Using least cost optimality to reliably simulate photosynthetic acclimation

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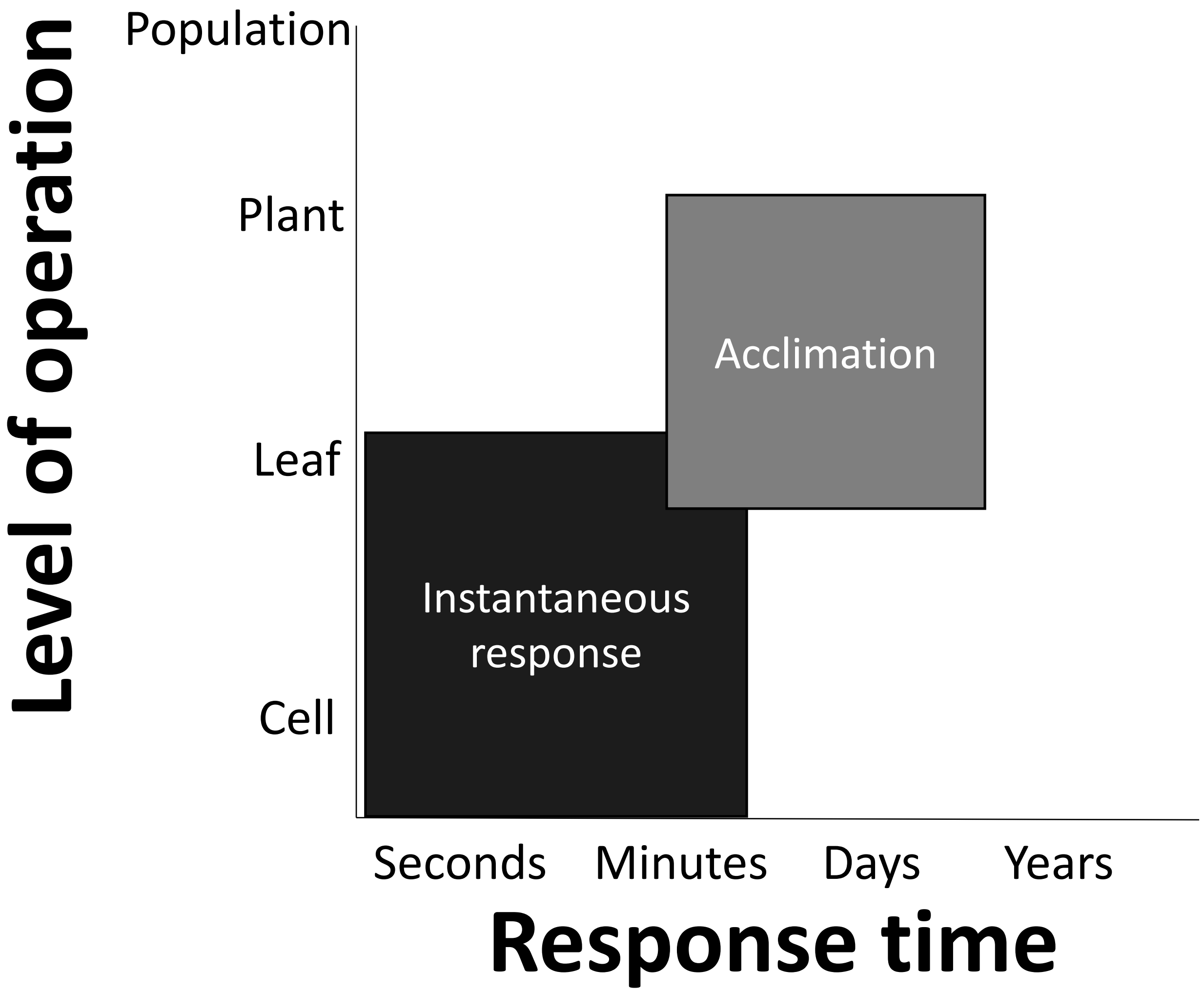
Plants acclimate to environmental conditions



Smith and Dukes (2013)

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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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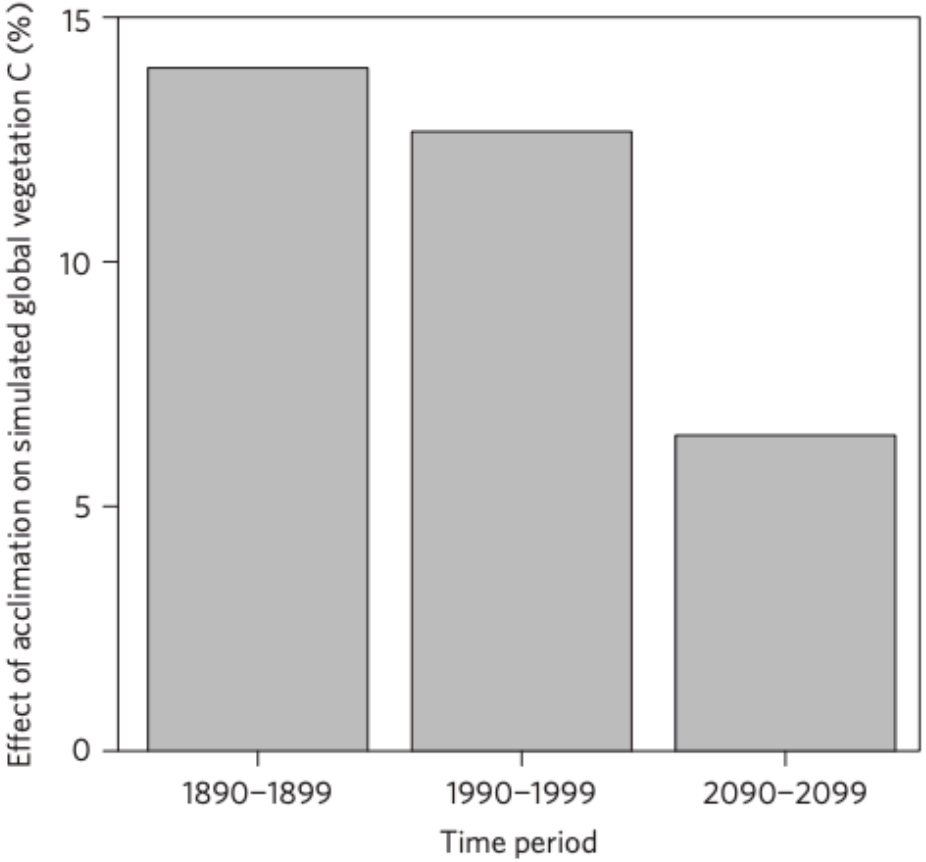
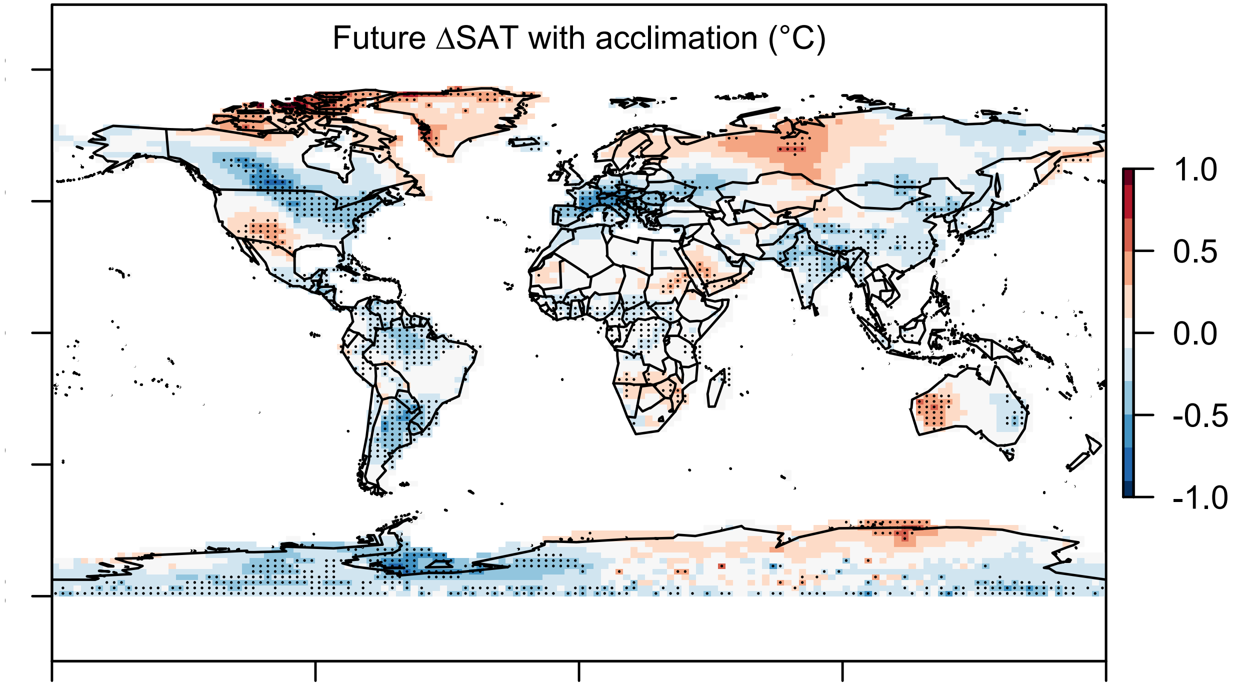
…and can possibly impact carbon cycling and climate

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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Lack of theory results in…

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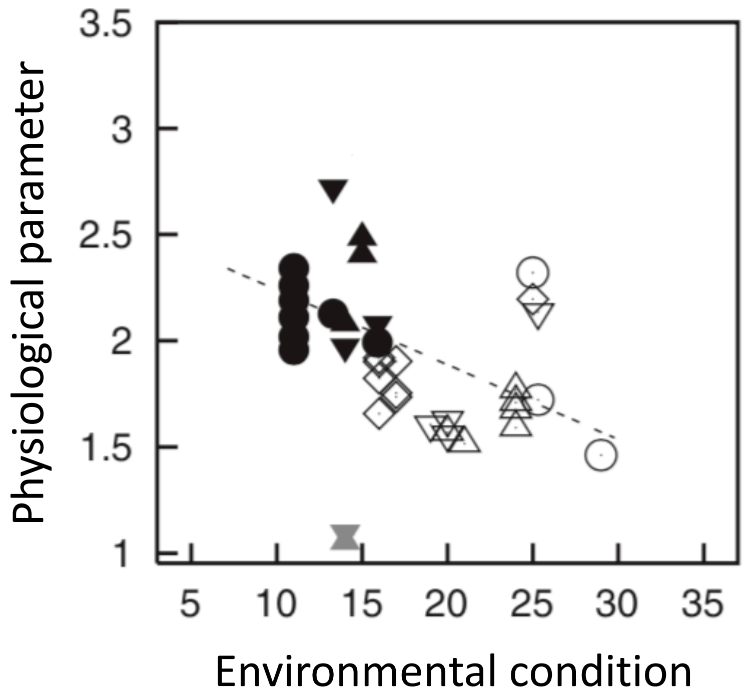
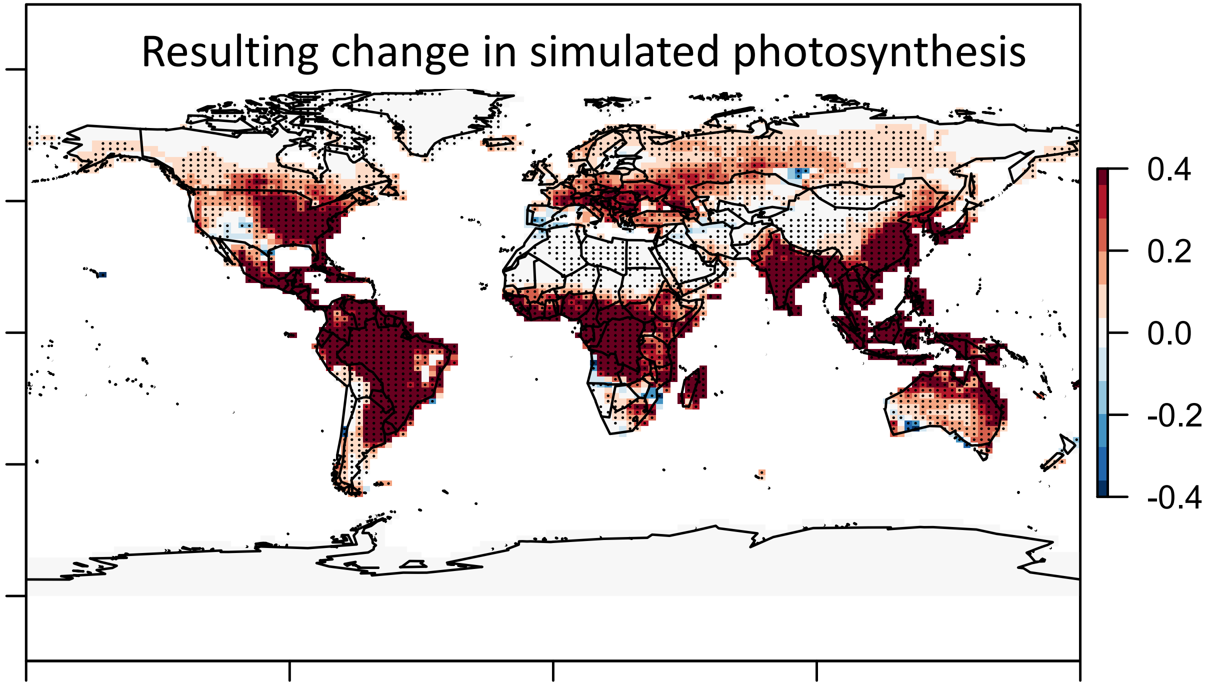
Lack of theory results in…

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





Kattge and Knorr (2007) *PC&E*

Smith et al. (2017) *JAMES*

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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}

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)

