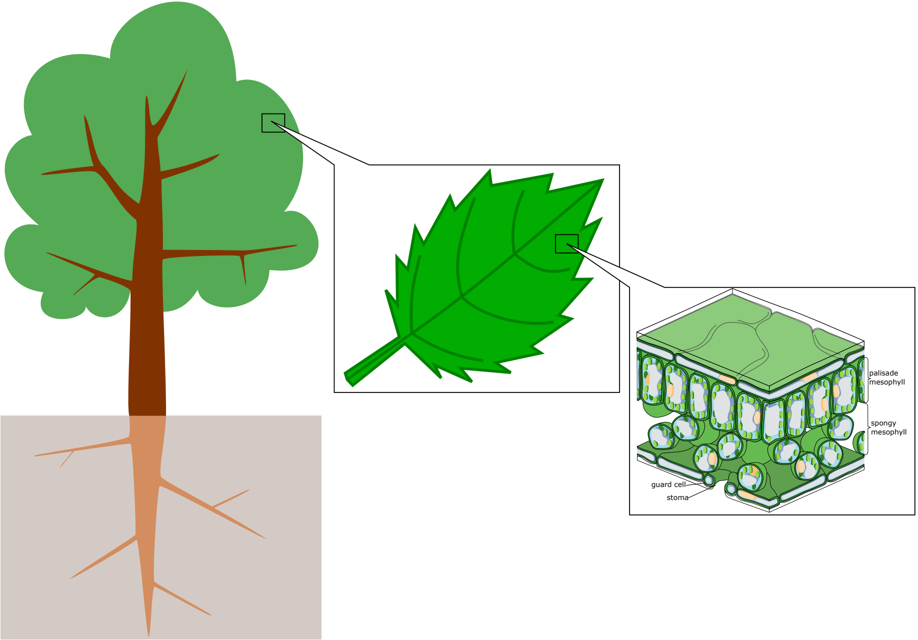
Plant Hydraulics and Stomatal Control

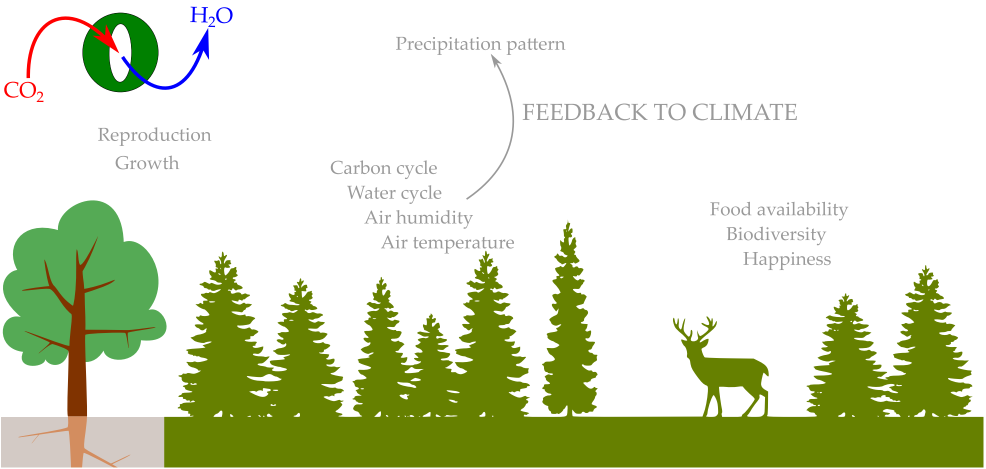
Yujie Wang

California Institute of Technology

April 29/30, 2020


palisade mesophyll
spongy mesophyll
guard cell
stoma

Significance of leaf gas exchange



Uncertainty in land surface system

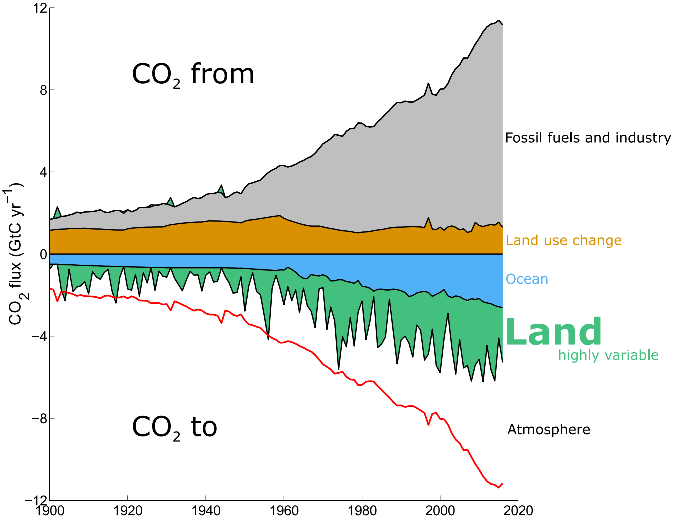
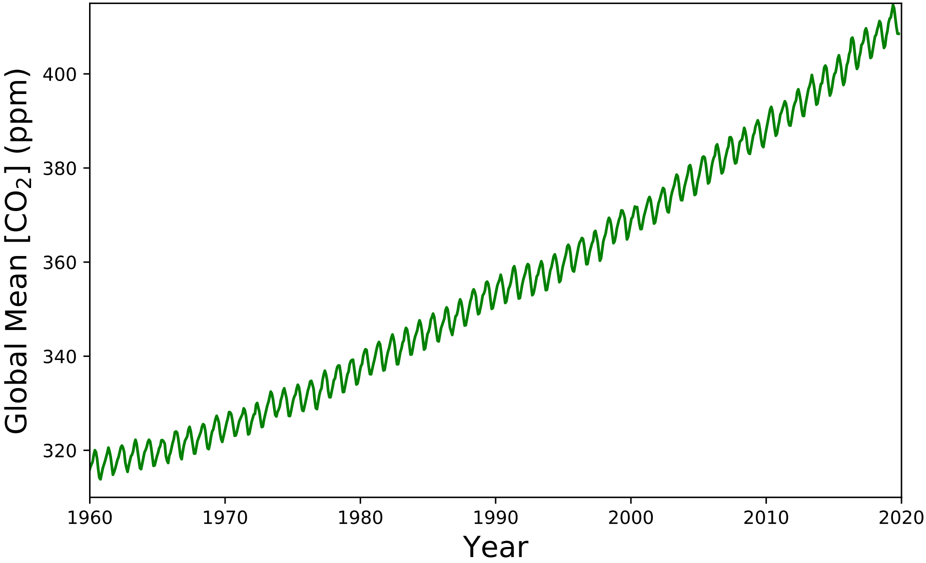
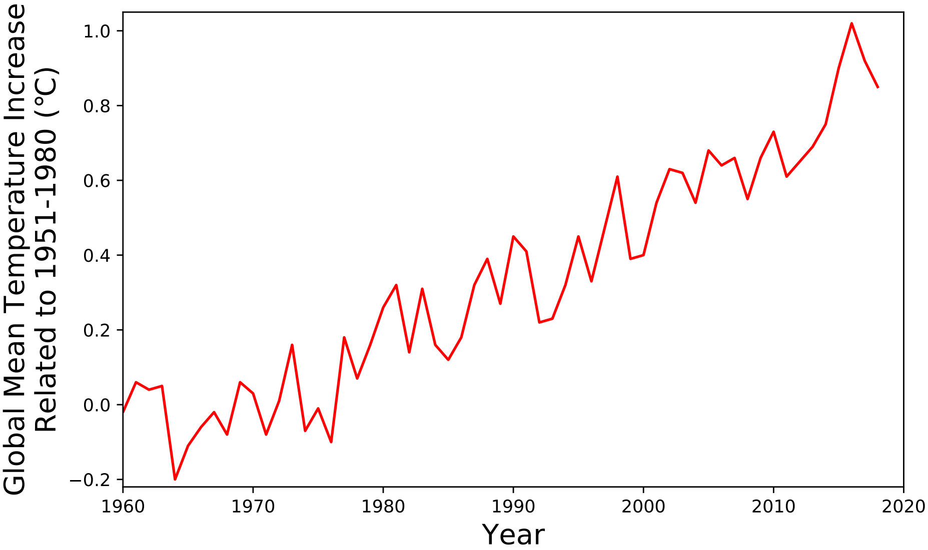


Figure adapted from Le Quéré et al. (2018)

Increasing CO_2 concentration



Increasing temperature



Soil moisture change

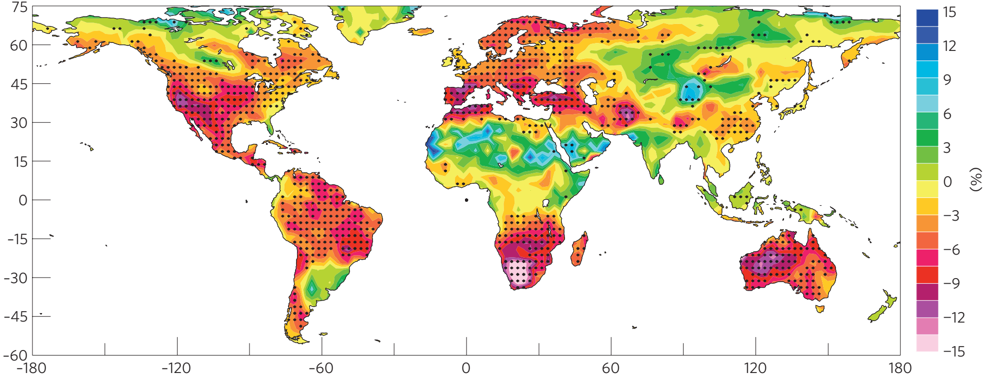


Figure from Dai (2013)

Role of land in the future

CO_2 Sink?

CO_2 Source?

