Modelling plant-nematode interactions to understand plant tolerance

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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

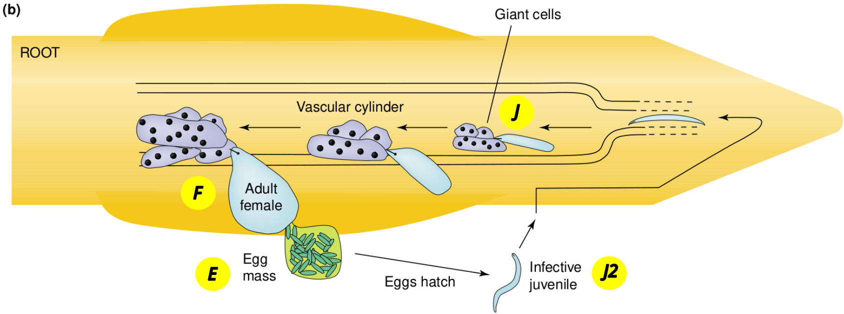
Main impacts

- stunted growth and wilting
- root deformation (galls)

RKN life cycle

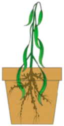
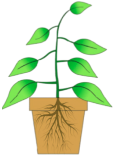
Specific impacts

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



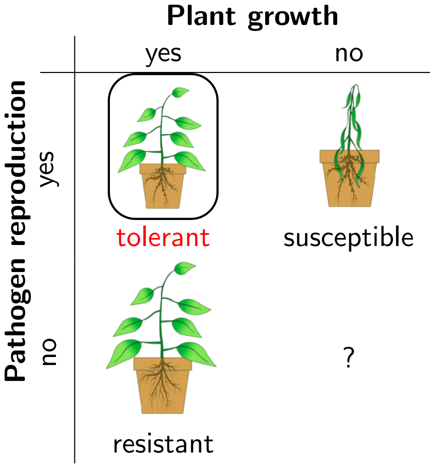
Context

Strong variability in plant response to RKN parasitism among crop species

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

Plant variability

Strong variability in plant response to RKN parasitism among crop species



Which mechanisms underlie plant tolerance?

Project vision

Our approach

- Experimental data on 3 plant species
- Model coupling plant ecophysiology and pest population dynamics

[1] Dewar, *Functional Ecology*, 1993
[2] Tankam et al., *Mathematical Biosciences*, 2020

Project vision

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	Plant physiology	Pest population dynamics
Ecological models[1]	yes	no
Epidemiological models[2]	no	yes

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Our model	yes	yes

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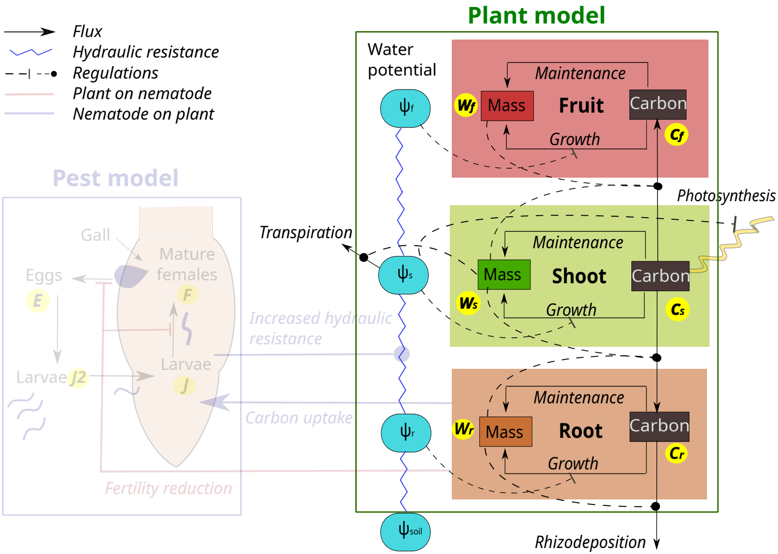
Outline

Plant model


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

Mathematical equations

$$\text{Shoot}\begin{cases}\dfrac{dW_s}{dt} = \\[2em] \dfrac{dC_s}{dt} = \\[2em] \end{cases}$$

$$\text{Root}\begin{cases}\dfrac{dW_r}{dt} = \\[2em] \dfrac{dC_r}{dt} = \\[2em] \end{cases}$$

$$\text{Fruit}\begin{cases}\dfrac{dW_f}{dt} = \\[2em] \dfrac{dC_f}{dt} = \\[2em] \end{cases}$$

Mathematical equations

$$
\text{Shoot}\begin{cases}
\dfrac{dW_s}{dt} = \\[2em]
\dfrac{dC_s}{dt} = \underbrace{\sigma_c f(\psi_s)}_{\text{Uptake}} \qquad - \underbrace{\dfrac{1}{W_s}\dfrac{dW_s}{dt}C_s}_{\text{Dilution}}
\end{cases}
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Carbon transport (T)

