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Modelling and control of managed ecosystems, from bioreactors to agroecosystems

Frédéric Grogard

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HABILITATION À DIRIGER DES RECHERCHES

Modelling and control of managed
ecosystems, from bioreactors to
agroecosystems

Frédéric GROGNARD

BIOCORE, Centre Inria d'Université Côte d'Azur

**Présentée en vue de l'obtention
de l'Habilitation à Diriger des
Recherches en**

Automatique, Traitement du Signal
et des Images
d'Université Côte d'Azur

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Contents

Remerciements	7
Introduction	9
1 Feedback control for nonlinear constrained systems	11
1.1 Control of structured nonlinear systems	12
1.2 Control in population dynamics	13
1.3 Control theory?	14
1.4 Collaborators	16
1.5 Representative paper	16
2 Control and stability of a bioreactor	17
2.1 Saturated control of a wastewater plant	17
2.2 Stability analysis of a bioreactor	19
2.3 Collaborators	20
2.4 Representative paper	20
3 Augmentative biological control	21
3.1 A first result	22
3.2 Which intra-specific interactions between predators?	26
3.2.1 Interfering predators	26
3.2.2 Cooperating predators	28
3.3 Take-home message and other results	32
3.4 Collaborators	32
3.5 Further consequences	33
3.6 Representative paper	33
4 Resistance deployment and host mixtures	35
4.1 Increasing genetic drift for resistance durability	36
4.2 Host mixtures and plant immunity	39
4.2.1 Extension	43
4.3 Collaborators	44
4.4 Representative paper	44

CONTENTS

5	Epidemiological modelling for tropical agriculture	45
5.1	Why EPITAG?	45
5.1.1	Anecdotally	45
5.1.2	Agriculture in Africa	45
5.1.3	Agriculture in Cameroon	47
5.1.4	Crop pests	47
5.2	Banana/plantain plant-parasitic nematode control	48
5.2.1	Banana/plantain in Cameroon	48
5.2.2	Radopholus similis	48
5.3	Control of the Coffee Berry Borer	53
5.3.1	Coffee in Cameroon	53
5.3.2	The coffee berry borer	53
5.4	Control of the Coffee Leaf Rust	56
5.4.1	Coffee in Cameroon	56
5.4.2	Coffee Leaf Rust (CLR)	56
5.5	Collaborators	61
5.6	Representative paper	61
6	Ongoing works and perspectives	63
6.1	Introductions for crop protection	63
6.2	Resistance deployment, priming and seasonality	65
6.3	Epidemiological modelling for tropical agriculture	65
6.4	Perspectives	66
	Bibliography	80
A	Curriculum Vitae	81
A.1	Identity	81
A.2	Formation	81
A.3	Professional experience	81
A.4	Teaching	82
A.5	Supervision	82
A.6	Collaborations and Projects	85
A.7	Responsibilities	87
A.8	Publications	88
A.8.1	Peer-reviewed journal papers	88
A.8.2	Peer-reviewed conference proceedings	91
A.8.3	Presentations at international conferences without proceedings	94
A.8.4	Book chapters	97
A.8.5	Edition	97
A.8.6	PhD thesis	97

CONTENTS

B	Positive control for global stabilization of predator-prey systems	99
C	Polytopic Lyapunov functions for persistence analysis of competing species	101
D	Natural enemies deployment in patchy environments for augmentative biological control	103
E	Host mixtures for plant disease control: benefits from pathogen selection and immune priming	105
F	Modelling and optimal strategy to control coffee berry borer	107

CONTENTS

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Introduction

My research has evolved over the years, from purely theoretical results in control theory during my PhD thesis at the Université catholique de Louvain and my post-doctoral stay in what was the Institut National Polytechnique de Grenoble, to more application inspired results since I arrived at Inria in Sophia Antipolis in 2003. Having been recruited as *Chargé de recherches* in the Comore project-team (Comore - Modelling and control of renewable resources) which is now the Biocore team (Biocore - Biological control of artificial ecosystems), I was expected to direct my research towards biological applications. Since then, my research contributes to the fields of **mathematical biology, theoretical ecology, control theory and dynamical systems applied to the life sciences**. In all those contexts, I have mostly concentrated on population dynamics models upon which I apply and develop methods of control theory and computational biology.

The present manuscript aims at presenting the course of my research work and at being somewhat coherent. It does not present everything I did in research. For instance, it omits or hardly mentions some papers I am quite fond of such as Lebon et al. (2014) that gave a novel perspective on the feedback loop of overcompensation in plant-herbivore interactions or Calcagno et al. (2014) that revisits the decades old Marginal Value Theorem that predicts the behavior of insects when confronted with resource patches, and warns about its incorrect usage. Since I have been working in research for quite some time, I had the pleasure of going back to some of my older results and took the liberty of emphasizing things I liked most inside or even outside my research work. For instance, I start my manuscript by presenting Watt's governor since I never had any occasion of mentioning it in any of my papers and it merges two of my interests: science and history; also I have always been fascinated by this device as it encompassed all the power of control theory before any theory was ever set. It was also for me the occasion to research a bit further and expose the challenges facing agriculture in Africa that are central to Chapter 5.

I opted to do a leisurely walk through my research work, more less in a chronological order, presenting new applications and new methodologies as I encountered them. As I said, I come from nonlinear control theory and started with that for my biological applications. Along the way, I encountered semi-discrete systems, bifurcation analysis, optimal control,... The idea behind all this is always to control or regulate the systems to some desired point. This is the point of view of control and not that of dynamical systems. In the latter, bifurcation analysis for instance is seen as a tool to explore all the possible situations that can occur when varying some parameter. In control, it is a way to identify the parameter values where the behaviour of the system is acceptable. In the end, I extracted one paper per chapter to illustrate and allow for a deeper dive into my work; these might not be my most cited papers but I picked them as they are illustrative of what I do and are not already detailed in the heart of the manuscript, some written for a control audience (see for instance Appendix B) and other for theoretical biologists

Introduction

(Appendix E).

This manuscript is faithful to my modelling and control philosophy. You should not expect to find in this manuscript large dimension models that try to meticulously represent every detail of a biological phenomenon with a lot of parameters that need to be fine-tuned. These play an important role in agronomy for instance and are necessary to understand the interconnections that take place in complex systems. However, I mostly develop models of small dimension that focus on one or two aspects of a phenomenon, in order to retain some genericity. The point is to identify generic properties of the models, delimit the impact of the aspect we are considering, and draw conclusions for control. From such results, we do not aim to directly go to the field and apply the preconisations that we draw. The point is more to give qualitative ideas of what should be done, to give insights into the phenomena, to give ideas for experiments,... However, small models can be more than that: a strong result of Olivier Bernard that has always impressed me is that his small model of anaerobic digestion could represent 95% of the variability observed in the data, in a digester in which population dynamics are very complex; this is as good or even better than any big model that could be designed.

I do not think however that one modelling approach is better than another, and in fact multi-models approaches are probably the most efficient, but with my background and my skills, theoretical analysis of small models is the track I can be the most efficient at.

1

Feedback control for nonlinear constrained systems

Control of industrial systems is a problem that dates back centuries, with Watt's centrifugal governor from 1788 that regulated the speed of an engine by controlling the flow of steam or fuel being a first emblematic example of successful regulation, that was instrumental in the onset of the industrial revolution (see Figure 1.1). Though Watt only adapted one of Christiaan

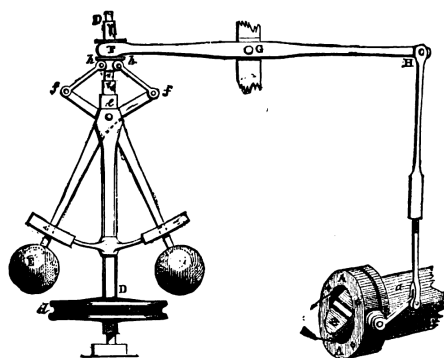


FIG. 4.—Governor and Throttle-Valve.

Figure 1.1: Illustration of Watt's centrifugal governor (from Routledge (1899)): if the engine speed increases, the balls move away from the axis and tend to shutter the steam valve to bring the speed down.

Huyghens' inventions, and though first examples of feedback controls are traced back to ancient water clocks of the IIIrd century B.C. (Mayr, 1970), this purely analogic controller was at the basis of a whole field of simple linear controllers that have been used in industry. Though its core principle was not really conceptualized, it opened the door to feedback control, that is the usage of online measurements to determine the action to be applied on the system to be controlled (as opposed to open loop control, where the control values are pre-determined and do not take online measurements into account). Watt's controller is in fact a proportional controller (P) in that its action is proportional to the deviation of the quantity of interest from its reference

1. Feedback control for nonlinear constrained systems

point; such controllers have been extended to the PID form, that is a form where the action is proportional to a weighted sum of the deviation, its integral and its derivative. Such controllers, when finely tuned, have proven to be extremely efficient in real life applications. They however encounter limitations when the system is not accurately represented by linear dynamics. In my early years as a researchers, I have encountered two applications where the nonlinearities were so strong and had such dramatic consequences that they had to be taken into account for the design of the controller: the cement mill (Grognaud et al., 2001) and the anaerobic digester (Grognaud and Bernard, 2006); in both cases, if the industrial plant drifts away a bit far from its normal operating conditions due to some perturbations, and is not adequately controlled, the system crashes: the cement mill becomes plugged and acidification washes out the biomass from the digester. Hence the necessity for designing control laws that take nonlinearities into account.

1.1 Control of structured nonlinear systems

During the 1990s, theoretical nonlinear control was expanding quickly, and my PhD thesis and postdoctoral stay were set in that field. My PhD thesis concentrated on the problem of stabilization by feedback, that is in using measurements of the whole state x to compute the control value, of the origin ($0 \in \mathbb{R}^n$) of nonlinear systems having certain structures. The general nonlinear stabilization problem consisted in considering the system

$$\dot{x} = f(x, u) \quad (1.1)$$

with $x \in \mathbb{R}^n$, $u \in \mathbb{R}$ and $f \in \mathcal{C}^1$, and to design a feedback control law $u = \alpha(x)$ that would ensure that the origin of the system

$$\dot{x} = f(x, \alpha(x)) \quad (1.2)$$

be at least asymptotically stable, and if possible globally asymptotically stable. At the time, the exploitation of the structure of the systems to develop control laws for large systems was central to many nonlinear control developments, starting from systems in feedback form:

$$\begin{cases} \dot{x}_1 &= f_1(x_1) & +x_2 \\ \dot{x}_2 &= f_2(x_1, x_2) & +x_3 \\ &\vdots & \\ \dot{x}_{n-1} &= f_{n-1}(x_1, \dots, x_{n-1}) & +x_n \\ \dot{x}_n &= f_n(x_1, \dots, x_n) & +u \end{cases} \quad (1.3)$$

with $x_i, u \in \mathbb{R}$. A classical stabilization approach of such a system consists in first building a control law $x_2 = \alpha_1(x_1)$ for the stabilization of $x_1 = 0$ in the first equation, which is then used as a basis to build a control law $x_3 = \alpha_2(x_1, x_2)$ for the stabilization of the origin of the (x_1, x_2) subsystem through a method called backstepping (Saberri et al., 1990). This method is then extended step by step until the control law $u = \alpha_n(x_1, \dots, x_n)$ that stabilizes the origin of \mathbb{R}^n is obtained. Conversely, the system

$$\begin{cases} \dot{x}_1 &= x_2 + g_1(x_2, \dots, x_n) \\ \dot{x}_2 &= x_3 + g_2(x_3, \dots, x_n) \\ &\vdots \\ \dot{x}_{n-1} &= x_n + g_{n-1}(x_n) \\ \dot{x}_n &= u \end{cases}, \quad (1.4)$$

1.2. CONTROL IN POPULATION DYNAMICS

with $x_i, u \in \mathbb{R}$ and the g_i functions of higher order close to 0, is in feedforward form and, based on a control law $u = \alpha_n(x_n)$ that stabilizes $x_n = 0$, methods were developed to build a new control law $u = \alpha_{n-1}(x_{n-1}, x_n)$ that stabilizes the origin of the (x_{n-1}, x_n) subsystem through small gain or forwarding approaches (Mazenc and Praly, 1996; Teel, 1996; Grogard et al., 1998). The idea of the small gain method is that x_n is brought to small values by the control u , so that $g_{n-1}(x_n)$ becomes small, and then u can control x_{n-1} to 0 without interference from the g_{n-1} term. This method is then extended step by step until x_1 is reached and all states are stabilized.

The backstepping approach allows for the construction of a control law from the top down in a lower triangular system while the forwarding approach builds the control law from the bottom up in an upper triangular system.

The contribution of the paper Grogard et al. (1999) was to find a middle ground between these two forms and develop a control law for a rate-limited feedforward system in the presence of feedback terms:

$$\begin{cases} \dot{x}_1 &= f_1(x_1) & +x_2 & +g_1(\dot{x}_2, \dots, \dot{x}_n) \\ \dot{x}_2 &= f_2(x_2) & +x_3 & +g_2(\dot{x}_3, \dots, \dot{x}_n) \\ & \vdots & & \\ \dot{x}_{n-1} &= f_{n-1}(x_{n-1}) & +x_n & +g_{n-1}(\dot{x}_n) \\ \dot{x}_n &= f_n(x_n) & +u & \end{cases} \quad (1.5)$$

In the absence of the $f_i(\dots)$ terms, system (1.5) would be in feedforward form, while in the absence of the $g_i(\cdot)$ terms, it would be in feedback form. The feedback control that we proposed in Grogard et al. (1999) was built recursively and ensured that the x_{i+1} variable controls the x_i variable "slowly", that is by having $g_i(\dot{x}_{i+1}, \dots, \dot{x}_n)$ staying small.

Beyond this result, my PhD thesis contained a hybrid control method for the stabilization of linear systems with bounded inputs (Grogard et al., 2002a), and the design of a dynamical system whose solutions converge to the duration of the times between switchings of the solution of a time-optimal control problem for linear systems with bounded inputs (Grogard and Sepulchre, 2001; Grogard et al., 2002b). The stabilization problem for such systems is indeed intrinsically nonlinear: if the saturation in its input is not taken into account, the action that is actually applied on the system can be much smaller than what is mandated by the control design, and so the behaviour of the system be degraded up to potential destabilization.

During my post-doctoral stay in Grenoble, I studied orbital stabilization, that is the stabilization of periodic orbits in a nonlinear system. The application this stemmed from was the biped robot, whose walking movement can be considered to be a periodic orbit, but I mainly stayed on the theoretical side (Grogard and Canudas de Wit, 2004, 2005).

1.2 Control in population dynamics

Since I arrived at Inria, I have had a few occasions to apply feedback control to biological systems since the classical design methods tend not to work, mainly due to the positivity constraints on the variables (often quantities or densities of populations) and on the control (often a flow rate, or a release rate). In two contexts, I could do so however: the first one is the design of a saturated control for a wastewater plant (see Section 2.1 for details) and the second one concerns the design of positive control for Lotka-Volterra and predator-prey systems. The design of positive feedback control laws has been of interest for a long time for Jean-Luc Gouzé, who

1. Feedback control for nonlinear constrained systems

was the head of Comore and then Biocore. It is however rarely tackled due to its complexity. We first considered general Lotka-Volterra systems in the form

$$\dot{x} = \text{diag}(x)(A(x - e) + bu)$$

with $x, e \in \mathbb{R}_+^n$, $A \in \mathbb{R}^{n \times n}$ skew symmetric and $b \in \mathbb{R}^n$ (and $\text{diag}(x)$ is the diagonal matrix with the x_i on its diagonal). When $\det(A) \neq 0$, such systems present a first integral in the form $V(x) = \sum_{i=1}^n (x_i - e_i \ln(x_i))$, which can be used as a Control Lyapunov Function based on which we have built the control law

$$u = \sigma(-{}^t b(x - e))$$

that globally asymptotically stabilizes the equilibrium e (with $\sigma(s) = 0$ when $s \leq 0$ and $\sigma(s) > 0$ otherwise) (Gronard and Gouzé, 2005).

A similar control was developed in Gronard et al. (2013) for the stabilization of an equilibrium with a small level of predators in a generalized form of the classical Rosenzweig MacArthur model (Rosenzweig, 1971):

$$\begin{cases} \dot{x} &= f(x) + g(x)y \\ \dot{y} &= h(x)y - my + u(x, y)y \end{cases} \quad (1.6)$$

with $x, y \in \mathbb{R}_+$ respectively the prey and predator densities, and where u represents the release of predators into the system. Supposing that we have a target level for the prey x^* , we easily compute the level of input required to ensure it is achieved at equilibrium ($\bar{u} = m - h(x^*)$). When some assumptions are satisfied, the equilibrium (x^*, y^*) is then stabilized with the control

$$u(x, y) = \sigma(\bar{u} - \gamma[(y - y^*) + \beta(x - x^*)])$$

with σ defined as earlier. The proof does not go through a Lyapunov function but we rather show the existence of a positively invariant and attractive region Ω connecting the equilibrium (x^*, y^*) and the y axis (see Figure 1.2); we then use the Poincaré-Bendixson theorem to show that the only possibility is for the solution to converge to the equilibrium. A follow-up article was then presented where the feedback control took the form of impulses applied at regular intervals, which corresponds better to the way introductions take place in a population, when compared to their classical modelling as continuous flow (Gronard, 2014). This discrepancy between continuous and impulsive actions will be further developed in Chapter 3.

1.3 Control theory?

My work is set in the field of ‘‘Control theory’’, which gives an original approach on the analysis and, obviously, control of dynamical systems. Indeed, control theory covers way more than the design of feedback control laws in an industrial context. It also encompasses related topics such as parameter identification, observation of non measured states, or stability analysis (Khalil, 2015). From these, stability analysis is an important component of my work through

- the computation of the eigenvalues of the Jacobian matrix evaluated at an equilibrium, or the application of the Routh-Hurwitz criterion on said matrix (linearisation or Lyapunov indirect method). This approach is central in several of my papers such as Lebon et al. (2014), Gronard et al. (2015) or Clin et al. (2021, 2022), where we identify parametric conditions for the stability of equilibria, from which we draw biologically relevant conclusions.

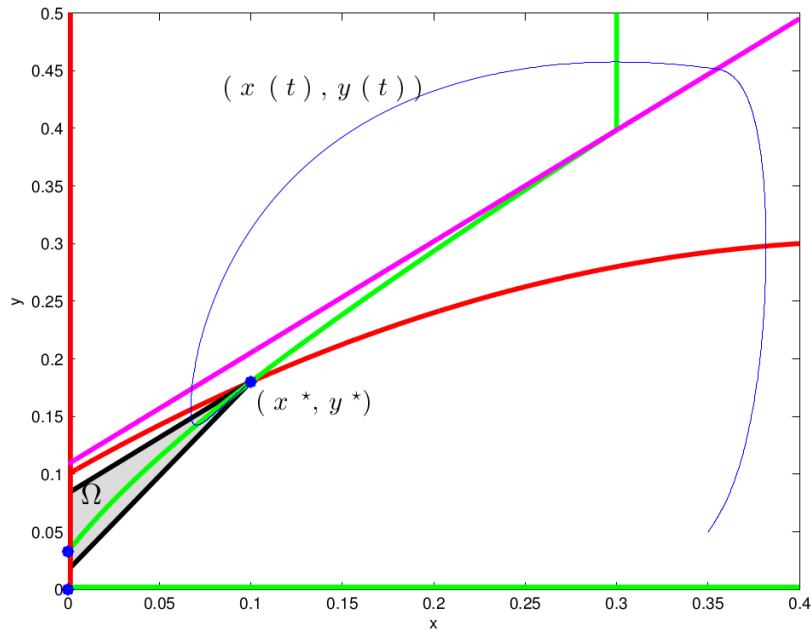


Figure 1.2: Stabilization of the point (x^*, y^*) , with the magenta line indicating the level above which $u = 0$, the red and green lines the x - and y -nullclines respectively, the shaded area Ω the positively invariant region, and the blue line a solution that converges to the equilibrium. (Grogard et al., 2013)

- the design of Lyapunov or Lyapunov-LaSalle functions (for Lyapunov direct method or LaSalle invariance principle), which is an art in itself. I for example designed a polytopic Lyapunov function in Grogard et al. (2007b) while Yves Fotso built one in Fotso Fotso et al. (2021), and I helped him exploit it to the fullest.
- more ad-hoc methods related to the problem at hand such as for example the use of Poincaré-Bendixson theorem to conclude on the stability of the equilibrium in the presence of a feedback control law (Grogard et al., 2001, 2013).

More on the boundary between applied mathematics and control theory is optimal control theory. It essentially consists in finding a control sequence $u(t)$ that maximizes or minimizes a cost functional. Classical examples of optimal control are ones that aim at minimizing the time or fuel required to achieve an objective. A comprehensive theory has been developed to obtain solutions for this family of problem, from variational methods to the maximum principle of Pontryagin (Pontryagin et al., 1962) on the theoretical side, indirect (Lenhart and Workman, 2007) and direct (Team Commands, Inria Saclay, 2019) methods on the numerical side. In the present manuscript, we use the tools of optimal control theory for the deployment of ecologically friendly crop protection methods to optimize profit of plantation in a tropical context, and to identify optimal behavior of organisms in an evolutionary context. Closer to control theory is the design of optimal control in feedback form, which we managed to do in Akhmetzhanov et al. (2011), but can also be achieved by setting the solutions of the open-loop optimal control problem in a Model Predictive Control framework that regularly recomputes the solution of the optimal control problem on the basis of the measurements (Propoi, 1963).

1. Feedback control for nonlinear constrained systems

1.4 Collaborators

These results were obtained:

- during my PhD thesis in Louvain-la-Neuve and Liège, under the supervisions of Rodolphe Sepulchre and Georges Bastin;
- during my post-doctoral stay in Grenoble, with Carlos Canudas-de-Wit;
- with Jean-Luc Gouzé, in part during his supervision of Jonathan Rault's thesis.

1.5 Representative paper

The following paper presents the control method built for system (1.6).

A26 (numbering corresponding to Section A.8) - F. Grogard, J. Rault, J.-L. Gouzé, "Positive control for global stabilization of predator-prey systems", IFAC NOLCOS 2013 Symposium, Toulouse, 2013. <https://doi.org/10.3182/20130904-3-FR-2041.00136>

See Appendix B for the complete paper.

2

Control and stability of a bioreactor

The bioreactor is the central tool of many industrial applications, be it wastewater treatment, microalgae production (for example for biofuel production), pharmaceutical applications, beer production,... and has been a major object of interest within the Comore-Biocore project team over the years, mainly driven by Olivier Bernard. The basic model of the chemostat, that is a constant volume continuous bioreactor, has been proposed by Jacques Monod in 1950 (Monod, 1950):

$$\begin{cases} \dot{s} &= D(s_{in} - s) - k\mu(s)x \\ \dot{x} &= (\mu(s) - D)x \end{cases}$$

where s is a substrate density, x a biomass density, D the dilution rate (input and output flow-rate divided by the volume of the reactor), s_{in} the substrate in the input, and $\mu(s)$ the biomass growth-rate. In that model, the terms containing D correspond to the in- and outflow of substrate and biomass from the reactor while the $\mu(s)x$ terms represent consumption of the substrate by the biomass (in the \dot{s} equation) resulting in biomass growth (in the \dot{x} equation). When $\mu(s)$ is in the Monod form ($\mu(s) = \frac{\mu_{max}s}{K_s+s}$), stability properties and control of the bioreactor, as well as what happens when several biomasses are put in competition for a single substrate is well known (a single biomass survives if the dilution rate is not too large). We tackled two problems in that family, that were quite complex: how can we control the model of a wastewater treatment plant to ensure that the substrate level (that is the pollution level) is brought below some predefined level? And what happens when there are several types of microorganisms in competition in a bioreactor?

2.1 Saturated control of a wastewater plant

Anaerobic digesters are bioreactors that contain a very complex network of microorganisms. A whole research area is devoted to the design of a model that would represent the complex set of biological reactions that take place (I.W.A.T.G.M.M.A.D., 2002). However, this very complex model contains far too many parameters for them to be easily identifiable and far too many

2. Control and stability of a bioreactor

variables to design a simple control law. With the latter objective in mind, a simpler model was developed (Bernard et al., 2001) that is only made of 4 equations, and that has been shown to represent 95% of variability in the data:

$$\begin{cases} \dot{x}_1 &= (\mu_1(s_1) - \alpha D)x_1 \\ \dot{x}_2 &= (\mu_2(s_2) - \alpha D)x_2 \\ \dot{s}_1 &= D(s_{1in} - s_1) - k_1\mu_1(s_1)x_1 \\ \dot{s}_2 &= D(s_{2in} - s_2) + k_1\mu_1(s_1)x_1 - k_2\mu_2(s_2)x_2 \end{cases}$$

where the acidogenic bacteria x_1 , consumes the organic substrate s_1 and produces through an acidogenesis step volatile fatty acids (VFA) s_2 with growth rate $\mu_1(s_1)$. The second population (methanogenic bacteria) x_2 , uses the VFA in a methanogenesis step as substrate for growth (at rate $\mu_2(s_2)$) and produces methane. μ_1 is an increasing and bounded function (like the Monod function) and μ_2 is first increasing and then decreasing to 0 as s_2 goes to $+\infty$. The second reaction is hence inhibited when the density of its own substrate becomes too large due to acidification. The difficulty for the operation of this process, illustrated by this simple model, is that x_2 needs s_2 to grow, but if s_2 becomes too large, it acidifies the reactor and stops methanogenesis, so that x_2 goes to 0 and s_2 accumulates.

Classically, a combination of both substrates called Chemical Oxygen Demand is measured online ($s_\lambda = s_1 + \lambda s_2$); this measure is an indicator of the quantity of oxygen that would be consumed by bacteria to degrade the organic substrate present in wastewater. In s_λ , the value of λ is the ratio between this demande for a gram of s_2 compared to a gram of s_1 . It is required by regulations that COD be brought below some $s_{\lambda max}$ value at the output of the reactor (which is the same value as the one in the reactor since the reactor is supposed to be perfectly mixed). In Grogard and Bernard (2006), we proposed a saturating control that takes the form illustrated on Figure 2.1. In that control law, D_{max} is given by the maximum dilution rate of the input and

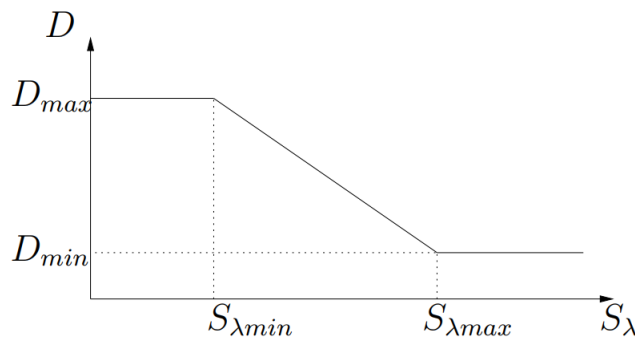


Figure 2.1: Form of the control law that ensures that s_λ be brought below $s_{\lambda max}$ (Grogard et al., 2013)

output valve, $s_{\lambda max}$ is the maximal admissible pollution at the output, and the other two values (D_{min} and $s_{\lambda min}$) are taken to make sure that the region $s_{\lambda min} \leq s_\lambda \leq s_{\lambda max}$ is attractive and positively invariant. The fact that the control needs to be positive and upper-bounded by D_{max} puts this problem squarely into the category of those handled in Chapter 1.

