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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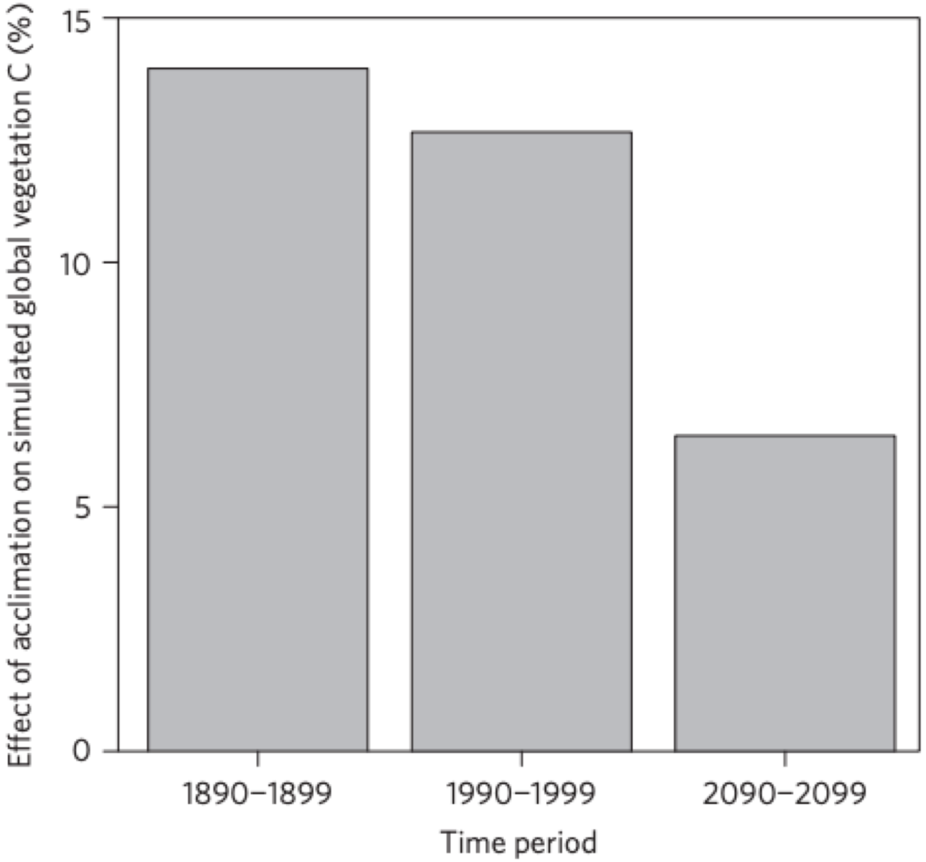
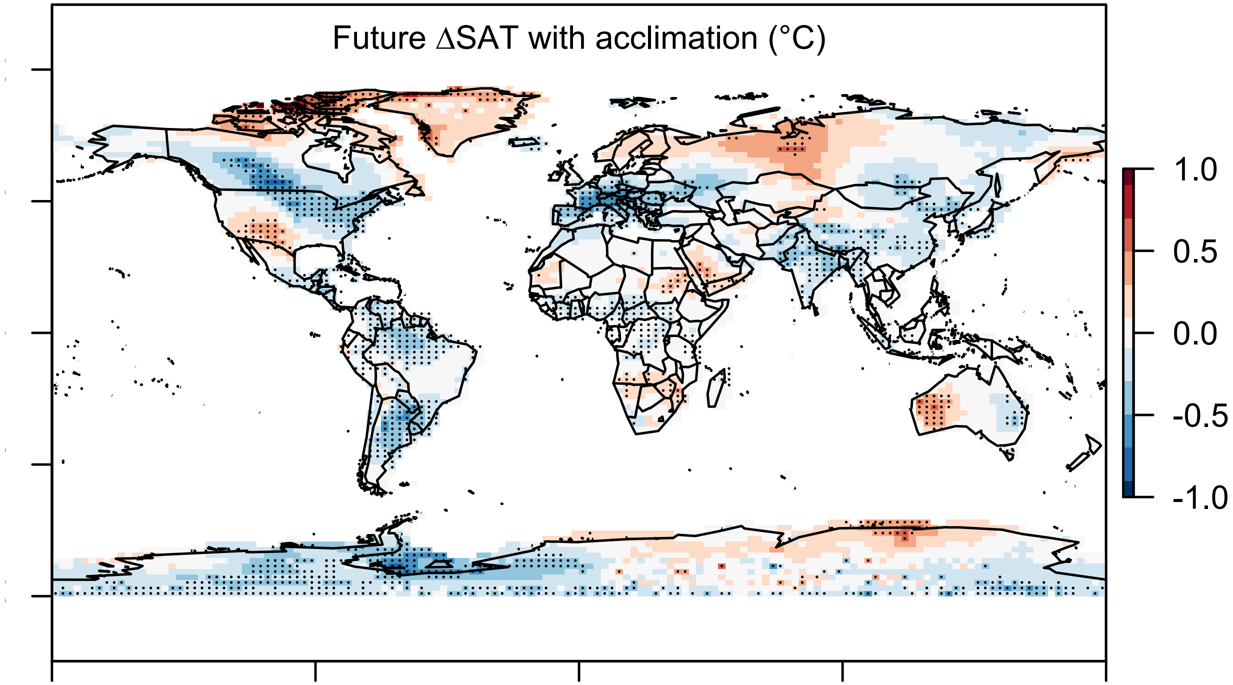
…and can possibly impact carbon cycling and climate

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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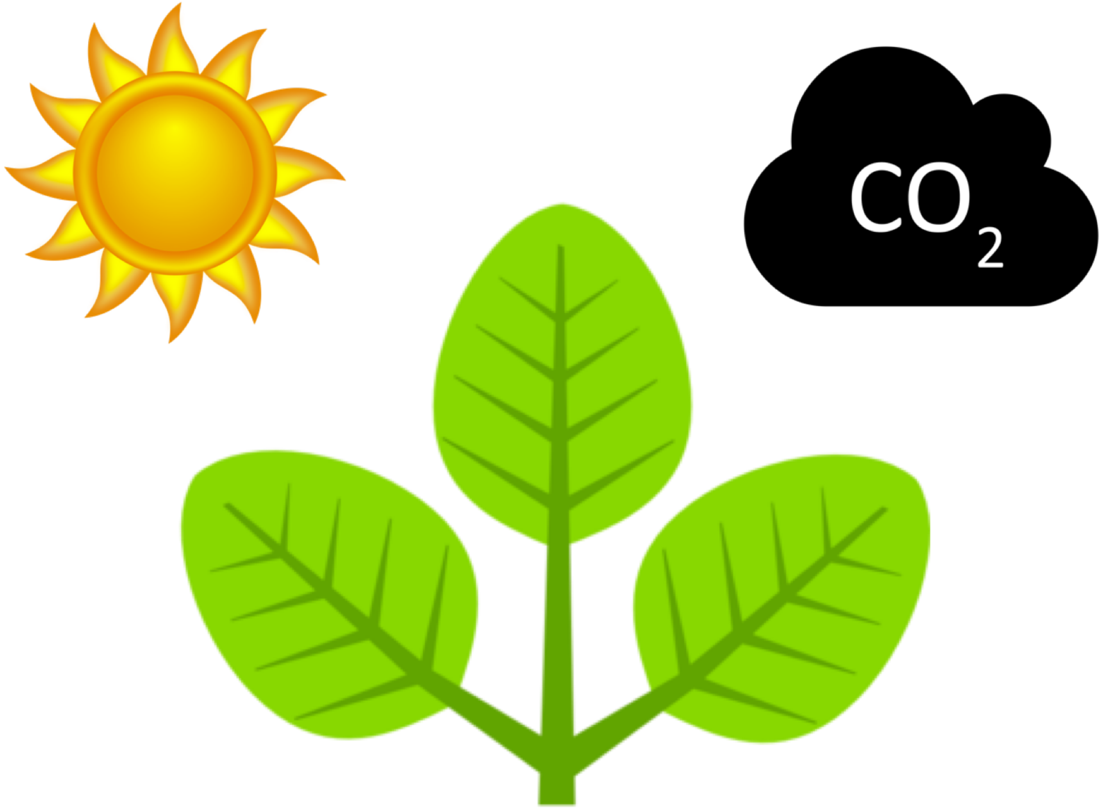
Biochemistry optimization: Coordination hypothesis



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)

$$A_j = A_c$$

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

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

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

Smith et al. (2019)

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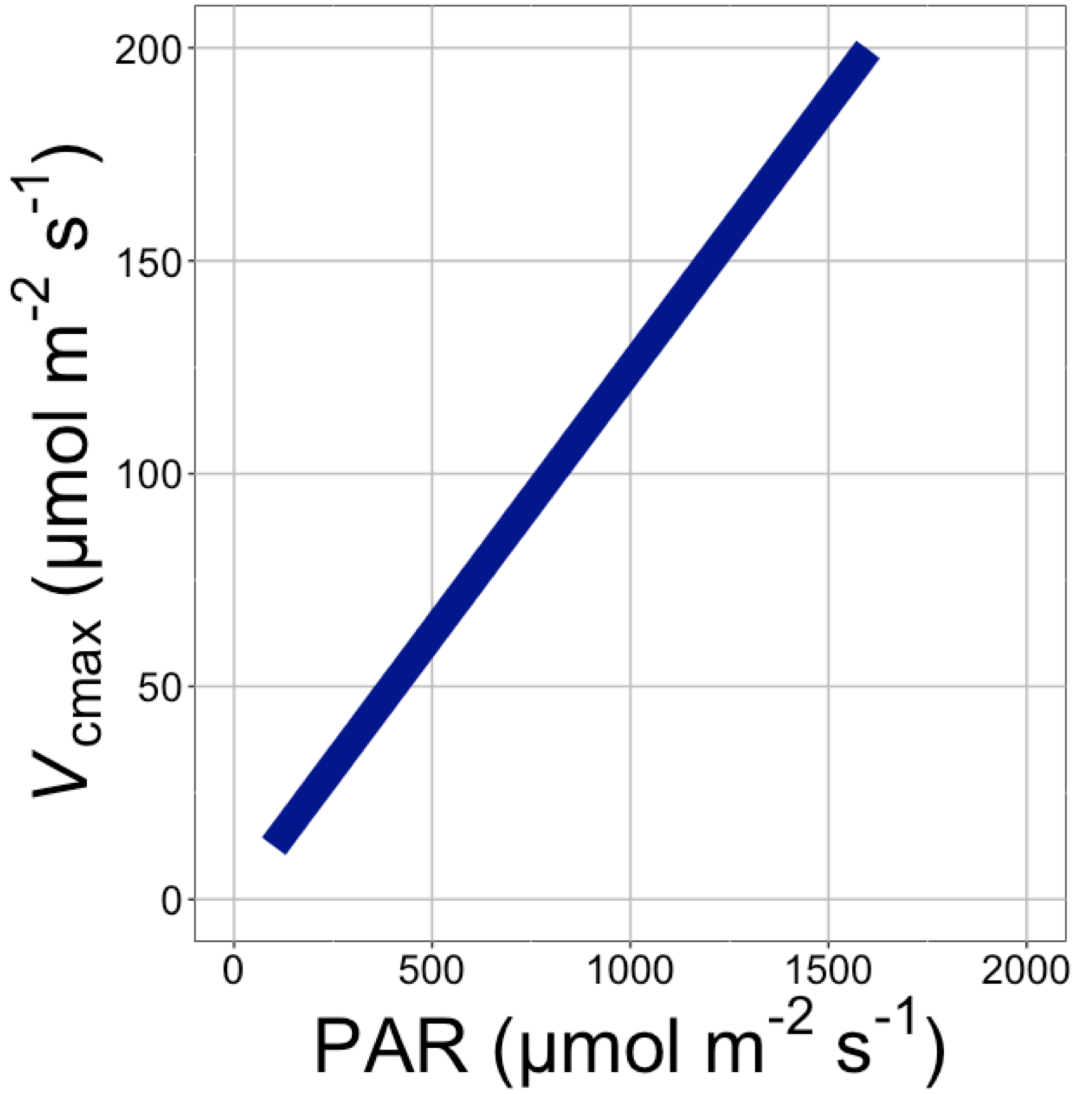

