# Using least cost optimality to reliably simulate photosynthetic acclimation

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# Acknowledgements


- Lawrence Berkeley National Lab
  - Bill Riley
  - Qing Zhu
- Smith Ecophysiology Lab
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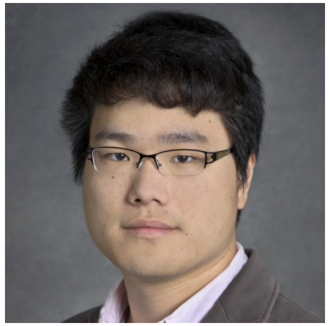
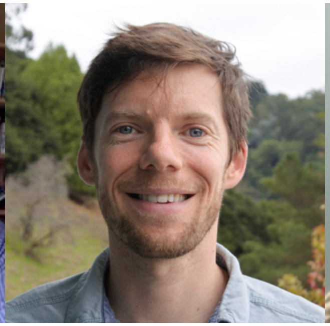
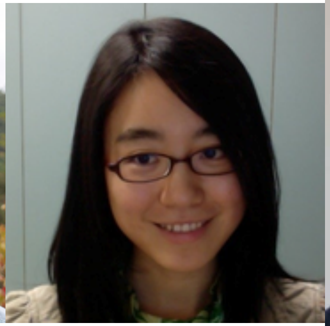
- Next Generation Ecosystem Modeling Group
  - Colin Prentice (Imperial College)
  - Trevor Keenan (UC Berkeley)
  - Wang Han (Tsinghua U)
  - Beni Stocker (ETH Zurich)

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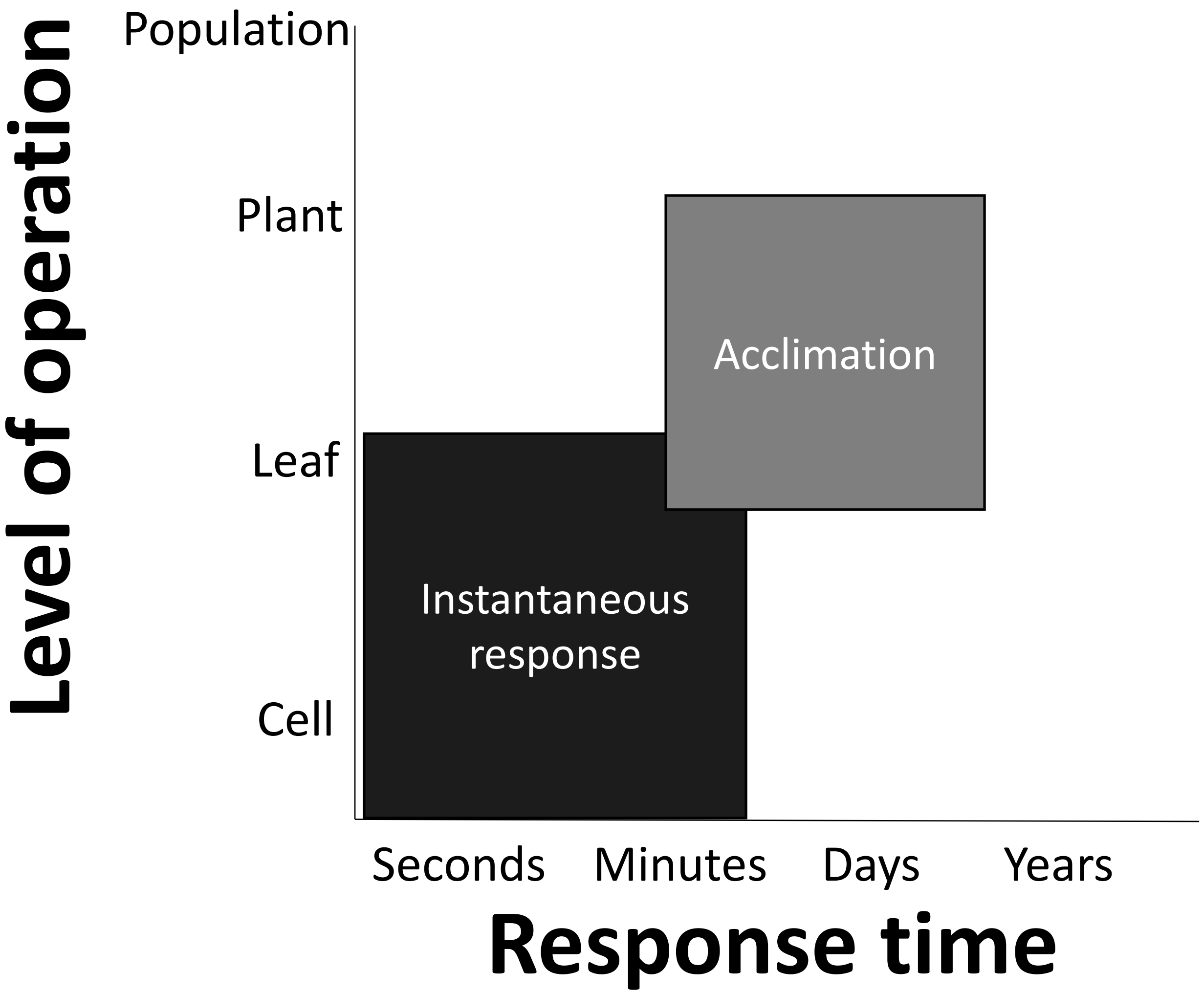
# Plants acclimate to environmental conditions




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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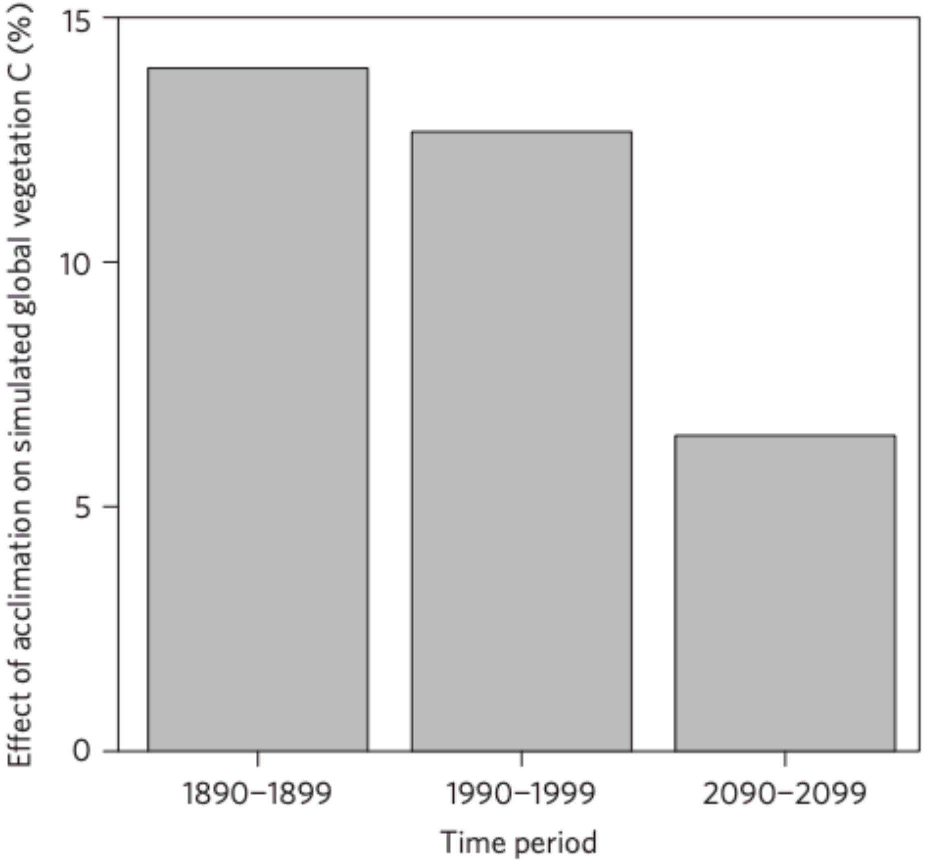
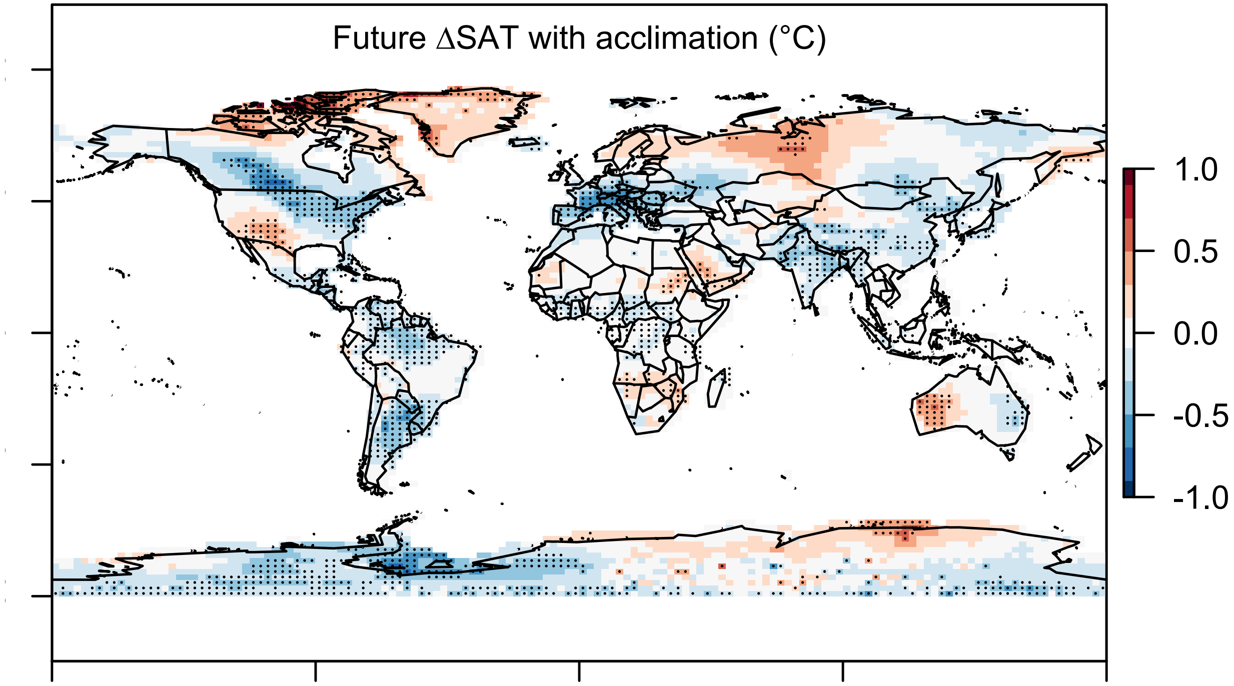
# …and can possibly impact carbon cycling and climate

## 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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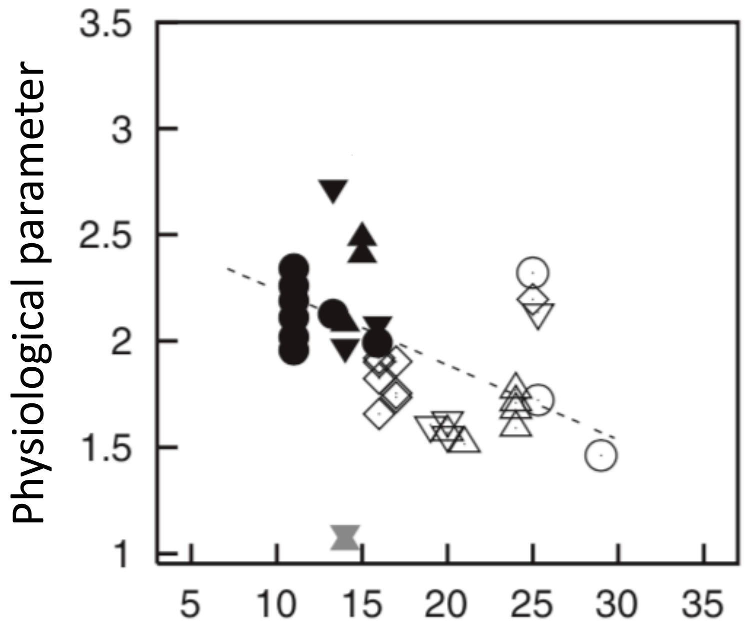
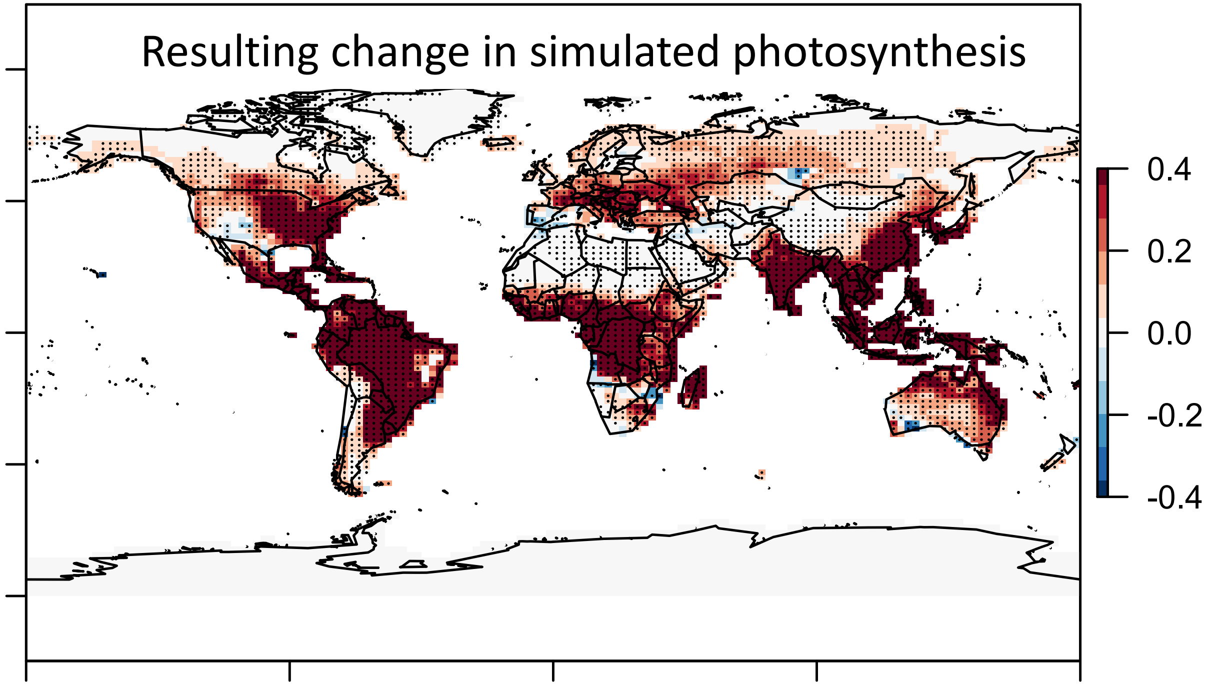
# Lack of theory results in…

