Coupling plant physiology and pest demography to understand plant-nematode interactions

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13th ECMTB, July 22-26, 2024, Toledo, Spain

Root-Knot Nematodes (RKN), *Meloidogyne spp.*

- small soil worms,
- obligate root endoparasites,
- ubiquitous polyphagous pest
- 14% of global crop losses worldwide [1]

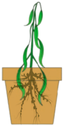
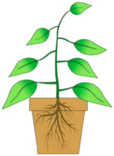
  [1] Djian-Caporalino, *EPPO Bulletin*, 2012

Main impacts

- root deformation (galls)
- stunted growth and wilting

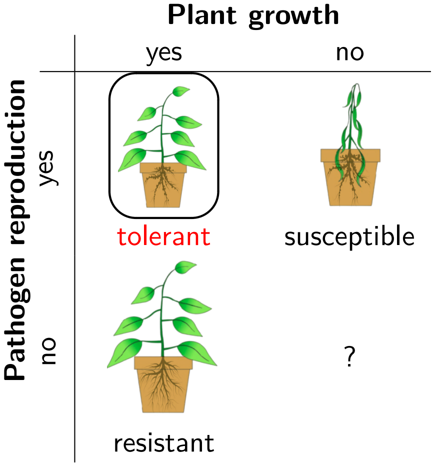
Plant variability

Strong variability in plant response to RKN parasitism among crop species

		Plant growth	
		yes	no
Pathogen reproduction	yes	 tolerant	 susceptible
	no	 resistant	?

Plant variability

Strong variability in plant response to RKN parasitism among crop species



Which mechanisms underlie plant tolerance?

Problematic

Host-Pathogen interactions

pest dynamics

plant physiology

Epidemiological modeling

(Tankam et al., Mathematical Biosciences, 2020)

(Nilusmas et al., Evolutionary applications, 2020)

Ecological modeling

(Thornley, Annals of botany, 1972)

(Dewar, Functional Ecology, 1998)

Problematic

Host-Pathogen interactions

pest dynamics → Epidemiological modeling

plant physiology → Ecological modeling

Epidemiological modeling

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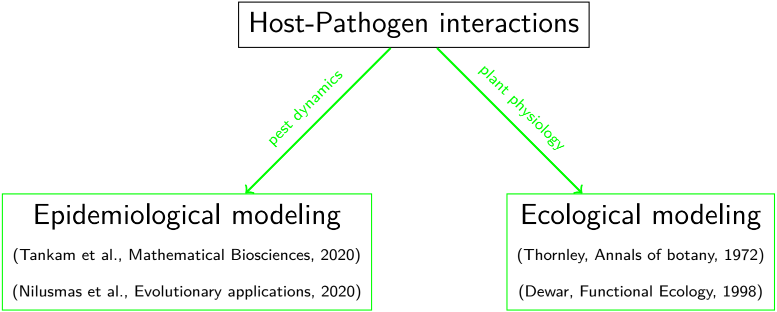
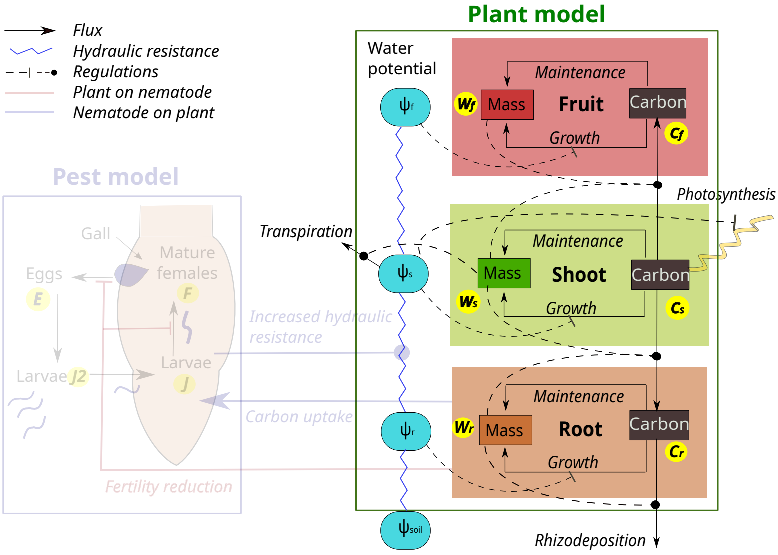


Approach

- Model coupling plant ecophysiology & pest population dynamics
- Experimental data on 2 plant species (tomato & pepper)

Plant model


Flux
Hydraulic resistance
Regulations
Plant on nematode
Nematode on plant
Plant model
Water potential
ψf
ψs
ψr
ψsoil
Maintenance
Mass
Fruit
Carbon
Growth
Wf
Cf
Shoot
Ws
Cs
Root
Wr
Cr
Photosynthesis
Transpiration
Rhizodeposition
Pest model
Gall
Mature females
Eggs
E
F
Larvae
Larvae J2
J
Increased hydraulic resistance
Carbon uptake
Fertility reduction

Mathematical equations

$$
\text{Shoot}\begin{cases} \dfrac{dW_s}{dt} = \\ \\ \dfrac{dC_s}{dt} = \\ \end{cases}
$$

$$
\text{Root}\begin{cases} \dfrac{dW_r}{dt} = \\ \\ \dfrac{dC_r}{dt} = \\ \end{cases}
$$

$$
\text{Fruit}\begin{cases} \dfrac{dW_f}{dt} = \\ \\ \dfrac{dC_f}{dt} = \\ \end{cases}
$$

Mathematical equations

$$\text{Shoot}\begin{cases} \dfrac{dW_s}{dt} = \\ \dfrac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} \underbrace{- \dfrac{1}{W_s}\dfrac{dW_s}{dt}C_s}_{\text{Dilution}} \end{cases}$$