V_{cmax} increases with light because of greater electron transport

Smith et al. (2019)

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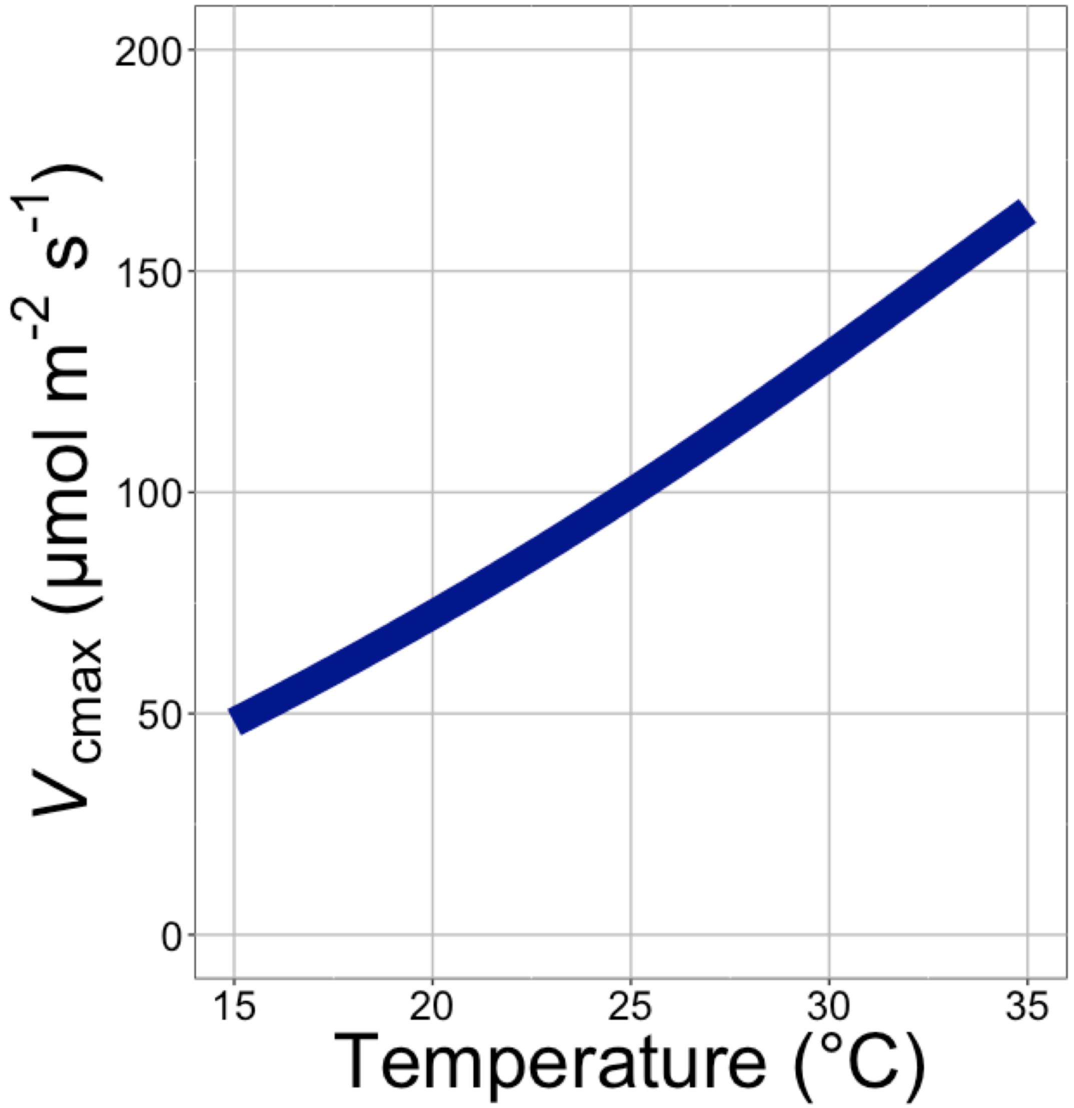
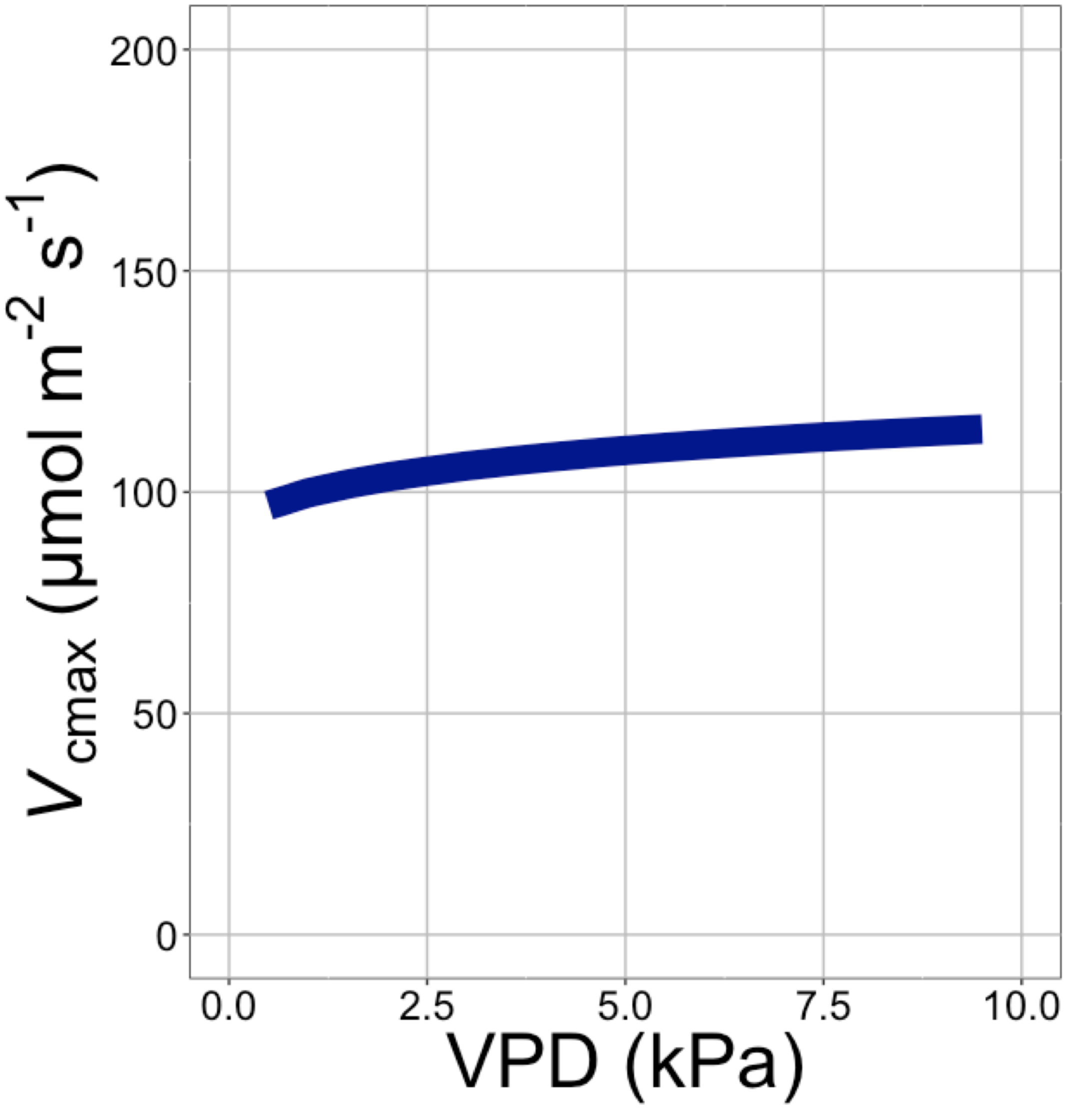


V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019)

nick.smith@ttu.edu



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

Smith et al. (2019)

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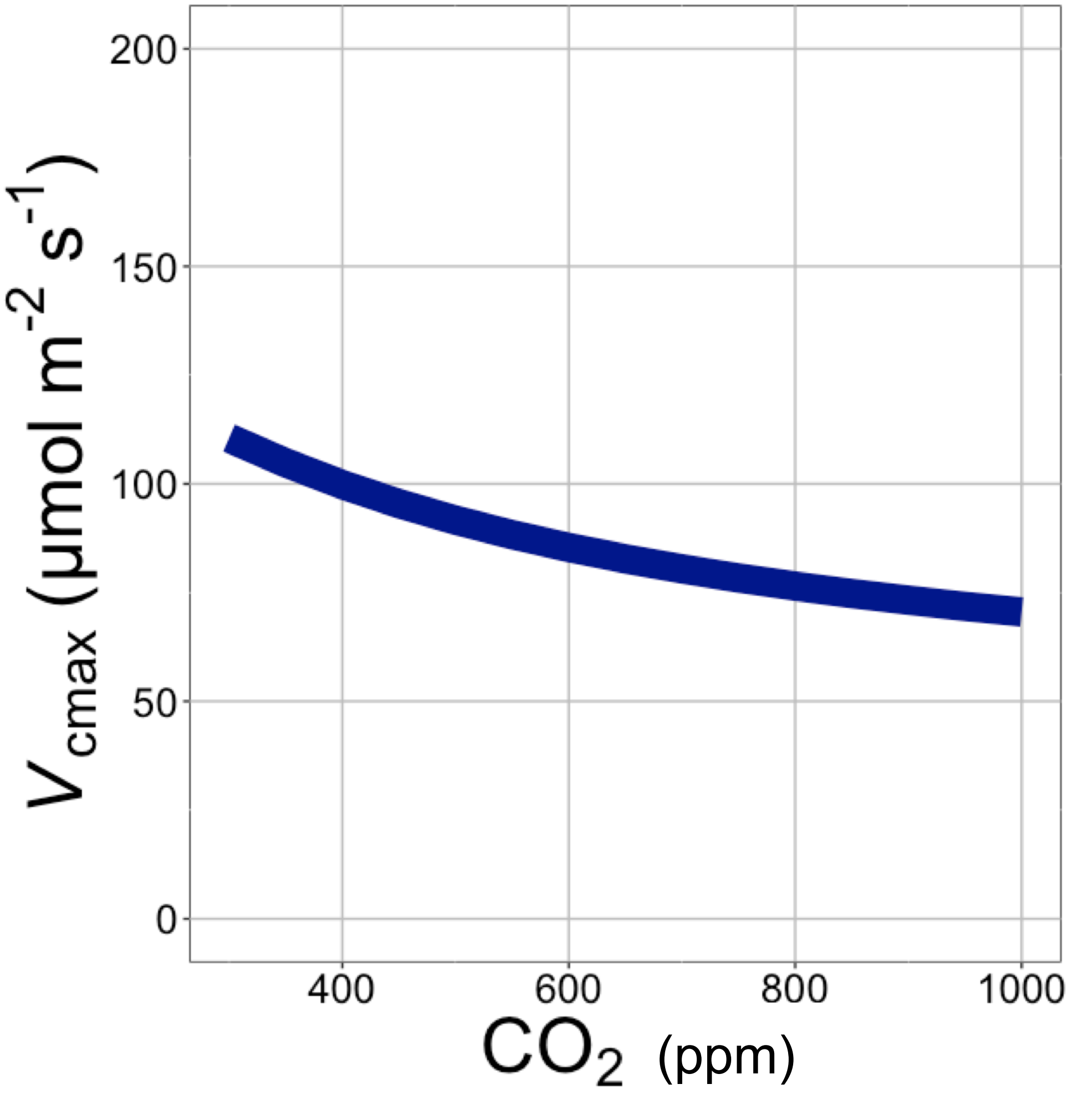