- 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}

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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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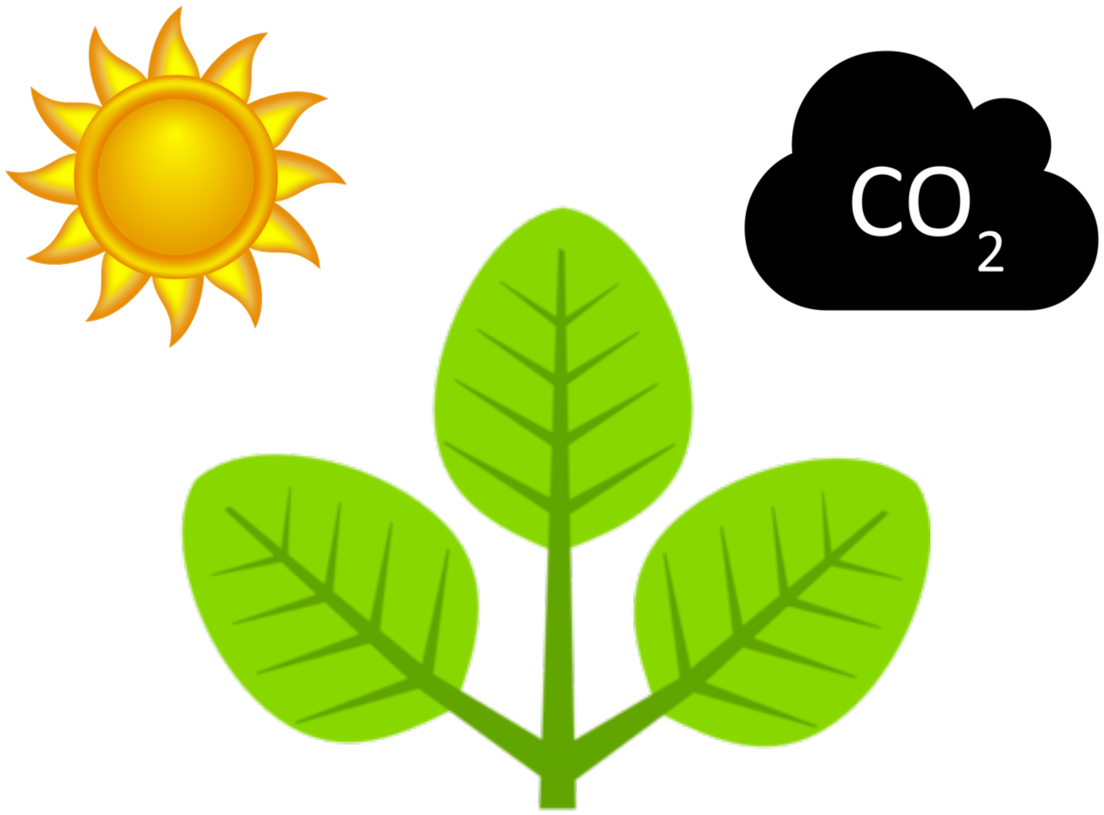
# Biochemistry optimization: Coordination hypothesis




Optimal setup = equal limitation by all factors

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

$$A_j = A_c$$

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

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

Smith et al. (2019)

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

Smith et al. (2019)

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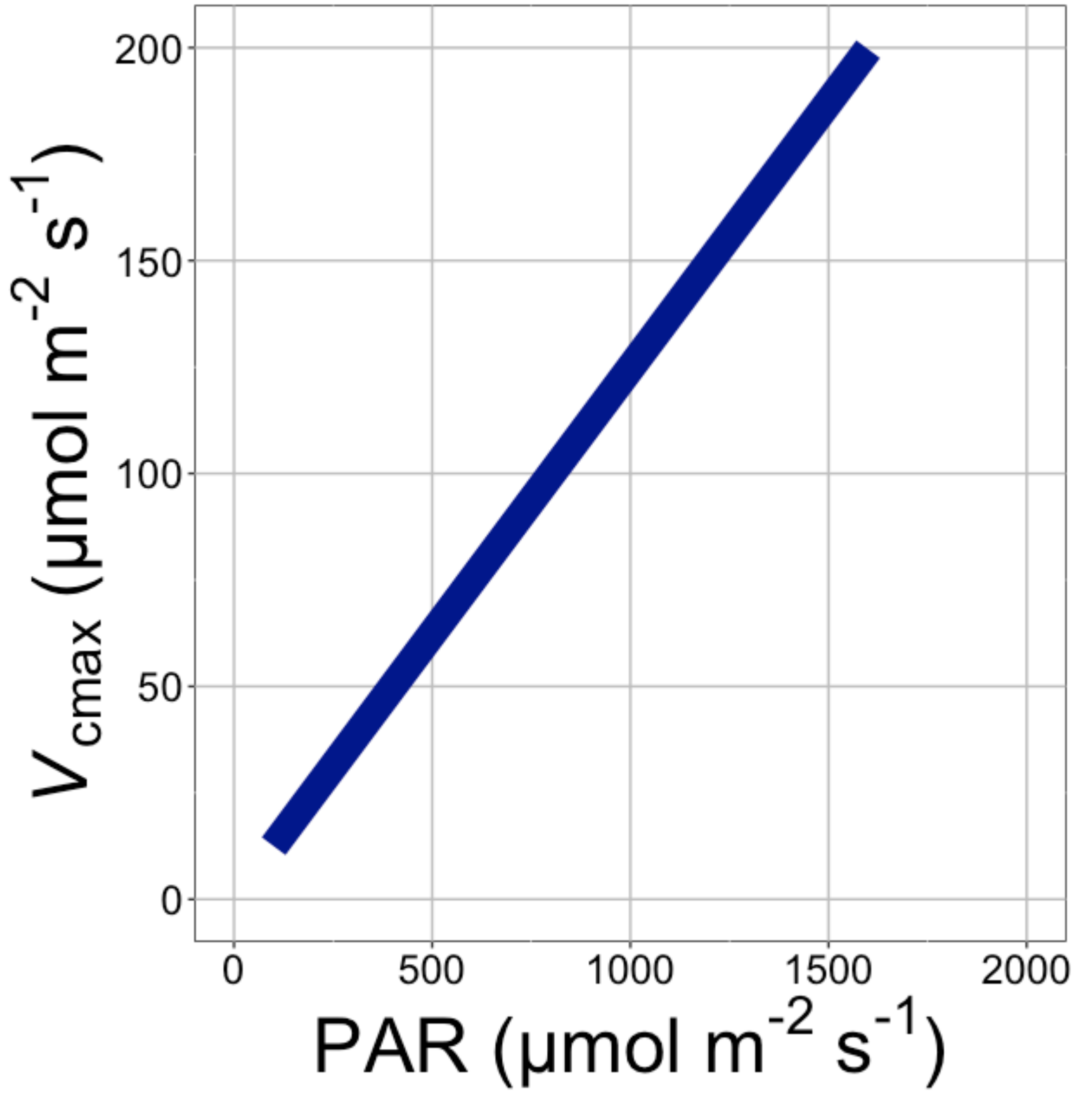


*$V_{cmax}$* increases with light because of greater electron transport

Smith et al. (2019)

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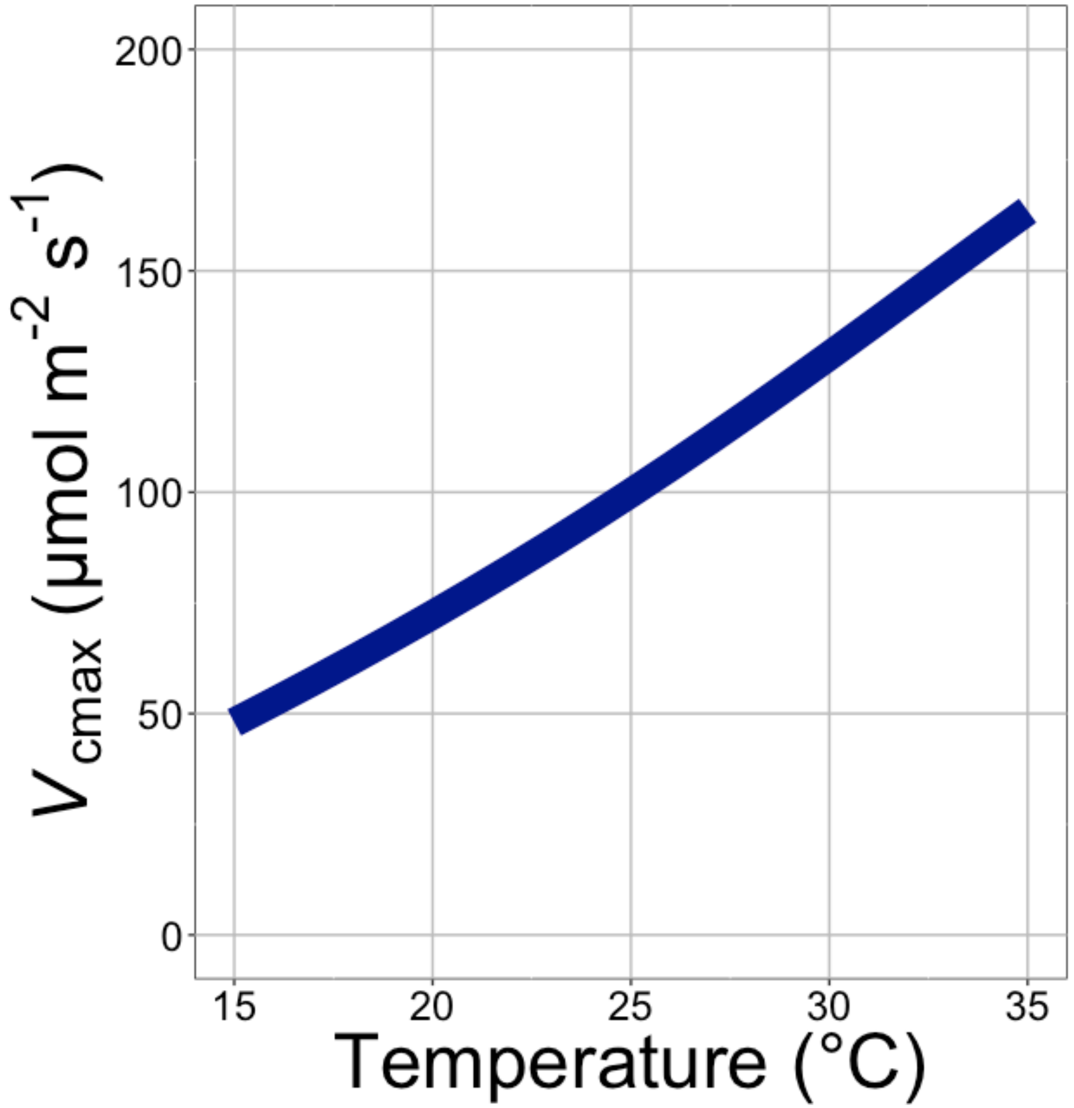


$V_{cmax}$ increases with temperature because of greater electron transport and photorespiration

Smith et al. (2019)

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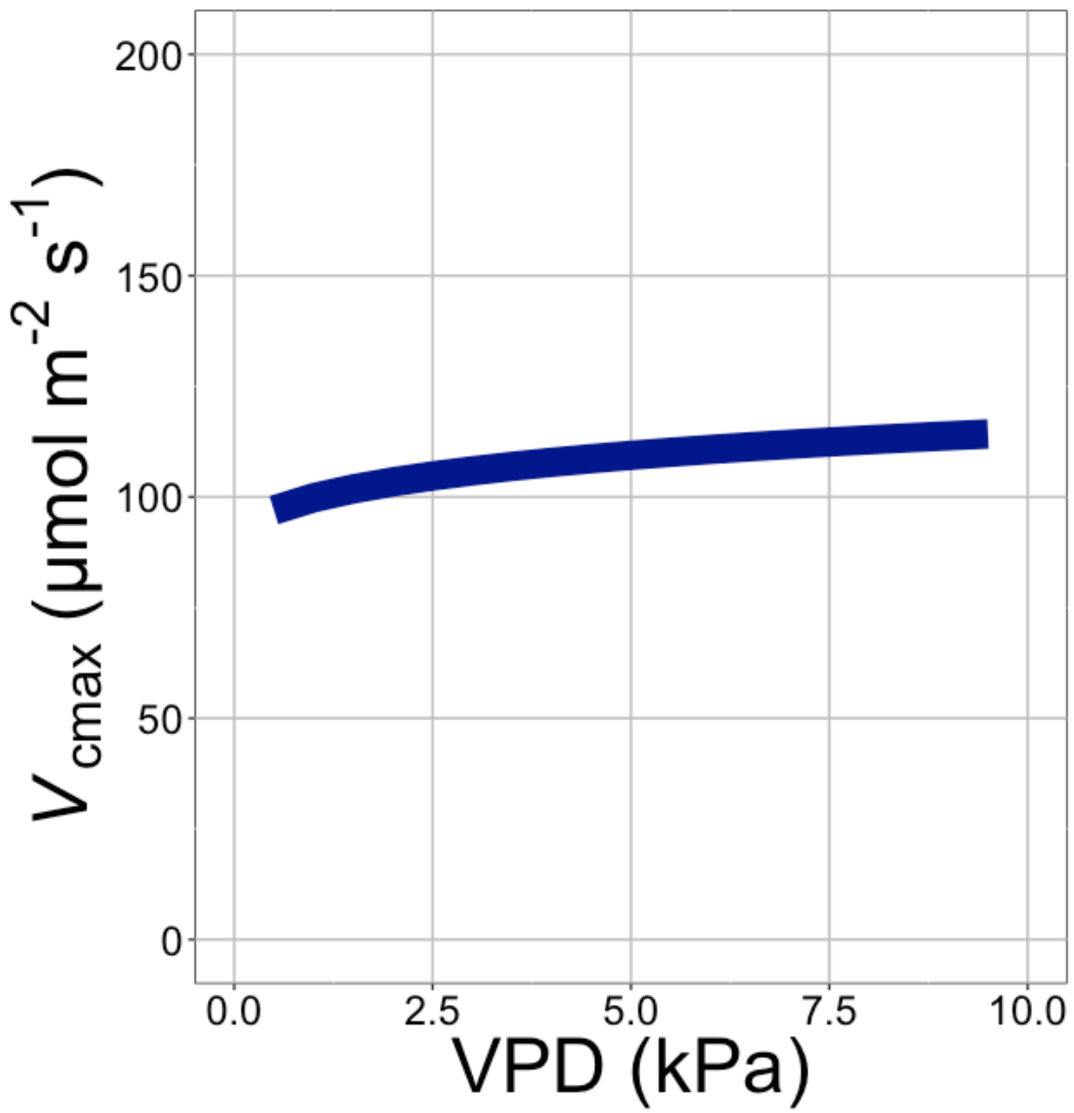


