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► **To cite this version:**

Israël Tankam Chedjou, Suzanne Touzeau, Frédéric Grognard, Ludovic Mailleret, Jean-Jules Tewa. A multi-seasonal model of the dynamics of banana plant-parasitic nematodes. CARI'2018 - 14. Colloque Africain sur la Recherche en Informatique et en Mathématiques Appliquées, Oct 2018, Stellenbosch, South Africa. hal-01871510

HAL Id: hal-01871510

<https://inria.hal.science/hal-01871510v1>

Submitted on 10 Sep 2018

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A multi-seasonal model of the dynamics of banana plant-parasitic nematodes

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This work is supported by EPITAG, an Inria Associate team part of the LIRIMA (<https://team.inria.fr/epitag/>).



ABSTRACT. In this paper, a hybrid multi-seasonal model is proposed to describe the action of *Radopholus similis* with banana plants' roots. On one side a general Holling type II predator-prey model with stage structuration of the predators is coupled including a host-parasite dynamic with a parasite free living stage. On the other side, at a certain period called inter-seasonal time, a decay equation is given, consisting essentially in the exponential decay of free living pest when hosts are lacking. The switching between these two continuous systems is given by discrete laws and the switchings are repeated season after season. The proposed model is reduced and analysed and relevant constants like the basic reproduction number and the minimal inter-season duration for pest eradication are computed. Numerical simulation are provided.

RÉSUMÉ. Dans cet article, un modèle hybride multi-saisonnier est proposé pour décrire l'action de *Radopholus similis* sur les racines des bananiers. D'un côté, un modèle proie-prédateur de Holling type II avec une structuration par stade des prédateurs est couplé avec une dynamique hôte-parasite incluant un stade libre des parasites. De l'autre côté, sur un temps dit inter-saisonnier, une équation de désintégration est donnée, consistant essentiellement en la décroissance exponentielle de la population de parasite libre en absence d'hôte. La commutation entre ces deux systèmes continus est donnée par des lois discrètes et les commutations sont répétées saison après saison. Le modèle proposé est réduit puis analysé et des constantes révélatrices comme le taux de reproduction de base et la durée minimale d'inter-saison pour l'éradication des ravageurs sont calculées. Des simulations numériques sont fournies.

KEYWORDS : Mathematical modelling; *Radopholus similis*; Multi-seasonal model; Semi-discrete model; Parasit-host dynamics; Slow-fast dynamics; Model reduction;

MOTS-CLÉS : Modélisation mathématique; *Radopholus similis*; Modèle multi-saisonnier; Modèle semi-discret; Dynamique hôte-parasite; Dynamique lent-rapide; Réduction de modèle;



1. Introduction

Banana cultures are hampered by several parasitic factors like plant-parasitic nematodes, insect pests or soil-borne fungi that seriously threaten the sustainability of these systems by decreasing yield, causing plant toppling or requiring intensive pesticide use. The nematode *Radopholus similis* is the most significant parasitic nematode of the banana plant and the banana plantain plant in the world [8]. The infestation by the *Radopholus similis* causes damages going from simple roots lesion reducing the production to the fall of the seedlings. These damages are due to the fact that the nematodes destroy the roots tissue by feeding on. Hence, *Radopholus similis* is one of the most regulated pests of banana plant [5] but its control still implies toxic nematicides which are not always efficient.

After describing briefly the biology of *R. Similis*, we propose a general model that will be reduced and summarily analysed then provide some numerical result.

2. Biological background and model formulation

The burrowing nematode *Radopholus similis* is a phytophagous nematode that attacks the roots of host plants. Like most nematodes in its family, the Pratylenchidae family, it is an obligate parasite. The following observations show that, it can only feed on living roots, which explains why: (i) it occurs mainly in roots and rhizomes, and little in the soil; the ratio of population density in soil and roots (expressed as the number of nematodes per gram) is generally less than 1/100; (ii) in roots, maximum densities are observed at the edges of necrotic areas or between necrotic zones, and not in necrotic root sections [1]. In absence of host, the population of nematodes therefore decreases. Exponential model fairly well describes the decay of the nematode population in the absence of a host [3].