Shoot

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

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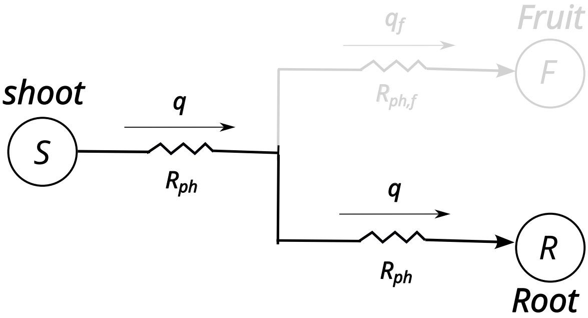
Carbon transport (T)

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



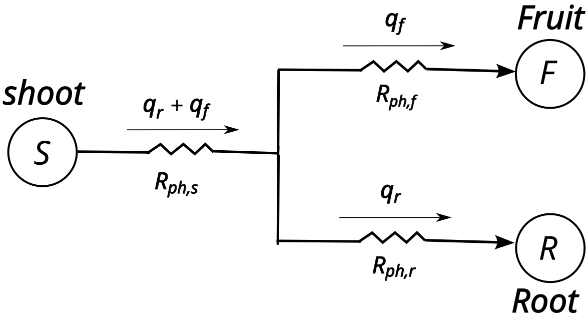
Then,

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

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

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

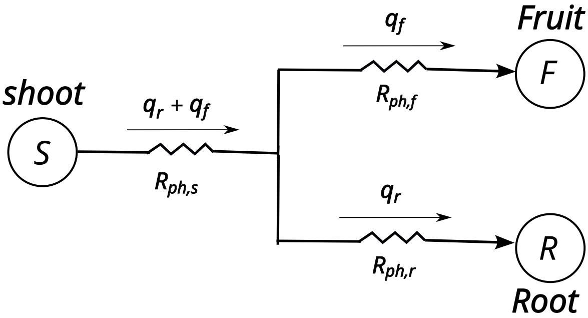
Carbon transport (T)



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

$$
\text{Shoot}\begin{cases}
\dfrac{dW_s}{dt} = \underbrace{k_s f(\psi_s)\dfrac{C_s}{K_s+C_s}W_s}_{\text{Growth}} - \underbrace{\gamma_s\left(\dfrac{K_m^n}{K_m^n+C_s^n}\right)W_s}_{\text{Mortality}},\\
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\end{cases}
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\text{Root}\begin{cases}
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\text{Fruit}\begin{cases}
\dfrac{dW_f}{dt} = \underbrace{k_f f(\psi_f)\dfrac{C_f}{K_f+C_f}W_f}_{\text{Growth}} - \underbrace{\gamma_f\left(\dfrac{K_m^n}{K_m^n+C_f^n}\right)W_f}_{\text{Mortality}},\\
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\end{cases}
$$

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

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

Plant model calibration

Experimental data

- 3 plant species: tomato, pepper, cucurbit
- 2 plant categories:
  - control
  - inoculated by nematodes
- destructive measures, 3 points in time:
  - plant: fresh and dry masses for shoot, root and fruit
  - nematodes: number of galls, egg masses and nematode/gall
- 6 replicates (90 plants)

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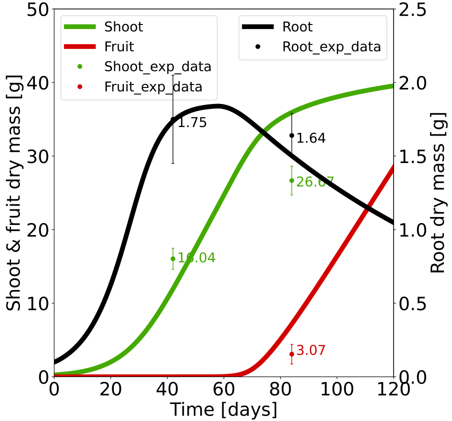
  - inoculated by nematodes
- destructive measures, 3 points in time:
  - plant: fresh and dry masses for shoot, root and fruit
  - nematodes: number of galls, egg masses and nematode/gall
- 6 replicates (90 plants)

Strategy

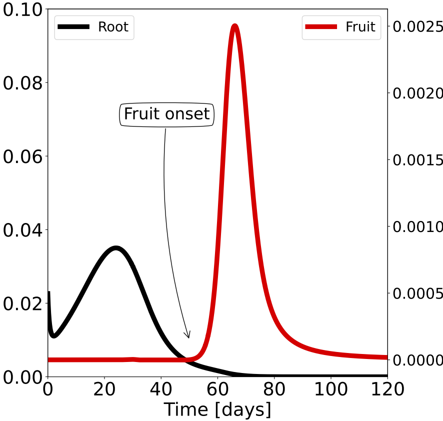
- Plant model calibration on **control data**
- Full model calibration on inoculated data [ongoing work]