$V_{cmax}$ increases with VPD because of lower stomatal conductance

Smith et al. (2019)

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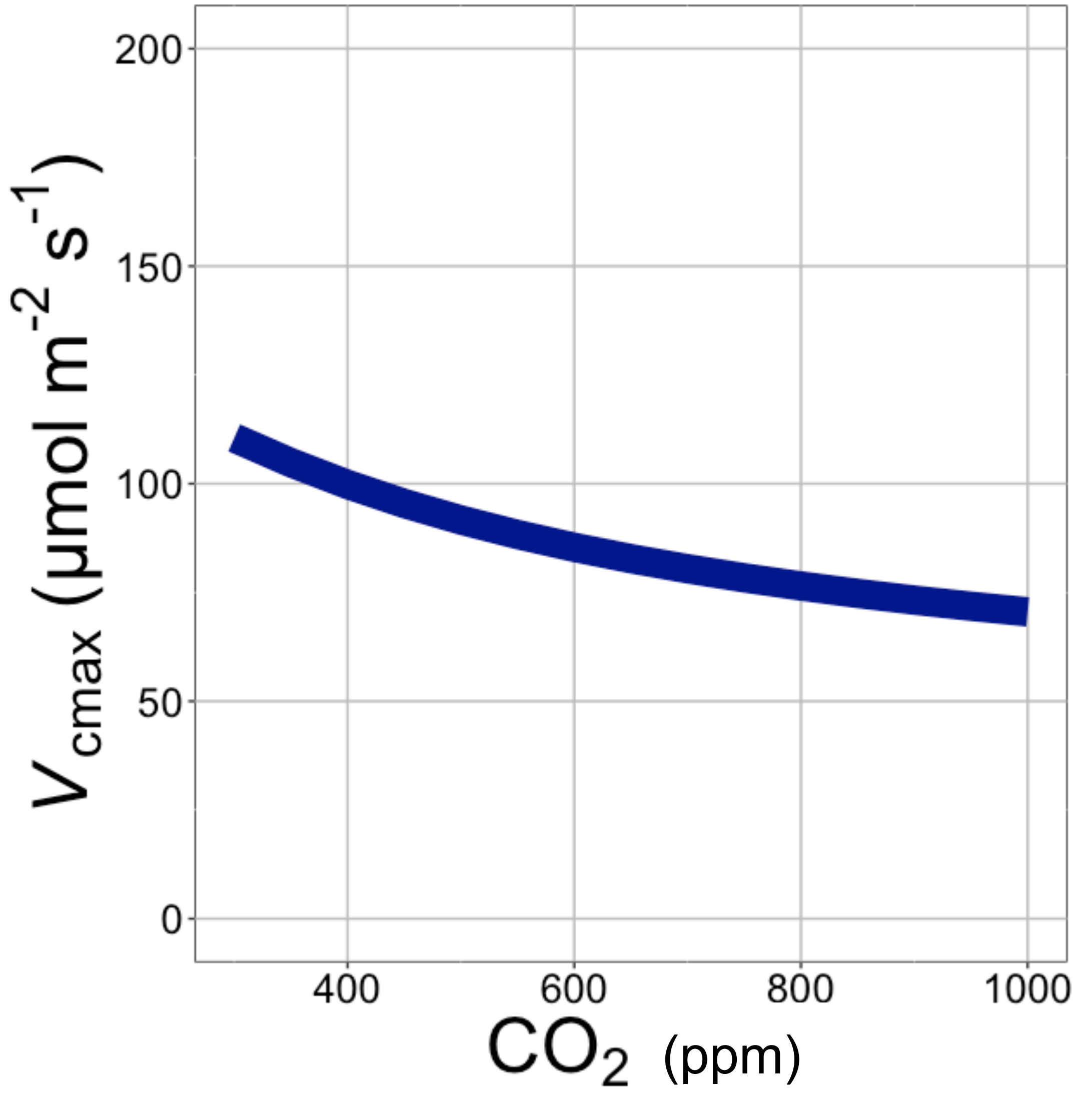


$V_{cmax}$ decreases with $CO_2$ because of greater $CO_2$ in the leaf

Smith et al. (2019)

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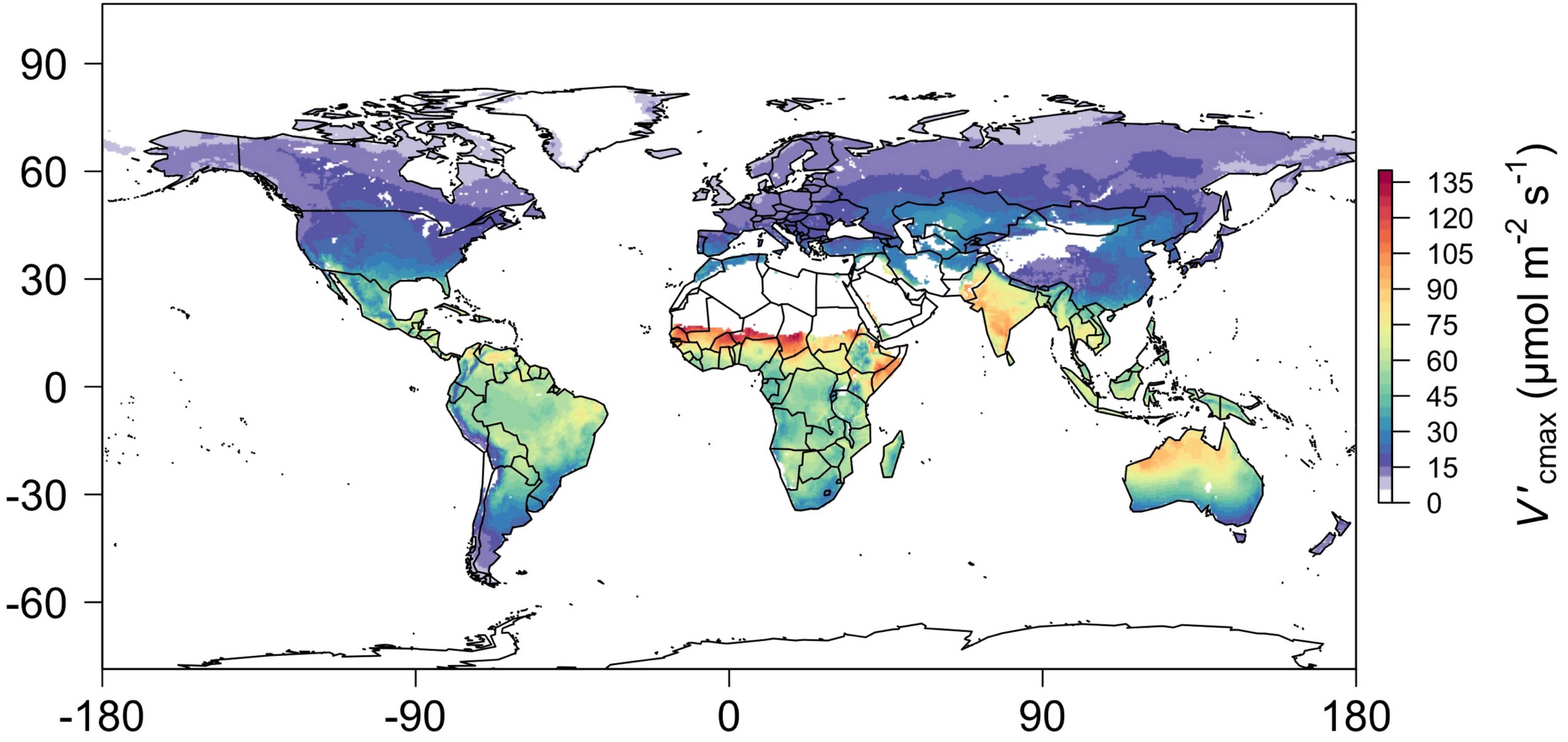
# Global, optimally acclimated traits!




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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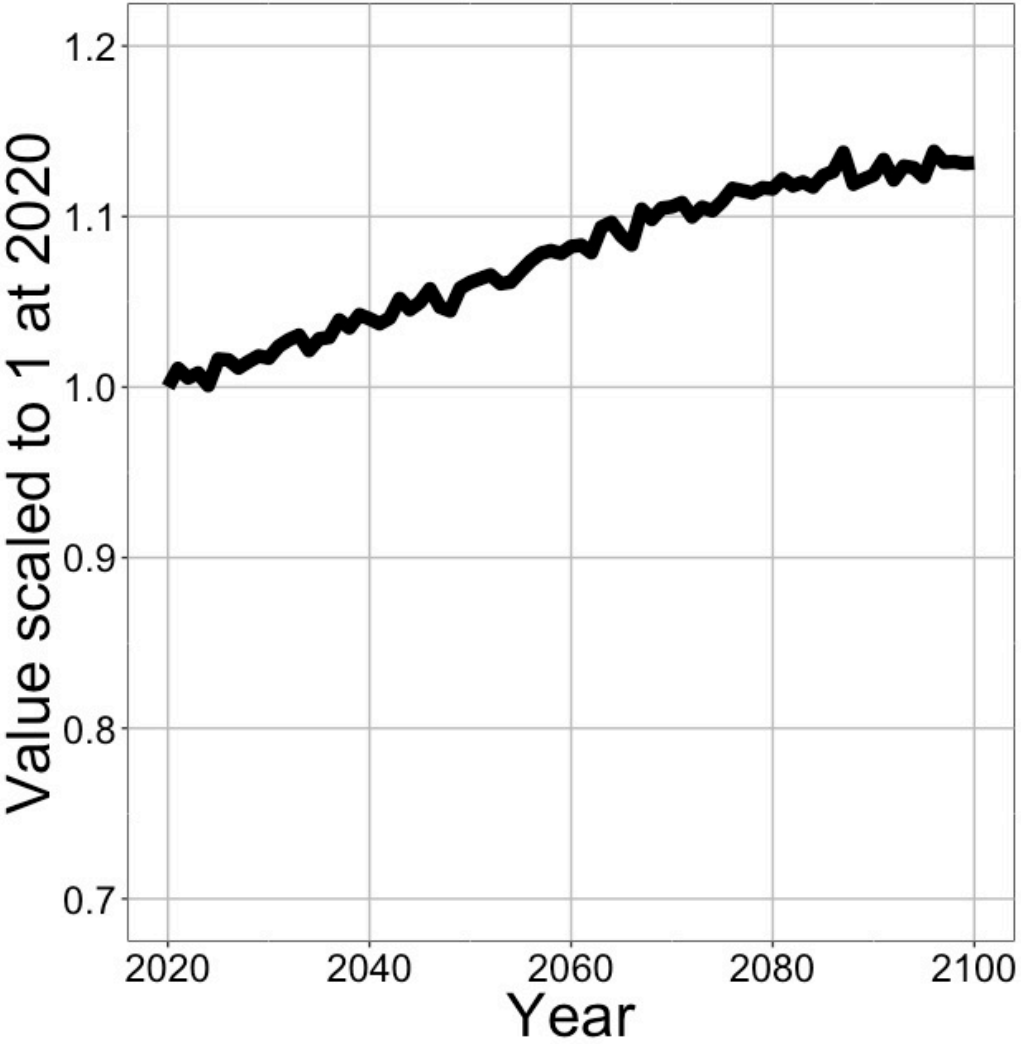
# Photosynthesis increases in future




Net Photosynthesis

Smith et al. (in prep)