Concerning banana plant biology and cultivation, its roots are continuously produced until the flowering [2]; subsequently, the newly emitted roots are mainly related to successive suckers. After a complete season of culture of banana -10 to 12 months- it is advisable to remove all the old plant roots before planting healthy suckers, in order to avoid the nematodes to directly infest suckers roots from the infested roots. The crop rotation or the fallow strategies consisting in leaving the soil free of any nematodes host for a while in order to insure sufficient decay of nematodes population in the soil and reduce the infestation.

According to the previous biological background, the following assumptions are made:

- There are two compartments for nematodes: free nematodes in the soil (P) and nematodes infesting the roots (X).
- There is one compartment for healthy roots (S).
- There are several cropping seasons with an inter-season that match the duration of the fallow or the alternative culture duration.
- During one cropping season, banana roots grow logistically [4] until the flowering. The duration d until the flowering is usually 7 months and a cropping season usually lasts $t_f = 11$ months. If τ is the duration of the inter-season, we let $T = t_f + \tau$ be the combined duration of the banana cropping and the alternative cropping (or the fallow).

– The logistic growth of the roots during a cropping season is then given by: $\frac{dS}{dt} = g(t, S)$ where the function $g(t, S)$ is defined by

$$g(t, S) = \rho(t)S\left(1 - \frac{S}{K}\right).$$

The form of the function $\rho(t)$ within the $(n + 1)$ th season follows:

$$\rho(t) = \begin{cases} \rho & , \quad t \in \{0\} \cup]nT, nT + d], \\ 0 & , \quad t \in]nT + d, nT + t_f]. \end{cases} \quad (1)$$

Where ρ is the growth rate of the roots during the growth phase.

– At the end of a season, the roots of the plants are torn off. We assume that a small fraction q (that can be null) of infesting nematodes remains in the soil. This fraction corresponds to the nematodes that leave the roots toward the soil at the removal or the non-fresh roots that are left in the soil during the removal.

– When free pests contact plant roots (S) with a rate β , they infest the roots and start feeding on it with a saturated response as well as in Holling type II functional response, which is well-suited for invertebrates [6]. In the absence of experimental data, it seems coherent to rely on this functional response, since nematodes are invertebrates.

– The infesting parasites have a natural mortality μ .

– Infesting nematodes use a part of their food to reproduce inside (proportion γ) or outside (proportion $1 - \gamma$) the roots.

– In the absence of hosts, free nematodes undergo an exponential decay with a rate Ω .

This assumptions result in a three-dimensional semi-discrete model; a switched system, coupled to two sets of recurrence equations and one set of ordinary differential equations, define the model.

During the cropping, i.e $t \in \{0\} \cup]nT, nT + t_f]$, free nematodes (P) and infesting nematodes (X) interact with the healthy roots according to the following switching system:

$$\begin{cases} \frac{dP(t)}{dt} & = -\beta P(t)S(t) + \alpha a(1 - \gamma) \frac{S(t)X(t)}{S(t) + \Delta} - \Omega P(t), \\ \frac{dS(t)}{dt} & = \rho(t)S(t)\left(1 - \frac{S(t)}{K}\right) - a \frac{S(t)X(t)}{S(t) + \Delta}, \\ \frac{dX(t)}{dt} & = \beta P(t)S(t) + \alpha a\gamma \frac{S(t)X(t)}{S(t) + \Delta} - \mu X(t). \end{cases} \quad (2)$$

With the initial conditions $P(0) = P_0$, $S(0) = S_0$, $X(0) = 0$.

Where $\Delta > 0$ is the half-saturation constant.

In the following, we will term the dynamics of (2) during the $\{0\} \cup]nT, nT + d]$ interval "the first subsystem of (2)" while "the second subsystem of (2)" will concern $]nT + d, nT + t_f]$, with $\rho = 0$.

When roots are removed, only free parasites and a fraction q of infesting nematodes survive. So, for $t = nT + t_f$:

$$\begin{cases} P(nT + t_f^+) & = P(nT + t_f) + q.X(nT + t_f), \\ S(nT + t_f^+) & = 0, \\ X(nT + t_f^+) & = 0. \end{cases} \quad (3)$$

where the + superscript will always indicate the instant that directly follows.

