Modelling plant-nematode interactions to understand plant tolerance

Joseph Penlap, Suzanne Touzeau, Frédéric Grognard, Valentina Baldazzi

MacBiosCore seminar 2023











Outline

Context

- Plant model
- Plant-Nematode interactions
- Model calibration

Context

Root-knot nematodes

- microscopic endoparasites feeding on plant roots
- more than 5000 host species concerned
- changes in root architecture
- wilting of vegetative part, yield reduction
- 14% of global crop losses worldwide



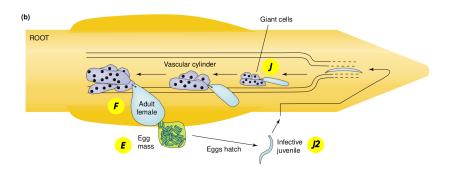




Root-knot nematodes

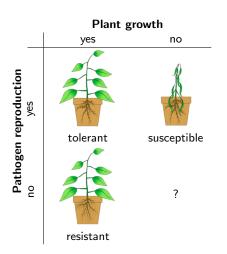
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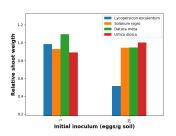




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• Strong variations in the extent of damages within and among plant species



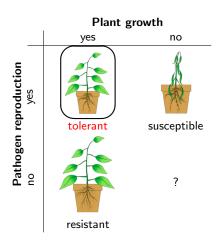


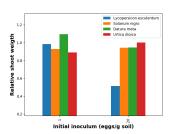
- Resistance is efficient but
 - few resistant genes identified
 - only for a few species
 - may favour the emergence of virulent nematodes
- Interest for tolerance
- Several possible mechanisms reported
 - high root growth rate
 - better water and nutrients uptake

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delayed senescence ...

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delayed senescence ...

Aim

Better understand the mechanisms behind (differential) plant susceptibility to nematodes

6/27

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Research question

Which are the **physiological mechanisms** behind **plant tolerance**?

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Aim

Better understand the mechanisms behind (differential) plant susceptibility to nematodes

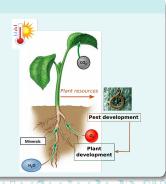
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Which are the physiological mechanisms behind plant tolerance?

Approach

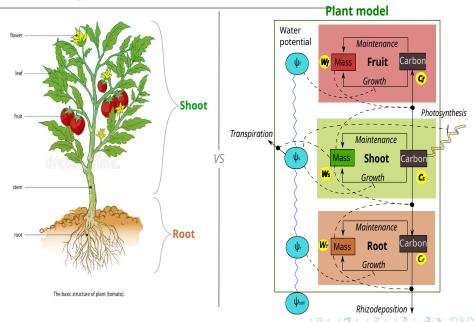
Coupled modeling of plant physiology and pest population dynamics

- better representation of pathosystem dynamics
 - interplay between plant and pest dynamics
- better prediction of plant growth rate and yield
- screening of interesting plant phenotypic traits



Plant model

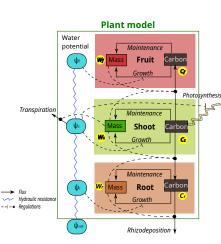
Plant description



Plant description

- 3 plant compartments:
 - shoots
 - roots
 - fruits
- 2 resources:
 - carbon (structural and free)
 - water
- Uptake, transport and allocation through plant compartments
 - growth and respiration processes
 - regulatory functions with respect to the water status of the plant

Thornley (1972), Dewar (1991)



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Shoot
$$\begin{cases} \frac{dW_s}{dt} = \\ \frac{dC_s}{dt} = \end{cases}$$
Root
$$\begin{cases} \frac{dW_r}{dt} = \\ \frac{dC_r}{dt} = \end{cases}$$
Fruit
$$\begin{cases} \frac{dW_f}{dt} = \\ \frac{dC_f}{dt} = \end{cases}$$

$$\begin{cases} \frac{dW_s}{dt} = \\ \frac{dC_s}{dt} = \underbrace{\frac{\sigma_c f(\psi_s)}{U_{\text{ptake}}}} \\ \\ \text{Root} \begin{cases} \frac{dW_r}{dt} = \\ \\ \frac{dC_r}{dt} = \end{cases} \end{cases}$$

