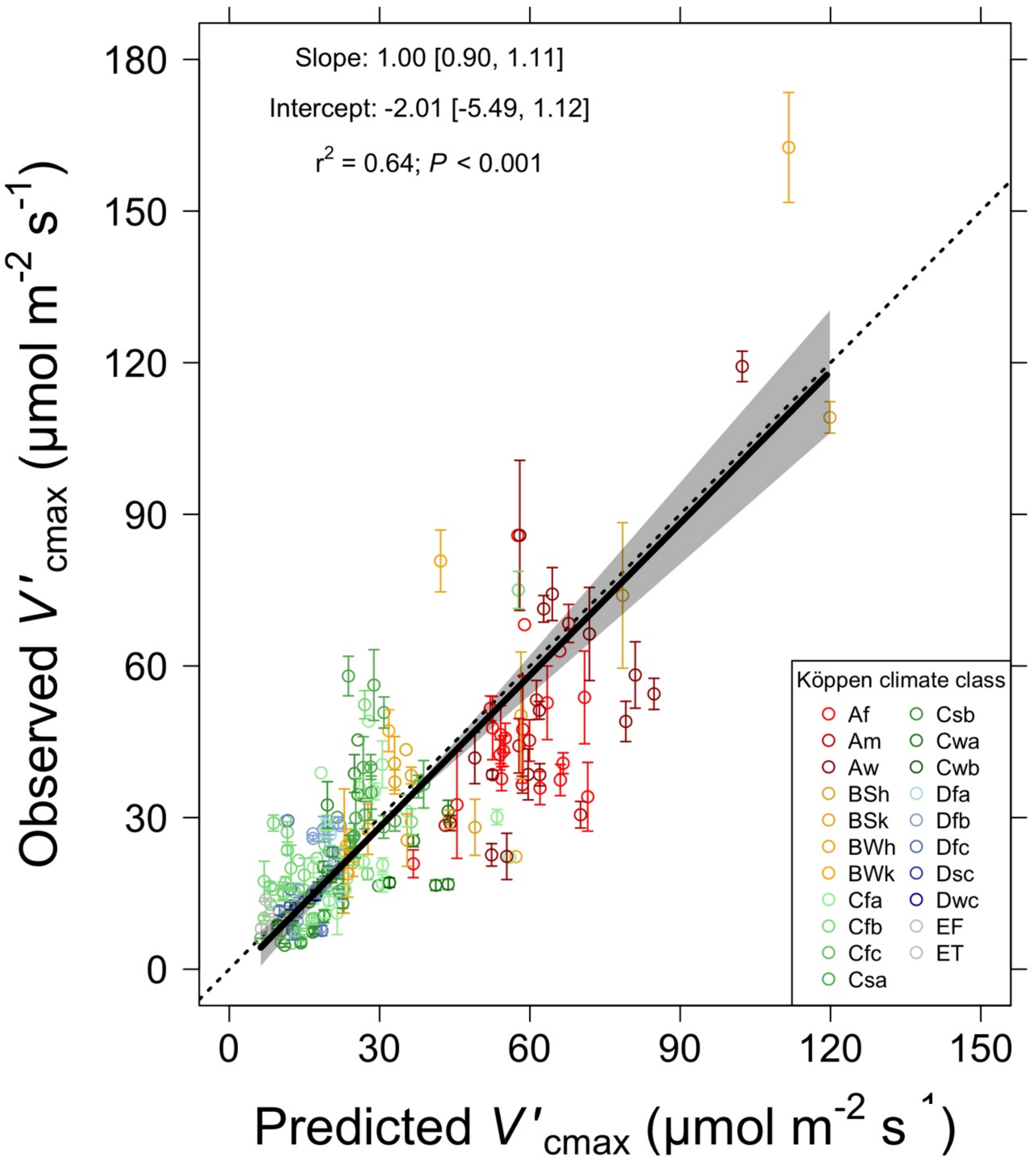

Optimal V_{cmax} is similar to observed values

Smith et al. (2019)

