Modeling optimal leaf area and photosynthetic capacity from plant traits and climate

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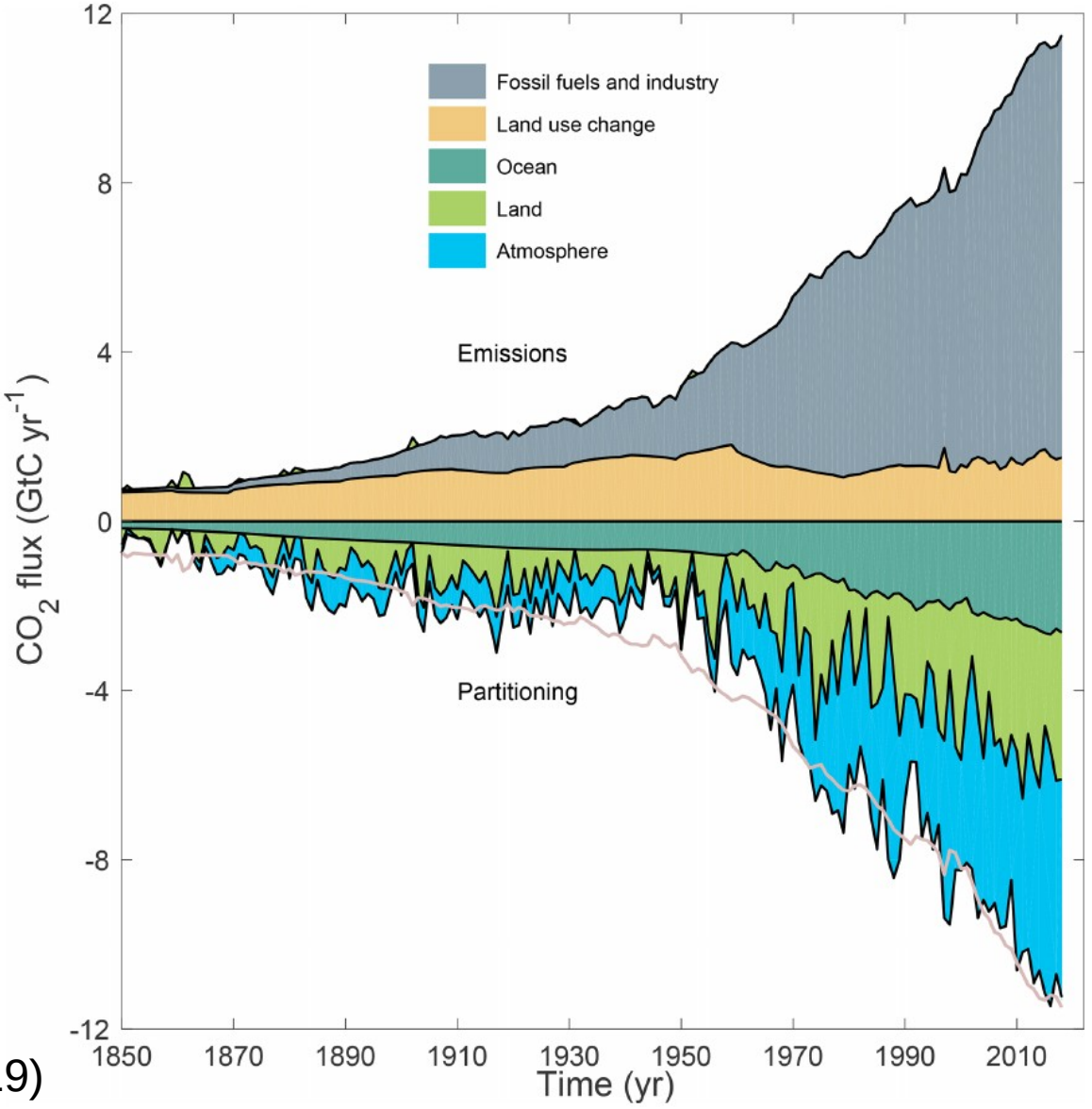
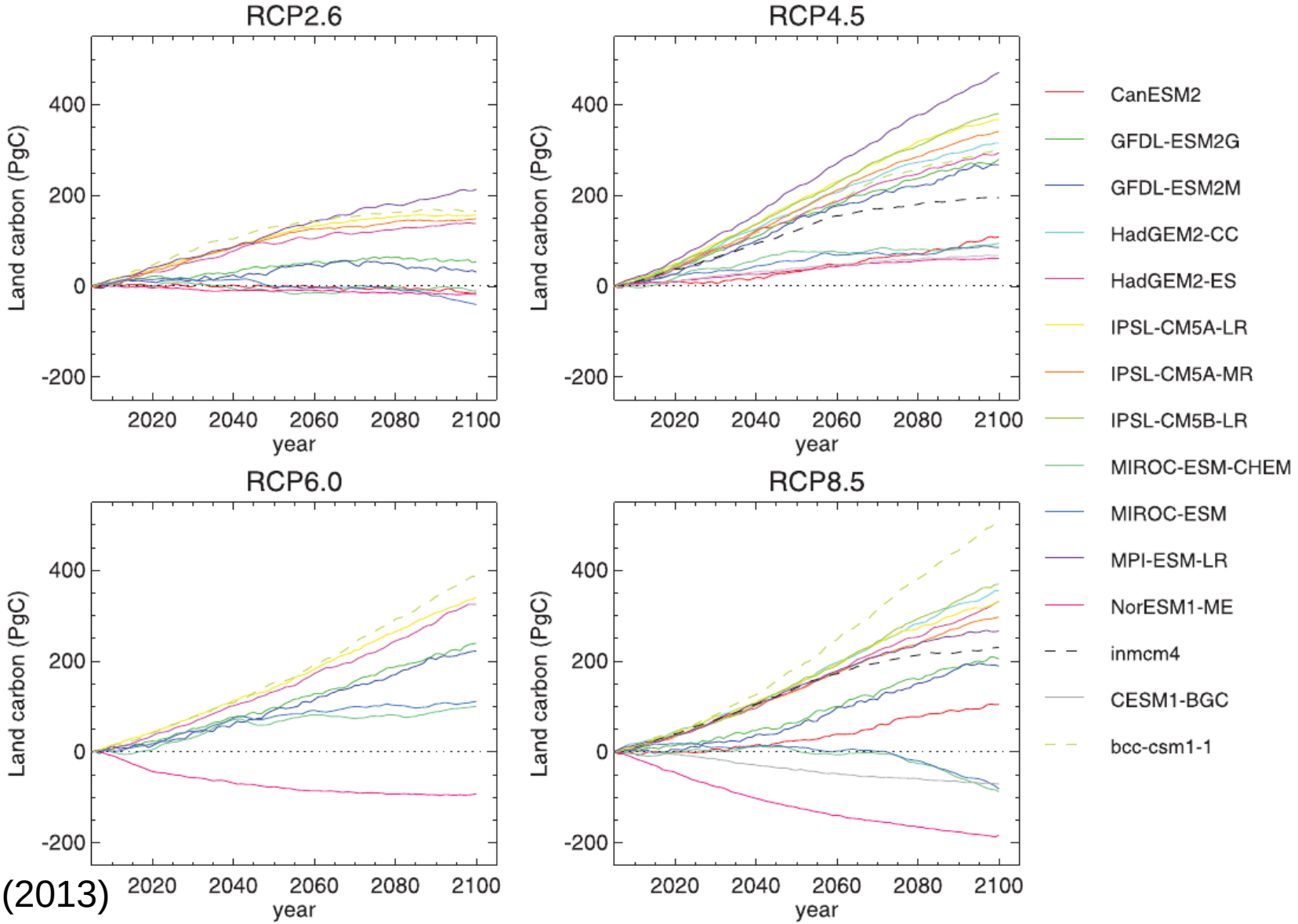


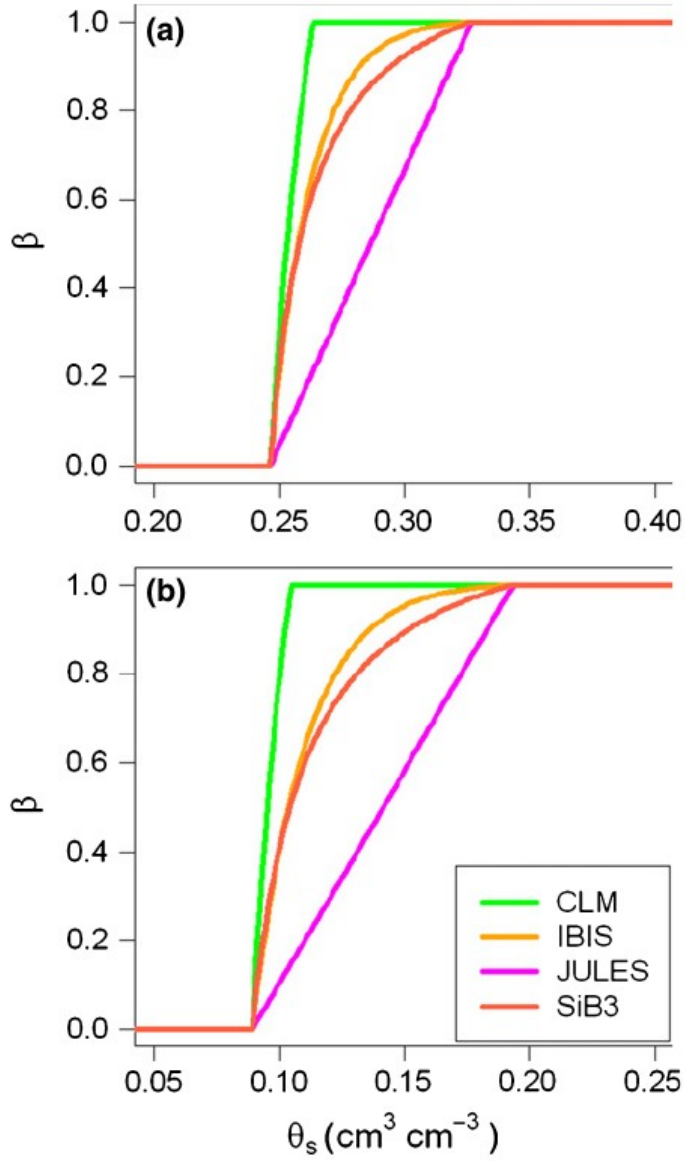
Friedlingstein et al. (2019)



Jones et al. (2013)

Stomatal behavior

- Ball-Berry model: $G = g0 + g1 * RH * A / Cs$
- Leuning model: $G = g0 + g1 * A / (Cs - \Gamma) / (1 + VPD/d0)$
- Medlyn model: $G = g0 + 1.6 * (1 + g1/\sqrt{D}) * A / Ca$
- … …

