Controlling burrowing nematodes in banana roots based on an epidemiological model with variable infestation density

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Crop protection

SUSTAINABLE DEVELOPMENT GOALS

- Population & food demand are increasing
  "By 2050, global agricultural production must increase by 70% [...] to meet the demand from a population of 9 billion" [FAO]
- Crop pests, diseases and weeds threaten food security
  20–40% of crop yields destroyed every year
- Agriculture is a major sector for employment and revenues in many (developing) countries
  nearly 80% of working poor live in rural areas [FAO]

➥ Controlling crop pests is a major issue

- Chemical pesticides:
  - negative impact on human health & the environment
  - variable effectiveness, induce pest resistance
  - high financial and labour costs

➥ Need for sustainable control methods

2 ZERO HUNGER

1 NO POVERTY

3 GOOD HEALTH AND WELL-BEING

15 LIFE ON LAND

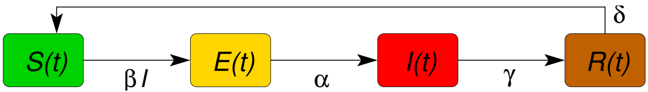
12 RESPONSIBLE CONSUMPTION AND PRODUCTION

Epidemiological modelling

Compartmental models to represent the dynamics (progression over time) of an infectious disease in a population, where individuals are:

Susceptible = healthy, naive
Exposed = infected, latent, non infectious
Infected = infectious
Recovered = immune, resistant / removed

E.g. SEIRS model



$$\begin{cases} \dot{S} = -\beta I\, S + \delta R \\ \dot{E} = \beta I\, S - \alpha E \\ \dot{I} = \alpha E - \gamma I \\ \dot{R} = \gamma I - \delta R \end{cases}$$

Constant population: $P = S(t) + E(t) + I(t) + R(t) > 0$

Equilibria ($\dot{S} = \dot{E} = \dot{I} = \dot{R} = 0$):

- disease-free (DFE): $S^* = P$, $E^* = I^* = R^* = 0$
- endemic (with disease) if $\gamma < \beta P$

Number of secondary cases generated by an average index case during its entire infectious period, when introduced in a fully susceptible population

$\mathcal{R}_0$ is a threshold (DFE local stability)

- $\mathcal{R}_0 < 1 \rightarrow$ no epidemic, infection cannot settle in
- $\mathcal{R}_0 > 1 \rightarrow$ epidemic

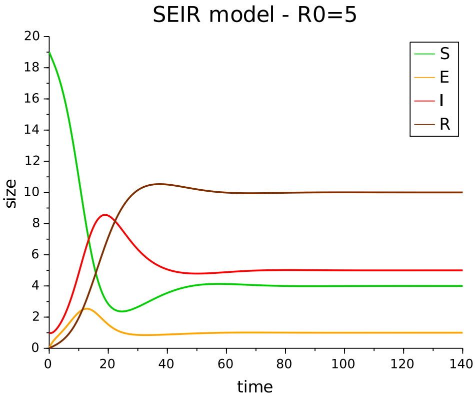
E.g. SEIRS model

$$\mathcal{R}_0 = \frac{\beta P}{\gamma}$$

If $\mathcal{R}_0 < 1$: stable DFE

If $\mathcal{R}_0 > 1$:

- unstable DFE
- endemic equilibrium



Plant epidemiology

Epidemiological models for human populations, but also animal and **plant** populations

Plant & crop specificities

- Definition of a (healthy/infected) individual: plant/tree, (part of) leaf, root, fruit...?

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- Plants affected by diseases and pests: grazers, phytophagous insects...
- Plants don't move: "contacts" via vectors, wind, water, free-living pathogen stages...
- Plants usually don't recover, but variable susceptibility
- Crops managed by humans: planting, harvest, partial environmental control...
- Seasonality plays an important role in annual & perennial crops

Banana burrowing nematodes (*Radopholus similis*)

Rosendahl

A: [Jesus, Agron Sustain Dev 2014]; B: M. MacClure, Univ. Arizona; C: [Zhang, EJPP 2012]

- **Banana**, including plantain: major staple food – *Cameroon: 2% GDP*
  - herbaceaous flowering plant, *ca.* 5 m $\rightarrow$ bunch 20–60 kg
  - cycle: *ca.* 11 months
- **Burrowing nematodes**: develop, feed and reproduce in roots
  - obligate root endoparasites, < 1mm
  - sexual reproduction or hermaphroditism, males not infective
  - life cycle: 20-25 days
- Severe **crop losses** due to root damages
  - reduced nutrient and water uptake
  - weakened anchor roots, up to plant toppling