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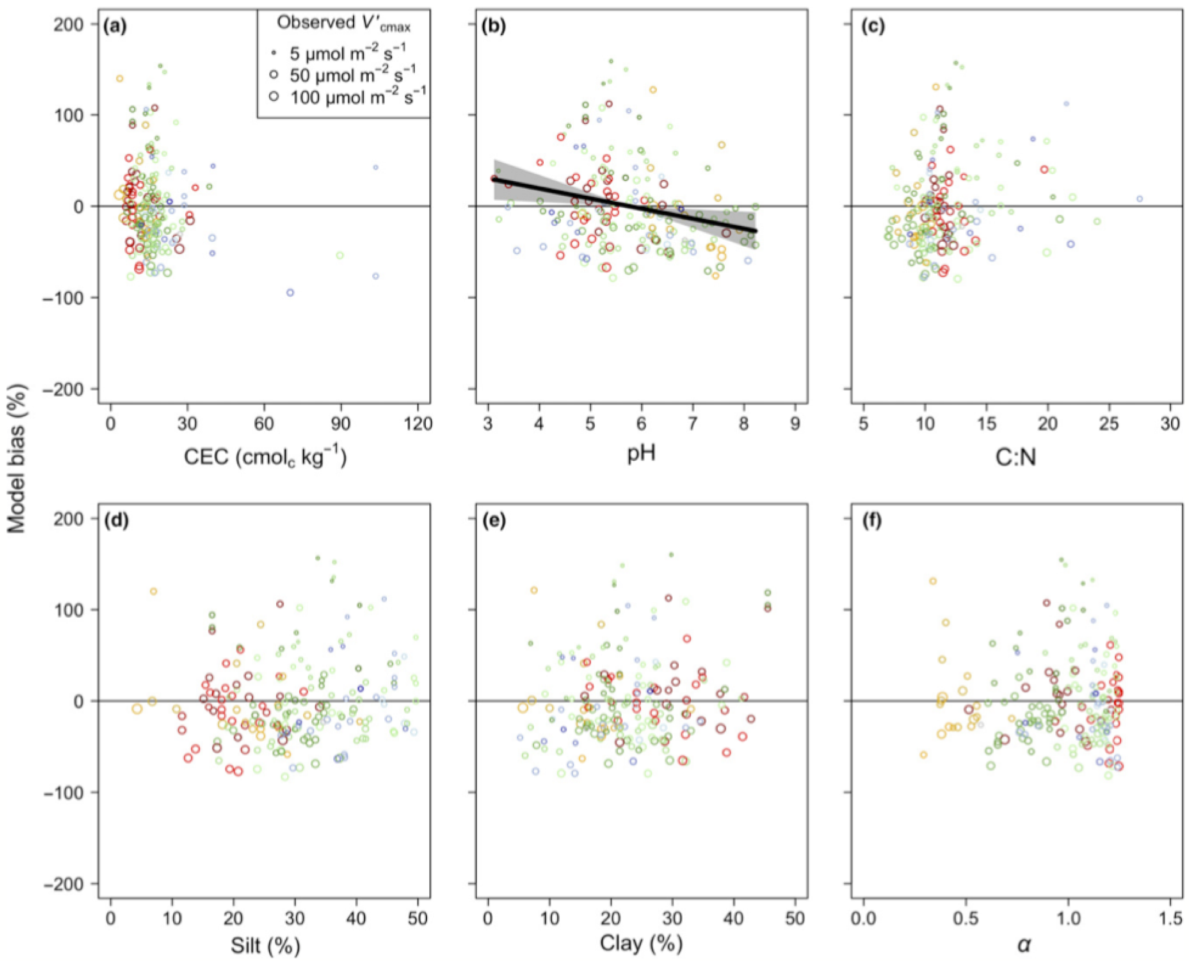
There is little effect of soils on V_{cmax}



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

Smith et al. (2019)

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Does it work under future conditions?

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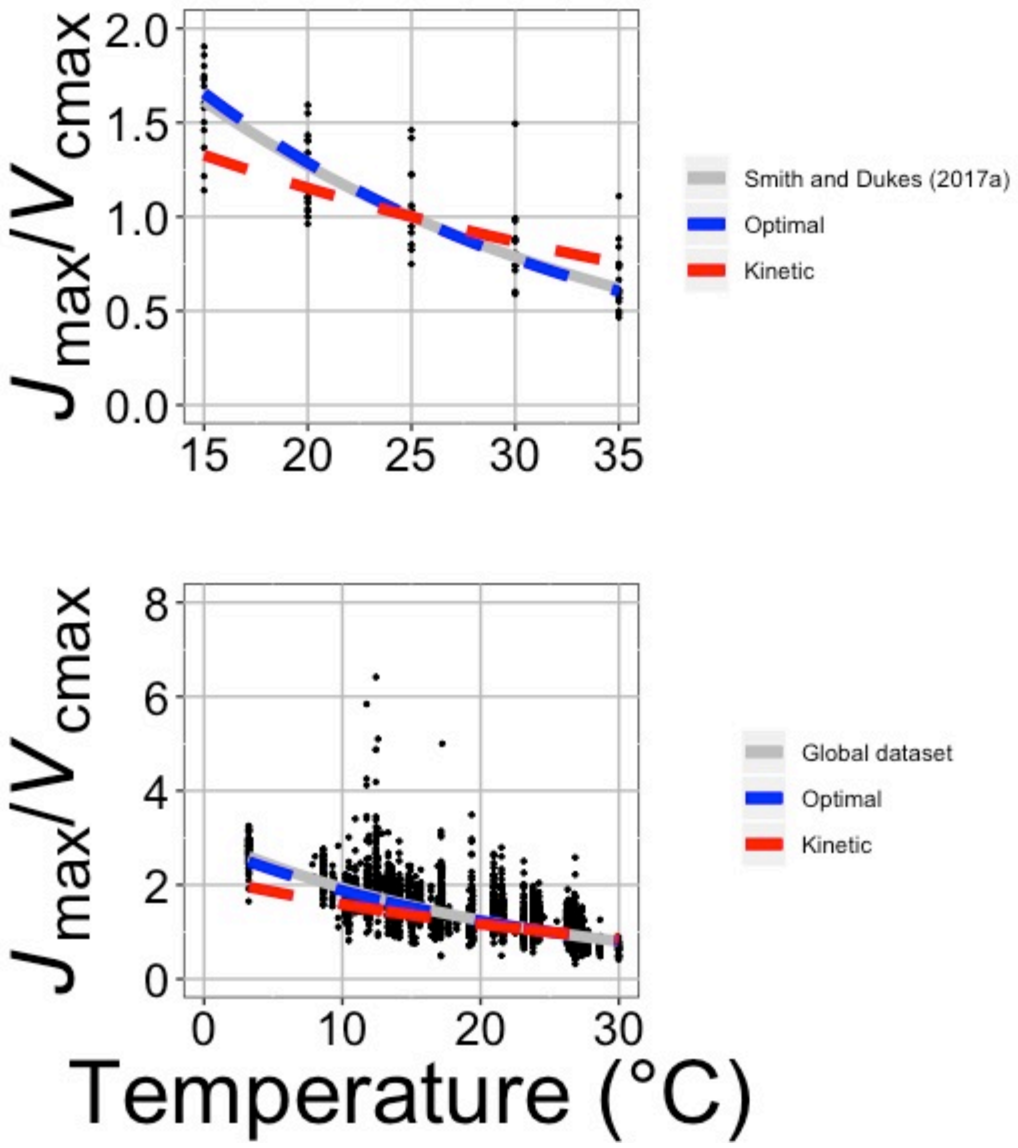