Optimal photosynthesis

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

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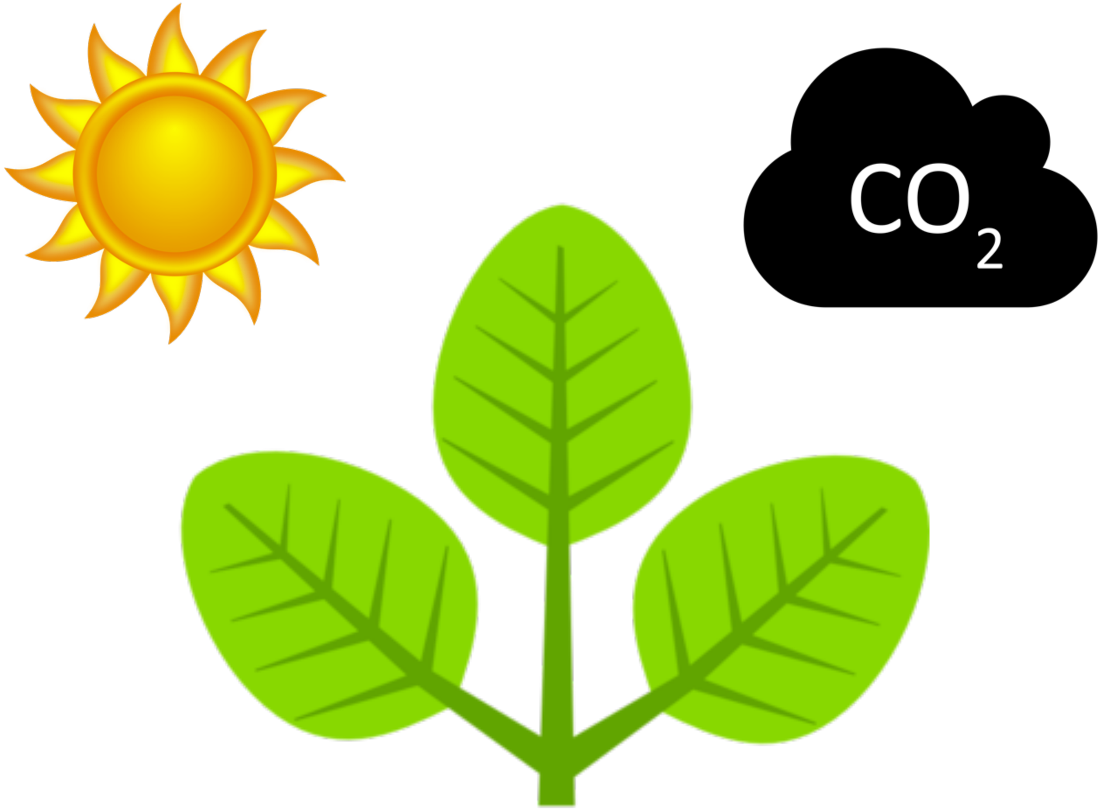
Biochemistry optimization: Coordination hypothesis



Optimal setup = equal limitation by all factors

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

$$A_j = A_c$$

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

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

Smith et al. (2019)

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

Smith et al. (2019)

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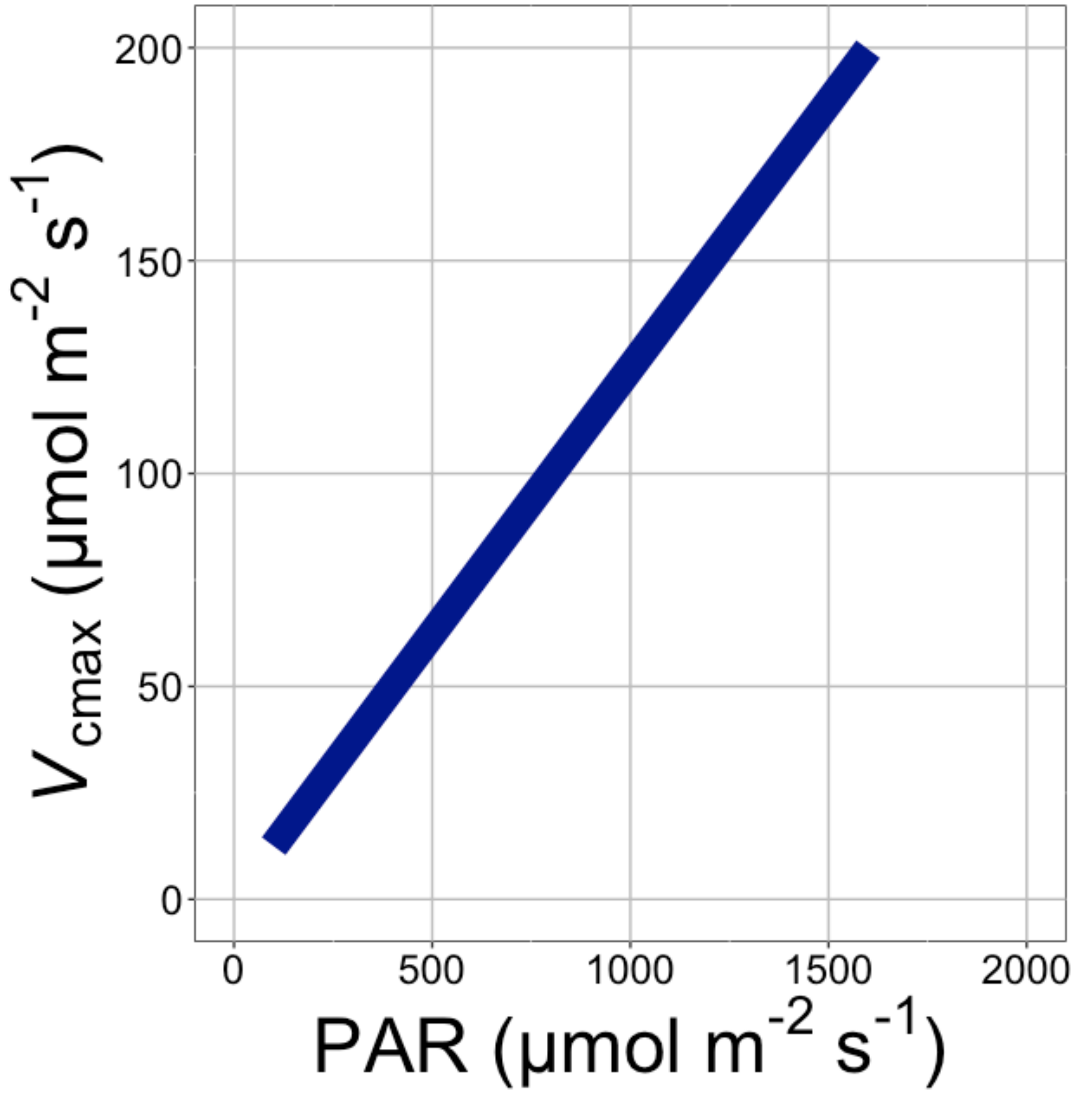

V_{cmax} increases with light because of greater electron transport

Smith et al. (2019)

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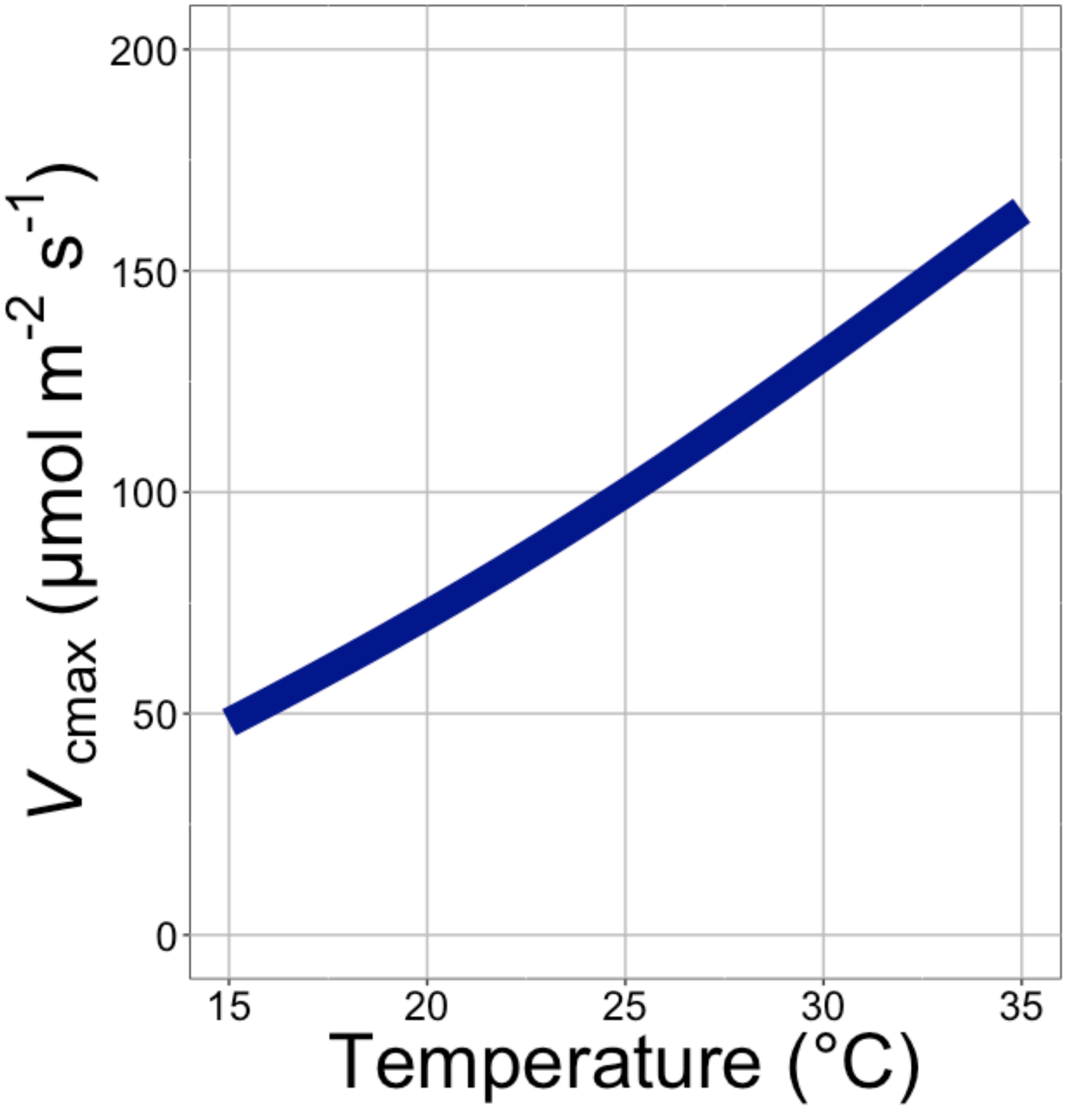

V_{cmax} increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019)

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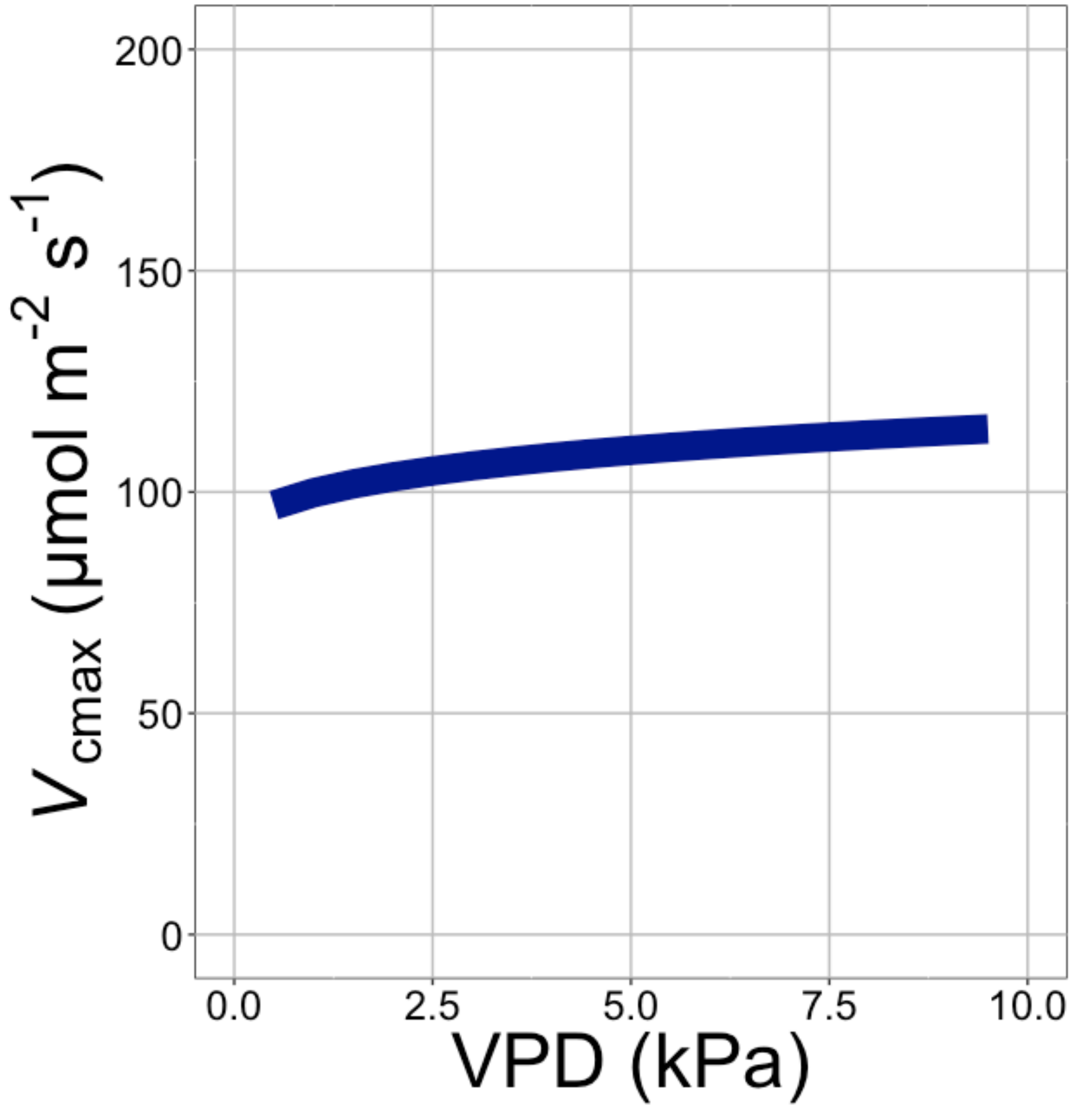

V_{cmax} increases with VPD because of lower stomatal conductance

Smith et al. (2019)

