Improve leaf gas exchange modeling with gain vs. risk optimization

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University of Utah

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Why we model leaf gas exchange?*

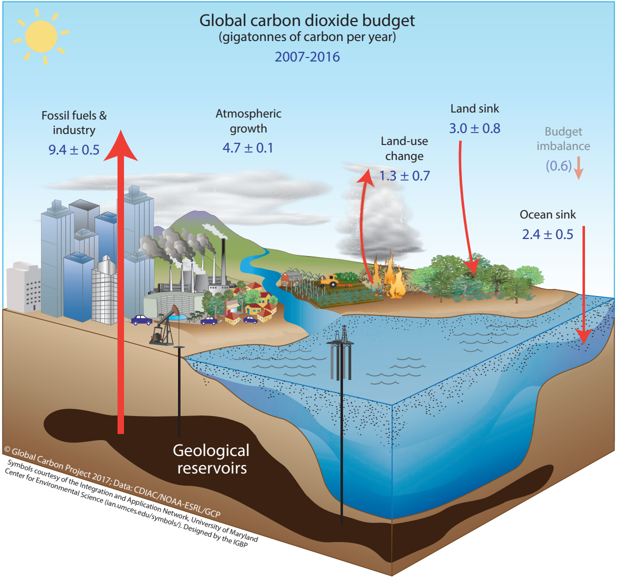

*Figure from Le Quéré et al. (2018)

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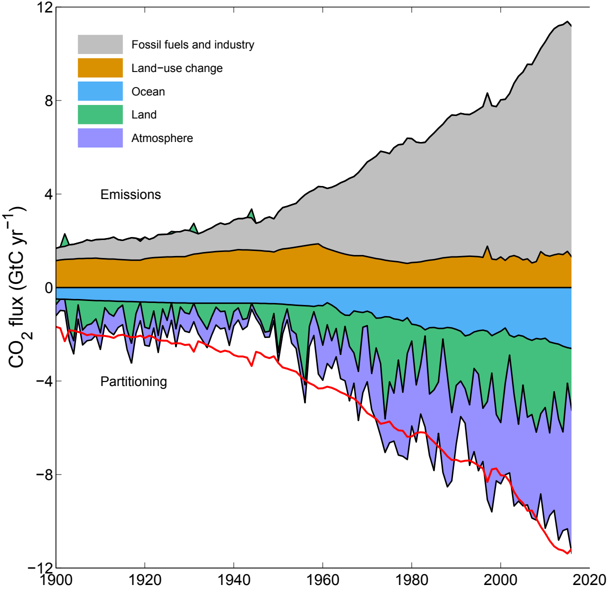


*Figure from Le Quéré et al. (2018)

Why we model leaf gas exchange?*

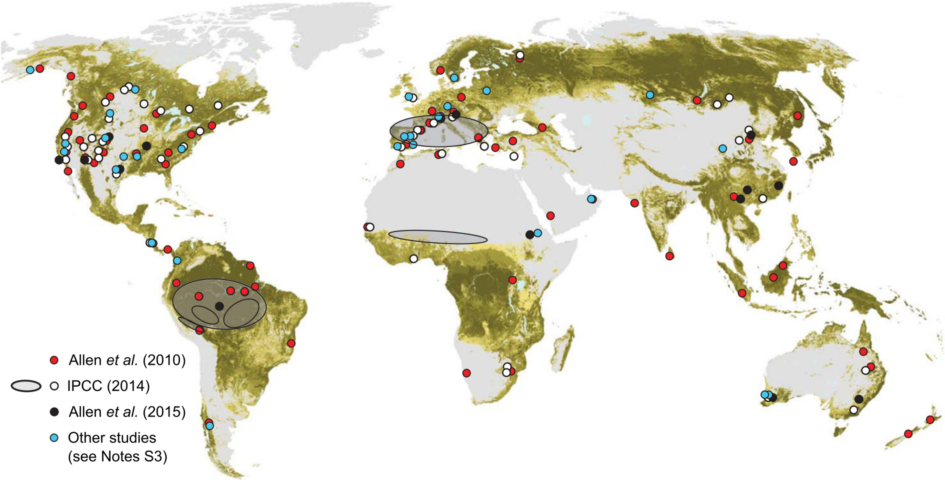
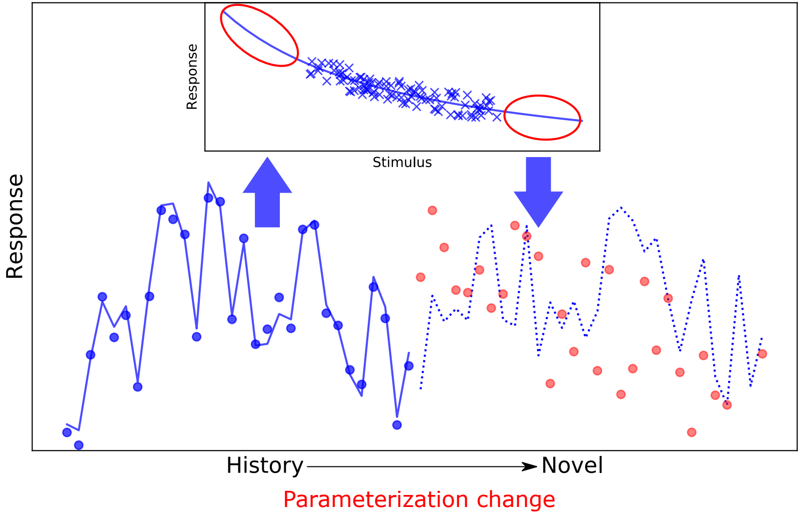
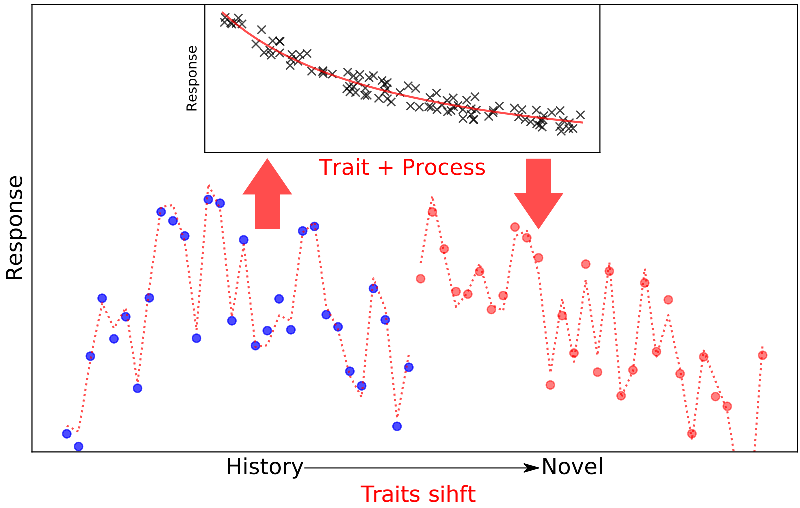


*Figure from Hartmann et al. (2018)