Photosynthetic traits change with temperature in ways expected from optimization

Data = -0.051 °C^{-1}

Predicted = -0.048 °C^{-1}

Smith and Keenan (in review)

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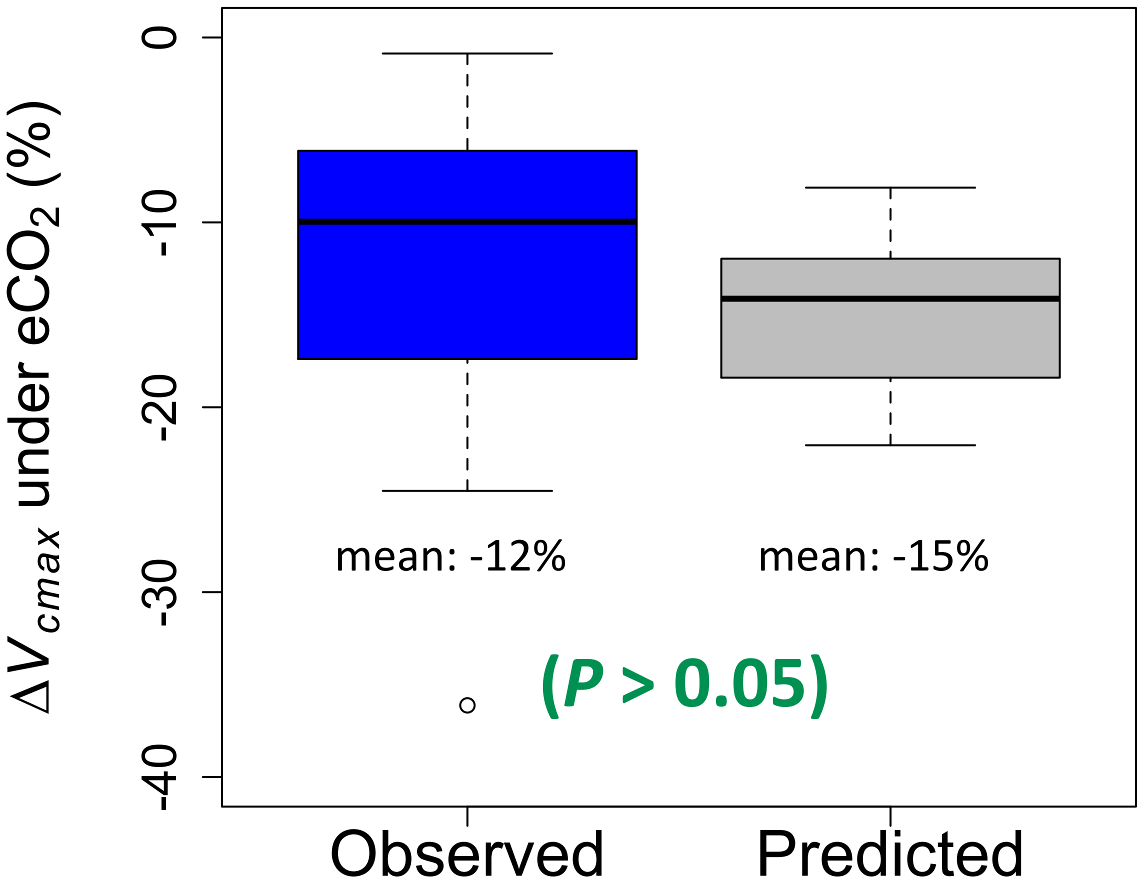
Photosynthetic traits change with future conditions in ways expected from optimization



Smith and Keenan (in review)

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We now have an acclimation model for C_3 and C_4 species!