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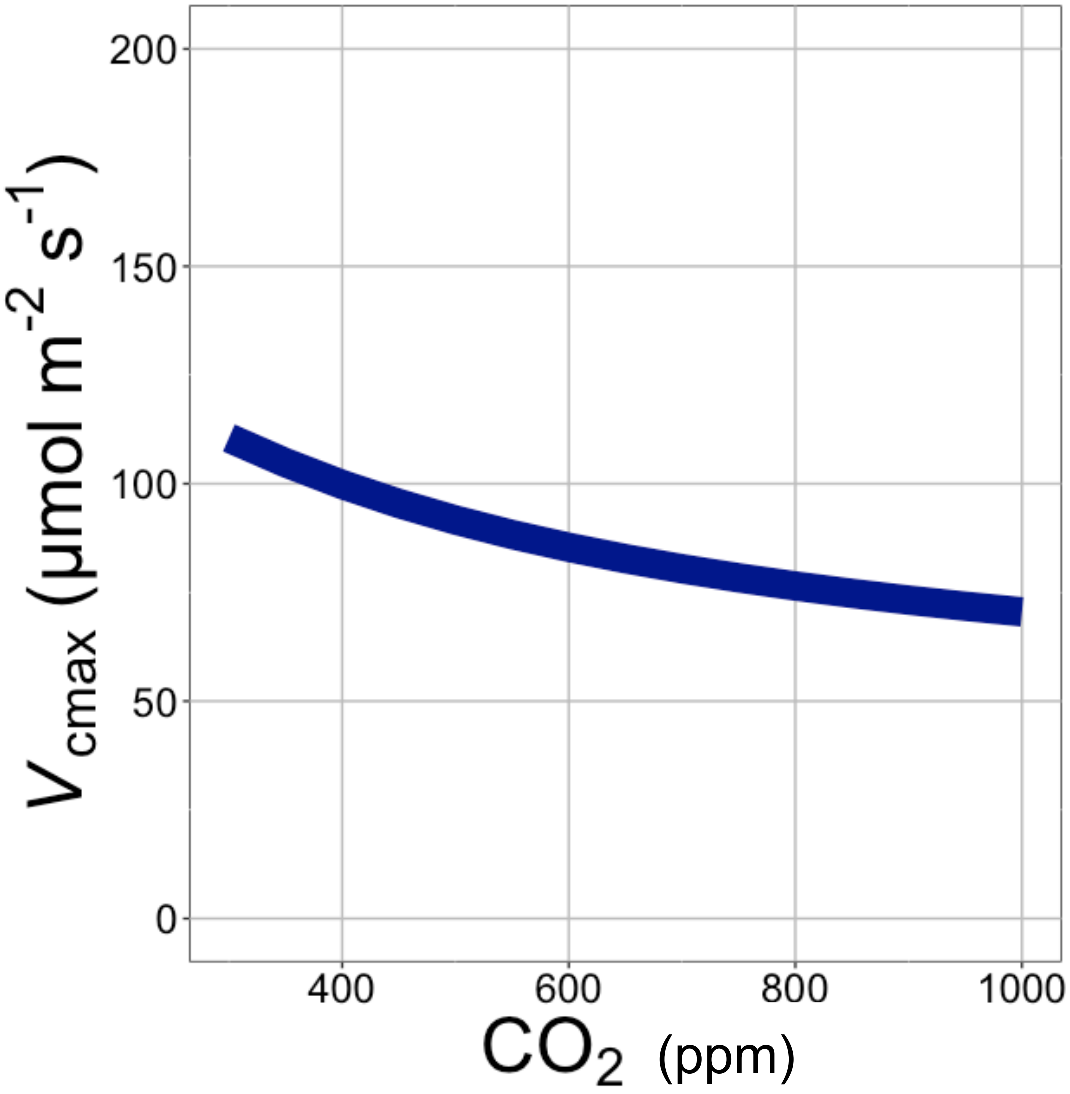

V_{cmax} decreases with CO_2 because of greater CO_2 in the leaf

Smith et al. (2019)

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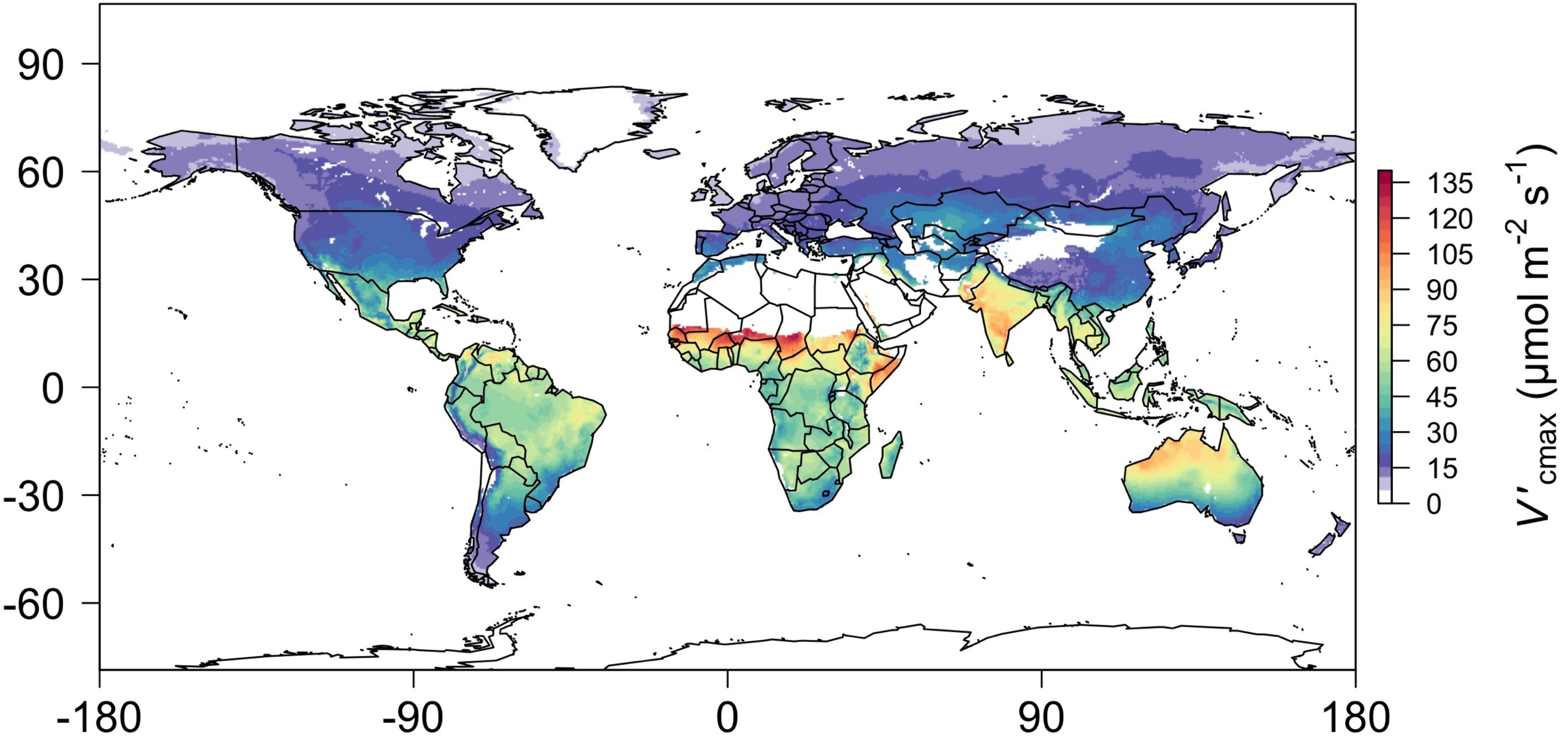
Global, optimally acclimated traits!



Smith et al. (2019)

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Important note: optimality model adds no free parameters to Farquhar model 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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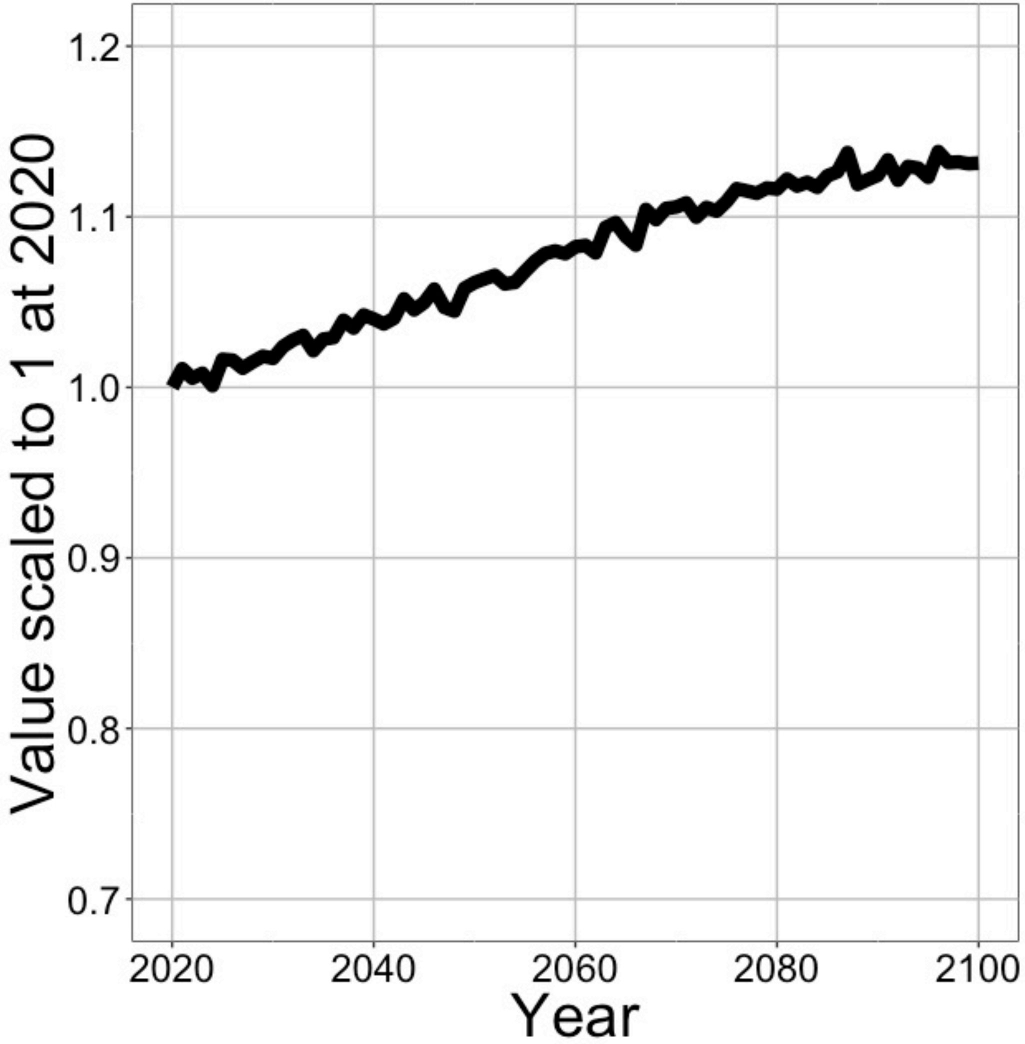
Photosynthesis increases in future



Net Photosynthesis

Smith et al. (in prep)

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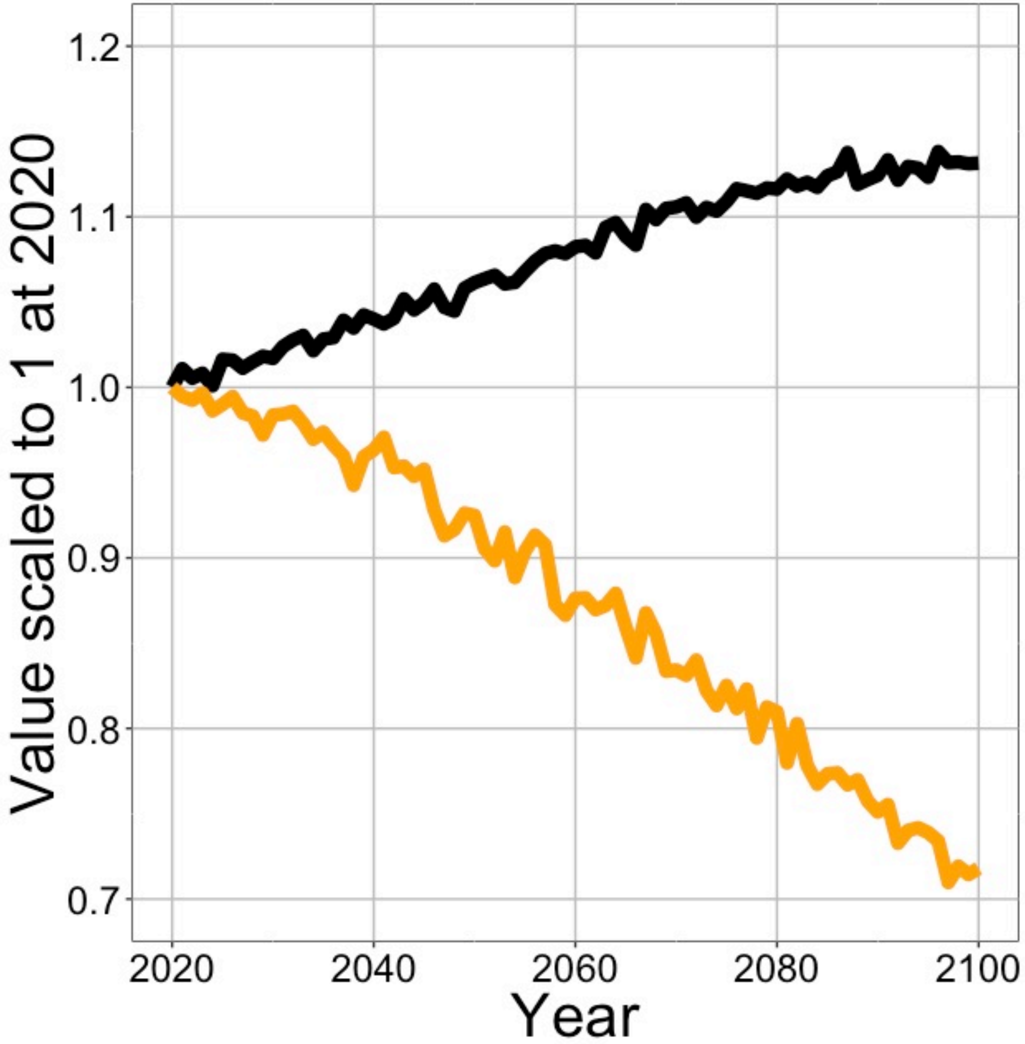
Photosynthesis increases in future
(at lower nutrient use)