I tackled other control problems in the bioreactor, mainly an optimal control problem in a simple model of photobioreactor under natural light, where the objective was to maximize the microalgae productivity. It needed to take into account that no production occurred by night,

2.2. STABILITY ANALYSIS OF A BIOREACTOR

and that some of the biomass present at night would disappear due to respiration. Through the Pontryagin Maximum Principle, we obtained several possible open-loop periodic control patterns, depending on the parameters. A typical one would be that the dilution rate is equal to zero at the beginning of the day to ensure growth of the microalgae, followed by a singular arc where the dilution is constant and intermediate and by a period of maximum dilution/harvesting before the night, where the dilution is stopped (Grogard et al., 2010, 2014).

2.2 Stability analysis of a bioreactor containing competing bacteria and microalgae

A major problem was tackled during the thesis of Pierre Masci that I supervised with Olivier Bernard, that of the endpoint of the competition of microalgae, and two types of bacteria, in a bioreactor with a single substrate (Grogard et al., 2015). It is a bit isolated in my work, but it was a major endeavour.

Resource-based competition between microorganisms species in continuous culture has been studied extensively both experimentally and theoretically, mostly for bacteria through Monod and Contois "constant yield" models, or for phytoplankton through the Droop "variable yield" models. For homogeneous populations of N bacterial species (of Monod type, Armstrong and McGehee (1980)) or N phytoplanktonic species (of Droop type, Hsu and Hsu (2008)), with one limiting substrate and under constant dilution rate, the theoretical studies indicated that competitive exclusion occurs: only one species wins the competition and displaces all the others. The winning species expected from theory is the one with the lowest "substrate subsistence concentration" s^* , such that its corresponding equilibrium growth rate is equal to the dilution rate D (Smith et al., 1995). For the Contois model, we showed in Grogard et al. (2007b) that all species capable of surviving at s^* would survive at equilibrium through the use of a non-smooth Lyapunov function that I proposed and termed "polytopic". We later used this same function in Robledo et al. (2012).

In Grogard et al. (2015), we tackled the problem of having the three families of microorganisms together in a bioreactor with a single substrate and constant input:

- bacteria x_i characterized by Monod-like growth $\alpha_i(s)$, which corresponds to bacteria in suspension in the medium;
- bacteria y_j characterized by Contois-like growth $\beta_j(s, y_j)$ where β is naturally increasing in s , but is decreasing in y_j for intraspecific competition; this growth-rate corresponds to attached or flocculating bacteria where the access to the substrate can be density-dependent.
- microalgae z_k characterized by two-step Droop dynamics: a substrate uptake rate $\rho_k(s)$ and a growth rate $\gamma_k(q_k)$ built on the cell-quota q_k .

2. Control and stability of a bioreactor

All put together, this leads to the model

$$\begin{cases} \dot{s} &= D(s_{in} - s) - \sum_{i=1}^{N_x} \alpha_i(s)x_i - \sum_{j=1}^{N_y} \beta_j(s, y_j)y_j - \sum_{k=1}^{N_z} \rho_k(s)z_k \\ \dot{x}_i &= (\alpha_i(s) - D)x_i \\ \dot{y}_j &= (\beta_j(s, y_j) - D)y_j \\ \dot{z}_k &= (\gamma_k(q_k) - D)z_k \\ \dot{q}_k &= \rho_k(s) - f_k(q_k) \end{cases} \quad (2.1)$$

with $f_k(q_k) = \gamma_k(q_k)q_k$
and $s, q_k \in \mathbb{R}^+$, $s_{in}, D \in \mathbb{R}_*^+$ and $x_i(0), y_j(0), z_k(0) \in \mathbb{R}_*^+$ for $i \in \{1, \dots, N_x\}$,
 $j \in \{1, \dots, N_y\}, k \in \{1, \dots, N_z\}$

The end-result is the one that we expected by putting all three families of bacteria together, but requires an arduous proof: the system settles at a level s^* , which corresponds to the smallest s^* of the three types of microorganisms taken separately. If it corresponds to the Contois type, the equilibrium is the same as the Contois one; if it corresponds to one of the other two, the corresponding winning species survives, together with all the Contois bacteria that can survive at that substrate level.

2.3 Collaborators

These results were obtained:

- with Olivier Bernard, in the framework of the Telemac European project;
- with Olivier Bernard and Éric Benoît in the framework of Pierre Masci's thesis, which I co-supervised. With the additional help of Andrei Akhmetzhanov, whose post-doctoral stay I co-supervised, for the optimal control problem.
- with Alain Rapaport, Frédéric Mazenc, Jean-Luc Gouzé and Gonzalo Robledo-Veloso for the works around polytopic Lyapunov functions.

2.4 Representative paper

As a complement to the results of the present section, the following paper builds a polytopic Lyapunov function for stability analysis of an equilibrium in a chemostat with intraspecific competition.

J7 - F. Grogard, F. Mazenc and A. Rapaport, "Polytopic Lyapunov functions for persistence analysis of competing species," *Discrete and Continuous Dynamical Systems-Series B*, vol. 8, no. 1, pp. 73-93, 2007. (<https://hal.inria.fr/inria-00000873/file/polytopicdef.pdf>)

See Appendix C for the complete paper.

3

Semi-discrete systems for augmentative biological control

My research took a major turn when, in 2005, Ludovic Mailleret who had been freshly hired at INRA Sophia Antipolis, came to give a seminar on the first questions he was considering. Before that point, I had tried to integrate into the applications that were central to the Comore project-team: bioreactor control in (Grogard and Bernard, 2006; Grogard et al., 2007b) that were already covered in the present manuscript, and metabolo-genetic network stability and control (Ndiaye et al., 2006; Grogard et al., 2006, 2007a) that will not be covered here.

Ludovic Mailleret brought an application that had already been considered within Comore, but was not carried by anyone: biological control for ecologically friendly crop protection. "Classically", crops are protected from pests through the use of chemical pesticides. Their formidable efficiency has led to their massive use and abuse. However, there are several drawbacks to their usage. The first one concerns non-target organisms, the primary one being humans, that can be harmed through their ingestion, either when applying them or when consuming agricultural products. These non-targets organisms can also be small mammals, insects,... whose service is crucial in the environment such as pollinating bees (Metcalf, 1994) or natural enemies of herbivore insects that kept the herbivore population in check (King and Powell, 1992), and whose eradication could trigger an explosion of the pest population. Pesticides also apply selection pressure on the pest population: when applying a massive dose of pesticides, only a fraction of the pest population survives, the fraction that possess resistant genes to the pesticide. Since these survivors do not need to compete with their non resistant co-specifics, they are free to expand, transmitting their resistant trait to their offspring, and take up the whole ecological niche, rendering the pesticide useless (Roush and Tabashnik, 2012). As a consequence, many chemical pesticides were banned, resulting in situations where no pesticide is either efficient enough or even allowed to control some pests. There is therefore a need for development of alternative, ecologically friendly, crop protection methods. This was our conviction in 2005, and this was the goal of the Ecophyto 2018 plan that was set in 2009 in France to reduce the amount of pesticide use by half by 2018; since the goal could not be achieved a new plan, Ecophyto 2, set

3. Augmentative biological control

the target at 2025... One of the alternative methods that could be used is biological control, that is the use of living organisms, such as predators, parasitoids or pathogens, to control a pest; these organisms are the biocontrol agents. Several different biological control techniques can be implemented:

- *Conservation* biological control, which consists in making sure that the biocontrol agent, which is already present in the environment, can thrive and hence control the pest. This can be achieved by installing birdhouses for insect-eating passerines in the field or the orchards or making alternative food available for the biocontrol agent in the field; though we noted in Mickaël Teixeira Alves' thesis that the distraction effect of alternative food should not be neglected when assessing its use (Teixeira-Alves et al., 2011, 2010).
- *Classical* biological control, which aims at the establishment of natural enemies that are initially not present in the field, to control the pest. This method is especially relevant when targeting invasive pests, by importing its natural enemies from its original location.
- *Augmentative* biological control, which consists in massively and repeatedly releasing biocontrol agents in the field. This method is especially relevant if little or no reproduction of the biocontrol agent can be achieved in the field, so that no long-term establishment can occur without repeated releases.

These approaches are more appealing than chemical pesticides for obvious reasons, but it is not all rosy. There can be unintended consequences of the release of exotic organisms into the environment (Simberloff, 2012), with the biocontrol agent targeting non-target species, or taking up the ecological niche of some native species. Also, some potential biocontrol agents that show lots of promise in the lab are total failure in the field, most often due to their failed integration in the complexity of the foodweb.

3.1 A first result

The questions that Ludovic brought were related to the optimization of the release of biocontrol agents in an augmentative context. Given a pest-biocontrol agent pair (or equivalently a prey-predator pair), how to best deploy the biocontrol agent in terms of quantity and repartition over time.

To give a relevant answer to that question, we wanted to make sure that the release process was modelled accurately. Indeed, in a classical control context, we would have put the system in the format of equation (1.1), with u the release rate of biocontrol agents. However, predators cannot be released in real life through a continuous flow. It should explicitly be considered that batches of predators would be brought into the field all at once.

We were not the first to consider such questions, as impulsive events occurring as perturbations of continuous processes had already a long list of applications in life sciences, from pulse vaccinations to harvesting and, as in our case of interest, pest management (Mailleret and Lemesle, 2009). Of interest in the pest management context were the developments of Prof. Lansun Chen's group of the Academia Sinica in Beijing; their first result concerned the Rosenzweig Mac Arthur model with periodic impulses:

$$\begin{cases} \dot{x} &= rx(1 - \frac{x}{K}) - \frac{cx}{x+h}y \\ \dot{y} &= \frac{bx}{x+h}y - my \\ y(nT^+) &= y(nT) + p, \quad n \in \mathbb{N} \end{cases} \quad (3.1)$$

3.1. A FIRST RESULT

where $x, y \in \mathbb{R}_*^+$ are the prey (pest) and predator (biocontrol agent) densities, T is the release period, p the quantity released at time nT , and nT^+ , the time just after the release occurred (Liu and Chen, 2003). While interesting, this work and the many similar ones that would follow (Liu et al., 2004, 2005a,b), went into directions that did not correspond to our sensibilities: mainly it considered explicit functions in the model, and the bulk of its work concerned what would occur if the pest free solution was unstable through bifurcations that would lead to chaos. From our control theoretician points of view, we were mainly interested in the global stabilization of a pest-free solution, with generic growth and predation functions, and we wanted to have a result that could be of meaningful interest for the crop grower. Indeed, the result of Theorem 3.2 of Liu and Chen (2003) indicates that the pest-free solution is (locally) asymptotically stable in (3.1) if

$$p > \frac{rmh}{c}T$$

from which we can conclude that if enough predators are released each time or if it is done frequently enough, pest eradication would occur. This is totally expected as, in both cases, the total quantity of biocontrol agents released would be increased. A question whose answer was harder to decipher from that is the impact of release frequency on this eradication, if we do not modify the total number of predators released over the crop growth duration. For that, we replaced the discrete equation with

$$y(nT^+) = y(nT) + \mu T, \quad n \in \mathbb{N}$$

where μ is now the predator release rate. The modification looks trivial written like that, but no one had looked at these equations through that lense before. With that simple notation modification, we were able to decouple the released rate from the release frequency and could give answers to the question: "For a given release rate, is it advised to release small amounts of biocontrol agents frequently or large amounts rarely". It is to that question that we tried to give a first answer in Mailleret and Grogard (2006) and Mailleret and Grogard (2009). We considered the system

$$\begin{cases} \dot{x} = f(x) - g(x)y \\ \dot{y} = h(x)y - my \\ y(nT^+) = y(nT) + \mu T, \quad n \in \mathbb{N} \end{cases} \quad (3.2)$$

where $f(x)$ denotes the prey's growth rate, $g(x), h(x)$ and m denote the predators' functional response, that is its prey uptake rate per capita, numerical response, that is its resulting growth rate per capita, and mortality rate, respectively. Since biological processes are always difficult to model accurately, we only assumed general qualitative hypotheses on the functions $f(\cdot)$, $g(\cdot)$ and $h(\cdot)$:

Hypotheses 1 (H1) (Mailleret and Grogard, 2009) *Let $f(\cdot)$, $g(\cdot)$ and $h(\cdot)$ be locally Lipschitz functions on \mathbb{R}^+ such that:*

- (i) $f(0) = 0$
- (ii) $g(0) = 0$, $g'(0) > 0$ and $\forall x > 0$, $g(x) > 0$
- (iii) the function $\frac{f(x)}{g(x)}$ is upper bounded (for $x > 0$)
- (iv) $h(0) = 0$ and $\forall x > 0$, $h(x) \geq 0$

3. Augmentative biological control

A large part of the predator-prey functions encountered in the literature fit these hypotheses: (H1-i) only indicates that no spontaneous generation of pests is possible; $f(\cdot)$ might be constant, linear, logistic or model an Allee effect *etc...*(H1-ii) means that there is no prey consumption as the prey level is zero and that if some prey are present, the predator are able to find and consume them. Moreover, $g(x)$ is supposed to be increasing at the origin. As a consequence $g(x)$ may be linear or of the Monod type (termed Holling I and II in the ecological context). No hypotheses are made on the numerical response $h(x)$ except (H1-iv) which is verified by most classical numerical responses (but does not account for intra-predatory interference nor Allee effects for the predators). Notice that according to the different types of biocontrol strategies recalled in the introduction, $h(x) = 0$ for all x would correspond to a purely augmentative biocontrol as the introduced biocontrol agent does not reproduce, while $h(x) > 0$ for positive x would allow for some possible establishment of the predator as in the classical type of biocontrol.

We then obtained the following theorem:

Theorem 1 (Mailleret and Grogard (2009)). *Under Hypotheses 1, model (3.2) possesses a “pest free” T -periodic solution*

$$(x_p(t), y_p(t)) = \left(0, \frac{\mu T e^{-m(t \bmod T)}}{1 - e^{-mT}} \right) \quad (3.3)$$

which is locally asymptotically stable if and only if

$$\mu > \frac{mf'(0)}{g'(0)}, \quad (3.4)$$

and globally asymptotically stable if

$$\mu > mS \triangleq m \sup_{x \geq 0} \frac{f(x)}{g(x)}. \quad (3.5)$$

This theorem, as most theorems we obtained in this field was proven in three step:

1. Identify the pest-free T periodic solution by considering the semi-discrete system without pest;
2. Identify the local stability condition either by applying a very convenient theorem of Lakmeche and Arino (2000) or by computing the linearization of the system around the pest-free T periodic solution. The latter yields a system in the form $\dot{z} = A(t)z$ with $A(\cdot)$ T -periodic, which can be analyzed using Floquet theory (Floquet, 1883). Indeed, we can compute its monodromy matrix that maps $z(nT^+)$ onto $z((n+1)T^+)$. This computation is sometimes simple, as is the case here, when the solution of $\dot{z} = A(t)z$ takes the form of a matrix exponential, or more complex when it has to go through the computation of the principal matrix solution. Anyways, stability of the semi-discrete system is deduced from the eigenvalues of the monodromy matrix.
3. Obtain a global attractivity condition in a more ad-hoc manner. In the present case, we build the function

$$G(x(t)) - G(x_0) = m \int_{x_0}^{x(t)} \frac{1}{g(s)} ds,$$

that satisfies

$$\lim_{t \rightarrow +\infty} G(x(t)) = -\infty \Leftrightarrow \lim_{t \rightarrow +\infty} x(t) = 0. \quad (3.6)$$

because $g(x) = 0$ only in $x = 0$ from Hypothesis 1.

$$\begin{aligned} G(x(t)) - G(x_0) &= m \int_{t_0}^t \frac{\dot{x}(\tau)}{g(x(\tau))} d\tau, \\ &= \int_{t_0}^t \left(\frac{mf(x(\tau))}{g(x(\tau))} - m(\tilde{y}(\tau) + y_p(\tau)) \right) d\tau. \end{aligned} \quad (3.7)$$

where $\tilde{y}(t) = y(t) - y_p(t)$ is the predator error coordinate for which we can show that

$$\tilde{y}(t) \geq \min(0, \tilde{y}_0) e^{-m(t-t_0)}. \quad (3.8)$$

Using (3.7) and the definition of S in (3.5), we then have for all $t \geq t_0$

$$\begin{aligned} G(x(t)) - G(x_0) &\leq \int_{t_0}^t \left(mS - my_p(\tau) - m \min(0, \tilde{y}_0) e^{-m(\tau-t_0)} \right) d\tau, \\ &= m \left[\int_{t_0}^{\lfloor \frac{t}{T} \rfloor + 1)T} (S - y_p(\tau)) d\tau + \left(\left\lfloor \frac{t}{T} \right\rfloor - \left\lfloor \frac{t_0}{T} \right\rfloor - 1 \right) \int_0^T (S - y_p(\tau)) d\tau \right. \\ &\quad \left. + \int_{\lfloor \frac{t}{T} \rfloor T}^t (S - y_p(\tau)) d\tau + \frac{1}{m} \min(0, \tilde{y}_0) \left(e^{-m(t-t_0)} - 1 \right) \right], \end{aligned} \quad (3.9)$$

since $y_p(t)$ is T -periodic. It is clear that the first, third and fourth term of the right hand side of (3.9) are upper bounded. Now, suppose that (3.5) holds, then

$$\int_0^T (S - y_p(\tau)) d\tau = \int_0^T \left(S - \frac{\mu T e^{-m\tau}}{1 - e^{-mT}} \right) d\tau < 0, \quad (3.10)$$

so that, since $\lfloor \frac{t}{T} \rfloor$ goes to infinity as t does, the right hand side of (3.9) goes to $-\infty$. Then, condition (3.5) implies that $x(t) \rightarrow 0$; one can also prove that \tilde{y} converges to zero as well, and hence $y(t)$ towards $y_p(t)$.

Condition (3.5) is only sufficient, and works as if $h(x) = 0$, that is as if there was no predator growth possible, as in a purely augmentative context. In that case, if we consider $T \rightarrow 0$, we have $y(t) \rightarrow y_p(t) = \frac{\mu}{m}$ as $t \rightarrow +\infty$, so that the x dynamics then follow

$$\dot{x} = f(x) - g(x) \frac{\mu}{m}$$

The origin of this equation is then globally asymptotically stable if and only if $\dot{x} < 0$ for all x , that is $g(x) \frac{\mu}{m} > f(x)$ for all x , which is equivalent to (3.5). Hence, in the purely augmentative case with $T \rightarrow 0$, the sufficient condition (3.5) is also necessary.

It is to be noted that this result describes a way to control the pest population. It is however not feedback control in the sense that was presented in Chapter 1. No measurements of the state are used to design the control action. This makes sense in many agricultural contexts: for example, in flower production, no damage is tolerated on the plants, so that action has to be taken before pests or damages are noticed; also, most of the time, no measures are available in practice. In contrast with these results, actual state dependant impulses are proposed in Tang and Cheke (2008) where the impulse occurs when the state reaches a certain threshold while impulsive feedback control in a set-up where the impulses occurs every T time instants is proposed in Grogard (2014).

The most natural way of optimizing the release frequency is to choose the T value that minimizes the release budget through the release rate threshold. We see however that both

3. Augmentative biological control

thresholds given by (3.4) and (3.5) are independent of T . This is therefore not an avenue that can be pursued for optimization. Hence, the paper Mailleret and Grognaud (2009) was completed by an optimization analysis that demonstrated that, in a prophylactic context where biocontrol agent releases aim at reducing the worst-case damage incurred when a pest invasion occurs at a random time, the best choice is to take T as small as possible.

3.2 Which intra-specific interactions between predators?

In subsequent years, Ludovic and I have co-supervised two PhD theses on this topic, the one of Sapna Nundloll and the one of Nicolas Bajoux. What we wanted to do was to acknowledge that model (3.2) had limitations, in the sense that the functional and numerical response, as well as the mortality rate reasonably needed to be complexified to take nature's complexity into account. We then modified the prey/predator interaction characteristics to represent a wider range of pest/biocontrol agents pairs. In essence, in our subsequent developments, we studied

$$\begin{cases} \dot{x} &= f(\cdot) - g(\cdot)y \\ \dot{y} &= h(\cdot)y - m(\cdot)y \\ y(nT^+) &= y(nT) + \mu T, \quad n \in \mathbb{N} \end{cases}$$

with various generic forms of $f(\cdot)$, $g(\cdot)$, $h(\cdot)$ and $m(\cdot)$ functions.

3.2.1 Interfering predators

In Sapna's thesis, we considered intraspecific interference or competition between the predators for the access to the prey. Such a competition is known to occur in arthropods that are used in biological control (Visser et al., 1999; Flowers et al., 2006) and so needs to be taken into account in our models. For this, we produced a model in Nundloll et al. (2010b) with negative predator density dependence in the functional and numerical responses, in the form

$$\begin{cases} \dot{x} &= f(x) - g\left(\frac{\alpha(x)}{\beta(y)}\right)y \\ \dot{y} &= h\left(\frac{\alpha(x)}{\beta(y)}\right)y - my \\ y(nT^+) &= y(nT) + \mu T, \quad n \in \mathbb{N} \end{cases} \quad (3.11)$$

with $f(0) = g(0) = h(0) = 0$, $g(\cdot)$ and $h(\cdot)$ positive and increasing and f logistic-like ($f(x) < 0$ for x larger than some \bar{x} , which ensures that x stays smaller than \bar{x}). Also

$$\begin{aligned} a_1x &\leq \alpha(x) \leq a_2x \\ b_0 + b_1y &\leq \beta(y) \leq b_0 + b_2y \end{aligned} \quad (3.12)$$

With that form we wanted to produce a generalization of the Beddington DeAngelis functional response (Beddington, 1975; De Angelis et al., 1975)

$$g(x, y) = \frac{ax}{h + bx + cy}$$

that is the simplest form for the representation of interference between predators, for access to the prey. With $b_0 = 0$, our form also leads to ratio-dependant functional responses (Arditi and Ginzburg, 1989). As in model (3.2) we opted to go beyond models with specified functions and obtained a stability result that is summarized in Figure 3.1. The stability threshold is represented by the grey region and not a simple line due to the sector condition (3.12); above

3.2. WHICH INTRA-SPECIFIC INTERACTIONS BETWEEN PREDATORS?

the grey region, pest eradication is ensured while below it, non eradication is guaranteed. The threshold is increasing with T : if T is larger the release rate μ needs to be larger. This can be explained by the fact that, for a given μ , if T is increased, larger individual releases take place so that the predator population presents large spikes at which predator interference is intense and limits the efficiency of the releases. Hence for a given μ^* illustrated on the figure, stability is ensured for T smaller than \underline{T}^* and instability is guaranteed for T larger than \overline{T}^* . The dual result of this stability conclusion is that, for a given release rate μ , convergence to the pest-free solution is faster for T smaller.

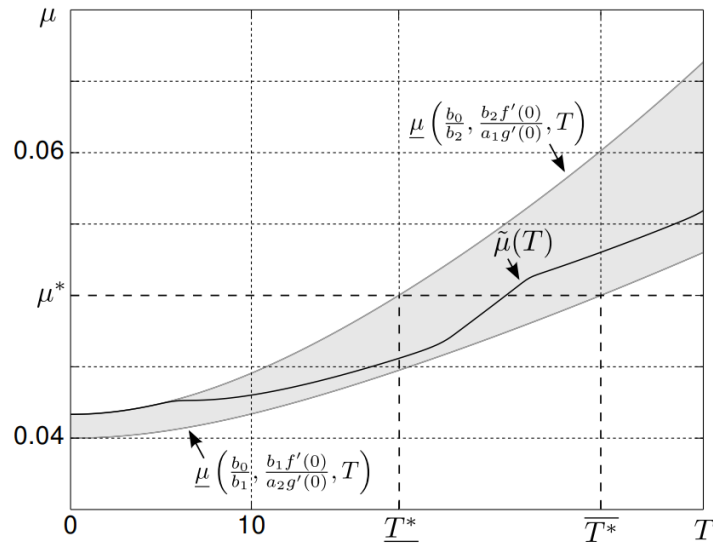


Figure 3.1: Stability zones for model (3.11) in the (T, μ) space. When μ is above the grey zone, asymptotic stability of the pest-free periodic solution is guaranteed; when it is below the grey zone, it is unstable (Nundloll et al., 2010b).

Since we opted for modelling that qualitatively represents the pest/biocontrol, and not a finely calibrated model to data, our results informs the growers by giving qualitative recommendations. In the present case, it tells to rather release small quantities of biocontrol agents frequently.

Validation

These results were tested at Institut Sophia Agrobiotech (ISA) on the thrips *Frankliniella occidentalis*, a pest of numerous vegetable and fruit plants. The predatory spider mite *Neoseiulus cucumeris* feeds on the immature forms of this thrips and can be used for biocontrol. This validation was achieved in two phases: we first tested if there was interference between spider mites for access to the prey and we then implemented two different biocontrol strategies and compared them to a control experiment without any biocontrol.

For the test of existence of interference between the biocontrol agents, we put 1 spider mite on a leaf disk with thrips on the one hand, and compared this situation with the same setup with 5 spider mites on an identical leaf disk. And we scaled this experiment to leaves. As can be seen on Figure 3.2, the per capita consumption between the two predator densities is different in both cases, with a significant reduction of the per capita predation with the predator density.

3. Augmentative biological control

This confirms that *N. cucumeris* are interfering predators.

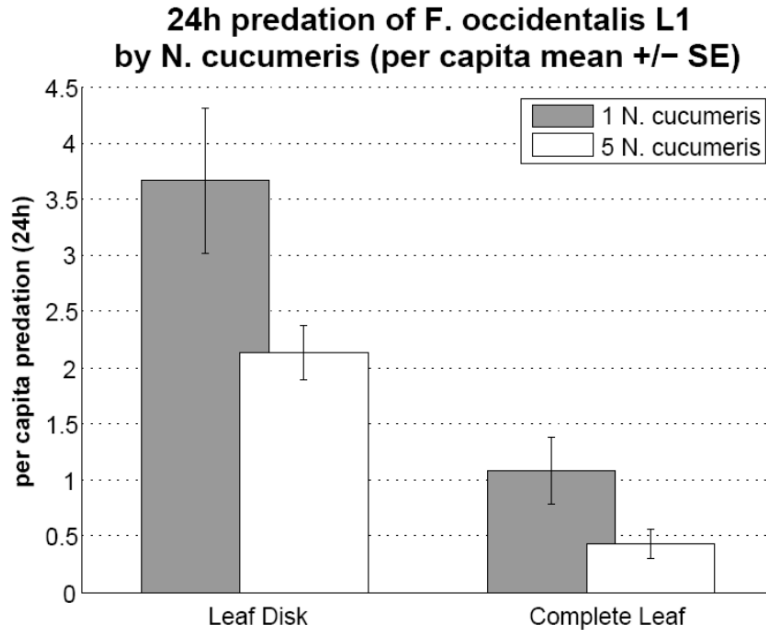


Figure 3.2: Comparison of per capita predation by *N. cucumeris* on *F. occidentalis* over 24 hours on leaf disks and leaves with respectively 1 and 5 predatory mites.

In order to validate our convergence results, we realised experiments at ISA in greenhouse boxes where spider mites were first introduced before thrips populations were put in, and we compared three modes of introductions: spider mites releases every week and every four weeks with the same release rate, and a control experiment without releases. On Figure 3.3, a thrips explosion is noticed in the control group while the weekly release seems more efficient than the monthly release at controlling the pest population. Unfortunately, this result that we "see" on the figure is not necessarily statistically significant. Despite that, it is a kind of validation of our theoretical result, which brought Sapna's thesis full circle.