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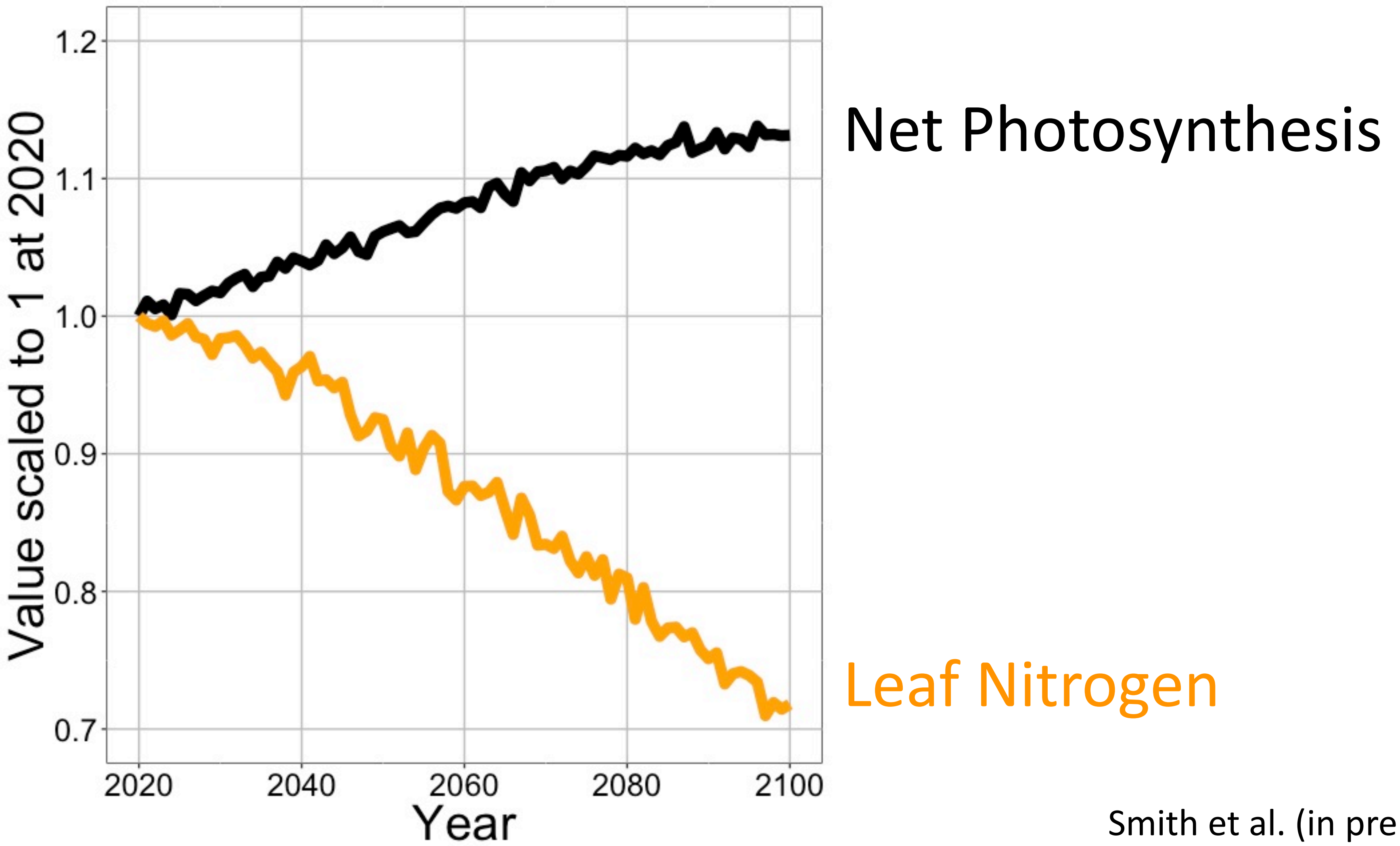
# Photosynthesis increases in future (at lower nutrient use)




Smith et al. (in prep)

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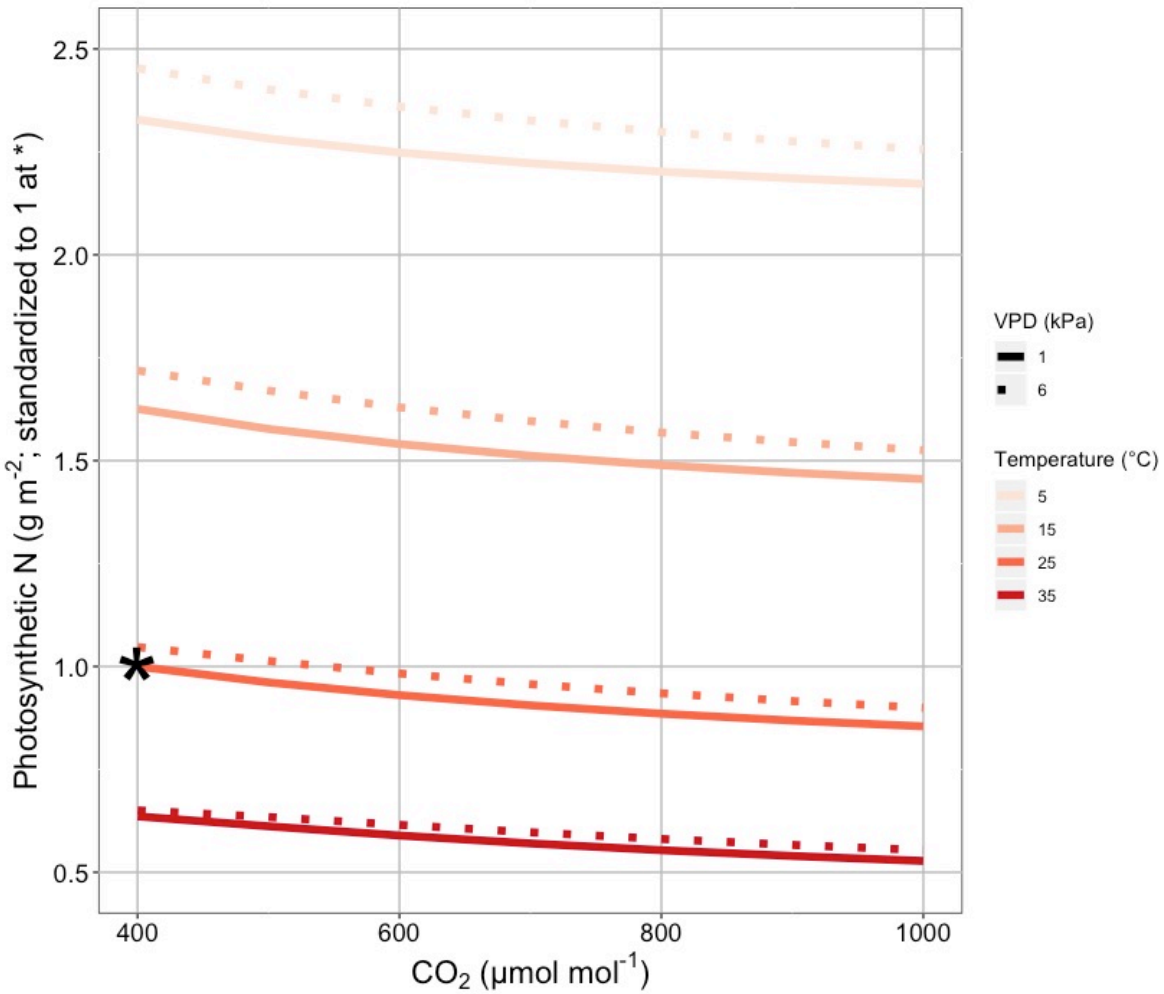
# Leaf N declines due to warming and $eCO_2$




Smith & Keenan (in review)

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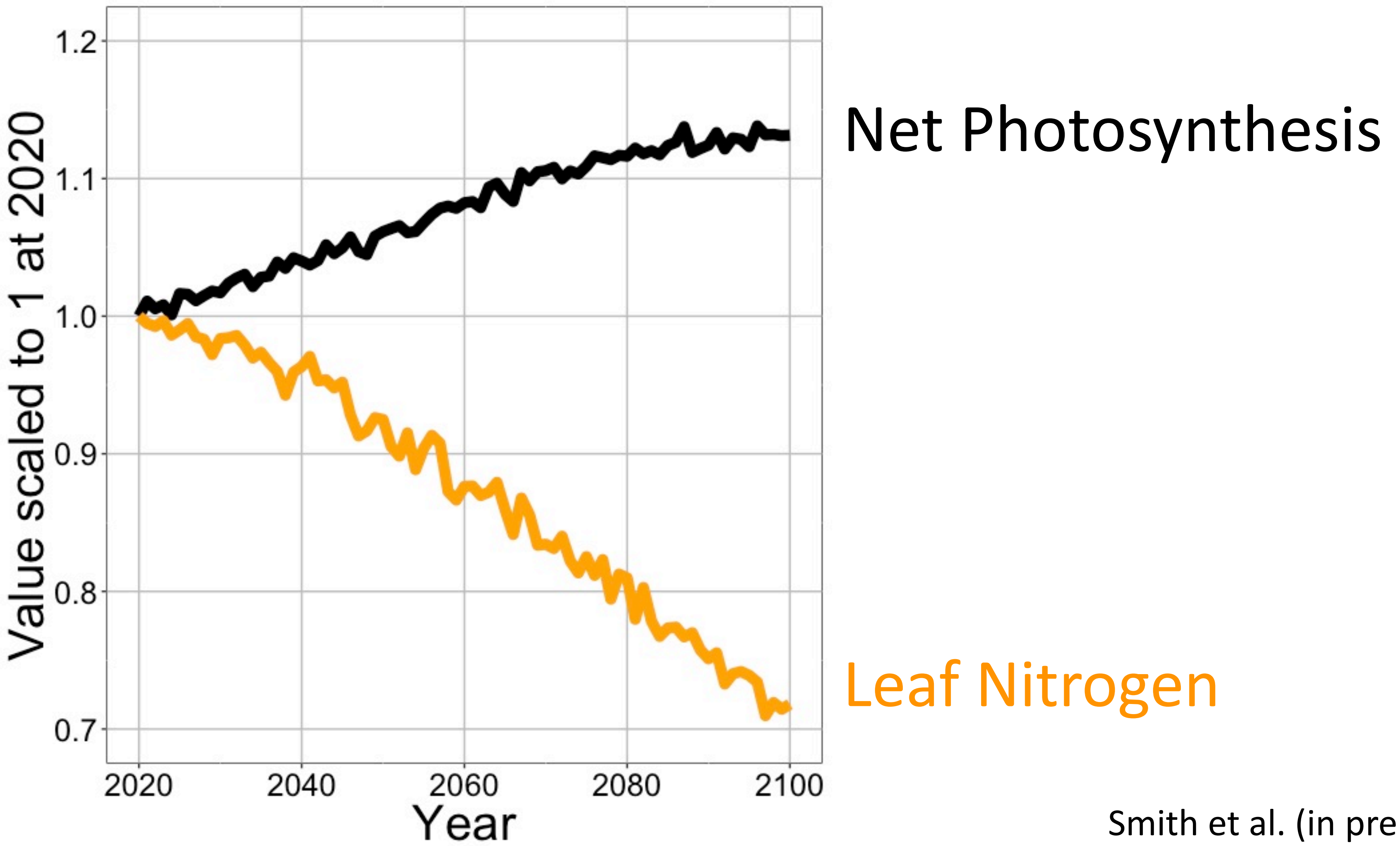
# Photosynthesis increases in future
# (at lower nutrient use)




Smith et al. (in prep)

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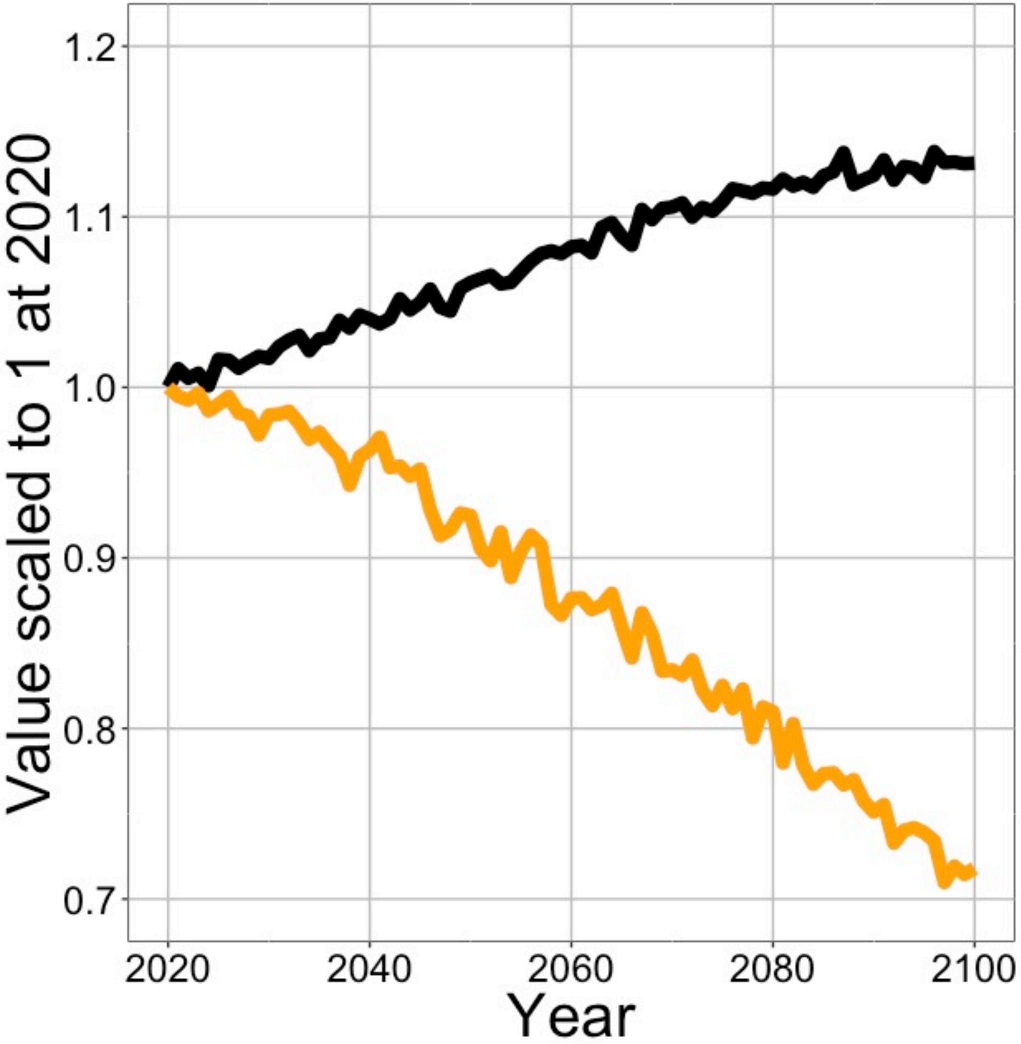
# Photosynthesis increases in future (at lower nutrient use)

Base ELM shows <5% change in leaf N




Smith et al. (in prep)

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# 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

↓

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**

Smith et al. (in prep)