Helen Scott
TTU

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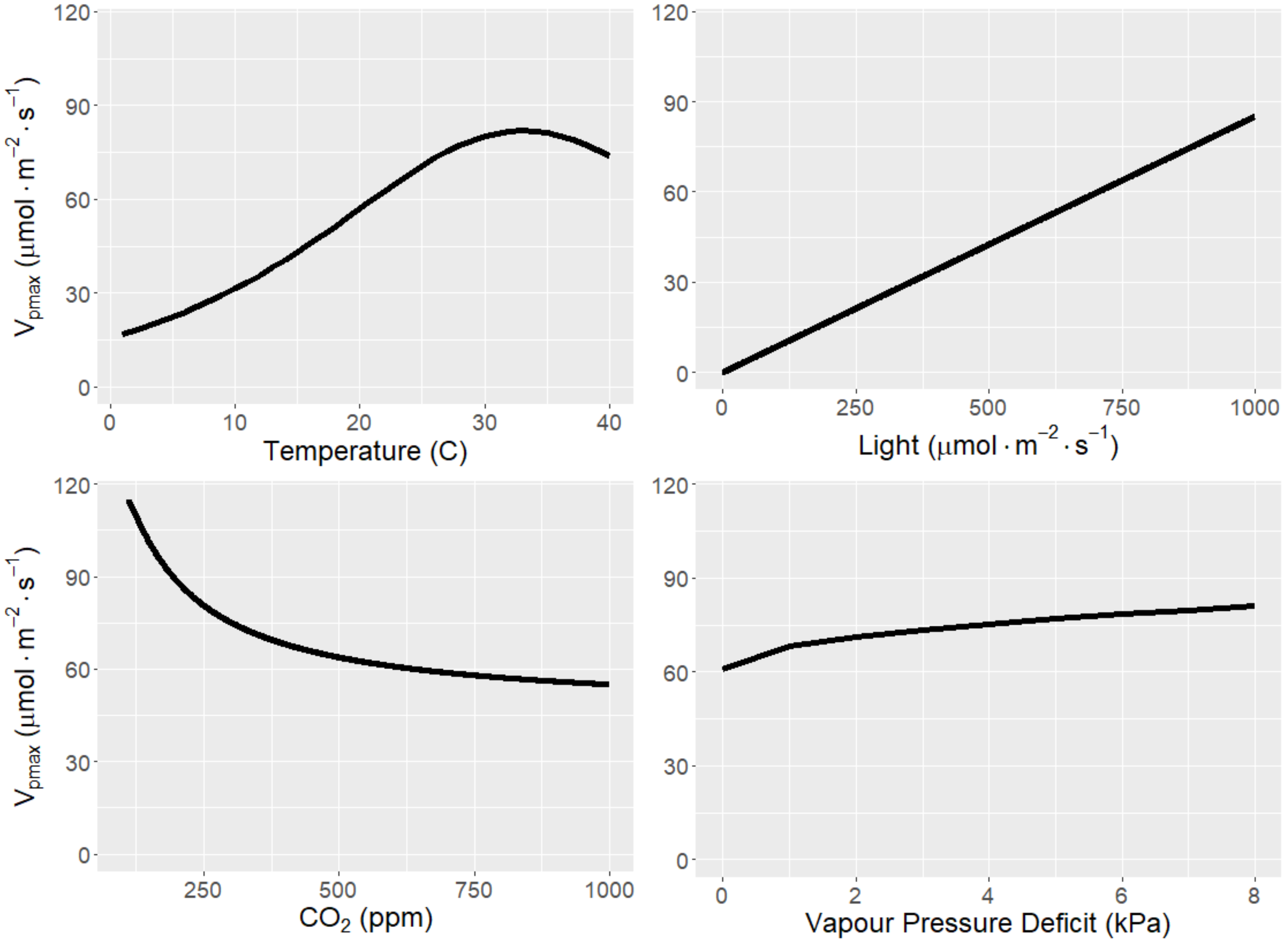
Photosynthetic biochemistry responds similarly in C_4 leaves as C_3 leaves



Scott and Smith (in prep)