When there is no host plant, i.e $t \in]nT + t_f, (n + 1)T]$, the remaining free nematodes undergo a decay:

$$\begin{cases} \frac{dP(t)}{dt} = -\Omega P(t), \\ \frac{dS(t)}{dt} = 0, \\ \frac{dX(t)}{dt} = 0. \end{cases} \quad (4)$$

At the beginning of a new season of banana plants, i.e. $t = (n+1)T$, fresh healthy roots are added through new suckers. The equation translating the process follows:

$$\begin{cases} P((n+1)T^+) = P((n+1)T), \\ S((n+1)T^+) = S_0, \\ X((n+1)T^+) = 0. \end{cases} \quad (5)$$

The system formed by the equations (2 - 5) represents our multi-seasonal nematodes-banana interaction model. This type of multi-seasonal model exists in the literature for another nematode, *Meloidogyne incognita* [7].

3. Model reduction and analysis

Proposition 1 – *The problem (2- 5) admits a solution that is unique for any initial condition and continuous on any interval $]nT, nT + t_f]$ and $]nT + t_f, (n+1)T]$, with $n \in \mathbb{N}$.*

– *The state variables remain non-negative over the time.*

– *The transition law of free nematodes from one banana cropping season to the next is given by*

$$P((n+1)T) = [P(nT + t_f) + qX(nT + t_f)]e^{-\Omega\tau}. \quad (6)$$

Proof.

– The equation (4) with initial condition (3) easily satisfies the Cauchy-Lipschitz conditions. Hence the conclusion directly follows on the intervals $]nT + t_f, (n+1)T]$. Furthermore, each subsystem of equation (2) is a well-posed Cauchy problem. The first subsystem has $P_0, S_0, 0$ as initial condition when $n = 0$ and the initial conditions are given by (5) when $n \geq 1$. The second subsystem has the value of the solution of the first subsystem as initial condition. Therefore, since S is bounded and the (P, X) dynamics are linearly bounded, the switched system (2) admits a unique continuous solution on $\{0\} \cup]nT, nT + t_f]$.

– We first consider $n = 0$ and denote by $W = (P, S, X)$ the state vector and $W(0)$ the initial condition. As these state variables represent biological quantities, we set $W(0) \geq 0$. The structure of the model then ensures that the state variables remain non-negative in the course of time. Besides, the discrete rule (5) ensures that if the non-negative orthant is positively invariant for season n then the initial condition for season $n+1$ will be positive, hence the same conclusion will follow for $n \geq 1$.

– Let $t \in]nT + t_f, (n+1)T]$, $n \in \mathbb{N}$.

We solve $\frac{dP}{dt} = -\Omega P$ with initial condition $P(nT + t_f^+) = P(nT + t_f) + q.X(nT + t_f)$ to obtain $P((n+1)T) = [P(nT + t_f) + qX(nT + t_f)]e^{-\Omega\tau}$. ■

The proposition 1 shows that the problem (2-5) is well posed. In the next proposition, we reduce the first subsystem of equation (2) to a Rosenzweig-MacArthur model, by introducing a new state variable $N = P + S$ that represents the total number of nematodes and using the singular perturbation theory.

Proofs of propositions (2 - 4) are left in appendix.

Proposition 2 *The first subsystem of equation (2) can be reduced to the system:*

$$\begin{cases} \dot{S} &= \rho S \left(1 - \frac{S}{K}\right) - a \frac{SN}{S + \Delta}, \\ \dot{N} &= \alpha a \frac{SN}{S + \Delta} - \mu N, \end{cases} \quad (7)$$

With initial conditions $S(nT^+) = S(0) = S_0$, $N(nT^+) = N(0) = P(nT)$.

Where $N = P + X$; assuming that the primary infestation is very fast (β is high) and the free pest P tends very fast to 0 and using the singular perturbation theory for slow-fast dynamics [11]. The states of the second subsystem will then be initialized with the final values of the first subsystems taking $P(nT + d^+) = 0$ and $X(nT + d^+) = N(nT + d)$;

REMARK. — According to Proposition 2, the number of free pest is null in the reduced first subsystem. That is a good approximation when β has a high value.

Thus, we consider that there is no free pest at the input of the second subsystem of equation (2) and that, at the same input, the number of infesting parasites X is therefore equal to the sum N of the two. In the following proposition, we therefore compute the values of the pest level and the roots biomass in the neighbourhood of the pest free solution.

