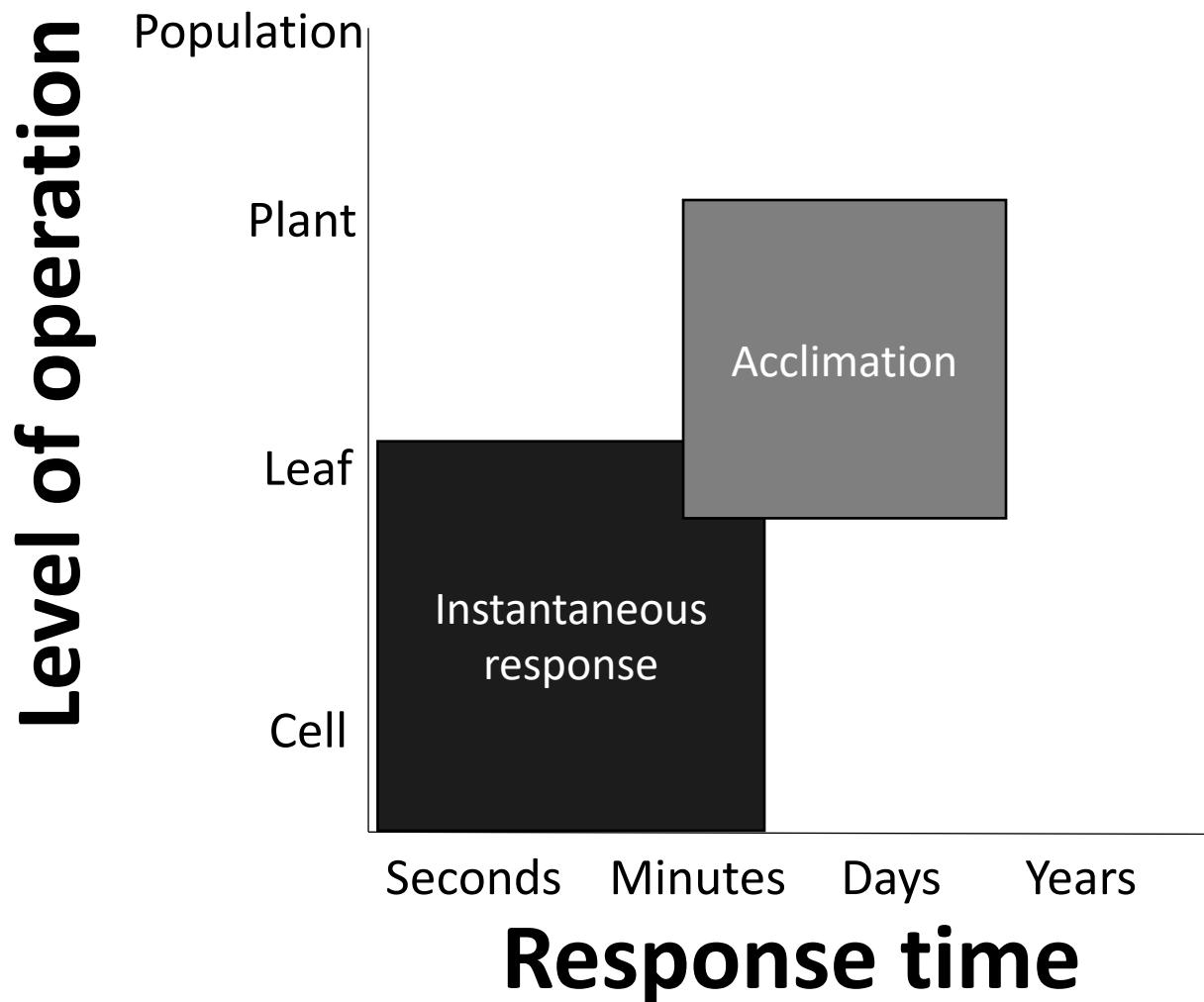


Using least cost optimality to reliably simulate photosynthetic acclimation

Nick Smith

Department of Biological Sciences
Texas Tech University

Plants acclimate to environmental conditions



Photosynthetic acclimation is ubiquitous and well known...

CO₂: Bazzaz (1990)

Ann. Rev. Ecol. Syst. 1990, 21:167–96
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THE RESPONSE OF NATURAL ECOSYSTEMS TO THE RISING GLOBAL CO₂ 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)

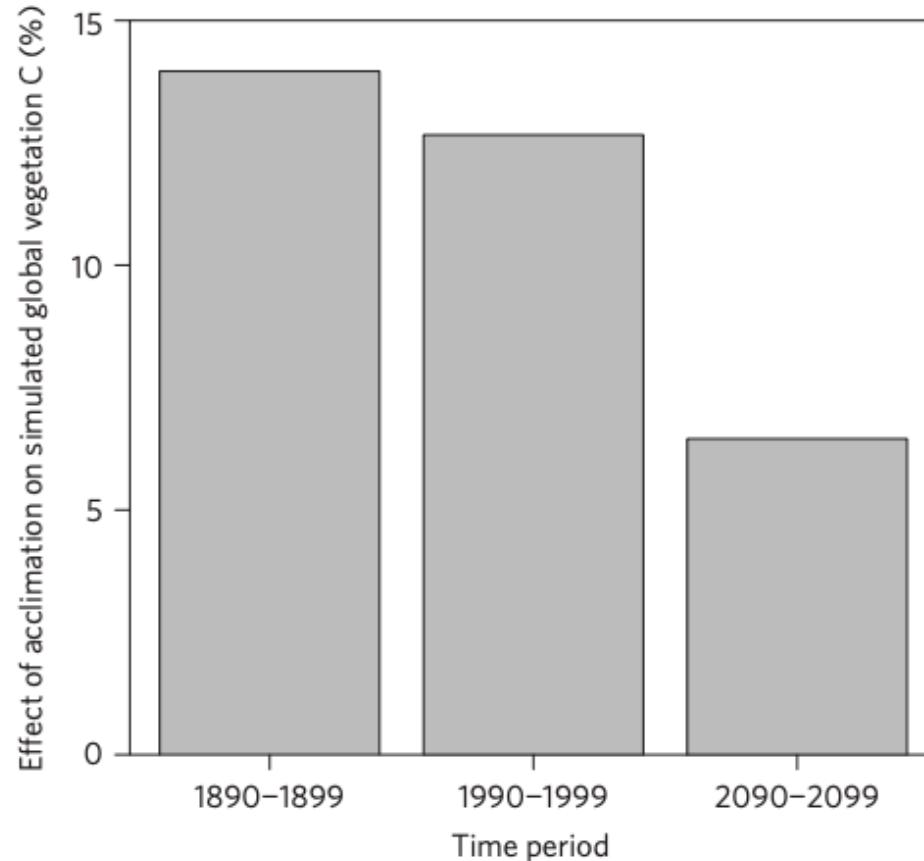
Ann. Rev. Plant Physiol. 1980, 31:491–543
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PHOTOSYNTHETIC RESPONSE AND ADAPTATION TO TEMPERATURE IN HIGHER PLANTS

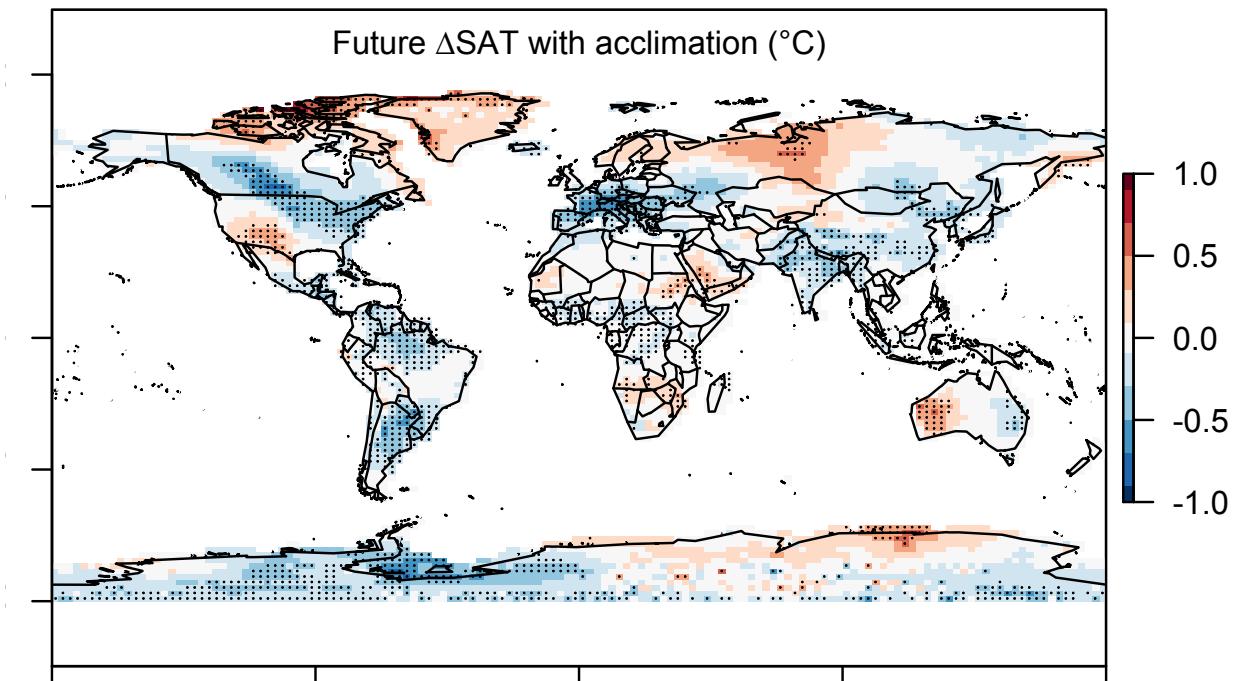
Joseph Berry and Olle Björkman¹

...and can possibly impact carbon cycling and climate

Acclimation increase future C storage by ~6%



Acclimation alters future temperature by >1°C

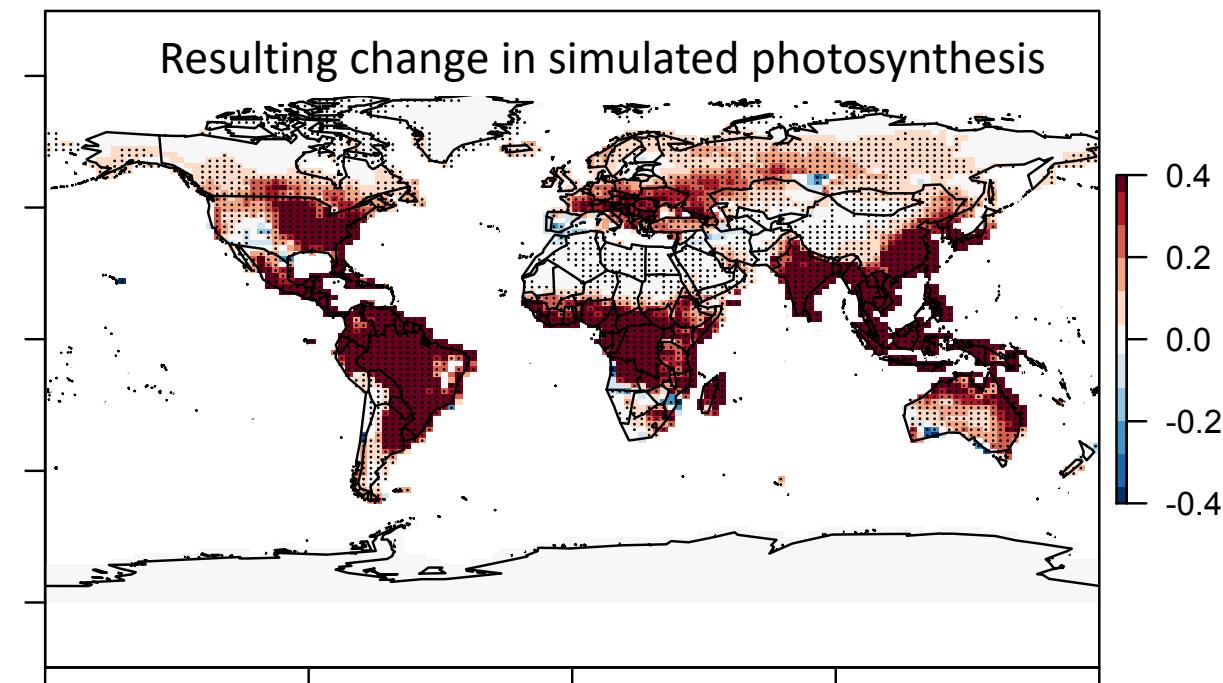
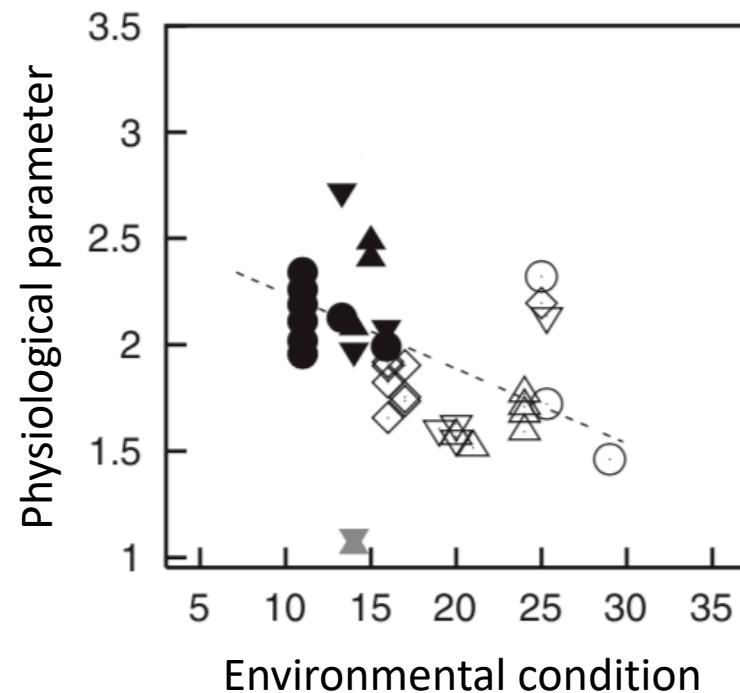


Here's the problem:
No theoretical model for
photosynthetic acclimation exists

Lack of theory results in...

Lack of theory results in...