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

$$-\underbrace{\frac{1}{W_s}\frac{dW_s}{dt}C_s}_{\text{Dilution}}$$

$$-\underbrace{\frac{1}{W_r}\frac{dW_r}{dt}C_r}_{\text{Dilution}}$$

$$-\underbrace{\frac{1}{W_f}\frac{dW_f}{dt}C_f}_{\text{Dilution}}$$

$$\begin{cases} \frac{dW_s}{dt} = \\ \frac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} - \frac{1}{W_s} \underbrace{(T_r + T_f + T_a)}_{\text{Transport}} \\ \end{cases} - \underbrace{\frac{dW_r}{dt}}_{\text{Uptake}} = \\ \\ \text{Root} \begin{cases} \frac{dW_r}{dt} = \\ \frac{dC_r}{dt} = \frac{1}{W_r} \underbrace{T_r}_{\text{Transport}} \\ \end{cases} - \underbrace{\frac{1}{W_r} \frac{dW_f}{dt}}_{\text{Dilution}} \\ \end{cases} - \underbrace{\frac{1}{W_r} \frac{dW_f}{dt}}_{\text{Dilution}} \\ \end{cases}$$

Dilution

Shoot
$$\begin{cases} \frac{dW_s}{dt} = \underbrace{k_s f(\psi_s) \frac{C_s}{K_s + C_s}}_{\text{Growth}} \\ \frac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} - \frac{1}{W_s} \underbrace{(T_r + T_f + T_a)}_{\text{Transport}} - \underbrace{(f_c \quad) k_s f(\psi_s) \frac{C_s}{K_s + C_s}}_{\text{Growth}} \\ \end{cases} - \underbrace{\frac{1}{W_s} \frac{dW_s}{dt}}_{\text{Dilution}} \\ \text{Root} \begin{cases} \frac{dW_r}{dt} = \underbrace{k_r f(\psi_r) \frac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{(f_c \quad) k_r f(\psi_r) \frac{C_r}{K_r + C_r}}_{\text{Growth}} \\ \end{cases} - \underbrace{\frac{1}{W_r} \frac{dW_r}{dt} C_r}_{\text{Dilution}} \\ \end{cases}$$

$$= \text{Fruit} \begin{cases} \frac{dW_f}{dt} = \underbrace{k_f f(\psi_f) \frac{C_f}{K_f + C_f}}_{\text{Growth}} \\ \end{cases} - \underbrace{\frac{1}{W_f} \frac{dW_f}{dt} C_r}_{\text{Transport}} \\ \underbrace{\frac{dC_f}{dt} = \frac{1}{W_f} \underbrace{(T_f + T_a)}_{\text{Transport}} - \underbrace{(f_c \quad) k_f f(\psi_f) \frac{C_f}{K_f + C_f}}_{\text{Growth}} \\ \end{cases} }_{\text{Dilution}}$$

$$\begin{aligned} & \begin{cases} \frac{dW_s}{dt} = \underbrace{k_s f(\psi_s) \frac{C_s}{K_s + C_s}}_{Growth} \\ \end{cases} \\ & \begin{cases} \frac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{Uptake} - \frac{1}{W_s} \underbrace{(T_r + T_f + T_a)}_{Transport} - \underbrace{(f_c + r_{g,s}) \, k_s f(\psi_s) \frac{C_s}{K_s + C_s}}_{Respiration growth} - \underbrace{r_{m,s} \left(\frac{C_s^n}{K_m^n + C_s^n}\right)}_{Maintenance respiration} - \underbrace{\frac{1}{W_s} \frac{dW_s}{dt} \, C_s}_{Dilution} \\ \end{aligned}$$

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Shoot
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Joseph Penlap