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Mathematical equations

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Mathematical equations

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\text{Shoot}\begin{cases}
\dfrac{dW_s}{dt} = \underbrace{k_s f(\psi_s)\dfrac{C_s}{K_s + C_s}W_s}_{\text{Growth}} \\
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\end{cases}
$$

$$
\text{Root}\begin{cases}
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$$

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\end{cases}
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$$\text{Fruit}\begin{cases} \dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}W_f}_{\text{Growth}} \\ \dfrac{dC_f}{dt} = \dfrac{1}{W_f}\underbrace{(T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,f})\, k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}}_{\text{Respiration growth}} \underbrace{- \dfrac{1}{W_f}\dfrac{dW_f}{dt}C_f}_{\text{Dilution}} \end{cases}$$

Mathematical equations

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$$\begin{cases} \dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r)\dfrac{C_r}{K_r + C_r} W_r}_{\text{Growth}} \\ \dfrac{dC_r}{dt} = \dfrac{1}{W_r}\underbrace{T_r}_{\text{Transport}} - \underbrace{(f_c + r_{g,r})\, k_r f(\psi_r)\dfrac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{r_{m,r}\left(\dfrac{C_r^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_r}\dfrac{dW_r}{dt} C_r}_{\text{Dilution}} \end{cases}$$

Fruit

$$\begin{cases} \dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f + C_f} W_f}_{\text{Growth}} \\ \dfrac{dC_f}{dt} = \dfrac{1}{W_f}\underbrace{(T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,f})\, k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}}_{\text{Growth}} - \underbrace{r_{m,f}\left(\dfrac{C_f^n}{K_m^n + C_f^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_f}\dfrac{dW_f}{dt} C_f}_{\text{Dilution}} \end{cases}$$

Mathematical equations

$$\text{Shoot}\begin{cases}\dfrac{dW_s}{dt} = \underbrace{k_s f(\psi_s)\dfrac{C_s}{K_s + C_s}W_s}_{\text{Growth}}\\[2ex]\dfrac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} - \dfrac{1}{W_s}\underbrace{(T_r + T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,s})\, k_s f(\psi_s)\dfrac{C_s}{K_s + C_s}}_{\text{Growth}} - \underbrace{r_{m,s}\left(\dfrac{C_s^n}{K_m^n + C_s^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_s}\dfrac{dW_s}{dt}C_s}_{\text{Dilution}}\end{cases}$$

$$\text{Root}\begin{cases}\dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r)\dfrac{C_r}{K_r + C_r}W_r}_{\text{Growth}}\\[2ex]\dfrac{dC_r}{dt} = \dfrac{1}{W_r}\underbrace{T_r}_{\text{Transport}} - \underbrace{(f_c + r_{g,r})\, k_r f(\psi_r)\dfrac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{r_{m,r}\left(\dfrac{C_r^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{c_{rh}\, C_r}_{\text{Rhizodeposition}} - \underbrace{\dfrac{1}{W_r}\dfrac{dW_r}{dt}C_r}_{\text{Dilution}}\end{cases}$$

$$\text{Fruit}\begin{cases}\dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}W_f}_{\text{Growth}}\\[2ex]\dfrac{dC_f}{dt} = \dfrac{1}{W_f}\underbrace{(T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,f})\, k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}}_{\text{Growth}} - \underbrace{r_{m,f}\left(\dfrac{C_f^n}{K_m^n + C_f^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_f}\dfrac{dW_f}{dt}C_f}_{\text{Dilution}}\end{cases}$$

Mathematical equations

Shoot

$$\begin{cases} \dfrac{dW_s}{dt} = \underbrace{k_s f(\psi_s)\dfrac{C_s}{K_s + C_s} W_s}_{\text{Growth}} - \underbrace{\Gamma_s W_s}_{\text{Natural mortality}} - \underbrace{\Gamma_s \left(\dfrac{K_m^n}{K_m^n + C_s^n}\right) W_s,}_{\text{Additional mortality due to carbon shortage}} \\ \dfrac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} - \dfrac{1}{W_s}\underbrace{(T_r + T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,s})\, k_s f(\psi_s)\dfrac{C_s}{K_s + C_s}}_{\text{Growth}} - \underbrace{r_{m,s}\left(\dfrac{C_s^n}{K_m^n + C_s^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_s}\dfrac{dW_s}{dt} C_s}_{\text{Dilution}} \end{cases}$$

Root

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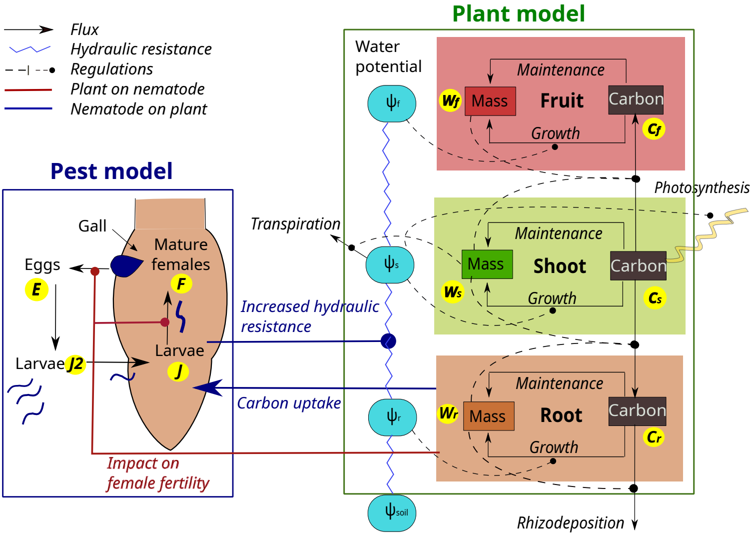
Fruit

$$\begin{cases} \dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f + C_f} W_f}_{\text{Growth}} - \underbrace{\Gamma_f W_f}_{\text{Natural mortality}} - \underbrace{\Gamma_f \left(\dfrac{K_m^n}{K_m^n + C_f^n}\right) W_f,}_{\text{Additional mortality due to carbon shortage}} \\ \dfrac{dC_f}{dt} = \dfrac{1}{W_f}\underbrace{(T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,f})\, k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}}_{\text{Growth}} - \underbrace{r_{m,f}\left(\dfrac{C_f^n}{K_m^n + C_f^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_f}\dfrac{dW_f}{dt} C_f}_{\text{Dilution}} \end{cases}$$