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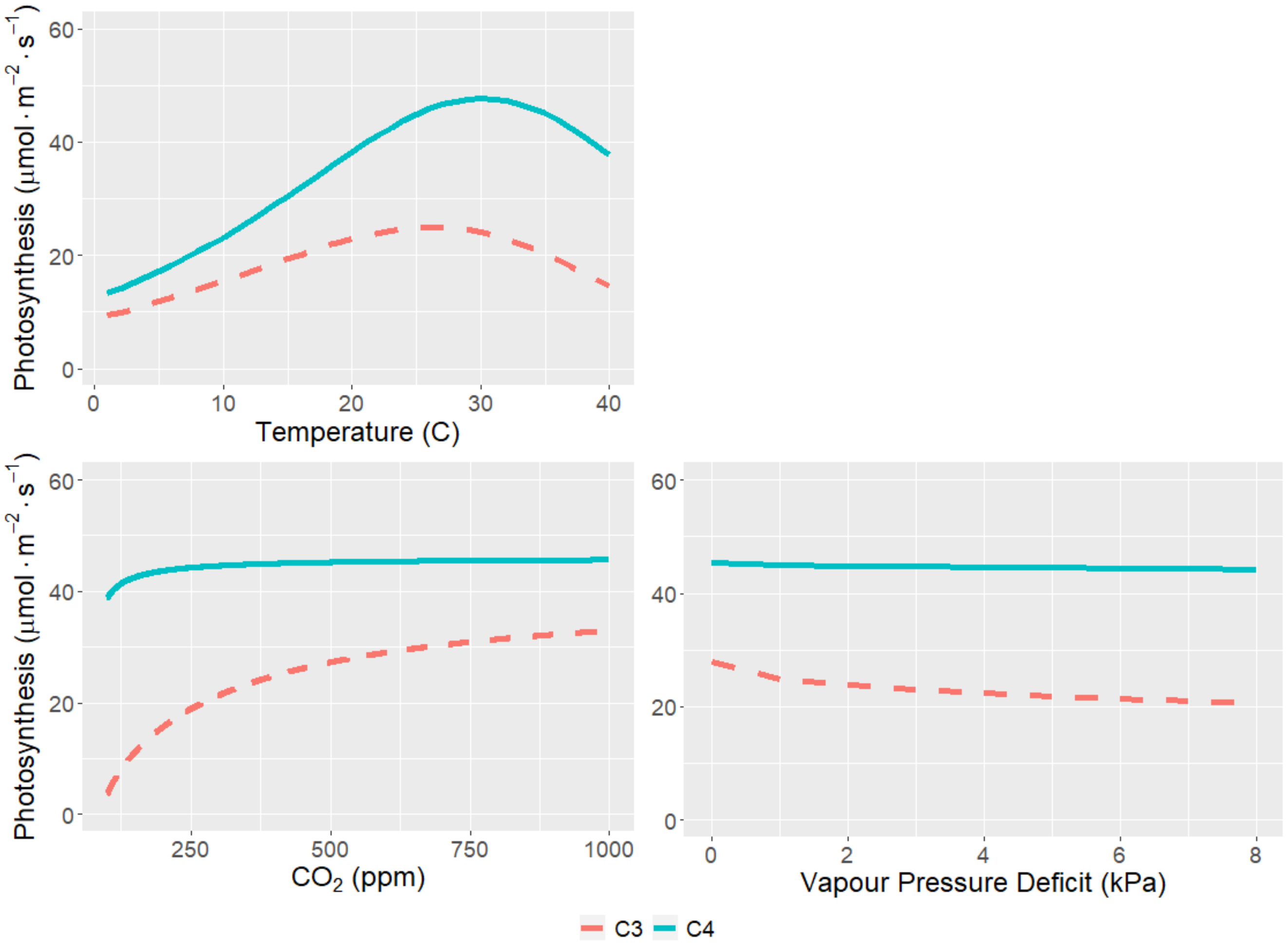
As expected, C_4 species are most benefitted under hot, dry, low CO_2 conditions



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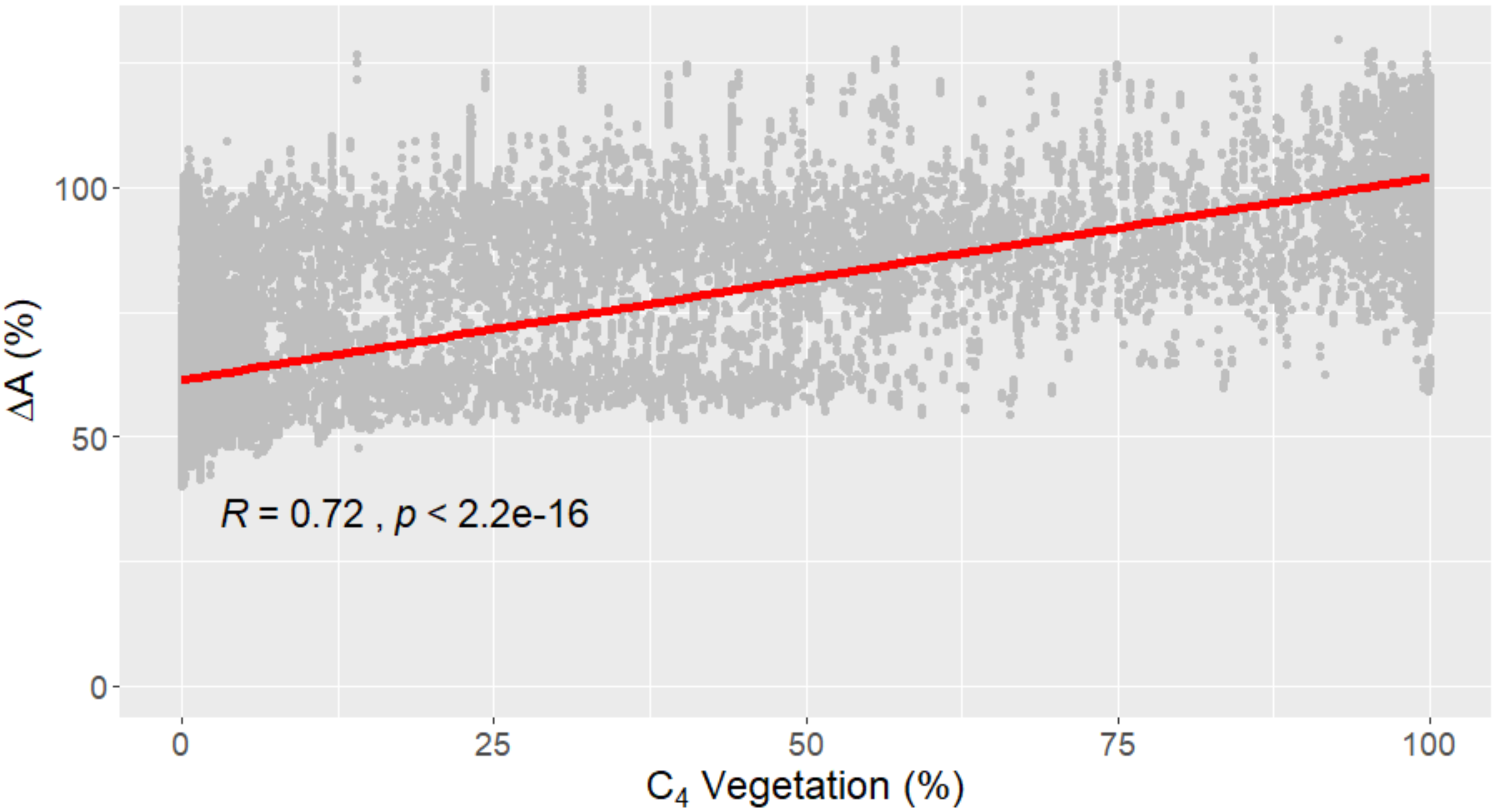
This correlates with C_4 cover