Leaf gas exchange through stomata

PLANT PHYSIOLOGY

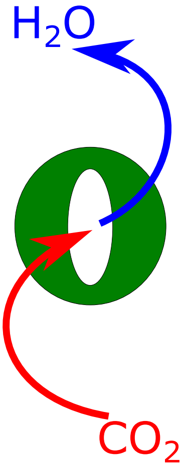
Abscisic acid

Leaf turgor pressure

Hydraulic conductance

Photosynthetic capacity

Mesophyll conductance



ENVIRONMENT

Atmospheric CO_2

Vapor pressure deficit

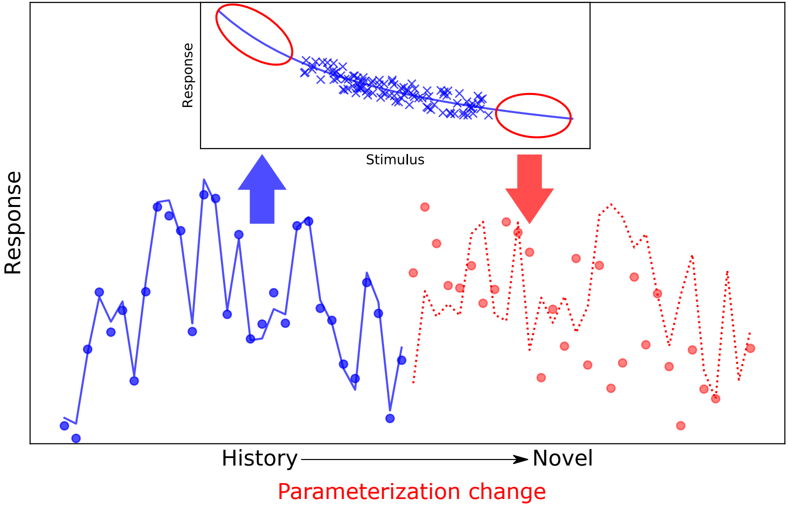
Air temperature

Solar radiation

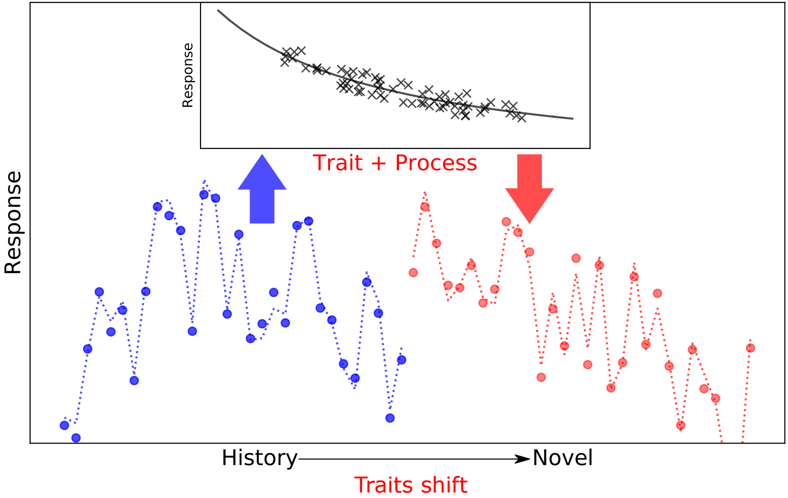
Wind speed

Soil moisture

The easiest way—statistical regression approach



A better way—physiological trait-based approach



A better way—challenges

- How to model stomatal behavior from traits?
- How to model the shift of traits?

What we know

PLANT PHYSIOLOGY

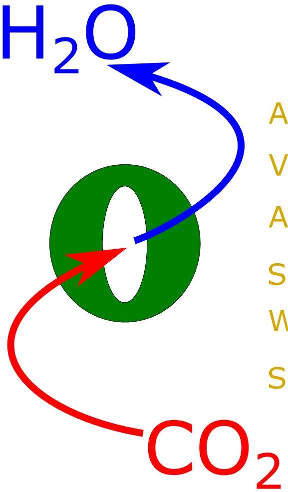
Abscisic acid

Leaf turgor pressure

Hydraulic conductance

Photosynthetic capacity

Mesophyll conductance



ENVIRONMENT

Atmospheric CO_2

Vapor pressure deficit

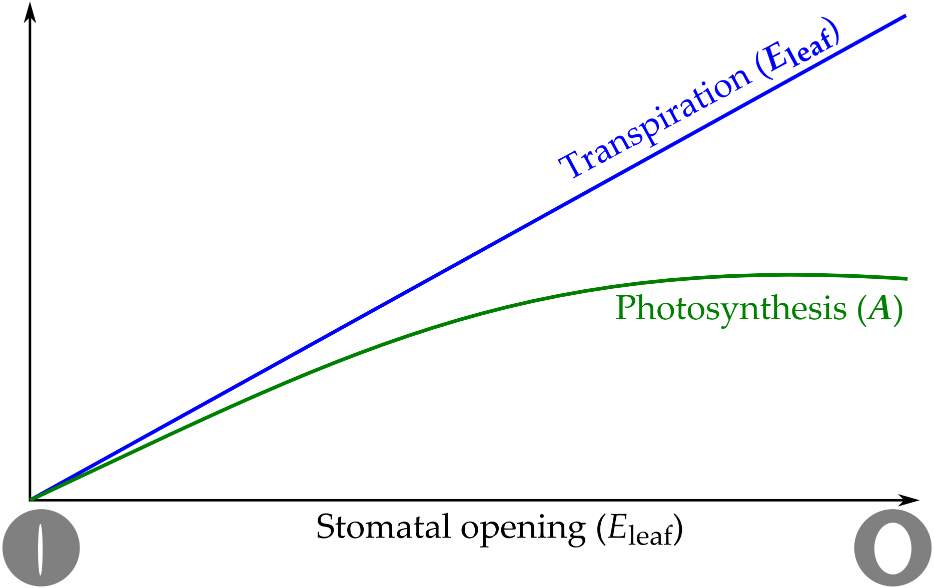
Air temperature

Solar radiation

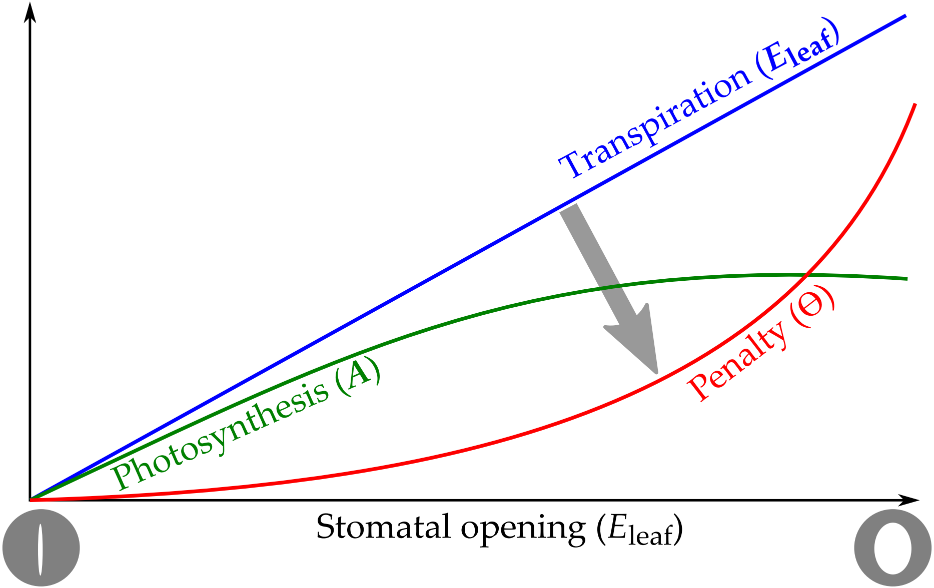
Wind speed

Soil moisture

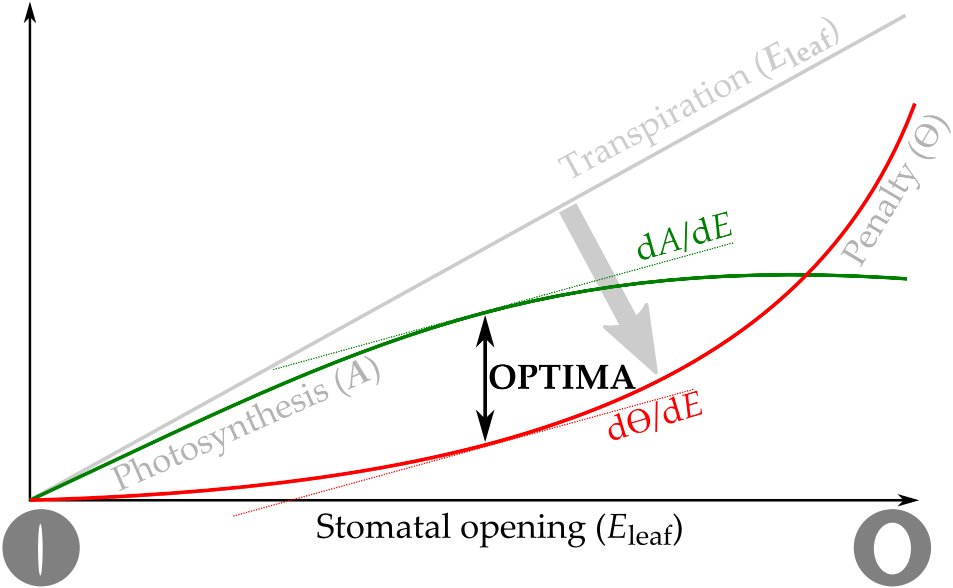
Quantify transpiration and photosynthesis