Model dynamics

Tomato plant **biomass**



carbon transport



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

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

Global sensitivity analysis

Goal: Identifying the most influential parameters

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

Method

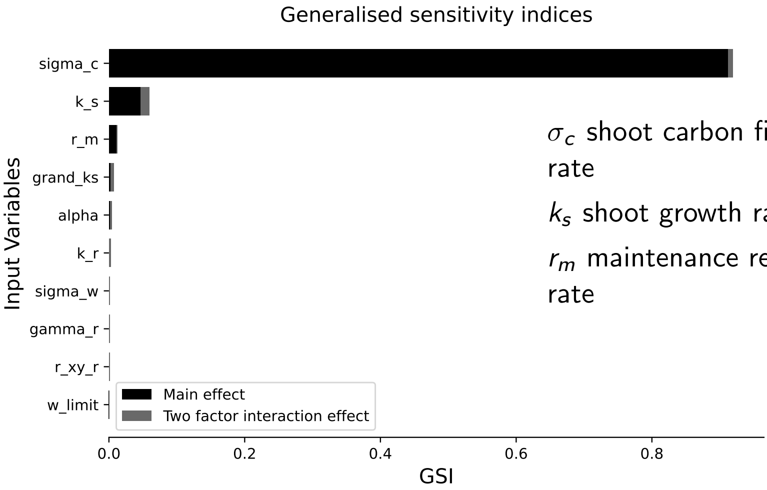
1. fractional factorial design to explore parameter space
2. PCA to reduce output and capture its variability
3. ANOVA to compute sensitivity indices (SI)

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

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

Global sensitivity analysis

Plant model used to screen plant traits that most affect the **total biomass** (shoot + root + fruit) dynamics



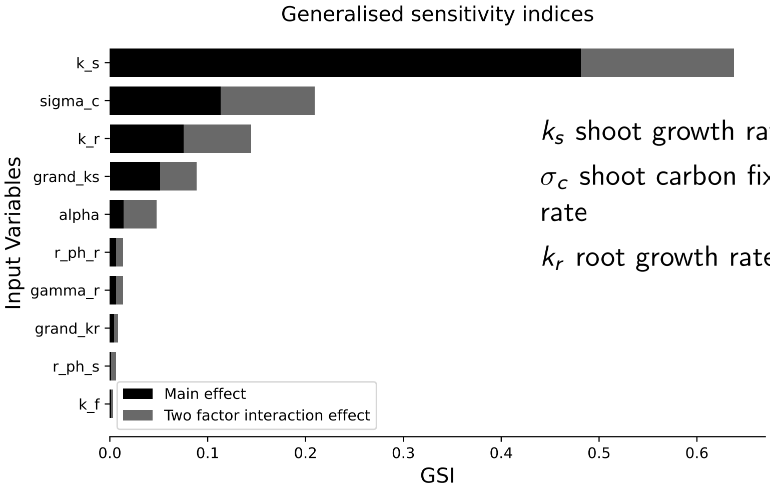
σ_c shoot carbon fixation rate

k_s shoot growth rate

r_m maintenance respiration rate

Global sensitivity analysis

Plant model used to screen plant traits that most affect **root biomass** (W_r) dynamics