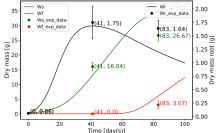
$$\text{Shoot} \begin{cases} \frac{dW_s}{dt} = \underbrace{k_s f\left(\psi_s\right) \frac{C_s}{K_s + C_s} W_s}_{\text{Growth}} - \underbrace{\gamma_s W_s}_{\text{Natural senescence}} - \underbrace{\gamma_s \left(\frac{K_m^n}{K_m^n + C_s^n}\right) W_s}_{\text{Additional drop due to carbon shortage}} \\ \frac{dC_s}{dt} = \underbrace{\sigma_c f\left(\psi_s\right)}_{\text{Uptake}} - \underbrace{\frac{1}{W_s} \left(T_r + T_f + T_a\right)}_{\text{Transport}} - \underbrace{\left(f_c + r_{g,s}\right) k_s f\left(\psi_s\right) \frac{C_s}{K_s + C_s}}_{\text{Growth}} - \underbrace{r_{m,s} \left(\frac{C_s^n}{K_m^n + C_s^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\frac{1}{W_s} \frac{dW_s}{dt} C_s}_{\text{Dilution}} \\ \frac{dW_r}{dt} = \underbrace{k_r f\left(\psi_r\right) \frac{C_r}{K_r + C_r} W_r}_{\text{Growth}} - \underbrace{\gamma_r W_r}_{\text{Natural senescence}} - \underbrace{\gamma_r W_r}_{\text{Additional drop due to carbon shortage}} \\ \frac{dC_r}{dt} = \underbrace{\frac{1}{W_r} \underbrace{T_r}_{\text{Transport}} - \left(f_c + r_{g,r}\right) k_r f\left(\psi_r\right) \frac{C_r}{K_r + C_r}}_{\text{Natural senescence}} - \underbrace{r_{m,r} \left(\frac{C_n^n}{K_m^n + C_r^n}\right)}_{\text{Maintenance respiration}} - \underbrace{\frac{1}{W_r^{1-\beta}} C_r}_{\text{Plittion}} - \underbrace{\frac{1}{W_r} \frac{dW_r}{dt} C_r}_{\text{Dilution}} \\ \frac{dW_f}{dt} = \underbrace{k_r f\left(\psi_r\right) \frac{C_r}{K_f + C_r} W_f}_{\text{Growth}} - \underbrace{\gamma_f W_r}_{\text{Natural senescence}} - \underbrace{\gamma_f \left(\frac{K_m^n}{K_m^n + C_r^n}\right) W_f}_{\text{Natural senescence}} \\ \frac{dC_r}{K_m^n + C_r^n} - \underbrace{\frac{1}{W_r} \frac{dW_r}{dt} C_r}_{\text{Dilution}} \\ \frac{dC_r}{K_m^n + C_r^n} - \underbrace{\frac{1}{W_r} \frac{dW_r}{dt} C_$$

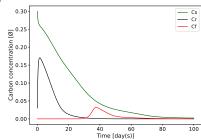
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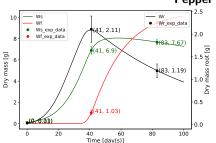
Plant dynamics

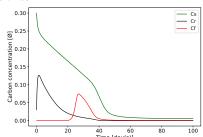






Pepper plants



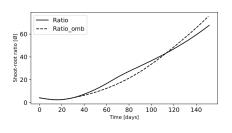


Test of plant model: environmental scenarios

The model is able to react correctly to a panel of environmental scenarios:

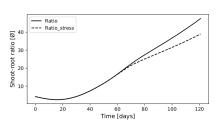
allocation towards the most limiting resource

