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

Joseph Junior Penlap Tamagoua, Suzanne Touzeau, Frédéric Grognard, Valentina Baldazzi

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INRAE, Institut Sophia Agrobiotech & Inria Sophia

PHARE workshop, Rennes, France

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

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

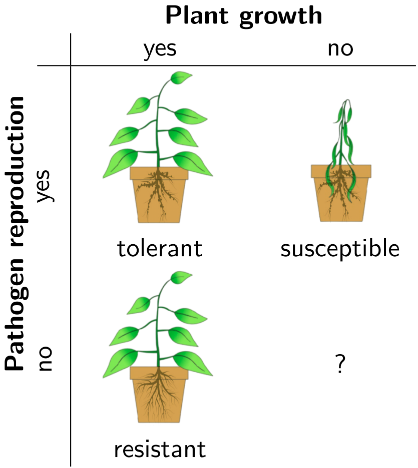
[1] Djian-Caporalino, *EPPO Bulletin*, 2012

Main impacts

- root deformation (galls)
- stunted growth and wilting

Plant variability

Strong variability in plant response to RKN parasitism among crop species



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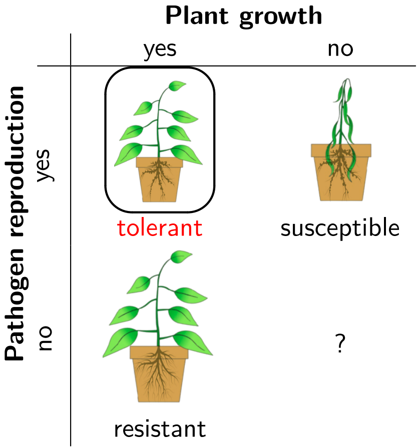


Which mechanisms underlie plant tolerance?

Modelling

Traditionally,

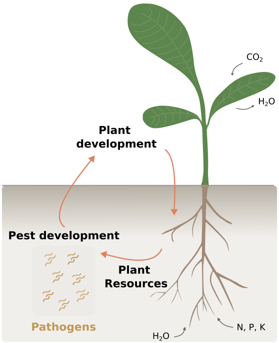
- **Ecological models**: focus on pathogen population dynamics
- **Ecophysiological models**: focus on plant growth and abiotic factors

However, plant-pest dynamics are **strongly coupled**

- Pests divert plant resources for development
- Pest development affects plant physiology
  - resource allocation to damaged organs
  - growth vs defence metabolism

Approach: Coupled modeling of plant physiology and pest population dynamics

- better prediction of plant growth and yield
- screening of interesting plant phenotypic traits



Plant Model

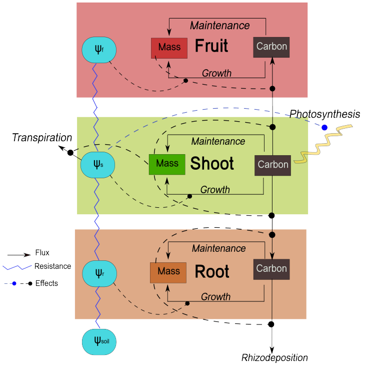
Inspired from Transport-Resistance models (Thornley 1972, Dewar 1991)