V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf

Smith et al. (2019)

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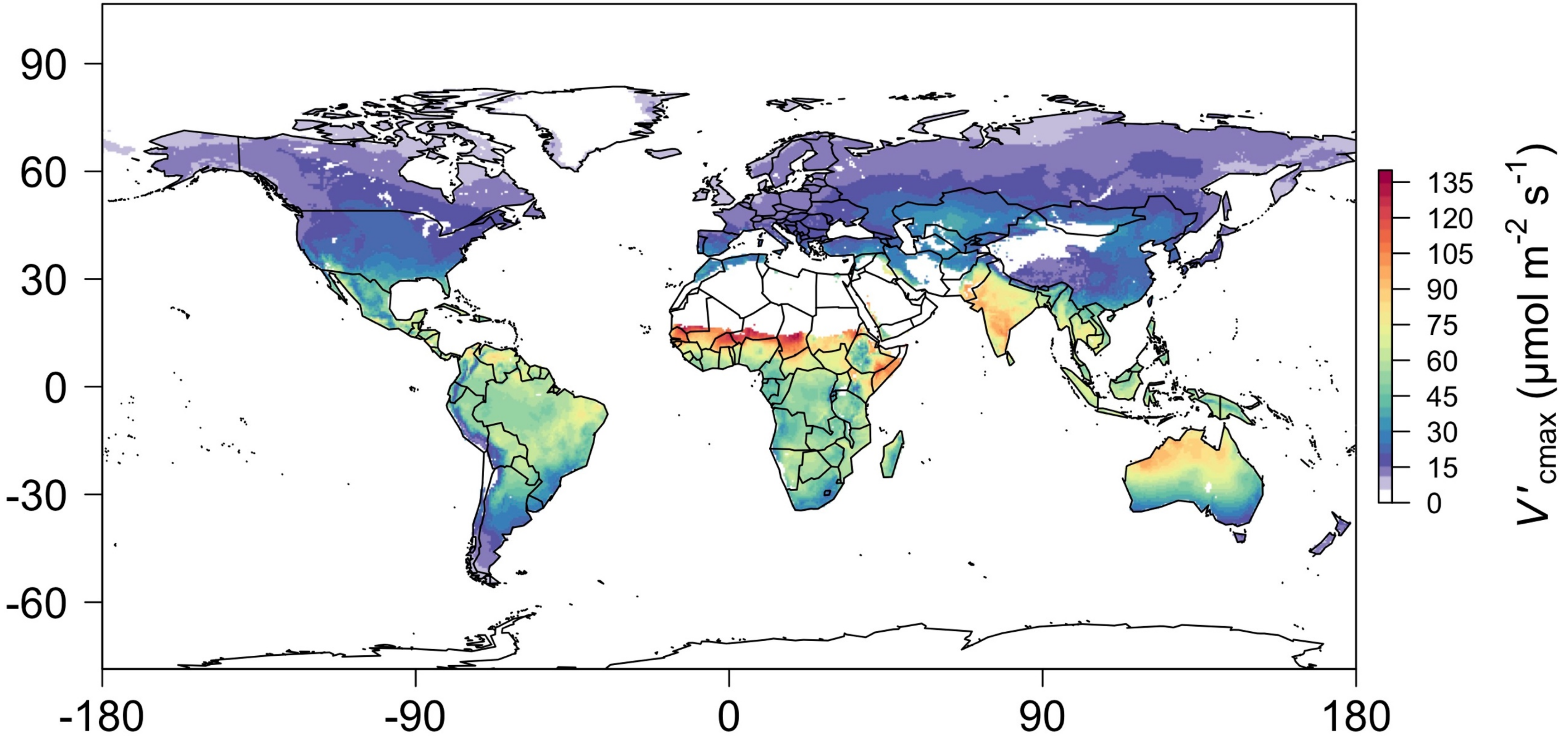
Global, optimally acclimated traits!



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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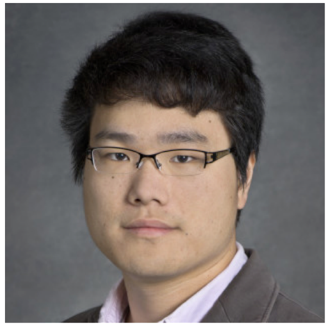
Let's run a model out into the future!



E3SM Energy Exascale Earth System Model

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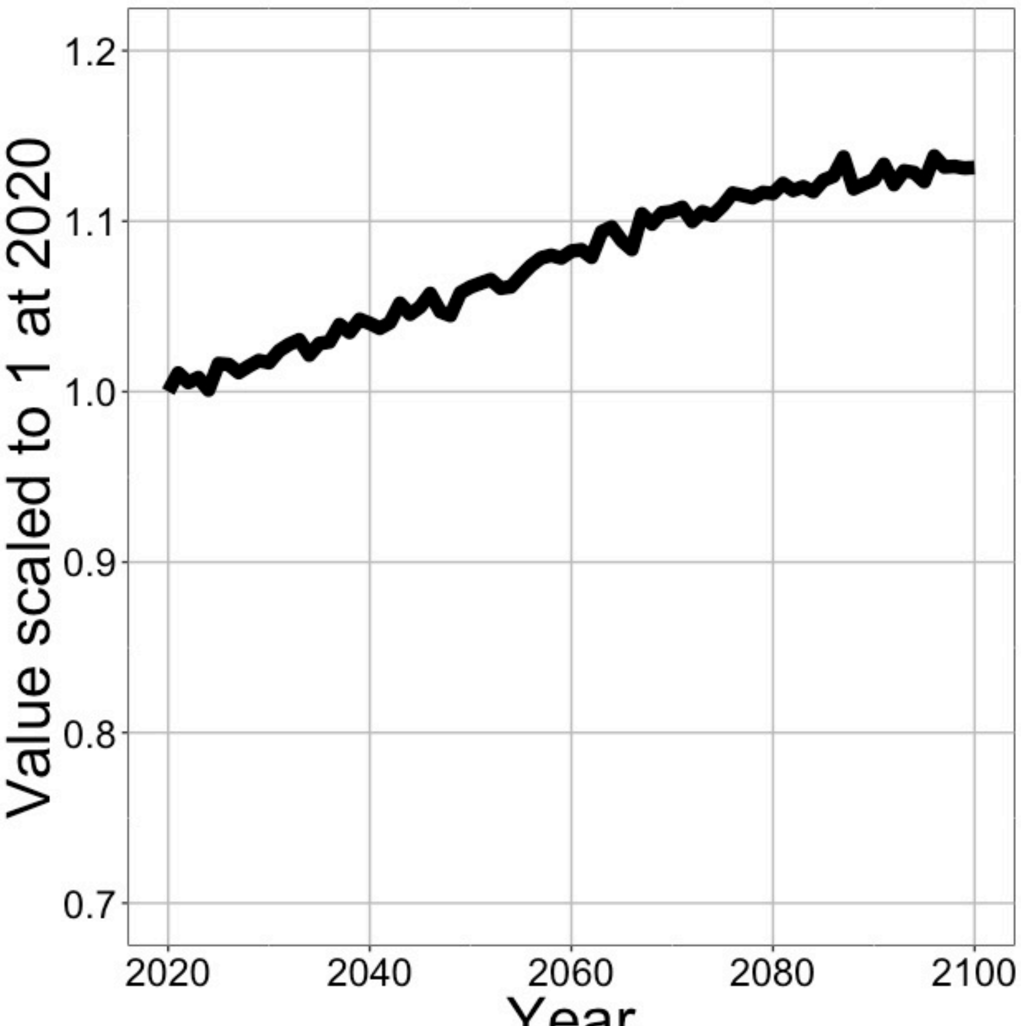
Photosynthesis increases in future



Net Photosynthesis

Smith et al. (in prep)