Shading



$$\sigma_c \to \sigma_c/2$$

Water stress



$$\Psi_{soil}
ightarrow -200 MPa$$

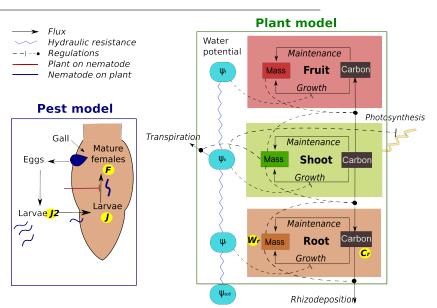
$$Ratio = \frac{W_s}{W_r}$$

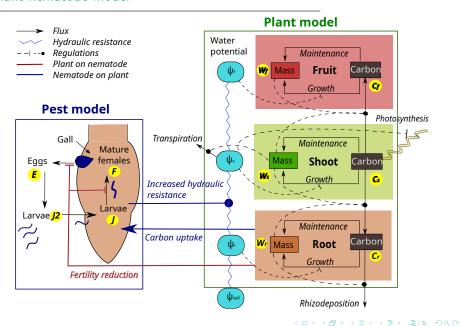
Plant-Nematode interactions

- Hijack of cell machinery amplifies carbon sink in root galls M.G.K. Jones. et al. 1981
- Increased hydraulic resistance R. Dorhout, F.J. Gommers, 1991
- Change in plant vascularization Bartlem et al. 2014
- Inhibition of photosynthesis by water stress and/or interference between synthesis and translocation of growth hormones - B. Loveys and A. F. Bird, 1994
- Decrease of respiration intensity T. Mateille, 1994
- Changes in glucose metabolism, nucleogenesis, proteogenesis... T. Mateille, 1994
- Nematode growth rate and body size depend on food supply McLeod et al. 2001
- Host physiological stress affects egg production and sex ratio -Ferris et al. 1984,
 Snyder et al. 2006
- No effect of nitrogen fertilization on nematodes development Spiegel et al. 1982

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Plant-nematode model





RKN model:

Free
$$\begin{cases} \frac{dE}{dt} = \underbrace{rF}_{\text{Egg laying}} - \underbrace{hE}_{\text{Egg hatching}} - \underbrace{\mu_e E}_{\text{Mortality}} \\ \frac{dJ_2}{dt} = \underbrace{hE}_{\text{Egg hatching}} - \underbrace{\beta J_2 W_r}_{\text{Larvae infection}} - \underbrace{\mu_j J}_{\text{Mortality}} \end{cases}$$
Inside root
$$\begin{cases} \frac{dJ}{dt} = \underbrace{\beta J_2 W_r}_{\text{RKN entry}} - \underbrace{\eta J}_{\text{Maturation}} - \underbrace{\mu_j J}_{\text{Mortality}} \\ \frac{dF}{dt} = \underbrace{\eta J}_{\text{Maturation}} - \underbrace{\mu_F F}_{\text{Maturation}} \end{aligned}$$

Plant roots:

$$\mathsf{Root} \left\{ \begin{array}{l} \frac{dW_r}{dt} = \underbrace{k_r f(\psi_r) \frac{C_r}{K_r + C_r} W_r}_{\mathsf{Growth}} - \underbrace{\gamma_r W_r}_{\mathsf{Natural senescence}} - \underbrace{\gamma_r \left(\frac{K_m^n}{K_m^n + C_r^n}\right) W_r}_{\mathsf{Additional drop due to carbon shortage}} \\ \frac{dC_r}{dt} = \underbrace{\frac{1}{W_r}}_{\mathsf{Transport}} \underbrace{T_r}_{\mathsf{Transport}} - \underbrace{(f_c + r_{g,r}) k_r f(\psi_r) \frac{C_r}{K_r + C_r}}_{\mathsf{Growth}} - \underbrace{r_{m,r} \left(\frac{C_r^n}{K_m^n + C_r^n}\right)}_{\mathsf{Maintenance respiration}} - \underbrace{c_{rh} \frac{1}{W_r^{(1-\beta)}} C_r}_{\mathsf{Rhizodeposition}} - \underbrace{\frac{dW_r}{dt} C_r}_{\mathsf{dilution}} \right\} \\ \end{array} \right.$$

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RKN model:

Free
$$\begin{cases} \frac{dE}{dt} = \underbrace{r(C_r) F}_{\text{Egg laying}} - \underbrace{h E}_{\text{Egg hatching}} - \underbrace{\mu_e E}_{\text{Mortality}} \\ \frac{dJ_2}{dt} = \underbrace{h E}_{\text{Egg hatching}} - \underbrace{\beta J_2 W_r}_{\text{Larvae infection}} - \underbrace{\mu_{J_2} J_2}_{\text{Mortality}} \end{cases}$$
Inside root
$$\begin{cases} \frac{dF}{dt} = \underbrace{\Omega(C_r) \beta J_2 W_r}_{\text{RKN entry}} - \underbrace{\eta J}_{\text{Maturation}} - \underbrace{(\mu_j + \mu_r) J}_{\text{Mortality}} \\ \frac{dF}{dt} = \underbrace{(1 - \theta(C_r)) \eta J}_{\text{Maturation}} - \underbrace{(\mu_F + \mu_r) F}_{\text{Mortality}} \end{cases}$$