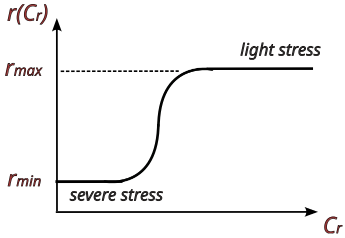
Integrated plant-pest model

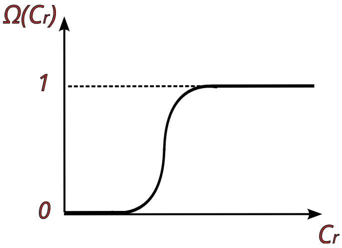


Plant status on RKN development

$$\text{Free}\begin{cases}\dfrac{dE}{dt} = \underbrace{r(C_r)\,F}_{\text{Egg laying}} - \underbrace{h\,E}_{\text{Egg hatching}} - \underbrace{\mu_e\,E}_{\text{Mortality}}\\[2ex] \dfrac{dJ_2}{dt} = \underbrace{h\,E}_{\text{Egg hatching}} - \underbrace{\beta\,J_2\,W_r}_{\text{Larvae infection}} - \underbrace{\mu_{J_2}\,J_2}_{\text{Mortality}}\end{cases}$$

$$\text{RKN}\begin{cases}\dfrac{dJ}{dt} = \underbrace{\Omega(C_r)\,\beta\,J_2 W_r}_{\text{RKN entry}} - \underbrace{\eta\,J}_{\text{Maturation}} - \underbrace{\mu_j\,J}_{\text{Mortality}}\\[2ex] \dfrac{dF}{dt} = \underbrace{\eta\,J}_{\text{Maturation}} - \underbrace{\mu_F\,F}_{\text{Mortality}}\end{cases}$$

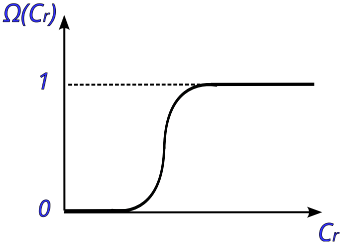


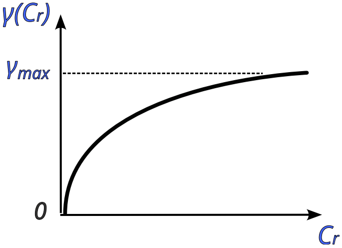


RKN effects on plant growth

Root

$$
\begin{cases}
\dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r)\dfrac{C_r}{K_r + C_r} W_r}_{\text{Growth}} - \underbrace{\gamma_r \left(1 + \dfrac{K_m^n}{K_m^n + C_r^n}\right) W_r}_{\text{Mortality}} - \underbrace{\Omega(C_r)\,\epsilon\,\beta\,J_2\,W_r}_{\text{Infected roots}} \\
\dfrac{dG}{dt} = \underbrace{\Omega(C_r)\,\epsilon\,\beta\,J_2\,W_r}_{\text{Gall formation}} + \underbrace{k_g f(\psi_r)\dfrac{C_r}{K_r + C_r} G}_{\text{Growth}} - \underbrace{\Gamma_r\,G}_{\text{Natural mortality}} \\
\dfrac{dC_r}{dt} = \dfrac{1}{(W_r + G)} \underbrace{T_r}_{\text{Transport}} - \underbrace{(f_c + r_{g,r})\left(\dfrac{k_r W_r + k_g G}{W_r + G}\right) f(\psi_r)\dfrac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{r_{m,r}\left(\dfrac{C_r^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{c_{rh} C_r}_{\text{Rhizodeposition}} \\
\qquad - \underbrace{\dfrac{C_r}{(W_r + G)}\left(\dfrac{dW_r}{dt} + \dfrac{dG}{dt}\right)}_{\text{dilution}} - \underbrace{\gamma(C_r)\,F}_{\text{RKN feeding}}
\end{cases}
$$





Calibration of models

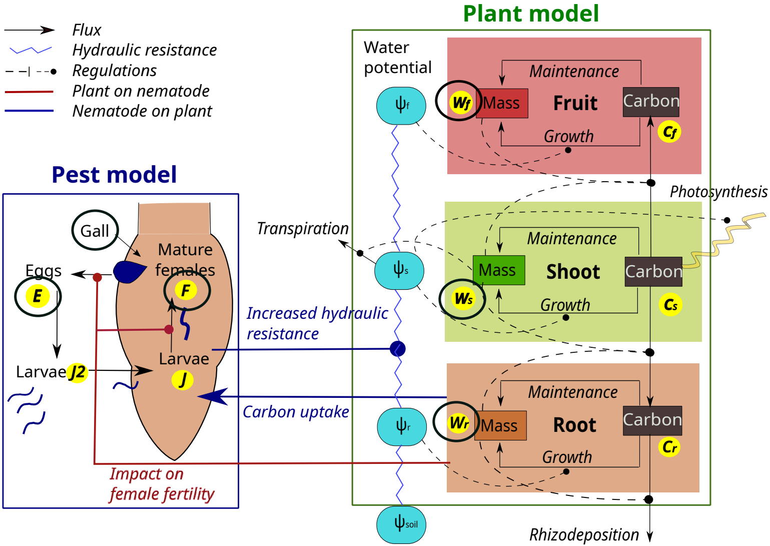
Steps

- select parameters to be estimated based on **sensitivity analysis**
- least squares **criterion** between model simulations and data
- find parameter values that minimize the criterion
  - Global search: ARS (Adaptive Random Searches)
  - Local search: Nelder-Mead from *minimize()* python module

Strategy

- calibration of plant model on control data
- calibration of plant-RKN model on inoculated plants & RKN data

Which data?