Translation to water penalty



Optimal stomatal opening



Stomatal optimization

$$\max(A(E_{\text{leaf}}) - \Theta(E_{\text{leaf}}))$$

The optimal solution is:

$$\frac{\mathrm{d}A}{\mathrm{d}E} = \frac{\mathrm{d}\Theta}{\mathrm{d}E}$$

Wolf et al. (2016)

1. Quantify $A(E_{\text{leaf}})$
2. Quantify $\Theta(E_{\text{leaf}})$
3. Test different optimization models
4. Way forward—long-term prediction

Symbols

A Photosynthesis;

Θ Penalty;

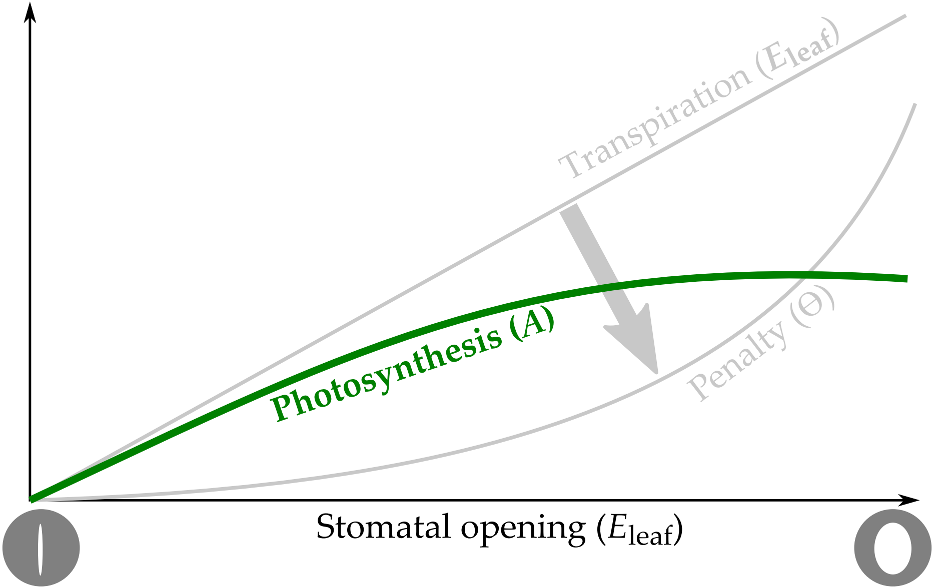
E, E_{leaf} Transpiration;

$\mathrm{d}A/\mathrm{d}E$ Marginal carbon gain;

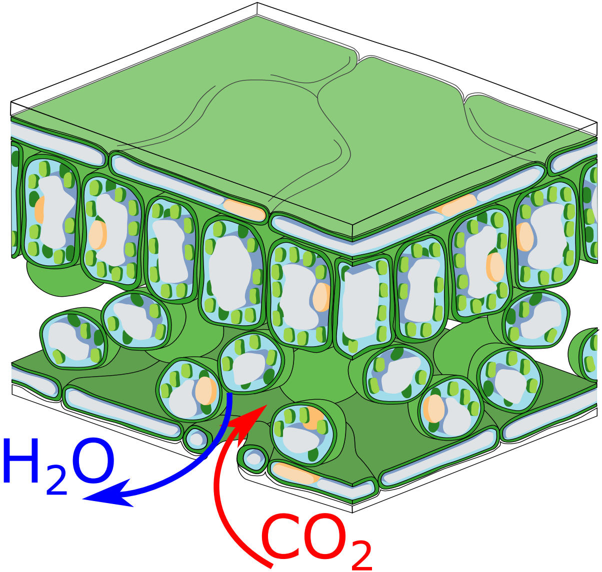
$\mathrm{d}\Theta/\mathrm{d}E$ Marginal water penalty.

Part I
Quantify Carbon Gain

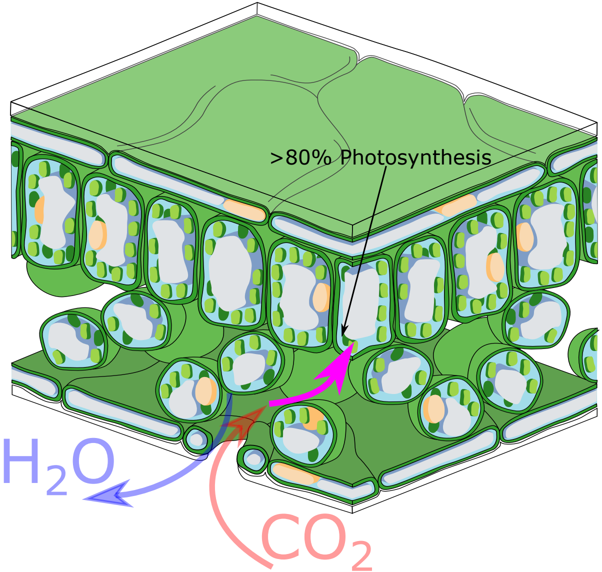
Quantify carbon gain—photosynthesis (A)



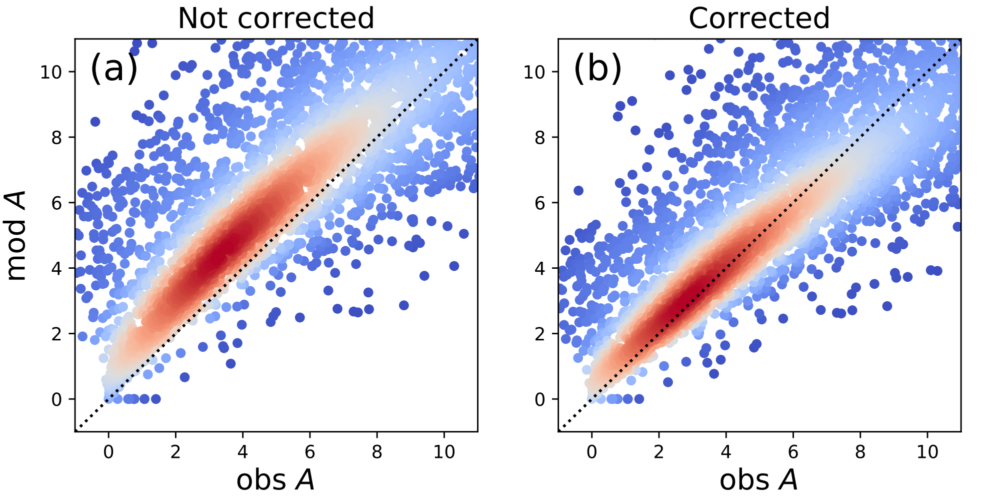
Classic photosynthesis model



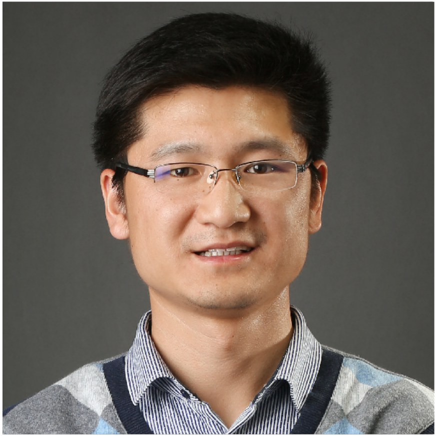
The "missing" components



Improvement of modeled A



BREAKING NEWS



华中农业大学熊栋梁课题组博士后招聘

熊栋梁 / 2019-05-30

一、课题组简介

华中农业大学植物科学技术学院熊栋梁课题组拟招聘博士后研究人员3-4名。课题组隶属于作物遗传改良国家重点实验室和农业部长江中下游作物栽培与耕作重点实验。其中作物遗传改良国家重点实验室连续5次被评为优秀国家重点实验室，是唯一获此殊荣的农业科研类国家重点实验室，也是依托高校所建生命科学类唯一获此殊荣的国家重点实验室。实验室具备一流的作物生物学研究平台。

课题组致力于：I. 挖掘作物高产、高效、高抗及高生态系统服务价值的生理功能性状；II. 多尺度上解析植物生理功能与生长环境之间的互作机制；III. 开发基于功能性状调控的作物高产高效管理技术。近5年，课题组已在New Phytologist、Plant Cell & Environment、Journal of Experimental Botany等植物学主流学术期刊发表论文15篇。课题组网站：www.dlxiong.org。