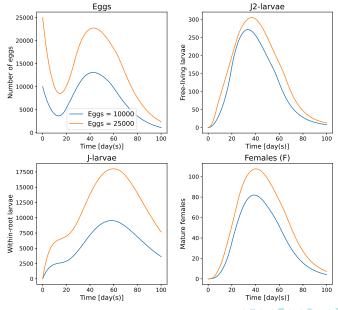
Plant roots:

$$\mathsf{Root} \left\{ \begin{array}{l} \frac{dW_r}{dt} = \underbrace{k_r f(\psi_r) \frac{C_r}{K_r + C_r} W_r}_{\mathsf{Growth}} - \underbrace{\gamma_r W_r}_{\mathsf{Natural senescence}} - \underbrace{\gamma_r \left(\frac{K_m^n}{K_m^n + C_r^n}\right) W_r}_{\mathsf{Additional drop due to carbon shortage}} - \underbrace{\frac{\Omega(C_r) \epsilon \beta J_2}{\mathsf{Successfully infected roots}}}_{\mathsf{Successfully infected roots}} \\ \frac{dC_r}{dt} = \underbrace{\frac{1}{W_r}}_{\mathsf{Transport}} \underbrace{T_r}_{\mathsf{Crowth}} - \underbrace{(f_c + r_{g,r}) k_r f(\psi_r) \frac{C_r}{K_r + C_r}}_{\mathsf{Growth}} - \underbrace{r_{m,r} \left(\frac{C_r^n}{K_m^n + C_r^n}\right)}_{\mathsf{Maintenance respiration}} - \underbrace{c_{rh} \frac{1}{W_r^{(1-\beta)}} C_r}_{\mathsf{Rhizodeposition}} - \underbrace{\frac{1}{W_r} \frac{dW_r}{dt} C_r}_{\mathsf{Gluttion}} \\ - \underbrace{\gamma \frac{C_r}{C_r + K_\gamma} F}_{\mathsf{Dematode feeding}} F - \underbrace{\rho \Omega(C_r) \beta}_{\mathsf{Gall formation}} \underbrace{J_2}_{\mathsf{Gall formation}} \\ \underbrace{J_2}_{\mathsf{Nematode feeding}} \underbrace{J_2}_{\mathsf{Gall formation}} + \underbrace{J_2}_{\mathsf$$

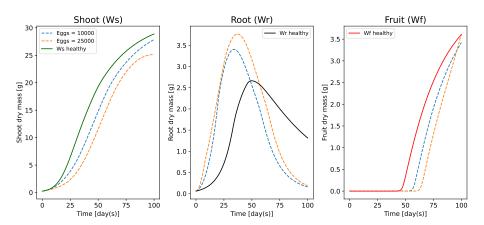
 $\begin{array}{c} \mathsf{Plant} \to \mathsf{Nematodes} \ \mathsf{effects} \\ \mathsf{Nematodes} \to \mathsf{Plant} \ \mathsf{effects} \end{array}$

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Preliminary Simulation plant-pest model



Preliminary Simulation plant-pest model



Model calibration

Calibration strategy

- Highly complex and non-linear model
- More than 30 parameters
- Few data available in literature

Calibration strategy

- Highly complex and non-linear model
- More than 30 parameters
- Few data available in literature
- Dedicated experiments
- 2-steps calibration strategy:
 - Calibration of the plant model on data from healthy plants
 - data processing
 - global sensitivity analysis
 - numerical estimation of sensitive parameters
 - Calibration of the plant-nematode model on data from infected plants
 - global sensitivity analysis: nematode parameters
 - numerical estimation of sensitive parameters

Plant model Calibration

- Dedicated experiments
- 2-step calibration strategy:
 - Calibration of the plant model on data from healthy plants
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Work in progress!