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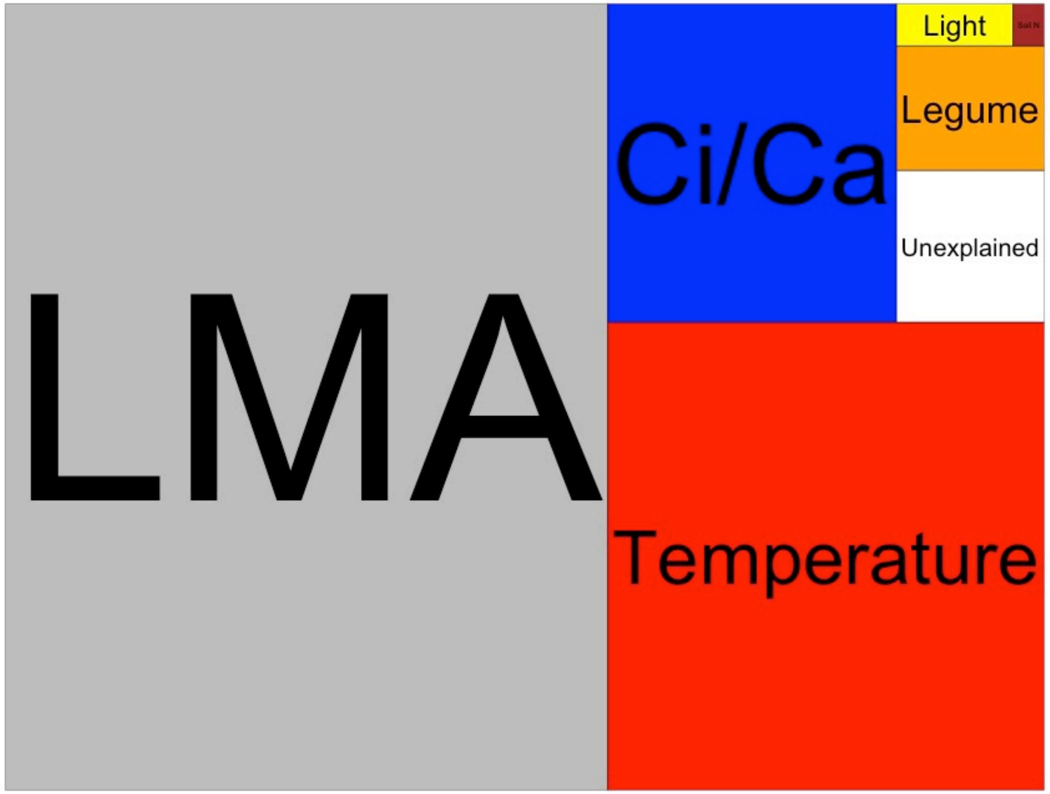
# Globally, N addition little impact on leaf N




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

nutrient network

Smith et al. (in prep)

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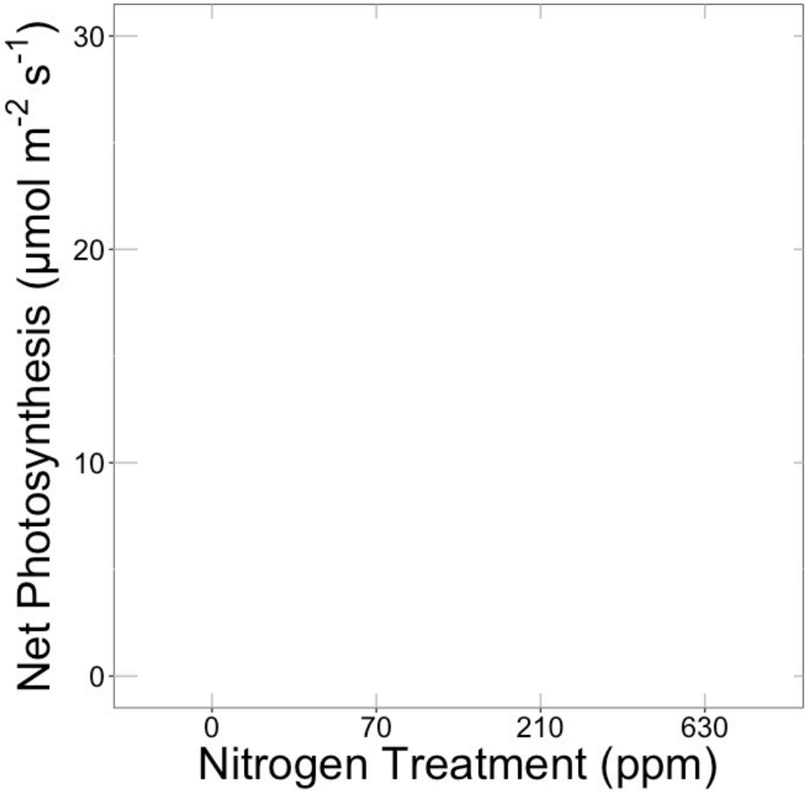
# Does photosynthesis respond to soil N?




Waring and Smith (in prep)

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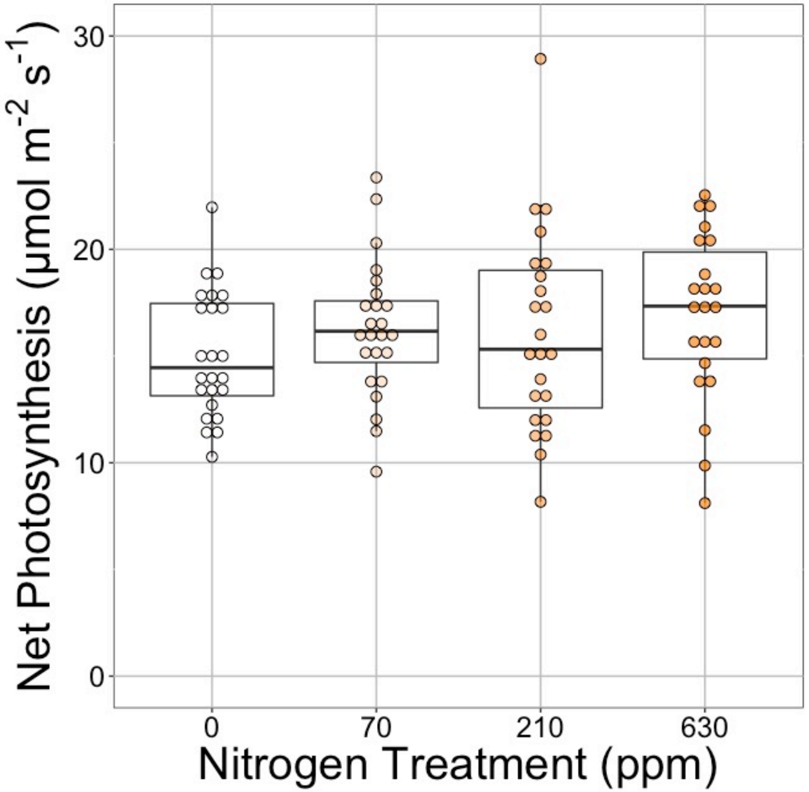
# Photosynthesis does not change with soil N

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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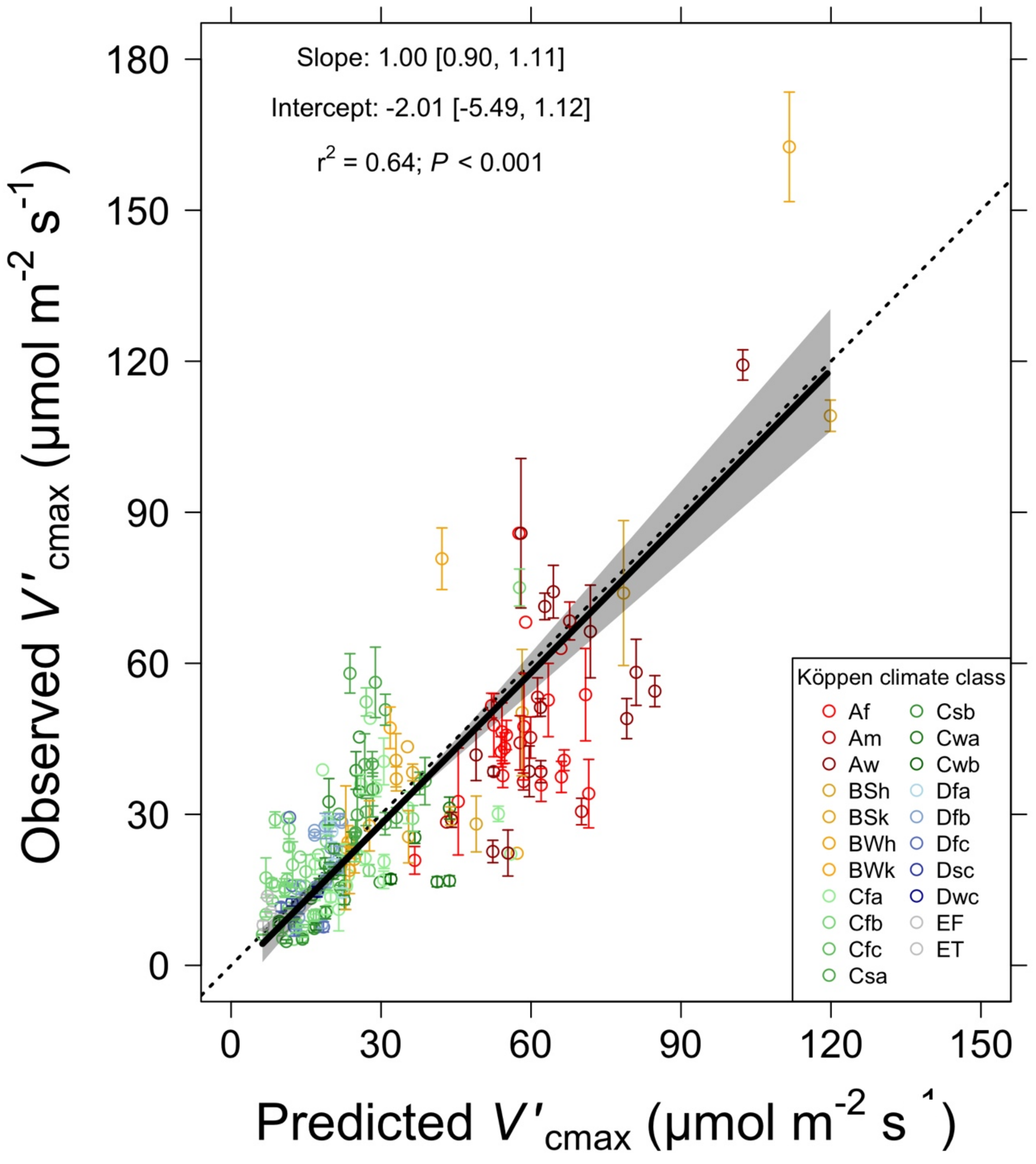


# Optimal $V_{cmax}$ is similar to observed values

Smith et al. (2019)

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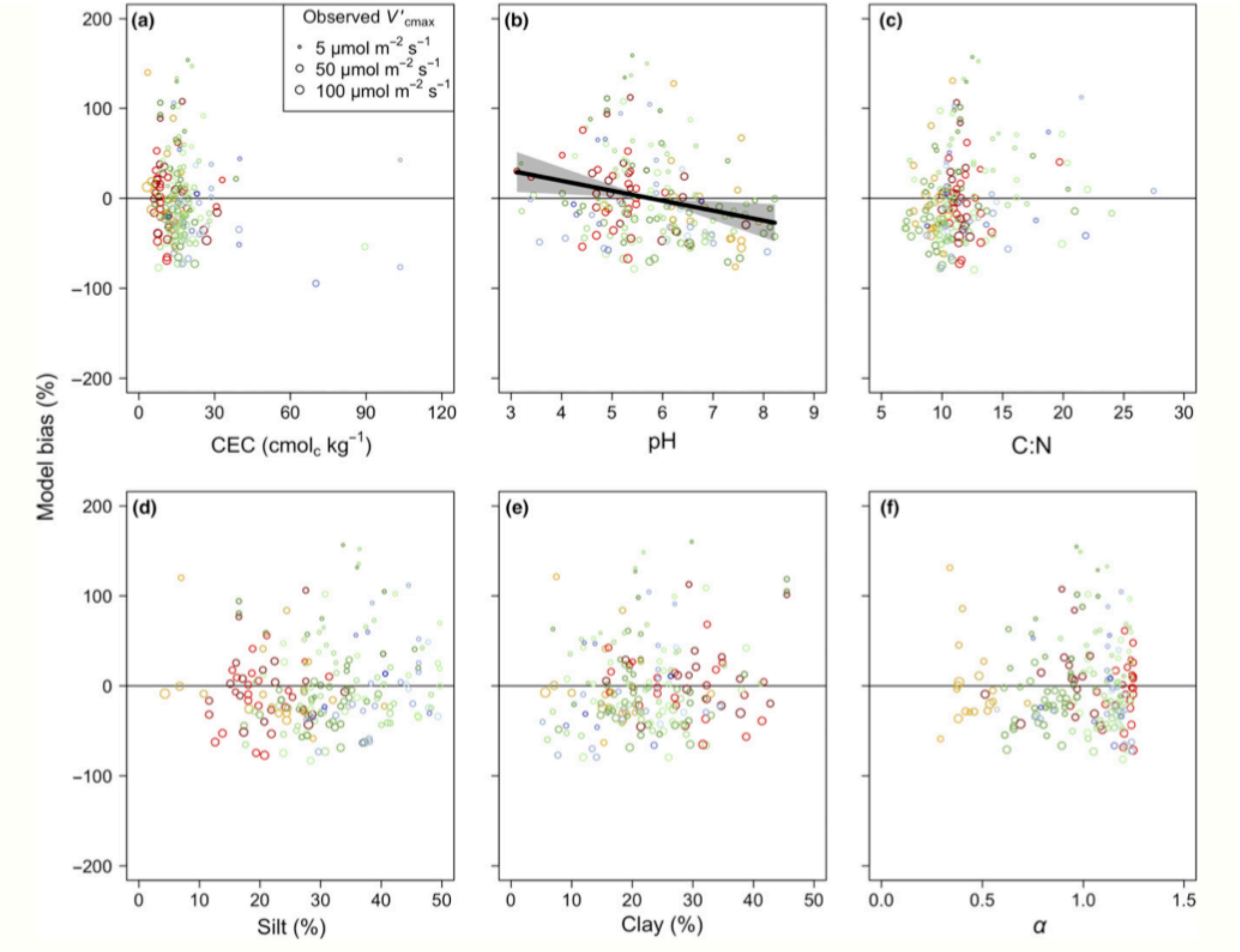
# There is little effect of soils on $V_{cmax}$