Banana burrowing nematodes (*Radopholus similis*)

Rosendahl

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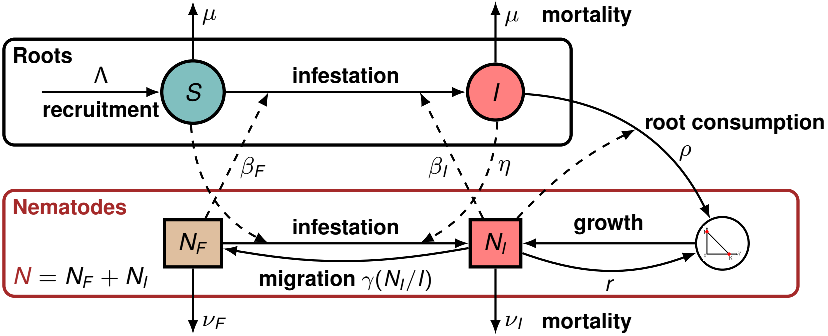
- **Pest control methods**
  - chemical nematicides: harmful to environment and human health
  - soil sanitation & vitroplants [Israël TANKAM CHEDJOU's PhD]
  - tolerant or resistant banana cultivars
  - biological control: biostimulants (to enhance plant defense)

How to control banana burrowing nematodes to optimize profit?



$$\dot{S} = -(\beta_F N_F + \beta_I N_I) S + \Lambda - \mu S$$

Prop: $S, N_F \geq 0$; $I, N_I > 0$; bounded

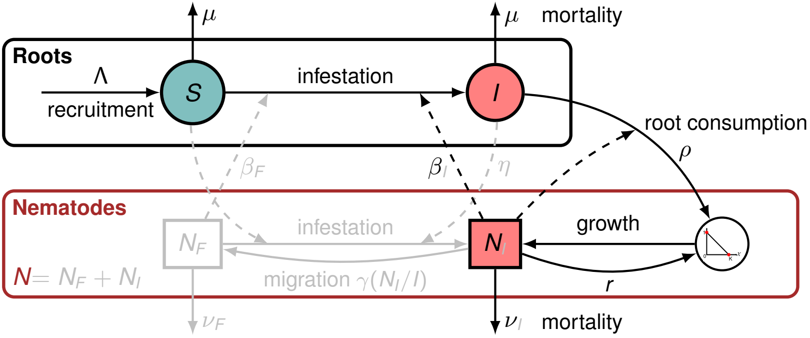
$$\dot{I} = +(\beta_F N_F + \beta_I N_I) S - \rho N_I \frac{I}{\alpha + I} - \mu I$$

variable infestation density $X = N_I / I$

$$\dot{N_F} = -c_\beta \beta_F (S + \eta I) N_F + \gamma \left(1 + \frac{N_I}{\kappa I}\right) N_I - \nu_F N_F$$

$$\dot{N_I} = +c_\beta \beta_F (S + \eta I) N_F - \gamma \left(1 + \frac{N_I}{\kappa I}\right) N_I + \left(r + c_\rho \rho \frac{I}{\alpha + I}\right) N_I \left(1 - \frac{N_I}{\kappa I}\right) - \nu_I N_I$$

Reduced model



$$\dot{S} = -(\beta_F N_F + \beta_I N_I) S + \Lambda - \mu S$$

$$\dot{I} = +(\beta_F N_F + \beta_I N_I) S - \rho N_I \frac{I}{\alpha + I} - \mu I$$

$$\dot{N_F} = -c_\beta \beta_F (S + \eta I) N_F + \gamma \left(1 + \frac{N_I}{\kappa I}\right) N_I - \nu_F N_F$$

Hyp: fast infestation

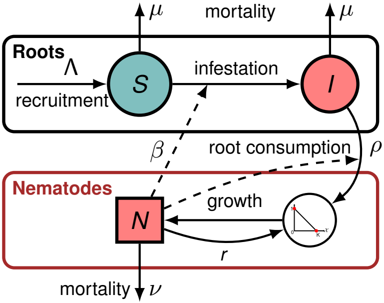
$$\dot{N_I} = +c_\beta \beta_F (S + \eta I) N_F - \gamma \left(1 + \frac{N_I}{\kappa I}\right) N_I + \left(r + c_\rho \rho \frac{I}{\alpha + I}\right) N_I \left(1 - \frac{N_I}{\kappa I}\right) - \nu_I N_I$$

