

Models for Miridae, a Cocoa insect pest. Application in control strategies.*

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Abstract

Cocoa mirid, *Sahlbergella singularis*, is one of the major pests of cocoa in West Africa. It is responsible of several damages in plots. In this paper, we mainly study the dynamics of this pest and its control. Based on biological and ecological partial knowledge, we develop two cooperative mathematical models that aim to describe the time dynamics of the cocoa mirids. We first develop a cooperative stage-structured model, derived qualitative results. Then, assuming that all parameters are or not periodic, we obtain conditions that allow the persistence or not of the population along the year. Then, we derive a two-stage cooperative time-delay model, with two delays, that takes into account the nymph maturation period and the females maturation period. A sensitivity analysis is provided for both models. We illustrate our theoretical results with numerical simulations and show that the delayed system provides the best results compared to real observations. Finally, we focus on chemical control, that is commonly used in Cameroon, and compare it to a new biological control, mixing mating disrupting and trapping. We discuss the results and provide future perspectives based on this work.

Keywords: *Sahlbergella singularis*; cocoa pest; mathematical models; delays; pest control; simulation.

1 Introduction

Cacao is a cash crop mainly cultivated in African countries (Ivory Coast, Ghana, Nigeria and Cameroon) that ensures around 72% of the world production [ICCO 2016]. Cocoa (*Theobroma cacao*) is essential for the livelihood of millions of small producers in Africa especially in Cameroon [2]. African production of cocoa is seriously impacted by two important diseases the Cocoa Swollen Shoot Virus (CSSV) and the black pod rot (up to 80-90% losses) [28] and by the damage caused by two pests: *Sahlbergella singularis* and *Distantiella theobroma* known as mirid bugs or cacao capsids ([10]; [14]). These species, which originate from the forests of central Africa, have very similar

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life histories and regularly live together in cacao-based agroforestry systems [13]. In Cameroon, *Sahlbergella singularis* is nowadays the most common and the most harmful species for the production. Mirid bugs feed preferentially on *Theobroma cacao* but other species like *Cola nitida*, *Ceiba pentandra* are known to be alternative hosts when cacao resource is unavailable. The immature (five instars) and adult stages of these sucking insects used to feed on the sap of young semi-lignified branches, on plant tissues by injecting a digestive saliva, on buds and on fruits [46, 18, 15, 34]. Mirid damage on the pod are relatively superficial since the pods cortex is very thick. In general mirids attacks on the pods are characterized by black dots (feeding lesion) around the peduncle of mature pods. Indeed, there is no obvious link between the intensity of feeding lesions on mature pods and an impact on beans quality [47]. Very few losses are noted at this stage. However, lesion caused to young fruit (less than 10 cm and less than 2 months old), called cherelle, increase fruit abortion and impact directly the ongoing production [47]. This fruit stage is vulnerable to mirids attacks. Indeed, the most harmful damage that is also the less obvious to quantify is the damage caused to cocoa vegetative growth parts. Those lesions prevent sap circulation favouring leaves fall and branches death that is characteristic of mirids attacks. Extensive feeding by mirids on branches results in the degradation of the canopy of discrete groups of trees which can be up to one hundred and are referred as mirid pockets. Mirid pockets are generally located in the sunniest areas of plantations [15]. The impact of mirids on cacao tree is a long term impact as cacao is a perennial plant which can produce for more than 20 years. Damage of mirid bugs on the cocoa tree are cumulated over time and can lead to premature ageing of plantations and to the rapid death of the most severely damaged trees [17, 46, 27]. Losses due to mirids are difficult to estimate, but can reach 30 – 40% of potential production ([1, 8]) depending on the system management strategy. In fact, mirids attacks are known to be the most harmful in full sun plantations. In multi-strata and highly diversified [22, 32, 45] cacao based agroforestry system as the one that is widespread in Cameroon, shade management is a relevant option to control mirid population [15]. But shade management is a long term process that is sometimes difficult to set up for the farmers given antagonistic effects on black pod disease. Whatever the type of system considered, synthetic insecticides of the neonicotinoid family, such as λ -cyhalothrine and Imidacloprid [25, 10], are still the main input used to control these pests [37]. Since 1970, the economic threshold for phytosanitary intervention has been fixed at 0.7 mirids/tree in Cameroon [15] and 0.6 mirids/tree in Ghana [40]. These indicators based on mirid populations are however difficult to evaluate regarding the ecology of the species. In fact, it is challenging to count mirids individuals (immatures and adults) on the field since they used to hide during the day to avoid direct light. It is likely a relatively low level of mirid population can cause important damage in the plantation. Mirids do not pullulate in the plantations even during the peak period. Due to controversial effects of chemical insecticide use, alternative cocoa pest control methods have been developed including cultural management, varietal management [21], as well as semio-chemical management, using synthetic sexual pheromone traps [35] or the use of plant extracts as pesticides [10]. Considering the difficulty to estimate mirid population and to obtain long-term data on the field, the mathematical approach appears as the most relevant option to forecast the efficiency of control strategy. In that sense, the aim of this work is to develop some (generic) mathematical models of mirid population to better predict its time evolution in a plot under different management strategies. A first compartmental model, with constant or periodic parameters, is developed based on the mirid life cycle. We make theoretical analysis, a sensitivity analysis and provide numerical simulations. Then, we develop a second model, a time delayed model, based on the previous one, in order to better take into account the

developmental or maturation time in some stages. After a brief theoretical analysis, we provide numerical simulations without and with control efforts, and we discuss the results.

The paper is organized as follows. In section 2, we formulate a first ODE model considering the resource as constant or periodic function: for this model, we make a theoretical study (its global dynamical properties), a sensitivity analysis and numerical simulations. In section 3, we formulate a delayed model. After a brief study, we do some numerical simulations and we compare with the previous model without delay. In section 4, we compare chemical and biological controls and discuss their efficiency. Finally, in Section 5 we conclude and propose several experimental and theoretical studies in order to improve our knowledge and extend our work.

2 Mirids ODEs models

In order to build the models, we recall here what we know about the biology and ecology of Mirids. The life cycle of *S. singularis* is composed of three stages: egg stage, nymph stage and adult stage that develop mainly on pods either on shoots. The eggs are individually inserted into the host plant tissues [33] principally in the cortex of pods and sometimes under the bark of young shoots [26]. The incubation period of eggs is on average 15 days with a minimum of 9 days [48] and a maximum of 21 days [31] before reaching nymph stage. Mirid *S. singularis* has a very long life cycle (eggs to adults). It is on average 40 days with a minimum of 36 days [12] and a maximum of 50 days [13]. The percentage of hatching eggs is globally 96.53% as the eggs are protected in the pods cortex. During the five nymph instars, the individuals move within a cacao tree by walk to feed on the pods and shoots. The nymphs are able to feed just after the eggs hatching. Twenty five days are needed to complete the nymph development considering 5 days in average per instar [13]. Globally, the total nymph survivorship is around 68% [11]. The average daily rate of survival of the nymphs (considering all the five instars) was estimated around 98.5% (estimated using biological data). At the emergence there is on average one female for 0.71 male [13] (this gives a sex ratio $r = 1/1.71 \approx 0.58$; in fact, sex ratio varies between 0.5 and 0.6). Females *S. singularis* mate with one male 6 to 10 days after their emergence. The first eggs are observed in average 10 days after emergence, so 4 to 8 days after mating (estimated using biological data). Indeed, after this mating period females are considered as mature. On average 72.1% of immature females become mature females [12]. After the emergence, adults (males and females) fly from one cocoa tree to another ensuring the spatial dispersion of the individuals and causing the spatial distribution of the damage in the plots. It is likely the females do not lay all their eggs on the same pod. The average fecundity per female is around 50.7 larvae or 52.5 eggs and the fecundity period lasts on average 16 days [46, 27, 48, 7, 16]. The daily survival of mirids adult is around respectively 98.14% for immature females, 92.8% for mature females and 93% for males (estimated thanks to [7, 31, 48, 13, 46]). On average, 50 to 60 days are needed to obtain a new generation of mirids [13]. This long life period for an insect to grow is a key factor for the dynamic of mirid populations.

Mirids population dynamics varied greatly during the year. Density of population is likely to be influenced by pods availability on the trees and by external conditions like weather [15]. The mirid population is low on cocoa during the period from February to March. From June to July, the populations start to grow more or less rapidly. The peak of the population appears between September and November when the pods are almost mature [13, 38, 7, 39]. It is also assumed that unfavourable climatic conditions (high temperature and low pluviometry) can cause declining

fertility of females and increased mortality of individuals [15] that lead to lower mirid populations observed in plantations from November-December to June.

We now formulate a model based on the life cycle of *S. singularis*, summarized in Fig. 1. We use a stage structured model. We consider three main stages in the development of the mirid: the egg stage (E), the nymph stage (L) (nymphs and pupae) and the adult stage, subdivided into immature female (F_1), mature female (F_2) and male (M). According to the flow diagram given in

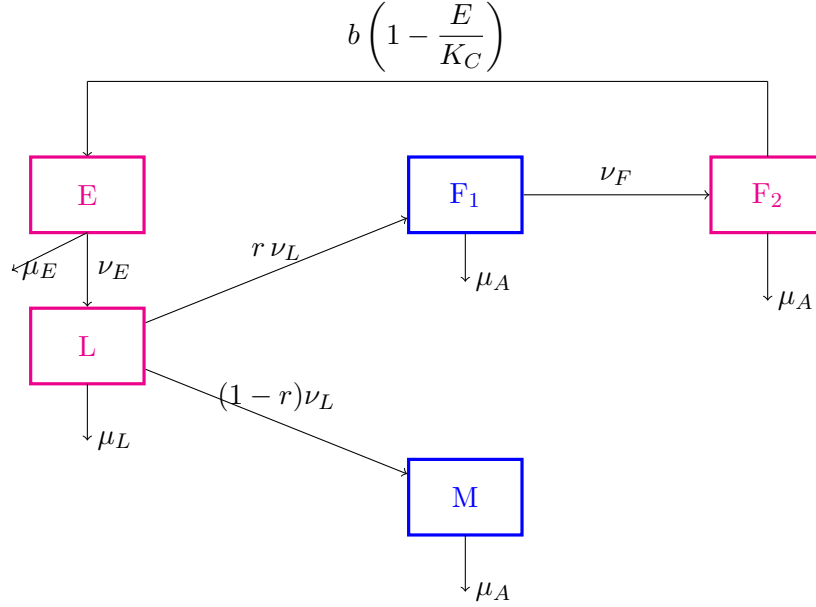


Figure 1: Life cycle of *Sahlbergella singularis*

Fig. 1, we derive the following ODES model:

$$\begin{cases} \dot{E} = b F_2 \left(1 - \frac{E}{K_C}\right) - (\nu_E + \mu_E) E, \\ \dot{L} = \nu_E E - (\nu_L + \mu_L) L, \\ \dot{F}_1 = r \nu_L L - (\nu_F + \mu_A) F_1, \\ \dot{F}_2 = \nu_F F_1 - \mu_A F_2, \\ \dot{M} = (1 - r) \nu_L L - \mu_A M, \end{cases} \quad (1)$$

with non-negative initial conditions:

$$\begin{cases} E(0) = E^0, & L(0) = L^0, & F_1(0) = F_1^0, \\ F_2(0) = F_2^0, & M(0) = M^0. \end{cases} \quad (2)$$

The biological parameters are described as follows: r is the sex ratio; b is the mean number of eggs laid by an adult female mirid per day that have emerged as nymphs, K_C is the maximal carrying capacity related to the mean daily number of pods per area (ha), μ_E , μ_L and μ_A represents respectively the eggs, nymphs and adults daily mortality rate, ν_E and ν_L are respectively the transition rate from the egg to nymph stage and the nymph to adult stage; $(1/(\nu_E + \mu_E))$ and $(1/(\nu_L + \mu_L))$ are respectively the mean time a mirid stays in the egg and nymph stage (measured in days); ν_F is the transition rate from the immature female stage to mature female stage; $1/(\nu_F + \mu_A)$ is the mean lifespan of an immature female mirid, measured in days.

The non linear term $r b F_2 \left(1 - \frac{E}{K_C}\right)$ is related to a specific behaviour of some insects species, like *Aedes* mosquito [19, 20], and also mirids, known as skip-oviposition behaviour. Indeed, according to expert's knowledge, mirids (*S. singularis*) are able to select their breeding sites. Some cocoa trees, particularly suitable for nymph development, show greater damage, which leads to the degradation of the foliage and the formation of orthotropic (or greedy) shoots [11]. Thus, if breeding sites, in a given area, already contain a lot of eggs, then females will not deposit eggs or only very few. That is why, the oviposition rate $r b F_2$ is limited by the available space in breeding sites, $\left(1 - \frac{E}{K_C}\right)$, which implies that the birth rate in the eggs compartment is modeled by the non linear term $r b F_2 \left(1 - \frac{E}{K_C}\right)$. Table 1, page 5, summarizes the parameters and their biological meaning.

| Parameters | Biological significance | Unit |
|------------|---|--------------------|
| b | Mean number of eggs laid by a mature female | days ⁻¹ |
| K_C | Maximal carrying capacity related to the mean daily number of pods per ha | |
| $1/\nu_L$ | Duration of the development of nymphs | days |
| $1/\nu_F$ | Time necessary for an immature female to become mature | days |
| μ_L | Mortality of nymphs | days ⁻¹ |
| μ_A | Mortality of adults | days ⁻¹ |
| μ_E | Mortality of eggs | days ⁻¹ |
| $1/\nu_E$ | Time necessary for an egg to become nymph | days |

Table 1: Parameters of model (1).