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

Smith et al. (2019)

# Does it work under future conditions?

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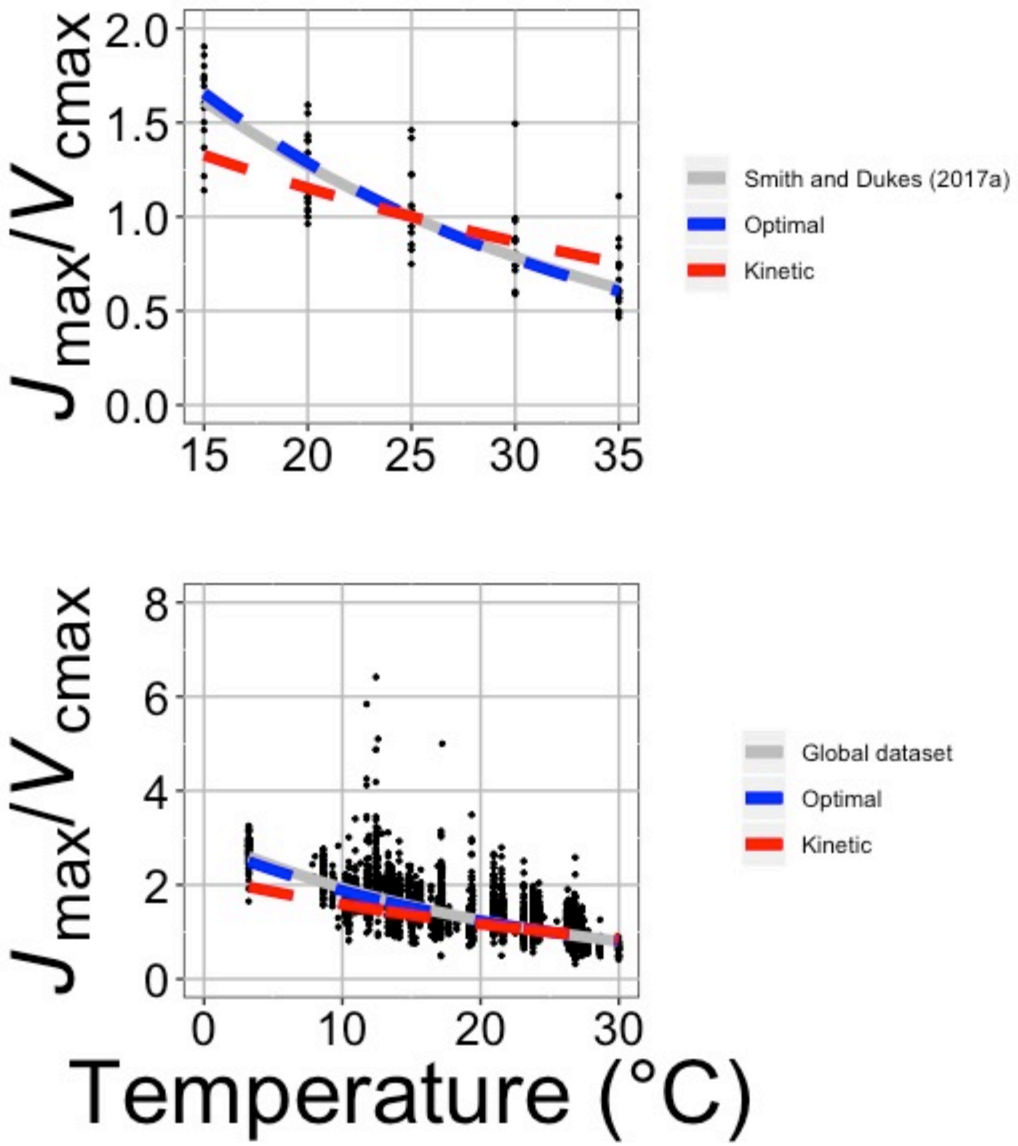


# Photosynthetic traits change with temperature in ways expected from optimization

Data = -0.051 °C$^{-1}$

Predicted = -0.048 °C$^{-1}$

Smith and Keenan (in review)

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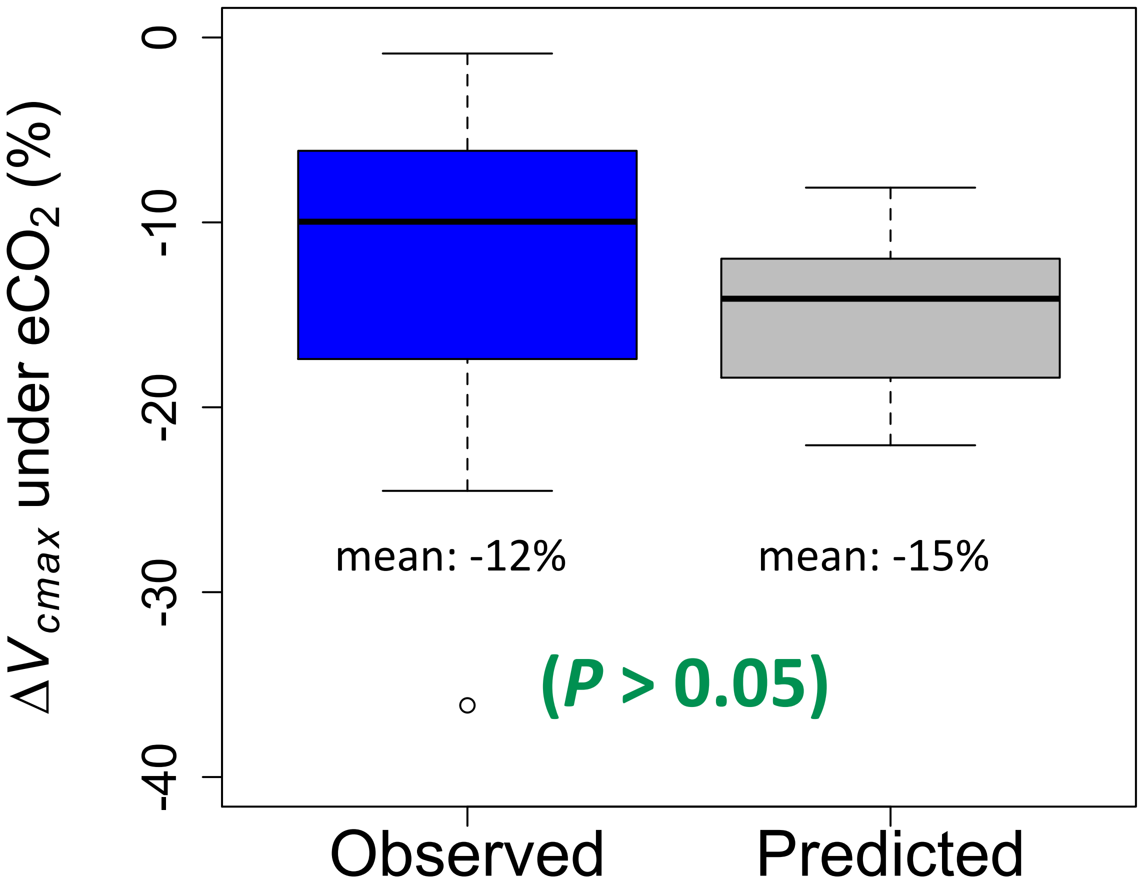
# Photosynthetic traits change with future conditions in ways expected from optimization




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
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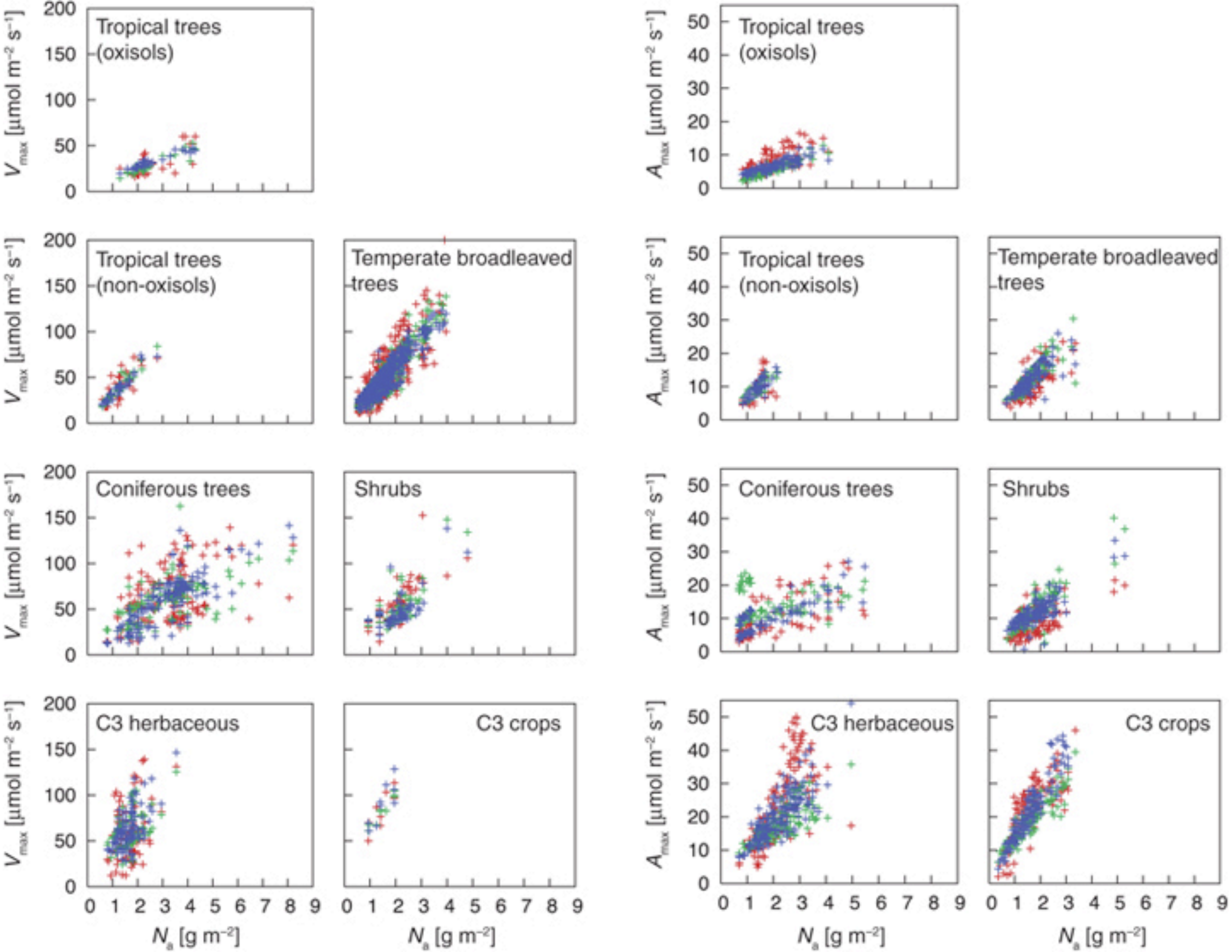
- Photosynthetic demand determines leaf N, not the other way around




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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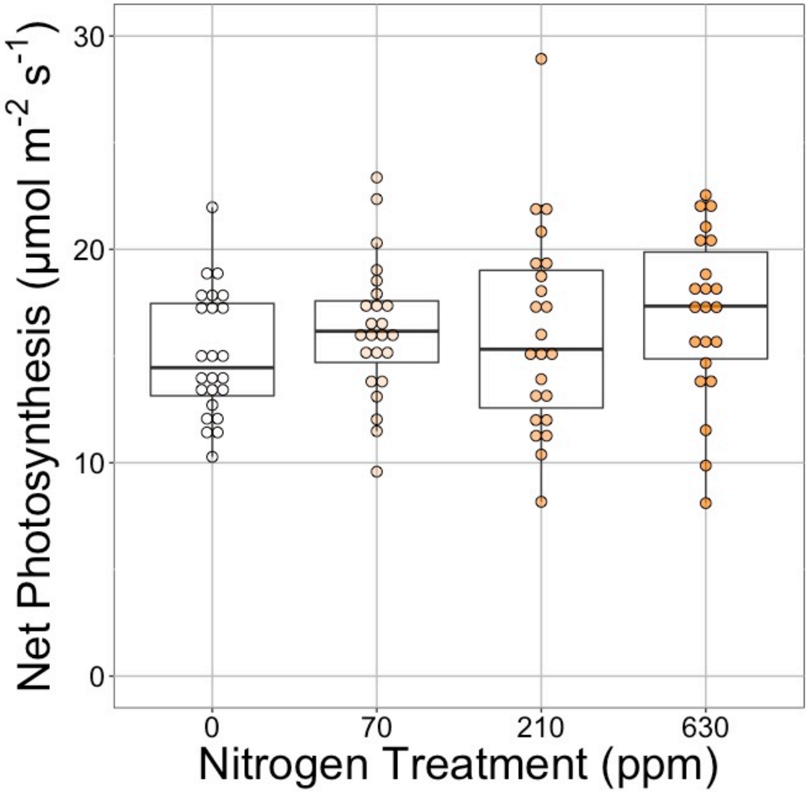
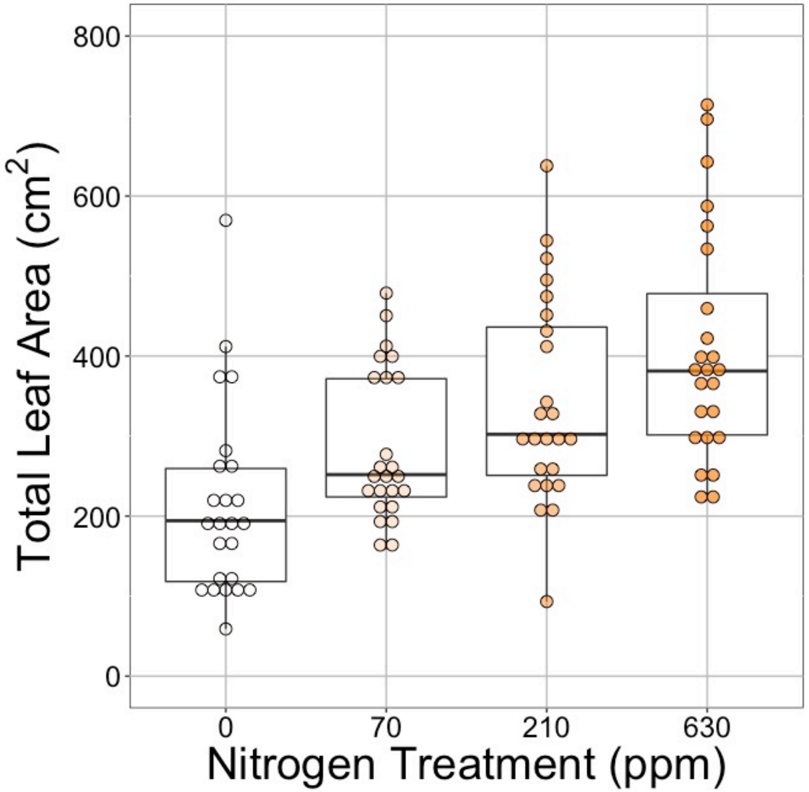
# Soil N determines # of leaves?

