

CARBON GAIN AND RISK IN MODELING LEAF GAS EXCHANGE

WANG, Yujie

Sperry Lab, University of Utah

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- Global climate change
- Modeling leaf gas exchange

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- Mesophyll limitation
- Model solution
- Improvements

Quantify Θ

- Potential penalties
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- Model review
- The Cowan & Farquhar model
- The Sperry model
- A new model

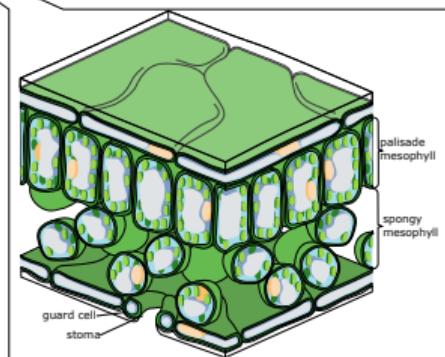
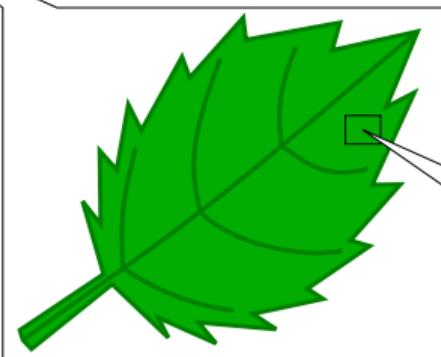
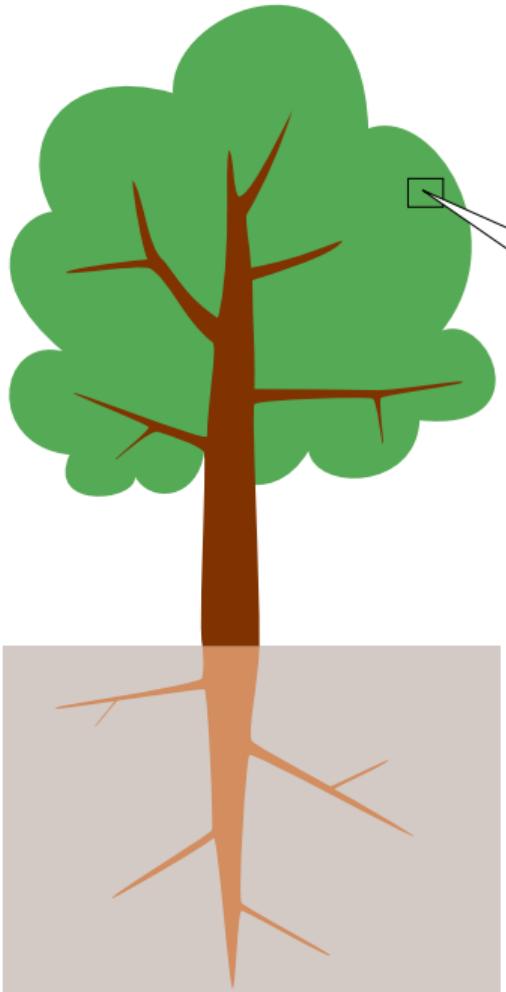
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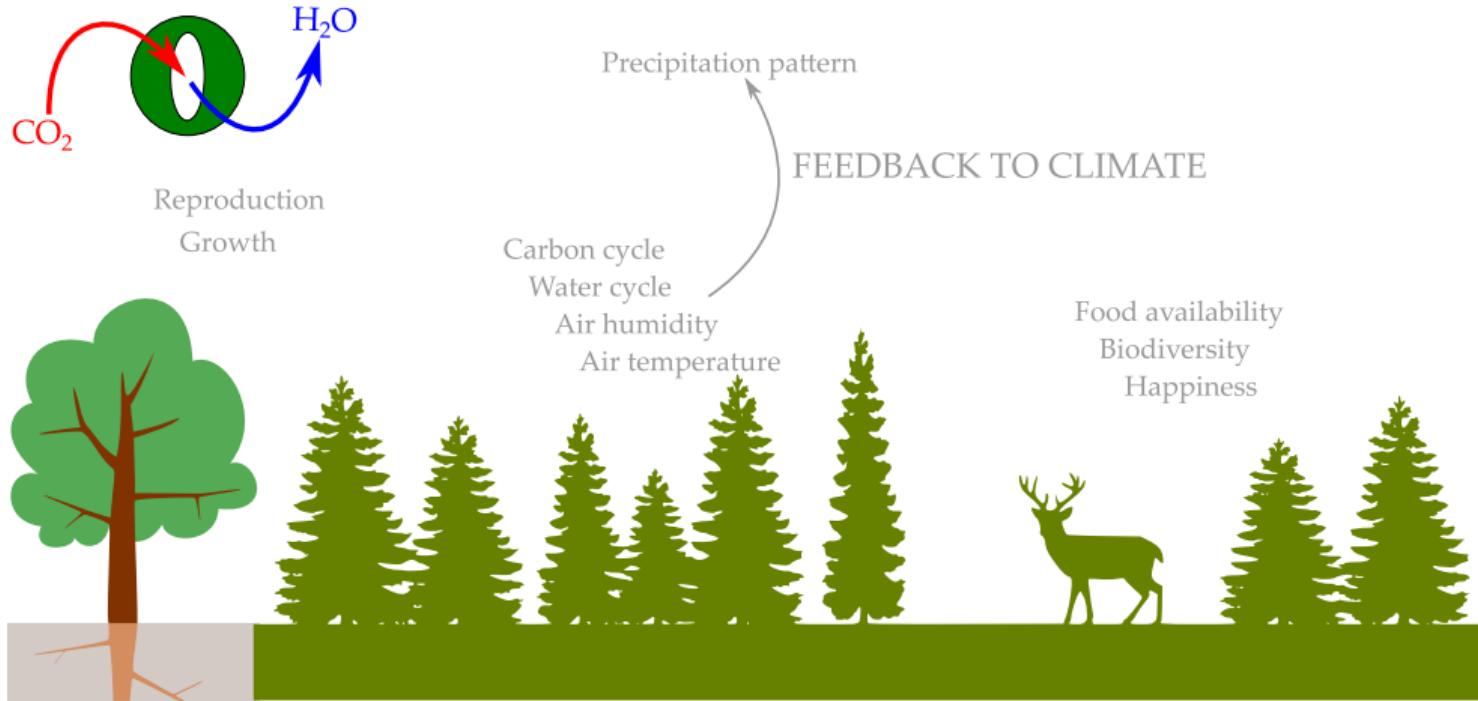
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Significance of leaf gas exchange



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Uncertainty in land surface system

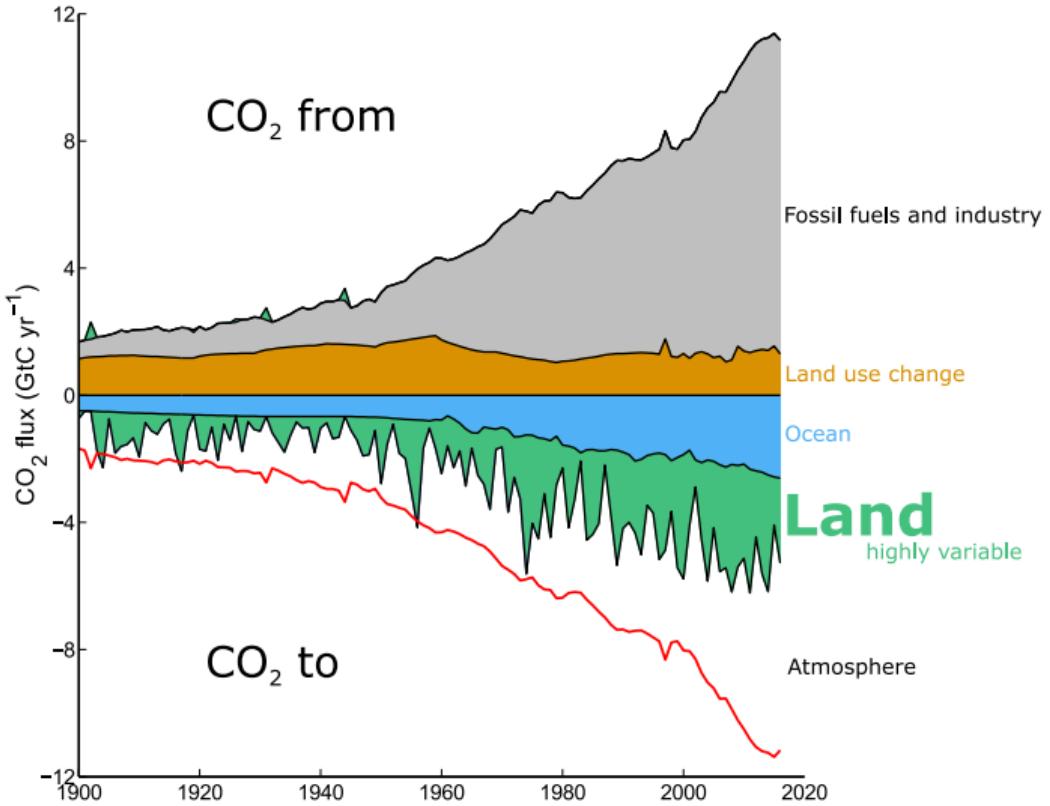


Figure adapted from Le Quéré et al. (2018)

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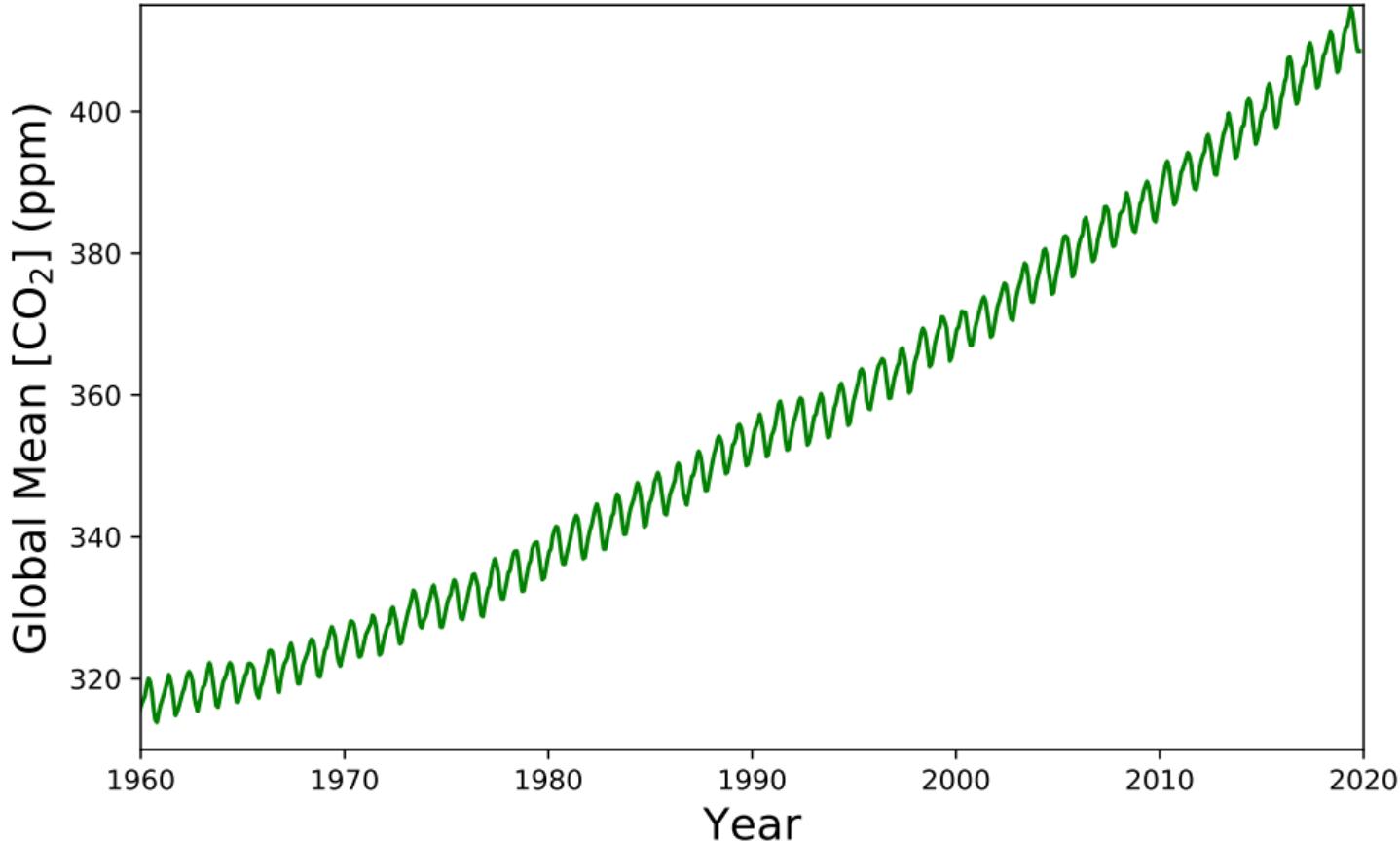
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Increasing CO₂ concentration



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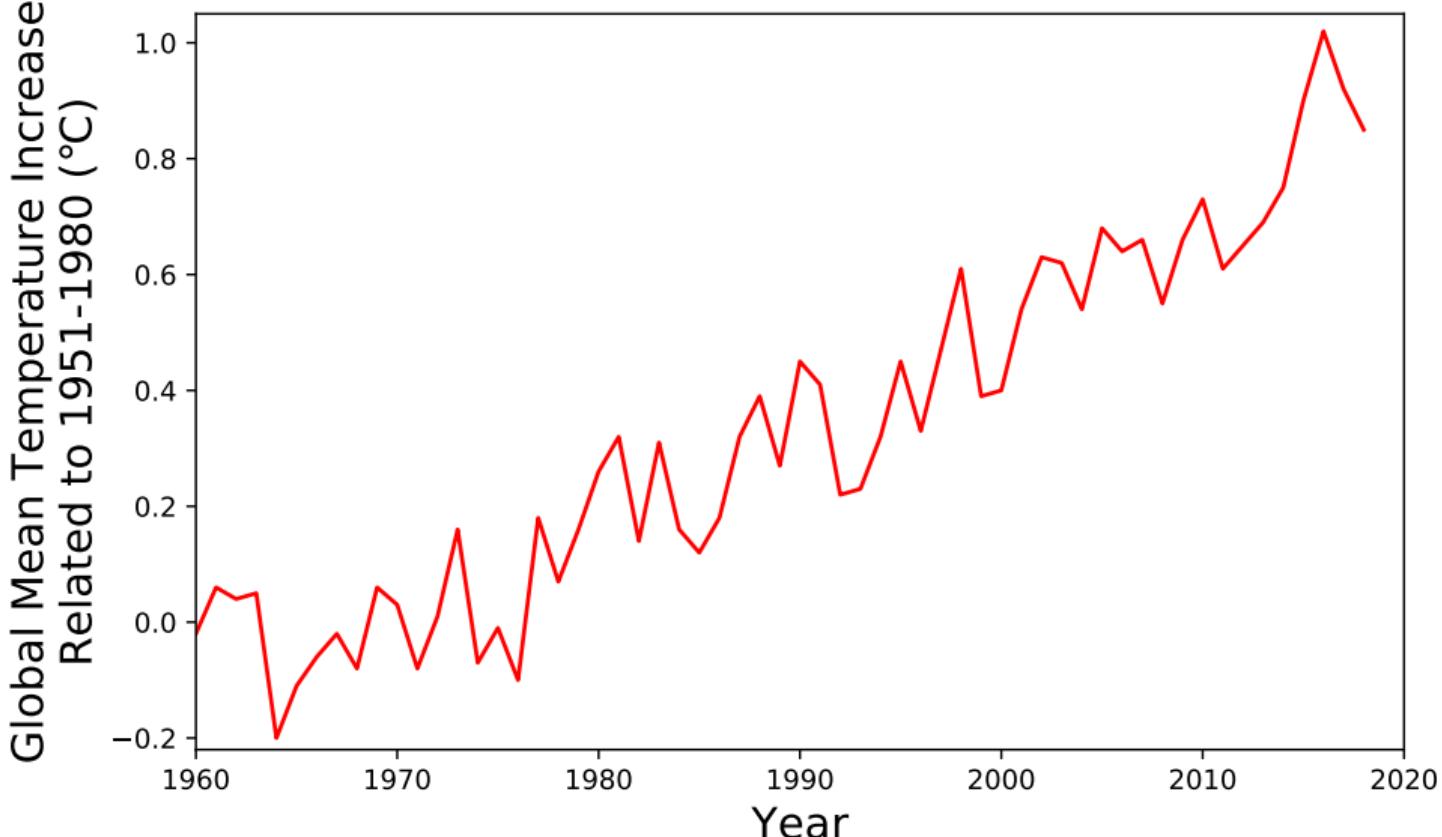
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Increasing temperature



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Soil moisture change

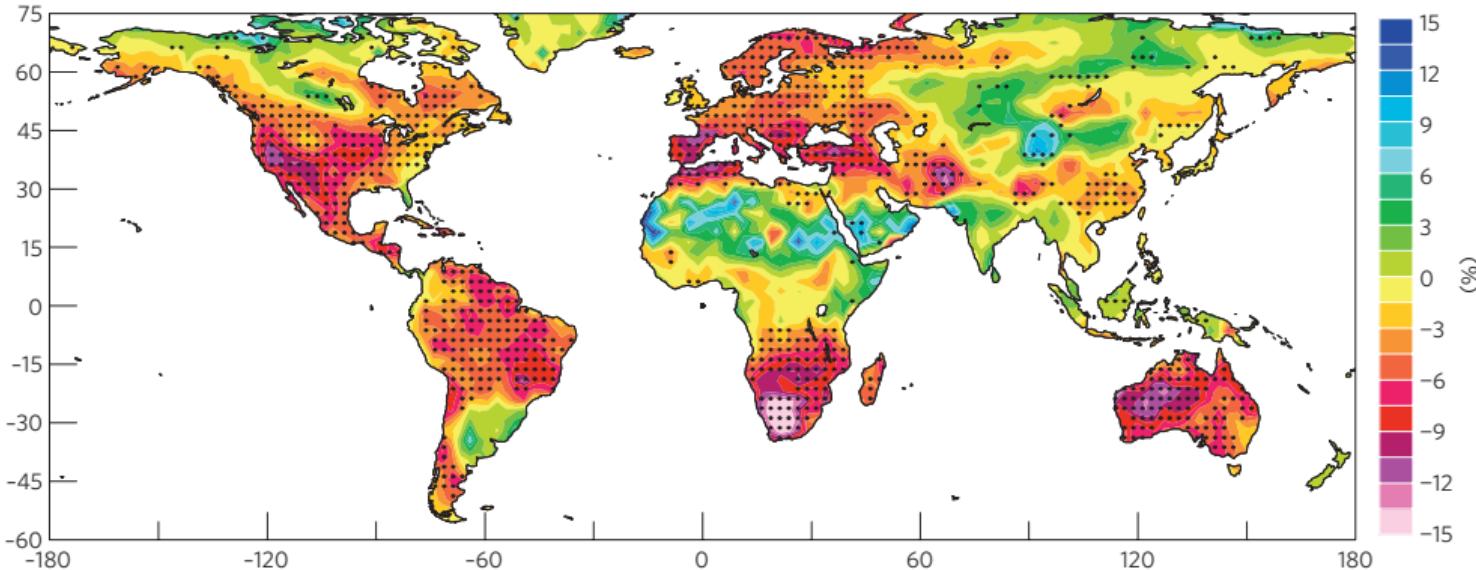


Figure from Dai (2013)

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Role of land in the future

CO₂ Sink?

CO₂ Source?