The right-hand side of system (1) is continuously differentiable (\mathcal{C}^1). Then, using the Cauchy-Lipschitz theorem, system (1) has a unique maximal solution. If the initial data are in \mathbb{R}_+^5 , the solutions stays in \mathbb{R}_+^5 : $E = 0$, $L = 0$, $F_1 = 0$, $F_2 = 0$ and $M = 0$ are vertical and horizontal null lines respectively. Thus, the trajectories can not cut these axes: so model system (1) is biologically well posed. It is straightforward to show that the compact

$$\Omega = \{(E, L, F_1, F_2, M) \in \mathbb{R}_+^5; E(t) \leq K_C, L(t) \leq \frac{\nu_E K_C}{\nu_L + \mu_L}, F_1(t) \leq \frac{r \nu_L \nu_E K_C}{(\nu_L + \mu_L)(\mu_A + \nu_F)}, \quad (3)$$

$$F_2(t) \leq \frac{r \nu_L \nu_F \nu_E K_C}{\mu_A(\nu_L + \mu_L)(\nu_F + \mu_A)} \text{ and } M(t) \leq \frac{(1-r) \nu_L \nu_E K_C}{\mu_A(\nu_L + \mu_L)}\}$$

is positively invariant by (1).

Now, we will derive some quantitative analysis of system (1). Let us consider the following threshold

$$\mathcal{N}_0 = \frac{r b \nu_L \nu_F \nu_E}{\mu_A(\nu_E + \mu_E)(\nu_F + \mu_A)(\nu_L + \mu_L)}. \quad (4)$$

\mathcal{N}_0 represents the mean number of adults female produced by one adult female over its lifespan. It is sometimes called the basic offspring number.

Lemma 2.1 *System (1) has two possible equilibria:*

- (i) *a trivial equilibrium $X^0 = (0, 0, 0, 0, 0)$ which always exists*

(ii) a positive equilibrium $X^* = (E^*, L^*, F_1^*, F_2^*, M^*)$, defined as follows:

$$\begin{aligned} E^* &= \frac{(\mathcal{N}_0 - 1)}{\mathcal{N}_0} K_C, \quad L^* = \frac{\nu_E}{\nu_L + \mu_L} E^*, \quad F_1^* = \frac{r \nu_E \nu_L}{(\nu_L + \mu_L)(\nu_F + \mu_A)} E^*, \\ F_2^* &= \frac{r \nu_E \nu_L \nu_F}{\mu_A(\nu_L + \mu_L)(\nu_F + \mu_A)} E^* \quad \text{and} \quad M^* = \frac{(1 - r) \nu_E \nu_L}{\mu_A(\nu_L + \mu_L)} E^*. \end{aligned} \quad (5)$$

which exists when $\mathcal{N}_0 > 1$.

It is straightforward to verify that system (1) is a cooperative system [44]. We briefly recall its definition. Let us consider an n -dimensional autonomous differential system:

$$\dot{x} = f(x), \quad x(0) = x_0 \quad (6)$$

where $\Omega \subseteq \mathbb{R}^n$ is an open subset, and f is a given vector function, i.e $f = (f)_i$, such that $f : \Omega \rightarrow \mathbb{R}^n$ is continuous. System (6) is called cooperative if for every $i, j \in \{1, 2, \dots, n\}$ such that $i \neq j$, the function $f_i(x_1, \dots, x_n)$ is monotone increasing with respect to x_j . For cooperative systems, like (6), the global asymptotic stability of an equilibrium can be studied using the following theorem:

Theorem 2.1 (see Theorem 6 [5]) *Let $a, b \in \Omega$ such that $a < b$, $[a, b] \subset \Omega$ and $f(b) \leq 0 \leq f(a)$; where $[a, b] = \{x \in \mathbb{R}^n, a_i \leq x_i \leq b_i, i = 1, \dots, n\}$. Then (6) defines a (positive) dynamical system on $[a, b]$. Moreover, if $[a, b]$ contains a unique equilibrium p then p is globally asymptotically stable on $[a, b]$.*

The dynamic of system (1) is summarized in the following theorem:

Theorem 2.2 *Assume that $(E^0, L^0, F_1^0, F_2^0, M^0) \in \Omega$.*

- (i) *When $\mathcal{N}_0 \leq 1$, the trivial equilibrium X^0 is globally asymptotically stable, which means that the mirid population will dwindle until extinction, whatever the initial population.*
- (ii) *When $\mathcal{N}_0 > 1$, the trivial equilibrium X^0 is unstable, and the positive equilibrium X^* is globally asymptotically stable, which means that the mirid population persists.*

Proof It suffices to verify the assumptions of theorem 2.1.

- (i) When $\mathcal{N}_0 \leq 1$, model system (1) has only the trivial equilibrium X^0 . By taking $a = 0$ and

$$b = \left(K_C, \frac{2\nu_E K_C}{\nu_L + \mu_L}, \frac{3r \nu_L \nu_E K_C}{(\nu_L + \mu_L)(\nu_F + \mu_A)}, \frac{4r \nu_E \nu_L \nu_F K_C}{\mu_A(\nu_L + \mu_L)(\nu_F + \mu_A)}, \frac{2(1 - r) \nu_E \nu_L K_C}{\mu_A(\nu_L + \mu_L)} \right),$$

we have $f(a) = 0$ and $f(b) \leq 0$. Thus, according to Theorem 2.1, the trivial equilibrium X^0 is globally asymptotically stable on $[0, b]$, hence on Ω when $\mathcal{N}_0 \leq 1$.

- (ii) When $\mathcal{N}_0 > 1$, there exists $\varepsilon > 0$ such that $\mathcal{N}_0 > 1 + \varepsilon$. Let E_ε sufficiently small such that

$$\begin{aligned} E_\varepsilon &\leq \varepsilon, \quad L_\varepsilon = \frac{\nu_E(1 + \varepsilon)}{(\nu_L + \mu_L)\mathcal{N}_0} E_\varepsilon, \quad F_{1\varepsilon} = \frac{r \nu_L(1 + \varepsilon)}{(\nu_F + \mu_A)\mathcal{N}_0} L_\varepsilon, \\ F_{2\varepsilon} &= \frac{(\nu_E + \mu_E)(1 + \varepsilon)^2}{b\mathcal{N}_0^2} E_\varepsilon, \quad M_\varepsilon = \frac{(1 - r) \nu_L(1 + \varepsilon)}{\mu_A \mathcal{N}_0} L_\varepsilon \end{aligned}$$

Let $b_\varepsilon = (E_\varepsilon, L_\varepsilon, F_{1\varepsilon}, F_{2\varepsilon}, M_\varepsilon)$. Then, from the right-hand side of (1) and the fact that $\mathcal{N}_0 > 1 + \varepsilon$ and $K_C \gg 1$, we deduce:

$$f(b_\varepsilon) \geq \begin{pmatrix} \varepsilon (\nu_E + \mu_E)(1 + \varepsilon)^2 \left(1 - \frac{1 + \varepsilon}{K_C}\right) E_\varepsilon \\ \nu_E \left(1 - \frac{1 + \varepsilon}{\mathcal{N}_0}\right) E_\varepsilon \\ r \nu_L \left(1 - \frac{1 + \varepsilon}{\mathcal{N}_0}\right) L_\varepsilon \\ \nu_F \left(1 - \frac{1 + \varepsilon}{\mathcal{N}_0}\right) F_{1\varepsilon} \\ (1 - r) \nu_L \left(1 - \frac{1 + \varepsilon}{\mathcal{N}_0}\right) L_\varepsilon \end{pmatrix} > 0.$$

Hence, according to Theorem 2.1, equilibrium X^* is globally asymptotically stable on $[b_\varepsilon, b]$. Since b_ε can be selected to be smaller than any $x > 0$, we have that X^* is asymptotically stable on Ω with basin of attraction $\tilde{\Omega} = \Omega \setminus \{(0, 0, 0, 0, 0)\}$. This also implies that X^0 is unstable.

2.1 Sensitivity analysis

It is important to know the relative importance of some factors that maintain or not a mirid population. We may estimate the sensitivity index of \mathcal{N}_0 with respect to a parameter p , as follows:

$$\gamma_p^{\mathcal{N}_0} = \frac{\partial \mathcal{N}_0}{\partial p} \cdot \frac{p}{\mathcal{N}_0} \quad (7)$$

Straightforward calculation leads to the following result:

$$\begin{aligned} \gamma_r^{\mathcal{N}_0} &= \gamma_b^{\mathcal{N}_0} = 1, & \gamma_{\nu_E}^{\mathcal{N}_0} &= \frac{\mu_E}{\nu_E(\nu_E + \mu_E)}, \\ \gamma_{\nu_L}^{\mathcal{N}_0} &= \frac{\mu_L}{\nu_L(\nu_L + \mu_L)}, & \gamma_{\nu_F}^{\mathcal{N}_0} &= \frac{\mu_F}{\nu_F(\nu_F + \mu_A)}, \\ \gamma_{\mu_E}^{\mathcal{N}_0} &= -\frac{1}{\nu_E + \mu_E}, & \gamma_{\mu_L}^{\mathcal{N}_0} &= -\frac{1}{\nu_L + \mu_L}, & \gamma_{\mu_A}^{\mathcal{N}_0} &= -\frac{\nu_F}{\mu_A(\nu_F + \mu_A)} \end{aligned}$$

Clearly, r and b have the strongest impact on \mathcal{N}_0 . However, this gives us only partial informations. In particular, we will now focus on the variables E , L , F_1 , F_2 and M . That is why, we derive some global sensitivity analysis using two well-known methods: the eFast and the LHS-PRCC methods. The eFast method given in Fig.2, page 9, highlights first-order effects (main effects) and total effects (main and all interaction effects) of the parameters on the Model Outputs. Complementary to the eFast method, we derived a LHS-PRCC sensitivity analysis given in Fig.3, page 10. LHS-PRCC stands for Latin Hypercube Sampling and PRCC for Partial rank correlation coefficient. These two methods give complementary information. Indeed the PRCC method provides mainly information about how the outputs is impacted if we increase (or decrease) the inputs of a specific parameter while the eFast indicates which parameter uncertainty has the greatest impact on the output variability (see for instance [36] for further explanations).

In Table 2, page 8, we provide ranges of values for the model parameters. These ranges were estimated based on the Data obtained by Babin and collaborators.

| Parameters | Range | Source |
|------------|---------------|-----------|
| r | [0.5, 0.6] | estimated |
| b | [1.5; 4] | estimated |
| K_C | [1, 10000] | estimated |
| ν_L | [1/35, 1/10] | estimated |
| ν_F | [1/10, 1/6] | estimated |
| μ_L | [1/100, 1/10] | estimated |
| μ_A | [1/100, 1/10] | estimated |
| μ_E | [1/100, 1/10] | estimated |
| ν_E | [1/10, 1/20] | estimated |

Table 2: Range of values for the parameters of system (1).

As expected, variation of the carrying capacity K_C has strong an impact on all variables, and also μ_A . For the transition rates ν_L , ν_E , ν_F , and the mortality rate μ_L , their impact is weaker, but according to the LHS-PRCC analysis, is not negligible. Thus obviously, among all parameters, the parameters K_C , μ_A , ν_L , ν_E , ν_F , and μ_L are the most important parameters to estimate. Finally, according to the sensitivity analysis method that is considered b does not have the same impact. However, we think that this is an important parameter too.

2.2 Mirid system with periodic coefficients

In this section, we consider the previous model, but with periodic time-dependent parameters, since we know that most of the parameters may depend on the environment. In fact, mirids dynamics vary greatly during the year; density of populations is likely to be influenced by pods avail ability on the trees. In [12], it is admitted that lower mirid populations observed in the plots during a certain period of the year is due to the declining fertility of females and increasing mortality of individuals. Thus it seems that development parameters (longevity, fecundity, mortality) of mirids vary depending on season. We assume that all those parameters are T -periodic functions and are bounded: below, by a non negative minimal value, and above by a positive maximal value, that is $p_{min} \leq p(t) \leq p_{max}$ for all $t \geq 0$, and $p = r, b, \mu_L, \mu_A, \mu_E, \nu_L, \nu_F, \nu_E$ or K_C . We also split the carrying capacity in two parts, $K_C(t) + C$: $K_C(t)$, the mean number of pods available for breeding, and C , the alternative breeding sites including other tree hosts, like *Cola nitida*, *Ceiba pentandra* [11]. Thus, Model (1) becomes

$$\begin{cases} \dot{E} = b(t) F_2 \left(1 - \frac{E}{C + K_C(t)} \right) - (\nu_E(t) + \mu_E(t)) E, \\ \dot{L} = \nu_E(t) E - (\nu_L(t) + \mu_L(t)) L, \\ \dot{F}_1 = r(t) \nu_L(t) L - (\nu_F(t) + \mu_A(t)) F_1, \\ \dot{F}_2 = \nu_F(t) F_1 - \mu_A(t) F_2, \\ E(0) = E^0, \quad L(0) = L^0, \quad F_1(0) = F_1^0, \quad F_2(0) = F_2^0 \end{cases} \quad (8)$$

In fact system (8) enters the family of periodic concave cooperative system with a concave non-linearity ([30],[43]).

