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

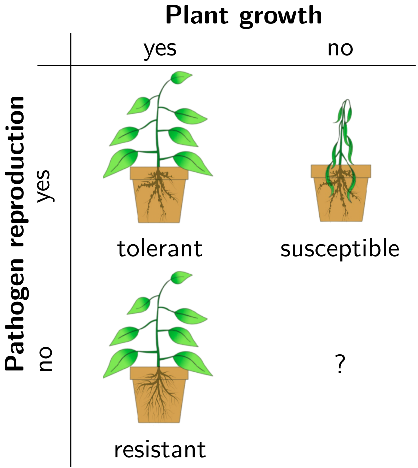
Joseph Penlap, Suzanne Touzeau, Valentina Baldazzi, Frédéric Grognard

INRAE / UMR 1355 ISA / M2P2 & Inria / MACBES

IPN Lab meeting, Sophia Antipolis, France

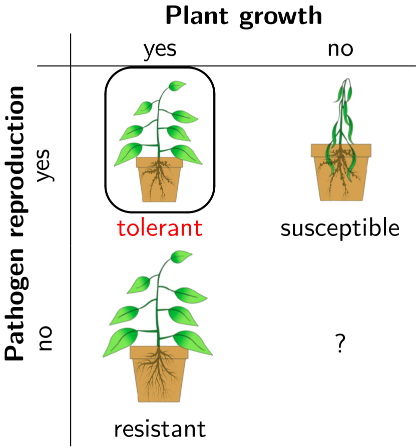
Plant variability

Strong variability in plant response to RKN parasitism among crop species



Plant variability

Strong variability in plant response to RKN parasitism among crop species

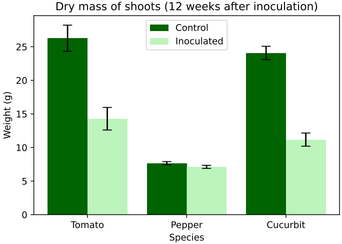


Which mechanisms underlie plant tolerance?

Experimental data (ArchiNem project)

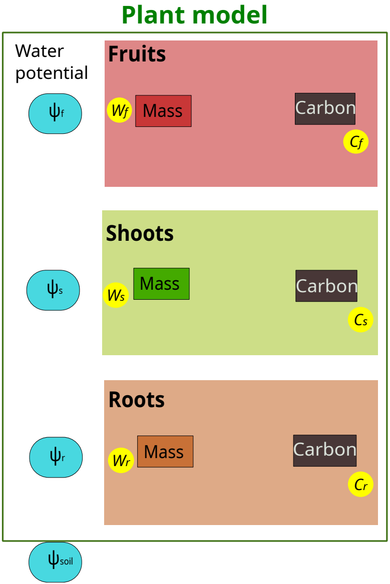
- 3 plant species: tomato, pepper, cucurbit
- 2 plant categories:
  - control
  - inoculated by nematodes
- 3 points in time (T0, T6 = 6 wai, T12 = 12 wai)
- 6 replicates*category / point

- weekly number of leaves
- destructive measures:
  - **plant**: fresh and dry masses for shoot, root and fruit
  - **nematodes**:
    - number of galls (T6)
    - egg masses (T6, T12)
    - egg per egg masses (T6, T12)
    - soil-extracted larvae (T12)

