

Modeling the adaptive behavior of an agricultural pest population

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In this work, we formulate a model describing the growth of a pest population with seasonal diapause at the larval stage. The model includes the insect resistance to chemical treatments and their adaptation against a hostile environment. It consists on the description of three classes: the immature stage that includes eggs, larvae and pupae, and two mature stages corresponding to the vulnerable adult stage and the insecticide resistant adult stage. The main result consists in an analytical approach for the existence of a non-negative periodic solution. The proof uses comparison results and Kamke's Theorem for cooperative systems. As an important illustration, a threshold type result on the global dynamics of the pest population is given in terms of an index R . When $R \leq 1$, the trivial solution is globally asymptotically stable. When $R > 1$, the positive periodic solution is globally asymptotically stable. Numerical simulations confirm the analytical results.

Keywords: *seasonal diapause; resistance to insecticides; monotone systems; global attractivity; numerical simulations.*

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1. Introduction

With global warming, the risk of contamination of vineyards by the European Grapevine Moth is increasing day by day in the world, and particularly in the Mediterranean basin, see [1]. This pest should be considered as a potential dangerous pest on a worldwide scale. Damages are caused during the larval stage. Thus, some research have been conducted to study the behavior and the life cycle of the insect *Lobesia-Botrana* (see [2–9]), and the references therein. The acquisition of this knowledge gradually allowed the construction of mathematical models able to describe with varying precision degrees the evolution in time and space of the insect densities, see also [2, 3, 6], and the references therein. The integrated pest management programs usually includes chemical, and biological controls that acts at different stages of the pest. The most used one is based on the dispersion of pheromones to act on the mating disruption, see [10, 11].

Chemical control has been extensively used to reduce the proliferation of the pest population, however, in some areas, the insect has developed resistance to different classes of chemical insecticides, see for instance [5]. This resistance represents a major obstacle to the sustainability of pest control. Understanding insect resistance is particularly important when the treatment needs to use larger quantities, or new and more expensive pesticides to effectively control pest populations.

The insect develops a mechanism of resistance under the form of a genetic mutation which destroys the ingested pesticides. This mutation disrupts the hormonal functioning of the insect, and the individuals enter an early diapause, or delays their emergence in the adult phase.

However, only a few studies have investigated the phenomenon of *Lobesia-Botrana* diapause which is still not very well understood. This latter is a strategy adopted by the insect to survive in the harsh environmental conditions. Among other causes that induce insect diapause, we cite the photoperiod (short day and long night), and the gradual drop in temperature. In general, diapause consists of 03

phases, the first is called normal growth or pre-diapause, it consists of storing energy in the form of reserves to maintain the metabolism. In the second phase, development is slowed down or interrupted, this period is called diapause. The last stage corresponds to the awakening or activation of development, it is called post-diapause, see [4]. In [12] a model is investigated to analyze the impact of insecticides control on mosquitoes without diapause. In [13], the authors consider the following scalar delay differential equation

$$x'(t) = -dx(t) + f(1 - \alpha)\rho x(t - \tau) + \alpha\rho x(t - 2\tau), \quad (1)$$

with a proportion constant α with which the population undergoes a diapause, f is a function. They establish global continuation of a branch of periodic solutions through the Hopf bifurcation analysis.

In [14], the authors consider the diapause as an independent growth process. An important property of the proposed model is that the rate of change of the population may jump instantaneously. In [14], the dynamics of seasonal mosquito population when juveniles enter into diapause is given by the following model: let $L(t)$, and F_1 be respectively the density of the immature and mature population. During the normal period

$$\begin{cases} \frac{dL}{dt} = b(F_1(t)) - b(F_1(t - \tau))e^{-\mu_L\tau} - \mu_L L, \\ \frac{dF_1}{dt} = b(F_1(t - \tau))e^{-\mu_L\tau} - \mu_{F_1} F_1, \end{cases} \quad (2)$$

during the diapause period,

$$\begin{cases} \frac{dL}{dt} = -\mu_L L, \\ F_1 \text{ decreases to zero continuously,} \end{cases} \quad (3)$$

during the post-diapause period,

$$\begin{cases} \frac{dL}{dt} = b(F_1(t)) - b(F_1(t - \tau - \tau_d))e^{-\mu_L\tau - \mu_L\tau_d} - \mu_L L, \\ \frac{dF_1}{dt} = b(F_1(t - \tau - \tau_d))e^{-\mu_L\tau - \mu_L\tau_d} - \mu_{F_1} F_1. \end{cases} \quad (4)$$

The second term in the normal period represents the maturation of the immature born at previous time $(t - \tau)$. The diapause duration is assumed to be τ_d .

The intraspecific competition among immatures is ignored during the normal period. As it is mentioned in [14], one feasible way to incorporate competition is to add a density dependent term, which gives difficult theoretical analysis of the system (2)–(4).

Understanding the impact of insecticides and the behavior of the pest is challenging. To respond to this challenge, we propose a model that includes (a) diapause in the larval stage, (b) resistance of adults to insecticides, and (c) adaptation of the new generation against hostile environment. To account for (d) intraspecific competition in the larval stage, the model has been developed by introducing a quadratic nonlinear term. The study of the model is achieved by an alternative approach, namely the theory of monotone systems which is adapted for systems structured on three periods with continuous transition. We need to ensure for system (5)–(7) that the transition does not lead to a jump in the wrong direction. Note that important contributions have been made on monotone dynamical systems in [15–17] to cite a few.

We present our model in Section 2. With the help of preliminaries of Section 3, we establish the main results in Section 4. The global dynamics is analyzed in Section 5. We illustrate the analytical results with numerical solutions in Section 6. Concluding remarks are given in Section 7.

2. Model description

During her lifetime, the female can lay more than 300 eggs. Eggs remain until natural death or emerge into larvae, after seven to eleven days in the spring, but only three to five days in the summer.