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



So, we developed a mechanistic model of photosynthetic acclimation

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

Least cost theory

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

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$



Must predict optimal rates of both

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$

Optimal photosynthesis

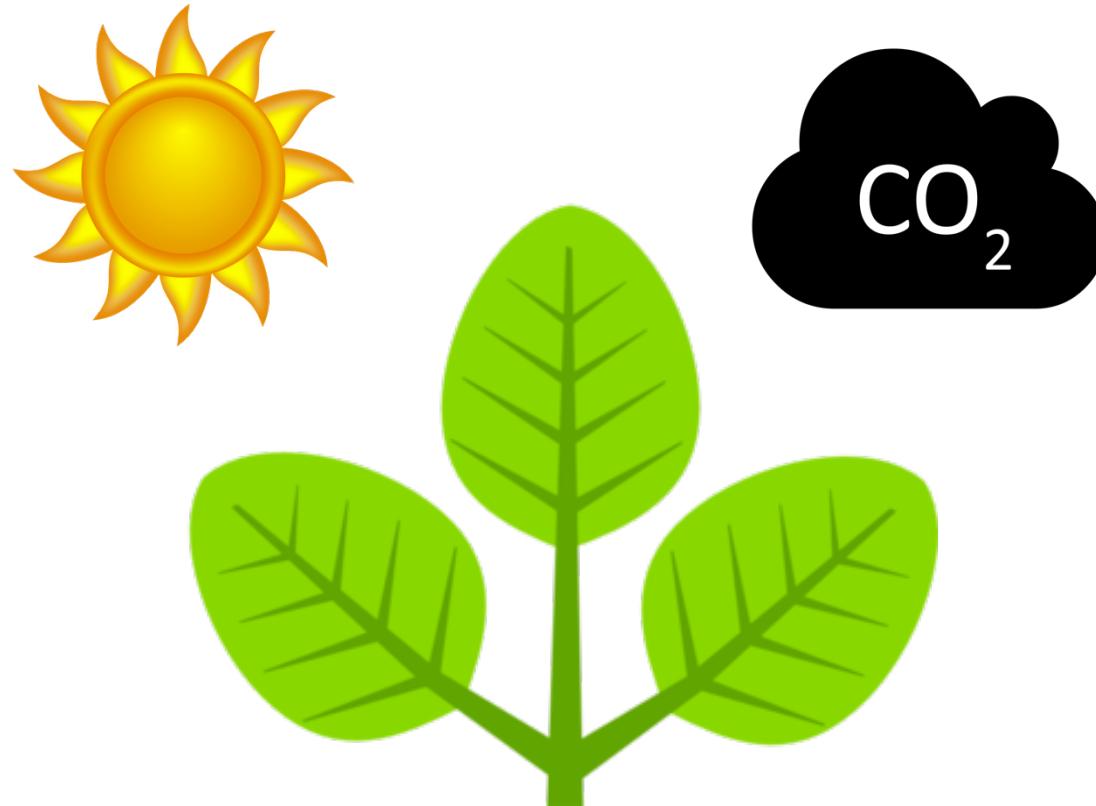
Photosynthesis = $f\{\text{stomatal conductance,}$
 $\text{photosynthetic biochemistry}\}$

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

Optimal photosynthesis

Photosynthesis = $f\{\text{stomatal conductance,}$
photosynthetic biochemistry}

Biochemistry optimization: Coordination hypothesis



Optimal setup =
equal limitation
by all factors

Optimally:

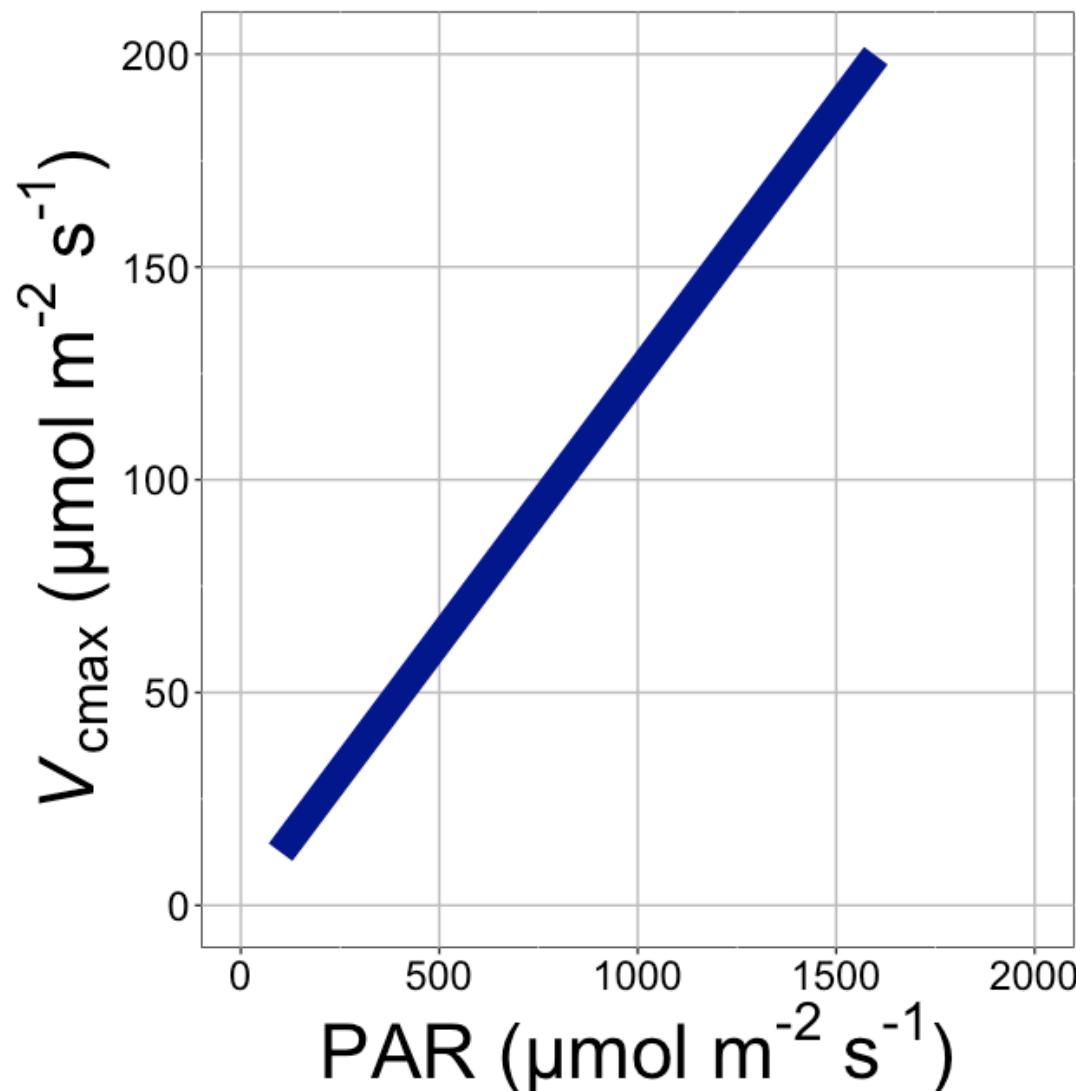
electron transport-limited (A_j) = Rubisco-limited (A_c)

$$A_j = A_c$$

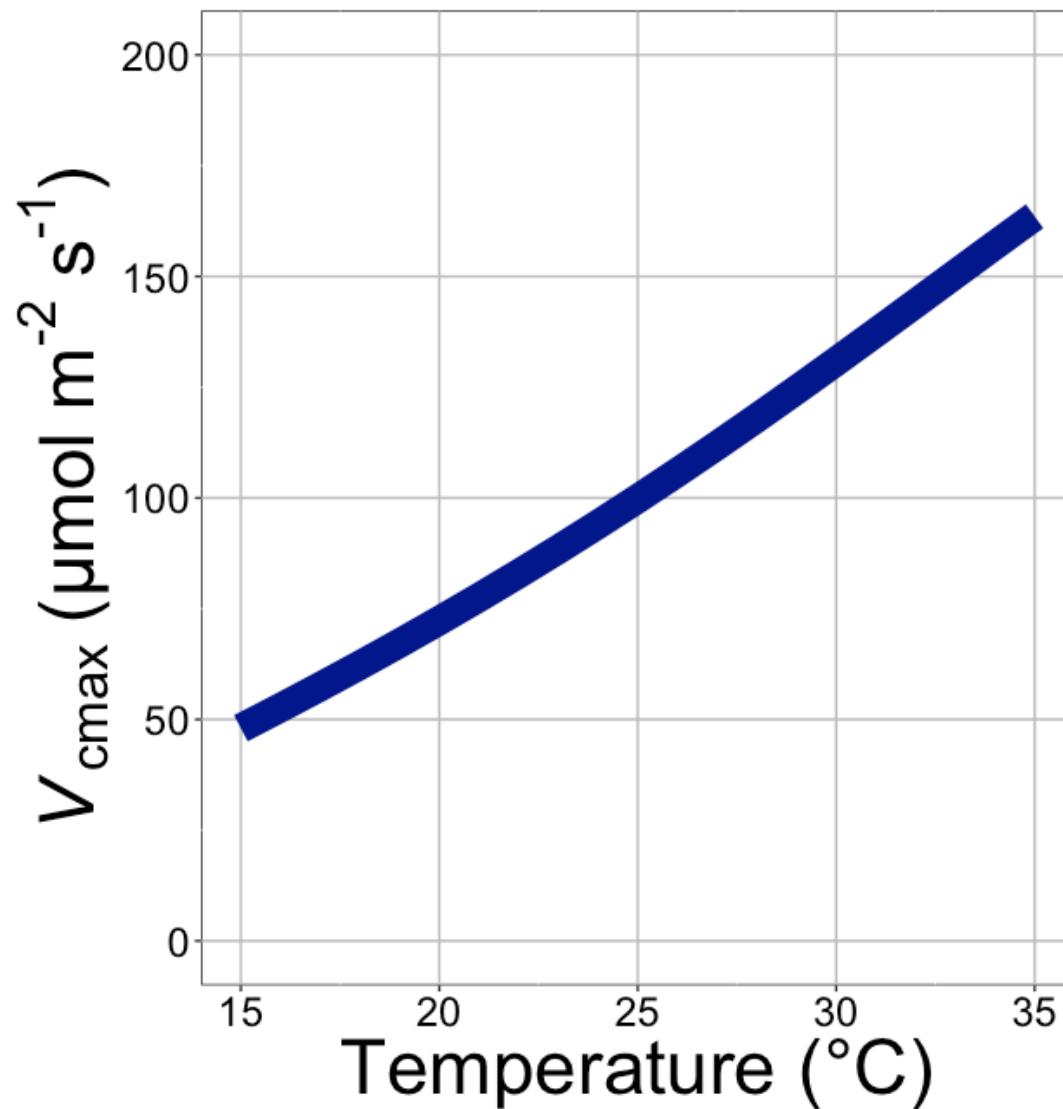
$$A_j = f\{\text{light}, T, CO_2\}$$

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

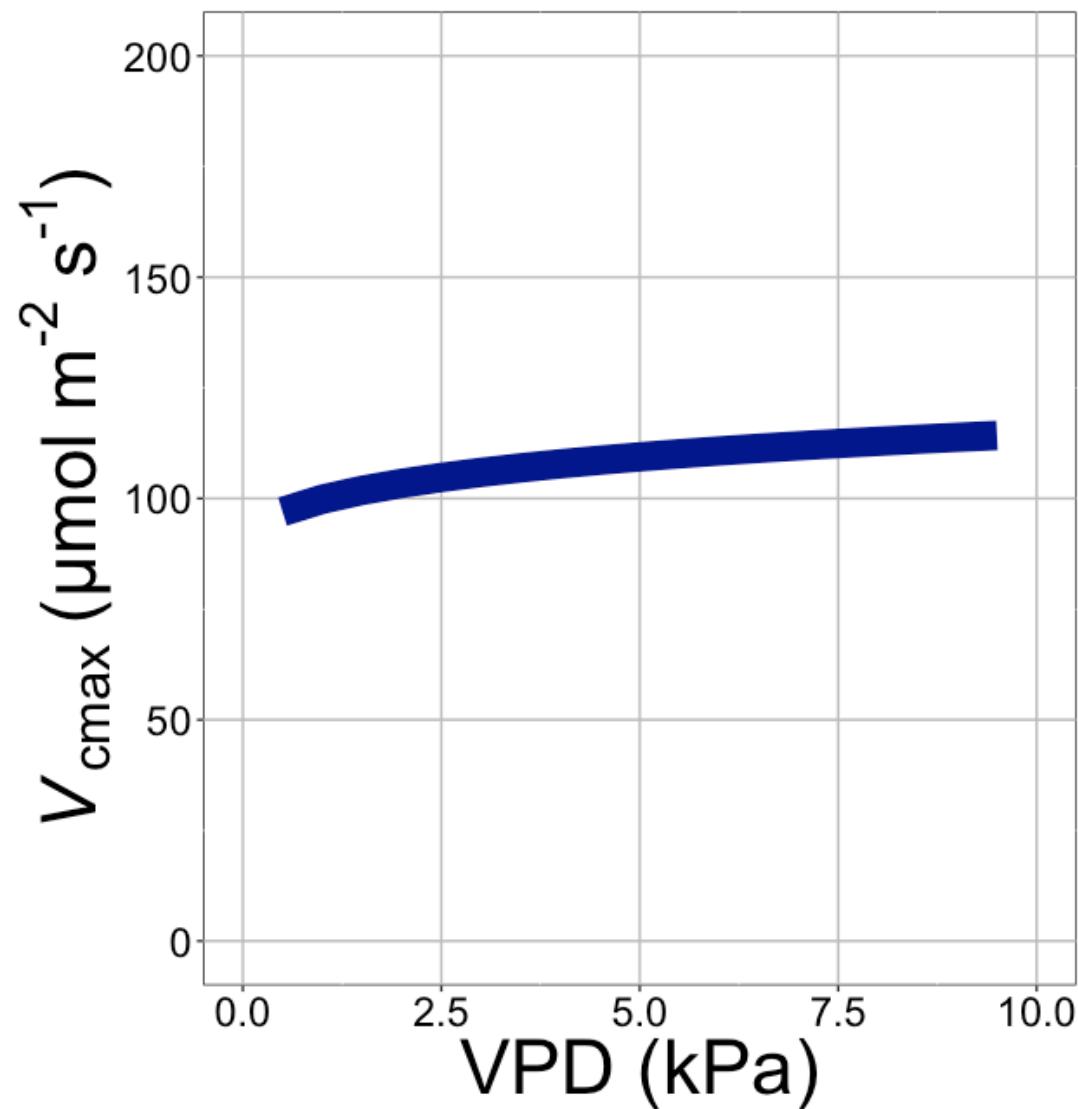
$$V_{\text{cmax}} = f \{\text{light}, T, CO_2\}$$