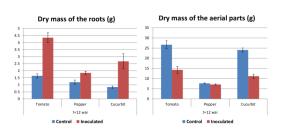


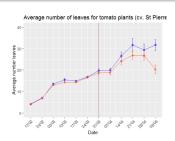
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ArchiNem project (INRAE 2020-21)

Experimental data available on 3 contrasted species (tomato, pepper, curcubit)

- Plant growth, physiology (healthy and infected)
 - Shoot, root, fruit dry mass (destructive): 3 time-points
 - Leaf number: 12 time-points
- 6 replicates per time-point





Collaboration with C. Caporalino (INRAE)

Data processing

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

Allometric relation: shoot weight vs leaf number

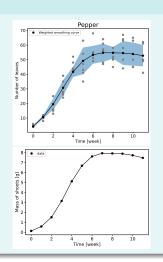
- Spline smoothing of leaf data
 average dynamics
- Calibration of a general allometric relation (3 time-points x 3 species)

$$M = a_i L^b$$
, $i = \text{species } 1, 2, 3$

M = shoot dry mass, L = number of leaves

 \Downarrow

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



Multi-variate global sensitivity analysis

inputs : 26 parameters, reference value $\pm 30\%$

outputs: Shoot and root dry masses dynamics (vector)

 $\boldsymbol{method:} \ \mathsf{R} \ \mathtt{multisensi} \ \mathsf{package} \ (\mathsf{PCA-} \ \mathsf{and} \ \mathsf{ANOVA-based})$

Multi-variate global sensitivity analysis

inputs : 26 parameters, reference value $\pm 30\%$

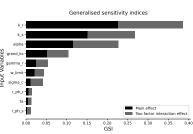
outputs : Shoot and root dry masses dynamics (vector)

method: R multisensi package (PCA- and ANOVA-based)

Shoot growth

Generalised sensitivity indices k.s. grand_ks. ta sigma_c | wide sigma_c |

Root growth



8 sensitive parameters (1 parameter fixed from litterature data):

 k_s shoot growth rate

 k_r root growth rate

 σ_c shoot carbon fixation rate

 K_s shoot growth dynamics

t_a active C transport to fruit

 γ_r root senescence rate

 α vascular architecture

w_{limit} water stress sensitivity

Numerical parameter estimation

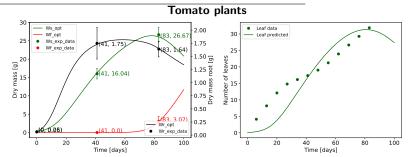
- 1 calibration per species considered
- Estimation of 7 (sensitive) parameters
- Weighted (π) least-square function for real and reconstructed mass data:

$$\underbrace{\frac{\pi}{N_{i}} \sum_{i=1}^{N_{i}} \left(\frac{M_{sol}^{i} - M_{data}^{i}}{std^{i}} \right)^{2}}_{Dry \ mass \ data} + \underbrace{\frac{(1-\pi)}{N_{j}} \sum_{j=1}^{N_{j}} \left(\frac{M_{sol}^{j} - M_{pred}^{j}}{M_{pred}^{j}} \right)^{2}}_{Reconstructed \ data \ from \ leaf \ number}$$

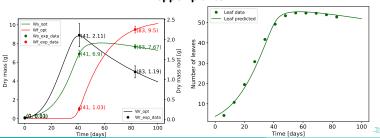
2-step estimation strategy:

- Global search (differential evolution algorithm)
- Local search around solution of step 1 (least square)

Calibrated plant model







On-going work and perspectives

- Calibration of RKN-related parameters on data from infected plants
- Identification of key physiological and architectural traits underlying plant tolerance to RKN infestation
- Multi-seasonal² effect of plant tolerance: **crop rotations** (tolerant, susceptible and resistant plants), management practices, effect of environmental conditions...



Collaborators:

INRAE collegues:

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- L. Pagès
- C. Doussan

Master students

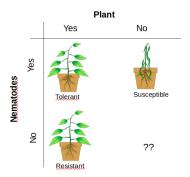
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- C. Bourgade

- E. Ceci
- A. Canaud



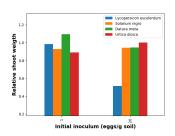
Phenotypic variability

• Strong variations in the extent of damages within and among plant species



Aim

Better understand the mechanisms behind (differential) plant susceptibility to nematodes



- Resistance is efficient but
 - few resistant genes identified
 - only for a few species
 - may favour the emergence of virulent nematodes
- Interest for tolerance
- Several possible mechanisms reported
 - high root growth rate
 - better water and nutrients uptake
 - delayed senescence ...