Empirical approach — curve fitting

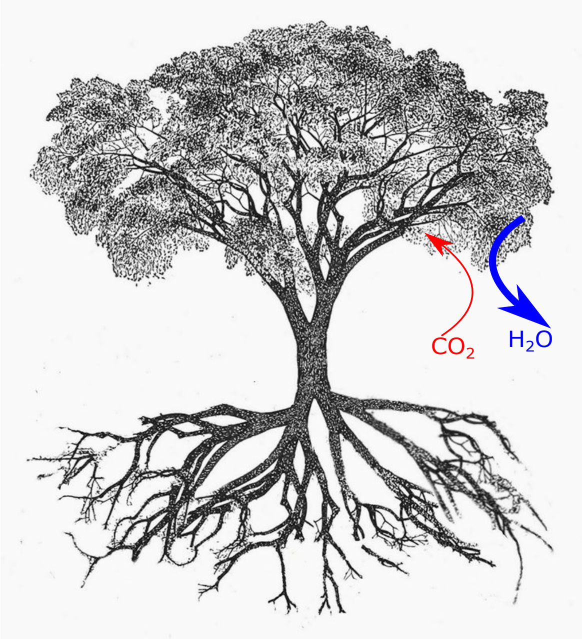


Optimality approach — goal oriented

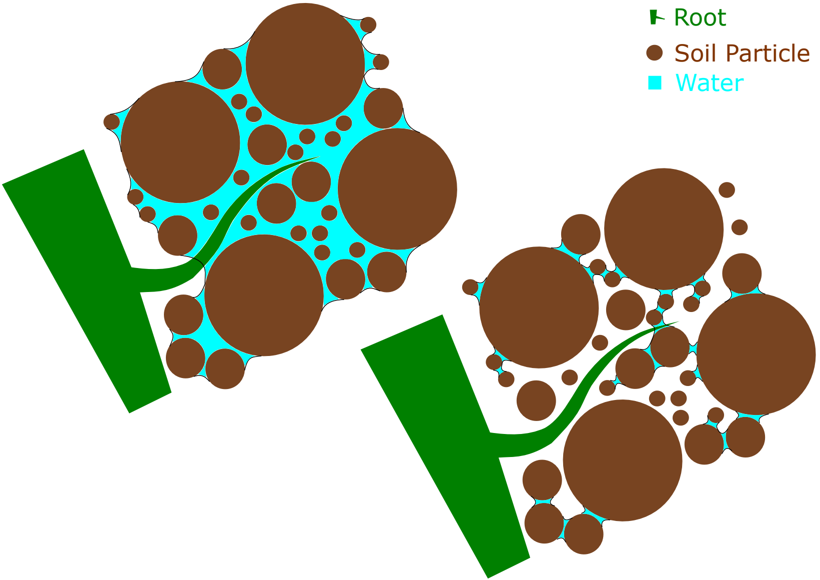


Trees have to use water

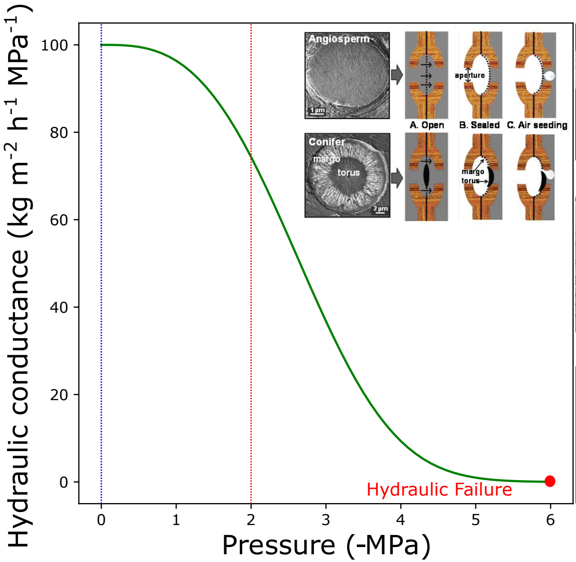
- H_2O is smaller
- H_2O gradient is higher