After a few days, larvae die by natural death or evolves into pupae. Individuals stay approximately seven days before emerging into adult.

The first adults emerge in April or May, and those of later generation in August or September.

The insect makes 3 or 4 generations per year depending on the climate, for example in Spain, Italy, and Greece, the insect can produce up to 4 generations. Between, August and September, the larvae feed inside the berries, hence the last generations causes enormous damage, see [8]. We divide the population into two classes, juvenile and adult individuals. The juveniles stage includes all pre-adult stages like eggs, larvae, and pupae. We suppose that once an adult emerges from the larvae stage, it is exposed to insecticides.

Let $F_1(t)$ be the density of females at time t , that are vulnerable to insecticides, and let $F_2(t)$ be the density of resistant females at time t . Let $L(t)$ be the density of juveniles at time t . Each year, the population spend three periods, the normal period of length T_1 , the diapause period of length τ , and the post-diapause period from $T_2 = T_1 + \tau$ to 1, where 1 denotes one year.

a) The normal period ($0 \leq t \leq T_1$). Before the diapause period, the population evolves with a logistic law during the time interval $(0, T_1)$,

$$\begin{cases} \frac{dL}{dt} = \lambda_1 F_1 + \lambda_2 F_2 - rL - \mu_L L - cL^2, \\ \frac{dF_1}{dt} = \rho rL - \mu_{F_1} F_1 - \delta F_1, \\ \frac{dF_2}{dt} = (1 - \rho)rL - \mu_{F_2} F_2, \end{cases} \quad (5)$$

where λ_1 is the birth rate of the vulnerable females, λ_2 denotes the birth rate of resistant females. The juvenile competition rate is given by the parameter c . The rate at which juveniles develop into adults is given by r . The parameter μ_L represents the juveniles mortality, and μ_{F_1} , μ_{F_2} are respectively the mortality rate of vulnerable and resistant females. The parameter, $1 - \rho$ is the mutation rate to resistant insect. The term $-\delta F_1$ represents the mortality induced by insecticides.

b) The diapause period ($T_1 \leq t \leq T_2$). During the diapause period, all individuals stop growing in an adverse environment. In this case, the dynamics of the population is described by

$$\begin{cases} \frac{dL}{dt} = -\mu_L L, \\ \frac{dF_1}{dt} = -\mu_d F_1, \\ \frac{dF_2}{dt} = -\mu_d F_2. \end{cases} \quad (6)$$

The adults disappear, hence, we assume that the mortality rates μ_d , is very high. The length of the diapause period is $\tau = T_2 - T_1 \geq 0$.

c) The post-diapause period ($T_2 \leq t \leq 1$). In this period, juveniles survive through the diapause and emerge into adults. The model is given by the system

$$\begin{cases} \frac{dL}{dt} = \lambda_1 F_1 + \lambda_2 F_2 - rL - \mu_L L - cL^2, \\ \frac{dF_1}{dt} = \gamma_1 L(t - \tau) - \mu_{F_1} F_1 - \delta F_1, \\ \frac{dF_2}{dt} = \gamma_2 L(t - \tau) - \mu_{F_2} F_2, \end{cases} \quad (7)$$

where γ_1 is the rate of vulnerable females coming from larvae with diapause. Note that γ_2 represents the rate that a larvae emerges to a resistant adult. At the pupae stage some individuals adapt their abilities against hostile environment.

We shall describe a solution of the problem (5)–(7). Let $u(t, u_0)$ be a solution of system (5)–(7). The trajectory of the solution $u(t, u_0)$ starts at the point $(0, u_0)$, where

$$u_0 = (L(0), F_1(0), F_2(0)),$$

and moves along the solution of problem (5) until the moment $t = T_1$. At the time $t = T_1$, it continues along the solution of system (6) with initial point

$$(T_1, u(T_1, u_0))$$

till the moment $t = T_2$. At the time $t = T_2$, the trajectory moves along the solution of system 7 with initial conditions

$$(\varphi(t), F_1(T_2), F_2(T_2)),$$

where

$$\varphi(t) = L(t), \quad T_2 - \tau \leq t \leq T_2$$

is the history segment in the diapause period.

Taking into account the seasonal effects, the system (5)–(7) are considered respectively in the periods $[n, T_1 + n]$, $[T_1 + n, T_2 + n]$, and $[T_2 + n, 1 + n]$, where n is the n -th year.

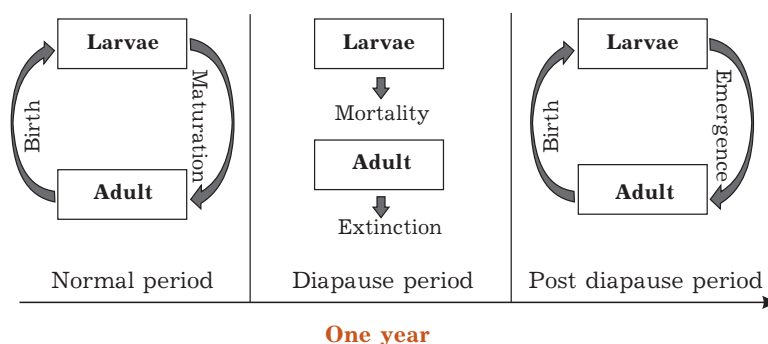


Fig. 1. Diagram describing the life cycle of Lobesia-Botrana over one year.

Remark 1. For clarity, in the previous diagram, we only consider the most important biological traits for each stage.

3. Preliminaries

In this section, we establish some preliminary results on ODEs systems of cooperative type. Let $a, b \in \mathbb{R}^n$.

Definition 1. We write $a \leq b$, if $b - a \in \mathbb{R}_+^n = \mathbb{R}_+^n = \{x \in \mathbb{R}^n : x \geq 0\}$. We write $a < b$, if $b - a \in \mathbb{R}_+^n \setminus \{0\}$. We write $a \ll b$, if $b - a \in \text{Int}(\mathbb{R}_+^n)$.