Definition 2.1 *Let us consider a n -dimensional autonomous differential system:*

$$\dot{x} = F(t, x), \quad x \in \mathbb{R}^n \quad (9)$$

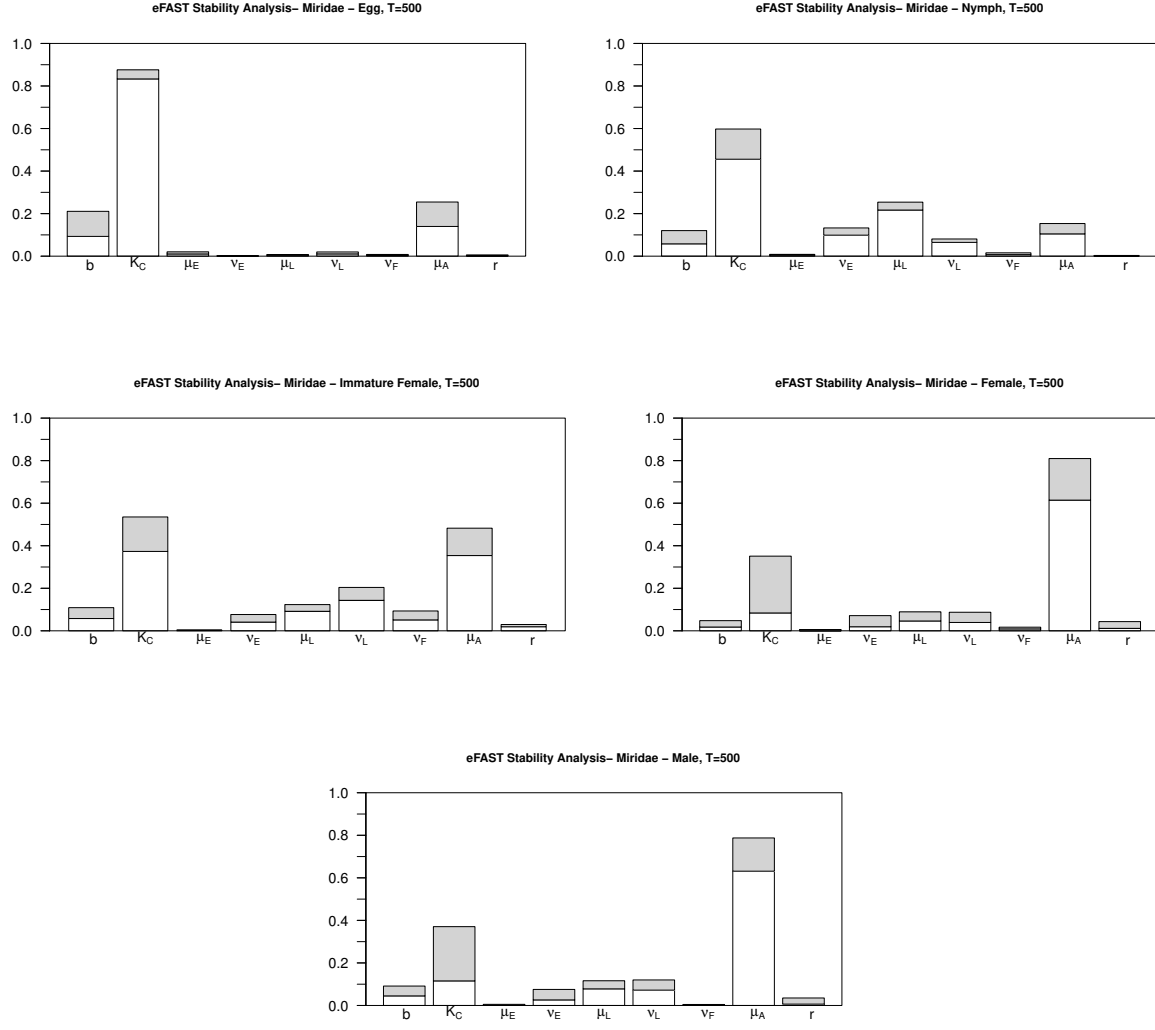


Figure 2: e-FAST Sensitivity analysis at $T = 500$. White bar: first-order effects; Sum of white and grey bars: total effect.

The system of differential equations (9) is called cooperative with concave non-linearities if

$$(i) \quad \frac{\partial F_i}{\partial x_j} \geq 0, \quad i \neq j \text{ for each } (t, x) \in \mathbb{R}_+ \times \mathbb{R}_+^n.$$

$$(ii) \quad x > y > 0 \text{ implies } D_x F(t, y) > D_x F(t, x).$$

We will use a theorem (Theorem 3.1, see appendix B) proved in [43]. We have:

$$F(t, x) = \begin{pmatrix} b(t) F_2 \left(1 - \frac{E}{C + K_C(t)} \right) - (\nu_E(t) + \mu_E(t)) E \\ \nu_E(t) E - (\nu_L(t) + \mu_L(t)) L \\ r(t) \nu_L(t) L - (\nu_F(t) + \mu_A(t)) F_1 \\ \nu_F(t) F_1 - \mu_A(t) F_2 \end{pmatrix},$$

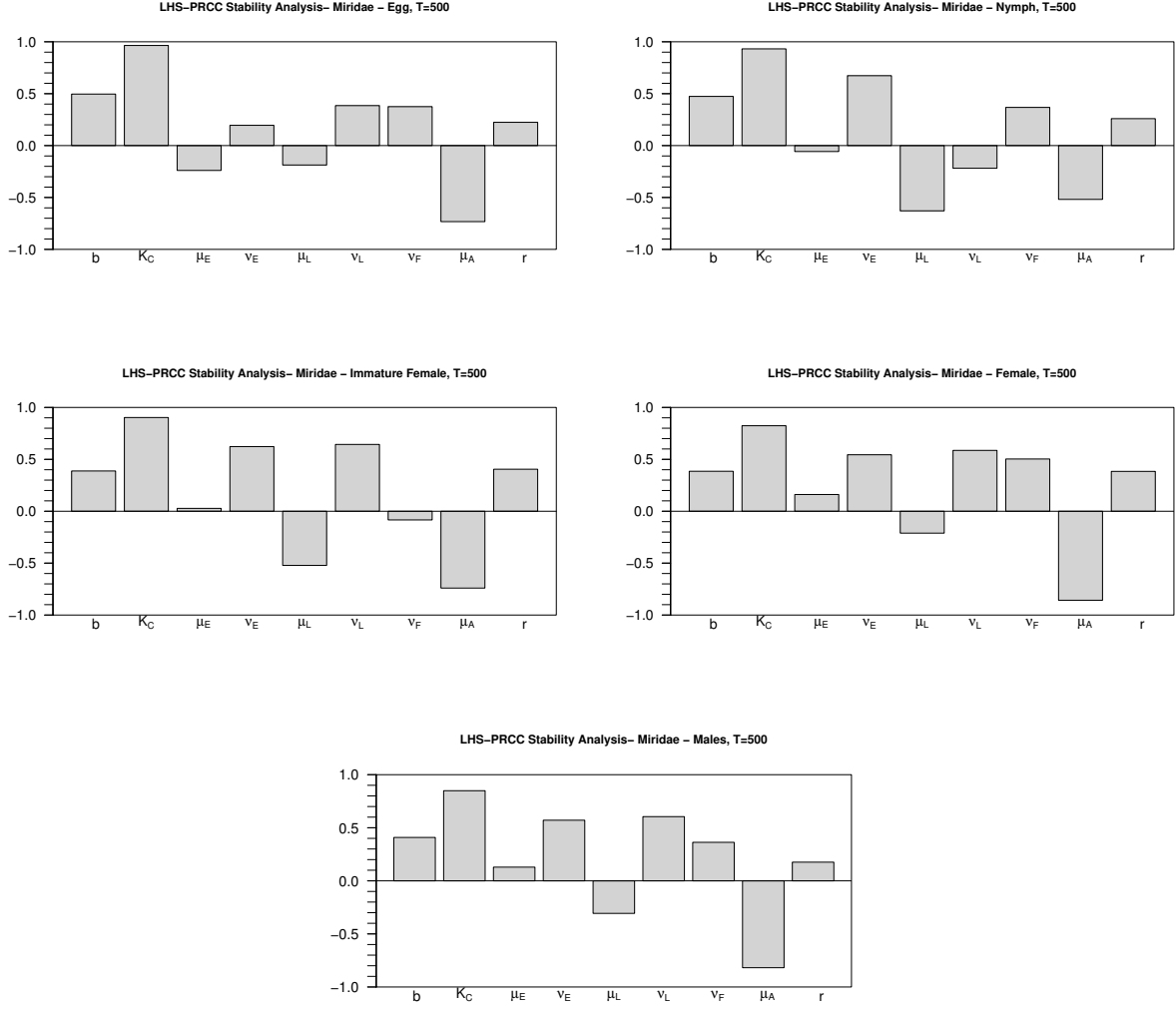


Figure 3: LHS-PRCC Sensitivity analysis at $T = 500$.

where $x = (E, L, F_1, F_2)^T$. Obviously, F is continuously differentiable and T -periodic. According to Cauchy-Lipschitz theorem, we have existence of a positive and bounded solution. Since all time-dependent parameters are positive, we verify easily property (i) in Definition 2.1.

Let us compute the Jacobian

$$D_x F(t, x) = \begin{pmatrix} -\left(\nu_E(t) + \mu_E(t) + \frac{b(t)F_2}{K_C(t) + C}\right) & 0 & 0 & b(t) \left(1 - \frac{E}{K_C(t) + C}\right) \\ \nu_E(t) & -(\nu_L(t) + \mu_L(t)) & 0 & 0 \\ 0 & r(t)\nu_L(t) & -(\nu_F(t) + \mu_A(t)) & 0 \\ 0 & 0 & \nu_F(t) & -\mu_A(t) \end{pmatrix}$$

It is straightforward to verify (ii) in Definition 2.1. In addition, $D_x F(t, x)$ is irreducible for each $(t, x) \in \mathbb{R} \times \mathbb{R}_+^n$. Thus, Theorem .1 applies to system (9) and we deduce that every solution x , with $x(t_0) \geq 0$, can be continued in $[t_0, \infty]$ with $x(t) \geq 0$ for $t \geq t_0$.

Now, let us compute $D_x F(t, 0)$, that is

$$D_x F(t, 0) = \begin{pmatrix} -(\nu_E(t) + \mu_E(t)) & 0 & 0 & b(t) \\ \nu_E(t) & -(\nu_L(t) + \mu_L(t)) & 0 & 0 \\ 0 & r(t)\nu_L(t) & -(\nu_F(t) + \mu_A(t)) & 0 \\ 0 & 0 & \nu_F(t) & -\mu_A(t) \end{pmatrix}$$

According to Theorem .1, if the Floquet multipliers of $D_x F(t, 0)$ lie inside or on the unit circle, then $\lim_{t \rightarrow \infty} x(t) = 0$. In contrary, if any Floquet multiplier lies outside the unit circle, and according to the fact that $F(t, 0) \equiv 0$ and x is a bounded solution, we deduce that system (9) has a unique non-zero T -periodic solution $x_{per}(t)$.

In general, the determination of Floquet multipliers is extremely difficult. That is why, we will now consider an additional result [30] recalled in Appendix B (see Theorem .2). This is an algebraic criterion, related to the study of $A(t) = D_x F(t, 0)$.