3.2.2 Cooperating predators

In Nicolas Bajoux's thesis, we considered predators behaving to the opposite to those in Sapna's thesis, and presenting positive predator density dependence in the functional response. This represents a form of Allee effect (Allee et al., 1949). Stephens and Sutherland (1999) defined two levels of effects: 'component' and 'demographic' Allee effects. A component Allee effect is defined as a positive relationship between one component of individual fitness and population size or density. A demographic Allee effect refers to a positive relationship between the mean fitness of the population, i.e. its per capita growth rate, and population size or density. In Bajoux et al. (2017), we introduced component Allee effects into the predation relationship of a slight modification of model (3.2):

$$\begin{cases} \dot{x} = f(x) - g(x)y \\ \dot{y} = h(g(x))y - d(g(x))y \end{cases} \quad (3.13)$$

3.2. WHICH INTRA-SPECIFIC INTERACTIONS BETWEEN PREDATORS?

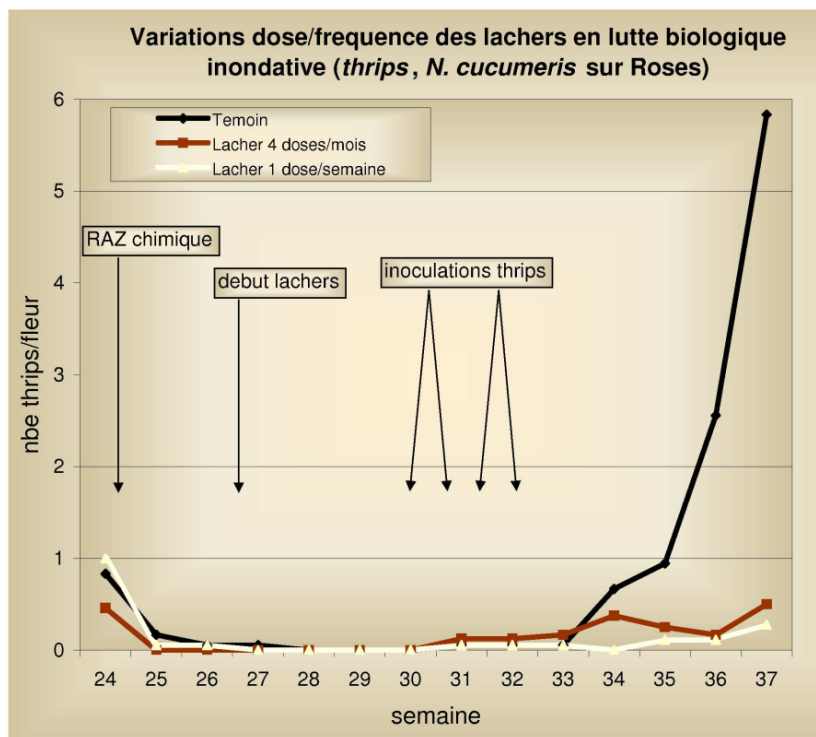


Figure 3.3: Illustration of thrips population over time. After chemical wipe-out of the populations on week 24, comparison of weekly (white line) and monthly (red line) biocontrol agents release strategies with a control group (black line) where no action is taken. Releases start on week 27 and thrips pest are introduced between weeks 30 and 33.

3. Augmentative biological control

where the numerical response $h(\cdot)$ directly depends on the functional response as predator growth naturally depends on its predation rate (functional response); similarly, the death rate of the predators is decreasing with predation as the death rate of the predators will be higher when it feeds too little (following Terry (2014a)).

Courchamp et al. (2008) listed various kinds of component Allee effects that could be contributing to demographic effects. In the present work, we considered two of them:

1. mechanisms linked to reproduction such as the mate-finding Allee effect which is the difficulty to find mates when populations are small, or cooperative breeding which makes it difficult for a social population to breed offspring at low population size
2. mechanisms related to survival such as cooperative anti-predator behavior or alterations of the foraging efficiency resulting from the difficulty to locate or capture resources when the population is small, *e.g.* for species hunting in herd.

The first kind only modulates the numerical response $h(\cdot)$, and we chose to represent it through a function $q_r(y)$. The second one modulates the functional response $g(\cdot)$, and so indirectly the numerical response and mortality; we represent it through a function $q_f(y)$. In both cases, $q_i(y)$ satisfies $q_i(0) = q_{i_0}$, $q_i(y) \in [0, 1]$, $q'_i(y) \geq 0$ and $\lim_{y \rightarrow +\infty} q_i(y) = 1$. Full efficiency of the functional and numerical responses are only achieved for y going to infinity. Note that q_{i_0} is not necessarily equal to 0 as there can be some residual foraging or reproduction efficiency even at very low density. The resulting model is then

$$\begin{cases} \dot{x} = f(x) - g(x)q_f(y)y, \\ \dot{y} = h(g(x)q_f(y))q_r(y)y - d(g(x)q_f(y))y, \\ y(nT^+) = y(nT) + \mu T \end{cases} \quad (3.14)$$

Developments similar to those of the previous section yielded both local and global asymptotic stability results for the periodic pest-free solution. This time, the conditions were (Bajeux et al., 2017)):

$$\int_0^T q_f(y_p(\tau))y_p(\tau)d\tau - \frac{f'(0)}{g'(0)}T > 0. \quad (3.15)$$

for local asymptotic stability and

$$\int_0^T q_f(y_p(\tau))y_p(\tau)d\tau - ST > 0 \quad (3.16)$$

for global asymptotic stability of the pest-free solution, with S defined in (3.5) and $y_p(t)$ in (3.3) (replacing m with $d(0)$). Also, it should be noted that, when $q_f(y)$ is identically equal to 1, these two conditions are equivalent to (3.4) and (3.5) of our first result. Since $q_f(\cdot) \leq 1$, conditions (3.15) and (3.16) are harder to satisfy so that Allee effects will impose that μ be taken larger. A final point should be made about the fact that the reproductive Allee effect $q_r(\cdot)$ has no impact on the stability conditions. This is exactly true for the local stability condition which is necessary and sufficient. Our global stability condition is only sufficient though, and we are only certain that it is necessary when $S = \frac{f'(0)}{g'(0)}$ so that both LAS and GAS conditions are equivalent. When they are not, there can be situations where the pest-free solution is LAS

3.2. WHICH INTRA-SPECIFIC INTERACTIONS BETWEEN PREDATORS?

and not GAS (Terry, 2014b), situations where the impact of $q_r(\cdot)$ can be felt. We illustrated that point on a particular example

$$\begin{cases} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \left(\frac{b_0 x}{x + x_h}\right) \left(\frac{y}{y + \alpha_f}\right) y, \\ \dot{y} = \left(\frac{b_0 x}{x + x_h}\right) \left(\frac{y}{y + \alpha_f}\right) \left(\frac{y}{y + \alpha_r}\right) y - d_0 y. \end{cases} \quad (3.17)$$

based on the Rosenzweig MacArthur model with $q_f(y) = \frac{y}{y + \alpha_f}$ and $q_r(y) = \frac{y}{y + \alpha_r}$. We compared two situations with $\alpha_f > 0$, one where $\alpha_r > 0$ that we termed the RF-model with both foraging and reproductive component Allee effects, and the other where $\alpha_r = 0$ that we termed the F-model with only a foraging component Allee effects. We identified the different stability regions in the (T, μ) parameter plane on Figure 3.4, based on the aforementioned theoretical result, but we also identified regions where we noted numerically that global stability is achieved without the theoretical condition (3.16) being satisfied. We note two things on that figure: 1) the thresholds are μ -functions that are decreasing with T so that, for a given μ , stability is achieved for larger T values, to the contrary of the interference situation of the previous section; 2) there is indeed a zone in which the reproductive Allee effect prevents global stability (in the RF model) while global stability is achieved numerically when only foraging Allee effect is present (the "numerically GAS (F) - LAS (RF)" region of the figure).

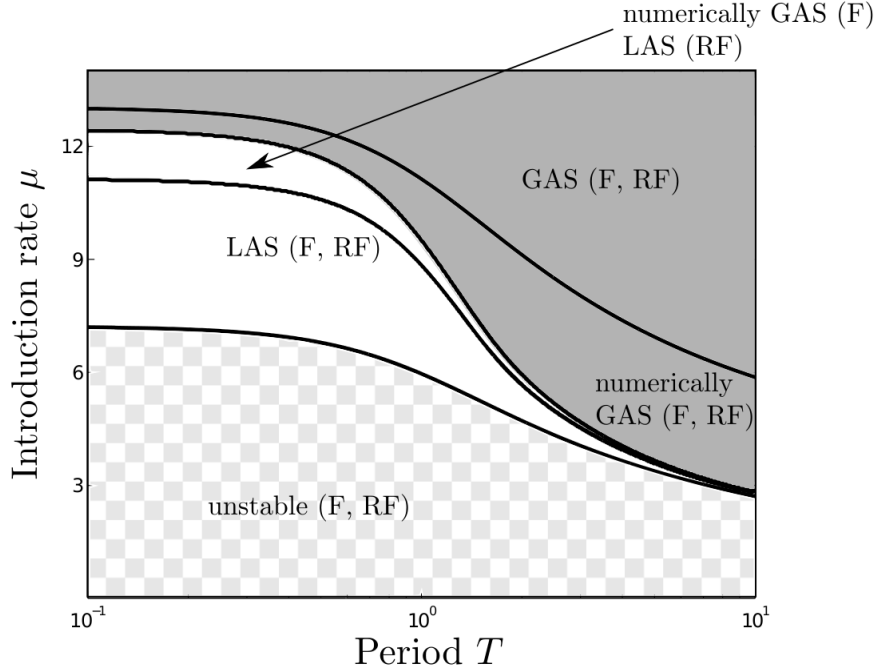


Figure 3.4: Stability conditions of pest-free solution as functions of T (in logarithmic scale) and μ . The RF- and F- models are compared. Thresholds (3.15) and (3.16) are the lower and upper curves respectively. The "numerically GAS" regions are the ones where condition (3.16) is not satisfied, but we could check that all initial conditions yielded pest eradication. The white region is the one where the impact of $q_r(\cdot)$ is identified. (Bajeux et al., 2017)

3. Augmentative biological control

3.3 Take-home message and other results

As a conclusion from these three main results, we see that the recommendation for a choice of release strategy strongly depends on the kind of intra-specific interactions that exists between the predators. There is no "one size fits all", and experiments like the one we did at the end of Sapna's thesis need to be performed to inform the choice of strategy.

I chose to only illustrate three main results. In this line of work, and in the 17 years since we started together, we covered many other bases:

1. In Nundloll et al. (2010a), we have compared predators who present interference upon predation as in Section 3.2.1, with squabbling predators which, due to overcrowding or cannibalism, present a quadratic mortality rate.
2. In Bajeux et al. (2019), we added stochasticity in the introduction process in the 1D model with Allee effect proposed in Gruntfest et al. (1997). Stochasticity is present in the size of the release as the effective population that is released is quite uncertain due to the mortality that takes place before or during the release; also, we added catastrophes wiping-out the population through a Poisson process. The aim here was to bring the population from 0 to some threshold level where the Allee effect was overcome. We could compute the Mean First Passage Time at this level as in Drury (2007) to determine whether frequent and small introductions or rare and large ones are preferable in terms of optimizing the introduction process. Intense stochasticity in the introductions can reverse the conclusion drawn in Section 3.2.2.
3. In Nundloll et al. (2008), we added impulsive harvesting to model 3.2 in two situations: 1) the harvesting period is a multiple of the biocontrol agent introduction period, situation that occurs when harvest take place annually; 2) the introduction period is a multiple of the harvesting period, situation that occurs when harvesting is very frequent, such as in horticulture in greenhouses where flowers are harvested weekly.
4. In Ghosh et al. (2015), we studied introduction processes with a spatial component by considering two patches following model (3.2) and diffusion between the two patches. In that situation, frequent and small releases should be preferred. It is in that paper that we first introduced what we termed our semi-numerical technique. Indeed, when computing the monodromy matrix of $\dot{z} = A(t)z$, we cannot here use exponential forms, and we need to compute the solutions of the system with the elements of the classical orthonormal basis as initial conditions to fill the matrix. From there stability is deduced from the computation of the eigenvalues. We termed this method semi-numerical because only some elements of the analysis are purely numerical, as opposed to the necessity of computing thousands of solutions of the system to ensure stability.
5. As a complement to all this, we validated some of the results through individual based computations in the internship of David Davtian (Mailleret et al., 2018).

3.4 Collaborators

These results were obtained with Ludovic Mailleret

- with him alone for initial works

3.5. FURTHER CONSEQUENCES

- in the context of Sapna Nundloll's thesis (interfering predators), Nicolas Bajeux's thesis (cooperating predators) and Mickaël Teixeira Alves's thesis (conservation biocontrol);
- during the 6 month visit of Bapan Ghosh (National Institute of Technology, Meghalaya), during his PhD thesis in the context of the PULSPOP project;
- in the internships of David Davtian.

3.5 Further consequences

Inria project teams have a 12-year lifespan. In 2010, the Comore project-team then had to evolve. My close collaboration with Ludovic had been ongoing for 5 years; hence we collectively decided to fully integrate the crop protection theme into our new project team by making Biocore a common project-team with Institut Sophia Agrobiotech, with Ludovic a full-time member. In 2013 and 2015, this partnership with INRA(E) allowed us to host two new INRA(E) researchers, Suzanne Touzeau and Valentina Baldazzi. In 2023, I will be the leader of a new common project-team where modelling for crop protection will play a larger role, birthed from Biocore. This project-team will be named Macbes: "Modelling and Control of Biological and Ecological Systems".

3.6 Representative paper

The following paper details the results obtained during the visit of Bapan Ghosh, with the introduction of space in our models through the definition of a two-patch environment:

J19 - B. Ghosh, F. Grogard, L. Mailleret, Natural enemies deployment in patchy environments for augmentative biological control, vol. 266 (1), pp.982-999, 2015. (<https://dx.doi.org/10.1016/j.amc.2015.06.021>)

See Appendix D for the complete paper.

3. Augmentative biological control

4

Resistance deployment and host mixtures

In the arsenal of non-pesticide measures that can be deployed to fight pests, plant resistance takes a large role when dealing with plant pathogens such as fungi, viruses, or bacteria. Through intrinsic genetic mechanisms, resistances in plants prevent or limit pest invasion or pathogen infection. However, if they are not carefully managed, resistance breakdown occurs, *i.e.* the pests or pathogens more or less rapidly overcome the resistance through adaptive evolution. The crop cultivar carrying this resistance gene then needs to be replaced by crops bearing new resistant genes. As resistant genes are limited resources, durability of crop resistance needs to be ensured in order to not become powerless in the face of pathogens.

Plant qualitative resistances, *i.e.* resistances that almost totally prevent any plant infection result from a molecular relationship governed by the gene-for-gene concept (Flor, 1971). Either the plant is susceptible (does not possess a resistant gene), so that all strains of a pathogen can infect, or the plant is resistant so that avirulent (or wild-type) pathogens cannot infect it; only those pathogens that do not carry the avirulence allele, that we will term the resistance-breaking types, can infect. This yields a 2×2 matrix of interaction between the wildtype (WT) or resistance-breaking (RB) pathogens, and the susceptible (S) and resistant (R) plants, among which only the WT-R pairing does not lead to infection success (Brown and Tellier, 2011).

Remark: *In the present manuscript, "susceptible" is taken to mean "not resistant" as is done in plant epidemiology. It does not mean "not infected" as in human epidemiology. For the latter, we will rather use the term "healthy" or "uninfected".*

Deploying massively novel resistant cultivars would then seem an all-efficient crop protection method as no RB-pathogen would exist to create infection. It does however not often lead to long-term crop protection, even if a resistance-breaking pathogen is not initially present (Brown, 2015). Indeed, it often suffices for one or two mutations to occur in the pathogen population for a resistance-breaking individual to appear (Lecoq et al., 2004), which can happen very quickly in fast evolving organisms such as fungi or bacteria. Once the RB variant has appeared in a resistant monoculture, it has a disproportionate selective advantage over the WT variant and can spread very fast, even if it was less efficient at infecting susceptible plants than WT variants

4. Resistance deployment and host mixtures

(Brown, 2015).

Different methods have been proposed to limit the effect of this massive selection pressure favoring RB variants: plant cultivar rotations over time as in Nilusmas et al. (2020), plant mixtures (Mundt, 2002), or more generally a large heterogeneity of the cultivars over time and space (Gilligan, 2008). Pyramiding qualitative resistance with quantitative resistances has also been shown to be a promising tool to increase the durability of the qualitative resistance (Palloix et al., 2009). These quantitative resistances do not block infections, and are controlled by Quantitative Trait Loci (QTLs) in the genetic background of the plant; they reduce the fitness of the pathogen by impacting one or more of the infection traits, such as viral load, infection initiation efficiency, or controlling bottleneck size acting on virus populations at inoculation.

4.1 Increasing genetic drift for resistance durability in host mixtures

After several years where our focus had been on biological control for crop protection, we started studying resistance deployment with the internship and then PhD thesis of Elsa Rousseau in 2012. Through a collaboration with experimentalists and modellers of INRA Avignon (B. Moury and F. Fabre), Elsa did a PhD thesis that was truly interdisciplinary, starting with one year of experiments in Avignon and then completing her thesis in Biocore for the modelling aspects. She was mainly focused on bottlenecks occurring during infection. Indeed, four evolutionary forces are known to affect the installation of a RB variant in a field: mutation, migration, selection and genetic drift. The first two are linked to the appearance of the RB variant, from within or from without, and the latter two to the success of its installation; we will mainly focus on the latter two. We have already touched on how massive resistant plant deployment had a strong selection effect in favour of RB-variants. Genetic drift produces random fluctuations in the evolution of variant frequencies, eventually purging variants regardless of whether they are beneficial, neutral or harmful for resistance breakdown (Zhan et al., 2015). It is generally evaluated with the effective population size N_e , defined as the number of individuals passing their genes to the next generation (Charlesworth, 2009). If the effective population size is small, there are strong bottlenecks in the infection process where only a small number of individuals take part in the effective infection, and there is a high probability that a beneficial mutant (to the pathogen), such as a RB-variant, be eliminated at that point; otherwise installation is mainly driven by selection.

Through experiments lead by Elsa and Lucie Tamisier who did her PhD thesis concurrently in Avignon, Tamisier et al. (2017) showed that N_e was indeed controlled by Quantitative Trait Loci in pepper plants so that they could take part in the production/selection of new resistant cultivars. Elsa then showed among other things that effective population size during infection (more than that at inoculation) could limit the installation of RB variants (Rousseau et al., 2018). Also, we developed a method to identify virus effective population size N_e and selection coefficient s without neutral markers, from another large scale experiment lead by Elsa involving the growth of hundreds of pepper plants, manual infestation by a mixture of virus variants, leaf harvest at several stages of its growth followed by High Throughput Sequencing of the leaves to identify their viral content (Rousseau et al., 2017); this was a challenging problem as most existing methods to identify N_e required the genetic markers studied to be neutral (Nei and Tajima, 1981; Williamson and Slatkin, 1999; Berthier et al., 2002), and the methods developed to estimate s needed that N_e be known or negligible (Vitalis et al., 2014; Illingworth et al., 2012). In our case, we followed the evolution of alleles linked to the ability to counter a quantitative

4.1. INCREASING GENETIC DRIFT FOR RESISTANCE DURABILITY

resistance, hence intrinsically non-neutral markers. As the probability of fixation of mutation is strongly linked to the product $N_e \times s$, identifying both from data obtained is crucial. Our method relied on the simulation of the evolution of variant frequencies and the estimation of the parameters through maximum likelihood.

Stemming from these results we developed a model to identify in which situations acting on QTLs that can reduce effective population size could be the most beneficial (Rousseau et al., 2019). We wanted to identify what benefit could be drawn by exploiting such QTLs when confronted with different disease intensities, different plant mixture proportions φ , different bottleneck levels N_e^R , and different proportions f_{RB} of RB variants present at equilibrium within any given susceptible plant. This f_{RB} value will be very important; if it is very small, it means that the RB-variants have an important competitive disadvantage when compared to WT-variants when confronted to susceptible plants, as there is an important fitness cost linked to the resistance breaking ability. If f_{RB} is close to 0.5, there is no fitness cost linked to resistance breaking. To measure the improvement linked to the addition of N_e QTLs to resistant plants, we took as reference a field with only susceptible plants (N^S plants) that satisfy

$$\frac{dI^S}{dt} = \beta_0 \frac{I^S(N^S - I^S)}{N^S} \left(1 - e^{-N_e^S}\right), \quad (4.1)$$

with $I^S(0) = 1$. This model is in a classical SI form (Kermack and McKendrick, 1927) where the total number of plants is constant so that the density of healthy plants $S^S = N^S - I^S$, with I^S the density of infected plants. Also we assumed that the number of virus particles surviving all bottlenecks results from a Poisson distribution of mean N_e^S , so that the probability that at least one virus particle survives all bottlenecks is the opposite of the event leading to zero virus particles surviving, that is $1 - e^{-N_e^S}$, which we put as a factor modulating infection rate. Model (4.1) will serve as a reference to identify the potential intensity of the infection through the computation of the Area Under the Disease Progress Curve (AUDPC)

$$A_0 = \int_0^{n_d} p_i^S(t) dt = \frac{1}{\beta_0} \ln \left(1 + p_i^S(0) \left(e^{\beta_0 n_d} - 1\right)\right)$$

for this model, where n_d is the duration of the crop, $p_i^S(t) = I^S(t)/N^S$, and $1 - e^{-N_e^S}$ has been neglected because $N_e^S = 10^4$. AUDPC is a classical measure to assess the efficiency of resistant cultivar deployment (Jeger and Viljanen-Rollinson, 2001); the smaller it is, the less damage there are.

A simple way of extending model (4.1) is by adding a resistant plants compartment, so that

$$\begin{cases} \frac{dI^S}{dt} &= \left(\beta_0 \frac{I^S(N^S - I^S)}{N^S} + \beta_0 \frac{I^R(N^S - I^S)}{N^S} \right) \left(1 - e^{-N_e^S}\right) \\ \frac{dI^R}{dt} &= \beta_0 \frac{I^R(N^R - I^R)}{N^R} \left(1 - e^{-N_e^R}\right) + \beta_0 \frac{I^S(N^R - I^R)}{N^R} \left(1 - e^{-N_e^R f_{RB}}\right) \\ I^S(0) &= 1, I^R(0) = 0. \end{cases}$$

where $I^i(N^j - I^j)$ corresponds to the infection of plants of types j coming from plants of type i . Also, the probability that one particle survives the bottleneck in resistant plants depends on the origin of the infection: if the origin is another resistant plants, all particles initiating are RB so that, in average, N_e^R particles initiate the infection; if the origin is a susceptible plants, transmitted particles are a mixture of WT and RB types, among which a proportion f_{RB} are RB so that, in average, only $N_e^R f_{RB}$ particles are RB and can initiate the infection.

4. Resistance deployment and host mixtures

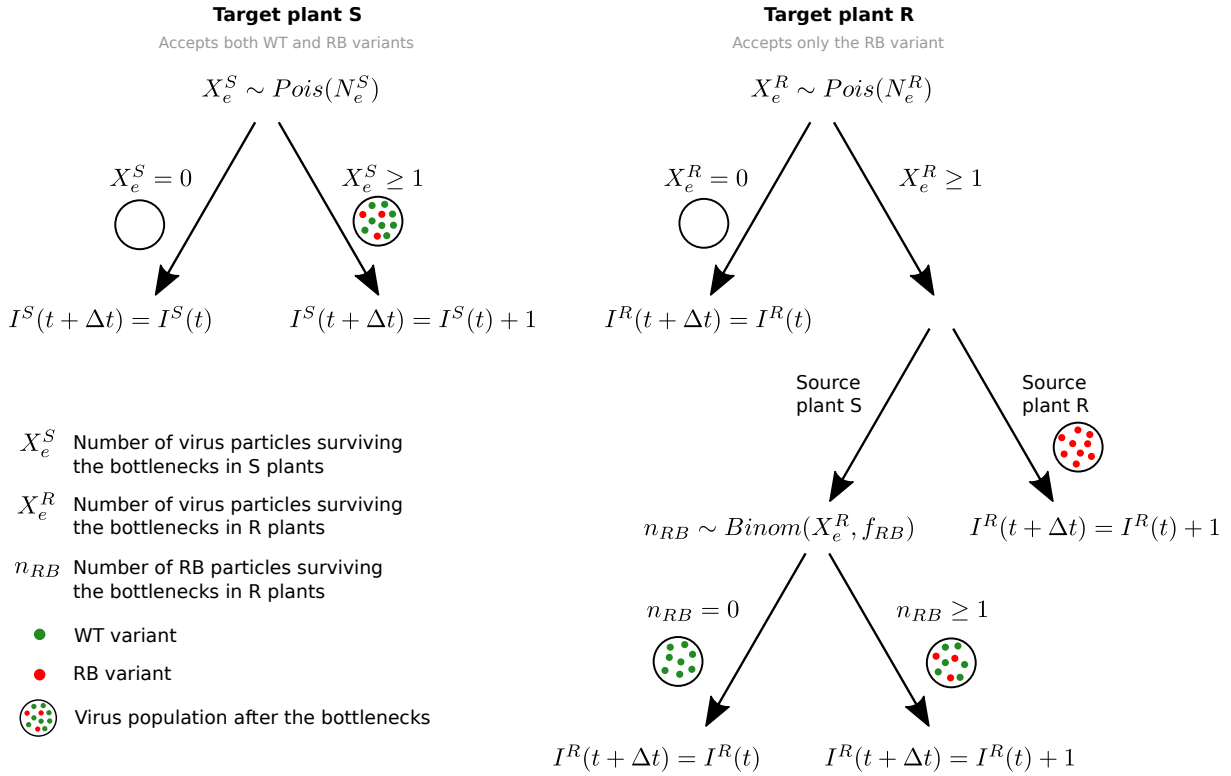


Figure 4.1: [Figure by Elsa Rousseau in Rousseau et al. (2016)] Infection process of a new plant in three steps following a Gillespie algorithm defining the waiting time until the next contact event between an infected and a healthy plant (Wilkinson, 2006) :

- 1) the time to next event follows an exponential distribution $\Delta t \sim Exp\left(\sum_{i,j} \beta_0 \frac{I^i(N^j - I^j)}{Np}\right)$ (not illustrated on the figure). Once the waiting time is known, the varieties of the source and target plants are determined after a draw in a Uniform distribution, by looking at where it falls in the vector of added contact rates.
- 2) the number of particles X_e^i trying to initiate the infection in a plant of type i follows a Poisson distribution from which we can directly infer the success or failure of infection for the $S \rightarrow S$, $R \rightarrow S$ and $R \rightarrow R$ transmissions (if the number of particles is non-zero, the infection succeeds).
- 3) in the $S \rightarrow R$ transmissions case, only a proportion f_{RB} of the particles in the plant of origin can infect the plant of destination; the binomial distribution in the figure determines if one of them is present in the X_e^R particles trying to infect a R plant; if yes ($n_{RB} \geq 1$), infection occurs.

4.2. HOST MIXTURES AND PLANT IMMUNITY

Since the bottlenecks, when related QTLs are exploited, can be very small, there is a need for the model to be stochastic, describing one by one the infection of new plants. This model is described in detail in Rousseau et al. (2019), and is best illustrated on Figure 4.1.