The n -dimensional interval is defined by $[a, b] = \{x \in \mathbb{R}^n : a \leq x \leq b\}$.

Let $D \subset \mathbb{R}^n$ be an open domain. Consider the system of ODE's

$$\begin{cases} x'(t) = f(x(t)), & x \in D, \quad t > 0, \\ x(t_0) = x_0. \end{cases} \quad (8)$$

We denote by $x(t, x_0)$, a solution of (8). If $f: D \rightarrow \mathbb{R}^n$ is differentiable on a convex D , then the system (8) is said to be cooperative if the Jacobian matrix $\frac{df}{dx}$ is a Metzler matrix, for $x \in D$, and $t \geq 0$, i.e. its diagonal entries are nonnegative.

Assume that f is C^1 , and there exists $b > 0$, such that $f(b) \leq 0$, with $f(0) = 0$. Suppose the system (8) is cooperative, then

Lemma 1. For any $x_0 \in [0, b]$, the system (8) has a solution $x(t, x_0)$ satisfying $x(0, x_0) = x_0$, and $x(t, x_0) \in [0, b]$, for all $t \geq 0$.

Proof. Since f is C^1 , Cauchy–Lipchitz theorem implies that (8) has an unique solution $x(t, x_0)$ defined on a maximal interval of existence $[0, T_{\max}]$. Since the system is cooperative, then Kamke's theorem, (see [15]) implies that the solution is monotone with respect to initial values, i.e. if $a \leq b$, then

$$x(t, a) \leq x(t, b) \text{ for } t \geq 0.$$

Hence for $0 \leq x_0 \leq b$, we obtain that

$$0 = x(t, 0) \leq x(t, x_0) \leq x(t, b).$$

From proposition 3.2.1 in [15], it follows that the solution $t \rightarrow x(t, b)$ is nonincreasing. We deduce that

$$0 = x(t, 0) \leq x(t, x_0) \leq x(t, b) \leq x(0, b) = b. \quad \blacksquare$$

Now we consider the delayed system

$$\begin{cases} x'(t) = f(x(t), x(t - \tau)), & x \in \mathbb{R}^n, \quad t > 0, \\ x(t) = \varphi(t), & -\tau \leq t \leq 0, \end{cases} \quad (9)$$

where $f: \mathbb{R}^n \times \mathbb{R}^n \rightarrow \mathbb{R}^n$ is C^1 , and the initial condition $\varphi \in C([- \tau, 0]; \mathbb{R}^n)$, for some $\tau \geq 0$. The order relation on $C([- \tau, 0]; \mathbb{R}^n)$ is induced by the positive cone

$$\{\varphi \in C([- \tau, 0]; \mathbb{R}^n) : \varphi \geq 0\}.$$

For $\varphi \in C([- \tau, 0]; \mathbb{R}^n)$, we denote by $x(t, \varphi)$ a solution of (9). We define $\widehat{\varphi} \in C(R; \mathbb{R}^n)$ by the relation $\widehat{\varphi}(t) = \varphi(t)$, for all $t \in [- \tau, 0]$.

The system (9) is cooperative if $f(x, y)$ satisfies

$$\frac{\partial f_i}{\partial x_j} \geq 0 \text{ for all } i \neq j, \quad \text{and} \quad \frac{\partial f_i}{\partial y_l} \geq 0 \text{ for all } i, l.$$

Assume that f is C^1 , and there exists $b > 0$, such that $f(b, b) \leq 0$, with $f(0, 0) = 0$. Suppose the system (9) is cooperative, then

Lemma 2. For any $\varphi \in C([- \tau, 0]; \mathbb{R}^n)$, such that $\widehat{0} \leq \widehat{\varphi} \leq \widehat{b}$, the system (9) has a solution $x(t, \varphi)$, with $0 \leq x(t, \widehat{\varphi}) \leq \widehat{b}$ for all $t \geq 0$.

Proof. Since f is C^1 , then (9) has a local solution defined on a maximal interval of existence $[0, T_{\max}[$, see [18]. Since the system is cooperative, Th. 1.1 in [15] implies that

$$0 = x(t, \widehat{0}) \leq x(t, \widehat{\varphi}) \leq x(t, \widehat{b}) \text{ for all } t \geq 0.$$

Corollary 2.2 in [15] implies that the map

$$t \rightarrow x(t, \widehat{b})$$

is nonincreasing. We deduce that

$$0 \leq x(t, \widehat{\varphi}) \leq x(t, \widehat{b}) \leq x(0, \widehat{b}) = \widehat{b} \text{ for all } t \geq 0. \quad \blacksquare$$

Let $U = [0, b]$, $b \in \mathbb{R}_+^n$, and $b \gg 0$, or $U = \mathbb{R}_+^n$.

Let $f: U \rightarrow U$ be a continuous map.

Definition 2. f is said to be

- i) monotone on U if $x_1 \geq x_2 \Rightarrow f(x_1) \geq f(x_2)$;
- ii) strongly monotone if $x_1 > x_2 \Rightarrow f(x_1) \gg f(x_2)$;
- iii) subhomogeneous if $f(\lambda x) \geq \lambda f(x)$, $\forall \lambda \in [0, 1]$, $\forall x \in U$.
- iv) strictly subhomogeneous if $f(\lambda x) > \lambda f(x)$, $\forall \lambda \in (0, 1)$, $x \in U$, with $x \gg 0$.

4. Main results

Definition 3. A function u is called a solution to system (5)–(7) if i) u is absolutely continuous with respect to Lebesgue measure, ii) u satisfies (5)–(7), whenever u is differentiable.

We assume that $T_1 + 2\tau < 1$.

Remark 2. We will need this assumption when we consider step method for delayed equations.

Theorem 1. For any $u_0 \in \mathbb{R}_+^3$, there exists $b \in \mathbb{R}_+^3$, such that the system (5)–(7) has a unique solution $u(t, u_0)$ satisfying $u(0, u_0) = u_0$, and $u(t, u_0) \in [0, b]$, for all $t \geq 0$.