Net Photosynthesis

Leaf Nitrogen

Smith et al. (in prep)

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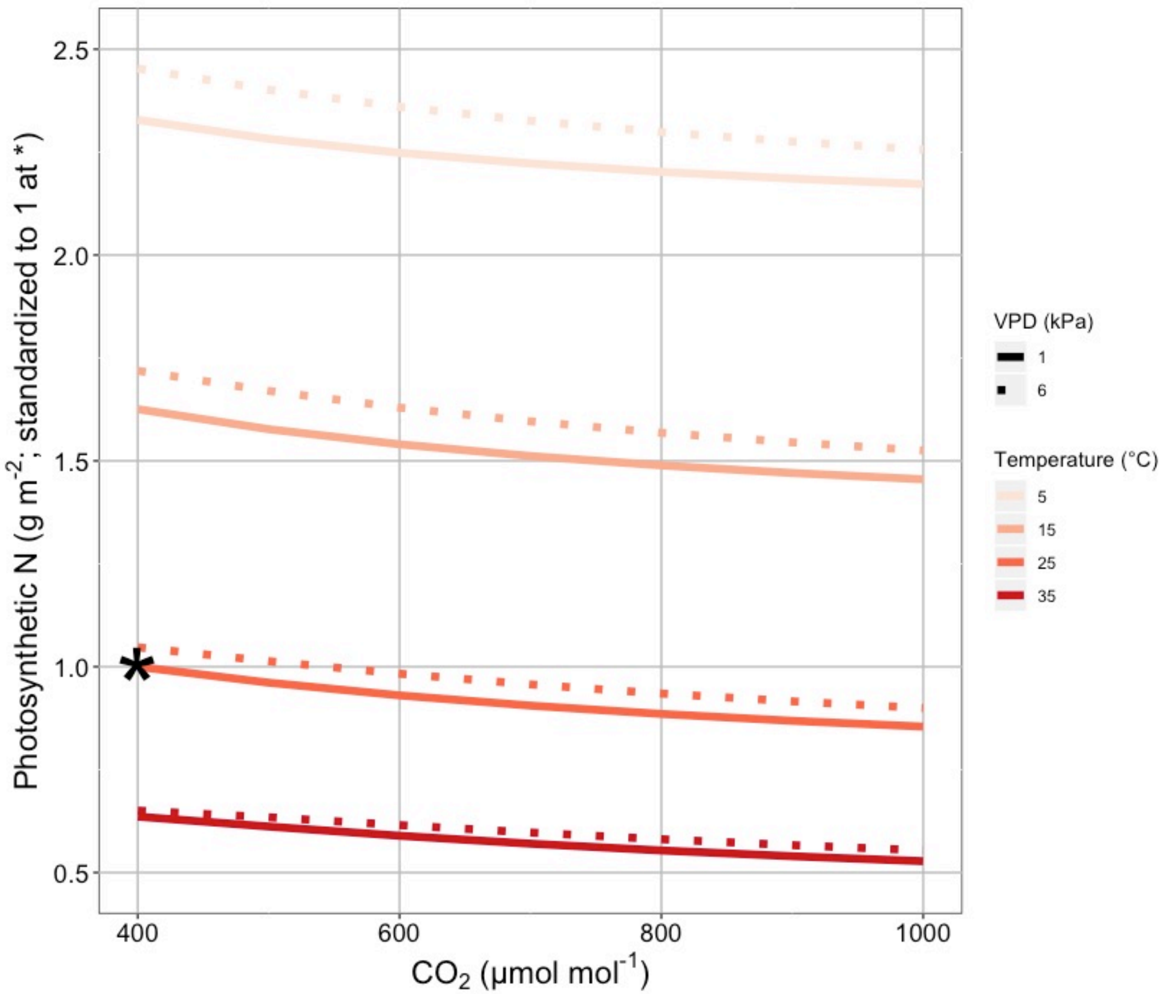
Leaf N declines due to warming and eCO_2



Smith & Keenan (in review)

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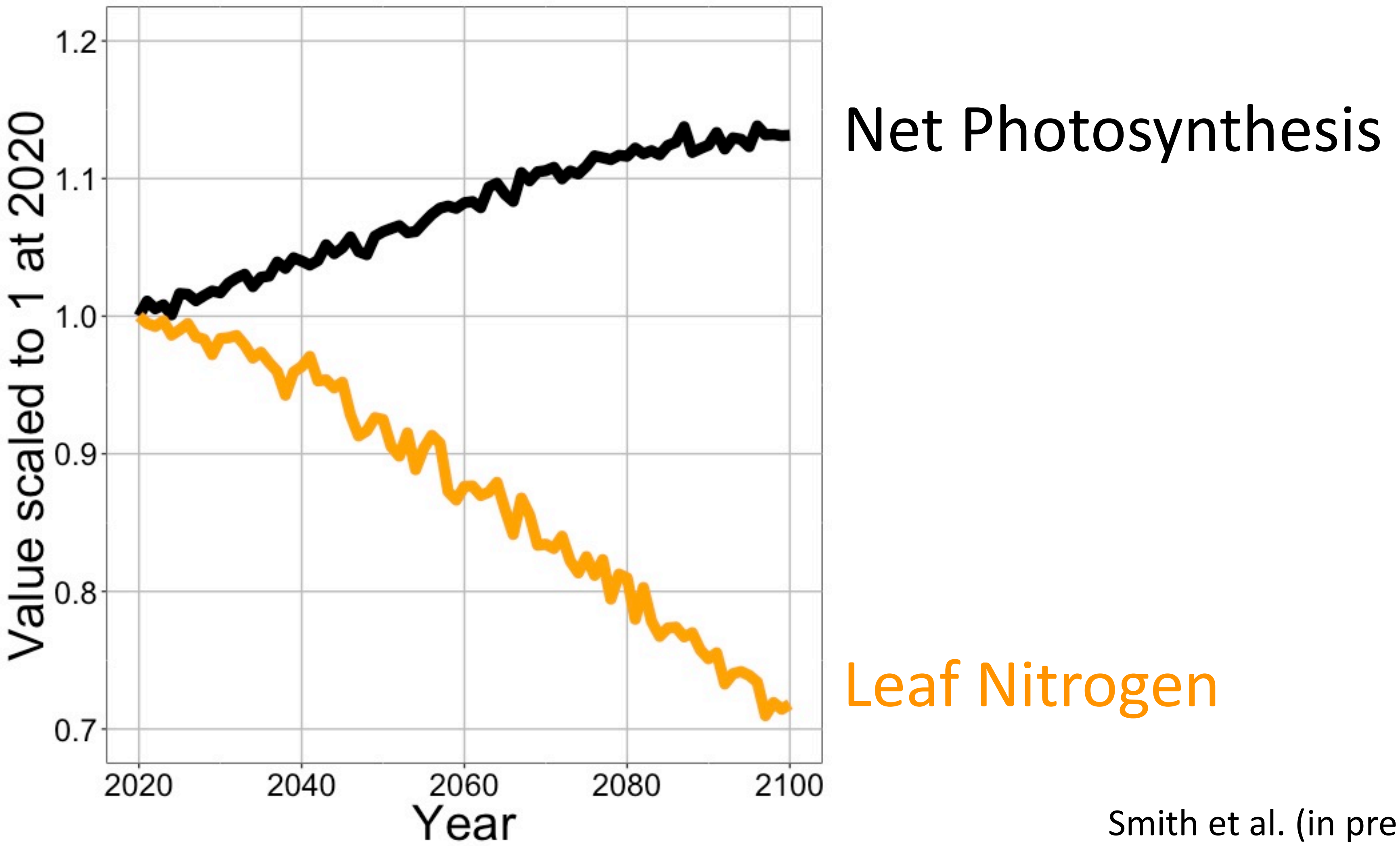

Smith et al. (in prep)

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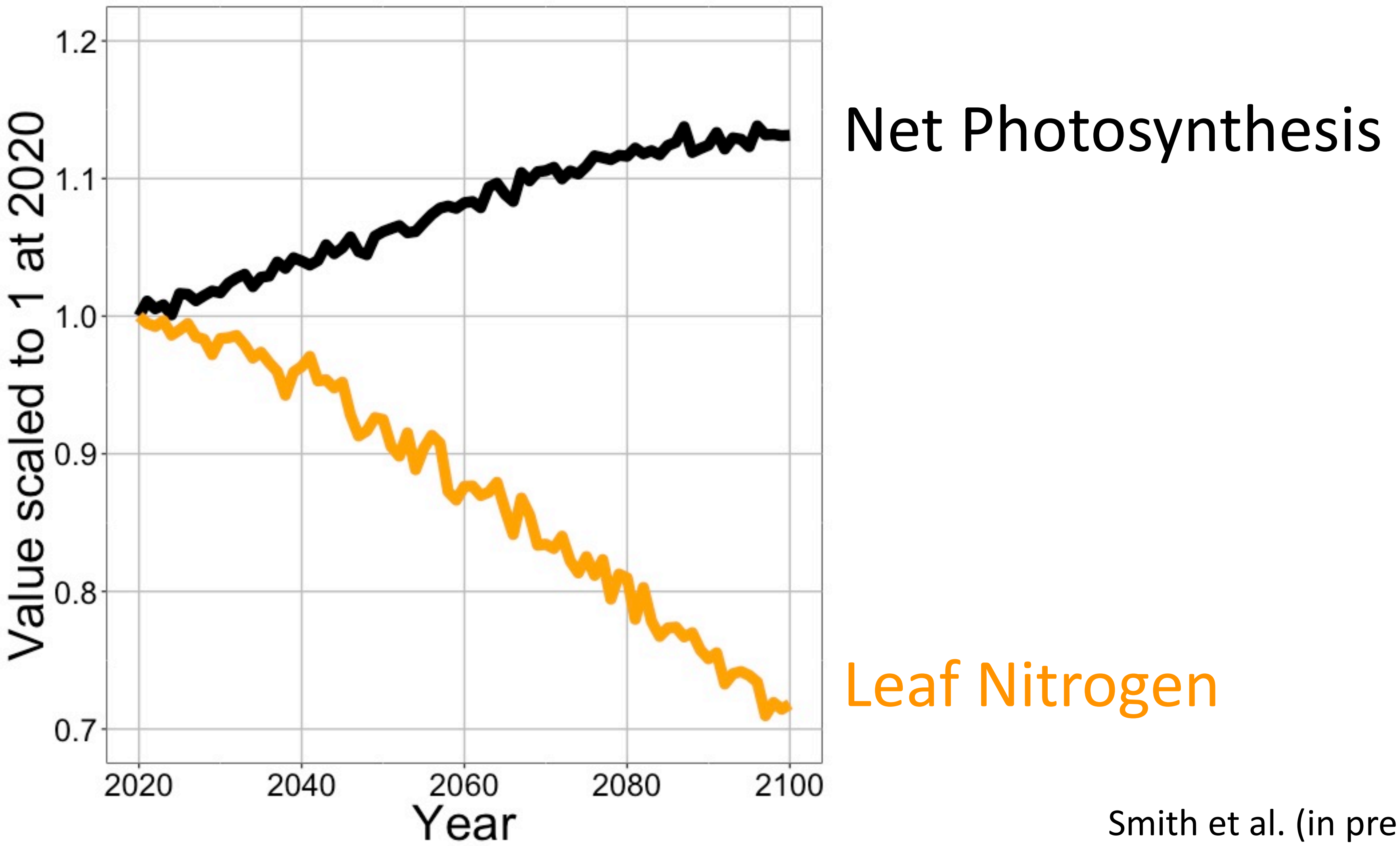
Photosynthesis increases in future
(at lower nutrient use)

Base ELM shows <5% change in leaf N



Smith et al. (in prep)

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

$\downarrow$

Photosynthesis

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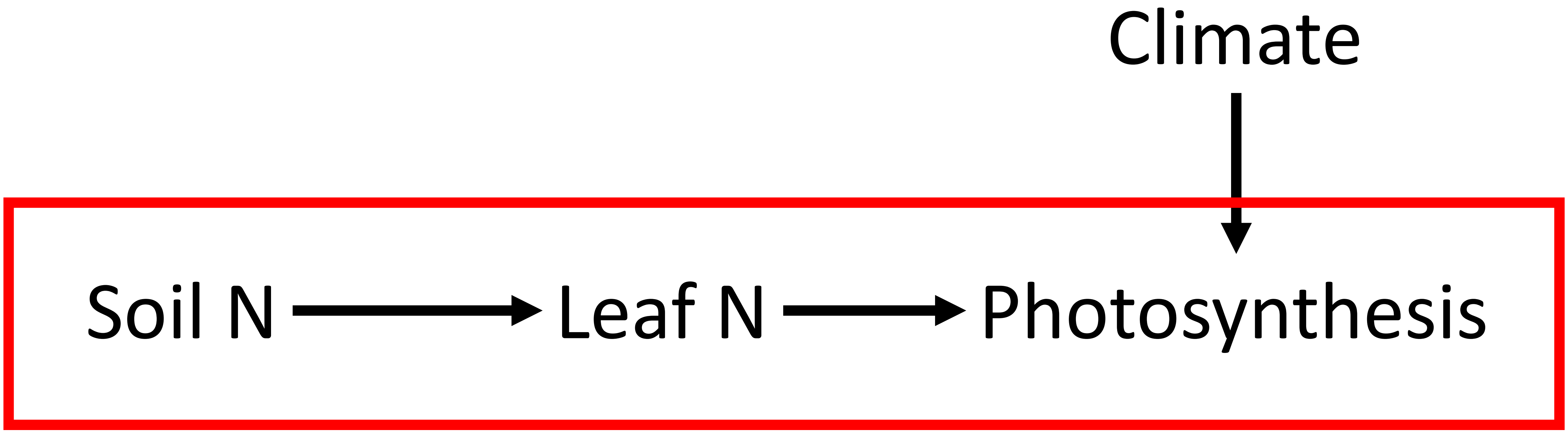
Let’s check this assumption



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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

