

CARBON GAIN AND RISK IN MODELING LEAF GAS EXCHANGE

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- Leaf gas exchange
- Global climate change
- Modeling leaf gas exchange

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- Mesophyll limitation
- Model solution
- Improvements

Quantify Θ

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

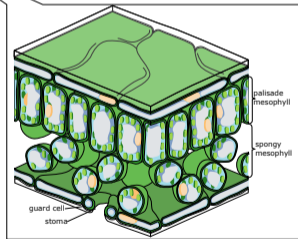
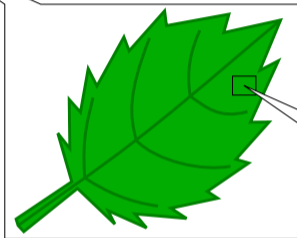
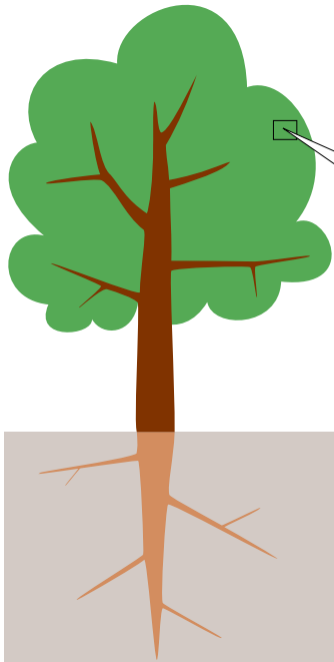
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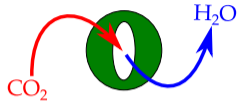
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Significance of leaf gas exchange



Reproduction
Growth

Precipitation pattern

FEEDBACK TO CLIMATE

Carbon cycle
Water cycle
Air humidity
Air temperature

Food availability
Biodiversity
Happiness



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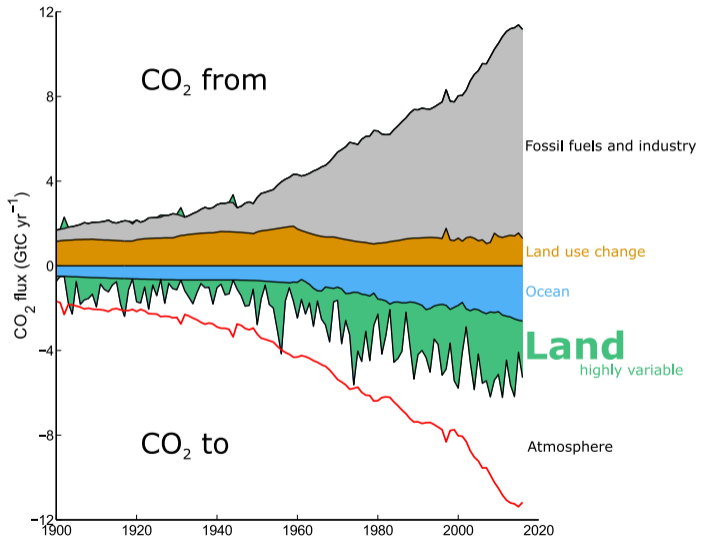


Figure adapted from Le Quéré et al. (2018)

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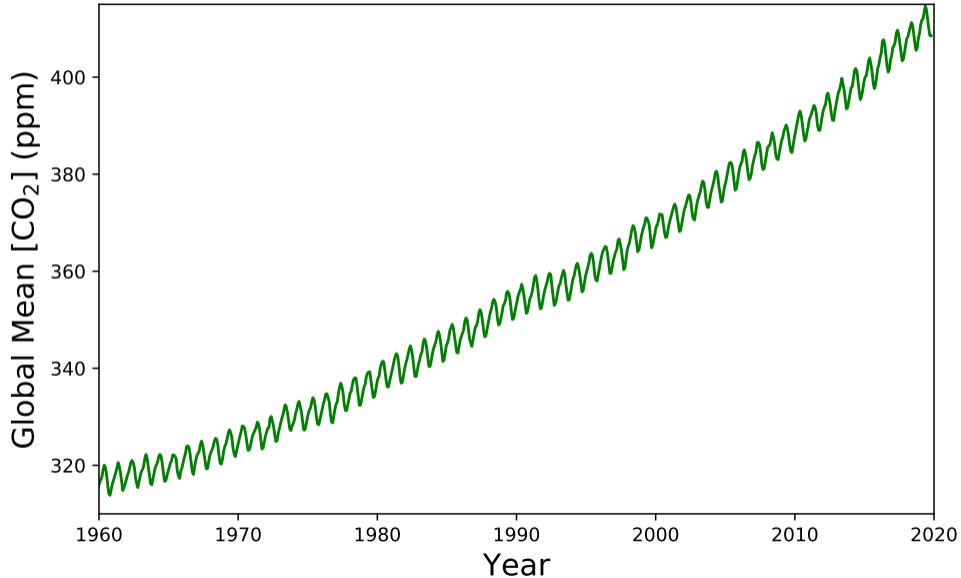
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Increasing CO₂ concentration



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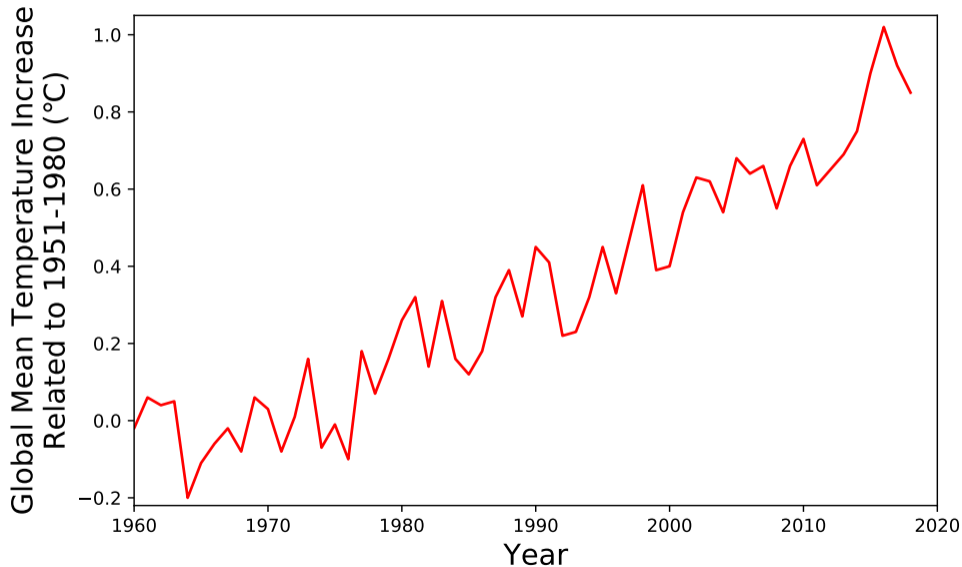
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Increasing temperature



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Soil moisture change

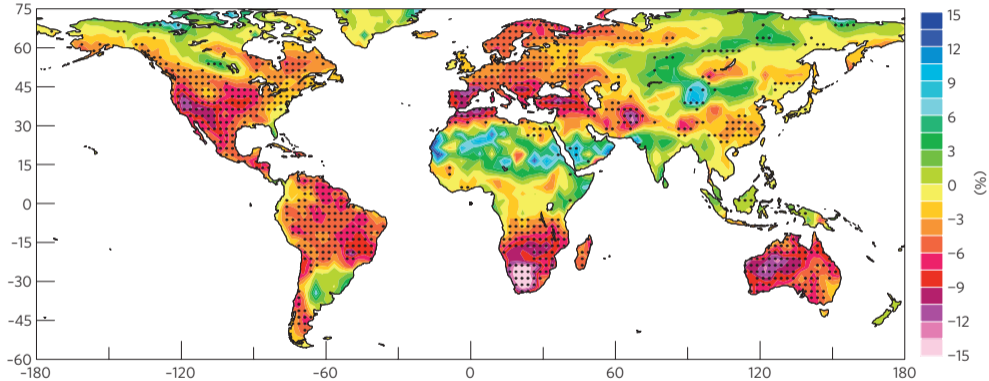


Figure from Dai (2013)

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Role of land in the future

CO₂ Sink?

CO₂ Source?

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Leaf gas exchange through stomata

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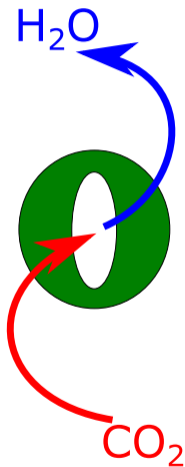
Abscisic acid

Leaf turgor pressure

Hydraulic conductance

Photosynthetic capacity

Mesophyll conductance



ENVIRONMENT

Atmospheric CO_2

Vapor pressure deficit

Air temperature

Solar radiation

Wind speed

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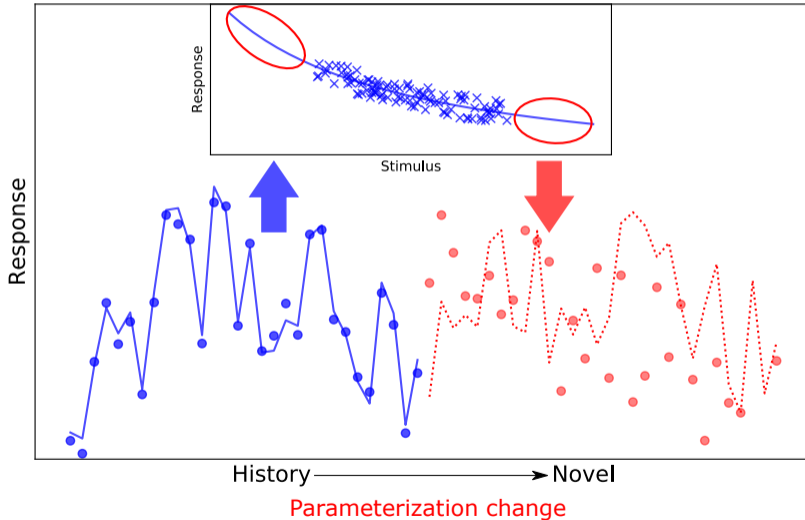
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The easiest way—statistical regression approach



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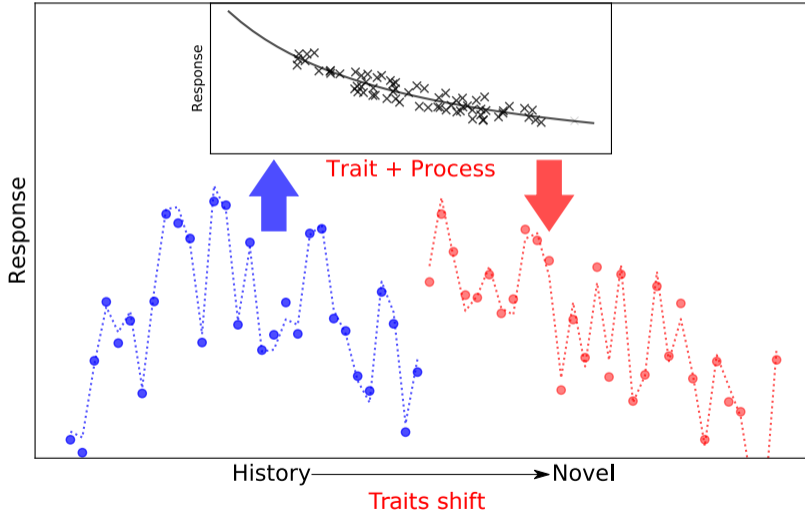
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A better way—physiological trait-based approach