Proposition 3 *In the neighbourhood of the Pest Free Solution (PFS),*

– For all $n \in \mathbb{N}$ and $t \in [0, d]$, the solution of equation (7) is given on $]nT, nT + d]$ by

$$N(nT + t) = P(nT) e^{-\mu t} \int_0^t \frac{\alpha a S^*(\tau)}{S^*(\tau) + \Delta} d\tau \quad (8)$$

$$S(nT + t) = S_0 - \int_0^t F(\xi) \exp\left(-\int_0^\xi \rho \left(1 - \frac{2S^*(\tau)}{K}\right) d\tau\right) d\xi \times \exp\left(\int_0^t \rho \left(1 - \frac{2S^*(\tau)}{K}\right) d\tau\right), \quad (9)$$

– For all $n \in \mathbb{N}$ and $t \in]nT + d, nT + tf]$.

There exists a matrix $\Pi(t)$ detailed in appendix such as

$$S(t) = S^*(t) - a \frac{S(nT + d)}{S(nT + d) + \Delta} X(t)$$

and

$$\begin{pmatrix} P(t) \\ X(t) \end{pmatrix} = \Pi(t - (nT + d)) \cdot \begin{pmatrix} 0 \\ N(nT + d) \end{pmatrix}$$

Where $S^*(t) = \frac{S_0 K}{S_0 + (K - S_0) e^{-\rho t}}$

From this result, one can now compute the basic reproduction number of the pest and the minimal inter-season duration that leads to the disappearance of the pest. That is the aim of the following proposition.

Proposition 4 *(Pest eradication)*

We have the following results:

1) For all $n \in \mathbb{N}$, the persistence of free nematodes is given by

$$P(nT) = P_0 e^{-n\Omega\tau} \delta^n \left[\Pi_{1,2}(t_f - d) + q \Pi_{2,2}(t_f - d) \right]^n, \quad (10)$$

Where

$$\delta = \exp\left(-\mu d + \int_0^d \frac{\alpha a S^*(\tau)}{S^*(\tau) + \Delta} d\tau\right) = N(d)/P_0.$$

2) The basic reproduction number is given by

$$\mathcal{R}_0 = e^{-\Omega\tau} \delta [\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d)]. \quad (11)$$

3) The minimal inter-season duration τ_0 such as the pest will disappear over time as soon as $\tau > \tau_0$ is given by

$$\tau_0 = \frac{\ln([\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d)]\delta)}{\Omega}. \quad (12)$$

4. Numerical simulations

We consider the parameters values in Table 1. In Figure 1, we compare the difference in behaviour between the system and its reduced form for different values of β within a season. In Figure 2, we illustrate the behaviour of the reduced system in the neighbourhood of the pest free equilibrium. Since $N = P+X$ and $P = 0$ in the first substem, such as $N = X$ in this same subsystem, the value X (number of infesting nematodes) will always be the one represented instead of N . With the considered parameters, we obtain $\tau_0 = 8.04$. The figure 2 illustrates the behaviour of the pest with τ taking different values: $\tau \ll \tau_0$, $\tau < \tau_0$, $\tau > \tau_0$, $\tau \gg \tau_0$.

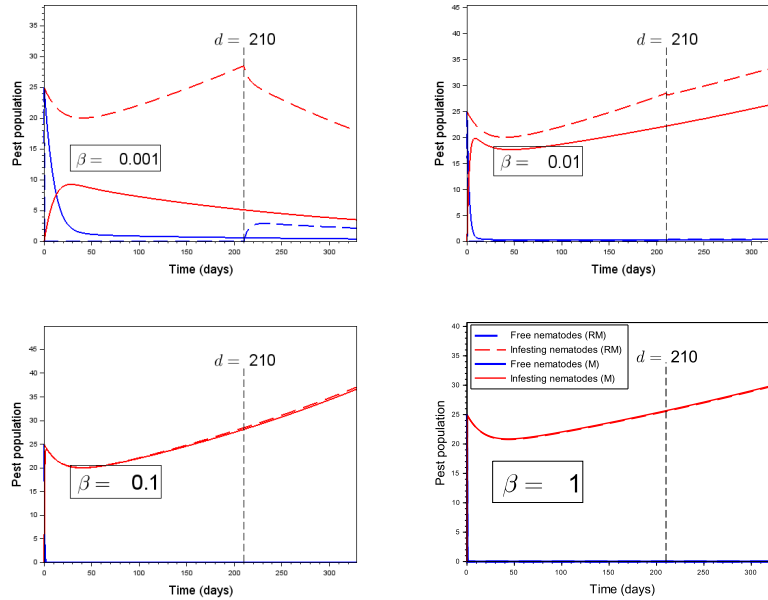


Figure 1. Comparison between the model (M) and its reduced form (RM) for different values of β .