+ weekly number of leaves

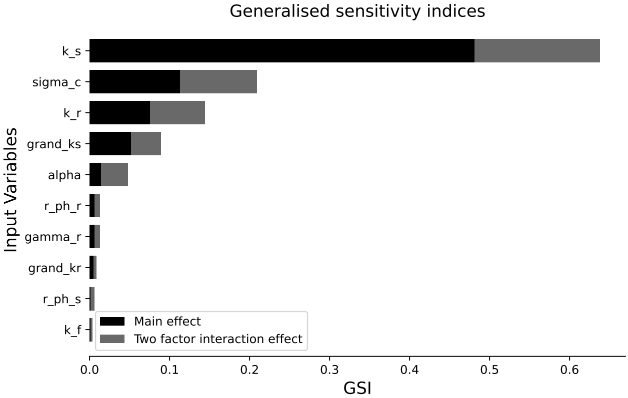
Calibration of plant model

Global sensitivity analysis on plant model

Features

- **goal**: identify the most influential parameters
- **inputs**: 26 parameters, **outputs**: W_s, W_r, W_f, C_s, C_r, C_f

Plant traits that most affect **root biomass** (W_r) dynamics



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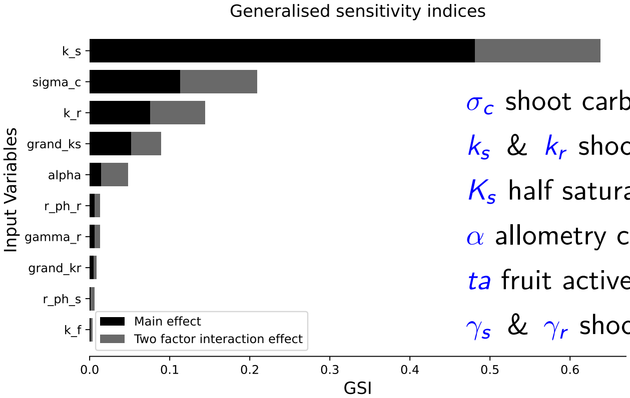


σ_c shoot carbon fixation rate

k_s & k_r shoot and root growth rates

K_s half saturation coef. of shoots

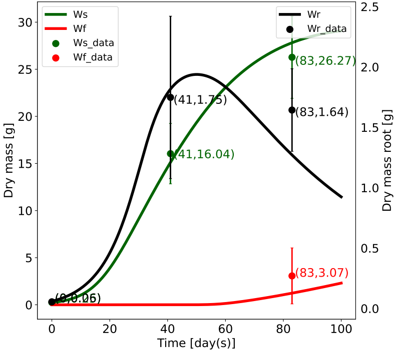
α allometry coefficient

ta fruit active transport rate

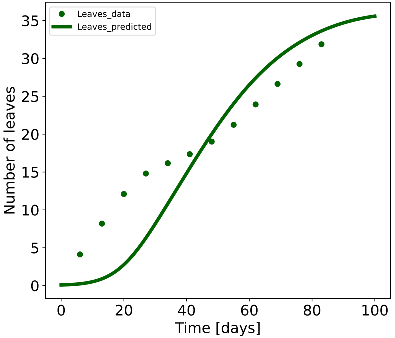
γ_s & γ_r shoot & root mortality rates

Tomato parameter estimation

Tomato dynamics

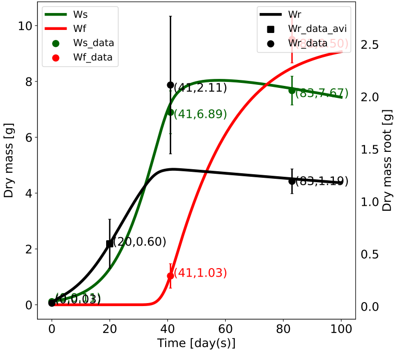


Predicted number of leaves

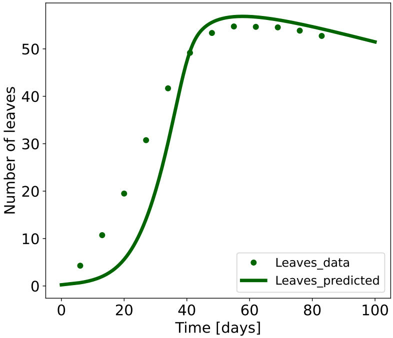


Pepper parameter estimation

Pepper dynamics



Predicted number of leaves



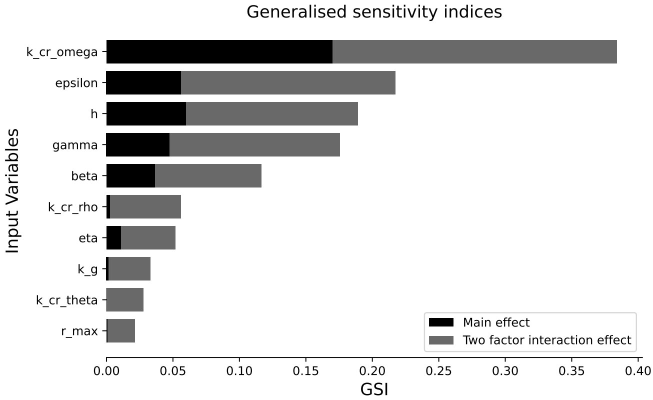
Calibration of full model

Global sensitivity analysis on full model

Features

- **inputs**: 15 parameters, **plant parameters are fixed**
- **outputs**: W_s, W_r, W_f, C_s, C_r, C_f, Eg, J_2, J, F, G