Through extensive simulations, we studied a measure that we termed "Additional relative benefit", to identify the interest of pyramiding N_e^R -reducing QTLs with a qualitative resistance by comparing identical epidemiological situations, with the same proportion of resistant plants, only differing in the presence/absence of the QTL. An additional relative benefit of 0 indicates that the QTLs have no impact on the AUDPC while an additional relative benefit of 100 shows that the AUDPC is brought down to 0, so that infestation has not developed. In Figure 4.2, we studied the impact of four parameters:

- Ω_{int} , the intensity of the epidemic if there were only susceptible plants, computed as the mean proportion of plants infected over the year. Ω_{int} is strongly linked to β .
- f_{RB} , the proportion of resistant-breaking viruses present in a susceptible plant, at equilibrium.
- φ , the proportion of resistant plants in the field.
- N_e^R , the intensity of the bottlenecks imposed by the QTLs, pyramided on the qualitative resistance.

Figure 4.2 is best read column by column as f_{RB} values induce very different figures. When f_{RB} is very small ($= 10^{-4}$), there is no need to have very narrow bottlenecks N_e^R . If N_e is reduced from 10^4 (which is the situation that we defined as the one without bottleneck QTLs) to any value of N_e between 1 and 100, similar additional relative benefits are achieved, as there are very few RB particules in the inoculum. When f_{RB} is very large ($= 0.5$), there are so many RB variants in the inoculum that bottleneck inducing QTLs have hardly any impact on the infection level. The case where the pyramiding strategy has more clearly an impact is for intermediate values of f_{RB} ($= 0.01$). In that case, the largest improvement linked to N_e is achieved in the top left of the three figures: 80% additional relative benefit can be achieved when deploying 100% of resistant plants with as small as possible bottlenecks. In summary, if f_{RB} is very small, not much effort needs to be done to reduce damages; if f_{RB} is large, no improvement can be hoped for. The best prospect of N_e reducing QTLs sits in the intermediate range.

4.2 Host mixtures and plant immunity

Going back to situations where only qualitative resistances are used, we considered the impact of plant immunity on the spread of resistance-breaking variants, first in Pauline Clin's M2 internship that I co-supervised with Frédéric Hamelin and then in her PhD thesis, of which I am not a co-supervisor, but in which I take an important part.

This work was initially set up in the same framework as Elsa's work, with mixtures of susceptible and qualitatively resistant plants, with WT and RB pathogens. We added one element to the equation, stemming from the observation that, in biotrophic pathogens (those feeding on living host tissues), an interaction between a wild-type pathogen and a resistant genotype generally triggers a hypersensitive response: the plant blocks the infection process by killing its own cells around the point of infection. Such a strong defense response may result in the plant

4. Resistance deployment and host mixtures

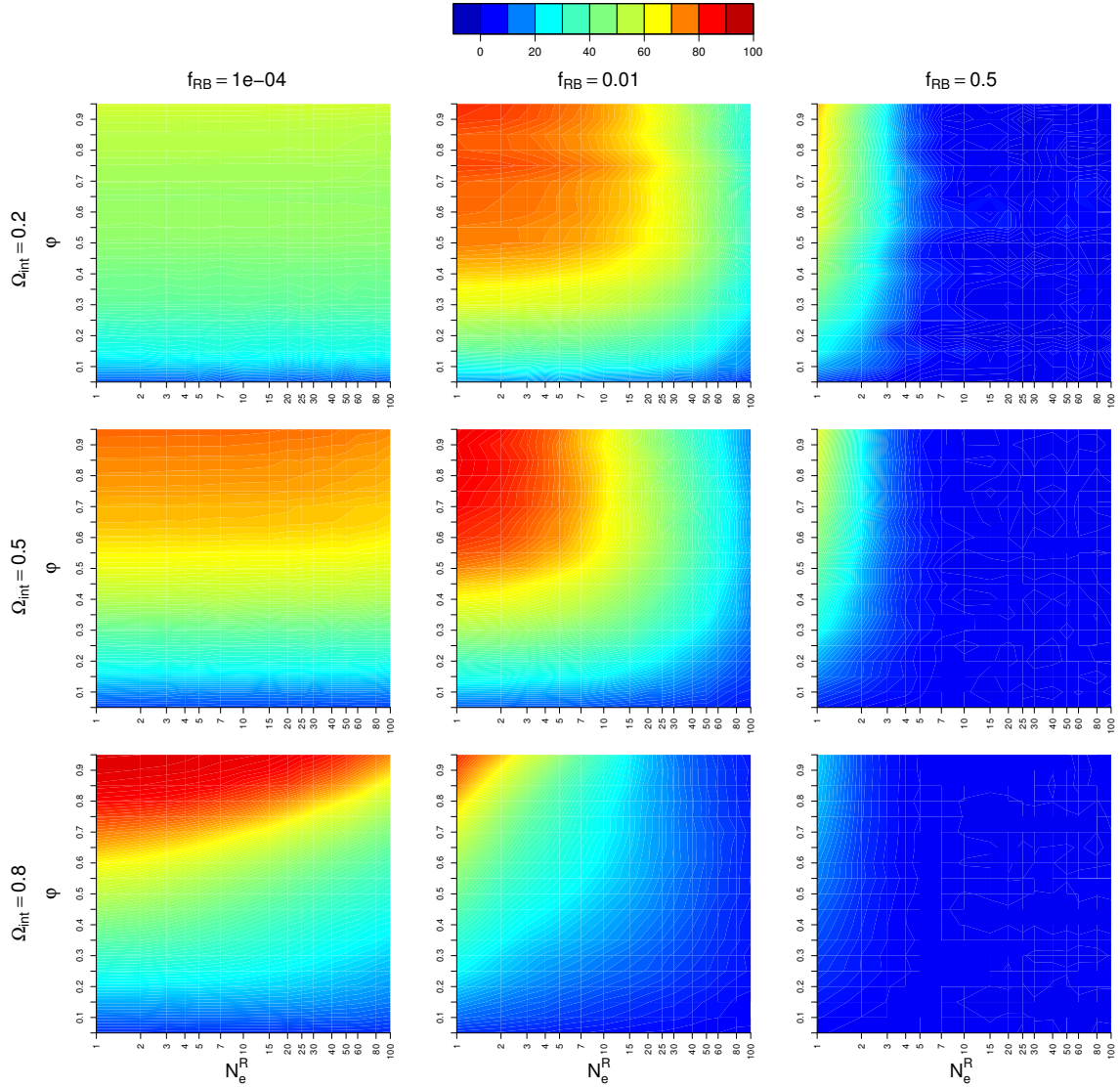


Figure 4.2: Additional relative benefit as a function of four parameters representative of the host, the virus, the vectors and the field. Contour plots representing the additional relative benefit as a function of the proportion of resistant plants φ on the y-axis and of the virus effective population size N_e^R in R plants on the x-axis. Three graphics lines represent three contrasted values of the intensity of epidemic Ω_{int} (defined on the left of the lines). Three graphics columns represent three contrasted values of frequencies of the virulent variant in susceptible plants f_{RB} (defined on top of the columns). The legend of colors is indicated on top of the graphics.

4.2. HOST MIXTURES AND PLANT IMMUNITY

being primed against future infections by RB pathogens. Immune priming is defined as increased defense to pathogen infections following previous exposure to a pathogen or an elicitor (Tidbury et al., 2012). In the plant disease epidemiology literature, and in particular in host mixtures with gene-for-gene interactions, priming corresponds to the elicitation of specific defense responses which can lead to “induced resistance” (Lannou et al., 1995; Tellier and Brown, 2008). This phenomenon might explain situations where host mixtures have been surprisingly effective, such as in large scale experiment on rice blast in the Yunnan province of China (Zhu et al., 2000). In that experiment, the disease was reduced by 94% in the mixture when compared to purely susceptible plants and, more interestingly, the prevalence in resistant plants was reduced when compared to purely resistant fields, which was interpreted as a protection of the resistant plants by the susceptible ones through some sort of priming effect.

The purpose of our work in Clin et al. (2021) was then to propose a model through which evaluating the effect of priming on resistance-breaking pathogens and on the disease prevalence. In building our model, we considered a mixture of susceptible and resistant plant hosts in constant proportions $1 - p$ and p respectively, in a field with a total plant density N (p is equivalent to φ in the previous section). The density of uninfected susceptible host is S_s . The density of uninfected resistant host is S_r . The density of resistant host primed by the WT is S_r^* . The density of susceptible hosts infected by the WT is I_s . The densities of susceptible and resistant hosts infected by the RB genotype are J_s and J_r , respectively. Although susceptible plants may be co-infected by the WT and the RB genotype, we do not allow for coinfections for simplicity. We consider that the plant is present yearlong and we ignore seasonality in climatic conditions for simplicity. We have $S_s = N_s - I_s - J_s$, and $S_r = N_r - S_r^* - J_r$.

We assume the resistance-breaking (RB) pathogen genotype incurs a cost which reduces its transmission rate by a factor $0 \leq c \leq 1$ relative to the wild-type (WT). Such a cost has been demonstrated and measured in many types of parasites since for example Klittich et al. (1986) and Cruz et al. (2000).

We assume that priming is triggered by an infection attempt initiated in a susceptible host towards a resistant one; it is then lost at a rate $\gamma > 0$ and can last for several weeks to months (Fu and Dong, 2013). We suppose that priming instantaneously reduces the probability that a resistant host be infected by a RB genotype by a factor $0 \leq \rho \leq 1$ (priming effect). Note that, when $\rho = 1$, priming is fully effective and no infection can take place, while it has no effect when $\rho = 0$.

We assume that infected hosts remain infectious until harvest, as is the case for most plant viruses and many other parasites. The rate at which a host is replaced with an uninfected one (due to harvesting and replanting) is α . It corresponds to the inverse of the length of the growing period. The transmission rate of the WT is β . The forces of infection of the WT and RB genotypes are therefore, respectively: $F = \beta I_s$, and $G = (1 - c)\beta(J_s + J_r)$.

$$\begin{cases} \dot{I}_s &= \beta I_s S_s - \alpha I_s, \\ \dot{S}_r^* &= \beta I_s S_r - (1 - \rho)(1 - c)\beta(J_s + J_r)S_r^* - (\gamma + \alpha)S_r^*, \\ \dot{J}_s &= (1 - c)\beta(J_s + J_r)S_s - \alpha J_s, \\ \dot{J}_r &= (1 - c)\beta(J_s + J_r)S_r + (1 - \rho)(1 - c)\beta(J_s + J_r)S_r^* - \alpha J_r. \end{cases} \quad (4.2)$$

We re-scale variables and parameters according to

$$x = \frac{I_s}{N}, \quad m = \frac{S_r^*}{N}, \quad y = \frac{J_s}{N}, \quad z = \frac{J_r}{N}, \quad t^* = \alpha t, \quad R = \frac{\beta N}{\alpha}, \quad \nu = \frac{\gamma + \alpha}{\alpha} \geq 1,$$

with the parameter R corresponding to a basic reproduction number (Madden et al., 2007), that

4. Resistance deployment and host mixtures

is the mean number of secondary infections produced by a pathogen able to infect N hosts with transmission rate β during an average time $1/\alpha$. Any relevant pathogen necessarily has $R > 1$, otherwise it would go extinct without any need of intervention by the crop grower. In these new dimensionless variables, system (4.2) becomes

$$\begin{cases} \dot{x} &= Rx[(1-p) - x - y] - x, \\ \dot{m} &= Rx(p - m - z) - (1-\rho)(1-c)R(y+z)m - \nu m, \\ \dot{y} &= (1-c)R(y+z)[(1-p) - x - y] - y, \\ \dot{z} &= (1-c)R(y+z)(p - m - z) + (1-\rho)(1-c)R(y+z)m - z. \end{cases} \quad (4.3)$$

We define the total prevalence of the disease as the proportion of infected hosts in the plant population $P = (I_s + J_s + J_r)/N = x + y + z$, as we assume that primed plants are neither infectious nor present any symptom.

In Clin et al. (2021), we then propose an extensive analysis of the equilibria, their positiveness, and their stability as a function of the parameter values, and illustrate the resulting prevalence values. We show that there are four possible equilibria types: i) the pathogen free equilibrium $(0, 0, 0, 0)$ that always exists; ii) an equilibrium with only WT pathogens $(\hat{x}, \hat{m}, 0, 0)$ that only exists (in the sense that it is positive) if $R(1-p) > 1$, that is if its basic reproduction number over the proportion $(1-p)$ of plant upon which it can grow is larger than 1; iii) an equilibrium with only RB pathogens $(0, 0, \hat{y}, \hat{z})$ that only exists if its own basic reproduction number satisfies $R(1-c) > 1$; iv) a coexistence equilibrium $(\bar{x}, \bar{m}, \bar{y}, \bar{z})$ that only exists if the other three exist and are unstable (which requires $p < c$ and a more complex condition on ρ exhibited in Clin et al. (2021)). We have also shown that only one of them is asymptotically stable at a time. The main tools used are simply the analysis of algebraic inequalities to ensure positiveness, and the analysis of the eigenvalues, or the Routh-Hurwitz criterion, of the jacobian matrix of system (4.3) evaluated at the equilibria.

Our result concerning the impact of priming on the prevalence is best illustrated on Figure 4.3. It illustrates the prevalence P at equilibrium as a function of the proportion p of resistant plant without (panel A) and with priming (panel B). In both panels A and B, it is seen that the prevalence initially decreases from $p = 0$ until $p = \hat{p}$ or p^* , without any RB-type at equilibrium because $R(1-p)$, the basic reproduction number of the WT-variants, is there much larger than $R(1-c)$, basic reproduction number of the RB-types. Also, since in that region the density of plants actually available for the WT-types decreases with P , the prevalence naturally decreases; prevalence decreases through a dilution effect of the susceptible plants. On the other end, for large p values ($p > c$), there are no WT-types that can survive; hence, as the landscape then appears homogeneous for the RB-variant which does not differentiate between susceptible and resistant plants, prevalence is necessarily constant. Finally, there is a coexistence region between the two. In the absence of priming (panel A), prevalence is also constant there; indeed, with $m = 0$ in (4.3), the growth of the RB-variants takes the form

$$\frac{d}{dt}(y+z) = (y+z)[(1-c)R(1-P) - 1]$$

which shows that the total prevalence at equilibrium is equal to $P = 1 - \frac{1}{R(1-c)}$ and hence independent of p . The growth of the RB-variant takes place in the space the susceptible ones leave, as also shown by the crossing dashed and dotted segments inside the violet region. In the presence of priming, things are quite different: due to priming which hampers RB-type growth, more resistant plants are required for the RB-type to establish, so that the region of decrease in the pink region extends longer, and the prevalence plunges below the one of the blue

4.2. HOST MIXTURES AND PLANT IMMUNITY

region. Once RB-types can establish themselves, the prevalence then increases. The strength of this result is that it then shows the existence of an optimal proportion for the deployment of resistant plants p^* , and that by choosing p just below that value, RB-variants cannot persist in the system, hence preserving the effectiveness of the resistance.

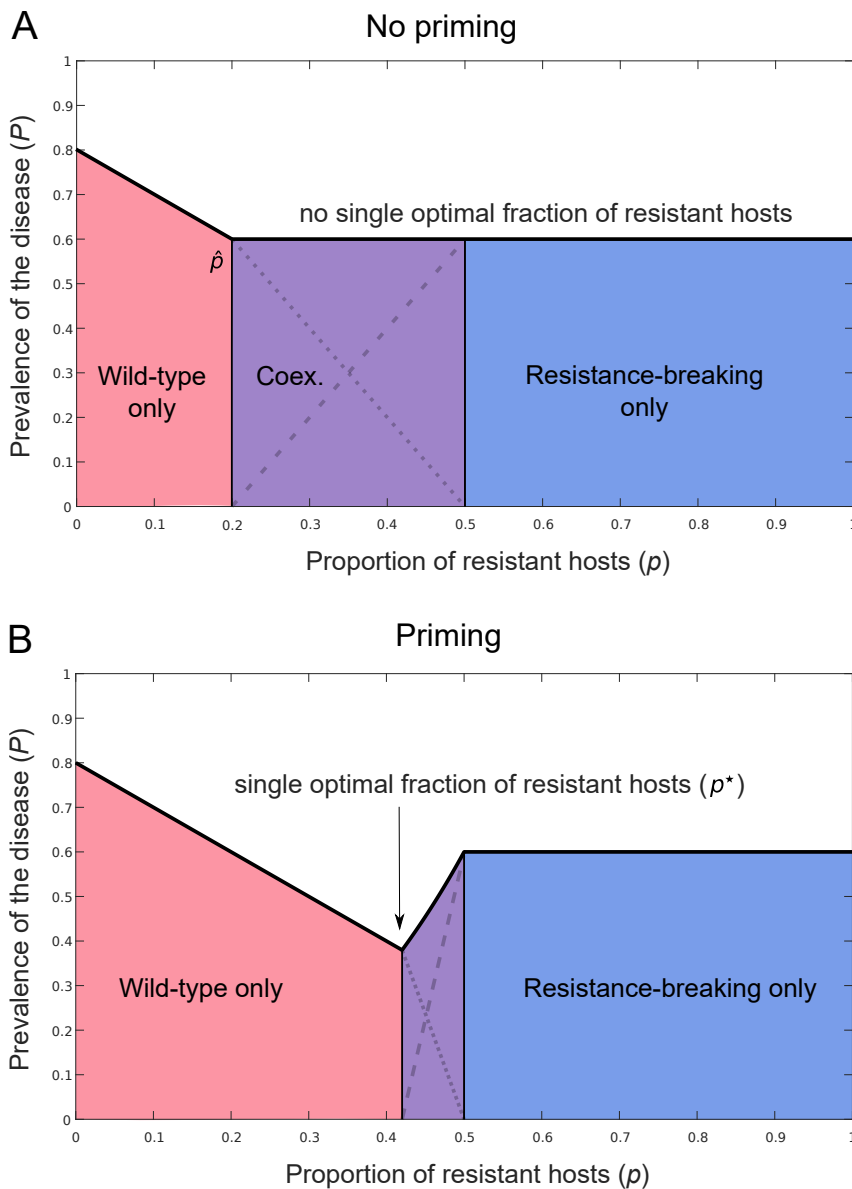


Figure 4.3: The total prevalence of the disease (P) as a function of the proportion of resistant hosts p . Panel A shows the baseline without priming ($\rho = 0$): all p such that $\hat{p} \leq p \leq 1$ equally minimize the disease prevalence. Panel B shows the effect of priming ($\rho = 0.8$): there is a single optimal fraction of resistant host p^* . Other parameter values: $c = 0.5$, $R = 5$, and $\nu = 1$. The crossing lines in the coexistence region represent the prevalences of the WT (P_w : dotted line) and RB genotype (P_b : dashed line).

4.2.1 Extension

Instead of considering a mixture of susceptible and resistant plants, we considered a mixture of n types of resistant plants of the same plant, all at the same density $\frac{N}{n}$. More specifically a

4. Resistance deployment and host mixtures

multiline mixture, which is here defined as the mixtures of plants that are identical in all points except in their resistance. We supposed that each plant carries a single resistance gene, and that all genes induce the same fitness cost c in a resistant breaking pathogen; a pathogen being able to break k different resistance genes is termed a pathogen of virulence complexity k , and sees a reduction of its transmission rate by a factor $(1 - c)^k$ (Groth, 1976; Tellier and Brown, 2007). In Clin et al. (2022), we studied the dynamics of variants of all complexities and first showed (through simulations) that the densities of all variants of the same complexity converge to each other. We then analysed the behavior of the resulting model where all variants of the same complexity have the same density and showed analytically that only one complexity k^* , persists in the pathogen population at endemic equilibrium. This virulence complexity turns out to be the one that maximizes $\phi_k = kR(1 - c)^k$, which emerges as a metric of fitness as it combines the fitness of a pathogen of virulence complexity k when it infects a host ($R(1 - c)^k$) with the number of different host types it can infect (k). In the end, we obtain that increasing n drastically reduces disease prevalence. Supposing that priming occurs when a variant that does not carry a given resistant-breaking allele tries to infect a plant that carries the corresponding resistance genes, we then observe an important reduction of the number of resistance genes to be deployed in order to bring the prevalence below some threshold level. Hence confirming, in that framework also, that host mixtures and priming can greatly help control plant pathogens.

4.3 Collaborators

These results were obtained with Ludovic Mailleret

- in the context of Elsa Rousseau’s PhD thesis with Frédéric Fabre (INRA(E) Bordeaux) and Benoît Moury (INRA(E) Avignon), and Pauline Clin’s thesis with Frédéric Hamelin (Agrocampus Ouest) and Didier Andrivon (INRAE Rennes).
- in the internships of Elsa, Pauline and Mélanie Bonneault, who I co-supervised with Elsa.

4.4 Representative paper

The following paper presents the main results of Section 4.2.1 about the equi-mixture of n resistant plant variants:

J34 - P. Clin, F. Grogard, D. Andrivon, L. Mailleret, F.M. Hamelin, Host mixtures for plant disease control: benefits from pathogen selection and immune priming, *Evolutionary applications*, 2022. (<https://dx.doi.org/10.1111/eva.13386>).

See Appendix E for the complete paper.

5

Epidemiological modelling for tropical agriculture

5.1 Why EPITAG?

5.1.1 Anecdotally

In the middle of 2016, I was concerned with the end of the PhD theses of Elsa Rousseau and Nicolas Bajoux, when Jean-Luc and then Suzanne came into my office, talking to me about an existing collaboration between Inria (Gauthier Sallet) and Cameroon (Samuel Bowong) that could not go on due to Gauthier's departure. This collaboration needed shelter in some other Inria team. Without thinking too much about it, I agreed that Suzanne put my name on the project, which was to become EPITAG. Little did I know...

EPITAG has now been running from January 2017, and renewed in January 2020, as an Inria associate team between Biocore and a group of mathematicians in Cameroon, scattered between Yaoundé, Douala, and Dschang. This collaboration really runs through the PhD students, who Suzanne and myself co-supervise with Cameroonian professors, and who spend at least 5 months each (non-COVID) year in Biocore.

These students are brilliant and dedicated to grasping the opportunity of pursuing their research in France, where they can do it full time, as opposed to when they are in Cameroon, where their status as PhD students without pay impose that they find some other money-making activity. They are an inspiration and the real engine of the work presented in this chapter.

In this chapter, I will mainly concentrate on the presentation of the models that were used for our analyses and developments of control strategies. I will however start by exposing the challenges agriculture faces in Africa, and in particular in Cameroon.

5.1.2 Agriculture in Africa

Agriculture is central to most of Africa's economies, whether for subsistence in rural areas or for export of commodities, fueling its developing economies. Though it now accounts for

5. Epidemiological modelling for tropical agriculture

only 15.5% of Sub-Saharan African countries' GDP (World Bank Data, 2018a), its impact in term of people's lives is way larger as agriculture accounts for 54% of the employment in Sub-Saharan Africa (World Bank Data, 2018b). Moreover, even though they are not employed in the agriculture sector per se, even more people are involved if all stakeholders are taken into account: traders, vendors on markets, and people growing some crops as a side job.

Also, African agriculture is facing a daunting challenge, that of feeding an ever-growing population. Africa's population, which was 250 millions in 1955, is now at 1.3 billions and projected to top 2 billions by 2050, among which a mounting proportion lives and will live in urban areas. For now, African agriculture has not been up to the task, as countries have had to rely more and more on imports to feed their urban populations for cereals, poultries,... This is not only explained by population growth, as local agriculture production has risen steadily at the same rate as population growth, but is more a consequence of changing diets (more precisely, increased food intake), and export policies of other zones, such as the European Union or China, that flood Africa with low-price food through their subsidies (Rakotoarisoa et al., 2012).

African agriculture production has risen through the exploitation of new land and the reduction of fallow periods, but its productivity has barely improved since the 1970s. The FAO lays the blame on soil degradation due to continuous cultivation with too little use of fertilizers and soil amendment techniques aimed at maintaining soil quality; fertilizer usage is way below international standards (OECD-FAO, 2016), which may or may not be a good thing. The aim is to increase this productivity while fitting into the Sustainable Development Goals of the United Nations.

This productivity problem is compounded with global change, whose consequences will be multiple over agriculture potential in Africa: reduced agricultural land use due to submergence of coastal regions, increased aridity in the tropical high agricultural potential regions, loss of the semi-arid lands of East Africa, and increased prevalence of farm pests and diseases (Ngaira, 2007).

In this chapter, we will concentrate on the crop protection side of things in order to deal with current pests and their future increase. Africa is indeed the continent which suffers the most important crop losses to pests (Oerke, 2006); for instance potato culture in Central Africa suffers 50% losses to pests, compared to 24% in North West Europe. This is due in part to the limited efficiency and intensity of the crop protection strategies, but also to the very favourable conditions for insect pests in tropical regions.

Chemical pesticide usage has penetrated Africa about 80 years ago, but its misuse has been rampant, especially in the myriad of small farms which dominate the agricultural landscape in Africa, because of "(i) absence of clear instructions, (ii) illiteracy of farmers, (iii) lack of knowledge on risks from bad uses, (iv) uses of pesticides on crops for which the product was not homologated, and (v) difficulties to properly prepare the solution to be used, and poor respect of dosage", as stated in Pouokam (2019). Moreover, many pesticides that are the subject of a worldwide ban due to their toxicity can still be found in Africa. Also, pesticide exposure during application or pesticide residue presence in food sold in local markets is of little concern for authorities, so that pesticides are a major source of health hazards for the population; only fruits and vegetables for export are subject to close monitoring of their pesticide content.

Despite this dark picture, Africa is on the low end of pesticide usage in the world, way behind Asia, which consumes more than half of the yearly pesticide production (FAO Statistics, 2017). In order to improve their productivity, African farmers will need to implement crop protection actions. However, they will have to avoid the "all-pesticide" approach of the intensive

cultures in Europe, Asia, and America if they want to achieve sustainable development without harming their health as well as that of the consumers. Also, intensive pesticide usage leads to an expensive, and often losing, arms'race with the pests, which often develop resistances to the pesticides, as stated in the introduction of Chapter 3.

5.1.3 Agriculture in Cameroon

Cameroon is a country in Sub-Saharan Africa, just North of the Equator line, on the Atlantic Coast. Its population, which was of 4.7 millions in 1955, is now over 26 millions people. Agriculture represents 14.4% of its GDP and 30% of its export value (OEC World, 2020). It employs 46.6% of Cameroon's population, mostly in small exploitations. Long having had a self-sufficient agriculture, and even being the breadbasket of the region as a net exporter of agricultural products, Cameroon now imports low-price goods from Europe and Asia, which has put many of its small farmers in jeopardy. Moreover, the current fragile equilibrium has the potential of being permanently disrupted by climate change, as the semi-arid plains in the North could potentially dry out due to the high temperatures and the tropical plains could be subject to more frequent extreme rain events that regularly ruin the whole crops. Moreover, the periodicity of rainy and dry seasons is already perturbed by global change.

However, Cameroon, with its varied ecological zones and two principal climatic zones (marked by rainy and dry seasons of different intensities), has the potential of developing a booming agriculture if government and farmers engage in its modernization (Abia et al., 2016). Also, political unrest in the english-speaking western part of the region and non-democratic institutions pose a permanent threat and prevent progress in the agricultural sector. Self-sufficiency would save the country billions of dollars every year.

The main subsistence crops include plantains, beans, potatoes, yams, cassava (manioc), corn, and oil palm in the south and peanuts, millet, and cassava in the north. Most day-to-day food has hence the potential of being produced locally, to the exception of rice.

Cameroon's main cash crops are cocoa (4th largest producing country in 2016, 15% of exports), bananas and plantains (7.2%), cotton (4.2%) and coffee (1.5%). As a strong point of Cameroon's exports, these cultures are vital to Cameroon's economy and its productivity needs to be improved if the country's population is to have its quality of life improved and, even more importantly, its life expectancy lengthened; it was at 58.5 years in 2017, with important discrepancies between the socio-economic classes, compared to 82.5 years in France. Cameroon needs the revenues of these exports as a stepping stone to its economic development and to improve its health system, its education, ...