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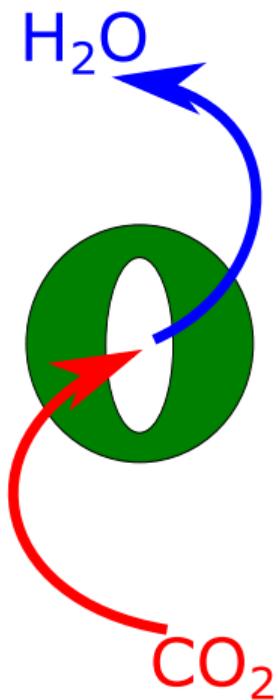
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Leaf gas exchange through stomata

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

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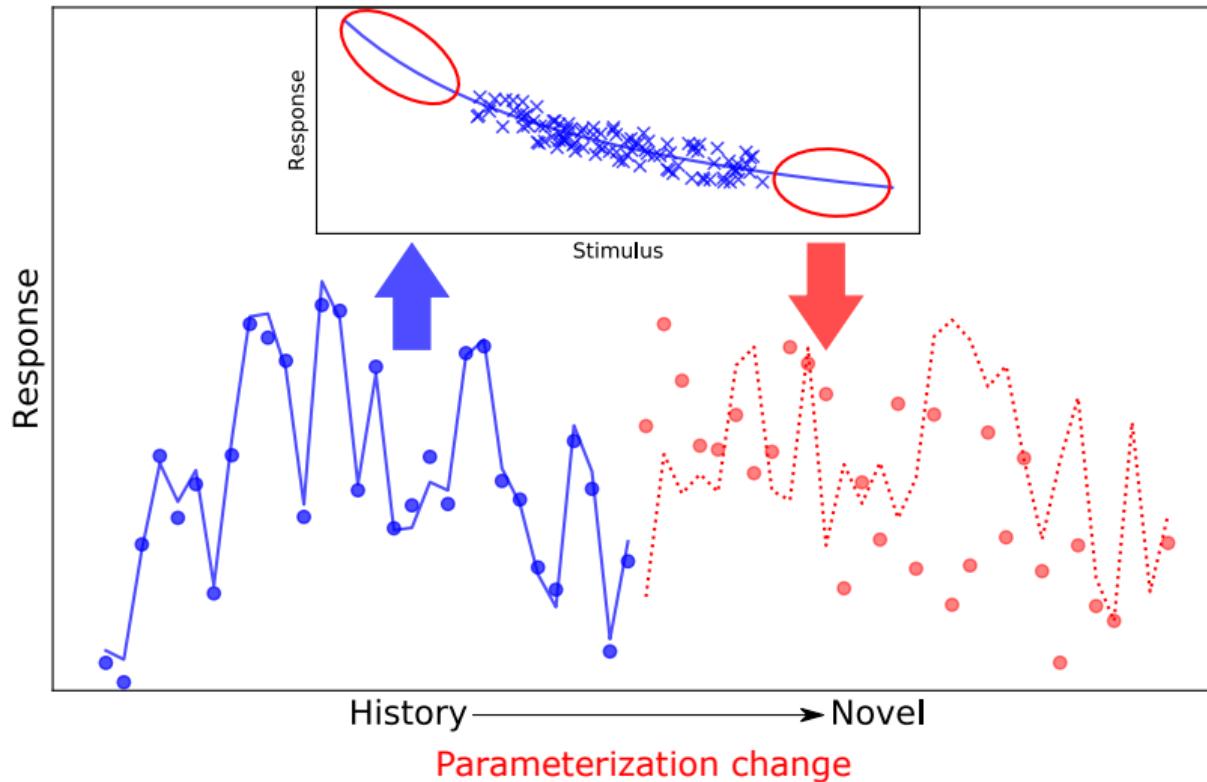
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The easiest way—statistical regression approach



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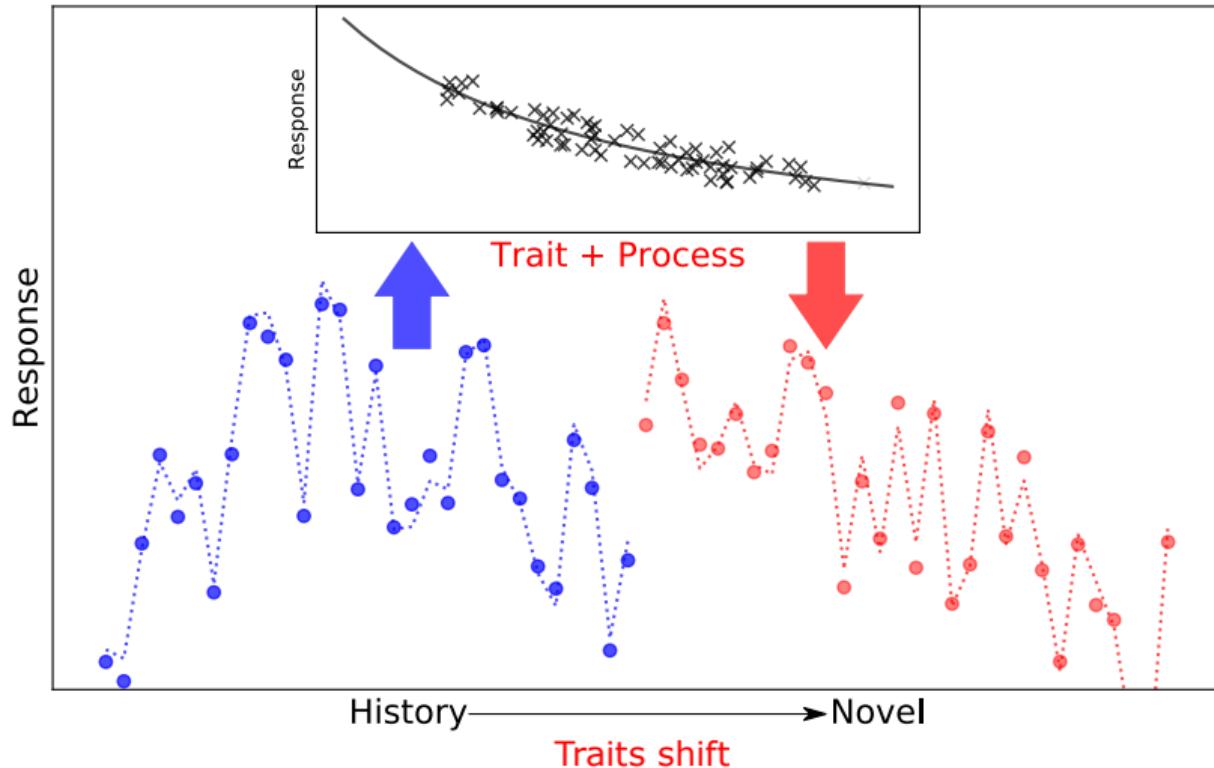
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A better way—physiological trait-based approach



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A better way—challenges

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

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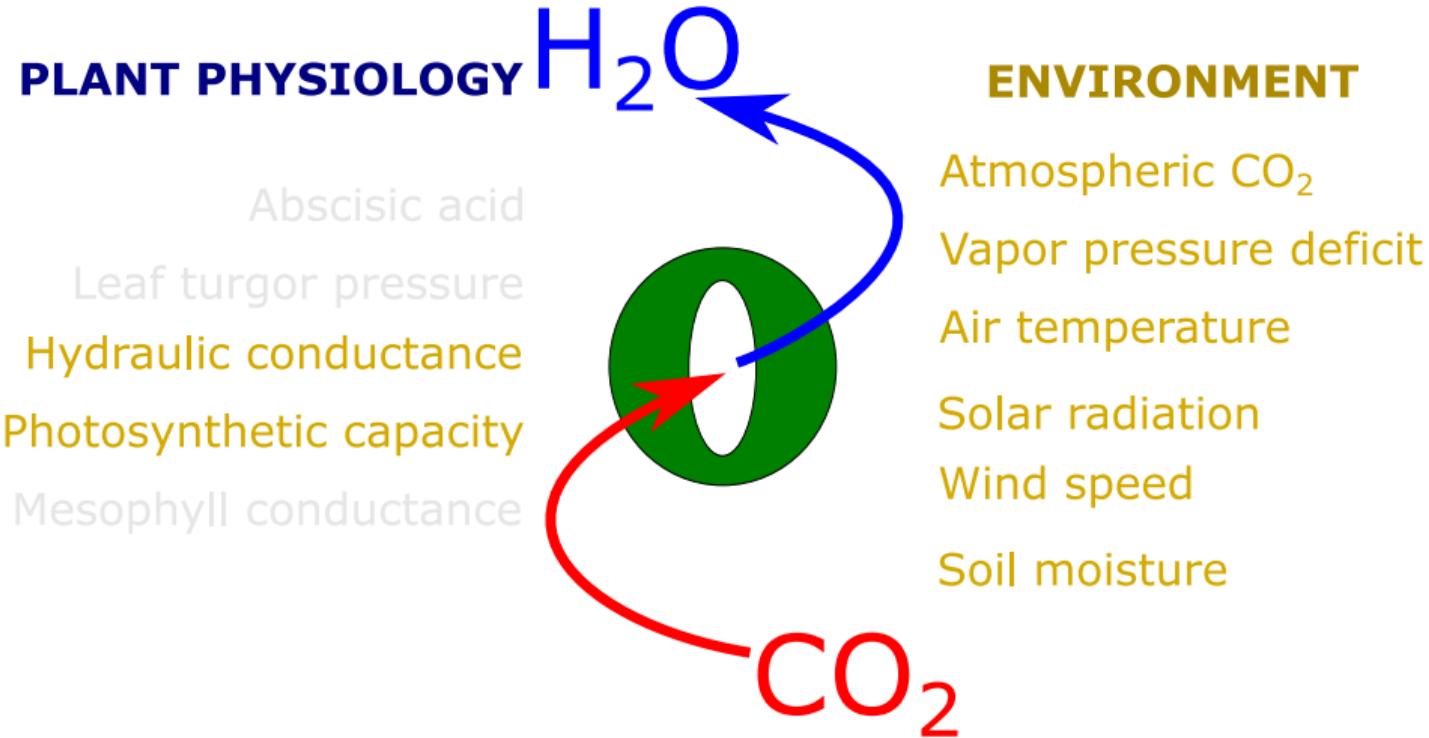
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What we know



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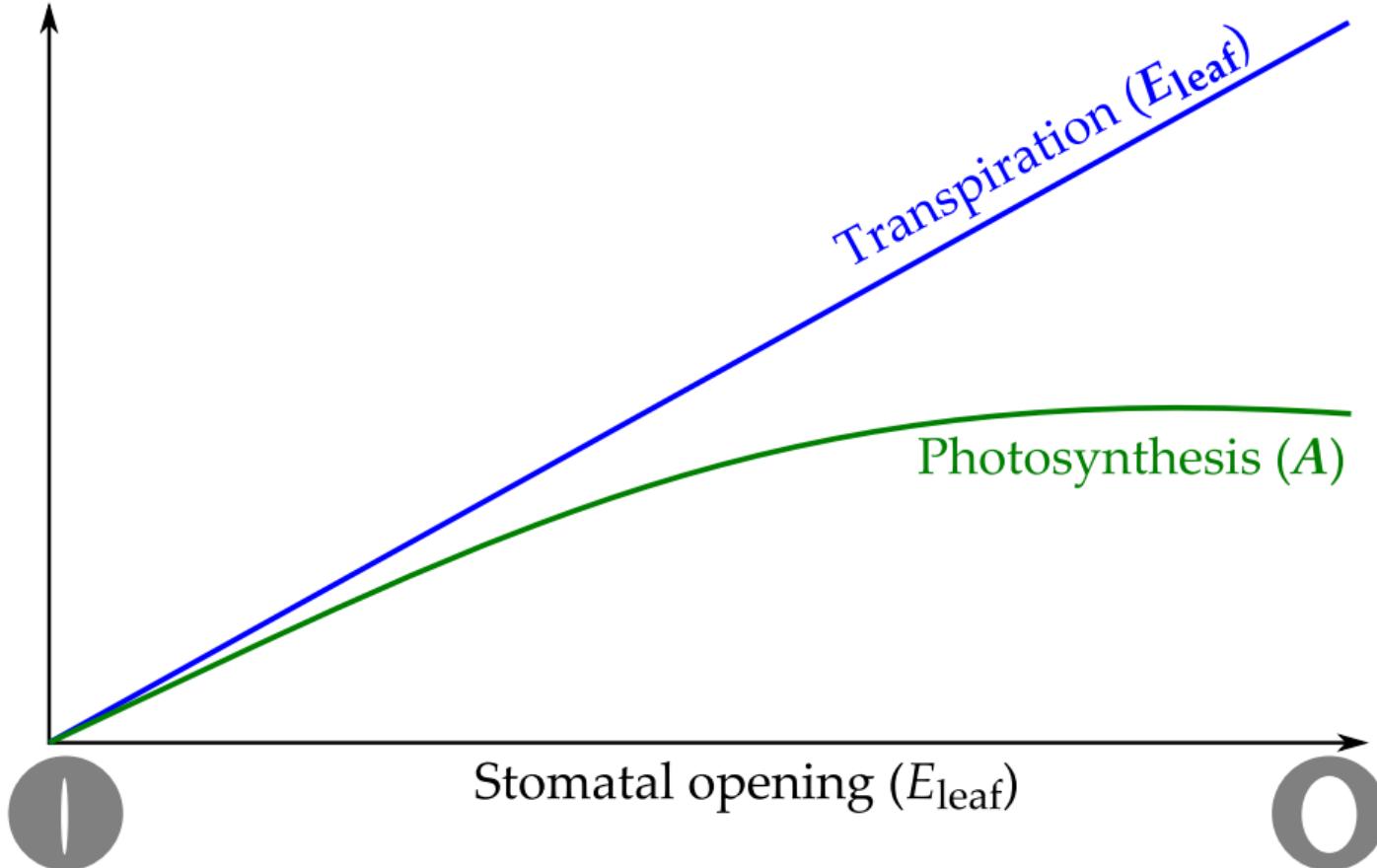
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Quantify transpiration and photosynthesis



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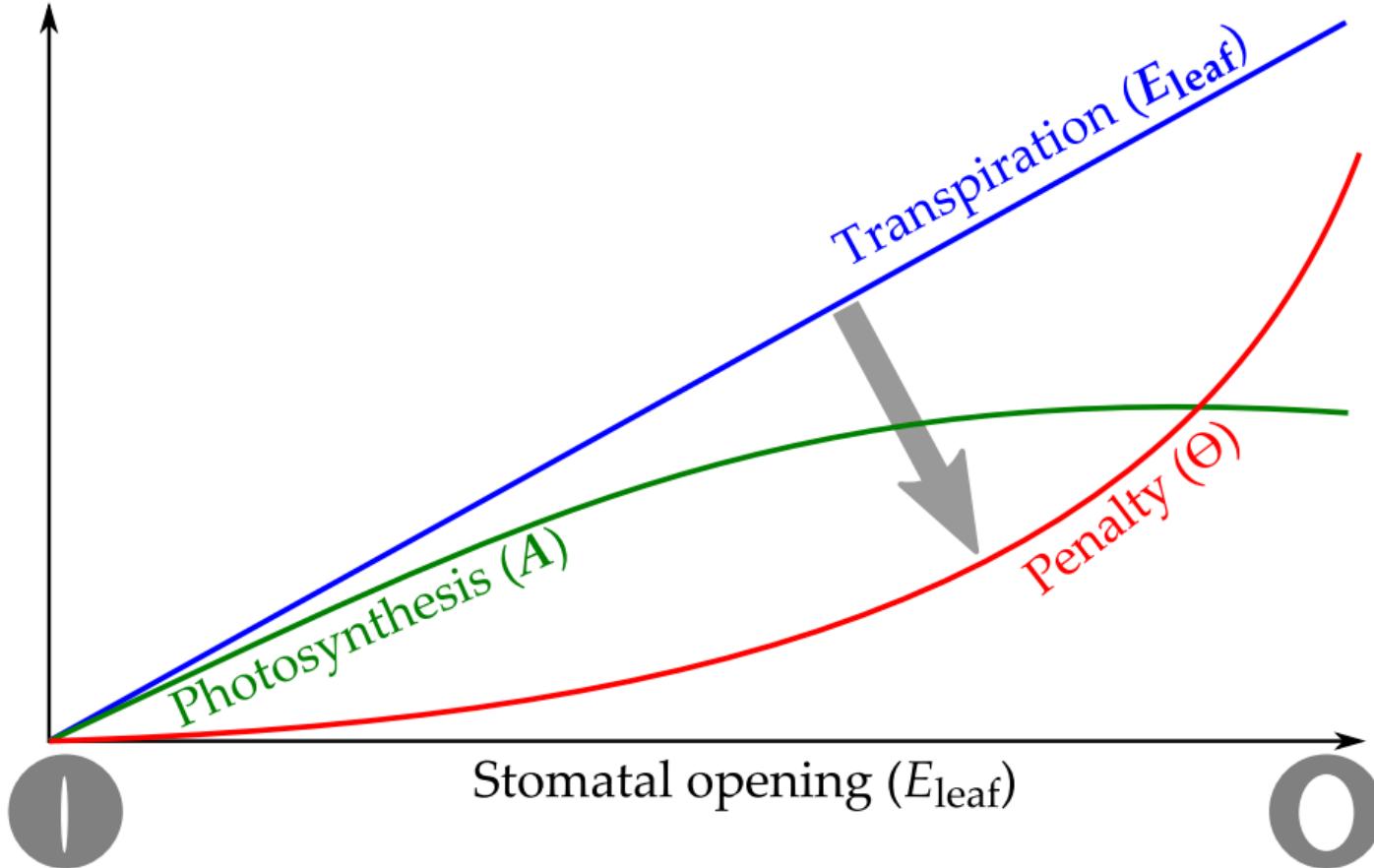
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Translation to water penalty



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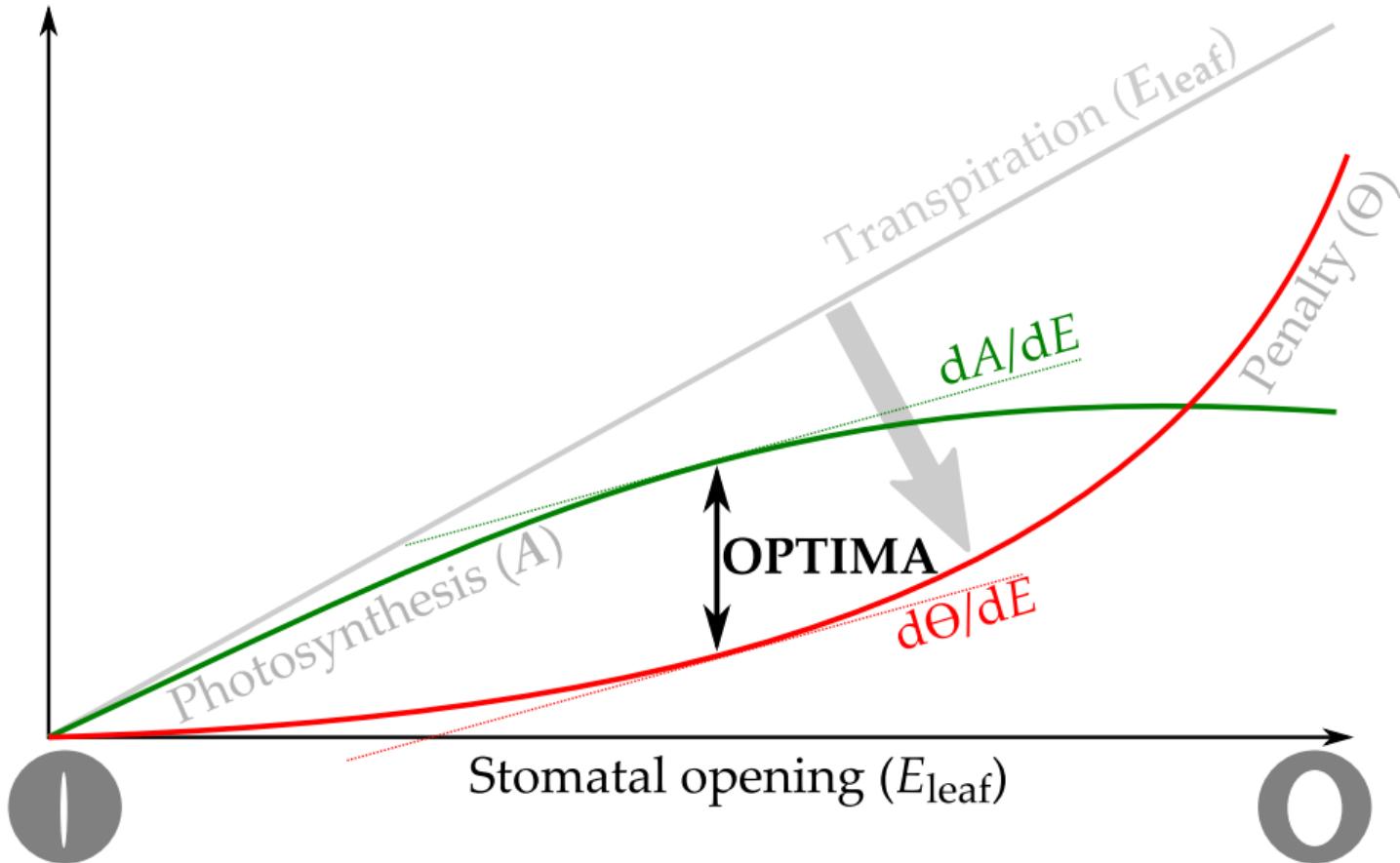
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Optimal stomatal opening



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Stomatal optimization

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

The optimal solution is:

$$\frac{dA}{dE} = \frac{d\Theta}{dE}$$

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

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Symbols

A Photosynthesis;
 Θ Penalty;
 E, E_{leaf} Transpiration;
 dA/dE Marginal carbon gain;
 $d\Theta/dE$ Marginal water penalty.