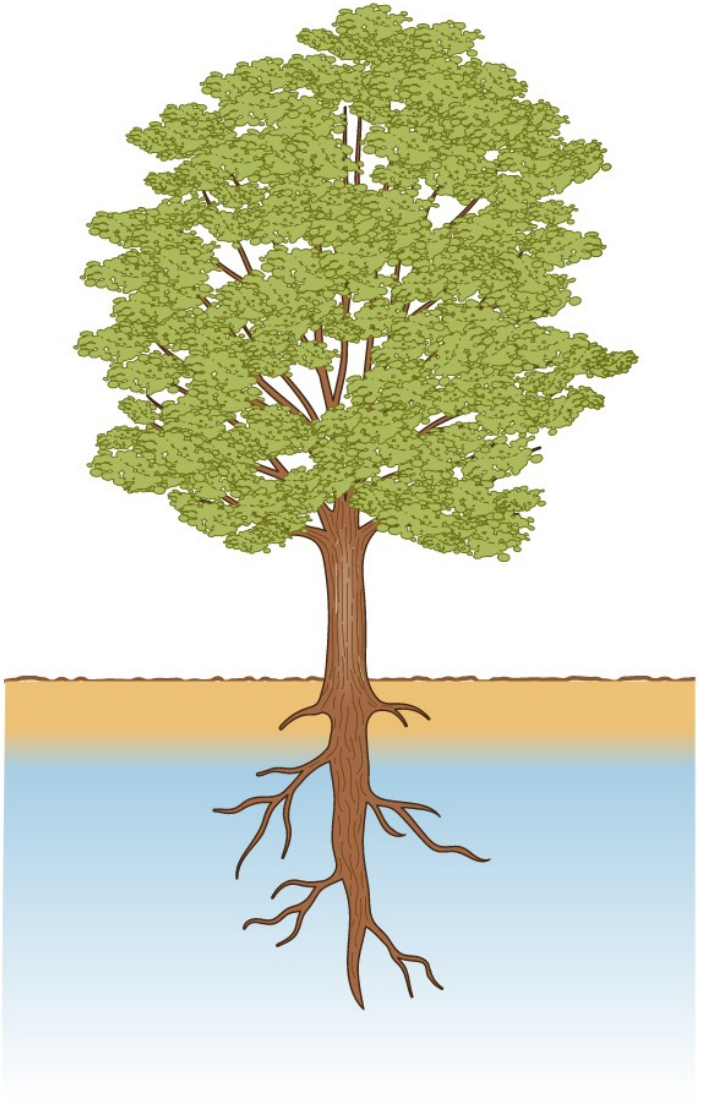


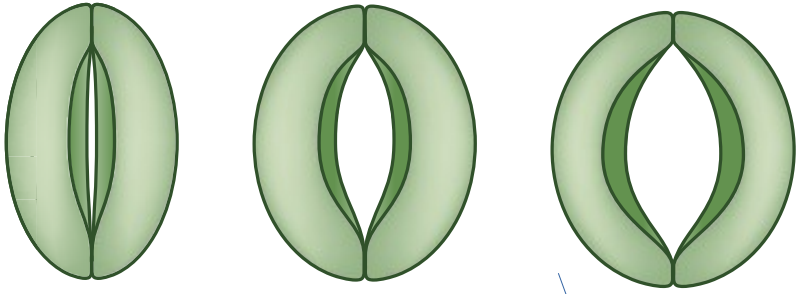
Powell et al. (2013)

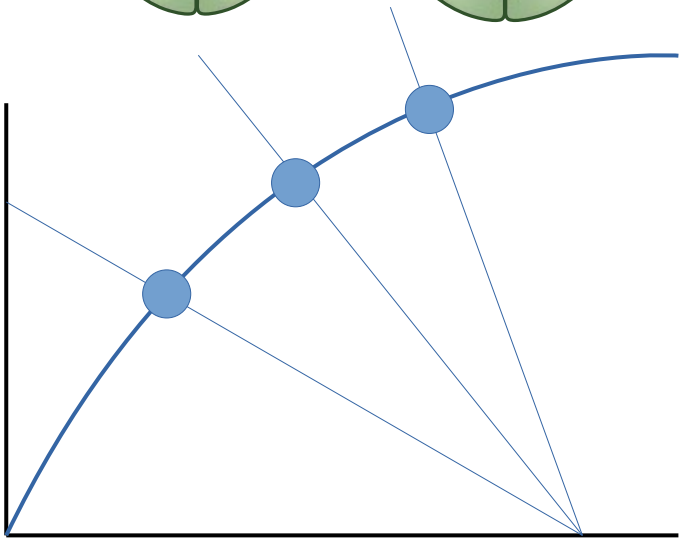
- PROBLEMS
- Environment is changing
- Plants are changing
- KEYS
- Better modeling of the climate
- Better parameterization of plants

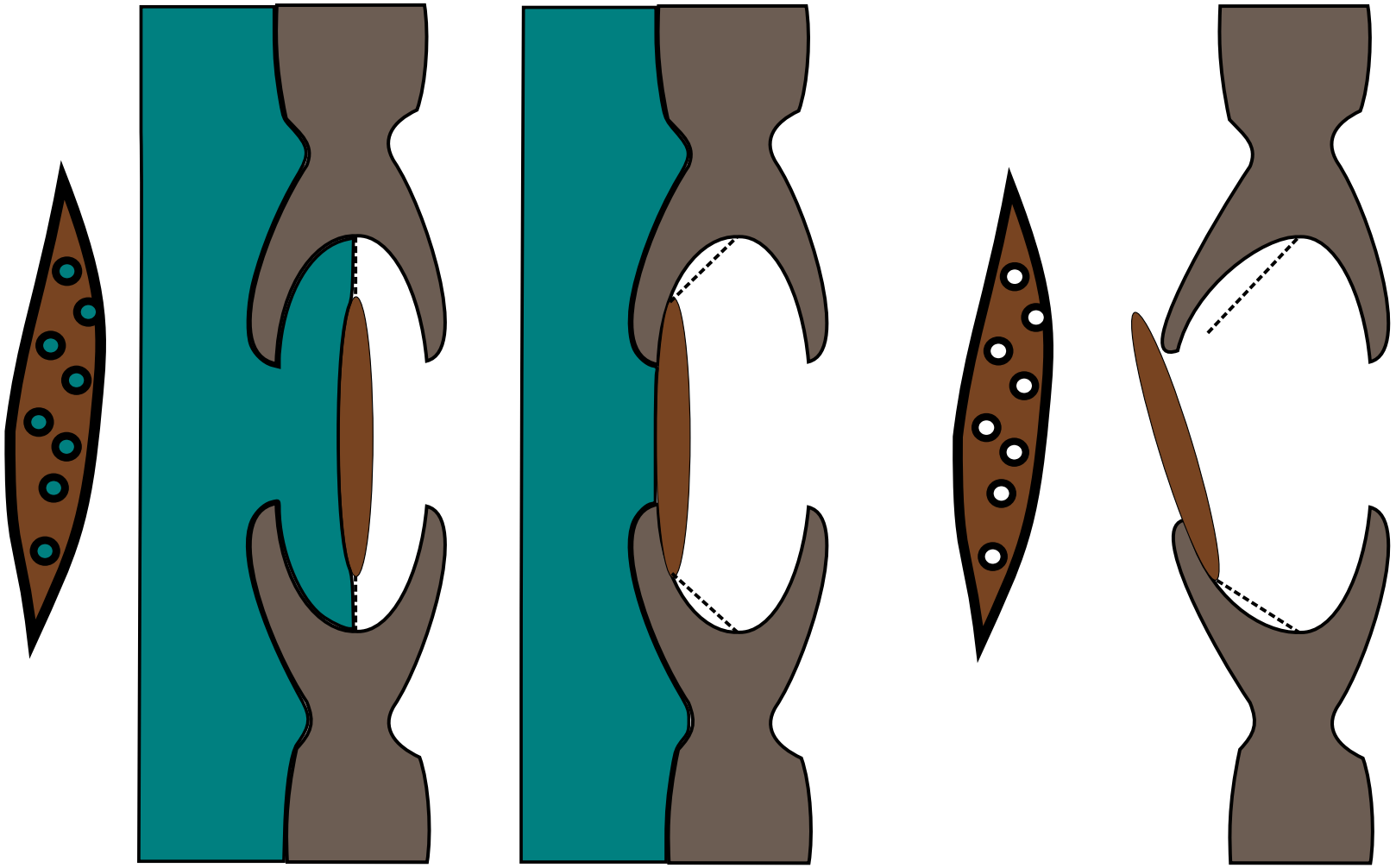
First Step

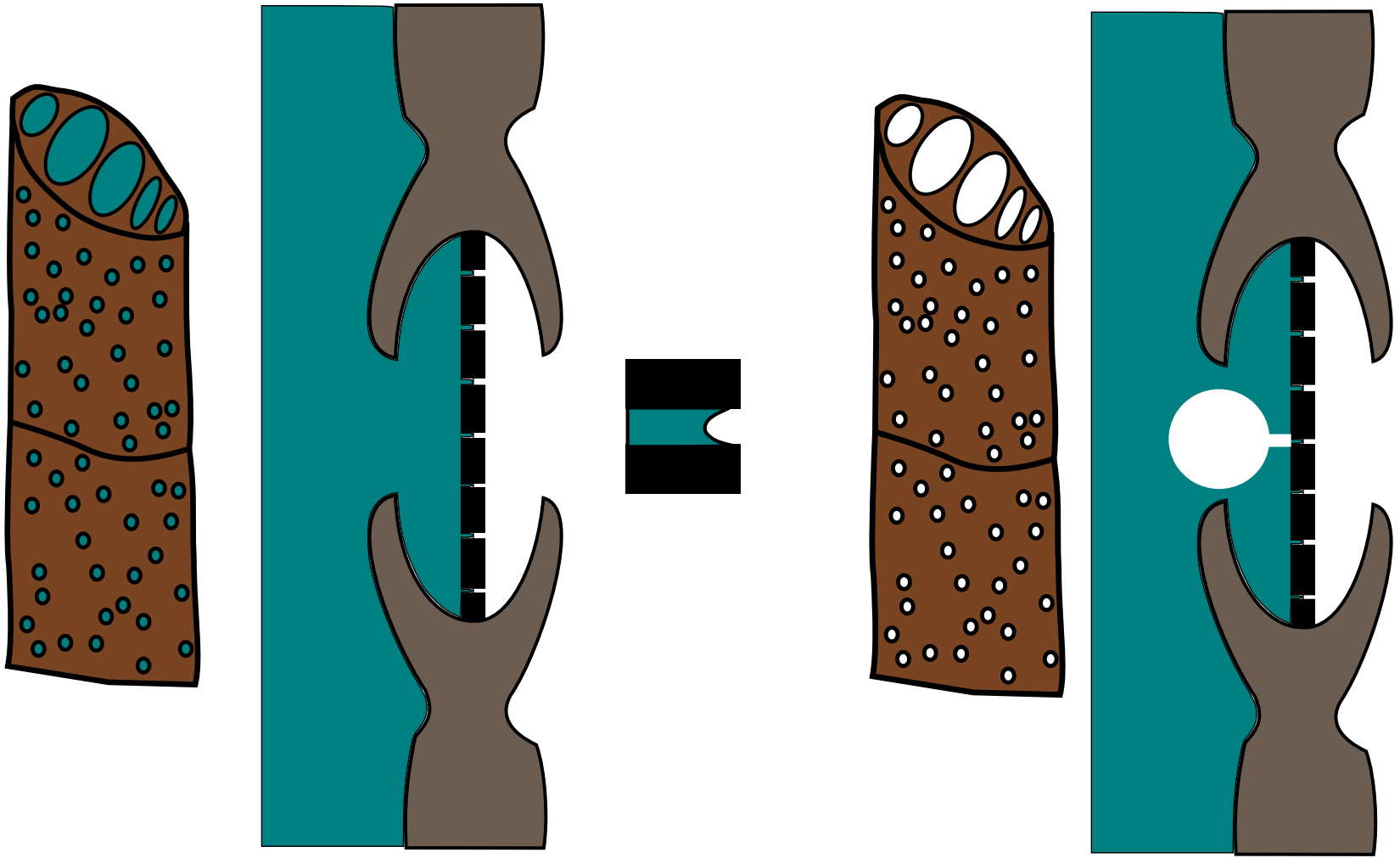
- Modeling stomatal behaviors using optimization theory
- Maximize (carbon gain – carbon risk)