Equilibria

Reduced model:

$$\dot{S} = -\beta NS + \Lambda - \mu S$$
$$\dot{I} = +\beta NS - \rho N \frac{I}{\alpha + I} - \mu I$$
$$\dot{N} = \left(r + c_\rho \rho \frac{I}{\alpha + I} \right) N \left(1 - \frac{N}{\kappa I} \right) - \nu N$$

with $r > \nu$



- **Pest-free equilibrium** (PFE)
  - model not defined for $I = 0 \rightarrow$ equivalent system $(S, I, \mathcal{X} = N/I)$

Pest-free equilibria (PFE)

Reduced system $(S, I, \mathcal{X})$:

$$\dot{S} = -\beta\mathcal{X}IS + \Lambda - \mu S$$
$$\dot{I} = \beta\mathcal{X}IS - \mu I - \rho\mathcal{X}\frac{I^2}{\alpha+I}$$
$$\dot{\mathcal{X}} = \left(r + c_\rho\rho\frac{I}{\alpha+I}\right)\mathcal{X}\left(1-\frac{\mathcal{X}}{K}\right) - (\nu-\mu)\mathcal{X} - \beta S\mathcal{X}^2 + \rho\frac{I}{\alpha+I}\mathcal{X}^2$$

Two pest-free equilibria ($I = 0$, $S = \Lambda/\mu$) with different infestation densities $\mathcal{X}$:

$$\zeta_1 = \left(\frac{\Lambda}{\mu}, 0, 0\right)$$

Jacobian matrix at ζ_1:

$$\begin{pmatrix} -\mu & 0 & 0 \\ 0 & -\mu & 0 \\ 0 & 0 & r-\nu+\mu \end{pmatrix}$$

with $r > \nu$

$\Rightarrow$ ζ_1 always unstable

$$\zeta_2 = \left(\frac{\Lambda}{\mu}, 0, \mathcal{X}^0\right), \text{ with } \mathcal{X}^0 = K\mu\frac{r-\nu+\mu}{r\mu+K\beta\Lambda}$$

Jacobian matrix at ζ_2:

$$\begin{pmatrix} -\mu & -\beta\frac{\Lambda}{\mu}\mathcal{X}^0 & 0 \\ 0 & \frac{r\mu^2}{r\mu+K\beta\Lambda}(\mathcal{R}-1) & 0 \\ -\beta(\mathcal{X}^0)^2 & \frac{c_\rho\rho}{\alpha}\mathcal{X}^0\left(1-\frac{\mathcal{X}^0}{K}\right) + \frac{\rho}{\alpha}(\mathcal{X}^0)^2 & -(r-\nu+\mu) \end{pmatrix}$$

with $\mathcal{R} = \frac{\Lambda\beta K}{\mu^2}\left(1-\frac{\nu}{r}\right)$

$\Rightarrow$ ζ_2 LAS if $\mathcal{R} < 1$, unstable if $\mathcal{R} > 1$

Equilibria

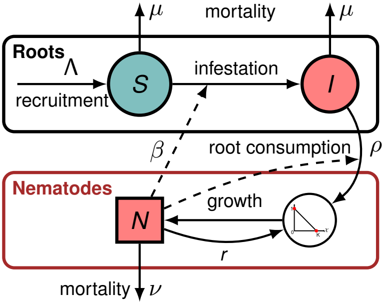
Reduced model:

$$\dot{S} = -\beta NS + \Lambda - \mu S$$

$$\dot{I} = +\beta NS - \rho N \frac{I}{\alpha + I} - \mu I$$

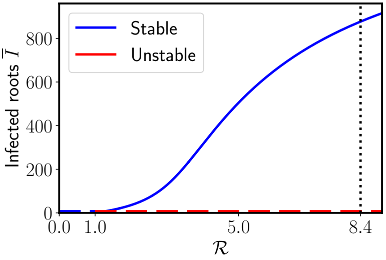
$$\dot{N} = \left(r + c_\rho \rho \frac{I}{\alpha + I} \right) N \left(1 - \frac{N}{\kappa I} \right) - \nu N$$