Proof. First, we assume $n = 0$. Assume that the initial value

$$u_0 = (L(0), F_1(0), F_2(0)) > 0.$$

Let L^m be a positive number large enough such that

$$L^m \geq \frac{1}{c} \left\{ \frac{\lambda_1 \rho r}{\mu_{F_1} + \delta} + \frac{\lambda_2 (1 - \rho) r}{\mu_{F_2}} - r - \mu_L \right\},$$

and

$$F_1^m > \frac{\rho r L^m}{\mu_{F_1} + \delta}, \quad F_2^m > \frac{(1 - \rho) r L^m}{\mu_{F_2}}.$$

Let

$$b^m = (L^m, F_1^m, F_2^m).$$

If $f(L, F_1, F_2)$ denotes the right hand side of (5) it is clear that

$$f(b^m) < 0.$$

Hence Lemma 1 implies that system (5) admits a solution $u(t, u_0)$ that satisfies

$$0 \leq u(t, u_0) \leq b^m \quad \text{for } 0 \leq t \leq T_1.$$

In the diapause period, the system (6) has a solution that satisfies

$$\begin{aligned} L(t) &= L(T_1) e^{-\mu_L(t-T_1)}, \\ F_1(t) &= F_1(T_1) e^{-\mu_{F_1}(t-T_1)}, \\ F_2(t) &= F_2(T_1) e^{-\mu_{F_2}(t-T_1)}, \end{aligned}$$

where the initial value at time $t = T_1$ satisfy

$$(L(T_1), F_1(T_1), F_2(T_1)) = u(t, T_1) \leq b_m.$$

Hence

$$0 \leq u(t, u_0) \leq b^m \quad \text{for } T_1 \leq t \leq T_2.$$

Let $g(x(t), x(t - \tau))$ denotes the right hand side of system (7). We choose b^l such that

$$b^l = (L^l, F_1^l, F_2^l),$$

where

$$\begin{aligned} L^l &\geq \frac{1}{c} \left\{ \frac{\lambda_1 \rho r}{\mu_{F_1} + \delta} + \frac{\lambda_2 (1 - \rho) r}{\mu_{F_2}} - r - \mu_L \right\}, \\ F_1^l &> \frac{(\rho r + \gamma_1) L^l}{\mu_{F_1} + \delta}, \quad F_2^l > \frac{((1 - \rho) r + \gamma_2) L^l}{\mu_{F_2}}. \end{aligned}$$

This gives that

$$g(b^l, b^l) < 0.$$

Note that

$$F_1^l \geq F_1^m, \quad F_2^l \geq F_2^m,$$

and

$$u(T_2, u_0) \leq b^m \leq b^l.$$

Lemma 2 implies that system (7) has a solution such that

$$0 \leq u(t, u_0) \leq b^l \quad \text{for } T_2 \leq t \leq 1,$$

where the initial value $u_0 = (\varphi, F_1(T_2), F_2(T_2))$ and

$$\varphi(t) = L(t) \quad \text{for } T_2 - \tau \leq t \leq T_2.$$

The same arguments hold for the case $n \geq 1$. We conclude that system (5)–(7) has a continuous solution satisfying

$$0 \leq u(t, u_0) \leq b = b^l \quad \text{for all } t \geq 0. \quad \blacksquare$$

Let $\phi_t(u_0)$ be the semiflow generated by the system (5)–(7), that is $\phi_t(u_0)$ is the solution $u(t, u_0)$ of system (5)–(7) satisfying $u(0, u_0) = u_0$, then we obtain the following lemma.

Lemma 3. i) $\phi_0(u_0) = u_0$. ii) $\phi_{t+1}(u_0) = \phi_t(\phi_1(u_0))$, for all $t \geq 0$. iii) The map $u_0 \rightarrow \phi_t(u_0)$ is continuous on \mathbb{R}^3 for every $t \geq 0$.

Proof. Due to the lack of a specific reference, we give a proof in the appendix B. ■

Lemma 4. The semiflow $\phi_t(u_0)$ is strictly monotone with respect to u_0 .

Proof. Let

$$u_0 < v_0.$$

Without loss of generality, assume that

$$L(t, u_0) < L(t, v_0).$$

If there exists $\tau > 0$ such that

$$\phi_\tau(u_0) = \phi_\tau(v_0),$$

then, in the normal period, the function L of the system (5) satisfies an equation of the form

$$\frac{dL}{dt} = a(t) - rL - \mu_L L - cL^2,$$

with $a(t) = \lambda_1 F_1(t) + \lambda_2 F_2(t)$. By uniqueness of the solution, we deduce that

$$L(t, u_0) = L(t, v_0), \quad \forall t \geq 0,$$

but this contradicts the hypothesis $L(t, u_0) < L(t, v_0)$. Hence the flow is strictly monotone, it follows that

$$\phi_t(u_0) = (L(t, u_0), F_1(t, u_0), F_2(t, u_0)) < (L(t, v_0), F_1(t, v_0), F_2(t, v_0)) = \phi_t(v_0) \text{ for } 0 \leq t \leq T_1.$$

In the diapause period, it is clear from the expression of the solutions that

$$\begin{aligned} L(t, u_0) &= L(T_1, u_0)e^{-\mu_L(t-T_1)} < L(T_1, v_0)e^{-\mu_L(t-T_1)}, \\ F_1(t, u_0) &= F_1(T_1, u_0)e^{-\mu_L(t-T_1)} < F_1(T_1, v_0)e^{-\mu_L(t-T_1)}, \\ F_2(t, u_0) &= F_2(T_1, u_0)e^{-\mu_L(t-T_1)} < F_2(T_1, v_0)e^{-\mu_L(t-T_1)}. \end{aligned}$$