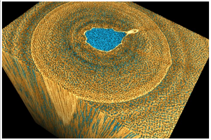


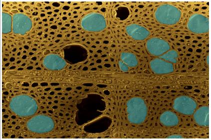
Root water uptake



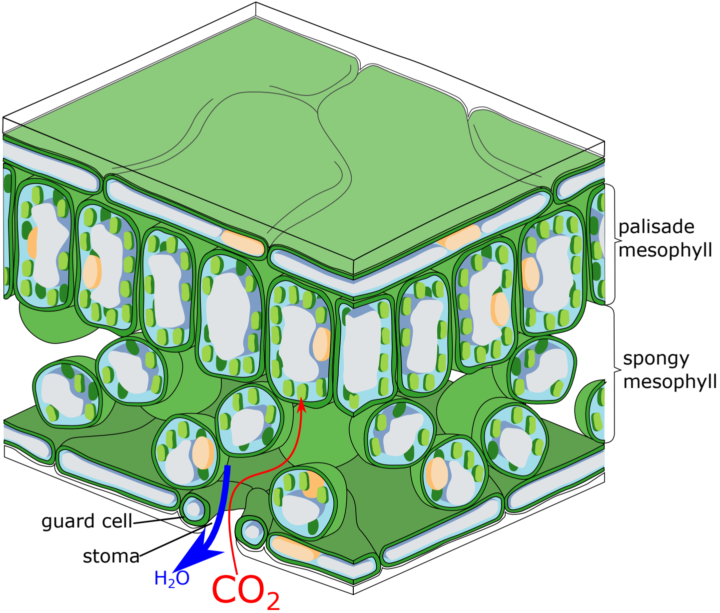
Xylem water transport



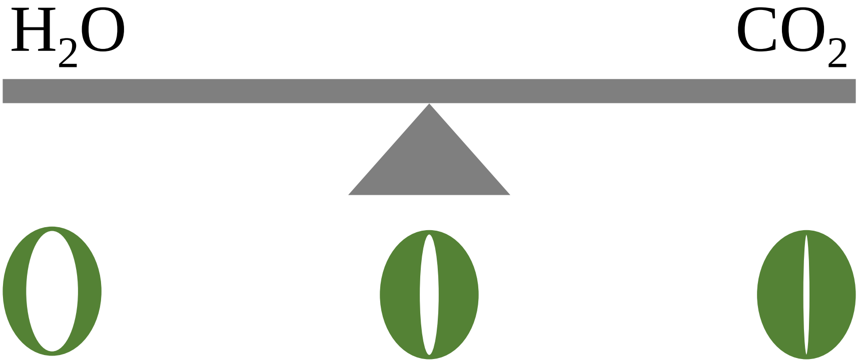




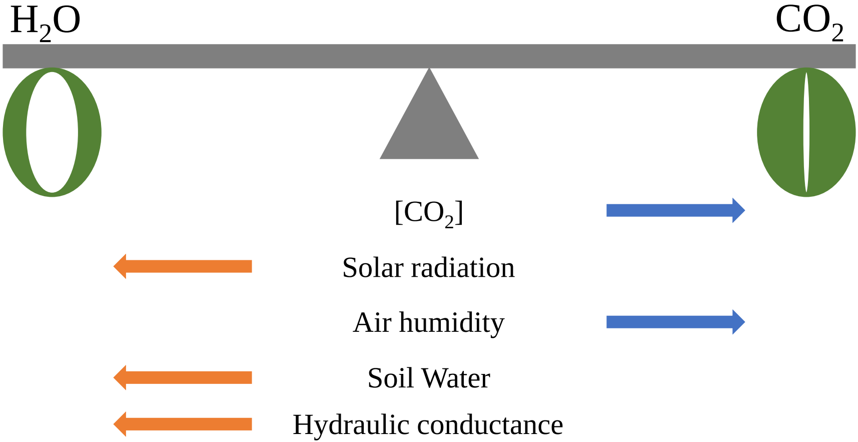
Leaf gas exchange



Water for carbon trade-off



Water for carbon trade-off



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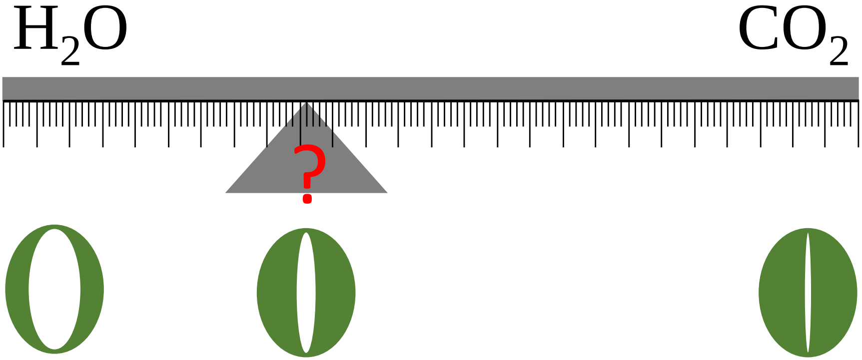
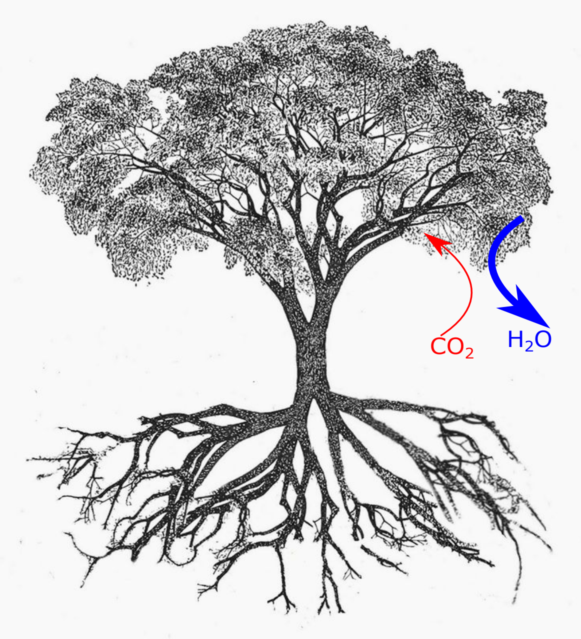


Benefit from water use

Photosynthesis — $\boldsymbol{A}$.

Costs/Risks from water use — Θ

- Efficiency
- Transport
- Resource



Optimal water use*

$$max(A - \Theta)$$

$$\Downarrow$$

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

*Wolf et al. (2016)

What is A or $\frac{dA}{dx}$?

What is Θ or $\frac{d\Theta}{dx}$?

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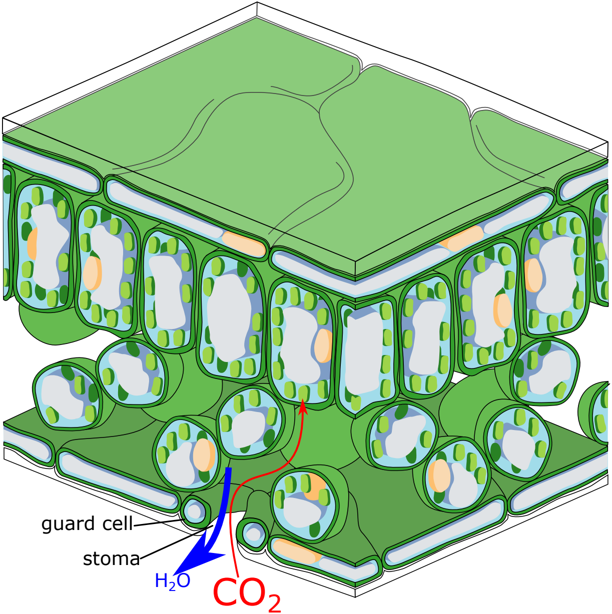
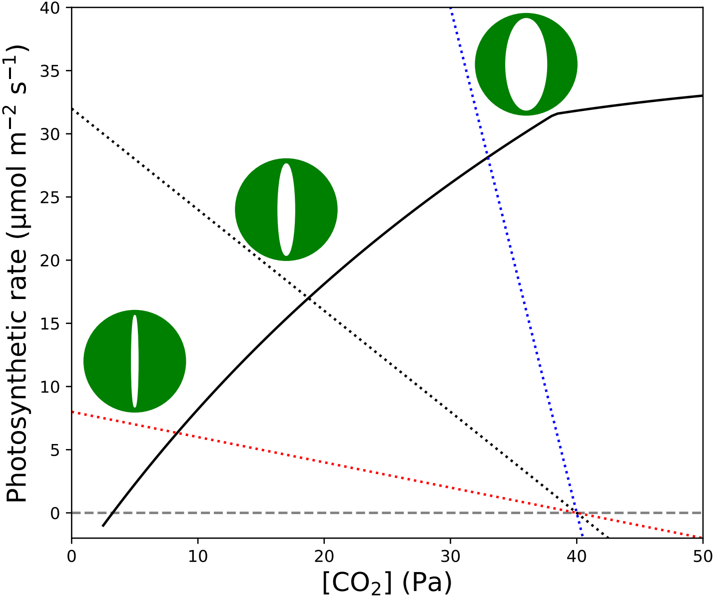
Leaf gas exchange