Let us estimate \underline{A} and \overline{A} , lower and upper bounds of Matrix $A(t)$. Using the fact that all time-dependent parameters have positive lower and upper bounds, we deduce

$$\underline{A} = \begin{pmatrix} -(\nu_{E,max} + \mu_{E,max}) & 0 & 0 & b_{min} \\ \nu_{E,min} & -(\nu_{L,max} + \mu_{L,max}) & 0 & 0 \\ 0 & r_{min}\nu_{L,min} & -(\nu_{F,max} + \mu_{A,max}) & 0 \\ 0 & 0 & \nu_{F,min} & -\mu_{A,max} \end{pmatrix}$$

and

$$\overline{A} = \begin{pmatrix} -(\nu_{E,min} + \mu_{E,min}) & 0 & 0 & b_{max} \\ \nu_{E,max} & (\nu_{E,min} + \mu_{E,min}) & 0 & 0 \\ 0 & r_{max}\nu_{L,max} & -(\nu_{F,min} + \mu_{A,min}) & 0 \\ 0 & 0 & \nu_{F,max} & -\mu_{A,min} \end{pmatrix}.$$

Then according to Theorem .2, we have to study the principal minors of $-\underline{A}$ and $-\overline{A}$. All diagonal terms of $-\underline{A}$ and $-\overline{A}$ are positive. In fact it suffices to compute $\det(-\overline{A})$ and $\det(-\underline{A})$, that is

$$\det(-\overline{A}) = -(\nu_{E,min} + \mu_{E,min})(\nu_{L,min} + \mu_{L,min})(\nu_{F,min} + \mu_{A,min})\mu_{A,min} + b_{max}r_{max}\nu_{E,max}\nu_{L,max}\nu_{F,max},$$

$$\det(-\underline{A}) = (\nu_{E,max} + \mu_{E,max})(\nu_{L,max} + \mu_{L,max})(\nu_{F,max} + \mu_{A,max})\mu_{A,max} - b_{min}r_{min}\nu_{L,min}\nu_{F,min}.$$

Thus $\det(-\overline{A}) \geq 0$ if

$$b_{max}r_{max}\nu_{L,max}\nu_{F,max} \geq (\nu_{E,min} + \mu_{E,min})(\nu_{L,min} + \mu_{L,min})(\nu_{F,min} + \mu_{A,min})\mu_{A,min},$$

and $\det(-\underline{A}) < 0$ if

$$(\nu_{E,max} + \mu_{E,max})(\nu_{L,max} + \mu_{L,max})(\nu_{F,max} + \mu_{A,max})\mu_{A,max} < b_{min}r_{min}\nu_{L,min}\nu_{F,min}.$$

In fact, the previous results are related to the time dependent basic offspring number

$$\mathcal{N}_0(t) = \frac{r b(t)\nu_E(t)\nu_L(t)\nu_F(t)}{\mu_A(t)(\nu_E(t) + \mu_E(t))(\nu_F(t) + \mu_A(t))(\nu_L(t) + \mu_L(t))},$$

such that $\mathcal{N}_{0,min} \leq \mathcal{N}_0(t) \leq \mathcal{N}_{0,max}$, where

$$\mathcal{N}_{0,min} = \frac{r_{min} b_{min}\nu_{E,min}\nu_{L,min}\nu_{F,min}}{(\nu_{E,max} + \mu_{E,max})(\nu_{L,max} + \mu_{L,max})(\nu_{F,max} + \mu_{A,max})\mu_{A,max}},$$

and

$$\mathcal{N}_{0,max} = \frac{r_{max} b_{max} \nu_{E,max} \nu_{L,max} \nu_{F,max}}{(\nu_{E,min} + \mu_{E,min}) (\nu_{min} + \mu_{min}) (\nu_{F,min} + \mu_{A,min}) \mu_{A,min}}.$$

According to Theorem .2, we deduce

Theorem 2.3 :

- (i) If $\mathcal{N}_{0,max} \leq 1$, then the solution of system (8) converges to the trivial equilibrium X^0 .
- (ii) If $\mathcal{N}_{0,min} > 1$, then system (8) admits a unique periodic solution that attracts all initial condition in Ω .

According to the sensitivity analysis, an interesting and particular case is when we assume that all parameters are constant, except K . Then $\bar{A} = \underline{A}$, and thus $\mathcal{N}_{0,max} = \mathcal{N}_{0,min} = \mathcal{N}_0$. Thus, theorem 2.3 reduces to

Theorem 2.4 (i) If $\mathcal{N}_0 \leq 1$, then the solution of system (8) converges to the trivial equilibrium X^0 .

- (ii) If $\mathcal{N}_0 > 1$, then system (8) admits a unique periodic solution which attracts all initial condition in Ω .

In fact, we recover the same results than for the constant parameters problem, except that the constant positive equilibrium is now periodic of period T .

It is important to notice that K_C constant is relevant in the case where the cocoa production is almost constant along the year. This is realistic in Central America where there is no real seasonality. By contrast, in Cameroon, they are two rainy season: a long one, and a short one. There the seasonality is clearly marked, which has an impact on cacao production. That is why we consider a periodic function for K_C .

Numerical simulation

Now, we will illustrate our theoretical results. We will use the values of the monthly mean number of pods using data extrapolated, obtained in Cameroon, from [16] to construct our periodic function $K_C(t)$. According to the data from [16] and the knowledge about the mean number of pods over the year, our daily estimated data are recapitulated in Table 3. We suppose that the

| Months | Jun | Jul | Aug | Sept | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun |
|----------|-----|--------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|-------------------|-----|-----|-----|-----|
| $K_C(t)$ | 0 | $\frac{32000}{31}$ | $\frac{160000}{31}$ | $\frac{416000}{30}$ | $\frac{544000}{31}$ | $\frac{304000}{31}$ | $\frac{416000}{31}$ | $\frac{120000}{31}$ | $\frac{8000}{28}$ | 0 | 0 | 0 | 0 |

Table 3: Mean number of pods per days

function $K_C(t)$ is periodic, of period $T = 365$ days. We use the cubic spline interpolation to derive the time evolution of $K_C(t)$ along a year. Using cubic Hermite spline, we obtain a polynomial interpolation (Daily estimation of $K_C(t)$) given in Fig. 4, page 13. Figure 4, page 13 represents the daily estimation of pods number in the plot. $K_C(t)$.

When the parameter K_C is constant, we used a classical scheme already well implemented under matlab (ode23s) for numerical simulations and we consider that the number of pods K_C is constant, we evaluate the average daily value estimated with the data of Table 3, that is

$$\bar{K}_C = \frac{1}{365} \int_1^{365} K_C(t) dt.$$

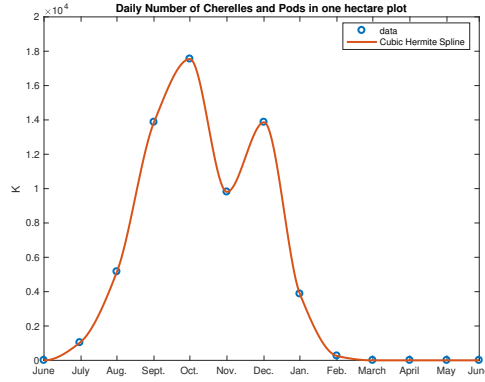


Figure 4: Daily estimation of $K_C(t)$ along a year

. When K_C is periodic, following [6], we consider a nonstandard numerical scheme to preserve most of the qualitative properties of the continuous model, like positivity, equilibria, stability and instability whatever the time step $\Delta t > 0$. We consider the values of parameters given in Table 4. We illustrate our numerical simulations for two values of C : $C = 5$ and $C = 100$. All the given values have been estimated thanks to [7, 31, 48, 13, 46].

| Parameters | Case $\mathcal{N}_0 < 1$ | Case $\mathcal{N}_0 > 1$ | Source |
|-----------------|--------------------------|--------------------------|--------------|
| r | 0.58 | 0.58 | [13] |
| b | 3.28 | 3.28 | Estimated |
| ν_E | 1/15 | 1/15 | Estimated |
| ν_L | 1/25 | 1/25 | Estimated |
| ν_F | 1/10 | 1/10 | Estimated |
| μ_E | 0.05 | 0.001 | Estimated |
| μ_L | 0.15 | 0.03 | Estimated |
| μ_A | 0.15 | 0.07 | Estimated |
| \mathcal{N}_0 | 0.6103 | 9.0002 | Equation (4) |

Table 4: Values of constant parameters

In Fig. 5, page 14, we illustrate the theoretical results when the carrying capacity K_C is constant, that is $\overline{K}_C = 5482$, with initial conditions $(E, L, F_1, F_2, M) = (0, 0, 0, 10, 10)$. As expected, when $\mathcal{N}_0 < 1$, the population decays till extinction, while, when $\mathcal{N}_0 > 1$, the population reaches rapidly the positive equilibrium. However, in Cameroon, having a constant number of pods along the year is not realistic. That's why in the next simulations, we consider a more realistic case, with the same parameters values. In Figs. 6 and 7, page 14, we illustrate the previous results when the carrying capacity K_C is periodic. However, in the case where $\mathcal{N}_0 > 1$, the dynamic of mirids follows the dynamic of pods, as expected. However, the size of the population seems to be large compared to real observations (see for instance [16]).

3 A model with delays

In the previous section, we studied the time evolution of mirid population as if the transition

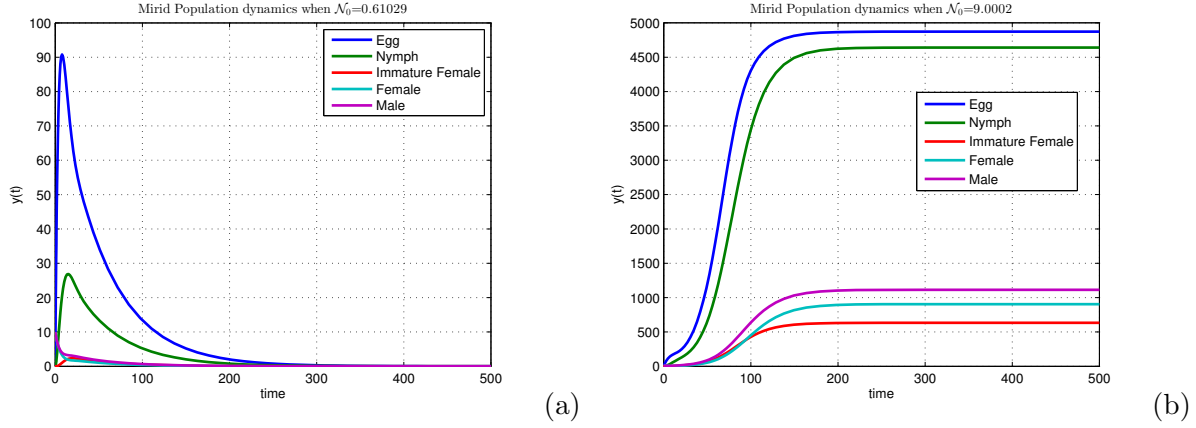


Figure 5: Time Evolution of mirid population when $K_C = 5482$; (a) $\mathcal{N}_0 < 1$; (b) $\mathcal{N}_0 > 1$.

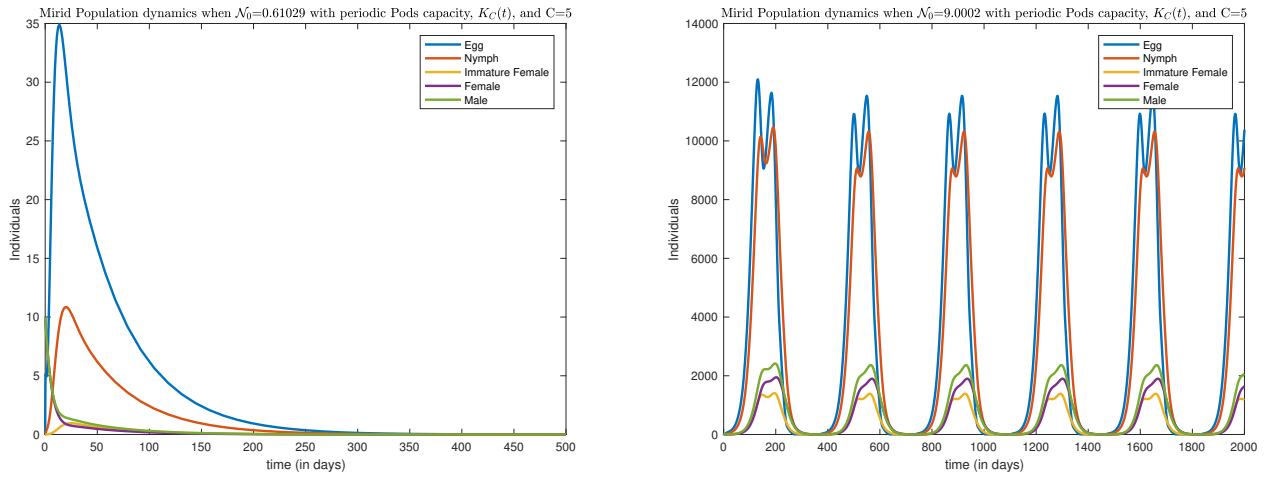


Figure 6: Time Evolution of mirid population when K_C is periodic and $C = 5$; (a) $\mathcal{N}_0 < 1$; (b) $\mathcal{N}_0 > 1$.

to one stage of development to another is immediate. Biologically, this is not correct: let us return on the biological life cycle of *S. singularis* given in Fig. 8, page 15. In fact, each individual needs to stay a certain amount of time in each compartment to complete its stage, in particular in the egg, nymph and non-mature female stages: there exists τ_1 days between egg-laying and appearing of new nymphs; τ_2 days between nymphs and emergence to adults. In addition, female needs τ_3 days to become mature before being able to lay eggs. In this section, we will take into account some of these previous times leading to time-delayed model with delays.

