# Thoughts on improving $C_4$ photosynthesis in TBMs

**Nick Smith**

**w/ contributions from Helen Scott, Zinny Ezekannagha, Cameron Merryman, and USGS Powell Center $C_4$ working group**

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# Quick physiology reminders

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# Photorespiration

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# Photorespiration

- Rubisco : RibUlose – 1,5 – BISphosphate Carboxylase and Oxygenase
- Catalyzes $CO_2$ and $O_2$
- Catalyzing $O_2$ leads to “wasteful” respiration (loss of $CO_2$)
- Increases as $O_2$ increases
- Increases with temperature

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# 2 types of photosynthesis systems in TBMs

- $C_3$: Most plants
- $C_4$: Separate carbon acquisition and sugar creation in space

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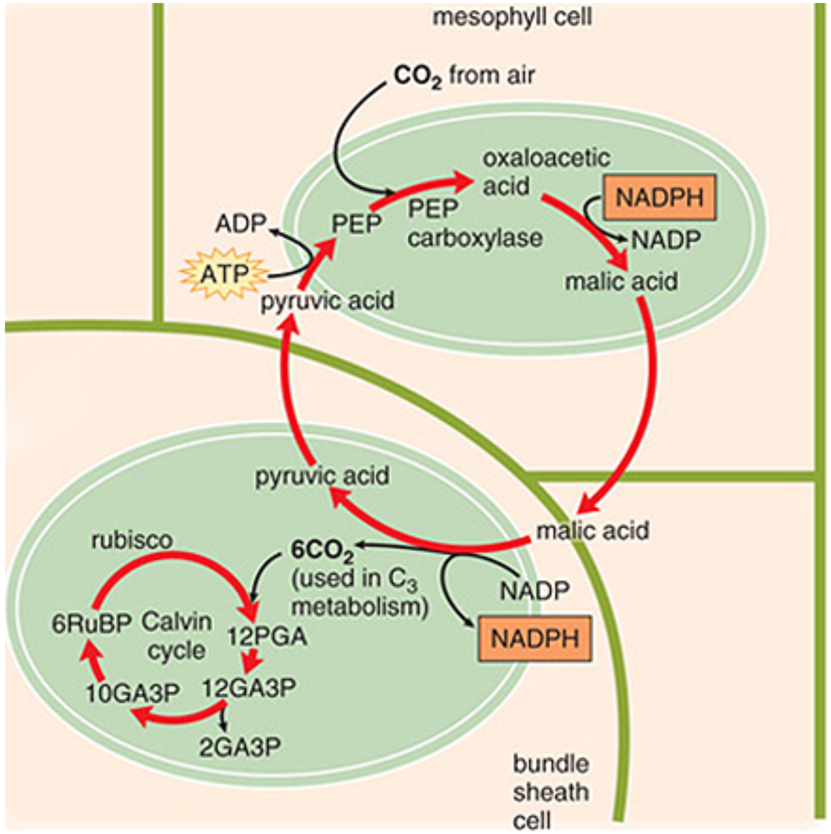
# $C_4$ photosynthesis

- PEP carboxylase captures $CO_2$ and creates a 4 carbon sugar in mesophyll
- Moves sugar to bundle sheath, where $CO_2$ is removed
  - Bundle sheath cells surround veins
- Calvin cycle progresses as normal
- "Costs" a little extra ATP



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# $C_4$ photosynthesis - benefits

PEP carboxylase is not an oxygenase

- Good at capturing $CO_2$
- Good in low $CO_2$ environments
- Good in hot, dry environments
  - Can close stomata

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# Current representation of $C_4$ photosynthesis in TBMs

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*Aust. J. Plant Physiol.*, 1992, **19**, 519–38

# Coupled Photosynthesis–Stomatal Conductance Model for Leaves of $C_4$ Plants*

*G. James Collatz*[A], *Miquel Ribas-Carbo*[B] *and Joseph A. Berry*[A]

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# Collatz et al. (1992)

- Photosynthesis is limiting rate of three processes:
  - Rubisco carboxylation ($A_c$)
  - Light-related processes ($A_j$)
  - PEP carboxylation ($A_p$)
- Governing equations
  - $A_c = V_{cmax,25} * f(T_{leaf})$
  - $A_j = \phi I$
  - $A_p = k_{p,25} * f(T_{leaf}) * C_i$

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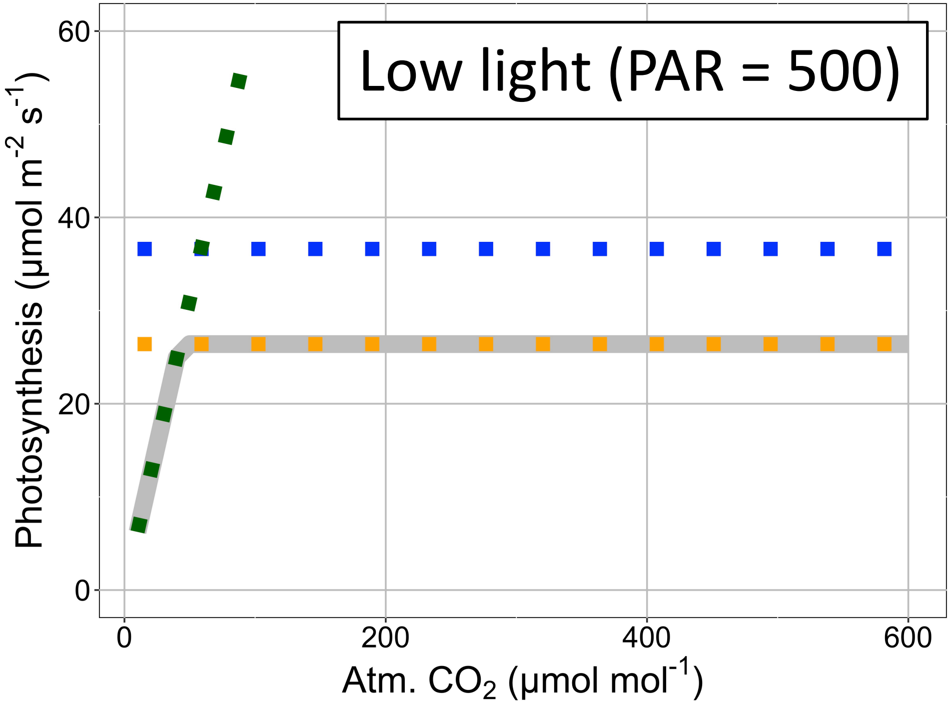
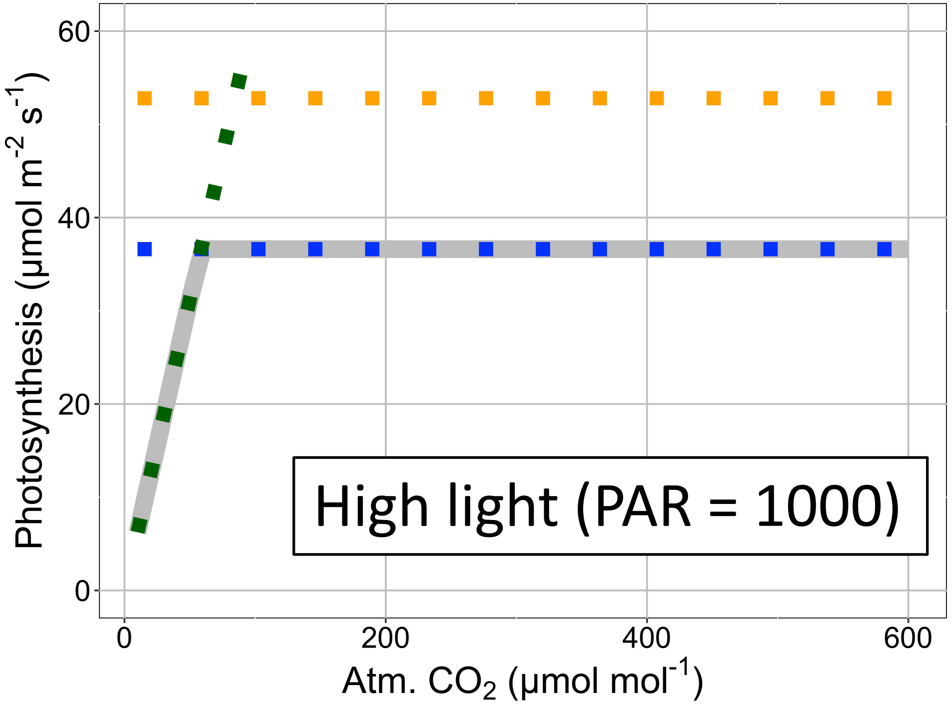



# Collatz model instantaneous $CO_2$ responses




Rubisco carboxylation ($A_c$)
Light-related processes ($A_j$)
PEP carboxylation ($A_p$)