## No change ($P = 0.42$)




## 91% increase ($P < 0.05$)




Waring and Smith (in prep)

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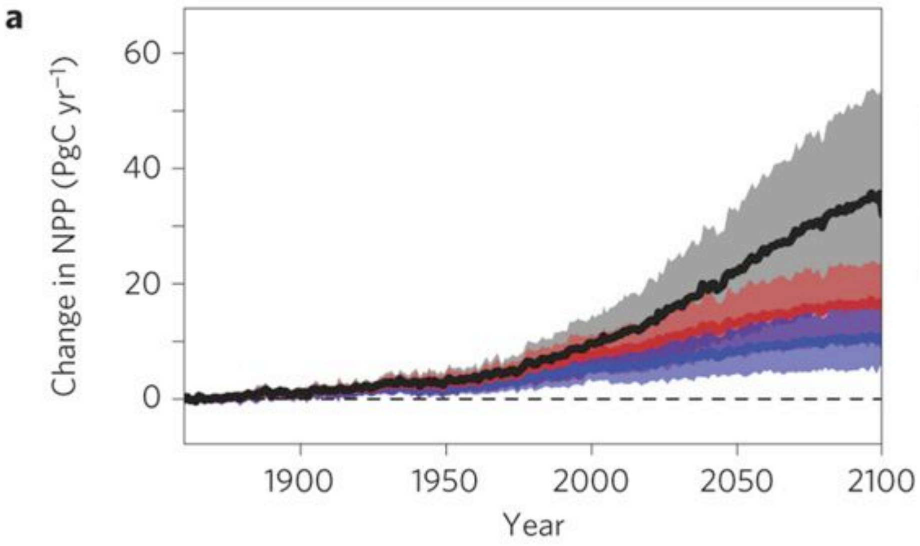
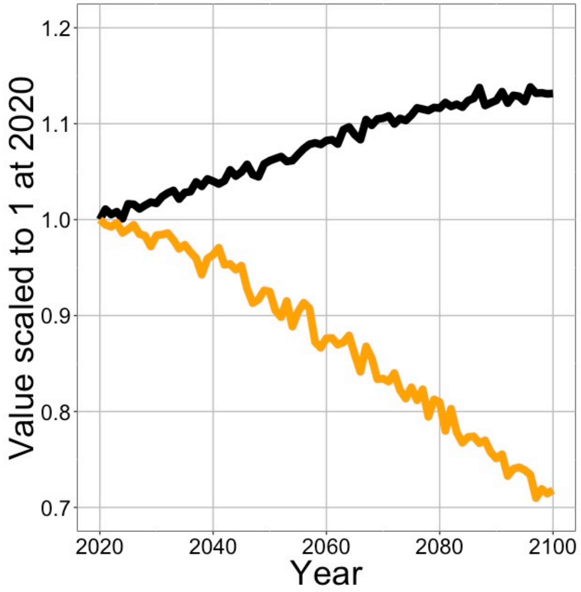
# Next steps: How might this effect simulated nutrient limitation?




"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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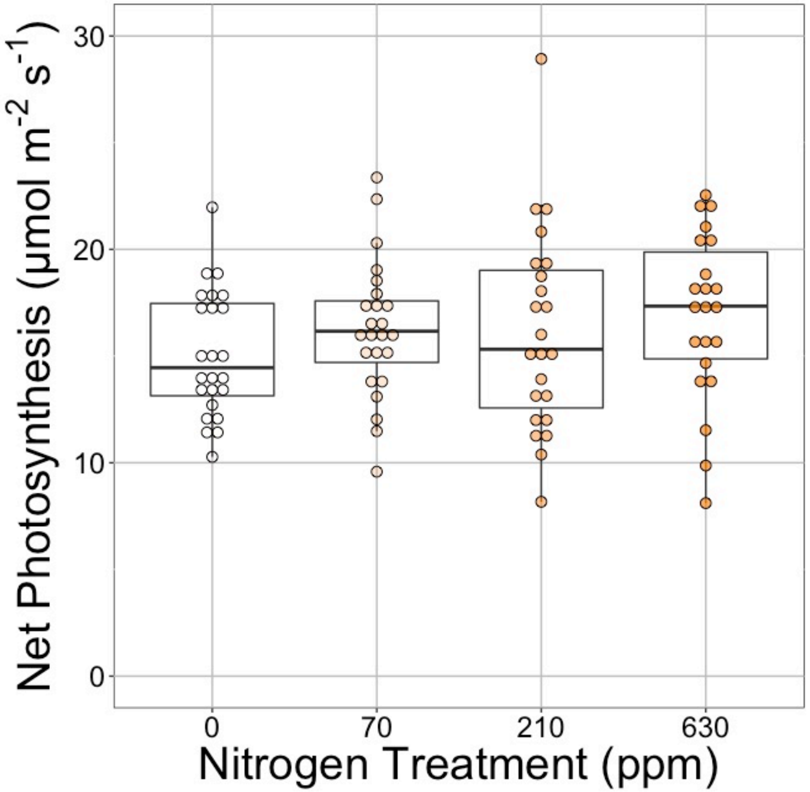
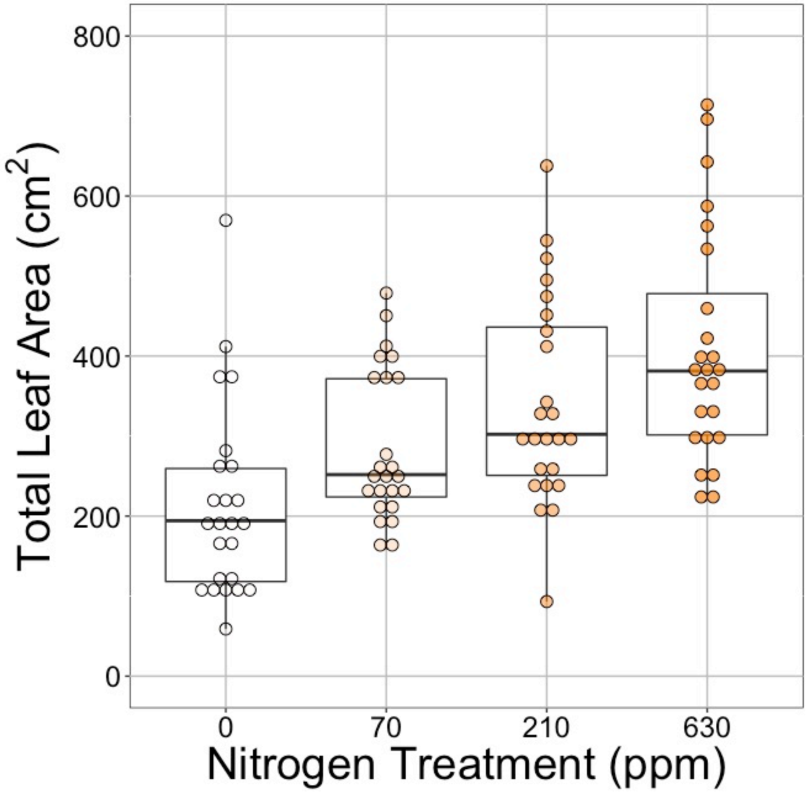
# Leaf area, but not photosynthesis increases with N addition

## No change (P = 0.42)




## 91% increase (P < 0.05)




Waring and Smith (in prep)

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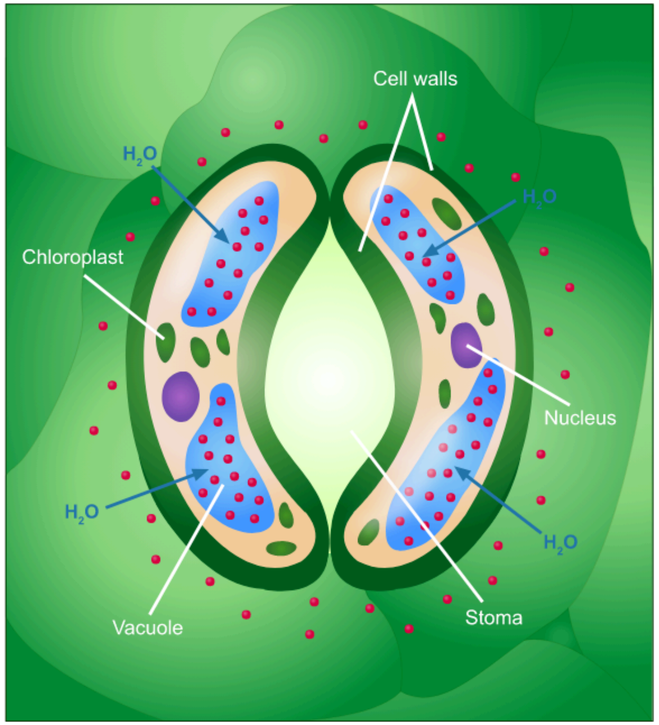


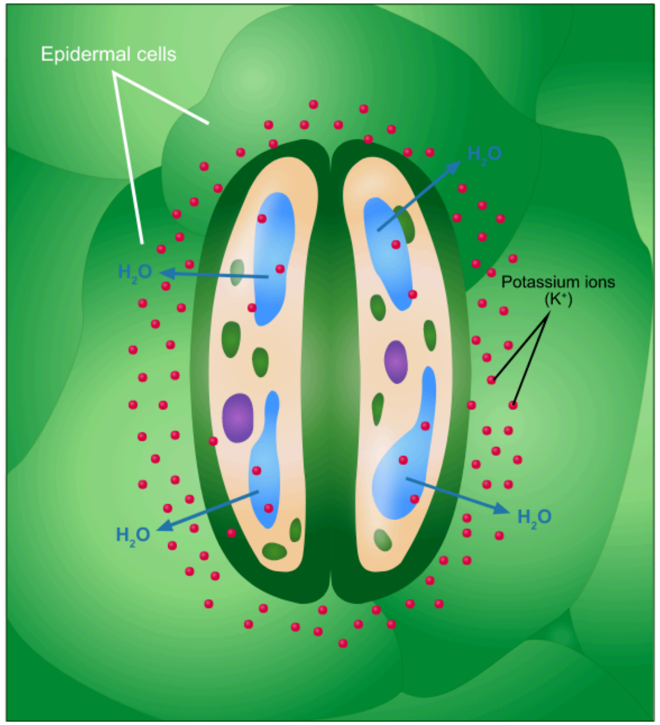


## Open stomata:

Benefits

- High $CO_2$ influx

Costs

- High water outflux

## Closed stomata:

Benefits

- Low water outflux

Costs

- Low $CO_2$ influx

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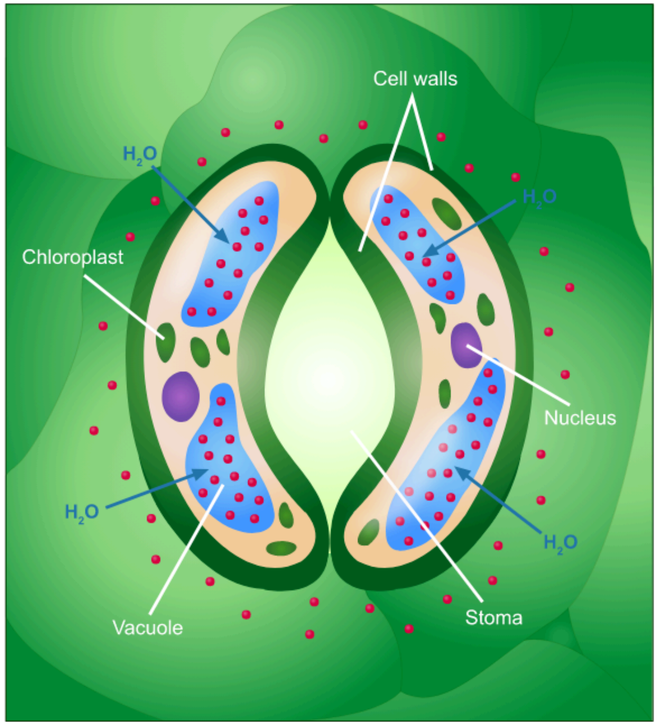