Scott and Smith (in prep)

Some takeaways

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- Optimal leaf biochemical setup is determined by climate

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- Optimal leaf biochemical setup is determined by climate
- Plants mine for nutrients to get the most leaves at the optimal setup

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Some takeaways

- Optimal leaf biochemical setup is determined by climate
- Plants mine for nutrients to get the most leaves at the optimal setup
- Photosynthetic demand determines leaf nutrients, not the other way around

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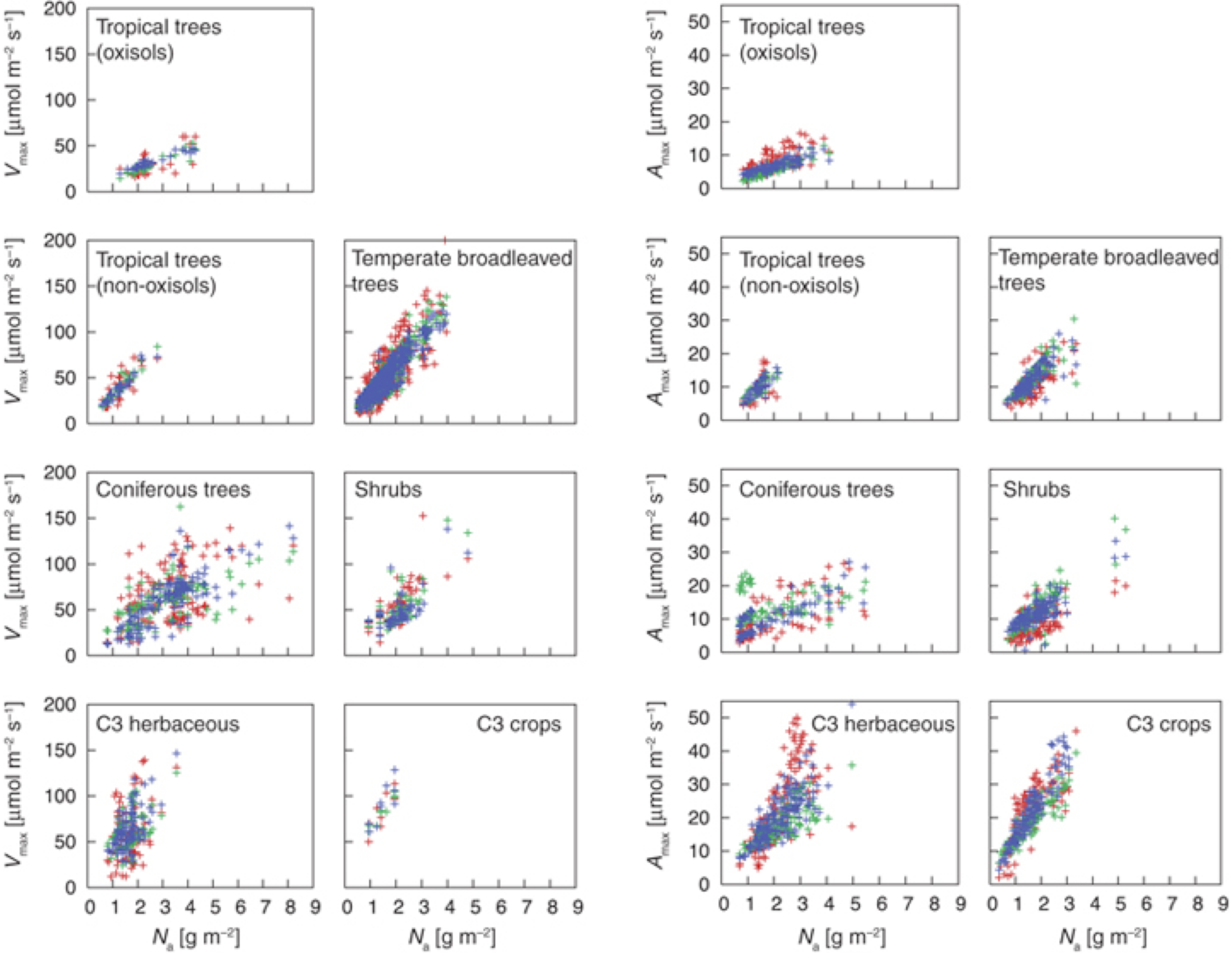