二、研究方向

1、气孔功能进化；

2、植物抗旱与水分高效利用；

3、作物高光效（**需有分子遗传、基因编辑等现代生物技术基础**）；

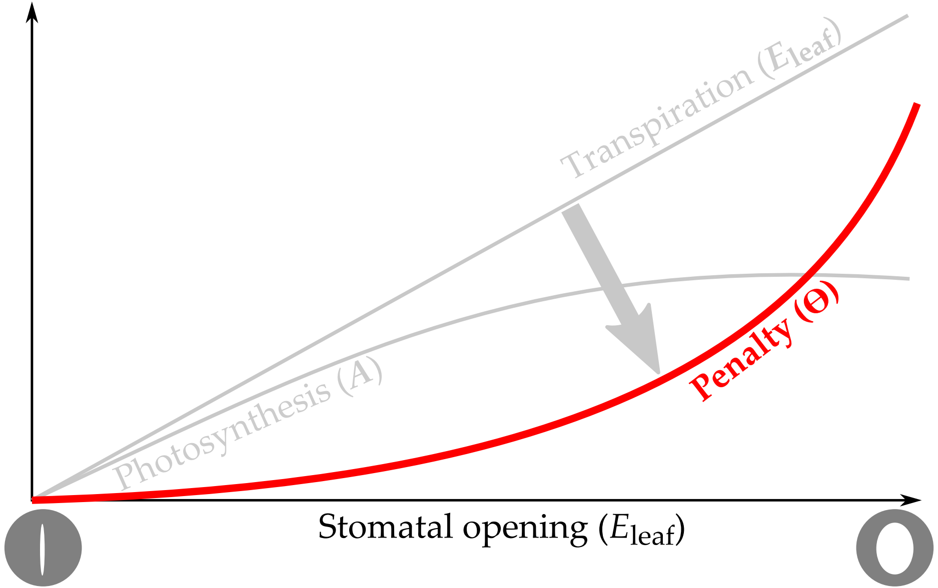
4、热烈欢迎具有数、理、信息或工程背景的博士加盟发展交叉科学。

✓ Quantify $A(E_{\text{leaf}})$

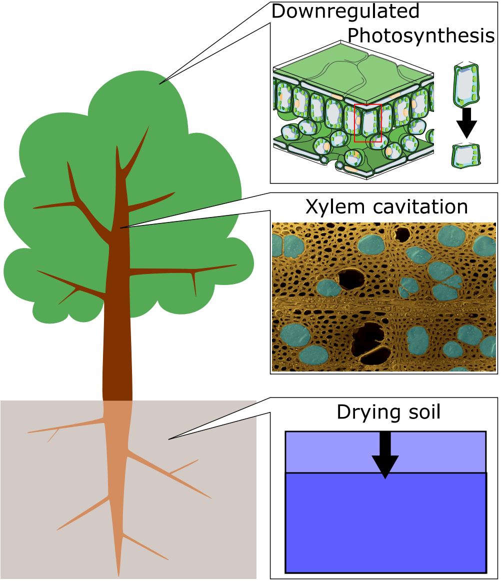
2. Quantify $\Theta(E_{\text{leaf}})$
3. Test different optimization models
4. Way forward—long-term prediction

Part II
Quantify Water Penalty

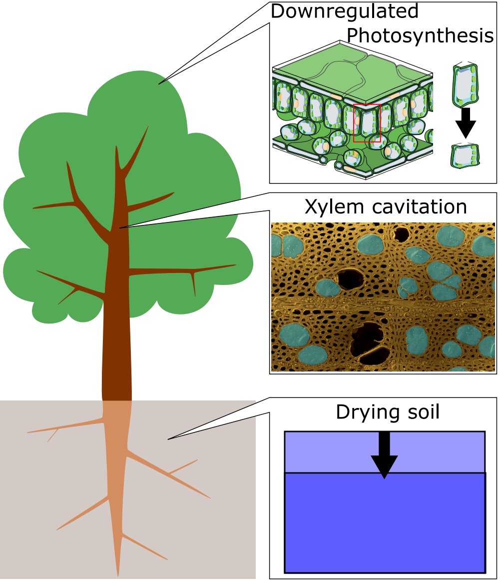
Quantify water penalty (Θ)



Causes of water penalty (Θ)



Models based on different Θ



Holtta *et al.* (2017)
Dewar *et al.* (2018)
Huang *et al.* (2018)
... ...

Wolf *et al.* (2016)
Sperry *et al.* (2017)
Anderegg *et al.* (2018)
Eller *et al.* (2019)
... ...

Cowan & Farquhar (1977)
... ...
Manzoni *et al.* (2013)
Prentice *et al.* (2014)
Lu *et al.* (2016)
... ...

Model reviewed

Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($d\Theta/dE$ or $d\Theta'/dE$)	Criteria I–III	Response Criteria IV–VII DCPK	Fitting parameters
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{leaf}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{leaf}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et al., 2014)	$\Theta = A \cdot \left(1 - \frac{1}{c_E E_{leaf} + c_V V_{cmax}}\right)$	$\frac{d\Theta}{dE} = \frac{A}{E_{leaf} + \frac{c_V}{c_E} V_{cmax}}$	YNY	YYNN	c_E, c_V
Lu	(Lu et al., 2016)	$\Theta = \frac{E_{leaf}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Wolf-Anderegg	(Wolf et al., 2016) (Anderegg et al., 2018)	$\Theta = aP^2 + bP + c$	$\frac{d\Theta}{dE} = \frac{2aP + b}{K}$	YYN	NNYY	a, b, K_{rhiz}
Sperry	(Sperry et al., 2017)	$\Theta = A_{max} \cdot \left(1 - \frac{K}{K_{max}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{max}}{K_{max}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{max,0}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{leaf}}{E_{crit}}$	$\frac{d\Theta}{dE} = \frac{A}{E_{crit} - E_{leaf}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{ww} \cdot \frac{SC}{SC_{max}}$	$\frac{d\Theta'}{dE} = \frac{A}{SC_{max} - SC} \cdot \frac{dSC}{dE}$	YYY	YYYY	SC_{max}, K_{rhiz}, anatomy
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{ww} \cdot \frac{P}{P_{crit}}$	$\frac{d\Theta'}{dE} = \frac{A}{K \cdot (P_{crit} - P)}$	YYY	YYYY	K_{rhiz}

New Phytologist

Review

Tansley review

A theoretical and empirical assessment of stomatal optimization modeling

Author for correspondence:
Yujie Wang
Tel: +1 626 395 2021
Email: wyujie@caltech.edu

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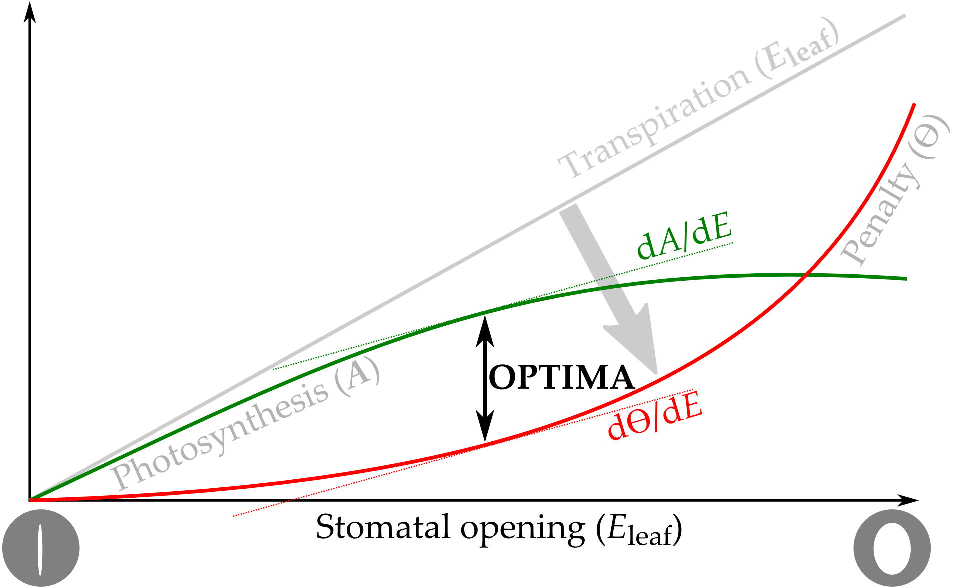
Yujie Wang[1], **John S. Sperry**[1], **William R. L. Anderegg**[1], **Martin D. Venturas**[1] and **Anna T. Trugman**[2]

[1]School of Biological Sciences, University of Utah, Salt Lake City, UT 84112, USA; [2]Department of Geography, University of California Santa Barbara, Santa Barbara, CA 93106, USA

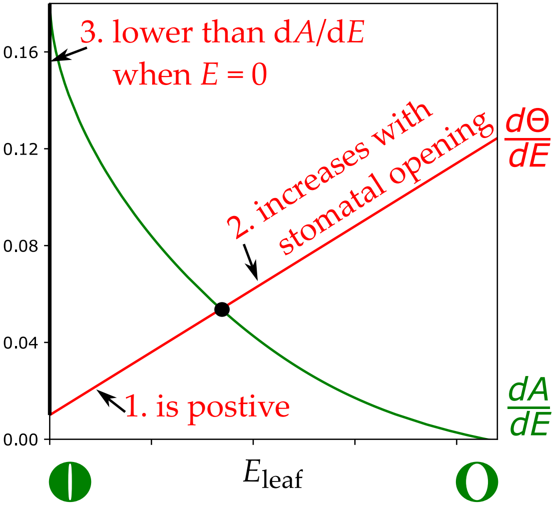
Contents

Mathematical tips

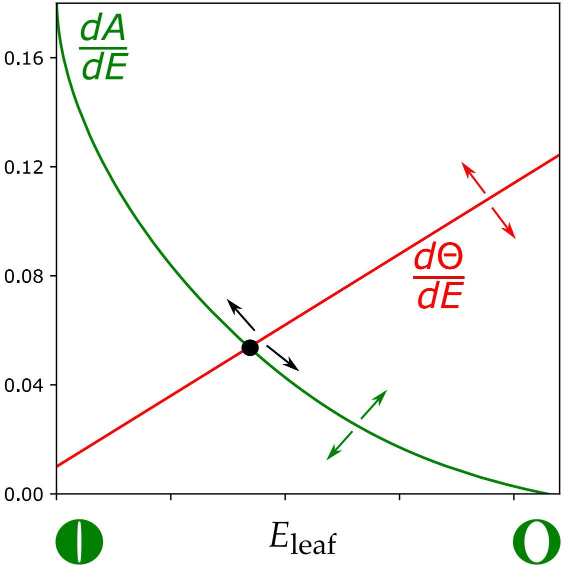


Criteria for a unique solution

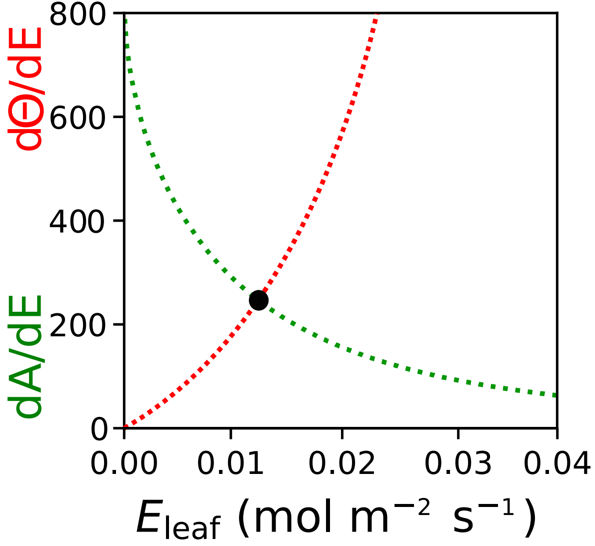
$$\frac{\mathrm{d}A}{\mathrm{d}E} = \frac{\mathrm{d}\Theta}{\mathrm{d}E}$$