In the post-diapause period, system (7) becomes an ODE on the interval $[T_2, T_2 + \tau]$,

$$\begin{cases} \frac{dL}{dt} = \lambda_1 F_1 + \lambda_2 F_2 - rL - \mu_L L - cL^2, \\ \frac{dF_1}{dt} = \gamma_1 L(T_1, u_0)e^{-\mu_L(t-\tau-T_1)} - \mu_{F_1} F_1 - \delta F_1, \\ \frac{dF_2}{dt} = \gamma_2 L(T_1, u_0)e^{-\mu_L(t-\tau-T_1)} - \mu_{F_2} F_2. \end{cases}$$

On the interval $[T_2, T_2 + \tau]$, the solution $F_1(t, u_0)$ is given by

$$F_1(t, u_0) = e^{-(\delta+\mu_{F_1})(t-T_2)} \gamma_1 L(T_1, u_0) e^{-\mu_L(t-\tau_1-T_1)} + \int_{T_2}^t e^{-(\delta+\mu_{F_1})(s-T_2)} \gamma_1 L(T_1, u_0) e^{-\mu_L(s-\tau-T_1)} ds.$$

This gives that

$$\begin{aligned} F_1(t, u_0) &< e^{-(\delta+\mu_{F_1})(t-T_2)} \gamma_1 L(T_1, v_0) e^{-\mu_L(t-\tau_1-T_1)} \\ &\quad + \int_{T_2}^t e^{-(\delta+\mu_{F_1})(s-T_2)} \gamma_1 L(T_1, v_0) e^{-\mu_L(s-\tau-T_1)} ds = F_1(t, v_0). \end{aligned}$$

Similarly, we obtain that

$$F_2(t, u_0) < F_2(t, v_0).$$

Hence

$$\frac{dL(t, u_0)}{dt} < \lambda_1 F_1(t, v_0) + \lambda_2 F_2(t, v_0) - rL(t, u_0) - \mu_L L(t, u_0) - cL^2(t, u_0).$$

By comparison principle, see appendix B, we obtain that

$$L(t, u_0) < L(t, v_0).$$

By a similar method, we extend the comparison to the interval $[T_2, 1]$, and step by step, the inequalities will be established on $[n, n+1]$, $\forall n \in N$. ■

Lemma 5. *The flow $\phi_t(u_0)$ is strictly sub-homogeneous.*

Proof. Let $u_0 \gg 0$. Then by the previous lemma, $\phi_t(u_0) \gg 0$. Let $\lambda \in (0, 1)$, and $h_1(u)$ be the right hand side of system (5), then h_1 is strictly sub-homogeneous. Let $v(t) = \lambda u(t, u_0)$, where $u(t, u_0)$ is a solution of system (5)–(7) satisfying $u(0, u_0) = u_0$. Let $w(t) = u(t, \lambda u_0)$ be a solution of system (5)–(7) satisfying $w(0) = \lambda u_0$. Then,

$$\frac{dv}{dt} = \lambda \frac{du}{dt} = \lambda h_1(u) < h_1(\lambda u) = h_1(v).$$

This implies that

$$\frac{dv}{dt} - h_1(v) < 0 = \frac{dw}{dt} - h_1(w).$$

By comparison principle, see [19], we obtain that

$$v = (\lambda L(t, u_0), \lambda F_1(t, u_0), \lambda F_2(t, u_0)) \leq w = (L(t, \lambda u_0), F_1(t, \lambda u_0), F_2(t, \lambda u_0)).$$

If $v = w$, then we will have

$$\frac{dv}{dt} - h_1(v) = 0 < 0 = \frac{dw}{dt} - h_1(w),$$

and this constitutes a contradiction. It follows that $v < w$. As in the diapause period, the system is linear, we obtain that

$$v \leq w.$$

In the post-diapause period, since the system (7) is cooperative, Kamke's theorem for delayed equations, (see [15]) implies that $v \leq w$. Hence

$$\phi_1(\lambda u_0) > \lambda \phi_1(u_0). \quad \blacksquare$$

Theorem 2. *For any $u_0 \in \mathbb{R}_+^3$, there exists a nonnegative 1-periodic solution $u^*(t)$ of system (5)–(7).*

Proof. Consider the Poincaré operator

$$\begin{aligned} P: \mathbb{R}_+^3 &\rightarrow \mathbb{R}_+^3, \\ u_0 &\rightarrow \phi_1(u_0). \end{aligned}$$

Then P is continuous, maps $[0, b]$ into itself, $P([0, b])$ has compact closure in \mathbb{R}^3 , strongly monotone, and sub-homogeneous. By Theorem 2.1 in [20], and Theorem 3.2 in [21] we will have that for any $u_0 \in \mathbb{R}_+^3$, there exists a nonnegative point $e = e(u_0)$ such that

$$\lim_{m \rightarrow +\infty} P^m(u_0) = e.$$

Since P is continuous,

$$P(e) = P\left(\lim_{m \rightarrow +\infty} P^m(u_0)\right) = \lim_{m \rightarrow +\infty} P^{m+1}(u_0) = e,$$

and $u^*(t) = u(t, e)$ is a 1-periodic solution of system (5)–(7). ■

5. Global dynamics of the pest population

It is clear that $(0, 0, 0)$ is an equilibrium for the system (5)–(7). The linearized system at $(0, 0, 0)$ becomes on $(0, T_1)$,

$$\begin{cases} \frac{dL}{dt} = \lambda_1 F_1 + \lambda_2 F_2 - rL - \mu_L L, \\ \frac{dF_1}{dt} = \rho rL - \mu_{F_1} F_1 - \delta F_1, \\ \frac{dF_2}{dt} = (1 - \rho)rL - \mu_{F_2} F_2, \end{cases} \quad (10)$$

on (T_1, T_2) ,

$$\begin{cases} \frac{dL}{dt} = -\mu_L L, \\ \frac{dF_1}{dt} = -\mu_d F_1, \\ \frac{dF_2}{dt} = -\mu_d F_2, \end{cases} \quad (11)$$

and on $(T_2, 1)$,

$$\begin{cases} \frac{dL}{dt} = \lambda_1 F_1 + \lambda_2 F_2 - rL - \mu_L L, \\ \frac{dF_1}{dt} = \gamma_1 L(t - \tau) - \mu_{F_1} F_1 - \delta F_1, \\ \frac{dF_2}{dt} = \gamma_2 L(t - \tau) - \mu_{F_2} F_2. \end{cases} \quad (12)$$

Let $P(t)$ be the solution of the linearized system (10)–(12). Let R be the spectral radius of the Poincaré map $P(1)$, then we have the threshold type result on the global dynamics of the pest population.