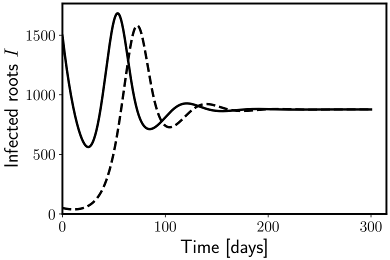
with $r > \nu$



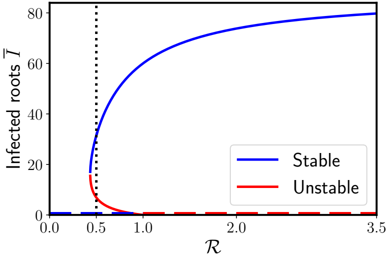
- **Pest-free equilibrium** (PFE)
  - system $(S, I, \mathcal{X} = N/I)$
  - LAS if $\mathcal{R} < 1$, with threshold $\mathcal{R} = \frac{\Lambda\beta\kappa}{\mu^2}\left(1 - \frac{\nu}{r}\right)$
- **Endemic equilibria** (EE)
  - no explicit expression (degree-4 polynomial)
  - if $\mathcal{R} < 1$: 0, 2 or 4 equilibria
  - if $\mathcal{R} > 1$: 1 or 3 equilibria
- **Bifurcation analysis** (parameter β)
  - reference parameters
  - reduced recruitment (Λ) and nematode growth (r)

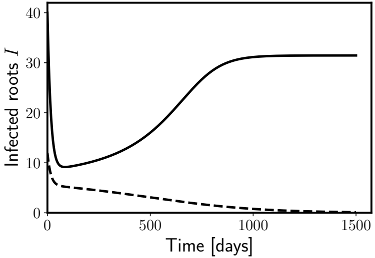
- **Forward bifurcation:** $\mathcal{R} > 1 \Rightarrow$ existence & stability of a unique EE (unstable PFE)





- **Backward bifurcation:** $\mathcal{R} < 1$ does not ensure pest eradication (stable PFE)





Control

Biological control: biostimulants to enhance plant defense, i.e. reduce infestation

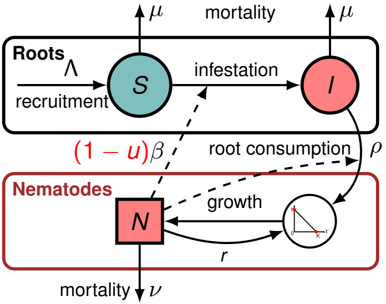
Controlled model:

$$\dot{S} = -(1-u)\beta NS + \Lambda - \mu S$$

$$\dot{I} = +(1-u)\beta NS - \rho N \frac{I}{\alpha + I} - \mu I$$

$$\dot{N} = \left(r + c_\rho \rho \frac{I}{\alpha + I}\right) N \left(1 - \frac{N}{\kappa I}\right) - \nu N$$

with $0 \leq u \leq u_{\max} \leq 1$



Optimal control

Finite time horizon: $[0, t_f]$
Admissible controls: $\mathcal{U} = \{u \in L^\infty([0, t_f]) : 0 \leq u \leq u_{\max} \leq 1, \ \forall t \in [0, t_f]\}$

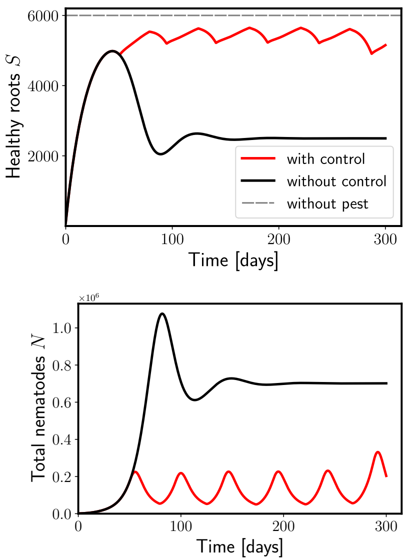
Optimal control problem

Find $u^\star \in \mathcal{U}$ to maximise profit (yield − control costs) during a cropping season, while minimising infestation at the end of the season (reasonable yield for next season)

$$u^\star : \max_{u \in \mathcal{U}} \mathcal{J}(u) = \underbrace{B_S \int_0^{t_f} S(t)dt}_{\text{yield}} - \underbrace{B_u \int_0^{t_f} u(t)dt}_{\text{costs}} - \underbrace{B_I \, I(t_f)}_{\text{penalty}}$$