Parameter	Value	Ref.	Parameter	Value
Ω	$0.0495^{(1)} \text{ day}^{-1}$	[3]	β	$10^{-1} \text{ g}^{-1} \cdot \text{day}^{-1}$
μ	$0.05 - 0.04^{(2)} \text{ day}^{-1}$	[9]	γ	0.5
K	$\geq 143^{(3)} \text{ grammes (g) in Costa Rica}$	[10]	a	$10^{-4} \text{ g} \cdot \text{day}^{-1}$
S_0	$60^{(4)} \text{ g}$	[10]	α	650 g^{-1}
t_f	$300 - 360^{(5)} \text{ days}$	[12]	q	5%
d	Berangan: 210-240 days Cavendish: 180-210 ⁽⁶⁾ days	[12]	P_0	25
			Δ	60 g
			ρ	0.06 days^{-1}

Table 1. Values of the parameters.⁽¹⁾ We consider the soil as an andosol with a null matrix potential. ⁽²⁾ We consider the average. ⁽³⁾ We consider the value 150. ⁽⁴⁾ We consider an approximation of the sucker survey critical level ⁽⁵⁾ We take the average value. 330 ⁽⁶⁾ We take the value 210.

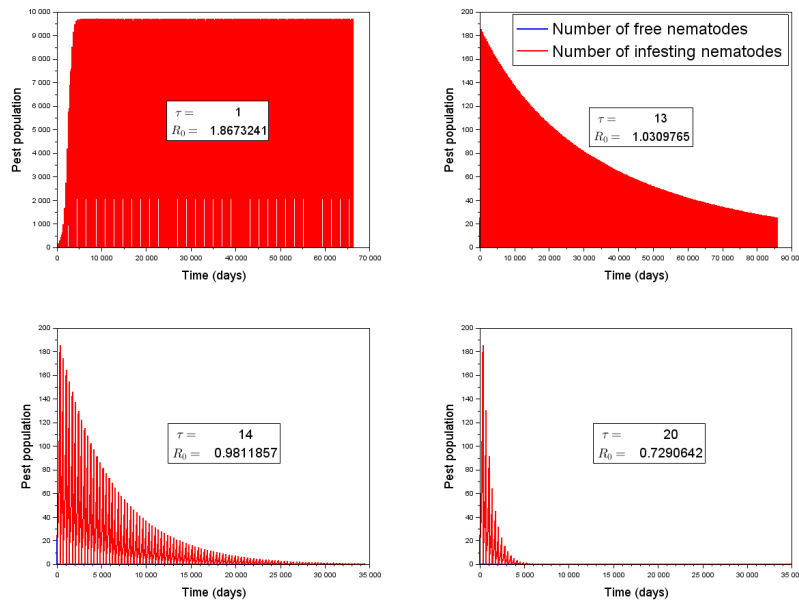


Figure 2. Pest dynamics for different values of τ when $\tau_0 = 11.78$.

REMARK. — In figure 2, free pest levels are very low and really appear when there is no host (during the inter-season) through the fraction q of infesting remaining in the soil upon extraction of the roots.

Conclusion

Nematode-host models have not undergone enough development in theory and practical applications in the field of biomathematics in the case of *Radopholus similis*. So, in

this paper, we have studied a simple model for this kind of interaction with a saturated response and taking in account both free and infesting stages of nematodes. We have obtained a threshold on the duration of the inter-season such as the pest level tends to zero over time when that threshold is crossed. We also computed the basic reproduction number of the nematodes. All this work was done after we reduced the model by using the singular perturbation theory for slow-fast dynamics. Our numerical simulation results confirm that when the duration of the inter-season τ passes through the critical value τ_0 , the pest tends to disappear. The ability to compute the basic reproduction number and the critical duration of the inter-season developed in this paper might help lead to more sophisticated strategies of control of *Radopholus similis* in agricultural fields.

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Appendix 1: Proof of Proposition 2

Let's first consider the first subsystem of equation (2), i.e. $t \in]nT, nT + d[$. Let $N = P + X$ and consider the system in (P, S, N) .