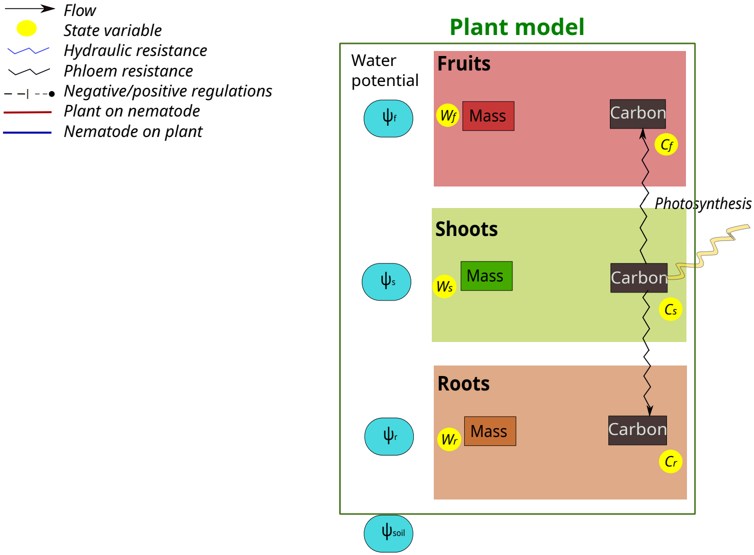


Integrated plant-pest model

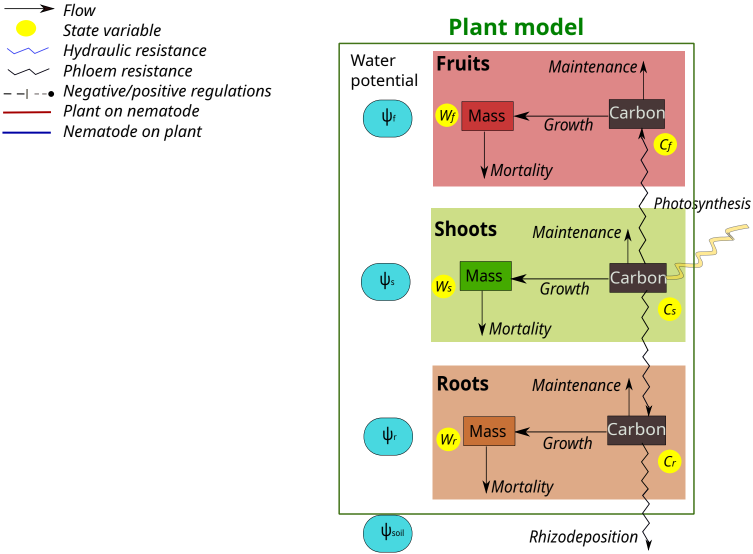
Flow
State variable
Hydraulic resistance
Phloem resistance
Negative/positive regulations
Plant on nematode
Nematode on plant