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QUANTIFY CARBON GAIN

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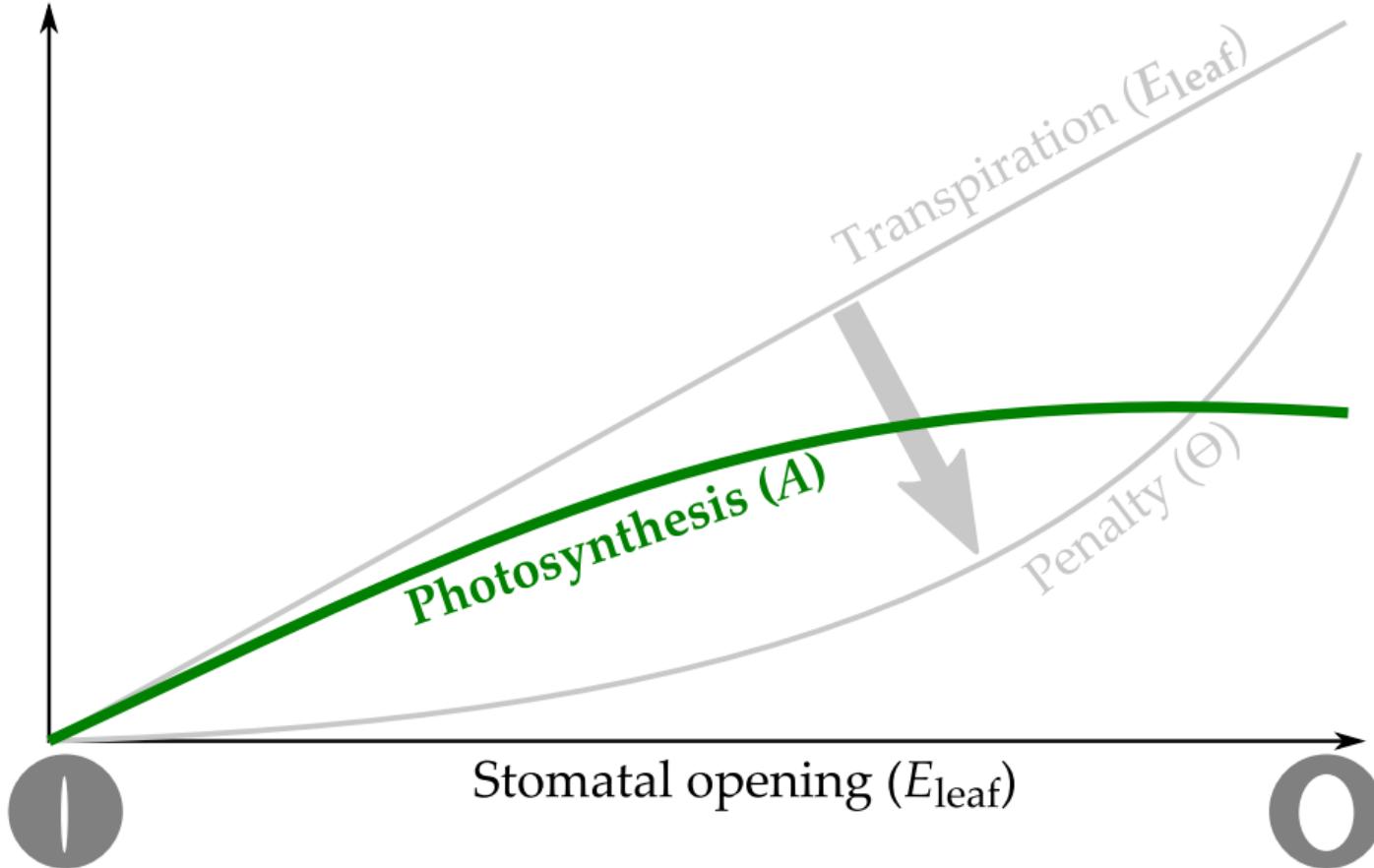
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Quantify carbon gain—photosynthesis (A)



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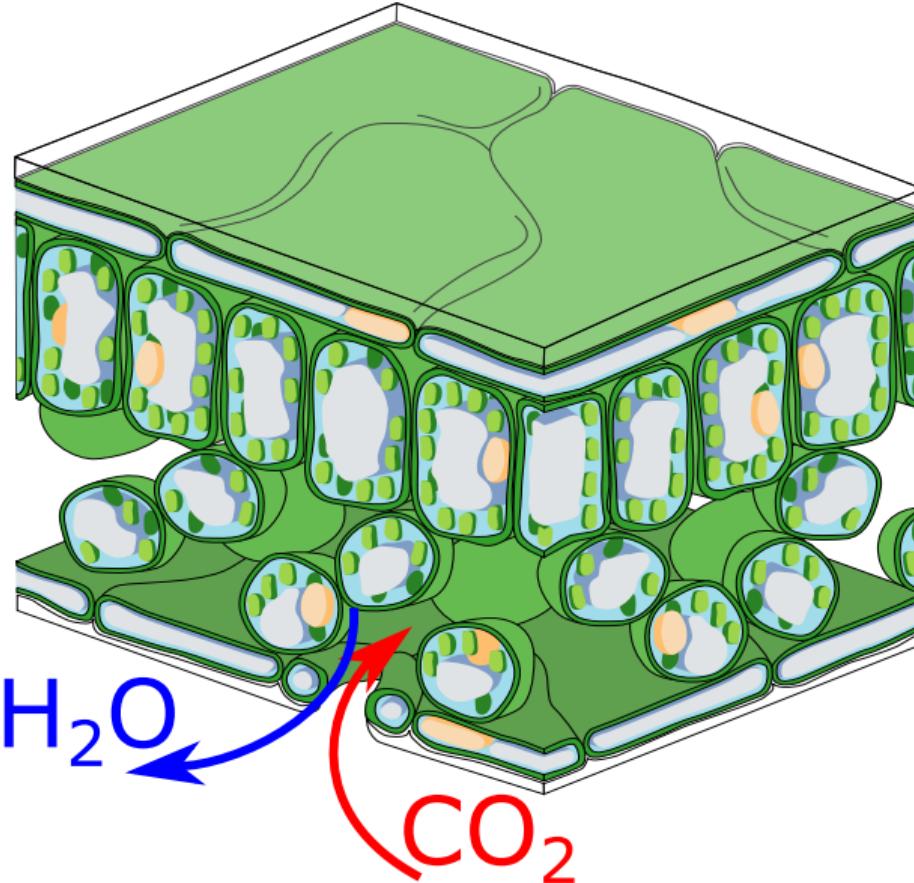
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Classic photosynthesis model



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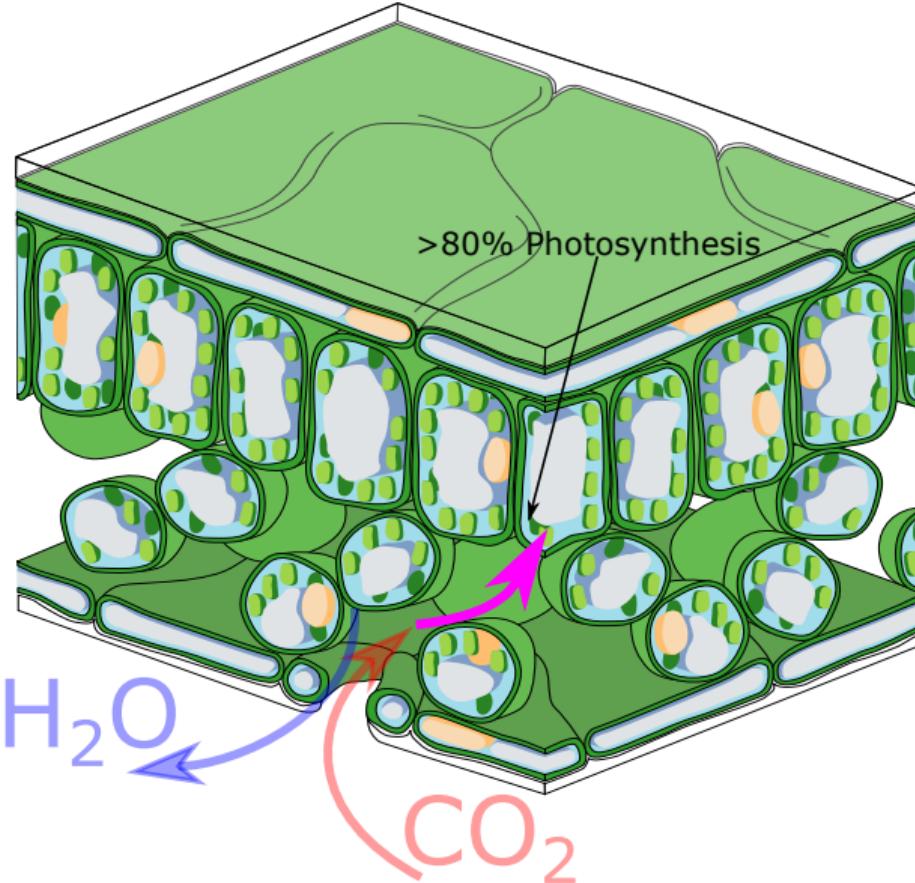
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The “missing” components



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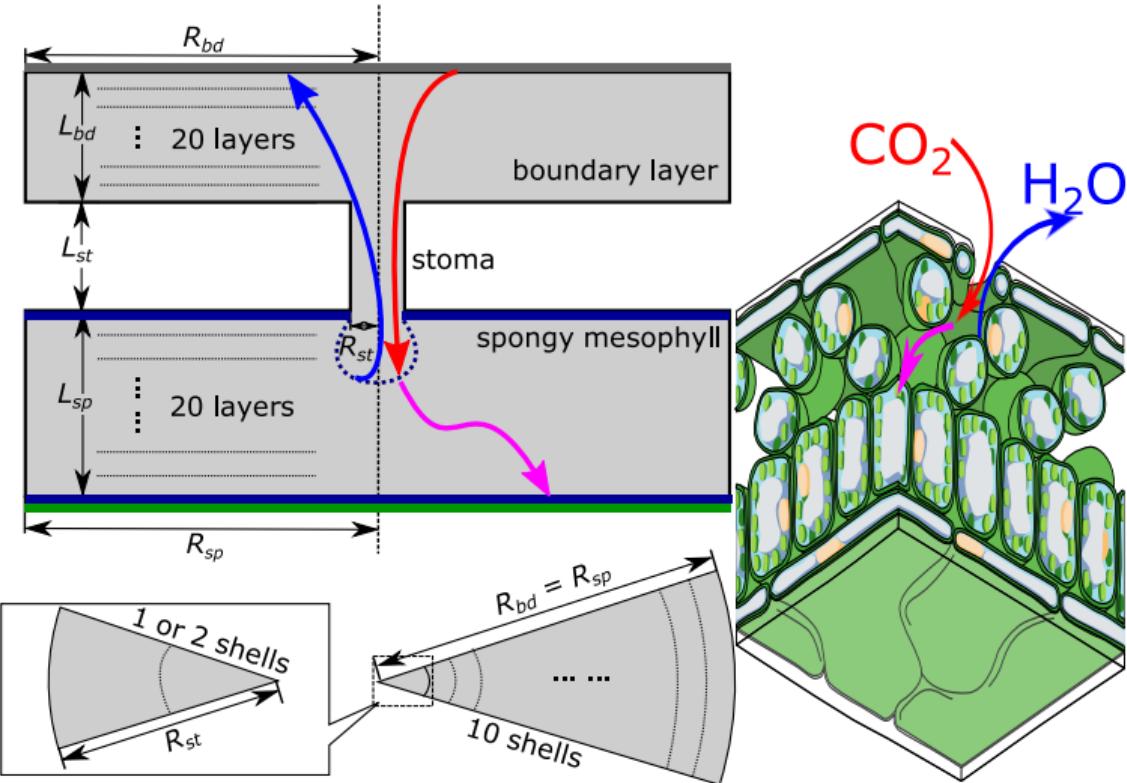
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Mesophyll limitation



Wang et al., (in review)

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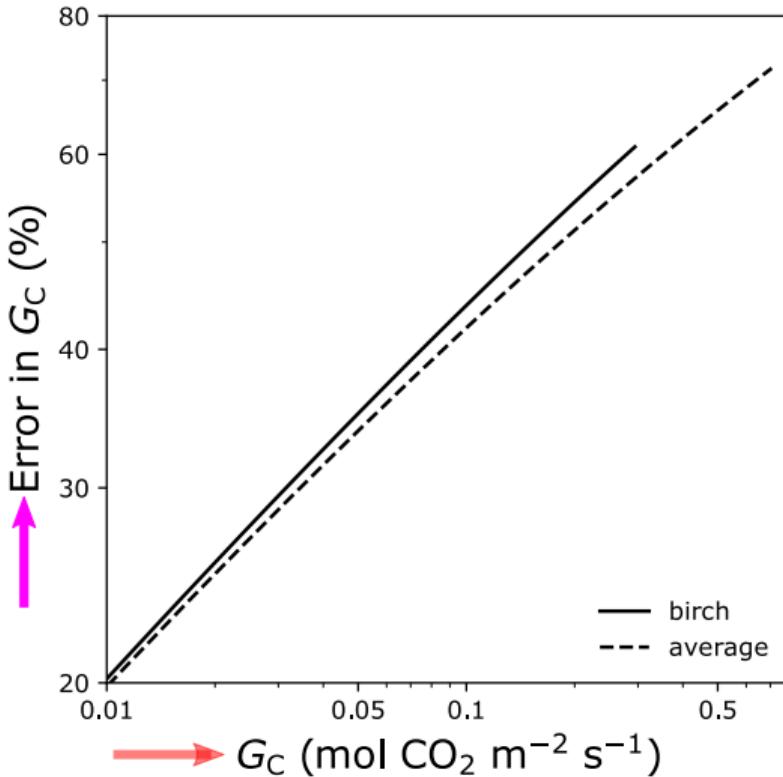
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Mesophyll limitation as an “error”



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Improved photosynthesis model

$$G_C' = \frac{G_C}{1 + a \cdot G_C^b}$$

classic model

corrected model

A mathematical equation comparing a 'classic model' term G_C with a 'corrected model' term G_C' . The corrected model is represented by a fraction where the numerator is the classic model term G_C , and the denominator is a correction factor $1 + a \cdot G_C^b$. A red arrow points from the G_C term in the denominator to the G_C term in the numerator. A pink arrow points from the G_C' term on the left to the left side of the equation.

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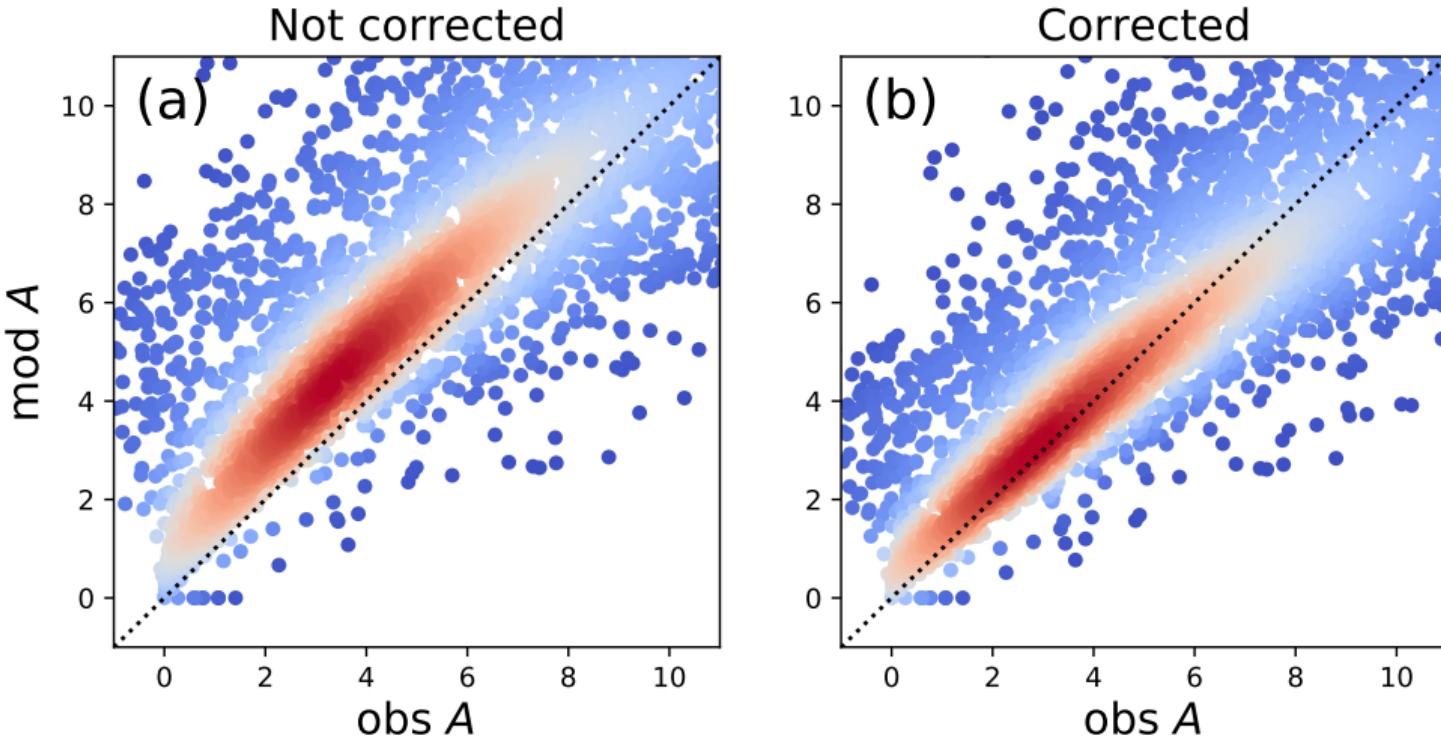
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Improvement of modeled A



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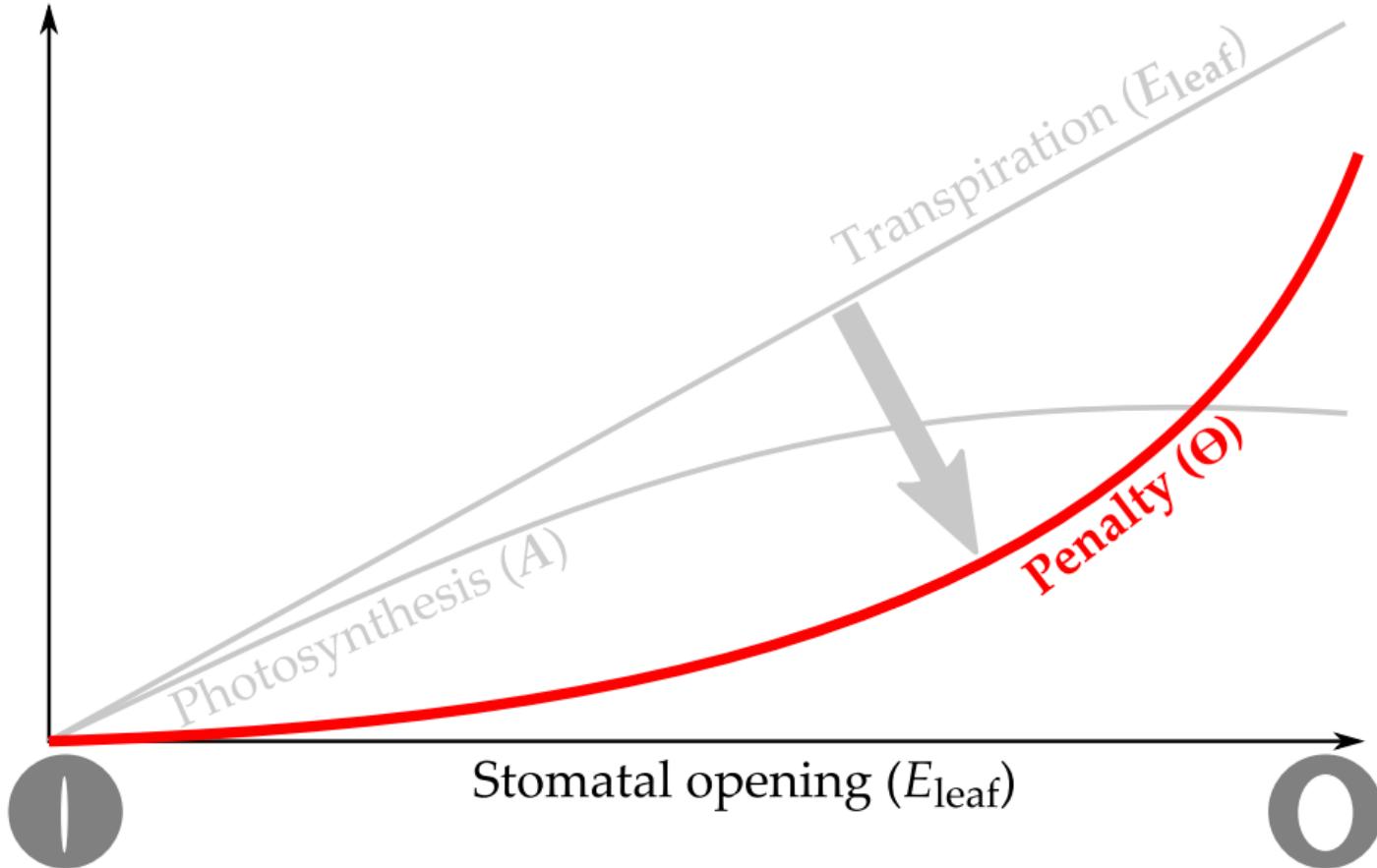
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Quantify water penalty (Θ)