5.1.4 Crop pests

As most crops, the cash crops are produced by small farmers and long have been hampered by administrative inadequacies in the state-run commodity buying agency, which has prevented farmers from modernizing their infrastructures and renewing their trees (New Agriculturist, 2001). There are numerous ways productivity could be improved in the face of climate change: the increased use of inorganic fertilizers, animal droppings, and vegetal wastes in the soil, the use of improved seeds that will preserve productivity in arid regions, crop rotation or improved irrigation (Abia et al., 2016). In this chapter, and in EPITAG in general, we have considered the aspect of crop protection against the most problematic pests. In EPITAG, these are or have been pursued in PhD theses about pest control on three of the four main crops in Cameroon:

5. Epidemiological modelling for tropical agriculture

- Cocoa plant mirids (PhD student: Myriam Djoukwe Tapi, University of Douala; Supervisors: L. Bagny-Beilhe, S. Bowong, Y. Dumont; defended in june 2020).
- Plantain plant-parasitic nematodes (PhD student: Israël Tankam Chedou, University of Yaoundé I; Supervisors: F. Grognard, L. Mailleret, J.-J. Tewa, S. Touzeau; defended in april 2021).
- Coffee Berry Borers (PhD student: Yves Fotso Fotso, University of Dschang; Supervisors: S. Bowong, F. Grognard, S. Touzeau, B. Tsanou; defended in january 2022).
- Coffee Leaf Rust (PhD student: Clotilde Djuikem, Inria; Supervisors: S. Bowong, F. Grognard, S. Touzeau; defended in january 2023).

In this chapter, I will then concentrate on the two crops I have worked on: banana/plantain and coffee.

5.2 Banana/plantain plant-parasitic nematode control

The banana plant is not a tree, as it is often wrongfully called, but a herbaceous flowering plant of the genus *musa* whose stem looks like a trunk and only lasts for a year, the time it takes for it to grow and bear a single banana bunch. The bananas are the berries of the plant, but they are seedless when edible and hence do not participate in the reproduction of the plant; there exist however banana varieties whose fruits present seeds, but these bananas are (physically) inedible because of these big and hard seeds. Reproduction in edible banana plants then takes place through the development of a new sucker arising from the rhizome near the existing plants; it is hence a form of asexual (clonal) reproduction (ProMusa, 2020).

5.2.1 Banana/plantain in Cameroon

Banana plants are endemic to Southeast Asia and Australia and are now cultivated all around the globe, across the tropics and subtropics, mainly for local consumption. Its two main producers are India, with 30 million tons and China with 11 million tons per year, but they hardly export any; on the other hand Ecuador is the leading banana exporter in the world with 7700 tons, with the Philippines second at 3900 tons per year (FAO, 2020). Cameroon is in the top ten of the producers at around 5500 tons per year (dessert banana + plantain) and of the exporters.

Plants of the genus *musa* are roughly divided into two categories: dessert bananas and plantains. The former are appreciated as dessert all over the world and the latter is mostly consumed cooked, with 73% of its production and consumption taking place in West and Central Africa (Robinson and GalánSaúco, 2010). In Cameroon, plantain is a basic food for day to day consumption, and represents 86% of the country's banana production. Bananas and plantains are hence central for Cameroon, both as cash crops and staple food.

5.2.2 *Radopholus similis*

Both banana and banana-plantain cultures are hampered by plant-parasitic nematodes, insect pests and soil-borne fungi, that seriously threaten the sustainability of these systems by decreasing yield, causing plant toppling or requiring intensive pesticide use. The burrowing nematode *Radopholus similis* is the most significant parasitic nematode of the banana and plantain plants

5.2. BANANA/PLANTAIN PLANT-PARASITIC NEMATODE CONTROL

in the world (Sarah, 1993). It is a phytophagous nematode that attacks the roots of host plants and causes damages, ranging from simple root lesions that reduce the production to the toppling of the plant. Hence, *R. similis* is one of the most regulated pests of banana plants (Hockland et al., 2006).

In Israël Tankam Chedjou’s thesis, we proposed a model to design control strategies avoiding pesticide use and relying rather on fallow deployments associated with uprooting of the banana plant and plantation of a new, nematode-free, vitroplant. Banana cropping taking place in tropical regions in Cameroon, fallows are hence unconstrained in duration, as banana cropping does not need to follow any seasonal pattern as it would in temperate regions. This gives freedom in the optimization of fallow durations. This fallow approach contrasts with more traditional production methods where the banana plant for the next season stems from a shoot of the previous season and hence keeps its infected roots; in that situation nematode control is achieved through pesticides.

Because of the large number of factors and the complexity of interactions between plants and pests, mathematical models are invaluable tools to improve the efficacy of sustainable agricultural practices, especially for soilborne pest control. In the early 90s, Gilligan (1990, 1995) proposed some models that described the dynamics of soilborne pathogens, that were subsequently generalized by Gubbins et al. (2000). Optimization of fallow deployment strategies for soilborne pest control in the literature is rare and rather unsophisticated though. Van den Berg and Rossing (2005) designed optimal rotation strategies between host and fallows by deciding whether or not to deploy a one-year fallow of fixed-length, based on a statistical model. Other models, also worthy of interest, sought for optimal rotation strategies between good and bad hosts, which has similarities with fallows as it presents the principle of reducing pathogen populations in the absence of a good host (Taylor and Rodriguez-Kábana, 1999; Van Den Berg et al., 2006; Van den Berg et al., 2012; Nilusmas et al., 2020).

We initially presented our model at the CARI conference (Tankam Chedjou et al., 2018), and used it in three subsequent journal papers:

- In Tankam Chedjou et al. (2020), we compared the fallow approach with pesticide usage and showed that, provided fallows are of sufficiently long (and constant) duration, the nematode-free periodic solution is asymptotically stable in a multi-seasonal context.
- In Tankam Chedjou et al. (2021b), we fixed a horizon (15 years) and optimized the (non-constant from year to year) fallow deployment over that horizon.
- In Tankam Chedjou et al. (2021a), we summarized things and considered cases where fallows are not applied every year, but alternate with seasons where the previous year’s root is the basis for the new plant.

Israël’s thesis considered several cropping seasons so that we built a multi-seasonal compartmental model which represents the root-pests continuous dynamics within the growing season with discrete transitions from the end of one season to the beginning of the next following the semi-discrete formalism presented in Chapter 3. Considering a single plant and homogeneous repartition of nematodes in the roots, we assumed that the plant-pest dynamics can be represented through three variables: free nematodes in the soil (P), infesting nematodes in the roots (X), and the biomass of functional roots of the banana plant (S).

During a cropping season, banana roots grow logistically (Gregory, 2006) until the flowering at which moment root development stops. The duration of the growth period, *i.e.* the time

5. Epidemiological modelling for tropical agriculture

elapsed between the start of the cropping season and the flowering of the plant, is termed d ; the total duration of a cropping season is termed D . We denote the starting point of the $(k + 1)$ -th season by t_k , and we set $t_0 = 0$ as the starting point of the first season. The logistic growth of the roots during a cropping season is therefore given by:

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

where

$$\rho(t) = \begin{cases} \rho & \text{for } t \in (t_k, t_k + d], \\ 0 & \text{for } t \in (t_k + d, t_k + D]. \end{cases}$$

Free pests (P) infest the plant roots (rate β). They undergo natural mortality (rate ω). Infesting pests (X) feed on the plant roots with a Holling type II-like functional response $\frac{aSX}{S+\Delta}$ that is well-suited for invertebrates (Holling, 1966). They undergo natural mortality (rate μ). This mortality rate differs from the mortality rate in the soil because the environments are different. The root, which serves both as host and food for the nematode, is more favourable to pest survival than the soil ($\mu < \omega$). When infesting nematodes feed, the ingested root biomass is used for growth and for reproduction. A proportion γ of the offspring stays in the roots (hence becomes X), while the rest exits the roots (and becomes P) (Hugon and Picard, 1988). α is the conversion rate of ingested biomass into pests.

Free nematodes and infesting nematodes then interact with the functional roots during the cropping season, *i.e.* for $t \in (t_k, t_k + D]$, according to the following system:

$$\begin{cases} \frac{dP(t)}{dt} = -\beta P(t)S(t) + \alpha a(1 - \gamma) \frac{S(t)X(t)}{S(t) + \Delta} - \omega P(t), \\ \frac{dS(t)}{dt} = \rho(t)S(t)\left(1 - \frac{S(t)}{K}\right) - a \frac{S(t)X(t)}{S(t) + \Delta}, \\ \frac{dX(t)}{dt} = \beta P(t)S(t) + \alpha a \gamma \frac{S(t)X(t)}{S(t) + \Delta} - \mu X(t). \end{cases} \quad (5.1)$$

with the initial conditions $P(0^+) = P_0$, $S(0^+) = S_0$, $X(0^+) = X_0$.

At the end of a cropping season, *i.e.* at $t = t_k + D$, the plant is uprooted. Since uprooting is imperfect, we assume that a fraction r of the roots remains in the soil, containing $rX(t_k + D)$ nematodes, which we put in the free pool as the left-over roots quickly die out and cannot be considered fresh roots hosting nematodes anymore. This leads to the following switching rule for $k \in \mathbb{N}$:

$$\begin{cases} P(t_k + D^+) = P(t_k + D) + rX(t_k + D), \\ S(t_k + D^+) = 0, \\ X(t_k + D^+) = 0. \end{cases} \quad (5.2)$$

In the absence of hosts, during the fallow, free pests undergo an exponential decay Chabrier et al. (2010):

$$\frac{dP(t)}{dt} = -\omega P(t) \quad \text{for } t \in (t_k + D, t_{k+1}]. \quad (5.3)$$

where $t_{k+1} = t_k + D + \tau_{k+1}$ with τ_{k+1} the duration of the fallow after the $k + 1$ -th cropping season. At the beginning of each cropping season, a pest-free vitroplant is planted Chabrier and Qu  n  herv   (2003). Hence, $S(t_{k+1}^+) = S_0$ and $X(t_{k+1}^+) = 0$. Solving equation (5.3) with the

5.2. BANANA/PLANTAIN PLANT-PARASITIC NEMATODE CONTROL

initial condition given by (5.2) then leads to the following transition rule:

$$\begin{cases} P(t_{k+1}^+) = \left(P(t_k + D) + rX(t_k + D) \right) e^{-\omega\tau_{k+1}}, \\ S(t_{k+1}^+) = S_0, \\ X(t_{k+1}^+) = 0, \end{cases} \quad (5.4)$$

The system formed by equations (5.1) and (5.4) form the multi-seasonal model with fallow. This is schematically displayed in Figure 5.1.

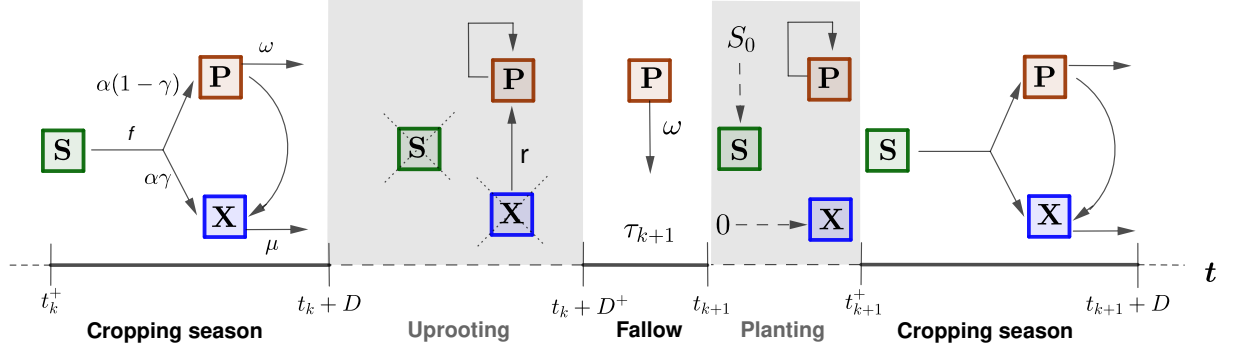


Figure 5.1: Schematic representation of the multi-seasonal plant-nematode dynamics with uprooting and pest-free vitroplant planting. Interactions between fresh roots (S), free nematodes (P), and infesting nematodes (X) during the cropping seasons correspond to Eq. (5.1). Switching between the cropping seasons corresponds to Eq. (5.4) when a fallow of duration τ_{k+1} is introduced between the parent plant uprooting and the planting of a pest-free vitroplant. On the time axis, plain lines represent the continuous course of time, whereas dotted lines and grey backgrounds represent discrete times and phenomena (parent plant cutting or uprooting, vitroplant planting). Boxes represent model variables, plain arrows population flows, dashed arrows planting and crossed-out boxes uprooting (Tankam Chedjou et al., 2021a).

In Tankam Chedjou et al. (2020), we set all τ_k equal to a single τ and performed the stability analysis of the periodic nematode-free solution for system (5.1) and (5.4), through the method exposed in Chapter 3. It gave us a threshold level for τ above which nematode eradication is achieved in the long run.

In Tankam Chedjou et al. (2021b), we fixed the horizon T_{max} (e.g. 15 years) and optimized the profit over this horizon. Following Serrano (2005); Ngo-Sammick (2011) we obtained the profit over one season as

$$R_k = m \int_{t_k+d}^{t_k+D} S(t)dt - c \quad (5.5)$$

with the first term the yield (*i.e.* the price obtained from the mass of banana produced per plant) and the second term the fixed cost of a vitroplant, where the banana mass over the period of interest depends on the infestation level, and so on the fallows applied during the previous intercroppings. Hence, over the fixed horizon, we wished to find the fallow durations that maximize

$$R(\tau_1, \dots, \tau_n) = \sum_{k=0}^n R_k \quad (5.6)$$

From switching rule (5.4), long fallow durations τ_k lead to the reduction of the soil infestation. Equation (5.5) shows that the seasonal yield is linked to fresh root biomass that depends on the

5. Epidemiological modelling for tropical agriculture

infestation level throughout the season. Increasing the fallow durations to drastically reduce the pest population increases the yield of each season. However, on a fixed and finite time horizon that spans several seasons, increasing the fallow durations may reduce the number of cropping seasons and hence the multi-seasonal profit.

We analyzed this maximization problem and showed that, under some monotonicity hypothesis, its solution needed to have its last cropping period finishing exactly on T_{max} , whatever the number of fallows and cropping seasons it contained.

The algorithmic aspect of this resolution is not complex. First we note that the maximum number of fallows is $n_{max} = \lfloor \frac{T_{max}}{D} \rfloor - 1$ since there cannot be more than $\frac{T_{max}}{D}$ cropping season over the horizon. Our algorithm then goes through all possible number of fallows from 1 to n_{max} and, for each n , it identifies the optimal (τ_1, \dots, τ_n) through an adaptive random search (ARS) algorithm, which consists in exploring a given bounded space, by alternating variance-selection and variance-exploitation phases (Walter and Pronzato, 1997). An example of result of this optimization is given in Figure 5.2, where we see that the fallows are concentrated mainly at the beginning of the cropping period to ensure that the plantation is clean of nematodes for most of the cropping seasons. Note that there are 11 cropping seasons and 10 fallows (averaging 37 days), while it would have been possible to squeeze 12 cropping season and 11 fallows (averaging 4 days) over T_{max} . However, the additional cropping season does not compensate yield losses linked to the high level of nematodes due to the short fallow periods.

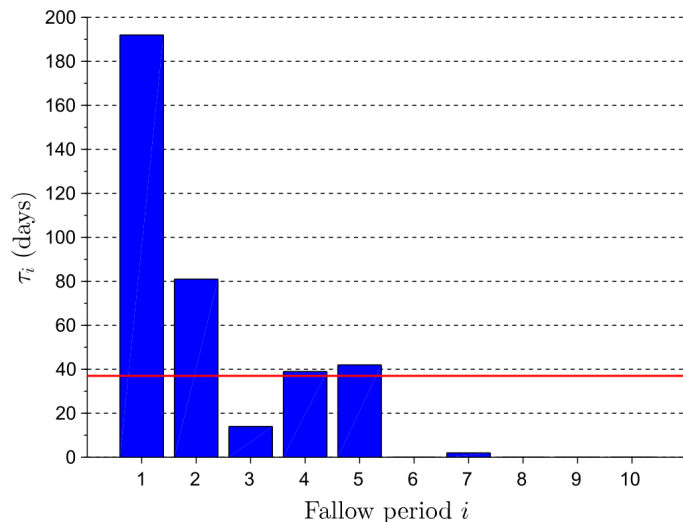


Figure 5.2: Optimal distribution of fallow periods for time horizon $T_{max} = 4000days$. The maximal profit is obtained for 11 cropping seasons and 10 fallows: $\tau^* = (192, 81, 14, 39, 42, 0, 2, 0, 0, 0)$ (in days). The red line corresponds to the average fallow period $\tau = 37$ days. (Tankam Chedjou et al., 2021b).

In Tankam Chedjou et al. (2021b), we have also performed the same optimization while first adding a hard cap on the fallow durations and, in a second instance, by adding a penalty term to the profit to ensure that the fallow repartition is not too far from the situation where all fallows are identical. This way, we ensure that the banana/plantain grower is not exposed to too large variations in his revenues. In all cases, we have shown that fallow deployments can be a viable alternative to the heavy pesticide use that currently prevails

5.3 Control of the Coffee Berry Borer

The coffee tree is a perennial plant, belonging to the Rubiaceae family, which has persistent leaves. The productivity stage (flowers and fruits) begins after 3 years and lasts for 20 years on average. Flowers appear at the end of branches and require a lot of humidity for their development. The annual productivity period lasts 7 to 11 months depending on coffee species and cultivars, as well as climate.

5.3.1 Coffee in Cameroon

As stated earlier, coffee is one of the cash crops of Cameroon, though it is dwarfed by cocoa production. It is mainly produced in two regions: the littoral region with the Moungo department and the West region (from which our PhD students come from). Climatic conditions are indeed very diverse in Cameroon and coffee cannot be grown everywhere. Due to the decreasing price of the coffee commodity and the deteriorating state of the infrastructures, coffee production is however decreasing over the years in Cameroon (-40% from 2005 to 2016). There are mainly two coffee cultivars that are grown worldwide: robusta and arabica, the latter being more fragile but more expensive (twice the price of robusta (Statista Data, 2022)); robusta represents 90% of the production in Cameroon (Office National du Cacao et du Café, 2017). Cameroon is a very small coffee producer when compared to the bigger ones such as Brasil and Columbia, but coffee is still important for its economy and attempts are being made by the National Office for Cocoa and Coffee to increase its production over the next years.

Coffee is mainly grown in small farms in Cameroon. As opposed to what happens in Ivory Coast for example, there a single harvest per year in Cameroon as its production is punctuated by the rainy and dry seasons: with a single rainy period per year from April to November, there is a single harvest between November and December.

5.3.2 The coffee berry borer

The most devastating pest of coffee is *Hypothenemus hampei* Le Pelley (1968); Damon (2000), a coffee berry borer hereafter denoted by CBB. It is an insect that develops in coffee berries at different stages of ripening. Originally from Central Africa, CBB can now be found in most coffee growing countries throughout the world Le Pelley (1968). It can cause yield losses of 30–35% and it deteriorates the berry quality with up to 100% of berries perforated at harvest time Ochoa Milián et al. (1989). Worldwide damages are estimated at more than USD 500 million each year Vega et al. (2003).

The coffee berry growth is divided into several stages that are characterised by the berry colour. After flowering, the berry successively goes through the green, yellow, red and black colours and becomes fully mature when it is red, after 6–9 months Aristizábal et al. (2016). The CBB life cycle is composed of four stages: egg, larva, nymph and adult (male and female) Damon (2000). All these stages take place inside the coffee berries, and we will term females at these stages “infesting females”. The female lays one to three eggs per day during approximately 20 days and remain inside the berry to take care of their offspring until they die. There is a 10:1 female-to-male sex ratio Silva et al. (2012); Damon (2000). The larvae, nymphs, males and young females remain inside the coffee berry, together with the founder female. The males mate with the young females of their generation. A few days after fertilisation, females leave the berry and become winged “colonising females” to find other uninfested berries for oviposition. Only

5. Epidemiological modelling for tropical agriculture

one female infests each berry as they need to dig a hole through their sole possible access, that is the apex of the berry, and super-parasitism is rarely observed in a plantation as colonising females can usually detect infested coffee berries, thanks to that hole.

Coffee berry borer control worldwide is mainly based on cultural practices, which consist in removing dropped berries and strip-picking trees after harvest or stump pruning Damon (2000); Aristizábal et al. (2016). Chemical insecticides are used with their known health risks, so alternative control methods have been developed, such as trapping, using attractive traps to capture colonising CBB as they emerge from the berries Dufour and Frérot (2008), and biological control. The most commonly used biocontrol agents are parasitoids (*Prorops Nasuta*, *Phymastichus coffea*), predators (*Cephalonomia stephanoderis*, *Cathartus quadricollis*) and entomopathogenic fungi (*Beauveria bassiana Vuillemin*) Damon (2000); Aristizábal et al. (2016).

In Yves Fotso Fotso's thesis, we proposed a model to design control strategies avoiding pesticide use. We initially presented our model at the CARI conference (Fotso Fotso et al., 2018), and used it, as well as evolutions, in four subsequent journal papers:

- In Fotso Fotso et al. (2021), we proposed a model analysis, and developed an optimal control strategy to maximize a penalized form of profit, based on the release of entomopathogenic fungi.
- In Fotso Fotso et al. (2022b), to appear, we developed a berry-age-structured version of this model, hence obtaining a model in partial derivative equations, to account for CBB preference for mature berries. Yves analyzed well-posedness of the problem, the asymptotic behaviour of the dynamics, as well as presented simulations for different values of the basic reproduction number.
- In Fotso Fotso et al. (2022c), submitted for publication, we developed an optimal control strategy for the latter PDE model. This approach aims at maximizing a penalized form of profit, based on the release of entomopathogenic fungi and trap deployments to catch colonizing females.
- In Fotso Fotso et al. (2022a), almost completed, we set our ODE model in a seasonal framework and optimize the harvesting and cleaning of the plantation at the end of the year, to maximize profit.

Needless to say that my technical contributions to the PDE papers Fotso Fotso et al. (2022b) and Fotso Fotso et al. (2022c) were minor.

In our first work (Fotso Fotso et al., 2021), we developed an optimal control approach for the continuous application of entomopathogenic fungi that kill CBB as it tries to enter a berry. For that, we developed a berry (s) - colonising female (y) - infesting female (z) - fungi (v) model of the dynamics relying on a number of hypotheses.

We supposed that there is constant berry production during the cropping season (rate Λ), and that there are enough males for fertilisation of the females, so that the colonising female production term takes the simple form ϕz . We represent the infestation through a ratio-dependent function $f(s, y) = \beta \frac{sy}{y + \alpha s}$. Ratio-dependence (Arditi and Ginzburg, 1989, 2012, Chapters 1 and 6) is particularly adapted to this pathosystem as there is a one-to-one interaction between CBB and berries; if we had fixed $\alpha = 1$, this relationship would be totally symmetric, which would make sense as infestation takes place through the encounter of one CBB with one berry, both exiting then the candidate pools for infestation (the colonising female becomes an infesting female and the healthy berry becomes infested); we added α to give us some freedom. With a

5.3. CONTROL OF THE COFFEE BERRY BORER

ratio-dependent function, when healthy berries are largely outnumbered by colonising females ($s \ll y$), berries determine the infestation response ($f(s, y) \approx \beta s$), and vice versa. The definition of f is extended to $f(0, 0) = 0$ Kuang and Beretta (1998). Parameter β represents the infestation rate per unit of time, α the infestation half saturation constant, while $\varepsilon = 1 \text{ CBB/berry}$ is simply a conversion constant to ensure that there is unit coherence.

$$\begin{cases} \dot{s} = \Lambda - \beta \frac{sy}{y + \alpha s} - \mu s \\ \dot{y} = \phi z - \varepsilon \beta \frac{sy}{y + \alpha s} - \mu_y y \\ \dot{z} = \varepsilon \beta \frac{sy}{y + \alpha s} - \mu_z z \end{cases} \quad (5.7)$$

We thoroughly analyzed this model in Fotso Fotso et al. (2021), showing the boundedness of its solutions, its basic reproduction number \mathcal{R}_0 , and demonstrating the global asymptotic stability of the CBB-free equilibrium when \mathcal{R}_0 is smaller than 1 through the construction of a Lyapunov function. Upon a request from a reviewer we also managed to obtain a closed form for the computation of the Effective Reproduction Number, which was not trivial at all:

$$\mathcal{R}_e(t) = \int_t^{+\infty} \int_t^\tau \phi \varepsilon \beta \frac{s(\hat{t})}{y(\hat{t}) + \alpha s(\hat{t})} e^{-\varepsilon \beta \int_t^{\hat{t}} \frac{s(r)}{y(r) + \alpha s(r)} dr - \mu_y(\hat{t}-t) - \mu_z(\tau-\hat{t})} d\hat{t} d\tau \quad (5.8)$$

as well as an approximated value of this number. While the basic reproduction number gives information on the onset of the epidemic in an entirely susceptible population, the value of the time-dependant effective reproduction number $\mathcal{R}_e(t)$ when compared to 1 indicates if the epidemic is expanding, endemic or contracting. At time t , it is defined as the average number of secondary cases per infectious case present at time t (Gostic et al., 2020). The importance of this value has been put into evidence in the context of the COVID epidemic.

Let us denote by $v(t)$ the fungus load at time t . The dynamics of the entomopathogenic fungus on the berries can be modelled as:

$$\dot{v}(t) = -\gamma v(t) + h(t),$$

with initial condition $v(0) \in \mathbb{R}_+$. Parameter γ denotes the natural decay rate of the fungus. The function $h(t)$ represents the fungus application rate at time t , with an upper bound $h_M > 0$. The effect of the fungus is limited and saturates at $\xi \in (0, 1)$:

$$\sigma(v) = \frac{\xi v}{v + k},$$

So, we obtain the following control system:

$$\begin{cases} \dot{s} = \Lambda - (1 - \sigma(v))\beta \frac{sy}{y + \alpha s} - \mu s \\ \dot{y} = \phi z - \varepsilon \beta \frac{sy}{y + \alpha s} - \mu_y y \\ \dot{z} = (1 - \sigma(v))\varepsilon \beta \frac{sy}{y + \alpha s} - \mu_z z \\ \dot{v} = -\gamma v + h(t) \end{cases} \quad (5.9)$$

with initial conditions $(s(0), y(0), z(0), v(0)) \in \mathbb{R}_+^4$, where we have to determine the value of $v(t)$ that would limit the pest damage. In Fotso Fotso et al. (2021), we proposed an optimal control approach to that design where we aim at maximizing the functional

$$\mathcal{J}(x, h) = \zeta_s s(t_f) - \int_0^{t_f} Ch(t) dt - \zeta_y y(t_f), \quad (5.10)$$

5. Epidemiological modelling for tropical agriculture

which is a measure of the profit penalised with the final population of colonising females which, if it is too large, would seriously hamper the possible profit of the next season. The first term of the objective functional represents the crop yield, that is the harvest of healthy coffee berries at the end of cropping season multiplied by the coffee berry price ζ_s . The second term represents the control cost, with C the price of a fungus unit, and the third term is the penalty term.