Smith et al. (in prep)

nutrient network

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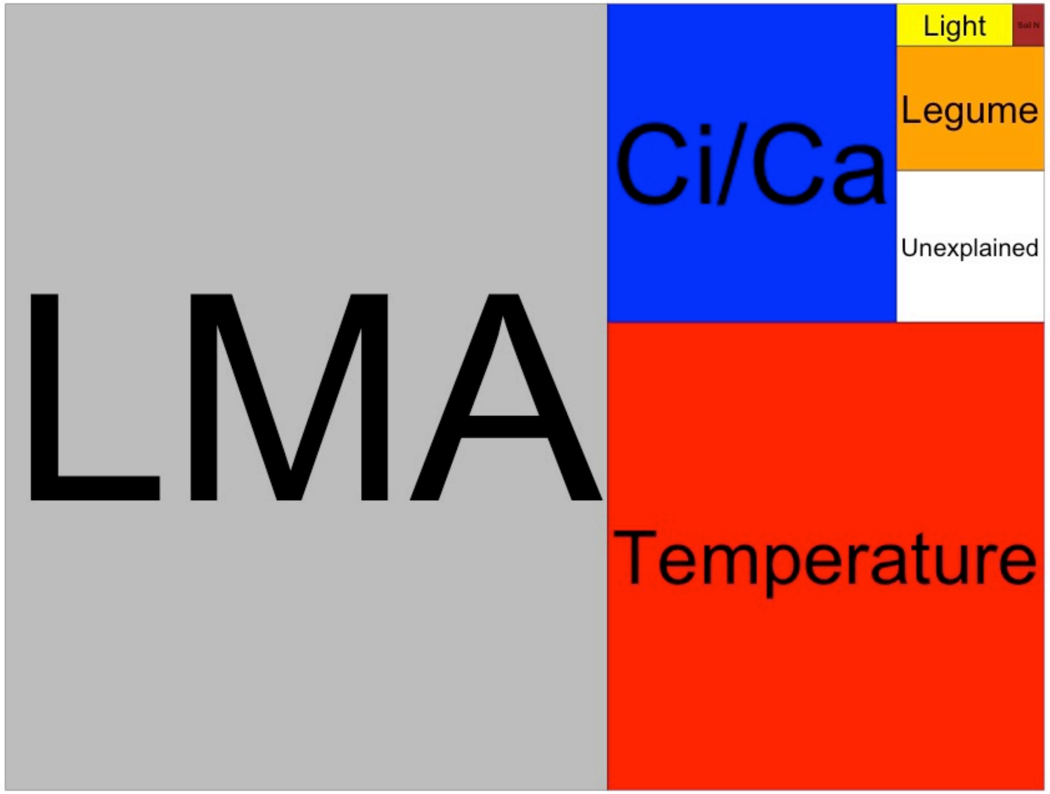
Globally, N addition little impact on leaf N



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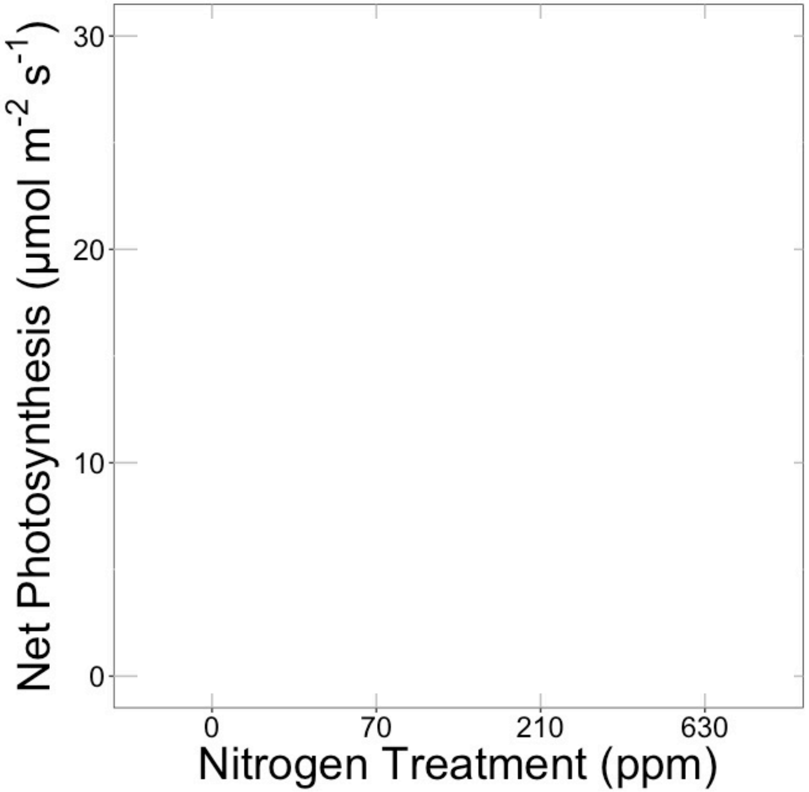

Waring and Smith (in prep)

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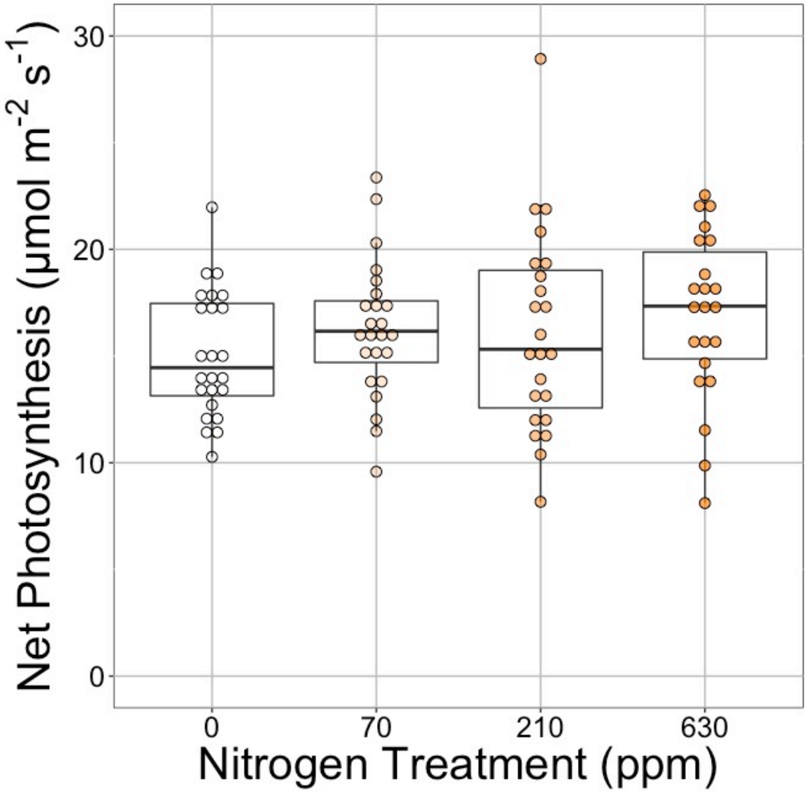
Photosynthesis does not change with soil N

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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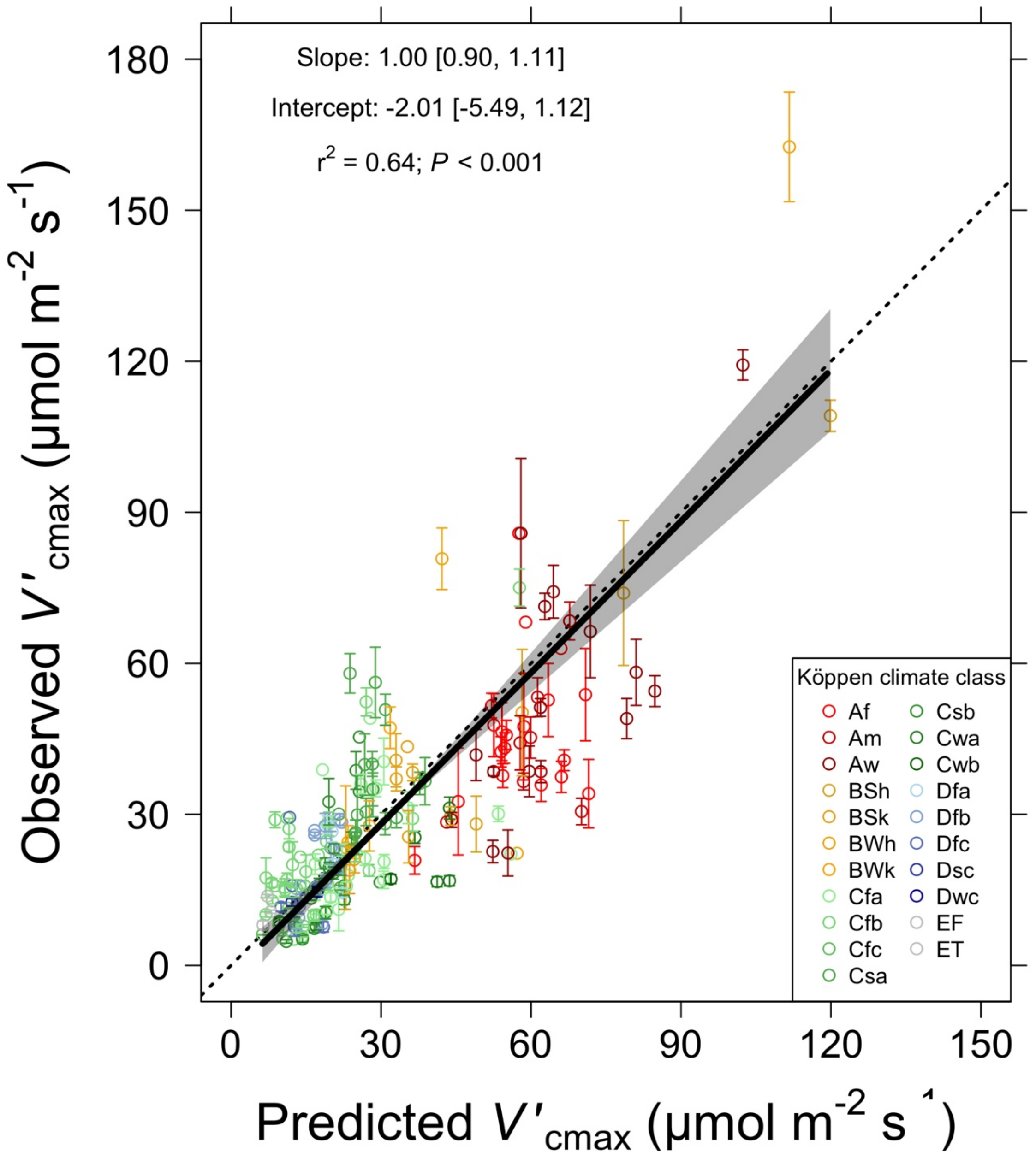

Optimal V_{cmax} is similar to observed values

Smith et al. (2019)

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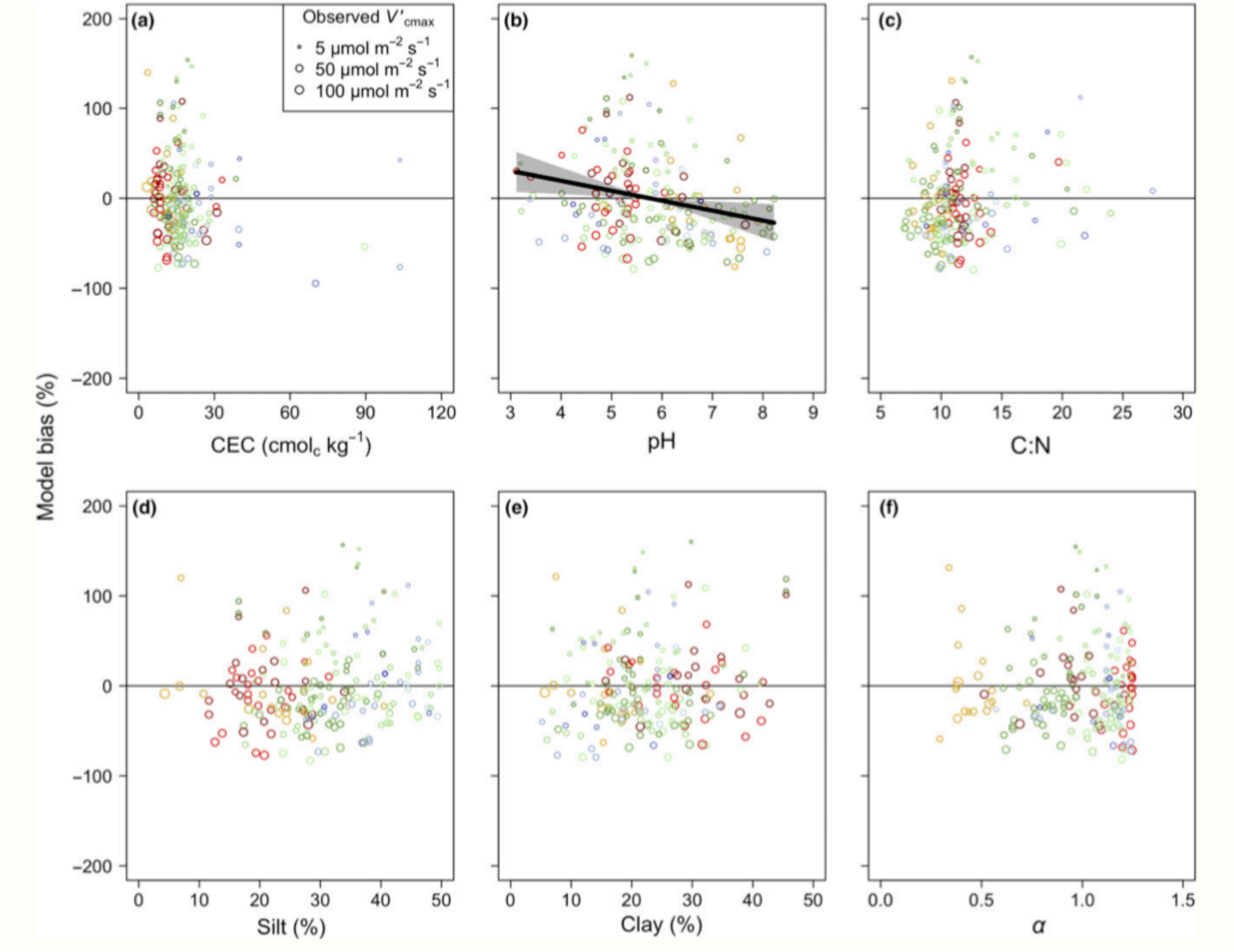
There is little effect of soils on V_{cmax}



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

Smith et al. (2019)

Does it work under future conditions?