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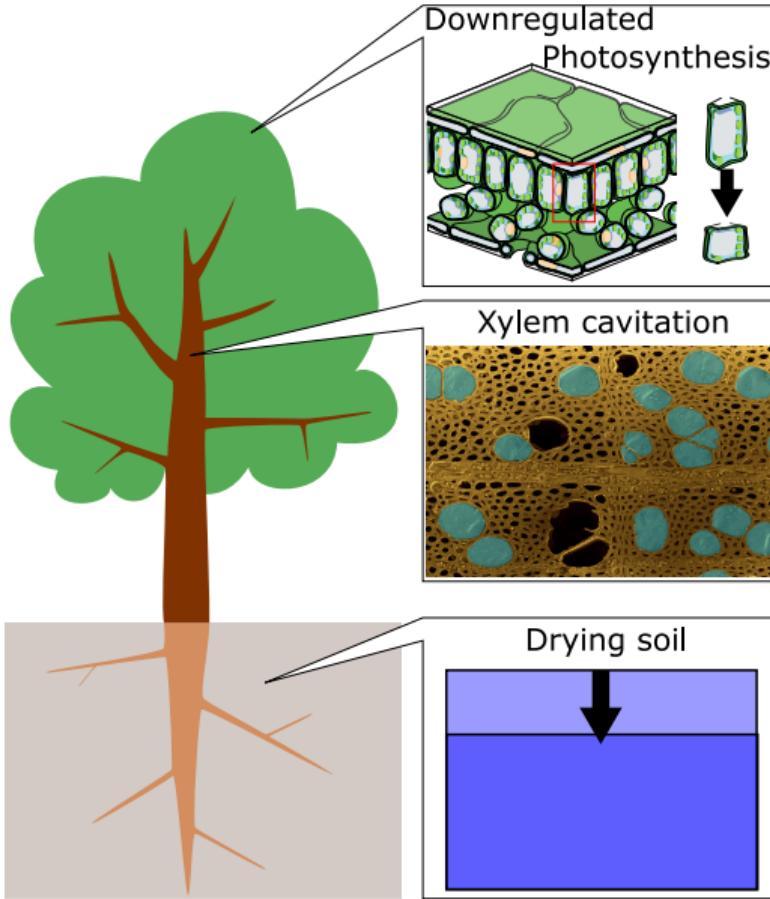
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Causes of water penalty (Θ)



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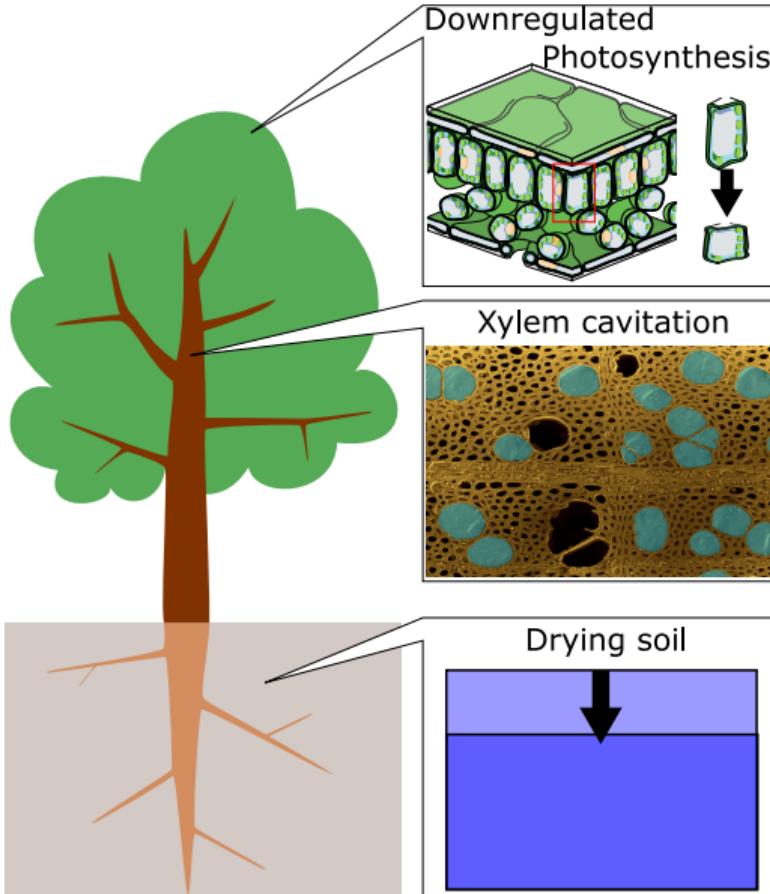
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Models based on different Θ



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)

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Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($d\Theta/dE$ or $d\Theta'/dE$)	Response		
				Criteria I-III	Criteria IV-VII	Fitting parameters
<u>DCPK</u>						
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}

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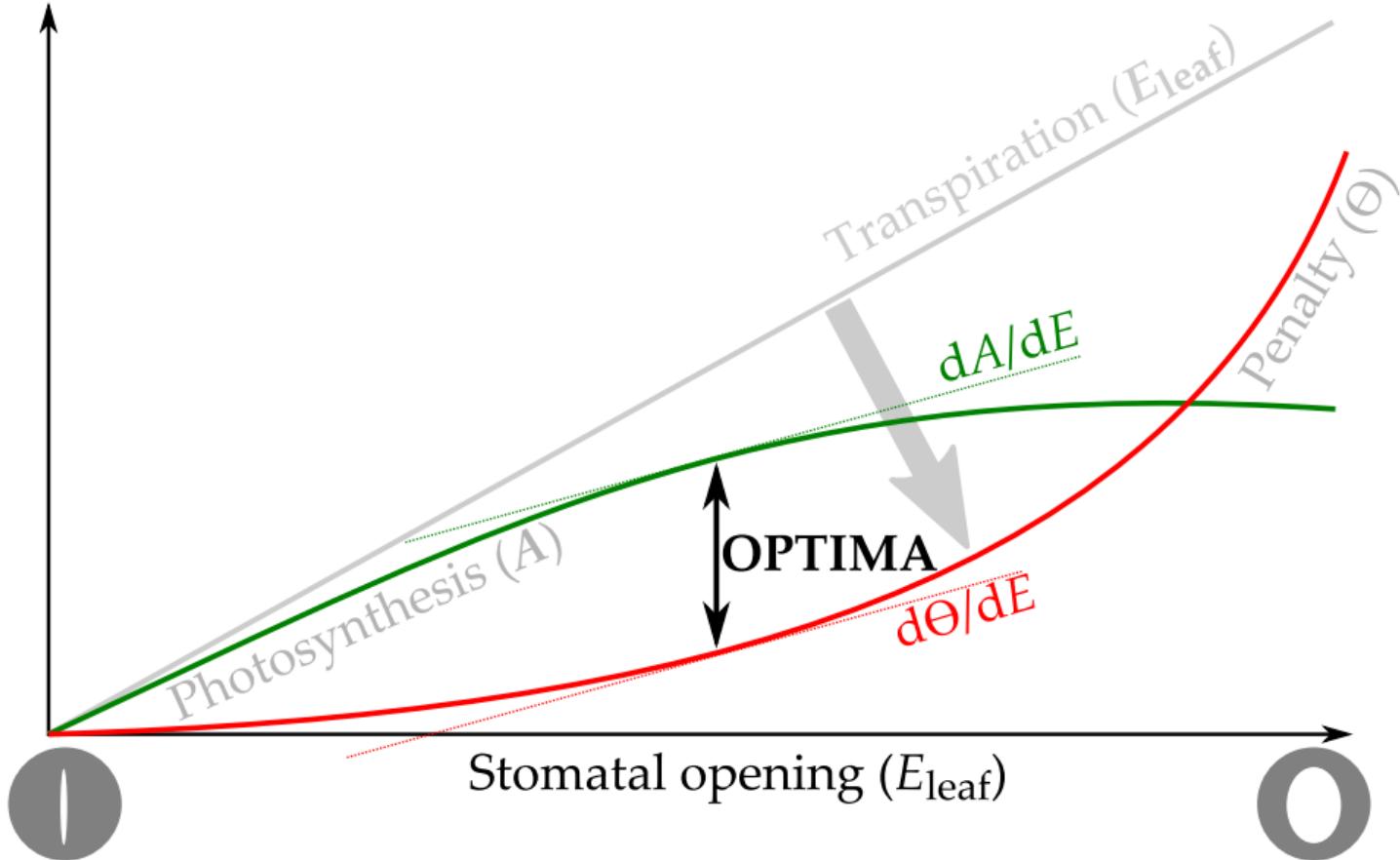
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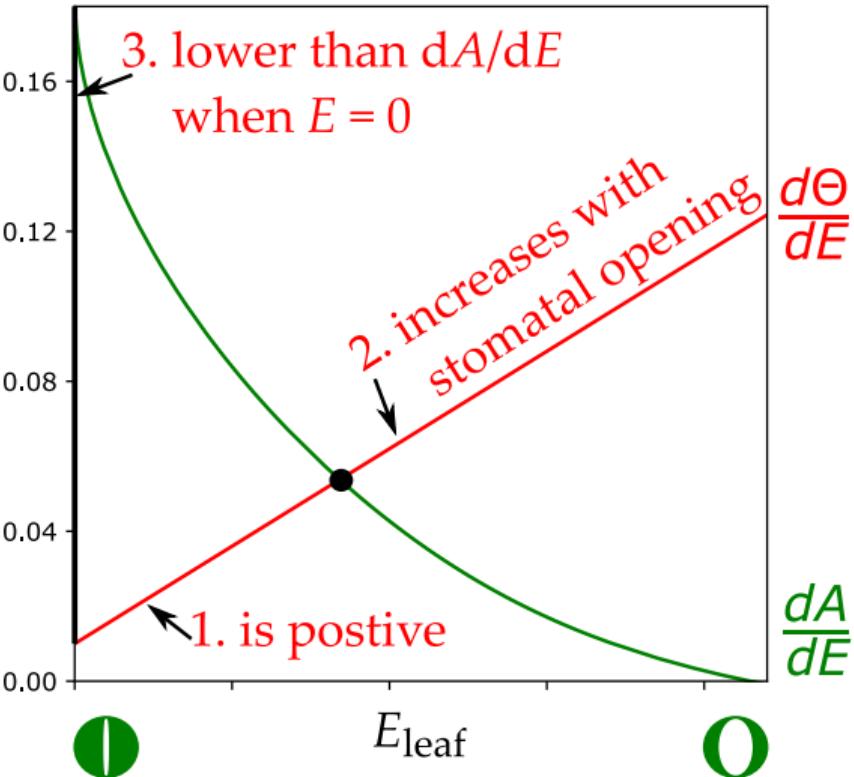
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Criteria for a unique solution

$$\frac{dA}{dE} = \frac{d\Theta}{dE}$$



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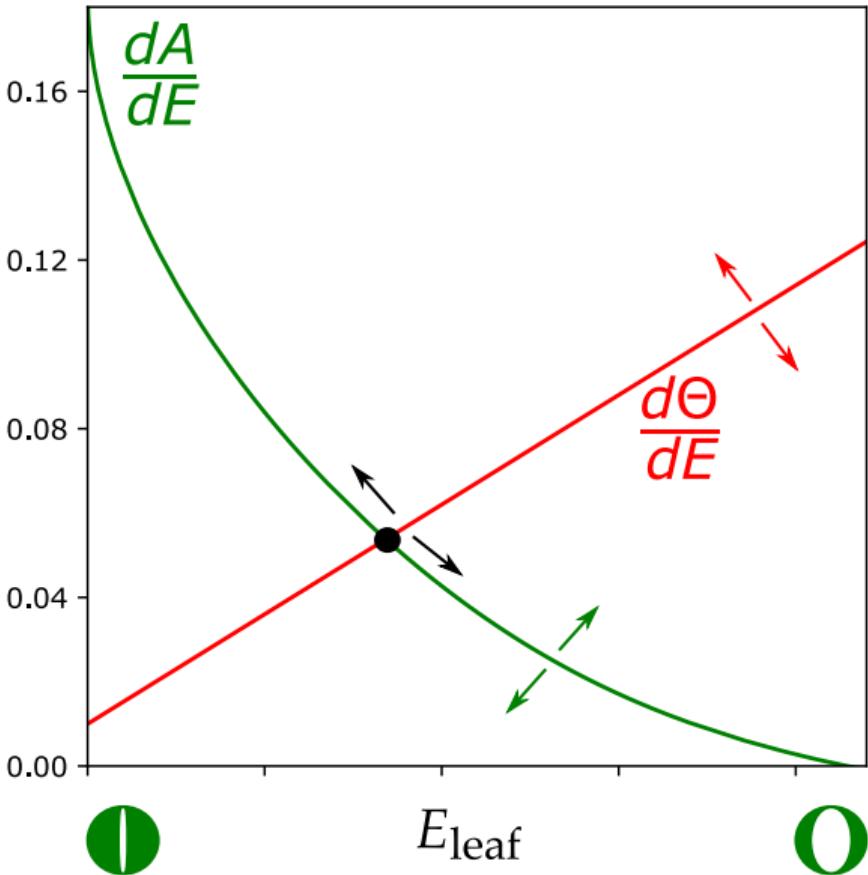
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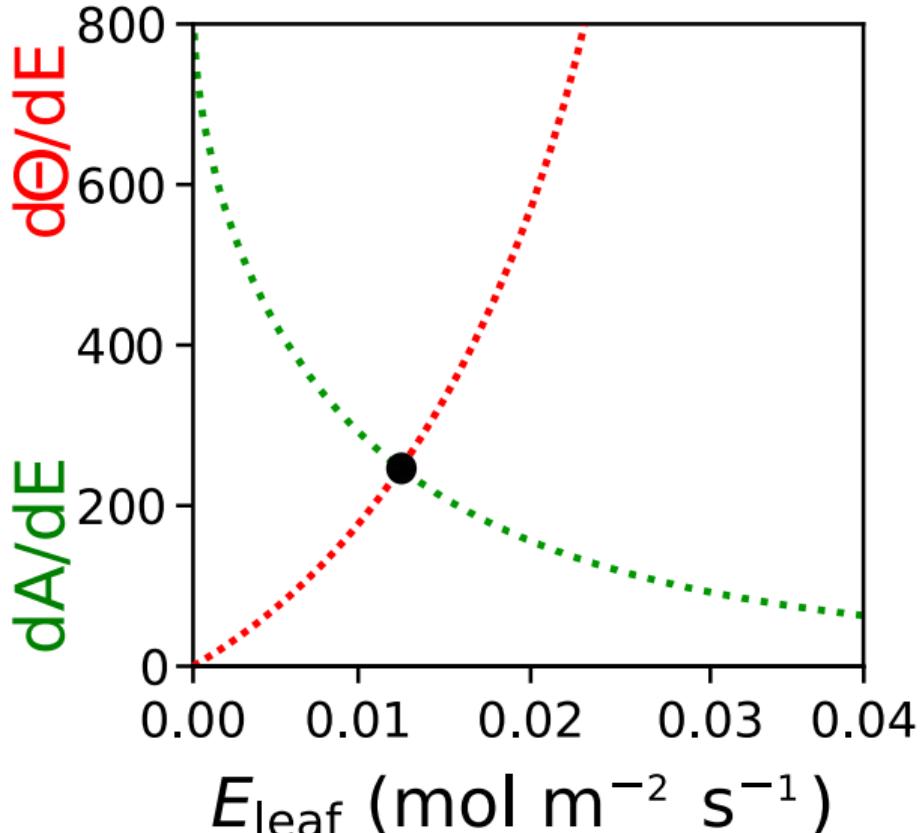
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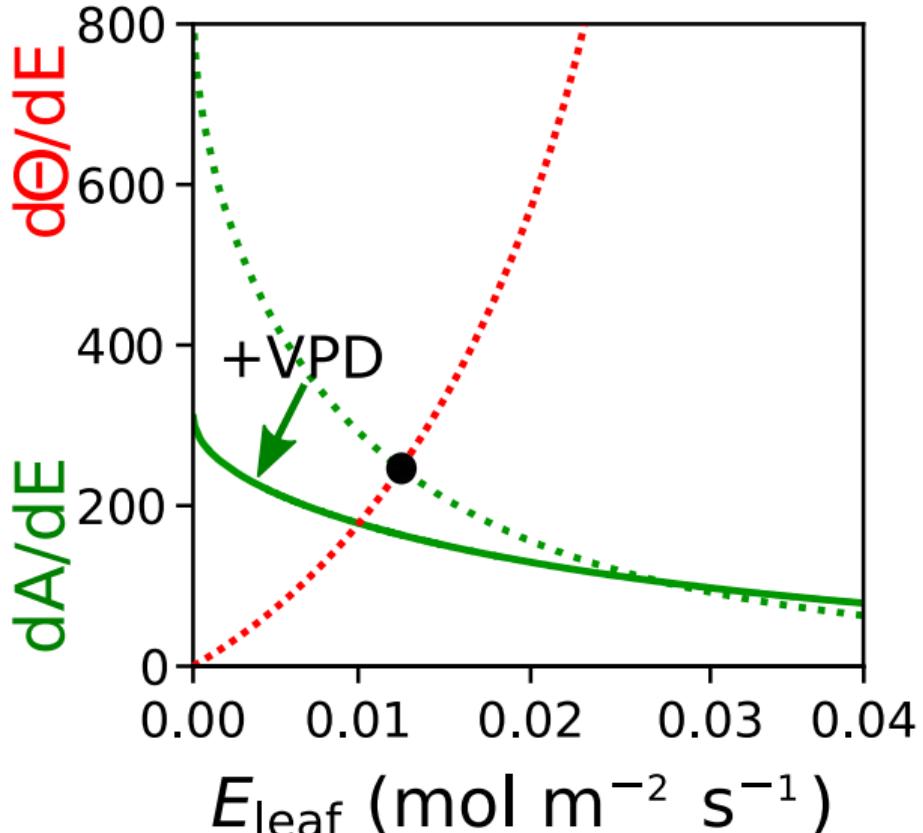
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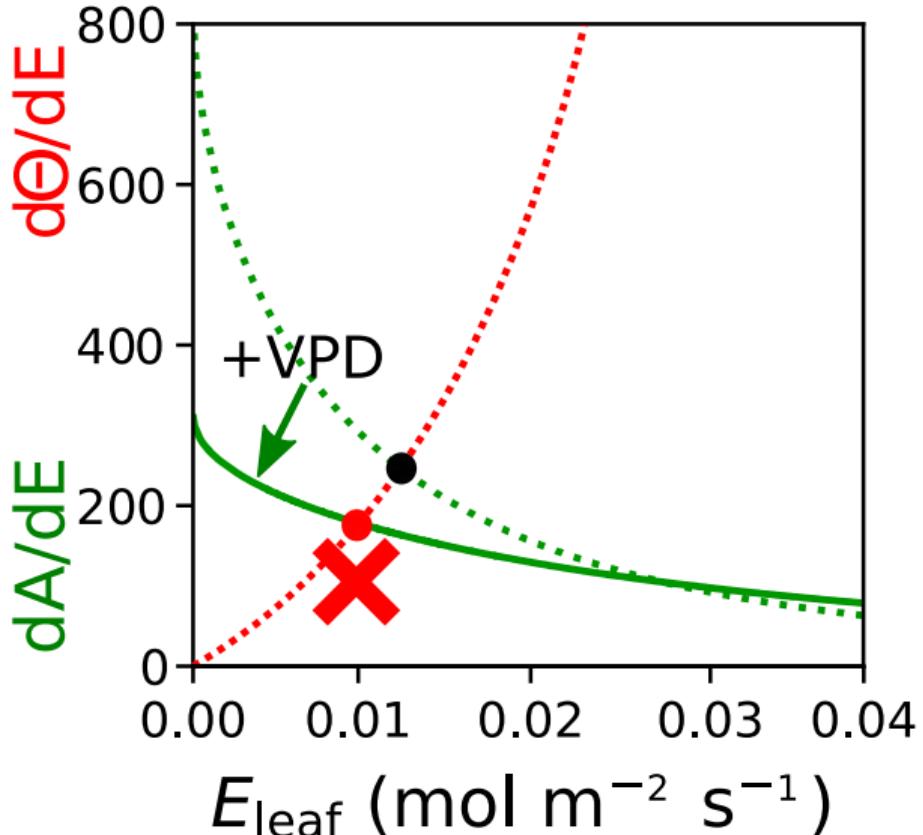
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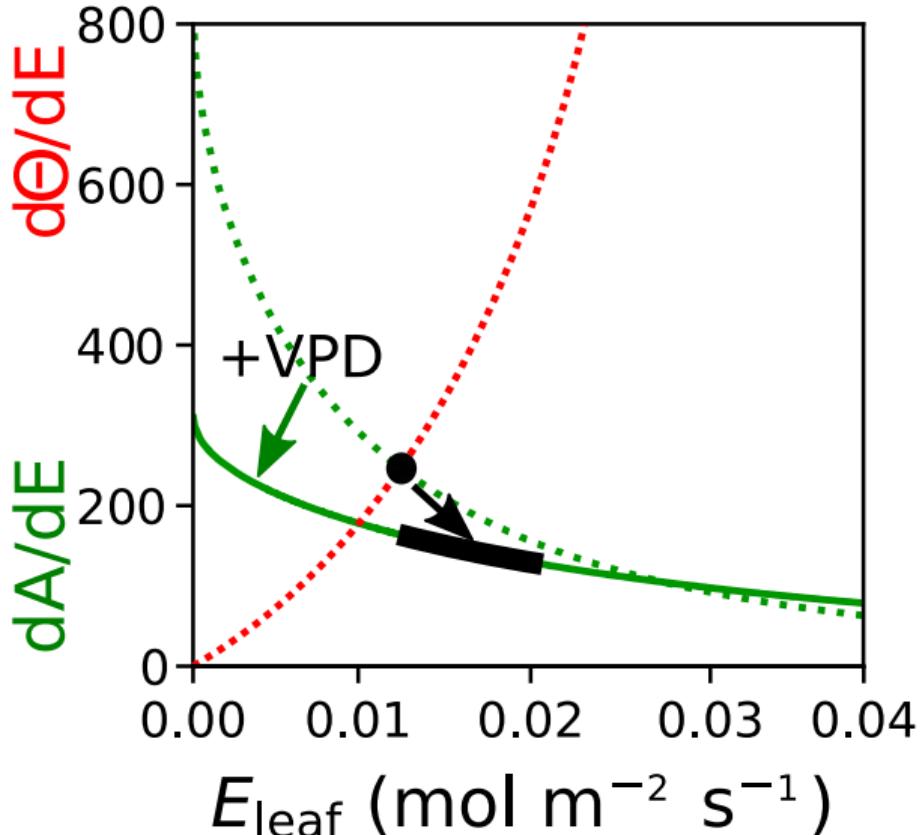
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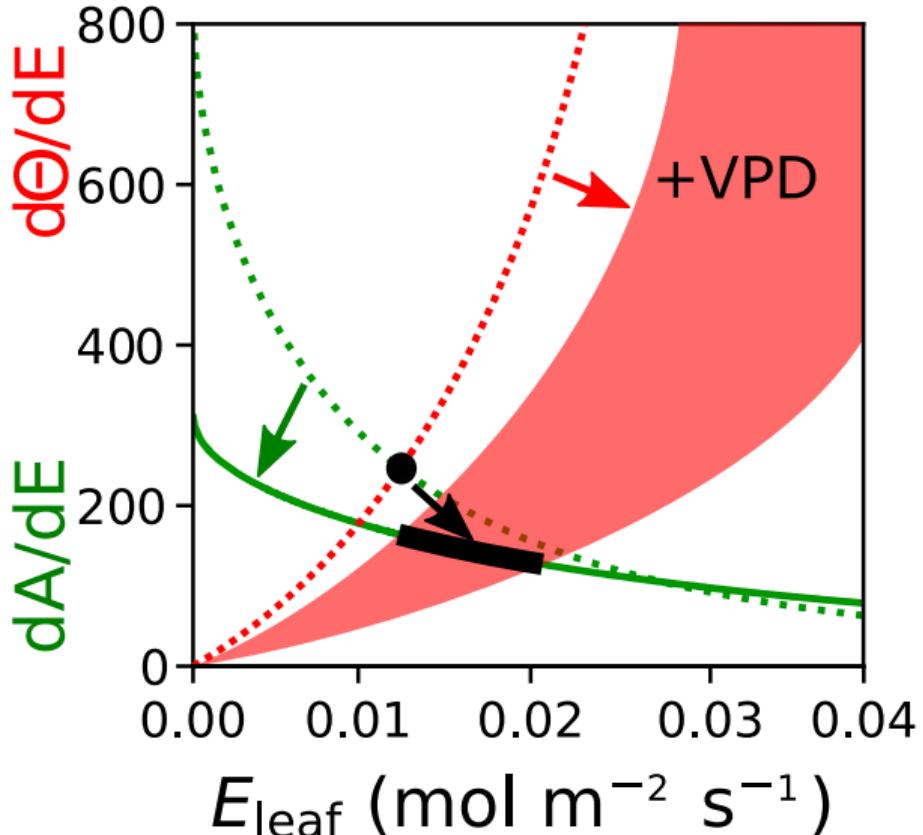
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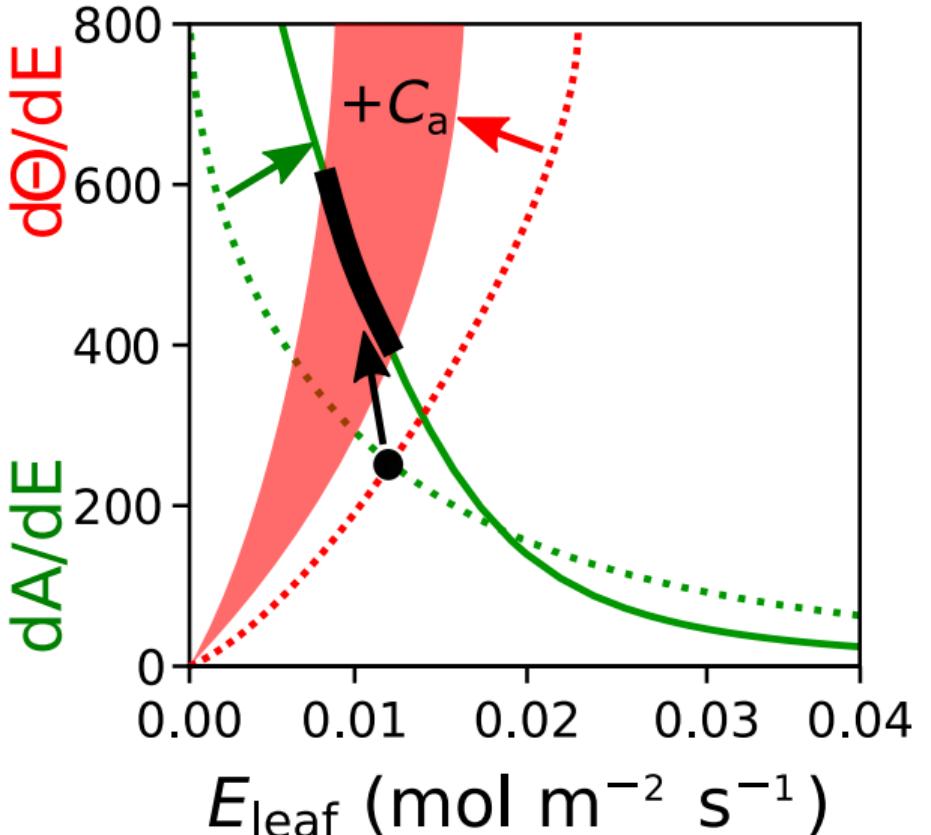
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5. increases with higher CO₂