Theorem 3. *The following statements hold for system (5)–(7).*

- i) if $R \leq 1$, then 0 is globally asymptotically stable in \mathbb{R}_+^3 .
- ii) if $R > 1$, then there exists a unique positive 1-periodic solution $u^*(t)$ which is globally asymptotically stable in $\mathbb{R}_+^3 \setminus \{0\}$.

Proof. Suppose that the derivative $D\phi_1$ exists at $(0, 0, 0)$. Let $r(D\phi_1(0))$ be the spectral radius of the operator $D\phi_1(0)$, then $r(D\phi_1(0)) = R$, and Theorem 2.3 in [22] gives

- i) if $r(D\phi_1(0)) \leq 1$, then 0 is globally asymptotically stable for system (5)–(7) in \mathbb{R}_+^3 .
- ii) if $r(D\phi_1(0)) > 1$, then there exists a unique positive 1-periodic solution $u^*(t)$ for system (5)–(7), which is globally asymptotically stable in $\mathbb{R}_+^3 \setminus \{0\}$. ■

6. Numerical simulations

In this section, we illustrate our theoretical results with numerical simulations. The population parameters are summarized in Table 1. We discuss the biological meaning of some figures. All parameters are positive, and measured per day, except the time of the diapause, which is given in months.

Remark 3. Figures 3 and 5 show that the vulnerable females die out and the resistant females very rapidly take over.

Table 1. Parameters of the model (5)–(7).

Parameter	Definition	Values	Source
λ_1	birth rate of vulnerable	0.02 – 4.5	[1, 2]
λ_2	birth rate of resistant	0.02 – 4.5	[1, 2]
r	rate at which juvenils develop into adult	0.01 – 0.8	[1, 2]
c	juvenile competition rate	0 – 0.02	given
μ_L	juvenile mortality rate	0.1 – 0.85	[2]
μ_{F_1}	vulnerable mortality rate	0.1 – 0.87	[2]
μ_{F_2}	resistant mortality rate	0.1 – 0.87	[2]
$(1 - \rho)$	the ratio of mutation to resistant moth	0 – 1	given
γ_1	rate of vunerables coming from larvae with diapause	0.1 – 0.9	[2]
γ_2	rate of resistants coming from larvae with diapause	0.1 – 0.9	[2]
δ	insect mortality induced by insecticides	[0, 0.5]	[12]
τ	diapause duration	4 – 8	[4]

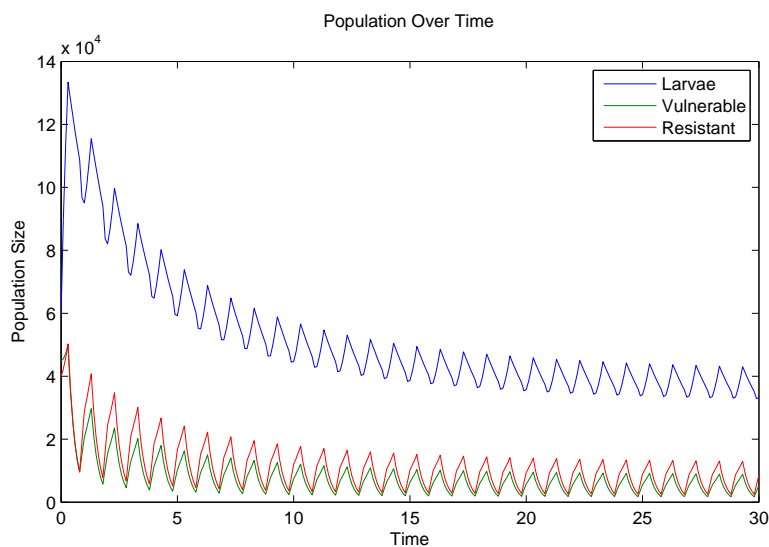


Fig. 2. Pest population abundance for the parameters $\lambda_1 = 4.5$, $\lambda_2 = 4.5$, $r = 0.8$, $\mu_L = 0.4$, $c = 0.00001$, $\rho = 0.5$, $\mu_{F_1} = 0.02$, $\delta = 0.4$, $\mu_{F_2} = 0.02$, $\mu_d = 2.81$, $\gamma_1 = 0.05$, $\gamma_2 = 0.8$, $\tau = 4.8$. This figure shows that the population persists and the solution tends to an oscillatory solution.