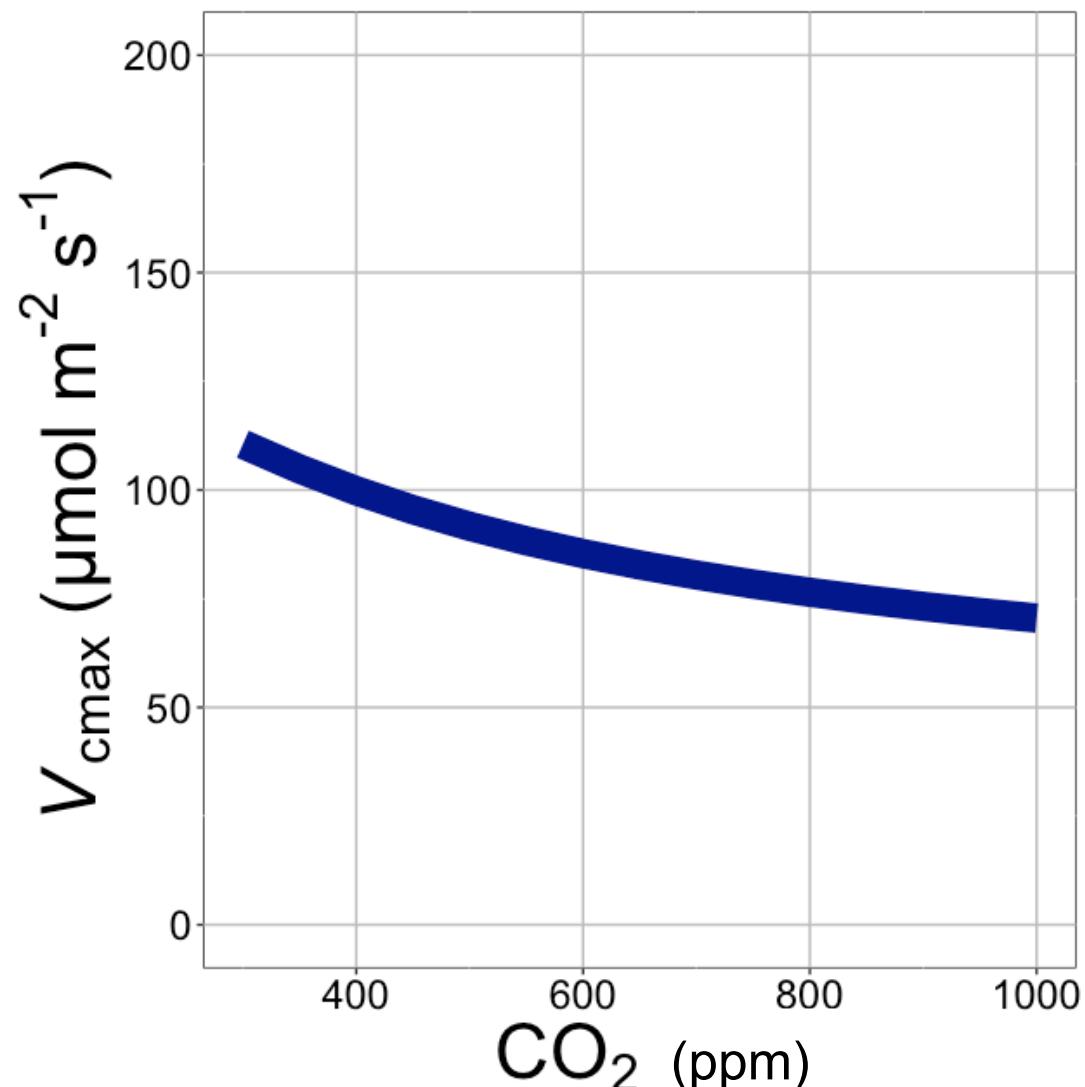
$V_{c\text{max}}$ increases
with light because
of greater electron
transport



$V_{c\max}$ increases
with temperature
because of greater
electron transport
and
photorespiration

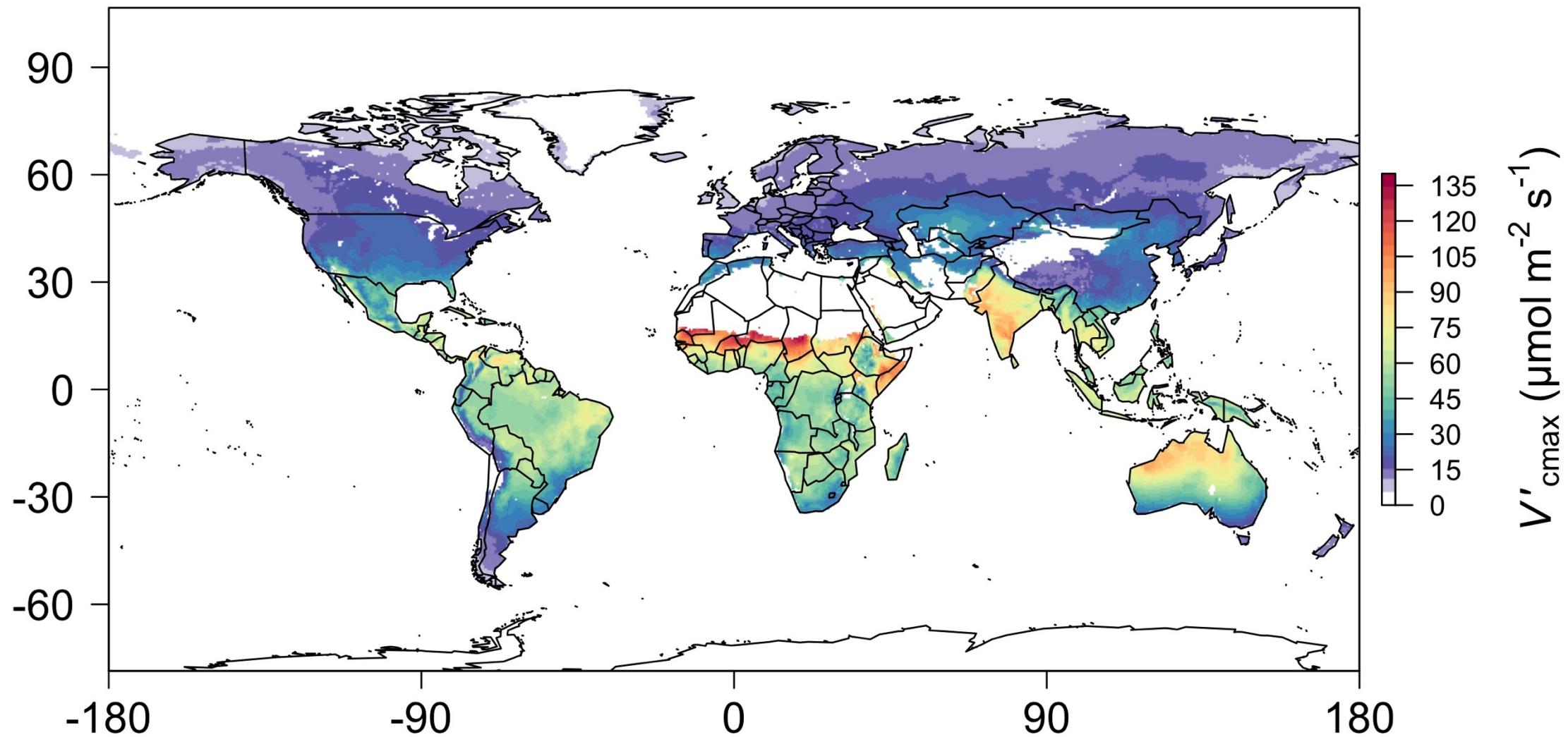


$V_{c\max}$ increases
with VPD because
of lower stomatal
conductance



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

Global, optimally acclimated traits!



Important note: optimality model adds no free parameters to Farquhar model and dynamically predicts most

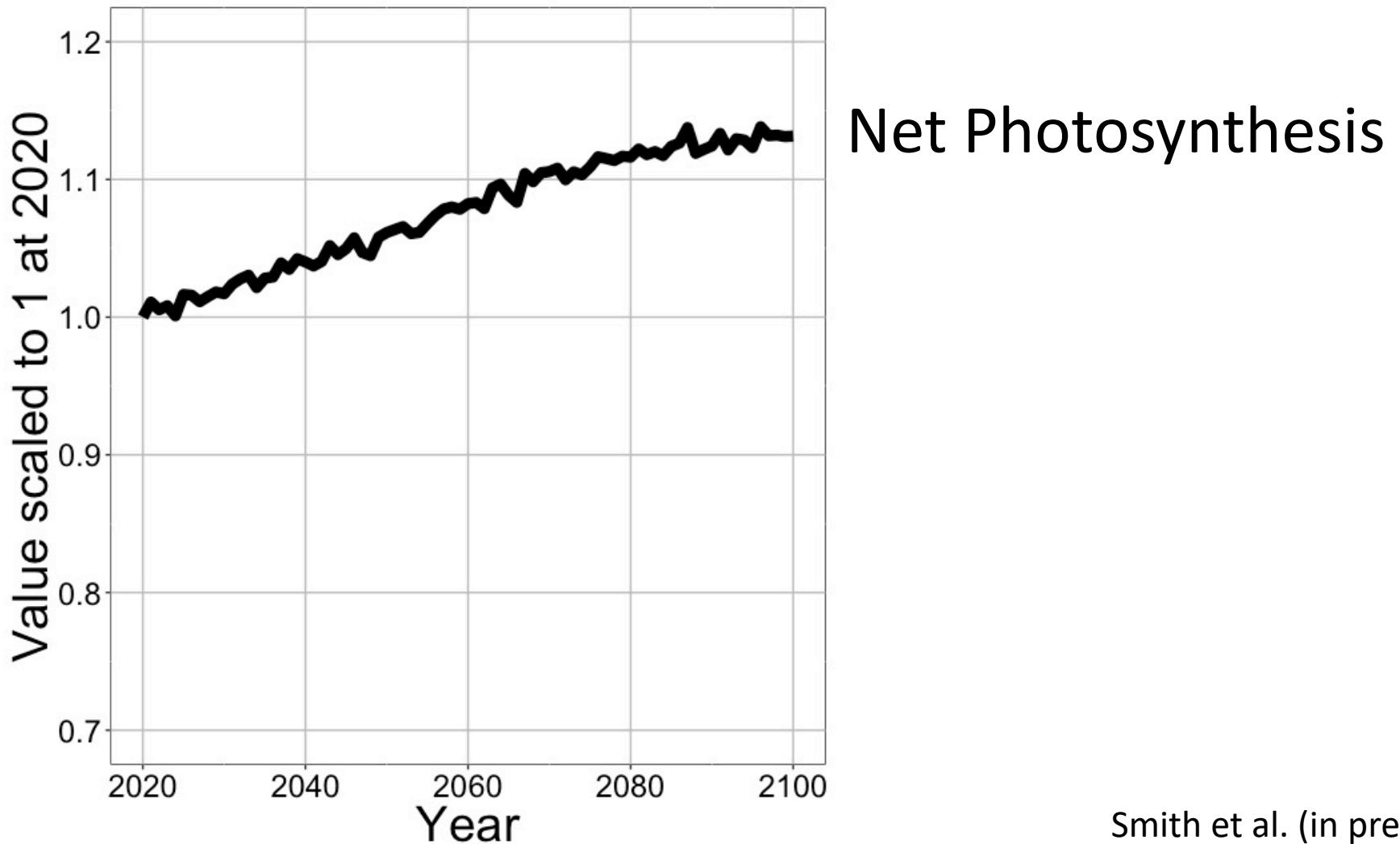
Important note: adds
acclimation, while reducing
parametric uncertainty

Let's run a model out into the future!