Assuming that β is large, let $\beta = \frac{\beta'}{\varepsilon}$, $0 < \varepsilon \ll 1$ and $\tau = \frac{t}{\varepsilon}$. The new time τ is called *fast time*. The system with derivatives according to τ is written:

$$\begin{cases} \frac{dP}{d\tau} &= -\beta'PS + \varepsilon\alpha a(1-\gamma)\frac{S(N-P)}{S+\Delta} - \varepsilon\Omega P, \\ \frac{dS}{d\tau} &= \varepsilon\rho S\left(1 - \frac{S}{K}\right) - \varepsilon a\frac{S(N-P)}{S+\Delta}, \\ \frac{dN}{d\tau} &= \varepsilon\alpha a\gamma\frac{S(N-P)}{S+\Delta} + \varepsilon(\mu - \Omega)P - \varepsilon\mu N, \end{cases} \quad (13)$$

When $\varepsilon = 0$, we then define the *fast equation* by

$$\frac{dP}{d\tau} = -\beta'PS$$

Which admits an equilibrium $\bar{P} = 0$ that is asymptotically stable because $S > 0$ (we will have proven that the trajectories are positive).

The *slow equation* is written as

$$\begin{cases} \dot{S} &= \rho S\left(1 - \frac{S}{K}\right) - a\frac{SN}{S+\Delta}, \\ \dot{N} &= \alpha a\gamma\frac{SN}{S+\Delta} - \mu N, \end{cases} \quad (14)$$

Which corresponds to a Rosenzweig-MacArthur model. The Tychonov theorem ensures that

$$\begin{aligned} \lim_{\varepsilon \rightarrow 0} P(t, \varepsilon) &= 0, \quad t \in]nT, nT + d[\\ \lim_{\varepsilon \rightarrow 0} (S(t, \varepsilon), N(t, \varepsilon)) &= (\bar{S}(t), \bar{N}(t)), \quad t \in]nT, nT + d[\end{aligned}$$

Where (\bar{S}, \bar{N}) is the solution of equation (14) and $(P(t, \varepsilon), S(t, \varepsilon), N(t, \varepsilon))$ is the solution of the perturbed system:

$$\begin{cases} \varepsilon\dot{P} &= -\beta'PS + \varepsilon\alpha a(1-\gamma)\frac{S(N-P)}{S+\Delta} - \varepsilon\Omega P, \\ \dot{S} &= \rho S\left(1 - \frac{S}{K}\right) - a\frac{S(N-P)}{S+\Delta}, \\ \dot{N} &= \alpha a\frac{S(N-P)}{S+\Delta} + (\mu - \Omega)P - \mu N. \end{cases}$$

Appendix 2: Proof of Proposition 3

- The Pest Free Solution is written for all $t \in [0, d]$, $\begin{pmatrix} S^*(t) \\ N^*(t) \end{pmatrix} = \begin{pmatrix} \frac{S_0 K}{S_0 + (K - S_0)e^{-\rho t}} \\ 0 \end{pmatrix}$.

Considering the deviation variables $\tilde{S} = S(t) - S^*(t)$ and $\tilde{N} = N(t) - N^*(t) = N(t)$, one can write the deviation system as

$$\begin{cases} \dot{\tilde{S}} &= \rho(\tilde{S} + S^*(t))\left(1 - \frac{\tilde{S} + S^*(t)}{K}\right) - \frac{a(\tilde{S} + S^*(t))\tilde{N}}{\tilde{S} + S^* + \Delta} - \rho S^*(t)\left(1 - \frac{S^*(t)}{K}\right), \\ \dot{\tilde{N}} &= \frac{\alpha a(\tilde{S} + S^*(t))\tilde{N}}{\tilde{S} + S^* + \Delta} - \mu\tilde{N}, \\ \tilde{S}(0) &= 0, \tilde{N}(0) = N(0) = P_0. \end{cases} \quad (15)$$

In a neighbourhood of the PFS, the system is equivalent to

$$\begin{pmatrix} \dot{\tilde{S}} \\ \dot{\tilde{N}} \end{pmatrix} = \begin{pmatrix} \rho\left(1 - \frac{2S^*(t)}{K}\right) & -\frac{aS^*(t)}{S^*(t) + \Delta} \\ 0 & -\mu + \frac{\alpha aS^*(t)}{S^*(t) + \Delta} \end{pmatrix} \cdot \begin{pmatrix} \tilde{S} \\ \tilde{N} \end{pmatrix} \quad (16)$$