Now, it is possible to take into account different biological facts. In particular, based on the literature, we know that after deposition, eggs need (in mean) $\tau_1 = 15$ days to hatch and enter the nymphs compartment. b always represents the mean daily number of eggs laid by an adult female. $\tau_2 = 25$ days represent the required time for nymphs to achieve their development and become adults. So only a proportion $e^{-\tau_2 \mu_L}$ of Nymphs will survive and become adults, . Thus $\nu_E e^{-\tau_2 \mu_L} E(t - \tau_2)$ represents the transition rate from eggs to adults, after τ_2 days in the Nymphs compartment. The term $re^{-\tau_3 \mu_A}$ represents the proportion of immature adults that will deposit

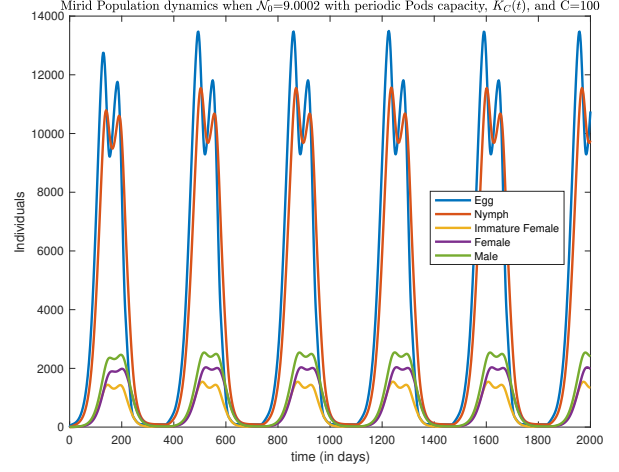
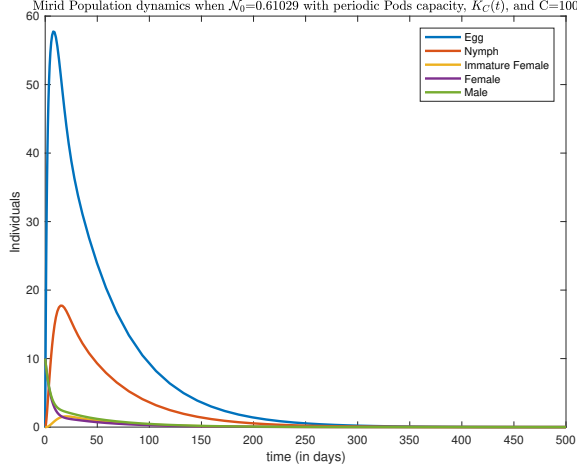


Figure 7: Time Evolution of mirid population when K_C is periodic and $C = 100$; (a) $\mathcal{N}_0 < 1$; (b) $\mathcal{N}_0 > 1$.

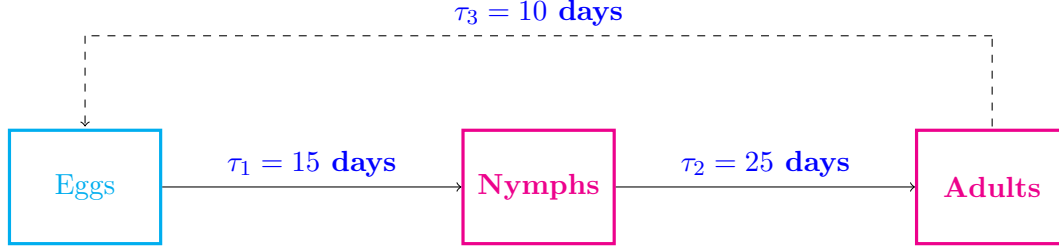


Figure 8: Life cycle of *S. singularis*

eggs, after τ_3 of maturation.

Altogether, we obtain the following "two-delays" model:

$$\begin{cases} \frac{dE}{dt} = r b e^{-\tau_3 \mu_A} A(t - \tau_3) \left(1 - \frac{E}{K_C}\right) - (\nu_E + \mu_E) E, \\ \frac{dA}{dt} = \nu_E e^{-\tau_2 \mu_L} E(t - \tau_2) - \mu_A A \end{cases} \quad (10)$$

$A = F_1 + F_2 + M$ and this is why the sex ratio r enters the E equation in Eq. (10). System (10) can be rewritten as follows:

$$\begin{cases} \frac{dx_1}{dt} = \alpha x_2(t - \tau_3) \left(1 - \frac{x_1}{K_C}\right) - \beta x_1, \\ \frac{dx_2}{dt} = \gamma x_1(t - \tau_2) - \delta x_2, \end{cases} \quad (11)$$

where

$$\alpha = r b e^{-\tau_3 \mu_A}, \quad \beta = \nu_E + \mu_E, \quad \gamma = \nu_E e^{-\tau_2 \mu_L}, \quad \delta = \mu_A.$$

The right-hand side of system (11) is continuous and Lipschitzian in x . Thus, according to the standard theory of Delay Differential Equations [29], system (11) admits a unique solution for each continuous initial condition $\varphi \in \mathcal{C}([-\tau; 0], \mathbb{R}^2)$ where $\tau = \max(\tau_3, \tau_2)$. We denote $\mathcal{C}([-\tau; 0], \mathbb{R}^2)$ the

Banach space of continuous functions mapping the interval $[-\tau; 0]$ into \mathbb{R}^2 with the topology of uniform convergence; i.e. for $\varphi \in \mathcal{C}([-\tau; 0], \mathbb{R}^2)$, the norm of φ is defined as $\|\varphi\| = \sup_{-\tau \leq \theta \leq 0} |\varphi(\theta)|$ where $|\cdot|$ is a norm of \mathbb{R}^2 .

Let

$$\mathcal{D} = \left\{ x \in \mathbb{R}_+^2 / x_1 \leq K_C, \quad x_2 \leq \frac{\gamma K_C}{\delta} \right\}$$

System (11) can be rewritten as follows

$$x'(t) = f(x(t), x(t - \tau_3), x(t - \tau_2)) = f(x, Y), \quad (12)$$

where $Y = (x(t - \tau_3), x(t - \tau_2))$. Following [44], it is important to notice that system (8) without delays reduces to a cooperative irreducible system. In fact the delayed system is cooperative too. Indeed, according to [44, 42], we can show that f verifies the quasimonotone condition, defined as follows in [44, 42]

$$\phi, \psi \in \mathcal{D}, \phi \leq \psi \text{ and } \phi_i(0) = \psi_i(0) \text{ implies } f_i(\phi) \leq f_i(\psi). \quad (13)$$

In fact, it suffices to use Theorem 4.5 [42], page 308, i.e. to show that f is cooperative to deduce that (13) holds for f , that is

$$\frac{\partial f_i}{\partial x_j}(x, Y) \geq 0, \quad \text{for } i \neq j, \quad (14)$$

$$\frac{\partial f_i}{\partial y_j^k}(x, Y) \geq 0, \quad \text{for all } i, j, k. \quad (15)$$

Obviously, since the non-delayed model is cooperative, condition (14) is verified. Let us now check condition (15):

$$\frac{\partial f_1}{\partial y_1^1}(x, Y) = 0, \quad \frac{\partial f_1}{\partial y_2^1}(x, Y) = \alpha \left(1 - \frac{x_1}{K_C}\right) \geq 0, \quad (16)$$

$$\frac{\partial f_2}{\partial y_1^2}(x, Y) = \gamma > 0, \quad \frac{\partial f_2}{\partial y_2^2}(x, Y) = 0. \quad (17)$$

Since the previous conditions are verified we deduce that f is quasi-monotone, which implies that if the initial condition is positive (with at most one zero component), then the solution x is still non-negative, i.e. $x(t) \geq 0$.

Similarly, using the fact that the initial condition $\phi \in \mathcal{D}$, we have $x_1 \leq K_C$, and $x_2 \leq \frac{\gamma K_C}{\delta}$, for $t \in [-\tau, 0]$. Using these inequalities in (11), we infer that this is still true when $t \in [0, \tau]$. Iterating this reasoning, we finally deduce that $x(t) \in \mathcal{D}$ for all $t \geq 0$.

A direct computation shows that system (11) admits two equilibria: the trivial ones, $\mathbf{0} = (0, 0)$, and

$$\mathbf{x}^* = \left(\left(1 - \frac{\beta\delta}{\alpha\gamma}\right) K_C, \frac{\gamma}{\delta} \left(1 - \frac{\beta\delta}{\alpha\gamma}\right) K_C \right) = \left(\left(1 - \frac{1}{\mathcal{R}}\right) K_C, \frac{\gamma}{\delta} \left(1 - \frac{1}{\mathcal{R}}\right) K_C \right),$$

when $\mathcal{R} > 1$ where

$$\mathcal{R} = \frac{\alpha\gamma}{\beta\delta} = \frac{r b \nu_E e^{-\tau_2 \mu_L - \tau_3 \mu_A}}{\mu_A (\nu_E + \mu_E)}. \quad (18)$$

Note that

$$\mathcal{R} = \frac{\alpha\gamma}{\beta\delta} = \frac{r b \nu_E e^{-\tau_2 \mu_E - \tau_3 \mu_A}}{\mu_A (\nu_E + \mu_E)} < \mathcal{N} = \frac{r b \nu_E \nu_L \nu_F}{\mu_A (\nu_E + \mu_E) (\nu_L + \mu_L) (\nu_F + \mu_A)}.$$

Thus, for some parameters values, we may have $\mathcal{N} > 1$ and $\mathcal{R} < 1$.

There is no need to study the stability/instability of the equilibria. Indeed, according to [44] (Chapter 5), there is a nice property pointed out about cooperative irreducible time-delay systems: the asymptotic stability of each equilibrium is preserved for the delay differential system (8), whatever the values taken by the delays. In particular, when $\mathcal{R} \leq 1$ ($\mathcal{R} > 1$), all orbits are attracted by $\mathbf{0}$ (\mathbf{x}^*). In other words, to study the long term behaviour of cooperative time-delay systems it suffices to study the cooperative systems without delay(s).

This result implies that the use of delays does not change the long-time behaviour of the time-dependent system (8). However, when the system is non-autonomous and periodic, its behaviour may be different in the transient period from the non-delayed non-autonomous periodic system as it is showed in the forthcoming simulations (see Fig. 11, page 21), and Fig.12, page 21).

Remark 3.1 *The previous time-delayed system is considered with fixed delays. A possible extension, for future work would be to consider time varying delays, $\tau_i(t)$, since it seems obvious to consider that the developmental time in each stage may change according to environmental parameters, like temperature, rainfall.... Finally, distributed delays could be considered. Unfortunately for both cases, we do not have data.*

Finally, like for the non-delayed model, it is interesting to provide a global sensitivity analysis at different time $T = 100$ and $T = 500$: see Fig. 9, page 18. Clearly, the parameters μ_L , and μ_A are the most sensitive parameters, and the delays play mainly a role in the transient phase ($T = 100$) and no more at equilibrium, contrary to the carrying capacity, K_C , even if this parameter is far less sensitive than in the previous non-delayed model. This clearly shows the importance of estimating efficiently these parameters in different environmental or semi-field conditions. It also very interesting to compare the sensitivity analysis between two models that are supposed to model the same system.

Numerical simulation

Now, we illustrate all the different stability cases, i.e. when $\mathcal{R} < 1$ and $\mathcal{R} > 1$. The time-delayed Model is solved using Matlab and the dde23 function. In Table 4, page 13 we summarize the parameters values used in the next simulations but we attribute the new values of parameter μ_L . Then, the values of parameters for those simulations are consigned in Table 5, page 19.

| Parameters | Case $\mathcal{R} < 1$ | Case $\mathcal{R} > 1$ | Source |
|---------------|------------------------|------------------------|---------------|
| b | 3.28 | 3.28 | Estimated |
| τ_2 | 25 | 25 | Estimated |
| τ_3 | 10 | 10 | Estimated |
| μ_A | 0.1 | 0.07 | Estimated |
| r | 0.58 | 0.58 | [13] |
| μ_L | 0.1 | 0.03 | Estimated |
| ν_E | 1/15 | 1/15 | Estimated |
| μ_E | 0.001 | 0.001 | Estimated |
| \mathcal{R} | 0.566 | 6.28 | Equation (18) |