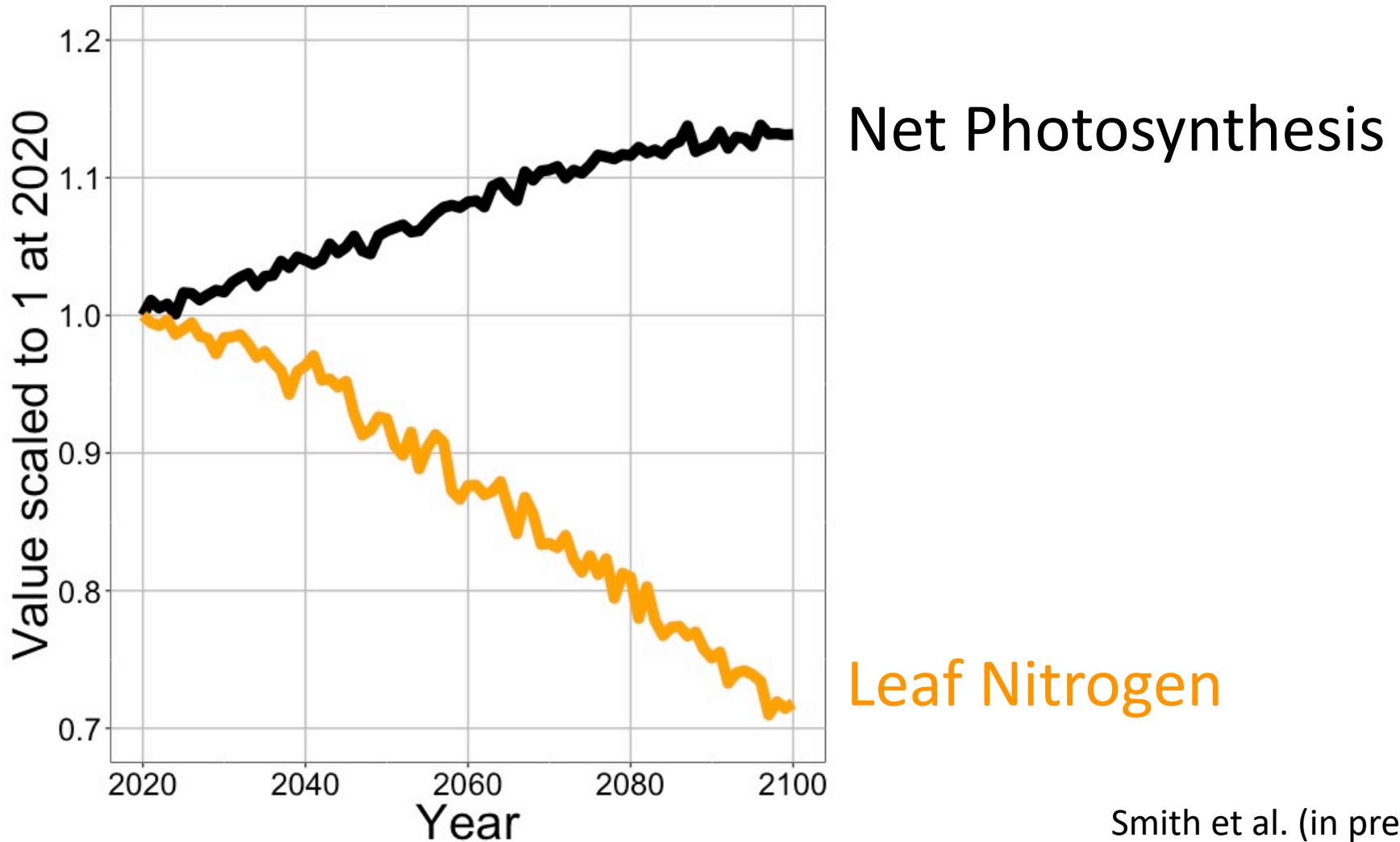


Energy Exascale
Earth System Model

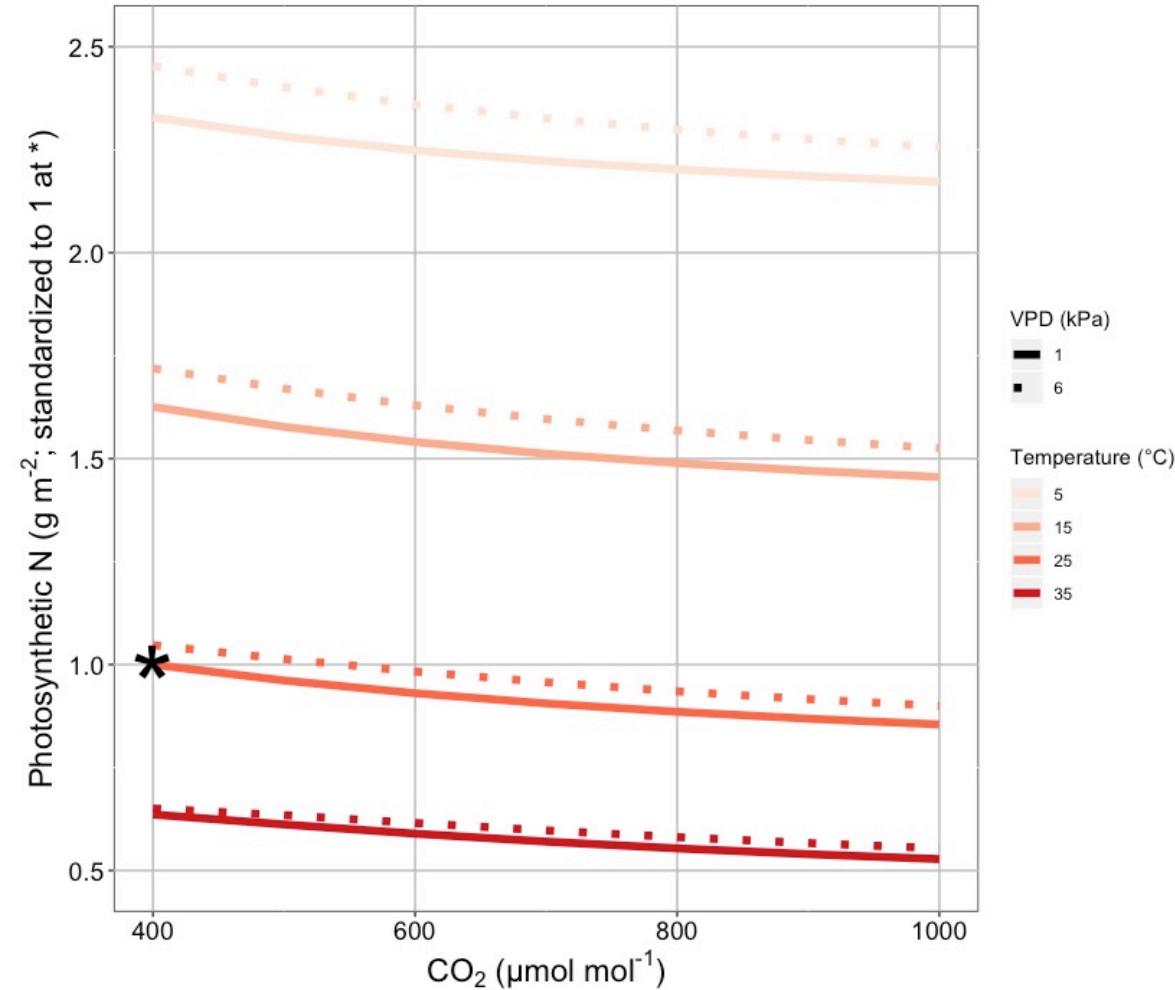
Photosynthesis increases in future



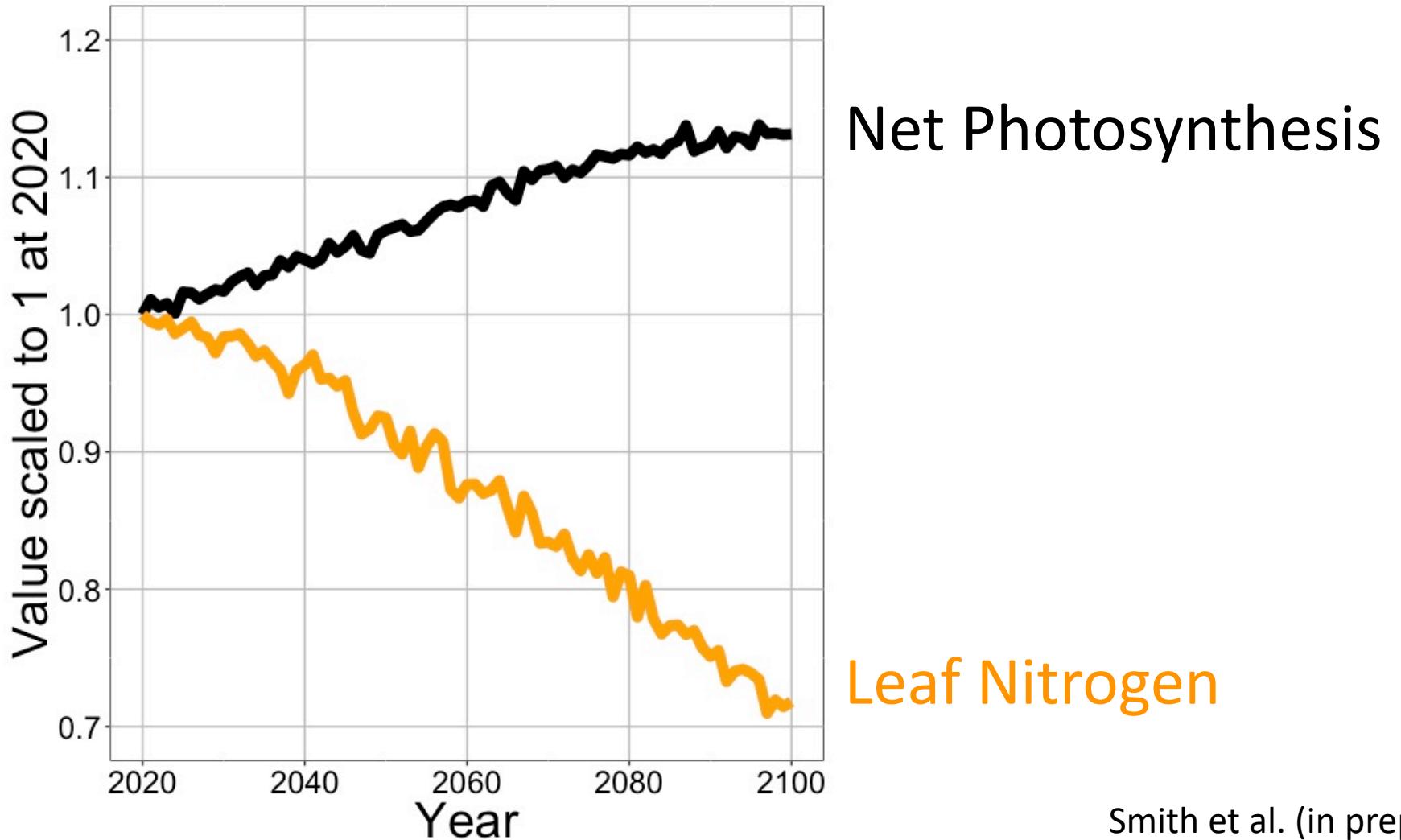
Photosynthesis increases in future (at lower nutrient use)



Leaf N declines due to warming and eCO₂

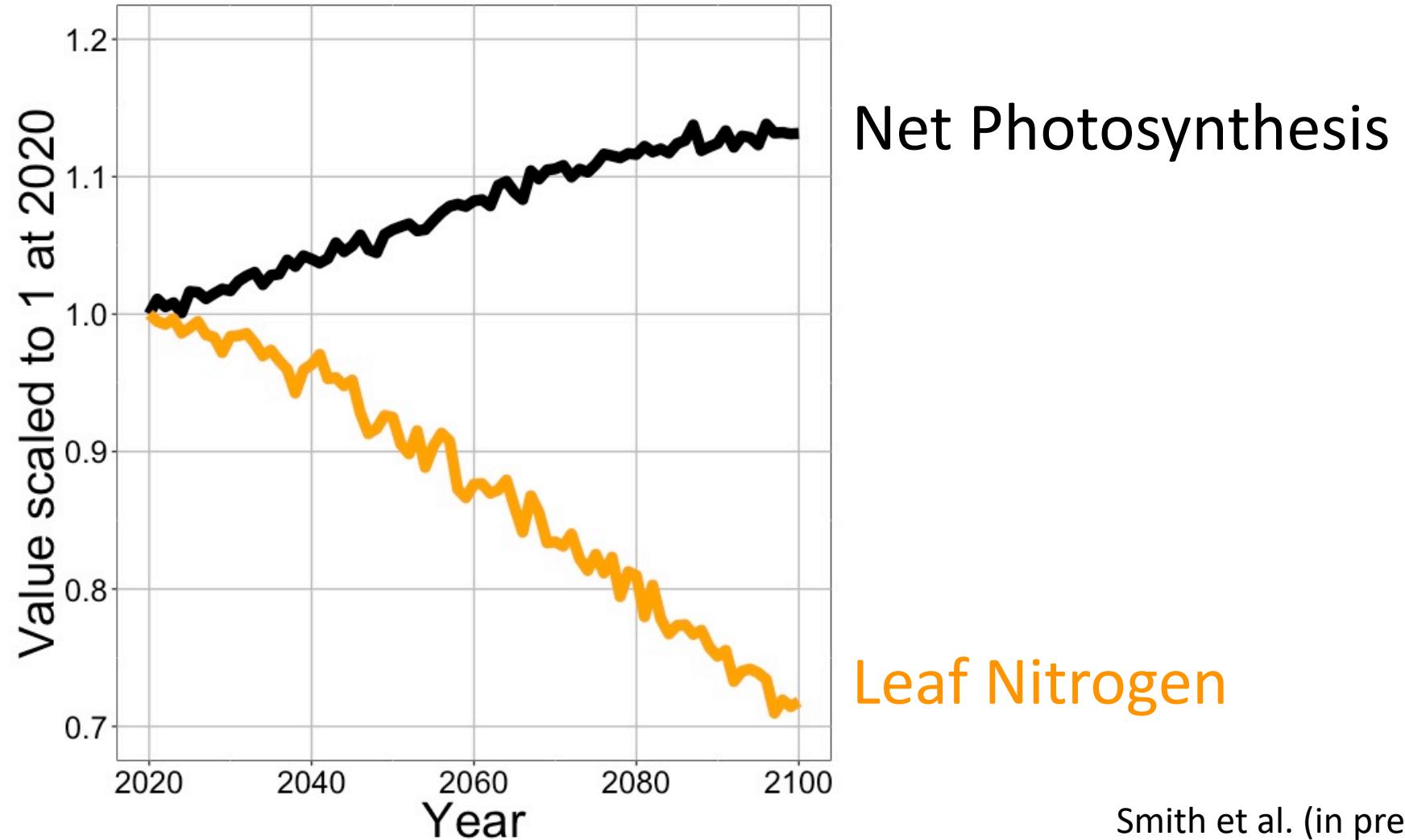


Photosynthesis increases in future (at lower nutrient use)



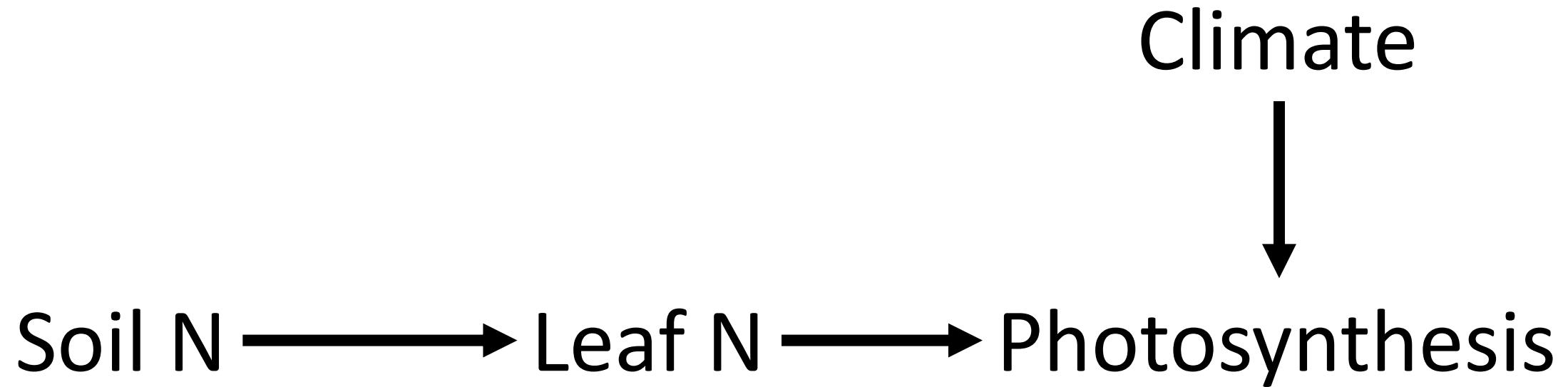
Photosynthesis increases in future (at lower nutrient use)

Base ELM
shows <5%
change in
leaf N

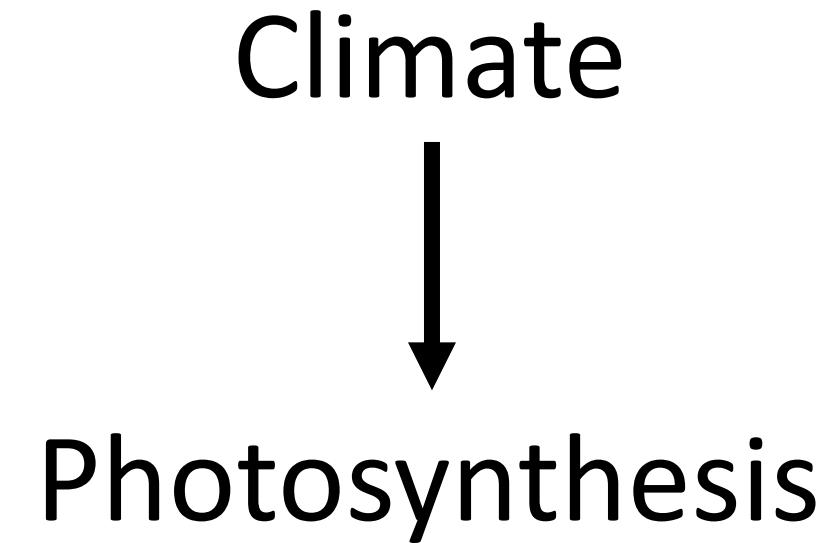


What does this all mean and is it real?