That leads to the equation in \tilde{N}

$$\dot{\tilde{N}} = \left(-\mu + \frac{\alpha aS^*(t)}{S^*(t) + \Delta}\right)\tilde{N},$$

whose solution is given by

$$\tilde{N}(t) = P_0 e^{-\mu t + \int_0^t \frac{\alpha aS^*(\tau)}{S^*(\tau) + \Delta} d\tau}.$$

One can now replace this expression in (16) and let $F(t) := \frac{aS^*(t)}{S^*(t) + \Delta}\tilde{N}(t)$ to obtain the equation in \tilde{S} :

$$\dot{\tilde{S}} = \rho\left(1 - \frac{2S^*(t)}{K}\right)\tilde{S}(t) - F(t), \quad \tilde{S}(0) = 0.$$

That leads to the solution

$$\tilde{S}(t) = - \int_0^t F(\xi) \exp\left(- \int_0^\xi \rho\left(1 - \frac{2S^*(\tau)}{K}\right) d\tau\right) d\xi \times \exp\left(\int_0^t \rho\left(1 - \frac{2S^*(\tau)}{K}\right) d\tau\right).$$

Assuming that the solutions remain close enough to the PFS over the seasons, we obtain the result by changing $P(0)$ in $P(nT^+) = P(nT)$.

– On $]nT + d, nT + t_f]$, the second subsystem of equation 2 is written

$$\begin{cases} \dot{P}(t) &= -\beta P(t)S(t) + \alpha a(1 - \gamma)\frac{S(t)X(t)}{S(t) + \Delta} - \Omega P(t), \\ \dot{S}(t) &= -a\frac{S(t)X(t)}{S(t) + \Delta}, \\ \dot{X}(t) &= \beta P(t)S(t) + \alpha a\gamma\frac{S(t)X(t)}{S(t) + \Delta} - \mu X(t). \end{cases} \quad (17)$$

With initial conditions $P(nT + d^+) = 0$, $X(nT + d^+) = N(nT + d)$ and $S(nT + d^+) = S(nT + d)$ from the system (14).

The pest free equilibrium (PFE) can be written $Y_P(t) = \begin{pmatrix} P_p(t) \\ S_p(t) \\ X_p(t) \end{pmatrix} = \begin{pmatrix} 0 \\ S^*(d) \\ 0 \end{pmatrix}$.

Considering the deviation variables $\tilde{P}(t) = P(t) - P_p(t) = P(t)$, $\tilde{S}(t) = S(t) - S_p(t)$, $\tilde{X}(t) = X(t) - X_p(t) = X(t)$, one can write the equation in the new variables as:

$$\begin{cases} \dot{\tilde{P}} &= -\beta\tilde{P}(\tilde{S} + S^*(d)) + \alpha a(1-\gamma) \frac{(\tilde{S} + S^*(d))\tilde{X}}{\tilde{S} + S^*(d) + \Delta} - \Omega\tilde{P}, \\ \dot{\tilde{S}} &= -a \frac{(\tilde{S} + S^*(d))\tilde{X}}{\tilde{S} + S^*(d) + \Delta}, \\ \dot{\tilde{X}} &= \beta\tilde{P}(\tilde{S} + S^*(d)) + \alpha a\gamma \frac{(\tilde{S} + S^*(d))\tilde{X}}{\tilde{S} + S^*(d) + \Delta} - \mu\tilde{X} \end{cases} \quad (18)$$

And the Jacobian matrix $J = \begin{bmatrix} -\beta S^*(d) - \Omega & 0 & \alpha a(1-\gamma) \frac{S^*(d)}{S^*(d) + \Delta} \\ 0 & 0 & -a \frac{S^*(d)}{S^*(d) + \Delta} \\ \beta S^*(d) & 0 & -\mu + \alpha a\gamma \frac{S^*(d)}{S^*(d) + \Delta} \end{bmatrix}$.