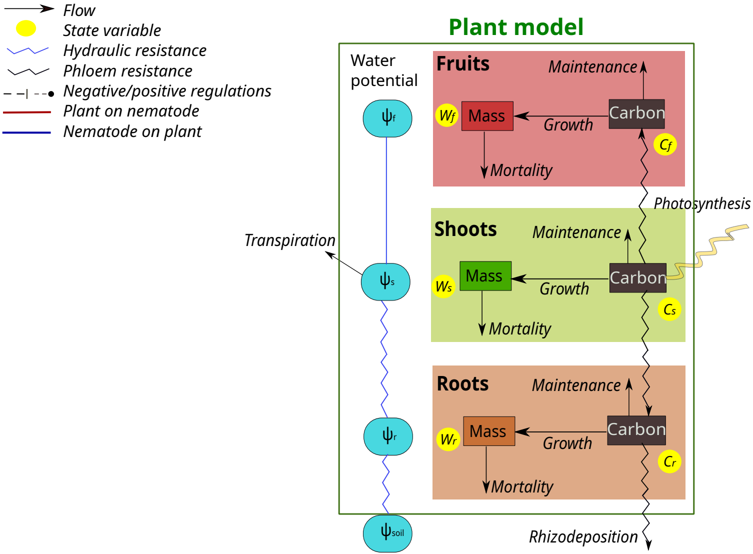
Integrated plant-pest model



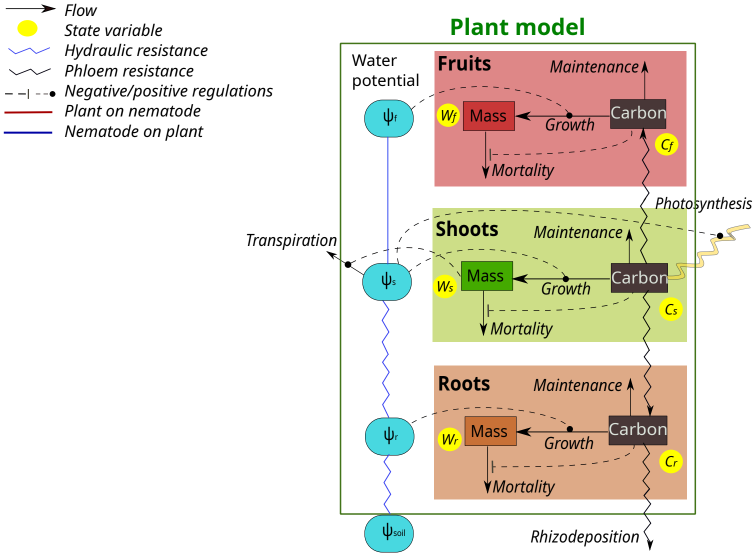
Integrated plant-pest model



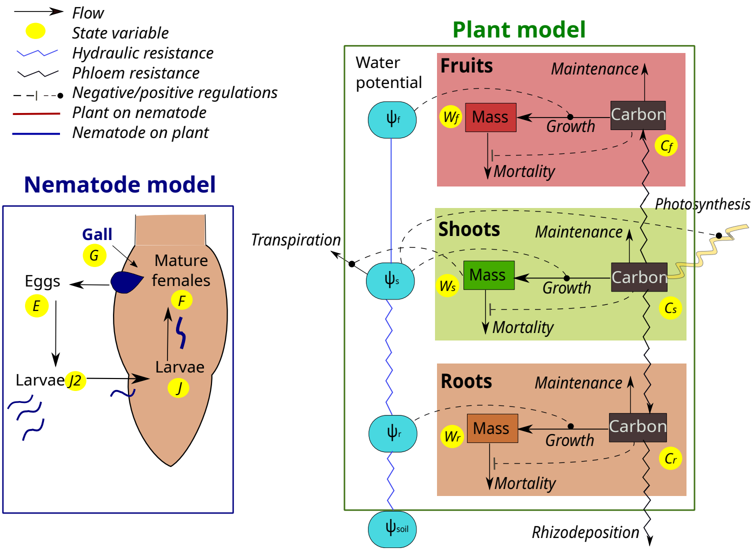
Integrated plant-pest model



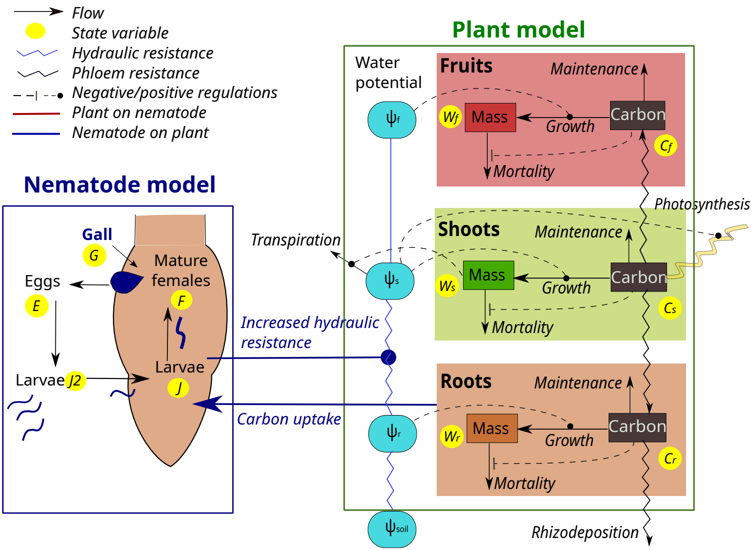
Integrated plant-pest model



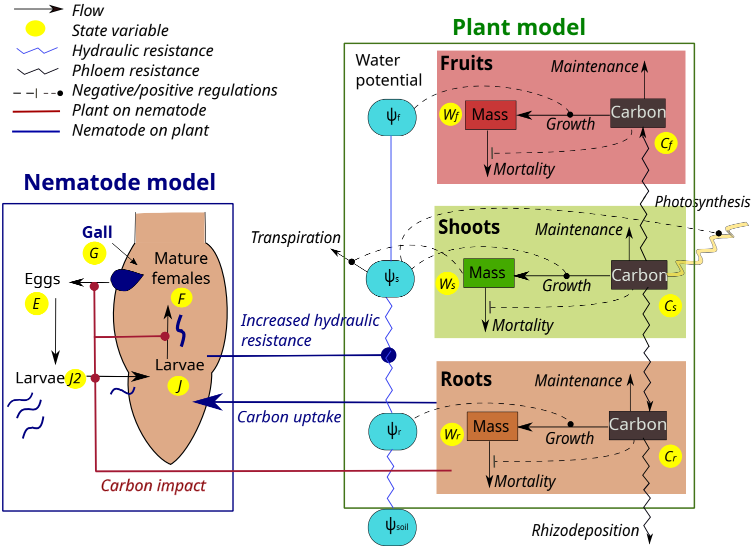
Integrated plant-pest model



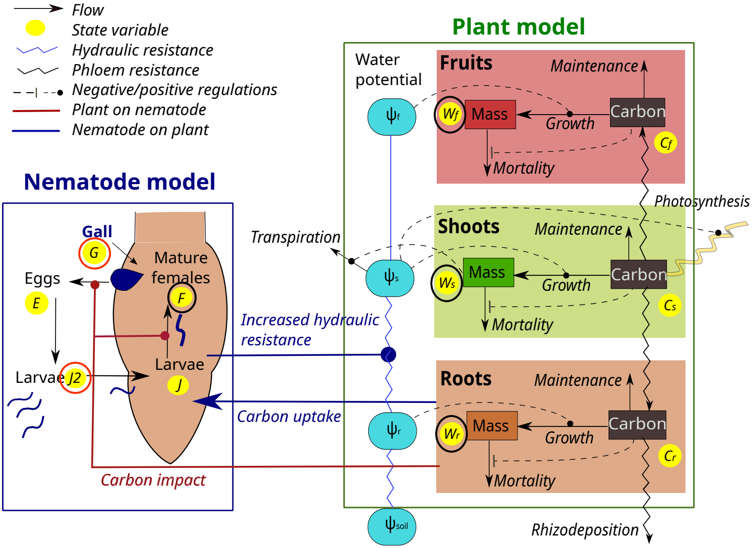
Integrated plant-pest model



Integrated plant-pest model



Integrated plant-pest model