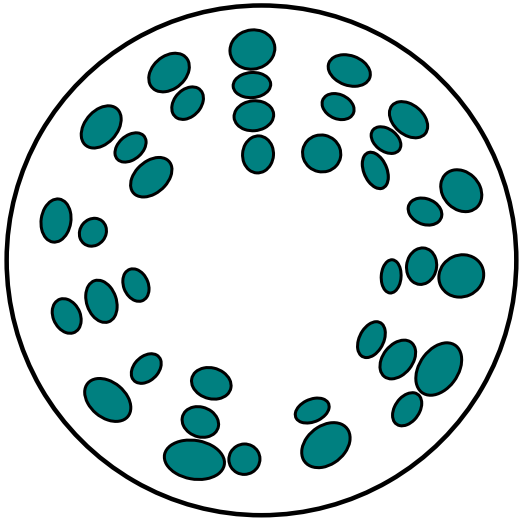


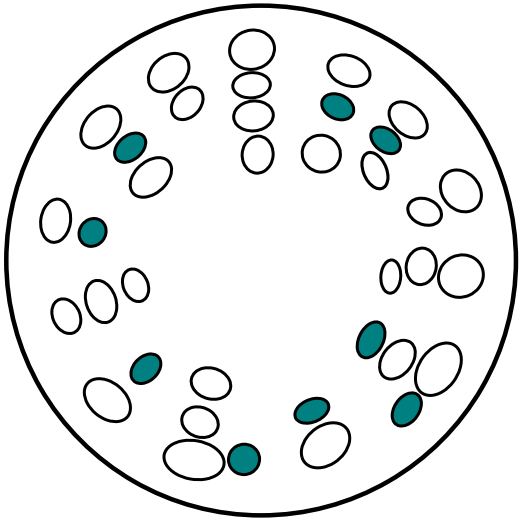


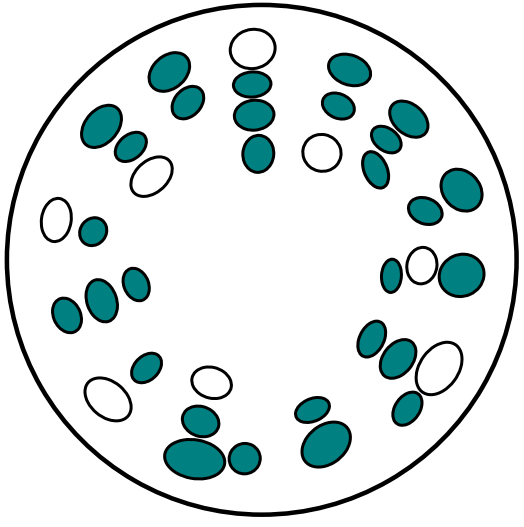


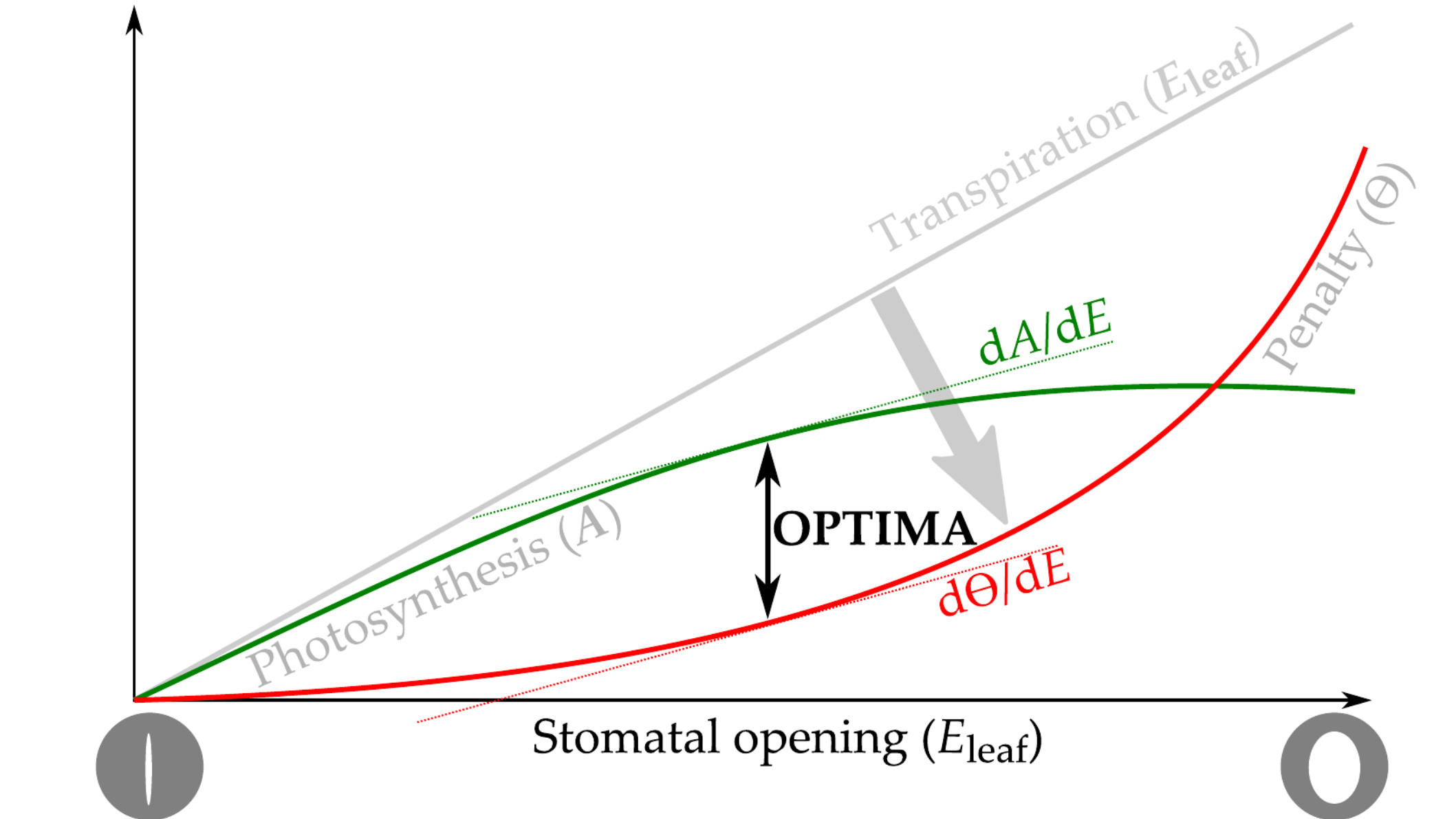




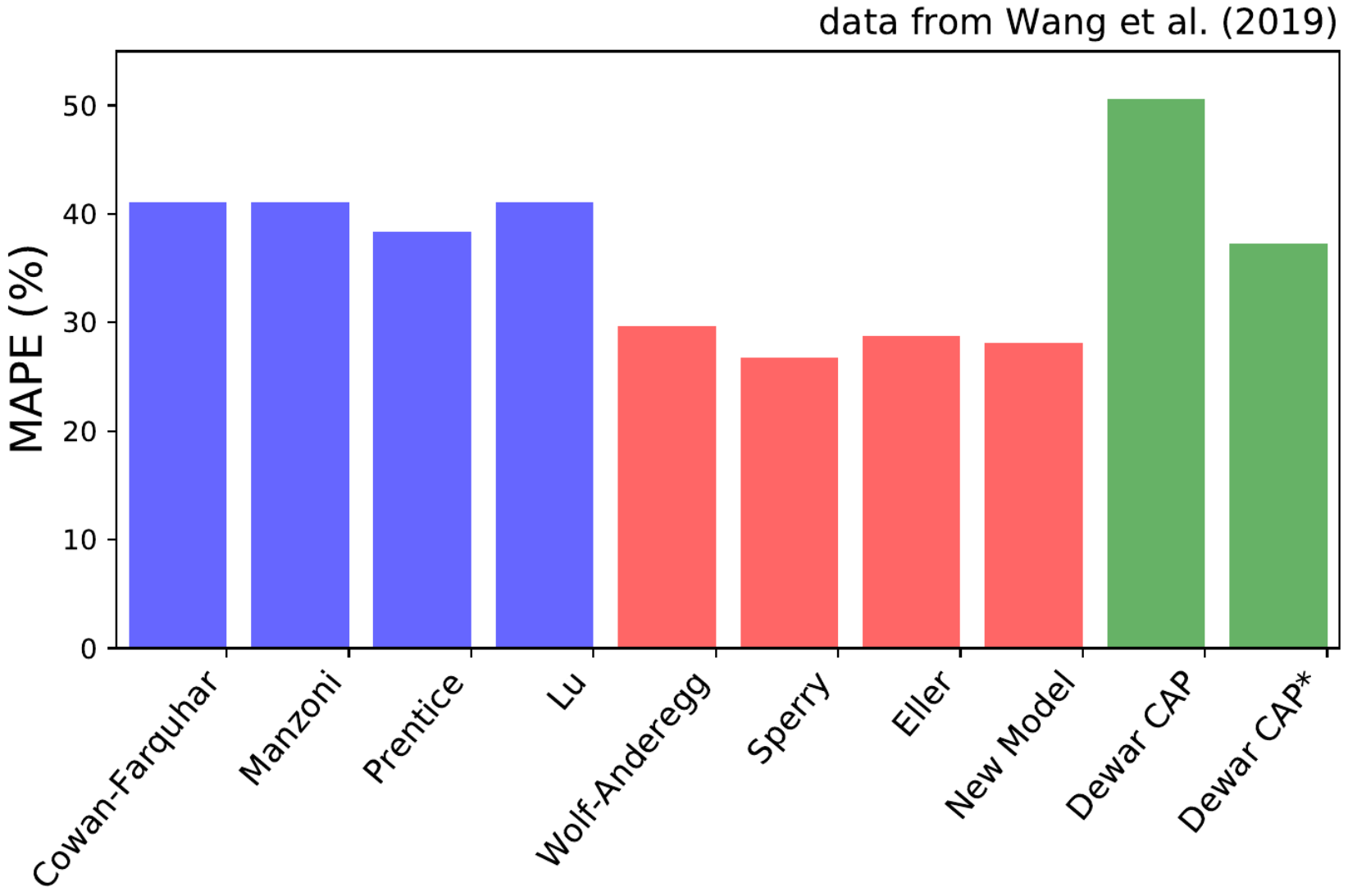







Transpiration (E_{leaf})
Penalty (Θ)
dA/dE
Photosynthesis (A)
OPTIMA
dΘ/dE
Stomatal opening (E_{leaf})