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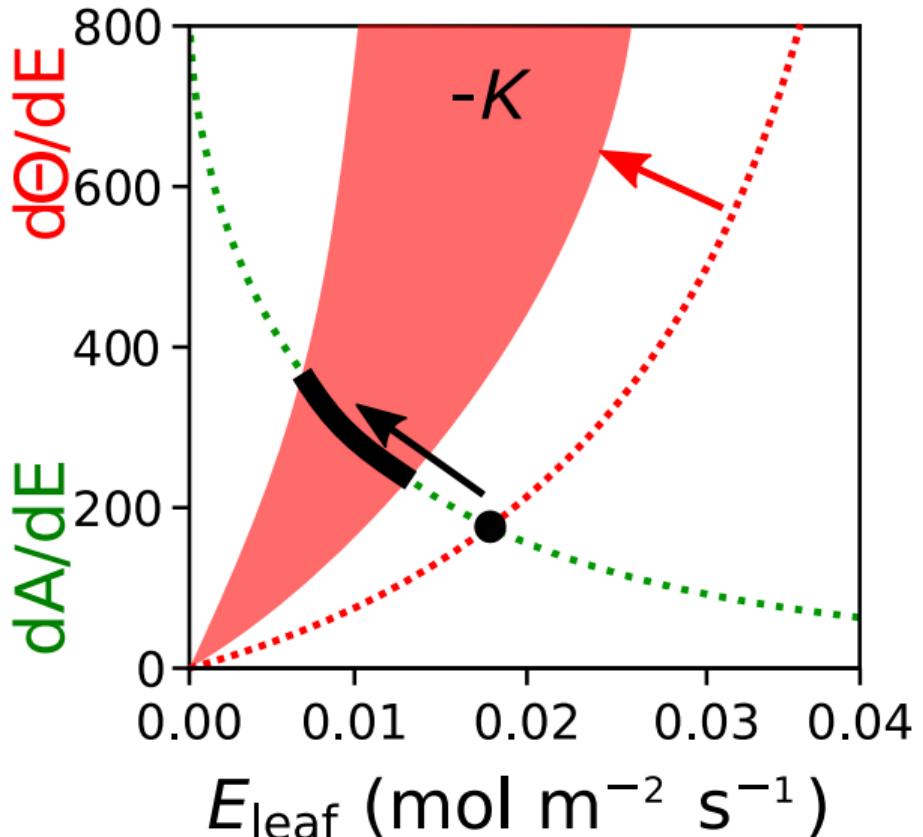
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6. increases with drier soil



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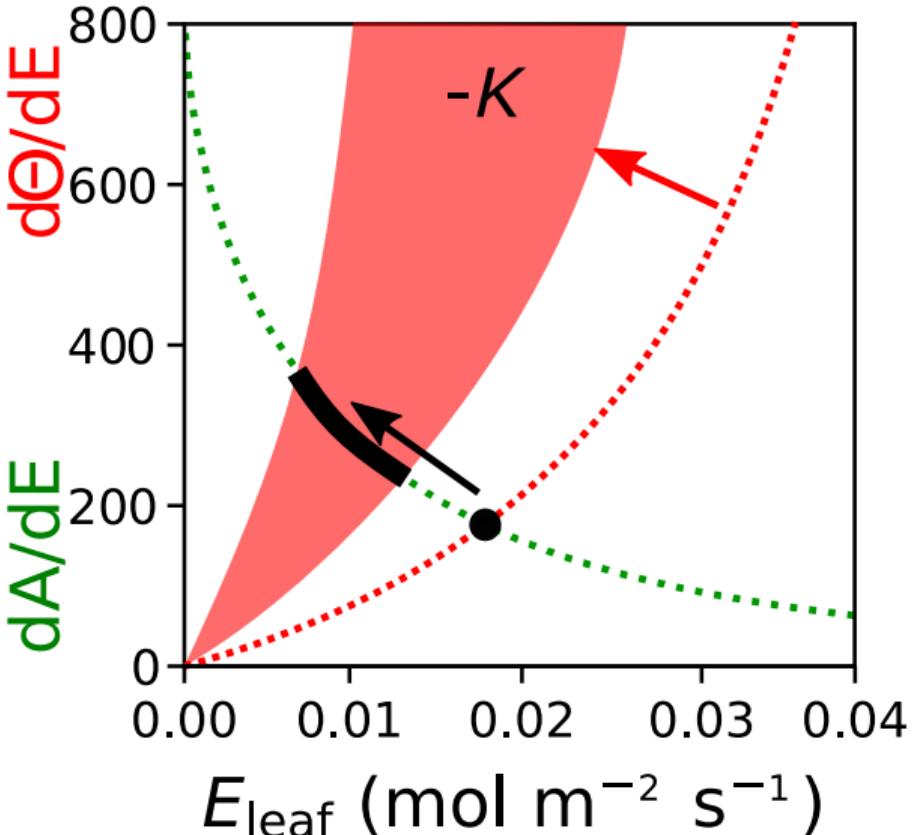
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7. increases with lower hydraulic conductance



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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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				Criteria I-III	Criteria IV-VII	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}

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Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($d\Theta/dE$ or $d\Theta'/dE$)	Response		
				Criteria I-III	Criteria IV-VII	Fitting parameters DCPK
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}

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Example 1: The Cowan-Farquhar model

Criterion

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

Marginal penalty

$$\frac{d\Theta}{dE} = \frac{1}{\lambda}$$

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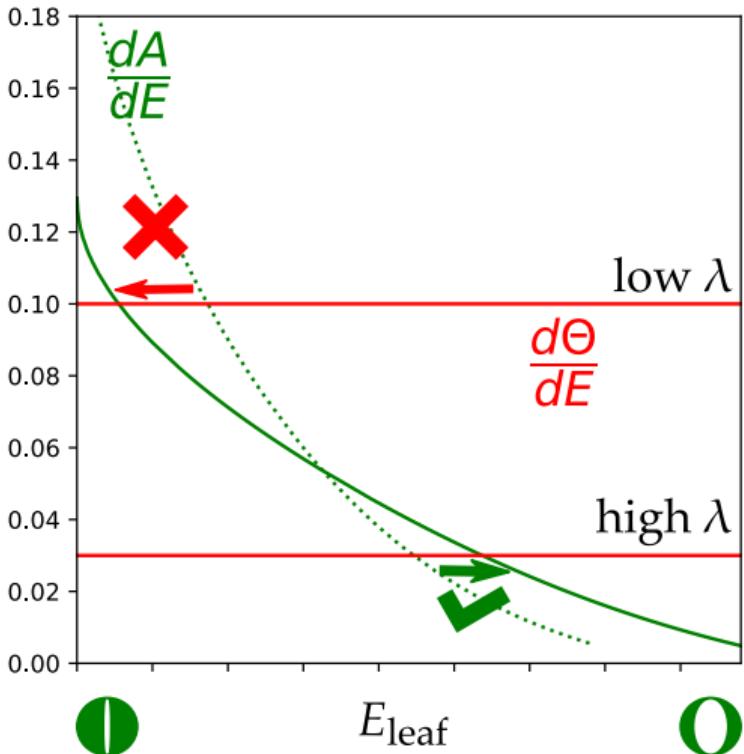
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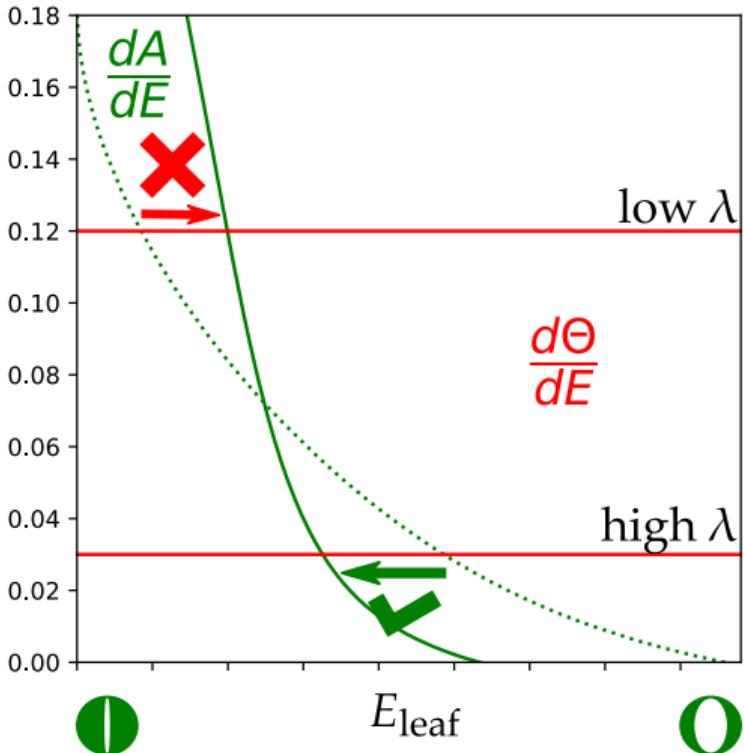
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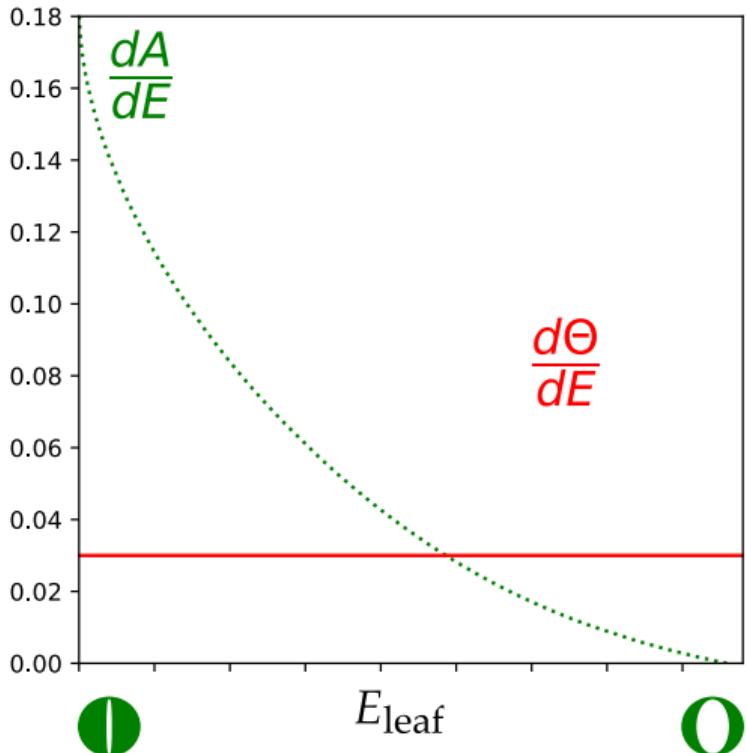
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				Criteria I-III	Criteria IV-VII	Fitting parameters
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{leaf}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{leaf}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	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}

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Example 2: The Sperry model

Optimization criterion

$$\max \left(\frac{A}{A_{\max}} - \left(1 - \frac{K}{K_{\max}} \right) \right), K = \frac{dE}{dP}$$

Marginal penalty

$$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{\max}}{K_{\max}}$$

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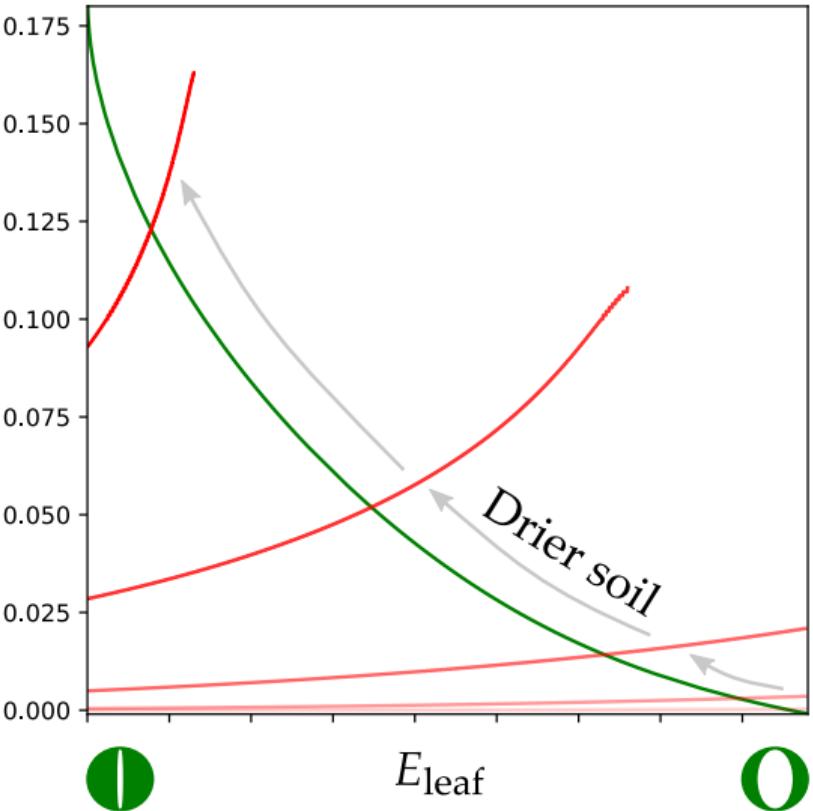
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				Criteria I-III	Criteria IV-VII	Fitting parameters
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Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{leaf}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et 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	YYYY	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}

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Example 3: A new model

Criterion

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

Marginal penalty

$$\frac{d\Theta}{dE} = \frac{A}{E_{\text{crit}} - E_{\text{leaf}}}$$

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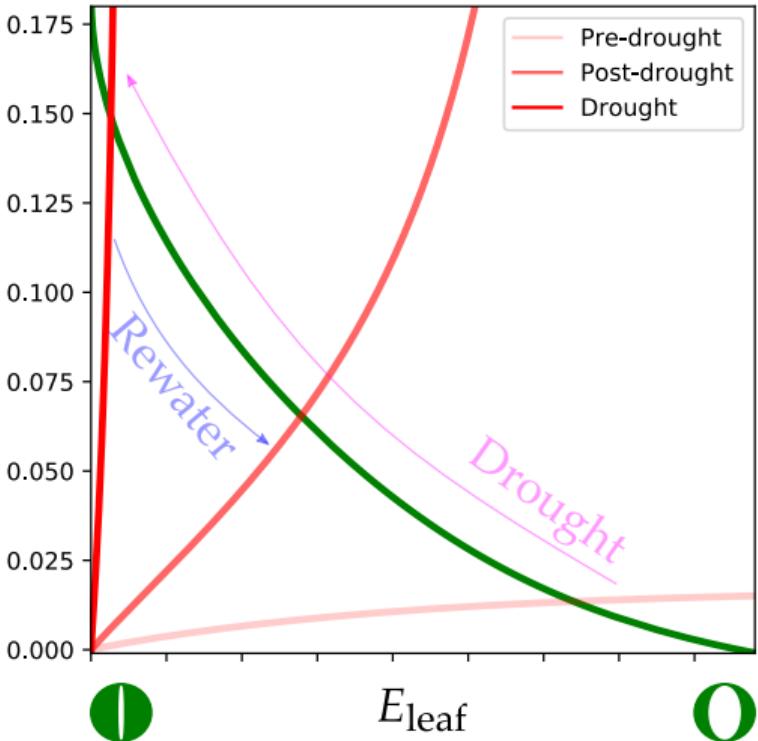
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- ✓ Quantify $A(E_{\text{leaf}})$
- ✓ Quantify $\Theta(E_{\text{leaf}})$

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

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Wang et al. (2019)

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Venturas et al. (2018)