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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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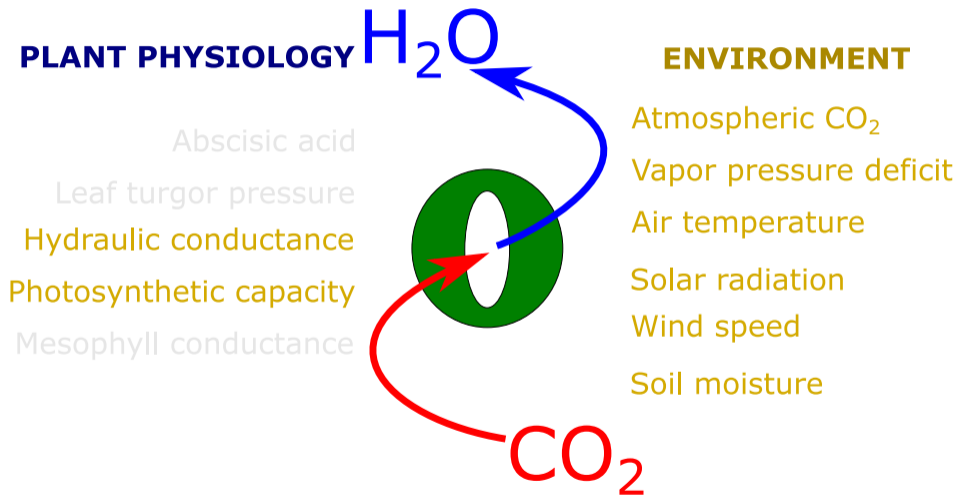
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What we know



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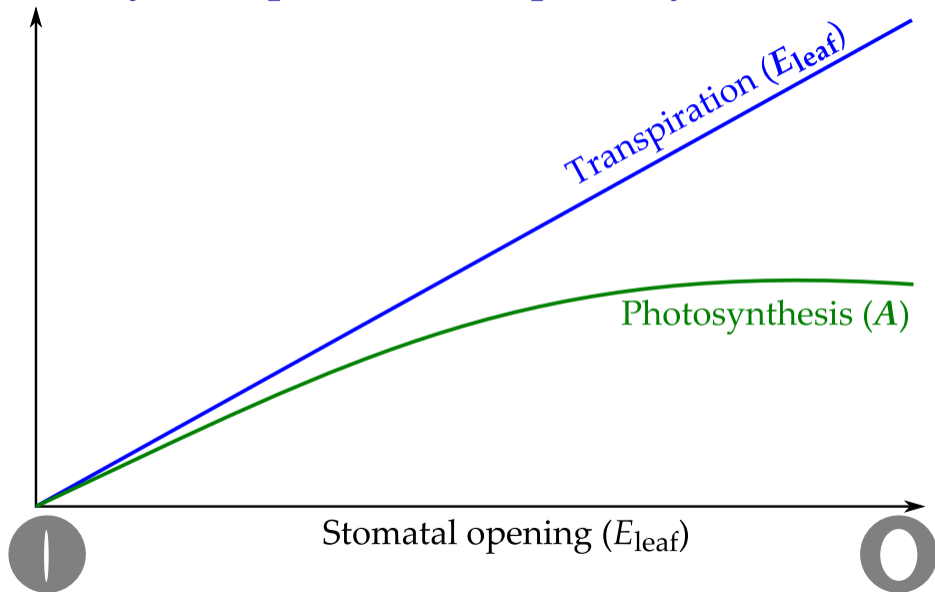
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Quantify transpiration and photosynthesis



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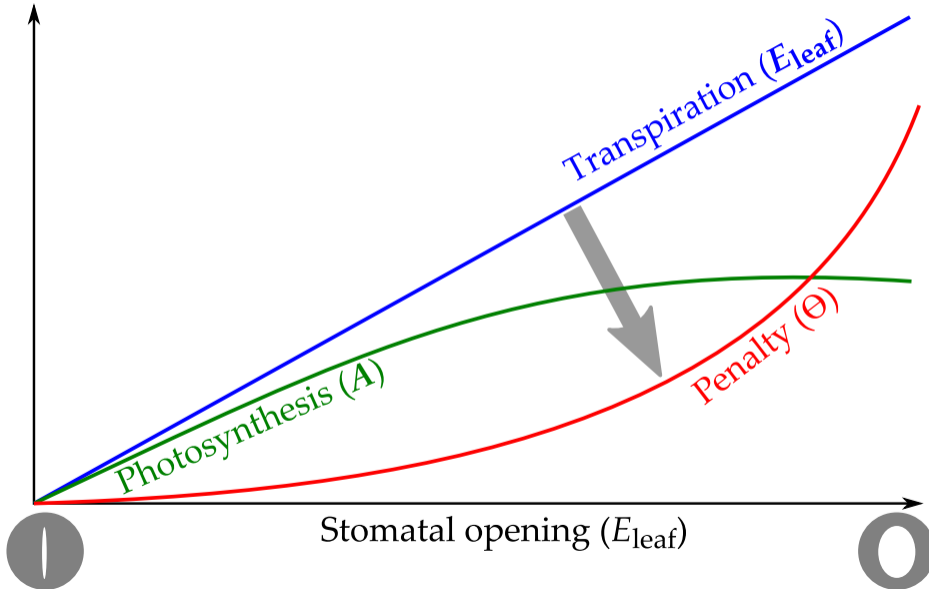
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Translation to water penalty



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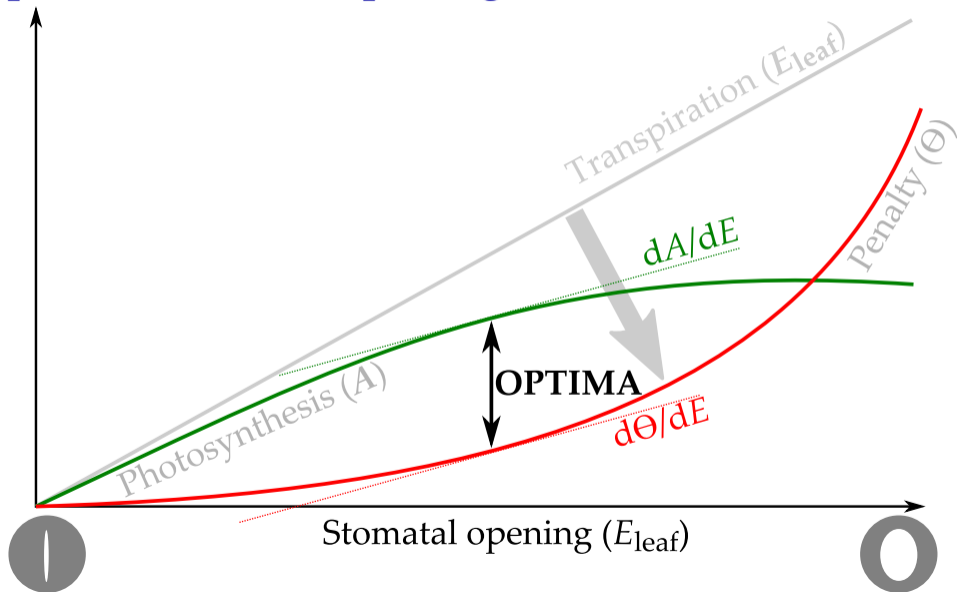
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Optimal stomatal opening



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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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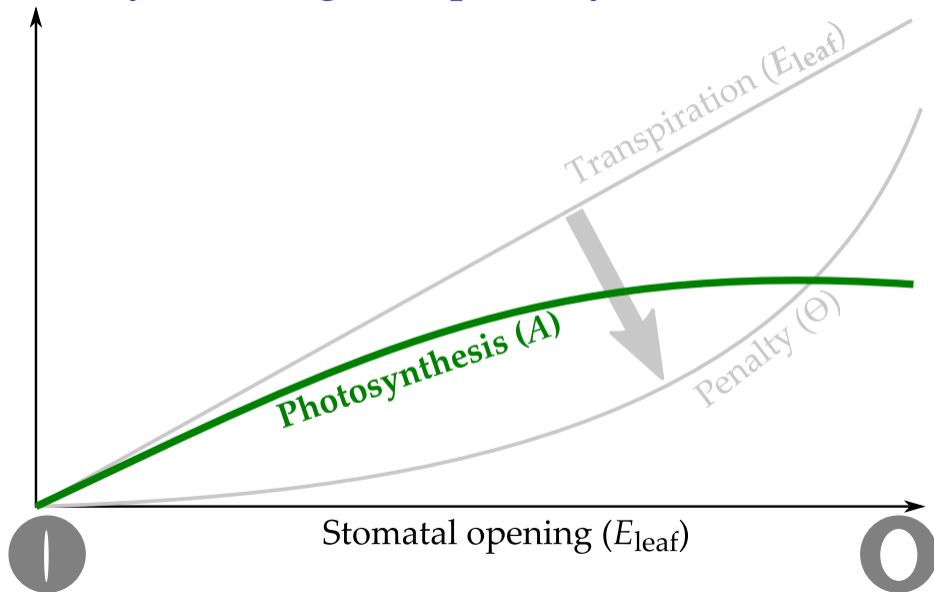
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Quantify carbon gain—photosynthesis (A)



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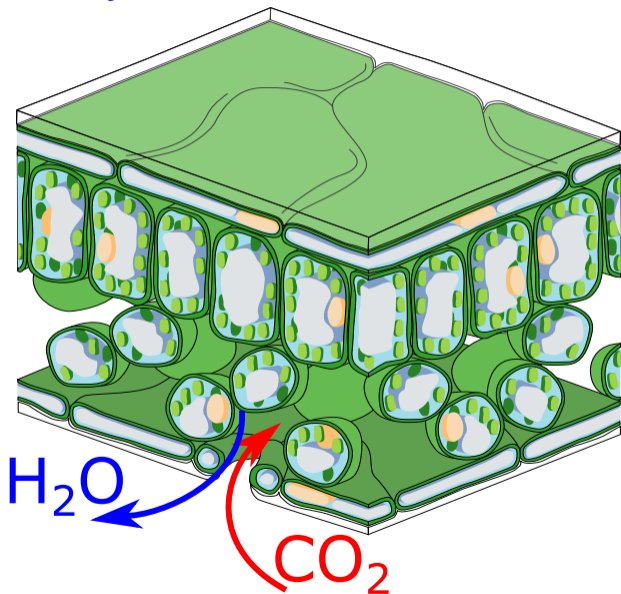
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Classic photosynthesis model