Through the application of Pontryagin's Maximum Principle, we identified conditions for saturated control (at 0 or h_M), as well as conditions for having singular solutions.

To solve our optimal control problem numerically, Yves used the BOCOP software Team Commands, Inria Saclay (2019); Bonnans et al. (2019), an open source toolbox in which the optimal control problem is approximated by a finite dimensional optimisation problem. For our simulations, we considered that, at the beginning of a cropping season, there are no berries, so $s(0) = 0$. Moreover, we assumed that there are only colonising females, as infesting females were eliminated from the plantation when berries were manually removed during the preceding harvest, so $z(0) = 0$. We also assumed that the entomopathogenic fungus is absent in the plantation, so the initial load $v(0) = 0$. In Fotso Fotso et al. (2021), we considered several different initial loads of colonising females, but we here only illustrate the intermediate case: $y(0) = 10^4$ colonising females. In Figure 5.3, there are 6 panels. Most notable, on panel (a), we see that the quantity of berries after 250 days, at the time of harvest, is reduced by 60% when comparing the healthy plantation (black curve) with the infected plantation without control measures (blue curve); optimal control (red curve) brings that harvest reduction down to 25%. In panel (b), we see that the colonising females at the end of the season, which will initiate the following year's infestation are about halved by the control. In panel (e), we see that the control is bang-singular-bang, with an initial phase where h is at its maximal level to bring the fungus-load to a sufficient level, and a final phase where it is at zero as the investment is not worth it anymore at such a late phase. The optimal control type depends on the initial condition. In the case where $y(0) = 10^6$, the control structure is *bang(0)-singular-bang(0)*. Whatever the initial CBB density, Beauvaria succeeds in reducing the damage through different application sequences depending on the initial condition.

5.4 Control of the Coffee Leaf Rust

The coffee tree is still a perennial plant, belonging to the Rubiaceae family,... (see Section 5.3).

5.4.1 Coffee in Cameroon

Coffee is still an important commodity for Cameroon... (see Section 5.3.1).

5.4.2 Coffee Leaf Rust (CLR)

Coffee leaf rust (CLR) is a disease caused by a basidiomycete fungus, *Hemileia vastatrix*, that affects coffee trees and propagates through the production of uredospores. The fungus *H. vastatrix* is a compulsory parasite, that is it only lives and develops on coffee leaves. It attacks the lower leaves of the coffee tree and causes premature defoliation, which reduces the photosynthetic capacity and weakens the tree. CLR is the most serious leaf disease of the coffee tree known to date Muller et al. (2008). It has direct and indirect economic impacts on coffee production. Direct impacts include decreased quantity and quality of yield. In some cases, more than 70%

5.4. CONTROL OF THE COFFEE LEAF RUST

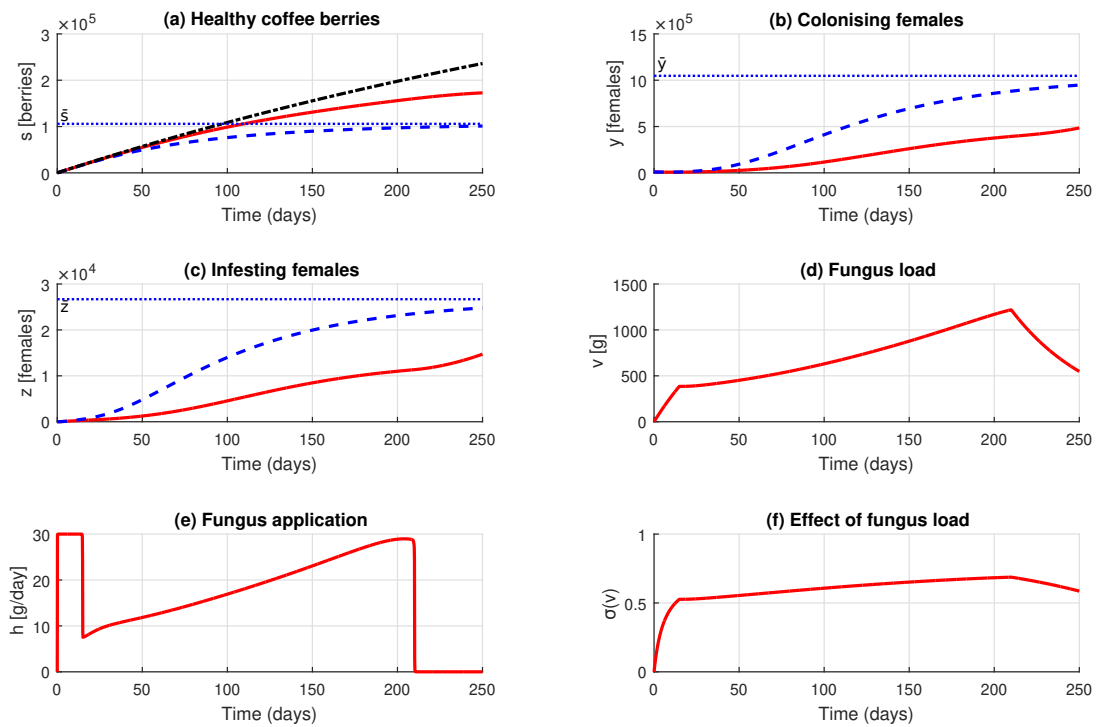


Figure 5.3: Simulation of system (5.7) without control (dashed blue curves) and system (5.9) with optimal control (plain red curves), for initial condition $s(0) = z(0) = v(0) = 0$ and $y(0) = 10^4$ colonising females. The healthy berry growth without pest is also represented in (a) (dash-dotted black curve). The coexistence steady state without control is indicated in (a–c) (dotted blue lines). (Fotso Fotso et al., 2021)

5. Epidemiological modelling for tropical agriculture

of the coffee production is lost Grée (1993). Indirect impacts include increased costs to control the disease. Control methods include fungicide application Capucho et al. (2013), cultural practices Avelino et al. (2004) including stumping of diseased plants, the use of resistant cultivars Arneson (2000), and biocontrol by fungal and bacterial parasites Vandermeer et al. (2014); Arroyo-Esquivel et al. (2019). These methods induce significant labor and material costs and, in the case of stumping, a year-long decline in production. To better control this fungus, it is necessary to understand the disease propagation and what conditions favor its development and dispersal.

Clotilde Djuikem developed an initial PDE model for the spread of CLR in a plantation over space and time during her master thesis at the University of Douala under the supervision of Samuel Bowong and Roger Tagne Wafo. When she came to Biocore for a stay after her master, Suzanne Touzeau and myself helped put that model into a seasonal framework in order to take into account the fact that the rainy season is favourable for coffee tree growth and the expansion of CLR, while the dry season less so. This allowed her to develop analytical results on her model, a control method to reduce the impact of CLR, and relevant simulations that she presented at the Biomath 2019 conference in Bedlewo (Djuikem et al., 2019). From there, her talk was selected for publication in a special issue of *Mathematical Modelling of Natural Phenomena* linked to the conference (Djuikem et al., 2021).

We started from there to build a semi-discrete model with a simplified ODE version of her PDE model (which included latency of the CLR infection and leafless branches) for the rainy season, and a single discrete-time event to represent the dry season dynamics, which are in essence simpler. This yielded

$$\begin{aligned} & \text{Rainy season for } t \neq nT : \\ & \begin{cases} \dot{S} = \Lambda - \omega\nu U \frac{S}{N} - \mu S, \\ \dot{I} = \omega\nu U \frac{S}{N} - (\mu + d)I, \\ \dot{U} = \gamma I - (\nu + \mu_U)U, \\ \dot{B} = \delta_S S + \delta_I I - \mu_B B; \end{cases} \end{aligned} \quad (5.11)$$

Dry season:

$$\begin{cases} S(nT^+) = \varphi_S S(nT), \\ I(nT^+) = \varphi_I I(nT), \\ U(nT^+) = \varphi_U U(nT), \\ B(nT^+) = 0; \end{cases}$$

where $S(t)$, $I(t)$, $U(t)$, $B(t)$ and $N(t) = S(t) + I(t)$ represent the number of healthy leaves, infected leaves, uredospores, berries and total number of leaves, respectively, at time t ; with $0 < \varphi_S, \varphi_I, \varphi_U < 1$ and φ_U close to 0 (Djuikem et al., 2022). During the production period with length $T > 0$ which represents the rainy season, the recruitment of healthy leaves occurs at rate Λ . Uredospores are deposited on all leaves at rate ν . Since the conditions are favourable during the rainy season, they germinate with efficiency rate ω and the healthy leaves become infected leaves. All leaves undergo natural mortality with baseline rate μ and the infected leaves have an additional mortality rate d due to the disease. Uredospores are produced by infected leaves at rate γ and lose their ability to infect coffee leaves at constant rate μ_U . Healthy and infected leaves produce the berries with constant rates δ_S and δ_I , respectively and $\delta_S > \delta_I$. At the end of the production period, harvest occurs instantaneously and we consider that the dry

5.4. CONTROL OF THE COFFEE LEAF RUST

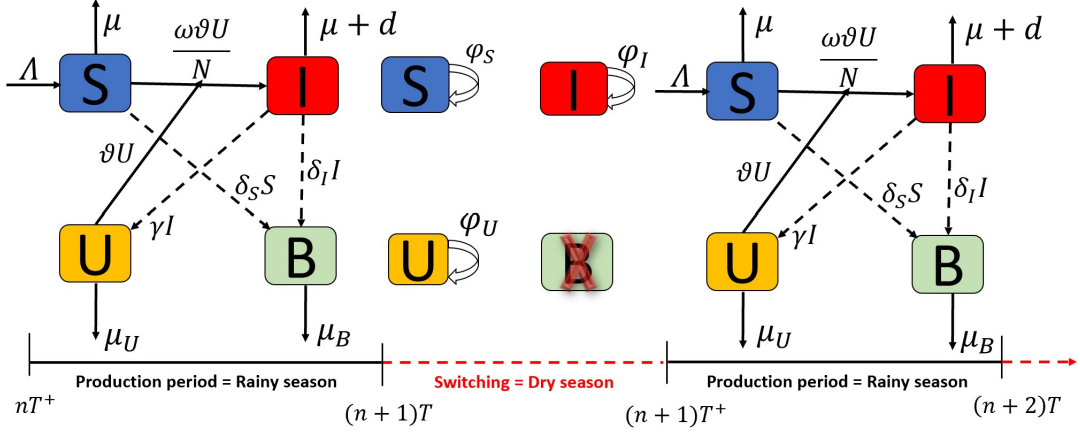


Figure 5.4: Diagram of the CLR multi-seasonal model. Model equations are given in system (5.11). State variables are: healthy branches (S), infectious branches (I), uredospores (U) and berries (B). T corresponds to the length of rainy season and n the year number.

season or non-production period can be summarised in a discrete time event due to the slow growth of leaves during that period. The impact of harvest and dry season reduces the number of healthy leaves, infected leaves and uredospores with rates φ_S , φ_I and φ_U respectively. Using the fact that uredospores lose their ability to infect quickly, we assume that φ_U is very close to 0. The representation of this evolution in the coffee plantation over a multi-year period, gives the multi-seasonal model, given in Figure 5.4, with the continuous dynamics during the rainy season and switching event for the dry season. Note however that this model is not CLR-coffee tree specific. It could hold for any pathogen spreading through spores (mostly fungi), infecting perennial fruit trees in a seasonal environment. Up to a correct calibration of the parameters, and verifying that this simplified form is not too simple for the considered dynamics. In Djuikem et al. (2022), we have identified a positively invariant region

$$G = \left\{ (S, I, U, B) \in \mathbb{R}_+^4 \mid S(t) + I(t) \leq \frac{\Lambda}{\mu}, U(t) \leq \frac{\gamma\Lambda}{\mu(\nu + \mu_U)}, \right. \\ \left. B(t) \leq \frac{\Lambda(\delta_S + \delta_I)}{\mu\mu_B} \right\}$$

for system (5.11) by upper-bounding the dynamics, and then followed the methodology exposed in Chapter 3 on system (5.11) without the berry dynamics, by first identifying the periodic disease-free solution (PDFS) $X^T(t) = (S^T(t), 0, 0)$ with

$$S^T(t) = \frac{\Lambda}{\mu} \left[1 - \frac{(1 - \varphi_S)e^{\mu T}}{e^{\mu T} - \varphi_S} e^{-\mu(t-nT)} \right]. \quad (5.12)$$

and then considering the linearization of the system around that solution which yields

$$\tilde{X}(nT^+) = \text{diag}(\varphi_S, \varphi_I, \varphi_U) e^{AT} \tilde{X}((n-1)T^+). \quad (5.13)$$

with $X = (S, I, U)$, $\tilde{X} = X - X^T$ and

$$A = \begin{pmatrix} -\mu & 0 & -\omega\nu \\ 0 & -(\mu + d) & \omega\nu \\ 0 & \gamma & -(\nu + \mu_U) \end{pmatrix}.$$

5. Epidemiological modelling for tropical agriculture

Local asymptotic stability of the PDFS ensues from stability conditions on discrete system (5.13) obtained through Jury conditions (Wang, 2012):

$$\mathcal{R} = \frac{\varphi_I}{2\beta} \left[(\beta + k_1 - k_2)e^{\lambda_1 T} + (\beta - k_1 + k_2)e^{\lambda_2 T} \right] < 1 \quad (5.14)$$

with

$$\begin{cases} k_1 = \mu + d, & k_2 = \nu + \mu_U, \\ \alpha = k_1 + k_2, & \beta = \sqrt{(k_1 - k_2)^2 + 4\gamma\omega\nu}, \\ \lambda_1 = -\frac{\alpha}{2} - \frac{\beta}{2} \text{ and } \lambda_2 = -\frac{\alpha}{2} + \frac{\beta}{2}. \end{cases}$$

The global aspect comes from the observation that the (I, U) subsystem is cooperative, and can be upper-bounded by the linearised system, whose equilibrium is globally asymptotically stable. From Kamke's theorem Coppel (1965), we then have global asymptotic stability of $X^T(t)$. We then set ourselves in an introduction context similar to that of Chapter 3: we want to introduce Λ_p hyperparasites P per production season to control the CLR dynamics and release them over the year in m batches of $\frac{\Lambda_p}{m}$ individuals, and identify, for a given Λ_p , what the best choice of m is. We suppose that the hyperparasite consumes the uredospores, which results in the following (U, P) dynamics during the rainy season:

$$\begin{cases} \dot{U} = \gamma I - (\nu + \mu_U)U - aP \frac{U}{K + U}; \\ \dot{P} = eaP \frac{U}{K + U} - \mu_P P. \end{cases} \quad (5.15)$$

Also, we can model the introduction process and the dry season for the hyperparasite through the following discrete events:

$$\begin{aligned} \text{Predator releases for } j \in \{1, \dots, m-1\}: & \quad P\left(nT + \frac{j}{m}T^+\right) = P\left(nT + \frac{j}{m}T\right) + \frac{\Lambda_P}{m}; \\ \text{Dry season and initial predator release:} & \quad P(nT^+) = \varphi_P P(nT) + \frac{\Lambda_P}{m}; \end{aligned} \quad (5.16)$$

We conducted a stability analysis through the usual linearization around the periodic disease free solution, that lead us to the integration of a system in the form $\dot{X}_p = A(t)X_p$ so that, as opposed to what we obtained in (5.13), we cannot use the matrix exponential of $A(t)$ and instead need to take a semi-numerical approach as we did in Ghosh et al. (2015). Through that, we saw that, in case of low mortality rate μ_p of the hyperparasite, $m = 1$ should be favoured (one release per year), while in the case of high mortality rate $m \rightarrow +\infty$ should be preferred, that is an almost continuous hyperparasite introduction. This is explained by the fact that, when the mortality rate is low, a large unique release ensures a quick reduction of the CLR population and the introduced hyperparasites survive over the long run, while if the mortality rate is high, such a unique release would initially be efficient, but the hyperparasite population would quickly disappear and allow for the CLR to rise back. The effect of release frequency is illustrated in Figure 5.5, where we see that $m = 5$ ensures CLR eradication while $m = 1$ does not.

The last aspect of Clotilde's thesis concerns developments on the stability analysis of a model of CLR-coffee tree dynamics that is structured in stage of the host (young J_x and mature M_x) and epidemiological status (healthy X_S , latent X_L , infectious X_I or dry leaves X_R), as well as

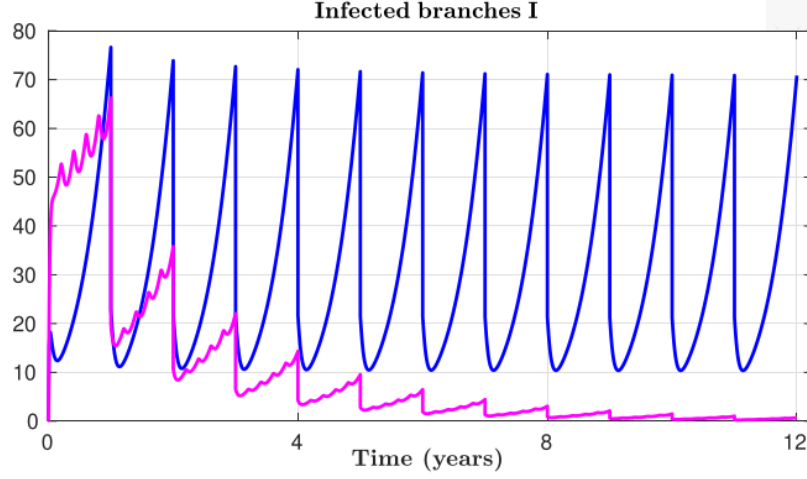


Figure 5.5: Impact of release frequency on the stability for high predator mortality rate $\mu_P = 0.1/\text{day}$. Dynamics of infected branches I for parameter values for $m = 1$ (blue curve) and $m = 5$ (magenta curve)

uredospores U and coffee berries B . This yields a large model

$$\left\{ \begin{array}{l} \dot{J}_S = r_0 M_1 - r_1 M J_S - \frac{\omega_1 \nu U}{J+M} J_S - (\beta + \mu_J) J_S, \\ \dot{J}_L = \frac{\omega_1 \nu U}{J+M} J_S - (\beta + \theta + \mu_J) J_L, \\ \dot{J}_I = \theta J_L - (\beta + \alpha + \mu_J) J_I, \\ \dot{M}_S = \beta J_S - \frac{\omega_2 \nu U}{J+M} M_S - \mu_M M_S, \\ \dot{M}_L = \beta J_L + \frac{\omega_2 \nu U}{J+M} M_S - (\theta + \mu_M) M_L, \\ \dot{M}_I = \beta J_I + \theta M_L - (\alpha + \mu_M) M_I, \\ \dot{M}_R = \alpha M_I - (\mu_M + d) M_R, \\ \dot{U} = \gamma_1 J_I + \gamma_2 M_I - (\nu + \mu_U) U, \\ \dot{B} = \delta_1 M_S + \delta_2 M_L + \delta_3 M_I + \delta_4 M_R - \mu_B B, \end{array} \right. \quad (5.17)$$

for which we analyze the existence and stability of equilibria, yielding bifurcation analysis indicating on what parameters the practitioner can act to limit the expansion of the pathogen.

5.5 Collaborators

These results were obtained with Suzanne Touzeau (INRAE and Biocore) and Samuel Bowong (Université Yaoundé 1, Cameroon), in the context of EPITAG. We all co-supervised Israël Tankam Chedjou, Yves Fotso Fotso and Clotilde Djuikem, with the additional supervision of Ludovic Maillert and Jean-Jules Tewa (Université Yaoundé 1, Cameroon) for Israël, and Berge Tsanou (Université de Dschang) for Yves.

5.6 Representative paper

The following paper presents the main results of section 5.3 and develops analytical and numerical results for the optimal control of the CBB population. :

J32 - Y. Fotso Fotso, S. Touzeau, B. Tsanou, S. Bowong, F. Grogard, Modelling and optimal strategy to control coffee berry borer, *Mathematical Methods in the Applied Sciences*, Wiley,

5. Epidemiological modelling for tropical agriculture

2021. (<https://dx.doi.org/10.1002/mma.7726>).

See Appendix F for the complete paper.

6

Ongoing works and perspectives

My current and future works are in the footsteps of what my research has been up to now. With the exception of the chemostat that was discussed in Chapter 2, all other aspects should see further developments in the coming years. As already stated, I will be heading the new Inria team Maches, that will be created at the end of this year or at the beginning of the next. In this team, there will be researchers of Inria, CNRS (Institut de Pharmacologie Moléculaire et Cellulaire) and INRAE (Institut Sophia Agrobiotech), working on modelling and control at the cell level and in agroecosystems. Maches will come from the splitting of the Biocore team between researchers working on oceanography and bioreactors, and our future group. Hence, I will probably be less involved in work concerning the bioreactor, though it is not ruled out.

I will still be working on feedback control as exposed in Chapter 1; however, constraints might not be the main driver of the complexity in my future works. As my initial formation in control theory tells me, feedback control is most of the time the most robust way of controlling a system. However, when the system is nonlinear, it quickly becomes difficult to design. My most recent developments of control law have mostly been the design of controls in the open-loop form, such as the optimal control results that we have obtained, mainly in Section 5. Open-loop control laws are notoriously less robust than closed-loop ones; however, as stated earlier, we can transform an open-loop optimal control into feedback control by setting it into a Model Predictive Control framework that regularly recomputes the solution of the optimal control problem on the basis of the measurements (Propoi, 1963).

My ongoing and future works now mainly map onto Chapter 3-5 of this thesis.

6.1 Introductions for crop protection

Outside of EPITAG, I currently do not have an ongoing research topic that exactly maps Chapter 3 where biological control is understood as relying on the release of predators or parasites of the pest. However, we currently have two research projects on the Sterile Insect Technique (CeratiTIS Corse - 2019-2023, and SuzuKIISS:ME - 2022-2025). These projects are at the inter-

6. Ongoing works and perspectives

face between academic research and applications as professional agricultural organisations are partners. They concern the control of two types of fruit flies (*Ceratitis capitata* and *Drosophila suzukii*) that are pests of citrus fruits, peaches, apricots, plums, grapes on the one hand and red fruits in greenhouses on the other. The Sterile Insect Technique consists in the massive release of sterile males of a given pest species, obtained through irradiation, in order to reduce the reproductive potential of the population (Knipling, 1955). Matings between wild females and sterile males produce unviable offspring; this technique would then be especially efficient if females only mate once as, in this case, mating with a sterile male would totally remove any offspring from the mated female. For example, *Drosophila suzukii* is known to mate at most twice, with the sperm of the first male being at the origin of most offspring, which is close to that hypothesis (Chen et al., 2022). Note however that monogamy leaves the crop exposed to incoming already inseminated females upon which the local sterile males would have no effect (Barclay, 2005).

Up to now, we have developed models in the framework of Kévan Rastello and Marine Courtois' internships in 2021, concerning *Ceratitis capitata*, and we currently work on modelling for *Drosophila suzukii* in Crésus Kounoudji's internship in 2022. Kévan's model aimed at representing the multi-year dynamics with impulses representing the simplified winter-dynamics where only a small proportion ϕ of the larvae survive:

$$\begin{cases} \dot{L} = \gamma \frac{M}{k+M} \frac{1}{1+\beta F} F - rL - \mu_L L, \\ \dot{F} = r(1-p)L - \mu_F F, \\ \dot{M} = rpL - \mu_M M. \end{cases} \quad \begin{cases} L((n+1)T) = \phi L(nT + \tau), \\ F((n+1)T) = 0, \\ M((n+1)T) = 0. \end{cases}$$

where L, F and M are the larvae, males and females of *Ceratitis*. The probability of giving offspring for a female is given by $\frac{M}{k+M} \frac{1}{1+\beta F}$ where the first factor is linked to the mating probability and the second one to the competition between the females for access to the fruits where they lay their eggs. Also, r is the larval emergence rate, p is the sex ratio, T is the duration of a year, and τ the duration of the season that is favourable to the fruit flies.

Marine's extension explicitly considered the presence of sterile males and short circuited the larva phase to give

$$\begin{cases} \dot{S} = -\mu_S S + \sigma \\ \dot{F} = -\mu_F F + r(1-p) \frac{M+\epsilon\eta S}{k+M+\eta S} \frac{1}{1+\beta F} F \\ \dot{M} = -\mu_M M + rp \frac{M+\epsilon\eta S}{k+M+\eta S} \frac{1}{1+\beta F} F \end{cases}$$

where S is the density of sterile males and σ their release rate. We see here how the presence of sterile males can impact the wild insect dynamics. It occurs through the $\frac{M+\epsilon\eta S}{k+M+\eta S}$ mating probability. Initially considering $\epsilon = 0$ and $\eta = 1$, the S at the denominator reduces the mating probability of a female with a fertile male because the total number of males $M + S$ is larger, so that the fertile males are diluted. Parameters η and ϵ modulate that impact. Indeed, η is usually smaller than 1 as it represents some form of desirability/fitness of the sterile males relatively to the fertile males; it is usually less than 1 as they have undergone some irradiation. Parameter ϵ represent some residual fertility among the "sterile" males, as it is not always possible to irradiate enough to obtain perfectly sterile males while keeping these males fit enough so that they have a chance to reproduce.

We have obtained preliminary results on these models, but this will be the focus of more extensive work in the framework of Marine Courtois's PhD thesis starting in octobre 2022 that

6.2. RESISTANCE DEPLOYMENT, PRIMING AND SEASONALITY

will especially analyse, through modelling, the impact of different phenomena on the efficiency of SIT: polyandry of the females, the trade-off between sterilization efficiency and male fitness, the presence of females in the releases, or the potential damage that the females that have mated with sterile males can anyway produce on the fruits.

6.2 Resistance deployment, priming and seasonality

In Coraly Soto’s master thesis, we have considered exactly the situation described in Section 4.2 from Clin et al. (2021), except that we added seasonality. Model (4.3) runs during the cropping season, with $\alpha = 0$ since no harvesting takes place during that time of the year, and we suppose that survival forms are produced by the pathogen that stays in the environment during the winter, and re-infect the clean crop that is re-planted at the beginning of the next cropping season. We observed that, if fitness cost for the RB-variants only is present during the cropping season, the results are identical to those of Pauline. If a fitness cost is added to the overwintering capacity of the RB-variants, things change more. We also considered planting resistant plants that are already primed, which could be done by spraying spores of avirulent pathogens on the resistant plants, as studied in (Calonnec et al., 1996), or by elicitor spraying (Tidbury et al., 2012).

These results are currently in their initial developments, and will be pursued during the final months of Pauline Clin’s PhD thesis or subsequently. They currently lack a more systematic exploration of the possible configurations, as well as sensitivity analyses to the various parameters. Also, Coraly’s internship aimed at putting only the first result of Pauline’s thesis into a seasonal framework. The other results, concerning the mixtures of n different hosts carrying different resistance genes, will need to be put in a seasonal framework to extend them from perennial tropical crops to annual plants in temperate regions.

An other important aspect of our future works on resistance is exposed in the opinion note Saubin et al. (2021), that has been published in “Molecular Ecology” with a consortium of researchers with whom we have (re-)submitted an ANR research project in 2022. The objective of this collaboration between modellers that are specialists in epidemiological/evolutionary modelling and biologists that study the molecular aspects of resistance breakdown, is to introduce information on the genetic dynamics of resistance breakdown in epidemiological models, and so obtain population genetics models that will inform resistance deployment to limit damage and curtail resistance breakdown.

6.3 Epidemiological modelling for tropical agriculture

The EPITAG associate team, that initiated this topic, has been extended until 2024. Through the three PhD theses that we co-supervise(d), we considered three important crop-pest pairs whose economic impact on often poor countries is major. Two of the these have been completed and Clotilde Djuikem’s thesis will be defended on January 5th, 2023.