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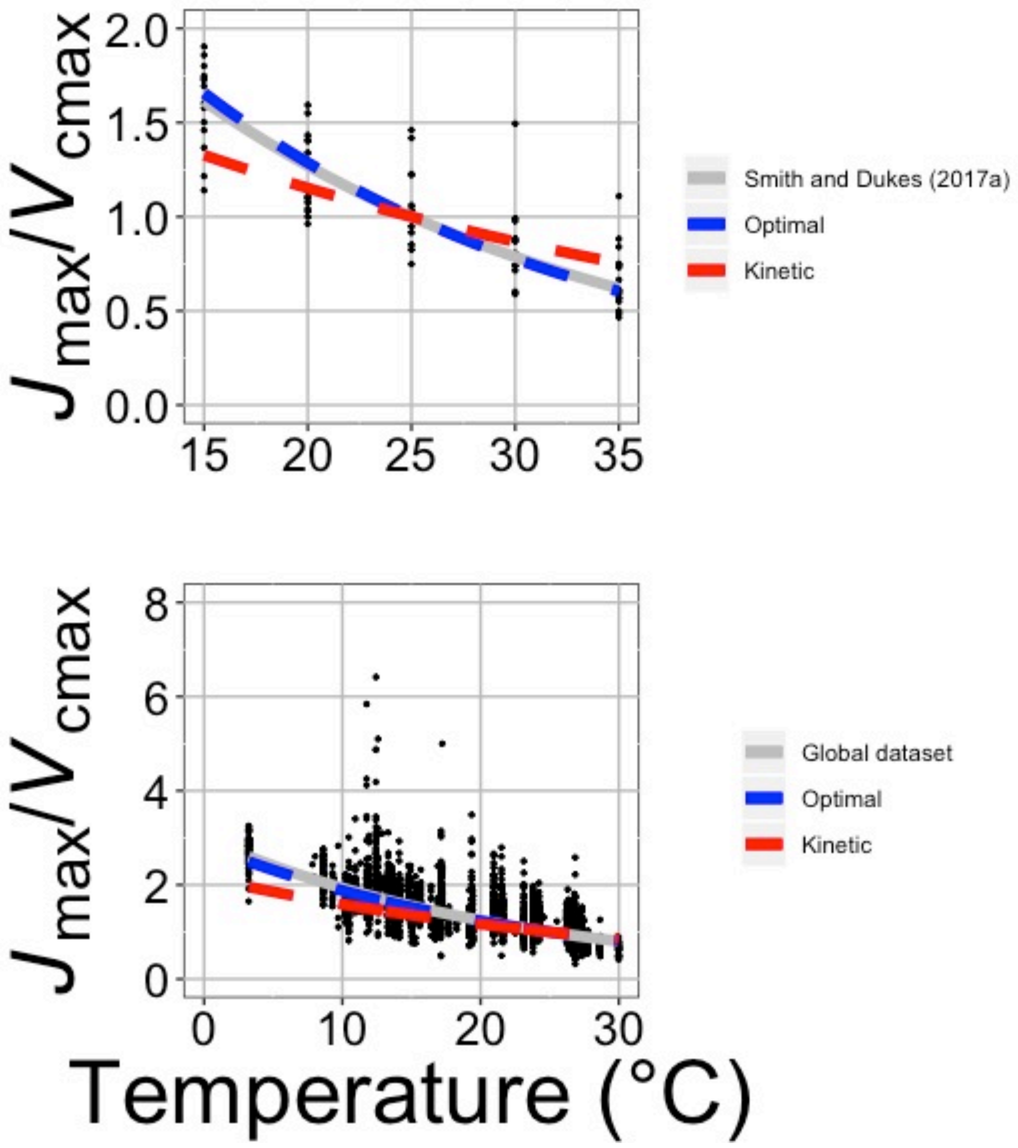

Photosynthetic traits change with temperature in ways expected from optimization

Data = -0.051 °C^{-1}

Predicted = -0.048 °C^{-1}

Smith and Keenan (in review)

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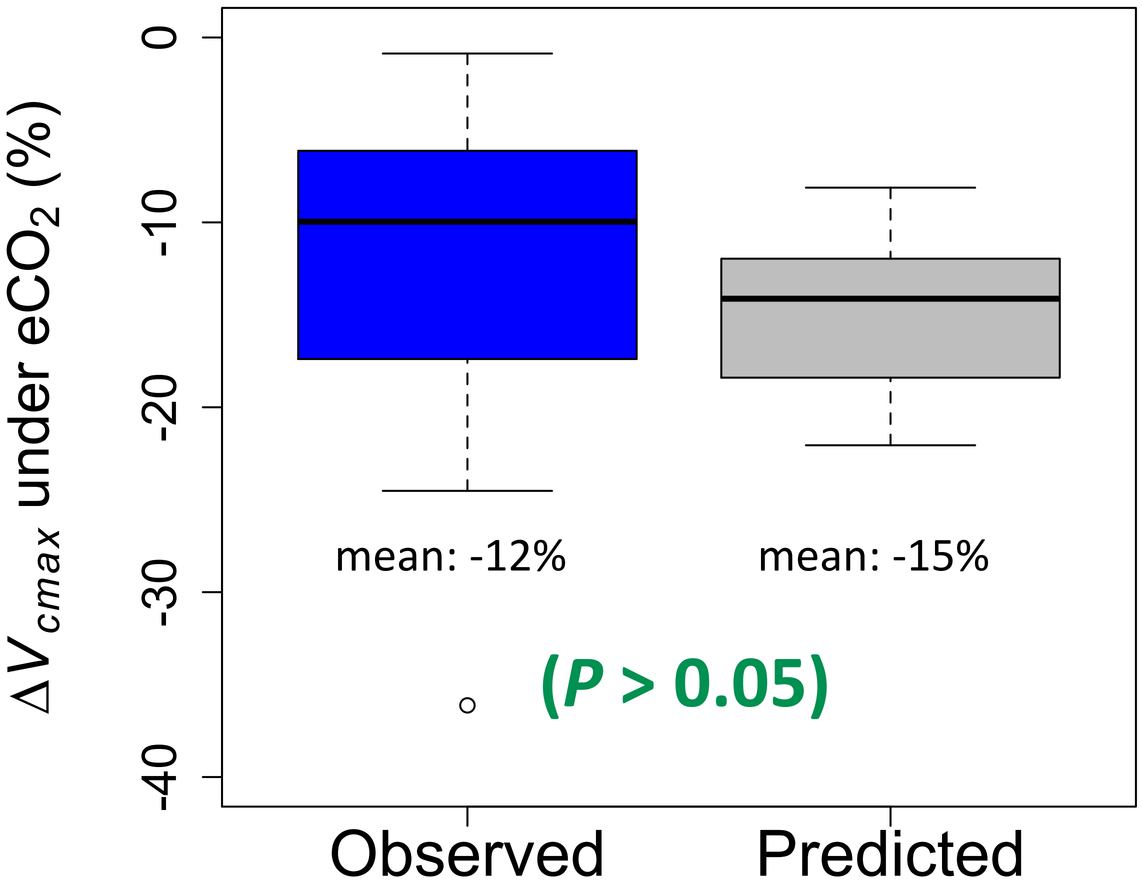
Photosynthetic traits change with future conditions in ways expected from optimization



Smith and Keenan (in review)

Implications

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- Optimal leaf biochemical setup is determined by climate

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- Plants mine for N to get the most leaves at the optimal setup

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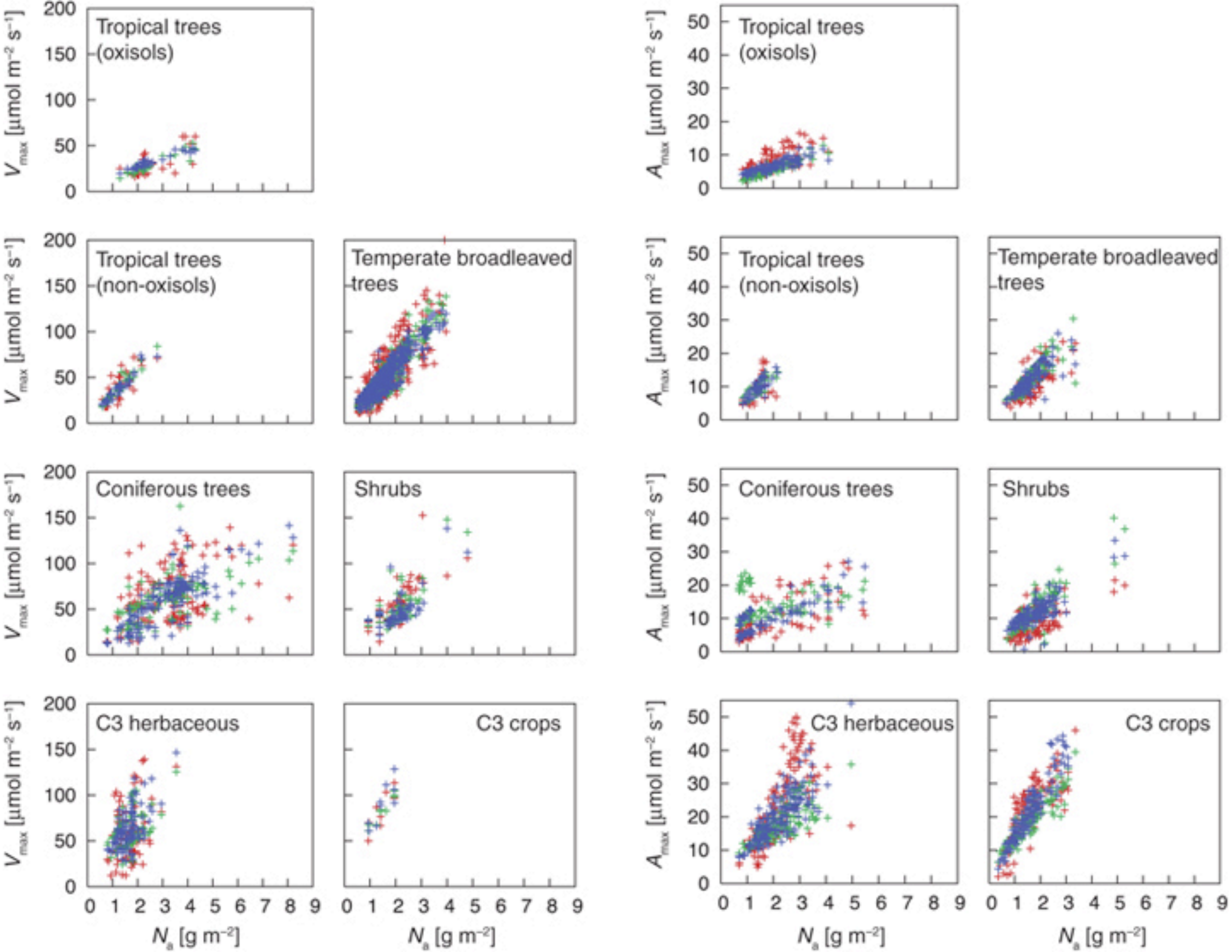
- Optimal leaf biochemical setup is determined by climate
- Plants mine for N to get the most leaves at the optimal setup
- Photosynthetic demand determines leaf N, not the other way around



Axes need flipped

Kattge et al. (2009)

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 # of leaves (before canopy closure)

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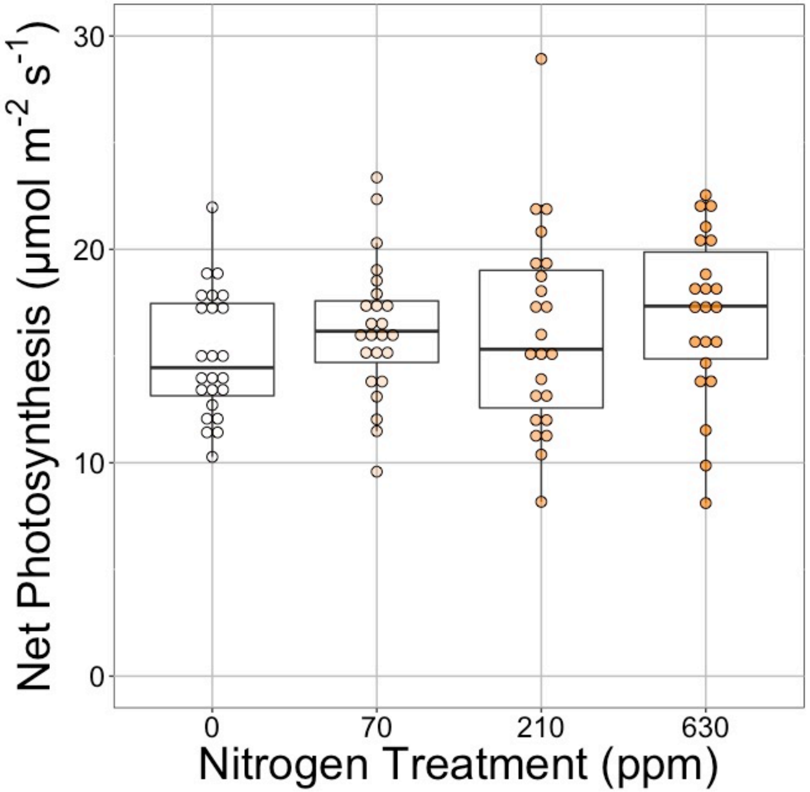
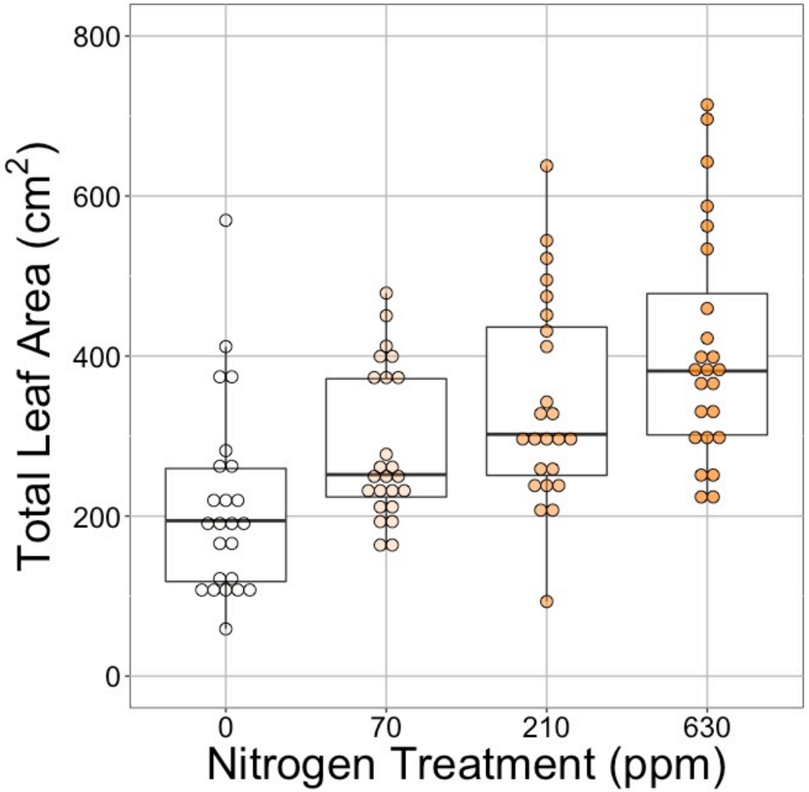
Soil N determines # of leaves?