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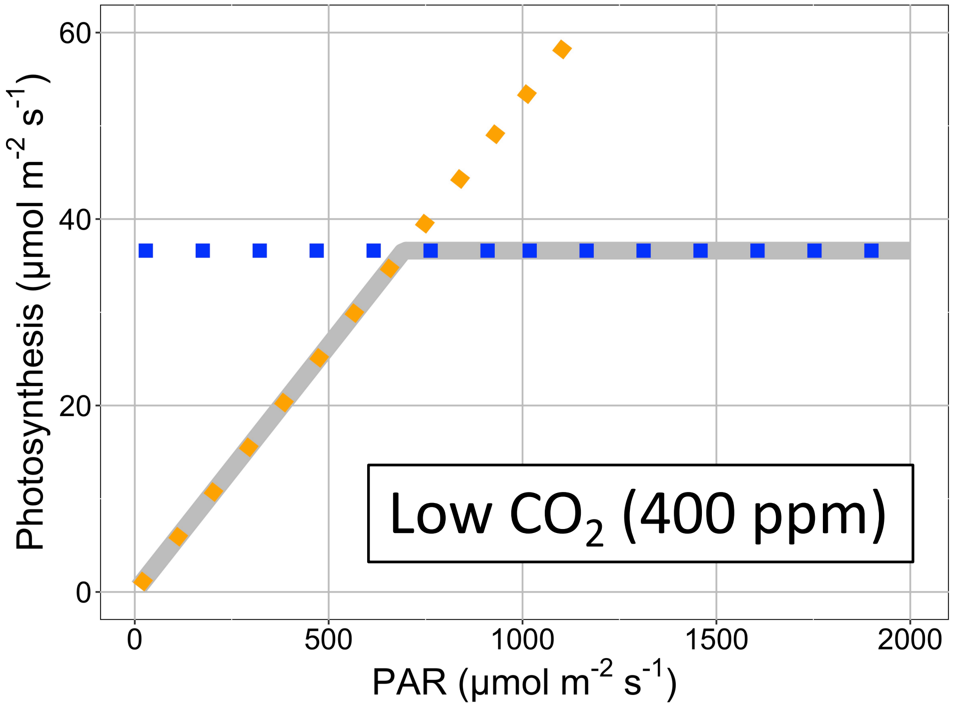


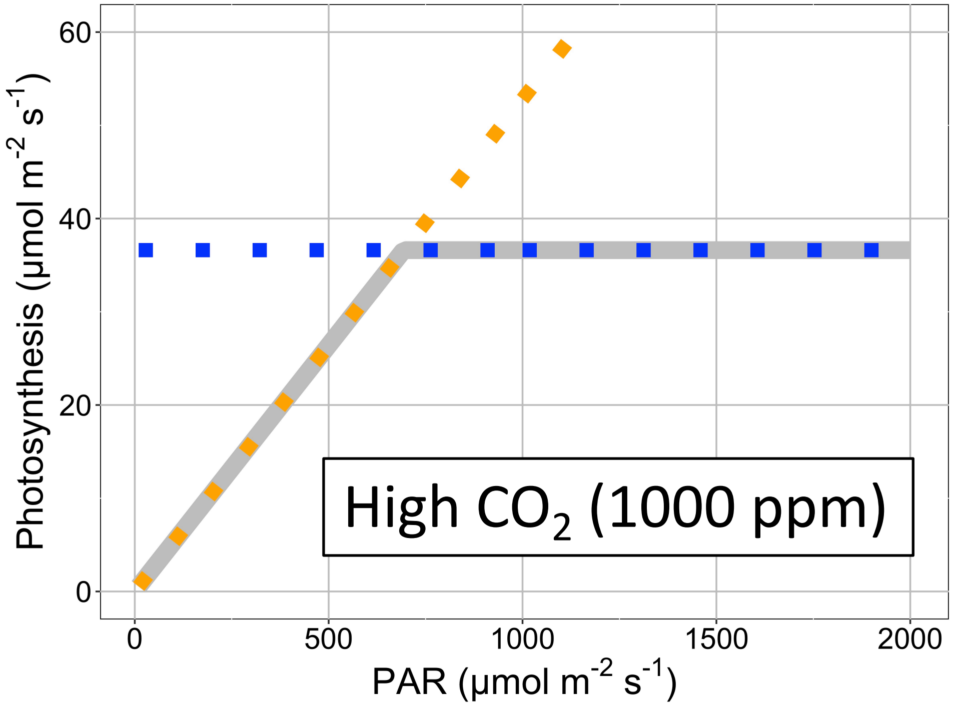


# Collatz model instantaneous light responses

Rubisco carboxylation ($A_c$)

Light-related processes ($A_j$)

PEP carboxylation ($A_p$)

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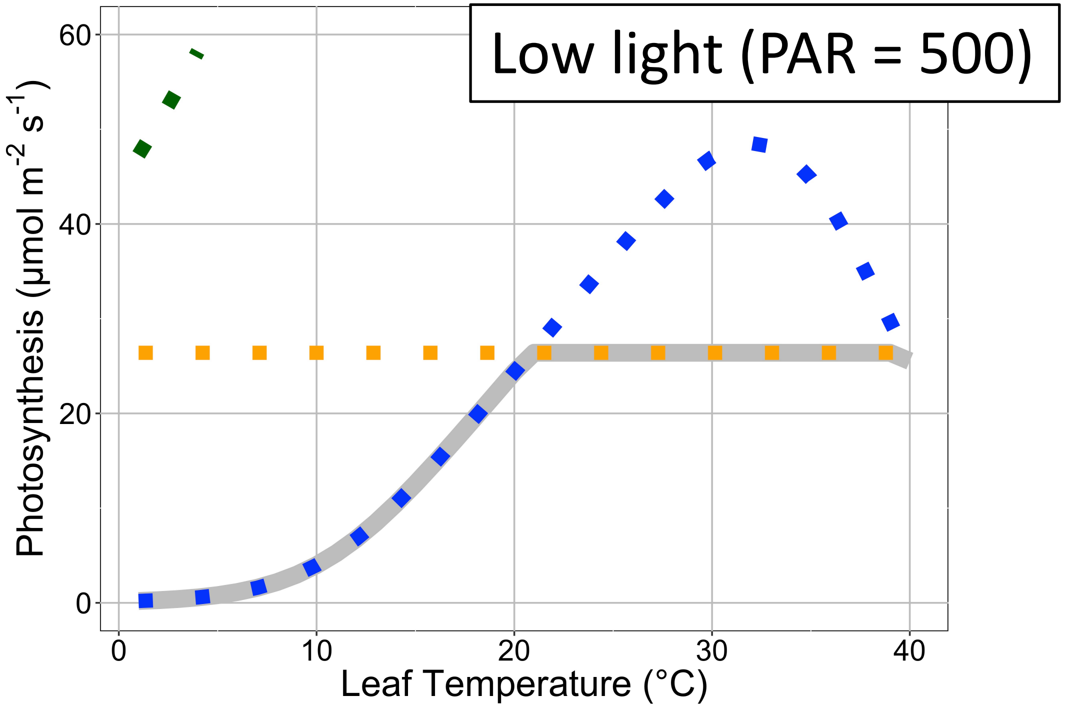
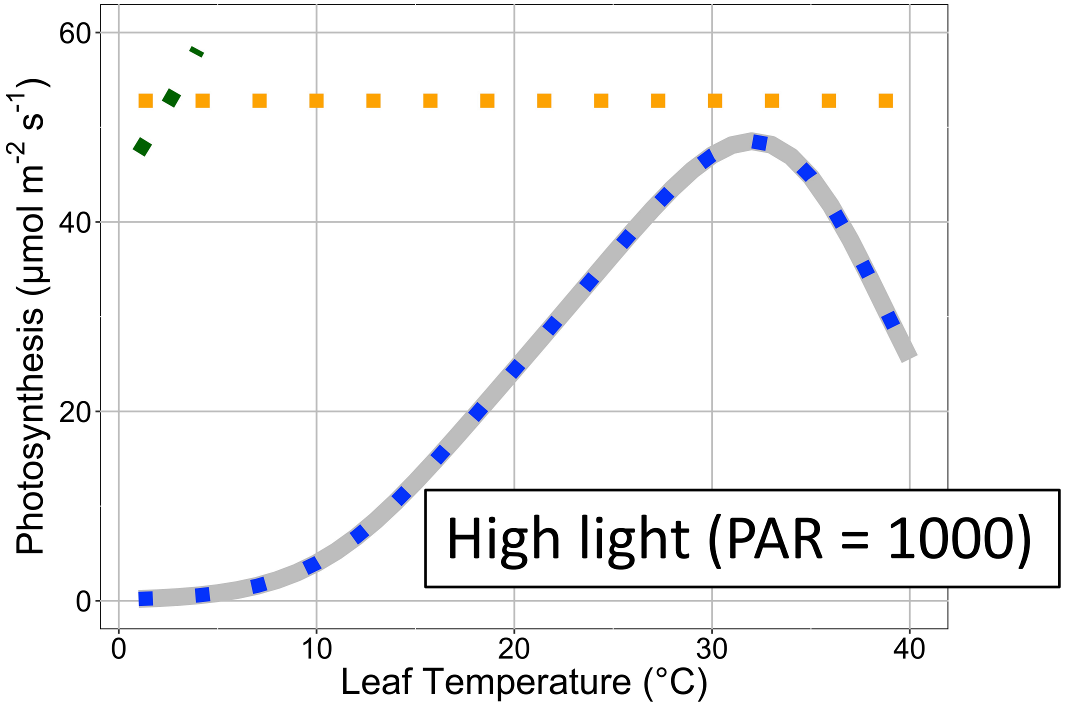



# Collatz model instantaneous temperature responses




Rubisco carboxylation ($A_c$)
Light-related processes ($A_j$)
PEP carboxylation ($A_p$)