Table 5: Values of constant parameters for the time-delay model

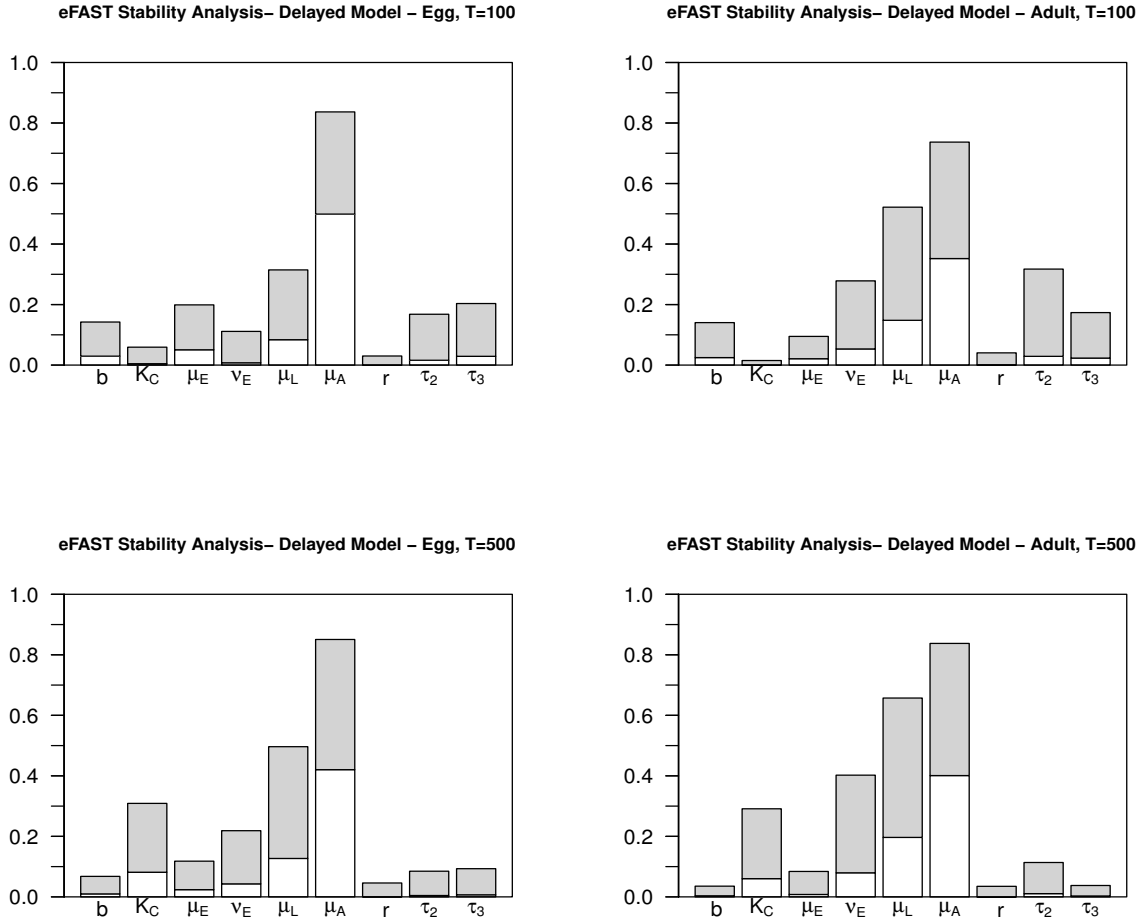


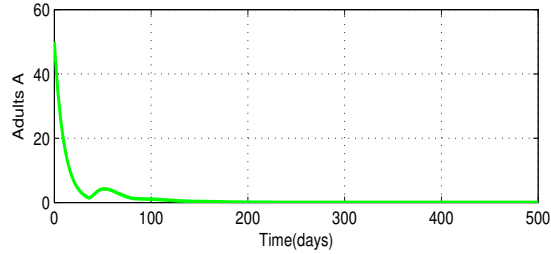
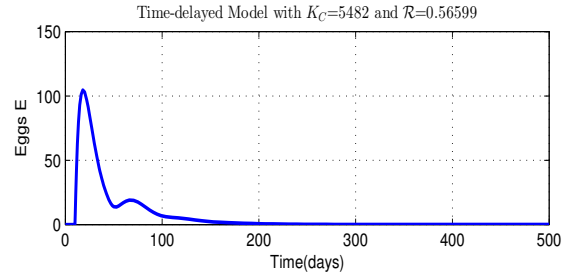
Figure 9: E-Fast Sensitivity analysis of the Time-Delay Model

We now derive numerical simulations with $K_C = 5482$ constant and K_C periodic, like in the previous section. We choose as initial conditions $(E(0), A(0)) = (0, 50)$.

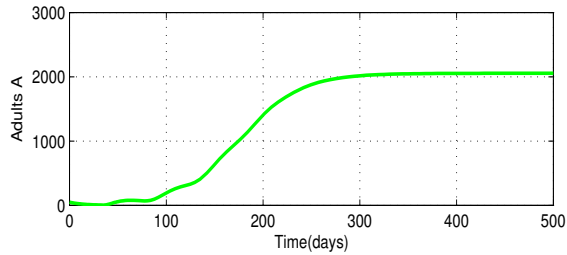
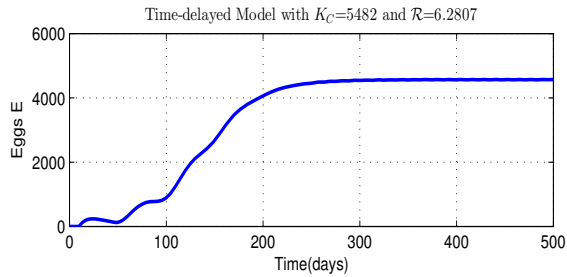
In Fig. 10, page 20, we illustrate the previous results when the carrying capacity K_C is constant. When $\mathcal{R} < 1$, mirids population decays till extinction and when $\mathcal{R} > 1$, mirids population converge to a positive equilibrium.

As expected, when t goes to infinity, the time-delayed model with constant parameters responds exactly like the non-delayed model, except that the threshold parameters is not exactly the same. When $\mathcal{R} < 1$ (> 1), the system converges to the trivial (positive) equilibrium. In fact, with the same parameters, the deterministic model may converge to the positive equilibrium, while the time-delay model converges to the trivial equilibrium.

Figs. 11, page 21 and 12, page 21 represent the time evolution of mirids with K_C periodic and for different values for C , namely $C = 5$ and $C = 100$. When $\mathcal{R} \leq 1$, mirid population decays rapidly till extinction, whatever the values taken by C . In contrary, when $\mathcal{R} > 1$, mirid population converges to a periodic solution, as expected, but with different amplitudes related ted



(a)

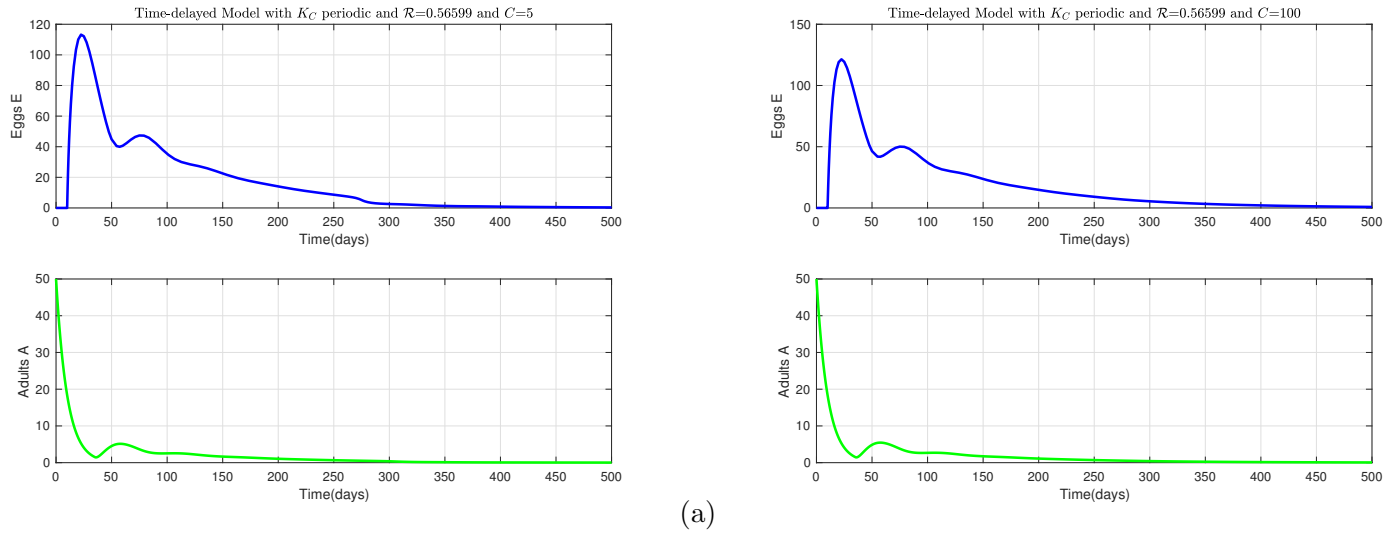


(b)

Figure 10: Time evolution of the Eggs and Adult Compartments for the time-delay model with constant parameters, $K_C = 5482$, with: (a) $\mathcal{R} < 1$, (b) $\mathcal{R} > 1$

to C , indicating the importance of alternative resources in the maintenance and the size of the population. The simulations seem to be in good agreement with field observations. It seems also to be obvious that the removal of alternative resources should be part of control strategies to lower the impact of the mirids. Compared to the time-delayed model, the non-delayed model overestimates the population. Thus, even if from the mathematical point of view the long term behaviour is the same, the time-delayed model provides better estimate of the population size along the year than the non-delayed model.

We would like to emphasize that our study was very difficult because of the lack of population data. Many parameters values were estimated using raw data obtained in the field by Babin, in 2008, in Cameroon. We use these data to estimate several parameters like mortality of eggs, nymphs and adults (μ_E , μ_L and μ_A), fecundity of adults female (b), the mean duration of immature



(a)

Figure 11: Time evolution of the Eggs and Adult Compartments for the time-delay model with constant parameters, K_C periodic, such that $\mathcal{R} < 1$, with: (a) $C = 5$ (b) $C = 100$.

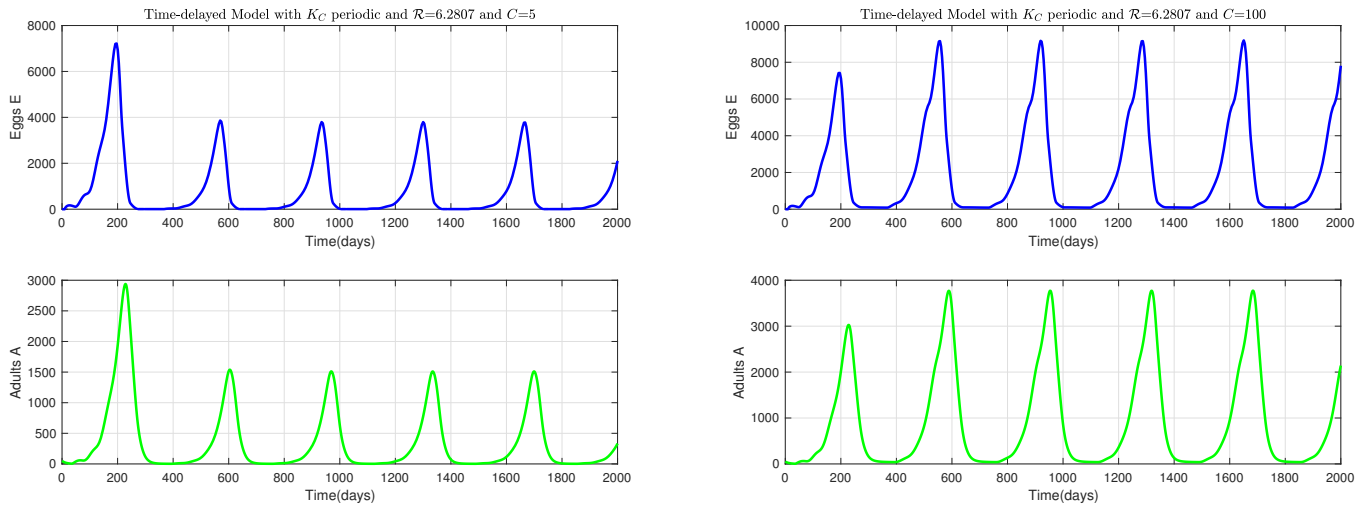


Figure 12: Time evolution of the Eggs and Adult Compartments for the time-delay model with constant parameters, K_C periodic, such that $\mathcal{R} > 1$, with: (a) $C = 5$ (b) $C = 100$.

females stage ($1/\nu_F$) and the mean necessary time for development of eggs. For some parameters (the sex-ratio r , the mean duration of egg stage ($1/\nu_E$) and the mean duration of nymph stage ($1/\nu_L$)), we used data from [12] because it was the last experiment on *S. singularis* life cycle, realized in Cameroon. The most difficult data to obtain was the daily evolution of pods number in the plot. Using data from [16] and also based on our knowledge about the mean pods density per hectare, we construct our periodic function $K_C(t)$ which represent the daily appearance of pods and cherelles in the plot. However, mirids also feed and lay eggs on young shoots that lead to important damage able to cause the destruction of the tree over the years. It will be important to take into account this aspect and model the daily appearance of young shoots in the plot by a function ($S(t)$ for example). Then, it will be relevant to know the mirid frequency of feeding on host plants to have a good idea about the parameter C because the time-evolution of mirids also depends on it considering that if C is large, the level of mirid population increase. In our numerical simulations, we attributed to this parameter two values $C = 5$ and $C = 100$. According to these results, we suggest that it will be important to have several experiences in the field: to better estimate the daily appearance on pods and shoots in the plot, to have a good idea about the parameters of development of mirids and also to better estimate the parameter C .

4 About Mirid Controls

Several methods are used to control mirid population among which:

- cultural management, based on managing the system structure and composition to create unfavorable conditions for the development of mirids populations.
- varietal management, which consists in replacing the cacao varieties traditionally cultivated with more resistant and/or tolerant varieties to mirid attacks.
- chemical management, based on chemical insecticide used. This is the most widespread and efficient strategy to control mirid population in Cameroon. The chemical insecticides are applied twice to three times a year [10] (see also the CIRAD report published for cocoa producers.)
- semio-chemical management which consists of using synthetic sexual pheromone traps [35] which increases adult mortality (trapping), and prevents male insects finding females and mating (mating-disruption), and thus reduces the fecundity of female.
- last but not least, as showed in the previous simulations, a reduction of mirids alternative host (resources), i.e. decrease C , is also essential to have an efficient control.