Axes need flipped

Kattge et al. (2009)

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Some takeaways

- Optimal leaf biochemical setup is determined by climate
- Plants mine for N to get the most leaves at the optimal setup
- Photosynthetic demand determines leaf N, not the other way around
- Soil nutrient availability determines biomass investment

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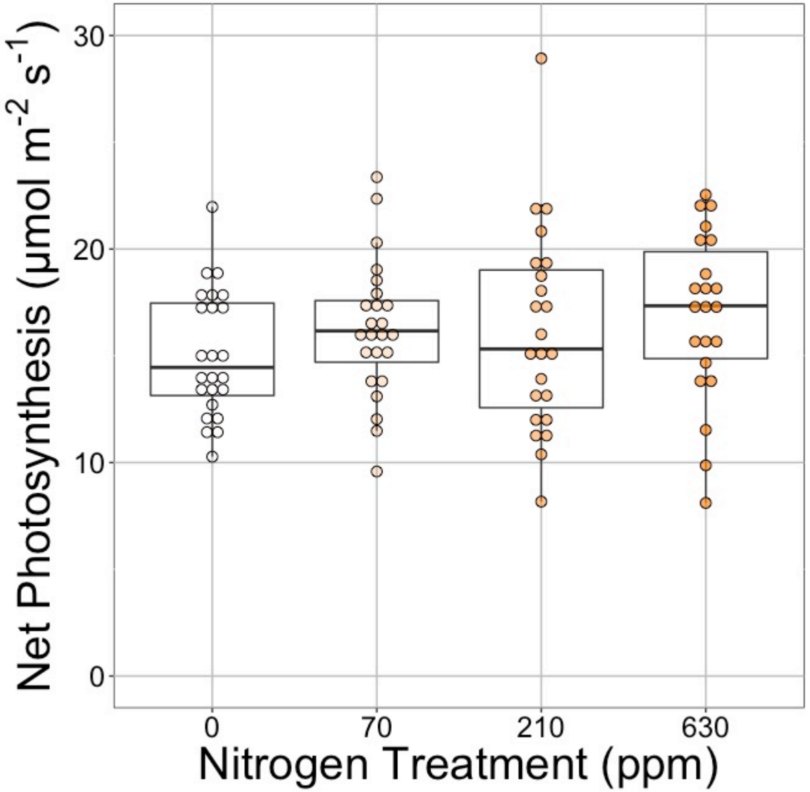
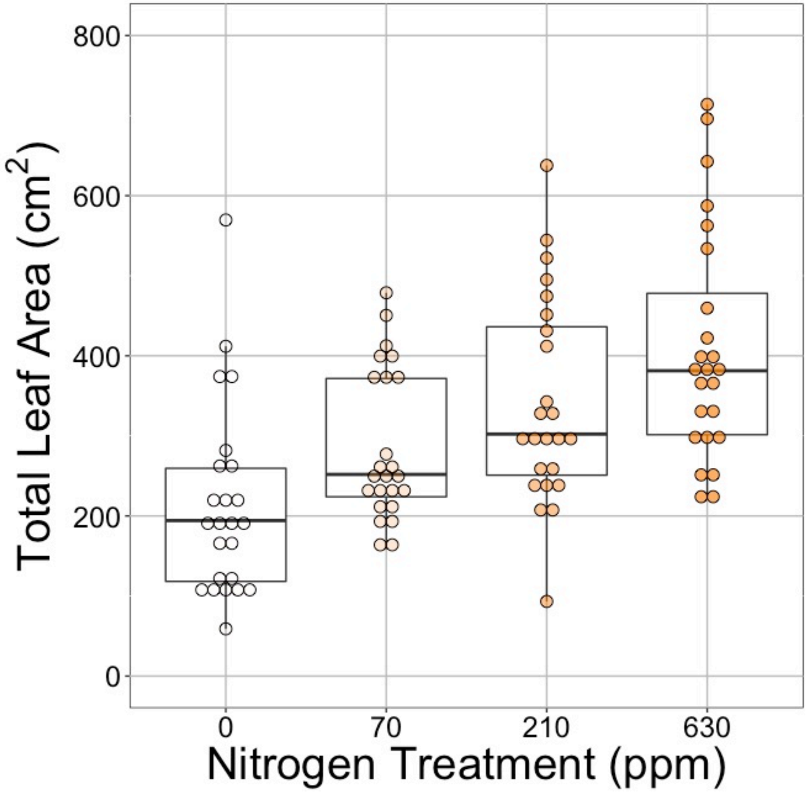
No change (P = 0.42)