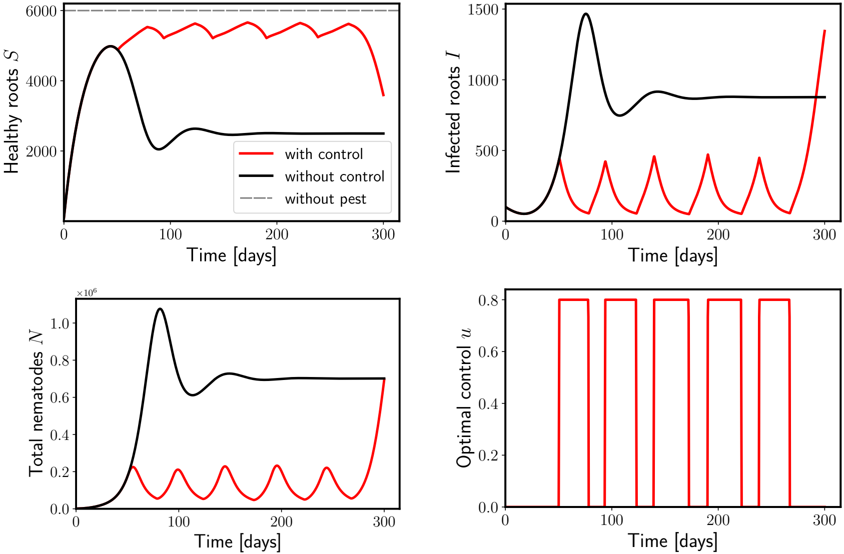
- Pontryagin's Maximum Principle → **bang-bang** solution
- Direct method, **BOCOP** software (bocop.org or github)

Optimal control



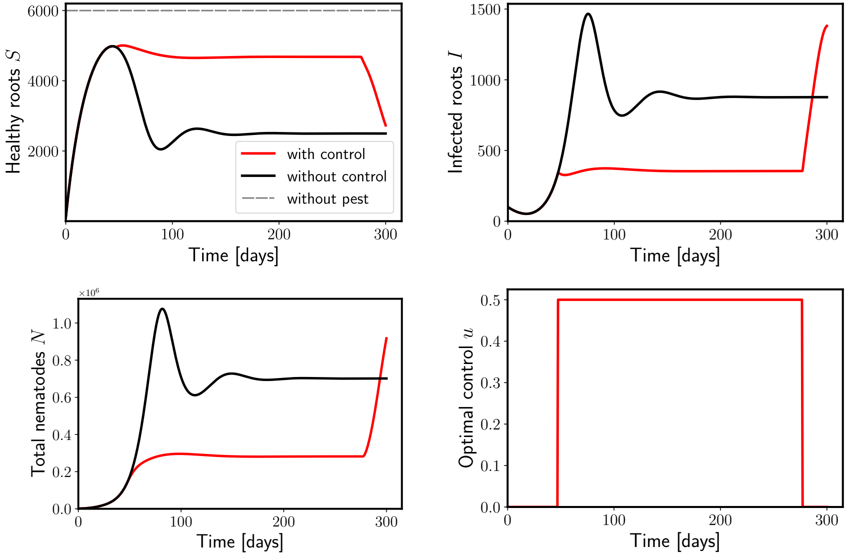
“Oscillating” and efficient optimal control

Optimal control: no penalty



No pest control at the end of the season, to reduce control costs

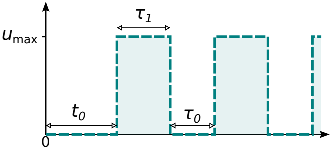
Optimal control: reduced u_{max}

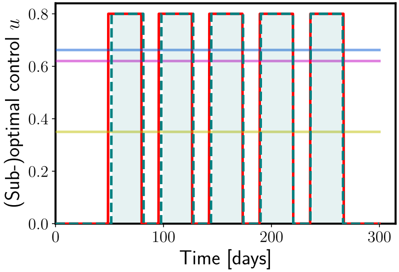


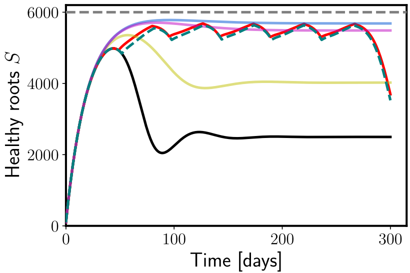
Less efficient but "cheaper" control costs → no more oscillations

Sub-optimal controls

- **Constant controls**
  - average of the optimal control:
    $u_a = \frac{1}{t_f}\int_0^{t_f} u^\star(t)dt$
  - static optimisation at endemic equilibrium
    $u_e : \max_{u\in[0,u_{\max}]} \overline{\mathcal{J}}(u) = B_S\overline{S}(u) - B_u u$
  - optimisation with constant control
    $u_c : \max_{u\in[0,u_{\max}]} \mathcal{J}(u) =$
    $\int_0^{t_f} (B_S S(t,u) - B_u u)dt$
- **Periodic control**
  - 3-parameter optimisation:
    $u_p(t)$