Understanding the population dynamic of *S. singularis* is crucial for monitoring, forecasting and, then, controlling this pest population. Recent work in Ghana indicates (using the visual hand-height assessment method) that mirid populations (predominately nymphs) began to increase rapidly in April with an initial peak in May, followed by a rapid build-up in June [9]. In Cameroon, mirid /population is low on cacao from February to March. From June to July, the populations start to grow more or less rapidly depending on external conditions like weather and fruits production on the trees. The peak of the population appears between September and November when the pods are almost mature [12].

In Cameroon, mirids populations are mainly controlled by chemical insecticides. Three treatments are recommended per year: in June/July and August/September (propagation of mirids population); in November/December [25]. We will consider the impact of one treatment, two treatments and, finally three treatments. We will make a comparative study of treatments applied in systems with cacao only, $C = 5$, and in agroforestry systems composed of cacao and associated trees that could be secondary resource for mirids, $C = 100$.

According to the expert's knowledge and field observations, the insecticide has a decaying death rate over 8 weeks, that is summarized in Table 6: .

| | | | | | | | | | | |
|----------------------------------|---|---|-----|-----|-----|------|-------|------|----|----|
| Time (in days) after the release | 1 | 3 | 8 | 16 | 24 | 32 | 40 | 48 | 56 | 60 |
| Insecticide death rate | 1 | 1 | 0.9 | 0.2 | 0.1 | 0.05 | 0.025 | 0.01 | 0 | 0 |

Table 6: Time dependent death-rate of chemical treatment

Remark 1 *Synthetic insecticides like λ -cyhalothrine and Imidacloprid have a long residual effect, but it depends on several environmental factors, like rainfall. That is why Table 6 provides only a feedback from field experts according to the locations in Cameroon where these treatments have been studied and are already used.*

We start our numerical simulations at the end of June, a period where the number of pods is increasing in the plot. We treat the plot respectively one, two, or three time(s) per year, as recommended to Cacao producers. We compare the efficacy between each treatment. The periods of treatment are given as follows:

- **Treatment One** with only one application per year: (beginning of) July ($t = 395, 760, 1125, 1490, 1855$).
- **Treatment Two** with two applications per year: July ($t = 395, 760, 1125, 1490, 1855$) and September ($t = 457, 822, 1187, 1552, 1917$) (see [25], page 20).
- **Treatments Three** with three applications per year: July ($t = 395, 760, 1125, 1490, 1855$), September ($t = 457, 822, 1187, 1552, 1917$), and November ($t = 518, 883, 1248, 1613, 1978$) (see [25], page 20).

It is worth to mention that the periodicity of the two last treatments coincides with the duration of the chemical treatment after spreading. In Figs. 13, page 23, Fig. 14, page 23, and Fig. 15, page 24, we present the results obtained with the different treatments in two cases: $C = 5$ and $C = 100$. The case $C = 5$ represents a full cacao crops, while $C = 100$ may represent a cacao crop in an agro-forestry system, where additional resources (host trees) are available for mirids.

We summarize in Table 7, page 23 the impact of each treatment in the reduction of the wild population.

| | Treatment 1 | Treatment 2 | Treatment 3 |
|-----------|-------------|-------------|-------------|
| $C = 5$ | 74.8% | 92.9% | 97.8% |
| $C = 100$ | 58.7% | 84.8% | 94.1% |

Table 7: Efficacy of each treatment - Percentage of reduction of the wild population

As expected, 2 treatments are sufficient (more than 90% reduction of the population) when C is small. An additional (third) treatment is particularly recommended when C is large, i.e. $C = 100$. These results are relevant with real observations in different type of plots, at least in Cameroon.

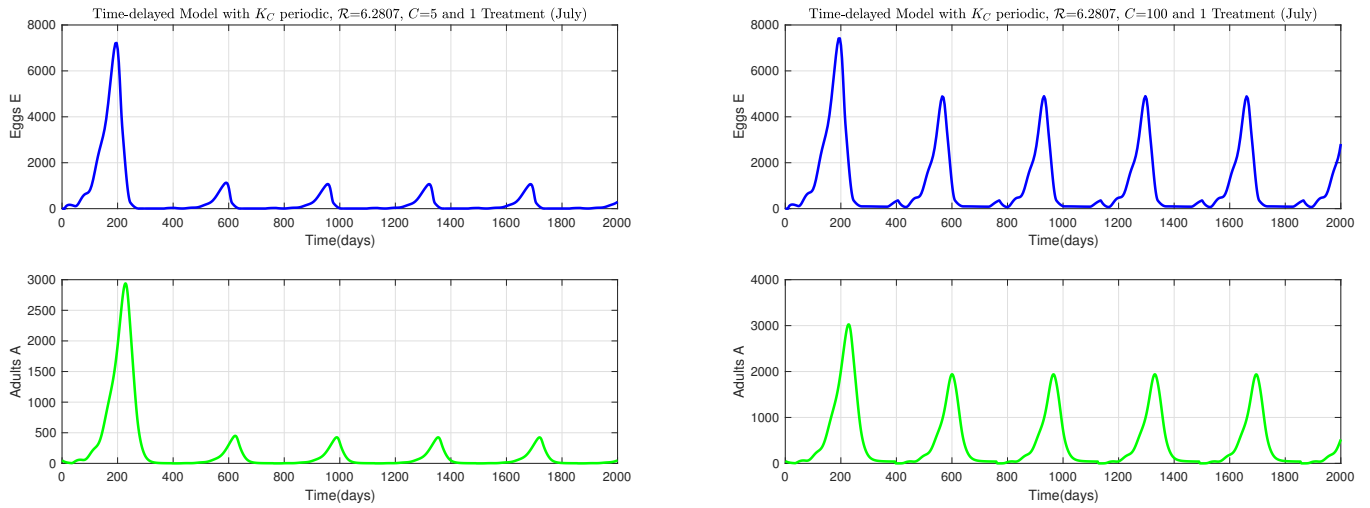


Figure 13: Time evolution of Mirids using only one treatment in the plot per year: (a) $C = 5$, (b) $C = 100$.

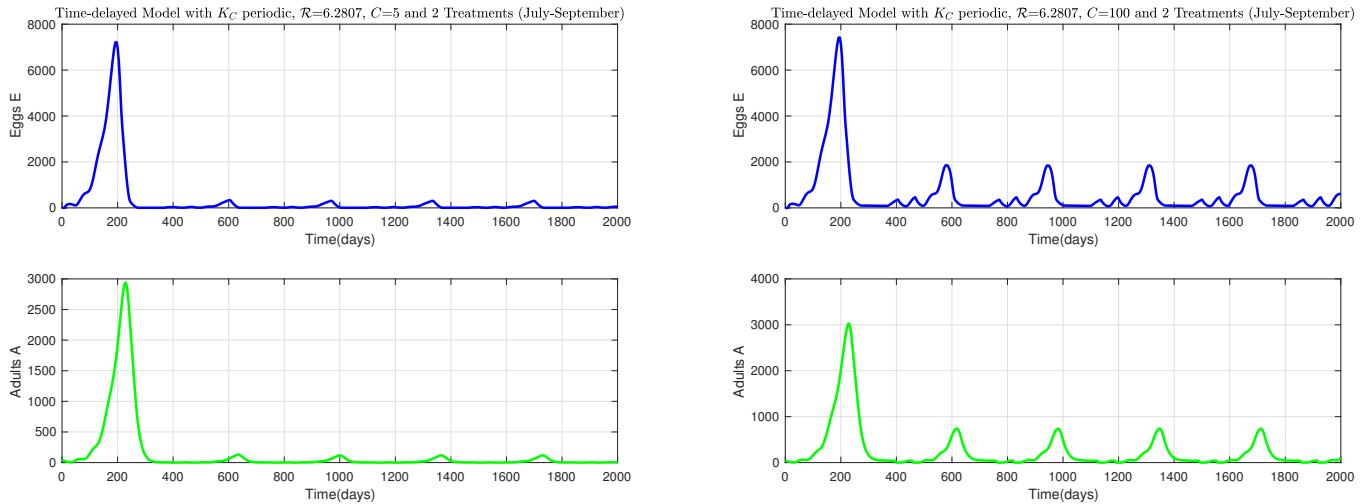


Figure 14: Time evolution of Mirids using two treatments per year in the plot: (a) $C = 5$, (b) $C = 100$.

Although chemical insecticides are very efficient to control mirids, their recurrent use is widely questioned due to the immediate adverse effects that they cause in ecosystems via environmental pollution (impact non targeted species), induce resistance in the mirid population, and to the toxic effects on human health. In addition, these chemical products are very expensive. That is why, it could be more advantageous to consider sustainable control strategies, like for instance, mating disruption and trapping [35, 41]. Mating disruption consists of introducing an artificial stimuli,

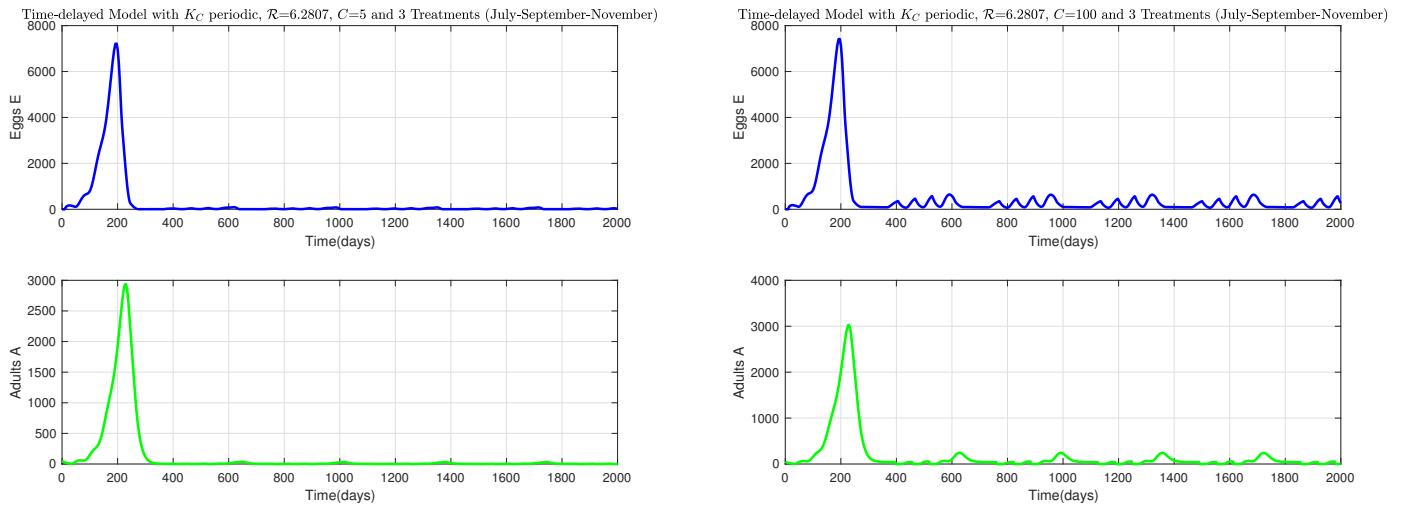


Figure 15: Time evolution of Mirids using three treatments per year in the plot: (a) $C = 5$, (b) $C = 100$.

like pheromones or para-pheromones, to confuse individuals, and, thus, disrupt mate localization, leading to long-term reduction of the population. In our case, we roughly assume that this implies a decrease of the female fecundity. Thus, for instance, if we reduce the daily female fecundity from 3.28 to 2, the mirid population decreases: see Fig.16, page 24.

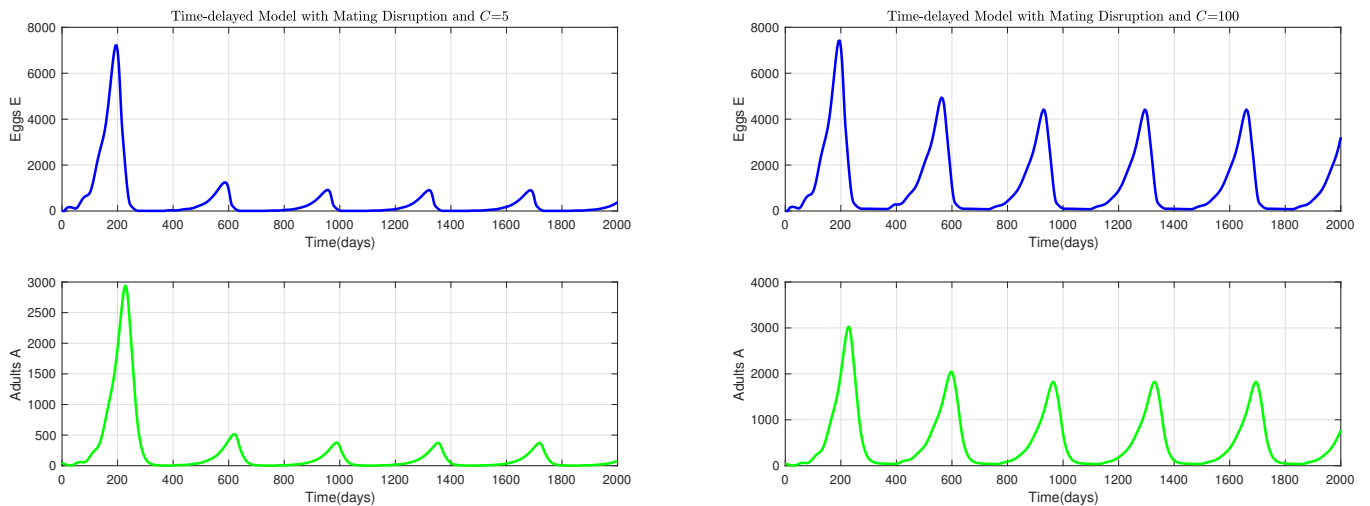


Figure 16: Time evolution of Mirids with control using mating disruption: (a) $C = 5$, (b) $C = 100$.