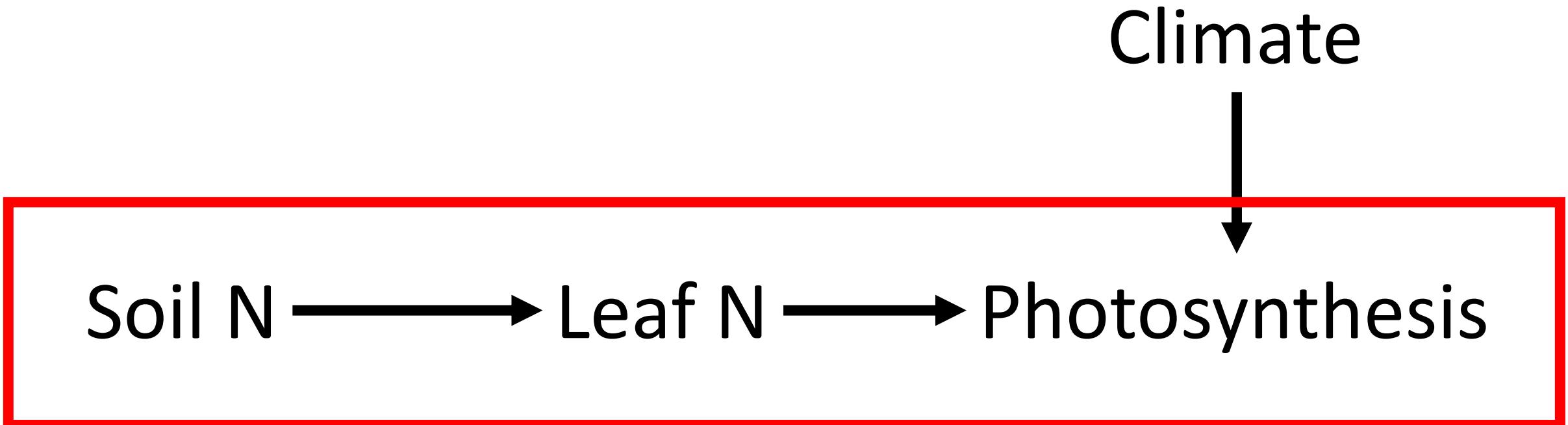
A typical LSM photosynthesis scheme



Least cost optimality model



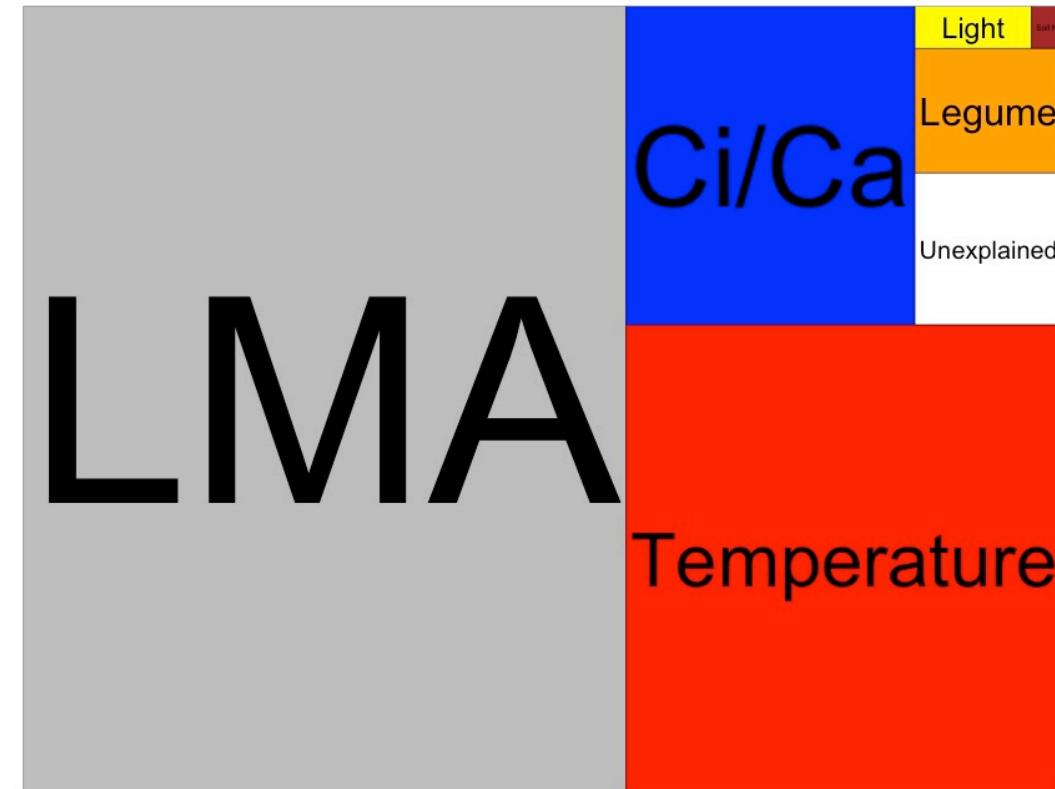
Let's check this assumption



Does leaf N respond to soil N?

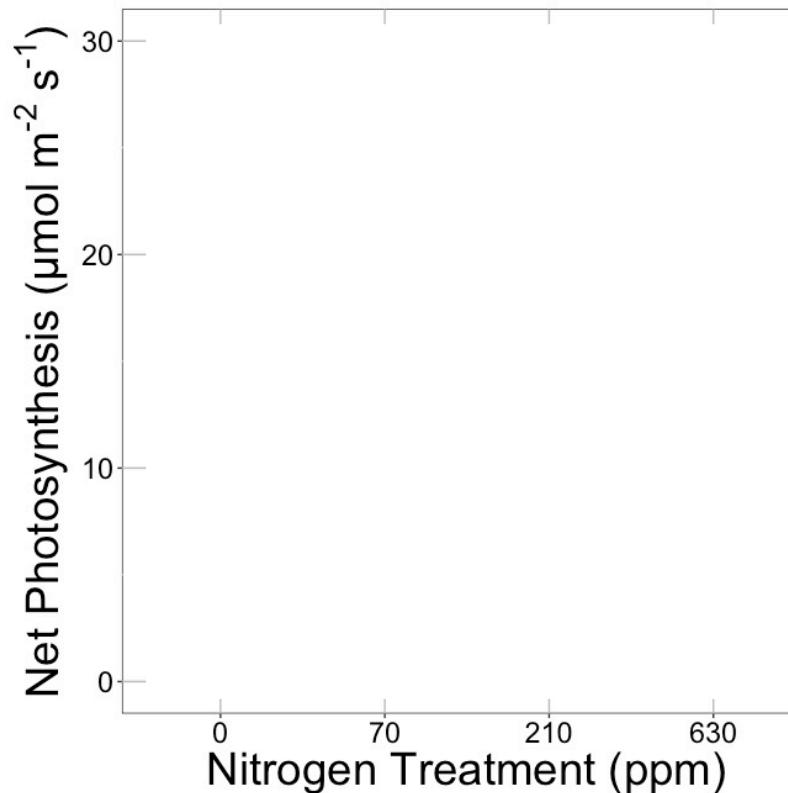
Each box is proportional to the variance in leaf N explained by each variable

Globally, N addition little impact on leaf N



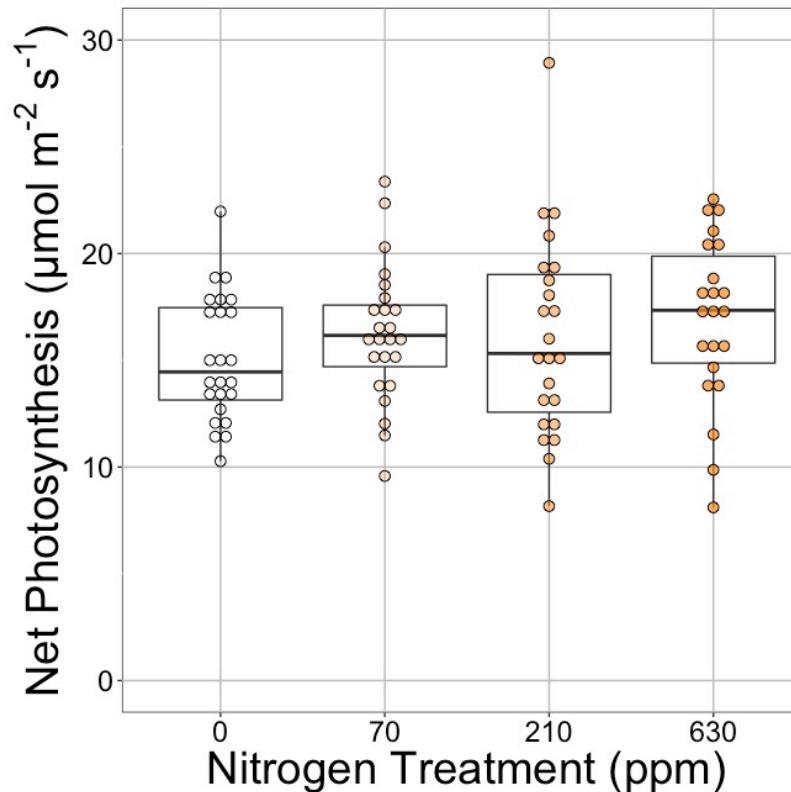
Each box is proportional to the variance in leaf N explained by each variable

Does photosynthesis respond to soil N?



Photosynthesis does not change with soil N

No change ($P = 0.42$)

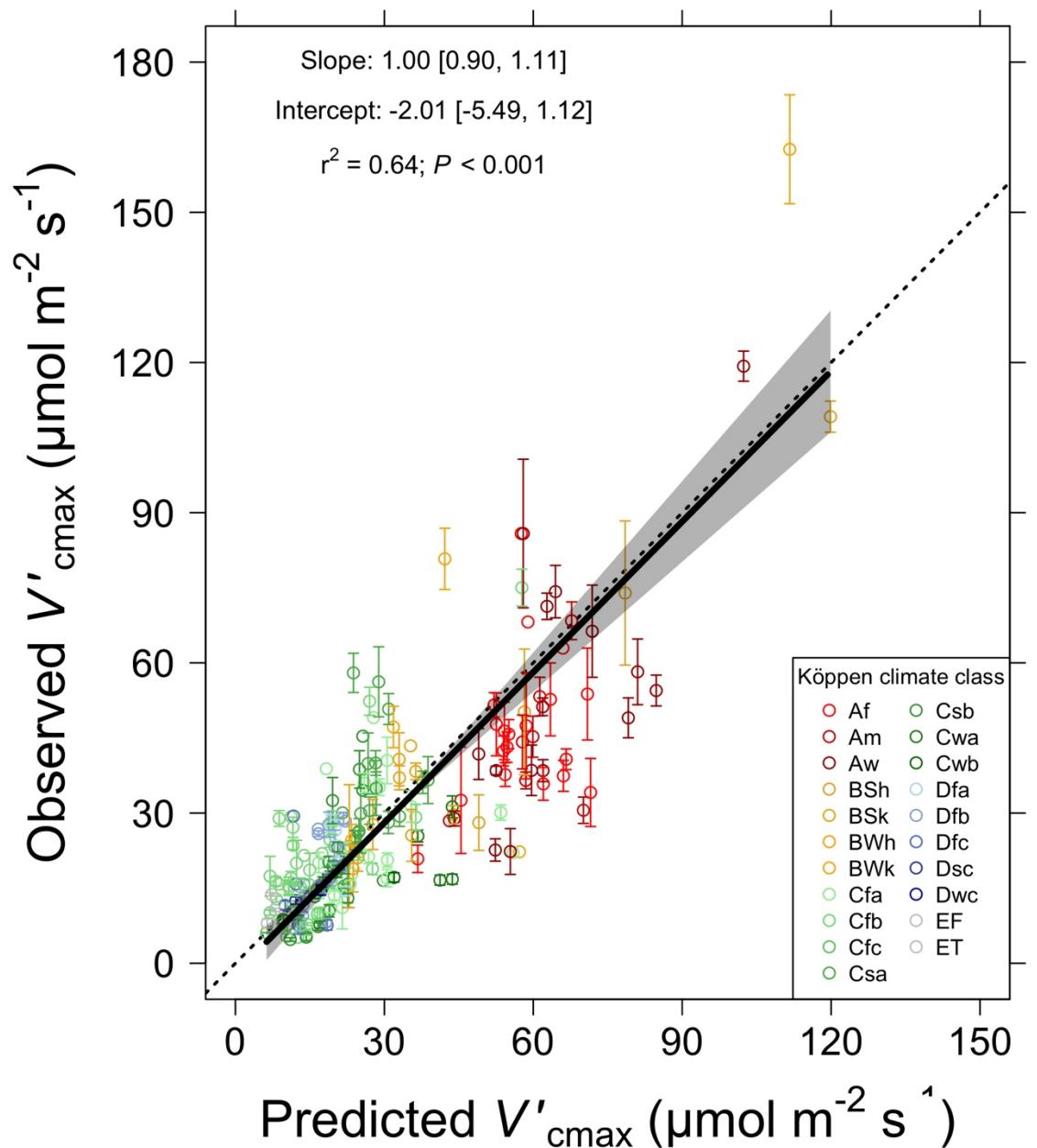


How does the optimality model do?