+ weekly number of leaves

Calibration procedure

Two-phases strategy

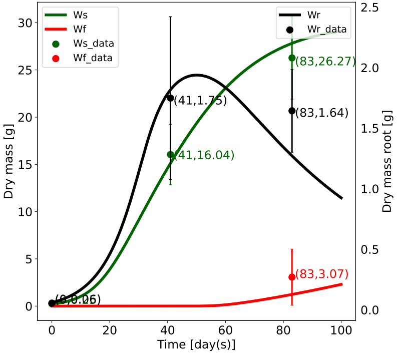
- calibration of plant model on control data
- calibration of plant-RKN model on inoculated plants & RKN data

Steps

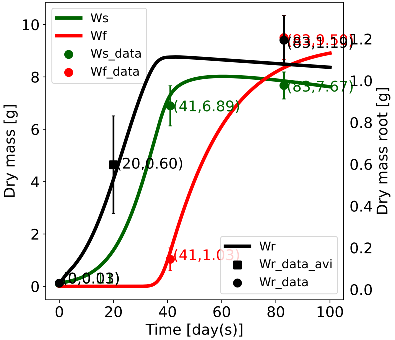
- select parameters to be estimated based on **sensitivity analysis**
- find parameter values that minimize the criterion
  - Global search: ARS (Adaptive Random Searches)
  - Local search: Nelder-Mead from *minimize()* python module