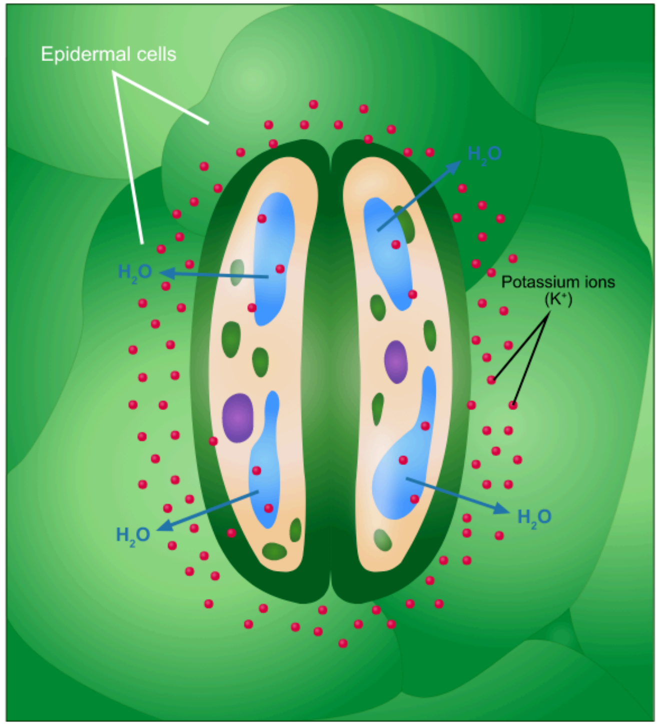


## Open stomata:

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 $V_{\mathrm{cmax}}$

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# 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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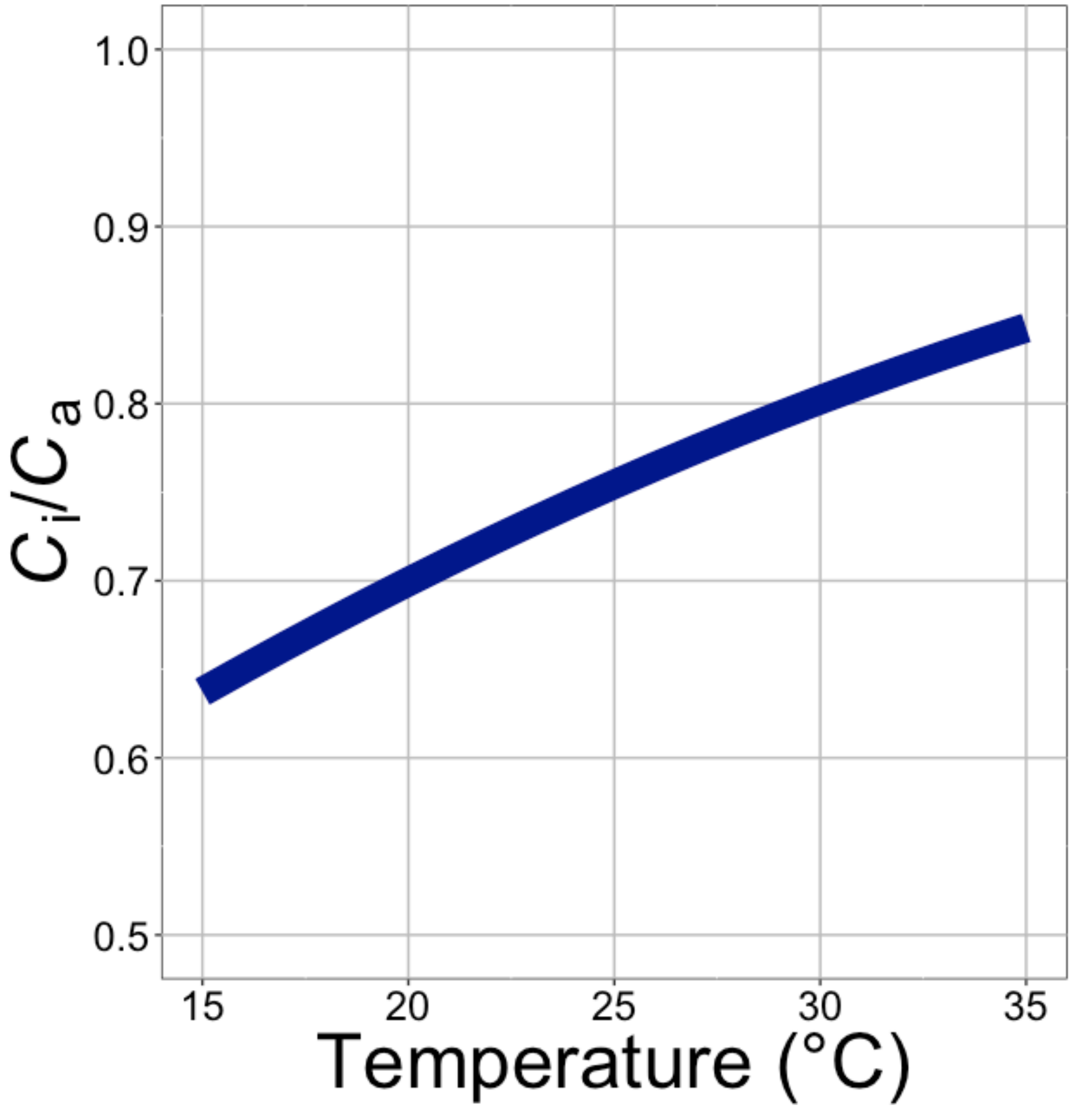


$C_i/C_a$ increases with temperature because of greater photorespiration

Smith et al. (2019)

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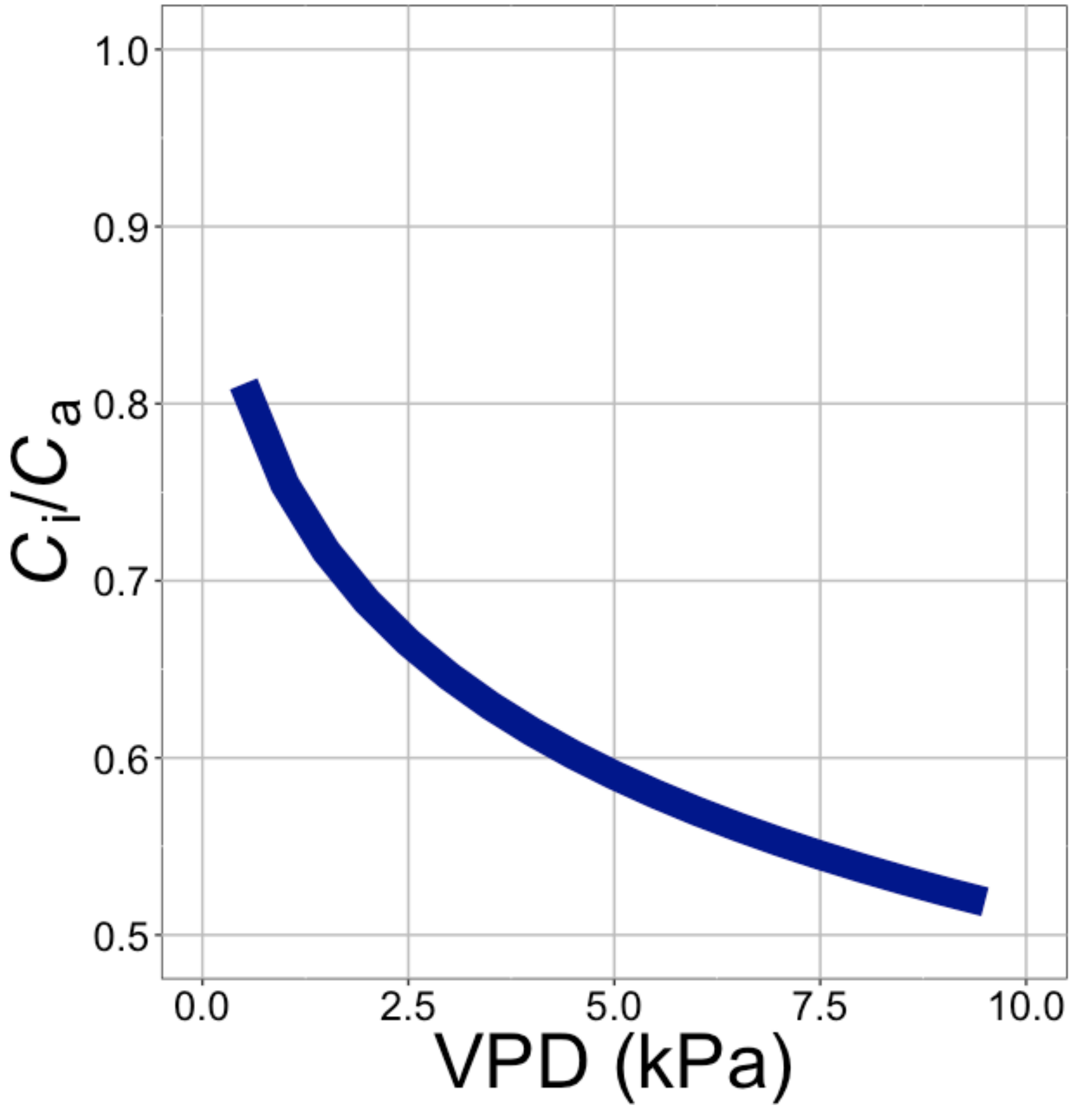


$C_i/C_a$ decreases with VPD because of greater water loss

Smith et al. (2019)

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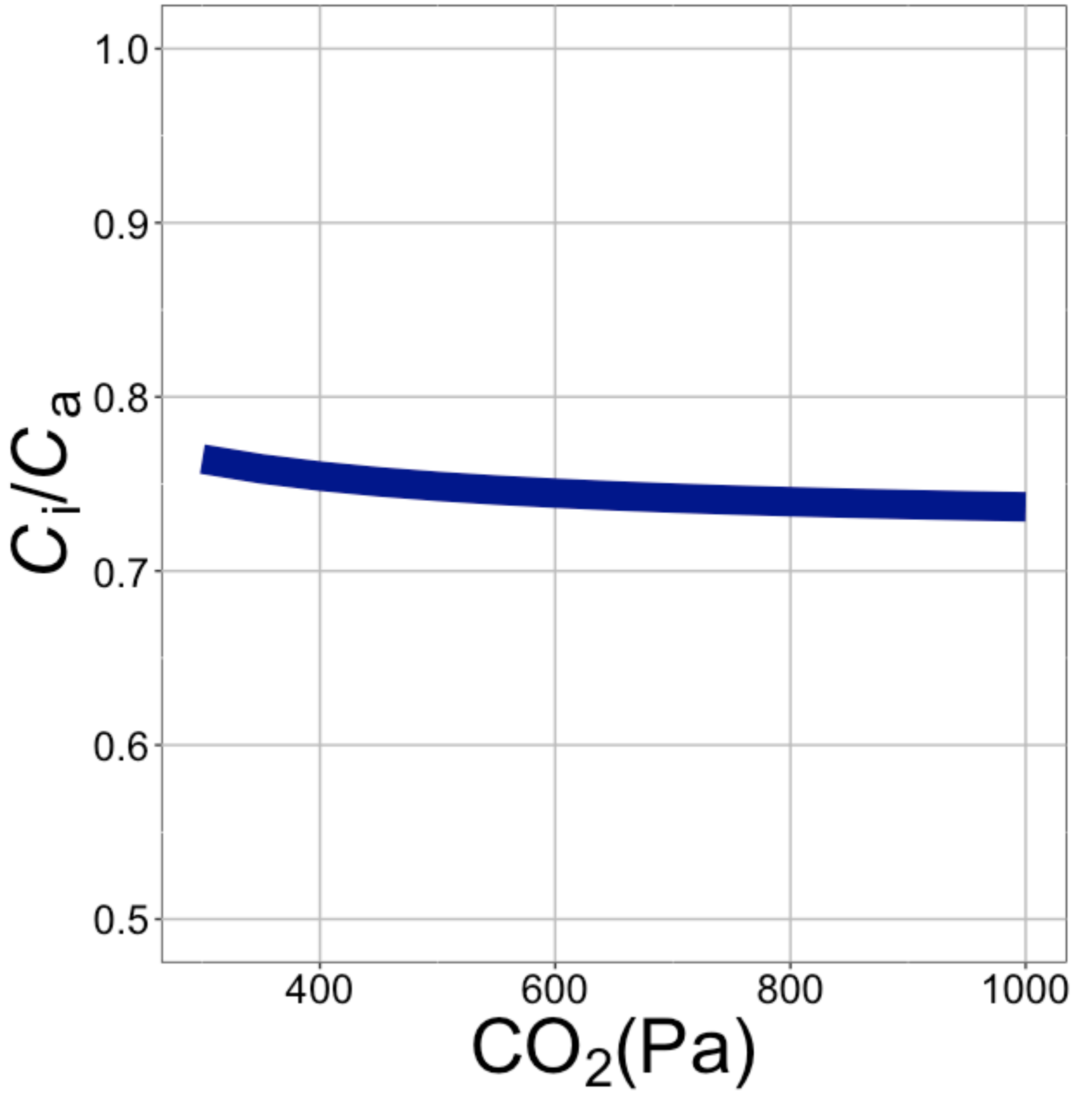


$C_i/C_a$ decreases with $CO_2$ because of lower openness needed to satisfy Rubisco

Smith et al. (2019)

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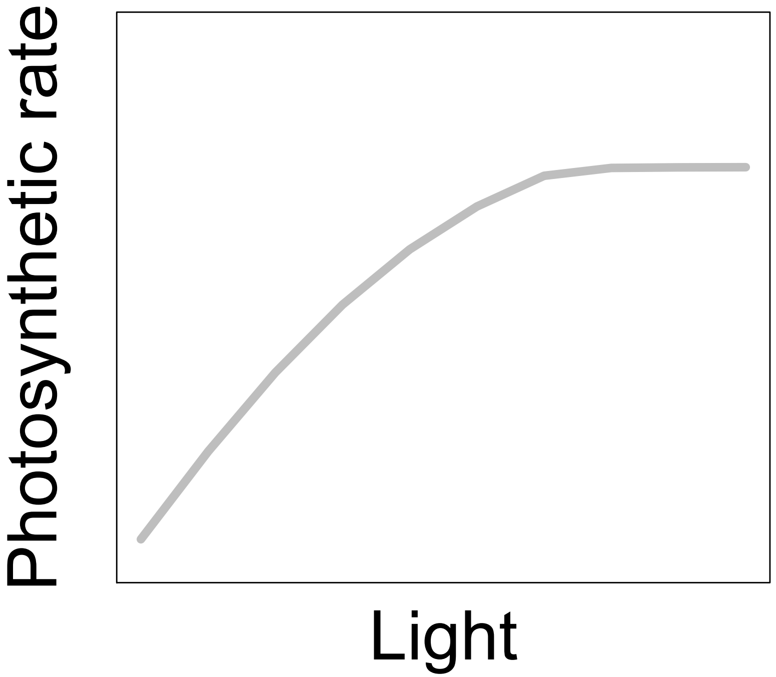
# Photosynthetic acclimation can be seen as the change in the instantaneous responses with longer-term exposure

Acclimated to high light



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