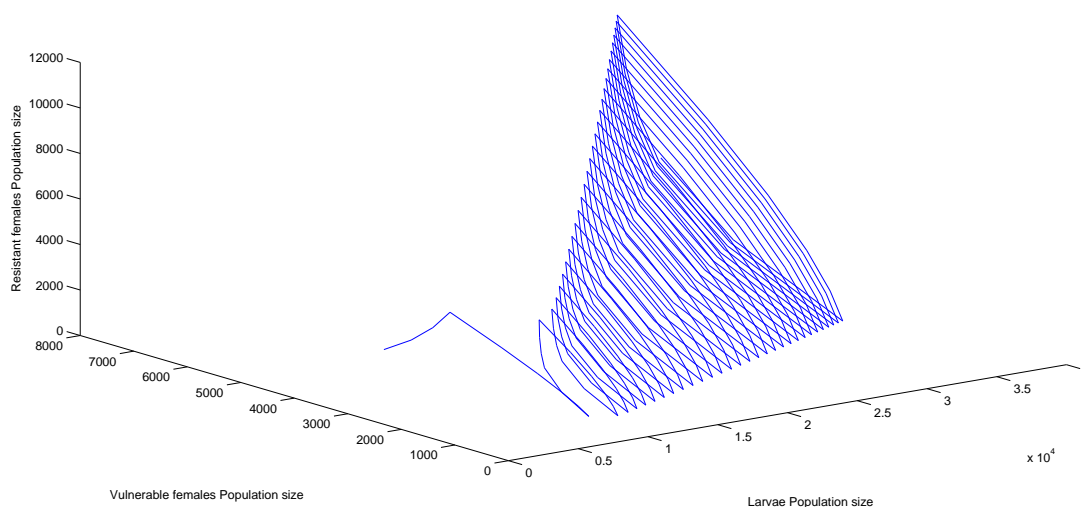


Fig. 3. Phase portrait corresponding to the persistence case.

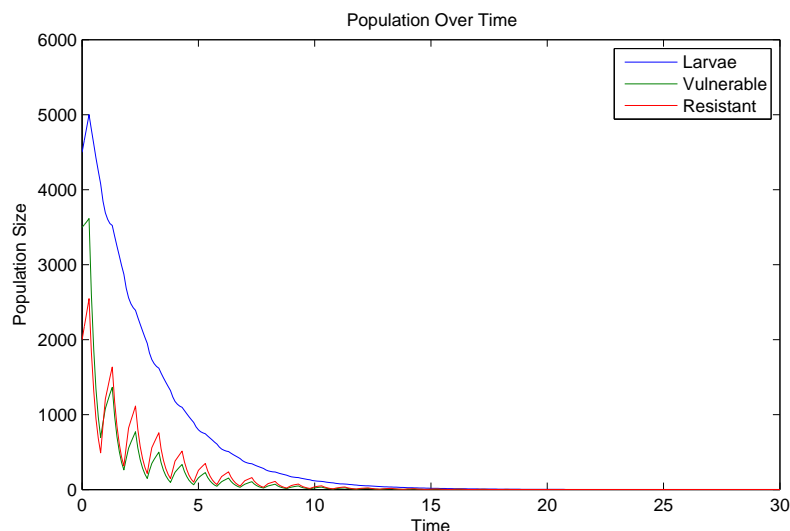


Fig. 4. Pest population abundance for the parameters $\lambda_1 = 1$, $\lambda_2 = 1$, $r = 0.8$, $\mu_L = 0.4$, $c = 0.00001$, $\rho = 0.5$, $\mu_{F_1} = 0.02$, $\delta = 0.4$, $\mu_{F_2} = 0.02$, $\mu_d = 2.81$, $\gamma_1 = 0.05$, $\gamma_2 = 0.8$, $\tau = 4.8$. This figure shows that the population goes to extinction.

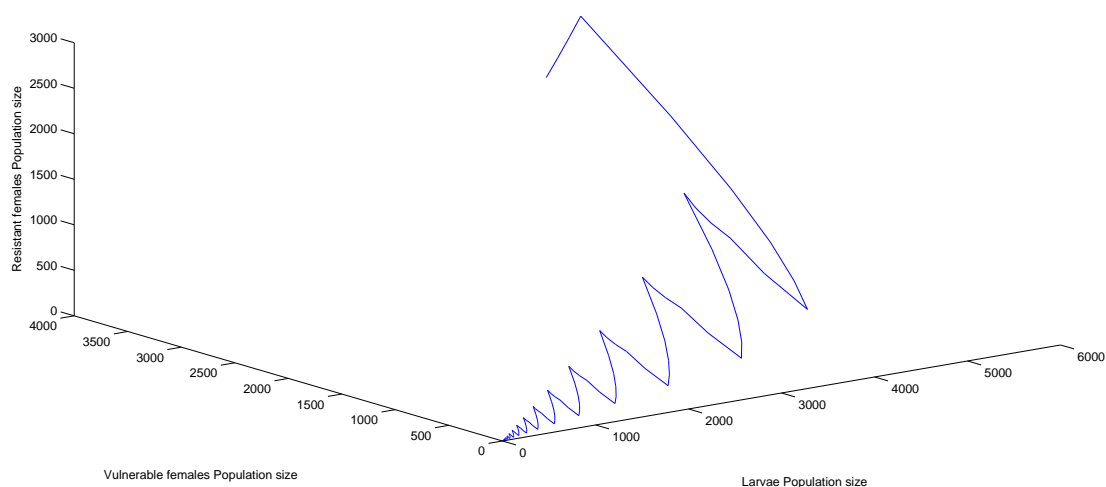


Fig. 5. Phase portrait corresponding to the extinction case.

7. Concluding remarks

To control the pest, modern vineyards rely mainly on insecticides. This causes insecticide resistance. Despite the dramatic impact of resistance to insecticides and diapause on Agriculture, few works are devoted to them. To better understand these traits, we have discussed a structured model with two life stages, juveniles and reproducing adults.

The life cycle of the population is divided in three periods: pre-diapause, diapause, and post-diapause stage. The overlapping generations is described by delay differential equations. The competition term in the model may be explained by non-native individuals colonizing new habitats. The model (5)–(7) is not autonomous. We present a systematic study using monotone systems theory. The present study provides insights on the possibility of estimating for a given date and stage the density

of individuals. The dynamics is described in terms of an index R obtained by the spectral radius of the Poincaré operator of the linearized problem around the extinction equilibrium. Numerical simulations confirm the obtained theoretical results.

Although the model is reasonably simplified, it can be modified to take into account other stages, such as the equation of eggs, and pupae. Hence, the method used can be adapted to cover a wide set of systems provided they are quasi-monotone in each period.