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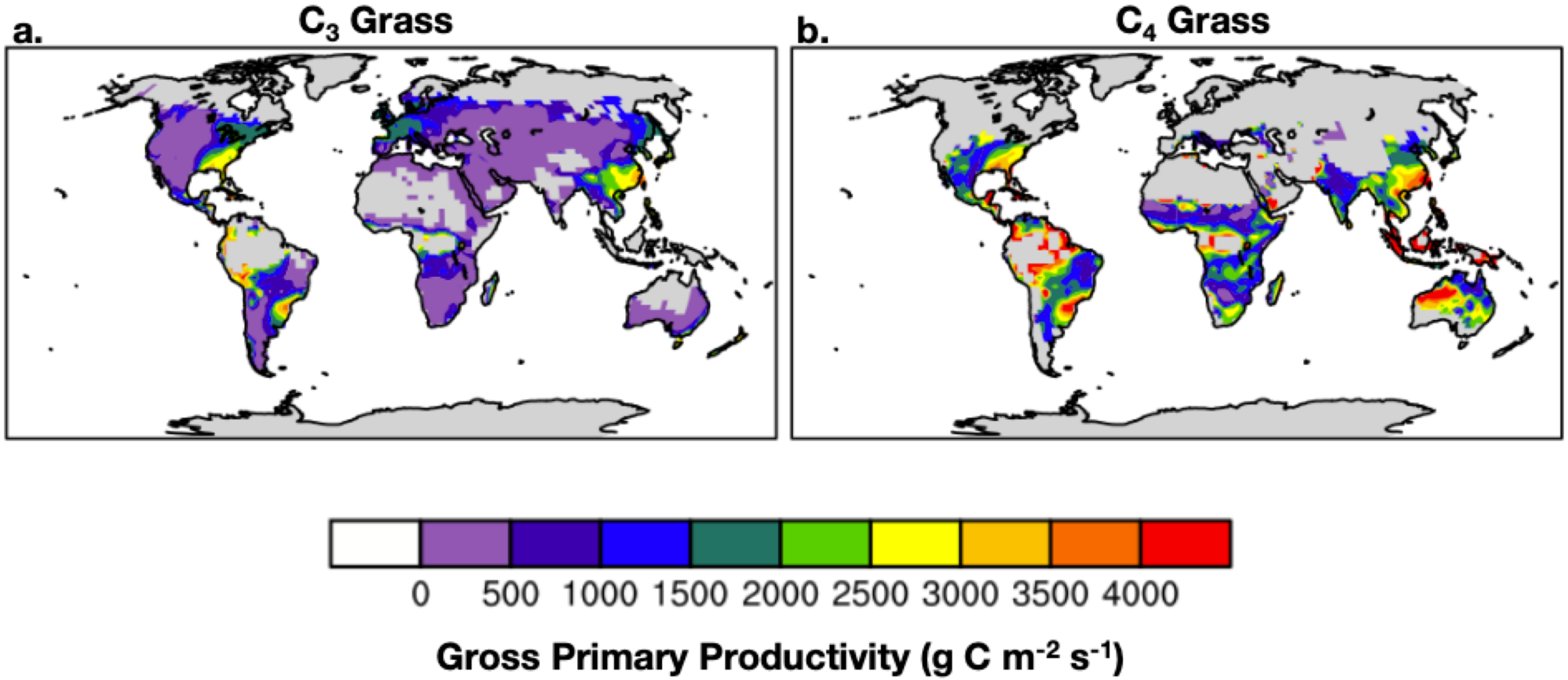
# $C_4$ grasses can be rather productive in ESMs



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# Collatz model issues

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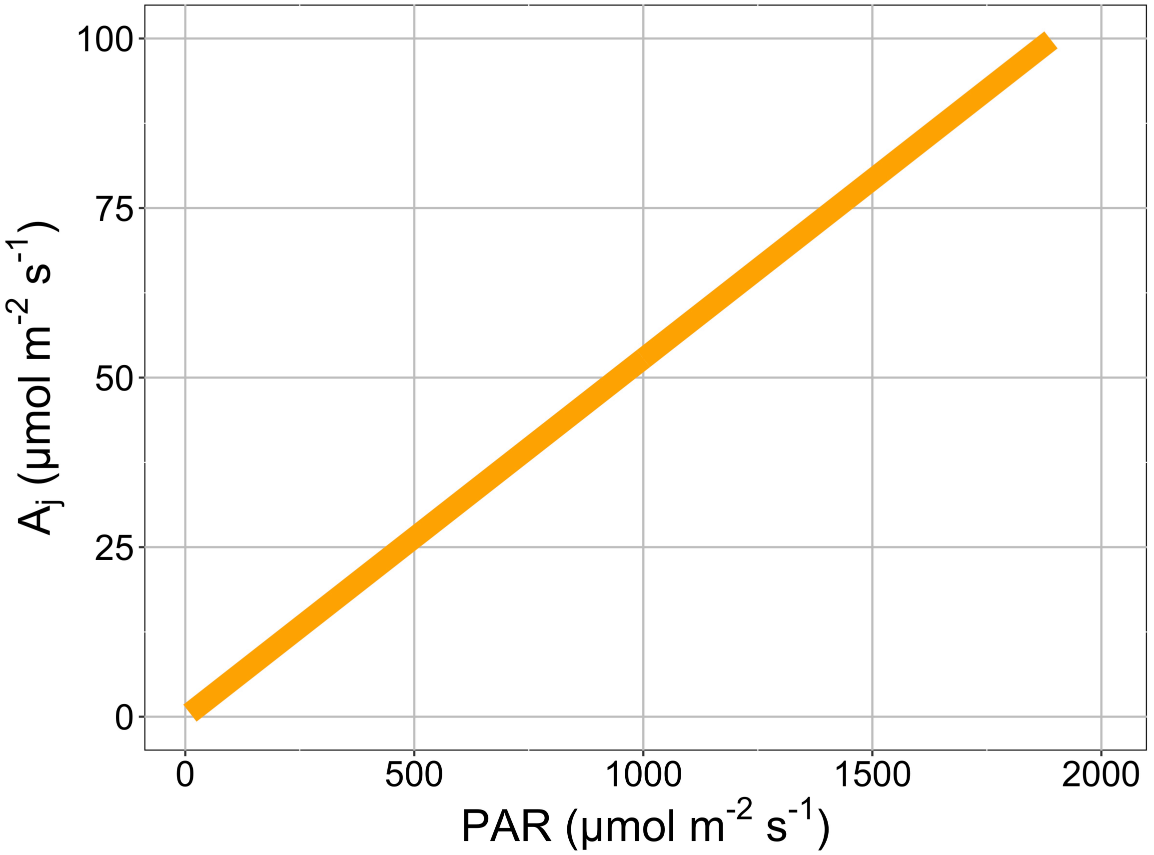
# Issue 1: light response

- Non-mechanistic linear light response



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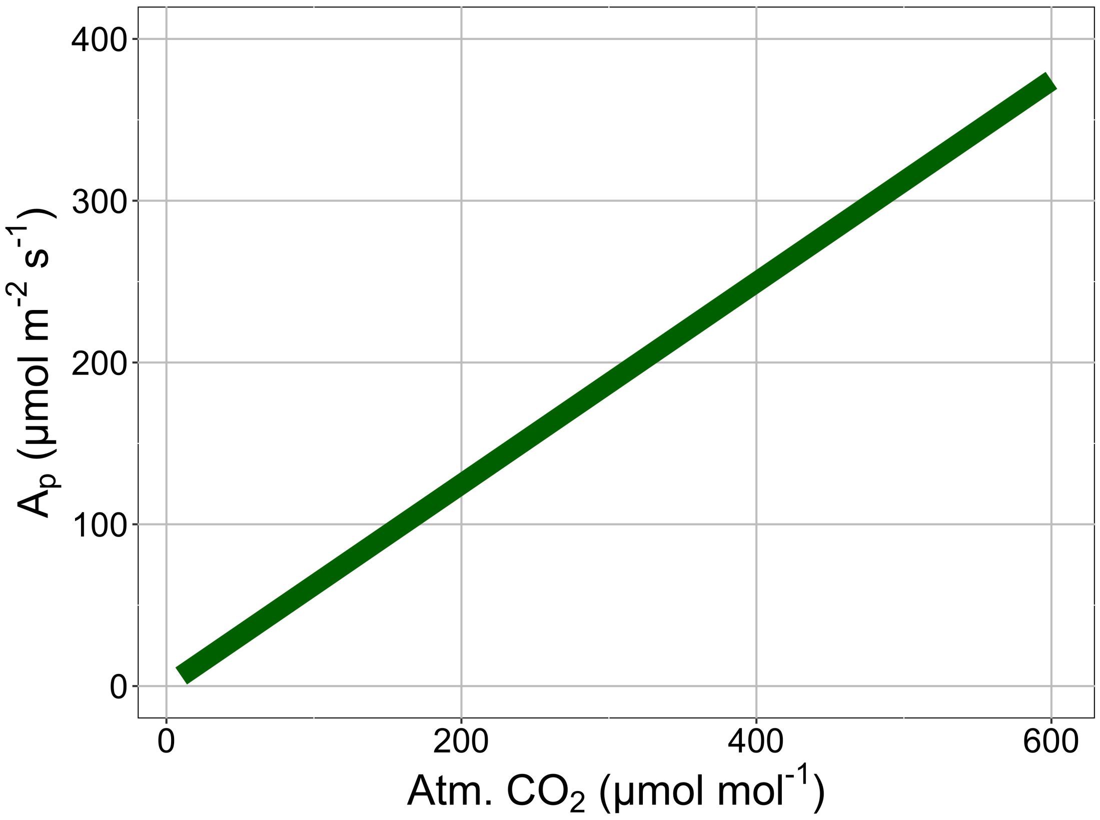
# Issue 2: PEP response

- Linear, no $CO_2$ saturation (no M-M kinetics)