3 Compartments

- Roots, Shoots and Fruits

2 Resources

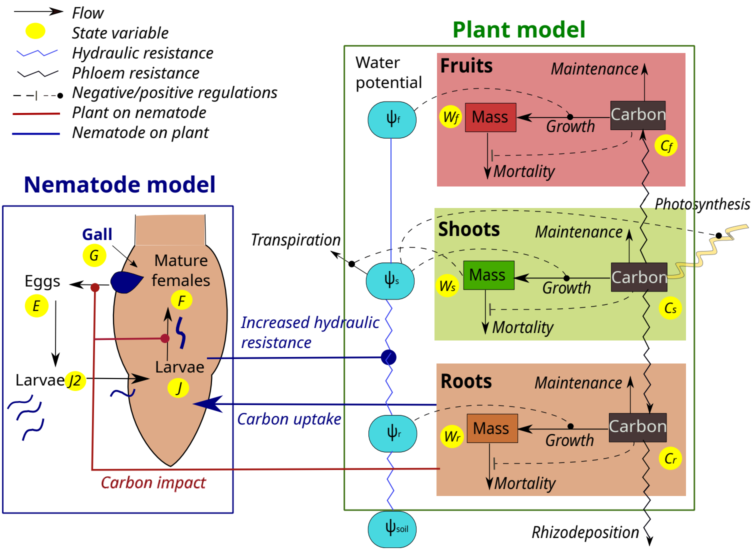
- Carbon
- Water



Processes

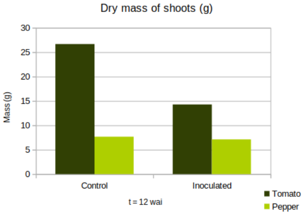
- Carbon balance
  - C uptake, transport and allocation
  - maintenance and growth respiration
  - rhyzodeposition
- Water transport: water potential
- Regulatory functions with respect to the water status of the plant

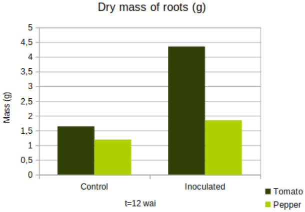
Integrated plant-pest model



Calibration Data

- 2 plant species: tomato, pepper
- 2 plant categories:
  - control
  - inoculated by nematodes
- 6 replicates/condition
- 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





Calibration procedure

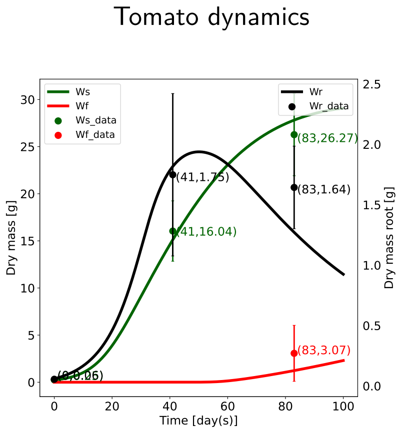
Two-phases strategy

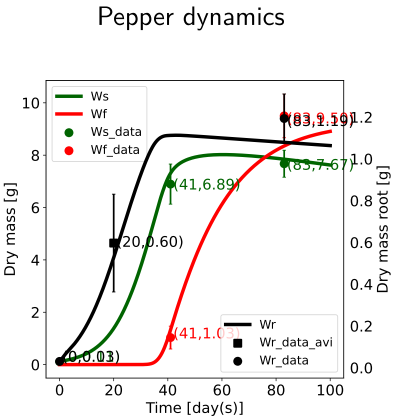
- calibration of plant model on control data
- calibration of plant-RKN model on inoculated plants & RKN data

Steps

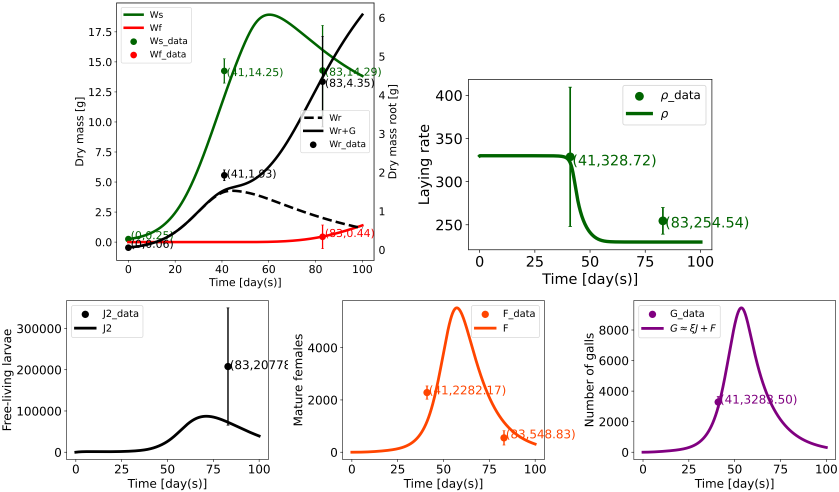
- select parameters to be estimated based on **sensitivity analysis**
- least squares **criterion** between model simulations and data
- find parameter values that minimize the criterion
  - Global search: ARS (Adaptive Random Searches)
  - Local search: Nelder-Mead from *minimize()* python module