Criteria for responses to the environment



4. decreases with higher VPD (drier air)



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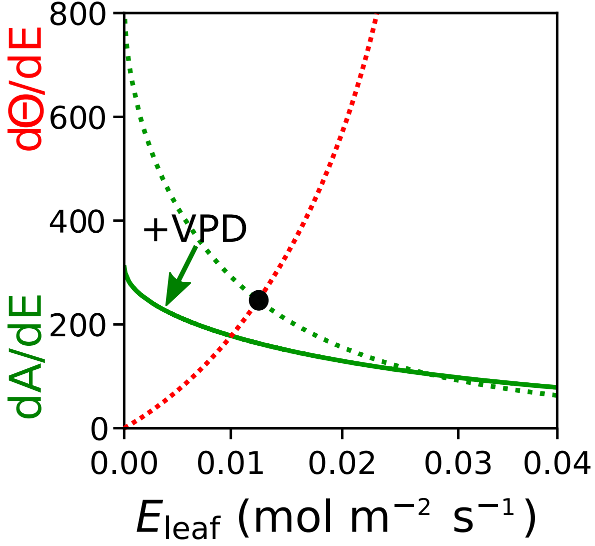

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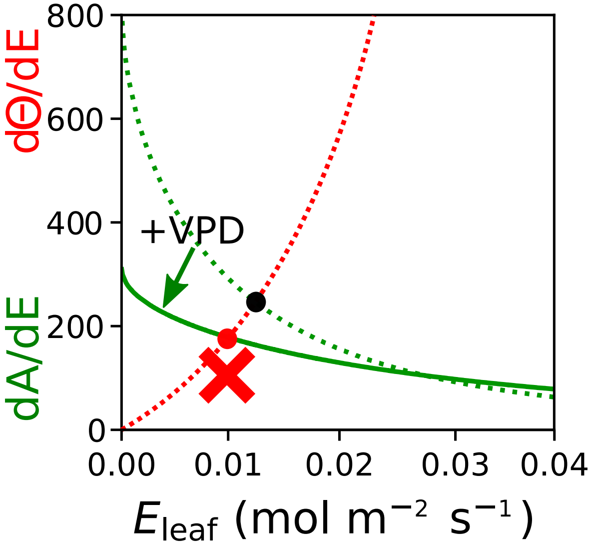

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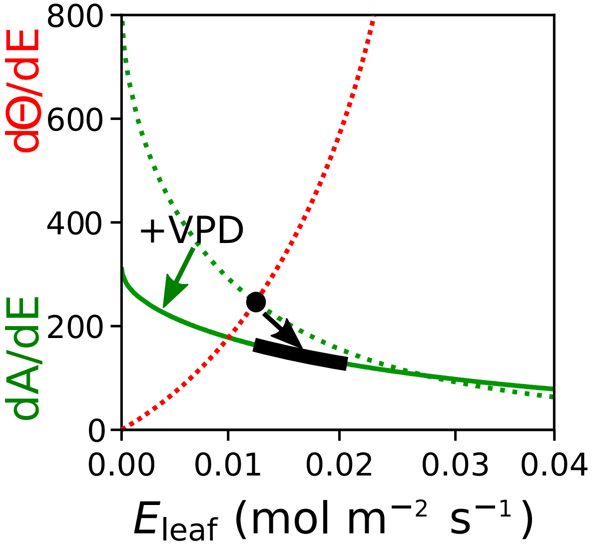

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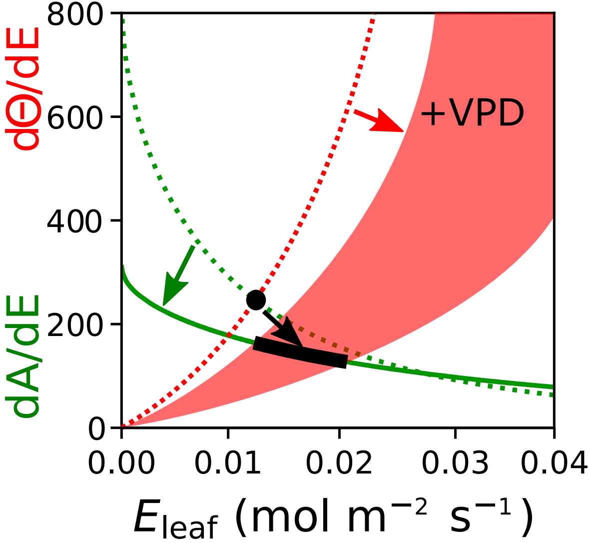
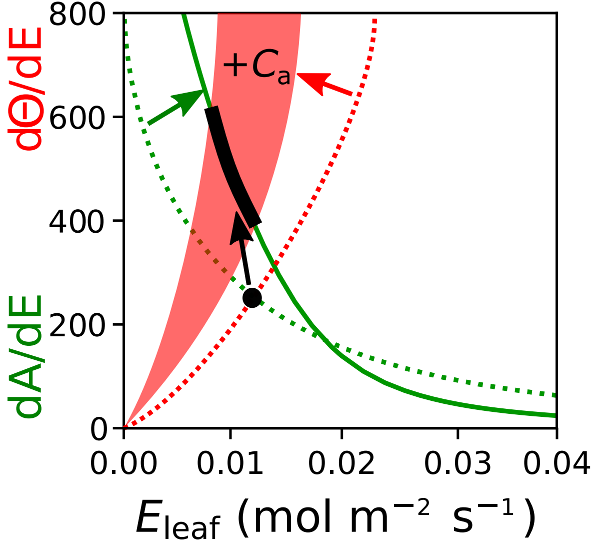
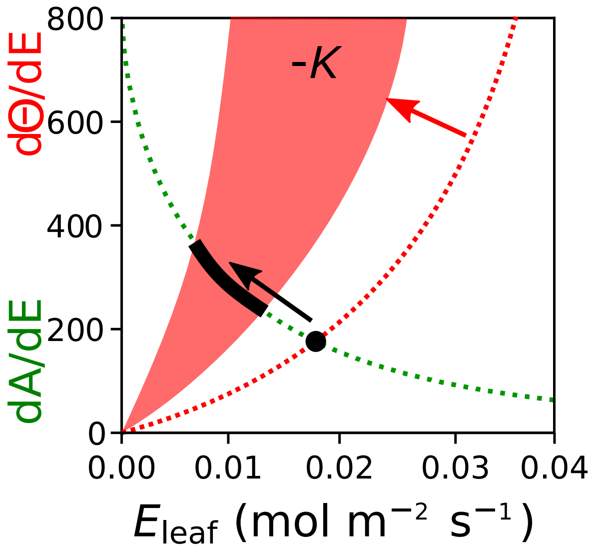


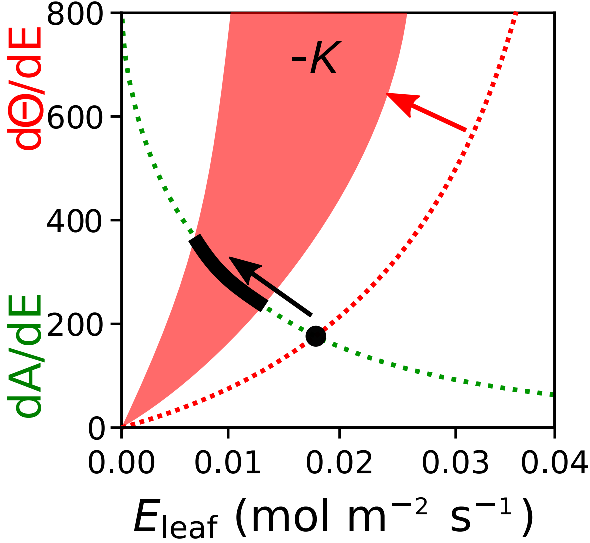
5. increases with higher CO_2



6. increases with drier soil



7. increases with lower hydraulic conductance



Criteria for $d\Theta/dE$

Criteria for a unique solution

1. $d\Theta/dE > 0$
2. $d\Theta/dE \Uparrow$ when $E_{leaf} \Uparrow$
3. $d\Theta/dE < dA/dE$ when $E_{leaf} = 0$

Criteria for stomatal responses

4. $d\Theta/dE \Downarrow$ when air gets drier
5. $d\Theta/dE \Uparrow$ when $[CO_2] \Uparrow$
6. $d\Theta/dE \Uparrow$ when soil gets drier
7. $d\Theta/dE \Uparrow$ when hydraulic conductance $\Downarrow$

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Example 1: The Cowan-Farquhar model

Criterion

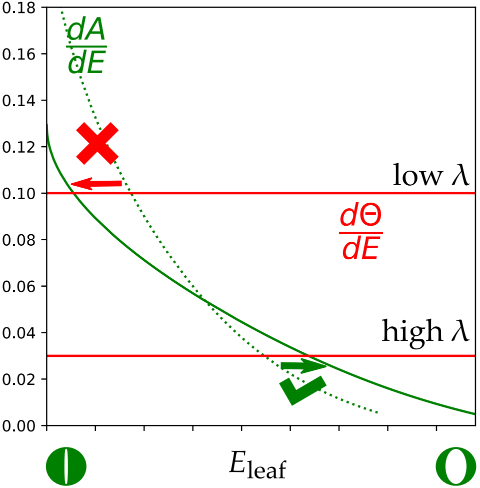
$$\max\left(A - \frac{E_{\text{leaf}}}{\lambda}\right)$$