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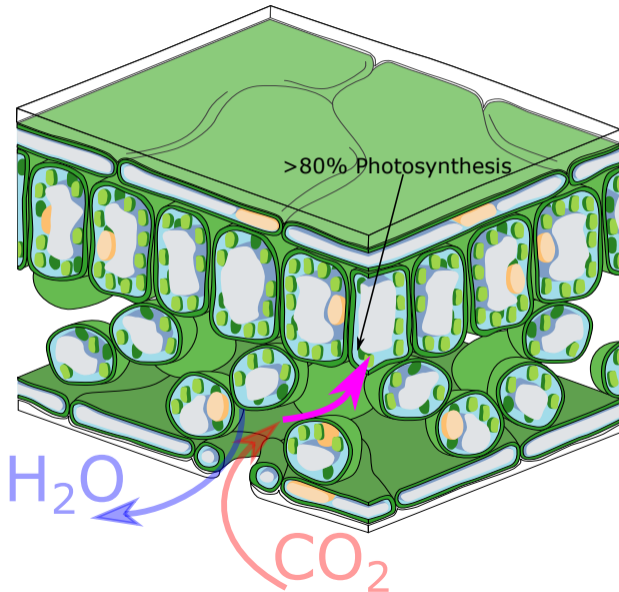
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The “missing” components



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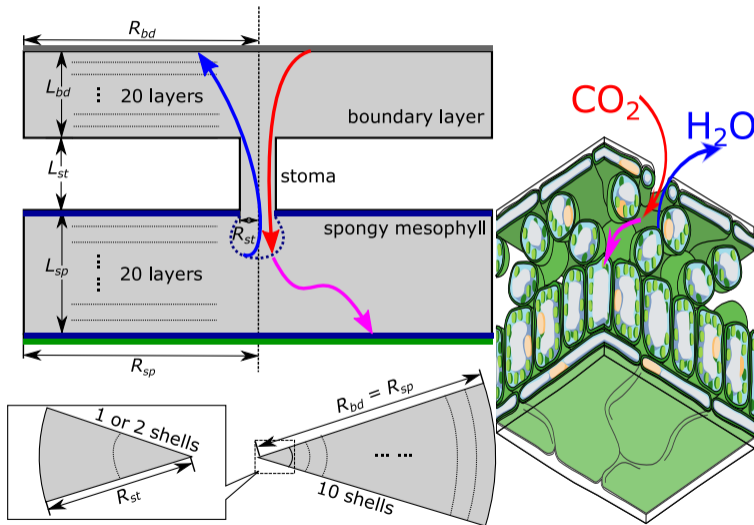
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Mysophyll limitation



Wang et al., (in review)

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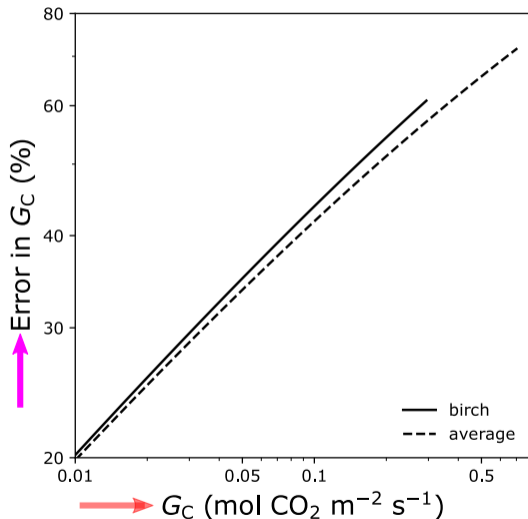
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Mesophyll limitation as an “error”



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Improved photosynthesis model

classic model

$$G_C$$

corrected model

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

The diagram illustrates the relationship between the classic model and the corrected model. A red arrow points from the text "classic model" to the term G_C in the numerator of the equation. A magenta arrow points from the text "corrected model" to the entire equation, which defines G'_C .

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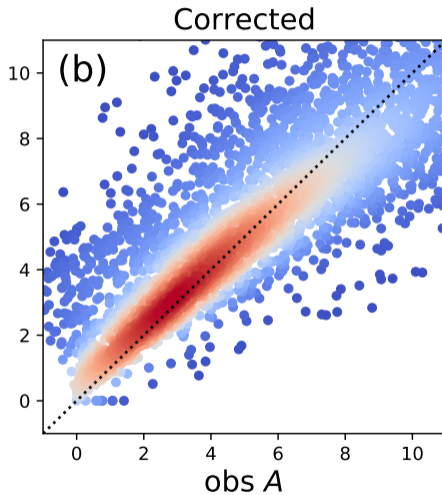
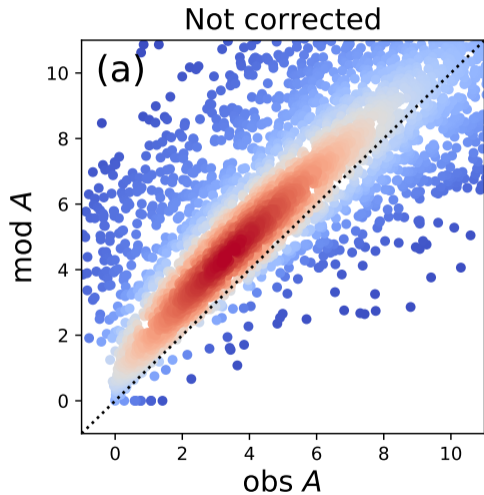
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Improvement of modeled A



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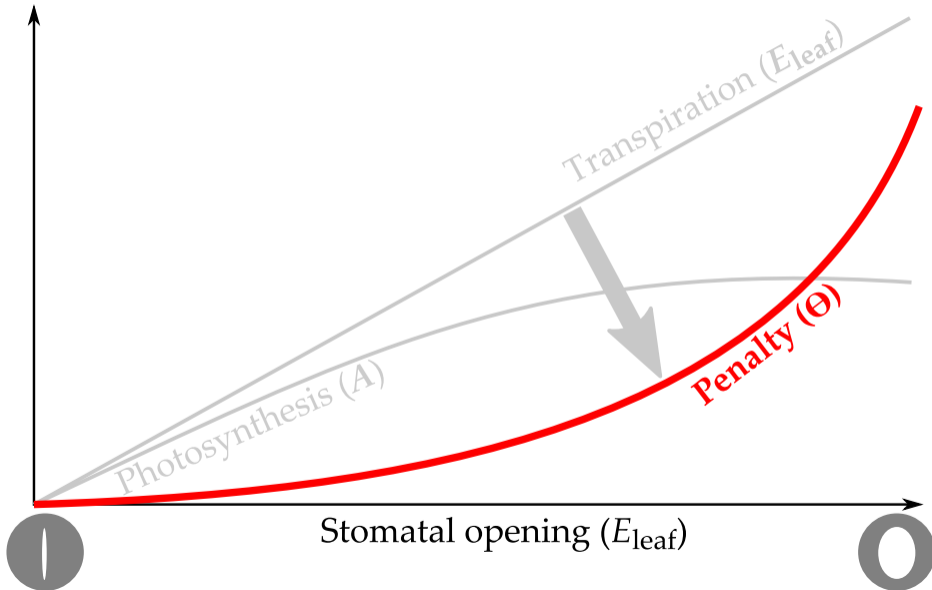
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Quantify water penalty (Θ)



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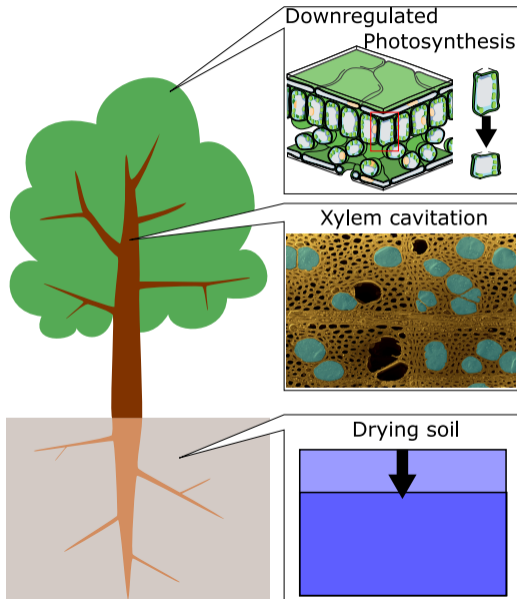
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Causes of water penalty (Θ)



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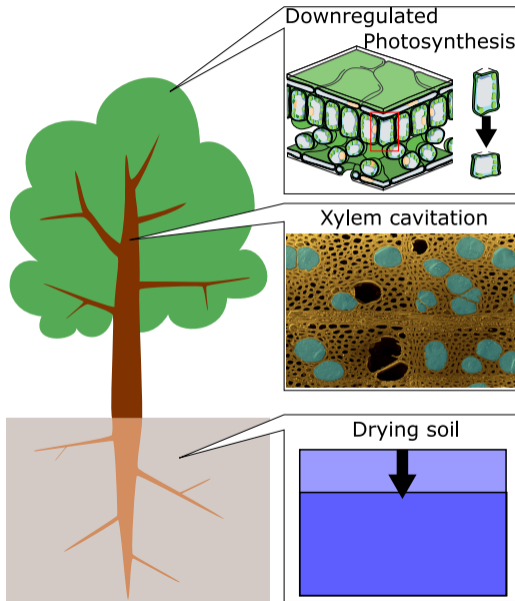
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Models based on different Θ



Holttä *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 DCPK	Fitting parameters
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{\text{leaf}}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et al., 2014)	$\Theta = A \cdot \left(1 - \frac{1}{c_E E_{\text{leaf}} + c_V V_{\text{cmax}}}\right)$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{leaf}} + \frac{c_V}{c_E} V_{\text{cmax}}}$	YNY	YYNN	c_E, c_V
Lu	(Lu et al., 2016)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	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)	$\Theta = A_{\text{max}} \cdot \left(1 - \frac{K}{K_{\text{max}}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{\text{max}}}{K_{\text{max}}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{\text{max},0}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{\text{leaf}}}{E_{\text{crit}}}$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{crit}} - E_{\text{leaf}}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{\text{ww}} \cdot \frac{SC}{SC_{\text{max}}}$	$\frac{d\Theta'}{dE} = \frac{A}{SC_{\text{max}} - SC} \cdot \frac{dSC}{dE}$	YYY	YYYY	$SC_{\text{max}}, K_{\text{rhiz}}, \text{anatomy}$
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{\text{ww}} \cdot \frac{P}{P_{\text{crit}}}$	$\frac{d\Theta'}{dE} = \frac{A}{K \cdot (P_{\text{crit}} - P)}$	YYY	YYYY	K_{rhiz}