After some stalling of the collaboration due to the covid pandemic, new collaboration avenues are however open, with two students who will be coming to Sophia Antipolis from february to april with the support of the INRAE-TSARA program (Transformer les Systèmes Alimentaires et l’Agriculture par la Recherche en partenariat avec l’Afrique) and the French embassy in Cameroon:

6. Ongoing works and perspectives

- Aurélien Kambeu-Youmbi who is pursuing a PhD thesis under the supervision of Berge Tsanou at the University of Dschang since 2020. His PhD work does not necessarily target a specific plant-pest ecosystem, but develops a framework for the inclusion of budgetary aspects in the fight against a generic pest through the use of ... pesticides. He has written a model with his supervisor, and we have given comments. We hope we will be able to make the last adjustments to his model when he comes so that it can result in something relevant that will be worth publishing.
- Frank Kemayou-Mangwa is starting his PhD thesis under the supervision of Samuel Bowong at the University of Douala. His PhD work concerns the development of an age-structured model of the banana/plantain-radopholus similis pathosystem (with only the age of the banana plant taken into account). As he is currently starting his PhD thesis, his model is very preliminary.

6.4 Perspectives

These were ongoing or almost ongoing works that are directly in the tracks of what I have done previously. Within the Macbes project, we aim at going further in the developments aimed at expanding the control of pests and pathogens through ecologically friendly methods. I will pursue two tracks in the next years:

- The first one concerns plant-pest interactions. Except in the epidemiological context of Chapter 5, I have brushed on that topic mainly in the context of Audrey Lebon's thesis. This resulted in the paper Lebon et al. (2014) about the overcompensation plants are capable of due to attacks by herbivores: in some situations the presence of herbivores triggers compensation mechanisms that result in more plant biomass than if the attack had not occurred. In future works, we will more readily include the plant compartment when considering pests in order to have estimates of their impact on crop yield. We will do that through ecophysiological modelling in which we will represent the impact of the presence of the pests on plant physiology, by evaluating for instance water and carbon cycle and photosynthesis. This approach will be at the core of the starting PhD thesis of Joseph Penlap that considers the impact of root nematodes on fruit plants.
- The other theme should wrap all the topics of this manuscript together, feedback control and crop protection. Indeed, I argued that feedback control was not relevant for crop protection as online measurements are not available and cropped plants lose too much value if we do not intervene before damages or pests can be spotted. The latter, which is especially true in flower culture, is much less so for fruits, as long as the pests do not damage the fruits. The relevance of feedback control then hinges on the availability of online measurements. The use of aerial photographs to detect diseases was already talked about in Colwell (1956) as the diseases could have a visible effect on the plants; however, nowadays, the information on the disease can be tracked through RGB, spectral or thermal sensors as diseases have effects on the color, chemical composition, gaseous exchanges,... of the plants. The objective of this prospective research avenue would be to integrate such measurements in a feedback loop in which biocontrol agents release timing and quantities is computed as a function of the measurements.

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Curriculum Vitae

A.1 Identity

Last name : GROGNARD	First Name : Frédéric David Gilbert
Date of birth : 28 août 1973	Place of birth : Uccle (Belgium)
Nationalities : Franch, Belgian	
Address:	Inria. BIOCORE team. 2004 route des Lucioles. 06902 Sophia Antipolis.
Website:	http://www-sop.inria.fr/members/Frederic.Grognard/
Keywords:	dynamical systems, ordinary differential equations, population dynamics, control, plant epidemiology biological control, evolution, resistance durability.

A.2 Formation

1992-1997 Université catholique de Louvain [Louvain-la-Neuve, Belgium] Engineer in applied mathematics

Thesis: Nested linear low-gain design for semiglobal stabilization of feedforward systems (Supervisors: R. Sepulchre, G. Bastin and L. Praly)

1997-2001 Université catholique de Louvain [Louvain-la-Neuve, Belgique] PhD in Applied Sciences

Thèse: Control of constrained systems: closed-loop, open-loop, and hybrid solutions (Supervisors: R. Sepulchre, G. Bastin).

A.3 Professionnal experience

10/97- 09/01 Fonds National de la Recherche Scientifique: Aspirant F.N.R.S. at CESAME (UCL). Collaborator of Université de Liège, Service Systèmes (10/99-09/01).

A. Curriculum Vitae

10/01- 09/02 Institut National Polytechnique de Grenoble: Post-doctoral fellowship at Laboratoire d'Automatique de Grenoble. Grant from the NACO2 Research Training Network of European Commission.

10/02- 10/02 Visiting researcher at CESAME (UCL).

11/02- 12/02 Inria Sophia-Antipolis: Post-doctoral fellowship in the COMORE project-team. Grant of the TELEMAT project (Telemonitoring and advanced telecontrol of high yield wastewater treatment plants).

01/03-12/04 Inria Sophia-Antipolis: second class researcher (CR2) in the COMORE project-team.

01/05-08/18 Inria Sophia-Antipolis: first class researcher (CR1) in the COMORE project-team. and then the BIOCORE project-team.

09/18-12/21 Inria Sophia-Antipolis: normal class researcher (CRCN) in the BIOCORE project-team.

01/22-... Inria de l'Université Côte d'Azur: Hors Classe researcher (CRHC) in the BIOCORE project-team.

A.4 Teaching

2004-2011 "Control for biological systems" in the Biological Oceanography master (Paris VI university): 3h/year

2005 "Modelling, control and observation of biological systems" (ISIA - Mines de Paris): 11h

2007-... "Mathematics for biology" to MAM4 students at Polytech'Nice (Applied Mathematics and Modelling track, 2nd year of engineering) : 18h/year

2010-... "Ordinary differential equations" to MAM3 students at Polytech'Nice (Applied Mathematics and Modelling track, 1st year of engineering) : 13h lessons and 26h exercises.

2019-... "Elements of mathematical modelling" in the MSc RISKS - MSc Environmental Hazards and Risks Management de l'Université Côte d'Azur: 18h lessons and 18h exercises.

2019-... Co-head of the MSc RISKS, with Dennis Fox.

A.5 Supervision

Post-doctoral fellows:

1. Andrei R. Akhmetzhanov (2009-2011 - 15 months): Adaptive behavior in a seasonal consumer-resource dynamic (co-supervision L. Mailleret and P. Bernhard)
2. Ivan (Y)egorov (2016-2017 - 12 months): ESS strategies for biotrophic pathogens (co-supervision F. Halkett, L. Mailleret and P. Bernhard).

Theses:

A.5. SUPERVISION

1. Sapna Nundloll (2006-2010, Université de Nice Sophia Antipolis, ED STIC, co-supervision -50%- with L. Mailleret; director J.-L. Gouzé) Dos and don'ts in augmentative biological control: insights from mathematical modelling;
2. Pierre Masci (2007-2010, UNS ED STIC, co-director -50%-; director O. Bernard), Control and optimization of ecosystems in bioreactors for bioenergy production;
3. Mickaël Teixeira-Alves (2009-2013, UNS ED STIC, director; co-supervision -50%- with L. Mailleret), Indirect interactions between prey: modelling and influence of the behavior of a common predator;
4. Audrey Lebon (2011-2014, Univ. Montpellier II ED SIBAGHE, co-supervision -25%- with L. Mailleret; Directeur Y. Dumont), Coupled plants-pests-natural enemies modelling in a biological control context;
5. Elsa Rousseau (2012-2016, UNS ED STIC; co-supervision -20%- with B. Moury, L. Mailleret, F. Fabre; director O. Bernard), Impact of genetic drift and selection on the durability of plant resistance to viruses.
6. Nicolas Bajoux (2013-2017, UNS ED STIC; co-supervision -50%- with L. Mailleret; director J.-L. Gouzé), Influence of density dependence in impulsive models of population dynamics.
7. Israël Tankam Chedjou (2015-2021, Université de Yaoundé 1 - Cameroon, co-supervision -40%- with L. Mailleret, S. Touzeau; direction: J.-J. Tewa), Modeling, analysis and control of plantain plant-parasitic nematodes.
8. Yves Fotso Fotso (2017-2022, Université de Dschang - Cameroon, co-supervision -50%- with B. Tsanou et S. Touzeau; direction S. Bowong), Modeling, analysis and control of coffee berry borers.
9. Clotilde Djuikem (2019-2023, Université Côte d'Azur, co-supervision -50%- with S. Touzeau; direction J.-L. Gouzé), Modelling and control of perennial plant phytopathogens.
10. Joseph Penlap (2022-..., Université Côte d'Azur, co-direction -33%- with V. Baldazzi and S. Touzeau)

Theses individual monitoring committees:

1. Méline Saubin (2019-2022, Université de Lorraine), supervision F. Halkett and P. Frey.
2. Pauline Clin (2020-2022, Université de Rennes 1), supervision F. Hamelin, D. Andrivon and L. Mailleret.
3. Christos Bountzouklis (2020-..., Université Côte d'Azur); supervision D. Fox and E. di Bernardino.

Master internships¹:

1. Guillaume Salicis (M2 INSA Rouen, 2004), Examples of Gene Regulation Models (co-supervision J.-L. Gouzé);

¹L3 indicates a License 3 internship or 1st year of engineering study, duration 1 month; M1 indicates an internship of Master 1 or 2nd year of engineering study, duration 3 months; M2 indicates an internship of Master 2 or 3rd year of engineering study, duration 6 months

A. Curriculum Vitae

2. Kolayinka Bouraïma (M2 Univ. Orsay, 2005), Study of Models of Gene Regulation Networks (co-supervision J.-L. Gouzé);
3. Sapna Nundloll (M2 Imperial College, 2006), The effect of harvest on biological control (co-supervision L. Mailleret);
4. Pierre Masci (M2 Polytech'Nice Sophia, 2007), Selection of species of microorganisms by controlled competition (co-supervision O. Bernard);
5. Jia Zhu (M1 INSA Toulouse, 2008), Enrichment and immigration in an intra-guild predation model (co-supervision L. Mailleret);
6. Adrien Morvan (M1 Polytech'Nice Sophia, 2009), Optimal consumption/reproduction strategy for crop pests (co-supervision L. Mailleret);
7. Elodie Girard (M1 INSA Lyon, 2010), Modeling pest spread in fragmented environments (co-supervision L. Mailleret & V. Lemesle);
8. Aurore Lebrun (M1 Polytech'Nice Sophia, 2010), Modeling the propagation of a mutation during the spatial expansion of a population (co-supervision L. Mailleret & T. Guillemaud);
9. Elsa Rousseau (M2 INSA Lyon, 2011), Design and study of a model for the sustainable management of virus-resistant plant varieties in a landscape (co-supervision V. Lemesle, L. Mailleret, F. Fabre & J. Coville);
10. Audrey Lebon (M2 Supagro, 2011) Development of a plant-pest model in the context of biological control (co-supervision Y. Dumont - CIRAD & L. Mailleret);
11. Nicolas Bajoux (M1 Polytech'Nice Sophia, 2012), Inundative biological control and the Allee effect in predators (co-supervision L. Mailleret);
12. Perside Gbehounou (M1 Polytech'Nice Sophia, 2012), Modeling the evolution of viral diseases in plants in an agricultural landscape (co-supervision L. Mailleret & F. Fabre);
13. Nicolas Bajoux (M2 Polytech'Nice Sophia, 2013), Influence of density dependence in impulsive models of population dynamics (co-supervision L. Mailleret, G. Robledo Veloso - Universidad de Chile);
14. Mélanie Bonneault (M1 INSA Lyon, 2015), Design and study of a model for the sustainable management of virus-resistant plant varieties in an agricultural landscape (co-supervision E. Rousseau & L. Mailleret);
15. Julien Guégan (M1 Polytech'Nice Sophia, 2017), Evolution of life history traits of phytopathogenic fungi (co-supervision L. Mailleret);
16. Olivier Faure (M1 Polytech'Nice Sophia, 2017), Augmentative Biological Control - optimizing natural enemies deployment (co-supervision L. Mailleret);
17. Pauline Clin (M2 Université de Rennes 1, 2018), Acquired systemic resistance, varietal mixtures and evolutionary epidemiology of plant-pathogen interactions (co-supervision F. Hamelin - Agrocampus Ouest);
18. David Davtian (M1 Université Côte d'Azur, 2018), Multi-agent modeling for the study and optimization of biological introductions (co-supervision L. Mailleret).
19. Jessica Gourdon (L3 Polytech'Nice Sophia, 2020), Optimization of containment for the fight against COVID-19 (co-supervision L. Mailleret).

A.6. COLLABORATIONS AND PROJECTS

20. Marine Courtois (M1 Biodiversité, Ecologie et Evolution, 2021), Modeling for the sterile insect technique to control the fruit fly (co-supervision L. Mailleret, S. Touzeau, L. Vanoudenhove).
21. Kevan Rastello (M1 Modélisation des systèmes écologiques, Université de Rennes 1, 2021). Control for sterile insect technique to control fruit fly (co-supervision L. Mailleret, S. Touzeau, L. Vanoudenhove).
22. Jan-Luka Fatras (L3 Sorbonne Université, 2021), Optimization of fallow distribution for banana plantations (co-supervision S. Touzeau).
23. Coraly Soto (M1 Université Côte d’Azur, 2021), Consideration of plant immunity in the context of the deployment of resistant plants in seasonal agrosystems (co-supervision L. Mailleret).
24. Crésus Kounoudji (M1 Aix-Marseille Université, 2022), Modeling population dynamics of *Drosophila suzukii* (co-supervision L. Mailleret, S. Touzeau, L. Vanoudenhove).

End of semester projects for Polytech’Nice ²

1. 06/2012: Spatio-temporal optimization for biological control (with L. Mailleret, 4 students)
2. 01/2016: Analysis, simulation and optimization of a stochastic population introduction process (with L. Mailleret, V. Calcagno et N. Bajeux, 4 students)
3. 06/2019: Mathematical and computer modeling of the sterile insect technique (with L. Mailleret, 3 students)
4. 06/2020: Construction and calibration of an epidemiological model of COVID-19 (with L. Mailleret, 3 students).

End of studies project for Polytech’Nice ³

1. 09-2021-02/2022: C. Soto, Differentiated fitness costs in the context of the deployment of resistant plants in seasonal agrosystems, (with L. Mailleret).

A.6 Collaborations and Projects

European projects:

- TELEMAT (Tele-monitoring and Advanced Tele-control of High-Yield Wastewater Treatment Plants: 2002-2005);
- HYGEIA (Hybrid Systems for Biochemical Network Modeling and Analysis: 2006-2008)

Bilatéral actions:

- PAI Tournesol project (Belgium, communauté française) “Dynamic modeling and stability of dynamic networks”, with CESAME, Université catholique de Louvain, Belgique (2004), coordinator.

²3 week full-time projects with MAM4 students

³6 month part-time project for a MAM5 student

A. Curriculum Vitae

- PULSPOP project "PULses in Spatial POPulation dynamics" with Indo-French Centre for Applied Mathematics (IFCAM), with Institut Sophia Agrobiotech and National Institute of Technology, Meghalaya, India (2016-2017)
- EPITAG with Cameroon (see Inria financing).

ACI/ANR

- MathResoGen, Mathematical methods for the identification of critical actors in biochemical processes regulated by a gene network (ACI IMPBIO 2004-2006),
- Shamash, Production of lipid biofuels by microalgae (ANR Bioénergies, 2007-2009);
- Symbiose, Study and Optimization of Microalgae-Anaerobic Bacteria Coupling for Biological Energy Production from Primary Biomass and Organic Waste (ANR Bioénergies, 2009-2011);
- Gemco, Model reduction, experimental validation, and control for the gene expression machinery in *E. coli* (ANR Blanc, 2010-2013);
- Facteur 4, Non-GMO microalgae performance enhancement (ANR Bio-Matières et Energies, 2012-2015).
- Purple Sun, coupling the production of microalgae with photovoltaic panels (ANR-13-BIME-004: 2013-2017).
- Funfit, trait-based approach linking individual fitness of fungal plant pathogens to ecological strategies (ANR Blanc, 2013-2018), **co-coordination** with P. Frey (biologist of INRAE Nancy).
- Maximic: design and implementation of control strategies in a bacterium to maximize its production of a high value-added product (2018-2021).
- SuzuKIISS:ME, Managing *Drosophila* SuzuKII with Super Sterile Insects: Maturation and Efficiency (partners CBGP, CTIFL, INRAE, Université Côte d'Azur, 2022-2025) - AAP Ecophyto maturation.
- Submitted in 2022: Endurance (ENhanced DURability AgaiNst Crop Enemies - *responsible of WP*) and BEEP (Behavioural Epidemiology and Evolution of Plant Pathogens).

Inria

- Coordination of Color projects funded by Inria Sophia Antipolis for the initiation of new collaborations: Lutins&Co (Biological control, interactions between and within guilds and ecology, partners INRA Sophia Antipolis and I3S-CNRS, 2007) and Erbacé (Evolution of Resistances of Bio-aggressors during their Expansion, partners CIRAD and INRA Avignon, 2010).
- Associated team EPITAG (Epidemiological Modeling and Control for Tropical Agriculture, 2017-2024) between Biocore and mathematics laboratories in Cameroon. Funding for the missions of co-supervised Cameroonian students.

INRA(E) Participation in several projects funded by the SPE (Plant Health) department of INRA(E):

- 2007-2009: IA2L (Antagonistic interactions between auxiliaries: consequences for biological control) with INRA Sophia Antipolis

A.7. RESPONSIBILITIES

- 2009-2011: RBHS (Role of biodiversity and spatio-temporal heterogeneities in the distribution of pests and their natural enemies in biological regulation phenomena) with INRA Sophia Antipolis
- 2010-2012: Eco-Tuta (Ecology of communities in agro-ecosystems and implications for the biological control of an invasive species: the case of *Tuta absoluta* on tomato) with INRA Sophia Antipolis
- 2011-2013: Propagules (Effect of different components of propagule pressure on the success of establishment of a biological control aid) with INRA Sophia Antipolis.
- 2012-2014: Spatial dynamics (Integration of behavioral and demographic approaches to the spatial dynamics of insect populations) with INRA Sophia Antipolis and Agro-campus Ouest.
- 2017-2019: ABCD (Augmentative Biological Control; optimizing natural enemies Deployment) with INRA Sophia Antipolis.
- 2019-2021: Immune (Immunity and Mathematical Modeling to Unify Epidemiology) with Agrocampus Ouest.

Participation in the Metacarpe project (Modelling the evolution of life history traits related to the aggressiveness of biotrophic parasitic fungi: application to the rust-poplar pathosystem) funded by the SPE-GAP-EFPA-EA departments (2009-2012).

Participation in the "Take Control" project, "Deployment strategies of plant quantitative resistance to take control of plant pathogen evolution," of the PRESUME call for projects of the INRA SMAch Metaprogram.

Agropolis Coordination of the project "Dynamics and evolution of life history traits in plant pathogens and pests" funded by the Agropolis foundation (partners CIRAD, INRA Nancy, INRA Rennes, INRA Sophia, 2009-2010).

Ecophyto • Project-call "Territorial levers to reduce the use and risks associated with phytopharmaceuticals". Project "CeratiTIS Corsica - Territorial Management of Ceratitis in Corsica by the Sterile Insect Technique." (partners AREFLEC, FAO/IAEA, Tragsa, INRA, CIRAD, GREDEG, CTIFL, 2019-2023)

- Project-call "How to combine alternative operational levers to synthetic plant protection products for integrated crop protection?". CACOLAC project - COncceptual Framework for the analysis of combinations of Agroecological Levers (INRAE PACA partners, Paris Institute of Ecology and Environmental Sciences, 2023-2026).

Ministry of Agriculture Representative of Inria in UMT FIORIMED (Unité Mixte Technologique) centered on horticulture (2015-...).

A.7 Responsibilities

Reviewer for journals in Control (Automatica, IEEE Transactions on Automatic Control,...), Applied Mathematics (Nonlinear Analysis: Real World Applications,...) and Mathematical Biology (Journal of Mathematical Biology,...)

Participation in a jury (Maitre de Conférence position at University of Nice for teaching in botany and modelling, 2012)

A. Curriculum Vitae

Evaluation for the Italian Research and University Evaluation Agency (2012)

Member of the Council of the Doctoral School of Life and Health Sciences of the University of Nice (2012-2017)

Member of the Committee for the allocation of post-doctoral fellowships and delegations to Inria Sophia Antipolis (2013-2019).

Member of the Steering Committee of the Academy 3 of the University Côte d'Azur, Space, Environment, Risks and Resilience, (2015-...);

Member of the Specialized Scientific Commission "Mathematics, Bioinformatics and Artificial Intelligence" (CSS-MBIA) in charge of the individual evaluation of INRA researchers (2015-...);

Co-head (with Dennis Fox) of the MSc Environmental Hazards and Risks Management at the Université Côte d'Azur (2019-...)

Member of the scientific council of the Agroecosystems department (Agronomy and environmental sciences for agroecosystems) of INRAE (2020-...).

Head of the Inria Maches project-team (Modelling and Control of Biological and Ecological Systems, 2023-...)

A.8 Publications

My publications are available on HAL https://haltools.inria.fr/Public/afficheRequetePubli.php?idHal=frederic-grognard&CB_auteur=oui&CB_titre=oui&CB_article=oui&langue=Anglais&tri_exp=typdoc&tri_exp2=annee_publi&tri_exp3=date_publi&ordre_aff=TA&Fen=Aff&css=../css/VisuRubriqueEncadre.css or through my website.

A.8.1 Peer-reviewed journal papers

J1 F. Grognard, R. Sepulchre, G. Bastin, "Global stabilization of feedforward systems with exponentially unstable Jacobian linearization" *Systems & Control Letters*, vol. 37, no. 2, pp. 107-115, 1999. ([https://dx.doi.org/10.1016/S0167-6911\(99\)00011-0](https://dx.doi.org/10.1016/S0167-6911(99)00011-0))

J2 F. Grognard, F. Jadot, L. Magni, G. Bastin, R. Sepulchre, V. Wertz, "Robust stabilization of a nonlinear cement mill model", *IEEE Trans. on Automatic Control*, vol. 46, no. 4, pp. 618-623, 2001. (<https://dx.doi.org/10.1109/9.917663>)

J3 F. Grognard, R. Sepulchre, G. Bastin, "Improving the performance of low-gain designs for bounded control of linear systems", *Automatica*, vol. 38, no.11, pp. 1777-1782, 2002. ([https://dx.doi.org/10.1016/S0005-1098\(02\)00086-9](https://dx.doi.org/10.1016/S0005-1098(02)00086-9))

J4 F. Grognard, C. Canudas de Wit, "Design of orbitally stable zero-dynamics for a class of nonlinear systems", *Systems & Control Letters*, vol. 51, no.1, pp. 89-103, 2004. ([https://dx.doi.org/10.1016/S0167-6911\(03\)00209-3](https://dx.doi.org/10.1016/S0167-6911(03)00209-3))

J5 F. Grognard, Y. Chitour, G. Bastin, "Equilibria and stability analysis of a branched metabolic network with feedback inhibition," *Networks and Heterogeneous Media*, vol. 1, no.1, pp. 219-239, 2006. (<https://dx.doi.org/10.3934/nhm.2006.1.219>)

A.8. PUBLICATIONS

- J6 F. Grognaud, O. Bernard, "Stability analysis of a wastewater treatment plant with saturated control," *Water Science & Technology*, vol. 53, no.1, pp. 149-157, 2006. (<https://dx.doi.org/10.2166/wst.2006.017>)
- J7 F. Grognaud, F. Mazenc and A. Rapaport, "Polytopic Lyapunov functions for persistence analysis of competing species," *Discrete and Continuous Dynamical Systems-Series B*, vol. 8, no. 1, pp. 73-93, 2007. (<https://dx.doi.org/10.3934/dcdsb.2007.8.73>)
- J8 S. Nundloll, L. Mailleret, F. Grognaud, "The effect of partial crop harvest on biological pest control," *Rocky Mountains Journal of Mathematics*, vol. 38, no 5, pp. 1633-1661, 2008. (<https://dx.doi.org/10.1216/RMJ-2008-38-5-1633>)
- J9 L. Mailleret, F. Grognaud, "Global stability and optimisation of a general impulsive biological control model," *Mathematical Biosciences*, vol. 221-2, pp. 91-100, 2009. (<https://dx.doi.org/10.1016/j.mbs.2009.07.002>)
- J10 S. Nundloll, L. Mailleret, F. Grognaud, "Two models of interfering predators in impulsive biological control," *Journal of Biological Dynamics*, Vol. 4, pp. 102-114, 2010. (<https://dx.doi.org/10.1080/17513750902968779>)
- J11 S. Nundloll, L. Mailleret, F. Grognaud, "Impulsive biological control with intra-specific predator competition: global stability and convergence," *Bulletin of Mathematical Biology*, vol. 72, pp.2113-2138, 2010. (<https://dx.doi.org/10.1007/s11538-010-9531-6>)
- J12 A.R. Akhmetzhanov, F. Grognaud, L. Mailleret, "Optimal life-history strategies in seasonal consumer-resource dynamics," *Evolution*, vol. 65, no 11, p. 3113-3125, 2011. (<https://dx.doi.org/10.1111/j.1558-5646.2011.01381.x>)
- J13 G. Robledo, F. Grognaud, J.-L. Gouzé, "Global stability for a model of competition in the chemostat with microbial inputs," *Nonlinear Analysis: Real World Applications*, vol. 13, pp. 582-598, 2012. (<https://dx.doi.org/10.1016/j.nonrwa.2011.07.049>)
- J14 V. Calcagno, L. Mailleret, E. Wajnberg, F. Grognaud, "How optimal foragers should respond to habitat changes: a reanalysis of the Marginal Value Theorem," *Journal of Mathematical Biology*, Springer Verlag (Germany), vol. 69, no 5, pp.1237-1265, 2014. (<https://dx.doi.org/10.1007/s00285-013-0734-y>)
- J15 F. Grognaud, A.R. Akhmetzhanov, O. Bernard, "Optimal strategies for biomass productivity maximization in a photobioreactor using natural light," *Automatica*, vol. 50 (2), pp.359-368, 2014. (<https://dx.doi.org/10.1016/j.automatica.2013.11.014>)
- J16 A. Lebon, L. Mailleret, Y. Dumont, F. Grognaud, "Direct and apparent compensation in plant-herbivore interactions," *Ecological Modelling*, vol. 290, pp.192-203, 2014. (<https://dx.doi.org/10.1016/j.ecolmodel.2014.02.020>)
- J17 V. Calcagno, F. Grognaud, F.M. Hamelin, E. Wajnberg, L. Mailleret, "The functional response predicts the effect of resource distribution on the optimal movement rate of consumers," *Ecology Letters*, vol. 17, no 12, pp.1570-1579, 2014. (<https://dx.doi.org/10.1111/ele.12379>)
- J18 F. Grognaud, P. Masci, E. Benoît, O. Bernard, "Competition between phytoplankton and bacteria: exclusion and coexistence," *Journal of Mathematical Biology*, vol. 70 (5), pp. 959-1006, 2015. (<https://dx.doi.org/10.1007/s00285-014-0783-x>)

A. Curriculum Vitae

- J19 B. Ghosh, F. Grogard, L. Mailleret, Natural enemies deployment in patchy environments for augmentative biological control, vol. 266 (1), pp.982-999, 2015. (<https://dx.doi.org/10.1016/j.amc.2015.06.021>)
- J20 N. Bajeux, F. Grogard, L. Mailleret, Augmentative biocontrol when natural enemies are subject to Allee effects, *Journal of Mathematical Biology*, Springer Verlag (Germany), vol. 74 (7), pp.1561 - 1587, 2017. (<https://dx.doi.org/10.1007/s00285-016-1063-8>)
- J21 L. Tamisier, E. Rousseau, S. Barraillé, G. Nemouchi, M. Szadkowski, L. Mailleret, F. Grogard, F. Fabre, B. Moury, A. Palloix, Quantitative trait loci in pepper control the effective population size of two RNA viruses at inoculation, *Journal of General Virology*, Microbiology Society, 98 (7), pp.1923 - 1931, 2017. (<https://dx.doi.org/10.1099/jgv.0.000835>)
- J22 E. Rousseau, B. Moury, L. Mailleret, R. Senoussi, A. Palloix, V. Simon, S. Valière, F. Grogard, F. Fabre, Estimating virus effective population size and selection without neutral markers, *PLoS Pathogens*, Public Library of Science, 13 (11), pp.1-25, 2017. (<https://dx.doi.org/10.1371/journal.ppat.1006702>)
- J23 E. Rousseau, L. Tamisier, F. Fabre, V. Simon, M. Szadkowski, O. Bouchez, C. Zanchetta, G. Girardot, L. Mailleret, F. Grogard, A. Palloix, B. Moury, Impact of genetic drift, selection and accumulation level on virus adaptation to its host plants, *Molecular Plant Pathology*, Wiley, 19 (12), pp.2575-2589, 2018. (<https://dx.doi.org/10.1111/mpp.12730>)
- J24 N. Bajeux, F. Grogard, L. Mailleret, Influence of the components of propagule pressure, Allee effects, and stochasticity on the time to establish introduced populations, *Journal of Theoretical Biology*, Elsevier, 471, pp.91-107, 2019. (<https://dx.doi.org/10.1016/j.jtbi.2019.03.012>)
- J25 E. Rousseau, M. Bonneault, F. Fabre, B. Moury, L. Mailleret and F. Grogard, Virus epidemics, plant-controlled population bottlenecks and the durability of plant resistance, *Phil. Trans. R. Soc. B*, 374, 2019. (<http://doi.org/10.1098/rstb.2018.0263>)
- J26 I. Yegorov, F. Grogard, L. Mailleret, F. Halkett, P. Bernhard, A dynamic game approach to uninvadable strategies for biotrophic pathogens, *Dyn. Games Appl*, 10, pp.257-296, 2020. (<https://dx.doi.org/10.1007/s13235-019-00307-1>).
- J27 V. Calcagno, F. Hamelin, L. Mailleret, F. Grogard, How optimal foragers should respond to habitat changes: on the consequences of habitat conversion, *Theoretical Ecology*, Springer, 13 (2), pp.165-175, 2020. (<https://dx.doi.org/10.1007/s12080-019-00437-7>)
- J28 I. Tankam Chedjou, S. Touzeau, L. Mailleret, J.-J. Tewa, F. Grogard, Modelling and control of a banana soilborne pest in a multi-seasonal framework, *Mathematical Biosciences*, Elsevier, 322, pp.108324, 2020. (<https://dx.doi.org/10.1016/j.mbs.2020.108324>)
- J29 P. Clin, F. Grogard, L. Mailleret, F. Val, D. Andrivon, F.M. Hamelin. Taking advantage of pathogen diversity and immune priming to minimize disease prevalence in host mixtures: a model, *Phytopathology*, American Phytopathological Society, 2021. (<https://dx.doi.org/10.1094/PHYTO-09-20-0429-R>).