Marginal penalty

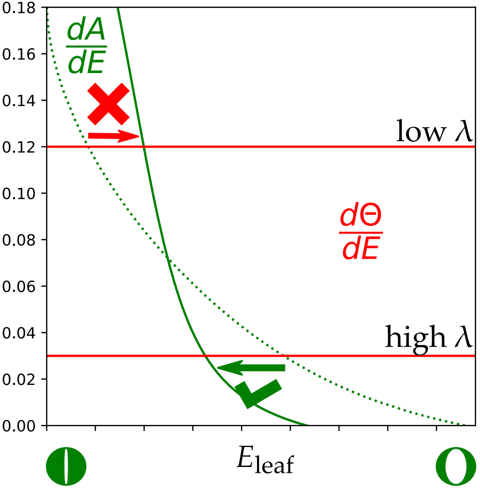
$$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = \frac{1}{\lambda}$$

Cowan and Farquhar (1977)

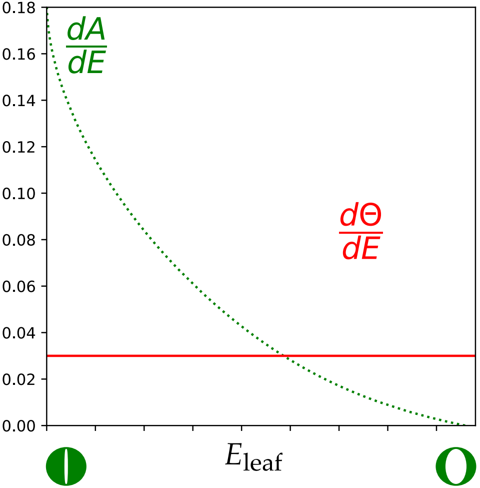
Response to VPD



Response to CO_2



Response to drought (history)



Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($\mathrm{d}\Theta/\mathrm{d}E$ or $\mathrm{d}\Theta'/\mathrm{d}E$)	Criteria I–III	Response Criteria IV–VII DCPK	Fitting parameters
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\mathrm{leaf}}}{\lambda}$	$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = \frac{1}{\lambda}$	YNN	NNNN	λ
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Sperry	(Sperry et al., 2017)	$\Theta = A_{\mathrm{max}} \cdot \left(1 - \frac{K}{K_{\mathrm{max}}}\right)$	$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = -\frac{\mathrm{d}K}{\mathrm{d}E} \cdot \frac{A_{\mathrm{max}}}{K_{\mathrm{max}}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{\mathrm{max},0}}\right)$	$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = -\frac{\mathrm{d}K}{\mathrm{d}E} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{\mathrm{leaf}}}{E_{\mathrm{crit}}}$	$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = \frac{A}{E_{\mathrm{crit}} - E_{\mathrm{leaf}}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{\mathrm{ww}} \cdot \frac{\mathrm{SC}}{\mathrm{SC}_{\mathrm{max}}}$	$\frac{\mathrm{d}\Theta'}{\mathrm{d}E} = \frac{A}{\mathrm{SC}_{\mathrm{max}} - \mathrm{SC}} \cdot \frac{\mathrm{dSC}}{\mathrm{d}E}$	YYY	YYYY	$\mathrm{SC}_{\mathrm{max}}$, K_{rhiz}, anatomy
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{\mathrm{ww}} \cdot \frac{P}{P_{\mathrm{crit}}}$	$\frac{\mathrm{d}\Theta'}{\mathrm{d}E} = \frac{A}{K \cdot (P_{\mathrm{crit}} - P)}$	YYY	YYYY	K_{rhiz}

Example 2: The Sperry model

Optimization criterion

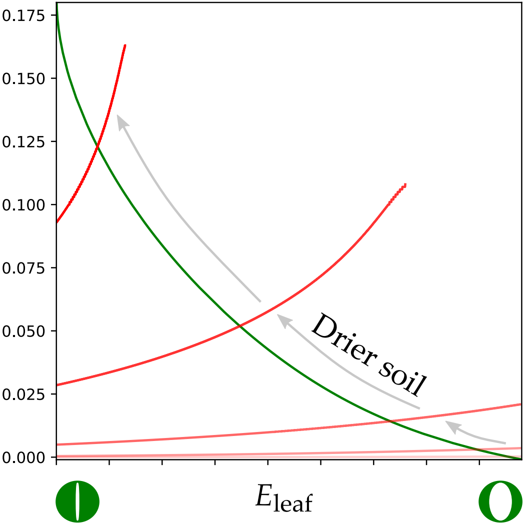
$$\max\left(\frac{A}{A_{\max}} - \left(1 - \frac{K}{K_{\max}}\right)\right), K = \frac{\mathrm{d}E}{\mathrm{d}P}$$

Marginal penalty

$$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = -\frac{\mathrm{d}K}{\mathrm{d}E} \cdot \frac{A_{\max}}{K_{\max}}$$

Sperry et al. (2017)

Response to drought



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New Model		$\Theta = A \cdot \frac{E_{\mathrm{leaf}}}{E_{\mathrm{crit}}}$	$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = \frac{A}{E_{\mathrm{crit}} - E_{\mathrm{leaf}}}$	YYY	YYYY	K_{rhiz}
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Example 3: A new model

Criterion

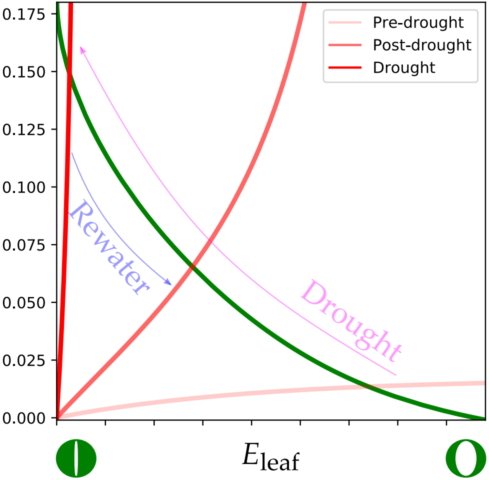
$$\max \left(A \cdot \left(1 - \frac{E_{\mathrm{leaf}}}{E_{\mathrm{crit}}} \right) \right)$$

Marginal penalty

$$\frac{\mathrm{d}\Theta}{\mathrm{d}E} = \frac{A}{E_{\mathrm{crit}} - E_{\mathrm{leaf}}}$$

Wang et al. (in press)

Response to drought



✓ Quantify $A(E_{\text{leaf}})$

✓ Quantify $\Theta(E_{\text{leaf}})$

3. Test different optimization models
4. Way forward—long-term prediction

Part III
Testing The Models

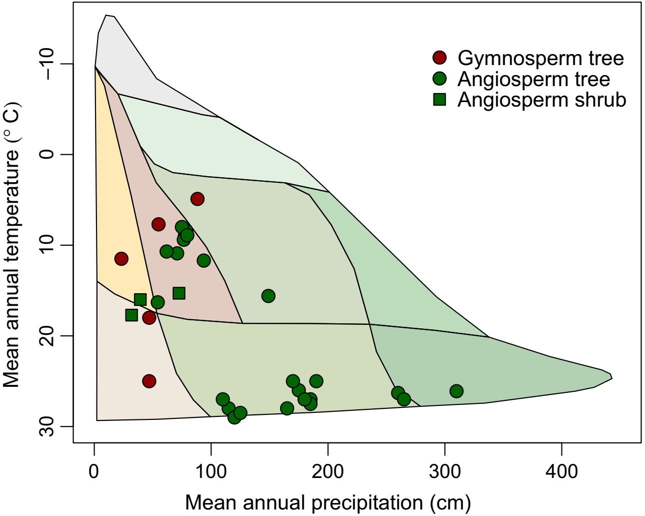
Birch dataset

Wang et al. (2019)

Aspen dataset

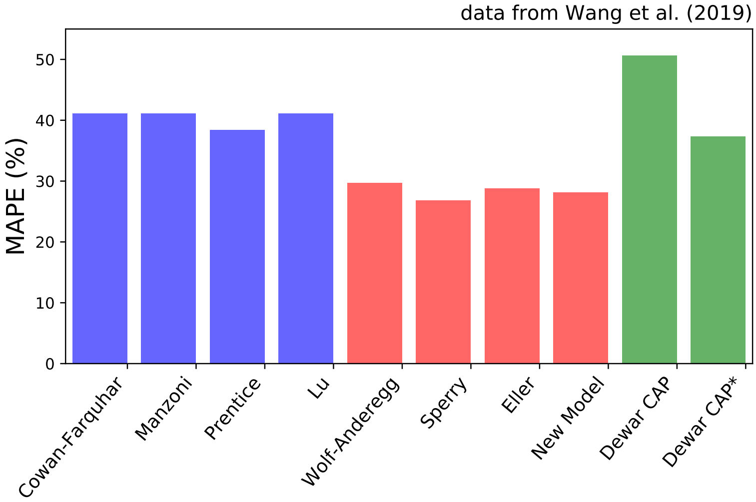
Venturas et al. (2018)