91% increase (P < 0.05)



Waring and Smith (in prep)

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Some takeaways

- Optimal leaf biochemical setup is determined by climate
- Plants mine for N to get the most leaves at the optimal setup
- Photosynthetic demand determines leaf N, not the other way around
- Soil N determines biomass investment
- Future conditions may provide relatively greater benefits to C_3 over C_4 species

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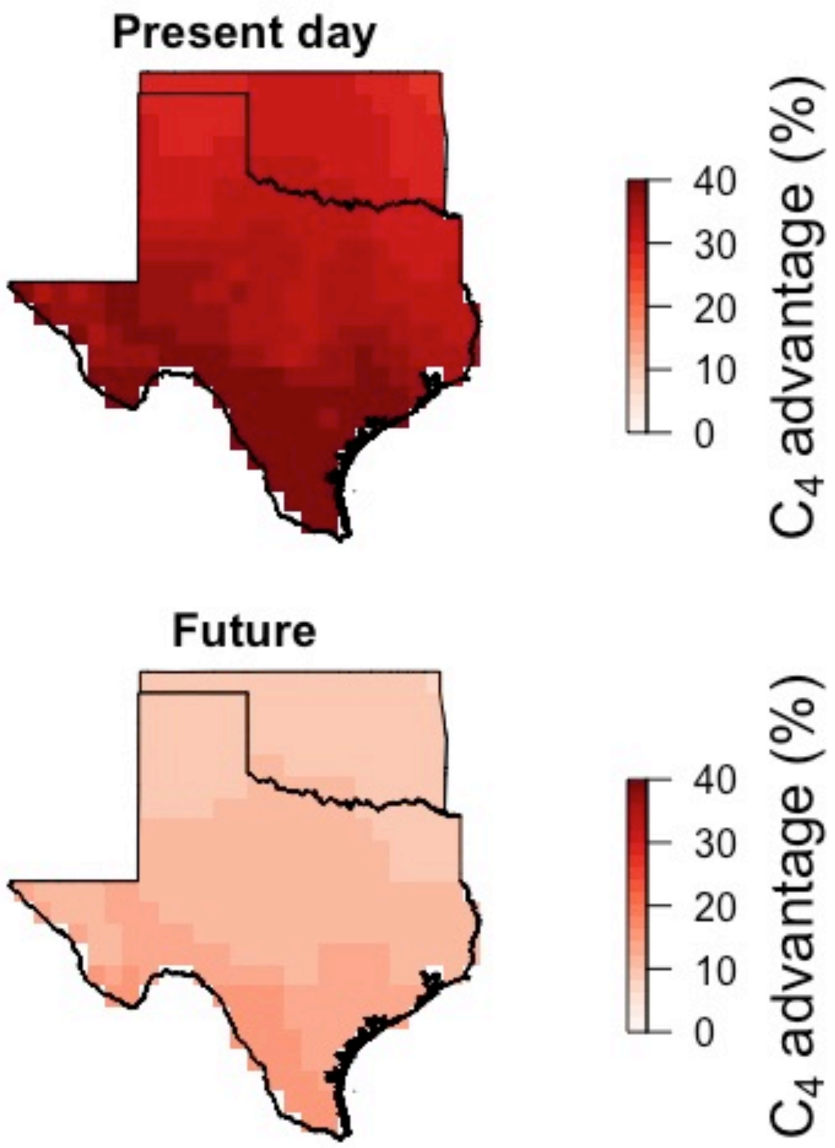

Scott and Smith (in prep)

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FATES implementation

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FATES implementation – Code changes

- No new parameters beyond Farquhar et al. (1980; C3) and Von Caemmerer (2000; C4)
  - Will need running mean environmental conditions
  - More tractable code?

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FATES implementation – Code changes

- New scheme
  1. Predict acclimated “basal rate” each time step using mean conditions
  2. Apply scalars to calculate photosynthesis at a given timestep (as already in model)
  3. Calculate leaf nutrient demand (reverse current leaf nutrient equations)
     - Use available nutrients to build optimal leaves
     - Leaf stoichiometry will vary with acclimation (i.e., leaf demand)
  4. Allocate any “saved” nutrients to new tissues
     - Model may already do optimal nutrient allocation?

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FATES implementation – Trait variability

- Variation would come from aboveground environmental variation
  - Need variation in environment the leaves are experiencing
- Spatial → variability across gridcells with climate variability
- Spatial → within gridcell would need to arise by changes in environment
- Temporal → within and across season variability as conditions change

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FATES implementation – "Tweakable" parameters

- Quantum efficiency of photosystem II
  - Including its temperature response
- Acclimation ”timescale”
- Acclimation "to what"?
  - Average conditions
  - Maximum conditions

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FATES implementation – Cool science questions

- C_3/C_4 competition
- Allocation responses*
- Nutrient feedbacks (whole plant and ecosystem)*
- Timescale of acclimation*
- Acclimation "to what"*

*Could be "strategy"-specific!

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Presentation available at:
www.github.com/SmithEcophysLab/seminar/2020_fates

Thanks!