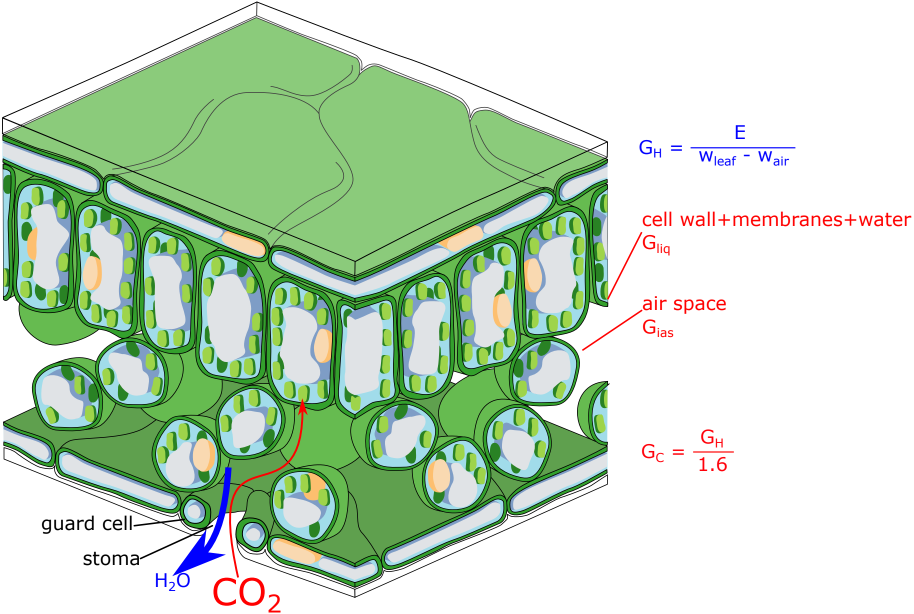
$$G_H = \frac{E}{w_{leaf} - w_{air}}$$

$$G_C = \frac{G_H}{1.6}$$

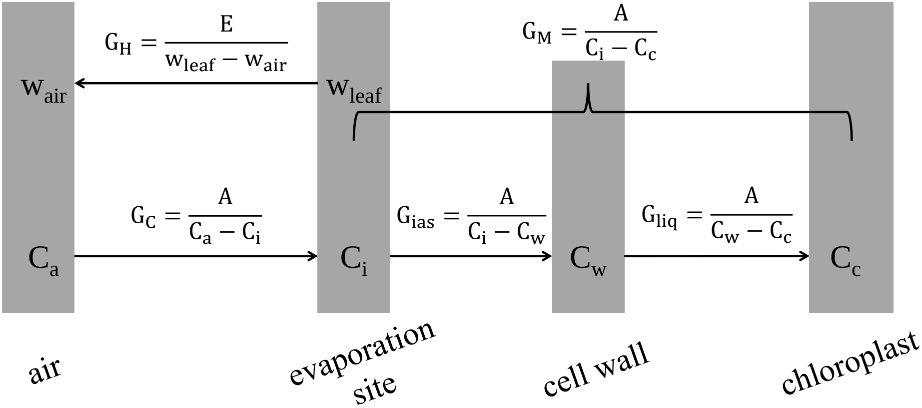
Leaf gas exchange



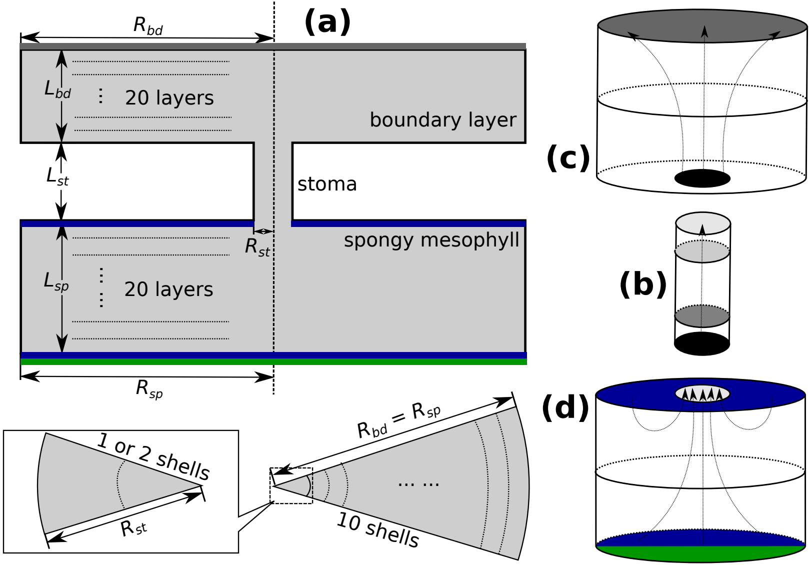
The neglected mesophyll conductance



Leaf gas exchange



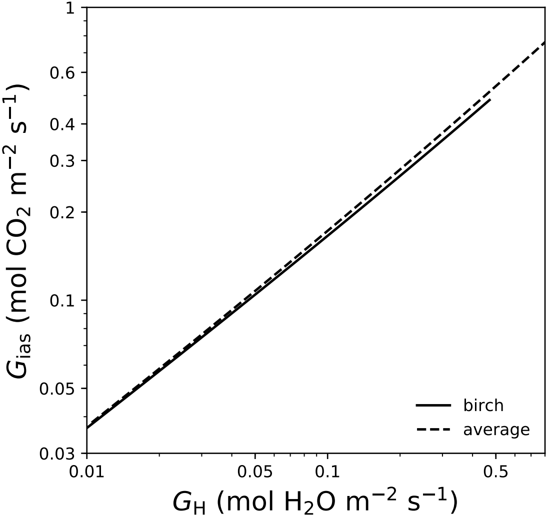
G_{ias} model*



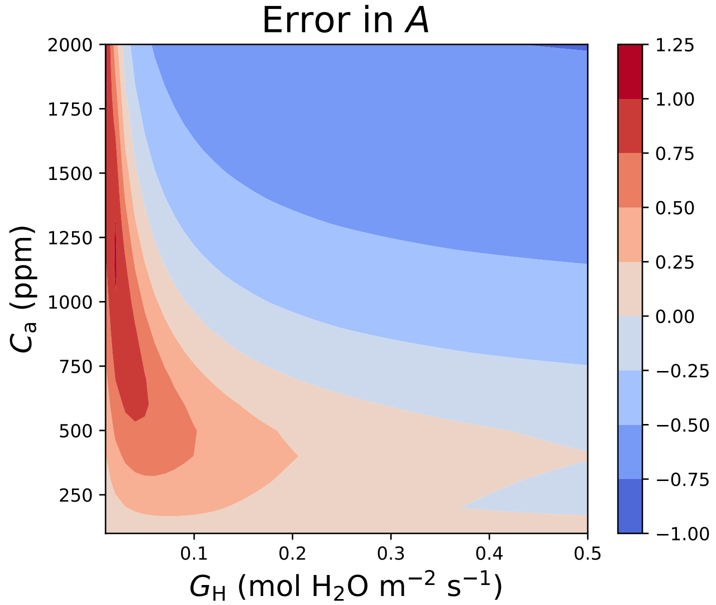
*Wang et al., (in review)

G_{ias} vs G_H

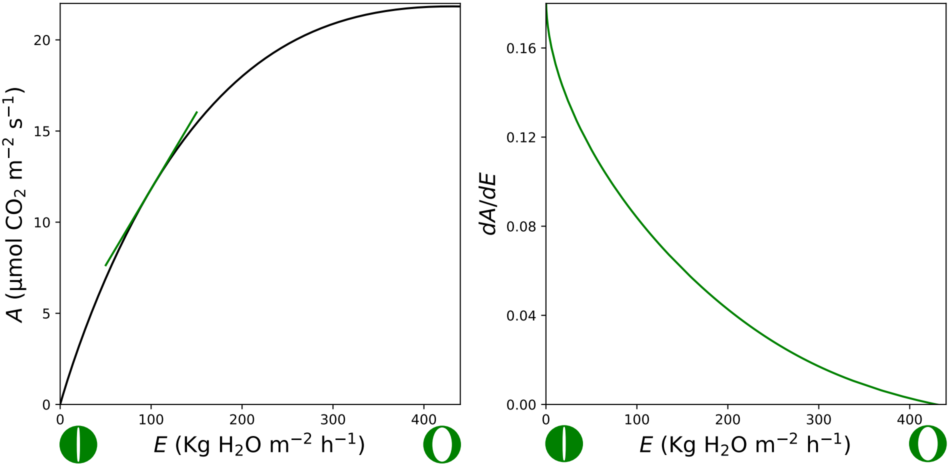
$$G_{ias} = a \cdot G_H^b$$



Estimation of A



Shape of A and dA/dE (α)