Anderegg dataset



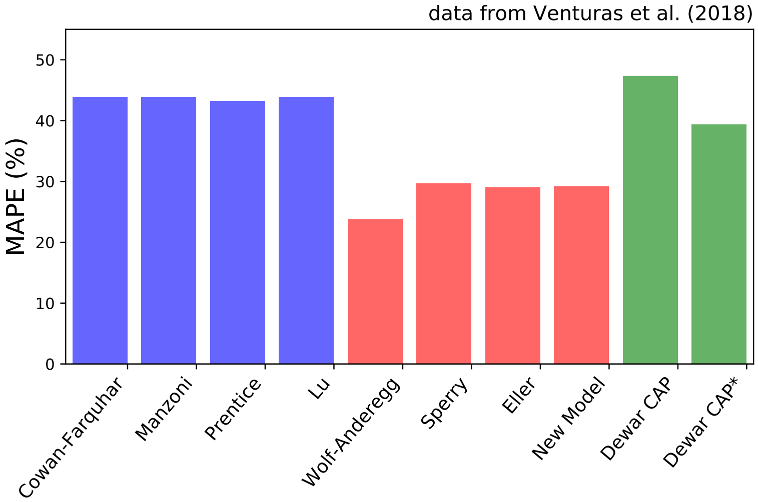
Anderegg et al. (2018)

Birch dataset

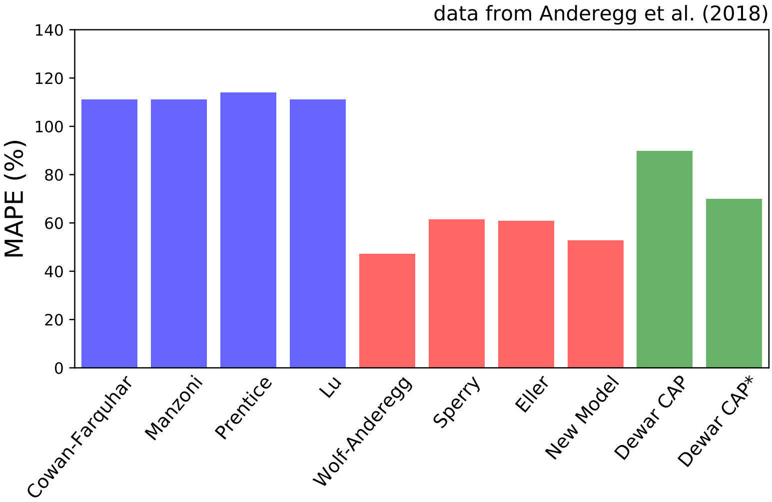


MAPE: mean absolute percentage error for A, P, and E

Aspen dataset



Anderegg dataset



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Take-home message

MATH is important.

Take-home messages

- Penalty is well represented by plant hydraulics
- Penalty is likely weighted by photosynthesis
- Trait-based models are very promising

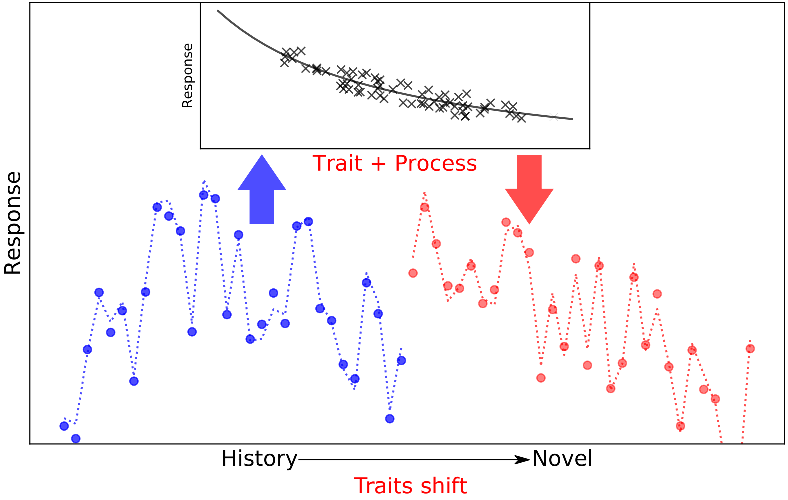
✓ Quantify $A(E_{\text{leaf}})$

✓ Quantify $\Theta(E_{\text{leaf}})$

✓ Test different optimization models

4. Way forward—long-term prediction

How about trait change?

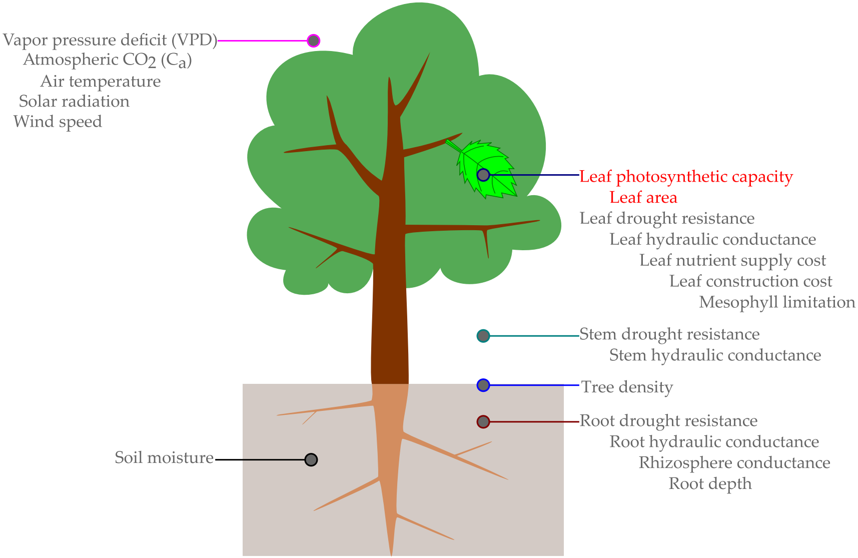


Part IV
Modeling Trait Shifts

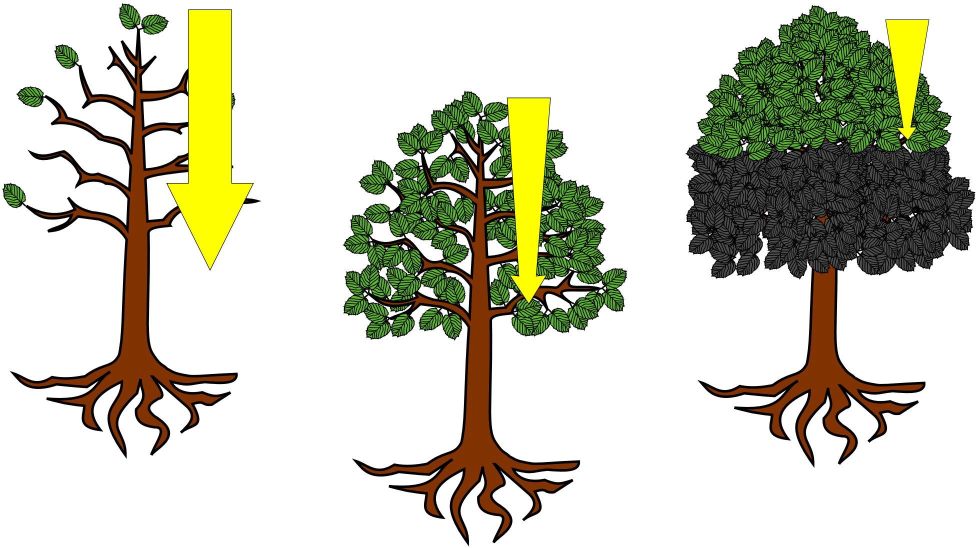
Disadvantages of trait-based model

- The model needs a lot of trait inputs;
- The traits are not constant spatially or temporally.

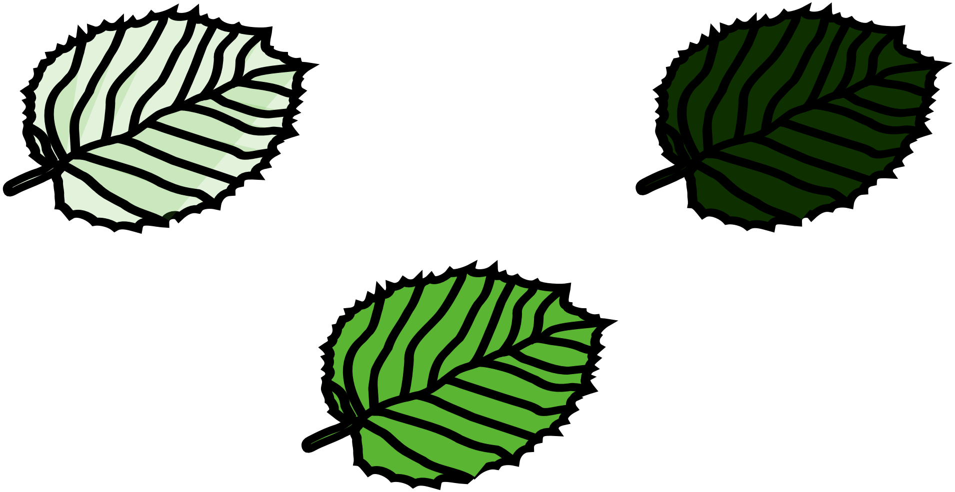
Environmental and physiological variables