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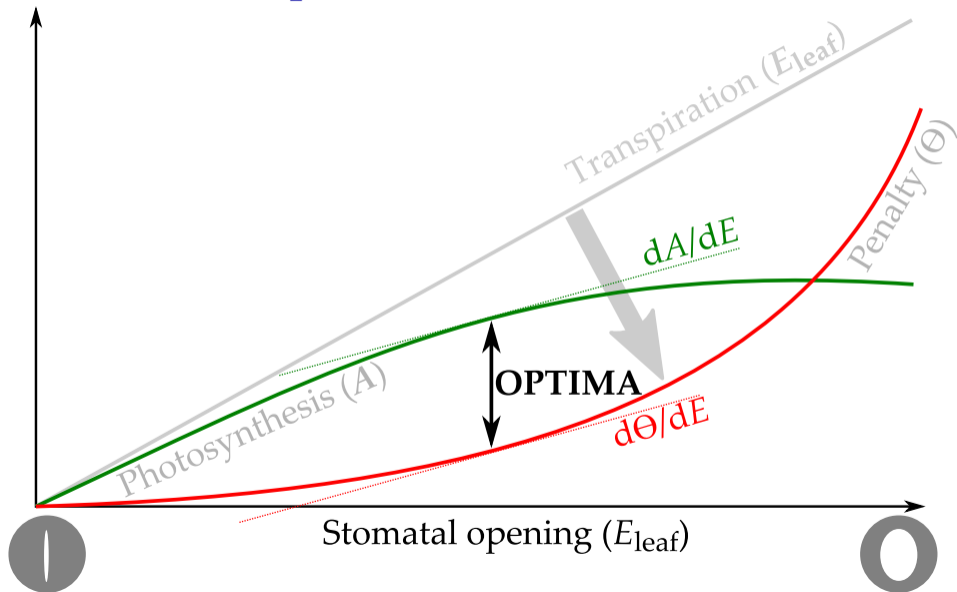
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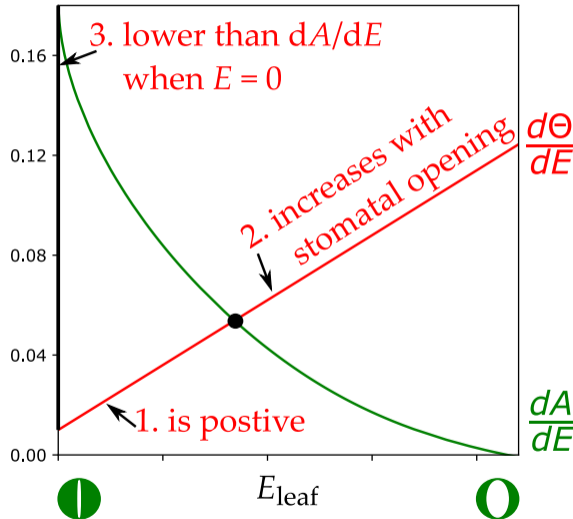
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$$\frac{dA}{dE} = \frac{d\Theta}{dE}$$



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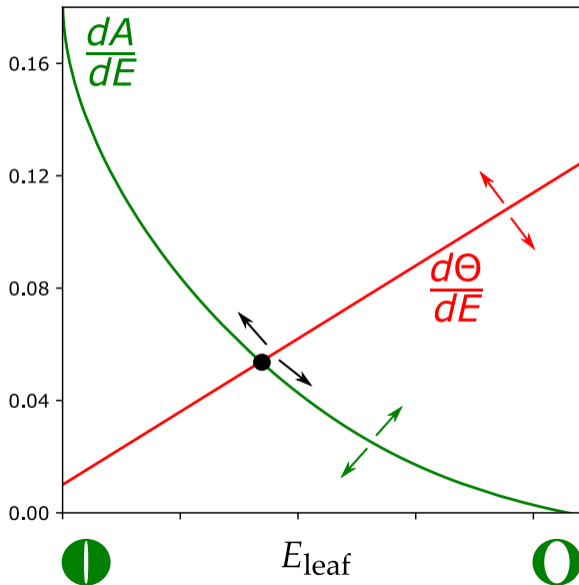
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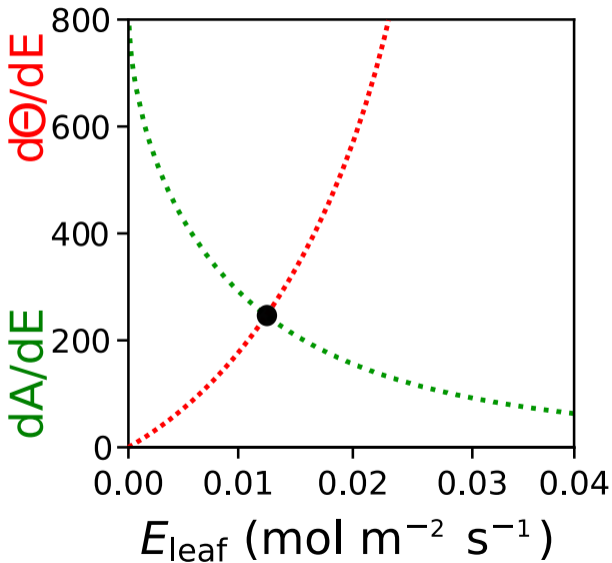
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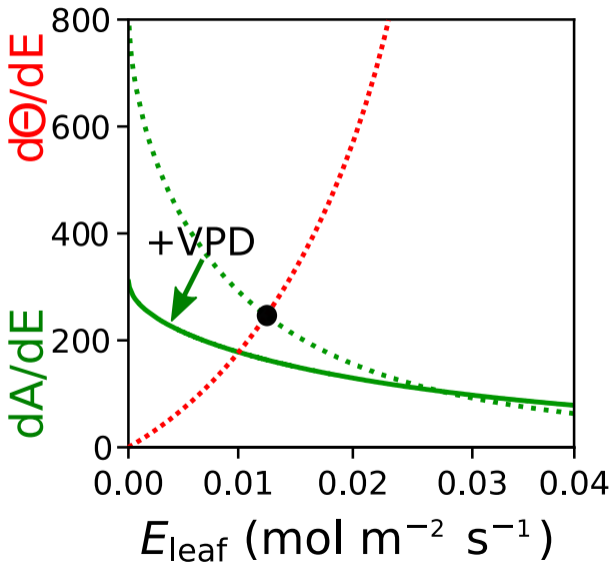
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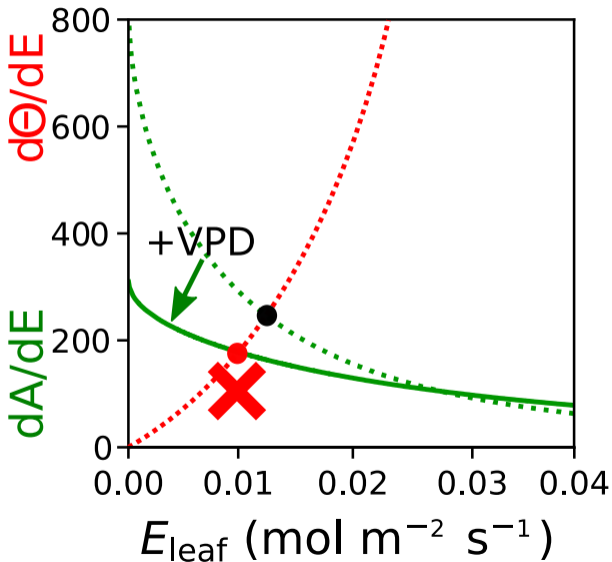
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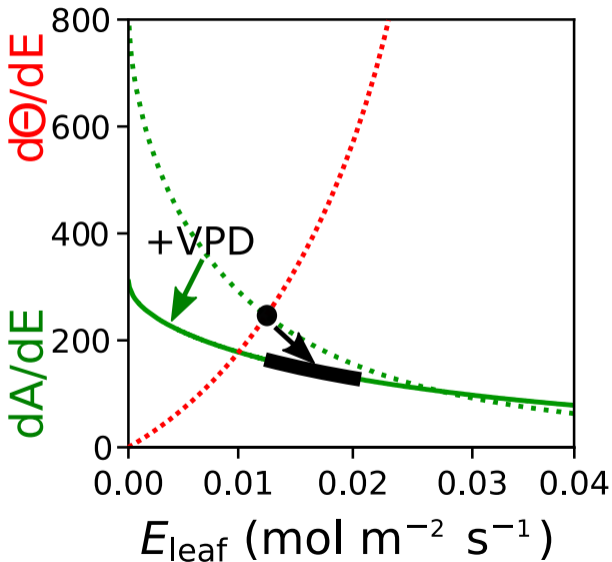
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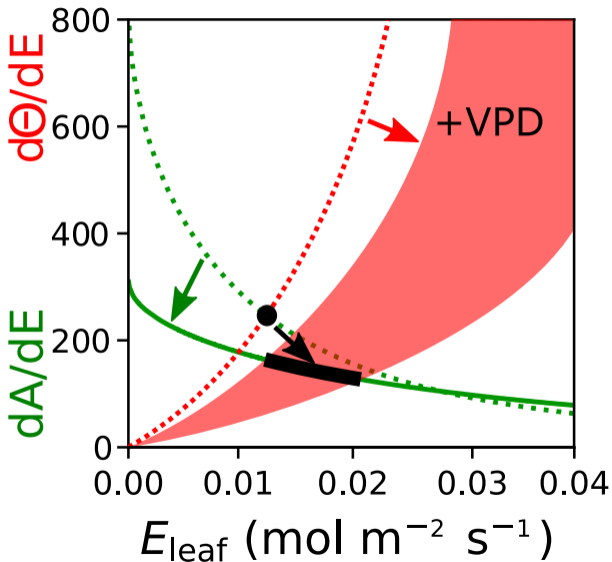
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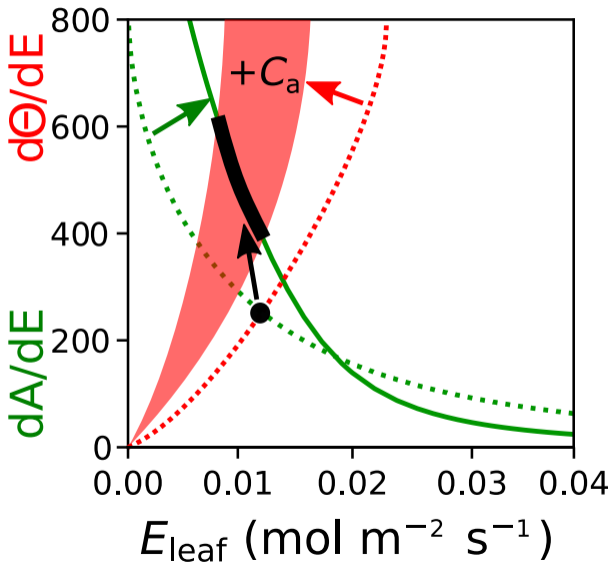
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5. increases with higher CO₂