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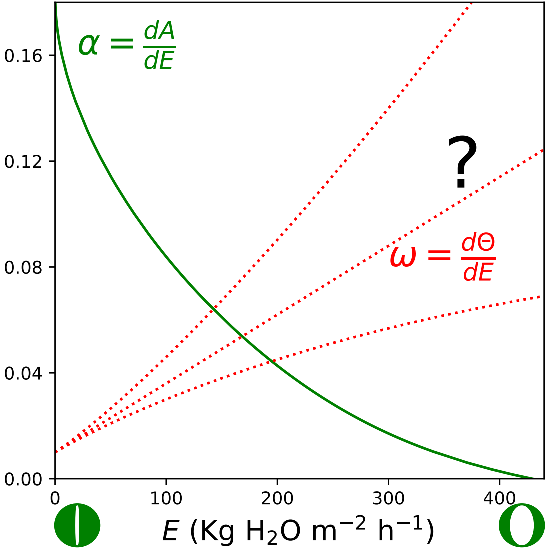
Optimality

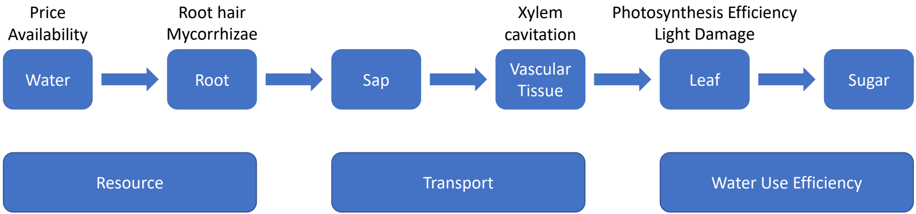
$$\alpha = \omega$$



Requirements for ω

1. $\omega > 0$
2. $\omega < \alpha$ when $E = 0$
3. $\omega \Uparrow$ when $E \Uparrow$

Sources for risk



Requirements* for marginal risk ($\omega = \frac{d\Theta}{dE}$)

1. $\omega > 0$
2. $\omega < \alpha$ when $E = 0$
3. $\omega \Uparrow$ when $E \Uparrow$
4. $\omega \Uparrow$ when soil gets drier
5. $\omega \Uparrow$ when $[CO_2] \Uparrow$
6. $\omega \Uparrow$ when air gets wetter
7. $\omega \Uparrow$ when hydraulic conductance $\Downarrow$

*Wang et al. (in prep)

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Optimization models

Model	Reference	Optimization Criterion	Risk	Marginal water price	Response to				Fitting Parameters
					C_a	D	P_{soil}	K	
CF	(Cowan & Farquhar 1977)	$\max(\int_0^{t_{total}} A \cdot dt)$ $\int_0^{t_{total}} E \cdot dt = E_{total}$	$\Theta = \lambda E$	$\omega = \lambda$	N	N	N	N	λ
Manzoni	(Manzoni et al. 2013)	$\max(\int_0^{t_{total}} A \cdot dt + A_{RE})$ $\int_0^{t_{total}} E \cdot dt = E_{total}$ $A_{RE} = \Lambda \cdot E_{remain}$	$\Theta = \Lambda E$	$\omega = \Lambda$	N	N	N	N	Λ
Prentice	(Prentice et al. 2014)	$\min\left(\frac{c_E E + c_V V_{cmax}}{A}\right)$ $c_E = \frac{con_E}{E}$	$\Theta = 0$	$\omega = 0$	N	N	N	N	c_E, c_V
Lu	(Lu et al. 2016)	$\max(f(P_{soil}) \cdot A(P_{soil}))$	$\Theta = \lambda E$	$\omega = \lambda$	N	N	N	N	λ
Hölttä	(Hölttä et al. 2017)	$\max(A)$ $A = A_{ww} \cdot \left(1 - \frac{SC}{SC_{max}}\right)$	$\Theta' = A_{ww} \cdot \frac{SC}{SC_{max}}$	$\omega' = \frac{A}{SC_{max} - SC} \cdot \frac{dSC}{dE}$	Y/N	Y/N	Y/N	Y/N	SC_{max}, phloem parameters
Huang	(Huang et al. 2018)	$\max(K_{xp} \cdot S_{xp} \cdot [P_{xy} - P_{ph}] \cdot SC_{ph})$	$\Theta = 0$	$\omega = 0$	N	N	N	N	S_{xp}, K_{xp}
Dewar CAP	(Dewar et al. 2018)	$\max(A)$ $A = A_{ww} \cdot \left(1 - \frac{P}{P_{crit}}\right)$	$\Theta' = A_{ww} \cdot \frac{P}{P_{crit}}$	$\omega' = \frac{A}{K \cdot (P_{crit} - P)}$	N	N	Y	N	
WAP	(Wolf et al. 2016; Anderegg et al. 2018)	$\max(A - \Theta)$	$\Theta = aP^2 + bP + c$	$\omega = \frac{2aP + b}{K}$	N	N	Y/N	Y/N	a, b
Sperry	(Sperry et al. 2017)	$\max\left(\frac{A}{A_{max}} - 1 + \frac{K}{K_{max}}\right)$	$\Theta = A_{max} \cdot \left(1 - \frac{K}{K_{max}}\right)$	$\omega = -\frac{dK}{dE} \cdot \frac{A_{max}}{K_{max}}$	Y	Y	Y	N	
Eller	(Eller et al. 2018)	$\max\left(A \cdot \frac{K}{K_{max,0}}\right)$	$\Theta = A \cdot \left(1 - \frac{K}{K_{max,0}}\right)$	$\omega = -\frac{dK}{dE} \cdot \frac{A}{K}$	Y	Y	Y	N	
Wang		$\max\left(A \cdot \left(1 - \frac{E}{E_{crit}}\right)\right)$	$\Theta = A \cdot \frac{E}{E_{crit}}$	$\omega = \frac{A}{E_{crit} - E}$	Y	Y	Y	Y	

Example 1: Cowan and Farquhar model*

Criterion

$$max(A - \lambda E)$$

Risk

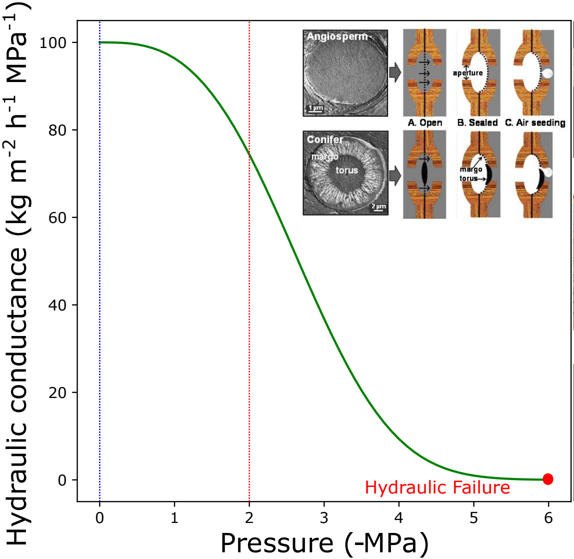
$$\omega = \lambda$$

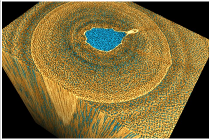
*Cowan and Farquhar (1977)