Plant model calibration:

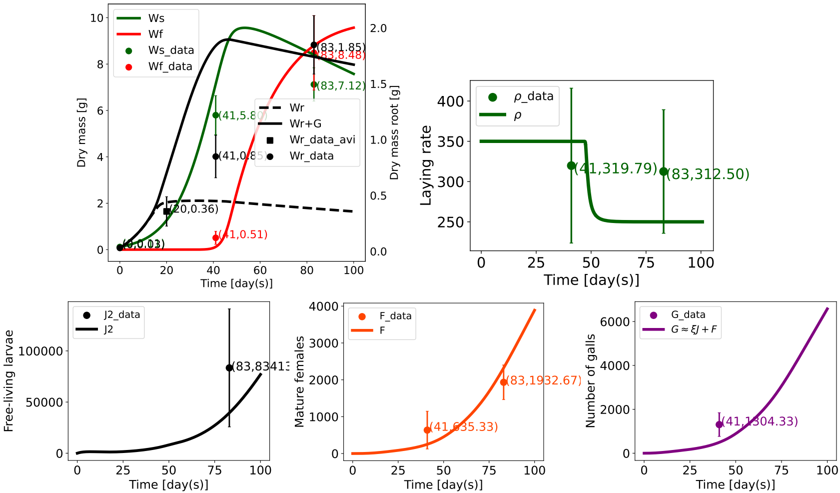




Plant-RKN model calibration: tomato

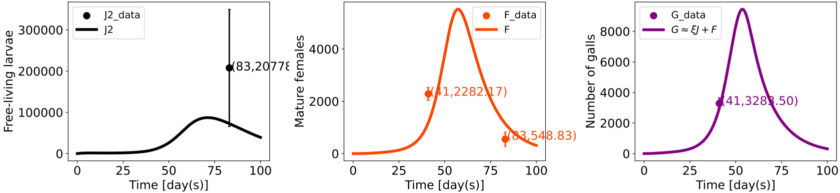


Plant-RKN model calibration: pepper

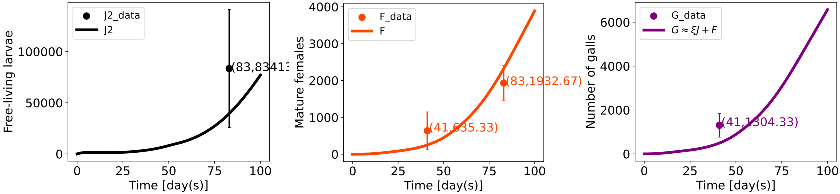


Different RKN dynamics for the two species

Tomato:

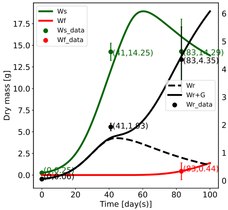


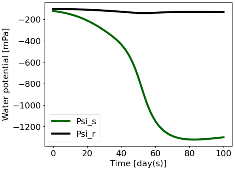
Pepper:

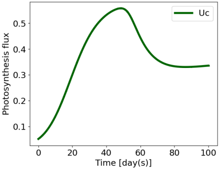


Different plant response to RKN

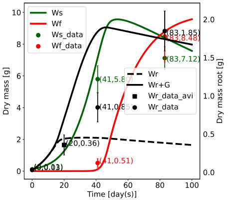
Tomato

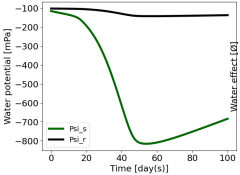


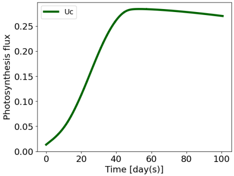




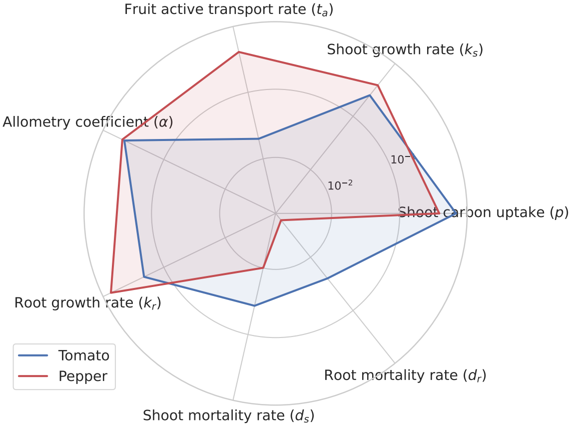
Pepper





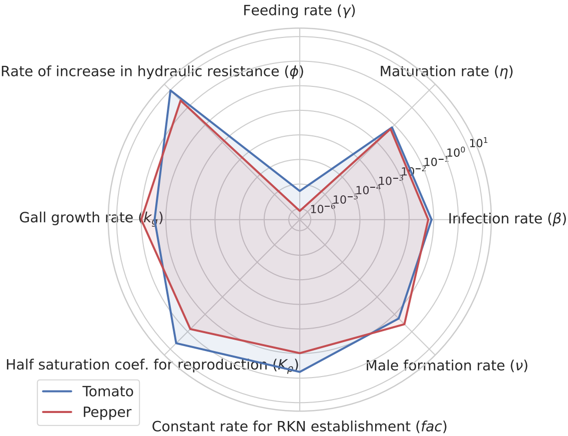


Tomato vs Pepper: Plant parameters



- Reduced mortality γ_r for pepper roots
- Faster C allocation towards fruits (active transport)

Tomato vs Pepper: RKN infection parameters



- Different plant-induced effect on RKN reproduction and establishement rates
- Reduced gall impact on plant hydraulic resistance for pepper

First simulations for virtual tomato plants

Are these traits really important for plant tolerance?

First simulations for virtual tomato plants

Virtual tomato plant

- reduced root mortality (pepper value)
- increased active transport to fruits (pepper value)

All other parametres are kept fixed to estimated values

Tolerance indices

$$TI_s = \frac{W_s^{inoc}}{W_s^{healthy}}, \qquad TI_f = \frac{W_f^{inoc}}{W_f^{healthy}}$$

First simulations for virtual tomato plants

Virtual tomato plant

- reduced root mortality (pepper value)
- increased active transport to fruits (pepper value)

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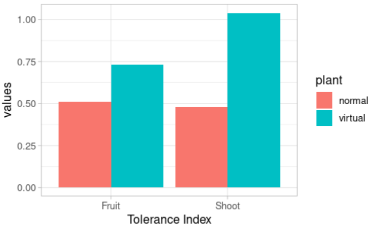
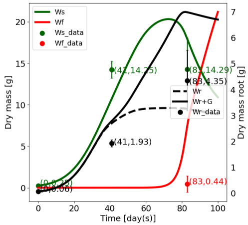
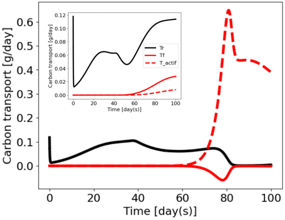


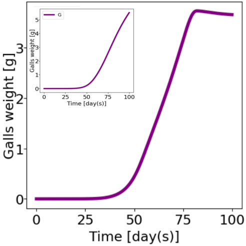


First simulations for virtual tomato plants

Fruit priority reduces
C transport towards roots

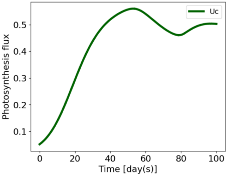


Reduced gall growth

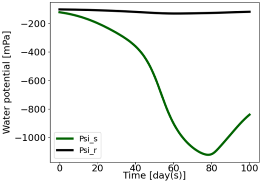


Low root mortality

Maintained photosynthesis rate



Reduced hydraulic impact



Conclusions & Perspectives

- mechanistic model of plant-RKN interactions
- good agreement with experimental data
    - estimation of interaction parameters

Perspectives

- *In silico* validation of tolerance traits
    - Numerical exploration of selected parameter combinations
- Robustness of tolerance traits
    - Infection scenarios (low, medium,high RKN virulence)
    - Time-horizon (multi-seasonal)
    - Impact of abiotic factors