Another way to control mirids is the use of traps. Traps increase the adult mortality rate, μ_A . For instance, if we increase the mortality μ_A from 0.07 to 0.1, we observe a great reduction of the level of mirid population (see the time evolution of mirids in Fig. 17, page 25). According to the sensitivity analysis, the adult mortality μ_A is a sensitive parameter for the delayed model such that any increase may have a strong negative impact on the population.

In general, combining the two previous methods of control (mating disruption and trapping),

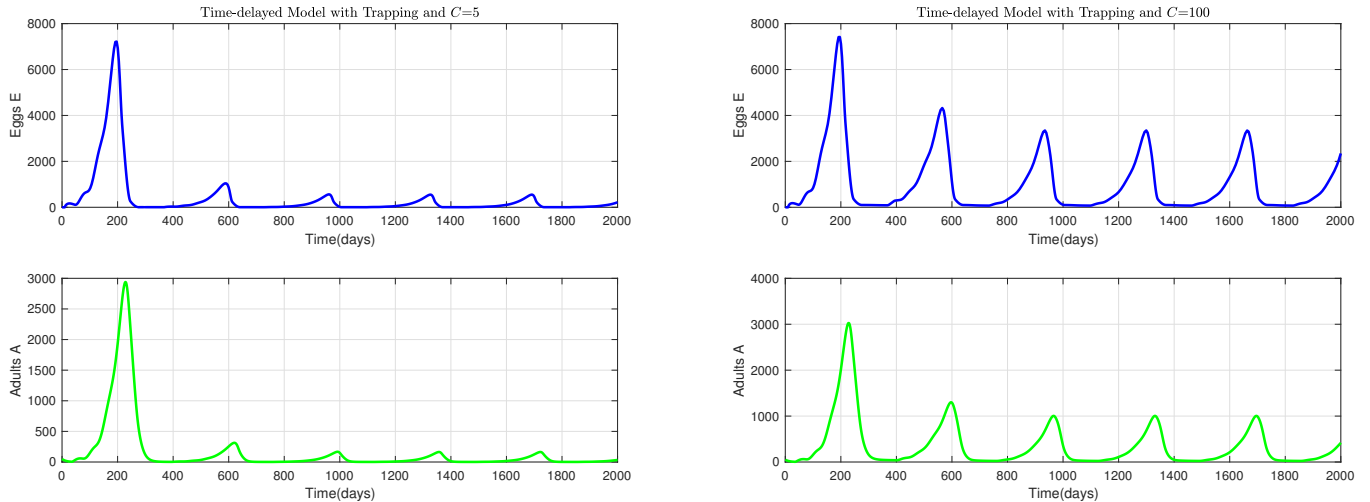


Figure 17: Time evolution of Mirids with control using trapping: (a) $C = 5$, (b) $C = 100$.

improve the previous results (see Fig. 18, page 26). This combination allows to reach a low level of population, right after the first year. . We summarize in table Table 8, page 25, the efficiency

| | Mating | Trapping | Trapping&Mating |
|-----------|--------|----------|-----------------|
| $C = 5$ | 70.5% | 85.5% | 96.5% |
| $C = 100$ | 49.4% | 71.0% | 90.1% |

Table 8: Efficacy of Trapping, Matting, and Trapping-Mating - Percentage of reduction of the wild population

of each control methods. According to the given results, it seems possible to have a very efficient control of mirids without using chemical control. Clearly the combination of Mating and Trapping gives the best results whatever the values taken by C . This is in good agreement with recent field experiments [41].

In the previous simulations, we showed that a biological control strategy (using Mating and Trapping) can be a very good alternative to the use of insecticides. Last but not least, if it is possible, the reduction of alternative hosts in the plots is also an additional way to improve the efficacy of both controls.

5 Conclusion

In this paper, we studied the dynamics of a cocoa pest, mirids. From the best of our knowledge it is the first time that mathematical models are developed to study mirid pest. We first build a generic stage-structured ODE model to simulate the dynamic of the pest population considering the resource (available cocoa pods and additional tree hosts) as constant or as a periodic function. Our model enters the family of cooperative system, which facilitates its study. Thus, we show that there exists a threshold parameters, \mathcal{N}_0 , also called the basic offspring number, that summarizes the dynamics of the system: when it is less than one, then the mirid population decreases till extinction; when it is greater than one, then mirids population persists. Then, based on the mirid's

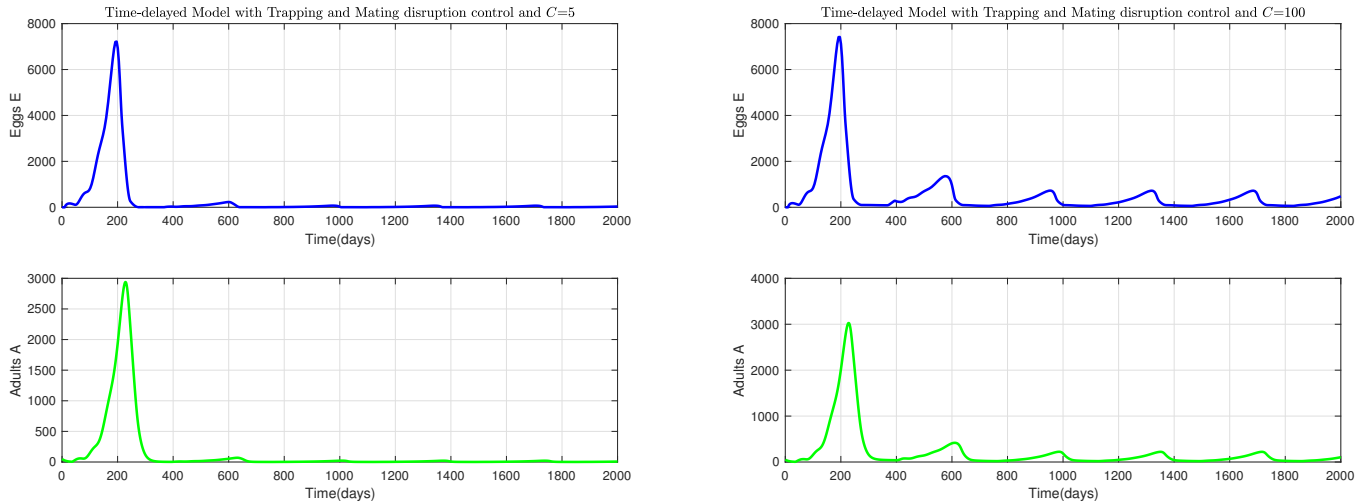


Figure 18: Time evolution of Mirids with control combining trapping and mating disruption; (a) $C = 5$, (b) $C = 100$.

development stages and times, we also develop a cooperative delay model with two delays. We derive a theoretical study and estimate the related basic offspring number, \mathcal{R} . We illustrate the theoretical results through numerical simulations. We show that the outputs of the delayed system are more realistic than the non-delayed ODE model. We also highlighted that the presence of additional hosts can help the capsid population to maintain when pods are not available. Last but not least, for both models, we derive a sensitivity analysis that shows that the carrying capacity and the mortality rates are the most sensitive parameters.

Another objective of our work was to study ongoing mirid control strategies in Cameroon. We evaluate the impacts of chemical control and biological control (using mating disruption and trapping). Chemical control is used since a long time in Cameroon. It is very efficient when, at least, 2 treatments per year are applied. Our numerical simulations are in good agreement with the phytosanitary recommendations. However, we show that mating disrupting and trapping can be as efficient as chemical control, while being less detrimental to the environment. Of course, the reduction of additional hosts will improve the efficacy of the control.

According to these preliminary results, several ways of study are possible: (i) to propose to entomologists and agronomists to set up new experiments in the field in order to obtain additional and new data to improve our knowledge, to estimate some biological and ecological parameters in different environmental conditions, to better model the time dynamic of the mirids, and thus to improve their control, (ii) to develop a model where mating disrupting and trapping are effectively modeled, like in [3, 4], (iii) to couple our models to a pod growth model in order to take into account the impact of mirids on cocoa pods, (iv) to take into account the spatial distribution of mirids using a Metapopulation approach [24], or a Partial Differential Equation approach [23].

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Appendix A: Mains results of Cooperative Systems

Here, we recall useful theorems (Theorem 3.1 in [43] and Theorem 5.5 in [30]).

Theorem .1 ([43], Theorem 3.1, page 1045) *Let $F(t, x)$ be continuous in $\mathbb{R} \times \mathbb{R}_+^n$, T -periodic in t for fixed x . and assume $D_x F(t, x)$ exists and is continuous in $\mathbb{R} \times \mathbb{R}_+^n$. Assume that if $x \geq 0$, with $x_i = 0$, then $F_i(t, x) \geq 0$, $1 \leq i \leq n$, $t \in \mathbb{R}$. Assume*

$$(M) \quad \frac{\partial F_i}{\partial x_j} \geq 0, \quad i \neq j, (t, x) \in \mathbb{R} \times \mathbb{R}_+^n$$

and

$$D_x F(t, x) \text{ is irreducible for each } (t, x) \in \mathbb{R} \times \mathbb{R}_+^n$$

(C) if $0 < x < y$, then $D_x F(t, x) \geq D_x F(t, y)$.

Then every solution of (9) with $x(t_0) \geq 0$ can be continued to $[t_0, \infty]$ with $x(t) \geq 0$ for $t \geq t_0$.

If $F(t, 0) \equiv 0$ and

$$z' = D_x F(t, 0)z \quad (19)$$

is the variational equation about $x \equiv 0$, then $\lim_{t \rightarrow \infty} x(t) = 0$ for every solution of (9) with $x(t_0) \geq 0$ provided all Floquet multipliers of (19) lie inside or on the unit circle in the complex plane. If any multiplier of (19) lies outside the unit circle, then one of the following holds: (a) every solution $x(t)$ of (9) with $x(t_0) \geq 0$ satisfies $\lim_{t \rightarrow \infty} x(t) = \infty$, or (b) (9) possess a unique nonzero T -periodic solution $q(t)$. In the latter case $q(t) > 0$ for all t and $\lim_{t \rightarrow \infty} x(t) = q(t)$ for every solution of (9) with $x(t_0) > 0$.

If $F(t, 0) \equiv 0$, then exactly one of the alternatives (a) or (b) occurs, except that $x(t_0) > 0$ is replaced by $x(t_0) \geq 0$ above.

Let $A(t)$ be a $n \times n$ continuous matrix in \mathbb{R} τ -periodic in t , denote

$$\begin{aligned} \overline{a_{ij}} &= \max_{0 \leq t \leq \tau} a_{ij}(t), & \underline{a_{ij}} &= \min_{0 \leq t \leq \tau} a_{ij}(t) \\ \overline{A} &= (\overline{a_{ij}}), & \underline{A} &= (\underline{a_{ij}}) \end{aligned}$$

Thus

$$\underline{A} \leq A(t) \leq \overline{A}, \quad \text{for } 0 \leq t \leq \tau.$$

Let p be a positive real number. In order to study system (8), we will use the following theorem:

Theorem .2 ([30], Theorem 5.5, page 203) *Let $F(t, x)$ be continuous in $\mathbb{R} \times \mathbb{R}_+^n$, T -periodic in t for a fixed x and assume $D_x F(t, x)$ exists and is continuous in $\mathbb{R} \times \mathbb{R}_+^n$. Assume that all solutions are bounded in \mathbb{R}_+^n and $F(t, 0) = 0$. Assume*

- $\frac{\partial F_i}{\partial x_j} \geq 0$, $(t, x) \in \mathbb{R} \times \mathbb{R}_+^n$
- and $A(t) = D_x F(t, 0)$ is irreducible for any $t \in \mathbb{R}$.
- If $0 < x < y$, then $D_x F(t, x) > D_x F(t, y)$.

Then

1. If all principal minors of $-\overline{A}$ are non-negative, then $\lim_{t \rightarrow +\infty} x(t) = 0$ for every solution of (9) in \mathbb{R}_+^n
2. If $-\underline{A}$ has at least one negative principal minor, then (9) possesses a unique positive T -periodic solution which attracts all initial conditions in \mathbb{R}_+^n .