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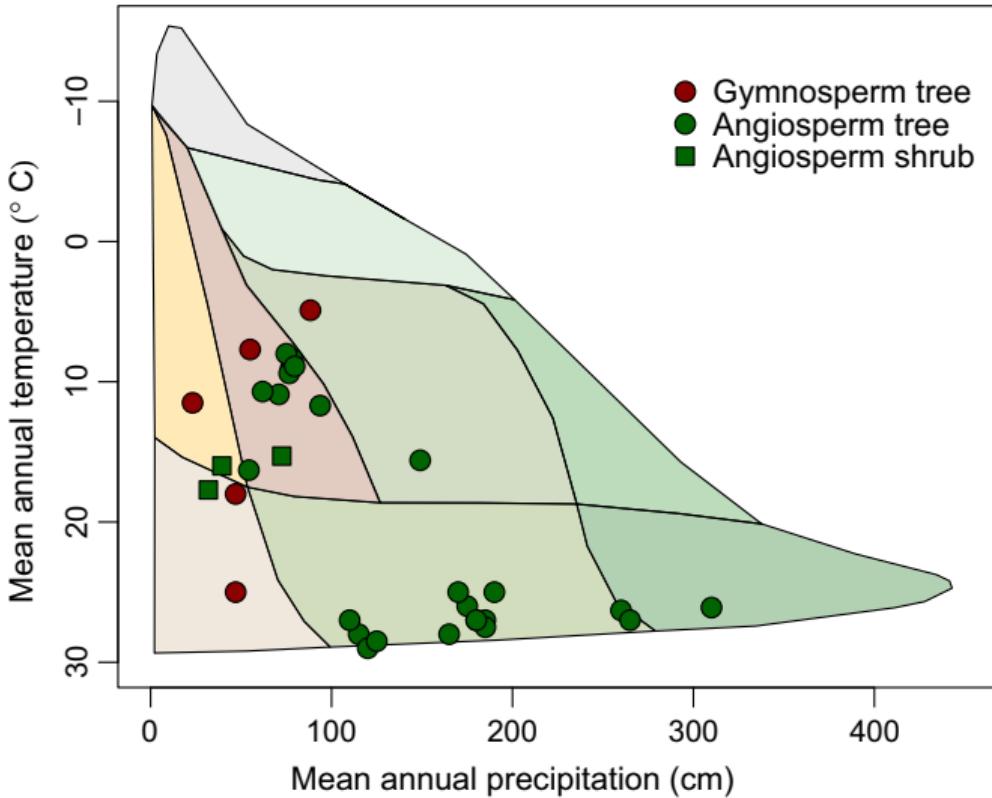
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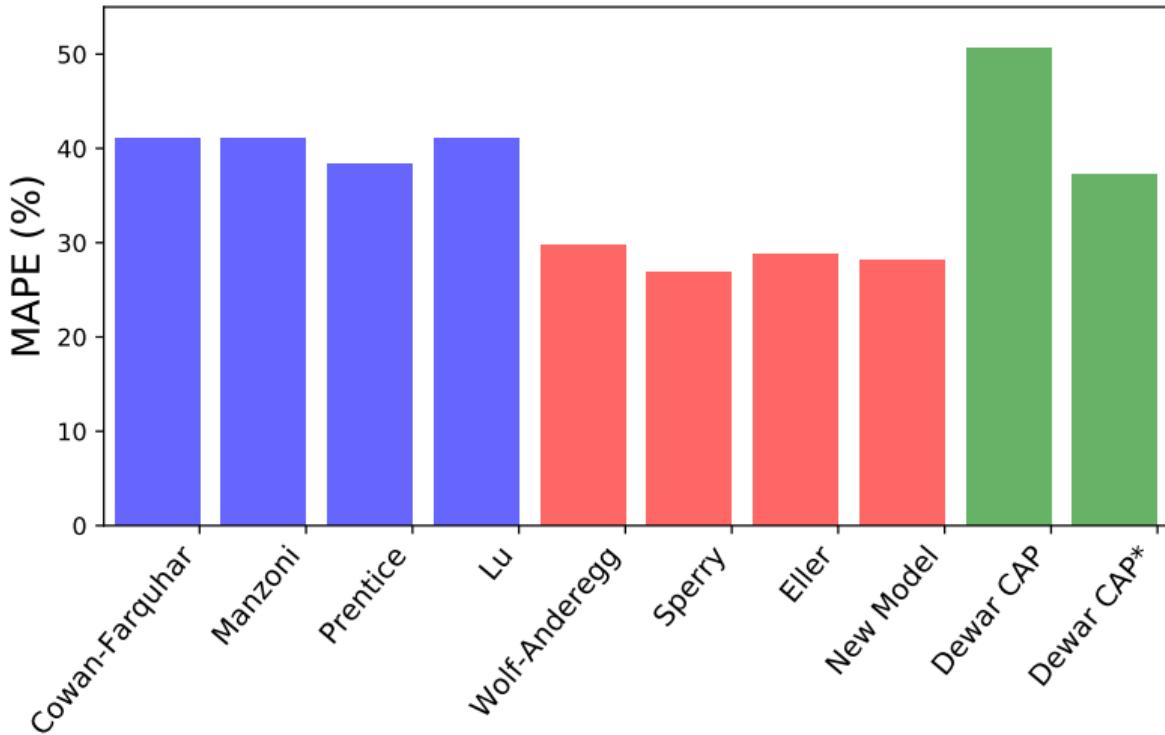
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Birch dataset

data from Wang et al. (2019)



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

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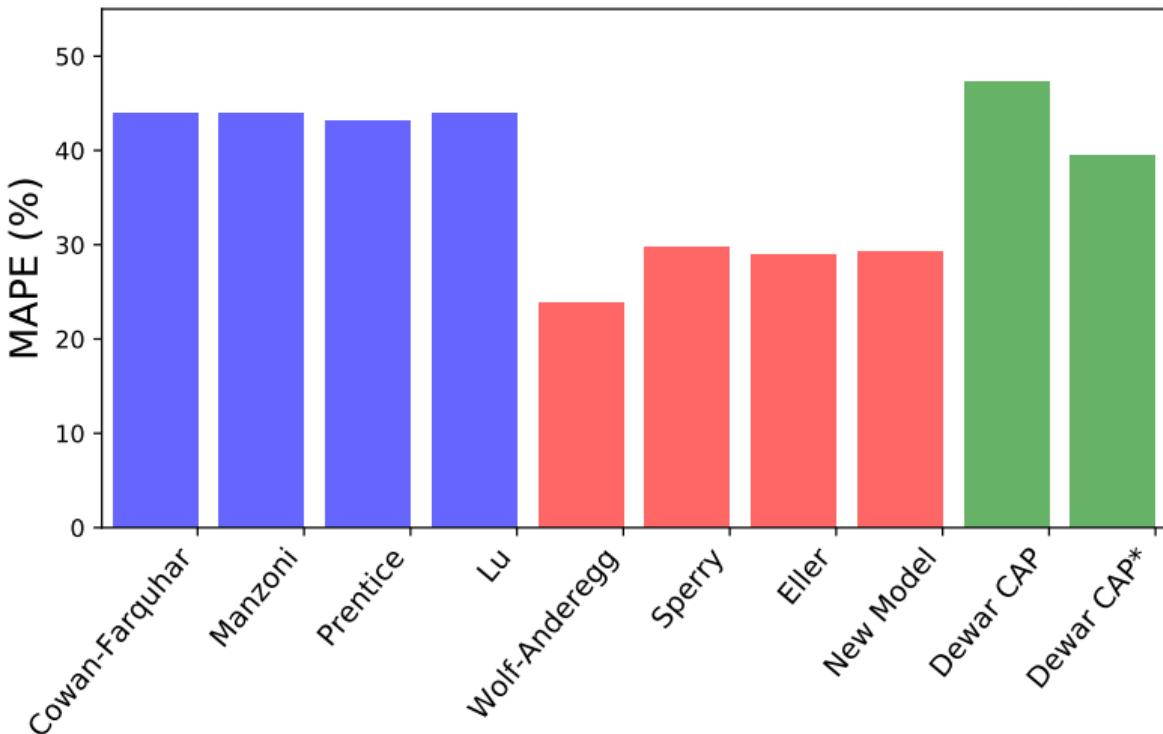
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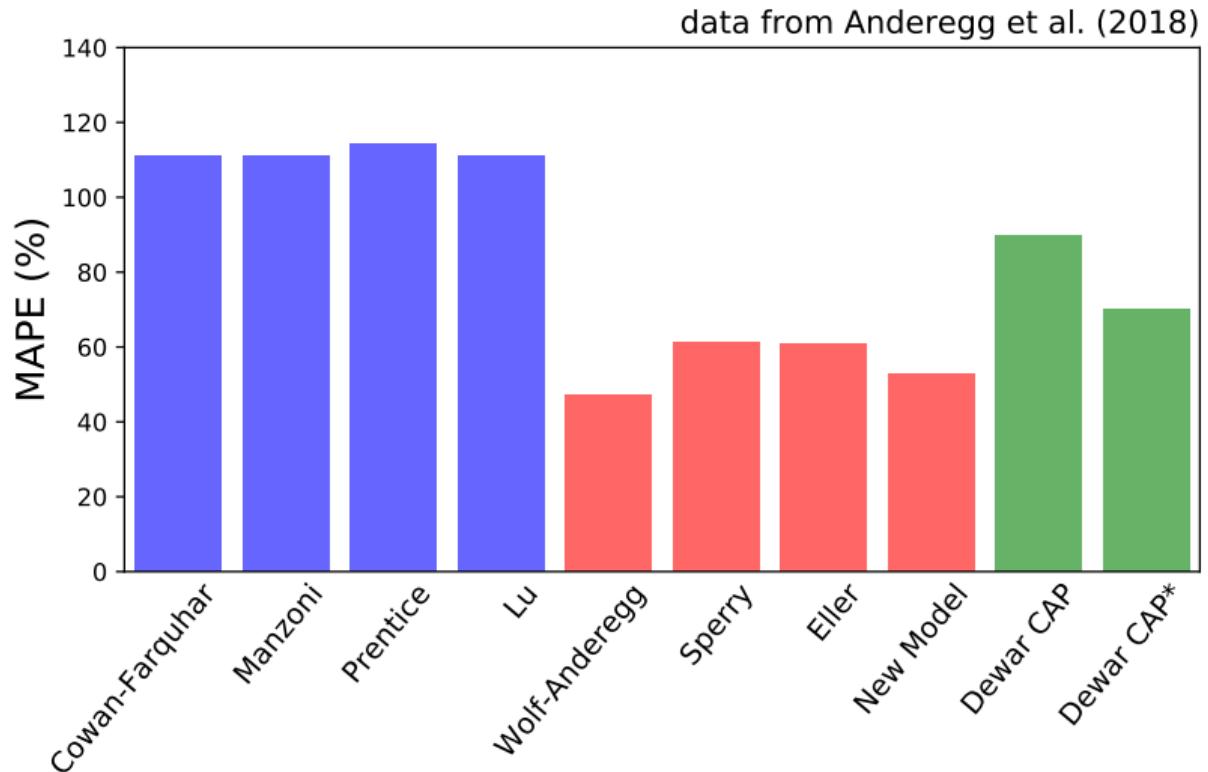
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Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($d\Theta/dE$ or $d\Theta'/dE$)	Response		
				Criteria I-III	Criteria IV-VII	Fitting parameters
Cowan- Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{leaf}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	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}

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Take-home message

MATH is important.

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Take-home messages

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

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

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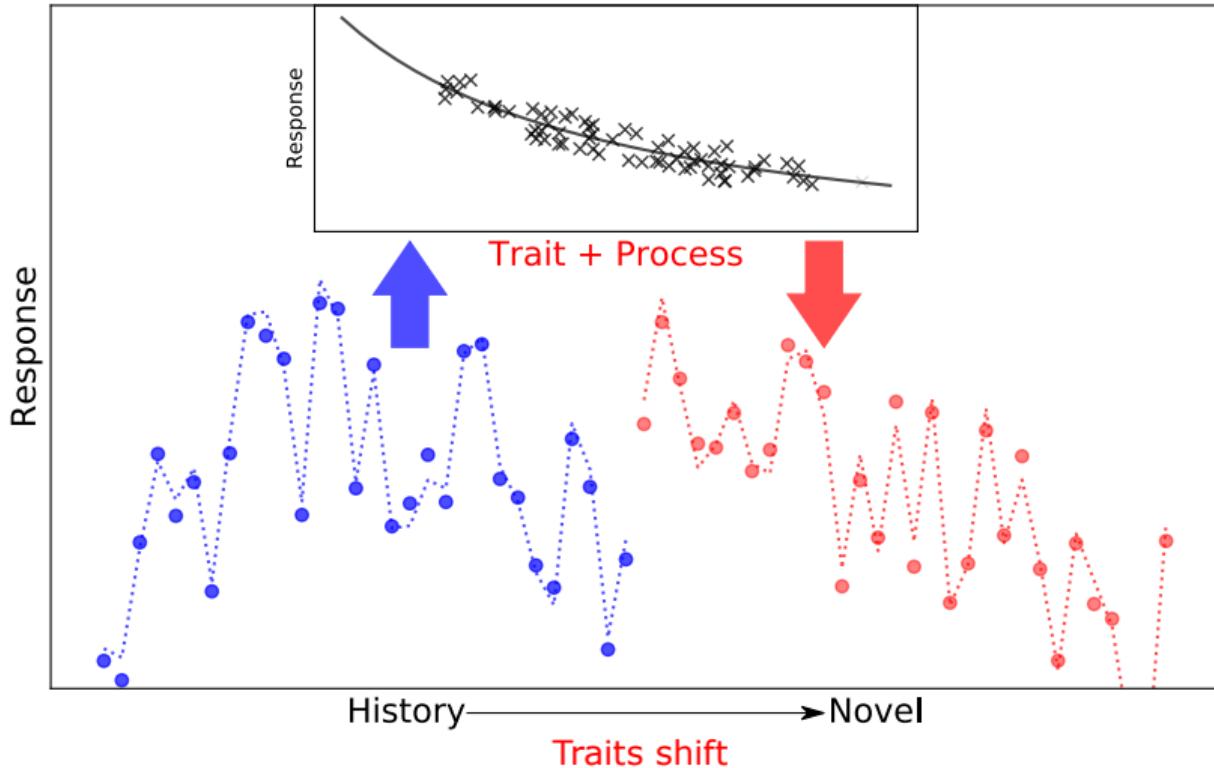
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How about trait change?



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PART IV

MODELING TRAIT SHIFTS

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Disadvantages of trait-based model

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

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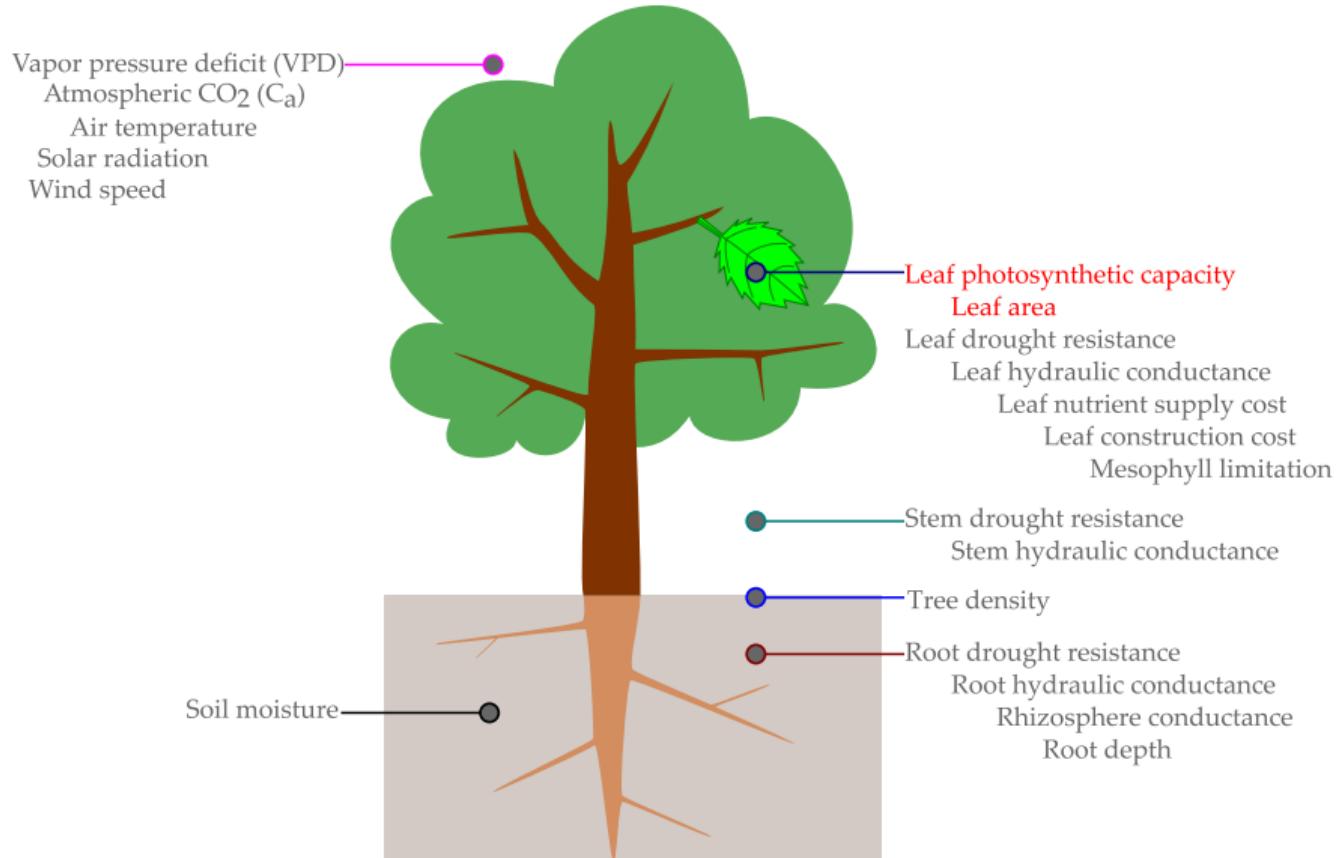
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Environmental and physiological variables



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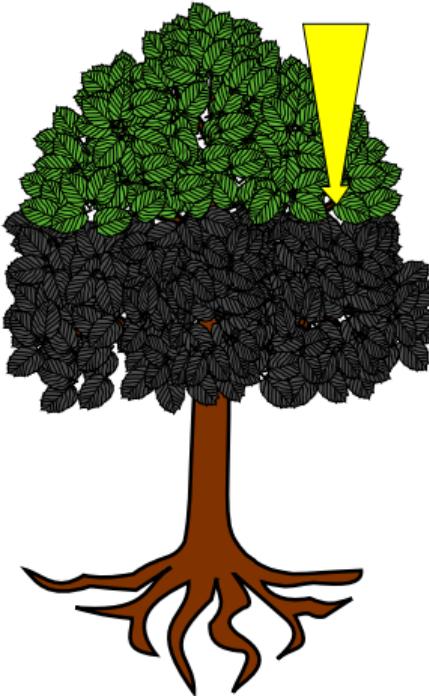
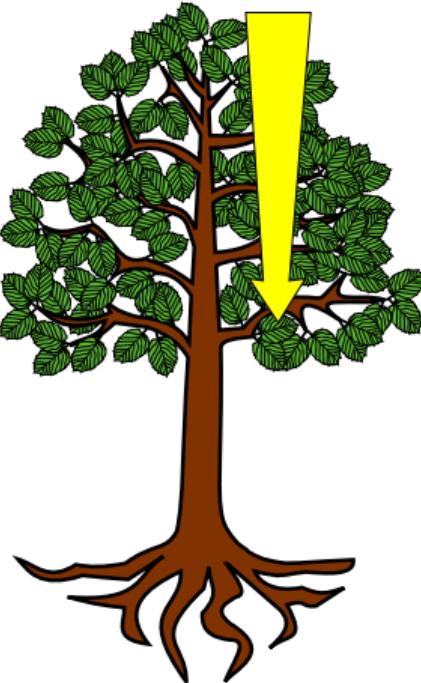
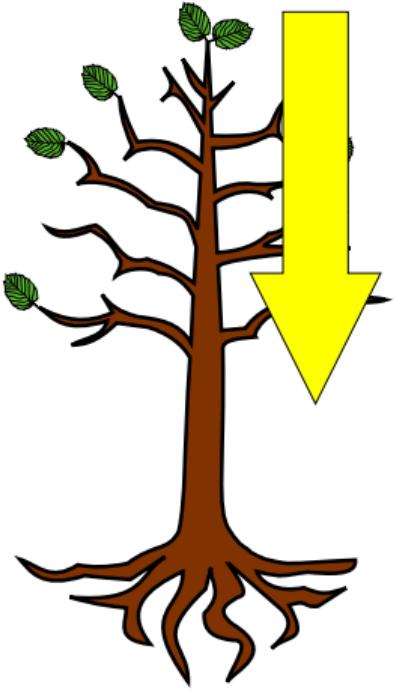
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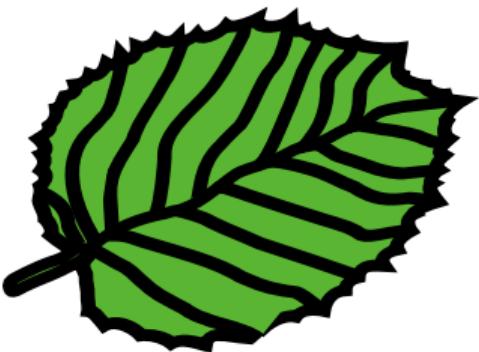
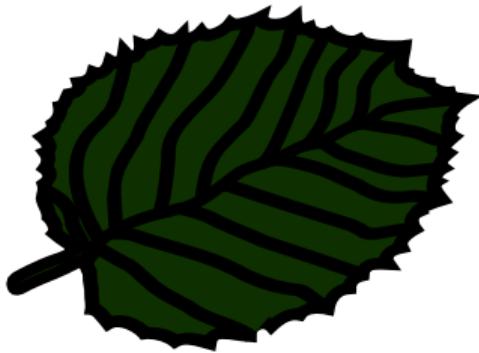
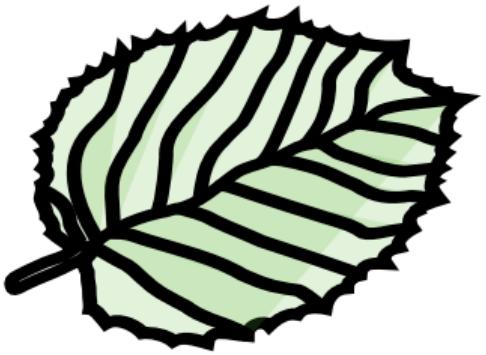
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Optimal leaf investment