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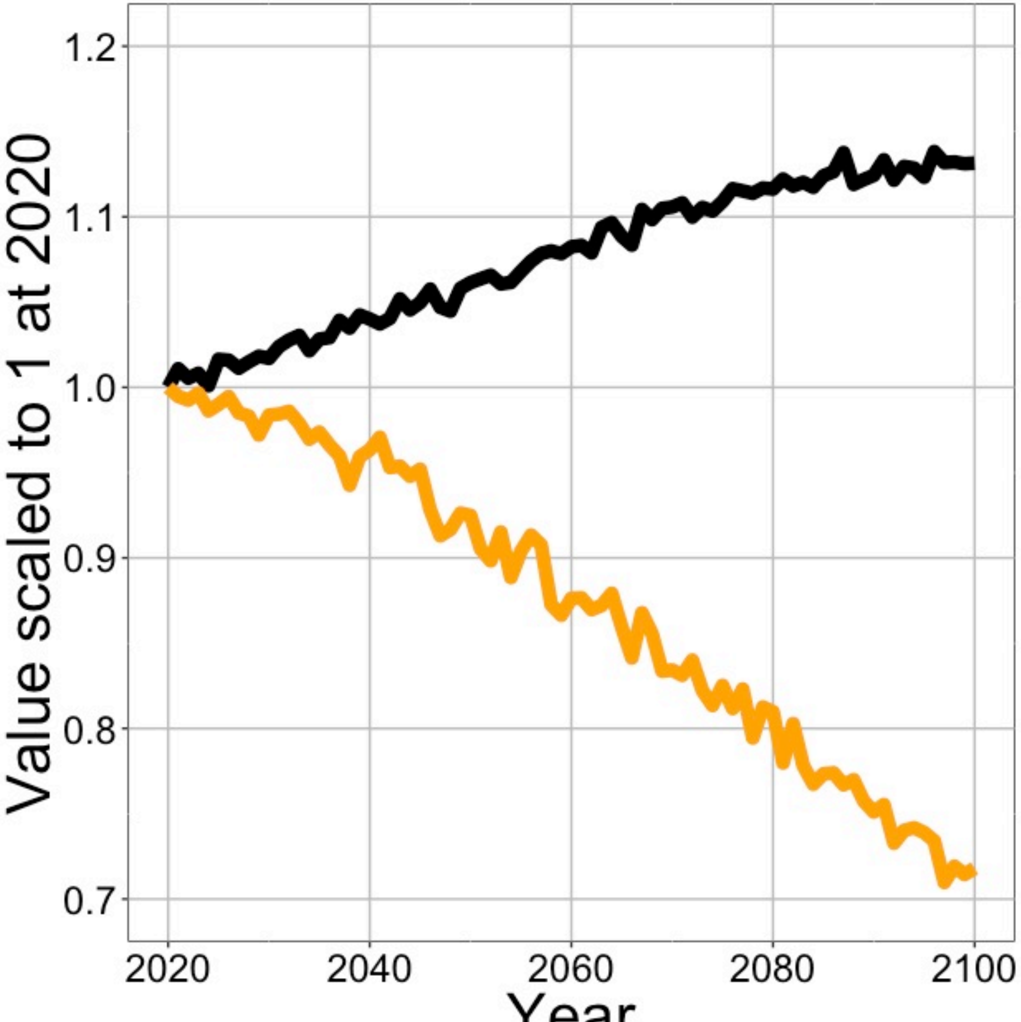
Photosynthesis increases in future
(at lower nutrient use)



Net Photosynthesis

Leaf Nitrogen

Smith et al. (in prep)

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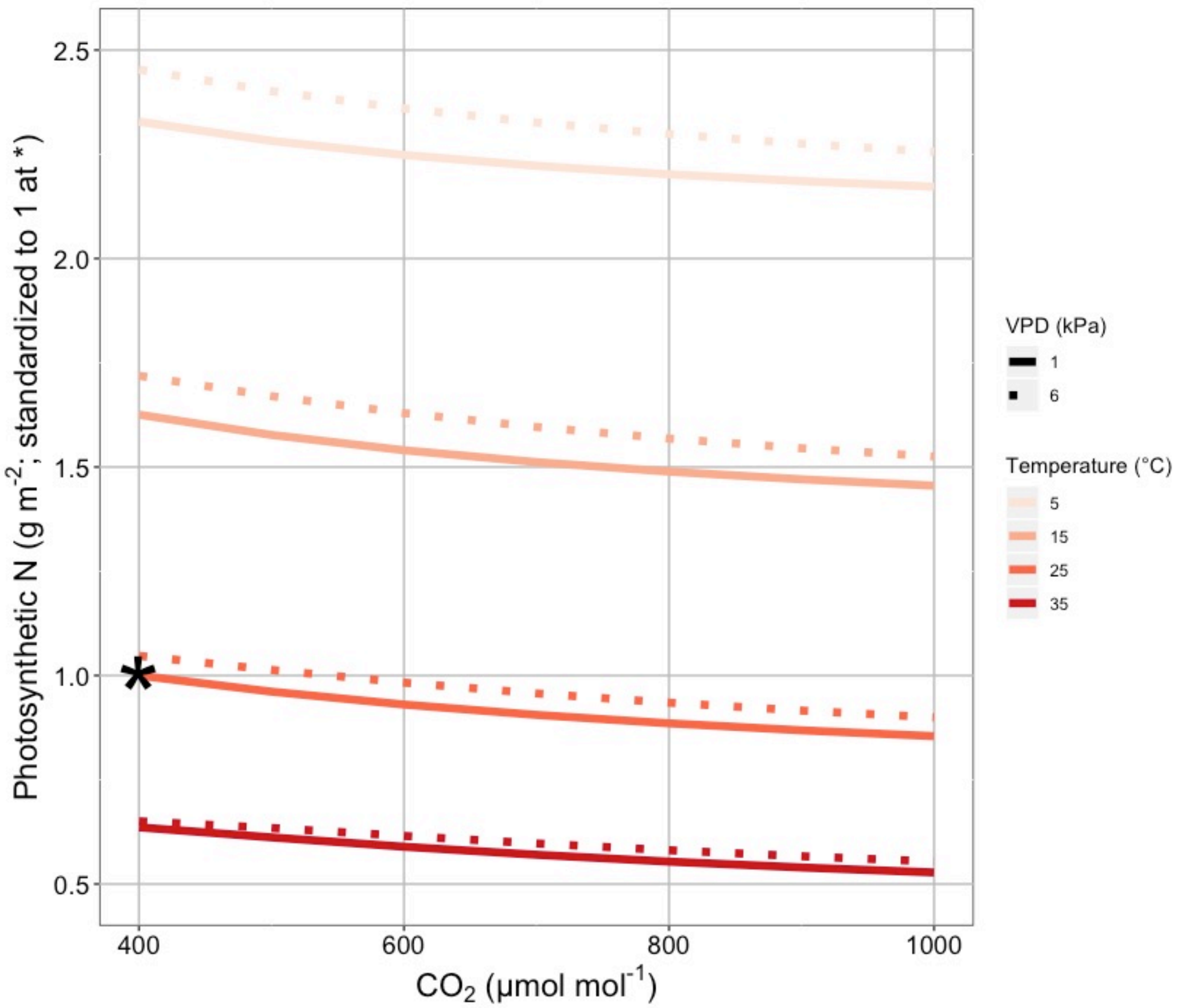
Leaf N declines due to warming and eCO_2



Smith & Keenan (in review)

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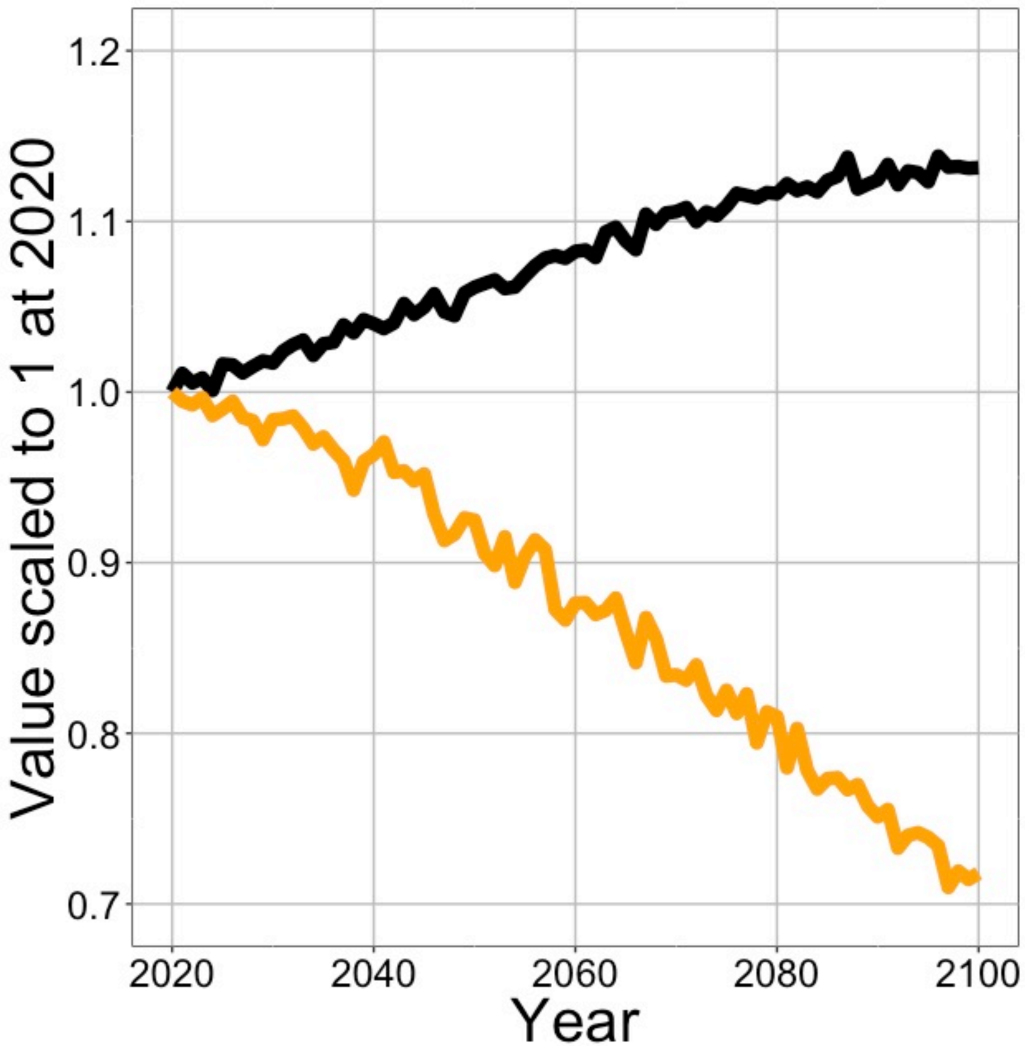
Photosynthesis increases in future
(at lower nutrient use)