Interaction traits that most affect **J-larvae** dynamics



Global sensitivity analysis on full model

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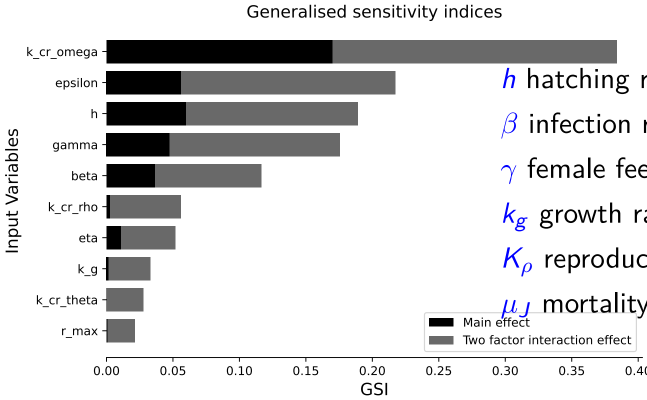
Interaction traits that most affect **J-larvae** dynamics



h hatching rate

β infection rate

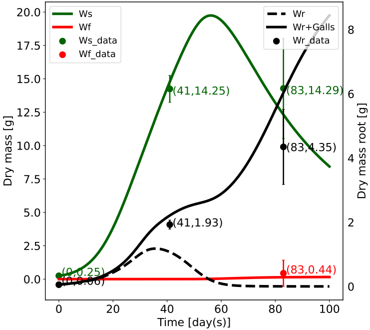
γ female feeding rate

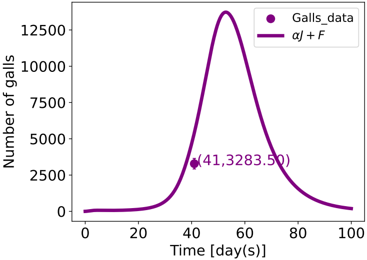
k_g growth rate of gall

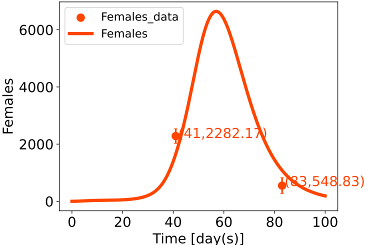
K_ρ reproduction hill constant

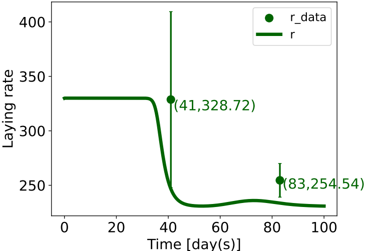
μ_J mortality rate of J-larvae

Calibration on tomato

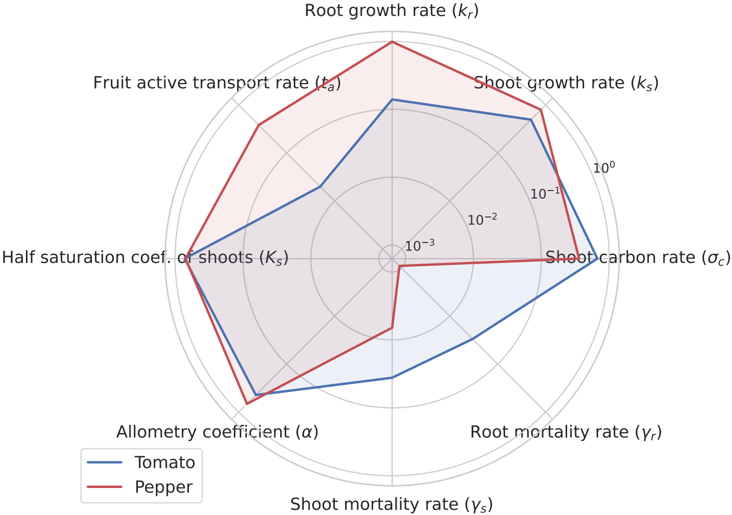






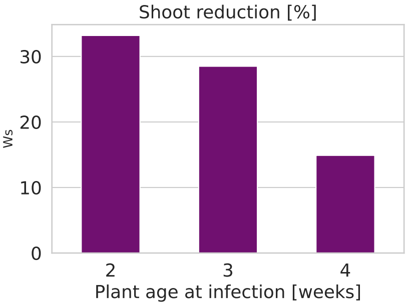


Plant parameter patterns (Tomato vs Pepper)

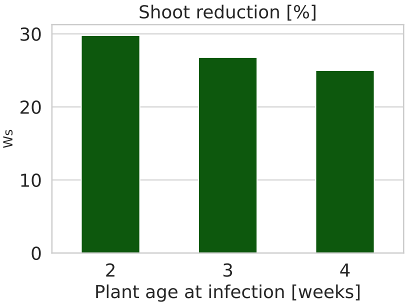


Shoot reduction vs plant age at infection

a. Cucumber dynamics
(Experimental results[1])



b. Tomato dynamics
(Model simulations)



[1] Kayani et al., *Crop Protection*, 2017

Conclusion

- **Modeling**
  - mechanistic model of plant functioning
  - plant model coupled to RKN population dynamics
- **Calibration**
  - plant parameters (8/26) & interaction parameters (6/15)
  - better estimates for pepper than tomato
  - estimation of pepper interaction parameters [ongoing]
  - comparison of dynamical patterns of 2 species: insights on the origin of tolerance [ongoing]


{thank you}

Global sensitivity analysis (GSA)

Goal: Identifying the most influential parameters

inputs : all parameters, **outputs** : model variables along time (vector)