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

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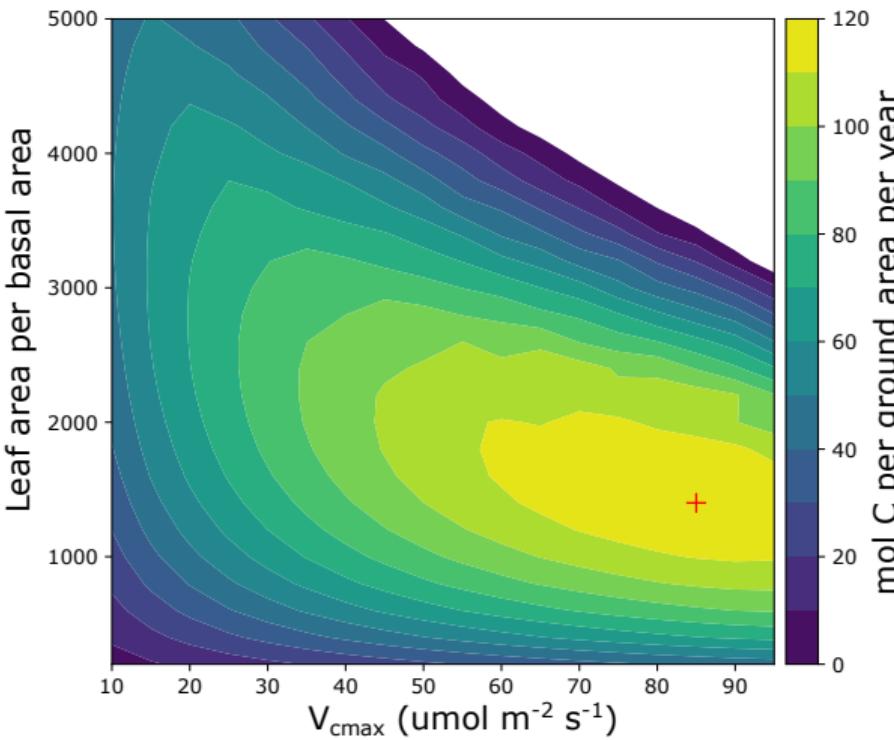
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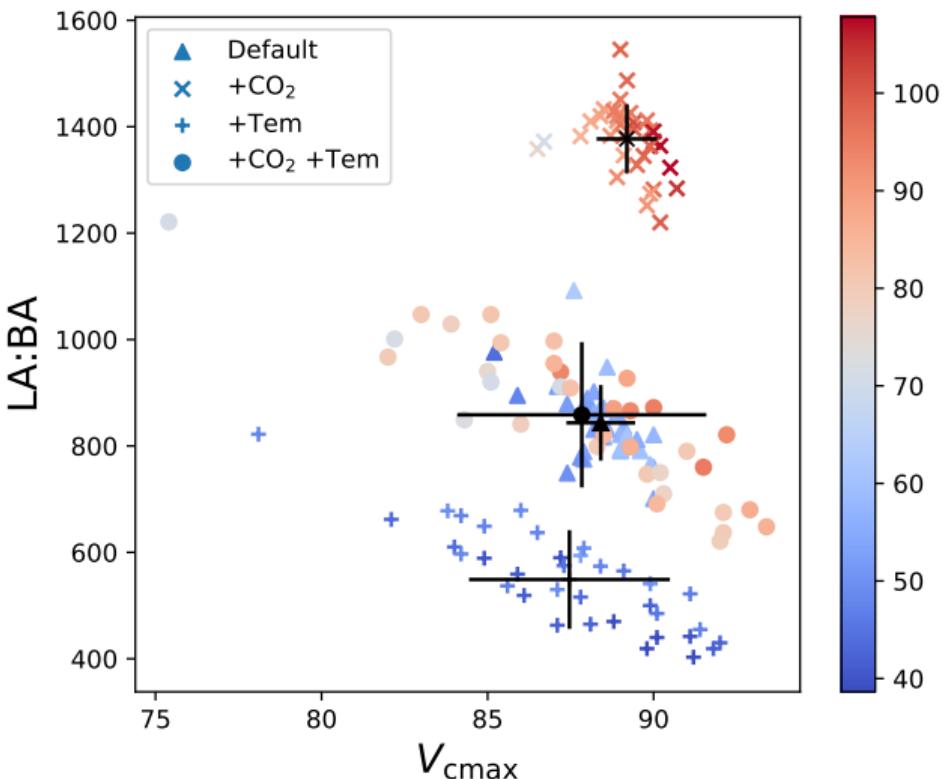
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Optimal leaf investment vs. climate



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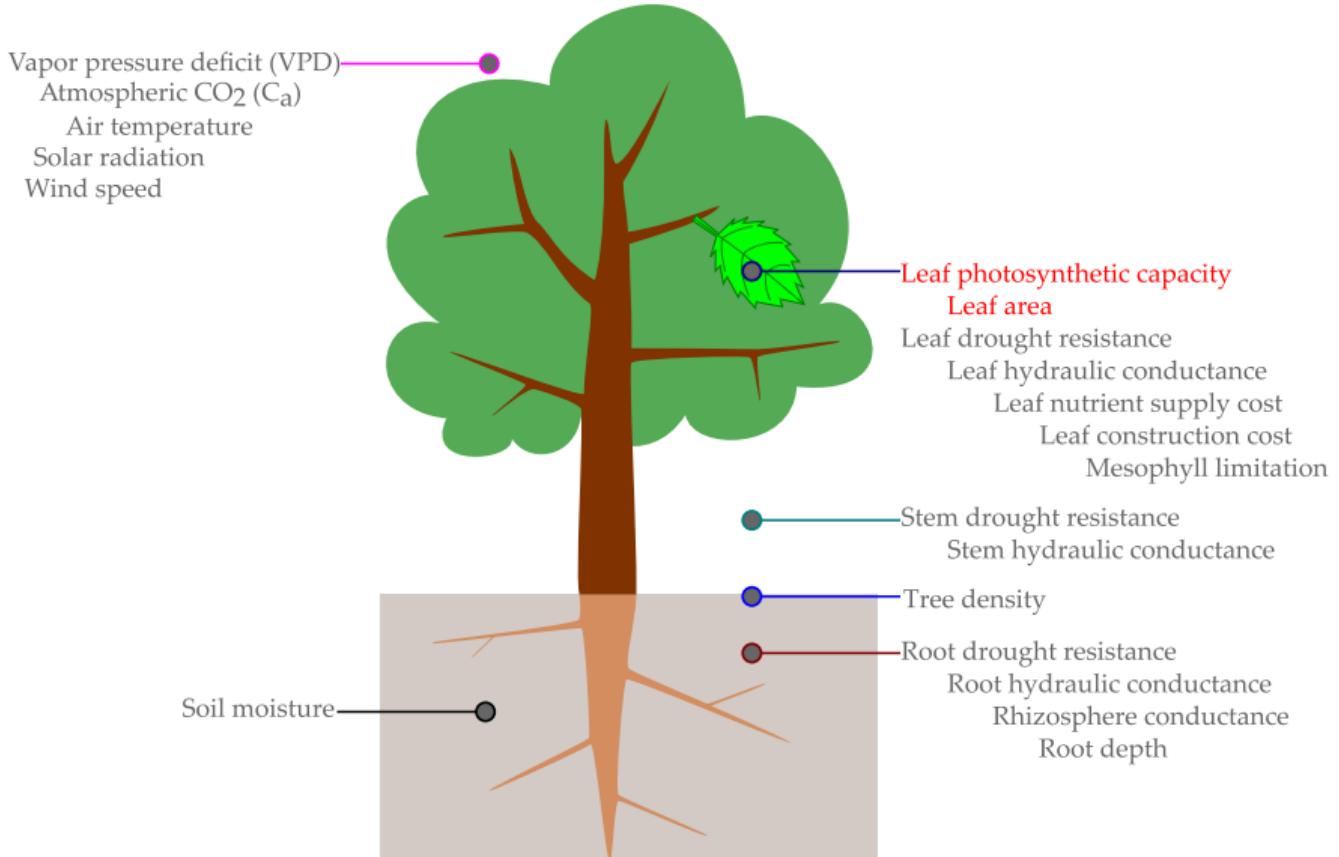
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Other traits?



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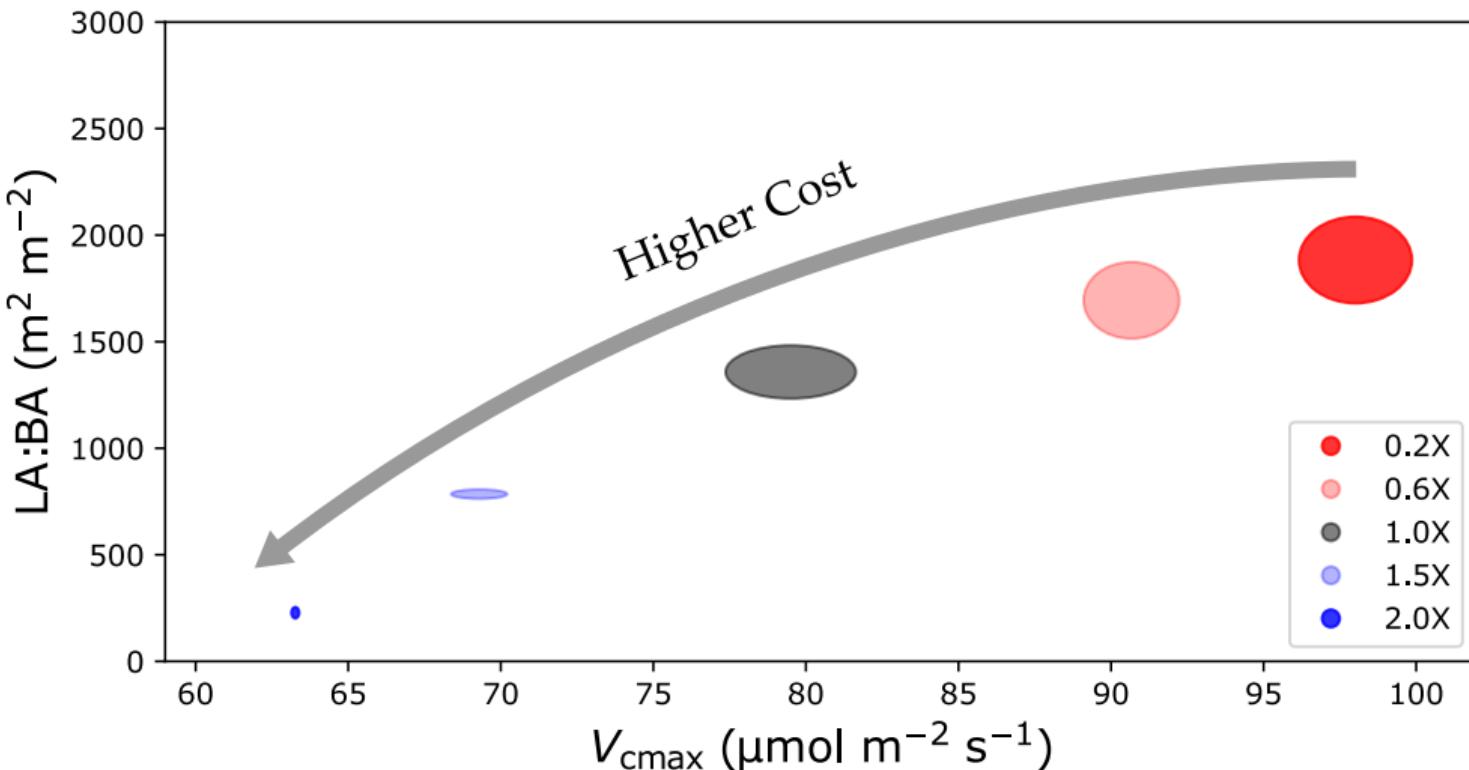
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Optimal leaf investment vs. carbon cost (LCBM)



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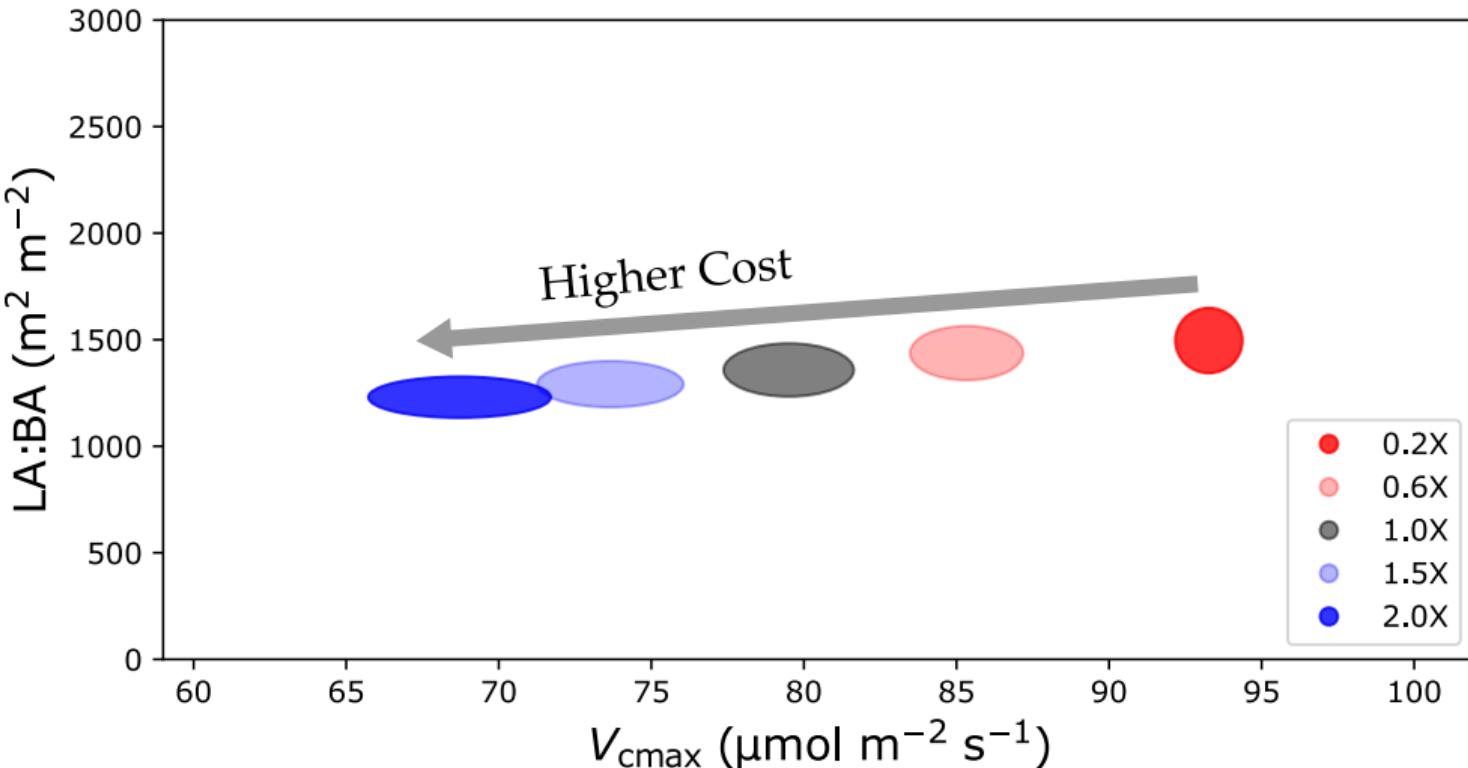
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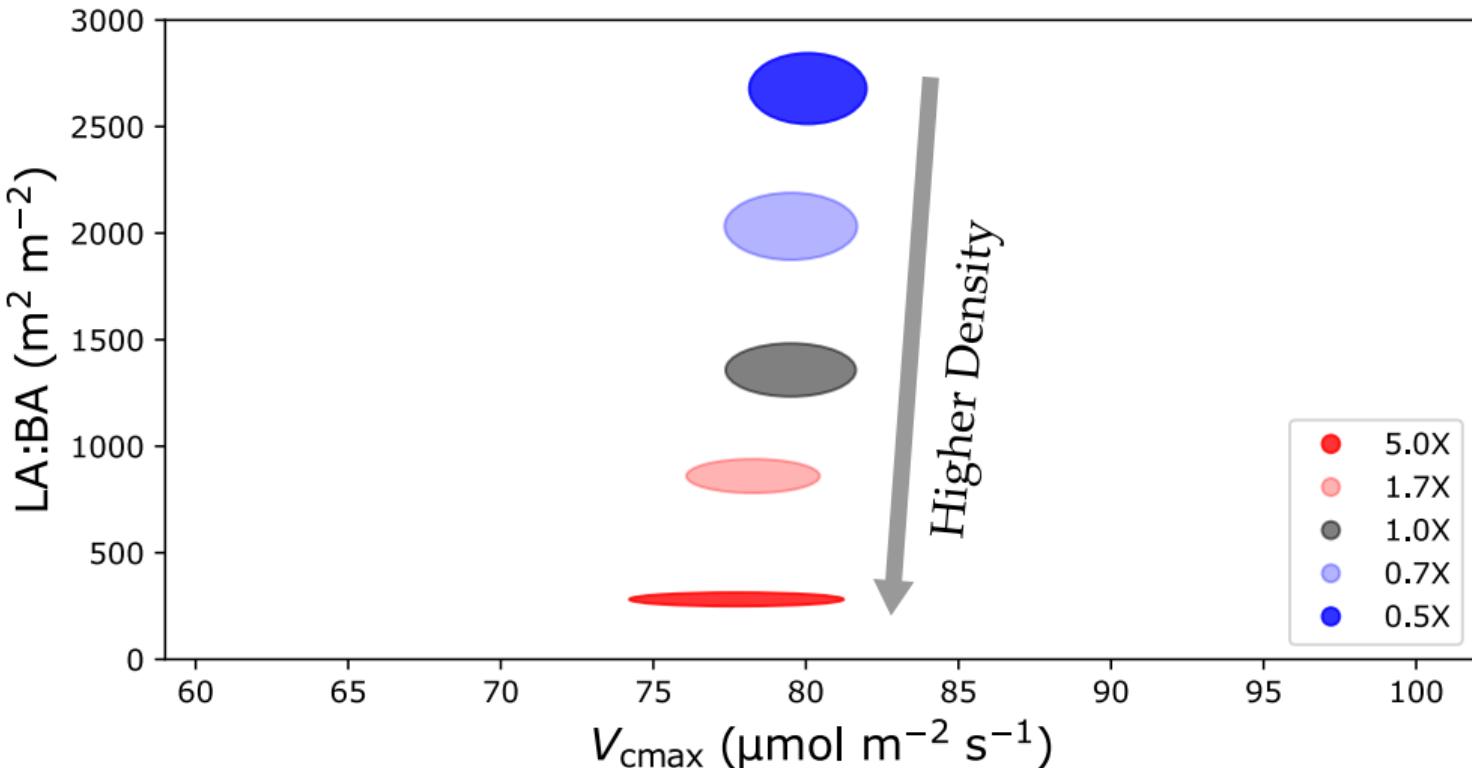
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Optimal leaf investment vs. stand density