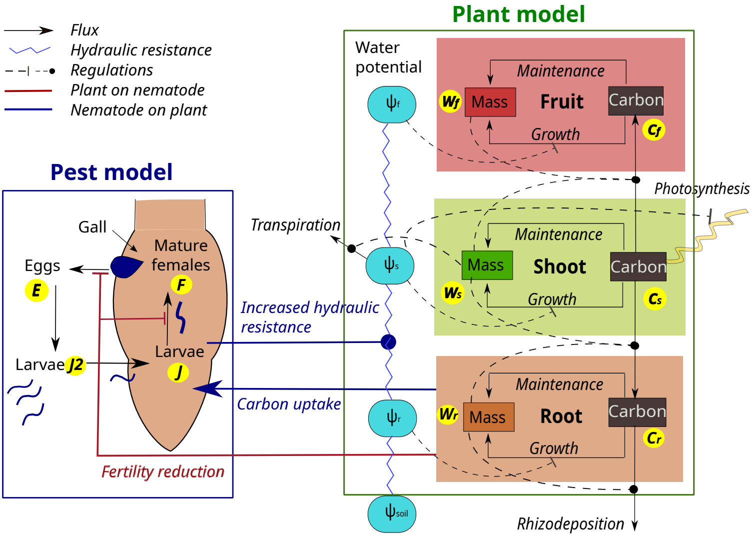


k_s shoot growth rate

σ_c shoot carbon fixation rate

k_r root growth rate

Integrated plant-pest model



Mathematical equations

Root
$$\begin{cases} \dfrac{dW_r}{dt} = \underbrace{k_r f(\psi_r) \dfrac{C_r}{K_r + C_r} W_r}_{\text{Growth}} - \underbrace{\gamma_r \left(\dfrac{K_m^n}{K_m^n + C_r^n} \right) W_r}_{\text{Mortality}} - \underbrace{\epsilon\beta\, J_2\, W_r}_{\text{Infected roots}} \\ \dfrac{dC_r}{dt} = \dfrac{1}{W_r} \underbrace{T_r}_{\text{Transport}} - \underbrace{(f_c + r_{g,r})\, k_r f(\psi_r) \dfrac{C_r}{K_r + C_r}}_{\text{Growth}} - \underbrace{r_{m,r} \left(\dfrac{C_r^n}{K_m^n + C_r^n} \right)}_{\text{Maintenance respiration}} - \underbrace{c_{rh} \dfrac{W_r}{W_r^{2-\beta}} C_r}_{\text{Rhizodeposition}} \\ \qquad - \dfrac{1}{W_r} \dfrac{dW_r}{dt} C_r - \underbrace{\gamma\, F}_{\text{RKN feeding}} - \underbrace{\kappa\epsilon\beta\, J_2\, W_r}_{\text{Gall formation}} \end{cases}$$

RKN
$$\begin{cases} \dfrac{dJ}{dt} = \underbrace{\Omega\, \beta\, J_2 W_r}_{\text{RKN entry}} - \underbrace{\eta\, J}_{\text{Maturation}} \underbrace{-(\mu_j + \mu_r)\, J}_{\text{Mortality}} \\ \dfrac{dF}{dt} = \underbrace{(1-\theta)\, \eta\, J}_{\text{Maturation}} \underbrace{-(\mu_F + \mu_r)\, F}_{\text{Mortality}} \end{cases}$$

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

Future work

- **Identification** of key physiological and architectural traits underlying **tolerance plant** to RKN infestation

- **Multi-seasonal**[2] effect of plant tolerance: **crop rotations** (tolerant, susceptible and resistant plants).

[2] Nilusmas et al., *Evolutionary Applications*, 2020


{thank you}

Control measures

Resistant varieties

Nematicide treatments

Solarisation

Water potential & hydraulic resistance

The **presence of galls** lowers the water and carbon transport along the xylem and phloem resp.

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

where ψ_{sol} the soil water potential and $E = \sigma_W W_s f(\psi_s)$ leaf transpiration.

without nematodes

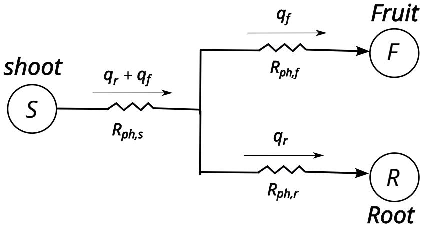
$$R_{sr} = \frac{r_{sr}}{W_r^{\alpha_r}},$$
$$R_{xy} = \frac{r_{xy,r}}{W_r^{\alpha_r}} + \frac{r_{xy,s}}{W_s^{\alpha_s}},$$
$$R_{ph} = \frac{r_{ph,r}}{W_r^{\alpha_r}} + \frac{r_{ph,s}}{W_s^{\alpha_s}} + \frac{r_{ph,f}}{W_f^{\alpha_f}}.$$

with nematodes

$$R_{sr} = \frac{r_{sr}}{(W_r + G)^{\alpha_r}},$$
$$R_{xy} = \frac{r_{xy,r}}{(W_r + G)^{\alpha_r}} + \frac{r_{xy,s}}{W_s^{\alpha_s}},$$
$$R_{ph} = \frac{r_{ph,r}}{(W_r + G)^{\alpha_r}} + \frac{r_{ph,s}}{W_s^{\alpha_s}} + \frac{r_{ph,f}}{W_f^{\alpha_f}}.$$

Carbon transport

The circulation flux[3] T of carbon in the phloem between the source and the sink is described by: $T = q\ C_s$



and therefore,

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

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

Active transport (T_a)

It requires energy from cells *ATP (Adenosine Triphosphate)* to occur

$$T_a = ta \times C_s \times W_f$$

Nematodes dynamics

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

$$\text{In the root}\begin{cases} \dfrac{dJ}{dt} = \underbrace{\Omega\beta J_2 W_r}_{\text{Nematode entry}} - \underbrace{\eta J}_{\text{Larvae maturation}} - \underbrace{\mu_j J}_{\text{Mortality}}\,, \\ \dfrac{dF}{dt} = \underbrace{(1-\theta)\eta J}_{\text{Maturation}} - \underbrace{\mu_F F}_{\text{Female mortality}} \end{cases}$$