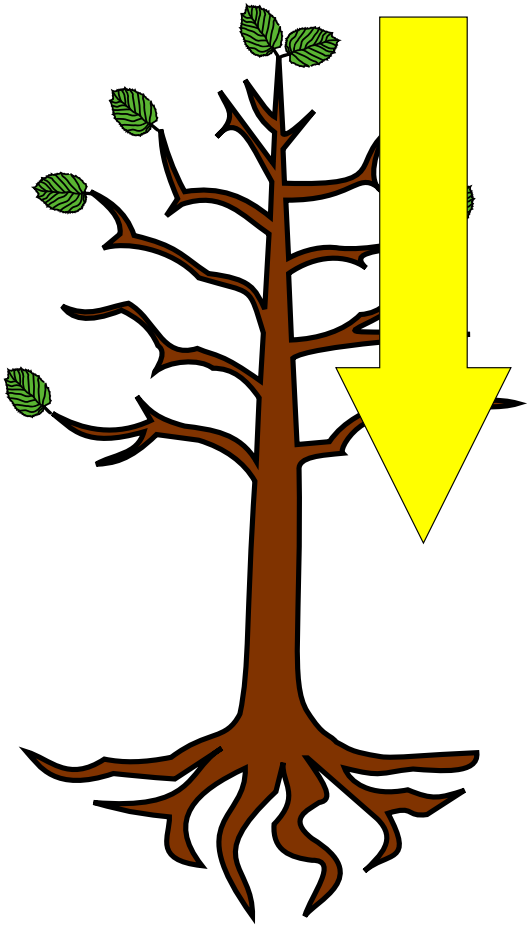
Model	Reference	Water Penalty (Θ or Θ')	Marginal Penalty ($d\Theta/dE$ or $d\Theta'/dE$)	Criteria I–III	Response Criteria IV–VII / DCPK	Fitting parameters
Cowan-Farquhar	(Cowan and Farquhar, 1977)	$\Theta = \frac{E_{leaf}}{\lambda}$	$\frac{d\Theta}{dE} = \frac{1}{\lambda}$	YNN	NNNN	λ
Manzoni	(Manzoni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

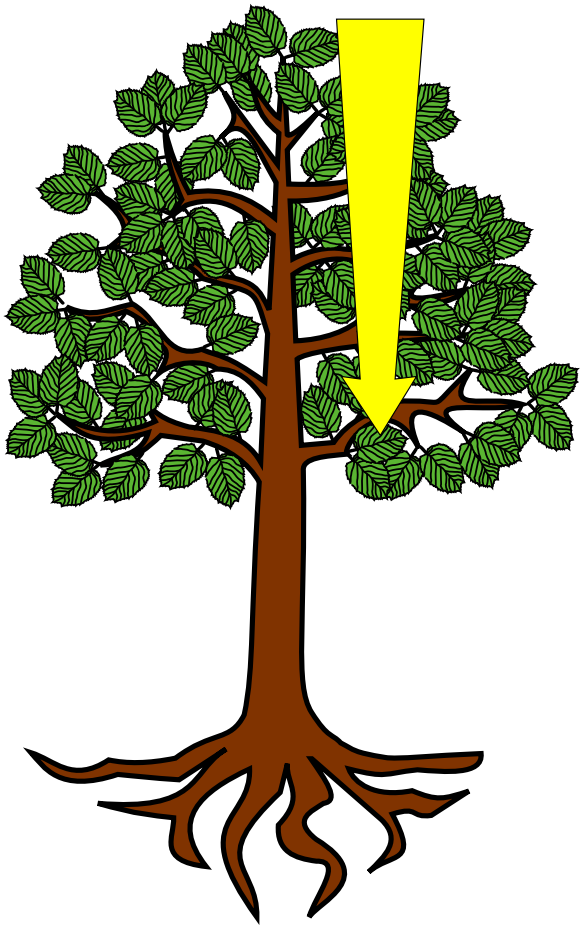


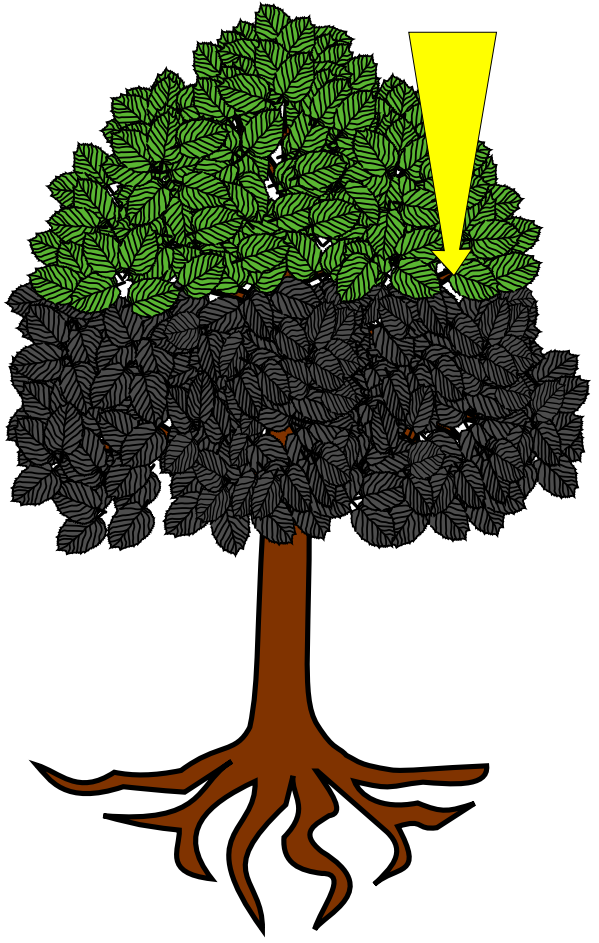
Wang et al. (2020)

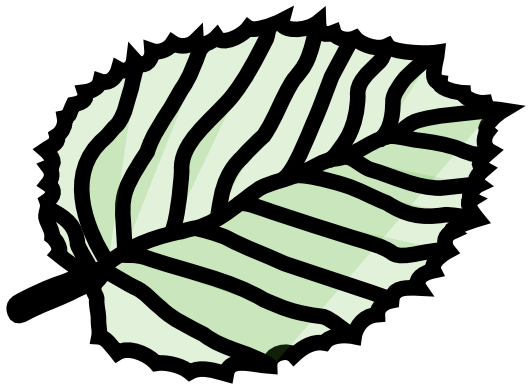
Second Step

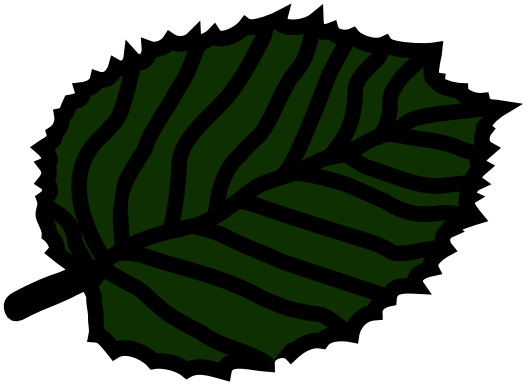
- Predict how plant traits change with the environment
- Optimizing leaf area and photosynthetic capacity