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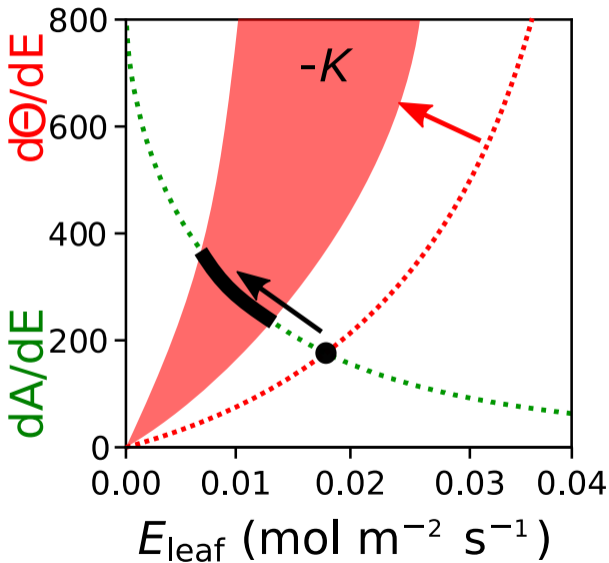
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6. increases with drier soil



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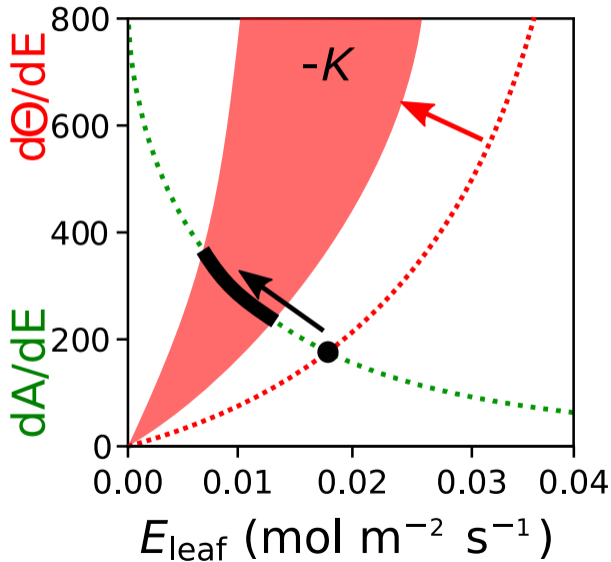
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7. increases with lower hydraulic conductance



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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 $E_{\text{leaf}} \uparrow$
3. $d\Theta/dE < dA/dE$ when $E_{\text{leaf}} = 0$

Criteria for stomatal responses

4. $d\Theta/dE \downarrow$ when air gets drier
5. $d\Theta/dE \uparrow$ when $[\text{CO}_2] \uparrow$
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 DCPK	
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{\text{leaf}}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et al., 2014)	$\Theta = A \cdot \left(1 - \frac{1}{c_E E_{\text{leaf}} + c_V V_{\text{cmax}}}\right)$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{leaf}} + \frac{c_V}{c_E} V_{\text{cmax}}}$	YNY	YYNN	c_E, c_V
Lu	(Lu et al., 2016)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	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)	$\Theta = A_{\text{max}} \cdot \left(1 - \frac{K}{K_{\text{max}}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{\text{max}}}{K_{\text{max}}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{\text{max},0}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{\text{leaf}}}{E_{\text{crit}}}$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{crit}} - E_{\text{leaf}}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{\text{ww}} \cdot \frac{SC}{SC_{\text{max}}}$	$\frac{d\Theta'}{dE} = \frac{A}{SC_{\text{max}} - SC} \cdot \frac{dSC}{dE}$	YYY	YYYY	$SC_{\text{max}}, K_{\text{rhiz}}, \text{anatomy}$
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{\text{ww}} \cdot \frac{P}{P_{\text{crit}}}$	$\frac{d\Theta'}{dE} = \frac{A}{K \cdot (P_{\text{crit}} - P)}$	YYY	YYYY	K_{rhiz}

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				Criteria I-III	Criteria IV-VII DCPK	
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{\text{leaf}}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et al., 2014)	$\Theta = A \cdot \left(1 - \frac{1}{c_E E_{\text{leaf}} + c_V V_{\text{cmax}}}\right)$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{leaf}} + \frac{c_V}{c_E} V_{\text{cmax}}}$	YNY	YYNN	c_E, c_V
Lu	(Lu et al., 2016)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	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)	$\Theta = A_{\text{max}} \cdot \left(1 - \frac{K}{K_{\text{max}}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{\text{max}}}{K_{\text{max}}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{\text{max},0}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{\text{leaf}}}{E_{\text{crit}}}$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{crit}} - E_{\text{leaf}}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{\text{ww}} \cdot \frac{SC}{SC_{\text{max}}}$	$\frac{d\Theta'}{dE} = \frac{A}{SC_{\text{max}} - SC} \cdot \frac{dSC}{dE}$	YYY	YYYY	$SC_{\text{max}}, K_{\text{rhiz}}, \text{anatomy}$
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{\text{ww}} \cdot \frac{P}{P_{\text{crit}}}$	$\frac{d\Theta'}{dE} = \frac{A}{K \cdot (P_{\text{crit}} - P)}$	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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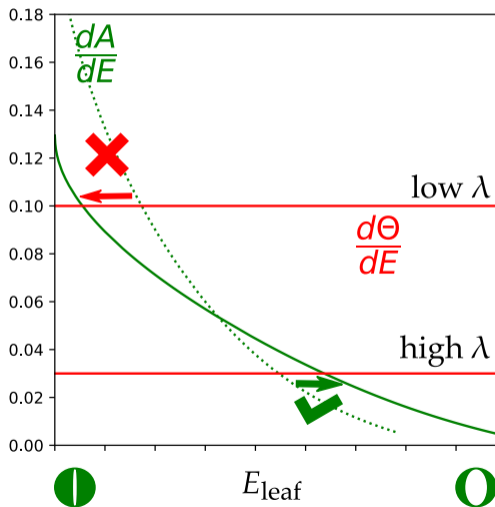
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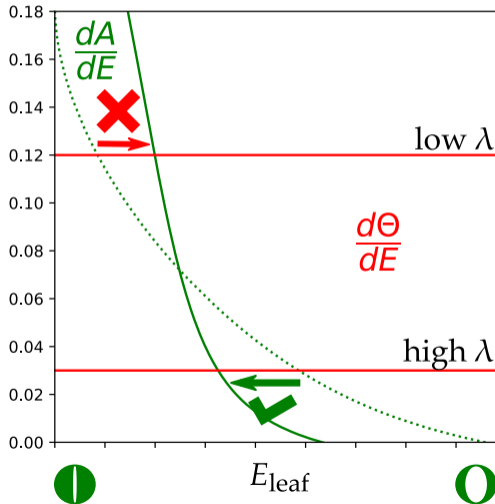
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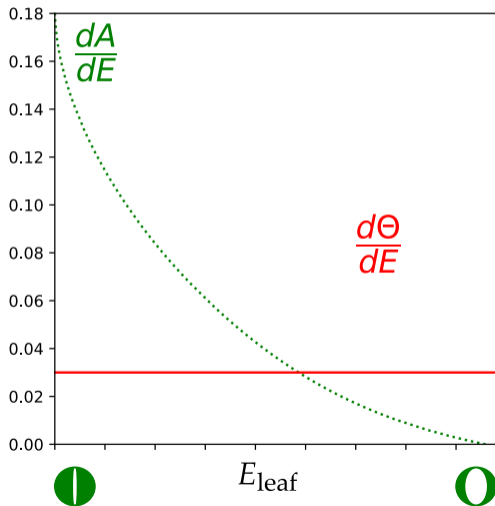
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				Criteria I-III	Criteria IV-VII DCPK	
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{\text{leaf}}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et al., 2014)	$\Theta = A \cdot \left(1 - \frac{1}{c_E E_{\text{leaf}} + c_V V_{\text{cmax}}}\right)$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{leaf}} + \frac{c_V}{c_E} V_{\text{cmax}}}$	YNY	YYNN	c_E, c_V
Lu	(Lu et al., 2016)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	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)	$\Theta = A_{\text{max}} \cdot \left(1 - \frac{K}{K_{\text{max}}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{\text{max}}}{K_{\text{max}}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{\text{max},0}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{\text{leaf}}}{E_{\text{crit}}}$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{crit}} - E_{\text{leaf}}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{\text{ww}} \cdot \frac{SC}{SC_{\text{max}}}$	$\frac{d\Theta'}{dE} = \frac{A}{SC_{\text{max}} - SC} \cdot \frac{dSC}{dE}$	YYY	YYYY	$SC_{\text{max}}, K_{\text{rhiz}}, \text{anatomy}$
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{\text{ww}} \cdot \frac{P}{P_{\text{crit}}}$	$\frac{d\Theta'}{dE} = \frac{A}{K \cdot (P_{\text{crit}} - P)}$	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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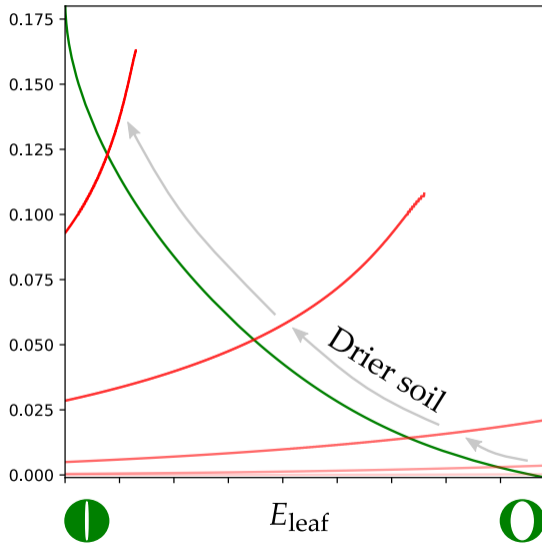
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				Criteria I-III	Criteria IV-VII DCPK	Fitting parameters
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni et al., 2013)	$\Theta = \frac{E_{\text{leaf}}}{\Lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\Lambda}$	YNN	NNNN	Λ
Prentice	(Prentice et al., 2014)	$\Theta = A \cdot \left(1 - \frac{1}{c_E E_{\text{leaf}} + c_V V_{\text{cmax}}}\right)$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{leaf}} + \frac{c_V}{c_E} V_{\text{cmax}}}$	YNY	YYNN	c_E, c_V
Lu	(Lu et al., 2016)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	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)	$\Theta = A_{\text{max}} \cdot \left(1 - \frac{K}{K_{\text{max}}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A_{\text{max}}}{K_{\text{max}}}$	YYY	YYYY	K_{rhiz}
Eller	(Eller et al., 2018)	$\Theta = A \cdot \left(1 - \frac{K}{K_{\text{max},0}}\right)$	$\frac{d\Theta}{dE} = -\frac{dK}{dE} \cdot \frac{A}{K}$	YYY	YYYN	K_{rhiz}
New Model		$\Theta = A \cdot \frac{E_{\text{leaf}}}{E_{\text{crit}}}$	$\frac{d\Theta}{dE} = \frac{A}{E_{\text{crit}} - E_{\text{leaf}}}$	YYY	YYYY	K_{rhiz}
Hölttä	(Hölttä et al., 2017)	$\Theta' = A_{\text{ww}} \cdot \frac{SC}{SC_{\text{max}}}$	$\frac{d\Theta'}{dE} = \frac{A}{SC_{\text{max}} - SC} \cdot \frac{dSC}{dE}$	YYY	YYYY	$SC_{\text{max}}, K_{\text{rhiz}}, \text{anatomy}$
Dewar CAP	(Dewar et al., 2018)	$\Theta' = A_{\text{ww}} \cdot \frac{P}{P_{\text{crit}}}$	$\frac{d\Theta'}{dE} = \frac{A}{K \cdot (P_{\text{crit}} - P)}$	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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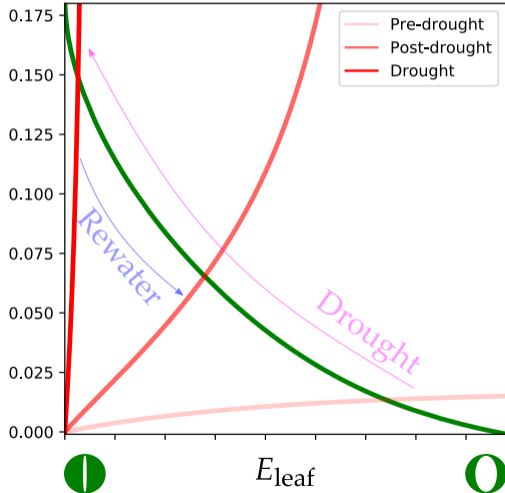
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- ✓ Quantify $A(E_{\text{leaf}})$
- ✓ Quantify $\Theta(E_{\text{leaf}})$
- 3. Test different optimization models
- 4. Way forward—long-term prediction