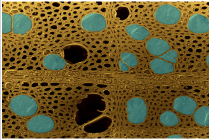
Cowan and Farquhar model marginal risk (ω)

1. $\omega > 0$
2. $\cancel{\omega < \alpha \text{ when } E = 0}$
3. $\cancel{\omega \Uparrow \text{ when } E \Uparrow}$
4. $\cancel{\omega \Uparrow \text{ when soil gets drier}}$
5. $\cancel{\omega \Uparrow \text{ when } [CO_2] \Uparrow}$
6. $\cancel{\omega \Uparrow \text{ when air gets wetter}}$
7. $\cancel{\omega \Uparrow \text{ when hydraulic conductance } \Downarrow}$

The consequence of transpiration







Example 2: Sperry model*

Criterion

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

Risk

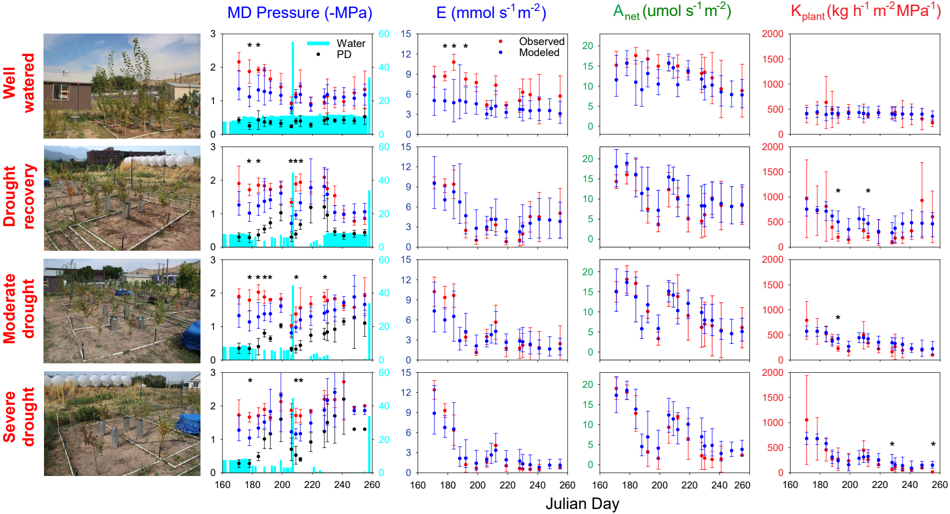
$$\omega = -\frac{dK}{dE} \cdot \frac{A_{\max}}{K_{\max}}$$

*Sperry et al. (2017)

Sperry model marginal risk (ω)

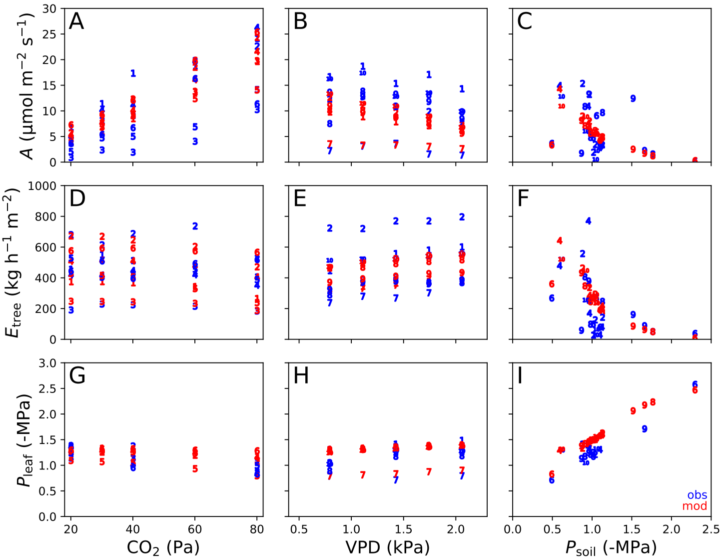
1. $\omega > 0$
2. $\omega < \alpha$ when $E = 0$
3. $\omega \Uparrow$ when $E \Uparrow$
4. $\omega \Uparrow$ when soil gets drier
5. $\omega \Uparrow$ when $[\mathrm{CO_2}] \Uparrow$
6. $\omega \Uparrow$ when air gets wetter
7. ~~$\omega \Uparrow$ when hydraulic conductance $\Downarrow$~~

Test Sperry model*



*Venturas et al. (2018)

Test Sperry model*



*Wang et al. (2019)

Example 3: Wang model *

Criterion

$$max(A - A \cdot \frac{E}{E_{\mathrm{crit}}})$$

Risk

$$\omega = \frac{A}{E_{\mathrm{crit}} - E}$$

* Wang et al. (in prep)

Wang model marginal risk (ω)

1. $\omega > 0$
2. $\omega < \alpha$ when $E = 0$
3. $\omega \Uparrow$ when $E \Uparrow$
4. $\omega \Uparrow$ when soil gets drier
5. $\omega \Uparrow$ when $[\mathrm{CO_2}] \Uparrow$
6. $\omega \Uparrow$ when air gets wetter
7. $\omega \Uparrow$ when hydraulic conductance $\Downarrow$

Model performances

Model	MAPE for birch (%)	MAPE for aspen (%)
CF	41.1	43.9
Manzoni	41.1	43.9
Prentice	226.8	267.8
Modified Prentice	38.4	43.2
Lu	41.1	43.9
Hölttä	-	-
Huang	226.8	267.8
Dewar CAP	82.5	76.4
WAP	29.7	23.8
Sperry	26.8	29.7
Eller	28.8	29.0
Wang	28.1	29.2

Optimization models

Model	Reference	Optimization Criterion	Risk	Marginal water price	Response to				Fitting Parameters
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WAP	(Wolf et al. 2016; Anderegg et al. 2018)	$\max(A - \Theta)$	$\Theta = aP^2 + bP + c$	$\omega = \frac{2aP + b}{K}$	N	N	Y/N	Y/N	a, b
Sperry	(Sperry et al. 2017)	$\max\left(\frac{A}{A_{max}} - 1 + \frac{K}{K_{max}}\right)$	$\Theta = A_{max} \cdot \left(1 - \frac{K}{K_{max}}\right)$	$\omega = -\frac{dK}{dE} \cdot \frac{A_{max}}{K_{max}}$	Y	Y	Y	N	
Eller	(Eller et al. 2018)	$\max\left(A \cdot \frac{K}{K_{max,0}}\right)$	$\Theta = A \cdot \left(1 - \frac{K}{K_{max,0}}\right)$	$\omega = -\frac{dK}{dE} \cdot \frac{A}{K}$	Y	Y	Y	N	
Wang		$\max\left(A \cdot \left(1 - \frac{E}{E_{crit}}\right)\right)$	$\Theta = A \cdot \frac{E}{E_{crit}}$	$\omega = \frac{A}{E_{crit} - E}$	Y	Y	Y	Y	

Conclusions on optimization model

To predict realistic stomatal behavior, ω must meet these requirements.