Steps

1. fractional factorial design to explore parameter space
2. PCA to reduce output and capture its variability
3. ANOVA to compute sensitivity indices (SI)

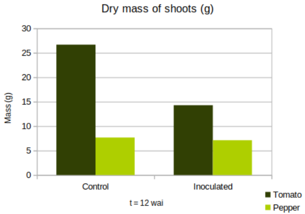
$$SI_{..} = \frac{SS_{..}}{TSS}, \qquad GSI = \sum_{k=1}^{components} SI_k \times inertia_k$$

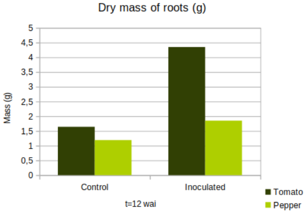
SS = sum of squares, TSS = total sum of squares

Data from ArchiNem project

- 2 plant species: tomato, pepper
- 2 plant categories:
  - control
  - inoculated by nematodes
- 6 replicates (90 plants)
- weekly number of leaves

- destructive measures, 3 points in time:
  - plant: fresh and dry masses for shoot, root and fruit
  - nematodes: number of galls, egg masses and egg per egg masses



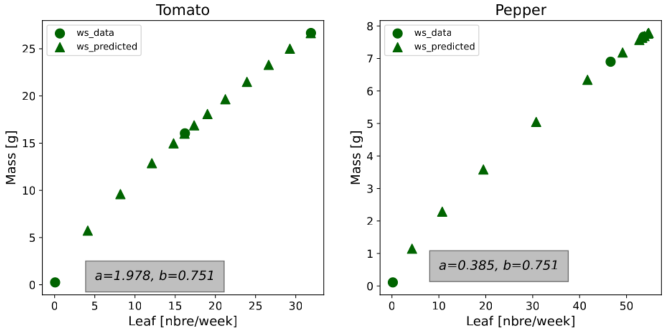


Allometric relationship

Equation

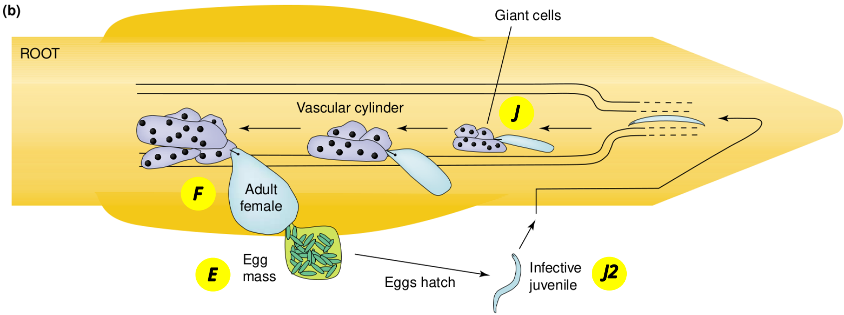
$$W_s^{\text{leaf}} = a\ L^b,$$

a, b allometric coefficients & weekly number of leaves (L).



Specific impacts

- clonal reproduction
- reduced water and nutrient uptake
- hijacking of plant resources (carbon)



Criterion for estimating plant parameters

Allometric relationship

$$W_s^{\text{leaf}} = a\ L^b,$$

a, b allometric coefficients & weekly number of leaves (L).

Cost function

$$err = \alpha_s \left[\frac{1}{2} \sum_{i=1}^{2} \left(\frac{\left(W_s^{sol}\right)_i - \left(W_s^{obs}\right)_i}{(W_s^{obs})_i} \right)^2 + \frac{1}{2} \sum_{i=1}^{2} \left(\frac{\left(W_r^{sol}\right)_i - \left(W_r^{obs}\right)_i}{(W_r^{obs})_i} \right)^2 + \left(\frac{W_f^{sol} - W_f^{obs}}{W_f^{obs}} \right)^2 \right]$$

$$+ \beta_s \underbrace{\left[\frac{1}{12} \sum_{i=1}^{12} \left(\frac{\left(W_s^{sol}\right)_i - \left(W_s^{leaf}\right)_i}{(W_s^{leaf})_i} \right)^2 \right]}_{\text{Addiotional data of Ws obtained via allometry}}$$

- α_s and $\beta_s = (1 - \alpha_s)$ are the weighted coefficients
- $\underset{k := \{s = shoot, r = root, f = fruit\}}{W_k^{sol} \text{ and } W_k^{obs}}$ are model predictions and data respectively.

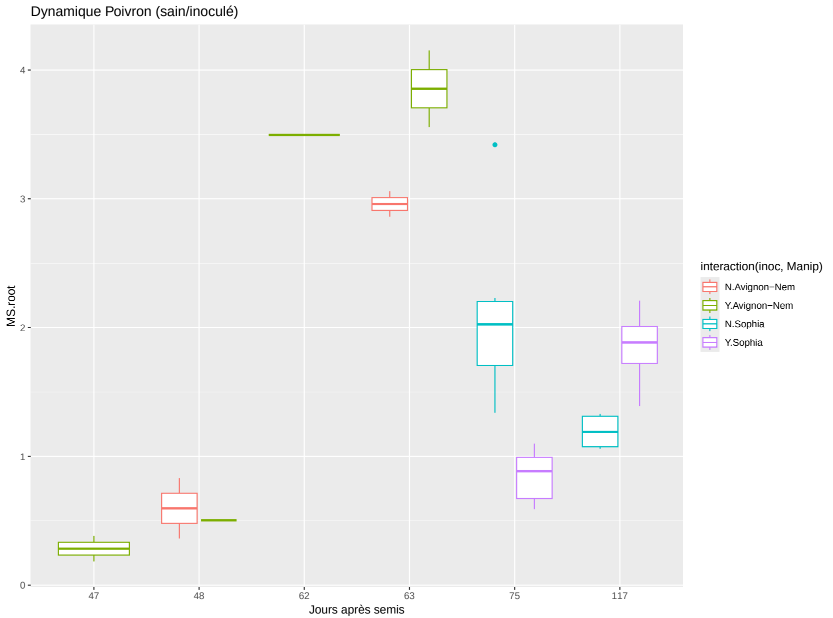
Criterion for estimating interaction parameters