Plant model calibration

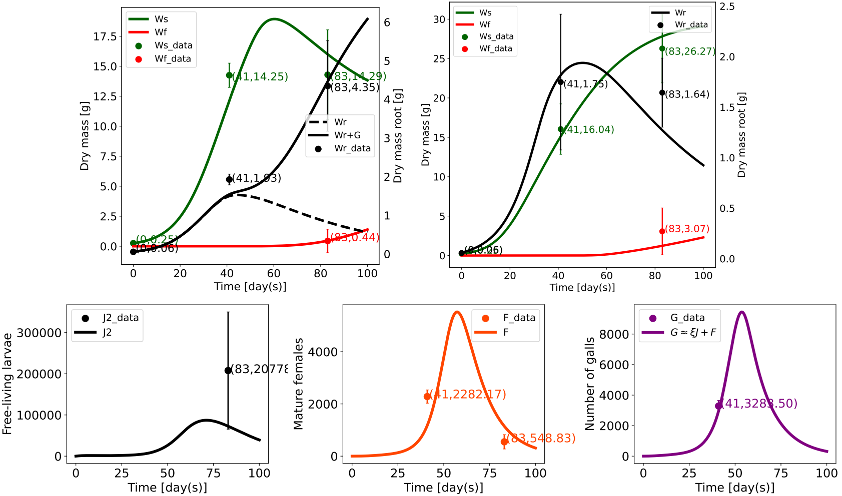
Tomato dynamics



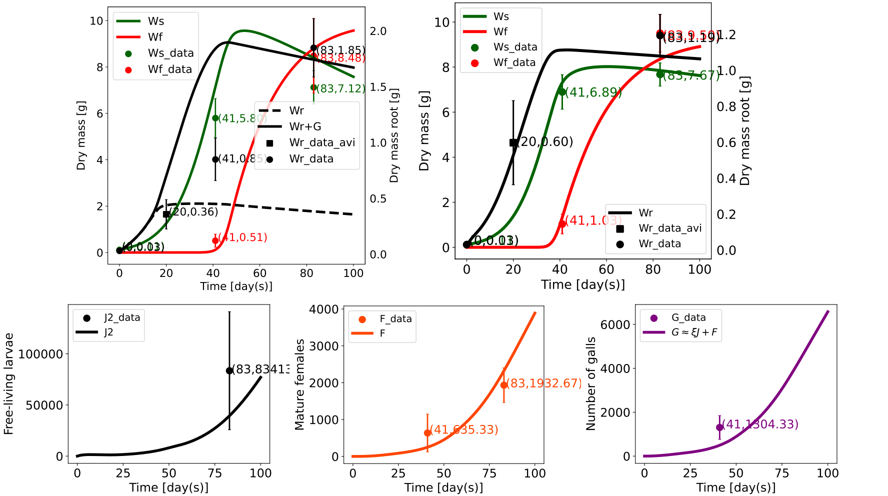
Pepper dynamics



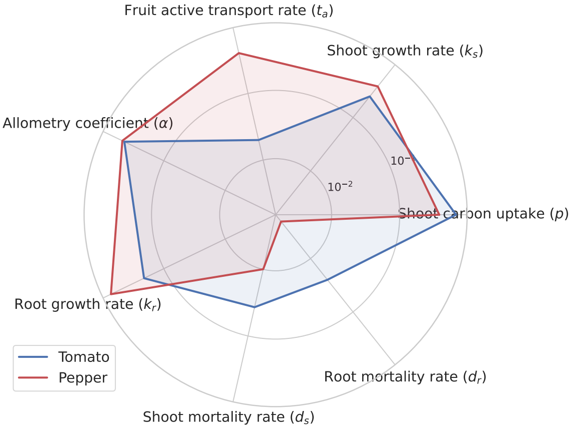
Plant-RKN model calibration: tomato



Plant-RKN model calibration: pepper



Tomato vs Pepper: Plant parameters



Pepper: reduced mortality γ_r, higher growth k_r, faster C allocation towards fruits t_a

First simulations for virtual tomato plants

Are these traits really important for plant tolerance?

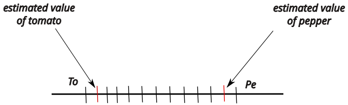
First simulations for virtual tomato plants

Are these traits really important for plant tolerance?

Virtual tomato plant

- root mortality rate (d_r)
- root growth rate (k_r)
- faster C allocation towards fruits (t_a)

Full factorial design



All other parametres are kept fixed to estimated values

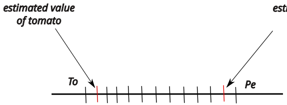
First simulations for virtual tomato plants

Are these traits really important for plant tolerance?

Virtual tomato plant

- root mortality rate (d_r)
- root growth rate (k_r)
- faster C allocation towards fruits (t_a)

Full factorial design



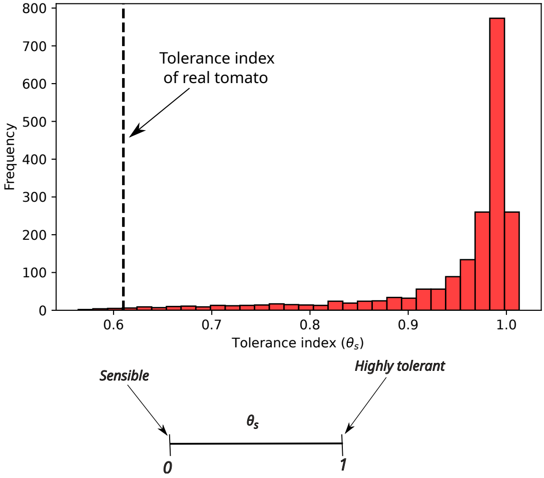
All other parametres are kept fixed to estimated values

Tolerance index (over the cropping season)

$$\theta_s = \frac{\text{Cumulative dry mass of } \textbf{infected} \text{ shoots}}{\text{Cumulative dry mass of } \textbf{healthy} \text{ shoots}}$$

Results

Tolerance indices



Conclusion: possible more tolerant tomatoes.