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TESTING THE MODELS

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Birch dataset



Wang et al. (2019)

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Venturas et al. (2018)

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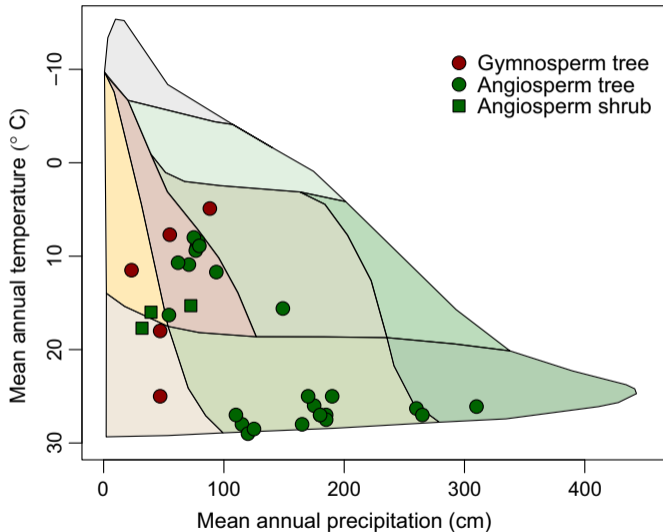
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Anderegg dataset



Anderegg et al. (2018)

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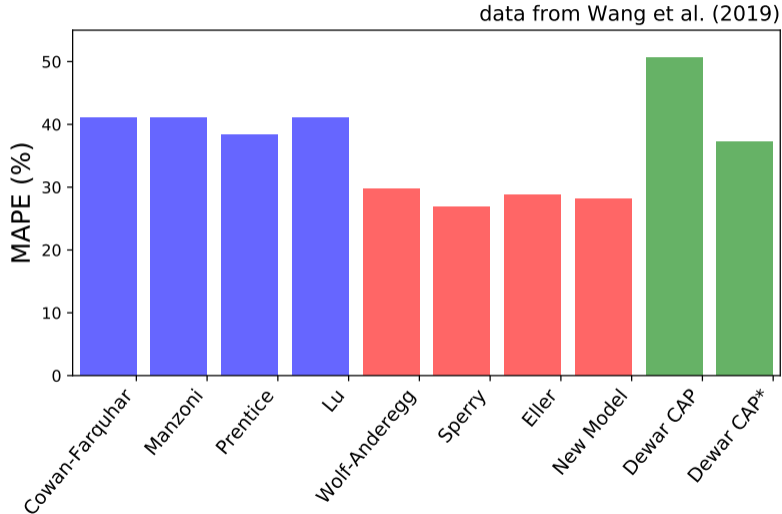
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MAPE: mean absolute percentage error for A, P, and E

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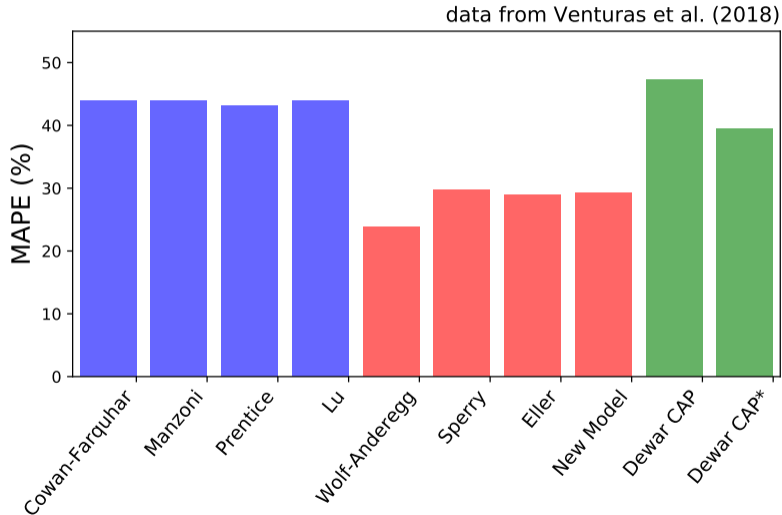
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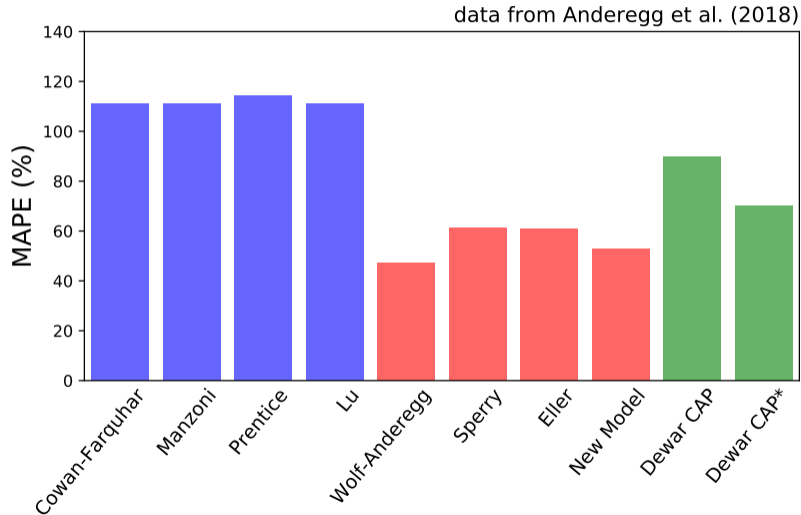
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Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($d\Theta/dE$ or $d\Theta'/dE$)	Response		Fitting parameters
				Criteria I-III	Criteria IV-VII DCPK	
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{\text{leaf}}}{\lambda}$	$\frac{d\Theta}{dE}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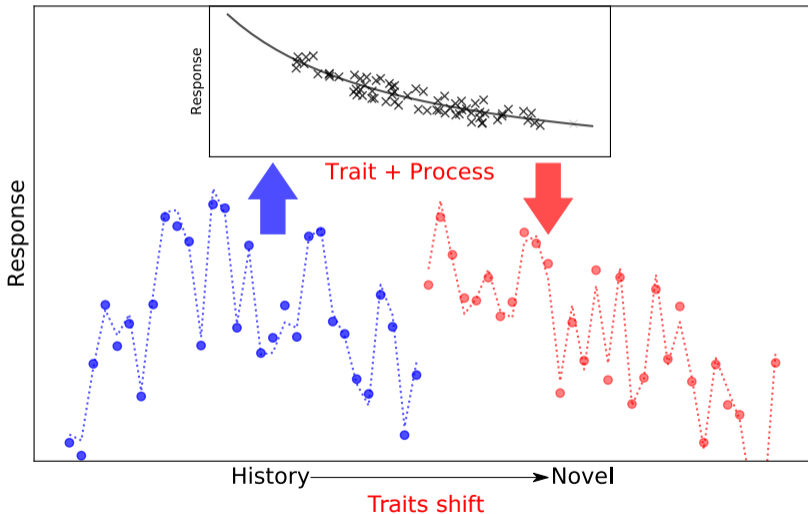
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How about trait change?



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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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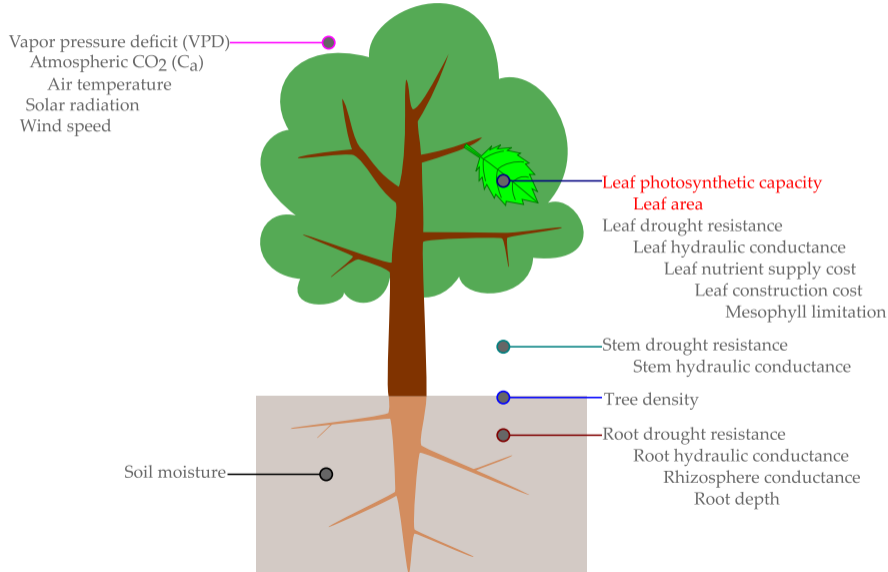
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Environmental and physiological variables