No change (P = 0.42)



91% increase (P < 0.05)



Waring and Smith (in prep)

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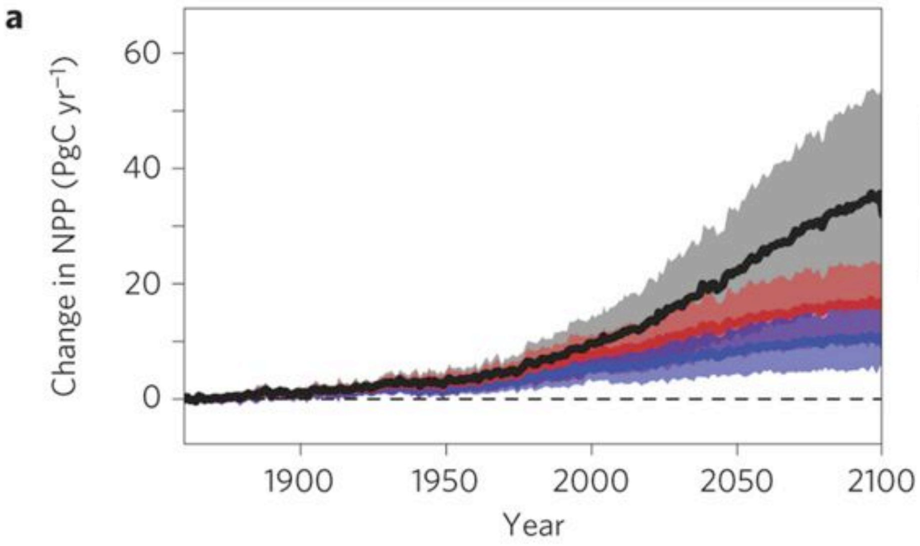
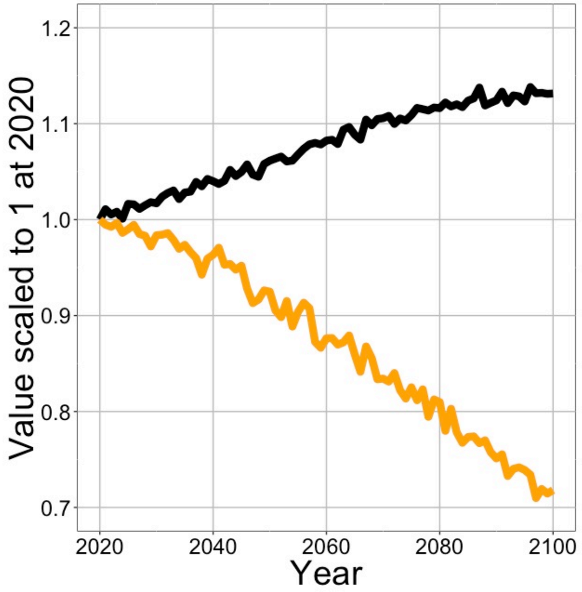
Next steps: How might this effect simulated nutrient limitation?



"No limitation" simulation

"Nutrient limitation" simulations



Net Photosynthesis

Leaf Nitrogen

Weider et al. (2015)

Smith et al. (in prep)

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Presentation available at:
www.github.com/SmithEcophysLab/seminar/lmwg_2020

Extra slides

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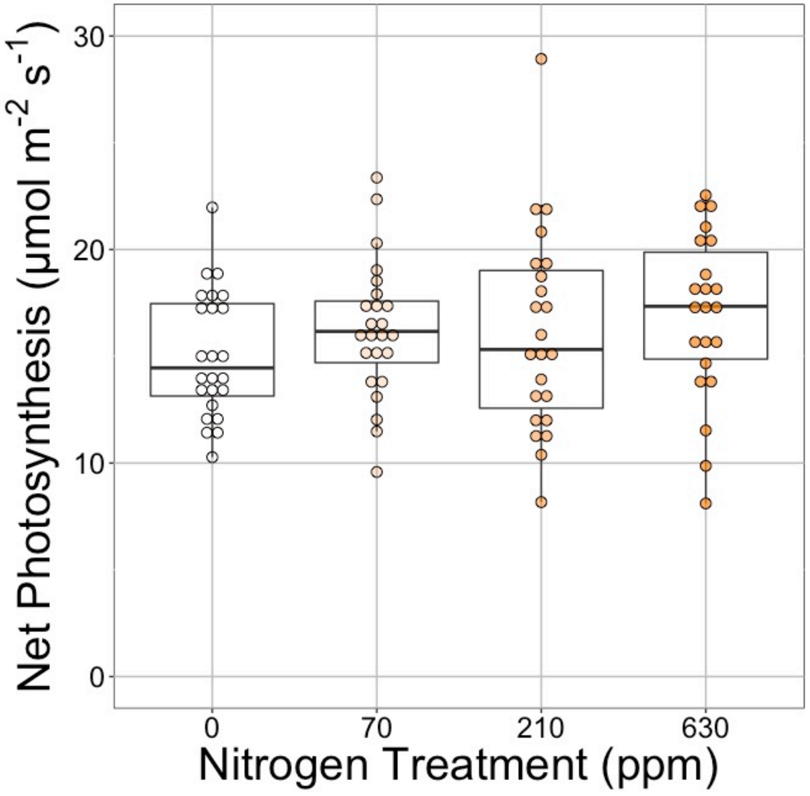
Leaf area, but not photosynthesis increases with N addition

No change (P = 0.42)



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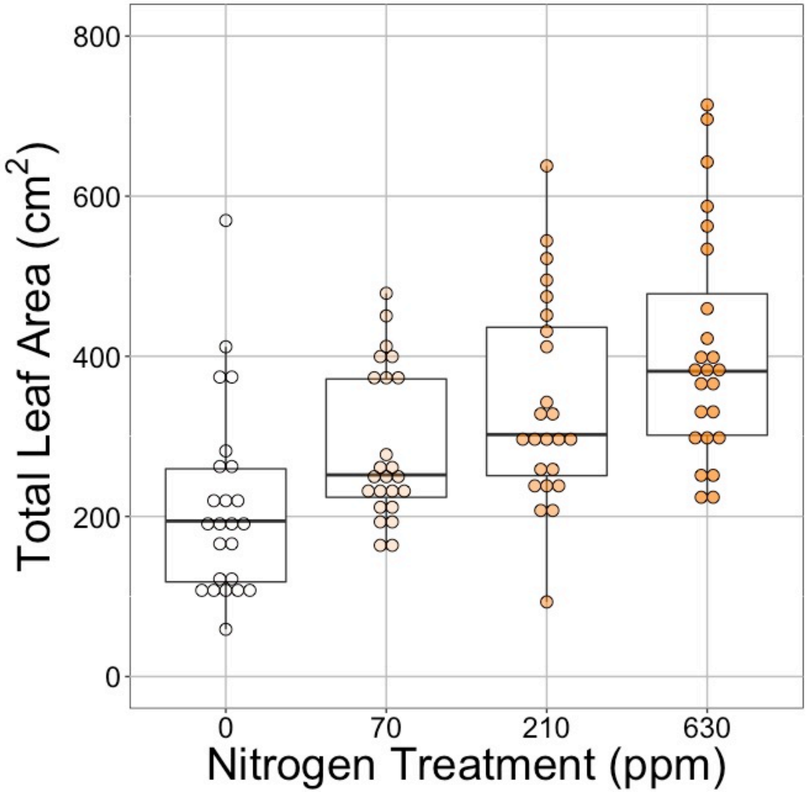

Waring and Smith (in prep)

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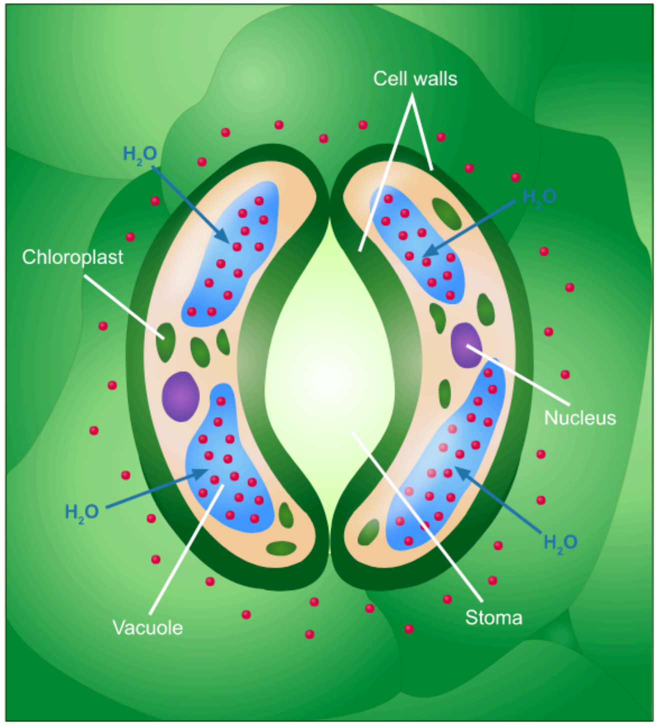

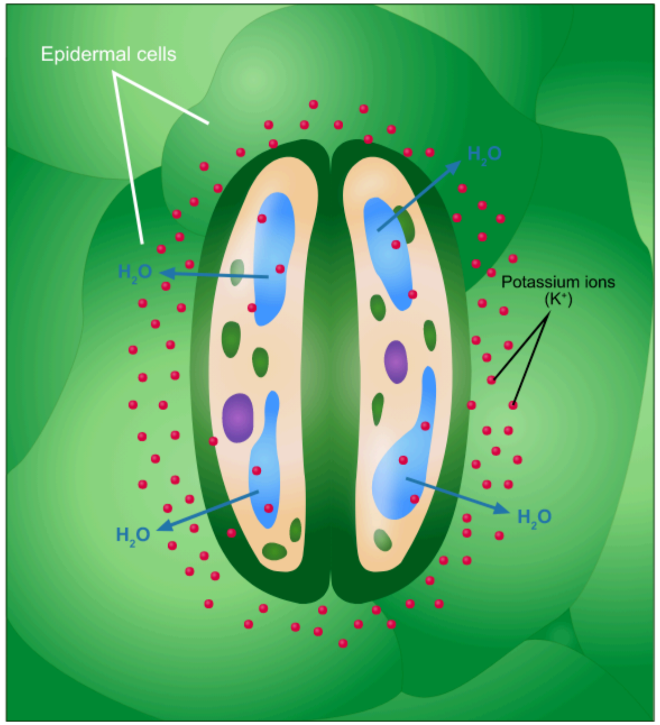

Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux

Closed stomata:

Benefits

- Low water outflux

Costs

- Low CO_2 influx

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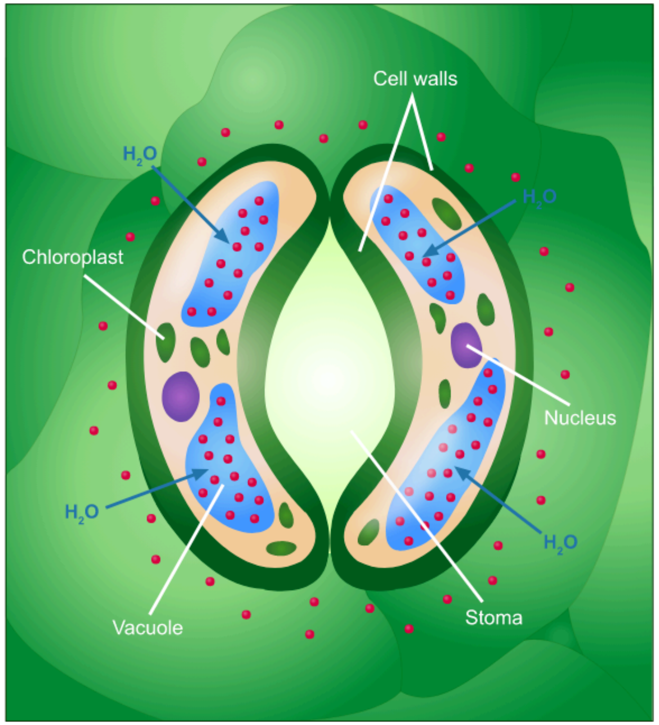

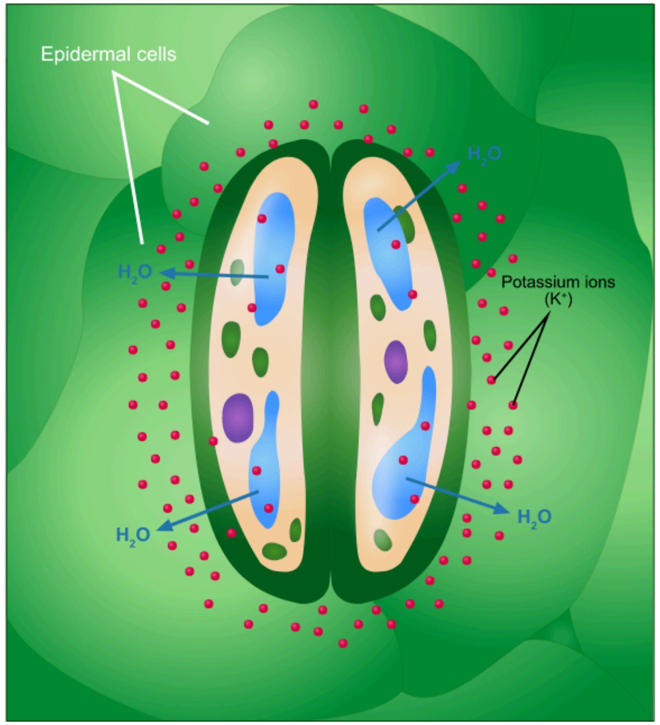

Open stomata:

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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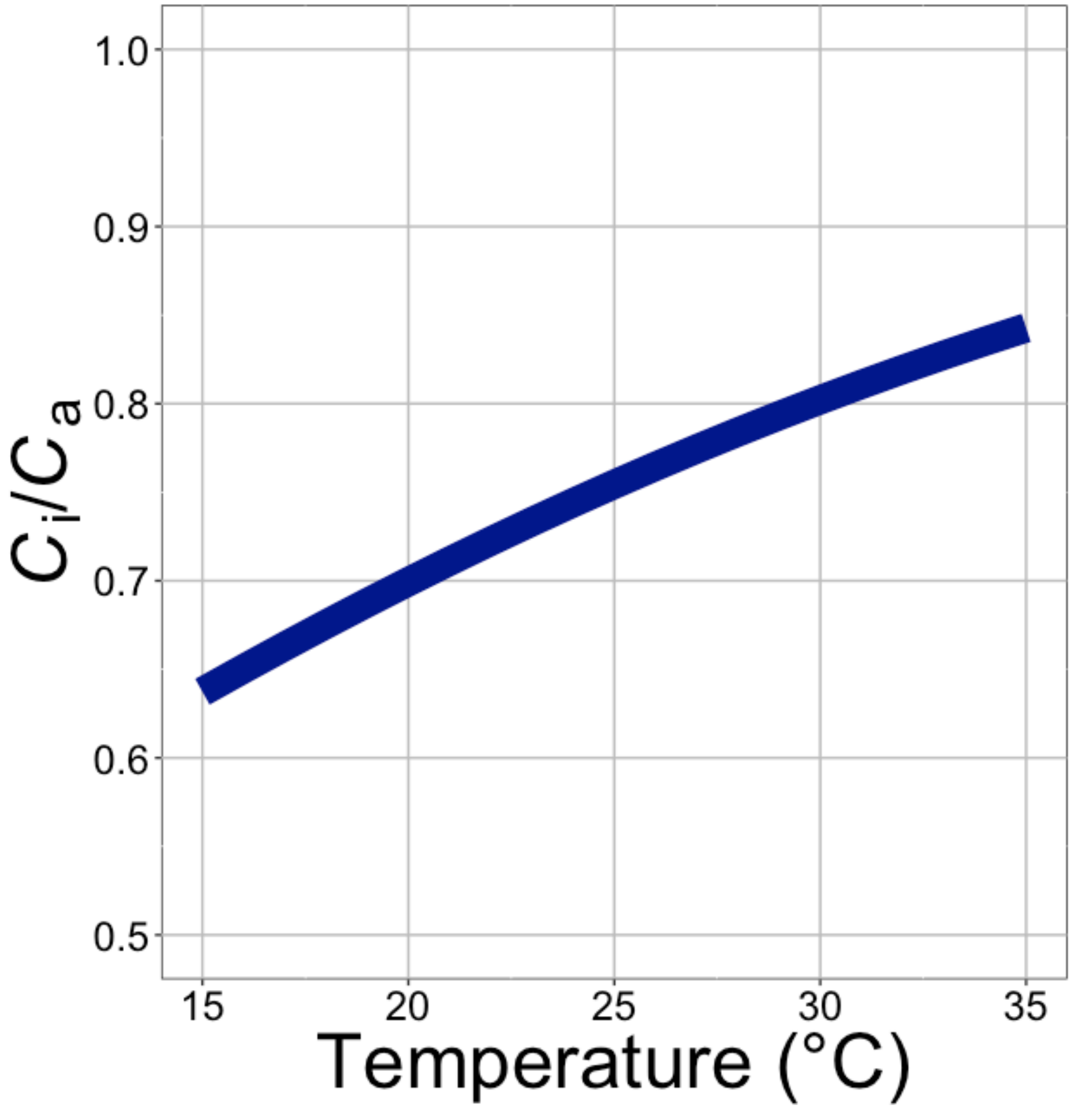

C_i/C_a increases with temperature because of greater photorespiration

Smith et al. (2019)

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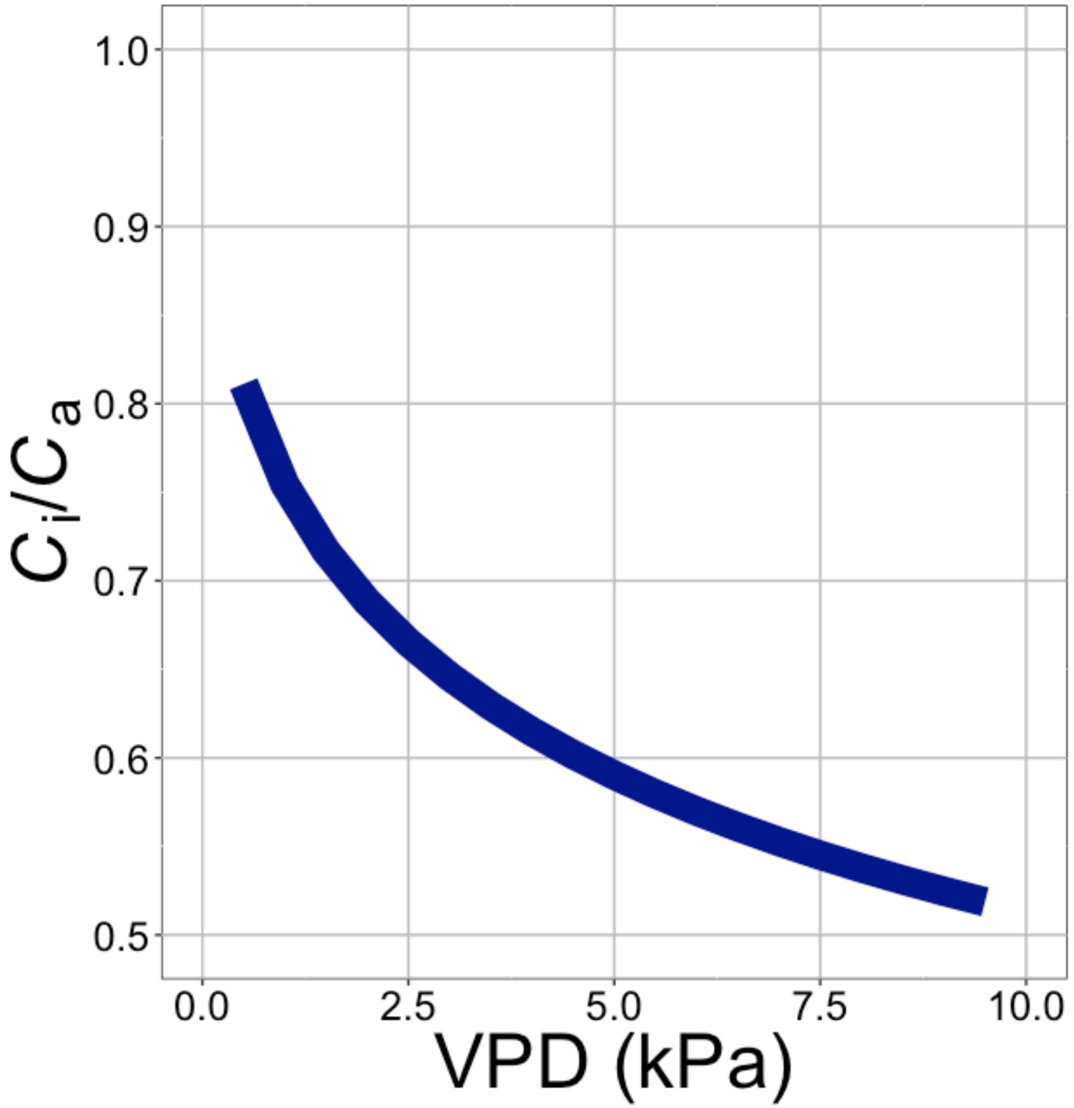

C_i/C_a decreases with VPD because of greater water loss

Smith et al. (2019)

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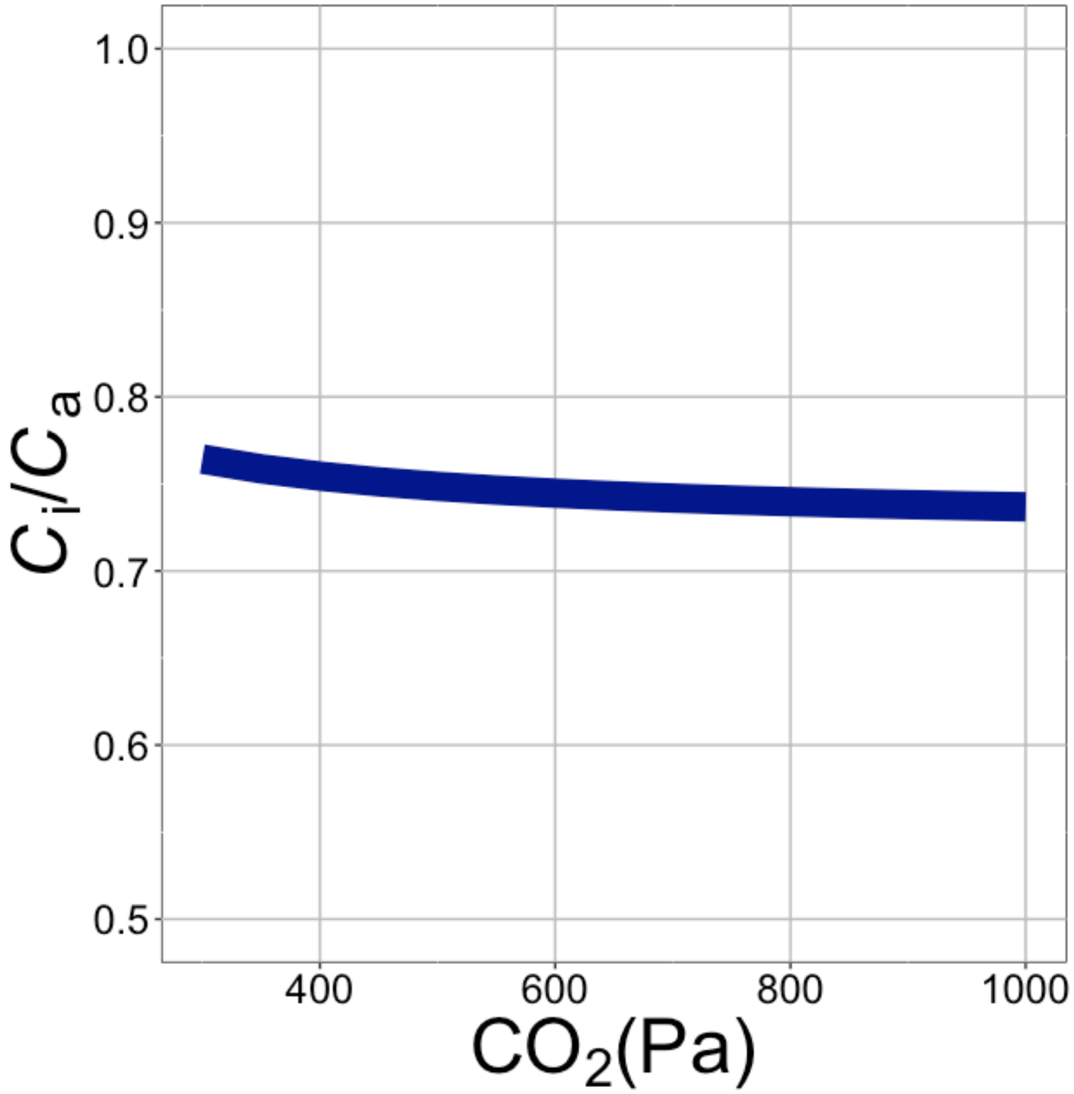

C_i/C_a decreases with CO_2 because of lower openness needed to satisfy Rubisco

Smith et al. (2019)

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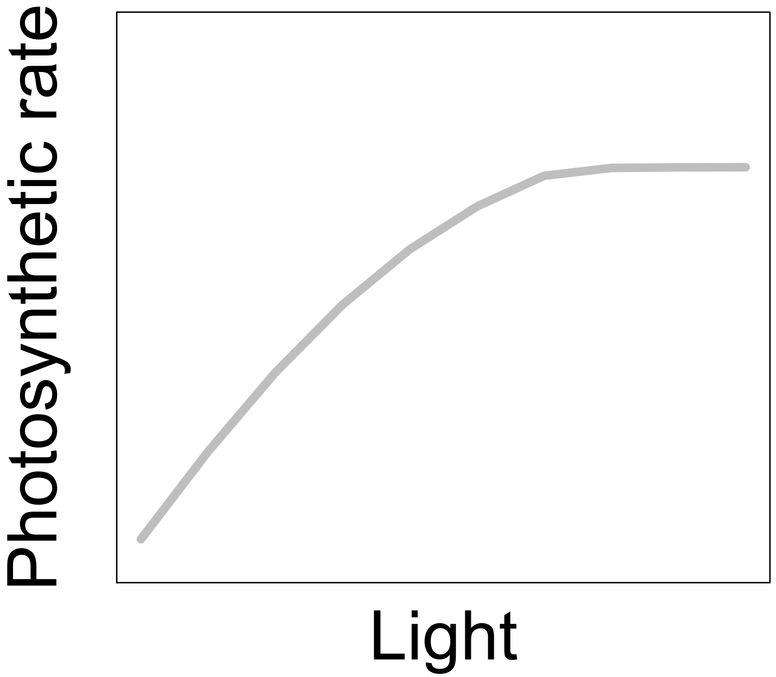
Photosynthetic acclimation can be seen as the change in the instantaneous responses with longer-term exposure

Acclimated to high light



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