Climate

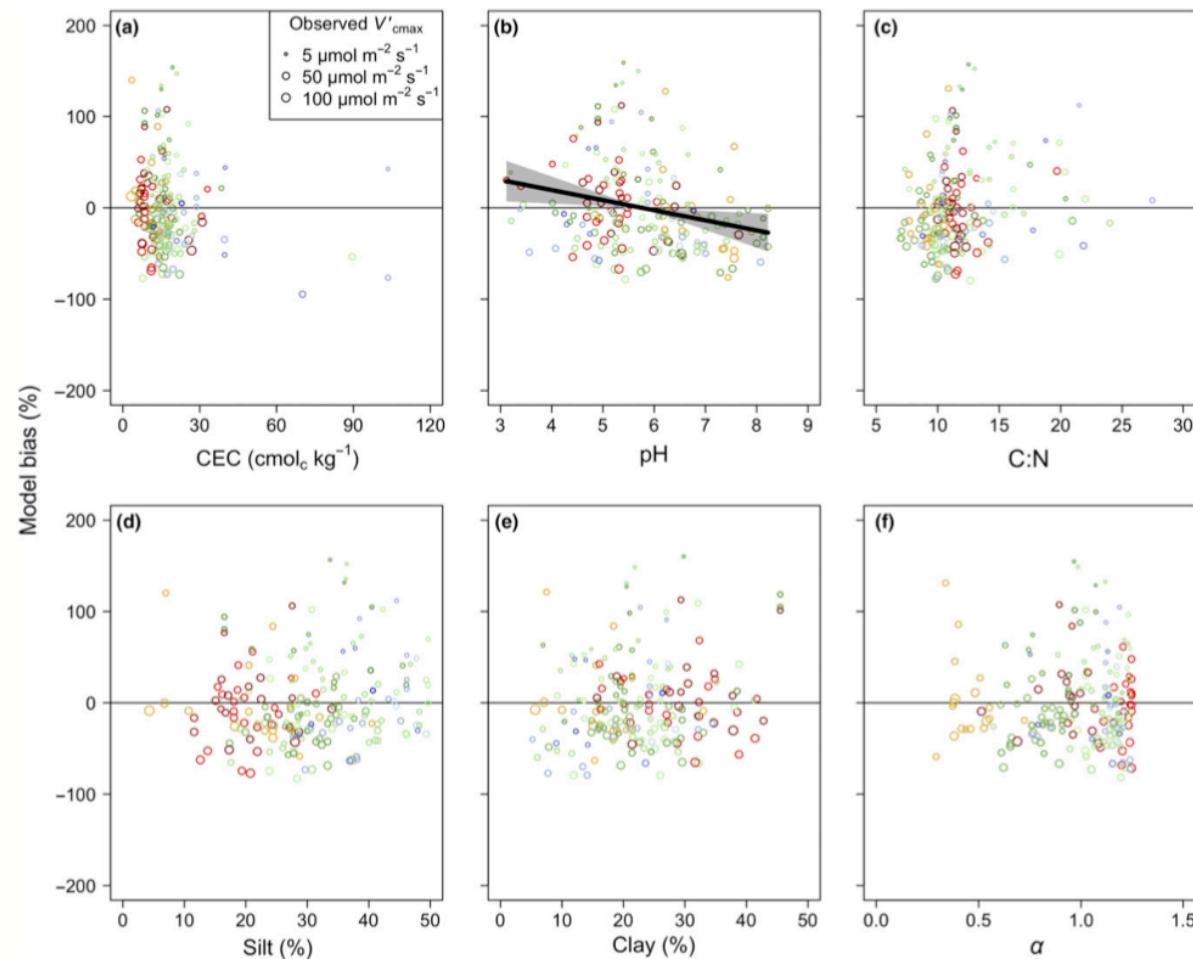


Photosynthesis



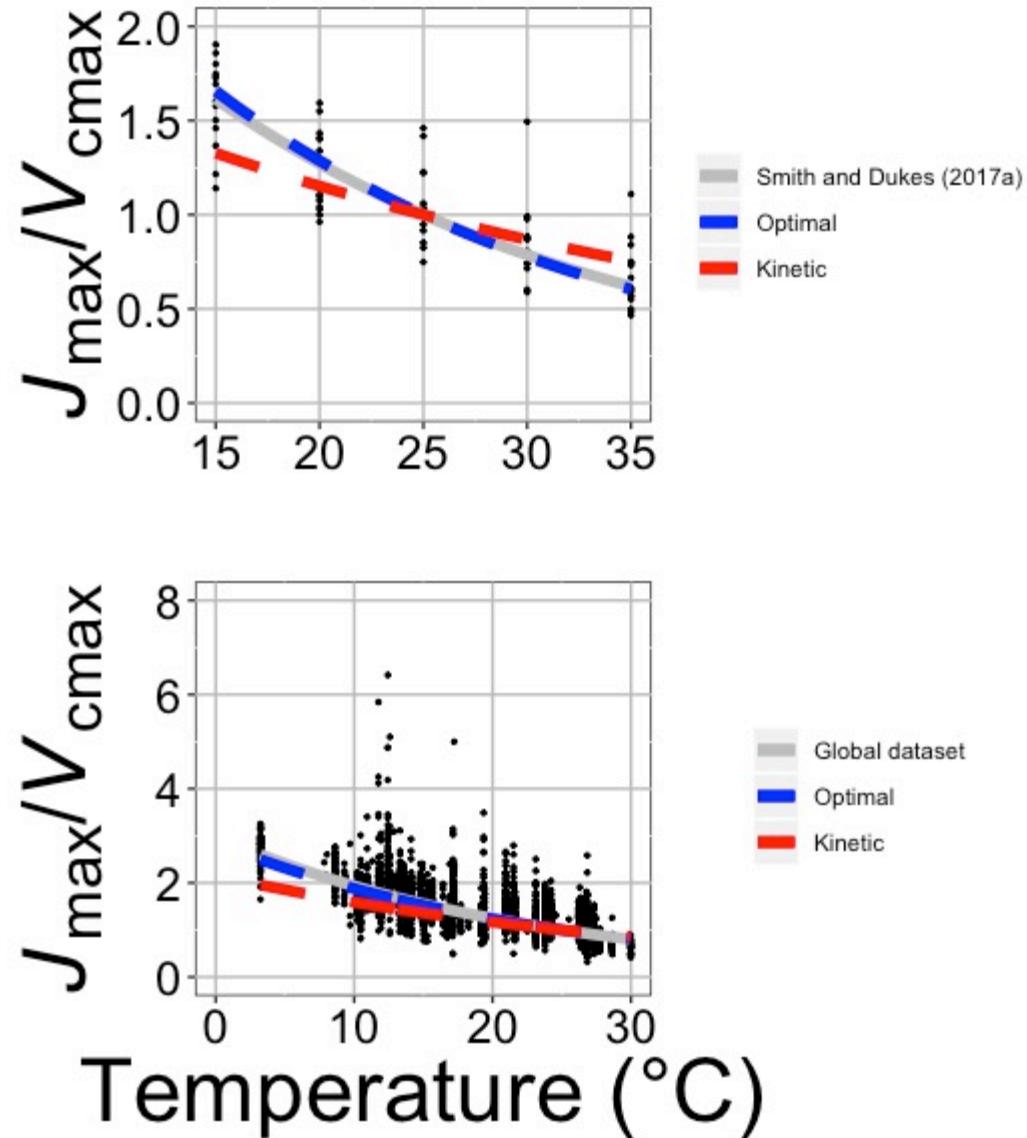
Optimal V'_{cmax} is
similar to
observed
values

There is little effect of soils on V'_{cmax}



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

Does it work under future
conditions?

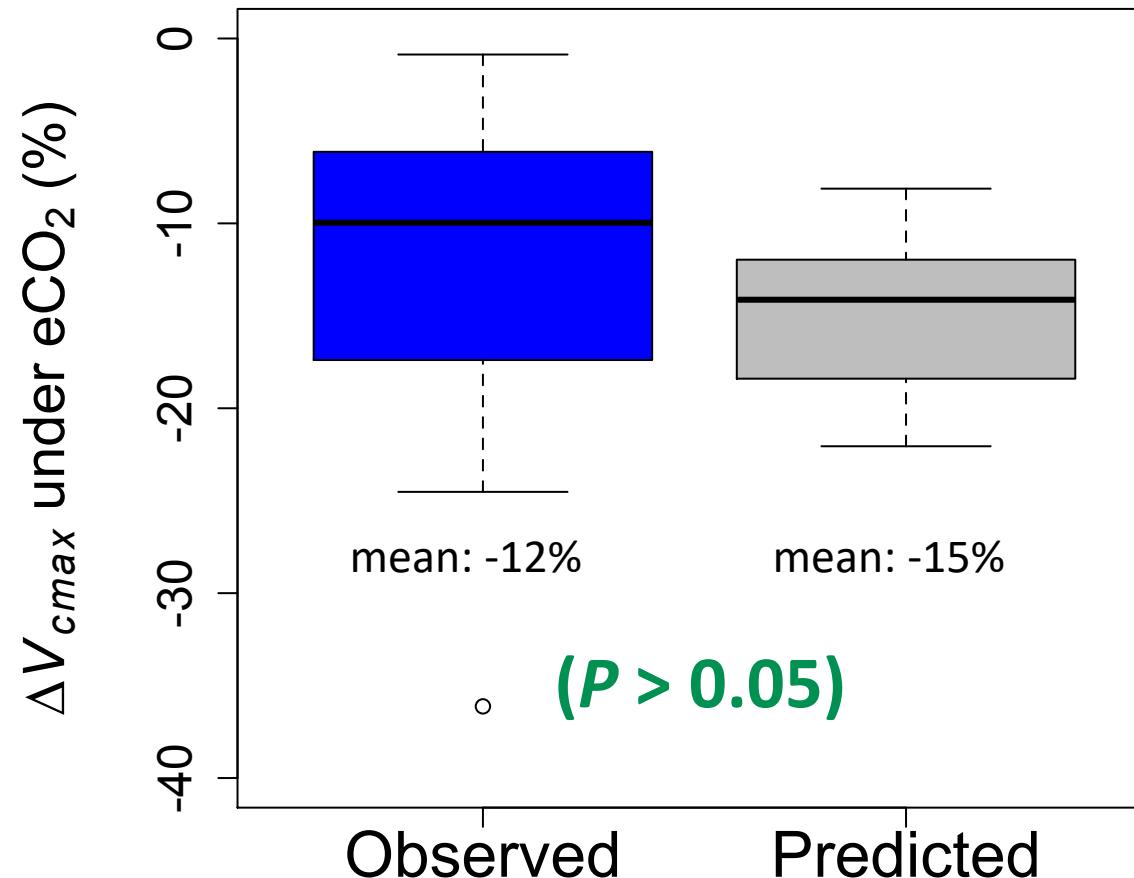


Photosynthetic traits change with temperature in ways expected from optimization

Data = $-0.051 \text{ } ^{\circ}\text{C}^{-1}$

Predicted = $-0.048 \text{ } ^{\circ}\text{C}^{-1}$

Photosynthetic traits change with future conditions in ways expected from optimization



Implications

Implications

- Optimal leaf biochemical setup is determined by climate

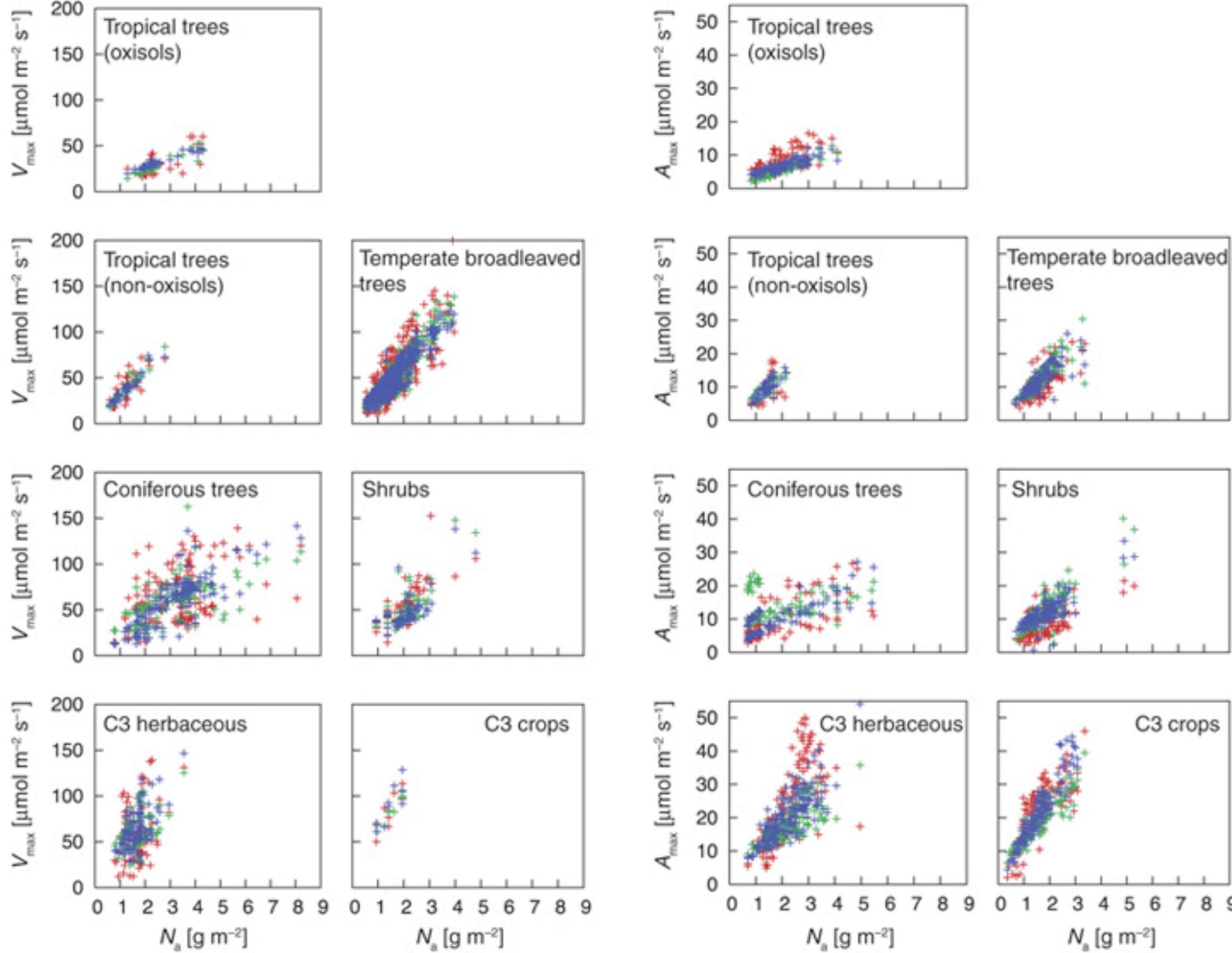
Implications

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

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

Axes need
flipped

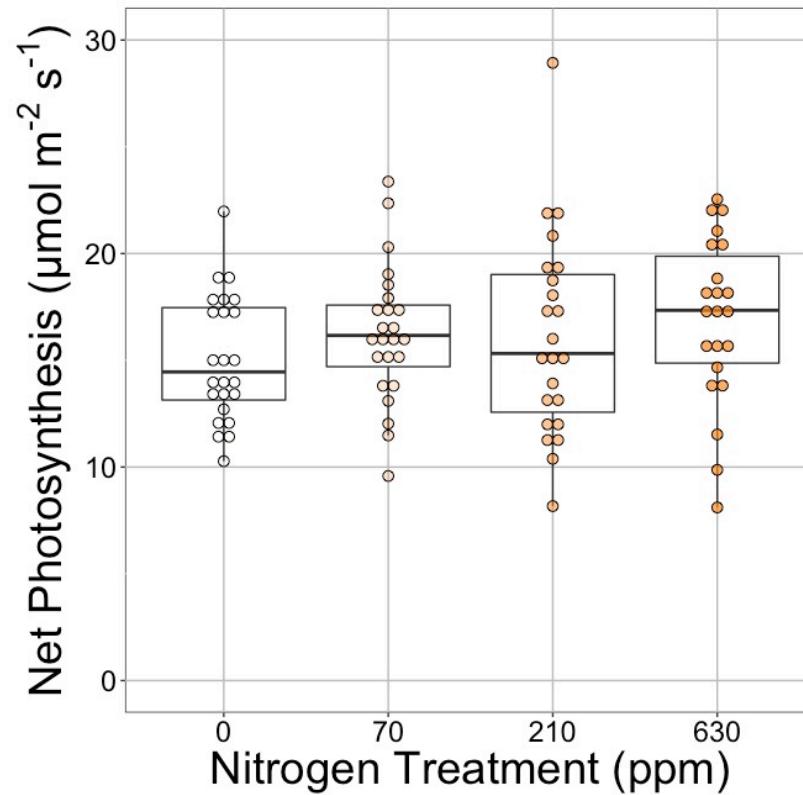


Implications

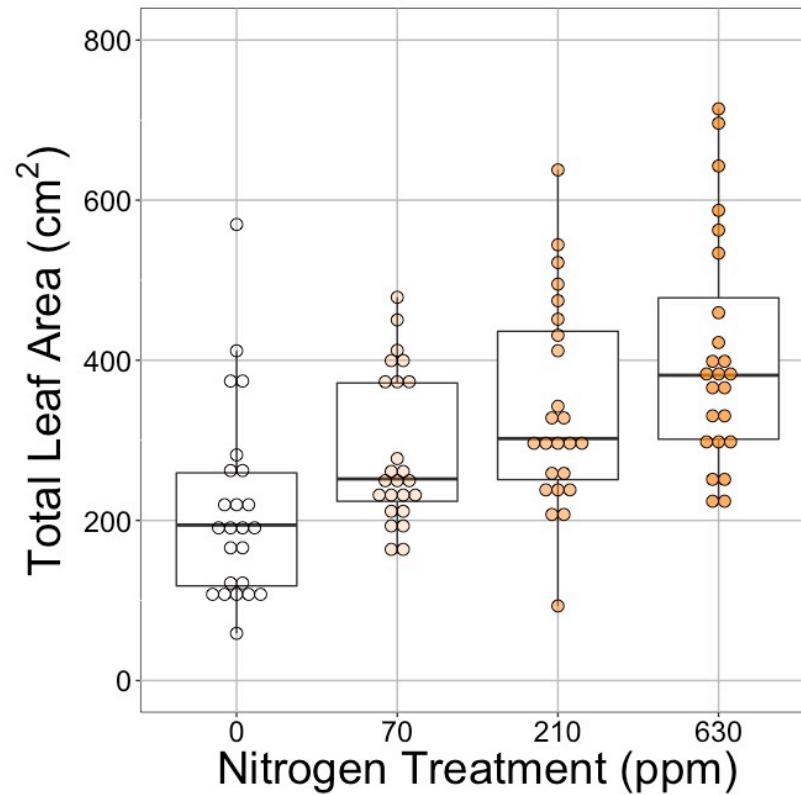
- Optimal leaf biochemical setup is determined by climate
- Plants mine for N to get the most leaves at the optimal setup
- Photosynthetic demand determines leaf N, not the other way around
- Soil N determines # of leaves (before canopy closure)

Soil N determines # of leaves?