1. $\omega > 0$
2. $\omega < \alpha$ when $E = 0$
3. $\omega \Uparrow$ when $E \Uparrow$
4. $\omega \Uparrow$ when soil gets drier
5. $\omega \Uparrow$ when $[\mathrm{CO_2}] \Uparrow$
6. $\omega \Uparrow$ when air gets wetter
7. $\omega \Uparrow$ when hydraulic conductance $\Downarrow$

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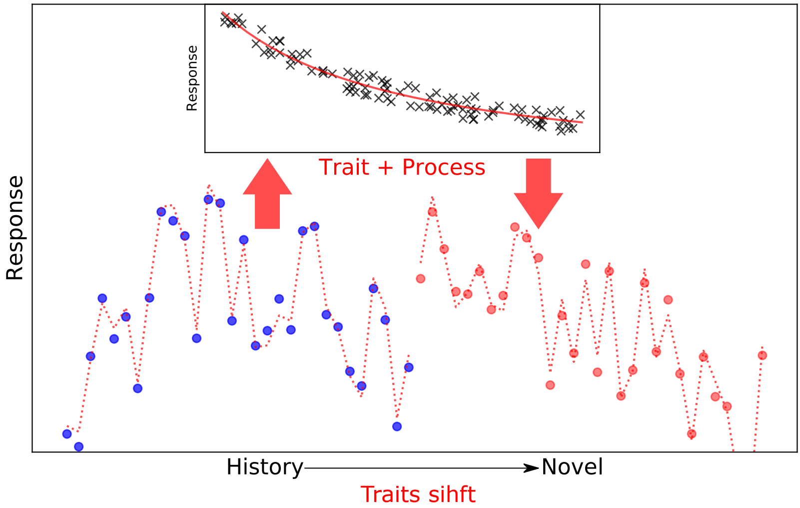
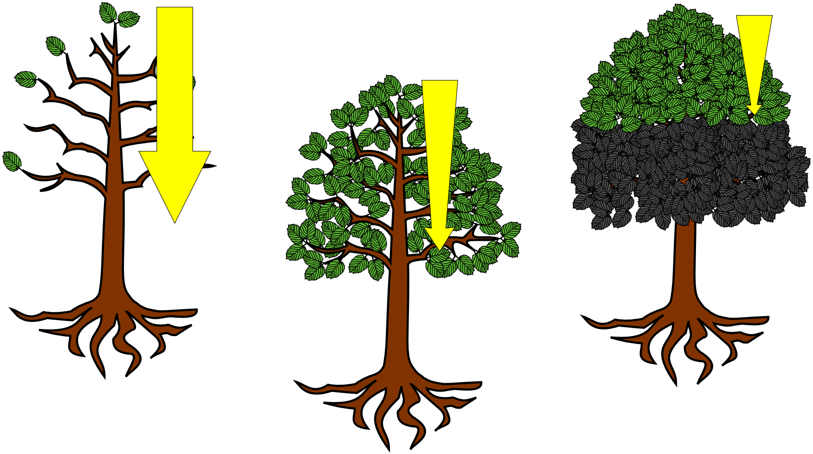
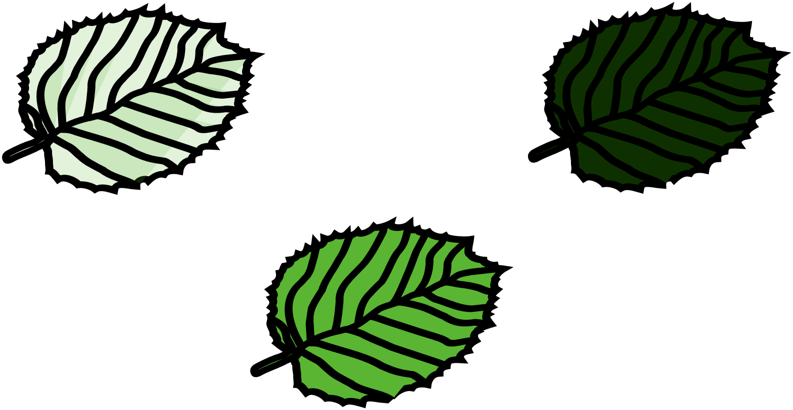
How to model the changing traits



Optimal leaf area



Optimal leaf photosynthesis



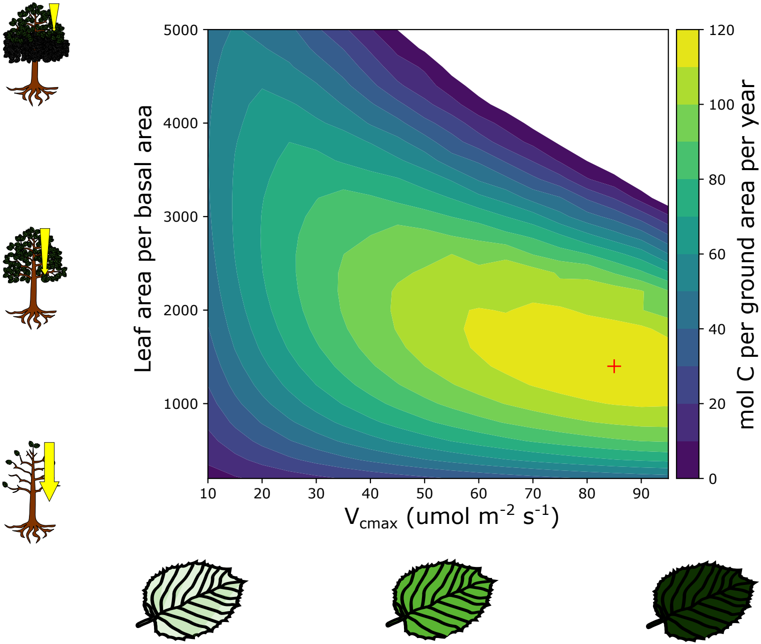
Optimal leaf investment*

Optimization criterion

$$max\left(\int A_{\mathrm{day}} - \int R_{\mathrm{night}} - C_{\mathrm{carbon}} - C_{\mathrm{nutrient}}\right)$$

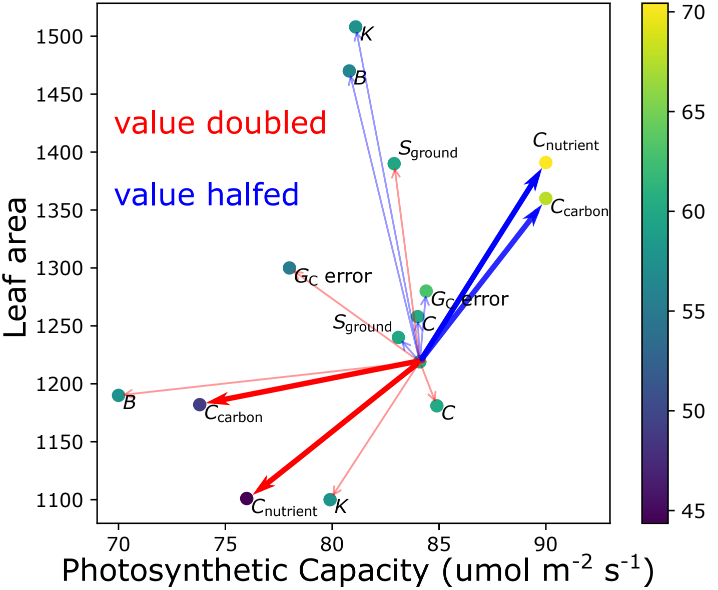
A_{day}	Net photosynthetic rate in the day
R_{night}	Respiratory rate in the night
C_{carbon}	Construction cost for carbon, $\propto$ leaf area
C_{nutrient}	Nutrient cost, $\propto$ leaf area $\times$ photosynthetic capacity