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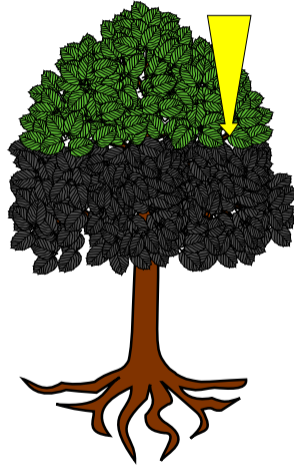
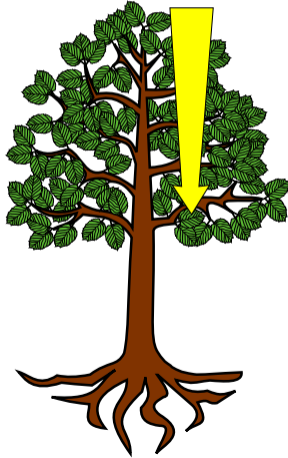
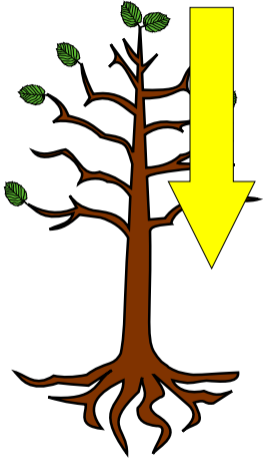
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Optimal leaf area



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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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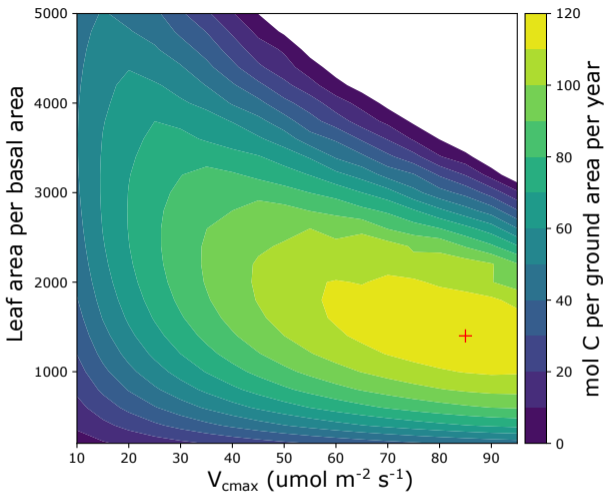
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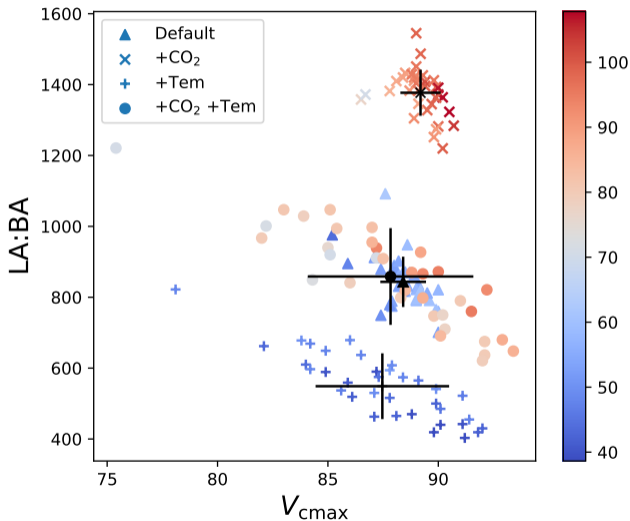
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Optimal leaf investment vs. climate



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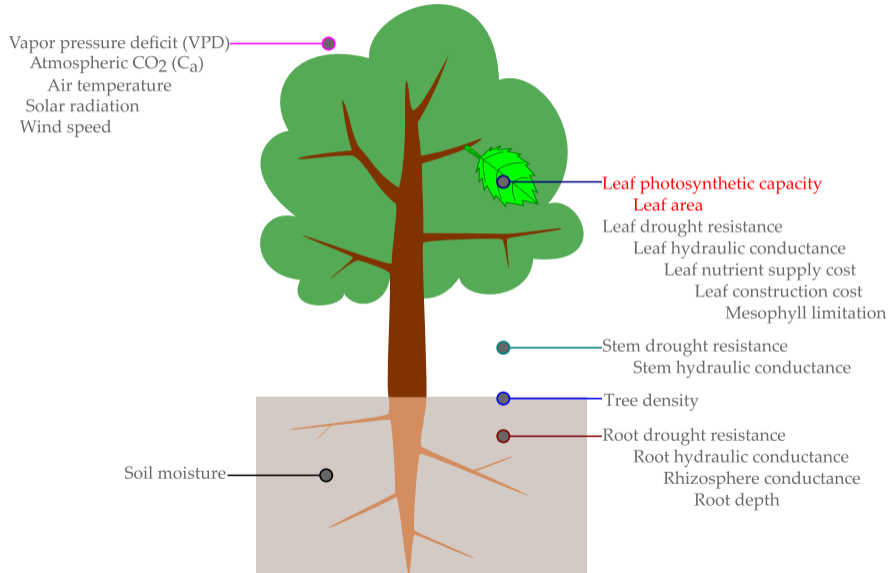
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Other traits?



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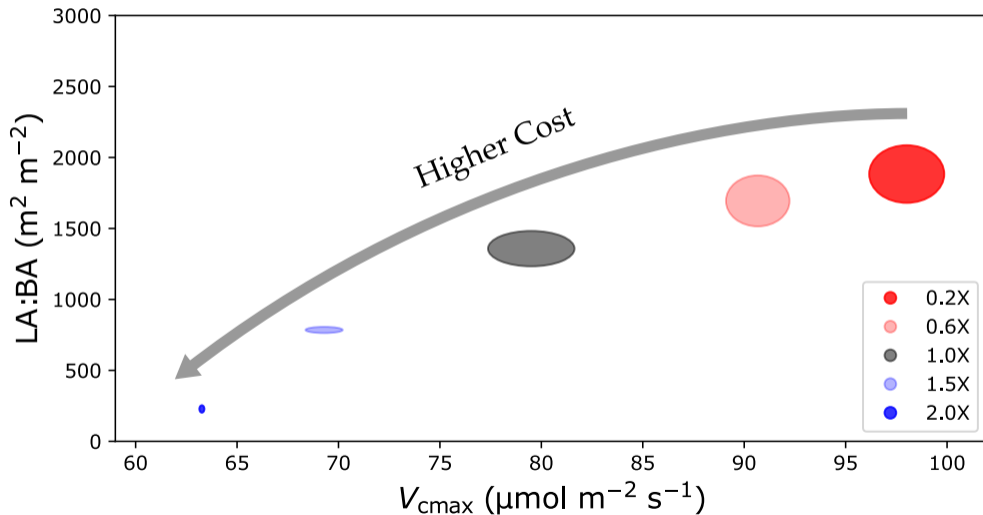
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Optimal leaf investment vs. carbon cost (LCBM)



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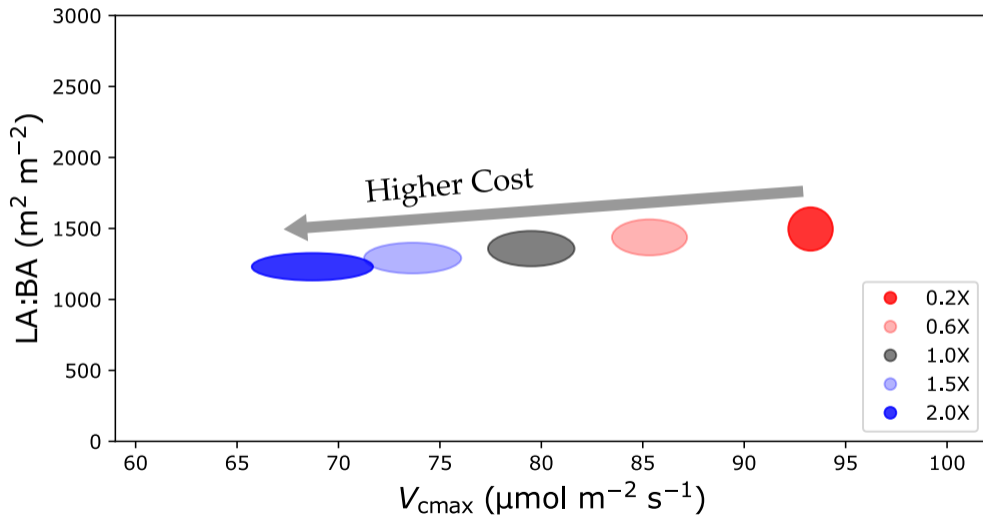
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Optimal leaf investment vs. nutrient cost (NS)



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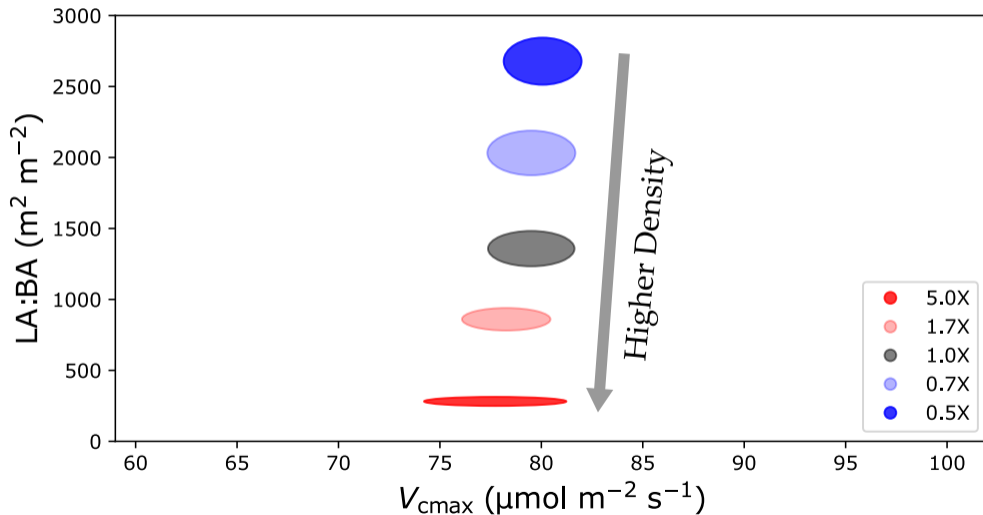
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Optimal leaf investment vs. stand density