It is clear from the monotony of the flow that the quantity of larvae which undergoes diapause contributes favorably in the persistence of the pest. If diapause is long, few larvae survive the next season. Unfortunately, with global warming, the diapause is getting shorter and, this means that the pest becomes more persistent.

The model contains several biological factors, in the absence of an explicit expression of the index R , we could not study analytically the sensitivity of R with respect to the various parameters, and it is very interesting to numerically study the sensitivity with respect to each parameter.

From Figures 2–5, we see the influence of parameters λ_1 , λ_2 on population dynamics. The study allows us to conclude that an efficient way to control the pest is to reduce the birth rates. An adequate technique is to combine the sterile male approach, see [23] with insecticides. Knowledge of the spatial distribution is important for developing efficient control of the pest. We did not consider spatial structure, and this will be the subject of the next step. To facilitate the analysis we have supposed that the diapause duration is constant. This duration may vary according to individuals and exposure to insecticides. This aspect can make the model difficult to analyze.

Appendix A

Comparison principle, see [24].

Theorem 4. Suppose $u(t)$ and $v(t)$ are continuous in the interval $[a, b]$ of the real line R , and differentiable on $(a, b]$, f is a continuous mapping from $R \times R$ to R , and

$$u(a) < v(a), \quad \frac{du}{dt} - f(t, u) < \frac{dv}{dt} - f(t, v) \quad \text{on } (a, b].$$

Then $u < v$ on $(a, b]$.

Appendix B: Proof of Lemma 3

Proof. i) is trivial.

ii) Note that $\phi_{t+1}(u_0)$ is the solution $v(t)$ of system (5)–(7) satisfying $v(0) = \phi_1(u_0)$. Let $w(t) = \phi_t(\phi_1(u_0))$, then $v(t)$, and $w(t)$ are solutions of the same system (5)–(7) verifying the same initial value

$$v(0) = w(0) = \phi_1(u_0).$$

By uniqueness, we obtain that $u = v$.

iii) Using ideas as in [25], let

$$\phi_t = (\phi_t^1, \phi_t^2, \phi_t^3),$$

be the semi-flow corresponding to system (5)–(7). By the continuity of the semiflow on post-diapause period, see [18] we obtain that for any $\varepsilon > 0$, there exists $\delta_1 > 0$, such that

$$\begin{aligned} \sup_{T_2 - \tau \leq s \leq T_2} \{ \|\phi_s^1(u_0) - \phi_s^1(u_0^*)\|, \|\phi_{T_2}^2(u_0) - \phi_{T_2}^2(u_0^*)\|, \|\phi_{T_2}^3(u_0) - \phi_{T_2}^3(u_0^*)\| \} &< \delta_1 \\ \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| &< \varepsilon, \quad T_2 \leq t \leq 1. \end{aligned}$$

Similarly, from the continuity property of the semi-flow in diapause period, we have that there exists $\delta_2 > 0$, such that

$$\|\phi_{T_1}(u_0) - \phi_{T_1}(u_0^*)\| < \delta_2 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \delta_1, \quad T_1 \leq t \leq T_2.$$

In a similar manner, from continuity property of the semi-flow in the normal period, we have there exists $\delta_3 > 0$, such that

$$\|u_0 - u_0^*\| < \delta_3 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \delta_2, \quad 0 \leq t \leq T_1.$$

It follows that

$$\|u_0 - u_0^*\| < \delta_3 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \varepsilon, \quad T_2 \leq t \leq 1.$$

Similarly, from continuity property of the semi-flow in diapause period, for any $\varepsilon > 0$, there exists $\rho_1 > 0$, such that

$$\|\phi_{T_1}(u_0) - \phi_{T_1}(u_0^*)\| < \rho_1 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \varepsilon, \quad T_1 \leq t \leq T_2,$$

and from continuity property of the semi-flow in the normal period, we obtain that there exists $\rho_2 > 0$, such that

$$\|u_0 - u_0^*\| < \rho_2 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \rho_1, \quad 0 \leq t \leq T_1.$$

It follows that

$$\|u_0 - u_0^*\| < \rho_2 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \varepsilon, \quad T_1 \leq t \leq T_2.$$

The continuity of the semi-flow in the normal period implies that there exists $\eta_1 > 0$ such that

$$\|u_0 - u_0^*\| < \eta_1 \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \varepsilon, \quad 0 \leq t \leq T_1.$$

We conclude that for any $\varepsilon > 0$, there exists $\delta = \min(\eta_1, \rho_1, \delta_3) > 0$, such that

$$\|u_0 - u_0^*\| < \delta \Rightarrow \|\phi_t(u_0) - \phi_t(u_0^*)\| < \varepsilon, \quad 0 \leq t \leq 1. \quad \blacksquare$$

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Моделювання адаптивної поведінки популяції шкідників сільського господарства

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У цій роботі формулюється модель, що описує ріст популяції шкідника зі сезонною діапаузою на стадії личинки. Модель включає стійкість комах до хімічних обробок та їх адаптацію до агресивного середовища. Вона складається з опису трьох класів: незрілої стадії, яка включає яйця, личинки та лялечки, і двох зрілих стадій, що відповідають уразливій дорослій стадії та стійкій до інсектицидів дорослій стадії. Основний результат полягає в аналітичному підході до існування невід’ємного періодичного розв’язку. Доведення використовує результати порівняння та теорему Камке для кооперативних систем. Як важливу ілюстрацію, наведено результат порогового типу щодо глобальної динаміки популяції шкідників у термінах індексу R . Якщо $R \leq 1$, то тривіальний розв’язок є глобально асимптотично стабільним. Якщо $R > 1$, то додатний періодичний розв’язок є глобально асимптотично стійким. Чисельне моделювання підтверджує аналітичні результати.

Ключові слова: *сезонна діапауза; стійкість до інсектицидів; монотонні системи; глобальне притягування; чисельне моделювання.*