Cost function

$$err = \alpha_c \underbrace{\left[\frac{1}{2} \sum_{i=1}^{2} \left(\frac{\left(W_s^{sol}\right)_i - \left(W_s^{obs}\right)_i}{(W_s^{obs})_i} \right)^2 + \frac{1}{2} \sum_{i=1}^{2} \left(\frac{\left(W_r^{sol}\right)_i - \left(W_r^{obs}\right)_i}{(W_r^{obs})_i} \right)^2 + \left(\frac{W_f^{sol} - W_f^{obs}}{w_f^{obs}} \right)^2 \right]}_{\text{Inoculated plant}}$$

$$+ \beta_c \underbrace{\left[\left(\frac{G^{sol} - G^{obs}}{G^{obs}} \right)^2 + \frac{1}{2} \sum_{i=1}^{2} \left(\frac{F_i^{sol} - F_i^{obs}}{F_i^{obs}} \right)^2 + \frac{1}{2} \sum_{i=1}^{2} \left(\frac{r_i^{sol} - r_i^{obs}}{r_i^{obs}} \right)^2 \right]}_{\text{Nematodes}}$$

- α_c and $\beta_c = (1 - \alpha_c)$ are the weighted coefficients
- G^{sol}, F^{sol}, r^{sol} are nematode model predictions of galls, females and egg-laying
- G^{obs}, F^{obs}, r^{obs} are nematode data


Dynamique Poivron (sain/inoculé)
MS.root
0
1
2
3
4
47
48
62
63
75
117
Jours après semis
interaction(inoc, Manip)
N.Avignon−Nem
Y.Avignon−Nem
N.Sophia
Y.Sophia

Carbon transport (T)

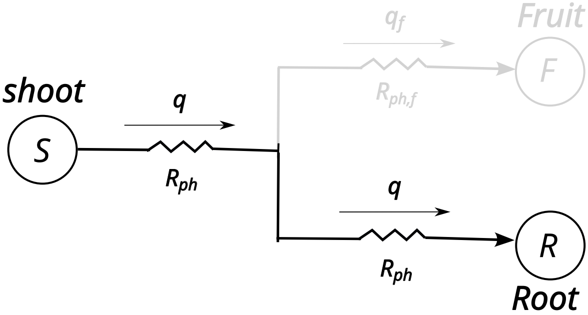
$$
\text{Shoot}\begin{cases}
\dfrac{dW_s}{dt} = \underbrace{k_s f(\psi_s)\dfrac{C_s}{K_s + C_s} W_s}_{\text{Growth}} - \underbrace{\Gamma_s \left(\dfrac{K_m^n}{K_m^n + C_s^n}\right) W_s}_{\text{Additional mortality due to carbon shortage}}, \\[2ex]
\dfrac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} - \dfrac{1}{W_s}\underbrace{(T_r + T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,s})\, k_s f(\psi_s) \dfrac{C_s}{K_s + C_s}}_{\text{Growth}} - \underbrace{r_{m,s}\left(\dfrac{C_s^n}{K_m^n + C_s^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_s}\dfrac{dW_s}{dt} C_s}_{\text{dilution}}
\end{cases}
$$

$$
\text{Root}\begin{cases}
\dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r)\dfrac{C_r}{K_r + C_r} W_r}_{\text{Growth}} - \underbrace{\Gamma_r W_r}_{\text{Natural mortality}} - \underbrace{\Gamma_r \left(\dfrac{K_m^n}{K_m^n + C_r^n}\right) W_r}_{\text{Additional mortality due to carbon shortage}}, \\[2ex]
\dfrac{dC_r}{dt} = \dfrac{1}{W_r}\underbrace{T_r}_{\text{Transport}} - \underbrace{(f_c + r_{g,r})\, k_r f(\psi_r) \dfrac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{r_{m,r}\left(\dfrac{C_r^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{c_{rh}\, C_r}_{\text{Rhizodeposition}} - \underbrace{\dfrac{1}{W_r}\dfrac{dW_r}{dt} C_r}_{\text{dilution}}
\end{cases}
$$

$$
\text{Fruit}\begin{cases}
\dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f + C_f} W_f}_{\text{Growth}} - \underbrace{\Gamma_f W_f}_{\text{Natural mortality}} - \underbrace{\Gamma_f \left(\dfrac{K_m^n}{K_m^n + C_f^n}\right) W_f}_{\text{Additional mortality due to carbon shortage}}, \\[2ex]
\dfrac{dC_f}{dt} = \dfrac{1}{W_f}\underbrace{(T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,f})\, k_f f(\psi_f) \dfrac{C_f}{K_f + C_f}}_{\text{Growth}} - \underbrace{r_{m,f}\left(\dfrac{C_f^n}{K_m^n + C_f^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_f}\dfrac{dW_f}{dt} C_f}_{\text{dilution}}
\end{cases}
$$

Carbon transport (T)