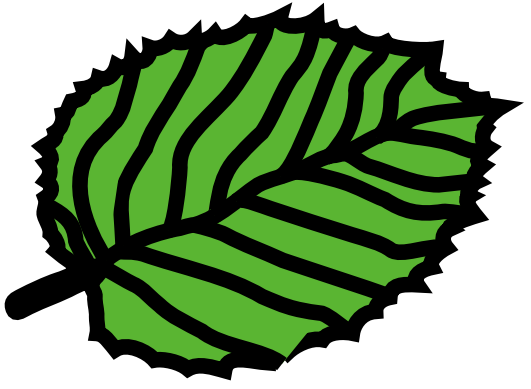










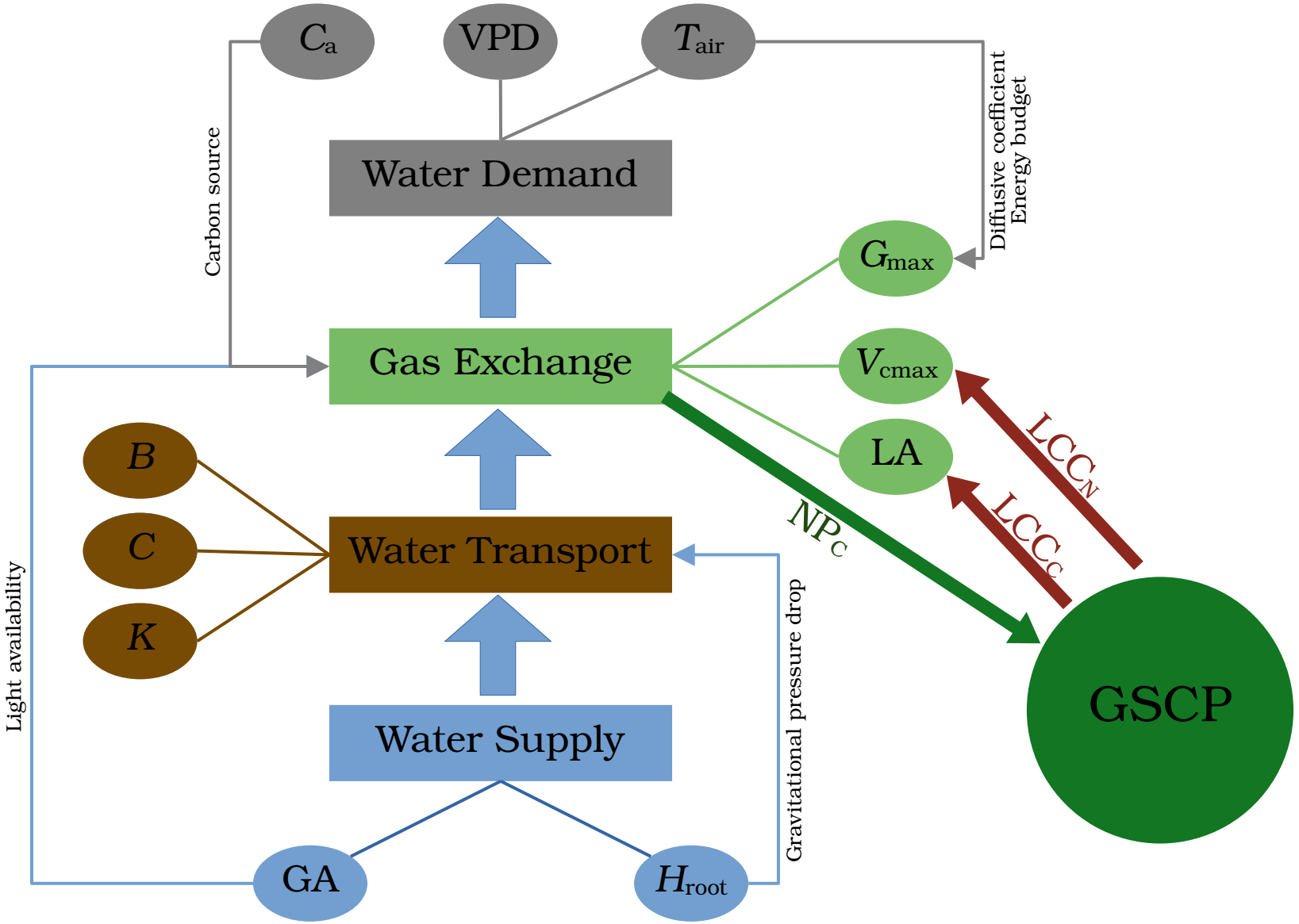


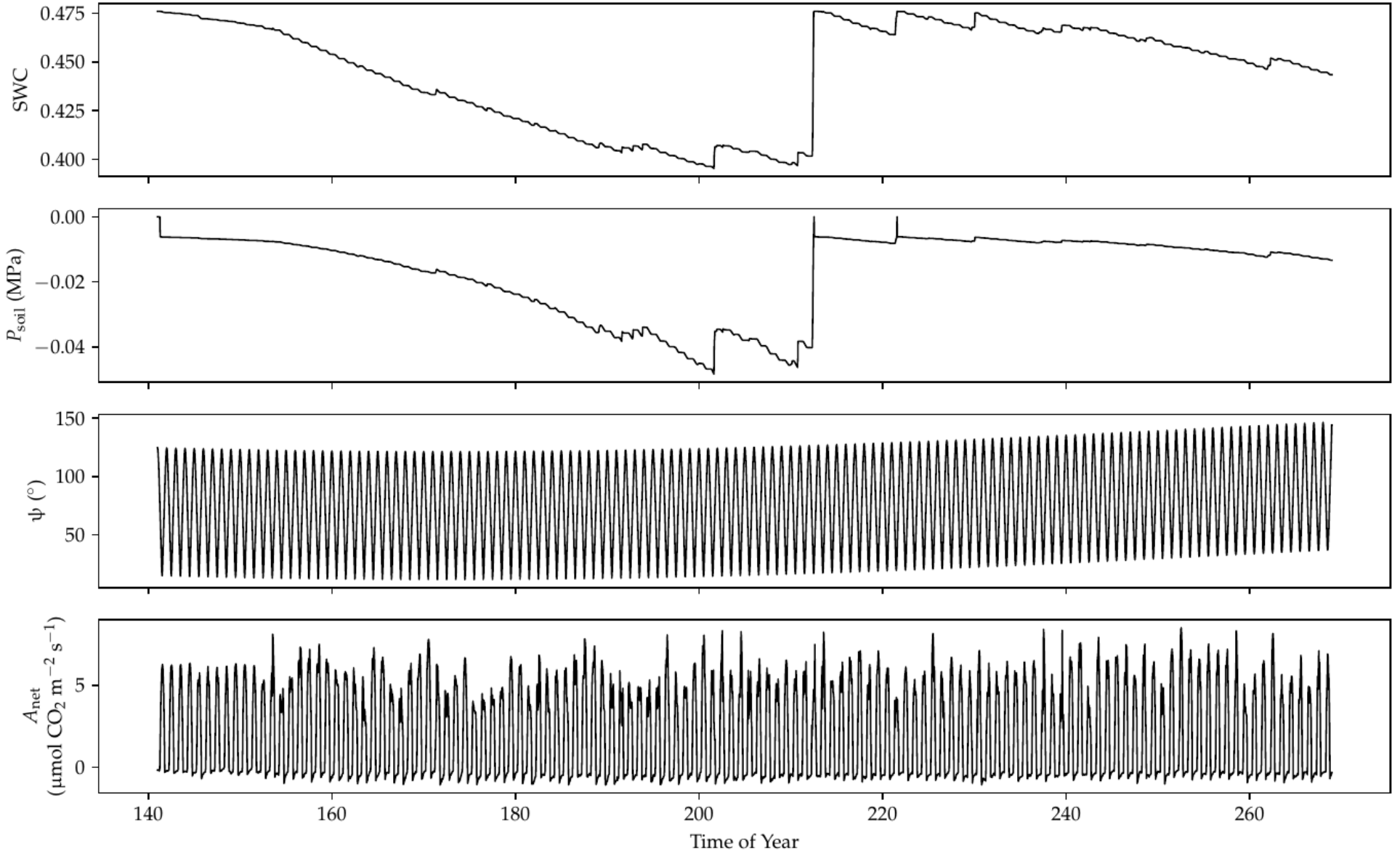
Assumptions

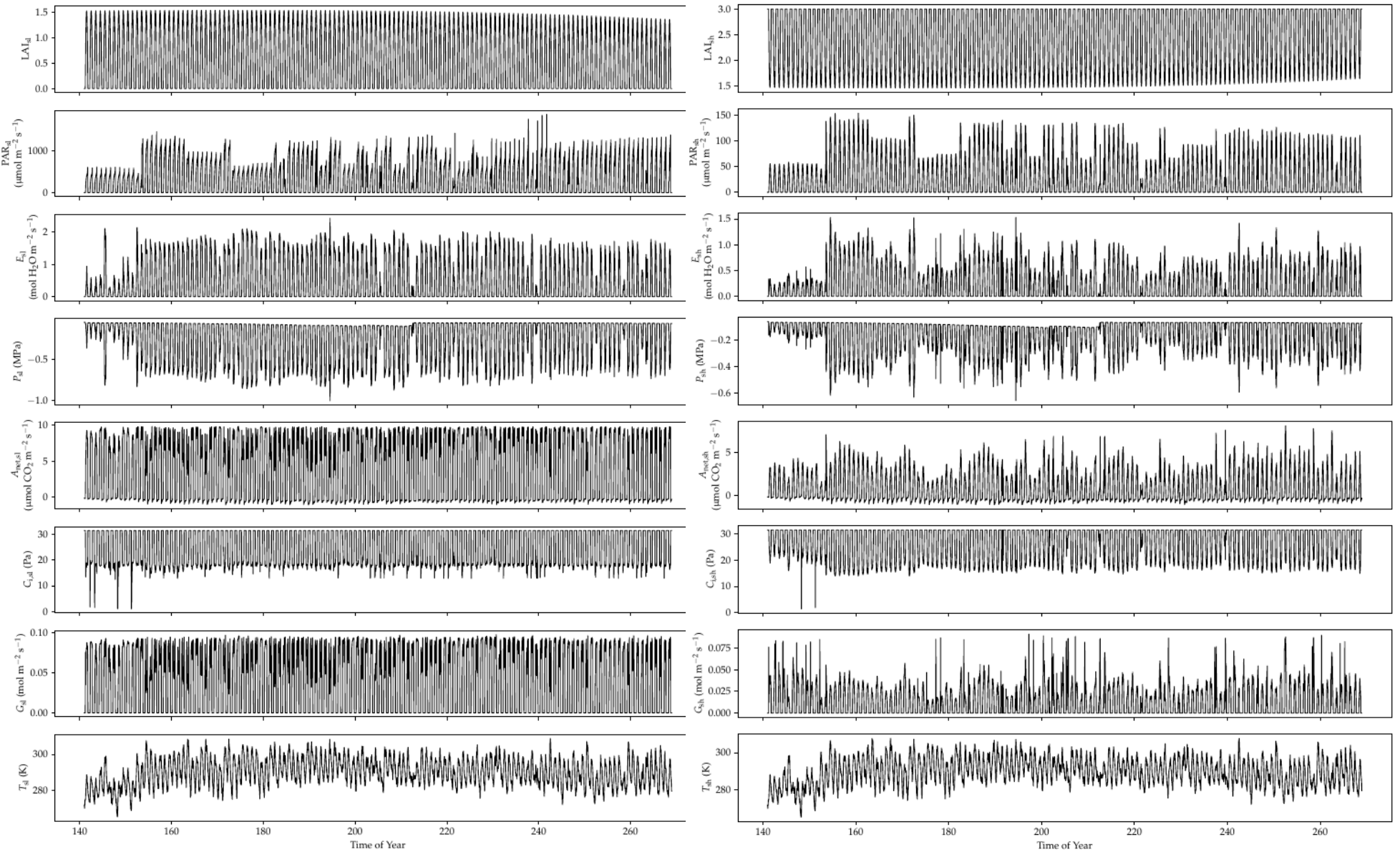
- Leaf biomass costs: LA * $invest_C$
- Leaf nutrient costs: LA * Vcmax * $invest_N$
- Total carbon gain: $\int A_{net}(t)$
- Maximize $\int A_{net}(t)$ – LA * $invest_C$ – LA * Vcmax * $invest_N$