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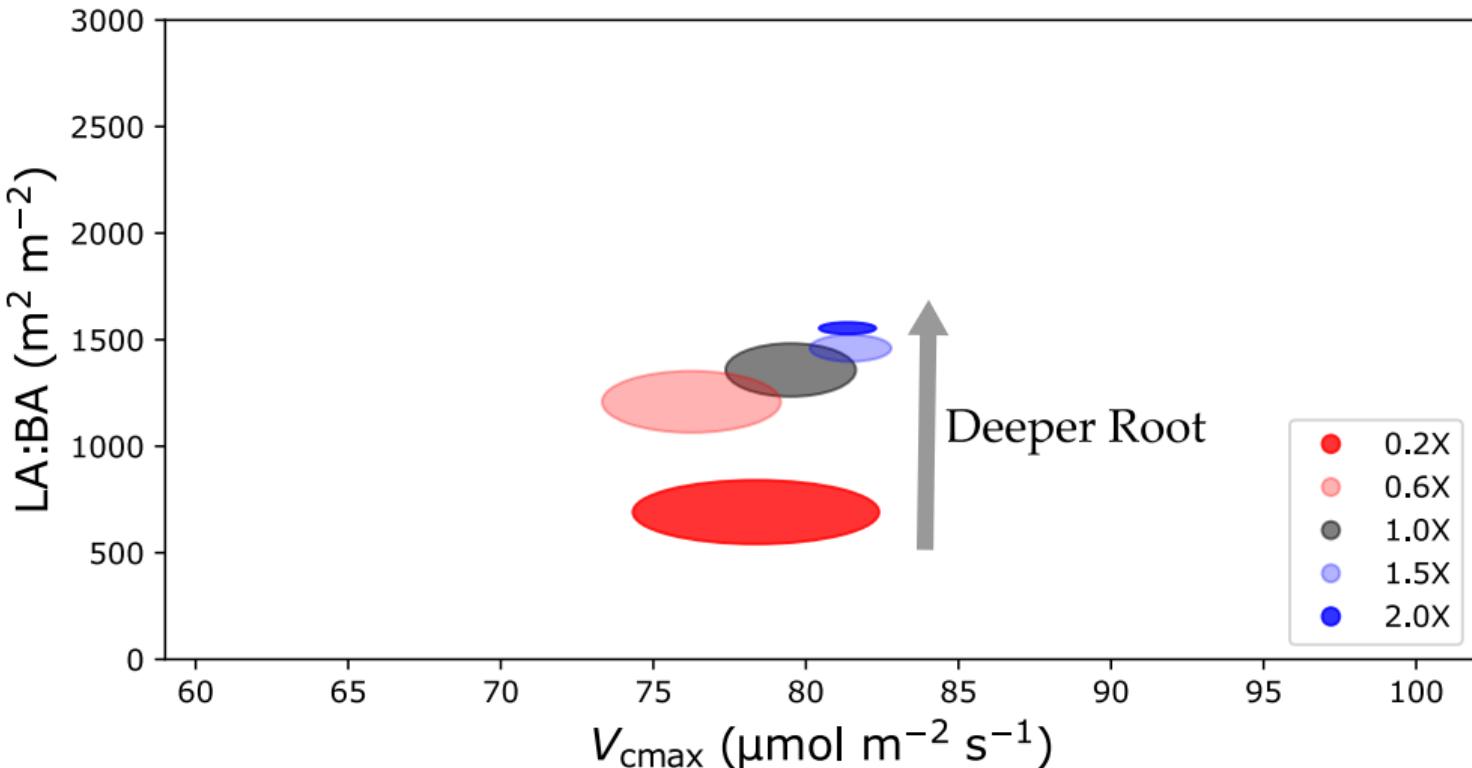
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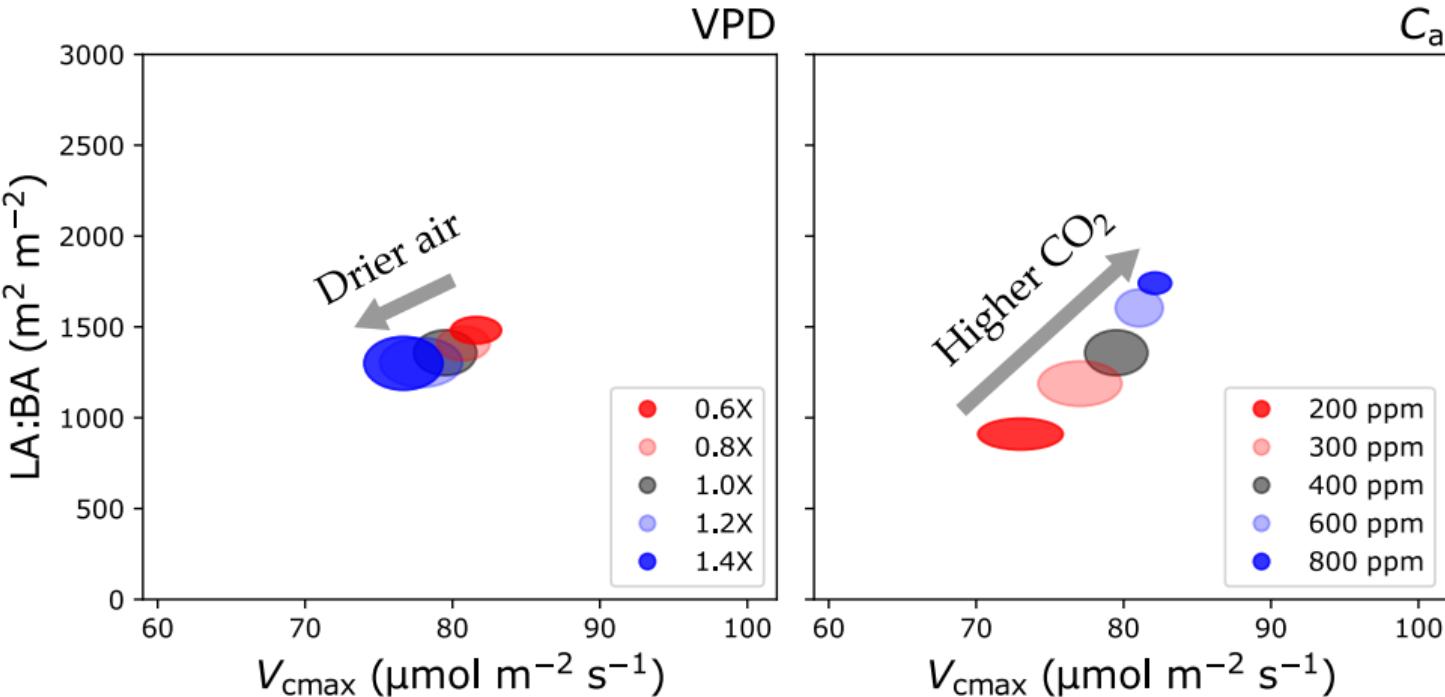
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Optimal leaf investment vs. VPD and C_a



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Major drivers for leaf investment

Plant traits

- ▶ Leaf construction costs (carbon and nutrients)
- ▶ Root depth

Environmental conditions

- ▶ Stand density
- ▶ VPD
- ▶ Atmospheric CO₂

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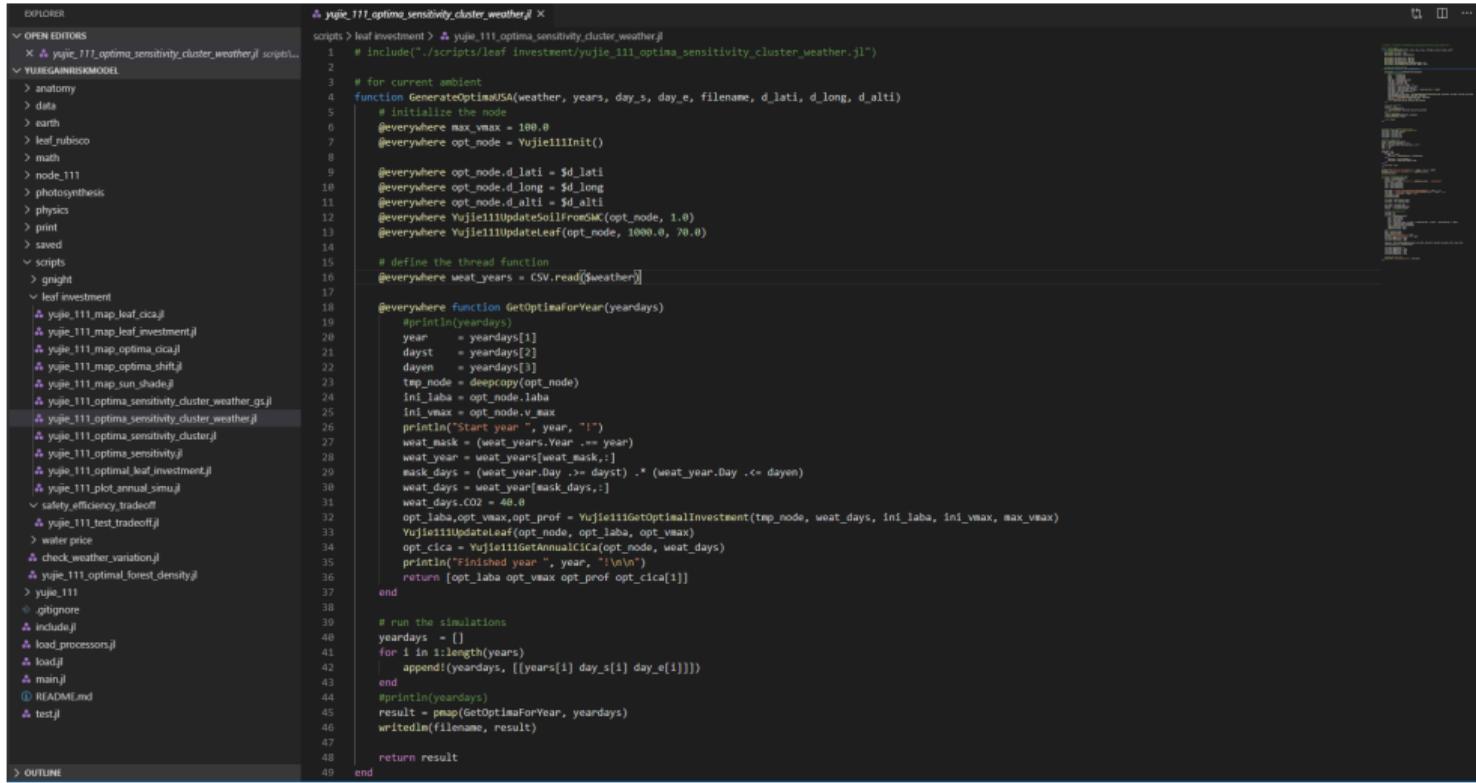
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```
scripts > leaf_investment > ▲ yujie_111_optima_sensitivity_cluster_weather.py
1 # include("./scripts/leaf_investment/yujie_111_optima_sensitivity_cluster_weather.jl")
2
3 # for current ambient
4 function GenerateOptimaUSA(weather, years, day_s, day_e, filename, d_lat, d_long, d_alt)
5     # initialize the node
6     @everywhere max_vmax = 100.0
7     @everywhere opt_node = Yujie111Init()
8
9     @everywhere opt_node.d_lat = $d_lat
10    @everywhere opt_node.d_long = $d_long
11    @everywhere opt_node.d_alt = $d_alt
12    @everywhere Yujie111UpdateSoilFromSMC(opt_node, 1.0)
13    @everywhere Yujie111UpdateLeaf(opt_node, 1000.0, 70.0)
14
15    # define the thread function
16    @everywhere weat_years = CSV.read("$weather")
17
18    @everywhere function GetOptimaForYear(yeardays)
19        #Println(yeardays)
20        year   = yeardays[1]
21        dayst  = yeardays[2]
22        dayen  = yeardays[3]
23        tmp_node = deepcopy(opt_node)
24        ini_laba = opt_node.laba
25        ini_vmax = opt_node.v_max
26        println("Start year ", year, "!")
27        weat_mask = (weat_years.Year .== year)
28        weat_year = weat_years[weat_mask,:]
29        mask_days = (weat_year.Day .>= dayst) .* (weat_year.Day .<= dayen)
30        weat_days = weat_year[mask_days,:]
31        weat_days.C02 = 48.0
32        opt_laba,opt_vmax,opt_prof = Yujie111GetOptimalInvestment(tmp_node, weat_days, ini_laba, ini_vmax, max_vmax)
33        Yujie111UpdateLeaf(opt_node, opt_laba, opt_vmax)
34        opt_cica = Yujie111GetAnnualCICA(opt_node, weat_days)
35        println("Finished year ", year, "\n\n")
36        return [opt_laba,opt_vmax,opt_prof,opt_cica[i]]
37    end
38
39    # run the simulations
40    yeardays = []
41    for i in 1:length(years)
42        append!(yeardays, [[years[i] day_s[i] day_e[i]]])
43    end
44    #Println(yeardays)
45    result = pmap(GetOptimaForYear, yeardays)
46    writedlm(filename, result)
47
48    return result
49 end
```

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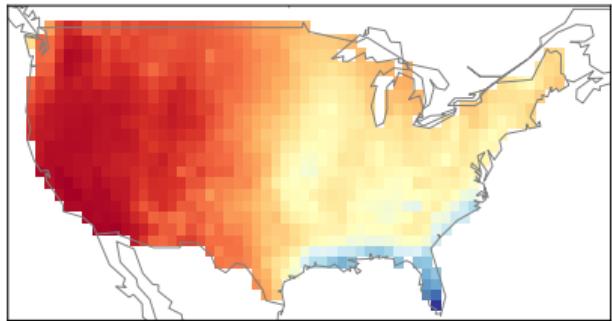
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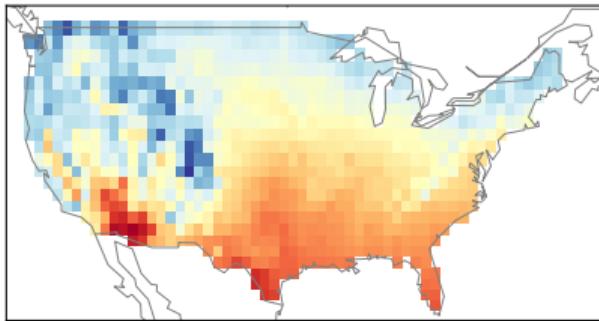
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Sensitivity to climate

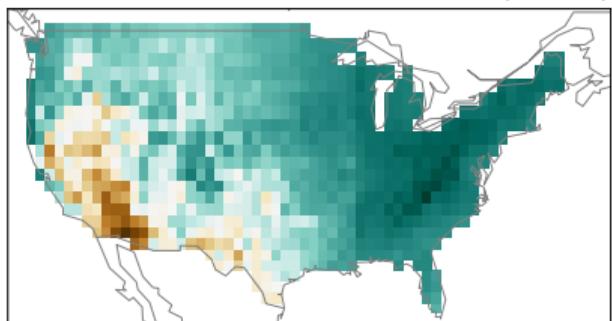
Mean growing season precipitation (mm)



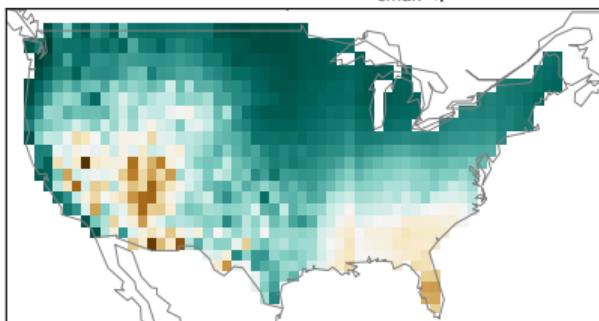
Mean growing season temperature ($^{\circ}\text{C}$)



LA:BA ($\text{m}^2 \text{ m}^{-2}$)



V_{cmax} ($\mu\text{mol m}^{-2} \text{ s}^{-2}$)



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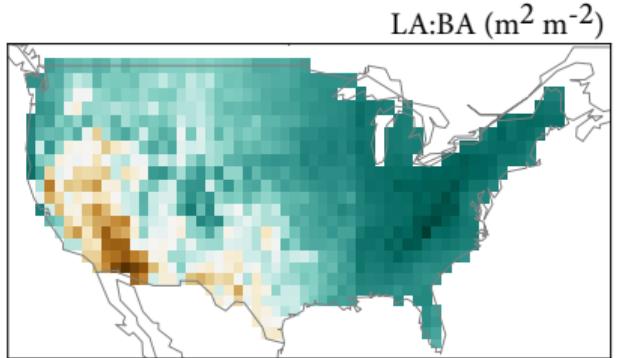
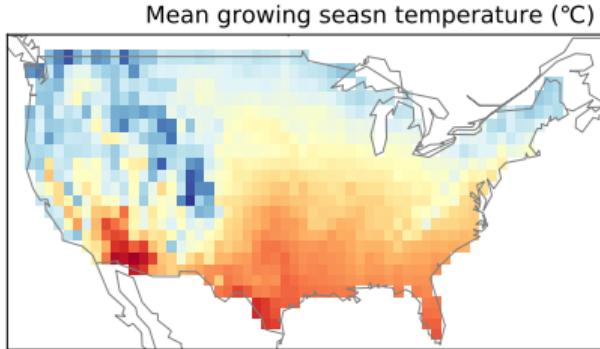
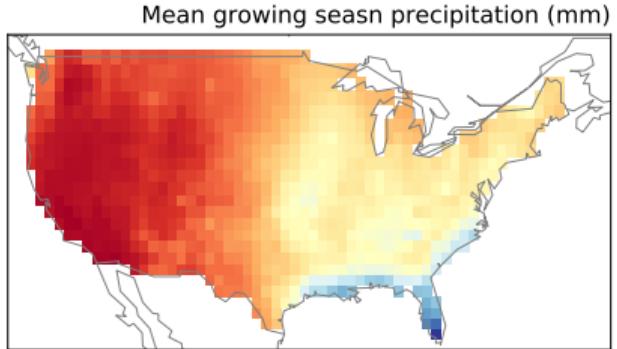
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- ✓ Quantify $A(E_{\text{leaf}})$
- ✓ Quantify $\Theta(E_{\text{leaf}})$
- ✓ Test different optimization models
- ✓ Way forward—long-term prediction

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- ▶ Incorporating gas-phase mesophyll conductance improves photosynthesis modeling
- ▶ Water penalty is linked to plant hydraulic integrity
- ▶ Water penalty is weighted by photosynthesis opportunity
- ▶ Leaf investment is very sensitive to leaf construction costs and root depth
- ▶ Future research on how traits coordinate and acclimate to the environment is required

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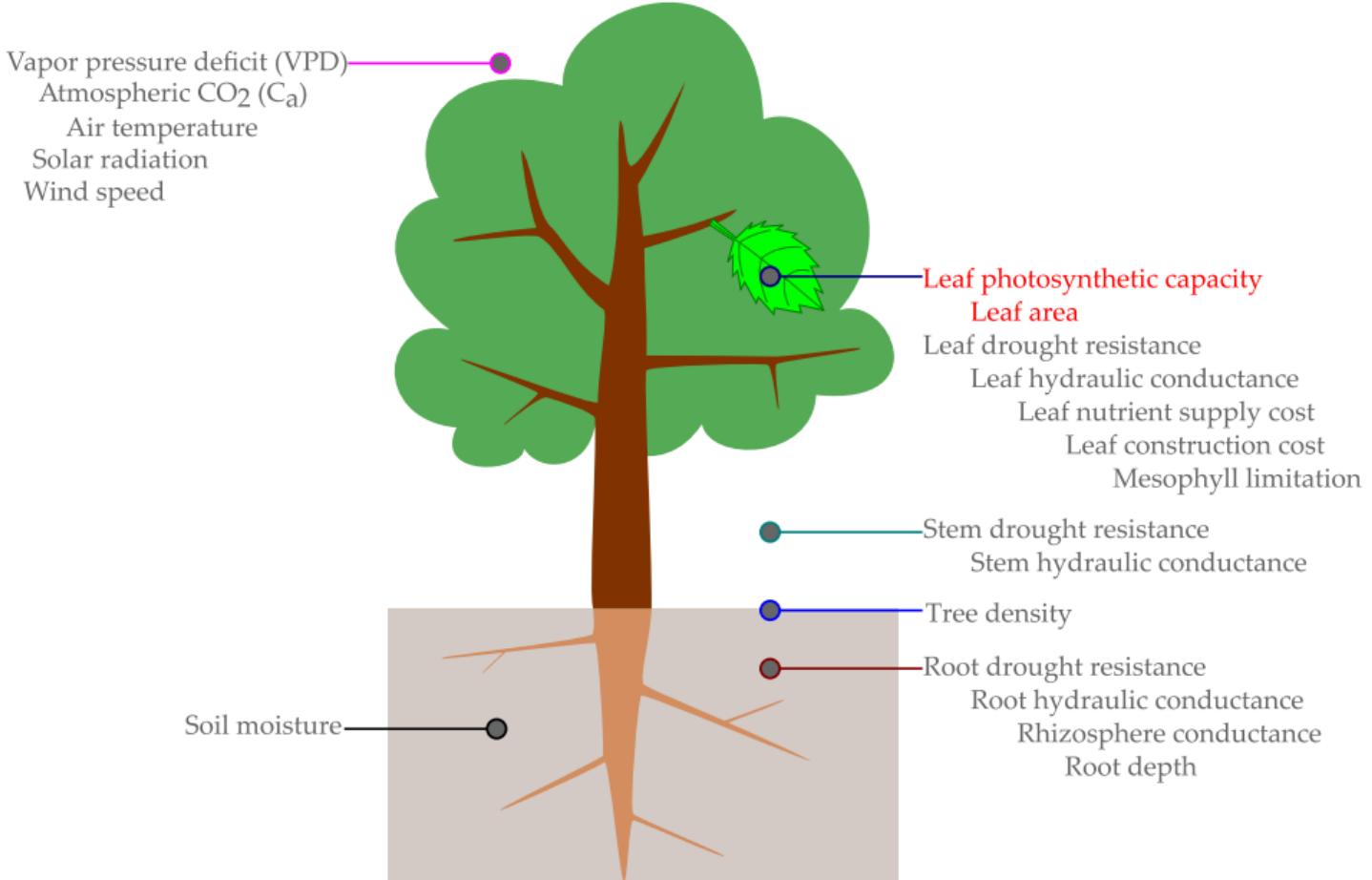
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Acknowledgments

Supervisory committee

- ▶ 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

School of Biological Sciences

- ▶ Shannon Nielsen
- ▶ April Mills
- ▶ Christopher Morrow



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