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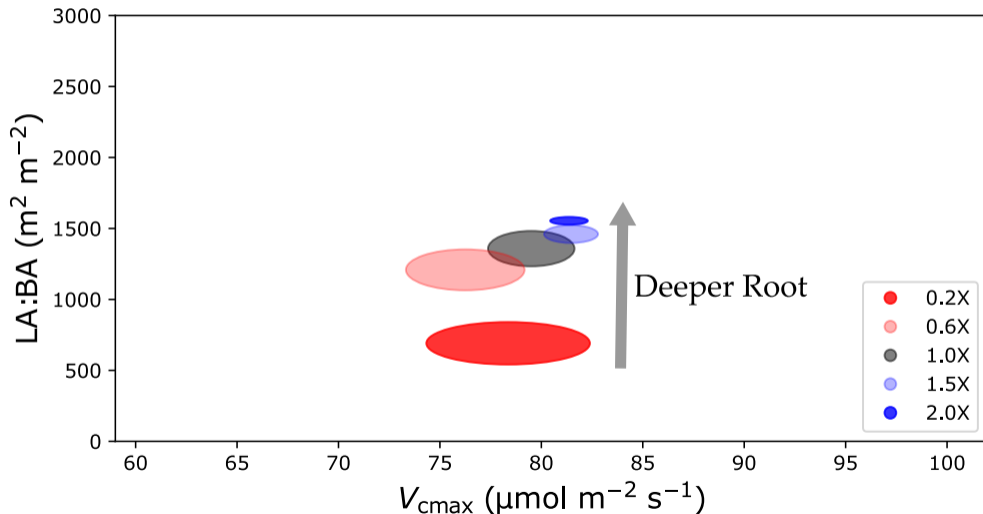
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Optimal leaf investment vs. root depth



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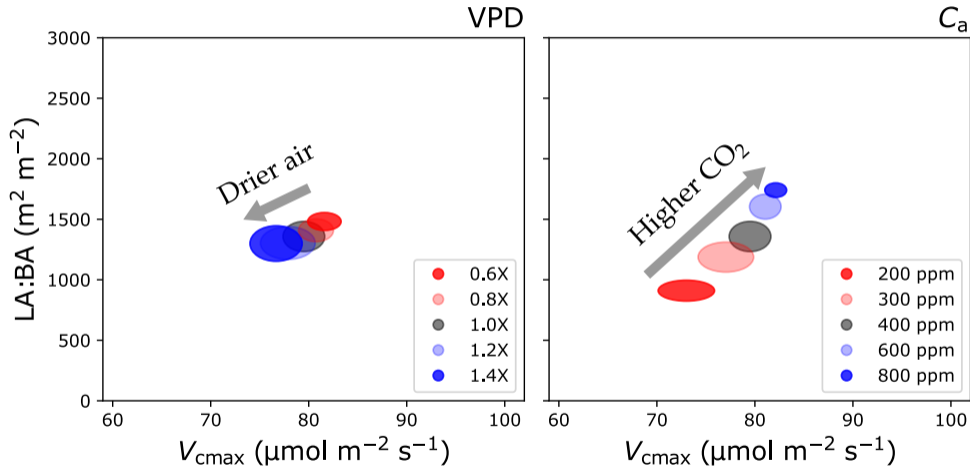
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Optimal leaf investment vs. VPD and CO₂



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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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Plant trees!



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```
OPENER
└─ OPEN EDITORS
  └─ yujie_111_optima_sensitivity_cluster_weather.jl scripts > leaf investment > yujie_111_optima_sensitivity_cluster_weather.jl
    └─ YUREGANBIRSKMODEL
      └─ anatomy
        └─ data
          └─ earth
            └─ leaf_rubisco
              └─ math
                └─ node_111
                  └─ photosynthesis
                    └─ physics
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                        └─ saved
                          └─ scripts
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                                                        └─ yujie_111_test_tradeoff.jl
                                                          └─ water price
                                                            └─ check_weather_variation.jl
                                                              └─ yujie_111_optimal_forest_density.jl
                                                                └─ yujie_111
                                                                  └─ .gitignore
                                                                    └─ include.jl
                                                                      └─ load_processors.jl
                                                                        └─ load.jl
                                                                          └─ main.jl
                                                                            └─ README.md
                                                                              └─ test.jl
                                                                              └─ OUTLINE
                                                                              └─ yujie_111_optima_sensitivity_cluster_weather.jl
                                                                              └─ scripts > leaf investment > yujie_111_optima_sensitivity_cluster_weather.jl
                                                                              └─ # 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_alti)
                                                                              └─ 5 # initialize the node
                                                                              └─ 6 @everywhere max_vmax = 100.0
                                                                              └─ @everywhere opt_node = Yujie111Init()
                                                                              └─ 9 @everywhere opt_node.d_lat = $d_lat
                                                                              └─ @everywhere opt_node.d_long = $d_long
                                                                              └─ @everywhere opt_node.d_alti = $d_alti
                                                                              └─ @everywhere Yujie111UpdateSoilFromSMC(opt_node, 1.0)
                                                                              └─ @everywhere Yujie111UpdateLeaf(opt_node, 1000.0, 70.0)
                                                                              └─ # define the thread function
                                                                              └─ @everywhere weat_years = CSV.read{weather}
                                                                              └─ 18 @everywhere function GetOptimaForYear(yeardays)
                                                                              └─ 19 #println(yeardays)
                                                                              └─ year = yeardays[1]
                                                                              └─ dayst = yeardays[2]
                                                                              └─ dayen = yeardays[3]
                                                                              └─ 23 tap_node = deepcopy(opt_node)
                                                                              └─ ini_laba = opt_node.laba
                                                                              └─ ini_vmax = opt_node.v_max
                                                                              └─ println("Start year ", year, "!")
                                                                              └─ weat_mask = (weat_years.Year .== year)
                                                                              └─ weat_year = weat_years[weat_mask,:]
                                                                              └─ mask_days = (weat_year.Day .>= dayst) .* (weat_year.Day .<= dayen)
                                                                              └─ weat_days = weat_year[mask_days,:]
                                                                              └─ weat_days.CO2 = 40.0
                                                                              └─ opt_laba,opt_vmax,opt_prof = Yujie111GetOptimalInvestment(tap_node, weat_days, ini_laba, ini_vmax, max_vmax)
                                                                              └─ Yujie111UpdateLeaf(opt_node, opt_laba, opt_vmax)
                                                                              └─ opt_cica = Yujie111GetAnnualCICA(opt_node, weat_days)
                                                                              └─ println("Finished year ", year, "!")
                                                                              └─ return [opt_laba opt_vmax opt_prof opt_cica{:}]
                                                                              └─ 37 end
                                                                              └─ 38
                                                                              └─ # run the simulations
                                                                              └─ 40 yeardays = []
                                                                              └─ for i in 1:length(years)
                                                                              └─ | append!(yeardays, [[years[i] day_s[i] day_e[i]]])
                                                                              └─ 42 end
                                                                              └─ 44 #println(yeardays)
                                                                              └─ result = pmap(GetOptimaForYear, yeardays)
                                                                              └─ 46 writedln(filename, result)
                                                                              └─ 47
                                                                              └─ 48 return result
                                                                              └─ 49 end
```

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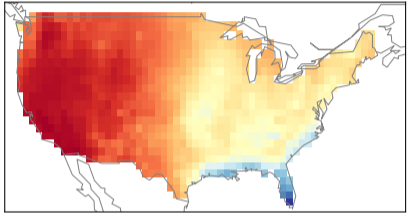
Trait shifts

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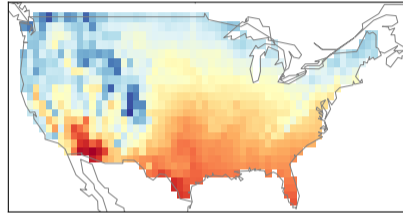
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Sensitivity to climate

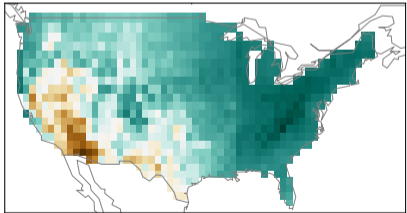
Mean growing season precipitation (mm)



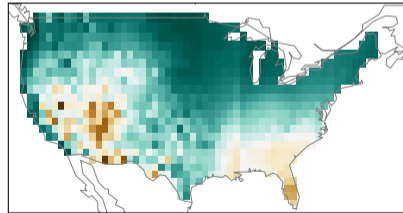
Mean growing season temperature (°C)



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



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



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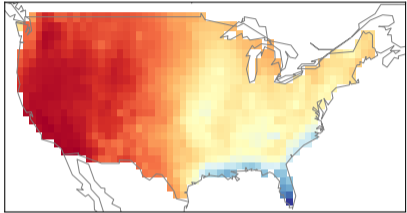
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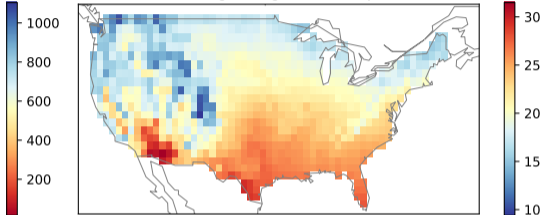
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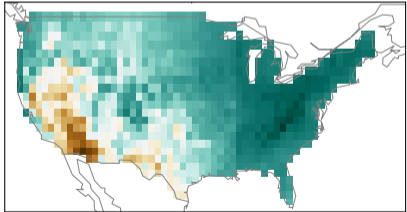
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Mean growing season temperature (°C)



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



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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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CLIMATE MODELING ALLIANCE



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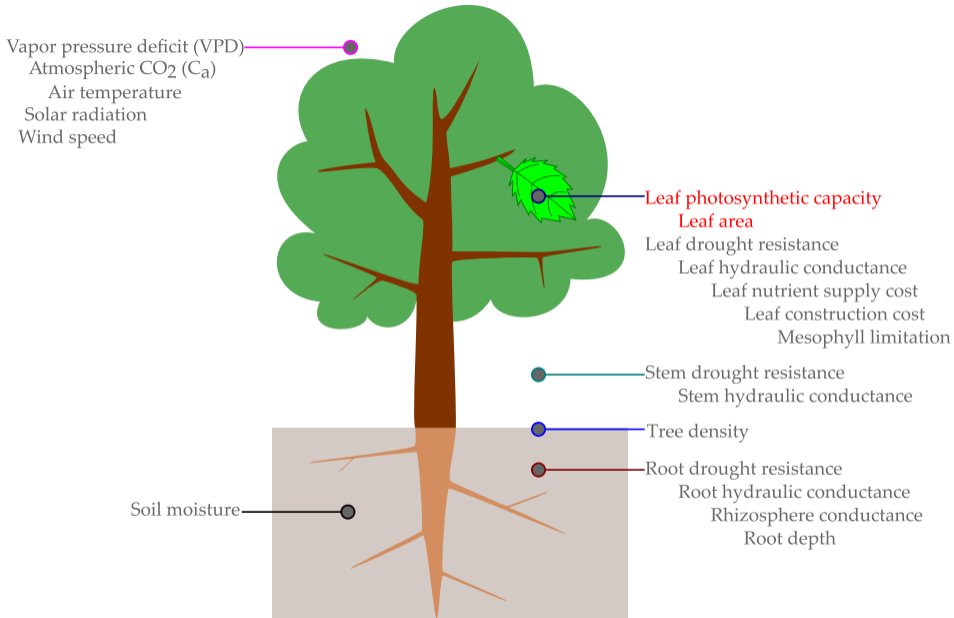
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Acknowledgments

Supervisory committee

- ▶ John Sperry
- ▶ Bill Anderegg
- ▶ Fred Adler
- ▶ David Bowling
- ▶ Jim Ehleringer
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