* Wang et al., (in prep)

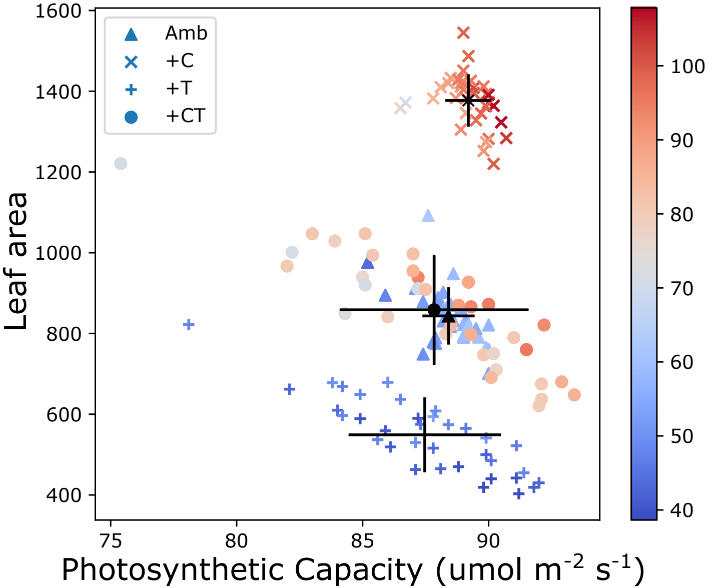


5000
4000
3000
2000
1000
Leaf area per basal area
10
20
30
40
50
60
70
80
90
Vcmax (umol m-2 s-1)
120
100
80
60
40
20
0
mol C per ground area per year

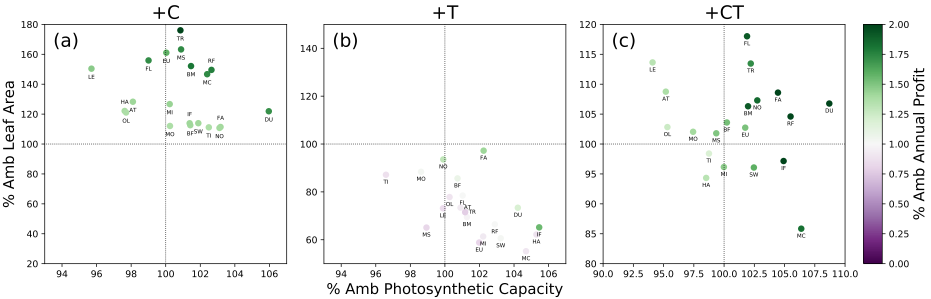
Optimal leaf investment vs. traits



Optimal leaf investment vs. climate



Optimal leaf investment shift



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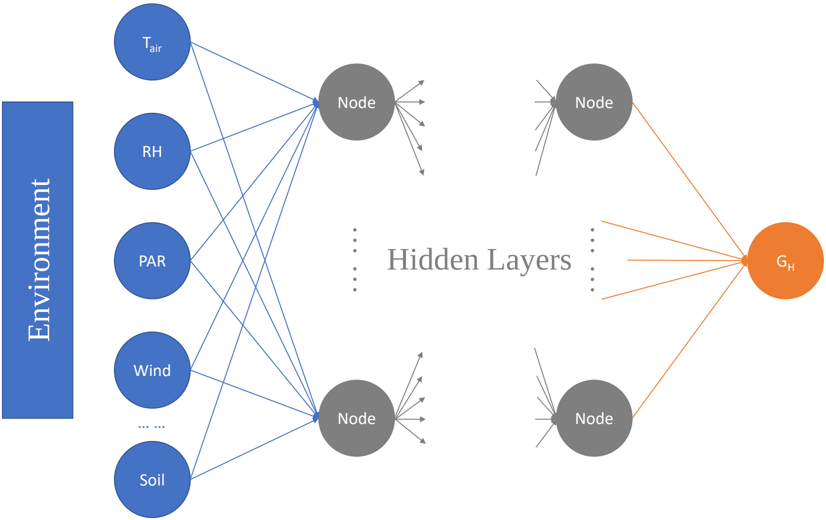
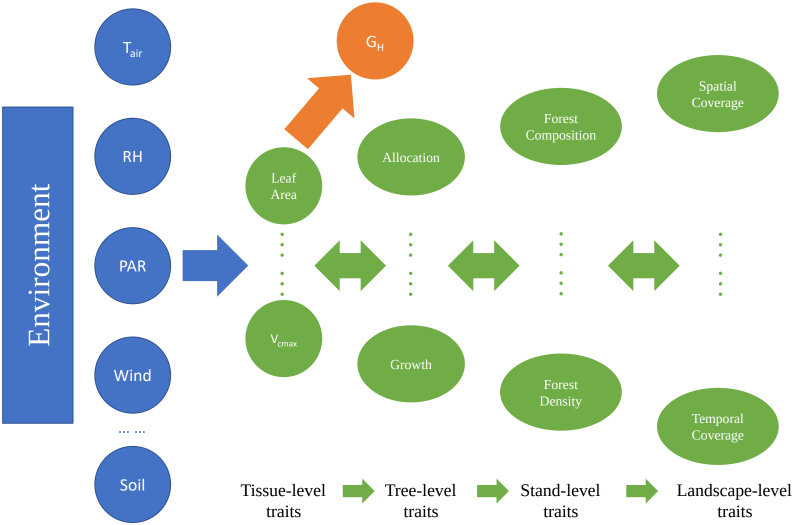
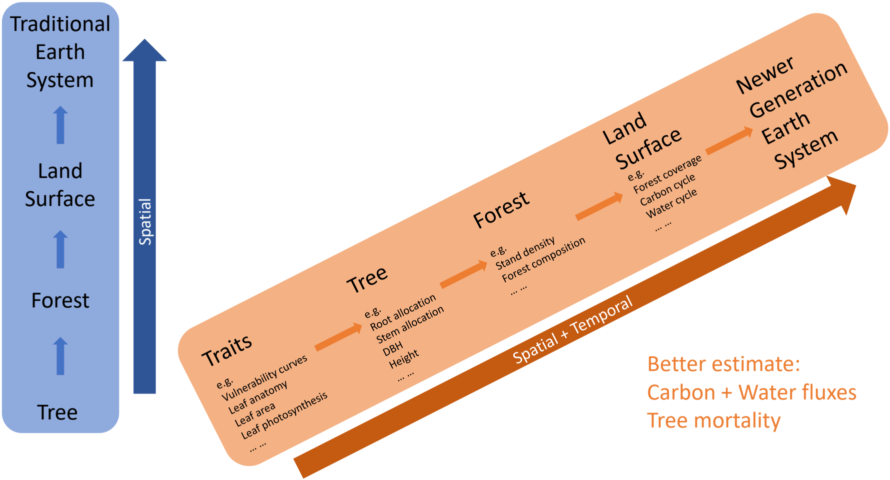
Empirically "learn" from history



Mechanistically “learn” from history



'Orange'print



Better estimate:
Carbon + Water fluxes
Tree mortality

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
- Grayson Badgley

THANKS