Net Photosynthesis

Leaf Nitrogen

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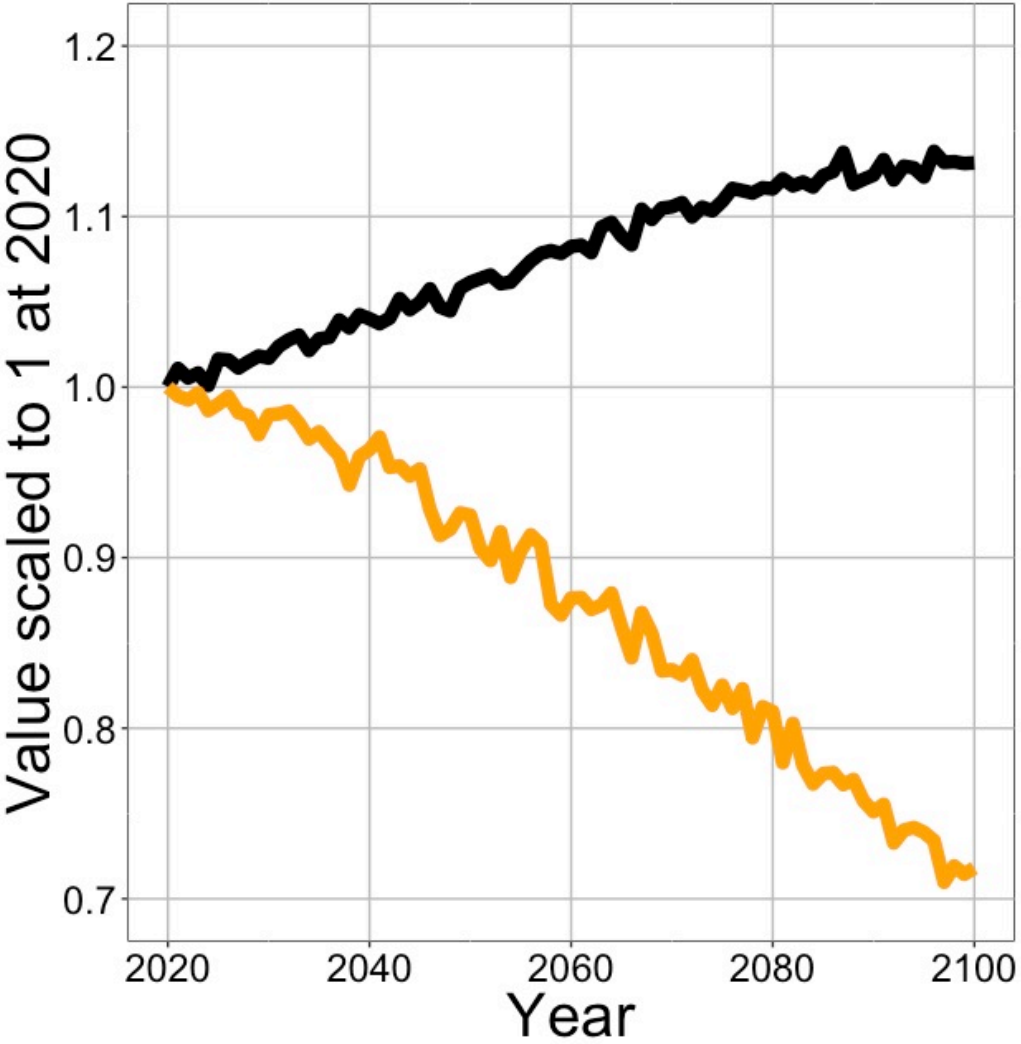
Photosynthesis increases in future
(at lower nutrient use)

Base ELM shows <5% change in leaf N



Net Photosynthesis

Leaf Nitrogen

Smith et al. (in prep)

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What does this all mean and is it real?

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A typical LSM photosynthesis scheme

$$
\begin{tikzcd}
 & & \text{Climate} \arrow[d] \\
\text{Soil N} \arrow[r] & \text{Leaf N} \arrow[r] & \text{Photosynthesis}
\end{tikzcd}
$$

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Least cost optimality model

Climate

↓

Photosynthesis

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Let’s check this assumption

Climate

↓

Soil N → Leaf N → Photosynthesis

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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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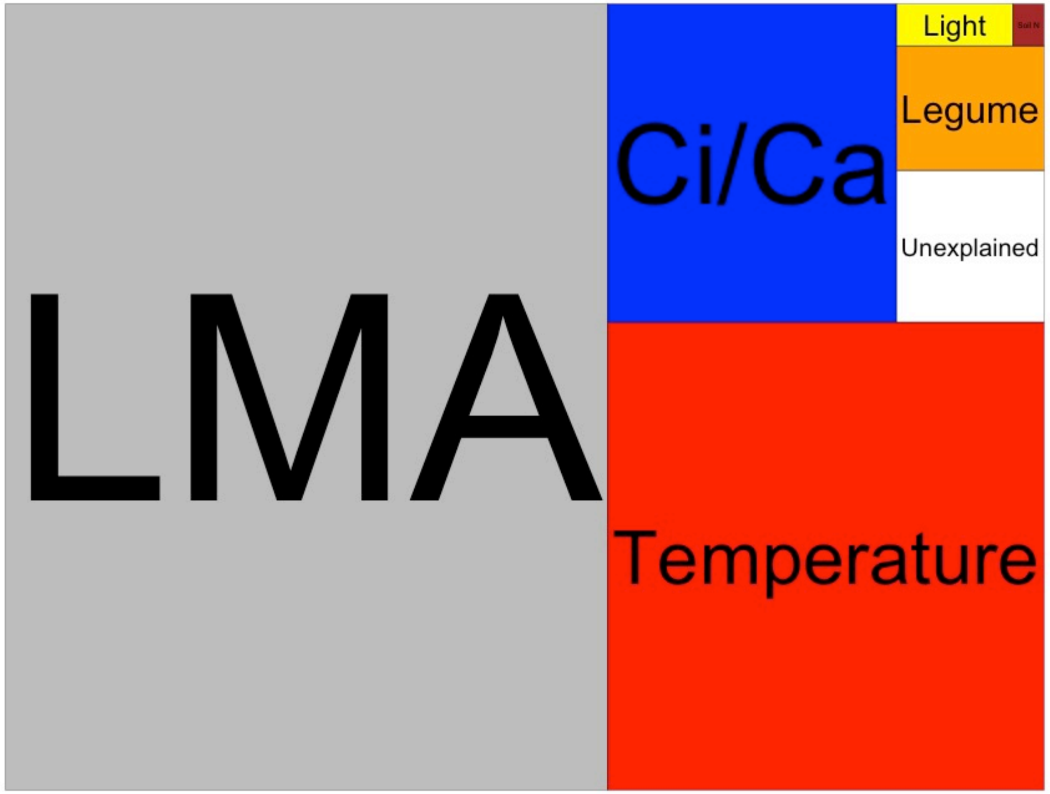
Globally, N addition little impact on leaf N



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

nutrient network

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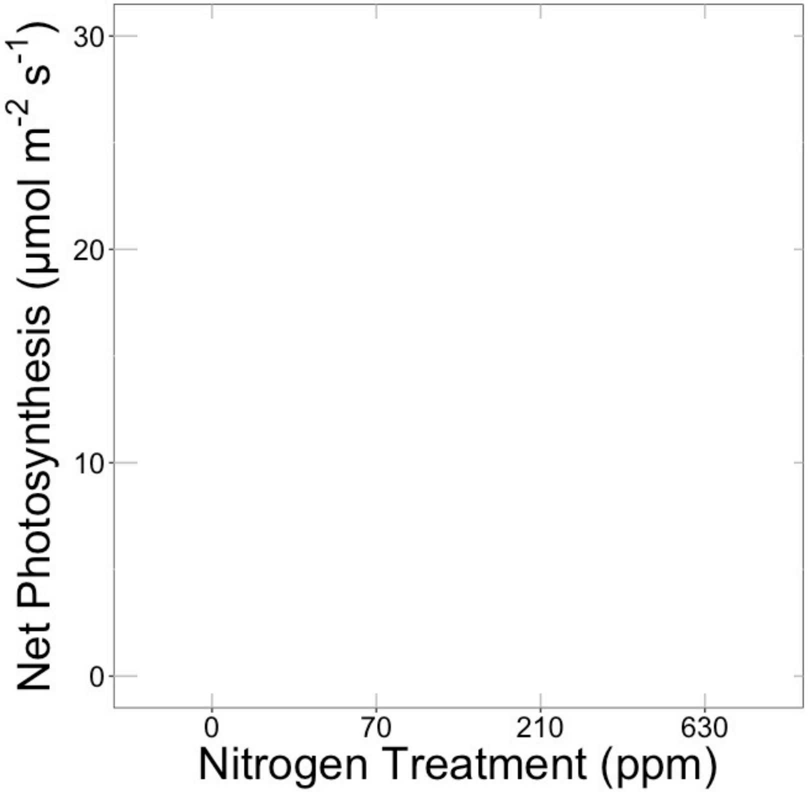
Does photosynthesis respond to soil N?



Waring and Smith (in prep)

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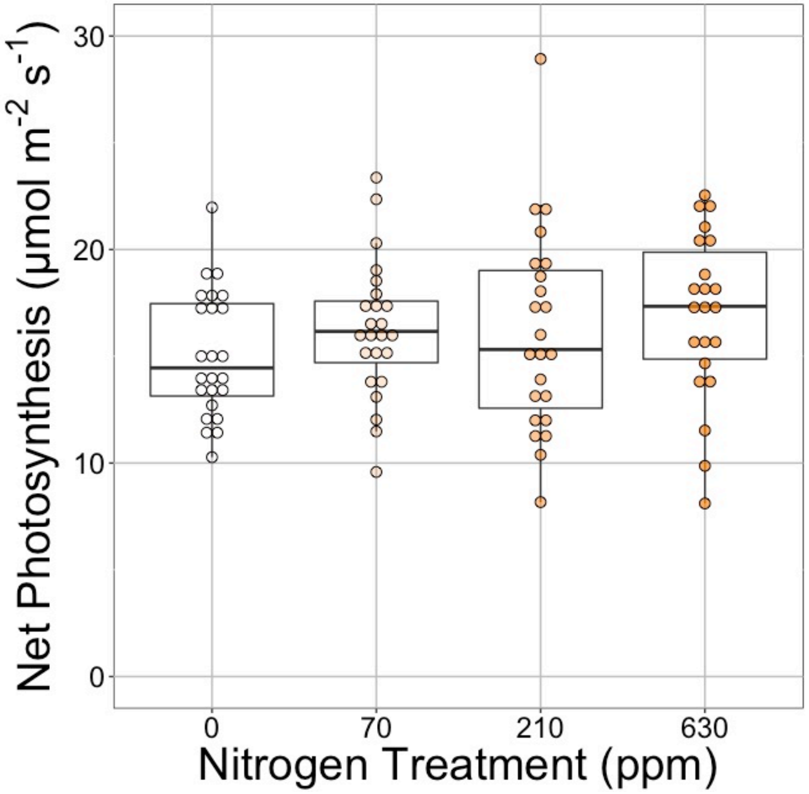
Photosynthesis does not change with soil N