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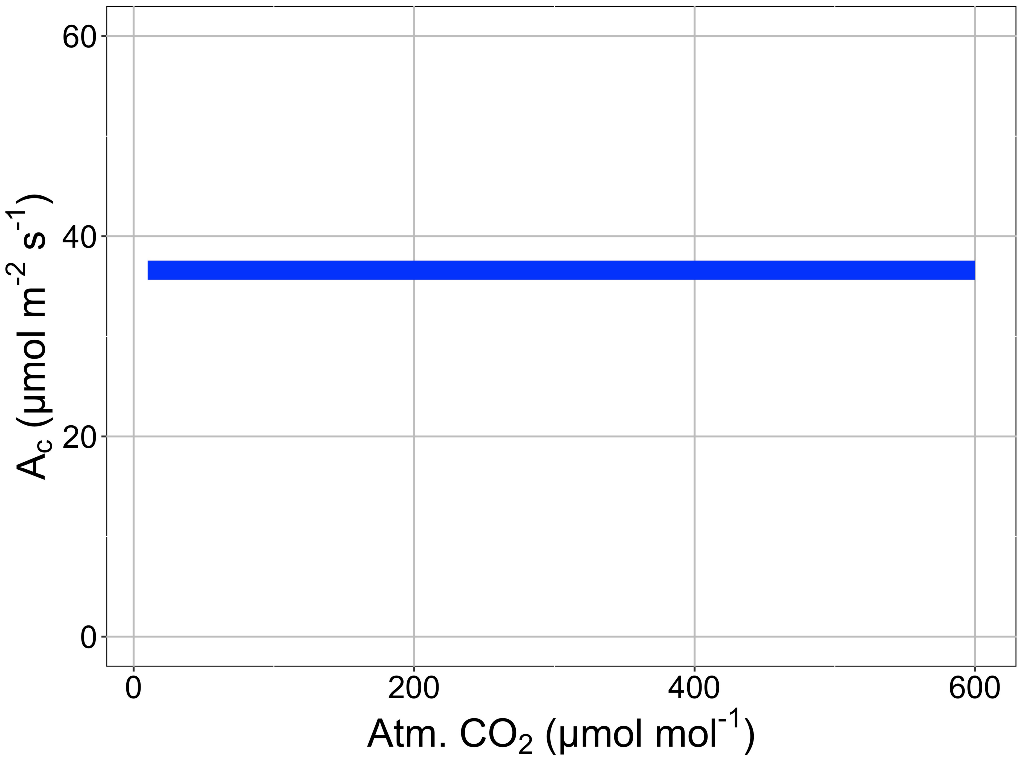
# Issue 3: Rubisco response

- No oxygenation or $K_m$, Rubisco assumed to be saturated with $CO_2$



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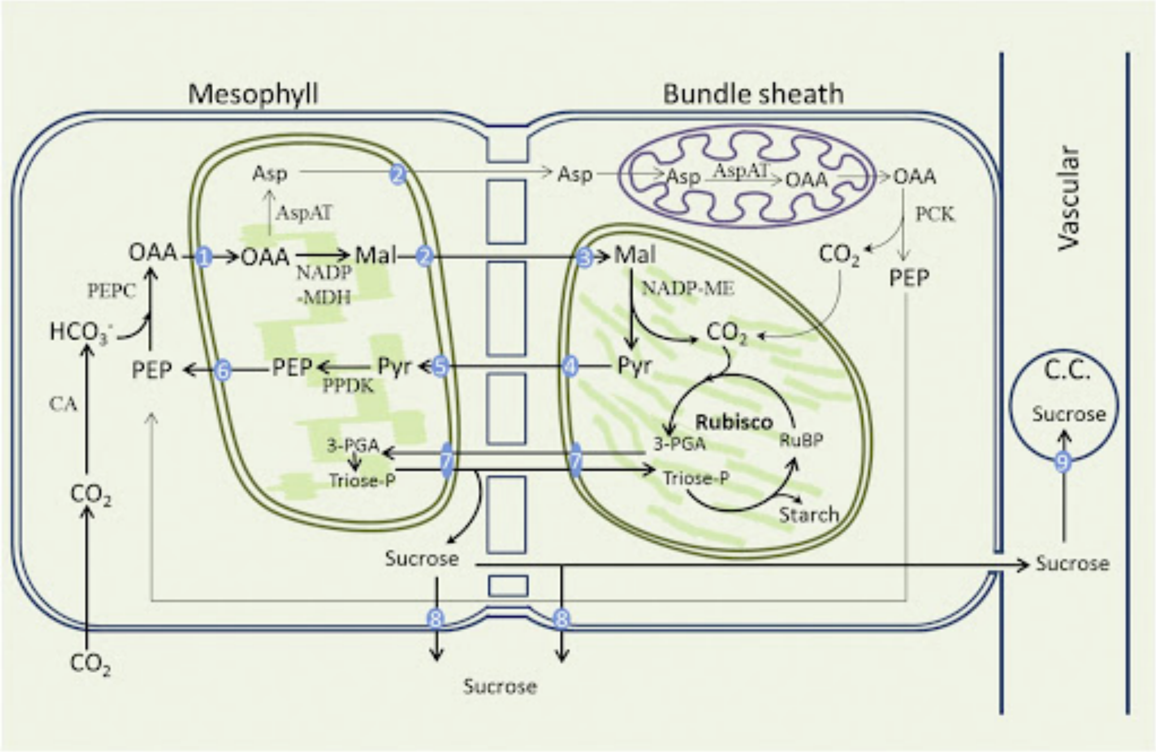
# Issue 4: Carbon

- No transfer of carbon between mesophyll and bundle sheath (i.e., no bundle sheath conductance or leakage)

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# Issue 5: parameterization

- Parameters are from 21 measurements on potted, fertilized *Z. mays*

# A proposed way forward

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# Previous models offer ways to address some of the current issues in ESMs

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**Coupled Photosynthesis–Stomatal Conductance Model for Leaves of $C_4$ Plants***

*G. James Collatz*[A], *Miquel Ribas-Carbo*[B] *and Joseph A. Berry*[A]

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**Appendix has mods for including:**

- Full PEP M-M kinetics
- Full Rubisco M-M kinetics
- Oxygenation
- Leakage
- BS conductance

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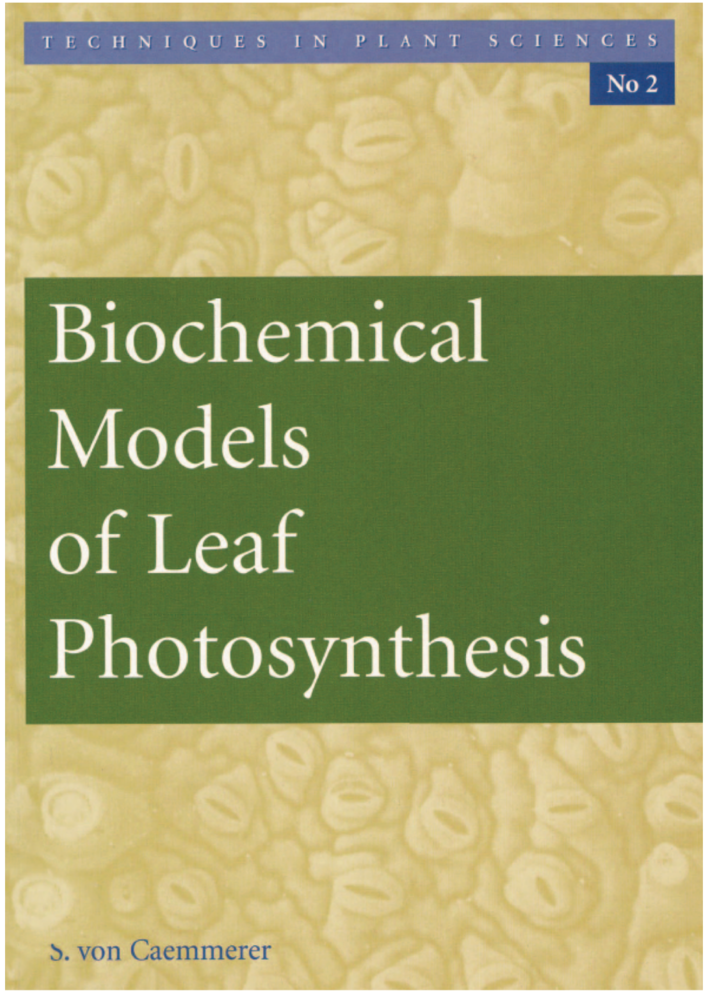
# Previous models offer ways to address some of the current issues in ESMs




**Chapter 4 has mods for:**

- Full PEP M-M kinetics
- Full Rubisco M-M kinetics
- Oxygenation
- Leakage
- BS conductance
- Light dependence of electron transport

Von Caemmerer (2000), and updated in Von Caemmerer (2022)

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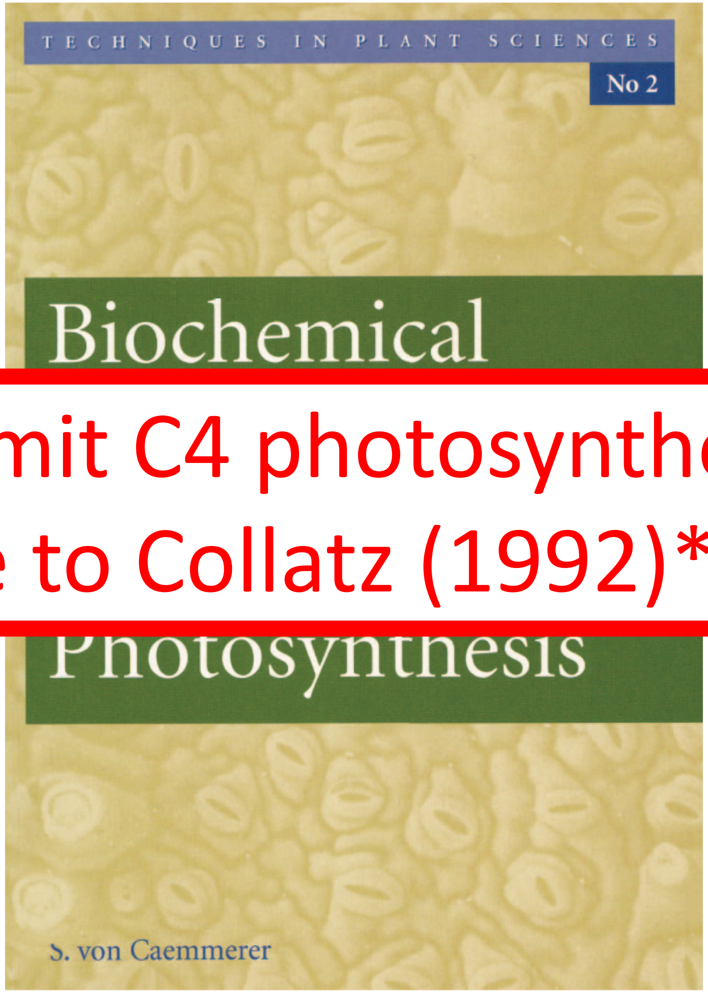
# Previous models offer ways to address some of the current issues in ESMs