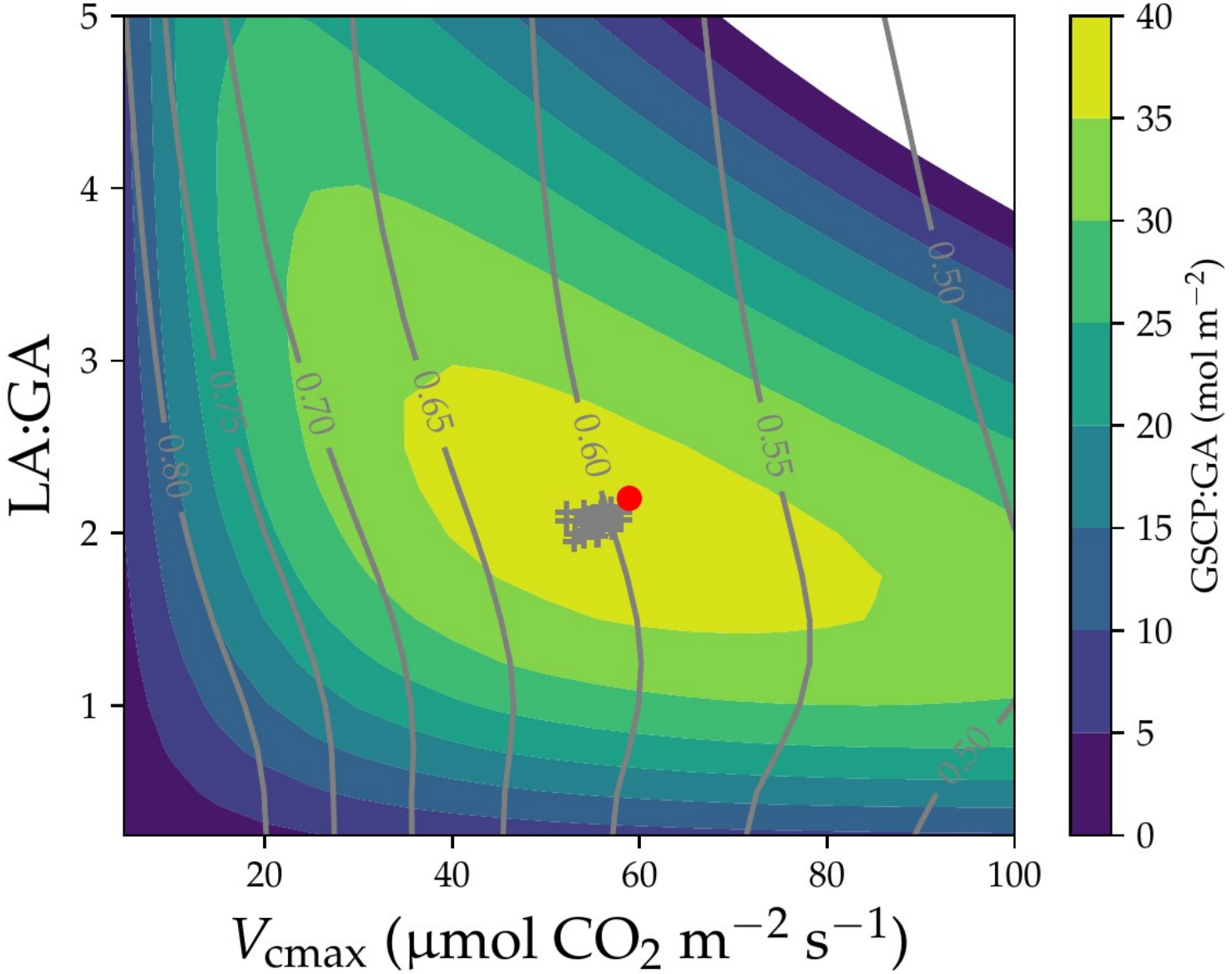
Difficulties

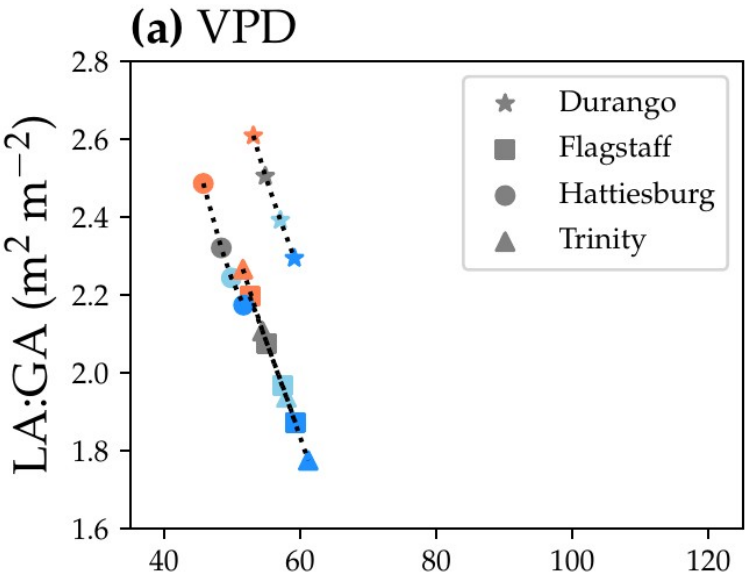
- Leaf investment is one-time investment
- It includes carbon biomass and nutrient costs
- Both costs are related to metabolism
- Experimentally difficult to tease apart the one-time investment from respiration
- Optimizing two variables from at least two unknowns

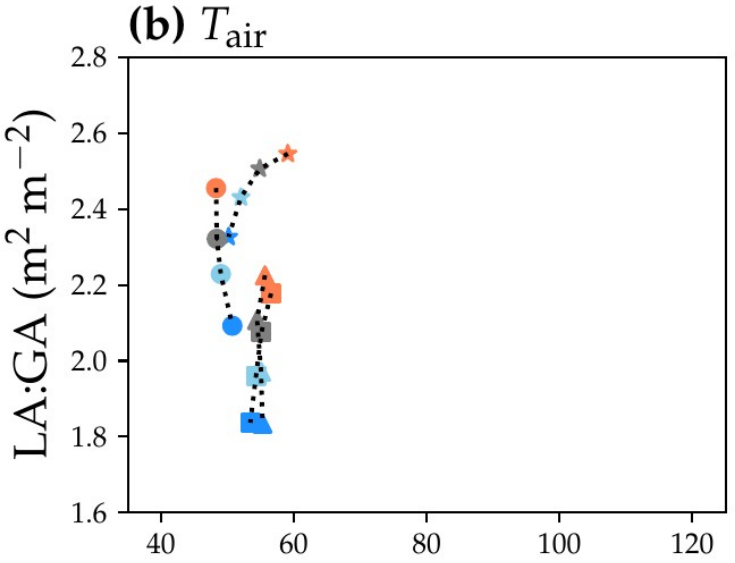

C_a
VPD
T_{air}
Carbon source
Diffusive coefficient
Energy budget
Water Demand
G_{max}
Gas Exchange
V_{cmax}
LA
LCC_N
LCC_C
NP_C
B
C
K
Water Transport
Light availability
Gravitational pressure drop
GSCP
Water Supply
GA
H_{root}

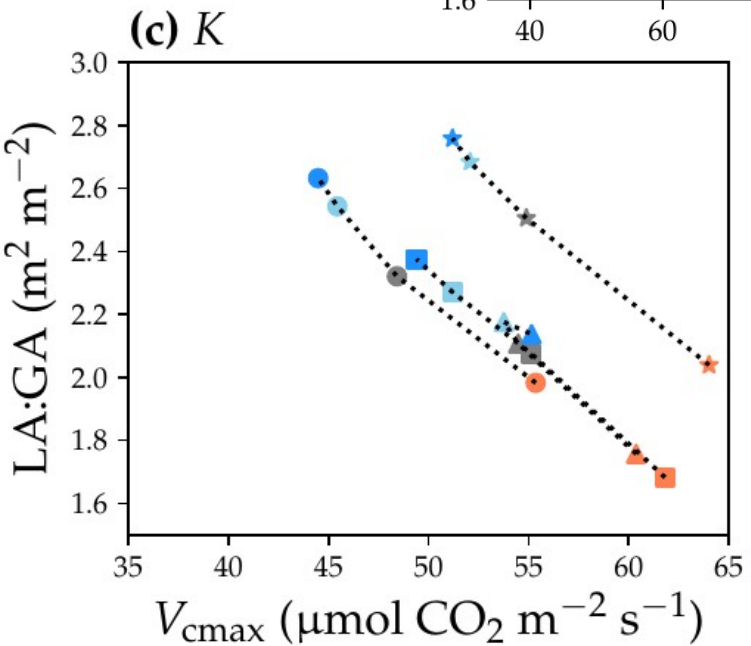

SWC
0.475
0.450
0.425
0.400
P_{soil} (MPa)
0.00
−0.02
−0.04
ψ (°)
150
100
50
A_{net} (μmol CO_2 m^{-2} s^{-1})
5
0
140
160
180
200
220
240
260
Time of Year

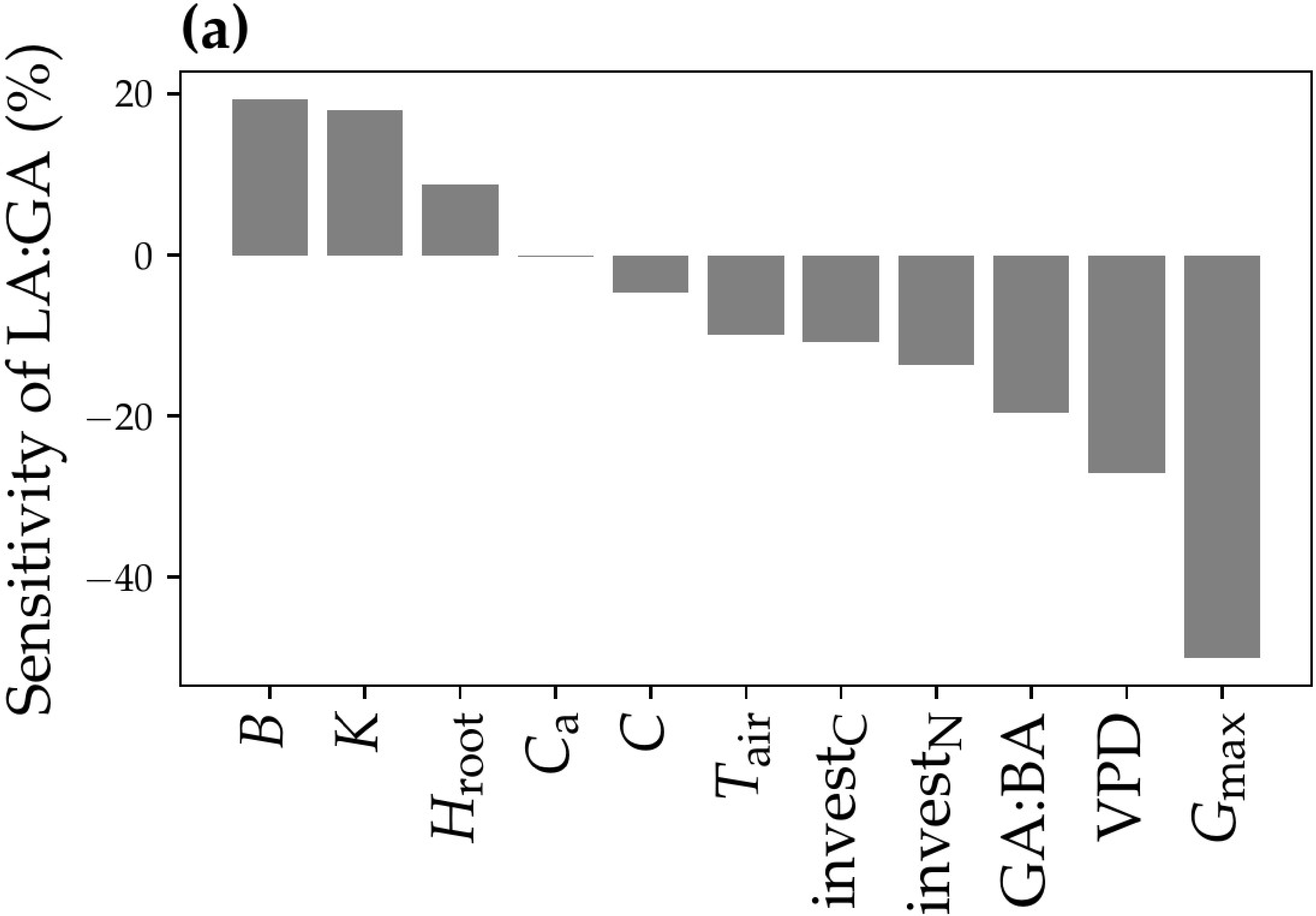

LAI_sl
LAI_sh
PAR_sl (μmol m⁻² s⁻¹)
PAR_sh (μmol m⁻² s⁻¹)
E_sl (mol H2O m⁻² s⁻¹)
E_sh (mol H2O m⁻² s⁻¹)
P_sl (MPa)
P_sh (MPa)
A_netsl (μmol CO2 m⁻² s⁻¹)
A_netsh (μmol CO2 m⁻² s⁻¹)
C_isl (Pa)
C_ish (Pa)
G_sl (mol m⁻² s⁻¹)
G_sh (mol m⁻² s⁻¹)
T_sl (K)
T_sh (K)
Time of Year
Time of Year