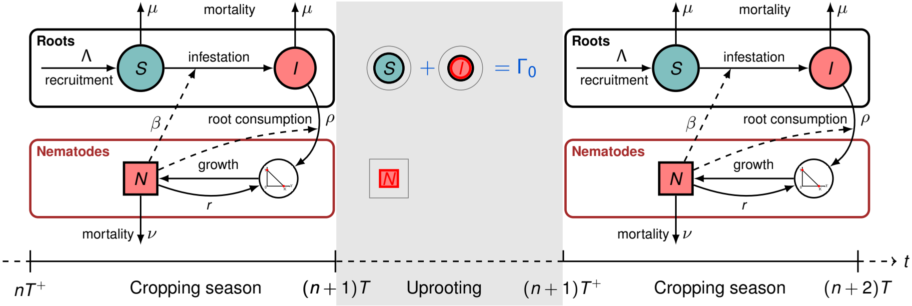
Best → worst control strategy:
$\mathcal{J}(u^\star) \simeq \mathcal{J}(u_p) > \mathcal{J}(u_c) \simeq \overline{\mathcal{J}}(u_e) > \mathcal{J}(u_a)$

Take home

How to control banana burrowing nematodes to optimize profit?

- Oscillating controls outperform constant controls
  - cheaper in terms of control costs
  - almost as efficient to maintain healthy root biomass and yield
  - for practical reasons, **apply periodic pest control**
- Efficient biocontrol is needed ($u_{\max} \geq 0.8$)
  - combine with other pest control methods, such as soil sanitation

Multiseasonal model



$$\dot{S} = -\beta N S + \Lambda - \mu S$$

$$\dot{I} = +\beta N S - \mu I - \rho N \frac{I}{\alpha + I}$$

$$\dot{N} = \left(r + c_\rho \rho \frac{I}{\alpha + I} \right) N \left(1 - \frac{N}{KI} \right) - \nu N$$

$$S(nT^+) = \Gamma_0 \frac{S(nT) + (1-\theta) I(nT)}{S(nT) + I(nT)}$$

$$I(nT^+) = \theta \Gamma_0 \frac{I(nT)}{S(nT) + I(nT)}$$

$$N(nT^+) = \theta \Gamma_0 \frac{N(nT)}{S(nT) + I(nT)}$$

Prop: $S \geq 0$; $I, N > 0$; bounded

Control $\theta < 1$

Periodic pest-free solution (PPFS): existence

Model not defined for $I = 0 \to$ equivalent system $(S, I, \mathcal{X} = N/I)$

$$\dot{S} = -\beta \mathcal{X} I S + \Lambda - \mu S \qquad S(nT^+) = \Gamma_0 \left(\frac{S(nT)+(1-\theta)I(nT)}{S(nT)+I(nT)} \right)$$

$$\dot{I} = \beta \mathcal{X} I S - \mu I - \rho \mathcal{X} \frac{I^2}{\alpha + I} \qquad I(nT^+) = \theta \Gamma_0 \frac{I(nT)}{S(nT)+I(nT)} \quad n \in \mathbb{N}^*$$

$$\dot{\mathcal{X}} = \left(r + c_\rho \rho \frac{I}{\alpha+I}\right) \mathcal{X} \left(1 - \frac{\mathcal{X}}{K}\right) - (\nu - \mu)\mathcal{X} - \beta S \mathcal{X}^2 + \rho \frac{I}{\alpha+I} \mathcal{X}^2 \qquad \mathcal{X}(nT^+) = \mathcal{X}(nT)$$

Expression: $Z^\star(t) = (S^\star(t), 0, \mathcal{X}^\star(t))$ with $Z^\star(t+T) = Z^\star(t)$

for $t \in [nT^+, (n+1)T]$

- $\dot{S} = \Lambda - \mu S \quad \Rightarrow \quad S^\star(t) = \frac{\Lambda}{\mu} + \left(\Gamma_0 - \frac{\Lambda}{\mu}\right) e^{-\mu(t-nT)}$
- $\dot{\mathcal{X}} = (r - \nu + \mu)\mathcal{X} - \left(\frac{r}{K} + \beta S^\star\right) \mathcal{X}^2 \quad \Rightarrow \quad \mathcal{X}^\star(t) = \frac{\mathcal{X}^\star(nT^+)}{\mathcal{X}^\star(nT^+)\omega_1(t) + \omega_2(t)}$

$$\text{with} \begin{cases} \omega_1(t) = \int_{nT}^{t} \left(\frac{r}{K} + \beta S^\star(s)\right) e^{-(r-\nu+\mu)(t-s)} ds \\ \omega_2(t) = e^{-(r-\nu+\mu)(t-nT)} \\ \mathcal{X}^\star(nT^+) = \frac{1 - e^{-(r-\nu+\mu)T}}{\omega_1((n+1)T)} \end{cases}$$