**All limit C4 photosynthesis relative to Collatz (1992)**

**Chapter 4 has mods for:**

- Full PEP M-M kinetics
- Full Rubisco M-M kinetics
- Oxygenation
- Leakage
- BS conductance
- Light dependence of electron transport

Von Caemmerer (2000), and updated in Von Caemmerer (2022)

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# New model (Scott and Smith, 2022)

JAMES | Journal of Advances in Modeling Earth Systems®

RESEARCH ARTICLE
10.1029/2021MS002470

**Key Points:**

- A parameter-sparse model of $C_4$ photosynthetic acclimation to changes in environmental conditions based on photosynthetic least cost theory
- Including acclimation will improve simulations of $C_4$ carbon assimilation and water/nutrient-use efficiencies under present/future conditions
- In simulated competition experiments with a similar $C_3$ model, $C_4$ photosynthesis becomes less advantageous under increased carbon dioxide

## A Model of $C_4$ Photosynthetic Acclimation Based on Least-Cost Optimality Theory Suitable for Earth System Model Incorporation

**Helen G. Scott[1] and Nicholas G. Smith[1]**

[1]Texas Tech University, Lubbock, TX, USA

**Abstract** Empirical studies have shown that plant photosynthetic responses to environmental change can vary over time due to acclimation, but acclimation responses are often not included in Earth System Models. Photosynthetic least cost theory can be used to develop models of photosynthetic acclimation that are simple and testable. The theory is based on the idea that plants will acclimate to minimize the ratio of carbon costs to photosynthetic assimilation rate (Prentice et al., 2014, https://doi.org/10.1111/ele.12211).

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(now at BU)

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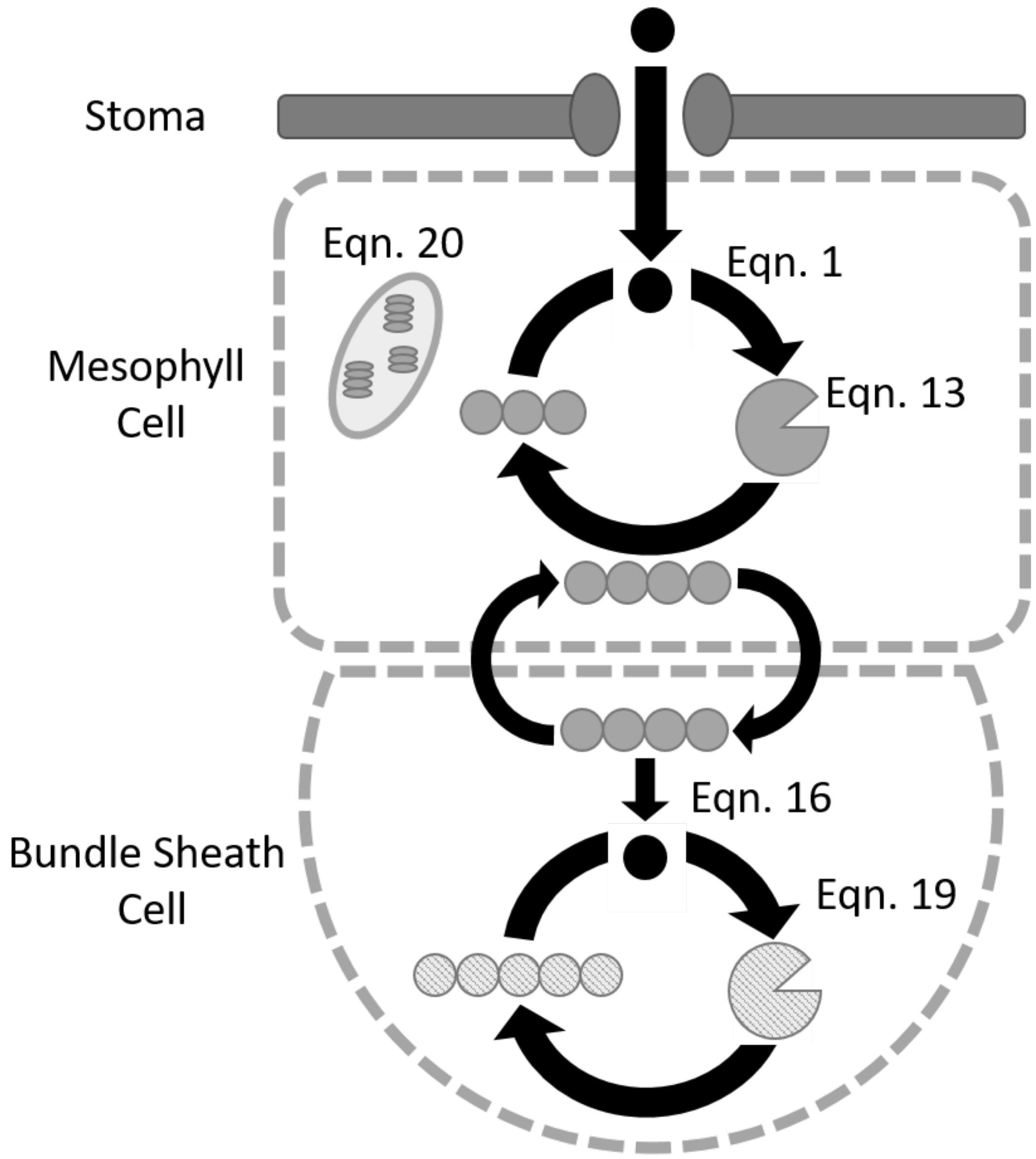
# New $C_4$ model features

- Von Caemmerer (2000)
  - Maximum PEP carboxylation
  - Rubisco kinetics
  - Oxygenation
  - Leakage
  - BS conductance
  - Light dependence of electron transport




Scott and Smith (2022)

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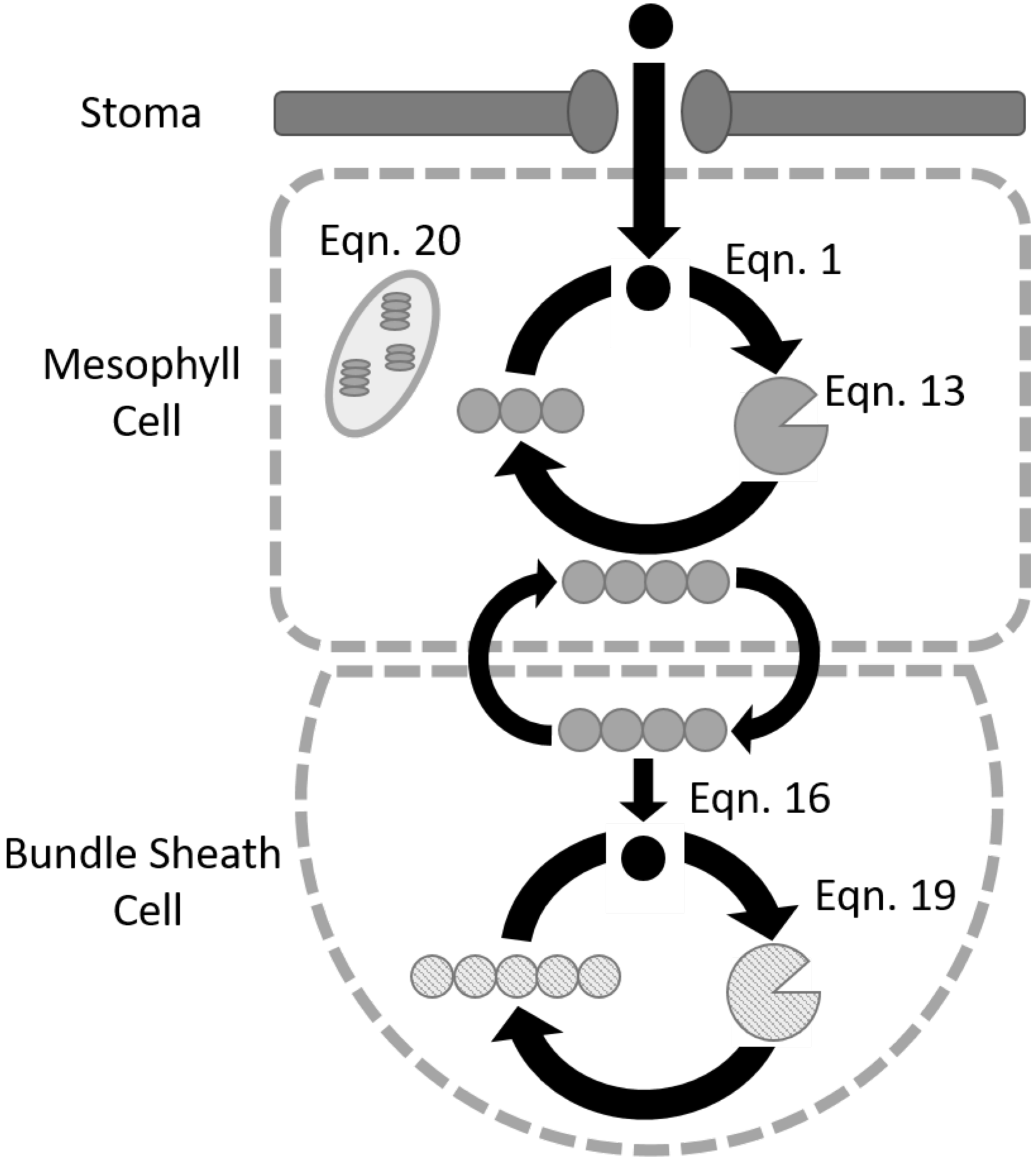
# New $C_4$ model features