In the neighbourhood of the PFE, system 18 is then equivalent to the linearised system

$$\dot{\tilde{Y}} = J\tilde{Y}, \quad \tilde{Y} = (\tilde{P}, \tilde{S}, \tilde{X}). \quad (19)$$

Since the second column of J is null, one just has to compute the exponential of At that will generate a local solution for \tilde{P} and \tilde{X} , where $A :=$

$$\begin{bmatrix} -\beta S^*(d) - \Omega & \alpha a(1-\gamma) \frac{S^*(d)}{S^*(d) + \Delta} \\ \beta S^*(d) & -\mu + \alpha a\gamma \frac{S^*(d)}{S^*(d) + \Delta} \end{bmatrix}.$$

We deduce \tilde{S} from $\dot{\tilde{S}} = -a \frac{S^*(d)}{S^*(d) + \Delta} \tilde{X}$, i.e.

$$\tilde{S}(t) = -a \frac{S_0}{S_0 + \Delta} \tilde{X}(nT + t).$$

Since A is a Metzler matrix, it admits two distinct real eigenvalues $\lambda_{1,2} = \frac{\text{tr}(A)}{2} \pm$

$\frac{1}{2}\sqrt{\text{tr}^2(A) - 4\det(A)}$ and we have $\Pi(t) = \begin{pmatrix} \Pi_{1,1}(t) & \Pi_{1,2}(t) \\ \Pi_{2,1}(t) & \Pi_{2,2}(t) \end{pmatrix}$, where

$$\Pi_{1,1}(t) = \frac{1}{\lambda_2 - \lambda_1} \left(e^{\lambda_1 t} (\lambda_2 + \beta S^*(d) + \Omega) - e^{\lambda_2 t} (\lambda_1 + \beta S^*(d) + \Omega) \right)$$

$$\Pi_{1,2}(t) = -\frac{1}{\lambda_2 - \lambda_1} \left(\frac{\alpha a(1-\gamma)}{S^*(d) + \Delta} (e^{\lambda_1 t} - e^{\lambda_2 t}) \right)$$

$$\Pi_{2,1}(t) = -\frac{1}{\lambda_2 - \lambda_1} \left(\beta S^*(d) (e^{\lambda_1 t} - e^{\lambda_2 t}) \right)$$

$$\Pi_{2,2}(t) = \frac{1}{\lambda_2 - \lambda_1} \left(e^{\lambda_1 t} \left(\lambda_2 + \mu - \frac{\alpha a S^*(d)}{S^*(d) + \Delta} \right) - e^{\lambda_2 t} \left(\lambda_1 + \mu - \frac{\alpha a S^*(d)}{S^*(d) + \Delta} \right) \right)$$

Appendix 3: Proof of Proposition 4

1) From equation (8), we have

$$N(nT + d) = P(nT)e^{-\mu d + \int_0^d \frac{\alpha a S^*(\tau)}{S^*(\tau) + \Delta} d\tau}.$$

Hence, $N(nT + d) = P(nT)\delta$.

Proposition 3 therefore involves

$$\begin{pmatrix} P(nT + t_f) \\ X(nT + t_f) \end{pmatrix} = \begin{pmatrix} \Pi_{1,1}(t_f - d) & \Pi_{1,2}(t_f - d) \\ \Pi_{2,1}(t_f - d) & \Pi_{2,2}(t_f - d) \end{pmatrix} \begin{pmatrix} 0 \\ \delta P(nT) \end{pmatrix}$$

Hence,

$$\begin{cases} P(nT + t_f) & = \Pi_{1,2}(t_f - d) \cdot P(nT)\delta \\ X(nT + t_f) & = \Pi_{2,2}(t_f - d) \cdot P(nT)\delta \end{cases}$$

So, according to the transition rule (6),

$$P((n+1)T) = [\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d)]P(nT)\delta e^{-\Omega\tau}$$

From where we deduce

$$P(nT) = P_0 e^{-n\Omega\tau} \delta^n [\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d)]^n.$$

2) Since $P(nT) \rightarrow 0$ iff

$$(\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d))\delta e^{-\Omega\tau} < 1, \quad (20)$$

We deduce $\mathcal{R}_0 = (\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d))\delta e^{-\Omega\tau}$.

3) We deduce τ_0 from the condition (20) above, by rearranging as $\tau > \frac{\ln([\Pi_{1,2}(t_f - d) + q\Pi_{2,2}(t_f - d)]\delta)}{\Omega} \equiv \tau_0$.