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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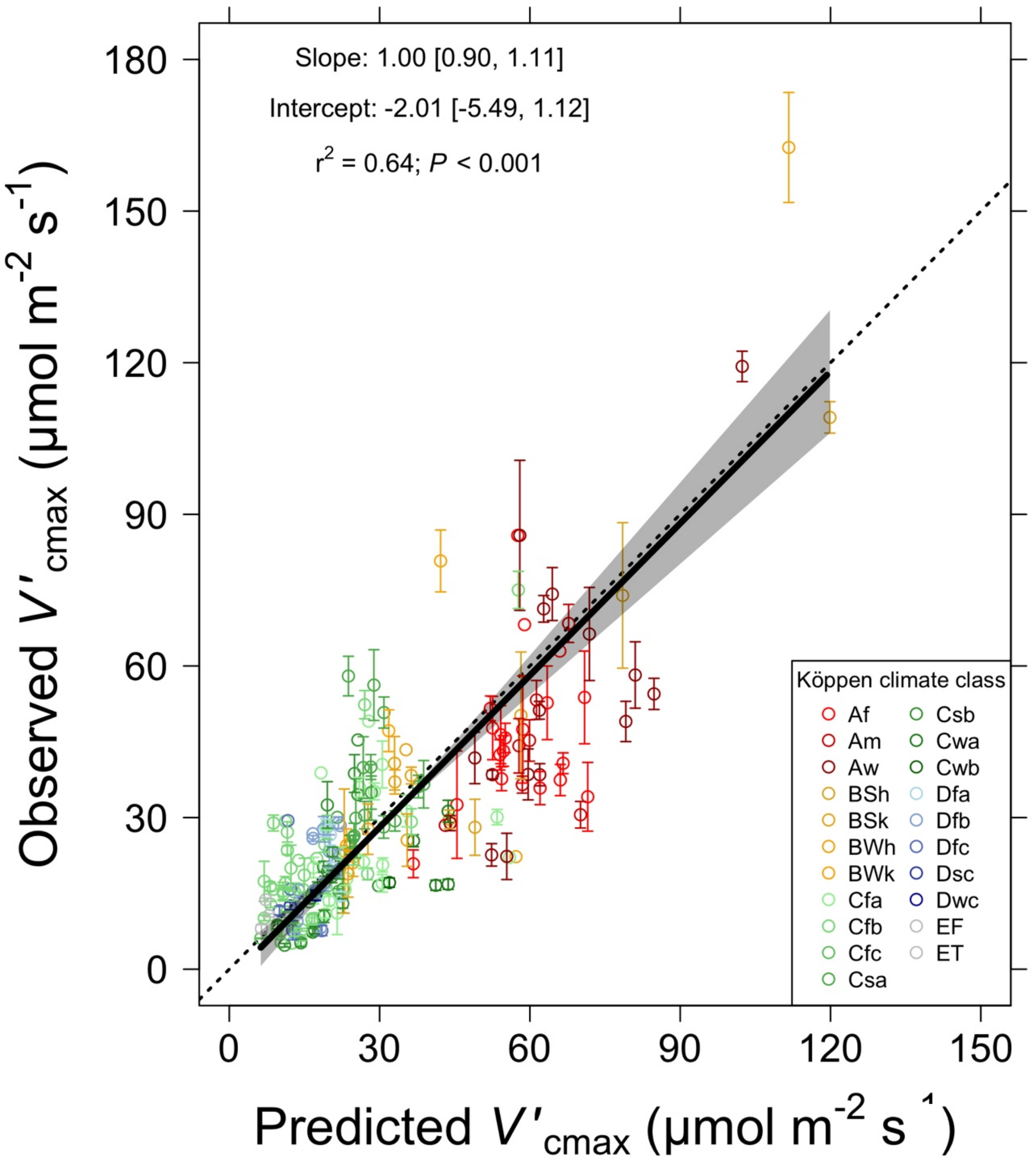

Optimal V_{cmax} is similar to observed values

Smith et al. (2019)

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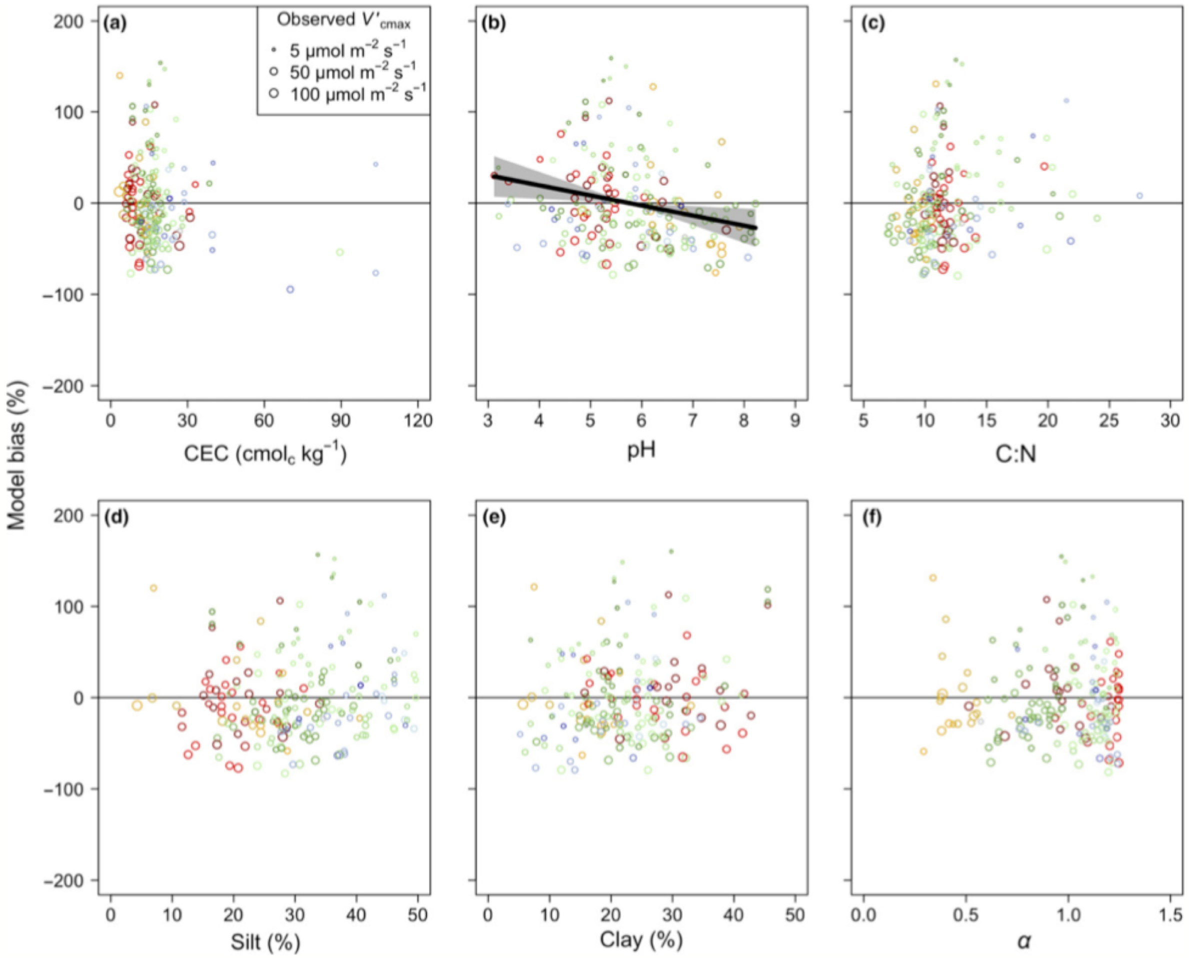
There is little effect of soils on V_{cmax}



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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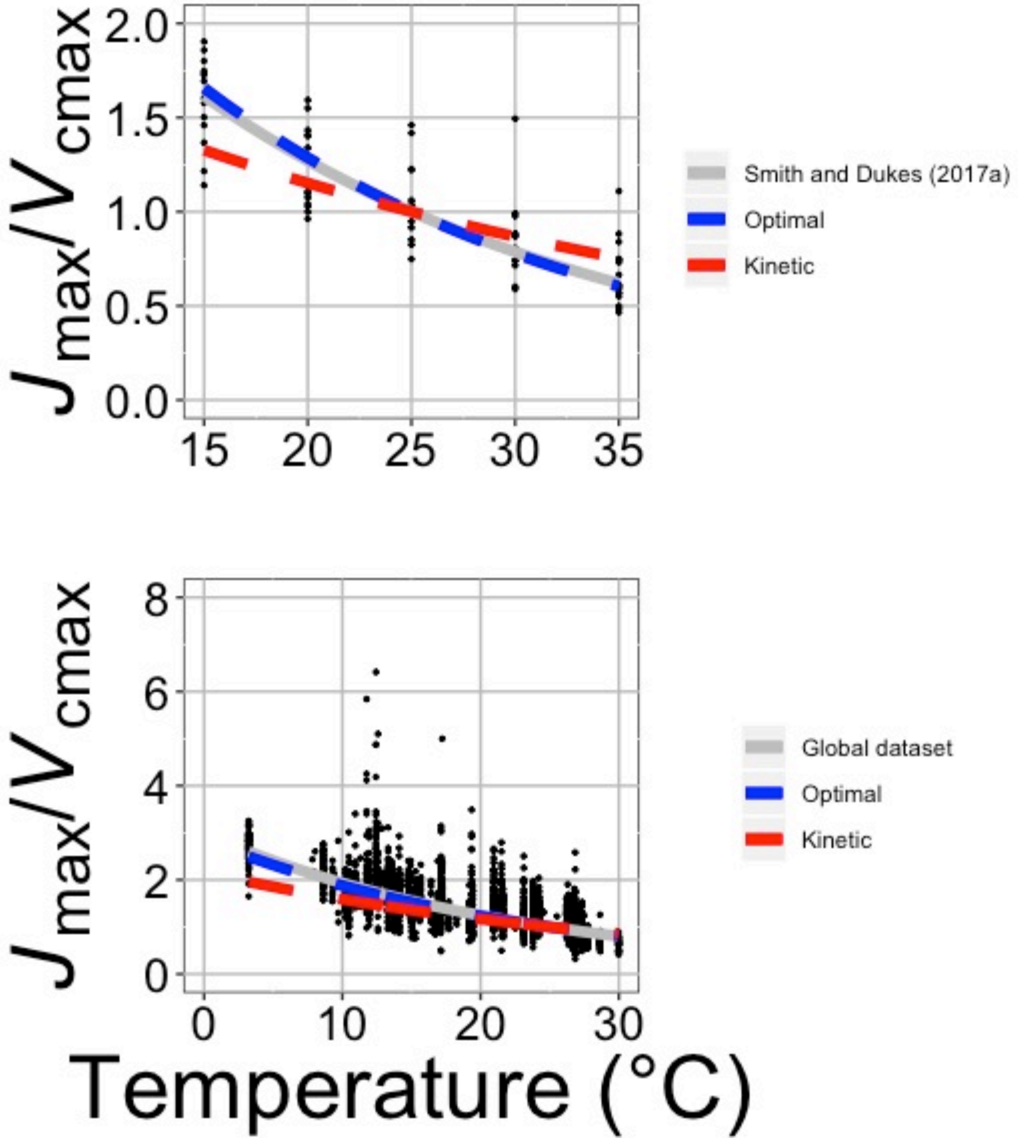

Photosynthetic traits change with temperature in ways expected from optimization

Data = -0.051 °C^{-1}

Predicted = -0.048 °C^{-1}

Smith and Keenan (in review)