Next steps

- Complete comparison between tomato and pepper traits (parameter values)
- Robustness of tolerance traits
  - infection scenarios (low, medium, high RKN virulence)
  - trade-off between tolerance vs soil infestation (epidemiological risk)

Collaborators:

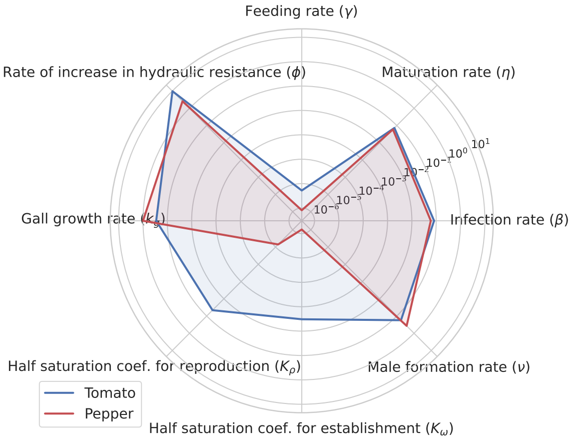
INRAE collegues:

- C. Caporalino
- L. Pagès
- C. Doussan

Master students

- T. Brenière
- N. Juazion-Graverolle
- C. Bourgade
- E. Ceci
- A. Canaud

Tomato vs Pepper: RKN infection parameters



Tomato: Higher effect of plant status on RKN reproduction K_ρ and establishement K_ω rates

Tolerance Index

Yield

$$\theta_s = \frac{\int_0^T W_s^{inoc}(t)dt}{\int_0^T W_s^{healthy}(t)dt},$$

Plant Model: Mathematical equations

Shoot

$$\begin{cases} \dfrac{dW_s}{dt} = \underbrace{k_s f_g(\psi_s)\dfrac{C_s}{K_s + C_s} W_s}_{\text{Growth}} - \underbrace{d_s\left(1 + \dfrac{K_m^n}{K_m^n + C_s^n}\right) W_s}_{\text{Mortality}}, \\ \dfrac{dC_s}{dt} = \underbrace{p\left(\dfrac{1}{K_u + W_s}\right) f_p(\psi_s)}_{\text{Uptake}} - \underbrace{\dfrac{1}{W_s}\left(T_r + T_f + T_a\right)}_{\text{Transport}} - \underbrace{(b + r_{g,s})\, k_s f_g(\psi_s)\dfrac{C_s}{K_s + C_s}}_{\text{Growth+Respiration}} - \underbrace{r_{m,s}\left(\dfrac{C_s^n}{K_m^n + C_s^n}\right)}_{\text{Maintenance}} - \underbrace{\dfrac{1}{W_s}\dfrac{dW_s}{dt} C_s}_{\text{Dilution}}, \end{cases}$$

Root

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

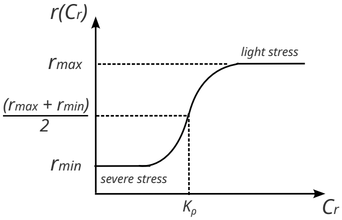
Fruit

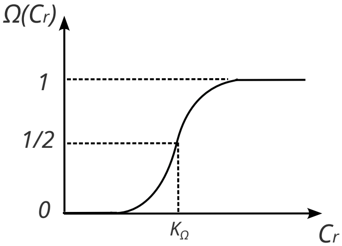
$$\begin{cases} \dfrac{dW_f}{dt} = \underbrace{k_f f_g(\psi_f)\dfrac{C_f}{K_f + C_f} W_f}_{\text{Growth}} - \underbrace{d_f\left(1 + \dfrac{K_m^n}{K_m^n + C_f^n}\right) W_f}_{\text{Mortality}}, \\ \dfrac{dC_f}{dt} = \underbrace{\dfrac{1}{W_f}\left(T_f + T_a\right)}_{\text{Transport}} - \underbrace{(b + r_{g,f})\, k_f f_g(\psi_f)\dfrac{C_f}{K_f + C_f}}_{\text{Growth+Respiration}} - \underbrace{r_{m,f}\left(\dfrac{C_f^n}{K_m^n + C_f^n}\right)}_{\text{Maintenance}} - \underbrace{\dfrac{1}{W_f}\dfrac{dW_f}{dt} C_f}_{\text{Dilution}}. \end{cases}$$