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- J30 I. Tankam Chedjou, F. Grogard, J.-J. Tewa, S. Touzeau. Optimal and sustainable management of a soilborne banana pest. *Applied Mathematics and Computation*, Elsevier, 397, pp.125883, 2021. (<https://dx.doi.org/10.1016/j.amc.2020.125883>).
- J31 I. Tankam Chedjou, F. Grogard, J.-J. Tewa, S. Touzeau. When and how to fallow: first steps towards banana crop yield improvement through optimal and sustainable control of a soilborne pest, *Journal of Interdisciplinary Methodologies and Issues in Science (JIMIS)*. 2021. (<https://dx.doi.org/10.18713/JIMIS-120221-8-4>)
- J32 Y. Fotso Fotso, S. Touzeau, B. Tsanou, S. Bowong, F. Grogard, Modelling and optimal strategy to control coffee berry borer, *Mathematical Methods in the Applied Sciences*, Wiley, 2021. (<https://dx.doi.org/10.1002/mma.7726>).
- J33 C. Djuikem, F. Grogard, R. Tagne Wafo, S. Touzeau, S. Bowong, Modelling coffee leaf rust dynamics to control its spread *Mathematical Modelling of Natural Phenomena*, EDP Sciences, 2021. (<https://dx.doi.org/10.1051/mmnp/2021018>).
- J34 P. Clin, F. Grogard, D. Andrivon, L. Mailleret, F.M. Hamelin, Host mixtures for plant disease control: benefits from pathogen selection and immune priming, *Evolutionary applications*, 2022. (<https://dx.doi.org/10.1111/eva.13386>).
- J35 Y. Fotso Fotso, S. Touzeau, B. Tsanou, F. Grogard, S. Bowong, Mathematical modelling of a pest in an age-structured crop model: the coffee berry borer case, *Applied Mathematical Modelling*, 2022. (<https://doi.org/10.1016/j.apm.2022.05.042>).
- J36 M. Saubin, C. Louet, L. Bousset, F. Fabre, I. Fudal, F. Grogard, F.M. Hamelin, L. Mailleret, S. Stoeckel, S. Touzeau, B. Petre, F. Halkett, Improving sustainable crop protection using population genetics concepts, *Molecular Ecology*, 2022, (<https://doi.org/10.1111/mec.16634>)

A.8.2 Peer-reviewed conference proceedings

- A1 F. Grogard, R. Sepulchre, G. Bastin, L. Praly, "Nested linear low-gain design for semiglobal stabilization of feedforward systems", *IFAC NOLCOS'98 Symposium*, Enschede, 1998), pp. 830-835.
- A2 F. Grogard, R. Sepulchre, G. Bastin, "Slow control for global stabilization of feedforward systems with exponentially unstable Jacobian linearization, 37th IEEE Conference on Decision and Control, Tampa, 1998, pp. 1452-1457.
- A3 F. Grogard, R. Sepulchre, G. Bastin, "Improved performance of low-gain control for linear systems with saturated input", *MTNS 2000*, Perpignan, 2000.
- A4 F. Grogard, R. Sepulchre, G. Bastin, "Control of linear systems with affine constraints: a gain-scheduling approach", 39th IEEE Conference on Decision and Control, Sydney, 2000, pp. 4785-4790.
- A5 F. Grogard, R. Sepulchre, J. De Dona, "Dynamical systems that compute time-optimal switchings", *IFAC NOLCOS 2001 Symposium*, St Petersburg, 2001.

A. Curriculum Vitae

- A6 F. Grognaard, R. Sepulchre, "Global stability of a continuous-time flow which computes time-optimal switchings", 40th IEEE Conference on Decision and Control, Orlando, 2001, pp. 3826-3831.
- A7 F. Grognaard, C. Canudas de Wit, "Design of orbitally stable zero-dynamics for a class of nonlinear systems", 41st IEEE Conference on Decision and Control, Las Vegas, 2002.
- A8 J. Perram, A. Shiriaev, C. Canudas-de-Wit, F. Grognaard, "Explicit formula for a general integral of motion for a class of mechanical systems subject to holonomic constraint", 2nd IFAC Workshop on Lagrangian and Hamiltonian Methods for Nonlinear Control, Sevilla, 2003.
- A9 Y. Chitour, F. Grognaard, G. Bastin, "Stability analysis of a metabolic model with sequential feedback inhibition," First Multidisciplinary International Symposium on Positive Systems: Theory and Applications (POSTA 2003), Rome, 2003.
- A10 F. Grognaard, R. Sepulchre, "Computation of time-optimal switchings for linear systems with complex poles", European Control Conference 2003, Cambridge, 2003.
- A11 F. Grognaard, Y. Chitour, G. Bastin, "Equilibria and stability analysis of a branched metabolic network with feedback inhibition," 9th International Symposium on Computer Applications in Biotechnology (CAB9), Nancy, France, 2004.
- A12 F. Grognaard, O. Bernard, "Stability analysis of a wastewater treatment plant with saturated control," 6th International Symposium on Systems Analysis and Integration Assessment (WATERMATEX 2004), Beijing, China, 2004.
- A13 F. Grognaard, J.-L. Gouzé, "Positive control of Lotka-Volterra systems," 16th IFAC World Congress, Prague, Czech Republic, 2005.
- A14 F. Grognaard, F. Mazenc, A. Rapaport, "Polytopic Lyapunov functions for the stability analysis of persistence of competing species", joint 44th IEEE Conference on Decision and Control and European Control Conference 2005, Sevilla, Spain, 2005.
- A15 I. Ndiaye, J.-L. Gouzé, F. Grognaard, "Etude d'un petit réseau métabolico-génétique par des techniques de systèmes monotones", RIAMS 2006 (Réseaux d'interactions : analyse, modélisation et simulation), Lyon, France, 2006..
- A16 A. Akhmetzhanov, P. Bernhard, F. Grognaard and L. Mailleret "Reproduction dynamics in a differential game between foraging predators and hiding preys", 13th International Symposium on Differential Games and Applications. Wroclaw, Pologne, 2008.
- A17 P. Masci, O. Bernard, F. Grognaard, "Continuous selection of the fastest growing species in the chemostat", 17th IFAC World Congress, Seoul, Korea, 2008.
- A18 S. Nundloll, L. Mailleret, F. Grognaard, "Global Stability in a General Impulsive Biological Control Model with Harvest", 17th IFAC World Congress, Seoul, Korea, 2008.
- A19 A. Akhmetzhanov, P. Bernhard, F. Grognaard, L. Mailleret, "Competition between foraging predators and hiding preys as a nonzero-sum differential game", International Conference on Game Theory for Networks (GameNets 2009), Istanbul, Turkey, 2009.

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- A20 P. Masci, O. Bernard, F. Grognaard, E. Latriille, J.-B. Sorba and J.P. Steyer, "Driving competition in a complex ecosystem: application to anaerobic digestion", European Control Conference 2009, Budapest, Hungary, 2009.
- A21 A. Akhmetzhanov, F. Grognaard, L. Mailleret and P. Bernhard, "Join forces or cheat: evolutionary analysis of a consumer-resource system". Fourteenth International Symposium on Dynamic Games and Applications. Banff, Canada, 2010.
- A22 P. Bernhard, F. Grognaard, L. Mailleret and A. Akhmetzhanov, "ESS for life-history trait of cooperating consumers facing cheating mutants", Fourteenth International Symposium on Dynamic Games and Applications. Banff, Canada, 2010.
- A23 P. Masci, F. Grognaard and O. Bernard, "Microalgal biomass surface productivity optimization based on a photobioreactor model," 11th International Symposium on Computer Applications in Biotechnology (CAB), Leuven, Belgium, 2010.
- A24 F. Grognaard, A. Akhmetzhanov, P. Masci, O. Bernard, "Optimization of a Photobioreactor Biomass Production Using Natural Light", 49th IEEE Conference on Decision and Control, Atlanta, USA, 2010.
- A25 A. Lebon, Y. Dumont, F. Grognaard, L. Mailleret, "Modelling Plant Compensatory Effects in Plant-Insects dynamics," 4th IEEE International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications (PMA), Shanghai, 2012.
- A26 F. Grognaard, J. Rault, J.-L. Gouzé, "Positive control for global stabilization of predator-prey systems", IFAC NOLCOS 2013 Symposium, Toulouse, 2013.
- A27 N. Bajeux, F. Grognaard, L. Mailleret, "Introduction strategies for biological control agents subject to Allee effects," 21st International Symposium on Mathematical Theory of Networks and Systems, Groningen, Netherlands, 2014.
- A28 F. Grognaard, "Feedback stabilization of predator-prey systems for impulsive biological control," 19th IFAC World Congress, Cape Town, South Africa, 2014.
- A29 I. Yegorov, F. Grognaard, L. Mailleret, F. Halkett, Optimal resource allocation for biotrophic plant pathogens, IFAC 2017 - 20th World Congress of the International Federation of Automatic Control, Toulouse, France, 2017.
- A30 Y. Fotso Fotso, F. Grognaard, B. Tsanou, S. Touzeau, "Modelling and control of coffee berry borer infestation" CARI'2018 - 14. Colloque Africain sur la Recherche en Informatique et en Mathématiques Appliquées, Oct 2018, Stellenbosch, South Africa
- A31 I. Tankam Chedjou, S. Touzeau, F. Grognaard, L. Mailleret, J.-J. 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
- A32 C. Djuikem, A. Yabo, F. Grognaard, S. Touzeau, Mathematical modelling and optimal control of the seasonal coffee leaf rust propagation, ADHS 2021 - 7th IFAC Conference on Analysis and Design of Hybrid Systems, IFAC, Jul 2021, Brussels, Belgium (online conference).

A. Curriculum Vitae

- A33 Y. Fotso Fotso, B. Tsanou, S. Bowong, S. Touzeau, F. Grogard, Optimal impulsive control of coffee berry borers in a berry age-structured epidemiological model, CARI'2022 - Colloque Africain sur la Recherche en Informatique et en Mathématiques Appliquées, Sep 2022, Tunis, Tunisia.

A.8.3 Presentations at international conferences without proceedings

I did the talk for C17, C24, C25 et C32 - otherwise, it is usually the PhD student or post-doc who did.

- C1 M. Teixeira-Alves, L. Mailleret, F. Grogard, Optimal foraging in Leslie-Gower predator-prey models with alternative food, Conference on Computational and Mathematical Population Dynamics, 2010, Bordeaux, France
- C2 A.R. Akhmetzhanov, F. Grogard, L. Mailleret, P. Bernhard, ESS versus cooperative behaviour in a consumer-resource model, Conference on Computational and Mathematical Population Dynamics, 2010, Bordeaux, France
- C3 A.R. Akhmetzhanov, F. Grogard, L. Mailleret, P. Bernhard, ESS versus cooperative behavior in a consumer-resource model, Workshop on Game Theory for Finance, Social and Biological Sciences, 2010, Warwick, United Kingdom
- C4 M. Teixeira-Alves, L. Mailleret, F. Grogard, Optimal foraging predators in Leslie Gower models with alternative prey, European Conference on Mathematical and Theoretical Biology, 2011, Krakow, Poland
- C5 A.R. Akhmetzhanov, P. Bernhard, F. Grogard, L. Mailleret, Dynamic game for optimal resource allocation of annual plants and grazing consumers, European Conference on Mathematical and Theoretical Biology, 2011, Krakow, Poland
- C6 V. Calcagno, F. Grogard, L. Mailleret, E. Wajnberg, Habitat quality and optimal foraging: the Marginal Value Theorem revisited, First Joint Congress on Evolutionary Biology (Evolution 2012), 2012, Ottawa, Canada
- C7 B. Ghosh, F. Grogard, L. Mailleret, Optimal natural enemies deployment in patchy environments for augmentative biological control, 9th European Conference on Mathematical and Theoretical Biology, Jun 2014, Goteborg, Sweden
- C8 L. Mailleret, V. Lemesle, F. Hamelin, V. Calcagno, F. Grogard, Modelling populations subjected to pulsed taking regimes, 9th European Conference on Mathematical and Theoretical Biology, Jun 2014, Goteborg, Sweden
- C9 E. Rousseau, J. Coville, A. Palloix, F. Fabre, L. Mailleret, B. Moury, F. Grogard, Protection of the durability of major resistance genes to plant viruses with quantitative resistance, a modeling approach, 9th European Conference on Mathematical and Theoretical Biology, Jun 2014, Goteborg, Sweden
- C10 N. Bajeux, F. Grogard, L. Mailleret, Les stratégies d'introduction d'agents de lutte biologique soumis aux effets Allee, 34ème Séminaire de la Société Francophone de Biologie Théorique, , May 2014, Saint Flour, France

A.8. PUBLICATIONS

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- C11 E. Rousseau, F. Fabre, L. Mailleret, A. Palloix, V. Simon, S. Valière, B. Moury, F. Grog-nard, Protecting the durability of major resistance genes to plant viruses with quantitative resistance, Conférence Jacques Monod, Apr 2014, Roscoff, France
- C12 E. Rousseau, F. Fabre, J. Coville, L. Mailleret, Alain Palloix, R.Senoussi, F. Grog-nard, B. Moury, Estimation of genetic drift and selection from next generation sequencing time-sampled data, SMBE Satellite meeting SMBEBA 2015, Investigating biological adaptation with NGS: data and models, 2015, Leicester, United Kingdom
- C13 L. Tamisier, E. Rousseau, S. Barraille, G. Nemouchi, M. Szadkowski, L. Mailleret, F. Grog-nard, F. Fabre, B. Moury, A. Palloix, Quantitative trait loci in pepper genome control the effective population size of two RNA viruses at inoculation, XVI-Eucarpia Capsicum and Eggplant Meeting, Sep 2016, Kecskemét, Hungary. pp.169–176
- C14 N. Bajeux, F. Grog-nard, L. Mailleret , Introduced populations in a stochastic world, European Conference on Mathematical and Theoretical Biology, Jul 2016, Nottingham, United Kingdom
- C15 E. Rousseau, B. Moury, L. Mailleret, R. Senoussi, A. Palloix, V. Simon, F. Grog-nard, S. Valiere, F. Fabre, Joint estimation of effective population size and selection coefficient without neutrel markers: method validation and application to experimental evolution of viruses, IPVE2016 - 13th International Plant Virus Epidemiology Symposium, Jun 2016, Avignon, France. pp.16
- C16 E. Rousseau, M. Bonneault, F. Fabre, B. Moury, L. Mailleret, F. Grog-nard, Genetic drift as a tool to increase the durability of plant qualitative resistance to viruses, IPVE2016 - 13th International Plant Virus Epidemiology Symposium, Jun 2016, Avignon, France. pp.135
- C17 E. Rousseau, M. Bonneault, F. Fabre, B. Moury, L. Mailleret, F. Grog-nard, Stochastic epidemiological model for the analysis of plant resistance break- down to pathogens sub- jected to genetic drift, Emerging trends in applied mathematics and mechanics (ETAMM 2016), May 2016, Perpignan, France
- C18 N. Bajeux, F. Grog-nard, L. Mailleret, V. Calcagno, Introduced populations in a stochastic world, Models in population dynamics and ecology, 2016, Marseille, France
- C19 F. Grog-nard, I. Yegorov, J. Guegan, L. Mailleret, F. Halkett, P. Bernhard, Uninvadable strategies for biotrophic pathogens, from dynamic games to adaptive dynamics 11th Euro- pean Conference on Mathematical and Theoretical Biology (ECMTB), Jul 2018, Lisbon, Portugal
- C20 Y. Fotso Fotso, S. Touzeau, S. Bowong, F. Grog-nard, L. Mailleret, B. Tsanou, Modelling and control of coffee berry borer infestation, ECMTB 2018 - 11th European Conference on Mathematical and Theoretical Biology, Jul 2018, Lisbon, Portugal
- C21 I. Tankam Chedjou, S. Touzeau, F. Grog-nard, L. Mailleret, J.-J. Tewa, An agricultural control of Radopholus similis in banana plantations, 11th European Conference on Math- ematical and Theoretical Biology (ECMTB), Jul 2018, Lisbon, Portugal

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- C22 F. Hamelin, P. Clin, F. Val, F. Grogard, Gene-for-gene epidemic models, systemic acquired resistance, and the evolution of plant parasites, 11th European Conference on Mathematical and Theoretical Biology (ECMTB), Jul 2018, Lisbon, Portugal
- C23 F. Hamelin, P. Clin, F. Val, F. Grogard, Gene-for-gene epidemic models, systemic acquired resistance, and the evolution of plant parasites, *MB²* 3rd Mathematical Biology Modelling Days of Besançon, Jun 2018, Besançon, France
- C24 F. Grogard, P. Clin, F. Val, F. Hamelin. Taking advantage of pathogen diversity and plant immunity to minimize disease prevalence. Computational and Mathematical Population Dynamics - CMPD5, May 2019, Fort Lauderdale, United States.
- C25 F. Grogard, I. Chedjou, Y. Fotso, S. Touzeau. Modelling, control, and optimization for tropical agriculture. Computational and Mathematical Population Dynamics - CMPD5, May 2019, Fort Lauderdale, United States.
- C26 I. Chedjou, S. Touzeau, F. Grogard, L. Mailleret, J.-J. Tewa. Agricultural control of *Radopholus similis* in banana and plantain plantations. International Conference on Mathematical Methods and Models in Biosciences - Biomath 2019, Jun 2019, Bedlewo, Poland.
- C27 Y. Fotso Fotso, S. Touzeau, S. Bowong, F. Grogard, L. Mailleret, B. Tsanou, Optimal control on a simple model of coffee berry borer infestation, International Conference on Mathematical Methods and Models in Biosciences - Biomath 2019, Jun 2019, Bedlewo, Poland.
- C28 C. Djuikem, F. Grogard, S. Touzeau, S. Bowong, Modelling and controlling fungus *Hemileia vastatrix*, a coffee pest, International Conference on Mathematical Methods and Models in Biosciences - Biomath 2019, Jun 2019, Bedlewo, Poland.
- C29 F. Halkett, I. Yegorov, F. Fabre, V. Ravigné, P. Frey, F. Grogard, Optimal infection dynamics in spore producing pathogens: reconciling theory with experiment for the study of host-parasite interactions, 3rd Wild Plant Pathosystems Conference, Sep 2019, Frankfurt, Germany.
- C30 C. Djuikem, F. Grogard and S. Touzeau, Impulsive model and hyperparasite-based bio-control of coffee leaf rust propagation, Conference on Mathematical Population Dynamics, Ecoepidemiology and Evolution, Apr 2021, Marseille, France (online).
- C31 P. Clin, F. Grogard, L. Mailleret and F. Hamelin, Host mixtures for plant disease control: from induced pathogen competition to the benefits of immune priming, Conference on Mathematical Population Dynamics, Ecoepidemiology and Evolution, Apr 2021, Marseille, France (online).
- C32 F. Grogard, S. Bowong, Y. Fotso Fotso, S. Touzeau, B. Tsanou, A multi-seasonal model of plant-pest interactions: the coffee berry borer, Conference on Mathematical Population Dynamics, Ecoepidemiology and Evolution, Jun 2022, Turin, Italie.
- C33 C. Djuikem, F. Grogard, S. Touzeau, Bifurcation analysis in a coffee leaf rust epidemiological model, 12th European Conference on Mathematical and Theoretical Biology (ECMTB), Sep 2022, Heidelberg, Allemagne,

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- C34 P. Clin, F. Grognaard, L. Mailleret, D. Andrivon, F.M. Hamelin, Host mixtures for plant disease control: benefits from pathogen selection and immune priming, 12th European Conference on Mathematical and Theoretical Biology (ECMTB), Sep 2022, Heidelberg, Allemagne,

A.8.4 Book chapters

- L1 Y. Chitour, F. Grognaard, G. Bastin, "Stability analysis of a metabolic model with sequential feedback inhibition " dans "Positive Systems: Theory and Applications. Proceedings of the First Multidisciplinary International Symposium on Positive Systems: Theory and Applications", L. Benvenuti, A. De Santis, L. Farina (Eds.), 2003.
- L2 F. Grognaard, C. Canudas-de-Wit, "Virtual constraints for the orbital stabilization of the pendubot," in "Nonlinear and adaptive control: theory and algorithms for the user", Ed. A. Astolfi, Imperial College Press, pp. 115-145, 2005.
- L3 L. Mailleret, F. Grognaard, "Optimal Release Policy for Prophylactic Biological Control" , in " Positive Systems Proceedings of the second Multidisciplinary International Symposium on Positive Systems: Theory and Applications (POSTA 06), Grenoble, France" , Eds. C. Commault, N. Marchand, Lecture Notes in Control and Information Sciences (LNCIS) 341, Springer-Verlag, p. 89-96, 2006.
- L4 F. Grognaard, J.-L. Gouzé, H. de Jong, "Piecewise-linear models of genetic regulatory networks: theory and example", in "Biology and control theory: current challenges", Eds. I. Queinnec, S. Tarbouriech, G. Garcia, S. Niculescu, Lecture Notes in Control and Information Sciences (LNCIS) 357, Springer-Verlag, p. 137-159, 2007.
- L5 A. R. Akhmetzhanov, L. Mailleret, F. Grognaard, P. Bernhard, "Join forces or cheat: evolutionary analysis of a consumer-resource system," Advances in Dynamic Games, Annals of the International Society of Dynamic Games, P. Cardaliaguet, R. Cressman (editors), Springer, p. 73-95, 2013.

A.8.5 Edition

- E1 "The Green Book of the Academy Space, Environment, Risk and Resilience", Editors: P.-J. Barre, C. Den Auwer, D. Fox, F. Grognaard, T. Guillot, M. Le Gourrierec, I. Manighetti, Université Côte d'Azur, 85 pp., ISBN: 978-2-9571154-0-2.

A.8.6 PhD thesis

- T1 F. Grognaard, "Control of constrained systems: closed-loop, open-loop, and hybrid solutions", Université catholique de Louvain, Louvain-la-Neuve (Belgium), October 2001, 138pp.

A. Curriculum Vitae

B

Positive control for global stabilization of predator-prey systems

A26 - F. Gognard, J. Rault, J.-L. Gouzé, "Positive control for global stabilization of predator-prey systems", IFAC NOLCOS 2013 Symposium, Toulouse, 2013. <https://doi.org/10.3182/20130904-3-FR-2041.00136>

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B. Positive control for global stabilization of predator-prey systems



Polytopic Lyapunov functions for persistence analysis of competing species

J7 - F. Gognard, F. Mazenc and A. Rapaport, "Polytopic Lyapunov functions for persistence analysis of competing species," *Discrete and Continuous Dynamical Systems-Series B*, vol. 8, no. 1, pp. 73-93, 2007. (<https://dx.doi.org/10.3934/dcdsb.2007.8.73>)

This paper can be accessed from <https://inria.hal.science/inria-00000873>

C. Polytopic Lyapunov functions for persistence analysis of competing species

D

Natural enemies deployment in patchy environments for augmentative biological control

J19 - B. Ghosh, F. Grogard, L. Mailleret, Natural enemies deployment in patchy environments for augmentative biological control, vol. 266 (1), pp.982-999, 2015. (<https://dx.doi.org/10.1016/j.amc.2015.06.021>)

This paper can be accessed from <https://hal.science/hal-01171118>

D. Natural enemies deployment in patchy environments for augmentative biological control

E

Host mixtures for plant disease control: benefits from pathogen selection and immune priming

J34 - P. Clin, F. Grogard, D. Andrivon, L. Mailleret, F.M. Hamelin, Host mixtures for plant disease control: benefits from pathogen selection and immune priming, *Evolutionary applications*, 2022. (<https://dx.doi.org/10.1111/eva.13386>).

This paper, main part and supporting information, can be accessed from <https://inria.hal.science/hal-03676499>

E. Host mixtures for plant disease control: benefits from pathogen selection and immune priming

F

Modelling and optimal strategy to control coffee berry borer

J32 - Y. Fotso Fotso, S. Touzeau, B. Tsanou, S. Bowong, F. Grogard, Modelling and optimal strategy to control coffee berry borer, *Mathematical Methods in the Applied Sciences*, Wiley, 2021. (<https://dx.doi.org/10.1002/mma.7726>).

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