- **Least cost acclimation**
  - PEP carboxylation
  - Rubisco carboxylation
  - Electron transport
  - Stomatal conductance




Scott and Smith (2022)

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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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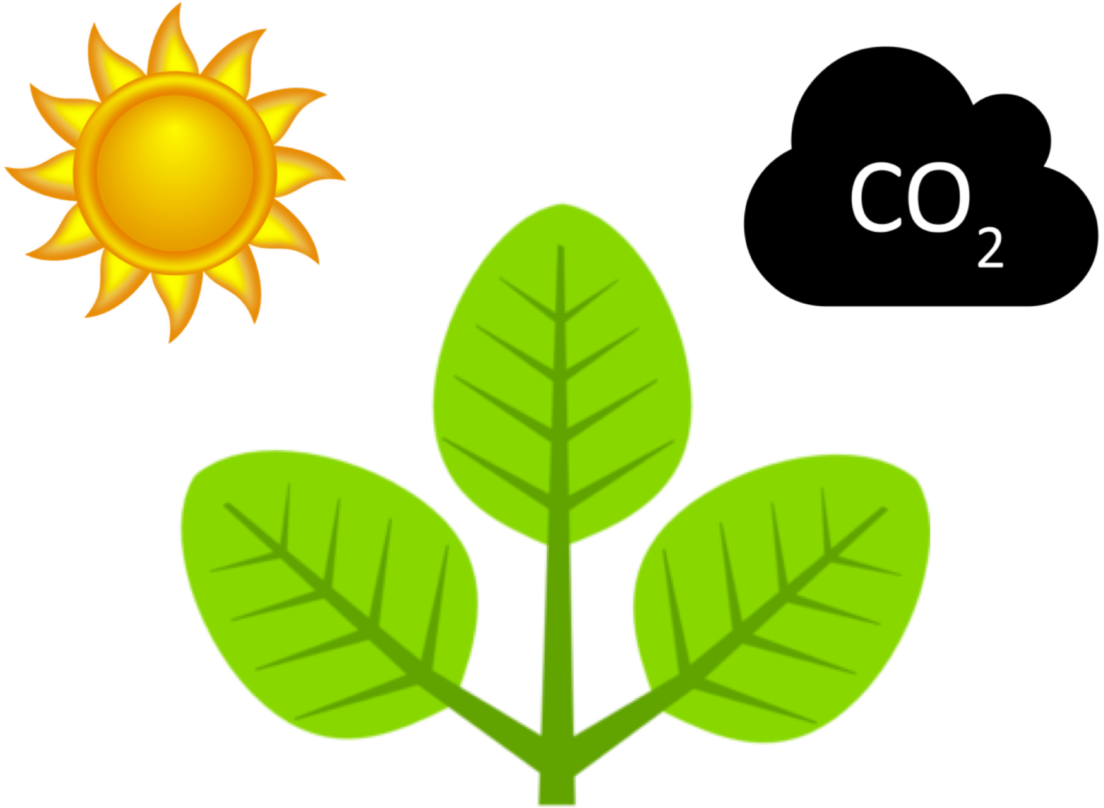
# Biochemistry optimization: Coordination hypothesis




Optimal setup = equal limitation by all factors

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

$$A_j = A_c = A_p$$

Scott and Smith (2022)

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

$$A_j = A_c = A_p$$

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

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

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

Scott and Smith (2022)

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# *Can rearrange the formulas to solve for acclimated traits*

$V_{cmax}$

$J_{max}$

$V_{pmax}$

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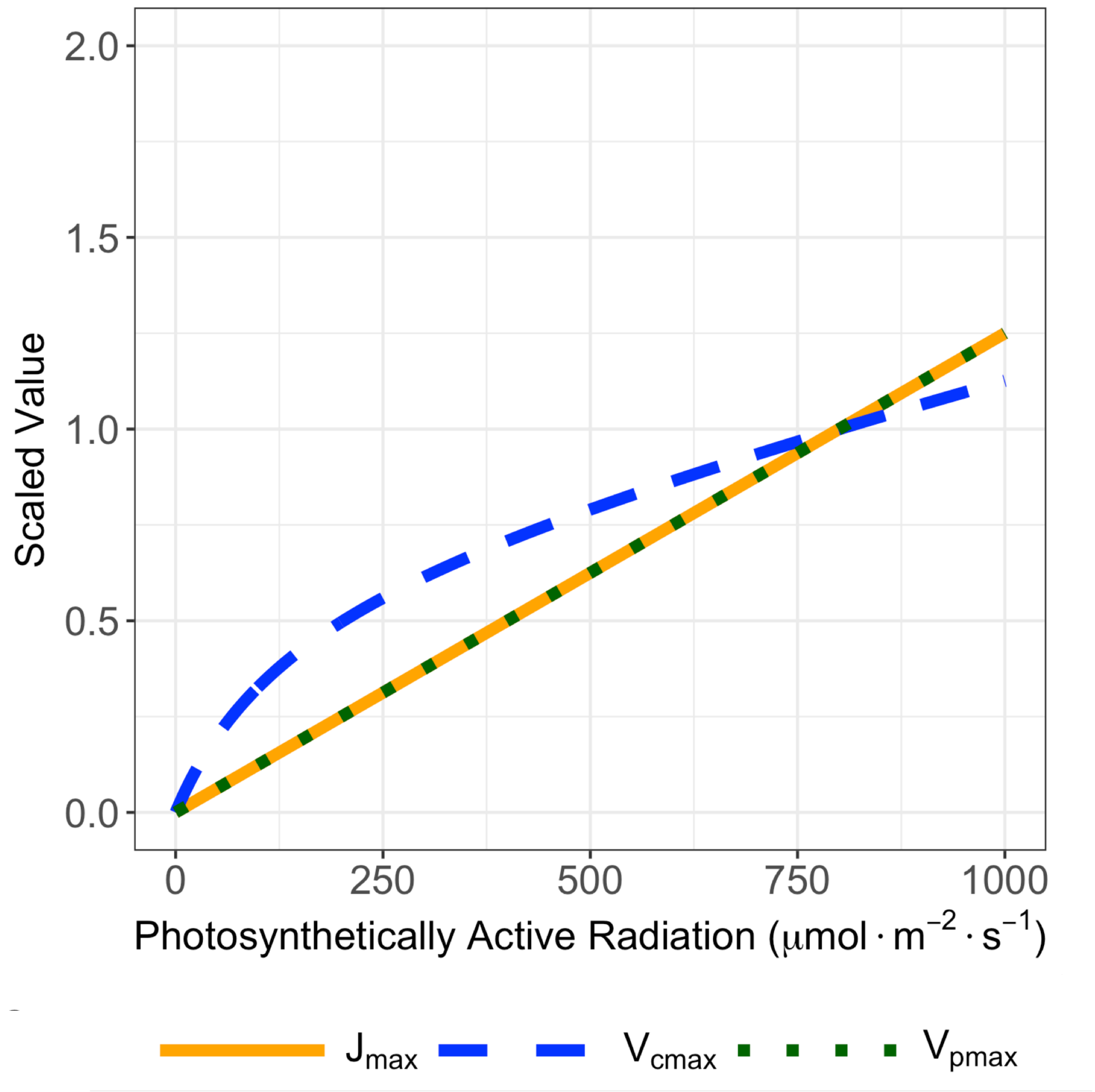