Collaborators:

INRAE collegues:

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

Master students

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

Plant Model: Mathematical equations

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

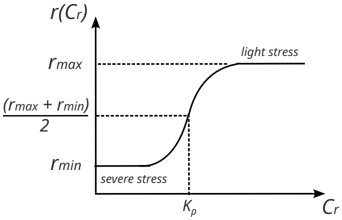
$$
\text{Root}\begin{cases}
\dfrac{dW_r}{dt} = \underbrace{k_r f_g(\psi_r)\dfrac{C_r}{K_r + C_r} W_r}_{\text{Growth}} - \underbrace{d_r\left(1 + \dfrac{K_m^n}{K_m^n + C_r^n}\right) W_r}_{\text{Mortality}}, \\
\dfrac{dC_r}{dt} = \underbrace{\dfrac{1}{W_r} T_r}_{\text{Transport}} - \underbrace{(b + r_{g,r})\,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

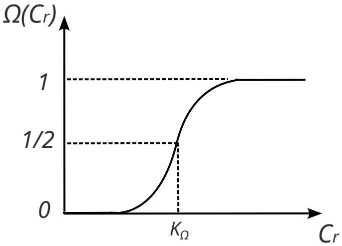
$$
\text{Fruit}\begin{cases}
\dfrac{dW_f}{dt} = \underbrace{k_f f_g(\psi_f)\dfrac{C_f}{K_f + C_f} W_f}_{\text{Growth}} - \underbrace{d_f\left(1 + \dfrac{K_m^n}{K_m^n + C_f^n}\right) W_f}_{\text{Mortality}}, \\
\dfrac{dC_f}{dt} = \underbrace{\dfrac{1}{W_f}\left(T_f + T_a\right)}_{\text{Transport}} - \underbrace{(b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

Plant status on RKN development

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

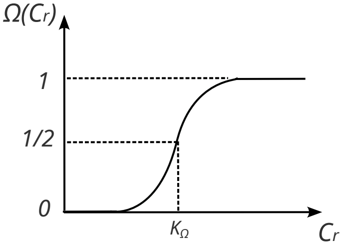
RKN
$$\begin{cases} \dfrac{dJ}{dt} = \underbrace{\Omega(C_r)\,\beta\,J_2 W_r}_{\text{RKN entry}} - \underbrace{\eta\,J}_{\text{Maturation}} - \underbrace{\mu_j\,J}_{\text{Mortality}} \\ \dfrac{dF}{dt} = \underbrace{\eta\,J}_{\text{Maturation}} - \underbrace{\mu_F\,F}_{\text{Mortality}} \end{cases}$$

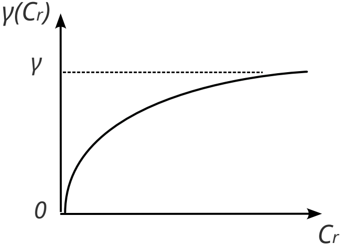




RKN effects on plant growth

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





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)

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

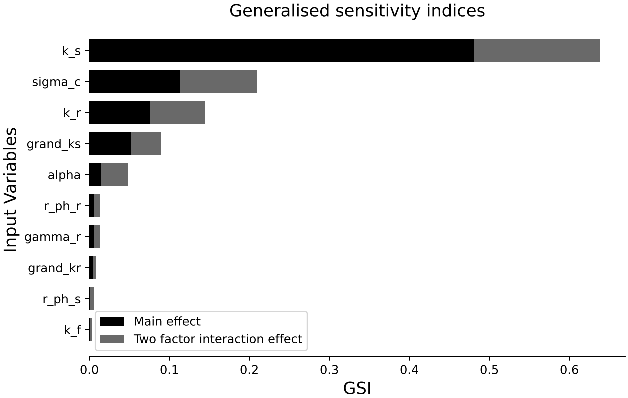
SS = sum of squares, TSS = total sum of squares