Plant status on RKN development

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

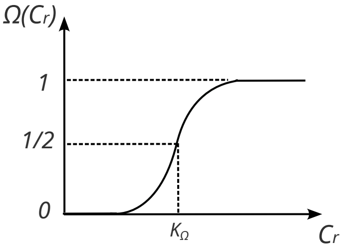
$$\text{RKN}\begin{cases}\dfrac{dJ}{dt} = \underbrace{\Omega(C_r)\,\beta\,J_2 W_r}_{\text{RKN entry}} - \underbrace{\eta\,J}_{\text{Maturation}} - \underbrace{\mu_j\,J}_{\text{Mortality}}\\[2ex] \dfrac{dF}{dt} = \underbrace{\eta\,J}_{\text{Maturation}} - \underbrace{\mu_F\,F}_{\text{Mortality}}\end{cases}$$

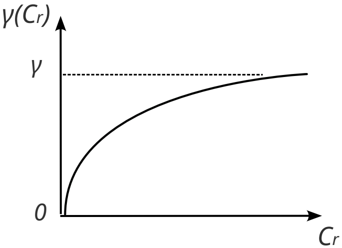




RKN effects on plant growth

$$
\text{Root}\begin{cases}
\dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r)\dfrac{C_r}{K_r + C_r}W_r}_{\text{Growth}} - \underbrace{\gamma_r\left(1 + \dfrac{K_m^n}{K_m^n + C_r^n}\right)W_r}_{\text{Mortality}} - \underbrace{\Omega(C_r)\,\epsilon\,\beta\,J_2\,W_r}_{\text{Successfully infected roots}} \\[2ex]
\dfrac{dG}{dt} = \underbrace{\Omega(C_r)\,\epsilon\,\beta\,J_2\,W_r}_{\text{Gall formation}} + \underbrace{k_g f(\psi_r)\dfrac{C_r}{K_r + C_r}G}_{\text{Growth}} - \underbrace{\Gamma_r\,G}_{\text{Natural mortality}} \\[2ex]
\dfrac{dC_r}{dt} = \dfrac{1}{(W_r + G)}\underbrace{T_r}_{\text{Transport}} \underbrace{-(f_c + r_{g,r})\left(\dfrac{k_r W_r + k_g G}{W_r + G}\right)f(\psi_r)\dfrac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{r_{m,r}\left(\dfrac{C_r^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{c_{rh}C_r}_{\text{Rhizodeposition}} \\[2ex]
\qquad - \underbrace{\dfrac{C_r}{(W_r + G)}\left(\dfrac{dW_r}{dt} + \dfrac{dG}{dt}\right)}_{\text{dilution}} - \underbrace{\dfrac{1}{(W_r + G)}\gamma(C_r)\,(F + J)}_{\text{Nematode feeding}}
\end{cases}
$$





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)

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

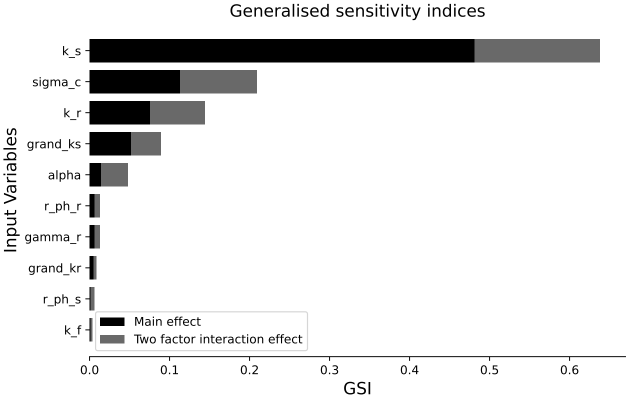
SS = sum of squares, TSS = total sum of squares

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

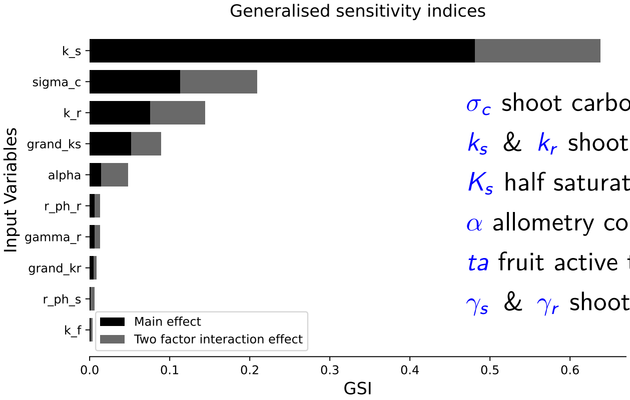


Global sensitivity analysis on plant model

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



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

Data processing

Objective: increase the number of data points by exploiting non-destructive measurements (leaf number)