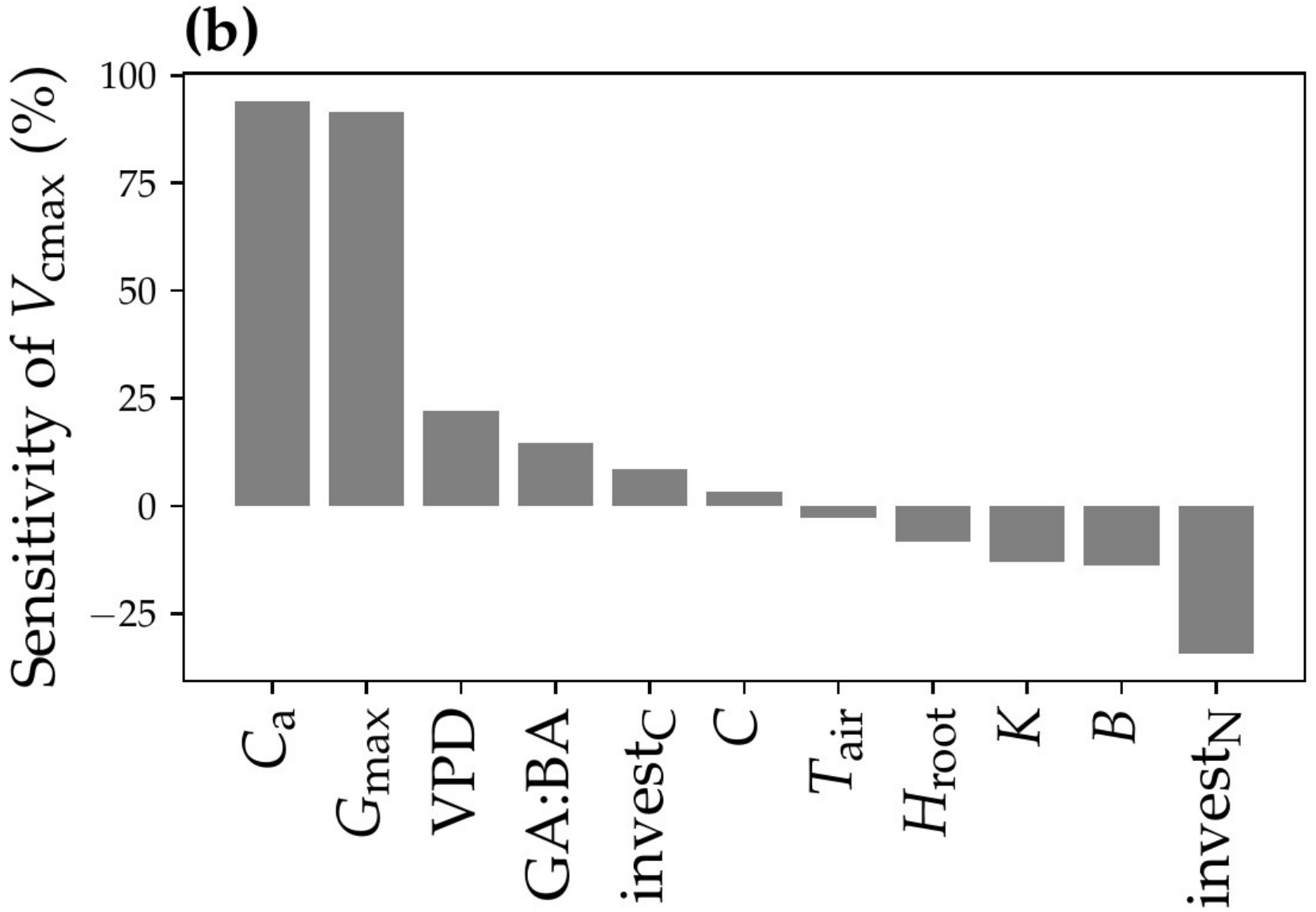

LA:GA
5
4
3
2
1
20
40
60
80
100
V_{cmax} (μmol CO_2 m^{-2} s^{-1})
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.50
40
35
30
25
20
15
10
5
0
GSCP:GA (mol m^{-2})


(a) VPD
Durango
Flagstaff
Hattiesburg
Trinity
LA:GA (m^2 m^{-2})
2.8
2.6
2.4
2.2
2.0
1.8
1.6
40
60
80
100
120


(b) T_{air}
LA:GA (m^2 m^{-2})
2.8
2.6
2.4
2.2
2.0
1.8
1.6
40
60
80
100
120

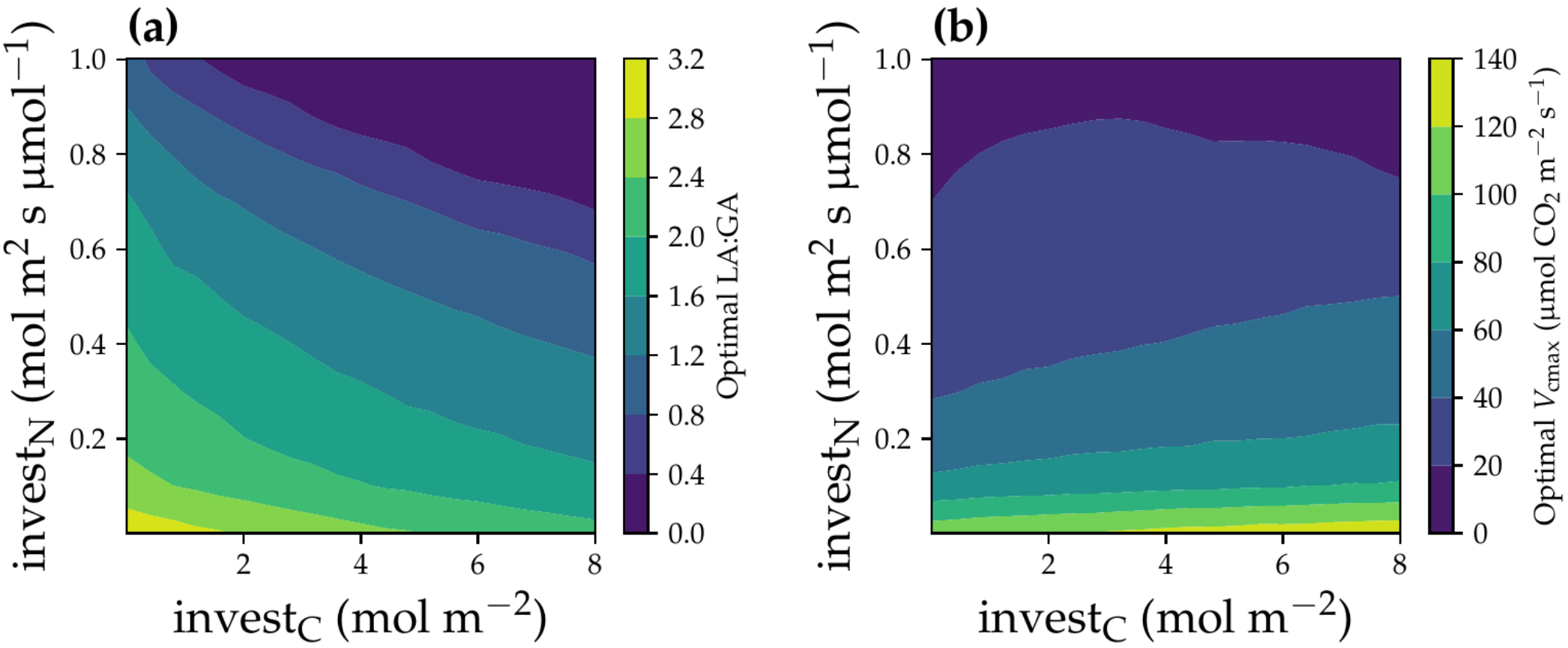

(c) K
LA:GA (m^2 m^{-2})
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
35
40
45
50
55
60
65
V_{cmax} (μmol CO_2 m^{-2} s^{-1})