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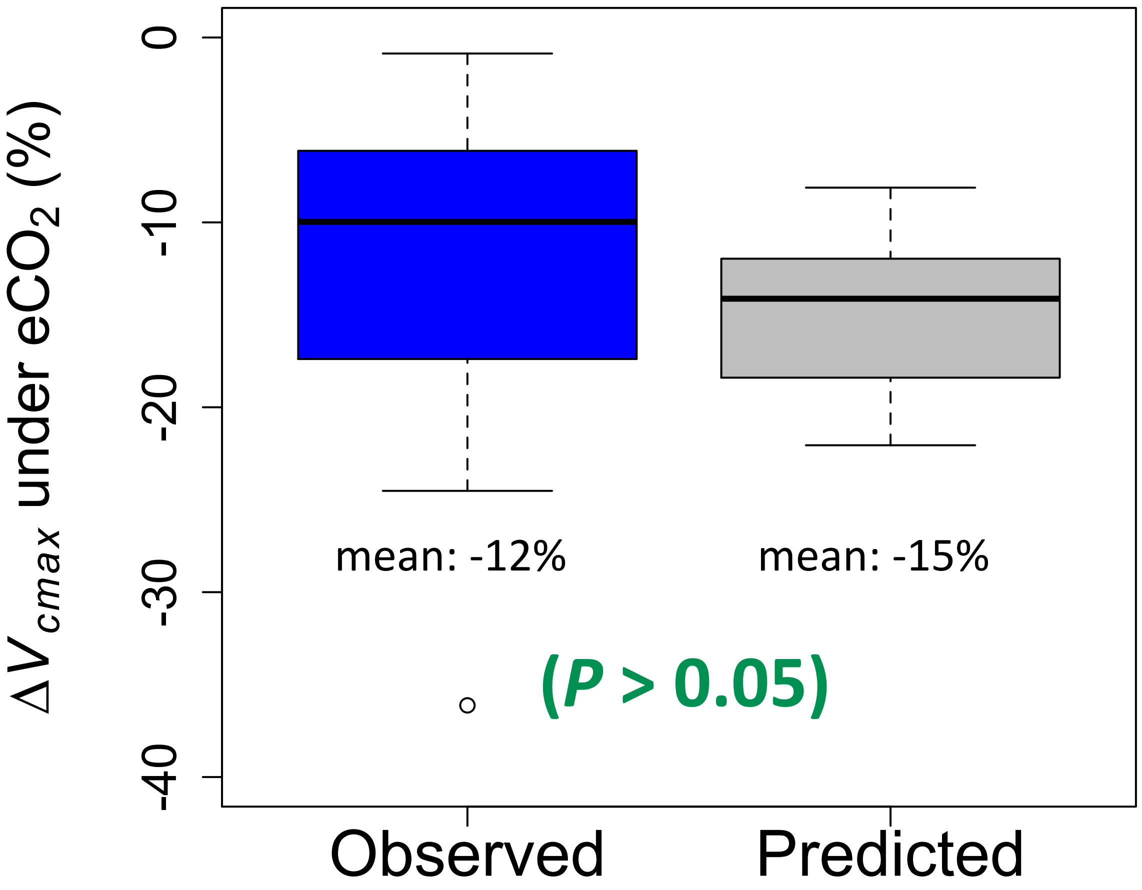
Photosynthetic traits change with future conditions in ways expected from optimization



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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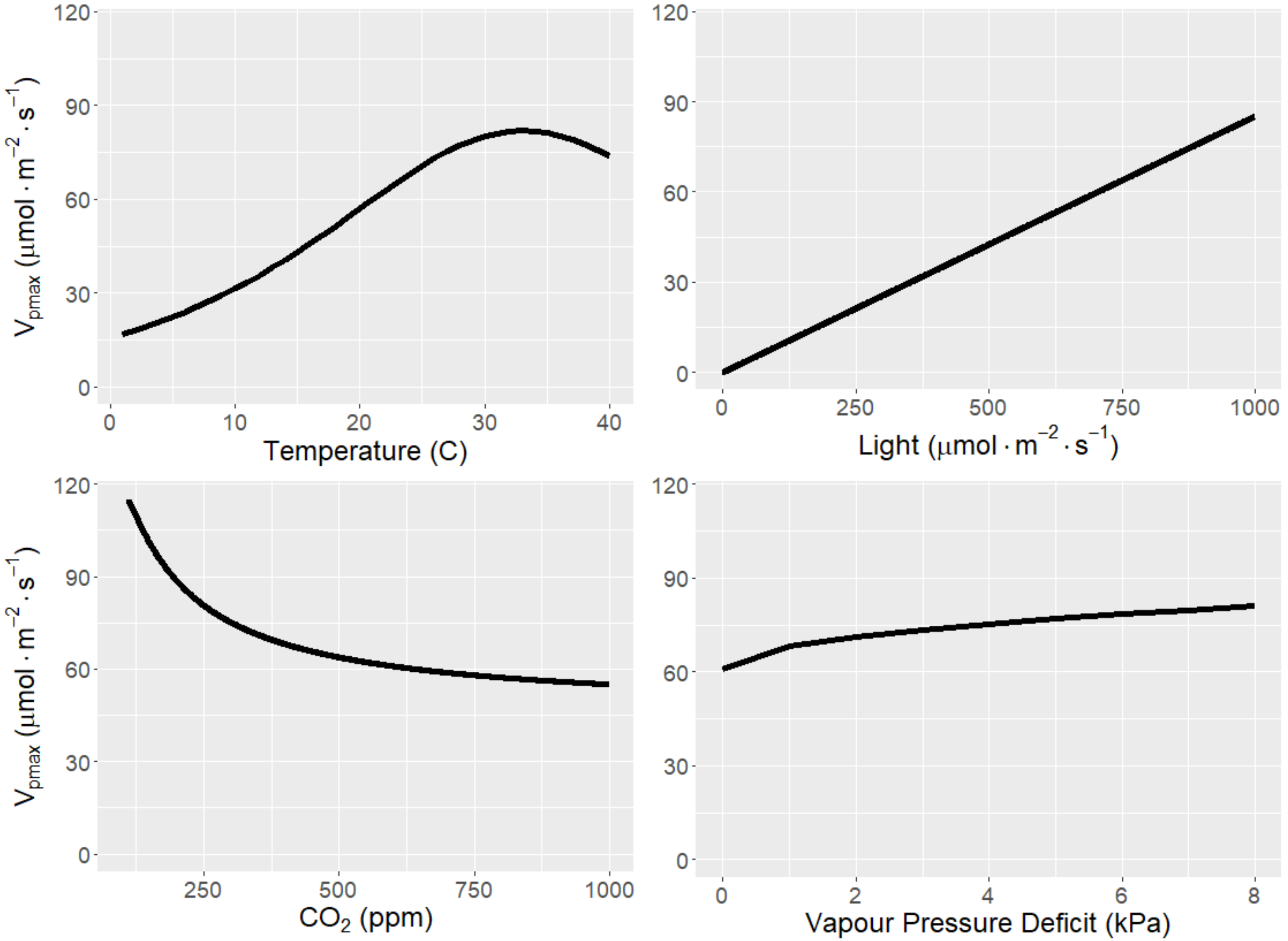
Photosynthetic biochemistry responds similarly in C_4 leaves as C_3 leaves



Scott and Smith (in prep)

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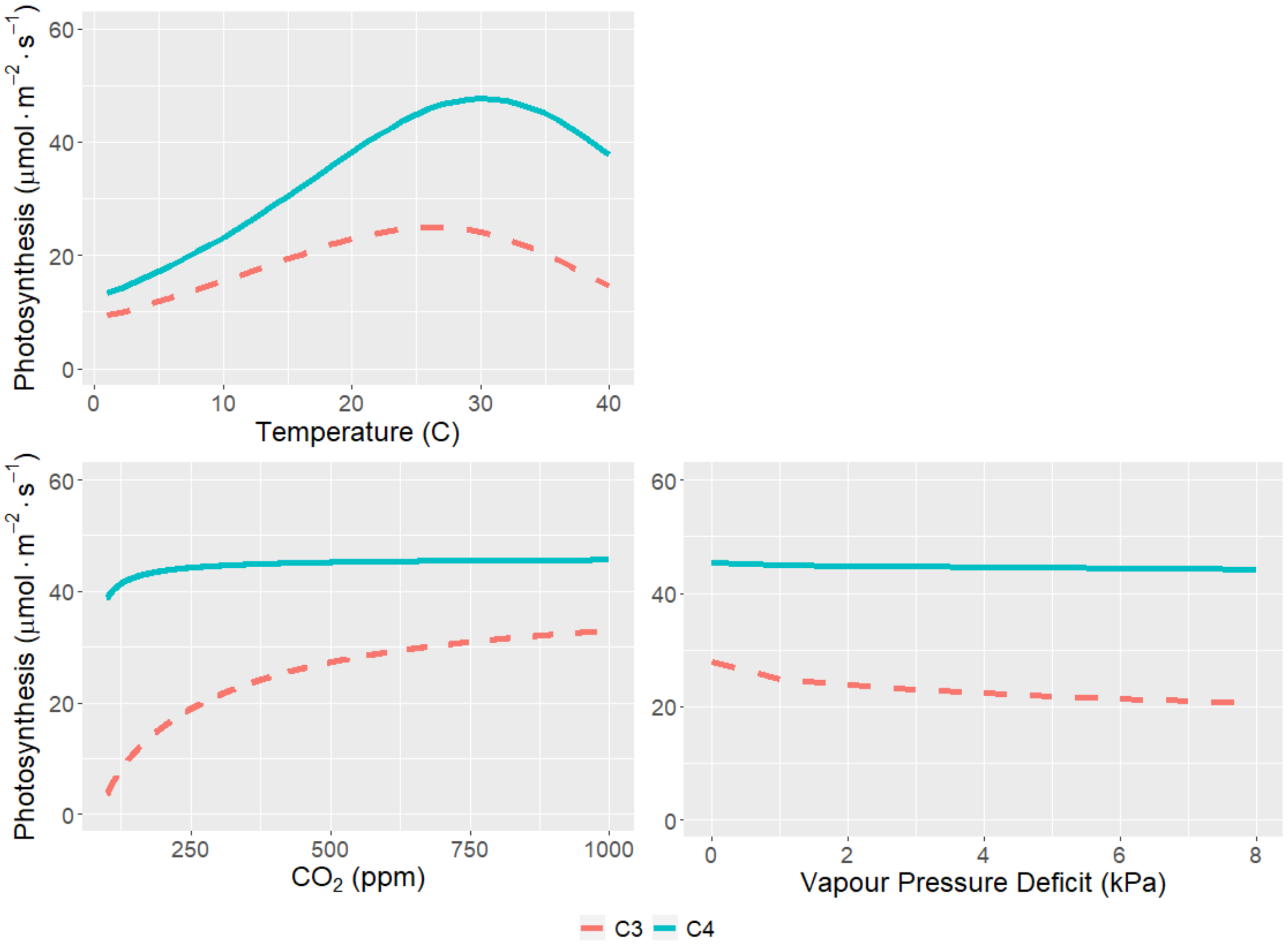
As expected, C_4 species are most benefitted under hot, dry, low CO_2 conditions



Scott and Smith (in prep)