Resource transport resistances

Water transport

$$R_{sr} = r_{sr} \left(Wr + G \right)^{-\alpha_r} \tag{1}$$

$$R_{xy} = \frac{r_{xy}}{W_r^{\alpha_r}} + \frac{r_{xy}}{W_s^{\alpha s}} \tag{2}$$

Carbon transport

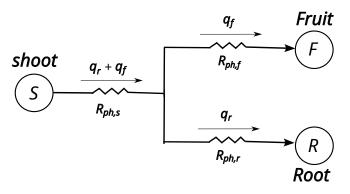
$$R_{ph} = \frac{r_{ph}}{W_s^{\alpha_s}} + \frac{r_{ph}}{(W_r + G)^{\alpha_r}}$$
 (3)

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ph Penlap MacBiosCore seminar October 16-19, 2023

Carbon transport (T)

The carbon flow³ T in phloem vessels $T = q C_s$, with q the volume flow rate,



Therefore,

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

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

◆□▶ ◆圖▶ ◆불▶ ◆불▶ 활발 虳♀♡

³Minchin et al., Journal of Experimental Botany, 1993

Male proportion

$$\theta(C_r) = \theta_{\text{max}} \frac{K_{\theta}}{C_r + K_{\theta}} \tag{4}$$

Reproduction rate

$$r(C_r) = r_{\min} + \frac{(r_{\max} - r_{\min}) C_r}{C_r + K_{repro}}$$
(5)

Establishment of the feeding site

$$\Omega(C_r) = \frac{Wcr^{\kappa}}{Wcr^{\kappa} + K_{\Omega}^{\kappa}}$$
 (6)

Global sensitivity analysis

Goal: Identifying the most influential parameters

inputs: 26 parameters, **outputs**: dry masses along time (vector)

Method

- fractional factorial design to explore parameter space
- PCA to reduce output and capture its variability
- 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

Joseph Penlap

Parameter set

TABLE 1 - Standard values for sensitivity analysis

Parameters	Description	Value	Interval
σ_C	Specific carbon fixation rate by the aerial part	0.4	± 30%
σ_W	Specific transpiration rate of aerial part	1.2	± 30%
$r_{ph,s}, r_{ph,r}, r_{ph,f}$	Xylem resistance coefficients to water flow	0.5, 0.5, 0.005	± 30%
$r_{xy,s}, r_{xy,r}, r_{xy,f}$	Phloem resistance coefficients to sap flow	5, 5, 0.1	± 30%
r_{sr}	Coefficient of resistance to water absorption by the roots	1	± 30%
k_s, k_r, k_f	Specific growth rates	0.14, 0.12, 0.6	± 30%
K_s, K_r, K_f	Half-saturation constants related to growth rate	0.1, 0.05, 0.01	± 30%
$\gamma_s, \gamma_r, \gamma_f,$	Mortality and leaf fall coefficients	0.1, 0.01, 0.001	± 30%
n, n_c, n_p, n_{hill}	Hill coefficients for transition, growth, photosynthesis and water regulation	10, 10, 10, 10	± 30%
W_{limit}	Transition coefficient from vegetative to reproductive phase	15	± 30%
K_c, K_p	Half-saturation constants related to the effect of water on growth and photosynthesis	-1400, -1600	3 fixed values
$\alpha_s, \alpha_r, \alpha_f$	Allometric coefficients	2/3, 2/3, 2/3	± 30%
$r_{s,m}, r_{r,m}, r_{f,m}$	Maintenance respiration coefficients for aerial, root and fruit compartments	0.001, 0.001, 0.001	± 30%
$r_{s,g}, r_{\tau,g}, r_{f,g}$	Growth respiration coefficients of aerial, root and fruit compartments	0.01, 0.01, 0.01	± 30%
c_{rh}	Rhizodeposition coefficient	0.1	± 30%
ta	concentration rate of carbon related to active transport	0.5	± 30%

- 26 parameters
- 3 levels for each parameter (reference value and ±30% of reference value)
- some reference values from literature