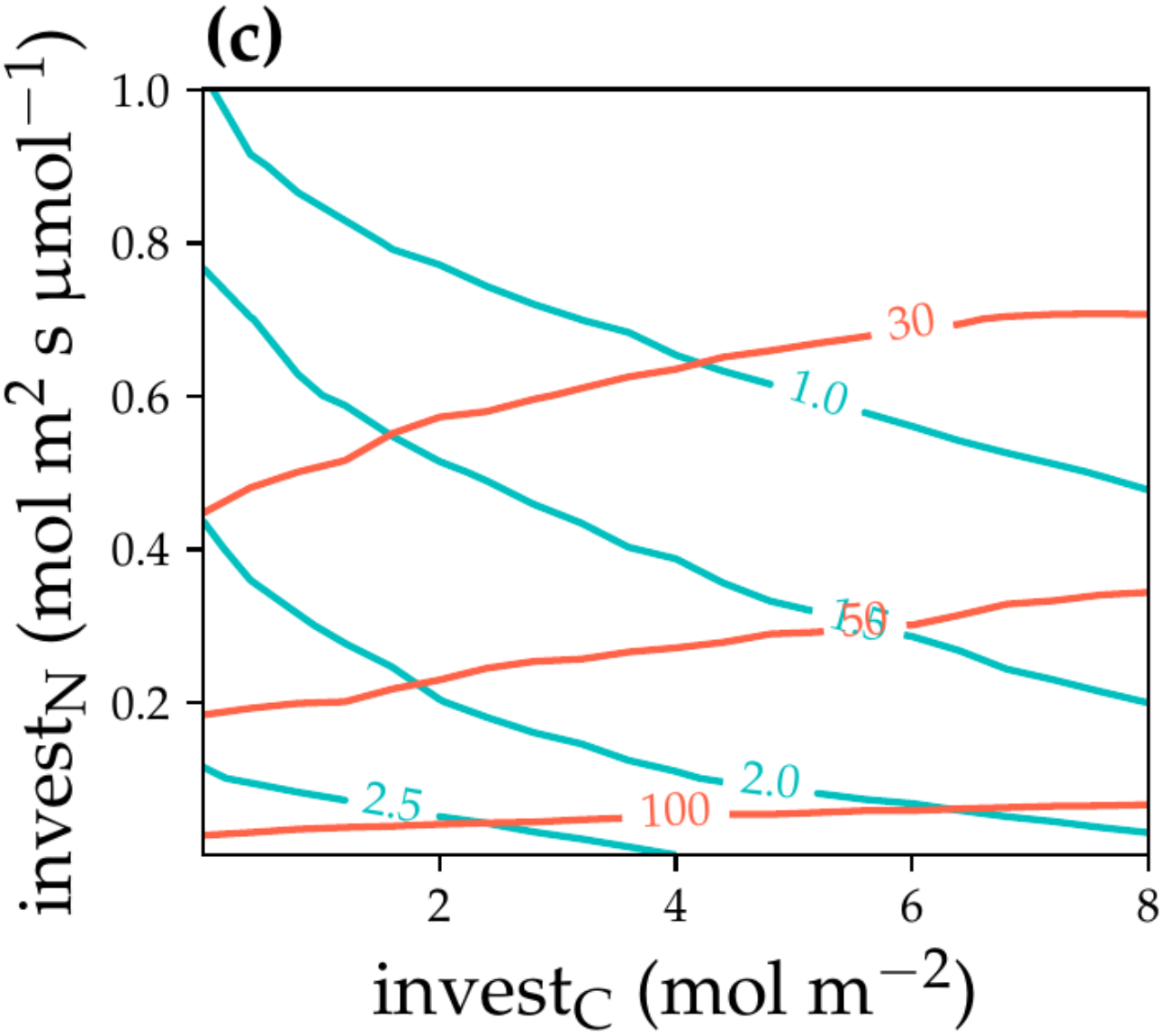

(a)
Sensitivity of LA:GA (%)
20
0
−20
−40
B
K
H_root
C_a
C
T_air
invest_C
invest_N
GA:BA
VPD
G_max

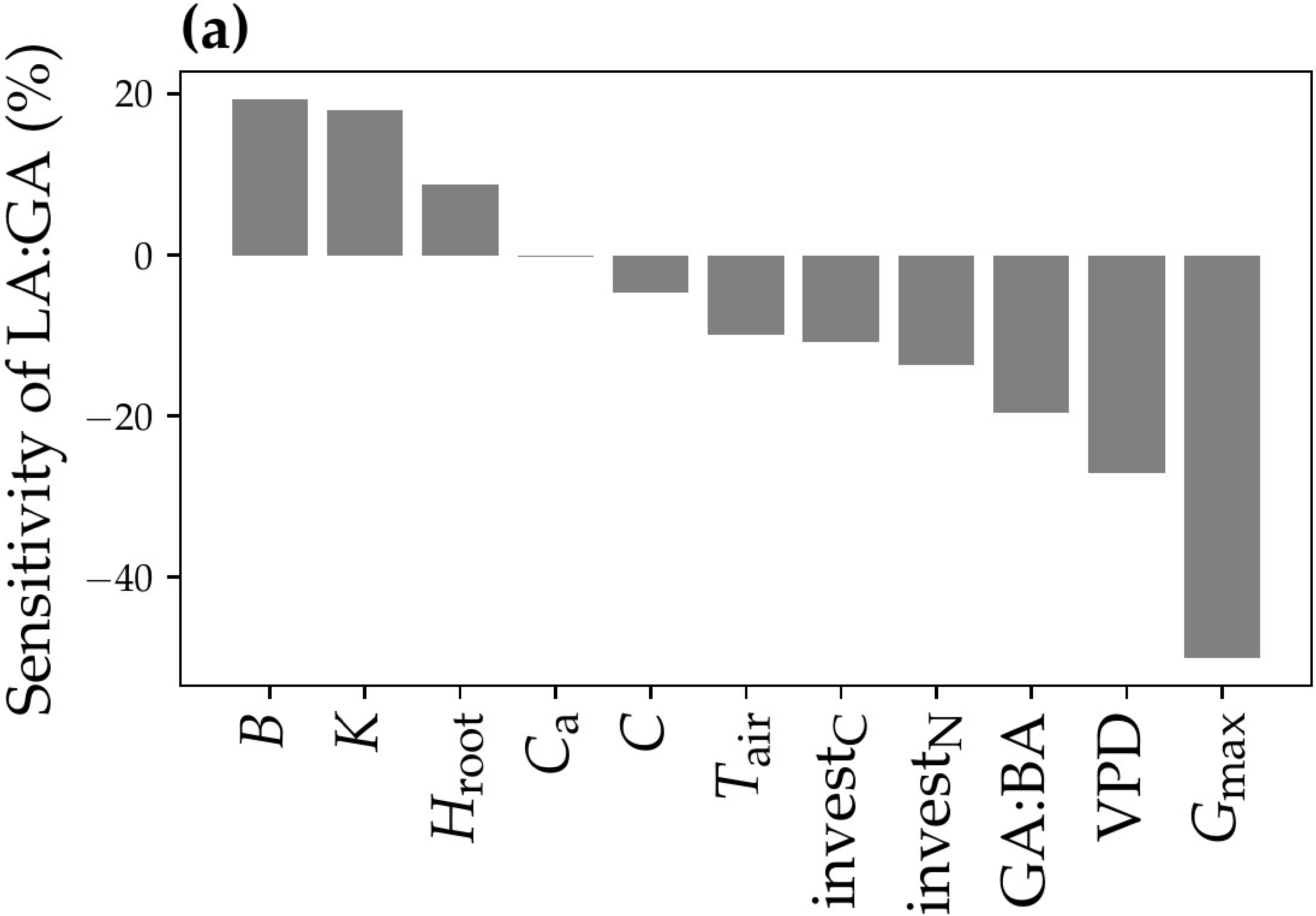

(b)
Sensitivity of V_{cmax} (%)
100
75
50
25
0
−25
C_a
G_{max}
VPD
GA:BA
$invest_C$
C
T_{air}
H_{root}
K
B
$invest_N$

Is the model useful?

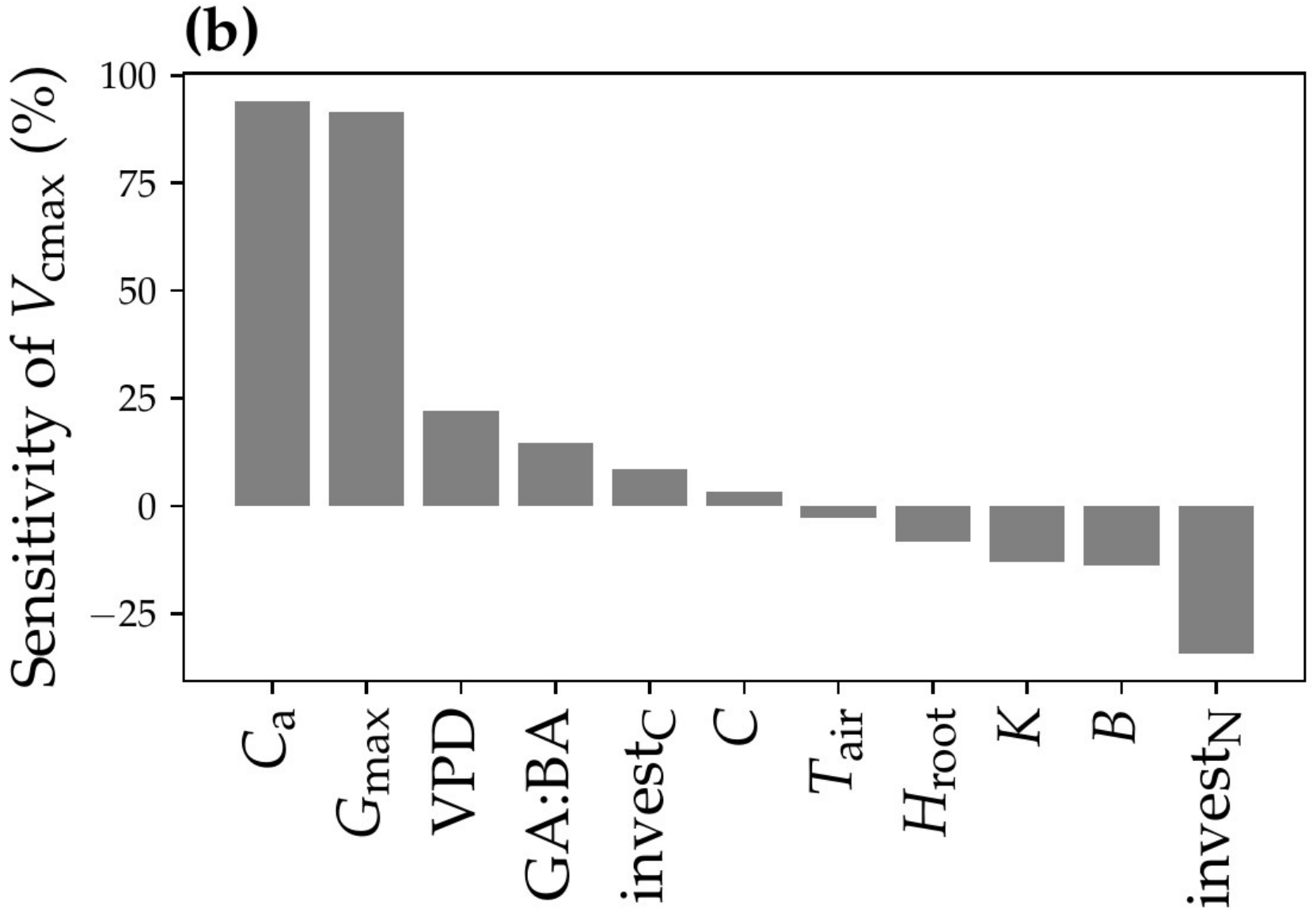
- $invest_C$ is unknown
- $invest_N$ is unknown


(a)
(b)
1.0
0.8
0.6
0.4
0.2
2
4
6
8
invest_N (mol m^2 s μmol^{-1})
invest_C (mol m^{-2})
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0.0
Optimal LA:GA
140
120
100
80
60
40
20
0
Optimal V_{cmax} (μmol CO_2 m^{-2} s^{-1})


(c)
1.0
0.8
0.6
0.4
0.2
2
4
6
8
invest_N (mol m^2 s μmol^{-1})
invest_C (mol m^{-2})
30
1.0
50
2.5
100
2.0



(a)
Sensitivity of LA:GA (%)
20
0
−20
−40
B
K
H_root
C_a
C
T_air
invest_C
invest_N
GA:BA
VPD
G_max


(b)
Sensitivity of V_{cmax} (%)
100
75
50
25
0
−25
C_a
G_{max}
VPD
GA:BA
$invest_C$
C
T_{air}
H_{root}
K
B
$invest_N$

Conclusions

- Plant hydraulic and leaf traits are important when modeling optimal leaf area
- Leaf traits are key drivers for optimal photosynthetic capacity
- The unknown leaf construction cost parameters can be estimated from known plant trait combinations

Acknowledgments

- University of Utah
- Sperry Lab
- Anderegg Lab
- Caltech
- Frankenberg Lab
- CliMA