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Important model assumptions

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Implications

- Optimal leaf biochemical setup is determined by climate

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Implications

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

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Implications

- 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

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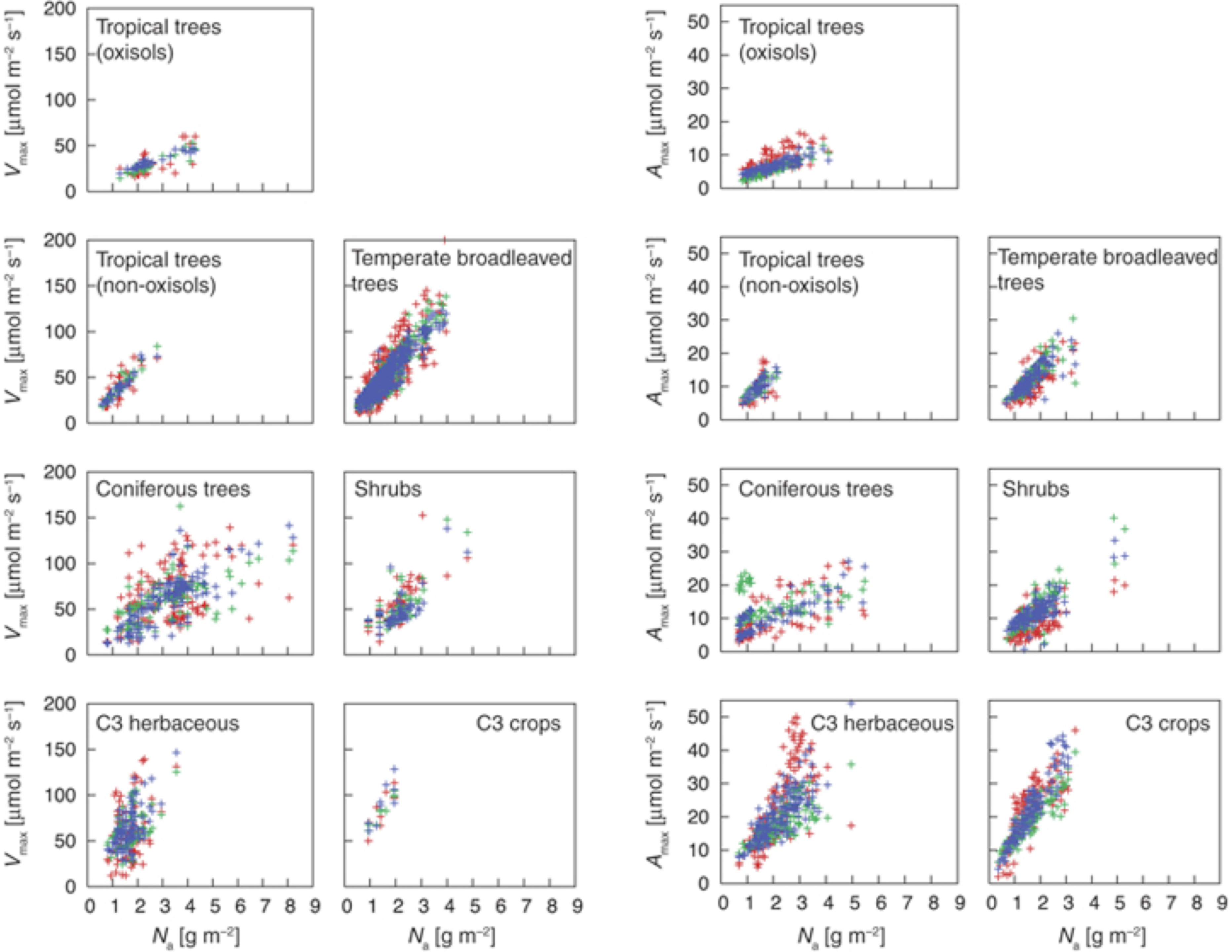

Axes need flipped

Kattge et al. (2009)

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Implications

- 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

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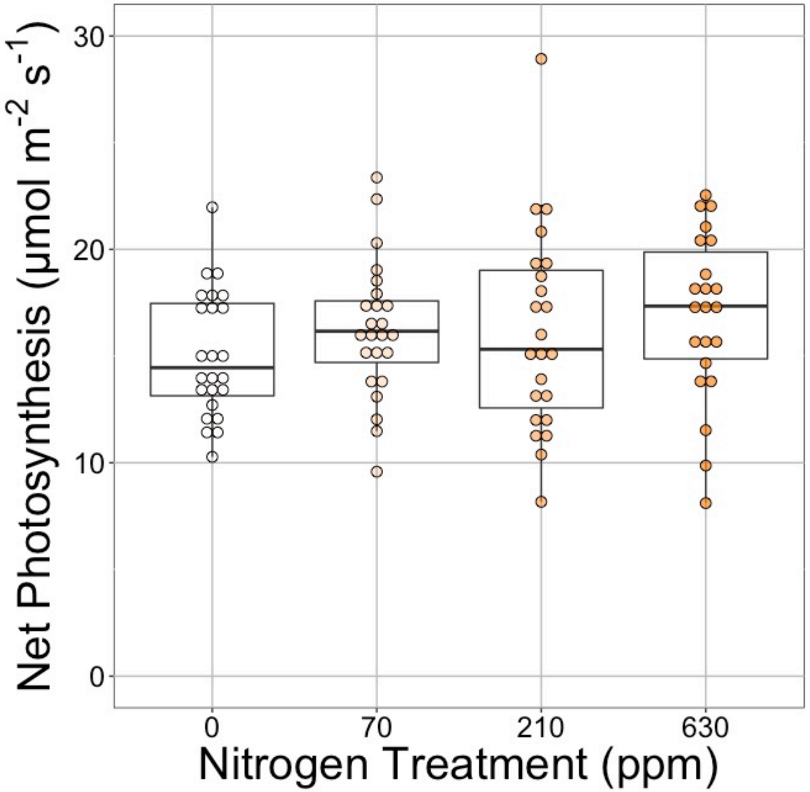
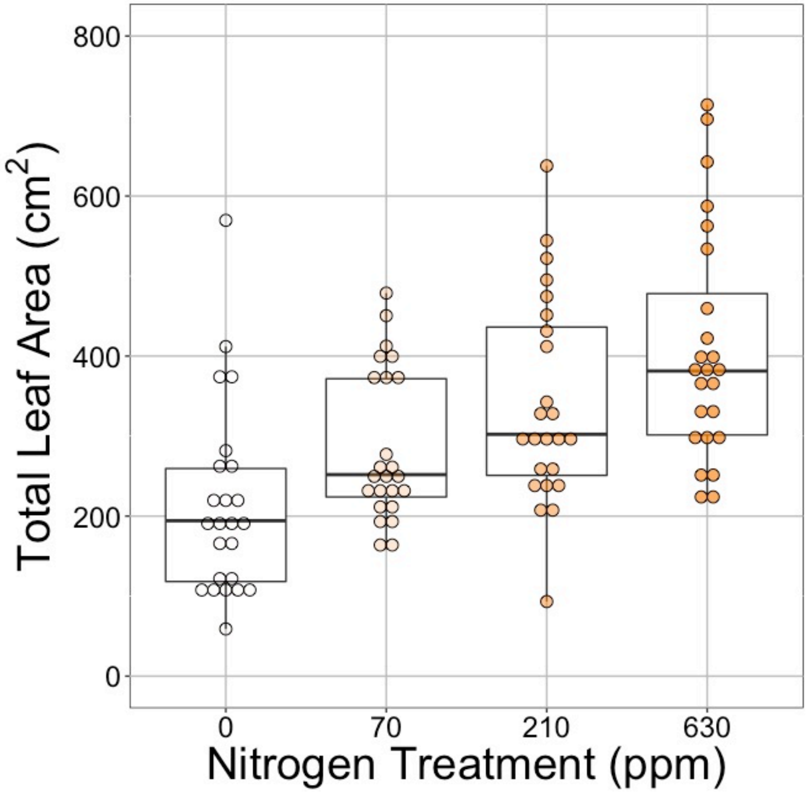
Soil N determines # of leaves?

No change (P = 0.42)



91% increase (P < 0.05)



Waring and Smith (in prep)

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Implications

- 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 benefit C_3 over C_4 species

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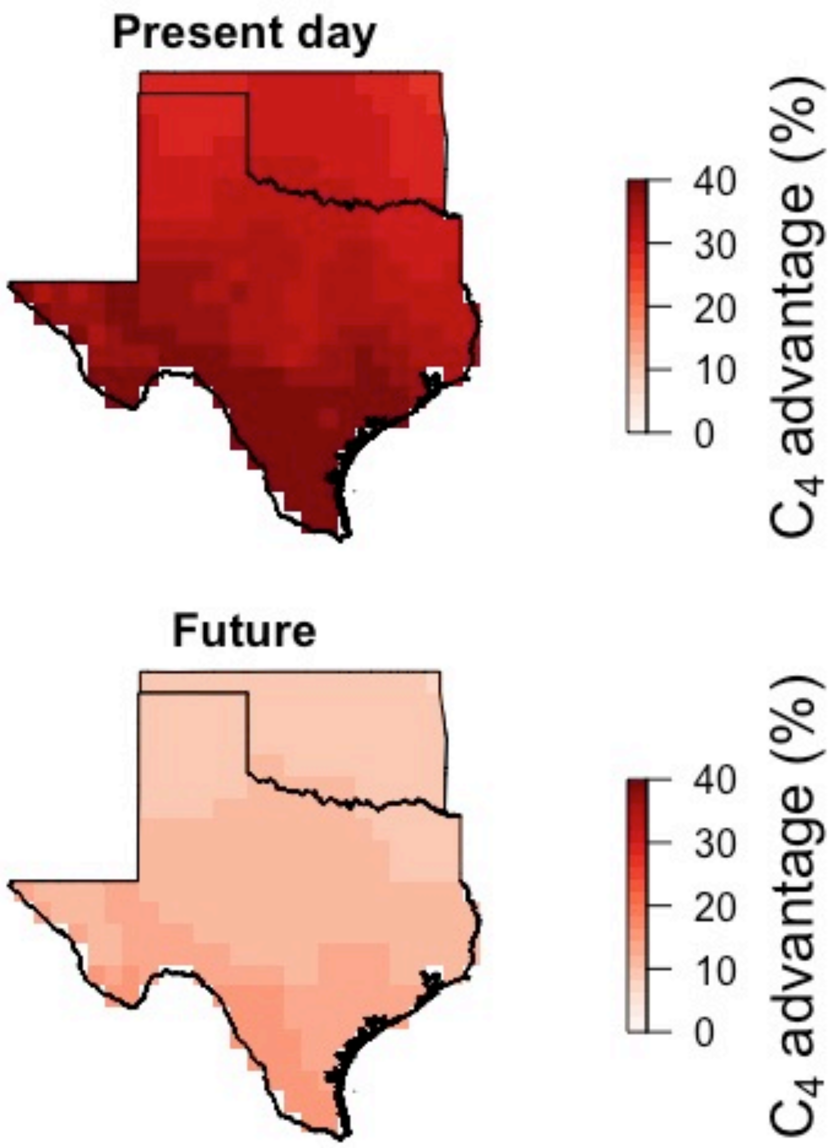

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FATES implementation

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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 (as already in model)
    3. Calculate leaf nutrient demand (reverse current leaf nutrient equations)
        - Use available N to build optimal leaves
        - Leaf C:N:P will vary with acclimation (i.e., leaf demand)

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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 – Practical application

1. Predict acclimated “basal rate” each time step using mean conditions
2. Apply scalars to calculate photosynthesis (as already in model)
3. Calculate leaf nutrient demand (reverse current leaf nutrient equations)
4. Reallocate “saved” nutrients to new tissues
   - Does model already do some sort of optimal nutrient allocation?

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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

Extra slides