More light = more investment in biochemical processes

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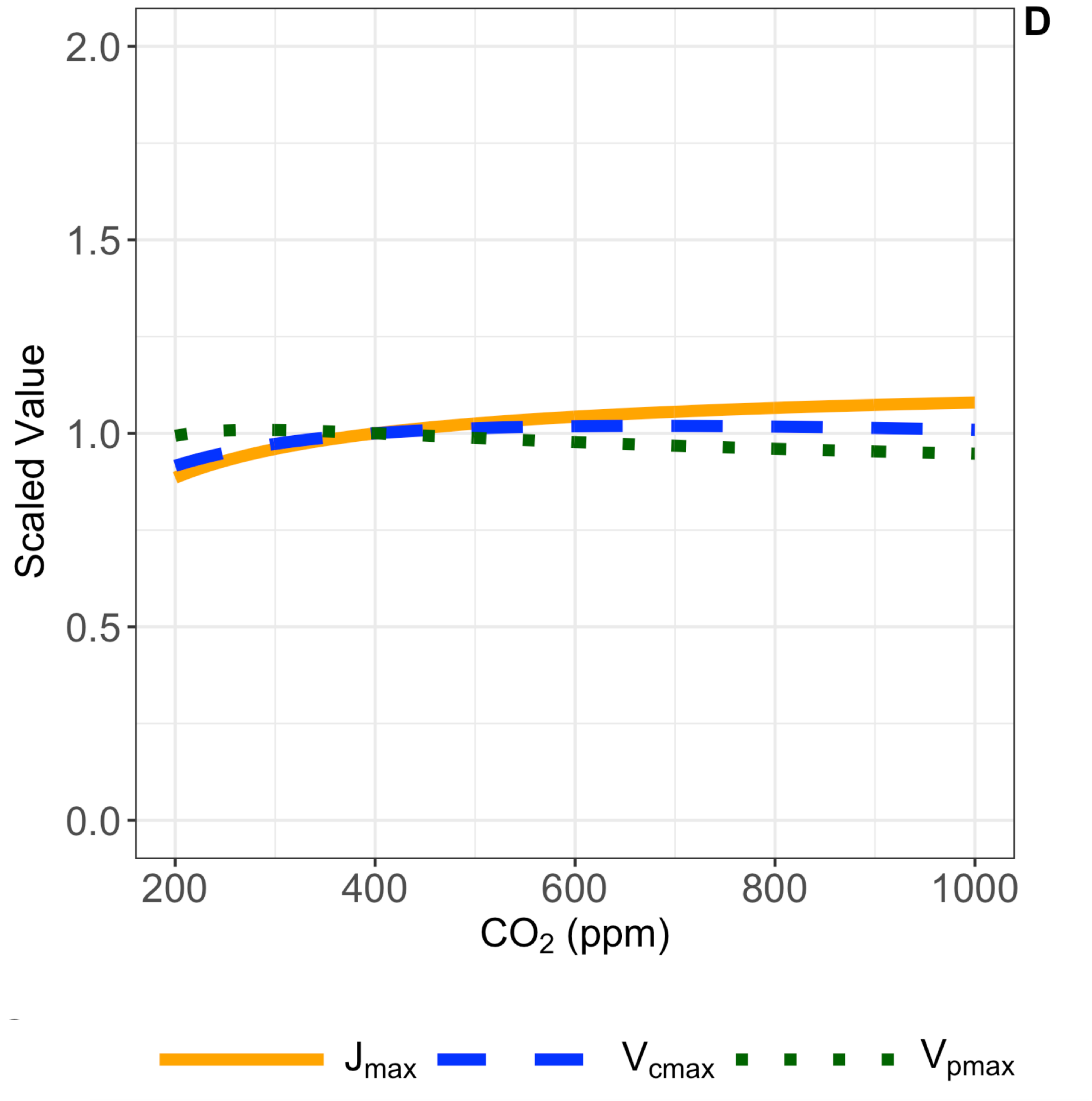


More $CO_2$ = less investment in PEP, more in electron transport

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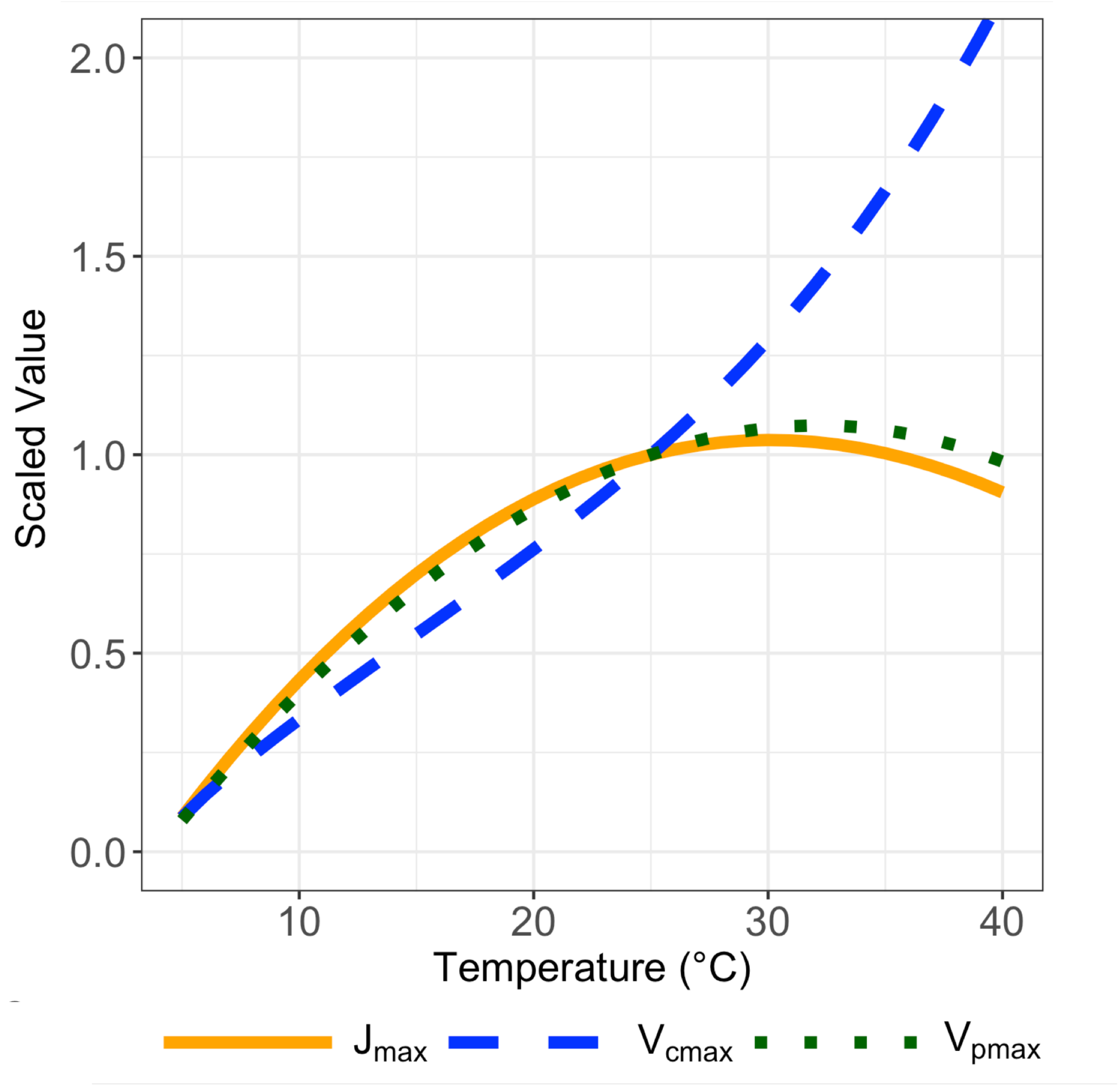


Higher T = faster rates, but less investment (not shown)

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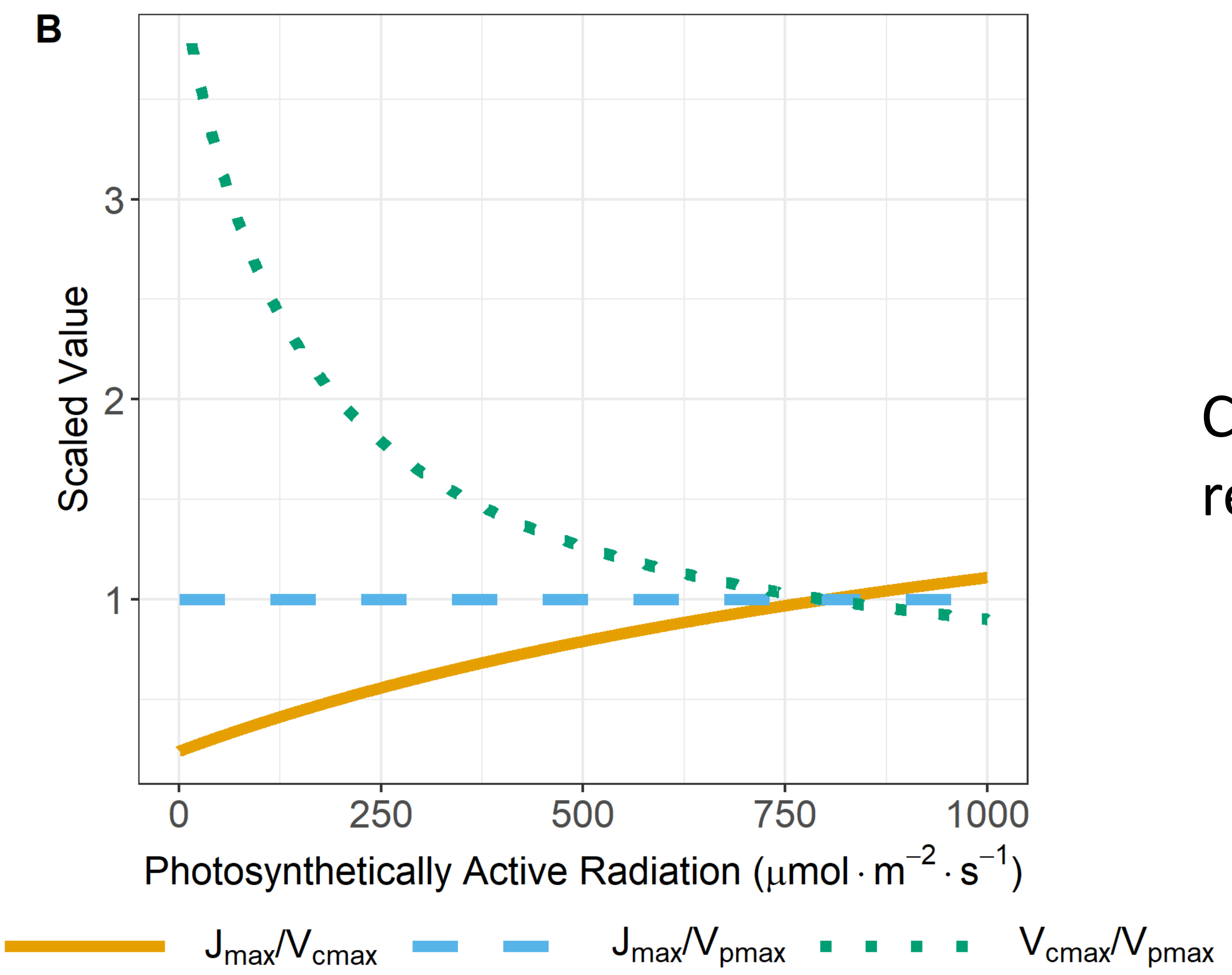


Can look at changes in relative investment

Scott and Smith (2022)

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# Does it work?