The carbon flow[3] T in phloem vessels $T = q\ C_s$, with q the volume flow rate



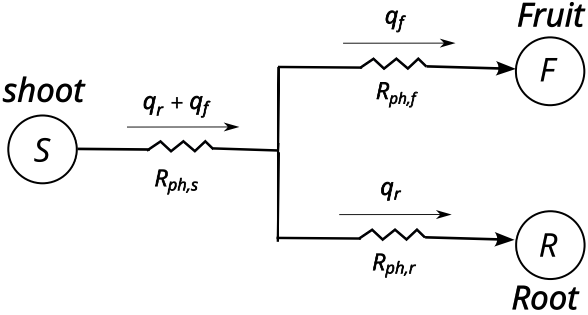
Then,

$$\begin{cases} (q_r + q_f) R_{ph,s} + q_r\ R_{ph,r} = (C_s - C_r) \\ (q_r + q_f) R_{ph,s} + q_f\ R_{ph,f} = (C_s - C_f) \end{cases}$$

$$\begin{cases} T = \dfrac{(C_s - C_r)}{R_{ph}} C_s \\ R_{ph,..} = \dfrac{r_{ph,..}}{W_{..}^{\alpha_{..}}} \end{cases}$$

[3] Minchin et al., *Journal of Experimental Botany*, 1993

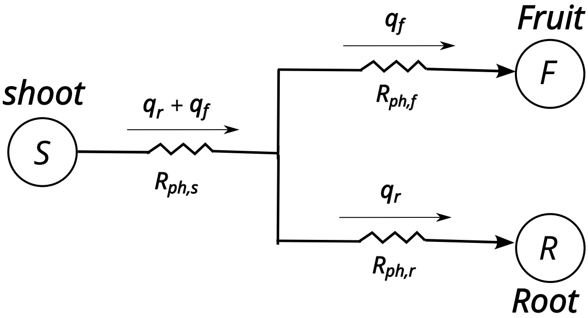
Carbon transport (T)



Therefore,

$$\begin{cases} (q_r + q_f)R_{ph,s} + q_r \; R_{ph,r} = (C_s - C_r) \\ (q_r + q_f)R_{ph,s} + q_f \; R_{ph,f} = (C_s - C_f) \end{cases}$$

Carbon transport (T)



Therefore,

$$\begin{cases} (q_r + q_f)R_{ph,s} + q_r \; R_{ph,r} = (C_s - C_r) \\ (q_r + q_f)R_{ph,s} + q_f \; R_{ph,f} = (C_s - C_f) \end{cases}$$

$$\begin{cases} T_r = q_r C_s \\ T_f = \left(\dfrac{W_s^n}{I^n + W_s^n} \right) q_f C_s \end{cases}$$

Water transport

Shoot

$$
\begin{cases}
\dfrac{dW_s}{dt} = \underbrace{k_s f(\psi_s)\dfrac{C_s}{K_s + C_s} W_s}_{\text{Growth}} - \underbrace{\Gamma_s\, W_s}_{\text{Natural mortality}} - \underbrace{\Gamma_s \left(\dfrac{K_m^n}{K_m^n + C_s^n}\right) W_s}_{\text{Additional mortality due to carbon shortage}}, \\[2ex]
\dfrac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} - \dfrac{1}{W_s}\underbrace{(T_r + T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,s})\, k_s f(\psi_s)\dfrac{C_s}{K_s + C_s}}_{\text{Growth}} - \underbrace{r_{m,s}\left(\dfrac{C_s^n}{K_m^n + C_s^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_s}\dfrac{dW_s}{dt} C_s}_{\text{dilution}}
\end{cases}
$$

Root

$$
\begin{cases}
\dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r)\dfrac{C_r}{K_r + C_r} W_r}_{\text{Growth}} - \underbrace{\Gamma_r\, W_r}_{\text{Natural mortality}} - \underbrace{\Gamma_r \left(\dfrac{K_m^n}{K_m^n + C_r^n}\right) W_r}_{\text{Additional mortality due to carbon shortage}}, \\[2ex]
\dfrac{dC_r}{dt} = \dfrac{1}{W_r}\underbrace{T_r}_{\text{Transport}} - \underbrace{(f_c + r_{g,r})\, k_r f(\psi_r)}_{\text{Growth}} - \underbrace{r_{m,r}\left(\dfrac{C_r^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{c_{rh}\, C_r}_{\text{Rhizodeposition}} - \underbrace{\dfrac{1}{W_r}\dfrac{dW_r}{dt} C_r}_{\text{dilution}}
\end{cases}
$$

Fruit

$$
\begin{cases}
\dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f + C_f} W_f}_{\text{Growth}} - \underbrace{\Gamma_f\, W_f}_{\text{Natural mortality}} - \underbrace{\Gamma_f \left(\dfrac{K_m^n}{K_m^n + C_f^n}\right) W_f}_{\text{Additional mortality due to carbon shortage}}, \\[2ex]
\dfrac{dC_f}{dt} = \dfrac{1}{W_f}\underbrace{(T_f + \mathrm{T}_a)}_{\text{Transport}} - \underbrace{(f_c + r_{g,f})\, k_f f(\psi_f)\dfrac{C_f}{K_f + C_f}}_{\text{Growth}} - \underbrace{r_{m,f}\left(\dfrac{C_f^n}{K_m^n + C_f^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\dfrac{1}{W_f}\dfrac{dW_f}{dt} C_f}_{\text{dilution}}
\end{cases}
$$

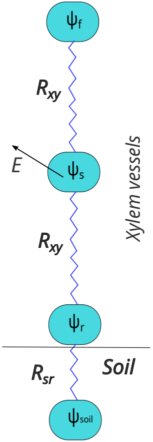
Water transport

Transpiration process E guiding water flow, $E = \sigma_W W_s f(\psi_s)$,

$$\psi_r = \psi_{sol} - R_{sr} E, \qquad \psi_s = \psi_r - R_{xy} E, \qquad \psi_f = \psi_s.$$

where ψ_{sol} the soil water potential and $R_{..}$ resistances.

$$R_{sr} = \frac{r_{sr}}{W_r^{\alpha_r}}, \qquad R_{xy,..} = \frac{r_{xy,..}}{W_{..}^{\alpha_{..}}}.$$



Water regulation function

$$f(\psi) = \frac{\psi^n}{K^n + \psi^n}$$