Allometric relation: shoot weight vs leaf number

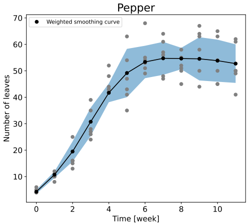
- Spline smoothing of leaf data
  - average dynamics
- Calibration of a general allometric relation (3 time-points x 3 species)

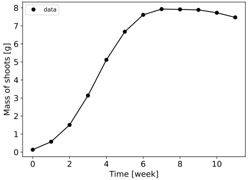
$$M = a\,L^{b_i}, \quad i = \text{species}\,1,2,3$$

M = shoot dry mass, L= number of leaves

$$\Downarrow$$

- Prediction of shoot dry mass from leaf data at 12 time-points





Criterion for estimating interaction parameters

Cost function

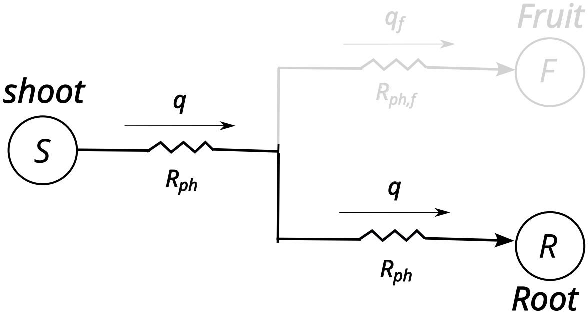
$$err = \alpha_c \underbrace{\left[\frac{1}{2} \sum_{i=1}^{2} \left(\frac{(W_s^{sol})_i - (W_s^{obs})_i}{(W_s^{obs})_i} \right)^2 + \frac{1}{2} \sum_{i=1}^{2} \left(\frac{(W_r^{sol})_i - (W_r^{obs})_i}{(W_r^{obs})_i} \right)^2 + \left(\frac{W_f^{sol} - W_f^{obs}}{w_f^{obs}} \right)^2 \right]}_{\text{Inoculated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

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

- 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

Carbon transport (T)

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



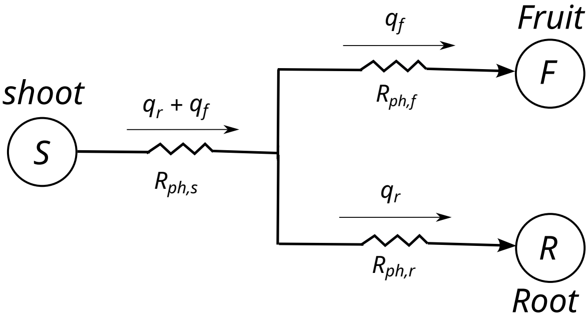
Then,

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

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

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

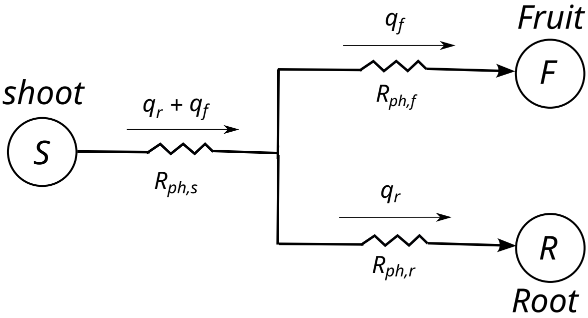
Carbon transport (T)



We get,

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

Carbon transport (T)



We get,

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

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

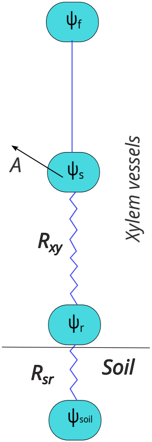
Water transport

Transpiration process A guides water flow, $A = \sigma_W W_s f(\psi_s)$,

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

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

$$R_{sr} = \frac{r_{sr}}{W_r^{\alpha_r}}, \quad R_{xy,z} = \frac{r_{xy,z}}{W_z^{\alpha_z}}, \quad z = \{s, r\}.$$



Water regulation function

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