Periodic pest-free solution (PPFS): stability

- **Perturbation**: $\widetilde{S} = S - S^\star$, $\widetilde{I} = I - I^\star = I$, $\widetilde{\mathcal{X}} = \mathcal{X} - \mathcal{X}^\star$ and set $\widetilde{Z} = (\widetilde{S}, \widetilde{I}, \widetilde{\mathcal{X}})$
- **Linearization** in $0_{\mathbb{R}^3}$: $\forall t \in (nT, (n+1)T]$, $\dot{\widetilde{Z}}(t) = A\widetilde{Z}(t)$ and $\widetilde{Z}(nT^+) = B\widetilde{Z}(nT)$

$$A = \begin{pmatrix} -\mu & -\beta S^\star \mathcal{X}^\star & 0 \\ 0 & \beta S^\star \mathcal{X}^\star - \mu & 0 \\ -\beta(\mathcal{X}^\star)^2 & \frac{c_\rho \rho}{\alpha} \mathcal{X}^\star \left(1 - \frac{\mathcal{X}^\star}{K}\right) + \frac{\rho}{\alpha}(\mathcal{X}^\star)^2 & (r - \nu + \mu) - 2\left(\frac{r}{K} + \beta S^\star\right)\mathcal{X}^\star \end{pmatrix}$$

$$B = \begin{pmatrix} 0 & \dfrac{-\theta\Gamma_0}{S^\star(nT)} & 0 \\ 0 & \dfrac{\theta\Gamma_0}{S^\star(nT)} & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

- **Solve equation**: $\dot{\widetilde{Z}}(t) = A\widetilde{Z}(t) \Rightarrow \widetilde{Z}(t) = \Phi_A(t)\widetilde{Z}(nT^+)$

$$\Phi_A(t) = \begin{pmatrix} e^{-\mu(t-nT)} & -m_1(t) & 0 \\ 0 & e^{\int_{nT}^t \left(\beta S^\star(s)\mathcal{X}^\star(s) - \mu\right) ds} & 0 \\ -m_2(t) & m_3(t) & e^{\int_{nT}^t a_3(s) ds} \end{pmatrix}$$

$a_3(t) = (r - \nu + \mu) - 2\left(\frac{r}{K} + \beta S^\star(t)\right)\mathcal{X}^\star(t)$ and m_1, m_2, m_3 strongly depends on PPFS

Periodic pest-free solution (PPFS): stability

- **Transition relation between jumps**:

$$\begin{cases} \widetilde{Z}(t) = \Phi_A(t)\widetilde{Z}(nT^+) \\ \widetilde{Z}((n+1)T^+) = B\widetilde{Z}((n+1)T) \end{cases} \Rightarrow \quad \widetilde{Z}((n+1)T^+) = M\widetilde{Z}(nT^+)$$

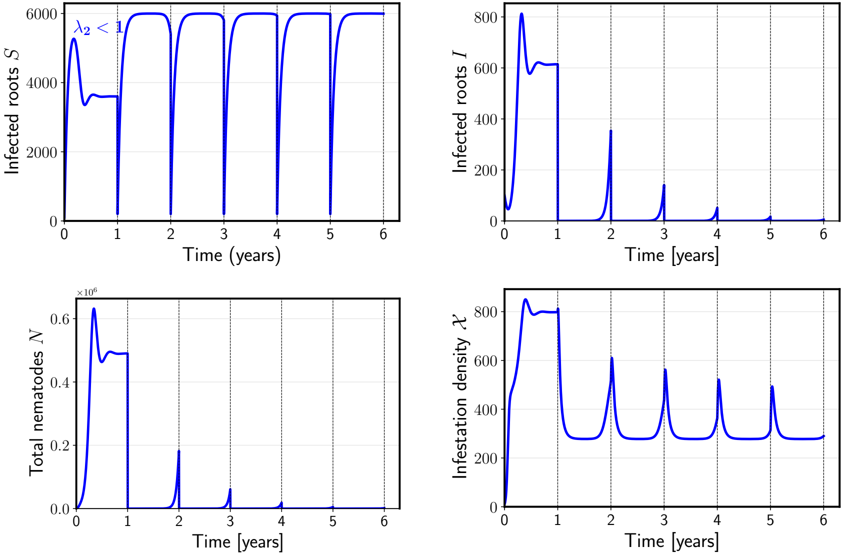
- **Monodromy matrix** $M = B\Phi_A((n+1)T)$:

$$M = \begin{pmatrix} 0 & \dfrac{-\theta\Gamma_0}{S^\star(nT)} m_1((n+1)T) & 0 \\ 0 & \dfrac{\theta\Gamma_0}{S^\star(nT)} e^{\int_{nT}^{(n+1)T}\left(\beta S^\star(s)\mathcal{X}^\star(s)-\mu\right)ds} & 0 \\ -m_2((n+1)T) & m_3((n+1)T) & e^{\int_{nT}^{(n+1)T} a_3(s)ds} \end{pmatrix}$$

- **Floquet multipliers** eigenvalues of M:

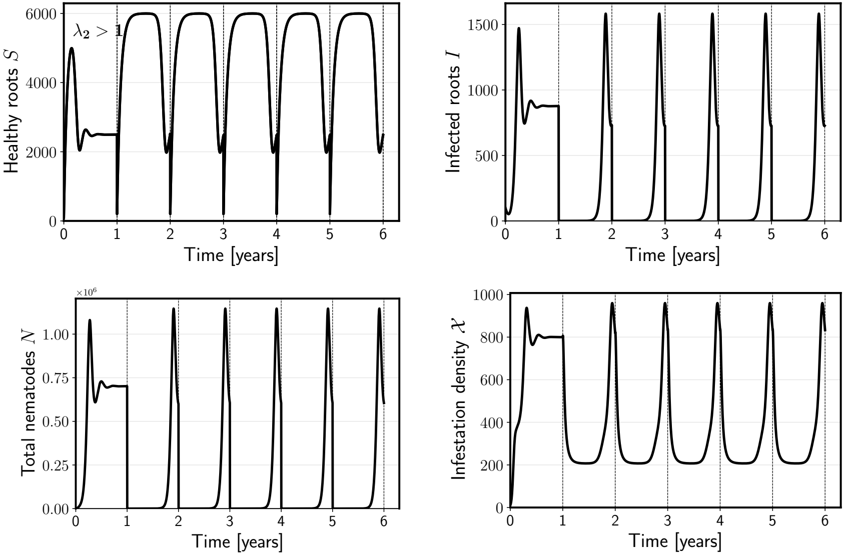
$$\begin{cases} \lambda_1 = 0 < 1 \\ \lambda_2 = \dfrac{\theta\Gamma_0}{S^\star(nT)} e^{\int_{nT}^{(n+1)T}\left(\beta S^\star(s)\mathcal{X}^\star(s)-\mu\right)ds} \\ \lambda_3 = e^{\int_{nT}^{(n+1)T} a_3(s)ds} < 1 \end{cases}$$

$\Rightarrow$ PPFS is LAS if $\lambda_2 < 1$ $\quad \rightarrow \lambda_2$: “semi-discrete” basic reproduction number



$\lambda_2 < 1 \Rightarrow$ PPFS is LAS

Periodic endemic solution



$\lambda_2 > 1 \Rightarrow$ unstable PPFS + *stable (numerically) periodic endemic solution*

ONGOING – Multiseasonal model: control

- Similar optimal control problem
  - Same control *u*: reduce infestation during cropping seasons
  - Maximise profit during *n* cropping seasons
  - Hybrid Pontryagin's Maximum Principle $\rightarrow$ **bang-bang or singular** solution
- Other control strategies
  - New control θ: reduce prevalence at uprooting
  - Discrete control
  - Combine both controls

Thanks!

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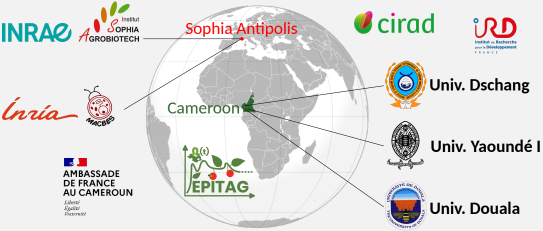
EPITAG = EPIdemiological modelling and control for Tropical AGriculture

French & Cameroonian scientists: background in applied mathematics, interest in crop diseases



More on EPITAG: https://team.inria.fr/epitag/