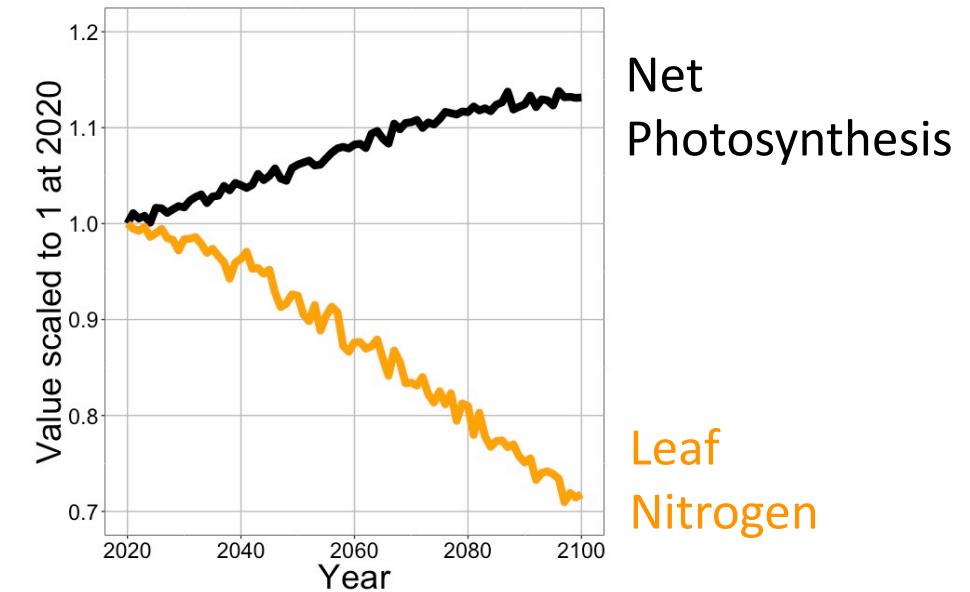
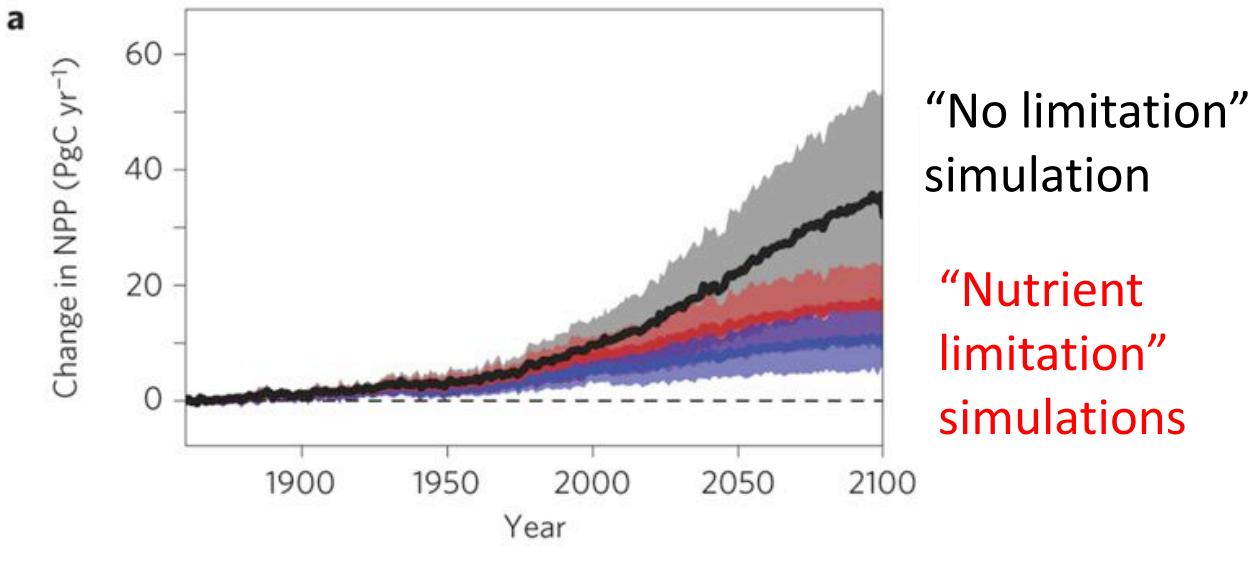
No change ($P = 0.42$)



91% increase ($P < 0.05$)

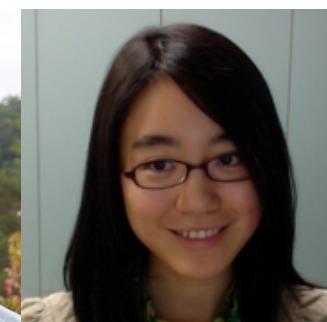
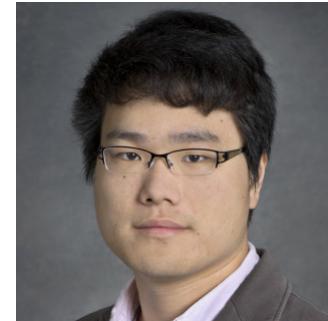


Next steps: How might this effect simulated nutrient limitation?



Acknowledgements

- Lawrence Berkeley National Lab
 - Bill Riley
 - Qing Zhu
- Smith Ecophysiology Lab
 - Lizz Waring (now AProf at Northeastern State U)
 - Helen Scott (now in industry)
 - Evan Perkowski (PhD student)
 - Risa McNellis (MS Student)
- Next Generation Ecosystem Modeling Group
 - Colin Prentice (Imperial College)
 - Trevor Keenan (UC Berkeley)
 - Wang Han (Tsinghua U)
 - Beni Stocker (ETH Zurich)



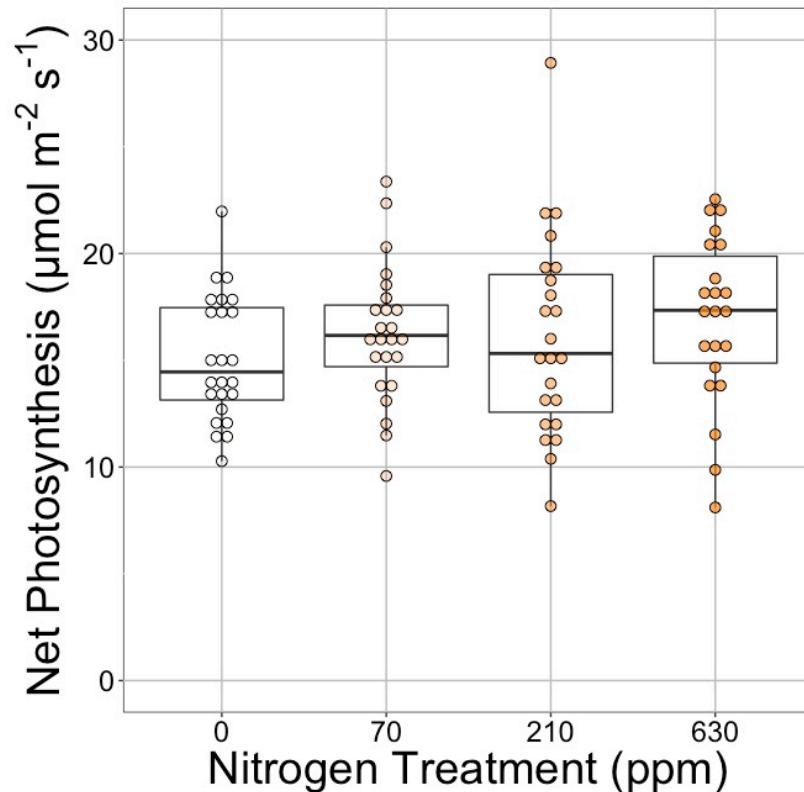
Presentation available at:
www.github.com/SmithEcophysLab/seminar/lmwg_2020



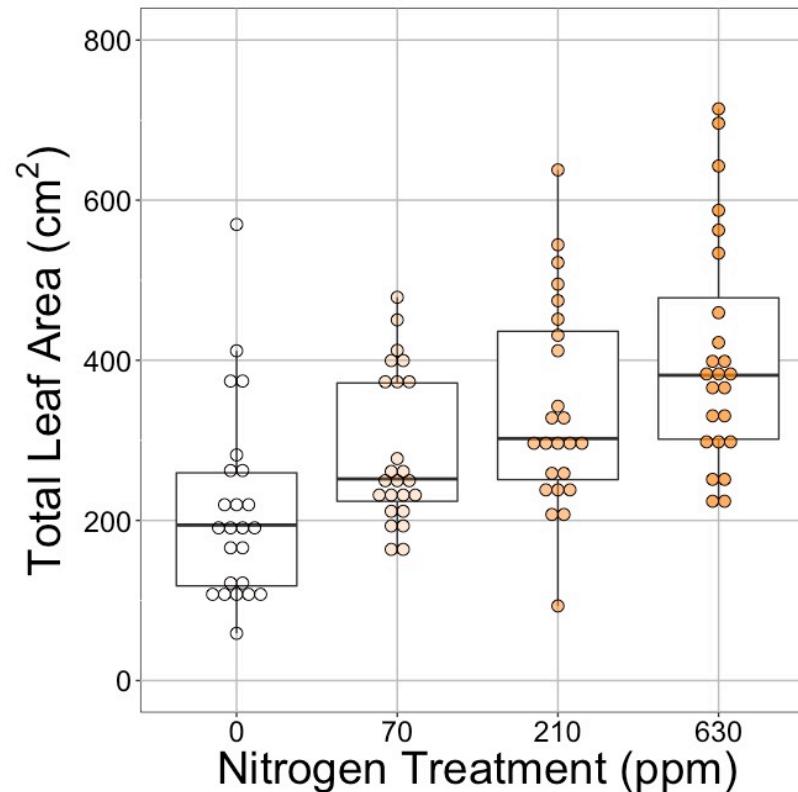
Extra slides

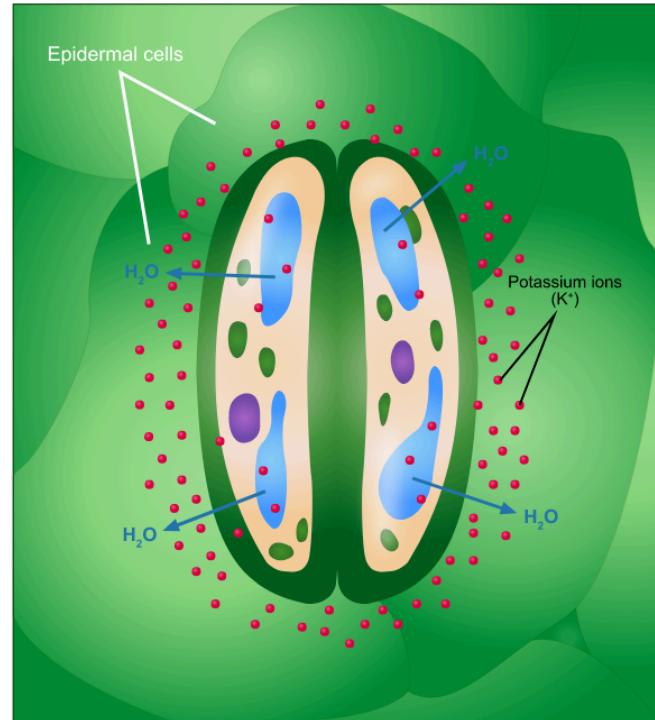
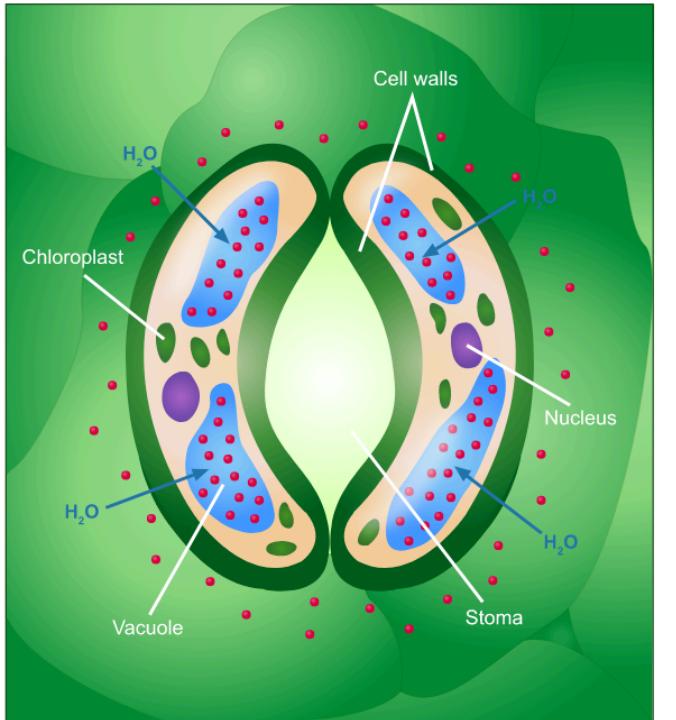
Leaf area, but not photosynthesis increases with N addition

No change ($P = 0.42$)



91% increase ($P < 0.05$)





Open stomata:

Benefits

- High CO_2 influx

Costs

- High water outflux

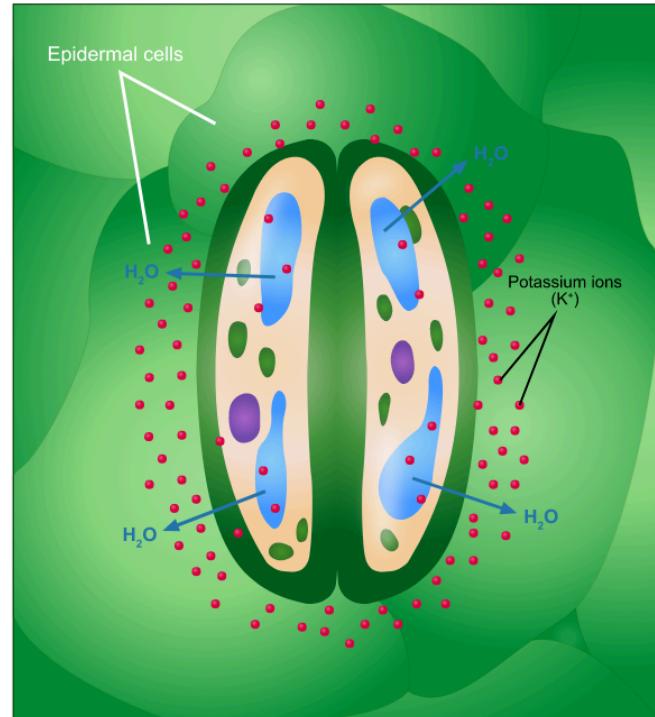
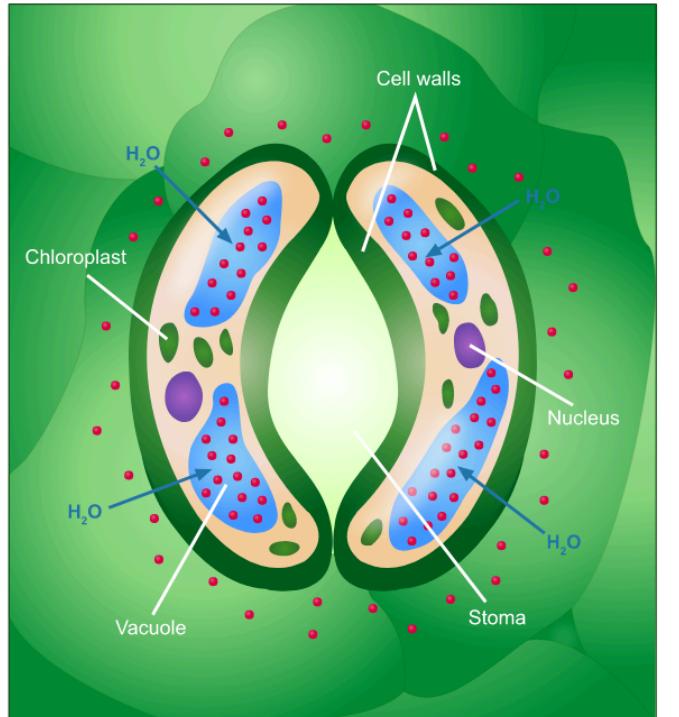
Closed stomata:

Benefits

- Low water outflux

Costs

- Low CO_2 influx



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

Optimal stomatal conductance

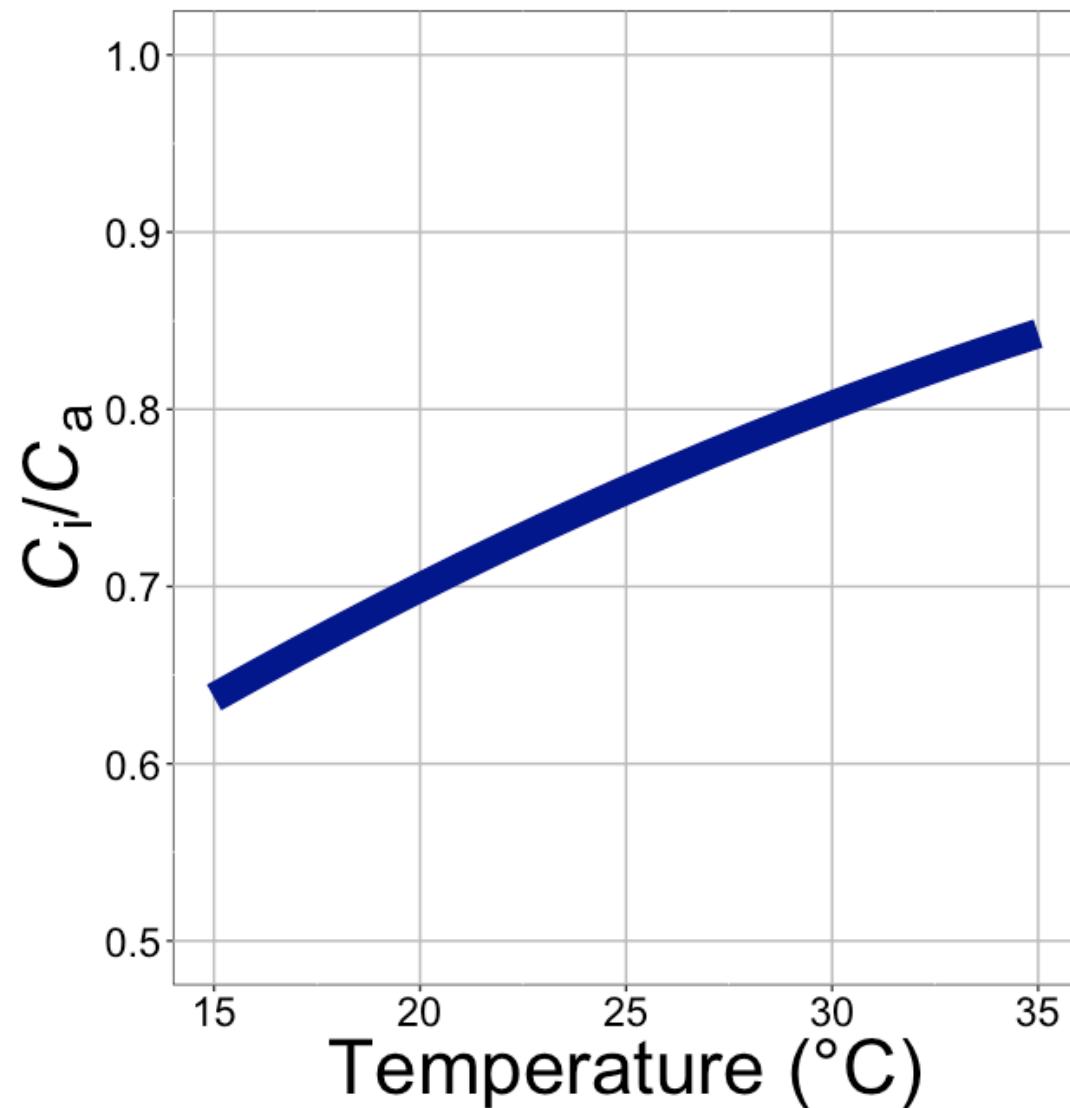
Optimal conductance maximizes photosynthesis
at least water loss and nutrient use

- Water loss is from transpiration
- Nutrient use is nutrients used to maintain Rubisco
 - Rubisco proxy is V_{cmax}

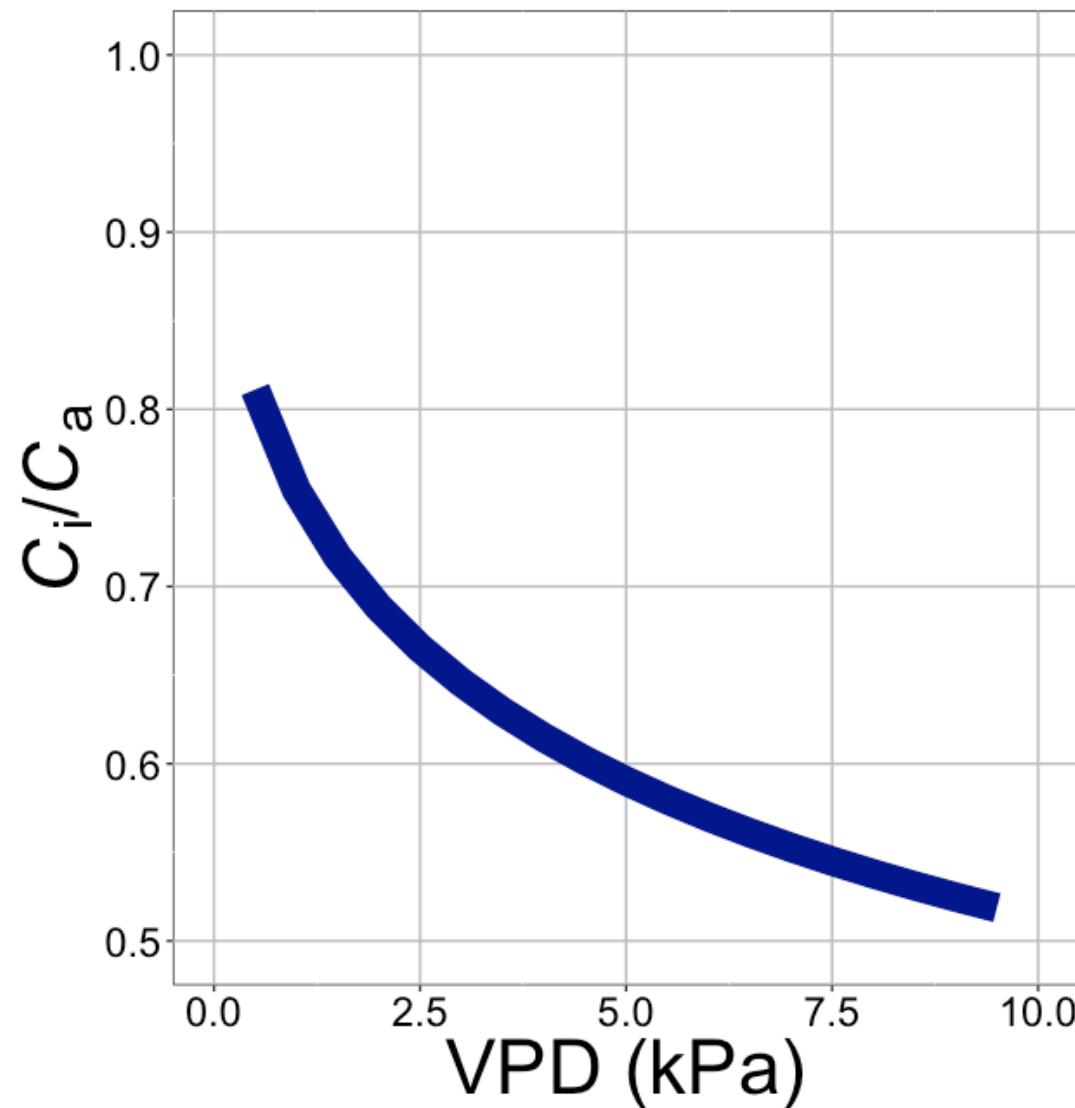
Stomatal conductance trait

The ratio of CO₂ in the leaf to CO₂ outside of the leaf (C_i/C_a)

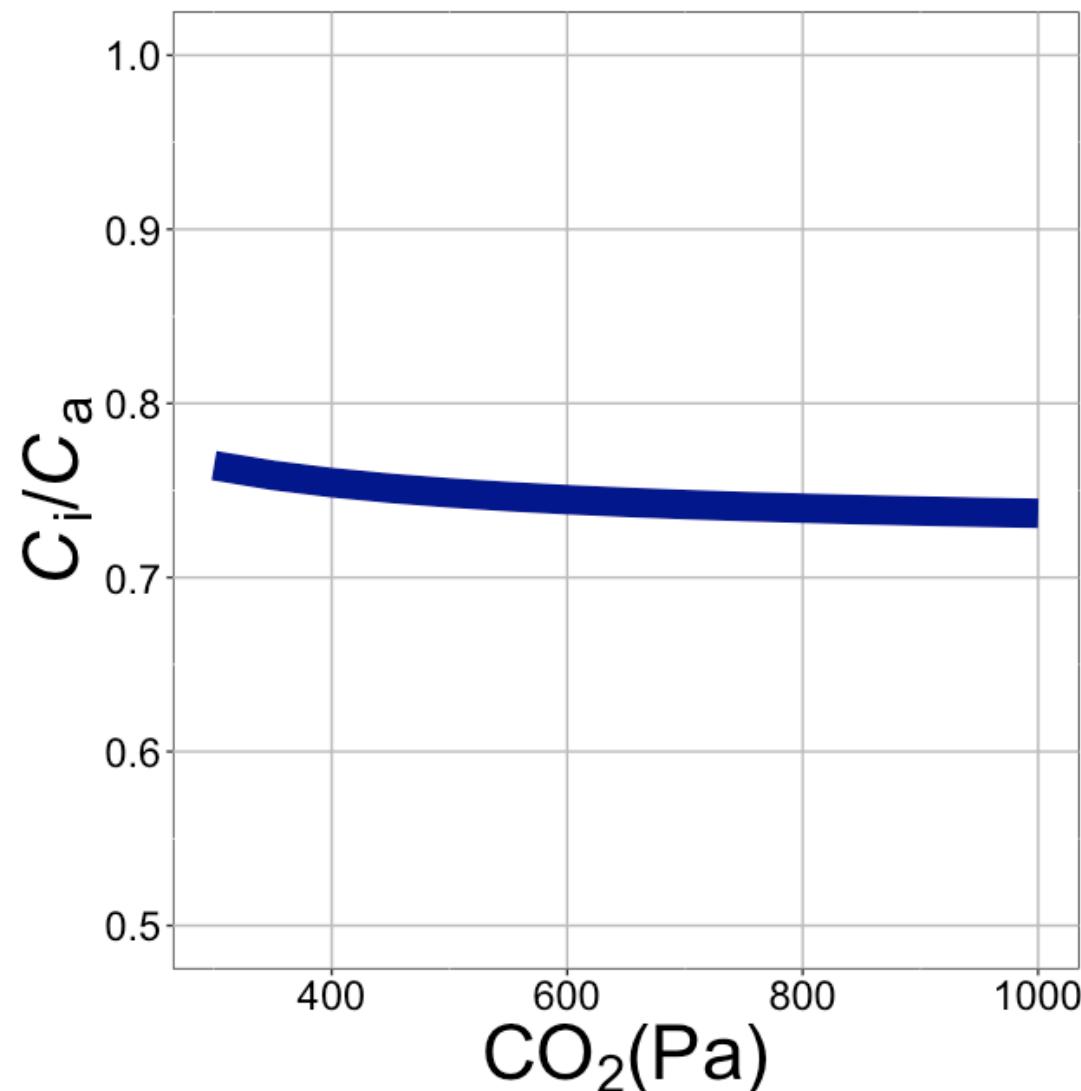
$C_i/C_a = f\{\text{temperature,}$
 $\text{CO}_2,$
 $\text{vapor pressure deficit}\}$



C_i/C_a increases
with temperature
because of greater
photorespiration



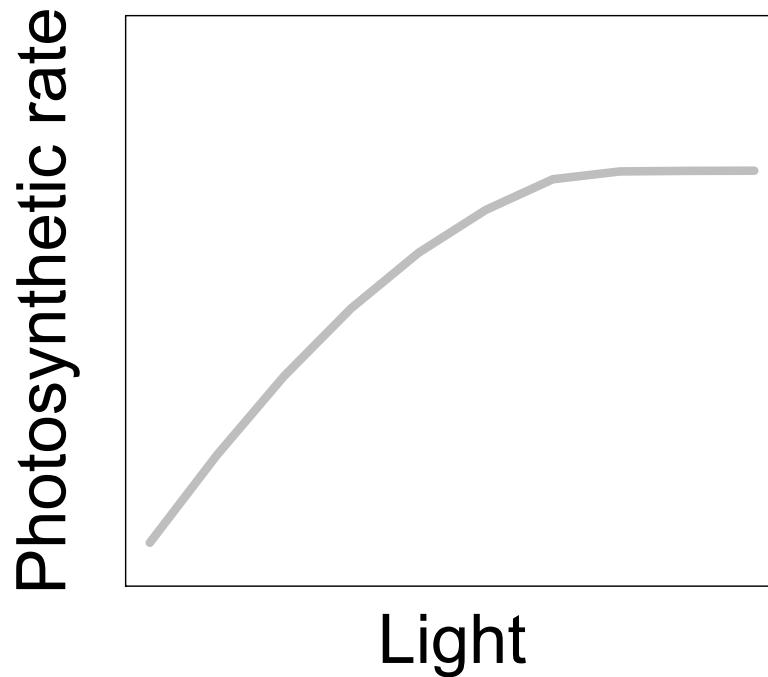
C_i/C_a decreases
with VPD because
of greater water
loss



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

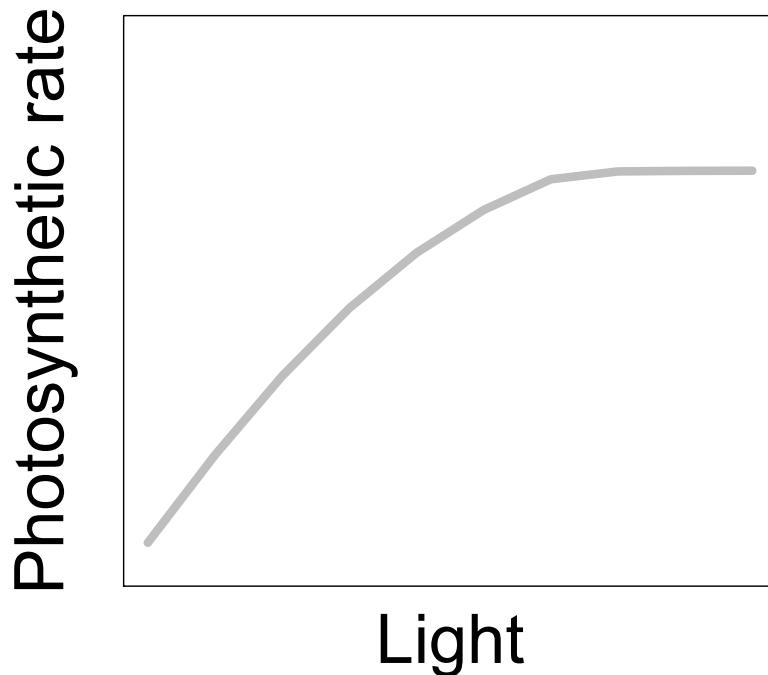
Photosynthetic acclimation can be seen as the change in the instantaneous responses with longer-term exposure

Acclimated to high light



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

Acclimated to high light



Acclimated to low light