Optimal leaf area



Optimal leaf photosynthesis



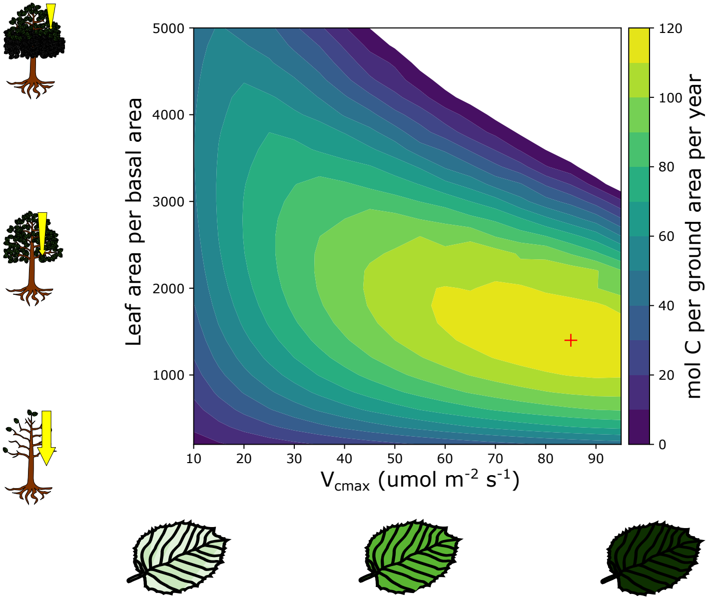
Optimal leaf investment

Optimization criterion

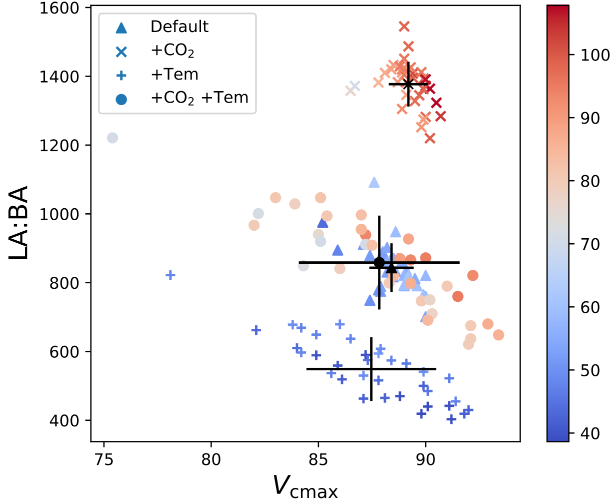
$$\max \left(\int A_{\text{day}} - \int R_{\text{night}} - \text{LCBM} - \text{NS} \right)$$

A_{day}	Net photosynthetic rate in the day
R_{night}	Respiratory rate in the night
LCBM	Leaf construction costs in carbon biomass
NS	Leaf construction costs in nutrient supply

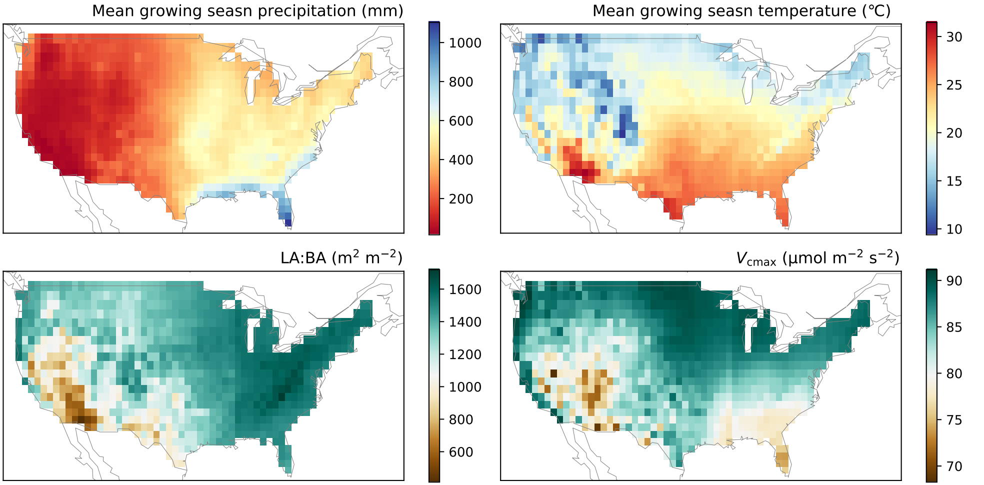
Wang et al., (in review)


Leaf area per basal area
5000
4000
3000
2000
1000
10
20
30
40
50
60
70
80
90
V_{cmax} (umol m^{-2} s^{-1})
120
100
80
60
40
20
0
mol C per ground area per year

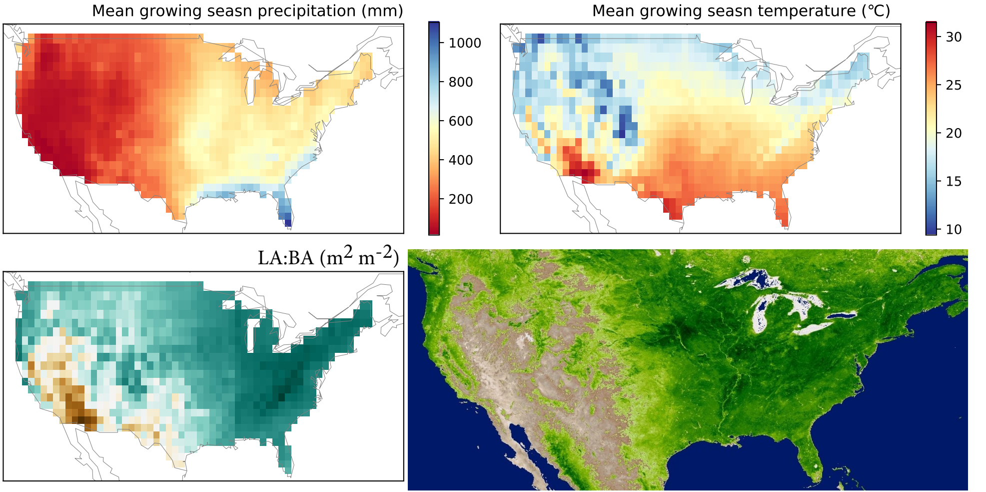
Optimal leaf investment vs. climate



Sensitivity to climate



Sensitivity to climate



- ✓ Quantify $A(E_{\text{leaf}})$
- ✓ Quantify $\Theta(E_{\text{leaf}})$
- ✓ Test different optimization models
- ✓ Way forward—long-term prediction

Conclusions

Conclusions

- Incorporating gas-phase mesophyll conductance improves photosynthesis modeling
- Water penalty is linked to plant hydraulic integrity
- Water penalty is weighted by photosynthesis opportunity
- Future research on how traits coordinate and acclimate to the environment is required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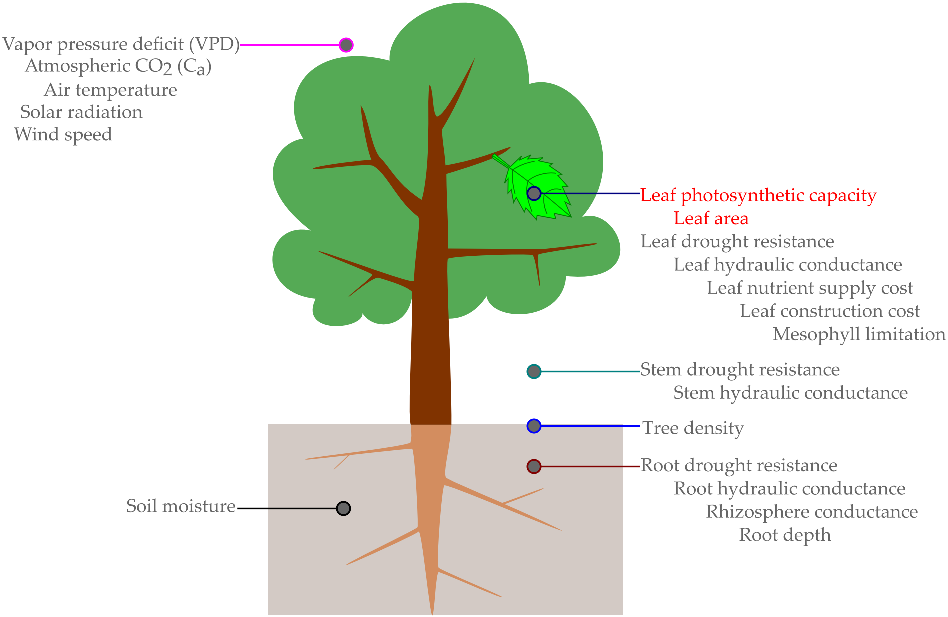
Vapor pressure deficit (VPD)
Atmospheric CO_2 (C_a)
Air temperature
Solar radiation
Wind speed
Leaf photosynthetic capacity
Leaf area
Leaf drought resistance
Leaf hydraulic conductance
Leaf nutrient supply cost
Leaf construction cost
Mesophyll limitation
Stem drought resistance
Stem hydraulic conductance
Tree density
Root drought resistance
Root hydraulic conductance
Rhizosphere conductance
Root depth
Soil moisture

Acknowledgments

University of Utah

- John Sperry
- Bill Anderegg
- Fred Adler
- David Bowling
- Jim Ehleringer
- Tom Kursar

Sperry lab

- I am the last one...

Anderegg lab

- Martin Venturas
- Anna Trugman
- Xiaonan Tai

This is not yet the end.

Stomata and agriculture

Questions

1. Should we make crops more and more resistant to drought?
2. How to optimize plant hydraulic function?
3. How to optimize water use strategy?

Q&A1

Should we make crops more and more resistant to drought?

No. Drought resistance is often coupled with low hydraulic efficiency.

Should we make crops more and more resistant to drought while being efficient as well?

No. Water use strategy is related to how the plant weighs the hydraulic risk.

Q&A2

How to optimize plant hydraulic function?

Set aside the gene engineering, there should be optimal hydraulic efficiency and safety combination, and finding this optimum is useful any way. Future gene editing may be guided by the coupling of stomatal control and plant hydraulics.

Q&A3

How to optimize water use strategy?

- The coupling of stomatal control and plant hydraulics may impede the gene engineering. Decoupling the two and then taking the Cowan-Farquhar optimum (constant marginal water use efficiency) might be useful.
- However, any gene engineering need to ensure that plants won't die from potential drought stress.