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

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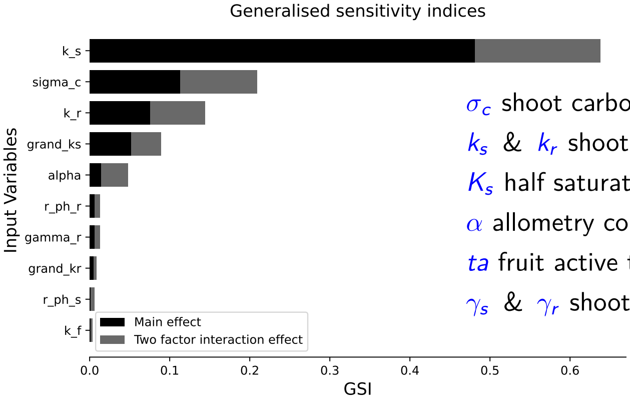


σ_c shoot carbon fixation rate

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

Data processing

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

Allometric relation: shoot weight vs leaf number

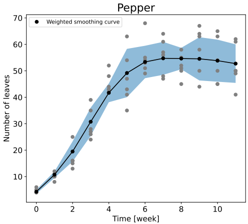
- Spline smoothing of leaf data
  - average dynamics
- Calibration of a general allometric relation (3 time-points x 3 species)

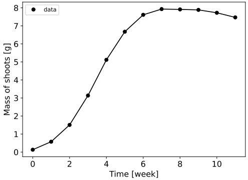
$$M = a\,L^{b_i}, \quad i = \text{species}\,1,2,3$$

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

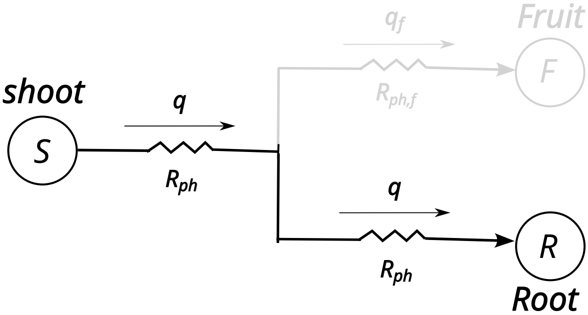
$$err = \alpha_c \underbrace{\left[\frac{1}{2} \sum_{i=1}^{2} \left(\frac{(W_s^{sol})_i - (W_s^{obs})_i}{(W_s^{obs})_i} \right)^2 + \frac{1}{2} \sum_{i=1}^{2} \left(\frac{(W_r^{sol})_i - (W_r^{obs})_i}{(W_r^{obs})_i} \right)^2 + \left(\frac{W_f^{sol} - W_f^{obs}}{w_f^{obs}} \right)^2 \right]}_{\text{Inoculated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

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

- 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



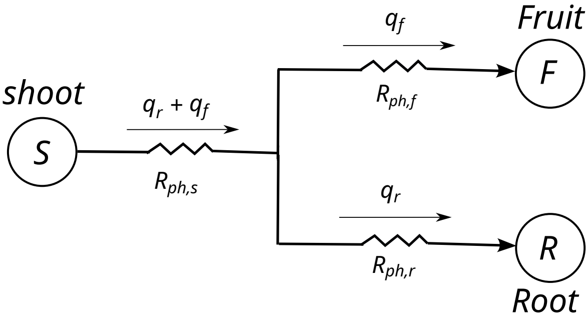
Then,

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

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

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

Carbon transport (T)



We get,

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

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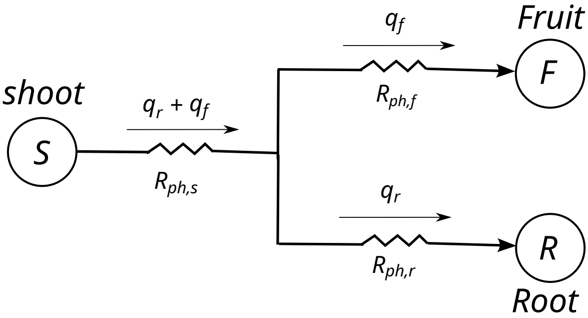


We get,

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

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

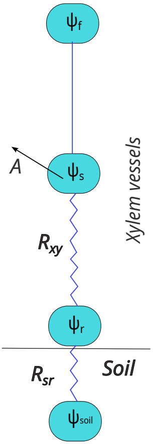
Water transport

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

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