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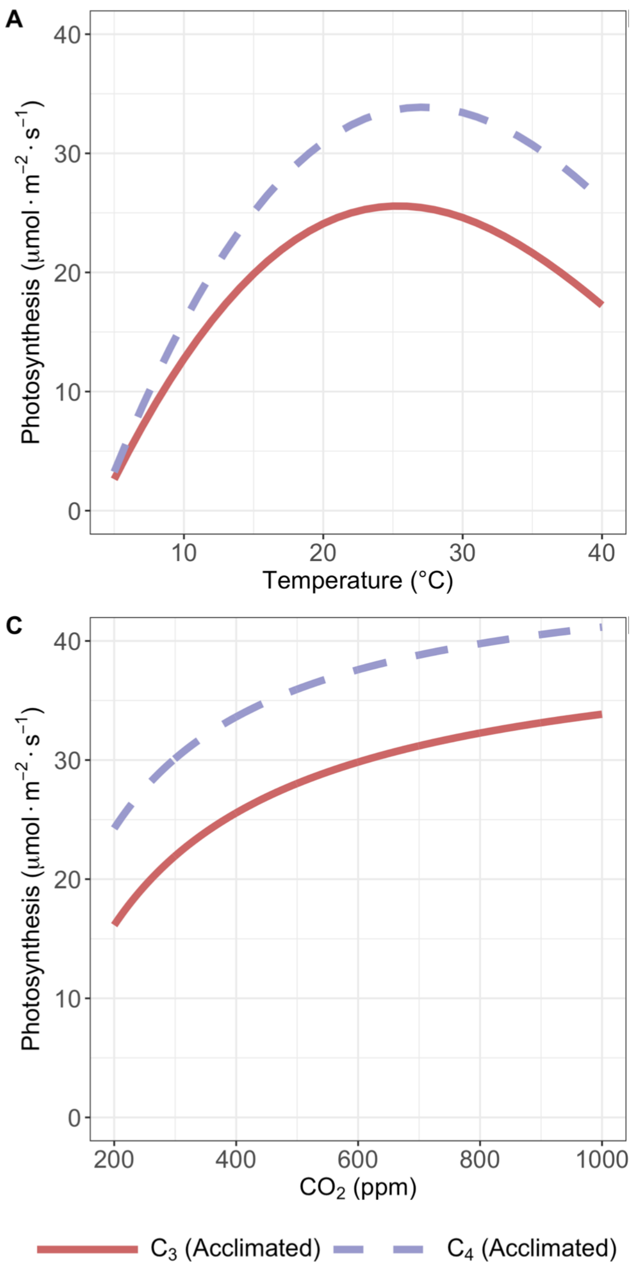
# Maybe?

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




20% benefit at 5°C to
40% benefit at 35°C

50% benefit at 200 ppm to
20% benefit at 1000 ppm

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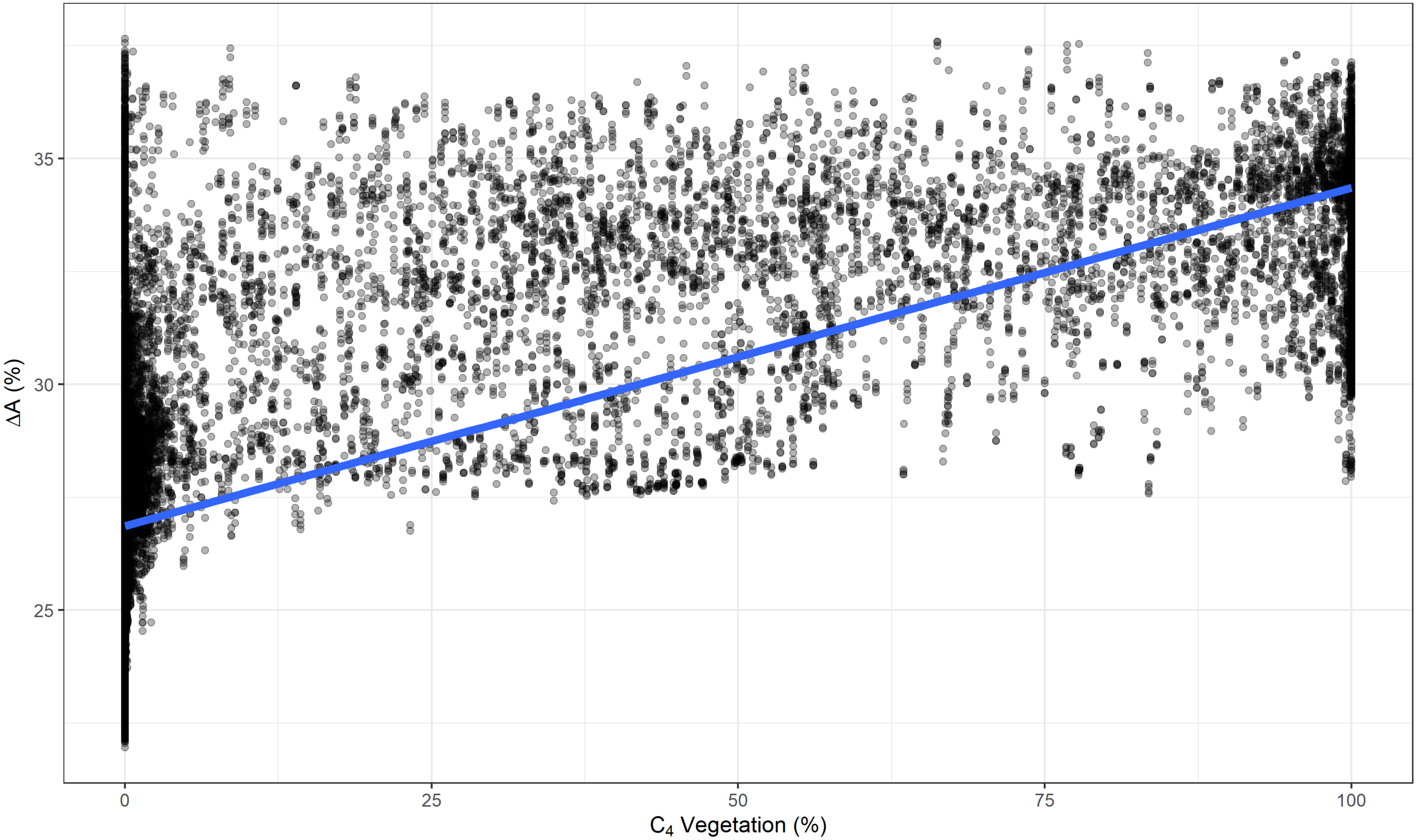
# Maybe?




The model tends to predict where $C_4$ species dominate

Still et al. (2003)

Scott and Smith (2022)

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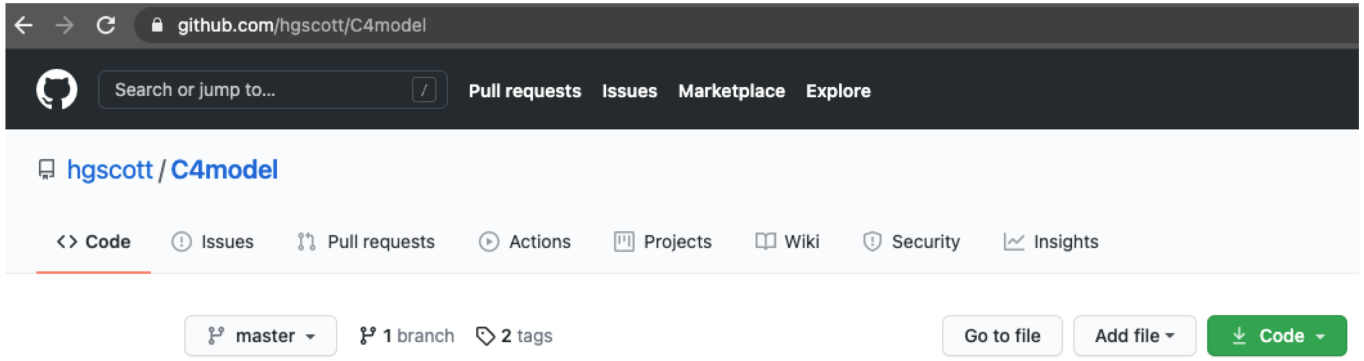
# Model considerations

- Parameters to incorporate soil water and nutrients (fixed at the moment)
- Need better light harvesting equations
- Could be used for ESM incorporation and/or asking ecological questions




github.com/hgscott/C4model (doi: 10.5281/zenodo.4420326)

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# Conclusions and future considerations

- Probably time to move away from simplistic representations of $C_4$ photosynthesis

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  - Unclear what the model-to-model variability is
    - Rogers et al. (2017) for C4?

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# Conclusions and future considerations

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    - Rogers et al. (2017) for C4?
  - Unclear all the options that exist
    - Whether they make a difference

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# Conclusions and future considerations

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- **Need more data to test different models**

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# Conclusions and future considerations

- Probably time to move away from simplistic representations of $C_4$ photosynthesis
  - Unclear what the model-to-model variability is
    - Rogers et al. (2017) for C4?
  - Unclear all the options that exist
    - Whether they make a difference
- **Need more data to test different models**
- Beyond leaf photosynthesis
  - Phenology
  - Allocation
  - ”Strategies” (e.g., fire adaptations)

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